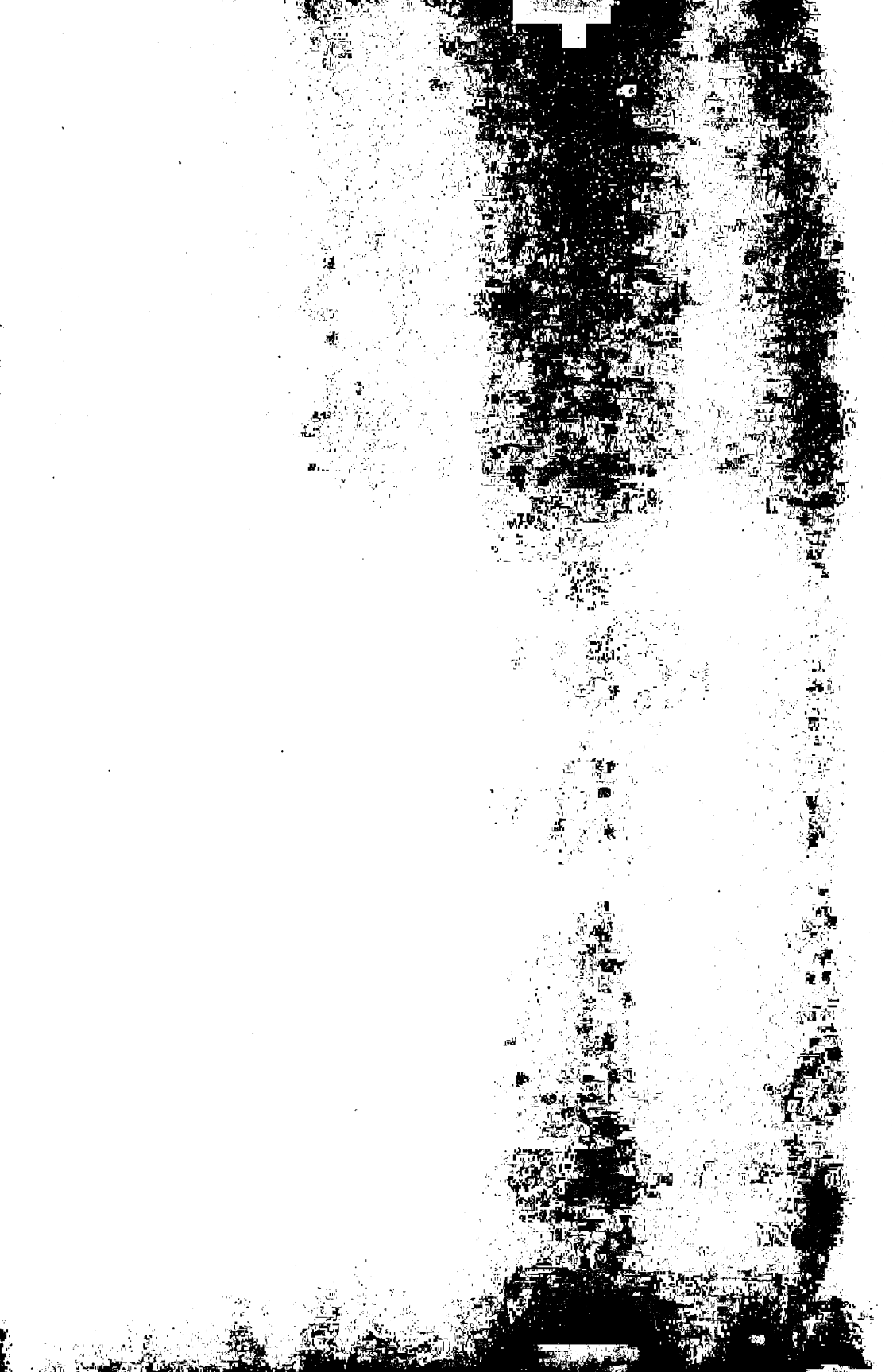
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Contents

Al-Mayah, A.-R. A. & Al-Shehbaz, I. A.: Chromosome numbers for some Leguminosae from Iraq 437
Arvidsson, L. & Lidén, M.: Galenia secunda (Aizoaceae) new to Europe 130
Behnke, H.-D.: Phloem ultrastructure and systematic position of Gyrostemonaceae 255
Böcher, T. W.: Cerastium alpinum and C. arcticum, a mature polyploid complex 303
Bremer, K.: The genus Peyrousea (Compositae) . 493
Brodie, H. J.: A key to the species of Cyathus (Nidulariaceae) 453
Brunkener, L.: Spore-producing and apical meristems in vascular plants – a comparison 189
Chaudhary, S. A.: Typification of Iris heylandiana Boiss. & Reut. 25
Chaudhary, S. A., Chaudhary, G. A. & Akram, M.: Karyotypes of some Iris taxa 263
Cotton, R. & Stace, C. A.: Morphological and anatomical variation of Vulpia (Gramineae) .. 173
Dahlgren, R., Jensen, S. R. & Nielsen, B. J.: Seedling morphology and iridoid occurrence in Montinia caryophyllacea (Montiniaceae) 329
Dixon, P. S. & Irvine, L. M.: Miscellaneous notes on algal taxonomy and nomenclature IV . 137
Eliasson, U.: Recent advances in the taxonomy of Myxomycetes 483
Elvers, I.: Flower-visiting lizards on Madeira 231
Eriksson, J. & Ryvarden, L.: A study of the genus Litschauerella (Corticiaceae) 461
Eriksson, J. & Ryvarden, L.: Laeticorticium pulverulentum (Corticiaceae) validated 466
Eriksson, J., Sunhede, S. & Torkelsen, A.-E.: Femsjonia peziziformis (Dacrymycetales) in North Europe 241
Frederiksen, S.: The Festuca brachyphylla group in Greenland 269
Gustavsson, L.-Å.: Drabopsis verna C. Koch (Brassicaceae) new to Europe 213
Hagström, E.: Vesiculomyces Hagström gen. nov. segregated from Gloeocystidiellum (Corticiaceae) 53
Haines, R. W. & Lye, K. A.: Studies in African Cyperaceae XV. Amphicarpy and spikelet structure in Trianoptiles solitaria 235
Hansen, A. & Lohmeyer, W.: New finds of Cornucopiae cucullatum (Poaceae) in Europe 203
Hedberg, I. & Hedberg, O.: Chromosome numbers of afroalpine and afromontane angiosperms 1
Heyn, C. C. & Herrnstadt, I.: Seed coat structure of Old World Lupinus species 427
Holm, L. & Holm, K.: A study of the Leptopeltidaceae 215
Hosni, H. A.: A new Tribulus species with winged carpels 261
Hosny, A. I.: New taxa of Zygophyllum from Egypt 467
Humphries, C. J.: A new genus of the Compositae from North Africa 155
Håkansson, H. & Stabell, B.: Identification of some species of Navicula 477
Jacobsen, N.: Chromosome numbers and taxonomy in Cryptocoryne (Araceae) 71
Jacobsen, N.: Cryptocoryne dewitii N. Jacobsen sp. nov. (Araceae) 381
Julin, E.: Some Bothnian subspecies in the Ranunculus auricomus complex: origin and dispersal 287
Kärnefelt, I.: Masonhalea, a new lichen genus in the Parmeliaceae 101
Kärnefelt, I.: Three new species of brown fruticose Cetraria 125
Kennedy, H.: An unusual flowering strategy and new species in Calathea 333
Khaleel, T. F.: Embryology of Trichodesma (Boraginaceae) 441
Løjtnant, B.: New and noteworthy species of Neottioideae (Orchidaceae) from Ecuador .. 163
Løjtnant, B.: Notes on the genus Epidendrum (Orchidaceae) in Ecuador 321
Løjtnant, B.: Species of Epidendroideae (Orchidaceae) new to Ecuador 417
Lye, K. A. & Haines, R. W.: Studies in African Cyperaceae XVI. New taxa of Isolepis R. Br. 311
Mattatia, J.: Amphicarpy and variability in Pisum fulvum 27
Merxmüller, H. & Strid, A.: A new species in the Cerastium alpinum group from Mt Olympus, Greece 469
Nannfeldt, J. A.: The species of Anthracoidea (Ustilaginales) on Carex subgen. Vignea with special regard to the Nordic species 351
Neuendorf, M.: Pardinae, a new section of Bomarea (Alstroemeriaceae) 55
Nordenstam, B.: A review of the Andean genus Cacosmia H.B.K. (Compositae–Liabeae) ... 279
Norlindh, T.: Garuleum subgen. Rutidocarpaea, a monotypic subgenus showing achene dimorphism 377

Oredsson, A. & Snogerup, S.: Drawings of Scandinavian plants 115–117. Epilobium L. sect. Epilobium 205
Pedersen, P. M.: Polytretus reinboldii, a rare brown alga in culture (Ectocarpales, Sorocarpaceae fam. nov.) 35
Renberg, I.: Fragilaria lata, a new diatom species 315
Sahlin, C. I.: Contribution to the Taraxacum flora of Nordrhein-Westfalen 61
Snogerup, B.: Chromosome numbers of Scandinavian Odontites species 121
Sohmer, S. H.: Notice for the exchange of duplicate voucher material 52
Strid, A.: A new species of Crepis from Mt Olympus, Greece 143
Strid, A.: Sisyrinchium laxum Otto ex Sims found in N Greece 473
Sunhede, S.: Morphology and intraspecific variation in Geastrum triplex Jungh. 403
Thomasson, K.: Two conspicuous desmids from Amazonas 41
Thomsen, H. A.: Chrysochromulina pyramidosa sp. nov. (Prymnesiophyceae) from Danish coastal waters 147
van der Werff, H.: Vascular plants from the Galápagos Islands: new records and taxonomic notes 89
Vánky, K.: Moesziomyces, a new genus of Ustilaginales 131
Wagner, P.: Vessel types of the monocotyledons: a survey 383
Wingfield, R.: A note on Fuirena ciliaris (Cyperaceae) and related species 319

Reviews of botanical literature

Ainsworth, G. C., Sparrow, F. K. & Sussman, A. S. (eds.): The Fungi, an advanced treatise. IV A. A taxonomic review with keys: Ascomycetes and Fungi Imperfecti. IV B. Basidiomycetes and lower Fungi (by N. Lundqvist) 109
Ayensu, E. S.: Leaf anatomy and systematics of New World Velloziaceae (by I. Nordal) 111
Brodo, I. M. & Hawksworth, D. L.: Alectoria and allied genera in North America (by O. Almborn) 253
Correns, C. E.: Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge (by O. Mårtensson) 112
Cramer, J. (ed.): Bibliotheca Lichenologica 1–5 (by O. Almborn) 251
Dixon, P. S. & Irvine, L. M.: Seaweeds of the British Isles. Volume 1, Rhodophyta. Part 1 (by T. Christensen) 499
Faegri, K. & Iversen, J.: Textbook of pollen analysis (by B. E. Berglund) 114
Ferguson, I. K. & Muller, J. (eds.): The evolutionary significance of the exine (by S. Nilsson) 115
Frey-Wyssling, A.: The plant cell wall (by E. Treiber) 116
Gams, W.: Cephalosporium-artige Schimmelpilze (Hyphomycetes) (by N. Lundqvist) ... 341
Gottschalk, W.: Die Bedeutung der Polyploidie für die Evolution der Pflanzen (by Á. Löve) 342
Harling, G. & Sparre, B. (eds.): Flora of Ecuador 1–5 (by K. Larsen) 117
Heywood, V. H.: Plant taxonomy (by G. Weimarck) 500
Hilliard, O. M.: Compositae in Natal (by K. Bremer) 500
Iwatzuki, Z., Vitt, D. H. & Gradstein, S. R.: Bryological herbaria. A guide to the bryological herbaria of the world (by O. Mårtensson) . 112
Jacobsen, H.: Das Sukkulentenlexikon (by B. Nordenstam) 249
John, B.: Population cytogenetics (by G. Weimarck) 500
Löve, Á., Löve, D. & Pichi Sermolli, R. E. G.: Cytotaxonomical atlas of the Pteridophyta (by B. Øllgaard) 250
Lundqvist, J. (ed.): Survey of the vegetation conditions in the catchment area of the river Vindelälven, northern Sweden (by Á. Löve) . 344
Lundqvist, J. & Wistrand, G.: Riverside vascular flora in the upper and middle catchment area of the river Skellefteälven, northern Sweden (by Á. Löve) 345
Miège, J. & Stork, A. L. (eds.): Origines des flores africaines et malgaches. Progrès–conservation–écologie (by M. Iwarsson) 118
Moore, D. M.: Outline studies in biology. Plant cytogenetics (by A. Strid) 119
Smith, P.: The chemotaxonomy of plants (by B. J. Nielsen and S. R. Jensen) 119
Stafgleu, F. A. & Cowan, R. S.: Taxonomic literature 1 (by O. Almborn) 349
Sybenga, J.: Meiotic configurations. A source of information for estimating genetic parameters (by A. Weimarck) 251
Thomas, E. & Davey, M. R.: From single cells to plants (by A. Weimarck) 501
Tzvelev, N. N.: Poaceae USSR (by Á. Löve) 347
Whittier, H. O.: Mosses of the Society Islands (by O. Mårtensson) 113

Index

The index covers only taxa which have been treated in more detail. New taxa and new combinations are printed in boldface. f indicates illustration(s) and m refers to a map. Each taxon is only indexed once per article.

Acalypha parvula 97
– sericea 97
Achyranthes aspera 93
Actinotaenium turgidum v. ligatum 47 f
Agapantheae 387
Agave americana 232
Alismatales 385
Alismatanae 385
Aloe arborescens 231 f
Altensteinia **fragosa** 163 f
– **nigrescens** 164
Alternanthera sessilis 93
Alyssum saxatile 256 f
Anthracoidea 356
– **arenaria** 365 f
– aspera 365
– **douglasii** 366 f
– eleocharidis 366 f
– fischeri 367
– **karii** 368 f
– turfosa 371 f
– **vankyi** 372 f
– **verrucosa** 372 f
Arachniodes denticulata 89
Aranae 395
Araucariaceae 195
Arecanae 394
Arthrodesmus longispinus 49 f
Astragalus laguriformis 437
– russelii 437
Axonopus compressus 99
Azima tetracantha 256 f
Batis maritima 256 f
Bifrenaria picta 417
Bomarea sect. **Pardinae** 55
– **ceratophora** 60 f
– pardina 56 f
Brachionidium tetrapetalum 417
Brassia 417
Bromeliales 391
Bromus 5
Cacosmia 279
– **harlingii** 283 f
– hieronymi 284 f
– rugosa 280 f
Calathea **gymnocarpa** 333 f
– **verecunda** 336 f
Callitriche 5 f
Campylocentrum colombianum 417
– fasciola 418
Carex subgen. Carex 353
– subgen. Indocarex 352
– subgen. Kuekenthalia 353
– subgen. Primocarex 353
– subgen. Vignea 352
– sect. Dioicae 352
– sect. Baldenses 352
– sect. Curvulae 352
– sect. Dispermae 354
– sect. Distichae 354
– sect. Ursinae 352
Cartonema 391
Cephalotaxaceae 195
Cerastium alpinum 304
– arcticum ssp. arcticum 306 f
– – ssp. **hyperboreum** 306
– – ssp. **procerum** 307 f
– edmondstonii 304
– **theophrasti** 469 f
Ceratiomyxa 483
Cetraria **arenaria** 124 f
– **australiensis** 127 f
– **fastigiata** 128 f
Chamaesyce lasiocarpa 96
Chrysochromulina **pyramidosa** 147 f
Cleome spinosa 256 f
Codonocarpus cotinifolius 256 f
Commelinanae 391
Cornucopiae cucullatum 203 m
Cosmarium **kostei** 41 f
– latipyramidatum v. **trapeziforme** 47 f
– patelliforme 49 f
– zonatum v. subcylindricum 49 f
Cotula abyssinica 6
Cranichis diphylla 164
– **pachnodes** 164 f
Crassula alba 5
– granvikii 5

Crepis **pawlowskii** 143 f
Cryptocentrum 418
Cryptocoryne 71 m
– affinis 78 f
– alba 79
– albida 78 f
– balansae 78 f
– beckettii 73
– bertelihansenii 78 f
– blassii 77 f
– bogneri 79
– ciliata 72 f
– costata 78 f
– crispatula 78 f
– **dewitii** 381 f
– griffithii 77 f
– jacobsenii 77 f
– lingua 79 f
– lucens 73
– lutea 76
– minima 77 f
– parva 73
– petchii 73
– pontederiifolia 76 f
– purpurea 77 f
– retrospiralis 79 f
– sarawacensis 77 f
– siamensis 77 f
– spiralis 73 f
– thwaitesii 79 f
– tonkinensis 78
– undulata 76 f
– usteriana 78 f
– verstegii 78 f
– walkeri 76
– wendtii 76 f
– willisii 73
– zewaldiae 77 f
Ctenitis pleiosorus 90
Ctenopsis 186
– sect. Ctenopsis 186
– sect. **Pseudocynosurus** 186
– cynosuroides 174 f
– gypsophila 174 f
– pectinella 174 f
Cuphea racemosa 97
Cupressaceae 194
Cyathus 453 f
Cycadaceae 194
Cyperus densicaespitosus 99
– odoratus 99
Delilia biflora 94
Dennstaedtia dissecta 90
Dichaea 418
Didymotheca tepperi 256 f
Digitaria decumbens 99
Diothonea gratissima 419
Dothiopeltis 226
– arunci 228 f
Drabopsis verna 213 m
Dryopteris parallelogramma 90
Echeveria atropurpurea 232
Echinosteliales 486
Echium nervosum 231 f
Elleanthus 166
Epidendrum 321
– cornanthera 322 f
– **echinatum** 324 f
– **garayii** 325 f
– **suavis** 327 f
Epilobium ciliatum 207 f
– glandulosum 205 f
Equisetaceae 191
Erechtites hieracifolia 94
Erythrodes arietina 166
Euastrum bahiense f. **minor** 45
– didelta var. quadriceps 45 f
– gessneri var. laticeps 44 f
– pinnatum 47 f
– platycerum var. eximium f. clausum 47 f
Femsjonia peziziformis 241 f m
Fernandezia ionanthera 419
Ferreyranthus excelsus 281
Festuca baffinensis 271 f m
– brachyphylla 269 f m
– – var. groenlandica 271 f m
– **hyperborea** 273 f m
– saximontana 274
Fragilaria constricta 318 f
– construens 318 f
– **lata** 315 f
Fucus bifidus 138
– corneus var. sesquipedalis 140
– crinalis 139
– pusillus 139
Fuirena ciliaris var. **apetala** 319
– microcarpa 320
– zambesiaca 320
Furcellaria fastigiata 137
– lumbricalis 137
Galenia secunda 130
Galinsoga urticaefolia 94
Garuleum subgen. **Rutidocarpaea** 377
– bipinnatum 378 f
Geastrum triplex 403 f
Gelidium 138
Ginkgoaceae 194
Gloeocystidiellum 53
Gnetinae 195
Gomphichis traceyae 166
Gyrostemonaceae 255
Gyrostemon ramulosus 256 f
Hanguana 387
Heliocauta 155
– **atlantica** 156 f m
– – var. **dasyphylla** 156
Hydrocotyle galapagensis 98
– umbellata 98
Hymenophyllum plumieri 89
Ipomoea pulchella 95
– stolonifera 95
Iris antilibanotica 264 f
– aucheri 263 f
– bismarckiana 264 f
– damascena 264 f
– haynei 266 f
– hermona 264 f
– heylandiana 25
– melanosticta 263 f
– nigricans 266 f

– nusairiensis 264 f
– palaestina 264 f
– paradoxa 256 f
– petrana 266 f
– postii 264 f
– samariae 266 f
– susiana 264 f
Isoetaceae 191
Isolepis **meruensis** 311 f
– setacea var. **aberdarica** 311 f
Jaegeria crassa 94
– gracilis 94
Kefersteinia laminata 419 f
Kniphofia thomsonii 5
Laeticorticium **pulverulentum** 466
Lathyrus pratensis 438
– vinealis 438
Lepanthes dasyphylla 419
– **villosa** 419 f
Leptopeltella perexigua 218
Leptopeltidaceae 215
Leptopeltis 218
– filicina 222 f
– **gregaria** 223 f
– **litigiosa** 221 f
– **lunariae** 216 f
– **nebulosa** 223 f
– pteridis 220 f
Leptosporangiatae 192
Liabum wrightii 281 f
Liceales 484
Lilianae 385
Liparis laticuneata 420 f
Lippia rosmarinifolia 96
Listerella 485
Litschauerella 461
– clematitis 465 f
Lupinus albicaulis 435 f
– albus 427 f
– angustifolius 428 f
– arboreus 435 f
– aschenbornii 435 f
– cosentinii 428 f
– graecus 427 f
– luteus 427 f
– micranthus 428 f
– montanus 435 f
– mutabilis 435 f
– palaestinus 428 f
– pilosus 428 f
– succulentus 435 f
Lycopodiaceae 190
Malaxis **hoppii** 421
– lobulata 421
– **nasuta** 421
Marattiaceae 192
Masonhalea 101 f m
– **richardsonii** 104
Maxillaria 422
Mayaca 391
Melinis minutiflora 99
Merremia umbellata 95
Micrasterias decemdentata 47 f
– **foersteri** 41 f
– truncata f. gibbosa 47 f
Moesziomyces 133
– **bullatus** 133 f
– **evernius** 135
– **globuligerus** 135
– **penicillariae** 135
Montinia caryophyllacea 329 f
Navicula amphipleuroides 478 f
– cryptolyra 476 f
– escorialis 478 f
– fenestrella 478
Octomeria grandiflora 423
Odontites litoralis 121 f
– rubra 121 f
– verna 121 f
Odontoglossum 423
Oldenlandia corymbosa 95
Oliveriana brevilabia 423
Oncidium cocciferum 423
Ophioglossaceae 191
Pachyphyllum 424
Palmorchis 168
Peltaria alliacea 256 f
Pentaschistis 5
Peperomia tequendamana 93
Petrocelis cruenta 138
Peyrousea 494
– umbellata 496 f m
Philesiaceae 386
Physalis peruviana 95
Physarales 489
Pinaceae 194
Pisum formosum 438
– fulvum 27 f m
– sativum 438
Pityphyllum laricinum 424
Planetella lironis 364
Pleurothallis 424
Podocarpaceae 195
Polygala galapageia 98
Polypodium astrolepis 90
Polytretus reinboldii 35 f
Ponthieva keraia 168
Psilochilus macrophyllus 168
– **physurifolius** 168
Psilotaceae 190
Pterichis 168
Ranunculus auricomus ssp. crassiusculus 287 m
– – ssp. **dactylophyllus** 288 f m
– – ssp. holanthus 289 m
– – ssp. inconspectus 292 m
– – ssp. obscurans 292 m
– – ssp. oligandrus 293 m
– – ssp. **pectinifolius** 294 f m
– – ssp. rotundellus 298 m
– monophyllus ssp. neumanii 298 m
Rhodophyllis divaricata 138
Rhynchosporeae 238
Rodriguezia carnea 424
Ronnigeria 228
– arctica 228 f
Salvia splendens 232
Scaphyglottis bicornis 424
Scinaia turgida 141
Scorpiurus muricatus 438
Selaginellaceae 190

Sesbania sesban 439
Sida glutinosa 98
Sisyrinchium laxum 473 f
Smilacaceae 386
Sobralia candida 170
– **melanothrix** 170
– rigidissima 171
Sorocarpaceae 39
Sorocarpus micromorus 37 f
Stemonaceae 386
Stemonitales 488
Synedra parasitica 318 f
Taraxacum **distantijugum** 61 f
– **eudontum** 62 f
– **fridenii** 69 f
– **oinopopodum** 64 f
– **semicurvatum** 65 f
– **virellum** 65 f
Taxaceae 195
Taxodiaceae 194
Thelypteris 91
Thyriopsis 228
Tillandsia insularis 98
Tolyposporium junci 131 f
Trianoptiles solitaria 235 f
Tribulus arabicus 261 f m
Trichiales 487
Trichocentrum recurvum 424
Trichodesma indicum 441 f
– zeylanicum 441 f
Tridax procumbens 95
Typhanae 394
Verbena brasiliensis 96
– townsendii 96
Vesiculomyces 53
– **citrinus** 53 m
Vicia ervilia 439
– hybrida 439
– koeieana 439
– narbonensis 439
– palaestina 439
– peregrina 439
– sativa 439
– sericocarpa 440
– tenuifolia 440
Vulpia 173
– sect. Monachne 187
– sect. Spirachne 187
– sect. Vulpia 187
– alopecuros 174 f
– ambigua 174 f
– bromoides 174 f
– ciliata 174 f
– fasciculata 174 f
– fontquerana 174 f
– geniculata 174 f
– inops 174 f
– myuros 194 f
– octoflora 174 f
Vulpiella 186
– tenuis 174 f
Zingiberanae 393
Zygophyllum **aegyptium** 467 f m
– decumbens var. **megacarpum** 467 m

Chromosome numbers of afroalpine and afromontane angiosperms

Inga Hedberg and Olov Hedberg

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Chromosome counts are reported for 200 afroalpine species of angiosperms from East Africa and Ethiopia. More than one collection was studied of 116 taxa, in 27 of which intraspecific polyploidy was discovered. Only diploids were recorded in 48.5%, only polyploids in 46.5%, both diploids and polyploids in 5%, which gives an overall polyploidy percentage of 49. This comparatively low figure suggests that the afroalpine flora has been relatively little exposed to major geographical changes in recent geological time. Counts are also reported for 7 afroalpine species of Cyperaceae and for 23 afromontane taxa, none of which are included in the percentage calculations. Taxonomic comments are given for a few genera.

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The afroalpine flora, occurring in isolated enclaves on the upper parts of the high East African and Ethiopian mountains (O. Hedberg 1951, 1957), provides unique opportunities to study speciation in connection with geographical isolation and adaptation to extreme environmental conditions (O. Hedberg 1964, 1969, 1970a, 1973, 1975a). Data on chromosome numbers and morphology have often contributed greatly to studies of evolution and speciation, and the percentage of polyploids in a flora may provide useful hints concerning its age and later development. In connection with our current studies on the origin and development of the afroalpine flora and of high mountain floras in general, it was therefore deemed desirable to procure as complete a list as possible of the chromosome numbers of afroalpine vascular plants. Detailed chromosome lists of this kind may also be of considerable interest for studies of generic affinities and angiosperm phylogeny in general (Raven 1975).

The publication has been delayed in the hope of getting the list more complete, but it now seems comprehensive enough to be worth publication. It comprises 182 of the 267 flowering plant species (the Cyperaceae excluded) known to be regular members of the East African afroalpine flora (O. Hedberg 1957), which means a coverage of 68%. We have also included 18 afroalpines from Ethiopia which are not found in East Africa. Only counts on tropical African material are considered. In addition 7 species of Cyperaceae and a few afromontane species (neither of which are considered in the calculation of polyploidy percentage) are included.

Material and methods

Most of the East African material used for this study was collected by O. Hedberg during field trips in 1948 (O. Hedberg 1951), 1967, 1970 and 1973, and by the authors together in 1971 (cf. I. Hedberg 1976). The bulk of the Ethiopian material was assembled by O. Hedberg in 1967 (O. Hedberg 1971) and 1973 (cf. O. Hedberg 1975a). In order to cover as many species and mountain populations as possible we have tried to get wherever possible both field fixations and seed samples.

All chromosome numbers reported here were counted on somatic mitoses in root tips. Mostly root tip sections were prepared but in some cases squash preparations were used (cf. I. Hedberg 1967, 1970).

The root tips for field fixation were taken from the same specimens that were later put in press as

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vouchers. Field fixations normally gave only one count per population, whereas we attempted to raise, fix and count 5 specimens from each seed sample. Voucher specimens for the latter consist either of the plants fixed or other specimens raised from the same batch of seeds (when those came into flower) or otherwise of specimens collected in the field from the same population which yielded the seeds. Vouchers of all counts are kept in the Botanical Museum, Institute of Systematic Botany, University of Uppsala (UPS).

The living material was kept in a cool greenhouse in the Botanic Garden of Uppsala University, during summer time in the open under shade. Whereas O. Hedberg has been responsible for most of the collecting and naming of the material, the bulk of the chromosome counts were performed or checked by I. Hedberg, and we are jointly responsible for the discussions and conclusions.

Unfortunately some groups of plants proved very difficult to examine cytologically with the methods employed – the number of counts reported e.g., for *Carex* and *Romulea*, bears little relation to the number of fixations made, and the few and inexact counts of *Alchemilla* have been left out. Such genera evidently demand special techniques.

One important difficulty in studies of polyploidy is to ascertain the basic chromosome numbers. In genera where several counts have been made, it may be reasonable to accept half of the lowest somatic number known as the basic number, but this may need adjustment as more numbers are discovered. Where monographic studies are known to us, we have usually followed the monograph in this respect. Thus *Gladiolus watsonioides* is treated as a diploid with $x = 15$. The basic number of *Cerastium* has earlier been assumed to be 18 (cf. e.g. Blackburn & Morton 1957), but since the somatic numbers 36 and 48 were found in this study in *Cerastium afromontanum* we must assume the basic number to be 6 instead of 18. Grasses like *Deschampsia caespitosa* with the somatic number 26 are treated here as diploids with $x = 13$ even if they must presumably result from secondary polyploidy. This means that the distinction between diploid and polyploid is sometimes rather schematical: *Deschampsia caespitosa* with $2n = 26$ and *Carduus keniensis* with $2n = 34$ are classified as diploids, whereas *Deschampsia flexuosa* with $2n = 28$ and *Carduus chamaecephalus* with $2n = 32$ are treated as tetraploids. But nevertheless this seems to be the most objective manner of classification. Obviously polyploidy percentages should always be taken as approximations only.

Polyploidy percentage

The discovery by Hagerup (1931) that the flora of Timbuctu contained a considerable number of polyploids and his hypothesis that these polyploids have arisen through the influence of climatic extremes stimulated a number of cytologists to explore the frequency of polyploids in other areas. Comparison of their results revealed that at least in NW Europe the percentage of polyploids increases towards higher latitudes (Tischler 1935, Löve & Löve 1943, 1971, Reese 1958). In some instances at least the frequency of polyploidy was also found to increase with altitude on a mountain, as on Mt Bismarck, New Guinea (Borgmann 1964) and on Mt Washington in USA (from c. 45% in the surrounding nemoral flora to 64% in the alpine belt, Löve & Löve 1967). But the snowfen communities of Knutshö, Norway, have a polyploidy percentage of 51 only (Gustafsson 1948), and the nival flora of the Swiss Alps contains barely 56% polyploids (Favarger 1956). Similarly the high mountain flora of the Caucasus contains no more than 49.5% polyploids as against 86% in the Pamir (Sokolovskaja & Strelkova 1962).

To explain the higher incidence of polyploidy towards higher latitudes and (sometimes) altitudes Löve & Löve (1943) suggested that polyploidy may represent an adaptation to a cold climate. This hypothesis was contested by Manton (1950) who considered that polyploidy is not "an adaptation to cold or any other climatic factor but that it is correlated rather with climatic or geographical upheavals however caused ... In a relatively undisturbed flora the incidence of polyploidy may therefore be expected to be low". From a genetical point of view Stebbins (1950) looked upon (allo)polyploidy as "a process which is most effective as a mean of enabling species groups which have reached a certain stage of depletion of their biotypes, and of sharp divergence of specific entities, to adapt themselves to new environmental conditions which arise relatively suddenly. It is much less important in stable environments and in diploid species which are still widespread and rich in ecotypic differentiation". From the point of view of phytogeography, the importance of the polyploidy percentage was formulated by Reese (1958, 1961): "the younger the flora, the higher the percentage of polyploids" (cf. also O. Hedberg 1961).

It was realized at an early stage that the percentage of polyploids may be a crude instrument for comparison of different floras, since the tendency to form polyploids is much higher in some groups than in others; it is usually stronger in monocots than in dicots.

Table 1. Summary of chromosome numbers counted and polyploidy percentage. – Only counts on tropical African material are considered. In calculating the percentage of polyploidy we have counted those species which contain diploid and polyploid strains both under diploids and under polyploids. The total number of afroalpine vascular plant species is probably larger than indicated here, since much has happened both concerning exploration and taxonomic revisional work after the survey in O. Hedberg 1957.

Category	Gramineae	Monocots excl. Cyperaceae	Compositae	Dicots	Angiosperms
Number of species occurring in the East African afroalpine flora	34	53	62	214	267
Number of species in which the chromosome number has been counted	28	42	43	140	182
Per cent species studied	82	79	69	65	68
Number of additional afroalpine species from Ethiopia studied	5	6	7	12	18
Only the diploid number found	6	9	34	88	97
Only one polyploid number found	21	29	13	50	79
Intraspecific polyploidy (diploid + polyploid)	4	5	–	5	10
Intraspecific polyploidy (2 or more polyploid races)	4	5	3	9	14
Percentage polyploids	74	74	32	41	49

But a detailed breakdown of available figures demonstrated that within each of the main families or family groups the same relation exists between latitude and percentage of polyploids (cf. Löve & Löve 1948, Blackburn & Morton 1957, Reese 1957, 1961). A breakdown for monocots and dicots and for the largest family of each in the afroalpine flora is given in Table 1.

In order to improve the usefulness of polyploidy spectra in estimating the age of a flora Favarger (1961) subdivided the polyploids (apart from taxa demonstrating intraspecific polyploidy) in the area into three groups: *paleopolyploids,* of which diploid ancestors and close relatives are unknown and probably extinct; *neopolyploids,* which in the area studied have replaced the diploid race(s) of the same species; and *mesopolyploids,* which can probably be derived from known diploid taxa in the same genus or closely related genera. In a "spectrum of relative age" Favarger groups diploids and paleopolyploids together as an ancient element against a middle-aged element (mesopolyploids) and a recent element (neopolyploids and taxa with intraspecific polyploidy). This method was intended to provide a better measure of the age of the flora than only the percentage of polyploidy. It was later stressed by Reese (1966) than Favarger's age index was not directly comparable to the polyploidy spectrum – instead of giving the age of establishment of a flora it attempted to give the phylogenetic age of it. A tentative attempt to subdivide our polyploids according to Favarger's method proved very difficult, since in order to distinguish between paleopolyploids, neopolyploids and mesopolyploids one must know the flora under consideration and other related floras very well both cytologically and taxonomically. To enforce a distribution of the afroalpine polyploids in this way would have necessitated a number of arbitrary decisions.

Another way of refining the use of polyploidy spectra was applied by Blackburn & Morton (1957) who introduced a *polyploidy index* reflecting also the level of polyploidy of each taxon. That method may obviously be of value in comparing the degree of polyploidy in one family between different geographical areas. But when one is comparing entire floras of widely diverging taxonomic composition it would seem to be less useful.

The polyploidy percentage of 49 obtained in this study (Table 1) is comparatively low – much lower than in the Arctic, and considerably

Table 2. Species displaying intraspecific polyploidy. ++ refer to cases where two ploidy levels were found in one batch of seedlings.

Taxa	Diploid and polyploid	Two different polyploids	Inter-mountain differences	Intra-population differences	References
Poa leptoclada	+	+	.	+	O. Hedberg 1957
Festuca abyssinica	+	.	.	+	
Anthoxanthum nivale	.	+	+	+	I. Hedberg 1976
Koeleria capensis	+	.	.	+	
Deschampsia flexuosa	.	+	+	.	O. Hedberg 1957
Pentaschistis borussica	+	.	.	++	
P. minor	+	.	+	+	
P. mannii	+	.	+	.	
Bromus leptocladus	.	+	.	++	
Luzula campestris var. *gracilis*	.	+	.	++	
Kniphofia snowdenii	+	.	.	+	Janaki Ammal 1950
K. thomsonii	+	.	+	.	
Cerastium afromontanum	.	+	.	+	
Ranunculus volkensii	.	+	+	.	
R. oreophytus	.	+	+	.	
Cardamine hirsuta	+	.	.	.	
C. obliqua	.	+	+	.	Jonsell 1976
Sedum meyeri-johannis	+	.	.	+	
Crassula granvikii	.	+	+	+	O. Hedberg 1957
C. alba	+	.	+	.	
Trifolium burchellianum ssp. *johnstonii*	.	+	.	.	
Callitriche stagnalis	+	.	+	.	
Peucedanum kerstenii	+	.	.	++	
Anagallis serpens ssp. *meyeri-johannis*	+	.	.	+	Taylor 1955
Cotula abyssinica	.	+	+	.	
Senecio johnstonii ssp. *cheranganiensis*	+	.	.	.	
S. schweinfurthii	.	+	.	+	
Guizotia reptans	+	.	+	.	

lower than, e.g., in the alpine belt on Mt Washington and on Mt Wilhelm mentioned above. It is more comparable to values from the high-mountain regions of Caucasus (49.5%, Sokolovskaja & Strelkova 1962) and to the nival zone in the Swiss Alps (56%, Favarger 1954). According to the above considerations this indicates that the afroalpine flora like the flora of the Caucasus has been relatively little disturbed by major climatic changes in recent times.

Taxonomic comments

The comparatively large material accounted for in this study enables us to estimate the amount of intraspecific polyploidy in the afroalpine flora. Two or more euploid numbers have been found in 28 taxa (Table 2), which represent 13% of the total number studied or 24% of the species from which more than one collection has been counted. In some cases at least there appears to be a difference in ploidy between different mountain populations. This may be compared to 46 cases of intraspecific polyploidy known among the 437 flowering plant species of Greenland (10.5%; see Jørgensen, Sørensen & Westergaard 1959).

An indication of the frequency of polyploidization is given by the fact that out of 54 sowings in which at least 2 plants were counted 4 gave two different euploid numbers (*Pentaschistis borussica, Bromus leptocladus, Luzula campestris* var. *gracilis* and *Peucedanum kerstenii*).

The cytological data mentioned seem to suggest that differences in ploidy within and between

populations may be important in connection with differentiation and speciation, for instance in *Anthoxanthum nivale, Deschampsia flexuosa, Pentaschistis, Ranunculus, Cardamine obliqua, Crassula, Callitriche stagnalis, Cotula abyssinica,* and *Guizotia reptans*.

Occurrence of two or more different chromosome numbers within what is believed to be one taxonomic species gives reason for detailed taxonomic studies to investigate whether the cytological differences are connected with morphological differences permitting taxonomic segregation. Some of the species enumerated in Table 2 have already been thoroughly scrutinized and found to display continuous variation, e.g. *Poa leptoclada, Anthoxanthum nivale, Deschampsia flexuosa, Cardamine obliqua,* and *Anagallis serpens* ssp. *meyeri-johannis* (for references see Table 2). For a few other species taxonomic comments are given below and for those as well as a few others more detailed studies on a larger material are called for.

Pentaschistis. A spontaneous triploid in *Pentaschistis* was reported by O. Hedberg (1952 p. 264) and later identified as *P. mannii* (Hedberg 1957 p. 34). The occurrence of intraspecific polyploidy in this species as well as in *P. minor* and *P. borussica* is confirmed by the counts presented here. We have found no morphological distinctions between the cytotypes in either case. As emphasized by Clayton (1970 p. 124) the genus is insufficiently collected in East Africa for a proper appreciation of variation among the species.

Bromus. The only difference so far discovered between the cytotypes is smaller spikelets in the hexaploid specimen, but in view of the wide and continuous variation described for this species by Clayton (1970 p. 70) this difference appears of no taxonomic value.

Kniphofia thomsonii. No significant morphological differences were discovered between the diploid and tetraploid specimens, nor was the tetraploid in any respect larger than the diploid.

Crassula granvikii. Friedrich (1973 p. 51) reports the number 48 for Ethiopian material of this species and the numbers 32 and 64 for Mt Kenya material of two forms growing together, assigned by him to the closely related species *C. rivularis* (Peter) Hutch. & E. A. Bruce, which was treated by O. Hedberg (1957 p. 100) as a synonym of *C. granvikii*. This variable species would evidently merit a detailed cytotaxonomic study.

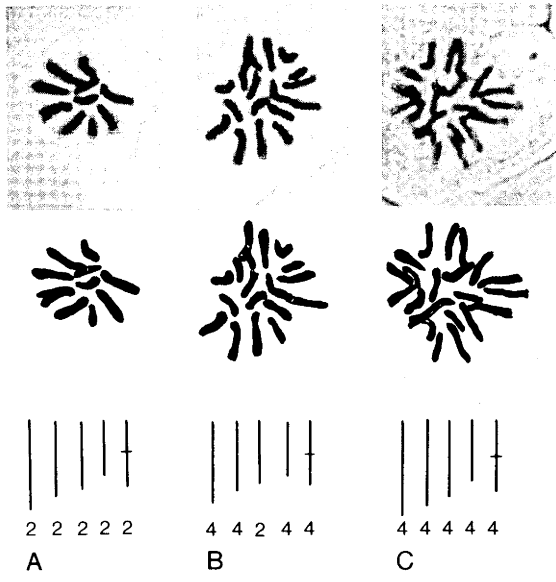


Fig. 1. Chromosome complements in three specimens of *Callitriche* from tropical Africa. – A: 2n = 10 (Hedberg 4234). – B: 2n = 18 (Hedberg 4351). – C: 2n = 20 (Hedberg 5574). – The figures give the number of each chromosome type. × c. 1500.

Crassula alba. Friedrich (1973 p. 58) gives the chromosome number of this species as 14 in material from Cameroons Mt, whereas *C. abyssinica* A. Rich. s. str. from Ethiopia (usually considered synonymous) gave 2n = 28.

Callitriche. As shown in the main list three different chromosome numbers were found within the material. Of those 2n = 10 has been reported earlier in *C. stagnalis* (Jørgensen 1923, Schotsman 1967), *C. obtusangula* (Schotsman 1967) and *C. cophocarpa* (Schotsman 1967); 2n = 20 in *C. stagnalis* (Jørgensen 1923) and in *C. platycarpa* (Schotsman 1967), whereas 2n = 18 is here reported for the first time. Hence the basic number n = 9 is added to the earlier reports from which four (five) basic numbers are known within the genus, viz. 3, 4, 5, (7?), and 19 (Schotsman 1967, who provisionally lists *C. brutia*, 2n = 28, as a diploid).

The chromosome numbers in the present material were counted in paraffin sections which

makes the material less suitable for studies of chromosome morphology (cf. I. Hedberg 1970 p. 157). It is, however, possible to distinguish certain types of chromosomes and thus to some extent to compare the different complements (Fig. 1). Obviously they have very much in common. In the diploid (2n = 10) the complement consists of four pairs of subterminals, one pair of which is considerably shorter than the rest, and one pair of medians (or submedians) slightly longer than the shortest subterminals. There are no difficulties in recognizing the two pairs of shorter chromosomes in different sections and it is also possible to distinguish the larger subterminals (Fig. 1A). In the 18-chromosomic specimens as well as in the tetraploid (2n = 20) four short subterminals can easily be recognized and also four medians (or submedians). It seems also possible to group the larger subterminals (Fig. 1 B, C).

Judging from the somatic number the species from Mt Kenya must probably be an allotetraploid arisen from hybrids between species with n = 4 and n = 5, respectively. This assumption is supported by the idiograms though not too much weight should be laid on the differences in length between the larger subterminals. Unfortunately differences in applied technique and illustrations makes it impossible to compare in detail the chromosome complements illustrated by Schotsman (1967) and those illustrated here. The only species with n = 4 so far known is *C. lusitanica*, the complement of which, however, as illustrated by Schotsman, lacks medians or submedians. It is also evident that the complements found in our African material agree much more with that found by Schotsman in *C. obtusangula* (Schotsman 1967 Pl. XIX, III_2:a1) than with those in *C. stagnalis* (Pl. XVIII, III:a–c).

The existence of the somatic number 18 might also explain the origin of the numbers 2n = 28 (*C. brutia*) and 2n = 38 (*C. hamulata*), respectively, since these could then have arisen through hybridization between specimens with n = 9 and with n = 5 and n = 10, respectively, followed by doubling. A fact supporting this hypothesis is that according to Schotsman a certain type of chromosomes is found in both *C. brutia* and *C. hamulata*. This type is said to be a median, longer than the other chromosomes. On the other hand, the medians found by us in the African material are not the largest in the complement, but as pointed out above the length of the chromosomes should be used with great care in comparisons, both within a complement and between different sets.

Because of the limited material available we refrain from taxonomic conclusions, the more so since a comprehensive study of the group is being undertaken by Schotsman. The necessity of a careful cytological investigation of the whole genus in connection with such a study is obvious.

Cotula abyssinica. Our material indicates a very interesting polyploid series with the somatic numbers c. 32, c. 40, 48, and 54. The highest number was found in an ecologically very specialized variety which might prove worthy of a higher rank when more material becomes available (O. Hedberg 1971 p. 119). But between the other three cytotypes no significant morphological differences could be found.

The occurrence of two or more basic chromosome numbers within a genus is an interesting and inspiring challenge for further cytotaxonomic studies. In the afroalpine flora such cases occur in *Deschampsia, Andropogon, Stellaria, Ranunculus, Crassula,* and *Vicia,* each of which must be studied in a wider context.

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List of chromosome numbers

For ease of reference the taxa have been arranged in the same sequence as in O. Hedberg 1957, with additional taxa intercalated in relevant places. Species occurring only at lower levels on the mountains have been marked with an asterisk. + after the species epithet indicates that the chromosome number of the species in question is here reported for the first time. Apart from our own material we have included in this list relevant counts of afroalpine taxa published by other authors. For the survey of polyploidy we have included only counts from the afroalpine flora.

Under references in the list numbers without letters refer to collections by (I. &) O. Hedberg, whereas names of other collectors have been abbreviated as follows: B = S. W. Bie, C = M. J. Coe, C & K = Coe & Kirika, E = J. Eriksson, G = Gower, N = Nelson, T = M. Thulin. Literature references have been abbreviated in the usual manner. Herbarium abbreviations according to Holmgren & Keuken 1974.

Taxon	2n	Ploidy	Locality and altitude	Reference
Gramineae				
Andropogon (x = 5, 9)				
amethystinus Steud. +	20	4 x	Galama Mts, 3750 m	4227
lima Stapf +	36	4 x	Mt Elgon, 3560 m	B 66275
			Mt Elgon, 3200 m	4466
Pennisetum (x = 9)				
clandestinum Hochst. ex Chiov.	36	4 x	Kilimanjaro, 2800 m	Tateoka 1965
Pentaschistis (x = 13)				
borussica (K. Schum.) Pilg.	26	2 x	Kilimanjaro, 3800 m, 3150 m	1176, O. Hedberg 1957, Tateoka 1965
	26	2 x	Mt Meru, 3450 m	B 66124: 1, 2, 5
	39	3 x	Mt Meru, 3450 m	B 66124: 4

Taxon	2n	Ploidy	Locality and altitude	Reference
minor (Ballard & C. E. Hubbard) Ballard & C. E. Hubbard +	26	2 x	Mt Elgon, 3800 m	4487
			Mt Kenya, 4250 m	4437
	52	4 x	Mt Kenya, 4350 m	1773, O. Hedberg 1957, Tateoka 1965
mannii Stapf +	26	2 x	Galama Mts, 3750 m	4208
	c. 39	3 x	Aberdare, 3900 m	1538, O. Hedberg 1952, 1957
	52	4 x	Mt Meru, 4560 m	2329, O. Hedberg 1957
trisetoides Pilg. +	26	2 x	Simien, 3600 m	5343
pictigluma (Steud.) Pilg. +	26	2 x	Simien, 4225 m	5440
			Bale Mts, 4050 m	5604
Festuca (x = 7)				
abyssinica Hochst. ex A. Rich. +	14	2 x	Simien, 4100–4200 m	5452, 5445
	28	4 x	Galama Mts, 3750 m	4179
			Bale Mts, 4300 m	5586
			Mt Kenya, 4350 m	1862, O. Hedberg 1957
			Kilimanjaro, 3150 m	Tateoka 1965
			Mt Meru, 3000 m	B 66131
cfr. *abyssinica* Hochst. ex A. Rich.	28	4 x	Simien, 4225 m	5429
pilgeri St.-Y.	28	4 x	Mt Kenya, 4200–4270 m	1901, 1928, O. Hedberg 1957
Poa (x = 7)				
ruwensoriensis (L.) Robyns & Tournay	42	6 x	Galama Mts, 3750 m	4207
			Ruwenzori, 4150 m	402, O. Hedberg 1957
leptoclada Hochst. ex A. Rich.	28	4 x	Mt Kenya, 3100 m	2020, O. Hedberg 1957
	42	6 x	Bale Mts, 4050 m	5595
			Ruwenzori, 3850–4300 m	602, 677, O. Hedberg 1957
			Mt Elgon, 4200 m	886
			Mt Kenya, 4500 m	1757
			Kilimanjaro, 3800–4600 m	1246, 1262, B 05, Tateoka 1965
			Mt Meru, 3150–4200 m	2342, 2406
schimperana Hochst. ex A. Rich.	42	6 x	Galama Mts, 3750 m	4178, 4198
			Bale Mts, 4050–4100 m	5597, 5644
			Muhavura, 3800–4100 m	2079, 2145, 2188
			Ruwenzori, 3850–4150 m	404, 499, 601, 717
			Mt Elgon, 3600 m	983
			Mt Kenya, 3100–4130 m	1780, 1781, 1956, 1965
			Kilimanjaro, 3800 m, 3100 m	1247, Tateoka 1965
kilimanjarica (Hedb.) Markgraf-Dannenb. +	42	6 x	Kilimanjaro, 3800 m	B 02
cfr. *simensis* Hochst. ex A. Rich +	42	6 x	Galama Mts, 3750 m	4209
			Simien, 3720 m	5367
cfr. *pumilio* Hochst. +	42	6 x	Bale Mts, 4300 m	5609
Koeleria (x = 7)				
capensis (Steud.) Nees	14	2 x	Simien, 4100 m	5450
			Galama Mts, 3750 m	4171
			Bale Mts, 4300 m	5585
			Mt Kenya, 3950 m	1873, O. Hedberg 1957
			Kilimanjaro, 3150 m	Tateoka 1965
			Cherangani Hills, 3250 m	Thulin 1970
	28	4 x	Kilimanjaro, 3125 m	B 66188

Taxon	2n	Ploidy	Locality and altitude	Reference
Helictotrichon (x = 7)				
elongatum (Hochst. ex A. Rich.) C. E. Hubbard	28	4 x	Galama Mts, 3750 m	4175
			Kilimanjaro 3120 m, 2900 m	B 66169, Tateoka 1965
milanjianum (Rendle) C. E. Hubbard +	28	4 x	Aberdare, 3200 m	4355
Deschampsia (x = 7, 13)				
caespitosa (L.) Beauv.	26	2 x	Galama Mts, 3750 m	4143
			Simien, 4050 m	5454
			Ruwenzori, 3450 m	363, O. Hedberg 1957
			Mt Elgon, 4000 m	860
flexuosa (L.) Trin. v. *afromontana* C. E. Hubbard	28	4 x	Galama Mts, 3750 m	4193
			Muhavura, 4100 m	2075, O. Hedberg 1957
			Mt Kenya, 3950 m	1840
			Kilimanjaro, 4100 m, 3100 m	1361, Tateoka 1965
	42	6 x	Ruwenzori, 3450 m	389, O. Hedberg 1952
Agrostis (x = 7)				
schimperana Steud.	42	6 x	Mt Elgon, 3200 m	4557
			Kilimanjaro, 3800 m	1248, O. Hedberg 1957, Tateoka 1965
sclerophylla C. E. Hubbard	28	4 x	Mt Kenya, 4350 m	1724, O. Hedberg 1957
taylori C. E. Hubbard	28	4 x	Muhavura, 3730 m	2247, O. Hedberg 1957
kilimandscharica Mez.	28	4 x	Muhavura, 3450 m	2113, O. Hedberg 1957
			Mt Elgon, 3560 m	B 66256
			Aberdare, 3500 m	4331
			Mt Kenya, 3700 m	4436
			Kilimanjaro, 3100 m	Tateoka 1965
quinqueseta (Steud.) Hochst. +	28	4 x	Muhavura, 3730 m	2249
trachyphylla Pilg.	28	4 x	Ruwenzori, 4200 m	412, O. Hedberg 1957
			Mt Kenya, 4200–4350 m	1725, 1768
volkensii Stapf	28	4 x	Aberdare, 3570–3900 m	1543, 1664, O. Hedberg 1957
			Mt Kenya, 4150 m	1907
			Kilimanjaro, 3100 m	Tateoka 1965
			Mt Meru, 3750 m	B 66130
gracilifolia C. E. Hubbard +	28	4 x	Simien, 4100 m	5449
	c. 28	4 x	Mt Elgon, 3200 m	4461
producta Pilg.	28	4 x	Kilimanjaro, 3100 m	Tateoka 1965
Colpodium (x = 4)				
chionogeiton (Pilger) Tzvel.	8	2 x	Mt Kenya, 4250–4450 m	1902, 1759, O. Hedberg 1952, Melderis 1956
			Kilimanjaro, 4830 m, 3800 m	1253, B 35
hedbergii (Meld.) Tzvel.	8	2 x	Simien, 3600–3700 m	5361, 5492
			Bale Mts, 4100–4150 m	5645, 5618
			Mt Elgon, 3580 m	908, O. Hedberg 1952, Melderis 1956

Taxon	2n	Ploidy	Locality and altitude	Reference
Bromus (x = 7)				
leptoclados Nees +	28	4 x	Galama Mts, 3700 m	4235
			Mt Meru, 2400 m	4927: 1, 3, 4, 5
	42	6 x	Mt Meru, 2400 m	4927: 2
			Mt Kenya, 3020 m	4402
Anthoxanthum (x = 5)				
nivale K. Schum.	20	4 x	see I. Hedberg 1976	
	60	12 x	see I. Hedberg 1976	
aethiopicum I. Hedb.	20	4 x	see I. Hedberg 1976	
Cyperaceae				
Scirpus				
setaceus L.	c. 56		Aberdare, 3500 m	4332
Carex				
runssoroensis K. Schum. var. *aberdarensis* Kük.	c. 50		Mt Kenya, 3900 m	4415
conferta Hochst.	c. 52		Mt Elgon, 3560 m	B 66287
	c. 56		Kilimanjaro, 3120 m	B 66164
bequaertii Hochst. ex A. Rich.	c. 58		Mt Kenya, 3400 m	C &K 392: 1
simensis Hochst. ex A. Rich.	c. 70		Aberdare, 3500 m	4330
	70		Cameroons Mt	Morton 1961
fischeri K. Schum.	c. 56		Mt Elgon, 3200 m	4563
	c. 67		Mt Elgon, 3560 m	B 66265: 1
Eriocaulaceae				
Eriocaulon (x = 8)				
schimperi Körn. ex Engl.	c. 80	10 x	Bale Mts, 3950 m	5566
Juncaceae				
Juncus (x = 5)				
dregeanus Kunth	c. 35	c. 8 x	Aberdare, 3300 m	4328
	c. 40	8 x	Mt Elgon, 3200 m	4553
Luzula (x = 3)				
abyssinica Parl.	24	8 x	Galama Mts, 3750 m	4180
			Mt Kenya, 4200 m	1766, Nordenskiöld 1951
			Kilimanjaro, 3800 m	1216, Nordenskiöld 1951
			Mt Meru, 3750 m	B 66129
campestris (L.) DC. v. *gracilis* S. Carter +	24	8 x	Mt Elgon, 3000 m	4571: 2
	c. 30	10 x	Mt Elgon, 3000 m	4571: 4
	42	14 x	Cameroons Mt	Morton 1961
johnstonii Buchenau	42	14 x	Aberdare, 3070 m	1568, Nordenskiöld 1951
			Kilimanjaro, 3350 m	1365, Nordenskiöld 1951

Taxon	2n	Ploidy	Locality and altitude	Reference
Liliaceae				
Kniphofia (x = 6)				
snowdenii C. H. Wright +	12	2 x	Mt Elgon, 3200 m	4467
	18	3 x	Mt Elgon (offspring, cult.)	Janaki Ammal 1950
thomsonii Baker +	12	2 x	Mt Meru, 3450 m	B 66127: 1–5
	24	4 x	Mt Kenya, 3020 m	4398
Iridaceae				
Romulea (x = 9)				
fischeri Pax	74–78	polypl.	Et., Gama Mts, 3300 m	E 417, O. Hedberg 1962 a
	c. 70	polypl.	Mt Elgon, 3350 m	B 66304, Goldblatt 1971
keniensis Hedb.	28–30	polypl.	Mt Kenya, 4000 m	4821
Hesperantha (x = 13)				
petitiana (A. Rich.) Bak. v. *volkensii*	c. 75	6 x	Kilimanjaro, 3120 m	B 66174, Goldblatt 1971
Dierama (x = 10)				
pendulum (L. f.) Bak.	20	2 x	Cherangani Hills, 3240 m	Thulin 1970
			Kilimanjaro, 3000 m	4382
			Tropical Africa	Darlington & Wylie 1955
			Aberdare, 3350 m	5105: 1, 2
Gladiolus (x = 15)				
watsonioides Bak. +	30	2 x	Mt Kenya, 3900 m	4815
			Mt Meru, 3300 m, 3450 m	4761: 2, B 66102
Orchidaceae				
Disa (x = 9)				
stairsii Kränzl. +	36	4 x	Mt Kenya, 3020–3550 m	4400, 4278
Urticaceae				
Urtica (x = 12)				
massaica Mildbr. +	48	4 x	Mt Elgon, 3560 m	B 66282: 1, 2, 3
Polygonaceae				
Rumex (x = 9, 10)				
bequaertii De Wild.	40	4 x	Et., Garamba, 2900 m	E 268, O. Hedberg 1962 a
	c. 40		Cameroons Mt	Morton K 517, Morton 1961
* *ellenbeckii* Dammer	18	2 x	Et., Lake Awasa, 1750 m	E 527, O. Hedberg 1962 a
Oxygonum (x = 13)				
* *sinuatum* (Hochst. ex Steud.) Benth. & Hook. f. +	52	4 x	Kilimanjaro, 1300 m	1117

Taxon	2n	Ploidy	Locality and altitude	Reference
Portulacaceae				
Montia (x = 10)				
fontana L. ssp. *fontana*	20	2 x	Mt Kenya, 3850 m	4310
			Kilimanjaro, 3800 m	B 16
Caryophyllaceae				
Stellaria (x = 9, 13)				
sennii Chiov.	c. 52	4 x	Cherangani Hills, 3150 m	Thulin 1970
			Aberdare, 3000 m	4347
			Mt Meru, 2500 m	4943
* *mannii* Hook. f. +	36	4 x	Et., Arussi, 2400 m	Brink 27:3
Cerastium (x = 6, 13)				
afromontanum Th. Fr. jr. & H. Weim. +	36	6 x	Bale Mts	5523: 1, 2
			Mt Elgon, 3350 m	5073
			Aberdare, 3500 m	5034 A
			Mt Kenya, 3550 m	C & K 390
			Kilimanjaro, 3120–3550 m	B 66157
	48	8 x	Kilimanjaro, 3050 m	B 66241
octandrum Hochst. ex A. Rich. +	52	4 x	Simien, 3720 m	5371
			Bale Mts, 3200 m	5519: 2
			Mt Elgon, 3200 m	4458
Sagina (x = 10)				
abyssinica Hochst. ex A. Rich. ssp. *aequinoctialis* Hedb.	c. 60	6 x	Mt Elgon, 3450 m	220 a, O. Hedberg 1954
			Mt Kenya, 3400 m	C 412
			Kilimanjaro, 3500 m, 4130 m	4370, 1412
			Cameroons Mt	Morton 1961
afroalpina Hedb.	20	2 x	Mt Kenya	Mark 2
			Kilimanjaro, 4600 m	1250
Silene (x = 12)				
burchellii Otth. in DC.	24	2 x	Kilimanjaro, 3700 m	1291, O. Hedberg 1957
			Mt Meru, 3450 m	B 66125
			S. Africa	Nordenstam 1969
Uebelinia (x = 12)				
* *rotundifolia* Oliv. +	48	4 x	Kilimanjaro, 3000 m	4389
* *crassifolia* Th. Fr. jr. +	48	4 x	Cherangani, 3150 m	Thulin 1970
Ranunculaceae				
Delphinium (x = 8)				
macrocentrum Oliv.	16	2 x	Aberdare, 2550 m	Hedberg s.n., O. Hedberg 1957
Anemone (x = 8)				
thomsonii Oliv. +	16	2 x	Mt Elgon, 3500 m	4577
			Kilimanjaro, 3000–3050 m	4384, B 66231

Taxon	2n	Ploidy	Locality and altitude	Reference
Ranunculus (x = 7, 8)				
volkensii Engl.	c. 64	8 x	Mt Elgon, 3600 m	1019, O. Hedberg 1957
	80	10 x	Cherangani Hills, 2550 m	Thulin 1970
	c. 90	polypl.	Mt Kenya, 3000 m	4266
oreophytus Delile	32	4 x	Ruwenzori, 3900 m	507
			Cherangani Hills, 2850 m	Thulin 1970
			Aberdare, 3600 m	1617
			Mt Kenya, 3800–4200 m	1708, 4323
	64	8 x	Kilimanjaro, 3000	4375
* *multifidus* Forsk.	32	4 x	Cherangani, 2850 m	Thulin 1970
stagnalis Hochst. ex A. Rich.	28	4 x	Simien, 3850 m	5466
			Galama Mts, 3750 m	4145
			Mt Elgon, 3600–4000 m	994, 4520, 4482, O. Hedberg 1957
			Kilimanjaro, 4750 m	1256
Cruciferae				
Subularia (x = 7)				
monticola A. Br.	28	4 x	Mt Kenya	1727, 1804, O. Hedberg 1957
			Kilimanjaro	Jonsell 1976
Thlaspi (x = 7)				
alliaceum L.	14	2 x	Simien, 4225 m	5427, Jonsell 1976
Cardamine (x = 8)				
hirsuta L.	16	2 x	Simien, 3750 m	5395, Jonsell 1976
	32	4 x	Cameroons Mt	Morton 1961
obliqua Hochst. ex A. Rich.	36	4 x	Uluguru, 2400 m	Jonsell 1976
	56	7 x	Kilimanjaro, 2500 m	Jonsell 1976
	62		Simien, 3600 m	5348 b, Jonsell 1976
	c. 64	8 x	Bale Mts, 4000 m	5553, Jonsell 1976
	72	9 x	Mt Kenya, 3250 m	Jonsell 1976
			Mt Meru, 2900 m	4742, Jonsell 1976
**africana* L.	16	2 x	Kilimanjaro, 1500 m	4396
			Mt Meru, 2700 m	4741, Jonsell 1976
			Cameroons Mt	Morton 1961
Arabidopsis (x = 5)				
thaliana (L.) Heinh.	10	2 x	Simien, 3700 m	5433, Jonsell 1976
			Mt Kenya, 4000 m	C & K 290
Arabis (x = 8)				
alpina L.	16	2 x	Simien, 4225 m	5431, Jonsell 1976
			Chillalo, 3500 m	Jonsell 1976
			Bale Mts, 4000 m	Jonsell 1976
			Mt Kenya, 3900 m	O. Hedberg 1962 b, Jonsell 1976
			Mt Meru, 2800 m	Jonsell 1976
Oreophyton (x = 8)				
falcatum (A. Rich.) O. E. Schulz	32	4 x	Simien, 4225 m	5435, Jonsell 1976

Taxon	2n	Ploidy	Locality and altitude	Reference
Erophila (x = 8)				
verna (L.) F. Chev. s. lat.	c. 60		Bale Mts, 3950 m	5550, Jonsell 1976
Crassulaceae				
Sedum (x = 8)				
meyeri-johannis Engl.	16–18	2 x	Kilimanjaro, 3550 m	B 66221: 1, 2
	c. 44	6 x?	Kilimanjaro, 3800 m	B 10: 1, 2, 3
Crassula (x = 7, 8)				
granvikii Mildbr.	32	4 x	Bale Mts, 4150 m	5619
			Mt Kenya	Friedrich 1973
			Cherangani Hills, 2500 m	Thulin 1970
			Aberdare	4282
	c. 30		Mt Elgon, 3600 m	1022
	c. 40	5 x	Mt Elgon, 3350 m	B 66317: 2
	48	6 x	Ethiopia	Friedrich 1973
	64	8 x	Mt Kenya	Friedrich 1973
	c. 96	12 x	Mt Kenya	C 1959: 4
alba Forsk.				
(sub nom. *C. abyssinica* Forsk.)	14	2 x	Cameroons Mt	Friedrich 1973
(sub nom. *C. alba*)	28	4 x	Ethiopia, Dire Dawa	Friedrich 1973
Leguminosae				
Trifolium (x = 8)				
cryptopodium Steud. ex A. Rich. +	48	6 x	Bale Mts, 3950 m	5570
	c. 48		Mt Elgon, 3200 m	4456
burchellianum Ser. subsp. *johnstonii* (Oliv.) Gillett +	c. 48	6 x	Aberdare, 3200 m	4305
	96	12 x	Kenya, Kitale	Pritchard 1962, Britten 1963
acaule Steud. ex A. Rich.	16	2 x	Galama Mts, 3750 m	4126
			Trop. Africa	Frahm-Leliveld 1969
			Mt Elgon, 4000 m	4481
rueppellianum Fres.	16	2 x	Galama Mts, 3700 m	4237
			Kenya, Kitale	Pritchard 1962, Britten 1963
spananthum Thulin	16	2 x	S. Ethiopia	Thulin 1976 b
tembense Fres.	16	2 x	Mt Elgon, 3200 m	4457
			Kenya, Molo	Pritchard 1962
			Tanganyika, Mbulu	Pritchard 1962, Britten 1963
* *steudneri* Schweinf.	16	2 x	Et., Gibbi River, 1100 m	E 165(S), O. Hedberg 1962 a
elgonense Gillett +	16	2 x	Simien, 3600 m	5342
Lathyrus (x = 7)				
hygrophilus Taub. +	14	2 x	Mt Elgon, 3450 m	4503
Vicia (x = 6, 7)				
* *hirsuta* (L.) S. F. Gray	14	2 x	Mt Meru, 2450 m	4963
* *sativa* L.	12	2 x	Mt Meru, 2450 m	4964

Taxon	2n	Ploidy	Locality and altitude	Reference
Geraniaceae				
Geranium (x = 14)				
arabicum Forsk.	28	2 x	Kilimanjaro, 3120 m	B 66159: 1
			Galama Mts, 3750 m	4136
			Mt Kenya, 2500 m	4445
			Tanzania, Ngara distr.	Kokwaro 1969
* *ocellatum* Cambess. +	56	4 x	Cameroons Mt	3518 A
Oxalidaceae				
Oxalis (x = 6)				
corniculata L.	24	4 x	Kilimanjaro, 3120 m	B 66155: 1, 2
	c. 24	4 x	Mt Kenya, 2500 m	4441
Euphorbiaceae				
Euphorbia (x = 10)				
wellbyi N. E. Br. +	20	2 x	Mt Elgon, 3400 m	4550
Callitrichaceae				
Callitriche (x = 5, 9)				
stagnalis Scop.	10	2 x	Simien, 3650 m	5485
			Galama Mts, 3800 m	4234
	20	4 x	Bale Mts, 3950 m	5574
	18	2 x	Aberdare, 3000 m	4351
	18	2 x	Mt Kenya, 3020 m	4403
Malvaceae				
Malva (x = 7)				
verticillata L.	c. 76	polypl.	Simien, 3750 m	5476
Hypericaceae				
Hypericum (x = 8, 12)				
keniense Schweinf. +	24	2 x	Mt Elgon, 3200 m	4554
peplidifolium A. Rich. +	16	2 x	Galama Mts, 3750 m	4194
scioanum Chiov. +	16	2 x	Mt Elgon, 3500 m	4502
Violaceae				
Viola (x = 5, 6)				
eminii (Engl.) R. E. Fr. +	c. 72	12 x	Mt Elgon, 3200 m	4556
Onagraceae				
Epilobium (x = 18)				
stereophyllum Fres. +	c. 36	2 x	Galama Mts, 3750 m	4211

Taxon	2n	Ploidy	Locality and altitude	Reference
Umbelliferae				
Anthriscus (x = 8)				
sylvestris (L.) Hoffm.	16	2 x	Mt Kenya, 3350 m	1940, O. Hedberg 1957
Caucalis (x = 11)				
melanantha (Hochst.) Bth. & Hook. f. +	44	4 x	Et., S. Bale, 2000 m	E 386
Hapłosciadium (x = 11)				
abyssinicum Hochst. +	22	2 x	Mt Kenya, 4200 m	C s.n., Hedberg 1964 Fig. 75
			Kilimanjaro, 3800 m	B 105
Pimpinella (x = 9)				
kilimandscharica Engl. +	18	2 x	Mt Elgon, 3500 m	4500
Peucedanum (x = 11)				
kerstenii Engl.	22	2 x	Muhavura, 3800 m	2141, O. Hedberg 1957
			Ruwenzori, 3400 m	4895: 1, 2, 3, 4
			Mt Elgon, 3350 m	B 66301: 1, 3, 4
			Kilimanjaro, 3120 m	1206, B 156
	22	2 x	Kilimanjaro, 3850 m	B 66195: 2, 4
	44	4 x	Kilimanjaro, 3850 m	B 66195: 1
volkensii Engl. +	22	2 x	Kilimanjaro, 3800 m	1214
			Mt Meru, 3580 m	B 66138: 1–3
Heracleum (x = 11)				
elgonense (H. Wolff) Bullock +	22	2 x	Mt Elgon, 3500 m	4495
			Mt Kenya, 3800 m	73/06: 1, 2, 4, 5
Hydrocotyle (x = 9)				
monticola Hook. f. +	18	2 x	Mt Elgon, 3900 m	4531
* *mannii* Hook. f. +	18	2 x	Mt Kenya, 2500 m	4443
			Mt Meru, 2500 m	4942
Primulaceae				
Anagallis (x = 11)				
serpens Hochst. ex DC. subsp. *meyeri-johannis* (Engl.) P. Tayl.	22	2 x	Mt Elgon, 3600–3900 m	1040, 1042, O. Hedberg 1957
			Cherangani Hills, 3300 m	Thulin 1970
			Aberdare, 2900–3680 m	1547, 1651
			Mt Kenya, 2500 m	4446
			Kilimanjaro, 3000–3120 m	1329, 4378, B 66152: 1
	c. 64	6 x	Mt Kenya, 3100 m	1968
	c. 66	6 x	Aberdare, 2900 m	1513
	66	6 x	Aberdare, 3500 m	4333
			Mt Kenya, 3020–3350 m	4409, 4273
Ardisiandra (x = 17)				
* *wettsteinii* R. Wagner +	34	2 x	Et., Irgalem, 1800 m	E 619
			Mt Kenya, 3400 m	C & K 407

Taxon	2n	Ploidy	Locality and altitude	Reference
Gentianaceae				
Swertia (x = 10, 13)				
kilimandscharica Engl.	26	2 x	Mt Elgon, 3500 m	4501
			Cherangani Hills, 2850 m	Thulin 1970
			Aberdare, 3500 m	5040 A: 1, 2
			Kilimanjaro, c. 3000 m	4390, B 66248: 1–5
			Mt Meru, 2400–3600 m	4930: 2, 4, 5, B 66136 A: 2, 4
crassiuscula Gilg	20	2 x	Mt Elgon, 3800 m	4486
			Cherangani Hills, 3150 m	Thulin 1970
			Aberdare, 3600 m	1620, O. Hedberg 1957
			Mt Kenya, 3000–4200 m	1831, 4265, 4404, 4420
subnivalis Th. Fr. jr.	26	2 x	Mt Elgon, 3600 m	1018, O. Hedberg 1957
			Mt Kenya, 4130 m	1783
uniflora Mildbr. +	26	2 x	Mt Elgon, 3900 m	4533
volkensii Gilg	c. 26	2 x	Aberdare, 3900 m	1544, O. Hedberg 1957
	26	2 x	Mt Kenya, 4100 m	1787
macrosepala Gilg	26	2 x	Mt Muhavura, 4100 m	2076, O. Hedberg 1957
cfr. *macrosepala* Gilg (vel sp. nov.)	26	2 x	Bale Mts, 4050 m	5600
Boraginaceae				
Myosotis (x = 8, 9)				
abyssinica Boiss. & Reut.	48	6 x	Kilimanjaro, 3050 m	B 66238: 2, 4
			Cameroons Mt	Morton 1961
vestergrenii Stroh	18	2 x	Galama Mts, 3750 m	4141
			Mt Elgon, 3450 m	215, O. Hedberg 1957
			Aberdare, 3500–3600 m	1611, 5036 A: 1–5
keniensis Th. Fr. jr.	18	2 x	Bale Mts, 4000–4200 m	5631 b, 5575
			Mt Kenya, 4300 m	1729, O. Hedberg 1957
Lithospermum (x = 12)				
afromontanum H. Weim. +	24	2 x	Aberdare, c. 3500 m	4286: 1–3, 5048 A: 1–2
			Kilimanjaro, 3050 m	B 66250: 1
Cynoglossum (x = 12)				
* *geometricum* Baker & Wright +	24	2 x	Cameroons Mt, 2750 m	Morton K616, offspring (UPS)
Labiatae				
Salvia (x = 7, 8)				
merjamie Forsk. +	c. 42	6 x	Aberdare, 3300 m	4579: 2, 4
nilotica Juss. ex Jacq.	32	4 x	Mt Kenya, 3100 m	4317, Yakovleva 1933
			Burundi	Lewalle 1618
	30			Delestaing 1954
Satureja (x = 5, 11)				
biflora (Hamilt. ex D. Don) Briq.	30	6 x	Kilimanjaro, 3800 m	1223, O. Hedberg 1957
punctata (Bth.) Briq.	30	6 x	Cameroons Mt	Morton 1962
kilimandschari (Gürke) Hedb. +	22	2 x	Mt Kenya, 3950 m	C & K 270
			Kilimanjaro, 3100–3800 m	B 37: 2–5, 7–9, B 66165: 2, 3, 5

Taxon	2n	Ploidy	Locality and altitude	Reference
simensis (Bth.) Briq. +	22	2 x	Galama Mts, 3750 m	4218: 1–4
pseudosimensis Brenan	22	2 x	Cameroons Mt	Morton 1962
Stachys (x = 23)				
aculeolata Hook. f. +	46	2 x	Galama Mts, 3150 m	4301
			Mt Elgon, 3200 m	4561
			Aberdare, 3150 m	5069: 1, 3
	c. 42		Aberdare, 3500 m	5037 A: 1
Thymus (x = 7)				
schimperi Ronn. +	c. 30	4 x	Galama Mts, 3750 m	4168
Scrophulariaceae				
Celsia (x = 23)				
floccosa Benth. (incl. *C. scrophulariefolia* Hochst. ex A. Rich. and *C. brevipedicellata* Engl.)	46	2 x	Garamba 2900 m E. Trop. Africa	E 292: 3, 4 Håkansson 1926
Limosella (x = 10)				
africana Glück	40	4 x	Galama Mts, 3750 m	4134, 4192
			Ruwenzori, 4050 m	416, O. Hedberg 1957
			Mt Elgon, 3580 m	1021
			Mt Kenya	1765
macrantha R. E. Fr.	c. 60	6 x	Kilimanjaro, 4400 m	1343, O. Hedberg 1957
Sibthorpia (x = 9)				
europaea L.	18	2 x	Mt Elgon, 3350 m	O. Hedberg 1975 b
Veronica (x = 8, 9)				
abyssinica Fres.	48	6 x	Mt Kenya, 3400 m	C & K 400
			Kilimanjaro, 3050 m	B 66249: 1, 4, 5
			Cameroons Mt	Morton 1961
gunae Schweinf.	54	6 x	Mt Kenya, 4250 m	1813, O. Hedberg 1957
			Mt Elgon, 3600 m	941
	c. 54	6 x	Galama Mts, 3750 m	4131
glandulosa Hochst. ex Bth. +	c. 52	6 x	Mt Kenya, 3000 m	4405
			Kilimanjaro, 3100 m	B 66156
arvensis L.	16	2 x	Simien, 4225 m	5428
Zaluzianskya (x = 6)				
elgonensis Hedb.	12	2 x	Mt Elgon, 3800 m	4478: 1, O. Hedberg 1970 b
Bartsia (x = 7)				
macrocalyx	c. 28	4 x	Mt Elgon, 3450 m	259, O. Hedberg 1957

Taxon	2n	Ploidy	Locality and altitude	Reference
Selaginaceae				
Hebenstretia (x = 7)				
dentata	14	2 x	Mt Elgon, 3350 m	B 66316: 1–5
			Aberdare, 3000 m	B 66412: 1–5
			Kilimanjaro, 3100 m	B 66167: 1–5
			S. Africa	Sugiura 1939
Rubiaceae				
Anthospermum (x = 11)				
usambarense K. Schum. +	22	2 x	Mt Kenya, 3550 m	C & K 377
			Mt Meru, 3450 m	B 66118: 1–3
Galium (x = 11)				
ossirvaense K. Krause +	22	2 x	Mt Elgon	4476
glaciale K. Krause +	c. 36	4 x	Galama Mts, 3700 m	4236
	c. 44	4 x	Kilimanjaro, 3800	B 115:6
ruwenzoriense (Cort.) Chiov. +	c. 38	4 x	Mt Elgon, 3350 m	B 66334: 1, 2, 4
	38–42	4 x	Mt Meru, 3600 m	B 66142
	c. 36	4 x	Mt Meru, 3250 m	4899: 3–5
Valerianaceae				
Valeriana (x = 7, 8)				
volkensii Engl. +	28	4 x	Mt Elgon, 3300 m	4564
kilimandscharica Engl.	16	2 x	Mt Elgon, 3450–4050 m	210, 961, O. Hedberg 1967
			Mt Kenya, 4200 m	4427
			Kilimanjaro, 3500 m	4368
Dipsacaceae				
Dipsacus (x = 9)				
pinnatifidus Steud. ex A. Rich. +	18	2 x	Galama Mts, 3500 m	4187
			Kilimanjaro, 3050 m	B 66255: 1–6
Scabiosa (x = 8)				
columbaria L.	16	2 x	Mt Elgon, 3200 m	4468
Campanulaceae				
Campanula (x = 7)				
* *edulis*	56	8 x	Asella, 2700 m	Thulin 1976 a
			Ngorongoro, 2200 m	Thulin 1976 a
	c. 56		Mt Meru, 2450 m	4735: 1, 2
Wahlenbergia (x = 7)				
krebsii Cham. ssp. *arguta* (Hook. f.) Thulin	14	2 x	Asella, 2300 m	Thulin 1975
			Mt Kenya, 2800 m	Thulin 1975
			Kilimanjaro, 2850 m	Thulin 1975
			Mt Meru, 2500 m	4689

Taxon	2n	Ploidy	Locality and altitude	Reference
pusilla Hochst. ex A. Rich.	14	2 x	Mt Chilalo, 2900 m	Thulin 1975
			Aberdare, 3500 m	5028 A: 1, 2
			Kilimanjaro, 3500 m	Thulin 1975
			Mt Meru, 3450 m	Thulin 1975
Canarina (x = 17)				
* *abyssinica* Engl.	34	2 x	Mt Elgon, cult	O. Hedberg 1961
* *eminii* Aschers. ex Schweinf.	34	2 x	Mt Elgon, cult	O. Hedberg 1961
Lobelia (x = 6, 7, 13)				
* *aberdarica* R. E. Fr. & Th. Fr. jr.	28	4 x	Mau Range, 2700 m	1076
			Cherangani, 2850 m	Thulin 1970
* *bambuseti* R. E. Fr. & Th. Fr. jr. +	28	4 x	Mt Kenya	C 1960 s.n.
deckenii Schweinf. +	28	4 x	Kilimanjaro, 3100–3800 m	B 66229: 1, 4; 18: 1, 2, 6, 9
burtii E. A. Bruce	28	4 x	Mt Meru, 3200 m	2404, O. Hedberg 1967
keniensis R. E. Fr. & Th. Fr. jr. +	28	4 x	Mt Kenya	C & K 363
rhynchopetalum +	c. 28	4 x	Galama Mts, 3750 m	4191
telekii Schweinf.	c. 28	4 x	Mt Elgon, 4000 m	861, O. Hedberg 1967
			Kenya	Mabberley 1974
wollastonii E. G. Bak.	c. 28	4 x	Ruwenzori, 4150 m	400, O. Hedberg 1967
lanuriensis De Wild. +	c. 28	4 x	Ruwenzori	4891: 2, 5
minutula Engl. +	12	2 x	Aberdare, 3200 m	4350
lindblomii Mildbr. +	26	2 x	Mt Elgon, 3500 m	4499
	c. 26	2 x	Aberdare, 3550 m	4275
Monopsis (x = 7)				
stellarioides Urb. var. *schimperana* (Urb.) E. Wimm.	28	4 x	Mt Elgon, 3600 m	909 (offspring), O. Hedberg 1957
Compositae				
Dicrocephala (x = 9)				
alpina R. E. Fr. +	18	2 x	Galama Mts, 3750 m	4213, 4221
			Kilimanjaro, 3000–3125 m	4385 and offspring (3 plants)
				B 66191: 3, 4
Conyza (x = 9)				
subscaposa O. Hoffm. +	18	2 x	Mt Kenya	N s.n.
ruwenzoriensis (S. Moore) R. E. Fr. +	c. 54	6 x	Mt Elgon, 3500 m	4491
	c. 54	6 x	Aberdare, 3350 m	4580: 3
variegata Sch. Bip. ex A. Rich. +	18	2 x	Galama Mts, 3750 m	4197
Helichrysum (x = 7)				
odoratissimum (L.) Less.	c. 14	2 x	Mt Meru, 3450 m	B 66115: 1
	14	2 x	S. Africa	Nordenstam 1969
cymosum (L.) Less. ssp. *fruticosum* (Forsk.) Hedb. +	14	2 x	Mt Kenya	N s.n.
citrispinum Delile v. *hoehnelii* (Schweinf.) Hedb. +	14	2 x	Kilimanjaro, 3550 m	B 66210: 1–4

Taxon	2n	Ploidy	Locality and altitude	Reference
newii Oliv. & Hiern. +	14	2 x	Kilimanjaro, 3125–3800 m	B 66185: 2; 15: 1, 2
amblyphyllum Mattf. +	14	2 x	Mt Elgon, 3200 m	4454
chionoides Philipson +	14	2 x	Mt Kenya, 3600–4200 m	4435, 4802 (offspring, 2 plants)
meyeri-johannis Engl. +	14	2 x	Kilimanjaro, 3000 m	4386
formosissimum (Sch. Bip.) Sch. Bip. ex A. Rich. +	14	2 x	Mt Elgon, 3550 m	B 66261: 1
			Aberdare, 3500 m	5050 A: 3, 4
guilelmii Engl. +	14	2 x	Mt Meru, 3450 m	B 66112: 1, 3, 5
globosum Sch. Bip. ex A. Rich. (syn. *Gnaphalium schultzii* Mendonça)	14	2 x	Galama Mts, 3750 m	4152
			Cherangani Hills, 2650 m	Thulin 1970
* *foetidum* (L.) Moench	28	4 x	Cameroons Mt, 2600 & 2750 m	Morton K 566, 636
Stoebe (x = 8)				
kilimandscharica O. Hoffm. +	16	2 x	Mt Elgon, 3200 m	4551
Anthemis (x = 9)				
tigreensis J. Gay ex A. Rich.	18	2 x	Galama Mts, 3750 m	4229
			Mt Kenya	Turner & Lewis 1965
Cotula (x = 8, 9)				
cryptocephala Sch. Bip. ex A. Rich. +	c. 80	10 x	Simien, 3750 m	5477
			Mt Elgon, 3800 m	4515
abyssinica Sch. Bip. ex A. Rich. var. *abyssinica* +	c. 32	4 x	Mt Elgon, 3350 m	B 66305: 4
	c. 40	5 x	Aberdare, 3550 m	4296
	48	6 x	Mt Kenya, 2500 m	4440
var. *sessilis* Hedb. +	54	6 x	Galama Mts, 3750 m	4204
Artemisia (x = 9)				
afra Jacq. ex Willd.	18	2 x	Mt Elgon, 3200 m	4552
			Mt Elgon	Kawatani & Ohno 1964
Cineraria (x = 10)				
grandiflora Vatke	40	4 x	Mt Kenya, 3000 m	4397
			Mt Kenya	Turner & Lewis 1965
			Kilimanjaro, 3000–3125 m	4388; B 66181: 2–4
Senecio (x = 10)				
johnstonii Oliv. ssp. *elgonensis* (Th. Fr. jr.) Mabberley +	100	10 x	Mt Elgon, 3900 m	4534
* ssp. *cheranganiensis* (Cotton & Blakelock) Mabberley	c. 80	8 x	Cherangani, 2700 m	Thulin 1970
	20	2 x	Cherangani, 3300 m	Mabberley 1971
keniodendron R. E. Fr. & Th. Fr. jr. +	100	10 x	Mt Kenya, 4200 m	5017
mattirolii Chiov.	20	2 x	Ruwenzori, 4000 m	730 (offspring), O. Hedberg 1967
mattirolii Chiov. × *transmarinus* S. Moore	20	2 x	Ruwenzori, 4200 m	726 (offspring), O. Hedberg 1967

Taxon	2n	Ploidy	Locality and altitude	Reference
transmarinus v. *sycephyllus* (S. Moore) Hedb.	20	2 x	Ruwenzori, 3400 m	357 (offspring), O. Hedberg 1967
sotikensis S. Moore +	40	4 x	Mt Elgon, 3200 m	4453
purtschelleri Engl. +	40	4 x	Mt Kenya, 3950 m	C & K 277
			Kilimanjaro, 3550–3800 m	B 3: 1, 2, 4; B 7: 1, 2; B 13: 5; 66209: 2, 3; G 1959: 1
telekii (Schweinf.) O. Hoffm. +	20	2 x	Kilimanjaro	G 1959: 2
			Mt Meru, 3450 m	B 66101: 2
meyeri-johannis Engl. +	20	2 x	Kilimanjaro, 3600 m	4361
jacksonii ssp. *caryophyllus* (Mattf.) Hedb. +	20	2 x	Mt Elgon, 3400 m	4541
keniophytum R. E. Fr. +	20	2 x	Mt Kenya, 3850 m	4314, N s.n.
* *trichopterygius* Muschl. & Hiern. +	40	4 x	Aberdare, 3200 m	4352
schweinfurthii O. Hoffm.	c. 180	18 x	Mt Meru, 3450 m	B 66115: 1, Afzelius 1949
	c. 160	16 x	Mt Meru, 3450 m	66108: 3
	c. 140	14 x	Kilimanjaro, 3550 m	66220: 2
chillaloensis Cufod. +	40	4 x	Galama Mts, 3750 m	4214
cyaneus O. Hoffm. +	20	2 x	Kilimanjaro, 3125	B 66184: 1, 2, 3, 5
			Kilimanjaro	4570: 1, 2
unionis Sch. Bip. ex A. Rich. +	20	2 x	Galama Mts., 3750 m	4160
aff. *unionis* Sch. Bip. ex A. Rich.	40	4 x	Simien, 3650 m	5425: 1, 2, 3, 4
schultzii Hochst. ex A. Rich.	40	4 x	Simien, 3650 m	5488
nanus Sch. Bip. +	40	4 x	Bale Mts, 4100 m	5639
Euryops (x = 10)				
brownei S. Moore	c. 20	2 x	Aberdare, 3700 m	1550, O. Hedberg 1967
dacrydioides Oliv. +	20	2 x	Kilimanjaro, 3500 m	4369
prostratus B. Nord. +	20	2 x	Bale Mts, 4200 m	5615
Haplocarpha (x = 9, 15)				
rueppellii (Sch. Bip.) Beauverd	30	2 x	Galama Mts, 3750 m	4140
			Bale Mts, 4100 m	5621
			Cherangani Hills, 2850 m	Thulin 1970
	c. 30	2 x	Mt Kenya	N s.n.
schimperi (Sch. Bip.) Beauverd	+ 36	4 x	Galama Mts, 3750 m	4225
Guizotia (x = 15)				
reptans Hutch.	30	2 x	Aberdare, 3500 m	4329
	c. 60	4 x	Cherangani, 2850 m	Thulin 1970
Carduus (x = 8, 17)				
chamaecephalus (Vatke) Oliv. & Hiern. +	32	4 x	Mt Kenya, 4300 m	4425
			Mt Kenya, 4200 m	N s.n.
keniensis R. E. Fr. +	34	2 x	Mt Elgon, 3300 m	4575: 1, 3, 4, 5; B 66307: 1, 3, 4
**nyassanus* (S. Moore) R. E. Fr. +	34	2 x	Kilimanjaro	B 66192: 2–5
* *afromontanus* R. E. Fr. +	32	4 x	Mt Kenya	4835: 1–3

Taxon	2n	Ploidy	Locality and altitude	Reference
Dianthoseris (x = 4)				
schimperi Sch. Bip. ex A. Rich. +	8	2 x	Simien, 4225 m Mt Kenya, 3800–4200 m	5436 4817, N s.n.
Crepis (x = 4)				
oliverana (Kuntze) C. Jeffrey +	8	2 x	Mt Meru, 3450 m	B 66109: 1–3
cfr. *xylorhiza* Babc. +	8	2 x	Simien, 3600 m	5360
carbonaria Sch. Bip. +	8	2 x	Aberdare, 3500 m	5052A: 1, 2, 3, 5
suffruticosa Babc.	8	2 x	Mt Meru, 3800 m	Babcock 1947
Erigeron (x = 9)				
alpinus L. s. lat.	18	2 x	Galama Mts, 3750 m Bale Mts, 3950 m	4155 5554: 1, 2, 4, 5

Typification of Iris heylandiana Boiss. & Reut.

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Iris heylandiana Boiss. & Reut. is lectotypified and a new description of the taxon is given.

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Boissier (1882) described *Iris heylandiana* using as syntypes the specimens Olivier s.n., between Mosul and Baghdad (G) and Kotschy 307, between Diarbekir and Mardin (G). Dinsmore (1934) referred his specimen 21512 (BEI) to *I. heylandiana*. Mouterde (1966) considered Gombault 5769 (Herb. Leb. National Res. Counc.) to be this taxon. Recently, Chaudhary et al. (1976) cited a collection from NE Syria as *I. heylandiana* (?).

The author has had the opportunity of examining practically all the material cited by different authors as *I. heylandiana* from NE Syria and S Turkey. Boissier's syntypes are two entirely different taxa. Kotschy 307 is essentially the same as described by Foster (1890) as *I. gatesii*, a well-known taxon. Olivier's sheet does not match any other taxon known and is here selected as the type specimen of *I. heylandiana*.

Another enigmatic taxon is *I. maculata* Baker (1876). The sheet believed to be the original material (fide Brian Mathew, Kew) is in a poor state. Although the specimen (Aucher–Eloy–Berbier d'Orient 2136 (K); not 7136 as reported by Dykes 1912) looks very much like the type of *I. heylandiana*, it is difficult to say with certainty that the two are conspecific. With the exact locality unknown for this specimen and the condition of the material too poor for a definite determination it does not seem advisable to consider *I. heylandiana* to be synonymous with *I. maculata*.

Dinsmore 21512 cited by Dinsmore as *I. heylandiana* is neither this taxon nor *I. gatesii*. The material is apparently identical with that reported by Chaudhary et al. (1976) as *I. heylandiana* (?) from Darbassyeh, NE Syria. Nor is Gombault 5769 from near Ras-Al-Ain, cited by Mouterde (1966), *I. heylandiana*. The latter sheet has the name *I. gombaultii* written on it in Dinsmore's hand. Study of fresh material from the above two locations is essential to assign these specimens their taxonomic status.

A description of the lectotype of *I. heylandiana* is given here.

Iris heylandiana Boiss. & Reut.

Boiss. & Reut. 1882, in Boiss., Fl. Orient. 5: 130–131 (p. p.); non Dinsmore 1934, nec Mouterde 1966, nec Chaudhary et al. 1976. – Orig. coll.: Iraq, between Mosul and Baghdad, Olivier s.n. (G lectotype).

Plants about 40 cm tall. Rhizome not known. Leaves 7, 1.0–1.2 cm wide, up to 20 cm long, falcate to strongly arched, completely or partly enclosing the peduncle. Stem leaf one, the node visible between the basal leaves or not. Flowers up to 15 cm tall from base of the valves, c. 9 cm wide; peduncle 11–14 cm; valves tightly clasping or only slightly inflated; ovary c. 2.5 cm long with a stalk 5 mm long; perianth tube about 2.5 cm long. Falls c. 6.5 cm long, 3.5 cm wide; beard linear of rather long, mamillate–papillate (not echinate), clavate hairs. Standards erect, c. 7 cm long, 4 cm wide, laterally reflexed.

Anthers c. 2 cm long; filaments 1 cm long. Style branches c. 4.5 cm long, 2 cm wide or less, rather oblique (like in *I. auranitica* Dinsm.), wider than the combined width of the two lobes. Pollinator tunnel open ventrally. Pod not known.

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Amphicarpy and variability in Pisum fulvum

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Amphicarpy in *Pisum fulvum* Sibth. & Sm. is basically genetically determined but shows variation among populations. The potential for developing subterranean flowers may appear also in normally non-amphicarpic populations. However, inherent phenological differences among populations affect occurrence and extent of formation of subterranean fruits. The degree of amphicarpy may also be influenced by growth conditions. Amphicarpy is negatively correlated with aerial vegetative growth and fruit yield; it is of obvious adaptive value in some habitats. *P. fulvum* is predominantly autogamous. Some characters apparently lacking ecological significance are strikingly constant within populations and seem to be distributed at random among populations. These characters show no correlation with amphicarpy. Amphicarpy in *Pisum* seems to be a relatively young phenomenon. The amphicarpic form series is taxonomically regarded as a variety. Its morphology, phenology, distribution and ecology are described.

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Pisum fulvum Sibth. & Sm. is an East Mediterranean plant, occurring in Israel, Jordan, Lebanon, S and W Syria, Cyprus and S Turkey (Gruenberg-Fertig 1966). Like many other annual legumes in this region, it is a very polymorphic species, showing a wide range of variability in several morphological characters. Variability was found to occur between populations, and sometimes also within populations.

The amphicarpic form, described as var. *amphicarpum* Warb. & Eig (Warburg & Eig 1926), is of particular biological and ecological interest. From present records, this form is fairly frequent in Israel (Zohary 1972, Mattatia 1976), rare in Syria and Lebanon (Mouterde 1970), and not known from the other parts of the distribution area of the species. In the morphology and biology of the subterranean reproductive organs, amphicarpy of *P. fulvum* closely parallels the same phenomenon in two other legumes from this region, i.e., *Vicia sativa* ssp. *amphicarpa* (Plitmann 1973, Mattatia 1976) and *Lathyrus ciliolatus* (Mattatia 1977). However, it differs from the latter in two major respects: (1) Amphicarpic and non-amphicarpic forms cannot be distinguished by any definite diagnostic character, apart from amphicarpy itself. They differ only in some quantitative characters, which fall within the general range of variability of the species. (2) Amphicarpy was described to occur to a varying degree in different populations of *P. fulvum*. This feature was originally pointed out by Warburg & Eig (1926) as "different grades" of amphicarpy, and is also reflected from the data of Ben-Ze'ev & Zohary (1973), who described among the lines of *P. fulvum* "small amphicarpic type", "large, slightly amphicarpic type", "nonamphicarpic type" etc. This variability may lead to the impression that amphicarpy in this species is not constant and a facultative character. Thus Zohary (1937) maintained that amphicarpy in *P. fulvum* is not constant and depends on growth conditions, such as the depth of germination, and therefore concluded that the amphicarpic form cannot be considered as a taxonomic unit. Hylander (1946), on the other hand, cited Samuelsson's view, that there was no need for naming an amphicarpic variety, as *P. fulvum* seems to be always amphicarpic.

The aim of the present study was to examine the constancy of amphicarpy in *P. fulvum* and the variation of this character, as related to the pattern of variation of other morphological characters. The study is based on field observations throughout the distribution area of the species in Israel and on plants grown in an experimental plot in the Department of Botany, the Hebrew University, Jerusalem.

The amphicarpic form of Pisum fulvum

A general description of *P. fulvum* appears in several East Mediterranean floras (e.g. Davis 1970, Post 1932, Zohary 1972). The following is a complementary description of the amphicarpic form.

Amphicarpic plants of *P. fulvum* produce, in addition to the aerial shoots, subterranean stolons, bearing flowers and fruit. The stolons develop from the cotyledonary buds, from axillary buds at the nodes of the subterranean part of the main axis, between the cotyledons and ground level, and sometimes also from basal nodes of aerial shoots lying on the ground; they are achlorophyllous, sub-terete, simple or 1–2-branched, up to 20 cm long, bearing at their nodes small laciniate scales. Growth of the stolons is diageotropic to slightly plagiogeotropic; the growing apex is recurved, thus protected from mechanical damage while penetrating the soil. The subterranean flowers are cleistogamous, resembling floral buds, reduced in size, 6–9 mm long, but they always contain all the floral organs as the aerial flowers. The corolla is colourless, or sometimes the standard is slightly tinged with pink to orange, due to some penetration of light to the upper soil layer. The subterranean pods are usually smaller than the aerial ones, or sometimes approaching them in size, 10–20(–25) mm long, containing 1–3(–4) seeds, which are on the average slightly larger than the aerial ones. The valves are relatively thin and indehiscent, in accordance with their dispersal ecology, sometimes splitting along the sutures, but not twisting.

The somatic chromosome number in amphicarpic lines was found to be $2n = 14$ (aceto-orcein root-tip squashes), which confirms previous counts in *P. fulvum* in general (Fedorov 1969, Ben-Ze'ev & Zohary 1973).

Variation in amphicarpy

Field studies and examination of available herbarium material (HUJ), have shown a wide range of variation in the occurrence and in the degree of development of subterranean reproductive organs, from well-developed stolons, flowers and fruits, to their complete absence. For simplicity, the various forms were classified into four categories: (1) Amphicarpic plants, with well-developed stolons and mature subterranean fruits at the time of maturation of the aerial fruits. (2) Plants with scanty and late development of subterranean organs. At the time of maturation of the aerial fruits, few minute floral buds or flowers could be found in the ground, borne on very thin and short stolons, or sessile in the axils of the cotyledons or scales on the main axis. Since this late development does not result in the formation of mature fruits, from the functional point of view these cases cannot be regarded as truly amphicarpic. (3) Plants with some fruits borne on short, small-leaved basal branches near ground level, sometimes partly hidden among plant debris and stones. Generally these basal pods develop from cleistogamous flowers and are sometimes intermediate between aerial and subterranean pods. This condition, termed as "sub-amphicarpic", may be regarded as transitional between basicarpy and amphicarpy. (4) Plants that according to present evidence have no subterranean stolons, flowers and fruits.

The distinction between these categories is not always clear-cut, and there are sometimes transitions between them. Thus in non-amphicarpic populations single plants were found to be "subamphicarpic" or to have single lately-formed subterranean buds. In some cases it is difficult to decide whether a partly exposed basal pod developed originally in the ground or whether it was covered after anthesis. Variation was also observed in the amphicarpic type. The number of subterranean fruits may be small (1–2), or greater (up to 10). In general, judging by the extent of development of the stolons and the number of subterranean fruits, the expression of amphicarpy is weaker than in the amphicarpic *Vicia* and *Lathyrus* (Mattatia 1976).

Distribution and ecology

The general distribution of *P. fulvum* in Israel is mainly in the Mediterranean phytogeographical territory (Zohary 1972), with some extensions to the Irano-Turanian territory in sub-Mediterranean bathas at the margins of the Samarian and Judean Deserts (Fig. 1). *P. fulvum* occurs in rather diffuse populations in open formations like batha, at the edges of fallow and cultivated fields, and sometimes at margins or clearings of garigue and maquis. Whereas there appears to be no clear pattern in the distribution of the non-amphicarpic forms, it seems from the present evidence that the amphicarpic populations are concentrated in the higher mountainous parts of the distribution area of the species: in the Judean Mts, mainly at the higher altitudes, around Bethel, Jerusalem and Hebron, in Samaria, Mt Gilboa, the Upper Galilee and Mt Hermon. In those regions the amphicarpic plants often grow in grazing areas. They thrive particularly in rocky slopes, in gravelly soils and stony habitats, such as gravel heaps and stony edges of terraces. Under such conditions, density in amphicarpic populations is locally higher than in non-amphicarpic ones. This is due to the fact that a considerable number of plants originate from subterranean fruits, which are topochorous and synaptospermous dispersal units. Owing to the amphicarpic habit, the populations persist in the same microhabitat year after year.

The breeding system

Like *P. sativum* (Hayward 1938) and the wild species of peas (Ben-Ze'ev & Zohary 1973), *P. fulvum* is predominantly autogamous. This was repeatedly confirmed by bagging of floral buds, which yielded mature pods and highly germinable seeds. The flowers are sometimes reduced in size, and then may be cleistogamous. Even in chasmogamous flowers, the anthers usually dehisce prior to anthesis. However, as indicated by the general pattern of variation, allogamy may also take place occasionally.

According to Ben-Ze'ev & Zohary (1973), vigorous and fully fertile hybrids were obtained by crossing amphicarpic and non-amphicarpic lines, though no information is provided on the inheritance of amphicarpy in the hybrids obtained.

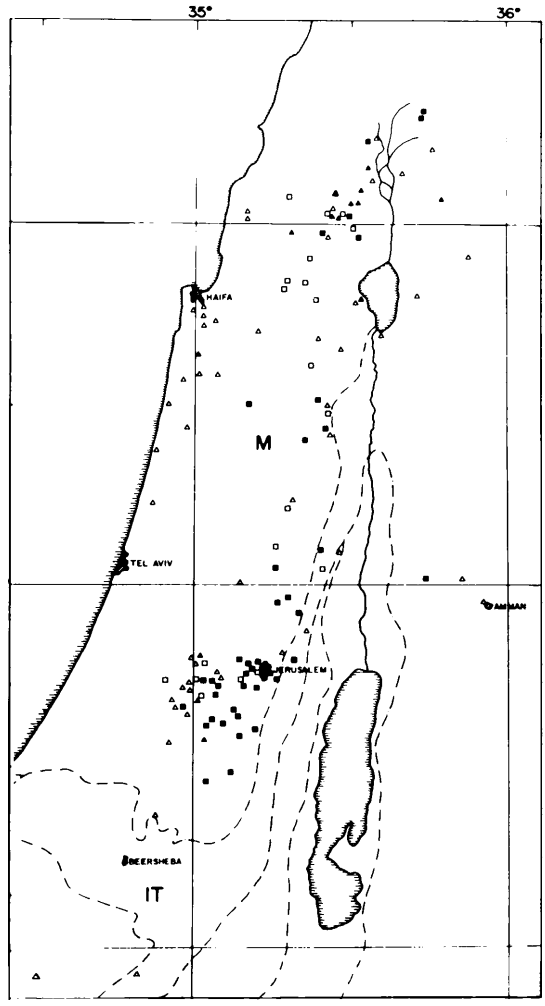


Fig. 1. Populations of *Pisum fulvum* in Israel examined with reference to amphicarpy. – Filled squares: amphicarpic. Unfilled squares: late subterranean flowering. Filled triangles: sub-amphicarpic. Unfilled triangles: Not amphicarpic by present evidence.

Constancy of amphicarpy

In order to study the constancy of amphicarpy and the relationships between it and other morphological characters, the following experiments have been carried out. Plants of ten different populations, five amphicarpic and the rest of the other types, were grown under equal conditions in Jerusalem. Scarified seeds, collected in the natural habitats, were sown at a depth of 4–5 cm in beds of terra-rossa mixed with polyuritan crumbs. In eight cases parallel experiments have been carried out on terra-rossa covered with a layer of limestone gravel. These conditions

Table 1. Differential characters of two populations of *Pisum fulvum*. 1: Jerusalem, Neve Sha'anan. 2: Mt. Carmel, Nahal Kelah.

Character	1	2
Habit	plants few-branched; branches 10–30(–50) cm	plants many-branched; branches 25–75(–100) cm
Margins of leaflets	incised; lobes round-elongate, 3–5 mm	serrate; teeth small, acute
Average length of flowers	1.2–1.3 mm	1.4–1.5 mm
Colour of seeds	orange-brown to light brown	dark brown, punctate
Amphicarpy	present	absent

imitate natural habitats of the amphicarpic form. The plants were grown outdoors under natural conditions. About half of the plants of each group were taken out at the time of ripening of the aerial fruits for examination of subterranean organs, and the rest were examined after withering.

Plants from one amphicarpic population and one non-amphicarpic population were grown for three successive generations. A comparison of some characters of the mother-populations, which proved to be constant during the course of the experiment, is given in Table 1. Some parameters concerned with amphicarpy are compared in Table 2.

The experimental plants generally conformed with the mother-populations in the occurrence and in the extent of development of subterranean reproductive organs. In some cases, plants from populations that have been regarded by field observations as non-amphicarpic or subamphicarpic, developed in the ground minute stolons with few floral buds or small flowers (Fig. 2 E), which, however, did not form mature fruits due to their late development.

Observation on the ontogeny and phenology of plants from amphicarpic lines has shown that the development of stolons starts approximately at the time of secondary branching of aerial shoots, about 3–5 weeks after the emergence of the seedling (Fig. 2 A). At this time, elongation of the main axis is slowed down or has ceased. The rate of vegetative growth is generally slower than in non-amphicarpic plants growing under the same conditions. Subterranean floral buds could be observed in January and February, approximately at the time of differentiation of aerial buds, or in some cases even earlier. At the onset of aerial flowering, usually during March–April, developing fertilized ovaries and young fruits were observed in the ground. Flowers which develop later in the season may wither before maturing fruits. These facts point out the significance of the phenology and time factor and their influence on differences in amphicarpy between populations.

In the two populations compared in Tables 1 and 2, flowering of the amphicarpic plants started 1–2 weeks earlier than in the non-amphicarpic ones. Their flowering season was markedly shorter, so that fruit maturation was earlier. This is in correlation with the differences in the extent of vegetative growth prior to anthesis, and is well reflected in the fruit yield.

Table 2. Comparison of parameters of two populations of *Pisum fulvum*, as in Table 1. 1 is amphicarpic and 2 is non-amphicarpic. Results for two years of cultivation under equal conditions are compared (mean values of 6 plants in 1973, 12 plants in 1974; standard errors of most means given).

Parameter	1973		1974	
	1	2	1	2
Longest branch (cm)	43.5 ± 2.5	74.5 ± 5.1	44.3 ± 3.3	105.2 ± 4.7
Number of aerial pods	17.0 ± 2.2	53.7 ± 7.1	20.0 ± 3.7	90.5 ± 9.4
Dry weight of aerial organs (g)	4.301	9.526		
Cumulative length of stolons (cm)	65.7 ± 5.3	5.3 ± 1.0	46.0 ± 4.1	10.2 ± 4.1
Dry weight of stolons and subterranean reproductive organs (g)	0.388 ± 0.07	0.036 ± 0.01	0.313 ± 0.07	0.017 ± 0.004
Number of subterranean pods	6.8 ± 1.1	0	4.0 ± 0.8	0
Total number of fruits	23.8	53.7	24.0	90.5

Some variable characters

Plant habit and yield. Although generally described as 15–30 cm (Zohary 1972) or 60 cm high (Mouterde 1970), plants may reach the height of 1 m. The extent of branching is also very variable. As in most annuals, variability in these characters is largely phenotypic. However, despite the wide range of variation, it has been repeatedly observed, both in the field and in the experiments, that the extent of vegetative growth is negatively correlated with amphicarpy. The same applies to the average number of flowers and fruit yield (Table 2).

Leaves. Apart from variation in size and in length of petiole and tendrils, which is mostly phenotypic, there is marked variation in the shape and indentation of leaves, which cannot be related to growth conditions or to geographical distribution. Margins of leaflets may be serrate or crenate to incised, with teeth of varying shape and size, from minute to 3–5 mm long. Generally there is uniformity in this character within a population, or sometimes two leaf types may occur together in one population, e.g., in an amphicarpic population from Jerusalem plants having either serrate or incised leaflets (var. *incisum* of Post 1932) occurred in approximately equal ratios. This was constant in two successive generations of cultivation. The plants of both leaf types were equally amphicarpic (Fig. 2 B–D).

Size of aerial flowers. Size varies in the range 10–17 mm. Flowers tend to be smaller at the beginning and end of the flowering season and under limiting conditions, and in extreme cases they may be cleistogamous. Differences between populations were constant but for such phenotypic variation. At least in some cases, small average flower size was found to be correlated with amphicarpy (Table 1).

Colour of flowers. Colour varies from brownish to yellowish orange. Within a certain range of phenotypic variability, colour is constant and usually similar in a given population. Sometimes more than one colour type may occur, e.g., in the population mentioned above, a light yellowish orange corolla was coupled with incised leaflets, and a darker orange corolla with serrate leaflets. In other cases colour was not correlated with any particular character.

Pigmentation of seeds. In the literature the seeds are invariably described as velvety-black (Post 1932, Zohary 1972). However, in some of the populations examined, seeds were orange-brown or light brown, seldom dark brown and punctate (Table 1). In two amphicarpic populations, both aerial and subterranean pods had light brown seeds. This fact and the constancy studies indicate that seed colour does not depend on growth conditions. In other cases amphicarpic plants had the typical black seeds.

It may be summarized that, of the characters studied, plant height, the extent of vegetative growth and fruit yield are correlated with amphicarpy, whereas leaf shape and pigmentation of flowers and seeds are randomly distributed among populations and are not correlated with any of the other characters studied.

Discussion

Experiments and observations have shown that amphicarpy in *Pisum fulvum* is genetically constant, although not uniform in degree in different lines. However, there are certain requirements for its full expression, and like other genotypical characters it can be modified by growth conditions. Much of the variation in amphicarpy encountered in natural habitats can be attributed to edaphic conditions, which affect the immediate environment of the subterranean reproductive organs. The soil is a rather unusual medium for development of buds and flowers and for processes like anthesis and fruit maturation. Therefore, even small changes in the edaphic conditions can be expected to affect the expressivity of amphicarpy.

The potential of forming subterranean floral buds and cleistogamous flowers under suitable conditions is of a rather wide occurrence in this predominantly autogamous species, which shows a tendency to cleistogamy also in aerial flowers. This potential is related to the hypogeal germination and to the fact that the cotyledonary and other axillary buds of the main axis are subterranean. Sporadic development of one of these buds, as described above, was also observed in some non-amphicarpic species of *Vicia* and *Lathyrus* (Mattatia 1976). It can be expected to occur at random in any of the species of the Vicieae with the above-mentioned



Fig. 2. Plants of *Pisum fulvum* grown under equal conditions in Jerusalem in constancy experiments. – A: 30-day-old seedlings, at the beginning of development of the subterranean stolons. – B: Comparison of leaf indentation in two biotypes of an amphicarpic population (Jerusalem, Giv'at-Ram). – C–D: Subterranean organs (right) and fruiting aerial branches (left) of the two biotypes as in Fig. B (aerial and subterranean pods

characters. However, there are two main requirements in order that such a development will result in amphicarpy: (1) that hypogeal branches will continue to develop but will remain subterranean; and (2) that the development of the subterranean organs will keep pace with that of the corresponding aerial organs and not lag behind it.

Amphicarpy probably involves more fundamental differences than the mere potential to develop subterranean buds. It is well known that in hypogeal seedlings (e.g. of *Pisum sativum,* Hayward 1938), development of the normally dormant cotyledonary buds into branches may be induced by decapitation. Such branches, however, grow vertically or obliquely to emerge from the ground as ordinary leafy shoots. In amphicarpic plants development of subterranean buds, including the cotyledonary buds, proceeds normally, without interference with the hormonal system by decapitation. This fact and the reduced growth of the main axis and more decumbent habit of amphicarpic plants suggest that in them apical dominance is less pronounced and that amphicarpy probably involves differences in the hormonal system. The latter point is suggested also by the diageotropic growth of the stolons.

The phenological aspects are also very important. The observations indicate that differences in the degree of amphicarpy depend largely on the time of differentiation of the subterranean reproductive organs and the onset of flowering and fruit-set, in relation to the life span of the plant. The formation of a subterranean branch or a floral bud late in the season should not be considered as amphicarpy, as it does not result in the maturation of fruits.

The pattern of variation of morphological characters in *P. fulvum* is characteristic of populations of predominantly inbreeding species with occasional outcrossing, as repeatedly described in annual legumes (Stebbins 1957, Heyn 1971). Successive autogamous generations bring about the establishment of characters in local biotypes, while occasional allogamy may lead to a burst of new variability. This breeding system makes possible the sympatric differentiation of new forms (Ehrendorfer 1968), while the strong tendency to autogamy and cleistogamy serves as effective means for reproductive isolation. Characters such as the indentation of leaves or the pigmentation of seeds, cannot be correlated with any ecological factor or with any other morphological character and seem to have no evident adaptive importance. This may explain their random distribution among populations. Amphicarpy, on the other hand, definitely has ecological significance, as it implies a diversification in the modes of reproduction and dispersal ecology. This involves a change of strategy in the allocation of resources. The formation of a whole system of non-photosynthetic subterranean stolons, specialized for reproduction only, comes at the expense of the photosynthetic system. It results in a reduced rate of vegetative growth and consequently in reduction of the total biomass and fruit yield of the amphicarpic plant as compared with the non-amphicarpic one (Table 2). Such changes certainly affect the competitive ability of the plants. Under suitable conditions, the successful formation of subterranean fruits is advantageous, as it assures the perpetuation of the amphicarpic population in a particular microhabitat from year to year. This is particularly so under conditions that may present some dangers to the aerial flowers and fruits (Warburg & Eig 1926). In such cases amphicarpy can be regarded as a very safe investment in a microhabitat which has proved to be suitable for the completion of life cycle of this particular biotype in the preceding season (cf. Zohary 1937, Koller & Roth 1964). Therefore the establishment of this character can be expected to be favoured by selection, despite the reduction in plant material and fruit yield associated with it. On the other hand, the formation of subterranean organs under conditions that will not permit their complete course of development to mature fruits will not contribute to survival and therefore represents a waste of resources. In such cases it can be expected that amphicarpy will tend to be gradually eliminated by selection. This can explain the distribution of amphicarpic populations in the mountainous region in gravelly soils and stony habitats. These types of habi-

before full maturation). – E: Comparison of plants of two populations, amphicarpic (left) and non-amphicarpic (right), as in Tables 1 and 2 (photographed in May, towards the end of the growing season).

tats can be regarded as the ecological niches of the amphicarpic plants, since the conditions prevailing in them, namely good drainage and ample aeration in the soil, enable amphicarpy and its ecological advantages to be fully expressed.

The facts that amphicarpy in *P. fulvum* is less pronounced and more variable than in the amphicarpic *Vicia* and *Lathyrus* (Mattatia 1976) may suggest that amphicarpy is a relatively young phenomenon in this species and still in the process of evolution and establishment by occasional hybridization and selection. The absence of a reproductive barrier between amphicarpic and non-amphicarpic lines (Ben-Ze'ev & Zohary 1973) strengthens this view.

The present study supports the taxonomic treatment of the amphicarpic form of *P. fulvum* as a variety (Warburg & Eig 1926). The same view is held by Ben-Ze'ev & Zohary (1973) on cytological evidence. However, the criterion for the amphicarpic variety should be the constant formation of mature fruits in the ground. Plants with late subterranean flowering should be excluded, although it is admitted that such a criterion, which incorporates phenological data, may involve practical difficulties.

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Polytretus reinboldii, a rare brown alga in culture (Ectocarpales, Sorocarpaceae fam. nov.)

Poul Møller Pedersen

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Polytretus reinboldii (Reinke) Sauvageau has shown a direct type of life history through several generations under various sets of culture conditions. The best development of erect filaments is obtained at low temperature (4–5°C), while higher temperature (15°C) strongly inhibits the formation of erect filaments and also affects their morphology. There is not an opening at each loculus along the surface of the plurilocular sporangium as previously assumed, but Reinke's sporangium must be considered a sorus of sporangia. The taxonomic position is rather close to the genera *Hummia* and *Sorocarpus*. A new family, Sorocarpaceae, is proposed to contain these three taxa, all of which have true hairs and sympodial branching.

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Reinke (1892) described this species as *Ectocarpus reinboldii*, based on material from Heligoland. Sauvageau (1900) changed the generic name to *Polytretus* with a reference to Reinke's illustrations, which show each loculus along the surface of the sporangium with an opening and also show true phaeophycean hairs. He considered the genus to form a connecting link between the Ectocarpaceae on one side, and the Sphacelariaceae, Cutleriaceae, and Tilopteridaceae on the other.

P. reinboldii seems to be a fairly rare alga with a limited distribution. Outside the type locality it has only been reported by Parke & Dixon (1968), Rosenvinge & Lund (1941), and Wærn (1958) from Great Britain, Denmark, and Sweden, respectively.

Material and methods

Polytretus reinboldii with plurilocular sporangia was collected by Tyge Christensen, growing on hand-sized stones at a depth of approximately 3 m at the island of Hirsholmen, NE of Frederikshavn, Denmark, on 8 March 1973. Unialgal cultures were established by pipetting germlings from crude cultures. The culture medium was a modification of Provasoli's ES (cf. Nielsen 1972), with an addition to the initial cultures of germanium dioxide to prevent growth of diatoms. The light source was Philips fluorescent tubes, warm white 29. The following sets of culture conditions have been used: (1) 4°C, 1100 lx, 16h light/8h dark (LD); (2) 4°C, 420 lx, LD; (3) 15°C, 2400 lx, LD; (4) 15°C, 690 lx, LD; (5) 5°C ± 2.5°C, 2500 lx, 8h light/16h dark (SD).

Results

Swarmers from the plurilocular sporangia are of normal phaeophycean type with a long anterior and a short posterior laterally inserted flagellum. Copulation has not been observed; after a period of swimming the swarmers round off and germinate unipolarly (Fig. 2A). The eyespot is visible in the initial stages of germination either in the rounded cell or in the germ-tube (Fig. 2A, arrows). By further vegetative growth a prostrate, uniseriate, branched system arises (Fig. 2B), which remains sterile under all conditions tested. Older prostrate systems are composed of roundish cells (Fig. 2C). At conditions 3 and 4 the plants mostly remain at this stage, eventually forming a hemispherical cushion. Only few erect filaments have been observed in this

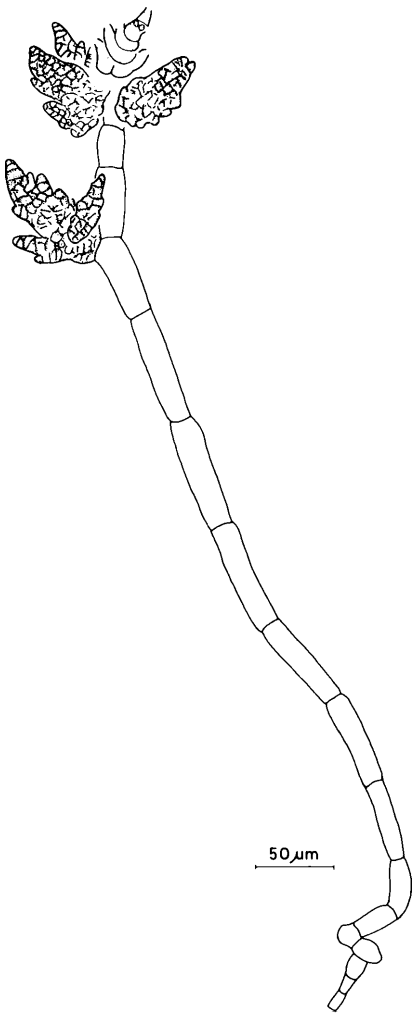


Fig. 1. Short, unbranched erect filament of *P. reinboldii* with apical, sessile sori; few such filaments develop at sets 3 and 4 conditions.

case, in a reduced form, few-celled, without vegetative laterals, developing normal sporangia at their tips (Fig. 1).

At sets 1, 2, and 5 vigorous growth of erect filaments occurs. These filaments are initially unbranched terminated by a phaeophycean hair. By sympodial branching the hair is pushed into a seemingly lateral position (Fig. 2D–F). The laterals formed may continue the vegetative growth (Fig. 2E) or may immediately form sporangia (Fig. 2F). At sets 1 and 2 the plants appear as small delicate bushes, while they have relatively fewer laterals at set 5. Their growth is diffuse intercalary.

The reproductive body of this species is called a plurilocular sporangium by Reinke (1892), his Pl. 41 Fig. 12 showing each loculus along the surface of the sporangium with an opening. A closer study has shown, however, that these are rather complex structures, better interpreted as sori. The initials may be few-celled laterals (often 3–6 cells), which are transformed in their entirety into sessile sori by numerous subdivisions (Fig. 4A), or they may be longer with transformation of the apical cells and subsequent development of laterals from some of the stalk-cells (Fig. 4B, C) giving a cluster of sori. Some of the initial divisions in the young sorus are longitudinal (Fig. 4E, arrows), and it must be assumed that several such divisions may occur in each link. At a later stage of development each link of the sorus is subdivided into well-separated clusters of cells (Fig. 4D), and at maturity each cell cluster is often prolonged into a tooth-like structure (Fig. 4G) representing the top of one sporangium with an apical opening through which the swarmers are released (Fig. 4H). Consequently, Reinke's plurilocular sporangium must be interpreted as a chain with each link being a whorl of sporangia. It is obvious that the longitudinal divisions in the sorus initial are often most frequent in the lower cells, which gives the sorus a conical outline as seen in Fig. 4G. Intercalary sori have been observed under set 5 conditions. As seen in Fig. 4F the apical and some lateral cells of the young sorus fail to form sporangia, and are instead prolonged into short, branched vegetative filaments. Further, the sori developed at SD are often longer and more slender with only initial development of whorled sporangia (Fig. 5). Unilocular sporangia-like and ascocyst-like cells as illustrated by Rosenvinge & Lund (1941) have never been observed in culture.

Discussion

The culture conditions tried in this study show that higher temperature (15°C) exerts a strong inhibitory effect on formation of erect filaments. This is in perfect agreement with the occurrence of *Polytretus* in nature, where it has been

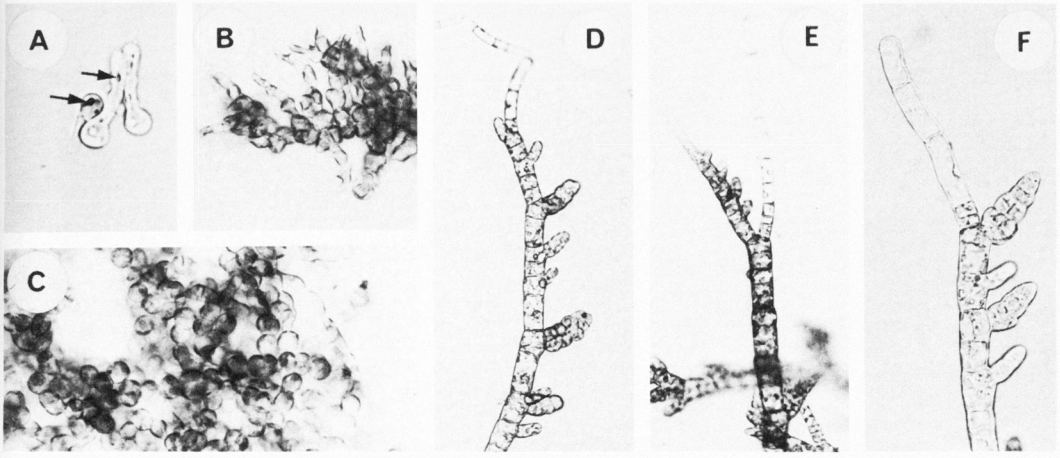


Fig. 2. Germination and sympodial branching of *P. reinboldii* in culture. – A: Germinating swarmers with still visible eye-spots (arrows). × 600. – B: Part of young, prostrate system. × 150. – C: Part of older prostrate system of roundish cells. × 150. – D: Initial stage of sympodial branching; the hair is in a subapical position. × 150. – E: Later stage of sympodial branching, the terminal hair is now in a seemingly lateral position. × 150. – F: Sympodial branching followed by immediate transformation of the lateral to a sorus. × 250.

found from March to June (I have no dates for the finds in Great Britain).

Rosenvinge & Lund (1941) mention that several of the sporangia found in Danish material from nature are actually chains of sporangia thus rather similar to those obtained under set 5 conditions, but they maintain that each loculus along the surface has an opening. I have found in all cases that several loculi have an opening in common, thus forming a sporangium together. The sori formed in culture may be very complex. Material from nature obviously often shows fewer loculi and no tooth-like prolongations deeming from illustrations in literature.

Basing on the sporangia Sauvageau (1900) suggested a connection from the Ectocarpaceae to the Sphacelariaceae, Cutleriaceae, and Tilopteridaceae through *P. reinboldii*. This connection seems not quite evident, as these taxa are widely separated from *Polytretus* by apical and trichothallic growth, respectively, and by the fact that the individual sporangium

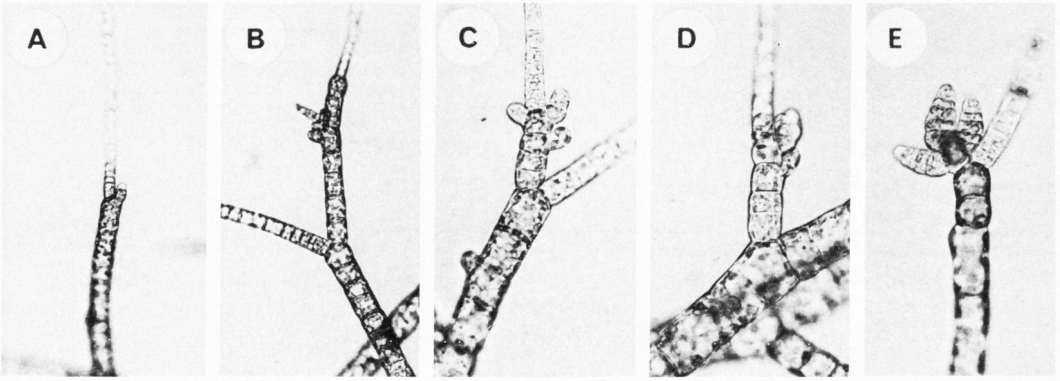


Fig. 3. Sympodial branching and sporangia development of *Sorocarpus micromorus* in culture. – A, B: Initial and later stages of sympodial branching (cf. Fig. 2D–F). × 150. – C–E: Development of sporangia from short laterals, often several from the same supporting cell (cf. Fig. 4 B). × 250.

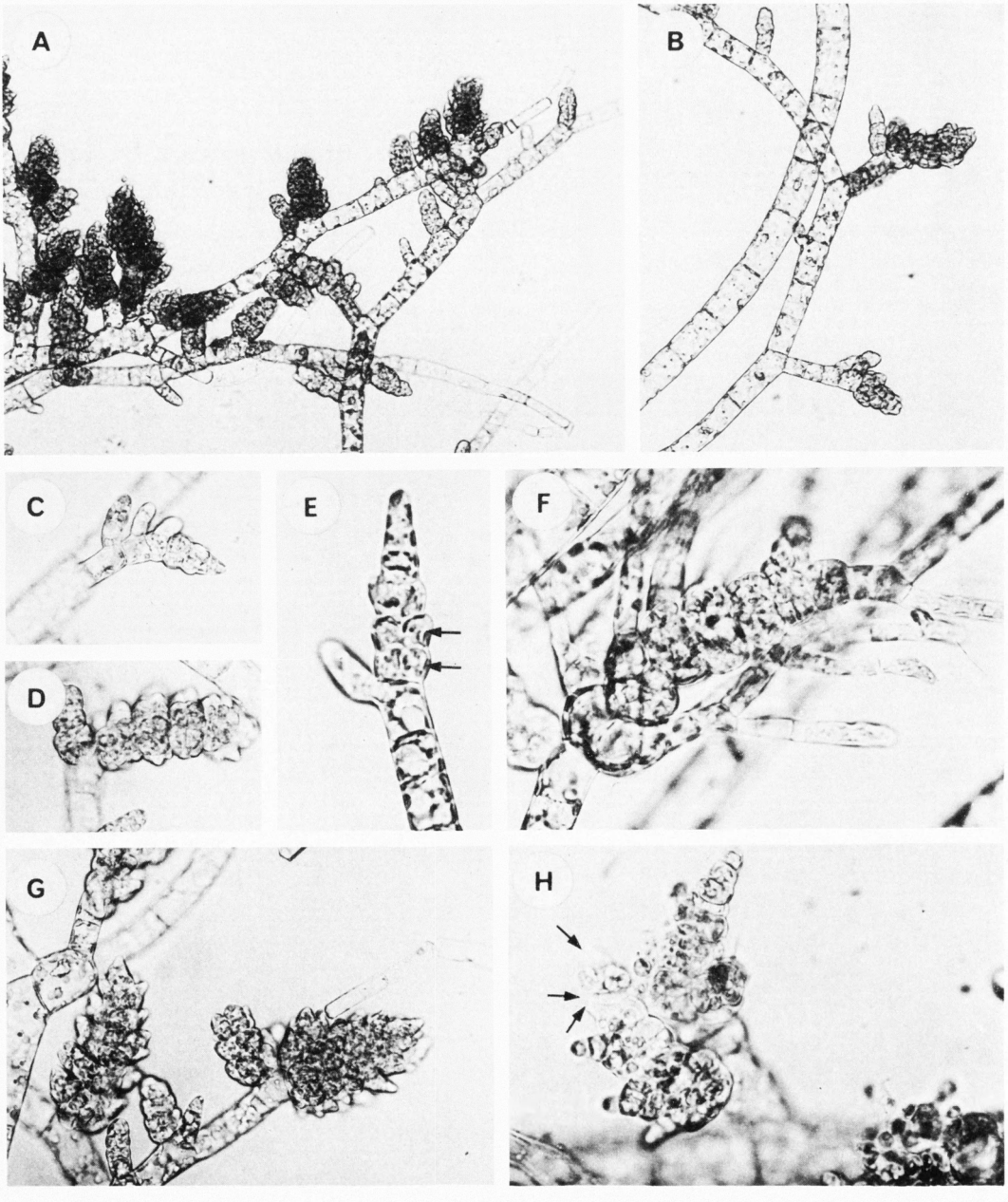


Fig. 4. Sporangia formation of *Polytretus reinboldii* in culture. – A: Mostly sessile sori on erect filaments. × 150. – B: Stalked sori and further development of sori from laterals of higher order. × 150. – C: Detail of stalked sorus with development of sporangia initials from the stalk-cells. × 250. – D: Each link subdivided into well-separated clusters of cells. × 250. – E: Longitudinal divisions (arrows) in the basal cells of an initial sorus. × 600. – F: Intercalary sorus formed under set 5 conditions. × 500. – G: Mature sori of conical outline with the individual sporangia prolonged into tooth-like structures. × 250. – H: Partly empty sori. Three openings of sporangia are indicated by arrows. × 500.

of *Polytretus* agrees with those of other members of Ectocarpales in principle.

In modern systematic treatments such as that by Christensen (1966) *Polytretus* is still included in the Ectocarpaceae together with genera without true hairs. There seems, however, to be particularly close relations with the genera *Sorocarpus* and *Hummia*.

The generic name *Hummia* needs a few comments. It was proposed by Fiore (1975) to replace *Farlowiella* Kornmann (Kuckuck 1956), which is said to be a homonym of *Farlowiella* Saccardo (1883). However, the name published by Saccardo (1883) is *Farlowia*, which was later changed to *Farlowiella* Saccardo (1891 p. 1100). In the same paper Fiore says that *Hummia onusta* (Kütz.) Fiore is the gametophytic generation of *Stictyosiphon subsimplex* Holden, which makes *Hummia* superfluous. Either this is bad nomenclature or Fiore should have mentioned the possible connection with *Stictyosiphon* with more reservation.

Polytretus, Sorocarpus and *Hummia* all have true phaeophycean hairs and all show sympodial branching. Further, the development of their sporangia is in principle the same. I have previously reported on the life history of *Sorocarpus micromorus* (Bory) Silva in culture (Pedersen 1974), though without giving detailed illustrations of sympodial branching and sporangia development. Fig. 3 shows sympodial branching (Fig. 3A, B) and young sporangia (Fig. 3C–E) of *S. micromorus*. There is a striking similarity to *P. reinboldii* (Fig. 2 D–F).

The sporangia formation of *Hummia* is also restricted to certain parts of laterals. As to possible unilocular sporangia there are only doubtful reports by Rosenvinge & Lund (1941) and Takamatsu (1936) for *Polytretus* and *Sorocarpus*, respectively. *Hummia, Polytretus,* and *Sorocarpus* are of course closely related to other hair-bearing genera that do not exhibit sympodial branching, such as *Protectocarpus* and apparently also *Kuckuckia*. However, in my opinion the sympodial branching is a specialized character. Also the sporangia formation, restricted to laterals, is more specialized compared e.g. with *Protectocarpus*, in which most of the cells of the erect filaments are potential sporangia. Consequently, I find it necessary to separate the genera *Polytretus, Sorocarpus,* and *Hummia* from the Ectocarpaceae and refer them to a separate new family, Sorocarpaceae, defined by the presence of true hairs and sympodial branching.

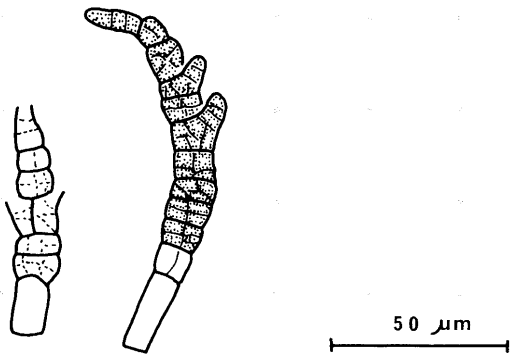


Fig. 5. One empty and one mature sorus composed of sporangia in chains with incipient development of sporangia in whorls (cf. empty sorus). Set 5 conditions.

Sorocarpaceae fam. nov.

Fila erecta a filis repentibus orta primum simplicia, quidque pilo vero terminatum, inde sub pilis ramigera sympodia ita formantia. Sori sporangiorum pluriloculariorum e ramulis orti, aut omnibus ramulorum cellulis subdivisis aut nonnullis in statu vegetativo manentibus, quoque sporangio ostio unico terminali aperto. Sporangia unilocularia vix formata. Genus typificum: *Sorocarpus* N. Pringsheim, 1863, p. 12, pl. 3A, Fig. 1–8.

Erect filaments initially unbranched with a terminal true hair, showing sympodial branching. Sori of plurilocular sporangia are formed by complete transformation of laterals or certain parts of laterals, each sporangium with a terminal opening. Unilocular sporangia hardly formed.

Acknowledgements. I am grateful to Tyge Christensen for the material of *P. reinboldii*, critical reading of the manuscript, and the Latin diagnosis.

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Two conspicuous desmids from Amazonas

Kuno Thomasson

Thomasson, K. 1977 04 15: Two conspicuous desmids from Amazonas. *Bot. Notiser 130:* 41–51. Stockholm. ISSN 0006-8195.

Two new species of desmids from the Amazonas area, namely *Micrasterias foersteri* and *Cosmarium kostei,* are described, and their phycocoenosis is analyzed.

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Some time ago the rotatorian specialist Walter Koste sent me photomicrographs of two curious desmids, both of which were unknown to me. There is quite a number of papers on Brasilian desmids but in some way these two have hitherto escaped observation. Both were frequent in a sample, which Dr Koste kindly placed at my disposal. The sample is labelled as follows:

GOB-13-75. Region Nhamundá, Probe Nr. 3, Terra Santa. Überschwemmte Wiese, sehr flach, 0,5–1,5 m, sehr viel Wasserpflanzen. 4. 7. 75. pH 5,4, μS 12, Sichttiefe 1,40 m. Netzprobe, die Maschenweite 100 μm. Leg. Gerd O. Brandorff, Max-Planck-Institut für Limnologie, Abt. Tropenökologie, Plön. Das Material wurde mit Hilfe des Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus gesammelt.

Cosmarium kostei Thom. sp. nov. – Fig. 1 C–E, 4

Cosmarium maximum; medium profunde constrictum incisura acutangula mox valde ampliata, apex complanatus, laevis, anguli apicales protracti, 1–3-cuspidati. Membrana crassa, porosa. Cellula 180–210 μm long., 140–163 μm lat. Iconotypus fig. nostra 1 E. Habit.: Brasilia, Amazonas.

The plant is biradiate; the semicells are in front view cup-shaped with mamillate corners. The apex is straight or slightly convex, the sinus is acute, and the thick cell wall is porous. It looks like a huge *Staurodesmus subpygmaeus* v. *spiniferus* (Scott & Grönbl.) Teil. Actually my first impression was that it might belong to the genus *Staurodesmus* because in the first studied specimens the corners terminated in a small spine. However, it soon turned out that there were mostly two spines, rarely three. The mamillate corners with spines might be interpreted as short processes, and if so, it would be natural to refer this plant to the genus *Staurastrum.* Furthermore, its relationship to *Cosmarium* might be considered; in e. g. *C. securiforme* v. *brasiliense* Grönbl. the radii of semicells are also drawn out into a kind of process. Of course, the shape is entirely different. The systematic position of this conspicuous plant thus remains somewhat uncertain. Most likely it is a *Cosmarium.*

Micrasterias foersteri Thom. sp. nov. – Fig. 1 A–B, 2, 3 A–E

Species magna, paululo latior quam longior; sinus apertus profundus; semicellulae 5-lobatae, omnis lobus lateralis incisione aperta invicem divisus. Semicellulae in medio processibus mammillatis ornatae. Cellula 200 μm long., 210–230 μm lat. Iconotypus fig. nostra 1 B. Habit.: Brasilia, Amazonas.

Contrary to the previous plant this one has a very complicated shape. On the whole it looks like an ordinary *Micrasterias.* The lateral lobes of order III are divided into a pair of lobes of order IV, one of which points, as a rule, outwards from the cell surface. There are two long mamillate processes on both sides of the isthmus; these are also directed outwards from

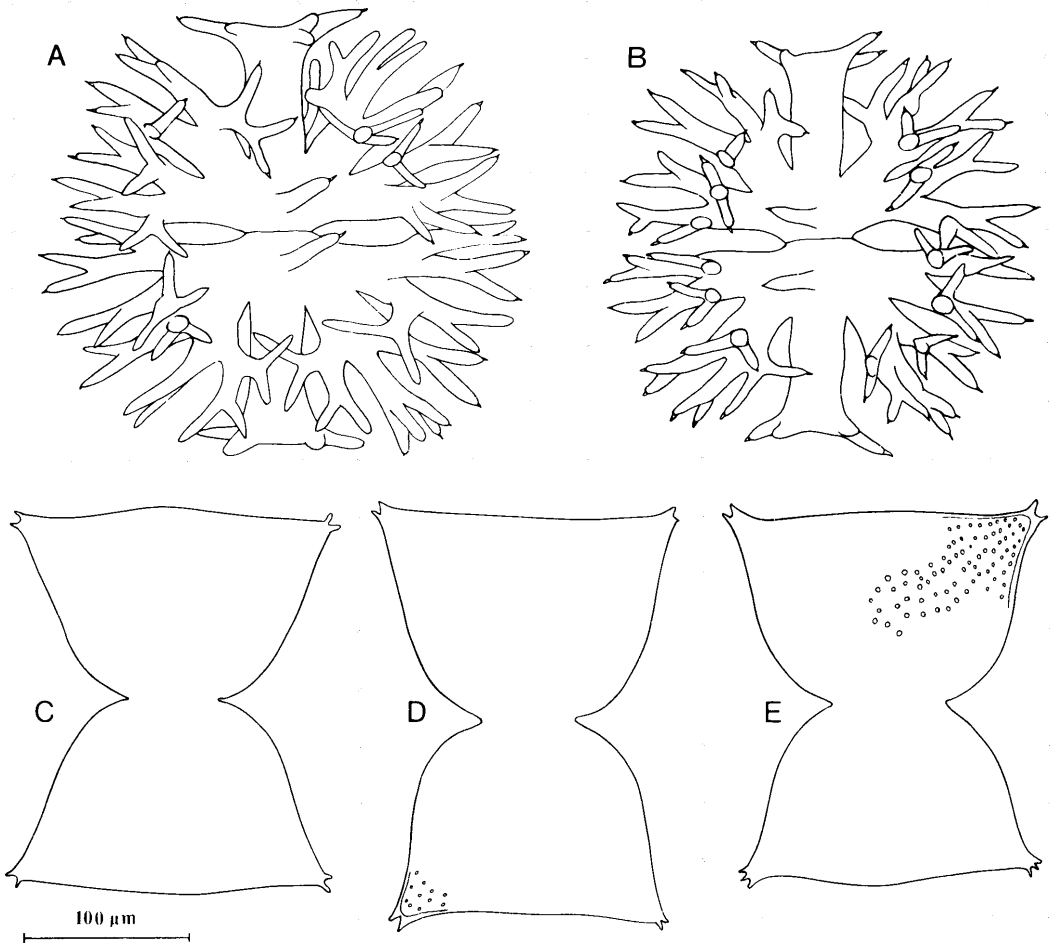


Fig. 1. A–B: *Micrasterias foersteri*. – B: Iconotype. – C–E: *Cosmarium kostei*. – E: Iconotype.

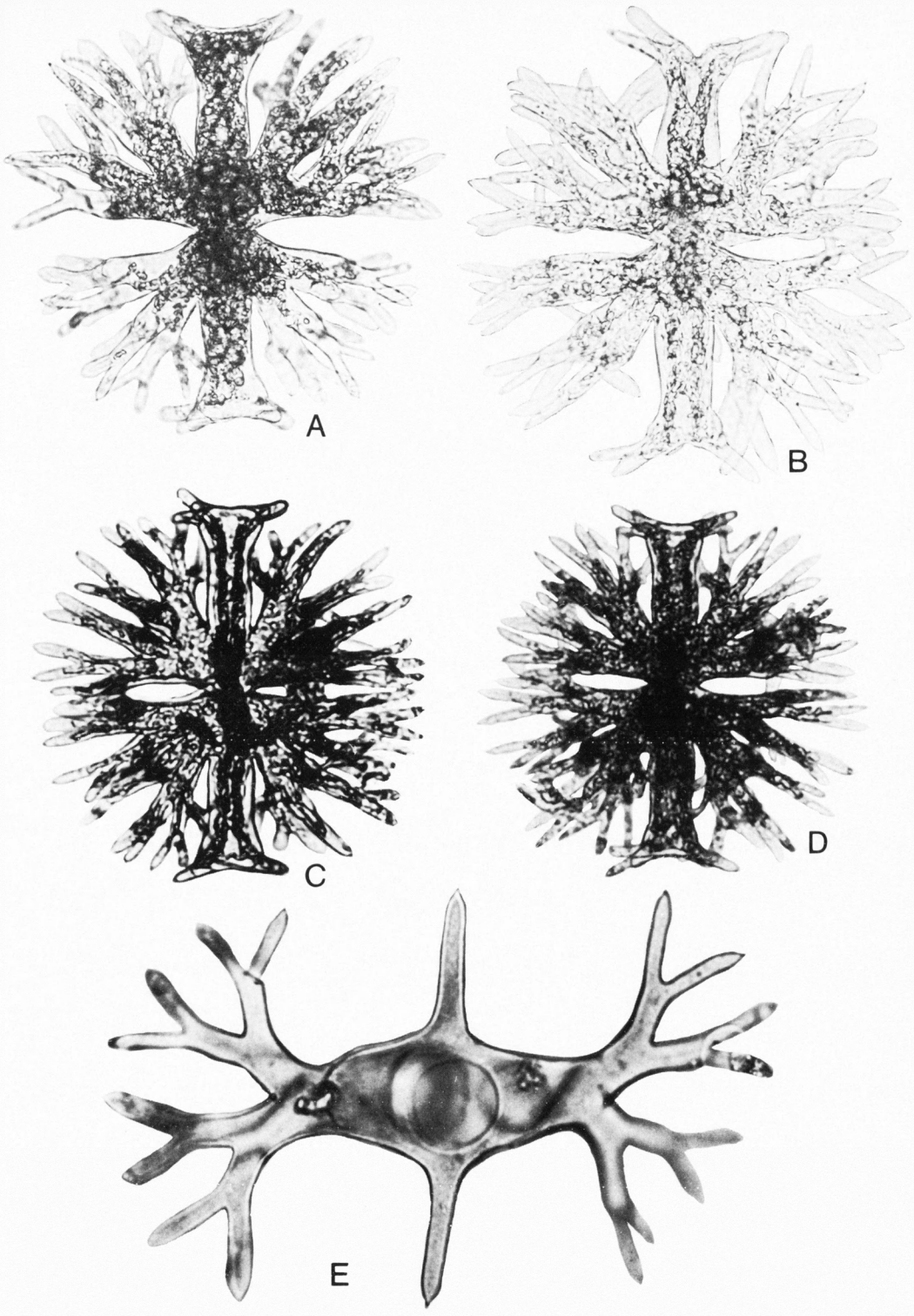
the cell surface. The mamillate drawn-out corners of polar lobes are double. The taxonomic problem with this curious plant is whether it is a *Micrasterias* or belongs to the genus *Allorgeia*. I consider it belongs most probably to the genus *Micrasterias*.

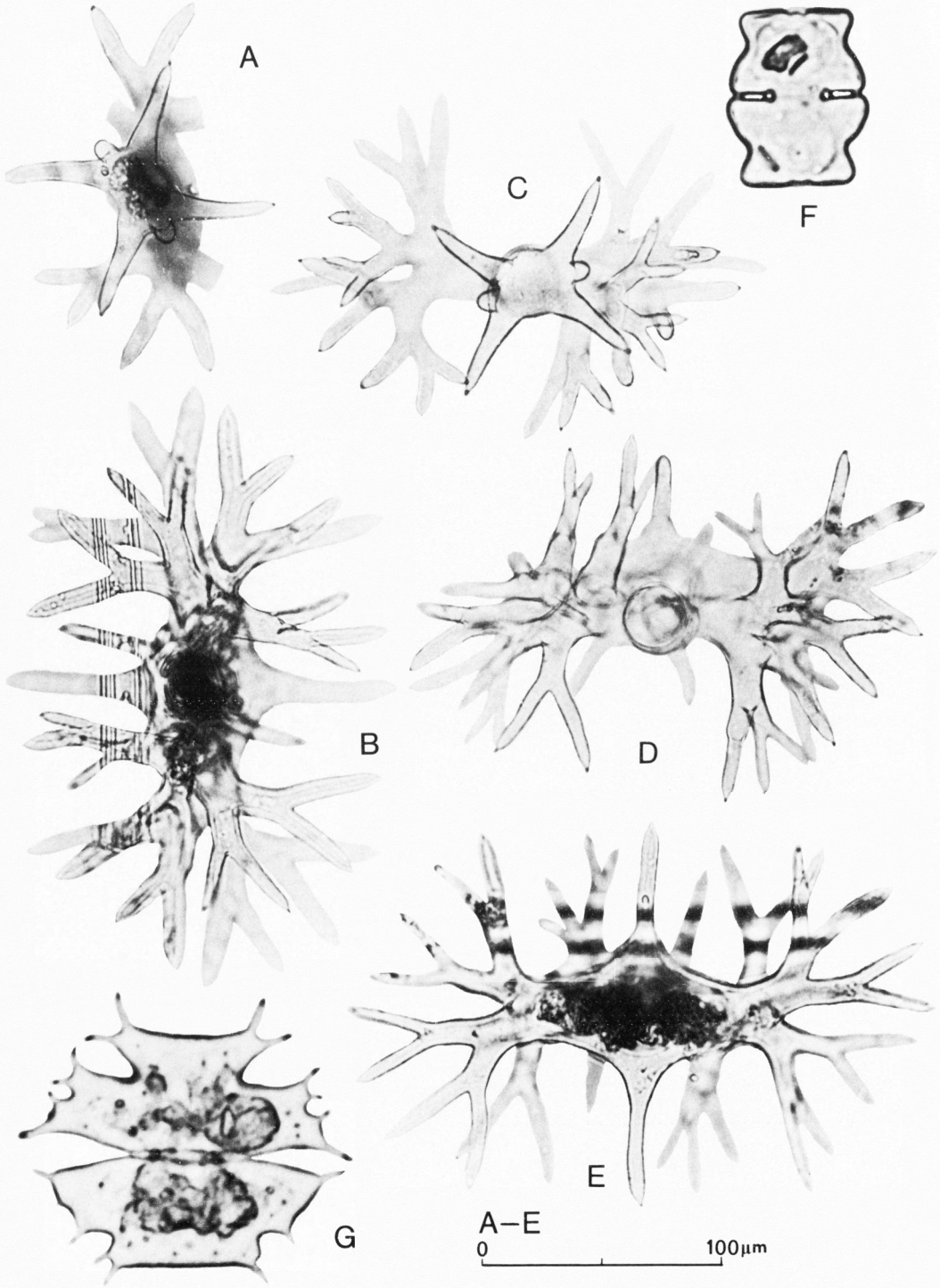
The sample, which was really a mini-sample of only about 3–5 mm^3, at first glance seemed to contain a few dozen taxa only. However, after some weeks of study, the occurrence of a considerable number of taxa was established. They are listed below in order to give some idea of the phycocoenosis in this kind of habitat. There are at least 50 more taxa, mainly diatoms, which I have not been able to identify.

Cyanophyta

Chroococcus dispersus (Keissl.) Lemm.
Cylindrospermum sp.
Gomphosphaeria lacustris Chod.

Fig. 2. A–E: *Micrasterias foersteri*. – A–D: Front view. – E: Basal view of semicell showing lateral lobes, and the mamillate projections on each side. – A–B × 300.


A
B
C
D
E
A–B
0
100 µm


A
C
F
B
D
E
G
A–E
0
100µm

Merismopedia glauca (Ehr.) Näg.
Oscillatoria limnetica Lemm.

Pyrrhophyta

Peridinium gatunense v. *madagascariense* (Lef.) Lef.
Peridinium sp.

Chromophyta

Chrysophyceae

Dinobryon bavaricum Imh.
D. cylindricum Imh.
D. sertularia Ehr.
Epipyxis alpina Hill. & Asm.
E. proteus (Wisl.) Hill. & Asm.
Mallomonas splendens (G. S. West) Playf.
Mallomonas sp.
Synura uvella Ehr.

Bacillariophyceae

Actinella guianensis Grun.
A. mirabilis Grun.
Melosira granulata (Ehr.) Ralfs
Rhizosolenia eriensis H. L. Smith
R. longiseta Zach.
Surirella sp.
Synedra acus Kütz.

Euglenophyta

Euglena sp.
Phacus curvicauda Swir.
Phacus sp.
Trachelomonas spinosa Stok.
T. volvocina Ehr.

Chlorophyta

Volvocales

Eudorina elegans Ehr.

Chlorococcales

Ankistrodesmus falcatus (Corda) Ralfs
Botryococcus braunii Kütz.
Coelastrum cambricum Arch.
Crucigeniella apiculata (Lemm.) Kom.
Dictyosphaerium pulchellum Wood
Dimorphococcus lunatus A. Br.
Oocystis sp.
Pediastrum boryanum (Turp.) Menegh.
P. tetras (Ehr.) Ralfs
Scenedesmus brasiliensis Bohl.
S. denticulatus v. *gracilis* Playf.
S. ecornis (Ralfs) Chod.
S. ecornis v. *disciformis* Chod.
S. quadricauda (Turp.) Bréb.
Selenastrum bibraianum Reinsch
Tetraedron caudatum (Corda) Hansg.
Treubaria setigera (Arch.) G. M. Smith

Chaetophorales

Chaetosphaeridium pringsheimii Kleb.

Zygnematales

Closterium closteroides (Ralfs) Luis & Reet.
C. closteroides v. *intermedium* (Roy & Biss.) Ruz.
C. costatum Corda
C. costatum v. *subtumidum* Racib.
C. gracile Bréb.
C. macilentum Bréb.
C. porrectum v. *borgei* (Borge) Först.
C. setaceum Ehr.
C. turgidum Ehr.
C. venus Kütz.
Pleurotaenium coronatum (Bréb.) Racib.
P. coronatum v. *fluctuatum* W. West
P. elatum (Turn.) Borge
P. elatum v. *alternans* (Nordst.) Grönbl.
P. minutum v. *latum* Kais.
P. subcoronulatum (Turn.) W. & W.
P. truncatum (Bréb.) Näg. – Long. 480 μm, lat. 75 μm.
P. truncatum v. *attenuatum* Krieg. – Long. 480 μm.
P. verrucosum (Bail.) Lund.
Docidium baculum Bréb.
D. hexagonum (Børg.) Krieg.
D. undulatum Bail.
Triploceras gracile Bail.
T. gracile v. *bidentatum* Nordst.
Ichtyocercus longispinus v. *amazonensis* Först.
Tetmemorus granulatus Bréb.
Euastrum abruptum Nordst.
E. bahiense f. *minor* Thom. n. f. – Euastrum forma ornatuque speciei simile, sed multo minus. Long. 25 μm.
E. biocellatum Scott & Croasd.
E. ciastonii Racib. – Cf. *E. flammeum* v. *subkalimantanum* Först.
E. ciastonii v. *apertisinuatum* Scott & Presc.
E. confusum Först.
E. cuspidatum Wolle
E. didelta v. *quadriceps* (Nordst.) Krieg. – Fig. 6 J; long. 100 μm. This plant resembles in shape *E. brasiliense* v. *convergens* Krieg. However, there are three large protuberances just above the isthmus. The semicells are stouter than in typical *E. didelta* v. *quadriceps*.
E. engleri Schmidle

Fig. 3. A–E: *Micrasterias foersteri*. – A: Vertical view, apical lobe. – B: Vertical view, upper lateral lobes. – C: Vertical view, apical lobe. – D: Vertical view, upper lateral lobes. – E: Vertical view, lower lateral lobes. – F: *Euastrum gessneri* v. *laticeps* forma. – G: *Micrasterias* sp.

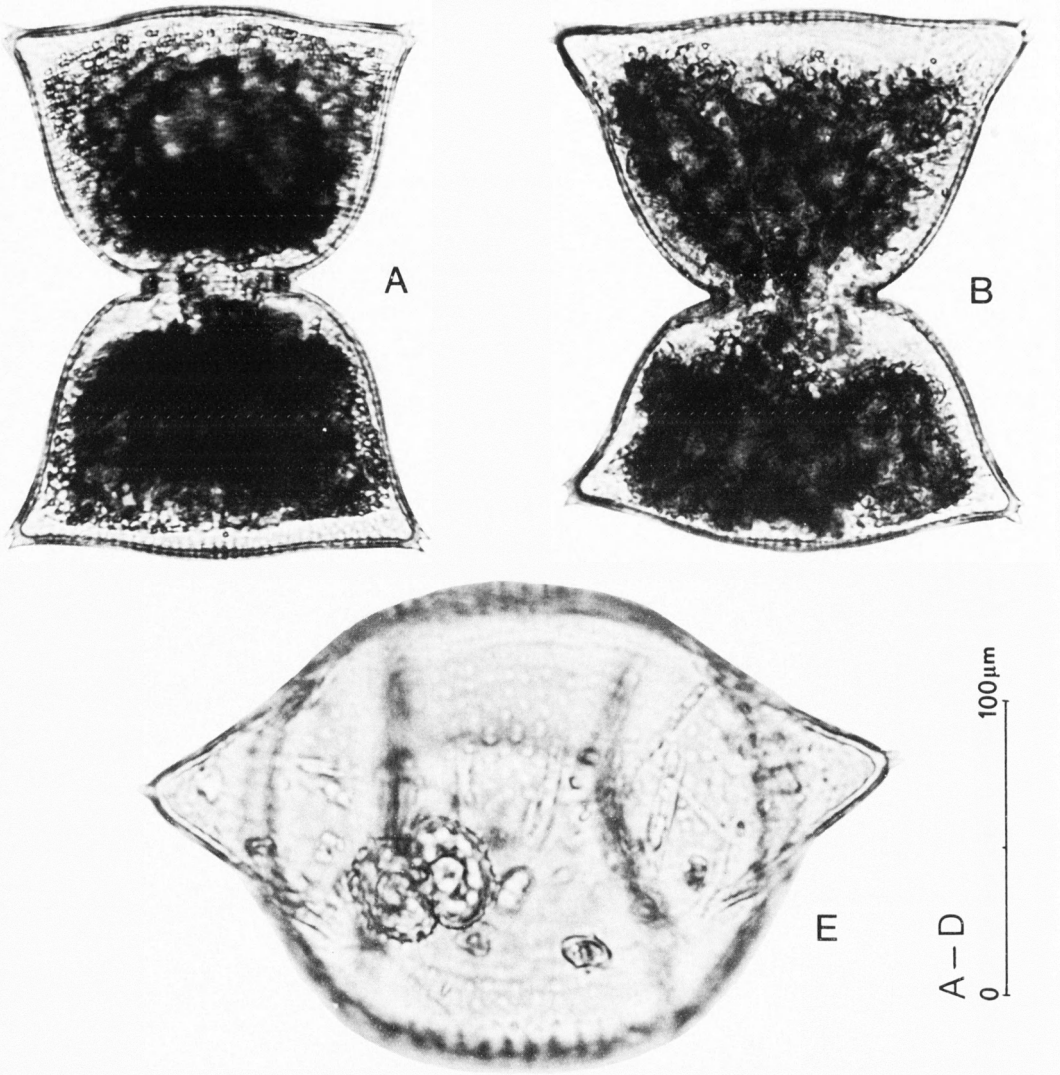
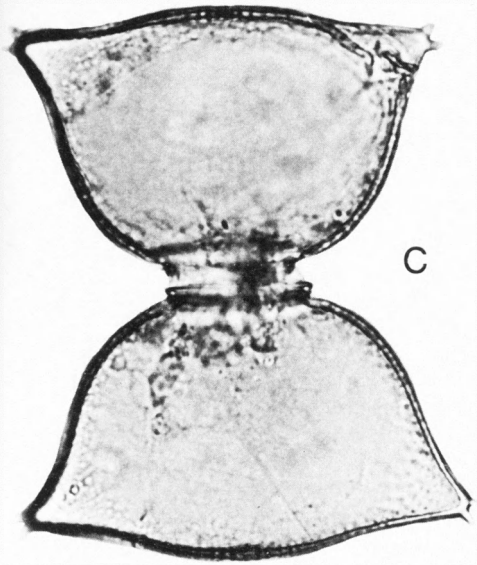
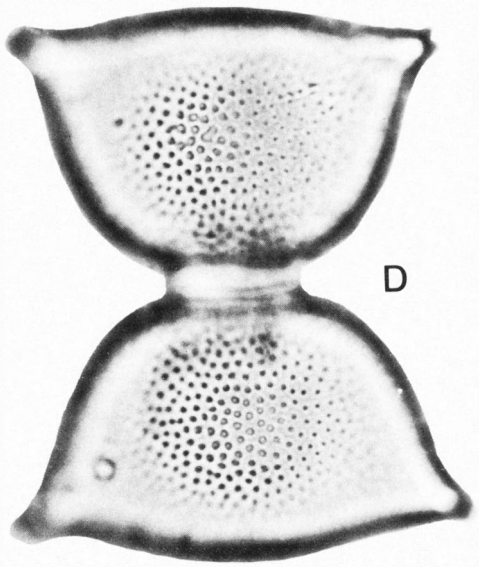


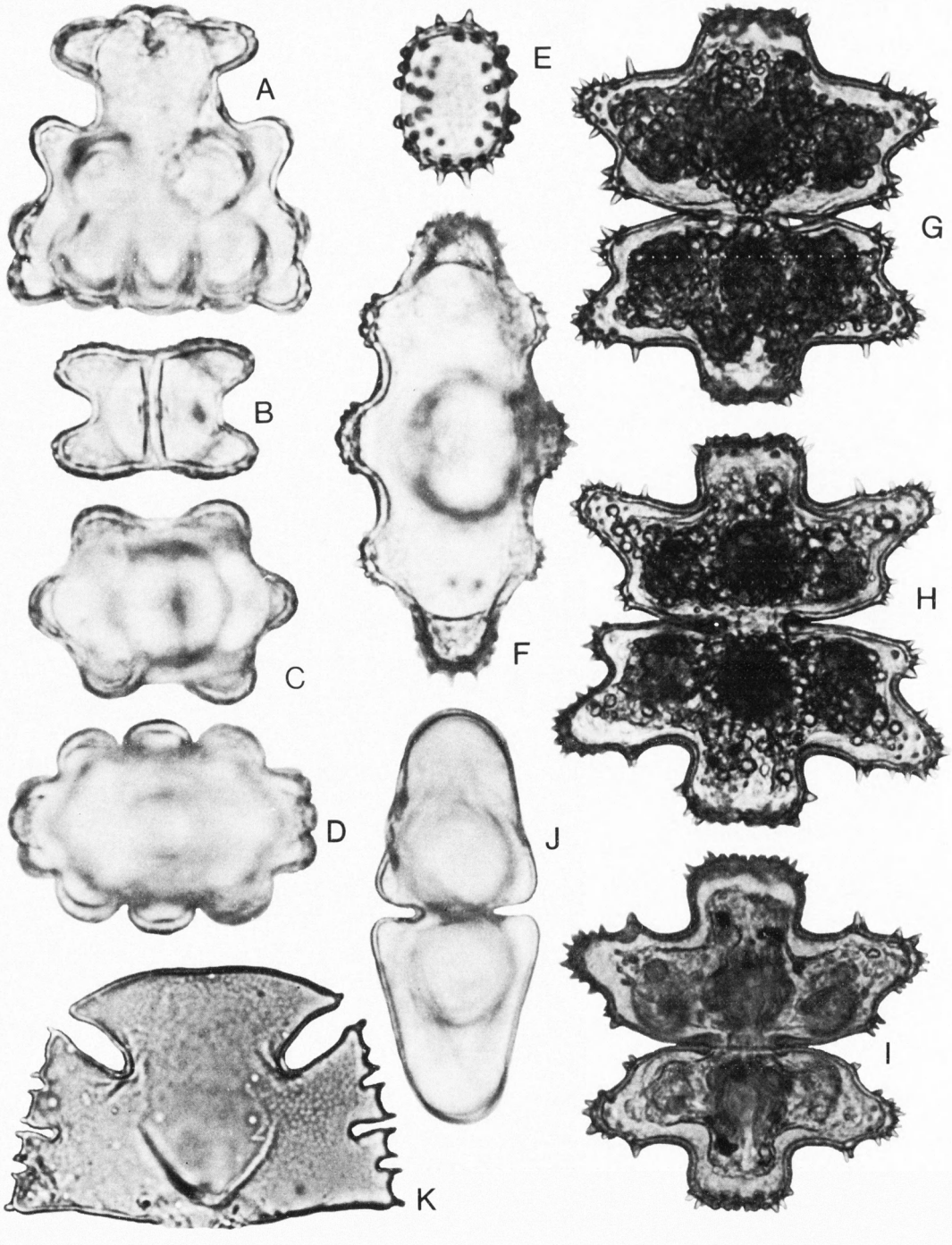
Fig. 4. *Cosmarium kostei*. A–D: Front view. – E: Vertical view.

E. evolutum (Nordst.) W. & W.
E. evolutum v. *glaziowii* (Børg.) W. & W. – Long. 56 µm.
E. evolutum v. *perornatum* Scott & Croasd.
E. flammeum v. *subkalimantanum* Först.
E. foersteri Scott & Grönbl.
E. gemmatum Bréb.
E. gessneri v. *laticeps* Scott & Prescott forma – Fig. 3 F. This is a small form, the length being only 28 µm, breadth 24 µm. It resembles *E. subincisum* Reinsch forma depicted by Krieger (1932) which is, however, a smaller plant.
E. humbertii v. *brasiliense* Krieg.
E. humbertii v. *brasiliense* f. *goyazense* Först. – Long. 28 µm, lat. 18 µm.
E. humerosum v. *evolutum* Krieg.
E. informe Borge – Long. 30 µm.
E. obesum Josh.
E. oculatum v. *cyclopicum* Först.
E. oculatum v. *suboculatum* Borge





E. paulense f. *caicarense* Först.
E. pinnatum Ralfs – Fig. 5 A–D. There are a number of figures of *E. humerosum* v. *evolutum* Krieg. which closely resemble *E. pinnatum*. However, the lateral supraisthmal protuberances are different.
E. platycerum v. *eximium* f. *clausum* Grönbl. & Scott – Fig. 5 E–I. Many morphae, formae, and varieties of *E. platycerum* Reinsch have been described. The taxonomical value of many of these taxa is doubtful. The morphological variation within the present population has been illustrated by Fig. 5 G–I.
*E. pirassununga*e Borge
E. quadrilobatum Scott & Grönbl. – Long. 23.5 μm, lat. 16 μm.
E. sinuosum Len.
E. sublobatum v. *kriegeri* f. *rotundatum* Först.
E. sublobatum v. *notatum* Grönbl. – With a granule just above the isthmus on each side.
E. subtrilobatum v. *gibbosum* Först.
E. umbonatum (W. & W.) Schmidle
E. validum W. & W.
Micrasterias alata Wall.
M. arcuata Bail.
M. arcuata f. *gracilis* W. & W.
M. decemdentata (Näg.) Arch. – Fig. 6 D. This plant is similar to the one designated as *M. decemdentata* in Borge (1918 Fig. 5: 22), later transferred to *M. abrupta* by Krieger (1939 p. 37). A rather similar plant has been figured by Krieger (1939 Fig. 104: 10) as *M. decemdentata*. For *M. abrupta* see West & West (1896 Fig. 14: 13–16), compare also Fig. 3: 10–12 and 4: 4–5 in Förster (1963).
M. depauperata v. *kitchellii* (Wolle) W. & W.
M. foersteri Thom.
M. foliacea Bail.
M. radiata v. *gracillima* G. M. Smith
M. radiata v. *groenbladii* Croasd.
M. radiosa v. *ornata* f. *elegantior* G. S. West
M. truncata f. *gibbosa* Thom. – The description of this taxon in Thomasson (1971) was not illustrated with a side view. Such a figure is given here (Fig. 5 J).
Micrasterias sp. – Fig. 3 G. Long. 36 μm, lat. 52 μm. This small *Micrasterias* is probably related to *M. abrupta* W. & W. However, having seen only two specimens I prefer to leave its taxonomic position open.
Actinotaenium cucurbitinum (Biss.) Teil.
A. globosum (Bulnh.) Teil.
A. peniomorphum v. *latius* (Scott & Presc.) Först.
A. turgidum v. *ligatum* (W. & W.) Teil. – Fig. 6 E–F represents an interesting morpha. The length of the plants is 100 μm, and the diameter 50 μm.
Cosmarium connatum Bréb.
C. contractum Kirchn.
C. costatum v. *subtumidum* Racib.
C. denticulatum v. *rotundatum* Lütkem.
C. denticulatum v. *rotundatum* f. *mediolaeve* Först.
C. depressum v. *elevatum* Borge
C. cf. *exasperatum* Josh.
C. furcatum Först.
C. geminatum v. *scottii* Först. – Long. 28 μm, lat. 30 μm.
C. groenbladii Thom.
C. isthmium v. *brasiliense* Grönbl.
C. kostei Thom.
C. lagerheimianum (Turn.) Scott & Presc. – Long. 96–120 μm, lat. 68–72 μm.
C. lagoense Nordst. – Incl. v. *amoebum* Först., long. 38(42) μm, lat. 28 μm.
C. lagoense v. *cornigerum* Nordst. – Syn. *C. lagoense* v. *octastichum* Först.
C. latipyramidatum v. *trapeziforme* Thom. var. nov. –


A
B
C
D
E
F
G
H
I
J
K
A–D
0
50µm
G–I
0
50µm
E-F, K-L
0
50µm

Long. 85–90 μm, lat. 65–70 μm. Semicellulae trapeziformis, angulis acutirotundatis, membrana dense porosa. Iconotypus fig. nostra 6 G.

C. moniliforme v. *pseudofuellebornii* Först.
C. monomazum v. *dimaziforme* Grönbl.
C. notochondrum W. & W. forma – The papillae are more like spines than in plants depicted by West & West and there is one protuberance on each side of the sinus.
C. ocellatum Eichl. & Gutw.
C. ornatum v. *pseudolagoense* Först.
C. patelliforme Borge – Fig. 6 H, I. Long. 108–116 μm, lat. 62–64 μm. These plants are a little smaller than those described by Borge (1903). However, the similar *C. contractum* v. *maximum* W. & W. is considerably smaller. I am not convinced about the taxonomic value of the apical depression mentioned by Borge.
C. polymorphum v. *groenbladii* Först. – Long. 26.5 μm, lat. 22 μm.
C. portianum Arch.
C. pseudoconnatum v. *borgei* Först.
C. pseudomagnificum v. *brasiliense* Först. – Long. 70–72 μm. This variety resembles *C. margaritiferum* v. *brasiliense* Först. One should always carefully consider the ornamentation of the cell wall.
C. pseudopachydermum Nordst. forma
C. pseudopyramidatum v. *borgei* Krieg. & Gerl. – Long. 88 μm.
C. pseudotaxichondrum v. *longii* (Tayl.) Scott
C. redimitum Borge
C. regnesii v. *productum* W. & W.
C. scrobiculosum Borge – The plants are a little smaller than those described by Borge (1903): Length 60 μm, breadth 40 μm. See also Fig. 139 in Grönblad (1945).
C. spinuliferum W. & W. – Long. 32 μm, lat. 26 μm.
C. subpraemorsum Borge – Long. 60 μm, lat. 40 μm.
C. trilobulatum v. *minutum* Först.
C. zonatum v. *subcylindricum* Grönbl. & Scott – Fig. 6 C. Long. 54–64 μm.
Xanthidium armatum (Bréb.) Rabenh.
X. armatum v. *circumornatum* Först.
X. fragile Borge
X. mamillosum (Grönbl.) Först.
X. multituberculatum Först. forma – With a large protuberance on each side of the isthmus.
X. regulare v. *asteptum* Norst. – Borge 1918 Fig. 3: 31.
X. regulare v. *pseudoregulare* (Borge) Bic. & Carv.
X. regulare Nordst. forma – Förster 1964 Fig. 27: 1.
Arthrodesmus borgei Thom.
A. impar v. *centrispinum* Scott & Grönbl.
A. longispinus Borge – This taxon was described by Borge (1903 Fig. 3: 35). Since then a number of plants of different shape have been lumped under that name. Fig. 6 A, B shows what this taxon should be like.
A. octocornis Ehr.
A. westii (W. & W.) Först. – Long. 40 μm, lat. 72 μm.
Staurodesmus calyxoides v. *marthae* (Grönbl.) Teil.
S. ceratophorus (Nordst.) Först.
S. cornutus (Wolle) Teil.
S. hebridarus v. *brasiliensis* Först. fac. 3 – Long. 40–44 μm.
S. incus (Bréb.) Teil. forma – Teiling 1967 Fig. 5: 5.
S. leptodermus v. *ikapoae* f. *elongatus* Grönbl. & Scott – Long. 42(96) μm.
S. mamillatus (Nordst.) Teil.
S. maximus (Borge) Teil. forma – Förster 1969 Fig. 30: 1.
S. minutissimus (Reinsch) Teil.
S. o'mearae (Arch.) Teil.
S. patens (Nordst.) Croasd.
S. phimus (Turn.) Thom. – Förster 1974 Fig. 8: 18.
S. psilosporus (Nordst. & Löfgr.) Teil. forma – Förster 1964 Fig. 25: 6–7.
S. validus (W. & W.) Thom.
S. wandae v. *pseudopterosporus* (Först.) Teil.
S. wandae (Racib.) Bourr. forma – Five-radiate, somewhat larger than those described by Raciborski. Spines considerably longer, length of cells 44 μm, with spines 88 μm.
Staurastrum binum v. *inaequale* Grönbl. & Croasd. – Long. 48(92) μm, lat. 28(80) μm. There are seven long upper spines and the same number of shorter and thinner lower spines which are directed towards the isthmus.
S. bituberculatum Först. – Long. 48–60 μm, lat. 40 μm.
S. brachiatum Ralfs
S. boergesenii v. *elegans* Borge
S. brasiliense Nordst.
S. brasiliense v. *porrectum* Borge
S. capitulum v. *tumidiusculum* (Nordst.) W. & W.
S. cerastes v. *pulchrum* Scott & Grönbl. – Long. 48(92) μm, lat. 28(80) μm. Most likely the plant described by Grönblad (1945) as *S. submanfeldtii* v. *convergens* is closely related to *S. cerastes* v. *pulchrum*.
S. circulus Grönbl.
S. columbetoides v. *basiaculeatum* Scott & Presc.
S. columbetoides v. *ginzbergeri* (Grönbl.) Scott
S. cosmaroides Nordst. – Long. 74 μm.
S. cosmaroides v. *tropicum* (Lagerh.) Borge – This plant is identical with the one figured in Bicudo 1969 Fig. 199. The size is: length 78 μm, breadth 40 μm. It is abundant in the sample.
S. diptilum Nordst.
S. elegantissimum v. *brasiliense* f. *triradiatum* Först. – Syn.: *S. oxyacantha* v. *majus* Scott & Grönbl. forma in Thomasson (1971).
S. elongatum v. *amazonense* Scott & Grönbl.
S. glabribrachiatum Först.
S. grallatorium v. *brasiliense* (Grönbl.) Först. – Syn.: *S. saltans* v. *brasiliense* Grönbl.
S. hystrix v. *brasiliense* Grönbl.
S. hystrix v. *floridense* Scott & Grönbl.
S. inconspicuum Nordst.
S. irregulare W. & W.
S. jurucuiense Thom.

Fig. 5. A–D: *Euastrum pinnatum*. – A: Front view. – B–D: Vertical views. – E–I: *Euastrum platycerum* v. *eximium* f. *clausum*. – E: Apex in vertical view. – F: Basal view. – G–I: Front views. – J–K: *Micrasterias truncata* f. *gibbosa*. – J: Side view. – K: Front view.

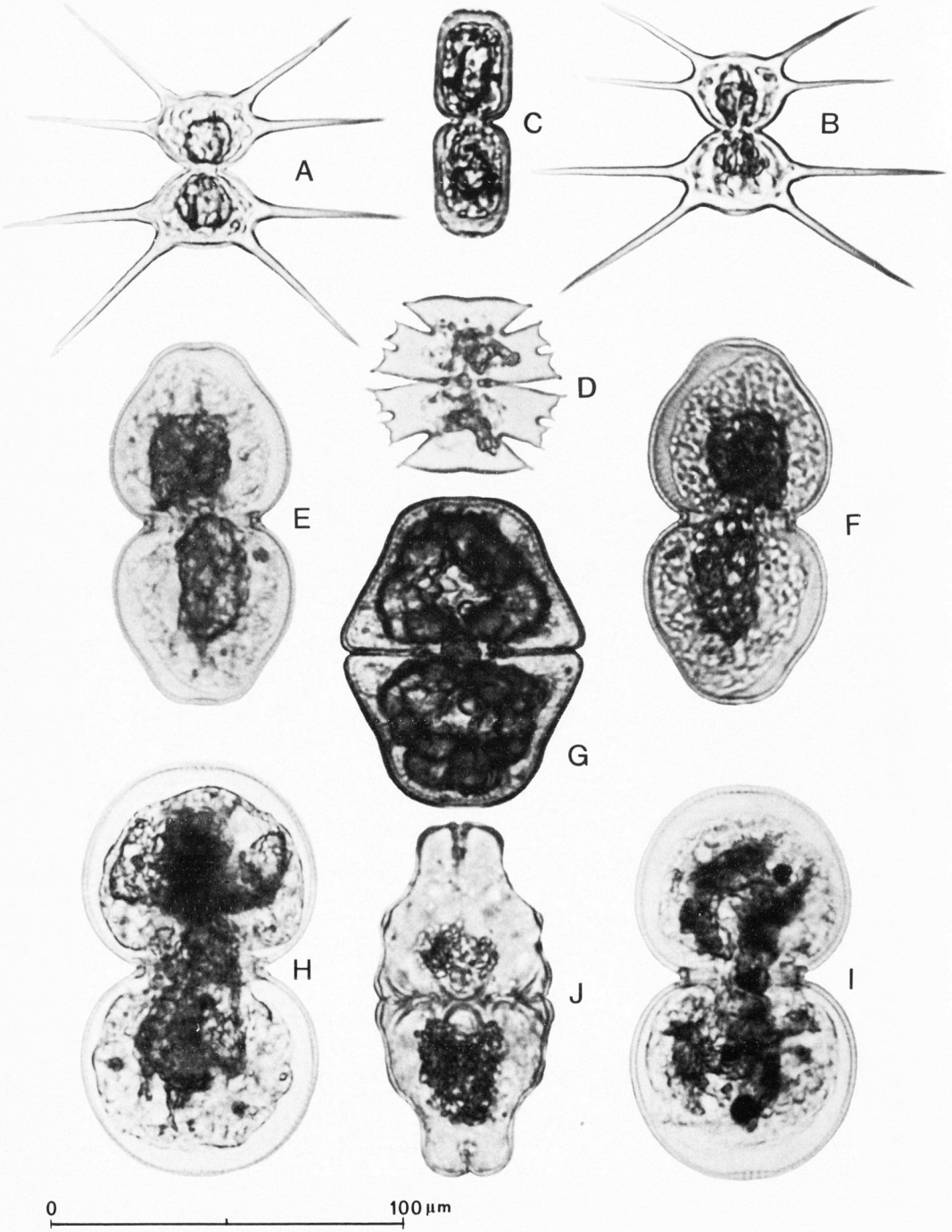


Fig. 6. A–B: *Arthrodesmus longispinus*. – C: *Cosmarium zonatum* v. *subcylindricum*. – D: *Micrasterias decemdentata*. – E–F: *Actinotaenium turgidum* v. *ligatum*. – G: *Cosmarium latipyramidatum* v. *trapeziforme*, iconotype. – H–I: *Cosmarium patelliforme*. – J: *Euastrum didelta* v. *quadriceps*.

S. laevispinum Biss. – Long. sine proc. 12 μm.
S. leptacanthum Nordst.
S. leptocladum v. *cornutum* Wille
S. leptocladum v. *insigne* W. & W.
S. longipes v. *evolutum* f. *gracillius* Först.
S. minnesotense Wolle
S. novae-caesareae v. *brasiliense* (Grönbl.) Först.
S. octoverrucosum v. *brasiliense* Först.
S. orbiculare v. *depressum* Roy & Biss. forma – Förster 1969 Fig. 33: 4.
S. penicilliferum Grönbl.
S. pseudozonatum v. *minutum* f. *rectum* Först.
S. quadrangulare v. *contectum* (Turn.) Grönbl. – Long. 20–22 μm.
S. rotula Nordst.
S. royi Turn.
S. spiculiferum Borge
S. stelliferum v. *evolutum* Thom.
S. tectum v. *ayayense* Grönbl.
S. teliferum v. *groenbladii* Thom.
S. tentaculiferum Borge
S. tetracerum Ralfs
S. trifidum v. *inflexum* W. & W.
S. trihedrale Wolle – The observed plant is similar in shape to the one figured by West & West (1896 Fig. 16: 29), being somewhat larger: length 54 μm, breadth 40 μm.
S. vestitum v. *subanatinum* W. & W.
S. wolleanum v. *brasiliense* Scott & Grönbl.
S. xiphophorum Grönbl. – Abundant.
S. zonatum Børg. – The specimens in this sample are 40–42 μm long, the breadth is 52 μm, the ornamentation of the apex is similar to the specimen figured by Grönblad (1945 Fig. 300). The plants are 5-radiate.
S. zonatum f. *elongata* Grönbl. – Long. 30(48) μm, 4-radiate.
Spondylosium panduriforme f. *limneticum* (W. & W.) Teil.
S. rectangulare f. *majus* Scott & Grönbl.
Sphaerozosma laeve (Nordst.) Thom.
Desmidium baileyi f. *tetragonum* Nordst.
D. curvatum Nordst.
D. cylindricum Grev.
D. elegans (Racib.) Grönbl.
D. gracilipes (Nordst.) Lagerh.
Bambusina longicollis (Nordst.) Grönbl.
Phymatodocis alternans Nordst.
P. nordstedtiana Wolle
Hyalotheca dissiliens (J. E. Smith) Bréb.

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Notice for the exchange of duplicate voucher material

S. H. Sohmer

The Herbarium of the University of Wisconsin-La Crosse has been the base for a number of floristic projects including a detailed project dealing with Navigation Pool 8 of the Upper Mississippi River. This area consists of that portion of the Upper Mississippi River and its flood plain impounded behind Lock and Dam No. 8 at Genoa, Wisconsin, and extending 47.5 km or 23.3 river miles, north to Lock and Dam No. 7 at Dresbach, Minnesota.

Two major series of collections have been made in this area; one series vouches for a study of the vascular flora and its succession on dredge material (material dredged from the navigation channel and piled along the edge of the channel) and the other vouches for a study dealing with the flora and phytosociology of all other sites, both aquatic and terrestrial, in this area. The total number of collections come to nearly 6000 numbers and over 20,000 specimens.

The first set of these collections will remain at UWL to vouch for these studies. I would like to distribute the duplicate sets for exchange to herbaria that will maintain these collections. The specimens have been identified, often by specialists of particularly difficult groups, and will be provided with 100% rag, heavy, detailed specimen labels with separate map labels that will pinpoint exact locations within the Navigation Pool. Individual arrangements can be made and we are rather open to exchange possibilities for this material. Please contact Dr S. H. Sohmer, Director, Herbarium, University of Wisconsin, La Crosse, Wisconsin 54601, USA.

Vesiculomyces Hagström gen. nov. segregated from Gloeocystidiellum (Corticiaceae)

Elisabeth Hagström

Hagström, E. 1977 04 15: Vesiculomyces Hagström gen. nov. segregated from Gloeocystidiellum (Corticiaceae). *Bot. Notiser 130:* 53–54. Stockholm. ISSN 0006-8195.

The new monotypic genus *Vesiculomyces* is described to accommodate *V. citrinus* (Pers.) Hagström (≡ *G. citrinum* (Pers.) Donk). A distribution map of this species is given.

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An investigation of the Nordic species of the genus *Gloeocystidiellum* Donk is being undertaken by the author. As a first result a new genus is here described to accommodate *G. citrinum* (Pers.) Donk, a species that deviates in several important characters from other species of *Gloeocystidiellum*.

Vesiculomyces Hagström gen. nov.

Fructificatio resupinata, effusa, albida–citrina–flavida, in vivo plus minusve tuberculata; systemate hyphali monomitico; hyphis tenuiter tunicatis, septatis non fibulatis, 1.5–3.5 μm latis; gloeocystidiis vesicularibus, demum apicaliter tubiformibus sinuosisque, quae in solutione sulphovanillini non tinguntur, 30–150 × 10–22 μm; basidiis flexuoso-cylindricis, 4-sterigmatibus, 23–75 × 4.5–8 μm; sporis subglobosis, tenuiter tunicatis, glabris, amyloideis, apiculo prominenti, 5.0 × 4.8 μm vel 4.9 μm diam.

Typus generis *Vesiculomyces citrinus* (Pers.) Hagström comb. nov. (≡ *Thelephora citrina* Pers., Mycol. europ. 1: 136 (1822).

Fructifications resupinate, effused, white to yellow, when fresh more or less tuberculose. Hyphal system monomitic, of thin-walled hyphae that are septate but not fibulate, 1.5–3.5 μm diam. Gloeocystidia without positive reaction to sulfo-aldehydes, terminal, bladder-like, later apically winding and tube-formed, 30–150 × 10–22 μm. No other sterile hymenial elements present. Basidia flexuous-cylindrical with 4 sterigmata, 23–75 × 4.5–8 μm. Spores subglobose, thin-walled, smooth, amyloid, with a prominent apiculus, 5.0 × 4.8 μm or 4.9 μm diam.

The generic name is derived from *vesicula* = small bladder, and *myces* = fungus, referring to the shape of the gloeocystidia.

Discussion

The main difference between *Vesiculomyces* and *Gloeocystidiellum* is the reaction of the gloeocystidia to sulfo-aldehydes. All species of *Gloeocystidiellum* s. str. show a positive reaction, the gloeocystidia becoming dark coloured in the test. There are some other characters contributing to make *V. citrinus* distinct from all species of *Gloeocystidiellum* viz. the lack of clamps, the almost spherical spores and the long and narrow basidia. Taken together these characters make *Vesiculomyces* stand out as a well delimited taxon. The segregation of *Vesiculomyces* allows a more precise circumscription of *Gloeocystidiellum* which can be described as having amyloid spores, gloeocystidia with positive reaction to sulfo-aldehydes but lacking acanthohyphidia and other hymenial elements characteristic of the genus *Aleurodiscus* Rabenh.

Amyloid spores is a very important character for the classification of species and genera of resupinate Basidiomycetes. Besides in *Gloeocy-*

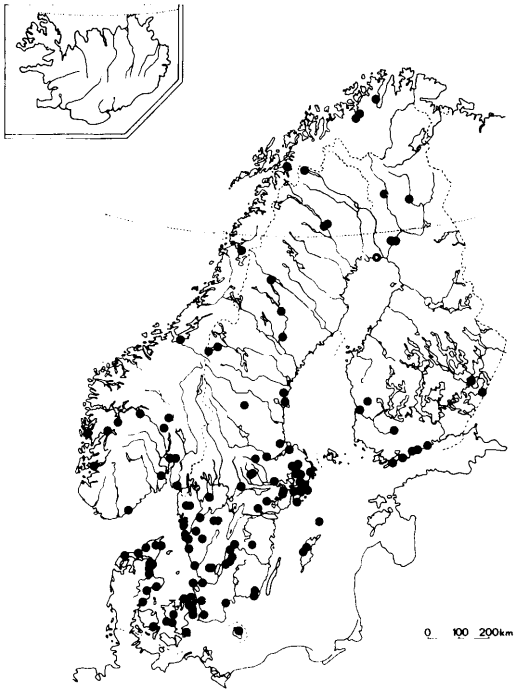


Fig. 1. *Vesiculomyces citrinus*. Known distribution in Northern Europe.

stidiellum and *Aleurodiscus* such spores are found in the related genera *Laxitextum* Lentz and *Scytinostromella* Parm., which differ from *Vesiculomyces* in having ornamented spores. Amyloid spores are also found in *Irpicodon* Pouz., in *Melzericium* Hauersl. and in *Amylocorticium* Pouz. However, these three genera are easily separated from *Vesiculomyces* by lacking gloeocystidia, possessing clamps and having spores of quite different shapes. *Melzericium* besides has pleurobasidia. Some other species with such basidia, in the genera *Xenasmatella* Oberw. and *Pseudoxenasma* Larss. & Hjortst., have amyloid spores as well. In Stereaceae such spores are found in most genera, for example *Stereum* Pers. per S.F. Gray, *Amylostereum* Boid. and *Xylobolus* Karst., but these differ in other respects. The stereoid genus *Laurilia* Pouz. (Echinodontiaceae) with amyloid, ornamented spores is in many respects different from *Vesiculomyces*.

The natural relationships between *Vesiculomyces* and other genera within Corticiaceae and consequently its place within the family are obscure, as is very often the case among the resupinate Basidiomycetes. The similarities with *Gloeocystidiellum* and *Aleurodiscus* may or may not be an indication of real affinity. *V. citrinus* is rather similar to the phlebioid fungi in hymenial configuration, having narrow basidia standing in a dense palissade. For practical reasons it is probably best to leave it in the vicinity of *Gloeocystidiellum*.

During the investigation of *Vesiculomyces citrinus* special attention has been given to intraspecific variation. Variation in colour, structure, thickness and size of the fruitbodies, the nature of hyphae, gloeocystidia, basidia and spores have been thoroughly studied. Preferences to different substrates have been considered. *V. citrinus* is clearly a uniform taxon. All available Nordic collections of *V. citrinus* from the following herbaria have been examined: GB, UPS, S, C, O, TRH, H, L, Lars Arvidsson, John Eriksson, Nils Hallenberg, Kurt Hjortstam, Åke Strid and Stellan Sunhede. The known distribution is shown in Fig. 1. Despite the bias resulting from over- and undercollecting it can be claimed that the fungus is more common in the southern parts of the investigated area.

The most common substratum for this species is decayed wood of coniferous trees lying on the ground. In the southern parts of the investigated area some 80% of the material has been found on coniferous wood and the corresponding number for the northern parts is somewhat higher. *Picea abies* seems to be the most common substrate according to the labels on the collections. *Pinus* is also often reported as a host. Some finds have been made on *Juniperus*, and a few other conifers have also occasionally been noted. At least seven genera of deciduous trees may serve as substratum, viz., *Betula*, which is quite common, *Alnus*, *Salix*, *Fagus*, *Populus*, *Quercus* and *Sorbus*. *V. citrinus* has also been found growing on mosses, on dead *Lenzites* and on soil. Detailed information and a list of the material studied will be included in a stencilled report to be published at the Botanical Department, University of Göteborg.

Acknowledgements. I am indebted to my supervisor, Dr John Eriksson, for valuable help with the present paper, and to Professor Åke Fridh for correcting the Latin.

Pardinae, a new section of Bomarea (Alstroemeriaceae)

Magnus Neuendorf

Neuendorf, M. 1977 04 15: Pardinae, a new section of Bomarea (Alstroemeriaceae). *Bot. Notiser 130:* 55–60. Stockholm. ISSN 0006-8195.

A new section of *Bomarea,* sect. *Pardinae,* is described. It is characterized by auriculate pollen grains and white petals. The section comprises two species: *B. pardina* Herb. and *B. ceratophora* sp. nov. *B. pardina* is distributed in the Andean region from Peru to S Colombia. *B. ceratophora* is known from the E slopes of the Andes of the provinces Tungurahua and Pastaza in Ecuador.

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The genus *Bomarea* (Alstroemeriaceae) was established by Mirbel in 1804 and comprises now about 100 species. However, this figure is very unreliable because of the lack of a modern revision. The genus is closely related to *Alstroemeria* L. but separated by the actinomorphic (sometimes slightly zygomorphic) flowers, the straight filaments and the leathery or somewhat fleshy mature capsules or berry-like fruits. *Alstroemeria* has zygomorphic flowers, curved filaments and dry capsules.

Bomarea is generally subdivided into three subgenera: *Wichuraea, Sphaerine* and *Bomarea* (Baker 1888). The largest of these, subgenus *Bomarea,* on which I am preparing a monograph, is usually split up into four groups of species, classified sections by Killip (1936). The principles of the division of subgenus *Bomarea* seem quite artificial, however, and make some obviously closely related species fall into different sections. A modern revision will entail a different grouping within the subgenus *Bomarea.* Two closely related species, one of which is described in the present paper as new to science, have characteristic pollen grains, quite different from those in other species of the genus. These two species constitute a natural group and warrant recognition as a separate section, *Pardinae.*

Sect. **Pardinae** Neuend. sect. nov.

Type species: *Bomarea pardina* Herb.

Inflorescentia thyrsus condensatus, cymulis unifloris ad quadrifloris. Segmenta perianthii inaequalia. Petala alba maculis fuscoviolaceis vel atroviolaceis. Pollinis grana auricula utraque parte sulci ornata.

Vines. Stems to 10 m long, glabrous. Inflorescence a condensed thyrse composed of one- to three- or rarely four-flowered cymules (Fig. 1). The youngest shoot-generation of the cymule always stunted (Fig. 2). Pedicels bracteate. Petals exceeding the sepals with about 1 cm, white to whitish grey, internally with numerous dark violet spots. Pollen grains with an auricle at each end of the sulcus (Fig. 3).

Two species belong to this section. The geographical distribution comprises Peru, Ecuador and southernmost Colombia, with a concentration to the Andean region in the N half of Ecuador.

Key to the species

Sepals without horn ..... 1. *B. pardina*
Sepals with a 0.6–0.8 cm long, curved horn just below the apex ..... 2. *B. ceratophora*

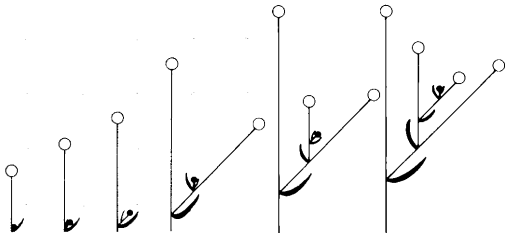


Fig. 1. *Bomarea pardina.* – Different cymule-types, youngest shoot-generation (flower) stunted. Length of axis enlarged.

1. **Bomarea pardina** Herbert – Figs. 4, 5 A–C

Bomarea pardina Herbert 1837 p. 120 – Orig. coll.: Hall 19 (K holotype).
Bomarea lyncina Herbert 1837 p. 398 – Orig. coll.: Mathews 1668 (K holotype).
Bomarea brachypus Kränzlin & Sodiro 1907 p. 40 – Orig. coll.: Sodiro 176/15 (B), Lehmann 7784? (B).
Bomarea grandiceps Kränzlin & Sodiro 1907 p. 40 – Orig. coll.: Sodiro 174/16 (B).
Bomarea pulchella Sodiro 1908 p. 55 – Orig. coll.: Sodiro 11/905 (cf. below).
Bomarea venusta Sodiro 1908 p. 55 – Orig. coll.: Sodiro 7/907 (cf. below).
Bomarea falcata Sodiro 1908 p. 56 – Orig. coll.: Sodiro s. n. (cf. below).

Illustrations: Herbert 1837, Pl. 14 fig. 1 (inflorescence) and Pl. 46 fig. 1 (as *Bomarea lyncina* Herb., part of inflorescence, leaf).

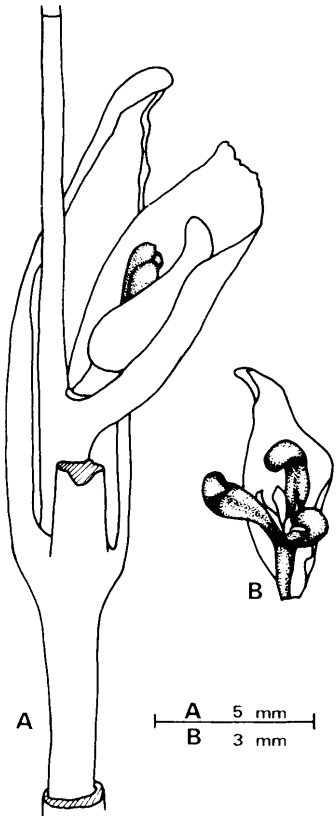


Fig. 2. *Bomarea pardina.* – A: Two-flowered cymule with a third stunted flower (flowering pedicels and bract removed) (Hitchcock 21174). – B: Stunted, bracteate flower (André 3787).

Stem rather slender, voluble, generally 3–5 m long, sometimes up to 10 m, glabrous. *Leaves* ovate to narrowly ovate, generally 6–13 cm long, 3–5 cm wide, cuspidate to acuminate at apex, obtuse at base, glabrous above, densely pilose to ± glabrous beneath. *Petioles* 0.5–1.5 cm long, with a flattened narrow margin. *Bracts* sessile, or with a short untwisted petiole, narrowly ovate, 1.0–2.5 cm long, 0.3–1.5 cm wide, acute to obtuse at apex, slightly puberulous. *Cymules* 10–30(–40), one-, two-, three- or rarely four-flowered, pedicels ± pilose, primary pedicels 1.0–1.5(–2.5) cm long. *Bractlets* ovate to narrowly ovate, 0.5–2.0 cm long, 0.3–0.6 cm wide, obtuse at apex, slightly puberulous. *Sepals* narrowly obovate to narrowly elliptic (Fig. 5 A, C), (3.6–)4.0–5.0(–5.8) cm long, 0.7–1.1(–1.4) cm wide, externally red and slightly puberulous, internally pale pink, often with a distinct boss 1–2 mm high c. 0.5 cm below the apex. *Petals* cuneate, unguiculate (Fig. 5 A–C), (4.0–)4.8–6.0(–6.8) cm long, 1.2–1.8(–2.0) cm wide, white to whitish grey, with reddish mid-nerve, internally with numerous, rather large, elliptic, dark violet spots on the lamina, externally with a few small spots at the margin. *Filaments* filiform, generally 0.5–1.0 cm shorter than the petals. *Anthers* elliptic, 0.6–0.8 cm long. Pollen grains (95–)110–120 μm long, with auricles (Fig. 3), flesh-coloured to pale violet. *Ovary* turbinate to subglobose, ± densely pilose. *Style* as long as the stamens, glabrous. Stigma branches c. 3 mm long. *Fruit* unknown.

Representative specimens. Colombia. Putumayo: Valle de Sibundoy, in the vicinity of Sibundoy, c. 2250 m, 10–11.XII. 1942, Schultes & Smith 3091 (US) – *Ecuador. Carchi:* Road Tulcán–Maldonado, c. 13 km SE of Maldonado, c. 2600 m, 1.III. 1974, Harling & Andersson 12337 (GB) – *Pichincha:* San Ignacio, km 23 on road Aloag–Sto. Domingo, 2000 m,

4.III. 1967, Sparre 14691 (S) – *Napo:* Near Archidona, 19.IV. 1935, Mexía 7254 (UC) – *Pastaza:* Mera, 1160 m, 28.XII. 1958, Harling 3741 (S) – *Bolívar:* Below San Jacinto de la Unión, ca 2300 m, 15.VIII. 1939, Asplund 8323 (S).

Bomarea pardina is rather uncommon in mountain rain forest and edge vegetation from 550 to 3000 m. The geographical distribution coincides with that of the section. Forty-seven collections have been examined. A list of investigated specimens is kept at the Botanical Museum, Göteborg.

Despite a rather large intraspecific variation, which probably depends on the large vertical distribution, *B. pardina* is very characteristic with the white, richly spotted petals, shorter unhorned sepals and auriculate pollen grains.

The pubescence of the lower leaf surface varies from densely pilose to more or less glabrous, and the cymules can be either one-, two-, three- or rarely four-flowered. A few of the inflorescences examined have both one- and two-flowered cymules. The leaves vary rather much in shape and size. The bracts and bractlets are longer and narrower in a compact inflorescence than in a lax one. In most of the collections from low elevations in eastern Ecuador, the sepals are wider (1.3–1.4 cm, Fig. 5 C) than in the material from the rest of the distribution area (0.7–1.1 cm, Fig. 5 A). The cymules in collections from low elevations (500–1000 m) bear at least two, often more, flowers, while one-flowered cymules prevail at high altitudes.

The type of *B. lyncina,* from Peru, (all other types mentioned are collected in the Andes of the N part of Ecuador), has three-flowered cymules and rather small leaves, which are almost glabrous beneath. The type of *B. pardina* has one-flowered cymules and the lower leaf surface is pilose. The type of *B. brachypus* agrees very well with that of *B. pardina.* Kränzlin's comment that the inflorescence of *B. brachypus* is quite different from that of *B. pardina* is not correct. Concerning *B. grandiceps,* Kränzlin states that it has very little similarity to *B. pardina,* with which Sodiro had identified it. This is rather confusing, since the types agree very well. The only dissimilarity is that *B. grandiceps* has longer leaves with the lower surface only slightly pilose. Also *B. pulchella* is similar to *B. pardina* with the exception that the leaves are glabrous. Sodiro

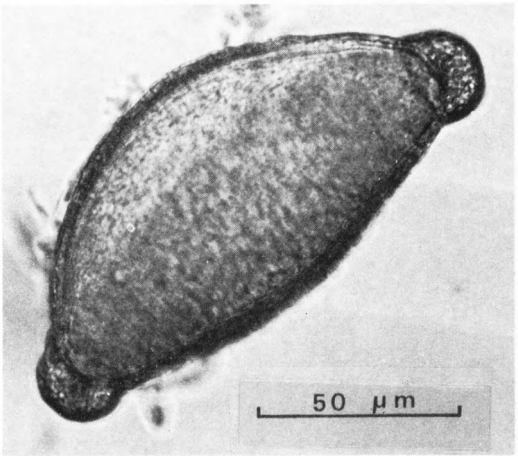


Fig. 3. *Bomarea pardina.* – Pollen grain (Harling 3741).

placed *B. pulchella* under the heading "Umbella simplici", but remarked that the pedicels are sometimes two-flowered. *B. venusta* and *B. falcata,* placed by Sodiro in the group "Umbella composita", also agree well with *B. pardina,* but have two- to three-flowered cymules and glabrous leaves. *B. falcata* was separated from *B. venusta* by its proportionately longer leaves.

I have only seen fragments of the types of *B. pulchella, B. falcata* and *B. venusta,* brought from the Sodiro herbarium in Quito to herbarium US by Mrs Mexía in 1934. Part of Sodiro's herbarium was sold to Herbarium Darwinion probably between 1924 and 1926, but the major part of Sodiro's original collections is still in Quito (Acosta-Solís 1969). It was earlier kept in Colegio San Gabriel, but is now placed in Bibliotheca Arvelio Espinoza. Since the material there is packed up and in no order it is unavailable. In Universidad Central, Quito (Q), one of Sodiro's duplicate collections is kept. The sect. *Pardinae* is represented here only by one specimen, labelled *B. grandiceps* (L. Andersson pers. comm.). Since there are no Sodiro collections at all at Universidad Católica in Quito (QCA), the types of *B. pulchella, B. falcata* and *B. venusta* are probably to be found in Bibliotheca Arvelio Espinoza.

From the material studied I do not believe that much importance should be attached to the difference in number of flowers per cymule and

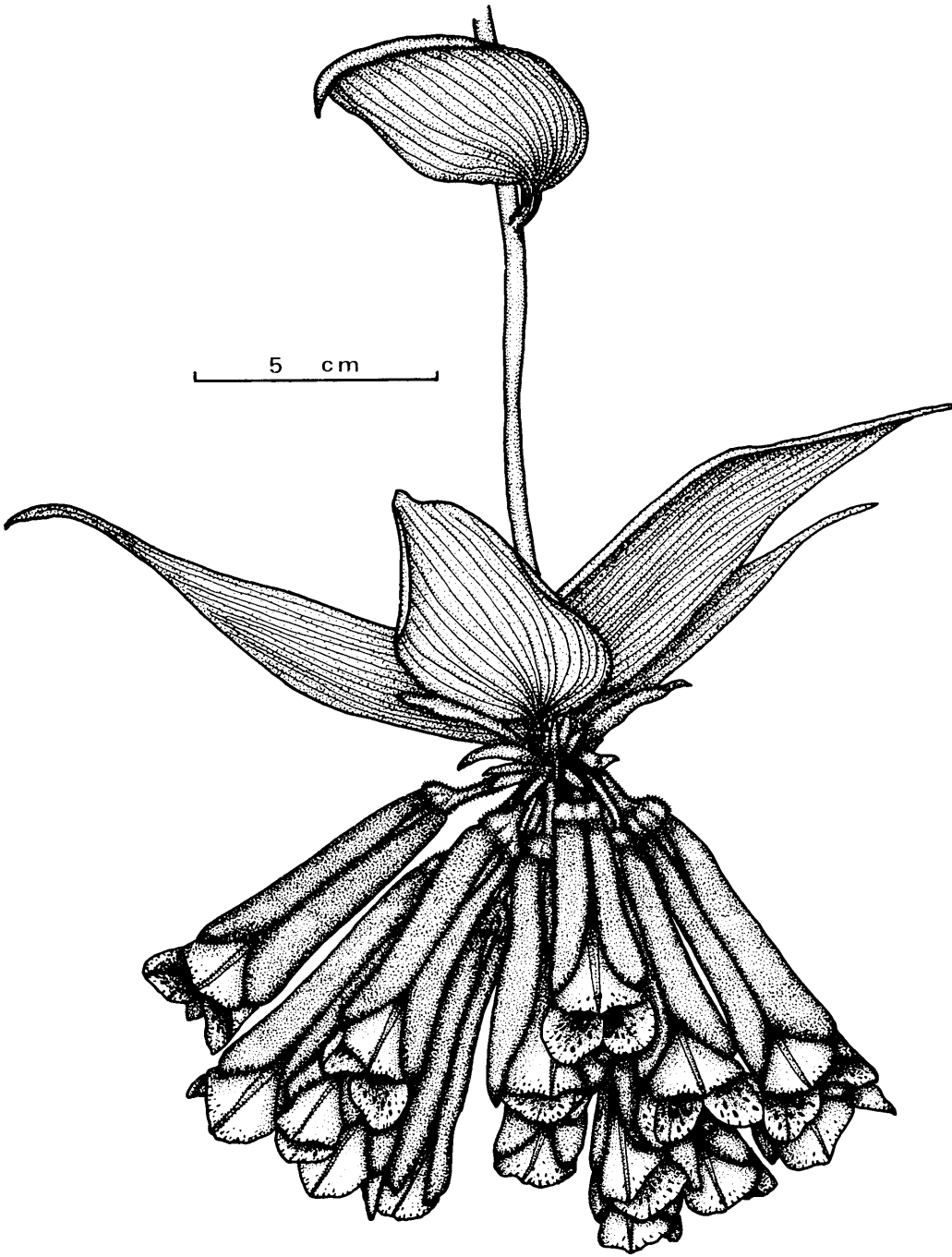
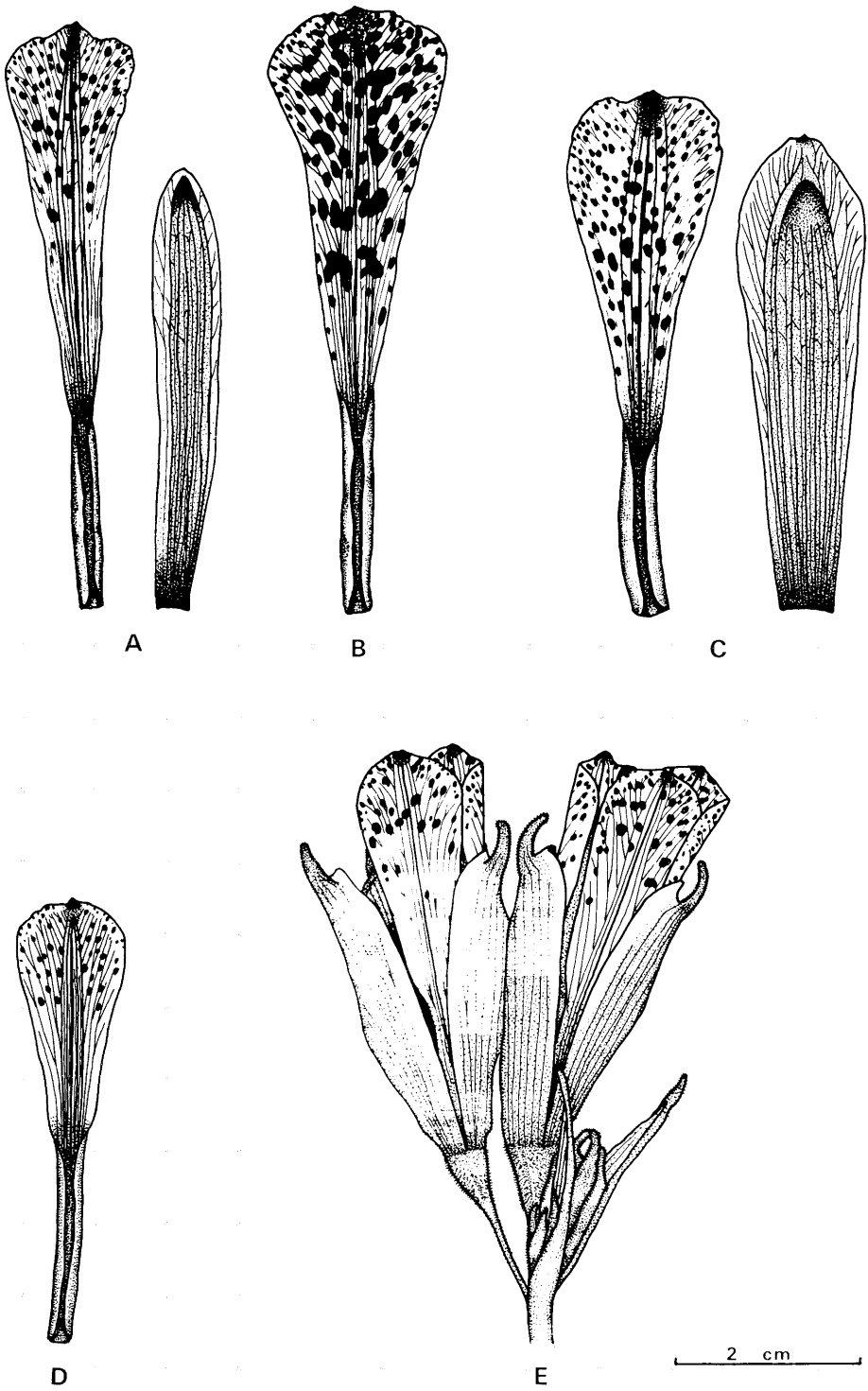


Fig. 4. *Bomarea pardina* Herb. – Habit (Harling & Andersson 12337).

Fig. 5. A–C: *Bomarea pardina*. – A: Petal and sepal (Hall 19). – B: Petal (Sparre 14691). – C: Petal and sepal (Mexía 7254). – D–E: *Bomarea ceratophora*. – D: Petal (Lugo 144). – E: Two-flowered cymule (Asplund 18550).


A
B
C
D
E
2 cm

the varying pubescence of the leaves. The highly variable species *B. pardina* could perhaps be divided into two or more subspecies, but more collections must be available before definite conclusions can be drawn.

2. **Bomarea ceratophora** Neuend. sp. nov. – Fig. 5 D–E

Orig. coll.: Asplund 18550 (S).

Bomareae pardinae Herb. affinis, differt foliis comparate angustioribus, 10–16 cm longis, 2–3 cm latis, subtus in nervis dense pilosis, floribus, si mediam magnitudinem respicias, minoribus, sepalis cornu crasso, curvo, 0.6–0.8 cm longo, paulo infra apicem instructis, petalis spathulatis, 4.5–4.9 cm longis, 1.2–1.4 cm latis, pollinis granis minoribus, 85–95 μm longis.

Stem slender, voluble, 3–4 m long, glabrous. *Leaves* narrowly ovate, 10–16 cm long, 2–3 cm wide, cuspidate at apex, obtuse at base, glabrous above, pilose on the nerves beneath. *Petioles* 1–1.5 cm long. *Bracts* sessile or with a short, untwisted petiole, narrowly ovate, 3–5 cm long, 0.5–1 cm wide, acute to obtuse at apex, slightly puberulous to ± glabrous. *Cymules* 15–50, two- or three-flowered, pedicels slightly pilose to ± glabrous, primary pedicels 2–3 cm long. *Bractlets* narrowly ovate, 1.7–3 cm long, 0.4–0.6 cm wide, slightly puberulous. *Sepals* narrowly obovate to narrowly elliptic, 3.3–4.0 cm long, 0.6–0.9 cm wide, with a 0.6–0.8 cm long, curved horn 2–3 mm below the apex (Fig. 5 E), externally light red and slightly puberulous, internally whitish. *Petals* spathulate, unguiculate (Fig. 5 D–E), 4.5–4.9 cm long, 1.2–1.4 cm wide, white with reddish mid-nerve and dark violet spots on both sides. *Filaments* filiform, as long as the petals or somewhat shorter, glabrous. *Anthers* elliptic, 0.5–0.7 cm long. Pollen grains (75–)85–95 μm long, with auricles, flesh-coloured. *Ovary* semiglobose to turbinate, ± densely pilose. *Style* as long as the petals, glabrous. Stigma branches 3–4 mm long. *Fruit* unknown.

Specimens studied. Ecuador. Tungurahua: Vicinity of Río Pastaza at Río Topo, 1240 m, 13.IX. 1933, Diels 1007 (B) – Colonia México, III. 1969, Lugo 652 (GB) – *Pastaza:* Mera, 1100 m, 21.XI. 1955, Asplund 18550 (S) – Mera, 1100 m, 26.VII. 1968, Lugo 144 (GB).

Bomarea ceratophora is known from the E slopes of the Andes in the central part of Ecuador. It is climbing in mountain rain forest.

B. ceratophora is closely related to *B. pardina,* but separated by the long horns on the sepals and the spathulate petals. Furthermore the flowers are generally smaller and the leaves longer and proportionally narrower.

Acknowledgements. I am indebted to Dr U. Eliasson for much advice and valuable criticism. I am also grateful to Professor G. Harling and Mr L. Andersson for help in various ways, and to Professor Åke Fridh for his help with the Latin diagnosis.

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Contribution to the Taraxacum flora of Nordrhein-Westfalen

Carl Ingemar Sahlin

Sahlin, C. I. 1977 04 15: Contribution to the Taraxacum flora of Nordrhein-Westfalen. *Bot. Notiser 130:* 61–70. Stockholm. ISSN 0006-8195.

The following new species are described: *T. distantijugum* Sahlin, *T. eudontum* Sahlin, *T. oinopopodum* Sahlin, *T. semicurvatum* Öllg., *T. virellum* Hagl. ex Sahlin and *T. fridenii* Sahlin, all belonging to sect. *Taraxacum*.

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During 1969–1975 I have had the opportunity of studying the *Taraxacum* flora of Nordrhein-Westfalen and of making six excursions in the area. About 140 species were found and determined. I estimate this figure to be equivalent to 40–50% of the total number of species in the area.

The most common species are *T. alatum* Lindb. fil., *T. ancistrolobum* Dt., *T. atrovirens* Dt., *T. exsertum* H., v. S. & Z., *T. hamatiforme* Dt., *T. lamprophyllum* M. P. Chr. and *T. pannucium* Dt. *T. alatum* is distributed throughout Europe. Five (excepting *T. exsertum*) have a suboceanic distribution in northern Europe and may be expected in such a list for Nordrhein-Westfalen. The *Taraxacum* flora of suboceanic Europe is well-known from the works of H. Dahlstedt, J. L. van Soest and his collaborators, M. P. Christiansen, and others. The majority of the species were identified without difficulty.

T. exsertum is a good example of a smaller group, which has a Dutch-German distribution, following the big rivers upstream from the Rhine Delta, with a slight extension to the sides. A second group of less common species enters Nordrhein-Westfalen from the southwest, extending to northern or central France. Finally, there is also an eastern element, a group of species especially found in the Sauerland. In these three geographical groups there remains a few undescribed species. I have chosen six of them to be treated here. All belong to the section *Taraxacum* (syn. *Vulgaria* Dt.)

My own collections (abbreviated CIS) are kept in my private herbarium. The voucher specimens of J. L. van Soest (abbreviated v. S.) are deposited in Rijksherbarium at Leiden (L).

T. distantijugum Sahlin sp. nov. – Fig. 1

Holotypus: Germany, Nordrhein-Westfalen, Kreis Meschede: a lay-by 4 km N of Meschede at the road to Lippstadt, 12.V. 1972 Sahlin (S).

Planta sat gracilis, 10–12 cm alta. *Folia* elliptica, gramineo-viridia, 3–4-juga, parce araneosa–sugglabra. Lobi laterales distantes, anguste deltoides–lineares, patentes–leviter retroversi, dorso sat recto et dentibus paucis tenuissimis et singulis robustis praeditis, in margine inferiore non raro denticule unico instructis, in apicem subsensim angustati. Lobus terminalis magnus et sagittatus, saepius in uni vel utroque latere semel aut bis profunde incisus, in apicem apiculatum, plerumque integer. Interlobia longa et angusta, plerumque integra vel interdum dentibus singulis instructa, vulgo piceimarginata–piceimaculata. Petiolus sat angustus, aeque ac dimidia–praecipua pars nervi mediani lucide rubro-violaceus. *Scapi* foliis superantes, ± roseocolorati et parce araneosi. *Involucrum* sat parvum, ad 15 mm altum, sat obscure viride, basi ovata. Squamae exteriores linearis, 1.5–2 mm latae et 8–10 mm longae, patentes, rubrocoloratae, in apicem sat sensim attenuatae, conspique marginatae. *Calathium* aureum. Ligulae marginales extus stria cano-violacea coloratae. Ligulae interiores apicibus non raro purpurascentibus. Antherae polliniferae.



Fig. 1. *Taraxacum distantijugum* Sahlin. Holotypus.

Stigmata sicca sat atra. *Achenium* parvum c. 2.6 mm longum (pyr. incl.), superne spinulosum caeterum tuberculatum et laeve, in pyramidem c. 0.3 mm longam, brevissimam conicam et sat abrupte abiens.

T. distantijugum is easy to recognize. Its leaves are particularly characteristic with their more or less black-violet coloured interlobes, the long and narrow lobes with few large teeth on the distal margin and the large incised terminal lobes. *T. distantijugum* does not seem to have any close relatives.

This species apparently represents the eastern element in the *Taraxacum* flora of Nordrhein-Westfalen. I have not seen the species in the western part of Germany or in France, but in Austria:

Austria. Burgenland: Leithagebirge, Kaisersallé at the road to Kaisersteinbruch, 15.V. 1976 CIS.

T. eudontum Sahlin sp. nov. – Fig. 2

Holotypus: The Netherlands, Zuid-Holland: Hazerswoude, Dorp 7.V. 1973 Sahlin & van Soest (S).

Planta mediocriter alta. *Folia* suberecta, oblongo-



Fig. 2. *Taraxacum eudontum* Sahlin. Holotypus.

lanceolata, sat laete viridia, araneosa, 5–7-loba. Lobi laterales sat approximati, non raro alternatis, superiores basi lata, deltoides, dorso ± convexo vulgo dente unico et robusto lobo ± parallelis praedito, in apicem saepe abrupte abeuntes et basi eiusdem interdum geniculata, apice sat longo, acutiusculo, patente–leviter retroverso et circa medium saepe ± dilatato, in margine inferiore ad basin apicis dente unico et robusto armifero; inferiores angustiores deltoides–falcati, in dorso sat crebre denticulatis–integro. Lobus terminalis sat parvus, hastato-triangularis, integer, supra lobulos basales interdum leviter incisum vel contractum, acutum. Anguli loborum obtusi vel interdum sat orbiculati et plicati. Petiolus angustus, pallidus; nervus medianus apicem versus leviter vinosus. *Scapi* foliis superantes, sub involucri ± floccosi, virescenties. *Involucrum* mediocre, ad 20 mm altum, sat atroviride. Squamae exteriores lanceolatae–late lanceolatae, 3–4 mm latae, 9–12 mm longae, arcuato-patentes, conspique marginatae, mucronatae, supra canescens saepe rubrocoloratae; interiores 2.5–3 mm latae. *Calathium* luteum, subradians. Ligulae marginales subtus stria cano-violacea coloratae. Ligulae interiores apicibus purpurascentibus. Antherae polliniferae. Stigmata sat lutescentia–virescentia. *Achenium* stramineum, c. 3.7 mm longum (pyr. incl.), vix 1 mm latum, superne spinulosum inferne parum rugosum–fere laeve, in pyramidem 0.5 mm longam, late conicam sensim abiens.

The geniculate lobes with the large tooth in the lower margin and the pallid petioles of *T. eudontum* are reminiscent of some of the species related to *T. undulatum* Lindb. fil. & Markl. Thus the species has been confused with *T. sinuatum* Dt. (1925). The petioles of the latter are, however, more or less red, often bright red. Its lobes are mostly deltoid and largely dentate. The terminal lobe of the outer leaves is small and triangular, that of the inner leaves long, broad and ovately triangular with a broad and more or less obtuse apex.

There are two forms of *T. sinuatum*. The second has been described as *T. surrigens* Dt. & Ohlsén (1935), but was later on recognized as *T. sinuatum* by Borgvall (1957). The two forms have achenes of different length. As Dahlstedt has given erroneous cone lengths for both (1925, 1935) I give new measurements (in mm):

Character	*sinuatum*	*surrigens*
Achene excl. cone	3.10–3.50	3.55–3.95
Cone	0.50–0.70	0.45–0.65

T. eudontum thus resembles the true *T. sinuatum*. It has pallid petioles, narrower and longer lobes, and a smaller terminal lobe abruptly

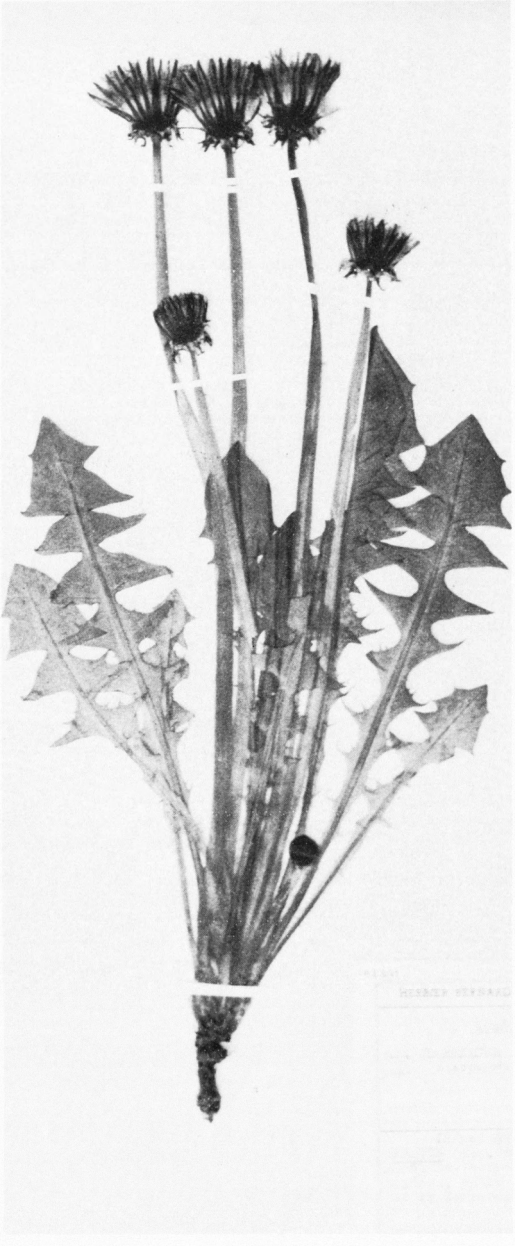


Fig. 3. *Taraxacum oinopopodum* Sahlin. Holotypus.

narrowed into a long and acute apex. Its achenes are a little shorter too. The small terminal lobe distinguishes *T. eudontum* from *T. undulatum* Lindb. fil. & Markl., *T. subaurosulum* M. P. Chr. and others.

T. eudontum is also related to a species group represented by *T. pannucium* Dt. and *T. macrolobum* Dt. It has earlier been identified with *T. lacerilobum* Dt. as there are some similarities to their leaves. But the latter differs considerably by having much narrower outer bracts, only 2 mm wide, and achenes 2.55 + 0.95 = 3.50 mm in length, according to my control of the type specimen in Oxford. The cone of *T. lacerilobum* is thus distinctly longer.

The Netherlands. Gelderland: Linge opposite Asperen, 7.V. 1960 v. S. et al.; 6.V. 1967 CIS, v. S. et al. – Buren, 7.V. 1960 v. S. et al. – Spijk, on Linge, 6.V. 1967 v. S. et al. – Stokkum, 3.V. 1953 v. S. – *Noord-Holland:* along the N. Holland Kanaal, 15.V. 1971 v. S. et al. – *Zuid-Holland:* Ablasserdam, humid pasture along Nieuwe boezen, and E Ameide along the river de Lek, 5.V. 1949 Haglund & v. S. (S). – Gouda, Scheepsvaart Kanaal and Waddriwver, both 12.V. 1958 v. S. – The Hague, Duin Tapijweg, 15.V. 1947 v. S. – Haastrech Stolwijk, 20.IV. 1957 Groot. – Leidschendam, Vliet, 4.V. 1941 v. S. – Poortugaal, on Oude Maas, 29.IV. 1967 v. S. & Zevenbergen; 29.IV. 1973 v. S. – Scheveningen, Pompstationsweg, 2.V. 1949 Haglund & v. S. (S). – Voorburg, the national motor road, 28.IV. 1949 v. S. – Brinkenhorstpolder, 25.IV. 1971 v. S. – Warmond, 6.V. 1953 v. S. – Woerden, at Valk Boumanlaan, 7.V. 1965 v. S. & v. d. Voo. – Zevenhuizen, 20.IV. 1948 v. S. – Zwammerdam, 7.V. 1965 Insje. – *Noord-Brabant:* Hoge en Lage Zwaluwe, lage Zwaluve and Jachthaven, 3.V. 1972 CIS & v. S.

Belgium. Luxemburg Belge: Marche-en-Famenne, 6.V. 1970 CIS.

Germany. Altenkirchen: 2 km W of Friesenhagen at the road to Bettorf, 11.V. 1972 CIS. – *Euskirchen:* Zülpich-Sinzenich and Blankenheim-Alendorf, 9.V. 1973 CIS.

France. Pas-de-Calais: Marquion 25 km ESE of Arras at Canal du Nord, 7.V. 1970 CIS.

T. oinopopodum Sahlin sp. nov. – Fig. 3

Holotypus: France, Essonne: the forest Verrières-le-Buisson between Verrères and Carrefour des Abbés, 12.V. 1973 de Retz (S).

Planta mediocris, 30 cm alta. *Folia* erecta, oblonga–spatulata, prasino-viridia, glabra, lobata. Lobi laterales sat approximati, oppositi vel non raro alternati, triangulares–subdeltoides, patentes, superiores integri et inferiores subulato-dentati, acuti. Lobus terminalus sat magnus, ovato-triangularis et hastatus, sat acutus, uno vel utrique latere profunde incisus vel uno–duobus dentibus praeditus. Anguli loborum obtusi. Petiolus sat angustus, aeque ac inferiore pars nervi mediani rubro-violaceis. *Scapi* foliis breviter superantes, glabri, virides. *Involucrum* sat parvum, 10–15 mm altum, olivaceo-viride, basi ovata. Squamae exteriores lineari-lanceolatae, 2–3 mm latae, c. 15 mm longae, recurvatae, supra griseo-virides, in apicem sensim

attenuatae, inconspique marginatae. *Calathium* aureum. Ligulae marginales extus stria cano-violacea ornatae. Ligulae interiores apicibus purpurascentibus. Antherae polliniferae. Stigmata sicca obscura. *Achenium* stramineum, 3.1–3.4 mm longum (pyr. incl.), ad medium latissimum superne breve spinulosum ceterum usque ad medium tuberculatum inferne laeve, in pyramidem 0.4–0.6 mm longam subcylindricam sat abrupte abiens.

At a first glance *T. oinopopodum* seems to belong to the same group as *T. hamatum* Raunk. and its relatives. It has, however, rather characteristic leaves and outer involucral bracts. At the moment no close relatives are known and *T. oinopopodum* stands isolated in the section.

The type collection is rather comprehensive. The description is based on this material. The species is also found in Nordrhein-Westfalen. Its three localities indicate a centre of distribution in southwestern or central France.

Germany. Euskirchen: Zülpich, between Geich und Zülpich, 9.V. 1973 CIS. – *Grevenbroich:* Oekoven, Römerstrasse 5.V. 1975 CIS.

T. semicurvatum H. Öllgaard sp. nov. – Fig. 4

Holotypus: Denmark, Jutland, TBU-distr. 25: Skibet, roadside c. 200 m W of the church, 26.V. 1970 Öllgaard (C).

Planta mediocris. *Folia* crispula, obscure viridia, interlobiis piceo-coloratis, lobis interdum ± piceo-maculatis, petiolis alatis–alatissimis, leviter roseis, nervis medianis leviter sordide-roseis. Folia exteriora linguata, araneosa, obtusa–subobtusa, c. 3 binilobi; lobis 10–13 mm latis, hamatis, subobtusis, integris vel dentibus singulis brevibus instructis; interlobiis 0–8 mm longis, alatis, leviter piceatis; integris vel uno dente instructis; lobo terminalis mediocri, marginibus superioribus valde convexis, saepe uno dente lato et brevi instructis, marginibus inferioribus rectis–paulum concavis. Folia intermedia late lanceolata, manifesto araneosa, c. 5 binilobi; lobis 13–15 mm latis, quoque lobo aut hamato, ad apicem sensim angustato, margine superiore partis basalis saepe dente praeteriente instructo, aut patente, parte basali lata, integra vel parce subulata, parte exteriore ± late lineari, ± porrecta, marginibus inferioribus omnium loborum integris (vel interdum levissime subulatis); interlobiis alatis, 5–15 mm longis (inter lobum terminalem et summos lobos interdum 0), ± piceatis, irregulariter ± dentosis; lobo terminali mediocri, late cordato–ovato, obtuso–subobtuso, marginibus superioribus convexis, saepe irregulariter incisis, dentatis vel sine dentibus, apicibus sectionum basalium saepe rotundatis, marginibus inferioribus rectis vel paullo concavis. Folia interiora intermediorum simila; lobis terminalibus majoribus; lobis magis dentatis, magis piceato-maculatis. *Scapi* foliis aequantes vel superantes, ± cupreo-colorati, araneosi, maxime in superiore parte. *Involucrum* 13–15 mm longum, c. 9 mm latum, obscure viride, levissime pruinosum, squamis exterioribus 2.5–4 mm latis, ad 16 mm longis, ± retroversis, supra griseo-viridibus, subtus obscure viridibus, apicibus leviter corniculatis, rubescentibus, non marginatis vel interdum inconspicue marginatis. *Calathium* convexum, c. 50 mm diam., sat obscure luteum, ligulis marginalisbus subtus stria griseo fusca ornatis, apicibus florum interiorum ± rubris. Antherae polline carentes vel (raro) parce polliniferae. Stylus et stigmata virescentes. *Achenium* griseo-fuscum, 3.8–4.0 mm longum (pyr. incl.), superne crasse spinulosum, saepe squamuloso-spinulosum, ceterum dense ± manifesto verrucosum, pyramide subconica, c. 0.5 mm longa, sat abrupte abiente.

I am indebted to H. Öllgaard for this description and the following remarks: *T. semicurvatum* is a characteristic species, which is easy to recognize by its crispate, tar-coloured leaves with fairly round terminal lobes, the slightly irregular lobes and the faintly rose petioles. As a rule no pollen is formed. However, in one head of a cultivated plant pollen was formed. Since all of more than 50 spontaneous plants investigated lacked pollen, the presence of pollen seems to be an exception. At present *T. semicurvatum* is known only from Denmark and Nordrhein-Westfalen:

Germany. Lübecke: Blasheim 3 km W of Lübecke, 9.V. 1969 CIS.

In my opinion *T. semicurvatum* is close to *T. scotiniforme* Dt. It differs by lacking pollen and by having shorter and more obtuse terminal lobes and paler petioles.

T. virellum Haglund ex Sahlin sp. nov. – Fig. 5

T. virellum Haglund ex Hylander: Förteckn. skand. växter I, ed. 3, 1941 p. 136, nomen.

Holotypus: Västergötland, Sweden: Borås, Daltorpsskolan (map 7 C 0 f), 6.VI. 1946 Sandberg (S). Cotypus fructifer: Borås, Ekenberg (7 C 0 f), 6.VI. 1937 Sandberg (S).

Planta mediocris, 15–40 cm alta. *Folia* erecta, sat oblonga, sat obscura et prasino-viridia, canescentia, 2- ad 5-lobata, araneoso-pilosa et sat firmula. Lobi laterales sat breves et lati deltoides–triangulares, superioribus in dorso convexulo et integris, inferioribus aeque ac lobi foliorum interiorum in dorso subrecto et subulato-dentatis, in apicem patentem et acutum. Lobus terminalis nunc sat magnus nunc minor, triangularis et hastatus, in apicem acutum et saepe mucronatum, in foliis exterioribus saepius in uno vel in utroque latere profunde incisus et supra

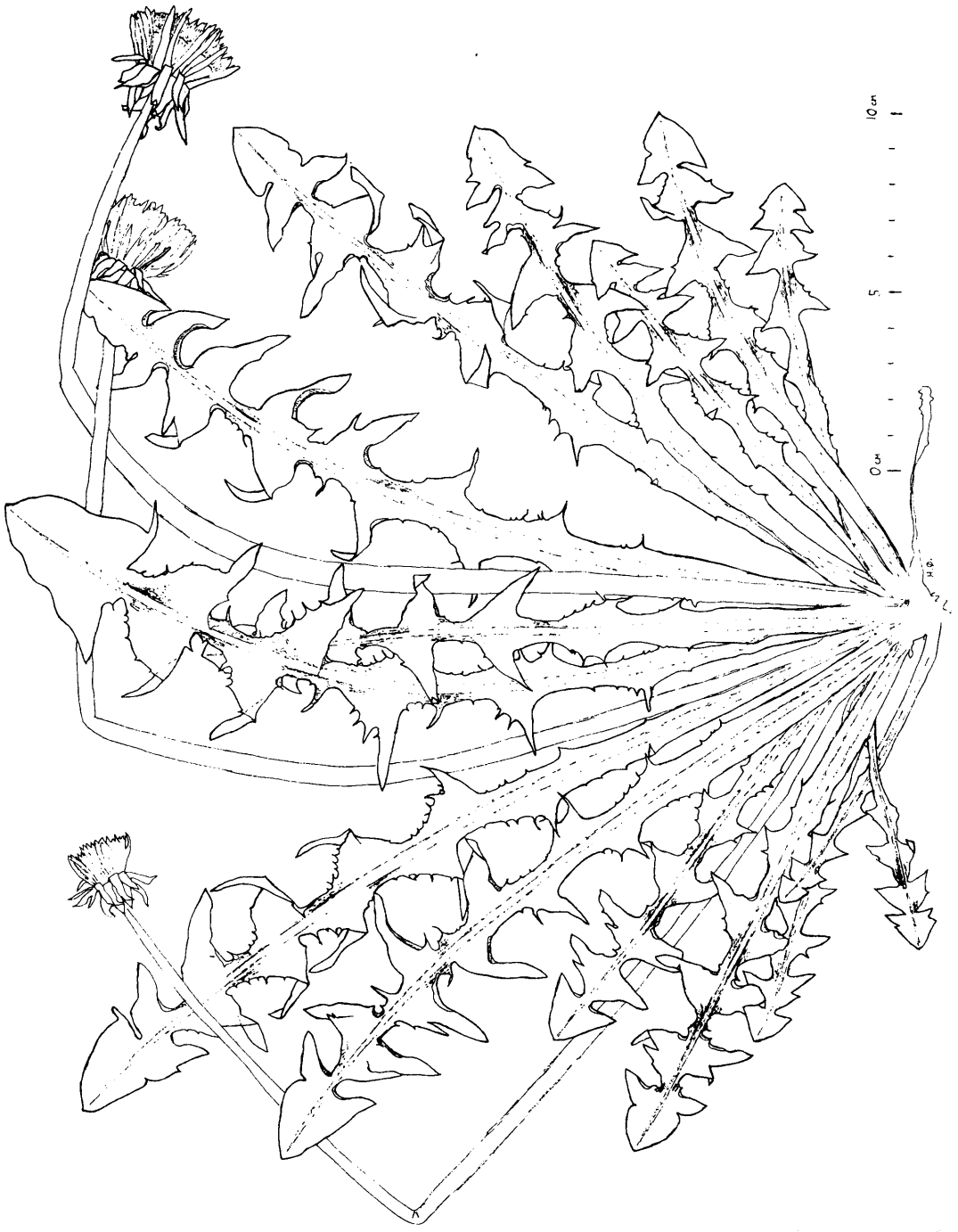


Fig. 4. *Taraxacum semicurvatum* Öllg. Holotypus. Öllgaard pinxit.

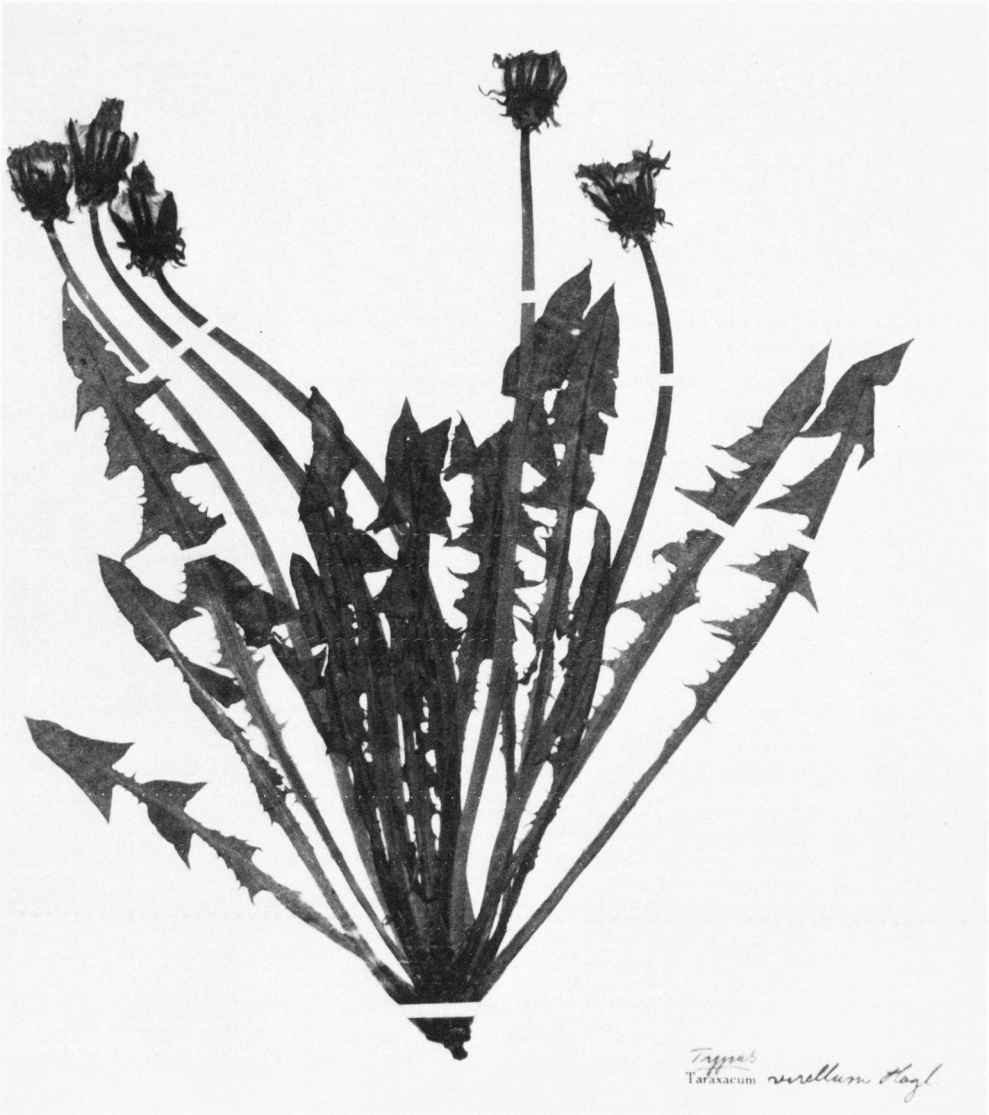


Fig. 5. *Taraxacum virellum* Haglund ex Sahlin. Holotypus.

incisuram margine rotundatus, in foliis interioribus supra lobulus basales semel et saepius profunde incisus. Interlobia in foliis interioribus sat angusta et subintegra vel dentibus singulis–pauci instructa, in foliis exterioribus nullis praedita. Petiolus subalatus, rubroviolaceus. *Scapi* foliis aequilongi vel ea breviter superantes, sub involucri ± araneosi, virides. *Involucrum* mediocre–sat parvum, ad 21 mm longum, olivaceo-viride, basi ovata. Squamae exteriores lineares, c. 2 mm latae et 14 mm longae, retroversae et apicibus saepe ± porrigentibus, supra laetiores, in apicem longum et sensim attenuatae, inconspique–haud marginatae. *Calathium* laete luteum ad suggil-vum, sat plenum. Ligulae marginales extus stria fusco-violacea ornatae, omnes dentibus croceis praediteae. Antherae polliniferae. Stigmata sicca sat obscura vel raro sublutea. *Achenium* hepaticum, 3.6–4.0 mm longum (pyr. incl.) et 0.8 mm latum, supra medium latissimum et sat breve et acute spinulosum, inferne ± laeve, in pyramidem anguste conicam 0.7–0.9 mm longam, sat abrupte abiens.



Fig. 6. *Taraxacum fridenii* Sahlin. Holotypus.

The leaves of *T. virellum* are very similar to those of *T. copidophyllum* Dt., but the involucres of the two taxa are quite different and they are not closely related. On the contrary, *T. virellum* seems to be related to *T. sterneri* Hagl., which grows in the same area on the European mainland. They differ *inter alia* by the hairiness of the leaves, the length of the outer bracts and the width of the petioles. *T. virellum* is also somewhat similar to, e.g., *T. fennorodiae* Hagl., but the latter and its relatives have shorter cusps on their achenes.

The localities of the two species *T. virellum* and *T. sterneri* are grouped in a zone around the Moselle. I have earlier described seven new species from this region (1975). My impression is that all have their centre of distribution in France and thus have entered Germany from SW. Representative specimens are:

Germany. Jülich, at the main road to Aachen, 6.V. 1970 CIS. – *Ingbert:* St. Ingbert-West, 10.V. 1970 CIS. – *Rhein-Hunsrück-Kreis:* Boppard on the Rhine, 3.V. 1971 CIS.

Sweden, Västergötland: Borås, Druvefors in a meadow on the river Viskan (7 C 0 f), 28.V. 1941, Hulta at the house of Good Templars (7 C 0 g), 6.VI. 1937, the fish ponds at Rya (7 C 1 f), 16.V. 1936, all Sandberg (S).

T. fridenii Sahlin sp. nov. – Fig. 6

Holotypus: Sweden, Västergötland: Trollhättan, a ravine 400 m N of Karlsberg (map 8 B 4 i), 27.V. 1960 Fridén (S).

Planta mediocris, c. 15–25 cm alta. *Folia* adscendentes, elliptica–ovalae, sat gramineo-viridia, canescentia, sat firmula. Folia extima et exteriora sat paucilobata, extima sat glabra ceteri araneosi; lobi laterales approximati, oppositi, triangulares, breves et basi sat lata, dorso recto et dentibus paucis praedito, in apicem brevem, patentem et subacutum; lobus terminalis mediocris, sat ovatus, hastatus, acutiusculus–subobtusus, supra lobulus basales interdum dentibus unis vel duobus et robustis praedito; anguli loborum plicati. Folia interiora integra et sinuosodentata vel paucilobata, araneosa; lobi laterales distantes, deltoides breves et basi sat lata, dorso raro dentatis interdum lobulato-inciso, in apicem patentem–recurvum; lobus terminalis saepe indistincte determinatus et grosse inciso, dentatus; interlobia et anguli loborum atrimarginata. Petiolus late alatus, pallidus. *Scapi* foliis breviter superantes, subaraneosi ad glabrescentes. *Involucrum* mediocre, c. 15 mm altum, olivaceo-viride. Squamae exteriores lineari-lanceolatae, 2.5 mm latae, c. 11 mm longae, patentes–recurvatae, superne laete griseo-virides et ± rubro-violaceae, subtus piceae, in apicem abrupte contractum et saepe ciliatum, anguste sed conspique marginatae. *Calathium* luteum–aureum, sat densum. Ligulae marginales sat breves, extus stria atroviolacea et marginibus rubro-purpureis–laete rubro-purpurea ornatae, omnes dentibus purpureis praeditae. Antherae polliniferae. Stigmata virescentia. *Achenium* fusco-olivaceum, 3.6–3.9 mm longum (pyr. incl.), supra medium latissimum, superne squamuloso-spinulosum, medio breve spinulosum et inferne ± valde tuberculatum, pyramis 0.65–0.85 mm longa, conico-cylindrica, interdum spinis binis et brevibus praedita, sat sensim abiens.

T. fridenii is characterized by its broad, pallid petioles, large, ovate or triangular terminal lobes and flowers with red stripes and red teeth. It is close to *T. insigne* Ekm., but the latter has a small terminal lobe of more triangular shape and its side lobes are often armed with a robust tooth. The flowers of *T. insigne* lack the red stripes and red teeth. The large terminal lobes and the broad petioles of *T. fridenii* are also reminiscent of *T. alatum* Lindb. fil. but *T. fridenii* differs markedly by its red-coloured flowers.

The species is named after L. Fridén Rev., Trollhättan, authority on the flora of Västergötland. Representative specimens are only found at three localities in the northern part of Trollhättan, Sweden. But the town has close connexions with the Continent by the canal navigation to the industries around Vänern. Thus a Dutch-German origin of this species might be assumed. It has also been preliminarily identified both in the Netherlands and Nordrhein-Westfalen, but reconsiderations of the specimens calls the determinations into question. These are my reasons for including its description in this paper, hoping that it will be recognized in Nordrhein-Westfalen.

Sweden. Västergötland (all map 8 B 4 i): Trollhättan, the ravine 400 m N of Karlsberg 26.V. 1954, 2.VI. 1954, 4.VI. 1957, 17.V. 1960, 2.VI. 1960 and 14.VI. 1963 Fridén (S); 24.V. 1968 Lundevall, CIS, v. S. and Såltin (H, L). – Trollhättan, the ravine W of Nybergskulla 2.VI. 1962, 14.VI. 1963 Fridén (S). – Trollhättan, the ravine S of Hult 27.V. 1954 Fridén (S).

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Chromosome numbers and taxonomy in Cryptocoryne (Araceae)

Niels Jacobsen

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Chromosome numbers for 34 species of *Cryptocoryne* are reported. They represent a heteroploid series with the secondary basic numbers 11, 14, 15, 17, 18. Triploids have been found in several species, and they, as well as some of the tetraploids and hexaploids, have reduced pollen fertility but are able to reproduce vegetatively. It is possible to make a subdivision of the genus based on chromosome number, morphology and geography. The basic evolutionary event in the genus was the establishment in different areas of taxa with different chromosome numbers. Upon this basis, adaptive radiation between different river systems has given rise to a great number of species, many of which are narrow endemics. The spathes of most of the species discussed are illustrated in colour. One new combination, viz., *C. sarawacensis* (Rataj) Jacobsen stat. nov. is made.

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Cryptocoryne is a natural but polymorphic genus. It occurs in India, Sri Lanka, Bangladesh, the Indo-Chinese peninsula, Java, Sumatra, Borneo, New Guinea, and the Philippine Islands. The species are aquatic or amphibic.

More than 60 species are known, and most of them are endemics, a feature rare in water plants. Many more species are likely to be discovered in the future. Since Engler's monograph in 1920, three major papers have appeared on the taxonomy of *Cryptocoryne,* viz., Petch (1928), de Wit (1971) and Rataj (1975 a); recently the present author (N. Jacobsen 1976) has dealt with the species of Sri Lanka. Chromosome numbers have previously been reported for about 20 species (Tjio 1948, Pancho 1971, Marchant 1972, Legro 1967, Legro in de Wit 1971, and Sarkar et al. 1976).

The present paper is a link in a project dealing with taxonomy and evolutionary patterns in *Cryptocoryne*.

Material and methods

The material was cultivated in the hothouses of the Botanical Garden of the University of Copenhagen. Many of the plants were originally imported commercially by aquarium dealers, and for these plants the exact origin is not known. Singapore is one of the main export centres for aquatic plants which are brought in from all over South and South East Asia. This has led to confusion as to the origin and natural distribution of the species. Importers' information should be taken with some caution.

Cytological preparations were made from root tips according to the method described by P. Jacobsen (1957) with smaller modifications. Excised roots were pretreated in 0.1% colchicine for three hours in the dark at 20°C and then fixed in lactic acid/alcohol at 0°C. For species with high chromosome numbers a saturated solution of alphamonobromonaphthalene was used for pretreatment. The meristematic regions were squashed in cold 45 % acetic acid, stained with pyronine for 20–30 minutes, and mounted in Canada balsam. Staining was improved if the fixations were stored for at least three days at −15°C. Fixations have been kept at this temperature for up to 18 months without any deleterious effects.

To estimate the male fertility, pollen was stained with cotton blue, and the percentage of well-developed, stained, non-vacuolized grains was calculated. Two hundred grains were counted twice and the mean was calculated. Strid (1970) describes the sources of error and the reliability of the method.

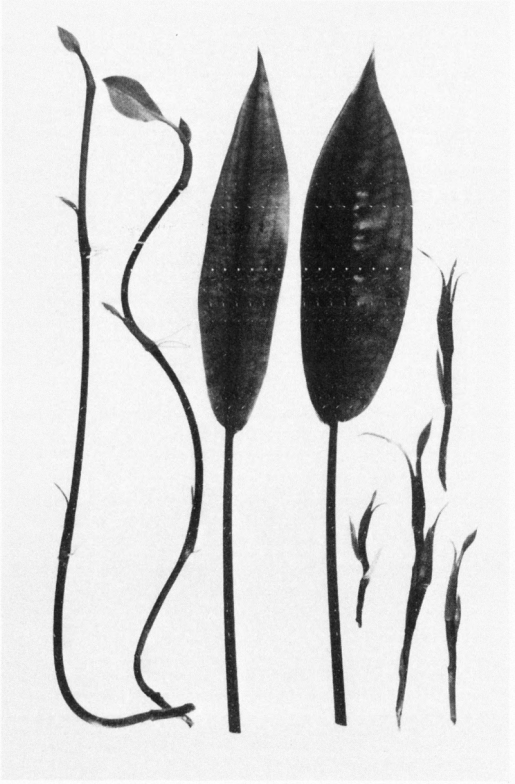


Fig. 1. *Cryptocoryne ciliata*. Leaves and runners of a plant with 2n = 22 (left) and 2n = 33 (right).

Voucher specimens are placed in the Botanical Museum, University of Copenhagen (C) under the number cited, and living plants are cultivated in the Botanical Garden.

Chromosome numbers previously reported

Comments on the counts are given under the species, but a general comment is given here.

Voucher specimens of Legro's (1967, 1971) counts do not exist, but I am inclined to regard most of them as correct. Two species, *C. grabowskii* Engler and *C. tortilis* De Wit, are reported to have 2n = 34 (Legro 1971). I have not had material of the two species.

Unfortunately, Marchant's (1972) voucher specimens are deposited very incompletely in the herbarium at Kew. It has only been possible to locate 7 herbarium specimens (of 14) which may originate from the plants studied by Marchant, but none of them is marked in any way. At Kew Gardens it has been possible to locate and obtain 3 living plants which may be identical with some of Marchant's material. "Kew Entry Numbers" (K.E.N.) do not always refer to single plants but are batch numbers that are applied to all plants received from the same source or shipment. After flowering and determination, the plants are given additional, unambiguous numbers (cf. Marchant 1972 p. 396 and 398, where several plants have the same number). Apparently only few of the *Cryptocoryne* at Kew Gardens had been verified when Marchant undertook his work. An attempt to match Marchant's plants with material from the herbarium and garden at Kew gave the following results: *C. affinis* K.E.N. 450(=430?)-63: One fertile herbarium specimen. – *C. affinis* K.E.N. 332-54: No material. – *C. beckettii* K.E.N. 518-49: Two fertile herbarium specimens, and one living plant. – *C. ciliata* K.E.N. 493-59: No material. – *C. ciliata* K.E.N. 460-67: One herbarium specimen. – *C. griffithii* K.E.N. 513-63: No material. – *C. longispatha* K.E.N. 723-68: One fertile herbarium specimen which has been determined by Rataj as *C. tonkinensis*. – *C. lutea* K.E.N. 358-57: No material. – *C. "nevillii"* K.E.N. 332-54: No material. – *C. purpurea* K.E.N. 86-68: Three sterile herbarium specimens with pickled spathes labelled: *affinis*, *cordata*, and *purpurea*. They belong to *C. affinis*, *C. griffithii*, and *C. purpurea*, respectively. – *C. thwaitesii* K.E.N. 102-67: The living plant at Kew Gardens has 2n = c. 102 and probably represents *C. blassii*. – *C.* cf. *wendtii* K.E.N. 309-67: One herbarium specimen which is *C. walkeri*. – *C. "willisii"* K.E.N. 533-48 and *C. "nevillii"* K.E.N. 533-48: Two living plants, *C. undulata* and *C. willisii* Reitz, respectively, were found at Kew Gardens. It could be that Marchant's count was made on the former. – *C.* sp. K.E.N. 203-53: No material. – *C.* sp. No. 2 K.E.N. 358-57: Two fertile herbarium specimens belonging to *C. beckettii* and one which was sterile.

Additional living plants at Kew Gardens: *C. bullosa* K.E.N. 450-63: It is a specimen of *C. wendtii* and cannot be Marchant's 530 (=550?)-63 *C. affinis*. – *C. undulata* K.E.N. 513-63: It cannot be Marchant's *C. griffithii* K.E.N. 513-63.

Rataj (1975 a) mentions several chromosome numbers but does not state the source of his information.

C. ciliata (Roxburgh) Schott – 2n = 22, 33

Material. 2n = 22: P 1958/1013 Bogor; NJ 2845 cult. – 2n = 33: 1671/6 cult.; NJ 2794 cult.; NJ 2895 cult.

Tjio (1948) reported 2n = 28 for this species. His work on tropical plants was done during a stay in Copenhagen. At that time a plant labelled *C. ciliata* was cultivated in the Botanical Garden. This plant flowered in 1956 and proved to be *C. beckettii*, and the count may refer to this species. It was not until 1958 that the Botanical Garden received true specimens of *C. ciliata*.

Legro (1971) reports 2n = 32, which could be a wrong count of 2n = 33. Marchant (1972) and Sarkar et al. (1976) reported 2n = 22.

The pollen of the plants with 2n = 33 is very defective (Table 1).

Rataj (1975 a) described two varieties of *C. ciliata,* viz., v. *ciliata* with 2n = 22 and v. *latifolia* Rataj with 2n = 32. My results fully agree with v. *ciliata* having 2n = 22 but indicate that v. *latifolia* has 2n = 33, and must be regarded as a triploid. The v. *ciliata* has rather narrow leaf-blades and long terranean, rooting stolons (up to 50 cm), which are quite firmly attached to the parent plant. The v. *latifolia* has short, erect, non-rooting stolons (up to 15 cm, branching at the internodes) which easily break off (Fig. 1). I can find no difference between the spathes of the two cytotypes.

Contrary to most of the other species *C. ciliata* has a very wide distribution. It is characterized by its terranean runners and by its habitat (close to the mouth of rivers). No doubt it has a greater colonizing ability than the other species, which are often more specialized ecologically. Nothing is known as to the distribution of the two cytotypes.

C. spiralis (Retzius) Fischer ex Wydler – 2n = 66, 88

Material. 2n = 66: Cook 327/73 Ernukalam, Kerala State; Cook 328/73 Ernukalam, Kerala State – 2n = 88: 1671/5 Calcutta; NJ 2970 cult.

Legro (1971) reported 2n = 42 (and 84), and Sarkar et al. (1976) reported 2n = 90.

The chromosome numbers indicate that the species may be tetra-, hexa-, and octoploid.

The numbers 2n = 66 and 88 indicate that *C. spiralis* may be placed together with *C. ciliata.* There are, however, differences in chromosome size and in the morphology of the plant (Fig. 2).

C. D. K. Cook, Zürich, made two collections of this species at Ernucalam, India. These plants are different from material in other parts of the range. Cook 327/73 has rather broad leaf blades with a rather long petiole, and the spathe has a very long and narrow limb. Cook 328/73 has almost linear leaves, reddish petioles, a dark green colour, and the spathe is short and compact. I can, however, find only quantitative differences between the forms, and de Wit (1971) and Rataj (1975 a) are probably right when they include *C. tortilis* and *C. huegelii,* respectively, in *C. spiralis.*

C. parva De Wit – 2n = 28

Material. 1671/16 Halloluwa; NJ 23-14 Halloluwa; NJ 22-4 Hiriwadunna.

Legro (1971) reported the same number.

C. willisii Reitz – 2n = 28

C. nevillii auct. non Trim. ex Hook. f.

Material. 1671/3 (= P 1914/114) cult.; P 1953/435 cult.; P 1966/353 cult.; NJ 2766 cult.; NJ 2897.

Legro (1971) reported the same number under *C. "nevillii".*

No material of the typical form with the yellow collar is known from nature. However, I collected some plants at Halloluwa with a dark purple collar, which no doubt belong to this taxon.

C. lucens De Wit – 2n = 28

Material. NJ 21-1 Peradeniya; NJ 21-2 Halloluwa; NJ 23-4 Halloluwa; NJ 24-3 Peradeniya; NJ 24-4 Peradeniya.

Legro (1971) reported the same number.

A specimen collected at Halloluwa, NJ 23-5, may belong to this species, but has a green limb with small purple warts and a purple collar. The leaves are larger than normally found in *C. lucens.* It is also possible that it is a hybrid.

C. beckettii Thwaites ex Trimen – 2n = 28

Material. 1671/4 cult.; NJ 2832 cult.; NJ 2902 cult.; Jayasuriya 2246 Rhuna National Park; NJ 22-2 Udamulle E of Kegalla; NJ 23-19 Halloluwa.

Legro (1971) and Marchant (1972) reported the same number. Tjio's (1948) report of 2n = 28 for *C. ciliata* no doubt refers to *C. beckettii.*

C. petchii Alston – 2n = 42

Material. 1671/12 cult.; P 1963/631 cult.; P 1965/336 cult.; P 1969/322 cult.; NJ 2769 cult.; NJ 2833 cult.; NJ 2847 cult.; NJ 2898 cult.

Legro (1971) reported the same number.

In my material there are several different variants, which can at times be hard to separate

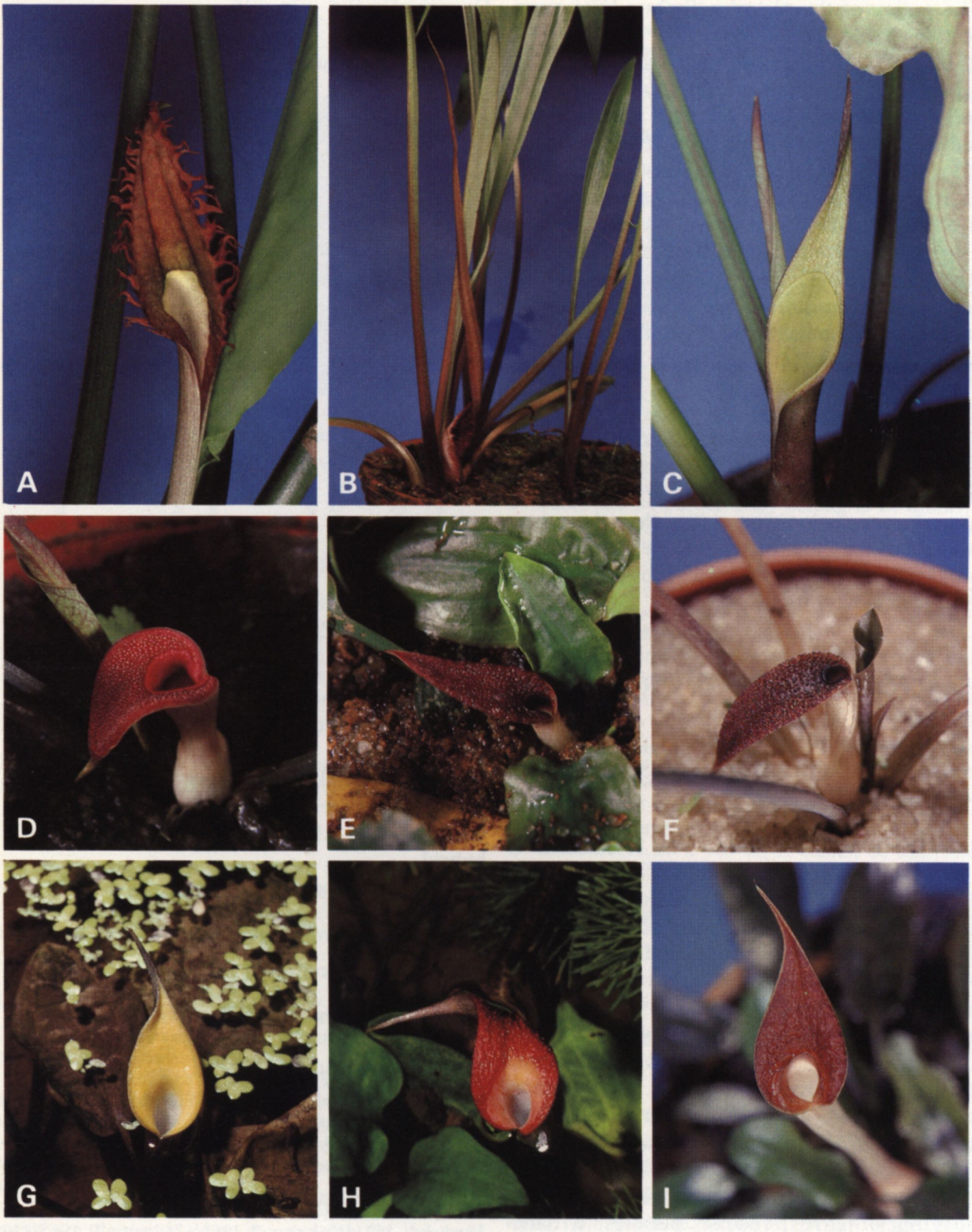


Fig. 2. A: *Cryptocoryne ciliata* (NJ 2845, 2n = 22). – B: *C. spiralis* (Cook 327/73, 2n = 66). – C: *C. pontederiifolia* (NJ 2963, 2n = 30). – D: *C. griffithii* (NJ 2805, 2n = 34). – E: *C. minima* (NJ 2990, 2n = 34). – F: *C. zewaldiae* (NJ 2912, 2n = 34). – G: *C. blassii* (1671/9, 2n = 102). – H: *C. purpurea* (P 1912/92, 2n = 34). – I: *C. jacobsenii* (NJ 2864, 2n = 34). – A, B × 0.5, I × 0.8, C–H × 1.0.

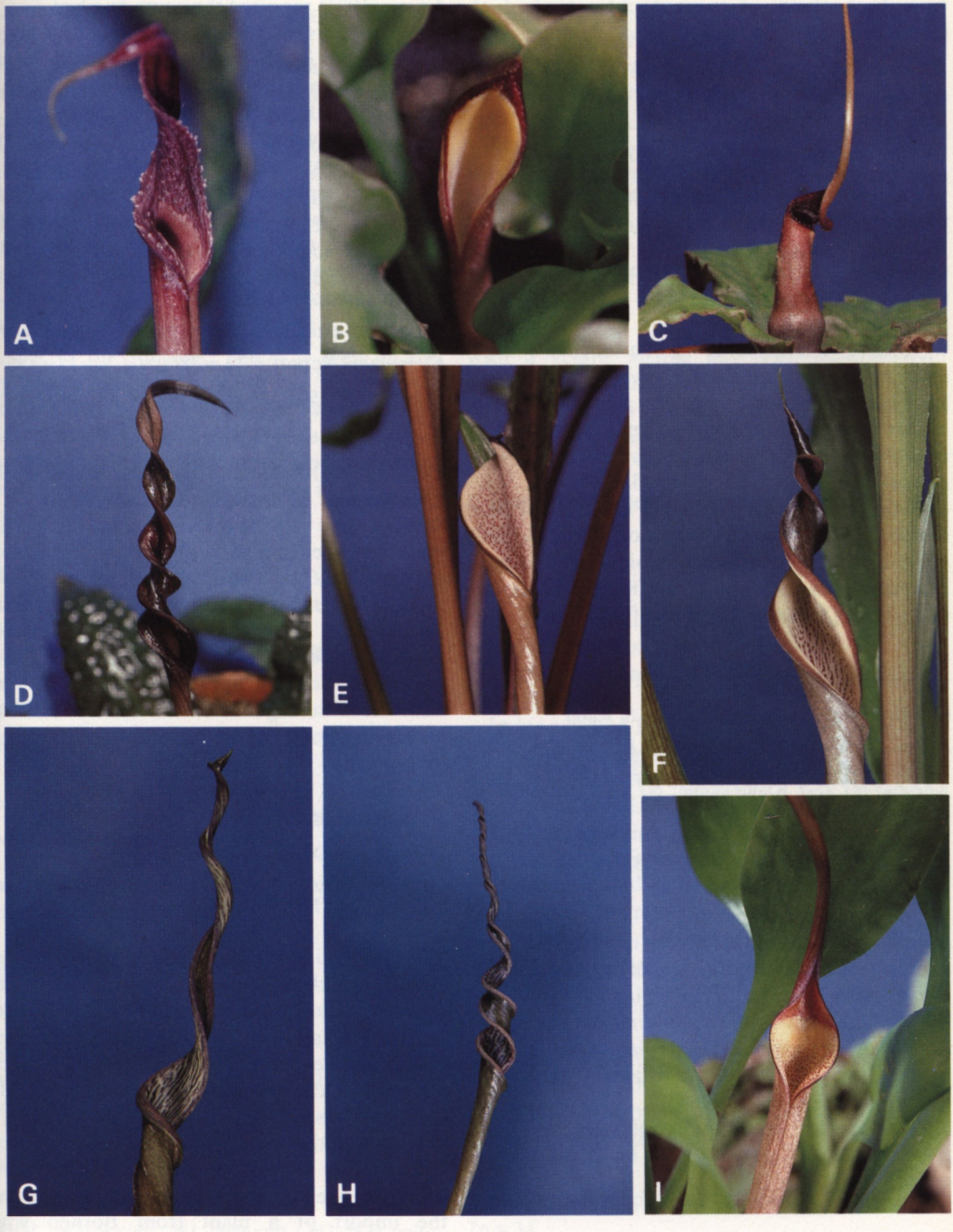


Fig. 3. A: *Cryptocoryne usteriana* (NJ 2875, 2n = 34). – B: *C. versteegii* (1671/8, 2n = 34). – C: *C. sarawacensis* (NJ 2954, 2n = 34). – D: *C. affinis* (1671/15, 2n = 34). – E: *C. costata* (NJ 2915, 2n = 36). – F: *C. albida* (1671/14, 2n = 36). – G: *C. balansae* (NJ 2893, 2n = 36). – H: *C. bertelihansenii* (Beusekom et al. 4486, 2n = 36). – I: *C. lingua* (NJ 2955, 2n = 36). – C–D × 0.8, E–I × 1.0, A–B × 1.6.

from *C. beckettii;* it is no doubt a triploid of *C. beckettii*. The pollen is highly defective.

C. wendtii De Wit – 2n = 28, 42

Material. 2n = 28: 1671/11 cult.; P 1961/342 cult.; P 1964/281 cult.; NJ 2474 cult.; NJ 2779 cult.; NJ 2867 cult.; NJ 2869 cult.; NJ 2924 cult.; NJ 2933 cult. – 2n = 42: 1671/11 a, Mi Oya; NJ 2781 cult.; NJ 2849 cult.; NJ 2855 cult.; NJ 2914 cult.

C. wendtii is one of the most polymorphic species in the genus. There are at least 8 different variants in cultivation in Copenhagen, with leaves classified as "green (normal), large red, small red, crisped red, brown, brown-green, long green, and small green."

Due to vegetative reproduction polymorphism is probably stable to some degree. The 2n = 42 plants have highly defective pollen.

Rataj (1975 a) established 5 varieties of this species. The species is polymorphic, but considering that it contains triploids, which only reproduce vegetatively, I find Rataj's basis for establishing these varieties insufficient.

C. undulata Wendt – 2n = 28, 42

C. willisii Engl. ex Baum; *C. axelrodii* Rataj

Material. 2n = 28: 1671/13 cult.; P 1961/338 cult.; NJ 2813 cult.; NJ 2825 cult.; NJ 22-1 Udamulle E of Kegalla; NJ 22-7 Kandekenne; NJ 23-2 Halloluwa – 2n = 42: NJ 3000 cult.

Legro (1971) reported 2n = 28 for *C. willisii* Engl. ex Baum.

One deviating specimen, NJ 3000, proved to have 2n = 42, and the discovery of a triploid form makes the situation quite parallel to that found in e.g. *C. wendtii*. The triploid plant differs from the diploid ones of *C. undulata,* by the much larger, silvery variegated, greyish green leaves, by the limb of the spathe which is brownish, and by the yellowish collar.

This species is in morphological respects rather close to *C. wendtii,* but lacks the purple collar.

C. lutea Alston – 2n = 28

Material. P 1963/629 cult.; P 1974/21 Halloluwa; NJ 2767 cult.; NJ 2817 cult.; NJ 2836 cult.; NJ 2853 cult.; NJ 23-1 Halloluwa; NJ 23-3 Halloluwa; NJ 23-6 Halloluwa; NJ 23-13 Halloluwa; NJ 23-20 Halloluwa.

Legro (1971) reported the same number.

C. lutea is rather polymorphic both in the leaves and in the colour and shape of the spathe; the latter can be pure yellow or densely sprinkled with purple on the outside.

C. legroi which has 2n = 42 (Legro 1971) is probably best considered a triploid form of *C. lutea,* quite parallel to *C. beckettii–C. petchii,* and to *C. wendtii* coll. Another unidentified plant which resembles *C. lutea* (NJ 2809 cult., see N. Jacobsen 1976) also has 2n = 42 and highly defective pollen.

C. walkeri Schott – 2n = 28

Material. P 1965/337 cult.; NJ 2913 cult.; NJ 2931 cult.

Legro (1971) reported the same number. The specimen at K marked K.E.N. 309-67 *C.* cf. *wendtii,* may be from the same plant as Marchant counted under that name, however, it is in fact a specimen of *C. walkeri.*

A feature most useful in the determination of this species is the broad, conspicuous collar zone, which does not rise from the surface of the rest of the limb. The spathe changes in shape and colour during anthesis as it is first stiff and green(ish), and later becomes leathery and yellow(ish).

C. pontederiifolia Schott – 2n = 30

C. sulphurea De Wit

Material. Bogner 1093 cult. (type of *C. sulphurea*); NJ 2963 cult.; NJ 2999 cult.

The species is characterized by the rather short spathe, which is brownish on the outside, and greenish yellow on the inside. The limb is rugose and has a large collar. The leaves are green but sometimes have a shining reticulate appearance which can resemble *C. sarawacensis*. The leaf margin is entire.

Uncertainties about the identity of this species have come from the presumed absence of inflorescences on the type specimen, and from the import of a plant from Borneo which resembled *C. pontederiifolia* but had a purple, caudate spathe. The Borneo plant was illustrated by van der Vlugt (1969) and by de Wit (1971) who referred it to *C. pontederiifolia*. Rataj (1975 a) described it as *C. pontederiifolia* ssp.

sarawacensis, and in the present paper it is given rank of species.

V. Sadilek, Brno, (pers. comm.) is of the opinion that *C. sulphurea* is identical with *C. pontederiifolia*. A renewed study of the holotype of *C. pontederiifolia* has revealed one crimpled spathe between the cataphylls. Although this spathe is in a bad condition I find it identical with the newly imported plant with a yellow spathe and the large collar described as *C. sulphurea*, and can thus confirm Sadilek's assumption.

W. Meijer informed me that he has collected the species on Sumatra, where it grew in the lower parts of the rivers, in the fresh water tidal zone. Part of these collections were brought to Java for cultivation, and it is possible that it is descendants of these Sumatra plants that have recently been shipped to Europe as aquarium plants.

C. griffithii Schott – 2n = 34

Material. NJ 2805 cult.; NJ 2861 cult. (WAG).

Fruiting has been observed in NJ 2805.

C. minima Ridley – 2n = 34

Material. NJ 2816 cult.; NJ 2990 cult.

C. zewaldiae De Wit – 2n = 34

Material. NJ 2912 cult.

This species is closely related to *C. minima*, but has much larger leaves.

C. siamensis Gagnepain – 2n = 68

Material. NJ 2946 cult. (WAG, C).

This species is closely related to *C. blassii*. The plant counted is the one illustrated by van Bruggen (1975).

C. blassii De Wit – 2n = 102

C. evae Rataj

Material. 1671/9 cult.; NJ 2846 cult.; NJ 2873 cult.; NJ 2807 cult.

The specimens counted were somewhat different in appearance, both with respect to leaves and spathes. The pollen is highly defective.

Rataj (1975 a) lists *C. blassii* as a synonym of *C. siamensis* v. *kerrii* (Gagnep.) Rataj. I consider, however, *C. evae* as a synonym of *C. blassii*. The latter one was described from emersed plants, which are smaller than the submersed ones (described as *C. evae*). I find no characteristics in *C. evae* which are not to be found in *C. blassii*.

C. blassii may be considered as a sterile hexaploid due to the chromosome number (2n = 6x = 102) and the highly defective pollen. *C. siamensis* is probably the tetraploid (2n = 4x = 68), but as yet no fertile diploid (2n = 34) with a yellow spathe has been encountered. There are great taxonomic difficulties within the group of species: *C. blassii, C. siamensis, C. cordata, C. grandis, C. kerrii* etc.

C. purpurea Ridley – 2n = 34

C. hejnyi Rataj

Material. NJ 3004 cult.; P 1912/92 cult.

The pollen is highly defective, and a hybrid origin may be possible.

Legro (1972) and Marchant (1971) reported the same number.

In his revision Rataj (1975 a) lists *C. purpurea* as a synonym for *C. cordata* Griffith. Furthermore, he describes *C. hejnyi* as a new species, a taxon which is identical with Tab. 7719 in Botanical Magazine. Apparently he is not aware of the fact that it is in the type description of *C. purpurea* Ridley states that Tab. 7719 is *C. purpurea* and not *C. griffithii*.

C. jacobsenii De Wit – 2n = 34

Material. NJ 2864 cult. (holotype in WAG).

This species differs from *C. purpurea* and *C. griffithii* by narrow, obtuse leaves, by the red, rough limb, and by the indistinct collar which is sprinkled with red.

C. sarawacensis (Rataj) Jacobsen stat. nov. – 2n = 34

Basionym: C. pontederiifolia Schott ssp. *sarawacensis* Rataj, Revision of the genus Cryptocoryne Fischer, Studie ČSAV č. 3, p. 62 (1975). – Holotype: Cult. Sumperk, 18.9. 1974 Rataj (PR 335235).

Material. NJ 2954 cult.

This species is characterized by the short tube, the caudate, purple, rugose limb which has a prominent blackish purple collar. The leaves are irregularly dentate with a slightly undulate margin, and they have a characteristic glossy, green colour, with irregular purple stripes.

Mr Sadilek informs me that material which he received from van der Vlugt was passed on to Rataj and was subsequently used as type material. My material came from de Wit, and no doubt also stems from van der Vlugt.

C. usteriana Engler – 2n = 34

Material. 1671/17 cult.; NJ 2875 cult.

Pancho (1971) reported 2n = 28. It is unlikely that this species has both the numbers recorded. Pancho (1971) also reported 2n = 28 for *C. pygmaea* Merrill. These counts are rather puzzling, as 2n = 28 has only been found in plants from Sri Lanka; however it is by no means inconceivable.

C. usteriana is perhaps the largest species in the genus as the leaves can reach a length of more than 150 cm.

C. affinis N. E. Brown ex Hook. f. – 2n = 34

Material. 1671/15 cult.; NJ 2792 cult.

Legro (1971) and Marchant (1972) reported the same number.

C. versteegii Engler – 2n = 34

Material. 1671/8 New Guinea.

Legro (1967, 1971) reported the same number.

C. costata Gagnepain – 2n = 36

Material. NJ 2915 cult.

This species is closely related to *C. albida*. *C. costata* has brown variegated leaves, and a rather short limb with circular spots, whereas *C. albida* has green leaves, and a rather long limb which has long spots.

C. albida Parker – 2n = 36

C. hansenii Hu; *C. korthausae* Rataj; *C. retrospiralis* ssp. *albida* (Parker) Rataj.

Material. 1671/14 Ranawang (type of *C. hansenii*); NJ 2952 cult.

In transferring *C. albida* Parker to a subspecies of *C. retrospiralis*, Rataj does not cite the correct holotype which is Parker 2735 (K), but instead cites Parker 3089 (B) which is another specimen collected three years later. Furthermore, Rataj established *C. korthausae* Rataj which is quite identical with *C. albida* (conf. N. Jacobsen 1974, de Wit 1971, 1975).

C. balansae Gagnepain – 2n = 36

Material. NJ 2893 cult.

C. balansae is closely related to *C. crispatula*.

C. bertelihansenii Rataj – 2n = 36

Material. Beusekom et al. 4077 Chaiyaphum (isotype); Beusekom et al. 4486 Chaiyaphum (isosyntype).

The two collections are somewhat different in appearance. The holotype has narrow, almost smooth, and green leaves, while the syntype has broader, undulate leaves which are brown with darker brown lines. The vegetative characters are constant in cultivation. However, colour slides at L of Beusekom et al. 4077 together with Fig. 3 H indicate that these two specimens may be forms of *C. crispatula* incl. *balansae*.

C. cf. **tonkinensis** Gagnepain – 2n = 36

Material. P 1969/306 cult.

Marchant (1971) gives 2n = 36 for *C. longispatha*, a plant quite identical with mine.

Rataj (1975 a) gave an account of the uncertainty regarding Gagnepain's description of *C. tonkinensis*, and I am, at present, not sure that the above-mentioned material really is *C. tonkinensis*.

C. cf. **crispatula** Engler – 2n = 54

Material. NJ 2984 cult.

This plant has not flowered so far, but the denticulations on the very narrow leaves are very characteristic for *C. crispatula*.

It is probable that the present plant is a triploid.

C. retrospiralis (Roxburgh) Kunth – 2n = 72

Excl. *C. retrospiralis* ssp. *albida* (Parker) Rataj

Material. NJ 2971 cult.; NJ 2950 Hahabalishwar, Maharashtia, W India.

Legro (1971) reported 2n = 28 which is most puzzling.

There is some uncertainty as to the interpretation of the species, because it was believed to have been found on the Indo-Chinese peninsula. This is apparently not true, and the species occurring there (e.g. *balansae, albida, crispatula, tonkinensis*), among other things, have a different chromosome number. *C. retrospiralis* has cylindrical leaves in the winter-form, a feature not recorded elsewhere, and it also has a very strongly developed system of negatively geotropic roots.

C. bogneri Rataj – 2n = 36

Material. NJ 2917 cult.; NJ 2934 cult.

C. alba De Wit – 2n = 36

Material. Hermsen s.n. Dehiwala (from type collection).

This species is closely related to *C. thwaitesii,* and may prove to be a colour variant.

C. thwaitesii Schott – 2n = 36

Material. NJ 14-1 Kottawa.

Legro (1971) reported 2n = 56. Marchant (1972), however, reported 2n = 42. At Kew Gardens there exists living plants labelled K.E.N. 102-67 *C. "thwaitesii".* This specimen has 2n = c. 102 and is probably *C. blassii,* although they have not flowered and therefore cannot be identified.

C. lingua Beccari ex Engler – 2n = 36

Material. NJ 2856 cult.; NJ 2928 cult.; NJ 2955 cult.

Legro (1967, 1971) reported 2n = 36. The chromosomes of this species are rather small.

Rataj (1975 a) suggested a close connection between *C. lingua* and *C. versteegii* on account of the thick, fleshy, green leaves, a feature which I would not regard as of great taxonomic importance, considering the differences in the spathe, in the distribution, and in chromosome number.

Fruiting specimens of *C. lingua* have been observed.

Male fertility

The values obtained are shown in Table 1. As expected, the pollen of the triploids is defective. *C. blassii* (hexaploid) also proved to have completely defective pollen. Several of the diploids have a somewhat reduced fertility, but it is very odd that e.g. *C. purpurea* has a fertility of 0% and *C. affinis* only has a fertility of 19%. A hybrid origin of *C. purpurea* is possible (*griffithii* × diploid *siamensis*-type?).

Hybrids

Several plants from e.g. Sri Lanka are deviating in appearance, and a hybrid origin is possible. The occurrence of triploids does complicate the situation, and allotriploids can be expected to have a deviating appearance.

Artificial hybrids have been reported by Legro (1963): *beckettii* × *lutea, beckettii* × *"nevillii"* (= *willisii*), and *wendtii* × *lutea,* but no further results have been published. Rataj (1975 a) reports artificial hybrids between, e.g., *beckettii* × *petchii* (3x), and *lutea* × *legroi* (3x), which does seem improbable.

Chromosome morphology

Although difficult to measure exactly, there is an obvious correlation between the different chromosome groups and the size of the chromosomes (Figs. 4–5). Unfortunately the same pretreatment could not be used for all the species, and in the illustrations given here, the chromosomes of *C. spiralis* and *C. retrospiralis* are not quite comparable with the others. Secondly, it was sometimes necessary to use late prophases in order to show the exact number. The different chromosome groups also proved to stain differently, especially *C. pontederiifolia,* and *C. bogneri* proved very difficult to handle, because of their diffuse heterochromatic ends.

The chromosomes of the genus are metacentric to submetacentric and the chromosomes showed heterochromatic ends, H-segments, most pronounced in the 22 and 28 groups.

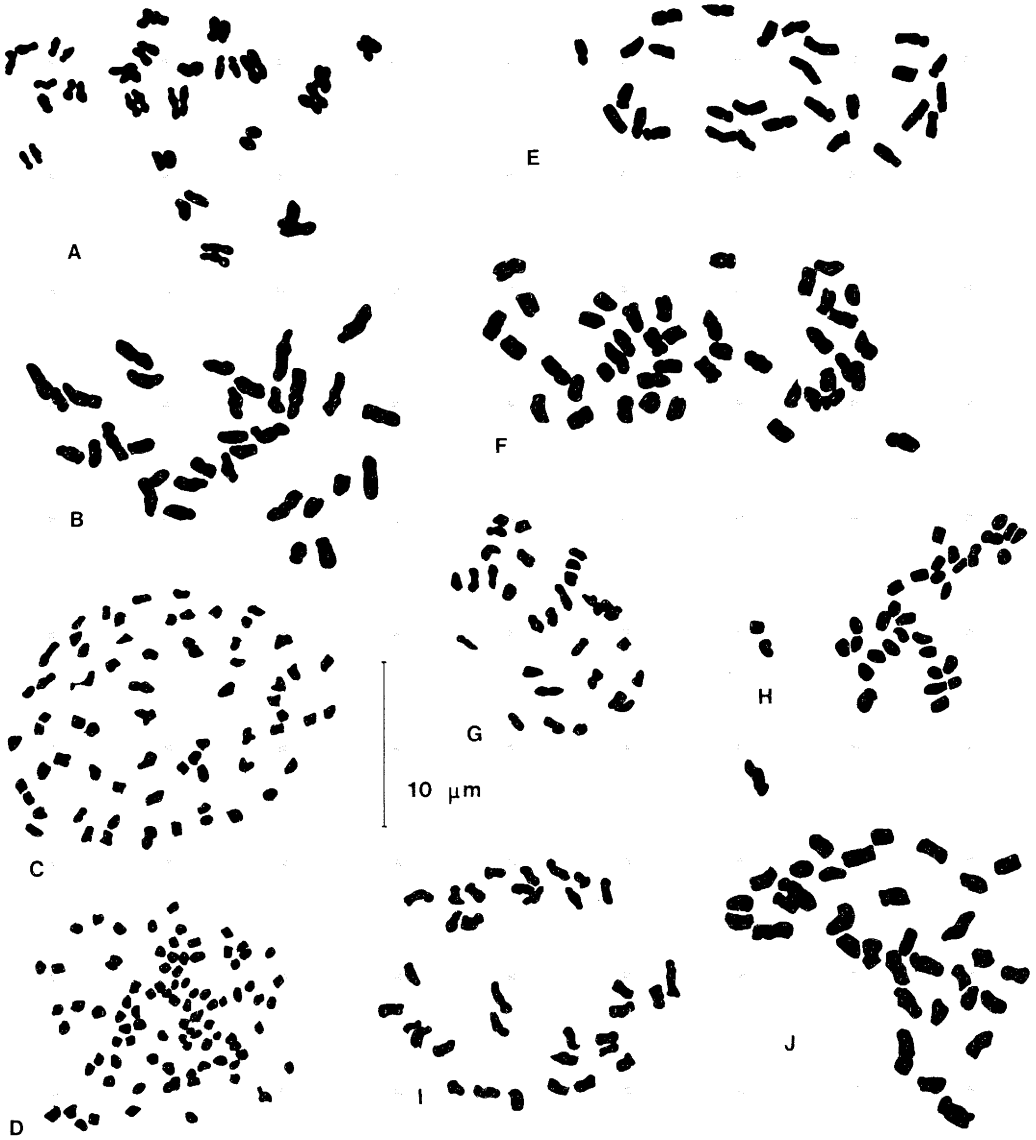


Fig. 4. Root tip mitoses. – A; *Cryptocoryne ciliata* 2n = 22 (P 1958/1013). – B: *C. ciliata* 2n = 33 (1671/6). – C: *C. spiralis* 2n = 66 (Cook 327/73). – D: *C. spiralis* 2n = 88 (1671/5). – E: *C. undulata* 2n = 28 (P 1961/542). – F: *C. wendtii* 2n = 42 (1671/11 a). – G: *C. pontederiifolia* 2n = 30 (NJ 2963). – H: *C. versteegii* 2n = 34 (1671/8). – I: *C. usteriana* 2n = 34 (1671/17). – J: *C. sarawacensis* 2n = 34 (NJ 2954).

In *C. spiralis* 3–4 small bodies occurred which may be satellites. However, sometimes they were not apparently associated with the other chromosomes (artifact?).

There are no karyological implications of the evolutionary direction of the aneuploid series.

Discussion

Subdivision of the genus Cryptocoryne

It is possible to make a subdivision of the genus *Cryptocoryne* on the basis of chromosome numbers, morphology and geography. The pres-

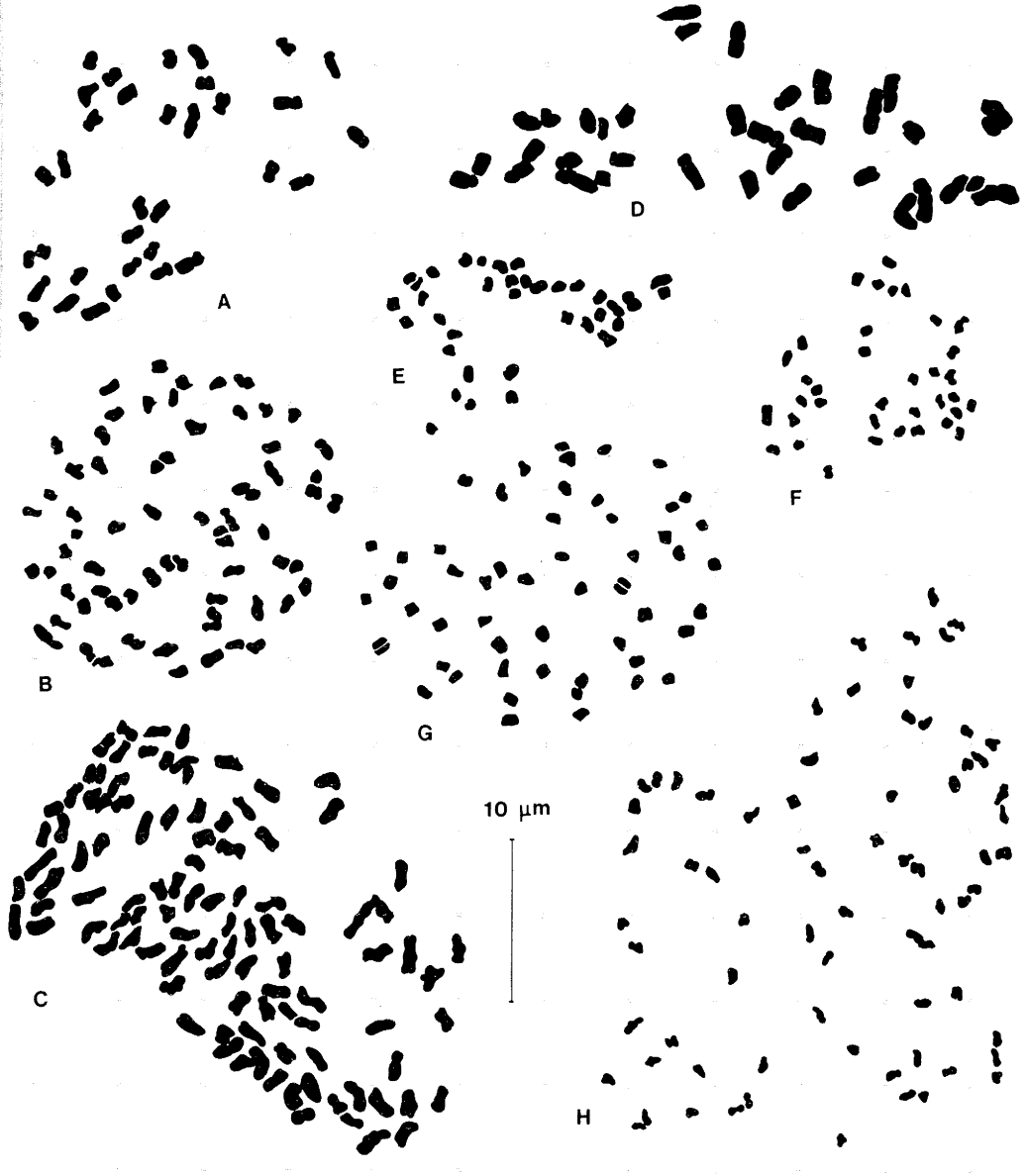


Fig. 5. Root tip mitoses. – A: *Cryptocoryne purpurea* 2n = 34 (P 1912/92). – B: *C. siamensis* 2n = 68 (NJ 2946). – C: *C. blassii* 2n = 102 (1671/9). – D: *C. thwaitesii* 2n = 36 (NJ 14-1). – E: *C. lingua* 2n = 36 (NJ 2856). – F: *C. albida* 2n = 36 (1671/14). – G: *C.* cf. *crispatula* 2n = 54 (NJ 2984). – H: *C. retrospiralis* 2n = 72 (NJ 2950).

ent material can be divided into eight groups, some of which have different basic numbers (Table 2). Generally there seems to be rather little morphological similarity between the different chromosome groups (Figs. 2–3) and they occupy different geographical areas (Fig. 6).

(1) *Cryptocoryne ciliata* – 2n = 22, 33. S Asia, widely distributed. The species is characterized by the large size, the thick green leaves and by the ciliate margin of the limb of the spathe (Fig. 2 A).

Table 1. Pollen stainability in different species of *Cryptocoryne*. Figures indicate number of specimens with the degree of ploidy given within parentheses.

Species	% stainable pollen									
	0	10	20	30	40	50	60	70	80	90	100
ciliata	1(3x)	1(3x)	1(3x)	.	.	.	.	1(2x)	.	1(2x)	
spiralis	.	.	.	.	.	.	.	.	2(8x)	2(6x)	
parva	.	.	.	.	.	.	.	.	.	1(2x)	
willisii	.	.	.	.	.	.	2(2x)	.	.	.	
lucens	.	.	.	1(2x)	.	.	1(2x)	.	.	.	
beckettii	.	.	.	.	.	1(2x)	.	2(2x)	1(2x)	1(2x)	
petchii	3(3x)	.	.	.	.	.	.	.	.	.	
wendtii	.	.	2(3x)	.	.	.	.	.	2(2x)	5(2x)	
undulata	2(3x)	.	.	.	.	.	2(2x)	.	.	.	
lutea	1(3x)	.	.	1(2x)	.	.	.	.	.	3(2x)	
walkeri	.	.	.	1(2x)	.	.	.	.	.	.	
pontederiifolia	.	.	.	.	.	.	.	.	.	1(2x)	
griffithii	.	.	.	.	.	.	.	.	.	1(2x)	
minima	.	.	.	.	.	.	.	.	1(2x)	.	
zewaldiae	.	.	.	.	.	.	.	.	.	1(2x)	
blassii	2(6x)	.	.	.	.	.	.	.	.	.	
purpurea	2(2x)	.	.	.	.	.	.	.	.	.	
sarawacensis	.	.	.	.	.	.	.	.	.	1(2x)	
usteriana	.	.	.	1(2x)	.	.	.	.	.	.	
affinis	.	1(2x)	.	.	.	.	.	.	.	.	
versteegii	.	.	.	.	.	.	.	.	1(2x)	.	
costata	.	.	.	.	.	.	.	.	.	1(2x)	
albida	.	.	.	.	.	.	.	.	1(2x)	.	
balansae	.	.	.	.	.	.	.	.	.	1(2x)	
bertelihansenii	.	.	.	.	.	.	1(2x)	.	.	.	
bogneri	.	.	.	.	.	.	.	.	.	1(2x)	
thwaitesii	.	.	.	.	.	.	1(2x)	.	.	.	
lingua	.	.	.	.	.	.	.	.	.	1(2x)	

(2) *Cryptocoryne spiralis* – 2n = 66, 88. India. The species is characterized by the narrow leaves, and the spathe which has a short tube and a long, twisted limb (Fig. 2 B).

(3) *Cryptocoryne beckettii* group – 2n = 28, 42. The species with 2n = 28 and 42 all come from Sri Lanka. They are morphologically uniform and clearly different from species coming from other parts of Asia. The leaves are lanceolate with a more or less rounded base. The spathe has a rather long tube and the shape of the limb is rather uniform in the different species. For the nomenclature and illustrations of the group, see N. Jacobsen (1976). The delimitation of the species is somewhat obscured by the different chromosome numbers within the same and closely related species. This group is more amphibious than most of the others, and is much better adapted to the terrestrial form of life.

(4) *Cryptocoryne pontederiifolia* – 2n = 30. Sumatra. The species is characterized by the short spathe with the long, yellow, rugose limb and the large collar (Fig. 2 C). On normally developed specimens there are numerous cataphylls.

(5) *Cryptocoryne griffithii* group and other species with an obscure relationship – 2n = 34, 68, 102. This group consists mainly of species with cordate leaves coming from the Indo-Chinese peninsula, Borneo and New Guinea. It is obviously heterogeneous, and a closer study may show that there are different karyotypes with the diploid number 2n = 34. On morphological grounds *C. minima*, *C. zewaldiae*, and *C. griffithii* are closely related (Fig. 2 E, F, D). This group of three species is probably related to *C. siamensis*, *C. blassii*, *C. jacobsenii*?, and *C. purpurea*? (Fig. 2 G, I, H), while *C. usteriana* (Fig. 3 A), *C. affinis* (Fig. 3 D), *C. sarawacensis* (Fig. 3 C), and *C. versteegii* (Fig. 3 B) stand rather isolated.

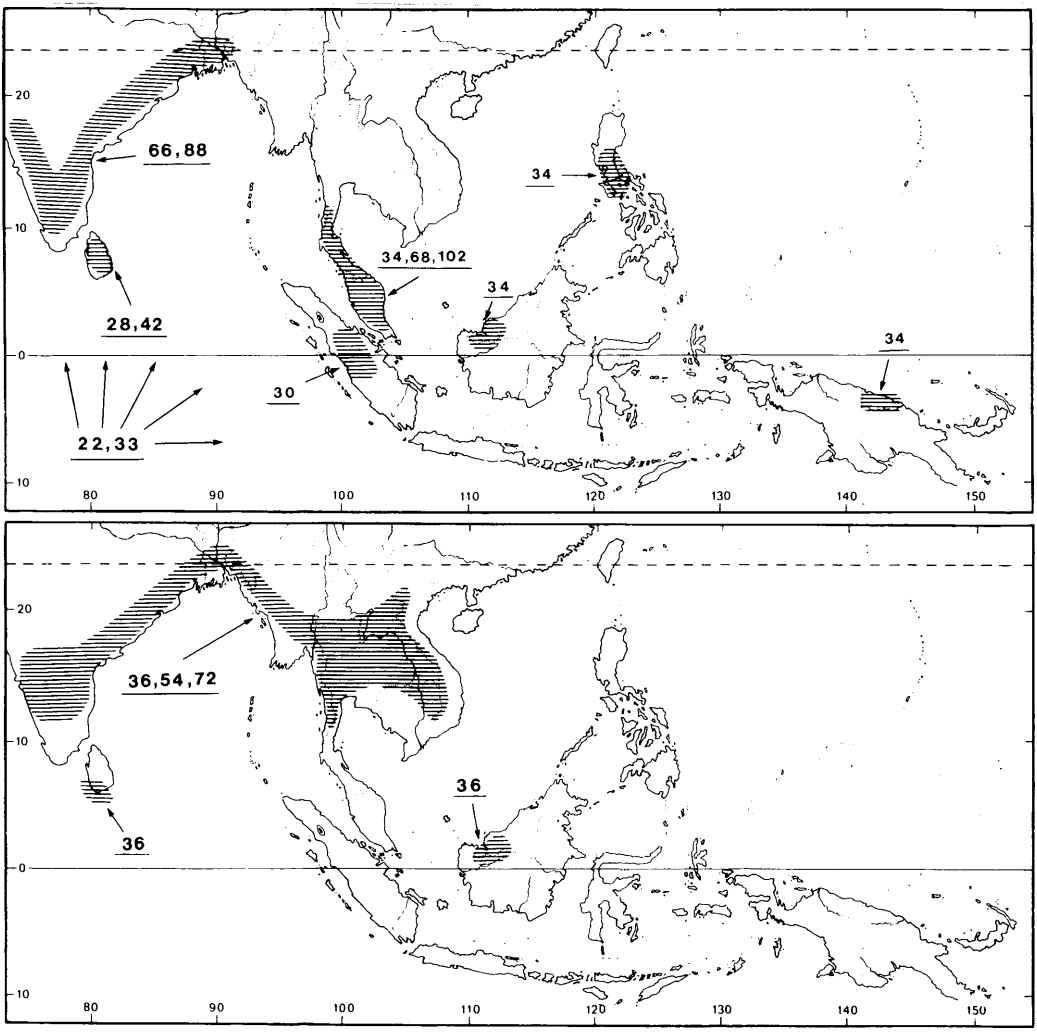


Fig. 6. The distribution of the different chromosome numbers.

(6) *Cryptocoryne albida* group – 2n = 36, 54, 72. Indo-Chinese peninsula to India. The group is characterized by the long, narrow leaves which are smooth, undulate or bullate. The limb of the spathe is more or less spirally twisted, and a collar is missing (Fig. 3 E–H). De Wit (1971) advocated a rather wide species concept, while Rataj (1975 a) was in favour of a narrow one. However, I believe that the species delimitation will prove to be different from both of the two interpretations.

(7) *Cryptocoryne thwaitesii* group – 2n = 36. Sri Lanka. Of these three broad-leaved species *C. alba* and *C. thwaitesii* are closely related, while *C. bogneri* is somewhat different with the short limb with the rough margin. The group is karyologically and morphologically very different from the *C. albida* group.

(8) *Cryptocoryne lingua* – 2n = 36. Borneo. The species is characterized by the spathulate, green leaves, and by the spathe with the caudate limb (Fig. 3 I). The rhizome is stout with numerous thick, white roots.

Table 2. The species of *Cryptocoryne* arranged according to their chromosome number, compared with the system proposed by Rataj (1975 a).

Species	Classification in Rataj 1975 a
2n = 22, 33	
ciliata	Subg. 2, sp. 5
2n = 66, 88	
spiralis	Subg. 1, sect. 1, sp. 1
2n = 28, 42	
parva	Subg. 4, sect. 9, spp. 25–27
willisii	
lucens	
beckettii	Subg. 4, sect. 10, spp. 28–31
petchii	
wendtii	
undulata	
lutea	
walkeri	
2n = 30	
pontederiifolia	Subg. 4, sect. 6, sp. 20 p.p.
2n = 34, 68, 102	
griffithii	Subg. 4, sect. 14, spp. 38–40
minima	
zewaldiae	
siamensis	Subg. 4, sect. 15, spp. 44–45
blassii	
purpurea	Subg. 4, sect. 16, sp. 50
jacobsenii	
sarawacensis	Subg. 4, sect. 6, sp. 20 p.p.
usteriana	Subg. 3, sect. 4, sp. 14
affinis	Subg. 4, sect. 12, sp. 36
versteegii	Subg. 4, sect. 7, sp. 22
2n = 36, 54, 72	
costata	Subg. 3, sect. 5, spp. 15–16 (+ 9b)
albida	
balansae	Subg. 3, sect. 4, spp. 9 (– 9 b)–13
bertelihansenii	
cf. *tonkinensis*	
cf. *crispatula*	
retrospiralis	
2n = 36	
bogneri	Subg. 4, sect. 8, sp. c. 24 a
alba	
thwaitesii	Subg. 4, sect. 6, sp. 18
2n = 36	
lingua	Subg. 4, sect. 7, sp. 21

A criticism of Rataj's system

In his revision of the genus *Cryptocoryne*, Rataj (1975 a) proposed a division into 4 subgenera and 17 sections. Table 2 shows Rataj's system compared with the sequence indicated by the chromosome numbers. A linear sequence often exaggerates minor differences, but apart from this there are evident differences:

(1) Rataj states that "*C. spiralis* belongs evolutionally to the oldest species of the genus showing with the whole subgen. *Saturina*" (= subgen. *Cryptocoryne*) "to the relationship with the genus *Lagenandra*". The arguments "the absence of the tube and the shape of the limb" can be seen as a convergent adaptation to a mainly emerse habitat. The chromosome number of *Lagenandra* is 2n = 36. Without any other arguments I think it venturous to state that a hexaploid-octoploid (?) species with the highest primary base number belongs to the oldest ones of the genus. Rataj places *C. ciliata* and *C. spiralis* in different subgenera. However, I find no greater differences (or similarities) between these two species than between any of the other chromosome groups, e.g. between the *C. beckettii* group and the *C. thwaitesii* group. Legro (1971) counted 2n = 34 for *C. tortilis* De Wit. Rataj regards the two species *C. tortilis* De Wit and *C. fusca* De Wit as conspecific with *C. ferruginea* Engler. However, even if one leaves out the different opinions regarding the status of the above mentioned taxa, it is not likely that a species with 2n = 34 belongs to a group which as far as is known has the base number x = 11. I can find no basis for the "evolutionary lines" as proposed by Rataj on pp. 22–25.

(2) Rataj placed the Sri Lanka species of the *beckettii* group with 2n = 28 in the middle of subgenus *Submersina*, which contains other groups with the chromosome number 2n = 34 and 2n = 36. On account of the chromosome number and the morphology of the 2n = 28 group, I find no close relationship between them and the rest of subgenus *Submersina* Rataj.

The distinguishing between two sections in this 2n = 28 group, viz., sect. *Nevillae* and sect. *Walkeriae*, which have "evolved independently", is not supported by the chromosome

numbers, nor do I find any basis for it in the morphology.

(3) Rataj places *C. pontederiifolia* ssp. *pontederiifolia* with 2n = 30 in the subgenus *Submersina,* and establishes *C. pontederiifolia* ssp. *sarawacensis* with 2n = 34.

(4) Rataj places *C. usteriana* with 2n = 34 in subgenus *Terrestrina,* section *Retrospiralae. C. usteriana* differs in many respects from the *albida* group. The bullate leaves have very prominent lateral nerves. The type collection has ovate as well as lanceolate leaves. The limb of the spathe has a collar and is not spirally twisted. The large cataphylls which are invariably present are very characteristic of the species.

(5) I do not agree with Rataj in placing *C. albida* (2n = 36) as a subspecies of *C. retrospiralis* (2n = 72). I believe that *C. albida* and *C. costata* are closely related. I find no reason to keep sect. *Retrospiralae* (excl. *C. usteriana*) and sect. *Costatae* apart. The backward twist of the limb of the spathe in *C. albida* and *C. costata* is just a matter of time after the opening. The general morphology of the young spathe is the same as in, e.g., *C. balansae.*

(6) *C. thwaitesii* and *C. bogneri* which both have 2n = 36 and come from Sri Lanka are placed in subgenus *Submersina* in section *Thwaitesiae* and section *Auriculatae,* respectively, and the two sections contain species from (1) Borneo, Malaya, and Sumatra and (2) Borneo and the Philippine Islands! Considering the strict endemism of most species and the chromosome numbers, which apparently have certain geographical correlations, I cannot find any support for placing them as Rataj does.

(7) *C. lingua* and *C. versteegii* have different chromosome numbers. Moreover, the embryo of *C. versteegii* is quite different as it has numerous plumulary processes, a feature only found in *C. ciliata.* I find no support for placing them in the same section.

The chromosome numbers

When interpreting chromosome numbers, primary base numbers are used. Thus it may be argued that x = 7 and x = 9 (or 6?) should be used instead of x = 14 and x = 18. However, this still leaves x = 15 and x = 17, and maybe even x = 11 to be explained. Supposing that aneuploidy occurs in addition to the primary basic numbers 7, 9, and 11, most combinations are possible, but I do not think that such arithmetics can be applied here. At present I find no morphological support for such a procedure.

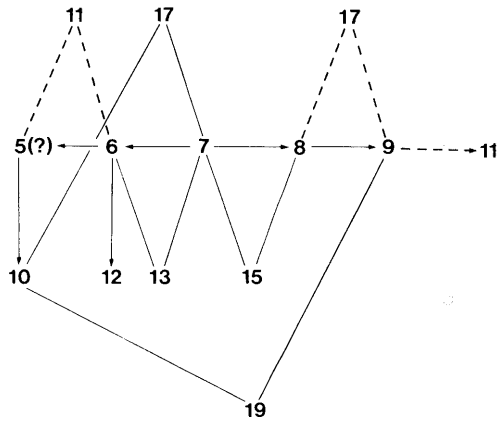


Fig. 7. Possible basic number relationships and direction of their evolution in the Araceae according to Marchant (1973).

The present chromosome counts in *Cryptocoryne* suggest that the chromosomal evolution has taken place at the secondary level, with large variation in chromosome number, in contrast to the closely related genus *Lagenandra* where only 2n = 36 has been found (*L. insignis, L. koenigii, L. lancifolia, L. meboldii, L. ovata, L. toxicaria,* and *L. thwaitesii,* Marchant 1972, N. Jacobsen unpubl.).

The formation and establishment of triploids, tetraploids, and hexaploids is very interesting. It is probable that the formation of triploid plants is an event which occurs with a higher frequency than is normally recognized (e.g. Alexander & Beckett 1973, Sandfaer 1970, Snogerup 1967).

Marchant (1973) pictures a possible chromosomal evolution within the Araceae (Fig. 7). It is striking that a scheme somewhat like it can be drawn for the genus *Cryptocoryne.* However, I do not consider the two situations quite comparable, as Marchant's table is based on a numerical interpretation of his results in the family as a whole.

Reproduction

The species of *Cryptocoryne* have to a great extent occupied niches in the rivers which are rarely inhabited by other plants. Part of their success is due to their rhizomes and subterranean runners which to some extent are protected under the soil, and at the same time are an excellent mode of reproduction. Examples of other phanerogams which have invaded the same habitat are species of *Crinum, Barclaya, Aponogeton* (van Bruggen 1968–73) and *Echinodorus* (Rataj 1975 b). The first three genera have bulbs or thickened rhizomes, whereas the latter often reproduces by means of plantlets formed in the inflorescence. The only other aquatic phanerogams which in radiation, speciation, and endemism resemble *Cryptocoryne* are the Podostemonaceae (Engler 1930, van Royen 1951–54, Willis 1926).

The ability for vegetative reproduction in *Cryptocoryne* opens possibilities for the establishment of more or less sterile populations, and it is obvious that many populations reproduce only vegetatively. Bothmer (1974) found a similar pattern in *Allium* from the Aegean Islands. Some species of the 2n = 28 group from Sri Lanka have developed numerous, short, bulb-like "runners" which are easily broken off.

Fruiting diploids have been observed several times in nature in the *C. beckettii* group, but only rarely in hothouses. Fruiting specimens of *C. griffithii, C. lingua,* and *C.* cf. *johorensis* have been observed in imported plants. Fruiting of triploid plants has not been observed.

Adaptive radiation

The evolution within the genus *Cryptocoryne* must be considered as an example of "island speciation", where the islands are the different river systems of South Asia.

The isolated rivers form the basis for the radiating evolution. The species occupy almost similar habitats throughout most of Asia. However, there is a diversification of the vegetative parts which undoubtedly must be adaptive. Also the differentiation of the inflorescence can in part be seen as an adaptation to the habitat of the plant, at least as to the character long tube versus short tube.

The occasional dispersal to new unoccupied river systems is of utmost importance in the evolution of the genus. Random factors, like genetic drift are likely to play a role. Long distance dispersal of rhizomes and runners must be taken into consideration, especially as the seeds have to germinate almost immediately.

An example which in several respects resembles the evolutionary pattern found in *Cryptocoryne,* is given by St. John (1966) for the genus *Cyrtandra* (Gesneriaceae) on the island of Oahu of Hawaiian Islands. *Cyrtandra* is found mostly in deep, wet ravines on the side of the volcano. These radiating river systems are separated from one another by relatively dry regions, so that geographically isolated, roughly similar habitats are found all around the island. In many cases, morphological characters that distinguish the species do not appear to have any selective value, which may be ascribed to geographic isolation in combination with the work of genetic drift.

Another interesting aspect is the influence of man, e.g. in Sri Lanka. 1000–2000 years ago large parts of the island were under cultivation (Mendis 1947), and it is very likely that the number of populations of *Cryptocoryne* diminished during that time. When the cultivated areas were abandoned, the remaining populations were able to reinvade formerly inhabited areas. This might have led to hybridisation and/or the establishment of new variants, which may partly explain why the taxonomy of the Sri Lanka species is so complicated.

The main evolutionary trend in the genus *Cryptocoryne* lies in the formation of the aneuploid series. When the plants proceed to a higher polyploid level their further evolution is probably often hindered by sterility.

Within *Cryptocoryne* there is a large diversification of the inflorescence, while the morphology and biology on the whole must be considered as rather uniform.

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Vascular plants from the Galápagos Islands: new records and taxonomic notes

Henk van der Werff

van der Werff, H. 1977 04 15: Vascular plants from the Galápagos Islands: new records and taxonomic notes. *Bot. Notiser 130:* 89–100. Stockholm. ISSN 0006-8195.

Thirty-five taxa are reported as being new for the Galápagos Islands, among them 8 species of *Thelypteris* (Polypodiaceae). Attention is drawn to a collection of *Thelypteris* that probably represents a new species. A key to the species of *Thelypteris* known from the archipelago is provided. Taxonomic and nomenclatural notes are made on taxa in the genera *Jaegeria* (Compositae), *Lippia* and *Verbena* (Verbenaceae), *Acalypha* (Euphorbiaceae), *Polygala* (Polygalaceae), *Hydrocotyle* (Umbelliferae) and *Tillandsia* (Bromeliaceae).

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From April 1974 to October 1975 the author conducted field work on the Galápagos Islands for a vegetation study of Santa Cruz and Volcán Alcedo, Isabela. Plants were collected on other islands as well. Thirty-five taxa are new for the archipelago. When determining the material, I found some changes in nomenclature to be necessary.

The first set of the collection is in U while a duplicate set will be deposited in CAS. A representative set will be deposited in an Ecuadorian Herbarium. The sequence of the taxa in the Flora of the Galápagos Islands (Wiggins & Porter 1971) is followed.

Hymenophyllaceae

Hymenophyllum plumieri Hook. & Grev.

Hook. & Grev., Icon. Fil. 2: pl. 123 (1829).

Collections: Isabela, the S slope of Cerro Azul, 750 m, van der Werff 2241 – San Cristóbal, summit area, 600 m, van der Werff 2190.

New for the Galápagos Islands. *H. plumieri* belongs to the section *Sphaerocionium,* which is characterized by the presence of hairs on veins and leaf margins and sometimes also on the leaf surface. *H. hirsutum,* reported by Morton (1947) from San Cristóbal, lacks hairs on the leaf surface, while such hairs are present in *H. plumieri.* The hairs are never numerous, but are always found on closer inspection. On the specimens from San Cristóbal they are quite sparse.

Both on San Cristóbal and Isabela this fern is terrestrial and found in wet areas, often on a slope with pendent leaves. The fronds are of a light colour and contrast rather sharply with the dark venation.

The Isabela specimens conform well with the Mille collection cited by Morton (1947). The specimens from San Cristóbal have fewer hairs, especially on the abaxial side, but otherwise conform.

H. plumieri is not common. On the mainland it is only reported from Ecuador, from where Morton (1947) cited 8 collections.

Polypodiaceae

Arachniodes denticulata (Swartz) Ching

Ching, Acta Bot. Sin. 10: 260 (1962).

Collection: San Cristóbal, on vertical walls of streambeds near the summit, 630 m, van der Werff 2188.

New for the Galápagos Islands. *A. denticulata* keys out in Wiggins & Porter (1971) to the group *Rumohra, Dryopteris* and *Polystichum*. It can be distinguished from the species of these genera by a combination of hairlike scales on the costae below, hairlike scales at the base of the stipe, laterally attached indusia and the semi-erect rhizome. *A. denticulata* is widespread on the American mainland.

Ctenitis pleiosorus (Hook. fil.) Morton

Morton, Leafl. West. Bot. 8: 190 (1957).

Collections: Isabela, a small crater on the S slope of Cerro Azul, 600 m, van der Werff 2244, 2256; same locality, but growing in a cave, van der Werff 2257 – Santa Cruz, Media Luna, 600 m, van der Werff 966.

C. pleiosorus is one of the few ferns endemic to the Galápagos Islands. It is fairly common but confined to the wetter zones.

Normally this species is not very tall and the description is based on medium-sized specimens. A few of the plants I collected were considerably larger (van der Werff 2256). The size of the pinnae, pinnulae and the branching of the veins in the pinnulae are quite different from that of medium-sized plants. Intermediates do exist and there are no differences in pubescence or scale characters. The measurements given below were obtained from the larger plants. Measurements from Wiggins & Porter (1971) are given in parentheses. Characteristics not mentioned do not differ from the description in the flora.

Fronds up to 25 dm tall (4–8 dm); stipe not measured separately but correspondingly larger, up to 7 mm thick (3–4 mm); length of the blades not measured separately; pinnae up to 30 cm long (8–12 cm); pinnulae up to 5 cm long (1.3 cm), 1.5 cm wide (0.4 cm), entire to incised 4/5 down to the costule; veins free, 1–4 times branched; sori up to 35 per pinnule (4–8), 2 mm in diameter (1 mm).

Dryopteris parallelogramma (Kunze) C. Alston

C. Alston, Amer. Fern J. 47: 92 (1957).

Collection: Isabela, in a small crater on the S slope of Cerro Azul, 600 m, van der Werff 2243.

New for the Galápagos Islands. *D. parallelogramma* will not key out to *Dryopteris* in Wiggins & Porter (1971) as it is very scaly but not very glandular. It differs from *D. patula,* the only other *Dryopteris* species known from the archipelago, by having bipinnate fronds, a densely scaly stipe and rhachis, and rufous brown rhizome scales. *D. patula* has bipinnate–pinnatifid to tripinnate fronds and few, light-coloured rhizome scales.

D. parallelogramma is rather widespread on the American mainland, ranging from Colombia to Argentina, mostly at higher altitudes (2500 m or more).

Dennstaedtia dissecta (Sw.) Moore

Moore, Ind. Fil. 305 (1861).

Collection: Isabela, from a small crater on the S slope of Cerro Azul, 600 m, van der Werff 2268.

New for the Galápagos Islands. Two other species of *Dennstaedtia* are known from the archipelago, *D. globulifera* and *D. cicutaria*. *D. dissecta* differs from *D. globulifera* by not having green alate axes of the pinnules, and from *D. cicutaria* by having larger sori (slightly over 1 mm in my specimens, 0.3–0.4 mm in *D. cicutaria*). *D. dissecta* occurs on the American mainland from Mexico to Bolivia.

Polypodium astrolepis Liebm.

Liebm., Vid. Selsk. Skr. B 1: 185 (1849).
Pleopeltis revoluta (Spr. ex Willd.) A. Reid Smith, Proc. Cal. Acad. Sci. ser. 4, 40: 230 (1975).

Collection: San Cristóbal, epiphyte on *Hippomane mancinella* near Tres Palos, 120 m, van der Werff 2174.

New for the Galápagos Islands. *Polypodium astrolepis* was recently transferred to *Pleopeltis*. As Wiggins & Porter only use the name *Polypodium,* I prefer not to introduce the name *Pleopeltis* here.

P. astrolepis has distinctly elongated sori up to 2 cm long. This characteristic distinguishes it from the rather similar *P. lanceolatum*. On San Cristóbal *P. astrolepis* is not uncommon as an epiphyte at middle elevations, mostly found on *Hippomane mancinella*. It occurs on the American mainland from S Mexico to Brazil.

Key to the species of Thelypteris known from the Galápagos Islands

1. Lamina bipinnate–bipinnatifid ..... *T. torresiana*
– Lamina pinnate or pinnate–pinnatifid 2
2. Basal veins of adjacent segments united in the sinus between the segments or united in the leaf tissue below the sinus with an excurrent veinlet running to the sinus 3
– Basal veins of adjacent segments not united and reaching the leaf margin slightly above the sinus 9
3. Lamina with conform terminal pinna; some hairs on the lower side of the rhachis forked 2–4 times; basal veins united with excurrent veinlet 4
– Lamina with pinnatifid apex; rhachis hairs not repeatedly branched; basal veins united in leaf tissue or meeting in sinus 5
4. Lamina pinnate, the pinnae crenate; 5 or 6 pairs of uniting veins per segment; frond with 4 or 5 pairs of pinnae ..... *T. poiteana*
– Lamina pinnate–pinnatifid, the pinnae lobed at least halfway down to the costa; only 1 or 2 pairs of veins united per segment. Frond with 7–9 pairs of pinnae ..... *T. tetragona* ssp. *aberrans*
5. Pseudovein running from the costa to the sinus between the segments; lamina coriaceous and glabrous; veins conspicuous, white, sometimes forked ..... *T. gardneriana*
– No pseudovein running from costa to sinus 6
6. Basal veins in adjacent segments united in leaf tissue and sending an excurrent veinlet to the sinus; rhizome erect or suberect ..... *T. quadrangularis*
– Basal veins in adjacent segments not united in leaf tissue but connivent in the sinus 7
7. Costae with some ciliate, castaneous scales below; basal segments of the lower pinnae reduced in size; rhizome creeping ..... *T. grandis*
– Costae without scales below 8
8. Rhizome erect; basal superior segments enlarged; veins on upper surface not hairy; lower pinnae not reduced in size ..... *T. patens*
– Rhizome creeping; veins on upper surface hairy; lower pinnae reduced in size ..... *T. conspersa*
9. Croziers covered with mucilage, aerophores present 10
– Croziers not covered with mucilage, aerophores present or absent 12
10. Rhachis with short, fasciculate hairs; aerophores at bases of pinnae 4 mm long; small aerophores present at bases of segments. Sori median ..... *T. thomsonii*
– Rhachis without fasciculate hairs; aerophores small, not present at the bases of segments 11
11. Rhizome erect, fronds caespitose. Stipe shorter than lamina. Rhachis glandular, distance between pinnae about 2 cm ..... *T. cheilanthoides*
– Rhizome creeping, fronds distant. Stipe as long as lamina. Rhachis not glandular. Distance between pinnae 0.6–0.8 cm ..... *T.* sp. nov.?
12. Indusia absent 13
– Indusia present 14
13. Sori elongated along veins ..... *T. linkiana*
– Sori round; rhachis densely and shortly hairy ..... *T. oligocarpa*
14. Rhachis glabrous below; costa below with few stramineous, adpressed scales ..... *T. pachirhachis*
– Rhachis pubescent below; no scales on costae below 15
15. Rhachis with stiff, short and non-septate hairs 16
– Rhachis with long (1.5– 2 mm), slender and multicellular hairs 17
16. Uncinate hairs present on lamina below ..... *T. oligocarpa*
– Uncinate hairs absent ..... *T. pilosula*
17. Well-developed pinnae up to 15 cm long, nearly always exceeding 10 cm. Segments with 12 or more pairs of veins; lamina with many sessile glands below ..... *T. balbisii*
– Well-developed pinnae up to 7 cm long. Segments with about 8 pairs of veins. Lamina with few red glands below ..... *T.* aff. *glandulosolanosa*

Thelypteris torresiana (Gaudich.) Alston

Alston, Lilloa 30: 11 (1960).

Collection: Pinta, Cerro Colorado, 220 m, T. de Vries s.n. (U).

New for the Galápagos Islands. *T. torresiana* is the only species of *Thelypteris* known from the archipelago with bipinnate–bipinnatifid fronds (cf. the key). It originates from tropical Asia and has been introduced into the American tropics.

Thelypteris gardneriana (Baker) Reed

Reed, Phytologia 17: 278 (1968).

Collections: San Cristóbal, on vertical walls of deep streambeds near the top, 600 m, van der Werff 2189; Adsersen 720 (C).

New for the Galápagos Islands. *T. gardneriana* is the only member of the subgenus *Steiropteris* known from the Galápagos Islands. The presence of a pseudovein running from the costa to the sinus between the segments is characteristic for this subgenus. *T. gardneriana* has coriaceous and glabrous fronds with conspicuous veins, which are almost white on the dark leaf tissue. Most mainland collections are from Brazil but a few records are from Colombia and Ecuador.

Thelypteris conspersa (Schrad.) A. Reid Smith

A. Reid Smith, Univ. Cal. Publ. Bot. 59: 60 (1971).

Collections: Santa Cruz, Wiggins 18.617a (DS); van der Werff 1755 – Isabela, Cerro Azul, van der Werff 2265, 2266.

New for the Galápagos Islands. A specimen identified as *T. kunthii* (Desv.) Morton belongs to *T. conspersa* (Wiggins 18.617a, DS). *T. conspersa* differs from *T. kunthii* by having reduced lower pinnae. Most mainland collections of *T. conspersa* are from S Brazil, but it is also known from the Andean countries.

Thelypteris grandis A. Reid Smith var. **pallescens** (C. Chr.) A. Reid Smith

A. Reid Smith, Univ. Cal. Publ. Bot. 59: 99 (1971).

Collections: Santa Cruz, Howell 9274 (CAS), Bowman 93 (CAS), Dawson E-23 (DS) – Isabela, Alcedo, van der Werff 1201.

T. grandis var. *pallescens* was reported by Smith (1971) from the archipelago. It was not included in Wiggins & Porter (1971).

T. grandis is widespread in tropical America, ranging from the Antilles and Costa Rica south to Bolivia. Four varieties have been described from the mainland of which only var. *pallescens* has been found in the Galápagos Islands.

Thelypteris cheilanthoides (Kunze) Proctor

Proctor, Bull. Inst. Jamaica, Sci. Ser., 5: 58 (1953).

Collection: Isabela, in a small crater on the S slope of Cerro Azul, 600 m, van der Werff 2242.

New for the Galápagos Islands. In addition to the characteristics mentioned in the key, *T. cheilanthoides* has submarginal sori that are partly covered by the reflexed leaf margin. It is widespread in tropical America.

Thelypteris thomsonii (Jenm.) Proctor

Proctor, Bull. Inst. Jamaica, Sci. Ser., 5: 65 (1953).

Collection: Isabela, in a small crater on the S slope of Cerro Azul, 600 m, van der Werff 2258.

New for the Galápagos Islands. See key for characteristics. The species is known from Jamaica, Hispaniola and Colombia.

Thelypteris oligocarpa (Humb. & Bonpl. ex Willd.) Ching

Ching, Bull. Fan Mem. Inst. Biol., Bot. 10: 253 (1941).

Collections: Isabela, in a cave above Villamil, Stewart 905 (CAS); in a small crater on the S slope of Cerro Azul, 600 m, van der Werff 2260, 2262, 2263 – Fernandina, Adsersen 937 (C).

New for the Galápagos Islands. *T. oligocarpa* belongs together with *T. linkiana* to the section *Uncinella* A. Reid Smith, characterized by the presence of uncinate hairs. *T. oligocarpa* has round sori with small, setose indusia that are sometimes hard to find. It is widespread in the West Indies and tropical America.

Thelypteris pachirhachis (Kunze ex Mett.) Ching

Ching, Bull. Fan Mem. Inst. Biol., Bot. 10: 253 (1941).

Collection: Santiago, in a *Cyathea weatherbyana* brake near the top, 750 m, van der Werff 2349.

New for the Galápagos Islands. For characteristics see the key. Mainland collections are from Venezuela and Colombia.

Thelypteris aff. **glandulosolanosa** (C. Chr.) Tryon

Tryon, Rhodora 69: 6 (1967).

Collection: Isabela, in a streambed on the W slope of Volcán Alcedo, 790 m, van der Werff 1263.

New for the Galápagos Islands. *T. glandulosolanosa* belongs to a group that Smith (1974) places in the section *Adenophyllum* A. Reid Smith of the subgenus *Amauropelta* (Kunze) A. Reid Smith because of its suberect rhizomes, sessile red glands and stramineous stipe with a dark base. This group is in need of revision and

consequently the identification is tentative. *T. glandulosolanosa* is known from Peru.

Thelypteris sp. nov.?

Collection: Isabela, from the SW slope of Cerro Azul, 750 m, van der Werff 2239.

This collection probably represents an undescribed species. It belongs to the subgenus *Amauropelta* (Kunze) A. Reid Smith. In some but not all of its characteristics it agrees with sect. *Blennocaulon* A. Reid Smith. It differs for instance by having a creeping rhizome with distant leaves. As the systematics of this group of ferns are rather confused I prefer to leave it unnamed until a revision of the genus has been made. It is included in the key as *Thelypteris* sp. nov.?

Description: Rhizome slender, creeping, up to 10 cm long and 0.4 cm thick. Tip of the rhizome and young leaves covered with some mucilage. Scales at rhizome very few, base of stipe almost glabrous. Stipe 10–25 cm, lamina 10–25 cm. Pinnae 20–25 pairs, up to 2.5 cm long and 0.5 cm wide. The lowermost pinnae (about 5 pairs) gradually reduced. The pinnae are pinnate or pinnatifid. Small aerophores present at the bases of the pinnae. Costae below with few dark scales and many stiff hairs, some of which are pluricellular. Veins dark, sunken in the leaf tissue, slightly widened towards the tip. Indusia absent, sporangia glabrous. Lamina coriaceous, a little shiny above.

I found this fern in only one locality on Cerro Azul, where fresh lava was overgrown by a thick layer of terrestrial mosses (*Thuidium delicatulum* (Hedw.) BSG and *Breutelia* sp. – Dr R. Gradstein and H. Sipman, pers. comm.). Apart from mosses and ferns few plants were present. The *Thelypteris* was creeping over the lava with only the laminae appearing above the moss layer, the stipes and rhizomes being completely hidden.

Thelypteris species excluded from the key

Thelypteris invisa (Sw.) Proctor var. *aequatorialis* (C. Chr.) Morton was reported from Santa Cruz. *T. invisa* is a hybrid between *T. grandis* and *T. serra* (Sw.) R. St. John (for an extensive discussion on the name *T. invisa*, see A. Reid Smith 1971) only known from Cuba, Haiti and Jamaica. All Galápagos material in DS and CAS identified as *T. invisa* turned out to belong to *T. grandis*.

T. kunthii (Desv.) Morton was reported from Santa Cruz. The specimens identified as *T. kunthii* in DS and CAS belong to *T. grandis* (Wiggins 18528) and *T. conspersa* (Wiggins 18.617a). *T. kunthii* is known from the West Indies and the Caribbean coast of Venezuela and Brazil. No collections are known from the W coast of S America and I do not think *T. kunthii* occurs on the Galápagos Islands.

Amaranthaceae

Achyranthes aspera L.

L., Sp. Pl. 204 (1753).

Collection: San Cristóbal, along a fresh water stream near Tres Palos, 150 m, van der Werff 2180.

New for the Galápagos Islands. *A. aspera* can be distinguished from the other Amaranthaceae known from the archipelago by its long (up to 20 cm or more) spikes with reflexed flowers and fruits. It is a common weed in tropical and subtropical regions.

Alternanthera sessilis (L.) R. Br.

R. Br., Prodr. 417 (1810).

Collection: San Cristóbal, common along the road near Tres Palos, 150 m, van der Werff 2179.

New for the Galápagos Islands. *A. sessilis* can be distinguished from other *Alternanthera* species in the archipelago by its creeping habit and large, obcordate utricles a little longer than the tepals. *A. sessilis* is a widespread weed in the tropics of the Old and New World.

Piperaceae

Peperomia tequendamana Trel.

Trel., Journ. Wash. Acad. Sci. 16: 207 (1926).

Collections: Isabela, SE rim of Alcedo, 1020 m, van der Werff 1970 – Santiago, epiphyte on *Zanthoxylum* near the summit, Adsersen 1070 (C) – Santa Cruz, in *Scalesia* forest near the two craters behind Santa Rosa, Adsersen 1311 (C).

New for the Galápagos Islands. *P. tequendamana* has opposite or alternate leaves like *P. petiolata*. However, *P. tequendamana* has densely rufous hirsute young shoots, petioles up to 2 cm long and the lower surface of the leaves are copiously black-dotted.

The Isabela collection is from the SE rim of the Volcán Alcedo where it grows as a creeping epiphyte on mossy branches of *Zanthoxylum fagara*. This habitat is much wetter than the preferred habitat of *P. petiolata* which is usually found in the lower *Scalesia* or Transition zones.

P. tequendamana is known from Colombia and Venezuela where it occurs at higher altitudes (2800–3700 m).

Compositae

Delilia biflora (L.) Kuntze

Kuntze, Rev. Gen. Pl. 333 (1891).

Collection: Isabela, near the tortoise nesting area in the NE part of the caldera of Alcedo, 740 m, van der Werff 1905.

New for the Galápagos Islands. *D. biflora* is an erect annual weed with leaves up to 6 cm. The two endemic *Delilia* species on the Galápagos Islands differ from *D. biflora* in several respects. *D. repens*, a fairly common plant in mesic forests, is a decumbent to trailing weed usually with small leaves (up to 3 cm). *D. inelegans*, collected only by Darwin, is erect and has larger leaves. It has three staminate and three pistillate flowers per head while *D. biflora* has only one staminate and one pistillate flower per head.

D. biflora is widespread in tropical America.

The name *Elvira* has often been used for this genus. The name *Delilia* is older and should therefore be used instead of *Elvira*.

Erechtites hieracifolia (L.) Raf. ex DC. var. **cacaloides** (Fisch. ex Spreng.) Griseb.

Griseb., Fl. Brit. W. Ind. 381 (1861).

Collection: Santa Cruz, from pasture land below Santa Rosa along the trail to El Chato, van der Werff 1372.

New for the Galápagos. For a discussion of the relationships between this species and *Senecio* and other genera, see Belcher (1956). *E. hieracifolia* var. *cacaloides* is a widespread weed in S America.

Galinsoga urticaefolia (H.B.K.) Benth. in Örsted

Benth. in Örsted, Vidensk. Meddel. Dansk Naturhist. Foren. København 1852: 102 (1852).

Collection: Santa Cruz, occasionally along the New Road, van der Werff 1284.

New for the Galápagos Islands. *G. urticaefolia* is a weedy species found in USA, C and S America and in Europe.

Jaegeria gracilis Hook. fil.

Hook. fil., Trans. Linn. Soc. Lond. 20: 213 (1847).
J. crassa Torres, Brittonia 20: 71 (1968).

Collections examined: Howell 9576, 9222, 9551a, 9006, 9204, Bowman s.n., Schimpf 91, Stewart 634, 637, Taylor G 34, Wiggins & Porter 633, 646, all in CAS – Colinvaux 347, 388, Wiggins 18.356, 18.774, 18.807, Itow 112, 30701-1, all in DS – van der Werff 957, 1175, 1154, 1353, 1401, 1509, 1528, 1678.

Cronquist recognised two species of *Jaegeria*, *J. gracilis* and *J. crassa*, in the Galápagos Islands. He uses the following differentiating characteristics:

J. gracilis: Involucral bracts thin and barely, if at all, wrapped around the edges of the subtended achene. Outer receptacular bracts slightly to strongly differentiated from the middle and inner ones, often somewhat clasping their achenes and occasionally approaching the structure and texture of those of *J. crassa*.

J. crassa: Involucral bracts thickened, wrapped around and fully enclosing the subtended achene, often some or even all of the bracts very like outer receptacular bracts; these are glabrous, strongly thickened, conspicuously grooved-striate, wrapped around and fully enclosing the achene. Larger, more robust and often less hairy than *J. gracilis*.

In addition to these differences I noticed that characteristic for *J. crassa* the number of flowers per head decreases to 15 (c. 50 in *J. gracilis*), that the achenes become fused with the receptacle and the head falls as a unit (achenes falling individually in *J. gracilis*), that the growth is erect (*J. gracilis* is trailing), and that it grows in forest (*J. gracilis* grows in wet, disturbed places).

Field observations and study of herbarium and

my own collections have revealed that we are not dealing with two distinct *Jaegeria* populations, but rather with one variable population. A large number of collections are intermediate between the *gracilis* and *crassa* extremes. The plants are found in wet, disturbed sites (especially the *gracilis* type) but sometimes the more stable forest habitat is invaded. It is the collections from the forest that show the *crassa* characteristics: increased size (leaves up to 10 cm), strongly thickened involucral bracts, reduction in the number of flowers per head and fusion between the receptacle and the achenes.

Carlquist (1974) cites several examples from islands in the Pacific of evolutionary changes in originally weedy species upon their spread to more stable habitats. One of the changes is very often a reduction in dispersal ability. *Jaegeria* on the Galápagos Islands seems to be another example of this process. Eventually, the forest type will possibly separate from the weedy type and each of them will become a distinct taxon. Nowadays, however, the intermediates are so numerous that it does not seem possible to recognise the extremes taxonomically.

Tridax procumbens L.

L., Sp. Pl. 900 (1753).

Collection: Santa Cruz, on the open roadside along the new road just outside Puerto Ayora, van der Werff 2238.

New for the Galápagos Islands. *T. procumbens* is a decumbent, stiff-hairy weed with yellow-flowered heads on long, erect peduncles. It is a pantropical weed; I saw it in great numbers along roads in Guayaquil and it has doubtlessly been recently introduced into the Galápagos Islands.

Convolvulaceae

Merremia umbellata (L.) Hallier fil.

Hallier fil., Bot. Jahrb. 16: 552 (1893).

Collections: Santa Cruz, along the road near Bella Vista, van der Werff 1289, 2044.

New for the Galápagos Islands. *M. umbellata* is the only member of the Convolvulaceae in the archipelago with bright yellow flowers. It has been reported from both the New and Old World tropics.

Ipomoea pulchella Roth

Roth, Nov. Pl. Sp. 115 (1821); O'Donnell, Lilloa 29: 221 (1959).

Collection: San Cristóbal, along the road from Baquerizo Moreno to El Progreso, 180 m, van der Werff 2170.

New for the Galápagos Islands. *I. pulchella* is a slender plant that can easily be distinguished from all other Galápagos *Ipomoeas* by its long, filiform and coiled peduncles. The leaves are palmately pentafoliolate. *I. pulchella* is pantropical.

Ipomoea stolonifera (Cyrill.) Gmel.

Gmel., Syst. Nat. ed. 13, 2: 345 (1791).

Collection: Isabela, common on sand dunes behind Villamil, van der Werff 2317.

New for the Galápagos Islands. *I. stolonifera* grows on sandy sea shores. *I. pes-caprae* occupies the same habitat but is purple-flowered, while *I. stolonifera* has white flowers with a yellow throat. It is reported from both the Old and New World tropics.

Rubiaceae

Oldenlandia corymbosa L.

L., Sp. Pl. 119 (1753).

Collection: San Cristóbal, from the airport near Puerto Baquerizo Moreno, van der Werff 2201.

New for the Galápagos Islands. *O. corymbosa* is a low, branched annual that differs from the other indigenous, herbaceous Rubiaceae by having several seeds in each of the two cells of the fruit. It is widely distributed in the tropics of both hemispheres.

Solanaceae

Physalis peruviana L.

L., Sp. Pl. ed. 2: 1670 (1763).

Collection: Santa Cruz, along the road near Sta Rosa, 400 m, van der Werff 1830.

New for the Galápagos Islands. *P. peruviana* is a perennial, pilose species that is considerably larger than the other *Physalis* species reported from the archipelago. A good difference is the size of the anthers: 3 mm in *P. peruviana*, 1.5–2.4 mm in the other species. According to Macbride (1962) *P. peruviana* is frequently cultivated for its edible fruit.

Verbenaceae

Lippia rosmarinifolia Anderss. var. **rosmarinifolia**

Anderss., Kongl. Svenska Vet.-Akad. Handl. 1853: 198 (1855).

L. rosmarinifolia var. *stewartii* Moldenke, Phytologia 14: 217 (1967).

Collections: Isabela, Volcán Alcedo, van der Werff 1038, 2331, 2337.

L. rosmarinifolia var. *rosmarinifolia* is known from Isabela, Fernandina and Pinta.

Moldenke (in Wiggins & Porter 1971) gives as diagnostic characteristics for var. *rosmarinifolia:* leaves entire or obscurely toothed. Var. *stewartii* is described as having pinnately lobed leaves. Howell, on the label of his collection no. 9585 (CAS), states that the juvenile leaves are lobed. My own field observations confirm this: van der Werff 2337 is a juvenile, non-flowering plant from the coast below Volcán Alcedo, and has distinctly lobed leaves. All flowering *Lippia* plants in the area had entire leaves. Apparently *L. rosmarinifolia* keeps the lobed leaves longer on the top of the volcanoes than in the coastal areas, but such plants with juvenile, lobed leaves do not deserve taxonomic recognition.

L. rosmarinifolia var. *latifolia* Moldenke, described from Santiago, also has entire or obscurely toothed leaves when mature and lobed leaves when juvenile.

Verbena brasiliensis Vell.

Vell., Fl. Flum. 17 (1825); Icones 1: pl. 40 (1827).

Collection: San Cristóbal, along the road near Tres Palos, 150 m, van der Werff 2182.

New for the Galápagos Islands. *V. brasiliensis* has distant leaves and short, densely flowered spikes in fascicles. In *V. litoralis* the spikes soon become elongate. *V. brasiliensis* is a widespread weed on the American mainland.

Verbena townsendii Svens.

Svens., Amer. Journ. Bot. 22: 253 (1935).

V. galapagosensis Moldenke, Phytologia 2: 55 (1941).

V. glabrata var. *tenuispicata* Moldenke, Phytologia 14: 283 (1967).

V. stewartii Moldenke, Phytologia 2: 56 (1941).

Collections examined: Isabela, Stewart 3317, 3318, 3319, 3320, Howell 9007, all in CAS; van der Werff 2280, 2286, 1172, 1192, 1218, 1897, 2152; Vagvolgyi s.n. (C) – Fernandina, Lynn Hendrix s.n. (DS), Adsersen 486, 512, 543, 572, 913, 920, 944, 969 (C) – Pinta, Adsersen 1148, 1189 (C); van der Werff 2124.

V. townsendii in this wide sense is known from Santa Cruz, Isabela, Pinta and Fernandina.

V. townsendii, V. glabrata var. *tenuispicata, V. galapagosensis* and *V. stewartii* have been separated on leaf characteristics by Moldenke (in Wiggins & Porter 1971). In these four species the leaves range from linear to lanceolate or oblong and from entire to lobed or deeply trifid. Since there were only few collections of these species it appears that Moldenke came to accept them by correlating leaf characteristics with locations. From a study of the herbarium material available, my own collections and field observations I conclude that the taxa mentioned belong to one single, extremely variable species.

There are great differences in leaf shape within the population of Alcedo, Isabela (the type locality of *V. galapagosensis*) where I collected repeatedly. Juvenile plants have relatively wide leaves and would be referred to *V. glabrata* var. *tenuispicata*. Some older plants have linear, entire leaves and would be called *V. galapagosensis*, while others have lobed leaves and are closer to *V. townsendii* or *V. stewartii*. On Cerro Azul old plants have greatly reduced leaves or have leafless flowering branches, while the leaves at the base of the plants are large. Thus, by using material from the upper or lower part of the same plant one can easily arrive at different identifications.

In open, wind-exposed locations the plants are decumbent and the stems regularly carry young shoots with juvenile leaves. Old parts have much narrower leaves. Even the isotypes of *V. stewartii, V. galapagosensis* and *V. townsendii*

(CAS) do not show the characteristics ascribed to these species.

Consequently, the lax-flowered, narrow-leaved *Verbena* plants from the Galápagos Islands should not be separated into four species but should all be called *Verbena townsendii* Svens.

Euphorbiaceae

Chamaesyce lasiocarpa (Kl.) Arthur

Arthur, Torreya 11: 260 (1911).

Collection: San Cristóbal, along the road outside Puerto Baquerizo Moreno, 50 m, van der Werff 2171.

New for the Galápagos Islands. Diagnostic characteristics of *C. lasiocarpa* are pubescent capsules, cyathia arranged in leafy dichasia and erect habit. It is known from the Antilles, C America and the northern part of S America.

Acalypha parvula Hook. fil.

Hook. fil, Trans. Linn. Soc. Lond. 20: 185 (1847).
A. parvula var. *chathamensis* (Robins.) Webster, Madroño 20: 263 (1970).
A. parvula var. *reniformis* (Hook. fil.) Muell-Arg., Linnaea 34: 48 (1865).
A. parvula var. *strobilifera* (Hook. fil.) Muell.-Arg., Linnaea 34: 47 (1865).

Collections: van der Werff 1026, 1087, 1094, 1100, 1138, 1241, 1250, 1731, 1812, 1853, 1953, 1996, 2053, 2071, 2141, 2147, 2149, 2200, 2274, 2275, 2351 from Santa Cruz, San Cristóbal, Pinzón, Santiago, Santa Maria, Española and Rábida.

A. parvula is known from all the larger islands with the exception of the northern islands Pinta, Marchena, Genovesa, Wolf and Darwin.

There is a wide variation within *A. parvula*. Webster (in Wiggins & Porter 1971) recognises four varieties. However, nowadays when more collections are available, it is clear that the size, pubescence and leaf characteristics used in Webster's key do not separate four taxa. The four varieties are "simply arbitrary assemblages of plants selected from a mosaic of clinal and microgeographic variation" (Webster 1970).

Acalypha sericea Anderss. var. **baurii** (Robins. & Greenm.) Webster

Webster, Madroño 20: 261 (1970).
A. sericea var. *indefessus* Webster, Madroño 20: 261 (1970).

Collections: Santa Cruz, van der Werff 1278, 1297, 1391, 1667, 1736, 1746, 2617 – Isabela, Volcán Alcedo, van der Werff 1180, 1467, 1502, 1525, 1534, 1861, 1980.

A. sericea var. *baurii* in this sense is known from Isabela, Santa Cruz and San Cristóbal.

My collections clearly show that both *A. sericea* var. *baurii* and var. *indefessus* occur on Santa Cruz and Volcán Alcedo, Isabela. On both locations plants from dry areas show characteristics of var. *indefessus*, whereas plants from wetter areas correspond with var. *baurii*. A number of plants are intermediate. Consequently, the varieties *baurii* and *indefessus* do not deserve separate recognition and var. *indefessus* should be regarded as a synonym of *A. sericea* var. *baurii*.

A. sericea var. *sericea* and var. *baurii* can be distinguished by the following characteristics:

var. *baurii:* Staminate spike curved, often pendent; its peduncle very short in relation to the fertile part; terminal pistillate spike generally absent, present in specimens from southern Santa Cruz; leaves with 17 or more teeth on each side.

var. *sericea:* Staminate spike erect; its peduncle about as long as the fertile part; terminal pistillate spike present; leaves with 8–15 teeth on each side.

My collections of *A. sericea* var. *baurii* from Alcedo and western and northern Santa Cruz all lack a terminal spike. However, several collections from southern Santa Cruz do have a terminal pistillate spike. Near the Caseta at southern Santa Cruz I found a large heterogeneous population of *Acalypha* (van der Werff 1413, 1414, 1415, 1417, 1419). Some plants belonged to *A. parvula*, which often has well-developed terminal spikes. Others were typical *A. sericea* var. *baurii* lacking a terminal spike. A great number of intermediates were also collected. In this locality *A. sericea* var. *baurii* interbreeds with *A. parvula*. Plants with a terminal pistillate spike but in other respects similar to ordinary *A. sericea* var. *baurii* probably represent introgression from *A. parvula*.

Lythraceae

Cuphea racemosa (L. fil.) Spreng.

Spreng., Syst. 2: 455 (1825).

Collection: Santa Cruz, open terrain near Media Luna, 540 m, van der Werff 1692.

New for the Galápagos Islands. Only one other species of *Cuphea* is known from the archipelago, viz. *C. carthagenensis*. This species has axillary, purple flowers while *C. racemosa* has a terminal raceme with almost white flowers. *C. racemosa* is found in tropical S America, extending northwards to Mexico and Cuba.

Malvaceae

Sida glutinosa Commers. ex Cav.

Cav., Mon. Cl. Diss. Dec., t. 2 (8) (1785).

Collections: Isabela, E slope of Volcán Alcedo, 750 m, van der Werff 1135; 1020 m, van der Werff 1987 – Santa Cruz, near the Puntudo, Adsersen 173, 622 (C).

New for the Galápagos Islands. *S. glutinosa* is immediately distinguished from other species of *Sida* known from the archipelago by being glandular-pilose. The leaves are up to 4 cm long and 2 cm wide, serrate, cordate at base, acuminate at tip and have a stellate pubescence. The flowers are pale orange. *S. glutinosa* is reported from the West Indies and Mexico to S America.

Polygalaceae

Polygala L.

L., Sp. Pl. 701 (1753).

The genus *Polygala* in the Galápagos Islands was recently discussed by Howell & Porter (1968). They recognise five taxa, one of which, *P. anderssonii* Robins., is puberulent and the remaining four glabrous. Other characteristics said to separate *P. anderssonii* from the glabrous taxa show partially overlapping ranges. The difference in ratio of aril length to seed length is not as well-marked as indicated in the key.

Among my collections of *Polygala* are two from Rábida, one (no. 1092) from near the coast and one from the top (330 m, no. 2354). The coastal collection keys out to *P. sancti-georgii* Riley var. *oblanceolata* Howell while the specimens from the top only differ in being puberulent. I found a similar situation on Volcán Alcedo, Isabela: the coastal plants (no. 1000) were glabrous, belonging to *P. galapageia* Hook. fil. var. *galapageia*, while plants growing inside the caldera near the fumaroles at 840 m (no. 1928) were puberulent but otherwise similar to the coastal plants.

I expect that intense collecting along an altitudinal gradient on Rábida or Alcedo will show that taxa which are glabrous at sea level become puberulent at higher altitudes and that *P. anderssonii* should be reduced to synonymy under *P. galapageia*. At this moment not enough material is available to support this change.

Umbelliferae

Hydrocotyle umbellata L.

L., Sp. Pl. 234 (1753).

Collections: Santa Cruz, open terrain near Cerro Crocker, 600 m, van der Werff 1689 – San Cristóbal, near the summit, Adsersen 805 (C).

New for the Galápagos Islands. There is only one previous collection of *Hydrocotyle* from the Galápagos Islands. This collection was at first regarded as belonging to *H. umbellata* (Robinson & Greenman 1895) but was later on (Robinson 1902) described as an endemic species, *H. galapagensis* Robinson. This species is extremely similar to *H. umbellata*, the only difference being the leaf margin, which is shallowly crenate in *H. umbellata* but double dentate in *H. galapagensis*. It is quite possible that the type specimen of *H. galapagensis* (originating from San Cristóbal from where *H. umbellata* is reported here) is nothing but an aberrant individual of *H. umbellata*.

Bromeliaceae

Tillandsia insularis Mez in DC.

DC., Monogr. Phan. 9: 765 (1896).
T. insularis var. *latilamina* Gilmartin, Phytologia 16: 163 (1968).

Collections examined: Gilmartin 875, 876, 877, 879, 882, 883, 884, 885, 886, 906, 908, 917, all in CAS; van der Werff 2316.

T. insularis has been reported from San Cristóbal, Santa Maria, Santa Cruz, Santiago, Isabela and Pinzón.

Gilmartin (1968) recognises two varieties in this endemic species. The var. *latilamina* has floral bracts with lepidote outer surface, partly purple leaf sheaths, 4.3–7 cm wide leaves and ascending spikes. In contrast the var. *insularis*

has glabrous outer floral bracts, not partly purple leaf sheaths, 2.4–4 cm wide leaves and spreading to recurved spikes.

These characteristics correlate with regard to size and vary between small and large specimens. Since large specimens are bulky and inconvenient to handle, quite a few older collections consist only of an inflorescence or part of an inflorescence, and a leaf rosette mounted on the same sheet. Usually the rosette comes from a small plant and the inflorescence from a larger one. This gives inaccurate information about the size of flowering plants. To illustrate this I will give the leaf widths of a number of flowering plants from two locations.

I measured 38 plants at Cerro Azul, Isabela. One had a leaf width of 4.0 cm, the others varied from 5.5 to 8.0 cm. At Pinzón I measured 20 plants: two were in the range ascribed to var. *insularis* (3.5 and 4.0 cm) and the remaining ranged from 4.3 to 8.0 cm. Only var. *insularis* had been reported from these localities. The data indicate that most flowering plants have a leaf width in the *latilamina* range but that a few small flowering plants are also found. Since large and small plants grow together extensively, there is no reason to keep them apart taxonomically.

Cyperaceae

Cyperus densicaespitosus Mattf. & Kuekenth.

Mattf. & Kuekenth., Pflanzenr. 4–20 (2): 597 (1936).

Collection: San Cristóbal, in mud along a fresh water stream near Fresh Water Bay, van der Werff 2175.

New for the Galápagos Islands. *C. densicaespitosus* is similar to *C. brevifolius* (Rottb.) Hassk. regarding inflorescence characteristics. However, it is a caespitose annual while *C. brevifolius* is a perennial with a slender, long-creeping rhizome. *C. densicaespitosus* is widespread in tropical America and Africa.

Cyperus odoratus L.

L., Sp. Pl. 46 (1753).

Collection: Santa Cruz, along the road near Santa Rosa, van der Werff 1829.

New for the Galápagos Islands. The rachilla in this species becomes corky after flowering and finally breaks into single-fruited segments. This characteristic is not found in any other species of *Cyperus* known from the archipelago. *C. odoratus* is a common pantropical species.

Gramineae

Axonopus compressus (Swartz) Beauv.

Beauv., Ess. Agrost. 12 (1812).

Collections: San Cristóbal, near El Junco lake, 660 m, van der Werff 2192 – Isabela, southern slope of Cerro Azul, 600 m, van der Werff 2289.

New for the Galápagos Islands. *Axonopus* resembles *Paspalum* in a number of characteristics but can easily be distinguished by its abaxial spikelets. Both areas where I collected *Axonopus* had large herds of free-roaming cattle. *A. compressus* is a widespread tropical grass.

Digitaria decumbens Stent

Stent, Bothalia 3: 150 (1930).

Collection: Santa Cruz, in pasture land near Santa Rosa, van der Werff 1838.

New for the Galápagos Islands. *D. decumbens* originates from South Africa and is widely introduced as a forage grass in the tropics. Unfortunately, in the Galápagos Islands this species easily escapes from cultivation and it threatens to overrun the native vegetation in the fern-sedge zone by means of vegetative reproduction. Locally, this grass is called "pangola grass".

Melinis minutiflora Beauv.

Beauv., Ess. Agrost. 54 (1812).

Collection: Santa Cruz, along the road near Santa Rosa, van der Werff 2087.

New for the Galápagos Islands. *M. minutiflora* is also an introduced forage grass. It does not spread as extensively as *Digitaria decumbens*, but is fairly well confined to the patches where it was planted.

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Polypodiaceae, Dr Harold N. Moldenke with *Verbena brasiliensis*, Dr T. M. Koyama, New York Botanical Garden, with the Cyperaceae and Dr John R. Reeder, University of Wyoming with the Gramineae. I would like to thank the Curator and Staff Members of the Botany Department of the California Academy of Sciences for their hospitality during my stay in San Francisco. Dr C. Berg, Prof. Dr A. L. Stoffers and Nita van der Werff-Clark critically read the manuscript. Finally I would like to thank Dr H. Adsersen and Dr T. de Vries for making their collections available to me, and the staff of the CDRS for their assistance during my stay in the Galápagos. Contribution no. 209 from the Charles Darwin Foundation.

Resumen

Desde abril de 1974 hasta octubre de 1975 se realisaron trabajos de campo en las Islas Galápagos (Ecuador), para estudiar la vegetación de la Isla Santa Cruz y de la Isla Isabela, especialmente el volcán Alcedo. Durante dicho estudio además hubo oportunidad de coleccionar plantas en otras islas. Se encontraron 35 especies nuevas para el archipiélago y en unos casos hubo necesidad de cambios de nomenclatura. La presentación de los datos es según la secuencia en la "Flora of the Galapagos Islands" de Wiggins & Porter (1971).

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Masonhalea, a new lichen genus in the Parmeliaceae

Ingvar Kärnefelt

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The new genus *Masonhalea* is segregated from *Cetraria* s. lat. on the basis of anatomy, morphology, ecology and chemistry. Its only species, *M. richardsonii* (Hook. in Richardson) Kärnef. is described and illustrated and a distribution map is provided.

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In recent decades lichenology has seen enormous advances in all areas of the field. New criteria for the delimitation of lichen genera have been developed as the large, early described, heterogeneous genera are re-evaluated. There has been an increasing trend to recognize smaller groups of more closely related species at generic rank (e.g. Hale 1965, Culberson & Culberson 1968, Brodo & Hawksworth 1977).

During my work on the brown fruticose *Cetrariae*, e.g. *C. islandica* and allied species, which comprise a well-defined natural group, I realized that *C. richardsonii* (previously referred to this aggregate) was unrelated to other species within the complex. This plant has puzzled lichenologists for more than a century. Nylander (1857) transferred the species from *Cetraria* to *Evernia*. Three years later he suggested that this taxon would be better accommodated in *Parmelia* (Nylander 1860 a) and later in the same year he placed the species in *Platysma* (Nylander 1860 b). Trevisan (1861) transferred the species to *Cornicularia*, while Howe (1915) in his revision of North American *Cetraria* noted that his inclusion of this species was only "tentative" and that it would be better placed in *Everniopsis*.

I find the species is sufficiently isolated from *Cetraria* and other genera in Parmeliaceae and warrants recognition as a separate genus. The new genus is named in honour of Dr Mason E. Hale, Jr. Dr Hale has been a leader in shaping modern taxonomic thought in lichenology, and has encouraged and inspired numerous young lichenologists. When I first became aware of the unique characters of this lichen, Dr Hale immediately recognized their significance.

I have examined all collections and exsiccatae of *Masonhalea* in BM, CANL, COLO, FH, MICH, MIN, MSC, LD, O, US, WIS. I also studied the plant in the field on the Seward Peninsula, Alaska, in 1973.

For anatomical investigations thalli were soaked in water for a few hours, sectioned with a freezing microtome at 10–15 μm and mounted in cotton blue. One collection was examined using a scanning electron microscope following Hale (1973). The presence of alectoronic acid is easily determined using UV light. However, collections from several populations from the whole distributional range were also tested using the standardized procedure of C. Culberson (1972).

Masonhalea Kärnef. gen. nov.

Typus generis: *Masonhalea richardsonii*.

Thallus prostratus, cartilagineus, e paucibus ramibus principalibus irregulariter vel dichotome divisis formatus, in statu sicco saepe rotundatus. Superficies superior obscure brunnea ad pallide olivacea, superficies inferior in partibus corticatis concolor, in partibus decorticatis alba vel caerulescens. Cortex superior crassissimus, e hyphis gelatinosis et valde pachydermaticis constans, cortex inferior comparate tenuis, e hyphis gelatinosis, aliquantum pachydermaticis et valde pachydermaticis constans. Medulla

Table 1. Comparison of *Cetraria* and *Masonhalea*.

Character	Brown fruticose *Cetrariae*	Other *Cetrariae*	*Masonhalea*
Upper cortex	thin paraplectenchymatous	thin paraplectenchymatous	thick prosoplectenchymatous
Thallus and lobes	erect fruticose, tubular or channelled, corticate on both sides, dying off from the basal parts	subfruticose or foliose, tubular or channelled or plane, in some erect fruticose, corticate on both sides, dying off from the basal parts	cartilaginous, prostrate, in dry condition often somewhat rounded, slightly channelled, lower surface only partly corticate
Branching	dichotomous or irregular from the basal parts	dichotomous or irregular from the basal parts, broad foliose forms almost unbranched	dichotomous or irregular, radiating in several directions, in one plane
Ecology	terricolous or corticolous, tuft-forming or growing in small colonies	terricolous or corticolous, tuft-forming or growing in small colonies	rolling freely on the ground, single individuals aggregate into large clumps

crassa compacta, alba. Algae prope corticem superiorum glomeratae, ad Trebouxiam pertinentes. Apothecia laterali-marginalia, sporae non septatae, hyalinae, ellipsoideae vel subglobosae. Pycnidia marginalia, microconidia bacillaria.

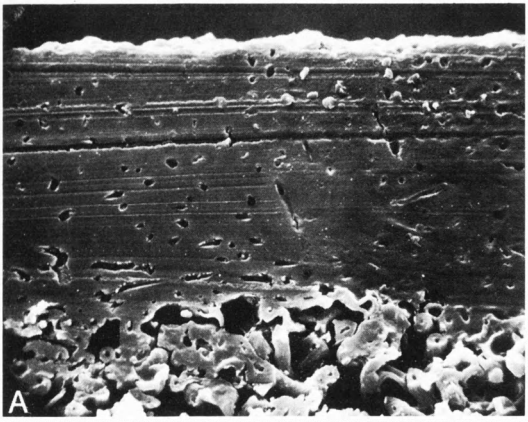
Thallus prostrate, cartilaginous, formed of a few major branches dividing irregularly or dichotomously, in dry condition often with a somewhat rounded habit. Upper surface dark brown to pale olive brown, lower surface concolorous on corticate portions of the thallus, or whitish to bluish on decorticate portions. Upper cortex very thick, composed of gelatinized and very thick-walled hyphae, lower cortex relatively thin, composed of gelatinized moderately thick-walled and thick-walled hyphae. Medulla thick and dense, white. Algae clustered near the upper cortex, *Trebouxia* type. Apothecia lateral-marginal, spores non-septate, hyaline, ellipsoidal to subglobose. Pycnidia marginal, microconidia rod-shaped.

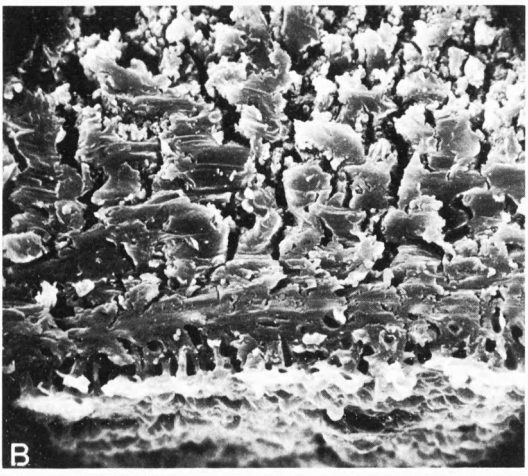
Delimitation of the genus

The new monotypic genus is segregated on a combination of characters (Table 1). The most important features are the structure of the upper cortex, the branching pattern, the partly decorticate lower surface and the ecology. Chemically *Masonhalea* does not show close affinity to *Cetraria*.

The thick upper cortex of *Masonhalea* is composed of thick-walled cells embedded in a dense matrix (Fig. 1 A, C). The cell walls are gelatinized and a homogeneous mass is formed where individual hyphae no longer are discernable. This kind of tissue is usually classified as being prosoplectenchymatous (Hale 1976, Jahns 1974) but sometimes as being scleroplectenchymatous (Degelius 1954). The upper cortex of *Cetraria* is relatively thin (15–40 μm) and formed of moderately thick-walled cells. Hale (1976) referred to this kind of cortical layer as being composed of pachydermatous (thick-walled) paraplectenchyma and it is characteristic of the Parmeliaceae. A similar cortical layer is also found in *Evernia, Everniopsis* and *Cornicularia* (e.g. *C. californica*). Other *Cornicullariae* have prosoplectenchymatous cortical layers (e.g. *C. normoerica*) or an unusual combination of both paraplectenchymatous and prosoplectenchymatous tissues (e.g. *C. aculeata*) (Hale 1976). *C. normoerica* has a thick upper cortex. However, this particular species differs markedly from other *Cornicullariae* (Henssen & Jahns 1973) and differs from *Masonhalea* morphologically, ecologically and chemically.

The thallus of *Masonhalea* is prostrate and its branching somewhat resembles that of an alga (*Chondrus*). The plant appears to initiate growth from one point and to divide horizontally in several directions, forming three or more major





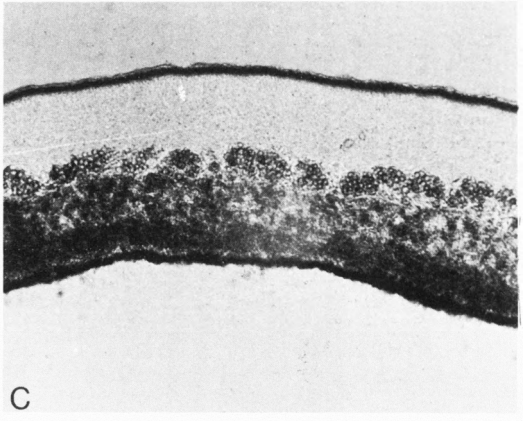


Fig. 1. Internal structure of *Masonhalea*. – A: L. S., upper cortex (Weber & Viereck 7071, US). × 660. – B: L.S., lower cortex. Above the cortex, the medulla with hyphae embedded in an extracellular compound (Weber & Viereck 7071, US). × 660. – C: Decorticate portion. From top upper cortex, clustered algal cells, medulla with extracellular compound (dark in light microscope) (Krog 303, O). × 50.

lobes which then divide dichotomously or irregularly (Fig. 2). The appearance is quite different from that of the erect, fruticose, dichotomously branched or foliose *Cetrariae*. The partly decorticate lower surface is another unique feature. These decorticate portions have sometimes erroneously been referred to as pseudocyphellae (Räsänen 1952). Pseudocyphellae, i.e. small cortical pores, are common in *Cetraria* and many other genera.

The ecological behaviour of the species is remarkable and differs from that of possibly related taxa. *Masonhalea* is usually not attached to the ground and actually rolls upon the other vegetation on the windy tundra. It is found as individual thalli or as fragments. Occasionally the individuals aggregate to form a large unorganized clump. Individual thalli or aggregates are sometimes also found in minor depressions on the tundra.

The orcinol depsidone alectoronic acid is the only secondary constituent found in *Masonhalea*. It is produced in large quantities and almost completely covers the medullary hyphae. The same substance is produced in a few *Cetraria* species (listed in C. Culberson 1969), e.g. *C. halei* and *C. pseudocomplicata,* but these species differ morphologically and have a thin paraplectenchymatous upper cortex. In addition *C. halei* contains atranorin and α-collatolic acid (Culberson & Culberson 1967).

Fruticose brown *Cetrariae* generally contain higher aliphatic acids, e.g. lichesterinic, protolichesterinic and rangiformic acids. These products are synthesized over the same acetate-polymalonate pathway as the aromatic com-

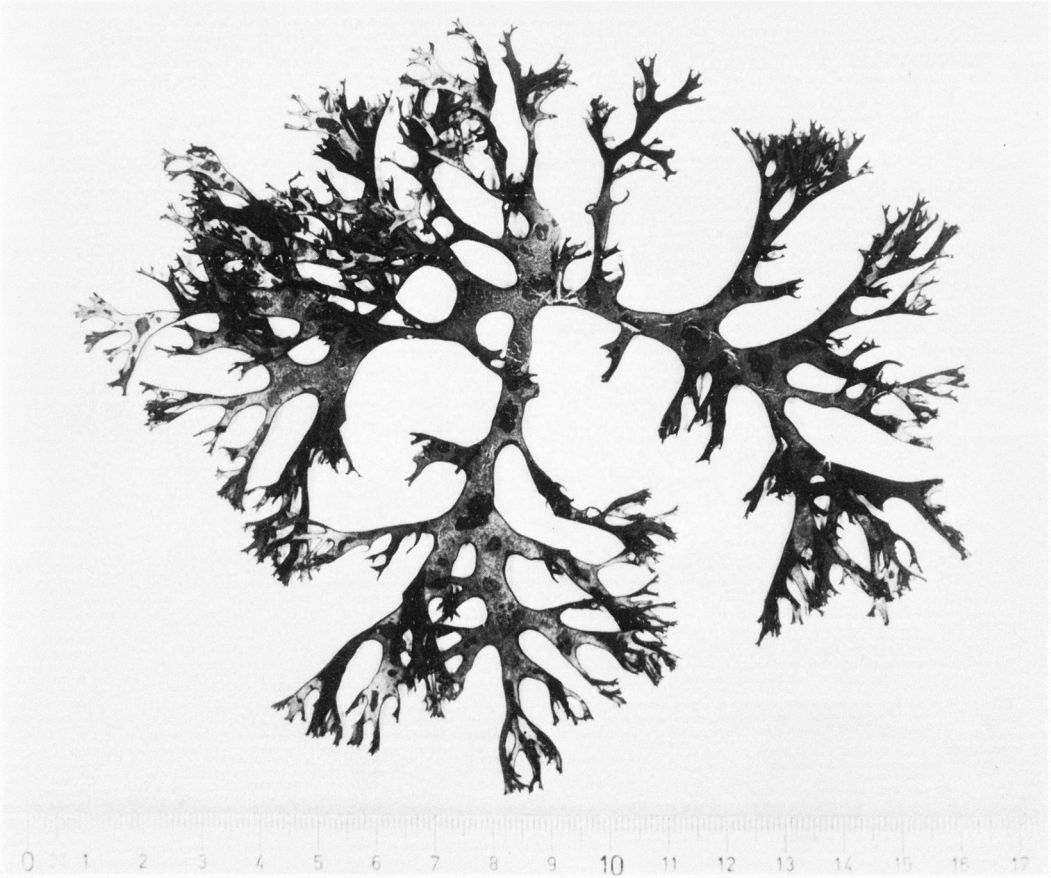


Fig. 2. *Masonhalea*. Lower surface with decorticate portions (Scotter 18687, CANL). Scale in cm and mm.

pounds (C. Culberson 1969) but are structurally different.

Masonhalea richardsonii (Hook. in Richardson) Kärnef. comb. nov.

Basionym: *Cetraria richardsonii* Hook. in Richardson, Bot. App. Narrat. Jour. Polar Sea (1823) p. 761. Lectotype: Barren grounds from Point Lake to the Arctic Sea, l.c. Captain Franklin, N. American Land Expedition 1820 (preserved in BM but belonging to K). – *Evernia richardsonii* (Hook. in Richardson) Nyl. in Mém. Soc. Imp. Scienc. Natur. Cherbourg 5 (1857) p. 99. – *Platysma richardsonii* (Hook. in Richardson) Nyl. Synops. Lich. 1 (1860) p. 306. – *Cornicularia richardsonii* (Hook. in Richardson) Trev. in Flora 44 (1861) p. 51.

Thallus prostrate (1–)3–5(–8) cm, formed of a few major branches dividing dichotomously or irregularly, in dry condition with a somewhat rounded habit. *Lobes* cartilaginous (0.5–)2–5(–20) mm broad with the margins weakly recurved inwards. *Upper surface* dark brown, chestnut brown or olive brown, dull or glossy, smooth. *Lower surface* concolorous on corticate portions of the thallus, smooth or wrinkled. Decorticate portions whitish or bluish. *Soralia* rare. *Upper cortex* 110–130 μm thick, prosoplectenchymatous, matrix colourless except for external pigmentation, c. 10 μm thick. Medulla 110–200 μm, hyphae about 3.5 μm in diameter, superficially covered with extracellular deposits (Fig. 1 B). *Algae* often in clusters of about 20 μm, concentrated near the upper cortex, green, spherical, c. 6 μm in diameter (Fig. 1 C). *Lower cortex* 30–40 μm thick, a thin layer of moderately thick-walled, slightly anticlinal cells

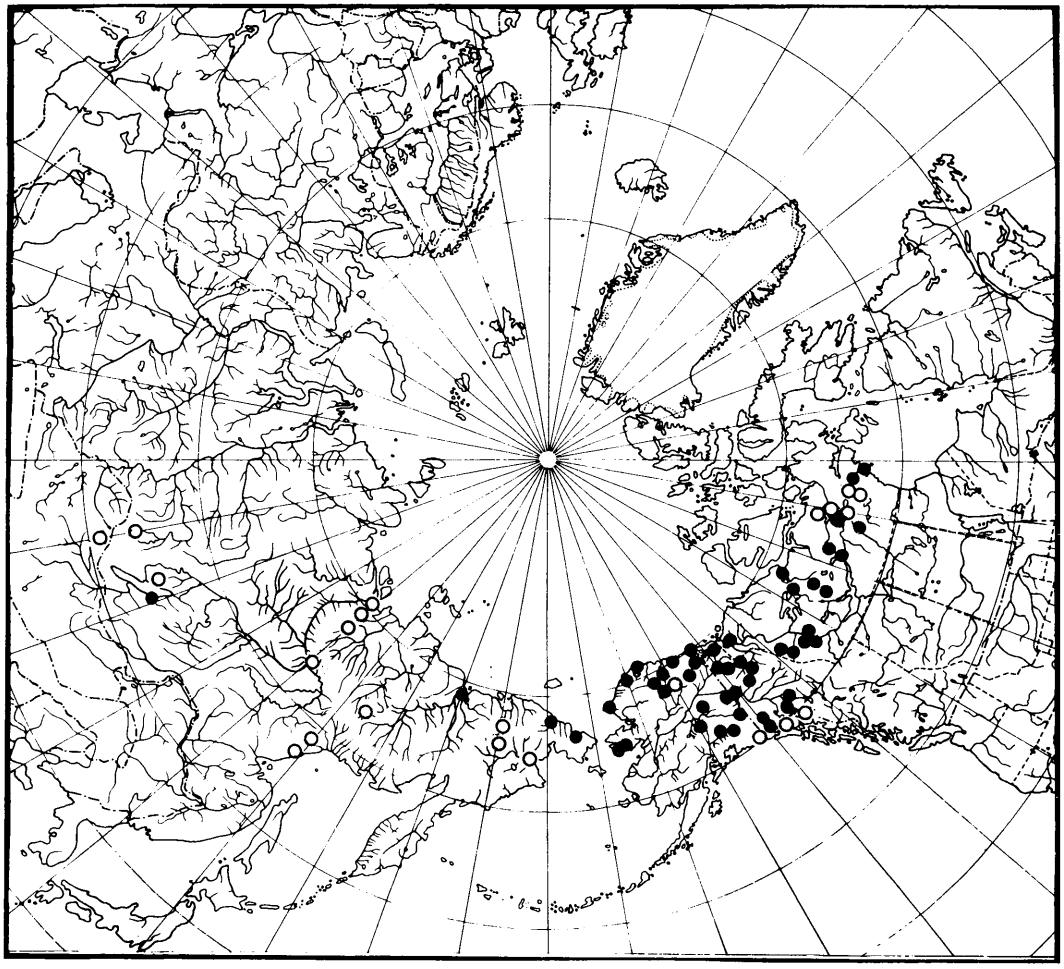


Fig. 3. Distribution of *Masonhalea*. Open circles in USSR from Rassadina (1950) and in North America from Thomson (1972).

covering a prosoplectenchymatous tissue, colourless except for a thin external pigmented portion, or lower cortex lacking, thickened medullary hyphae forming the lower surface. *Apothecia* rare, lateral, marginal; disc pale brown to brown, 0.5–3(–9) mm; hymenium 60–70 μm. *Asci* clavate to cylindrical, 10 × 40 μm. *Spores* 8 per ascus, non-septate, hyaline, ellipsoidal to subglobose, 6–6.5 × 3–6 μm. *Paraphyses* septate, c. 2 μm thick; hypothecium 30–40 μm, colourless. Pycnidia marginal, dark brown to black; microconidia rod-shaped, c. 0.75 × 5 μm. Medulla C −, K −, KC + pink, PD −, UV + bluish.

Nomenclature

Cetraria richardsonii was described in 1823 in a botanical appendix to Captain Franklin's *Narrative of a journey to the shores of the polar sea*. The appendix was written by John Richardson, surgeon and botanist on Franklin's first expedition, 1819–1822. We know from the preface to the appendix that William Jackson Hooker examined the lichens. Among the lichens *Dufourea arctica* was also described as new. Since both Hooker and Richardson were involved in the preparation of the lichen list, there is some question as to the authorship of the new taxa. Several new vascular plant species were described in the appendix and Richardson never wrote his name after a new epithet. In the same manner *D. arctica* has no author cited. On the other

hand after *C. richardsonii* (Hooker, Ms) was cited. I therefore conclude that *D. arctica* should be attributed to Richardson as *Dactylina arctica* (Richardson) Nyl. and *C. richardsonii* to Hooker as *Masonhalea richardsonii* (Hook. in Richardson) Kärnef.

Richardson's collections are presently in BM. One collection clearly refers to the first expedition of Captain Franklin and I have therefore selected it as lectotype. The type locality was noted in the appendix as "Barren Grounds from Point Lake to the Arctic Sea". Isotypes: Fort Enterprise, Franklin's 1 journey, herb T. Taylor (FH: Sprague); Amer. Arctica, Fort Enterprise, Richardson det. Hooker (208) (FH: Tuck.); Arctic N. America, barren soil, Richardson det. Hooker (MICH: Fink 12093).

Variation

M. richardsonii has a normal variation amplitude in lobe form and colour and infraspecific taxa have never been described. The decorticate portions of the lower surface seem to expand with increased lobe width. A specimen from Alaska (Krog 539, O) with thallus parts up to 2 cm wide had an almost completely decorticate lower surface. A few specimens were found with soralia-like structures (1969 Krog, O; Scotter 19977, CANL; Bird & Benson 30543, CANL; 1947 Scholander, MIN; Thomson, Lich. Arct. 92).

Reproductive structures

The anatomical structure of apothecia and pycnidia is parmeliaceous. Apothecia are probably rare and only a few fertile specimens were observed (Kanewskij 1916, O; Krog 428, O; Johnson 17, CANL; Johnston 238, FH; 1970 Mitchell, CANL; 1971 Ironside, CANL; 1899 Williams, FH: Howe; Cantlon & Gillis 57-537, MSC; Thomson, Lich. Arct. 92; Bostock 40, CANL). Pycnidia are usually inconspicuous and do not occur in large numbers. Microconidia were only found in one specimen (H: Nyl. 36150). Reproduction by sexual means must be of minor importance.

Distribution

M. richardsonii is an arctic-alpine tundra species with a northern Beringian distribution (Krog 1968). It radiates from the northern part of Alaska and easternmost Siberia. Westwards it reaches the Lena River valley and Lake Bajkal and eastwards it extends towards Hudson Bay (Fig. 3). Its distribution in North America was mapped by Thomson (1972) and its range in the USSR was presented by Rassadina (1950) and Savicz (1923).

M. richardsonii seems to be a poor ecological competitor when compared with associated species. Fragmentation and wind dispersal has probably led to the local success and modern distribution of this fascinating plant.

Acknowledgements. I am deeply grateful to Dr Ove Almborn, Lund, Dr Irwin M. Brodo, Ottawa, Dr Peter A. Bowler, Irvine (Ottawa) and Mr Thomas Karlsson, Lund for discussion of this work. Peter Bowler in particular showed a great interest in my work and he also revised the English text. The Sweden-America Foundation made it possible for me to visit Ottawa during 1976.

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Botanical literature

Ainsworth, G. C., Sparrow, F. K. & Sussman, A. S. (eds.) 1973: *The Fungi, an advanced treatise. IV A. A taxonomic review with keys: Ascomycetes and Fungi Imperfecti.* X + 621 pp., 93 figs., 70 pls. *IV B. Basidiomycetes and lower Fungi.* XIII + 504 pp., 74 figs., 27 pls. incl. 1 coloured pl. Academic Press, New York, London. Price bound $ 29.– + 28.–.

The present work is undoubtedly the most ambitious mycological survey in modern time. It covers all important biological aspects, which is rarely the case in comparable textbooks. The volumes 1–3 deal with the fungal cell, the fungal organism, and the fungal population, whereas the last two-part volume is strictly morphological–taxonomic. A great many authors have contributed.

The system follows Ainsworth & Bisby's *Dictionary of the Fungi* (1971) and embraces the fungi in a conventional sense, but excludes the Hydromyxomycetes and Labyrinthulales. Both books begin with a key to the classes, and end with a cumulative index of Latin names and authors. Most papers follow a common pattern: at first a definition of the group, a morphological survey, keys to families and genera, description of the families, and finally selected references. Representative species are mentioned, sometimes even type species. Most articles are illustrated with drawings and/or photographs.

There has been an aspiration to include as many genera as possible within the restricted space. In the Saprolegniales (M. W. Dick) even all species are mentioned, and in orders as large as Mucorales, Pezizales, Agaricales, and Uredinales practically all known genera (c. 65, 93, 145, 110 resp.) are keyed out. Compared with corresponding figures in *Dictionary* the Pyrenomycetes are covered to c. 50%, the Discomycetes to c. 80%, and the Loculoascomycetes to almost 75%, which is impressive. In the Hyphomycetes and Mycelia Sterilia the key with 595 genera is completed with a list of 1541 generic names (incl. synonyms, references, and type species). *Dictionary* accepts 930 genera and 475 synonyms.

A doubling of several genera and a few families occurs, but this has been accepted by the editors in order not to conceal unsolved, taxonomic problems. Thus, for instance, *Ceratiomyxa, Acrospermum,* Thraustochytriales, and ten genera in "Perisporiaceae" (pp. 82, 90, 169, 170) turn up in two or three places in the system. With single exceptions the articles maintain a high standard – what else could be expected from outstanding experts? The existing differences are mainly due to the nature of the group treated, such as number of genera, taxonomic difficulties, and stage of present knowledge.

The number of illustrations varies from none (Agaricales) up to 66 plates with 559 genera in the Hyphomycetes (W. B. Kendrick & J. W. Carmichael), where the generic identification is founded on fine drawings following Saccardo's practical spore type system. The vouchers should have been mentioned, however. The authors' radical opinions of the nomenclature of these fungi have led them to accept S. J. Hughes's proposal of Persoon (1801) as a starting point, which has resulted in many illegitimate name changes. Knowledge of the conidial ontogeny is a must in modern Deuteromycete taxonomy, and both Kendrick & Carmichael and B. C. Sutton in his interesting treatise of the Coelomycetes report this as far as it is known. Since this development is still unknown in many type species, not few generic names are dubious and hence excluded (in the Hyphomycetes no less than 400; see Kendrick

in *Taxon 23,* 1974). Other taxonomic problems refer to the kind of pycnidia or stromata. Thus, the Melanconiales seem to be more related to the Tubercularíales than to other Coelomycetes.

The treatment of well-known groups follows on the whole modern monographs and revisions, for example, as regards the Myxomycetes, Mucorales, Laboulbeniales, Pezizales, Ustilaginales, and Agaricales. But also the well-informed reader can find many items of interest here, such as a discussion of the still nebular origin of the slime moulds, the recent subclass division of the group (C. J. Alexopoulos), and two new families in Mucorales (by C. W. Hesseltine & J. J. Ellis). The Plasmodiophoromycetes have often been classified as parasitic slime moulds, but new cytological experiences seem to strengthen their affinity to higher zoosporic fungi (G. M. Waterhouse). The latter constellation forms here – like in many modern text-books – the Mastigomycotina. It is difficult to understand why this unnatural taxon has been created and accepted, when we finally have got rid of the "class" Phycomycetes. F. K. Sparrow gives a handy introduction to these fungi, based particularly on their zoospore morphology. Among the more interesting information is the suggestion that the absence of zoospore I in the Lagenidiales–Peronosporales could be primary, and that their zoospore II is thus not homologous to that of the Saprolegniales. The unexpressed consequence would be a splitting of the Oomycetes!

The Discomycetes (R. P. Korf) and Loculoascomycetes (E. S. Luttrell) have received admirable treatments with keys crammed with useful comments and references without being overloaded. The term 'interascicular' (p. 194), which is found in several publications of today, and probably originates from Luttrell, should be corrected to 'interascal'. There is no such basic word as 'asciculus'. From a taxonomic point of view one notices i.a. that the Patellariaceae are placed among the bitunicates, and the (plectomycetous?) Elaphomycetaceae among the truffles, which deviates from conventional systems. Plectomycetes has here received an unusually narrow circumscription by D. I. Fennel, who maintains one order only (Eurotiales s. lat.), and excludes i.a. all species with ostiolate perithecia or septate (!) spores.

Erysiphales is a well-defined group with a small number of clear-cut genera. In spite of this C. E. Yarwood treats the order very incompletely and mainly from his Californian horizon (8 genera out of some 20, and many omitted references), which is unsatisfactory in a book of this magnitude. Somewhat disappointing is also the chapter on the Pyrenomycetes by the eternal team E. Müller & J. A. von Arx. Even if their gigantic task is indeed impossible (a selection among some 800 genera), one could demand a more careful presentation of facts. Also the ordinal system is over-simplified, with Sphaeriales engulfing most of the other orders. A scrutiny of the treatment of the reviewer's own speciality, the Sordariaceae s. lat., has revealed many grave errors: Fig. 4 d is *Diplogelasinospora,* not *Apiosordaria;* the asci are said to lack an apical apparatus (p. 91), when most of the genera have such; *Ceriophora* (p. 110) should be *Cercophora* (*Ceriophora* is a different genus); *Hypocopra* in Xylariaceae (p. 123) is represented by the type of *Sordaria, S. fimicola,* an inexplicable lapsus! Many more examples could be given.

In the Basidiomycetes particularly the classification on the family level and higher is of interest. The traditional bipartition into Holo- and Phragmobasidiomycetes has been given a lower rank here, but the taxonomic importance of basidial septation is nevertheless stressed by a division of the jelly fungi (R. F. R. McNabb & P. H. B. Talbot), where those with one-celled basidia at last are transferred to the Holobasidiomycetes. Also in the Aphyllophorales recent ideas are confirmed: the pulverization of old genera as *Polyporus, Hydnum, Clavaria, Corticium* and their families, and the importance of anatomical characters. The authors have chosen a middle way with keys of cupuloid, thelephoroid, clavarioid, cantharelloid, hydnoid, and poroid groups. This means a certain overlapping of families and genera, but it is no disadvantage from a practical point of view. The reader will find much of interest here, such as R. H. Petersen's pruning of Corner's concept of the cantharelloid fungi, or Talbot's dissolution of the Thelephoraceae sensu Donk, or be surprised at D. N. Pegler's conventional circumscription of the Polyporaceae.

Overlapping problems are also demonstrated between agarics and Gasteromycetes. Many of the latter are found in the Agaricales as

gasteroid elements, and no less than seven families contain such; other Gasteromycetes are of more problematic affinity. A. H. Smith's and D. M. Dring's chapters anticipate a forthcoming, unorthodox taxonomy of this border field.

Highly informative is G. F. Laundon's outline of the complex and ambiguous terminology of spores, spore stages, and life cycles in the rust fungi. The author prefers to base the spore stages on morphology and not cytology, but the uredinologists are not unanimous on this point. A perplexing error is how he can call plasmogamy "diploidization" (p. 248) or say that the aeciospores germinate to a diploid thallus, when it is a matter of a dicaryotic phase.

The Fungi offers stimulating reading, and on most pages there are problems and details to discuss or comment upon, of which only a fraction can find room within an ordinary review. Although this 1125 page opus has its shortcomings, the final judgement must be marked positive. There is an enormous amount of information within these four covers, and for some fungus groups modern surveys and keys are presented for the first time. These two books (and the other three volumes too) will no doubt become the mycologists' bible for a long period to come.

Nils Lundqvist

Ayensu, E. S. 1974: *Leaf anatomy and systematics of New World Velloziaceae*. 125 pp., frontispiece, 24 figs., 51 plates. Smithsonian Contributions to Botany 15. Washington. Price (paper) $ 2.20.

Velloziaceae is a very interesting family of "woody" monocotyledons that has many distinct morphological, ecological and phytogeographical features. The family has been thoroughly studied the last few years, especially by L. B. Smith and E. S. Ayensu. The latter has been primarily interested in comparative leaf anatomy, and he surveyed species of the Old World in 1969. Five years later the corresponding work for the New World species has appeared. In these papers Ayensu has collected a great amount of leaf anatomical data. Velloziaceae must at the moment be one of the best-mapped plant families in that respect. The author has also contributed with new valuable methods, making it possible to deduce many anatomical details from old herbarium specimens.

The work under consideration here gives leaf anatomical data for 106 species of the genera *Vellozia* and *Barbacenia*. According to the revision by Smith (1962) this represents about 65% of the species known from the area. The main emphasis has been put on patterns of sclerenchyma, but information on hairs, epidermis, stomata, mesophyll and vascular bundles is given. In addition to detailed descriptions considerable weight is given to figure documentation: drawings of leaf surfaces (28 species), detailed drawings of transverse sections (42 species), scanning electron micrographs of epidermal and hair structures (20 species) and of stomata (22 species) and photos of transverse sections of nearly all the species examined. The drawings are very clear and good which also applies to most of the photographic documentation.

Ayensu has shown that in most cases the two genera can be separated on leaf anatomical data, especially by the sclerenchyma patterns. He also claims that each species exhibits distinct mesophyll and epidermal features that permit their individual identification. The material presented does perhaps not appear quite convincing on that point. But if it really is possible to distinguish the species the author ought to have systematized the results in an anatomical key. My reason for questioning the statement on specific identification is that the author himself demonstrates intraspecific variation in some species, whereas for many other species he only investigates one specimen.

My main criticism of the work is the lack of discussion and systematizing of the data. The impressive collection of data has not been set into any sort of reference frame. Since the data are put to such limited use the reading is less interesting than it could have been. And even if the aim of the work was only to present a sort of anatomical atlas (the title of the book promises more than that), the results and documentation should still have been presented more systematically.

Apart from this the author is to be praised for his endurance in procuring information. The

author's next work can be awaited with expectation and perhaps this will give some of the answers to the still many unsolved problems within the family: the delimitation of genera and the affinities between the taxa of the Old and the New World.

Inger Nordal

Correns, C. E. *Untersuchungen über die Vermehrung der Laubmoose durch Brutorgane und Stecklinge.* Jena 1899. Reprinted 1976 as Vol. 7 of Bryophytorum Bibliotheca. XXIV + 472 pp., illustrated. J. Cramer, Lehre. Price 120.–DM.

With this reprint an excellent, classical work has again become available. Carl Correns was the last pupil of Carl Nägeli, to whom also the book is dedicated. To most of us he is known as a famous geneticist and one of the rediscoverers of the Mendelian laws. But he was a clever and skilful morphologist too, and his early activity in the field of morphology of moss propagula, manifested in several papers, culminated in the present book. It treats the concept of propagula in its widest sense from fragile shoots and leaves to advanced gemmae-forming structures. Since the book certainly is new to younger bryologists, some notes about its content will be worthwhile.

The main content is divided into two parts. The first or special part (322 pp.) includes careful descriptions of propagula of a great number of genera and species ordered by families. A separate section here treats also those innovations from the stem which in the title of the book is called Stecklinge. The second part is a general one (166 pp.), and gives morphological and phylogenetical aspects of propagula from stem, leaves, protonema, sporophyte, etc. A second section here describes the development of propagula, how they get loose and are distributed. In two other sections germination, the conditions of germination, growth and development and the occurrence and conditions of formation are treated. The last section discusses the evaluation of propagula in taxonomic work and finishes with a survey of (key to) investigated species. There are 187 excellent figures, all drawings, in the text. A reference list and an index to taxa treated complete the volume.

The reproduction of text and illustrations in the reprint edition is clear and distinct. The format is almost the same as that of the original and fits the other volumes in the series (with the exception of the first one).

Olle Mårtensson

Iwatzuki, Z., Vitt, D. H. & Gradstein, S. R. 1976: *Bryological herbaria. A guide to the bryological herbaria of the world.* Bryophytorum Bibliotheca Vol. 8. 144 pp. J. Cramer, Lehre. Price 25.–DM.

The present book is, in addition to its general usefulness, also an excellent indication of how far the international cooperation between bryologists has advanced during the last decades. The demand for a special index of bryological herbaria was raised at the Colorado meeting of the International Association of Bryologists in 1973 by one of the authors (Dr Iwatzuki). According to the resolution, the material was collected by distribution of a questionnaire to the 735 herbaria listed in Index Muscorum but also to all members of I. A. B. In May 1975 when the main part of the questionnaires had been returned, the compilation work could start.

The index which can be considered as a continuation or supplement of Index Herbariorum embraces 292 herbaria with material of bryophytes available. Of these 44 refer to private (personal) collections. The herbaria are arranged alphabetically by city and their abbreviations are also those of I. H., and can be decoded by a separate index. For practical reasons the persons with private herbaria which lack herbarium abbreviations have been listed separately with reference to relevant city (and country) under which one has to look. The final list gives the cities with herbaria ordered alphabetically by countries.

Print and covers are those earlier adopted to the series. This guide to bryological herbaria is obviously as complete as one can expect and will be an indispensable and convenient tool in the taxonomic work on bryophytes.

Olle Mårtensson

Whittier, H. O. 1976: *Mosses of the Society Islands*. 410 pp., 101 figs. The University Press of Florida, Gainesville. Price (bound) $ 17.50.

The scientific – and romantic – interest in exotic islands does not seem to cease. Many of them are scientifically explored to an extent which leave many continents far behind. Most of these islands are created by fairly recent volcanic activity and are of great biohistorical and biogeographical interest. As far as bryophytes are concerned, two island groups of the southern Pacific have recently had their moss floras monographed: the Samoa Islands (Schultze-Motel 1974) and, now, the Society Islands by Dr Whittier. This last work is based on a dissertation from 1969.

The Society Islands form a central group in the southern Pacific. Tahiti is by far the largest and highest of the islands and the best explored from many points of view. The group embraces 13 other islands, but only 4 have been bryologically investigated: Moorea, the double islands Raiatea and Tahaa, and Bora Bora. The author gives an excellent view of the natural history and history of exploration of the islands.

It is not just the larger size of Tahiti which makes it predominate the present work. Its height (2237 m) is impressive for an island of its size (1036 km^2). Almost perpendicular walls up to 1000 m surround several of its valleys. The precipitation is extremely high, particularly on the windward (NE) side. In some elevated places in the central part of the island it is estimated to 2500 *cm*. Obviously this island should be a lovely place for bryologists.

The author applies the zonation introduced by Pappy (1948–58). The main vegetation belts are the maritime, mesotropical and hygrotropical zones, of which the first and third include several sub-zones. They are well defined by characteristic moss species. Drawings illustrate representative transects.

The systematic arrangement follows Brotherus' treatment in the second edition of *Die natürlichen Pflanzenfamilien*. There are keys to families, genera and species. For all taxa descriptions are given. More than a hundred species are illustrated by drawings from authentic specimens and references to other authentic illustrations are given. Synonyms, heterotypic as well as homotypic – and they are often many – are included and show together with the taxonomic discussions that the revision in many cases has been a difficult task, particularly so since the material is spread over herbaria in many countries. The author's own collections include more than 1700 numbers. The occurrence and ecology within the Society Islands, and the general distribution is reported for all species. There are only seven new descriptions (including four *Fissidens* species earlier described by the author and H. A. Miller jointly).

Before the revision about 400 species (the author here uses the word taxa in an unclear sense) have been reported from the islands. Now this number has been reduced to about 175. The author estimates the real number to about 200. Of the accepted species, less than 20 per cent are considered as endemic. Many elements indicate a relationship with other Polynesian islands, such as Hawaii, Marquesas Islands and New Zealand.

Of course, the composition of the moss flora is quite another than what we are familiar with in the northern temperate zone. For instance, Bryaceae is represented just by *Brachymenium indicum* and four *Bryum* species (of which *B. argenteum* is one), Mniaceae only by the cosmopolitan *Mnium (Rhizomnium) rostratum*, Grimmiaceae only by the endemic *Racomitrium papeetense* and Polytrichaceae by two species of *Pogonatum*. No *Andreaea* or *Sphagnum* species is reported. Instead we find species from many more or less exotic families, such as Calymperaceae, Hookeriaceae, Leucobryaceae, Meteoriaceae and Sematophyllaceae. Orthotrichaceae is not represented by its type genus but by two widespread *Zygodon* species and by eight *Macromitrium* species of which no less than six are endemic. Some of these tropical species are cosmopolitan in this belt, such as *Octoblepharum albidum* and *Rhizogonium spiniforme*. The world cosmopolite *Ceratodon purpureus* is not reported and in all probability is absent from the islands.

The bibliography (ten pages) has been worked out with care and seems to be very complete. The following glossary of terms could perhaps have been left out since one has to expect the users of this flora to know the terminology. In the index, keys as well as specific epithets are listed under the generic names.

The editor has made an attractive volume

bound in green cloth with the signatures intact and with broad margins. The printed text and the reproduction of illustrations are good, and the typography greatly facilitates the use of the book. Perhaps the generic names could have been in boldface or have been moved to the centre of the page. Serious misprints and inadvertences have not been met with hitherto. The price must be considered as low.

Mosses of the Society Islands is an excellent work which will be indispensable for the continued study of the mosses of the southern Pacific as a whole.

Olle Mårtensson

Fægri, K. & Iversen, J. 1975: *Textbook of pollen analysis*. 3rd revised edition. Munksgaard, Copenhagen. Price DKr 100.–.

For more than 25 years the "Fægri–Iversen book" has been the main textbook for pollen analysts dealing with Quaternary biostratigraphy. The first edition was published 1950, the second slightly revised edition 1964 and the third thoroughly revised edition in 1975. Due to Johannes Iversen's death in 1971, Knut Fægri alone had to prepare the final revision. He has consequently added important new knowledge to the text chapters. However, Iversen's excellent main contribution, the identification key of NW European pollen types, was completely revised already in 1964, and this key still stands out as the most important part of the book for pollen analysts in the daily microscope work.

The textbook covers the methods in the field, laboratory and at the microscope important for pollen analysts working with mainly bog and lake deposits of Late Quaternary age. The identification key is restricted mainly to pollen grains of spermatophytes growing in NW Europe. The authors do not regard the book as a textbook of pollen morphology. However, in the last edition the very comprehensive chapter on "The pollen grain, its form and function" is the very best introduction to pollen morphology, useful for pollen analysts as well as taxonomists.

The following comments are concentrated on the new information in the last edition.

The expanded chapter on pollen morphology seems to cover references to the most recent literature on the morphology, stratigraphy and chemistry of pollen grains. The terminology is distinct and carefully explained in text and figures. This is the basis for the identification key. Different terminological "schools" exist in pollen morphology, but the Fægri–Iversen terminology seems to be the most simple and logical, which is a prerequisite for a reliable pollen key. This chapter could possibly have been illustrated by more stereoscanning pictures.

The chapter on production and dispersal of pollen grains has also been expanded due to the growing amount of literature and knowledge within this field. Experimental studies on present-day pollen dispersal during the last few years have given pollen analysts an instrument for a more thorough interpretation of pollen diagrams. This knowledge has given the pollen analytical biostratigraphy a paleoecological approach. It should have been possible to add still more information to this chapter, and also some illustrations.

The three chapters on peat, sediment and field technique are in all editions of the textbook much too abbreviated. However, the reader obtains an introduction with the most important references. The field technique is fundamental for a good result of a pollen-analytical study, and this chapter should have been expanded and better illustrated.

In the chapter on pollen diagrams a pollen analyst is looking for advice in arranging the pollen types into ecological groups. I am convinced that the experienced authors do have important contributions in this respect.

New results from studies on pollen production, absolute pollen frequency diagrams and forest soil profiles are added to the chapter on interpretation of pollen diagrams. It makes this chapter extremely valuable.

The chapter on error has also been expanded, and it is better illustrated than before. In the chapter on statistical errors three pages have been added on numerical treatment. However, also in this respect the pollen-analytical method has been treated more in detail. The literature dealing with multivariate analysis of pollen data is growing enormously, and young pollen analysts, as well as older ones who are not trained in mathematics, need much more advice

than can be found in this textbook. However, within the near future we will get a textbook dealing exclusively with numerical methods in pollen analysis.

I would also like to say that the chapter on pollen-analytical zones is old-fashioned. The modern terminology for stratigraphy, used in Pre-Quaternary geology for decades, has been introduced into Scandinavian biostratigraphy. One would expect to be given advice, with illustrated examples, on the usage of this important tool for subdividing pollen diagrams. In this textbook it is only briefly mentioned and discussed.

The last part of the book comprises the identification key. Though other, more complete keys are prepared and will be printed in the future, this Iversen key will remain indispensable for decades. It is based on an enormous experience in pollen-analytical research on NW European vegetational history combined with pollen morphological studies. The restricted selection of taxa is based on this experience. The terminology is simple and logic. However, the pollen analysts miss the pteridophyte spores in the key, since these are normally included in the analyses.

The textbook contains a valuable reference list. However, the literature is enormous within this wide field of science. The authors have made a good selection, but some important references are missing.

The conclusion is that this partly new book on pollen analysis stands out as an indispensable textbook for pollen analysts dealing with geological and paleoecological problems, as well as for taxonomists dealing with pollen-morphological problems.

Björn E. Berglund

Ferguson, I. K. & Muller, J. (eds.) 1976: *The evolutionary significance of the exine*. Linnean Society Symposium Series 1. VII + 591 pp. Academic Press Inc. Ltd., London, New York. ISBN 012 253650 9. Price £ 28.–.

The present volume is based on some twenty papers presented at an international symposium on the evolutionary significance of the exine held in London and Kew in 1974 under the auspices of the Linnean Society and the International Commission for Palynology. Studies on pollen and spore morphology, exine ultrastructure, formation and function of exine, pollen dimorphism etc. are included.

Sporopollenin, usually confined to pollen and spore exines, is known to occur in fossil cysts already in the Devonian or even earlier. A morphological feature like the proximal triradiate suture functioning as the germination site has persisted for a long time and through many types of spores and pollen. The exine evidently has a long fossil history.

The exine formation of species of *Pinus*, *Cosmos* and *Lilium* is strikingly similar while the ontogeny of Hepaticae spore walls differs both from pteridophytes and angiosperms.

The pollen wall shows a certain plasticity during the pollen development and carries physiologically active materials both from the sporophytic parent (exine domaine) and the gametophyte (intine domaine). These materials (enzymes) play a part in compatibility control. The ontogeny of the pollen grain wall of various genera in the Liliaceae, Juncaceae and Cyperaceae suggest phylogenetic relationships which are not obvious in mature pollen grains.

Studies on the arrangement of pollen grains during meiosis (successive and simultaneous types) are relatively few although they are essential in order to understand polarity, symmetry and aperture position. A close correlation between the simultaneous-type meiosis and the acquisition of radially symmetrical grains is suggested.

The major part of the book is devoted to the morphology of spore and pollen walls in taxa of the Hepaticae, Musci, Pteridophyta and Angiospermae. The ultrastructure of the walls as revealed by electron microscopy brings new information which aids in interpreting the taxonomy and phylogeny of several taxa.

The mature spore walls of Hepaticae consist of intine and lamellated exine which is reminiscent of the endexine in certain pollen walls. The spore walls of the Musci, generally consist of intine (endospore), exine (exospore) and perine (perispore). The perine appears to be absent in the Hepaticae spores which, however, have a more prominent and variable wall ornamentation than the Musci spores. The fine structure of the spore walls (exospore) of

Pteridophytes varies from group to group with reference to, e.g., relative position of the lamellated and non-structured exospore parts.

Taxa from nearly 50 angiosperm families were pollen-morphologically investigated. Morphological trends have been particularly emphasized. Within angiosperm taxa pollen apertural configurations are referable to two main models, "successiformy" and "breviaxy". Successiformy (tricolpate–pericolpate–periporate) is found in, e.g., the Centrospermae, Rosidae and Asteridae (sensu Takhtajan). Periporate conditions are also present in the Malvales, but the geometrical principle is different. The end result is due to disappearance of ectoapertures and spiralization of apertures.

In a survey of families of the Ranalean complex it was concluded that ancestral angiosperm pollen grains are large, boat-shaped, psilate, atectate, monosulcate and probably without endexine. Two clear-cut pollen types are reported in the Annonaceae. Outside the Ranalean complex the following families were treated: Anacardiaceae, Dichapetalaceae, Labiatae, Onagraceae, Sapindaceae, Saxifragaceae, Umbelliferae, and Xanthorrhoeaceae. Pollen dimorphism was reported in the Sterculiaceae and Commelinaceae.

In the Labiatae the ultrastructure of the opercula are of special interest as they may explain a possible passage from an operculum to a normal mesocolpium, i.e. passage from tricolpate to hexacolpate conditions. Based on the ectexine fine structure a number of patterns are recognized in the Onagraceae. The typical viscin threads are morphologically variable. In the Sapindaceae morphological trends of vegetative parts, flowers, and pollen grains are compared. As a result a new classification of the Sapindaceae is proposed. The concept "stereostructure" is further defined and illustrated in the Saxifragaceae. Numerical analysis of palynological characters supports the observations based on stereostructural study of only the exine and endoapertures. In the five pollen types in the Umbelliferae the exine changes from type to type, i.e., ectexine evolves with the change of pollen type. A number of pollen groups are recognized in the Xanthorrhoeaceae, the monosulcate pollen grains being derived from the liliaceous stock and the spiraperturate ones pointing towards the Eriocaulaceae.

The volume is a masterpiece from an editorial point of view. The grouping and sequence of papers and illustrations are logical and exemplary, and the printing is of excellent quality. The editors' hope that the symposium would function as a guide directing future studies in palynology is entirely fulfilled. *The evolutionary significance of the exine* is an indispensable book for institutes, libraries and scientists engaged in palynology.

Siwert Nilsson

Frey-Wyssling, A. 1976: *The plant cell wall.* Allgemeiner Teil, Band III (Cytologie), Teil 4 des Handbuches der Pflanzenanatomie (2. A.) von K. Linsbauer, fortgeführt von G. Tischler u. A. Pascher. Dritte, völlig neubearbeitete Auflage. XI + 294 Seiten mit 193 Abbildungen und 28 Tabellen im Text sowie auf 20 Bildtafeln. Verlag Gebrüder Borntraeger, Berlin–Stuttgart. ISBN 3-443-14009-2. Preis (Leinenband) DM 176.–.

In der von K. Linsbauer gegründeten Serie *Handbuch der Pflanzenanatomie* ist nun die Monographie *Die Pflanzenzellwand* in dritter, völlig neubearbeiteter Auflage erschienen. Der Autor, Prof. Frey-Wyssling, ist als Fachmann und Fachautor zahlreicher Lehrbücher internationell so wohlbekannt, dass er keiner Introduktion bedarf und dass man automatisch eine klar konzipierte moderne Monographie der kompletten Zellwand erwartet.

Das Buch ist in drei Abschnitte gegliedert und zwar in die Ultrastruktur und Biogenese der Zellwand, in die Biochemie der Zellwand und schliesslich in die Biophysik der Zellwand.

Die Entwicklungsgeschichte (Entstehung, Ultrastruktur und Wachstum) der einzelnen Zellwandschichten (M, P, S und T) und ihre Veränderungen im dritten Entwicklungsschritt (Inkrustation) werden im ersten Abschnitt ausführlich besprochen, gleich wie die Entwicklung lokaler Wandveränderungen (Differenzierungen). Der Abschnitt ist mit vielen instruktiven Abbildungen und elektronenmikroskopischen Aufnahmen versehen. Auffallend ist vielleicht das Fehlen rasterelektronenmikroskopischer Aufnahmen, die durch ihren dreidimensionalen Bildcharakter dort, wo es nicht gilt Mikrofibrillen abzubilden, instruktives Bildmaterial liefern.

Der Abschnitt Biochemie der Zellwand gliedert sich in die Besprechung der Zellwände der niederen (Thallophyten) und höheren (Kormophyten) Pflanzen. Der Autor weist im Vorwort darauf hin, dass die biochemische Forschung in letzter Zeit den Wissensumfang so erweitert hat, dass im Rahmen dieser Monographie nur eine stark kondensierte Darstellung möglich ist. Dennoch erscheinen Fragen nach der Kettenlänge der Nativcellulose, deren Polydispersität und intermolekulare Wasserstoffbrückenbindung etwas zu stiefmütterlich behandelt zu sein. Jeder Autor einer solchen Monographie steht vor besonderen Schwierigkeiten, wenn es gilt das gegenwärtige Wissen über die Konstitution des Lignins und insbesondere der Hemicellulosen auf wenige Buchseiten zusammenzufassen. Vielleicht wären hier besondere Hinweise auf ausführlichere zusammenfassende Darstellungen am Platze gewesen.

Der Abschnitt Biophysik der Zellwand umfasst teils die optischen Methoden (Röntgenanalyse, Lichtbrechung und -Doppelbrechung, Lichtabsorption, Dichroismus usw.) und wichtigen Ergebnisse in der Erforschung von Zellwandstrukturen, teils die physikalisch-chemischen Eigenschaften der Zellwandsubstanzen wie auch der Zellen bezw. Zellgewebe. Die stärkere Betonung der Eigenschaften des Holzes (spez. Gewicht, Wasseraufnahme, Schrumpfung, Festigkeitseigenschaften usw.) machen diesen Abschnitt besonders interessant für den Holzforscher.

Die wichtige Literatur ist bis 1974/75 grossteils berücksichtigt, was dem Buch besondere Aktualität verschafft.

300 Jahre Zellwandforschung haben eine solche Fülle von Erkenntnissen gebracht, dass man dankbar sein muss, wenn ein so berufener Fachmann die wichtigen Ergebnisse in einer leicht lesbaren, weniger als 300 Seiten umfassenden Monographie zu einem geschlossenen Überblick über den gegenwärtigen Stand der Zellwandforschung zusammenfassen konnte.

Das Buch kann nicht nur warm allen Botanikern sondern auch den Holzforschern sowie Agrar- und Forstwissenschaftlern empfohlen werden.

Erich Treiber

Harling, G. & Sparre, B. (eds.) 1973–1976: *Flora of Ecuador 1–5*. Swedish Natural Science Research Council, Editorial Service, Stockholm. Price SKr 35 + 25 + 35 + 50 (paperback). – Address for subscription: Swedish Natural Science Research Council, Editorial Service, P.O. Box 23136, S-104 35 Stockholm 23, Sweden.

In 1973 the first instalment of Flora of Ecuador appeared containing 47 pages about the family Cyclanthaceae by G. Harling. Since then the following families have been dealt with: Tropaeolaceae (31 pages) by B. Sparre 1973, Onagraceae (46 pages) by Ph. A. Munz 1974, Columelliaceae (5 pages) by K. Fagerström 1975, Lentibulariaceae (15 pages) by P. Taylor 1975, Plantaginaceae (16 pages) by K. Rahn 1975, and Umbelliferae (71 pages) by E. Mathias and L. Constance 1976.

The work is sponsored by the Swedish Natural Science Research Council and the Chief Editors are G. Harling and B. Sparre and the Assistant Editor is Uno Eliasson. The flora is issued at irregular intervals. The families are numbered and the circumscription follows Ed. 12 of Engler's *Syllabus der Pflanzenfamilien*. Each family of a reasonable size is allotted its own fascicle. Very small families are treated together with larger ones, e.g. 182 Columelliaceae and 183 Lentibulariaceae.

The treatment follows traditional lines. New taxa are described in the flora. There are not many references under the families and genera, but as far as can be judged full synonymy is given. The descriptions are elaborate but by no means too long. All specimens are cited for every species. This is a policy which might prove rather troublesome in 10 years' time with the numerous expeditions being carried out in Ecuador at the moment. In any case it will make the flora increasingly expensive both to print and to buy. Today most floras have abstained from this procedure because printing costs are rising every year. Plantaginaceae are dealt with on 14 pages; one third of these are locality lists. Some species which have not yet been found in Ecuador, but are known from neighbouring countries, have been included. *Centella asiatica* is an example: in this case the 21 synonyms might have been printed continuously in order to save paper. Illustrations are few and of varying technique; the most elegant ones are

those illustrating the Umbelliferae. Some families are not illustrated at all. Let us hope that in the future it will be possible to find funds to finance more line drawings.

The above should not be interpreted as a serious criticism. All in all this is a very promising beginning for a flora which will be of enormous dimensions as the area to be treated harbours a unique richness in plant species. It is difficult to give an exact number since each new expedition brings back numerous undescribed species, at a rough guess based on a moderate species concept it could amount to about 18,000 species. Let us hope that the Editors will not accept splitters among their men.

Kai Larsen

Miège, J. & Stork, A. L. (eds.) 1975: *Origines des flores africaines et malgaches. Progrès–conservation–écologie.* Comptes rendus de la VIIIe réunion de l'AETFAT, Vol. 2. Boissiera 24 b, pp. 423–692. Genève.

The eighth meeting of the "Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale" (AETFAT) was held in Geneva in September 1974. The first volume of the congress report consists of 47 papers concerning mainly the topic of this meeting: "The origin of the flora of Africa and Madagascar and the nature of speciation" (review in Bot. Notiser 1975 p. 371). Volume II, which is considered here, contains 64 papers grouped under four more general themes: "Nature conservation; Ecology–Mapping, their problems in the African flora; Progress made in the study of the African flora and vegetation; Progress made in the mapping of the African flora and vegetation". Unfortunately these headings are not given in the text.

In the first paper on Nature conservation the urgency for the governments in Africa to get important vegetation types protected is underlined. Out of 43 countries consulted only 23 gave more or less extensive reports. Only 13 countries are making improvements in nature protection. The conclusion is not new but important: in most of the countries the lack of financial resources limits the progress in conservation of nature. The intentions of the Threatened Plant Committee (TPC) were presented in the second paper. Specialists are invited to collaborate and an international (African) Tropical Garden is suggested to function as a refuge for species on the verge of extinction.

Under the Ecology–Mapping heading some disparate papers are collected: Phytogeography of Basse-Casamance; Phytogeographic importance of the Loma Mountains; The origin of the termitophile flora of Haut-Shaba; Fibre plants in Ghana. Two papers treat exhaustively the vegetation and the rôle of the epiphytic vegetation in Uluguru Mountains. A multicoloured large map (1:50,000) with 30 vegetation units is interfoliated inside the cover. In the text five more vegetation units are described and mapped, as well as important environmental factors for the vegetation.

Of interest for a broad public is the announcement of four new flora projects: Flora Macaronesica, Flora of Cape Coast, Ghana, Flore général de la Côte-d'Ivoire and Flore du Rwanda. These floras are planned to be published in many volumes and in the last two about 80% of the species will be illustrated. The area covered by these new floras has already partly been treated in larger flora projects: Flora Europaea (the Azores), Flora of West Tropical Africa and Flore d'Afrique Central. Despite this it is justified to start new local floras which can give a more precise and current picture of taxonomy and phytogeography for their respective areas.

The last 150 pages of this volume are occupied by detailed progress reports of plant-collecting, flora-writing and vegetation-mapping for various regions of Africa. Some diverse papers can be mentioned: Ecologic studies in pasture land at IEMVT (Institut d'Elevage et de Médecine Vétérinaire des Pays Tropicaux); A list of orchids in Côte-d'Ivoire; The history of the botanical exploration in Gabon. In this part of the volume the principle to start all articles on right-hand pages has become too space-consuming. In a volume of totally 270 pages it is too much with 40 blank pages. The 29 less-than-one-page articles could have been set in continuation under a Short Reports-heading.

The last paper in Volume II is worth noticing

for all botanists working at herbaria and with determination of African or Madagascan plants. It is a catalogue of "Which families are treated where" for the main floras of tropical Africa, Das Pflanzenreich IV and Die Natürlichen Pflanzenfamilien ed. 2. In this long table of the families it is also indicated which families are absent in the area covered by each flora. This last article is a good example of the practically useful knowledge often presented in the AETFAT-reports.

The articles of the second volume deal with a variety of subjects out of which only a few have been mentioned here. To sum up, the eighth Comptes rendus is a good continuation of the tradition of AETFAT to survey the progress made in botanical taxonomy and ecology in Africa.

Mattias Iwarsson

Moore, D. M. 1976: *Outline studies in biology. Plant cytogenetics*. 64 pp. Chapman and Hall, London. ISBN 0 412 13440 3. Price £ 1.30.

This slim volume gives a readable, up-to-date account of classical plant cytogenetics, i.e. the study of chromosomes at the light microscopic level. Far from being exhausted this branch of study is alive and kicking – a fair percentage of the references are from 1970 and later.

The book is one in a series of texts called *Outline studies in biology* intended – according to the editor's foreword – as guidebooks, not textbooks, presenting the conceptual framework within which biological research is progressing. The author is an experienced cytotaxonomist who himself has made important contributions in the field. The emphasis is on the mechanics of chromosome behavior and to some extent on evolutionary aspects. There is virtually nothing on cytological techniques – here the reader is referred to standard texts like Darlington and La Cour: *The handling of chromosomes*.

Cytogenetics dates its origin as an independent although composite branch of science to the early years of this century when the chromosomal theory of inheritance was proven by the Morgan school. It is still possible to present some of the current work at the frontiers of the discipline without loosing sight of the founding fathers. Prof. Moore has achieved this goal remarkably well. The senior undergraduate who wishes to gain an insight into this important field could hardly be given a better introduction.

Arne Strid

Smith, P. 1976: *The chemotaxonomy of plants*. In E. J. W. Barrington & A. J. Willis (eds.), Contemporary biology series. 313 pp., 63 figs., 26 tables. Edward Arnold Ltd., London. Price £ 13.– (board), £ 6.50 (paper).

This is virtually the first student text about the use of chemical data in botanical taxonomy. P. M. Smith of Department of Botany, University of Edinburgh has written a book which is quite readable for botanists as well as for chemists, although for different reasons, as will be discussed below.

The text is divided into 3 parts the first of which deals with the inherent possibilities of chemistry as a tool in systematic botany. Chemical reactions are the basis for development of the whole phenotype of any plant and the information used for this is buried in the chemical composition of the DNA of the cells. The use of chemical information from plants is placed in perspective with other taxonomic activities of the botanist, and this part of the book appears to be valuable reading for the phytochemist starting on taxonomic work. The author recommends teamwork involving both chemists and biologists, and chemists producing results on their own "should suggest what changes (in classification) are to be made, in as strident a fashion as possible".

The second part comprises 9 chapters of which the first 6 deal with micromolecular compounds, i.e., amino acids, phenolics, carbohydrates etc. Each chemical group is described and accounts are given about their variation among plants, about their function and taxonomic value. Important groups of compounds such as quinones, polyacetylenes and glucosinolates are not mentioned at all which seems strange as a chapter has been devoted to the taxonomically unimportant fatty acids. Two chapters treat proteins and nucleic acids while one is devoted to the technique and use of serological methods.

Examples of applications of chemotaxonomic methods form the third part of the book. One chapter deals with "The Case of the Bacteria" where the morphological characters are not sufficient for classification and where chemical methods have been used for a long time. Another chapter contains examples of the use of chemotaxonomy at different levels, among these also the betalain story. Finally phylogeny and the use of protein sequences for construction of phylogenetic trees are discussed.

The author is apparently not a chemist. We have noticed many errors both in the formulas (in 7 of the 24 formulas on pp. 92–93) and in the text. In the section about anthocyanidins some of the information is erroneous and the term anthocyanin is not even used, which is strange as these are the natural flower pigments. Several minor misunderstandings and/or mistakes can be found in the chapters dealing with chemistry.

Trivial errors like the above-mentioned are not really serious. It is more important that the author seems uninterested in biosynthesis as shown in the quotation (p. 7): "Unlike biochemists, taxonomists and evolutionists are only incidentally interested in molecules from the standpoint of how they may be synthesized or what their function may be". To a certain degree this principle is followed through the book. Biosynthetic evidence is only used in the negative sense as the reader is often warned that a compound may be biosynthesized through different pathways in unrelated plants (which is appropriate). Unfortunately, the positive evidence which can be deduced from biosynthetic sequences has been almost completely ignored. An example is the large, homogeneous group of indole alkaloids biosynthetically derived from the iridoids, which are monoterpenes. The two groups are naturally connected and this should to some degree be correlated with their distribution. Such connections can only be discovered by the use of biosynthetic evidence or by deduction using biosynthetic principles. Full use of the available information will perhaps demand the teamwork advocated by the author – also when writing a book on chemotaxonomy.

Despite these mainly critical remarks we can recommend the book as an introduction to the subject for botanists and chemists planning to start chemotaxonomic research. The references provide an entry to the recent phytochemical literature. Teachers will welcome it for their students as a textbook on a subject that has been missing so far.

The majority of professional taxonomists who have apparently been conservative in their view upon chemical characters will find many examples of successful applications here, especially at family and lower level.

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Chromosome numbers of Scandinavian Odontites species

Britt Snogerup

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The chromosome number has been determined for 29 populations. Aneuploidy and aneusomaty have been observed. Karyotypes are given for *Odontites verna* (Bell.) Dum. (2n = 40), *O. rubra* (Baumg.) Opiz (2n = 18) and *O. litoralis* Fr. (2n = 18). Both mitosis and meiosis were studied. Two theories of previous possible misinterpretation of the chromosome number of the diploids are given.

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Within Scandinavia the following taxa of *Odontites* have been recognized by different authors:

Odontites verna (Bell.) Dum.
Odontites rubra (Baumg.) Opiz (*O. serotina* Dum.)
  ssp. *rubra*
  ssp. *rubra* var. *pallida* Lange
  ssp. *rubra* f. *tescaria* K. Joh.
  ssp. *pumila* (Nordst.) U. Schneider
Odontites litoralis Fr.
  ssp. *litoralis*
  ssp. *litoralis* var. *baltica* Eklund ex Markl.
  ssp. *fennica* Markl.

O. verna is known only as a weed. It is distinguished from *O. rubra* in being few-branched, the branches (mostly in the upper part of the stem) making an acute angle with the stem. *O. rubra* is much-branched, the branches arising from the base of the stem at an obtuse angle. *O. rubra* is the commonest species, occurring in grassland, salt marshes and as a weed. The epithet ssp. *pumila* has been given to an extremely low-growing salt-marsh ecotype (Pedersen 1963). The epithets *verna* and *rubra* have both been used in a collective sense.

O. litoralis grows in salt marshes and on the brackish shores of the Baltic and is distinguished from *O. rubra* in having the first flower at the 5th–7th node, leaves shorter than the internodes and the style shorter than the upper lip of the flower. The epithets ssp. *fennica* and var. *baltica* were given to local races from the brackish shores of the Gulf of Finland and of the Åland Islands respectively (Marklund 1955).

Material and methods

The seeds of *Odontites* do not germinate unless exposed to low winter temperatures and moisture for 12–18 weeks (Vallance 1951). Seeds were sown in pots in December and placed in open frames at the Botanical Gardens, Lund, for 18 weeks and then moved to a greenhouse (15°C). Within a week the seeds had germinated. Seedlings were pretreated with a saturated solution of 1,4-dichlorobenzene for 1 1/2–2 hours (Lepper 1968), fixed in absolute alcohol:acetic acid (3:1) overnight, stained with Feulgen (hydrolysis 10 mins.) according to Lepper (1968) and then treated with a 5% aqueous solution of pectinase for 2–3 hours. The squash technique described by Östergren & Heneen (1962) was used on meristematic tissues of the plumule and lateral root-initials. Cell division had ceased in the radicle. If the Feulgen staining proved too weak aceto-carmine was added to the preparation. To prevent bleaching the slides were left in acetone only till the astralon coverslip loosened.

Slides for investigating meiosis were made from flower buds fixed overnight in absolute alcohol, chloroform and glacial acetic acid (6:3:1) and stained overnight in HCl-carmine at 60°C (Snow 1963). Excess stain was removed in 70% alcohol. Anthers were crushed in 45% HAc and squashed in a drop of Hoyer's medium under a glass coverslip (Beeks 1955). PMCs, pollen mitoses and dividing somatic tissues were studied. Well spread-out chromosomes were found in terminal cells of some anther hairs.

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Table 1. Previously published chromosome numbers of *Odontites*.

Species	2n	Counted by
O. rubra	20	Witsch 1932 as *O. serotina*, Rottgardt 1956, Sorsa 1962, Schneider 1964
O. rubra	18	Greilhuber 1971
O. litoralis	20	Sorsa 1963, Schneider 1964
O. verna	40	Witsch 1932, Rottgardt 1956, Schneider 1964

Other methods for preparing slides for chromosome counts were less successful. Pretreatment with colchicine and hydroxychinoline gave rise to overcontraction. Stickiness occurred in such preparations as well as in sections fixed in Navashin-Karpechenko.

Voucher specimens are deposited at LD.

Chromosome numbers and karyotypes

The previously published chromosome numbers in *Odontites* are cited in Table 1. The number 2n = 20 for *O. litoralis* published by Rottgardt in Tischler (1950) and in Rottgardt (1956) refer to erroneously determined material of *O. rubra* (Pedersen 1963). In Fedorov (1969) the number 2n = 20 for *O. rubra* is also cited from Rohweder (1937) and Tischler (1937) and 2n = 40 for *O. rubra* from Tischler (1934) and Soó (1959), but no counts of their own are given in these works. In the same work 2n = 20 is cited for *O. verna* from Fagerlind (1937), which must be a misprint for Fagerlind (1936). Fagerlind discusses chromosome numbers but no counts of his own for *Odontites* are given. Greilhuber (1971) presumes that previous reports of 2n = 20 are the result of misinterpretation. The chromosomes of *Odontites* are small and often show stickiness.

My investigations confirm the diploid number found by Greilhuber. In both mitosis and meiosis I have found 2n = 18 for *O. rubra* and *O. litoralis*. In each of 4 populations out of 20 I have found 1 aneuploid plant (Table 2). Three of them had 2n = 20 and the fourth 2n = 22. This plant showed abnormal meiosis with the metaphase configurations 6^{I}, 5^{II}, 2^{III} or 6^{I}, 8^{II}. Laggards occurred at anaphase. Meiosis was not studied in the other 3 aneuploids.

The normal diploid chromosome complement consists of 18 metacentric to submetacentric chromosomes (Fig. 1A–C). The chromosomes show a gradual decrease in size from 3.5 μm to

Table 2. Chromosome number of Scandinavian *Odontites* species. N = number of plants investigated. – 1 = Pollen mitosis. – 2 = Material corresponding to Marklund's ssp. *fennica*. – 3 = Material corresponding to Marklund's ssp. *litoralis* var. *baltica*. – 4 = Material corresponding to K. Johansson's ssp. *rubra* f. *tescaria*.

Locality	n	2n	N
O. rubra			
Sweden, Skåne, Klagshamn, BS 14	9		3
Sweden, Skåne, Sjötorp, BS 117	9		1
Sweden, Skåne, Ljunghusen, BS 118	9	18	3
Sweden, Skåne, Skanör, BS 119	9	18	5
		20	1
Sweden, Öland, L. Vickleby, Widén 030119		18	1
Sweden, Öland, Ventlinge, Widén 030115		18	1
Sweden, Gotland, Bälsalvret, T. Karlsson 030203[4]		18	1
Finland, Regio aboënsis, Nauvo, Lillandet, BS 97	9		1
	11		1
O. litoralis			
Sweden, Gotland, Klintehamn, BS 33		18	1
Sweden, Sörmland, Dalbyö, Breviken, BS 18		18	2
Finland, Karelia australis, Vilniemi, BS 66[2]		18	1
		20	1
Finland, Karelia australis, Hämeenkylä, BS 69[2]		18	1
Finland, Karelia australis, Pyötsaari, BS 74[2]	9	18	5
Finland, Regio aboënsis, Korppoo, BS 87[3]		18	1
Finland, Regio aboënsis, Korppoo, Korposträm, BS 91[3]		18	1
Finland, Regio aboënsis, Väättäinen, Vohlo, BS 100	9	18	3
Finland, Regio aboënsis, Lepäinen, BS 104		18	1
		20	1
Finland, Regio aboënsis, Kittamaa, Pitkäluota, BS 101		18	1
Finland, Regio aboënsis, Kustavi, Hannula, BS 108		18	1
Finland, Regio aboënsis, Röölä, BS 115		18	1
O. verna			
Sweden, Skåne, Kiaby, BS 120	20^{1}		1
		38	1
Sweden, Gotland, Ardre, BS 22		40	1
Sweden, Gotland, Faludden, BS 47		40	1
		39	2
Sweden, Gotland, Vägumeviken, BS 53		40	1
Sweden, Gotland, Tingstäde, BS 60	20^{1}	40	4
		38	1
Sweden, Gotland, Othem, BS 63		40	1
		38	1
Sweden, Gotland, Martebo, BS 61	20^{1}		2
Sweden, Gotland, Friggars, BS 64		40	1
		39	1
Sweden, Gotland, Fide, BS 45		40	1

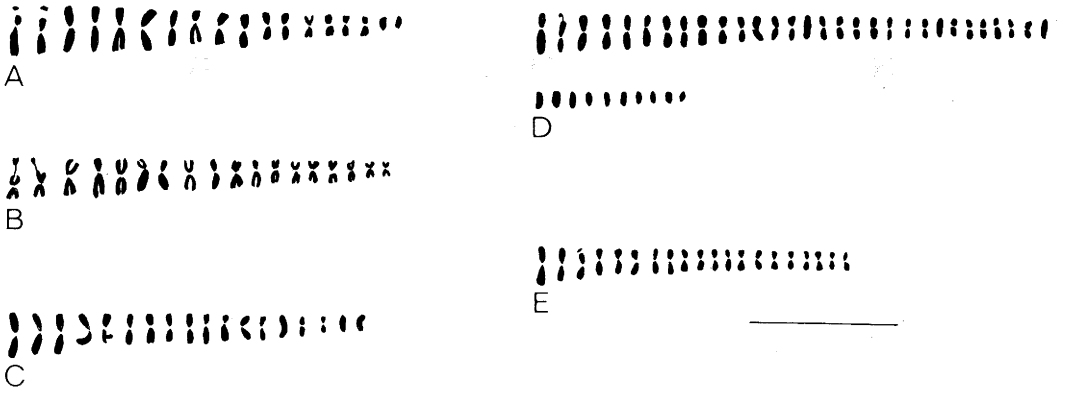


Fig. 1. Karyotypes of *Odontites*. – A: *O. rubra* (BS 119). 2n = 18. – B: *O. litoralis* (BS 33). 2n = 18. – C: *O. litoralis* (BS 74), material corresponding to Marklund's ssp. *fennica*. 2n = 18. – D: *O. verna* (BS 60). 2n = 40. – E: *O. verna* (BS 60). n = 20, pollen mitosis. – Scale 10 μm.

1 μm. A satellite is often visible on one of the longest pairs.

For *O. verna* I have found the numbers 2n = 38, 39, 40 (Table 2). The euploid number of *O. verna* is 2n = 40, which is confirmed in the pollen mitosis (Fig. 1 E). I have also found aneusomaty in some individuals where the numbers 36, 38, 39 and 42 are found together with the euploid number.

The chromosomes are metacentric to submetacentric. They range from 3 μm to 1 μm with a gradual decrease in size from the largest to the smallest. One of the longest pairs has a satellite (Fig. 1D).

In PMCs of *O. rubra* and *O. litoralis* one bivalent usually divides precociously giving the impression of 10 bivalents instead of 9 (Fig. 2B). At pachytene, diplotene and diakinesis a strongly staining aggregation can be seen on the nucleolus. It is probably heterochromatin belonging to the satellite chromosomes. The nucleolus is visible until late diakinesis. In counts made at diakinesis this aggregation could possibly be interpreted as a separate bivalent (Fig. 2C). Meiosis was normal in nearly all cells investigated.

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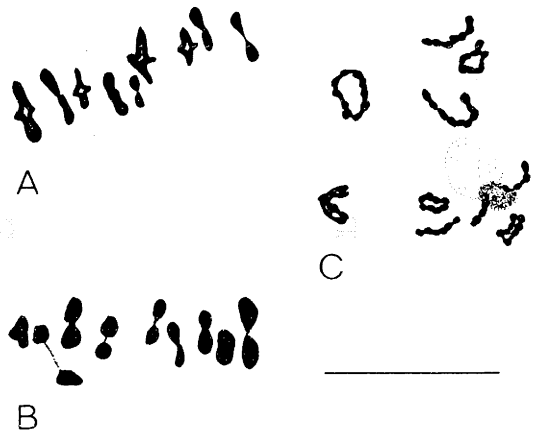


Fig. 2. PMCs of *Odontites*. – A: Metaphase I, *O. rubra* (BS 119). – B: Metaphase I, *O. litoralis* (BS 74), material corresponding to Marklund's ssp. *fennica*. One bivalent is in the process of dividing. – C: Diplotene–diakinesis, *O. rubra* (BS 14). A darkly staining aggregation is visible on the satellite chromosome and the nucleolus. – Scale 10 μm.

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Three new species of brown fruticose Cetraria

Ingvar Kärnefelt

Kärnefelt, I. 1977 06 30: Three new species of brown fruticose Cetraria. *Bot. Notiser 130:* 125–129. Stockholm. ISSN 0006-8195.

C. arenaria Kärnef. sp. nov., an American lowland species growing on sand and distributed from New England to the Great Plains of western Canada, with a disjunct occurrence in Colombia and *C. australiensis* W. Weber ex Kärnef. sp. nov., an alpine species from Australia, New South Wales, Snowy Mountains, are described and illustrated. *C. fastigiata* (Del. ex Nyl. in Norrl.) Kärnef. stat. nov., based on an infraspecific taxon of *C. delisei*, is redescribed, illustrated and one table is presented comparing it with *C. delisei*.

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When working with the brown fruticose *Cetrariae* I first noticed *C. arenaria* and *C. fastigiata* on herbarium specimens under other names. Only after having studied the plants in the field (*C. arenaria* in Maryland, Wisconsin, Massachusetts and Michigan and *C. fastigiata* in Alaska) did I become convinced of their status.

C. australiensis has been distributed in Lich. Exs. COLO 454 as *Coelocaulon australiense*, unpublished. For morphological, anatomical and chemical reasons the species is better accommodated among the brown *Cetrariae*.

A more extensive presentation of these species is to appear in a monograph (Kärnefelt in prep.).

I have examined all collections of *C. arenaria* and *C. fastigiata* in ABSL, CANL, COLO, FH, H, LE, LD, MICH, MIN, MSC, NEBC, S, UPS, US, WIS. Thin layer chromatography was carried out according to the method described by Culberson (1972).

C. arenaria Kärnef. sp. nov.

Holotypus: Michigan, on sandy soil, 35 miles west of St. Ignace on U.S. 2, 5.9 miles west of junction of M117 to Newberry, Mackinaw Co., 1949 Imshaug 5449 (LD).

Thallus fruticosus (1–)3–4(–7) cm longus, pars proximalis plerumque longe indivisa, partes distales pluries divisae. *Laciniae* (0.5–)1–4(–12) mm latae, leviter canaliculatae, partibus planis, marginibus hic inde pontibus connectis, dichotome divisae. *Superficies inferior* cinereo-brunnea vel pallide cinerea, raro obscure brunnea, laevis vel longitudinaliter porcata, opaca vel nitida. *Superficies superior* concolor vel saepe obscurior, laevis sed saepe rugis transversalibus distantibus munita, nitida, interdum opaca. Partes basales raro rubentes. *Pseudocyphellae marginales* plerumque praecipue partibus distalibus perspicuae. *Pseudocyphellae laminales* plerumque paucae, minutissimae, sed aliquando in partibus thalli expansis numerosae. *Margines laciniarum* prominentiis acicularibus, 0.5–1 mm longis munitae. *Apothecia* rarissima, marginalia ad apices laciniarum posita, discus 0.5–3 mm, obscure brunneus. *Sporae* octonae, hyalinae, ellipsoideae, 3.5–4 × 5.5–6 μm. *Pycnidia* rara terminalia in prominentiis maginalibus posita, microconidia bacillaria, circa 1 × 5 μm. Medulla K−, C−, KC−, PD−.

Thallus fruticose (1–)3–4(–7) cm large, proximally with usually long undivided portions and distally more densely branched. *Lobes* (0.5–)1–4(–12) mm broad, weakly channelled and with plane parts, lobe margins here and there folded together and connected with thallus bridges, dichotomously branched. *Lower surface* greyish brown to pale greyish, rarely dark brown, smooth or weakly ridged along the lobes, dull or glossy. *Upper surface* concolorous or often darker, smooth but with sparse transverse wrinkles, usually glossy, sometimes dull. Basal parts only rarely reddish. *Marginal pseudocyphellae*

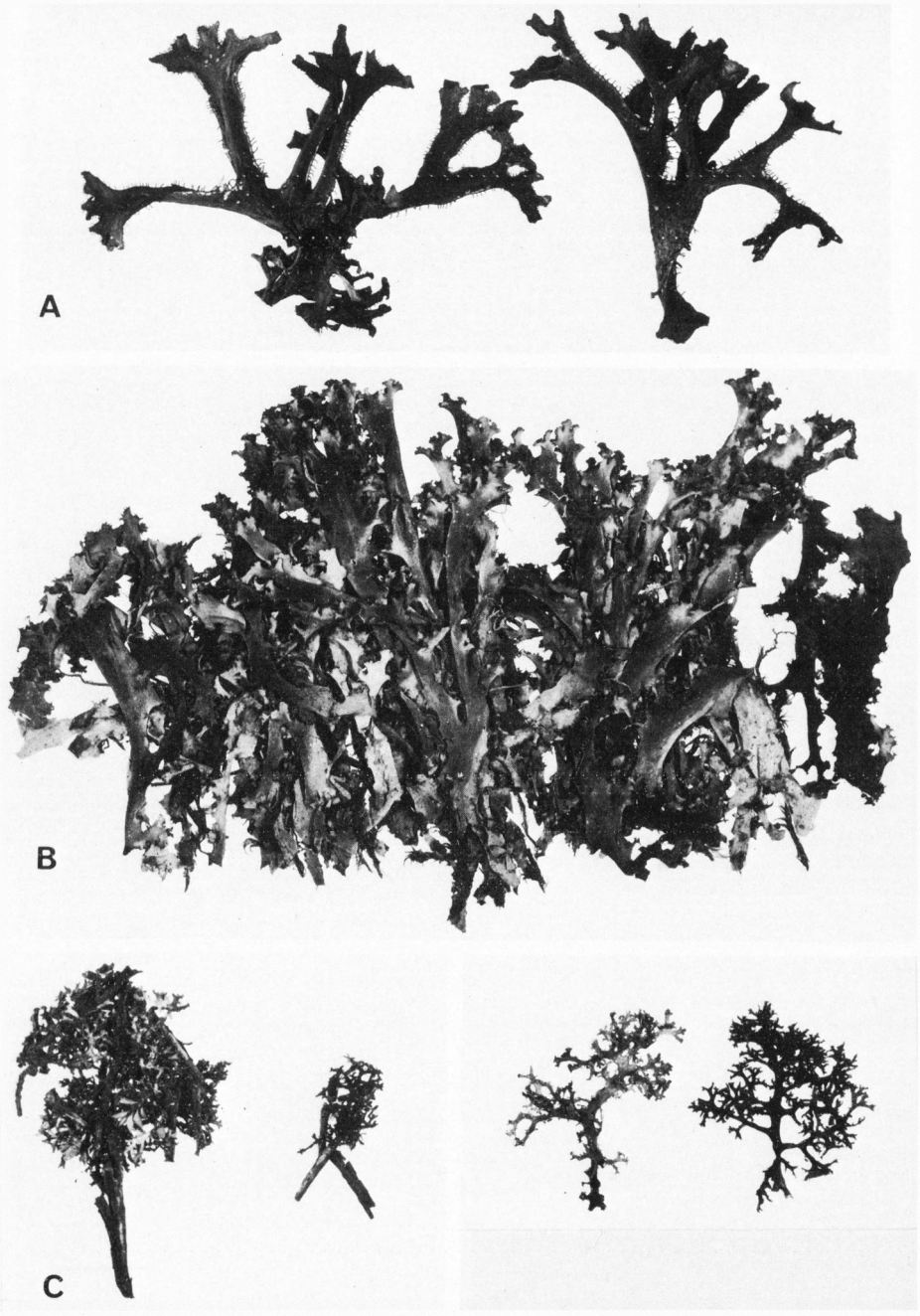


Fig. 1. A: *C. arenaria*. Minnesota, Polk Co., 1953 Thomson 17005 (WIS). – B: *C. fastigiata*, rather luxuriant specimen. Petsamo, 1931 Räsänen (H). – C: *C. australiensis*. Left specimens, New South Wales, 1968 Weber & McVean L-49746 (COLO); right specimens, 1967 Weber & McVean L-47321 (COLO). – All illustrations in natural size.

usually distinct, especially on the upper parts of the thallus. *Laminal pseudocyphellae* usually uncommon and very small, but occasionally numerous on expanded thallus parts and then larger. *Marginal projections* 0.5–1 mm long, acicular. *Apothecia* marginal on the lobe ends, very rare, disc 0.5–3 mm, dark brown. *Spores* 8 per ascus, hyaline, ellipsoidal, 3.5–4 × 5.5–6 μm. *Pycnidia* on top of the marginal projections, very rare; microconidia rod-shaped, about 1 × 5 μm. Medulla K−, C−, KC−, PD−.

C. arenaria (Fig. 1A) differs from *C. islandica* mainly in the acicular marginal projections and in the absence of distinct laminal pseudocyphellae. Otherwise the taxon has usually been referred to as *C. islandica* subsp. *crispa* (Brodo 1968) or as *C. ericetorum* (Taylor 1968) because of the PD negative medulla. *C. arenaria* also differs from *C. ericetorum* in the acicular marginal projections and the less channelled and flatter lobes. Chemically *C. arenaria* differs from *C. islandica* in the absence of fumarprotocetraric acid. However, the two species contain the same aliphatic compounds (lichesterinic and protolichesterinic acids). *C. arenaria* and *ericetorum* prove to have different aliphatic compounds when tested in the B-system (Culberson 1972) for the identification of lichen products.

C. arenaria is mainly a North American lowland species preferring sandy environments. The species is fairly common on the Atlantic seaboard from Maine, Massachusetts, Rhode Island, Connecticut to New York (Long Island). Inland it is found in Vermont, Pennsylvania, Maryland, Virginia, West Virginia and Ohio. However, the best-known localities are along the shores of Lake Michigan and Lake Huron. There has been a general agreement among American lichenologists that these plants merit nomenclatural recognition (Imshaug 1957). *C. arenaria* is also found on the eastern shore of Lake Superior and on the northern shore of Lake Ontario. The species occurs only scattered in Wisconsin, Minnesota, Manitoba, Saskatchewan and Alberta. *C. arenaria* also occurs in an isolated locality in Colombia, South America.

The species is named because of its preference for sandy situations.

Cetraria australiensis W. Weber ex Kärnef. sp. nov.

Holotypus: Australia, New South Wales, Snowy Mountains, Kosciusko State Park, summit of Mount Stilwell, Kangaroo Range, 1981 m.s.m., above Charlottes Pass, abundant locally on windswept heath of *Epacris petrophila–Baeckia gunniana*, occurring locally entangled in broom-like masses on dead twigs, 1968 Weber & McVean (Lich. Exs. COLO 454) (COLO).

Thallus fruticosus aliquantum *C. delisei* minutae similis, 1–2(–3) cm longus, pars basalis ad circa 0.5 cm, indivisa, partes distales densissime divisae, partes basales et laciniae principales 1.5–2 mm latae, saepe porcis longitudinalibus praeditae. *Laciniae* irregulariter vel dichotome divisae, 0.5–1 mm latae, fere planae vel laevissime canaliculate. Margines medio crassiores. *Superficies inferior* flaveo-brunnea vel obscure brunnea, laevis et opaca. *Superficies superior* concolor vel plerumque inferiore obscurior, laevis et opaca. Pars basalis laeviter rubens. *Pseudocyphellae marginales* punctiformes in superficie inferiore positae. *Margines laciniarum* prominentiis dispersis, circa 0.5 mm longis et cilis paucis, aliquanto divisis, 1–2 mm longis munitae. *Apothecia* ignota. *Pycnidia* rara terminalia prominentiis marginalibus praedita, microconidia bacillaria circa 1 × 6 μm. Medulla K−, C−, KC−, PD−.

Thallus fruticose somewhat resembling a tiny *C. delisei*, 1–2(–3) cm large, with an unbranched basal portion, about 0.5 cm, and distally more densely branched, basal part and main lobes 1.5–2 mm broad, often with longitudinal ridges. *Lobes* irregularly or dichotomously branched, 0.5–1 mm broad, almost plane or very weakly channelled. The margins usually thicker than the central parts. *Lower surface* yellowish-brown to dark brown, smooth and dull. *Upper surface* concolorous or usually darker, smooth and dull. Basal parts pale reddish. *Marginal pseudocyphellae* dot-like. *Marginal projections* about 0.5 mm, scattered. On the edges also a few branched cilia c. 1–2 mm long. *Apothecia* not known. *Pycnidia* rare, on top of the marginal projections; microconidia rod-shaped about 1 × 6 μm. Medulla K−, C−, KC−, PD−.

The species is accommodated in the group of brown *Cetrariae* because of the lobe form, the marginal pseudocyphellae on the lower surface and the marginal projections with terminal parmeliaceous pycnidia (Fig. 1C).

The cortical layers, 30–70 μm thick, consist of pachydermatous paraplectenchyma overlying a prosoplectenchymatous tissue. The medulla, 140–190 μm thick, is composed of loosely interwoven hyphae 3–6 μm thick. The algae of *Trebouxia* type, each 10–15 μm in diameter, are

Table 1. Comparison of *C. delisei* and *C. fastigiata*.

Species	Lobes	Lobe tips	Lower surface	Pseudocyphellae
C. delisei	weakly channelled to plane	acute or at least partly acute on wider lobes	smooth or wrinkled	marginal and laminal usually distinct
C. fastigiata	subtubular and cucullate	more obtuse	smooth and pitted	marginal almost indiscernible, laminal few, poorly developed

spread through the medulla or concentrated near the upper cortex.

The species produces lichesterinic and protolichesterinic acids, common in this group of lichens.

C. australiensis is only known from the Snowy Mountains in Australia, where it grows unattached but intertangled amidst twigs of small alpine shrubs or on the ground in protected depressions.

Cetraria fastigiata (Del. ex Nyl. in Norrl.) Kärnef. stat. nov.

Cetraria delisei (Bory ex Schaer.) Nyl. var. *fastigiata* Del. ex Nyl., Flora 52 p. 444 (1869), nomen nudum. – *Cetraria delisei* (Bory ex Schaer.) Nyl. ssp. *fastigiata* ("**C. fastigiata*") Del. ex Nyl. in Norrl., Not. Sällsk. Fauna Fl. Fenn. Förh. 13 p. 323 (1873). – *Cetraria hiascens* (Fr.) Th. Fr. var. *fastigiata* (Del. ex Nyl. in Norrl.) Wainio, Meddel. Soc. Fauna Fl. Fenn. 6 p. 119 (1881) and Ark. Bot. 8 (4) p. 23 (1909). – *Lectotype* (selected here): Finland, Enontekis, Hetta, 1867 Norrlin det. Nylander (H).

Thallus fruticose (1–)3–4(–6) cm large. *Lobes* 2–5 mm broad, canaliculate or almost tubular, dichotomously branched and the margins cucullate with short branchlets, lobe tips obtuse, basal parts more weakly channelled or plane up to 15 mm wide. *Lower surface* dark brown, grey-brown, yellow-brown or pale brown, smooth and pitted, usually glossy. *Upper surface* concolorous, more pitted, dull or glossy. *Marginal pseudocyphellae* very narrow and almost indiscernible. *Laminal pseudocyphellae* sparse and poorly developed. *Marginal projections* 0.1–1 mm, sparse or absent, rarely on the lobe tips. *Apothecia* marginal on the lobe ends, disc 2–10 mm, usually with a slightly wavy margin, dark brown or brown. *Spores* 8 per ascus, hyaline, ellipsoidal, 2.4–3.6 × 6–8.4 μm. *Pycnidia* on top of the marginal projections, dark brown; microconidia rod-shaped, about 0.5 × 5 μm. Medulla K−, C+, KC−, PD−. Contains gyrophoric and hiascinic acids.

The epithet, taken from a Delise herbarium name, was first mentioned by Nylander (1869), but without an acceptable description. A valid description was published a few years later by Nylander in Norrlin (1873). In this work Norrlin adopted Nylander's habit of marking infraspecific units above variety with an asterisk, as in the case of *C. fastigiata*.

C. fastigiata is readily distinguished from its closest relative *C. delisei* on the structure of the lobes and pseudocyphellae (Table 1). The lobes of *C. fastigiata* (Fig. 1 B) resemble more closely those of *C. cucullata* or *C. kamczatica* than the more finely divided lobes of *C. delisei*.

C. fastigiata is a poor competitor on the arctic tundra and occurs chiefly where minor depressions and bare spots form niches. It is also found in depressions in northern boreal bogs. Only rarely is *C. fastigiata* found in other habitats. The same kind of habitats are exploited by other brown *Cetrariae*, e.g. *C. andrejevii*, *C. delisei* and *C. nigricascens*. However, these species all have a much wider ecological amplitude and *C. fastigiata* consequently is the least successful.

C. fastigiata is found on Newfoundland, scattered in the Canadian Arctic and in Alaska. On the Eurasian continent *C. fastigiata* is distributed in the easternmost part of Siberia and from the Urals to northern Scandinavia.

Acknowledgements. I am very grateful to Dr Teuvo Ahti, Helsinki and Professor Rolf Santesson, Stockholm for nomenclatural and taxonomic comments on *C. fastigiata* and to Dr Irwin M. Brodo, Ottawa, Dr Richard C. Harris, Ann Arbor and Dr Henry A. Imshaug, East Lansing, for comments on *C. arenaria*. I gratefully acknowledge the honour Dr William A. Weber, Boulder, has paid me in allowing me to describe his unpublished Australian species. I am also grateful to Dr Ove Almborn, Lund, for criticism of the work and for correcting the Latin descriptions. The

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Galenia secunda (Aizoaceae) new to Europe

Lars Arvidsson and Magnus Lidén

Arvidsson, L. & Lidén, M. 1977 06 30: Galenia secunda (Aizoaceae) new to Europe. *Bot. Notiser 130:* 130. Stockholm. ISSN 0006-8195.

Galenia secunda (L. fil.) Sonder is reported from the province of Cadiz, S Spain. The species is native to S Africa. It probably came to Europe by human activity.

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In 1968 a specimen of *Galenia secunda* (L. fil.) Sonder was collected in S Spain. As far as we know, no *Galenia* has been collected in Europe before. The Spanish plant agrees well with the description given by Adamson (1956) except that the leaves are alternate only in the upper parts of the stems. Some specimens in S, determined by Adamson, also have opposite leaves, however, and Sonder (1862) states that the young leaves are often opposite. Our plant is rather robust with large flowers (perianth lobes 3.0–3.2 mm long), red anthers and a gynoecium with five styles. It agrees well with the type in herb. Thunberg (UPS). *Galenia secunda* is evidently very close to *G. pubescens* (E. & Z.) Druce, which is said to be green and less hairy and with perianth segments 2.0–2.5 mm. Both species are very polymorphic and many subspecific taxa have been described. However, the somewhat larger flowers and the dense hairiness of our specimen seem to justify our determination.

The Spanish specimen (prov. Cadiz, 2 km N Chiclana de la Frontera, 21.4. 1968, Strandhede et al. 826 (GB)) was found on saline soil near the Atlantic Ocean in company with *Arthrocnemum glaucum, A. perenne, Beta macrocarpa, Limoniastrum monopetalum, Mesembryanthemum nodiflorum, Salsola soda* and *Suaeda vera.*

Galenia secunda probably came to Europe by human activity. The plant is indigenous to South Africa (Adamson 1956) and southern Namibia (Friedrich 1972). It has also been collected in Florida, USA (Curtis 6869 (S) "the seeds evidently brought in ballast") and in Adelaide, S Australia (Kaspiew 35 (S)).

The occurrence of *Galenia secunda* in Europe is not very remarkable since several other species of the Aizoaceae have been naturalized here. At least seven of the eleven species of Aizoaceae mentioned in Flora Europaea (Tutin 1964) originate from S Africa.

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Moesziomyces, a new genus of Ustilaginales

Kálmán Vánky

Vánky, K. 1977 06 30: Moesziomyces, a new genus of Ustilaginales. *Bot. Notiser 130:* 131–135. Stockholm. ISSN 0006-8195.

A new genus of Ustilaginales, *Moesziomyces,* is described. The genus is characterized by many-spored, permanent spore balls in which the spores are bound together by surface ornaments appearing as meshes, or at the margins as thin irregular wings, when the spores are separated. There is no columella in the sori. The following new combinations are made: *Moesziomyces bullatus* (Schröt.) Vánky (type species of *Moesziomyces*), *M. evernius* (H. Syd.) Vánky, *M. globuligerus* (Berk. & Br.) Vánky and *M. penicillariae* (Bref.) Vánky.

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The genus *Tolyposporium* was erected by Woronin (1882) for *Sorosporium junci* Schröter. A description of *T. junci* is provided for comparison with the species segregated here in the new genus *Moesziomyces*.

Tolyposporium junci (Schröt.) Woronin

Sori small, tumor-like (Fig. 1 A, B) in the flowers (often involving only part of the inflorescence, the capsule or only the base of the inflorescence and spreading to the adjacent bracts and rachis), less often in the stems, forming a naked, black, granular agglutinated spore mass, composed of spore balls. *Spore balls* (Figs. 1 C, 2 A–C) variable in form and size, globose, subglobose, elongated or irregular, 16–50(–80) μm long, opaque, dark chestnut-brown to black-brown, composed of 3–40 or more spores. *Spores* (Figs. 1 D, 2 D) subglobose to more or less angular, often rounded cuneiform and irregular, (6.4–)8–13.6(–16) μm in diameter, chestnut-brown to black-brown, smooth on the contact surface and provided with irregular warts on the free, slightly convex surface. The wall is unequally thick and may vary from 0.5–4 μm within the same spore. *Type* on *Juncus bufonius* L., Silesia, Carlowitz near Breslau (at present Wroclaw, Poland), coll. J. Schröter.

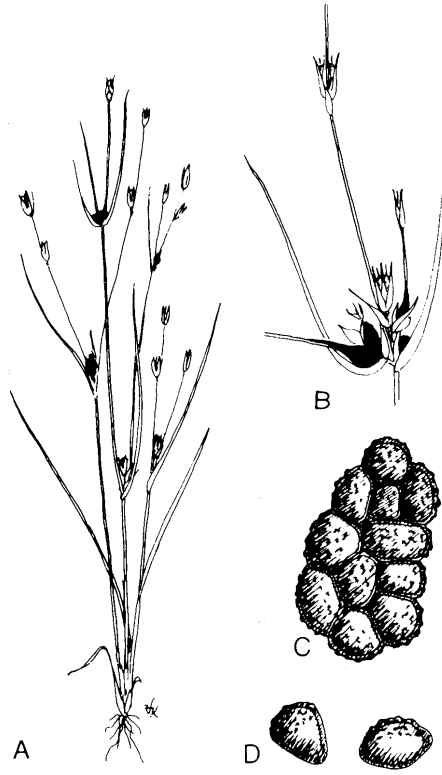


Fig. 1. *Tolyposporium junci* on *Juncus bufonius*. – A: The host plant with the fungus sori, × 0.6. – B: The sori, × 3. – C: Spore ball, × 625. – D: Spores, × 625.

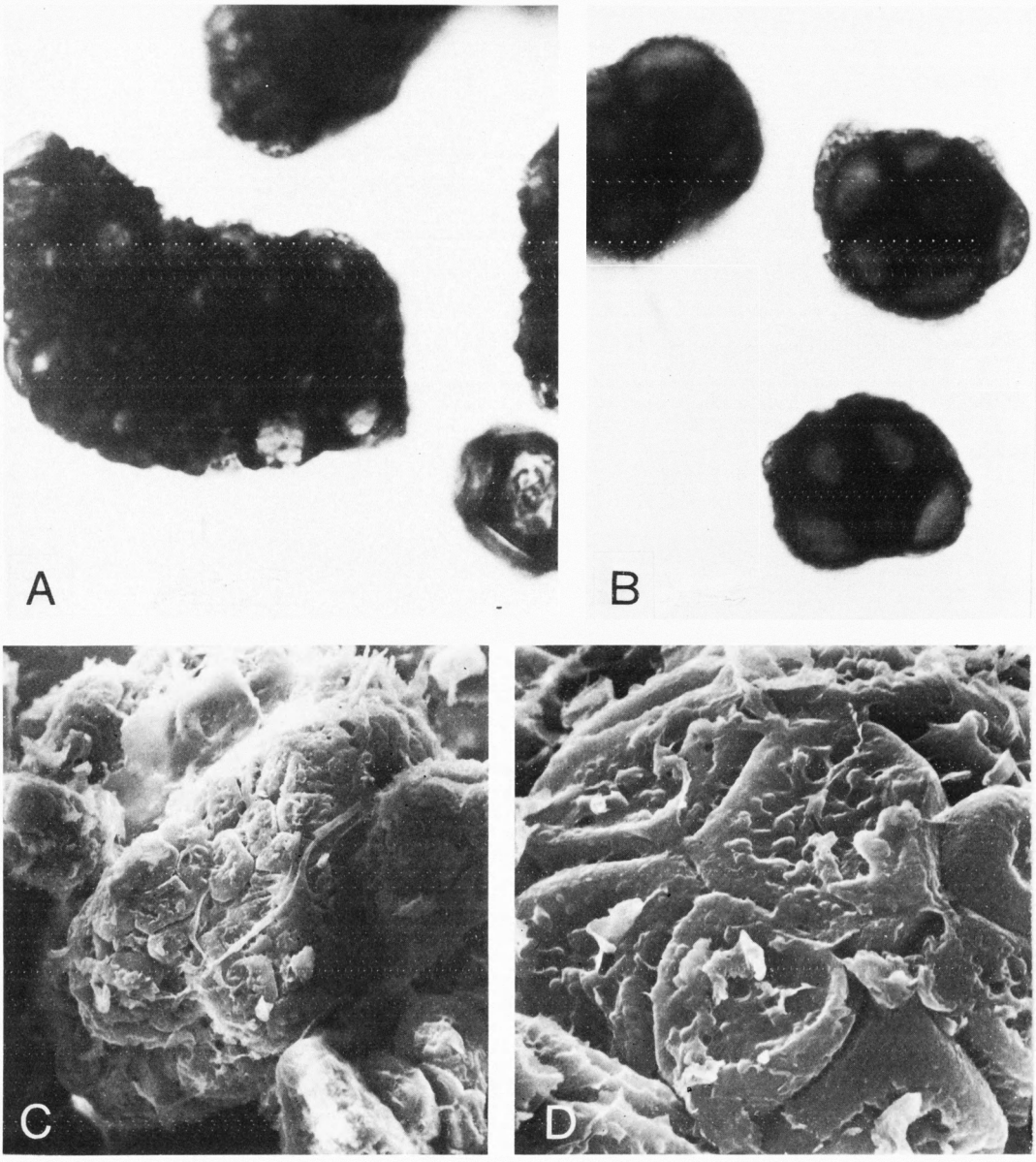


Fig. 2. *Tolyposporium junci*. – A, B: Spore balls, LM × 1100. – C: Spore balls, SEM × 630. – D: Spores in a spore-ball, SEM × 2420.

Distribution: on *Juncus bufonius* L.: Europe, N. America; on *J. capitatus* Weig.: Europe (Poland, Sweden).

The heterogeneity of Tolyposporium

Over the years numerous species of fungi with spore balls and an uncertain systematic position have been included in the genus *Tolyposporium*. Consequently this genus became heterogeneous

containing species with widely different morphology and biology. So far about 40 species have been referred to this genus. Some of them belong to the genus *Thecaphora,* e.g. *Tolyposporium davidsonii* Dietel & Holway which in fact is conspecific with *Thecaphora pilulaeformis* Berkeley & Curtis, on *Isocoma veneta* (Compositae), or *Tolyposporium iresine* Elliot which is *Thecaphora iresine* (Elliot) H. S. Jackson on *Iresine celosina* (Amaranthaceae). Several species of *Tolyposporium* turned out to belong to the genus *Sorosporium,* e.g. *T. anthistiriae* P. Henn., *T. cenchri* Bref., *T. christensenii* Ragunath, *T. everhartii* (Ellis & Galloway) Dietel, *T. filiferum* Bussee, *T. tristachidis* (Sydow) Zundel. *Tolyposporium cocconii* Morini on the leaves of *Carex* spp. belongs to the genus *Schizonella* with all the characteristics of this genus, except for one: the spores in pairs are agglutinated in smaller or larger balls. *Tolyposporium crepidis-rubrae* (Jaap) Ciferri is a species of *Entyloma. T. glabrum* Ciferri belongs to the genus *Sphacelotheca; T. bursum* (Berk.) Mc Alpine to the genus *Ustilago; T. junci* Lind (non Woronin) is *Cintractia lidii* Liro and *T. junci* (Schröt.) Woron. *β. johansonii* Blytt on *Juncus bufonius* is *Urocystis johansonii* (Lgh.) Magnus. The genus *Glomosporium* (type: *T. leptideum* Sydow, in the seeds of *Chenopodium album* L.) was separated from the genus *Tolyposporium. Tolyposporium eriocauli* Clinton was recently transferred to the genus *Dermatosorus* (Whitehead & Thirumalachar 1972). Several species of *Tolyposporium* are Fungi Imperfecti e.g. *T. chloridis* P. Henn. (!), *T. pampeanum* Speg., *T. philippinense* H. & P. Sydow, *T. reticulatum* Speg. and *T. volkensii* P. Henn. (!).

Apart from the above-mentioned species, the genus *Tolyposporium* is still rather heterogeneous. However, there is a group of 4 or 5 species with common characteristics which are still quite different from the type of the genus (*T. junci* (Schröt.) Woron.). For this small group of fungi belonging to the family Ustilaginaceae, it proves necessary to set up a separate genus, for which I propose the name *Moesziomyces,* in honour of the Hungarian mycologist Gusztáv Moesz (1873–1946).

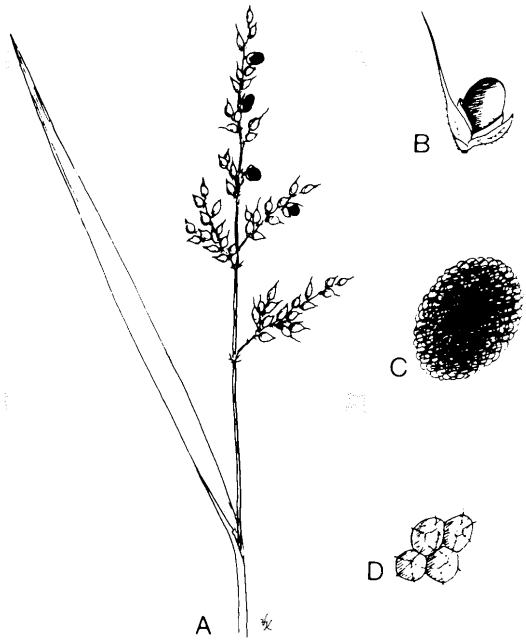


Fig. 3. *Moesziomyces bullatus* on *Echinochloa crus-galli.* – A: The host plant with the fungus sori, × 0.6. – B: One sorus in a spikelet, × 3. – C: Spore ball, × 140. – D: Spores, × 625.

Moesziomyces Vánky gen. nov.

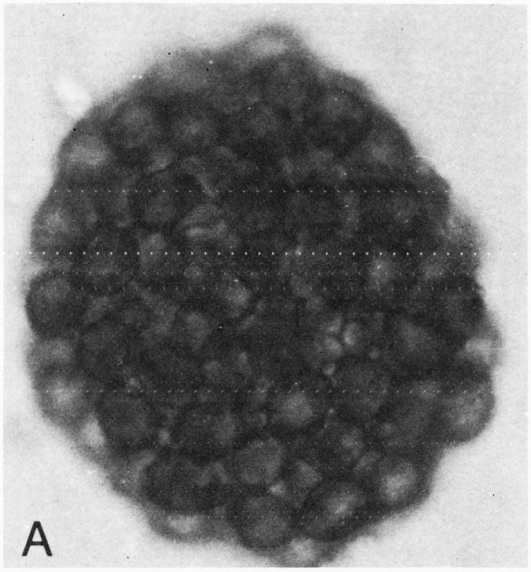
Typus generis: *Moesziomyces bullatus* (Schröter) Vánky.

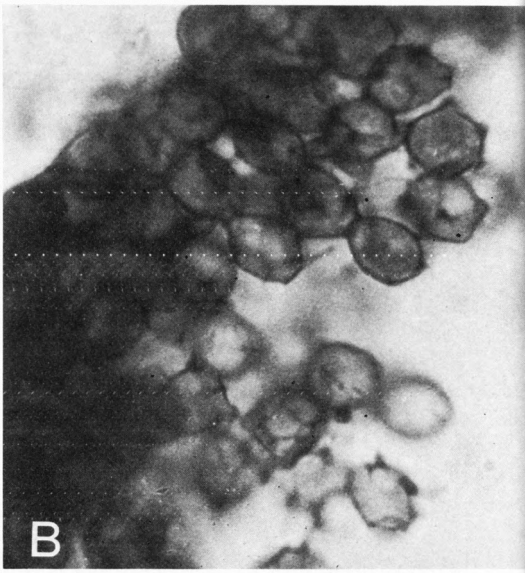
Sori ovariicoli, sine columella; sporae in glomerulis multisporis ornamentis superficialibus firme conjunctae, haec aspectu macularum irregularium reticuli vel, ad margines sporarum separatarum, alarum irregularium.

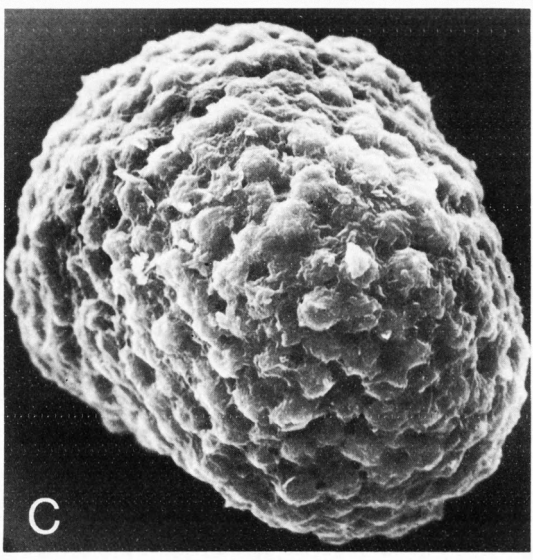
Sori in the ovaries, without columella. *Spores* in many-spored spore balls firmly agglutinated by surface ornaments appearing as irregular meshes, or at the margins as thin irregular wings when the spores are separated.

Moesziomyces bullatus (Schröter) Vánky comb. nov.

Sorosporium bullatum Schröt., Abh. Schles. Ges. Vaterl. Cultur, Abth. Naturw. Med. 1869–72: 6, 1869. – *Tolyposporium bullatum* (Schröt.) Schröt., Krypt. Fl. Schles. 3: 276, 1887. – *Type* on *Panicum crus-galli* L. (=*Echinochloa crus-galli* (L.) Beauv.), Germany, Silesia, near Liegnitz (at present Legnica in Poland), Sept. 1869, coll. Schneider, in Rbh. Fgi. eur. 1489 (!).







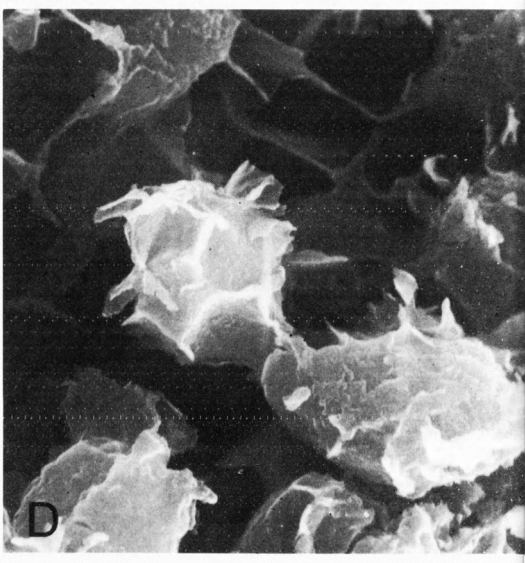


Fig. 4. *Moesziomyces bullatus*. – A: Young spore ball, LM × 1100. – B: Spores, LM × 1100. – C: Spore ball, SEM × 500. – D: Spores, SEM × 2450.

Sori in the ovaries (Fig. 3A, B), usually infecting occasional ones, globose to ovoidal, 2.5–4 mm in length, covered by a smooth, first green, later brown membrane which ruptures irregularly disclosing a granular, black-brown spore mass composed of spore balls. The sori lack a columella and are often detached entirely. *Spore balls* (Figs. 3C, 4A, C) varying in shape and size, globose, subglobose, ovoidal, elongate to irregular, dark brown, opaque, 50–220 × 60–320 μm in diameter, composed of many (often several hundred), firmly agglutinated spores. *Spores* (Figs. 3D, 4B, D) globose, ovoidal to irregular, slightly polyhedral, 6.4–8(–8.8) × 7.2–10.4(–12)

μm in diameter, semi-hyaline to light yellowish-brown, bound together by surface ornaments appearing as meshes, or at the margins as thin irregular wings, when the spores are separated (Fig. 4D). The immature spores are round, while the mature spores often become slightly polyhedral as a result of mutual pressure.

Distribution: on different species of *Echinochloa:* Asia, Europe and North America.

Moesziomyces evernius (H. Sydow) Vánky comb. nov.

Tolyposporium evernium H. Syd., Ann. Myc. 37: 443, 1939. – *Type* in the ovaries of *Paspalum distichum* L., Akalgarh, Punjab, W. Pakistan, coll. S. Ahmad (!).

Tolyposporium paspali Langdon, Papers Univ. Queensland, Dept. Biol. 2(9): 4, 1948. – *Type* in the ovaries of *Paspalum distichum* L., Enoggera Creek, Ashgrove, Brisbane, Queensland, Australia, 2.III. 1943, coll. R. F. N. Langdon (!).

Distribution: on *Paspalum distichum* L.: Asia (China, India, W. Pakistan), Australia.

Moesziomyces globuligerus (Berkeley & Broome) Vánky comb. nov.

Thecaphora globuligera Berk. & Br., Trans. Linn. Soc. Lond., Bot. II, 1: 407, 1880. – *Tolyposporium globuligerum* (Berk. & Br.) Ricker, Journ. Myc. 11: 112, 1905. – *Type* in the ovaries of *Leersia hexandra* Swartz, Brisbane River, Queensland, Australia.

Testicularia leersiae Cornu, Ann. Sci. Nat. Bot. VI. 15: 275, 1883. – *Ustilago leersiae* Durieu, in Cornu, Ann. Sci. Nat. Bot. VI. 15: 274, 1883. – *Type* in the ovaries of *Leersia hexandra* Swartz, Algeria, VIII. 1862, coll. M. Letourneaux.

Distribution: on *Leersia hexandra* Swartz: Africa (Algeria, Ivory Coast, Morocco, Nyasaland, Uganda), N. and S. America, Asia (India), Australia; on *L. japonica* Makino: Asia (China).

Moesziomyces penicillariae (Brefeld) Vánky comb. nov.

Tolyposporium penicillariae Bref., Unters. Gesammt. Mycol. 12: 154, 1895. – *Type* in the ovaries of *Penicillaria spicata* Willd., about Febr. 1891, coll. A. Barclay.

Tolyposporium senegalense Spegazzini, Ann. Museo Nac. Hist. Nat. 26: 118, 1914. – *Type* in the ovaries of *Penicillaria typhoidea* Fig. & De Not., W. Africa: Senegal, Dakar, XII. 1913, coll. C. Spegazzini.

Distribution: on *Pennisetum glaucum* (L.) R. Br. (= *P. americanum* (L.) Schum., = *P. typhoideum* L., = *Penicillaria typhoidea* Fig. & De Not., = *P. spicata* (L.) Willd.): Africa (common), S. Asia (India).

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Miscellaneous notes on algal taxonomy and nomenclature IV

Peter S. Dixon and Linda M. Irvine

Dixon, P. S. & Irvine, L. M. 1977 06 30: Miscellaneous notes on algal taxonomy and nomenclature IV. *Bot. Notiser 130:* 137–141. Stockholm. ISSN 0006-8195.

(1) The correct name for the North Atlantic species of *Furcellaria* is *F. lumbricalis* (Huds.) Lamour. (2) *Petrocelis cruenta* J. Ag. must be typified by material at LD, in Herb. Alg. Agardh. 27581. (3) *Rhodophyllis divaricata* (Stackh.) Papenf. must be typified by the original description of *Fucus bifidus* Huds., in the absence of material. (4) With regard to names applying to species of *Gelidium* it is shown that *G. corneum* var. *latifolium* must by typified by material collected at Sidmouth, now at E; that *Fucus pusillus* Stackh. must be typified, provisionally, by material at BM; that *Fucus crinalis* Turn. must be typified by material in BM-K; and that *Fucus corneus* var. *sesquipedalis* Clem. must be typified by material at LD, in Herb. Alg. Agardh. 32975. (5) *Scinaia turgida* Chemin must be typified by material at LD, in Herb. Alg. Agardh. 32180.

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The following notes refer to further taxonomic and nomenclatural problems detected during preliminary work for the first volume (Rhodophyta) of the forthcoming *Seaweeds of the British Isles* (Dixon & Irvine 1977).

The correct name for the North Atlantic species of Furcellaria

The genus *Furcellaria* was described by Lamouroux (1813 p. 45, reprint p. 25) and at the time he included two species, *F. lumbricalis* (based upon *Fucus lumbricalis* var. α Turn.) and *F. fastigiatus* (based upon *Fucus lumbricalis* var. β Turn.). The former species was selected as the lectotype of the genus *Furcellaria* by La Pylaie (1829 p. 66).

Lamouroux's reference is to Turner (1802 p. 317–320) where the latter distinguishes varieties α and β of *Fucus lumbricalis* having either 'lineari-lanceolate cylindrical binate pods, often an inch long' or 'apices very short, diaphanous, of an ovate, or ovato-lanceolate form, compressed, and of a pale-pink colour'. Later, Turner (1808 p. 11) calls these varieties α *lumbricalis* and β *fastigiatus*. From the accompanying illustrations, it is clear that the former represents tetrasporangial plants and the latter spermatangial plants of the species currently but erroneously known as *Furcellaria fastigiata* (L.) Lamour. Turner gives a number of references under his *F. lumbricalis* var. β but *Fucus fastigiatus* L. (1753 p. 1162) is not among them. In fact, in both 1802 (p. 309, p. 315) and 1808 (p. 9) Turner gives *F. fastigiatus* L. as the basionym of *Fucus rotundus* var. γ *fastigiatus* (L.) Turn. Although Linnaeus's plant was shown by Drew (1958 p. 750) also to be representative of the taxon under discussion, she comments that "those familiar only with the usual form found on the Atlantic shores might well be excused for being uncertain of its identity ... Waern ... considers the specimen now selected as the type (Pl. 62 a) to be 'like an old piece of *Furcellaria fastigiata*, which may be found dropped on the roads of Gotland', i.e. what is known in those parts as Kräkel. Comparison of the specimen of Pl. 62

and photographs of Baltic specimens of *F. fastigiata* given by Waern certainly support this statement." A combination based upon *Fucus fastigiatus* L. would however be a later homonym of *Furcellaria fastigiata* Lamour. Drew also investigated the application of the binomial *Fucus lumbricalis* Huds. (1762 p. 471). There is a specimen bearing this name in the Herbarium of the British Museum (Natural History) (BM) which appears to have belonged to Hudson and since Hudson changed the name later (1778 p. 589, *Fucus furcellatus*) it must be an early specimen if not the type. It is proposed to accept this specimen provisionally as having lectotype status. As shown by Drew, it is a typical plant of the species under consideration. Under *Fucus lumbricalis* var. α, Turner (1802) quotes a number of references including '*Fucus lumbricalis*' in Gmelin (1768 p. 108, t.6, f.2) and Goodenough & Woodward (1797 p. 204). Both of these works attribute the binomial to Hudson (1762 p. 471), so the combination becomes *F. lumbricalis* (Huds.) Lamour., the correct name for the taxon in the genus *Furcellaria*.

The typification of Petrocelis cruenta J. Agardh

The species *Petrocelis cruenta* was described by J. Agardh (1851 p. 490) without citing any specimens, but giving the habitat as 'ad oras Hiberniae, Angliae et Galliae'. The Irish record is evidently based on Harvey (1847 pl. 117, as '*Cruoria pellita*') and the English one upon Berkeley (1833 pl. 1, fig. 3, as '*Chaetophora pellita*'), both of which are quoted by J. Agardh, the latter with a query. In the Agardh Herbarium at Lund (LD) are two specimens, nos. 27580 and 27581, sent by the brothers Crouan from Brest, collected on 8th December 1849, which presumably provide the record for France. There is also a pencil sketch by J. Agardh apparently made from no. 27581, a mica preparation. This sketch shows the intercalary tetrasporangia with cruciately arranged tetraspores typical of the genus *Petrocelis* (first described by J. Agardh in the same publication) but not actually mentioned in the species description. Harvey, in his illustration, shows only undivided tetrasporangia and therefore it seems appropriate to select the Crouan specimen preserved on mica, Herb. Alg. Agardh. no. 27581, as the lectotype of *Petrocelis cruenta* J. Ag.

The typification of Fucus bifidus Huds.

Bifida divaricata Stackhouse (1809 p. 95, 97) is derived from *Fucus bifidus* Huds. (1778 p. 581) and shares the same type, as does *Rhodophyllis divaricata* (Stackh.) Papenf. (1950 p. 190) (*Rhodophyllis* Kützing (1847) has been conserved against *Bifida* Stackh.). Hudson's *Fucus bifidus* is a later homonym of *F. bifidus* S. G. Gmelin (1768 p. 201); the combination *Rhodophyllis bifida* must therefore be treated as a new name and attributed to Kützing (1847 p. 23). Papenfuss discussed the interpretation of the binomial *Fucus bifidus* Huds. and concluded that it is synonymous with *Rhodymenia palmetta* sensu Grev. (=*R. pseudopalmata* (Lamour.) Silva). The evidence for this assumption appears to be based on a statement by Turner (1809 p. 5) that Sir Thomas Frankland had sent him an original specimen of Hudson's, which Turner illustrates on Plate 73 (Fig. g). It is known, however, that Hudson's interpretations of his own 'species' changed a great deal over the years. In view of the information given by Frankland in an unpublished paper presented to the Linnean Society in June 1806 that his first correspondence with Hudson took place in 1782, when he sent specimens from Scarborough for identification, it seems likely that any specimens and comments passed to Frankland by Hudson represented the latter's later views. In fact, the wording of Hudson's original description: 'Fronds 1–1 1/2 inches, translucent, once and then immediately twice bifid, cuneiform or dilated towards the apex, flat, veinless, purple, diaphanous' would seem more closely to describe *Rhodophyllis divaricata* than *Rhodymenia pseudopalmata*. Further, the former species occurs not infrequently on the Hampshire coast (e.g. Southsea Castle), whilst the latter appears to be rare in the area. It seems reasonable, therefore, to accept Hudson's original description as the lectotype of *Fucus bifidus* and that it refers to the plant currently known as *Rhodophyllis divaricata*.

The typification of names applying to species of Gelidium

Identification of specimens of *Gelidium* has always been notoriously difficult, so much so that Bornet referred to it as "genre diabolique". The difficulties have been caused by the very great

morphological plasticity shown by all entities growing under different environmental conditions and by uncertainties in the application of names caused by improper typification.

Sequential observations of marked plants have indicated that there are only three species in the British Isles – *G. latifolium* (Grev.) Born. & Thur., *G. pusillum* (Stackh.) Le Jol., and *G. sesquipedale* (Clem.)Thur. This represents a marked reduction from the number of species accepted in the most recent revision in Europe (Feldmann & Hamel 1936). The attribution of species, sensu Feldmann & Hamel, is as follows:

Present treatment	Feldmann & Hamel
Gelidium latifolium	*G. attenuatum* *G. latifolium*
Gelidium pusillum	*G. crinale* *G. pulchellum* *G. pusillum*
Gelidium sesquipedale	*G. sesquipedale*

In general, the axes of the *G. pusillum* aggregate are cylindrical although the tips may become somewhat spathulate during the winter months while those of the *G. latifolium* aggregate are predominantly flattened but becoming more terete during the winter months. Both *G. latifolium* and *G. pusillum* occur on the Atlantic coast of Europe from southern Norway to Gibraltar (although of limited occurrence in the North Sea) and also in the Mediterranean. *G. sesquipedale*, in comparison, is one of the few species of the genus with little variation of external form other than in size. It is of rare occurrence in Devon and Cornwall, extending to Mauritania and into the Mediterranean.

Despite the need for accurate typification in a genus where the taxonomy has become so confused, little has been achieved. Dawson (1953) made a few comments on those entities which occurred on the Pacific coast of North America while Segi (1963) attempted to typify many epithets in the genus. The work of Dawson is somewhat unreliable while the supposed typifications of Segi are largely meaningless.

The following comments are offered on the typification of entities relevant to the British flora.

Gelidium corneum var. **latifolium**

This variety was described by Greville (1830 p. 143) on the basis of material from 'Trevone Bay, Cornwall, and Waldon rocks, Torbay, Mrs. Griffiths. Sidmouth and Torquay'. The Greville collection in the herbarium of the Royal Botanic Garden, Edinburgh (E), contains one sheet apparently with material from both Waldon Rocks and Trevone Bay, a second sheet with several specimens from Trevone Bay and a further sheet with a single specimen from Sidmouth. Of these, the single specimen from Sidmouth best shows the characteristics of the taxon, as now understood, and this has been selected as lectotype. The variety was given specific status by Bornet & Thuret (1876).

Fucus pusillus Stackh.

The original treatment of *Fucus pusillus* by Stackhouse (1795 p. 16) was based on material collected at Sidmouth. Attempts at typification were made by Dawson and Segi: Dawson (1953 p. 62) states 'the whereabouts of the original material unknown to the writer'; the comments by Segi (1963) refer to specimens of no relevance to the typification of *F. pusillus* Stackh.

Material possibly relevant to the typification has been found in two herbaria.

(1) The British Museum (Natural History), London (BM), possesses one sheet apparently received directly from Stackhouse himself. This sheet, with two small clumps of material, is annotated '*Fucus pusillus* Ner. Brit.' in Stackhouse's hand and 'J. Stackhouse' on the reverse in the same hand. A second specimen received through the Skrimshire herbarium is annotated '*Fucus pusillus*. Stackh. Ner. Brit. 6. This was sent to me by D. Turner, who had it from Mr. Stackhouse – 1797', in Skrimshire's hand.

(2) The Lamouroux herbarium at the Laboratoire de Botanique, Caen (CN) contains a specimen annotated '*Fucus pusillus* Ner. Brit.', in Stackhouse's hand, filed in carton 19, folder 153.

The first specimen listed above has been accepted provisionally as lectotype of *F. pusillus* Stackh.

Fucus crinalis Turn.

The description of *Fucus crinalis* given by Turner (1819 p. 4) is based on various collections, which

are cited as follows: 'On the English and Irish coasts. – Rocks in the sea at Sheringham in Norfolk. – At Sidmouth, growing on *F. abrotanifolius*. Mrs. Griffiths. – Near Ilfracombe. Mr. Hare. – Rocks at Kilmouth in Cornwall. Mr. Rashleigh. – At Brighton, forming large patches on the flat chalk-rocks about low water mark. Mr. Borrer. – Sides of Belfast Lough. Mr. Templeton'. In addition, Turner describes *β tricuspidatus*, based on material received from Mertens, originating on the French coast, to which Thore had applied the manuscript name *'Fucus tricuspidatus'*.

Turner was obviously uncertain as to the attribution of various entities now referable to the genus *Gelidium* since most specimens of that genus in his herbarium are inadequately labelled. This is in marked contrast to other genera, where specimens are fully labelled and, when used as the basis for an illustration, this is clearly stated.

The Kew algal collection, now at the British Museum (Natural History) contains the following material.

(1) A specimen labelled 'Sidmouth Nov 1807 Mrs. Griffiths', in Turner's hand.

(2) Several small clumps of material, associated with two labels, one annotated in Borrer's hand 'Fucus crinalis fr. Brighton July 1812'.

(3) Five specimens mounted on three small pieces of paper, two annotated 'Turner's Herb.', in Hooker's hand, and 'Gelidium crinale J. Ag.', in A. D. Cotton's hand. In addition, one is annotated in A. D. Cotton's hand: 'This is Turner's idea of *G. crinale* and may be taken as type f.[ide] WAS[etchell]'.

(4) Several specimens on small pieces of paper, associated with a label annotated 'From the sandpool Sidmouth around every side. The same as Mr. Stackhouse found small black tubercles scattered on the stem & leaves', in Mrs Griffiths's hand, with two other annotations, 'F. pusillus' and 'corneus var young', in unknown hands. In view of the statement by Turner that Mrs Griffiths's material was collected as an epiphyte on *F. abrotanifolius* and the uncertainty that the label refers to the material with which it is now associated, it would seem best to reject this material from consideration in the typification.

There have been various attempts to typify *Fucus crinalis*. Most accept the material from the Kew Herbarium which Setchell regarded as 'Turner's idea of *G. crinale'*. Setchell apparently removed a portion of this, as Gardner (1927 p. 277) refers to having 'examined a sterile fragment of the assumed type of *G. crinale* Turn., obtained from the Herbarium at Kew, England, by W. A. Setchell'. Dawson (1953 p. 64) comments that the type 'may be considered to be a specimen without locality data from the Turner Herbarium, now in Kew, England. It is annotated 'This is Turner's idea of *G. crinale* and may be taken as type. f. W.A.S.'; he also removed a fragment, now preserved in the Herbarium of the Allan Hancock Foundation, University of Southern California, Los Angeles (HAHF), as specimen 55234. The material Setchell, Gardner and Dawson were dealing with had at least passed through Turner's hands, even if it is of uncertain type status. Of the specimens Segi (1963 p. 514) comments on, however, none can be considered as type material of *Fucus crinalis* Turn.

Selection of the type locality has also posed problems. Turner states that his illustration was based on a specimen collected by Hare: 'to him I am indebted for the specimen here figured, as well as for the name now given to it'. Dawson uses this statement as an indication of the typification but then gives the type locality (Dawson 1953 p. 64) as 'rocks at Kilmouth, Cornwall, England'. This choice results from a misreading of the data presented by Turner due to the curious punctuation used by the latter. The Hare locality is, in fact, 'near Ilfracombe', the collection from Kilmouth, Cornwall having been made by 'Mr. Rashleigh'.

The specimen annotated by Setchell is probably the best choice which can be made at the present time, although the specimen should not be regarded as of higher status than provisional lectotype.

Fucus corneus var. **sesquipedalis** Clem.

This varietal epithet, the basionym of *Gelidium sesquipedale*, was applied by Clemente (1807 p. 317) to plants from Algeciras (Spain). The present location of Clemente's herbarium is unknown and there is every indication that it has been destroyed. There is material sent by Clemente to C. Agardh in the Agardh Herbarium at Lund (LD); a fragment sent by Clemente to Turner, which was present in the Kew Herbarium in 1958, cannot now be located in the material transferred to the British Museum (Natural History) (BM-K).

It would seem best to accept one of the Clemente specimens at Lund as being of provisional lectotype status; the most appropriate is Herb. Alg. Agardh. 32975.

The typification of Scinaia turgida Chemin

Setchell (1914) suggested that there were several species confused in Europe under the name *S. furcellata* (Turn.) J. Ag., now known as *S. forcellata* Biv. (see Dixon & Irvine 1977). Setchell's suggestion was taken up by Chemin (1926) who demonstrated that the entity known as *S. furcellata* var. *subcostata* J. Agardh differed markedly from *S. furcellata* var. *furcellata* in terms of structure, reproduction and spore germination. Chemin proposed that this variety be given specific status but used the epithet *turgida* on the grounds that it is more appropriate than *subcostata*. The later suggestion by Hamel (1930) that the epithet *subcostata* should be used is incorrect, since an epithet has no priority outside its rank.

S. turgida Chemin and *S. furcellata* var. *subcostata* J. Agardh share the same type i.e., the material collected in Tangier and now filed in the Agardh Herbarium, Lund (LD), as Herb. Alg. Agardh. 32180.

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A new species of Crepis from Mt Olympus, Greece

Arne Strid

Strid, A. 1977 06 30: A new species of Crepis from Mt Olympus, Greece. *Bot. Notiser* 130: 143–145. Stockholm. ISSN 0006-8195.

Crepis pawlowskii sp. nov. is described from beech forest on Mt Olympus. It is related to *C. geracioides* Hausskn. and *C. viscidula* Froel.

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Crepis pawlowskii Strid sp. nov. – Fig. 1

Herba perennis, 50–70 cm alta, e rhizomate obliquo surgens. *Folia* caudicalia 7–17 × 2–4 cm magna, oblanceolata, petiolis brevibus, profunde runcinate pinnatifida vel lyrata. *Caulis* a basi unicus, erectus, in media planta et supra ramificatus, 3–15 capitulis terminatus, folio caulino unico deminuto ramum infimum fulgente, foliolis ad ramificationes superiores bracteaceis. *Pedunculi* tenues, 3–8 cm longi, ad apices versus non incrassati. *Capitula* erecta circiter 40-flora. *Involucrum* cylindricum, 11–13 × 5–8 mm magnum, glabrum, minute nigro-papillatum. Foveolae receptaculi plerumque ciliis marginatae. *Corolla* 16–20 mm longa, saturate flava; tubus pilis crispis praesertim supra vestitus. *Achenium* glabrum, ad apicem versus attenuatum, nullum tamen rostrum manifestum formans, 8–10 carinis crassis aliisque tenuioribus costatum. *Pappus* albus, 6–8 mm longus, biserialis, pilis basi 30 μm crassis.

Perennial, 50–70 cm high. *Rhizome* oblique, 15–30 × c. 8 mm, bearing many long, fleshy fibres c. 1 mm in diameter. *Caudical leaves* 6–8, ascending, 7–17 × 2–4 cm, oblanceolate, acute to subobtuse, gradually attenuate into a narrow winged petiole c. 1/5 as long as the blade; deeply runcinate-pinnatifid to lyrate, the terminal lobe large, hastate, the lateral lobes narrow, distinctly retrorse; pubescent below, especially on the mid-vein, with white, eglandular, rather short and coarse hairs, glabrescent above. *Stem* single, erect, terete, fistulose, striate, branched at the middle and above, 3–15-headed; sparsely pubescent below, glabrescent above; with a single, 3–7 cm long, linear, entire cauline leaf at the lowest branching, and very small, bract-like leaves at the upper branchings. *Peduncles* suberect, slender, 3–8 cm long, not thickened towards the apex, without or with 1–2 minute bracts, nearly glabrous except for a tuft of crispate hairs just below the head. *Heads* erect, rather large, about 40-flowered; involucre cylindrical, 11–13 × 5–8 mm. *Outer bracts* 6–8, 1/4–2/5 as long as the inner, ovate-lanceolate, acute, margin somewhat scarious and often finely lacerate towards the apex. *Inner bracts* 12–16, linear-lanceolate, acuminate, ciliate in the apical 2–3 mm. Both outer and inner bracts glabrous on both sides, but especially the inner densely covered with minute black papillae on the upper surface, and with a dorsal crest near the apex. *Receptacle* flat, alveolate; the pits without rim, usually fringed with thin, white, 0.5–0.8 mm long cilia. *Corolla* 16–20 mm long, bright yellow; ligule 2–3 mm wide, teeth c. 0.4 mm long, subacute, with a crest of papillae. Corolla-tube 5–7 mm long, crispate-hairy, especially above. *Anther* tube c. 4.5 × 0.8 mm; appendages very small, oblong, obtuse; filaments c. 2 mm long. *Style* branches c. 2 mm long, uniformly thick, obtuse, greenish, with erecto-patent scabridity. Mature *achenes* not seen; half-mature ones medium brown, glabrous, 5–6 mm long, attenuate towards the apex but not distinctly beaked, with 8–10 coarse and some finer ribs, calloused at base, with a slightly expanded pappus disk at

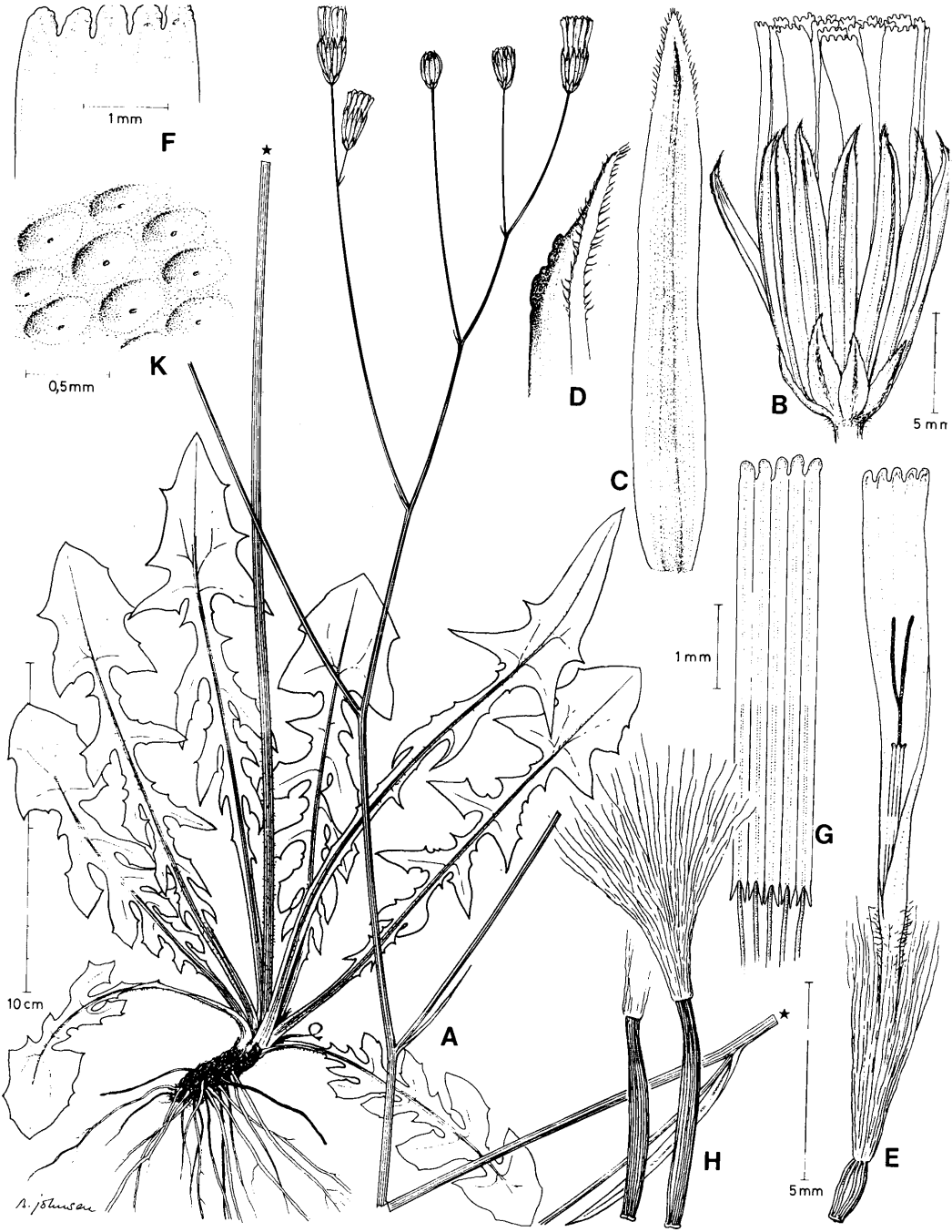


Fig. 1. *Crepis pawlowskii* Strid sp. nov. – A: Habit. – B: Capitulum. – C: Inner involucral bract seen from the outside. – D: Upper part of ditto, seen from the side to show dorsal crest. – E: Floret. – F: Upper part of ligule, to show papillate structure of teeth. – G: Anther tube. – H: Two half-mature achenes. – K: Part of receptacle to show alveolate structure (cilia not drawn, apparently sometimes lacking).

apex. *Pappus* white, 6–8 mm long, 2-seriate; pappus hairs c. 30 μm wide at the base.

Belonging to sect. *Desiphylion,* and apparently related to *C. geracioides* Hausskn. and *C. viscidula* Froel. (cf. Babcock, Univ. Calif. Publ. Bot. 22: 226–232, 1947), but distinct on account of its very reduced cauline leaves, slender peduncles which are not thickened towards the apex, glabrous involucre, often ciliate receptacular pits, and thinner pappus hairs.

The specific epithet commemorates the distinguished Polish botanist Professor B. Pawlowski who lost his life in a climbing accident on Mt Olympus in 1971.

Orig. coll. Greece, Thessaly, Mt Olympus: NW part, 8.2 km from the village of Petra along forest road to Kokkinoplos, 860 m, at the point where the road crosses lower part of Xerolakki Rema. *Fagus* forest in ravine. Strid & Kjellsson 11161, 4.6. 1976 (ATH holotype, C, LD isotypes). The species is only known from this gathering.

Acknowledgements. The field work on Mt Olympus was supported by a grant from the Carlsberg foundation. The Latin diagnosis was prepared by Dr T. Christensen, and the illustration by Mr B. Johnsen.

Chrysochromulina pyramidosa sp. nov. (Prymnesiophyceae) from Danish coastal waters

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Thomsen, H. A. 1977 06 30: Chrysochromulina pyramidosa sp. nov. (Prymnesiophyceae) from Danish coastal waters. *Bot. Notiser 130:* 147–153. Stockholm. ISSN 0006-8195.

Chrysochromulina pyramidosa sp. nov. is described on the basis of electron microscopy of shadowcast whole mounts, prepared from water samples collected in October 1975 at two localities in the Storebælt (Denmark). The saddle-shaped cell possesses two smooth flagella and a short haptonema. The cell surface is covered with scales of two types. The underlying scales are circular, flat, wide-meshed plates, whereas the outer scales have a pyramidal superstructure on an otherwise similar base-plate.

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The genus *Chrysochromulina* was established by Lackey (1939) to comprise a "three-flagellated", golden-brown organism observed in the Scioto river system of Ohio, U.S.A. Lackey (1939) stated that one flagellum was directed forwards; this one was heavier than the two others and was held rigid when the organism was at rest. The two other flagella were posteriorly directed and thinner, and when the cell rested, they were often kept undulating. The locomotory difference noted by Lackey was later ultrastructurally substantiated. Parke et al. (1955, 1962) showed that the anterior flagellum (haptonema in Parke et al. 1955) had a fine structure different from that of usual flagella. Christensen (1962) established a separate class – Haptophyceae – for this and related genera previously placed in the Chrysophyceae. Because of recent recommendations in the International Code of Botanical Nomenclature, Hibberd (1976) proposed that the name Haptophyceae should be replaced by the name Prymnesiophyceae.

Including the new taxon to be described below, there are now 29 named species of *Chrysochromulina,* 28 of which are brackish/marine. Only the generic type species *C. parva* Lackey thrives in freshwater. Leadbeater (1972) listed 22 species; the increase in number is due to the following species: *C. pontica* Rouchijainen (1966), *C. orbiculata* Rouchijainen (1972), *C. campanulifera* Manton & Leadbeater (1974), *C. adriatica* Leadbeater (1974), *C. birgeri* Hällfors & Niemi (1974), *C. spinifera* (Fournier) Pienaar & Norris (1976), and *C. pyramidosa* sp. nov.

Records of *Chrysochromulina* species from Danish waters are rather sparse, at least regarding the number of localities involved. *C. parva* has been recorded from the freshwater lake Haarupsande (Kristiansen 1971) and from the oligohaline lake Selsø (Wøldike 1973). Manton & Leadbeater (1974) reported 19 marine *Chrysochromulina* species from the east coast of North Jutland, five of them also from the west coast. Apart from these findings, a previously unpublished find of *C. ericina* Parke & Manton from the Kattegat bay Isefjorden (District Ks) is included in the check-list of Danish marine algae by Christensen & Thomsen (1974).

Investigations on marine nanoplankton flagellates from the Baltic, the Danish Sounds, and the Kattegat carried out during 1975/76 have provided new information on the occurrence of known *Chrysochromulina* species, and in addition have uncovered some apparently undescribed species.

The present paper deals with the description of *C. pyramidosa* sp. nov.

Chrysochromulina pyramidosa Thomsen sp. nov.

Cellula ephippioides, 3 μm longa, 4 μm lata; flagella bina 10–13 μm longa, haptonema 5–6 μm longum. Squamae dimorphae, aliis e laminis solum constitutis, aliis e laminis et machinis superimpositis. Squama prioris gregis orbicularis, circiter 0.7 μm diam., 24 costis radiantibus et 7–8 anularibus concentricis fere aequidistantibus ornata, costa anulari marginali aliis crassiore. Squama alterius gregis e lamina illius satis simili, 0.8–0.9 μm diam., 27–28 costis radiantibus et 8–9 anularibus ornata, anularibus interioribus aequidistantibus, marginali crassiore a vicina distantiore, et quattuor trabeculis crassis e margine laminae surgentibus machinam pyramidiformem super illam formantibus constituta.

In aqua subsalsa lecta salinitatis 14 ‰ temperaturae 11.5 graduum Celsii die 21 Oct. anni 1975 prope Asnæs e freto danico Storebælt hausta, figura 1 A typifica monstrata.

Cell saddle-shaped, 3 μm long × 4 μm wide; two flagella 10–13 μm long, and a haptonema 5–6 μm long. Scales of two types. Some are plate-like, circular, approximately 0.7 μm in diameter, with a pattern of radiating ridges (24 in number), and 7–8 nearly equidistant concentric rings, the ring at the edge being thicker than the others. The second type of scales have a plate-like base which is constructed in a similar way with a diameter 0.8–0.9 μm, 27–28 radiating ridges, and 8–9 concentric rings. The innermost rings are equidistant, the distance between the outermost thicker ring and the next ring somewhat greater. From the margin of the plate four thick struts branch off creating a pyramidal superstructure.

Found on October 21st 1975, in sea water samples from Asnæs, the Storebælt, Denmark. Salinity 14‰, temperature 11.5°C. Holotype Fig. 1 A.

Material and methods

The sub-surface water samples used for this investigation were collected in October 1975, at two localities in the Storebælt (Asnæs (55° 38.5′ N, 10° 46.5′ E) and Spodsbjerg (54° 56′ N, 10° 53′ E)), Denmark. The preparation of the whole mounts for electron microscopy took place on board the oceanographic vessel "Martin Knudsen".

The water samples were collected by means of a 5 l water bottle and immediately filtered through a 20 μm net in order to remove the larger organisms. The resulting nanoplankton suspension was concentrated by gentle centrifugation. Whole mounts were prepared by transferring small drops of the resuspended pellet of material onto carbon/formvar coated grids. Fixation was made in osmic vapour. After complete drying, the grids were washed for c. 10 min. in redistilled water in order to remove salt crystals. When completely dry, the grids were stored in gelatine capsules. The subsequent handling of the grids took place at the Institut for Sporeplanter, University of Copenhagen. Grids were shadowcasted with gold/palladium, and examined in a JEM-T8 electron microscope at the Institut for Sporeplanter.

Observations

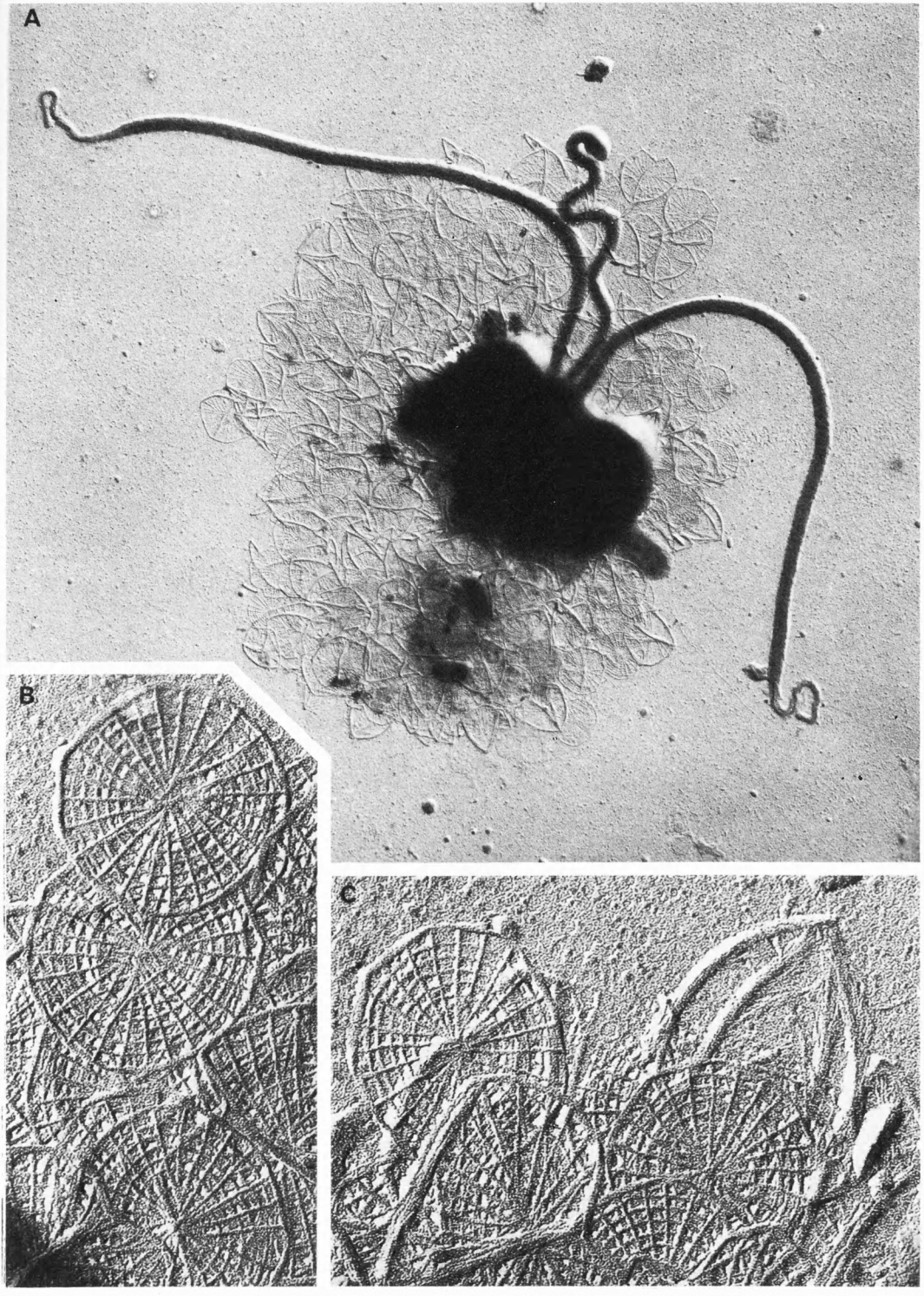
Chrysochromulina pyramidosa occurred in small numbers in the samples. The description of the external morphology is based on electron microscopical evidence only. Light microscopical information is not an absolute necessity for the description of a *Chrysochromulina* species. This is due to the fact that the by far most important specific characteristic within this genus is the scale structure, which can only be clarified by means of the electron microscope. In considering measurements of body size as well as length of flagella and haptonema, allowance must be made for shrinkage during processing of the cells for whole mounts.

The haptonema of *C. pyramidosa* measures 5–6 μm, which is about twice the body length and approximately half the length of the flagella (Fig. 1 A). The two flagella, which both end in a hairpoint (Fig. 1 A), differ slightly in length. The cell proper is saddle-shaped, with the flagella and the haptonema inserted in the apical depression (Fig. 1 A).

Two types of scales cover the cell body. The inner layer consists of circular, plate-like scales, approximately 0.7 μm in diameter (Fig. 1 B, C). These scales show a loosely woven pattern of radiating ridges (24) and 7–8 approximately equidistant concentric rings. The dorsal and ventral surfaces of these scales are virtually indistinguishable. All the ridges that form the scale are of equal thickness, with the exception of the outermost ring which is conspicuously thicker (Fig. 1 B).

The outer layer consists of more elaborate

Fig. 1. *Chrysochromulina pyramidosa* from Denmark. – A: Whole cell showing scales, a haptonema, and two flagella. Micrograph T 1075, × 9000. – B: Plate-like inner scales. Note thickened margins. Micrograph T 1530, × 50 000. – C: Mixture of scale types. Inner plate-like scale to the left. Pyramidal superstructure of scale from the outer layer to the right. Micrograph T 1530, × 50 000.


A
B
C

scales, made up of a subtending circular flat base plate, and a superstructure composed of four converging struts (Fig. 2A–C). The plate-like base, which in many respects is similar to the inner scale type described above, is 0.8–0.9 μm in diameter, and is formed by 27–28 radiating ridges and 8–9 concentric rings. The innermost rings are equidistant, whereas the distance between the outermost two rings is considerably greater (Fig. 2B, arrows). The outermost ring as well as the four struts that form a pyramidal structure (Figs. 1C, 2C) are thicker than the remainder of the meshwork.

Fig. 2A, C (arrowheads) shows some additional scale material between the four struts, apparently running from one strut to a point above the centre of the scale and back again to the neighbouring strut. A transverse section of the pyramidal superstructure thus presents itself as two right triangles joined together to form a cross. From Fig. 2B it appears, however, that this extra material is not always present.

Fig. 2D, E was kindly supplied by Professor I. Manton. They show some very similar scales from a water sample collected off the South African coast (November 13, 1972; 4 miles NW of Hout Bay Neck near Cape Town; 33° 57.6 S, 18° 16.9 E; 33 ft. depth, water temperature 12°C). The differences between the Danish and the African material are marginal. The simple plate-like inner scales of the latter are slightly larger (approximately 0.8 μm versus 0.7 μm) and have 9–11 concentric rings versus 7–8; otherwise they appear identical. The pyramidal scales seem to agree completely with those found in the Danish material. The interconnecting material between the four struts found on some of the pyramidal scales from the Danish material is apparently lacking in the equivalent South African scales.

In spite of minor differences the Danish and the South African material seem to represent the same species, suggesting that *C. pyramidosa* has a worldwide distribution.

Discussion

The presence of a haptonema and two flagella, the dimorphism of scales, and the structure of the apparently unmineralised scales together justify the inclusion of *C. pyramidosa* in the genus *Chrysochromulina*.

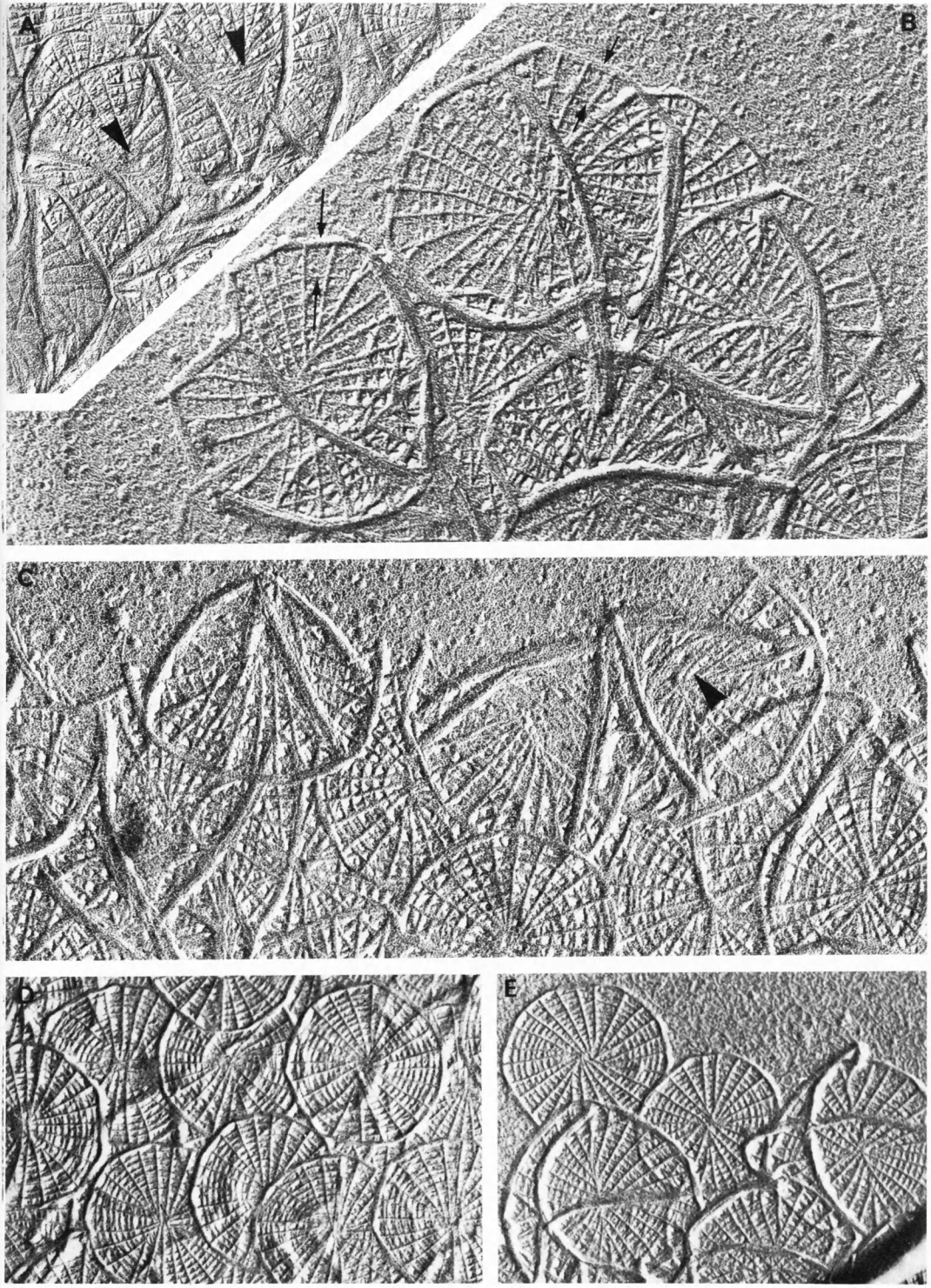
Scale structure alone is sufficient to distinguish *C. pyramidosa* from other species of the genus when observed in the electron microscope. The shape and size of the cell body and the length of the haptonema relative to the length of the flagella can be used for preliminary light microscopical determination. With regard to these characters, however, *C. pyramidosa* resembles *C. fragilis* Leadbeater (1972), *C. minor* Parke & Manton in Parke et al. (1955), and in particular *C. adriatica* Leadbeater (1974).

The pattern of ridges on the plate-like inner scales as well as on the subtending plates of the outer pyramidal scales is similar to that of *C. acantha* Leadbeater & Manton (1971), *C. parva* Lackey (1939) (Parke, Lund & Manton 1962), and *C. adriatica* Leadbeater (1974). The common feature is the sparse woven pattern dominated by delicate radiating ridges equally visible on both surfaces. The entire construction of the outer scales of *C. pyramidosa* also has a certain resemblance to that of *C. acantha*, the superstructure in both cases consisting of four struts. In *C. acantha* the struts support a central spine, whereas in *C. pyramidosa* they make up a pyramidal structure. A central spine supported by four struts is known from several other species of *Chrysochromulina*. In these species, however, the pattern on the lower part of the scale differs substantially from that found in *C. pyramidosa*.

The scale structures of *C. pontica* Rouchijainen (1966), *C. orbiculata* Rouchijainen (1972) and *C. birgeri* Hällfors & Niemi (1974) remain to be characterized on the basis of electron microscopy.

The haptonema of *C. pontica* measures up to

Fig. 2 A–C: *Chrysochromulina pyramidosa* from Denmark. – A: Scales from the outer layer. Arrowheads indicate the connecting scale material between struts. Micrograph T 1536, × 40000. – B: Scales from the outer layer. The arrows demarcate the gap between the two outer rings. Note the thickness of the outer ring and the struts as opposed to the remainder of the meshwork. Micrograph T 1534, × 50000. – C: Scatter of scales from both layers. The three scales from the outer layer at the top of the figure clearly show the pyramidal form. Arrowhead indicates scale material between struts. Micrograph T 1532, × 50000. – D, E: *Chrysochromulina pyramidosa* from the coast of South Africa (courtesy of Prof. I. Manton). – D: Scales from the inner layer. × 30000. – E: Pyramidal scales from the outer layer. × 30000.


A
B
C
D
E

70 μm, which definitely rules out any possibility of conspecificity between this species and *C. pyramidosa*.

C. birgeri has not only a quite different shape, but is also considerably larger than *C. pyramidosa*. A forthcoming paper will demonstrate important differences also on the electron microscopical level.

C. orbiculata may be conspecific with *C. minor* Parke & Manton in Parke et al. (1955), *C. fragilis* Leadbeater (1972), *C. adriatica* Leadbeater (1974), or *C. pyramidosa* sp. nov., the description by Rouchijainen (1972) being too little detailed to ensure positive identification. If future investigations demonstrate the presence of *C. pyramidosa* in the Black Sea, which is the type locality of *C. orbiculata*, one may claim that *C. pyramidosa* (described on the basis of electron microscopy only) and *C. orbiculata* (described on the basis of light microscopy only) are conspecific. With regard to *C. adriatica* the situation is the same. From a biogeographical point of view it seems probable that at any rate this latter species may well occur in the Black Sea (type locality: Kastel Bay, Adriatic Sea (Leadbeater 1974); also found in the Gulf of Elat, Red Sea (Thomsen 1977)). In both cases the specific epithet *orbiculata* takes priority.

If either *C. minor* or *C. fragilis* occurs in the Black Sea, *C. orbiculata* may be quoted as synonym to one of these (the specific epithets *minor* and *fragilis* take priority).

As pointed out by Black (1968) a significant parallelism exists between calcified and uncalcified members of the Prymnesiophyceae. A comparison of the scale structure in *Chrysochromulina* with that of a number of coccolithophorid genera clearly demonstrates that the calcified and the uncalcified genera do not represent two separate evolutionary lines (see Manton et al. 1975, 1976, 1977). The new species here described provides a remarkable example to this general observation. The pattern on the inner and the outer scales of *C. pyramidosa* shows obvious similarities with that on the scales and unmineralized coccoliths of the coccolithophorid *Wigwamma arctica* Manton in Manton et al. (1977), the main difference being a matter of degrees of symmetry. In both species four struts attach themselves to the thickened rim of the basal plate of some of the scales, converging above the plate to form a pyramidal, or tent-like, superstructure.

On account of the obvious similarities between *C. pyramidosa* and *W. arctica* it is quite likely that these two species are phylogenetically more closely related than e. g. *C. pyramidosa* and *C. campanulifera* Manton & Leadbeater (1974).

Continued investigations of marine nanoplankton will undoubtedly result in the demonstration of many more examples of evolutionary affinity between coccolithophorids and species of *Chrysochromulina*. Pending such observations and cultural experiments on some of the organisms, however, it is probably most convenient to maintain the traditional classificatory principle of keeping mineralized and unmineralized genera in separate families.

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A new genus of the Compositae from North Africa

Christopher John Humphries

Humphries, C. J. 1977 06 30: A new genus of the Compositae from North Africa. *Bot. Notiser 130:* 155–161. Stockholm. ISSN 0006-8195.

The new, monotypic North African genus *Heliocauta* is formally published and its relationship to other genera of the *Anthemis* complex is discussed.

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On the basis of a detailed morphological and anatomical study it is possible to show that *Anacyclus,* like several other currently recognised genera of the *Anthemis* complex is a paraphyletic assemblage. The affinities of the curious mat-forming alpine species named by Litardière & Maire (1924) as *Anacyclus atlanticus* were brought into question in a revision of the genus (Humphries in prep.) as the capitulum, floret and cypsela differ in most respects from those of the type species and its close allies. In this species there are also several character states which are not shared by other genera of the Anthemideae. Thus, it is placed into a new genus, *Heliocauta,* described below, and the reasons for its separation from *Anacyclus* are discussed.

Heliocauta Humphries gen. nov. – Figs. 1, 2

Herbae perennes humiles; caudex brevis, praemorsus. *Folia* basalia, rosulata, triternatisecta, segmentis ultimis brevibus linearibus. *Pedunculi* simplices, monocephali ex axillis foliorum orti. *Capitula* hemisphaerica, parva (7–11 mm diametro) homogama, discoidea, flosculis hermaphroditis fertilibus; receptaculum conicum paleaceum. *Anthodii phyllaria* (involucri bracteae seu squamae) triangularia vel oblongo-lanceolata, dorso viridia, margine scariosa fusco apice versus plus-minusve erosa. *Receptaculi phyllaria* (paleae) oblongo-linearia, carinata hyalina, scariosa apicibus obtusis serrulatis. *Flosculi* regulares hypocrateriformes; minuti (2.5–3.2 mm longi) lobis limbi parvis patentibus triangularibus apicibus fere cucullatis. *Antherae* basi obtusae; filamenta infra antherum tumida. *Stylus* teres, glaber, nectario conspicue lobato basi cinctus, ramis 2 brevibus divaricatis anguste oblongis apice paulo penicillatis. *Cypselae* anguste obcuneatae, leviter dorsoventraliter compressae, costis lateralibus 2, costis intermediis utrinque 1–3 obscuris apice truncatae; pappus coroniformis, minutus.

Typus: *Heliocauta atlantica* (Litard. & Maire) Humphries. Nomen ex ηελιοκαντεω oritur, ob capitulorum aspectum adustum.

Perennial creeping herb; stems short, reduced to a praemorse caudex. *Leaves* in a basal rosette, tripinnatisect, with tiny, linear, ultimate lobes; primary lobes in 3–6 opposite or subopposite pairs; rhachis flat or slightly canaliculate, narrowly triangular in outline, with a broad, hyaline, winged, sheathing base and 4–6 distinct veins. *Peduncles* simple, monocephalous, emerging from the leaf axils. *Capitulum* hemispherical, small (7–11 mm in diameter), homogamous, discoid with fertile, hermaphrodite florets; receptacle conical, paleaceous. *Phyllaries* in 3 rows, triangular to oblong-lanceolate, green on the dorsal surface, the margins scarious, brown at the apex, ± erose. *Receptacular scales* oblong-linear, carinate, hyaline scarious, the apex obtuse, serrulate. *Florets* regular, hypocrateriform, minute (2.5–3.2 mm long), the lobes patent, triangular in shape, with a somewhat cucullate apex. *Anthers* obtuse at the base, the filaments distinctly enlarged at the collar. *Style* terete, slightly swollen at the base, set in a con-

spicuous lobed nectary; style branches short, about the same thickness or slightly thicker than the shaft, truncate-penicillate at the tips. *Cypselas* narrowly obcuneate, terete to slightly dorsally-ventrally compressed with 2 distinct, vascularized lateral ribs and 1–3 obscure dorsiventral ribs; truncate, dark-brown or grey-black due to a dense tannin layer in the testa; the scalariform, thickened epicarp is invested, here and there, with linear series of dark-brown resin cells; pappus a minute, erose corona. *Cotyledons* anteriorly-dorsally orientated.

Heliocauta atlantica (Litard. & Maire) Humphries comb. nov.

Basionym: *Anacyclus atlanticus* Litard. & Maire, Mem. Soc. Sci. Nat. Maroc 4 (1): 13 (1924).

Caudex 2–4 mm crassus, interdum stolones emittens. *Folia* ambitu oblongo-lanceolata, 3–8 × 1–2.5 cm, plus-minusve glabra ad villosa. *Pedunculi* decumbentes, 3.5–15 cm longi, apicem versus parce villosi sed sub capitulo dense pubescentes. *Capitula* 7–11 mm diametro. *Anthodii phyllaria* circa 2 mm longa. *Flosculi* primo pallide flavis demum brunnescentibus, tubo 2.5–3.2 mm longi, lobis 0.1–0.3 mm longi. *Antherae* 1–1.5 mm longae. *Cypselae* 1.5–2 mm longae, fere 1 mm latae.

Stems 2–4 mm thick, occasionally producing stolons. *Leaves* oblong-lanceolate in outline, 3–8 × 1–2.5 cm, ± glabrous to densely villous. *Peduncles* decumbent, 3.5–15 cm long, sparsely to densely pubescent below the capitulum. *Capitula* 7–11 mm in diameter. *Phyllaries* c. 2 mm long. *Floret tubes* 2.5–3.2 mm long, lobes 0.1–0.3 mm long. *Anthers* 1–1.5 mm long at anthesis. *Cypselas* 1.5–2 mm long and up to 1 mm wide.

var. **atlantica**

Anacyclus atlanticus var. *eu-atlanticus* Maire in Jahandiez & Maire, Cat. Pl. Maroc 3: 767 (1934).

A variety from the Atlas mountains occurring on granitic or porphyritic rocks between 2900 and 3600 m.

Specimens seen: Grand Atlas, Reraya: rocailles porphyriques terreuses au Tizi-n-Tagherat 3300–3600 m, 22.7.1922, Maire (MPU holotype, P, LD, S isotypes) – Great Atlas mountains, Refuge Neltner, Djebel Toubkal, 3200 m, Polunin 2155 (BM); same locality, granite gravel and scree nr. stream, Newbould 490 (BM); same locality, 9600 ft., pastureland on granite bedrock, 9.7.1966, Lambert 119 (BM); same locality, 22.7.1976, C. J. & A. R. Humphries 101 (BM); same locality, 3500 m, 20.8.1951 Rauh 299 (M); same locality, 3600 m, 2.8.1951, Schoffer (M); same locality, 1933, Stodieck (M); Jbel Toubkal, nr. stream, 11,000 ft., 14.9.1955, Newbould 403 (BM) – Refuge d'Hangaye, vers 3000 m, Grand Atlas Central, 31.7.1938 in herb. Maire (MPU).

var. **dasyphylla** Humphries

Anacyclus atlanticus var. *vestitus* Humbert ex Jahandiez & Maire, Cat. Pl. Maroc 3: 768 (1934), nom. nud.

Varietas rara maroccana in montibus Grand Atlas (in parte orientali) et Moyen Atlas inter 2800 et 3500 m supra mare crescens, a var. *atlantica* indumento foliorum pilis densis simplicibus distinguenda.

An extremely rare variety from the eastern High Atlas and the Middle Atlas mountains occurring between 2800 and 3500 metres, distinguished from the type variety by its dense indumentum of simple hairs on the leaves.

Specimens seen: Grand Atlas, Ari Ayachi, Humbert (AL holotype, RAB); same locality, Sindsiert, 3600 m, Schmittfluren, 17.9.1953, Rauh 754 (M) – Middle Atlas, Chaine du Bou Iblane, 2800–3200 m, Emberger & Maire (AL, RAB) – Mont Bou Nacer, 3000 m, Emberger (AL, RAB).

Distribution and habitat

H. atlantica is known exclusively from wet, cold montane pastures in the Middle and High Atlas mountains, where it has only been found in 4 locations (Fig. 2), all of which are over 2900 m.

Cytology

Twenty-two plants of var. *atlantica* collected during August 1976 (C. J. & A. R. Humphries 101) from Jbel Toubkal (High Atlas) were cultivated at the Chelsea Physic Garden. After pre-treatment overnight in a saturated solution of paradichlorobenzene root-tips were stained in Feulgen and squashed in 45% acetic acid. Fresh buds were squashed directly in aceto-orcein.

The chromosome number, reported here for the first time, was found to be $2n = 18$, the most common number for diploids in the Anthemideae. There are nine pairs of meta- and submetacentric chromosomes, two pairs of which have satellites on their shorter arms. Meiosis was normal with 9 pairs of bivalents at metaphase I.

Taxonomic remarks

This interesting taxon was originally described by Litardière & Maire (1924) from material col-

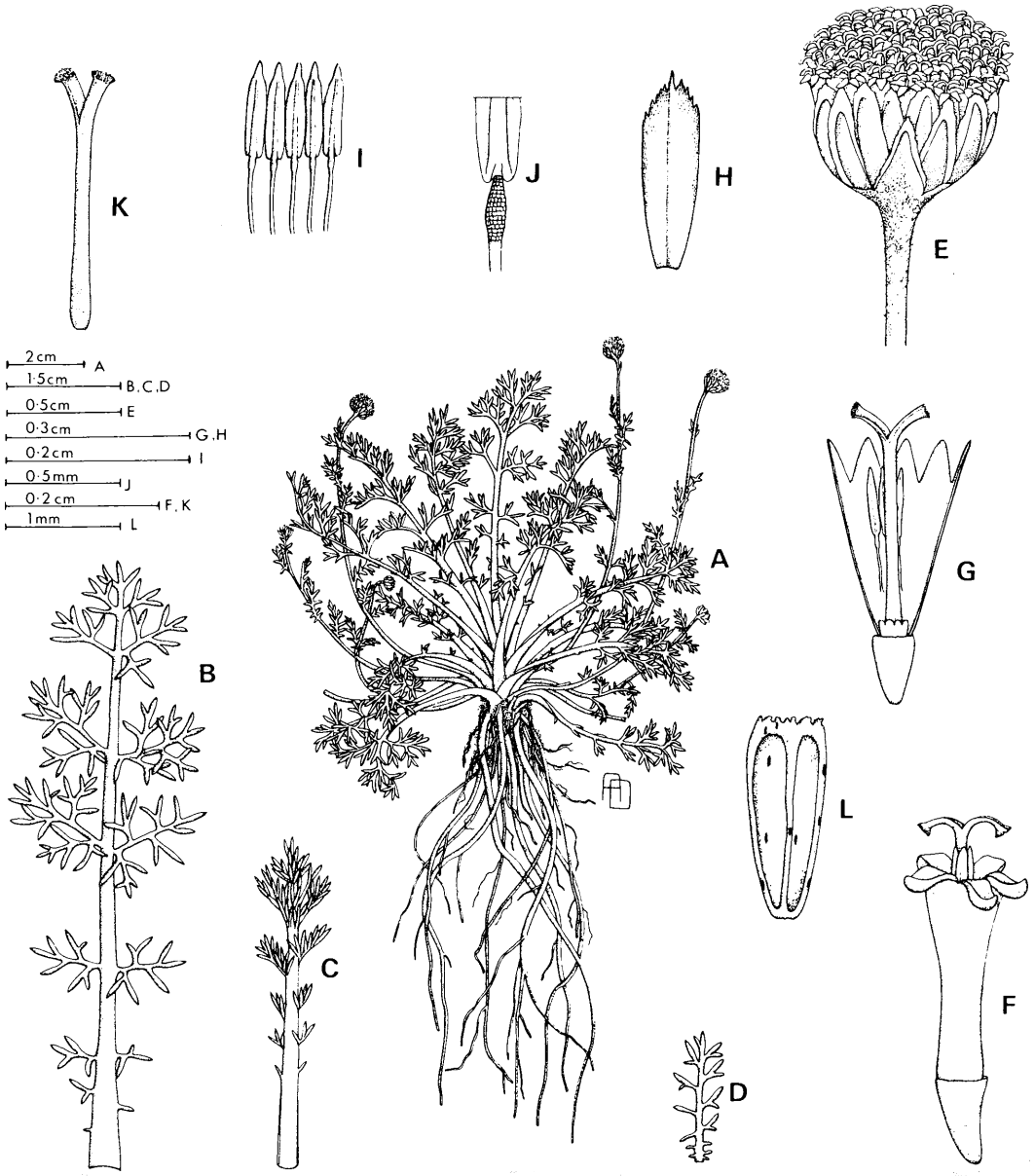


Fig. 1. *Heliocauta atlantica*. Based on live material (C. J. & A. R. Humphries 101). – A: Habit. – B: Mature leaf. – C: Young leaf. – D: Stem bract. – E: Flowering capitulum. – F: Floret at anthesis. – G: Dissected floret at anthesis. – H: Receptacular scale. – I: Anthers. – J: Filament collar and anther base. – K: Stigma. – L: Mature cypsela, anterior view.

lected in the High Atlas mountains: "In ditionis Ourika jugo Tachdirt (Maire 1921. nondum florens, Maire and Litardière, 1922) et in valle amnis Ouelga (Litardière, 1923); in ditionis Reraya valle amnis Ouenkrim (Litardière, 1923)."

Because *Heliocauta atlantica* resembles the two perennial varieties of *Anacyclus pyrethrum*

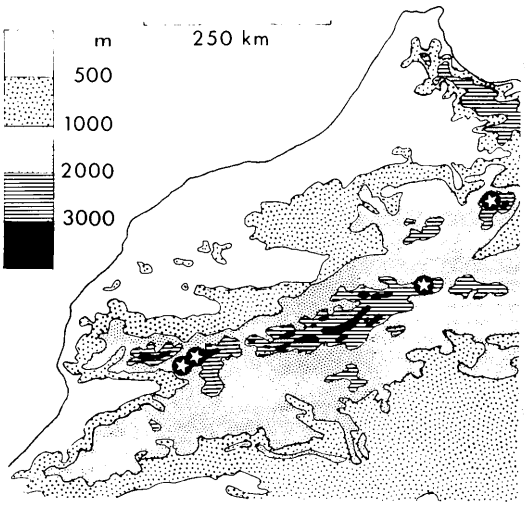


Fig. 2. Known range of *Heliocauta atlantica*.

(Humphries in prep.) in gross morphology Maire placed it in the same genus with the comment, "Affinis *A. pyrethro* L. et *A. depresso* Ball, a quibus valde differt caudice brevi praemorso radices fasciculates edenti (nec in radicem crassam palarem abeunti, capitulis minoribus homogamis, florescentia valde serotina etc. Sectioni Pyrethrariae DC etsi eligulatus, ob perennitatem, flosculos regulares, tubum compresseum et vegetationis modum adscribendus." This is clearly a classification mainly based on an overall resemblance in convergent characters, i.e. similar adaptations to the alpine environment in which both species occur. A more detailed examination shows that the two species are very different from each other.

Mature individuals of *A. pyrethrum* are characterised by the presence of a solitary, woody rootstock which can be up to four or five years old. The premorse stem of *H. atlantica*, on the other hand, produces at least three fasciculate roots (Fig. 1 A). Transverse sections show that these roots rarely survive for longer than two years. Instead perenniality is achieved by the development of stolons, capable of reaching lengths of up to 12 cm. Transverse sections of the protracted stem show that it can survive for two or three years. Both species produce an annual rosette of leaves which emerges from the centre of the perennating stocks. The flowering shoots in *A. pyrethrum*, homologous to the lateral branches of cauline corymbose cymes in other genera of the Anthemideae (Humphries in prep.), emerge during the month of February to form a rosette of procumbent shoots which flower at the tips from March until June. The decumbent flowering shoots of *H. atlantica* do not form flat rosettes but develop from the axils of the leaves and flower from August until October or November.

The flowers and fruits of *H. atlantica* differ in many respects from those of *Anacyclus*. The receptacular scales of the former are extremely narrow, delicate, carinate and chartaceous with an acuminate, brown-tipped apex and somewhat erose at maturity. By comparison the scales of *Anacyclus* are tough, mucronate and barely keeled but distinctly herbaceous at the base and centre, particularly in those from the outer parts of the capitulum. The heads of *Heliocauta* are homogamous consisting only of disc florets with regular corolla lobes. Homogamous heads are found in annual species of *Anacyclus* (*A. monanthos* and *A. valentinus*) but these frequently have zygomorphic corollas with two of the apical lobes longer than the other three. The cypselas of *Heliocauta* are also very different from anything to be found in *Anacyclus*, especially by the thin pericarp, the small ribs and the overall size (Figs. 1 L, 3). The epicarp consists of colourless, horizontally thickened cells and is invested with tanniniferous sphacelae which appear to be 4–7-celled resin glands (Fig. 1 L). The pappus is a tiny, marginal, toothed corona. In a transverse section of the pericarp a one-celled, scalariform epicarp (Fig. 3 C), a narrow 1–2-celled mesocarp and 3–5 sclerenchymatous ribs are shown. The deep brown colour is brought about by a very thick tanniniferous substance in the inner layers of the testa (Fig. 3 B).

The cypselas of *Anacyclus*, as in so many other genera of the Anthemideae, provide the unambiguous diagnostic features of the genus (Humphries in prep.). They are flattened in an anterior-dorsal plane with 2 lateral wings. The pericarp consists of a basal layer of sclerenchyma, some 2–3 cells thick covered by a 1–2-celled layer of parenchyma. The wings contain radially elongated parenchymatous tissue surrounding 2 laterally placed vascular bundles. The epicarp is covered with slime cells in linear series, as in *Heliocauta*, but they contain colourless mucilage. The pappus

varies in different species from a marginal rim to an anterior appendage.

Relationship to other genera

The representatives of the *Anthemis* and *Achillea* complexes in the Northern Hemisphere form a group of 11 related genera (Table 1). Although each possesses many differential features the individual taxa can be delimited on a few diagnostic character states of unique status, as these help to define monophyletic groups, an essential requirement for natural classifications (Hennig 1966). The most important features of this kind are obtained from the morphology of the cypselas and the capitulum. Other possibly useful character states are found in the type of embryo-sac development (Harling 1950, 1951) and in the distribution of secondary metabolites (Greger 1975, 1977, Harborne et al. 1970). A summary of useful morphological features of genera in the *Anthemis* complex together with *Achillea, Heliocauta* and *Sclerorhachis* is given in Table 1.

A detailed examination of the fruits in the genera of the *Anthemis* complex reveals a number of parallel morphological trends which tend to obscure actual relationships. Such features include the anteriorly-dorsally compressed cypselas of *Anthemis* section *Cota* which have 7–22 ribs and a similar number of vascular bundles in the pericarp (Wagenitz 1968, Kynčlova 1970, Reitbrecht 1974); the weakly monosymmetric shape, the barely visible ribs and the thin pericarp of the cypselas in *Chamomilla;* and the thick tanniniferous layers of the testa in the dark coloured cypselas of *Matricaria*. The presence of myxogenic cells on the pericarp represent a plesiomorphous condition as they are common to all of the main generic complexes in the Anthemideae. However, the resin-filled glands of the type found in *Heliocauta* have only been observed elsewhere in *Sclerorhachis*.

Heliocauta can immediately be distinguished together with *Anacyclus, Leucocyclus* and *Achillea,* from the remainder of the complex on the basis of slightly or completely anteriorly compressed cypselas with 2 distinct lateral ribs or wings containing only 2 vascular bundles in the pericarp wall. The remaining genera have more or less terete, angled, monomorphic, laterally compressed or even occasionally anteriorly-dorsally compressed cypselas but with at least 3, usually

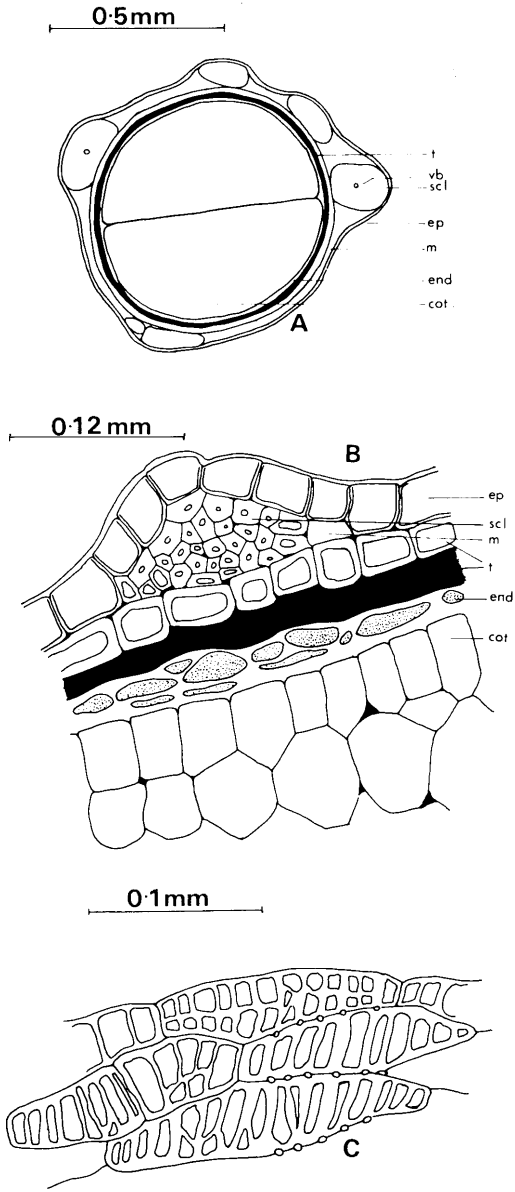


Fig. 3. Cypsela anatomy of *Heliocauta atlantica*. – A: T.s. across the median region. – B: T.s. in the region of a rib. – C: Surface view of the epicarp to show scalariform thickening of the cell walls. – cot cotyledon, end endosperm, ep epicarp, m mesocarp, scl sclerenchyma, t testa, vb vascular bundle.

Table 1. Morphological features of *Heliocauta, Achillea* and related genera. The characters are as follows:

1 Habit: a annual, b biennial, c perennial
2 Perennial habit: a rhizomes, b stolons
3 Receptacular scales: + present, − absent
4 Receptacular hairs: + present, − absent
5 Cypselas: + heteromorphic, − homomorphic
6 Cypsela symmetry: a terete/actinomorphic, b laterally compressed, c anteriorly/dorsally compressed, d zygomorphic
7 Number of vascular bundles in the pericarp
8 Number of cypsela ribs
9 Cypsela wings: + 2 wings, − absent
10 Cypsela parenchyma: a absent, b spongy, c single-layered, d multi-layered
11 Cypsela sclerenchyma: a absent, b hypodermic sclerocarp, c oval braced, d palisade, e multi-stranded, f 1–2-stranded
12 Pericarpic resin ducts and glands: + present, − absent
13 Pericarp lacunae: + present, − absent
14 Slime cells: − absent, a present, b sphacelate, c on ribs, d over whole surface
15 Number of nuclei in embryo-sac
16 Corolla: − not basally enlarged, a basally saccate, b anteriorly-dorsally overlapping fruit, c dorsally overlapping fruit
17 Cotyledons: a anteriorly-dorsally orientated, b laterally orientated

Genus	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Leucocyclus	c	a	+	−	−	c	2	±	+	c	e	−	−	c		b	
Achillea	c	a	+	−	−	c	2	2	−	b	f	−	−	c	2	−	b
Sclerorhachis	b		+	−	−	a b	4–5	0				+	−	c		−	
Heliocauta	c	b	+	−	−	c	2	3–5	−	b	f	+	−	−		−	a
Anacyclus	a c	(a)	+	−	−	c	2	0	+	b	e	−	−	d	1	(c)	a
Cladanthus	a		+	+	−	b		0	−	a	e	−	−	−	1	−	b
Anthemis sect. *Anthemis*	a–c	a	+	−	−	a	10	8–10	−	c d	e	−	−	(a)	4	−	a b
Anthemis sect. *Cota*	a–c	a	+	−	−	a c	22	22	−	d	c	−	−	−	4	−	b
Anthemis sect. *Ammanthus*	a		(+)	−	−	a		0–10	−			−	−	−		−	
Chamaemelum	a c	(a)	+	−	−	b	5	0	−	d	b d	−	−	−	1	a	b
Chamomilla	a		−	−	−	b	4–5	3	−	b	f	(+)	−	d	1	−	b
Matricaria	a c	(a)	−	−	−	b d	3	4–5	−	d	f	−	(+)	(a)	4	−	a b
Otospermum	a		−	−	+	a	5	5–6	−	d	e	−	−	−		−	

5–10, or even up to 22 vascular bundles in the pericarp wall. *Anacyclus* and *Leucocyclus* together form a monophyletic assemblage characterized by large cypselas with lateral wings and thick, continuously thickened pericarp walls. Grierson (1975) considers *Leucocyclus* to be unique on account of its vermiform leaves, the narrow wings on the cypselas and the dorsiventrally compressed disc corollas divided into 2 overlapping lobes at the base, which clasp the upper part of the cypsela on the anterior and dorsal faces.

By comparison both *Heliocauta* and *Achillea* have relatively tiny cypselas with 2 distinct lateral ribs rather than wings, and extremely thin pericarp walls (cf. Briquet 1916, Reitbrecht 1974, for details of *Achillea*). The relationship between *Heliocauta* and *Achillea* was originally suggested by phytochemical data. Greger (1977) has shown that the flavonoid profile of *Heliocauta* represents a widespread plesiomorphous pattern with compounds similar to those found in *Tanacetum, Artemisia, Anthemis* and *Achillea* although the exact profile is identical only to the one of *Achillea*. Morphologically, *H. atlantica* is closest to the montane species of the *Achillea barrelieri* (Ten.) Schultz Bip. – *A. oxyloba* (DC.) Schultz Bip. group of the European Alps, on the basis of the monocephalous heads, slender, brown-tipped receptacular scales, dark-brown margins on the phyllaries, cypsela size, pinnatisect leaves and its perennial habit.

Although *Achillea* is one of the largest genera in the Anthemideae and comprises a wide variation in many characters, *Heliocauta* cannot be included without a grave distortion of its coherent definition. Features of *Heliocauta* not found in any species of *Achillea* include the actual position of the vascular bundles in the ribs of the cypselas (basal rather than central), the horizontal wall thickenings of the cells in the pericarp, the variable strands of sclerenchyma

forming extra ribs and the small, erose coroniform pappus.

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New and noteworthy species of Neottioideae (Orchidaceae) from Ecuador

Bernt Løjtnant

Løjtnant, B. 1977 06 30: New and noteworthy species of Neottioideae (Orchidaceae) from Ecuador. *Bot. Notiser 130:* 163–172. Stockholm. ISSN 0006-8195.

Three species of Ecuadorian orchids are described as new, *Altensteinia fragosa* Løjtnant, *Cranichis pachnodes* Løjtnant and *Sobralia melanothrix* Løjtnant. Two new combinations, *Altensteinia nigrescens* (Schltr.) Løjtnant and *Psilochilus physurifolius* (Rchb. f.) Løjtnant are made. The latter two species and *Cranichis diphylla, Elleanthus amethystinus, E. haematoxanthus, E. sphaerocephalus, Erythrodes arietina, Gomphichis traceyae, Ponthieva keraia,* the genus *Palmorchis, Pterichis barbifrons, P. galeata, P. multiflora, Sobralia candida* and *S. rigidissima* are reported for the first time from Ecuador.

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The taxonomic decisions presented result from determination of a great number of orchids collected during the 1st and 2nd Danish Botanical Expedition to Ecuador (cf. Holm-Nielsen & Jeppesen 1968, Holm-Nielsen et al. 1975, Løjtnant 1977). The research was carried out at the Orchid Herbarium of Oakes Ames, Harvard. Without the comprehensive collections of type-material at AMES and the unique guidance of the curator Dr Leslie A. Garay, this work would not have been practicable.

The flowers and floral parts in Fig. 2 are drawn from material preserved in FAA, those in Figs. 1 and 3 are from dried material.

Altensteinia fragosa Løjtnant sp. nov.

Orig. coll.: Ecuador, prov. Napo, 10 km above Laguna de Papallacta on road Quito–Papallacta, road sides and grass páramo with numerous small lakes, 3800 m (78°07′ W, 0°20′ S), 5.6.1973, Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 6755 (AAU holotype).

Terrestris, erecta, 40 cm alta. *Radicibus* fasciculatis, crassis, pilosis. *Foliis* rosulatis, 4–5, glabris, lanceolato-ellipticis, lamina 4–6 cm longa, in medio 10–24 mm lata, petiolo c. 2 cm longo. *Scapo* simplici, tereti, vaginis c. 11 scariosis, sub anthesin jam emarcidis, imbricantibus obtecto, supra versus rhachidem parce puberulo. *Spica* dense multiflora, cylindrica, 9 cm longa, 11–14 mm in diametro. *Bracteis* hyalinis, ovato-lanceolatis, acuminatis, flores multo superantibus, sursum decrescentibus, primum erectis, deinde reflexis, margine erosulis, 1.5–2.5 cm longis. *Floribus* albescentibus, parvulis, inversis, glabris. *Sepalo postico* concavo, oblongo-elliptico, obtuso, uninervato, margine valde erosulo, 2.1 mm longo, 1.2 mm lato. *Sepalis lateralibus* valde concavis, oblique obovato-oblongis, uninervatis, margine valde erosulo, 3.2 mm longis, 1.2 mm latis. *Petalis* oblongo-ligulatis, obtusis, uninervatis, margine apicem versus irregulariter eroso-denticulato, 2.5 mm longis, 1 mm latis. *Labello* calceolato, trilobato; lobis incurvis, laceratis, lobis lateralibus expansis semi-orbicularibus, lobo medio triangulari; disco praecipue 5-nervato, nervis lateralibus ramosulis; juxta basin glandulis 2 subglobosis ornato; toto labello 2.3 mm longo, 1.6 mm lato. *Columna* brevi, *rostello* emarginato. *Ovario* sessili, cylindrico, apicem versus sparsim pilosulo.

Terrestrial, erect, 35 to 45 cm tall. *Roots* fasciculate, fleshy, pilose. *Leaves* 4–5, rosulate, glabrous, lanceolate-elliptic, basally produced into a 2 cm long petiole, including the petiole 4–6 cm long and 10–24 mm wide in the middle. *Scape* erect, terete, completely enclosed by c. 11 scarious sheaths which are evanescent during anthesis, those close to the rhachis partly pubescent. *Spike* dense, many-flowered, cylindric, 6–10 cm long and 11–14 mm in diameter excl. bracts. *Bracts* hyaline, ovate-lanceolate,

acuminate, much longer than the flowers, decreasing in size upwards, first erect, then with age reflexed in middle, with erose margins, 1.5–2.5 cm long. *Flowers* whitish, small, non-resupinate, glabrous. *Dorsal sepal* concave, oblong-elliptic, obtuse, one-nerved, with deeply erose margins, 2.1 mm long and 1.2 mm wide. *Lateral sepals* obliquely ovate-oblong, deeply concave, one-nerved, with prominently erose margins, 3.2 mm long and 1.2 mm wide. *Petals* oblong-ligulate, obtuse, 1-nerved with irregularly erose-denticulate margins towards the apex, 2.5 mm long and 1 mm wide. *Lip* calceolate, 3-lobed, lobes incurved, lacerate, lateral lobe when expanded semi-orbicular, the median lobe triangular; disc principally 5-nerved with lateral nerves branched, near the base with 2 subglobose glands, the whole lip up to 2.3 mm long and 1.6 mm wide. *Column* short; *rostellum* emarginate. *Ovary* sessile, cylindric, near the apex sparsely pilose.

This new species (Fig. 1) is distinguished from *A. riobambae* (Schltr.) Hawkes and *A. macra* (Schltr.) Hawkes by the erose sepals, erose-dentate petals, and by the more stalwart appearance and smaller flowers. In addition, it differs from *A. macra* by its long and acuminate bracts. The species is distinguishable from *A. leucantha* Rchb. f. and *A. paleacea* Kth. by the characteristics mentioned above and by the 3-lobed lip.

The specific name is descriptive of the margin of bracts, sepals and petals, *fragosus* meaning broken, rough, uneven.

The following collection is referable to this new species: Ecuador, prov. Imbabura, timber line vegetation on the hacienda Yura Cruz, 10 km N of Ibarra, páramo dominated by grass, 3700–3800 m (78°05′ W, 0°22′ N), 25.5.1973, Holm-Nielsen et al. 6481 (AAU).

Altensteinia nigrescens (Schltr.) Løjtnant comb. nov.

Basionym: *Aa nigrescens* Schltr. in Feddes Rep. Beih. 7: 49, 1920.

This species has formerly only been known from Cauca, Colombia, whence it has been described.

As *Aa* Rchb. f. hardly deserves the rank of a genus (cf. Schweinfurth 1958, Brieger 1974, Dunsterville & Garay 1976) the above new combination has been made.

Ecuador, prov. Imbabura, hacienda Yura Cruz, 10 km N of Ibarra, *Festuca* páramo and scrub (mainly in the quebradas), 3500–3600 m (78°05′ W, 0°22′ N), 25.5.1973, Holm-Nielsen et al. 6376 (AAU).

Cranichis diphylla Sw.

Sw., Prodr. Veg. Ind. Occ. 120, 1788.

This species, ranging from Mexico through C America and the West Indies to Peru (Schweinfurth 1940, 1958, Dunsterville & Garay 1972), has not formerly been reported from Ecuador, although it seems to be widely distributed in that country.

Ecuador, prov. Carchi, Valle de Maldonado, km 60 on road Tulcán-Maldonado, cleared slopes along road and denser cloud forest, 2700 m (78°04′ W, 0°51′ N) 18.5.1973, Holm-Nielsen et al. 5701, 5705 (AAU). – Prov. Loja, road Loja–Zamora, 1 km E of the pass (km 12), dry grass slopes, shrubby mountain slopes and elfin forest, 2725–2750 m (79°09′ W, 4° S), 17.4.1973, Holm-Nielsen et al. 3692 (AAU).

Cranichis pachnodes Løjtnant sp. nov.

Orig. coll.: Ecuador, prov. Carchi, Páramo El Angel, just before the pass on road El Angel-Tulcán, humid páramo vegetation with abundance of *Espeletia hartwegiana,* 3450–3500 m (77°54′ W, 0°41′ N), 14.5.1973, Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 5245 (AAU holotype).

Terrestris, erecta, gracilis, 50 cm alta, *Radicibus* fasciculatis, fusiformibus. *Foliis* basilaribus, 2, suberectis vel erecto-patentibus, longepetiolatis; lamina elliptica, acuta, usque ad 9 cm longa, 4 cm lata; petiolo 8–10 cm longo. *Scapo* stricto, apicem versus glanduloso-piloso, vaginis 7, acuminatis ornato. *Racemo* cylindrico, subdense multifloro, 3.5 cm longo. *Bracteis* patentibus, lanceolato-ellipticis, acuminatis, quam ovariis pedicellatis brevioribus, margine sparse glanduloso-pilosis. *Floribus* glabris, albidis, extus viridi suffusis. *Sepalo postico* late elliptico, subacuto, 4.2 mm longo, 1.8 mm lato, obscure 3-nervio. *Sepalis lateralibus* ellipticis, subacutis, 4.6 mm longis, 2.5 mm latis, obscure 2-nerviis. *Petalis* uninerviis, spathulatis, obtusis, 4 mm longis, 1.1 mm latis. *Labello* concavo, suborbiculari, obtuso, 4 mm longo, 2.5 mm lato; disco obscure 3-nervio, nervis obscure ramosis. *Rostello* simplici. *Ovario* cylindrico, glabro vel sparse puberulo.

Terrestrial, erect, slender, up to 50 cm tall. *Roots* fasciculate, fusiform. *Leaves* basal, 2–3, suberect to erecto-patent; lamina elliptic, acute, up to 9 cm long and 4 cm wide; petioles 8–13 cm long. *Scape* erect, glandular pilose with 4–7 acuminate sheaths. *Raceme* cylindric, subdensely many-flowered, 3.5–7 cm long. *Bracts* patent, lanceo-

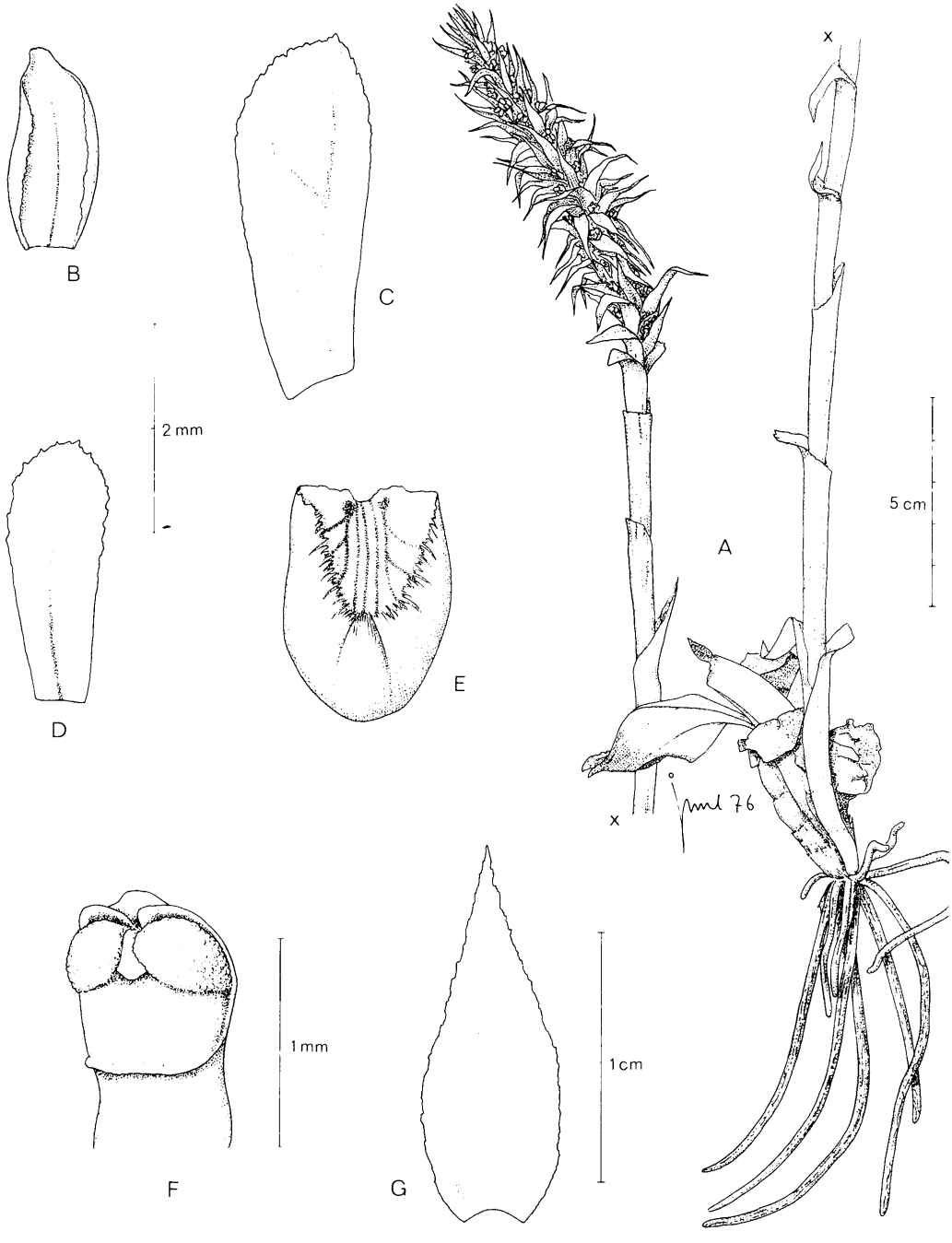


Fig. 1. *Altensteinia fragosa* (holotype). – A: Habit. – B: Dorsal sepal. – C: Lateral sepal. – D: Petal. – E: Lip. – F: Gynostemium. – G: Bract from the middle of the inflorescence.

late to elliptic, acuminate, shorter than the ovary, sparsely glandular pilose along the margins. *Flowers* glabrous, white, faintly greenish tinted, particularly on the outer side. *Dorsal sepal* broadly elliptic, obtusely acute, 4.2 mm long and 1.8 mm wide, inconspicuously 3-nerved. *Lateral sepals* elliptic, bluntly acute, 4.6 mm long and 2.5 mm wide, indistinctly 2-nerved. *Petals* l-nerved, spathulate, blunt, 4 mm long and 1.1 mm wide. *Lip* concave with green dots on the inner side, suborbicular, obtuse, 4 mm long and 2.5 mm wide, with 3 inconspicuous and indistinctly ramose nerves. *Rostellum* simple. *Ovary* cylindric, glabrous or sparsely pubescent at the base when young.

This new species (Fig. 2) is characterized by its spathulate petals and its indistinctly ramose and inconspicuous nerves on the lip. *Cranichis pachnodes* resembles *C. fendleri* Schltr., but is differentiated by a less rounded lip and by the characteristics mentioned above.

The specific name is descriptive of the cold habitat of the species, *pachnodes* meaning chilly or cold.

Elleanthus amethystinus (Rchb. f. & Warsz.) Rchb. f.

Rchb. f. in Walp. Ann. 6: 479, 1862. – Basionym: *Evelyna amethystina* Rchb. f. & Warsz. in Bonpl. 2: 113, 1854.

After comparing a copy at AMES of Reichenbach's drawing of the type of this species, it was obvious that our collection represents this rarely collected species, hitherto reported only from Peru and Colombia (Schweinfurth 1958).

Ecuador, prov. Loja, km 13 on Pan American Highway N of Loja, dry rocky slopes with scattered grass and shrubs, 2050 m (79°14′ W, 3°55′ S), 1.5.1973, Holm-Nielsen et al. 4635 (AAU).

Elleanthus haematoxanthus (Rchb. f. ex Lind.) Rchb. f.

Rchb. f. in Walp. Ann. 6: 485, 1863. – Basionym: *Evelyna haematoxantha* Rchb. f. ex Lind., Illustr. Hortic. 29: 51, 1882.

Hitherto only known from Colombia this species may now be acknowledged as part of the Ecuadorian flora.

Ecuador, prov. Zamora–Chinchipe, road Loja–Zamora, km 37, steep slopes covered with shrubs, 1750 m (79°04′ W, 3°59′ S), 18.4.1973, Holm-Nielsen et al. 3758 (AAU).

Elleanthus sphaerocephalus Schltr.

Schltr. in Feddes Rep. Beih. 27: 17, 1924.

Elleanthus sphaerocephalus, which is closely related to *E. cephalotus* Garay & Sweet and *E. sodiroi* Schltr., is recorded here for the first time from outside Colombia.

Ecuador, prov. Zamora–Chinchipe, road Loja–Zamora, km 54, steep clayey slopes with scattered shrub vegetation and dense herb cover, 1300 m (78°59′ W, 4°02′ S), 18.4.1973, Holm-Nielsen et al. 3784 (AAU).

Erythrodes arietina (Rchb. f. & Warm.) Ames

Ames, Orchidaceae 7: 66, 1922. – Basionym: *Physurus arietinus* Rchb. f. & Warm., Otia Bot. Hamb. 2: 52, 1881.

This inconspicuous but characteristic species, known from Brazil (type), Peru, and Venezuela (Foldats 1969), is reported here for the first time from Ecuador.

Ecuador, prov. Morona–Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34′ W, 3°29′ S), 23.4.1973, Holm-Nielsen et al. 4153 (AAU).

Gomphichis traceyae Rolfe

Rolfe in Kew Bull. 1916: 78.

Gomphichis traceyae has so far only been reported from Colombia, where it is widely distributed (Renz 1948). Although it is apparently common in the southern Ecuadorian dry scrub regions, it has undoubtedly been either overlooked or confused with the allied *G. alba* Lehm. & Kränzl. (cf. Kränzlin 1899, Renz 1948).

Ecuador, prov. Azuay, km 67 S of Cuenca on Pan American Highway, xerophytic scrub, 2–3 m high, intermingled with meadows and drier grass land, 3250 m (79°08′ W, 3°18′ S), 4.5.1973, Holm-Nielsen et al. 4933 (AAU). – Prov. Azuay, km 85 on Pan American Highway N of Loja, dry low scrub vegetation, more humid in small hollows and valleys, 2850–2950 m (79°11′ W, 3°35′ N), 3.5.1973, Holm-Nielsen et al. 4829 (AAU).



Fig. 2. *Cranichis pachnodes* (holotype, B isotype). – A: Habit. – B: Old inflorescence. – C: Dorsal sepal. – D: Lateral sepal. – E: Petal. – F: Flower. – G: Lip. – H: Gynostemium. – I: Anther.

The genus Palmorchis

The genus *Palmorchis*, which has its centre in northern S America and extends to Panama and Trinidad (Schweinfurth & Correll 1940), has not up to the present time been reported from Ecuador. Plants of *Palmorchis* are not rare in the Amazonian lowlands of Ecuador but due to their insignificant appearance they can easily be overlooked.

Despite the immature buds, the cited collection may be referable to *P. lobulata* (Mansf.) C. Schweinf. & Correll, which, according to Schweinfurth & Correll (1940) is known from Peru and Colombia. However, strangely enough, Schweinfurth (1958) excludes any mention of species of *Palmorchis* in his Orchids of Peru.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34′ W, 3°29′ S), 23.4.1973, Holm-Nielsen et al. 4154 (AAU).

Ponthieva keraia Garay & Dunsterv.

Garay & Dunsterv., Venz. Orch. Ill. 6: 382, 1976.

This species, which has recently been described as endemic to Venezuela, seems to be rather widespread. It is distinguished from the closely related Colombian *P. ochreata* Renz by the distinct horn on the lateral petals and by the cordate base of these floral segments.

Ecuador, prov. Azuay, km 91 on Pan American Highway N of Loja, dry scrub, 1–3 m high, 2900 m (79°10′ W, 3°25′ S), 5.5.1973, Holm-Nielsen et al. 5111 (AAU).

Psilochilus physurifolius (Rchb. f.) Løjtnant comb. nov.

Basionym: *Pogonia physurifolia* Rchb. f. in Nederl. Kruidk. Arch. 4: 324, 1858.

The genus *Psilochilus* is new to the flora of Ecuador; in fact the members of this small genus also seem to be rare in the two other northern Andean countries, Colombia and Peru (cf. Schweinfurth 1970, Garay 1974).

Psilochilus physurifolius (type from Guiana) is closely related to *P. macrophyllus* (Lindl.) Ames, which is described from Cuba. *P. physurifolius* is, in fact, often considered conspecific with *P. macrophyllus* (cf. Ames & Correll 1952, Foldats 1969). However, an examination of the types of the two taxa has shown that they are not conspecific. But it is deplorable that the flowers of the type of *P. physurifolius* were in very poor condition even at the time the species was described. In describing *Pogonia macrophylla*, Lindley (1858) writes: "There is one very like it in Schomburgk's collections, but my specimens of it are scarcely sufficient for publication." In the very same year Reichenbach (1858) based *Pogonia physurifolia* on the collection of Schomburgk mentioned above.

Vegetatively *P. physurifolius* and *P. macrophyllus* are differentiated by the following characters:

Character	*P. physurifolius*	*P. macrophyllus*
Leaves	acuminate, tapering	acute
Leaf base	tapering–rounded	cordate
Petiole	more than 1 cm	very short, leaf-base clasping the stem
Bracts	acuminate	acute to blunt

The Colombian *P. maderoi* (Schltr.) Schltr. may be conspecific with *P. physurifolius* (cf. Schlechter 1920). Thus *P. maderoi* resembles *P. physurifolius* in having a long claw to the lip unlike the short claw of *P. macrophyllus*.

Of the collections studied at AAU and AMES, the following are referable to *P. physurifolius*:

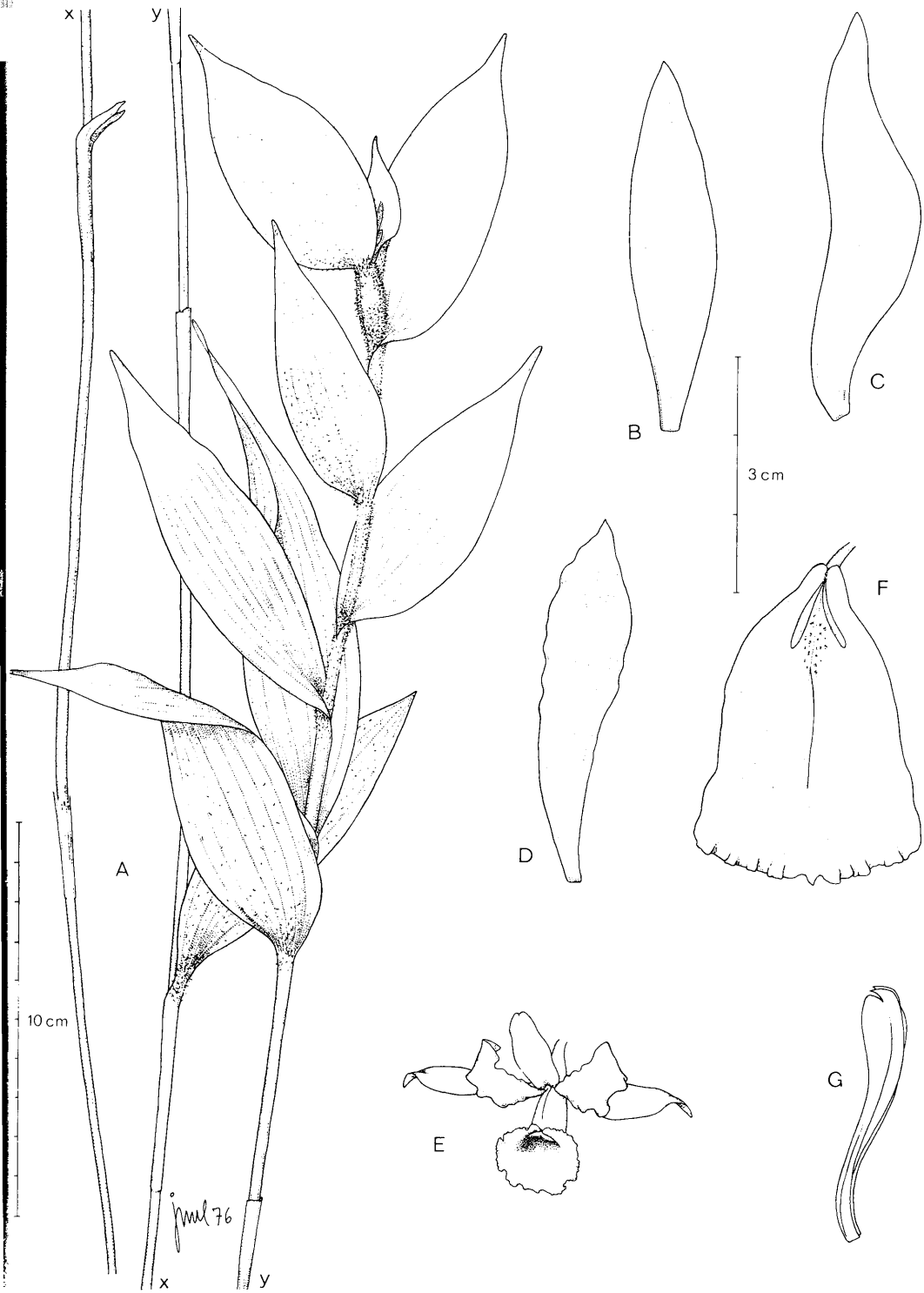
Venezuela, Bolivar, Cerro Venamo (parte Sur-Oeste), cerca de los límites con la Guayana Inglesa, 950–1150 m, 29–30.12.1963, Steyermark, Dunsterville & Dunsterville 92382 (AMES). – Merida, woods above las Cuadras, along Quebrada Molino, N of Torondoy, 1820–2255 m, 27.3.1944, Steyermark 55780 (AMES).

Ecuador, prov. Pastaza, Shell Mera rain forest, 2 km N of Shell Mera, 1050 m (78°03′ W, 1°29′ S), 6.6.1968, Holm-Nielsen & Jeppesen 340 (AAU).

Pterichis barbifrons (Kränzl.) Schltr.

Schltr. in Feddes Rep. Beih. 9: 127, 1921. – Basionym: *Prescottia barbifrons* Kränzl. in Engl. Bot. Jahrb. 54, Beibl. 117: 19, 1916.

Fig. 3. *Sobralia melanothrix* (holotype). – A: Habit. – B: Dorsal sepal. – C: Lateral sepal. – D: Petal. – E: Flower. – F: Lip. – G: Gynostemium.


x
y
A
10 cm
x
y
B
C
3 cm
D
F
E
G

This species, described from Peru, was regarded as being conspecific with *P. galeata* Lindl. by Schweinfurth (1941); however, comparisons with type material have shown that *P. barbifrons* is most likely a distinct species. It is distinguished from *P. galeata* by its glabrous sepals and bracts and by its linear falcate petals.

Apparently *P. barbifrons* is a rather common species in Ecuador; yet, because it has been considered identical with *P. galeata* up to now, it has only been reported from Peru.

Ecuador, prov. Carchi, Páramo El Angel, in the pass on road El Angel–Tulcán, very humid *Espeletia* páramo, 3750–3850 m (78°54′ W, 0°41′ N), 15.5.1973, Holm-Nielsen et al. 5450 (AAU). – Prov. Azuay, km 50 S of Cuenca on Pan American Highway, páramo, c. 3500 m (79°07′ W, 3°18′ S), 6–10.5.1973, Holm-Nielsen et al. 5128 (AAU). – Prov. Azuay, km 85 on Pan American Highway N, of Loja, dry, low scrub vegetation, more humid in small hollows and valleys, 2850–2950 m (79°11′ W, 3°35′ S), 3.5.1973, Holm-Nielsen et al. 4767 (AAU).

Pterichis galeata Lindl.

Lindl., Gen. Sp. Orch. 445, 1840.

This species has been reported from Peru (type), Bolivia, Colombia, and Venezuela and is hereby confirmed as being part of the Ecuadorian flora.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, above Pilaló, in cloud forest, mostly steep slopes, c. 3200–3300 m (78°56′ W, 0°58′ S), 8.4.1973, Holm-Nielsen et al. 3279 (AAU).

Pterichis multiflora (Lindl.) Schltr.

Schltr. in Engl. Bot. Jahrb. 45: 389, 1916. – Basionym: *Acrea multiflora* Lindl., Orch. Linden 26, 1846.

During this study the number of *Pterichis* species recognized as native to Ecuador has almost been doubled. Hitherto four species, *P. parviflora* (Lindl.) Schltr., *P. pauciflora* Schltr., *P. seleniglossa* Schltr. and *P. triloba* (Lindl.) Schltr. have been reported from Ecuador. Including the species in discussion, which, up to now, has only been known from Colombia (cf. Dunsterville & Garay 1966, 1976) the number has reached seven.

Ecuador, prov. Carchi, Páramo El Angel, in the pass on the road El Angel-Tulcán, very humid *Espeletia* páramo, 3750–3850 m (78°54′ W, 0°41′ N), 15.5.1973, Holm-Nielsen et al. 5453 (AAU).

Sobralia candida (Poepp. & Endl.) Rchb. f.

Rchb. f., Fl. Serres 8: 247, 1853. – Basionym: *Cyathoglottis candida* Poepp. & Endl., Nov. Gen. Sp. Pl. 1: 56, 1836.

This characteristic species has so far been known from Peru (type), Colombia, and Venezuela (Dunsterville & Garay 1961, Foldats 1969) and is now also reported from Ecuador.

Ecuador, prov. Zamora–Chinchipe, road Loja–Zamora, km 54, steep clayey slopes with scattered shrub vegetation and dense herb cover, 1300 m (78°59′ W, 4°02′ S), 18.4.1973, Holm-Nielsen et al. 3779 (AAU). – Also km 49, c. 1500 m, Holm-Nielsen et al. 3829 (AAU).

Sobralia melanothrix Løjtnant sp. nov.

Orig. coll.: Ecuador, prov. Pichincha, km 40–51 on road Santo Domingo de los Colorados–Quito, forested slopes along Rio Pilatón, 1100–1400 m (78°55′ W, 0°22′ S), 14.6.1973, Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 7150 (AAU holotype).

Terrestris, usque ad 1 m alta; caulibus erectis, infra vaginis emarcidis obtectis, supra foliosis. *Vaginis* adpressis, plus minusve pubescentibus. *Foliis* ovatis vel ovato–lanceolatis, acutis vel abrupte subacuminatis, sessilibus, cum vaginis articulatis, laminis subtus atropilosis, 7–14 cm longis, 2.3–3.2 cm latis. *Inflorescentiis* terminalibus, sessilibus, unifloris. *Floribus* succedaneis. *Sepalo postico* anguste elliptico, utrinque attenuato, acuto, 42 mm longo, 11 mm lato. *Sepalis lateralibus* oblique falcato–lanceolatis, acutis, vel subobtusis, margine undulatis, revolutis, 51 mm longis, 12 mm latis. *Petalis* obovato–oblanceolatis, acutis, margine undulatis, usque ad 44 mm longis, 10 mm latis. *Labello* e cuneata basi infundibuliformi, in ambitu subquadrato–obovato, antice subtruncato, minute apiculato, margine valde undulato et minute eroso-denticulato; disco in medio incrassato et alte unicarinato, basin versus carinis abbreviatis, oblique insertis ornato, inter carinas minute papilloso; toto labello 4 cm longo, 2.9 cm lato. *Columna* gracili, leviter sinuosa, apicem versus alata, juxta clinandrium falcata, usque ad 3 cm longa. *Ovariis* cylindraceis.

Terrestrial, up to 1 m tall, basal half leafless, provided with distinct evanescent sheaths. *Sheaths* appressed, more or less pubescent. Upper half of the stem leafy. *Leaves* ovate to ovate-lanceolate, acute to abruptly subacuminate, sessile, articulate with leaf sheaths, 7–14 cm long, 2.3–3.2 cm wide, leaf sheaths and the underside of the leaf blades dark pilose. *Inflorescence* terminal, single-flowered, flowers produced in succession from 3 pubescent, imbricating sheaths. *Flowers* with reddish brown sepals and petals and purple lip margined with white and

yellow in the throat. *Dorsal sepal* narrowly elliptic, attenuated in both ends, acute, 42 mm long, 11 mm wide. *Lateral sepals* obliquely falcate–lanceolate, acute to subobtuse with revolute, wavy margins, up to 51 mm long and 12 mm wide. *Petals* obovate–oblanceolate, acute, with undulate margins up to 44 mm long and 10 mm wide. *Lip* infundibuliform from a cuneate base, subquadrate–obovate in outline when spread, subtruncate in front, minutely apiculate, the truncate part heavily undulate and minutely erose-denticulate, disc thickened in the middle with a longitudinal, erect keel and with a pair of obliquely inserted short keels at the base, the area between the basal fleshy keels and the median carina minutely papillose, the base of the lip dorsally carinate, the whole lip 4 cm long and 2.9 cm wide at the truncate apex. *Column* sinuous, rather slender, winged towards the apex, terminating in a pair of falcate processes at the clinandrium, up to 3 cm long. *Ovary* cylindric.

This new species (Fig. 3) is distinguished from *S. atropubescens* Ames & C. Schweinf. and *S. lowii* Rolfe by the distinct keels on the lip. In addition, it differs from *S. atropubescens* by its larger flowers and from *S. lowii* by its considerably broader leaves and red-brown, not purple flowers.

Sobralia melanothrix resembles *S. atropubescens* from Costa Rica with its darkly pubescent sheaths and leaves. In fact, *S. melanothrix* and *S. atropubescens* seem to represent another example of the close phytogeographical relationship which exists between Costa Rica and Ecuador, and which Reichenbach (1878) has already pointed out.

It may be noted that the type of *S. atropubescens* does not measure more than 28 cm in height; the height differences between *S. atropubescens* and *S. melanothrix* taken from the diagnoses, however, can hardly be considered to have any significance because only the upper leaf-bearing part of *S. atropubescens* is present on the type sheet of that particular species.

The specific name is descriptive of the darkly pubescent sheaths and leaves, *melanos* meaning black, dark; and *thrix* meaning hair.

Sobralia rigidissima Lind. ex Rchb. f.

Rchb. f. in Bonpl. 2: 278, 1854.

Sobralia rigidissima has so far only been reported from the type locality in Colombia.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 24–25. steep rocky slopes with scrub, 1950–2100 m (79°05′ W, 3°59′ S), 15.4.1973, Holm-Nielsen et al. 3455 (AAU).

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Morphological and anatomical variation of Vulpia (Gramineae)

R. Cotton and C. A. Stace

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The genus *Vulpia* in its widest sense is reviewed. Almost all the 28 or so species in the world have been examined with respect to a wide range of morphological, anatomical and cytological characters, with due emphasis on caryopsis morphology and leaf anatomy, which have been neglected in the past. It is concluded that *Vulpiella* (one species) is a genus quite distinct from *Vulpia* and more properly placed close to *Cutandia*, and that *Ctenopsis* (four species) is also best recognised as a distinct genus, although close to *Vulpia*. Within *Vulpia* four well-defined groups are recognisable; these are given sectional status and their nomenclature and scope are set out in detail. Of the four, section *Monachne* (three species) occupies a key position, as it is intermediate between sections *Loretia* and *Vulpia* and is the section which section *Spirachne* most closely approaches.

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In its widest historical sense the genus *Vulpia* C. C. Gmel. contains some 28 species, among which five major groups have been recognised: *Vulpia, Loretia, Spirachne, Ctenopsis* and *Vulpiella*. These groups have at various times been given different taxonomic ranks, either as distinct genera or as subgenera or sections of *Vulpia*. The species assigned to these five groups are given in Table 1, in which the classification suggested by Maire (1955) and adopted by us in the first paper in this series (Cotton & Stace 1976) is provisionally used. *Vulpia, Loretia* and *Spirachne* are there considered as sections of *Vulpia*, and *Ctenopsis* and *Vulpiella* as distinct genera.

In addition to these five groups, other taxa have from time to time erroneously been included in *Vulpia*. Notable among these are *V. michelii* (Savi) Reichenb. and *V. tenuicula* Boiss. & Reut., for which the sectional name *Koelerioides* Willk. has been used (Willkomm & Lange 1870), but which are nowadays placed in the separate genus *Avellinia* Parl. in the tribe Aveneae. Species such as these are not covered in this account.

The five groups differ cytologically and geographically (Cotton & Stace 1976); on both counts *Vulpia* is the most diverse. In this group diploids (2n = 14) (*V. bromoides, V. fontquerana, V. membranacea, V. muralis, V. octoflora*), tetraploids (2n = 28) (*V. ambigua, V. ciliata, V. fasciculata*) and hexaploids (2n = 42) (*V. hirtiglumis, V. megalura, V. microstachys, V. myuros, V. persica, V. sciurea*) occur, and it has the widest distribution of all the groups, being found throughout Europe as far north as Scotland and S. Scandinavia, and in North Africa, W. and C. Asia, and North and South America. Several species have become naturalized in E. Asia, Australasia and C. and S. Africa. In the other four groups only diploids (2n = 14) have been recorded and the species are restricted to the Mediterranean region. Chromosome numbers of *Loretia* and *Spirachne* are given in Cotton & Stace (1976). In *Ctenopsis* and *Vulpiella* we know of only one published chromosome count each: *Ctenopsis delicatula* from Portugal (Fernandes & Queirós 1969) and *Vulpiella tenuis* from Tunisia (Kerguélen 1975).

Table 1. Species of *Vulpia* sensu lato allocated to the genera and sections recognised by Maire (1955).

Vulpia C. C. Gmel. section **Vulpia**

V. ambigua (Le Gall) More
V. antofagastensis Parodi
V. bromoides (L.) S. F. Gray
V. ciliata Dumort.
V. fasciculata (Forsk.) Samp.
(*V. membranacea* auct.)
V. fontquerana Melderis & Stace
V. hirtiglumis Boiss. & Hausskn.
V. membranacea (L.) Dumort.
(*V. longiseta* (Brot.) Hackel)
V. microstachys (Nutt.) Benth.
V. muralis (Kunth) Nees (*V. broteri* Boiss. & Reuter)
V. myuros (L.) C. C. Gmel.
(incl. *V. megalura* (Nutt.) Rydb.)
V. octoflora (Walt.) Rydb.
V. persica (Boiss. & Buhse) Krecz. & Bobr.
V. sciurea (Nutt.) Henr.

Vulpia section **Loretia** (Duval-Jouve) Boiss.

V. alopecuros (Schousboe) Dumort.
V. geniculata (L.) Link
V. ligustica (All.) Link
V. litardiereana (Maire) A. Camus
V. obtusa Trabut
V. pauana (Font Quer) Font Quer
V. setacea Parl.
V. sicula (C. Presl) Link

Vulpia section **Spirachne** (Hackel) Boiss.

V. inops (Del.) Hackel

Ctenopsis De Not.

C. cynosuroides (Desf.) Paunero
C. delicatula (Lag.) Paunero
C. gypsophila (Willk. ex Hackel) Paunero
C. pectinella (Del.) De Not.

Vulpiella (Trabut) Burollet

Vulpiella tenuis (Tineo) Kerguélen
(*V. incrassata* (Salz. ex Loisel.) Burollet)

Variation in morphology is of obvious importance in taxonomy at all levels, and that in *Vulpia* has been documented in many publications. Anatomical variation in grasses has, however, mostly been applied to the taxonomy of the higher ranks, and only more recently to that of species and genera. Leaf anatomy of *Vulpia* was mentioned by Pée-Laby (1898), Lewton-Brain (1904) and Burr & Turner (1933), but only as uncritical descriptions of one or two species. Later Paunero (1963, 1964) gave detailed descriptions of the leaf epidermal anatomy of many species of *Vulpia* (including *Vulpiella*) and *Ctenopsis*.

Although there are many floristic accounts of parts of the genus *Vulpia*, and other accounts covering specialised aspects such as leaf epidermis, a broad review of the whole genus covering a very wide range of structural aspects, which is essential for the proper understanding of any genus, has not previously been attempted. In this paper we present the results of such a survey of the above five groups and discuss this in relation to their taxonomy. Specific limits are not in general covered here, but it is necessary to adopt four changes from the names used in Cotton & Stace (1976): *Vulpia fasciculata* (Forskål) Samp. for *V. membranacea* (L.) Dumort.; *V. membranacea* (L.) Dumort. for *V. longiseta* (Brot.) Hackel; *V. muralis* (Kunth) Nees for *V. broteri* Boiss. & Reuter; and *V. myuros* f. *megalura* (Nutt.) Stace & Cotton for *V. megalura* (Nutt.) Rydb. Reasons for these changes have been given by Stace & Cotton (1976a, 1976b, 1977).

Material and methods

Material studied consisted of wild collected plants or plants grown from wild collected caryopses (c. 450 collections), and herbarium specimens from BM, K, LISI, LTR and MANCH. Vouchers of all the wild collections subsequently cultivated are preserved in LTR.

Measurements were made on spikelets taken from the middle portion of the inflorescence or of a panicle branch, since these exhibited the least variation. Unless otherwise noted the size range of characters given is the range of means calculated for each specimen, and not the range of extremes.

The second culm leaf below the inflorescence was used for anatomical work. For internal anatomy leaves were variously hand-sectioned, sectioned with a freezing microtome, or wax-embedded and sectioned with a rocking microtome. Preparation of epidermises followed the technique of Clarke (1960), with some modifications. After softening in hot 88 % lactic acid the abaxial epidermis was isolated by laying it on a slide and scraping away the adaxial epidermis and internal tissues from above with a sharp scalpel. In the isolation of the adaxial epidermis it was necessary to cut away the tough abaxial epidermis and its associated sclerenchyma with a scalpel held at a narrow angle to the leaf, before scraping away the soft mesophyll. The terminology used to describe the leaf epidermis follows that of Metcalfe (1960).

We have examined material of all the species named in Table 1 except *V. obtusa*, which is only a doubtfully distinct species. For ease of reference, for the most part in this paper we use the names of the five groups without qualification as to rank. However, the species are referred to as belonging to one of the three genera *Vulpia*, *Ctenopsis* and *Vulpiella*, although in the case of *Vulpia* their allocation to the sections *Vulpia*, *Loretia* or *Spirachne* is indicated. The abbreviation *V.* stands for *Vulpia*; *Vulpiella* is never abbreviated.

Results

The grasses considered here are typically pooid (festucoid) in their major characteristics. Within the five groups under review the morphological and anatomical characters of greatest taxonomic value are as follows.

Growth habit

All species, with the exception of *V. setacea*, *V. sicula* and *V. litardiereana* (*Loretia*) are annuals. This pattern persists in cultivation, although certain specimens of *V. alopecuros* and *V. geniculata* (*Loretia*) showed a response to warm, humid glasshouse conditions by rooting at the lower nodes of some culms.

Branching of all species, including the perennial ones, is intravaginal only, in contrast to that in the related perennial genus *Festuca*, where both intravaginal and extravaginal branching occurs.

Vivipary, the premature germination of the caryopses while still attached to the inflorescence, has been observed only in one sample of *V. ciliata* (*Vulpia*), from Ardingly, E. Sussex, England.

Inflorescence characters

Exsertion. The degree of exsertion of the inflorescence at and after anthesis is a valuable specific character within certain groups of *Vulpia*. In particular, it is a discriminant between *V. bromoides* and *V. myuros*, and a partial discriminant between *V. membranacea* and *V. fasciculata*. This character is, however, subject to ecophenetic variation, for in very dry conditions the normally exserted inflorescences of *V. bromoides* may become included in the uppermost leaf-sheath and closely resemble those of *V. myuros*. We have observed this condition in material of *V. bromoides* from a wall-top in Ireland and from shingle-banks in England.

Branching. In *Vulpia* and *Loretia* inflorescences range from branched panicles with long pedicels to subspicate racemes. The most extreme examples of the latter occur in *V. alopecuros* (*Loretia*) and *V. persica* (*Vulpia*). All the species of *Ctenopsis* have very sparsely branched inflorescences and in *C. pectinella* they are more or less spicate. In species with racemose or spicate inflorescences the pedicels are borne on only two of the three faces of the triquetrous rhachis, and the inflorescences are therefore secund. This is particularly marked in *C. pectinella*. *Vulpiella* and *Spirachne* have paniculate inflorescences.

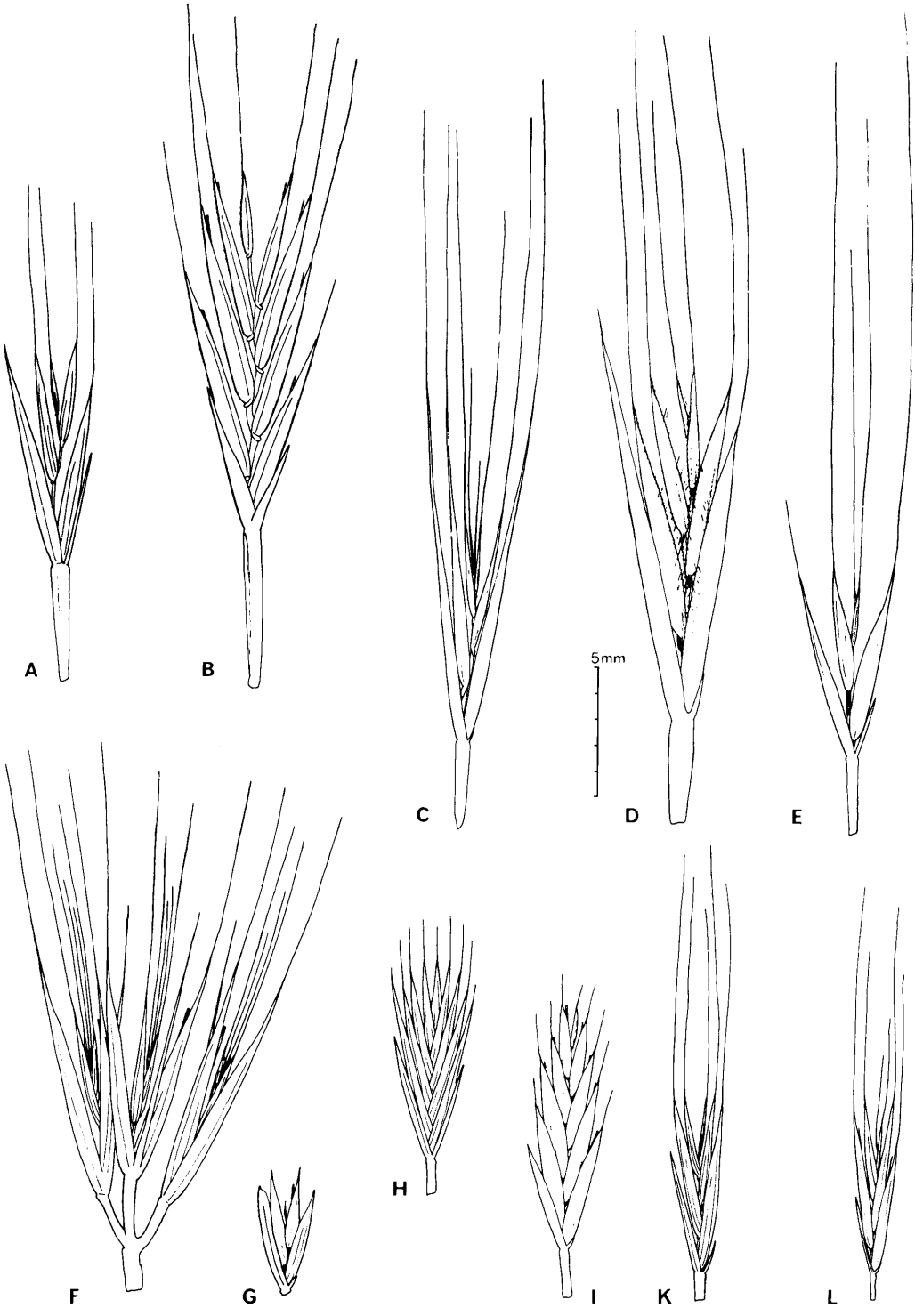
Pedicels. In *Loretia*, *Spirachne* and three species of *Vulpia* (*V. membranacea*, *V. fasciculata*, *V. fontquerana*) the long pedicels are conspicuously dilated and flattened distally (Fig. 1). Dilation is scarcely developed in other species, even where the pedicel is very long.

Pulvini. Well developed pulvini are present in the axils of panicle branches and pedicels in *V. microstachys* agg. (*Vulpia*). These swell after anthesis and cause the branches or spikelets to become strongly divergent or even reflexed. In *Vulpiella* pulvini are present, but the branches do not become reflexed. Pulvini are not found in other species, but are characteristic of certain related genera such as *Scleropoa* and *Cutandia*.

Spikelet groups. In *Spirachne* the spikelets, each with a distinct pedicel, are arranged in constant groups of three on top of a common pedicel–like panicle-branch (Fig. 1F). In all other species the spikelets are borne independently.

Spikelet characters

Aestivation. In most plants of *Spirachne* the normal distichous arrangement of glumes and florets has become twisted so that these parts form a gradual spiral around the rhachilla. This unique character was described in detail by Hackel (1880), when first recognising *Spirachne* as a subgenus of *Vulpia*, although he also recognised a variant which exhibited the normal


A
B
C
5mm
D
E
F
G
H
I
K
L

distichous arrangement (var. *subdisticha* Asch. & Hackel, cf. Maire 1955).

Glumes. In all but two species the two glumes are distinctly unequal, the lower being not more than three-quarters the length of the upper. In the genus *Festuca*, on the other hand, the lower glume is almost always more than three-quarters the length of the upper. In *V. inops* (*Spirachne*) the two glumes (including awns) are subequal in length, but the lower glume is much narrower than the upper and has a shorter body and longer awn (Fig. 1 F), while in *V. octoflora* (*Vulpia*) the lower glume is up to 7/8 as long as the upper (Fig. 1 H). It is sometimes more useful to express glume length in relation to the length of the adjacent lemma; *V. sicula* and *V. setacea* may be separated by this character (upper glume longer than adjacent lemma in *V. setacea*, shorter in *V. sicula*).

In extreme cases the lower glume is very short and veinless, or has one minute vein (Fig. 1). This is the case in all species of *Ctenopsis* and in certain species of *Loretia* (*V. alopecuros, V. ligustica*) and *Vulpia* (*V. membranacea, V. fasciculata, V. ciliata, V. ambigua*). Nevertheless both *Loretia* and *Vulpia* possess other species with relatively long lower glumes (Fig. 1); up to 3:5 the length of the upper in *V. geniculata* (*Loretia*), up to 3:4 in *V. bromoides* (*Vulpia*), and up to 7:8 in *V. octoflora* (*Vulpia*). In *Vulpiella* the ratio is approximately 3:4 (Fig. 1 B).

Glume-ratio is therefore a very important diagnostic criterion in *Vulpia* and related genera. Care is needed, however, to make measurements only on spikelets which are not terminal on the inflorescence or on its branches, for in such spikelets the lower glume is often much longer than usual.

The number of veins is generally 0–1 in the lower glume and 1–3 in the upper glume, the higher numbers in each case being associated with the longer and broader glumes. In *Spirachne* there are 3 and 5 veins respectively.

In most species the glumes are acuminate or sharply acute at the apex. In *V. ciliata* and *V. ambigua* (*Vulpia*) the upper glume is hyaline at the apex, which frequently breaks off, giving the false impression that the apex is blunt. In *Spirachne* and *V. membranacea* and *V. fasciculata* (*Vulpia*) the upper glume has an awn up to as long as the body, while in *V. fontquerana* (*Vulpia*) and annual species of *Loretia* the upper glume is also characteristically, though more shortly, awned.

The glumes are mostly rounded dorsally but in *Ctenopsis cynosuroides* and *C. pectinella* the upper glume is keeled distally.

Glume pubescence is reviewed under lemma.

Sterile florets. As in most pooid grasses, the 1–2(–3) most apical florets in each spikelet are reduced in size and male or sterile in the majority of the species. However, two other patterns also occur.

In *V. ciliata* and *V. ambigua* (*Vulpia*) there are only 1–3 fertile florets, but 3–7 distal sterile florets. The lemmas of the latter exceed those of the former in length and width (and in *V. ciliata* bear a different pattern of indumentum), but have shorter awns (Fig. 2 B, C). The paleas of the sterile florets are reduced or absent.

In *V. membranacea, V. fasciculata* and *V. fontquerana* (*Vulpia*) there is a congested group of 2–6 very small sterile florets (Fig. 1 C, E). This pattern also occurs in *Spirachne*, where there is only one fertile floret, just as there often is in *V. fontquerana*.

Rhachilla. The lowest floret is more or less sessile within the glumes, but the rest are separated by rhachilla segments which provide useful taxonomic characters in terms of length, shape and indumentum. In *V. membranacea, V. fasciculata* and *V. fontquerana* (*Vulpia*) and in *Spirachne* the apical group of sterile florets is borne on a long slender rhachilla segment which separates this group from the fertile florets.

Dispersal units. In most species the unit of dispersal is a single floret with the next higher rhachilla segment, the spikelet disarticulating at the base of each floret and leaving the pedicel and two glumes on the parent plant. There is usually no abscission layer at the base of sterile or male florets, so the most distal fertile floret carries

Fig. 1. Spikelets of representative species of *Vulpia* sensu lato. – A: *V. geniculata*. – B: *Vulpiella tenuis*. – C: *V. fasciculata*. – D: *V. alopecuros*. – E: *V. fontquerana*. – F: *V. inops*. – G: *Ctenopsis pectinella*. – H: *V. octoflora*. – I: *Ctenopsis gypsophila*. – K: *V. myuros*. – L: *V. ambigua*.

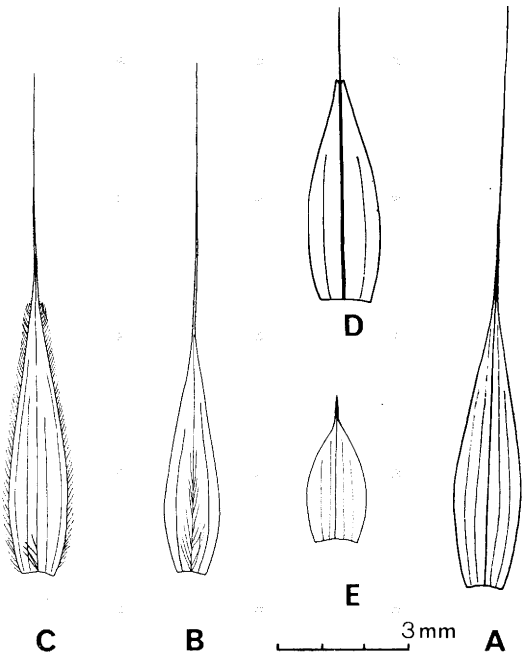


Fig. 2. Lemmas of representative species of *Vulpia* sensu lato. – A: *V. bromoides*. – B: *V. ciliata* (from fertile floret). – C: *V. ciliata* (from sterile floret). – D: *Vulpiella tenuis*. – E: *Ctenopsis gypsophila*.

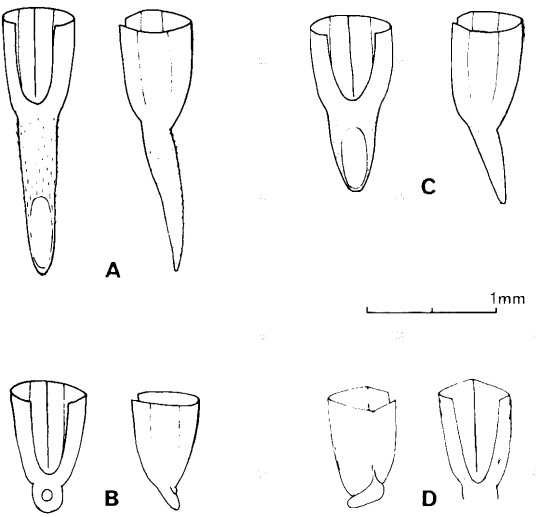


Fig. 3. Adaxial and lateral views of lemma calluses of representative species of *Vulpia* sensu lato. – A: *V. fontquerana*. – B: *V. fasciculata*. – C: *V. bromoides*. – D: *Vulpiella tenuis*.

with it any more distal sterile ones. Such a unit is thus particularly bulky in *V. ciliata, V. ambigua, V. fontquerana, V. fasciculata,* and *V. membranacea* (*Vulpia*). In plants of the first three of these species bearing spikelets with only one fertile floret, all the florets therefore fall as a single unit. In all these species the antrorsely hispid lemmas are efficient in penetrating fur and clothing, etc., and act as a dispersal agency.

In *V. fasciculata* and *V. membranacea* (*Vulpia*) and in *Loretia* abscission occurs less readily below each floret, but in addition there is an abscission layer at the base of the pedicels. Hence the dispersal units are mixtures of single fertile florets, single fertile florets with one or more sterile florets attached, and whole spikelets. The last are particularly characteristic of *V. alopecuros* (*Loretia*). In these species abscission sometimes occurs at the base of each rhachilla segment rather than above it. The antrorsely hispid, distally dilated pedicels are efficient in dispersing whole spikelets.

In *Spirachne* there is little abscission within or below each spikelet, but it regularly occurs at the base of the ultimate panicle branch bearing three spikelets, so that the unit of dispersal is three spikelets (with a total of three fertile florets).

In *Vulpiella* abscission often occurs also at the position of the pulvini, at the base of the pedicels and panicle branches, a feature shared with the related genus *Cutandia* but scarcely developed in the pulvinate *V. microstachys* (*Vulpia*).

Floret characters

Callus. The callus appears to be derived from the most basal part of each rhachilla segment, and the lemma arises from it. In most species the line of disarticulation lies adjacent to and below the callus, so that it forms the most basal part of each separated, ripe floret. In the majority of species considered here it is a thickened, glabrous, horse-shoe-shaped structure, approximately 0.1–0.2 mm in the plane of the longitudinal axis of the lemma (Fig. 3 C, D). However, in *V. alopecuros* (*Loretia*) and *V. fasciculata* and *V. membranacea* (*Vulpia*) it is much longer (0.5–0.8 mm), pointed and antrorsely hispid (Fig. 3 B), while in *V. fontquerana* it is 1–1.5 mm, antrorsely hispid and sharply pointed (Fig. 3 A). In the last case the callus is about as long as the rest of the

rhachilla segment, the florets thus being separated by 2–3 mm, and serves as an effective agent of dispersal. In the other three species, on the other hand, the spikelets often fall as a single unit, so the pointed callus plays a much lesser role in dispersal.

Lemma. The usual features of the lemma such as size, shape, number and prominence of veins, length of awns and pubescence are all important diagnostic characters, but many of them vary at or even below the species level.

The longest lemmas (excluding awns) are found in *V. alopecuros* (*Loretia*), *V. fasciculata* and *V. membranacea* (*Vulpia*), where they may be up to c. 18 mm long, and the shortest in *V. sciurea* (*Vulpia*), where they are only 2.5–3.5 mm long. It must be emphasised that these measurements apply to only the two lowest florets, and are extremes of means. More distal florets usually have smaller parts, those of apical, sterile florets often being minute, and exceptional spikelets can often be found where even the basal florets have measurements outside those given above. We consider that mean basal lemma length is the most satisfactory measurement for diagnostic purposes. Lemma width is seldom of diagnostic value, but it can be used to separate *V. bromoides* (1.3–1.9 mm) and *V. muralis* (0.8–1.3 mm) (*Vulpia*).

In *Vulpia*, *Loretia*, *Spirachne* and *Ctenopsis* the lemma is narrowed at the apex into an awn of varying length, often longer than the lemma itself (Fig. 2A–C). In *Ctenopsis* (Fig. 2E) and some species of *Vulpia* the awns are shorter, the extreme being found in *C. pectinella*, with awns up to c. 1 mm only. The lemma is mostly very gradually narrowed at the apex, but in *Ctenopsis* and a few *Vulpia* species it is more abruptly so. In *Vulpiella* (Fig. 2D) the lemma is slightly but distinctly notched at the apex, and the awn arises from the termination of the midrib at the base of the notch, as in the genus *Cutandia*.

In *Vulpia*, *Loretia*, *Spirachne* and *Ctenopsis* the lemmas are mostly 5-veined and rounded on the back, although in *C. pectinella* they are somewhat keeled and in *V. ciliata* and *V. ambigua* (*Vulpia*) they often possess only 3 veins (Fig. 2B, C). In all cases the veins are usually rather inconspicuous. In *Vulpiella*, on the other hand, the lemmas are conspicuously 3-veined and strongly keeled on all 3 veins (Fig. 3D). In lemma characters, therefore, *Vulpiella* closely resembles the genus *Cutandia*. It must be noted that in both *Cutandia* and *Vulpiella* microscopic examination of cleared lemmas usually shows an extra pair of very weakly developed veins.

Lemma (and glume) pubescence is a very variable character, but its pattern of variation is sometimes of great interest. In some species no variation has been recorded, e.g. *V. membranacea* (*Vulpia*), where the lemmas are glabrous apart from antrorsely directed pricklets on the awn and veins. But in most species variation occurs from totally glabrous to densely pubescent lemmas. The pubescence of the glumes and lemmas, and of the margins, veins and other surfaces of the lemma, often varies independently, so that a great many combinations are possible. These are particularly numerous in *V. alopecuros* (*Loretia*) where they were treated in detail by Maire (1955), and in *V. microstachys* (*Vulpia*), in which many segregates have been described based on these and other characters (Lonard & Gould 1974). *V. megalura* (*Vulpia*) is in fact only a variant of V. *myuros* with ciliate lemmas and we therefore recognise it as only a forma of the latter (Stace & Cotton 1976 b). In most species the variant with densely pubescent lemmas is much less common than the subglabrous variant, but in *V. hirtiglumis* (*Vulpia*) the reverse is the case, only one example of this species without pubescent lemmas having been seen by us. *V. ciliata* and *V. sciurea* (*Vulpia*) and *V. alopecuros* (*Loretia*) are also more often pubescent than not. *V. ciliata* differs from *V. ambigua* mainly in its lemma pubescence, being hairy on the margins and dorsal midline in the former but glabrous or scabrid in the latter. There are also small differences in floral measurements between these two species, which are more or less allopatric. There are, however, occasional glabrous variants of *V. ciliata* (var. *imberbis* (Vis.) Halácsy) which occur among typical variants well outside the geographical range of *V. ambigua*.

Palea. The paleas provide relatively few diagnostic characters. In all the species they are 2-keeled, bifid at the apex and slightly shorter than to as long as the lemmas, but small specific differences in overall shape, degree of apical notching and pubescence do occur. Palea length

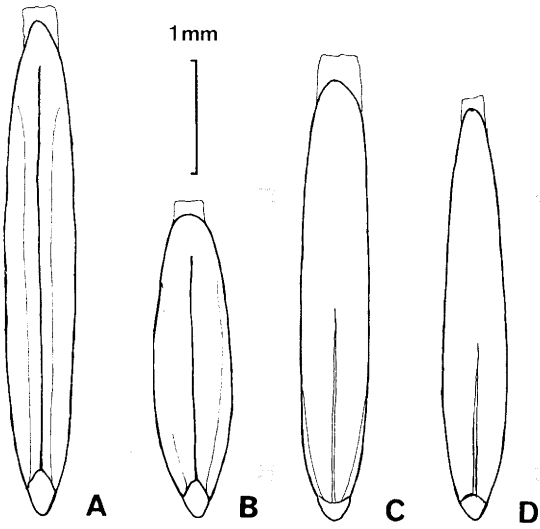


Fig. 4. Adaxial views of caryopses of representative species of *Vulpia* sensu lato. – A: *V. myuros*. – B: *V. octoflora*. – C: *Vulpiella tenuis*. – D: *Ctenopsis cynosuroides*.

may be a slightly better discriminant than lemma length in separating *V. fasciculata* from *V. membranacea* (*Vulpia*).

Stamens. In *Loretia, Spirachne, Ctenopsis* and *Vulpiella* there are usually three stamens, which become exserted at anthesis, although the anther size and the degree of exsertion varies a good deal. Thus in *C. pectinella, C. cynosuroides, C. gypsophila* and *Spirachne* the anthers are only c. 0.4–1.4 mm and appear just beyond the lemma tip at anthesis, whereas in species of *Loretia* they are mostly 2–4 mm and pendent on long filaments. Occasionally, plants of these groups with only 1 or 2 stamens have been recorded (cf. Maire 1955).

In *Vulpia* there is a greater range in such stamen characters. *V. fasciculata* and *V. membranacea* have 1–3 anthers which are 0.7–2 mm and just exserted at anthesis; *V. fontquerana* has 3 anthers 0.5–0.8 mm and also just exserted at anthesis; and the other species have usually a single anther 0.3–0.8 mm and included at anthesis. In the third group occasional specimens are encountered with 2 or 3 anthers, or in which the anther just protrudes at anthesis or slightly exceeds 0.8 mm, but basically it is a group of cleistogamous, self-pollinated grasses. Within it, *V. ciliata* and *V. ambigua* represent extremes; they are ephemeral, cleistogamous grasses with a single anther 0.4–0.6 mm long. However, we have seen specimens of *V. myuros* in England and of *V. muralis* in Sicily with a single, well-exserted anther, and similar examples of the American species have been reported by Lonard & Gould (1974) and Kannenberg & Allard (1967). *V. persica* has 1–3 small anthers, and there is no justification for Bor's (1970) referring it to *Loretia*. The undehisced anthers are either yellowish or deep violet in colour, and we have seen both colour variants on different plants in the same population of several species. Similar variation is found in a great many grasses of varying relationships, and seems to be of very little taxonomic significance.

Ovary and lodicules. These organs provide relatively few taxonomic characters. In *Vulpiella* the lodicules are ovate and rather irregularly toothed at the apex, whereas in *Vulpia, Loretia, Spirachne* and *Ctenopsis* they are usually narrower and are conspicuously bifid, the relative lengths and shapes of the two teeth varying from species to species. In lodicule characters *Vulpiella* resembles the genus *Cutandia* rather than *Vulpia* and its allies.

The ovary is glabrous in most species, and provided with two terminal or subterminal styles. However, in all species of *Loretia* except *V. alopecuros*, in *V. fasciculata* (*Vulpia*), and in *Spirachne* it is conspicuously pubescent at the apex. This character is a constant discriminant between *V. fasciculata* and *V. membranacea*, which are otherwise extremely difficult to separate. It should be noted that in Paunero (1964) the drawings of the spikelets (Figs. 21, 22) of these two species have become transposed, so that the ovary of *V. fasciculata* wrongly appears glabrous.

Caryopsis. The caryopsis varies from linear to narrowly elliptic in outline, with a short embryo visible at the base of the abaxial (dorsal) surface. The species with the relatively broadest caryopsis (ratio c. 1:4) is *V. octoflora* (*Vulpia*) (Fig. 4 B), and those with the narrowest ones (ratio c. 1:7) are *V. membranacea, V. fasciculata, V. myuros* (Fig. 4A), *V. ciliata* and *V. ambigua* (*Vulpia*). Those species with a pubescent ovary-tip retain this characteristic on the ripe caryopsis. According to Paunero (1963) the apex of the caryopsis is

papillose in *Ctenopsis delicatula* and *C. cynosuroides*, and smooth in *C. gypsophila* and *C. pectinella*, but we have not observed such a difference.

The abaxial surface is rounded in *Vulpia*, *Loretia*, *Spirachne* and *Ctenopsis*, but strongly carinate in *Vulpiella*, producing a more or less trigonous caryopsis. The edges of the caryopsis are rolled round on to the adaxial side to produce a groove which obscures the hilum to varying degrees in different species.

The hilum is very narrow and almost as long as the caryopsis in *Vulpia*, *Loretia* and *Spirachne* (Fig. 4A, B), but less than half as long in *Ctenopsis* and *Vulpiella* (Fig. 4C, D).

The palea is wrapped round the caryopsis and in *Vulpia*, *Loretia*, *Spirachne* and *Vulpiella* is firmly adherent to it, but in *Ctenopsis* the caryopsis remains more or less free from the palea.

Leaf characters

Morphology. Leaf morphology is not very variable. All the species possess flat leaf-blades which, however, become convolute as the season advances. In dry conditions this often takes place well before flowering.

A few species show conspicuously dilated upper leaf-sheaths, this character being particularly well displayed in *V. fasciculata* (*Vulpia*) and to a lesser extent in other species where the inflorescence is partially enclosed in the uppermost leaf-sheath at anthesis.

The membranous ligules show some variation in length, which is particularly useful in separating *C. delicatula* (0.1–0.5 mm), *C. gypsophila* (0.5–1.5 mm) and *C. cynosuroides* (1–2.5 mm).

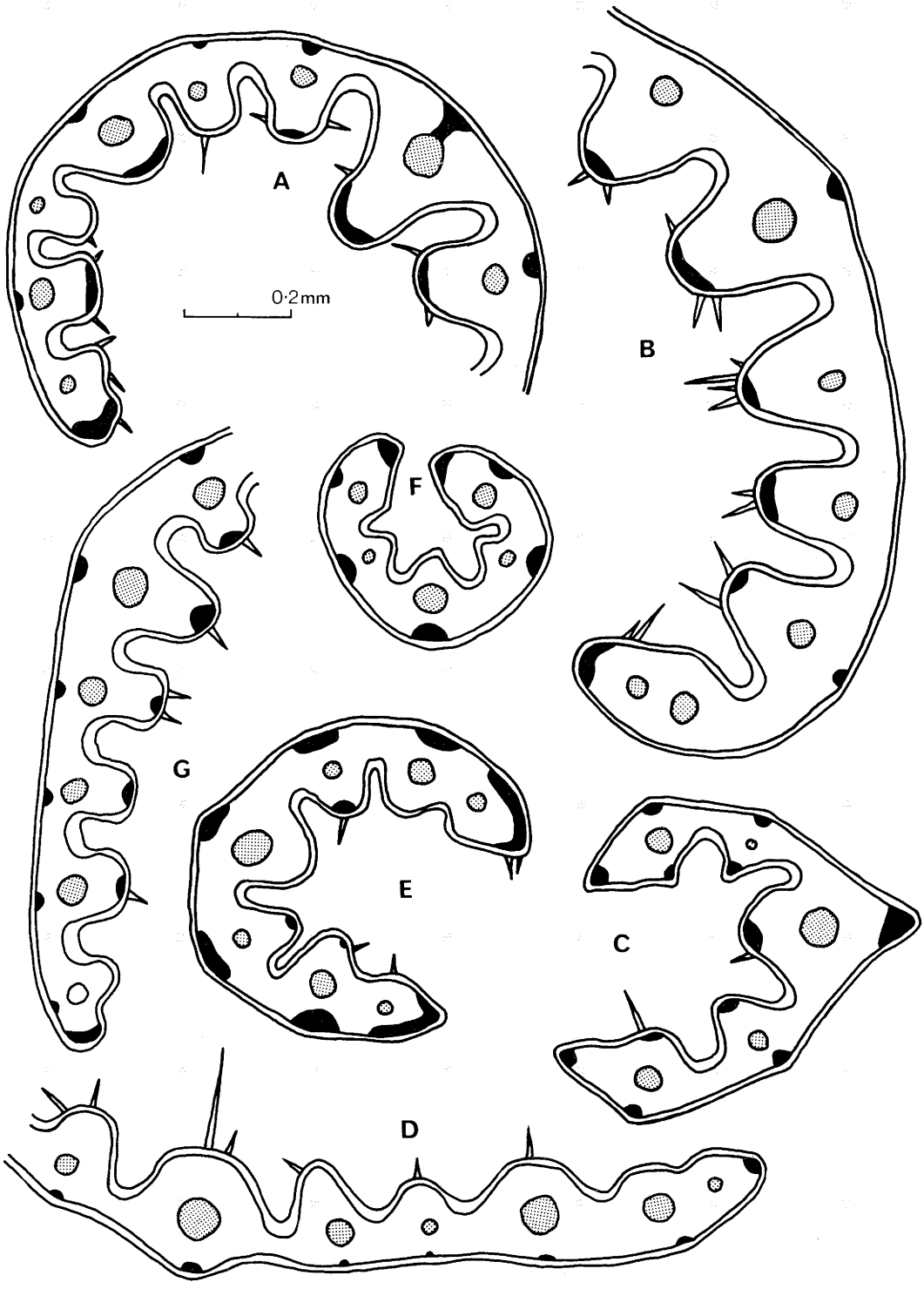
Internal anatomy. The anatomical details of the leaves follow the typical festucoid pattern described by Metcalfe (1960).

The adaxial surface of the leaf-blade is strongly ribbed, each rib corresponding to the position of a vascular bundle, the most prominent of which is the midrib itself (Fig. 5). In most species there are approximately 9–13 veins across the leaf width, the midrib and the third one on either side being larger than the others, but frequently some of the smaller veins are missing or there are extra ones. In *Ctenopsis* and *Spirachne* there are usually only 5–7 veins, which alternate between large and small.

Bundles (caps) of fibres above and below each vein, especially the midrib, and at the leaf margins, are developed to varying extents. They are distinctly better developed in *V. fasciculata*, *V. membranacea* and *V. fontquerana* (*Vulpia*), *Loretia*, *Vulpiella* and (especially) *Ctenopsis* than in *Spirachne* and the rest of *Vulpia*. In some cases, especially in *Vulpiella* and *Spirachne*, the epidermal cells contiguous with the sclerenchyma bundles, particularly on the abaxial surface, are lignified and very narrow in cross section, as is equally clearly seen on epidermal preparations. *Spirachne* (Fig. 5C) is also distinctive in that the abaxial leaf surface is keeled on the midrib and major lateral veins, whereas it is more or less rounded or flat in all other species. The differences in the bulliform cells of *V. myuros* f. *myuros* and f. *megalura* given by Lonard & Gould (1974) were not observable in our material.

Epidermis. The epidermal anatomy is again typically festucoid (Metcalfe 1960), but variation within this pattern occurs. The abaxial epidermis exhibits two major zones, costal and intercostal, but on the adaxial epidermis there is a narrow intermediate zone between the two, and the intercostal zone can be subdivided into central bulliform and marginal stomatal regions. On both epidermises long cells, short cells, hairs and stomata may occur.

The epidermises of *Vulpia*, *Loretia*, *Spirachne*, and *Ctenopsis* are very similar. On the abaxial epidermis (Fig. 6A) the long cells are very long, parallel sided and have tightly undulate anticlinal cell-walls in the intercostal zones. The short cells vary greatly in abundance, but are generally present in both costal and intercostal zones. They are very short, with smooth walls, and vary in the degree to which they are single or paired; single short cells are either cork-cells or prickle-bases, whereas double short cells consist of two cork-cells, a cork-cell and a silica-cell or a cork-cell and a prickle-base. In the costal zone up to about four adjacent short cells may occur. On the abaxial surface all the hairs are prickles: short, more or less conical, thick-walled hairs arising from a short cell. They are present on the leaf margin and to varying degrees (but never frequent) in the costal and intercostal zones. Stomata are only of sporadic


A
0·2mm
B
F
G
E
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D

occurrence on the abaxial epidermis; when present they are confined to the intercostal zones.

On the adaxial epidermis (Fig. 6 B), except close to the margins, the long cells are straight-walled, and short cells (apart from hair- or prickle-bases) rather infrequent and more or less confined to the costal and intermediate zones. Hairs are generally much more abundant than on the abaxial epidermis, but may or may not be confined to the costal zone. In almost all cases at least the majority of hairs in the costal zone are macrohairs, often mixed with prickles and sometimes with intermediate types. Microhairs and papillae are absent. The density of macrohairs varies considerably from species to species and to some extent within species and, of course, constitutes the macroscopic character 'leaf pubescence'. Macrohairs are absent from the material seen of *V. sciurea* (*Vulpia*) and *C. pectinella*, and prickles too (except on the leaf margin) from that of the latter; material of all the other species examined possesses both macrohairs and prickles. The stomatal zone consists of modified (shorter) long cells with rows of stomata bearing the typically gramineous paired subsidiary cells. The bulliform cells are large, thin-walled cells with flattened ends.

Within *Vulpia*, *Loretia*, *Spirachne* and *Ctenopsis* variation is thus virtually confined to the frequency, distribution and pairing of short cells and the frequency of prickles on the abaxial epidermis, and the frequency and distribution of prickles and macrohairs on the adaxial epidermis, and the quantitative differences observed are not well correlated with any of the four taxonomic groupings. Moreover, it is possible, with the examination of further material, that many of the apparent interspecific differences would disappear. Epidermal characters of this sort, possibly distinguishing *V. fasciculata* and *V. membranacea* (*Vulpia*), have been given by Stace & Cotton (1976 a).

The epidermal characters of the single species of *Vulpiella* (Fig. 6C, D) differ markedly from the above. The main differences are as follows:

(1) Short cells are confined to the costal zones on both epidermises.

(2) Short cells on both epidermises are often in pairs or greater units, or separated by longer short-cells.

(3) Short cells on both epidermises are much longer than in the other taxonomic groups, and mostly with markedly undulate anticlinal walls.

(4) Silica cells all have markedly undulate anticlinal walls and occur in the costal zones of both epidermises.

(5) Long cells on the abaxial epidermis have straight anticlinal walls, and are conspicuously wider at their midpoint than at their ends.

(6) There are more stomata in the intercostal zone on the abaxial epidermis.

(7) Hairs are absent from the abaxial epidermis.

(8) Prickles are present in the costal zone but hairs are otherwise absent from the adaxial epidermis.

The list of differences is impressive, and moreover leads to a much closer resemblance between abaxial and adaxial epidermises of *Vulpiella* than between those of the other four groups.

Table 2. Stomatal length and chromosome number in two species groups of *Vulpia*. Stomatal lengths are ranges of means (in three cases only one collection measured).

Species	2n	Stomatal length (μm)
V. myuros	42	34–57
V. hirtiglumis	42	53
V. bromoides	14	24–39
V. muralis	14	29–43
V. octoflora	14	39
V. fasciculata	28	33–59
V. membranacea	14	26–41
V. fontquerana	14	36

Stomatal length. Although there is not a good overall correlation between chromosome number (Cotton & Stace 1976) and stomatal length, within certain critical species groups of *Vulpia* it is better. Table 2 shows that the hexaploids *V. myuros* and *V. hirtiglumis* have on average longer stomata than the three related diploids, and that the tetraploid *V. fasciculata* has on average longer stomata than its two related diploids.

Fig. 5. Leaf-sections of representative species of *Vulpia* sensu lato. – A: *V. alopecuros*. – B: *V. fasciculata*. – C: *V. inops*. – D: *V. myuros*. – E: *Ctenopsis gypsophila*. – F: *Ctenopsis pectinella*. – G: *Vulpiella tenuis*. – Shaded regions: vascular bundles. Black regions: sclerenchyma.

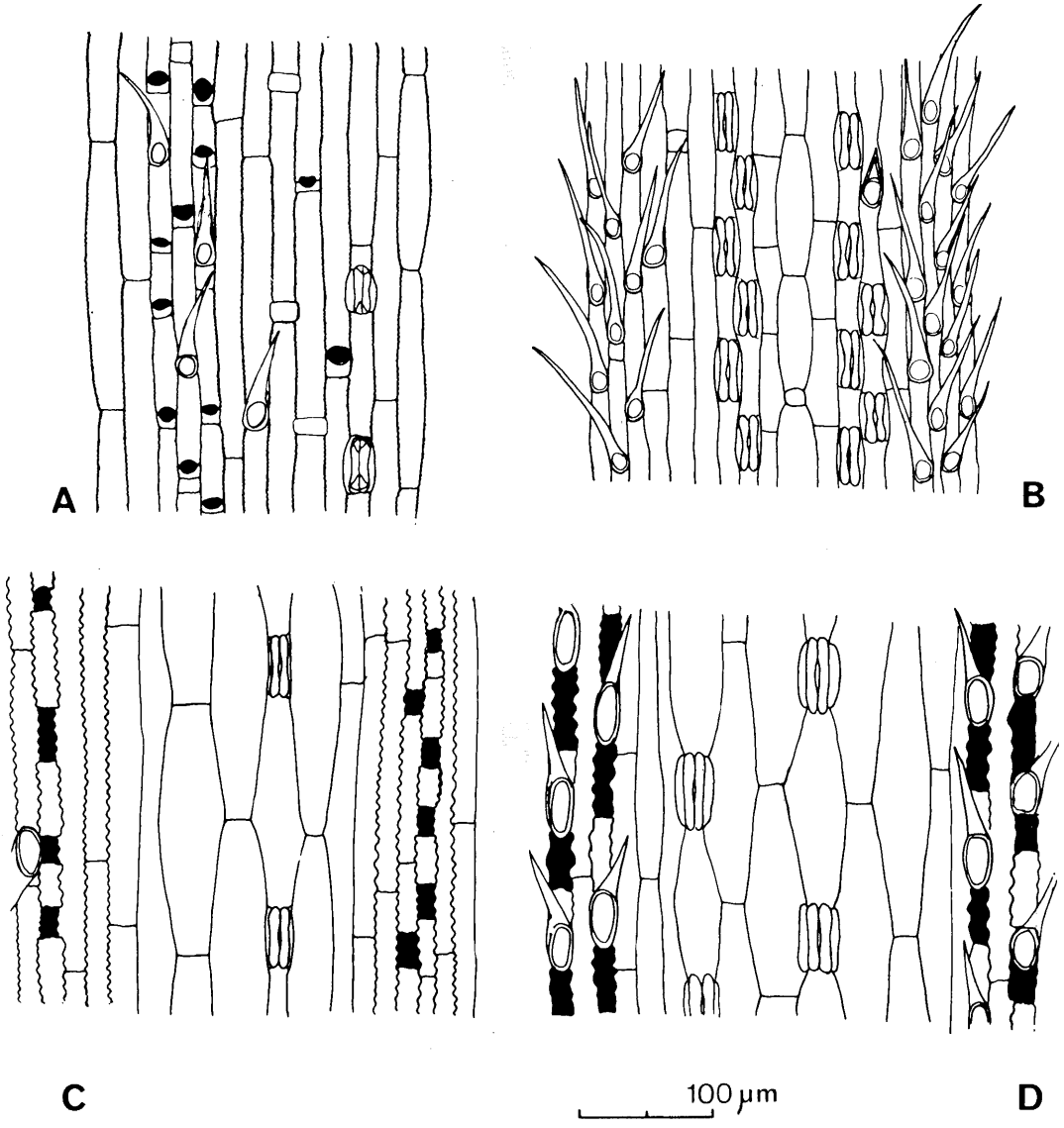


Fig. 6. Epidermises of *Vulpia alopecuros* (A, abaxial; B, adaxial) and *Vulpiella tenuis* (C, abaxial; D, adaxial). – Black regions: silica-cells.

Discussion

The morphological and anatomical characters previously surveyed clearly serve to differentiate taxa at all levels. Hence, it is possible to define each of the five taxonomic groups recognised and various subgroups within some of them, as well as the individual species and infraspecific taxa.

Vulpiella

Of the five groups, *Vulpiella* is clearly the most distinct. It differs from *Vulpia*, *Loretia*, *Spirachne* and *Ctenopsis* in the well-developed pulvini at the base of the inflorescence branchlets, at which disarticulation takes place; in the 3-veined, 3-keeled lemmas with a notched apex; in the broad,

irregularly toothed lodicules; in the trigonous caryopsis with a short hilum; and in a considerable number of features of the leaf epidermis (notably the straight-walled long cells and the relatively long, undulate-walled silica-cells on both epidermises). Many of these characters are traditionally considered important diagnostic features in the Gramineae, and together they provide convincing evidence that *Vulpiella* and *Vulpia* are not congeneric. In all its important characters the single species of *Vulpiella* most closely resembles the genus *Cutandia*, which will be reviewed in a later paper; it is simply the long awns and non-divaricating inflorescence branches of *Vulpiella* which give it a superficial resemblance to *Vulpia*. We are therefore of the opinion that Duval-Jouve (1880) and Camus (1943) were wrong in placing this species in *Loretia* Duval-Jouve and in *Vulpia* subgenus *Loretia* section *Incrassatae* A. Camus respectively.

Ctenopsis

Ctenopsis differs from the other three groups in its relatively short, broad caryopses which have a short hilum and which lie more or less free from the palea at maturity, although we are not aware that these characters have been stressed by previous workers. Traditionally (cf. Maire 1955) *Ctenopsis* has been treated as a monotypic genus (type species *C. pectinella*), but Paunero (1963) added to it the other three species in Table 1. These have been usually included in *Vulpia*, although the name *Narduretia* has also been coined for them (Huguet del Villar 1925). *C. pectinella* is certainly the most distinctive of the four species, particularly with regard to its sessile spikelets, keeled, shortly-awned lemma apex and glabrous leaf epidermis, but in general the characters surveyed here support Paunero's broader concept of the genus. It is additionally characterized by its simple, secund inflorescence, large abaxial bundles of leaf sclerenchyma, minute lower glume, rather abruptly narrowed lemmas often with rather short awns, keeled upper glume in two species, and 3 short, slightly but distinctly exserted anthers. While arguments could be made for including *Ctenopsis* in *Vulpia*, we feel that at least equally strong arguments exist for recognising it as a distinct genus and we therefore prefer to follow Paunero's treatment.

Vulpia, Loretia and Spirachne

There are good differences between *Loretia* and *Vulpia* if, for the present, we set aside *V. fasciculata, V. membranacea* and *V. fontquerana*. *Loretia* has chasmogamous florets with three long anthers, well developed leaf-sclerenchyma, and distally dilated pedicels with a basal abscission layer, while in *Vulpia* the florets are cleistogamous (or nearly so) with often a single, short anther, the leaf-sclerenchyma is less abundant, and the pedicels are unthickened and lack an abscission layer. These are clear differences which, in the absence of *V. fasciculata* and its two allies, would strongly suggest generic separation for *Vulpia* and *Loretia*.

V. fasciculata and *V. membranacea* are very closely related and have been much confused in the past (Stace & Cotton 1976 a); many authors have not recognised them as distinct species (cf. Maire 1955). *V. fontquerana*, a recently discovered endemic from SW. Spain (Melderis & Stace 1968), is much more distinct, but nevertheless obviously closely related. The three share in common the general facies and short anthers of *Vulpia*, and the well developed leaf-sclerenchyma, distally dilated pedicels and usually 3, exserted anthers of *Loretia*. Moreover, spikelet disarticulation of *V. fontquerana* is as in *Vulpia*, whereas that of the other two species is as in *Loretia*, and the hairy ovary apex of *V. fasciculata* is found elsewhere in *Loretia* but not in *Vulpia*. These facts clearly show that *V. fasciculata, V. membranacea* and *V. fontquerana* form a well-defined taxon somewhat intermediate between *Loretia* and *Vulpia*. This group is further characterized by the well-awned upper glumes, the distinctive apical group of sterile florets and the very well developed, pointed basal callus. It (or those members of it under study at the time) has previously been described as section *Monachne* (Dumortier 1824) and section *Intermediae* (Camus 1943).

Spirachne is clearly most similar to *Monachne* of the above 3 groups, with which it shares the apical group of sterile florets, 3 short, slightly exserted anthers, the awned upper glume and distally dilated pedicels. It is, however, unique in its groups of three spikelets (each usually with a spiral aestivation), subequal glumes and keeled leaves.

Thus, within the genus *Vulpia*, excluding

Vulpiella and *Ctenopsis*, four major groups are recognisable. Within each of these there is variation roughly proportional to the number of species, but in our opinion it does not warrant recognition of further supra-specific categories. Some of this variation is parallel within the four groups. For example the glume ratio shows a wide range of variation in *Vulpia, Monachne* and *Loretia*, the range being greatest in *Vulpia* and least in *Monachne*, and awn-length is similarly variable. The existence of parallel variation within many species, regardless of the group to which they belong, has been pointed out previously, particularly with regard to pubescence.

Within each of the two largest groups, *Vulpia* and *Loretia*, there are species or groups of species with distinctive, exceptional features. Notable among these is the perennial habit in *V. sicula, V. setacea* and *V. litardiereana* (*Loretia*); the characteristic group of apical sterile florets and 3-veined lemmas in *V. ciliata* and *V. ambigua* (*Vulpia*); the subsessile spikelets in *V. persica* (*Vulpia*); and the pulvinate inflorescence branches in *V. microstachys* (*Vulpia*).

Relationship to Festuca

The closest relations of *Vulpia* (including *Loretia, Monachne* and *Spirachne*) are *Ctenopsis*, discussed above, *Nardurus*, to be discussed in a later paper, and *Festuca*. *Festuca* and *Vulpia* have been traditionally separated by up to six characters, none of which, however, forms an absolute criterion. Hence *V. sicula* and its two allies are perennials, *V. geniculata, V. setacea* and others have well-branched panicles, *Loretia* has chasmogamous florets, *V. octoflora* and *Spirachne* have subequal glumes, *V. octoflora* has rather abruptly narrowed and shortly awned lemmas, and *V. geniculata* and *V. bromoides* have relatively broad caryopses; all these characters are typical of *Festuca*. Nevertheless it is possible to separate the two genera by a combination of characters and, although it is admittedly simply a practical convenience, we prefer this to their amalgamation.

Of the four groups of *Vulpia, Loretia* is obviously the most similar to *Festuca*, forming a link between *Festuca* and the other three groups.

Taxonomic conclusions

We consider *Vulpiella, Ctenopsis* and *Vulpia* to be separate genera, but the status of these and the ranks accorded the four groups within *Vulpia* will remain a matter of subjective judgement unless numerical taxonomic studies can produce an acceptable objective system.

Loretia, Vulpia and *Spirachne* are all distinct groups which might well merit recognition at the generic level but for the fact that *Monachne* clearly links the former two and *Spirachne* seems closer to *Monachne* than to the others. Therefore we recognise these four groups as sections of *Vulpia*. We consider this classification to be the most useful and practical, but it is clearly a phenetic, not a phylogenetic, one.

Within *Ctenopsis, C. pectinella* is distinct from the other three species and the two groups merit sectional status.

The following conspectus sets out the classification we have adopted, together with the most important supra-specific synonyms and an indication of the scope of each taxon. A more detailed taxonomic description of all the taxa, including the species, will be given in a later paper.

Vulpiella (Trabut) Burollet

Basionym: *Cutandia* subg. *Vulpiella* Trabut
Type species: *Cutandia incrassata* (Salzm. ex Loisel.) Bentham = *Vulpiella tenuis* (Tineo) Kerguélen
Other synonyms: *Cutandia* sect. *Vulpecula* Hermann; *Vulpia* subg. *Loretia* sect. *Incrassatae* A. Camus, pro parte excl. typ.
Monotypic

Ctenopsis De Not.

Type species: *C. pectinella* (Del.) De Not.

Sect. **Ctenopsis**

Synonym: *Festuca* subg. *Vulpia* sect. *Pectinula* Hermann
Monotypic

Sect. **Pseudocynosurus** (Willk.) Cotton & Stace, comb. nov.

Basionym: *Vulpia* sect. *Pseudocynosurus* Willk., in Willk. & Lange, Prodr. Fl. Hisp. 1: 91 (1861)
Type species: *V. delicatula* (Lag.) Dumort. = *C. delicatula* (Lag.) Paunero
Other synonyms: *Narduretia* Huguet d. Villar; *Festuca*

subg. *Vulpia* sect. *Ctenopsis* sens. Hermann, non sens. orig.
Other species: *C. gypsophila* (Willk. ex Hackel) Paunero; *C. cynosuroides* (Desf.) Paunero

Vulpia C. C. Gmel.

Type species: *V. myuros* (L.) C. C. Gmel.
Synonyms: *Mygalurus* Link; *Dasiola* Raf.; *Chloamnia* Raf.; *Distomomischus* Dulac

Sect. **Vulpia**

Synonym: *Vulpia* subg. *Euvulpia* sect. *Articulatae* A. Camus
Species included: All species under sect. *Vulpia* in Table 1 with the exception of the three included under sect. *Monachne* below

Sect. **Monachne** Dumort.

Type species: *V. uniglumis* (Ait.) Dumort. = *V. fasciculata* (Forsk.) Samp.
Synonym: *Vulpia* subg. *Euvulpia* sect. *Intermediae* A. Camus
Other species: *V. membranacea* (L.) Dumort.; *V. fontquerana* Melderis & Stace

Sect. **Spirachne** (Hackel) Boiss.

Basionym: *Vulpia* subg. *Spirachne* Hackel
Type species: *V. inops* (Del.) Hackel
Monotypic

Sect. **Loretia** (Duval-Jouve) Boiss.

Basionym: *Loretia* Duval-Jouve
Lectotype species: *L. geniculata* (L.) Duval-Jouve, selected here, = *V. geniculata* (L.) Link
Other synonyms: *Vulpia* subg. *Pseudofestuca* Rouy; *Vulpia* subg. *Loretia* sect. *Festucoides* A. Camus & sect. *Incrassatae* A. Camus, pro parte incl. typ.
Other species: All species under sect. *Loretia* in Table 1.

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Spore-producing and apical meristems in vascular plants – a comparison

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A comparison, mainly based on literature between the organization of spore-producing and apical meristems is made in various groups of vascular plants. The comparison is carried out only with respect to the occurrence of periclinal divisions in the superficial cell layer of the meristems and concerning the pteridophytes also in respect to the number of initials. The two kinds of meristems are reported to be undifferentiated (unstratified) in pteridophytes and differentiated in angiosperms except for the roots of a number of angiosperms. During the evolution a transition from undifferentiated to differentiated apical meristems and spore-producing meristems probably has occurred. In most gymnosperms studied the spore-producing meristems have attained the more advanced stage while the shoot apical meristems of most genera still are quite undifferentiated or show intermediate conditions.

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The distinguished British morphologist, Bower (1896), stated that the study of the sporangia of a vascular plant should be carried out in the light of a knowledge of the segmentation of its apical meristems. He considered that the earliest development of the sporangia in the main corresponds to the growth of the apical meristems of the same plant. According to this view plants with tunica-corpus differentiated (stratified) shoot apices should have sporangia which originate from two separate initial layers (epidermal and subepidermal initials) and that plants with undifferentiated (not tunica-corpus differentiated, unstratified) shoot apices should have sporangia which are derived from the outermost cell layer of the mother organ. Bower's statement also implies that the organization of all apical meristems of a plant is essentially similar. Later Allen (1946), Foster & Gifford (1959) and Fagerlind (1961, 1971) discussed the correlation between the structure of spore-producing meristems and that of shoot apical meristems. However, no detailed comparison between the two types of meristems within different groups of vascular plants has been performed. For that reason this survey of the organization of shoot and root apical meristems as well as spore-producing meristems has been carried out. On the basis of this information an attempt has been made to compare the two kinds of meristems.

Apical meristems are unlimited contrary to spore-producing ones and exhibit various patterns of zonal structure which do not occur in sporangia. On that account no comparison between the meristems is made in regard to cytohistological zonation and to the degree of mitotic activity in different cell complexes except for the rate of periclinal divisions in the outermost cell layer. The comparison is carried out only with respect to the occurrence of periclinal divisions in the superficial cell layer of the meristems and concerning the pteridophytes also with respect to the number of initials. With meristem initial(s) is (are) here meant the cell or the cells from which all meristem tissue ultimately is derived. In this paper the descriptions of vegetative meristems generally refer to fully developed shoots and roots.

Within many systematic groups the information about the organization of apical meristems and/or spore-producing meristems is insufficient or lacking. Since there is very little information on the structure of the meristems in question of one and the same plant the comparison between the meristems has been made between different plants of the species or between different species of the genus. In some cases there are

contradictory reports in the literature respecting a certain type of meristem of a species or a genus which may be due to many reasons. The structure of the meristem may be different in different individuals of the species or in various species of the genus. The investigations perhaps do not refer to the same stage of development and the meristem may show different organization during the ontogeny. Furthermore the same meristem may have been interpreted in various ways by different authors. It seems, however, that at least most species of a genus usually show the same organization concerning a certain meristem in regard to the presence or absence of a discrete outer layer and in regard to the number of initials (one or more). Even if the present paper is a preliminary report it will give information on whether Bower's theory is correct.

The reports on the ontogeny of the sporangia are partly based on the author's own investigations (Brunkener 1973, 1975). In the present paper the results from the author's preliminary studies on vegetative shoot apices and on strobili of some gymnosperms are also mentioned. The references concerning a certain taxon in most cases represent only a selection of works.

Pteridophytes

The growth of the pteridophyte shoots is initiated from one or more cells in the superficial layer. In some genera, however, the frequency of periclinal divisions in the surface at the summit of the apex is low or very low. Most investigations about the roots show that there is a single apical initial or a layer of initials immediately inside the root cap. The sporangia in all pteridophytes are initiated from one or more cells in the outermost layer of the mother organ.

Thus the spore-producing meristems and the shoot apical meristems of pteridophytes and the root apical meristems of at least most pteridophytes are undifferentiated which agrees with Bower's theory. Below some reports are mentioned in which the initials of the apical meristems are described to be stratified or to show a tendency to stratification. Moreover, an attempt has been made to compare the number of initial cells (one or more) of the sporangia and of the apical meristems of shoots and roots.

Psilotaceae

The apical meristem of the rhizome and the aerial shoot of *Psilotum* (Ford 1904, Bierhorst 1954) and the rhizome of *Tmesipteris* (Sykes 1908) is reported to possess a single, large apical cell. Wardlaw (1945) found that such a cell usually can be observed but that it is difficult to refer the development of the meristem to the division of a single cell.

Regarding the sporangium Bower (1894, 1908) could not definitely say that there is only one initial cell. Fagerlind (1961) was of the same opinion concerning *Psilotum* while Bierhorst (1968) stated that the sporangium of both genera originates from a group of surface cells. The author's studies on *Psilotum* have shown that the initiation of the sporangium at least sometimes can be traced to the division of a single mother cell.

Lycopodiaceae

Turner (1924) reported that the apical growth of the shoot of *Lycopodium* proceeds from two groups of cells. A few superficial cells give rise to the "dermatogen" and the "periblem" while another group of cells immediately below the surface group produces the "plerome". Härtel (1938) and Freeberg & Wetmore (1967) described a group of superficial initials from which all the stem tissue is ultimately derived. Bhambie & Puri (1963) arrived at the same result but spoke about a more or less discrete superficial layer.

According to Bruchmann (1874), Stokey (1907) and Guttenberg (1964) the root apical meristem grows from four independent superimposed tiers of initials which give rise to calyptrogen, dermatogen, periblem and plerome.

The sporogenous tissue is derived from several initial cells (Bower 1908, Brunkener 1973).

Selaginellaceae

The shoot apical meristem is variable according to the species and sometimes even within the same species (Bruchmann 1909a, Wand 1914, Popham 1951). In certain species a single, usually tetrahedral apical cell has been demonstrated, while in other species two such cells or more often several initials have been described. Bruchmann (1909a) reported that in *Selaginella poulteri* young shoot apices show a single apical cell, whereas older branches may show several initials. In *S. gracilis*, Wand (1914) described a group of initials in the main shoots but a single apical initial in older lateral shoots. Bhambie & Puri (1963), however, never found signs of a single apical initial and believed that

throughout *Selaginella* there is a group of large conspicuous initials in the shoot apical meristem.

Also the organization of the root apex seems to vary from species to species. A single apical cell has been demonstrated in some of the few investigated species (Guttenberg 1964, 1966, Webster & Steeves 1967). Webster & Steeves maintained that the number and distinctness of the initials may vary even during the development of the root. In *S. martensii* they found in several roots that the cap is derived from separate initials. Bruchmann (1909 b) described a stratified initial group with two distinct tiers in *S. spinulosa* and three such tiers in *S. lyallii*. According to Guttenberg (1966) species of *Selaginella* with a single apical initial in the shoots also have such a cell in the roots while other species with a group of superficial initials in the shoots exhibit a stratified initial region in the roots. It is, however, too early to propose this, since only a few species have been compared in this respect. Moreover, an investigation of *S. densa* (Webster & Steeves 1963) does not support this view.

The sporogenous tissue arises from a group of initials (Bower 1908, Brunkener 1973).

Isoetaceae

The stem apex of *Isoetes* (West & Takeda 1915, Guttenberg 1966) and *Stylites* (Rauh & Falk 1959) show a few superficial initials, which rarely divide periclinally. Bhambie & Puri (1963) described for *Isoetes* a discrete superficial layer at the summit of the apex but found some periclinal divisions on the sides. They suggested that the zone of cells inside the outermost layer at the summit is a self-perpetuating complex.

In regard to the root apex of *Isoetes* Bruchmann (1874) and Guttenberg (1964) reported a meristem with common initials for calyptrogen and dermatogen and separate initials for periblem respectively plerome. Rauh & Falk (1959) arrived at the same result regarding *Stylites*. In *Isoetes* Paolillo (1963) observed two initial groups, one that produces the procambium and the inner cortex and one that gives rise to the rest of the root. On the contrary, Bhambie (1972) described in *Isoetes* a group of common initials responsible for the formation of all parts of the root.

The sporogenous tissue is derived from a number of initials (Smith 1900, Bower 1908).

Equisetaceae

A tetrahedral apical cell is present in the shoot apex as well as in the root apex. According to the prevalent view this cell is actively dividing. Buvat & Liard (1953) and D'Amato & Avanzi (1968), however, reported that the apical cell in established shoot apices divides very rarely and is devoid of histogenetic potencies.

Regarding the sporangium Bower (1894) and Campbell (1940) always, and Goebel (1880) at least in most cases, found only one initial. Fagerlind (1961) was of the opinion that it is almost impossible to prove this. According to my own studies it appears that at least in some cases there is a single initial.

Ophioglossaceae

Campbell (1911) and Sen (1968) reported that the apex of the rhizome of *Ophioglossum* possesses a central initial that, however, cannot be designated as a typical apical cell. In contrast to this a layer of prismatic superficial initials has been observed by Gewirtz & Fahn (1960), Bhambie & Senger (1971, quoted from Bhambie 1972) and McAlpin & White (1974). Also in the shoot apex of *Botrychium* and *Helminthostachys* a single apical cell (Campbell 1911) or a group of initials (Bhambie & Senger 1971, quoted from Bhambie 1972) has been described. Stevensen (1976 b) stated that the shoot apex of *Botrychium* cytohistologically is composed of three zones of "initials". A zone of surface "initials" usually contains a conspicuous centrally located apical cell, from which all parts of the shoot are derived.

For the root apex of *Ophioglossum* a tetrahedral apical cell has been reported (Campbell 1911, Gewirtz & Fahn 1960, Sen 1968, Bhambie & Rao 1973). Campbell (1911) observed this condition also in *Botrychium* and *Helminthostachys*. He stated, however, that in all three genera the apical cell is replaced by several more or less equivalent initials in older roots. This was confirmed by Bhambie & Rao (1973) with reference to *Ophioglossum*.

The sporangium of *Ophioglossum* generally arises from a few initials but sometimes there is probably only one (Brunkener 1973). *Botrychium* and *Helminthostachys* in most cases show a single initial (Bower 1908).

Marattiaceae

A pyramidal or prismatic apical cell predominates in the apex of the stem of the young sporeling, whereas a group of equivalent initial cells occur in older shoot apices (Charles 1911, West 1917, Campbell 1918).

Corresponding conditions have been described for the root apices (Campbell 1911, West 1917, Guttenberg 1966). In thicker roots, however, there is from the beginning a number of equivalent initials.

The sporangium generally originates from a single initial (Bower 1908).

Leptosporangiatae

According to the classical view on the shoot apex of the leptosporangiate ferns the growth proceeds from a single apical cell with two or three cutting faces (Popham 1951, Wardlaw 1951, Clowes 1961, Guttenberg 1966, Foster & Gifford 1974). The results from several recent investigations support this concept of an active apical cell (Hébant-Mauri 1975, Stevenson 1976 a). In *Osmunda,* however, Steeves (1963) found that a distinct apical initial may be identified in dormant shoot apices but cannot be recognized in actively growing ones. McAlpin & White (1974), who examined 19 leptosporangiate genera stated that most of them do not show a single apical cell which divides in a regular, predictable sequence. They described a promeristem consisting of many "initials" but, like many other authors, did not use the term initials for the cell or the cells from which all the tissue of the shoot is ultimately derived. In the shoot apex of *Dennstaedtia* Stevenson (1976 a) distinguished a number of "initials" which are derived from a prominent apical cell. He emphasized that the apical cell is a constituent of the fern apical meristem and considered that the efforts of Hagemann (1964), De Albertis & Paolillo (1972), McAlpin & White (1974) and other authors to discount totally the presence of an apical cell is untenable.

In the root apices of the leptosporangiate ferns a single, usually tetrahedral apical initial has been demonstrated. Guttenberg (1966) and Bhambie & Rao (1973), however, found that a single apical initial in young roots of *Osmunda* is replaced by a number of equally prominent initials in older or thicker roots. In *Azolla* the apical cell of the root apex is reported to cut off a single root cap cell (Clowes 1961). Subsequently the root grows partly from the apical cell, partly from a group of cells which originates from the first root cap cell and gives rise to the root cap. According to Avanzi & D'Amato (1967) the single apical cell in the root apex of *Marsilea* behaves as a typical initial only during the early development of the root. Later the cell becomes quiescent in the sense that it does not divide or divides rarely, whereas the surrounding cells still are meristematic. Other authors such as Bhambie & Rao (1973) also found a tendency to the presence of a quiescent centre in the roots of some leptosporangiate ferns. Clowes (1967) stated that the occurrence of a single tetrahedral apical cell and the very obvious derivative pattern in the surrounding tissues does not prove that the apical cell divides to give rise to this pattern. This cell pattern merely shows that there has been a genetic relationship in the past.

The sporangium of the Leptosporangiatae with the exception of the Osmundaceae is derived from a single mother cell. In the Osmundaceae, however, the sporogenous tissue can be traced in origin to a single cell.

Discussion

Shoot apical meristems of vascular cryptogams are undifferentiated. In *Lycopodium* and *Isoetes,* however, there is a weaker or stronger tendency to the elimination of periclinal divisions in the superficial layer at the summit of the apex. In mature roots of *Lycopodium,* a few *Selaginella* species, *Isoetes, Stylites* and *Azolla* a differentiated initial group in the apex has been reported. Bhambie & Puri (1963), however, described a common group of initials in roots of *Isoetes* and Esau (1965) stated that all tissues of the root in vascular cryptogams are derived either from a single apical cell or from a number of initial cells arranged in one tier.

Since a sporangial initial in many pteridophytes in appearance does not diverge from adjacent meristematic cells and since its daughter cells at first are not divergent, it is in many cases very difficult or impossible to determine the number of initials. Often it can be decided that the first sporogenous cells of a sporangium arise through periclinal divisions of a few cells while it is uncertain whether the latter originate from a single sporangium initial. In certain cases it is also

Table 1. Number of initials of shoot and root apices and of sporangium primordia in pteridophytes. – [1] Reports of one initial in some species and more initials in other species. – [2] Reports of one initial in young apices and more initials in older apices of the same plant (species).

Taxon	Shoot apex	Root apex	Sporangium primordium
Psilotum	one	–	one (at least in some cases)
Tmesipteris	one	–	one or more?
Lycopodium	more	more	more
Selaginella	one or more[1 2]	one or more[1]	more
Isoetes	more	more	more
Equisetum	one	one	one (at least in some cases)
Ophioglossum	one or more[1]	one or more[2]	more (in general)
Botrychium	one or more[1]	one or more[2]	one (in general)
Helminthostachys	one or more[1]	one or more[2]	one (in general)
Marattiaceae	one or more[2]	one or more[2]	one (in general)
Leptosporangiatae (excl. Osmundaceae)	one or more[1]	one	one
Osmundaceae	one or more[2]	one or more[2]	one

difficult to establish whether there is one or more initials in the apical meristems. Accordingly the comparison between the spore-producing meristems and the apical meristems in regard to the number of initials in many cases must be very uncertain. More detailed information about the number of sporangium initials in pteridophytes has been given earlier (Brunkener 1973).

Since there are different opinions about the mitotic activity of the apical cell in the fern shoot and root and since the number of species which have been thoroughly investigated in this respect is low, no satisfactory generalization about the role of the apical cell can be made. White (1971) considered, however, that it seems possible that the single apical cell of the typical fern shoot and root might be active during the early development of the organ but becomes more or less quiescent when the organ matures. This condition has also been reported in the shoot apex of *Equisetum* (Buvat & Liard 1953, D'Amato & Avanzi 1968) and may be observed in all pteridophytes with an apical cell in the shoot and root apex. If the apical cell really loses the ability to divide, the growth of the adult organ consequently proceeds from a group of initials. If the apical cell, however, is not quiescent but divides at times it must be regarded as the single true initial.

The number of initials (one or more) of the apical meristems in shoots and roots and of the spore-producing meristems are summarized in Table 1 which is partly generalized. When a single apical cell is present the cell is here considered to show at least a certain degree of mitotic activity and therefore can be regarded as a true initial. In most groups of pteridophytes the number of initials in the root corresponds to that of the shoot of the same species (genus).

The number of initials (one or more) of the apical meristems and that of the spore-producing meristems agree in *Lycopodium, Isoetes* and many species of *Selaginella* and of the Leptosporangiatae and at least sometimes in *Psilotum* and *Equisetum*. In the Marattiaceae the single initial of the sporangium corresponds to the condition in the apical meristems only in very young plants. In respect to the Ophioglossaceae the number of initials of the spore-producing meristems seems to agree with that of the shoot apices only in some species and with that of either young or old root apices.

In shoot and root apices within the Marattiaceae and the Osmundaceae and in root apices within the Ophioglossaceae a single apical cell is often reported to be gradually replaced by a group of equivalent cells. This ontogenetic development supports the view that a meristem with a single initial represents a more primitive stage than a meristem with a number of initials. The defenders of this opinion also emphasize the occurrence of a single apical cell in many algae and bryophytes. On the basis of this view it can be stated that the more advanced evolutionary stage has been attained in many pteridophytes but in some of them not with regard to all meristems. Thus the transition from the stage with one to the

stage with several initials obviously can take place in a meristem independently of the conditions in other meristems. Meristems in which an apical cell is more or less quiescent or is replaced by a number of initials may be regarded as transitional forms between meristems with a single permanent initial and meristems with several permanent initials. In some pteridophytes the spore-producing meristem originates, sometimes from a single initial, sometimes from a few initials. This condition may also be considered a transition from meristems which always show a single initial to meristems which always show two or more initials. On the contrary, however, it can be suggested that a spore-producing meristem with several initials is more primitive than one with a single initial in accordance with the general view that the eusporangiate pteridophytes are phylogenetically more primitive than the leptosporangiate ones.

Gymnosperms

Cycadaceae

All studies on the shoot apices show that the growth proceeds from some initials in the superficial layer (Johnson 1951).

According to the few investigations about the ontogeny of the sporogenous tissue the microsporangia as well as megasporangia arise from two-layered initial groups (Brunkener 1973).

Ginkgoaceae

In both long and short shoots the initials of the apex belong to the outermost layer (Foster 1938).

Starr (1910) reported that the sporogenous tissue of the microsporangium probably originates from a single subepidermal cell. The megasporangium is derived from a two-layered initial group (Brunkener 1973).

Pinaceae

In all investigated genera periclinal divisions are common in the superficial layer of the shoot apex (Korody 1937, Allen 1947, Sacher 1954). My own studies on young male and female strobili in *Pinus mugo, P. sylvestris, Picea abies, P. pungens, Pseudotsuga taxifolia, Tsuga canadensis, Larix decidua* and on young male strobili in *Abies veitchii* as well as my studies on vegetative shoot apices of these species also show that these apical meristems are undifferentiated.

The microsporangium arises from the surface layer. The sporogenous tissue of the megasporangium originates directly (*Pinus, Tsuga*) or either directly or indirectly (*Pseudotsuga, Larix, Picea*) from the superficial layer (Brunkener 1973). In the first case ("direct origin") a cell in the outermost layer cuts off a sporogenous cell. In the latter case ("indirect origin") an inner cell arisen in this way cannot be regarded as sporogenous. On the contrary the cell gives rise to a small group of cells of which the inner cells are somatic and one or a few of the outer cells, that is immediately inside the outermost layer of the ovule, produce the sporogenous tissue (Brunkener 1973 p. 375).

Taxodiaceae

In most of the species studied the initial region of the shoot apical meristem is obviously undifferentiated but the frequency of periclinal divisions in the initials is definitely lower than in the Pinaceae (Cross 1943). In *Taxodium*, however, the periclinal divisions in the outermost layer appear to be absent in the permanent shoots contrary to the deciduous shoots (Cross 1943).

The microsporangium of *Taxodium* (Coker 1903, Vasil & Sahni 1964), *Cryptomeria* (Erspamer 1952, Singh & Chatterjee 1963) and *Cunninghamia* (Brunkener 1973) and the megasporangium of *Cryptomeria* (Singh & Chatterjee 1963) are reported to originate from two initial layers. According to Shaw (1896) the same condition seems to exist in the megasporangium of *Sequoia*.

Cupressaceae

Periclinal divisions in the superficial layer of the shoot apex have been observed in *Chamaecyparis* (Hejnowicz 1957), *Libocedrus* (Jackman 1960), *Callitris, Juniperus, Thuja* (A. Pillai 1963 b) and *Cupressus* (S. K. Pillai 1963). In *Thujopsis*, however, Seeliger (1955) found, with few exceptions, a discrete outer layer. In *Juniperus communis* I have investigated the apical meristem of lateral buds and in *Chamaecyparis pisifera, Thuja occidentalis* and *Callitris* sp. the apical meristem of various lateral branches. In *Juniperus* 147 periclinal divisions (mitoses or cell

pairs, which clearly show that mitoses just have occurred) were recorded in the outer layer at the summit of the shoot apex in 109 of the 118 buds studied during the period July–October (147/109-118). The corresponding value was for *Chamaecyparis* 4/4-46 (September, October), for *Thuja* 4/4-38 (July, August) and for *Callitris* 22/16-28 (in greenhouse).

Almost all investigations of the Cupressaceae show that the sporangia arise from two distinct initial layers. The rate of periclinal divisions in the outermost layer of the generative axis of *Juniperus communis* at the time of megasporangium initiation does not seem to be as high as previously (Brunkener 1973) was suggested. Therefore, the megasporangium can be said to arise sometimes directly and sometimes indirectly from the outermost layer (cf. Pinaceae). The microsporangium of *Juniperus communis* is remarkable owing to the occurrence of occasional periclinal divisions in the outer of the two initial layers. The inner cell produced by such a division can give rise to sporogenous cells.

Cephalotaxaceae

Singh (1961 a, b) demonstrated that the shoot apical meristem of *Cephalotaxus* possesses superficial initials, whereas the microsporangium as well as the megasporangium originates from two-layered primordia.

Podocarpaceae

The growth of the shoot apex of *Podocarpus* (Johnson 1951, Jackman 1960, Pillai & Pillai 1974), *Dacrydium* and *Phyllocladus* (Jackman 1960) proceeds from some cells of the outermost layer.

The microsporangium of *Podocarpus* and *Acmopyle* originates from two distinct layers of mother cells (Brunkener 1973) and to judge from the drawings made by Lawson (1923 a, b) the same condition seems to exist for the megasporangium of *Microcachrys* and *Pherosphaera*.

Araucariaceae

In *Araucaria* (Griffith 1952, S. K. Pillai 1964) and *Agathis* (Jackman 1960, Pillai & Pillai 1974) the apical shoot meristems are tunica-corpus organized.

From Burlingame's (1913) illustrations it is evident that the primordium of the microsporangium of *Araucaria* is two-layered.

Taxaceae

In lateral buds of *Taxus baccata* I have found periclinal divisions in the outermost cell layer at the summit of the apex (15/13-22, August, September). In young generative secondary shoots the result was 45/32-40. According to Kemp (1943) the shoot apex of *Torreya* grows from an undifferentiated group of initial cells.

In *Taxus* the mother cells of the microsporangium are arranged in two distinct layers. The same condition is reported for both types of sporangia in *Torreya* (Coulter & Land 1905, Kemp 1959). In *Taxus*, however, the first sporogenous cells of the megasporangium originate directly or sometimes probably indirectly from the outermost layer of the mother organ (Brunkener 1973).

Gnetinae

In *Gnetum* (Johnson 1951, Fagerlind 1954, Pillai & Pillai 1974) and in *Ephedra* (Gifford 1943, Seeliger 1954, Fagerlind 1971, Pillai & Pillai 1974) older shoots have tunica-corpus differentiated meristems. In *Welwitschia* Rodin (1953) and Martens & Waterkeyn (1963) detected occasional periclinal divisions in the superficial layer of the shoot apex. Fagerlind (1954), however, emphasized that the activity of the apical meristem ceases very early and that corresponding young stages of *Gnetum* and *Ephedra* also show periclinal divisions in the outermost layer.

According to the summary of Schnarf (1933) the initials of the microsporangium and megasporangium of the three genera are arranged in two layers. Fagerlind (1961, 1971) who confirmed this with respect to the microsporangium showed that the sporogenous tissue of the megasporangium in the Gnetinae is derived from the superficial cell layer.

The limited amount of information on the apical structure of strobili shows that they are organized as the vegetative apices in respect to the presence or absence of a tunica-corpus (Guttenberg 1966, Gifford & Corson 1971). Fagerlind (1971), however, found occasional periclinal divisions in the "pseudotunica" of both

male and female strobili of *Ephedra* which exhibits tunica-corpus differentiated vegetative shoot apices.

Root apical meristems

According to older literature the root apices of gymnosperms have separate initials for the stele (plerome), whereas the other parts of the root are derived from common initials. The reports, however, refer to embryonic roots. Allen (1947) and Wilcox (1954) studied older roots and recognized a group of common initials for all the tissues of the root in *Pseudotsuga* respectively *Abies*. Allen distinguished three and Wilcox two groups of temporary initials which are derived from the central group of permanent initials. Also in the Cycadaceae and *Ginkgo* a common group of initials for all the tissues of the root has been reported (A. Pillai 1963 a). On the basis of available literature Guttenberg (1964) distinguished two separate groups of initials in primary roots of gymnosperms. He considered, however, that the independent initials for plerome later become inactive and that the growth of the root then proceeds from a common group of initials. A. Pillai (1964) studied the root apices of 27 species belonging to 14 genera and 5 families within the Coniferae and found that all species exhibit two separate initiating zones. One central initiating zone is responsible for the growth of the stele and the central region of the root cap (columella). The other zone of initials which is situated around the stelar pole and the proximal end of the columella (as a hollow cylinder) gives rise to the cortex and the peripheral region of the root cap. Thus the two groups of initials distinguished by A. Pillai are not arranged in superimposed tiers as was described in older literature. In the root apex of *Ephedra* A. Pillai (1966) observed three separate groups of initials. There is a discrete layer of stelar initials that is situated immediately above a layer of columella initials. The initiating zone for the cortex and the peripheral region of the cap surrounds the stelar pole and the proximal part of the columella.

A. Pillai (1966) has suggested an evolutionary trend in the organization of the root apex in gymnosperms. The most primitive type with an undifferentiated initial region occurs in the Cycadaceae and *Ginkgo*. The Coniferae exhibits a more advanced type with two separate groups of initials and *Ephedra* which has three such groups probably represents the most advanced type. The occurrence of a quiescent centre in the root apices has been demonstrated in many angiosperms but the available information is yet too insufficient to justify a generalization regarding the presence of such a region in gymnosperm roots.

Discussion

A comparison between the root and shoot apical meristem shows that both types of meristems are undifferentiated in the Cycadaceae and in *Ginkgo*. On the basis of A. Pillai's view (1964) the root apical meristem of the Coniferae with two specially arranged groups of initials agrees neither to the unstratified shoot apex of most conifers nor to the two-layered one in certain other conifers. Nor in *Ephedra* the root apical organization with three groups of initials corresponds to the stratification of the shoot meristem. If, however, Guttenberg's (1964) suggestion that gymnosperms have common initials in the root apex is correct, the organization of the shoot and root apical meristem agrees in most gymnosperms.

In Table 2 the frequency of periclinal divisions in the superficial cell layer of the shoot apex at the summit and of the sporangium primordia is mentioned very approximately. No reports concerning the roots are noted in the table since the roots of most investigated gymnosperms (A. Pillai 1964, 1966) show a special organization that does not occur in shoot apices or sporangium primordia. It must be emphasized that the table is based upon few investigations and therefore is strongly generalized. It is difficult to compare the frequency of periclinal divisions of different studies since the frequency almost always is related with such vague expressions as "periclinal divisions are rather common" or "periclinal divisons occur occasionally". Moreover, in many gymnosperms more or less pronounced seasonal variations can be observed with respect to the rate of periclinal divisions in the superficial layer. During a certain period numerous such periclinal divisions can be detected but during another period the apical meristem gives the expression of being tunica-corpus differentiated. If such variations are reported in the literature the period with the

highest frequency is represented in the table. Furthermore the conditions in main and lateral shoots may be different as in *Taxodium*. In certain gymnosperms the megasporangium-producing meristem at first is tunica-corpus organized but later shows a higher or lower frequency of periclinal divisions in the outermost layer. Since these divisions do not give rise to sporogenous tissue they have been neglected in the table. Many genera are incompletely or not at all investigated with reference to the meristems in question. In almost all gymnosperm genera the structure of the sporangia is described but only few studies give information about whether the early primordium is undifferentiated or differentiated. The information in the table, however, presumably corresponds to the condition in most genera within a respective family.

It is evident from the table that the arrangement of the initials of the microsporangium in general corresponds to that of the megasporangium of the same genus (family). Furthermore, it is clear that the structure of the spore-producing meristems on the whole agrees with that of the apical shoot meristems in the Pinaceae. This condition is possibly valid also respecting the Araucariaceae. In the Gnetinae only the meristem of the microsporangium corresponds to that of the shoot apex. In *Juniperus communis* the shoot apex relatively often exhibits periclinal divisions in the superficial layer. Such divisions also occur in the outer layer of the spore-producing meristems but in a much lower frequency. Thus the latter meristems show a strong tendency to tunica-corpus differentiation and one can speak about only a certain degree of accordance between these meristems and the shoot apical meristem. In most gymnosperms it seems to be no such accordance. Some genera, however, such as *Cryptomeria, Taxodium, Chamaecyparis, Cupressus* and *Thuja,* which have sporangium initials arranged in two discrete layers, possess shoot apices which show a stronger or weaker tendency to tunica-corpus organization.

In all gymnosperm seedlings anticlinal as well as periclinal divisions occur in the superficial cells of the shoot apical meristem (Guttenberg 1961). In some families this condition becomes permanent in the fully developed shoot while in other families the rate of periclinal divisions decreases more or less. Accordingly one can speak about an intermediate type of meristem between, on one side, clearly undifferentiated shoot meristems as in the Cycadaceae and the Pinaceae, and, on the other side, tunica-corpus organized shoot meristems in the Araucariaceae and the Gnetinae. Most investigated genera of the Taxodiaceae and the Cupressaceae and some genera of the Podocarpaceae and *Taxus* appear to have apical shoot meristems of such an intermediate type. The Taxodiaceae and the Cupressaceae seem to be the most heterogeneous families in this connection, since undifferentiated and tunica-corpus differentiated meristems as well as meristems of the intermediate type have been described. The shoot apical meristem of *Taxodium distichum* indicates that even a single plant can be heterogeneous in this respect.

In harmony with the condition in the shoot apices intermediate types also occur between undifferentiated and differentiated sporangium primordia. The microsporangium primordium of *Juniperus communis* and the megasporangium

Table 2. The approximate frequency of periclinal divisions in the superficial layer of the shoot apical meristem and of the micro- and megasporangium in gymnosperms. – P = Periclinal divisions are reported to occur very often or often. – (P) = Periclinal divisions are reported to occur occasionally, relatively rarely or rarely. – O = Periclinal divisions are reported to occur very rarely or never (tunica-corpus organization).

Taxon	Shoot apical meristem	Micro-spor-angium primor-dium	Mega-spor-angium primor-dium
Cycadaceae	P	O	O
Ginkgoaceae	P	O	O
Pinaceae	P	P	P, (P)
Taxodiaceae			
Taxodium	(P), O	O	–
other genera	P, (P)	O	O
Cupressaceae			
Juniperus	P	(P)	(P)
Thujopsis	O	–	–
other genera	(P)	O	O
Cephalotaxaceae	P	O	O
Podocarpaceae	P, (P)	O	O
Araucariaceae	O	O	–
Taxaceae			
Taxus	(P)	O	(P)
Torreya	P	O	O
Gnetaceae	O	O	(P)
Ephedraceae	O	O	(P)
Welwitschiaceae	O	O	(P)

primordium of *Pseudotsuga, Larix, Picea, Juniperus* and *Taxus* can be regarded as belonging to an intermediate type of meristem. The young microsporophyll of *Juniperus communis* has a discrete outer layer and the microsporangium primordium is stratified. However, when the cells of the inner initial layer of the primordium begin to divide periclinally, or at a later point of time, the outer cell layer occasionally can cut off a single cell that can give rise to sporogenous cells. The megasporangium-producing meristem of *Pseudotsuga, Larix, Picea, Juniperus* and *Taxus* is organized in another way. The mother organ does not show a discrete outer layer and the sporogenous tissue is derived directly or indirectly from superficial cells.

Angiosperms

The shoot apical meristems of all investigated angiosperms with a few exceptions are reported to be tunica-corpus organized. The number of layers in which only anticlinal divisions occur may fluctuate during the ontogeny of the plant, in connection with the initiation of leaves and under the influence of environmental factors. Thielke (1951, 1965) detected periclinal divisions in the outermost layer of the apex at the summit in young fast growing shoots in some species of *Saccharum* and *Erianthus*. The organization of the apices, however, changes and later only normal tunica-corpus differentiation can be observed. Also in a few other genera occasional periclinal divisions in the outermost layer of the shoot apex have been reported but may be regarded as pathologic changes. There is relatively little information about the apical meristems of inflorescences and flowers but it seems as if also these meristems are tunica-corpus differentiated (Guttenberg 1960, Esau 1965).

According to Hanstein's histogen theory (1868) the root apical meristem of angiosperms is initiated from a group of mother cells, the histogen initials, which are arranged in three discrete, superimposed tiers. However, in many angiosperms it has been demonstrated that the histogens are not as discrete as was previously thought. Guttenberg (1960) summarized the information on root apical organization in angiosperms and distinguished two principal types, the closed and the open. The closed type exhibits three discrete and superimposed initial groups which are responsible for the development of the plerome, periblem, dermatogen and root cap. The open type has common initials for all tissues of the root or for all tissues except for the plerome. Transitional forms between the two types are also described. Both the principal types are found in dicotyledons as well as in monocotyledons. Guttenberg stated that the two basic types are developed from a closed type in the embryonic root. Later this type of organization is retained or replaced by the open type.

According to Clowes (1959, 1961, 1967) the apical meristem of the root in most angiosperms and perhaps in most vascular plants has a quiescent centre, which consists of many cells which divide rarely or never. The quiescent centre is shaped like a hemisphere and the cells on the surface of this quiescent complex may be regarded as the initials of the meristem. Clowes emphasized that the degree of quiescence in a root may vary and that the boundary between the region and the surrounding initials fluctuates in position. Several other investigators as Byrne & Heimsch (1968, 1970), also described a quiescent centre in the roots of certain angiosperms. Authors as Popham (1958) and Guttenberg (1960, 1964), however, were doubtful about the existence of such a region. Even if there are contradictory views about the structure of the root apex it is evident that a large number of angiosperms shows a differentiated (stratified) root apical meristem that, however, only partly harmonizes with the tunica-corpus organization of the shoot apex. The stratification of the root meristem does not agree with that of the shoot meristem since the divisions in the root "histogens" do not occur in the same manner as in the tunica layers.

Both the microsporangium and the megasporangium are derived from differentiated initial groups which accordingly corresponds to the organization of the shoot meristem.

Conclusions

During the evolution a transition from undifferentiated to differentiated apical meristems and spore-producing meristems probably has occurred. This change can evidently take place at different points of time in apical meristems and spore-producing meristems. In most gymno-

sperms studied the spore-producing meristems have attained the more advanced stage while the shoot apical meristems of most genera still are quite undifferentiated or show intermediate conditions.

This review shows that Bower's theory about the accordance between the organization of the spore-producing meristems and that of the apical meristems is partly correct. The pteridophytes and angiosperms at large can be regarded as homogeneous groups in this respect whereas the gymnosperms exhibit varying conditions with pteridophyte as well as angiosperm characters. With reference to the organization of the spore-producing meristems and the apical shoot and root meristems the gymnosperms, therefore, as in many other respects, can be considered a transitional group between pteridophytes and angiosperms.

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New finds of Cornucopiae cucullatum (Poaceae) in Europe

Alfred Hansen and W. Lohmeyer

Hansen, A. & Lohmeyer, W. 1977 06 30: New finds of Cornucopiae cucullatum in Europe. *Bot. Notiser 130:* 203–204. Stockholm. ISSN 0006-8195.

Cornucopiae cucullatum is reported as new to the islands of Crete and Kos (E Aegean region). Its general distribution is reviewed.

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The authors have found the small annual grass *Cornucopiae cucullatum* L. (for description and illustration see Bor 1968 p. 300) as new to the islands of Crete and Kos (E Aegean region). On Crete it was found in April 1976 by WL in the village of Skisma (Schima), c. 7 km W of Aghios Nikolaos, prov. Merabello. On Kos it was found in a number of localities in 1974–76 by AH (Fig. 1).

Cornucopiae cucullatum always grows under rather wet conditions: on the borders of ditches, small ponds and rivulets, and also in areas waterlogged during winter but dry in summer. On Kos it is often associated with *Oenanthe prolifera*.

The species has clearly an eastern total distribution (map in Colosante & Ricci 1972) and previous finds in Europe are few and mostly old. It has been found on the islands of Patmos (Sibthorp & Smith 1806) and Rhodes (Fiori 1938) in the E Aegean area, and on the island of Gozo, Maltese Islands (Sommier 1911). There is also a recent record from C Italy, near Latina in Agro Pontini (Colosante & Ricci 1972).

The species might still be present on Patmos and Rhodes since these islands lie within its probable native area. On Gozo only a single plant was found growing in a ditch, and the find probably represents an occasional introduction only. Colosante & Ricci (1972) regard, although with some reservations, the occurrence in Agro Pontini as native. They refer to the fact that a number of other E Mediterranean plants have their westernmost occurrences in C Italy.

Outside Europe *C. cucullatum* is known from Turkey (probably widespread in the S and W parts), Lebanon, W Syria and Israel (Boissier 1884, Post 1896, Post & Dinsmore 1933, Thiébaut 1953, Mouterde 1966), Iraq (Rechinger 1964, Bor 1968) and doubtfully Iran (Parsa 1950, not mentioned by Bor 1970). It is said to be more or less common in Israel and Lebanon (Post 1896, Thiébaut 1953) but from other areas only very few finds have been published and most of them are old. The species is probably much overlooked

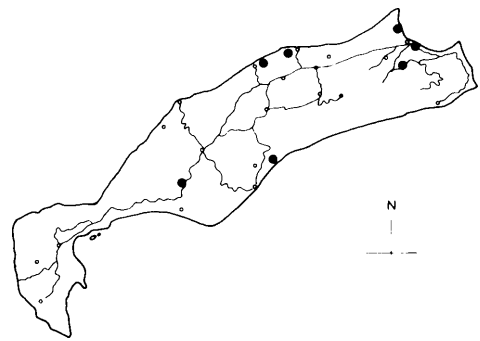


Fig. 1. Localities for *Cornucopiae cucullatum* on the island of Kos. Scale 1:625,000.

and further field work will undoubtedly shed new light on its true distribution and frequency.

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Drawings of Scandinavian plants 115–117

Epilobium L. sect. Epilobium

Alf Oredsson and Sven Snogerup

Oredsson, A. & Snogerup, S. 1977 06 30: Drawings of Scandinavian plants 115–117. Epilobium L. sect. Epilobium. *Bot. Notiser 130:* 205–211. Stockholm. ISSN 0006-8195.

Drawings and descriptions are given for *E. glandulosum* Lehm. and for two Scandinavian form series included under *E. ciliatum* Raf. without taxonomic rank.

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These species are recent introductions in the area, but are well established and spreading. They belong to an American group recognized by its characteristic seed surface, with markedly papillate ridges. Autogamy seems to be dominant in the group, but occasional cross-fertilisation gives rise to hybrids both within the group and with European species. The former at least seem to be relatively fertile, and the taxonomy of the group is difficult. A revision is now being carried out by professor Raven, St Louis. The populations of various minor areas are often quite constant within themselves but differ from one another. This may reflect the introduction of a few presumably rather homozygous biotypes.

The descriptions given below are made on Scandinavian material only and are certainly not valid for the entire American material of these species. Two form series are here presented as *E. ciliatum* form A and *E. ciliatum* form B respectively. They differ in several characters so that in Scandinavia they are just as easily separated as are pairs of related species in other parts of the genus. Professor Raven (pers. comm.), however, states that they will be treated together in his revision. Under these circumstances we find it unwarranted to retain a different taxonomy for the introduced forms in Europe.

115. **Epilobium glandulosum** Lehmann 1830

Perennial herb, (20–)40–90(–110) cm high. Plant sparingly branched, producing one or a few (7–)15–30(–45)-flowered inflorescences, small specimens often unbranched with an apical inflorescence more than half of the plant height. Turions formed late in the autumn, at the surface, sessile or at the end of stolons up to 10 mm long with small spathulate leaves, as dense rosettes of c. 10, broadly obovate, obtuse, glabrous, fleshy, entire to weakly serrate leaves 8–15 mm long, first pale reddish, later dark reddish or in shaded positions pure green.

Stem (1.5–)2.5–4(–6) mm thick, terete, with weak lines below the leaf margins, lines often inconspicuous on older stem parts. Stem subglabrous to sparsely hairy below, often more densely so on the lines, gradually more hairy upwards, in apical part usually rather densely hairy, most hairs glandular, 0–0.3 mm, erect to incurved, some eglandular, incurved to adpressed, 0.2–0.4 mm long.

Lower and middle leaves opposite, most bracts usually alternate, leaves not decurrent, their bases often united. Basal leaves smaller, with a petiole up to 10 mm long, obovate-spathulate to lanceolate, subentire. Middle cauline leaves (35–)50–90 mm long, (15–)20–30(–35) mm broad, sessile or with a petiole up to 2 mm long, ovate to narrowly ovate, acute, basally subentire, in


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middle and upper part sharply but often irregularly serrate with largest teeth usually c. 0.5 mm high. Bracts rather large, like the middle cauline leaves, only the upper ones slightly smaller, more lanceolate in form and often more distinctly petiolated. Basal and middle cauline leaves subglabrous, upper ones sparsely hairy chiefly on petiole, margin and veins, hairs smaller than those of the stem and predominantly glandular.

Pedicels first erect, in fruit erectopatent. Young buds obovoidal, later ± broadly ellipsoidal, with a distinct mucro 0.2–0.3 mm long. Sepals (3.5–)4.5–5 mm, connate to c. 1.5 mm at base, narrowly ovate to lanceolate, green to reddish, usually sparsely glandular, denser on connate part, rarely also with some eglandular hairs. Petals (6–)6.5–7.5(–8.5) mm, notched to 1–2 mm, ± pinkish-purple or often rather light pinkish. Anthers (0.5–)0.7–0.9 mm, long filaments (2.5–)3.5–6 mm, short filaments 1.5–2.7 mm, usually less than half as long as the long ones. Pistil equalling or slightly shorter than the long stamens, stigma capitate.

Capsule stalk (5–)10–15 mm. Capsule 50–60(–70) mm, sparsely to moderately hairy but young ovaries more densely hairy, usually with glandular hairs only but rarely with some eglandular ones as well. Seeds 1.0–1.3(–1.4) mm long, 0.4–0.5(–0.6) mm broad, ± narrowly obovoidal, basally acute, apically obtuse, ventrally flattened with inconspicuous lines, neck inconspicuous or up to 0.05 mm, dorsal surface with c. 25 prominent, papillose edges, chalazal hairs 32–40(–45), 6–7.5 mm long. Flower homogamous, anthers often opening at bud stage.

E. glandulosum has a rather irregular distribution in S and C Scandinavia, with centres around Stockholm and Göteborg, in Västergötland and in S Skåne. It occurs in waste places, loading places, roadsides and similar localities, but in several places has also invaded ditch margins, shores of lakes and rivers etc. It must be regarded as established, and new localities are to be expected anywhere in the area.

E. glandulosum is indigenous in N America.

Known hybrids: with *E. montanum, palustre, parviflorum, roseum* and *tetragonum.*

116. **Epilobium ciliatum** Rafinesque 1808, form A

E. rubescens auct. scand.

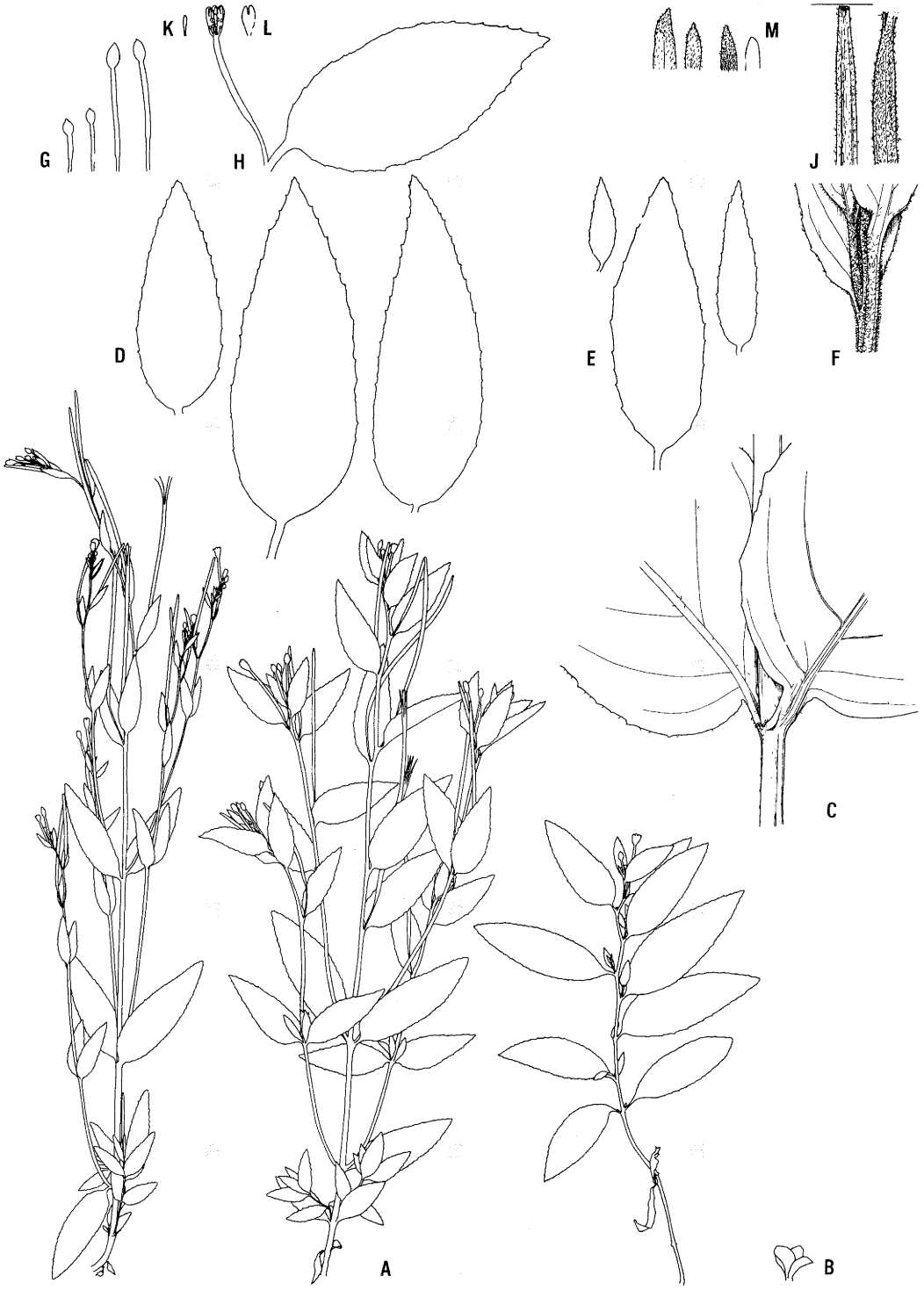
Perennial herb, (15–)30–60(–80) cm high. Plant branching from the base or rarely in denser vegetation only in upper part, with branches emerging at a very sharp angle, producing several or in small specimens only one 5–15(–20)-flowered inflorescences. Often forming adventitious shoots from basal internodes, similar to small individual plants. Turions formed late in the autumn, sessile or on stolons up to 5 mm long, at surface, as rosettes of 5–10 leaves usually broadly obóvate, subentire, glabrous, somewhat fleshy, reddish. Sometimes not forming specialized turions but regenerating from the basal parts of the previous year's plants.

Stem 1–5 mm thick, terete, with weak lines below leaf margins, lines inconspicuous in older stem parts. Stem glabrous to subglabrous below, gradually more hairy upwards, apically moderately to densely hairy, with incurved to adpressed eglandular hairs 0.2–0.4 mm long and glandular, patent to incurved ones 0–0.25 mm long.

Basal and middle cauline leaves opposite, most bracts alternate, not decurrent, bases of opposite leaves usually united. Basal leaves smaller, with a petiole 5–10 mm long, obovate-spathulate to lanceolate, subentire. Middle cauline leaves (25–)35–60(–110) mm long, (7–)10–20(–27) mm broad, with a petiole 2–8(–12) mm long, narrowly ovate or rarely lanceolate, acute, sharply but often irregularly serrate in middle and upper part with teeth less than 0.5 mm, in basal part entire to subentire. Upper leaves gradually smaller and often more lanceolate in form. Basal and middle cauline leaves subglabrous to completely glabrous, usually with only few and very small hairs on the margin, upper bracts often slightly more hairy, especially on margins and veins.

Pedicels erect in bud and flower, in fruit erect to erectopatent. Young buds obovoidal, later ± broadly ellipsoidal with a distinct mucro c. 0.2 mm long. Sepals 3–4.5(–5) mm, connate to 1–1.5 mm at base, narrowly ovate to lanceolate, usually reddish especially on the margins, moderately hairy, denser on the basal part, with chiefly

Fig. 115. *Epilobium glandulosum* Lehm. – A: Habit, × 1/3. – B: Winter bud, × 1/2. – C: Stem node, × 2.5. – D: Cauline leaves, × 1. – E: Upper leaves, × 1. – F: Upper stem part, × 2.5. – G: Buds, × 1. – H: Flower, ×1. – J: Apical part of capsule, × 2.5. – K: Style, ×1. – L: Petal, × 1. – M: Sepals, × 2.5.


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eglandular hairs. Petals 4.5–6.5 mm, notched to 1–1.5 mm, white or rarely light pink. Anthers 0.5–0.7 mm, long filaments 2.5–4 mm, short filaments 1.2–2.2 mm, usually about half as long as the long ones. Pistil usually shorter than the long stamens, sometimes no longer than the short ones, stigma capitate.

Capsule stalk 10–25(–35) mm in the basal part of the inflorescence, in the apical part shorter. Capsule (50–)60–75(–85) mm, young ovaries densely hairy, ripe fruits moderately so, with both glandular and eglandular hairs like those of the stem. Seeds 1.1–1.3 mm long, 0.4–0.45 mm broad, narrowly obovoidal, basally acute, apically obtuse, with a neck up to 0.05 mm long, ventrally flattened, dorsally with c. 25 prominent, papillose edges, chalazal hairs 30–40, 6.5–8.5 mm long. Flower homogamous, anthers often opening at bud stage.

E. ciliatum form A is commonest around Stockholm and Göteborg and on Gotland, but has also been observed in scattered places all over S and C Scandinavia. It is locally well established and probably spreading. Its relationship to form B requires further investigation. The two forms are normally well separated, but fertile specimens and populations presumed to be intermediate and probably hybridogenous have been observed. Form A occurs in the same sort of habitats as form B and *E. glandulosum* and often together with them.

E. ciliatum form A is indigenous in N America.

Known hybrids: with *E. montanum, palustre, roseum* and *tetragonum*.

117. **Epilobium ciliatum** Rafinesque 1808, form B

E. adenocaulon auct. scand.

Perennial herb, (25–)50–100(–130) cm high. Plant branching apically, or rarely from the base to form several or in dwarfed specimens rarely only one, (5–)10–20(–30)-flowered inflorescences. Turions formed late in the autumn at the surface, sessile or at the end of stolons up to 10 mm long with small, spathulate leaves, as dense rosettes of broadly obovate to elliptical, entire, glabrous, fleshy leaves 10–15 mm long, dark reddish or in shaded position rarely almost pure green.

Stem (1–)2–4(–8) mm thick, terete, with weak lines below the leaf margins, lines often inconspicuous on older stem parts. Stem subglabrous below, gradually becoming more hairy upwards, in apical part moderately hairy with incurved to adpressed eglandular hairs 0.2–0.4 mm long and erect to incurved, glandular ones 0–0.2 mm long.

Most leaves opposite or nearly so, usually only upper bracts alternate, not decurrent, leaf bases usually not united. Basal leaves smaller, with a short or up to 10 mm long petiole, obovate-spathulate, subentire. Middle cauline leaves (30–)50–90(–140) mm long, (8–)15–25(–40) mm broad, sessile or with a petiole up to 3 mm long, narrowly ovate, acute, sharply but often ± irregularly serrate with the largest teeth usually c. 0.5 mm high. Upper leaves gradually smaller and often somewhat narrower in form, usually with a petiole 1–3 mm long. Basal and middle cauline leaves subglabrous or sparsely hairy chiefly on the margin and sometimes also on the veins, upper bracts usually sparsely and sometimes more uniformly hairy, hairs smaller than those of the stem.

Pedicels first erect, in fruit erectopatent. Young buds obovoidal, later ± broadly ellipsoidal, with a distinct mucro c. 0.2 mm long. Sepals (3–)4–4.5 mm, connate to c. 1.5 mm at base, narrowly ovate to lanceolate, green to rather strongly reddish, sparsely to moderately hairy, denser on the connate part, with both glandular and eglandular hairs. Petals 4–6.5(–7.5) mm, notched to 1.5–1 mm, ± pinkish purple or rarely very light pink to white. Anthers 0.6–0.9 mm, long filaments 2.5–3.5 mm, short filaments 1.2–2 mm, usually at least half as long as the long ones. Pistil equalling or slightly exceeding the long stamens, stigma capitate.

Capsule stalk 4–8(–10) mm. Capsule (45–)50–60(–70) mm, sparsely to moderately hairy but young ovaries densely hairy, with glandular as well as eglandular hairs like those of the stem. Seeds (1.0–)1.1–1.3(–1.4) mm long, 0.4–0.45 mm broad, narrowly obovoidal, basally acute, apically obtuse, ventrally flattened with inconspic-

Fig. 116. *Epilobium ciliatum* Raf., form A. – A: Habit, × 1/3. – B: Winter bud, × 1/2. – C: Stem node, × 2.5. – D: Cauline leaves, × 1. – E: Upper leaves, × 1. – F: Upper stem part, × 2.5. – G: Buds, × 1. – H: Flower, × 1. – J: Apical parts of capsules, × 2.5. – K: Style, × 1. – L: Petal, × 1. – M: Sepals, × 2.5.


G
K
L
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uous lines, neck less than 0.05 mm, dorsal surface with c. 25 prominent, papillose edges, chalazal hairs 32–35(–40), 7–9 mm long. Flower homogamous, anthers often opening at bud stage.

E. ciliatum form B is rather common in S and C Scandinavia. It is indigenous in N America and has probably been introduced separately in several different places. It occurs on rubbish heaps, loading places and roadsides, but has also invaded ditch margins, shores of lakes and rivers, tracks and gardens. It is apparently spreading rapidly, and may be found anywhere in the area, generally S of c. 63°N.

Known hybrids: with *E. palustre, parviflorum, roseum* and *tetragonum*.

Fig. 117. *Epilobium ciliatum* Raf., form B. – A: Habit, × 1/3. – B: Winter bud, × 1/2. – C: Stem node, × 2.5. – D: Cauline leaves, × 1. – E: Upper leaves, × 1. – F: Upper stem part, × 2.5. – G: Buds, × 1. – H: Flower, × 1. – J: Apical parts of capsules, × 2.5. – K: Style, × 1. – L: Petal, × 1. – M: Sepals, × 2.5.

Drabopsis verna C. Koch (Brassicaceae) new to Europe

Lars-Åke Gustavsson

Gustavsson, L.-Å. 1977 06 30: Drabopsis verna C. Koch (Brassicaceae) new to Europe. *Bot. Notiser 130:* 213–214. Stockholm. ISSN 0006-8195.

Drabopsis verna C. Koch is reported from Lefka Ori on Crete. This Irano-Turanian species is previously known from C Anatolia and eastwards to W Himalaya. A description of the specimens from Crete is given.

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Drabopsis verna C. Koch

Koch, Linnaea 15: 253 (1841) – *Arabidopsis verna* (Koch) N. Busch, Fl. Cauc. Crit. 3, 4: 457, 460 (1909).

Arabis scapigera Boiss., Ann. Scienc. Nat. Ser. 2, 17: 54 (1842).

Arabis nuda Bel. ex Boiss., Ann. Scienc. Nat. Ser. 2, 17: 54 (1842) – *Sisymbrium nudum* (Bel.) Boiss., Fl. Or. 1: 214 (1867) – *Drabopsis nuda* (Bel.) Stapf, Denkschr. Akad. Wiss. Wien, Math.-Nat. Kl. 51, 2: 298 (1886) – *Arabidopsis nuda* (Bel.) Bornm., Beih. Bot. Centralbl. 28, 2: 535 (1911).

Collection: Crete, Nomos Canea, Lefka Ori, 5.5 km SE–ESE of the village of Omalos. Somewhat moist, stony ground close to snow patches, together with *Crocus sieberi* Gay, on a NW-facing slope, 1800–1850 m, 8.5. 1973, Gustavsson 2196 (LD).

This Irano-Turanian species is new to Europe. It is previously known from C and E Anatolia, Transcaucasia, Iraq, Iran, Afghanistan, C Asia, W Pakistan and W Himalaya. The occurrence on Crete is phytogeographically remarkable in that it extends the distribution of the species more than 1000 km westwards (Fig. 1).

The Irano-Turanian element as a whole is poorly represented on Crete, more richly represented on the S and C mainland of Greece. Among Irano-Turanian species occurring on Crete can be mentioned *Acantholimon androsaceum* (Jaub. & Spach) Boiss., *Atraphaxis billardieri* Jaub. & Spach and *Mattiastrum lithospermifolium* (Lam.) Brand.

D. verna belongs to the group of relict species with a very disjunct distribution on the eastern Mediterranean mountains (cf. Greuter 1972). It probably belonged to the flora of Crete before the island was isolated from the Anatolian continent, i.e. during the upper Miocene to Pliocene (Meulenkamp 1971, Creutzburg 1963).

All the Cretan material was flowering and some specimens bear immature fruits. The plants are extremely small, laying near the lower limit of the range of variation. The siliquae are much shorter than previously described for the species, probably because they are not fully developed. With regard to the most variable characters of the species the morphology of the Cretan plants is as follows: *Stem* single, 0.7–2.0 cm, pubescent, with stalked, branched hairs with 2–4 rays. *Leaves* spathulate to oblong-spathulate, entire, up to 5.5 × 2.1 mm, pubescent, with branched hairs especially on the margins. *Pedicels* in fruit up to 1.0 mm. *Sepals* 1.3–1.5 × 0.6–0.8 mm with simple and branched hairs. *Petals* 1.8–2.2 × 0.5–0.7 mm. *Siliquae* up to 8 mm long and 0.8 mm broad, pubescent, with branched hairs with 2 and 3 rays.

In comparison with the descriptions given in most oriental floras, e.g. Davis (1965) and Rechinger (1968), the plants from Crete also deviate in having pubescent siliquae. Such plants have been described as *Arabidopsis verna* (C.

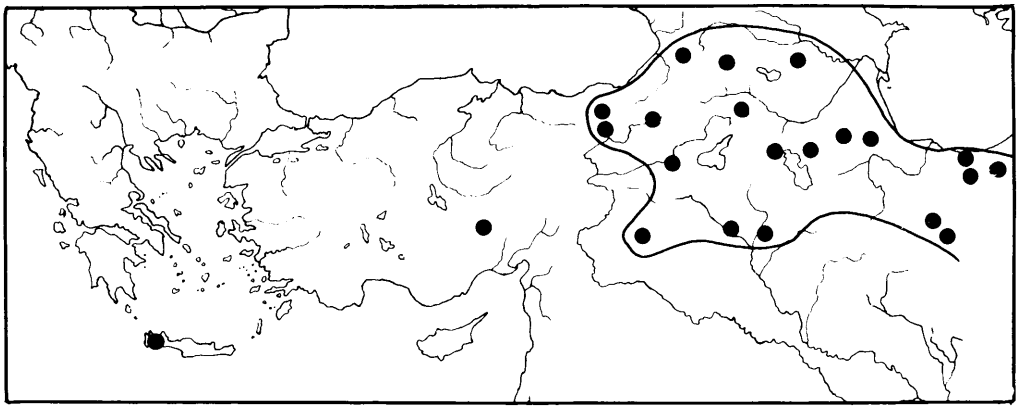


Fig. 1. Distribution of *Drabopsis verna* in the westernmost part of the total area of distribution, according to literature records and herbarium sheets seen by me.

Koch) N. Busch var. *hebecarpa* N. Busch, in contrast to var. *leiocarpa* N. Busch with glabrous siliquae. According to herbarium material specimens with pubescent siliquae are rare, but do sometimes occur growing together with plants with normally glabrous siliquae. Such mixed collections have been seen from N Iran and Russian Armenia. The specimens of the Cretan collection have constantly pubescent siliquae.

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A study of the Leptopeltidaceae

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The family Leptopeltidaceae von Höhnel ('Phacidiales') has been amended to comprise unitunicate genera only, viz. *Leptopeltis* von Höhnel s. lat., *Dothiopeltis* E. Müller, and *Ronnigeria* Petrak. *Dothithyrella* v. Höhn., *Leptopeltopsis* Petr., and *Moeszopeltis* Petr. are included in the synonymy of *Leptopeltis*. The following new combinations have been published: *Leptopeltis litigiosa* (Desm.) L. & K. Holm, *L. gregaria* (Petr.) L. & K. Holm, *L. nebulosa* (Petr.) L. & K. Holm, and *L. lunariae* (Fuckel) L. & K. Holm.

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The family Leptopeltidaceae was established by von Höhnel (1917 p. 417, as 'Leptopeltineen') to accommodate 'Phacidiales' with subcuticular ascocarps. With Höhnel's circumscription the taxon was highly heterogeneous, comprising elements as disparate as *Leptopeltis* and *Rhytisma*. No wonder that other investigators, like Theissen & Sydow (1918), and Nannfeldt (1932) did not recognize the group, referring the type genus, *Leptopeltis*, to the 'Hemisphaeriales'; the former authors considered *Leptopeltis* to be related to *Stigmatea*.

The Leptopeltidaceae was revived again as a taxonomic group by Petrak (1947 a) who restricted the family to the genera *Leptopeltis* and *Leptopeltella*, only. He did not express an opinion about its position in the Ascomycete system. Petrak's article is the most thorough study so far devoted to these fungi, and it has definite merits, in addition to the improved circumscription of the family. He noticed the existence of the 'hypostroma' in the host tissues, with differences in different species, which he utilized as taxonomic characters. Moreover, he described two new valid pteridicolous species, viz. *Leptopeltopsis nebulosa*, and *Moeszopeltis gregaria*, referring each of them to a new genus of its own. Petrak had a very narrow generic concept, guided i.a. by presumed differences in spore septation.

In a second article, published simultaneously, Petrak (1947 b) reported on the so-called *Microthyrium arcticum* Oud., a saprophyte on leaves of *Potentilla* spp. He considered this species to be a true member of the Leptopeltidaceae, referring it to the new monotypic genus *Ronnigeria*. We agree with Petrak's classification, though it has been criticized by other workers.

Another noteworthy contribution was made by von Arx (1964) who included some further genera in the family, viz. *Dothithyrella*, and *Dothiopeltis*. The first-mentioned genus had earlier been classified among the Microthyriales, but von Arx rightly recognized its close affinity with the Leptopeltidaceae. *Dothiopeltis* also clearly belongs here. Otherwise von Arx followed Petrak rather closely, though with a somewhat broader generic concept, uniting *Dothithyrella* and *Leptopeltis* (under the name *Pycnothyrium*). Concerning the general relationships von Arx classified the family among the Dothiorales, a view first held by Müller & von Arx (1962).

The Leptopeltidaceae have recently been treated anew by von Arx & Müller, in their survey of the bitunicate Ascomycetes (1975); here the family has been considerably enlarged

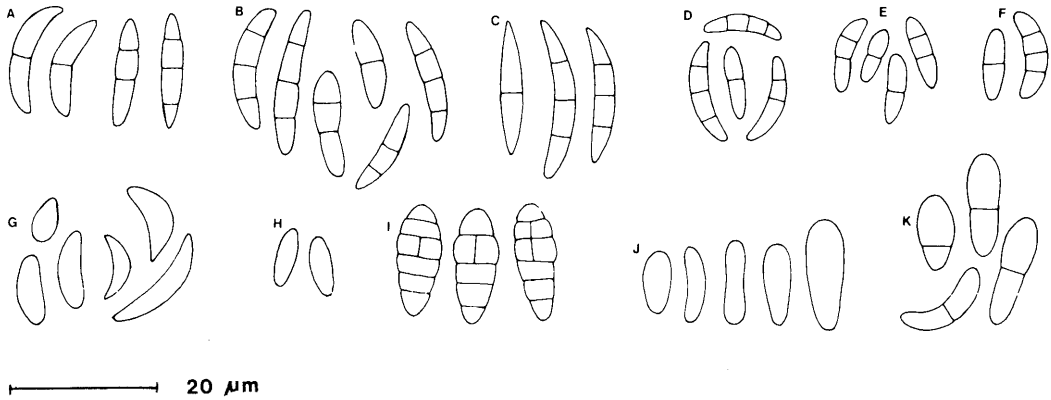


Fig. 1. Spores. – A: *Leptopeltis pteridis*. – B: *L. litigiosa*. – C: *L. filicina*. – D: *L. nebulosa* (on *Athyrium filix-femina*). – E: *L. nebulosa* (on *Lastrea dryopteris*). – F: *L. nebulosa* (on *Dryopteris filix-mas*). – G: *L. gregaria*. – H: *L.* sp., no. 576 b. – I: *Dothiopeltis arunci*. – J: *Ronnigeria arctica*. – K: *Leptopeltis lunariae*. – All × 1,000.

again, also including genera such as *Aulographum, Aulographina, Lembosina,* and *Morenoina*.

In our opinion the Leptopeltidaceae should certainly be recognized as a distinct group, appropriately of family rank, but restricted to the genera *Leptopeltis* s. lat., *Dothiopeltis,* and *Ronnigeria,* only. As will be shown the group is quite distinct from other superficial 'Hemisphaeriales' by the ascus structure.

Two morphological problems

Ascus structure

Most hemisphaeriaceous fungi are apparently bitunicate, and the Leptopeltidaceae have also been regarded as such, e.g. by von Arx & Müller (1975), and Luttrell (1973). This view, however, seems to be erroneous. Personally, we have never observed a *Leptopeltis* ascus exhibiting the 'Jack in the box' mode of dehiscence. A negative indication may not be very convincing, but some traits of the ascus microstructure certainly are. We refer to the TEM micrographs in Fig. 6.

For the ultrastructural studies the material (dried herbarium specimens) was prefixed in 2.5 % glutaraldehyde in 0.1 M sodium cacodylate buffer, pH 7.2, at room temperature for 48 h, and postfixed in 2 % $KMnO_4$ for 1 h. It was dehydrated in a graded ethanol series, embedded in Epon, and sectioned with a LKB Ultrotome I equipped with a Du Pont diamond knife. The sections were poststained in 2 % uranyl acetate for 20 min. and in Reynold's lead citrate for 6 min. For examination a JEOL 100 B transmission electron microscope was used, operating at 60 kV.

The ascus wall is thickened at the apex, and the lower part of the thickened region extends downwards as an annular projection into the apical epiplasm. Moreover, traces of a cylindrical ring of electron transparent material can be discerned in the apical thickening. An ascus tip structure of this kind is commonplace among the Unitunicatae, but unknown among the Bitunicatae. The pictures do not permit any definite conclusions as to ascus wall stratification; apparently fresh material is necessary for obtaining unequivocal pictures. However, it is becoming gradually apparent that even the Unitunicatae possess a complex ascus wall, composed of several strata (cf. Bellemère 1975, Codron 1974, Schrantz 1970).

Interthecial threads

Another morphological problem of prime importance is the true nature of the interthecial threads, present in the ascocarps of *Leptopeltis* and *Dothiopeltis*. This question has hardly been discussed, and not much clarification can be obtained from the literature. Petrak (1947 a) called them 'Paraphysoiden', as did von Arx (1964); according to the latter they represent remnants of the interthecial 'tissue': 'Die fädig faserigen Paraphysoiden gehen aus dem durch die Asci verdrängten Binnengewebe hervor' (von

Arx 1964 p. 185). However, the two illustrations in von Arx's paper seem contradictory: fig. 2 (*Leptopeltopsis lunariae*) is in accordance with the cited concept, with interthecial filaments, attached above and below; fig. 1 (*Pycnothyrium litigiosum*) rather illustrates true paraphyses. The term 'paraphyses' is used by von Arx & Müller (1975).

We have found no evidence of the interthecial filaments being true paraphyses but are inclined to interpret them as paraphysoids, in the sense of Chesters (1938), i.e. true filaments, not compressed remnants of a pseudoparenchyma. It is worth noting that they are lacking in *Ronnigeria*, the ascocarp centrum of which seems to be made up of a rapidly dissolving pseudoparenchyma, apparently composed of short-celled, adherent hyphae. It seems conceivable that such hyphae may develop into paraphysoids in the course of evolution. In several bitunicate Hemisphaeriales, on the contrary, the interthecial filaments are reported to be pseudo-paraphyses.

General description and discussion

The Leptopeltidaceae s. str. can be briefly characterized as follows:

Ascocarps supracuticular, or mostly subcuticular, scutate–crustose; scutellum one-layered, of generally radially arranged cells, ± square in surface view; basal layer often poorly developed, hyaline or ± pigmented. No superficial *mycelium*, but often an intramatrical *'hypostroma'*. *Interthecial filaments* numerous–none, septate, often with gelatinous walls. *Asci* oblong, sessile, 'unitunicate', wall apically thickened with an annular 'collar' projecting downwards, I−. *Spores* thin-walled, hyaline, generally allantoid or fusiform, continuous or mostly with 1–3 transverse septa, rarely muriform. *Conidial states* common, generally of the *Leptothyrium*, rarely of the *Pycnothyrium* type.

Saprophytes, particularly common on the petioles of ferns, also in the leaves and stems of various dicotyledons.

Type genus: *Leptopeltis* von Höhnel.

The family seems to be very isolated, and at present we cannot assign it a better place than that given by von Höhnel, among the 'Phacidiales', which is admittedly an expedient for the time being. The Leptopeltidaceae are a very homogeneous group, and it seems reasonable to accommodate most of them in one genus, i.e. *Leptopeltis*. This means a considerable lumping as the generic segregation has been extensive, based mainly on two sets of characters: spore septation and hypostroma structure.

Hypostroma

As regards this vegetative structure the variation in amount as well as in texture is considerable, and each species has its pattern of variation, as rightly pointed out by Petrak, though he overestimated the interspecific differences.

Ronnigeria is altogether devoid of a hypostroma, and *Leptopeltis litigiosa* and *L. lunariae* have at most traces of it, whilst in *Dothiopeltis arunci* it is more in the form of loose hyphae (Fig. 4 B). In the other species it is generally well developed, often completely filling up several host cells, not only in the epidermis, but also in the underlying cortex. Moreover, the hypostroma is not restricted to the matrix cells just beneath the ascocarps but may extend considerably outwards.

The hypostroma is generally pseudoparenchymatous, of ± isodiametric cells, forming a textura angularis or a textura globulosa. In *Leptopeltis nebulosa* and *L. gregaria* it is mainly made up of globose cells (Fig. 5), whilst the angular cells dominate in *L. filicina* and *L. pteridis*. These species were described by Petrak (1947 a) as having a stroma of very small, rather thick-walled cells, a somewhat exaggerated statement. It is true that the cell size is less than in *L. nebulosa* and *L. gregaria*, but it is not as minute as indicated by Petrak, generally being 5–7 μm. In *L. filicina* we have only seen normal thin-walled cells, whilst in *L. pteridis* the hypostroma is, in fact, partly slightly scleroplechtenchymatous, with somewhat thickened cell walls (Fig. 4 A), though thin-walled cells are common. With regard to the hypostroma *L. filicina* and *L. pteridis* are very similar.

Apart from the pseudoparenchymatous tissue there is often a loose hyphal network, or, quoting Petrak (1947 a p. 246), the stroma is 'teils aus reichverzweigten, kurzgliedrigen, durchscheinend grau- oder hell olivenbraun gefärbten Hyphen bestehend, teils pseudoparenchymatisch, durchscheinend olivenbraun'. This statement originally referred to *Leptopeltis nebulosa*

only (cf. Fig. 5 A), and the said condition was the basis for the erection of the genus *Leptopeltopsis*, but it also applies to *L. gregaria* (Fig. 5 B), and to some extent even to *L. filicina* and perhaps to other species as well. In fact, *L. gregaria* and *L. nebulosa* are strikingly similar in hypostroma characters, and these by no means justify the assigning of those species to different genera.

To sum up: differences exist in hypostroma structure, but they are not sufficiently clear-cut to justify a generic segregation.

Spore septation

Spore septation is the other parameter employed in generic delimitation within the Leptopeltidaceae. Although extremely important on the specific level, it has, however, been utilized as the basis for a large number of schematic, ill-founded Ascomycete genera. In this case the foundation is particularly shaky, as the alleged differences are largely illusive, based on immature material. Petrak e.g. believed *Leptopeltis filicina* to be amerosporous, and *L. pteridis* (=*L. aquilina*) and *L. nebulosa* to be didymosporous, whilst in fact they are all phragmosporous at maturity. Petrak's misconception largely contributed to his erecting the genera *Leptopeltina* and *Leptopeltopsis*.

The only genus which can be kept apart from *Leptopeltis* on sporological grounds is *Dothiopeltis*, characterized by its muriform spores, and it is chiefly a matter of opinion whether to unite them or not.

The consequences of the above considerations will apparently be a large-scale lumping, resulting in an extensive synonymy. The three genera recognized by us can easily be distinguished.

Key to the genera

1. Dictyosporous ..... *Dothiopeltis*
   Amerosporous, didymosporous or phragmosporous 2
2. Interthecial threads present ..... *Leptopeltis*
   Interthecial threads absent ..... *Ronnigeria*

Leptopeltis von Höhnel

von Höhnel, Ber. Deutsch. Bot. Ges. 35: 418 (in clave) (1917) – *Leptopeltina* Petrak, Sydowia 1: 240 (1947), non Spegazzini 1923 – *Leptopeltinella* Petrak, Sydowia 5: 187 (1951) – Type: *Leptopeltis filicina* (Lib.) von Höhnel, Ber. Deutsch. Bot. Ges. 35: 422.

Dothithyrella von Höhnel, Ann. Mycol. 16: 171 (1918) – Type: *D. litigiosa* (Desm.) von Höhnel.

Leptopeltella von Höhnel, Ber. Deutsch. Bot. Ges. 35: 418 (in clave) (1917) – Type: *L. perexigua* sensu von Höhnel.

Moesziella Petrak, Ann. Mycol. 25: 323 (1927) – Type: *M. pulchella* Petrak.

Moeszopeltis Petrak, Sydowia 1: 241 (1947) – Type: *M. gregaria* Petrak.

Leptopeltopsis Petrak, Sydowia 1: 243 (1947) – Type: *L. nebulosa* Petrak.

Pycnothyrium Diedicke sensu von Arx, Acta Bot. Neerl. 13: 183 (1964), non sensu orig.

Nomenclatural comments

The nomenclature was unfortunately more confused because of Petrak's erroneous typification of *Leptopeltis* by '*L. aquilina*', i.e. *L. pteridis*, with the consequent introduction of the superfluous names *Leptopeltina* and *Leptopeltinella*. Von Höhnel definitely stated that *L. filicina* is the type: unfortunately the wrong typification was accepted and perpetuated by von Arx & Müller.

Another mistake was the adoption of the name *Pycnothyrium*. This genus was established by Diedicke (1913 p. 175) for two imperfect fungi, *Pycnothyrium gracile* Died. (described as new), and *P. litigiosum* (Desm.) Died., the latter name based on *Leptostroma litigiosum* Desm. As pointed out by e.g. von Höhnel, Desmazières's original material in fact represents an immature, perfect state. For this reason von Arx argued that the name *Pycnothyrium* ought to apply to the perfect state, taking precedence over the younger *Dothithyrella*. This argumentation is, however, untenable. As is evident from the description, *Pycnothyrium* is a genus of Fungi Imperfecti; if Desmazières's original material does not fit Diedicke's description, it cannot serve as type for *Pycnothyrium* either (something which von Arx apparently took for granted); then the other species, *P. gracile*, must be selected as the type. Diedicke himself did not designate one.

Infrageneric taxonomy

Generally, the species delimitation does not seem to be very problematic, a condition related to the pronounced host-specificity prevailing in the genus; '*Leptopeltella perexigua*' only, is said to be plurivorous. Useful taxonomic characters can be drawn particularly from the spore type, but also from the hypostroma. Ascocarp shape, on the other hand, is too variable to be of much

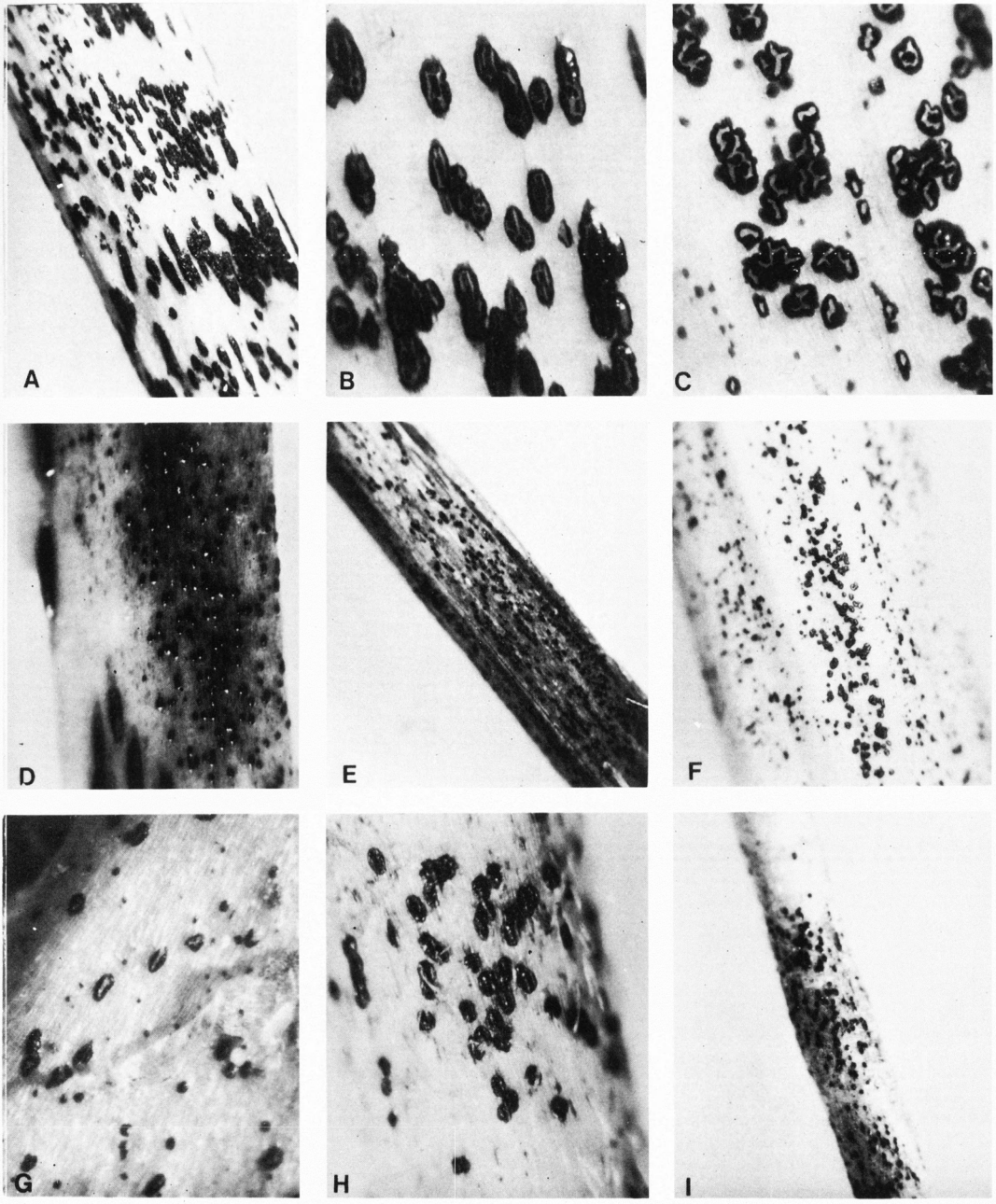


Fig. 2. Ascocarps in surface view. – A: *Leptopeltis pteridis*, ×6. – B: idem, ×25. – C: *L. litigiosa*, ×25. – D: *L. nebulosa*, ×12. – E: idem, ×6. – F: *L. litigiosa*, ×6. – G: *L. filicina*, ×25. – H: *L. gregaria*, ×25. – I: idem, ×6.

value: it can vary from circular to linear and ramified in the same species and within one collection, although a certain type may dominate; for instance most ascocarps of *Leptopeltis litigiosa* are circular. The mode of dehiscence is also very variable. Elongate ascocarps mostly open by an elongate fissure whilst the round ones open by a star-like or circular slit, or completely irregularly (cf. Fig. 2).

A character evidently of some importance is the degree of pigmentation in the basal layer, this being hyaline, if present at all, in *Leptopeltis pteridis, L. litigiosa,* and *L. filicina,* whilst strongly pigmented in *L. lunariae; L. gregaria* and *L. nebulosa* are intermediate in this respect.

Leptopeltis is a small genus, even with our wide circumscription. So far there are only seven known and named species; besides we have a few collections of uncertain status, on *Matteuccia* (see under *L. nebulosa*), and in the *lamina* of *Dryopteris filix-mas* (*Leptopeltis* sp. no. 6). The material at hand is insufficient for formal treatment. No doubt there still remains a great deal to discover – the Leptopeltidaceae have been badly neglected in spite of their frequency. They are easily overlooked though, and above all, they are seldom encountered in a well developed state. Obviously they become rapidly *passés* after ripening – most material collected by us has been either immature or dead, and the same is true for the few herbarium specimens seen.

The recognized species are presented in the following survey, with notes on diagnostic characters, host-range, distribution, and nomenclature; for detailed descriptions we refer mainly to Petrak's and von Arx's papers, though they should be taken with reserve in some respects.

Proposing a formal subgeneric hierarchy seems premature, but some suggestions may be made. A unique position is held by *Leptopeltis pteridis,* on account of its non-radiate scutellum and partly scleroplectenchymatous hypostroma. *L. litigiosa,* too, stands somewhat apart because of its supracuticular ascocarps. The other pteridicolous species, *L. filicina, L. nebulosa,* and *L. gregaria,* are apparently closely allied. *L. lunariae* probably stands close to *'Leptopeltella perexigua'* (a species not seen by us) and may be related to *Dothiopeltis*.

Key to the species of Leptopeltis

1. On ferns 2
   On dicots 7
2. Shield distinctly radiate 3
   Mature shield not radiate; on *Pteridium* ..... 1. *L. pteridis*
3. Ascocarps supracuticular; on *Pteridium* ..... 2. *L. litigiosa*
   Ascocarps subcuticular; on other hosts 4
4. Spores continuous (always?) 5
   Spores finally septate 6
5. In petioles of *Lastrea phegopteris* ..... 5. *L. gregaria*
   In the leaf-blade of *Dryopteris filix-mas* ..... 6. *L.* sp.
6. Spores narrowly fusiform, with ± pointed ends; on *Dryopteris* ..... 3. *L. filicina*
   Spores broadly fusiform, with obtuse ends; on various ferns ..... 4. *L. nebulosa*
7. Spores 2-celled; on *Lunaria* ..... 7. *L. lunariae*
   Spores 4-celled; on various hosts ..... 8. *'Leptopeltella perexigua'*

1. **Leptopeltis pteridis** (Mouton) von Höhnel

von Höhnel, Ann. Mycol. 15: 304 (1917) – *Gloniella filicina* (Lib.) Mouton f. *Pteridis* Mouton, Bull. Soc. Roy. Bot. Belg. 28(2): 80 (1889) – Type: Belgium, 'sur les stipes morts du Pteris aquilina' (n.v.).

Leptopeltis aquilina Petrak, Sydowia 1: 237 (1947) – *Hypoderma aquilinum* Rehm, Ber. Nathist. Ver. Augsburg 26: 68 (1881) – *Schizothyrium aquilinum* Rehm, Disc.-Fl. 75 (1888) – non *Sphaeria aquilina* Fr., Syst. Mycol. 2: 522.

Exs.: Krieger, F. sax. 1169 (*'Aulographum filicinum'*) (S) – Rehm, Asc. 270 (*'Hypoderma aquilinum'*) (S), Asc. 1227 (*'Aulographum filicinum'*) (S) – Thümen, Myc. univ. 73 (*'Hysterium aquilinum'*) (UPS).

Fig. 1A, 2A, B, 4A.

Ascocarps subcuticular, often densely scattered, ± elliptic, elongated along the petioles or veins, c. 0.3 mm long, mostly several confluent into larger crusts, up to 2–3 mm. *Hypostroma* well developed, partly slightly scleroplectenchymatous, of small cells, mostly 5–7 μm, first hyaline, later dark. *Asci* oblong, up to 30 × 12 μm, mostly

8-spored, but spore abortion is common. *Spores* mostly allantoid, with obtuse or somewhat acute ends, 12–15 × 3–4 μm, usually 2-celled, but 3- and 4-celled spores occur. *Interascicular threads* numerous.

In dead leaves of *Pteridium aquilinum,* especially the petioles, but also in the foliar veins. Common, as is the imperfect state, *Leptothyrium pteridis* Ehrenb. ex Fr.

This species is generally recognized even macroscopically by the relatively large black ascocarps, looking like tar spots, much more conspicuous than the smaller and lighter *L. litigiosa,* which is always present (see under this species). In the microscope it is easily identified by the non-radiate shield, composed of a textura angularis – not textura epidermoidea, as stated by von Arx & Müller (1975 p. 29). This deviating structure is apparently secondary; originally the scutellum cells are radially arranged.

The ascocarps occur even in the leaf segments, but as far as we have observed, always subcuticularly in the veins – according to Petrak (1947 a p. 235) they may even grow subepidermally in the mesophyll, then considerably deviating in morphology.

With regard to the nomenclature we must admit that the identification with Mouton's fungus may be somewhat problematic. We have followed von Höhnel who apparently had not examined type material, and it cannot be excluded that Mouton's description was at least partly based upon *Leptopeltis litigiosa.* Several authors, such as Rehm and Petrak, and more recently von Arx & Müller, have identified this fungus with *Sphaeria aquilina* Fr., a species taken by others to be a *Mycosphaerella.* Both interpretations are erroneous – as it is apparent from the description and the original material, *Sphaeria aquilina* is a *Leptostroma.*

2. **Leptopeltis litigiosa** (Desm.) L. & K. Holm, comb. nov.

Leptostroma litigiosum Desmazières, Ann. Sci. Nat. Bot. ser. 2, 19: 338 (1843) – *Microthyrium litigiosum* Sacc., Michelia 1: 496 (1879) – *Dothithyrella litigiosa* von Höhnel, Ann. Mycol. 16: 171 (1918) – *Pycnothyrium litigiosum* Died. sensu von Arx 1964 et auct. rec., non sensu Diedicke – Type: Moug. & Nestl., Stirpes Crypt. 673 (UPS!).

Exs.: Desm., Pl. Crypt. Fr. 1327 (n.v.) – Lundell & Nannf., F. exs. suec. 664, 778 (UPS) – Moug. & Nestl. Stirpes Crypt. 673 (UPS).

Fig. 1 B, 2 C, F, 3 A.

Ascocarps densely scattered, supracuticular, generally occurring in abundance and ± covering large parts of the petioles. Solitary ascocarps usually circular, c. 0.1 mm diameter, but often several confluent into crusts up to 1 mm large. *Shield* radiate, splitting irregularly or often with a star-like or circular fissure. *Hypostroma* none or almost none. *Asci* oblong, 25–30 × 10–12 μm. *Spores* generally allantoid, (11–)15–18(–20) × 2.5–3.5 μm, long 2-celled but finally (always?) 4-celled.

On dead petioles of *Pteridium aquilinum.*

An extremely common fungus, at least in Scandinavia, where it seems to be the constant companion of its host. The bracken is cosmopolitan, and *L. litigiosa* also perhaps, but very little is known about its distribution. It is apparently restricted to *Pteridium* – the old unverified record of an occurrence on *Osmunda* (Desmazières 1843) is surely erroneous.

Leptopeltis litigiosa often grows intermixed with *L. pteridis,* but they are easily distinguishable, even by sight, as rightly pointed out by von Höhnel l.c.: 'Während die *Dothithyrella* kleine rundliche, braunschwarze, fast matte Fruchtkörper besitzt, zeigt der zweite Schlauchpilz [=*L. pteridis*] stets längliche oder lanzettenförmige pechschwarze, stark glänzende Stromata'. The difference in brilliancy is due to the difference in habitat – supracuticular, and subcuticular, respectively. Microscopically they are easy to distinguish by the different shield textures, whereas the spores are very similar; *L. litigiosa,* though, seems to have slightly longer and narrower spores, which more often become 4-celled.

An imperfect form was described by Diedicke (1913 p. 175) as *Pycnothyrium litigiosum;* its existence was denied by von Höhnel (1918 p. 171) but confirmed by Grove (1937 p. 198). We have not seen it. Von Arx (1964 p. 185) also reported a conidial state, but according to his description most likely belonging to *Leptothyrium.*

With regard to the nomenclature it can be noted that Desmazières in his protologue cited *Sclerotium pteridis* Pers., but as this name is a *nomen nudum,* the epithet *litigiosum* is not endangered.

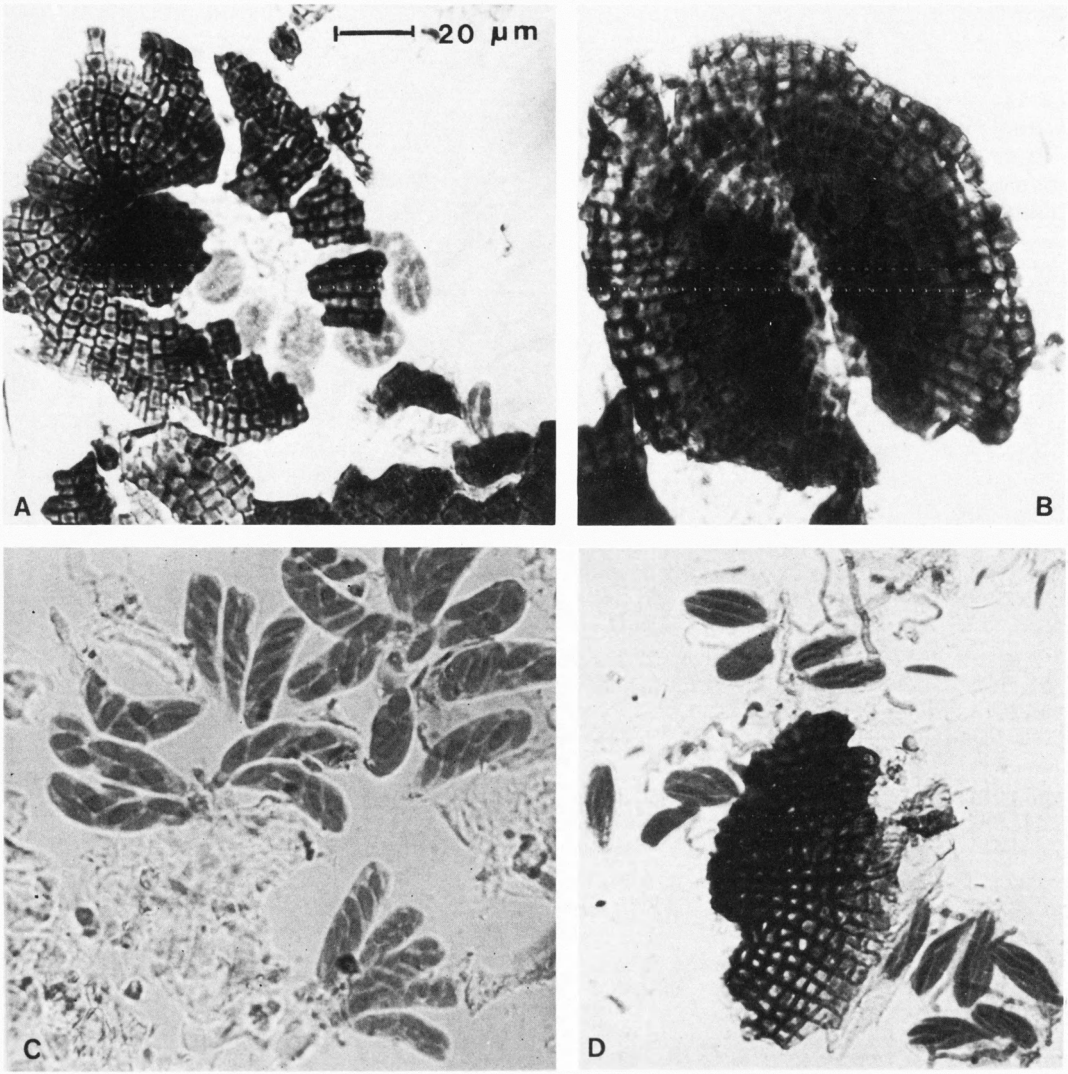


Fig. 3. A: *Leptopeltis litigiosa,* shield and asci. – B: *L. gregaria,* shield. – C: *Ronnigeria arctica,* asci. – D: *L. filicina,* part of shield and asci. – All × 530.

3. **Leptopeltis filicina** (Lib.) von Höhnel

von Höhnel, Ber. Deutsch. Bot. Ges. 35: 358 (1917) – *Aylographum filicinum* Libert, Pl. Crypt. Ard. 275 (1834) – Type: Belgium, 'Ad stipites Aspidii Filicis maris' (BR!S!).

Aporia Jaapii Rehm, Abh. Bot. Ver. Brandenburg 47: 84 (1905) – *Leptopeltinella Jaapii* Petrak, Sydowia 5: 187 (1951) – Type: Germany, Schleswig-Holstein, Sattenfelde, *Dryopteris spinulosa,* 23.VI.1904, Jaap (S!).

Exs.: Jaap, F. sel. 82 (S) – Libert, Pl. Crypt. Ard. 275 (BR, S) – (Krieger, F. sax. 1169 & Rehm, Asc. 1227 = *L. pteridis*) (S).

Fig. 1C, 2G, 3D.

Matrix: Dryopteris spp., as *D. filix-mas, D. assimilis, D. dilatata, D. spinulosa;* in the petioles and larger veins.

Ascocarps scattered, subcuticular, linear–elliptic. *Hypostroma* mainly of textura angularis, of isodiametric cells, 5–7 µm. *Asci* oblong, c. 30 × 10 µm, 8-spored. *Spores* fusiform, often termi-

nally pointed, 18–20 × 3–4(–4.5) μm, finally (always?) 4-celled.

This species is characterized by its narrow spores, generally pointed at the ends. We can find no support for the recognition of *Aporia jaapii* as a separate taxon – a large amount of material, collected on various members of the *Dryopteris dilatata* complex, seems to agree perfectly with the form on *Dryopteris filix-mas*. When Rehm described *Aporia jaapii* he was evidently ignorant of *Leptopeltis filicina* – otherwise, in all probability, he would have referred his fungus to this species. Certainly Petrak (1947 a) claimed that there were two different taxa, *Aporia jaapii* differing by 'oft etwas kleineren Fruchtkörper und durch die am Rande meist viel heller gefärbten Zellen der Deckschicht, deren Radialwände dicker sind als die Querwände. Auch sind die Sporen der *A. Jaapii* im Durchschnitt etwas grösser' (pp. 239–240). However, these alleged differences are imaginary. Even in the 'true' *L. filicina*, the marginal scutellum cells are almost hyaline, with the radial walls thicker than the transverse ones. Petrak did not see any mature spores, nor did Rehm, who claimed them to be one-celled in *Aporia jaapii*. His type material is immature but 2-celled spores occur.

Leptopeltis filicina is of course easily distinguishable from *L. litigiosa*, and by no means only a 'Substratform', as suggested by von Arx (1964 p. 185). It is probably rather common and widespread in Scandinavia; we have seen material from the Swedish provinces of Skåne, Uppland, Dalarna, and Hälsingland, and from Möre og Romsdal in Norway.

4. **Leptopeltis nebulosa** (Petrak) L. & K. Holm, comb. nov.

Leptopeltopsis nebulosa Petrak, Sydowia 1: 244 (1947) – Type: Czecho-Slovakia, Moravia pr. Podhorn, in dead petioles of *Athyrium filix-femina*, 2.V.1925, leg. Petrak (n.v.).

Fig. 1D–F, 2D, E, 5A, 6.

In aspect similar to the preceding species, *L. nebulosa* is very easily distinguishable, though, by the *spores* which are shorter and relatively broader, with obtuse ends, often allantoid, (8–)10–11 × (2.5–)3–3.5 μm, long 2-celled but finally, at least sometimes (always?), with 3 septa. *Asci* 20–25 × 10–12 μm. *Basal layer* present, ± pigmented below. *Hypostroma* well developed, mostly pseudoparenchymatous, of textura angularis–textura globulosa, cells 5–8 μm diameter, with dark cells.

In the petioles of various ferns.

Leptopeltis nebulosa is apparently a common fungus on *Athyrium filix-femina*, though hitherto known only from the type collection. We have seen a great amount of material on this host from Sweden (Skåne, Uppland, and Gästrikland). Moreover, the species can obviously occur on other hosts too. We have one collection on *Dryopteris filix-mas*, which in every respect is a perfect match of *L. nebulosa*: Norway, Möre og Romsdal, c. 4 km NE of Gjöra, close to the river Driva, 1.VII.1975, 666 a.

The occurrence on *Dryopteris filix-mas* may be exceptional, but this is certainly not the case with another host, viz. *Lastrea dryopteris*. No *Leptopeltis* has so far been recorded on this fern, but we have 5 collections agreeing closely with *L. nebulosa:*

Sweden: Uppland. Uppsala, 25.V.1975, 577 a. – Alunda, pr. Hävermossen, 2.VI.1976, 582. – *Västmanland.* Nora pr. Kerstinbo, 21.V.1975, 571 a. – *Dalarna.* Sundborn, Mjölnarvallen, 884 b.

Norway: Sör-Tröndelag. Oppdal, Gisnafallet, 29.VI.1975, 638.

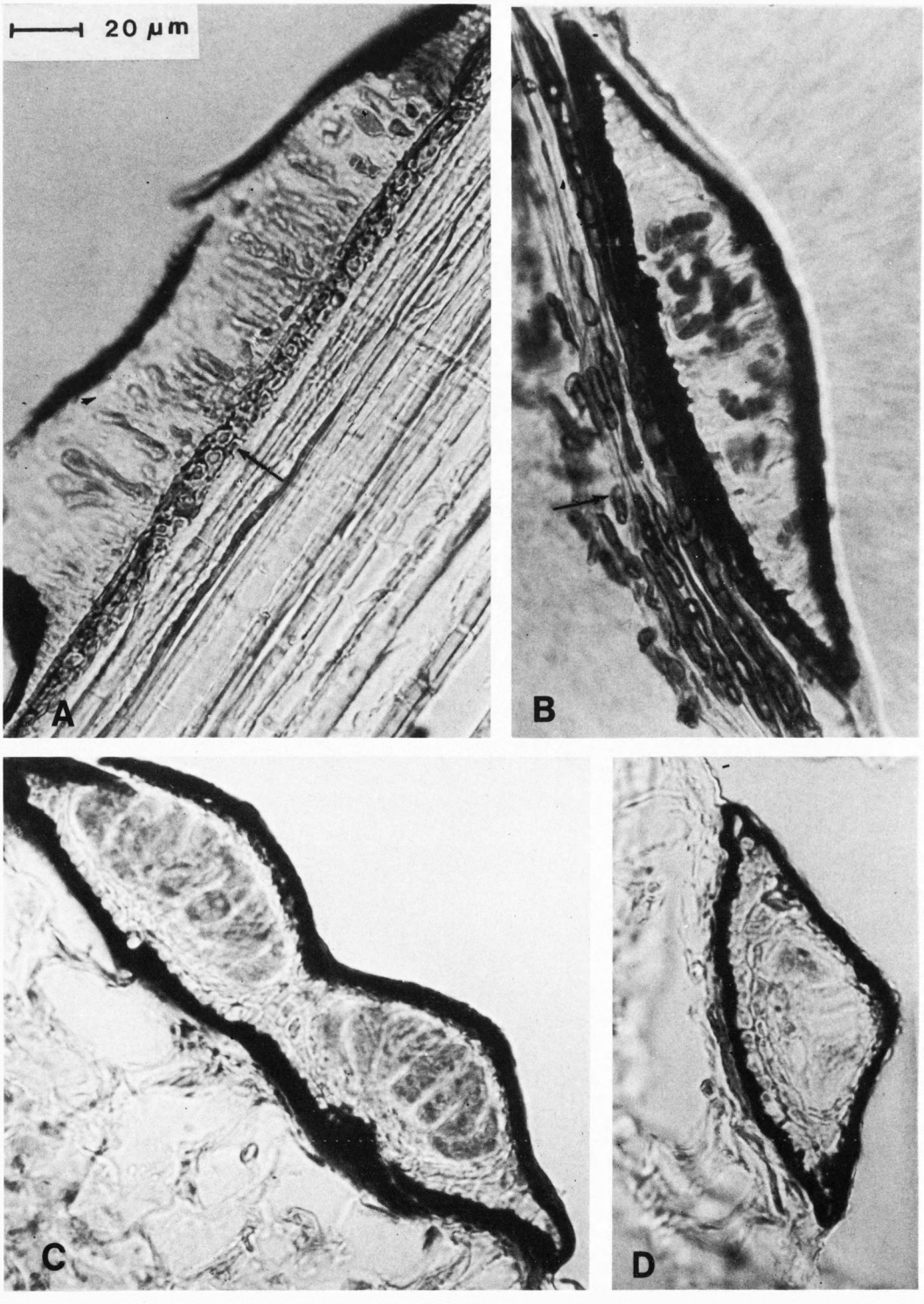
We can also report the occurrence on *Matteuccia struthiopteris* of a *Leptopeltis*, which possibly belongs to *L. nebulosa*. We have 6 Swedish collections, from Uppland, Gästrikland, and Torne Lappmark, but none is in a state to permit a safe determination. The hypostroma is suggestive of *L. nebulosa*.

5. **Leptopeltis gregaria** (Petrak) L. & K. Holm, comb. nov.

Moeszopeltis gregaria Petrak, Sydowia 1: 241 (1947) – Type: Norway, Sogn, Naeröy-dal ['Naerae-Tal, Sagnefjord' l.c.], on dead petioles of *Lastrea phegopteris*, 10.VI.1936, leg. Ade (n.v.).

Fig. 1G, 2H, I, 3B, 5B.

Ascocarps often densely scattered, broadly elliptic–subcircular, usually 100–150 μm long, opening by a longitudinal slit. *Basal layer* present, the cell walls adherent to the substratum being darkly pigmented. *Hypostroma* well devel-


20 µm
A
B
C
D

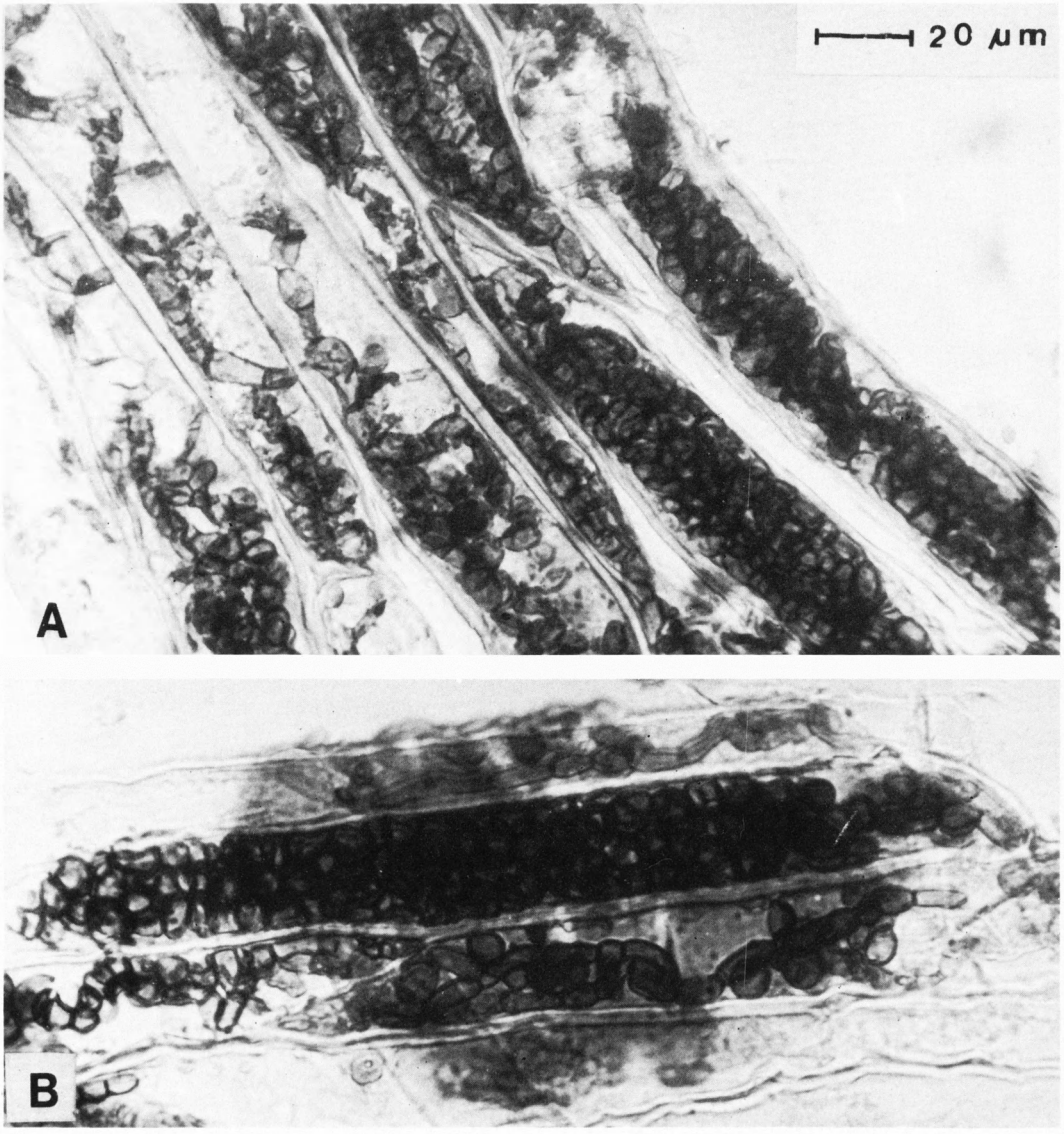


Fig. 5. Hypostromata in host tissue. – A: *Leptopeltis nebulosa*. – B: *L. gregaria*. – All × 610.

oped, mostly of textura globulosa, partly of textura angularis, of comparatively large, dark cells up to 10 µm. *Asci* normally with 8 spores but the number is extremely variable; supernumerary spores are frequent and we have seen asci with up to c. 16 spores. Petrak (1947 p. 243) reported 4- and 6-spored asci. The *spores* are also exceptionally variable in size and shape. Normally they are ± ellipsoidal, 10–12 × 3–4 µm, always(?) continuous.

Fig. 4. Sections of ascocarps. – A: *Leptopeltis pteridis*, hypostroma by the arrow. – B: *Dothiopeltis arunci*, hypostroma by the arrow. – C, D: *Ronnigeria arctica*, with conspicuous basal layer but no interthecial threads. – All × 530.

This species is apparently restricted to *Lastrea phegopteris*, and seems to be rather common, though so far only recorded from the type collection. It is characterized i.a. by the unicellular spores. We do not exclude the possibility of sundry spores becoming septate, but this is apparently exceptional.

Specimens seen: Sweden: Gästrikland. Hille par., Brännsågen, 21.V.1975, 563. – *Dalarna.* Sundborn par., Mjölnarvallen, 22.VI.1974, 198; 21.VI.1975, 596, 597; 23.VII.1975, 708.

Norway: Möre og Romsdal. c. 4 km NE of Gjöra, 1.VII.1975, 662.

6. **Leptopeltis** sp.

Fig. 1H.

Ascocarps subcuticular, densely clustered and often confluent, on both sides of the leaf blade, circular, c. 50 μm diameter, 25 μm high; basal layer pigmented on the underside. No hypostroma. *Asci* oblong, generally 17–20 × 10–12 μm, usually 8-sporous, but supernumerary spores occur. *Spores* oblong, continuous, hyaline, 7–10 × 2.5–3 μm.

Specimen seen: Sweden: Uppland, Uppsala, 'Predikstolen', last year's fronds of *Dryopteris filix-mas*, 25.V.1975, 576 b.

An extremely interesting fungus, unique by its habitat, growing abundantly in the leaf blade, outside the veins. It probably represents a new species, but because of the limited material we confine ourselves to this mention.

7. **Leptopeltis lunariae** (Fuckel) L. & K. Holm, comb. nov.

Microthyrium Lunariae Fuckel, Fungi rhenani 2471 (1872); Jahrb. Nass. Ver. Naturk. 27/28 p. 53 (1873) – *Gloniella lunariae* von Höhnel, Fragm. Mykol. 1004 (1919) – *Leptopeltopsis lunariae* von Arx, Acta Bot. Neerl. 13: 187 (1964) – Type: Austria, Kirchdorf, dead stems of *Lunaria rediviva*, leg. Schiedemayer (S!).

Fig. 1K.

Ascocarps superficial, densely scattered, elliptic, up to 0.3 mm long, but often confluent into larger crusts, intimately mixed with the imperfect form (*Leptothyrium lunariae* Kunze). *Shield* radiate, a thin basal layer present, with dark cell walls. No hypostroma. *Asci* oblong–cylindrical, 40–45 × 12 μm, 8-spored. *Spores* ellipsoid–fusiform, hyaline, 10–14 × 4–5 μm, with one, often submedian septum.

The species is known to us from the type collection only, which, however, is very rich. It is plainly distinct from the pteridicolous species, i.a. by the distinct basal layer, but is probably a close ally of the following species.

8. **'Leptopeltella perexigua'** von Höhnel

von Höhnel, Ber. Deutsch. Bot. Ges. 35: 422 (1917) – *'Pycnothyrium perexiguum'* von Arx, Acta Bot. Neerl. 13: 186 (1964) – non *Hysterium perexiguum* Spegazzini.

?*Moesziella pulchella* Petrak, Ann. Mycol. 25: 323 (1927) – Type: Czecho-Slovakia, Moravia, pr. Weisskirchen (Hranice), dead stems of *Senecio fuchsii*, 1925, leg. Petrak (W?).

Unfortunately no material of this species has been available for study, but judging from the descriptions published, it seems to be a true *Leptopeltis*, characterized i.a. by a distinct, dark basal layer, and by 4-celled spores. According to Petrak and von Arx, it is the perfect state of the very common and plurivorous *Leptothyrium vulgare* (Fr.) Sacc., a fungus, reported by others to be the imperfect form of *Hypoderma commune* (Fr.) Duby (e.g. Grove 1937 p. 163).

For the time being the fungus is probably devoid of a correct name. The epithet *'perexigua'* must be dropped, as it is based on a misinterpretation: von Höhnel erroneously identified his fungus with *Hysterium perexiguum* Speg. We have examined the type (Italy, Belluno, in dead stems of *Angelica silvestris*, 28. IX. 1879, leg. Spegazzini, LPS!) and can verify that it is hysteriaceous, having nothing to do with the Leptopeltidaceae. Consequently, it is the turn of *Moesziella pulchella* Petr., if it is synonymous, as claimed by Petrak. The correct name would then be *Leptopeltis pulchella* (Petrak), but without an autopsy we refrain from making the formal combination.

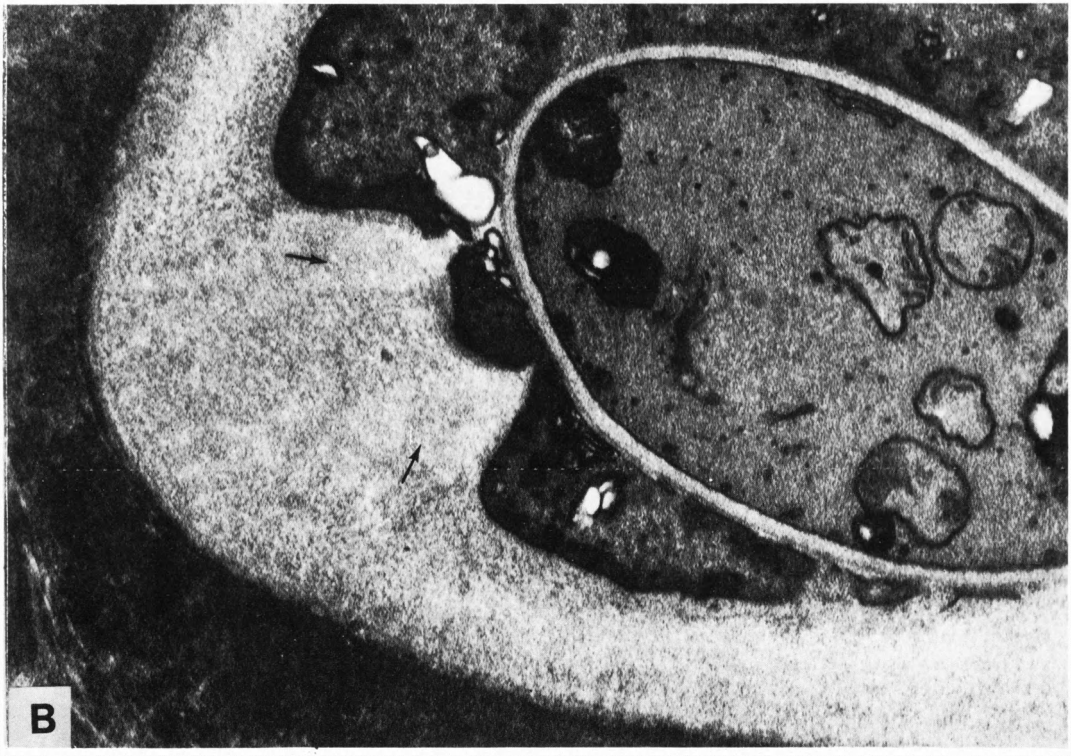
Dothiopeltis E. Müller

Müller, Sydowia 10: 197 (1957).

This genus was erected for the sole species *D. arunci* and is still monotypic. It is closely related

Fig. 6. *Leptopeltis nebulosa*, electron micrographs. – A: Ascus, × 8,000. – B: Ascus tip, a cylindrical electron-lucent ring by the arrows. × 30,000.


A


B

to *Leptopeltis* and the taxa might well be united. It seems reasonable, though, to keep *Dothiopeltis* as a separate genus, because of the muriform spores and the well developed basal layer.

Dothiopeltis arunci E. Müller

Müller, Sydowia 10: 197 (1957) – Type: Switzerland, St. Gallen, in dead stems of *Aruncus silvestris*, 25.V.1955, E. Müller & H. Schüepp (UPS isotypus!).

Fig. 1I, 4B.

Ascocarps scattered, subcuticular, elliptical in aspect in surface view, up to 0.2 mm long. *Shield* radiate, opening by a longitudinal slit. *Basal layer* well developed, up to 10 μm thick, of 1–2 layers of angular cells with strongly pigmented walls. *Hypostroma* poorly developed. *Interthecial threads* fairly numerous, with 2–3 septa. *Asci* ± oblong, c. 30 × 12 μm, 8-spored. Spores variable in form, ± irregularly ellipsoidal, hyaline, mostly 14–17 × 5–6 μm, generally with 4–5 transverse septa and one longitudinal septum in one or two central segments.

For a detailed description we refer to Müller's paper, though in some respects our findings are at variance with his. We have not seen the basal layer as strongly developed as in his Fig. 1d, nor are we able to confirm the existence of a 'Mittelsäule', i.e. a central, sterile part of the ascocarp.

Dothiopeltis arunci seems to be a very distinct species, but is so far only known from the type collection.

Ronnigeria Petrak

Petrak, Sydowia 1: 310 (1947). – Type: *Ronnigeria arctica* (Oud.) Petrak l.c.

This genus, so far monotypic, is remarkably deviating by the absence of interthecial threads. The asci, however, are exactly the *Leptopeltis* type, and Petrak was certainly quite right when referring the genus to this family, though the relationship has been denied by von Arx & Müller (1954 p. 399).

Ronnigeria arctica (Oud.) Petrak

Petrak, Sydowia 1: 310 (1947) – *Microthyrium arcticum* Oudemans, Versl. Meddel. Kon. Akad. Wetensch., Afd. Natuurk., ser. 3. 2: 160 (1885) – Type: Novaja Zemlya, *Potentilla fragiformis*, VIII. 1881, M. Weber (n.v.).

Fig. 1J, 3C, 4C, D.

Ascocarps mostly densely crowded, often confluent, amphigenous, subcuticular, solitary ones lenticular, generally 100–125 μm diameter. *Shield* irregularly radiate, basal stratum well developed, of 3–4 cell layers, the undermost one with strongly incrusted walls. No interthecial threads, no hypostroma. *Asci* rather few, ± oblong, c. 35–40 × 10–12 μm, 8-spored. *Spores* continuous, hyaline, 8–12(–15) × 2.5–4(–5) μm, very variable in form and size, oblong–ellipsoidal, often slightly cuneiform.

In dead leaves, especially the lamina, of *Potentilla* spp.

For a full description, see Petrak (1947 b). Evidently the fungus has an arctic-alpine distribution. It is widely spread in the Arctic and is quite common in northern Scandinavia, on *Potentilla crantzii* (even found on *P. hyparctica*). However, it is apparently not coextensive with *P. crantzii;* this plant is common around Uppsala, where the fungus seems to be lacking. Petrak found it on a collection from Austria, Burgenland, which was the first, and still seems to be the sole, record from Central Europe.

Excluded genera

As mentioned in the introduction, several fungi have been wrongly referred to the Leptopeltidaceae by various authors. Most of the 13 genera, originally included by von Höhnel, are evident outsiders and need not be considered; an exception is *Thyriopsis* Theissen & Sydow which was reintroduced by Müller & von Arx (1962) and still kept in the family by von Arx & Müller (1975). In the latter work some further taxa were included, viz. *Aulographum* Lib., *Aulographina* v. Arx & Müller, *Lembosina* Theissen, and *Morenoina* Theissen. These had been placed among the Asterinaceae by the same authors in 1962, a classification which is definitely to be preferred, as they are all bitunicate. This is also the case for *Thyriopsis*, which seems to be fairly closely related to e.g. *Lembosina*.

In 1919 von Höhnel erected the new genus *Lichenopeltella*, based on *Microthyrium maculans* Zopf, a parasite in the thallus of *Umbilicaria hirsuta*. He stated that the fungus 'stellt eine

neue Gattung dar, die wegen des fast oberflächlichen Wachstums am besten neben der subcuticulären *Leptopeltella* gestellt werden kann' (1919 p. 553). Von Höhnel was, however, more superficial than the fungus, which in fact is basally immersed in the lichen thallus, as is also illustrated by Müller & von Arx (1962 p. 239, fig. 82), who followed von Höhnel's classification. *Lichenopeltella maculans* has bitunicate asci and seems to be akin to *Mycosphaerella*.

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Flower-visiting lizards on Madeira

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The Madeiran lizard *Lacerta muralis dugesii* has been observed to visit flowers of the introduced species *Aloë arborescens* and of the indigenous *Echium nervosum* in a manner very similar to that of ordinary pollinating visitors. It is suggested that this lizard-flower interrelationship may be looked upon as a possible model of a palaeo-ecological connection between pre-angiosperms and reptilian pre-birds.

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The fauna of the Atlantic island of Madeira includes only one species of reptiles: an indigenous form of the wall lizard, *Lacerta muralis dugesii,* which is very abundant, especially in the vicinity of human settlements. In sunny weather it can be seen on rocky precipices, on house walls, on stone fences etc.

This lizard has been observed visiting the flowers of different plants – obviously to lap up nectar in the flower. A short account of two closely followed cases will be related here.

Observations

Aloë arborescens is a South African shrubby xerophyte, reaching a height of 0.5–2 metres. This species is grown frequently on Madeira as an ornamental plant. From October to February it carries dense, upright racemes of pendant, brightly red flowers. In its native surroundings it is ornithogamous, as is indicated by the vivid colour of the flowers and the very rich nectar production. On Madeira frequent visits are made by honey bees (Fig. 1A) and sometimes by indigenous birds, this is also true where other introduced plants are concerned (cf. Vogel 1954 p. 328).

On Cape Garajau, a high cliff on the southern shore of Madeira, a religious monument has been erected, surrounded by a horizontal, gravelled plain. On one side of the plain there is a small, stone-walled shed. This shed and the walls supporting the plain is the site of a great number of lizards. Around the place dense populations of *Aloë arborescens* are growing; some of the plants stand very close to the shed (Fig. 1 B).

In December 1976 observations were made of numerous visits of lizards in the flowers of these plants (Fig. 1C). This *Lacerta* population comprised animals of varying size; the flowers were exploited only by the young, still small individuals, which could poke their heads into the interior of the flowers. The adult lizards, who could no longer enter the legitimate way did not attempt any nectar thefts.

New observations were made on Cape Garajau in February 1977. The *Aloë* specimens along the shed wall were in a postfloral stage and although other plants in the vicinity still carried flowers, no lizards could be seen in them.

However, in the natural vegetation on the slopes of the cape another plant species was now in full bloom, viz. *Echium nervosum.* This shrub, reaching a height of c. 1 metre, is endemic to the Madeiran archipelago. It carries very conspicuous inflorescences: numerous cymes of light blue flowers, densely packed to form a heavy, upright spike-like construction. The nectar

production is rich, frequently attracting visitors, viz. pollinating insects.

On one point of Cape Garajau where the stone wall supporting the gravelled plain rises from the surrounding natural ground, two small *Echium* shrubs were flowering. The inflorescences of these were frequently visited by the *Lacerta* population from the adjacent wall (Fig. 1D). In the *Echium* flowers the nectar was available to lizards of any size; they could just sit on the inflorescence and rapidly dip their tongues into the flowers.

The distance between the *Aloë* plants exploited by the shed lizards in December and the *Echium* plants exploited by the wall lizards in February is c. 30 metres. The *Lacerta* population which had become accustomed to nectar drinking in the *Aloë* flowers may have moved over to the *Echium* plants later on. Though it does seem more probable that the populations stick within very limited territories, with the result that the different plants were visited by different lizard populations.

The flower-lizard inter-relationship observed may thus be provoked when a suitable flower grows just in front of a lizard-wall. Two other observations were made under these conditions, indicating such an incentive behind the adaptation of the lizards to the flowers. Firstly a visit of a lizard in flowers of *Echeveria atropurpurea* (in the Madeira Botanical Garden February 1967) was observed, and secondly a group of lizards visiting *Salvia splendens* (in the Sta Catarina Park in central Funchal, February 1977). A fifth plant species where Madeiran *Lacerta* specimens have been observed among the flowers is *Agave attenuata* (observations in February 1967, 1970 and 1977). In this case, however, it cannot with certainty by claimed that the purpose of the visits was that of lapping nectar.

As to the *Aloë*, the *Echium* and the *Salvia*, the lizards were observed to approach the flowers by climbing up along the stems of the plants, as well as by jumping directly through the air from the adjacent stone wall or from other branches of the plants. They showed the same versatile agility in such jumps as may be seen among lizards hunting for insects on the room walls in houses in the tropics.

Discussion

Very little attention has been given to the possibility that reptiles may have any importance as pollinators. The small and agile lizards that can be observed among flowers in the warmer parts of the world are typically carnivorous, and their hard, sleek body surface does not seem at all suitable for pollen carriage. To them the inflorescences of plants probably chiefly mean hunting grounds for insects.

During earlier periods in Earth history the situation may, however, have been different. Coprolites from the Permian and Jurassic indicate that reptiles have been browsing on the flowers of those days (Schweitzer 1968, Harris 1945, 1956, cf. also Faegri & van der Pijl 1966 p. 20). In a recent palaeobotanical treatise on angiosperm origin, reptiles have actually been mentioned as a possible alternative to beetles as original pollinators (Hughes 1976 p. 57).

At the present time birds are important pollinators. If similar ties existed in the Jurassic, they would have involved pre-angiosperms and pre-birds, which underwent a more or less contemporary evolution. In this respect the close relationship between birds and reptiles should be considered; the birds might even be classified as a group among the reptiles (von Huene 1956).

Probably the relationship observed on Madeira is rather unusual: it is so striking that it could hardly have escaped notice had it been of more common occurrence. However, the biological interest of the observations does not primarily lie in the fact that the lizards might bring about some cross-pollination in the few plants they visit. Since their behaviour so closely follows that of ordinary pollinators, it might instead be taken as a sign that an ethological basis for ecological relationships with flowers may be present among reptiles. Thereby is an interesting question raised: is what we today call ornithogamy directly derived from pollination by reptiles among early angiosperms?

The figures are reproductions from part-pictures of pairs of stereoscopic colour photographs. The three-dimensional realism of the originals cannot be communicated. Biologists visiting Stockholm are, however, invited to call upon the author to inspect the originals.

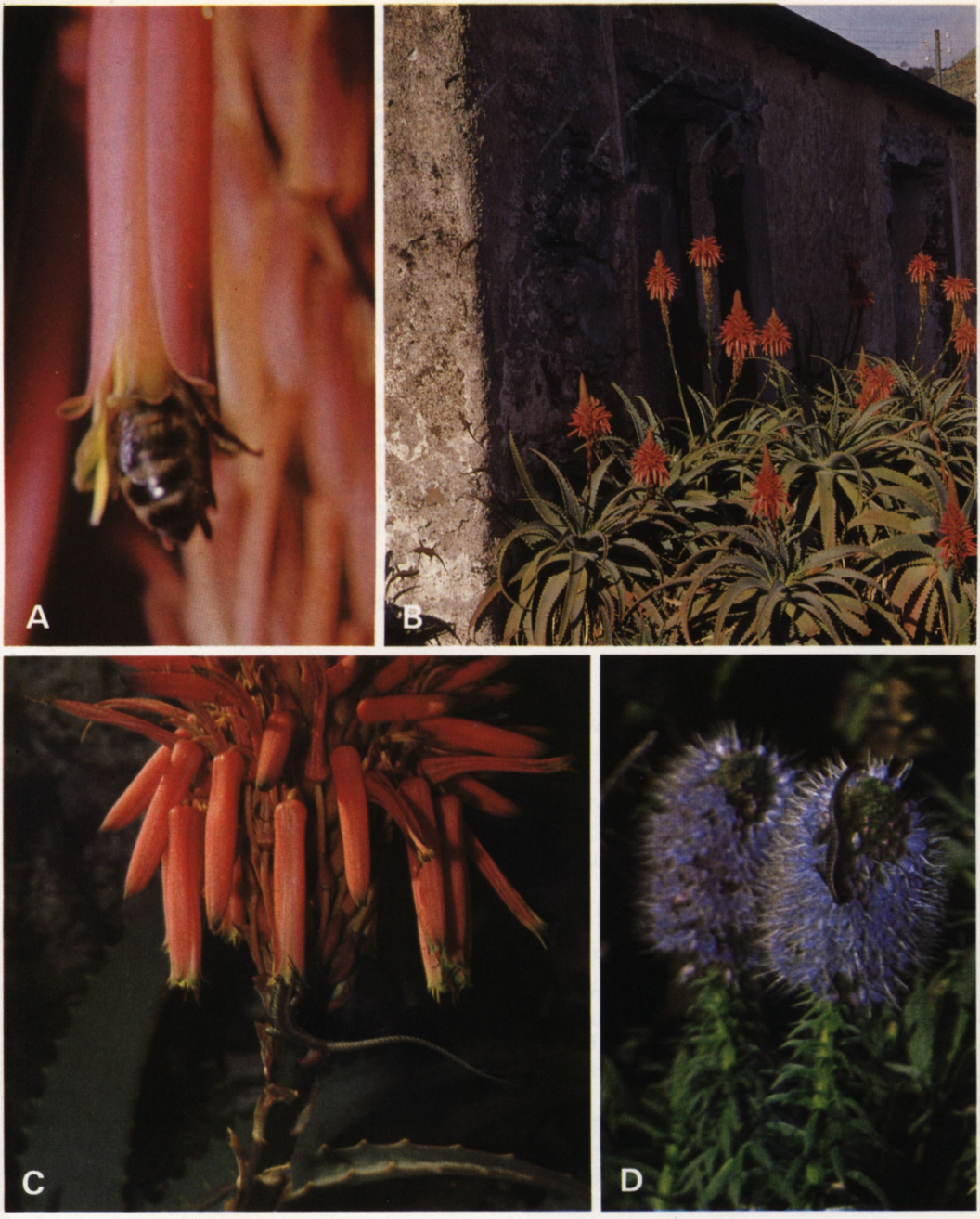


Fig. 1. A: Honey-bee in a flower of *Aloë arborescens*. – B: *Aloë arborescens* at a stone-walled shed. To the left on the sunny side some lizards (*Lacerta muralis dugesii*). – C: An inflorescence of *Aloë arborescens*. A young lizard is sucking nectar. – D: Inflorescences of *Echium nervosum* visited by a lizard drinking nectar. – Madeira, Cape Garajau, December 1976 (A–C) and February 1977 (D). Photo Ivar Elvers.

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Studies in African Cyperaceae XV

Amphicarpy and spikelet structure in Trianoptiles solitaria

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The morphology of *Trianoptiles solitaria* (C. B. Cl.) Levyns is described and illustrated. This South African plant has basal spikelets, each reduced to a solitary female flower enclosed in a utricle probably representing a modified glume, in addition to the 2-flowered aerial spikelets. New leafy culms and basal spikelets spring together, as multiple buds, in the axils of the leaves. In these features it is highly specialised. The 3- or 4-glumed aerial spikelet shows a monopodial structure particularly clearly and this, rather than a cymose structure, is probably characteristic of other Rhynchosporeae.

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The genus Trianoptiles Fenzl

The genus *Trianoptiles* was described by Fenzl in Endl. Gen. Pl., p. 113 (1836). The type species is *Trianoptiles capensis* (Steud.) Harv. in Gen. S. Afr. Pl. ed. 2, p. 422 (1868), based on *Ecklonea capensis* Steud., in Flora 1829, p. 138. However the generic name *Ecklonea* Steud. had to be rejected because it had previously been used for a genus of seaweeds.

The genus *Trianoptiles* is closely related to *Carpha* R. Br., but differs in having hypogynous bristles feathered at the base, 3-fid at the apex (Clarke 1898 for *Ecklonea*). However, Clarke (1898 p. 271) writes "The structure of the spikelet and flower in this plant is so exactly that of *Carpha* that it might be better to sink the genus in *Carpha*." Pfeiffer (1930) merged the two genera.

However when the basal female flowers were discovered (Levyns 1943), new evidence supporting the separation of the two genera came to light. Verbelen (1970) found the embryo to be of the *Fimbristylis* type in both genera, but in *Trianoptiles* the embryo has a distinct capitellate top-like form. The vegetative anatomy in the two genera also differs in several characters (Metcalfe 1971).

Therefore in this work we have accepted the genus *Trianoptiles* as being separate from *Carpha*, although we realize that they are closely related.

Description

Trianoptiles solitaria (C. B. Cl.) Levyns is a dwarf South African annual growing in seasonally damp areas of the Cape Flats, first described by Clarke (1900 p. 759) as *Ecklonea solitaria*. It is one of the three species of its genus, all rather similar and all confined to the Cape Province (Levyns 1943, Adamson & Salter 1950, Phillips 1951). It produces two kinds of fruit, one aerial, the other at ground level. Thus it is amphicarpous, as are several species of *Bulbostylis* and *Scirpus* recently reviewed by Haines (1971) and Raynal (1976), and now placed in *Abildgaardia* and *Schoenoplectus* (Haines & Lye 1977). It is discussed here because it is a very good example of the habit in the classic sense

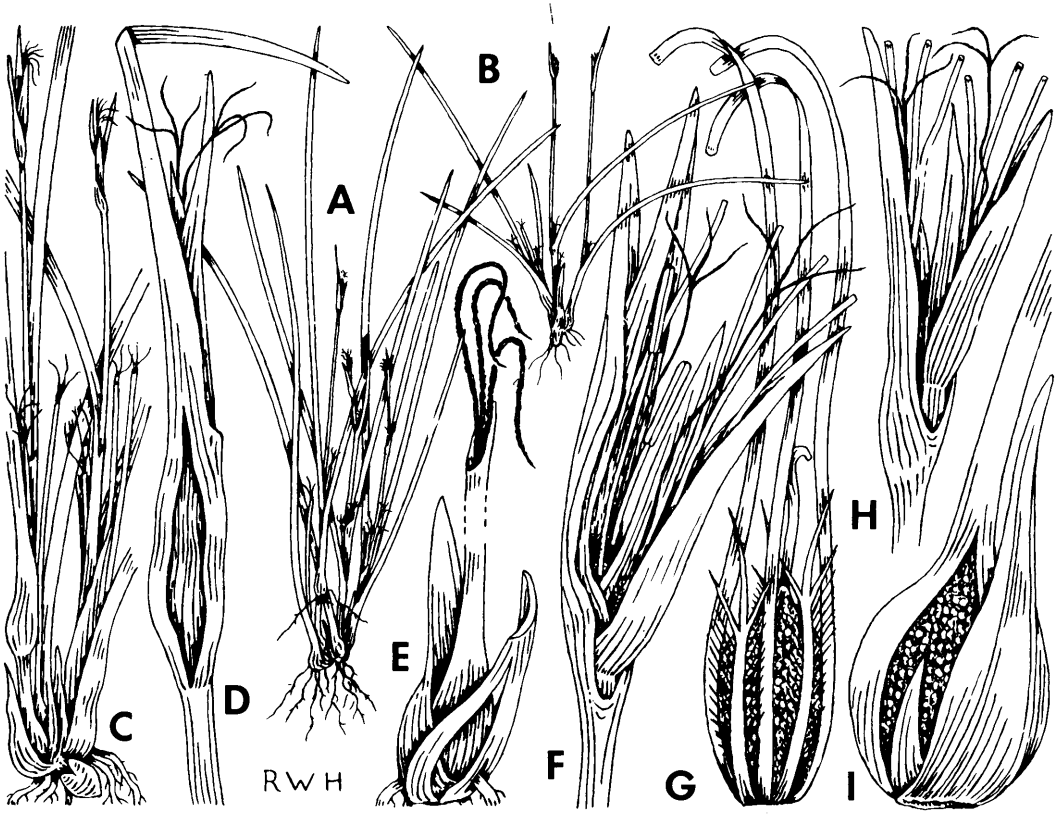


Fig. 1. *Trianoptiles solitaria* drawn from Lye 6697, Rondebosch, Cape Province, S. Africa. – A, B: Habit. – C: Culms and basal flowers, with the achene case from which the seedlings grew. –D: Aerial inflorescence in fruit, the basal glume split. – E: Basal spikelet. – F: Aerial spikelet with 4 glumes. –G: Flower in fruiting stage with perianth and filaments. – H: Aerial spikelet with 3 glumes, the lowermost fertile. – I: Basal fruit with its split utricular base.

of Zohary (1937) and Hylander (1946), as illustrating a possible way by which amphicarpy can be developed and as a basis for reconsideration of the disputed spikelet structure in Rhynchosporeae.

The plant is tufted, new culms developing in the axils of the leaves of the older culms (Fig. 1A, B). The fruit from which the plant grew may be preserved as a split shell at its base (Fig. 1C). Each culm bears up to 3 foliage leaves and ends in a 2-flowered spikelet, with or without additional lateral spikelets below. Solitary female flowers are found at the plant base, their stigmas raised high above the ground surface on long styles.

The internodes at the base of the culm are more elongated than in most tufted sedges, so that the roots growing from successive nodes come to form tiers one above the other. Raynal (1967) found similar elongated basal internodes in some specimens of *Lipocarpha chinensis* and noted that they might be mistaken for stolons: "il faut se défier de prendre pour des stolons des tiges allongées verticalement ou presque". They are illustrated in a form of *Abildgaardia* (*Fimbristylis*) *hispidula* by Lye (1971 Fig. 2) and in *Pycreus elegantulus* and *P. lanceolatus* by Haines & Lye (1977). In the *Lipocarpha* Raynal (1967) ascribed their development to "un ensablement dans le lit d'un cours d'eau", the *Abildgaardia* was surrounded by windblown sand and the *Pycreus* plants were growing on silt. In *Trianoptiles* they appear to be normal formations, possibly developed in adaption to life in the rich, though temporary, turf that springs up after rains.

The aerial spikelet may have 3 (Fig. 1D, H) or

4 (Fig. 1 F) glumes, the uppermost always empty, the lowermost also empty when there are 4. The flower bases are hidden in the glumes, only the ends of the long 3-branched styles and the filaments, from which the anthers soon drop, protruding. The flower has a 3-partite perianth of flattened bristles, each bristle trifid at the tip and long-ciliate on the margins (Fig. 1 G). The achenes are elliptic, often splitting the lowest glume as they expand (Fig. 1 D), with a hard coat bearing tubercles in longitudinal rows. At fertilization, which, as usual in Cyperaceae, precedes anthesis, the perianth is poorly developed and its cilia adpressed but later it grows and its cilia spread. The fruit disarticulates with the perianth and persistent filaments remaining attached, possibly as an aid to dispersal.

The solitary female flower at the plant base is reduced to a pistil without trace of any perianth or stamens. It is closely surrounded by a long-necked utricle with an oblique opening from which the style or its 3 branches protrude (Fig. 1 E), the arrangement closely resembling that in *Carex*. Enfolding the swollen base of the utricle there is often a short wide scale, probably a prophyll such as is commonly found at the base of the lateral, as opposed to the terminal, spikelets of Cyperaceae (Haines 1966, Raynal 1971). If this is the case the utricle must be a modified glume, not a modified prophyll as in *Carex*.

When fertilised, presumably by pollen from the aerial spikelets of the same or a neighbouring plant, the basal flowers form globular achenes, heavier than the aerial fruits. Encased in their utricles and old leaf bases they stay in place even after the plant has died. The specimen shown in Fig. 1 C grew from such a fruit. The fruits at the base of each culm ripen before the aerial fruits at its apex.

Clarke found the basal fruits resulting from these flowers in *Trianoptiles capensis* (Steud.) Harv., the type species of the genus. But though he was familiar with the similar fruits in *Bulbostylis humilis* and *B. brevicaulis* and in these species described them correctly, in *Trianoptiles* he described (1898) and figured (1909) the utricle necks and bodies as "slender rhizomes" and "minute bulbils". Schönland (1922) also figured the fruits but without indicating their nature. Later writers have recognised their true nature, but usually make no mention of the utricle, which encloses the pistil so tightly that it appears to have been missed. However, Levyns (1943) describes the female spikelet as "consisting of 2–4 tightly sheathing bracts and a terminal flower, the basal portion of the spikelet subterranean, only the narrow, tubular tip of the uppermost bract and the style branches projecting".

The annual habit and reduced unisexual 1-flowered basal spikelets forming large fruits fixed in place to grow during the next wet season are typical of amphicarpous plants and can be paralleled to *Schoenoplectus lateriflorus* and *articulatus*, for example (Haines 1971, Raynal 1976). The reduction of the aerial inflorescence to one or a few spikelets with only 2 flowers in each is peculiar to the species. The early ripening of the basal fruits is common in amphicarpous species but their enclosure in a utricle is unique.

Development of amphicarpy

In most Cyperaceae the buds in the axils of the lower leaves or sheaths grow into new culms, either directly or by first forming stolons which end in new culms. The buds nearer the culm apex form inflorescence branches of the panicle or anthela as the case may be, subtended by the inflorescence bracts. An intermediate group of leaves either subtend buds which do not develop except in emergencies when the plant apex is destroyed or have no buds at all in their axils. Such an arrangement is described in, for example, *Scirpus sylvaticus* by Irmisch (1855) and Monoyer (1934) and generalised by Mora (1960) and others.

In *Trianoptiles* there are usually no empty axils (Fig. 2 A–C). Haines (1971) suggested that in amphicarpous sedges the "intermediate emergency buds" might "have become specialised to give the basicaulous flowers". But here conditions are more complex, and at the same time more easily examined as the elongation of the internodes makes dissection relatively easy even in the dry specimen.

At the base of each new culm the scales are delicate and soon wither leaving the basal flowers in their axils exposed. No new shoots form in this region but there may be two flowers, each presumably representing a 1-flowered spikelet, in a single axil.

The lowest foliage leaf (Fig. 2A–C, f^1) subtends a complex with a well developed

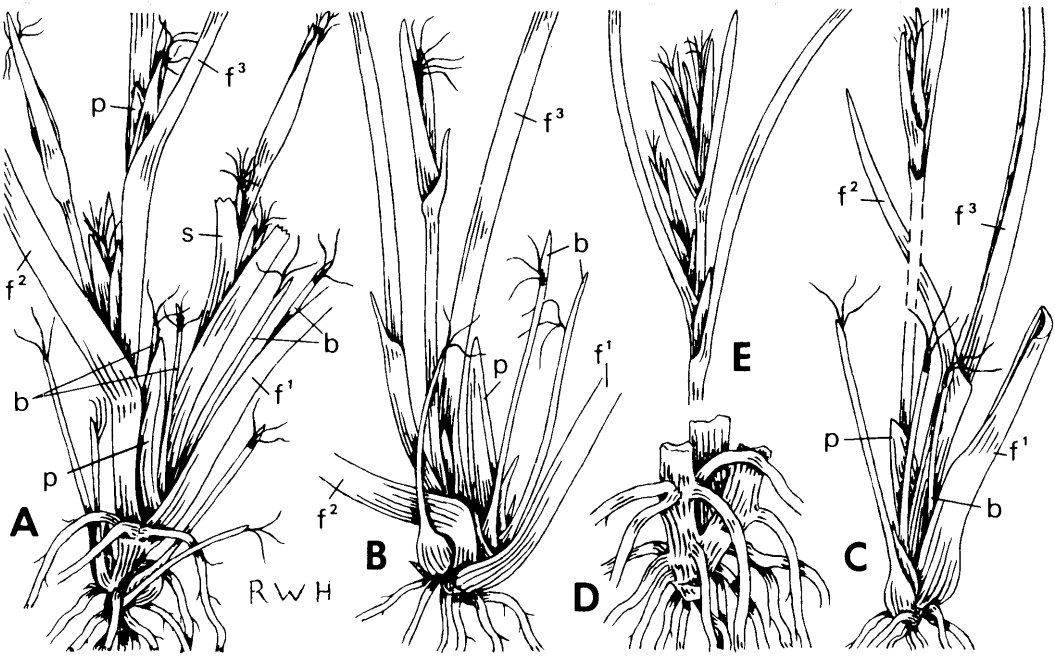


Fig. 2. Branch systems of *Trianoptiles*, the parts spread to expose the axils. – A–C: Culm bases with basal flowers and new culms. – D: Remains of a plant from a previous season. – E: Apex of a strong culm with terminal and lateral spikelets. – b basal flower; f foliage leaf; p prophyll; s leafy shoot.

prophyll (p), one or more basal spikelets (b) and, usually, a new leafy shoot (A and C, s). The second leaf (f^2) may subtend a leafy shoot, a stalked or sessile spikelet or a combination of these, but, in the material investigated, no basal type spikelet. The third and any succeeding leaves subtend only solitary sessile spikelets of an aerial type, or, in the case of the uppermost leaf of weak shoots, they may be empty.

Multiple branching in a single leaf axil is widespread in Cyperaceae. The branches may arise in succession, each from the axil of a prophyll of an earlier axis as in the inflorescence fragments of *Rhynchospora corymbosa* and *Scleria naumanniana* drawn and analysed by Haines (1966). Or the branches may arise independently, each with its own prophyll, as the pair of spikelets placed side by side or one before the other, in tandem, in *Carex utricularia* (Schulz 1887). There may be many branches in complex arrangement as in the inflorescence of *Cyperus papyrus* (Schumann 1892, Raynal 1971), and when they are crowded the prophylls may be lost as in *Schoenus nigricans* (Haines 1966). The arrangement in *Trianoptiles*, with basal flowers and new culms set together in the leaf axils appears unique in Cyperaceae and must be an extreme specialization, probably based on a less developed type of multiple budding in an ancestral species.

Spikelet in Rhynchosporeae

Since the work of Pax (1886) and Čelakovský (1887) the spikelet of Rhynchosporeae and Sclerieae has been considered to be a cymose structure or rhipidium. Each flower above the first was said to terminate an axis springing from the axis below (Fig. 3 E, F) and this produced a major distinction from Scirpeae and Cypereae where the structure was monopodial, with the flowers set laterally on a simple rachilla (Fig. 3G, H).

However, Schumann (1890) and Holttum (1948), on the contrary, found no essential difference in the spikelet structure between Scirpeae and Rhynchosporeae, describing both as being monopodial in structure. Kern (1962)

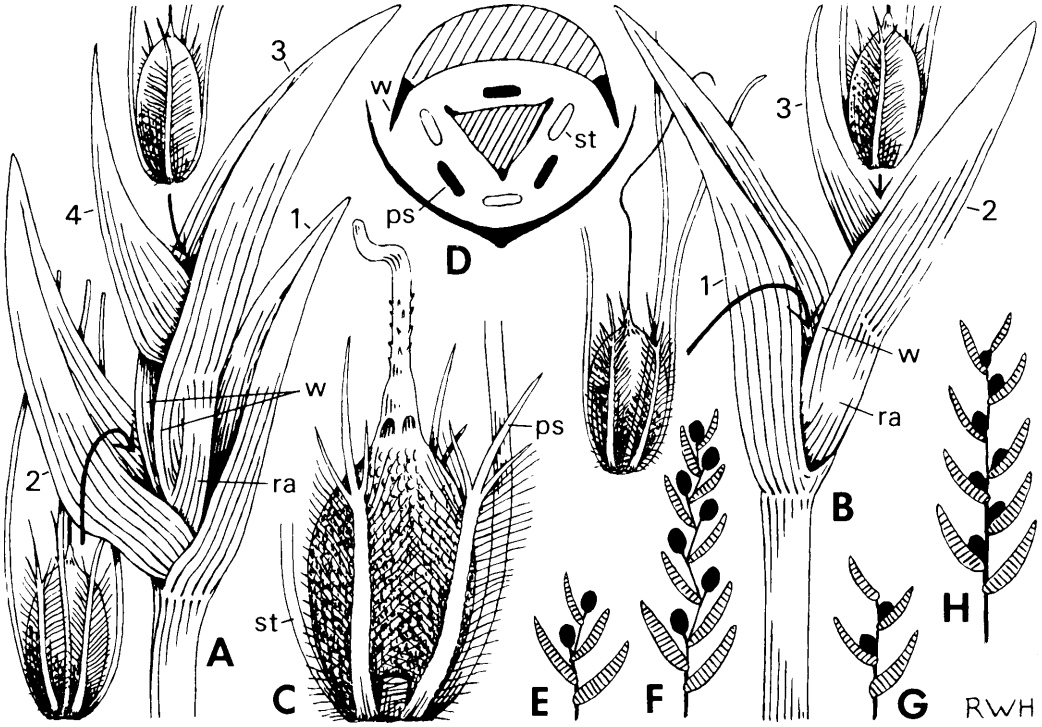


Fig. 3. Spikelet arrangement in *Trianoptiles* and other Rhynchosporeae. – A, B: Dissections of 4- and 3-glumed spikelets. – C: Fruit with perianth bristles. – D: Plan of a flower in position. – E, F: Diagrams of spikelets of cymose structure. – G, H: Diagrams of spikelets of monopodial structure. – ps perianth segment; ra rachilla; st stamen; w wing.

agreed that the spikelets were similar but described both as cymose. Haines (1966) showed in *Schoenus, Rhynchospora* and *Scleria* how each flower was enwrapped by the margins of the glume above that which subtended it, so giving a false impression that it was a terminal structure. Raynal (1971) from new evidence based on the structure of the rachilla, showed that in *Cyperus* at least the structure was monopodial.

Phillips (1951) described the aerial spikelets of *Trianoptiles* as "cymose, with 3–5 more or less distichous bracts and in most cases two perfect flowers associated with the 2 uppermost bracts". However, in reality the simple uncrowded spikelet shows the monopodial structure particularly clearly (Fig. 3 B). The lower flower is enwrapped by wing-like extensions (w) of the glume subtending the upper flower and the uppermost glume is empty.

In a 4-glumed spikelet (Fig. 3 A) the lowermost glume (1) is clearly empty. Glume 2 has a flower in its axil. The rachilla is continued (ra) with a hollow facing the flower and partly enclosing it. A pair of wings (w) are continued downwards from glume 3 along the margins of the rachilla and these help to deepen the hollow. Glume 3 subtends the upper flower which is again enclosed laterally by the wings of the empty glume 4. The flower is set with the median stamen and style-branch abaxial (C, D) as in Scirpeae and Cypereae and the 3 perianth bristles alternate with the stamens as the major segments of a *Fuirena* (Clarke 1898).

Since glume 4 is attached to the rachilla at about the same level as 3 it might be reasonable to consider the upper flower as being set above it, as stated by Phillips. But that would leave glume 3 empty, a most improbable situation. In the 3-glumed spikelet (Fig. 3 B) the arrangement is similar but the lowermost glume 1 of the 4-glumed

type is missing. The wing-like extensions of glumes 3 and 4 enwrapping the flowers below are to be found in many species of *Cyperus*, forming Kükenthal's (1936) "alae", considered by him as belonging to the rachilla rather than the glumes. They are less familiar in Rhynchosporeae.

An extension of either the cymose or monopodial system could result in a many-flowered spikelet (Fig. 3 E or G to F or H). But since E is clearly wrong for *Trianoptiles*, F is presumably wrong for Rhynchosporeae with several flowers, up to 5 in *Schoenus* (Haines 1966), over 30 in *Rhynchospora candida* (Haines & Lye 1977). Indeed it is doubtful if the cymose structure would ever have been proposed if such well developed spikelets had been examined by the earlier workers.

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Femsjonia peziziformis (Dacrymycetales) in North Europe

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Femsjonia peziziformis (Lév.) Karst. (Dacrymycetales) is treated with regard to its occurrence in North Europe. *F. peziziformis* is the only known species in this area. A detailed investigation of its morphology has been made. Intraspecific and intergeneric relations are discussed. Notes on the ecology are given, and the distribution in North Europe is mapped. The species is recorded as being new to Denmark and Norway.

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The genus *Femsjonia* was established by E. Fries, who described *F. luteoalba* (Fries 1849) and named the genus after his home parish of Femsjö in Småland. Since then the genus has only appeared once in Scandinavian mycological literature (Karsten 1876). It has therefore been looked upon as being extremely rare in this part of the world. The next report concerning its occurrence in Scandinavia is given by McNabb (1965) who regards three taxa described by Karsten as being synonymous with *Femsjonia luteoalba* and the older *Exidia pezizaeformis* Lév. During the last few years the species has been collected a few times in the Nordic countries. This is also the first report of the fungus from Denmark and Norway. In Estonian SSR several collections have been made during the last three decades (Fig. 5).

Outside Europe two other species have been described, viz. *F. orientalis* Kobay. (Kobayasi 1939 p. 217) and *F. pezizoidea* (P. Henn.) McNabb (McNabb 1965 p. 226). *F. natalensis* Cooke and *F. radiculata* (Fr.) Martin are species excludendae (McNabb 1965 p. 227).

Femsjonia peziziformis (Lév.) Karst.

Karst., Bidr. Finl. Nat. Folk 25 (=Mycologia fennica 3): 352, 1876. – *Exidia pezizaeformis* Lév., Ann. Sci. Nat. Bot. III, 9: 127, 1848.

Femsjonia luteoalba Fr., Summa Veg. Scand. II: 341, 1849. – Neotypus Eriksson & Jacobsson 19602.

Dacrymyces mesentericus Karst., Finl. Basidsv. 459, 1889. – Lectotypus Karst. 1556.

Dacrymyces radicellatus Karst., Hedwigia 29: 178, 1890. – Holotypus Karst. 1559.

Ditiola conformis Karst., Fungi Fenn. Exs. 629; Not. Sällsk. F. Fl. Fenn. Förh. 13 (=Symb. Myc. Fenn. 2): 223, 1873. – Lectotypus Karst. 1554.

Dacrymyces conformis (Karst.) Neuh., Ark. Bot. 28 A(1): 44, 1936.

Fruitbodies single or gregarious, often confluent, sessile or with a short stalk, when fresh mostly 5 to 10 mm in diameter, sometimes larger, at first circular, pustulate to discoid, convex, plane, or slightly concave. Old fruitbodies more irregular (Figs. 1, 2A, B), bright yellow when young, darkening to dull or brownish yellow when old, fleshy to firmly gelatinous; hymenium at first even and smooth, in old specimens more or less wrinkled (Fig. 2A); underside white in young fruitbodies, dull yellow in old ones. *Hyphal system* monomitic, hyphae fibulate (Fig. 3F, G), in the tramal part of the fruitbody thinwalled, 2–3

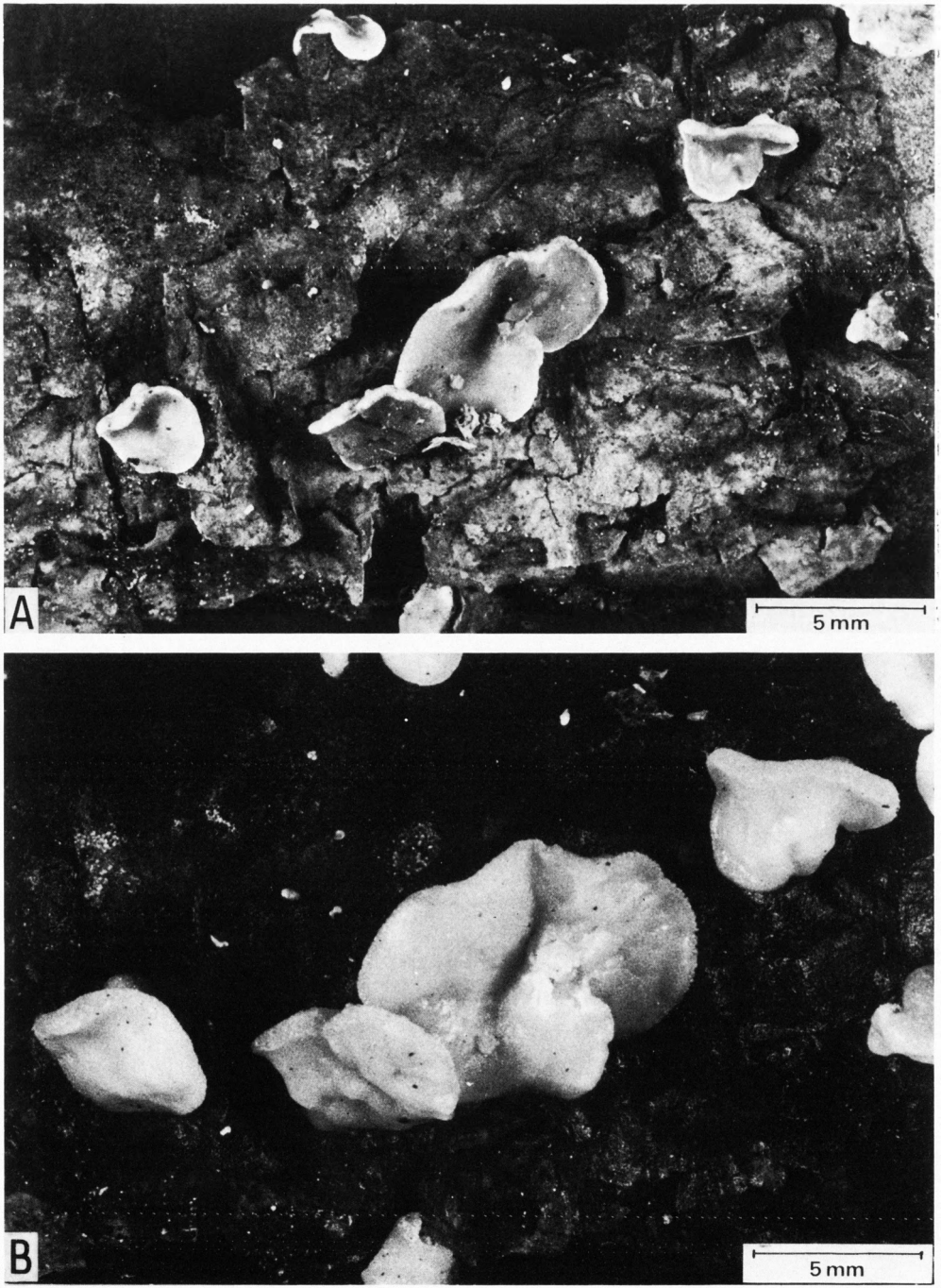


Fig. 1. Fruitbodies of *Femsjonia peziziformis* on *Pinus sylvestris*. – A: Dry specimens. Note the pezizoid shape. – B: The same specimens in wetted state. The fruitbodies have swollen considerably. – Coll. Sunhede 6695. Photo: S. Sunhede.

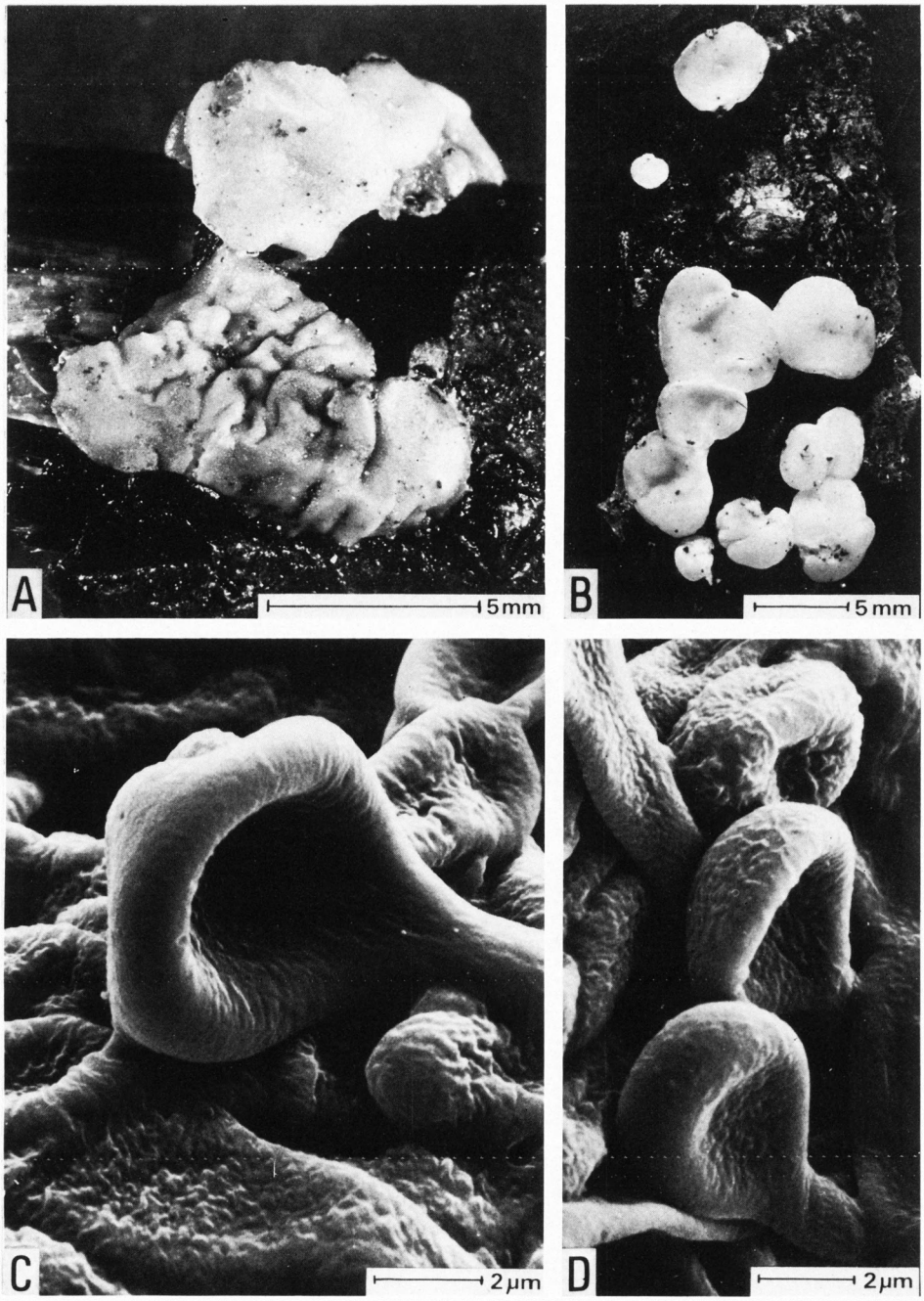
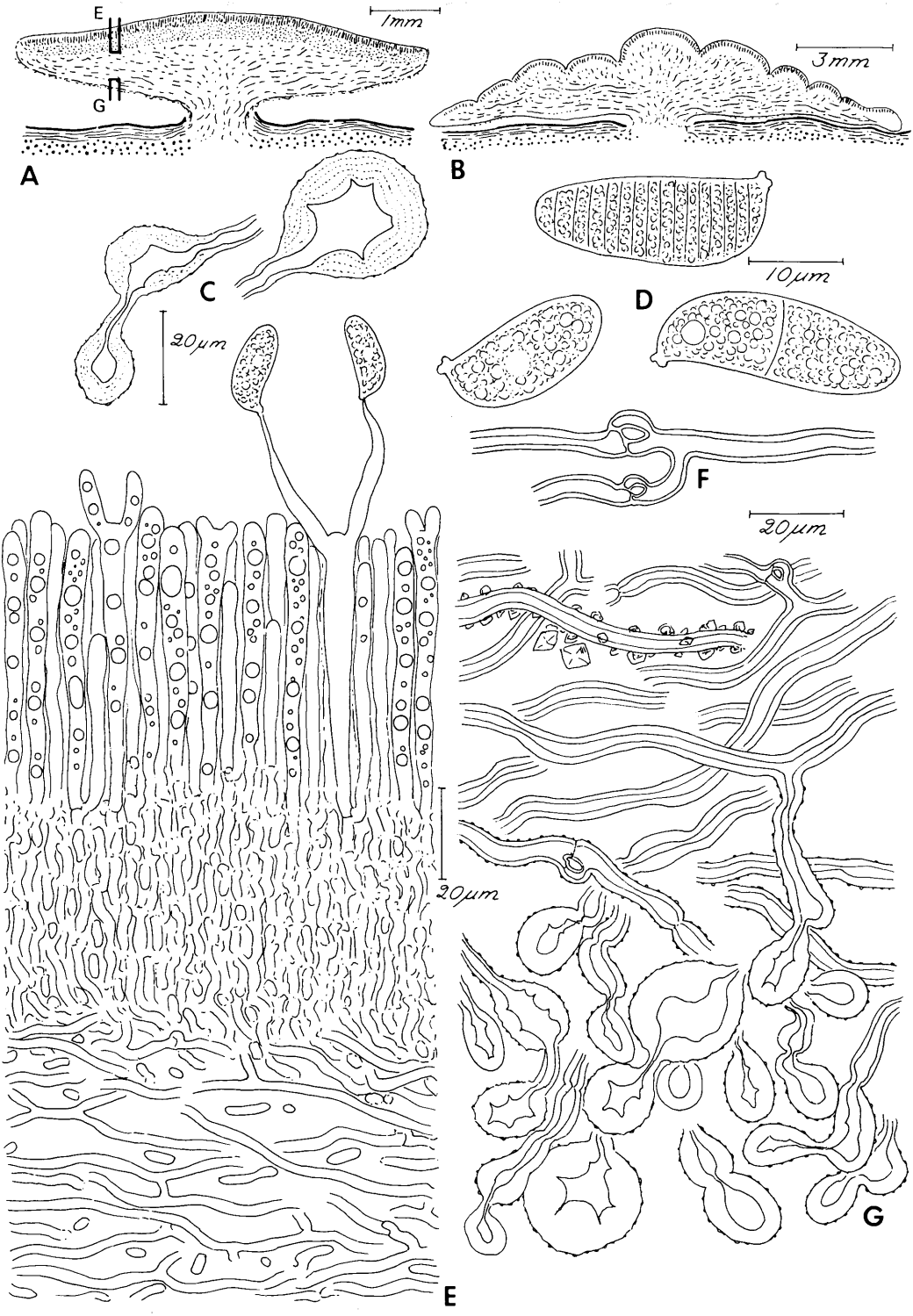


Fig. 2. *Femsjonia peziziformis*. – A: Two fresh fruitbodies on a branch of *Corylus avellana*. Note the wrinkled surface of the lower specimen. Coll. Hallingbäck 19603. – B: Both separate and coalescing pezizoid, fresh fruitbodies on a fallen branch of *Quercus*. Coll. Eriksson & Jacobsson 19602. – C, D: SEM-pictures of hyphae from the underside of a fruitbody. C shows one and D three clavate–globose apices of hyphae, all more or less collapsed. Also note the rough, wrinkled or finely tuberculate surface of the hyphae. – Photo: S. Sunhede, T. Hallingbäck & L. Ryvarden.


E
G
1mm
A
3mm
B
C
20µm
10µm
D
F
20µm
20µm
E
G

μm wide, richly branched, arranged more or less parallel, in the subhymenium densely united; hyphae of the white cover of the underside coarser, c. 4–5 μm wide, with thick, gelatinous walls, often encrusted with small grains in mature specimens (Fig. 3G), apically swollen into more or less isodiametric, thickwalled cells with a rough, wrinkled or finely tuberculate surface (Figs. 2C, D, 3G). *Basidia* first cylindrical, then slightly clavate, 65–100 μm long, sometimes more, 5–6 μm wide, with numerous yellow oil-drops in the protoplasm and with a basal clamp; sterigmata two, stout, at first obtuse, then subulate, 25–30 μm long or more, and basally c. 4 μm wide (Fig. 3 E). Basidia in mature specimens forming a dense palisade. No specially differentiated sterile hyphae elements (paraphysoids, dikaryophyses) were observed. The sterile hyphae seen between the basidia are rather young hymenial hyphae, participating in the basidium production (Fig. 3 E). *Spores* narrowly ellipsoid, broadly subcylindrical or slightly suballantoid, usually broader towards the base, mostly 25–32 × 8–10 μm but rather variable in size and shape (Fig. 4), thinwalled, smooth, non-amyloid, non-cyanophilous; in microscopical preparations made from hymenial parts several spores septated by thin parallel septa into 2–16 cells (Figs. 3D, 4); spores in the sporeprint studied were non-septate; when these spores were placed in a drop of water most of them became 2–16-septate after 30 hours and initials of germ conidia could be seen, after 48 hours a few developed germ conidia were observed (Fig. 4 B, K), the largest ones being ellipsoid, ab. 2 × 1 μm, and filled with yellow oil. One spore attached to a fruitbody was found to have produced numerous oblong conidia (Fig. 4C), reaching a size of 3.5 × 1.5 μm, all conidia developed from the convex, abaxial side of the spore.

Femsjonia peziziformis is easily recognized by its conspicuous discoid, bright yellow fruitbodies with white undersides and by its large spores. It looks very much like a Discomycete, e.g. a large species of *Helotium*. It is reminiscent of the closely related genus *Ditiola*, but the fruitbodies are wider and not so obviously stalked. In *Ditiola* fruitbodies are produced in large numbers, often in hundreds, whereas in *Femsjonia* they occur in a much smaller number or even singly.

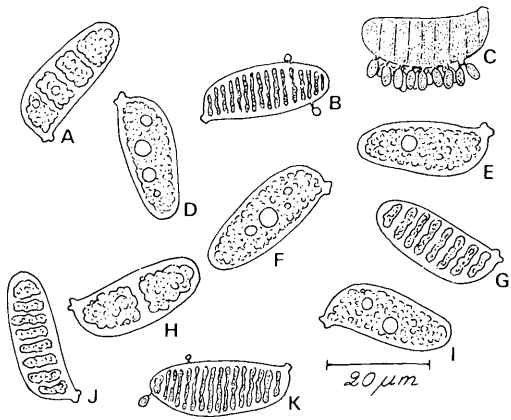


Fig. 4. Spores of *Femsjonia peziziformis*. – A–K: 1-, 2-, 4-, 8-, and 16-celled spores. – B, K: Two 16-celled spores with two young conidia each. – C: Spore with several oblong conidia, all from the convex, abaxial side of the spore. – Del. J. Eriksson.

History and taxonomy

The fungus was described by Fries (1849) and for a long time it was known as *Femsjonia luteoalba*. However, there was a species described earlier by Léveillé (1848) as *Exidia pezizaeformis*. Karsten (1876 p. 352) referred it to the genus *Femsjonia* Fr. Bourdot & Galzin (1928 pp. 71, 72) considered *Femsjonia luteoalba* and *F. pezizaeformis* as distinct species. The former was characterized by aseptate spores and by growing on deciduous wood as *Betula, Prunus padus* and *Quercus*. The latter was said to have 12–24-septate spores and to grow on coniferous wood. Later Bourdot (1932 pp. 206, 207) described the spores of *F. luteoalba* as 5–10-septate and those of *F. pezizaeformis* as multiseptate. McNabb (1965 p. 226) expresses a different opinion: "As the spores of *F. peziziformis* are tardily septate, it is doubtful whether these distinctions

Fig. 3. Microanatomy of *Femsjonia peziziformis*. – A: Section through fruitbody, showing position of the Figs. E and G. – B: Section through old fruitbody with wrinkled hymenium. – C: Cellular hyphal apices from the underside of the fruitbody. – D: Spores, 1-, 2-, and 16-celled. – E: Section through part of the hymenium with basidial palisade, subhymenium, and tramal hyphae. – F: Part of hyphae from the underside of the fruitbody. – G: Section through hyphal layer on the underside of the fruitbody. – Coll. Dissing & Sivertsen 7.IX. 1973. Del. J. Eriksson.

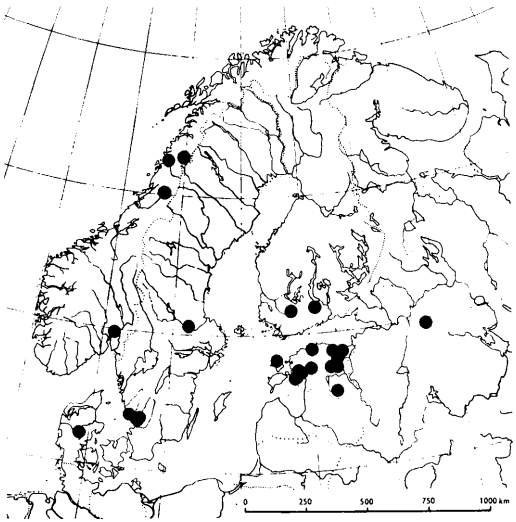


Fig. 5. Known distribution of *Femsjonia peziziformis* in North Europe.

can be maintained, and I prefer to regard Bourdot and Galzin's two species as different-aged collections of a single species."

Léveillé (1848) wrote the epithet *pezizaeformis,* which, however, according to the International Code 1972 art. 73 should be considered to be an orthographic error and should be changed to *peziziformis*. This change was made by McNabb (1965).

As to the generic arrangement with *Femsjonia* as a separate genus, we do not want to make any definite decisions, but we are of the opinion that the genera *Dacrymyces, Ditiola* and *Femsjonia* are very close to each other. The large spores and the general appearance of *Femsjonia peziziformis* make the species easily recognizable but these differences are hardly acceptable for generic separation. Another difference from *Ditiola* is the cellular swellings in the apical part of the sterile hyphae, which as a rule cover the exterior of the fruitbody in *F. peziziformis* (Figs. 2C, D, 3G). The exterior of the fruitbodies of *Ditiola* is also white, composed of coarse hyphae, similar to those in *F. peziziformis* but without the apical swellings. Moreover the hyphae of *Ditiola* are non-fibulate. Whether or not these differences can be looked upon as sufficient for generic separation is a matter for future discussion.

As there seems to be no authentic material left of *Femsjonia luteoalba* Fr. we designate the collection Eriksson & Jacobsson 19602 as the neotype of *Femsjonia luteoalba* Fr. This collection of many well developed fruitbodies is from the same geographic region as the original specimen from Femsjö.

Ecology and distribution

All North European specimens, except for three on *Pinus,* have been found on various deciduous woods, viz. *Alnus incana* (3 specimens), *Betula pubescens* (1), *B. verrucosa* (1), *Betula* sp. (17), *Corylus avellana* (2), *Quercus petraea* (1), and *Quercus* sp. (1). There seems to be no material left from Fries but he notes "Trunc. Betulae ad Femsjö" (Fries 1849 p. 341). All specimens have been found on twigs and trunks of decaying wood.

F. peziziformis is able to grow under very varying climatical conditions, e.g. in the mild, humid climate of Jylland, the oceanic climate of Central and Northern Norway, and the rather continental climate of East Norway, Central Sweden, Estonian SSR and South Finland (Fig. 5). Most of the specimens (26) were collected during August–December but there was also one collection in May. In spite of its rather conspicuous appearance few collections of *F. peziziformis* have been made in North Europe (except for Estonian SSR) indicating that the fungus may be rare at least in some regions. The collections are scattered and there is no definite distributional pattern (Fig. 5). For the distribution outside North Europe see i.a. Martin (1952), McNabb (1965) and Raitviir (1971).

Collections

The herbarium abbreviations are in accordance with Holmgren & Keuken (1974). The Swedish specimens are in the private herbaria of the authors in Göteborg; the Estonian specimens are in TAA, the Finnish ones in H. When possible the specimens are cited from south to north in each country, except for Estonian SSR.

Denmark: Jylland, Aarhus amt, Hörby lunde on *Quercus petraea* 1.X. 1950 B. & J. Eriksson 5004 (UPS).

Finland: Tavastia australis, Tammela, Mustiala, on *Betula* 20.XII. 1865 Karsten 1556; on *Betula* 4.V. 1872 Karsten 1558; on *Betula* 18.IX. 1894 Karsten 1553 – Tammela, Mustiala, Särkjärvi, on *Alnus incana* 20.IX. 1867 Karsten 1552, 1554 – Tammela, Mustiala, Salois, on *Betula* 19.IX. 1890 Karsten 1559 – Hollola, Tiirismaa, on *Betula* 1889? Wainio 1555.

Norway: Oslo, Østmarka, Sølvdobla, on *Betula* 9.IX.

1956 Eftestøl (O) – *Nord-Trøndelag,* Namnsskogan, on *Betula* 24.XII. 1974 Tønsberg (O) – *Nordland,* Rana, – Utskarpen, on *Betula* 12.IX. 1976 Torkelsen 773/76 (O) Rana, Lasken, Rundfjell, on *Betula* 7.IX. 1973 Dissing & Sivertsen (TRH) – Rana, Ørtfjellmoen bro–Rundfjell, on *Betula* 9.IX. 1975 Sivertsen (TRH).

Sweden: Halland, Breared parish, Askarebygget, on *Corylus avellana* 16.XI. 1975 Hallingbäck 19603 – *Småland,* Femsjö parish, "Betulae ad Femsjö" (Fries 1849 p. 341) – *Halland,* Tvååker parish, Sibbarp, on *Quercus* sp. 16.X. 1975 Eriksson & Jacobsson 19602 – *Dalarna,* Garpenberg parish, Garpenbergs gård, on *Pinus sylvestris* 29.VIII. 1974 Sunhede 6695.

Estonian SSR: Distr. Haapsalu, Kulli, on *Betula* 14.VIII. 1960 Raitviir – Virusaar, on *Corylus avellana* 10.X. 1958 Parmasto – *Distr. Harju,* Vikipalu, on *Betula* 14.XI. 1959 Raitviir – *Distr. Hiiumaa,* Tahkuna, on *Betula* 1.IX. 1960 Raitviir – *Distr. Jõgeva,* Enniksaare, on *Betula* 30.IX. 1958 Kalamees – Kurista, on *Betula* 3.X. 1960 Kalamees – Voore, on *Betula verrucosa* 17.IX. 1970 Parmasto – *Distr. Pärnu,* Avaste on *Betula pubescens* 9.IX. 1952 Parmasto – Eidapere, on *Betula 17.X. 1959 Raitviir – Distr. Rakvere,* Jõetaguse, on *Alnus incana* 7.VIII. 1961 Kalamees – Põlula, on *Betula* 11.VIII. 1958 Raitviir – *Distr. Võru,* Sõmerpalu, on *Pinus sylvestris* 19.IX. 1952 Parmasto.

Russian SSR: Distr. *Tikhvin* (Leningrad region), Rugui, on *Pinus* 20.VIII. 1961 Bondartseva (TAA). – One specimen (in H) from the Kola region cited by Karsten as *Ditiola conformis* is *Dacrymyces* sp.

Acknowledgements. We are indebted to the directors and curators of the following herbaria for loan of specimens: H, O, TAA, TRH, and UPS. We are most grateful to Dr J. Lepiksaar, Göteborg and Dr A. Raitviir, Tartu, who have helped us with the mapping of the Estonian localities, to Professor J. A. Nannfeldt, Uppsala for reading the manuscript and to Professor Å. Fridh, Göteborg for discussions on Latin orthography.

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Botanical literature

Jacobsen, H. 1970: *Das Sukkulentenlexikon*. 589 pp, 1063 figs. Gustav Fischer, Jena. Price DM 48:– (cloth).

Although this standard work has been on the market for a number of years, as yet it has not received attention in this journal. It deserves to be mentioned as a useful dictionary of succulent plants, covering about 6,500 species belonging to 355 genera of various families. Only the cacti are excluded, being similarly dealt with in Backeberg's well-known 'Kakteenlexikon'.

The contents have been condensed in order to be accommodated in a single volume. The essential information given includes short descriptions, indications of origin, and hints about cultivation. Larger genera are provided with keys to sections and species.

The extensive list of synonyms at the end may give the impression of a critical treatment throughout, but this is naturally not the case. Where most genera are concerned the author simply lists species in alphabetical order without attempting to evaluate their taxonomic status.

The work claims to cover all succulents (except cacti) described prior to 1970. Irrespective of the hazards of definition however, it must be stated that the coverage is far from complete. Many genera, which have not been subject to recent revision, are quite stepmotherly treated. Take one example from the succulent Liliaceae, only 14 species of *Bulbine* are listed, which is less than half the number of species described. Among the succulent Compositae *Othonna* can be mentioned as a taxonomically intricate and as yet unrevised genus, and many omissions and inconsistencies can also be noted here.

The problem of defining a succulent has been referred to above. Considering the rather incomplete coverage of truly succulent genera, one is surprised to find *Welwitschia* (although with an apology) represented, as well as a number of halophytes lacking horticultural interest. Also, the inclusion of certain bulbous plants seems quite arbitrary (e.g., *Ammocharis, Haemanthus, Litanthus*), as the majority of well-known bulbs are not treated (*Agapanthus, Allium, Lilium, Urginea*, etc.).

Apparently the book should be used with great caution. There are also inconsistencies in the phytogeographical information. In many cases the distribution area is roughly outlined, but all too frequently only the type locality is cited, which may give a false impression where the range is concerned.

The large and phytogeographically important genus *Zygophyllum* is remarkably maltreated. The distribution of the genus is given as the Canary Islands, and the only species mentioned is *Z. fontanesii*.

Unfortunately the nomenclature is not always in accordance with the rules. Some proposed new taxa are apparently not validly published due to the lack of Latin diagnoses, e.g. the new sections and subsections of *Cotyledon*.

The illustrations are mainly black-and-white photographs of cultivated plants. They are plentiful and useful, but not all of them are beautiful.

The above may suffice to warn the reader about uncritical digestion of the contents of this nevertheless impressive work. In spite of numerous errors and shortcomings, the book is a useful source of information and a handy tool for quick reference on a vast subject.

Bertil Nordenstam

Löve, A., Löve, D. & Pichi Sermolli, R. E. G. 1977: Cytotaxonomical atlas of the Pteridophyta. XVIII + 398 pp. J. Cramer, Vaduz. ISBN 3-7682-1103-7. Price DM 150:–.

For many years cytological data on the Pteridophyta have been scattered in several compilations, making it necessary to look up at least 8 sources for information about a particular taxon. This has made the search for information on this group rather inconvenient and time-consuming. Chiarugi's and Fabbri's works have long proved their value as sources of information of this kind, but the rapid accumulation of data since their publications has greatly increased the need for a modern synthesis. The Chiarugi and Fabbri chromosome tables might stand as models for such a work, although one could wish that information on the geography of counted specimens had been added.

Now Löve, Löve & Pichi Sermolli's *Cytotaxonomical atlas of the Pteridophyta* has been published. It deviates in principle and detail from Chiarugi's and Fabbri's works. The points of criticism are too numerous to be dealt with in detail. A few examples of the types of error in which this book abounds will have to suffice.

The authors deliberately exclude hybrids and supposedly incorrect counts although the critieria for exclusion of counts are not clear. Publications before Anno Mantoni (1950) have been omitted unless their information fits in with the classification of the atlas. At the same time many later undocumented counts are included although in my opinion they strongly need reassessment.

Taxa have been arranged according to a forthcoming classification, to be published in *Webbia* by Pichi Sermolli. It represents an extreme splitting into families and genera. This is not the place to discuss classification, but it must be mentioned that the names of original publications have not been followed. Taxa have been distributed according to the new system with the necessary new combinations. The original identification is brought among other synonyms. In some cases the synonymy is incorrect e.g. *Phlegmariurus taxifolius* (Sw.) Löve & Löve is a Tropical American species, not Indian as is the cytologically examined plant quoted. The latter was identified as *Lycopodium hamiltonii* var. *petiolatum* (*Lycopodium taxifolium* Spring nom. non val.)

Sometimes chromosome numbers alone, even very approximate ones, seem to have determined the grouping of species. Thus *Lycopodiella caroliniana* is cited as $2n = 78$, in line with the supposed $x = 13$ of this genus. *Lycopodium meridionale* is cited as $2n = c.\ 138$ which is made to correlate with $x = 17$ of *Lycopodium*. Far from being members of two different genera these two species are very closely related, perhaps even conspecific, and the actual number is now known to be $n = 35$ or multiples.

All counts have been cited as somatic numbers, although the majority of counts were made from meiotic material. All meiotic counts except those of known agamosporous species have simply been doubled for the sake of uniform citation. Since meiotic and somatic counts of agamosporous ferns are equal, this practice is a source of error because of the probability of undiscovered agamospory among the cited taxa.

The citation of counts is not always faithful, e.g. Manton 1950 indicated "2n = at least 260" for *Lycopodium selago*. This is cited in the *Atlas* as c. 264.

The practice of giving the supposedly correct number for each species in addition to actual counts is superfluous in most cases, whilst in other cases it is potentially misleading. Misinterpretations of approximate counts have been the cause of taxonomically wrong conclusions as for example the instance of *Lycopodium meridionale* already mentioned. In *Palhinhaea cernua* (*Lycopodium* among friends) it requires a strong faith to find the suggestions of $2n = 208, 260, 338$ and 416 convincing as supposedly correct numbers, considering the actual cited counts were 208, 220, 272, c. 330, c. 340, and 416.

The derivation of base numbers presented are often confusing or directly misleading, especially where aneuploid evolution is involved in a group of genera. Thelypteridaceae forms a natural evolutionary group, the lowest meiotic numbers of which form an almost complete aneuploid series 27–36. In the atlas the lowest meiotic number has been given in brackets as a secondary base number in some genera, but not in all. All numbers except prime numbers of the series have been divided to give a lower possible base number. This results in a base number series of 7, 9, 12, 15, 17, 29, 31, which does not make sense without excessive mental acrobatics. The calculations of base numbers seem rather arbitrary.

In Thelypteridaceous genera with n = 36 and multiples, 12 was chosen as the base number although it could equally well be 9 (or 3, 4, 6, or 18!).

The literature references for Lycopodiaceae are seriously confused. I have not been able to check them all, but in the first ten pages I found 10 errors, all referring to counts by Löve & Löve! A count of *Lycopodium selago* was omitted from the book as stated in the introduction p. xi. Later on page 4 the same reference was used for *Lycopodium clavatum*.

I have only examined here Lycopodiaceae s. lat. in detail, but random samples from the rest of the book leave little hope that it is better.

In conclusion it should be said that this book does not meet the need we have for a modern compilation. There are too many omissions, misquotations, misstatements, and misjudgements to be excused, and as a result we still have to check all the same references as before. It is feared that this book will have a harmful influence on future work on the Pteridophyta. It should never have been published.

Benjamin Øllgaard

Sybenga, J. 1975: *Meiotic configurations. A source of information for estimating genetic parameters*. 251 pp. Springer-Verlag, Berlin, Heidelberg, New York. ISBN 3-540-07347-7, 0-387-07347-7. Price DM 68:– (clothbound).

The present volume is the first of a planned series of monographs on theoretical and applied genetics from Springer's publishing house. Several branches of genetics covered by the series are of interest to many plant taxonomists, for example evolutionary genetics, population genetics, ecological genetics, biometrical genetics and cytogenetics.

Sybenga's book is devoted to the quantitative analysis of observations on meiotic configurations with emphasis on their bearing on recombination. The author presents numerous mathematical formulae, diagrams and photomicrographs to help the reader to obtain the maximum amount of information from the slides.

For practical reasons the analysis of crossing-over is dealt with first. Observations at different levels of resolution are taken into account, ranging from direct and exact determination of number and location of chiasmata and of the chromatids involved in specified chromosomes, to indirect estimation of recombination from bivalent number. In the latter case the chiasma frequency can only be inferred from the number of "bound" chromosome arms. The effects at different meiotic stages of structural and numerical deviations are analysed in detail.

Analysis of chromosome pairing is largely dependent on the availability of satisfactory models, since it is rarely possible to observe actual pairing direct. A number of such models are described and applied to various cases, and their merits and shortcomings discussed.

The last part of the book is devoted to the analysis of chromosome orientation and segregation.

The cytogeneticist, or the taxonomist using cytogenetic methods, will certainly gain much from a study of Sybenga's book. Not only will it enable more relevant conclusions to be drawn from the observations but I am also convinced that the researcher will actually see more than before on his slides, after he has been made more aware of the meaning of the microscopically observable features of meiotic configurations.

Anna Weimarck

Cramer, J.(ed.): *Bibliotheca Lichenologica*. A series of original papers and reprints of books on lichens.

1. Hannemann, B. 1973: *Anhangsorgane der Flechten*. Ihre Strukturen und ihre systematische Verteilung. IV + 123 pp., 3 tables, 181 drawings and microphotographs. J. Cramer, Lehre, Germany. Price DM 50:– (paperbound as the following volumes).

2. Awasthi, D. D. 1975: *A monograph of the lichen genus Dirinaria*. IV + 108 pp., 16 distribution maps, 59 figures in 15 plates. Gantner Verlag, Vaduz, Liechtenstein. ISBN 3-7682-5452-6. Price DM 40:–.

3. Wunder, H. 1974: *Schwarzfrüchtige, saxicole Sippen der Gattung Caloplaca (Lichenes, Teloschistaceae) in Mitteleuropa, dem Mittelmeergebiet und Vorderasien*. II + 186 pp., 9

plates. J. Cramer, Lehre. ISBN 3-7682-0924-5. Price DM 40:–.

4. Jürging, P. 1975: *Epiphytische Flechten als Bioindikatoren der Luftverunreinigung, dargestellt an Untersuchungen und Beobachtungen in Bayern*. II + 164 pp., 43 maps, diagrams and tables. Gantner Verlag, Vaduz. ISBN 3-7862-0964-4. Price DM 50:–.

5. De Wit, T. 1976: *Epiphytic lichens and air pollution in the Netherlands*. 115 pp., 114 maps, diagrams and tables. Gantner Verlag, Vaduz. ISBN 3-7682-1059-6. Price DM 60:–.

The various series of botanical works issued by the publisher J. Cramer during the last few decades have included several papers on lichens. *"Dissertationes Botanicae"* is a collection of theses for the Ph.D. degree. Some of them deal with lichenology, viz. No. 4, G. Eigler, *Studien zur Gliederung der Flechtengattung Lecanora* (1969), No. 9, K. Kalb, *Flechtengesellschaften der vorderen Ötztaler Alpen* (1970) and No. 17, V. Wirth, *Silikatflechten-Gemeinschaften im ausseralpinen Zentraleuropa* (1972). The upsurge of interest in lichens during the last few years has resulted in a special series *"Bibliotheca Lichenologica"*.

Anhangsorgane der Flechten is an account of the morphology of the appendix organs of lichens and an effort to use these in taxonomy. The paper has been presented as a Ph.D. thesis at the Free University of Berlin under Professor J. Poelt. The authoress has devoted much attention to the terminology of rhizines, hairs, holdfasts, etc. including a detailed survey of the extensive literature. Many of these organs attach the lichen to its substrate, whereas others have no apparent function.

The terms met with in previous works, for instance by Lindau and Frey, have often been used in different senses. Instead of defining the existing terms the authoress has sometimes preferred to create new ones, such as "Rhizopten", "Rhizohyphen" and "Lichenorhizen". In the reviewer's opinion, the result of this procedure is that the present complex terminology has become still more chaotic.

The concluding chapters contain a comprehensive survey of the lichen system with a discussion of the availability of the appendix organs as auxiliary taxonomic characters.

The majority of the lichen species now referred to the genus *Dirinaria* have mostly been recognized as a subgenus or section of *Physcia*. With the delimitation given in the monograph by Dr D. D. Awasthi (Lucknow, India) it seems to be a well-defined genus in the Physciaceae.

26 species are recorded. 4 species and 4 varieties or forms are described as new. A great many taxa have been recombined. The author has been successful in finding material suitable for lectotypification of all relevant taxa except *D. applanata* and *D. confluens*. In these two cases neotypes have been proposed.

The accepted taxa are fully described together with fairly detailed lists of specimens seen. The taxonomic revision is preceded by brief general chapters on history, morphology, chemistry, ecology, etc.

Dirinaria is a pantropical genus extending to eastern North America, South Africa, eastern Australia and Japan. No species occur in Europe. Distribution maps are provided for all 26 species.

The cosmopolitan genus *Caloplaca* (incl. *Blastenia*) is one of the largest lichen genera including about 500–600 species. Some groups have been studied recently but like many other genera of crustose lichens it is badly in need of a monographic revision.

The present study by Dr H. Wunder was initiated by Professor J. Poelt and has been used as Ph.D. thesis at the Free University Berlin. It has a limited scope treating mainly the *Caloplaca variabilis* group, i.e., saxicolous species (mainly on calcareous rocks) with black apothecia. 8 species are recognized and described in detail, some of them with varieties. The author has seen about 1,600 collections from the major Herbaria in Europe, but only a selected number of stations are quoted.

The numerous taxa described by various authors have been carefully checked. Lectotypes have been selected in almost all cases, and no less than 22 species and 26 varieties are placed in synonymy. Some taxa are recombined. The well known species *C. variabilis* has been neotypified as no type material referable to Persoon has been traced. 3 species described by Hue and probably belonging to this group have been omitted as no types were available in Paris (PC). In the experience of the reviewer most of Hue's

material, even from his last years, can be found in PC. However, this requires a personal visit to the Paris Herbarium and a good portion of patience and luck.

The author explicitly states that the group does not constitute a natural unit. In addition, he also treats two species from the *ferruginea* group, which normally have rusty-red apothecia sometimes changing to blackish-brown or black.

The influence of polluted air on the lichen vegetation has been studied for more than a century. The literature on this topic has been exceedingly abundant during the last few decades. A comprehensive survey of the various kinds of research carried out in this field was presented in 1973 under the title of *"Air pollution and lichens"* (ed. Ferry et al.). Cf. review in Bot. Notiser 1974 p. 155.

Many years ago Arnold (*Zur Lichenenflora von München,* 1891–1901) drew attention to the fact that various species of lichens are lacking or are on the decline in the central parts of Munich. The recent work by Dr P. Jürging (Lehrstuhl für Landschaftsökologie, München) gives a broad account of the "air hygienic" situation in the Munich area during the past decade. Following Sernander's classical terminology he has distinguished several zones, viz. "Flechtenwüste", "Innere Kampfzone", "Mittlere Kampfzone", "Äussere Kampfzone" and "Normalzone". His map from 1968 has been followed up by later studies from 1973–1974 showing that certain species of foliose lichens recorded as extinct have reappeared owing to improved air conditions in the central part of the city. The map from 1968 should be compared with maps showing the precipitation of dust and the emission of sulphur dioxide in the same area and at the same time.

Fumigation experiments were performed in nature using some of the most important pollutants, viz. SO_2, HCl, HF, NH_3 and CO. The techniques used and the damage caused to the relevant lichen species are discussed in some detail.

The author has studied the behavior of certain epiphytic lichen species in areas with varying pollution. He has mainly chosen foliose lichens that are sensitive to varying extents, e.g., *Anaptychia ciliaris, Evernia prunastri, Hypogymnia physodes, Lobaria pulmonaria, Xanthoria parietina* and several species of *Parmelia, Physcia* and *Ramalina*. It is remarkable that he draws very little attention to *Lecanora conizaeoides,* otherwise known as the most resistant lichen in polluted areas. The reason is that he seems to consider *L. conizaeoides* to be an ecological modification of *L. varia* caused by the special conditions in urban areas.

Holland is known as one of the most polluted areas in Europe. This fact has been noted in various works, not the least by Dr J. J. Barkman, the eminent specialist in the sociology of epiphytic mosses and lichens. One of his students, Dr T. De Wit, (Rijksinstituut voor Natuurbeheer, Leersum, Holland) has published a thesis which gives a comprehensive survey of the present relation of air pollution to lichen vegetation in this country.

A large number of species of epiphytic lichens on trees throughout the Netherlands have been listed using a 5 km square grid as a basis. Distribution maps of 20 lichen species are given. Comparison with data from around 1950 reveals a decline almost everywhere in the country. The area between Rotterdam and Amsterdam has become especially impoverished.

As in the preceding work results of fumigation experiments are presented. In addition to the gases used by Dr Jürging, Dr De Wit has also used C_2H_4, O_3 and a combination of SO_2 and O_3. Even low concentrations of these air pollutants cause significant morphological damage to the lichen species investigated.

Ove Almborn

Brodo, I. M. & Hawksworth, D. L. 1977: *Alectoria and allied genera in North America.* Opera Botanica 42. Stockholm. 164 pp., 1 + 67 figures and distribution maps. ISBN 91-546-0211-1. ISSN 0078-5237. Price SKr 87:– (libraries SKr 145:–).

The first attempt to provide a monograph on the North American species of the lichen genus *Alectoria* was made by Howe (1911) who accepted 10 species. Du Rietz (in a preliminary *Synopsis Lichenum,* 1926) recognized 19 species all over the world. In the following decades Gyelnik, Räsänen, Motyka and others (all notori-

ous splitters) "revised" the genus, or parts of it, in various ways. Their work resulted in the publication of numerous more or less vague and superfluous taxa. The present volume by I. M. Brodo (Ottawa, Canada) and D. L. Hawksworth (Kew, England) is a necessary clearing-up in this jungle.

There is a tendency today to divide large lichen genera into smaller perhaps more "natural" units of generic rank. Poelt et al. have segregated *Physconia* and *Physciopsis* from *Physcia* and *Heterodermia* from *Anaptychia*. Hale has recently proposed a subdivision of *Parmelia* (s. latissimo) into 10 genera. Following this trend Brodo and Hawksworth have split the old *Alectoria* into 4 genera, viz. *Alectoria* Ach. s. str. (8 species in North America), *Bryoria* gen. nov. (the name derived from *Bryopogon* and *Alectoria;* 27 species), *Pseudephebe* Choisy (2 species) and *Sulcaria* Bystr. (1 species). Useful characters for the delimitation of these genera have been found, for example, to be the cortical structure and the presence or absence of certain chemical compounds.

Alectoria s. str. comprises *A. nigricans, ochroleuca* and *sarmentosa* (with ssp. *vexillifera*), etc. Under *Bryoria,* which is divided into 5 sections, we meet with the well-known species *B. chalybeiformis, bicolor, nitidula, simplicior, implexa, fremontii* and others. *Pseudephebe* will hopefully be the permanent generic name for *P. minuscula* and *pubescens,* which for many years have vacillated between *Alectoria* and *Parmelia. Sulcaria* is represented by the new species *S. badia,* which is tentatively placed here in addition to *S. sulcata* and *S. virens,* both known from Asia only.

Alectoria nidulifera Norrl. is recorded as *Bryoria furcellata* (Fr.) comb. nov. The Friesian epithet, which is older, can be avoided under *Alectoria* as the combination *A. furcellata* exists for another species. Unfortunately, this procedure has not been possible under *Bryoria. A. jubata* is treated as a *nomen confusum* (Art. 69 in the Code of Nomenclature) and *A. prolixa* is considered a synonym of the same taxon.

Among the 38 species recorded from North America 9 are described as new. A great many combinations transferring both North American species and others to the accepted genera are made.

Each species is described in detail often with photographs and always with distribution maps. The numerous taxa described by previous workers have been carefully checked and typified which has resulted in long lists of synonyms. In addition to the maps there are fairly exhaustive lists of localities seen by the authors and represented in the major North American Herbaria.

The taxonomic treatment is preceded by comprehensive and well-illustrated chapters on Anatomy and morphology, Chemistry, Taxonomic concepts, Ecology, Distribution, and Importance to man and nature.

As many of the species treated are widely distributed in the Northern Hemisphere this monograph will also be most useful to the European reader.

The authors have worked jointly on this project since 1970. This method has been somewhat unusual among lichenologists, but has evidently many advantages. Errors and omissions caused by one author can be corrected by the other. The reviewer sincerely recommends this form of cooperation for future monographic works on lichen taxonomy.

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Phloem ultrastructure and systematic position of Gyrostemonaceae

H.-Dietmar Behnke

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The three species of Gyrostemonaceae investigated contain S-type sieve-element plastids. Starch grain morphology and occurrence was tentatively compared with data from sieve-element plastids of other members of Capparales. Similarities were found in Bataceae and Salvadoraceae. The companion cells of *Gyrostemon ramulosus* regularly include protein-containing vacuoles which by their development and contents are comparable with dilated ER-cisternae of Brassicaceae and Capparaceae. The results exclude the family from Phytolaccaceae and Centrospermae as a whole and support a position close to Capparales.

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The small family Gyrostemonaceae (5 genera, 17 species), until quite recently, has almost unanimously been allied with Centrospermae, where it was either included in Phytolaccaceae or recognized as a separate family. Early doubts with regard to the position of Gyrostemonaceae came from studies of their pollen grains which are unique among Centrospermae but in some features resembled those of Bataceae, a family also doubtfully allied with Centrospermae (Erdtman 1952, Prijanto 1970 a, b). Flower morphology also provided data emphasizing the isolated position of Gyrostemonaceae: centripetal development of stamens is not found elsewhere in Centrospermae, while the presence of rudimentary glandular stipules again finds a parallel in Bataceae (Eckardt 1971, cf. Eckardt 1976). Then, a survey on the chromosome numbers of Gyrostemonaceae established their base number to be n = 14 (Keighery 1975) which is uncommon in Centrospermae thus implying their separation from both Phytolaccaceae and the order Centrospermae as a whole.

Recently, Goldblatt et al. (1976) considered results from palynology, cytology, chemical analysis and ultrastructure of sieve-element plastids and concluded that the family should be removed from Centrospermae. The presence of glucosinolates suggested a relationship with Capparales. After carefully weighing morphological, chemical and other characters Dahlgren (1975) also favoured an inclusion of Gyrostemonaceae in Capparales or, alternatively, its placing in a closely related separate order.

Details of phloem ultrastructure have proved useful in providing additional criteria for the circumscription of higher taxa in angiosperms (Behnke 1972, 1977). In this investigation two features have been tested with regard to their possible evidence for the assignment of Gyrostemonaceae to Capparales (s.l.): (1) S-type sieve-element plastids (recorded in part by Goldblatt et al. 1976), and (2) the occurrence of dilated cisternae. The presence of glucosinolates in Capparales generally coincides with the presence of so-called myrosin cells, usually idioblasts, the vacuoles of which give a positive reaction to protein staining. In addition, dilated cisternae of endoplasmic reticulum are described for a great number of taxa from Brassicaceae and Capparaceae (Iversen 1970, Behn-

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ke 1977). Dilated cisternae occur in a few different cell types among which the most prominent are phloem-parenchyma cells and, as can be demonstrated with the transmission electron microscope, always contain protein material. Myrosin cells and dilated cisternae have both been regarded as potential sites of glucosinolate and/or myrosinase (glucosinolate-hydrolyzing enzyme) activity in capparalean plants. As glucosinolates have been recorded for Gyrostemonaceae it is appropriate to screen their phloem parenchyma for the presence of dilated cisternae.

Material and methods

Material. Gyrostemonaceae: *Codonocarpus cotinifolius* (Desf.) F. Muell., *Didymotheca tepperi* F. Muell. ex Walter (both collected in Northern Territory, Australia, by J. R. Maconochie) and *Gyrostemon ramulosus* Desf. (raised from seeds at the Botanical Garden, Copenhagen, 1976/276).

Bataceae: *Batis maritima* L. (one plant shipped from Texas and then grown at the Zoologisches Institut, Universität Heidelberg).

Salvadoraceae: *Azima tetracantha* Lam. and *Salvadora persica* L. (both from the Botanical Garden, Copenhagen).

Capparaceae: *Cleome spinosa* Jacq. (from the Botanical Garden, Bonn).

Brassicaceae: *Alyssum saxatile* L. (from the Botanical Garden, Bonn) and *Peltaria alliacea* Jacq. (from the Botanical Garden, Heidelberg).

Methods. Stem parts of the taxa mentioned were cut into longitudinal sections by hand and were immediately immersed into a fixing fluid containing a combination of formaldehyde and glutaraldehyde. Postfixation with osmic acid, dehydration with acetone, embedding and polymerisation in epoxy resins were carried out according to standard procedures. Ultrathin sections of phloem-containing parts were examined and photographed with a Siemens Elmiskop 101.

Plastids

The sieve-element plastids of the three species of Gyrostemonaceae examined are clearly of the starch-storing S-type. No protein accumulations have been detected. Every sieve-element plastid contains several roughly spherical starch grains of different size (Fig. 1 A–D). The grains are completely surrounded by a small coat of particulate, darkly stained material. There is usually a narrow light zone between the starch grain and the coat (Fig. 1 A–D, arrows). As in other plants investigated in this respect, the matrix contents of the sieve-element plastids are gradually reduced during the development of the sieve elements, to judge from their stainability properties: compare Fig. 1 A and B (young cells) with Fig. 1 D (a so-called mature sieve-element).

The species investigated (25) from other families within Capparales (sensu Dahlgren 1975) except for *Brassica chinensis* (Favali & Gerola 1968) and *Capparis cyanophallophora* (with P-type plastids) also contain S-type sieve-element plastids. However, starch grains very similar to those recorded in Gyrostemonaceae have hitherto only been found in Bataceae and Salvadoraceae (*Azima, Salvadora*) (Fig. 1 E, F). In *Azima* at least (Fig. 1 F, arrows), the light zone separating the coat can be seen. Among the other Capparales investigated the starch grains are predominantly ovoid and variable in size (Fig. 1 G–I). They are often accompanied by or disintegrated into small particles.

Protein-containing vacuoles

The stem phloem of *Gyrostemon ramulosus* has been carefully screened for the presence of dilated cisternae of ER. No inclusions of the type seen in Brassicaceae and Capparaceae have been detected. However, protein-containing vacuoles were found to be a regular component of companion cells of *Gyrostemon* sieve tubes. These vacuoles are derived from cisternal ER which contains some amorphous material and is almost agranulate when extending (Fig. 2 A, B). As soon as it has widened up to a vacuole-like compartment it already contains distinct protein filaments (Fig. 2 C). Finally the protein-containing vacuole extends considerably, parallel to the longitudinal axis of the companion cell: lengths of over 20 μm have been measured while their diameter is only 1–2 μm (Fig. 2 D). The protein filaments are orientated roughly longitudinally inside the vacuole. Their over-all diameter is about 50 nm; due to their bent course, their length is not possible to determine. The 50 nm filaments (Figs. 2 D, 3, double arrows) look like being composed of helically arranged subunits (Fig. 3, boldface arrow). The subunits probably first assemble into smaller, 20–25 nm broad entities (Fig. 3, arrow) before combining to form the 50 nm filaments. The membrane surrounding the entire organelle is completely devoid of ribosomes; it obviously corresponds to a normal tonoplast (Fig. 3, T).

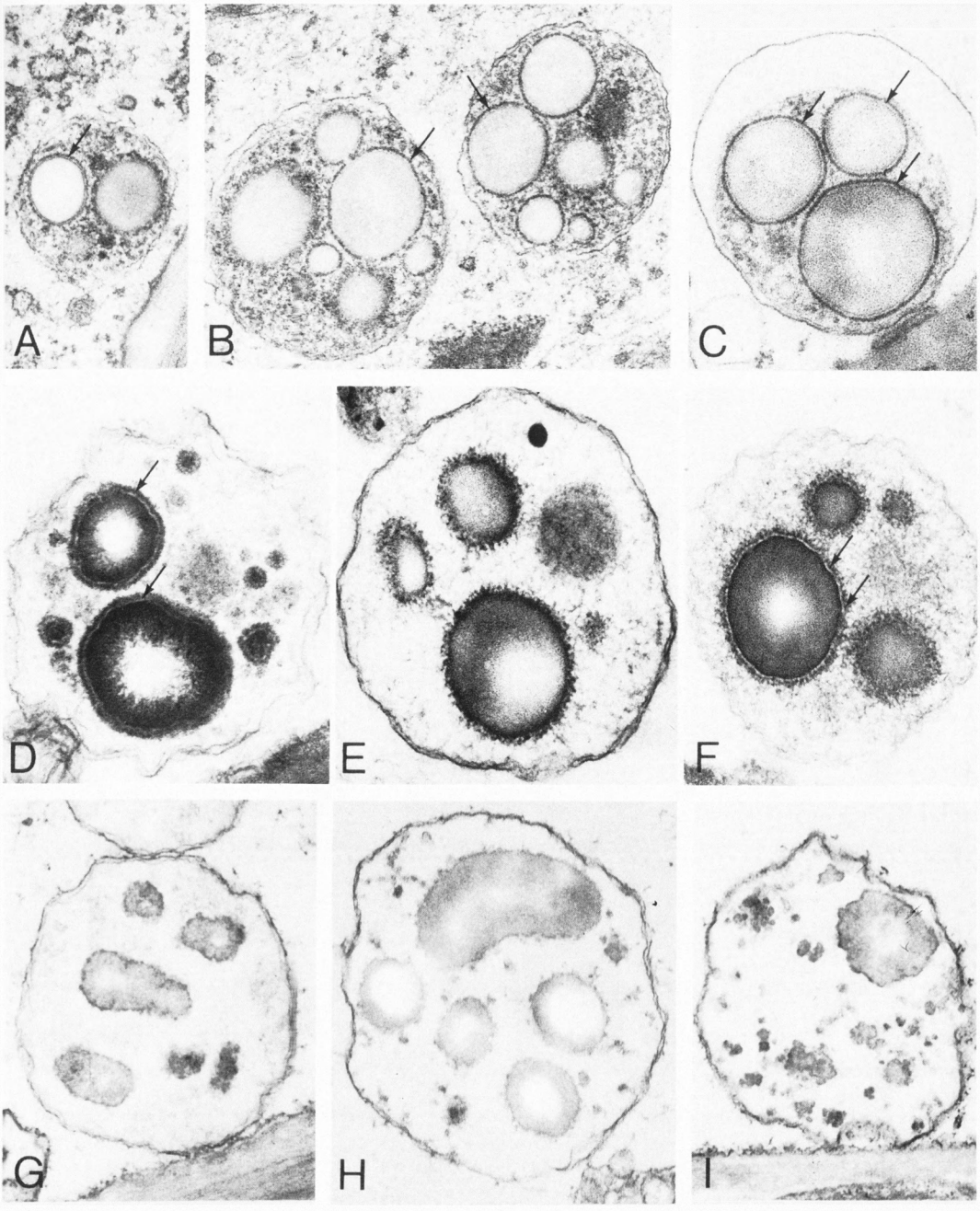
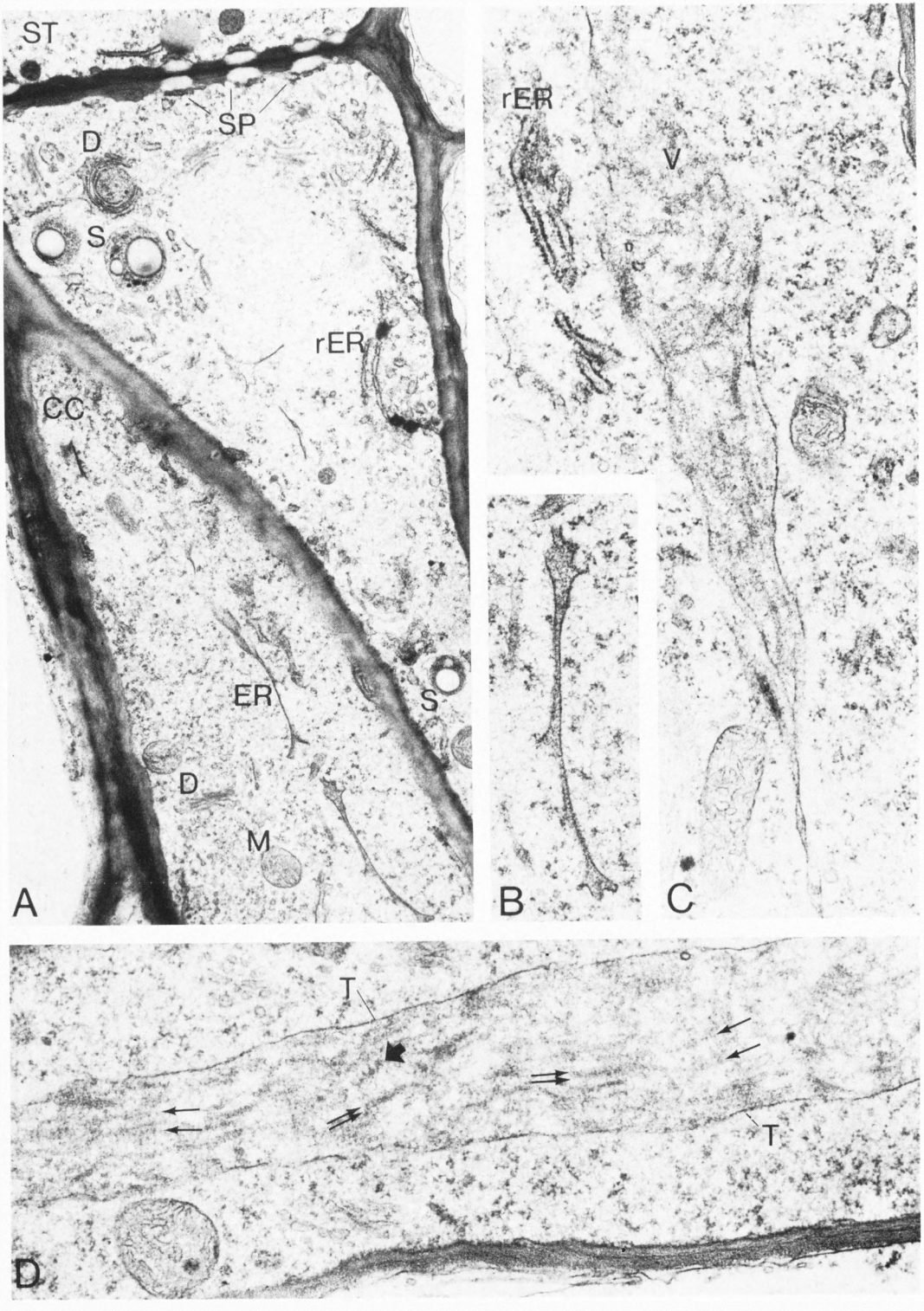


Fig. 1. S-type sieve-element plastids of Gyrostemonaceae and other members of Capparales (s.l.). – A: *Gyrostemon ramulosus* (Gyrostemonaceae). ×30,000. – B, C: *Didymotheca tepperi* (Gyrostemonaceae). Young sieve-element in B, plastid of mature sieve-element with dislocated envelope, due to aberrant fixation procedures, in C. Both ×30,000. – D: *Codonocarpus cotinifolius* (Gyrostemonaceae). ×40,000. – E: *Batis maritima* (Bataceae). ×40,000. – F: *Azima tetracantha* (Salvadoraceae). ×40,000. – G: *Alyssum saxatile* (Brassicaceae). ×40,000. – H: *Peltaria alliacea* (Brassicaceae). ×30,000. – I: *Cleome spinosa* (Capparaceae). ×30,000. – Arrows point to light zone between starch grain and surface coat.


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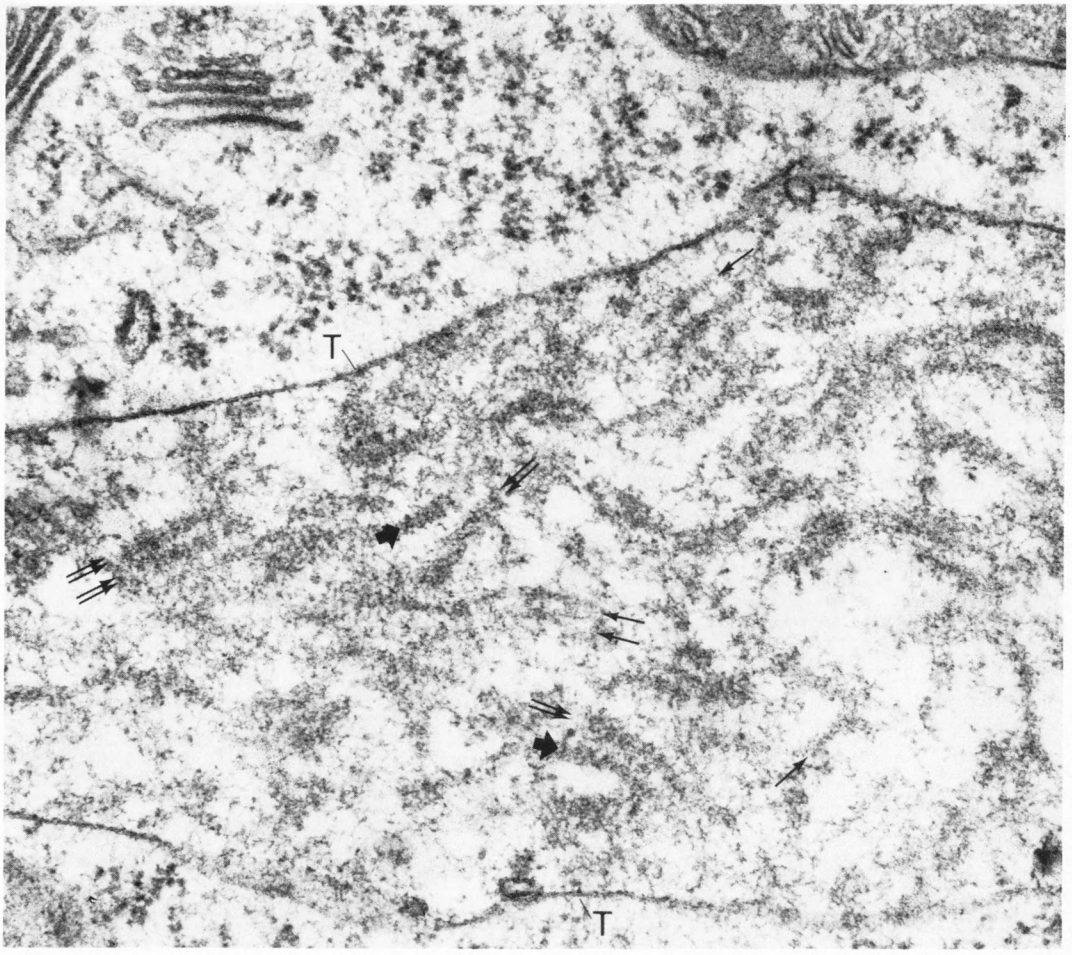


Fig. 3. Part of a protein-containing vacuole from companion-cell cytoplasm of *Gyrostemon ramulosus*. Vacuole surrounded by tonoplast (T) contains protein filaments (double arrows, diameter about 50 nm) which sometimes show composition of helically arranged subunits (boldface arrows); single arrows point to smaller (about 25 nm) filaments. ×50,000.

Discussion

The presence of S-type sieve-element plastids clearly distinguishes Gyrostemonaceae from the P-type containing order Centrospermae and is strong evidence against its inclusion in Phytolaccaceae (Behnke 1976). The more general use of S-type plastids as positive markers for the alignment of a taxon has still to be achieved since no reliable criteria which enable a general

Fig. 2. Protein-containing vacuoles in companion cells of *Gyrostemon ramulosus*. – A: Longitudinal section of stem phloem with sieve-tube (ST) and companion cell (CC). D dictyosome, ER agranular ER in companion cell, rER granular ER in sieve tube, M mitochondrium, S S-type plastid, SP sieve plate pores. ×12,000. – B: Agranular, slightly dilated ER of companion cell. ×25,000. – C: Companion cell with protein-containing vacuole (V) and granular ER (rER). ×25,000. – D: Protein-containing vacuole of companion cell surrounded by tonoplast (T) and including small (single arrows) and broad filaments (double arrows), partly showing helical arrangement of subunits (boldface arrow). ×25,000.

subclassification of this plastid-type, have as yet been worked out. It can be assumed, however, that, apart from ontogenetic changes, the phenotype of starch grains is genetically fixed like that of protein deposits. A first attempt at using the morphology of starch grains from sieve-element plastids as a taxon-specific feature has been undertaken by Behnke (1974) who found that the starch grains in Gymnospermae were usually club-shaped. The present comparison of starch-grain morphology and occurrence in sieve-element plastids of Capparales (s.l.) may perhaps lead towards further investigations. There seems to be a close similarity between Gyrostemonaceae, Bataceae and Salvadoraceae, whereas the core families Brassicaceae, Capparaceae, and Resedaceae stand somewhat apart.

The protein-containing vacuoles in the companion cells of *Gyrostemon ramulosus* find their counterpart in the dilated cisternae of Brassicaceae and Capparaceae. Although on superficial inspection they look quite different, they have some attributes in common: (1) they occur in phloem-parenchyma, (2) derive from endoplasmic reticulum, and (3) contain morphologically defined protein material. Therefore, both organelles may be interpreted as being the quantitative variations of one pattern, e.g. the exclusion of (enzyme?) proteins from its reaction site. The vacuoles in the companion cells of *Gyrostemon,* still of a limited size, would thus represent an intermediate between dilated cisternae of Brassicaceae and the protein-containing vacuoles of the glucosinolate species *Drypetes roxburghii,* which extend over almost the entire lumen of the phloem-parenchyma cell (Jørgensen et al. in prep.). From these results the conclusion can be drawn that Gyrostemonaceae are close to but not within the core-group families of Capparales.

To summarize: data from phloem ultrastructure favour considerations to include Gyrostemonaceae and other glucosinolate-containing families peripheral to Capparales (s. str.) in a separate but closely related order (see e.g. Dahlgren 1975).

Acknowledgements. The author is extremely grateful to J. R. Maconochie, Alice Springs, Australia, who several times collected material of the three Gyrostemonaceae species and also fixed some specimens at their natural habitat. Without his generous help this study would not have been possible. T. J. Mabry, Austin, sent a potted *Batis maritima* from the Gulf coast; R. Dahlgren, Copenhagen, gave permission to use a seedling of *Gyrostemon ramulosus* raised for his studies; L. B. Jørgensen, Copenhagen, helped to find species of interest for this study in the Botanical Garden, Copenhagen and assisted during their fixation; Mrs E. Grünbacher took care of the *Batis* plant in Heidelberg; Miss B. Schmidt, Miss A. Rüskens and Mrs D. Laupp gave technical assistance and conducted the photographical work. I would like to express my sincere thanks to all these people. The work was supported by grants from the Deutsche Forschungsgemeinschaft.

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A new Tribulus species with winged carpels

Hasnaa A. Hosni

Hosni, H. A. 1977 09 15: A new Tribulus species with winged carpels. *Bot. Notiser 130:* 261–262. Stockholm. ISSN 0006-8195.

Tribulus arabicus H. Hosni sp. nov. is described and illustrated. It is distinguished from the other *Tribulus* species with winged carpels by its larger flowers and fruits. It is believed to be endemic in S Arabia.

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Up to now, four species of *Tribulus* with winged carpels have been known, viz. *T. longipetalus* Viv., *T. bimucronatus* Viv., *T. pterocarpus* Ehrenb. and *T. pterophorus* Presl. The first three seem to be confined to the arid zones in N Africa and eastwards in Palestine, Iraq, Arabia, Iran and India. *T. pterophorus* is only known from Arabia and S Africa.

The author is preparing a thesis under the title "A revision of the *Tribulus* species with winged carpels in the Old World" under the supervision of Professor M. N. El Hadidi. During the revision of the material in BM, CAI, CAIM and K, a new species was recognized. It is described here as *T. arabicus*. The differences between the species of *Tribulus* with winged carpels can be summarized as follows.

Key to Tribulus species with winged carpels

1. Fruit over 5 mm diameter 2
– Fruit less than 5 mm diameter ..... *T. bimucronatus*
2. Flower 2–2.5 cm diameter 3
– Flower 0.8–1 cm diameter 4
3. Carpels with hairy dentate wings ..... *T. arabicus*
– Carpels with glabrous entire wings ..... *T. pterophorus*
4. Carpels with hairy dentate wings ..... *T. longipetalus*
– Carpels with glabrous entire wings ..... *T. pterocarpus*

Tribulus arabicus H. Hosni sp. nov. – Fig. 1

Frutex erectus, ad 100 cm altus omnino dense hirsutus, cinerascens; internodia 7–25 mm longa. *Folia* paripinnata, 4–7-jugata, 8–35 mm longa, foliola oblonga 5–7 mm longa, 3–4 mm lata; stipulae basi ovatae superne acuminatae 6 mm longae, 4 mm latae. *Flos* magnus 2.5 cm diam. *Pedicellus* 15 mm longus. *Sepala* lanceolata 7 mm longa, 2 mm lata. *Petala* flava obovata sepalis multo longiora 15 mm longa, 10 mm lata. *Stamina* 10, petalis breviora 5–8 mm longa. *Ovarium* 2 mm diam.; stylus brevis 1 mm longus, stigma gracile 3 mm longum. *Fructus* ellipticus 9 mm longus 7 mm latus, dense hirsutus. *Carpella* postice punctata 9 mm longa 1.5 mm lata, alis 2 cristatis 2.5 mm latis striatis trapeziformibus margine dentatis basi interruptis munita.

Holotypus: Yemen, Lower Wadi Najran (18°30'N, 45°0'E), 16.7. 1962, Zeller s.n. (BM).

Woody erect shrub up to 100 cm high, densely hairy, greyish-green; internodes 7–25 mm long. *Leaves* paripinnate, 8–35 mm long with 4–7 pairs of leaflets; leaflets 5–7 mm long and 3–4 mm broad, oblong; stipules ovate at the base, lanceolate above, 6 mm long and 4 mm broad.

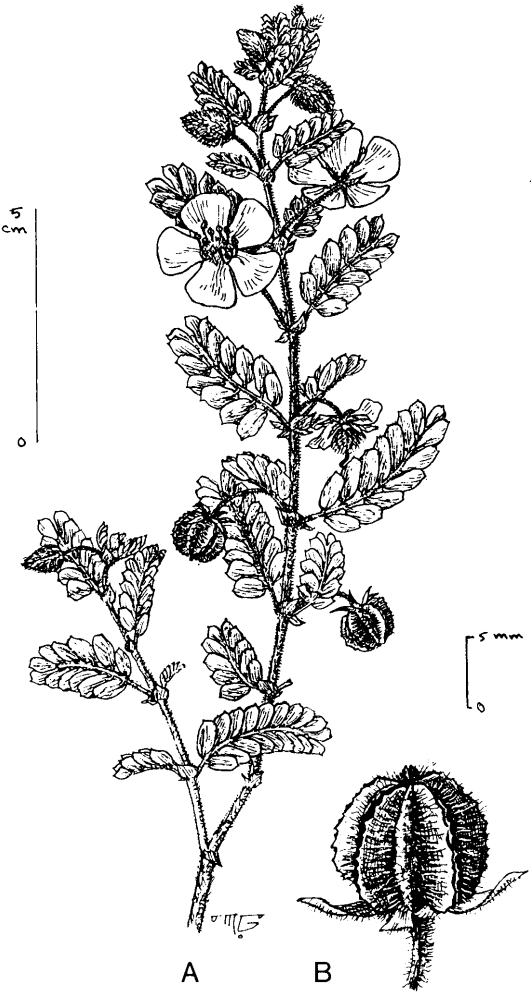


Fig. 1. ***Tribulus arabicus***. – A: Flowering branch. – B: Fruit.

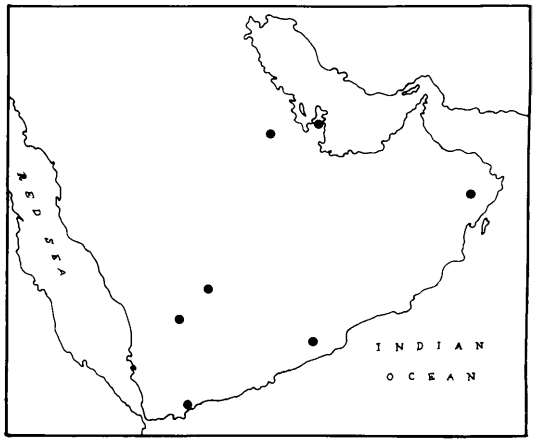


Fig. 2. *Tribulus arabicus*. Known distribution.

Flowers large, 2.5 cm across. *Pedicels* 15 mm long. *Sepals* 7 mm long and 2 mm broad. *Petals* yellow, obovate, longer than the sepals, 15 mm long and 10 mm broad. *Stamens* 10, shorter than the petals, 5–8 mm long. *Ovary* spherical, 2 mm broad; style short, 1 mm long, stigma slender, 3 mm long. *Fruit* elliptic, 9 mm long and 7 mm broad, densely hirsute. *Carpels* dorsally punctate, 9 mm long, 1.5 mm broad, with two marginal wings 2.5 mm broad, crusted, striate, trapeziform, margins dentate, interrupted at the base.

Distribution: Endemic in S Arabia: Rub El Khali, Yemen, Hadramout, Oman and Qatar (Fig. 2).

Collections: Saudi Arabia. Nefud Dahi, 12. 1951, Popov 503 (BM, K) – Rub El Khali, 12. 1946, Zeller (BM) – Rub El Khali, Arq Artha, 2. 1952, Popov, Tilin & Gililand 4158 (K).

Arab Republic of Yemen: Lower Wadi Najran, 7. 1962, Zeller (BM holotype, CAI).

Democratic Republic of Yemen: Aden, W of Wadi Mitan, 5. 1962, Stewart 689 (K) – Hadramout, 3. 1938, Feild 8A (K) – Hadramout, Adraj, 1939, Philpy (BM) – 100 m NE of Zumukh, Hadramout, 10. 1950, Guichard & Had 412 (BM, CAI).

Oman: Oman, 1. 1952, Lee (BM).

Qatar: Umm Bab, 4. 1975, Obeid 156 (CAI).

Acknowledgements. I wish to thank the staff of the Herbaria which I have consulted, especially Miss D. Hillcoat (BM) and Mr M. Forman (K) for the facilities they allowed me. Thanks are also due to Dr W. Stearn (BM) for his kind help with the Latin diagnosis, and to Mr M. El-Gohari (Assuit University, Egypt) for help with Fig. 1. The financial support of Sven and Dagmar Salén Foundation, Stockholm, is gratefully acknowledged.

Karyotypes of some Iris taxa

Shaukat A. Chaudhary, Ghulan Ahmad Chaudhary and Muhammad Akram

Chaudhary, S. A., Chaudhary, G. A. & Akram, M. 1977 09 15: Karyotypes of some Iris taxa. *Bot. Notiser 130:* 263–267. Stockholm. ISSN 0006-8195.

Chromosome numbers of 16 *Iris* taxa of the subgenera *Limniris*, *Scorpiris* and *Susiana* are reported. Their karyotypes are presented and illustrated.

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The classification problems within the genus *Iris* are becoming increasingly complex with each new taxonomic and/or cytologic report e.g. Rodionenko (1961), Weymouth & Chaudhary (1974), Gustafsson & Wendelbo (1975), Chaudhary et al. (1976). The accumulation of such data eventually, however, should lead to a more widely acceptable and rational classification of the genus. The present study is a continuation of an effort to investigate cytological characteristics of *Iris* taxa.

Methods

The cytological observations were made from root-tip squashes following the usual propionic-carmine staining technique after pretreatment with 0.002 mol/lt 8-hydroxyquinoline solution for 2–3 hours at c. 15°C. As many dividing cells as possible were studied for karyotype analyses, never less than 10 cells per taxon. The karyological nomenclature proposed by Levan et al. (1965) has been followed and the four groups of chromosomes referred to according to their r values: m (r = 1.0–1.7), sm (r = 1.7–3.0), st (r = 3.0–7.0) and t (r > 7.0).

Subgenus Limniris Tausch ex Spach

I. melanosticta Bornmüller

Material. S Syria, between Gezira and Daraa, Chaudhary & Kirkwood s.n. (BEI).

Chromosome number and karyotype. 2n = 24 (Fig. 1 A). m-chromosomes: 5 pairs, I, VI, VII, IX and XI (r = 1.0, 1.4, 1.3, 1.7 and 1.7, respectively). sm-chromosomes: five pairs, II, V, VIII, X and XII (r = 1.8, 2.7, 2.3, 1.9 and 2.0, respectively). st-chromosomes: two pairs, III and IV (r = 3.5 and 3.6, respectively). The members of pairs II, III, IV and VIII have short and/or long arms of unequal length. These inequalities in pairs III and VIII do not interfere with their separation into chromosome groups but the members of pairs II and IV are so unequal (r = 1.4 and 2.2 for II and 2.8 and 4.2 for IV) that they could be placed into different groups. Satellites are found on pairs IV and XII.

Previous report. 2n = 24 (Simonet 1952).

Subgenus Scorpiris Spach

I. aucheri (Baker) Sealy

I. fumosa Boiss. & Hausskn. in Post & Dinsmore 1934 and Mouterde 1966. – *I. sindjarensis* Boiss. & Hausskn. in Post & Dinsmore 1934 and Mouterde 1966.

Material. N Syria, Qilaat Simaan, Chaudhary s.n. (BEI); Bishmishly, Chaudhary & Kirkwood s.n. (BEI).

Chromosome number and karyotype. 2n = 24

(Fig. 1 B). m-chromosomes: four pairs, I, II, IV and VIII (r = 1.0, 1.1, 1.3 and 1.4, respectively). sm-chromosomes: four pairs, III, V, VI and XI (r = 1.9, 2.0, 2.0 and 2.0, respectively). st-chromosomes: four pairs, VII, IX, X and XII (r = 5.0, 3.3, 3.6 and 3.0, respectively). Satellites are found on pair X.

I. nusairiensis Mouterde

Material. Syrian desert, 32 km E of Homs, Chaudhary & R. A. Shad s.n. (BEI).

Chromosome number and karyotype. 2n = 20 (Fig. 1 C). m-chromosomes: two pairs, I and II (r = 1.5 for each). sm-chromosomes: three pairs, III, VIII and X (r = 1.8, 2.6 and 2.6, respectively). st-chromosomes: five pairs, IV, V, VI, VII and IX (r = 4.1, 3.7, 7.0, 3.3 and 3.8, respectively). No satellites could be observed.

I. postii Mouterde

Material. Syrian desert, near Ayn-al-Baida, Chaudhary & A. R. Shad s.n. (BEI).

Chromosome number and karyotype. 2n = 20 (Fig. 1 D). m-chromosomes: nine pairs, I–IX (r = 1.0, 1.0, 1.1, 1.2, 1.4, 1.0, 1.4, 1.1 and 1.1, respectively). st-chromosomes: one pair, X (r = 5.0). Prominent satellites are found on pair X.

I. palaestina (Boiss.) Klatt

Material. Lebanon, along Sidon highway near Khaldeh, S. & Z. Chaudhary s.n. (BEI).

Chromosome number and karyotype. 2n = 24 (Fig. 1 E). m-chromosomes: four pairs, I, II, XI and XII (r = 1.2, 1.1, 1.4 and 1.5, respectively). st-chromosomes: eight pairs, III–X (r = 5.5, 6.3, 6.0, 5.8, 6.8, 6.0, 5.6 and 5.2, respectively). Prominent satellites are found on pair IV.

Previous report. 2n = 24 (Simonet, unpublished?, as cited by Werckmeister 1967).

Subgenus Susiana Spach

The investigated species in this group have exclusively t-chromosomes.

I. bismarckiana Damman & Sprenger

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. 2n = 20 (Fig. 1 F). The chromosomes can be divided into two groups, one consisting of four large chromosome pairs and the other of six small, the latter gradually decreasing in length. Satellites are found on two pairs of the "small" group.

I. hermona Dinsmore

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. 2n = 20 (Fig. 1 G). As in *I. bismarckiana*, the chromosomes can be divided into two groups of four and six pairs, respectively. Satellites are found on two pairs of the "small" group.

Previous report. 2n = 20 (Simonet 1952).

I. antilibanotica Dinsmore

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. 2n = 20 (Fig. 1 H). The chromosome pairs constitute the usual two length-groups but because of the relatively small difference between pairs IV and V there is no sharp discontinuity between the two groups. Satellites are found on one pair in the "small" group.

Previous report. 2n = 20 (Simonet 1952).

I. damascena Mouterde

Material. Syria, Jabl Qasyoun (type locality), A. Khateeb 27–75 (BEI).

Chromosome number and karyotype. 2n = 20 (Fig. 1 I). Two length-groups which are not very well defined, just as in *I. libanotica*. Satellites are found on one pair in the "small" group.

I. susiana Linnaeus

Material. The material was obtained from Mr W. P. van Eeden, Noodwijk, Holland.

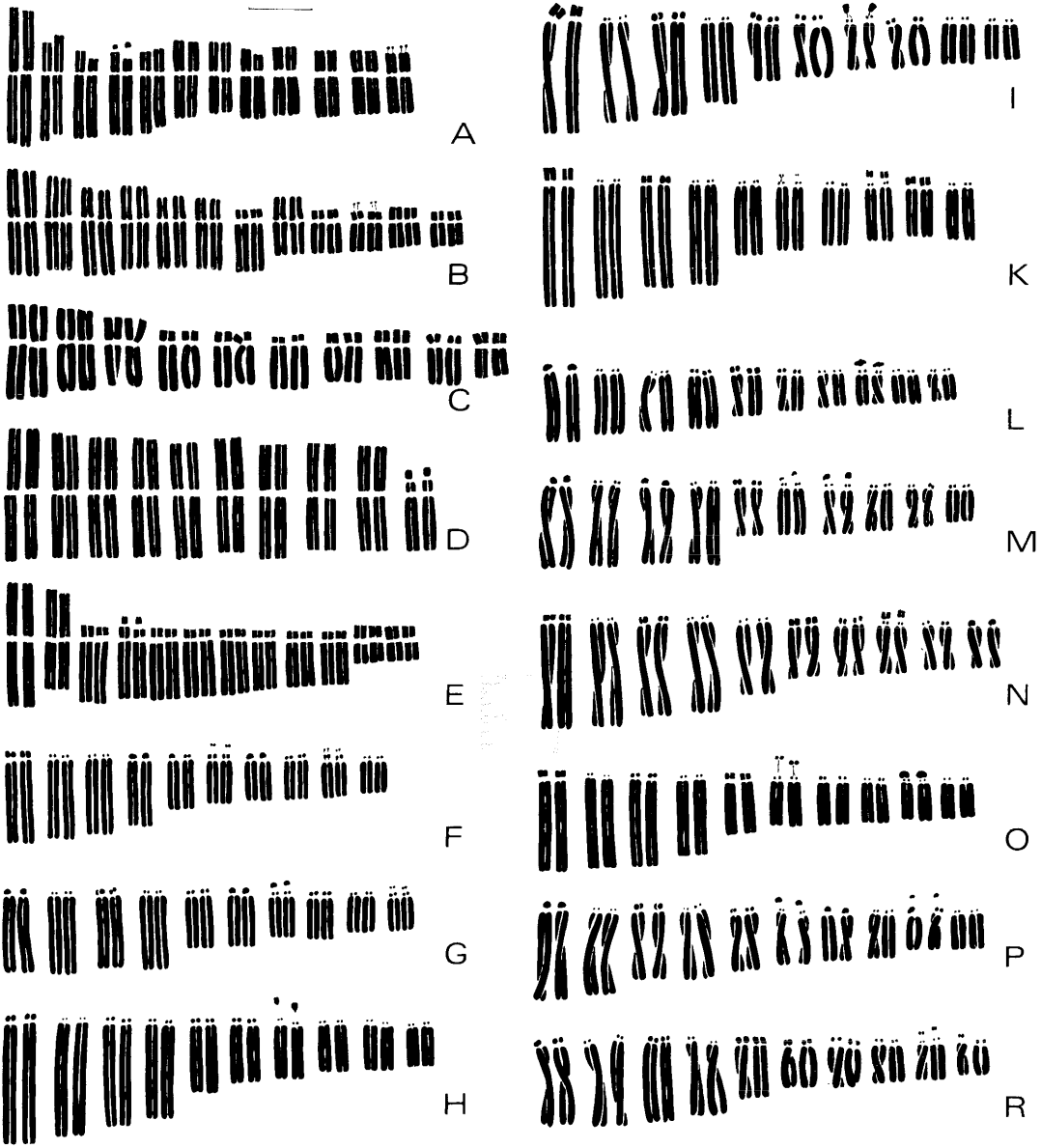


Fig. 1. Karyotypes of *Iris*. – A: *I. melanosticta*. – B: *I. aucheri*. – C: *I. nusairiensis*. – D: *I. postii*. – E: *I. palaestina*. – F: *I. bismarckiana*. – G: *I. hermona*. – H: *I. antilibanotica*. – I: *I. damascena*. – K: *I. susiana*. – L: *I. samariae*. – M: *I. haynei*. – N: *I. petrana*. – O: *I. nigricans*. – P: *I. paradoxa*. – R: *I.* sp. – Scale 5 μm.

Chromosome number and karyotype. 2n = 20, 21 (Fig. 1 K). Two well defined length-groups as in *I. bismarckiana*. Satellites are found on two pairs of the "small" group.

In some of the material investigated, an additional chromosome was found, with the same size and morphology as the members of the smallest pair. This taxon has been under cultivation for a long time and its origin is controversial. The karyotype, however, is of the Sofarana type of Weymouth & Chaudhary (1974). van Eeden, who supplied the material, comments that "it seems *Iris susiana* (material) is all imported (into Holland) from Turkey, each year."

Previous reports. 2n = 20 (Simonet 1932, Mitra 1956).

I. samariae Dinsmore

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. 2n = 20 (Fig. 1 L). The chromosome pairs do not fall into different length-groups, instead there is a continuous decrease in size. Prominent satellites are found on one of the smaller pairs.

Previous report. 2n = 20 (Simonet 1952).

I. haynei (Baker) Mallett

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. 2n = 20 (Fig. 1 M). Two distinct length-groups as in *I. bismarckiana*. Satellites are found on two pairs of the "small" group.

I. petrana Dinsmore

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. 2n = 20 (Fig. 1 N). As in *I. libanotica* the dividing line between the two length-groups is not very sharp. Satellites are found on one pair of the "small" group.

I. nigricans Dinsmore

Material. Jordan, between Karak and Madaba, 1975, R. Avolizzi (BEI).

Chromosome number and karyotype. 2n = 20 (Fig. 1 O). Two not very well defined length-groups as in *I. libanotica*. Satellites are found on two pairs of the "small" group.

Previous report. 2n = 20 (Simonet 1952).

I. paradoxa Steven

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. 2n = 20 (Fig. 1 P). Two not very well defined length-groups as in *I. libanotica*. Satellites are found on two pairs of the "small" group.

Previous reports. 2n = 20 (Delaunay 1928, Simonet 1934).

Iris sp.

Iris heylandiana in Chaudhary et al. (1976).

Material. The material was obtained from the Aril Society International, collected by Dr Barkouda of Damascus University near Ras-al-Ain in NE Syria.

Chromosome number and karyotype. 2n = 20 (Fig. 1 R). Two not very well defined length-groups as in *I. libanotica*. Satellites are found on one pair of the "small" group.

Comments

The karyotypes presented in this report show that the variation in chromosome morphology of the species in subgenus *Scorpiris* is rather large as compared to the variation of the species in subgenus *Susiana*. In the former subgenus the karyotypes vary from predominantly symmetrical to predominantly asymmetrical while *Susiana* is characterized by an asymmetrical karyotype.

Acknowledgements. The authors want to express their sincere thanks to the Aril Society International, USA, and particularly its members Mr Herbert McKusick, Mr Clay Osborne and Mr Thomas Wilkes who have helped in the procurement of research material and in arranging grants for the study.

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The Festuca brachyphylla group in Greenland

Signe Frederiksen

Frederiksen, S. 1977 09 15: The Festuca brachyphylla group in Greenland. *Bot. Notiser 130:* 269–277. Stockholm. ISSN 0006-8195.

The *Festuca brachyphylla* group consists of non-viviparous species especially characterized by very short anthers (less than 1.3 mm). In Greenland three species are recognized within this group, viz. *F. brachyphylla* Schult. & Schult. (2n = 42), *F. baffinensis* Polun. (2n = 28), and *F. hyperborea* Holmen ex Frederiksen (2n = 28). The latter species is validated and typified. The taxonomy and distribution of the species is discussed, and dot maps are presented for Greenland.

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In Greenland all native species of *Festuca* belong to sect. *Ovinae* Fr. The following species have been reported: *F. rubra* L. s.l., *F. vivipara* (L.) Sm., *F. brachyphylla* Schult. & Schult., *F. baffinensis* Polun., and *F. hyperborea* Holmen ex Frederiksen. In this paper the three latter species, all characterized by the very short anthers, are treated.

Collections from BM, C, DAO, GH and O have been studied.

Spikelets were always measured in the middle of the panicle. The measurements refer to the length of the glumes and the three lowest lemmas excluding the arista.

Cross-sections of the leaves were prepared according to Frederiksen (1974).

Only synonyms published on material from Greenland have been listed.

Lists of specimens examined of *F. brachyphylla* var. *groenlandica, F. baffinensis,* and *F. hyperborea* will be sent on request.

Festuca brachyphylla Schult. & Schult.

Scholander 1934 p. 69 p.p.; Seidenfaden & Sørensen 1937 p. 92 p.p.; Böcher 1938 p. 210; Sørensen 1943 p. 48; Holmen 1952 p. 28; Jørgensen et al. 1958 p. 29; Raup 1965 p. 16; Böcher et al. 1968 p. 256. – *Type:* Edwards, Melville Island 1819–20 (BM lectotype, selected here).

F. brevifolia R. Br. non Mühlenberg, nom. illeg. – Lange 1857 p. 115 quoad Vahl, Godthåbs Fj. (Baals Revier); Vahl, Upernaviârsuk; non quoad Vahl, Umanak 1836; Rink, Qaersut (Karsuk); Devold & Scholander 1933 p. 138.

F. ovina L. ssp. *brevifolia* Hack. – Ostenfeld & Lundager 1910 p. 15 p.p.

F. ovina L. var. *brevifolia* (R. Br.) S. Wats. – Sørensen 1933 p. 137 p.p.

F. ovina L. var. *alpina* (Gaud.) Koch f. *subspicata* Lange 1887 p. 302. – *Type:* Warming & Holm, Ikertôq, 13.VII. 1884; Warming & Holm, Kangerdluarssuk tugdleq, 5.VIII. 1884 (C syntypes).

F. ovina L. var. *borealis* Lange 1880; basionym *F. brevifolia* R. Br. non Mühlenberg.

F. ovina L. var. *alpina* (Gaud.) Koch sensu Lange 1880 p. 179 non (Gaud.) Koch.

F. ovina L. var. *tenuifolia* (Sibth.) Sm. sensu Lange 1880 p. 179 non (Sibth.) Sm.

Until 1940, when *F. baffinensis* was established by Polunin, the taxa now known as *F. brachyphylla, F. baffinensis,* and *F. hyperborea* were treated as one species only. This was first known as *F. brevifolia* R. Br. (Brown 1823) but as that name turned out to be a later homonym for *F. brevifolia* Mühlenberg 1817, it was changed by Schultes & Schultes, who referred to the description of Brown (Schultes & Schultes 1827). The types of *F. brevifolia* R. Br. and *F. brachyphylla* Schult. & Schult. are consequently identical. It was collected on Melville Island during Captain Parry's first voyage in 1819–20; at least two specimens were collected,

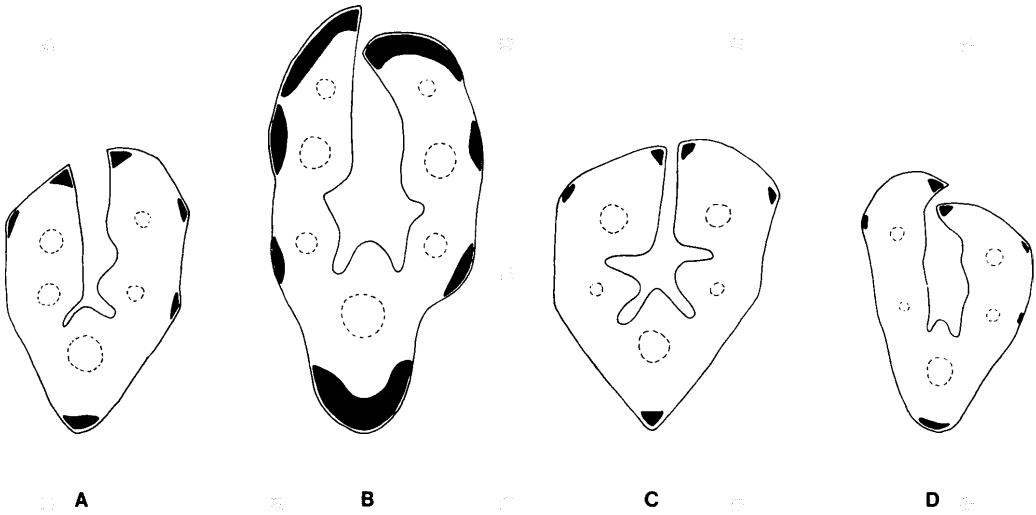


Fig. 1. Cross-sections of leaves, mechanical tissue black. – A: *F. brachyphylla* var. *brachyphylla*. – B: *F. brachyphylla* var. *groenlandica*. – C: *F. baffinensis*. – D: *F. hyperborea*. – ×60.

one by Ross and one by Edwards, and both were later studied by Brown. In the opinion of Schultes & Schultes the Ross collection hardly agreed with Brown's description, as the basal leaves were smaller, and the sheath of the upper culm leaf was comparatively long (Schultes & Schultes 1827). It is thus in agreement with Schultes & Schultes to choose the other collection, that of Edwards, as the lectotype of *F. brachyphylla*. The collection of Ross belongs to *F. hyperborea*, described below. However, it is a poorly developed specimen with an exceptionally short culm.

In the Arctic area there is some variation within *F. brachyphylla*, but apparently one chromosome number only, viz. 2n = 42 (Hedberg 1967, Holmen 1952, 1964, Johnson & Packer 1968, Jørgensen et al. 1958, Mosquin & Hayley 1966, Packer & McPherson 1974, Žukova 1965 a, 1965 b, Žukova & Tichonova 1973, Žukova et al. 1973, Frederiksen unpubl.). The few counts on 2n = 28 reported for *F. brachyphylla*, are most likely to be referred to material of *F. hyperborea* or *F. baffinensis* (Flovik 1938, Mosquin & Hayley 1966, Žukova 1965 a). The specimen (M & M-6458) cited by Mosquin & Hayley (1966), has been determinated by me as *F. hyperborea*.

F. brachyphylla normally has a very weak mechanical tissue in the basal leaves (Fig. 1 A), but in the southern parts of Greenland a morphologically not quite distinct form appears, characteristically with strongly developed mechanical tissue; this form is quite different from var. *groenlandica* discussed below.

Outside the Arctic, in high-alpine areas in Colorado and neighbouring states, there are forms of *F. brachyphylla* with smaller spikelets and a very slender habit. In such plants 2n = 28 has been counted (Holmen 1964, Mosquin & Hayley 1966).

The distribution of *F. brachyphylla* is circumpolar. On the American continent it extends as far as Colorado, following the Rocky Mountains. In the Flora Arctica URSS (Tolmačev 1964) *F. brachyphylla* also comprises *F. baffinensis* and *F. hyperborea*; I have only seen *F. brachyphylla* s.str. from Novaja Zemlja, but it has been reported from several places in the Sovjet Union (Žukova & Petrovskij 1972, Žukova & Tichonova 1973, Žukova et al. 1973). In Greenland it is widespread, though apparently rare in the northern and south-eastern parts (Fig. 2).

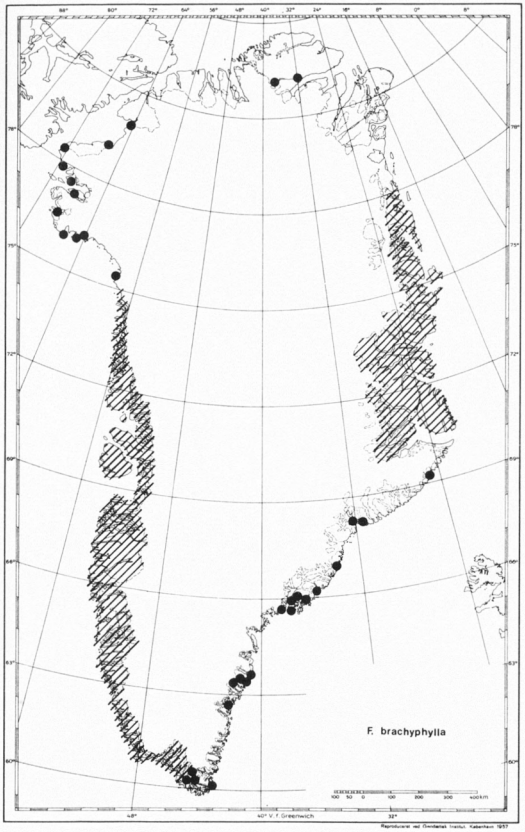


Fig. 2. Known distribution of *F. brachyphylla* in Greenland.

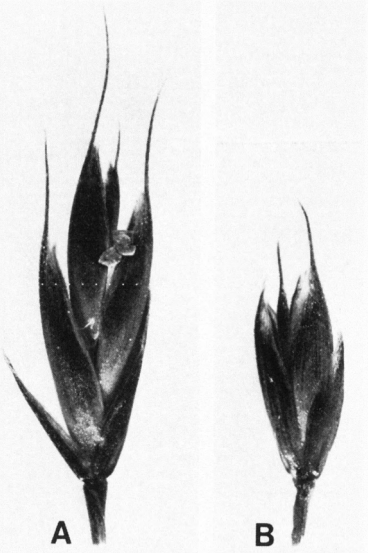


Fig. 3. Spikelets. – A: *F. brachyphylla* var. *brachyphylla*. – B: *F. brachyphylla* var. *groenlandica*. – Both Astrup et al. GBU 865, Skjoldungen Distr., Eqalungmiut, 1970 (C). – ×8.

Festuca brachyphylla var. **groenlandica** Schol.

Scholander 1934 p. 69; Böcher 1938 p. 210; Böcher et al. 1968 p. 258. – *Type:* Devold & Scholander, Greenland, Eqalungmiut (Dr. Maries Dal), 24.VII. 1932 (C holotype); 12.VIII. 1932 (O syntype); Devold & Scholander, Greenland, Finnsbu 24.VII. 1932 (O syntype); 14.VIII. 1932 (C, O syntypes).

As stated by Scholander (1934), this variety deviates in several characters from var. *brachyphylla* (Table 1). The most obvious are the very dense panicle, with smaller and broader spikelets, and the shorter, somewhat curved arista (Fig. 3). The mechanical tissue of the basal leaves is well developed in var. *groenlandica* (Fig. 1 B). The taxonomical value of this character has been judged very differently; among others Hackel (1882), Saint-Yves (1925) and Komarov (1934) regarded it as being a very important character. Studies by Bidault (1963) seem to show that it is to some extent independent of the environment, whereas Kjellquist (1961) came to the conclusion that it could not be used within his material of *F. rubra*. In my opinion the character is important but has to be used with great care. In var. *groenlandica* nearly all specimens studied show a distinctly stronger development of the mechanical tissue than is normally seen in var. *brachyphylla*. Nevertheless, as there seem to be some transitions, and since the distribution of var. *groenlandica* lies within that of var. *brachyphylla*, it is reasonable to keep the taxon on varietal level.

F. brachyphylla var. *groenlandica* seems to be restricted to Greenland, where it is found especially on the east coast (Fig. 4).

Festuca baffinensis Polun.

Holmen 1952 p. 26; Holmen 1957 p. 120; Jørgensen et al. 1958 p. 29; Raup 1965 p. 17; Fredskild 1966 p. 20; Böcher et al. 1968 p. 256. – *Type:* Polunin 706, Baffin Island, 12.IX. 1934 (GH holotype not seen, disappeared? CAN, BM isotypes).

F. brachyphylla Schult. & Schult. sensu Scholander 1934 p. 69 p.p.

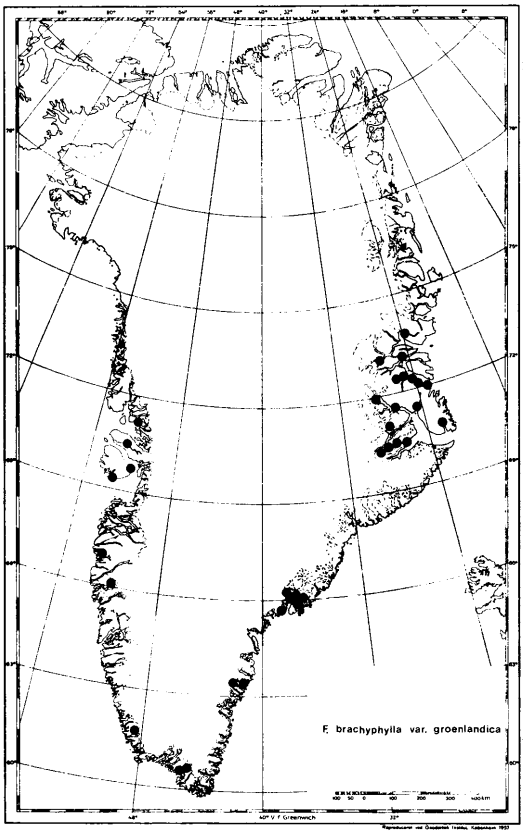


Fig. 4. Known distribution of *F. brachyphylla* var. *groenlandica*.

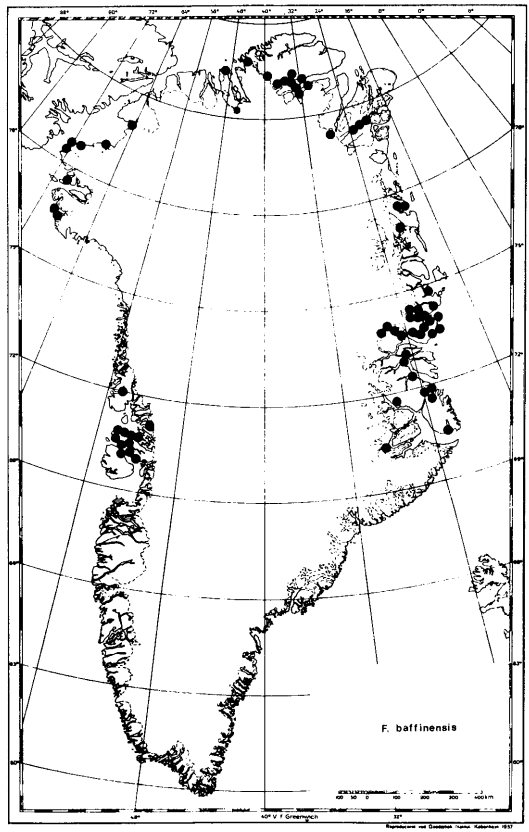


Fig. 5. Known distribution of *F. baffinensis* in Greenland.

F. brevifolia R. Br. non Mühlenberg, nom. illeg. sensu Lange 1857 p. 115 quoad Vahl, Umanak 1836; Rink, Qaersut (Karsuk); non quoad Vahl, Godthåbs Fj. (Baals Revier); Vahl, Upernaviârsuk.

F. ovina L. ssp. *brevifolia* Hack. sensu Ostenfeld & Lundager 1910 p. 15 p.p.

F. ovina L. var. *brevifolia* (R. Br.) S. Wats. – Ostenfeld 1923 p. 230 quoad Th. Wulff, Gunnar Anderson Dal, 11.VII. 1917; Th. Wulff, I. P. Koch Fj., 20.VI. 1917; Sørensen 1933 p. 137 p.p.

F. ovina L. var. *borealis* Lange 1880 p. 179 quoad Rink, Niaqornat (Niakornak); Rink, Qaersut (Karsuk); Vahl, Umanak, 1836; Copeland & Pansch, Jackson Isl.; Lange 1871 Tab. 2706.

Lange regarded *F. brevifolia* R. Br. as a synonym to *F. ovina* L. var. *borealis* but added that he had never seen the specimens of Brown (Lange 1871); nearly all the specimens determinated by him as *F. brevifolia* (1857) or *F. ovina* var. *borealis* (1880) belong in fact to *F. baffinensis*.

F. baffinensis is normally very easy to recognize because of its hairy upper culm and its short, broad panicle of glossy spikelets (Table 1). A few specimens have been seen in which the culm is very sparsely hairy, and these may form transitions between *F. baffinensis* and *F. brachyphylla* or *F. hyperborea*. As in *F. brachyphylla* the mechanical tissue in the basal leaves is very poorly developed (Fig. 1 C).

The distribution seems to be circumpolar, arctic-alpine. In America it is found as far south in the Rocky Mountains as Colorado (Weber 1961). In Eurasia the distribution is not known in detail but I have seen specimens from Svalbard and Novaja Zemlja, and it has been

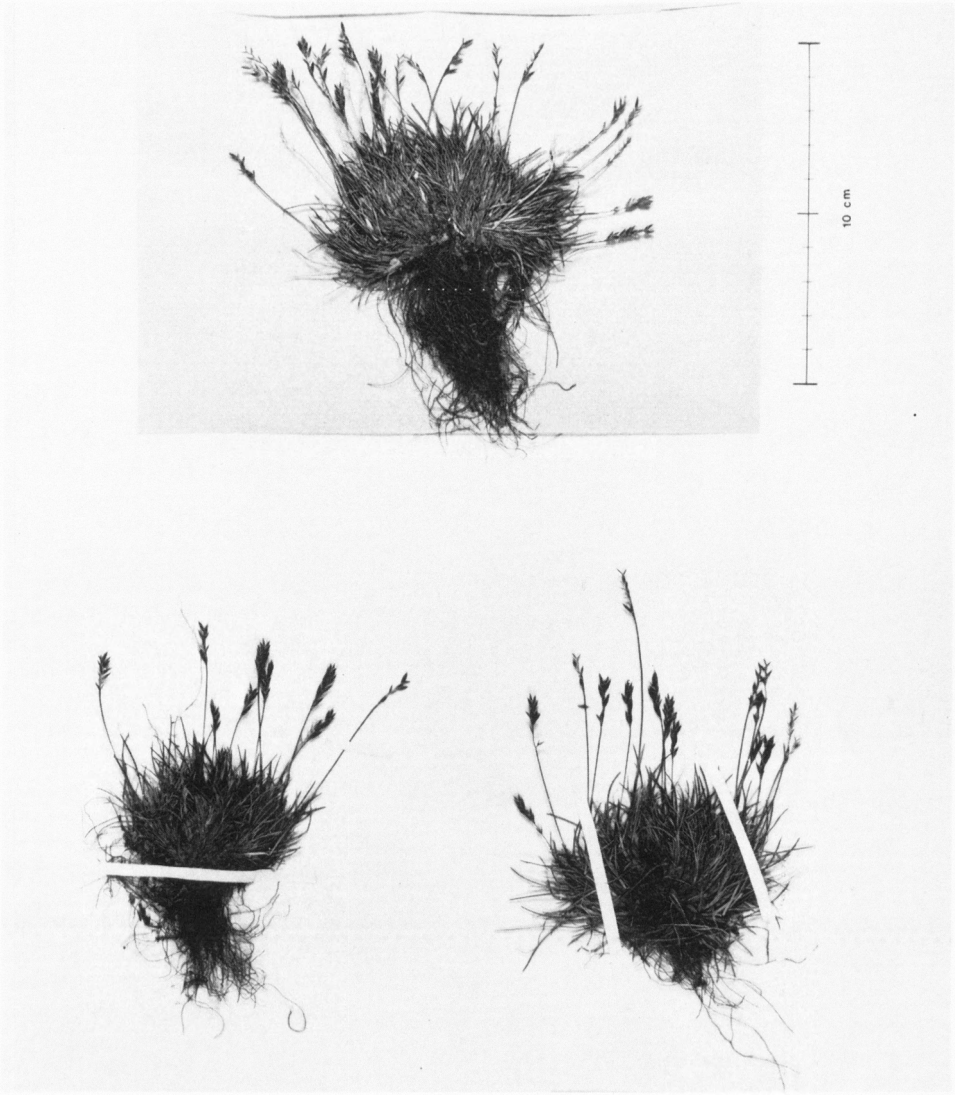


Fig. 6. Type specimen of *F. hyperborea*.

mentioned from the island of Wrangel (Žukova 1965 b), and the province of Chukotsk (Žukova & Tichonova 1973). In Greenland it is restricted to the northern areas with relatively basic rocks (Fig. 5).

Festuca hyperborea Holmen ex Frederiksen

Holmen 1952 p. 28; Holmen 1957 p. 120; Jørgensen et al. 1958 p. 29; Fredskild 1966 p. 20; Böcher et al. 1968 p. 258. – *Type:* Holmen 8078, Greenland, Jørgen Brøndlund Fj., 28.VII. 1950 (C holotype).

F. brachyphylla Schult. & Schult. sensu Scholander 1934 p. 69 p.p.

F. ovina L. var. *brevifolia* (R. Br.) S. Wats. – Ostenfeld 1923 p. 230 quoad Th. Wulff, Black Cape, 4.VI. 1917; Th. Wulff, I. P. Koch Fj., 20.VI. 1917; Th. Wulff, Cape Salor, 29.VI. 1917; Th. Wulff, John Murray Isl., 3.VII. 1917; Th. Wulff, Sommerdal, 14.VII. 1917; Th. Wulff, Dragon Point, 19.VII. 1917; non quoad Th. Wulff, Gunnar Anderson Dal, 11.VII. 1917; Th. Wulff, I. P. Koch Fj., 20.VI. 1917.



Fig. 7. *F. hyperborea*. Detail of the panicle of the type specimen. – ×2.

F. ovina L. var. *supina* (Schur) Hack. sensu Sørensen 1933 p. 137 non (Schur) Hack.; Böcher 1938 p. 211.

F. hyperborea was recognized by Holmen (1952), but the name was never validly published; nevertheless the species has been accepted by most botanists working on the Arctic flora. The following description of *F. hyperborea* is based on the type pointed out by Holmen (1952), and the material in C determinated by him. Holmen (1952) supposed that *F. hyperborea* is identical to *F. ovina* L. var. *supina* (Schur) Hack. sensu Sørensen (1933), which is undoubtedly correct. In fact the Arctic collections of Sørensen have nothing to do with *F. ovina* var. *supina*, which is known to occur in Central Europe (Schur 1866), where *F. brachyphylla* and its allies have never been found.

Gramen perenne, laxe caespitosum, glaucum, pruinosum, opacum. *Culmi* 5–15 cm alti, omnes vel saltem exteriores caespitum majorum geniculati vel procumbentes. *Folia* basalia 2–5 cm longa, curva, breviter acuta, sclerenchymate satis debile. Folium superius culmi lamina brevi, raro plus quam 5 mm longa, saepe omnino deficiente, vagina paulum inflata. *Paniculus* brevis vix ultra 20 mm longus, subfusiformi-ovoides, plerumque primarios solum ramos formans, e paucis spiculis compositus. *Lemma* lanceolato-ovale, violaceum, ad apicem versus scaberulum. *Arista* brevis, saepe curva, subterminalis. *Anthera* 0.4–0.7 mm longa. *Numerus chromosomatum* 2n = 28.

Illustrations: Figs. 6, 7.

Perennial grass. Loosely tufted, at least the outer culms of large tufts geniculate or prostrate. The plant glaucous, pruinose, opaque. *Culms* rarely exceeding 15 cm. *Basal leaves* rarely more than 5 cm, recurved, quickly tapering. Mechanical tissue in the leaf blade very weak (Fig. 1 D). Upper culm leaf with or without a very short blade (5 mm), the sheath somewhat inflated. *Panicle* short, rarely exceeding 20 mm, normally simply branched, with few spikelets. When measured after the method given in the introduction, spikelets are 4.4–6.8 mm; third lemma in these spikelets 3.0–4.4 mm, lanceolate-ovate, purple, scabrous towards the tip. *Arista* short, on the third lemma 1.4–2.0 mm, often curved or geniculate, subterminal. *Anthers* 0.4–0.7(–0.8) mm. *Chromosome number* 2n = 28 (Holmen 1952).

As mentioned by Holmen (1952, 1957), *F. hyperborea* is very closely related to *F. brachyphylla*, while *F. baffinensis* is more isolated. There are some intermediates between *F. brachyphylla* and *F. hyperborea*, but nevertheless it seems reasonable to keep them as separate species, partly because of the morphological differences and the difference in chromosome number, and partly because of differences in distribution.

The difference in chromosome numbers between *F. brachyphylla* s.str. and *F. hyperborea* must impose a strong reproductive isolation, and there is nothing to suggest that hybridization takes place. The tetraploid specimens of *F. brachyphylla* reported from Colorado (cf. above) obviously have nothing to do with *F. hyperborea*.

The distribution is characteristically high-arctic, and the species seems to be restricted to areas with relatively basic rocks. The distribution outside Greenland is not known in detail, but the species has been mentioned from Svalbard (Rønning 1961), Iceland (Löve & Löve

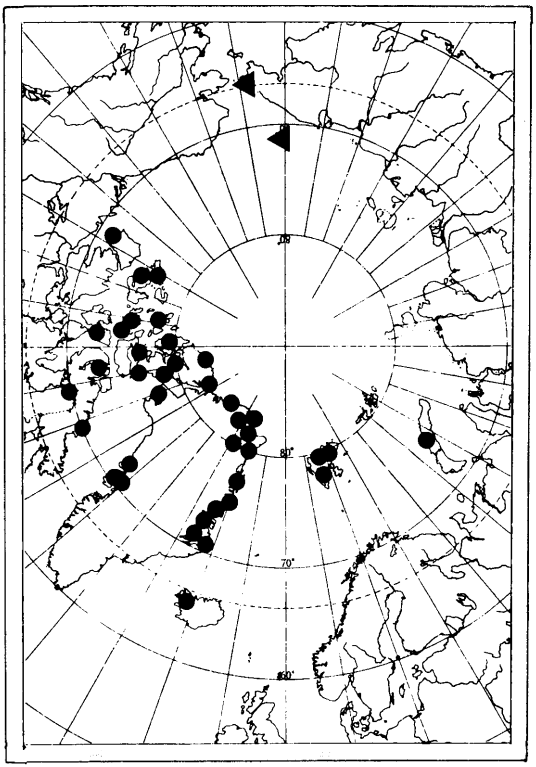


Fig. 8. Known distribution of *F. hyperborea*. ● specimens examined, ▲ references from the literature.

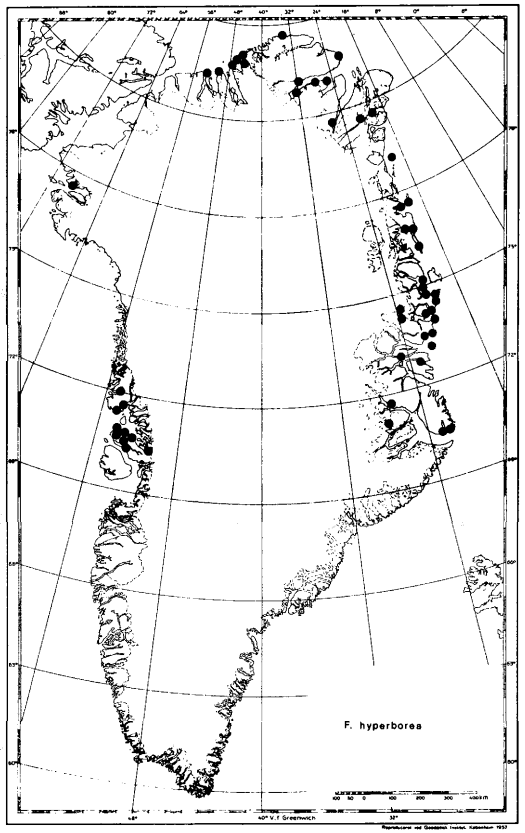


Fig. 9. Known distribution of *F. hyperborea* in Greenland.

1956), arctic America (Hedberg 1967), and from the province of Chukotsk and the island of Wrangel in USSR (Žukova & Petrovskij 1972, Žukova & Tichonova 1973, Žukova et al. 1973). It is not known from the American mainland and only from a few places on the Eurasiatic mainland (Fig. 8). In Greenland it has nearly the same distribution as *F. baffinensis*, and is thus restricted to areas with basic rocks (Fig. 9).

Final remarks

In addition to the species found in Greenland there seems to be only one more North American species in the group treated here. This is *F. saximontana* Rydb. from the northern parts of America, which is similar to *F. brachyphylla* and like the latter has 2n = 42 (Bowden 1960). *F. saximontana* differs from *F. brachyphylla*, for instance, by having strong mechanical tissue (Saint-Yves 1925). I have not studied the type specimen of Rydberg but neither the description (Rydberg 1909), nor the specimens in C, suggest that *F. saximontana* should be conspecific to any of the taxa treated here. Contrary to *F. brachyphylla* var. *groenlandica* it has an open panicle with fewer and larger spikelets, and a long and erect arista.

The viviparous taxa of *Festuca* occurring in the Arctic have sometimes been regarded as being closely related to the group treated here (cf. Ostenfeld & Lundager 1910, Ostenfeld 1923, Sørensen 1933, Holmen 1964). However, the former always have higher chromosome numbers, viz. 2n = 49, 56, and 63 (Jørgensen et al. 1958, Holmen 1964, Johnson et al. 1968, Frederiksen unpubl.). Normally they have no flowers, but when anthers are occasionally

Table 1. Summary of characters in the species of the *Festuca brachyphylla* group in Greenland.

F. brachyphylla var. *brachyphylla*	*F. brachyphylla* var. *groenlandica*	*F. baffinensis*	*F. hyperborea*
Densely tufted	Densely tufted	Densely tufted	Loosely tufted
Plant normally fresh green, more or less shining	Plant fresh green to glaucous	Plant fresh green, normally shining	Plant glaucous, pruinose, often opaque
Basal leaves 5–10 cm, straight or almost so, long tapering	Basal leaves 6–15 cm, straight, long tapering	Basal leaves 3–10(–14) cm, straight or almost so, long tapering	Basal leaves 2–5 cm, recurved, short tapering
Mechanical tissue in basal leaves normally weak	Mechanical tissue in basal leaves well developed	Mechanical tissue in basal leaves weak	Mechanical tissue in basal leaves weak
Culm 10–30 cm, glabrous or almost so	Culm 14–37 cm, glabrous or almost so	Culm 5–20(–30) cm, in its upper half densely tomentose of short curved hairs	Culm 5–15 cm, glabrous or almost so
Culms erect	Culms erect	Culms erect	Culms often prostrate or geniculate
Upper culm leaf normally about 10 mm. Sheaths not inflated	Upper culm leaf with relatively long blade (10–50 mm). Sheaths not inflated	Upper culm leaf with a blade normally exceeding 10 mm. Sheaths inflated	Upper culm leaf with an extremely short blade 0–5(–15) mm. Sheaths inflated
Panicle with few or more spikelets, (15–)30–50 mm, often branched, open, lanceolate, green or purple	Panicle with many spikelets, 20–50 mm, always branched, lanceolate, green or purple	Panicle normally with few spikelets, dense, 15–35 mm, often branched, broadly ovate, dark purple	Panicle with few spikelets, seldom exceeding 20 mm, normally simple, lanceolate-ovate, normally purple
Spikelets 5.0–6.6 mm	Spikelets 4.2–5.6 mm	Spikelets 6.2–7.5 mm	Spikelets 4.4–6.8 mm
Lemma almost glabrous or scabrous towards the tip. Third lemma 3.3–4.6 mm	Lemma almost glabrous or scabrous towards the tip. Third lemma 2.9–3.4(–3.7) mm	Lemma almost glabrous, glossy. Third lemma 3.7–5.0 mm	Lemma scabrous towards the tip. Third lemma 3.0–4.4 mm
4–8 flowers in the spikelets	3–5 flowers in the spikelets	3–6 flowers in the spikelets	3–6 flowers in the spikelets
Arista erect or almost so, terminal. Arista on the third lemma (1.2–)2.1–2.5 mm	Arista more or less curved. Arista on the third lemma (0–)0.8–2.1 mm	Arista erect, terminal. Arista on the third lemma 1.7–3.3 mm	Arista curved or geniculate, subterminal. Arista on the third lemma 1.4–2.0 mm
Anther (0.6–)0.7–1.1 mm	Anther 0.8–1.3 mm	Anther 0.4–0.7(–0.8) mm	Anther 0.4–0.7(–0.8) mm
2n = 42	2n unknown	2n = 28	2n = 28

developed these are 1.6–2.1 mm long, i.e. distinctly longer than in *F. brachyphylla* and its allies (Table 1).

Acknowledgements. The author wishes to thank professor A. Strid, lektor K. Jakobsen, and lektor I. Friis for valuable discussions during the work on the manuscript. Moreover I wish to thank lektor T. Christensen for translating the diagnosis into Latin.

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A review of the Andean genus Cacosmia H.B.K. (Compositae–Liabeae)

Bertil Nordenstam

Nordenstam, B. 1977 09 15: A review of the Andean genus Cacosmia H.B.K. (Compositae–Liabeae). *Bot. Notiser 130:* 279–286. Stockholm. ISSN 0006-8195.

The small genus *Cacosmia* H.B.K. is restricted to the Andes of Ecuador and Peru. Three species are recognized, one of which is described as new, viz. *C. harlingii* B. Nord. In the type species, *C. rugosa* H.B.K., three varieties are distinguished.

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Cacosmia H.B.K. was established in 1818 as a monotypic genus of the Heliantheae (Humboldt, Bonpland & Kunth 1820; text available in 1818). Cassini (1828, 1830) more aptly associated the genus with *Liabum* and its allies in the subtribe "Liabeae" of the Vernonieae. Lessing (1831, 1832) and De Candolle (1836) treated *Cacosmia* in the same taxonomic context. The latter also simultaneously described *Clairvillea quinquenervia* DC. as a new monotypic genus of the subtribe "Flaverieae" (=Flaveriinae) of the Senecioneae. De Candolle soon realized that his *Clairvillea* was merely a synonym of *Cacosmia* (De Candolle 1838 p. 265). He noted, however, that *Clairvillea quinquenervia* differed somewhat from *Cacosmia rugosa,* mainly in pubescence, and he added, "An var.? An species propria?" (1838 p. 266). Steudel (1840) formally transferred De Candolle's species to *Cacosmia*. The two taxa are now treated as varieties of *C. rugosa*.

Bentham (in Bentham & Hooker 1873) violated Cassini's natural arrangement by removing the Liabeae from the Vernonieae to the Senecioneae, except for *Cacosmia,* which he assigned a position in the heterogeneous tribe Helenieae. He admitted, however, that it was "somewhat anomalous" there (Bentham 1873 p. 381). Hoffmann (1890) followed Bentham, and the systematic position of *Cacosmia* remained obscure for some time. Cabrera (1954) re-established the connection to the *Liabum* group, and further evidence to the same effect was presented by Skvarla & Turner (1966 a, b). The Liabeae are now recognized as a separate tribe closest to the Vernonieae (Robinson & Brettell 1974, Nordenstam in print). The closest relative of *Cacosmia* appears to be the recently described genus *Ferreyranthus* Robinson & Brettell, which also has a similar distribution.

There is a range of similarities between *Cacosmia* and *Ferreyranthus* extending from gross morphological features like habit, leaf shape and tomentum, to micromorphological characters like stylar pubescence and achenial wall crystals. The latter are elongate and rod-shaped in contrast to the short prismatic crystals of, e.g., the genus *Liabum* sensu stricto (Fig. 1). *Ferreyranthus* is significantly distinct, however, in a number of important characters, e.g. the setose and pappose achenes.

Until recently *Cacosmia* was generally regarded as monotypic, although considerable variability was noted by several authors, and Bentham (in Bentham & Hooker 1873 p. 396) wrote, "Species 2 v. 3". The polymorphism first received taxonomic recognition with Hieronymus (1901), who distinguished three varieties. A study of the genus was recently taken

up independently by the present author and Robinson, who published a new species and a new variety (Robinson 1976).

The present revision is based on herbarium material in BM, GB, K, P, S and US (abbreviations according to Holmgren & Keuken 1974). A third species is added, and the genus now comprises altogether five taxa.

Cacosmia H.B.K.

Humboldt, Bonpland & Kunth 1820 p. 289; Kunth 1823 p. 509; Sprengel 1826 p. 588; Lessing 1829 p. 338, 1831 p. 705, 1832 p. 152; De Candolle 1836 p. 98; Jameson 1865 p. 72; Bentham in Bentham & Hooker 1873 p. 396; Hoffmann 1890 p. 252.

Clairvillea De Candolle 1836 p. 636, 1838 p. 265.

Erect branching shrubs. *Stems* and branches laxly lanate and/or hirsute with articulated hairs. *Leaves* opposite, shortly petiolate or subsessile with stem-sheathing connate 'semi-stipules', flat, ovate–lanceolate; upper surface bullate-rugose, green, glabrous or setose; lower surface densely tomentose. *Capitula* several–many in terminal corymbose-paniculate inflorescences, heterogamous, radiate. *Involucre* narrowly oblong-ovoid. Involucral bracts ca 20–25, imbricated in 5–6 series, ovate–lanceolate, somewhat coriaceous, green, brown or purplish, obtuse (outer) to acute (inner), glandular or subglabrous. Receptacle flat–convex, alveolate. *Corolla glands* stipitate–subsessile, with a stalk of two cell-rows and a larger, thick-walled terminal cell. *Corolla hairs*, if present, thin, flexuous, consisting of a single cell-row. *Ray-florets* usually 5, female, ligulate, yellow or greenish yellow to dirty white or orange-coloured. *Style* filiform, bilobed, hispidulous from about the middle or subglabrous, basally glabrous. *Disc-florets* usually 6, perfect. Corolla funnel-shaped, 5-lobed, yellow to greenish white. *Anthers* dorsifixed (filament inserted slightly below the middle of the theca), basally obtuse–subacute, ecaudate; apical appendage ovate, obtuse. Endothecial cells shortly oblong or almost isodiametric, with few thickenings mainly on horizontal walls. *Style* filiform-cylindric with a dilated base on a short nectary, densely hispidulous in the distal half or more, bilobed, with continuous stigmatic surfaces on the inside of the branches. *Achenes* oblong, somewhat compressed or subtriquetrous, subhomomorphic (those of the disc less compressed and more 4–5-angular), glabrous, faintly ribbed, 8–10-veined, with numerous elongate prismatic wall crystals. *Pappus* 0.

Species 3, Ecuador, Peru. Type: *C. rugosa* H.B.K.

Key to the species and varieties of Cacosmia

1. Involucre predominantly green or yellowish. Leaf-margins distinctly denticulate (1. *C. rugosa*) 2
– Involucre predominantly brown or purple. Leaf-margins indistinctly denticulate 4
2. Upper leaf surface ± glabrous (softly pubescent along veins, rarely sparsely setose) 3
– Upper leaf surface evenly and ± densely setose ..... 1 c. *C. rugosa* var. *kingii*
3. Stem pubescence mainly hirsute with numerous articulated hairs ..... 1 a. *C. rugosa* var. *rugosa*
– Stem pubescence white-lanate–floccose without coarser articulated hairs ..... 1 b. *C. rugosa* var. *nivea*
4. Involucre ± purple, 5–6 mm long. Rays orange-coloured. Corollas without long hairs ..... 2. *C. harlingii*
– Involucre dark brown–purplish brown, 7–8 mm long. Rays yellow. Disc corollas villous with conspicuous long hairs ..... 3. *C. hieronymi*

1. C. rugosa H.B.K.

Humboldt, Bonpland & Kunth 1820 p. 290. – *Orig. coll.:* Humboldt & Bonpland no. 3312, Ecuador, Saraguro (P holotype, isotypes in B: herb. Willdenow and P: ex herb. Bonpland et ex herb. Schultz Bip.).

Clairvillea quinquenervia De Candolle 1836 p. 636. – *Cacosmia quinquenervia* (DC.) Steudel 1840 p. 377. – *Orig. coll.:* Dombey s.n., Peru (P holotype, prob. isotypes in P: Dombey 255, ex herb. Schultz Bip. et ex herb. Drake).

According to information kindly submitted by Dr A. Lourteig, the number 3312 in the journal of Humboldt and Bonpland has a description written by Bonpland and the name "*Cacosmia rugosa* n. sp." added by Kunth. The matching specimen in the Humboldt and Bonpland herbarium is the holotype, also named by Kunth. I have seen this specimen only in microfiche. There is an isotype in Willdenow's herbarium in B, another in P from Bonpland's herbarium, and in P also a fragment from the Willdenow specimen.

A further specimen in Bonpland's herbarium (P) represents a different collection from Gonzanamá in Ecuador. In the present taxonomy it belongs to var. *nivea* (q.v.).

Erect–ascending shrubs 1–4(–5) m tall. *Stems* white- or grey-lanate and often also hirsute with coarser, distinctly articulated hairs, sometimes glabrescent with age. *Leaves* shortly petiolate or subsessile, ovate or narrowly ovate, 1–9 cm long, 0.5–4 cm wide, acute–acuminate, with 3 or 5 main longitudinal veins and a finer reticulate venation pattern; margins laxly serrulate or callous-denticulate; upper side ± glossy green, setose or subglabrous; lower side densely white- or grey-tomentose. *Capitula* numerous in somewhat lax to fairly compact synflorescences, with rich or golden yellow florets (in one collection said to be greenish white). *Involucre* 5–7 mm long, 2.5–4 mm wide. Involucral bracts pale–dull green, sometimes with darker green or slightly brownish tips or margins; outer phyllaries ovate, obtuse, eglandular; inner phyllaries lanceolate, 5–6 mm long, acute, glandular on the lower half, with somewhat fimbriate-ciliate margins. *Ray-florets* (4–)5. Tube subcylindric, narrowest basally, 2–3.5 mm long, glandular with sessile and stipitate glands. Lamina concave or flat, elliptic-oblong, 3–7 mm long, 2–4 mm wide, 4-veined, abaxially glandular, apically trifid. *Style* branches subulate-filiform, 2.5–3.5 mm long, with shortly hispidulous outsides. *Achenes* oblong, 1.5–2 mm long, 0.6–0.9 mm wide, somewhat compressed-triquetrous with distinct lateral ribs and fainter ribs ad- and abaxially, brown. Disc-floret corolla 5–6 mm long, glandular with subsessile and stipitate glands and sometimes also a few (rarely many) apically thinner flexuous hairs; corolla lobes lanceolate, 2–2.5 mm long, acute, becoming rolled back. *Anthers* 2–2.7 mm long incl. appendage; base obtuse–subacute without distinct papillae. *Style* branches 0.5–1.2 mm long, semiterete, obtuse; style narrowly cylindric, thickest about the middle, densely hispidulous on the distal 1/2 or 2/3. *Achenes* as in ray-florets, but less compressed, somewhat 4- or 5-angled, 4–5-ribbed.

On the basis of stem and leaf pubescence three varieties of *C. rugosa* can be distinguished. They are quite characteristic and easily recognized (cf. the key), and transitional forms seem to be rare. Eglandular corolla hairs may be present in varying quantity, but never as copiously as in *C. hieronymi* (cf. Fig. 2 D, Fig. 3 H, I).

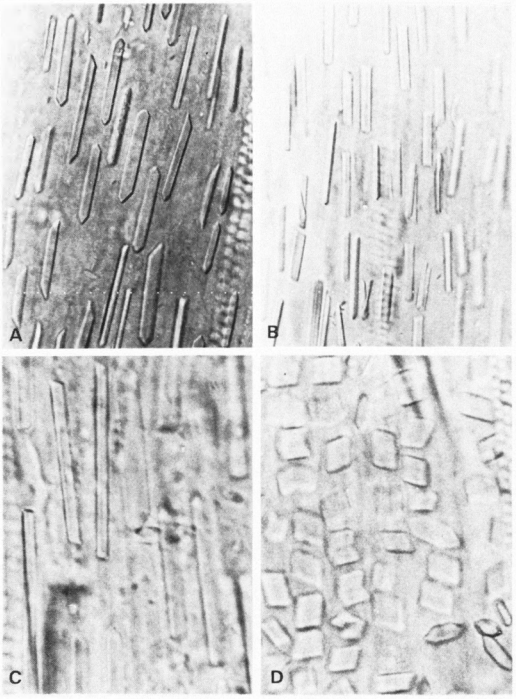


Fig. 1. Achenial wall crystals in the Liabeae. – A: *Cacosmia harlingii* (Harling 6050). – B: *C. hieronymi* (Asplund 17770). – C: *Ferreyranthus excelsus* (Hutchison & Wright 3854). – D: *Liabum wrightii* (Ekman 9253). – Photomicrographs by the author, ×c. 500.

1 a. **C. rugosa** var. **rugosa**

Illustr.: Humboldt, Bonpland & Kunth 1820 Plate 404; Lessing 1829 Plate 2 Figs. 31, 53–56; Hoffmann 1890 Fig. 122 A; Fig. 2 A–D.

Stems densely lanate and hirsute, the interwoven white hairs mixed with coarser, often brown- or purple-articulated hairs. Leaves acute; upper surface glabrous or nearly so, somewhat glossy green; lower surface densely white- or grey-tomentose.

Ecuador. Prov. Imbabura: S of Gonzales, 2700–3000 m, 1952, Fagerlind & Wibom 1293 (S) – Cajas, 3000 m, 1955, Asplund 17052 (S, US). – *Prov. Pichincha:* Prope Pifo, Sodiro (P) – Prope Pifo, 1897, Mille 582 (US). – *Prov. Chimborazo:* Vicinity of Huigra, mostly on the Hacienda de Licay, 1918, Rose 22204 (US) – Cañón of the Río Chanchán, ca 5 km N of Huigra, 5000–6500 ft, 1945, Camp E-3323 (K, P, US), Camp E-3454 (S) – Above Chunchí on road to Hacienda

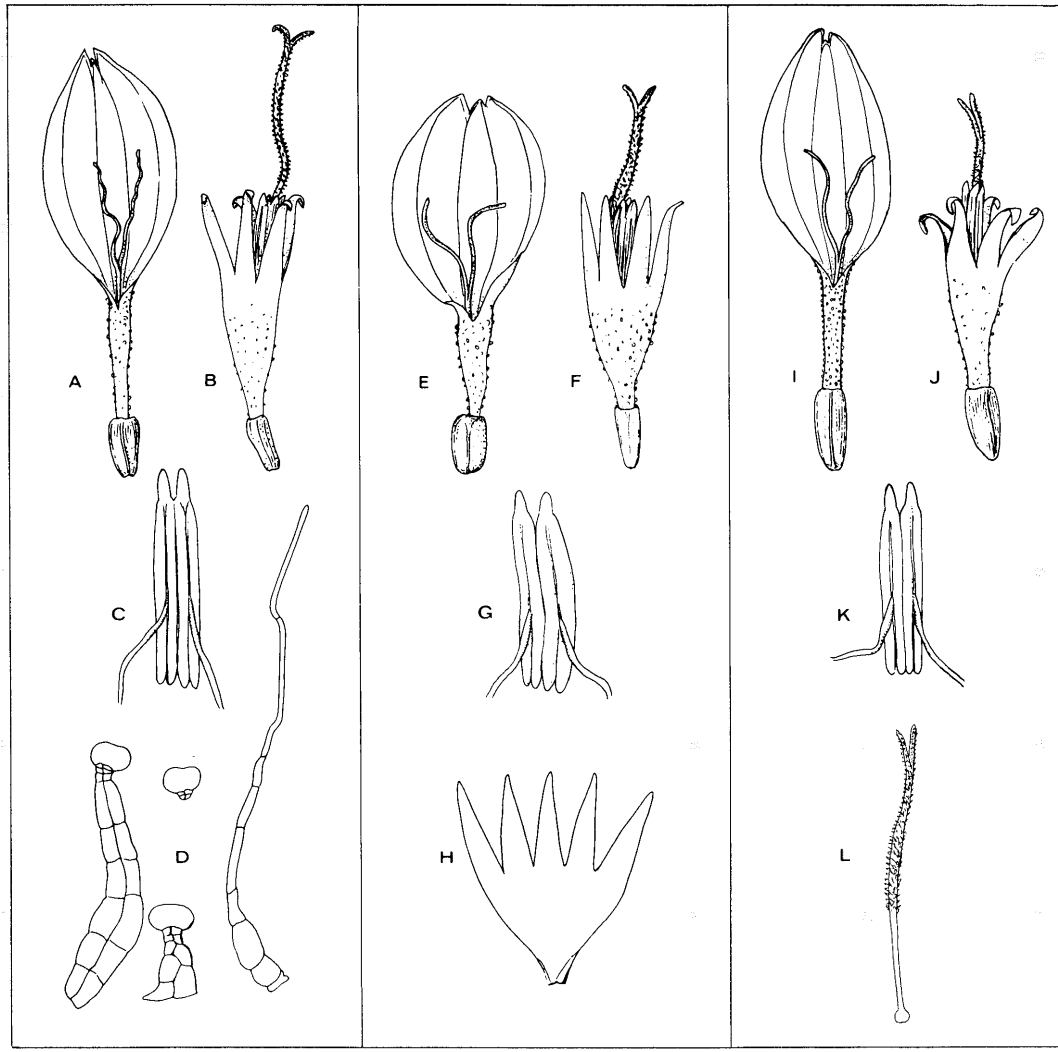


Fig. 2. *Cacosmia rugosa* var. *rugosa* (A–D), var. *nivea* (E–H) and var. *kingii* (I–L). – A, E, I: Ray-floret, ×6. – B, F, J: Disc-floret, ×6. – C, G, K: Anthers, ×12. – D: Corolla glands and hairs, ×100. – H: Corolla of disc-floret, laid out, ×6. – L: Style of disc-floret, ×6. – A–C: Harling & Andersson 14079, D: Hutchison & Wright 5031, E–H: Harling & Andersson 13467, I–L: Asplund 17938. – Del. auct.

Magna, Páramo de Cacheaco, 2500–3000 m, 1959, Barclay & Juajibioy 8305 (US). – *Prov. Cañar:* Between El Tambo and highest point on road from Cañar to Chunchí, 3100 m, 1959, Barclay & Juajibioy 8728 (US). – *Prov. Azuay:* Victoria de Portete, between division of road, SW of Cuenca, and Girón, 2820–2950 m, 1959, Barclay & Juajibioy 8339 (US). – *Prov. Loja:* Saraguro, Humboldt & Bonpland 3312 (P), herb. Willdenow 16749 (B non vidi, P fragment) – Vicinity of Saraguro, 1918, Rose 23135 (US) – Road from Loja to San Lucas, km 25, 2200 m, 1961, Dodson & Thien 568 (S, US) – Road Loja–Zaruma, near Chinches, 2400 m, 1974, Harling & Andersson 14079 (GB, S).

Peru. Dep. Piura. Prov. Huancabamba: W slope of Paso de San Cristobal, between Canchaqui and Huancabamba, 2800 m, 1947, Fosberg 27676 (US) – Abra de Porculla, entre Olmos y Jaén, 2000 m, 1959, Ferreyra 13738 (US). – *Dep. and Prov. Cajamarca:* Ca 1 km above and NE San Pablo, 2630 m, 1964, Hutchison & Wright 5031 (US). – *Dep. Libertad. Prov. Otuzco:* Usquil, 3000–3100 m, 1950, Ferreyra

7639 (US). – *Dep. Amazonas. Prov. Bongará:* Yambrasbamba–Pomacocha trail between Yambrasbamba and Yanayacu, 1900–2200 m, 1962, Wurdack 1016 (US).

Sine loco. "Peru", herb. Ruiz & Pavón (BM), "Huayaquil", Ruiz & Pavón (BM).

1 b. **C. rugosa** var. **nivea** Hieron.

Hieronymus 1901 p. 619. – *Orig. coll.:* Dombey s.n., Peru (holotype not traced; isotypes in P).

Clairvillea quinquenervia DC. – *Cacosmia quinquenervia* (DC.) Steud. – See under the species.

Illustr.: Fig. 2 E–H.

Stems and branches white-lanate without coarser articulated hairs, glabrescent with age. Leaves acute–acuminate; upper surface subglabrous and ± glossy green; lower surface densely white-tomentose.

Ecuador. Prov. Loja: Gonzanamá, Bonpland (P) – Summit and upper slopes of Cerro Villonaco, 2600–2750 m, 1974, Harling & Andersson 13467 (GB, S) – Road Loja–Zaruma, between Chinches and Sambi, 1700–2400 m, 1974, Harling & Andersson 14255 (GB, S).

Peru. Dep. Amazonas: Chachapoyas, 1840, Mathews 3075 (BM, K). – *Dep. Cajamarca. Prov. Chota:* Huambos, 2000 m, 1956, Soukup 4540 (US). – *Dep. Libertad:* Sunchubamba, upper Chicama Valley, 3100 m, 1957, Ellenberg 1765 (US). – *Dep. Huánuco. Prov. Huánuco:* Huánuco, hills, 1863, Pearce 62 (K) – Mito, 3000 m, 1922, Macbride & Featherstone 1386 (US) – Huallaga, by Chaglla (Dep.?) 3000 m, 1909–14, Weberbauer 6708 (US) – Mitotambo, arriba de Mito, 3000–3100 m, 1950, Ferreyra 6668 (US), Ferreyra 6901 (US) – Yanano, 2000 m, 1923, Macbride 4941 (S, US) – *Prov. Pachitea:* Panao, 2500 m, 1940, Asplund 13576 (S, US).

Sine loco. Peru, herb. Pavón (P), Peru, Pavón, ex herb. Schultz Bip. (P), "Huayaquil", Ruiz & Pavón (BM) – Peru, Dombey 255 (P), Dombey s.n. (P), Dombey s.n., ex herb. Schultz Bip. (P).

1 c. **C. rugosa** var. **kingii** H. Robinson

Robinson 1976 p. 48. – *Orig. coll.:* Fosberg 27777, Peru, Dep. Cajamarca, Prov. Jaén, Tabaconas, on Río Tabaconas, 20 km ESE Huancabamba, 1900 m, 11.VI. 1947 (US holotype).

Illustr.: Robinson 1976 p. 51–52: Fig. 2 I–L.

Stem pubescence as in var. *rugosa*. Leaves acute; upper surface ± densely setose, green; lower surface densely grey-tomentose.

Usually of a lower stature than the other varieties, normally about one metre tall. The presence of milky sap has been recorded from this taxon, but the distribution of this character in the genus needs further investigation, as pointed out by Robinson (1976).

Ecuador. Prov. Loja: Mountains of Cuenca and Loxa, Jameson (US, wrongly cited as *C. hieronymi* in Robinson 1976); sine loco, Jameson (S) – Loja, 2200 m, 1947, Harling 1596 (S) – Loja, S of the town, 2350 m, 1955, Asplund 17938 (S) – Loja, road to La Toma, 1958, 2400 m, Harling 5749 (S) – Cerro Villonaco, 20 km W of Loja along the road to Catomayo, 2200 m, 1967, Sparre 16259 (S) – Nudo de Cajanuma, 6 km S of Loja, 2400 m, 1967, Sparre 16573 (S) – Along the road to Zamora, ca 2 km E of Loja, 7000 ft, 1976, King & Garvey 6913 (US).

Peru. Dep. Amazonas. Prov. Chachapoyas: 1838, Mathews (K, P). – *Dep. Cajamarca, Prov. Jaén:* Above Tabaconas, 2300 m, 1912, Weberbauer 6304 (US) – Tabaconas, on Río Tabaconas, 20 km ESE Huancabamba, 1900 m, 1947, Fosberg 27777 (US).

2. **C. harlingii** B. Nord. sp. nov.

Orig. coll.: Harling 6050, Ecuador, Prov. Loja, Cariamanga, road to Amaluza, km 15, 22.VII. 1959 (S holotype, GB isotype).

Illustr.: Fig. 3 A–G.

A *C. rugosa* H.B.K. foliis non manifeste denticulatis, involucris partim purpureis, a *C. hieronymi* H. Robinson foliis majoribus, tomento caulium pilis articulatis intermixto, corollis pubescentia carentibus, ab ambabus ligulis aurantiacis differt.

A sparingly branching shrub ca 1 m high. *Stems* floccose-lanate with white interwoven hairs mixed with brownish articulated coarser hairs, becoming glabrescent with age, striate and brownish-purplish. *Leaves* in distant pairs, subsessile, ovate, up to 6.5 cm long and 3 cm broad, acute–acuminate, with three main longitudinal veins and a fine reticulate venation pattern; upper side green and glabrous except for some tomentum along the impressed veins; lower side white-tomentose; leaf-margin finely crenulate-serrulate without distinct teeth. *Capitula* rather densely corymbose-paniculate. *Involucre* 5–6 mm long, 2.5–3 mm wide, subglabrous, somewhat 5-angular with 20–25 phyllaries in 5 vertical rows, coriaceous–subscarious, faintly mid-veined, fimbriate-ciliate-margined; outer ones small, ca 1 mm long and wide, ovate with rounded tip; middle ones 2.5–3.5 mm long and 1.5 mm wide, ovate-oblong; inner ones ca 5 mm long and 1 mm wide, oblong-lanceolate, acute, densely glandular on the proximal half. *Ray-florets* 5, orange-

coloured. Tube 2–2.5 mm long, narrowly cylindric, occasionally split almost to the base, glandular, but without hairs. Lamina elliptic-oblong, 3.5–5 mm long, 1.5–2.3 mm wide, 4-veined, abaxially glandular, apically minutely trifid. *Disc-florets* 6. Corolla 4.5–5 mm long, glandular with scattered subsessile glands; lobes lanceolate, 1.5–2 mm long, 0.5 mm wide, without midvein, becoming recurved. *Anthers* 2 mm long incl. appendage, basally glabrous or minutely papillate, obtuse. *Style* densely hispidulous from about the middle; style branches 0.6–0.8 mm long, obtuse. *Achenes* (immature) oblong, somewhat flattened-triquetrous (esp. in the ray-florets) with 2 lateral ribs and 1 adaxial rib, glabrous, brown, apically truncate, ca 2 mm long and 1 mm wide, 10-veined.

The new species is named in honour of its collector, Professor Gunnar Harling, leader of the 'Flora of Ecuador' project. Distinctive features are the purplish involucre, the orange-coloured rays, and the absence of corolla hairs. The small size of capitula and rays is also noteworthy, especially in comparison to *C. hieronymi*.

Ecuador. Prov. Loja: Cariamanga, road to Amaluza, km 15, 1959, Harling 6050 (GB, S).

3. **C. hieronymi** H. Robinson

Robinson 1976 p. 46. – *Orig. coll.:* King 6702, Ecuador, Prov. Azuay, along the road to Loja, ca 6 km SE of Cumbe, 9600 ft, 4.II. 1974 (US holotype).

C. rugosa var. *arachnoidea* Hieronymus 1901 p. 601. – *Orig. coll.:* Lehmann nos. 5213 (isosyntype in K) and 7957 (isosyntype in US).

Illustr.: Robinson 1976 p. 50, 52; Fig. 3 H–M.

Much-branched shrubs 1–2 m high. *Stems* and branches floccose-lanate with a white–grey tomentum, with age glabrescent, striate, brownish. Internodes usually 1–4 cm long. *Leaves* shortly petiolate, narrowly ovate–lanceolate, acute, 1.5–5 cm long, 0.5–1.7 cm wide, green and glabrous above (except for some tomentum along the main veins), densely grey-tomentose below; margins bullate-crenulate without distinct teeth. *Capitula* ± densely corymbose-paniculate. *Involucral bracts* ca 25, ovate–oblong–lanceolate, up to ca 8 mm long and 2 mm wide (outer gradually smaller, to ca 1 mm), dark or purplish brown at least apically, faintly 1–3-veined, laxly tomentose – somewhat villous or subglabrous, with scattered dark glands on the outer ones and more densely set light glands basally on inner phyllaries; margins somewhat ciliate-villous. *Ray-florets* yellow or sulphur yellow. Tube cylindric, 2–5 mm long, glandular and laxly villous. Lamina elliptic-oblong, 5–8 mm long, 3–5 mm wide, 4–7-veined, apically tridentate. *Style* branches subulate, ca 2.5 mm long, minutely puberulous or subglabrous. *Disc-floret* corolla yellow or greenish yellow, 5–7 mm long, villous with thin flexuous hairs; lobes lanceolate, 2–2.5 mm long and ca 0.5 mm wide, rolled back. *Anthers* 2–2.5 mm long incl. appendage; base obtuse–subacute, distinctly papillate. *Style* densely hispidulous above the middle; style branches 0.4–0.6 mm long, obtuse. *Achenes* oblong, somewhat compressed-triquetrous (ray-florets) or somewhat 4–5-angular (disc-florets), 1.5–2 mm long, glabrous, faintly ribbed, brown.

This taxon was independently recognized as a distinct species by Dr H. Robinson and myself. It differs from other taxa of the genus by the smaller leaves without obvious marginal teeth, the more or less brown involucres, the condensed inflorescences, and the rich corolla pubescence. Apparently the species is restricted to southern Ecuador, which is obviously the centre of variation in the genus.

Ecuador. Prov. Cañar: Vicinity of Santa Rosa de Cañar, 1918, Rose 22666 (US) – N of Biblián, 2900–3200 m, 1974, Harling & Andersson 13246 (GB, S). – *Prov. Azuay:* About Cuenca, Jameson (?), ex herb. Hooker (K) – Supra Quinjed in Andibus mediis cuencanis, 2800–3200 m, Lehmann 5213 (K, wrongly labelled as Colombia, Popayán) – Prope Mariviña in prov. Cuenca, 2800–3200 m, Lehmann 7957 (US) – Páramo Alpacada, along Pan-American Highway 82 km S of Cuenca, 9500 ft, 1944, Wiggins 10810 (US) – Along Río Tarqui, 4–18 km S of Cuenca, 8300–9000 ft, 1945, Camp E-1890 (US) – Vicinity of Cuenca, near union of Ríos Tarqui and Yanuncay, 8200–8900 ft, 1945, Camp E-2635 leg. Prieto (K) – Cuenca, Cumbe, 3000 m, 1947, Harling 822 (GB, S) – Hacienda Pizhin on road from Cuenca to Oña, 2800 m, 1955, Asplund 17770 (GB, S) – Between Cumbe (2704 m) and ca 2800 m on southbound road, 1959, Barclay & Juajibioy 8435 (US) – S of Cumbe, 2700 m, 1968, Harling, Storm & Ström 8697 (GB, S) – Ca 6 km SE of Cumbe along the road to Loja, 9600 ft, 1974, King 6702 (US) – Road Cuenca–Loja, upper N slopes of Valle del Río León and S parts of Páramo de Tinajillas, 2800–3200 m, 1974, Harling & Andersson 14514 (GB) – Ca 39 km SE of Cumbe along the road to Loja, 10200 ft, 1976, King 6903 (US). – *Prov. Loja:* Between

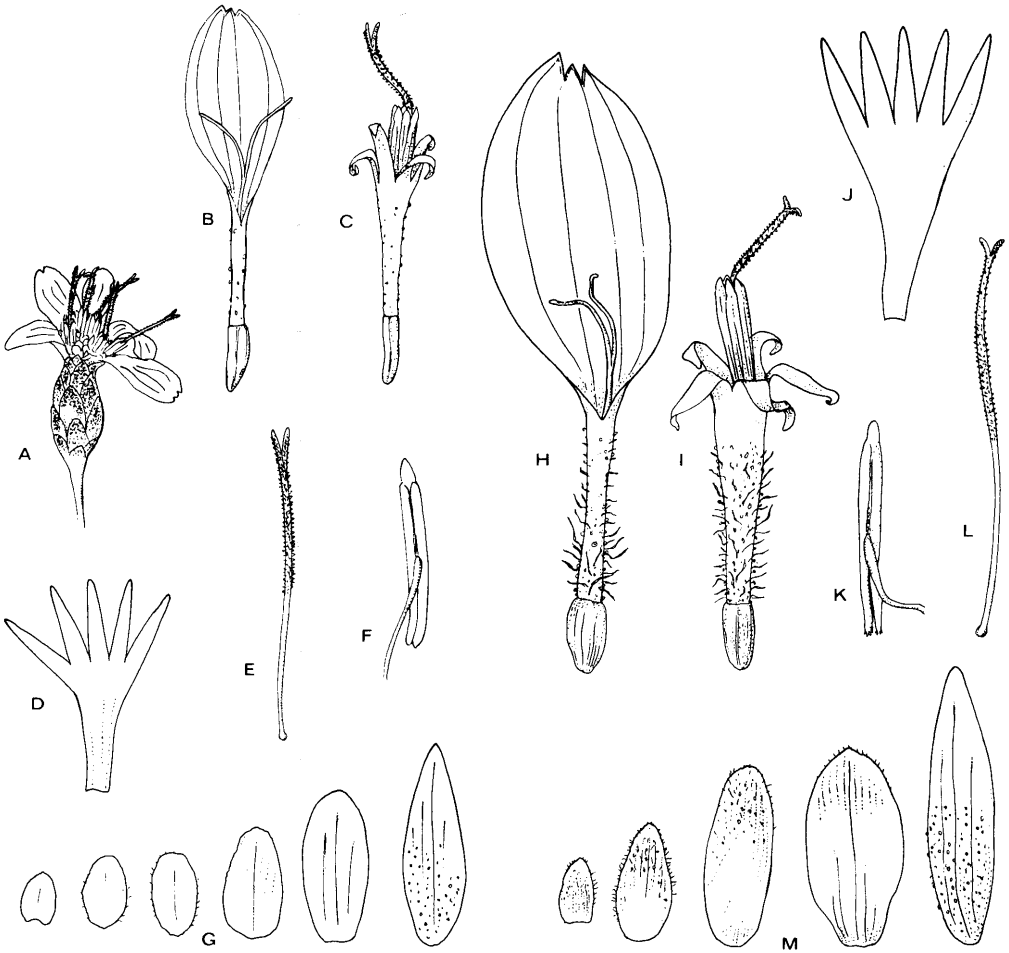


Fig. 3. *Cacosmia harlingii* (A–G: Harling 6050) and *C. hieronymi* (H–M: Asplund 17770). – A: Capitulum, ×3. – B, H: Ray-floret, ×6. – C, I: Disc-floret, ×6. – D, J: Corolla of disc-floret, laid out, ×6. – E, L: Style of disc-floret, ×6. – F, K: Anther, ×12. – G, M: Series of involucral bracts, ×6. – Del. auct.

San Lucas and Oña, 2200–3100 m, 1923, Hitchcock 21569 (US) – On road from Loja to Cuenca, 2900 m, 1961, Dodson & Thien 854 (S, US).

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Some Bothnian subspecies in the Ranunculus auricomus complex: origin and dispersal

Erik Julin

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Ranunculus auricomus ssp. *dactylophyllus* Julin ssp. nov. and ssp. *pectinifolius* Julin ssp. nov. are described and illustrated. Distribution maps of these and seven other subspecies are given. *R. monophyllus* ssp. *neumanii* has a western Bothnian distribution and seems to be of preglacial origin. *R. auricomus* ssp. *crassiusculus* and ssp. *inconspectus* are amphi-Bothnian and perhaps of preglacial origin. *R. auricomus* ssp. *holanthus*, ssp. *pectinifolius*, ssp. *rotundellus* and perhaps ssp. *dactylophyllus* seem to be indigenous and to have originated in the western Bothnian area in postglacial times. *R. auricomus* ssp. *obscurans* is eastern Bothnian and seems to be of postglacial origin. *R. auricomus* ssp. *oligandrus* seems to have spread from Estonia to Finland and thence to Sweden. Dispersal in hay and manure and, over longer distances, by shipping and road and railway traffic have all been important. All taxa are hemerophilous and some may be in danger of extinction due to reduction of suitable habitats.

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When it became clear in the 1930's that the *Ranunculus auricomus* group consists of apomictic (pseudogamous) microspecies, extensive collecting was started, by Gunnar Marklund in Finland and by John Axel Nannfeldt in Sweden, in order to describe the microspecies and establish their distributions. The basic material is still insufficient; nevertheless an analysis of the regions of origin and the migration routes of some biotypes is now possible.

Unfortunately little or nothing has been published on the taxonomy and distribution of the *R. auricomus* complex in Norway, Denmark or the southern part of the Baltic area.

The phytogeographically most interesting microspecies are those with comparatively large distribution areas and particularly those showing disjunctions. Some such microspecies, whose distribution areas at least in places reach the Gulf of Bothnia, are discussed in this paper.

The same terminology which was proposed in a previous paper (Julin 1967) has been used here: viz. *gynoclinium* is used for the pistil-bed and *androclinium* for the stamen-bed. *Interval* is that part of the receptacle which lies between the androclinium and the gynoclinium. The stipe of an individual carpel is called a *carpellophore*.

In Figs. 4 and 10, the oldest leaf is shown at top left-hand, the youngest at bottom right-hand side. Since the whole leaf series is rarely present on a single specimen, the leaves drawn are derived from several plants in the type collection.

Localities already published can be found in the references given under each subspecies. A complete list of all new localities has been deposited at the Museum of Natural History, Section for Botany, S-104 05 Stockholm 50, Sweden, and copies will be sent on request. The abbreviations of province names follow Hylander (1953), except that 'Klm' has been included in 'Sm' and 'Gbg' in 'Vg'.

R. auricomus L. ssp. **crassiusculus** Markl.

Marklund 1961 p. 37.

Localities: Ahti & Hämet-Ahti 1971, Julin & Nannfeldt 1966 (the information concerning Gstr is erroneous), Malmgren 1970, Marklund 1961. – *New localities:* Sweden: Srm 2, Upl 4, Gstr 2, Hls 6, Mdp 5, Hrj 4, Ång 12, Jmt 7, Vb 6, ÅsL 3, LyL 5, PL 2, LL 1. Norway: STrd 1.

This subspecies often occurs in damp places. It has a wide distribution on both sides of the

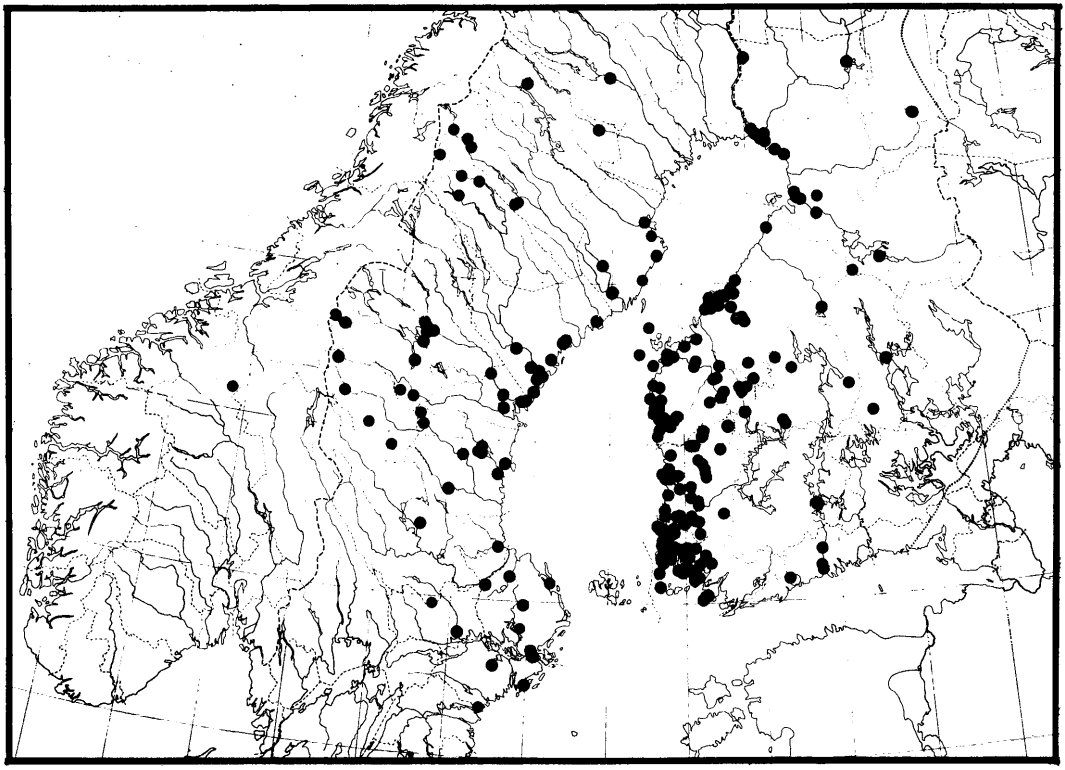


Fig. 1. Known distribution of *R. auricomus* ssp. *crassiusculus*.

Bothnian Gulf (Fig. 1). In Finland it is most common in the west. The occurrence of this subspecies is better known in Finland than in Sweden, which may explain the apparent difference in frequency in the two countries. In Sweden there are many inland localities near the mountains. However, these localities seem to be very much associated with human activities. With some hesitation, I consider this subspecies to be of preglacial origin.

R. auricomus L. ssp. **dactylophyllus**
Julin ssp. nov.

Holotypus: Suecia, Vestrobottnia, Vännäs, Vännfors, in prato ripario secus flumen Vindelälven 1.7. 1966 Julin (UPS).

Localities: Sweden: Srm 1, Upl 1, Gstr 1, Hls 8, Mdp 15, Hrj 1, Ång 20, Vb 13, PL 1. Finland: Ob 2.

Planta mediocriter alta vel parva, sat gracilis. *Caules* erecti, inferne violacei, ramum infimum sub angulo c. 45° emittentes. *Folia* rosularia ambitu semiorbicularia, basi plerumque lineam fere rectam formante. Folia exteriora multilobata, lobis lanceolatis, plerumque integerrimis. Folia intermedia et interiora multipartita, segmentis lanceolatis, acutis, integerrimis vel parce acuti-dentatis. Folia aestivalia multi- vel trilobata vel fere indivisa, acute triangulariter dentata. Laciniae foliorum caulinorum sat anguste lanceolati-lineares, integerrimae. *Flores* vel imperfecti, petalis omnibus abortivis, vel – saepissime – perfecti, ad 18 mm diametro. Sepala pallida. Stamina numerosa capitulum pistillorum rotundum superantia. Torus obovate oblongus, albidus, dense pilosus, pilis disparibus, non eadem longitudine. Carpellophora apice mediocriter longa, basi brevia. Androclinium intervallo perbrevi aliquanto crassius.

A medium-sized, rather slender plant, with erect stems which are violet basally. The lowermost branch emerges at an angle of c. 45°. *Basal leaves* semiorbicular in outline. Exterior basal leaves multilobate, their lobes lanceolate, usually entire. Central and inner leaves multipartite, their parts lanceolate, acuminate, entire or with a few acuminate teeth. Summer leaves mul-

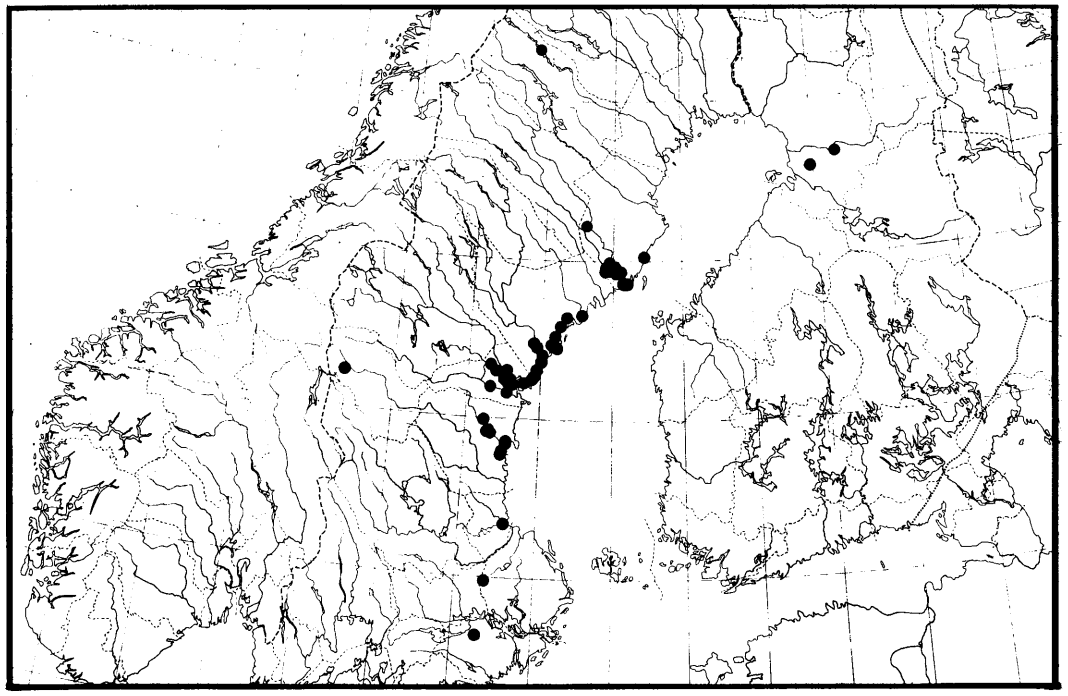


Fig. 2. Known distribution of *R. auricomus* ssp. *dactylophyllus*.

tilobate, trilobate or almost entire, with acuminate, triangular teeth. Segments of cauline leaves rather narrow, lanceolate–linear, entire. *Flowers* either imperfect, with all petals abortive or, most frequently, perfect, up to 18 mm in diameter. Sepals pale. Stamens numerous, overtopping the rounded head of pistils. Receptacle obovate–oblong, densely pubescent, whitish. Upper carpellophores of the receptacle of medium length, lower carpellophores short. Androclinium somewhat thicker than the interval, which is very short.

Some features of ssp. *dactylophyllus* are reminiscent of *R. monophyllus*, e.g. the intermixture of short hairs among the long ones on the receptacle and the shape of the basal leaves. Whether or not bladeless sheaths are present basally is uncertain. Such sheaths are characteristic for *R. monophyllus*, but usually disappear during anthesis and can only be studied on young, fresh material. The 'species' limits within the *R. auricomus* complex are vague (Marklund 1954, 1961, Marklund & Rousi 1961, Julin & Nannfeldt 1966). However, in our present state of knowledge, e.g. the hairs on the ripe carpels are denser and somewhat longer than in *R. monophyllus*, this subspecies should be included in *R. auricomus*.

This subspecies occurs in e.g. alder fens, valley bottoms, relatively damp pastures and paddocks, and in more or less natural, damp meadows. Its continuous distribution is confined to a small part of the W coast of the Bothnian Gulf (Fig. 2), where it may have originated in postglacial time (cf. ssp. *holanthus* and ssp. *pectinifolius*). According to this hypothesis, however, the outlying localities present difficulties, especially since some of them, e.g. that in Härjedalen, seem to be spontaneous. Together with the morphological similarity with *R. monophyllus* this may indicate that ssp. *dactylophyllus* is nevertheless of preglacial origin.

R. auricomus L. ssp. **holanthus** Markl.

Marklund 1964 p. 22.

Localities: Marklund 1964. – *New localities:* Sweden: Gstr 14, Hls 6, Mdp 13, Ång 35, Jmt 1, Vb 11. Finland: Ab 1. Norway: Nrd 1.



Fig. 3. *R. auricomus* ssp. *dactylophyllus*. Holotype. – Below right: Receptacle, ×20.

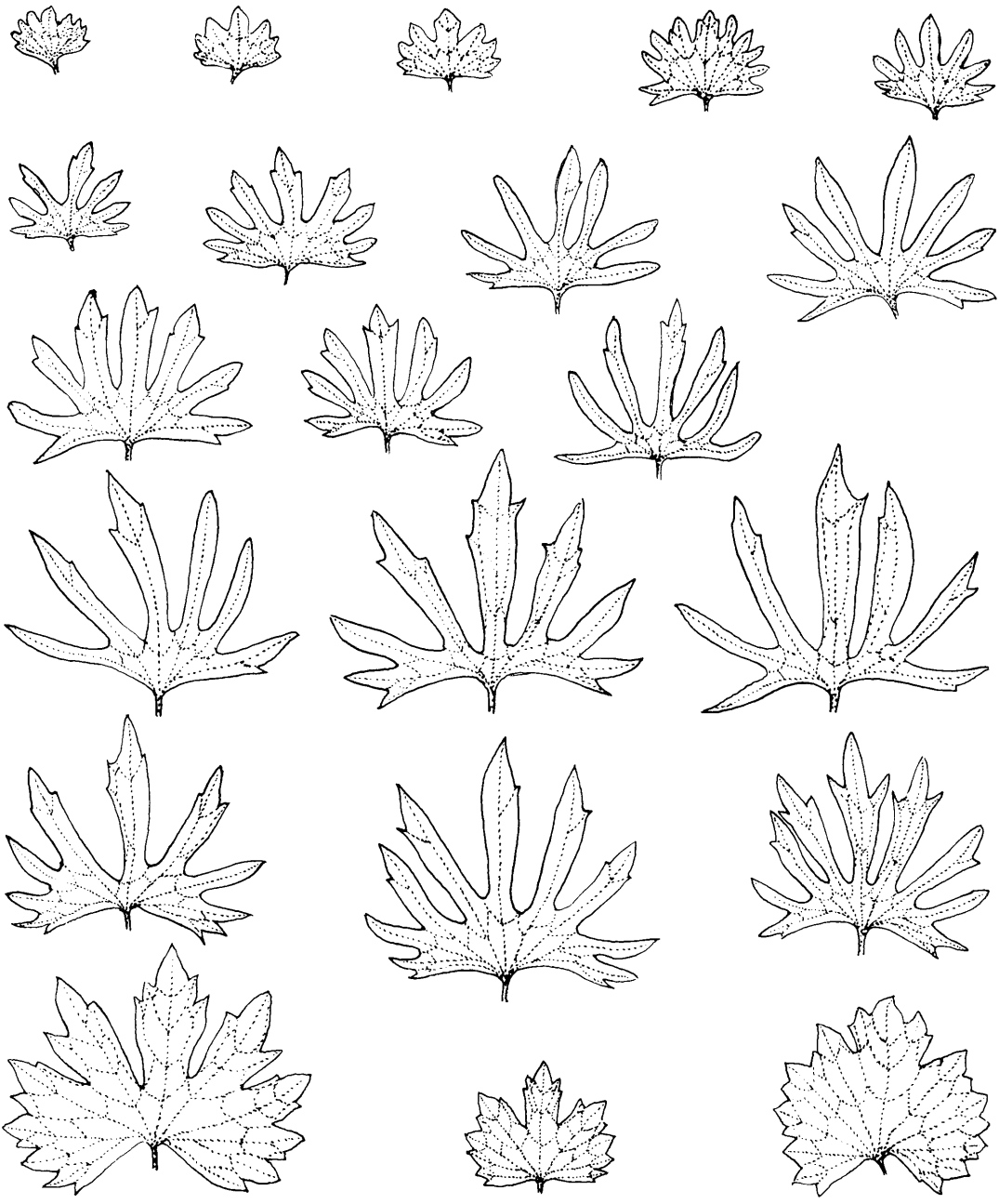


Fig. 4. *R. auricomus* ssp. *dactylophyllus*. Basal leaves of the type collection.

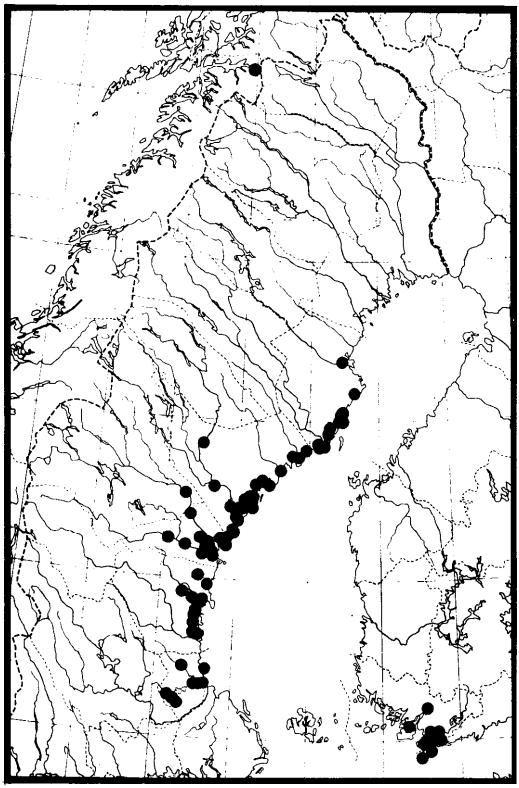


Fig. 5. Known distribution of *R. auricomus* ssp. *holanthus*.

The main Swedish distribution of this subspecies lies within a narrow belt along the W coast of the Bothnian Gulf (Fig. 5). It has almost certainly evolved within this area, and is consequently of postglacial origin. The many coastal localities indicate that dispersal by shipping, and by traffic along the old coastal road, has been important.

The Finnish localities are the result of an introduction from Sweden (Marklund 1964). In the middle of the thirteenth century the south coast of Finland was colonized from Sweden. The settlers came partly from the area around the lake Mälaren and partly from the coastal region of S Norrland. *R. auricomus* ssp. *holanthus* is restricted to those areas where Swedish is spoken; it does not occur in the adjacent Finnish-speaking parishes.

The Norwegian find was made by the present author on 14.7. 1965. The locality was on an abandoned farm near the railway station of Katterat, in the innermost part of the Rombakfjord just where a stream flows into the fjord. In the same locality ssp. *pectinifolius* was also found. The two subspecies occurred near each other, in patches covering 20–30 m^2 each. The occurrences of both these subspecies so far away from their main areas of distribution is most likely due to dispersal by railway traffic. In view of the size of the clusters, the occurrences are not very recent and may well date back to the construction of the Kiruna–Narvik railway-line which was opened for provisional traffic in 1902. Close to the locality there was a stable for the horses which were used when the railway was under construction. Some of the hay for the horses was imported from Sweden, most probably by rail from the eastern part of Medelpad province where both subspecies are common.

Assuming that ssp. *holanthus* colonised its Norwegian locality when the railway was under construction, the annual increase can be estimated as being 0.7 m^2. If only local dissemination has occurred this rate of spread seems reasonable. The increase of its area in Finland has been much more rapid. Here it is a question of a rural landscape, where the activities of the peasants and of their domestic animals have greatly facilitated dispersal.

R. auricomus L. ssp. **inconspectus** Markl.

Marklund 1961 p. 63.

Localities: Ahti & Hämet-Ahti 1971, Marklund 1961, Olofsson 1961. – *New localities:* Sweden: Sm 1, Srm 2, Nrk 1, Vrm 2, Upl 5, Dlr 1, Hls 2, Mdp 1, Hrj 1, Ång 3, Jmt 5, Vb 6, LyL 2.

Like ssp. *crassiusculus,* this subspecies often occurs in very damp places, has a wide distribution on both sides of the Bothnian Gulf (Fig. 6), and is predominantly western in Finland. The apparent differences in frequency between Finland and Sweden are probably due to the same cause as mentioned under ssp. *crassiusculus*.

With some hesitation I consider ssp. *inconspectus* to be of preglacial origin.

R. auricomus L. ssp. **obscurans** Markl.

Marklund 1961 p. 83.

Localities: Julin & Nannfeldt 1966, Marklund 1961,

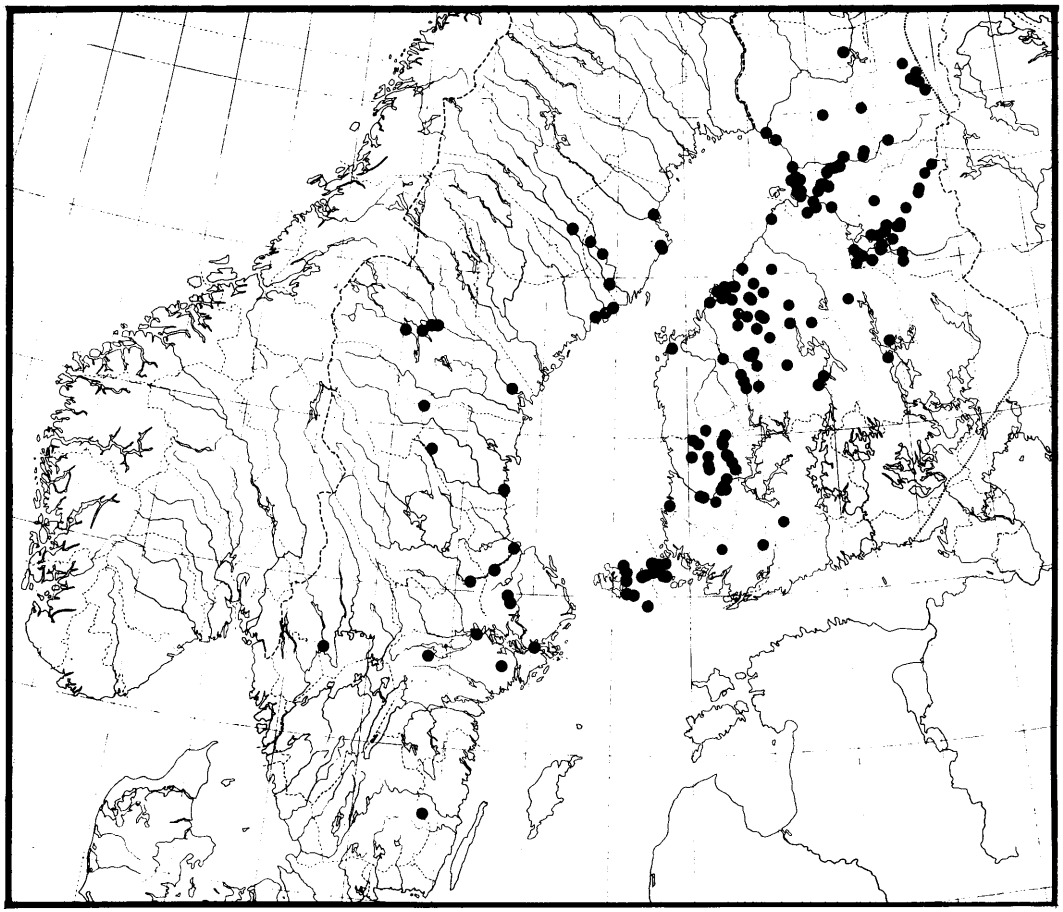


Fig. 6. Known distribution of *R. auricomus* ssp. *inconspectus*.

Olofsson 1961. – *New localities:* Sweden: Sk 2, Sm 1, Ög 1, Vg 1, Srm 3, Upl 2, Ång 3, Vb 13, LyL 2. Finland: Al 1.

This subspecies is very common on the Åland Islands and on the SW coast of the Finnish mainland, and probably originated there in postglacial times (Fig. 7). In Sweden, scattered occurrences are found from the province of Uppland southwards to Skåne, with an outlying, more concentrated area around the town of Umeå and along the valleys of the rivers Umeälven and Vindelälven in Västerbotten province, where it probably arrived by shipping from Finland.

R. auricomus L. ssp. **oligandrus** Markl.

Marklund 1961 p. 88.

Localities: Julin 1964 a, Marklund 1961, Olofsson 1961. – *New localities:* Sweden: Ög 6, Srm 7, Nrk 3, Upl 2, Vrm 1, Gstr 1, Hls 1, Mdp 7, Ång 6, Vb 4, Nb 36, LL 2, TL 4. Finland: Sa 1. USSR: Estonia 16, Latvia 2.

This subspecies has an eminent capacity for colonising man-made habitats and for otherwise benefiting from human activities in nature (Marklund 1954, 1961). This is especially clear for the N Swedish occurrences, e.g. around the town of Haparanda ssp. *oligandrus* is one of the most troublesome of garden weeds and between

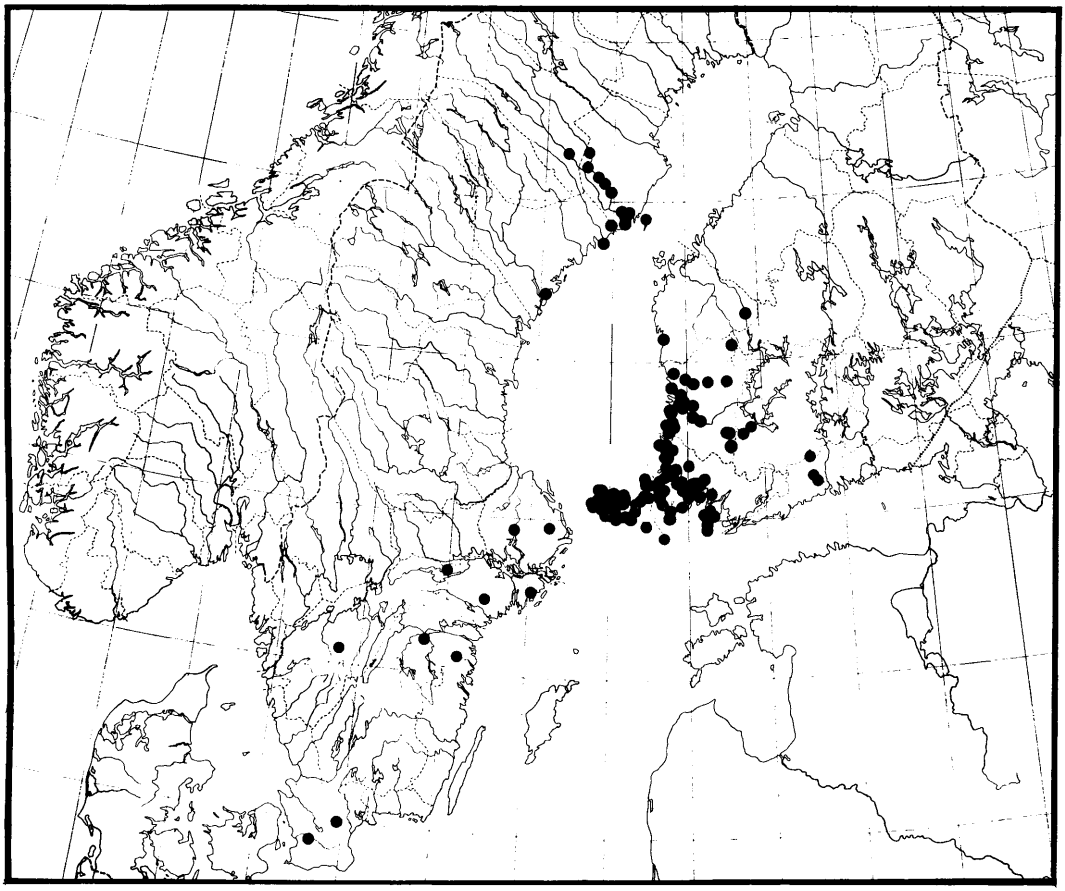


Fig. 7. Known distribution of *R. auricomus* ssp. *obscurans*.

Piteå and Älvsby it can be found at even the smallest of railway stations. Most of the inland localities in N Sweden have originated by dispersal along the railways.

A prime reason for the extensive distribution of this subspecies may be its capacity of growing vigorously in man-made habitats. It has the most extensive distribution area of all our subspecies of Goldilocks. There are also some records from Estonia and Latvia, many more than could be expected considering the low number of collections of *R. auricomus* available from these areas. The subspecies may in fact be very common there.

Judging from the map (Fig. 8) ssp. *oligandrus* would appear to have originated in postglacial times in S Finland, since it seems to be most common there nowadays. However, considering its rapid spread in recent times, its close connection with man-made habitats, and its discontinuous range, especially in Sweden but also in W Finland, I consider it more probable that ssp. *oligandrus* migrated into Finland from the SE during the postglacial and thence spread to Sweden.

R. auricomus L. ssp. **pectinifolius** Julin ssp. nov.

Holotypus: Suecia, Medelpadia, Selånger, Solbacken in pascuo betuloso 22.6. 1962 Julin (UPS).

Localities: Sweden: Hls 1, Mdp 21, Ång 12, Vb 1. Norway: Nrd 1.

Planta mediocriter alta. *Caules* plerumque curvati, graciles, inferne violacei, ramos sub angulo angusto emittentes; caules laterales subtus pilosi. *Folia* rosu-

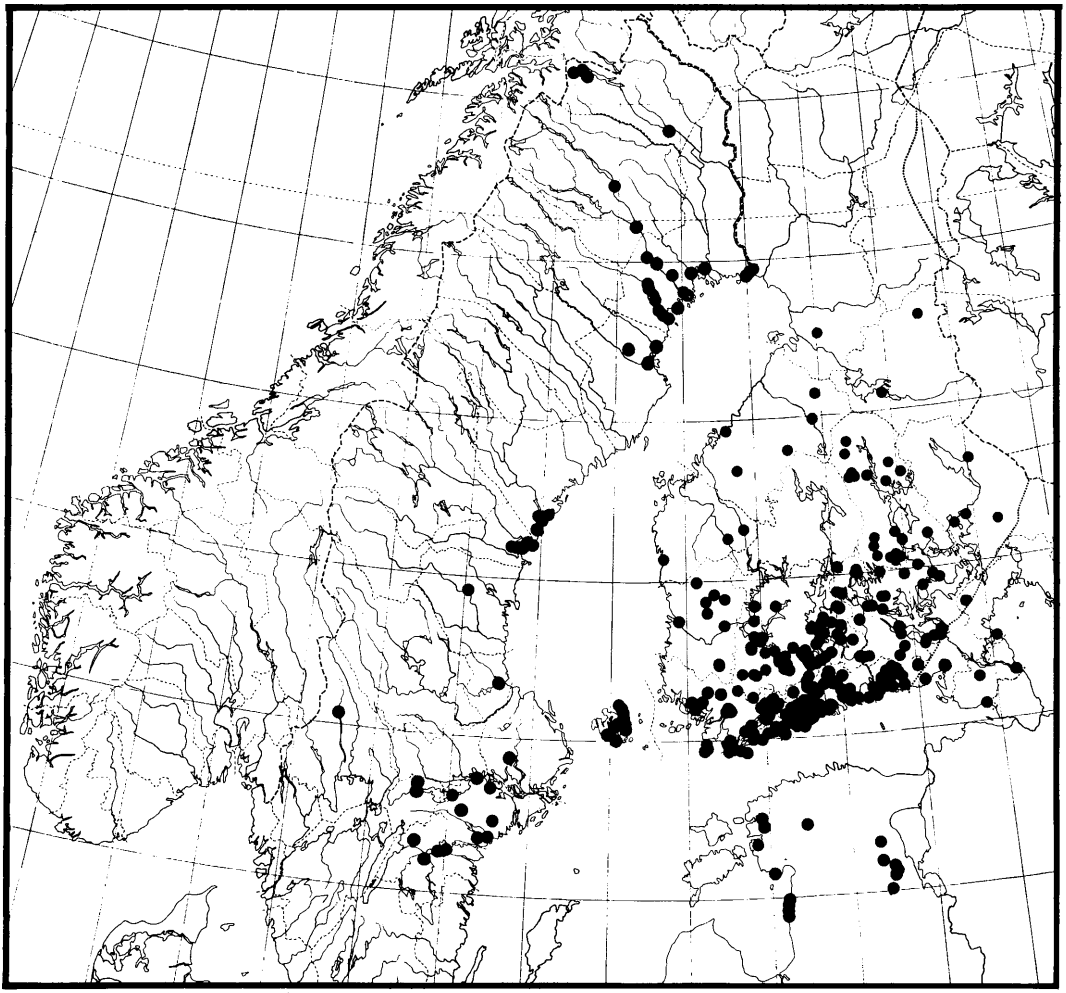


Fig. 8. Known distribution of *R. auricomus* ssp. *oligandrus*.

laria exteriora parva, reniformia, indivisa, obtruncate crenata. Folia sequentia ambitu reniformia, multilobata, lobis apice dilatatis, crenatis vel integerrimis. Folia intermedia ambitu fere orbicularia, multipartita, segmento medio ± late cuneato, dente apicali lato, obtuso et dentibus lateralibus minoribus praedito, vel indiviso vel profunde trilacinulato et petiolulato, segmentis lateralibus cuneatis. Folium sequens multipartitum, segmentis anguste lanceolatis, petiolulatis, integerrimis vel parce dentatis vel lacinulatis, sinu basali peraperto. Folia interiora multipartita, segmentis lanceolatis vel lanceolati-cuneatis, acutis, acute dentatis vel lobulatis. Folia aestivalia reniformia, trilobata, lobo medio rotundate cuneato, lobis lateralibus latis, leviter lobulatis vel indivisis, lobis (lobulis) late breviterque acute mammiformi-dentatis, sinu basali fere 90°. Laciniae foliorum caulinorum mediocres ad sat longae, lineari-lanceolatae, obtusulae, integerrimae vel – validiores folii infimi – interdum dente vel lacinula una alterave praeditae. *Flores* vel valde imperfecti, petalis omnibus vel plurimis abortivis vel interdum perfecti, petalis bene evolutis, c. 20 mm diametro. Sepala apice rubro-violacea. Stamina numerosa apicem capituli pistillorum superantia. Torus parvus, breviter obovatus ad ovatus, glaber; carpellophora mediocriter longa; intervallum breve.

A medium-sized plant with generally curved, slender stems, which are violet basally. The branches emerge at an acute angle. Lateral stems pubescent basally. Exterior *basal leaves* small, reniform, entire, truncately crenate. Sub-



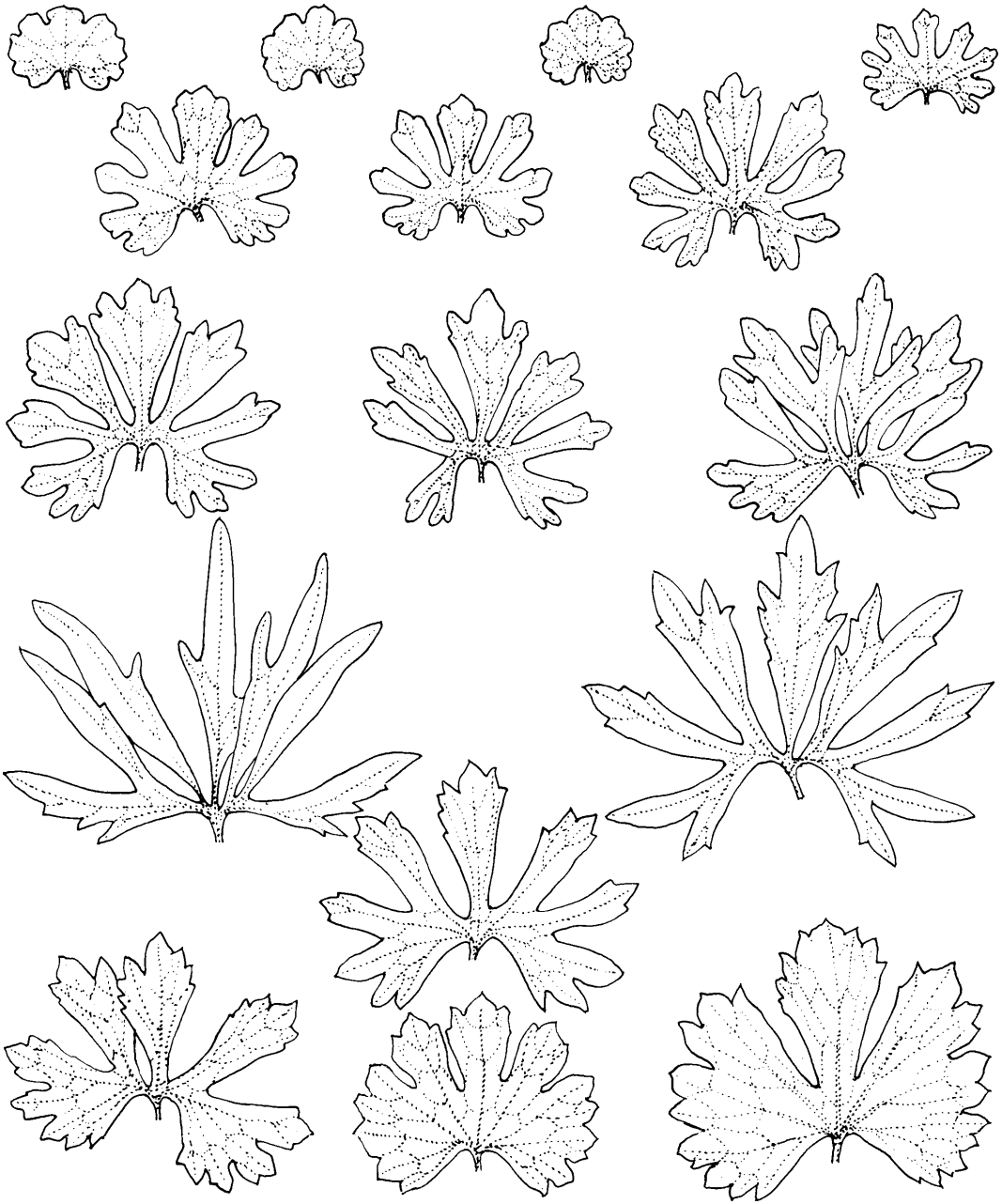


Fig. 10. *R. auricomus* ssp. *pectinifolius*. Basal leaves of the type collection.

Fig. 9. *R. auricomus* ssp. *pectinifolius*. Holotype. – Below right: Receptacle, ×20.

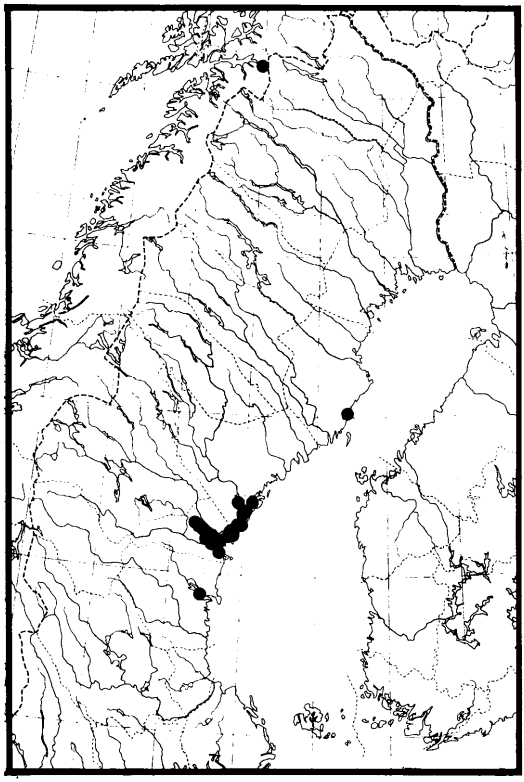


Fig. 11. Known distribution of *R. auricomus* ssp. *pectinifolius*.

sequent leaves reniform in outline, multilobate, lobes broader above, crenate or entire. Central leaves nearly orbicular in outline, multipartite, their median part more or less broadly cuneate with a broad, obtuse terminal tooth and smaller lateral teeth, either entire or more or less deeply trisected, shortly petiolulate, their lateral parts cuneate. The subsequent leaf multipartite, its parts narrowly lanceolate, petiolulate, entire or sparsely toothed or laciniate, the basal angle very open. Interior leaves multipartite, their parts lanceolate or lanceolate-cuneate, acuminate, acuminately toothed or lobulate. Summer leaves reniform, trilobate, median lobe roundly cuneate, lateral lobes broad, slightly lobulate or undivided, lobes (lobules) broad and short, with acuminate, nipple-shaped teeth, basal angle c. 90°. Segments of the cauline leaves moderately to fairly long, linear-lanceolate, a little obtuse, entire or – the most vigorous segments of the lowest leaf – sometimes possessing a few teeth or slender lobes. *Flowers* either imperfect, with all or most petals abortive, or sometimes perfect, with well-developed petals, c. 20 mm in diameter. Sepals purple apically. Stamens numerous, overtopping the head of pistils. Receptacle small, shortly obovate to ovate, glabrous; carpellophores moderately long; interval short.

This subspecies occurs in e.g. pastures and paddocks, relatively dry meadows, roadsides, lake- and sea-shore meadows, valley bottoms, alder fens and alder woods. Its main distribution area is a narrow belt along the W coast of the Bothnian Gulf (Fig. 11), where it almost certainly originated in postglacial times. There is also an extremely disjunct occurrence in N Norway, obviously the result of recent long-distance dispersal (cf. the discussion under ssp. *holanthus*, which has a very similar distribution).

R. auricomus L. ssp. **rotundellus** Markl.

Marklund 1961 p. 109.

Localities: Julin & Nannfeldt 1966, Malmgren 1970, Marklund 1961, Olofsson 1961. – *New localities:* Sweden: Vg 1, Srm 4, Upl 32, Vsm 2, Gstr 1.

This subspecies probably originated in the W part of the central postglacial area of evolution of the *R. auricomus* group (Fig. 12). It has probably been spread by shipping to Finland as well as to some of its more peripheral localities in Sweden. The Swedish W coast locality is in the Göteborg Botanical Gardens (a single plant).

R. monophyllus Ovcz. ssp. **neumanii** Julin

Julin 1964 b p. 487.

Localities: Julin 1964 b. – *New localities:* Sweden: Vg 4, Dlr 3, Hls 1, Mdp 19, Ång 6, Jmt 9, Vb 2, LyL 1, LL 1. Norway: Opl 7, STrd 8.

The discovery of these new localities (Fig. 13) has altered the picture presented by my previous map of this taxon (Julin 1964 b). My impression that ssp. *neumanii* has a preglacial origin has been strengthened. The localities in Falbygden (Västergötland province) may date back to the Middle Ages, since the mediaeval packway between Norway and Denmark passed

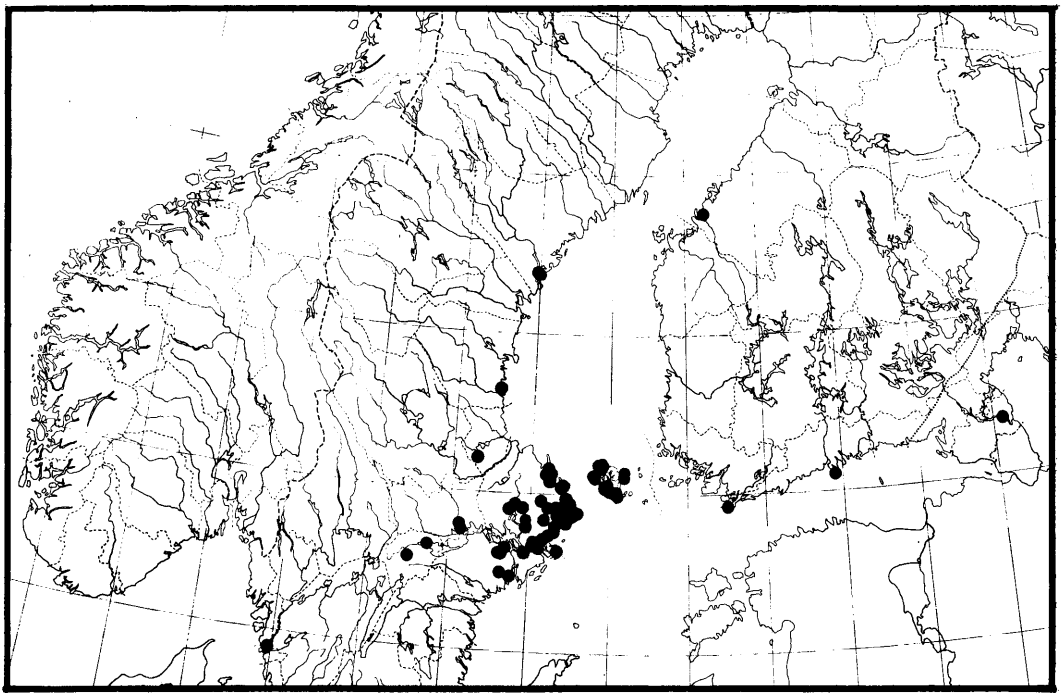


Fig. 12. Known distribution of *R. auricomus* ssp. *rotundellus*.

through this area (Nannfeldt, pers. comm.). The four northernmost Swedish localities are at railway stations and thus probably of later date.

The collective species *R. monophyllus* Ovcz. seems to comprise a number of fairly old, arctic subspecies. Its preglacial area, perhaps like that of *R. auricomus* var. *glabratus* Lynge (*R. lyngei* H. Sm.; Marklund & Rousi 1961), may have been extensive. Marklund (1965) considers that the subspecies of *R. monophyllus* reached Finland from the east. Without taking sides, I would like to draw attention to another possibility. A migration route southwards from the northern Norwegian ice-free refugia was already open by 8000 B.C., whereas immigration from the east seems to have been impossible for a long period of time because of formerly greater extent of the present White Sea (see e.g. Hultén 1971 p. 36). For ssp. *parvulifrons* Markl. and ssp. *boreigenus* Markl. at least, an immigration from the north appears to be the most probable alternative. I imagine that Marklund had something like that in mind when he gave the latter subspecies its name.

The general lack of knowledge of the detailed distributions of the various subspecies of *R. monophyllus* in N Finland presents a great difficulty. Further collecting is urgently needed before the phytogeographical problems connected with this taxon can be finally solved.

Possible means of dispersal

Goldilocks have no specialized means for dispersal. Their diaspores are small, relatively heavy and normally fall to the ground when ripe. They are viable only for a short period after ripening.

Dispersal by water seems to be of little importance. Fresh, fully ripe nutlets sink at once. Ripe nutlets, kept in a herbarium for some years, sank after few hours when put in water. To the best of my knowledge, Hesselman's (1897 p. 99) observation is the only report of the dispersal

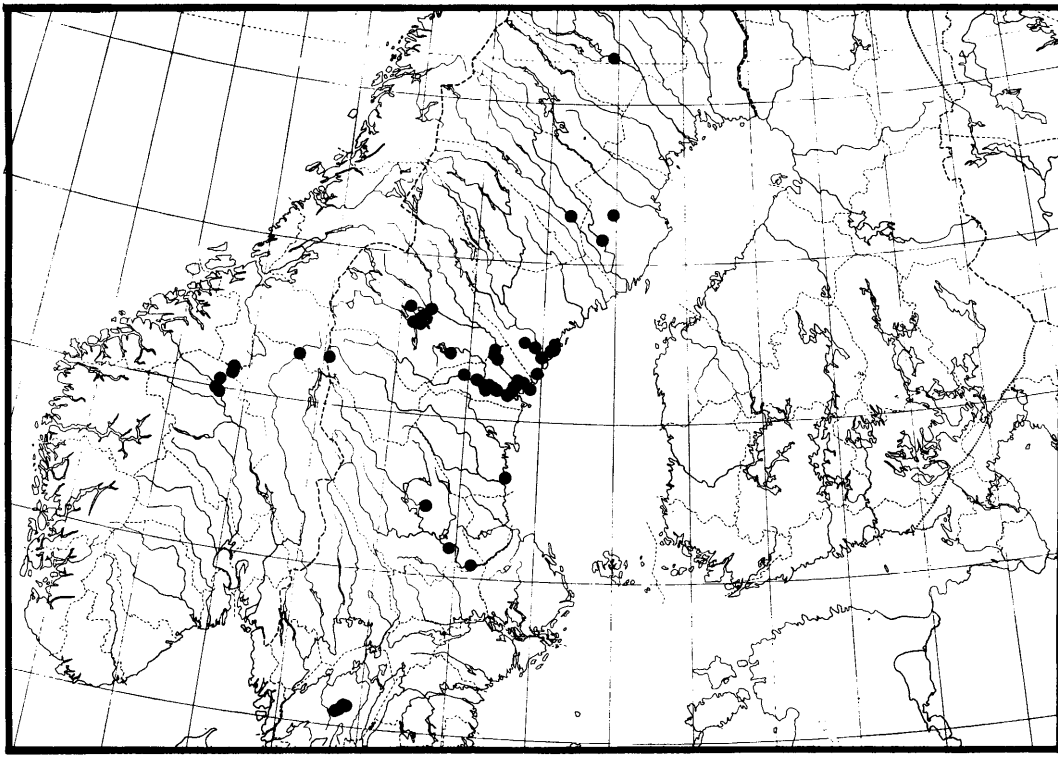


Fig. 13. Known distribution of *R. monophyllus* ssp. *neumanii*.

of Goldilocks by water. Only a single nutlet was caught in a drag-net after rowing c. 250 km. Water dispersal can only be of importance along fairly rapidly-flowing water-courses.

Dispersal with imported grass-seed (like *Hieracium;* Hylander 1943) has not been demonstrated, but should not be discounted (Julin 1965 p. 30).

Dispersal with manure. Goldilocks are not as acrid and poisonous as some other *Ranunculus* species. Nevertheless they are avoided by grazing animals, especially when they grow in pure stands. Therefore they are usually only swallowed by accident. As far as I know, the germination ability of nutlets, after passing through the alimentary canal of animals, has not been experimentally investigated. However, Paul Olofsson, who has a long experience as a farmer, emphatically claims that Goldilocks can be spread with manure, partly via the droppings of grazing animals, partly via the manure spread on natural meadows, which was at least formerly common on Vårdö, Åland (Olofsson 1961).

Rasch (1970), working on material from Gotland, also considered grazing animals to be of importance for the dispersal of Goldilocks, but apparently thought dispersal to be synzoochoric.

Before the activities of man and his domestic animals provided a means of dispersal for the Goldilocks, dispersal by wild animals, perhaps by the reindeer in particular, must have formed one of the most important factors.

Dispersal with hay. This was particularly important in the past, when a lot of the hay crop came from "natural" meadows (Olofsson 1961). In N Finland and Sweden, where Goldilocks are generally rather rare, they often occur near hay-barns.

Around Swedish country churches various subspecies of *R. auricomus,* derived from different parts of the parish, can often be found.

These accumulations may well date back to the days when people travelled to church by horse and carriage. The Goldilocks may have been introduced in the hay brought as fodder for the horses, or in the horse droppings.

Dispersal by shipping. For long periods of time shipping on the Gulf of Bothnia was subject to two special circumstances: viz. the Bothnian trade restrictions and the fishery along the coast of C Norrland carried on by fishermen from towns in C Sweden.

The Bothnian trade restrictions date back to the Middle Ages and were abolished in 1765. They imposed a ban on the ports of the Gulf of Bothnia to trade with any other place than Stockholm. Ballast for the return journey, when the cargo as a rule was lighter, was thus obtained from within the area of vigorous postglacial evolution of new taxa of Goldilocks, viz. the provinces of Södermanland, Uppland, the Åland archipelago and SW Finland.

The organized Bothnian coast fishery also started in the Middle Ages; in 1646 authorised fishing-vessels were sent northwards from the towns of Gävle, Öregrund, Strängnäs, Nyköping, Södertälje and Stockholm. Later several other towns were granted the same privilege. Along the coast of Norrland these fishermen established seasonal habitations to which they brought their goats and sometimes a few cows, and also hay for fodder. This type of fishery gradually came to an end in the late nineteenth century (Vedin 1939, Frödin 1958).

These two conditions may have contributed to the relatively richer flora of Goldilocks found along the SW part of the Bothnian coast, as compared with the NW part.

Dispersal by road and rail traffic. Dispersal along roads occurred in connection with the transport of hay, and also via horse droppings. The old coastal road along the Swedish side of the Gulf of Bothnia, as well as the roads leading inland up the large valleys in Norrland must have been of great importance.

Hay transport was also an important factor where dispersal by railway traffic was concerned, e.g. see *R. auricomus* ssp. *oligandrus*.

Hemerophily and survival

Most taxa in the *Ranunculus auricomus* complex are more or less hemerophilous. Nevertheless, all the subspecies treated here, with the possible exception of ssp. *oligandrus*, seem to be indigenous. The hemerophilous habit is more marked in the northern parts of the distribution areas and in the extreme north all occurrences are on man-made habitats.

Olofsson (1961) has described the ecological conditions for the rich flora of Goldilocks on the Åland Islands and pointed out that the number of suitable habitats has been gradually reduced, especially by the ploughing-up of natural meadows. However, he considered that local, man-made habitats, or new coastal habitats created by natural processes such as land uplift, may help to conserve the diversity of the *Ranunculus auricomus* flora.

Olofsson's reasoning may hold true for Swedish conditions too. Nevertheless, the future for the Goldilocks seems uncertain. Large-scale dispersal in hay and manure no longer occurs. Chemical weed control damages the existing populations. Hay-fields and pastures, preferred habitats for the Goldilocks, are being transformed into arable land, or afforested. When grazing and mowing cease, the Goldilocks become crowded out by more competitive species.

Apomictic taxa have fewer possibilities of adapting to changing ecological conditions than do sexually-reproducing taxa. When the changes in their habitats have reached a certain limit they will disappear. With their small distribution areas and their dependence on former agricultural practices, many of the subspecies in the *R. auricomus* complex are therefore probably now threatened with extinction.

Acknowledgements. My sincere thanks are due to Professor J. A. Nannfeldt, Uppsala, and to the late Dr G. Marklund, Helsingfors, for valuable information and stimulating discussions. In addition Professor Nannfeldt kindly kept me informed about recent acquisitions of Goldilocks in UPS, and read through the manuscript critically. I am also greatly indebted to the Directors of the Herbaria and to the many private persons who have kindly put material at my disposal.

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Cerastium alpinum and C. arcticum, a mature polyploid complex

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Cerastium alpinum (2n = 72, 144) and *C. arcticum* (2n = 54, 108) together constitute a polyploid complex which has now reached the mature stage and is exclusively composed of high polyploids. Some deviating numbers are probably derived from the euploid series. The nature of the intergradation and diversity in the complex and the role of hybridization are discussed. Two new subspecies are proposed to cover the truly arctic representatives of the *C. arcticum* group. *C. arcticum* ssp. *procerum* (Lange) Böcher comb. nov. seems to be restricted to Greenland and W Spitzbergen, while *C. arcticum* ssp. *hyperboreum* (Tolm.) Böcher comb. nov. extends from NE Canada to Novaya Zemlya but does not occur in Scandinavia. *C. arcticum* ssp. *arcticum* is atlantic-montane centering in the Faeroes and radiating to Scotland, Scandinavia, Iceland and southernmost Greenland.

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Hultén (1956) treated the *Cerastium alpinum* complex as a "case of worldwide introgressive hybridization". Without denying hybridization to be fundamental for the understanding of the structure and origin of the complex it may be advantageous to visualize this taxonomically troublesome group as a polyploid complex. It is not the intention to unravel the *C. alpinum–C. arcticum* complex in detail, but to discuss it in the light of experiences gained from other polyploid complexes.

The classical polyploid pillar complex comprises basic diploid taxa, which are morphologically distinct and reproductively separated, and polyploids which intergrade and form series of poorly defined entities. This model is impossible to transfer directly to the situation in the *C. alpinum–C. arcticum* complex. This complex has reached a level higher than tetraploidy, and clearly belongs to the category of mature complexes. Stebbins (1971) assumes that such complexes originated during Pleistocene and Pliocene.

Polyploid complexes contain at the higher ploidy levels entities which cannot be regarded as species in the traditional sense. These entities are neither uniform, nor well demarcated. On the other hand they may represent characteristic, perhaps common character combinations which are either resulting from a preference to certain environmental conditions or are due to historical events (survival and isolation in refugia, changes in biotype contents during migrations). Taxonomists would, in such cases, have to use their experience by estimating which characters they would prefer when they have to draw more or less artificial demarcation lines between the entities. In a case like *C. alpinum–C. arcticum* ecological and geographical evidence should be considered together with the morphological and cytological facts.

Hybridization

The *Cerastium alpinum–C. arcticum* complex falls naturally into two groups, the *C. arcticum*

group with 2n = 54, 108 and the *C. alpinum* group with 2n = 72, 144.

Asplund (1918) discusses the possibility of hybridization between *C. alpinum* and *C. arcticum*. He says that although hybrids have been recorded from Scandinavia it is doubtful whether intermediate specimens in the high Arctic should be evaluated as hybrids. Here the species are autogamous and the intermediate specimens do not produce bad pollen which is the case with Scandinavian hybrids. According to Warming (1920) *C. alpinum* and *C. arcticum* (*"C. latifolium"*) from Dovre, Norway, are usually self-pollinating or, where the plants locally are gynomonoecious, the female plants are probably pollinated by insects. Judging from the available chromosome counts crossing may be difficult. *C. alpinum* seems to consist mainly of octoploids (2n = 72) while *C. arcticum* is most often dodecaploid (2n = 108). Fertilization between gametes with n = 36 and n = 54 may not be easy and no plants with 2n = 90 have been recorded.

Possible origins of Cerastium arcticum

In the *Cerastium alpinum–C. arcticum* complex no diploid original species have been recorded. But it seems justified to discuss the alpine *C. latifolium* group as a relatively original and perhaps ancient group. According to counts by Favarger & Söllner (1949) and Söllner (1952, 1953) the *C. latifolium* group consists of tetraploids (2n = 36). The species (*C. latifolium, C. uniflorum* and *C. pedunculatum*) vary a great deal and intermediates have been described, but according to Merxmüller (1950) the many forms may largely be modifications and not species hybrids. The species of the *C. latifolium* group resemble members of the *C. arcticum* group to such an extent that they can be thought of as possible ancestors of *C. arcticum* s.l.

Söllner (1953) was the first who discussed the evolution of the polyploidy in the *C. arcticum* group. He suggested that *C. arcticum* ssp. *arcticum* (*"C. edmondstonii"*) with 2n = 108 might have arisen after chromosome doubling in a theoretical hexaploid, which might in turn be the result of a cross between *C. alpinum* (2n = 72) and *C. latifolium* (2n = 36). It is not unlikely that *C. latifolium* s.l. is one of the ancestors of the *C. arcticum* group, but it is difficult to imagine that *C. alpinum* could have contributed with as much as two genomes each with 18 chromosomes. Anyway, the type of pubescence of *C. arcticum* ssp. *arcticum* is very unlike that of *C. alpinum*. It is probably impossible to point out a recent taxon which could have been the other ancestor.

As the first step in the evolution one should perhaps suggest the formation of a triploid hybrid between a species related to *C. latifolium* (2n = 36) and an extinct, diploid *"pre-alpinum"* (2n = 18). The hybrid (2n = 27) would probably be sterile and by doubling give an allohexaploid, fertile entity with 2n = 54. Again this might, after a second doubling, give rise to plants with 2n = 108. If two allohexaploids of slightly different origin and genetical constitution were joined, the final step would result in double allododecaploids. According to this scheme *C. arcticum* might be polyphyletic, a possibility which would fit in with the taxonomic subdivision of the species given below.

Although most of the counts referable to *Cerastium arcticum* s.l. are dodecaploid (2n = 108), two hexaploid counts (2n = 54) are mentioned by Löve & Löve (1975), one from Greenland (Böcher & Larsen 1950) and one from Mt Chibiny (Kola Peninsula) by Sokolovskaja & Strelkova (1960). Both counts are listed under *C. hyperboreum* Tolm. by Löve & Löve (1975), presumably since Böcher et al. (1968) mentioned 2n = 54 for *C. arcticum* var. *vestitum* Hult. which was listed as a synonym for *C. hyperboreum* by Hultén (1956).

With regard to the material from Kola very little information is given by Sokolovskaja & Strelkova (1960). They refer their plant to *C. alpinum*. The material from Greenland is discussed under *C. arcticum* ssp. *procerum* below.

Cerastium arcticum Lange ssp. **arcticum**

C. edmondstonii (Wats.) Murbeck & Ostenfeld in Bot. Notiser 1898 p. 246 (1898) – *C. arcticum* ssp. *edmondstonii* (Wats.) Löve & Löve in Acta Horti Gotoburgensis 20 p. 110 (1956).

It seems impossible to maintain ssp. *edmondstonii* as a separate entity because the type of *C. arcticum* from S Greenland and Iceland is almost identical to material from Iceland and the Faeroes referred to *C. edmondstonii* (Fig. 1).

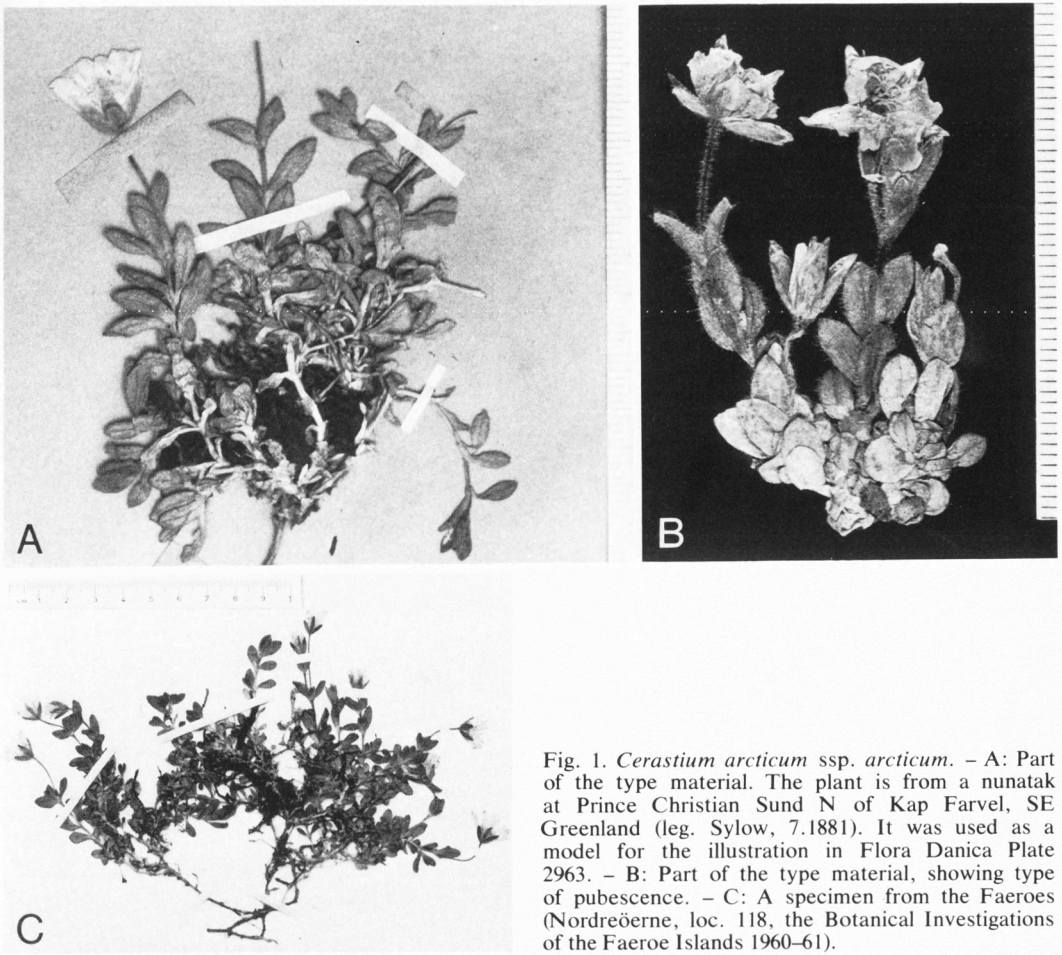


Fig. 1. *Cerastium arcticum* ssp. *arcticum*. – A: Part of the type material. The plant is from a nunatak at Prince Christian Sund N of Kap Farvel, SE Greenland (leg. Sylow, 7.1881). It was used as a model for the illustration in Flora Danica Plate 2963. – B: Part of the type material, showing type of pubescence. – C: A specimen from the Faeroes (Nordreöerne, loc. 118, the Botanical Investigations of the Faeroe Islands 1960–61).

Thus, according to the rules, the name *C. arcticum* has to cover plants which originate from environments which are not typically arctic, e.g. the Faeroes, the Shetlands, Scotland and the Kap Farvel area in S Greenland. *C. arcticum* is very typical and very uniform in the Faeroes. According to Ostenfeld "*C. edmondstonii*" is "pretty distinct from the alpine *C. latifolium* but verges towards another alpine species *C. uniflorum*". He concludes that the Faeroese plant belongs to a small north-Atlantic group of species (e.g. *Alchemilla faeroensis*) which is common all over the Faeroes but otherwise has a limited distribution. This view was also held by Simmons (1906) who doubts that the true "*C. edmondstonii*" is present on Greenland. After having studied the rich material labelled *C. edmondstonii* in C I have come to a similar conclusion. This taxon appears to be very distinct. It is common on all the islands but less frequent in the lowlands (Hansen 1966 map p. 49, "*C. arcticum*"). From this centre it radiates towards Iceland and the coastal mountains in S Greenland, Scandinavia and Scotland, but many populations found in these areas are less typical, perhaps because they have undergone introgression from other dodecaploids which they have met. Icelandic specimens referred to *C. arcticum* var. *vestitum* are clearly intermediate.



Fig. 2. *Cerastium arcticum* ssp. *procerum*. – A: The type material, from W Greenland (Holm & Warming 1884). – B: Specimens from the head of the Buksefjord, Greenland, 53°56' N (leg. Jon Feilberg, G.B.U. 5565). It has grown in north-exposed rock-crevices. Note reduced number of flowers but long internodia.

The number 2n = 108 was attached to *C. arcticum* Lange by Löve & Löve (1975). However, in their paper on the Icelandic flora (Löve & Löve 1956) they say that Icelandic material of two types which they call ssp. *arcticum* and ssp. *edmondstonii* as well as plants which appear to be fertile hybrids between them have 2n = 108. The same chromosome number was given for "ssp. *edmondstonii*" from the Shetlands (Söllner 1953) and Scotland (Brett 1954).

Brett (1954) reports formation of multivalents in *C. arcticum* from Scotland but adds that the disjunction of the chromosomes appeared to be regular. However, in a flower bud from Snowdon, meiosis was highly deviating with unpaired chromosomes, laggards, bridges and fragments in every PMC. A few seedlings had 2n = c. 126 which might be explained as the results of hybridization.

Cerastium arcticum ssp. **hyperboreum** (Tolm.) Böcher comb. nov.

Basionym: *C. hyperboreum* Tolmatchev in Skr. Svalbard Ishavet 34 p. 6, Plate I Fig. 1 (1930) – *C. arcticum* var. *sordidum* Hultén in Svensk Bot. Tidskr. 50 p. 456 (1956) – *C. arcticum* var. *vestitum* Hultén in Svensk Bot. Tidskr. 50 p. 453 (1956).

Hultén (1956) did not accept Tolmatchev's *C. hyperboreum* as a distinct species. Instead, he referred the material to his two varieties *C.*

arcticum var. *sordidum* and var. *vestitum*. The two varieties are not well separated morphologically, although I prefer to keep var. *sordidum* as a variety under this subspecies.

C. arcticum ssp. *hyperboreum* seems to be well circumscribed ecologically and geographically, being typically arctic, ranging from NE America and Greenland to Spitzbergen and Novaya Zemlya. It does not reach Scandinavia. Areas where ssp. *hyperboreum* and ssp. *arcticum* overlap are W Spitzbergen, N Iceland, middle Greenland, NE Labrador and S Baffin. This area needs to be investigated more carefully. My impression is that the occurrence of ssp. *procerum* in Greenland and W Spitzbergen complicates the matter, at least as far as Greenland is concerned.

The chromosome number 2n = 108 has been reported for material that clearly belongs to this subspecies. Holmen (1952) states this number for plants collected by him in Peary Land, and the material from this area belongs almost exclusively to var. *sordidum*. Holmen's count was referred to in Böcher et al. (1968 p. 129).

The material with 2n = 108 (n = 54) from Clavering Island in NE Greenland (Jørgensen et al. 1958 p. 57, Fig. 85) also probably belongs to var. *sordidum* or var. *vestitum* which are abundant on that island. However, there are no specimens bearing indication regarding the chromosome numbers.

Cerastium arcticum ssp. **procerum** (Lange) Böcher comb. nov.

Basionym: *C. alpinum* γ *procerum* Lange in Meddel. Grønland 3 p. 245 (1887) – *C. arcticum* var. *procerum* (Lange) Hultén in Svensk Bot. Tidskr. 50 p. 451, Plate III Fig. 1 (1956).

There is no doubt about the existence in Greenland of a coarse and tall, not densely tufted entity which has a type of pubescence reminiscent of that in *C. arcticum* ssp. *arcticum* but which is very different in other respects. Lange (1887) draws attention to the divaricate cymes and the long pedicels, characters that seem to be very useful. I prefer to evaluate the taxon as a subspecies mainly because it seems to cross occasionally with other members of the 108 chromosome group. The material to be regarded as the type was collected in W Greenland in 1884 by Holm and Warming (Fig. 2 A).

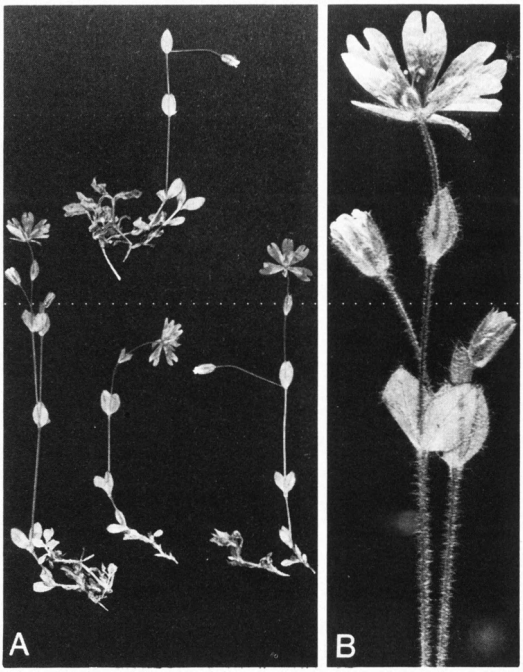


Fig. 3. *Cerastium arcticum* ssp. *procerum*. – A: Material grown from seeds from Fredskild 797. – B: Detail.

In 1957 Bent Fredskild collected a very vigorous, 30 cm tall, loosely tufted plant at Sermermiut S of Jakobshavn, W Greenland. The plant (Fredskild 797) grew in manured soil. Plants grown from seed had 2n = 108 and were lower and had shorter leaves (Fig. 3). The original plants as well as the offspring had green, pubescent leaves but no *alpinum* hairs. They clearly belong to ssp. *procerum*. Fredskild 5659, Perdlertutkuat, 69°58' lat. N, Nordfjord, Disko Island is very similar, being about 30 cm, loosely tufted with 6–7 cm long pedicels and ripe capsules measuring up to 2 cm. It is also green, not lanate, and has long and narrow, tapering–pointed sepals. It grew in a south-exposed knee-high *Salix* shrub, in other words under favourable conditions. Another specimen from a moss-marsh by a brook in the same locality reached a height of 16 cm and had smaller leaves, but the same long pedicels and capsules. Here the cymes are reduced to one flower on a long, often projecting pedicel, cf. similar specimen from Buksefjord (Fig. 2 B).

A hexaploid collection (2n = 54) mentioned by

Böcher & Larsen (1950) was originally referred to var. *vestitum* due to its type of pubescence. However, considering the habit and leaf size it is clearly more suitably accommodated in ssp. *procerum*. The plants (Jakobsen 882, 2.9. 1947, Niaqornat, 70°47' lat. N, 53°40' long.) seem to have been loosely tufted with 8–12 cm long stems and cymes of (1–)2(–4) flowers. The sepals are tapering with scarious margins and acute apices. The petals are twice as long as the sepals. Leaves, stems and pedicels are pubescent with long, light yellowish hairs and short glandular ones particularly on the stems and pedicels. The pedicel of the lowermost flower in a cyme of three often projects at almost right angles to the stem below.

Both hexaploids and dodecaploids have thus been found in ssp. *procerum*. The principle of including races with different chromosome numbers under the same name has been used in other polyploid complexes, e.g. the *Phacelia magellanica* complex (Heckard 1960) or the *Campanula rotundifolia* complex (Böcher 1960).

The Cerastium alpinum group

The many counts cited in Löve & Löve (1975) show that most plants of this group are octoploids (2n = 72). However, Brett (1954) found 2n = c. 144 in material of "*C. alpinum*" from Abisko in N Sweden.

Among the octoploids are *C. alpinum* ssp. *alpinum* and ssp. *lanatum* (Lam.) Simk., *C. glabratum* Hartm. (*C. alpinum* ssp. *glabratum* (Hartm.) Löve & Löve), *C. regelii* Ostenf. and *C. beeringianum* Cham. & Schlecht.

Some additional records are mentioned below together with a few remarks.

C. alpinum ssp. *lanatum*. – Angmagssalik, E Greenland (coll. T. Hatting 1958). B 29. 2n = 72, n = 36 – Disko, Lyngmarksfjeldet, 300 m (coll. TWB). B 21. 2n = 72 – Qapiarfik N of Jakobshavn, W Greenland (coll. TWB). B 32. 2n = 72, n = 36. During anaphase I some bridges were observed while acentric fragments could not be detected. – Kangersuneq S of Christianshåb, W Greenland (coll. TWB). B 35. 2n = 72 – Hasselsfjeld, Søndre Strømfjord, W Greenland. B 4832. n = 36. During anaphase I a number of univalents were observed lagging. n = 36 was counted at anaphase II which appeared almost normal – Akureyri, Iceland. B 38. 2n = 72. The cultivated plants had small leaves with densely spaced long white hairs.

C. glabratum. – Ankerlien, Kåfjorddalen, Troms, Norway (coll. G. Halliday). 2n = 72 was counted in plants raised from seeds.

C. regelii or perhaps *C. arcticum* × *regelii*. – Ny-Ålesund, W Spitzbergen (coll. N. Foged 1958). 2n = 82–86. A few seedlings gave rise to plants which were close to *C. regelii*. They died before a close study was possible.

C. beeringianum ssp. *terrae-novae* (Fern. & Wieg.) Hult. – Montreal. Counts of root-tip mitoses resulted in a number lower than 72 (perhaps 68). The plants grew perfectly well and resembled those pictured by Hultén (1956 Plate V).

Discussion

The *Cerastium alpinum–C. arcticum* complex is a mature high polyploid complex, but following the thoughts of Stebbins (1971 p. 169) it has to be considered as being among the declining complexes where the diploid ancestors have become extinct. However, although being mature and without ample possibilities of further increase in ploidy the complex is not evolutionarily stagnant. Jørgensen et al. (1958) discuss hybrids between entities belonging to the two euploid series (*C. alpinum* and *C. arcticum*), thereby approaching the views advanced by Hultén (1956). Also the deviating numbers found by Brett (1954) and by me (in a plant related to *C. regelii*) suggest that crossing can still take place even at a high polyploid level and in spite of most entities usually being autogamous.

However, crossing between recent high polyploids is probably of secondary importance for the understanding of the intergradation and variation in the complex. Alloploid evolution involving crossing between genomes of 9 or 18 chromosomes and doubling of the hybrid products has probably taken place as repeated cycles two or three times in both groups. The resulting entities which we see today may be composed of up to 12 or 16 genomes each with 9 chromosomes. The genomes have different, although related, genetic constitutions and usually many genomic parts are present 2–8 or more times enabling permanent heterozygosis for several alleles of the same genes, which serves as a buffer against genetic change. High polyploid entities thereby have firmly incorporated a great ecological versatility but have not lost the possibility of gene exchange. In our case where the various genomes probably contain considerable genetic material in common with the original now extinct diploids we may

set up a model according to which each specimen (biotype) is composed of different numbers of modified (genetically changed) basal genomes which we might call *"latifolium"*, *"lanatum"*, *"alpinum"*, *"glabratum"* and *"regelii"*. A low number of such modified *alpinum* genomes and a higher number from *latifolium* might give *C. arcticum* ssp. *arcticum*, while ssp. *procerum* might contain modified *latifolium*, *alpinum* and *glabratum* genomes and ssp. *hyperboreum* would perhaps mainly involve modified *latifolium* and *lanatum* genomes.

The great ecological amplitude in the *arcticum* group enables it to find suitable ecological niches from the maritime foggy and subarctic Faeroe mountains (ssp. *arcticum*) to the deserts of high arctic Peary Land (ssp. *hyperboreum*). But at the same time we find a more or less clinal transition from green subglabrous rather loosely tufted small-leaved biotypes to grizzled, hairy, more densely tufted or pulvinate ones. As we proceed to low-arctic middle W Greenland we gradually find relatively high-growing, loosely tufted, subglabrous, rather large-leaved biotypes. These transitions suggest that a selection is taking place or has taken place among the multitude of available combinations in the complex. Therefore the transitional types should not be regarded merely as hybrids between well circumscribed taxa. They may largely be due to long-time selection of the best adapted combinations within this wide-ranging polyploid complex.

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Studies in African Cyperaceae XVI

New taxa of Isolepis R. Br.

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Isolepis meruensis R. Haines & K. Lye sp. nov. and *I. setacea* (L.) R. Br. var. *aberdarica* R. Haines & K. Lye var. nov. are described and illustrated from East African material. *I. meruensis* is related to *I. cernua* (Vahl) Roem. & Schult., but has larger spikelets, glumes, crested anthers and a different nutlet. *I. setacea* var. *aberdarica* differs from var. *setacea* in the culm-base and has more reduced leaves. One new combination is made, viz. *I. trollii* (Kükenth.) K. Lye comb. nov.

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Isolepis meruensis R. Haines & K. Lye sp. nov. – Fig. 1

Herbae annuae, glabrescentes. *Culmus* 1–15 cm altus et 0.2–0.4 mm latus. *Folia* ad vaginas reducta. *Anthela* simplex, 1–2-spiculosa. *Spiculae* 2.5–5.0 mm longae et 1.5–2.0 mm latae, 15–25-florae. *Squamae* dense imbricatae, ovatae, obtusae, fuscae, 1.2–1.4 mm longae; *carina* viridis. *Stamina* 3. *Stylus* trifidus. *Nux* 0.7–0.8 mm longa et 0.7–0.8 mm lata, globosa, conspicue apiculata, brunnea, minute punctulata.

Typus speciei: Vesey-FitzGerald 6295, 3.VI. 1969. Tanzania, Arusha National Park, Meru Crater, Njeku gorge, 8400 ft (EA holotype).

A slender annual with 5–15 cm long and 2–4 mm thick culms and rather conspicuous brown or purple leaf-sheaths. *Leaf-blades* absent or consisting of an up to 1 mm long limb; very rarely an up to 2 cm long leaf-blade is found. *Inflorescence* a terminal spike, or very rarely with two spikes. Major inflorescence-bract glume-like, but with a short leafy limb, not overtopping the spikelet except in immature spikelets. *Spikelets* ovate to conic, 2.5–5.0 mm long and 1.5–2.0 mm wide, 15–25-flowered. *Glumes* 1.2–1.4 mm long, light to dark reddish-brown, broadly ovate with a rounded apex, a green midrib which ends below the apex, and several minor lateral nerves; marginal uncoloured border present. *Stamens* 3; anthers with a prominent projection. *Style* short but with 3 long branches. *Nutlet* 0.7–0.8 mm long and 0.7–0.8 mm wide, triangular, rounded in outline and with a short apiculus; surface brown, minutely punctate.

In edge of muddy pool, 2560 m (8400 ft). Only known from the type collection.

This species is somewhat similar to *I. cernua* (Vahl) Roem. & Schult., but has larger spikelets and glumes, apiculate anthers and a different nutlet.

Isolepis setacea (L.) R. Br. var. **aberdarica** R. Haines & K. Lye var. nov. – Fig. 2

Herbae perennes, glabrescentes. *Rhizoma* erecta. *Culmus* 3–10 cm altus et 0.3–0.6 mm latus. *Folia* bis 2 cm longa vel ad vaginas reducta. *Anthela* simplex, 1–2-spiculosa. *Spiculae* 3–5 mm longae et 1.5–2.5 mm latae, ovatae, fuscae, 10–15-florae. *Squamae* dense imbricatae, 1.5–1.8 mm longae, ovatae, brunneae vel fuscae; *carina* viridis. *Stamina* 3. *Stylus* trifidus. *Nux* 0.8–1.0 mm longa et 0.7–0.8 mm lata, obovata, striatula, conspicue apiculata.

Typus speciei: Lye 74/86, 1974. Kenya, Aberdares Mts, near the road on the West Escarpment, just outside Mt Aberdares National Park (EA holotype).

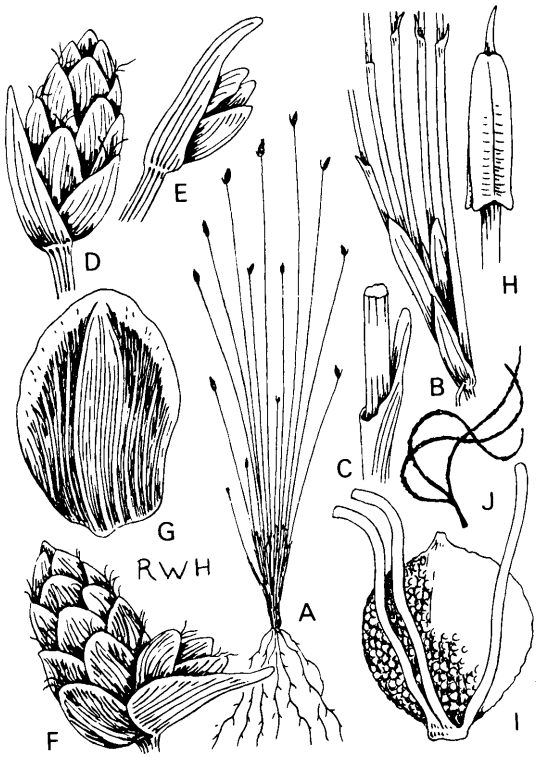


Fig. 1. *Isolepis meruensis*. – A: Habit, ×0.5. – B: Shoot-base, magnified. – C: Detail from culm showing throat of leaf-sheath. – D, E: Mature and young spikelet with bract. – F: Atypical inflorescence with 2 spikelets. – G: Glume. – H: Crested anther. – I: Achene with 3 filaments. – J: Style with 3 long branches. – Drawn from the holotype.

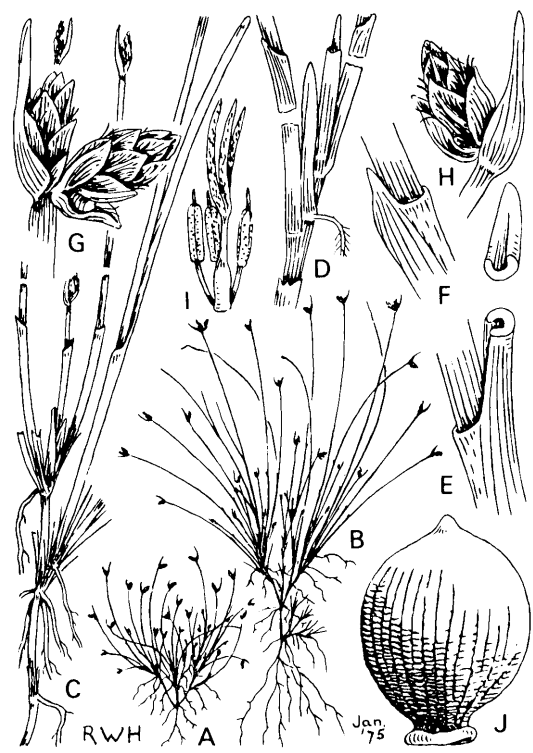


Fig. 2. *Isolepis setacea* var. *aberdarica*. – A, B: Habit, ×0.5. – C, D: Shoot-bases, magnified. – E: Detail from culm showing throat of leaf-sheath with leaf-blade. – F: Detail from culm showing throat of leaf-sheath without leaf-blade. – G, H: Inflorescences consisting of 2 and 1 spikes respectively. – I: Flower consisting of 3 stamens and a gynoecium with 3-branched style. – J: Mature achene. – Drawn from the holotype.

A low perennial forming flat and rounded tussocks 8–15 cm in diameter; the centre of the tussock consisting of numerous crowded slender and branched rhizomes, rooting at the nodes. *Branches* extra-axillary in origin, each branch ending in a group of curved culms. *Culms* 3–10 cm long and 0.3–0.6 mm thick, somewhat flattened, glabrous. Earlier culms with several nodes and bearing leaves with grey to brown sheaths and long green channelled limbs, later with only two nodes, one at the base of the bud-subtending prophyll, the other at the base of a tubular limbless sterile sheath. *Inflorescence* a solitary spikelet or an anthela consisting of two sessile spikelets. Inflorescence-bracts glume-like, but the excurrent green midrib sometimes longer than the spikelet. *Spikelets* 3–5 mm long and 1.5–2.5 mm wide, ovate, brown, 10–15-flowered. *Glumes* 1.5–1.8 mm long, oval, concave, light to dark brown with usually shortly excurrent green midribs, all fertile. *Stamens* 3. *Style* with 3 branches. *Nutlet* 0.8–1.0 mm long and 0.7–0.9 mm wide, grey, triangular, obovate to almost rounded in outline, and with a short apiculus; surface longitudinally ridged with transverse bars, shiny.

In mountain-moorland, on soil newly laid bare. Only recorded from Aberdares Mountains in Kenya.

This variety differs from var. *setacea* in having a different culm base, shorter bracts and more reduced leaves.

Isolepis trollii (Kükenth.) K. Lye comb. nov.

Basionym: Scirpus trollii Kükenth. in Feddes Repert. 53 p. 72 (1944).

The type is from the Uluguru Mountains in Tanzania (Troll 4916; B).

Fragilaria lata, a new diatom species

Ingemar Renberg

Renberg, I. 1977 09 15: Fragilaria lata, a new diatom species. *Bot. Notiser 130:*315–318 Stockholm. ISSN 0006-8195.

Fragilaria lata (Cleve-Euler) Renberg comb. nov. is described and illustrated with light and scanning electron micrographs. It is compared with *Synedra parasitica, F. construens* and *F. constricta.*

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In the palaeolimnological investigation of the lake Prästsjön, province of Västerbotten, northern Sweden, a rich material of a number of *Fragilaria* species was obtained (Renberg 1976). One of these, at that time simply called *Fragilaria* sp. a, is here described as *Fragilaria lata,* and four subspecific taxa of *Synedra parasitica* (W. Sm.) Hust. and one of *Fragilaria construens* (Ehr.) Grun. published by Cleve-Euler (1953) are shown to be synonymous with *F. lata.*

Material and methods

The museum slides studied (from S and S-PA) are those present in A. Cleve-Euler's and Å. Berg's collections which are labelled with the names of lakes cited by Cleve-Euler (1953) as the localities for the subspecific taxa of *S. parasitica* and *F. construens* in question. A number of slides in R. W. Kolbe's collection (S-PA) have also been examined.

My own collections, from a number of lakes in Västerbotten and Lapland, consist of subfossil material from sediment cores, recent material from surface sediments and samples of the epiphytic and planktic diatom floras.

The description is based on specimens collected in the lakes Prästsjön and Lillträsket in the province of Västerbotten. In certain samples in the sediment core from Prästsjön, valves of *Fragilaria lata* comprise about 5 % of the total number of diatom valves found (Renberg 1976). The type material, on the other hand, as well as the other museum material examined, contains only single valves.

The light micrographs show specimens taken from core samples from Prästsjön and surface sediment samples from Lillträsket. The valves were cleaned with hydrogen peroxide, embedded in Hyrax and photographed under a Wild M20 microscope using a Photo-Automatic camera and Agfa Gevaert Pan AHl film. The scanning electron micrographs were taken with a Cambridge Stereoscan S4 and a Jeol JSM-P15 microscope. The counts of striae were made on light micrograph prints at 5000 × magnification.

Fragilaria lata (Cleve-Euler) Renberg comb. nov.

Basionym: *Synedra parasitica* (W. Sm.) Hust. var. *parasitica* ("var. *genuina* Mayer") f. *lata* Cleve-Euler 1953 in K. Sven. Vetenskapsakad. Handl. Ser. 4, Bd. 4, No. 1, p. 56, fig. 372 a, e (S-PA).

Synedra parasitica var. *intermedia* Cleve-Euler 1953 p. 57, fig. 372 f.

Synedra parasitica var. *subconstricta* sensu Cleve-Euler 1953 p. 57, fig. 372 h, non Grunow 1880–1881 in Van Heurck, Syn. T. 45, fig. 29.

Synedra parasitica "var. *genuina* × var. *subconstricta*" Cleve-Euler 1953 fig. 372 i.

Fragilaria construens (Ehr.) Grun. var. *binodis* (Ehr.) Grun. f. *bigibba* (Cleve-Euler) Cleve-Euler 1953 p. 35, pro parte, fig. 346 x, y, non fig. 346 w = var. *bigibba* A. Cleve 1895 p. 35, fig. 28, which probably is the true *F. construens* var. *binodis.*

Cells in ribbon-like colonies or solitary. Frustules in girdle-view narrowly rectangular, girdle very narrow. Length of pervalvar axis ca 4–5 μm. Valve mantle striated. Small forms, especially, often with short striae, of only a few

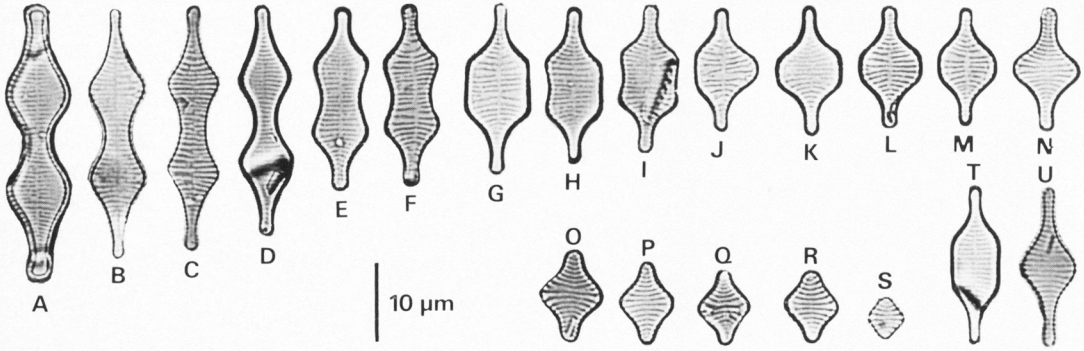


Fig. 1. Light micrographs of *Fragilaria lata* (× 1000); T and U are two unusual forms.

puncta, on valve mantle between ordinary continuous striae. Valve face flat, bilaterally symmetrical. Valve mantle almost perpendicular to valve face.

Valve shape very variable. Large forms narrowly oblong, deeply constricted medially and with elongated apices, sometimes slightly capitate. Intermediate forms oblong, sometimes square, often slightly constricted medially and with elongated apices, occasionally slightly capitate. Small forms either rhombic or almost circular, or rhombic or circular with elongated apices.

Length of apical axis 4–35 µm, of transapical axis 3–9 µm. A very narrow axial area often present, but sometimes lacking. Striae punctate, ca 50 puncta per 10 µm, radiate, in the middle of the valve face in larger forms, parallel. 15–17 striae per 10 µm (mean 16) along the margin of the valve face, generally one more when measured along the axial area. No ocellus has been observed. Linking spines present on the margin of the valve face, even at the apices.

Ecology. In acidic lakes (pH 5–6), probably non-planktic.

Slides examined. *Norway*. *Hordaland*. Lindås par., Gåsetjønn, PEK No. 8, surface sediment, water depth 10–12 m, leg. Kaland, coll. Aasheim, Bergen, det. Renberg.

Sweden. *Södermanland* (all leg. Silfversparre, coll. Kolbe (S-PA), det. Renberg). – Nacka par., Ulvsjön, No. VIII. 40, bottom sample, water depth 4.2 m, 23.III.1948 – Tyresö par., Långsjön 2, No. VIII. 37, bottom sample, water depth 2.4 m, 20.III.1948 – Tyresö par., Trehörningen I, No. VIII. 58, core sample from 2 m, II.1948 – Österhaninge par., Bylsjön, No. VIII. 20, bottom sample, water depth 2 m, 18.I.1948.

Västmanland. Ölsjön, bottom sediment near the shore, water depth 0.7 m, 4.IX.1941, coll. et det. Cleve-Euler (S).

Västerbotten (all leg., coll. (UME) et det. Renberg). – Umeå par., Prästsjön 142, subfossil sediment, 14.IV.1972 – Umeå par., Lill-Tavelsjöavan, surface sediment, 28.II.1974 – Sävar par., Svarttjärn, surface sediment, 12.III.1974 – Degerfors par., Lilltträsket 430, surface sediment, 15.III.1972.

Åsele lappmark (all leg. et coll. Berg (S-PA), det. Cleve-Euler). – Örträsk par., Örträsk 11:1 (right-hand coverslip), 1922 – Örträsk par., Örträsk 8:2 E and 8:3 E, 1923 – Örträsk par., Örträsk 8:4 E, 1923 (lectotype).

Discussion

Since most of the material of *Fragilaria lata* is subfossil it has been difficult to decide whether this species forms any kind of colonies, or only occurs as solitary cells. Colonies, or even two valves belonging to different frustules yet attached together, have never been observed in any of the cleaned material which has been studied. When sediment samples suspended in a drop of water were examined, colonies composed of a few cells, joined together valve-to-valve, were found, indicating that *Fragilaria lata* does form ribbon-like colonies. These are obviously readily disrupted, as for instance during routine cleaning processes.

This species is probably often overlooked because of its small size and its superficial resemblance to *Fragilaria construens* and its varieties, *F. constricta* and *Synedra parasitica* under the light microscope. The characters observable under the scanning electron microscope, however, quite easily differentiate it from

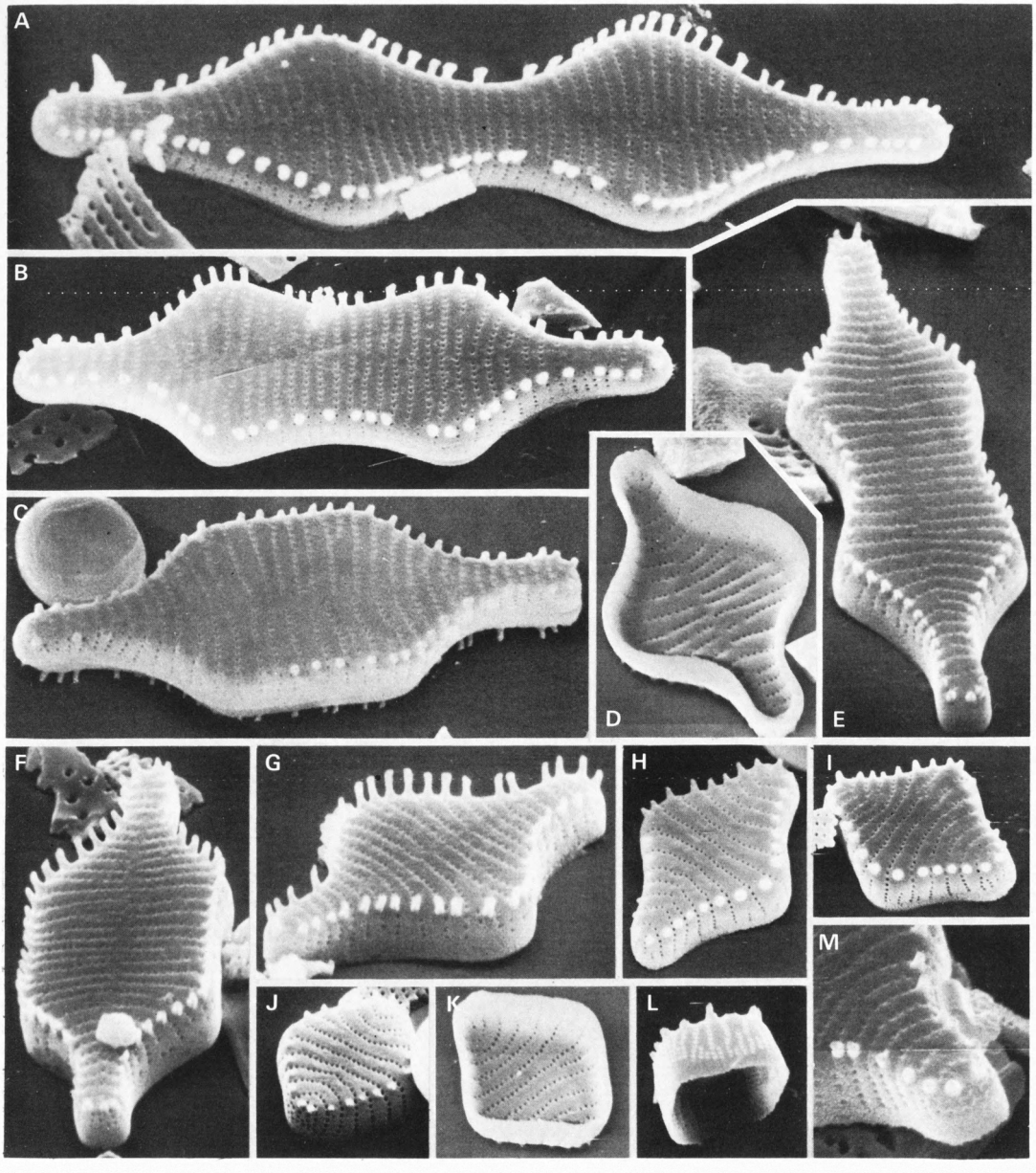


Fig. 2. Scanning electron micrographs of *Fragilaria lata*. – A–L ×c. 4000, M ×c. 6000.

these species (Fig. 3), but there are also distinct differences which can be seen under the light microscope. *S. parasitica* has marginal striae, *F. construens* has a large axial area and *F. constricta* is generally larger and has a different valve outline. Certain forms of *F. lata* may also be confused with *F. hungarica* var. *tumida* Cleve-Euler (1953 p. 40, fig. 349 n), see also Renberg (1976 p. 148, fig. 5), which, however, has an ocellus and is more densely striated.

The external shape of *Fragilaria lata* is variable. Its fine structure, however, is not.

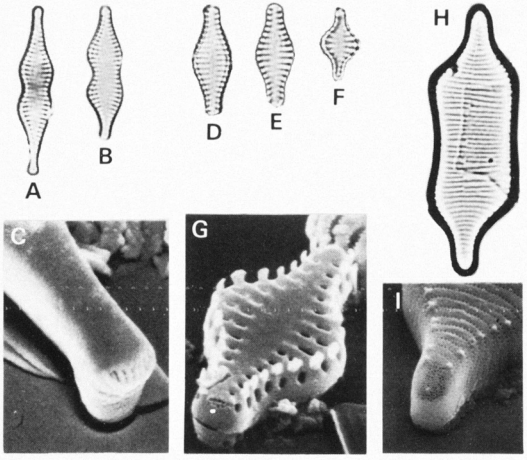


Fig. 3. A, B: Light micrographs of *Synedra parasitica* (×1000). – C: Scanning electron micrograph showing the apical ocellus of *S. parasitica* (×8000). – D–F and G: Light and scanning electron micrographs of *Fragilaria construens* (×1000 and ×3750 respectively). – H: Light micrograph of *F. constricta* (×1000). – I: Scanning electron micrograph showing the large-sized ocellus of *F. constricta* (×2400).

Irrespective of size, all valves have about the same number of striae and puncta per 10 μm. Small and intermediate forms were commoner than the large forms in the present material. Valves of abnormal shapes and striation patterns were occasionally encountered.

The variation in external shape exhibited by *Fragilaria lata* is quite reasonable since valve shape in diatoms becomes gradually simplified in the course of successive cell divisions (Geitler 1932). There is one fact, however, which indicates that the observed variation is not continuous. The micrographs (Fig. 1) and a statistical treatment of all available data show that valve width (length of transapical axis) of small and intermediate forms is not less than that of large forms, but more commonly the reverse is true. It is therefore uncertain whether the largest forms (Fig. 1 A–F) are capable of yielding the whole spectrum of forms which have been observed, even though it is a well-known fact (Geitler 1932) that the relative valve width of pennate diatom species may diminish to a lesser degree than would be expected in the course of repeated cell divisions.

The investigations carried out up to now are too limited to substantiate whether or not the observed range of variation is environmentally induced and ecologically significant, or genetically fixed, i.e. whether a separation of subspecific taxa would be justified within *Fragilaria lata*.

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A note on Fuirena ciliaris (Cyperaceae) and related species

R. Wingfield

Wingfield, R. 1977 09 15: A note on Fuirena ciliaris (Cyperaceae) and related species. *Bot. Notiser 130:* 319–320. Stockholm. ISSN 0006-8195.

Fuirena ciliaris (L.) Roxb. var. *apetala* Wingfield var. nov. is described from Tanzania and differences between it and similar 'apetalous' varieties of related African species are pointed out. Additional localities are given for *F. microcarpa* K. Lye and *F. zambesiaca* K. Lye.

R. Wingfield, Botany Department, University of Dar es Salaam, P. O. Box 35060, Dar es Salaam, Tanzania.

Fuirena ciliaris (L.) Roxb. var. **apetala** Wingfield var. nov.

Orig. coll.: Tanzania, 5 km S of Tanga, 1.1. 1970, Botany students in DSM 1501 (DSM holotype, EA, K isotypes).

A var. *ciliaris* squamis hypogynis absentibus differt.

Var. *ciliaris* is much commoner in the area than is var. *apetala*. I have seen intermediates in only one locality (Wingfield 2039). The intermediate plants have some fruits with no hypogynous scales, and others, sometimes in the same head, with one or rarely two scales of normal *F. ciliaris* appearance. The scales are fully developed when present.

The intermediate plants were growing mixed with both varieties, the ratio of var. *ciliaris* to var. *apetala* (including intermediates) being about 15:1. The intermediates are less frequent than var. *apetala* but I give no ratio, since in order to be sure a plant is not intermediate, one would have to examine every flower, which is impracticable. Out of about 300 plants from this site, examined quickly, I found only four intermediates.

The new variety is readily distinguishable from *F. microcarpa* K. Lye on fruit characters (the character states of *F. microcarpa* are given within parentheses): fruit 0.7–0.8 × 0.5 mm, c. 3/4 as wide as long (0.5 × 0.3 mm, c. 1/2 as wide as long), opaque (translucent), brown when ripe (pale green), with more prominent angles, the faces of the fruit being more or less flat in T. S. (markedly convex); also, the mature spikelets are larger, at least 5 × 1.7 mm, disregarding the bristles and the part where the glumes have fallen off (up to 4 × 1.5 mm).

It is less easy to distinguish the new variety from *F. leptostachya* Oliv. var. *nudiflora* C. B. Cl. and from corresponding, theoretically possible but still unknown, 'apetalous' varieties of *F. angolensis* (Schinz) K. Lye and *F. sagittata* K. Lye.

In *F. leptostachya* and *F. angolensis* the ligule is hairy, whereas in *F. ciliaris* it is nearly or quite glabrous (sometimes minutely ciliate). The fruit of *F. leptostachya* is smaller (c. 0.5 × 0.4 mm) than in *F. ciliaris*, with the sides frequently more convex (seen from top of fruit), the fruit of *F. sagittata* is larger (0.9–1.1 × 0.5–0.6 mm according to Lye) than in *F. ciliaris*.

F. leptostachya, *F. angolensis* and *F. sagittata* are not known to be sympatric with the new variety, their nearest known populations being as follows: *F. leptostachya* var. *leptostachya*, 40 km W of Dar es Salaam, lowest altitude 130 m; *F. leptostachya* var. *nudiflora*, 560 km W of Dar es Salaam at 1320 m; *F. angolensis*, 500 km WSW of Dar es Salaam (Ruaha National Park) and 330 km WNW of Tanga

(Tarangire National Park), lowest altitude 850 m; *F. sagittata*, 380 km W of Dar es Salaam, lowest altitude 1080 m. *F. ciliaris* var. *apetala* grows between 0 and 40 m.

Additional collections: Tanzania, 7 km SW of Dar es Salaam, Kilwani Pond by Pugu Road, 40 m, 17.7. 1971, Wingfield 1692 (DSM, K) – 28 km NNW of Dar es Salaam, 200 m S of Log Cabins, 15.7. 1972, Wingfield 2039 (DSM, K; only the intermediates from this collection were kept).

Fuirena microcarpa K. Lye

K. Lye in Bot. Notiser 127:111 (1974).

The holotype of this species is really Wingfield 2100 (not 1638 as stated by Lye), the data Lye gives being from 2100. The holotype is at DSM, isotypes at C, EA, K, NU, MO. No. 1638, which I did not send to Lye, but which was mentioned on the label of 2100, is the same species but from 4 km further west, at Dar es Salaam University campus, 14.7. 1971 (DSM, EA, K).

The fruit is relatively narrower than those of *F. leptostachya* and *F. ciliaris* (both of which have varieties without hypogynous scales), being about 1/2 as wide as long (not 3/4 as in the latter species), and is pale green in life when shed. The fruit-wall is rather translucent and glassy-looking (not brown and opaque as in the latter two species).

F. microcarpa ranges in height from 5 to 30 cm. It grows mixed with *F. ciliaris* var. *ciliaris* (3–66 cm tall), but I have found no intermediates although I have examined several hundred plants from mixed populations.

The known altitudinal range of *F. microcarpa* is 30–910 m.

Additional collections: Tanzania, Selous Game Reserve, 8°38'S, 38°29'E, c. 175 m, 15.8. 1976, K. Vollesen in MRC 3936 (DSM, EA, K) – Mozambique, Bandula, 910 m, 6.4. 1952, Chase 4548 (BM).

Fuirena zambesiaca K. Lye

K. Lye in Bot. Notiser 127:109 (1974)

This species was recorded from Mozambique and SE Tanzania by Lye. The two collections cited below extend its known range: 0°49'S to 14°50'S, altitude 0–850 m.

A search at several relevant herbaria (BM, BR, DSM, EA, MO, NA, WAG) by me in Dec. 1975–Jan. 1976 revealed no further collections of this species, or of *F. microcarpa*. The only other collection of either found at K (S. Hooper in letter, June 1973) was one of *F. zambesiaca* by Schlieben from near Madaba, near Kilwa in SE Tanzania, which is presumably the one referred to by Lye.

Additional collections: NE Tanzania, 25 km NNW of Dar es Salaam, sea-level, 15.7.1972, Wingfield 2041 (DSM, EA, K, MO, NU) – Kenya, Tana River, Seven Forks, 850 m, 3.3. 1974, S. A. Robertson 206 A (DSM, EA, MO: mixed with *F. angolensis* 206 B).

Notes on the genus Epidendrum (Orchidaceae) in Ecuador

Bernt Løjtnant

Løjtnant, B. 1977 09 15: Notes on the genus Epidendrum (Orchidaceae) in Ecuador. *Bot. Notiser 130:* 321–328. Stockholm. ISSN 0006-8195.

One new species, *Epidendrum echinatum* Løjtnant, is described, and the new combinations *E. garayii* Løjtnant (based on *Pleuranthium cardiochilum* Garay) and *E. suavis* (Rchb. f. & Warsz.) Løjtnant are made. *E. isomerum* is reported for the first time from S America and the following species are reported for the first time from Ecuador: *E. aggregatum, E. anthoceros, E. anthropophorum, E. carnosiflorum, E. cornanthera, E. densifolium, E. elleanthoides, E. evectum, E. funckii, E. ionodesme, E. jajense, E. lacustre, E. macbridei, E. pachyphyton, E. rolfeanum, E. sertorum, E. suaveolens* and *E. suavis.*

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The taxonomic decisions presented are a result of determining the orchids collected by the 1st and 2nd Danish Botanical Expeditions to Ecuador (Holm-Nielsen & Jeppesen 1968, Holm-Nielsen et al. 1975).

The drawings of flowers and floral parts are made from material preserved in FAA.

Epidendrum aggregatum Lindley

Lindl. in Hooker, J. Bot. 3:84, 1841.

This rare and conspicuous species, which can grow more than 2 m tall and have the appearance of a small tree, has hitherto only been known from very few collections from Peru.

Schweinfurth (1959) cites a specimen collected in Colombia, distr. Cauca (von Sneidern 855) under the name of *E. aggregatum,* but a study of this specimen at AMES has shown that it hardly belongs to *E. aggregatum* because the lateral sepals are acute and not spathulate and the floral segments are too large (lateral sepals 15×4 mm, petals 14×2 mm). Furthermore, the leaves are broader (up to 2.7 cm in contradistinction to 1.7 cm in the type of *E. aggregatum*).

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 33, dry rocky slopes with grass and scattered shrubs, 1800–1850 m (79°04′ W, 3°59′ S), 21.4.1973, Holm-Nielsen et al. 4148 (AAU).

Epidendrum anthoceros Linden & Reichenbach f.

Lind. & Rchb. f. in Bonpl. 2:281, 1854.

Epidendrum anthoceros has hitherto only been reported from Venezuela, Colombia (type) and Peru (Schweinfurth 1959, Foldats 1970, Dunsterville & Garay 1976).

Ecuador, prov. Napo, between Cuyuja and Papallacta, 10 km E of Papallacta on road to Baeza, rocky slope along the road, 2800–2900 m (78°01′ W, 0°21′ S), 5.6.1973, Holm-Nielsen et al. 6858 (AAU).

Epidendrum anthropophorum Reichenbach f.

Rchb. f. in Bonpl. 4:215, 1856.

This species, the description of which is based upon material of uncertain origin collected by Ruiz and Pavón, can now be reported from Ecuador. Although also known from Colombia (Leslie A. Garay, pers. comm.), the only sample

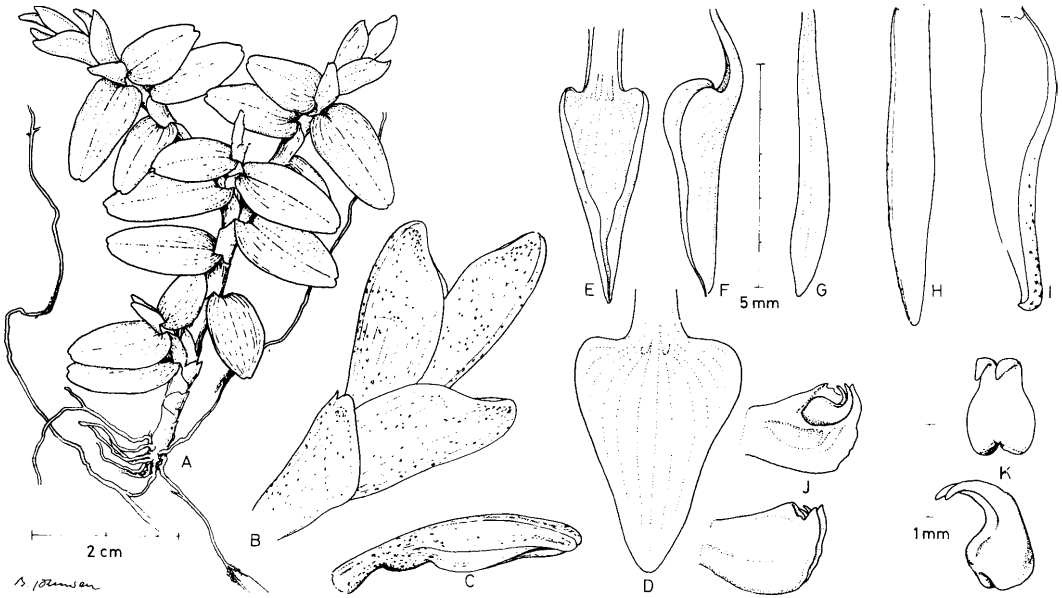


Fig. 1. *Epidendrum cornanthera*. Holm-Nielsen et al. 7026 (AAU). – A: Habit. – B: Inflorescence showing the lepidote bracts. – C: Bud (lepidote). – D: Lip, spread out. – E–F: Lip. – G: Petal. – H: Dorsal sepal. – I: Lateral sepal. – J: Column. – K: Anther.

of this species in AMES is Barclay & Juajibioy 8074 which, like our collection, comes from the surroundings of Pilaló.

Ecuador, prov. Cotopaxi, around Pilaló, 2400 m (79°02' W, 0°57' S), 1.7.1968, Holm-Nielsen & Jeppesen 1130 (AAU).

Epidendrum carnosiflorum C. Schweinfurth

C. Schweinf. in Bot. Mus. Leafl. 11: 87, 1943.

This species has so far only been reported from the type locality in Peru.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, c. 2300 m, 17.4.1973, Holm-Nielsen et al. 3753 (AAU).

Epidendrum cornanthera Lehmann & Kränzlin– Fig. 1

Lehm. & Kränzl. in Engl. Bot. Jahrb. 26: 463, 1899.

This poorly known species of *Epidendrum* has only been known previously from Colombia. It is not very rare but has seldom been collected, no doubt due to the fact that it is tiny and inconspicuous. It is closely related to the widespread neotropical *E. strobiliferum* and to the Venezuelan *E. strobiloides* Garay & Dunsterv., but it is distinguished from them by e.g. the form of the anther (see Fig. 1 and Dunsterville & Garay 1966).

Ecuador, prov. Pichincha, "Finca Carlita", at km 13 on road Santo Domingo de los Colorados–Chone, secondary rain forest and slopes with secondary herb vegetation, 550 m (79°14' W, 0°15' S), 10.6.1973, Holm-Nielsen et al. 7026 (AAU).

Epidendrum densifolium Kränzlin

Kränzl. in Feddes Rep. 1: 186, 1905.

Evidently, this species has so far only been known from Peru (Schweinfurth 1944, 1959).

Ecuador, prov. Azuay, km 85 on Pan American Highway N of Loja, dry low scrub vegetation, more humid in small hollows and valleys 2850–2950 m (79°11' W, 3°35' S), 3.5.1973, Holm-Nielsen et al. 4813 (AAU).

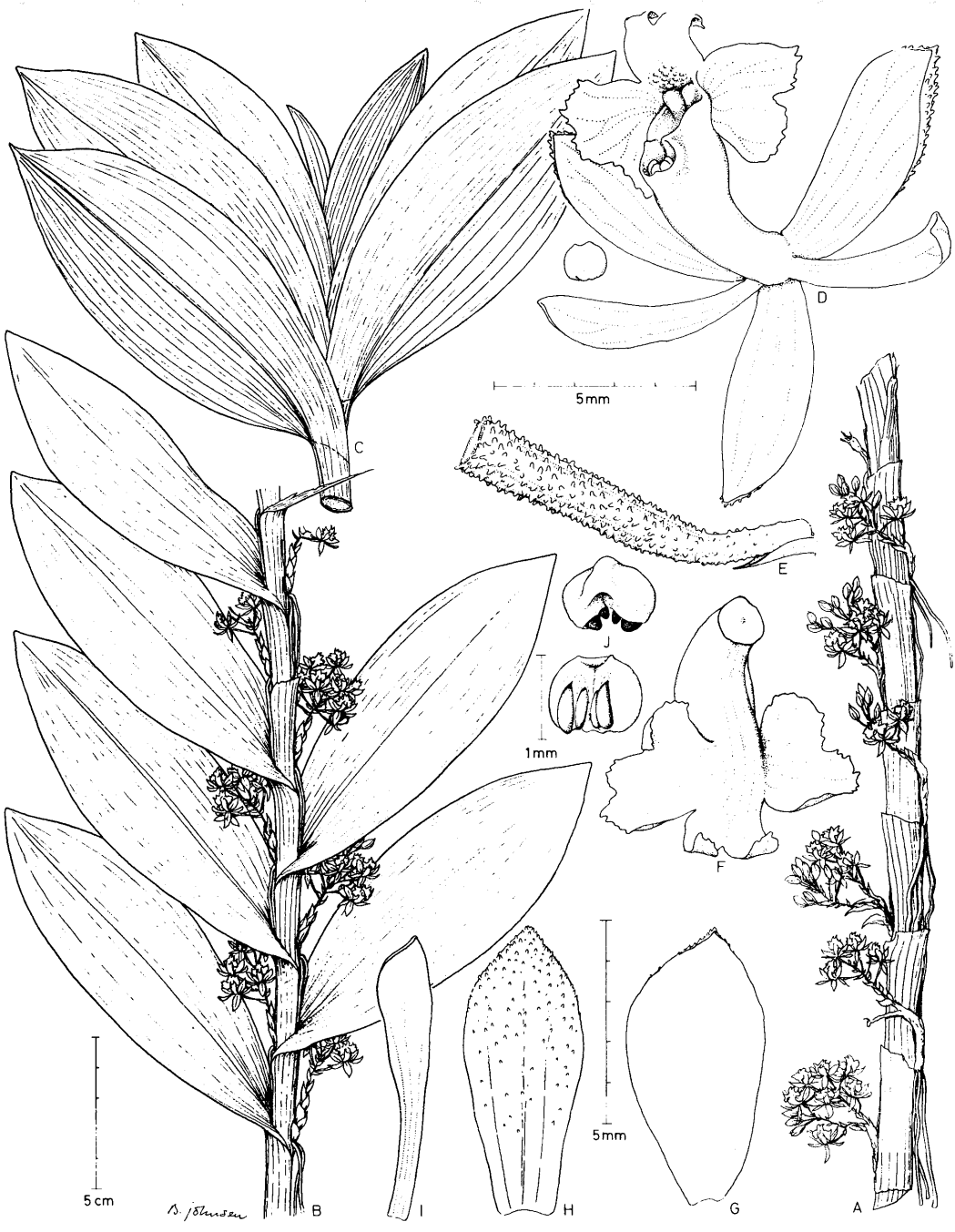


Fig. 2. *Epidendrum echinatum*. Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 3001 (AAU holotype). – A–C: Lower, middle, and upper part of the stem. – D: Flower. – E: Bract, pedicel, and ovary. – F: Lip, seen from behind. – G: Lateral sepal. – H: Dorsal sepal. – I: Petal. – J: Anther.

Epidendrum echinatum Løjtnant sp. nov. – Fig. 2

Orig. coll.: Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, rocky slopes with rain forest, c. 800–950 m (79°10' W, 0°55' S), 5.4.1973, Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 3001. 1.5 m high tufted shrub. Terrestrial on wet cliff in the rain forest. Flowers greenish white, sometimes violet tinged (AAU holotype).

Terrestris, caespitosis, usque ad 1.5 m alta; *rhizomate* valde abbreviato; *radicibus* fasciculatis, carnosis, glabris; *caulibus* erectis, simplicibus, dense foliosis, inferne denudatis, vaginis adpressis obtectis; *foliis* distichis, anguste obovatis, acutis, basin versus sensim angustatis, sessilibus, usque ad 15 cm longis, 4.5 cm latis; *inflorescentiis* caulinis, foliis oppositis, brachycladis vel simplicibus, patentibus; *pedunculo* vaginis obtecto, usque ad 3.5 cm longo; *rhacide* brevi, satis dense multifloro; *bracteis* ovatis, acutis vel subacuminatis usque ad 2 mm longis; *ovario* pedicellato, echinato, usque ad 1 cm longo; *sepalo* postico obovato, obtuso, extus echinato, usque ad 7 mm longo, 3 mm lato; *sepalis lateralibus* oblique obovatis, obtusis, extus echinatis, usque ad 7 mm longis, 3.5 mm latis; *petalis* lineari-oblanceolatis, obtusis, margine supra erosulo, usque ad 7 mm longis, 1.3 mm latis; *labello* e basi cordata, 3-lobo, lobis lateralibus dolabriformibus vel transverse reniformibus, plus minusque lobulatis, margine erosulo, 2.5 mm longis, lobo intermedio subquadrato, bilobato, margine erosulo, 2 mm longo latoque; disco incrassato, basin bicalloso; *columna* clavata, arcuata, 5 mm longa.

This new species belongs to sect. *Pleuranthium* Rchb. f. It is distinguished from all other known species of that section by the relatively short, narrowly obovate leaves and the densely echinate petioles, ovaries and sepals.

The specific name is descriptive of the echinate petioles, ovaries and sepals, echinatus meaning prickly.

Epidendrum elleanthoides Schlechter

Schltr. in Feddes Rep. Beih. 7: 132, 1920.

Originally described from Colombia, this species is now reported from Ecuador, close to the Peruvian border.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 14, mountain ridges with elfin forest and open bogs, 2750–2770 m (79°09' W, 4°S), 19–20.4.1973, Holm-Nielsen et al. 3837 (AAU).

Epidendrum evectum Hooker

Hook. in Bot. Mag. 97: t. 5902, 1871.

Epidendrum evectum, presumably described on material from Colombia, is usually included in the polymorphic *E. elongatum* Jacq. However, it should be regarded as a distinct species, since it has considerably larger and brighter purple flowers, thicker, succulent leaves and more robust stems. The collections below are apparently the first records of *E. evectum* from Ecuador.

Ecuador, prov. Pichincha, road Santo Domingo de los Colorados–Quito, above Tandapi (Cornejo Astorga), montane forest, river beds and roadsides, 2300–2450 m (78°43' W, 0°27' S), 12.6.1973, Holm-Nielsen et al. 7105, 7109, 7111, 7112 (AAU). – Prov. Cotopaxi, Quevedo–Latacunga road, 2–5 km W of Pilaló, steep rocky slopes in montane forest, 2200–2350 m (79° W, 0°55' S), 8.4.1973, Holm-Nielsen et al. 3199 (AAU).

Epidendrum funckii Reichenbach f.

Rchb. f. in Linnaea 22: 839, 1849.
E. brachycladium Lindl., Fol. Orch. Epidendrum 60, no. 186A, 1853.
E. brachycladium Lindl. β *crassipes* Lindl., Fol. Orch. Epidendrum 60, no. 186B, 1853. – *E. crassipes* (Lindl.) Kränzl. in Engl. Bot. Jahrb. 54, Beibl. 117: 25, 1916. – *E. crassipes* (Lindl.) Schltr. in Feddes Rep. Beih. 6: 69, 1919.

Epidendrum funckii has been reported from Peru, Bolivia, Colombia (type) and Venezuela (Lindley 1853, Schlechter 1919, Schweinfurth 1956, 1959). However, until now it has not been reported from Ecuador. *E. funckii* is unlikely to be rare in Ecuador, but it has often been confused with forms belonging to the polymorphic *E. elongatum* Jacq. (*E. secundum* auct. non Jacq.).

The specific epithet is normally spelled "*funkii*", but as the taxon is named in honour of its first collector, Nicholas Funck, it should be spelled as above. Schlechter (1919) based his superfluous combination *E. crassipes* on *E. brachycladium* Lindl. var. *crassipes* Lindl. but cited Reichenbach f. as the author of var. *crassipes*. Accordingly there has been confusion

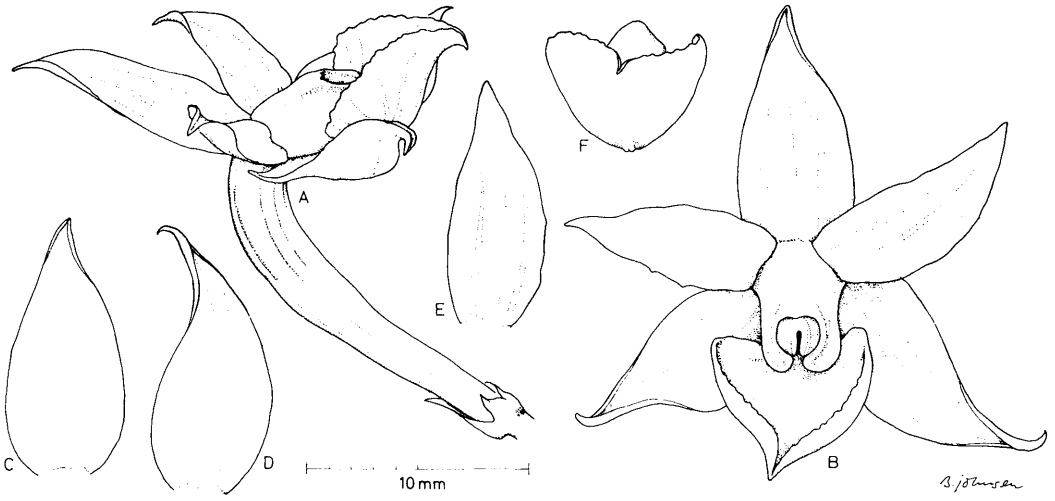


Fig. 3. *Epidendrum garayii*. Holm-Nielsen et al. 6477 (AAU). – A–B: Flower. – C: Dorsal sepal. – D: Lateral sepal. – E: Petal. – F:Lip.

concerning the synonymy of *E. funckii*. The full synonymy is therefore given above.

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on road Tulcán–Maldonado, steep forested slopes, 2100–2200 m (78°06' W, 0°54' N), 20.5.1973, Holm-Nielsen et al. 6052 (AAU). – Prov. Pichincha, km 40–51 on road Santo Domingo de los Colorados–Quito, forested slopes along Río Pilatón, 1100–1400 m (78°55' W, 0°22' S), 14.6.1973, Holm-Nielsen et al. 7175 (AAU).

Epidendrum garayii Løjtnant comb. et nom. nov. – Fig. 3

Based on: *Pleuranthium cardiochilum* Garay in Arquiv. Jard. Bot. 12:181, 1952.

A study of the collection mentioned below, which is referable to *Pleuranthium cardiochilum* Garay, has revealed that the flowers are terminal and not axillary. Hence the species should be excluded from *Pleuranthium*. Moreover, in my opinion *Pleuranthium* (Rchb. f.) Benth. can easily be accommodated in *Epidendrum;* see Reichenbach (1849), Lindley (1853), Bentham (1881), Bentham & Hooker (1883), Williams (1952) and Garay (1956).

Since the binomial *Epidendrum cardiochilum* L. O. Wms. (in Am. Orch. Soc. Bull. 9: 4, 1940) is already published the new name given above has been adopted.

P. cardiochilum was described from Ecuador: Ost-Cordillera von Riobamba, 3200 m (not 300 m as stated in the original description), coll. Rimbach 801! (S). This is evidently the second record for this species.

Ecuador, prov. Imbabura, timberline vegetation on Hacienda Yura Cruz, 10 km N of Ibarra, 3700–3800 m (78°05' W, 0°22' N), 25.5.1973, Holm-Nielsen et al. 6477 (AAU).

Epidendrum ionodesme Schlechter

Schltr. in Feddes Rep. Beih. 7:134, 1920.

In most publications *E. ionodesme* is considered to be conspecific with *E. paniculatum* Ruiz & Pavón. However, it differs considerably from the type of *E. paniculatum* both in habit and in the form of the lip and in my opinion should be treated as a separate species.

Because this species has previously been included in *E. paniculatum* it is difficult to give distributional data for it. However, it seems only to have been reported from Colombia previously.

Ecuador, prov. Carchi, Valle de Maldonado, km 60 on road Tulcán–Maldonado, cleared slopes along the road and denser cloud forest, 2700 m (78°04' W, 0°51' N), 18.5.1973, Holm-Nielsen et al. 5693; also at 2600 m, 21.5.1973, no. 6216 (AAU).

Epidendrum isomerum Schlechter

Schltr. in Feddes Rep. 2:132, 1906.

The collections cited below are the first reports of *E. isomerum* from S America. The species is previously known from Mexico, Guatemala (type), British Honduras, Costa Rica and Panama.

Ecuador, prov. Pichincha, "Finca Carlita", at km 13 on road Santo Domingo de los Colorados–Chone, secondary rain forest and slopes with secondary herb vegetation, 550 m (79°14' W, 0°15' S), 10.6.1973, Holm-Nielsen et al. 7032, 7038 (AAU).

Epidendrum jajense Reichenbach f.

Rchb. f. in Bonpl. 2:20, 1854.

This rare species has hitherto been reported from Peru, Colombia and Venezuela (type) (Garay 1972).

Ecuador, prov. Pichincha, "Finca Carlita", at km 13 on road Santo Domingo de los Colorados–Chone, secondary rain forest and slopes with secondary herb vegetation, 550 m (79°14' W, 0°15' S), 10.6.1973, Holm-Nielsen et al. 7042 (AAU).

Epidendrum lacustre Lindley

Lindl., Fol. Orch. Epidendrum 50, no. 157, 1853.

Contrary to the opinion of Ames (1924), this species does seem to occur throughout the American tropics; it is previously known from Nicaragua, Costa Rica, Venezuela (type), Colombia and Peru. It seems to be uncommon in the Andean regions, however, since it has not been reported from Ecuador previously and since it was unknown also from Peru until recently (Schweinfurth 1970).

Epidendrum obessum Ames, conspecific with *E. lacustre*, was reported from prov. Chimborazo in Ecuador by Wiggins (1950). However, the collection cited in Wiggins's report belongs to *E. spectatissimum* Rchb. f. (Leslie A. Garay, pers. comm.).

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 24–25, steep rocky slopes covered with scrub, 1950–2100 m (79°05' W, 3°59' S), 15.4.1973, Holm-Nielsen et al. 3475 (AAU).

Epidendrum macbridei C. Schweinfurth

C. Schweinf. in Bot. Mus. Leafl. 11:94, 1943.

Epidendrum macbridei, described from Peru, has apparently not been reported from elsewhere until now.

Ecuador, prov. Morona-Santiago, Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner", km 140 on road Loja–Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900–1000 m (78°34' W, 3°37' S), 26–27.4.1973, Holm-Nielsen et al. 4594 (AAU).

Epidendrum pachyphyton Garay

Garay in Orquideologia 8:182, 1973.

This species, described from Colombia in 1973 and found in Venezuela in 1974 (Dunsterville & Garay 1976), is now reported from Ecuador.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 33, dry rocky slopes with grass and scattered shrubs, 1800–1850 m (79°04' W, 3°59' S), 21.4.1973, Holm-Nielsen et al. 4126 (AAU).

Epidendrum rolfeanum Lehmann & Kränzlin

Lehm. & Kränzl. in Engl. Bot. Jahrb. 26:468, 1899.

Up to now, this species has apparently been known only from Colombia.

Ecuador, prov. Napo, 1 km E of the oil pump station on road Papallacta–Baeza, gallery vegetation along Río Papallacta, 2050 m (78° W, 0°21' S), 6.6.1973, Holm-Nielsen et al. 6979 (AAU).

Epidendrum sertorum Garay & Dunsterville

Garay & Dunsterv., Venz. Orch. Ill. 5:100, 1972.

Epidendrum sertorum, closely related to the variable and widely distributed *E. difforme* Jacq. and recently described from Venezuela, is now reported from Ecuador.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34' W, 3°29' S), 23.4.1973, Holm-Nielsen et al. 4248 (AAU).

Epidendrum suaveolens Ames

Ames in Sched. Orch. 1:21, 1922.

This conspicuous species, closely related to *E. mojandae* Schltr., *E. pichinchae* Schltr.,

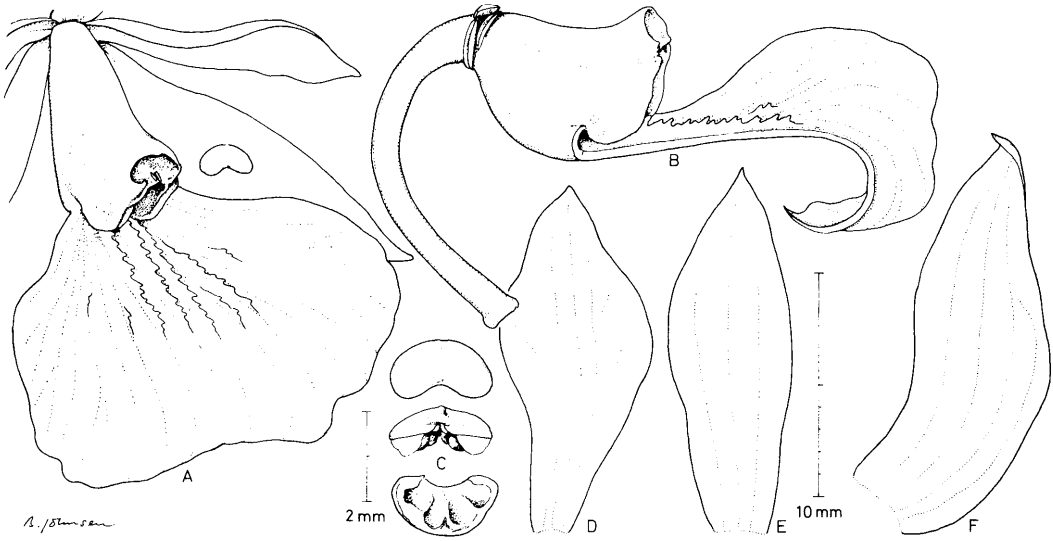


Fig. 4. *Epidendrum suavis*. Holm-Nielsen et al. 3205 (AAU). – A: Lip and gynostemium. – B: Gynostemium and the lip in bisection, showing that the claw of the lip is adnate to the face of the column. – C: Anther. – D: Petal. – E: Dorsal sepal. – F: Lateral sepal.

E. torquatum Lindl. (types from Ecuador) and *E. pastoense* Schltr. (type from Colombia) has hitherto only been reported from Colombia (type) and Venezuela (Dunsterville & Garay 1975, Garay 1975).

Ecuador, prov. Napo, between Cuyuja and Papallacta, 10 km E of Papallacta on road to Baeza, rocky slope along the road, 2800–2900 m (78°01' W, 0°21 S), 5.6. 1973, Holm-Nielsen et al. 6855 (AAU).

Epidendrum suavis (Reichenbach f. & Warscewicz) Løjtnant comb. nov. – Fig. 4

Basionym: *Diothonea suavis* Rchb. f. & Warsc. in Bonpl. 2:112, 1854.

Epidendrum suavis, like *E. diothonaeoides* Schltr. (type from Ecuador), has the general appearance of a *Diothonea*. A study of the type of *D. suavis* from the Reichenbach Herbarium in Vienna, however, revealed that the claw of the lip is adnate to the face of the gynostemium and that the labellum and gynostemium therefore do not meet at an angle as they do in *Diothonea* (Fig. 4). For this reason the species is here transferred to *Epidendrum*.

Epidendrum suavis, although a spectacular species, is rarely collected. It was described from Peru and is now, for the first time, recorded outside that country.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, 2–5 km W of Pilaló, steep rocky slopes in montane forest, 2200–2350 m (79°W, 0°55' S), 8.4. 1973, Holm-Nielsen et al. 3205; also at the timberline, 3450–3500 m (78°56' W, 0°58' S), 8.4.1973, no. 3301 (AAU).

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Seedling morphology and iridoid occurrence in Montinia caryophyllacea (Montiniaceae)

Rolf Dahlgren, Søren Rosendal Jensen and Bent Juhl Nielsen

Dahlgren, R., Jensen, S. R. & Nielsen, B. J. 1977 09 15: Seedling morphology and iridoid occurrence in Montinia caryophyllacea (Montiniaceae). *Bot. Notiser 130:* 329–332. Stockholm. ISSN 0006-8195.

The cotyledons of *Montinia caryophyllacea* Thunb. are unusual in possessing fused petioles. The plumule breaks through laterally and gradually forces the fused petioles aside. Dried leaf material of full-grown plants was found to contain a previously unknown iridoid gentiobioside, here named montinioside, structurally related to compounds usually found in *Deutzia, Viburnum* and members of Valerianaceae. The available evidence suggests a peripheral position for Montiniaceae in Cornales, or close-by.

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The family Montiniaceae consists of two or three genera, viz. *Montinia, Grevea* and probably also *Kaliphora*. *Montinia* is monotypic: the single species *M. caryophyllacea* extends from the Cape Province of South Africa to northern Namibia. *Grevea* has two species in East Africa (Tanzania and Kenya) and one species on Madagascar (Milne-Redhead 1955). *Kaliphora* is monotypic: *K. madagascariensis* is endemic on Madagascar. The latter species has usually been placed in Cornaceae, but a probable affinity to Montiniaceae is suggested by Capuron (1969), Airy Shaw (1973) and Krach (1976). Pollen morphology also supports this assignation (Hideux 1972).

According to Gibbs (1974) the family Montiniaceae has been described as new three times: by Kerner (1891), Nakai (1943) and Milne-Redhead (1955). Its ultimate taxonomic position has remained uncertain. Kerner (1891) placed it in Myrtiflorae and Milne-Redhead in Myrtales, a logical position judging from its epigynous tetramerous flowers and the sometimes opposite leaves. In fact, *Montinia* has been placed as an anomalous genus at the end of Onagraceae already by Bentham & Hooker (1862) and Baillon (1877). Airy Shaw (1973) pointed out possible connections with such divergent families as Celastraceae, Cucurbitaceae, Onagraceae and Escalloniaceae, which clearly demonstrates the great taxonomic problems involved. Although Dahlgren (1975) included the family in Celastrales, the most commonly proposed affinity of *Montinia* or Montiniaceae as a whole is with Saxifragaceae s.lat., particularly with Escalloniaceae, into which the genus was included by Hutchinson (1973). Takhtajan (1969) accepted the family as such and placed it in Saxifragales, while Schulze-Menz (1964), Cronquist (1968) and Thorne (1968) included *Montinia* (and *Grevea*) in Saxifragaceae s.lat.

Raven (1975) and Goldblatt (1976) report a chromosome number for *Montinia* of n = 34, a relatively high number. Krach (1976) shows that the main features of the seeds of *Montinia* and *Grevea* agree, but deviate so much from those of the genera of Escalloniaceae that familial separation is justified. The embryo was found to be small-celled and the cotyledons 4 times as long as the hypocotyl. The endosperm lumen accumulates fatty oils and protein and the testa was found to be 3-layered. According to

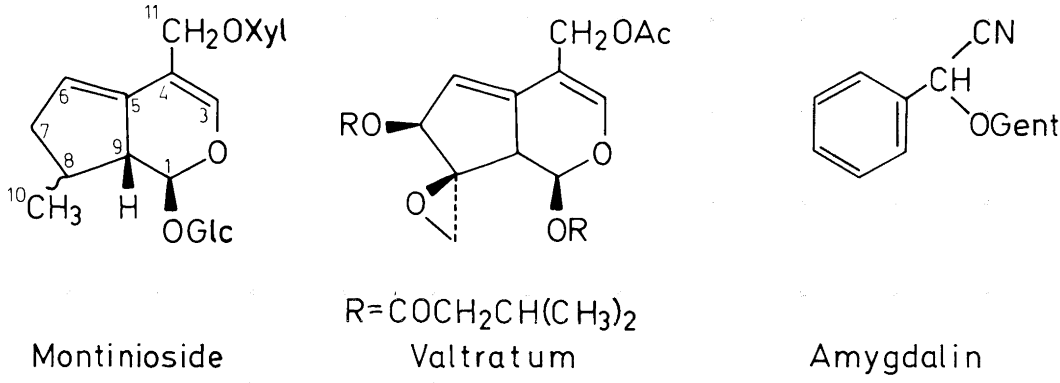


Fig. 1. Montinioside, an iridoid found in *Montinia caryophyllacea*, and two model compounds mentioned in the text.

Schulze-Menz (1964) the members of Montiniaceae have unitegmic ovules. Metcalfe (1955), who studied the anatomy of *Montinia* and *Grevea*, found that great differences exist between the genera. However, neither possessed intraxylary phloem, which is noteworthy since Milne-Redhead regarded them as Myrtalean.

In view of these facts and the common opinion that Montiniaceae is a woody member of the former Saxifragaceae s.lat. – and one with unitegmic ovules like Hydrangeaceae and Escalloniaceae – its likely affinity is Cornalean. As most of the families included by Dahlgren (1975) in Cornales often contain iridoids, a test for these compounds in *Montinia caryophyllacea* was considered relevant.

Occurrence of iridoid glycosides

A synonym of *Montinia caryophyllacea* is *M. acris* L. fil., referring to the sharp taste of its leaves. This might suggest the presence of glucosinolates. However, preliminary tests on the seeds by M. G. Ettlinger and E. Asmussen at the Ørsted Institute, Copenhagen, gave no indication of the presence of a thioglucosidase that hydrolyzes glucosinolates.

Dry leaf and stem material, kindly supplied by Dr J. Rourke, Compton Herbarium, Kirstenbosch Botanic Gardens, South Africa, was examined for iridoids. It yielded a new gentiobioside, which we have named montinioside.

Ground material (19 g) was extracted with ethyl acetate in a Soxhlet apparatus yielding 1.5 g of crude glycosides. These were dissolved in water and the solute passed through neutral alumina. This gave a syrup containing 1.3 g (7 %) of montinioside. The data after silica gel ($CHCl_3$-MeOH; 3:1) chromatography are: $[\alpha]_D^{20}$ – 14° (*c* 0.6 in MeOH) – λ_{max}^{MeOH} = =251 nm (log ε 3.83) – ^{1}H NMR spectrum (90 MHz, D_2O, DSS): 6.61 ppm (br. *s*, H-3); 5.70 ppm (br. *d*, J = 1 Hz, H-6); 5.15 ppm (*d*, J = 9 Hz, H-1); 4.36 ppm (*m*, 3 H, 11-CH_2-O-Xyl and H-1″); 1.18 ppm (*d*, J = 6 Hz, 10-CH_3) – ^{13}C NMR spectrum (22.63 MHz, D_2O, diox.): 145.0 ppm (*d*, J = 191 Hz, C-3); 135.3 ppm (*s*, C-5); 123.1 ppm (*d*, J = 164 Hz, C-6); 110.2 ppm (*s*, C-4); 103.6 ppm (*d*, J = 170 Hz, C-1); 102.3 ppm (*d*, J = 160, C-1″); 99.5 ppm (*d*, J = 163 Hz, C-1′); 76.7 (1C), 76.4 (2C), 73.4 (2C) and 70.1 (2C) ppm (d's, C-5′, C-3, C-2 and C-4 of the two glycosyl units, respectively); 67.4 ppm (*t*, J = 150 Hz, C-11); 65.7 ppm (*dd*, J = 142/152 Hz, C-5″); 61.3 ppm (*t*, J = 146 Hz, C-6′); 53.1 ppm (*d*, J = 131 Hz, C-9); 40.7 ppm (*t*, J = *ca* 135 Hz, C-7); 38.1 ppm (*d*, J = 128 Hz, C-8); 19.3 ppm (*q*, J = 126 Hz, C-10). After boiling with mineral acid for 2 h, glucose and xylose was detected in the hydrolysate, using TLC and authentic compounds.

A provisional structure for montinioside is shown in Fig. 1. Comparison with the model compounds valtratum (Thies 1968, Thies et al. 1973) and methyl xyloside gave satisfactory correspondence with the appropriate functionalities in ^{1}H and ^{13}C NMR, respectively, viz. the ^{1}H NMR signals of H-3 and H-6 of valtratum are found at 6.72 and 5.86 ppm, compared to 6.61 and 5.70 ppm for montinioside. With the exception of C-1″, all the ^{13}C NMR absorption arising from the glucosyl and xylosyl moieties of montinioside fall within a range of 0.7 ppm of the corresponding signals from those of other iridoid glucosides and methyl β-xyloside, respectively. The coupling constant $J_{1,9}$ = 9 Hz points to the *trans* relationship of H-1 and H-9, leaving only

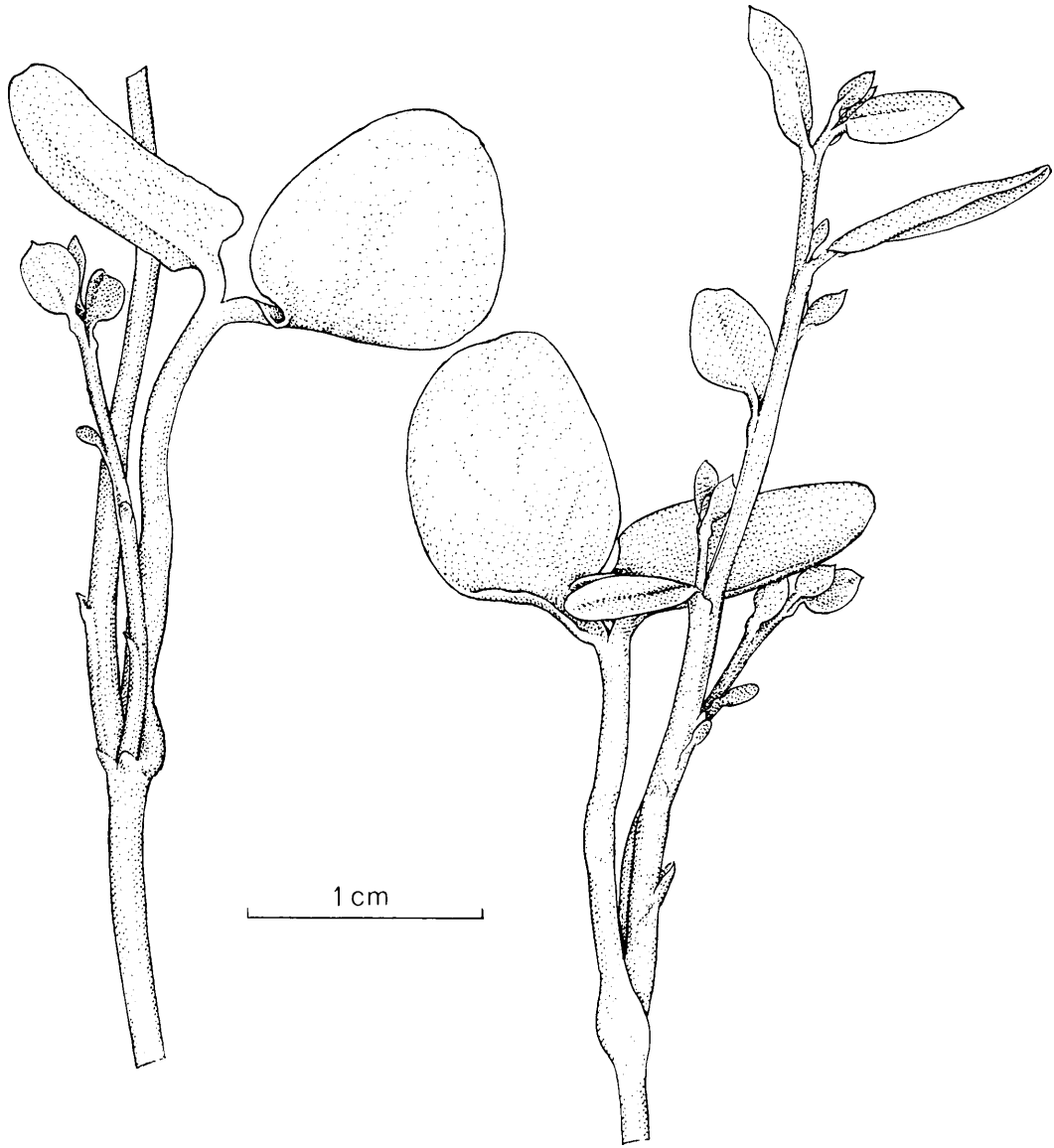


Fig. 2. Seedling of *Montinia caryophyllacea*.

the stereochemistry at C-8 to be determined. Finally, the UV-spectrum of montinioside corresponds to that of valtratum ($\lambda_{max}^{MeOH} = 256$ nm; log ε 4.04).

The presence of a 5,6-double bond and an 11-CH_2OH group is a combination that has so far only been found in *Valeriana* iridoids. This is the first example of an iridoid containing a sugar different from glucose.

Work on the elucidation of the full structure of montinioside is in progress and will be reported elsewhere.

Seedling morphology

The unusual cotyledons of *Montinia* had already been observed by one of us (Dahlgren) and by Dr B. Peterson, Gothenburg, in 1957, although

the observations were neither documented nor reported at that time. The present material was grown from seed (kindly supplied by Dr J. Rourke, South Africa) in the Botanic Garden of the University of Copenhagen.

Very young seedlings have a normal appearance. The elliptic-ovate cotyledons, with a somewhat truncate apex, seem to be subsessile, or have petioles which are less than one mm in length. However, the plumule, when breaking through, appears laterally some 10–15 mm below the bases of the cotyledon laminae, indicating that in fact the petioles of the cotyledons are connate. The stem (Fig. 2) on and above the level of the base of the cotyledon petiole, bears a number of small, scale-like leaves. Lateral branches develop in the axils of some of these and even – as seen in Fig. 2 – in the axil of the first leaf which develops above the cotyledons. In the material studied the first leaves following the cotyledons were constantly alternate. The leaf base is conspicuously pulvinous.

Conclusion

The assembled morphological evidence, including the presence of unitegmic ovules and the lack of intraxylary phloem, in combination with the presence and kind of iridoids, indicate a possible position of Montiniaceae in the order Cornales or close-by. The iridoids agree most closely with those found in *Deutzia* (Hydrangeaceae), *Viburnum* (Sambucaceae) and Valerianaceae of the orders Cornales and Dipsacales (Jensen et al. 1975). Iridoids have not been recorded in members of Celastrales, Myrtales or Saxifragales, in so far as these orders are circumscribed by Dahlgren (1975). The assignation of Montiniaceae to any of these orders, therefore, is not supported by the present results.

The fused petioles of the cotyledons in *Montinia caryophyllacea* is a peculiarity that should be looked out for in possibly-related genera.

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An unusual flowering strategy and new species in Calathea

Helen Kennedy

Kennedy, H. 1977 09 15: An unusual flowering strategy and new species in Calathea. *Bot. Notiser 130*:333–339. Stockholm. ISSN 0006-8195.

Two new species of *Calathea* (Marantaceae) are described: *C. gymnocarpa* from Panama and Costa Rica and *C. verecunda* from Panama. *C. gymnocarpa* exhibits a type of mass flowering, a phenomenon previously unknown in *Calathea*, which is accompanied by the disintegration of the bracts and prophylls.

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Calathea gymnocarpa Kennedy sp. nov. – Fig. 1, 2 A, B

Planta ad 1.4 m alta. Folia rosulata, petioli parte superiori glabra; lamina supra glabra, inferne minutissime tomentosa, trichomis uncinatis, statu juvenili, ovata acuminata supra viridia striata, lineis parallelis geminatis rubris vel albidis, inferne purpurea; lamina, statu maturo, elliptica vel oblongo-elliptica supra viridia, inferne griseo-viridia. Bracteolae mesophyllaque nulla. Bractea prophylla que fugacia. Florescentia circa una hebdomas.

Perennial rosulate herb, 0.8–1.5 m high, bearing 4–8 leaves. The inflorescence is terminal on the leafy shoot and is subtended by a bladeless sheath. *Cataphylls* rotting away, usually absent on flowering individuals, narrowly ovate, apex mucronulate, green abaxially in adults, purple in juveniles, minutely tomentose. *Leaf blade* leathery, tough, elliptic to oblong-elliptic, apex broadly obtuse to rounded, occasionally with an acumen, base unequal, rounded, abruptly shortly acuminate at the junction of the blade to the pulvinus, the midrib depression extending into the upper part of the pulvinus, 22–62 cm long and 16–35 cm wide in innermost leaf, 58–84 cm long and 30–43 cm wide in others. Leaf blade in juveniles shiny, dark green above with single or paired pink or white lines paralleling the lateral veins; dark red-purple below. Subadult leaf blade green above with two broad, longitudinal yellow-green bands (one on either side of the midrib); grey-green tinged purple below. Adult leaf blade deep green above, shiny in young leaves, dulling with age, glabrous, midrib yellow-green, glabrous, toward leaf base subglabrous; blade dull grey-green below, minutely tomentose (hairs recurved, occasionally straight, less than 0.3 mm) mainly along veins and midrib, midrib yellow-green. *Pulvinus* broadly elliptic in cross-section, dark olive-green to yellow-green, glabrous, often acuminately extended along the upper side of the petiole, confluent with the petiole, (1.2–)4–7.5 cm long in innermost leaf, 5.3–9(–12) cm long in others. *Petiole* green, sparsely minute tomentose (hairs mostly straight, less than 0.3 mm), occasionally absent, when present up to 18 cm long. *Leaf sheath* not auriculate, membranaceous, the margins rapidly disintegrating, green to dark green, minutely tomentose (hairs straight, less than 0.3 mm), (3.1–)22–50(–66) cm long. *Stem* green, minutely tomentose (hairs straight or bifurcate), internode between bladeless sheath and innermost leaf up to 55 cm.

Inflorescence terminal, the scape bearing 2, occasionally 1, bladeless sheaths below the inflorescence, the bladeless sheath subtending the inflorescence often similar to the bracts, caducous, densely minute appressed tomentose, 6–18 cm long. Inflorescence 1 per shoot, ovoid, (8–)

9–15 cm high and 6–10 cm in diameter. *Bracts* numerous (over 30), membranaceous, spirally arranged, lower bracts ovate, middle and upper bracts narrowly ovate, apex somewhat eccentric, sub-obtuse to acute in lowermost bracts, acute to acuminate in upper ones, 3.5–5.1 cm high and (0.8–)1.1–1.8(–2.1) cm wide. Outer surface of bract pale green basally in very young bracts, the bracts quickly dying, turning a pale tan to cream-yellow, somewhat translucent at apex and margins, densely puberulent; inner surface glabrous. Each bract subtending up to 5 potential flower pairs, usually only 3 actually mature. *Prophyll* membranaceous, not truly bicarinate, the "carina" represented by two somewhat raised areas, ovate to narrowly elliptic, apex acute, translucent tan, densely minute puberulent; glabrous within, 2.3–3.5 cm high and 0.95–1.4 cm wide. *Secondary bracts* absent. *Bracteoles* absent. The common pedicel of the flowers cream, densely appressed tomentose, 2.5–4 mm long in flower, in fruit up to 1.3 cm, individual pedicels subequal, 1.5–3 mm long.

Sepals fugacious, membranaceous, often wrinkled at base, narrowly elliptic to narrowly ovate-elliptic, apex acute to acuminate, translucent tan, lower half sparsely pilose, upper half appressed pilose, (2.1–)2.4–2.9 cm long and (0.4–)0.5–0.85 cm wide. *Corolla tube* cream to pale yellowish, appressed pilose (hairs to 1 mm), 1.5–2.3 cm long, staminal tube 0.8–1.2 cm long; corolla lobes subequal, elliptic, slightly sigmoidal, apex acute, pale cream, sparsely minute pilose (hairs less than 0.3 mm), 2.6–3.8 cm long and (0.5–)0.7–0.95 cm wide. *Outer staminode* obovate, apex obtuse, faintly orange to apricot-colored, paler at margins, (1.8–)2–2.6 cm long and 1–1.4 cm wide. *Callose staminode* elliptic to broadly rhombic-obovate, petaloid, apical half reflexed, apex retuse, cream at base, pale orange above, darker centrally, (1.6–)1.9–2.8 cm long and 1.1–1.75 cm wide. *Cucullate staminode* cream apically, basal portion apricot, 0.8–0.9 cm long and 0.5–0.8 cm wide, provided with a subterminal filiform appendage. *Filament* with lateral petaloid appendage c. 1 mm; anther free, 3–4 mm long. Style and stigma golden. *Ovary* cream-tan, densely villous (hairs tan), 2.5–3 mm high and 3–3.5 mm in diameter. *Capsule* fleshy, rough, obconoid, pale tan turning orange to red-orange at maturity, 1.3–1.4 cm high and c. 1.8 cm wide, occasionally the basal 1–3 mm of the shriveled sepals remains attached. *Seeds* usually 3 per capsule, smooth, subtrigonous to rotund, dark blue, 6–9 mm high and c. 6–7 mm in diameter, bearing a basal white aril to 2.5 mm high.

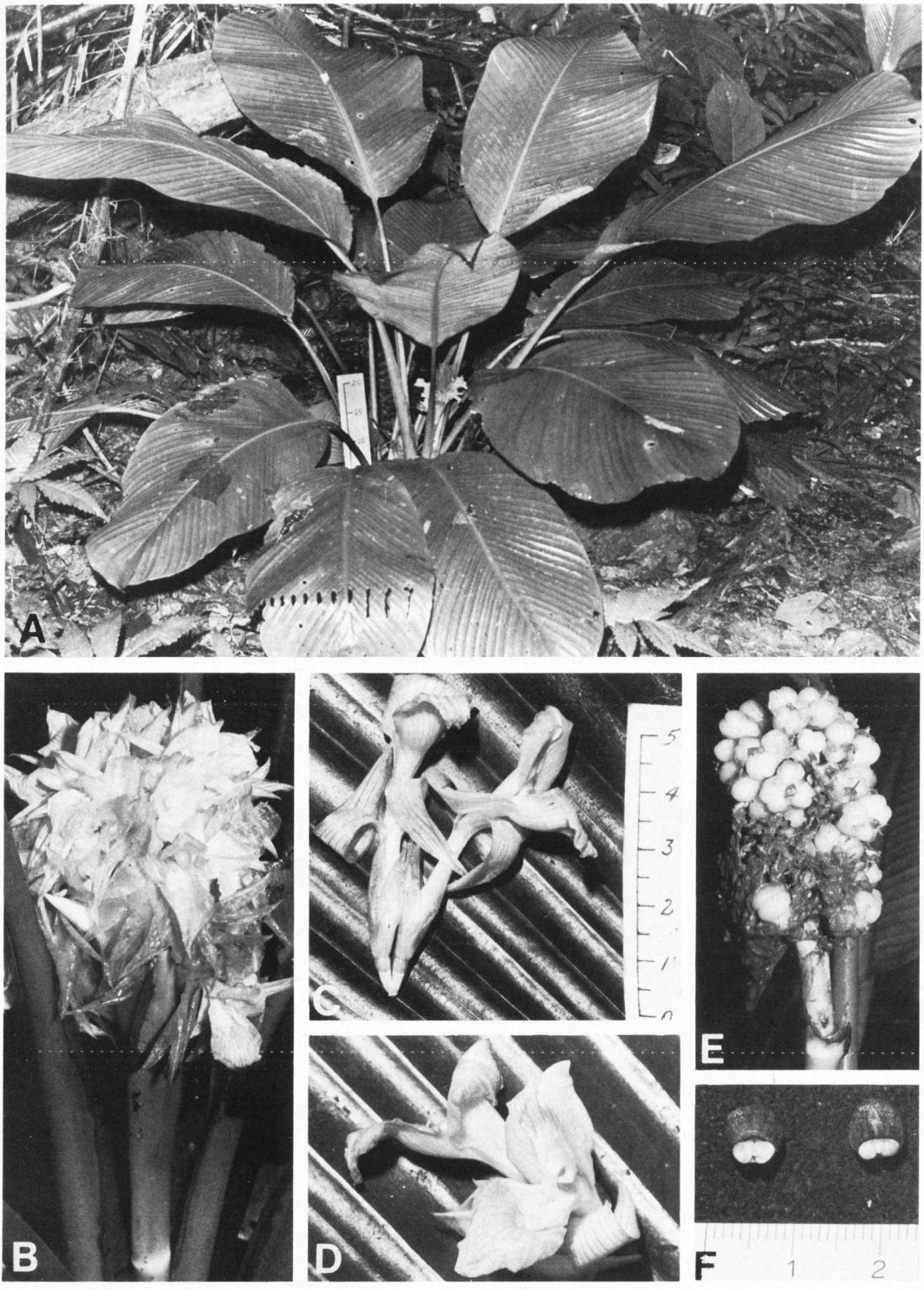
Type. Panama. Prov. Colón, Río Guanche, c. 1.5 miles upstream from the bridge, 10–20 m, wet lowland evergreen forest, 4.9.1974, Kennedy, Maas, Dressler & Toft 3393 (holotype F 1790971 and 1790970, isotypes F, GH, MO, U, US).

Other collections. Panama. Prov. Bocas del Toro, Almirante, Filo de Almirante, 1.12.1971, Kennedy & Dressler 1313 (F) – Costa Rica. Prov. Puntarenas, 10 km in on Pacific trail from Rincón, Osa Productos Forestales land, Osa Peninsula, 200 m, 2.3.1965, Lent 442 (F) – Prov. Heredia, original wet forest and cocoa plantation on the property of Dr L. Holdridge, c. 2 km upstream on the Río Puerto Viejo, c. 100 m, 10°23' N, 83°59' W, 5–6.1.1967, Burger & Matta U. (F) – Cultivated. Flowered at Kew 1914, Sander 485 (K) from material of Forget (Forget 2).

Calathea gymnocarpa flowers mainly during the rainy season, July through December. A fruiting specimen has been collected as late as early March. It occurs in the lowland evergreen wet forest and is found within the forest, in moderate to deep shade, as scattered individuals though occasionally it is locally abundant. It occurs in the wetter forests along the Atlantic lowlands of Costa Rica and Panama and the wet forests around the Golfo Dulce, Costa Rica, on the Pacific coast.

Calathea gymnocarpa can readily be distinguished from all other Central American Marantaceae by the distinctive pattern on the juvenile foliage. The upper leaf surface is dark green with pink or white lines paralleling the lateral veins; the lower leaf surface is red-purple. As a flowering individual, this species is distinguished by its capitate inflorescence, short flowering period (c. 1 week), the absence of secondary bracts (interphylls) and bracteoles,

Fig. 1. *Calathea gymnocarpa*. A: Habit. – B: Inflorescence in flower. – C: Flowers on upper surface of leaf. – D: Tripped flower showing shape of callose and outer staminodes; note pollen in the stigma. – E: Inflorescence in fruit; note the disintegrating bracts at left. – F: Seeds. – Scale in cm.


A
B
C
D
E
F
1
2

the rapidly disintegrating bracts and prophylls and the resultant cluster of exposed maturing capsules. These latter adult characteristics also distinguish this species from the related South American Calatheas which exhibit the same juvenile foliage pattern. The recurved hairs on the underside of the leaf distinguish the juveniles of *C. gymnocarpa* from other similarly patterned juveniles. There is a gradual transition in leaf pattern from the striped juvenile through the subadult pattern to the loss of the pattern altogether in the adult. The pattern on any given leaf is fixed, the type of pattern depends largely on the size (food reserves?) of the plant when that leaf was produced. If the rhizome of a mature plant is divided into small pieces, the new shoots will bear juvenile foliage, whereas if the rhizome is divided into a couple of moderate-sized pieces the new shoots will exhibit subadult foliage patterns.

The specific epithet *gymnocarpa* refers to the exposed position of the capsules after the covering bracts have rotted away. This species was observed to be pollinated by *Eulaema speciosa* at the type locality.

Flowering and fruiting in Calathea gymnocarpa

The flowering period of a single individual of *Calathea gymnocarpa* is quite short, probably lasting only a week or so. All the bracts in the lower third to half of the inflorescence bear flowers the first day. By the second or third day all the bracts in the inflorescence bear mature flowers. The time between the anthesis of the first pair of flowers and second pair of flowers within a bract is very short. During flowering, the bracts begin to disintegrate and, within a week or so, both the bracts and prophylls have rotted off, revealing the cluster of developing capsules. This short flowering time is quite unusual in the Marantaceae. Though mass flowering is known for a number of tropical trees and shrubs (Janzen 1967, Gentry 1974), it has not been reported in *Calathea* and is not known in any other species of Central American Marantaceae. In the majority of Calatheas, only a few flowers are produced each day over a long (over 2 months) period; both mature capsules and flowers can be found together on the same inflorescence.

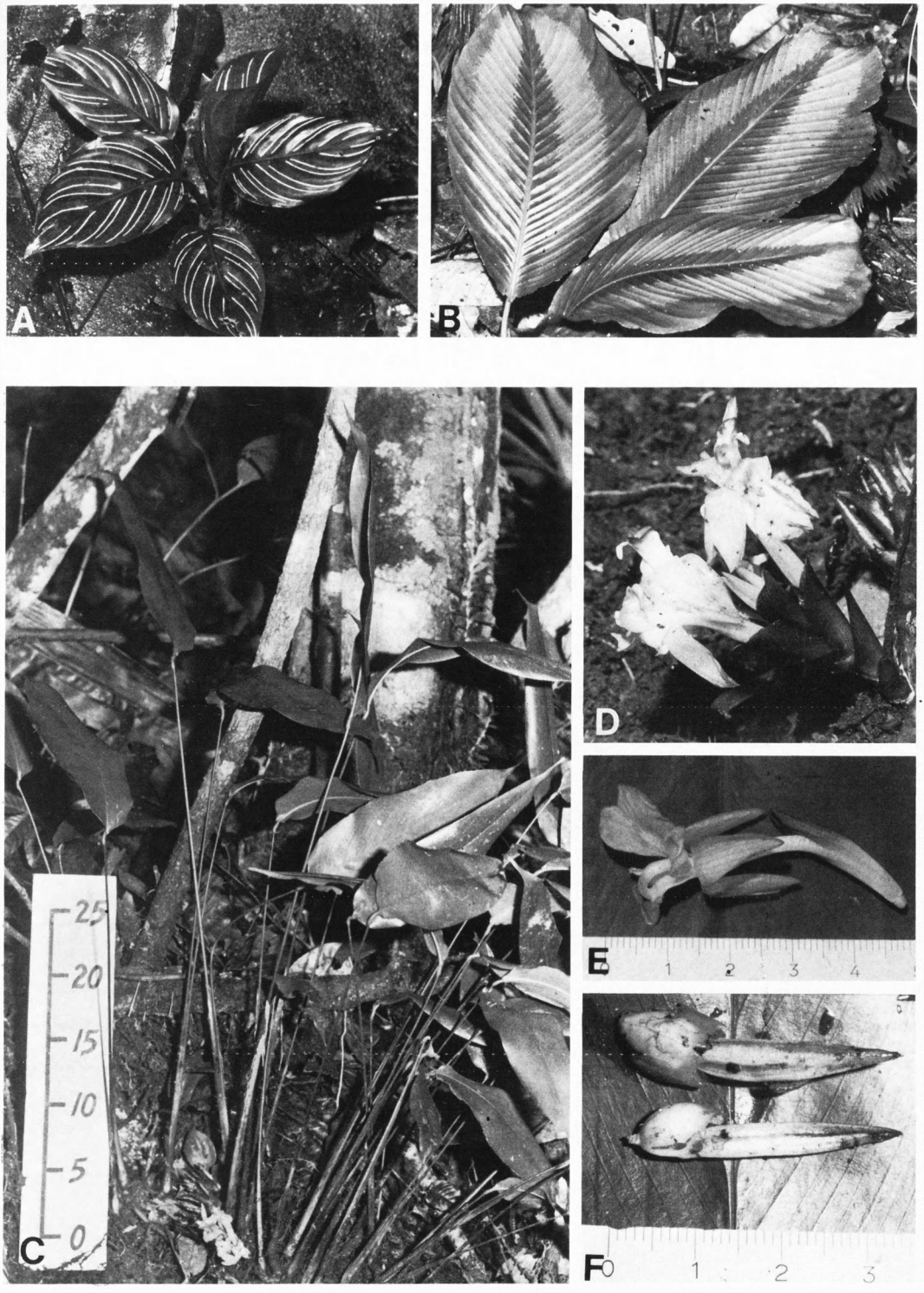
Another unusual aspect of the reproductive biology of *Calathea gymnocarpa* is the rapid disintegration of the bracts and prophylls which begins during flowering. In this species, both the secondary bracts (interphylls) and the bracteoles have been lost, whereas the secondary bracts (and usually bracteoles as well) are present in related species. However, in the most closely related species, *C. inocephala* (O. Ktze) Kennedy & Nicolson, the bracteoles are also absent. The bracts also die back shortly after the initiation of flowering in the related species *C. inocephala, C. altissima* (P. & E.) Koernicke and *C. grandis* Petersen, but in these species the bracts, or remnants thereof, remain on the inflorescence.

The bracts of a *Heliconia* which occurs with *C. gymnocarpa* at the Río Guanche locality also disintegrate completely and leave a cluster of capsules closely resembling that of *C. gymnocarpa*. In the *Heliconia* the capsules are red rather than orange or red-orange. The habit of the *Heliconia* is likewise similar to *C. gymnocarpa* and is rather atypical for *Heliconia*. The convergence in inflorescence position and manner of fruit presentation suggests that there has been selection for utilization by both species of a common dispersal agent, most probably a bird. Clearly a detailed study of the biology of both the *Calathea* and *Heliconia* is needed to understand the evolutionary significance of the striking similarity between them.

Calathea verecunda Kennedy sp. nov. – Fig. 2 C–F

Planta ad 70 cm alta. Folia 1–2, raro 3–4; lamina, pulvino, petiolo et vagina utrinque glabra. Spica e rhizomate; bractis 6–15 glabris, extus atropurpureis, intus viridibus; paria florum bracteolis 4 comitata; prophyllis bicarinatis ad 1.6 cm longis, ovatis ellipticisve, glabris, apice rotundata; corollae tubo ad 3.1 cm longo, albo; staminodiis exteriore et calloso pallide purpureis.

Fig. 2. A–B: *Calathea gymnocarpa*. A: Juvenile foliage. – B: Subadult foliage. – C–F: *Calathea verecunda*. C: Habit. – D: Inflorescence. – E: Flower on upper surface of leaf. – F: Capsule with persistent calyx on leaf. – Scale in cm.


A
B
C
25
20
15
10
5
0
D
E
1
2
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4
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Perennial, rhizomatous herb, 30–70 cm high. *Rhizome* 0.3–0.8 cm in diameter. Shoots bearing 1–2, rarely 3 or 4 leaves. *Cataphylls* thin, papery, narrowly ovate, apex obtuse, mucronulate, green when young, often dried up on mature individuals, glabrous; innermost cataphyll 13–28 cm long. *Leaf blade* pliable, somewhat leathery, narrowly ovate, apex caudate-acuminate, base obtuse to rounded, junction of blade to pulvinus abruptly shortly acuminate, 15–31 cm long and (4–)5–8 cm wide. Leaf blade above dark green, glabrous, midrib lighter green, glabrous; leaf surface below slightly lighter, almost concolorous, glabrous. *Pulvinus* oval in cross-section, strongly curved, olive-green, glabrous, articulate with petiole, 0.5–1(–1.5) cm long. *Petiole* round in cross-section, deep green, glabrous, 17–47 cm long. *Leaf sheath* not auriculate, dark green, darker at base with slight purplish tinge, glabrous, (3.5–)7–23 cm long; base of sheath swollen, pale white-tan or pinkish. *Stem* tan, tinged pinkish.

Inflorescences one to two associated with a leafy shoot, arising directly from the rhizome, ovoid, bracts imbricate, 2.5–4.2 cm high and 1.7–2.2 cm in diameter. *Peduncle* purple, glabrous, 0.9–4.5 cm long. *Bracts* 6–12(–15) in number, herbaceous, spirally arranged, ovate to narrowly ovate, apex acute to acuminate, upper bracts longer and narrower than basal ones, apex subpatent, 1.9–2.5 cm high and 1.2–1.7 cm wide. Outer surface of bract red-purple at the very base, the rest dark purple, glabrous; inner surface green, glabrous; each bract subtending 2 or more flower pairs. *Bicarinate prophyll* membranaceous, narrowly ovate, apex acute, translucent faint greenish, tinged purple apically, glabrous, 1.5–2 cm high and 0.5–0.6 cm wide, carina to carina, 0.8–1 cm wide, total width. *Secondary bracts* membranaceous, ovate to elliptic, apex rounded, translucent faint greenish, tinged purple apically, glabrous, 1.2–1.6 cm high and 0.4–0.8 cm wide. *Bracteoles* 4 per flower pair, 2 lateral, channeled, and 2 central, channeled, faint greenish to transparent below, apex tinged purple, glabrous, 0.9–1.8 cm high and 0.2–0.6 cm wide, the lateral ones longer and wider than the central ones.

Sepals herbaceous, narrowly obovate, apex acute to obtuse, lower 1/2 white, green above, apical margin tinged purple, glabrous, 2.3–2.4 cm long and 0.3–0.45 cm wide. *Corolla* tube white, glabrous, 3–3.1 cm long; corolla lobes subequal, ovate-elliptic, apex obtuse, the margins inrolled appearing acute, white, occasionally tinged purple at the apex, glabrous, 1.7–1.8 cm long and 0.6–0.8 cm wide. *Outer staminode* transverse broadly elliptic, clawed at base, apex emarginate, lavender, the basal portion white, 1.4–1.6 cm long and 1.3–1.5 cm wide. *Callose staminode* almost totally fleshy, apex obtuse to irregular, white below, apex light to dark purple, 1–1.1 cm long. *Cucullate staminode* white, 0.6–0.7 cm long and 0.5–0.6 cm wide, provided with a subterminal filiform appendage. *Filament* white with lateral white petaloid appendage to 1.5 mm wide; anther white, 2 mm long. Style and stigma white. *Ovary* cream-white, smooth, glabrous, 2.5–3 mm high and c. 2 mm wide. *Capsule* obconoid, trigonous, apical edge of one face irregularly tridentate, white to light green, 1–1.1 cm high and 0.8–0.9 cm wide; crowned by a persistent, live, enlarged calyx. *Seeds* usually 3 per capsule, trigonous, rugose on the outer surface.

Type. Panama. Prov. Panamá, La Eneida, region of Cerro Jefe, 3.3.1973, Dressler 4285 (holotype F 1790790, isotypes MO, US).

Other collections. Panama. Prov. Panamá, km 20 on the El Llano–Carti road, 22.2.1973, Kennedy & Dressler 2575 (DUKE, PMA); km 12–13 on the El Llano–Carti road, evergreen wet forest, 380–420 m, 25.2.1976, Kennedy & Dressler 3517 (F).

This species flowers mainly in the dry season, February through May. It occurs in moderate to deep shade within the forest on well-drained slopes, often near the base of large trees.

Calathea verecunda is distinguished from other Central American species by the inflorescence borne on a separate shoot directly from the rhizome (not terminating a leafy shoot); by the glabrous leaf blade, pulvinus, petiole and sheath; by the 6–15 dark purple, glabrous bracts and almost totally fleshy callose staminode. It is similar to *C. bachemiana* E. Morren in aspect but differs in having a plain green rather than a patterned leaf, a shorter (1.6 versus 2.3 cm) outer staminode, a callose staminode dissimilar in shape to the outer staminode and a lavender rather than a white flower. *Calathea verecunda* differs from the other species of *Calathea* which have the inflorescence(s) borne

on a separate leafless shoot by the following characters: the absence of claviculate bracteoles, the narrowly ovate leaf, and the glabrous bracts and pulvinus.

This species was referred to for several years as *Calathea* "unknown", as numerous seedlings and vegetative individuals were found but flowering individuals were still unknown, hence the epithet *verecunda,* meaning modest, shy or bashful.

Acknowledgements. I wish to thank Dr Robert Dressler for making possible the collection of these species in the field and Dr John Fay for his help with the Latin descriptions.

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Botanical literature

Gams, W. 1971: *Cephalosporium-artige Schimmelpilze (Hyphomycetes)*. X + 262 pp., 137 figs., 3 plates. Gustav Fischer Verlag, Stuttgart. Price (bound) 86 DM.

A great number of exceedingly different fungi have been placed in the genus *Cephalosporium* Corda (1839). Most of them are mould-like Hyphomycetes, which produce simple or ramified, sometimes synnematous, usually hyaline conidiophores with phialides and dry, one-celled conidia in chains, or slimy conidia in heads. The difficulty in circumscribing *Cephalosporium* and "allied" genera, such as *Acremonium, Paecilomyces,* and *Verticillium,* has resulted in numerous transfers of species between these and other genera. In spite of the recent studies published by several authors, no overall survey of these fungi was available. This is what Gams has tried to provide, and his task has not been easy. Not least the perusal of the literature must have been laborious, since accounts of the species have appeared in many different kinds of publications.

The general part of the monograph includes sections on methods, morphology, history, unaccepted genera, correlated Ascomycete genera, a full bibliography, and a key to all *Cephalosporium*-like genera in the widest sense. The special part contains descriptions, nomenclature, keys to and illustrations of the taxa, lists of cultures and of the herbarium specimens studied, and a list of excluded species (not complete). A third part provides surveys of certain ecological groups (species present in soil, on plants, chitin, animals, fungi, man, and antibiotic-producing species). The work ends with a glossary, an English translation of all keys, and an index.

The imperfect genera dealt with are: *Acremonium* (82 species), *Tilachlidium* (1), *Septofusidium* gen. nov. (1), *Monocillium* (13), *Verticillium* (20, light-coloured species only), and *Aphanocladium* gen. nov. (2). Unnamed conidial states of *Emericellopsis* (5), *Calonectria* (1), *Wallrothiella* (1), and some marginal species are also included. Two genera, 39 species, 3 sections, 5 "series", one name, and some 70 combinations are new, the last-mentioned mostly in *Acremonium*. *Cephalosporium* itself, however, is excluded because its original species are probably Phycomycetes of the genus *Mortierella*.

Gams uses a special terminology, which is partly his own, to describe different modes of growth on agar, the ramifications of the conidiophores, the position of the phialides, and the shape of the conidia. Notwithstanding, most of these terms seem superfluous. 'Ellipsoidal', for example, tells as much about the conidial form as "homopolar-polysymmetrisch" (p. 9), a term borrowed from palynology. To distinguish between synnema and coremium (p. 6) also goes against current practice. The author's ambition is understandable, however, bearing in mind the difficulties in finding diagnostic characters for these organisms.

In the discussion, some phenomena of taxonomic importance are pointed out. A catenate or capitate arrangement of the conidia seems to be specific characters only or even modifications strongly influenced by different substrates and moisture conditions. Substrate type and the age of the colonies govern the form and size (length) of the conidia. Not even the pigmentation and ornamentation of the conidia and conidiophores appear to be useful as generic characters.

These aspects have led Gams to adopt a wide generic concept, as is manifested by his

treatment of i.a. *Acremonium* and *Verticillium*. The former genus has conidial states in several Ascomycete families, and has devoured the whole of *Gliomastix* (as a section) and some species of *Paecilomyces*. Many *Nectria* imperfects form another section. This is disputable taxonomically, but is dictated for practical reasons. The dilemma lies in the acceptance of form-genera, which conflicts with a striving towards natural groups correlated with possible perfect states. It is the reviewer's opinion that if the *Nectria* imperfects be recognized as a section, one might just as well separate them at generic level, and, if not, then the section would be better deleted.

In *Gliomastix* s.str. the species possess pigmented conidia, but are related to hyaline-spored species, all of which have "chondroid" hyphae with thick, light-refractive walls. It would perhaps have been preferable to have kept *Gliomastix* at generic level in the one or the other sense. *Verticillium* has also become an unwieldy genus by the inclusion of species from both the Hypocreaceae and Clavicipitaceae. In other cases the classification adopted is simpler. *Monocillium*, for example, is easily defined in morphological terms, and, besides, belongs to only one perfect genus, *Niesslia*.

There are some nomenclatural errors. *Acremonium* sect. *Simplex* contains the type of the generic name and must thus bear the name *Acremonium*. The five "series" in *Gliomastix* are not validly described and series *Murorum* shall be named *Gliomastix*. *Acremonium* sect. *Nectrioidea* has not been typified and is accordingly illegitimate. Nor is it clearly indicated whether the types of all the new specific names are based on dried or living specimens. The present rules do not permit typifications based on living cultures, a clause laid down already in the 1966 Code of Nomenclature.

The author has been painstaking with the type investigations, but in many cases there was simply no material available. He has been very restrictive in his use of old names if there were any doubts attached, and he has also adopted a fairly narrow species concept. It is easy to sympathize with his motives here, but a number of name changes will certainly follow when the older type collections are eventually traced. Gams founds his descriptions mainly on living cultures (in Baarn), and has evidently revised only a few samples in other herbaria.

The present monograph is on the whole very impressive. One must appreciate this serious effort to bring order and system into such a difficult group of fungi. Gams has also arranged the text in a very straightforward manner, to which e.g. the synoptic key to *Acremonium*, the ecological surveys, and the translations for English-speaking readers bear witness. The author is to be congratulated on having produced a work of lasting value.

Nils Lundqvist

Gottschalk, W. 1976: *Die Bedeutung der Polyploidie für die Evolution der Pflanzen*. Fortschritte der Evolutionsforschung, Band 7. 511 pp., numerous figs. Gustav Fischer Verlag, Stuttgart. ISBN 3-437-30221-3. Price DM 210:–.

Discovery is a cumulative process, which includes not only the important phase of collecting and describing data of objective facts, but perhaps still more the philosophical evaluation that places new observations into their reasonable perspective. Because of the great importance of the latter, every scientific approach is, at a certain stage, in need of a basic synthesis of what has become known by aid of the descriptive and comparative methods. If that synthesis is comprehensive enough, then, at least for a time, a periodical upgrading through partial reviews is usually satisfactory, until adjustments in the general philosophical position require a new and extensive revaluation. This is true in all branches of knowledge, but it is perhaps most important in the disciplines related to organic evolution, the correct explanation of which is basic to most of the biological sciences and their practical application.

To paraphrase Kipling, there may be nine and sixty ways in which the evolution of life has proceeded. Extensive investigations of the part of this event that has been called speciation indicate that it may not be a continuous process as frequently suggested but a stratified stability of ladderlike advances, each step of which apparently being protected from oblivion by something called reproductive isolation. Numerous studies of many plants seem to indicate that the complex phenomenon of poly-

ploidy may have been the most important of these processes in eukaryotic plants with a localized centromere. Since no other genetical incident has been as widely investigated by population geneticists, its relative significance may, of course, be somewhat overrated; but that does not diminish the fact that polyploidy is a very important evolutionary process.

An issue so significant and so extensively studied must be reviewed and synthesized regularly so that its implication can be appraised and its progress directed into areas of possible neglect. Such reviews have, indeed, been published a few times for certain aspects of polyploidy, although still nobody seems to have attempted to compile a comprehensive philosophical and interpretative synthesis that could help to find its exact place in the modern understanding of life and thus clarify many observations that still appear to be ambiguous.

The main reason for the lack of a general synthesis of our present knowledge of polyploidy is probably the magnitude of the task, because few biologists have the energy or even ability for a detailed scrutiny, digestion and philosophical evaluation of more than ten thousand reports and books in which polyploidy has been described and discussed during the past three quarters of a century. Perhaps the solution lies in an organized division of the work between carefully selected members of a team of conscientious and energetic specialists who afterwards could together compose, as a kind of a conclusion, a comprehensive philosophical summary on basis of the more special reviews. At present such a team seems to be nonexistent, or perhaps its possible organizer and leader is nodding?

The most extensive digest of any part of the polyploid process has just become available in a book on the significance of polyploidy for the evolution of plants, written by Professor Werner Gottschalk of the University of Bonn, who is also the author of a synopsis of the evolutionary significance of gene mutations. After having examined a substantial part of the tremendous literature on the subject, he places the main emphasis on a survey of the characteristics of experimentally produced polyploids because he is of the opinion that this is necessary for establishing a firm basis for the identification of natural polyploids. Even that is a gargantuan task. Although the author has avoided the much needed philosophical part of the explanation, and the importance of polyploidy for speciation by forming an effective reproductive barrier between gene pools in which its fundamentality for evolution is most significant, and, therefore, limited his search to a single, albeit important, area of the subject, he has, in the view of this reviewer, succeeded amazingly well in writing a synopsis of considerable weight.

Professor Gottschalk divides his treatment into eighteen chapters. The essential chapters discuss experimental and natural polyploids, anorthoploids, aneuploids, and the distribution of polyploids, with an emphasis on means to identify and distinguish autoploids and alloploids in nature. Of course, some of the chapters are more detailed than others, for various reasons, and some are by necessity shallow for lack of information. It is a pity that the introductory chapter, on theoretical viewpoints for the evaluation of polyploid plants, is rather incomplete and philosophically weak, as are some conclusions regarding certain other basic phenomena elsewhere in the synopsis, but weaknesses of that kind are amply compensated for by the genuine thoroughness of the descriptive chapters that form the bulk of the book.

In such a large text all geneticists will find a wealth of important observations gathered from many sources. It is, however, inevitable that some specialists may join issue on various conclusions or even question the wisdom of the selection of references by the exclusion of others, and the size of the work makes it ideal for nitpickers. The present reviewer would have liked to see a more solid evaluation of the differences between various kinds of polyploids based on their assumed origin and later evolution and a more advanced classification into groups than is met with in the system adopted, which is essentially that of Stebbins in 1938, when less than one-fifth of the literature on the subject had been published. It could also have been emphasized more strongly that most of the knowledge of the physiology of polyploids is based on much too few and much too preliminary investigations published a generation ago so that the field is actually widely open for a modern and extensive attack which could benefit immensely from being connected with sound ecological observations. From the point

of view of some readers, it may seem unfortunate that the author apparently follows the 18th century philosophy of nominalism in his weak concept of the taxonomic categories, as is prevalent among many modern botanists but certainly contrary to all genetical and evolutionary concepts that are strictly empirical and materialistic. Furthermore, the author tends to accept uncritically most original reports, even when later papers, which he frequently ignores, have corrected their mistakes. Therefore, some of his conclusions and a few of the most elaborate tables must be taken with a grain of salt. This is, for instance, the case with Tables 6 and 7 which are characterized by the inclusion of many old and very doubtful examples of socalled "intra-specific polyploidy", which itself is an idea that may look as a nominalistic anachronism in a book on evolution. Actually, much too many of the almost 200 examples of such "species" are worthless because they were originally based on direct misidentification, downright misunderstanding, or lack of taxonomic skill by the original authors so that a more critical scrutiny would have reduced them to perhaps a handful of still doubtful cases. But a strict adherance to the uncritical principle adopted ought to have increased such "examples" manifold because even the socalled scientific literature abounds in superficial observations.

In the important discussion on the frequency of autoploids and alloploids it is, correctly, pointed out that the great majority of such plants are intermediate, whereas pure autoploids and strict alloploids are claimed to be rare. I am in no doubt that this is correct as far as their success and natural occurrence is concerned. However, I would like to add the observation, based on numerous studies of large samples of germinating seeds of many species of gymnosperms, monocots and dicots, that strict autoploids seem to be formed in a low permille frequency in all plants of which large samples have been studied, and perhaps in all populations of all plants; but if a seed gives rise to an autoploid individual, this plant is likely to be weak and soon selected away, which may be the reason for that such polyploids are rare under natural conditions. Likewise, a special emphasis could have been given the important remark by Müntzing and only hinted at in the book, that strict alloploids, produced from completely sterile hybrids between unrelated species, are likely to be entirely missing and to occur only in theory except after a thorough secondary differentiation of intermediate polyploids has taken place, for the simple reason that species with fully unrelated chromosomes cannot hybridize. Such minor remarks that could be made also on some other questions demonstrate the difficulties that any scientist must inevitably encounter when attempting such a wide synthesis, but small inaccuracies of fact and especially of judgement are human and cannot be escaped even by the most careful of compilers. And none of the more or less trite comments above can lessen the fact that the author has succeeded unusually well in his difficult task.

As a conclusion it is only fair to admit that it is the nature of most synoptic work not to be complete or even exact, although this text is unusually thorough and inclusive in the fields it covers. It was planned to embrace only some of the literature on the significance of polyploidy in evolution. For practical reasons the author shuns all discussion on the more general significance of polyploidy that some readers might have preferred. Therefore, the book may fall short of satisfying the need for an interpretative synthesis of polyploidy as a whole, but its virtue lies in its comprehensiveness rather than in its completeness in the areas it wants to cover. There has apparently been some difficulty in composing the bibliography of about 2500 titles, because some papers mentioned in the text are missing. The register is hardly sufficient for a work of this magnitude, and a few but insignificant printing errors will probably please those who find such matters to be important. But since this is by far the most important review of polyploidy ever published, it must be highly recommended to all botanists and geneticists interested in population biology, basic or applied, and, especially, to those working in the fields of evolutionary botany.

Áskell Löve

Lundqvist, J. et al. 1974: *Survey of the vegetation conditions in the catchment area of river*

Vindelälven, northern Sweden. 332 pp., 10 figs., 37 plates and 10 tables. SNV PM 409. Statens Naturvårdsverk, Stockholm.

Lundqvist, J. & Wistrand, G. 1976: *Riverside vascular flora in the upper and middle catchment area of the river Skellefteälven, northern Sweden*. 175 pp., 19 figs., 3 maps and 8 tables. Växtekologiska Studier 9. Uppsala. ISBN 91-7210-806-6.

From times immemorial human progress has depended upon the wise and effective exploitation of natural resources. Until the scientific method was invented, attempts to regulate even simple phenomena were frequently so groping that success was easily replaced by disaster. This is amply documented by history even from Scandinavia, when great lakes or rivers were tampered with through mistaken foresight. Even during recent times technological advance without scientific planning has sometimes caused unexpected harm so that unwarranted pollution or other disturbances by technologically desirable projects has endangered animals and plants and even human habitations over large areas, though such difficulties are frequently counteracted by natural regulation when time passes.

A continued but scientifically guided regulation of natural phenomena is certainly required for the improving of the conditions of life even for others than the fortunate few in all parts of the world. Of these conditions, the harnessing of energy seems to be the most widely discussed at present, not least because it is frequently connected with dangerous pollution or disturbance of other vitally important natural resources or with the impairing or destruction of ecosystems that may be essential for present or future production of food, maintenance of health, or simply for the well-being of human beings who still do not live on bread alone.

Sweden, which leads the development of the welfare state that the entire world will hopefully enjoy in the centuries to come, also stands in the front in the exploitation of water power which forms one of the essential pillars of its industrial strength. During the past generation, most of the large Swedish rivers have been thoroughly developed for hydroelectric power by aid of artificial reservoirs that sometimes have caused the transformation or even extinction of irreplaceable vegetation at the same time as it has led to the quieting of some of the most beautiful waterfalls in the world. In most cases this technological progress has been preceded by some biological investigations on which were based recommendations for modifications that favorably counteracted some of the negative effects of the technologically desirable projects and, sometimes, even led to their rejection.

Two recent publications demonstrate the approaches and methods of Swedish botanists studying the ecosystems of large river valleys before and after the technologists exploit them for much needed electrical power. The first of these, which is a survey of the condition of the vegetation in the catchment area of the river system Vindelälven in northern Sweden, is a 1974 report of a detailed floristic and ecological study that was initiated by the great late ecologist Professor G. Einar Du Rietz in 1961 and carried out by several well qualified botanists under the able leadership of Dr Jim Lundqvist, who compiled the report. This river is in its lowest parts confluent with the river Umeälven, which was heavily exploited during the past two decades, whereas Vindelälven remains largely unregulated so that it is a worthy object for vegetation studies of a resource prior to technological progress. The second book is a similar study of the river Skellefteälven, which is one of the most thoroughly exploited river systems in northern Scandinavia. Several ecologists have investigated this area in cooperation with the authors of the report, Dr Jim Lundqvist and Dr Gunnar Wistrand, who claim in the introduction that the regulation of this river system, made mainly during the past 15 years, has been so severe that a considerable part of the original ecosystems may be regarded as totally destroyed. In other words, the two publications describe a boreal ecosystem before and after a severe and perhaps disastrous exploitation.

The Vindelälven book begins with an historical review of botanical studies of this large area, which was visited by Linnaeus in 1732 and by some later botanists, although more extensive observations on the flora were hardly made until during the present project. The topographical and geological conditions are summarily described, as are also the effects and characteristics of various human activities since

the colonization of the area began in the 18th century. The bulk of the book, however, reviews the zonation and floristic composition of the vegetation of the river banks and valleys which reach from the spruce forests of the lowlands through the pine forests and mixed forests of the montane areas to the birch forests and tundra zones of the subalpine and alpine regions. The floristic composition at numerous sites has been analysed exactly and in great detail both qualitatively and quantitatively to demonstrate the wide variation and extreme richness of the vegetation. It is a pity that the magnitude of the task has not yet allowed a detailed phytosociological analysis of all sites studied, because that would evidently also have shown an unusual assemblage of plant associations at various stages of development. The floristic review concludes with a survey, by Gunnar Wistrand, of the distribution and lower limits of the alpine plants and a review of some of the rare species met with in the area, and a chapter, by Sten Nordenstam, on the many species of the apomictic genus *Hieracium* that are characteristic of this part of northern Sweden. Then come a few conclusions concerning nature protection, by Jim Lundqvist. There is an index of species mentioned in the text, and the book ends with 37 excellent photographs.

The Skellefteälven text reviews first the geography of the area and surveys the exploitation of this large river valley as explained by aid of an impressive map of the extensive regulation of the river, before delving into a discussion of the flora of the region as influenced by the recent technological advance. As could be expected, the vegetation near still undeveloped tributaries and on the mostly unaffected mountains remains conspicuously rich in species, and the plant associations in these places are undisturbed, whereas the flora of the riverbanks within the regulated area has been drastically reduced so that many of the lowland species seem to have been exterminated and most of the associations deranged beyond recognition. Fortunately, there have been left some pockets of less disturbed forests rich in species from where some plant associations might perhaps disperse for a partial recovery of the area when the artificial situation has stabilized, although complete recovery may require considerable and expensive human assistance. The destruction could, of course, have been minimized and the recovery simplified if a study like that of the Vindelälven had preceded the technical exploitation and been used as a basis for the selection of protected areas from where vegetation could invade the affected grounds, without restraining the certainly necessary technical development.

The investigations of these large river systems and the vegetation that is dependent upon them could be used as models for the planning of extensive exploitation in other parts of the world. They clearly show that even modest floristic-ecological studies by taxonomically competent ecologists are of the greatest importance in planning large technological projects in such a way that even drastic engineering projects could avoid disastrous effects on other natural resources. It is evident that the vegetation near Skellefteälven has been seriously though hardly irrepairably hurt because the mistaken but well-intentioned eagerness of the technologists blinded their foresight and even the biologists may have been sleeping on their guard. Similar mistakes caused by a lack of proper safety measures are still being made in connection with mining and industrialization in many parts of the world, especially where the supply of conscientious and properly competent floristic ecologists is scarce or where their rare existence is ignored by technologists and bureaucrats who themselves may have little understanding for the need for an environmental protection so they are satisfied by only paying for socalled environmental impact studies that are worthless because they were made without honest qualifications that border to fraudulence. These superb Swedish studies could not have been done by ecologists without a profound floristic training, and they would also have been impossible if the flora of Scandinavia had not been thoroughly covered by critical and modern flora manuals, which are the most important tools of botanists of either basic or applied learning.

The energy requirements of the industrial welfare state seem to increase exponentially as long as the population explosion is not effectively restrained. Since hydroelectric power evidently is less expensive and less polluting than other presently available energy, it is understandable that those who are responsible

for industrial progress find it desirable to utilize every available river to the utmost. Presently, all but four large Swedish rivers have been ultimately harnessed, and the time is rapidly nearing when those that are left also have to be utilized. Perhaps it is permissible to suggest, however, that the politicians and technologists look into the hardly unreasonable wish that these rivers could for ever be left untouched by developers so that unborn generations will be able to enjoy limited recreation in the pristine surroundings of great Scandinavian waterways and to profit from the natural beauty that always has stimulated the creative minds of poets and thinkers. The Vindelälven area seems to be a most ideal Scandinavian reservate for a total protection against all socalled developments, at the same time as the present study could serve as the first step towards an extended and detailed biological and geographical research and restricted experimentation. Perhaps most of all, a strict but scientifically guided conservation of such an area could create a northern Scandinavian enclave for effective conservation of the natural genetical diversity of the biota and thus become the first and most essential step towards establishing a worldwide network for the protection of the genepools which form the basis for life on planet earth.

Áskell Löve

Tzvelev, N. N. 1976: *Zlaki SSSR–Poaceae USSR*. 788 pp., 9 figs., 16 tables with drawings. Nauka, Leningrad. Price 5.26 rubel.

Until recently, the classification of grasses into genera and species has been based largely on the structure and arrangement of their spikelets. Emphasis on such characteristics led to some very artificial groupings so that natural genera were split and unrelated groups united. During the past four to five decades, beginning with the extensive review of the cytology of grasses by Avdulov, increasing attention has been devoted to evolutionary and anatomical aspects. These studies have yielded much evidence of relationship and resulted in a more natural classification, although further investigations and experiments are still needed before all genera and species of grasses can be satisfactorily circumscribed and placed logically in the new evolutionary system.

A critical review of all the grasses of the world has never been compiled, and most of the available manuals are largely outdated because they were either published before or ignored the recent revolution in grass systematics. Therefore, a modern manual of the many grasses of the Soviet Union, by N. N. Tzvelev, is highly welcome, and hopefully it will soon lead to similar manuals for other large areas.

The book includes a considerable proportion of the species and genera of this large family, which has been estimated to comprise perhaps 500 genera and about 8000 biological species. It first reviews the history of exploration of the flora and especially the grasses of this region, and then explains the modern background of the revision in great detail on more than 40 pages. Since this is the most concentrated and comprehensive review of the principles of modern grass systematics available in any language, it is to be hoped that the author soon will find it possible to publish it separately in English or German to make it available to others working with the classification of grasses. The bulk of the text is devoted to the taxonomic part, which begins with a description of the family Poaceae and a sixteen pages long key to the 177 genera that are included in the book. The genera are grouped into 28 tribes and numerous subtribes.

Every genus is given its valid Latin name, with proper references to authors and synonyms, if any, and then described in detail. Types or lectotypes are listed for each genus and a mention made of the diversity and of the general distribution of the taxon as a whole. When more than a single species are met with, a comprehensive key follows, aided by some good drawings of taxonomically important details. Thereafter, sections, if any, are concisely described, often with types or lectotypes mentioned, before each species is listed without description except in keys but with proper nomenclatural references, information on flowering times, distribution, the somatic chromosome number if known, and certain other pertinent information when available.

The classification at the generic level reflects the modern idea that all the species of a good genus must be related through a linear-branched

evolution from a common ancestor. Although other characters are utilized for their identification, the author puts a strong emphasis on basic chromosome number and karyotypes to delimit the higher categories down to the generic level. The common basic numbers in grasses are x = 5, 7 and 9, but the highest number is x = 12 and the lowest x = 2, which is represented in the Soviet Union by the genera *Colpodium* s.str., *Molineriella* and *Zingeria*. Most of the generic names are, naturally, familiar to botanists elsewhere although some have been little used, but many are circumscribed more exactly than has been customary, and others are new because the more precise concept requires splitting of collective units or the lumping of others that have been found to be biologically similar.

One of the more important groups for which a new and improved classification is presented is the tribe Triticeae, which is subdivided into three subtribes and seventeen genera on basis of recent experimental and karyological evidence. The subtribe Triticinae comprises the genera *Elymus* s.str., *Elytrigia*, *Agropyron* s.str., *Eremopyrum*, *Heteranthelium*, *Amblyopyrum*, *Aegilops*, *Triticum*, *Dasypyrum* and *Secale*. The subtribe Hordeinae includes the genera *Hystrix*, *Leymus*, *Psathyrostachys*, *Hordeum*, *Hordelymus* and *Taeniatherum*, whereas the subtribe Henrardiinae contains only the genus *Henrardia*. This is a great improvement from the conventional treatment of these taxa as a few unnatural and collective genera some of which combining genera here grouped into different subtribes, although one may wonder why a part of *Aegilops* as here defined has not been transferred to *Triticum*, and why the perennial genus *Critesion* has been left as a subgenus of the otherwise annual *Hordeum* s.str. with which it can hardly be hybridized experimentally. Since some of the genera cross occasionally, the author accepts a few hybrid genera to accommodate these ephemeral taxa of the tribe. Although the present reviewer agrees with this treatment, he believes that the author is biologically and nomenclaturally mistaken when among these hybrid groups are listed the experimentally produced alloploid species of *Triticale*, which are, indeed of hybrid origin as are all alloploids, but certainly not hybrids in the correct sense of the term; these species may either be logically classified in the genus *Triticum* as the species *T. aestivosecale* and *T. turgidosecale* as proposed by Mac Key, or as these two species in the genus *Triticale* as described by von Tschermak, not Müntzing, whereas the name of the primary hybrid seems to be *Triticosecale* Wittm.

Other remarkable improvements are too numerous to be mentioned. A few perhaps illogical conclusions have, however, not been avoided, as, e.g., the incomplete splitting of the genera *Briza* and *Brachypodium*, and the acceptance as distinct genera of some groups that cross easily, as, e.g., *Danthonia* and *Sieglingia*, *Phippsia* and *Puccinellia*, and *Calamagrostis* and *Ammophila*, and the sinking of the recently described genus *Arctopoa* in *Poa*. One may even question why the author refrains from transferring the subgenus *Schedonorus* from *Festuca* to *Lolium*, as is supported by extensive experimental evidence, or from separating the other subgenera of *Festuca* as genera in their own right, since their species never cross. There are a few genera that remain collective as indicated by two or more basic chromosome numbers referred to in the book, but the author has apparently preferred to be cautious in dividing them for some reasons not stated. But perhaps it is not fair to even hope that a specialist as thoroughly consistent as the author of this book never will fail in following strictly the same exact biological definition when treating so many critical genera.

Although the very advanced generic concept may disturb some agrostologists who have neglected the recent revolution in grass systematics, the species concept of the author is not likely to strike botanists from northern and central Europe as being unduly advanced, since he follows the Linnaean and biological concepts that Scandinavian botanists of note have adopted for two centuries, defining this category mainly by aid of its reproductive barrier but describing it morphologically. This is a great deviation from the Wettstein-Komarov species concept of the Flora SSSR. However, since the author apparently has a limited understanding of the significance of certain cytological characteristics as strong indicators of the occurrence of reproductive barriers, he sometimes fails to recognize the fact that it is illogical to include units separated by such characteristics

as geographical races only. Therefore, he sometimes reduces morphologically, geographically and cytologically well defined species to the rank of subspecies. But perhaps some lack of logic is excusable in the light of the generally high biological quality of this immense work – even Homer sometimes nodded.

The book about the grasses of the Soviet Union is a work of a magnitude that very few botanists could have undertaken. There is no book like it in any language. It seems to have been printed in only 2900 copies. Perhaps one may conclude with the wish that the able author could spend his time in composing a similar text for all the grasses of the world so that we may at long last get a modern and complete manual of these most important of plants.

Áskell Löve

Stafleu, F. A. & Cowan, R. S. 1976: *Taxonomic literature*. A selective guide to botanical publications and collections with dates, commentaries and types. 2nd ed. Vol. 1: A–G. XL + 1136 pp. Regnum vegetabile Vol. 94. Bohn, Scheltema & Holkema, Utrecht. ISBN 90 313 0225 2. Price (bound) DFl 275.

The publication of Stafleu, *Taxonomic literature*, in 1967 was a great event in the history of botanical documentation (cf. review in *Bot. Notiser* 122 (1969) p. 146). In his preface Stafleu stressed the words "selective guide" in the subtitle. As a rule only major works were recorded, not papers printed in periodicals. There was a preponderance of literature from Central and Western Europe as well as of literature on phanerogams. Cryptogams and paleobotany were treated briefly, a great number of important authors and works being omitted.

Less than ten years later the first volume of a much enlarged new edition of the same work has appeared. Dr Cowan (Washington, D.C.) has joined Dr Stafleu (Utrecht) as co-author. Stafleu has organized a group working on "Taxonomic documentation" at Utrecht. A similar team is working with Cowan at the Smithsonian Institution. With this broad background, including much aid from libraries and private botanists all over the world, it will hopefully be possible to complete two further volumes and a supplement (with addenda and indices) within the next eight years.

To judge from the present volume the coverage of the vast field of taxonomic botany is at least six times as much in ed. 2 as in the previous version. The temporal coverage is more or less defined by the years 1753 and 1940 with a special emphasis on the period between 1870 and 1914, in which descriptive plant taxonomy reached its highest achievements. A few earlier authors, e.g., Bauhin, C. and J., Boerhaave and Dillenius, have been included. This is important from a nomenclatural point of view as their works were often quoted by Linnaeus. The Swedish reader, especially if he is a cryptogamist, will notice that C. Agardh, J. G. Agardh, E. Fries, Th. M. Fries and others have now been treated in detail.

The presentation of the material follows, as a rule, the same principles as in ed. 1. However, the entries on collections, biography and bibliography contain much richer information. As stated in the preface, the work has now become a "bibliography of bibliographies". Additions are handwriting (references to published examples of an author's handwriting) and eponymy (i.e. information on the use of authors' names for generic names of plants or for titles of journals).

Other interesting news proposed standard abbreviations of authors' names and of book-titles. It is a well-known fact that authors' names have been abbreviated in very different ways, cf. the often diverse usage in Flora Europaea and in the International Code of Botanical Nomenclature. Admittedly, the choice proposed here is subjective and it may be difficult to be consistent. The four Swedish botanists mentioned above are cited as C. Agardh, J. Agardh, Fr. and Th. Fr. in the present work. The Frieses have mostly been abbreviated in this way, at least by Swedish authors, whereas the short forms proposed for the Agardhs conflict with common international usage (though this is not quite uniform) Ag. and J. Ag. (or J. G. Ag.) among phycologists.

This volume concludes with two useful indexes, one to titles of the works cited (with the author's name in brackets), another to names of authors, collectors, botanical artists, etc.

and to generic names of plants derived from personal names. Complete cumulative indices will follow in the supplement.

It is unavoidable that a few misprints (for instance in Swedish book titles) and other shortcomings can be found in the enormous material presented here. The reviewer will restrict himself to some minor remarks.

The destruction of the greater part of the Berlin Herbarium in 1943 is characterized as "one of the greatest catastrophes ever suffered by plant taxonomy". Under several German botanists (e.g. Engler) we read "Herbarium and types B (mostly destroyed)". However, according to recent information from staff members of the Berlin Herbarium. the catastrophe was not quite so total as has been believed. In many cases it has been possible to restore plant material saved. Hence a plant taxonomist searching for types presumably located at Berlin before 1943 should inquire at Berlin before writing B† in his monograph.

Types and collections of bryologists are sometimes (e.g. under Dusén) reported as located at the Section for Paleobotany, Natural History Museum, Stockholm (S-PA). In fact, all collections of recent plants (including bryophytes and pteridophytes) were transferred to the Section for Botany (S) at the beginning of the 1970's. S-PA has now collections of fossil plants only.

The only botanist still alive recorded in this volume is Gunnar Degelius (b. 1903). However, the statement "Herbarium and Types UPSV" is not correct. His collections (mainly lichens) were housed there earlier, but since the beginning of the 1960's they are in his home at Askim, near Göteborg, Sweden. The Botanical Museum at Göteborg (GB) can also arrange loans from his private herbarium.

Searching for an envoi to conclude this article the reviewer finds words such as "comprehensive", "indispensable", etc. to be not strong enough. It can suffice to state that taxonomic botanists all over the world eagerly await the forthcoming volumes of this standard work.

Ove Almborn

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The species of Anthracoidea (Ustilaginales) on Carex subgen. Vignea with special regard to the Nordic species

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The taxonomic delimitation, position and structure of *Carex* subgen. *Vignea* is critically reviewed. The high number of intra- and inter-sectional, almost always sterile, hybrids is a characteristic feature. It is fundamental for an understanding of the host ranges of the smuts. The pattern of variation within *Anthracoidea* is also discussed. The Swedish (=Nordic) species on *Vignea* are *A. arenaria* (H. Syd.) Nannf. comb. nov., *A. aspera* (Liro) Kukk., *A. fischeri* (Karst.) Kukk., *A. karii* (Liro) Nannf. comb. nov., and *A. turfosa* (H. Syd.) Kukk. *Cintractia glareosa* Liro is found to be synonymous with *A. aspera*, *Ustilago caricis* β *leioderma* Lgh. with *A. arenaria*, and *Cintractia caricis-dioicae* Lehtola with *A. karii*. *A. vankyi* Nannf. sp. nov. from Central Europe, *A. douglasii* [Shear] Nannf. sp. nov. and *A. verrucosa* (Savile) Nannf. stat. nov. from North America, and *A. eleocharidis* Kukk. from North America and Asia are also dealt with.

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In two previous papers (Nannfeldt & Lindeberg 1957 and 1965) the echinosporous species and those infecting subgen. *Carex* sect. *Acutae* were dealt with in detail. Following Kukkonen's (1963) monographic studies the generic name *Anthracoidea* (instead of *Cintractia*) was adopted in 1965. The present paper deals with the smut species which attack *Carex* subgen. *Vignea* (Beauv.) Kük. and which were left aside by Kukkonen to avoid duplication of work. The late Mrs Brita Lindeberg had already made some preliminary studies on these smuts, but the main part of the work has fallen upon the present author, who regrets the long delay in its completion.

The fourth and concluding paper is in preparation, viz. a list of all the Swedish (=Nordic) species of *Anthracoidea* (some 30 in number), their hosts and distributions, together with keys and short descriptions.

The abbreviations of the names of the provinces of Sweden and Norway and the floristical districts of Finland follow Hylander (1953).

Sect. *Acutae* is a well-circumscribed group comprising a large number of critical, often highly polymorphous species, which as a rule hybridize freely and whose hybrids are often fertile to some extent and give rise to polymorphous hybrid swarms. No hybrids with any other section are known with certainty.

The subgen. *Vignea* also comprises a large number of hybridizing species, but the species are as a rule 'small' but distinct and their hybrids completely sterile (except in sect. *Arenariae?*). They often form groups of closely allied species, distinguished by minute but very constant characters, e.g. the species grouped around *C. canescens*.

As a background for a better understanding of the specialization and speciation within the smuts under consideration, some comments upon the current classification of *Carex*, with special regard to *Vignea*, will be given.

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Features of Carex taxonomy

In Fennoscandia *Carex* has of old (following Fries 1845) been schematically divided into three groups *(Monostachyae, Homostachyae,* and *Heterostachyae).* These reappear almost unchanged in three of the four subgenera accepted by e.g. Kükenthal (1909) in his classical monograph and by most recent authors. Only their names have been changed, to *Primocarex, Vignea,* and *Eucarex (Carex)* respectively. The fourth subgenus *(Indocarex)* is mainly subtropical–tropical and is unrepresented in the North European flora.

These subgenera are of differing statuses. It has now become evident that *Primocarex* is by no means the primitive group which Kükenthal and others considered it to be. It has also turned out that the taxonomic limits towards *Kobresia, Schoenoxiphium* and *Uncinia,* as well as the phylogenetic connections between these genera, are highly debatable (cf. e.g. Krechetovitch 1936, Nelmes 1951, 1952, Savile & Calder 1953, and Kukkonen 1963).

The subgenus Indocarex

It seems fairly certain that *Indocarex,* characterized by bisexual 'spikes' and the presence of utriculiform cladoprophylls, is a natural group and also a relatively primitive one.

The female flower of *Carex* is borne laterally on a bracteolate branchlet which emerges from the axil of a glume, the bracteole being transformed into the utricle. A female spike (or the female part of a bisexual spike) is thus morphologically not a simple spike. However, the use of this term causes no misunderstanding.

The cladoprophyll is the bracteole ("prophyll") of the lateral spike. It may be ochreiform or utriculiform. Kukkonen's (1963 p. 30) definition is unsatisfactory.

Already Raunkiær (1899 p. 519) was inclined to regard the *"Carices homostachyae acroarrhenae tristigmaticae",* which roughly correspond to *Indocarex,* as the most primitive of all *Carices* and he coined the name *Protocarices* for them. All the other groups could be derived from the *Protocarices* through 'reductions' in various directions, e.g. in the number of spikes and stigmata and by the suppression of either sex in the individual spikes. Due to their publication in Danish and in a non-taxonomic monograph, Raunkiær's ideas remained practically unnoticed. Quite independently, Krechetovitch (1936) and Nelmes (1951) later put forward very similar ideas.

The few records of ovariicolous smuts on *Indocarex* are certainly – at least mainly – of *Farysia* species and Dr Kukkonen informs me (in litt. 28. XII. 1976) that all samples of smutted *Indocarices* seen by him were infected by *Farysia.* However, one of the two European species, viz. the Mediterranean *C. distachya* Desf. has been reported as infected by *Ustilago* (or *Anthracoidea) caricis* in Portugal (Lagerheim 1889 p. 127) and North Africa (Zambettakis 1970 p. 361). The description and drawings given by the latter author do not rule out *Anthracoidea,* but the spore drawings show very sparse, small warts, at least 5 μm apart. In this connection I cannot withhold the impression that *C. distachya* is far from being a typical *Indocarex.*

The subgenus Vignea

The diagnostic characters of *Vignea* are bisexual spikes and the lack of cladoprophylls. The bulk of the subgenus (sensu Kükenthal) forms a natural but certainly not primitive group, whose connections with the rest of the genus are obscure. Nelmes (1951) is inclined to derive also this subgenus from *Indocarex,* and Savile & Calder (1953) suggest that some relationship exists between it and that part of subgen. *Carex* which they include in their new subgenus *Kuekenthalia.*

It is evident that at least two of Kükenthal's sections should be excluded from *Vignea,* viz. *Baldenses* and *Curvulae,* both monotypical. They are tristigmatic and Kükenthal himself suggested affinities within subgen. *Carex,* for *C. curvula* with *Frigidae* and for *C. baldensis* in the vicinity of *Pallescentes.* A totally different disposition for *C. curvula* was proposed by Ivanova (1939), who transferred it to *Kobresia.* Kukkonen's (1963 p. 69) observation that the *curvula* smut is very close to *A. lindebergiae* Kukk. on *K. simpliciuscula* points in the same direction.

On the other hand, two sections which Kükenthal had placed in *Primocarex,* viz. *Dioicae* and *Ursinae,* should be added to *Vignea*

and, following Mackenzie (1935), *Ursinae* might even be better included in *Heleonastes*.

Savile (1951 p. 326) and Savile & Calder (1953 p. 170) suggest that a tristigmatic species, *C. leiophylla* Mack., placed in the notoriously unnatural section *Atratae* (subgen. *Carex)* should have its position close to *C. maritima (Foetidae),* because of their general similarity and especially because they are the only known hosts for a most distinctive smut, *Planetella lironis* Savile, probably a close relative of *Anthracoidea*. This suggestion may be well-founded, but *C. leiophylla* seems to possess distinct ochreiform cladoprophylls. Raymond (1965 p. 27) found that *C. leiophylla* belongs to an otherwise Central-Asiatic complex grouped around *C. melanantha* C. A. Mey. and to be so close to *C. sabulosa* Turcz. that he regards them as conspecific. If Savile & Calder's suggestion gains support from future studies, this complex would occupy a key position phylogenetically.

The subgenus Primocarex

Primocarex sensu Kük. is a very heterogeneous assemblage of species having only one common character, viz. the single uni- or bisexual terminal spike. This is neither a proof of primitiveness nor one of monophyletic origin. On the contrary, the individual members have their "roots" in widely differing groups. It is true that a large percentage of the species show one character that undoubtedly is primitive, viz. a distinct rachilla. Nelmes (1952) and Savile & Calder (1953) have discussed these problems in detail and were able to find ± clear connections for more than half of the species with other groups, not only the subgenera *Vignea* (cf. above) and *Carex* but also *Kobresia, Schoenoxiphium* (?), and *Uncinia*.

Hylander (1966) is conservative, as is Chater (1977) in 'Flora Europaea', keeping *Primocarex* (sensu Kükenthal) almost intact and only transferring *Dioicae* to *Vignea*.

The subgenus Carex

The fourth subgenus (*Carex* or *Eucarex*) is characterized by possessing spikes of two kinds (both usually unisexual) and by ochreiform cladoprophylls. It is by far the largest of the subgenera, but is hardly monophyletic. It is divided into numerous sections, some of which (e.g. *Acutae*) are very natural, while others are obviously artificial. The relations between the sections have on the whole remained obscure.

Savile & Calder (1953), following up a suggestion by Mackenzie and taking also the smuts into consideration, tried to segregate a fifth subgenus (*Kuekenthalia*), which in their opinion represents a special line of evolution "governed largely by the development of seed dispersal mechanisms" and marked by "persistent styles and bladdery perigynia". The 'higher' links (*Collinsiae, Folliculatae, Lupulinae, Pseudocyperae, Squarrosae, Paludosae, Vesicariae,* and *Hirtae*) "certainly represent a natural entity" (Kukkonen 1963 p. 32). This has been known of old and is testified both by morphological features and the existence of numerous intersectional hybrids. Further proof is adduced by their smuts (cf. Nannfeldt & Lindeberg 1957 pp. 506–516, Kukkonen 1964 b). Kukkonen's results also suggest that *Granulares* belongs to the same natural group, although it does not possess persistent styles contiguous with the nuts. "Jointed" styles are also characteristic of *Hirtae,* whose affinity is testified beyond any doubt by intersectional hybrids. However, these sections cannot reasonably be treated as a subgenus coordinated with the rest of the subgenus *Carex,* and Hylander (1966) unites all the Nordic members into one section (*Paludosae*).

The 'lower' links in *Kuekenthalia* certainly have no connections at all with the 'higher' and probably have no close interconnections either. *Pauciflorae* may be close to *Uncinia* (cf. e.g. Nelmes 1952).

Taxonomic structure of Vignea

When the clearly misplaced species have been removed, the subgenus *Vignea* becomes a most natural and monophyletic assemblage. Very few (if any) primitive characters are to be found, unless the following feature of the utricle can be regarded as such, viz. "the orifice obliquely cleft dorsally and with dorsal suture more or less apparent" (Mackenzie 1935 p. 11). The number of stigmata is (almost always?) reduced to two, and the nuts are accordingly lenticular. No species has a rachilla. The lack of cladoprophylls is perhaps also a result of 'reduction'.

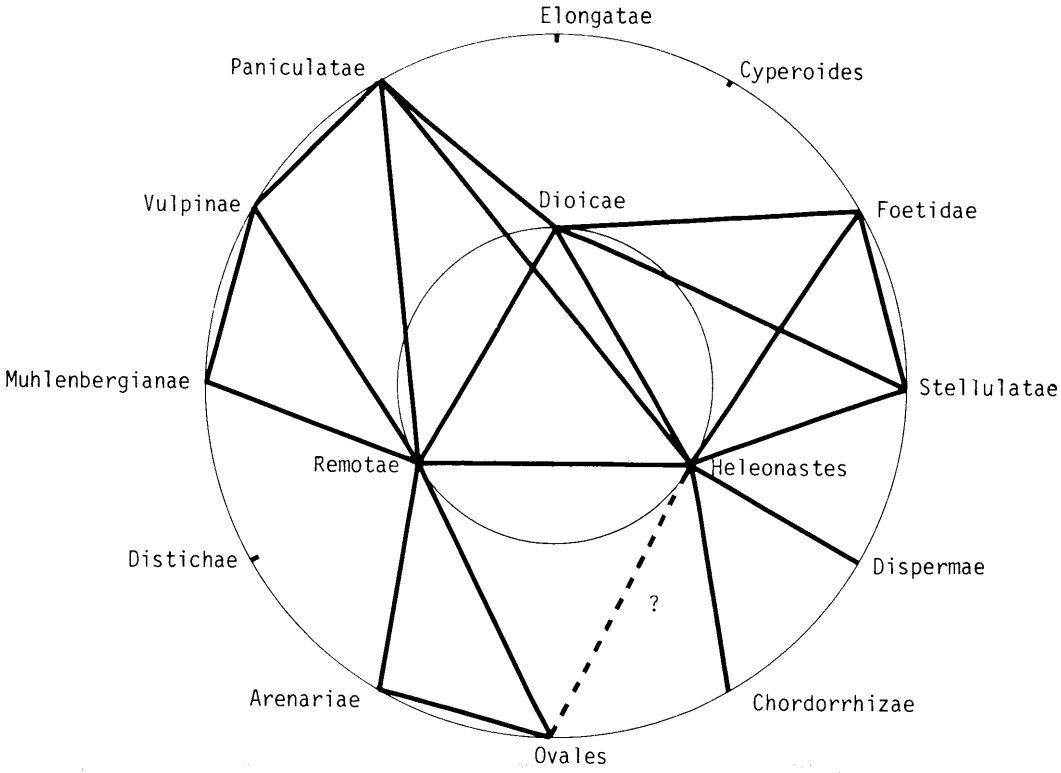


Fig. 1. Hybridization between the Nordic sections of *Carex* subgen. *Vignea*.

The members of *Vignea* are generally grouped into some 20 sections, most of which are natural. For the Nordic species I adopt Hylander's (1966) arrangement (cf. also Berggren 1969) with two exceptions. The most important differences from Kükenthal are that (1) *Dioicae* is transferred from *Primocarex* to *Vignea;* (2) *Canescentes* and *Tenuiflorae* are united into *Heleonastes;* (3) *Incurvae* (*C. maritima*) is included in *Foetidae* (Mackenzie 1935); and (4) *Remotae* (*C. remota*) and *Stellulatae* (*C. echinata*) are excluded from *Elongatae*.

In her treatment of *Vignea* in the Soviet Union Egorova (1966) includes some sections which are unrepresented in the Nordic countries, but otherwise the differences between her and Hylander's (1966) treatments are rather slight except for the sectional sequence and for the nomenclature. She retains *C. elongata* in *Canescentes* (=*Heleonastes*) and removes *C. disticha* from sect. "*Vignea*" (=*Arenariae*) placing it, together with some close allies, in a section of its own, *Holarrhenae*. Following Ohwi (1936), she excludes *C. disperma* from *Heleonastes* and treats it as a monotypical section, *Dispermae*.

Recent chromatographic and SEM studies by Toivonen (1974) and Toivonen & Timonen (1976) have confirmed the isolated position of *C. disperma*. In the ensueing pages it will thus be regarded as a separate section. In my opinion good reasons exist for separating *C. disticha* from *Arenariae*. This increases the number of Nordic sections to 15.

Chater's (1977) treatment in 'Flora Europaea' also deviates very little, except for nomenclature and sequence of sections.

Within certain sections the species are able to form sterile hybrids. Thus, in *Heleonastes*, with 9 Nordic species, 13 intrasectional hybrids are known within the area. In only one section (*Arenariae*) do ± fertile hybrids seem to occur (Sterner 1921). More remarkable is the occurrence of numerous intersectional hybrids, often

between species of rather different morphology (Fig. 1). *C. dioica* and *C. remota*, especially, participate in such crosses. In the Nordic countries *C. dioica* is known to cross with *Foetidae* (*C. maritima*), *Heleonastes* (8 species), and *Stellulatae* (*C. echinata*). Although in the Nordic countries *C. remota* is only known to hybridize with *Heleonastes* (*C. canescens*) and *Paniculatae* (2 species), on the Continent it is also reported to cross with *Arenariae* (2 species), *Muhlenbergianae* (2 species), *Ovales* (*C. leporina*), *Stellulatae* (*C. echinata*), and *Vulpinae* (2 species).

Further Nordic intersectional hybrids are: *Chordorrhizae* × *Heleonastes* (*C. canescens* × *chordorrhiza*, Flatberg 1972), *Dispermae* × *Heleonastes* (3 hybrids), *Heleonastes* × *Ovales* (*C. lachenalii* × *macloviana*, Sylvén 1958; in my opinion very doubtful), *Heleonastes* × *Paniculatae* (*C. appropinquata* × *canescens*), *Heleonastes* × *Stellulatae* (*C. canescens* × *echinata*), and *Paniculatae* × *Vulpinae* (*C. otrubae* × *paniculata*).

It is only thanks to the activity of such eminent Nordic experts as e.g. H. Lindberg and J. Montell in Finland, J. Lid in Norway, and C. G. Alm, Otto R. Holmberg, and G. Samuelsson in Sweden, that it has been possible to study so many reliably-named hybrids and their smuts.

From other parts of the world many more hybrid combinations are recorded (e.g. Kükenthal 1909, Suessenguth 1939), but most of them seem dubious and in strong need of critical sifting. However, they do not influence the present discussion.

The main traits of importance for the evaluation of host-ranges and evolution of *Vignea* parasites are therefore as follows:

(1) The bulk of *Vignea* forms a very natural entity, whose connections with the other subgenera of *Carex* are remote and obscure. It is thus very unlikely that *Vignea* should have any *Anthracoidea* smut in common with any of the other subgenera.

(2) The species of *Vignea* are as a rule 'small' and clearly distinct from each other, even if the morphological differences may be minute.

(3) The species can be grouped into some 20 sections, mostly natural and well-defined.

(4) The species are to a great extent able to hybridize intra- and inter-sectionally. Both kinds of hybrids are sterile (except those within *Arenariae*?).

(5) The sections are to a remarkably high degree "chained" together by intersectional hybrids (Fig. 1).

Advances in the taxonomic treatment of the Vignea smuts

The gradual development of the taxonomy of the black ovariicolous smuts on Caricoideae has progressed from a single omnivorous species, characterized mainly by its symptoms, to a genus of its own, *Anthracoidea*, with several tens of species distinguishable by means of an everincreasing number of microscopical characters.

The first *Vignea* smut to be described as distinct from the collective *Ustilago caricis* (Pers.) Roussel was the echinosporous *Tilletia fischeri* Karsten (1878 p. 10) on *C. canescens*.

Lagerheim (1888 p. 3) described the smut on *C. brizoides* as *U. caricis* β *leioderma* with "membrana sporarum perfecte glabra", in contrast to the 'Hauptart' with "Membran der Sporen körnig punktiert", but it is impossible to be sure what he considered to be the 'Hauptart'.

Magnus (1895 pp. 78–79) pointed out that the size of the spores and the verrucosity of the spore walls vary from one host to another and suggested that continued studies might show these differences to be of taxonomic value. Two *Vignea* smuts were mentioned: one (now *A. fischeri*) on *C. vulpina* (spores M = 13.5 × 10.3 μm) and one (now *A. eleocharidis;* cf. Magnus 1896) on *C. stenophylla* Wg. (spores M = 15.7 × 11.6 μm).

When H. Sydow (1924) initiated a more systematic subdivision of the *Carex* smuts, he found two *Vignea* smuts to be worthy of specific rank, viz. *Cintractia turfosa* on *C. dioica* and *Ci. arenaria* on *C. arenaria* (and *C. ligerica*?). For a third species, *Ci. microsora*, the host was also given as a *Vignea* but belongs in fact to subgen. *Carex* (Nannfeldt & Lindeberg 1957 p. 495).

Liro (1938) described three more *Vignea* smuts, viz. *Ci. aspera* on *C. chordorrhiza*, *Ci. glareosa* on *C. glareosa*, and *Ci. karii* on *C. brunnescens* (and some hybrids). The very common smut on *C. echinata* was referred to

Lagerheim's taxon, which had meanwhile been raised to specific rank as *Ci. leioderma* (Lgh.) Ciferri (1931 p. 45). The smut on *C. lachenalii* was the only Finnish *Vignea* smut left in the still very collective *Ci. caricis*. Liro also observed that the spore size on some hosts, e.g. *C. dioica*, showed an extraordinarily large variation.

Lehtola (1940), a pupil of Liro's, studied variation in spore size and germination of some *Carex* smuts, including those growing on four species of *Vignea*, viz. *C. chordorrhiza, diandra, dioica,* and *echinata*. The spore size of the smut on *C. chordorrhiza* (7 samples) showed only a normal variation, as did that on *C. echinata* (91 samples). The single sample from *C. diandra* agreed with the *chordorrhiza* smut with regard to spore size, wall ornamentation, and germination. He accordingly referred it to *Ci. aspera*. On the other hand, two amply different smuts were found on *C. dioica*, one (8 samples) with large spores and long, rod-shaped sporidia (the true *Ci. turfosa*) and the other (5 samples) with small spores and small ovoid sporidia (*Ci. caricis-dioicae* sp. nov.).

Savile (1952) in his studies of the North American smuts on Caricoideae took into consideration a number of previously neglected morphological characters and definitively split up the old collective *Ci. caricis*. He recognized 17 smut taxa (10 species and 7 varieties) for at least 90 host species, amongst them 24 species of *Vignea* carrying 10 smut taxa. Only two of these taxa were confined to *Vignea*, viz. *Ci. aspera* to *C. chordorrhiza* and *Ci. carpophila* var. *verrucosa* to *Ovales*.

In four cases he found two different smuts present on the same host species, e.g. both *Ci. fischeri* and *aspera* on *C. chordorrhiza* and both *Ci. carpophila* and *limosa* var. *limosa* on *C. gynocrates* Wormskj. Nannfeldt & Lindeberg (1957 p. 504) critizied Savile's way of delimiting his taxa too schematically, without taking into consideration that the (relatively few) samples he studied might in fact be connected by a series of forms showing continuous variation. Kukkonen (1964 b p. 175) showed this to be the case for the *chordorrhiza* smuts and he referred them all to *A. aspera*. On the other hand, the two *gynocrates* smuts are the same as those which Lehtola had found on the closely allied *C. dioica*.

The echinosporous *Ci. fischeri* was treated by Nannfeldt & Lindeberg (1957) and found to occur not only on *C. canescens* but also on several other species (and hybrids) of *Vignea* whereas Savile's records of this smut on species of subgen. *Carex* were referable to the rather similar *Ci. americana* sp. nov.

Kukkonen (1961 etc.) was the first person to provide a reliable survey of the genus. Out of regard to the studies by B. L. and the present author, he excluded most of the *Vignea* smuts from his investigations, dealing only with the three echinosporous species *A. fischeri, aspera* and *eleocharidis* (sp. nov.).

Subgenera and sections of Anthracoidea

Kukkonen (1963, 1972) found that it was possible to divide *Anthracoidea* into two subgenera, *"Euanthracoidea"* (=*Anthracoidea,* including *A. caricis,* the generic type) and *Proceres* (with *A. limosa* as the type). The crucial character is the mode of germination: either with short (mostly 7–15, exceptionally up to 30 μm long), subglobose–ovate sporidia, two or more usually produced per promycelial cell; or with long (50–80 μm), rod-shaped sporidia and only one produced per promycelial cell, respectively. Kukkonen & Raudakoski (1964) soon showed that this distinction was connected with a fundamentally different behaviour of the nuclei. In subgen. *Proceres* both of the two nuclei of each promycelial cell enter the young sporidium. In subgen. *Anthracoidea,* on the contrary, only one of the nuclei enters the sporidium and the other divides; when the second sporidium is about to be formed, one of the daughter nuclei enters that sporidium and the other divides once again; this procedure may be repeated several times. It seems very unlikely that such a change, combined with the change in sporidium shape (and size), should have occurred more than once within *Anthracoidea*.

With regard to taxonomic structure, *Anthracoidea* clearly belongs to the kind of taxa which Munk (1962) recognized as groups "in active evolution" where it is impossible to establish a "tree of evolution". Instead, if the variation of each individual character is studied separately, the "lines of variation" will be found to be combined into what Munk aptly describes as a "lattice work of crossing lines" or a "multi-

dimensional pattern of crossing lines". On the whole the "lines of variation" are the same in the two subgenera. As a rule, however, the individual characters vary within narrower limits within *Proceres* than within *Anthracoidea*.

There thus seems to be no truly echinosporous species amongst the *Proceres;* nor any species with very angular or irregular spores; nor any with very unevenly-thickened spore walls or light-refractive spots (cf. Kukkonen 1972 p. 1031). On the average the spores are larger than in subgenus *Anthracoidea,* and no really small-spored species is known. On the other hand, a species with very large spores belongs most probably to the *Proceres*. Nevertheless, because the sporidium (at least so far) provides the only reliable character, the assignment of a species to one or other of the subgenera, without knowing how it germinates, remains a ± qualified guess.

Subgenus *Anthracoidea* was divided by Kukkonen (1963) into three sections, based primarily on differences in spore shape and spore wall, viz. *"Angulosporae"* (= sect. *Anthracoidea;* including the generic type *A. caricis*), *Leiosporae* (type: *A. elynae* (H. Syd.) Kukk.), and *Echinosporae* (type: *A. subinclusa* (Koern.) Bref.). These sections may be useful for practical purposes but, as will be shown later, they are hardly monophyletic, nor are they sharply defined, since the diagnostic characters change gradually without sufficient discontinuities.

Sect. *Anthracoidea* is characterized by irregular–extremely irregular spores and unevenly thickened spore walls, the thickest points very often standing out as light-refractive spots. Sect. *Leiosporae* is characterized by regular, flattened spores and evenly or nearly evenly thickened, smooth or at the most very finely verrucose spore walls. An additional difference (Kukkonen 1963 pp. 25–26) is the size of the sporidia, which are slightly smaller in sect. *Anthracoidea* (M = 7–10 μm long) than in *Leiosporae* (M = 10–15(–20) μm long).

Nannfeldt & Lindeberg (1957) revised the five small-spored species with echinate spore walls known to them. Kukkonen (1963) added two species which have almost as high wall ornamentation but slightly larger spores, to form a third section, *Echinosporae,* characterized by "regular or, at most, slightly asymmetrical" spores and evenly thickened spore wall, covered with spines which are higher than broad. The only differences in the diagnosis from *Leiosporae* are therefore wall ornamentation and the lacking reference to sporidium size. (The sporidium lengths of these seven species are 6–15 μm.) One year later Kukkonen (1964 b; cf. 1969) treated the section monographically, adding another two species. He now allowed the spores to be also "moderately angular" and their walls "unevenly thickened, with light-refractive areas in the thickest places" or, in other words, of *"Angulosporae"* type.

The first five species dealt with were those with the highest wall ornamentation, reaching up to 2 μm. The emergences are usually called "spines" but this is rather inappropriate. They are best described as slender cylinders with very irregular sections, so slender that they are ± easily broken. They widen out and flatten apically and the tips may even tend to fuse. They parasitize sedges of the subgenera *Carex* (sects. *Paludosae* and *Acutae*) and *Vignea*. Their hosts are some ± exclusively hydrophilous species, as well as some less exacting ones, providing that they are growing close to open water. Savile (1954 pp. 742–743) suggested that the long "spines" are a habitat adaption, the spines serving to keep the spores afloat by means of trapped air bubbles, but Kukkonen (1964 b p. 176) showed that *Anthracoidea* spores remain afloat irrespective of the type of wall ornamentation.

The two additional species differ in several respects, both inter se and from the preceding ones. The wall ornamentation consists of ± conical spines with rounded tips, i.e. except in length they agree with the warts characteristic of so many members of the other sections and of *Proceres*. The ± arbitrary limit for inclusion in the *Echinosporae* is the possession of spines which are at least as high as broad.

One of these additional species (*A. aspera* on *C. chordorrhiza*) has medium-sized spores of the type characteristic for sect. *Anthracoidea,* with conical warts of rather unequal length, thus differing considerably from all the preceding species. Nevertheless, some North American samples of *C. chordorrhiza* have smuts so similar to *A. fischeri* that Savile (1952 p. 421) took them to be that species. Kukkonen (1964 b p. 173) has later shown that these samples are better placed under *A. aspera,* with which they are connected

by intermediates. Whether this also implies that these two smut species are closely related is another problem. A second species (*A. eleocharidis*) is characterized by its peculiar mode of germination (see below). A third (*A. calderi* (Savile) Kukk. on *Phyllostachyae;* subgen. *Carex*) is the only truly large-spored species known to germinate in the manner of the species of subgen. *Anthracoidea*.

It is hard to believe that all these species belong to a common evolutionary line. A comparable examination of the species grouped into the sections *Leiosporae* and *Anthracoidea* leads to analogous results.

Pattern of variation

Even within a single sorus, the *Anthracoidea* spores on the whole vary widely both in size and shape. The specific criteria ought as a rule therefore to be expressed as means, ranges, and frequencies.

Spore size

After Lehtola's (1940) fundamental biometrical studies spore size variation has been studied and discussed by several authors, e.g. by Nannfeldt & Lindeberg (1957, 1965) and especially by Kukkonen (1963). Here it is sufficient to point out that such studies, when critically evaluated, are among the most valuable tools for delimiting and describing a species, but are fortunately not needed for routine determinations. Extraordinarily wide amplitudes of means would suggest that genetical differences may be involved. *A. (Proceres) limosa* (H. Syd.) Kukk. on *Limosae* (subgen. *Carex*) is a good example. Here the degree of ornamentation is more variable than usual and the largest spores concentrate upon some of the principal hosts (Kukkonen 1963 pp. 17–22, 91–95).

Spore shape

In the species with the smallest spores (M = up to c. 18 μm) the spores are mostly ± isodiametric and rounded, subglobose or only moderately flattened (e.g. *A. subinclusa* and *echinospora*), but they may also be strongly flattened ("biscuit-shaped"), e.g. *A. karii*. In species with larger spores these are as a rule distinctly flattened and in plan view not isodiametric, i.e. if rounded ± elliptic. They may also be ± angular and are then subrectangular in plan view (as often in *A. heterospora*), subpentagonal or more irregular. In several species the spore contour is very irregular, with rounded protuberances and concavities, e.g. *A. caricis-albae* Kukk. and *irregularis* (Liro) Boidol & Poelt.

Spore wall

The spore wall only reaches its definitive thickness and colour late in development, although different species behave differently. Thus the presence in every mount of spores in (seemingly?) different stages of maturity is a characteristic of *A. heterospora*.

If the spores are rounded, their wall is mostly rather even in thickness, except that in distinctly flattened spores the rim as a rule has somewhat thicker walls. In angular or irregular spores the wall thickness is as a rule very uneven, thickest at the angles and in the protuberances. The "light-refractive spots" often observed in such spores represent a ± obligatory consequence of extreme, local wall thickenings rather than being an independent character.

Internal swellings

The internal swellings, first described by Savile (1952 p. 416), are organelles within the spore wall, of doubtful origin and doubtful function. They certainly have some taxonomic value at species level, but seem to be of little use above it and must on the whole be used with the utmost caution.

Some species, e.g. *A. inclusa* and *subinclusa*, seem to be totally devoid of such swellings, whereas others (such as the closely allied *A. americana*) show 1–6 clear swellings in almost every spore. In still other species (the majority?) swellings are present, but only discernible at certain stages and/or under certain conditions and/or in certain spores. In such cases it is not even clear whether all the spores of a given species form incipient swellings, or whether certain sori or populations may be totally devoid of them, and in the latter case whether this is genetically based or due to external conditions. *A. aspera* is such a species, studied in some detail by Kukkonen (1964 b p. 173, 1969).

Wall ornamentation

The wall ornamentation provides some of the most valuable taxonomic characters. The species with the highest "spines" ("sect. *Echinosporae*") have already been discussed. The spores of most species have a verrucose–verruculose surface, but when the ornamentation is minute it is almost indiscernible by light microscopy without the use of oil-immersion. Lagerheim (1888) described *U. caricis β leioderma* as an extreme taxon with (supposedly) smooth spores. It is true that the rather young spores, which predominate in the type collection, look almost smooth, but on closer examination traces of granulosity can be discerned and riper spores (both in this and in other collections from the same host) show distinct warts (Fig. 2). As far as known, no *Anthracoidea* has spores which, at all stages, are totally devoid of warts.

Gelatinous coat and mode of dispersal

The spores of *Anthracoidea*, like those of *Ustilago*, form within hyphae and are thus covered by a gelatinous coat during maturation (cf. Kukkonen & Vaissalo 1964 p. 247). This coat smooths the spore surface and produces an even contour if the warts are not high enough. As a rule the coat is rather thin and soon disappears, but in a few species the coat is much thicker and more persistent. Such a smut is *A. externa* (Griff.) Kukk. on *C. filifolia* Nutt. (*Primocarex–Filifoliae*), discussed by Savile (1952 p. 422) and by Kukkonen (1963 p. 71), who suggests that "the gelatinous sheath is probably an adaption of the smut to the extreme drought in the prairies, and the sheath protects the spores very well". Another example is a smut growing on *C. pachystylis* J. Gay (*Vignea–Divisae*), for which Golovin (1952 pp. 108–109) even coined a new genus, *Cintractiomyxa* (cf. Nannfeldt & Lindeberg 1957 p. 503). *A. scirpi* (Kühn.) Kukk. is yet a third smut with a noteworthy thick and persistent coat (Kukkonen 1963 p. 69). A gelatinous coat has also been observed in a few collections of *A. scirpoideae* Kukk. on *C. scirpoidea* (Kukkonen 1963 p. 78).

The presence of a thick and persistent gelatinous coat leads to the formation of sori that are hard and compact (not dusting) when dry, but deliquescent when wet. This implies a radical change in the mode of dispersal, from dispersal by air currents to dispersal with water (rain drops) or, in other words, from xerospory to gloiospory. In *A. externa* Kukkonen (1963 p. 71) observed how part of the spore mass floated down from older sori to surround the axis of the spike.

Conidial state

A few species (of both subgenera) are known to possess a conidial state of the genus *Crotalia* Liro (cf. Kukkonen & Vatanen 1968), which infects and deforms the host utricles (sometimes also the ovaries). The morphological differences between these states of various *Anthracoidea* species are very small. The conidial state appears only rarely, but with differing frequency in different species. It is impossible as yet to decide if more (all?) species are able to form conidia; however, if they exist, they are formed so rarely (under so special conditions?) or so ephemerally that they have been overlooked.

Germination

Variation in germinative features, of course, follows different lines in the two subgenera. In subgen. *Proceres* virtually only the size of the promycelial cells and the sporidia vary, whereas in subgen. *Anthracoidea* the sporidia vary in number, size and shape and the pseudosterigmata in length and branching.

A. scirpi, the only undoubted *Anthracoidea* parasitizing a host outside Caricoideae, is highly noteworthy. Its sporidia are extraordinarily long (up to 30 μm, M = 20 μm) and only one is formed from each promycelial cell. This reduction in number is perhaps not an independent character, but simply a consequence of the voluminous sporidia, the mother cells already becoming exhausted after producing the first sporidium. The deviant sporidia may indicate that *A. scirpi* has undergone a long independent evolution, and that it is not the result of a recent "escapade" of some *Carex*-inhabiting species. As Kukkonen (1967 p. 39) remarked, it is perhaps not merely by chance that the host (*Trichophorum caespitosum*) belongs to a group within the genus *Scirpus* sensu latissimo which deviates from the rest, and from the Scirpoideae on the whole, by possessing an embryo of "*Carex*

type" (Veken 1965), a type that otherwise is confined to Caricoideae–Cariceae.

A. eleocharidis represents an extreme in another direction. The 4–12 small sporidia (M = 6 μm long) are formed successively from each promycelial cell by sympodial prolification of the pseudosterigma, which eventually becomes zigzag-shaped, thus somewhat resembling the conidiophore of *Tritirachium* (Hughes 1953 p. 605).

In the other species the sporidia are relatively small (M = 7–13 μm long) and 2–4 are as a rule produced from each promycelial cell. The size and shape of sporidia and of pseudosterigmata afford good specific criteria, but seem to be of little value above species level, nor are they of any practical use for routine determinations.

The Anthracoidea species on Vignea

There are five Swedish (=Nordic) species of *Anthracoidea* on *Vignea,* and the European flora includes a further one.

Anthracoidea turfosa

One species, *A. turfosa,* belongs to *Proceres.* It only attacks members of *Dioicae* and their hybrids with *Heleonastes.* These sedges also fall within the host range of the small- and "smooth"-spored *A. karii.* A trace infection by *A. turfosa* on *C. heleonastes* has been found once amongst heavily infected *C. dioica* and with infected *C. dioica* × *heleonastes* in the vicinity.

As far as is known, *C. davalliana* does not take this smut, only *A. karii.* The North American *C. gynocrates* Wormskj. takes both. The North American *C. exilis* Dewey does take *A. turfosa,* which accords well with the view that this sedge belongs to *Dioicae* (instead of *Stellulatae*).

A. turfosa is easily recognized by its large spores (M = 21–24 μm long) with evenly thickened and rather smooth walls.

Anthracoidea fischeri

A second species, the echinosporous *A. fischeri,* has been revised by Nannfeldt & Lindeberg (1957 pp. 516–518) and by Kukkonen (1964 b pp. 170–172, 1969). In the Nordic countries it parasitizes *Heleonastes* (principal host: *C. canescens*), *Holarrhenae* (i.e. *C. disticha*), and *Paniculatae* (*C. diandra*). From a Nordic point of view it has a decidedly eastern–northeastern distribution. The host spectrum mentioned above already arouses attention, for *Holarrhenae* seems to take a rather isolated position, not hybridizing with any other section. Just east of Fennoscandia, in Latvia, a member of a fourth section, *C. vulpina* (*Stenorrhynchae*) takes a smut with the same morphology, and reports of smutted *C. vulpina* from eastern Germany, Poland, and Czechoslovakia may also refer to *A. fischeri.* In western Canada (British Columbia) such smuts, sometimes together with the *Crotalia* state, have been found on *Ovales* (*C. bebbii* Olney), *Paniculatae* (*C. cusickii* Mack. and *diandra*), and *Stellulatae* (*C. ?interior* Bailey).

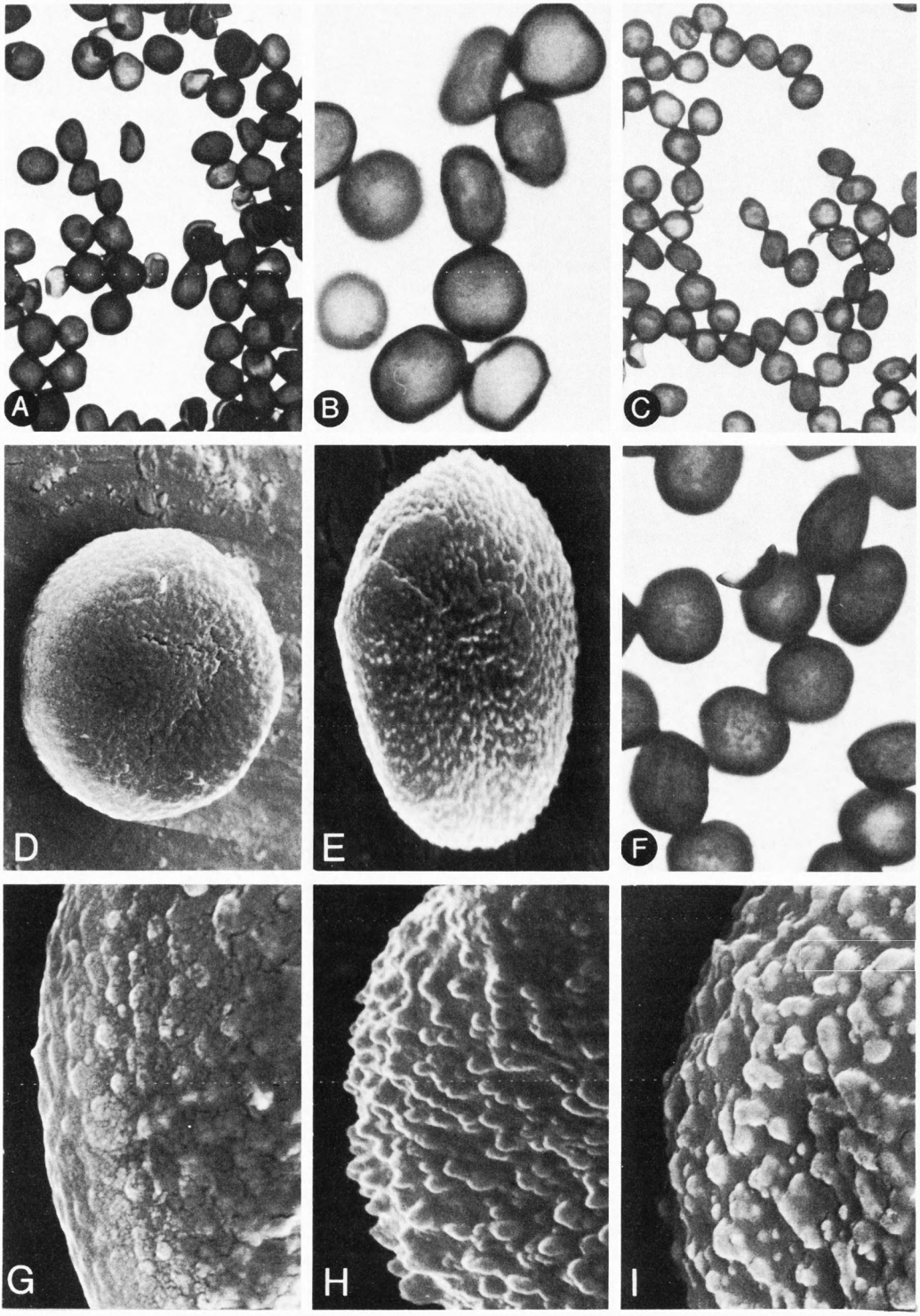
A. fischeri is easily recognized by its small subglobose spores (M = 14–16 μm) with long (1.0 μm), often apically flattened "spines". It is rather often accompanied by its conspicuous conidial state.

Anthracoidea aspera

A second echinosporous smut, *A. aspera,* with *C. chordorrhiza* (*Chordorrhizae*) as its principal host, has been treated in detail by Kukkonen (1964 b pp. 173–174, 1969).

A single sample found on *C. diandra* (*Paniculatae*) from Finland was studied by Lehtola (1940 pp. 79–81; cf. above), who found that the smut matched *A. aspera* so well, both as regards spore morphology and mode of germination, that he considered them to be conspecific, a view with which Kukkonen (1964 b) agreed although the voucher specimen cannot be found (Kukkonen in litt. 11.V. 1977). Unfortunately it is not known if smutted *C. chordorrhiza* also grew in the vicinity. Kukkonen (1964 b) also

Fig. 2. Spores of *Anthracoidea* species. – A, B, D, G: *A. karii* (A, B, D: Lundell & Nannf., F. exs. suec. 1573, on *C. echinata;* G: id. 1771, on *C. brunnescens*). – C, E, F, H, I: *A. arenaria* (C, F, I: Petr., Myc. gen. 1002, on *C. arenaria;* E, H: id. 1007, on *C. brizoides*). – A, C c. 400 ×; B, F c. 1100 ×; D, E c. 3000 ×; G, H, I c. 10,000 ×.


A
B
C
D
E
F
G
H
I

placed a smut from North America (Wyoming) on *C.* (?) *diandra* here.

Smuts on *Paniculatae* are on the whole very rare. A trace infection (a single sorus, UPS!) on *C. appropinquata* from the Swedish island of Gotland was also referred to *A. aspera* by Kukkonen (1964 b), and I agree. An old record of smut on *C. paniculata* (Tulasne 1847 p. 87 and repeated by numerous subsequent authors) cannot be substantiated, nor can the record by Lagerheim (1884 p. 104) of a smut on *C. diandra* from northern Sweden (Lule Lappmark) (Nannfeldt & Lindeberg 1957 p. 497).

Liro (1938 p. 22) based his *Ci. glareosa* on a single sample of smutted *C. glareosa* (*Heleonastes*) from the White Sea. The sample (H!) is not in a good condition, but the smut seems indistinguishable from *A. aspera,* as is a poor specimen (O!) on the same sedge from northernmost Norway.

A. aspera is characterized by slightly larger, oblong spores (M = 17–20 μm long), unevenly thickened walls with light-refractive spots and high, round-tipped papillae (up to 1.0 μm). The classification of the smuts on *C. glareosa* and on *Paniculatae* is only tentative.

Anthracoidea karii

Four taxa of small- and "smooth"-spored European *Vignea* smuts have been described, viz. *Ci. arenaria* (on *C. arenaria*), *Ci. caricis-dioicae* (on *C. dioica*), *Ci. karii* (on *C. brunnescens* and its allies), and *U. caricis β leioderma* (on *C. brizoides*). Liro (1938 pp. 25–27, 275–277) referred the smut very commonly found on *C. echinata* to *Ci. leioderma*. Lehtola (1940) and all subsequent authors followed.

The smallest spores (M = 14.3–16.1 μm long) are attributed to *Ci. caricis-dioicae* (Lehtola 1940 p. 82). On finding that her Swedish samples of a small-spored smut on *C. dioica* and *C. parallela* possessed decidedly larger spores (M = 15.9–18.3 μm long), B. L. hesitated to identify it as Lehtola's species, until we discovered (Nannfeldt & Lindeberg 1957 p. 564; cf. Kukkonen 1963 pp. 12–13) that on average Lehtola's measurements are 1.5 μm smaller than ours. Continued studies have convinced the present author that the *C. dioica* smut is morphologically indistinguishable from the *C. brunnescens* smut, and have shown that the numerous intersectional sedge hybrids are frequently infected by smuts of the same morphology.

During her studies B. L. also found that the *echinata* smut could not be kept apart from the *brunnescens* smut (i.e. *A. karii*) but did differ markedly from the *brizoides* smut (i.e. the original *Ci. leioderma*). My own extensive studies have confirmed her results, and the extremely rare hybrid *C. dioica* × *echinata,* in its single Swedish locality, was found to suffer from the same smut.

This implies a very wide host range, but all the hosts are directly or indirectly connected by (sterile) hybrids. The correct name of the composite species is *A. karii*. It is common and widespread on *C. dioica, parallela, echinata* and several members of *Heleonastes,* whereas it is rare or very rare on other, closely related members. Especially noteworthy is its rarity on *C. canescens*.

Anthracoidea arenaria

Judged from the type collection, *Ci. leioderma* looks at first sight very similar to *A. karii,* but closer examination reveals that the vast majority of the spores are immature and that spores approaching maturity are slightly longer, more oblong and irregularly angular, and their walls darker and unevenly thickened. This difference is confirmed by other collections from *C. brizoides,* for which the mean spore length is 16–20 μm. Some difference in verrucosity of the spores of the two smuts is just visible by light microscopy, but SEM reveals the difference to be real and very distinct (Fig. 2). The *brizoides* smut, instead, is morphologically indistinguishable from the smut found on *C. arenaria* (and *ligerica*). *A. arenaria* is the correct name for the consolidated species. For the sake of completeness it should be mentioned that Hirschhorn (1947 pp. 83–84) had already united these species, but this has not been generally accepted, because most of the other synonyms proposed in that paper are highly unjustifiable.

There are several records of smut on *C. leporina* (*Ovales*). Those that can be checked are mostly based on misnamed *C. brizoides*. A Bavarian record (Boidol & Poelt 1963 p. 18; M!) is correct, however. The smut agrees exactly with *A. arenaria,* and the host had been growing

amongst smutted *C. brizoides*. This is evidently a case of accidental infection.

The records of smutted *C. leporina* from Finland (Åland and Helsingfors; Liro 1938 p. 544) are inextricable. Dr Kukkonen (in litt. 28.XII. 1976) informs me that no voucher specimens can be found (destroyed during World War II?) and that, having got a detailed description of the Åland locality, he visited it without refinding the smut. Since there is no reason for suspecting a misidentification of the host, we are probably faced with two more cases of accidental infection (but by which smut?).

Anthracoidea vankyi

The remaining European species is the hitherto undescribed Central European *A. vankyi* on *C. muricata* s.lat. (i.e. *C. divulsa, pairae,* and *spicata; Muhlenbergianae*). It is known from Spain in the west to Poland and Romania in the east, and perhaps to Germany and the Netherlands in the north (cf. under General distribution). Although the potential hosts are also present in Norden, it has never been found there.

The spores are angular, or even irregular, with hemispherical protuberances, their wall is very unevenly thickened, with light-refractive spots in the thickest areas, and distinctly verrucose.

Anthracoidea in N America

The North American *Vignea* flora is much richer and more diversified than the European, and the same evidently applies to the *Anthracoideae*.

The European *A. aspera, fischeri, karii,* and *turfosa* occur in North America too, partly on other hosts, but *A. arenaria* seems to be absent, and it is an open question whether the smut found on *Muhlenbergianae* (*C. occidentalis* Bailey; Clinton 1904 p. 402, 1906 p. 33) is in fact *A. vankyi*.

The following taxa have been described from North America: *A. eleocharidis* (on *C. eleocharis; Physodeae*) and *Ci. carpophila* var. *verrucosa* (on *C. ebenea* and others; *Ovales*). A nomen nudum is *U. caricis* [var.] *douglasii* (on *C. douglasii; Physodeae*). They will be treated as full species in the subsequent text.

A. eleocharidis (Kukkonen 1964 a), with small echinulate spores, is also known from Asia on *C. stenophylla* (closely related to *C. eleocharis*). *A. verrucosa,* with small, distinctly verrucose spores, occurs on several closely allied sedges in western North America and extends its distribution to Greenland (on *C. macloviana*). *A. douglasii* is a relatively large-spored species, which Kukkonen (1963 p. 37, 1964 a p. 275) supposes to belong to *Proceres*.

Planetella lironis, found on *C. maritima* (*Foetidae*) and *C. leiophylla* (*Eucarex–Atratae?;* cf. above) from northern Canada, could be regarded as an aberrant *Anthracoidea* (cf. Kukkonen 1964 a p. 276). The reports of smutted *C. maritima* from Greenland (Allescher & Hennings 1897 p. 40 as *Ci. caricis*) and from Asia (see below) are certainly not based on *Planetella*.

A number of North American hosts, either not or only superficially studied by me, are certainly infected by one or other of the known smut species, but other hosts, especially the taxonomically more isolated ones, are likely to house further species as yet undescribed, e.g. *C. aenea* Fern. (*Ovales*), *bromoides* Schkuhr (*Elongatae* vel *Deweyanae*), *deweyana* Schw. (*Elongatae* vel *Deweyanae*), *praegracilis* Boott (*Divisae;* germination studied by Kukkonen 1964 a p. 275), *praticola* Rydb. (=*pratensis* Drej.; *Ovales*), *siccata* Dewey (=*foenea* Willd. sensu Svens.; *Arenariae*), *straminiformis* Bailey (*Ovales*).

Anthracoidea in S America

Two *Vignea* smuts have been described from South America, viz. *U. cariciphila* Spegazzini (1925 p. 152) from Argentina on *C. bonariensis* Desf. (*Bracteosae*) and *Ci. pannucea* Liro (1935 p. 5) from Colombia on *C. bonplandii* Kunth (*Elongatae* vel *Deweyanae*). The former was transferred to *Cintractia* by Ciferri (1931 p. 58) but is certainly a *Farysia* ("pulviscula verde-olivaceo vivo", "sporae parvae olivaceae"). The material of *Ci. pannucea* can no longer be found in H (Kukkonen in litt. 28.XII.1976), but Kukkonen informs me (in litt. 11.V.1977) that he has seen two samples that he considers to belong to this very peculiar species, viz. one on *C. bonplandii* from Colombia (16.IX.1953 Jamillo & Mora) and one on "*C. longii* Mack." from Venezuela (5.II.1944 Steyermark). He thinks the species is an *Anthracoidea*.

I have seen smuts on two other South American sedges, viz. on *C. nebularum* Phill. (*Foeti-*

dae fide Kük. or *Divisae* fide Egorova) from Patagonia (Dusén. H!; Liro 1938 p. 252 as *Ci. caricis*) and on *C. ? gayana* Desv. (*Divisae*) from Chile (Valparaiso, Dusén, S!). The two smuts look very similar and are probably conspecific. They seem to be close to *A. verrucosa*, but have a thicker and darker spore wall with more conspicuous warts.

Anthracoidea in Asia

Also from Asia two *Vignea* smuts have been described, viz. *Ci. variabilis* S. Ito (1935 p. 92, 1936) from Japan on *C. arenicola* Fr. Schm. (*Divisae*), but also on *C. caespitosa* (*Acutae*, subgen. *Carex*), and *Cintractiomyxa caricis* Golovin (1952 p. 108) from Kazakstan on *C. pachystylis* J. Gay (*Physodes*). I have seen neither of these, and Ito's species is certainly heterogeneous. I have seen a sample on *C. arenicola* (Korea: Sgou-ouen 30.V.1901 Faurie; Liro 1938 p. 238; H!) but this can hardly be Ito's species, because the spores are not echinulate but rather smooth, resembling those of *A. karii*. Golovin's species is one of those whose spores are surrounded by a thick gelatinous coat (cf. above).

There are on the whole very few records of *Anthracoidea* from Asia. Besides the new species, some records by Liro (1938) and the records of *A. eleocharidis* (see under this species) only a single further *Vignea* smut find has been recorded, viz. that of *Ci. caricis* on *C. maritima* (*Foetidae*) from India (Punjab) by Pavgi & Mundkur (1949 p. 108) and Mundkur & Thirumalachar (1952 p. 43). According to the description this smut could well be *A. karii*, to which *C. dioica* ×*maritima* is known to be susceptible.

Key to the Nordic black ovariicolous smuts on Carex subgen. Vignea

Some sufficiently known species not occurring in the Nordic countries have been included.

1. Spore wall with a broad (5–8 μm) dark equatorial band. Spores c. 10–16 × 9–14 μm. On *C. maritima* (and *C. leiophylla*) [Canada] ..... *Planetella lironis*
– Spore wall without such a band (*Anthracoidea*) 2
2. Spores large, 17–28 × 13–22 μm (M = 20.5–24 μm long), rounded or only moderately angular 3
– Spores small–medium-sized, 12–23(–26) × 8–19 μm (M = 16–20 μm long or, when spore shape very irregular, up to 21.5 μm) 4
3. Spore wall (almost) smooth. Internal swellings low, 1–2, rarely observed. On *Dioicae* and hybrids with *Heleonastes* ..... 5. *A. turfosa*
– Wall with distinct warts (0.2–0.3 μm high). Internal swellings not observed. On *C. douglasii* [W. North America] ..... *A. douglasii*
4. Spore wall almost smooth–verruculose, warts up to 0.3 μm high 5
– Wall distinctly echinate with warts or spines at least as high as broad (0.5–1 μm high) 8
5. Spore wall almost smooth 6
– Wall distinctly verruculose 7
6. Spores regularly rounded, 13–21 × 9–19 μm (M = 16–18.5 μm long). Wall evenly thickened. Internal swellings 2–3, often conspicuous. On *Dioicae*, *Heleonastes*, *Stellulatae*, and hybrids ..... 4. *A. karii*
– Spores often angular, 13–23 × 11–19 μm (M = 16–20 μm long). Wall often thicker at angles. Internal swellings present, but invisible in mature spores. On *Arenariae* ..... 1. *A. arenaria*
7. Spores rounded, in plan view subcircular–broadly elliptic, distinctly flattened, thin-walled (c. 1 μm). On *Ovales* [North America] ..... *A. verrucosa*
– Spores angular–irregular. Wall unevenly thickened (1.5–4 μm), sometimes with light-refractive spots in the thickest areas. On *Muhlenbergianae* [Central Europe] ..... *A. vankyi*
8. Spore wall unevenly thickened (c. 1–4 μm) with light-refractive spots in the thickest areas. Spines up to 1.0 μm high. On *C. chordorrhiza*, *C. glareosa*, *Paniculatae* etc. ..... 2. *A. aspera*
– Wall evenly thickened, relatively thin (c. 1.5 μm), no light-refractive spots 9
9. Spines up to 0.5 μm high, blunt. Internal swellings not observed. On *C. stenophylla* s.lat. [Canada, Asia] ..... *A. eleocharidis*
– Spines up to 1.0 μm high, often slightly flattened at tips. Internal swellings present. *Crotalia* state often conspicuous. On *Heleonastes* and hybrids, *C. disticha* etc. ..... 3. *A. fischeri*

1. **Anthracoidea arenaria** (H. Syd.) Nannf. comb. nov. – Fig. 2 C, E, F, H, I

Cintractia arenaria H. Syd., Ann. Myc. 22 p. 289 (1924). – Typus (selected here): *Carex arenaria;* Germany, Pommern, Rügenwaldemünde VII.1893 P. Sydow (Syd., Ust. 5; hololectotypus: Hb. Syd. S!).

Ustilago Caricis β leioderma Lgh., Mitt. Badisch. Bot. Ver. 1888 p. 37 (1888). – *Cintractia Caricis* var. *leioderma* ("lejoderma") Bub., Verh. Zool.-Bot. Ges. Wien 48 p. 24 (1898). – *Cintractia leioderma* Cif., Ann. Myc. 29 p. 45 (1931). – *Anthracoidea leioderma* Kochm. & Maj., Grzyby (Mycota) 5 p. 111 (1973). – Typus: *Carex brizoides;* Germany, Baden, Bromberg nr. Freiburg i. Br. VI. 1888 G. Lagerheim (holotypus: S!; isotypi: Roumeg., F. gall. 4717).

Ustilago Vigneae Fuss a. *V. Schreberi* Fuss, Arch. Ver. Siebenbürg. Landeskunde, N.F. 14 p. 446 (1878; nom. nud.).

Spores in plan view (13–)15–21(–23) × (11–)13–18 (–19) μm (M = 16–20 μm long), subcircular–subelliptic and evenly rounded or mostly moderately angular or even rather irregular and pointed at one or both ends, only slightly flattened (10–15 μm thick). Wall c. 1.5–2 μm thick, markedly thicker at angles (up to 3 μm), rather dark. Internal swellings distinct in young still thin-walled spores, not (or hardly) visible in mature. Surface of young spores practically smooth, but later with low warts (0.2–0.3 μm high), clearly visible. Germination not studied.

Matr.: (*Arenariae*) *C. arenaria, brizoides* L., *ligerica, praecox.* – (*Arenariae* × *Remotae*) *C. brizoides* × *remota.* – (*Ovales*) *C. leporina.*

Exs.: (On *C. arenaria*) Kochm., Myc. pol. 170; Kochm., Ust. pol. 22; Lundell & Nannf., F. exs. suec. 849; Petr., Myc. gen 1002; Rbh., Herb. myc., ed. II:396 (p.p.; "*Ust. urceol.*"); Samuelss., Fl. suec. exs. 348 Fung.; Smarods, F. latv. exs. 156 ("*Ci. Car.*"); Syd., Ust. 5 ("*Ust. Car.*"; typus), 14 ("*Ust. oliv.*"), 442 ("*Ci. Car.*"); Zillig, Ust. 2 ("*Ci. Car.*"). – (On *C. brizoides*) Crypt. čechosl. exs. Fungi 11 ("*Ci. Car.*"); Kochm., Myc. pol. 506; Krieg., F. saxon. 1851 ("*Ci. Car.*"); Krypt. exs. Vindob. 3234 ("*Ci. lejod.*"); Petr., Fl. Boh. Mor. exs. II:1 2107 ("*Ci. Car.*"); Petr., Myc. gen. 1007 ("*Ci. lejod.*"); Rbh., F. eur. 899 ("*Ust. urceol.*" on "*C. bryoides*"); Roumeg., F. gall. 4717 ("*Ust. Car.* var. *leiod.*"; typus); Schneid., Herb. Schles. P. 87 ("*Ust. urceol.*") fide Liro; Syd., Ust. 178 ("*Ci. Car.* var. *leiod.*"); Weese, Eumyc. sel. exs. 311 ("*Ci. Car.*"); Zillig, Ust. 71 ("*Ci. Car.*"), 74 ("*Ci. Car.*" on "*C. leporina*"). – (On *C. ligerica*) Baenitz, Herb. eur. 3465 Fung.; Syd., Myc. germ. 1875 ("*Ci. Car.*"); Syd., Myc. march. 238 ("*Ust. oliv.*"); Syd., Ust. 123 (*Ci. Car.*). – (On *C. praecox*) Const. & Negr., Herb. myc. rom. 2187 ("*A. car.*"); Syd., Myc. march. 2624 ("*Ust. Car.*").

Swedish distribution

On *C. arenaria:* Coextensive with the host, common and mostly abundant. – Sk, Bl, Öl, Gtl, Vg, Srm, Upl.

On *C. ligerica:* Probably common and coextensive with the host, which is rare and has a very restricted area. – Bl, Öl, Gtl.

Zundel's (1953 p. 22) report of this species on *C. brizoides* is erroneous. *C. brizoides* is not a member of the Swedish flora. Savulescu (1957 p. 774) lists a Swedish specimen under the heading *brizoides,* but on the next page the host is correctly given as *C. echinata.*

Occurrence in the other Nordic countries

Denmark: Coextensive with *C. arenaria* and common (cf. Lind 1913 p. 263; O. Rostrup 1935 p. 26). Not observed on *C. ligerica.*

Finland: *C. arenaria* has a very restricted area in the extreme south. Four recent finds of the smut (Nyl; H, UPS!). Not known on the introduced *C. praecox.*

Norway: Some finds (Östf, Vestf, VAgd) on *C. arenaria.*

General distribution

Probably coextensive in Europe with its principal hosts. This is one of the few *Anthracoideae* that are common in the Central European lowlands. A single sample has been seen on *C. brizoides* × *remota* (Germany, Rostock; Liro 1938 p. 275; UPS!) and one on *C. leporina* (Germany, Bavaria; Boidol & Poelt 1963 p. 18; M!) amongst infested *C. brizoides* (cf. above). – *C. arenaria* is introduced in North America but has not yet been found smutted there.

2. **Anthracoidea aspera** (Liro) Kukk.

Kukkonen, Ann. Bot. Soc. Vanamo 34:3 p. 73 (1963). – *Cintractia aspera* Liro, Mycoth. fenn. n. 41 (=Die Etiketten N:o 1–300 p. 15) (1934); Ann. Acad. Sci. Fenn. A:42 p. 18 (1938). – Typus: *Carex chordorrhiza;* Finland, Lapponia kemensis, Kittilä par., Sirkankylä 28.VII.1933 H. Roivainen & J. I. Liro (Liro, Mycoth. fenn. 41).

Cintractia scabra H. Syd., Ann. Myc. 33 p. 368 (1935). – Typus: *Carex chordorrhiza;* Sweden, Torne Lappmark, Kiruna, Ruopsok 8.VIII.1927 H. Smith (holotypus: Hb. Sydow S!; isotypi: Lundell & Nannf., F. exs. suec. ined.).

Cintractia glareosa Liro, Ann. Acad. Sci. Fenn. A:42 p. 22 (1938; diagn. german. tantum); Mycol. fenn., Die Etiketten N:o 301–600 p. 109 (1939). – Typus: *Carex glareosa;* Fennoscandia orientalis, Karelia keretina, Kantalaks, Pedosensk VII.1885 V. F. Brotherus (H!).

Spores subglobose–ellipsoid, usually slightly irregular or moderately angular, (15–)16–25

(–26) × 11–20(–22) μm (M = 17–20.5 μm long), slightly and irregularly flattened. Wall unevenly thickened, often with light-refractive spots in the thickest areas. Internal swellings 0–4, very variable in conspicuousness. Spines or warts of very different size, 0.1–1.0 μm high, tips rounded. Germination follows the pattern of subgen. *Anthracoidea* (fide Lehtola).

For detailed descriptions see Lehtola (1940 p. 74–81) and Kukkonen (1964 b p. 173, 1969 p. 271).

Matr.: (*Chordorrhizae*) *C. chordorrhiza*. – (*Paniculatae*) *C. appropinquata, diandra* fide Lehtola et Kukk. – (*Heleonastes*) *C. glareosa*.

C. glareosa does not take this smut in Greenland but *A. karii* instead, a fact which misled Savile (1952 p. 418) into regarding *Ci. glareosa* as a doubtful synonym of his *Ci. carpophila* var. *carpophila*. Liro's record (1938 p. 22) of *Ci. glareosa* from Greenland is based on E. Rostrup's (1888 p. 532) report of two finds of *U. caricis*. One (the Vahl specimen, C!) is *A. karii,* but the other is not to be found.

Exs.: (On *C. chordorrhiza*) Kari, F. exs. fenn. 103, 104; Liro, Myc. fenn. 41; Lundell & Nannf., F. exs. suec. 1554, 1555, ined.

Swedish distribution

On *C. appropinquata:* The only find (Kukkonen 1964 b p. 173; UPS!) consists of a single sorus (cf. above). – Gtl.

On *C. chordorrhiza:* In southern and central Sweden, perhaps restricted to the eastern parts. Increasing in frequency northwards. – Ög, Dlr, Hls, Jmt, LyL, LL, TL.

Occurrence in the other Nordic countries

Denmark: Unknown. *C. chordorrhiza,* the principal host, is very rare.

Finland: Known on *C. chordorrhiza* from all parts (Kukkonen 1964 b p. 174), evidently more common in the north. One find on *C. diandra* (Ob; Lehtola 1940 p. 79; doubtful, cf. above), one on *C. glareosa* from Fennoscandia orientalis (Kk; Liro 1938 p. 22).

Iceland: Unknown. Both *C. chordorrhiza* and *glareosa* are rather common.

Norway: Known on *C. chordorrhiza* from Akershus in the south to Troms in the north. One find on *C. glareosa* (Fnm; "prope Vadsöam" Deinboll; O!).

Spitzbergen: Not known. *C. glareosa* is a potential host.

General distribution

Liro (1938 p. 19) considered this smut (on *C. chordorrhiza*) to have a decidedly eastern distribution, being known from Russia and Siberia (cf. also Gutner 1941 p. 163) but not from Central Europe. The host, although almost circumpolar, is itself rather eastern in Europe (Hultén 1962 p. 94, map 85) and has become very rare in Central Europe. The smut is also known from North America (Alaska, British Columbia, Alberta, Ontario, Quebec) but there shows a greater morphological variability (Kukkonen 1964 b p. 174, cf. above). I have also seen a sample from Maine (K. K. Mackenzie 3194 Fung., S!).

Anthracoidea douglasii [Shear] Nannf. sp. nov. – Fig. 3 A, B

Ustilago Caricis [var.] *Douglasii* Shear var. nov. in Ell. & Ev., F. Columb. 1485 (1901; nom. nud.). – *Cintractia Caricis-Douglasii* Cif., Ann. Myc. 29 p. 43 (1931; nom. nud.). – Typus: *Carex douglasii;* U.S.A., Colorado, Gunnison 5.IX.1899 E. Bartholomew (Ell. & Ev., F. Columb. 1485; holotypus: S).

Sporae 16–27 × 14–20 μm (M = 21–22 μm longae), rotundatae vel raro paullum angulares. Paries 1.0–2.0 μm crassus, conspicue verrucosus, verrucis hemisphaericis, 0.2–0.3 μm altis, interdum binis confluentibus. Gibbera interna desunt.

Spores in plan view 16–27 × 14–20 μm (M = 21–22 μm long), subcircular–broadly elliptic, evenly rounded or subangular, moderately flattened (12–15 μm thick). Wall evenly thickened (1.0–2.0 μm thick), rather pale. Internal swellings not observed. Surface verrucose, warts 0.2–0.3 μm high, round or oblong, not infrequently confluent two and two, rather regularly spaced, forming no distinct pattern. Germination not studied.

Matr.: (*Divisae* fide Mack. vel *Douglasianae* fide Egorova) *C. douglasii* Boott.

Exs.: Ell. & Ev., F. Columb. 1485 (*"Ust. car. Dougl."*; typus); Ell. & Ev., N. Amer. F. 2259 (*"Ust. car."*); Griff., W. Amer. F. 209 (*"Ci. car."*), 209 a (*"Ci. car."*).

General distribution

May follow the host. Hitherto known from U.S.A. (Oregon, Nevada, Colorado) (Savile 1952 p. 427 as *Ci. limosa minor*).

Anthracoidea eleocharidis Kukk. – Fig. 3 F, H

Kukkonen, Trans. British Myc. Soc. 47 p. 274 (1964).

Spores in plan view 13–20(–21) × 11–15(–17) μm (M = 17–18 μm long), subcircular–elliptic, evenly rounded or slightly irregular, moderately flattened. Wall evenly thickened (1–1.5 μm). No inter-

nal swellings. Surface distinctly verrucose, warts up to 0.5 μm high, tips rounded. Germination follows the pattern of subgen. *Anthracoidea* (fide Kukkonen).

For full description and illustrations see Kukkonen 1964 a p. 274, 1964 b p. 172, 1969 p. 271.

Magnus (1895, 1896) found the mean spore length to be 15.7 μm in the collection studied (Bornmüller 1870), whereas I got M = 17.8 μm in the S copy of the same collection. My measurements were made in lactophenol and Magnus' certainly in water, which may explain the difference.

Matr.: (*Physodes*) *C. eleocharis* Bailey (type host), *stenophylla* Wg.

Exs.: 0.

General distribution

Known from Canada (Yukon) and U.S.A. (California) on *C. eleocharis* and from Central Asia (Iraq, Turkmenian S.S.R., Punjab, Kashmir) on *C. stenophylla* s.lat. Kukkonen (in litt. 11.V.1977) adds Turkey, Iran, and Afghanistan. The hosts belong to a widespread, almost circumpolar species complex, whose differentiation is still far from clarified (cf. e.g. Hultén 1962 p. 146, map 138, Raymond 1965 pp. 31–34, Egorova 1966 pp. 124–130). Although *C. stenophylla* s.str. is rather widely distributed in eastern and southeastern Europe, there are no European smut records.

3. **Anthracoidea fischeri** (Karst.) Kukk.

Kukkonen, Ann. Bot. Soc. Vanamo 34:3 p. 73 (1963).

For synonymy, detailed descriptions, illustrations, and exsiccata see Nannfeldt & Lindeberg (1957 pp. 516–519) and Kukkonen (1964 b pp. 170–171, 1969 p. 270).

Spores in plan view (13–)15–20(–22) × 10–18 μm (M = 16–18 μm long), circular–broadly elliptic and slightly flattened. Wall relatively thin with 1–5, mostly distinct internal swellings. Spines up to 1.0 μm high, rounded or slightly flattened apically. *Crotalia* state often present and conspicuous. Germination follows the pattern of subgen. *Anthracoidea* (fide Kukkonen).

Matr.: (*Heleonastes*) *C. ? arctaeformis* Mack. fide Kukk., *brunnescens* (& ×*canescens* ?), *canescens* (& ×*lachenalii* fide Liro & ×*lapponica* & ×*loliacea* & ×*mackenziei* & ×*tenuiflora*), *heleonastes, lapponica, mackenziei, tenuiflora*. – (*Stellulatae*) *C. ? interior* Bailey fide Kukk. – (*Paniculatae*) *C. cusickii* Mack. fide Kukk., *diandra*. – (*Vulpinae*) *C. vulpina*. – (*Holarrhenae*) *C. disticha*. – (*Ovales*) *C. bebbii* Olney fide Kukk.

Liro (1938 p. 528) listed *C. loliacea* as a host but Kukkonen (1964 b p. 171) found the sample to be *C. canescens* ×*loliacea*.

Swedish distribution

On *C. brunnescens:* The host grows almost all over Sweden except in the extreme south and becomes very common northwards. The single smut find is from the north. – Vb.

On *C. canescens:* Host common all over the country. The few smut finds only from the far north. Nevertheless a principal host? – Nb, LL, TL.

On *C. canescens* ×*lapponica:* One find on this little-known and certainly much overlooked hybrid. A neighbouring tuft had *A. karii*. – Nb (Överluleå par., Snödmossen 1929 O. R. Holmberg; UPS!).

On *C. canescens* ×*mackenziei:* The host is rather common in beach meadows wherever *C. mackenziei* grows. The smut is so far unknown from southern Sweden, where *C. mackenziei* is rare. – Gstr, Nb.

On *C. canescens* ×*tenuiflora:* One find only on this rather rare hybrid. – TL (Karesuando par., Karesvuopio 1929 E. Nordström; S!).

On *C. disticha:* The host is widespread in southern and central Sweden, but the smut is found only in the east. Certainly a principal host. – Ög, Upl, Gstr.

On *C. mackenziei:* Certainly much overlooked. The host is by far less conspicuous than its hybrid with *C. canescens,* and its culms wither early. Only two finds. – Gstr.

Occurrence in the other Nordic countries

Denmark: No finds. *C. canescens* and *C. disticha* are potential hosts.

Finland: Finds more numerous than in Sweden and on the whole concentrated to the north. *C. disticha* is found smutted only in the extreme south (Al, Ab) and *C. canescens* ×*mackenziei* has been found smutted from the north to Nylandia in the south. The known hosts are: *C. brunnescens* ×*canescens* (?), *canescens, c.* ×*lachenalii* (n.v.), *c.* ×*lapponica, c.* ×*loliacea, c.* ×*mackenziei, c.* ×*tenuiflora, diandra* (one find; Ob Tervola Loue 1961 Kukkonen 911; H, UPS!), *disticha, heleonastes, lapponica, mackenziei* (one find; Ab Painio 1969 Kukkonen; H, in litt. 11.V.1977), and *tenuiflora*. The then known finds were listed by Kukkonen (1964 b pp. 171–172).

The records by Liro (1938 pp. 20–22, 278–279, 528) are not all reliable, for he long considered that *C. canescens* and its hybrids were immune against *A. karii* (q.v.), *C. brunnescens* and its hybrids against *A. fischeri,* and in some cases he allowed the smuts to influence the determination of the host and vice versa.

Iceland: No finds. Potential hosts are *C. brunnescens, canescens,* and *mackenziei.*

Norway: Three finds only, on *C. canescens* (Hdm; O!) and on *C. canescens* ×*mackenziei* (Nrd, Trs; O!).

C. brunnescens, disticha, heleonastes, lapponica, and *tenuiflora* are further potential hosts.

General distribution

In striking contrast to the very wide host range of *A. fischeri* is its very limited geographical area. As pointed out previously (Nannfeldt & Lindeberg 1957 p. 517) the European distribution is decidedly northeastern. It is known on sect. *Heleonastes* only from Norway, Sweden and Finland (incl. Russian Fennoscandia) and on *C. disticha* only from Sweden and Finland. A morphologically indistinguishable smut on *C. vulpina* occurs in Latvia and a record of a small-spored smut (M = 13.5 × 10.3 μm) on the same host from eastern Germany (Brandenburg; Magnus 1895 p. 79, Jaap 1900 p. 262) also certainly belongs here, as also, probably, Eichler's report (sec. Kochman & Majewski 1973 p. 116) from Poland and Hruby's (1927 p. 156) from Czechoslovakia.

This species is also known from northwestern North America (Alaska, Distr. of Mackenzie, British Columbia) on *Heleonastes* (*C. canescens*) (Kukkonen 1964 b pp. 170–172). Morphologically indistinguishable smuts, on sects. *Ovales, Paniculatae,* and *Stellulatae* are also reported from northwestern North America (British Columbia) by Kukkonen (1964 b).

4. **Anthracoidea karii** (Liro) Nannf. comb. nov. – Fig. 2 A, B, D, G

Cintractia Karii Liro, Mycoth. fenn. n. 106 (=Die Etiketten N:o 1–300 p. 36) (1934); Ann. Acad. Sci. Fenn. A:42 p. 31 (1938). – Typus: *Carex brunnescens;* Finland, Lapponia enontekiensis, Enontekiö par., Vuontisjärvi, Peltovuoma 24.VII.1933 H. Roivainen & J. I. Liro (Liro, Myc. fenn. 106).

Cintractia Caricis-dioicae Lehtola, Acta Agral. Fenn. 42 p. 85 (1940). – Typus: *C. dioica;* Finland, no special collection designated.

Ustilago Vigneae Fuss b. *V. stellulatae* Fuss, Arch. Ver. Siebenbürg. Landeskunde N.F. 14 p. 446 (1878; nom. nud.).

Spores in plan view 13–21 × 9–19 μm (M = 16–18.5 μm long), subcircular–broadly elliptic, mostly very evenly rounded, only exceptionally slightly angular, strongly flattened (12–14 μm thick). Wall evenly thickened (up to 2 μm). Internal swellings 2–3, mostly distinct. Surface ranges from almost smooth to finely verruculose, warts up to 0.1 μm high, rounded, somewhat irregularly spaced but not forming a distinct pattern and not affecting the spore profile. Germination follows the pattern of subgen. *Anthracoidea* (fide Lehtola).

Matr.: (*Dioicae*) *C. davalliana, dioica, gynocrates* Wormskj., *parallela.* – (*Dioicae* × *Foetidae*) *C. dioica* × *maritima.* – (*Dioicae* × *Heleonastes*) *C. dioica* × *brunnescens* fide Liro & × *canescens* & × *heleonastes* & × *lachenalii* & × *tenuiflora, gynocrates* × ? *tenuiflora* fide Savile. – (*Dioicae* × *Stellulatae*) *C. dioica* × *echinata.* – (*Dispermae*) *C. disperma.* – (*Heleonastes*) *C. brunnescens* (& × *canescens* & × *lachenalii* & × *loliacea* & × *tenuiflora*), *canescens* (& × *heleonastes* & × *lachenalii* & × *lapponica* & × *loliacea* & × *tenuiflora*), *glareosa* (incl. *C. marina* Dewey), *heleonastes, lachenalii, lapponica, loliacea* fide Liro, *tenuiflora, trisperma* Dewey, *ursina* Dewey fide Fischer. – (*Stellulatae*) *C. angustior* Mack. fide Savile, *cephalantha* (Bailey) Bicknell fide Savile, *echinata, interior* Bailey fide Savile.

The four finds on *C. brunnescens* × *dioica* listed by Liro (1938 p. 32) may be either this species or *A. turfosa,* which has been seen on this hybrid from Norway, and the hosts may be hybrids with either *C. brunnescens* or *C. canescens* (cf. above under *A. fischeri*).

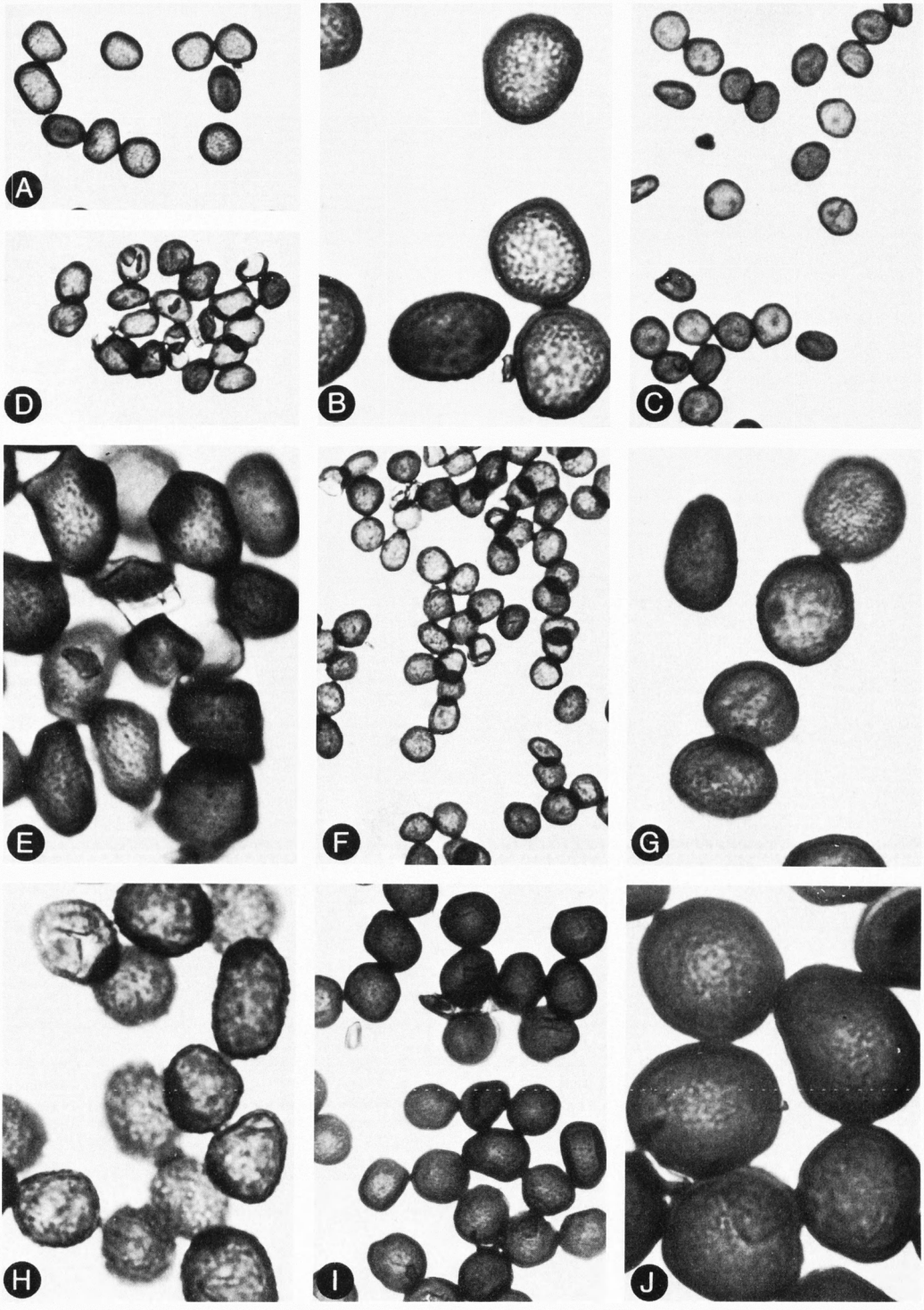
Exs.: (On *C. brunnescens*) Kari, F. exs. fenn. 277, 278; Liro, Myc. fenn. 106; Lundell & Nannf., F. exs. suec. 1571, 1572, 2761; Syd., Ust. 313 (*"Ust. Car."* on *"C. can."*); Vgr., M. rar. sel. 449 b (*"Ci. Car."*). – (On *C. canescens*) Kari, F. exs. fenn. 221; Liro, Myc. fenn. 769 (*"Ci. Fisch."*). – (On *C. canescens* × *loliacea*) Samuelss., Pl. Suec. exs. 364 Fung. – (On *C. canescens* × *tenuiflora*) Samuelss., Pl. Suec. exs. 367 Fung. – (On *C. cephalantha*) Seym. & Earle, Econ. F., Suppl. C5 (n.v.). – (On *C. dioica*) Lundell & Nannf., F. exs. suec. 645 b (*"Ci. turf."*, later changed into *"Ci. Car.-dioicae"*), 1568, 1569 (both as *"Ci. Car.-d."*), 2762. – (On *C. echinata*) Kari, F. exs. fenn. 105, 106, 276 a, 276 b (all as *"Ci. leiod."*); Linh., F. hung. 302 (*"Ust. Car."*); Liro, Myc. fenn. 153 (*"Ci. leiod."*); Lundell & Nannf., F. exs. suec. 1573, 1574 (both as *"Ci. leiod."*); Schneid., Herb. Schles. P. 183 (n.v.); Ust. Jugosl. 60 (*"Ci. baccata"*); Zillig, Ust. eur. 124 (*"Ci. Car."*). – (On *C. lachenalii*) Liro, Myc. fenn. 763 (*"Ci. Car."*); Lundell & Nannf., F. exs. suec. 2763, 2764. – (On *C. lapponica*) Lundell & Nannf., F. exs. suec. ined.

Swedish distribution

On *C. brunnescens:* So far unknown in the south, common towards the north. Evidently a principal host. – Hrj, Jmt, Nb, LyL, PL, LL, TL.

On *C. brunnescens* × *canescens* (nov. matr.): Two finds from one locality on this very rare (or at least much overlooked) hybrid. – TL (Kiruna, Vittangi 1928, 1929 O. R. Holmberg; LD!, UPS!).

Fig. 3. Spores of *Anthracoidea* species. – A, B: *A. douglasii* (typus). – C, G: *A. verrucosa* (Savile 28 248). – D, E: *A. vankyi* (typus). – F, H: *A. eleocharidis* (Turkmenistan, Melnik; UPS). – I, J: *A. turfosa* (typus). – A, C, D, F, I c. 400 ×; B, E, G, H, J c. 1100 ×.


A
D
B
C
E
F
G
H
I
J

On *C. brunnescens* ×*lachenalii:* This hybrid and the very similar *C. canescens* ×*lachenalii* are common in the north. The present author has made no attempt to check the determinations. – Jmt, LL, TL. (Liro (1938 p. 278) lists an additional collection (from TL) by O. R. Holmberg, because he considered the attack by *A. karii* as a proof that Holmberg's determination of the host as *C. canescens* ×*lachenalii* was incorrect.)

On *C. brunnescens* ×*loliacea:* This hybrid is not so rare. – Hrj, LL, TL.

On *C. brunnescens* ×*tenuiflora:* Only one find on this very rare hybrid. – TL (Kiruna, Perkosvuoma 1935 C. G. Alm 418 Fung; LD!. Together with smutted *C. canescens* ×*tenuiflora.*).

On *C. canescens:* The host is very common all over Sweden. The smut is found only in the north and very rarely even there. – Vb, LL, TL.

On *C. canescens* ×*dioica:* This hybrid occurs throughout the country but is found smutted only towards the north. – Dlr, Hrj, Jmt, LL.

On *C. canescens* ×*heleonastes* (nov. matr.): Only one find on this very rare hybrid. – TL (Kiruna, Ö. Soppero Pereojavuoma 1928 O. R. Holmberg; UPS!).

On *C. canescens* ×*lachenalii:* Probably rather common on this hybrid, which is not infrequent (as on the very similar *C. brunnescens* ×*lachenalii,* q.v.). – Hrj, LyL, TL.

On *C. canescens* ×*lapponica* (nov. matr.): Two finds on this rare and little-known hybrid. – Nb (see *A. fischeri*), TL (Karesuando 1928 O. R. Holmberg; LD!, a single sorus).

On *C. canescens* ×*loliacea:* This hybrid is known from Central and North Sweden but has been found smutted only in the north. – PL, TL.

On *C. canescens* ×*tenuiflora:* This rare hybrid, restricted to North Sweden, seems to take this smut rather often. Cf. Liro (1938 p. 279). – LL, TL.

On *C. dioica:* The host grows all over the country, but this smut has not been found in the southern provinces and increases in frequency and abundance towards the north. *C. dioica* is evidently a principal host, but *A. karii* is less common than *A. turfosa* on it. – Srm, Upl, Vstm, Dlr, Hls, Hrj, Jmt, Vb, Nb, LyL, PL, LL, TL.

On *C. dioica* ×*echinata* (nov. matr.): This hybrid is extremely rare in Sweden, although the parent species are widely distributed. The smut has only been found in one locality, but there repeatedly. – Hrj (Tännäs par., Fjällnäs 1934, 1935, 1936 O. Östergren; 1946 B. Borgström; all UPS!).

On *C. dioica* ×*tenuiflora* (nov. matr.): Only a single tuft of this hybrid is so far known (Holmberg 1929 a p. 6; 1929 b p. 28; Hylander 1966 p. 68) and this (as well as adjacent tufts of *C. canescens* ×*tenuiflora*) bore this smut. – TL (Kiruna, Perkosvuoma 1928 C. G. Alm & O. R. Holmberg; LD!, S!, UPS).

On *C. echinata:* Evidently coextensive with its host and one of the few *Anthracoideae* which also occurs in the southern provinces but increasing in frequency northwards as far as the host grows. A principal host. – Sk, Hl, Sm, Ög, Vg, Bh, Srm, Upl, Vstm, Nrk, Dlr, Hls, Hrj, Jmt, Mpd, Vb, Nb, LyL.

On *C. lachenalii:* Probably coextensive with its host. – Hrj, LyL, LL, TL.

On *C. lapponica* (nov. matr.): This long-neglected host species occupies a very restricted area in the north (Hultén 1971 map 350). Only one Swedish find of this smut. – TL (Kiruna, Valkikurkkio 1959 E. Julin; UPS!).

On *C. parallela:* Probably coextensive with its host but rarer than *A. turfosa.* – TL.

On *C. tenuiflora* (nov. matr.): Only one poor sample. – Nb (Tärendö par. at the Tärendö River c. 3 km N of the parish church 1959 C. G. Alm; UPS!).

Liro (1938 p. 32) records a find on *C. brunnescens* × *dioica* (LL, leg. Wichura). This sample has not been seen, and may be the same as that cited (1938 p. 36) as *Ci. turfosa* on *C. canescens* ×*dioica,* which could not be found either.

Distribution in the other Nordic countries

Denmark: Known only on *C. echinata* (cf. Lind 1913 p. 263). Two other potential hosts are *C. canescens* and *dioica.*

The Færoes: Known on *C. echinata* (cf. Möller 1945 p. 71). Only one other potential host, viz. *C. dioica.*

Finland: Reported by Liro (1938 pp. 31–32, 278–279, 530) as *Ci. karii* on *C. brunnescens* (and its hybrids with *dioica, lachenalii,* and *loliacea*), *canescens,* and *loliacea;* as *Ci. leioderma* (1938 pp. 26, 275–276, 529) on *C. echinata* (numerous additions in Lehtola 1940), and as *Ci. caricis* (Liro 1938 pp. 8, 526) on *C. lachenalii.* The first certain finds on *C. dioica* were reported by Lehtola (1940), who was the first to make a distinction between the two smuts on *Dioicae.* To the above hosts can now be added: *C. heleonastes* (nov. matr.; Lk: Muonio 9.VII.1914 J. Montell; LD!), *parallela* (Le, a single find, compared with nearly 20 of *A. turfosa*), and the following hybrids: *C. canescens* × *dioica, c.* ×*lachenalii, c.* ×*lapponica* (Lk), *c.* ×*loliacea* (Lk, Le), *c.* ×*tenuiflora* (Li), *dioica* ×*heleonastes* (nov. matr.; Lk: Muonio Lompolovuoma 7.VII.1921 J. Montell; H!). As in Sweden the smut becomes less frequent towards the south.

Iceland: Seen only on *C. echinata* (cf. Larsen 1932 p. 516). Potential hosts are *C. brunnescens, canescens, dioica, glareosa,* and *lachenalii.*

Norway: Seen on *C. brunnescens* (AAgd–Fnm), *canescens* (Trs), *dioica* (Hdm–Fnm), *echinata* (common to Nrd in the north), *lachenalii* (Trs, Fnm), *lapponica* (Trs), and *parallela* (STrd, Trs) as well as on the following hybrids: *C. brunnescens* ×*lachenalii* (Hdm, Busk, STrd), *br.* ×*loliacea* (Trs), *canescens* × *dioica* (Hdm, STrd), *c.* ×*lachenalii* (Busk, Hrd, Opl, STrd, Nrd, Trs, Fnm), *dioica* ×*lachenalii* (nov. matr.; STrd: Oppdal, Sandådal in Storlidalen 1940 J. Haugen, O!, and Trs: Storfjord between Lulle and Fawresvarre 1937 P. Benum, O!), and *d.* ×*maritima* (STrd; Liro 1938 p. 242 as "*Ci. turfosa* kleinsporige Form"; UPS!). Also in Norway the smut decreases in frequency southwards. Potential hosts are *C. glareosa, heleonastes, loliacea, tenuiflora,* and several hybrids.

Spitzbergen: Not known. *C. glareosa, lachenalii,* and *parallela* are potential hosts.

General distribution

The host spectrum of this smut is wide, several of the hosts are widely distributed, as is the smut itself, but as far as Europe is concerned it seems to be rare in or absent from large parts of the lowlands. It is most frequently collected and reported on *C. echinata* (Scotland, France, Germany, Latvia, Poland, Switzerland, Austria, Czechoslovakia, Hungary, Romania etc.). I have seen it on *C. brunnescens* from Switzerland and Austria (Tirol). Liro (1938 p. 278) reports it from Italy, and Schellenberg's report (1911 p. 75) of a Swiss smut on *C. canescens* probably refers to *A. karii* on mis-identified *C. brunnescens*. There are several finds on *C. davalliana*. There are very few records of smutted *C. dioica* and since no material has been available, no decision can be made whether the smut is *A. karii* or *A. turfosa*.

In North America the conditions in the north seem to be much the same as in northern Europe. Thus *A. karii* is known from Greenland on *C. brunnescens, br.* ×*lachenalii, canescens* ×*lachenalii, glareosa, lachenalii, parallela,* and *ursina;* and from Alaska on *C. brunnescens, canescens, disperma, gynocrates, g.* ×*tenuiflora* (?), *lachenalii,* and *loliacea*. As in Europe the smut becomes less frequent southwards and its host range narrower. It just extends into the United States but only on a restricted number of hosts, e.g. on *C. angustior* (New Haven, Vermont), *brunnescens* (Vermont), *cephalantha* (Vermont), *interior* (Maine), and *trisperma* (Michigan; Povah 1935 p. 153).

5. **Anthracoidea turfosa** (H. Syd.) Kukk. – Fig. 3 I, J

Kukkonen, Ann. Bot. Soc. Vanamo 34: 3 p. 24 (1963). – *Cintractia turfosa* H. Syd., Ann. Myc. 22 p. 289 (1924). – *Anthracoidea turfosa* Kochm. & Maj., Grzyby (Mycota) 5 p. 118 (1973). – Typus: *Carex dioica;* Norway, Finnmark, Alta Kåfjord VII.1895 G. Lagerheim (Syd., Ust. 75).

Spores in plan view (15–)17–26(–28) × (11–)13–22 (–25) μm (M = 22–24 μm long), rounded, broadly elliptic or rarely slightly irregular and angular, flattened (12–15 μm thick). Wall evenly thickened, dark, c. 2.5 μm thick. Internal swellings 1–2(–3), low, only rarely visible. Surface ranges from almost smooth to minutely verruculose; warts only 0.1 μm high or less, rounded or slightly elongate, occasionally confluent, somewhat irregularly spaced, but not forming a distinct pattern and hardly affecting the spore profile. Germination follows the *Proceres* scheme (fide Lehtola).

See Lehtola (1940 pp. 81–86).

Matr.: (*Dioicae*) *C. dioica* (& ×*parallela*), *exilis* Dewey, *gynocrates* Wormskj. fide Savile, *parallela.* – (*Dioicae* ×*Foetidae*) *C. dioica* ×*maritima.* – (*Dioicae* ×*Heleonastes*) *C. dioica* ×*brunnescens* & ×*canescens* & ×*heleonastes* & ×*lachenalii, parallela* ×*lachenalii.* – (*Heleonastes*) *C. heleonastes.*

The "kleinsporige Form" on *C. dioica* ×*maritima* mentioned by Liro (1938 pp. 17, 24) is *A. karii* (q.v.).

Boidol & Poelt (1963) cite *C. davalliana* and – with some doubts – also *C. baldensis* and *curvula* as hosts. Their *davalliana* sample (M!) shows typical *A. karii. C. baldensis* and *curvula* should be removed from *Vignea* (see above), and their smuts are specifically distinct. That found on *C. curvula* is close to *A. lindebergiae* (Kukk.) Kukkonen (1963 p. 63).

Exs.: (On *C. dioica*) Kari, F. exs. fenn. 101, 102; Krypt. exs. Vindob. 4504; Liro, Myc. fenn. 31, 779; Lundell & Nannf., F. exs. suec. 645 a; Syd., Ust. 75. [Non: Lundell & Nannf., F. exs. suec. 645 b (*"Ci. turf."*, corr. *"Ci. car.-d."*) q.e. *A. karii.*] – (On *C. parallela*) Krypt. exs. Vindob. 4402.

Swedish distribution

On *C. canescens* ×*dioica:* Restricted to the northern parts. – Hls, Ång, Vb, TL.

On *C. dioica:* Evidently coextensive with its host, commoner than *A. karii,* but likewise increasing in frequency and abundance towards the north. – Sm, Gtl, Vg, Bh, Srm, Upl, Vrm, Dlr, Hls, Hrj, Jmt, Ång, Nb, ÅsL, LyL, LL, TL.

On *C. dioica* ×*heleonastes:* Rare hybrid. – Hrj, TL (3 finds in all; cf. Liro 1938 p. 242).

On *C. dioica* ×*parallela* (nov. matr.): One find on this rare and little-known hybrid. – ÅsL (Vilhelmina par., Ransarluspen 1946 O. Rune 76 Fung.; S!, UPS!).

On *C. heleonastes:* A single sorus together with heavily infected *C. dioica* and with infected *C. d.* × *heleonastes* in the vicinty. – Hrj (Tännäs par., V. Malmagen 1933 J.A.N. 4664: UPS!; cf. Liro 1938 p. 242).

On *C. lachenalii* ×*parallela:* – TL (2 finds).

On *C. parallela:* coextensive with its host and much commoner than *A. karii.* – LyL, LL, TL.

Occurrence in the other Nordic countries

Denmark: No finds. *C. dioica* is a potential host. The Færoes: Ditto.

Finland: As Liro (1938) did not distinguish between the two smuts on *Dioicae* all his records need to be re-examined. Lehtola (1940) found *A. turfosa* to be more common than *A. karii* and to be scattered all over the country. It is also common on *C. parallela.* I have seen it (in H) on the following hybrids, viz. *C. canescens* ×*dioica* (Lk), *dioica* ×*parallela* (Le, one find), and *lachenalii* ×*parallela* (Le).

The record (Liro 1938 p. 35) on *C. dioica* ×*heleonastes* is erroneous. The spores are immature but nevertheless the smut can be identified as *A. karii.*

Iceland: Some finds on *C. dioica.*

Norway: As in Sweden coextensive with *C. dioica* and *parallela,* commoner than *A. karii* and increasing in frequency and abundance towards the north. Seen

also on the following hybrids: *C. brunnescens* × *dioica* (nov. matr.; Tel: Tinn, the Selstali fens 1933 J. Lid; O!), *canescens* × *dioica* (Oslo; Aurtjern at Ödegård (c. 1/2 km S of Nöklevatn) M. N. Blytt; O!), *dioica* × *lachenalii* (nov. matr.; Opl: Dovre, Midthö (at Vålåsjö) 980 m s. m. 1950 J. Lid; O!), and *dioica* × *maritima* (nov. matr.; Nrd: Narvik, Fagernes 1909 L. Trafvenfelt; UPS!).

Spitzbergen: No finds. *C. parallela* is a potential host.

General distribution

The host range of *A. turfosa* is rather narrow, as is its distribution. Apparently it does not follow its hosts everywhere, but is restricted to the northern regions. No finds are known from continental Europe, but it is uncertain whether some finds of smutted *C. davalliana* and *dioica* belong here and not to *A. karii* (q.v.).

In North America it is known on *C. gynocrates* (Quebec; Savile 1952 p. 426 as *Ci. limosa* var. *limosa*) and *exilis* (Quebec; Savile 1952 p. 427 as *Ci. pratensis;* Labrador, H!; and Nova Scotia fide Kukkonen in litt. 11.V.1977), but it is an open question whether other records on *C. exilis* belong here or perhaps to *A. karii.*

Anthracoidea vankyi Nannf. sp. nov. – Fig. 3 D, E

Typus: *Carex pairae;* Romania, Transilvania, in alpibus Csíki-havasok (M. Ciucului), mons Öcsém 1630 m s.m. 12.VII.1962 K. Vanky (holotypus: UPS, isotypus: Hb. Vanky).

Sporae 15–23(–26) × 12–20 μm (M = 18–21.5 μm longae), angulatae vel irregulares, elongatae, rarius ± isodiametricae. Paries valde inaequalis, 1.5–4 μm crassus, areolis crassissimis interdum ut loci lucem repercutientes apparentibus, verruculis c. 0.2 μm altis.

Spores 15–23(–26) × 12–20 μm (M = 18–21.5 μm long), angular–irregular, slightly and irregularly flattened, in plan view rarely ± isodiametric, mostly elongated, sometimes subtriangular or even subcordate, sometimes ± apiculate at one end. Wall of very uneven thickness (1.5–4 μm), often with light-refractive spots in the thickest areas. Internal swellings not observed. Surface distinctly verruculose, warts c. 0.2 μm high. *Crotalia* state not observed. Germination not studied.

Matr.: (*Muhlenbergianae*) *C. muricata* sensu lato, i.e. *divulsa, pairae,* and *spicata* (=*contigua* Hoppe). (No attempts have been made to revise the host determinations.)

Exs.: 0.

Additional specimens

France: Dépt Alpes-Maritimes, Fontan in the Roja Valley 435 m (*C. divulsa*) 1963 F. Oberwinkler 4801 (M!). – Switzerland: Kt Wallis, Saas-Fee (*C. pairae* det. W. Koch) 1945 E. Mayor (ZT!); Zermatt 1876 Körnicke (H fide Kukkonen in litt. 11.V.1977); Zermatt-Zmutt (*C. pairae,* det. W. Koch) 1934 E. Gäumann (ZT!). – Italy: Trento, Rhaetian Alps, "Veltlin, unmittelbar nördlich Tirano, an der Strasse nach Pra Campo" 460–520 m s. m. (*C. divulsa*) 1965 W. Dietrich, E. Mayr, H. Hertel 5079 (M!). – Romania: Montibus Bîrsei, Poiana Brasov (*C. divulsa* ssp. *chabertii*) 1967 P. Olaru & M. Danciu (LD!, S!).

General distribution

So far, specimens have been seen from the Alps and Transilvania. The *"muricata"* smut recorded from France (Dépt Hautes-Alpes; Massenot 1953 p. 404) and Poland (Walbrzych; Kochman & Majewski 1973 pp. 115–116), according to description and illustrations, exactly matches *A. vankyi.* Provided that the host determinations are correct other European records of *"muricata"* smut also certainly belong here, e.g. those from various parts of Switzerland by Körnicke (1877 p. 39), Boudier & Fischer (1894 p. CCXL), Schellenberg (1911 p. 75), Cruchet & Mayor (1918 p. 63), and Blumer (1946 p. 68), from Spain (Sierra Nevada) by Maire (sec. Massenot 1953 p. 404), from Germany (Leipzig) by Savulescu (1957 p. 788), from the Netherlands (Maastricht) by Oudemans (1893 p. 598). No finds from northern Europe. The identity of the smut on the North American *C. occidentalis* Bailey is unknown.

Anthracoidea verrucosa (Savile) Nannf. stat. nov. – Fig. 3 C, G

Cintractia carpophila (Schum.) Liro var. *verrucosa* Savile, Can. J. Bot. 30 p. 420 (1952). – Typus: *Carex ebenea;* U.S.A., Wyoming, Medicine Bow Mts, L. Marie 21.VIII.1941 W. G. Solheim 2009 (Myc. Saximont. exs. 439; n.v.).

Spores in plan view 14–23 × 13–17 μm (M = 18.5–20 μm), subcircular–broadly elliptic, regularly rounded, only exceptionally slightly angular, strongly flattened (9–12 μm thick). Wall thin (c. 1 μm), evenly thickened and rather pale, often with 1–3 internal swellings. Surface distinctly verrucose, warts rounded, rather evenly spaced, up to 0.3 μm high, distinctly visible in profile. Germination not studied.

Calculated from Ciferri's (1931 p. 48) measurements the mean spore length of Syd., Ust. 314, is only 16.6 μm, whereas I got M = 18.6 and 19.7 μm respectively, from two slides of the same collection. Ciferri probably

measured the spores in water, and I – as always – in lactophenol, which may explain the difference.

Matr.: (*Ovales*) *C. ebenea* Rydb., ? *festivella* Mack., *macloviana* (incl. ssp. *pachystachya* (Cham.) Hult.), and according to Kukkonen (in litt. 11.V.1977) ? *illota* L. H. Bailey, *phaeocephala* Piper, *preslii* Steudel, *subfusca* W. Boott, and (*Bracteosae*) *C. hoodii* Boott.

Exs.: Myc. Saximont. exs. 439 (*C. ebenea;* typus; n.v.); Syd., Ust. 314 (*C. "festivella"; "Ci. car."*).

General distribution

To the known North American distribution (Alaska, British Columbia, Wyoming) southeastern Greenland can now be added (Akorninarmiut, "Dronning Marias Dal" 1931 B. Björlykke, O!, and 1932 J. Devold & P. F. Scholander, O!; Umanak Innfjorden 1932 J. Devold, O!) on *C. macloviana*. These finds have been published as *Ci. caricis* by Hagen (1947 p. 284; cf. Savile 1952 p. 420). Smutted *C. macloviana* is not reported from Europe.

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Garuleum subgen. Rutidocarpaea, a monotypic subgenus showing achene dimorphism

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Norlindh, T. 1977 12 30: Garuleum subgen. Rutidocarpaea, a monotypic subgenus showing achene dimorphism. *Bot. Notiser 130:* 377–380. Stockholm. ISSN 0006–8195.

Garuleum bipinnatum (Thunb.) Less., conspecific with *Dimorphotheca multifida* DC., is described and illustrated. Style characters show that the species belongs to *Garuleum;* it deviates, however, in having outer disc florets which are capable of producing well-developed achenes similar to those of *Dimorphotheca.* The latter condition may be the original one in *Garuleum.* The pollen morphology also deviates from that of the type species of *Garuleum.* The species is referred to a monotypic subgenus, *Garuleum* subgen. *Rutidocarpaea* (DC.) T. Norl. comb. nov. (basionym *Dimorphotheca* sect. *Rutidocarpaea* DC.).

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The genus *Garuleum* Cass. belongs to the Compositae–Calenduleae. It occurs in South and Southwest Africa and comprises only eight species. In his treatment of *Garuleum,* De Candolle (1836) also included *G. bipinnatum,* which was first collected by Thunberg in the Hantam ("Hantum") Mountains of Calvinia District, described by him as *Osteospermum bipinnatum* (Thunberg 1800, 1823) and transferred to *Garuleum* by Lessing (1832).

When publishing his new species *Dimorphotheca multifida* in 1838, De Candolle obviously failed to compare it with the very similar collections which he had determined about two years earlier as *Garuleum bipinnatum;* otherwise he would certainly have discovered that they were identical. By adding a question-mark, De Candolle indicated his doubts as to whether or not the species really belonged to *Dimorphotheca.* He established the section *Rutidocarpaea* to accommodate this species and noted that it resembled *Dimorphotheca* because the achenes of the disc florets were "plano-compressis", but that the disc florets were sterile.

A closer investigation showed that this taxon does not belong to *Dimorphotheca;* style characters determine its position in *Garuleum.* However, within *Garuleum* the species is unique in having disc florets which produce achenes with ripe seeds. Furthermore, it differs from the type of *Garuleum* (*G. pinnatifidum* (L'Hérit.) DC.) in that its pollen grains lack horizontal tectal areas and have a greater number of spines which are more closely set, etc. (Fig. 2; Praglowski unpubl.). In my opinion *G. bipinnatum* should be referred to a subgenus of its own and I have chosen to retain De Candolle's name, *Rutidocarpaea,* which thus has to be transferred to *Garuleum:*

Garuleum subgenus **Rutidocarpaea** (DC.) T. Norl. comb. nov.

Dimorphotheca sect. *Rutidocarpaea* De Candolle 1838 p. 72. – Typus: *Dimorphotheca multifida* DC. (= *Garuleum bipinnatum* (Thunb.) Less.)

Differt a subgenere *Garuleo:* floribus disci hermaphroditis fertilibus, achaeniis disci exterioribus semen includentibus illis *Dimorphothecae* similibus (floribus interioribus non fructificantibus).

The genus *Garuleum* merits further investigation, which should include pollen morphology;

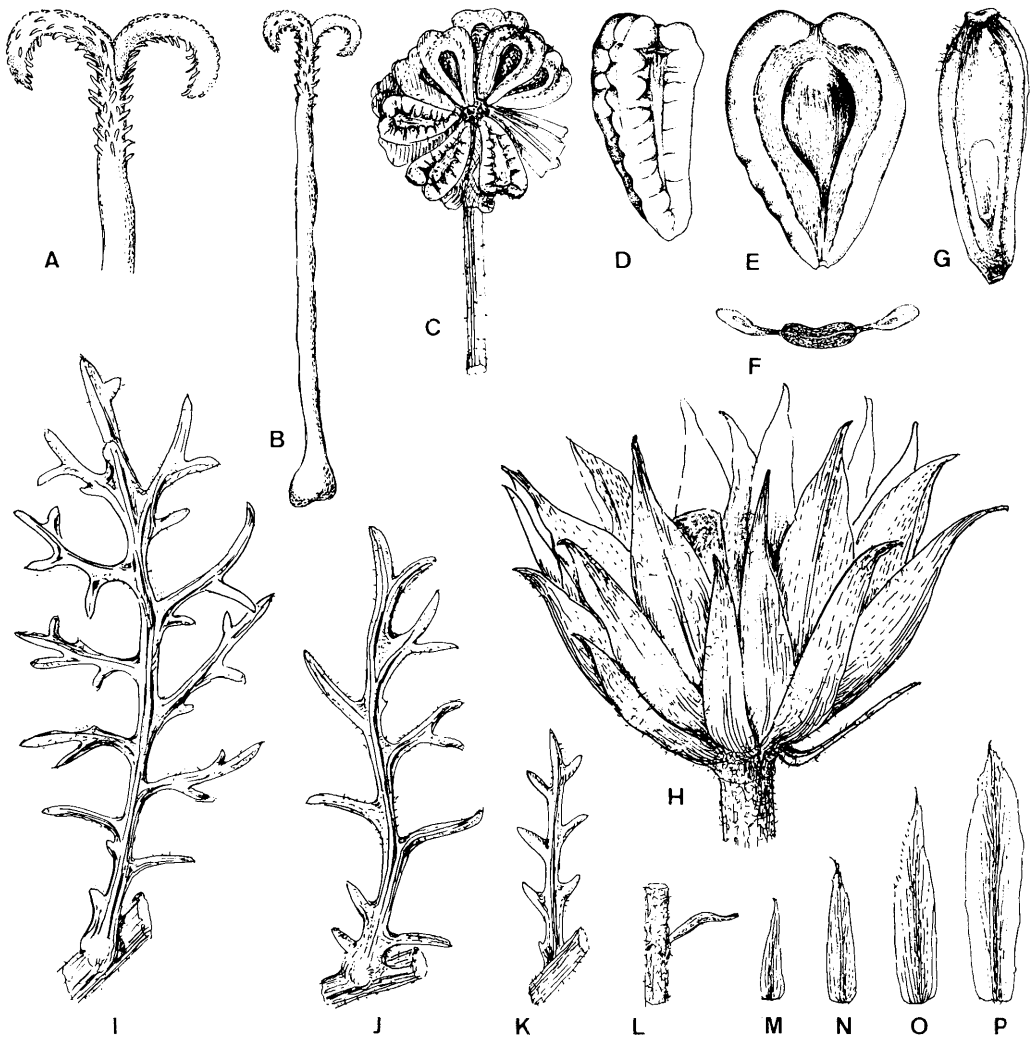


Fig. 1. *Garuleum bipinnatum*. – A: Upper part of style of disc floret, ×28. – B: Style of disc floret; note the bulbous base. ×14. – C: Capitulum with mature achenes of ray and disc florets, ×2. – D: Achene of ray floret, ×6.5. – E: Achene of outer disc floret with a well developed seed, ×6.5. – F: Cross section of achene of disc floret; the 14 years-old seed was somewhat shrivelled but still contained viscous oil, ×6.5. – G: Achene of inner disc floret with an abortive seed in the ovary, ×6.5. – H: Involucre; the achenes have fallen off. ×5.5. – I–K: Leaves from lower, middle and upper part of stem, ×3.5. – L: Part of peduncle with bract, ×3.5. – M–P: Series of involucral scales; M outermost, P innermost, ×5.5. – A, B: Wall s.n., Albany Distr., Committees Drift, 8.VIII.1938 (S). – C–G, M–P: Norlindh 5683, Albany Distr., Great Fish River Valley, 6.X.1963 (S). – H–L: Thunberg 20814, Calvinia Distr., Hantam Mountains, XI–XII.1774 (UPS).

this will probably result in the recognition of several sections.

Garuleum bipinnatum (Thunb.) Less. – Fig. 1,2

Lessing 1832 p. 194; De Candolle 1836 p. 309; Harvey 1865 p. 92; Marloth 1932 p. 243.

Osteospermum bipinnatum Thunberg 1800 p. 167 et ed. Schultes 1823 p. 717; Juel 1918 p. 717. – Holotype: Thunberg Herb. No. 20814, Calvinia "in Hantum" (UPS).

Dimorphotheca multifida De Candolle 1838 p. 73; Harvey 1865 p. 422. – Orig. coll.: Ecklon & Zeyher, Albany (G-DC No. 413 lectotype).

Perennial herb or subshrub, aromatic, viscid, with scattered short-stalked glands, up to 1.5 m tall. *Stems* arising from a woody rootstock up to 3 cm in diam., erect or ascendent, usually branched; stems and branches terete, striate or slightly furrowed, glabrous, in lower parts ± lignescent and covered by a brown-grey bark and remnants of leaf-sheaths, 1.5–3(–4) mm thick; internodes (except basal ones) 0.5–3 cm long. *Leaves* alternate, glabrous, 1–4 cm long, bipinnatipartite as well as pinnate, with lobes linear, subulate; primary lobes 3–6 on each side, up to 10 mm long; leaves decreasing in size and degree of lobation towards the inflorescence. *Capitula* solitary at the ends of stem and branches or more often arranged in loose corymbs; peduncles varying greatly in length, up to 12 cm, provided with few-dentate or entire bracts and upwards often densely covered with short-stalked glands. *Involucre* hemispheric, 5–8 mm high; scales imbricate, ± glandular (-puberulous) on the back, acuminate, 2–3-seriate, outer ones narrowly lanceolate, c. 3–4 mm long, innermost ones narrowly oblong-lanceolate, 5–6 mm long, with whitish-scarious margins and often violet tips. *Ray florets* (15–)20–25; ligule variously coloured, yellow, white (in two collections), blue, mauve, purple, violet etc., about twice as long as the involucre. *Disc florets* c. 60, yellow, about equalling the involucre; style branches provided with more or less distinct stigmatic papillae along margins. *Achenes* of ray florets glabrous, compressed triangular-obpyramidate, with angles partly entire, partly crenate, and sides irregularly cross-furrowed, truncate at apex, 4–5 mm long. Achenes of disc florets glabrous; outer ones surrounded by a wing with stiff, thickened margin, obovate and slightly emarginate at the tip or almost obcordate, c. 5 mm long and c. 3.5 mm broad; inner, sterile ones thin, pellucid, narrowly obovate, 5–6 mm long and c. 2 mm broad.

Garuleum bipinnatum is a xerophilic plant confined to the Cape Province, where it occurs mainly in the Karroo region. Some sixty herbarium specimens have been studied. Specimens having well-developed seeds, or nearly so, in the achenes of the outer disc florets are known from the following districts: Albany, Graaff Reinet, Laingsburg, Murraysburg and Oudtshoorn.

When visiting the Great Fish River Valley in 1963 I encountered specimens which agreed with De Candolle's *D. multifida,* except for the fact that the achenes of the outer disc florets contained well developed seeds. The specimens (Norlindh 5683) grew under favourable conditions and had bipinnatipartite leaves with numerous linear lobes.

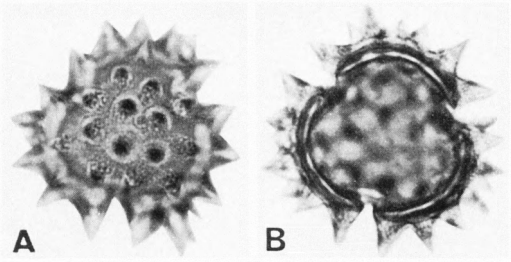


Fig. 2. Acetolysed pollen grains of *Garuleum bipinnatum*. – A: Polar view, high focus. – B: Optical cross section. – ×1000. Photomicrographs by Yvonne Arremo.

It seems that the achenes of the ray florets are nutritionally favoured, since in general they produce mature seed. The achenes of the outer disc florets probably develop only when nutrition is in excess. The achenes of the inner disc florets either do not receive sufficient food or they are sterile and the development of their ovaries is incomplete. There are numerous disc florets in each head but normally only a few of them produce ripe achenes, probably only under especially favourable conditions.

More detailed, recently obtained information about the variability of the flower colour in *Garuleum bipinnatum* has proved that it cannot be used as a distinguishing character, as earlier suggested by me.

Garuleum bipinnatum seems to be at an evolutionary stage, at which the female fertility of the disc florets is about to be lost. It is conceivable that the ancestral forms of *Garuleum* possessed fertile disc florets and that *G. bipinnatum* is primitive in this respect.

I intend to carry out supplementary investigations on the *Garuleum bipinnatum* complex. Above all, a better knowledge of the species would be gained by means of cultivation experiments.

Acknowledgements. I am very grateful to Dr J. Praglowski, Stockholm, for his palynological contri-

bution to this paper, and to Miss Rita Baechler for the excellent illustrations. Thanks are also due to Dr Dorothy Guy-Ohlsson, who kindly checked the English. – The study is based mainly on material from the following herbaria: B, G, G-DC, PRE, S, UPS (abbreviations in accordance with Holmgren & Keuken 1974) and I wish to thank all those who have placed specimens at my disposal.

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Cryptocoryne dewitii N. Jacobsen sp. nov. (Araceae)

Niels Jacobsen

Jacobsen, N. 1977 12 30: Cryptocoryne dewitii N. Jacobsen sp. nov. (Araceae). *Bot. Notiser 130:* 381–382. Stockholm. ISSN 0006-8195.

A new species of *Cryptocoryne* from Papua, New Guinea is described and illustrated.

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Cryptocoryne dewitii N. Jacobsen sp. nov.

Folia circiter 15 cm longa; laminae supra obscure virides, subtus pallidiores, 7–8 cm longae, anguste ovales, basi cordatae, margine leviter undulatae, in herbario complanatae irregulariter dentatas se praebentes. Spatha circiter 8 cm longa; tubus circiter 2 cm longus; limbus circiter 5 cm longus, anguste ovalis vel lanceolatus, lacteus vel flavidus, basi albidus, supra obscurior, extus cinnamomeus; collare faucale nullum; tubus inferior ut videtur alveolis nullis. Spadix circiter 1 cm longus; stigma ovale, breviter pedicellatum; corpora olfactoria irregularia; flores masculi circiter 30.

Holotypus die 16 Augusti anni 1971 in silva palustri paulum supra mare prope Kiunga Airstrip tractus Kiungensis regionis Papuanae Western District insulae New Guinea sub numero NGF 46818 a P. Katik lectus, siccus in Herbario Smithsoniano (US) depositus, isotypis in Herbario Leydensi (L) et Herbario Laensi (LAE).

The drawing is a reconstruction of the specimen at LAE. However, as the middle part of the spathe is missing, the spathe of the US specimen has been inserted instead. The upper part of the spathe is missing in the L specimen.

No stolons are present on the herbarium specimens, but they were doubtless broken off when the plants were dug up.

The species was found in lowland forest in the central western part of Papua, at an altitude of c. 70 m. The short tube of the spathe indicates an amphibious habit, and the plants were probably emersed at the time of flowering. The leaves are covered with a thin layer of mud and ochre. The colour of the limb was described as cream by the collector. The colours fade somewhat on drying and it is no longer possible to describe the colouration of the spathe more precisely. The outside of the limb seems to be more brownish than the rest. The herbarium specimens have denticulate leaf margins, an artefact obviously caused by pressing the slightly undulate leaf margins of the live plant.

The species is endemic to New Guinea, where *C. ciliata* (Roxb.) Schott and *C. versteegii* Engl. also occur. Rataj (1975) cited the collection of this new species under *C. versteegii* Engl., a species characterized by its green, fleshy leaves with an almost triangular leaf-blade (Engler 1920, de Wit 1971), a spathe with a yellow throat and collar and a very short, rugose, purple limb (Jacobsen 1977).

Cryptocoryne dewitii is characterized by ovate leaves with a slightly undulate margin, the rather wide, yellow to cream opening of the spathe, a rather flat, elongate limb, and the absence of a collar.

The species is named in honour of Prof. H. C. D. de Wit, nestor of the *Crypto's*.

Acknowledgement. I should like to thank Tyge Christensen for the Latin translation.

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Wit, H. C. D. de 1971: *Aquarienpflanzen.* Stuttgart.



Fig. 1. *Cryptocoryne dewitii*. – A: Habit.– B: Limb of the spathe. – C: Spadix. – A ×0.7, B ×1.6, C ×8.

Vessel types of the monocotyledons: a survey

Peter Wagner

Wagner, P. 1977 12 30: Vessel types of the monocotyledons: a survey. *Bot. Notiser 130:* 383–402. Stockholm. ISSN 0006-8195.

A literature survey of the occurrence of vessel types in roots, stems and leaves of the monocotyledons is presented. The information is arranged according to the classification suggested by Dahlgren, *Bot. Notiser 128:* 119–147 (1975). An agreement between type and distribution of vessels, systematic position, and habit is shown. Some minor modifications in the classification of the monocotyledons are suggested, e.g. *Hanguana* is better placed in Asparagales than in Poales, Bromeliales show greater affinity to Commelinaceae than to Lilianae in vessel characteristics and *Mayaca* and *Cartonema* deviate in their vessel anatomy from what is normal in Commelinales.

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The aim of the present compilation is to give an account of the distribution of vessels and vessel types in roots, stems and leaves of the monocotyledons. The system of classification used is mainly that suggested by Dahlgren (1975). Sometimes families suggested by Huber (1969) are preferred, in which case the appropriate taxon has been marked 'sensu Huber'. The perforation types found in the individual families and genera are tabulated at the end of this paper.

The information in this paper has been compiled from the various sources mentioned in the References. Whenever possible, information concerning the late metaxylem was used, because any differences in specialization are more pronounced in this part of the xylem. However, whether the information given concerns the metaxylem as a whole, or only the late metaxylem, is not always clearly stated in the papers. This may have distorted the picture to some degree. Systematic differences between authors also seem to be present. In the families dealt with in Cheadle's papers the frequency of scalariform perforation plates is invariably higher than e.g. in Metcalfe's 'Anatomy of the monocotyledons'.

The origin and specialization of vessels in the xylem of all parts of the plant in the monocotyledons were studied by Cheadle in a series of papers (1942–44). Using the principles outlined by Frost (1930) he concluded that vessel members originated from tracheids, that vessel members with long, scalariform perforation plates on very oblique end walls are the most primitive and that vessel members with simple perforation plates on transversely-placed end walls are the most specialized. During the phylogenetic development between these extremes, the vessel members have become shorter and, when thick, tend to have walls of constant width (Cheadle 1943 a). He established that the length of cells and the thickness of their walls, as well as their pitting details, should be used with great caution as indicators of specialization. The perforation plate is the most reliable tool for that purpose. He further concluded that vessels first originated in the roots, because in many plants vessels are found nowhere else and because the vessel members in the roots of species in which vessels are present throughout the plant are more specialized than similar elements in the shoot system; furthermore, the vessel members in the roots of species which lack vessels elsewhere are in general less specialized than those found in the roots of species in which vessels are widespread. Vessel members, however, may become more specialized in roots of species in which the shoot system lacks vessels (e.g. Alliaceae).Vessels originate, then, from the base

of the stem upwards. This upward progression is paralleled by a change from vessels with long, scalariform perforation plates to vessels with short scalariform plates with few bars and simple perforations. In those species in which vessels occur in the stems and leaves, the perforation types of the vessels in the roots are always the most specialized and those in the leaves the most primitive (Cheadle 1943 b). In a few genera vessels are present in the roots and leaves and not in the stems (e.g. *Dracaena, Cordyline*), but no species is known in which the vessel perforation types are more specialized in the shoot system than in the roots.

The development and specialization of vessels in the late metaxylem preceded the similar development in the early metaxylem. The vessel members in the early metaxylem are never more specialized than those in the late metaxylem. Whatever the degree of specialization of the perforation plates in the late metaxylem, any type of perforation plate, excepting the more specialized, may occur in the early metaxylem. In some species vessels may be absent from the early metaxylem, but no cases have been reported in which vessels are present in the early but not in the late metaxylem (Cheadle 1944). Differences in specialization are more clearly seen when the late, rather than the early, metaxylem in all organs is compared (Cheadle 1944). Later studies by Cheadle and others have not affected these conclusions.

Huber (1969) proposed another view on the development of the vessel system. He suggested that vessels were originally present in both root, stem and leaves. In some evolutionary trends vessels were preserved in all parts and the vessel members eventually became more specialized (i.e. simple perforations were developed); in other trends the vessels in the shoot system, or eventually (in aquatics) in the entire plant, were lost. Huber argues, in opposition to Cheadle, that the root is a conservative organ and is therefore not prone to develop new cell types. It is more likely that it preserves cell types which have already been lost by the more progressive shoot system. Against this view, it may be argued that in spite of the unquestionably conservative anatomical characteristics of the root, this does invariably possess the most advanced vessel types in the whole plant, whether the stem and/or leaves possess vessels or not. This is unaffected by the fact that the progression of vessel specialization from the late to the early metaxylem is slower in the roots than elsewhere (Cheadle 1944).

Huber further argues that aquatic forms without vessels, mainly found in Alismatanae and Lemnaceae, are very specialized forms. Consequently, the absence of vessels must also be regarded as an advanced characteristic. This assumption is sustained by the occurrence of relatively advanced perforation types in the root vessels of the fairly 'primitive' marsh plants within Alismatanae (Alismataceae, Butomaceae).

Cheadle has established the unidirectional specialization of the vessels in the monocotyledons. The progression tracheid–scalariform perforation–simple perforation is irreversible. If vessels ever occurred in the ancestors of the above mentioned aquatics, their failure to develop is therefore a reduction in specialization, as there is no evidence that tracheids have ever been derived from vessels (Cheadle 1953). If the absence of vessels is a result of a reduction of the xylem, then this absence represents an advanced feature and does not contradict Huber's view concerning the advanced nature of the aquatics. This conceivable reduction in the xylem of the aquatics does go counter to the afore-mentioned general trend, that monocotyledons with vessels only in the roots have primitive vessels. To correlate and evaluate the degree of specialization of characteristics (and their phylogenetic significance) a large random sample is needed (Frost 1930), but the aquatic monocotyledons investigated are neither many, nor at random. According to my view they are more correctly treated as forming exceptions to the general evolutionary trend.

It should be emphasized that the irreversible specialization of the perforation plate makes this a most useful character for ruling out certain suggested phylogenetic relationships (Cheadle 1955, Cheadle & Tucker 1961). Vessel distribution and vessel characters, however, may only either suggest or confirm such relationships. Fig. 1, which depicts the distribution of the characteristics of vessels in the roots, stems and leaves of the monocotyledons, reveals certain features. In every order the roots invariably possess the most specialized vessels, if vessels are present at all. With a few exceptions in Asparagales

(Dracaenaceae, Dasypogonaceae, Nolinaceae and Xanthorrhoeaceae), in Velloziales and one genus (*Phytelephas*) in Arecanae, the degree of vessel specialization decreases in stems and leaves, even in the most advanced orders (e.g. Poales). The more primitive organization level in stems and leaves is, in some orders, expressed by a higher frequency of scalariform perforation plates (in the order as a whole, not necessarily in the individual genera) e.g. Poales, Cyperales, Juncales, Eriocaulales, Arecales, in others it is shown by an increase in the number of genera without vessels e.g. Bromeliaceae, Asparagales, Liliales, Stemonales, Velloziales, Haemodorales and Zingiberales. In certain cases vessels are not present at all in the shoot system, e.g. Arales, Philydrales, Taccales, Alismatales. A feature which is not evident from the figure or table is that the vessels in the stems and leaves are often of a more primitive type than those in the roots, since they have longer perforation plates with more numerous bars on the oblique end-walls. Sometimes the change in perforation type from root to stem is so pronounced that a shift from vessels to vessel tracheids takes place e.g. in Pontederiales and Philesiaceae.

It is also true that vessels are present in the shoot systems of orders in which plants with long internodes are prevalent e.g. Poales, Juncales, Eriocaulales, Cyperales, Typhales, Arecales and Dioscoreales. In orders in which bulb- or corm-forming plants are frequent, vessels are often not present in the shoot system, e.g. Asparagales, Liliales.

Alismatanae

Alismatales. Vessels are absent in stems and leaves but present in the roots of the investigated members of this order.

The perforation plates are scalariform (*Hydrocleys, Echinodorus*), scalariform and simple (*Limnocharis*) or predominantly simple (most species of Alismataceae; Stant 1964, 1967). This does not support the supposition, sometimes put forward, that Alismatales may be related to Ranunculales, because vessels are present in the stems and leaves, as well as in the roots, of the latter order.

Hydrocharitales. In the few members of this order studied vessels were only found in the roots of *Butomus*. Vessels are totally absent in Hydrocharitaceae and Aponogetonaceae, which probably represents a reduction, as hypothesized by Cheadle (1942) and Carlquist (1975). The vessels of *Butomus* have simple (Stant 1967) or mostly simple (Cheadle 1942) perforations.

Zosterales. Most aquatic genera of this order lack vessels. Vessels occur in roots of the marsh plants *Scheuchzeria* and *Triglochin*, but also in the investigated species of *Potamogeton;* the perforations are scalariform (Cheadle 1942).

Najadales. No members possess vessels (Cheadle 1942).

The general trend in Alismatanae seems to be that most land (marsh) plants have vessels in the roots but not in the stems and leaves. At least the more advanced aquatics entirely lack vessels. Scalariform perforation plates are found in Scheuchzeriaceae, Juncaginaceae and *Potamogeton*. Simple and scalariform perforations are found in *Butomus* and Alismataceae. Vessel characteristics seem to be highly correlated with growth habit and hence cannot be used indiscriminately for taxonomic purposes. Alismatales can be distinguished from Hydrocharitales by the possession of poly-aperturate pollen grains and a curved embryo, the presence of secretion vessels and the lack of anthocyanine pseudobases.

Lilianae

Dioscoreales. In the species studied vessels with scalariform perforation plates are present in roots, aerial stems and petioles, absent in leaf laminae and rhizomes (Braun 1957, Ayensu 1972). According to Cheadle's (1953) concept the presence of vessels in stems is a fairly advanced feature, a view supported (in this order) by the presence of highly-specialized xylem – and phloem – glomeruli in the nodes. Huber (1969) regards the presence of vessels in roots and stems as a rather primitive feature and derives several families within Lilianae from Dioscoreaceae, which he claims also forms a link with the dicotyledons. The presence of the above-mentioned xylem glomeruli makes the postulated primitiveness of the xylem disputable.

Stemonales. All the investigated species have

root vessels with scalariform perforation plates; one, or perhaps two, species are known (both in Stemonaceae) which also have stem vessels with scalariform perforations (Tomlinson & Ayensu 1968). This supports the proposal by Huber (1969) and Ayensu (1968 a) that Stemonaceae, especially *Stemona* itself, are related to Dioscoreales. The presence of vessels (with scalariform perforations) only in the roots (Cheadle 1970) is a common feature among Lilianae and this characteristic is therefore not useful in assessing the affinities of Trilliaceae. The families are grouped together on a basis of absence of septal nectaries, presence of long connective appendages and on fruit anatomy.

Asparagales. In Smilacaceae scalariform perforations are found in the vessels. All the species investigated have vessels in the roots, 7 of 11 in the stems and 8 of 15 in the leaves (Cheadle 1970). Most taxa agree with Dioscoreaceae in the type and distribution of vessels to which family Smilacaceae is also for other reasons considered to be related (Huber 1969).

Some variation exists within Philesiaceae. In the roots, vessels with simple, or mostly simple, perforations are found in *Behnia* and *Eustrephus* (Fahn 1954 b, Cheadle & Kosakai 1975), vessels with simple and scalariform perforations (Cheadle & Kosakai 1975) or mostly simple (Fahn 1954 b) in *Geitonoplesium,* vessels with scalariform perforations (Cheadle & Kosakai 1975) or vessel-tracheids (Fahn 1954 b) in *Lapageria, Luzuriaga,* and *Philesia* and vessels with scalariform perforation plates in *Petermannia.* In the stems, Fahn (1954 b) found vessels with scalariform perforations in *Geitonoplesium* and vessel-tracheids in *Lapageria* and *Luzuriaga*; he reported finding only tracheids in the other genera which he investigated. Cheadle & Kosakai (1975) found vessels with scalariform perforations in *Eustrephus, Geitonoplesium, Lapageria, Luzuriaga, Philesia* and *Petermannia,* and tracheids only in *Behnia.* In the leaves, Fahn (1954 b) found vessel-tracheids in *Geitonoplesium.* Cheadle & Kosakai (1975) were uncertain about the presence of vessels (with scalariform perforations) in the leaves of *Eustrephus.* The discrepancies between the results of Fahn and of Cheadle and Kosakai, which may seem greater than they actually are, are due to the fact that the vessels are often very few and difficult to recognize, since they very much resemble tracheids. The heterogeneity of the family, most clearly seen in Fahn's results, may be taken to support Huber's conception that the family should be divided into smaller units (Philesiaceae, Luzuriagaceae and Petermanniaceae). The vessel distribution of *Petermannia* supports an affinity with Philesiaceae, rather than with Smilacaceae as is sometimes suggested (Tomlinson & Ayensu 1969).

In Convallariaceae the vessels in the roots have scalariform (*Aspidistra*), mostly scalariform, or mostly simple perforations (*Convallaria*). Some species in Polygonateae even have vessels (with scalariform perforations) in the stem (Cheadle & Kosakai 1971). Members of Herreriaceae have vessels with scalariform perforations in the stems, the roots not having been studied. Species of Asparagaceae have vessels with simple perforations in the roots and vessels with scalariform perforations in the stems (Cheadle & Kosakai 1971). In Ruscaceae a shift takes place from a primitive type, in which vessels, with scalariform perforation plates, are present only in the roots, to a presumably more advanced type with vessels with simple perforations in the roots and vessels with scalariform perforations in the stems; Cheadle (1970 p. 50) points out that he does not understand this mode of distribution. The occurrence of vessels in the stems of some of the genera in the families mentioned above may suggest a certain phylogenetic relationship with Smilacaceae, yet the perforations present in the root vessels are generally more advanced in type.

In Dracaenaceae and Nolinaceae sensu Huber (1969) the species studied have vessels in the roots and leaves, but not in the stems; vessel perforations in the leaves are scalariform, but are probably simple in the roots (Cheadle 1942). Cheadle (1943 b) suggests that the production of large numbers of tracheids in the bundles of the secondary tissues (both genera show secondary thickening) compensates for the failure to develope vessels. Carlquist (1975) notes that the establishment of a continuity between the vessels in the secondary tissues and the vessels in the upper primary stem would be a virtual impossibility morphogenetically; he also suggests stem succulence as providing an explanation. The species of Asteliaceae sensu Huber (1969) have vessels with scalariform perforation plates

in the roots, but no vessels in the shoot system; those of Dianellaceae sensu Huber (1969) have vessels with mostly simple or with simple and scalariform perforation plates in the roots and likewise no vessels elsewhere (Cheadle & Kosakai 1971). Vessel characteristics seem to support Huber's assumption that the four last-mentioned families form quite separate groups.

Vessels with simple perforations were found in all the investigated species of Xanthorrhoeaceae, except in *Baxteria* and *Kingia,* which have scalariform perforations. Vessels occurred only in the roots, except in two genera (*Acanthocarpus* and *Xanthorrhoea*) in which vessels with long, scalariform perforation plates are found in the leaves. Arber (1925) found vessel cells in the stem of *Xanthorrhoea minor,* but Fahn (1954 a) found only tracheids. No vessels are present in the rhizomes. Secondary thickening occurs in *Lomandra, Xanthorrhoea* and possibly in *Kingia*. The type and distribution of the vessels do not contradict Huber's supposition that Xanthorrhoeaceae, Dracaenaceae and Asteliaceae are closely allied, but it does not support his theory that a closer relationship exists between *Xanthorrhoea* and Asteliaceae and between Dracaenaceae and the remaining genera in Xanthorrhoeaceae.

Hanguana (Hanguanaceae) has no vessels in either stems or leaves; the roots were not studied. The absence of vessels from the shoot system agree with the condition found in several families in Asparagales, but is in disagreement with a position in Flagellariaceae, in which family the genus is often placed. Smithson (1957) also reported other anatomical characters which separate *Hanguana* from *Flagellaria* and *Joinvillea,* but which suggest a certain relationship with Xanthorrhoeaceae.

In Asphodelaceae and Anthericaceae vessels are present in the roots and in seven of the genera studied also in the stems. The perforation plates in the root vessels are almost exclusively simple, except in Kniphofieae, in which scalariform as well as simple perforations are found, and in *Borya,* in which the perforations are scalariform. The perforations in the stem vessels are scalariform except in *Tricoryne* in which also simple perforations occur (Cheadle & Kosakai 1971). Secondary thickening occurs in *Aloe.* (Tomlinson & Zimmermann 1969). As far as vessel characteristics are concerned these two families, and Aphyllanthaceae sensu Huber, agree completely. They are kept separate mainly because of the occurrence of saponins in Asphodelaceae and because of differences in the embryo, microsporogenesis and karyotype.

In Agavaceae vessels are present in the roots. Perforations are simple in *Agave* and scalariform in *Hosta* (Cheadle & Kosakai 1971). Secondary thickening occurs in *Agave* and *Furcraea* (Tomlinson & Zimmermann 1969). *Hosta,* because of its herbaceous habit, is an atypical genus within Agavaceae. The vessel perforation type also resembles that found in *Hemerocallis* (Hemerocallidaceae), which Huber (1969), however, does not consider is related to *Hosta*.

In Hyacinthaceae and Alliaceae vessels are absent from the shoot system, but present in the roots. In Hyacinthaceae the perforations are scalariform and – in 5 of 22 investigated genera – scalariform and simple; in one genus (*Milula*) the perforations are mostly simple (Cheadle & Kosakai 1971). In Alliaceae the perforation plates are simple, simple and scalariform or (in *Agapanthus*) scalariform. It is noteworthy that the most primitive member of the family with regard to vascular characters, *Agapanthus,* is grouped together with the more advanced *Tulbaghia* in the tribe Agapantheae; Cheadle (1969) also notes that they are "bad tribe mates".

All the species of Amaryllidaceae studied have vessels only in the roots, the perforations being exclusively scalariform (Cheadle 1969). Huber (1969) considers this family to be the most advanced one in Asparagales; the vessel characteristics agree with those found in Hyacinthaceae, but are less advanced than those found in Alliaceae, Anthericaceae and Asphodelaceae.

In Hypoxidaceae vessels with scalariform perforation plates are found in the roots, though *Campynema* is possibly totally devoid of vessels (Cheadle 1968). Huber (1969) supposes that this family is more closely related to Asteliaceae than to Amaryllidaceae. Since in both families the vessels have scalariform perforations neither possibility can be excluded.

In the roots of Velloziaceae the vessel perforations are simple. Ayensu (1968 b) claims that all the species studied – except *Vellozia elegans* – have vessels with scalariform perforations in the leaves, but no vessels in the stem. He questions Cheadle's (1968) statement that vessels with scalariform perforations occur in the stems and

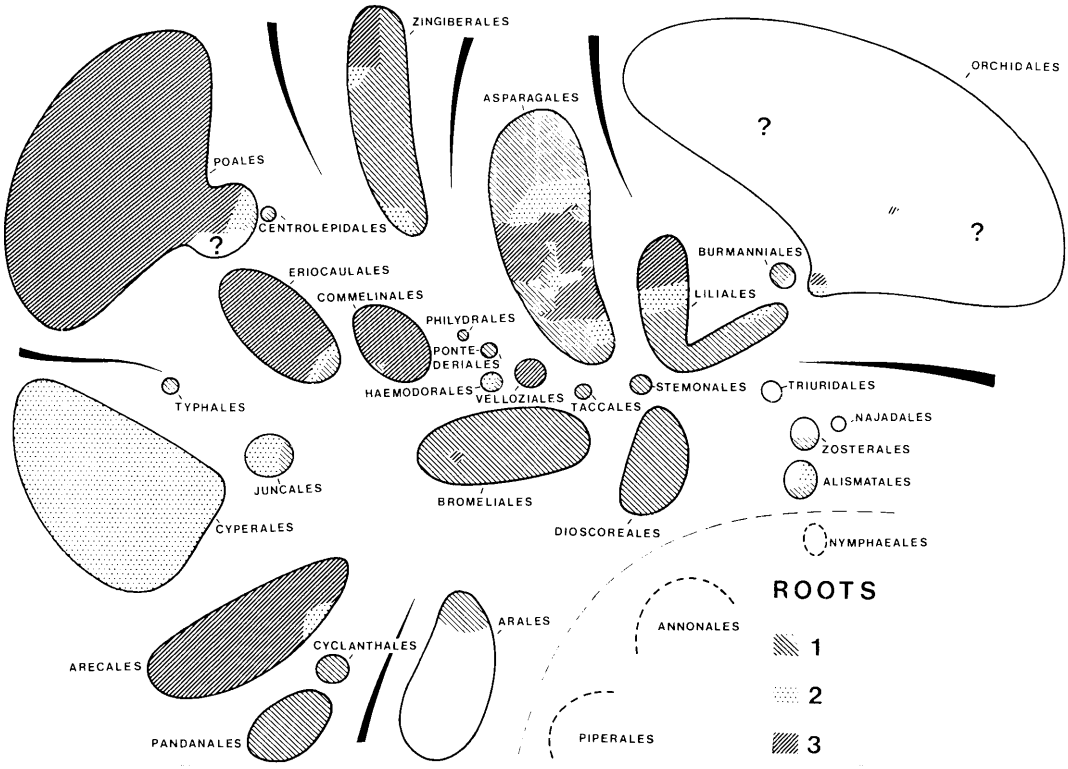


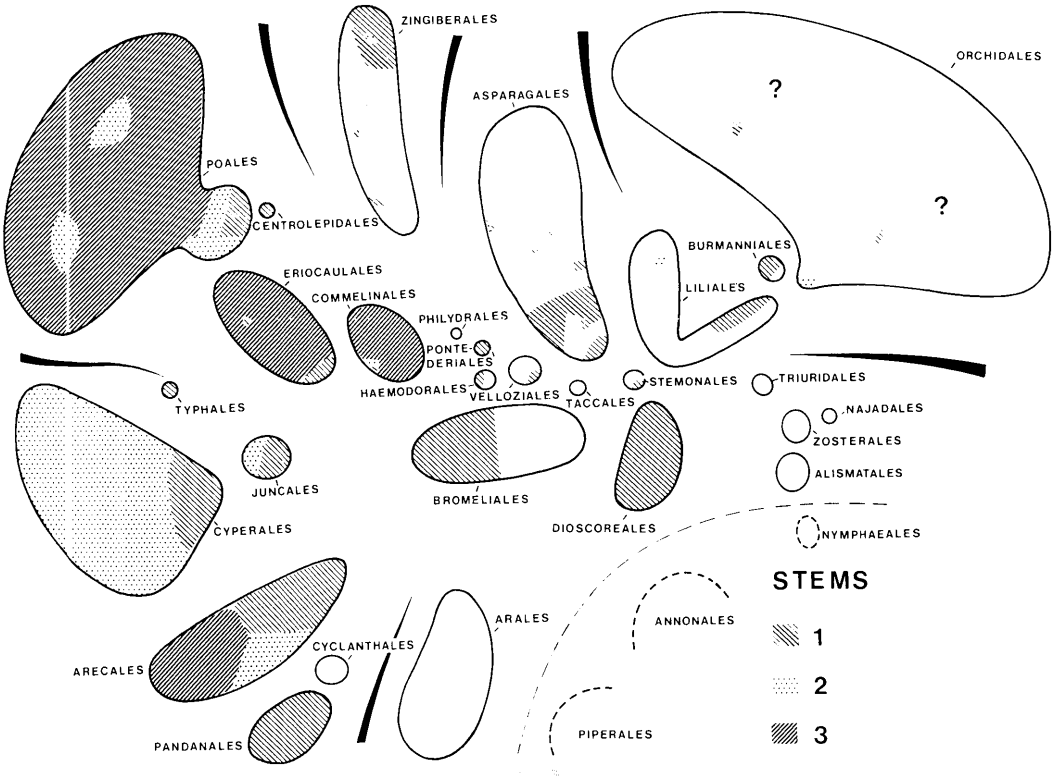
Fig. 1. Distribution of vessel types in roots, stems and leaves of the monocotyledons. The graphic representation of the orders is drawn up by Dahlgren and based on his system (Dahlgren 1975). Modifications have been made in accordance with a current revision of the system being carried out by Dahlgren and Huber, University of Hamburg. In the diagrams all the families have fixed places within the orders. – 1: Vessels with scalariform perforations only or vessel tracheids. – 2: Vessels with simple and scalariform perforations. – 3: Vessels with simple perforations only. – Orchidaceae is insufficiently investigated. No information was available about the presence of vessels in the stems and roots of some minor groups in Asparagales and in the roots of Flagellariaceae and Ecdeiocoleaceae. In Dioscoreales vessels are present in the petioles but not in the lamina; evidence is conflicting regarding their presence in the leaves of Restionaceae.

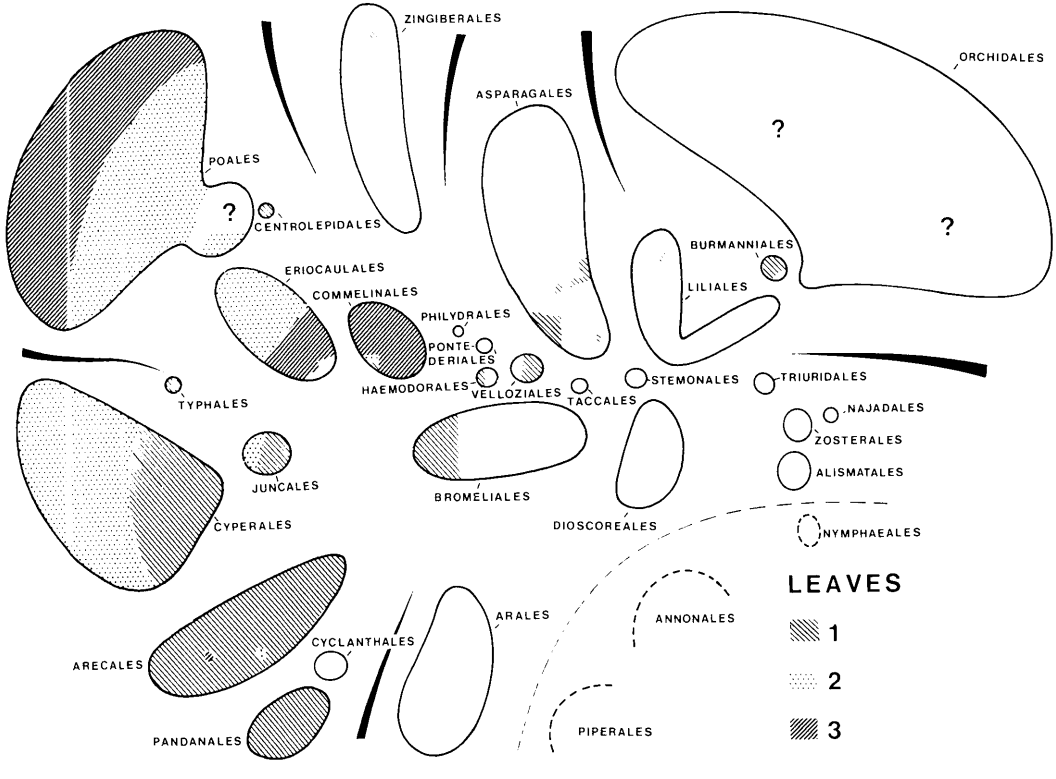
he assumes that macerated preparations may be contaminated with root material, because these cling tightly around the stem. Fahn (1954 b) found no vessels in the leaves of *Vellozia elegans*. Huber (1969) suggests that this family is best placed in an order of its own, Velloziales.

In Tecophilaeaceae vessels with scalariform perforations occur in the roots, but not elsewhere, an organization level equivalent to that found in the less specialized families within Asparagales (Cheadle 1969).

Liliales. The genera of Colchicaceae have vessels, with scalariform perforations, in the roots only (Cheadle & Kosakai 1971).

In Iridaceae most species have vessels with simple, or mostly simple, perforations in the roots, whereas the shoot system is devoid of vessels (Cheadle 1963). Two groups however deviate from this general condition, viz. (1) *Sisyrinchium,* in which vessels with mostly simple perforations occur in the stem and vessels with scalariform perforations occur in the leaves (in two species at least, in two other species only tracheids are present in the leaves), and (2) *Aristea, Klattia, Patersonia* and *Witsenia,* in which the vessels in the roots, as in Colchicaceae, have scalariform or mostly scalariform perforations (vessels are not present elsewhere in the plants). As regards vessel charac-


ZINGIBERALES
ASPARAGALES
ORCHIDALES
?
?
POALES
CENTROLEPIDALES
ERIOCAULALES
COMMELINALES
PHILYDRALES
PONTEDERIALES
HAEMODORALES
VELLOZIALES
TACCALES
BURMANNIALES
LILIALES
STEMONALES
TRIURIDALES
NAJADALES
ZOSTERALES
ALISMATALES
NYMPHAEALES
TYPHALES
JUNCALES
CYPERALES
BROMELIALES
DIOSCOREALES
ARECALES
CYCLANTHALES
ARALES
ANNONALES
PANDANALES
PIPERALES
STEMS
1
2
3


ZINGIBERALES
ASPARAGALES
ORCHIDALES
?
?
POALES
?
CENTROLEPIDALES
ERIOCAULALES
COMMELINALES
PHILYDRALES
PONTEDERIALES
HAEMODORALES
VELLOZIALES
TACCALES
BURMANNIALES
LILIALES
STEMONALES
TRIURIDALES
NAJADALES
ZOSTERALES
ALISMATALES
NYMPHAEALES
TYPHALES
JUNCALES
CYPERALES
BROMELIALES
DIOSCOREALES
ARECALES
CYCLANTHALES
ARALES
ANNONALES
PANDANALES
PIPERALES
LEAVES
1
2
3

teristics the latter group comes closest to Colchicaceae. The above-mentioned conditions support the tribal division suggested by Huber (1969). In *Klattia, Schizostylis* and *Witsenia* secondary thickening occurs (Tomlinson & Zimmermann 1969).

In Alstroemeriaceae vessels with scalariform perforations are found in the roots of *Bomarea, Schickendantzia* and *Alstroemeria*; in *Alstroemeria aurantiaca* the root vessels have mostly scalariform perforations. In the four genera investigated by Cheadle & Kosakai (1975), vessels with scalariform perforations were found in the stems. Huber (1969) regards the family as closely related to Colchicaceae and Liliaceae. The presence of vessels in the stems is a feature in common with *Sisyrinchium*.

Vessels are present in the roots of all the genera investigated in Liliaceae and Melanthiaceae, except in *Petrosavia,* in which genus no vessels occur. The perforation plates are scalariform (Cheadle & Kosakai 1971). In *Sandersonia* and *Tricyrtis* vessels with scalariform perforations are also present in the stem. The absence of vessels in *Petrosavia* (vessel tracheids may be present in the roots, the identification is difficult) may be connected with its saprophytic habit. Stant (1970) suggested placing *Petrosavia* in Triuridaceae, because of its anatomy, though with reservations. There is a fair possibility that parallel evolution has occurred, since Triuridaceae are likewise saprophytic. Colchicaceae, Liliaceae and Melanthiaceae agree in vessel characters. They are kept separate because of the presence of alkaloids, steroid saponins and raphides of calcium oxalate in Melanthiaceae.

Triuridales. Vessels are not present at all in the four Triuridales species investigated (only one of which is mentioned by name, viz. *Andruris sciaphila*). This feature is probably due to the mycoparasitic habit of the members of this family (Carlquist 1975).

Burmanniales. Burmannia disticha and *B. longifolia,* two autotrophic species, have vessels with scalariform perforation plates in roots, stems and leaves (Carlquist 1975). This is rather surprising considering their systematic position, although vessels do occur in the stems and leaves of Orchidales. None of the mycoparasitic species have been studied.

Orchidales. In Apostasiaceae the genus *Adactylus* has vessels, with mostly simple perforations, in the roots and vessels with simple and scalariform perforations in the stems; according to Cheadle (1968) it is devoid of vessels in the stems. In *Neuwiedia lindleyi* the presence of vessels in the roots is questionable (Cheadle 1968) and if present at all only scalariform perforations are found. According to Solereder & Meyer (1930) *Neuwiedia griffithii* has vessels with simple and scalariform perforations in the roots. In *Apostasia* vessels do occur in the stem, although the perforation type was not described. In Cypripediaceae *Phragmipedium* (5 spp.), *Cypripedium* (11 spp.) and *Selenipedium* (2 spp.) vessels with simple perforations are found in the roots. No vessels are found in *Paphiopedilum* (7 spp.) None of the genera investigated had vessels in the stems or leaves (Rosso 1966).

In Orchidaceae vessels are present in the roots of *Pogonopsis, Dendrobium, Vanda* and *Vanilla*; the perforation type is not described for any taxon, excepting *Vanilla aromatica,* in which the perforation plates are simple. Solereder & Meyer (1930) enumerate 8 genera with vessels in the stems, the perforation-type, however, being described only for two of them, and 6 genera with no vessels.

In *Epidendron* and *Scaphyglottis* vessels with scalariform perforations are present in the leaves. Cheadle (1942) mentions that one out of four species has vessels with simple and scalariform perforations in the roots and three have vessels with scalariform perforations, five out of 15 species have vessels with scalariform perforations in the stems (in 2 further species vessels are perhaps present in the stems). Generic names are only given exceptionally, however. According to the system of Dahlgren (1975) one of these genera would be placed in Cypripediaceae.

The insufficiency of the data on vessel characters in this order makes an assessment of the interrelationships almost impossible. A comparison with the conditions in other orders is also impeded by the presence of water-storing tissues (velamen) in the roots of Orchidales. The confusion is made worse by the suggestion of Withner et al. (1974) that the tracheids are vascular tracheids and that the absence of vessels should therefore be regarded as an advanced feature. However, it seems that the

vessel types found in Cypripediaceae and Apostasiaceae are no less advanced then those found in Orchidaceae. According to Cheadle & Tucker (1961) and Carlquist (1975 fig. 8 p. 106) the vessels in Orchidaceae are generally more primitive than those in Apostasiaceae.

Haemodorales. The roots of most genera in both tribes of Haemodoraceae have vessels with mostly simple perforation plates. *Tribonanthes, Dilatris* and *Lanaria,* however, have scalariform perforations. In two genera in Haemodoreae, viz. *Lachnanthes* and *Xiphidium,* vessels are present in the shoot system. In *Lachnanthes* the presence of vessels in the leaves is uncertain (Cheadle 1942, 1968), while in *Xiphidium* the presence of vessels in the stems (Cheadle 1942) or in stems and leaves (Cheadle 1968) is doubtful. The remaining genera are devoid of vessels in either stems or leaves. Cheadle (1969) advocated a certain relationship between Haemodoraceae and Tecophilaeaceae. In the four species of Philydraceae investigated vessels with scalariform perforations are found in the roots and not elsewhere (Cheadle 1968, Fahn 1954 b). In this respect the family is considered to be more primitive than Haemodoraceae. The presence of scalariform perforation plates is a feature in common with Pontederiales, which also includes marsh (and aquatic) plants.

Taccales. The four species of Taccaceae studied have root vessels only, with long scalariform perforations; as the cell membrane may be present between some of the bars, the cells may be regarded as vessel tracheids (Cheadle 1968, Fahn 1954 b). Huber (1969) mentions the scalariform perforations as a feature in common with the dioscoreoid Liliiflorae.

Pontederiales. All the genera studied in Pontederiaceae have vessels with scalariform perforation plates in the roots; *Eichhornia crassipes, Heteranthera limosa* and perhaps *Pontederia cordata* also have vessels with scalariform perforations in the stems (Cheadle 1970). The type and distribution of vessels does not contradict the suggested relationship with Philydraceae and Haemodoraceae (Huber 1969), although the vessels in the latter family are of a more advanced type.

Bromeliales. In Bromeliaceae 14 of the 16 genera investigated have vessels with scalariform perforation plates in the roots, two have only simple perforations, 10 out of these 16 genera have vessels with scalariform perforations in the stems (*Aechmea* and *Dyckia* include species with or without vessels in the stems) and 7 have vessels with scalariform perforations in the leaves (Tomlinson 1969). The frequent occurrence of vessels in roots, stems and leaves indicates a relationship with families in Commelinales. However, since the perforation plates are simple in the latter order, this is considered more advanced. Within Lilianae, Bromeliaceae stand nearest to Dioscoreales with regard to vessel characteristics. Bromeliaceae is included in Lilianae because of the presence of steroid saponins, septal nectaries and helobial endosperm, but in several other features it agrees better with Commelinanae.

Commelinanae

Commelinales. In the 32 genera of Commelinaceae investigated vessels with simple perforations are found in roots, stems and leaves. In *Commelina, Rhoeo, Tradescantia* and *Zebrina,* however, scalariform perforation plates as well are found in stems and leaves (Tomlinson 1969, Cheadle 1942). In regard to vessel features the phylogenetic level of this family is the same as e.g. Xyridaceae and Poaceae. The genera of Xyridaceae studied have vessels with simple perforations in roots, stems and leaves (Tomlinson 1969).

Mayaca in the monogeneric Mayacaceae has vessels with long scalariform perforation plates in roots and stems and perhaps also in the leaves (Tomlinson 1969, Cheadle 1953). The vessels in the leaves may be vessel tracheids. The evolutionary line leading to Mayacaceae, like that leading to Cartonemataceae, apparently separated from the main line leading to Commelinaceae at a stage before vessels with simple perforations had been developed. *Cartonema spicatum* (Cartonemataceae) has mostly simple perforations in the root vessels, although a few scalariform are found too (Tomlinson 1969). Vessels are not present in stems and leaves at all, in which respect *Cartonema* differs conspicuously from other taxa in Commelinales.

In Rapateaceae the tribes Saxofridericieae and Schoenocephalieae have vessels with scalariform perforation plates in roots and stems. In the

tribe Monotremeae simple perforations are present in the wider vessels of the roots, whereas scalariform perforations are present in the narrower ones; vessels with simple perforations are found in stems. In Rapateeae all genera have scalariform perforations in the roots and stems, except *Spathanthus* which has simple perforations (Carlquist 1969). Thus, within this family, the vessels exhibit a wide range of variation, from "rather primitive" (Saxofridericieae, Schoenocephalieae, Rapateeae p.p.) to "rather advanced" (Monotremeae, *Spathanthus*) conditions. In general, they are less advanced than the vessels found in Xyridaceae and Commelinaceae.

Eriocaulales. According to Tomlinson (1969) vessels with simple and, less frequently, scalariform perforations are found in roots, stems and leaves in all Eriocaulaceae genera studied, except *Tonina*, in which the stem has vessels with long, scalariform perforation plates. Cheadle (1942) states that *Eriocaulon articulatum* has scalariform perforations in all organs.

Juncales. Within Juncaceae the vessel characters in the genus *Juncus* vary. According to Cheadle & Kosakai (1973) four of the species studied have simple perforations in the roots and two have mostly scalariform, the remaining species varying between these extremes. In the stems five out of 12 species have mostly simple perforations, one scalariform and simple, and six mostly scalariform. In the leaves the perforations are simple and scalariform in two species, mostly scalariform in five, and only scalariform in three. In *Luzula* the root vessels have simple or mainly simple perforations, in the stems simple and scalariform perforations are found, in the leaves simple and scalariform or mainly scalariform. In the remaining genera the vessels in the shoot system have scalariform perforation plates and in the roots they have mostly or only scalariform (*Rostkovia*) except *Distichia*, in which the root vessels have mostly simple perforations. Cutler (1969) reported simple, scalariform and reticulate perforation plates in the vessels of these genera. It is evident that *Juncus* and *Luzula* are anatomically the most advanced genera in the family and *Rostkovia* the most primitive.

Thurnia (Thurniaceae) has vessels with scalariform perforations in roots, stems and leaves (Cutler 1969). Cheadle & Kosakai (1973) reported mostly scalariform perforations in the root vessels. As regards vessel characteristics this genus together with *Rostkovia* constitutes the most primitive part of Juncales.

Cyperales. In Cyperaceae Cheadle (1955) and Cheadle & Kosakai (1972) found vessels in roots, stems and leaves. Simple perforation plates prevail in the roots. In Cariceae mostly simple perforations are seen in the stems and mostly scalariform in the leaves. In Cryptangieae vessels with mostly scalariform perforations are present in the stems and leaves, except in *Cryptangium, Everardia* and *Lagenocarpus*, in which scalariform perforations only are found in both stems and leaves. The tribes Cypereae and Sclerieae have mostly simple to simple and scalariform perforation plates in the stems and simple and scalariform, or mainly scalariform, in the leaves. In Hypolytreae the stem vessels have mainly scalariform perforations and mostly or exclusively (*Chorizandra sphaerocephala*) scalariform perforations in the leaves. In Rhynchosporeae the vessels have mostly scalariform to scalariform and simple perforations in the stems and mostly scalariform in the leaves. Two species of *Cladium* and *Oreobolus* have scalariform plates only in both stems and leaves. *Carpha, Caustis* (one sp.), *Costularia, Cyathochaeta* and *Mesomelaena* (one sp.) have exclusively scalariform perforations in the leaves. The Scirpeae genera have vessels with simple and scalariform perforations in the stems and simple and scalariform or mainly scalariform in the leaves.

In tabular form Metcalfe (1971) reported on perforation types in 49 genera. The observations were made on longitudinal sections and the tables give only information about the observation of a perforation type in a given organ, not about the frequency of the different types. Metcalfe's results are therefore difficult to compare with those of Cheadle & Kosakai. The latter authors write that they "found no discrepancy in those species we had in common (with Metcalfe) except for our identification of scalariform perforation plates in addition to simple ones in a few organs". From the results of Cheadle & Kosakai and – to a certain extent – also from those of Metcalfe, it is evident, that vessels found in Cariceae and Cypereae

have attained a more advanced level than those in Hypolytreae, Cryptangieae and Rhynchosporeae. Generally speaking, Cyperaceae exhibit more advanced vessel features than Juncales.

Centrolepidales. In the investigated genera in Centrolepidaceae vessels occur in roots, stems and leaves, except *Trithuria filamentosa,* which has no leaf vessels. Scalariform and reticulate perforations are found in the stems and mostly reticulate in the rhizomes (Cutler 1969).

Poales. Restionaceae. In the genera studied by Cutler (1969) vessels with simple perforation plates are present in the roots. The rhizomes of *Cannomois, Elegia, Hypolaena, Lyginia, Restio monocephalus* and *Staberoha* have vessels with simple perforations, whereas those of *Chondropetalum* have vessels with scalariform or fenestriform perforations. The erect stems of five genera studied had simple perforations, two genera had mostly simple, three genera had simple and scalariform and 10 genera scalariform perforations. 3 genera included species with either simple or scalariform to mostly simple perforations. Cheadle (1955) reported that in the roots of the ten species he studied, two had simple perforations, four mostly simple, three simple and scalariform and one mostly scalariform. In the stems of 12 species studied, one had simple perforations, four mostly simple, six simple and scalariform and one scalariform. In the leaves of 11 species he found vessels with mostly simple perforations in one, simple and scalariform in five, mostly scalariform in two, and in three species scalariform perforations only. Cutler (1969) found no vessels in the leaves.

Flagellariaceae. *Joinvillea* (sometimes placed in its own family, Joinvilleaceae) has vessels with mostly simple perforations in the stem and with scalariform perforations in the leaves; in the leaf-sheaths mostly simple perforations are seen. No information exists about vessels in the roots (Tomlinson 1969, Fahn 1954 b). *Flagellaria* has simple and scalariform perforations in the vessels of stems and leaf-sheaths, whereas the leaf laminae have vessels with scalariform perforations (Tomlinson 1969, Fahn 1954 b). (*Hanguana* is included under Asparagales.) In the stem of *Ecdeiocolea* (Ecdeiocoleaceae) vessels with simple and scalariform perforation plates occur; the perforation type in the root vessels has not been described (Cutler 1969).

Poaceae. According to Metcalfe (1960) all the grass genera investigated have vessels with simple perforations in roots, stems and leaves. Cheadle (1955) stated that the roots had simple perforations in 57 of 58 species studied and mostly simple in one. Simple perforations were found in the stems of 55 of 69 species investigated and mostly simple ones in 14. In the leaves, simple perforations were found in 33 of 63 species, mostly simple perforations in 26 and simple and scalariform plates in one species. The families of Poales agree with the other Commelinanae in having vessels in roots, stems and leaves. Restionaceae, Flagellariaceae and Ecdeiocoleaceae have more primitive vessel perforation types in stems and leaves than Poaceae. Poaceae, together with Commelinaceae, Xyridaceae and Eriocaulaceae, represent the highest organization level attained within Commelinanae.

Zingiberanae

Zingiberales. In Lowiaceae *Orchidantha* has vessels with scalariform perforations in the roots; the shoot system is devoid of vessels (Fahn 1954 b, Tomlinson 1959). Within Strelitziaceae, *Ravenala* has vessels with scalariform perforations in the roots, while in *Phenakospermum* and *Strelitzia* this type of vessel occurs in the stems as well, simple perforation plates being intermixed with scalariform in the root vessels of *Phenakospermum.* In *Heliconia* (Heliconiaceae) vessels with scalariform perforations occur in the roots only (Tomlinson 1969, Cheadle 1942).

In *Musa* and *Ensete* of Musaceae, vessels are present in the roots, their perforation plates being mostly simple, although scalariform and reticulate plates are also seen. Vessels with scalariform perforations have been found in the inflorescence axis of *Musa* (Tomlinson 1969, Cheadle 1942).

In *Alpinia,* Zingiberaceae, the root vessels have simple perforations, according to Solereder & Meyer (1930), scalariform according to Tomlinson (1969), while in *Catimbium, Elettaria* and *Elettariopsis* they have simple and scalariform or mostly scalariform perforations (Tomlinson 1956, 1969). In the remaining 15 genera investi-

gated the perforation type is exclusively scalariform. Cheadle (1942) and Solereder & Meyer (1930) claimed that *Hedychium* is completely devoid of vessels, although Tomlinson (1956) reported finding vessels with scalariform perforation plates in the roots. Cheadle (1942) stated that in seven out of ten species (in his paper Zingiberaceae includes Costaceae) vessels are present in the stems; this was later corrected by Tomlinson (1956), who states that only one, *Renealmia,* has stem vessels. Within Costaceae, *Costus, Dimerocostus* and *Tapeinochilus* have vessels with scalariform perforations in the roots only, but in *Dimerocostus* also in the stem (Tomlinson 1956). In *Canna* (Cannaceae) the root vessels have mostly simple perforations (Tomlinson 1961).

In the genera of Marantaceae studied by Tomlinson (1969) vessels occurred in both roots and stems. In *Donax, Halopegia, Hypselodelphis, Ischnosiphon, Marantochloa, Megaphrynium* and *Thaumatococcus* the root vessels have simple perforations, while in the remaining 10 genera they have scalariform perforations only. The perforation plates in the stem vessels are scalariform, except in *Hypselodelphis,* where there are simple ones as well.

The vessel characters of Zingiberales are less advanced than those of Commelinanae, and on a level with those of Asparagales and Liliales. Rather primitive perforation types are found in the roots of Strelitziaceae, Lowiaceae, Heliconiaceae, Musaceae and Costaceae, while vessels with primitive perforation plates also occur in the stems of one or two genera in Strelitziaceae and Costaceae. Zingiberaceae possess more advanced vessel types in the roots than do the other families, but vessels are found in the stems of one genus only. In *Canna* the roots have vessels with perforation plates of advanced type and simple perforations are rather frequent in the roots of Marantaceae. In the latter family, vessels in the stems are not uncommon in genera with well developed stems and therefore the vessel type of this family may be considered the most advanced within Zingiberales.

Typhanae

Typhales. Sparganium (Sparganiaceae) and *Typha* (Typhaceae) have vessels with scalariform perforation plates in roots, stems and leaves (Cheadle 1942). Neither the type nor the distribution of vessels contradict the often-assumed connection with Pandanales and agree with the condition found in various Commelinanae genera as well. In Arecales, with which group a certain affinity is also suggested, the vessels have more advanced perforation types in the roots and sometimes also in the stems, a fact which does not however exclude some kind of relationship. Typhales, if related to Arecales at all, must have separated from the ancestors of this order before the simple perforation type had developed. Similar considerations apply to the relationships with groups within Commelinanae. In Araceae (Arales) vessels with scalariform perforations are found only in the roots and as regards vessel anatomy this family is distant from Typhales.

Arecanae

Arecales. In 20 out of 26 palm genera investigated the root vessels had simple perforations, two (*Verschaffeltia* and *Chamaerops*) had mostly simple, and two (*Nypa* and *Chamaedorea*) scalariform perforations only (Tomlinson 1961 b). In 10 of the genera investigated the stem vessels had simple perforation plates, three had mostly simple, two simple and scalariform and 10 genera had exclusively scalariform perforation. In *Phytelephas* no vessels were found in the stem, although they were present in the leaves. Vessels with simple perforations are found in the leaves of *Plectocomia,* while vessels with simple and scalariform plates are present in *Calamus* leaves. In the leaves of the remaining species scalariform perforations prevail, while eight genera have reticulate as well. Cheadle (1942) found simple and scalariform perforation plates in the roots of 21 species (the simple perforation plates prevailed in the late metaxylem): in the stems he found vessels with simple and scalariform plates in eight species and vessels with scalariform alone in 15, and in the leaves of 22 species he found scalariform perforation plates.

In the palms the occurrence of vessels in roots, stems and leaves supports the assumed connection with Pandanales. In the latter order, however, the perforation plates are scalariform and it ought therefore be regarded as the more primitive. The vessel characters do not rule out affinities to groups within Poales and Cyperales.

Relationships with Cyclanthales seem to be more distant, because of the primitive vessel tracheids found in that order. Vessel features indicate no relationship of Arecales with Arales.

Pandanales. Freycinetia and *Pandanus* have vessels with scalariform perforations in roots, stems and leaves (Cheadle 1942). This does not contradict the assumed relationships with Arecales, Typhales and Cyclanthales.

Cyclanthales. In the roots and leaves of the genera of Cyclanthaceae studied vessel tracheids with very long scalariform 'perforation plates' are present, while in the stems only tracheids have been found (Fahn 1954 b). A connection with Pandanales, or perhaps with Arecales (in Arecales no stem vessels are present in *Phytelephas*) cannot be excluded. It must be emphasized, however, that the vessel tracheids represent a much more primitive type of conductive system than that found in Pandanales and Arecales.

Aranae

Arales. In Araceae *Acorus* and *Arisaema* have vessels with scalariform perforations in the roots. *Lemna* and *Spirodela* (Lemnaceae) are completely devoid of vessels (Cheadle 1942). If the occurrence of vessels only in the roots is regarded as a primitive feature (as suggested by Cheadle) it is hardly possible to derive Arales from the ancestors of Arecanae. On the other hand, a common origin with groups close to Asparagales does not seem unlikely. If the absence of vessels is regarded as a reduction, then it represents an advanced feature, in which case it would be more justifiable to derive Aranae from ancestors of Pandanales. A comparison of the vessel characters of Piperales and Arales (a connection between these two families is sometimes suggested) would lead to an absurd conclusion, however, since there is no proof that the conductive system in fact arose in the same way in these two families.

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Data base

The following table lists the types of perforation plates occurring in roots, stems and leaves of the monocotyledonous genera, for which information was found in the literature. The only results that can be accepted without reservation are those from papers in which information is given on the actual genera and species studied. Information given about the perforation types of families or tribes only, has been entered under the name of the family or tribe stated by the author. Cheadle often gives information about vessel types for a whole family, not for the individual genera. Therefore only those genera for which a detailed anatomical description is found are included in the table. Where information on specific genera is given, this has been inserted in the table under the generic name.

The descriptions have been standardized and classified into five groups (which coincide with those used by Cheadle). Results from papers in which the proportion of different perforation types are not given, have been classified by the present author if possible. If no information was given about the vessel characteristics of specific organs or genera, a blank entry has been made in the table.

Code to the table: si exclusively simple perforations – si>sc mostly simple perforations – sc=si scalariform and simple perforations in about equal numbers – sc>si mostly scalariform perforations – sc exclusively scalariform perforations – – absence of vessels demonstrated – + vessels present but perforation type unknown – sc* vessel tracheids. – Punctuation marks: , is used if a family or a genus comprises species deviating from each other as regards perforation types, / is used when conflicting evidence on the perforation type is found in the literature and ; is used if two perforation types are described from an organ without any information about their frequency. – is used if the perforation types vary between the classes noted.

Taxon	Root	Stem	Leaves
Alismatales			
Limnocharitaceae			
Hydrocleys	sc	–	–
Limnocharis	si=sc	–	–
Alismataceae			
Alisma	si>sc	–	–
Baldellia		–	–
Damasonium		–	–
Echinodorus	sc	–	–
Limnophyton	si>sc	–	–
Luronium	si>sc	–	–
Ranalisma		–	–
Sagittaria 2 spp.	si>sc	–	–
Wisneria	si>sc	–	–
Hydrocharitales			
Butomaceae			
Butomus	si>sc	–	–
Hydrocharitaceae			
Vallisneria	–	–	–
Elodea	–	–	–
Aponogetonaceae			
Aponogeton	–	–	–

Taxon	Root	Stem	Leaves
Zosterales			
Scheuchzeriaceae			
Scheuchzeria	sc	–	–
Juncaginaceae			
Triglochin	sc	–	–
Potamogetonaceae			
Potamogeton 5 spp.	sc	–	–
Ruppia	–	–	–
Zosteraceae			
Zostera	–	–	–
Zannichelliaceae			
Zannichellia	–	–	–
Najadales			
Najadaceae			
Najas	–	–	–
Dioscoreales			
Dioscoreaceae[1]	sc	sc	
Stemonales			
Stemonaceae			
Croomia	sc	–	–
Stemona	sc	sc	–
Stichoneuron	sc	sc?	–
Trilliaceae			
Medeola	sc	–	–
Paris 4 spp.	sc	–	–
Scoliopus	sc	–	–
Trillium 2 spp.	sc	–	–
Asparagales			
Smilacaceae	sc	sc,–	sc,–
Heterosmilax 4 spp.			sc,–
Rhipogonum 4 spp.			–
Smilax 7 spp.			
Philesiaceae			
Behnia	si>sc	–	
Eustrephus 2 spp.	si	sc/–	sc?/–
Geitonoplesium	si=sc/si>sc	sc	sc*/–
Lapageria	sc*/sc	sc*/sc	–
Luzuriaga 5 spp.	sc*/sc	sc*/sc	–
Philesia	sc*/sc	–/sc	–
Petermannia	sc	–/sc	–
Convallariaceae			
Convallarieae			
Convallaria	si>sc		–
Aspidistreae			
Aspidistra	sc	–	–
Polygonateae[2]	si=sc,sc>si	sc,–	–
Ophiopogoneae[3]	si=sc,sc	–	
Herreriaceae			
Herreria 4 spp.		sc	
Asparagaceae			
Asparagus 4 spp.	si	sc	
Ruscaceae			
Ruscus 2 spp.	sc	–	
Danae	sc	sc	
Semele	si	sc	
Nolinaceae			
Nolina	si?	–	sc

Taxon	Root	Stem	Leaves
Dracaenaceae			
Dracaena	si?	–	sc
Asteliaceae[4]	sc	–	–
Dianellaceae[5]	si=sc,si>sc	–	–
Phormiaceae			
Xanthorrhoeaceae			
Acanthocarpus	si	–	sc
Baxteria	sc?	–	–
Calectasia 2 spp.	si	–	–
Chamaexeros 2 spp.	si	–	–
Dasypogon 2 spp.	si	–	–
Kingia	sc	–	–
Lomandra 34 spp.	si	–	–
Xanthorrhoea 14 spp.	si	–/sc	sc
Hanguanaceae			
Hanguana		–	–
Asphodelaceae			
Asphodeleae p.p.	si	–,sc	
Agrostocrinum		sc	
Asphodelus		sc	
Bulbine 4 spp.		–	
Bulbinopsis		–	
Herpolirion		–	
Nanolirion		–	
Aloineae[6]	si	–	
Kniphofieae[7]	si=sc	–	
Anthericaceae			
Asphodeleae p.p.[8]	si	–,sc	
Anthericum		sc	
Arthropodium 2 spp.		sc	
Caesia 2 spp.		–,sc	
Johnsonieae[9]	si,sc	–,sc>si	–
Borya	sc		
Johnsonia		sc	
Tricoryne		sc>si	
Aphyllanthaceae	si>sc	–	–
Aphyllanthes			
Agavaceae			
Hosta 2 spp.	sc	–	–
Agave	si	–	–
Hemerocallidaceae			
Hemerocallis	sc	–	–
Hyacinthaceae			
Scilleae[10]	sc>si	–	–
Albuca 2 spp.	si=sc		
Camassia	si=sc		
Dipcadi	si=sc		
Drimia	sc		
Drimiopsis	sc		
Eucomis	sc		
Galtonia	si=sc		
Hyacinthus	sc		
Lachenalia 2 spp.	sc		
Litanthus	sc		
Muscari	sc		
Ornithogalum 3 spp.	si=sc		
Polyxena 2 spp.	sc		
Rhadamanthus	sc		

Taxon	Root	Stem	Leaves
Bowieeae[11]	sc	–	–
Miluleae			
Milula	si>sc		
Massonieae			
Massonia	sc		
Alliaceae			
Agapantheae	sc>si	–	–
Agapanthus 3 spp.	sc		
Tulbaghia 4 spp.	si		
Allieae[12]	si>sc	–	
Gilliesieae[13]	si=sc	–	–
Amaryllidaceae			
Galantheae[14]	sc	–	–
Amaryllideae[15]	sc	–	–
Crineae[16]	sc	–	–
Zephyrantheae[17]	sc	–	–
Haemantheae[18]	sc	–	–
Ixiolirieae	sc	–	–
Ixiolirion			
Eucharideae[19]	sc	–	–
Eustephieae			
Phaedranassa	sc	–	–
Hippeastreae[20]	sc	–	–
Narcisseae			
Narcissus 2 spp.	sc	–	–
Hypoxidaceae			
Campynema	–/sc?	–	–
Curculigo 2 spp.	sc	–	–
Hypoxis 7 spp.	sc	–	–
Pauridia	sc	–	–
Velloziaceae			
Barbacenia 3 spp.	si	–	–/sc
Barbaceniopsis	si	–	sc
Vellozia 2 spp.	si	–/sc	–/sc
Tecophilaeaceae[21]	sc	–	–
Liliales			
Colchicaceae			
Iphigenieae[22]	sc	–	–
Colchiceae			
Colchicum	sc	–	–
Anguillarieae[23]	sc	–	–
Uvularieae[24]	sc	–	–
Iridaceae			
Sisyrinchieae[25]	si	–,si>sc	–,sc
Sisyrinchium 4 spp.		si>sc	–,sc
Aristeae	sc,si>sc	–	–
Aristea 3 spp.	sc		
Klattia 2 spp.	sc		
Patersonia 3 spp.	sc		
Schizostylis	si>sc		
Witsenia	sc		
Tigrideae[26]	si	–	–
Irideae[27]	si	–	–
Ixieae[28]	si>sc	–	–
Croceae[29]	si	–	–
Gladioleae[30]	si	–	–
Antholyzeae[31]	si>sc	–	–
Alstroemeriaceae			
Alstroemeria 3 spp.	sc>si,sc	sc	–

Taxon	Root	Stem	Leaves
Bomarea 3 spp.	sc	sc	–
Leontochir		sc	–
Schickendantzia	sc	sc	–
Liliaceae[32]	sc	–	–
Melanthiaceae			
Narthecieae	sc	–	–
Aletris			
Veratreae[33]	sc	–	–
Tricyrtideae[34]	sc	sc	–
Heloniadeae[35]	sc	–	–
Petrosavia	–/sc	–	–
Triuridales			
Triuridaceae			
Andruris 4 spp.	–	–	–
Burmanniales			
Burmanniaceae			
Burmannia 2 spp.	sc	sc	sc
Thismiaceae			
Corsiaceae			
Orchidales			
Apostasiaceae			
Adactylus	si>sc	si=sc/–	
Apostasia		+	
Neuwiedia	si=sc/–?		
Cypripediaceae			
Cypripedium 11 spp.	si	–	
Paphiopedilum 7 spp.	–	–	–
Phragmipedium 5 spp.	si	–	–
Selenipedium 2 spp.	si	–	–
Orchidaceae			
Appendicula		+	
Dendrobium	+	–	
Dichaea		sc	
Epidendrum		–	sc
Habenaria		–	
Isochilus		+	
Neottia		+	
Oncidium		–	
Phalaenopsis		–	
Physosiphon		+	
Pleurothallis		+	
Pogonopsis	+		
Renanthera		–	
Scaphyglottis			sc
Thunia		+	
Vanilla 2 spp.	si	sc	
Vanda	+	–/+	
Haemodorales			
Haemodoraceae			
Haemodoreae[36]	si>sc	–	–
Dilatris	sc		
Lachnanthes		sc	sc?
Lanaria	sc		
Xiphidium		sc?	sc

Taxon	Root	Stem	Leaves
Conostyleae[37]	si>sc	–	–
Tribonanthes 3 spp.	sc		
Philydraceae[38]	sc	–	–
Orthothylax	sc	–	–
Taccales			
Taccaceae			
Schizocapsa	sc*	–	–
Tacca 3 spp.	sc*	–	–
Pontederiales			
Pontederiaceae			
Eichhornia 2 spp.	sc	–,sc	–
Heteranthera 3 spp.	sc	–,sc	–
Monochoria 6 spp.	sc	–	–
Pontederia 2 spp.	sc	–,sc?	–
Reussia	sc	–	–
Bromeliales			
Bromeliaceae			
Acanthostachys	sc	sc	sc
Aechmea	sc	sc,–	–
Ananas	sc	–	–
Billbergia	sc	–	–
Cryptanthus	sc	sc	sc
Dyckia	sc	sc,–	–
Guzmania	sc	sc	–
Hechtia	sc	sc	sc
Hohenbergia	sc	sc	sc
Neoglaziovia	sc	–	–
Nidularium	sc	–	–
Ochagavia	sc	–	–
Orthophytum	sc	sc	sc
Pitcairnia	si	sc	sc
Quesnelia	sc	–	–
Vriesia	si	sc	sc
Commelinales			
Commelinaceae			
Aneilema 8 spp.	si	si	si
Anthericopsis	si	si	si
Aploleia	si	si	si
Ballya	si	si	si
Belosynapsis 2 spp.	si	si	si
Callisia 6 spp.	si	si	si
Campelia	si	si	si
Cochliostema 2 spp.	si	si	si
Coleotrype	si	si	si
Commelina 10 spp.	si	si>sc	si>sc
Cuthbertia 2 spp.	si	si	si
Cyanotis 16 spp.	si	si	si
Dichorisandra 2 spp.	si	si	si
Floscopa 2 spp.	si	si	si
Forrestia	si	si	si
Geogenanthus	si	si	si
Gibasis 2 spp.	si	si	si
Hadrodemas			si
Murdannia 5 spp.	si	si	si
Palisota 4 spp.	si	si	si
Phaeosphaerion		si	si
Pollia 5 spp.	si	si	si
Polyspatha 2 spp.	si	si	si
Rhoeo	si	si>sc	si>sc
Setcreasea	si	si	si
Siderasis			si
Stanfieldiella	si	si	si
Tinantia	si	si	si
Tradescantia 12 spp.	si	si>sc/si=sc	si>sc/si=sc
Triceratella	si	si	si
Tripogandra 3 spp.	si	si	si
Zebrina	si	si/si=sc	si/si=sc
Mayacaceae			
Mayaca 3 spp.	sc	sc	sc*/sc?
Cartonemataceae			
Cartonema	si>sc	–	–
Xyridaceae			
Abolboda 3 spp.	si	si	si
Achlyphila	si	si	si
Xyris 30 spp.	si	si	si
Rapateaceae			
Rapateeae			
Cephalostemon	sc	sc	–
Duckea 3 spp.	sc	sc	–
Rapatea 7 spp.	sc	sc	–
Spathanthus 2 spp.	si	si	si
Monotremeae[39]	si=sc	si	–
Schoenocephalieae[40]	sc	sc	–
Saxofridericieae[41]	sc	sc	–
Eriocaulales			
Eriocaulaceae[42]	si>sc	si>sc	si>sc
Eriocaulon 8 spp.	si/sc?	si/sc?	sc
Tonina		sc	
Juncales			
Juncaceae	si–sc>si	si>sc–sc>si	si>sc–sc
Distichia 2 spp.	si>sc		sc/–
Juncus 28 spp.	si–sc>si	si>sc–sc>si	si=sc–sc
Luzula 12 spp.	si,si>sc	si=sc	si=sc,sc>si
Marsippospermum	sc>si	sc	sc
Oxychloe 3 spp.	sc>si	sc	sc
Prionium	sc>si	sc	sc
Rostkovia	sc	sc	sc
Thurniaceae			
Thurnia 2 spp.	sc>si/sc	sc	sc
Cyperales			
Cyperaceae			
Cariceae[43]	si>sc	sc>si–si=sc	sc>si
Carex* 45 spp.	si	si;sc	si,sc
Schoenoxiphium* 3 spp.	si;sc?	si;sc	si;sc
Uncinia* 4 spp.		si;sc	
Cryptangieae[44]	si>sc	sc>si,sc	sc>si,sc

Taxon	Root	Stem	Leaves
Afrotrilepis 2 spp.	si	si;sc	si;sc?
Calyptrocarya* 2 spp.	sc		
Cephalocarpus		si;sc	si
Coleochloa		si	si
Cryptangium°		sc	sc
Didymiandrum	si	sc	
Everardia°		sc	sc
Lagenocarpus* 2 spp.		sc	sc
Cypereae[45]	si>sc	si=sc–si>sc	sc>si–si=sc
Cyperus* 13 spp.		si;sc?	
Kyllingia 2 spp.		si;sc?	si;sc
Mariscus* 6 spp.		si	si;sc?
Pycreus 2 spp.		si	
Hypolytreae	si=sc–si>sc	sc>si	sc,sc>si
Chorizandra°			sc
Chrysithrix*	si;sc?	si;sc	si;sc
Hypolytrum 13 spp.	sc	sc	sc
Lepironia		si	
Mapania		sc	
Scirpodendron	si;sc	sc	
Rhynchosporeae[46]	si>sc	sc>si–si=sc	sc>si
Asterochaete		si	si
Carpha°			sc
Caustis* 3 spp.	si;sc?	si,sc	sc,sc>si
Cladium* 4 spp.	sc,sc>si	sc,sc>si	sc,sc>si
Costularia°			sc
Cyathochaeta*		si	si,sc?
Dichromena		si	
Elynanthus	si	si;sc	si
Epischoenus* 2 spp.	si	si	
Evandra		sc	
Gahnia* 5 spp.		si;sc	si
Gymnoschoenus*			si;sc?
Lepidosperma* 3 spp.	si,sc?		si
Machaerina* 3 spp.		si,sc?	sc/si;sc?
Macrochaetium		sc	
Mesomelaena* 3 spp.	si	si	si;sc?
Neesenbeckia		si	si;sc?
Oreobolus°		sc	sc
Ptilanthelium		si	
Reedia*	si	si;sc	si;sc?
Rhynchospora* 3 spp.		si	si
Schoenus* 6 spp.		si	sc
Tetraria* 4 spp.		si	si;sc
Tetrariopsis*		si;sc	si
Trianoptiles*		sc	si
Sclerieae[47]	si>sc	si=sc–si>sc	sc>si–si=sc
Scleria* 10 spp.		si;sc	si
Scirpeae[48]	si>sc	si=sc	sc>si–si=sc
Eleocharis* 4 spp.		si	
Eriophorum* 3 spp.		si	si
Ficinia* 4 spp.		sc	si;sc?
Fuirena		si	si
Lipocarpha* 2 spp.		si;sc	si;sc?
Scirpus* 14 spp.	si	si;sc	
Centrolepidales			
Centrolepidaceae			
Aphelia 4 spp.		sc	sc
Centrolepis 8 spp.		sc	sc
Gaimardia 3 spp.		sc	sc
Pseudalepyrum 2 spp.	sc	sc	sc
Trithuria 2 spp.	sc	sc	sc,–
Poales			
Restionaceae	si	si–sc	si>sc–sc
Anthochortus		sc	–
Calorophus 3 spp.	+	si	–
Cannomois 6 spp.	+	sc=si	–
Chaetanthus		si	
Chondropetalum	si	sc	–
Coleocarya		sc	
Dielsia 2 spp.		sc	
Elegia 21 spp.		sc	–
Harperia		sc	
Hopkinsia		si	–
Hypodiscus 9 spp.	+	sc=si	–
Hypolaena 7 spp.	+,si	sc,si	–
Lepidobolus 3 spp.	+	si	–
Leptocarpus 19 spp.	+	si,si>sc	–
Lepyrodia 17 spp.	+	sc=si	–
Loxocarya 6 spp.		+	–
Lyginia 2 spp.	+	sc	
Mastersiella 5 spp.	+	si>sc	–
Meeboldina		sc	
Onychosepalum		+	
Phyllocomos		sc	–
Restio 85 spp.	+,si	sc	–/sc*
Sporadanthus	+	si>sc	–
Staberoha 5 spp.	si	+	–
Thamnochortus 20 spp.	+	si	–
Willdenowia 8 spp.		sc,sc=si	–
Flagellariaceae			
Flagellaria		si>sc	sc>si
Joinvillea 2 spp.		si>sc	sc,si>sc
Ecdeiocoleaceae			
Ecdeiocolea	+	sc=si	–
Poaceae[49, 50]	si–si>sc	si–si>sc	si–si=sc
Zingiberales			
Lowiaceae			
Orchidantha 3 spp.	sc	–	–

Taxon	Root	Stem	Leaves
Strelitziaceae			
Phenakospermum	sc>si	sc	–
Ravenala 3 spp.	sc	–	
Strelitzia 5 spp.	sc	sc	–
Heliconiaceae			
Heliconia 7 spp.	sc	–	–
Musaceae			
Ensete 3 spp.	si=sc	–	–
Musa 7 spp.	si>sc	–	–
Zingiberaceae			
Aframomum	sc	–	–
Alpinia 4 spp.	si/sc	–	–
Brachychilum	sc	–	–
Boesenbergia	sc	–	–
Burbidgea	sc	–	–
Camptandra 2 spp.	sc	–	–
Catimbium 2 spp.	sc>si	–	–
Cautleya	sc	–	–
Curcuma 2 spp.		–	–
Elettaria	si=sc	–	–
Elettariopsis	sc>si	–	–
Geostachys	sc	–	–
Globba 4 spp.	sc	–	–
Hedychium 4 spp.	sc/–	–	–
Hornstedtia 2 spp.	sc	–	–
Kaempferia 6 spp.	sc	–	–
Renealmia 2 spp.	sc	sc	–
Roscoea 3 spp.	sc	–	–
Scaphochlamys 3 spp.	sc	–	–
Zingiber 2 spp.	sc	–	–
Costaceae			
Costus 9 spp.	sc	–	–
Dimerocostus	sc	sc	
Tapeinochilus	sc	–	–
Cannaceae			
Canna 5 spp.	si>sc	–	–
Marantaceae			
Ataenidia	sc		
Calathea 12 spp.	sc		
Ctenanthe	sc		
Donax	si		
Halopegia	si		
Hypselodelphis	si	si>sc	
Ischnosiphon	si		
Maranta 2 spp.	sc		
Marantochloa 6 spp.	si	sc	
Megaphrynium	si		
Monotagma 2 spp.	sc		
Phrynium	sc		
Sarcophrynium	sc	sc	
Stromanthe 3 spp.	sc		
Thalia 2 spp.	sc	sc	
Thaumatococcus	si	sc	
Trachophrynium	sc		
Typhales			
Sparganiaceae			
Sparganium 5 spp.	sc	sc	sc?
Typhaceae			
Typha 2 spp.	sc	sc	sc
Arecales			
Arecaceae			
Areca	si	sc	sc
Bactris 2 spp.	si	si	sc
Borassus	si	si	sc
Calamus 11 spp.	si	si	si=sc
Caryota 6 spp.	+	+	+
Chamaedorea	sc	sc	sc
Chamaerops	si>sc	si>sc	sc
Chrysalidocarpus	si	sc	sc
Coccothrinax			sc
Copernicia			sc
Corypha	si		
Cryosophila			sc
Daemonorops	si	si	sc
Elaeis	si	si	sc
Howeia	si	sc	sc
Hyphaene 2 spp.	si	si	sc
Latania	si		sc
Licuala	si	sc	sc
Livistona	si	sc	sc
Lodoicea			sc
Myrialepis		si	sc
Nannorhops			sc
Nypa	sc		
Paurotis			sc
Phoenix	si	sc	sc
Pholidocarpus			sc
Phytelephas	si	–	sc
Pinanga		sc	sc
Plectocomia	si	si	si
Pritchardia			sc
Ptychosperma	si	sc	sc
Raphia	si	si	sc
Raphidophyllum		si>sc	sc
Rhapis		sc	sc
Sabal			sc
Salacca	si	si	sc
Sclerosperma		si=sc	
Serenoa	si	si=sc	sc
Thrinax			sc
Trachycarpus		si>sc	sc
Trithrinax			sc
Veitchia			sc
Verschaffeltia	si>sc		
Wallichia	si		
Washingtonia			sc
Zombia			sc
Pandanales			
Pandanaceae			
Freycinetia	sc	sc	sc
Pandanus 2 spp.	sc	sc	sc

Taxon	Root	Stem	Leaves
Cyclanthales			
Cyclanthaceae			
Carludovica	sc*	–	sc*
Cyclanthus	sc*	–	sc
Ludovia	sc	–	sc
Arales			
Araceae[51]	sc		
Lemnaceae[52]	–	–	–

[1] *Dioscorea* (97 spp.), *Rajania* (4 spp.), *Tamus* (2 spp.), *Stenomeris* (2 spp.), *Avetra, Trichopus* – [2] *Clintonia, Drymophila* (2 spp.), *Maianthemum, Polygonatum, Smilacina* (2 spp.) – [3] *Liriope, Mondo* – [4] *Astelia, Milligania* (3 spp.) – [5] *Dianella* (4 spp.), *Stypandra* (2 spp.), *Walleria* – [6] *Aloe* (10 spp.), *Apicra* (3 spp.), *Chortolirion, Gasteria* (2 spp.) – [7] *Blandfordia* (2 spp.), *Kniphofia, Notosceptrum* – [8] Also *Chamaescilla, Chlorophytum* (2 spp.), *Chlorogalum, Dichopogon, Paradisea, Thysanotus* (2 spp.), *Xeronema* – [9] Also *Bartlingia* (3 spp.), *Sowerbaea* – [10] Also *Scilla* (2 spp.), *Urginea, Veltheimia* (2 spp.) – [11] *Bowiea, Eriospermum, Schizobasis* – [12] *Allium* (6 spp.), *Bloomeria, Brodiaea, Muilla, Nothoscordum* (2 spp.) – [13] *Miersia, Trichlora* – [14] *Galanthus, Leucojum* (2 spp.) – [15] *Amaryllis, Brunsvigia* (2 spp.), *Nerine* (4 spp.) – [16] *Ammocharis, Crinum* (6 spp.), *Cybistetes, Cyrtanthus, Vallota* – [17] *Cooperia* (2 spp.), *Gethyllis, Zephyranthes* (2 spp.) – [18] *Buphane, Clivia* (2 spp.), *Haemanthus* (2 spp.), *Strumaria* (2 spp.) – [19] *Calostemma, Eucharis, Eurycles, Hymenocallis, Stenomesson* (2 spp.) – [20] *Hippeastrum* (2 spp.), *Sprekelia* – [21] *Conanthera* (2 spp.), *Cyanella* (2 spp.), *Odontostomum, Tecophilaea* – [22] *Androcymbium* (2 spp.), *Ornithoglossum, Reya* – [23] *Anguillaria, Baeometra, Dipidax, Neodregea* – [24] *Gloriosa, Kreysigia, Schellhammeria, Uvularia* (2 spp.), *Walleria* – [25] *Bobartia, Diplarrhena, Libertia, Orthrosanthus* – [26] *Ferraria, Hexaglottis, Homeria* – [27] *Dietes, Hermodactylus, Iris* (7 spp.), *Moraea* (2 spp.) – [28] *Dierama* (2 spp.), *Freesia, Geissorhiza, Hesperantha, Ixia, Lapeyrousia, Micranthus, Pillansia, Watsonia* – [29] *Galaxia, Romulea* (2 spp.), *Syringodea* (2 spp.) – [30] *Babiana* (2 spp.), *Crocosmia, Gladiolus, Melasphaerula, Sparaxis* (2 spp.), *Synnotia, Tritonia* (3 spp.), *Tritoniopsis* – [31] *Anaclanthe, Anapalina* (3 spp.), *Antholyza, Curtonus, Petamenes* – [32] *Calochortus, Erythronium, Fritillaria, Lilium* (4 spp.), *Tulipa* – [33] *Veratrum, Zygadenus* – [34] *Sandersonia, Tricyrtis* – [35] Also *Chaemaelirion, Chionographis, Helonias, Ypsilandra* – [36] Also *Haemodorum* (4 spp.), *Phlebocarya, Wachendorfia* – [37] Also *Anigozanthos* (4 spp.), *Blancoa, Conostylis* (4 spp.), *Macropidia* – [38] Also *Helmholtzia, Philydrum, Pritzelia* – [39] *Maschalocephalus, Monotrema* (4 spp.) *Potarophytum, Windsorina* – [40] *Guacamaya, Epidryos, Schoenocephalium* (3 spp.) – [41] *Phelpsiella, Saxofridericia* (2 spp.), *Stegolepis* (2 spp.) – [42] Also *Lachnocaulon* (3 spp.), *Leiothrix, Paepalanthus* (4 spp.), *Syngonanthus* (2 spp.) – [43] Genera of Cyperaceae investigated by Cheadle & Kosakai and Metcalfe are marked *, whereas genera studied only by Cheadle & Kosakai are marked° and those mentioned only by Metcalfe are unmarked– [44] Also *Becquerelia** – [45] Also *Dulichium*°, *Remirea* – [46] Also *Tricostularia*° – [47] Also *Diplacrum*°, *Kobresia*° (2 spp.) – [48] Also *Bulbostylis*°, *Fimbristylis*° (2 spp.) – [49] Genera of Poaceae investigated (genera mentioned by Metcalfe (1950) and Cheadle (1955) are marked *, whereas genera studied only by Cheadle are marked ° and those mentioned only by Metcalfe are unmarked): *Acroceras, Aegilops* (3 spp.), *Aeluropus, Agropyron** (4 spp.), *Agrostis** (2 spp.), *Aira, Alloteropsis* (2 spp.), *Alopecurus* (3 spp.), *Ammophila**, *Ampelodesmos, Andropogon** (2 spp.), *Anomochloa, Anthochloa, Anthoxanthum**, *Apluda, Aristida* (5 spp.), *Arrhenatherum, Arthraxon, Arundinaria*°, *Arundinella* (2 spp.), *Arundo**, *Avena** (2 spp.), *Beckeropsis* (3 spp.), *Bothriochloa* (2 spp.), *Bouteloua**, *Brachiaria* (4 spp.), *Brachypodium* (2 spp.), *Bromuniola, Bromus** (8 spp.), *Brylkinia, Buchloe, Calamagrostis**, *Calamovilfa, Capillipedium, Catapodium, Cenchrus** (3 spp.), *Centotheca, Chloris** (6 spp.), *Chrysopogon, Cleistachne, Coelachne* (3 spp.), *Coelachyrum, Coix, Coleanthus, Cortaderia* (2 spp.), *Corynephorus, Cymbopogon* (5 spp.), *Cynodon* (3 spp.), *Cynosurus, Cyrtococcum* (2 spp.), *Dactylis**, *Dactyloctenium* (2 spp.), *Danthonia** (16 spp.), *Deschampsia**, *Desmostachya, Deyeuxia, Diarrhena, Dichanthium* (3 spp.), *Dichelachne, Digitaria** (5 spp.), *Dimeria, Distichlis, Echinochloa** (2 spp.), *Ectosperma, Ehrharta* (2 spp.), *Eleusine* (2 spp.), *Elymus* (6 spp.), *Elyonurus* (2 spp.), *Enneapogon, Eragrostiella, Eragrostis* (6 spp.), *Eriachne, Erianthus, Euchlaena, Euchlaezea, Euclasta, Eulalia* (2 spp.), *Festuca* (5 spp.), *Fingerhuthia, Garnotia, Glyceria** (2 spp.), *Gymnopogon* (4 spp.), *Gynerium*°, *Hakonechloa, Helictotrichon* (3 spp.), *Hemarthria, Heteranthelium, Heteranthoecia, Heteropogon, Hierochloe* (2 spp.), *Hilaria*°, *Holcus** (2 spp.), *Hordelymus, Hordeum** (4 spp.), *Hyparrhenia, Imperata, Indopoa, Isachne* (3 spp.), *Ischaemum* (2 spp.), *Koeleria* (2 spp.), *Lagurus, Lamarckia, Leersia** (2 spp.), *Leptaspis, Leptocarydion, Leptochloa* (2 spp.), *Lolium**, *Lophatherum, Loudetia* (2 spp.), *Lycochloa, Lygeum, Megastachya, Melica** (3 spp.), *Melinis, Micraira, Microlaena, Microstegium, Miscanthidium, Miscanthus* (2 spp.), *Molinia* (2 spp.), *Muhlenbergia**, *Munroa, Nardus, Neurolepis* (2 spp.), *Neyraudia*°, *Olyra, Oplismenus* (2 spp.), *Orcuttia, Oropetium, Oryza, Oryzopsis** (3 spp.), *Panicum** (7 spp.), *Parapholis, Pariana* (3 spp.), *Paspalidium, Paspalum** (4 spp.), *Pennisetum* (2 spp.), *Pentapogon, Perotis* (2 spp.), *Phaenosperma, Phalaris** (3 spp.), *Pharus, Phleum**, *Phragmites**, *Phyllorachis**, *Plectrachne* (3 spp.), *Pleioblastus*°, *Pleuropogon*°, *Poa** (3 spp.), *Pogonarthria, Pogonatherum, Polypogon* (2 spp.), *Pommereulla, Psammochloa, Pseudanthistiria, Puccinellia* (2 spp.), *Rhynchelytrum, Rhytachne, Richardsiella, Rottboellia, Saccharum* (3 spp.), *Sacciolepis* (4 spp.), *Schizachyrium, Secale**, *Setaria** (5 spp.), *Sieglingia, Snowdenia, Sorghum**, *Spartina** (2 spp.), *Sphaerocaryum, Spinifex, Sporobolus** (9 spp.), *Stenotaphrum* (2 spp.), *Stipa* (6 spp.), *Streptochaeta, Streptogyna, Tetrarrhena, Themeda* (4 spp.), *Thysanolaena**, *Tragus* (2 spp.), *Tridens?, Trikeraia, Triplopogon, Tripsacum**, *Triraphis, Trichachne, Tristachya* (2 spp.), *Triticum** (3 spp.), *Uniola, Urochloa, Vetiveria, Zea**, *Zizania** – [50] Genera of Bambuseae investigated: *Arthrostylidium* (2 spp.), *Arundinaria* (12 spp.), *Atractocarpa, Bambusa* (2 spp.), *Cephalostachyum, Chloothamnus, Chusquea** (2 spp.), *Dendrocalamus** (2 spp.), *Dinochloa, Gigantochloa, Greslania, Guadua, Guaduella, Melocalamus, Melocanna, Merostachys, Nastus* (2 spp.), *Ochlandra, Oreobambos, Oxytenanthera, Phyllostachys** (6 spp.), *Pseudostachyum, Puellia, Schizostachyum, Shibataea* (2 spp.), *Thyrsostachys* – [51] *Acorus, Arisaema* – [52] *Lemna, Spirodela.*

Morphology and intraspecific variation in Geastrum triplex Jungh.

Stellan Sunhede

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Swedish material of *Geastrum triplex* Jungh. has been studied in the field and in the laboratory. The morphology and intraspecific variation of mature or nearly mature fruitbodies are described and illustrated with photographs and drawings. More than 3150 fruitbodies have been investigated. SEM-pictures show spores, capillitial threads and the surface of the endoperidium. The use of the name *Geastrum triplex* Jungh., instead of *G. indicum* (Klotzsch) Rauschert, is explained.

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The author has studied the biology and collected fruitbodies of *Geastrum* species in southern Sweden during more than 450 days in the field the last seven years (mainly September–December). Especially the islands of Öland, Gotland and Gotska Sandön have been investigated. This is the second paper discussing the morphology and intraspecific variation in mature or nearly mature fruitbodies of Swedish species of *Geastrum*. An earlier paper (Sunhede 1974 b) dealt with *G. umbilicatum* Fr.; in that paper the great variation in different characteristics of mature fruitbodies of *Geastrum*, as well as the importance of field experience, was pointed out.

The material of *Geastrum triplex* Jungh. examined in this study comprises c. 2700 specimens from the author's herbarium and c. 450 specimens from GB, LD, S, UPS and UPSV. For methods, see Sunhede (1974 b). Unless otherwise stated, all measurements of fruitbodies have been made on dry specimens. Routine investigations with the microscope have been performed in 2% KOH, in lactic blue and Melzer's reagent. All measurements reported were made in KOH. Spores were also measured in lactic blue. There was no significant difference in spore measurements between KOH and lactic blue preparations. I prefer the KOH preparations because the spore outline is more distinct. The basidial development in *G. triplex* will be discussed in a forthcoming paper.

Exoperidium

Young fruitbodies, just prior to opening, are often partly or wholly visible on the ground (Fig. 2 A, B). They are rounded with a small tip at the top, more or less onion-shaped, rarely irregular, light brownish and 1.5–6 cm broad or more (Figs. 2 A, B, E, F; 4 C; 5 A: j). At the base of loosened, unexpanded specimens there may be a mycelial tuft consisting of whitish hyphae intermixed with debris (Fig. 4 C: b, e, f, j, k). The exoperidium splits from the apex in a stellate manner, more or less deeply, into 3–10 (mostly 5–7) regular or irregular rays of varying shape (Figs. 2 A, B, C; 4 B: c; 5 B; 7 B). The rays often recurve under the unsplit part of the exoperidium (Figs. 1 B, D, F, 3 A: d–j; 4 A: a, c, B: b, d, f) but may also take up other positions (Figs. 3 A: a, B; 4 B: c; 5 A: d). The margins of the rays may be recurved (Figs. 3 A: a, 4 A: a, c, B: c). The rays are non-hygroscopic.

The exoperidium of expanded fruitbodies may be saccate (Figs. 1 A, D; 4 B: a, b; 5 A: f, h), somewhat saccate (Fig. 5 A: d, e, i), plane (Fig. 5 A: c, g) or arched (Figs. 1 F, 4 A: a, c; 5 A: a, b). The frequency of the different shapes is illustrated in Fig. 7 B. The maximal diameter of expanded fruitbodies (cf. Fig. 3 A) varies between 2.3. and 15.1 cm. A specimen with the

exoperidium forced out into stellate configuration (cf. Fig. 5 B) had a maximum diameter of 18 cm. When collected in the field (as rather fresh) the corresponding diameter was 22.4 cm.

The fleshy pseudoparenchymatic layer in a fresh, just opened fruitbody is whitish to sordid white and up to 5 mm thick or more. The colour changes with age to pale buff to brown of different shades. Older specimens (Fig. 1 E, F) are dark brown. In expanding fruitbodies the central region of the fleshy layer often breaks loose from that of the rays (Fig. 2 C) forming a collar or a cup around the endoperidium (Figs. 1 A–D, F; 4 A: a, c, d). The pseudoparenchymatic layer of the rays may crack in different ways or peel off. With wet conditions in nature the fleshy tissue seems to gelatinize gradually but it may persist for a long time. When drying the fleshy layer shrinks, becomes hard and brittle, and its colour changes to some degree.

The middle, fibrous layer of the exoperidium is rarely – even in old specimens – totally free from pseudoparenchymatic and mycelial remnants. When free (Fig. 4 B: e) it is pale brownish to dirty grey and papery coriaceous.

The third and the outermost layer, the mycelial stratum, is brownish, rather thick and persistent. It often cracks radially in a characteristic pattern (Fig. 3 C), or sometimes more irregularly. The mycelial layer may begin to crack in unexpanded fruitbodies (Fig. 2 B, arrows). Generally, it is free or nearly free from dirt and debris (Fig. 2 A, B). The basal mycelium (cf. Fig. 4 C: b) leaves a scar at the point of attachment when the expanding fruitbody is loosened from the ground (Figs. 3 C; 4 B: d).

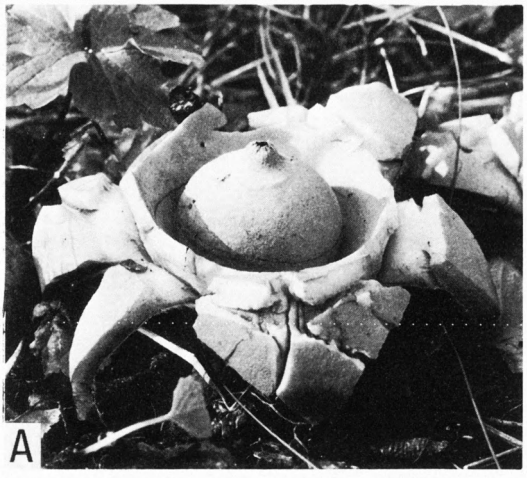
Endoperidium

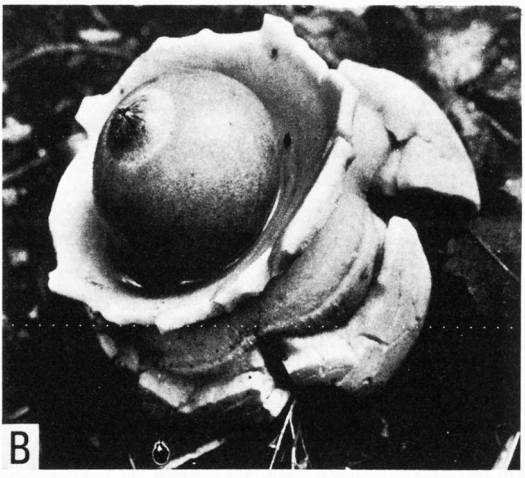
The endoperidium is often sessile. A short pedicel (stalk) may be seen when the fleshy layer of the exoperidium has disappeared (Figs. 4 B: e; 5 A: i; 6 A: b, c, B: k). The pedicel is rounded to oblong in cross section. The endoperidium is generally more or less globose, but may be depressed globose, depressed, laterally compressed, pyriform, obpyriform, oblong (seen from above) or irregular. The size, shape and position of the peristome also influence the general shape of the endoperidium. Examples of the variation in size and shape are given especially in Figs. 3 A; 5; 6 A but also in Figs. 1; 2 A, C; 3 D, E; 4 A, B. An apophysis occurs rarely (Fig. 6 B: k). The maximum diameter of the endoperidium is 10.8–54 mm and the height (normal peristome included) is 10–41 mm. The outer side of the endoperidial wall is smooth. The colour is generally of rather pale greyish or pale brownish shades or sometimes seemingly darker brown due to spore deposits. Argillaceous endoperidia are rarely observed. Endoperidia with dark areas or spots of unknown origin have been observed in a few specimens (Fig. 3 E).

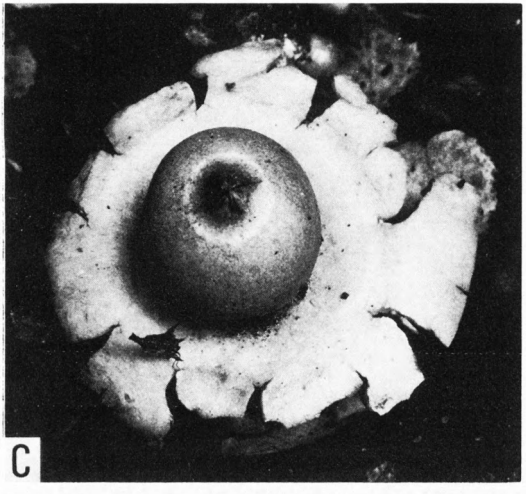
There is normally one stoma, usually at the top of the endoperidium, but specimens with two and six stomata have been observed (Figs. 3 D; 6 A: p, q). A stoma is rarely lacking (Fig. 6 A: g). Besides the true stoma there may be one or more regular holes in the endoperidial wall, made by insects, e.g. the beetle *Lycoperdina succincta* L. Such holes function in spore liberation (Sunhede 1974 a).

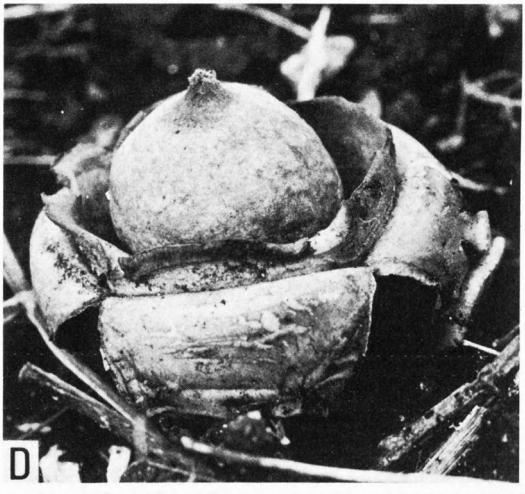
The peristome is mostly fibrillose. It is often well delimited (definite) from the rest of the endoperidium, due to different colour (darker or lighter) and/or through topographical demarcation (Figs. 1 B, C; 2 A, C, D; 3 A: a; 6 B: a, b, d–j). It is sometimes indefinite (Figs. 1 D, E; 6 B: c). The normal peristome is often more or less mammiform (Figs. 1 A–E; 4 A: a, c, d; 6 A: a–c) and up to 6 mm high. It is sometimes prolonged into a beak (Figs. 1 F; 2 D; 6 A: k, B: i). The peristome field is more or less circular (up to 15 mm or more in diameter) but may be oblong (Fig. 6 B: g, j). Occasionally there is only a

Fig. 1. *Geastrum triplex*. Fully expanded fruitbodies, in natural habitat, most of them with the rays recurved under the exoperidial discs. – A–C: Fresh specimens with an intact, whitish fleshy layer. – D: Rather fresh fruitbody where the fleshy layer has nearly dried up. – E, F: Older specimens with a dark-brown fleshy layer. – A, D, E: Exoperidia saccate. – B, C, F: Exoperidia arched. – A–F: The central part of the fleshy layer has formed a collar around the endoperidium. The collar may be deeply cup-shaped (A, B, D), shallowly cup-shaped (F) or plane (C). The collar in (C) is cracked at its margin. – A–C, F: Specimens with a well defined peristome field. – D, E: Endoperidium with an indefinite peristome-field. – A–E: Endoperidia with mamilla-like peristome. – F: Endoperidium with the peristome prolonged into a beak. – A, D: Bohuslän, Marstrand 14.X.1974. – B, C: Västergötland, Göteborg 10.X.1974. – E, F: Gotland, Bunge parish 4.XII.1972. Photo: Stellan Sunhede.

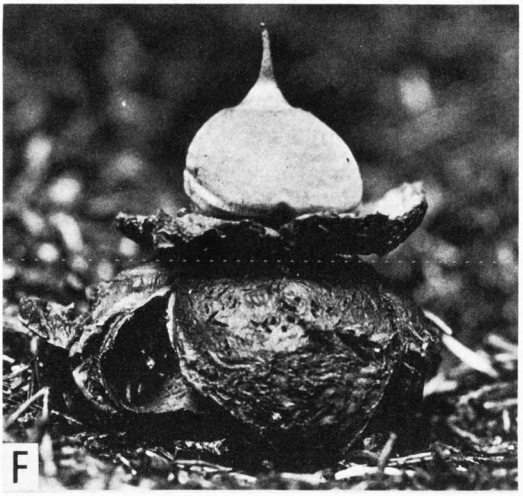

A


B


C


D


E


F

simple hole surrounded by the non-fibrillose endoperidial wall (Fig. 6 A: h, i). Examples of the shape, height and position of the peristome are given especially in Figs. 1; 2 D; 5 B and 6.

From the inner side of the endoperidial wall capillital threads radiate towards a central capillitial mass emerging from a pseudocolumella (Fig. 7 A: a, b, d). Capillitial threads from the top of the pseudocolumella may occasionally be so long that a bundle of them protrudes through the stoma. In vertical section through the center of the pseudocolumella, it appears to be more or less club-shaped or sometimes rounded (Figs. 2 E: e, F: e; 7 A: a, b, d, e, h). In cross section it is normally round to oblong (Fig. 7 A: c, f, g, i).

Microscopic characteristics

The *spores* are normally globose and, including the processes, the diameter is (4–)4.5–5.5(–6) μm. Smaller but not fully developed spores have been observed. The processes vary in shape and size. They are often high warts with a more or less flat top, but may be plate- or ridge-shaped (straight or curved) and have a height reaching 3/4 μm. Younger spores are cyanophilous but most of the fully developed, well pigmented spores do not stain blue. Their reaction in Melzer's reagent appears to be negative. The colour of the spore wall in KOH is yellow-brown. The processes have a darker tint.

The SEM pictures (Fig. 8 A–C) show the processes to be cylindrical or somewhat conical with rounded or flat, often expanded, tops. Sometimes the processes coalesce. The sides may be furrowed and there may be root-like ridges at the base of the processes.

The brown *capillitial threads* are more (Fig. 7 A: l) or less thick-walled, have gradually narrowing tips (Fig. 7 A: m) and a diameter of (1.5–)2–9(–11) μm. They may be smooth or nearly so or have a cyanophilous cover of warts or matter of different shapes (Figs. 7 A: l, m; 8 D–F). They do not stain in Melzer's reagent. Their colour in KOH is yellow-brown.

In a vertical section through the centre of the endoperidium the whitish *pseudocolumella* clearly stands out against the brown mass of capillitial hyphae and spores (Fig. 2 E). The hyphae of the pseudocolumella gradually pass into capillitial threads so that there is no distinct border to the pseudocolumella in a mature fruitbody (Figs. 2 E; 7 A: a, b, d). The interwoven hyphae from the centre of the tough pseudocolumella are thick-walled, cyanophilous and (1.5–)2–7.5 μm broad.

The hyphae of the *endoperidial wall* (Figs. 7 A: n, o; 8 A) are thick-walled and (1.5–)2–5(–7) μm broad.

The *pseudoparenchymatic layer* of the exoperidium consists of bladder-like cells (Fig. 7 A: p) of varying sizes. The hyphae of the *fibrous layer* are thick-walled (like those in Fig. 7 A: n, o), cyanophilous and 2–6(–8) μm broad. The *mycelial layer* is built up of thin-walled (or slightly thick-walled) hyphae with clamp connections (Fig. 7 A: j, k) and (1.5–)2–5(–6) μm broad. Similar hyphae are sparsely distributed on other sites of the fruitbody (cf. Fig. 8 A, arrow).

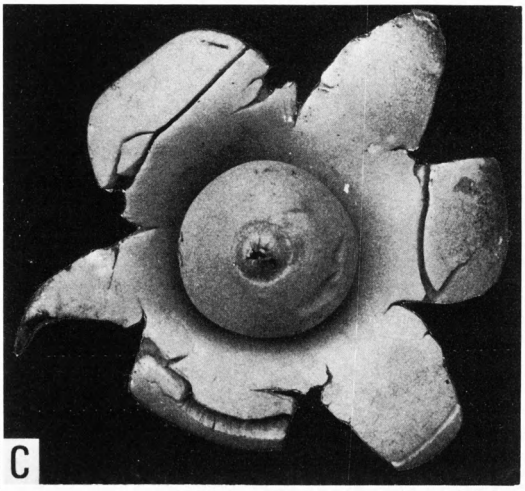
Discussion

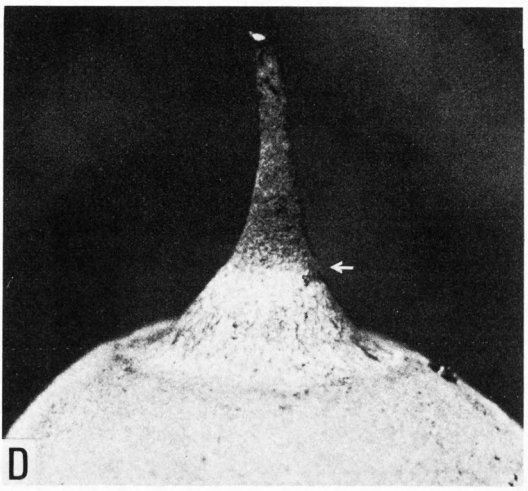
Junghuhn (1840 p. 287) described *Geastrum triplex* (ut *Geaster*) on specimens from Java. I have examined the type collection (Herb. F. Junghuhn in H. L. B. No. 97) kept in Leiden. It consists of one divided, unexpanded, onion-shaped specimen and eight expanded ones. The specimens are severely damaged, possibly due to insects. In five of them there is no endoperidium (except some remnants in two fruitbodies). On the four remaining specimens the peristome and other parts of the endoperidial wall are

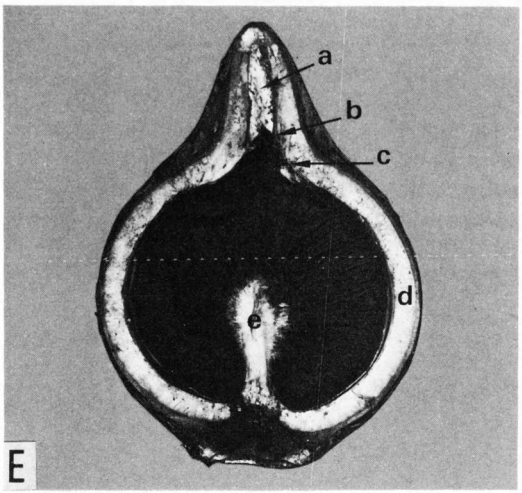
Fig. 2. *Geastrum triplex*. Fruitbodies. – A, B: Young epigeal fruitbodies in natural habitat. – A: Two onion-shaped specimens and one where the exoperidium has recently split to expose an endoperidium with a well defined mouth area. – B: Young onion-shaped fruitbody just splitting at the top. Note the cracks in the mycelial layer (arrows). – C: Fresh expanded specimen where the central part of the fleshy layer begins to break loose from that of the rays. – D: Endoperidium with a beak-like peristome. The arrow marks the height of a normal peristome, compare (b) in (E) and (F). Note the well defined peristome field. – E, F: Vertical sections through the centre of two young fruitbodies where the exoperidium still enclose the endoperidium and the gleba. (d) fleshy layer of the exoperidium and (e) pseudocolumella. – E: Prominently onion-shaped fruitbody where the peristome is prolonged into a beak (a), like that seen in (D). (b) and (c) correspond to the same letters in (F). – F: Subglobose fruitbody with an almost mature gleba. The arrows (b) and (c) mark the height of the peristome. – A, B: Bohuslän, Marstrand 14.X.1974. – D: Sunhede 5600. Photo: Stellan Sunhede.

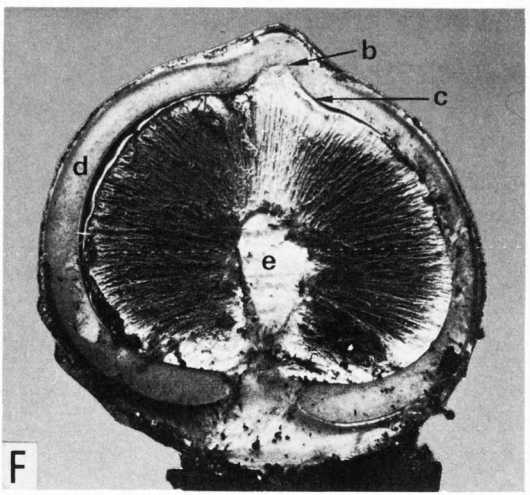

A


B


C


D


a
b
c
d
e
E


b
c
d
e
F

destroyed. In all the expanded specimens there are remnants of a pseudoparenchymatic collar. Fig. 3 on Junghuhn's plate also shows a deep pseudoparenchymatic cup around the endoperidium. The peristome of the endoperidium on his Figs. 2 and 3 is very similar to that of Fig. 6 B: a in this paper.

Palmer (1968 p. 116) notes: "Junghuhn's plate shows a deeply cupulate specimen with a blue endoperidium which I have never seen in European specimens". In Swedish specimens, I have not observed endoperidia with that pale bluish-grey colour that is shown on Junghuhn's Figs. 2 and 3, but pale grey or whitish grey endoperidia occur. The colour of the endoperidial wall of the fruitbodies in the type specimen is brownish but there are areas with a whitish or greyish tint. In the light microscope there seems to be a slight difference in the spore ornamentation compared with most spores in Swedish specimens. I do not think that this difference is taxonomically significant.

Palmer, who examined part of the type collection, noted: "... found it so severely insect-damaged that, although it looked like what I would call *G. triplex,* I was reluctant to form any definite conclusions". We have to be careful when dealing with incomplete fruitbodies of *Geastrum*. However the similarities between the Swedish specimens and the type (together with Junghuhn's description and Figs.) are so great compared with the differences mentioned that I consider them to be the same taxon. The best preserved specimen in the type collection is designated as lectotype.

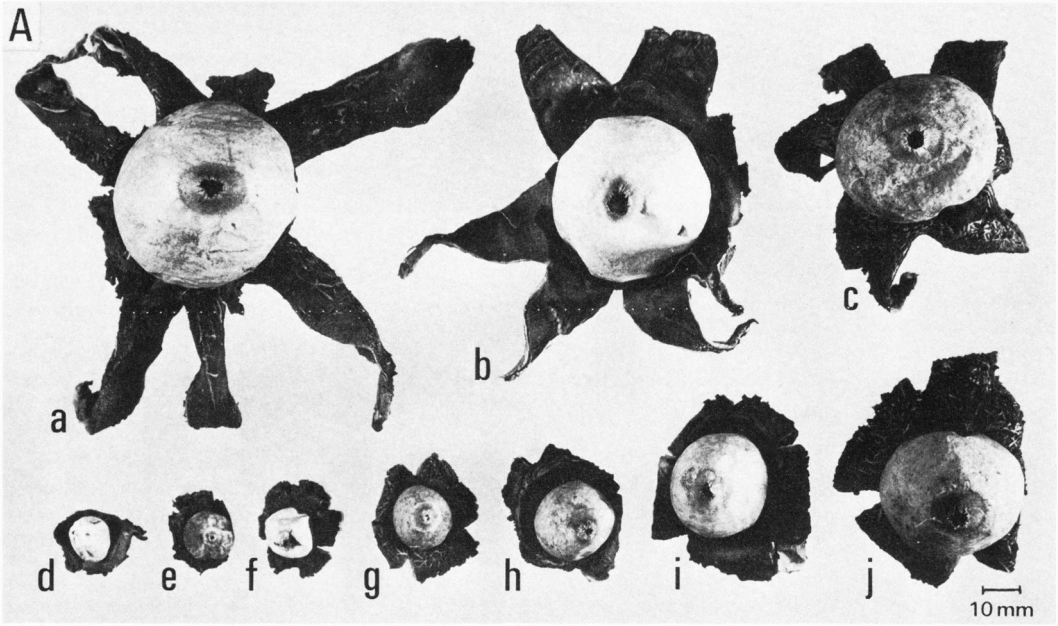
Klotzsch (1832) described *Cycloderma indicum* om material from "India occidentali". Hollós (1904 p. 53) who examined the material in Berlin stated that it was an immature fruitbody of *Geastrum triplex* Jungh. Lloyd (1904) was not sure of the identity of *C. indicum* but was of the opinion that it could not be an unopened *G. triplex*. Rauschert (1959) made the combination *Geastrum indicum* (Klotzsch) Rauschert on the basis of Hollós's (1904) report. The type of *Cycloderma indicum* was probably destroyed during the second world war (Palmer 1968). The description and the figures by Klotzsch are not detailed enough to show whether the fungus is *G. triplex* or another fungus. The epithet *indicum* can be considered to be a nomen dubium.

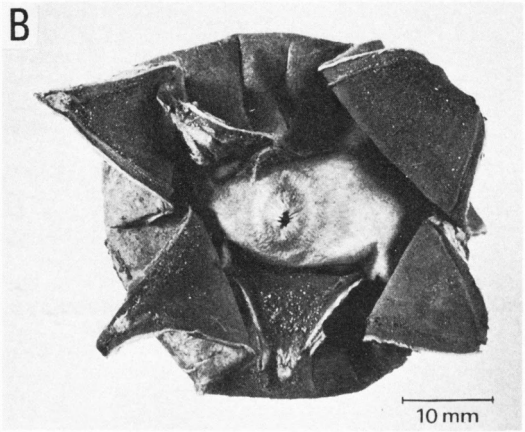
Unexpanded fruitbodies of *G. triplex* may have a root-like basal plug of mycelium and debris. I have seen this only on a Hungarian specimen growing on sandy soil near Pécs. Rounded young unexpanded fruitbodies (Fig. 4 C: e, i) show in section a normal mammiform mouth (Fig. 2 F). Young prominently onion-shaped fruitbodies (Fig. 4 C: a, b) show in section a mouth prolonged into a beak (Fig. 2 E: a). This beak normally breaks when the exoperidium bursts and remnants of it may sometimes be seen at the end of the rays. Such specimens were called *G. cryptorhynchus* by Hazslinszky (1874, 1876). Sometimes, however, the beak remains intact even in expanded specimens (Fig. 1 F; 2 D; 6 A: k, B: i). The beak is not hollow. Remnants of it may remain as a plug in the stoma (Fig. 6 B: f, h). Specimens where the exoperidial rays are prolonged into slender tips (Fig. 5 B: b, c) originate from prominently onion-shaped young fruitbodies.

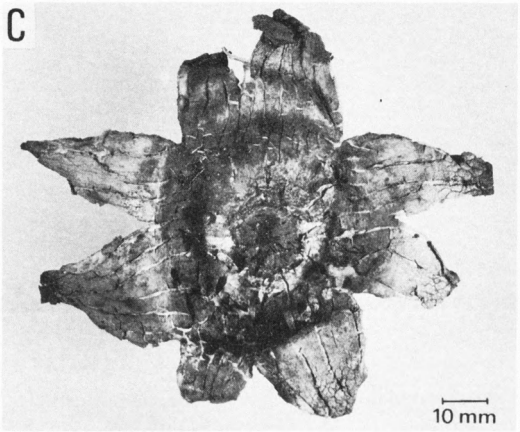
Most of the fully expanded specimens of *G. triplex* have a pseudoparenchymatic collar or cup. Such "triplex-collars" or "cups" may, even though rather rare, be present in other non-hygroscopic species of *Geastrum*. I have observed this phenomenon in *Geastrum coronatum* Pers., *G. fimbriatum* Fr., *G. minimum* Schw., *G. quadrifidum* Pers., *G. rufescens* Pers., *G. umbilicatum* Fr. (Sunhede 1974 b) and *Trichaster melanocephalus* Czern.

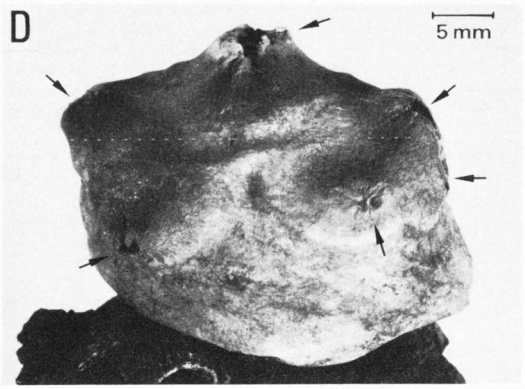
As a deviation from the normal the endoperidium of *Geastrum* spp. may have two or more peristomes. Staněk (1952 a, b) reports this deviation in nine species from Czechoslovakia. The phenomenon seems to be rare in *G. triplex* where only five specimens with two and one

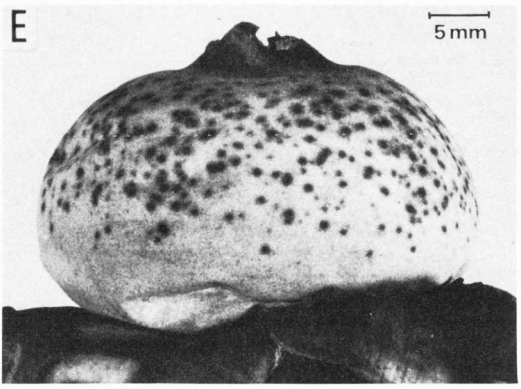
Fig. 3. Fruitbodies of *Geastrum triplex*. All, except (E), are dry. – A: Variation in size of fruitbodies, specimens rather old and dark. All, except (a), have some or all of their rays recurved under the exoperidial discs. (a) with an elliptical well-defined peristome field. – B: Fruitbody which has dried during the splitting of the exoperidium and where the rays have bent (back) over the endoperidium. – C: Specimen seen from below, where the exoperidial rays under wet condition have been forced into one plane. Note the radiating cracks in the mycelial layer and the dark central scar where the fruitbody was earlier attached to the mycelium in the ground. – D: Polystomatous fruitbody with six stomata (arrows). – E: Endoperidium (wetted) with dark areas and dots of unknown origin. – D: Sunhede 2102. – E: Sunhede 5588. Photo: Stellan Sunhede.


A
a
b
c
d
e
f
g
h
i
j
10 mm


B
10 mm


C
10 mm


D
5 mm


E
5 mm

with six stomata (Figs. 3 D, 6 A: p, q) were found among 3150 specimens examined.

For further information concerning *G. triplex* the reader is referred to Hollós (1904), Lohwag (1929), Palmer (1955, 1968), Staněk (1958), Demoulin (1968), Reid (1976), Boiffard (1976) and literature cited in these works.

The investigation has shown that the morphological variation within *G. triplex* is unexpectedly large and that no character alone is quite reliable för determinations. When normally developed the fungus is characteristic and easily determined, but for less experienced observers deviating specimens may be difficult to recognize, especially when they grow singly. I have not found any significant variation between fruitbodies from different mycelia except that in size a.s.o. directly depending on humidity and fertility of the soil, nor any geographical variation in the Swedish material of *G. triplex*. There is no reason to believe that Swedish specimens named *G. triplex* represent more than one taxon.

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– 1974 b: Studies in Gasteromycetes. II. Notes on the morphology and intraspecific variation in Geastrum umbilicatum Fr. *Bot. Notiser 127:* 376–391.

Fig. 4. Fruitbodies of *Geastrum triplex*. – A: Fresh specimens. (a) with a deep pseudoparenchymatic cup around the endoperidium, (d) with a shallow cup and (c) with a disc-shaped collar. (b) is a longitudinal section through the right ray in (a). The thick black line in the section represents the mycelial and fibrous layer of the exoperidium and the clear area the pseudoparenchymatous tissue. (a, c, d) the margins of at least the basal halves of the rays are recurved. – B: Dry fruitbodies. (a, b, f) rather small, saccate to somewhat saccate specimens where no pseudoparenchymatic collar has developed. (c) old fruitbody, where the margins of the rays are enrolled from both edges. (d) specimen seen from below with the rays recurved under the exoperidial disc. Note the central mycelial scar. (e) fruitbody with only the fibrous layer of the exoperidium and a short endoperidial stalk (arrow) remaining. – C: Shape and size of young fruitbodies. (a–f, i–k) fresh and (g, h, l, m) dry specimens. (g, l) one fruitbody seen from different angles. (b, e, f, j, k) specimens with basal mycelial tufts.

Fig. 5. *Geastrum triplex*. Dry fruitbodies, simplified drawings. – A: (a–i) vertical sections through the axis of fruitbodies showing the curvature of the exoperidium and the position and to some extent the shape of the endoperidium (dotted area). (c, d) with a prominent pseudoparenchymatic collar. (i) slightly stalked endoperidium. (a, b) exoperidium arched, (c, g) exoperidial disc plane or nearly so, (d, e, i) somewhat saccate and (f, h) prominently saccate. (j) young fruitbody (Hungarian specimen) with a root-like plug of whitish hyphae intermixed with debris. – B: Fruitbodies (from above) where the exoperidia under wet conditions have been forced into a horizontal plane. Note the more or less regular splitting of the exoperidium, the depth to which it has been cleft, the shape of the rays and the form of the endoperidia. (b, c) exoperidial rays with slender tips. – A: j Sunhede 3575.

Fig. 6. *Geastrum triplex*. – A: Variation in shape and size of endoperidium and peristome shown in side views (a–p) and top views (q–s). All endoperidia are dry except that in (c) which is wetted and has swollen. (b) dry state of specimen in (c). (l, m) and (p, q) two fruitbodies in different wiews. (a–p) position of exoperidium only indicated. (b, c) short-stalked endoperidium. (g) specimen with no stoma, (p, q) with two stomata. (h) endoperidium with an irregular hole in the wall. (k) endoperidium with a prolonged peristome. (o) endoperidium with a hat-shaped rest of the exoperidium covering the mouth. – B: (a–j) details of different types of peristomes. All specimens dry except that in (b). (a) is the same specimen as (b). Note the fringed peristome edge in (a). (a, b, d–j) endoperidia with a more or less definite peristome-field. (c) with an indefinite peristome-field. (f, h) stoma plugged with hyphae from the region marked with (a) in 2 E. (g, j) one specimen with an elongated peristome-field seen in different views. (i) peristome prolonged into a beak, partly covered with a hat of exoperidial remnants. (k) dry specimen with an apophysis and with a short endoperidial stalk.

Fig. 7. *Geastrum triplex*. – A: Shape of the pseudocolumella and microscopical characteristics. (a, b, d) vertical sections through the centre of the endoperidium and through the exoperidium showing the shape of the pseudocolumella. Capillitial threads from the inner side of the endoperidial wall radiate towards a central capillitial mass emerging from the pseudocolumella. (c, f, g, i) are horizontal sections through the broadest part of pseudocolumellas. (e, h) side views of a flat pseudocolumella from different angles. (j) young thin-walled and (k) somewhat thick-walled older clamp-bearing hyphae from the mycelial layer. (l) part of a thick-walled capillitial thread with a narrow lumen and with cyanophilous matter on the surface. (m) end of a capillitial thread with well-defined cyanophilous matter on the surface. (n, o) thick-walled hyphae from the endoperidial wall. (p) section through the fleshy layer of a fresh specimen showing bladder-like hyphal cells. – B: Diagrams showing variation of different characteristics of the fruitbody. The analyzed characteristics are: number of exoperidial rays, hape of exoperidium (see below) and largest diameter of endoperidium. s = saccate, [s] = somewhat saccate, p = plane and a = arched.

Fig. 8. *Geastrum triplex*. SEM photos of endoperidial surface, spores and capillitial threads. – A: Endoperidial surface with spores. Most of the hyphae are thick-walled, the arrow points at a thin-walled collapsed hypha. – B, C: Spores from Swedish specimens except that in C: c which is from the type specimen. – D, E, F: Segments of capillitial threads covered with irregular as well as well-defined cyanophilous matter. – A: 2100 ×. – B: 14000 ×. – C: a, b 7300 ×; c 8000 ×; d 7600 ×. – D, E: 6300 ×. – F: 4700 ×. – Photo: Stellan Sunhede.

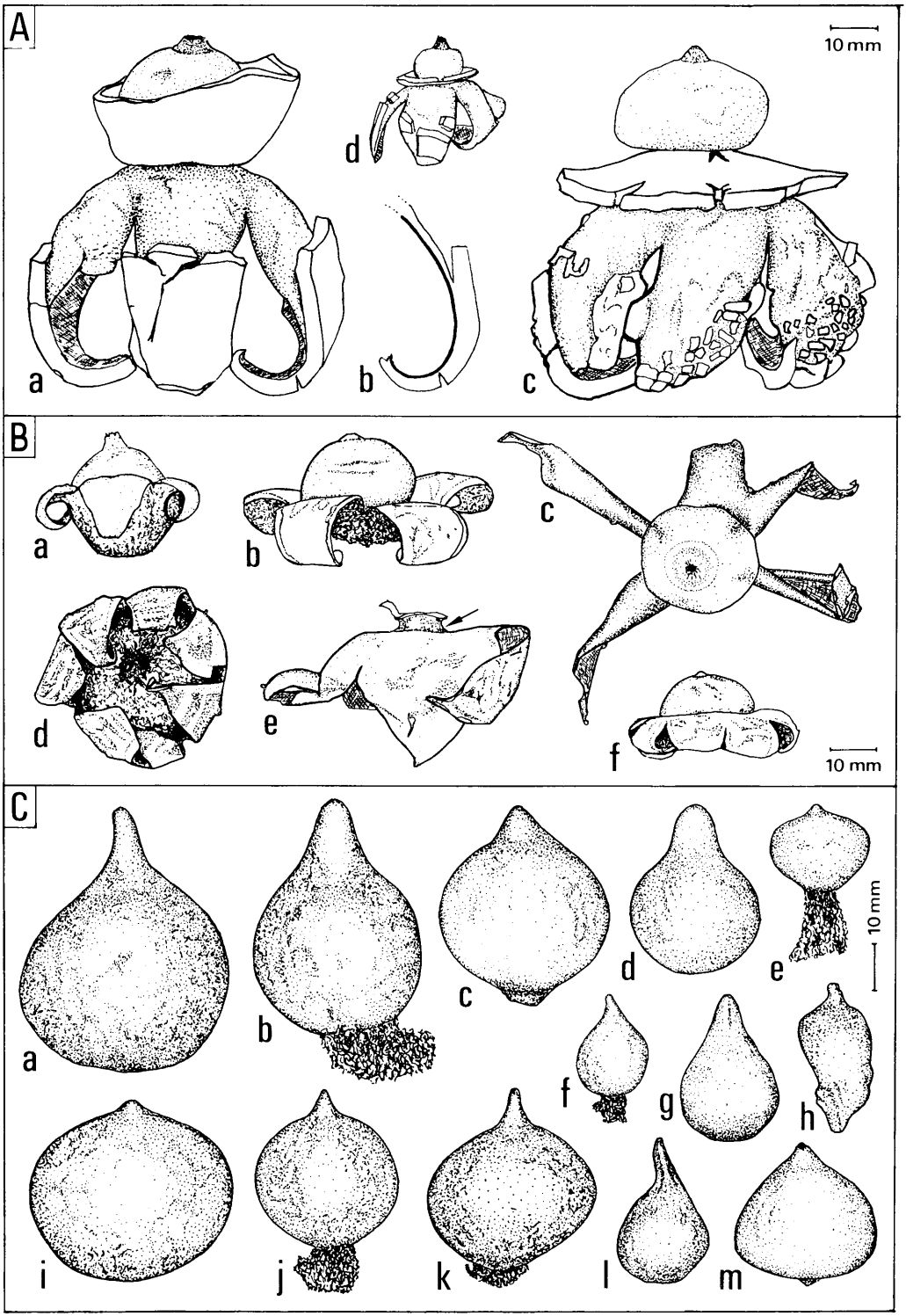


Fig. 4.

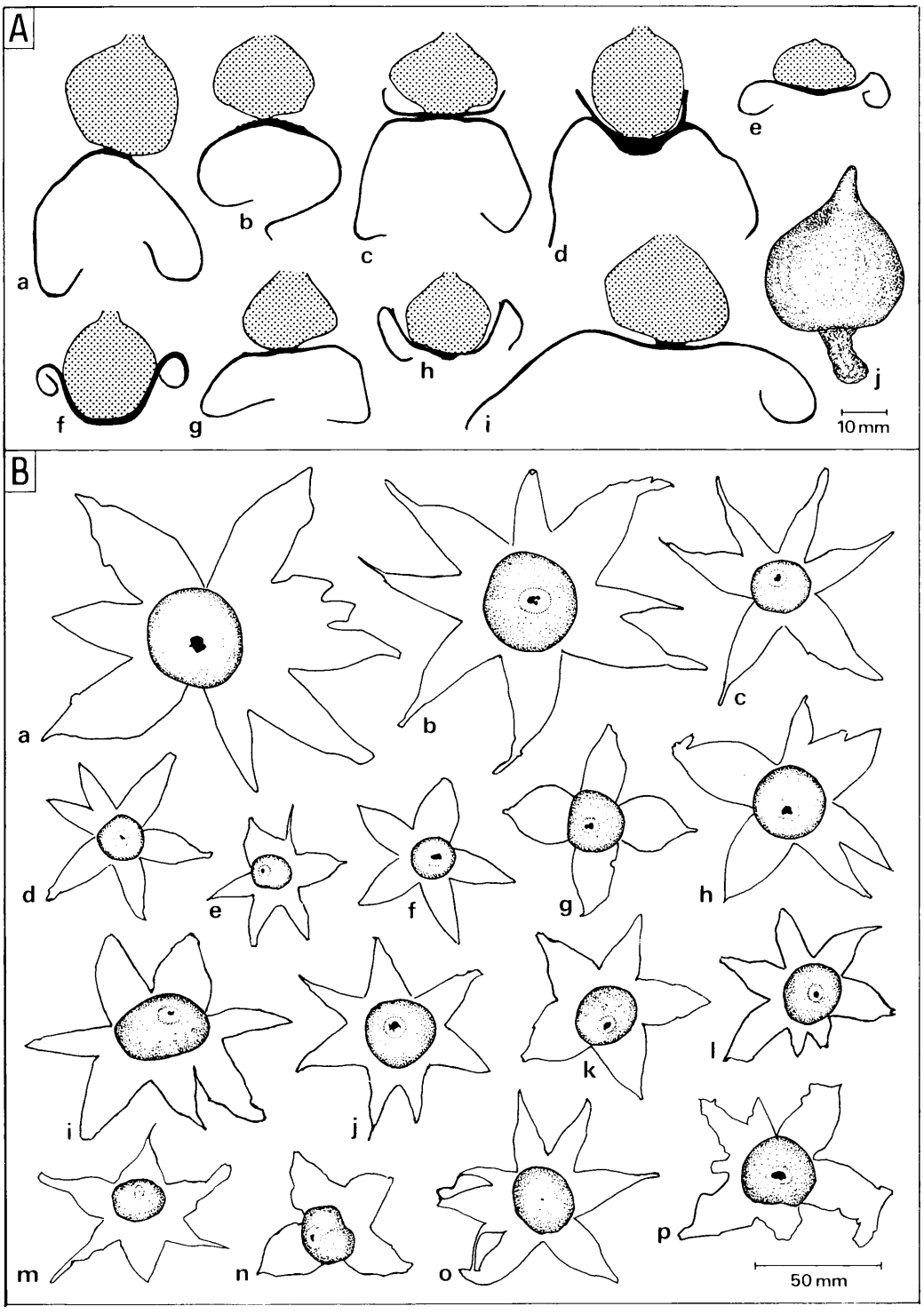


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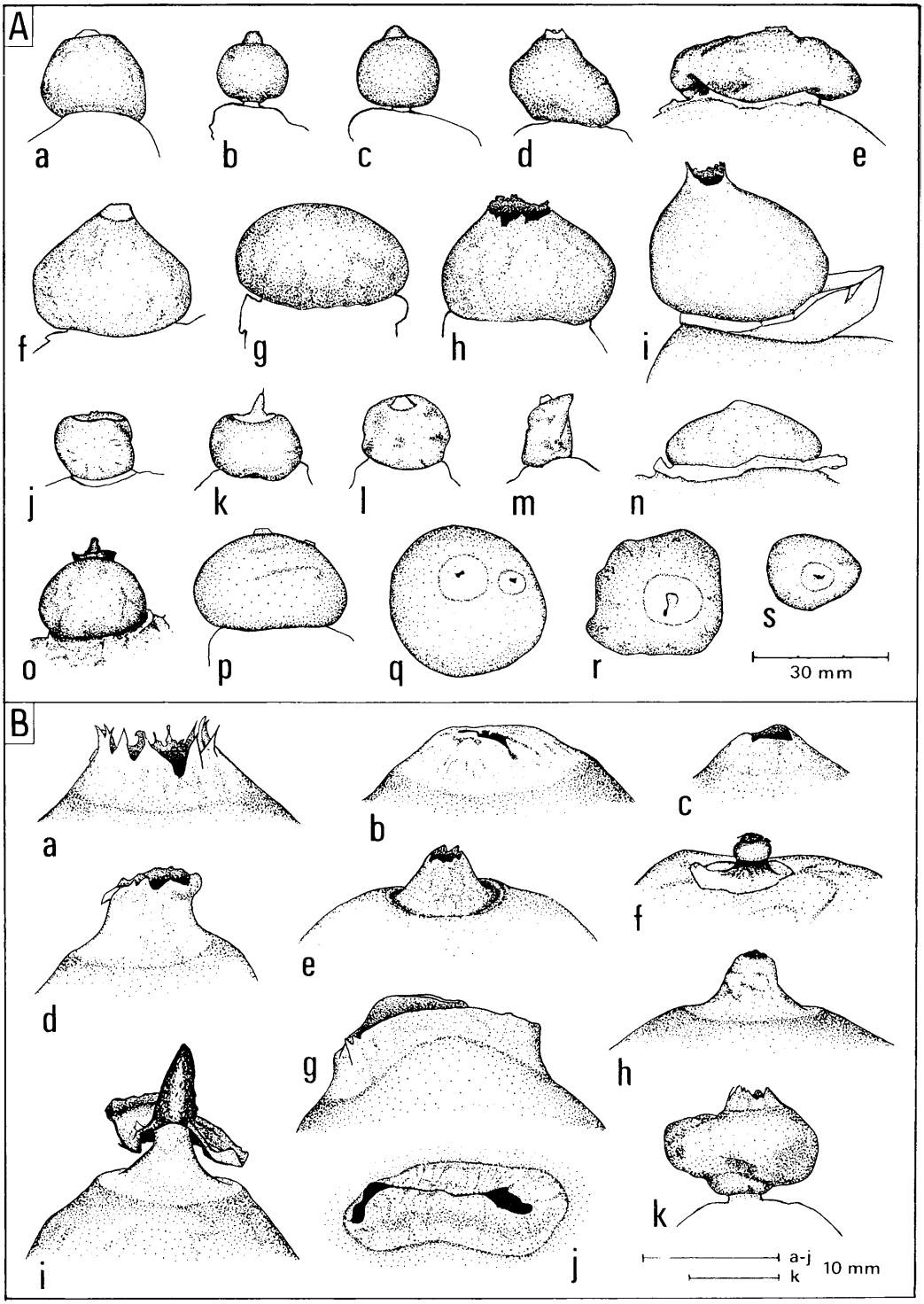


Fig. 6.

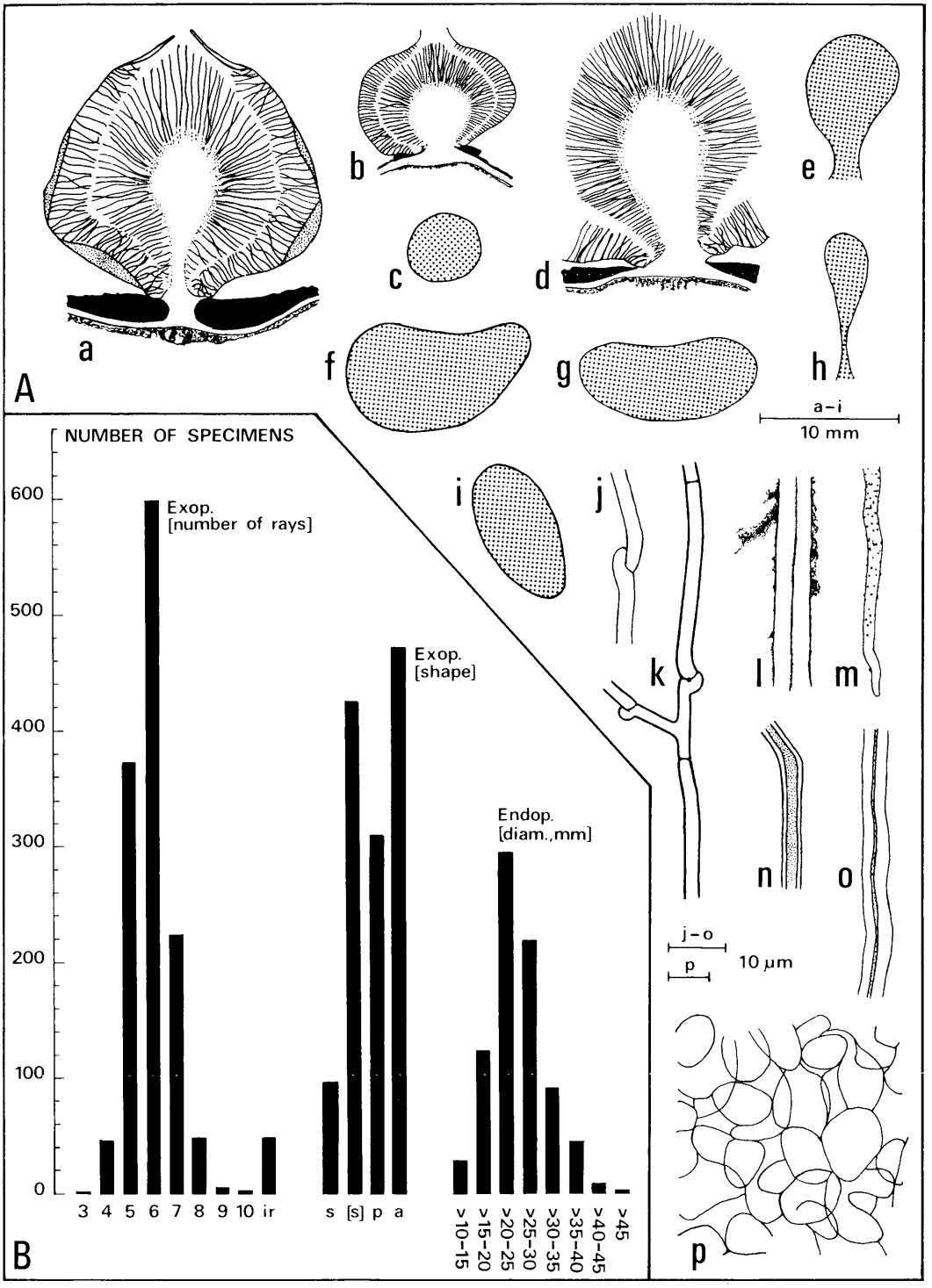

A
a
b
c
d
e
f
g
h
a–i
10 mm
B
NUMBER OF SPECIMENS
600
500
400
300
200
100
0
Exop.
[number of rays]
3 4 5 6 7 8 9 10 ir
Exop.
[shape]
s [s] p a
Endop.
[diam.,mm]
>10–15
>15–20
>20–25
>25–30
>30–35
>35–40
>40–45
>45
i
j
k
l
m
n
o
j–o
p
10 µm
p

Fig. 7

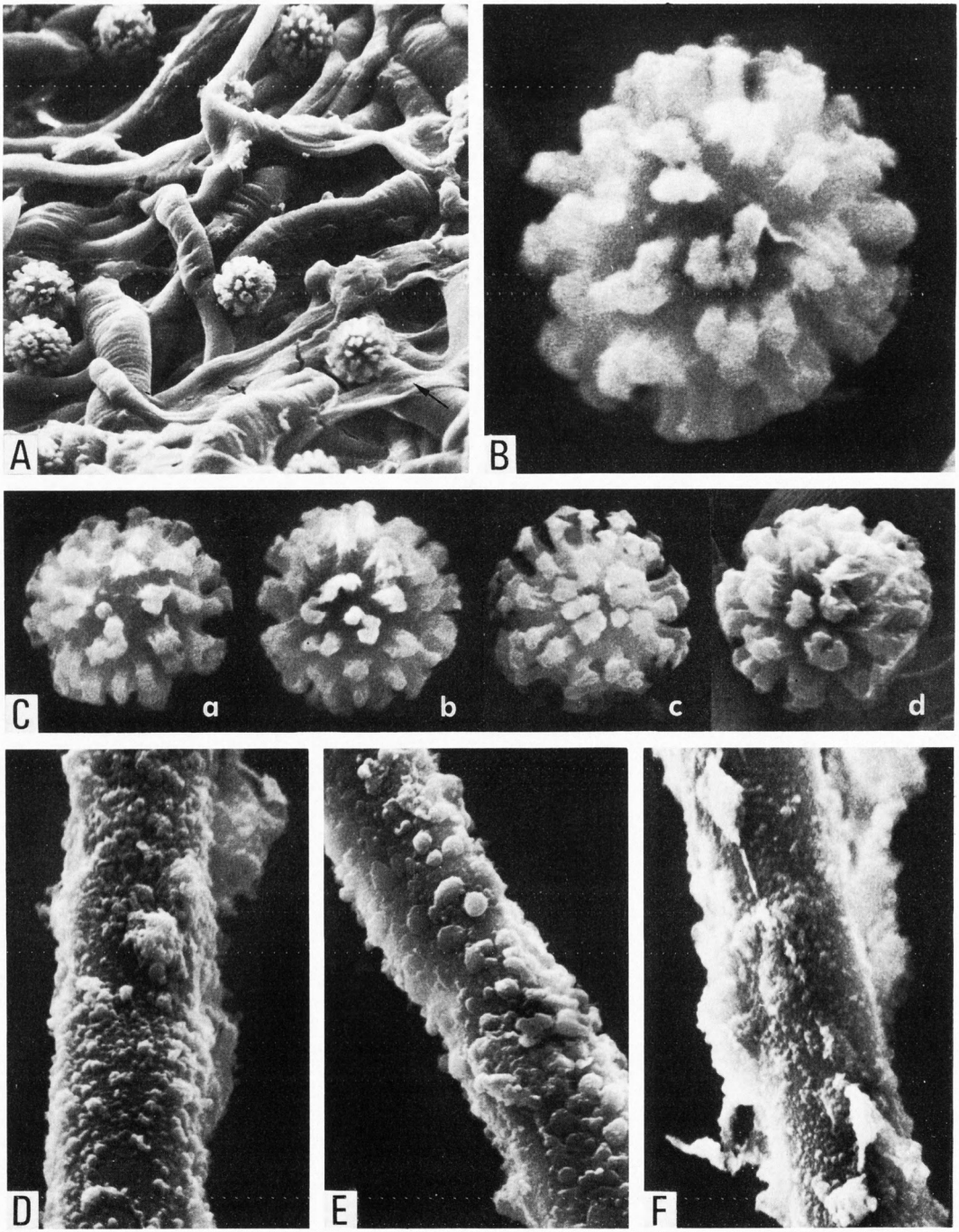


Fig. 8.

Species of Epidendroideae (Orchidaceae) new to Ecuador

Bernt Løjtnant

Løjtnant, B. 1977 12 30: Species of Epidendroideae (Orchidaceae) new to Ecuador. [AAU Ecuador project, contribution no. 9.] *Bot. Notiser 130:* 417–425. Stockholm. ISSN 0006-8195.

Lepanthes villosa Løjtnant is described as new and the new combinations, *Malaxis hoppii* (Schltr.) Løjtnant and *M. nasuta* (Schltr.) Løjtnant are made. Four species, *Dichaea lankesteri, Maxillaria campanulata, M. foliosa* and *M. friedrichsthalii* are reported for the first time from S America and 42 other taxa are reported as new to Ecuador.

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The species enumerated here are new to Ecuador (except for *Cryptocentrum jamesonii* and *C. latifolium*), and *Dichaea lankesteri, Maxillaria campanulata, M. foliosa* and *M. friedrichsthalii* are also new to S America. The collections were made during the 1st and 2nd Danish Botanical Expeditions to Ecuador (Holm-Nielsen & Jeppesen 1968, Holm-Nielsen et al. 1975). Most of the determinations were made during my stay at the Orchid Herbarium of Oakes Ames, Harvard University in 1976.

The first set of the collections are deposited at AAU. Duplicate sets have been sent to AMES, SEL, S, MO, HB, K, MBM, COL, QCA and Q. The drawings of flowers and floral parts have been made from material preserved in FAA.

Bifrenaria picta (Schltr.) C. Schweinf.

C. Schweinf. in Bot. Mus. Leafl. 11: 246, 1944.

Collected in the area around the Bomboiza Mission in prov. Morona-Santiago in SE Ecuador according to Padre Angel Andreetta who donated this plant to us. Holm-Nielsen et al. 4327 (in cultivation and preserved in FAA). – Also Colombia (type) and ?Panama (Schweinfurth 1944 b).

Brachionidium tetrapetalum (Lehm. & Kränzl.) Schltr.

Schltr. in Feddes Rep. Beih. 7: 241, 1920.

The type collection from Colombia is the only one hitherto known of this species (cf. Garay 1956). It is perhaps conspecific with *B. serratum* Schltr. from Peru (Leslie A. Garay, pers. comm.), but the type of that taxon was destroyed during World War II.

Ecuador, prov. Carchi, Páramo El Angel, in the pass on the road El Angel–Tulcán, very humid *Espeletia* paramo, 3750–3850 m (78°54'W, 0°41'N), 15.5.1973, Holm-Nielsen et al. 5454.

Brassia rhizomatosa Garay & Dunsterv.

Garay & Dunsterv., Venz. Orch. Ill. 3: 46, 1965.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, tropical rain forest and old *Citrus* plantation, c. 700 m (79°11'W, 0°55'S), 5.4.1973, Holm-Nielsen et al. 2967. – Also Venezuela.

Brassia spathacea Lind. & Rchb. f.

Lind. & Rchb. f. in Bonpl. 2: 279, 1854.

Ecuador, prov. Napo, 1 km E of the oil pump station on the road Papallacta–Baeza, gallery vegetation along Rio Papallacta, 2050 m (78°W, 0°21'S), 6.6. 1973, Holm-Nielsen et al. 6982. – Also Colombia.

Campylocentrum colombianum Schltr.

Schltr. in Feddes Rep. Beih. 7: 205, 1920.

Ecuador, prov. Los Rios, surroundings of Montalvo (foothills of the Andes, c. 40 km E of Babahoyo), rain forest with coffee and cocoa plantations, 100–200 m (79°17'W, 1°47'S), 30.3–2.4.1973, Holm-Nielsen et al. 2595, 2639. – Also Colombia.

Campylocentrum fasciola (Lindl.) Cogn.

Cogn. in Mart. Fl. Bras. 3,6: 520, 1906.

Ecuador, prov. Los Rios, surroundings of Montalvo (foothills of the Andes, c. 40 km E of Babahoyo), rain forest with coffee and cocoa plantations, 100–200 m (79°17'W, 1°47'S), 30.3–2.4.1973, Holm-Nielsen et al. 2719. – Also Guatemala, Br. Honduras, Honduras, Costa Rica, Panama, West Indies, Venezuela, Br. Guiana (type), Surinam, Brazil, Peru and Colombia.

Cryptocentrum hoppii Schltr.

Schltr. in Feddes Rep. Beih. 27: 103, 1924.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4241. – Also Colombia.

Cryptocentrum jamesonii Benth.

Benth. in Benth. & Hook., Gen. Pl. 3: 557, 1883.

A comparison of the types of *C. jamesonii* (Ecuador) and *C. calcarata* (Schltr.) Schltr. (Costa Rica) has shown that they are probably conspecific. The lip of *C. calcarata* is, like that of *C. jamesonii,* evenly tapered from the concave base and the constrictions described and illustrated by Schlechter (1906, 1913, 1931) represent folds rather than constrictions. There seems, however, to be a slight difference in leaf width: 3–5 mm in the type of *C. jamesonii,* occasionally up to 7 mm in *C. calcarata.*

C. lehmannii (Rchb. f.) Garay is easily distinguishable from *C. jamesonii* (Garay 1958). *C. lehmannii* is a rarely collected species described from Ecuador and it has not been recorded from outside that country. However, I found a Colombian specimen of it (Lehmann 8582, Colombia, West Andes of Popayan, 1500–2300 m, AMES) among the undetermined material of *Cryptocentrum* at AMES.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 33, dry rocky slopes with grass and scattered shrubs, 1800–1850 m (79°04'W, 3°59'S), 21.4.1973, Holm-Nielsen et al. 4124.

Cryptocentrum latifolium Schltr.

Schltr. in Feddes Rep. Beih. 19: 247, 1923.

The collection cited below belongs to the typical variety of this species, which seems to have been reported from Costa Rica (type) and Panama only. However, its var. *brachypetalum* Garay is known from a few collections from Colombia and Ecuador (Garay 1953). The Ecuadorean specimen of *Cryptocentrum* illustrated by Withner (1959) as *C. jamesonii* represents the typical form of *C. latifolium.*

Besides the species of *Cryptocentrum* reported here, we have found three further but yet unidentified species in Ecuador.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, tropical rain forest and old *Citrus* plantation, 700 m (79°11'W, 0°55'S), 5.4.1973, Holm-Nielsen et al. 2962. – Quevedo–Latacunga road, rocky slopes with rain forest, 800–950 m (79°10'W, 0°55'S), 5.4.1973, Holm-Nielsen et al. 3008.

Dichaea anguina Schltr.

Schltr. in Feddes Rep. 27: 82, 1929.

Ecuador, prov. Morona-Santiago, Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner", km 140 on the road Loja–Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900–1000 m (78°34'W, 3°37'S), 26–27.4.1973, Holm-Nielsen et al. 4487. – Also Bolivia (type) and ? Venezuela (Schweinfurth 1967).

Dichaea brachypoda Rchb. f.

Rchb. f., Beitr. Orch. Centr.-Amer. 78, 1866.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 33, dry rocky slopes with grass and scattered shrubs, 1800–1850 m (79°04'W, 3°59'S), 21.4.1973, Holm-Nielsen et al. 4131. – Also Costa Rica (type), Venezuela, Surinam, Colombia and Brazil.

Dichaea lankesteri Ames

Ames in Sched. Orch. 4: 56, 1923.

Ecuador, prov. Pichincha, "Finca Carlita", at km 13 on the road Santo Domingo de los Colorados–Chone, secondary rain forest and slopes with secondary herb vegetation, 550 m (79°14'W, 0°15'S), 10.6.1973, Holm-Nielsen et al. 7034. – Prov. Cotopaxi, Quevedo–Latacunga road, km 46 from Quevedo, NE-exposed slopes with rain forest, c. 600 m (79°11'W, 0°55'S), 4.4.1973, Holm-Nielsen et al. 2901. – Also Costa Rica (type) and Honduras.

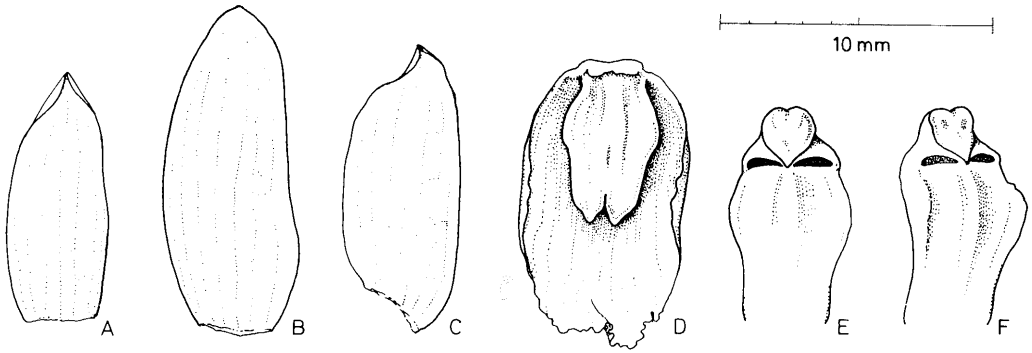


Fig. 1. *Kefersteinia laminata*. – A: Dorsal sepal. – B: Lateral sepal. – C: Petal. – D: Lip. – E–F: Column. – Holm-Nielsen et al. 6058.

Dichaea maculata Poepp. & Endl.

Poepp. & Endl., Nov. Gen. ac Sp. Pl. 2: 3, 1838.

Ecuador, prov. Morona-Santiago, Shuinia Nait, small mountain ridge c. 8 km SE of Misión Bomboiza, tropical rain forest, 900–1000 m (78°33'W, 3°30'S), 24.4.1973, Holm-Nielsen et al. 4420. – Also Peru (type) and Costa Rica.

Dichaea tenuis C. Schweinf.

C. Schweinf. in Amer. Orch. Soc. Bull. 21: 510, 1952.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4199. – Also Peru.

Diothonea gratissima Rchb. f.

Rchb. f. in Bot. Zeit. 10: 772, 1852.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, above Pilaló, in cloud forest, mostly steep slopes, c. 3200–3300 m (78°56'W, 0°58'S), 8.4.1973, Holm-Nielsen et al. 3275. – Also Colombia (cf. Schweinfurth 1944 a).

Fernandezia ionanthera (Rchb. f. & Warsz.) Schltr.

Schltr. in Feddes Rep. 16: 349, 1920.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 14, mountain ridges with elfin forest and open bogs, 2750–2770 m (79°09'W, 4°S), 19–20.4.1973, Holm-Nielsen et al. 3985. – Also Peru.

Kefersteinia laminata (Rchb. f.) Schltr.

Schltr. in Feddes Rep. Beih. 7: 267, 1920.

This species has apparently been known from the type collection only, which is of uncertain origin (Colombia?). It belongs to the genus *Kefersteinia* because it has a substigmatic longitudinal keel on the column (Fig. 1).

It is generally assumed that Reichenbach gave his species the alternative name *Kefersteinia laminata;* however, he only referred the species to the section *Kefersteinia* within the genus *Zygopetalum*. The legitimate combination under *Kefersteinia* was made incidentally by Schlechter. B. J. Jackson listed in 1895 the name *Kefersteinia laminata* in Index Kewensis, but this combination is not valid since it was listed merely as a synonym to *Zygopetalum laminatum*.

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on the road Tulcán–Maldonado, steep forested slopes, 2100–2200 m (78°06'W, 0°54'N), 20.5.1973, Holm-Nielsen et al. 6058.

Lepanthes dasyphylla Rchb. f.

Rchb. f. in Flora 69: 557, 1886.

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on the road Tulcán–Maldonado, steep forested slopes, 2100–2200 m (78°06'W, 0°54'N), 20.5.1973, Holm-Nielsen et al. 6072, 6073. – Also Colombia.

Lepanthes villosa Løjtnant sp. nov. – Fig. 2

Orig. coll.: Ecuador, prov. Carchi, Valle de Maldonado, km 67 on the road Tulcán–Maldonado, montane forest, 2400 m (78°04'W, 0°53'N), 20.5.1973, Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 6151. Epiphyte, pendent. Labellum red-brown. Flowers purple-brown with smaller pale greenish areas. Leaves with red-brownish veins (AAU holotype).

Plantae epiphyticae, pendentes; *caulibus primariis*

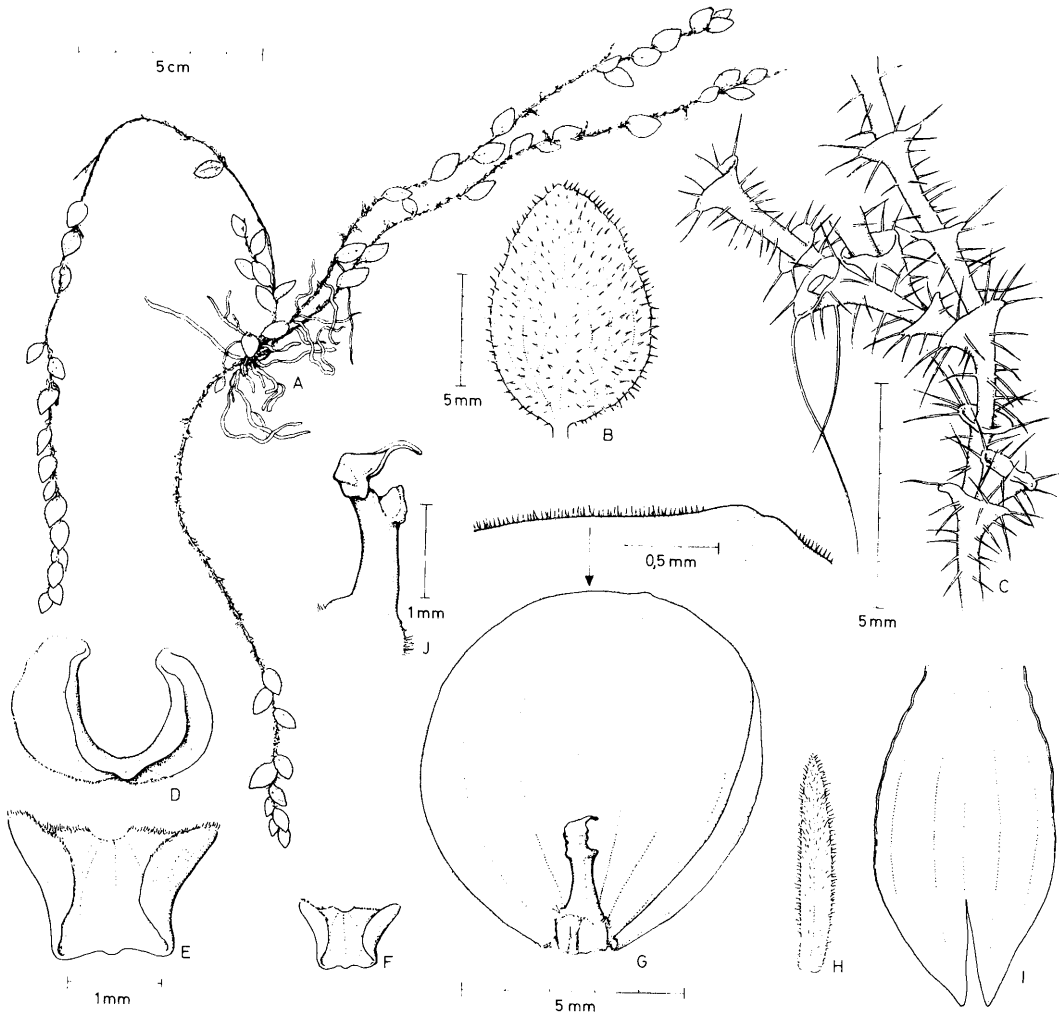


Fig. 2. *Lepanthes villosa*. – A: Habit. The plant is pendent under natural conditions. – B: Leaf. – C: Stems. – D–F: Lip. – G: Dorsal sepal and column. – H: Petal. – I: Lateral sepals. – J: Column. – Holotype.

gracilibus, simplicibus vel parum ramosis, vaginis infundibuliformibus, setis acutis obtectis; *caulibus secundariis* perpaucis, unifoliatis; *foliis* ellipticis, carnosis, dense setosis, in vivo usque ad 13 mm longis, 8.5 mm latis, 3-nerviis; *inflorescentiis* solitariis, unifloris; *pedunculo* folio breviore; *sepalo postico* orbiculari, hemisphaerico, valde concavo, margine ciliato, 7-nervio, 8.5 mm longo, 8 mm lato; *sepalis lateralibus* inter se usque ad tertiam partem apicalem connatis, ovato-lanceolatis, acutis, 4-nerviis, usque ad 8.5 mm longis, 4 mm latis; *petalis* lineari-lanceolatis, uninerviis, villosis, usque ad 5 mm longis, 0.7 mm latis; *labello* reniformi, minute apiculato, 3-nervio, usque ad 1.5 mm longo, 2.5 mm lato; *columna* gracili; *rostello* porrecto.

This new species differs from all hitherto described species of the section *Brachyclada* Rchb. f. by the long, linear and villose petals.

The specific name is descriptive of the villose petals, villosa meaning hairy.

Liparis laticuneata C. Schweinf.

C. Schweinf. in Bot. Mus. Leafl. 15: 104, 1951.

The leaves of our collection are somewhat smaller (up to 2.5 × 1.6 cm) and the lips are slightly broader and shorter than those of the

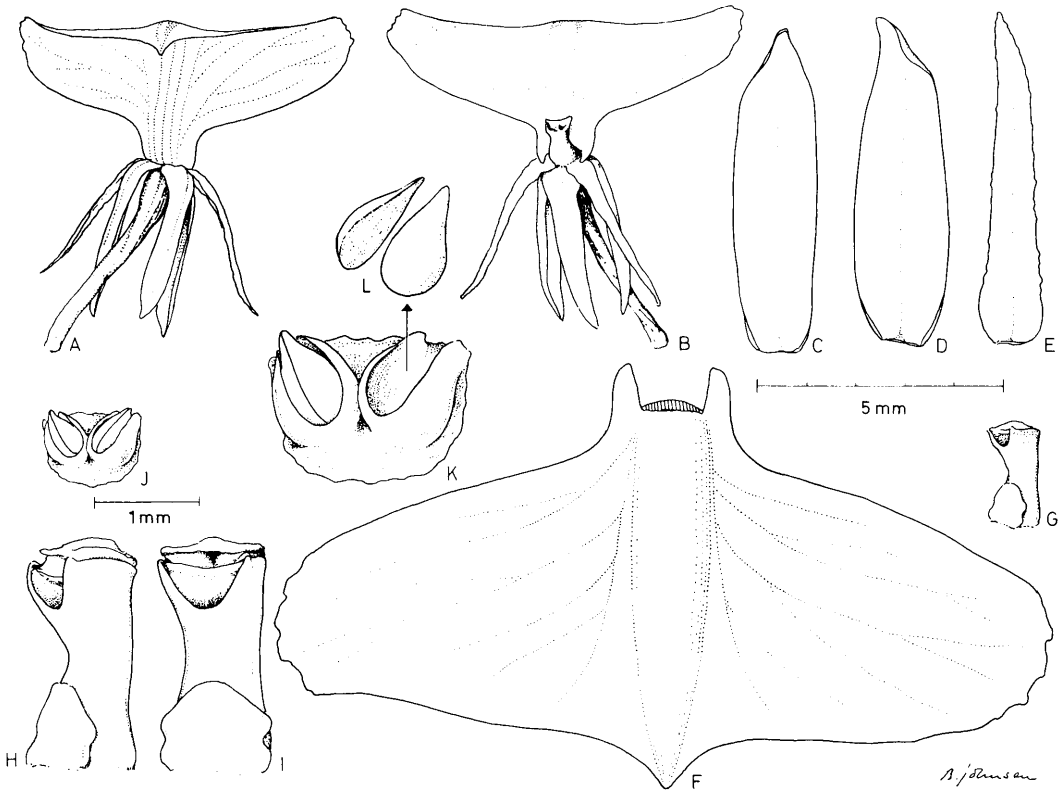


Fig. 3. *Liparis laticuneata*. – A–B: Flower from the lower part of the inflorescence. – C: Dorsal sepal. – D: Lateral sepal. – E: Petal. – F: Lip, spread out. –G–I: Column. –J–K: Anther. – L: Pollinia. – Holm-Nielsen et al. 4646.

type. However, the flowers vary even within a single inflorescence: the flowers situated lower down are thus bigger and have shorter and broader lips than the upper flowers (Fig. 3).

Ecuador, prov. Loja, km 51 on Pan American Highway of Loja, shrub, 2–4 m high, dominated by xerophytic vegetation, 2900 m (79°15'W, 3°45'S), 1.5.1973, Holm-Nielsen et al. 4646. – Also Peru.

Malaxis hoppii (Schltr.) Løjtnant comb. nov.

Basionym: *Microstylis Hopii* Schltr. in Feddes Rep., Beih. 27: 21, 1924.

Since the genus *Microstylis* Nutt. ex Lindl. is easily accommodated within *Malaxis* Soland. ex Sw. the above new combination has been made. The epithet should be spelled *hoppii* since the species is named to honour the collector, W. Hopp.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 24–25, steep rocky slopes, covered with scrub, 1950–2100 m (79°05'W, 3°59'S), 15.4.1973, Holm-Nielsen et al. 3451. – Also Colombia.

Malaxis lobulata L. O. Wms.

L. O. Wms. in Lilloa 5: 6, 1939.

Ecuador, prov. Azuay, km 91 on Pan American Highway N of Loja, dry scrub, 1–3 m high, 2900 m (79°10'W, 3°25'S), 5.5.1973, Holm-Nielsen et al. 5109. – Also Colombia.

Malaxis nasuta (Schltr.) Løjtnant comb. nov.

Basionym: *Microstylis nasuta* Schltr. in Feddes Rep. 27: 35, 1929.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, above Macuchi, low herb and grass vegetation on stony-clayey soil, c. 1600 m (79°03'W, 0°56'S), 6–

9.4.1973, Holm-Nielsen et al. 3039, 3043, 3428. – Also Bolivia.

Maxillaria affinis (Poepp. & Endl.) Garay

Garay in Caldasia 8: 527, 1962.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, common in rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4249. – Also Colombia and Peru (type).

Maxillaria brachybulbon Schltr.

Schltr. in Feddes Rep. Beih. 19: 55, 1923.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4198. – Also Honduras, Costa Rica (type), Panama, Venezuela and Colombia.

Maxillaria campanulata C. Schweinf.

C. Schweinf. in Bot. Mus. Leafl. 5: 94, 1938.

The original description of *M. campanulata* states that the species has several inconspicuous warts in the middle of the lip near the base. Our collection fits the type except in having a small cluster of unicellular hairs instead of warts in the middle and near the base of the lip. These hairs break off easily, leaving scars which resemble small warts. It is my opinion that the warts described by Schweinfurth represents scars of the above-mentioned unicellular hairs. The hairs may represent food-hairs, since this type of pollinator attractant as well as pseudopollen is common within *Maxillaria* (Porsch 1908, Pijl & Dodson 1969).

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on the road Tulcán–Maldonado, steep forested slopes, 2100–2200 m (78°06'W, 0°54'N), 20.5.1973, Holm-Nielsen et al. 6047. – Also Costa Rica.

Maxillaria christobalensis Rchb. f.

Rchb. f. in Bot. Zeit. 10: 857, 1852.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4242, 4245. – Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner" km 140 on the road Loja-Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900–1000 m (78°34'W, 3°37'S), 26–27.4.1973, Holm-Nielsen et al. 4537. – Also Peru.

Maxillaria equitans (Schltr.) Garay

Garay in Bot. Mus. Leafl. 18: 208, 1958.

Ecuador, prov. Morona-Santiago, Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner" km 140 on the road Loja-Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900–1000 m (78°34'W, 3°37'S), 26–27.4.1973, Holm-Nielsen et al. 4515. – Also Peru, Colombia (type), Brazil, Guyana and Venezuela.

Maxillaria foliosa Ames & C. Schweinf.

Ames & C. Schweinf. in Sched. Orch. 8: 60, 1925.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4195. – Also Costa Rica.

Maxillaria friedrichsthalii Rchb. f.

Rchb. f. in Bot. Zeit. 10: 858, 1852.

Ecuador, prov. Morona-Santiago, Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner" km 140 on the road Loja-Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900–1000 m (78°34'W, 3°37'S), 26–27.4.1973, Holm-Nielsen et al. 4536. – Also from Mexico to Br. Honduras, Guatemala (type) and Panama.

Maxillaria mapiriensis (Kränzl.) L. O. Wms.

L. O. Wms. in Caldasia 5: 16, 1942.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 39, rocky area with steep scrub-covered slopes, 1600–1650 m (79°04'W, 3°59'S), 21.4.1973, Holm-Nielsen et al. 4034. – Also Bolivia (type), Colombia and Venezuela.

Maxillaria nasuta Rchb. f.

Rchb. f., Beitr. Orch. Centr.-Amer. 104, 1866.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4247. – Also from Mexico to Guatemala, Costa Rica (type), Venezuela, Colombia, Peru and Bolivia.

Maxillaria parviflora (Poepp. & Endl.) Garay

Garay in Bot. Mus. Leafl. 21: 258, 1967.

Ecuador, prov. Morona-Santiago, Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner" km 140 on the road Loja-Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900–1000 m (78°34'W, 3°37'S), 26–27.4.1973, Holm-Nielsen et al. 4519, 4520. – Also Peru.

Maxillaria platyloba Schltr.

Schltr. in Feddes Rep. Beih. 9: 104, 1921.

Ecuador, prov. Loja, road Loja–Zamora, 1 km W of the pass (km 13), dry grass slopes, shrubby mountain slopes, and elfin forest, 2725–2750 m (79°09'W, 4°S), 17.4.1973, Holm-Nielsen et al. 3662; also at km 14, 2750–2770 m, 19–20.4.1973, Holm-Nielsen et al. 3946. – Also Peru.

Octomeria grandiflora Lindl.

Lindl. in Bot. Reg. 28: misc. 64, 1842.

Besides the cited collection of *O. grandiflora,* a different but fruiting species of *Octomeria* was collected in prov. Morona-Santiago and it is certain that several species of *Octomeria* will yet be discovered in the Amazonian part of Ecuador. The genus is new to Ecuador.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 24–25, steep rocky slopes, covered with scrub, 1950–2100 m (79°05'W, 3°59'S), 15.4.1973, Holm-Nielsen et al. 3445. – Also Trinidad, Venezuela, ? Bolivia and Brazil (type).

Odontoglossum auriculatum Rolfe

Rolfe in Kew Bull. 1892: 140.

Ecuador, prov. Carchi, Valle de Maldonado, km 60 on the road Tulcán–Maldonado, cleared slopes along the road and denser cloud forest, 2700 m (78°04'W, 0°51'N), 18.5.1973, Holm-Nielsen et al. 5702; also at km 67, 2600 m (78°04'W, 0°53'N), 21.5.1973, Holm-Nielsen et al. 6215. – Also Venezuela and Colombia (type ?).

Odontoglossum longipes Rchb. f. & Warsz.

Rchb. f. & Warsz. in Bonpl. 2: 100, 1854.

Schweinfurth (1970) was inclined to believe that *O. longipes* is conspecific with *O. longifolium* Lindl. from Ecuador. However, after examining records of the types of both species, I hesitate to concur with Schweinfurth's view that the differences between *O. longipes* and *O. longifolium* are merely a result of ecological differences.

Ecuador, prov. Loja, road Loja–Zamora, 1 km W of the pass (km 13), dry grass slopes, shrubby mountain slopes, and elfin forest, 2725–2750 m (79°09'W, 4°S), 17.4.1973, Holm-Nielsen et al. 3686. – Also Peru.

Odontoglossum rhynchanthum Rchb. f.

Rchb. f. in Gard. Chron. 1,3: 380, 1887.

Reichenbach described the species as "*Odontoglossum rhynchanthum* X" as he thought it might be a hybrid between *O. purum* Rchb. f. and *O. lindleyanum* Rchb. f. & Warsz., both from "New Granada". It is uncertain whether *O. rhynchanthum, O. purum,* and *O. lindleyanum* are described upon material from what is now known as N Ecuador or from Colombia. We found *O. rhynchanthum* close to the Colombian border, together with *O. armatum* Rchb. f. and *O. auriculatum* Rolfe, two species which are closely related to *O. purum* and *O. lindleyanum.*

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on the road Tulcán–Maldonado, steep forested slopes, 2100–2200 m (78°06'W, 0°54'N), 20.5.1973, Holm-Nielsen et al. 6066.

Odontoglossum scabiosum (Kränzl.) Schltr.

Schltr. in Feddes Rep. Beih. 7: 284, 1920.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 14, mountain ridges with elfin forest and open bogs, 2750–2770 m (79°09'W, 4°S), 19–20.4.1973, Holm-Nielsen et al. 3956, 3984. – Also Colombia.

Odontoglossum spathaceum Lindl.

Lindl., Fol. Orch., Odontoglossum 18, no. 50, 1852.

Ecuador, prov. Carchi, Valle de Maldonado, km 53 on the road Tulcán–Maldonado, steep slopes in cloud forest, 3150–3250 m (78°03'W, 0°50'N), 17–18.5.1973, Holm-Nielsen et al. 5614. – Prov. Imbabura, timber line vegetation on the Hacienda Yura Cruz, 10 km N of Ibarra, 3700–3800 m (78°05'W, 0°22'N), 25.5.1973, Holm-Nielsen et al. 6487. – Prov. Cotopaxi, Quevedo–Latacunga road, above Pilaló, at the timber line, 3450–3500 m (78°56'W, 0°58'S), 8.4.1973, Holm-Nielsen et al. 3298. – Also Colombia.

Oliveriana brevilabia (C. Schweinf.) Dressl. & N. Will.

Dressl. & N. Will. in Amer. Orch. Soc. Bull. 39: 324, 1970, in adnot.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 33, dry rocky slopes with grass and scattered shrubs, 1800–1850 m (79°04'W, 3°59'S), 21.4.1973, Holm-Nielsen et al. 4123. – Also Peru (type) and Colombia.

Oncidium cocciferum Rchb. f. & Warsz.

Rchb. f. & Warsz. in Bonpl. 2: 101, 1854.

Ecuador, prov. Carchi, Valle de Maldonado, km 67 on the road Tulcán–Maldonado, montane forest, 2400 m

(78°04'W, 0°53'N), 20.5.1973, Holm-Nielsen et al. 6149. – Also Colombia (type) and Peru.

Pachyphyllum pectinatum Rchb. f.

Rchb. f., Xen. Orch. 3: 22, 1878.

Ecuador, prov. Carchi, Valle de Maldonado, km 67 on the road Tulcán–Maldonado, montane forest, 2600 m (78°04'W, 0°53'N), 21.5.1973, Holm-Nielsen et al. 6223. – Also Bolivia (type) and Peru.

Pachyphyllum squarrosum Lindl.

Lindl. in Ann. & Mag. Nat. Hist. 15: 107, 1845.

Ecuador, prov. Carchi, Valle de Maldonado, km 53 on the road Tulcán–Maldonado, steep slopes in cloud forest, 3250–3300 m (78°03'W, 0°50'N), 22.5.1973, Holm-Nielsen et al. 6252. – Also Colombia.

Pityphyllum laricinum (Kränzl.) Schltr.

Schltr. in Feddes Rep. Beih. 7: 163, 1920.

Ecuador, prov. Zamora-Chinchipe, road Loja–Zamora, km 24–25, steep rocky slopes, covered with scrub, 1950–2100 m (79°05'W, 3°59'S), 15.4.1973, Holm-Nielsen et al. 3437. – Also Peru.

Pleurothallis gelida Lindl.

Lindl. in Bot. Reg. 27, misc.: 91, 1841.

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on the road Tulcán–Maldonado, steep forested slopes, 2100–2200 m (78°06' W, 0°54'N), 20.5.1973, Holm-Nielsen et al. 6077. – Prov. Cotopaxi, Quevedo–Latacunga road, steep rocky slopes along Río Pilaló with scattered trees, subtropical rain forest on fat clay, 1200–1300 m (79°09'W, 0°52'S), 7.4.1973, Holm-Nielsen et al. 3110, 3111. – Also from Florida, C America and the West Indies (type) to Colombia and Peru.

Pleurothallis rhopalocarpa Schltr.

Schltr. in Feddes Rep. Beih. 10: 43, 1922.

Ecuador, prov. Carchi, Valle de Maldonado, km 67 on the road Tulcán–Maldonado, montane forest, 2600 m (78°04'W, 0°53'N), 21.5.1973, Holm-Nielsen et al. 6227, 6228. – Also Bolivia.

Rodriguezia carnea Lindl.

Lindl. in Bot. Reg. 29, misc.: 72, 1843.

R. carnea will certainly prove to have a wider distribution in the equatorial Andes than indicated by the scarce collections as *R. carnea* is easily confused with *R. lanceolata* Ruiz & Pavón (*R. secunda* H.B.K.) which is often reported to be widely distributed in the American tropics. *R. carnea* differs from *R. lanceolata* by the lip which is distinctly constricted and bilamellate in the middle and not cuneate at the base.

Ecuador, prov. Napo, Archidona (77°48'W, 0°54'S), 27.6.1968, Holm-Nielsen & Jeppesen 1018. – Also Colombia.

Scaphyglottis bicornis (Lindl.) Garay

Garay in Bot. Mus. Leafl. 21: 255, 1967.

Ecuador, prov. Carchi, Valle de Maldonado, km 67 on the road Tulcán–Maldonado, montane forest, 2400 m (78°04'W, 0°53'N), 20.5.1973, Holm-Nielsen et al. 6150, 6156; also at 2600 m, 21.5.1973, Holm-Nielsen et al. 6221. – Also Colombia (type) and Venezuela.

Trichocentrum recurvum Lindl.

Lindl. in Bot. Reg. 29, misc.: 9, 1843.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78°34'W, 3°29'S), 23.4.1973, Holm-Nielsen et al. 4197. – Also Guyana.

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Seed coat structure of Old World Lupinus species

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The seed surface of 8 Old World *Lupinus* species was studied by SEM. At least 4 different seed coat patterns were discerned, according to which the species are arranged in four groups: (1) *L. albus* L. and *L. graecus* Boiss. & Sprun.; (2) *L. luteus* L.; (3) *L. angustifolius* L. and *L. micranthus* Guss.; (4) *L. pilosus* Murr., *L. palaestinus* Boiss. and *L. cosentinii* Guss. For comparison 6 New World species were also examined: *L. albicaulis* Torr., *L. arboreus* Sims, *L. aschenbornii* S. Schau., *L. montanus* H. B., *L. mutabilis* Sweet and *L. succulentus* Dougl. These were all found to have a comparatively uniform seed coat pattern.

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The data presented here are part of a wider biosystematic research project on native *Lupinus* populations in Israel, the aims of which have been explained elsewhere (Pazy et al. 1977). To assess interspecific relationships, characters not previously studied in *Lupinus* are being investigated.

To study the inter- and intraspecific variation of the seed coat of Old World lupins, several accessions of each of the 6 species (7 taxa) growing in Israel were examined; for comparison two other Mediterranean and 6 New World species were also investigated.

Material and methods

The sources of the seeds studied are listed in Table 1. Seeds were either collected by us in the field or obtained from various seed collections, more rarely taken from herbarium material. Vouchers are deposited in our seed collection or at HUJ.

In a preliminary study hand-cut sections of dried seeds were studied under a light microscope. The main investigations were SEM studies of seeds coated with gold-palladium, using a Cambridge S4/10 microscope. The micrographs were taken in the central part of the seed coat.

Observations

The general seed coat structure of *Lupinus*, as seen in the hand sections, agrees with that reported for other Leguminosae (Corner 1951, 1976). The different seed coat patterns are the result of differences in the organization of the uppermost layer, the palisade cells, and of various substances deposited on their surface. The following species groups were discerned.

(1) *L. albus* and *L. graecus* (Fig. 1).

The testa surface is strongly granulated. It is also covered with ridges either arranged in a regular pattern which makes the surface appear foveolate (*L. albus*, Fig. 1 A, B) or irregularly scattered (*L. albus*, Fig. 1 C, D; *L. graecus*, Fig. 1 E, F). According to the distance between the ridges, these may represent elevated cell walls or some parts of cell walls. It is possible that the foveolate appearance of some *L. albus* seed coats is due to the collapse of the tangential cell walls (cf. Brisson & Peterson 1976).

(2) *L. luteus* (Fig. 2).

The testa surface is covered with shallow, "volcano-like", protuberances which differ from those of the preceding group in shape and pat-

tern. Each protuberance probably corresponds to a single cell. Their upper margin is surrounded by a thick amorphous layer which we assume to be cutinous. Otherwise, the seed surface is smooth, not covered by granules as in *L. albus* and *L. graecus*.

We compared seeds from wild populations from Israel (Fig. 2 A, B) and the Iberian peninsula (Fig. 2 C, D) with seeds from a cultivated line (Fig. 2 E). The shape and spacing of the protuberances on the seed coats of *L. luteus* from Israel seem to differ slightly from those of the plants from other sources. Fig. 2 F shows an extreme case, which must be regarded, however, with some suspicion, because these seeds were obtained from a herbarium specimen and might not have reached full maturity.

(3) *L. micranthus* and *L. angustifolius* (Fig. 3).

The testa looks as if it had been strewn over with some amorphous substance. This covering is mainly formed of short 'threads', which lie between and on top of the rounded protuberances. In *L. albus* and *L. graecus* the surface granulation has a different appearance.

Some variation occurs within the group. The diameter of the protuberances is smaller in *L. micranthus* (Fig. 3 A, B) and *L. angustifolius* var. *angustifolius* (Fig. 3 C, D) than in *L. angustifolius* var. *basalticus* (Fig. 3 E). The large seeds of a sample of *L. angustifolius*, probably an introduced species in Israel, have a less granulated surface and the shape of the protuberances is somewhat different (Fig. 3 F).

(4) *L. palaestinus, L. pilosus* and *L. cosentinii* (Fig. 4).

The seed coat structure of all these species, known as the rough-seeded lupins, is generally similar. We consider the protuberances to be fascicled palisade cells. They are much larger than those of the other species and are discernible without optical aids. In *L. pilosus* (Fig. 4 A), which has the largest protuberances, they may exceed 300 μm in height, about twice the height of those of *L. palaestinus* (Fig. 4 B). In the single sample of *L. cosentinii*, they seem even shallower and wider.

The surface of each protuberance (Fig. 4 D) most resembles the continuous surface of the seeds of some of the species from the New World (Fig. 5 A–C).

In these three species a thin membrane covers the whole seed below the tops of the protuberances. However, it is easily torn apart, even after careful handling, like in nature, and only fragments remain (Fig. 4 B).

(5) Species from the New World (Fig. 5).

Six out of a total of at least 100 New World species were chosen at random. Their seed surfaces are fairly similar, being irregularly ridged, smooth or granular, perhaps most resembling that of *L. albus* and *L. graecus*. They vary, however, in the extent of granulation and in the shape and arrangement of the ridges.

Discussion

Species for which a close relationship has been previously proven or assumed, have a similar seed coat structure. *L. albus* and *L. graecus* (group 1) are closely related, and the latter is often assumed to be the wild progenitor of the former (for a summary see Gladstones 1974, who regards them as varieties of the same species). *L. palaestinus, L. pilosus* and *L. cosentinii* (group 4) are generally considered to have many morphological characters in common. The first two have the same chromosome number (Pazy et al. 1977); *L. cosentinii*, though differing in chromosome number, has even been united with *L. pilosus* to form a single species (*L. varius* L.; Amaral Franco & Pinto da Silva 1968, Chamberlain 1970, Zohary 1972).

Similarity of seed coat structure, however, may also occur in species which are not closely related: *L. angustifolius* and *L. micranthus* (group 3) differ greatly in morphological characters as well as in chromosome numbers. Their seed coat structures, however, are very similar.

Intraspecific variation has been found in some cases: e.g. native and introduced *L. angustifolius* (Fig. 3 C–E and 3 F); wild and cultivated *L. luteus* (Fig. 2 A–D and 2 E), in the latter case confirmed by cytogenetic studies (Kazimierski & Kazimierska 1975).

No comprehensive SEM studies of the seeds of leguminous genera seem to have been published yet (Brisson & Peterson 1976 p. 492). In any case, the variation displayed by the Old World species of *Lupinus* seems impressive and the contrast with the relative uniformity of the seed coats of the six New World species is striking. Further studies of a wider array of New

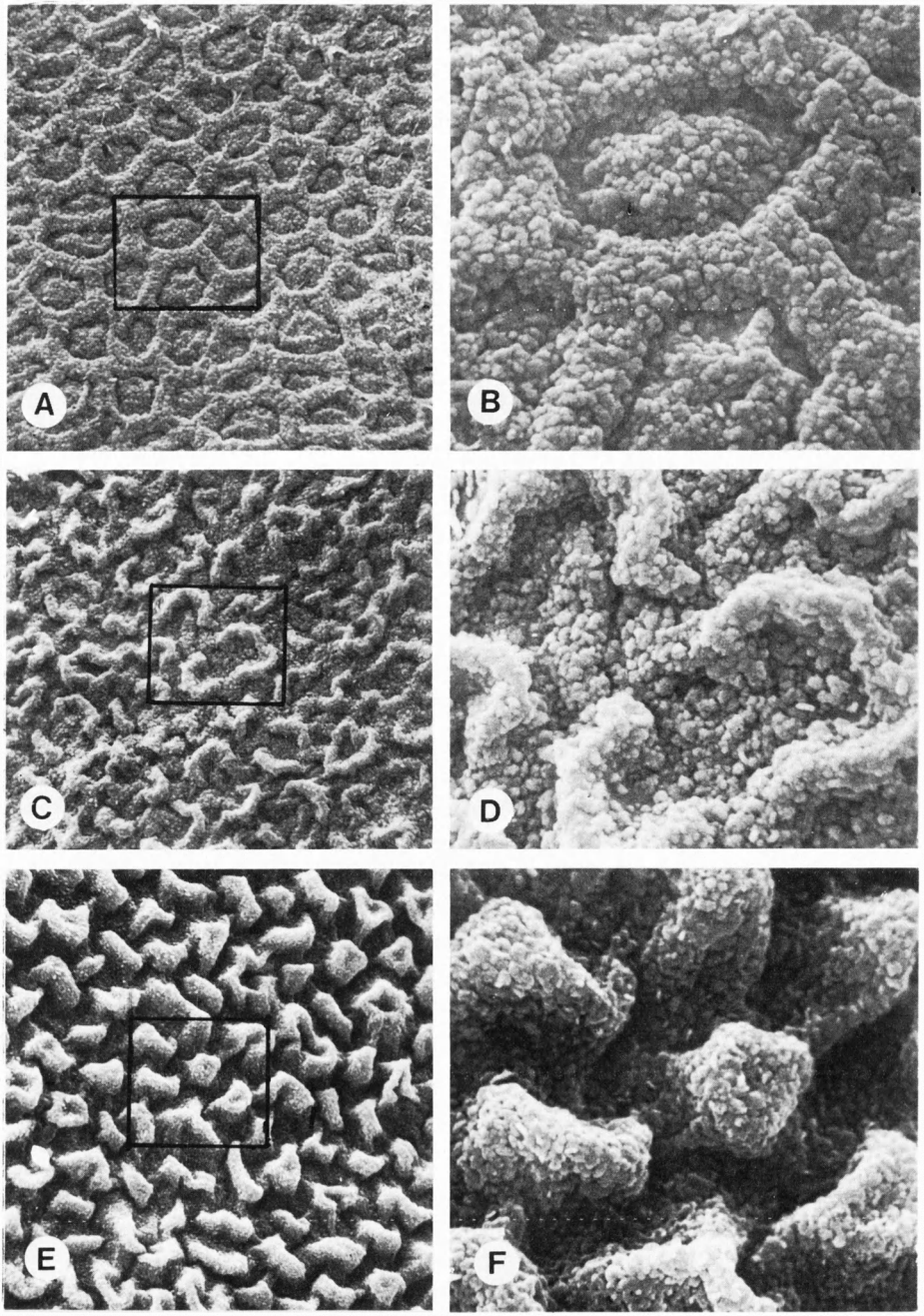


Fig. 1. Seed coats. A–D: *L. albus*. – A, B: Regularly ridged. – C, D: Irregularly ridged. – E, F: *L. graecus*. – A, C, E × 650, B, D, F × 2600.

Table 1. Collections of *Lupinus* species studied. – Old World species: *L. albus* to *L. pilosus*. New World species: *L. albicaulis* to *L. succulentus*.

Species	Reference	Origin	Fig.
L. albus L.	C/14	Cult. (Bot. Garden, HUJ)	
	C/11	Cult. (Pl. Introd. Service, Bet Dagan)	
	Herb. HUJ	Cult.? Golan Heights, Birket Ram	1 A, B
	C/22	Cult. (A. Horovitz, Tel-Aviv)	1 C, D
	C/55	Cult. (E. A. Bell, King's College, London No. 7)	
L. angustifolius L. var. *angustifolius*	ANG-P/75-3	Israel, Sharon Plain, Nordia	
	ANG-P/75-4	Israel, Sharon Plain, Raanana junction	3 C, D
L. angustifolius var. *basalticus*	C/3	Israel, W. Galilee (A. Horovitz Lb-21)	3 E
	C/4	Israel, W. Galilee (A. Horovitz Lb-20)	
	C/5	Israel, W. Galilee (A. Horovitz Lb-24)	
	ANG-P/76-12	Israel, Upper Galilee, Yiron (introduced)	3 F
L. cosentinii Guss. (*L. varius* ssp. *varius*)	C/18	Morocco (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	4 E, F
L. graecus Boiss. & Sprun.	C/20	Greece (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	1 E, F
L. luteus L.	C/58	Israel, Sharon Plain, Herzliya (Pl. Introd. Serv., Bet-Dagan, as *L. aureus*)	2 A, B
	LUT-P/75-4	Israel, Sharon Plain, Raanana junction	
	Herb. HUJ	Israel, Sharon Plain, Gan Shmuel	2 F
	C/19	Cult. (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	
	Herb. HUJ	Spain, Algeciras	
	C/17	Portugal, Cult. (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	2 C, D
	C/21	Cult. (Wageningen)	2 E
L. micranthus Guss.	MIC-P/75-5	Israel, W. Galilee, Kefar Liman	3 A, B
	MIC-P/75-6	Israel, Upper Galilee, Mt. Meron	
	C/37	Crete, Paleochora-Kandanos (J. Katznelson No. 30)	
L. palaestinus Boiss.	PAL-P/75-2	Israel, Sharon Plain, Ilanoth	4 B–D
	C/10	Israel, Sharon Plain, Tel Barukh	
	PAL-P/75-1	Israel, Sharon Plain, Tel-Tsur	
L. pilosus Murr. (*L. varius* ssp. *orientalis*)	C/2	Israel, Shomron, Wadi Milek (A. Horovitz Lv-31)	4 A
	C/7	Israel, Jezreel Valley, Dovrath–Tel Adashim	
	C/8	Israel, Upper Galilee, Rosh Pinna	
	PLO-P/76-11	Israel, Upper Galilee, Amiad	
	C/9	Israel, Lower Galilee, Mitspe	
	PLO-P/76-10	Israel, Upper Jordan Valley, N of Ein Gev	
	C/23	Crete (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	
	C/56	Crete, Kandanos (J. Katznelson No. 32 A)	
L. albicaulis Torr.	C/40	? (E. A. Bell, King's College, London)	5 F
L. arboreus Sims	Herb. HUJ	California, Rose 33228	5 B
L. aschenbornii S. Schau.	Herb. HUJ	Mexico, Rudd 1028	5 C
L. montanus H. B.	Herb. HUJ	Mexico, Rudd 1029	5 E
L. mutabilis Sweet	C/24	Cult. (Zentr. Inst. Genet. Kulturpfl. Gatersleben)	5 A
	C/41	Cult. (E. A. Bell, King's College, London)	
L. succulentus Dougl.	Herb. HUJ	California, Rudd 3436	5 D

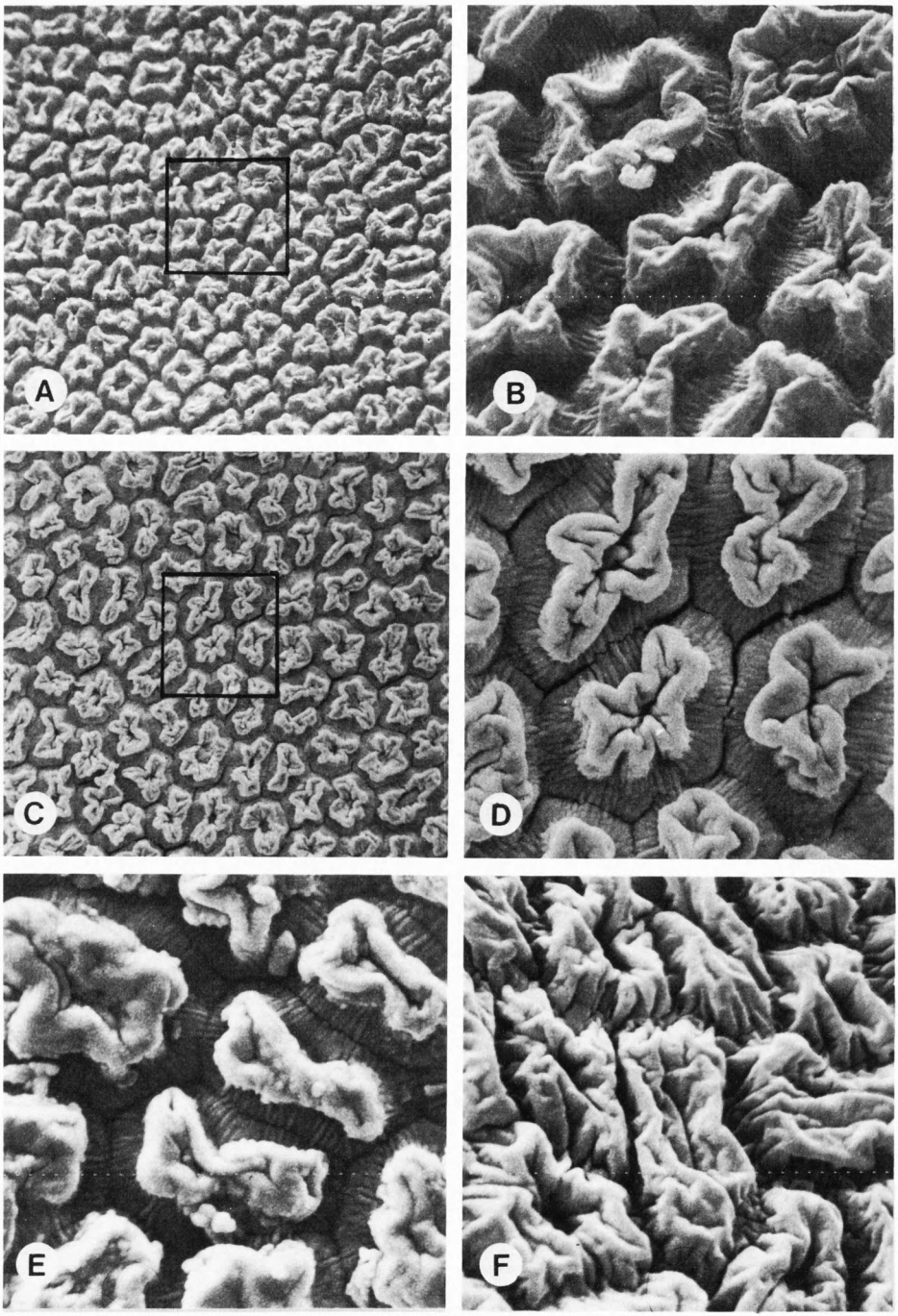


Fig. 2. Seed coats of *L. luteus*. – A, B: Plant growing wild in Israel. – C, D: Plant growing wild in Portugal. – E: Cultivated plant. – F: Herbarium specimen. Seeds perhaps immature. – A, C ×650, B, D–F ×2600.

World species are desirable to discover whether or not this uniformity is representative. The observations made so far, seem at all events to agree with the patterns of chromosome numbers found for the Old World lupins (cf. Pazy et al. 1977). According to the variation in both seed surface and chromosome number, the relatively few Old World *Lupinus* species may be regarded as being representatives of isolated species groups.

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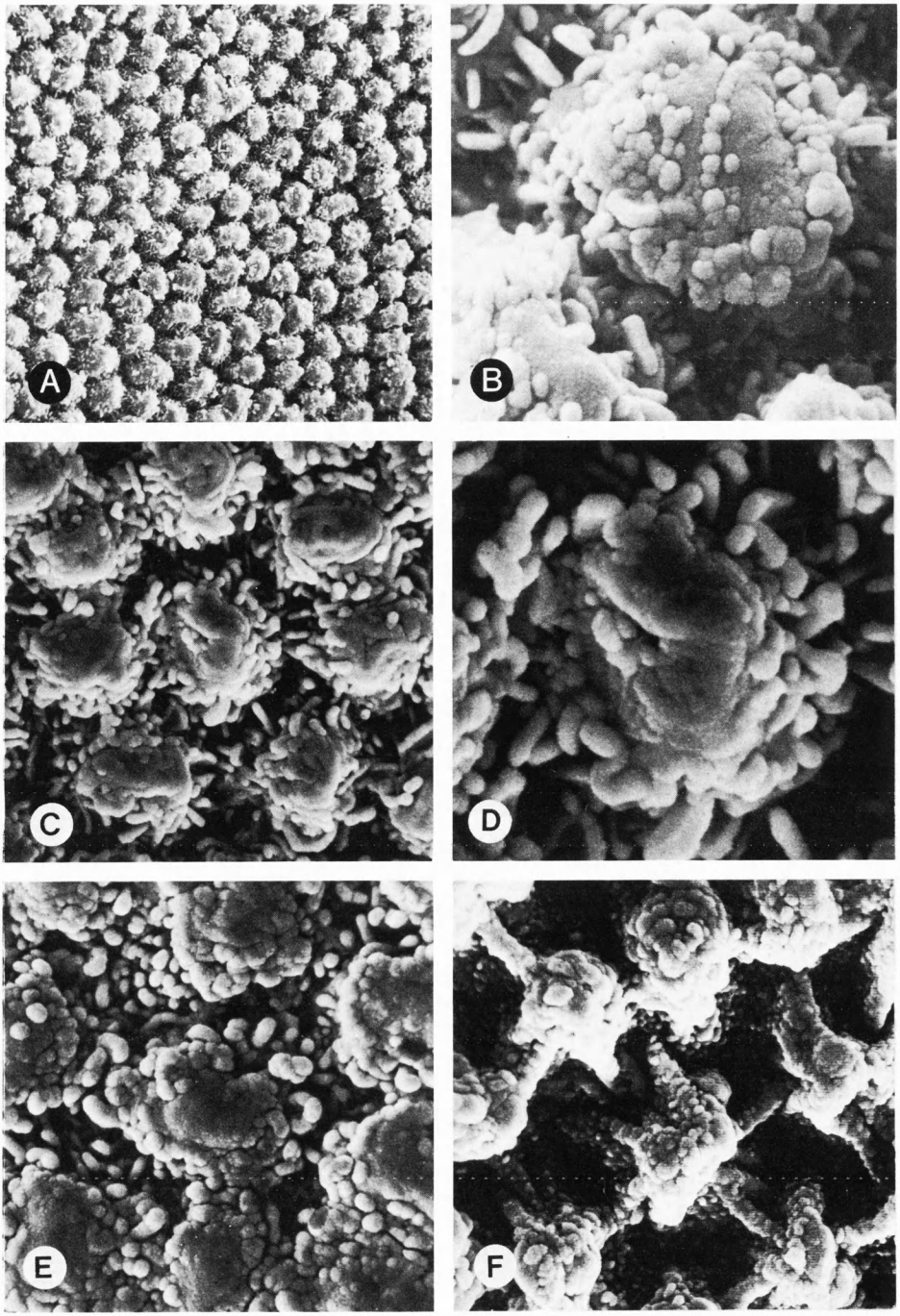


Fig. 3. Seed coats. – A, B: *L. micranthus*. – C, D: *L. angustifolius* var. *angustifolius* – E: *L. angustifolius* var. *basalticus*. – F: *L. angustifolius*. Introduced (?). – A × 650, B, D × 6500, C, E, F × 2600.

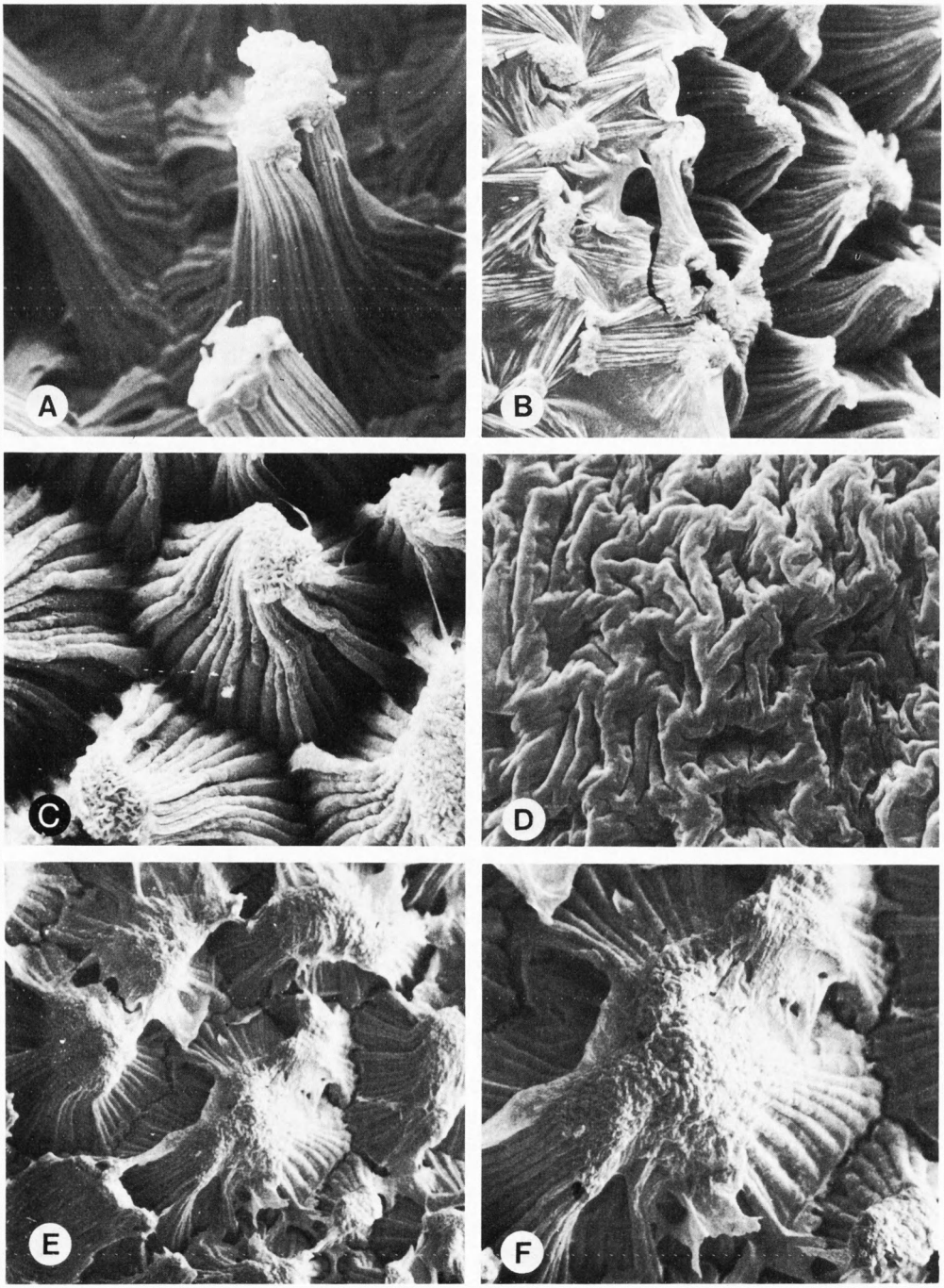


Fig. 4. Seed coats. – A: *L. pilosus*. – B–D: *L. palaestinus*. – B: Part of the seed with intact membrane. – C: Seed coat without membrane. – D: Surface of fascicled palisade cells. – E, F: *L. cosentinii*. – A, B, E × 130, C, F × 260, D × 2600.

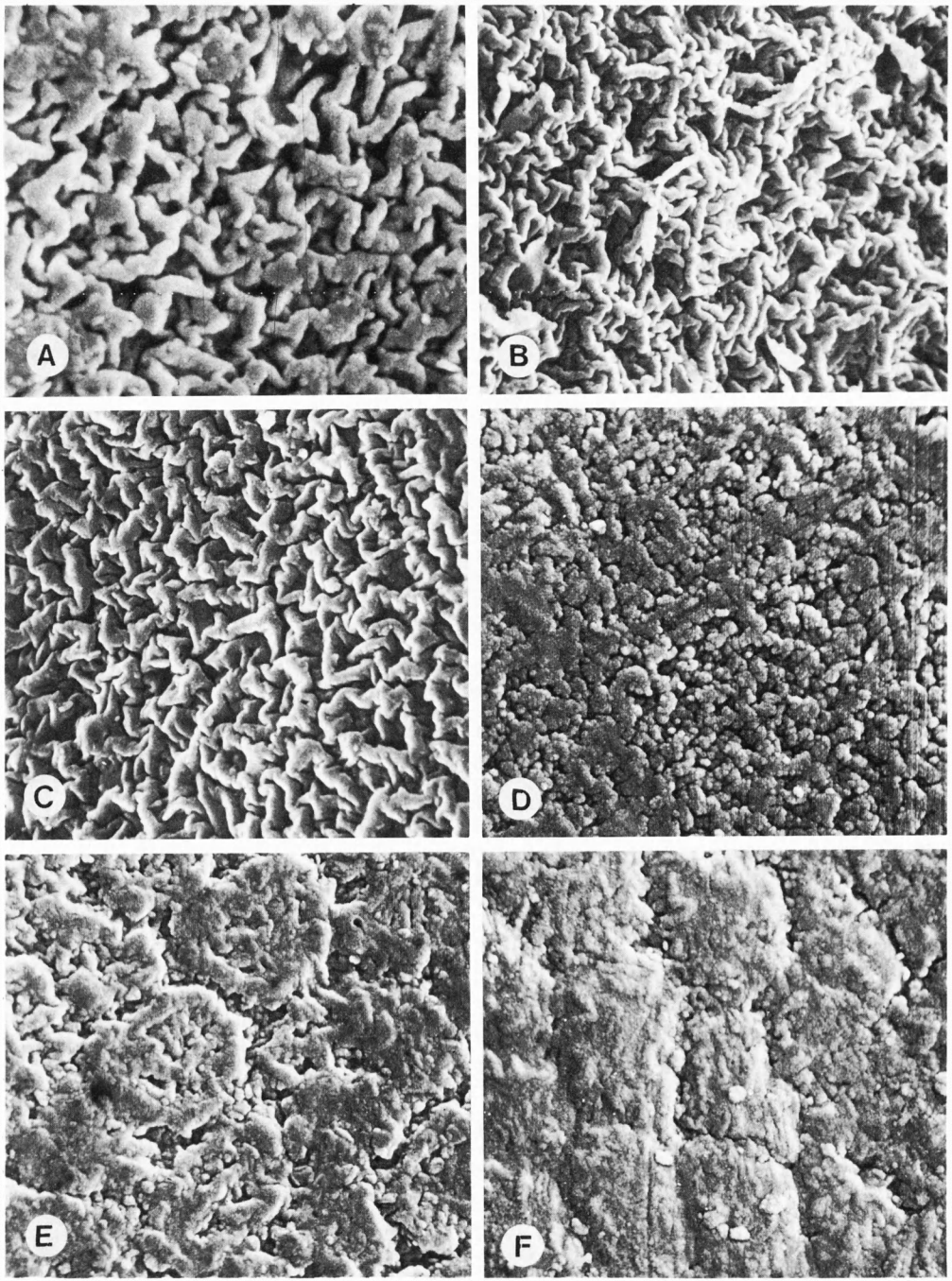


Fig. 5. Seed coats. – A: *L. mutabilis*. – B: *L. arboreus*. – C: *L. aschenbornii*. – D: *L. succulentus*. – E: *L. montanus*. – F: *L. albicaulis*. – All × 2600.

Chromosome numbers for some Leguminosae from Iraq

Abdul-Ridha A. Al-Mayah and Ihsan A. Al-Shehbaz

Al-Mayah, A.-R. A. & Al-Shehbaz, I. A. 1977 12 30: Chromosome numbers for some Leguminosae from Iraq. *Bot. Notiser 130:* 437–440. Stockholm. ISSN 0006-8195.

Chromosome numbers are reported for 79 collections representing 49 species in 19 genera of Leguminosae. Of these, 12 are first reports. Observations deviating from those of previous reports are discussed. Meiotic irregularities were observed in several species. The karyotypes of a few species are described for the first time.

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In the present paper, chromosome counts are reported for wild and cultivated species of Leguminosae from Iraq. Unless otherwise indicated, the counts given here are in accordance with those of previous reports as listed in the indices edited by Fedorov (1969) and Moore (1973, 1974), and are presented without further comment. For those species where meiosis was not quite regular, the types of irregularities are briefly discussed. The nomenclature follows Townsend (1974).

Flower buds or root tips were fixed in Carnoy's fluid. Meiotic material was squashed in aceto-carmine or aceto-orcein after treating the buds with boiling HCl for a few seconds and then washing them in water for 15–30 minutes. Most root tips were pretreated with 0.002 M 8-hydroxyquinoline for 3–4 hours at room temperature. Roots of *Vigna* species and of *Lathyrus vinealis* were pretreated with 0.5% colchicine for 2–3 hours at room temperature. Most root tips were squashed in aceto-carmine following the conventional method. Those of the genera *Medicago* and *Melilotus* were squashed in aceto-orcein after boiling them in the stain for 5 minutes and twice repeating the boiling process. Lacto-propionic-orcein was used for the roots of *Glycyrrhiza* and *Onobrychis* following the procedure of Dyer (1963).

Under each species, the chromosome number(s) given is followed by the name(s) of the physiographic districts and localities for the material on which the chromosome count(s) were made. We have followed Guest (1966) in assigning each physiographic district to a given locality. The abbreviations IAS and AAM stand for I. A. Al-Shehbaz and A. A. Al-Mayah respectively. An asterisk following the diploid number indicates that the count was made from the somatic cells of the pistil. All other diploid counts were obtained from root tips. All voucher specimens are deposited in the Baghdad University Herbarium (BUH), where they are available for inspection.

This paper is part of a M. Sc. thesis submitted by the senior author to the University of Baghdad.

Albizia lebbeck (L.) Benth. – n = 13. LCA: Wazeeriya, Baghdad, AAM 75205 (cult.). This is probably the second count for this species, after that made by Patil (1958).

Amorpha fruticosa L. – n = 20. LCA: Wazeeriya, Baghdad, AAM 76146 (cult.).

Astragalus dactylocarpus Boiss. – n = 8. LCA: Sudur, AAM 7631. This is the first report for this species.

Astragalus laguriformis Freyn – 2n = 14. MAM: Sharanish, AAM 75280. This is the first report for this species. All chromosomes are medium-sized. Two pairs are metacentric and the remaining five pairs are submetacentric.

Astragalus mossulensis Bunge – n = 8. LEA: Wadi Al-Ahmar, N of Muqdadiya, AAM 75149. Ledingham & Rever (1963) previously reported 2n = 32 for this species.

Astragalus russelii Banks & Sol. – n = 8. DSD:

Jabal Sanam, AAM 76415. This is the first report for this species. Townsend (1974) indicated that the species is restricted to northern and north-central Iraq. However, we have examined a large number of specimens that were not available to him, and the species does seem to extend all the way to the southern part of the country.

Astragalus zubairensis Eig – n = 8. DWD: Ukhaidhir, AAM 76136. This is the first report for this species.

Glycyrrhiza glabra L. var. *glandulifera* (Waldst. & Kit.) Reg. & Herd. – n = 8. LBA: Mikhrag, N of Fao, AAM 75192. This is the first report for this variety. It agrees with the other reported counts for the species, as well as with counts reported for other species of the genus.

Hymenocarpus circinnatus (L.) Savi – n = 8. MRO: Bekhal, IAS & AAM 76194.

Lathyrus annuus L. – n = 7. LCA: Saddat Al-Hindiya, AAM 7641.

Lathyrus aphaca L. – n = 7, 2n = 14*. LBA: Mikhrag, N of Fao, AAM 7620. LCA: Saddat Al-Hindiya, AAM 7642.

Lathyrus chloranthus Boiss. & Bal. – n = 7, 2n = 14*. MRO: Nawanda, southern slope of Algird Dagh, IAS & AAM 76295. This is the first report for this species.

Lathyrus cicera L. – n = 7, 2n = 14*. MAM: Sulaf, IAS & AAM 76229.

Lathyrus gorgoni Parl. – n = 7, 2n = 14*. LEA: Harooniya, AAM 7657.

Lathyrus inconspicuus L. – n = 7, 2n = 14*. MAM: Bamerni, near Sarsang, IAS & AAM 76260.

Lathyrus pratensis L. – n = 7. MRO: Sidikan, IAS & AAM 76287. Chromosomal fragments were occasionally observed. The association of two bivalents with the nucleolus at diakinesis indicates that secondary constrictions are present on two out of the seven pairs of chromosomes.

Lathyrus tuberosus L. – n = 7. MRO: Between Darband and Chouman, IAS & AAM 76296.

Lathyrus vinealis Boiss. & Noë – 2n = 14. MRO: Hirdi, IAS & AAM 76289; Haj Omran, IAS & AAM 76302. This is the first report for this species. The karyotype is made up of a pair of long metacentric chromosomes, a pair of long submetacentric chromosomes, four pairs of medium-sized submetacentric chromosomes and one pair of small metacentric chromosomes.

Lens orientalis (Boiss.) Hand.-Mazz. – n = 7, 2n = 14*. MRO: Chouman, IAS & AAM 76173. This is the first report for this species. Counts of n = 7 were reported for other species of the genus.

Lotus corniculatus L. var. *corniculatus* – n = 6, 2n = 12*. LBA: Ma'qil, AAM 7607. Diploids and tetraploids based on x = 6 have been reported for this genus.

Medicago sativa L. – 2n = 32. DSD: Najaf, AAM 75132 (cult.). LBA: Mikhrag, N of Fao, AAM 75193 (cult.).

Melilotus alba Med. – n = 8, 2n = 16. LBA: Basra, AAM 75183.

Melilotus indica (L.) All. – n = 8, 2n = 16. LCA: Baghdad, AAM 7531.

Onobrychis crista-galli (L.) Lam. – n = 8, 2n = 16*. DGA: Adhaim, AAM 7510.

Onobrychis galegifolia Boiss. – 2n = 16. MAM: Amadiya, AAM 75218. This is the first report for this species.

Onobrychis haussknechtii Boiss. – 2n = 16. FPF: Badra, IAS & AAM 76154. This is the first report for this species.

Pisum formosum (Stev.) Alef. – 2n = 14. MAM: Swara Tuka, AAM 75332. This is the first report for this species. All the chromosomes are nearly equal in size. Six pairs are submetacentric, one of which has a secondary constriction. The seventh pair is metacentric.

Pisum sativum L. – n = 7. MAM: Sulaf, IAS & AAM 76227. MRO: Bekhal, IAS & AAM 76191. In a few cells six bivalents and two univalents were observed at diakinesis and first metaphase. Lagging chromosomes were occasionally observed at first anaphase.

Scorpiurus muricatus L. var. *subvillosus* (L.) Lam. – n = 7, n = 8. LEA: Wadi Al-Ahmar, AAM 7547. In some plants eight bivalents were observed in most cells at first metaphase. However, few cells showed seven bivalents and two

univalents. In other plants seven bivalents, or five bivalents and four univalents were observed. This taxon certainly needs a more detailed study in Iraq. Heyn & Raviv (1966) showed that polyploidy based on x = 7 is involved in all the morphological extremes they studied in this species.

Securigera securidaca (L.) Deg. & Doerfl. – n = 6. LBA: Basra, AAM 7518.

Sesbania cannabina (Retz.) Poir. – n = 6. LCA: Baghdad, AAM 75241 (cult.). This is the first report for the species.

Sesbania sesban (L.) Merrill – n = 6. LCA: Baghdad, AAM 76340 (cult.). In a few cells five bivalents and two univalents were observed at first metaphase, while in others lagging chromosomes were seen at second anaphase.

Sophora gibbosa (DC.) Yakovl. – n = 9. DLJ: Thirthar, AAM 76522. This is the first report for the species. Counts of n = 9 have been reported previously for many species of the genus.

Trifolium echinatum M.B. – n = 8. LEA: Harooniya, AAM 7555.

Vicia assyriaca Boiss. – n = 6. MAM: Between Amadiya and Sulaf, IAS & AAM 76221. MRO: Bekhal, IAS & AAM 76186. Our count for the species differs from that (2n = 14) reported by Plitmann (1970).

Vicia ervilia (L.) Willd. – n = 7. MAM: Between Dohuk and Zawita, IAS & AAM 76249. MRO: Chouman, IAS & AAM 76174. – 2n = 14. MJS: Karsi, IAS & AAM 75123. The karyotype of this species is made up of one pair of small acrocentric chromosomes with satellites, a pair of medium-sized metacentric chromosomes, a pair of long metacentric chromosomes, two pairs of long submetacentric chromosomes and two pairs of long acrocentric chromosomes.

Vicia faba L. (all cult.) – n = 6. LBA: Mikhrag, N of Fao, AAM 7611. DSD: Safwan, AAM 7651. n = 7, 2n = 14. LCA: Baghdad, AAM 75450.

Vicia hybrida L. – n = 6, 2n = 12*. MAM: Between Dohuk and Zawita, IAS & AAM 76217. MRO: Salah ad-Din, IAS & AAM 76206; Bekhal, IAS & AAM 76189. FPF: Koma Sang, near Mandali, IAS & AAM 76151. Five bivalents and two univalents were occasionally observed at first metaphase, while one or two lagging chromosomes were seen in a few cells at first anaphase.

Vicia koeieana Rech. f. – n = 7. MRO: Bewas, IAS & AAM 76281: Hirdin, IAS & AAM 76283; Bassan, IAS & AAM 76293. Our count agrees with the earlier one reported by Plitmann (1970). In the three collections cited above, a number of meiotic irregularities were observed. A few cells showed five bivalents and a quadrivalent or six bivalents and two univalents at first metaphase. One or two lagging chromosomes or one or two chromosomal bridges were observed in many cells at first anaphase.

Vicia michauxii Spreng. – n = 7, 2n = 14*. MAM: Between Dohuk and Zawita, IAS & AAM 76254; Sulaf, IAS & AAM 76237. MRO: Salah ad-Din, IAS & AAM 76203; Chouman, IAS & AAM 76170. The only previous count available for this species is 2n = 12. This was made by Coutinho some 32 years ago (Fedorov 1969).

Vicia narbonensis L. – n = 7. MAM: Sulaf, IAS & AAM 76223; Kani Sang, IAS & AAM 76224; Zawita, IAS & AAM 76246. MRO: Chouman, IAS & AAM 76168; Bekhal, IAS & AAM 76187. Chromosomal fragments or one or two lagging chromosomes were observed in a few cells at first or second anaphase.

Vicia palaestina Boiss. – n = 7, 2n = 14*. MRO: Bekhal, IAS & AAM 76190. MJS: Karsi, IAS & AAM 75124. Four bivalents and six univalents were occasionally observed at first metaphase.

Vicia peregrina L. – n = 7, 2n = 14*. MAM: Sulaf, IAS & AAM 76230. MRO: Salah ad-Din, IAS & AAM 76202. Six bivalents and two univalents were observed in a few cells at first metaphase. Our counts agree with those reported by Kuzmanov & Markova (1973) and Zohary (1972) but not with those of Plitmann (1970).

Vicia sativa L. var. *sativa* – n = 6, 2n = 12*. MRO: Bekhal, IAS & AAM 76188; Salah ad-Din, IAS & AAM 76208. FPF: Mandali, IAS & AAM 76152. LCA: Baghdad, AAM 7646.

Vicia sativa var. *amphicarpa* Boiss. – n = 5, 2n = 10*. LCA: Saddat Al-Hindiya, AAM 7640. In many cells four bivalents and two univalents or three bivalents and four univalents were

observed at first metaphase. Plitmann (1973) and Kuzmanov & Markova (1973) have reported n = 7 for this species.

Vicia sericocarpa Fenzl – n = 6, 2n = 12*. MRO: Chouman, IAS & AAM 76178. Lagging chromosomes or chromosomal fragments or bridges were occasionally observed at first anaphase.

Vicia tenuifolia Roth – n = 7. MAM: Sarsang, IAS & AAM 76241; Zawita, IAS & AAM 76245. Six bivalents and two univalents or five bivalents and four univalents were observed in a few cells at first metaphase. Chromosomal fragments were occasionally seen at first anaphase. All the previous counts for this species reported 2n = 24, although counts of 2n = 14 and 2n = 28 have been reported for *V. cracca* L. Townsend (1974) stated that the Iraqi material which he treated as *V. tenuifolia* was intermediate between the typical plant and *V. cracca* subsp. *stenophylla* Vel. Davis (1970), on the other hand, considered *V. tenuifolia* to be a subspecies of *V. cracca*. Our cytological findings are thus compatible with the view held by Davis.

Vicia villosa Roth – n = 7. MRO: Hirdin, IAS & AAM 76284; Haj Omran, IAS & AAM 76297; Bassan, IAS & AAM 76292.

Vigna radiata (L.) Wilczek – 2n = 22. MAM: Sharanish, AAM 75303 (cult.).

Vigna unguiculata (L.) Walp. – 2n = 22. LCA: Adhamiya, Baghdad, AAM 76306 (cult.).

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Embryology of Trichodesma (Boraginaceae)

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The embryology of *Trichodesma indicum* R. Br. and *T. zeylanicum* R. Br. has been studied. The development of the anther conforms to the dicotyledonous type. The tapetal cells become multinucleate and the nuclei tend to fuse and form polyploid nuclei. A few cells, underlying the archesporial initials on the connective side of the anther, enlarge and become vacuolated and multinucleate, resembling the tapetum. The pollen grains are shed at the two-celled stage. The stylar canal is filled with a transmitting tissue which extends over the micropyle of the anatropous ovules and abuts onto the placenta, behaving like an obturator. The megaspore tetrads are linear in *T. indicum* and consistently T-shaped in *T. zeylanicum*. A tendency towards nucellar apospory was observed in both species. The aposporic embryo sacs degenerate at the two-nucleate (sometimes at the four-nucleate) stage. The endosperm is nuclear. Embryo development follows the Asterad type, conforming to the Polygonum variation in *T. indicum* and the Lamium variation in *T. zeylanicum*. The pericarp is differentiated into a one-layered epicarp, a 6–8-layered, resiniferous mesocarp and a one-layered endocarp with radially elongated cells. The cells bordering the interlocular septum become strongly thickened and behave like the endothecial cells in the anther. The seed coat is 8–10-layered with a tanniniferous innermost layer.

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The genus *Trichodesma* belongs to the tribe Cynoglosseae (Boraginaceae) and includes about 21 species distributed within tropical and subtropical Africa, Asia and Australia. In South India, this genus is represented by two species, viz. *Trichodesma indicum* and *T. zeylanicum* (Gamble 1928).

Extensive morphological, anatomical and cytological studies have been made on the subfamily Boraginoideae. Recent work is that of Khanna (1964 a, b) on *Trichodesma amplexicaule, Mertensia platyphylla* and *M. paniculata,* Fathima (1967) on *Trichodesma zeylanicum,* Nagaraj & Fathima (1968) on *Adelocaryum coelestinum* and Khaleel (1974) on *Cynoglossum denticulatum.*

The present investigation deals with anther development, micro- and megasporogenesis, development and organization of the megagametophyte, fertilization, endosperm and embryo development, and the structure and development of the pericarp and seed coat in *Trichodesma indicum* R. Br. and *T. zeylanicum* R. Br.

Material and methods

The material was collected from various localities near to Bangalore, Bannerghatta and Mysore in Mysore State, India. Young flower buds, open flowers, fruits and nutlets were fixed in FAA and embedded in paraffin wax. Sections, 5–15 μm thick, were cut and stained in Heidenhain's iron alum haematoxylin with eosin as a counterstain. Sections of fruits and seeds were stained with safranin and fast green. Fresh ovules were dissected to study the endosperm. They were also treated with lactic acid or KOH at 50–60°C and stained with cotton blue to study the course of the vascular strands.

Flower

The flowers of *Trichodesma* are actinomorphic, bisexual and hypogynous. The calyx consists of five densely hispid lobes that are hastate at the base in *T. indicum* and rounded in *T. zeylanicum*. The corolla consists of five pale-blue petals united to form a tube, which in *T. zeylanicum* is equal in length to that of the rounded lobes. Two glandular spots are present on each lobe at the throat of the corolla tube in *T. indicum*. The stamens are connivent, densely hirsute, and their tips are spirally twisted, ending in hair-like points. The ovary is superior, bicarpellary, syncarpous and bilocular in the early stages, but later becomes quadrilocular due to the development of a false septum, each locule then containing a single anatropous ovule on an axillary placenta. The style is terminal and the stigma is simple. The fruit is pyramidal, containing a central quadrangular carpophore with four bays each bearing an ovoid, oblong nutlet adnate to the torus. The nutlets are smooth. The floral parts develop in an acropetal succession.

The stylar canal consists of a transmitting tissue composed of compactly arranged, elongated, glandular cells. The transmitting tissue extends over the micropyle and abuts onto the placenta, behaving like an obturator (Fig. 3 A, B). It continues spreading along the upper part of the funiculus and finally covers the upper part of each locule. It persists until the later stages of embryo development.

Microsporogenesis and anther development

Trichodesma indicum and *T. zeylanicum* are protandrous. A young anther in transection is rounded in outline and consists of a mass of homogeneous cells. It soon becomes four-lobed and a plate of four to five hypodermal cells, each possessing conspicuous nuclei and dense cytoplasm, develops in each of the four lobes (Fig. 1 A). Periclinal divisions in these cells result in the formation of a primary parietal layer and a primary sporogenous layer (Fig. 1 B). The primary parietal layer divides periclinally to form two secondary parietal layers (Fig. 1 C). The outer secondary parietal layer divides again, while the inner one functions as the tapetum (Fig. 1 D, E). Thus the anther wall consists of four layers, viz., epidermis, endothecium, middle layer and tapetum (Fig. 1 E). The tapetal cells are uninucleate initially but become multinucleate in later stages with the appearance of vacuoles in the cytoplasm (Fig. 1 E). The nuclei in some of these cells have a tendency to aggregate and fuse, forming polyploid nuclei with many nucleoli. After its cells have elongated radially and tangentially, at about the time the microspores are formed, the endothecium develops fibrillar bands of thickenings. The middle layer degenerates and the outer tangential walls of the epidermal cells become heavily cutinized (Fig. 1 N). The development of the anther wall thus corresponds to the dicotyledonous type (Davis 1966).

A few cells which underly the archesporial initials on the connective side of the anther, enlarge and become vacuolated. They become binucleate when the archesporial cells divide and later multinucleate, resembling the tapetal cells (Fig. 1 B–D). They persist until microsporogenesis is completed and then degenerate along with the tapetal cells. They appear to take part in the nutrition of the developing microsporocytes before the tapetal cells are formed.

The cells of the primary sporogenous layer undergo a number of periclinal and anticlinal divisions to form a massive sporogenous tissue (Fig. 1 C–E). The microsporocytes enlarge and become rounded before dividing meiotically (Fig. 1 F–H). The cell divisions are simultaneous and result in tetrahedral and decussate microspore tetrads (Fig. 1 I, K). In *T. zeylanicum* isobilateral tetrads are also formed. The microspores separate and develop a thick wall (Fig. 1 L, M). The centrally placed nucleus migrates to one side of the microspore and divides mitotically to form a lenticular generative cell and a large vegetative cell. The generative cell detaches itself and becomes engulfed in the cytoplasm of the vegetative cell and lies near the nucleus of the same (Fig. 1 M). The pollen grains are triporate and possess a smooth exine. They are shed at the two-celled stage.

Anther dehiscence takes place at the junction of the pollen sacs, where the endothecial cells lack fibrillar thickenings and the epidermal cells are slightly smaller. Each locule opens out independently (Fig. 1 O, P).

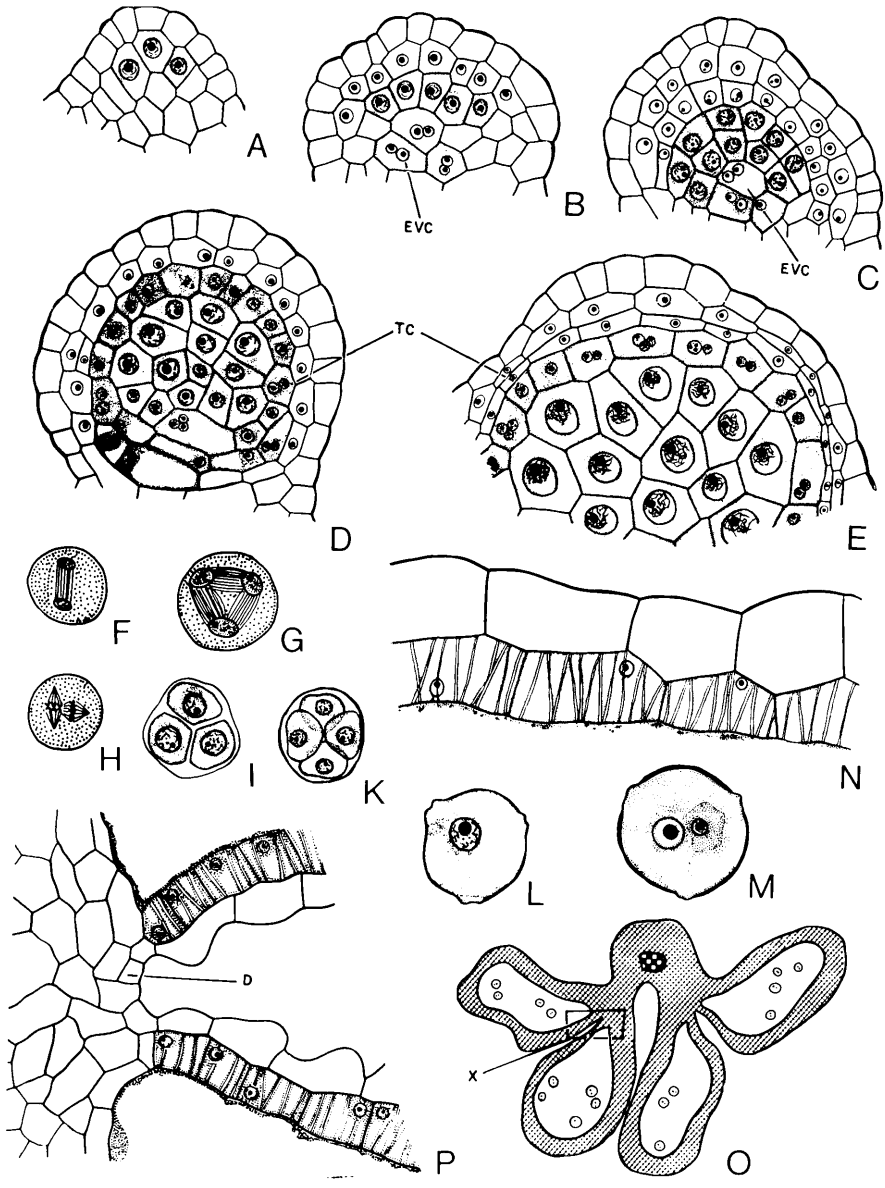


Fig. 1. Microsporogenesis and anther development in *Trichodesma indicum*. – A: TS of anther lobe showing archesporial initials. – B: TS of anther lobe showing primary parietal cells, primary sporogenous cells and enlarged vacuolated cells. – C: TS of anther lobe showing secondary parietal layers, sporogenous cells and enlarged vacuolated cells. – D: TS of anther lobe showing wall layers, tapetum and sporogenous tissue. – E: TS of portion of anther lobe showing wall layers, tapetum and microsporocytes. – F–H: Meiosis. – I, K: Tetrahedral and decussate microspore tetrads. – L, M: Pollen grains. – N: TS of portion of anther wall showing epidermis, fibrillar endothecium and degenerating tapetum. – O: TS of anther showing the region of dehiscence. – P: Portion marked X in Fig. 1 O enlarged. – A–H, N, P × 265, I–M × 530, O × 30. – D region of dehiscence, EVC enlarged vacuolated cells, TC tapetal cells.

Megasporogenesis and megagametophyte development

The ovules are anatropous, unitegmic and tenuinucellar. They arise on the axillary placenta as small papillate outgrowths and are supplied with a single vascular strand which branches inside the massive integument, the branches running close to the epidermis.

A single hypodermal archesporial initial differentiates in the nucellar dome and is recognizable by its dense cytoplasm and conspicuous nucleus. Occasionally two to three archesporial cells differentiate. However, only one of them functions further and the others degenerate (Fig. 2 A, B). The functional archesporial cell enlarges and becomes the megasporocyte (Fig. 2 C). Meiotic divisions in the megasporocyte result in linear tetrads in *Trichodesma indicum* (Fig. 2 D–F) and T-shaped tetrads in *T. zeylanicum*. The chalazal megaspore enlarges and functions further, while the three micropylar spores degenerate (Fig. 2 G–I).

The development of the gametophyte corresponds to the Polygonum type (Maheshwari 1950), see Fig. 2 H–L. The antipodals degenerate after fertilization. The two polar nuclei fuse either during or after fertilization.

The cells of the nucellar epidermis become disorganized at about the time that a four-nucleate gametophyte is formed. The surrounding nucellar cells also become crushed during this process, which brings the gametophyte into direct contact with the innermost layer of the integument (Fig. 2 K, L). However, no endothelium is organized.

A tendency towards nucellar apospory was observed. The aposporic embryo sacs initiate as enlarged cells below the archesporial cells and range from four to twelve in number (Fig. 2 B, C). They develop the characteristic vacuolation of aposporic embryo sacs and attain a regular polarity, thus simulating two-nucleate embryo sacs (Fig. 2 D–F). They seldom develop further and degenerate as the normal gametophyte enlarges. Rarely, however, they may reach a four-nucleate stage. The remnants of crushed, degenerating aposporic embryo sacs are visible during the various stages of gametogenesis as dark-staining masses.

Endosperm

The endosperm is nuclear, conforming to the Borago type (Svensson 1925). Division of the primary endosperm nucleus always precedes that of the zygote (Fig. 3 C) and about 16–32 free nuclei are formed (Figs. 3 D–G, 4 A, B). After a few more divisions, centripetal wall formation takes place, as a result of which the endosperm becomes cellular (Fig. 4 C–F). At this stage, small granules of reserve food material are found in the endosperm cells. When the embryo has reached the heart-shaped stage, most of the endosperm is consumed, leaving only one or two layers of cells. The endosperm is completely consumed as the embryo reaches maturity, so that none remains in the seed.

Embryo

The development of the embryo conforms to the Asterad type. In *Trichodesma indicum*, it develops according to the Polygonum variation and in *T. zeylanicum* according to the Lamium variation (Johansen 1950).

The zygote enlarges considerably before it divides transversely, resulting in the formation of a short terminal cell *ca* and a long basal cell *cb* (Figs. 5 A, B, 6 A, B). The next division in the terminal cell *ca* is by a vertical wall, whereas the basal cell *cb* divides by a transverse one, resulting in a T-shaped proembryonal tetrad (Figs. 5 C, D, 6 C). The upper two tiers of cells in the proembryonal tetrad are designated as *ci* and *m*. The two juxtaposed cells formed by the division of the cell *ca* divide vertically in a plane perpendicular to the previous one and organize the quadrant *q* (Figs. 5 F–I, 6 D–F). Meanwhile, the middle cell *m* divides vertically and the basal cell *ci* divides transversely resulting in an eight-celled embryo, the cells of which are placed in four tiers and are designated as *n'*, *n*, *m* and *q* respectively (Figs. 5 E, 6 F). In *T. indicum* this is followed by a transverse division in the cells *q* forming two tiers of an octant *l* and *l'* (Fig. 5 K, L). The cell *m* undergoes two vertical divisions (Fig. 5 K). The four cells of the tier *m* thus formed, and of the tier *l'* undergo periclinal divisions to form dermatogen *de* (Fig. 5 L, M). Further divisions in the embryonal mass after the second periclinal division are irregular (Fig. 5 M–S). The region *l* forms the stem tip, tier *l'*

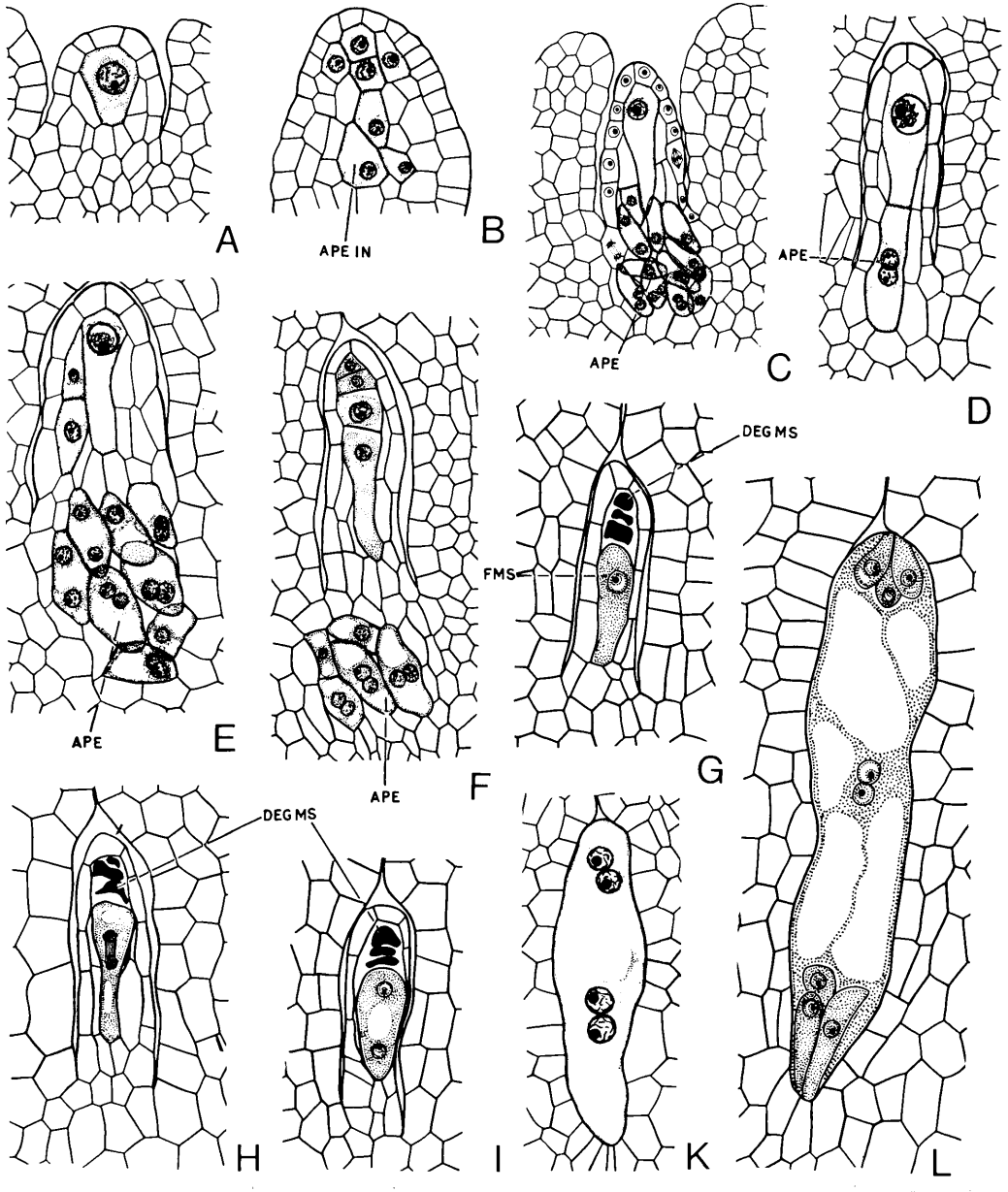


Fig. 2. Megasporogenesis and megagametophyte development in *Trichodesma indicum*. – A: LS of nucellus showing an archesporial cell. – B: LS of nucellus showing multiple archesporium and aposporic embryo sac initials. – C–E: LS of nucellus showing megasporocyte and aposporic embryo sacs. – F: LS of nucellus showing linear tetrad of megaspores and aposporic embryo sacs. – G–L: LS of nucellus showing successive stages in the development of the megagametophyte. – APE aposporic embryo sacs, APE IN aposporic embryo sac initials, DEG MS degenerating megaspores, FMS functional megaspore. – All × 310.

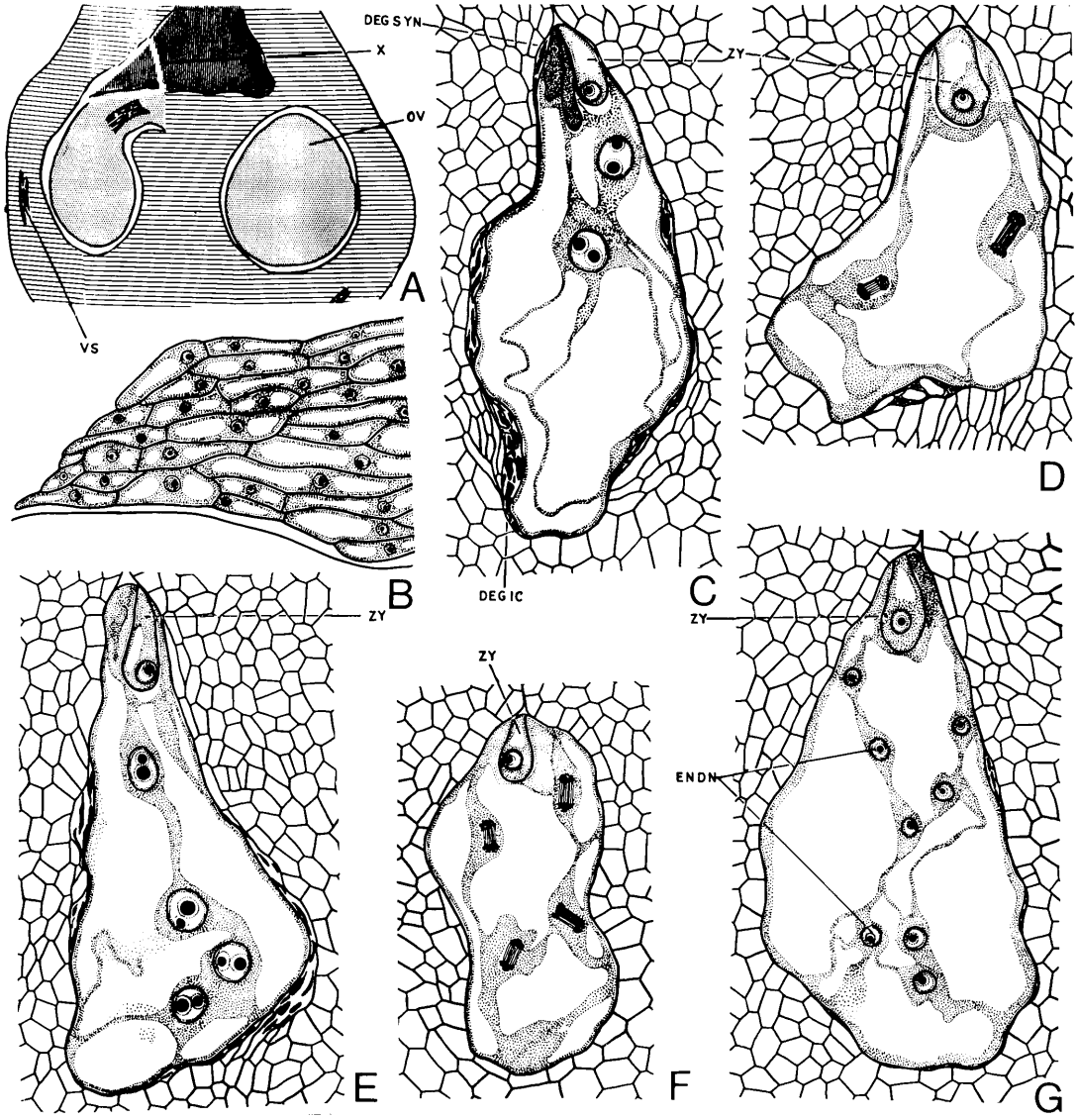


Fig. 3. *Trichodesma zeylanicum*. – A: LS of ovary showing obturator. – B: Portion marked X in Fig. 3 A enlarged. – C–G: LS of ovule showing zygote and successive stages in the development of the endosperm. – DEG SYN degenerating synergids, DEG IC degenerating cells of the integument, ENDN endosperm nuclei, OV ovule, VS vascular strand, ZY zygote. – A × 35, B × 325, C–G × 230.

gives rise to a part of the hypocotyl, while the remaining portion of the hypocotyl is derived from *m*. By this time the cell *n* has divided vertically and *n'* undergoes a transverse division to form *o* and *p* (Fig. 5 L–N). A suspensor of three to four cells is formed by two successive transverse divisions of *p* (Fig. 5 S). The terminal cell of the suspensor may undergo an oblique or a vertical division (Fig. 5 O, S). Cell *o* also divides forming two superposed cells, of which the upper after a transverse and the lower after a vertical division together form the initials for the

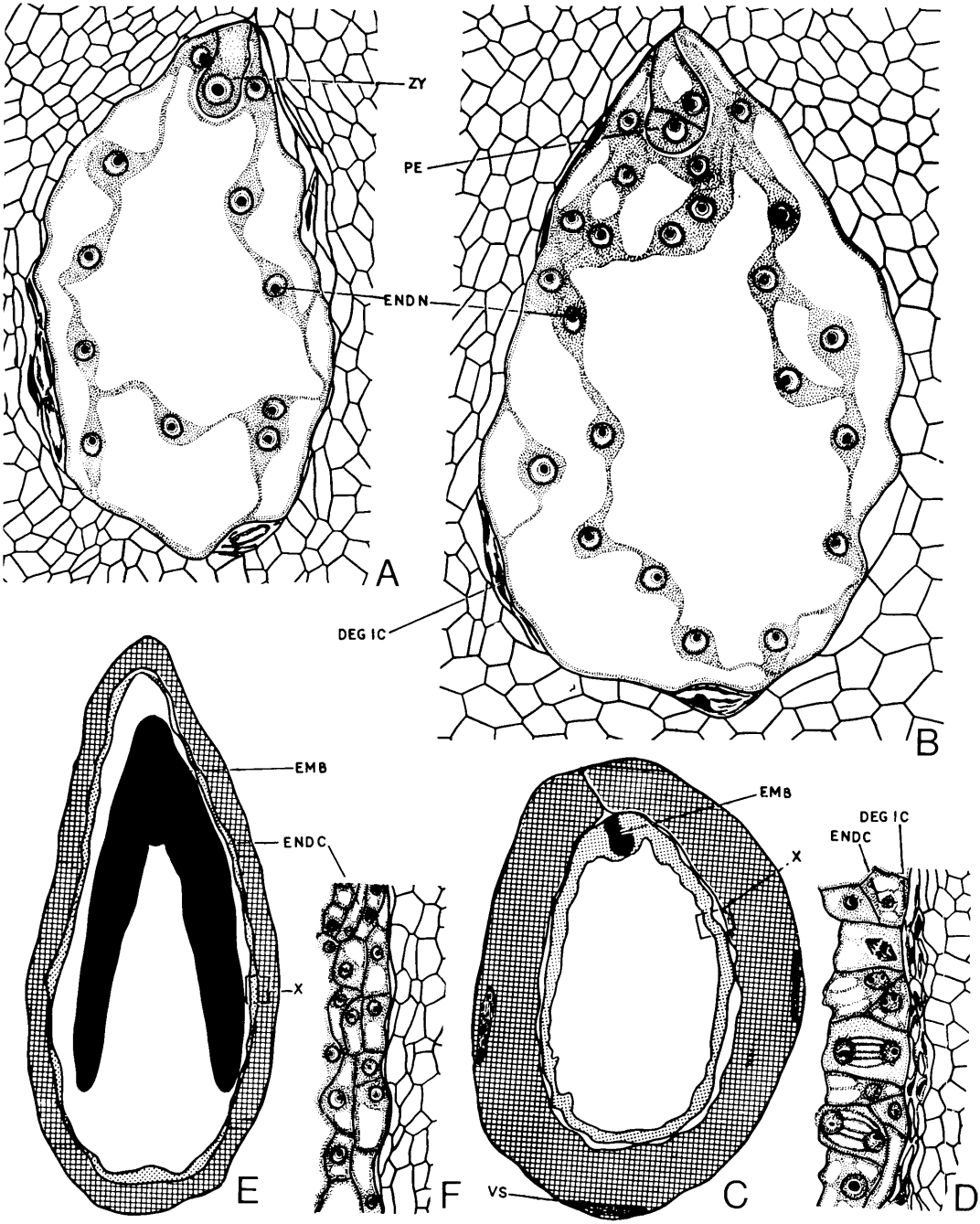


Fig. 4. Development of the endosperm in *Trichodesma zeylanicum*. – A: LS of ovule showing zygote and multinucleate endosperm. – B: LS of ovule showing 2-celled embryo and multinucleate endosperm. – C: LS of ovule showing globular embryo and cellular endosperm. – D: Portion marked X in Fig. 4 C enlarged. – E: LS of seed showing embryo with cotyledons and endosperm. – F: Portion marked X in Fig. 4 E enlarged. – DEG IC degenerating integument cells, EMB embryo, END C endosperm cells, ENDN endosperm nuclei, PE proembryo, VS vascular strand, ZY zygote. – A, B × 230, C × 35, D, F × 200, E × 20.

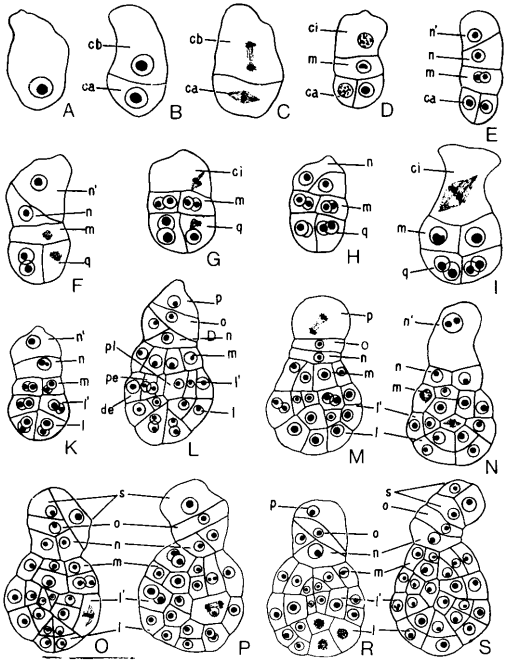


Fig. 5. Development of embryo in *Trichodesma indicum*. – Abbreviations as given under Fig. 6. – All × 150.

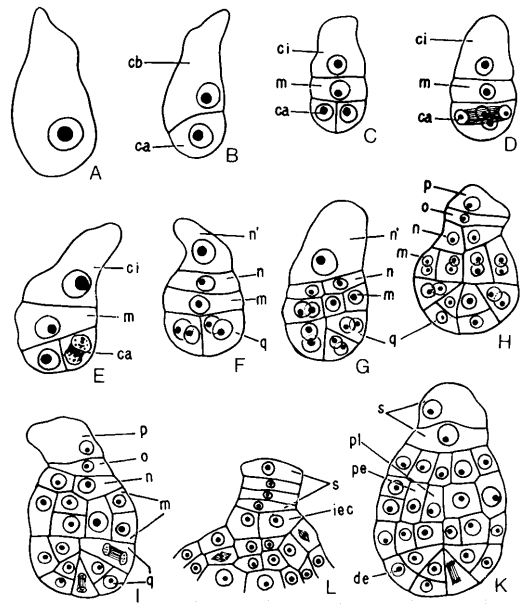


Fig. 6. Development of embryo in *Trichodesma zeylanicum*. – *ca* apical cell, *cb* basal cell, *ci* lower daughter cell of *cb*, *de* dermatogen, *iec* initials for root cortex, *l* upper tier of octant, *l'* lower tier of octant, *m* middle cell of tetrad, *n* upper daughter cell of *ci*, *n'* lower daughter cell of *ci*, *o* upper daughter cell of *n'*, *p* lower daughter cell of *n'*, *pe* periblem, *pl* plerome, *q* quadrant, *s* suspensor. – All × 150.

root, while the two cells formed by *n* give rise to the root cortex. Therefore, the cell *ca* contributes to the development of the embryo proper and a portion of the hypocotyl, while the cell *cb* gives rise to the hypophysis, hypocotyl and suspensor. Embryo development thus corresponds to the Polygonum variation of the Asterad type (Johansen 1950).

In *T. zeylanicum* a sixteen-celled embryo arises by a bipartition of each cell of the eight-celled embryo. Cell *n'* divides by a transverse wall to form *o* and *p*, the cell *n* meridionally into two juxtaposed cells and the two cells of the tier *m* divide by vertical walls to form four circumaxially placed cells (Fig. 6 G, H). The four elements of *q* undergo divisions by oblique walls, each wall having its outer insertion almost in the centre of the peripheral wall and its inner insertion at a point about a half to three-quarters of the way along the horizontal wall which separates *q* from *m* (Fig. 6 G, H). Of the cells thus formed, the upper cell nearest to the axis gives rise to the epidermal initials and subepidermal initials. The outer cells, away from the axis, undergo vertical divisions and become continuous with the epidermal initials (Fig. 6 I –L). The inner cells divide tangentially to form the periblem *pe* and the plerome *pl* respectively (Fig. 6 K). Thus the entire apical cell is destined for the formation of the cotyledonary portion and the stem apex.

The portion *m* consists of four circumaxially placed cells at the 16-celled stage of the embryo. They divide by vertical walls and separate the epidermal initials. Later on, transverse divisions in the derivatives of these cells result in the hypocotyledonary portion of the embryo (Fig. 6 G–I). The lower portion of the hypocotyl is formed by *n*. The cell *o* may undergo a transverse division or give rise directly to the initials for the root cap, *iec* (Fig. 6 L). The cell *p* divides once or twice by transverse walls and forms a 2–4-celled suspensor (Fig. 6 L). The sequence of development thus conforms to the Lamium variation of the Asterad type (Johansen 1950).

Pericarp

During the early stages of development, the pericarp consists of undifferentiated parenchymatous cells, with a well-developed epidermis made up of tangentially elongated cells (Fig. 7 A, B). In the mature fruit the pericarp is divisible into an endocarp, a mesocarp and an epicarp.

Before fertilization a young ovary shows eight to ten layers of cells, with the vascular strand traversing the centre (Fig. 7 A, B). After fertilization the inner epidermis of the ovary wall is gradually transformed into the endocarp, after its cells have developed thickenings along the inner tangential walls (Fig. 7 C–F). The mesocarp consists of six to eight layers of resiniferous cells. The cells of the outer epidermis elongate vertically and develop thickenings all over their outer tangential and radial walls. They become heavily cutinized during the later stages and constitute the epicarp (Fig. 7 C–F).

The cells bordering the interlocular septum are elongate and resemble those of the pericarp during the early stages, but as the epicarp differentiates the inner tangential and the radial walls of these cells become strongly thickened and possess a narrow, triangular lumen (Fig. 7 E, G). These cells behave similarly to those of the endothecium in the anther. They appear to help in the dispersal of the nutlets. The three to four layers of cells which underly these thickened cells are thin-walled and parenchymatous; they are followed by the innermost cells which are reticulately thickened (Fig. 7 G).

Seed coat

The seeds are oblong and the seed coat is undifferentiated during the early stages of development. Mature seeds possess a thin, papery seed coat. At the mature megagametophyte stage the integument is composed of 20–22 layers of cells (Fig. 8 A, B). Immediately after fertilization, the cells of the inner layers of the integument start to break down continuously until the mature embryo is formed (Fig. 8 C–H). At this stage the seed coat consists of about ten layers of cells, subdivided into an epidermal layer of tanniniferous cells, a middle zone of parenchymatous cells and an inner zone of thickened cells. The vascular strand runs close to the epidermis (Fig. 8 G). The seeds are never released from the fruit; the dispersal unit is the nutlet.

Discussion

A regular placental obturator is absent in Boraginoideae. However, in *Trichodesma indicum* and *T. zeylanicum,* as well as in *T. amplexicaule* (Khanna 1964 b), the stylar canal is filled with a transmitting tissue which extends over the micropylar region and behaves as an obturator. A similar feature has been observed in *Mertensia platyphylla* (Khanna 1964 a).

In the species of *Trichodesma* under study, a few cells underlying the archesporium become tapetal in function by developing vacuoles and undergoing precocious nuclear divisions. Such a feature has not been reported in any other member of Boraginaceae, excepting *Cynoglossum amabile* (Millsaps 1940), in which the first row of meristematic cells adjacent to the sporogenous tissue develop into a tapetum.

Occurrence of nucellar apospory in Boraginaceae was first reported for *Cynoglossum denticulatum* (Khaleel 1974). Four to five aposporic embryo sac initials differentiated just below the archesporial cells and developed up to the 2- or 4-, rarely 8-nucleate stage. However, they all degenerated as the normal gametophyte enlarged. Subsequently this phenomenon has also been reported for *Cordia alba* and *C. obliqua* (Khaleel 1975). In *C. alba* the aposporic embryo sacs occur in the form of six to eight enlarged binucleate cells. However, they thereafter degenerate, providing an additional source of nutrition for the gametophyte. In *C. obliqua,* not only is the number of aposporic embryo sac initials six to twelve, but the phenomenon itself is much more advanced. The aposporic embryo sacs develop up to the eight-nucleate stage, following the same sequence of cell divisions as the normal gametophyte, compete with the same and eventually suppress it by their vigorous enlargement. *T. indicum* and *T. zeylanicum* show similarities with *C. denticulatum* and *C. alba* in this aspect. The frequent enlargement of the nucellar cells, with a definite polarity and embryo sac like appearance suggests a tendency towards nucellar apospory. The aposporic embryo sac initials are four to twelve in number and differentiate below the archesporial cell. They rarely develop up to the four-nucleate stage

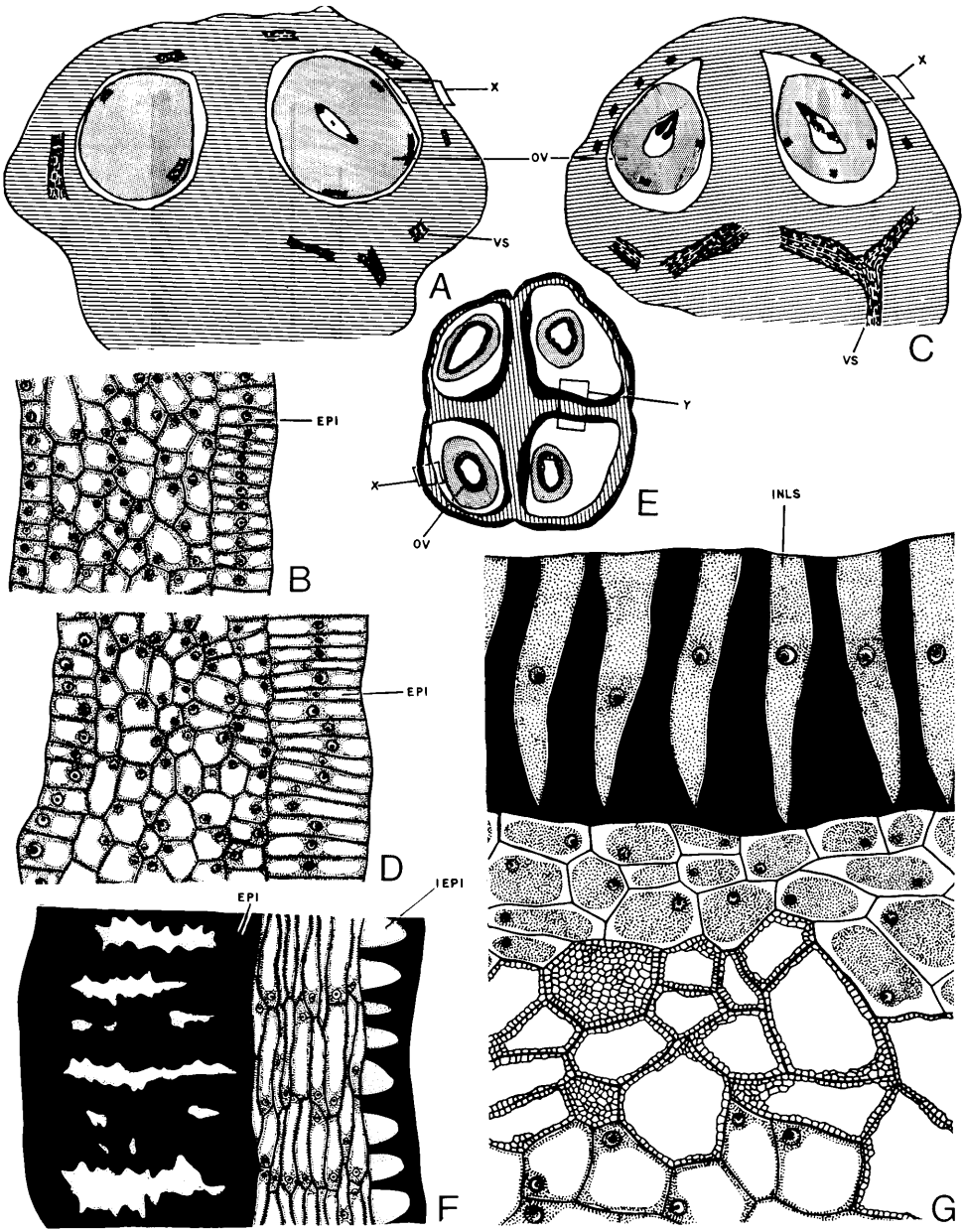


Fig. 7. Development of pericarp in *Trichodesma zeylanicum*. – A: LS of ovary with mature megagametophyte. – B: Portion marked X in Fig. 7 A enlarged. – C: LS of ovary with nuclear endosperm. – D: Portion marked X in Fig. 7 C enlarged. – E: TS of mature fruit. – F: Portion marked X in Fig. 7 E enlarged. – G: Portion marked Y in Fig. 7 E enlarged. – EPI epidermis, IEPI inner epidermis, INLS interlocular septum, OV ovule, VS vascular strand. – A × 30, B, D, F × 290, C × 20, E × 5, G × 150.

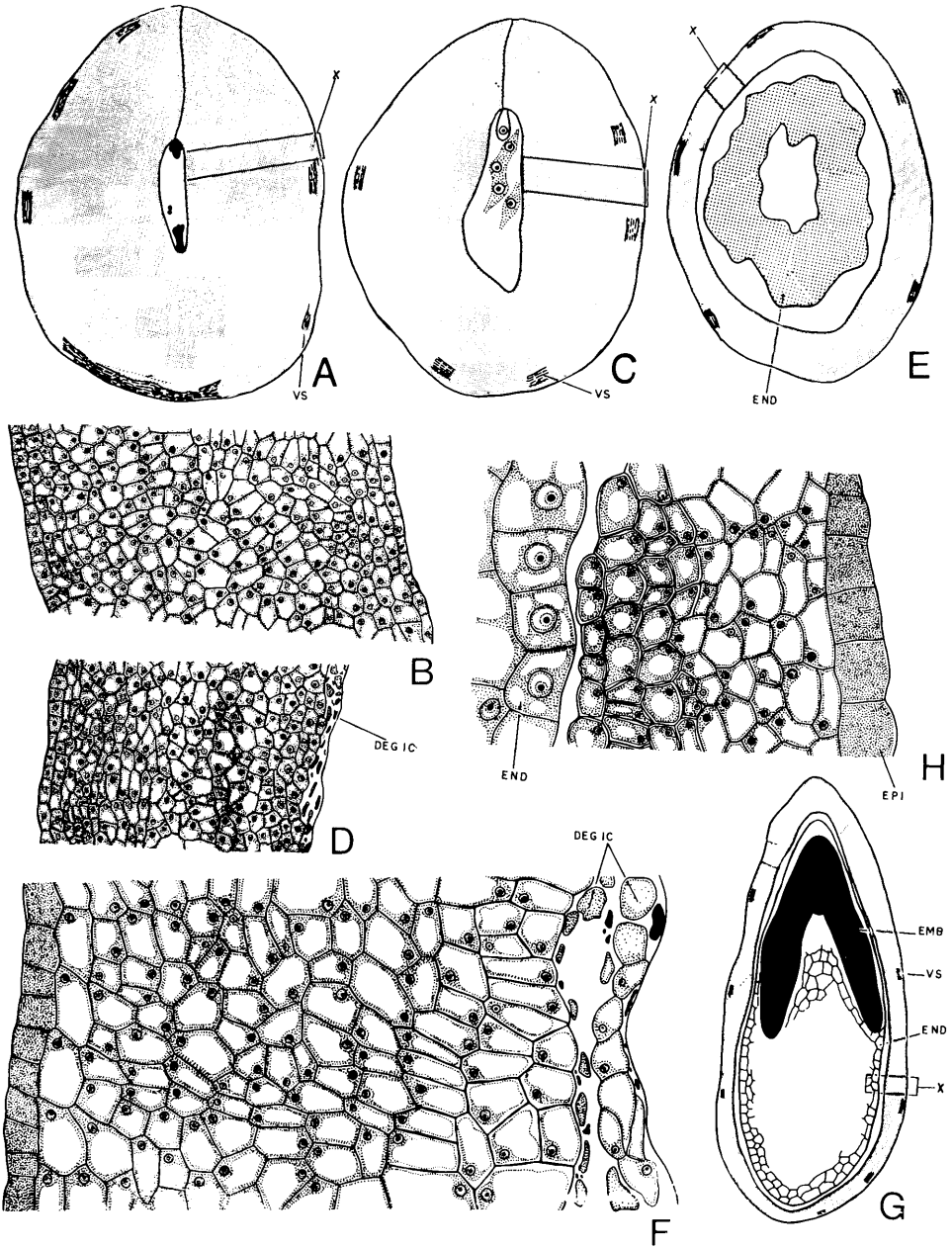


Fig. 8. Development of seed coat in *Trichodesma zeylanicum*. – A: LS of ovule with a mature megagametophyte. – B: Portion marked X in Fig. 8 A enlarged. – C:LS of ovule with 4-nucleate endosperm. – D: Portion marked X in Fig. 8 C enlarged. – E: TS of ovary with multinucleate endosperm. – F: Portion marked X in Fig. 8 E enlarged. – G: LS of mature seed. – H: Portion marked X in Fig. 8 G enlarged. – DEG IC degenerating integument cells, EMB embryo, END endosperm, EPI epidermis, VS vascular strand. – A, C × 90, B, D, E × 150, F, H × 300, G × 15.

and degenerate as the normal gametophyte enlarges.

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A key to the species of Cyathus (Nidulariaceae)

Harold J. Brodie

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A dichotomous key to the forty-two species of the fungus genus *Cyathus* (Nidulariaceae) is presented. Salient characters employed in the key are described, annotated and illustrated.

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Because only forty-two species in the fungus genus *Cyathus* are recognized as valid in my recently published monograph of the Nidulariaceae (Brodie 1975), it might appear that a key for identification could be constructed with ease. I was reluctant to produce such a key, for a number of reasons which were discussed in some detail in my monograph. The most cogent reason is my conviction that too many *Cyathus* species are still known only from scanty collections. Moreover, any key which can really guide a mycologist who lacks experience with this group of fungi must separate groups of species on the basis of divaricating phrases which are as unequivocal as possible, and the "all or none" nature of such descriptions tends to encourage too great a reliance on the key itself as a substitute for careful phrase-by-phrase comparison with the full official descriptions.

However, several mycologists have urged that a key should be published and the present paper is offered in an effort to meet the apparent need.

Terms used in the key

The terms have been listed approximately in the order in which they appear in the key.

In my monograph (Brodie 1975) I discussed at length the difficulties involved in applying the various criteria by means of which the species of *Cyathus* have been separated. This discussion was intended to alert mycologists to an awareness of the range of variation that exists in almost all species in colour, shape, size, etc. The reader should therefore consult the monograph (pp. 126–132) before using the accompanying key. For the convenience of those who may not have the monograph at hand, an illustrated glossary is given herewith to define or explain as clearly as possible the terms used in the present key. Page numbers cited in the key give the principal reference *in my monograph* to the species concerned.

The *first time* each term or descriptive phrase is used in the key, reference is made by brackets (T 1 to T 36 inclusive) which indicate corresponding items in the list of notes and illustrations.

T1 *Peridium* (Fig. 1 A). The fruit body as a whole, exclusive of the basal emplacement if this structure is present.

T2 *Plicate* (Fig. 1 A, G, M, X). Ridged, grooved or folded parallel to the length of the peridium. In some species, the external plicae may be hidden because of the shaggy outer surface (Fig. 1 X). As a precaution, hairs should be rubbed off one specimen if there is doubt as to whether it is externally plicate or not.

T3 *Not plicate or non-plicate* (Fig. 1 B, F, H, L, N, O, Y). An occasional specimen of a non-

plicate species will show some lengthwise folds as the result of drying, but such folds are not regular in width or spacing. Moreover, in some plicate species, the folds are very faint; in such cases they are regularly distributed, however (Fig. 1 D). Many species are plicate internally (Fig. 1 G, X) in addition to externally.

T4 *Tunica present* (Fig. 1 R). The tunica when present is an outermost layer of the peridiole. It can frequently be identified with certainty by using a needle to pick at a moist peridiole under the binocular microscope. More certain identification usually necessitates examination of a free-hand section of a peridiole, when a tunica is then seen as a firm (sometimes flimsy) layer of hyphae on the outside of the firmer darker cortex (a one-layered cortex is shown in Fig. 1 I, a two-layered in Fig. 1 K but no tunica is present in either).

T5 *Tunica absent* (Fig. 1 G, I, K). When there is no tunica at all, the peridiole usually appears dark and shiny on the outside (Fig. 1 G). In free-hand sections, a delicate tunica may easily be lost; for this reason, it is wise to examine sections of more than one peridiole.

T6 *Peridium dark-coloured* (Fig. 1 B, X). Colour intensity provides a useful key divarication but should be considered cautiously because of the variation in colour within certain species. Most descriptions refer to the colour of dry specimens. The colour is usually some shade of brown, from buff to deep chocolate or almost black.

T7 *Peridium light-coloured* (Fig. 1 D). As noted above, a few specimens of such a species as shown in Fig. 1 D may be considerably darker than others. The colour range is from ivory or grey to light buff.

.8 *Outer surface of peridium hirsute, shaggy, woolly* (Fig. 1 B, hirsute; Fig. 1 N, shaggy; Fig. 1 H, woolly). There are many degrees of "woolliness"; in general what is meant is seen in the contrast between the uneven lengths of hyphae making up the covering (Fig. 1 H) and the even length of the hyphae composing the outer wall of a species such as the one shown in Fig. 1 F.

T9 *Outer surface of peridium covered with fine matted hairs* (Fig. 1 C, F). Hyphae of outer layer of wall essentially all of the same length giving the appearance of a *fine* pile (Fig. 1 F) as compared with a coarse or shaggy pile (Fig. 1 H). Such a fine pile is commonly called the *tomentum.*

T10 *Peridia provided with long conspicuous hairs* (Fig. 1 O; Fig. 1 T, lower half; Fig. 1 D, lower half). The hairs are *in addition* to a fine under pile and stand out as easily-discerned bristles of various sorts as in Fig. 1 O, T. There are also long hairs in the woolly types (e.g. Fig. 1 H) but the hairs are irregular, usually matted and not specifically oriented *downwards* as they are clearly in Fig. 1 T.

T11 *External hairs aggregated into conical tufts* (Fig. 1 O). Shown clearly at the bottom of Fig. 1 O. Note that such tufts are *conical:* compare Fig. 1 T, where aggregation of hyphae produces long hairs, but not cones of hairs.

T12 *External hairs aggregated into mounds* (Fig. 1 N). This condition is frequently referred to in descriptions as *tufted tomentum.*

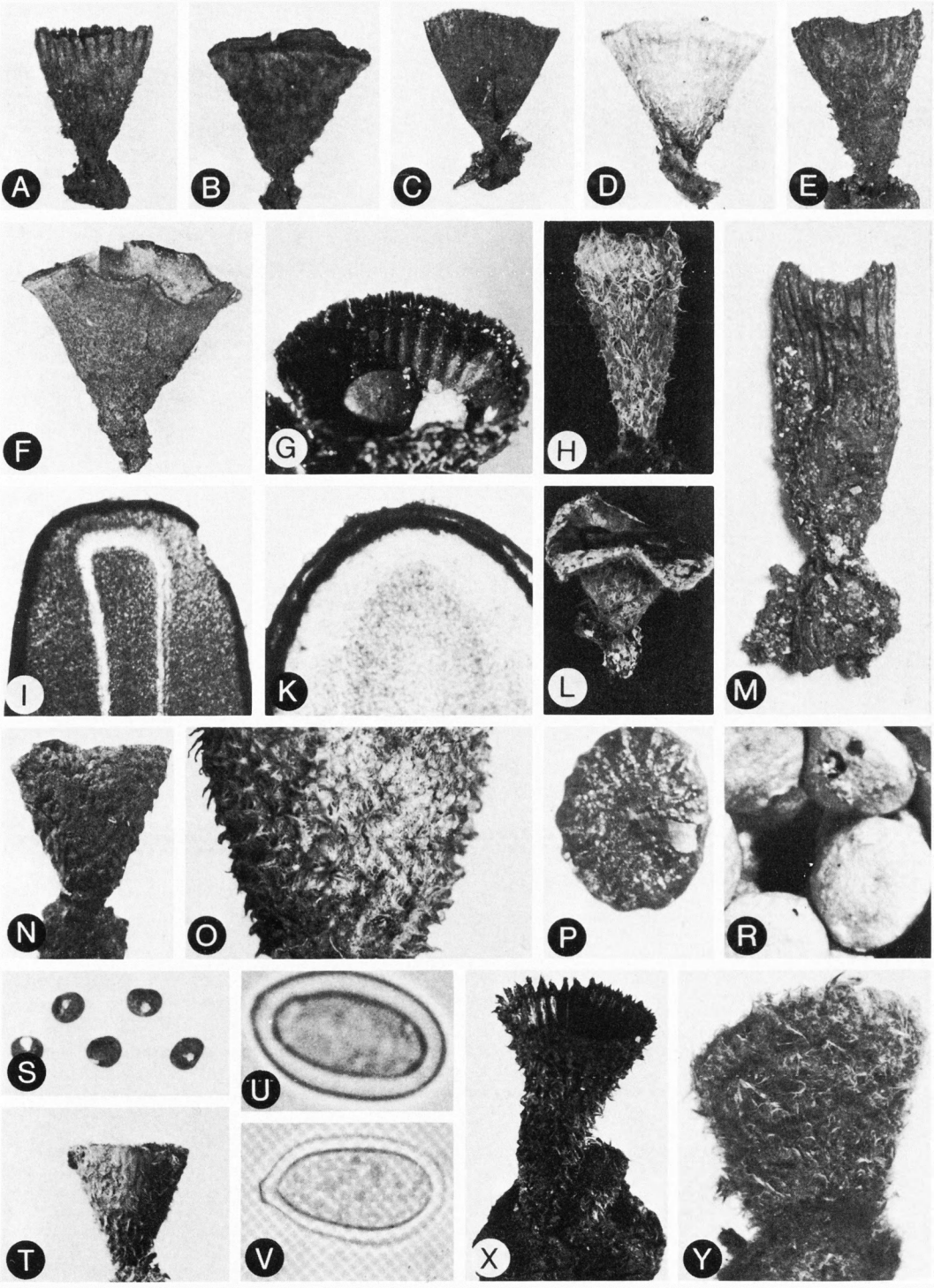
T13 *External hairs distinctly curled* (= curly tomentum, etc. of descriptions) (Fig. 1 Y). This is a woolly tomentum but hyphae or groups of hyphae form tight curls, easily seen under a binocular microscope.

T14 *Peridia slender* (= not broad relative to height) (Fig. 1 H, M). Such types often have a slender base but not invariably.

T15 *Peridia broad* (= broad relative to height). Fig. 1 F especially, and Fig. 1 A–D, N, T.

T16 *Peridia flaring out widely at the mouth* (Fig. 1 L, B). There is an abrupt change in the angle of the peridium wall in the upper third.

Fig. 1. Taxonomic features, *Cyathus* (for details see text under Terms used in the key). Photographs are similar to many I have published in various journals but in no case identical. – A: *C. poeppigii,* × 3. – B: *C. triplex,* × 3. – C: *C. berkeleyanus,* × 3. – D: *C. bulleri,* × 3. – E: *C. limbatus,* × 3. – F: *C. earlei,* × 3. – G: *C. poeppigii,* × 7. – H: *C. stercoreus,* × 6. – I: *C. limbatus,* × 70. – K: *C. gracilis,* × 90. – L: *C. olla,* × 3. – M: *C. gayanus,* × 4. – N: *C. intermedius,* × 4. – O: *C. gracilis,* × 10. – P: *C. crispus,* × 20. – R: *C.* sp. indet., × 20. – S: *C. olla,* × 2. – T: *C. pallidus,* × 4. – U: *C. gracilis,* × 1500. – V: *C. africanus,* × 2000. – X: *C. striatus,* × 5. – Y: *C. crispus,* × 6.


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T17 *Peridia not flaring out* (Fig. 1 A, C, N). No abrupt change in angle of wall. Note: as might be expected, there are many intermediate conditions, e.g. Fig. 1 E, F, X.

T18 *Spores ellipsoid* (Fig. 1 U, V). The spore outline approximates an ellipse with one dimension markedly exceeding the other.

T19 *Spores ovoid, globose, etc.* (not illustrated). These terms are used in the ordinary sense. Note: there is often considerable variation in shape among spores of a single specimen. If most are ellipsoid, that is the term used.

T20 *Spores apiculate* (Fig. 1 V). A distinct projection of some kind is visible at one end of the spore, at least under the oil immersion lens. According to present views this should be called a hilum; the term 'apiculate' is retained because it is used so frequently in older publications.

T21 *Spores not apiculate* (Fig. 1 U). No distinct projection at either end.

T22 *Peridia small or large* (no reference to illustrations is made because peridia are shown at various magnifications). These terms are helpful only in a very general way since within one species (e.g. *Cyathus stercoreus*) peridia may vary from 3 mm in height to as much as 10 mm).

T23 *Emplacement conspicuous, compact* (Fig. 1 M, N, X). The hyphae incorporate some substrate, and the basal structure is a *firm mass* which usually remains attached to the peridium proper.

T24 *Emplacement conspicuous, byssoid* (Fig. 1 Y). Basal hyphae only loosely aggregated, never a firm ball.

T25 *Emplacement inconspicuous* (Fig. 1 T, D).

T26 *Peridioles regular in outline* (circular or ellipsoid) (Fig. 1 G).

T27 *Peridioles irregular in outline* (reniform or subtriangular) (Fig. 1 S).

T28 *Peridioles smooth* (Fig. 1 G, R).

T29 *Peridioles wrinkled.* May be radiately wrinkled (Fig. 1 P) or irregularly wrinkled (not illustrated).

T30 *Cortex one-layered* (Fig. 1 I).

T31 *Cortex two-layered* (Fig. 1 K). Again, caution is urged! A one-layered cortex overlaid by a tunica may easily be classified as a two-layered cortex. In a true two-layered cortex, each layer is dense and of approximately the same width in section.

T32 *Mouth (or lip) of peridium setose* (Fig. 1 X).

T33 *Mouth of peridium not setose* (Fig. 1 F).

T34 *Mouth of peridium fimbriate* (Fig. 1 G). Note: at very high magnification, some hyphae of the lip or mouth can always be seen even in a specimen such as shown in Fig. 1 F which would be designated "not fimbriate".

T35 *Peridia with slender stalk* (Fig. 1 B, C).

T36 *Peridia without (clearly defined) stalk* (Fig. 1 E, H).

Key to the groups of Cyathus

1. Peridia (T1) distinctly plicate (T2) or ridged lengthwise, externally or internally or both 2
– Peridia distinctly not plicate (T3) or ridged lengthwise 3
2. Tunica present (T4); peridia dark (T6) or light-coloured (T7), hirsute to shaggy (T8) ... Group VII (p. 173)
– Tunica absent or extremely delicate and fragile; peridia mostly very dark; peridioles dark . Group VI (p. 171)
3. Peridia covered externally by fine, matted hairs (T9) but very few or no long, conspicuous hairs (T10) ..... Group I (p. 154)
– Peridia woolly externally and provided with conspicuous, long hairs 4
4. Tunica absent; peridioles shiny black ..... Group V (p. 168)
– Tunica present; peridioles not shiny black 5
5. External hairs of dark-coloured peridium distinctly aggregated into conical tufts (T11) or into mounds (T12); peridia mostly slender (T14), not broad at mouth relative to height ..... Group IV (p. 164)
– External hairs of peridium not clearly aggregated into tufts (T9), peridia mostly broad relative to height (T15) 6
6. Peridia mostly light-coloured and (outside) having conspicuous, long, downward-pointing hairs (T10); spores mostly ovoid (T19), thin-walled ..... Group II (p. 161)
– Peridia mostly dark-coloured; long hairs rare or inconspicuous; spores mostly ellipsoid (T18), thick-walled ..... Group III (p. 163)

Group I

The *olla* group; peridia commonly *flaring out widely* (T16) in the upper third, clearly not longitudinally ridged, though sometimes weakly transversely ridged on the inside; comparatively smooth-textured, the tomentum consisting of fine, appressed hairs; in some, aggregated into tufts or low mounds but usually *devoid of long, conspicuous hairs;* spores mostly ovoid, thin-walled.

Like many other species, *C. olla* appears in many "forms" which differ from one another in size, colour and form. The only one of these to which I applied a name is forma *anglicus* (Lloyd) Brodie, a description of which is given in my monograph (Brodie 1975 p. 155).

1. Peridia small (T22), not over 5 mm in height or breadth, usually less 2
– Peridia larger, mostly 7 mm wide at mouth or more, up to 15 mm 3
2. Spores small, ovoid, 8–9 × 12–14 μm ..... *C. pygmaeus* Lloyd (p. 157)
– Spores longer, ellipsoid, 10–12 × 18–20 μm ..... *C. minimus* Pat. (p. 157)
3. Spores with obvious apiculus (T20) ..... *C. africanus* Brodie (p. 159)
– Spores without obvious apiculus (T21) 4
4. Peridia thick-walled; mouth abruptly flared outwards, recurved; emplacement conspicuous (T23, T24); peridioles large, irregular (T27) in outline ..... *C. olla* (Batsch) ex Pers. (p. 154)
– Peridia not conspicuously thick-walled; mouth not abruptly flaring outwards 5
5. Cortex two-layered (T31); peridia internally shiny white or silvery 6
– Cortex one-layered (T30); peridia internally not shiny white or silvery 7
6. Spores globose, 8 μm ..... *C. canna* Lloyd (p. 158)
– Spores ovoid, 10–12 × 12–22 μm ..... *C. earlei* Lloyd (p. 156)
7. Peridia 5–6 mm in height and width 8
– Peridia 10–17 mm high, 7–10 mm wide 9
8. Spores small, 4 × 5–6 μm; cups with straight sides ..... *C. microsporus* Tul. (p. 158)
– Spores large, variable, 8–12 × 10–12 μm ..... *C. colensoi* Berk. (p. 156)
9. Spores ellipsoid, 5–8 × 8–11 μm 10
– Spores ovoid, 11 × 13 μm, thick-walled ..... *C. badius* Kobay. (p. 160)
10. Interior of cups dark brown, faintly plicate ..... *C. hookeri* Berk. (p. 159)
– Interior of cups light brown, not plicate ..... *C. confusus* Tai & Hung (p. 160)

Group II

The *pallidus* group; peridia *not* distinctly *flaring out abruptly* at the mouth (T17), mostly light-coloured and not plicate; basal texture of peridium wall fine, but bearing *conspicuous, long, downward-pointing hairs*. Inner peridium wall smooth. Spores mostly ovoid, thin-walled. Tunica thin.

1. Peridia small, mostly 5–6 mm in height or width; sides of peridia curved; colour pale straw, light buff, occasionally darker; spores mostly ellipsoid, 4–8 × 8–15 μm ..... *C. pallidus* Berk. & Curt. (p. 161)
– Peridia large, mostly 7–8 mm in height or width; sides of peridia straight; colour pale buff with a yellow tinge; spores mostly subglobose, 5–7 × 5–9 μm ..... *C. julietae* Brodie (p. 161)

Group III

The *triplex* group; peridia mostly *dark*-coloured, sometimes having faint plication, visible *only* internally; outer surface with a few spreading (sometimes tufted) hairs; inner surface smooth, silvery white; cortex one-layered, subhomogeneous *or* distinctly two-layered, spores mostly ellipsoid, thick-walled; tunica thin or absent.

1. Mouth of peridium beset with conspicuous stiff setae (T32); tunica absent; peridioles large and conspicuously plump ..... *C. setosus* Brodie (p. 164)
– Mouth of peridium lacking conspicuous setae (T33); tunica present; peridioles not conspicuously plump 2
2. Spores 8–10 μm long; cortex one-layered; peridioles 1–1.5 mm; external hairs in occasional tufts ..... *C. sinensis* Imaz. (p. 164)
– Spores 12–14 μm long or more; cortex two-layered; peridioles 2 mm or more; external hairs not in tufts ..... *C. triplex* Lloyd (p. 163)

Group IV

The *gracilis* group; peridia not plicate *or* extremely faintly plicate; tomentum hyphae *clearly* aggregated into nodular (T12) or pyramidal tufts (T11). Spores ellipsoidal, moderately thick-walled; tunica thin.

1. Peridia slender, with slender stalk (one third length of whole peridium); external hairs aggregated into sharp, conical tufts; cortex two-layered ..... *C. gracilis* Brodie (p. 164)
– Peridia not slender or long-stalked; external hairs aggregated into low irregular mounds; cortex one-layered 2
2. Peridium wall thin (0.1–0.2 mm); no stiff conspicuous hairs around mouth (T33); spore walls thin (1.5–2 μm) 3
– Peridium wall thick (0.3 mm); conspicuous stiff hairs around peridium mouth (T34); spore wall thick (2.5–4 μm) ..... *C. crassimurus* Brodie (p. 167)
3. Peridium very faintly (and broadly) plicate inside; tomentum of broad nodules; peridioles 1.3–1.5 mm; spores 10–12 × 18–22 μm ..... *C. elmeri* Bres. (p. 167)
– Peridium not plicate externally or internally; tomentum in small, sharply defined nodules (T12); peridioles 2 mm; spores 10 × 16 μm ..... *C. intermedius* (Mont.) Tul. (p. 166)

Group V

The *stercoreus* group; peridia *not plicate;* outer peridium wall bearing abundant hairs of irregular length, giving a *shaggy* or woolly appearance; peridioles *black* or dark, devoid of tunica; spores *large, subglobose.*

1. Spores large, 30–40 μm or more, globose 2
– Spores small, 8–16 μm, ellipsoid ..... *C. fimicola* Lloyd in Stev. & Cash, nom. illeg. (p. 169)
2. Few long, shaggy hairs; hairs of tomentum often aggregated into low mounds; reddish band just below outer lip of peridium ..... *C. pictus* Brodie (p. 169)
– Many long, shaggy hairs; hairs of tomentum sometimes irregularly adherent but not into mounds; no band on peridium mouth; peridioles conspicuously shiny black ..... *C. stercoreus* (Schwein.) de Toni (p. 168)

Group VI

The *poeppigii* group; peridia *distinctly plicate* externally and internally; outer peridium wall hirsute to shaggy, in age wearing to smooth, strong brown; *peridioles dark* to black; spores large, globose or ellipsoid; tunica absent.

1. Peridioles small, 1 mm, rarely 1.5 mm 2
– Peridioles larger, minimum 1.75 mm, maximum 3 mm 3
2. Peridia gold-coloured to pinkish brown; external hairs in tight curls (T13); peridioles radiately wrinkled (T29) ..... *C. crispus* Brodie (p. 181)
– Peridia not gold or pinkish; external hairs not in curls; peridioles black, not wrinkled (T28); on manure ..... *C. costatus* Lloyd in Stev. & Cash nom. illeg. (p. 172)
3. Peridia dark brown 4
– Peridia light brown, russett or olive, irregularly shaggy externally 6
4. Peridia narrow and tall (to 15 mm); peridioles 3 mm, spores subglobose, large, 20–32 μm ..... *C. gayanus* Tul. (p. 172)
– Peridia broadly conic, 10 mm high or less; peridioles 2 mm 5
5. Plicae marked and close, the grooves about 0.5 mm apart; spores large, 30–50 μm *C. poeppigii* Tul. (p. 171)
– Plication less marked but distinct and coarse, the grooves about 0.75–1 mm apart; spores 10–12 × 16–22 μm ..... *C. limbatus* Tul. (p. 172)
6. Peridia shiny brown; spores 11–15 × 16–22 μm, thin-walled .... *C. olivaceo-brunneus* Tai & Hung (p. 173)
– Peridia inside not shiny brown; spores smaller, 8.5–10 × 16–19 μm, thick-walled ..... *C. cheliensis* Tai & Hung (p. 173)

Group VII

The *striatus* group; peridia distinctly *plicate* internally, sometimes obscurely so externally; outer peridium wall hirsute to shaggy; spores mostly ellipsoidal; *tunica present;* emplacement firm and conspicuous in many species (T23).

1. Peridia strikingly elongate, 12–20 mm high, not over 7 mm wide, externally dark brown, shaggy 2
– Peridia not usually elongate, mostly in range, 7–10 mm high, 6–8 mm wide 3
2. Peridioles 2.5–3 mm; spores ellipsoid, 11–13 × 5–6 μm, thick-walled ... *C. novae-zeelandiae* Tul. (p. 176)
– Peridioles 1 mm; spores ovoid, 8 × 5 μm ..... *C. chevalieri* Hariot & Pat. (p. 177)
3. Peridioles distinctly ellipsoid (T26) and rugulose (T29); spores ellipsoid, 10 × 16 μm ..... *C. ellipsoideus* Brodie (p. 181)
– Peridioles circular in outline or irregular (T27), not ellipsoid or rugulose 4
4. Peridioles small, 1 mm or less; peridia only faintly plicate externally; cups ferrugineous ..... *C. rudis* Pat. (p. 177)
– Peridioles larger, mostly 2 mm (range 1.5–3 mm) 5
5. Peridium wall thick; external hairs distinctly aggregated into tufts; emplacement large, solid; peridia grey-coloured, rarely light fawn ..... *C. helenae* Brodie (p. 175)
– Peridium wall not thick; external hairs not in tufts; emplacement variable (T24, T25) 6
6. Peridia very pale, linen-coloured, outside having a few long, down-pointing hairs; epiphragm snow white with tawny hyphal tufts ..... *C. bulleri* Brodie (p. 179)
– Peridia usually darker brown 7
7. Peridia externally very dark brown, almost black, internally conspicuously white or silvery; peridia wide and short; spores ellipsoid, 12 × 16–22 μm 8
– Peridia in various shades of brown, internally not contrasting white or silvery 9
8. Peridioles small, not over 1.5 mm ..... *C. nigro-albus* Lloyd (p. 176)
– Peridioles larger, 2 mm or more ..... *C. montagnei* Tul. (p. 176)
9. Peridioles mostly irregular in outline, angular or triangular; spores not less than 8–5 × 10–20 μm 10
– Peridioles not angular in outline 11
10. Outer lip of peridium with band of tufted reddish-brown hyphae ..... *C. annulatus* Brodie (p. 179)
– Lip devoid of distinct, coloured band ..... *C. striatus* (Huds.) ex Pers. (p. 173)
11. Spores very small, subglobose, 4–7 × 6–9 μm; peridioles variable in size, commonly elliptical in outline ..... *C. berkeleyanus* (Tul.) Lloyd (p. 178)
– Spores larger, ovoid to globose, 6.5 × 9–11 μm; peridioles circular in outline *C. pullus* Tai & Hung (p. 179)

Comments

The keys presented herewith have been used with a fair degree of success by graduate students in botany who had little or no previous acquaintance with Birds' Nest Fungi. Undoubtedly, however, difficulties will be encountered by some persons using the keys; I should, therefore, be grateful to have such difficulties reported to me so that adjustments can be made if possible. As is true for any key that embraces all the recognized species in the world, the matter of geographical distribution as given in descriptions or monographs should not be overlooked. If, for example, erroneous judgement in the use of a dichotomy in the key should lead to the identification of a specimen collected in central Canada as *Cyathus colensoi,* which is known only from New Zealand and Australia, one should consider the identification as highly improbable. It is possible, however, for exotic species to appear adventitiously, especially in greenhouses and on imported nursery stock (Brodie 1975).

Addendum

In a recently-published review (*Kew Bull. 32:* 260–261), D. M. Dring has stated that I am incorrect in my use of the term 'double-layered cortex'. Recording to Dring, "the outer part of the 'double-layered cortex' is so obviously in reality just a part of the tunica, being constructed of filamentous not isodiametric cells as is the true cortex". Only further research will resolve the problem of the proper nomenclature to be applied. Meanwhile, the descriptive terms as I have used them herein do serve to separate the taxonomic entities covered by the keys.

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A study of the genus Litschauerella (Corticiaceae)

John Eriksson and Leif Ryvarden

Eriksson, J. & Ryvarden, L. 1977 12 30: A study of the genus Litschauerella (Corticiaceae). *Bot. Notiser 130:* 461–465. Stockholm. ISSN 0006-8195.

An examination of authentic Bourdot-Galzin material of *Litschauerella* showed that there is only one species in the genus as we know it today. Spore size and spore ornamentation, previously used as specific characters, are shown to be very variable and no discontinuity could be demonstrated which would support a separation into several species. The typification of *Peniophora clematitis* Bourd. & Galz. and *P. abietis* Bourd. & Galz. is discussed.

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In connection with our treatment of the genus *Litschauerella* Oberw. (Eriksson & Ryvarden 1976 p. 838) we found that the previous arrangement of species in the genus was difficult to maintain. The reason was that SEM pictures revealed the spore ornamentation to be far more variable than previously assumed. In our provisional treatment, we recognized two species, one growing on *Clematis* (*Peniophora clematitis* Bourd. & Galz.) with spores about 5 μm in diameter, and one (*Peniophora abietis* Bourd. & Galz.), growing on conifer wood with spores somewhat larger, viz. 7–9 μm in diameter. Oberwinkler (1965) also accepted two species although he put them in different genera. However, Weresub (1961), Boidin (1958) and Liberta (1960) treated the species as synonyms. Weresub (1961 pp. 1480–1581) gave very detailed descriptions of the two species based on syntype material from L, S, TRTC and UPS. She noticed particularly the difference in spore size between specimens from the two types of substrate. Both she and Boidin (1958) noticed that in some specimens collected on *Clematis,* there occurred some very large spores, up to 15 μm in diameter. Boidin considered these spores to be a result of polyploidy.

Our SEM pictures published in 1976 show that spores from collections made on *Clematis* have more or less cubical warts with a square base, while those from the coniferous hosts seem to have more or less rounded warts with a rounded base. However, a collection from Sweden (Eriksson 4157) has more or less smooth spores. Furthermore a collection made by Corbière has spores with somewhat elongated ridges, partly fused together to form a more irregular ornamentation. All other characters, such as cystidia (which are very distinctive in *Litschauerella*) and hyphae were the same, and it was clear that if a separation into several species was desirable, it would have to be based exclusively on the spores.

However, we were suspicious when it appeared that, possibly, 4 species were contained within this restricted number of collections. Further, many spores that appeared smooth under the light microscope, appeared distinctly ornamented when viewed under the scanning electron microscope. Thus, it would be impossible, if the species concepts were to be based on the spore ornamentation alone, to determine the species without the aid of a scanning electron microscope.

Table 1. Authentic and examined collections of *Litschauerella clematitis,* all collected by Galzin, except for number 10 (collected by L. Corbière).

Number	Galzin number	Bourdot number	Herb.	Locality (all in France)	Date	Substrate (according to labels)	Spore size (μm)
1	–	7920	S	Pl. de l'Aveyron, Trou d'Enfer, près Millau	8.V.1911	*Clematis alba*	5.5–15
2	6935	–	PC	Aveyron, Arnac	10.XI.1910	Sapin pectiné (*Abies pectinata*)	7–9
3	7573	–	S	Aveyron, Loubotis	Nov. 1910	*Clematis alba*	4.5–6
4	8949	7933	S	Aveyron, Pisse Vielle, près St. Sernin	26.IV.1911	*Clematis*	5
5	9640	7949	PC	Aveyron, Bouisson	4.VII.1911	*Clematis*	5
6	9486	7987	S	Aveyron, Arnac	29.V.1911	Sapin	5
7	10389	8946	S	Aveyron, Labastide	11.XI.1911	Genévrier (*Juniperus*)	9–12
8	15869	–	PC	Aveyron, Pisse Vieille	25.VII.1911	*Clematis*	4–5
9	17605	14866	PC, U	Aveyron, St-Estève	5.V.1915	*Juniperus*	7–9.5
10	–	32950	PC	Manche, Cherbourg	17.VI.1921	*Pinus*	7–7.5

In an effort to solve some of the problems mentioned above, we borrowed all available material collected or determined by Bourdot and Galzin (Table 1). The spores in all collections were measured and then photographed under a scanning electron microscope.

Spore size

It is apparent from Table 1 that most collections made on coniferous substrates have spores 7–12 μm in diameter. However, collection no. 6, made on *Abies,* has spores which are only about 5 μm in diameter (10 spores measured). This size is within the normal range for collections made on *Clematis* (see Table 1). The substrates have evidently not been mixed as the specimen lived on a piece of bark about 2 × 2 cm and about 4 mm thick and *Clematis* has thin, herbaceous stems.

Although most of the collections made on *Clematis* have rather small spores, 4–6 μm in diameter, there are some spores in collection no. 1 which reach 15 μm in diameter (see Fig. 2 B).

Thus, on both types of substrates there are specimens which deviate from the normal range of spore sizes. The inevitable conclusion is that spore size cannot be used as a character to separate the species in *Litschauerella* based on the facts now available.

Spore ornamentation

Fig. 1 A and B show the spores of two collections, both made on *Picea.* It is evident that the warts vary in shape from cubical to rounded. Fig. 1 C illustrates a form (from *Picea*) with weakly developed ornamentation, while Fig. 1 D shows more or less smooth spores (a collection made on *Picea*), probably slightly shrunken during drying. Fig. 2 A illustrates the spores from the Corbière collection (10 in Table 1) which was made on *Pinus* in France. Here the ornamentation is deviating from that of the other collections on coniferous substrates.

Fig. 2 B is a picture of the large spores from Bourdot 7920 collected on *Clematis* at the type locality and on the same date as the type. It is evident that the ornamentation is of the same

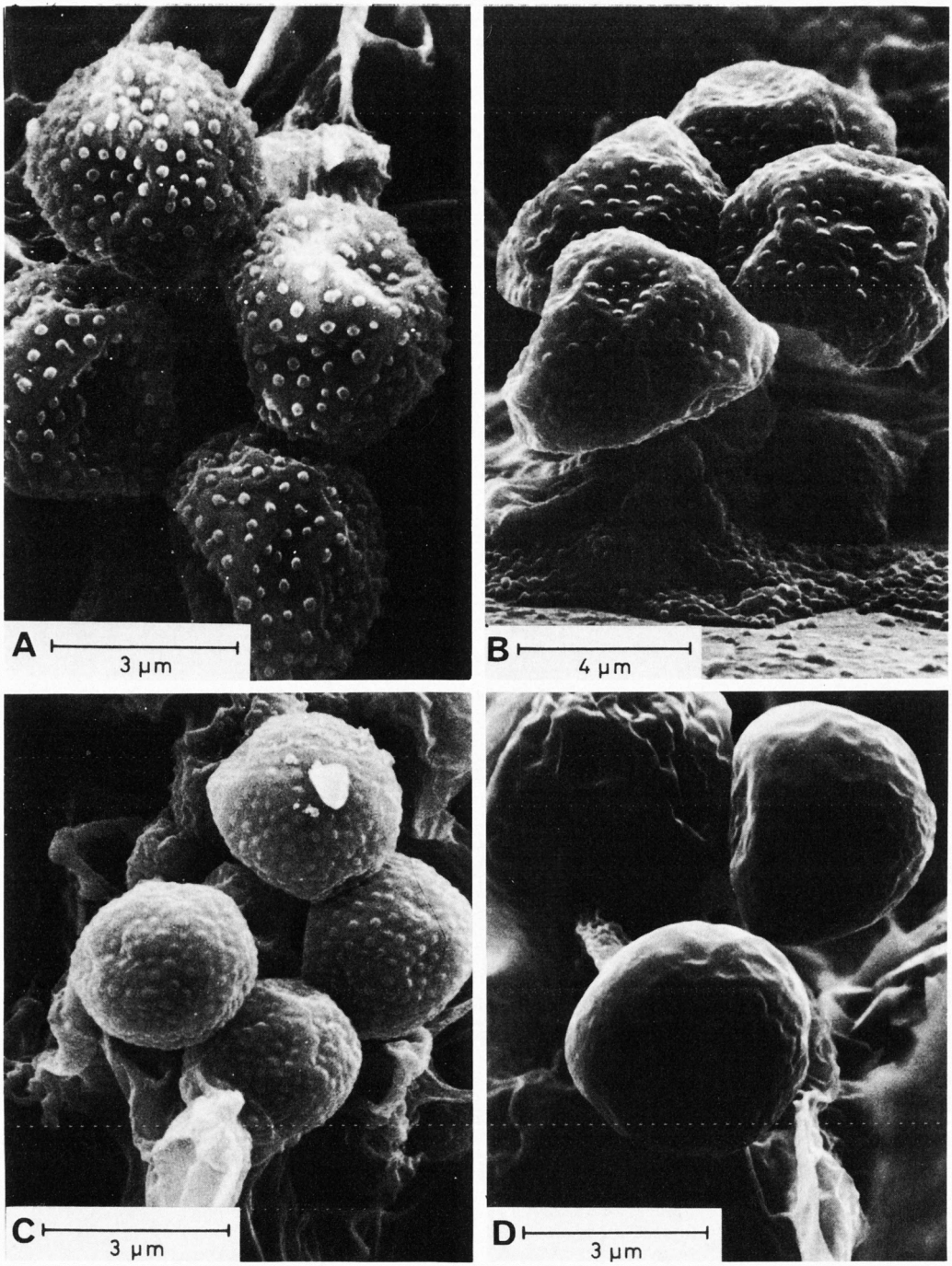


Fig. 1. Scanning electron micrographs of spores of *Litschauerella clematitis*. – A: Form from coniferous substrate with well developed warts. Hjortstam 3787 c. – B: Form from coniferous substrate with low, rounded warts. Larsson 2029. – C: Form from coniferous substrate with weakly developed warts. Eriksson 8570. – D: Form from coniferous substrate with almost smooth spores. Eriksson 4157. – Photo: Leif Ryvarden.

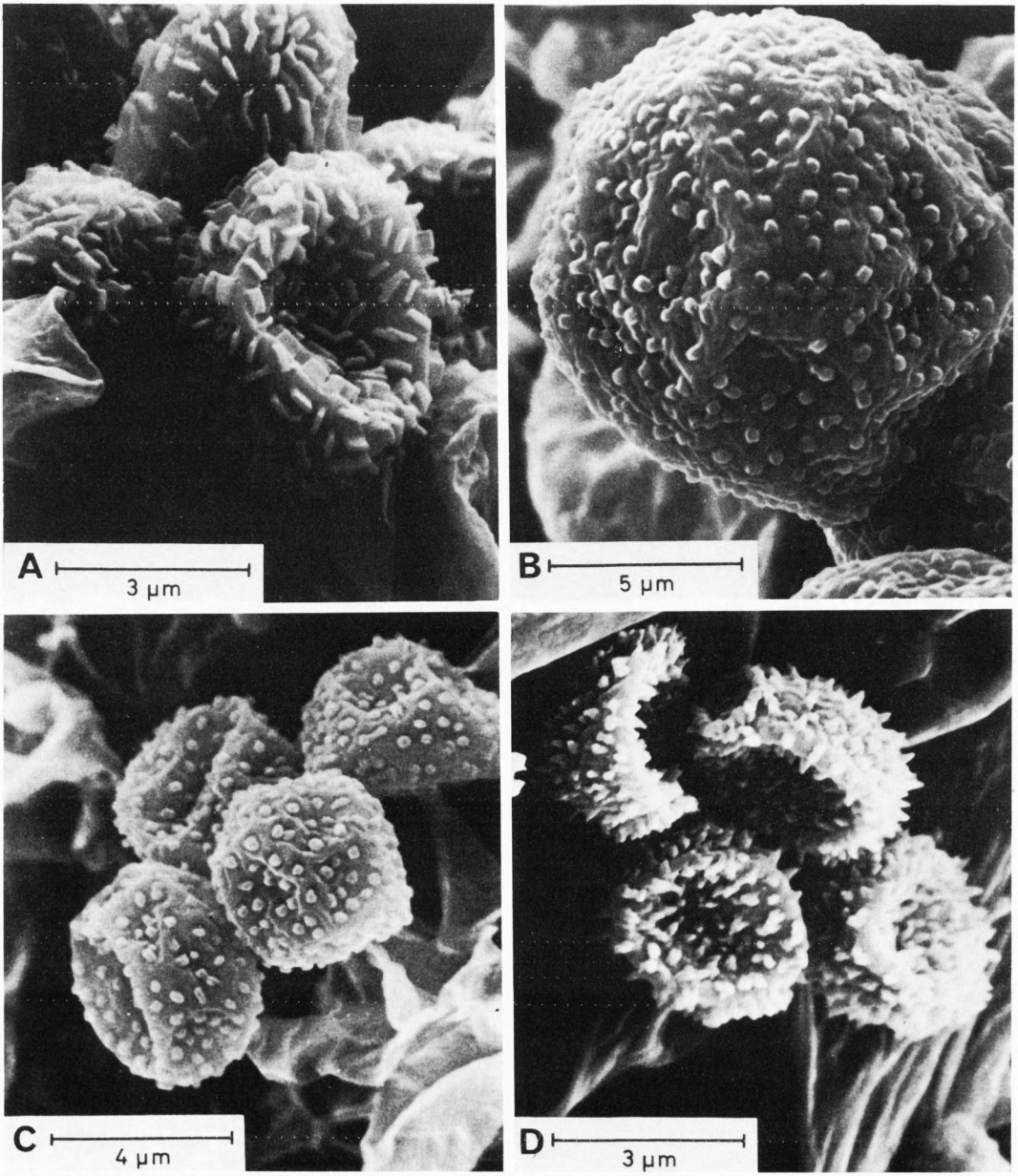


Fig. 2. Scanning electron micrographs of spores of *Litschauerella clematitis*. – A: Form with short plates on the spores, on *Pinus*. Corbière 5. – B: Form from *Clematis* with large spores. Bourdot 7920. – C: Form from *Clematis* with spores of normal size, cf. Fig. 2 B. Galzin 15869. – D: Form from *Clematis* with conical warts. Galzin 7573. – Photo: Leif Ryvarden.

type as that on the spores from collections made on conifer wood. Fig. 2 C shows spores from a collection made on *Clematis,* but which are of normal size. Fig. 2 D shows spores of a collection also made on *Clematis* (coll. no. 3) but with another type of ornamentation. With regard to other characters it is in complete accordance with the other ones made on *Clematis*.

Conclusion

Spore ornamentation is very variable and there are transitions from smooth spores to ornamented ones at least from coniferous substrates. Further, on both types of substrates, there are deviating forms which clearly indicate that spore ornamentation is not a stable character.

We have come to the point of view that there is only one species in *Litschauerella, L. clematitis* (Bourd. & Galz.) Erikss. & Ryv., and that there is no sound basis for separating the taxa involved into several species. A separation must eventually be based on spore ornamentation, and would necessitate the use of a scanning electron microscope and would be without value for mycologists in general.

Typification

P. clematitis. Weresub (1961) selected as lectotype coll. Bourdot 7943–Galzin 9001, but Oberwinkler (1965) challenged this view. He proposed Galzin 9640 as lectotype as it "stimmt exact mit der Originalbeschreibung überein", which was not the case, according to Oberwinkler, with the lectotype selected by Weresub. We have not taken SEM pictures of Bourdot 7943, but of Bourdot 7920 which was collected at the same locality on the same day and also on *Clematis* (Fig. 2 B). We measured the spores and found that some of them reached 15 μm in diameter, although the majority measured about 5 μm in diameter. This is in accordance with the original diagnosis, and we see no reason to reject Weresub's choice.

P. abietis. Weresub (1961) selected as lectotype the collection Galzin 9468–Bourdot 7988. This collection has spores deviating from the normal size for collections made on coniferous substrate (see Table 1, coll. no. 6). In his original description Bourdot states that the spores are 6–8 μm in diameter. Thus, the selected lectotype is somewhat abnormal, and we propose Galzin 6935 as new lectotype for *P. abietis*.

Acknowledgements. The curators of the herbaria in Paris, Uppsala and Stockholm are thanked most sincerely for their cooperation in lending us authentic Bourdot–Galzin material. We also wish to thank Dr L. Weresub, Ottawa, for valuable suggestions and Dr J. Ginns, Ottawa, for revising the English text.

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Laeticorticium pulverulentum (Corticiaceae) validated

John Eriksson and Leif Ryvarden

Eriksson, J. & Ryvarden, L. 1977 12 30: Laeticorticium pulverulentum validated. *Bot. Notiser 130:* 466. Stockholm. ISSN 0006-8195.

Laeticorticium pulverulentum Erikss. & Ryv. is validly published, rectifying a previous invalid publication.

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Laeticorticium pulverulentum Eriksson & Ryvarden sp. nov.

A Laeticorticio roseo differt sporis minoribus, autumno maturis, et statu imperfecto pulverulento.

Typus: Sweden, Uppland, Vänge par., Fiby urskog, on *Populus tremula,* 1937-10-26, Lundell 2030 (Herb. Eriksson).

In the Corticiaceae of North Europe vol. 4 (Eriksson & Ryvarden 1976) we made a mistake in proposing two different ranks simultaneously for the same taxon. In doing so, we violated article 34 of the International Code of Botanical Nomenclature, and none of the names is validly published. We want to rectify this error and therefore propose it as a species here.

Acknowledgements. We want to thank professor J. A. Nannfeldt and Dr L. Weresub for drawing our attention to the invalidity of our previous publication of *L. pulverulentum.*

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New taxa of Zygophyllum from Egypt

Amal I. Hosny

Hosny, A. I. 1977 12 30: New taxa of Zygophyllum from Egypt. *Bot. Notiser 130:* 467–468. Stockholm. ISSN 0006-8195.

Zygophyllum decumbens Del. var. *megacarpum* A. Hosny var. nov. and *Z. aegyptium* A. Hosny sp. nov. are described and illustrated.

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Zygophyllum sect. *Bipartia* v. Huyssteen comprises 2 species in Egypt. *Z. simplex* Del. is widespread in Africa and the W parts of Asia. It shows considerable variation in leaf shape, colour of petals and stamens and in fruit size. In Egypt, however, it is fairly constant and the variation exhibited seems to be related to differing environmental conditions. *Z. decumbens* Del. is restricted to the Red Sea region. In Egypt a robust variety is present which differs from the type in having larger flowers and fruits. It is here described as *Z. decumbens* var. *megacarpum*.

The species of *Zygophyllum* sect. *Mediterranea* Engler are all closely allied and are often confused. The author is preparing a thesis, entitled "Revision of the *Zygophyllum* species of sections *Bipartia* v. Huyssteen and *Mediterranea* Engler in Egypt", under the supervision of Professor M. N. El Hadidi. During revision of the material of *Z. album* L. fil. in BM, CAI, CAIM and K, it turned out that at least two species and several varieties have been included under this name. One new species from this complex, *Z. aegyptium,* is described here.

Zygophyllum decumbens var. **megacarpum** A. Hosny var. nov.

Holotypus: Egypt, Eastern Desert (Da. sept.), Cairo–Suez road, 115 km from Cairo, 4.1976, N. El Hadidi and A. Hosny s.n. (CAI).

Frutex quam varietas typica robustior, usque ad 35 cm altus. Inflorescentia cymosa ter vel quater ramificans. Flores magni, sepala 3 × 2 mm, petala 4 × 1.5 mm, stamina 8–10, filamenta 3.5 mm longa. Capsula magna, turbinata, 4–6 × 4–8 mm, pedicello 6.5 mm.

More robust than the type, up to 35 cm. Inflorescence cymose, branched 3–4 times. Flowers large, sepals 3 × 2 mm, petals 4 × 1.5 mm, stamens 8–10, filaments 3.5 mm. Capsule turbinate, 4–6 × 4–8 mm, pedicel 6.5 mm.

Distribution: Along the Red Sea coasts of Sudan and Somalia, and along the coasts of the Gulf of Aden. In Egypt (Fig. 2) along the Cairo–Suez road and in wadis along the Red Sea coast.

Zygophyllum aegyptium A. Hosny sp. nov. – Fig. 1

Holotypus: Egypt, Mediterranean region (Mma), Ras El Bar near Damietta, 7.1976, A. El Gazzar s.n. (CAI).

Differt a *Z. albo* ramis floriferis ad nodos bifloris vel trifloris (in *Z. albo* unifloris) et capsulis majoribus.

Green, glabrous shrub 30–60 cm high; internodes cylindrical, slightly hairy, 2.5–4 cm. Leaves 2-foliolate, leaflets unequal, obovate to oblanceolate, 7–11 mm long, apex rounded; petiole cylindrical, 9–16 mm; stipules minute. Inflorescence cymose with 2–3 flowers at each node. Flowers stalked, pedicel 2 mm; sepals 5, ovate, 4 × 2 mm; petals 5, spathulate, 5 × 3 mm, white; stamens 10, filaments 3 mm, staminal scales 2 mm long, entire; ovary spherical, hairy, style 1 mm, terminal. Capsule glabrous or slightly hairy,

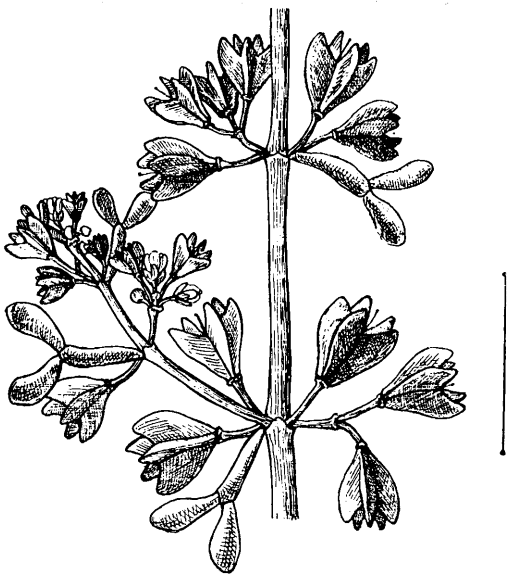


Fig. 1. *Zygophyllum aegyptium*. Scale 2 cm.

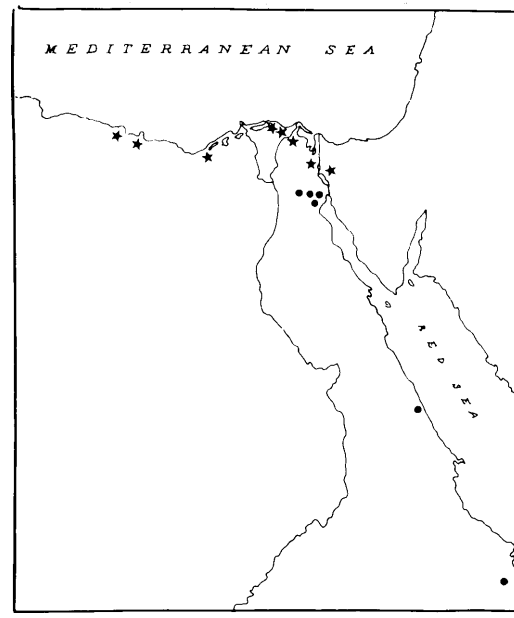


Fig. 2. Distribution of ★ *Zygophyllum aegyptium*, ● *Z. decumbens* var. *megacarpum*.

obconical, 5-partite, 5–9 mm long, 5–8 mm broad, apex retuse; pedicel short, 4–5 mm.

Z. aegyptium is easily distinguished from *Z. album* since the flowering branches bear 2–3 flowers at each node (only one in *Z. album*). This makes *Z. aegyptium* look more luxuriant during the flowering stage. The difference is even more marked during the fruiting stage. The branches of *Z. album* are lax, bearing only one capsule at each node and the capsule itself hardly exceeds 5×5 mm. In *Z. aegyptium*, the branches bear several capsules at each node and the capsules are larger, thereby giving the branches a characteristic, dense appearance.

Distribution: Mediterranean region and the Isthmic Desert in Egypt (Fig. 2). Specimens from Tunisia, Libya and Cyprus were also seen by the author.

Collections: Egypt. Western Mediterranean region: Mersa Matrouh, 7.1959, Ghabour (CAI) – Ras El Hekma, growing on sandy dunes, 5.1963, Täckholm et al. (CAI) – Alexandria, El Maks, 5.1908, Bornmüller 10504 (BM). – *Eastern Mediterranean region:* Burg El Borollos, 9.1952, Kassas (CAI) – Emad, 3 km W of Burg El Borollos, 8.1961, Täckholm et al. (CAI) – Baltim, 8.1968, El Hadidi (CAI) – Along the road from Damietta to Ras El Bar, 8.1961, Täckholm & Kassas (CAI) – Ras El Bar, 7.1976, El Gazzar (CAI). – *Isthmic desert:* Desert road between Qantara and Ismailia, 7.1952, Amin (CAI) – E bank of Suez Canal at Ismailia, Lupton (BM).

Acknowledgements. I am most grateful to Miss D. Hillcoat and Dr W. Stearn (BM) and to Mr L. Forman (K) for herbarium facilities. The drawings were made by Mr M. El-Gohari. Financial support from the Salén Foundation, Stockholm, is gratefully acknowledged.

A new species in the Cerastium alpinum group from Mt Olympus, Greece

Hermann Merxmüller and Arne Strid

Merxmüller, H. & Strid, A. 1977 12 30: A new species in the Cerastium alpinum group from Mt Olympus, Greece. *Bot. Notiser 130:* 469–472. Stockholm. ISSN 0006-8195.

Cerastium theophrasti Merxm. & Strid is described from calcareous scree in the summit area of Mt Olympus. It differs from related taxa by its glandular pubescence and larger seeds with long, acute tubercles. The chromosome number, 2n = 36, is the lowest yet recorded in the *C. alpinum* complex.

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Cerastium theophrasti Merxm. & Strid sp. nov. – Fig. 1

Cerastium uniflorum "Murith" (recte: Clairv.) var. *mitkaënse* Wagner, Feddes Repert. 38: 282 (1935).

Cerastium alpinum L. var. *glanduliferum* Koch sensu Stojanov & Jordanov, God. Sof. Univ. 34: 173 (1938).

Cerastium uniflorum Clairv. sensu Quézel & Contandriopoulos, Candollea 20: 55 (1965).

Orig. coll. Greece. Mt Olympus, summit area, E-facing slope below the peak of Mitikas, along path to Refuge C, 2700 m, calcareous scree, Strid 13029, 10.7.1977 (ATH holotype, C, G, LD, M, W, isotypes).

Herba caespitosa, perennis, ubique dense glandulosopilosa. Inflorescentia (1–)2(–3)-flora, pedunculis post anthesin deflexis. Bracteolae omnino herbaceae vel apice anguste scariosae. Sepala lanceolata, margine scariosa. Petala alba, bifida, sepalis circiter 1.4 longiora. Capsula paene recta ostio haud obliquo. Semina 1.45–1.75 mm longa, tuberculis longis acutis dense obsita. Numerus chromosomatum 2n = 36.

Caespitose perennial with a thin, more or less vertical, branched root and numerous, prostrate to ascending, 2–6 cm long non-flowering shoots. *Flowering shoots* ascending to erect, 4–9 cm long. *Stems* and peduncles terete, 0.6–0.8 mm in diameter. *Leaves* on non-flowering and flowering shoots similar, opposite, narrowly elliptical to oblanceolate, obtuse, 7–11(–14) × 2.5–4 mm, crowded towards the apex of non-flowering shoots; internodes on flowering shoots 5–14 mm. Older parts of stems rather densely covered with dead, inward-curving leaves which are obovate to broadly oblanceolate and somewhat smaller than the green leaves. *Inflorescence* 1–2- or occasionally 3-flowered; the flowers emerging in the axils of a pair of bracts which are entirely herbaceous and similar to the uppermost leaves, though somewhat smaller. *Peduncles* 10–25 mm, straight and erect at anthesis, conspicuously deflexed (but remaining straight) after anthesis. First flower usually lacking *bracteoles;* second flower with a pair of herbaceous (or sometimes scarious-tipped), elliptical, acute, 3–5 × 1–2 mm large bracteoles attached 1/4–1/3 from the base of the peduncle. *Sepals* lanceolate, subacute, 5–7 × 2–2.5 mm, with a scarious margin which is usually c. 0.5 mm wide near the apex and extends almost to the base in 2 of the sepals, narrower and confined to the upper 1/3 in the others. Whole plant, including stems, leaves, bracts, bracteoles, peduncles and calyces, densely covered with straight, spreading, colourless *glandular hairs* (white in dried material) which are 0.15–0.20 mm long on the leaves, somewhat longer and more variable (up to 0.45 mm) on the peduncles; whole plant thereby sticky; *eglandular hairs lacking*. *Flowers* broadly campanu-

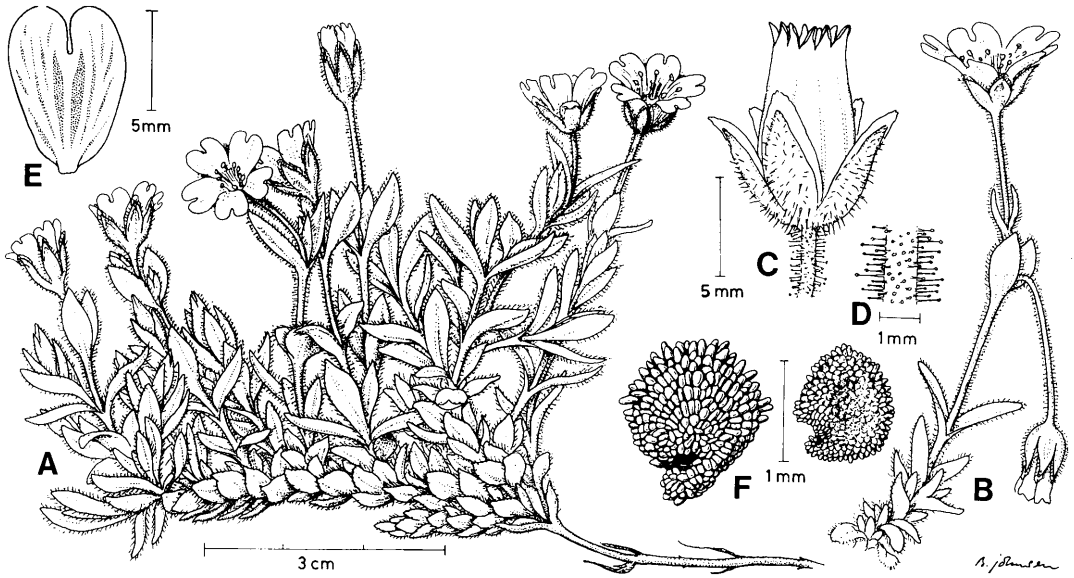


Fig. 1. *Cerastium theophrasti,* drawn from a cultivated specimen (Strid 9874). – A: Habit. – B: Inflorescence. Note the deflexed pedicel after flowering. – C: Ripe capsule. – D: Portion of pedicel to show glandular pubescence. – E: Petal. – F: Seed of *C. theophrasti* (left) compared with seed of *C. alpinum* from Britain (right).

late, with a sweet scent. *Petals* obovate, 7–9.5 × 4.5–5.5 mm, white except for the pale greenish base, with coarse, raised veins above, bifid to 1/4–1/3. *Filaments* subulate, 4–5 mm long, outward-curving, white, with small (c. 0.6 × 0.4 mm), dorsifixed, versatile, yellow anthers which dehisce c. 2 days before the stigmas become receptive. *Ovary* spherical at anthesis, pale green, smooth, c. 2 mm in diameter. Styles c. 3 mm long, white, outward-curving and slightly expanded in the upper part, papillose and receptive on the upper one mm of the adaxial side. *Mature capsule* 8–10 mm long, nearly straight, c. 4 mm wide at the base, gradually tapering and c. 3 mm wide at the apex (below the teeth); teeth c. 0.8 mm long, triangular, subacute, patent, with recurved sides; mouth of capsule not oblique. *Seeds* medium brown, 1.45–1.75 mm, acutely long-tuberculate, the tubercles rugose at base. *Chromosome number* 2n = 36.

Since the type collection was gathered on an excursion with the Botanical Society 'Theophrastos' of Copenhagen we find it appropriate to let the specific epithet commemorate the father of botany as well as the society named after him.

Other collections: Olympos, 2600 m, J. Wagner, Iter Graecum 1934, 1.8.1934 (M, type of *C. uniflorum* var. *mitkaënse*) – Auf Felsen und Felsschotter auf den Gipfeln Skala und Skolion, auf cca. 2700–2900 m Meereshöhe; in Ritzen der Felsmauer, auf den Gipfeln Stefani und Mitika, cca. 2800–2900 m, Stojanov & Jordanov, 21.–25.7.1937 (apparently in SOM, not seen) – Skolio, 2900 m, Stamatiadou 3972, 2.8.1968 (ATH) – Ditto, 2700–2750 m, Stamatiadou 6867, 10.7.1969 (ATH) – Am Mytikas-Gipfel, 2917 m, Roessler 6413, 4.7.1968 (M) – Grosschutthang an der Stefani-Nordwand, 2600 m, Sauer, 28.7.1969 (Herb. Univ. Saarbrücken) – Hagos Antonios, in saxosis calc., 2600–2700 m, Rechinger 38773, 27.7.1970 (M, W) – Summit area of Ag. Antonios, 2700–2800 m, Strid 1313, 24.7.1970 (C) – N and W slopes of Ag. Antonios, 2650 m, calcareous scree, Strid 1410, 27.7.1970 (C) – Ridge between Skala and Mitikas, 2800–2900 m, calcareous scree and rock crevices, Strid 1483, 28.7.1970 (C, W) – Skolio-Gipfel, 2900 m, Greuter 9720, 26.7.1971 (ATH, G) – S of Skala peak, 2740 m, glacial cirque with humid limestone scree, Kornaś 97, 26.–30.8.1973 (KRA) – Osthänge der Skala, 2600–2800 m, Podlech 25797, 10.8.1973 (M) – Above Refuge A, along path to Ag. Antonios, 2600 m, calcareous scree, Strid 9874 & 10092, 19.8. & 22.8. 1975 (seed coll., cult. in Bot. Garden Copenhagen, vouchers in C).

Cerastium theophrasti is fairly widespread in the summit area of Mt Olympus, where it grows on calcareous scree and occasionally in rock crevices. It is strictly alpine and has not been

recorded below c. 2600 m. It grows together with several other Olympus endemics such as: *Alyssum handelii, Rhynchosinapis nivalis, Potentilla deorum, Achillea ambrosiaca* and *Festuca olympica*. The following species are also frequently found in association with *Cerastium theophrasti: Arenaria conferta, Minuartia verna* ssp. *idaea, Paronychia rechingeri, Silene saxifraga, Ranunculus brevifolius, Cardamine carnosa, Saxifraga spruneri, S. sempervivum, Euphorbia capitulata, Thymus cherlerioides, Linaria alpina, Veronica thessalica, Galium degenii, Carex laevis* and *Sesleria coerulans*.

Cerastium theophrasti flowers from the end of June to the beginning of August. Plants cultivated outdoors in Copenhagen flowered from the end of May to mid-June. The flowers are protandrous and have a faint but distinct sweet scent. Seed-setting occurs very rapidly after flowering; in the cultivated material ripe seeds developed in about three weeks. In cultivated plants all the flowers become conspicuously deflexed after anthesis (Fig. 1 B). This is less obvious in some of the collections from nature, and the flowers of 1-flowered inflorescences and the second and third flowers of 2–3-flowered inflorescences may remain more or less erect. There is some individual variation in the number of flowers per inflorescence, some individuals or populations having predominantly one-flowered, others two-flowered or occasionally three-flowered inflorescences.

Possibly related taxa

In habit there is a striking similarity with *C. uniflorum* L. and other taxa of the *C. latifolium* group. The completely different shape of the seeds appears to rule out any close relationship, however, and the similarity in habit may be due to convergent evolution imposed by the same habitat (alpine screes). In the *C. latifolium* group the seeds have a loose testa which is shallowly and irregularly rugose, whereas in *C. theophrasti* the testa is firmly attached to the rest of the seed and is densely covered with long, acute tubercles.

In our opinion the species undoubtedly belongs in the *C. alpinum* group, a complex which can by no means be regarded as fully understood. The following features seem to exclude the possibility that the Olympus plant should be conspecific with *C. alpinum* s. lat.:

(1) The chromosome number $2n = 36$, which is the lowest yet recorded in the group. The most widespread chromosome number for *C. alpinum* s. lat. is $2n = 72$, reported from Arctic North America, Greenland, Iceland, Scandinavia, Great Britain, the Alps, the Central Plateau, the Pyrenees and the Sierra Nevada (see Küpfer 1974 and references in Hess, Landolt & Hirzel 1967 and Fedorov 1969). $2n = 108$ has been counted in material from Canada, Greenland and Scotland, and $2n = 144$ has been reported from northernmost Sweden (see op. cit. and Löve & Löve 1975). The lowest number so far reported for the *C. alpinum* complex is $2n = 54$ in material from Greenland (Böcher & Larsen 1950, Jørgensen et al. 1958) and Arctic Russia (Sokolovskaya & Strelkova 1960). According to Böcher (1977) the chromosome number $2n = 108$ (occasionally $2n = 54$) is confined to *C. arcticum* whereas *C. alpinum* s. str. has $2n = 72$ ($2n = 144$ reported only once). Incidentally, the chromosome number $2n = 36$ for *C. theophrasti* should not be taken to indicate any relationship with the *C. latifolium* group (where this number is prevalent) since $2n = 36$ is the commonest chromosome number found in *Cerastium* species.

(2) The seeds which are larger than those of *C. alpinum* and have longer tubercles (see Fig. 1 F).

(3) The complete absence of long, soft, eglandular hairs which (except in completely glabrous forms) are always present in the *C. alpinum* group and are indeed a diagnostic feature for that group.

In addition, the following differences also exist, although less distinct and perhaps less important:

(4) The short petals (c. 1.4 times as long as the sepals, whereas they are about twice as long as the sepals in *C. alpinum* s. lat.).

(5) The tendency for the inflorescence to be one-flowered and without bracteoles, a feature otherwise unknown in the *C. alpinum* group.

(6) The deflexed fruiting peduncles, which at least are not a regular feature of *C. alpinum* s. lat.

There are also two rather poorly known Balkan

species whose possible affinities with *C. theophrasti* should be considered.

(1) *C. runemarkii* Möschl & Rech. fil. – Described as having "seeds 0.7–0.8 mm, minutely muricate". Even if these seeds may not have been quite ripe they certainly appear to be very different from the seeds of *C. theophrasti,* which are twice as large and have long, acute tubercles. More important, perhaps, *C. runemarkii* has no glandular hairs, but has long, straight, eglandular hairs. The sepals also seem narrower and the capsule somewhat shorter and narrower. Conspecificity with *C. theophrasti* is thus ruled out, although it seems likely that *C. runemarkii* also belongs in the *C. alpinum* group s. lat. rather than in the *C. uniflorum* group. Its chromosome number, incidentally, is also 2n = 36. *C. runemarkii* is only known from the type collection from the summit area of the Aegean island of Naxos (c. 950 m).

(2) *C. hekuravense* Jáv. – According to the description this species should only have glandular hairs. If this is correct, it would constitute a similarity with the Olympus plant. In other respects, however, there seem to be great differences. The leaves of *C. hekuravense* are said to be broader (5–7 mm) and acute, the inflorescence 3–7-flowered, the bracts and bracteoles possess scarious margins, the petals are longer (13 mm!) and the seeds are smooth ("semina laevia"). If the seeds are as described, then *C. hekuravense* has no connection with *C. theophrasti* and does not belong in the *alpinum* group at all (where it was tentatively placed by Jalas in Flora Europaea). It was described from the 2500 m high limestone mountain Hekurave in Albania, and phytogeographically it would make sense to have the same species here as on Mt Olympus, but the description seems to rule out this possibility. According to information from Budapest (BP) the type is likely to have been destroyed in the Second World War.

The nearest localities to Mt Olympus for *C. alpinum* seem to be in southern Bulgaria (Pirin planina), where it is represented by ssp. *lanatum* (Lam.) Asch. & Graebn. The record "Gr" for *C. alpinum* in Flora Europaea (1: 140, 1964) may be based on the report by Stojanov & Jordanov (1938 p. 173).

Acknowledgements. Strid's field work in Greece was financed by a grant from the Carlsberg Foundation. The Latin diagnosis was prepared by Dr T. Christensen and the drawings made by Mr B. Johnsen.

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Sisyrinchium laxum Otto ex Sims found in N Greece

Arne Strid

Strid, A. 1977 12 30: Sisyrinchium laxum Otto ex Sims found in N Greece. *Bot. Notiser 130:* 473–475. Stockholm. ISSN 0006-8195.

Sisyrinchium laxum Otto ex Sims, a South American species, has been found on flats just N of Mt Olympus. Apparently this is the first record from Europe. The characteristics and affinities of the species are discussed.

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Three species of the predominantly American genus *Sisyrinchium* have been reported from Europe. *S. bermudiana* L. is a native of E North America and W Ireland, and has been introduced in England and probably elsewhere in Europe. *S. montanum* Greene, a related species originating in E North America and frequently confused with *S. bermudiana,* is widely naturalized in C Europe and appears to be spreading, the most recent records being from Romania (Rösler 1971) and Bulgaria (Kolev 1972). Concerning the taxonomy and nomenclature of these species, see Ingram (1967) and Ward (1968). A third species, *S. californicum* (Ker-Gawl.) Dryander, native of California and Oregon, is naturalized in Ireland.

The three above-mentioned species are all perennial and rather large-flowered. In 1976 a small-flowered, annual to biennial species, subsequently identified as *S. laxum* Otto ex Sims, was discovered in N Greece. The locality is: Macedonia, Nom. & Ep. Pierias, flats at N foot of Mt Olympus, 3.6 km from the village of Fotina along main road to Katerini, 140 m. Strid & Kjellsson 11313, 9.6.1976 (ATH, C, K, LD). The plants were found in a meadow in an agricultural area, chiefly at the edge of a small waterhole and by tracks left by a heavy vehicle, i.e. in places where the soil was damp to wet and the vegetation sparse.

Description

Annual to biennial, 5–15 cm tall, with thin fibrous roots. *Leaves* all or nearly all basal, linear-ensiform, 30–60 × 1.5–3 mm, with scabrid margins, not becoming dark on drying. *Stems* 2–8 per plant, ascending to suberect, much longer than the leaves, c. 0.8 mm wide, narrowly winged, with scabrid margins. Stem bearing a single, 2–4-flowered inflorescence. *Spathevalves* subequal, herbaceous, lanceolate-ensiform, 15–25 × 2–3 mm, with scarious margins and minutely scabrid keel. *Pedicels* slender, much exceeding the spathes; flowers more or less erect, fruiting pedicel arcuate or nodding. *Flowers* c. 10 mm long and 9–15 mm in diameter; tepals subequal. Lower part of corolla urceolate, greenish yellow, sparsely villous outside; expanded part of tepals broadly elliptical, apiculate, pale blue with darker stripes, becoming dark violet blue in throat. *Filaments* connate for up to 3/4 of their length; filamentous shaft expanded and densely glandular-pubescent below, cylindrical and glabrous above. *Anthers* more or less triangular in transection, arranged as to form a yellow triangle in throat of corolla. *Style* about as long as the filaments, style branches slender, appearing inbetween the anthers. *Ovary* broadly ellipsoid to ovoid, glandular-pubescent when young. *Capsule* globose-trigonal, 3–4 mm, medium brown, smooth.

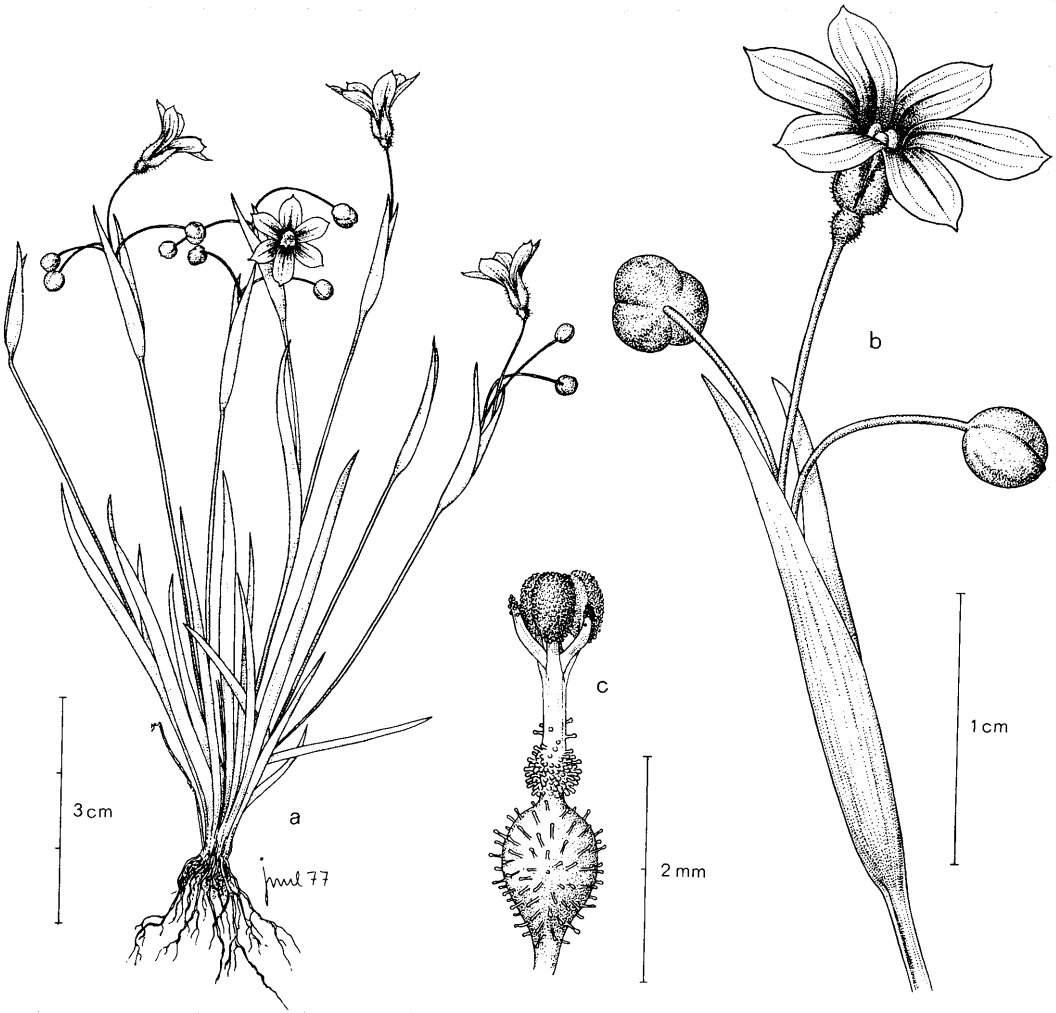


Fig. 1. *Sisyrinchium laxum,* Strid & Kjellsson 11313. Drawing based on dried material and photographs. – A: Habit. – B: Inflorescence. – C: Petals removed to show glandular-pubescent ovary, filamentous shaft with dense glandular pubescence below, anthers, and style-branches.

Seeds triquetrous, c. 0.8 mm, alveolate, black. *Chromosome number* 2n = 32.

Seeds were sown in the Copenhagen Botanical Garden on March 25, 1977. Only two germinated, after about three weeks, but the plants flowered very sparsely in the rather cool summer of 1977. Still in the end of September they have fresh green leaves; they are likely to survive a mild winter and flower in the next summer. The plants collected in nature were most probably growing as annuals, however, germinating in the early spring or possibly in the autumn, and withering in mid-summer when the site becomes completely dry.

Discussion

Our plant belongs to a taxonomically difficult group of South American species, and there is some confusion as to the application of names. According to the key in Johnson (1938) it clearly matches *S. laxum* Otto ex Sims in Curtis' Bot.

Mag. 49: tab. 2312 (1822), and there is indeed a good agreement with the original drawing and description of this species in which it is interesting to note that it is said to have "survived the last winter [in Chelsea] exposed to the open air." *S. laxum* differs from *S. micranthum* Cav., Diss. 2: 345, tab. 191 fig. 2 (1788), according to Johnson, in the larger corolla, subequal spathevalves, glandular-pubescent ovary, in the fact that it does not darken on drying, and in the more southern, temperate distribution. The widely used name *S. iridifolium* HBK, Nov. Gen. 1: 324 (1816) apparently belongs in the synonymy of *S. micranthum* (Johnson 1938 p. 392 and Marais in litt.). Ravenna (1968 p. 286), however, regards *S. laxum* as a synonym of *S. iridifolium* ssp. *iridifolium*, and *S. micranthum* as a separate species. *S. micranthum* was described from Peru, and the original drawing is somewhat mysterious, showing a plant with a single branched, leafy stem. With the available information it seems most reasonable to follow Johnson, according to whom our plant is definitely *S. laxum*.

Johnson recorded *S. laxum* from S Brazil, Uruguay, Argentine, Paraguay and Chile, and also noted that it "occurs as an adventive species in Europe". It seems nowhere to be mentioned in the European literature, however, and it is not clear on what Johnson based this statement.

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Identification of some small species of Navicula

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Light and electron microscopy have been used to identify some small *Navicula* species in a sediment from Halvarp bog in southern Telemark, Norway. The profile contained *N. amphipleuroides* Hust. and *N. cryptolyra* Brockmann. The relationships between *N. amphipleuroides, N. fenestrella* Hust. and *N. escorialis* Simonsen are discussed.

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A sediment profile from Halvarp bog in southern Telemark, Norway, has been investigated in order to determine former shoreline levels in this area (Stabell 1976). Specimens of small *Navicula* species are dominant in some of the samples. Correct identification of these specimens were therefore considered important both stratigraphically and ecologically.

Scanning electron microscopy showed that two species of *Navicula* were present: *N. cryptolyra* Brockmann and a species belonging to the group characterized by a large hyaline area and short marginal striae (i.a. *N. amphipleuroides* Hust., *N. fenestrella* Hust. and *N. escorialis* Simonsen). After comparison with slides at the "Friedrich Hustedt Arbeitsplatz", Bremerhaven, we managed to identify the latter species as *N. amphipleuroides*.

Phase-contrast light microscopy (LM), with a plan-apochromatic oil-immersion objective and scanning electron microscopy (SEM) were used. The SEM studies were made by HH in a Cambridge EM at the Zoological Institute, University of Lund.

The terminology follows Anonymous (1975).

Navicula amphipleuroides and related species

Table 1 shows the main differences between *N. amphipleuroides, N. fenestrella* and *N. escorialis* as they are reported in the literature.

Hustedt (1955) described and illustrated both *N. amphipleuroides* and *N. fenestrella*. He pointed out that *N. amphipleuroides* differs from *N. fenestrella* "by the somewhat curved raphe, the distant central pores and the median rib". Simonsen (1959) gave a very brief description of *N. escorialis*. He did not mention any median rib but it is visible in the illustrations. In 1962 Hustedt provided a new description of *N. fenestrella:* "Mittelrippe sehr schmal, zuweilen an einer oder beiden Seiten von einer zarten Punktreihe begleitet". He made *N. escorialis* synonymous with *N. fenestrella*. Van Landingham (1975) considered both *N. fenestrella* and *N. escorialis* to be synonymous with *N. amphipleuroides*.

We consider that *N. fenestrella* is a distinct species, characterized by the straight raphe and the missing median rib, as stressed in the original description (Hustedt 1955). His later description (Hustedt 1962) makes the difference between *N. amphipleuroides* and *N. fenestrella* obscure. However, we know this species only from the description and illustration; we have not been able to find any material agreeing with this description in spite of careful search. In the Beaufort material no *N. fenestrella* had been especially marked. A slide from the Hustedt Collection No. N 202,13b, containing material from Snigsfjord, Norway, was examined by LM.

Table 1. Differences between some species of *Navicula* according to the literature.

Character	*amphipleuroides* (Hustedt 1955)	*fenestrella* (Hustedt 1955)	*escorialis* (Simonsen 1959)	*fenestrella* (incl. *escorialis*) (Hustedt 1962)
Median rib	strong	absent	present	narrow
Raphe	slightly curved	straight	straight, sometimes slightly curved	often curved, sometimes one or two rows of punctae
Central pores	distant	close	.	.
Length (μm)	8–12	c. 8	7.5–9	7–9
Breadth (μm)	4.5–5.5	5	4–5.5	4–5.5
Number of striae/10 μm	20–24	c. 20	18–20	c. 20

However, even this slide was difficult to examine, because no particular specimen had been marked. The only material referred to *N. fenestrella* by Hustedt (after the publication of the species) which we have seen, is the Hustedt Collection No. N 397,85; material from Eckernförder Bucht (15 m), collected by Dr Simonsen; in fact this is the material on which Simonsen (1959) described *N. escorialis* and, as far as can be seen in LM, it is similar to the specimen shown here (Fig. 1 B).

We also found, after examination of slides at Bremerhaven by LM, that *N. amphipleuroides* (Hustedt Collection No. N 10,38; material from Beaufort, N.C., Hafen; specimen marked with a circle, Fig. 1 A) differs from *N. escorialis* (Simonsen Collection Di 289; material from Profil Winds Grav, 5 m, grauer Feinsand mit kleinen Steinen, *Zostera*, 25.11.1955; Fig. 1 B). No extension of the striae towards the raphe was seen in *N. escorialis*. However, according to Simonsen (pers. comm.) this character shows considerable intraspecific variation. We think this depends on whether the frustule is seen from the inner or from the outer side.

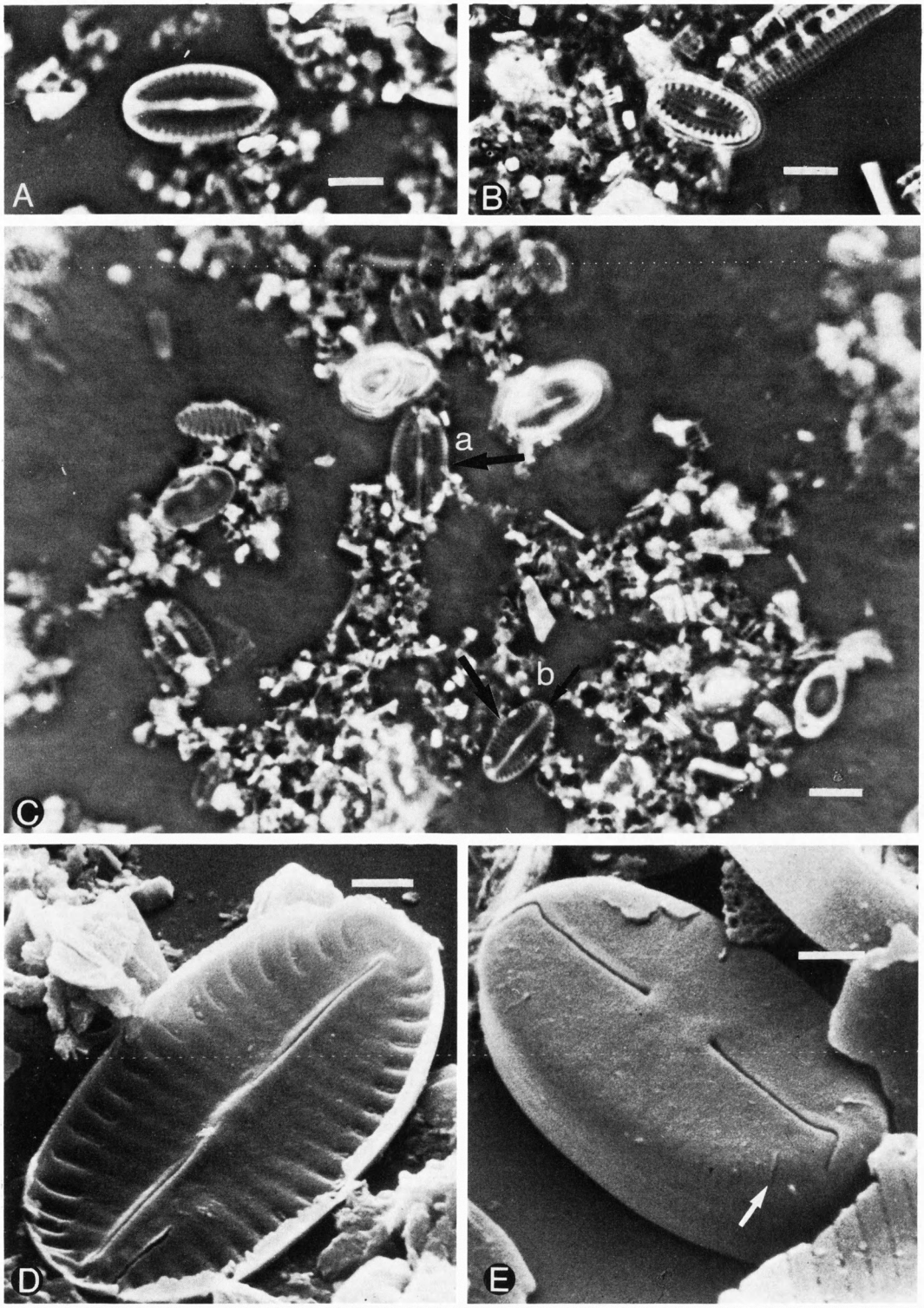
Navicula amphipleuroides Hust.

Hustedt 1955 p. 30, Pl. 5 Fig. 33, 34; Hustedt 1962 p. 175, Fig. 1308.

The *Navicula* specimens in the Halvarp samples show an extension of the striae towards the raphe and appear to have a strong median rib. We have therefore identified them as *N. amphipleuroides*. The following observations have been made on the Halvarp material (Fig. 1 C–E).

The central pores are not always far apart; the distance apart ranges from 0.8 to 1.5 μm. Both the central area and the areas at the polar ends are strongly light refractive (Fig. 1 C).

Fig. 1. A: *Navicula amphipleuroides* from the Beaufort material (Hustedt Collection No. N 10,38) (LM; photo HH). – B: *N. escorialis* from the Profil Winds Grav (Simonsen Collection Di 289) (LM; photo HH). – C: Specimens from the Halvarp bog sample (LM; photo BS). a *N. cryptolyra*, b *N. amphipleuroides* (note light-refractive areas). – D: *N. amphipleuroides*. SEM, interior view of a valve showing the somewhat thickened central nodule. – E: *N. amphipleuroides*. SEM, exterior view of a frustule showing the layer covering the marginal striae and a small split of the membrane (arrow). – Scale unit 5 μm (A–C), 1 μm (D, E).


A
B
a
b
C
D
E

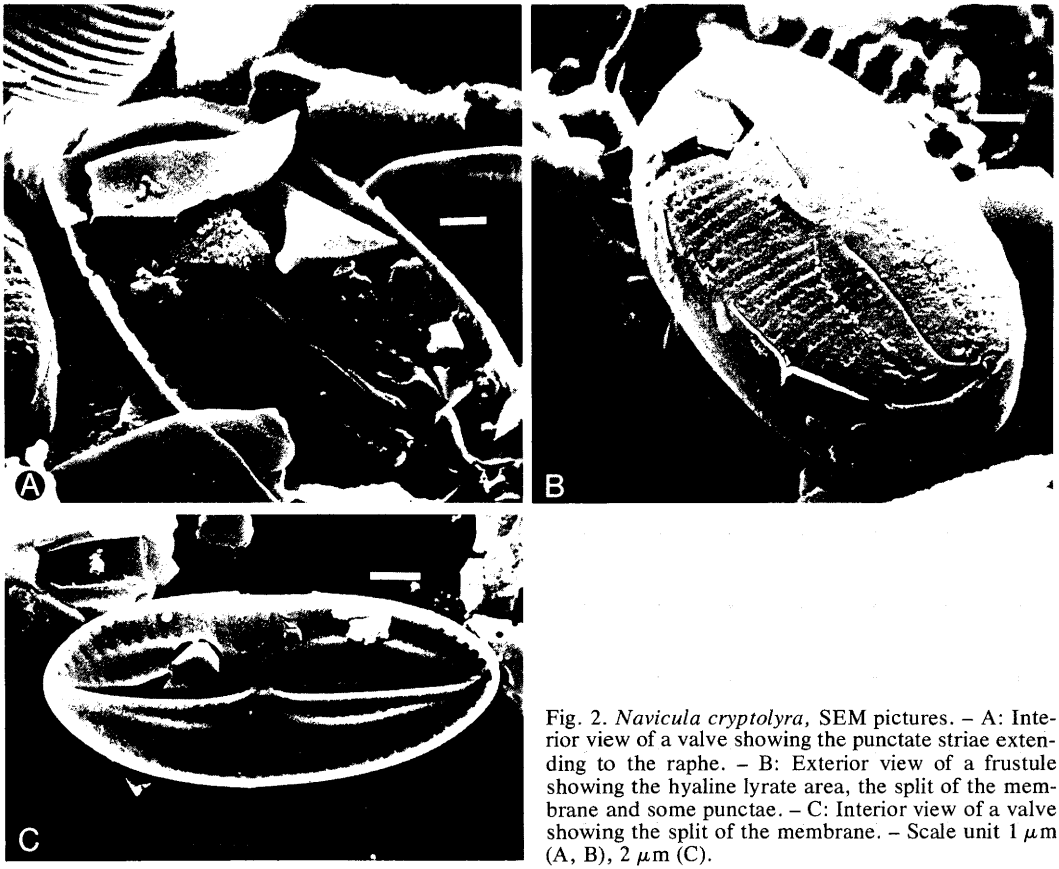


Fig. 2. *Navicula cryptolyra,* SEM pictures. – A: Interior view of a valve showing the punctate striae extending to the raphe. – B: Exterior view of a frustule showing the hyaline lyrate area, the split of the membrane and some punctae. – C: Interior view of a valve showing the split of the membrane. – Scale unit 1 μm (A, B), 2 μm (C).

The walls of the fissures seem to be fairly thick (Fig. 1 D), giving the impression of a strong longitudinal rib in LM. A weak extension of the striae (furrows) towards the raphe is clearly visible on the inner surface of the valves (Fig. 1 D). The outer surface, however, seems to have a cover which makes the striation barely visible (Fig. 1 E).

Hustedt (1962) classifies *N. amphipleuroides* as a "Meeresform". In the profile from Halvarp we have not found *N. amphipleuroides* in the lowermost samples. *N. amphipleuroides* increases at the same time as *Dimerogramma minor* (Greg.) Ralfs and *Grammatophora oceanica* (Ehr.) Grun. decrease, which may indicate that it can live in water with a low salinity. Although *Melosira sulcata* (Ehr.) Kütz. increases together with *N. amphipleuroides,* this does not indicate marine conditions since *M. sulcata* is polyhalobous and pleio-euryhaline and therefore can live in water with a salinity as low as 3–5‰.

Navicula cryptolyra Brockmann

Brockmann 1950 p. 19, Fig. 22, 23; Hustedt 1962 p. 534, Fig. 1570.

Our specimens fit very well with the description given by Brockmann (1950). It was not easy to decide whether or not this species belongs to the *Lyratae* group of *Navicula* from LM studies alone, because the lateral areas are obscure (Fig. 1 C). This fact had already been noted by Brockmann (1950). As seen in Fig. 2 A, viewed from the inner side of the valve, the punctate striae are not interrupted by the lateral areas. In Fig. 2 B, viewed from the outer side of the valve, no striae are visible between the raphe

and the lateral areas. It was not possible to see whether the striae are hidden by another layer or not. Figs. 2 B, C, however, show other specimens in which the membrane has split in places, showing that there are in fact two layers. In the specimen in Fig. 2 B some punctae are visible near the raphe. Change of focus indicated that the punctation extends as far as the raphe, though sometimes interrupted by a conspicuous, hyaline, lyrate area. This feature sometimes makes identification by LM difficult.

Simonsen (1962) placed *N. cryptolyra* among the euryhaline mesohalobes, i.e. it is found in brackish water with a salinity of 0.2 to 30‰.

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Recent advances in the taxonomy of Myxomycetes

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A general survey is given of some of the results obtained and the ideas presented in taxonomic research on Myxomycetes during the last ten years. It is suggested that the Liceales, as presently circumscribed, may be an unnatural order and that *Licea variabilis* Schrad. will prove to have more in common with species of *Perichaena* Fries than with species of *Licea* s. str.

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During the past two decades increased interest has been devoted to research on the Myxomycetes and related groups of organisms. Improved culture techniques have increased our knowledge about the ultrastructure and physiology of several species. Many species, including a large number regarded as common, have resisted all attempts to get them grow and complete their life cycles under laboratory conditions. Hence, most cytological and physiological research has been restricted to a limited number of species, in the main on *Physarum polycephalum* Schw. Studies of cultures grown in moist chambers have resulted in the discovery of several types of organisms that seem to be related to Myxomycetes, but which may differ in morphological character, as well as in their life cycles. This has made the delimitation of the Myxomycetes as a taxonomic group more difficult but has led to a better understanding of the origin and phylogeny of the Myxomycetes.

Increased interest has also been focused upon Myxomycetes from a taxonomic point of view during the past two decades. A monographic treatment by Martin & Alexopoulos was published in 1969, the appearance of which has not only facilitated taxonomic studies by bringing together in one volume information from a large number of sources, but by virtue of critical discussion and emphasis on the need for further studies it has stimulated further research. Martin & Alexopoulos recognized c. 425 species, grouped into 53 genera. An additional c. 80 species and three genera have now been described (up to June 1977) as new to science. The present paper attempts to briefly survey some of the results obtained and the ideas presented in taxonomic research on Myxomycetes since the appearance of the above-mentioned monograph. However, the paper makes no claim to completeness in this respect. The endosporous orders are treated in the same sequence as in Martin & Alexopoulos (1969).

Ceratiomyxa

Although very divergent the genus *Ceratiomyxa* Schroet. has traditionally been included in monographic treatments of the Myxomycetes, so also by Martin & Alexopoulos (1969). *Ceratiomyxa* differs in having exospores, i.e. spore-like structures which are borne externally on individual stalks scattered over the surface of generally white-coloured, variously arranged, solidified plasmodial columns. All other genera produce their spores internally, in fructifications of various shapes. Also in its life cycle *Ceratiomyxa* differs in important respects from the endospor-

ous species, e.g. reversible protoplasmic streaming, a characteristic of endosporous Myxomycetes, seems to be absent. Upon germination the exospore produces a 4-nucleate protoplast, which forms a peculiar "thread" phase (Nelson & Scheetz 1976). This structure has not been seen in any endosporous species.

The systematic affinity of *Ceratiomyxa* has been much debated. Ultrastructural studies on *C. fruticulosa* (Müll.) Macbr. have revealed similarities to, as well as differences from, endosporous Myxomycetes (Scheetz 1972). Gilbert (1935) suggested that each exospore on its stalk might be interpreted as a single sporangium, homologous with that of an endosporous species. Olive (1970, 1975), in his revised classification of the Myxomycetes and associated organisms, referred the endosporous Myxomycete genera to a subclass of their own, the Myxogastria, while *Ceratiomyxa* was included in a separate subclass, the Protostelia. The Protostelia comprises organisms with minute fruiting bodies consisting of one to several spores borne on a hollow stalk. The trophic stage varies from simple amoebae to plasmodia in which there is no shuttle movement of the protoplasm. So far about ten genera have been recognized in the Protostelia. Olive interpreted the stalked exospore of *Ceratiomyxa* as a structure homologous with the sporocarp of other protostelids. Similarities, possibly indicating phylogenetic relationships with *Ceratiomyxa*, have been observed in the protostelid genera *Ceratiomyxella* Olive & Stoianovitch (1971 b) and *Protosporangium* Olive & Stoianovitch (1972). In the latter genus the plurinucleate plasmodia may assume a worm-like shape, reminiscent of the "thread" phase formed at a certain stage in the life cycle of *Ceratiomyxa*.

The Protostelia have been regarded as primitive organisms, conceivably ancestral to the endosporous Myxomycetes as well as to *Dictyostelium* and allied genera of cellular slime moulds. Although the ultrastructure and life cycles of several protostelids are incompletely known, and no doubt many further organisms remain to be discovered, the knowledge obtained so far seems to point to an affinity of *Ceratiomyxa* with protostelids rather than with endosporous Myxomycetes. Olive's classification is interesting and deserves serious consideration.

Liceales

The order Liceales, as traditionally circumscribed, is characterized mainly by the absence of a true capillitium. The assimilative stage is either a protoplasmodium or a phaneroplasmodium (Olive 1975 p. 108), which may indicate that the group is heterogeneous and unnatural. I believe that reclassification in the future will lead to changes in the circumscription of the order as a whole, as well as in the delimitation of some of the genera.

In the three genera *Licea* Schrad., *Cribraria* Pers. and *Dictydium* Schrad. the fructifications are normally sporangia (plasmodiocarps in one or two species of *Licea*), in the remaining five genera (*Tubifera* Gmel., *Dictydiaethalium* Rost., *Lycogala* Adans., *Enteridium* Ehrenb. (=*Reticularia* Bull.) and *Lindbladia* Fries) normally aethalia or pseudoaethalia. The aethalia and pseudoaethalia possess a pseudocapillitium. Aethalia and pseudoaethalia have been suggested to have evolved by the coalescence of sporangiate fructifications, and the pseudocapillitium is generally interpreted as representing remnants of the peridium (=wall) of the coalesced sporangia. In the sporangiate genera *Cribraria* and *Dictydium* the largest part of the peridium is fugacious, but certain remnants persist in the form of parallel ribs or a reticulum. Although the term pseudocapillitium is normally not applied in this case, this structure is of course homologous with a pseudocapillitium, providing that the theory about the origin of the pseudocapillitium in aethalioid and pseudoaethalioid species is correct. *Cribraria* and *Dictydium* are closely allied and the formal merger of the two genera (Nannenga-Bremekamp 1962) is wholly defensible. However, the two genera are generally easily distinguished and most myxomycetologists keep them separate for the purposes of convenience. The monotypic and pseudoaethalioid genus *Lindbladia* is closely associated with *Cribraria* and, as repeatedly pointed out in the literature (Macbride 1922, Lister 1925, Hagelstein 1944, Martin & Alexopoulos 1969, Nannenga-Bremekamp 1974), intermediate forms connect *L. tubulina* Fries with *C. argillacea* (Pers.) Pers. The two species also have a similar ecology. Both prefer coniferous wood and may sometimes be found together (Nannenga-Bremekamp 1974). *Cribraria* is a very difficult

genus taxonomically. About 30 species have been recognized. Although several species are well-defined, many taxa are highly variable and the characters of many species overlap. Alexopoulos & Sáenz Reynolds (1975) have described the taxonomic state of *Cribraria* as "well-nigh chaotic". The situation is further complicated by the fact that all attempts to grow *Cribraria* species from spore to spore-bearing stage under laboratory conditions have failed, making any study of the stability of morphological characters difficult.

In the genus *Licea,* as traditionally interpreted, the fructifications are completely devoid of both a capillitium and a pseudocapillitium. Martin & Alexopoulos (1969) recognized 19 species. At least six more species have been described up to now, viz. *L. synsporos* Nannenga-Bremekamp (1968), *L. deplanata* Kowalski (1972 a) (in the original description, Kowalski 1970 b, called *L. applanata*), *L. hepatica* Kowalski (1972 b), *L. retiformis* Nawavi (1973), *L. alexopouli* Blackwell (1974) and *L. bryophila* Nannenga-Bremekamp (1976). However, as recently pointed out by Alexopoulos (1976), the taxonomic importance of the absence or presence of a capillitium ought to be questioned in some cases. It is apparent that some species not closely related to the Liceales may also lack a capillitium, as for instance the genus *Squamuloderma* Kowalski (1972 c), but the presence of crystalline lime in the peridium and the possession of a phaneroplasmodium are characters that justify placing this taxon in the Physarales rather than in the Liceales. Five of the eight species recognized so far in the genus *Echinostelium* also lack a capillitium, but this genus differs in many important characters from the other Liceales genera and is therefore referred to a separate order.

It is well-known that the capillitium may be scantily developed in some species of *Perichaena* Fries, a genus of the Trichiales, and may even be absent in *P. corticalis* (Batsch) Rost., *P. quadrata* Macbr. and *P. syncarpon* Brooks (Keller 1971). That the capillitium may be totally absent in *Perichaena* is highly interesting from a taxonomic point of view. Alexopoulos (1976) has pointed out that *Licea retiformis* Nawavi, obviously referred to *Licea* because of the lack of a capillitium, could very well be accomodated within *Perichaena*. Nawavi (1973) also apparently had this possibility in mind when he noted the similarities of this species with members of the Trichiales. Of special interest in *L. retiformis* are the plasmodiocarpous fructifications and the type of plasmodium, described as intermediate between an aphanoplasmodium and a phaneroplasmodium. This type of plasmodium is characteristic of the Trichiales (Alexopoulos 1960), while what I would call "true" species of *Licea* have the "primitive" type of plasmodium, referred to as a protoplasmodium. Apart from *L. retiformis,* only one species in this genus forms plasmodiocarpous fructifications, namely *L. variabilis* Schrad. In my opinion this species also bears some resemblance to *Perichaena* species. Furthermore, the plasmodium of *L. variabilis,* as so far described (Sobels 1950, McManus 1966), is not a protoplasmodium but is reminiscent of that found in *Perichaena*. I suspect that *L. variabilis* will prove to have greater affinity with species of *Perichaena* than with those of *Licea* s. str.

As mentioned previously, in the Liceales, as at present circumscribed, both protoplasmodia and phaneroplasmodia occur. That phaneroplasmodia are known in some species could possibly indicate a relationship of some genera with the Physarales. Another possible indication of an affinity with the Physarales may be the presence of calcium in the dictydine granules of *Cribraria* and *Dictydium,* as demonstrated by Schoknecht (1975).

Listerella

The questioning of the taxonomic importance of the presence or absence of a capillitium, leads to interesting speculations on the affinity of the genus *Listerella* Jahn. This genus has small fructifications, generally 0.2–1 mm in diameter. The genus has been placed in the Trichiales due to the presence of a capillitium, which is often only scantily developed, however. The single species recognized, *L. paradoxa* Jahn, bears a strong resemblance to *Licea,* and even under a lens it is hardly possible to distinguish *Listerella* from species of *Licea,* subgenus *Licea*. Many authors have pointed out the great similarity in habit between the two genera. Martin & Alexopoulos (1969) write about *Listerella* that "this is essentially a *Licea* with a capillitium". Kowalski (1967, 1970 b) stressed the macroscopic similari-

ties between *Listerella* on the one hand and *Licea minima* Fries, *L. pusilla* Schrad. and *L. deplanata* (sub nomine *L. applanata*) on the other. He recommended that *Listerella* should be referred not only to the order Liceales but even to the family Liceaceae.

On the ground that *Listerella paradoxa* has smooth peridial lobes, while *Licea minima* and *L. pusilla* have wart-like processes along the margins of the lobes, Kowalski (1967) suggested that the capillitium of *Listerella* might represent an extension of the wart-like processes in *Licea*. In this connection it should be pointed out that *Licea kleistobolus* Martin has finger-like processes which penetrate into the sporangial cavity. These processes were originally interpreted by Lippert (1894) as a rudimentary capillitium. Martin & Alexopoulos (1969) believed them to represent elongations of the tubercles. Keller & Brooks (1971), who examined numerous collections of this species, found a continuous gradation from wart-like processes to tubular outgrowths.

Kowalski (1967) also hypothesized that "the capillitium of *Listerella*, since it appears to be attached at the margins of the peridial lobes, may represent a reduced state of the pseudocapillitium of the Liceales, and that the sporangia of *Listerella* and *Licea* are not sporangia, but highly reduced aethalia". Future research may elucidate the credibility of this hypothesis. Both genera possess the primitive type of plasmodium referred to as a protoplasmodium, a character which, together with the macroscopic similarities of the fructifications, mirrors the apparently very close relationship of the two genera.

In Europe most fructifications of *Listerella paradoxa* have been found on species of the lichen genus *Cladonia*. A Californian collection on an oak leaf differs in some respects (Kowalski 1967) from typical *L. paradoxa* and may perhaps represent a second species of this genus.

Echinosteliales

The order Echinosteliales comprises species which have minute, stalked sporangia and a protoplasmodium as the assimilative stage. The order was circumscribed by Martin & Alexopoulos (1969) to comprise the single genus *Echinostelium* de Bary. Later (Alexopoulos & Brooks 1971), the genera *Barbeyella* Meylan and *Clastoderma* Blytt, in general previously regarded as members of the Stemonitales, have also been included.

In *Barbeyella* only a single species is known, *B. minutissima* Meylan. *Clastoderma* also remained monotypic for a long time, with *C. debaryanum* Blytt as the only known species. However, during the last ten years another three species have been recognized, viz. *C. pachypus* Nannenga-Bremekamp (1968), *C. microcarpa* (Meylan) Kowalski (1975 a) and *C. dictyosporum* Lakhanpal & Mukerji (1976). The second of these species had originally been regarded as a variety of *Comatricha elegans* (Racib.) G. Lister. Eight species of *Echinostelium* have been recognized up to now (June 1977). One of these, *E. lunatum* Olive & Stoianovitch (1971 a), is the smallest known Myxomycete. Its fructifications are (ex. char.) 21–44 μm tall, the sporangia are 17–30 μm in diameter and are generally 4–8-spored. The recently described species *E. arboreum* Keller & Brooks (1976 b), in contradistinction to the condition in other members of the genus, possesses a persistent peridium attached to the capillitial threads. In this respect *E. arboreum* approaches the genus *Clastoderma*.

A special interest is attached to *Echinostelium*, since it is regarded as probably the most primitive Myxomycete genus. A study of the ultrastructure of the spore wall in *E. lunatum* and in a form of *E. minutum* de Bary has revealed interesting similarities with that of the protostelid genus *Cavostelium* Olive (Hung & Olive 1972), similarities which are believed to indicate a close phylogenetic relationship between protostelids and primitive Myxomycetes. When describing *E. coelocephalum*, Keller & Brooks (1976 b) pointed out that this taxon has spores which in size and markings are strikingly similar to those of *Pocheina rosea* (Cienk.) Loebl. & Tapp., an acrasid cellular slime mold. It seems quite possible that *Echinostelium* is a primitive genus through which other endosporous Myxomycetes evolved from protostelids or related organisms (Hung & Olive 1972, Olive 1975). Of the eight species of *Echinostelium* hitherto formally recognized, five lack a capillitium. Olive & Stoianovitch (1971 a) have intimated the possibility that the non-capillitial species could be referred to the protostelids, while the species with a capillitium could be

retained in the Myxomycetes. This shows how vaguely delimited the group Myxomycetes is at present.

Trichiales

The order Trichiales is characterized by fructifications with a generally well-developed capillitium, a pallid, white, brown or bright-coloured spore mass, and the absence of a columella. The assimilative stage seems to be intermediate in type between a phaneroplasmodium and an aphanoplasmodium. In *Trichia arundinariae* Rammeloo (1973) the plasmodium has been described (Rammeloo 1976 a) as intermediate in structure between a typical trichiaceous plasmodium and a phaneroplasmodium.

In modern taxonomic treatments (Martin & Alexopoulos 1969, Alexopoulos 1973, Nannenga-Bremekamp 1974, Farr 1976) the Trichiales is divided into two families, the Dianemaceae and the Trichiaceae. The main difference between the two families is that the capillitial threads are solid in the former and hollow in the latter. In the two first-mentioned taxonomic treatments, the Dianemaceae comprises the genera *Listerella, Dianema* Rex, *Minakatella* G. Lister and *Calomyxa* Nieuwl. However, as mentioned previously, Kowalski (1967) for good reasons has recommended that *Listerella,* which diverges from typical members of the Trichiales i.a. by its dark spore mass and in having a protoplasmodium as the assimilative stage, should be transferred to the Liceales, an arrangement accepted by Farr (1976). Nannenga-Bremekamp (1974) also included *Prototrichia* Rost. in the Dianemaceae. However, Kowalski (1967) demonstrated that the capillitium in this genus is basically tubular and recommended that the genus should be included in the Trichiaceae. More recently, Keller et al. (1973) have presented ultrastructural evidence that also *Minakatella* has a tubular capillitium, and they propose that this genus as well should be transferred to the Trichiaceae. Future studies may show whether the remaining two genera *Calomyxa* and *Dianema* have enough characteristics in common and are sufficiently distinct from other taxa to warrant retention of the Dianemaceae as a distinct family. Characters common to the two genera are the membranous peridium (*D. corticatum* List. being an exception in this respect, in having (ex char.) a two-layered peridium, the outer layer being cartilaginous and opaque), a solid capillitium at least partially attached to both the base of the sporangium and to the peridium, and pallid or yellowish-coloured spores under transmitted light (Kowalski 1967). Martin & Alexopoulos (1969) recognized five species of *Dianema* and one species of *Calomyxa*. Kowalski (1967) has described a further two species of *Dianema*. A second species of *Calomyxa* has been added by Farr & Kowalski (1974).

Ten genera were recognized in the Trichiaceae by Martin & Alexopoulos (1969). Although most of the genera are well-defined, many are closely related. In some genera, in which most of the species have many common characteristics and seem to comprise a natural group, one or several species may be divergent and have features in common with other genera. Several examples exist where, in important characters, one or two species narrow or even bridge the gap between established genera.

One of the most interesting genera in the Trichiaceae from a phylogenetic point of view is *Perichaena*. The genus has been monographed by Keller (1971), who recognized 13 species. The genus appears to have some clear affinities with some species of *Licea,* although the two genera are traditionally placed far apart in monographic treatments. As mentioned previously, there is evidence that the plasmodiocarpous species *Licea retiformis* and *L. variabilis* may lie closer to *Perichaena* than to the sporangiate species of *Licea*. It is interesting that *P. brevifila* Keller & Brooks (1971) may conceivably be interpreted as forming a link between the two genera. This species possesses (ex char.) an inconspicuous capillitium, consisting of short, simple to furcate, scattered threads attached to the inner sporangial wall. Keller & Brooks (1971) have suggested that this capillitium may be homologous with the finger-like processes of *L. kleistobolus* which enter the sporangial cavity.

Perichaena shares various morphological characters with several other genera and is important in any discussion of the phylogeny of the trichiaceous genera. While *Calonema* Morg. and *Oligonema* Rost. are so closely allied to *Perichaena* that they could probably be merged with it, other genera are more distinct, although

single species may narrow the gaps also to such genera. Keller (1971) suggested two possibilities concerning the evolutionary standing of *Perichaena*. Either it lies close to *Licea*, thereby forming the base of one or several lines leading to other trichiaceous genera, or it is itself derived from some other trichiaceous genera or genus.

Exemples of species within the Trichiaceae that have features which intergrade with those of other genera are *Arcyria stipata* (Schw.) A. Lister (similarities with *Hemitrichia*), *Calonema luteolum* Kowalski (1969) (affinities with *Oligonema* and *Perichaena*, ex char.), *Hemitrichia karstenii* (Rost.) A. Lister (probably more correctly regarded as a variety of *Trichia contorta* (Ditmar) Rost.) and *Perichaena minor* (G. Lister) Hagelst. (approaching *Hemitrichia* in possessing spiral structures on the capillitium). Although it is possible that some of the generic distinctions in the Trichiaceae are of an artificial nature, the family as a whole appears to form a natural group. The only affinity to another order seems to be the afore-mentioned, presumed, linkage of *Perichaena* with some species of *Licea*. The lime deposition sometimes seen in the peridium of some species of *Perichaena* has been suggested as a possible affinity with the normally lime-bearing species in the Physarales. However, Schoknecht & Keller (1975, 1977) have shown by chemical tests that the lime seen in the peridium of *Perichaena* is present in the form of calcium oxalate, often mixed with crystals containing silica, while in the Physarales the peridial lime consists of calcium carbonate and possibly calcium phosphate. Schoknecht & Keller also found that calcium oxalate crystals occur between two membranous peridial layers also in phases of *Perichaena* that appear limeless.

Stemonitales

Martin & Alexopoulos (1969) recognized fifteen genera in the order Stemonitales. They included here also *Clastoderma* and *Barbeyella*. As mentioned previously, these two genera have protoplasmodia and have since been transferred by Alexopoulos & Brooks (1971) to the Echinosteliales, an arrangement adopted by Alexopoulos (1973), Nannenga-Bremekamp (1974) and Farr (1976). If these genera are removed, the Stemonitales becomes a more natural taxon. It is characterized by an aphanoplasmodium and by a special type of sporophore development, generally called epihypothallic. Because of these important characteristics, Ross (1973) and Alexopoulos (1973) assigned this group the rank of a separate subclass, juxtaposed on the one hand to the other endosporous Myxomycetes and on the other to *Ceratiomyxa*. The epihypothallic mode of sporophore development means that the hypothallus, as the sporangial primordia begin to develop, is deposited directly onto the substratum on the underside of the plasmodium, and that the stalk is formed inside the sporangial protoplast. This type of sporophore development is only known in the Stemonitales and is regarded as an important character from a phylogenetic point of view. In the Echinosteliales, Trichiales and Physarales the sporophore development is subhypothallic, i.e. the hypothallus is formed on the upper side of the plasmodium. A continuous membrane encloses the sporangial initials. The sporangial protoplast passes through the interior of the stalk. The hypothallus is laid down on the substratum as the protoplasm moves upwards within the developing stalk (Alexopoulos 1966). The two types of sporophore development have been schematised by Ross (1973) and Alexopoulos (1973). The subhypothallic type is also considered to prevail in the Liceales, but this remains to be demonstrated.

Rammeloo (1976 a) has intimated that more than one plasmodium type probably occurs in the Stemonitales, so far as this order is circumscribed by e.g. Alexopoulos (1973), and it is possible that the group may be less uniform than is often supposed. One of the most divergent genera generally referred to this order is *Diachea* Fries. Developmental studies of this genus are still incomplete, but it differs morphologically in having both stalk and columella (when present) encrusted with lime, a character often interpreted as showing an affiliation with the Physarales. In most of the recent Myxomycete surveys (Martin & Alexopoulos 1969, Alexopoulos 1973, Nannenga-Bremekamp 1974), the genus has been included in the Stemonitales, but Farr (1974, 1976) preferred placing it in the Physarales.

Although, good agreement exists on the whole concerning the delimitation of the order Ste-

monitales, different opinions exist regarding the circumscription of several of the genera and the order is considered to be a difficult one taxonomically. Thirteen genera were accepted by Alexopoulos (1973); quite different systems, as regards generic delimitation, have been proposed by Nannenga-Bremekamp (1967, 1974). Developmental studies are regarded as important for the discovery of the natural relationships between several genera in this order. The importance of stalk structure and capillitium development in the creation of a natural system within the Stemonitales has been emphasized by Alexopoulos (1967) and Nannenga-Bremekamp (1967). Differences in these respects separate e.g. the genera *Comatricha* Preuss and *Stemonitis* Roth.

Physarales

The order Physarales is characterized by a dark spore mass and by the presence of lime deposits. A capillitium is present in all genera except *Squamuloderma* Kowalski (1972 c). The order is well-delimited, although different opinions exist as regards the genus *Diachea*. The stemonitaceous habit of this genus and similarities with *Lamproderma* in the structure of the capillitium and peridium have led most authors to include it in the Stemonitales. Farr (1974) attached great weight to the presence of lime in the stipe and columella and considered *Diachea* to lie closer to the Physarales than to the Stemonitales. The results of a microanalysis of the calcareous deposits in *D. leucopodia* (Bull.) Rost. (Schoknecht 1975) do not contradict a placement of the genus in the Physarales.

Physarales is generally divided into two families, the Physaraceae and the Didymiaceae. The former is characterized by a calcareous capillitium, the latter by a non-calcareous capillitium. In the former the peridial lime is present in the form of non-crystalline granules, in the latter the lime is either crystalline or granular.

Martin & Alexopoulos (1969) recognized eight genera in the family Physaraceae. Most of these are well-distinguished from one another, although in some other cases the delimitation of genera may be vague. For example, *Physarum* Pers., the largest genus among the Myxomycetes with about ninety species so far described and accepted, is only vaguely, and probably unnaturally, delimited from both *Badhamia* Berk. and *Craterium* Trent. The physaroid type of capillitium (calcareous nodes connected by threads of various structure) is found in *Physarum, Craterium* and *Fuligo* Hall. The last-named genus is generally separated from the other two by normally having aethalioid fructifications; the fructifications in *Physarum* and *Craterium* are sporangiate or plasmodiocarpous. *Craterium* is separated from *Physarum* by its more or less cyathiform sporangia, often with circumscissile dehiscence. However, both these characters may be variable and it is questionable whether they warrant its retention as a separate genus. *Badhamia* is characterized by a capillitium consisting of a network of calcareous tubes. This type of capillitium is often very characteristic, but capillitia intermediate in appearance between the physaroid and the badhamioid types do occur. In a few species a continuous variation may exist, from typically badhamioid to physaroid capillitia. The border-line between these two genera has been discussed by many authors. Among recent papers in which this matter is at least partially dealt with, those by Gottsberger (1971), Carter & Nannenga-Bremekamp (1972) and Mitchell & Nannenga-Bremekamp (1976) deserve mention. One species of *Badhamia, B. ainoae* Yamashiro, has a deviant type of capillitium, consisting of calcareous columns which extend from the base of the fructification up to the peridium. This divergent species has recently been transferred to a separate genus, *Badhamiopsis* Keller & Brooks (1976 a).

In the family Didymiaceae six genera were recognized by Martin & Alexopoulos (1969), in three of which, *Wilczekia* Meylan, *Physarina* Höhn and *Diderma* Pers., the peridial lime is amorphous and granular, whereas in *Mucilago* Micheli ex Batt., *Didymium* Schrad. and *Lepidoderma* de Bary it is crystalline. The monotypic genus *Wilczekia* lies very close to *Diderma* and the single species, *W. evelinae* Meylan, has been formally transferred to *Diderma* by Kowalski (1975 a). According to Kowalski (1972 c) the genus *Squamuloderma* should also be included in the Didymiaceae. The latter genus is unique in the Physarales by its lack of a capillitium. The genus was based on material obtained from moist chamber cultivation. Before the taxon was described its life cycle was studied and completed several times in the laboratory, but the lack of a capillitium

was a constant feature in all the fructifications obtained. For this reason the lack of a capillitium is believed to be a characteristic of the organism, rather than due to the environmental conditions. Kowalski (1972 c) recommended placing *Squamuloderma* in the Didymiaceae, because of the presence of crystalline lime in the peridium.

In an interesting and important paper, Schoknecht (1975) suggests that the taxonomic importance of the type of lime deposit is questionable in some cases. From laboratory cultivations it is now well-known that the environmental conditions can influence the amount of calcium secreted, and that lime may even be absent from the fructifications of normally lime-bearing species when these are grown under certain conditions. Further investigations are also needed to reveal whether species which normally produce amorphous lime could, under different environmental conditions, produce crystalline lime, or vice-versa. Farr (1974, 1976) has drawn attention to the fact that fructifications of *Diachea bulbillosa* (Berk. & Br.) A. Lister from tropical and subtropical collections contain crystalline lime, whereas in specimens from temperate zones the lime is granular. Whether this is due to climatic conditions or whether it is genetically controlled is still unknown. If it is genetically controlled, the interesting question arises as to whether or not this character alone may warrant splitting what is nowadays called *D. bulbillosa* into two species. As Farr (1974) has pointed out, this is largely a question of being consist, since in other cases great taxonomic importance has been attached to the structure of the lime deposits, e.g. it is the only character which separates the genera *Diderma* and *Didymium*.

The recently established genus *Protophysarum* Blackwell & Alexopoulos (1975) is very interesting phylogenetically. The single species so far known, *P. phloiogenum* Blackwell & Alexopoulos (1975), appeared on pieces of *Ulmus* bark placed in a moist chamber. The species was maintained in culture for many years and its life cycle and development investigated, before the genus and species were described taxonomically. Although reminiscent of a small *Lamproderma, Protophysarum* differs (ex char.) from species of the Stemonitales in certain important respects, e.g. its plasmodium, despite its small size, is a true phaneroplasmodium, and its sporangial development is subhypothallic. Blackwell & Alexopoulos (1975) accomodated *Squamuloderma* in the Physarales, family Physaraceae. It differs from the other genera of the Physarales by its apparent absence of lime deposits. However, ultrastructural studies have shown that lime is found in association with both the peridium and capillitium (ex char.). *Protophysarum* seems to be intermediate between the Echinosteliales and the Physarales and may be regarded as forming an evolutionary link between these two orders (Blackwell & Alexopoulos 1975).

Concluding remarks

Since the publication of the paper by Schoknecht & Small (1972) on scanning electron microscopy of Myxomycetes, scanning pictures have become frequent in taxonomic papers dealing with this group. These organisms are very suitable for this kind of structural investigation. Since certain structural differences may sometimes be difficult to validate taxonomically, laboratory cultivation appears necessary for a true understanding of the relationships and intraspecific variability of some species. Alexopoulos (1969) recommended that recourse to the results of experimental work should always be made in proposals for Myxomycete classification and that any revisions of genera and higher taxa, as well as descriptions of new taxa, should be preceded by experimental culture whenever possible so as to test, under differing environmental conditions, the validity of the taxonomic characters used. This recommendation is of course very sound, although at present unrealistic for genera which so far have resisted all attempts to grow them under laboratory conditions. Hitherto, c. 70 species have been cultured from spore to spore-bearing stage on agar in the laboratory. A list of these species has been compiled by Clark & Collins (1976), to which *Trichia persimilis* Karst. may now be added (Rammeloo 1976 b).

The relatively large number of Myxomycete species described during the past decade shows that much floristic work remains to be done. The Myxomycete flora on decaying wood is probably relatively well-known, but investigations of other ecological niches will, in many cases, probably yield interesting results. Good exam-

ples are provided by the newly-discovered species of snow-line Myxomycetes, i.e. species growing in the vicinity of melting snow, described by Kowalski (e.g. 1967, 1968 a, b, 1970 a, 1975 b). The bark of living trees has also been found to harbour a special Myxomycete flora (Keller & Brooks 1973, 1975, 1976 a, b, Keller et al. 1973, Brooks et al. 1977). No doubt many further species remain to be discovered. It is likely that many species now regarded as rare will subsequently prove to be much less so when their ecological demands have become better known. An example of this situation is *Barbeyella minutissima,* which, when first reported from the United States (Curtis 1968), was regarded as "exceedingly rare", but only a few years later it was designated "a common alpine Myxomycete" (Kowalski & Hinchee 1972), growing on leafy liverworts.

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The genus Peyrousea (Compositae)

Kåre Bremer

Bremer, K. 1977 12 30: The genus Peyrousea (Compositae). *Bot. Notiser 130:* 493–497. Stockholm. ISSN 0006-8195.

Peyrousea is a monotypic genus of the Compositae-Anthemideae from South Africa. The confused nomenclature is elucidated and the systematic position, morphology, variation and distribution of the genus are discussed.

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Peyrousea is a monotypic genus of the Compositae-Anthemideae from South Africa. The present investigation has been made in order to elucidate the nomenclature and taxonomy of the genus, especially its systematic position, morphology, variation and distribution.

Material. I have examined 82 collections from the following herbaria: BM, BOL, G, G-DC (only microfiche), K, M, NBG, P, PRE, S, SAM, UPS, UPS-THUNB (Herbarium Thunberg at UPS), W and Z (abbreviations according to Holmgren & Keuken 1974). A list of examined specimens is kept at the Museum of Natural History, Section for Botany, Stockholm.

History and nomenclature

This genus was established by Thunberg (1800 p. 163 without description, 1823 p. 700), who named it *Lapeirousia* after the French circumnavigator J. F. Galaup de La Pérouse. Thunberg had himself collected material of the plant and identified it as *Osmites calycina* Linné fil. (1781 p. 380). The new genus thus comprised the single species *Lapeirousia calycina*. However, the type specimen of *O. calycina* L. f. and, in consequence, also of *L. calycina* (L. f.) Thunb. is in the Linnaean herbarium in London, and it belongs to a species of *Relhania,* a genus entirely different from that of the plant in Thunberg's collection. This was clarified by Compton (1935 p. 71). Thunberg's unfortunate misidentification has been copied in the works of his successors. The names are typified by the *Relhania* specimen, but the descriptions cover the species of the genus treated here. Cassini (1822 p. 251), who found the epithet *calycina* inappropriate, thus changed the name to *Lapeirousia Thunbergii,* a superfluous name typified by the *Relhania* specimen. De Candolle (1838 p. 76) changed the generic name to *Peyrousea,* since Thunberg's name is a later homonym of *Lapeirousia* Pourr. (Iridaceae). He did not intend to describe a new genus, and the type species is *Peyrousea calycina* (L. f.) DC., again typified by the *Relhania* specimen. *Osmitiphyllum Kraussii* Sch. Bip. is yet another name, which belongs here although never validly published, since it was merely mentioned as a synonym for *P. calycina* (L. f.) DC. (Schultz Bipontinus 1844 p. 675).

De Candolle recognized two species within this genus. They were described from collections made by Burchell and differed in minor characters of the involucre. Later authors, including myself, have not accepted these collections as belonging to more than one species. These species were named *Peyrousea calycina,* discussed above, and *Peyrousea oxylepis* DC. The name of the latter species is a superfluous name, since in his synonymy De Candolle included *Cotula umbellata* Linné fil. (1781 p. 378), the epithet of which should have been adopted. This was realized by Fourcade (1932 p. 87), who made the combination *Peyrousea umbellata* (L. f.) Fourc.

Cotula umbellata was described by Linné fil.

from a specimen in the herbarium of Abraham Bäck, physician to the Swedish king and a friend of the elder Linnaeus. An account of this herbarium, as well as of those specimens used by Linné fil., has been given by Juel (1924) and Exell (1931), respectively. These specimens should now be in J. E. Smith's herbarium at the Linnean Society in London, but for some unknown reason the type of *Cotula umbellata* L. f. is missing. However, from the description it is obvious that it must have been based on a specimen belonging to the genus treated here. The South African plants in Bäck's herbarium were given to him by Thunberg, who certainly kept duplicates of all the species sent. *Cotula umbellata* L. f. was therefore most probably based on the same collection as that which Thunberg erroneously identified as *Osmites calycina* L. f. Specimens of this collection exist at Uppsala (UPS-THUNB) and Stockholm (S), and I have chosen one of these from the former herbarium as the lectotype.

Let us now return to the problem of the generic name. With *P. calycina* (L. f.) DC. as type species, *Peyrousea* becomes a synonym of *Relhania,* and there is no name for the genus in this treatise. This was indicated in my revision of *Relhania* (Bremer 1976 pp. 8, 27, 71). A new name could be constructed, but in my opinion the only acceptable solution is to retain the generic name *Peyrousea* by simply changing the type species to *P. umbellata* (L. f.) Fourc. Such a proposal will be put forward at the next International Botanical Congress and, consequently, I have continued to use the name *Peyrousea.*

The name of the genus has already been in danger once before. The International Botanical Congress in Cambridge in 1930 had decided that a name is illegitimate and must be rejected if it is a later homonym, even if the earlier homonym is itself illegitimate or treated as a synonym. This is precisely the case in this genus, since *Peyrousea* DC. is a later homonym for *Peyrousia* Poir., in turn a synonym of *Lapeirousia* Pourr. (Iridaceae). However, the so-called absolute homonym rule was accepted on the understanding that all well-known generic homonyms should be conserved, and *Peyrousea* DC. was one in a long list of names proposed for conservation by Rehder *et al.* (1935 p. 447). Accordingly, *Peyrousea* DC. was conserved by the Special Committee for Phanerogamae and Pteridophyta appointed by the International Botanical Congress in Amsterdam in 1935 (Green & Sprague 1940 p. 129). At that time the original collection of the type species was not examined. With *Peyrousea calycina* (L. f.) DC. as type species, the genus inevitably goes into synonymy under *Relhania,* although it is a conserved name. However, the name can still be saved by changing the type species, as explained above.

Peyrousea DC., nom. cons.

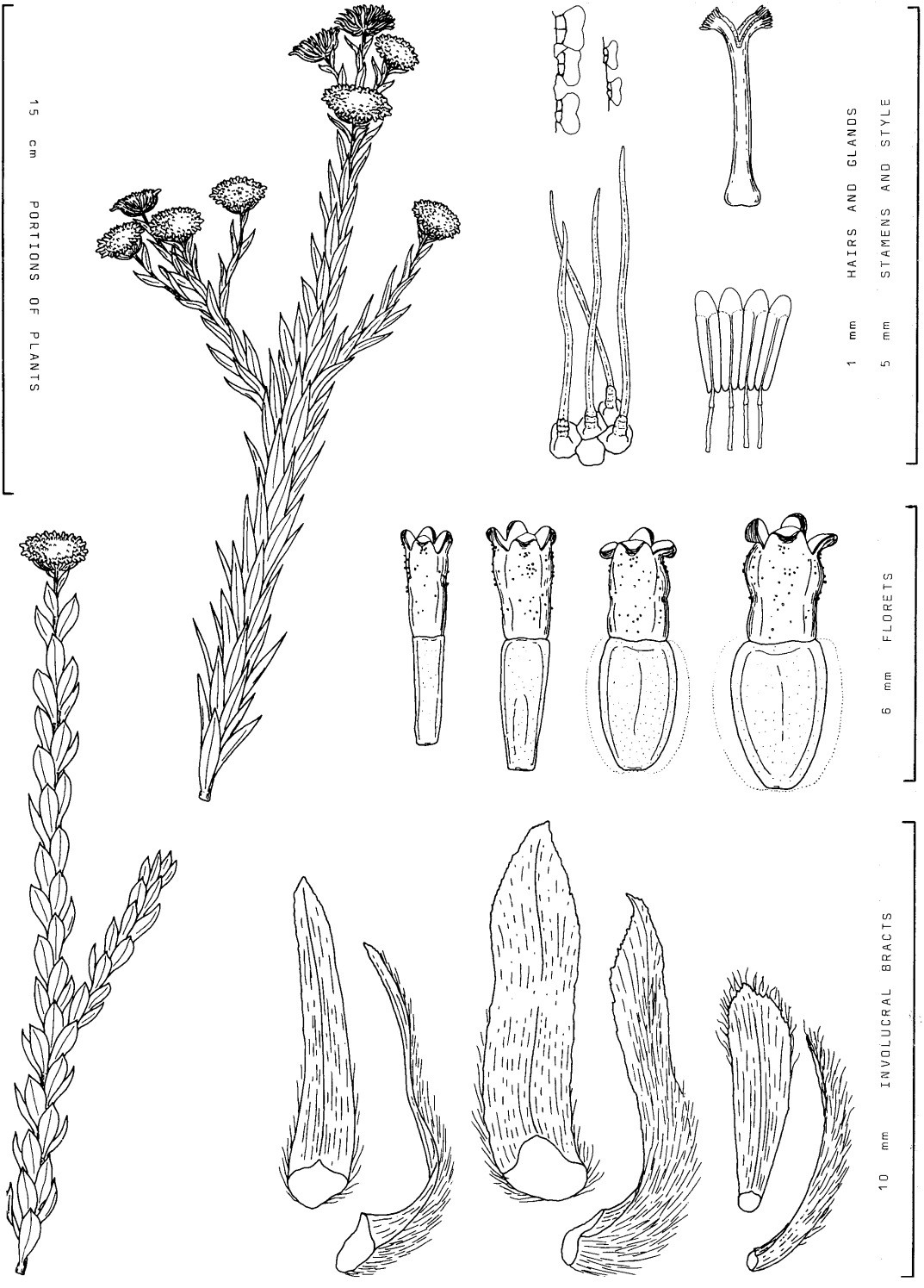
De Candolle 1838 p. 76 (non *Peyrousia* Poiret 1826 p. 363); Steudel 1841 p. 312 (*"Peurousea"*, sphalm.); Harvey 1865 p. 176; Bentham & Hooker 1873 p. 432; Hoffmann 1890 p. 283; Compton 1935 p. 71; Dyer 1975 p. 709. – Typus cons. prop.: *P. umbellata* (L. f.) Fourc. – Typus rej. prop.: *P. calycina* (L. f.) DC.

Lapeirousia auct. (non Thunberg 1800 p. 163; nec non Pourret 1788 p. 79); Cassini 1822 p. 251; Thunberg 1823 p. 700 (*"Lapeyrousia"*); Lessing 1832 p. 260 (*"Lapeyrousia"*).

The description given under the species applies to the genus, too, since only one species is accepted here.

Systematic position. There is still much work to be done on the South African genera of the Compositae-Anthemideae before we shall know anything definite about their interrelationships. With its entire leaves, *Peyrousea* looks rather anomalous in the Anthemideae, but it is generally placed in the "*Cotula*-group" of genera, characterized by compressed achenes. *Schistostephium* Less. is the most closely-related genus and it is even possible that *Peyrousea* and *Schistostephium* are sister groups, together forming a monophyletic unit. *Schistostephium* has a very similar floral morphology, especially

Fig. 1. *Peyrousea umbellata.* Features of plant parts, showing a common growth form, upper specimen (drawn from Compton 15801 in NBG), and a mountain form, lower specimen (Compton 5189 in NBG). From left to right the outer, middle and inner involucral bracts are shown in ventral and lateral views. The two left-hand florets have unripe achenes, while the two right ones have ripe, mucilaginous achenes. The hairs are drawn from a leaf; the involucral bracts have similar hairs. The smaller glands are from the achenes, while the larger ones are from the corolla. Similar glands, roughly intermediate in size, occur on the leaves and involucral bracts. (All details drawn from Compton 15801 in NBG.)


15 cm PORTIONS OF PLANTS
1 mm HAIRS AND GLANDS
5 mm STAMENS AND STYLE
6 mm FLORETS
10 mm INVOLUCRAL BRACTS

those species with homogamous capitula. Species with few, large capitula and few-lobed, almost entire leaves approach *Peyrousea* in habit. Another related genus is *Hippia* L. Thus we have here a group of three allied genera, but their mutual relationships deserve further study.

Peyrousea umbellata (L. f.) Fourc.

Fourcade 1932 p. 87; Compton 1935 p. 72. – *Cotula umbellata* Linné fil. 1781 p. 378. – *Peyrousea oxylepis* De Candolle 1838 p. 77, nom. superfl.; Harvey 1865 p. 176. – Holotypus: Thunberg, herb. Bäck, amissus? – Lectotypus: Thunberg, herb. no. 20508 (UPS-THUNB, isotypi in S).

Lapeirousia Thunbergii auct. (quoad descr., excl. syn.); Cassini 1822 p. 251. – *Lapeyrousia calycina* auct. (quoad descr., excl. syn.); Thunberg 1823 p. 700; Lessing 1832 p. 260. – *Peyrousea calycina* auct. (quoad descr., excl. syn.); De Candolle 1838 p. 77; Harvey 1865 p. 176.

Peyrousea argentea Compton 1935 p. 73. – Holotypus: Compton 4202 (BOL).

Nom. vern.: "Bels(kruie)" (Smith 1966 p. 616).

A little-branched shrub, up to 2 m high (fide coll.). *Stems* pubescent, densely leafy, gradually more sparsely upwards and thus often pedunculoid. *Leaves* alternate, erect–spreading, sessile, entire, elliptic, 8–40 mm long, 3–12 mm wide, acute and mucronate, mid-ribbed and sometimes with inconspicuous lateral veins, densely pilose with straight, appressed hairs. *Capitula* solitary or aggregated in a lax cyme at the end of the branches, homogamous. *Involucre* campanulate, 8–22 mm wide. Involucral bracts 25–70, 3–5-seriate, imbricated, firm, yellowish brown and the longest with a whitish or occasionally purplish tip, entire or serrulate apically, acute, mid-ribbed, dorsally densely pilose with straight hairs; outer bracts lanceolate, up to 8 mm long, middle bracts oblong, curved, 4.5–10 mm long, up to 2.5 mm wide, inner bracts narrowly obovate, up to 7 mm long. *Receptacle* flat–conical, nude. *Florets* 75–500, tubular, perfect. Corolla indistinctly divided into a cylindrical or somewhat compressed tube and a cyathiform–urceolate limb, 2.1–3 mm long, 0.8–1.7 mm wide, yellow, glandular, 4-lobed; lobes ovate-triangular, subcucullate. *Stamens* 4; apical anther appendage ovate; filament collar oblong, of subcubical cells. *Style* swollen at base, bifid; style-branches apically penicillate and truncate. *Achenes* obovate, strongly compressed dórsiventrally, with one distinct, somewhat winged, lateral rib on each side, 2.7–4.4 mm long, 1.7–3 mm wide, brown, minutely glandular, completely covered with myxogenic cells. *Pappus* O.

Flowering period mainly August–November, but flowering specimens have been collected from throughout the year.

Discussion. The morphology of this plant (Fig. 1) is characterized by many reductions. The capitula are homogamous with no rays, the receptacle is epaleate, the florets are tetramerous and the achenes have no pappus. Other characteristics are the thickened, subcucullate corolla lobes and the compressed, 2-ribbed achenes, mucilaginous when soaked in water. Furthermore, *P. umbellata* should not be difficult to recognize, with its entire, pubescent leaves and rather large, discoid capitula.

The leaves and involucral bracts are covered with a rather dense pubescence of more or less straight and appressed hairs. These hairs consist of a few, small, basal cells and a long, thick-walled, terminal cell. Few-celled glands are scattered over the corolla, achenes, involucral bracts and leaves. Those on the corolla are rather conspicuous, whereas those on the achenes are much smaller and are difficult to see. The glands on leaves and involucral bracts are roughly intermediate in size, rather sparsely scattered and hidden under the indumentum.

Whereas the floral morphology of this species is constant, both habit and foliage vary. The leaves are generally 15–30 mm long and rather densely set. A few collections have smaller leaves more scattered on the stems. Some of these collections are from outlying localities W of the main distribution area, e.g. Esterhuysen 23811 from Langeberg near Montagu, Esterhuysen 24755 from Swartberg N of Ladismith and Wurts 1359 from Sandberg W of Calitzdorp. However, I cannot grant these taxonomic recognition, since there are similar small-leaved plants present within the variation range shown by the main bulk of collections from the George, Knysna and Humansdorp area.

Plants from higher altitudes have a more condensed growth habit, with fewer capitula and smaller, densely pubescent leaves, which give the foliage a silvery appearance. These plants were described by Compton (1935 p. 73) as a new species, *Peyrousea argentea* Compt., but there is a continuous variation to the habit of

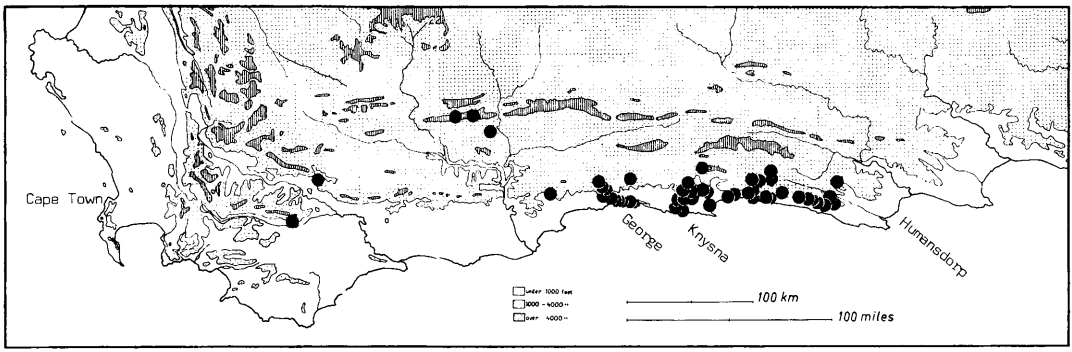


Fig. 2. Known distribution of *Peyrousea umbellata*.

lowland plants and the distinguishing characters, as described above, are quantitative and refer to the vegetative parts only. There are no differences within the capitula. Apparently the mountain plants constitute a high altitude ecotype. Since the variation is continuous, I cannot grant it any formal taxonomic rank.

Distribution (Fig. 2). *P. umbellata* mainly occurs along the Outeniqua and Tsitsikamma mountain ranges, in the southern Cape Province between George and Humansdorp. Most of the collections are from George and Knysna divisions, where it grows all the way from the coast up into the mountains. There is also one collection from Mossel Bay and a number of collections from further east, in Uniondale, Joubertima and Humansdorp divisions. It has been collected a few times in more western localities, viz. Sandberg W of Calitzdorp (Wurts 1359), Langeberg near Montagu (Esterhuysen 23811), Swartberg N of Ladismith (Esterhuysen 13948 and 24755), and Riviersonderend (Bayliss 57793). It grows on forest margins, on cliffs and in fynbos on hillsides and on the higher mountain slopes, from sea level to above 1500 m (fide coll..).

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Botanical literature

Dixon, P. S. & Irvine, L. M. 1977: *Seaweeds of the British Isles. Volume 1, Rhodophyta. Part 1, Introduction, Nemaliales, Gigartinales.* XI + 252 pp., 90 figs. British Museum (Natural History), London. ISBN 0-565-00781-5. Price £ 10.–.

This is the first part of a marine algal flora for which it has been set as an important goal to dig to the bottom in defining the species. For the first time in a Northwest-European marine flora the type is carefully indicated for each taxon, and when the type is a specimen, this specimen has been studied. Equally great efforts have been made to provide adequate illustrative material. All species are figured, and the present first part of the flora has original drawings in all cases except for one where no type material and no later finds are known. The search behind this achievement has been very considerable and provides a firm foundation for the taxonomic treatment.

In the standing conflict between 'lumpers' and 'splitters' the authors follow the principle of not combining species where this may make future critical work more difficult. They are at variance with Söderström as regards the distinctness of *Nemalion multifidum* from *N. helminthoides*, and with Feldmann & Hamel regarding the justification of several species of *Gelidium*, and in these cases follow their personal opinion as they do not expect this to block later weighing of specific characters. In the Acrochaetiaceae, on the other hand, they undertake no combination at all, though stating about various species that "their continued independence is highly unlikely". In these cases more knowledge of the variation and ecology of the doubtful species is needed for a final settlement, and it is found that such knowledge might perhaps never be provided if the species were precociously dropped in this flora. Similarly, the authors refrain from discussing the natural grouping of all these species, they arrange them alphabetically and refer to them all by the oldest generic name, *Audouinella*. In treating the complex in this way they offer the reader all available taxonomic information but at the same time do not force any personal opinion upon him. This is scientifically ideal, but some users may find themselves rather lost when left to a personal choice in these matters.

The work on typification has entailed a few name changes. Only one affects the general botanical public, namely that *Furcellaria fastigiata* must from now on be called *F. lumbricalis* (cf. this journal Vol. 130 p. 137). Nomenclatural problems are usually summarized so that the background for debatable choices is apparent.

Users of the book will find it easy to look up the information they want. A non-taxonomic key for the genera must necessarily await publication of the remaining two parts on red algae, but those who start with an uncertain identification, from memory or obtained with the help of a smaller flora, will find in each case a comparison of the genus in question with those it is likely to be confounded with. These very consistent comparative sections will be of particular use to many botanists. The information on occurrence, biology and variation is very complete, and also characteristic parasites and some epiphytes are mentioned.

The general appearance of the new flora is pleasing. The pages are small, relatively low and broad, making it easy to keep the book open alongside one's microscope without taking up too much table space. The illustrations are all line drawings; a few might have been made with greater care, such as those of *Gelidium* sections, and several are rather coarse, as if being made

for a somewhat smaller magnification, but all of them serve their purpose well.

Phycologists everywhere will look forward to the continuation of this work.

Tyge Christensen

Heywood, V. H. 1976: *Plant taxonomy*. Second edition. Studies in Biology 5. 63 pp. Edward Arnold, London. ISBN 0-7131-2609-4. Price £ 1.30.

To present plant taxonomy in a concise fashion and yet avoid a boring catalogue style is a difficult task in which Professor V. H. Heywood has succeeded admirably. The second edition of his little book, Plant Taxonomy, which has been brought entirely up to date, is an easily accessible introduction for students beginning their studies. It will certainly be a stimulus to the study of the subject in greater detail with the aid of more comprehensive textbooks. Some basic principles and a number of essential terms are explained. However, I greatly appreciate the fact that the emphasis has been placed on problems and methods rather than on descriptive text. It is a pleasure to recommend this little book to students of plant taxonomy.

Gunnar Weimarck

John, B. 1976: *Population cytogenetics*. Studies in Biology 70. 76 pp. Edward Arnold, London. ISBN 0-7131-2597-7. Price £ 1.50.

It is essential for a taxonomist to be familiar with variation and its causes at a level below that at which he is working. There is now a growing interest in population genetics among those who study taxonomy at the specific or subspecific level.

Chromosomes are doubly interesting in this context. Not only do they function as markers morphologically when they vary in number and structure, but as they contain genetic information they also play a functional part in the interplay between breeding individuals. Variation in the chromosome system may therefore affect variation in many respects at the populational level and may decisively effect the course of evolution.

Professor Bernard John is an expert on population cytogenetics and has produced a most interesting introduction to this topic. It is also of interest to the researcher. Variation in the organization, structure and number of chromosomes is intelligibly described and its effects on population structure accounted for by means of selected illustrative examples. A short section is devoted to the cytogenetics of speciation.

The number of typographic errors is, regrettably, far too high to be ignored. Some of them are disturbing, a few even ridiculous. The figure on p. 41 must surely have met with an accident. I do hope that in forthcoming editions these errors will be eliminated so that the positive impression the book makes will not be spoilt.

Gunnar Weimarck

Hilliard, O. M. 1977: *Compositae in Natal*. 659 pp., 25 figs. University of Natal Press, P O Box 375, 3201 Pietermaritzburg, South Africa. ISBN 0 86980 088 4. Price (cloth) R 24:–.

The floral richness of the Cape has led many a botanist to forget Natal, the easternmost province of South Africa. Nevertheless, with the high Drakensberg mountains on the Lesotho border and the grasslands which slope down to the coast of the Indian Ocean, Natal houses about 5000 species of flowering plants. Approximately 12 per cent of these belong to the Compositae, which is thus the largest family present. This book contains keys and descriptions for all the 640 species, distributed among 113 genera. This work represents a great step towards the completion of the Compositae volume of the 'Flora of Southern Africa', which is otherwise progressing deplorably slowly. The uninformed reader might suspect that this book is a mere compilation of results from earlier floras and revisions. On the contrary, it is the outcome of Dr Hilliard's own extensive research on this family over many years. It is obvious that the author herself is very familiar with both the living and herbarium material of the Natal Compositae.

There is a single key to all the genera as well

as a key to the separate tribes, followed by keys to the genera within each tribe. Those who already have some experience of the family will generally recognize the tribes and may thus be able to go straight-away to the tribal keys. Otherwise there is the key to all the genera. However, this runs to over 13 pages in length and will inevitably be time-consuming. There are also two long generic keys to the species of *Helichrysum* and *Senecio,* with nearly 125 species each. I have tested these keys on my own collections of Natal Compositae, especially *Helichrysum*. The keys work very well and generally there is no uncertainty when deciding between the alternatives. Related species have been brought together in the key and references are given to the notes and descriptions of those species that are difficult to key out.

The descriptions are concise, yet sufficiently informative. The author's extensive field experience vouches for distinct habit descriptions. This compensates to some extent for the scarcity of illustrations. The habit of about 20 species only are illustrated. Unjustly, this lack makes the book seem dull and stodgy.

The text is offset-printed from the original typescript, with its rather uneven right-hand margin. Names and synonyms are printed in boldface and italics. With the exception of the uneven margin, I have no objections to this printing method, which I suppose will be used more and more frequently for books in the future.

Kåre Bremer

Thomas, E. & Davey, M. R. 1975: *From single cells to plants*. 171 pp. Wykeham Publications (London) Ltd, London and Winchester. ISBN 0-85109-041-9 (paper), ISBN 0-85109-520-8 (cloth). Price £ 3.25 (cloth), £ 2.50 (paper).

The Wykeham Science Series consists of textbooks at a not-too-advanced university level. A novel feature is the intentionally pedagogic approach to the subject, and for this purpose the scientific author has been assisted by an experienced schoolmaster. The present book on plant tissue culture is a good example of the fruitfulness of this approach.

The totipotency of differentiated plant cells was postulated almost one and a half century ago but experiments were not successful until the 20s, and only during the last few decades has technique developed rapidly. The historical background of problems and methods is outlined in the first chapter. The second chapter is devoted to a rather comprehensive presentation of basic materials and methods. Culture mediums and schedules are given in an appendix. The rest of the book describes the culture of plant organs, vegetative and reproductive cells and protoplasts, and morphogenesis in cell cultures. The prospects for tissue culture research are also dealt with. The system of headings and subheadings makes the book very easy to read, and the main points are clearly summarized at the end of each chapter. The illustrations are abundant and informative.

Admittedly the main applications of plant tissue culture are at present in the fields of physiology and biochemistry. However, great achievements have also been made in plant breeding, and cytogenetics, morphology and systematics certainly gain, too, from adopting suitable tissue culture techniques. Embryo culture has long been employed to facilitate the production of certain hybrids, and promising results have recently been obtained from raising plants from protoplasts hybridized in vitro. The genetic analysis of plants has in many cases been made possible through raising haploids from pollen grains. Tissue culture will probably yield much information that is otherwise difficult or impossible to obtain.

It is to be hoped that the book by Thomas and Davey will also stimulate the employment of tissue culture techniques for taxonomic purposes.

Anna Weimarck