Drawings of Scandinavian Plants 97–99

Chenopodium L.

By Lennart Engstrand and Mats Gustafsson[1]

Department of Plant Taxonomy,
University of Lund,
Ö. Vallgatan 18—20,
S-223 61 Lund, Sweden

97. **Chenopodium opulifolium** SCHRAD. in KOCH et ZIZ. 1814

Annual, up to 1 m high, ascending to erect, usually divaricately branched. Stem angular, striated. Leaves alternate, pale green to greyish-green and glabrous to sparsely farinose above, greyish-green and conspicuously farinose beneath. Lower leaves petiolate, petiole about equal to or longer than lamina, cuneate at base, 1—5 cm long, about as long as broad, three-lobed to broadly rhombic and then with two prominent lateral teeth, lateral lobes with 2—3 broad, outward- to forward-pointing obtuse to acute teeth, middle lobe rather short and broad with 2—6 rather insignificant, obtuse to acute and forward-pointing teeth, apex obtuse, acute or apiculate. Upper leaves more or less petiolate, three-lobed to lanceolate, cuneate at base, entire to dentate, acute. Flowers situated in greyish, round, at least in the lower parts of inflorescences distinct glomerules, forming a loosely to rather compact, paniculate inflorescence. Flowers perfect, conspicuously farinose, 5-merous. Perianth lobes united at the most up to one half, ovate, greenish to brown in the centre, pale and membraneous in the most marginal parts, keeled on the back. The perianth entirely covers the seed. Pistil with a short style, and two slender, rather short stigmas papillate to the base. Stamens 5. Seeds horizontal, black, orbicular, 1.0—1.4 mm in diameter, with round margins. Testa lustrous, with radial furrows. Radicula short and broad, closely attached to the seed. Embryo annular.

Flowering time: July to August.

Chromosome number: 2n=18, 36, 54.

Variation: *C. opulifolium* varies, as do most *Chenopodium* species, in habit, height, size and shape of leaves and dentation on the margins. Two subspecies have been distinguished (cf. AELLEN 1960), but most of the Scandinavian material belongs to ssp. *opulifolium*.

Habit and distribution: *C. opulifolium* is a more or less occasional weed growing on most waste ground often in the vicinity of harbours, mills and factories. It has a wide area of distribution, but is probably only native to the Mediterranean parts of Europe, to the central parts of Asia and to Africa. In Scandinavia scattered localities throughout Denmark, in Sweden distributed northwards to the province of Medelpad, in Norway northwards to the province of Sör-Tröndelag and in Finland in the southernmost parts.

Comments: *C. opulifolium* is closely related to *C. album* and morphological transitions occur. However, according to AELLEN (1960), hybrid derivatives are rare. Typical specimens of *C. opulifolium* are distinguished from *C. album* by their long-petiolate, three-lobed leaves, which are about as long as broad and farinose beneath, and by their conspicuously farinose flowers.

[1] ENGSTRAND is responsible for the drawings and GUSTAFSSON for the text.

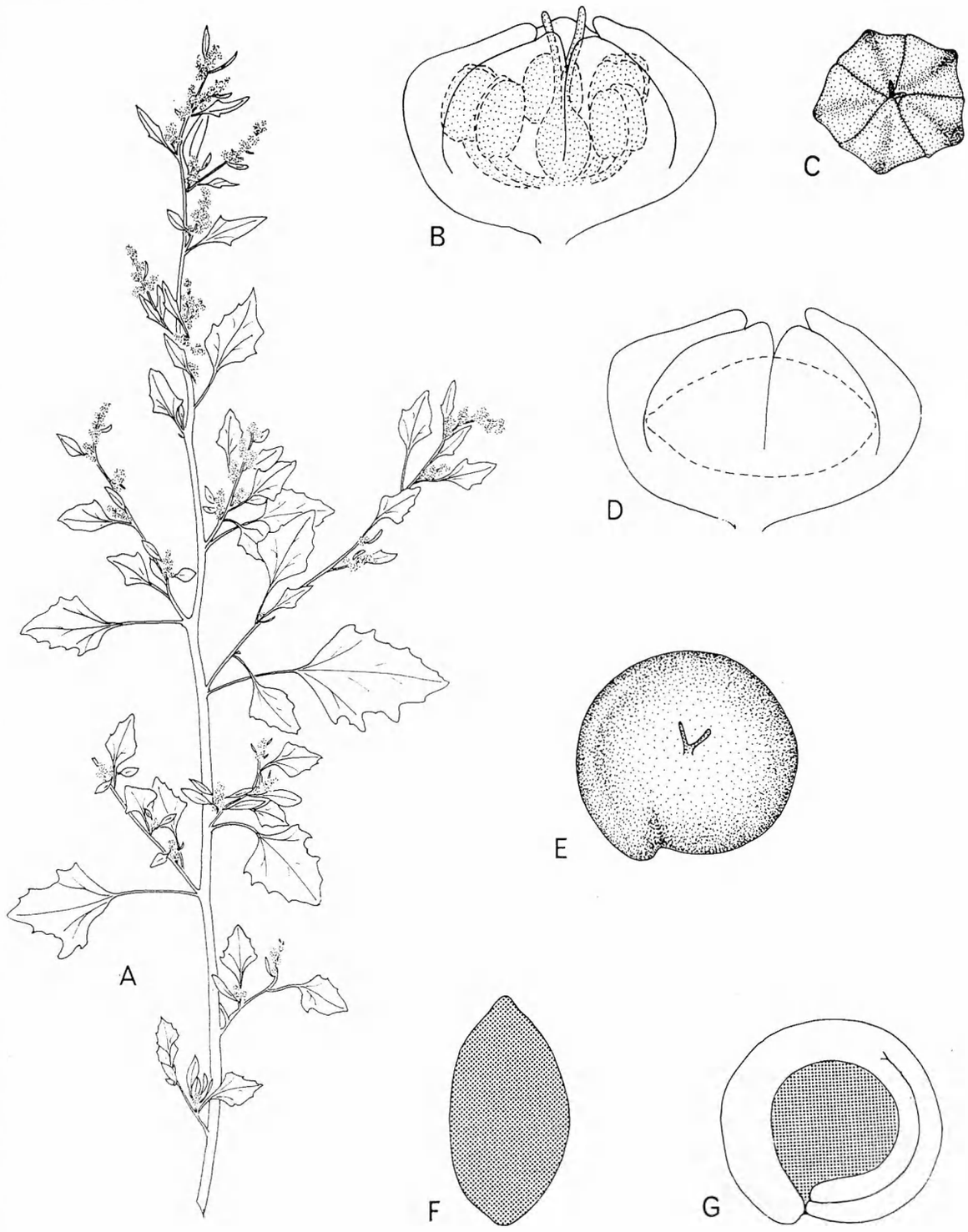


Fig. 97. *Chenopodium opulifolium* SCHRAD. — A: Habit (branch). — B: Hermaphrodite flower. — C: Perianth seen from above. — D: Fruit enclosed in the perianth. — E: Fruit with pericarp. — F: Seed in transection. — G: Section through a seed, showing the embryo. — A: ×0.5. — B, D—G: ×20. — C: ×8.

98. **Chenopodium suecicum** J. MURR. 1902

(Syn. *C. viride* sensu AELLEN 1960. For nomenclatural comments see HYLANDER 1945 and JÖRGENSEN 1973).

Annual, up to 1 m high, ascending to erect, usually branched. Stem angular, striated. Stem and shoots in young stages of development farinose, later becoming

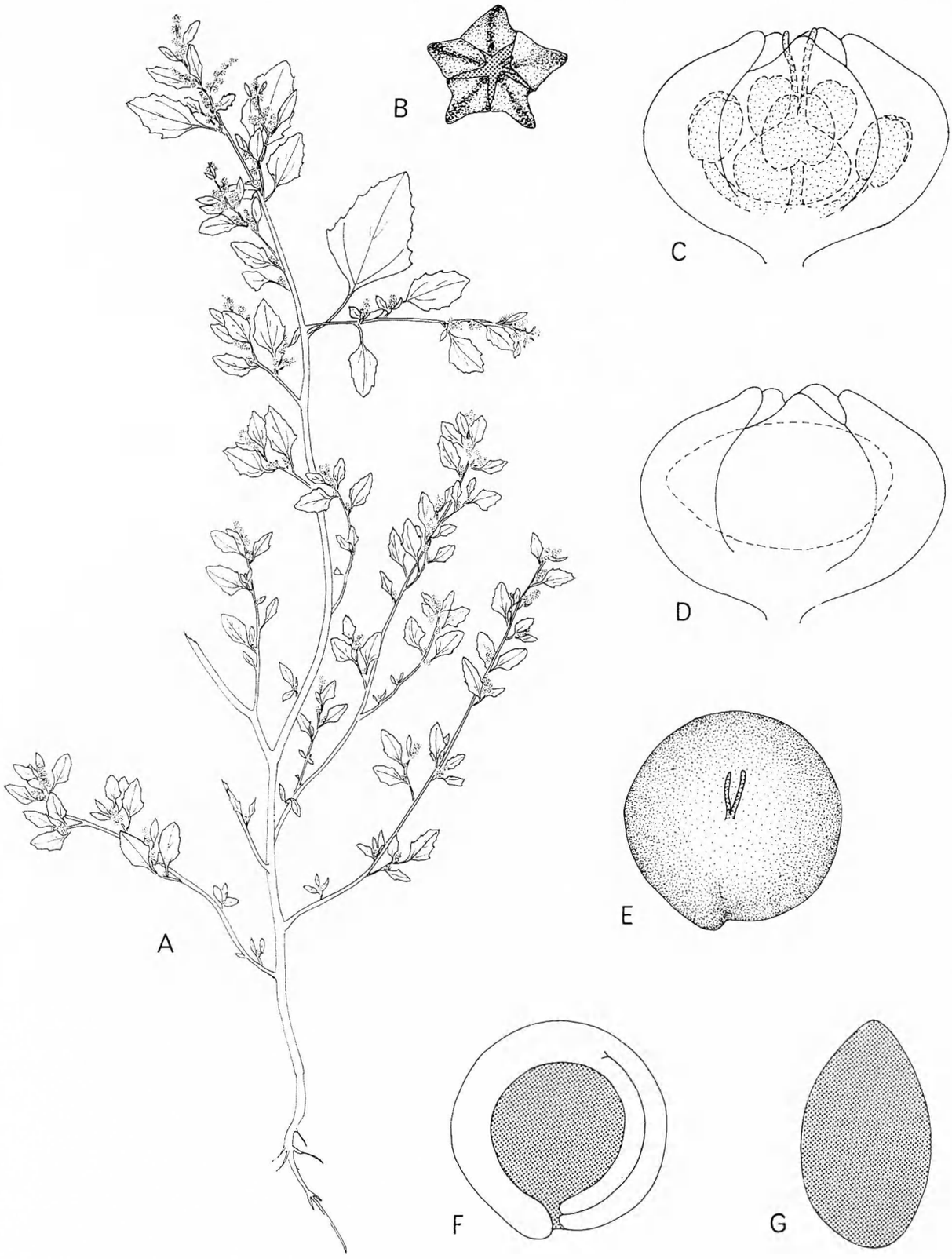


Fig. 98. *Chenopodium suecicum* J. MURR. — A: Habit. — B: Perianth seen from above. — C: Hermaphrodite flower. — D: Fruit enclosed in the perianth. — E: Fruit with pericarp. — F: Section through a seed, showing the embryo. — G: Seed in transection. — A: ×0.5. — B: ×8. — C—G: ×20.

glabrous. Leaves alternate, green to light green, glabrous to sparsely farinose above, green to greyish-green and conspicuously farinose beneath. Lower leaves long-petiolate, petiole about equal to or longer than lamina, more or less distinctly three-lobed, ovate to rhombic, cuneate at base, lamina usually 2—7 cm long, 1—5 cm broad, length about 1.5 times the breadth. Margins sharply dentate, except for the entire base, teeth prominent, acute, forward-pointing, the lowermost ones being largest. Apex acute. Upper leaves more or less petiolate, rhombic to lanceolate, cuneate at base, sharply dentate to entire. Flowers situated in rounded to oblong, usually distinct glomerules, forming a more or less leafy and rather loose and graceful panicle. Flowers perfect, usually conspicuously farinose, 5-merous. Perianth lobes united below, ovate, obtuse to acute, dark green to brown in the centre, light green to brown in the outer parts, only membraneous and transparant in the most marginal parts, distinctly and sharply but narrowly keeled on the back. The perianth only partly covers the seed. Pistil with a short style, and two long, filiform stigmas papillate to the base. Stamens 5. Seeds horizontal, at maturity attached to the perianth, black, orbicular, 1—1.5 mm in diameter, with rounded margins. Pericarp rather thin, whitish to yellowish-green, fairly firmly attached to the seed. Testa lustrous, with rounded to oblong, relatively shallow, radial grooves. Radicula short and broad, closely attached to the seed. Embryo annular.

Flowering time: July to August.

Chromosome number: 2n=18.

Variation: Most vegetative characters are variable, particularly the size and shape of lower leaves.

Habitat and distribution: *C. suecicum* is a more or less occasional weed growing on most waste ground, as gardens, farmyards, roadsides and in the vicinity of harbours and mills. It is a Eurasian species, distributed in the western and central parts of Europe, eastwards to Kamtschatka and Japan. In Scandinavia rather common in the southernmost parts, in Denmark from the eastern parts of Jylland to Sjælland, in Sweden from the province of Skåne to Västergötland—Uppland, rare further north. In Norway rather common in the vicinity of Oslo, rare and occasional northwards to Sör-Tröndelag, and in Finland most records are from the southern parts.

Comments: *C. suecicum* is closely related to *C. album* and hybrids are frequently formed in areas of sympatric distribution (cf. ILJIN 1936 and AELLEN 1960). Further, the leaf-shape of *C. suecicum* may resemble that of *C. opulifolium*. However, *C. suecicum* is distinguished from the other two species by the sculpturing of the testa, *C. suecicum* has a testa with radial, shallow grooves, the other species a smooth or furrowed testa.

99. **Chenopodium strictum** ROTH 1821

Annual, up to 1 m high, ascending to erect, branched. Stem angular, striated. Stem and branches glabrous to sparsely farinose, usually red-striped. Leaves alternate, the lowermost ones sometimes opposite, green and more or less reddish, glabrous above, usually farinose beneath. Lower leaves distinctly petiolate, petiole of varying length, broadly oblong to ovate, usually with almost parallel margins, cuneate at base, 2—6 cm long, 1—4 cm broad, length usually at least 1.5 times the breadth, entire to sparsely dentate. Apex mostly apiculate. Upper leaves petiolate, rhomboid to lanceolate, entire rarely dentate. Flowers situated in round to oblong, olivaceous or dull green glomerules, forming terminal, sparsely leafy, erect and rigid, spike-like inflorescences. Flowers perfect, glabrous or sparsely farinose, 5-merous. Perianth lobes united below, ovate, obtuse to acute, green in the centre, pale and membraneous in the outer parts, slightly keeled on the back. The perianth does not fully cover the seed. Pistil with a short style and two

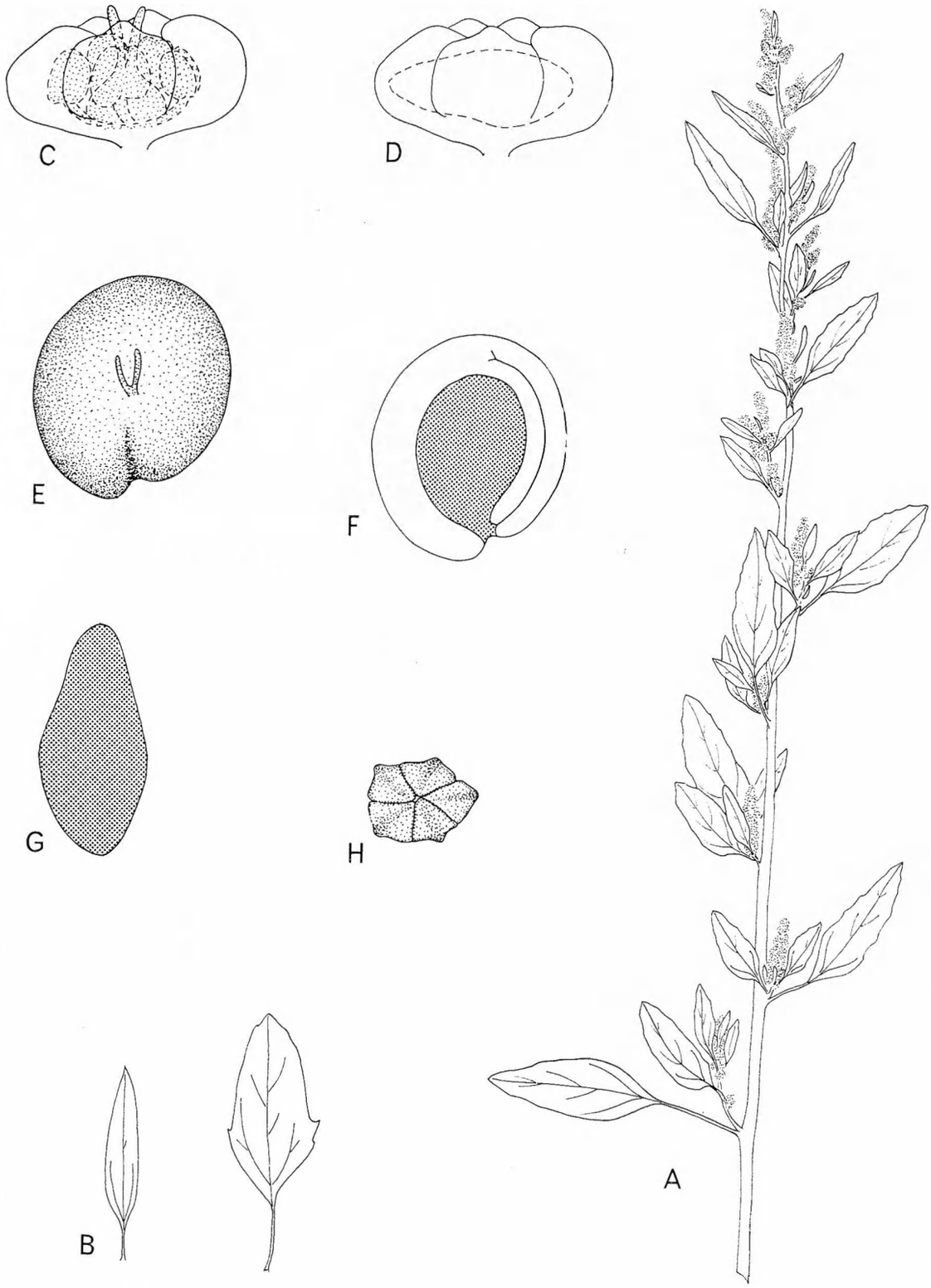


Fig. 99. *Chenopodium strictum* ROTH. — A: Habit (branch). — B: Diverging leaves. — C: Hermaphrodite flower. — D: Fruit enclosed in the perianth. — E: Fruit with pericarp. — F: Section through a seed, showing the embryo. — G: Seed in transection. — H: Perianth seen from above. — A—B: ×0.5. — C—G: ×20. — H: ×8.

stigmas papillate to the base. Stamens 5. Seeds horizontal, black, orbicular to ovoid, 0.9—1.3 mm in diameter, with round to slightly keeled margins. Pericarp rather thin, yellowish-green, easily detached from the seed. Testa lustrous, at low magnifications appearing smooth, at higher magnifications with more or less deep furrows, and sometimes with insignificant pits. Radicula rather prominent, the apex abruptly bent inwards towards the seed. Embryo annular.

Flowering time: End of August to September. In Scandinavia mature seeds are rarely developed.

Chromosome number: 2n=18, 36, 54.

Variation: Two distinct form-series have been distinguished, var. *strictum* and var. *glaucophyllum* (AELLEN) WAHL., mainly based on the appearance and colour of leaves, and differences in inflorescences (for details see AELLEN 1960). According to JÖRGENSEN (1973) *C. album* L. var. *microphyllum* BOENNINGH. ought to be transferred to *C. strictum,* but further study is needed to confirm this point.

Habitat and distribution: In Scandinavia *C. strictum* is a rare and more or less occasional weed, growing on waste ground, often close to harbours and railway-stations. It is probably native to Asia and in Scandinavia is only represented by single localities northwards to Gothenburg and Oslo.

Comments: *C. strictum* is closely related to and has often been included in *C. album* (cf. BRENAN 1964). But, according to AELLEN (1960) hybrids between these species are rare. The taxonomic treatment is a matter of opinion, but the authors prefer to follow AELLEN (1960) and keep it as a species. The most useful characters distinguishing *C. strictum* from *C. album* are: red-striped stem, not or scarcely dentate leaves with almost parallel, often reddish margins, olive-coloured almost glabrous flowers situated in rigid, erect, spike-like inflorescences, combined with the late flowering time.

LITERATURE CITED

AELLEN, P. 1960. Chenopodium. — In HEGI, Illustrierte Flora von Mitteleuropa, 2. Aufl., III (2). — München.

BRENAN, J. P. M. 1964. Chenopodium. — In "Flora Europaea" I. — Cambridge.

HYLANDER, N. 1945. Nomenklatorische und systematische Studien über nordische Gefässpflanzen. — Uppsala Univ. Årsskr. 1945 (7).

ILJIN, M. M. 1936. Chenopodium. — In KOMAROV, Flora SSSR VI. — Leningrad.

JÖRGENSEN, P. M. 1973. The genus Chenopodium in Norway. — Norwegian Journ. Bot. 20: 303—319.

Gunillaea and Namacodon. Two New Genera of Campanulaceae in Africa

Mats Thulin

THULIN, M. 1974 09 13. Gunillaea and Namacodon. Two new genera of Campanulaceae in Africa. — Bot. Notiser 127: 165—182. Lund. ISSN 0006-8195.

The new genera *Gunillaea* THULIN and *Namacodon* THULIN of Campanulaceae are described. *Gunillaea,* with two species, is distributed in tropical Africa from Angola to Mozambique and on Madagascar, while the monotypic *Namacodon* is restricted to Namibia (South West Africa). Their morphology, capsule dehiscence in particular, is discussed and comparisons are made with related genera such as *Prismatocarpus, Wahlenbergia, Peracarpa* and *Heterocodon. Gunillaea* is characterized by indehiscent capsules, which open tardily by the irregular decomposition of the pericarp between the persistent lateral nerves and further by hair-like projections on the testa. *Namacodon* is perhaps unique in Campanulaceae on account of its truly septicidal dehiscence. Other morphological characteristics are apical appendages of the connectives and pollen grains released in tetrads. Both genera are placed in the subtribe Wahlenberginae. Three new combinations are made, viz. *Gunillaea emirnensis* (A. DC.) THULIN, *G. rhodesica* (ADAMS.) THULIN and *Namacodon schinzianum* (MARKGR.) THULIN. The somatic chromosome number 2n=18 is reported for *Gunillaea rhodesica.*

Mats Thulin, Institute of Systematic Botany, University of Uppsala, Box 541, S-751 21 Uppsala 1, Sweden.

INTRODUCTION

During the revision of various African Campanulaceae, it has been found necessary in some cases to create new genera on the basis of previously unnoticed characters. Thus one species previously referred to the genus *Wahlenbergia,* viz. *W. emirnensis* A. DC.=*W. huillana* A. DC. and two species referred to the genus *Prismatocarpus,* viz. *P. rhodesicus* ADAMS. and *P. schinzianus* MARKGR. can hardly be placed in these or any other known genera. Two of the species, *Wahlenbergia emirnensis* and *Prismatocarpus rhodesicus* are closely related and are distributed in tropical Africa, with *W. emirnensis* also extending to Madagascar. They are placed in the new genus *Gunillaea.* The third, *Prismatocarpus schinzianus,* is endemic in South West Africa and is placed in the new monotypic genus *Namacodon.*

MATERIAL AND METHODS

The study is based on herbarium material from the following Herbaria, abbreviated as in the "Index Herbariorum" (LANJOUW & STAFLEU 1964): B, BM, BR, C, EA, G, G-DC, K, LISC, LISU, M, P, S, Z. All collections referred to in this paper have been seen by the author unless otherwise stated.

Specimens of *Gunillaea rhodesica* were also grown in greenhouses in the Uppsala Botanical Gardens from seeds obtained from the collection KORNAŚ 826.

Chromosome counts were made in root-tip sections prepared according to the paraffin method (fixative: Navashin-Karpechenko; stain: crystal violet).

For the anatomical studies flowers, fruits and seeds from herbarium material were softened in formalin for c. 10 days, paraffin-sectioned and stained with safranin and light green.

Pollen preparations were made according to the acetolysis method described by ERDTMAN (1952 pp. 6—9).

Gunillaea THULIN, gen. nov.

Genus novum, *Prismatocarpo* L'HÉR. et *Wahlenbergiae* SCHRAD. ex ROTH affine, sed ab ambobus capsula indehiscente, postremo inaequaliter inter nervos persistentes laterales aperiente differens.

Herbae annuae. Folia alterna, sessilia, plana, nervo medio infra protruso, nervis lateralibus indistinctis. Inflorescentia monochasialis, ± frondosa, floribus ± regularibus, bisexualibus proterandris. Calycis lobi (3—)4—5, accrescentes. Corolla campanulata, epigynica, (3—)4—5-loba. Stamina (3—)4—5, libera, filamentis basi fere linearibus vel dilatatis, ciliatis vel glabris. Pollinis grana tripora, spinulifera. Ovarium inferum, biloculare, ovulis numerosis. Stylus corolla brevior, bilobus, sursum pilis collectoribus vestitus, subtus glaber vel pilosus, eglandulatus vel ad basin loborum styli glandulis duabus munitus. Capsula pariete tenui, indehiscens, postremo inaequaliter inter nervos persistentes laterales aperiens. Semina numerosa; testa sulcata, interdum projecturis capilliformibus munita.

Annual herbs. Leaves alternate, sessile, flat; midvein protruding beneath, lateral veins obscure. Inflorescences ± frondose monochasia. Flowers ± regular, bisexual, protrandrous. Calyx lobes (3—)4—5, accrescent. Corolla campanulate, epigynous, (3—)4—5-lobed. Stamens (3—)4—5, free; filament bases almost linear to broadly winged, ciliate or glabrous. Pollen grains triporate, spinuliferous. Ovary inferior, 2-locular; ovules numerous. Style shorter than the corolla, 2-lobed, upper part with pollen-collecting hairs, lower part glabrous or hairy; two glands sometimes present at base of style lobes. Capsule thin-walled, indehiscent, tardily opening by the irregular decomposition of the pericarp between the persistent lateral nerves. Seeds numerous; testa sulcate, often with hair-like projections.

Type species: *G. emirnensis* (A. DC.) THULIN.

Genus consisting of two species distributed in tropical Africa and on Madagascar. The generic name is derived from my wife's Christian name.

KEY TO THE SPECIES

Corolla less than 5 mm long, shorter or longer than the calyx lobes. Style without glands ..... 1. *G. emirnensis*

Corolla 5—12 mm long, longer than the calyx lobes. Style furnished with two tiny glands immediately below the style lobes ..... 2. *G. rhodesica*

1. **Gunillaea emirnensis** (A. DC.) THULIN, comb. nov.

Basionym: *Wahlenbergia emirnensis* DE CANDOLLE 1839: 432. — Orig. coll.: BOJER s.n., Madagascar, Emirna, 1839 (G-DC holotype).

Wahlenbergia huillana DE CANDOLLE 1866: 333; HEMSLEY 1877: 479. — *Campanopsis huillana* (A. DC.) KUNTZE 1891: 379. — *Cervicina huillana* (A. DC.) HIERN 1898: 631. — Orig. coll.: WELWITSCH 1161, Angola, Huila, Lopollo—Lake Ivantâla, XII. 1859, I. 1860 (G holotype, BM, BR, C, K, LISU, M, P).

Wahlenbergia huillana A. DC. var *pusilla* DE CANDOLLE 1866: 333. — Orig. coll.: WELWITSCH 1160, Angola, Huila, Empalanca, II. 1860 (G holotype, BM, LISU).

Wahlenbergia huillana A. DC. var. *madagascariensis* P. DANGUY, nom. nud.? — This varietal name is written on the labels of some of the material in P, G and B. It was probably never published.

ILLUSTR.: Fig. 1; 3 F—K; 10 C, F.

Annual, ascending or decumbent, rarely erect herb, 4—40 cm tall, usually much-branched from the base. Stem ± hirsute, rarely glabrescent. Leaves narrowly elliptic to elliptic or oblanceolate, attenuate, acute to almost rounded, up to 8—40 mm long and 2—10 mm wide, ± hirsute or glabrous; margin slightly cartilaginous, ± undulate-crenate with small projecting teeth. Inflorescence not well demarcated, lax. Flowers sessile or shortly pedicellate; pedicel elongating in fruit up to 10 mm. Hypanthium narrowly obconical, 5—10-nerved, glabrous or hirsute. Calyx lobes

3—5, often of varying length, narrowly triangular to oblanceolate or narrowly oblong, 1.5—5(—10) mm long, glabrous or ± hirsute, sparsely dentate. Corolla white or blue, 2.4—4(—5) mm long; lobes 3—4(—5), united about halfway. Stamens 3—4(—5), 2—3.2 mm long; filament bases narrowly triangular to broadly angular obovate, glabrous or ciliate; anthers 0.6—1.6 mm long. Style glabrous or rarely hairy below; style lobes 2, 0.5—1.6 mm long, often slightly unequal in length, without glands at the bases; pollen-collecting hairs on style lobes only. Capsules up to 10 mm long, obovoid to narrowly obconical or cylindrical, often slightly curved upwards, prominently 5—10-nerved, glabrous or hirsute. Seeds elliptic, often ± reniform, slightly compressed, 0.5—0.8 mm long; testa sulcate, rarely with hair-like projections.

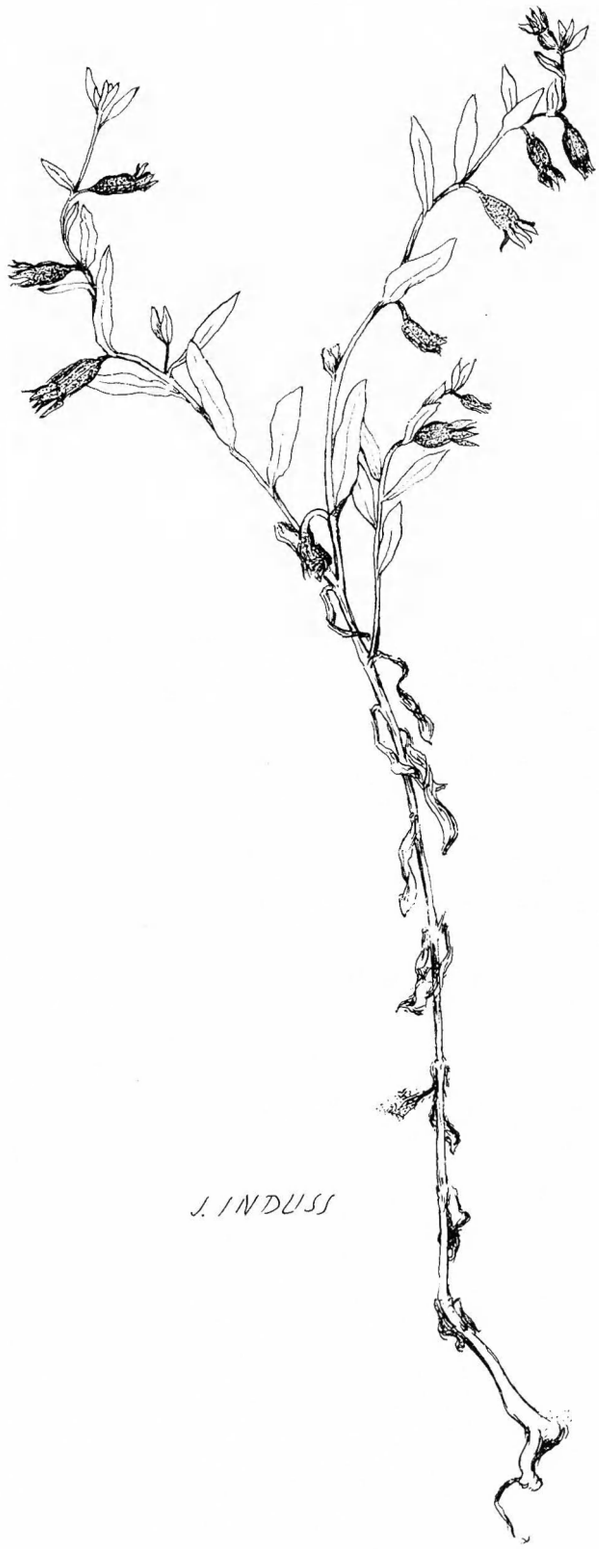


Fig. 1. *Gunillaea emirnensis*. — Flowering and fruiting specimen, ×0.6. Drawn from WILD 4151 (K), Rhodesia.

COLLECTIONS

ANGOLA. Huila, Lopollo—Lake Ivantâla, XII. 1859, I. 1860, WELWITSCH 1161 (BM, BR, C, G, K, LISU, M, P); Empalanca, II. 1860, WELWITSCH 1160 (BM, G, LISU).

TANZANIA. Ulanga, Taweta, XII. 1959, HAERDI 403/0 (EA, K).

ZAÏRE. Katanga, Kasa, Lufila R., XI. 1964, SYMOENS 11124 (BR).

ZAMBIA. North, Chambeshi flats, 50 km SE of Kasama, I. 1961, ROBINSON 4308 (EA, K, M). — East, Lundazi R., above dam, XI. 1958, ROBSON & FANSHAWE 667 (BM, BR, K). — South, Mapanza, XI. 1953, ROBINSON 361 (BR, K).

MALAWI. North, Nyika Plateau, Lake Kaulime, XI. 1958, ROBSON 627 (K); Rumpi, XII. 1964, ROBINSON 6287 (M).

RHODESIA. North, Urungwe, Mgunje, XI. 1953, WILD 4151 (K); Urungwe, Sanyati R., near junction of Fulechi R., X. 1957, PHIPPS 752 (BM, BR, EA, K, P). — Central, Salisbury, XI. 1919, EYLES 1944 (K, Z); Salisbury, Arthur's Seat, Hunyani R., XI. 1945, GREATREA 393 (K).

MADAGASCAR. Emirna, 1839, BOJER s.n. (G-DC); sine loco, HILSENBERG & BOJER s.n. (BM); sine loco, BARON 3615 (K, P); sine loco, 1898, Herb. E. DRAKE 751 (P); Nanisame, VII. 1905, D'ALLEIZETTE 209 (P); Tananarive, VI. 1906, D'ALLEIZETTE 534 (P); Bassin du Mangoro, VIII. 1912, PERRIER DE LA BATHIE 6972 (P); Distr. de Moramanga, Mangoro, near Ankarefo, XI. 1912, VIGUIER & HUMBERT 1158 (B, G, P); Distr. de Betafo, Iantsifitra, XI. 1912, VIGUIER & HUMBERT 1412 (P); Manankazo, NE of Ankazobe, IX.

1913, PERRIER DE LA BATHIE 6983 (P); Tananarive, X. 1914, PERRIER DE LA BATHIE 6946 (P); Andilamena, IX. 1922, PERRIER DE LA BATHIE 14991 (P); Tananarive, Fenoarivo, X. 1927, DECARY 5956 (P); Tananarive, X. 1928, DECARY 6851 (P); Lac Alaotra, IX. 1938, COURS 1289 (P); sine loco, X. 1950, BENOIST 192 (P); Mahazoarivo, VII. 1951, BENOIST s.n. (P); Tananarive, VIII. 1951, BENOIST s.n. (P); Ambohimandroso, XII. 1955, BOSSER 8843 (P); 14 km S of Fianarantsoa, X. 1970, KERAUDREN-AYMONIN & AYMONIN 25091 (P).

DISTRIBUTION AND HABITAT

Fairly wide-spread; very scattered localities throughout southern tropical Africa and Madagascar (Fig. 4 B).

Grows on sand or mud in more or less wet places such as river banks, shores of lakes, swamps or ricefields at altitudes of between 550 and 2150 m.

VARIATION

G. emirnensis is more variable than the fairly homogeneous *G. rhodesica*. Variation is considerable in a number of characters such as number of floral parts, pubescence of stem, capsule, style and filament bases, shape of capsule and number of lateral nerves on the capsule (Fig. 3 F—K). Most characters seem to vary independently, although some slight regional correlations may occur. Thus specimens with ciliate filament bases and hairy styles do not seem to occur on Madagascar. In continental Africa, however, these characters vary more or less independently and do not support infraspecific distinctions.

2. **Gunillaea rhodesica** (ADAMS.) THULIN, comb. nov.

Basionym: *Prismatocarpus rhodesicus* ADAMSON 1951: 123; ROESSLER 1966: 4. — Orig. coll.: FLANAGAN 3162, Rhodesia, Victoria Falls (BOL holotype, PRE). Not seen.

ILLUSTR.: Fig. 2; 3 A—E; 8 C; 10 A, B, E, H; 11 A, C—E).

Annual, usually erect herb, up to 60 cm tall, often much-branched from the base. Stems ± hirsute, at least below. Leaves narrowly elliptic to linear or narrowly oblanceolate, attenuate, ± acute, up to 12—50 mm long and 2—6 mm wide, ± hirsute; margin cartilaginous, ± undulate-crenate with small projecting teeth. Inflorescence usually well demarcated, lax. Flowers sessile or shortly pedicellate; pedicel elongating in fruit up to 25 mm. Hypanthium narrowly obconical, c. 10-nerved, glabrous or glabrescent. Calyx lobes (4—)5, narrowly triangular to narrowly oblanceolate, 3—6(—9) mm long, sometimes revolute, glabrous or ciliate, usually sparsely dentate. Corolla blue or white, 5—12 mm long, puberulous inside towards the base; lobes (4—)5, united up to about halfway. Stamens (4—)5, 4—5 mm long, filament bases dilated, almost cruciform, ciliate; anthers 2—2.5 mm long. Style hairly below; style lobes c. 0.8 mm long, with 2 tiny glands at the base; pollen-collecting hairs present on style lobes and immediately below them. Capsules up to 2 cm long, cylindrical or narrowly obconical, often slightly curved upwards, prominently c. 10-nerved and with the persistent style base forming a hard cone on the top. Seeds narrowly elliptic to elliptic, 0.5—0.7 mm long; testa sulcate, usually with hair-like projections.

COLLECTIONS

ANGOLA. Moxico, Cameia, XII. 1954, MACHADO 57 (LISC).

ZAÏRE. Kasai, Luisa, Lulua R., XI. 1921, ACHTEN 635 (BR).

NAMIBIA (SOUTH WEST AFRICA). Okavango, Kapuko Camp, 24 km W of Runtu, XII. 1955, DE WINTER 3798 (K, M); Diyona Camp, just beyond Nyangana Mission, I. 1956, DE WINTER 4174 (M). — Caprivi-Zipfel, Andara, Okavango R., III. 1958, MERXMÜLLER 1957 (M); Kakumba I., I. 1959, KILLICK & LEISTNER 3416 (K, M).

ZAMBIA. Barotseland, Sesheke Distr., GAIRDNER 442 (K); Matabele Plain, Senanga Distr., XII. 1950, REA 161 (K); Mongu Distr., Sandaula pontoon, XI. 1959, DRUMMOND & COOKSON 6367 (LISC); 8 km on Sandaula

pontoon—Kalabo road, XI. 1959, DRUMMOND & COOKSON 6386 (K); Mongu, XII. 1962, ROBINSON 5506 (K, M); Namushakende—Mongu, XI. 1964, LAWTON 1146 (K); Mongu, XI. 1965, ROBINSON 6704 (EA, K, M); Mongu Distr., Lealui, XII. 1965, ROBINSON 6751 (BR, EA, K, M). — West, Lake Ishiku—Ndola, X. 1953, FANSHAWE 430 (BR, K); Lake Chirengwa, 24 km SE of Ndola, XII. 1960, WILBERFORCE 36 (K). — South, Mumbwa, VII. 1912, MACAULAY 1015 (K); Livingstone Distr., Zambesi R., I. 1929, YOUNG 480 (BM); Victoria Falls, I. 1955, ROBINSON 1059 (K); Namwala, I. 1957, ROBINSON 2105 (BR, K); Machili Distr., X. 1960, FANSHAWE 5847 (BR, K); Machili R., XII. 1960, FANSHAWE 5950 (K); 3 km on Namwala—Kafue Nat. Park road, XII. 1962, VAN RENSBURG 1054 (K); Livingstone, Zambesi R., I. 1963, LAWTON 1022 (K); Namwala Distr., Kafue R. at Kalala, XII. 1963, MITCHELL 24/11 (BR, K); Livingstone, Zambesi R., I. 1972, KORNAŚ 826 (K).

ZAMBIA/RHODESIA. "Haut-Zambèse", KIENER s.n. (P); Victoria Falls, XII. 1904, ALLEN 118 (K); ibid., V. 1905, JEHEBER s.n. (G); ibid., II. 1906, ALLEN 288 (K).

RHODESIA. North, Zambesi R., near Binga, XI. 1958, PHIPPS 1363 (K). — West, Victoria Falls, II. 1912, ROGERS 5617 (K, Z).

MOZAMBIQUE. sine loco, X—XI. 1911, DAWE 497 (K).

DISTRIBUTION AND HABITAT

Scattered localities in tropical Africa, especially in the Zambesi R. basin (Fig. 4 A).

Grows in habitats similar to those of *G. emirnensis* at altitudes of about 1000 m. Both species generally appear during the rainy season and are apparently short-lived.

The species probably also occurs in Botswana. ADAMSON (1951 p. 124) mentions a collection, CURSON 710 (PRE) from Ngamiland, which he says represents a species allied to *Prismatocarpus rhodesicus*. It was not seen by me, but Ngamiland is very close to the known localities of *G. rhodesica* in Namibia and ADAMSON's description affords no reason for doubt. Moreover a specimen in K, HOLUB s.n., without locality has Botswana written on the cover.

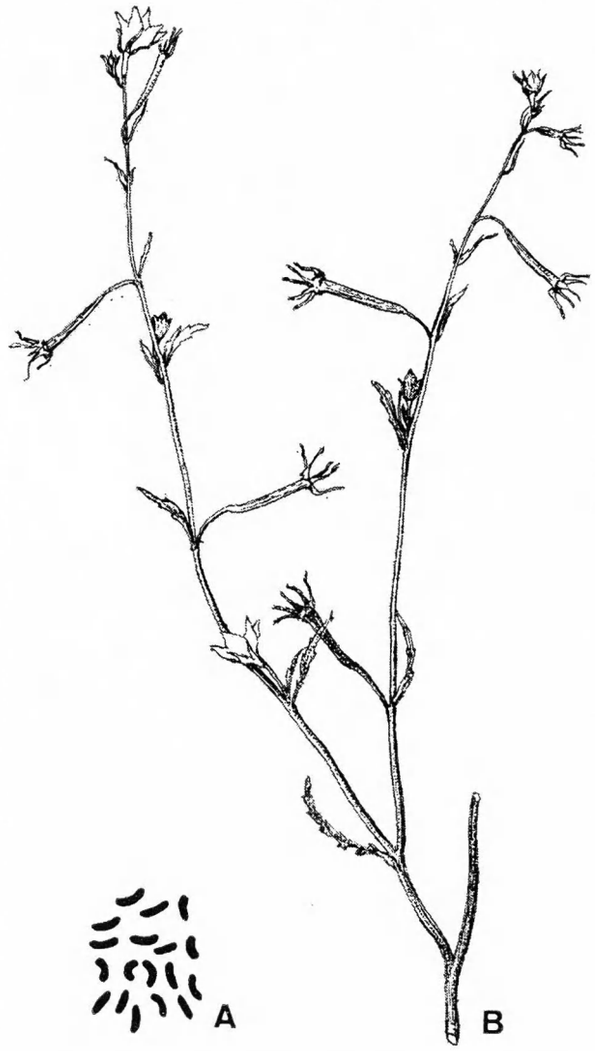


Fig. 2. *Gunillaea rhodesica*. — A: Somatic metaphase plate, ×1700. — B: Part of flowering and fruiting specimen, ×0.6. Drawn from ROBINSON 1059 (K), Zambia.

VARIATION

G. rhodesica shows variation mainly in the size of the flowers and in the length and shape of the capsules (Fig. 3 A—C). The latter are usually long and narrow, but sometimes they become shorter or thicker (WILBERFORCE 36, DAWE 497), thus approaching the shape common in *G. emirnensis*. Therefore small-flowered specimens can be rather similar to *G. emirnensis*. The most reliable characters for separating them are the glands at the base of the style lobes and the pollen-collecting hairs also present below the style lobes (Fig. 3 D), which never occur

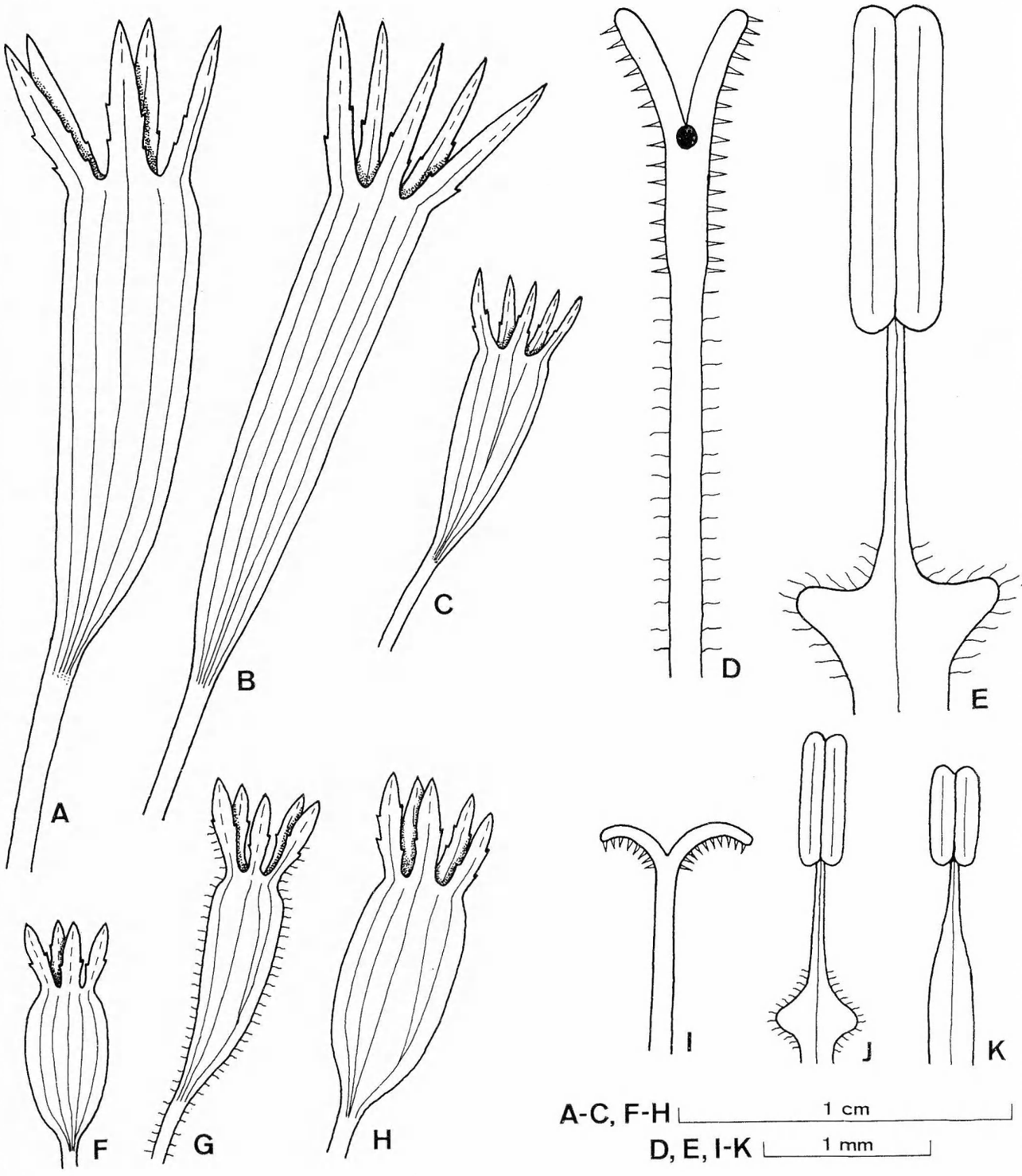


Fig. 3. A—E: *Gunillaea rhodesica*. — A—C: Capsules. — D: Style. — E: Stamen. — F—K: *Gunillaea emirnensis*. — F—H: Capsules. — I: Style. — J, K: Stamens. — The pollen-collecting hairs are drawn as cones in D and I. — A, D, E: DAWE 497, Mozambique. — B: ROBINSON 6751, Zambia. — C: WILBERFORCE 36, Zambia. — F, I, K: ROBSON 627, Malawi. — G, J: ROBINSON 6287, Malawi. — H: ROBINSON 4308, Zambia.

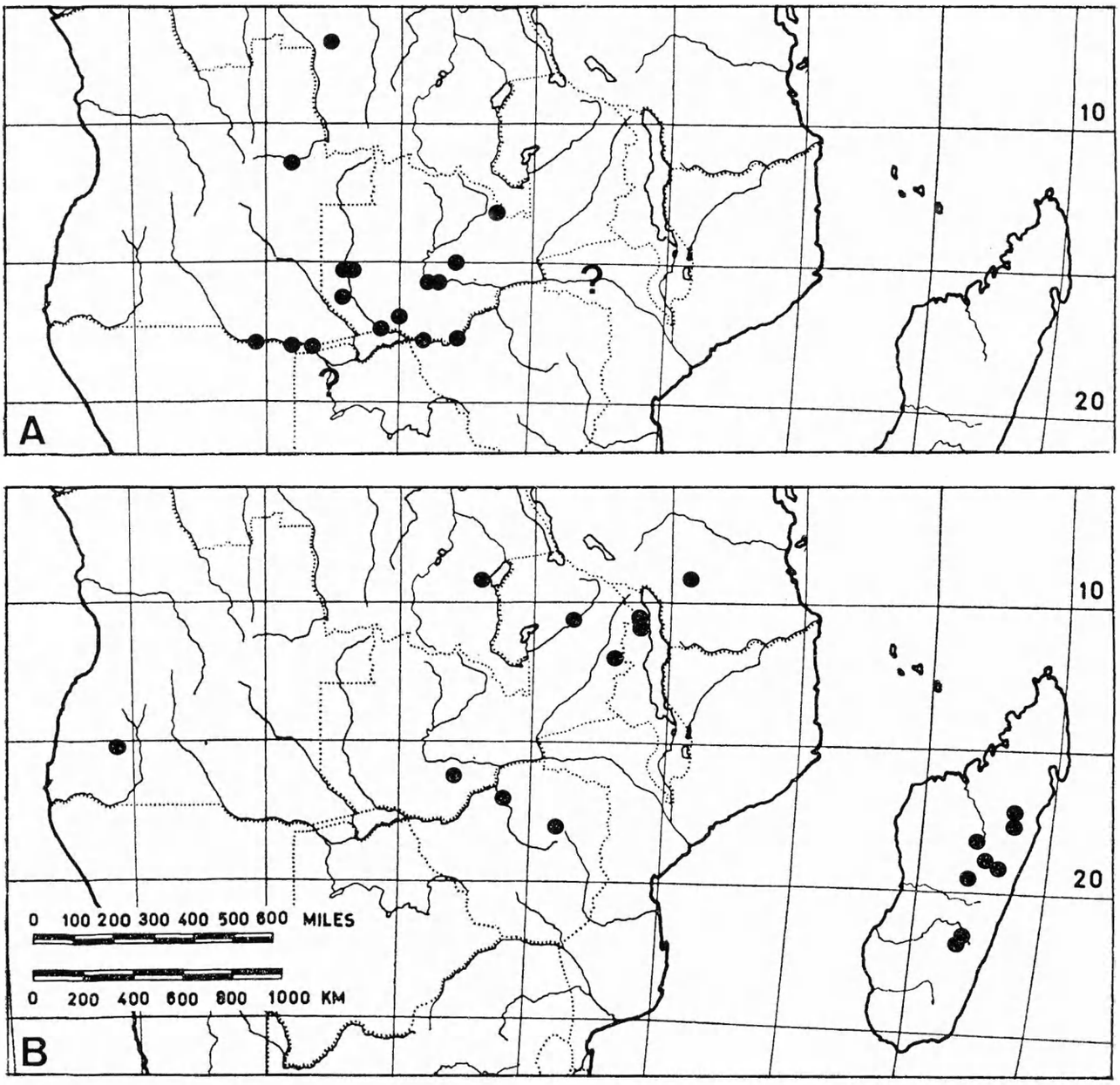


Fig. 4. Distribution of A: *Gunillaea rhodesica.* — B: *Gunillaea emirnensis.*

in *G. emirnensis.* The hair-like projections on the testa (Fig. 10 A, B, E) that are almost always found in *G. rhodesica* are only rarely and less abundantly present in *G. emirnensis.*

DISCUSSION

Previous Taxonomic Treatment

When describing the new species *P. rhodesicus* in his revision of the genus *Prismatocarpus,* ADAMSON (1951 p. 123) states it to be "not at all nearly related to any of the others", and places it as a species of uncertain affinity. In the introduction to the revision (op. cit. p. 93), he says the species "may be found to be generically distinct." He also points out its geographical isolation from the other species of the genus. He obviously did not, however, notice the difference in the dehiscence of the capsules. In a later paper (ADAMSON 1955), dealing with the phytogeography of the genus *Prismato-*

carpus, P. rhodesicus is not even mentioned.

Wahlenbergia emirnensis (usually called *W. huillana,* here reduced to synonymy), which has been known since 1839, has always been referred to *Wahlenbergia* (=*Cervicina*=*Campanopsis*), despite the fact that it lacks apical dehiscence of the capsule, i.e. by valves between the calyx lobes, which is characteristic of this genus.

Morphology

CAPSULE. The dehiscence of the fruits takes place in many different ways in Campanulaceae, and has been an important character for the delimitation of genera and supra-generic taxa within the family. In the tribe Campanulae, which is the only one of concern here, the main difference between the subtribes Campanulinae and Wahlenberginae of SCHÖNLAND (1889 p. 48) is the lateral dehiscence of the capsules in the former versus apical dehiscence in the latter.

When looking for parallels to the type of dehiscence found in *Gunillaea,* I briefly checked dehiscence in the genera *Peracarpa* and *Heterocodon,* both referred to Campanulinae by SCHÖNLAND (1889 p. 49).

Peracarpa HOOK. FIL. & THOMS., a monotypic Asian genus close to *Campanula* has a very thin membraneous pericarp. In the literature it is often stated to be indehiscent. However, in the specimens with ripe fruits seen by me, e.g. OHWI 3843 from Taiwan in UPS there are 3 basal pores in the capsule. This had been pointed out by DE CANDOLLE who placed it in the section Eucodon in *Campanula,* i.e. among species with basally dehiscent fruits (DE CANDOLLE 1839 p. 474). That there are basal pores, at least usually, is also admitted by FEER (1890 p. 619). However, as there is no "besonderer Dehiscenzapparat", the fruits are nevertheless characterized by him as being indehiscent. According to him the basal pores are merely the result of tension in the pericarp, which would not warrant describing the fruit as dehiscent. In the material studied by me, however, the pores are formed along clearly marked lines of dehiscence at the base, and the actual dehiscence takes place by the outward hygroscopic movement of the sclerenchymous parts of the septa near the base, i.e. in the same way as in the *Campanulas* having basal pores.

Heterocodon NUTT., a genus consisting of two species in Asia and North America respectively, is characterized by SCHÖNLAND (1889 pp. 49, 52) as having a capsule with "sehr dünner Wandung die sich seitlich in unregelmässiger Weise öffnet". It thus seems to open in a way very similar to that in *Gunillaea.* However, specimens of *H. rariflorum* NUTT. with ripe fruits present in UPS, e.g. HOWELL s.n. from Oregon, show a very thin pericarp, but have ± clearly marked lines of dehiscence laterally near the base of the capsule. Dehiscence takes place by the upward curving of the sclerenchymous outer part of the septa, i.e. in the same way as in *Campanula.* This is also indicated by some authors, e.g. HITCHCOCK, CRONQUIST, OWNBEY & THOMPSON (1959 p. 491), who describe the capsule as "opening tardily by inconspicuous irregular pores near the base."

Thus the two genera *Peracarpa* and *Heterocodon,* here briefly mentioned, belong without doubt to Campanulinae, and are closely related to *Campanula.* By reason of its lack of apical dehiscence one could believe that *Gunillaea* also belonged there. It is, however, highly probable that *Gunillaea* ought to be placed nearest to *Wahlenbergia* and *Prismatocarpus* in Wahlenberginae. The *Gunillaea* type of capsule (Fig. 10 H) might have derived from the *Wahlenbergia* type by loss of the apical valves in the latter, which would force the seeds to be freed laterally. A transverse section of an ovary of *G. rhodesica* is seen in Fig. 8 C and a capsule of the same species with a partly decomposed pericarp is shown in Fig. 10 H.

On the other hand the *Prismatocarpus* type of capsule (Fig. 8 D) could well have derived from the *Gunillaea* type by a thickening of the membraneous portions between the nerves of the capsule and the subsequent formation of longitudinal lines of dehiscence along them. (For further discussion of the capsule in *Prismatocarpus* see p. 175).

STYLAR GLANDS. The presence of the small stylar glands found in *Gunillaea rhodesica* (Fig. 3 D) is common in both *Wahlenbergia* and *Prismatocarpus,* whereas I do not know of any cases where similar glands occur in species of Campanulinae.

POLLEN. Pollen grains 3-porate, suboblate—spheroidal, equatorial diameter 42—52 μ. Exine generally 1.5—2.5 μ thick. Sexine thicker than nexine, which is thickened around the pores. Sexine with ± evenly spread spinules up to c. 0.8 μ long, mixed with smaller warts. Pore membranes smooth. Fig. 11 A, C—E.

The pollen grains of *Gunillaea* are similar to the ones found in *Wahlenbergia* and *Prismatocarpus,* but also to those in various genera in Campanulinae.

TESTA. The "hairs" usually present on the testa of *Gunillaea rhodesica* (Fig. 10 A, B, E) and sometimes also of *G. emirnensis* is an interesting feature not observed by me in *Wahlenbergia* or *Prismatocarpus.* It is not easy to guess their adaptive significance, if any. They may perhaps act as a kind of arresting mechanism for the seeds after the opening of the fruit, or they may possibly facilitate dispersal by water by increasing the surface of the seed. The "hairs" are not hygroscopic, however.

Cytology

The somatic chromosome number 2n=18 was counted in two specimens of *Gunillaea rhodesica* (offspring of the collection KORNAŚ 826). The chromosomes are small (1.5—2 μ) and of fairly uniform size (Fig. 2 A).

2n=18 has previously been counted in some species of *Wahlenbergia* (cf. FEDOROV 1969 p. 194; THULIN unpubl.). The basic number x=9 seems to be fairly common in this genus whereas it is almost unknown in *Campanula.* Only one count has been reported from *Prismatocarpus,* viz. 2n=34 in *P. campanuloides* (L. FIL.) SOND.=*P. strictus* A. DC. (SUGIURA 1942 p. 424). The reliability of many of SUGIURA's chromosome counts was, however, doubted by GADELLA (1964 pp. 42—43).

Namacodon THULIN, gen. nov.

Genus novum, *Prismatocarpo* L'HÉR. affine, sed ab eo differens gynoecio trimero, capsula per fissuras longitudinales tres septicida, connectivo antherae appendice apicali munito, et pollinis granis quae per tetrades liberantur.

Suffrutex. Folia alterna, sessilia, plana, nervo medio infra protruso, nervis lateralibus indistinctis. Flores solitarii, terminales, regulares, bisexuales, proterandri. Calyx et corolla quinquelobi. Stamina 5, libera, connectivis appendice apicali munitis, filamentis basi oblanceolatis, ciliato-pubescentibus. Pollinis grana tripora, spinulifera, quae per tetrades liberantur. Ovarium inferum, triloculare, ovulis numerosis. Stylus corolla brevior, trilobus, eglandulatus. Capsula per fissuras longitudinales tres septicida. Semina numerosa, late elliptica, complanata, fere laevia.

Type species: *N. schinzianum* (MARKGR.) THULIN.

Monotypic genus confined to Namibia (South West Africa). For further descriptions see under species.

The generic name from Great Namaland, the area in Namibia where the genus is mainly distributed, and -codon, "bell" (Greek).

Namacodon schinzianum (MARKGR.) THULIN, comb. nov.

Basionym: *Prismatocarpus schinzianus* MARKGRAF 1941: 465, 1942: 759 & 1950: 208; ROESSLER 1966: 4. — *P. junceus* SCHINZ 1900:

Fig. 5. *Namacodon schinzianum*. Part of flowering specimen, ×0.6. Drawn from v. WETTSTEIN 243 (M).

35, nom. illegit. (non BUEK in ECKLON & ZEYHER 1837: 383). — Orig. coll.: DINTER 806, Namibia, Windhoek, S side of the eastern Auas Mts., X. 1899 (Z holotype).

P. hildebrandtii auct. non VATKE 1874: 701; ADAMSON 1951: 107, p.p.

ILLUSTR.: Fig. 5; 6; 7; 8 A, B; 10 D, G; 11 B, F—H.

Erect shrublet, 30—40 cm tall, much-branched from the base, with long, ± erect branches. Stems ribbed, glabrous or sometimes puberulous at the base. Leaves alternate, sessile, flat, narrowly lanceolate to lanceolate, cuneate to truncate, acute, spreading, up to 15—25 mm long, 1.5—6 mm wide, rapidly diminishing in size upwards, glabrous or lower leaves sometimes puberulous; margin cartilaginous, slightly revolute, entire or sparsely dentate with teeth often directed slightly backwards; midvein visible beneath, lateral veins obscure. Flowers terminal, solitary, shortly pedicelled in bud, but pedicel elongating up to 3 cm in fruit, regular, bisexual, protrandrous. Hypanthium linear or slightly tapering at each end, 12—25 mm long, diffusely nerved, with 3 longitudinal furrows corresponding to the septa, glabrous. Calyx lobes 5, linear, 8—15 mm long, acute, entire, glabrous, ± erect. Corolla campanulate, epigynous, blue, 13—22 mm long; lobes 5, united almost halfway. Stamens 5, free, c. 10 mm long; filament bases oblanceolate, truncate, ciliate—pubescent; anthers c. 5 mm long; connective with a short but distinct apical appendage. Ovary inferior, 3-locular, ovules numerous. Style shorter than the corolla with pollen-collecting hairs all over, except in the basal part, eglandular; style lobes 3, 2—3 mm long. Capsule elongated, cylindrical—fusiform, 2.5—3.5 cm long, dehiscing septicidally by 3 longitudinal splits. Seeds numerous, broadly elliptic, strongly compressed, c. 0.8 mm long, almost smooth, brown, glossy.

COLLECTIONS

NAMIBIA (SOUTH WEST AFRICA). Windhoek, S side of the eastern Auas Mts., X.

1899, DINTER 806 (Z); Lichtenstein, II. 1923, DINTER 4478 (Z) & DINTER 4479 (S, Z); Khomas Hochland, Farm Friedenau, IV. 1939, GASSNER 87 (M); Binsenheim, I. 1956, VOLK 11184 (M); Farm Lichtenstein, I. 1958, MERXMÜLLER 1252 (M). — Rehoboth, Naukluft Mts., Kabiras, I. 1916, PEARSON s.n. (K); Areb, 1929, v. WETTSTEIN 243 (M); Gurumanas, I. 1935, DINTER 8296 (K, M); Naukluft, X. 1939, VOLK 820 (M); Claratal, 43 km SW of Windhoek, III. 1955, DE WINTER 2573 (K); Mica schist Mts., 40 km S of Windhoek, IV. 1958, DE WINTER 6053 (M); Gamsberg Mt., IV. 1963, NORDENSTAM 2384 (S); Gamsberg Mt., V. 1963, KERS 148 (M, S). — Lüderitz -Süd, Aus, VI. 1922, DINTER 3595 (BM, C, G, Z).

DISTRIBUTION AND HABITAT

Confined to the mountains in the central parts of Namibia at altitudes of about 1800—2000 m (Fig. 9). Grows on stony mountains, in crevices or among rocks and boulders. The species is very uniform throughout its area of distribution.

DISCUSSION

Previous Taxonomic Treatment

In his revision of the genus *Prismatocarpus,* ADAMSON (1951 p. 128) excludes *P. junceus* SCHINZ, nom. illegit. (nomenclatural synonym of *Namacodon schinzianum*) from the genus. He remarks: "as it was described as having a trilocular ovary, it probably does not belong to the genus". Nevertheless, among the five collections cited under *P. hildebrandtii* VATKE (ADAMSON 1951 p. 108), three doubtless belong to SCHINZ's species, the type of which ADAMSON apparently did not see. From the detailed original description of *P. hildebrandtii* (VATKE 1874 p. 701) it is evident, that it is distinct from *P. junceus* SCHINZ. According to VATKE *P. hildebrandtii* is a tiny annual with a 2-locular ovary, a corolla c. 2.5 mm long and calyx lobes 1.5 mm long. The type collection, MEYER 1869 from Hantamsberg in South Africa, was probably destroyed in Berlin. ADAMSON (loc. cit.) states it to be present "in herb Vienna", but according to Dr. G. LEUTE, who kindly checked the matter, it is not. The remaining specimen of *P. hildebrandtii* in ADAMSON's revision is ESTERHUYSEN 1422 (BOL) from Van Rhyns Pass, a specimen not seen by me. The species thus remains a dubious one, but is probably o local endemic in the Hantamsberg —Van Rhynsdorp area of the Cape Province. In any case it has nothing to do with the genus *Namacodon.* The new name *P. schinzianus* proposed by MARKGRAF 1941 p. 465) for *P. junceus* SCHINZ is therefore the correct basionym, when it is transferred to *Namacodon.*

Morphology

OVARY AND CAPSULE. *Namacodon* is superficially somewhat similar to several species of the genus *Prismatocarpus.* Nevertheless it displays a number of interesting features that makes it a very well-defined genus. Dehiscence of the fruit occurs in both genera by longitudinal lateral splits in the walls of the elongated capsules. There are, however, marked differences.

Prismatocarpus has a 2-locular inferior ovary with axile placentation. With age the septa often (?) more or less disappear, thus making the placentation appear almost free central. When the capsule is mature, the lines of dehiscence are formed from the sinuses of the calyx lobes down to the base of the capsule, splitting the now hard and sclerenchymous pericarp into 5 (or 4) segments, each corresponding to a calyx lobe (Fig. 8 D). The base of the style persists on top of the capsule as a hard often split cone, which finally drops off, as do the calyx lobes.

In *Namacodon* the ovary is 3-locular, with the septa persisting between the loculi. Along each septum a deep longitudinal furrow is formed in the capsule (Fig. 8 A). The lines of dehiscence are here not related to the calyx lobes, but are formed along the septa, the pericarp thus being split into 3 segments each

Fig. 6. *Namacodon schinzianum.* — A: Capsule after dehiscence, ×3.5. — B: Top of capsule with calyx and wilted corolla, ×5. Drawn from VOLK 11184 (M).

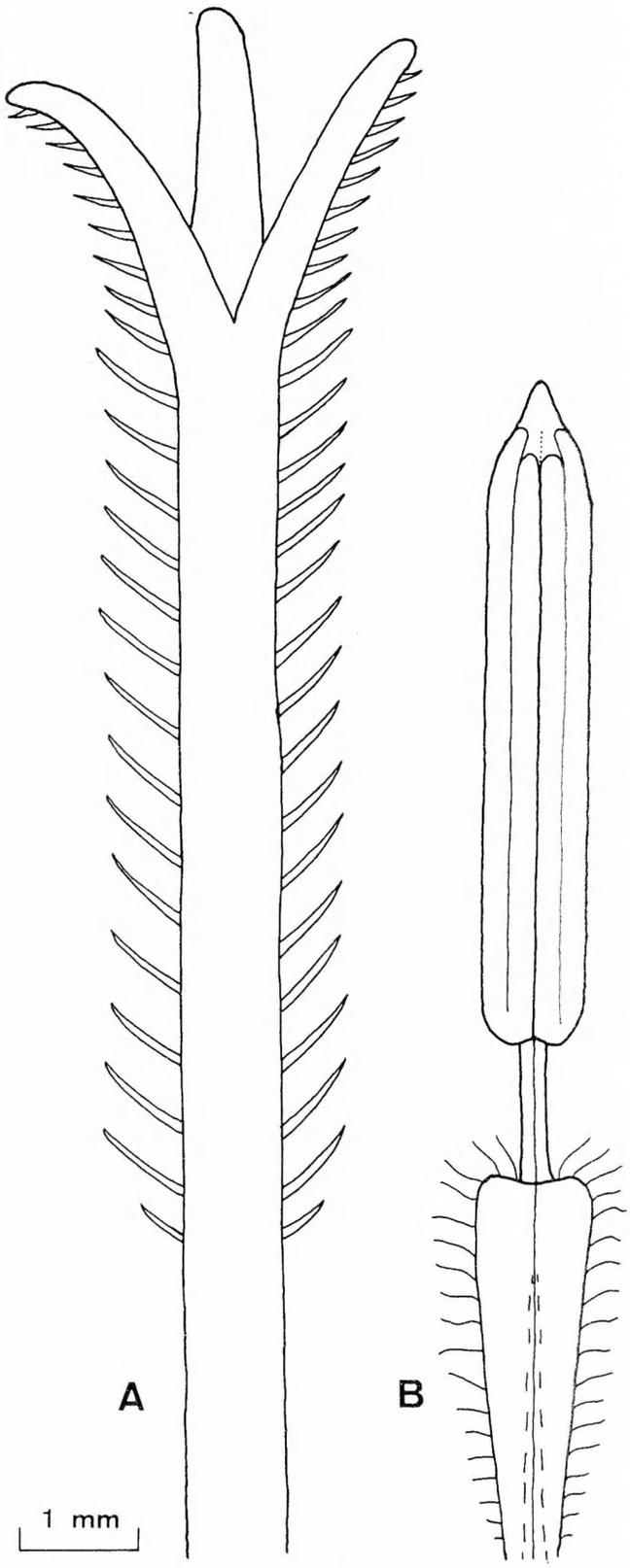


Fig. 7. *Namacodon schinzianum.* — A: Style. — B: Stamen. Drawn from GASSNER 87 (M).

corresponding to a carpel. The superficially very similar types of dehiscence found in *Prismatocarpus* and *Namacodon* are thus not homologous as the lines of dehiscence in the first case are determined by the structure of the calyx and in the latter by the carpels. The truly septicidal dehiscence in *Namacodon* seems to be unique indeed in Campanulaceae. I have not seen it reported elsewhere.

Furthermore, in *Namacodon* the three segments of the pericarp are actually actively pushed apart by a special mecha-

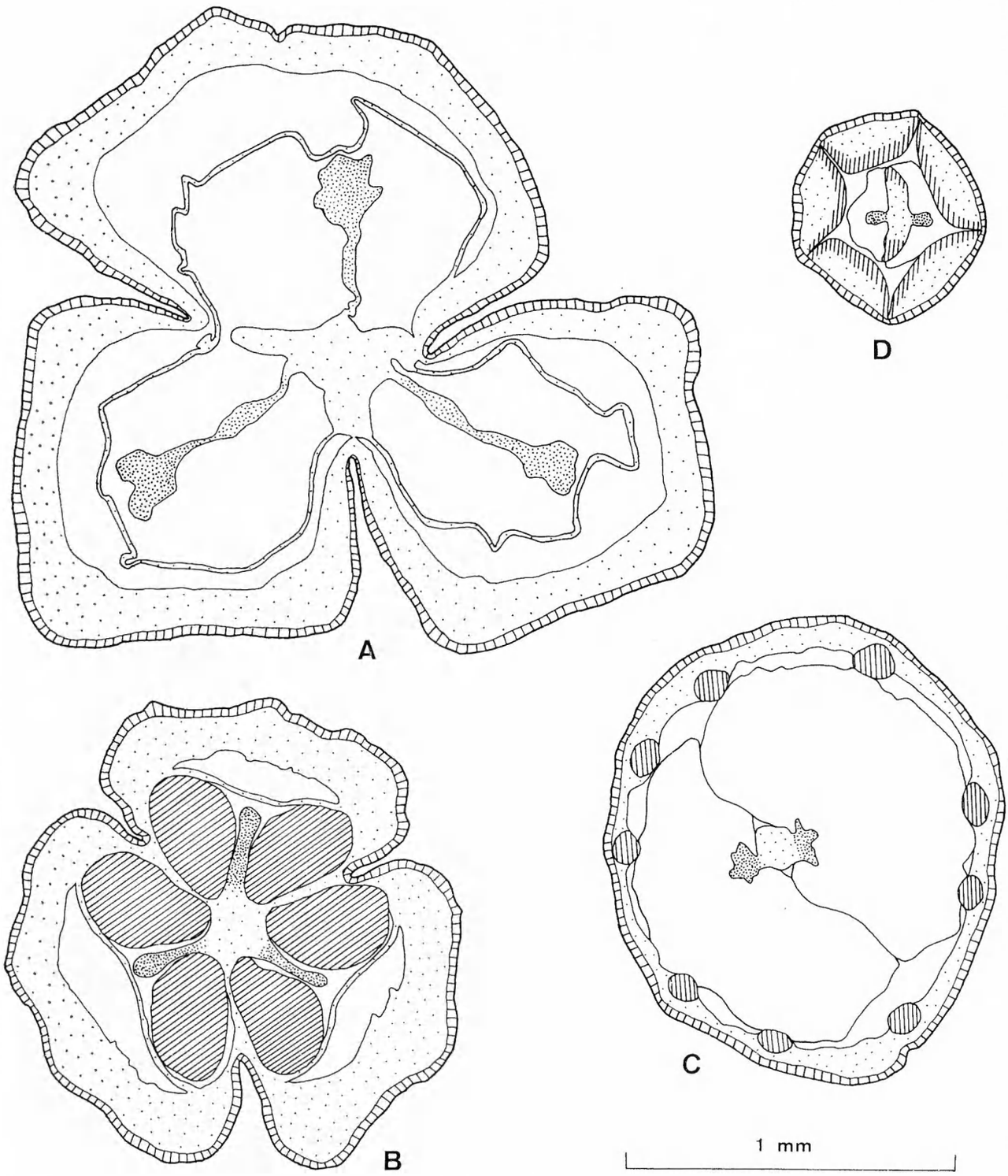


Fig. 8. Transversal sections of almost ripe capsules. — A: *Namacodon schinzianum,* from the middle of the capsule. — B: ibid., from the top of the capsule. — C: *Gunillaea rhodesica.* — D: *Prismatocarpus sessilis* ECKL. ex A. DC. var. *macrocarpus* ADAMS. — Dense dotting: placentas; sparse dotting: parenchyma; dense hatching: sclerenchyma; sparse hatching: epidermis. — A, B: VOLK 11184 (M). — C: FANSHAWE 5950 (K). — D: ESTERHUYSEN 13716 (UPS).

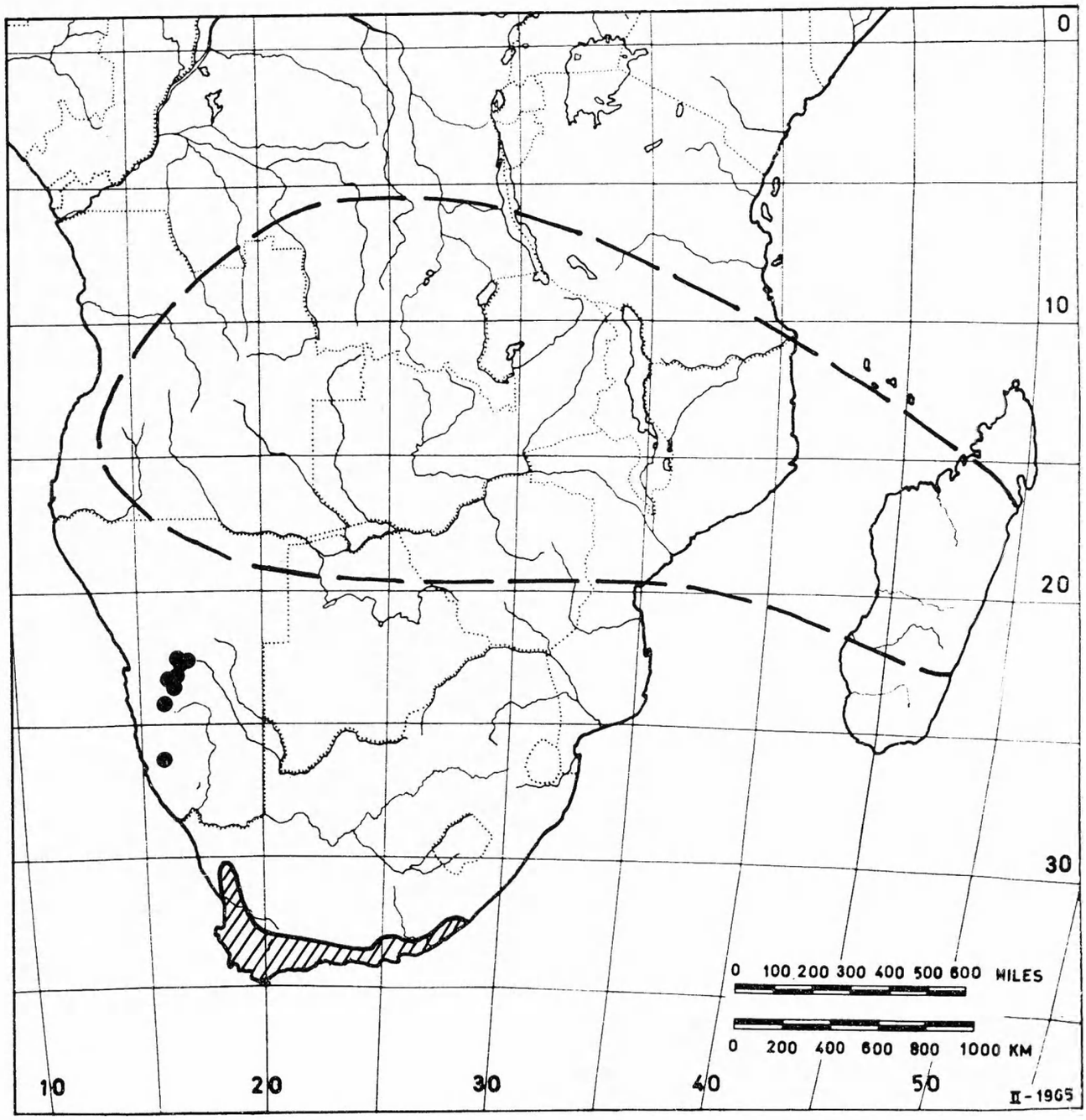


Fig. 9. Distribution of *Gunillaea* (broken line), *Prismatocarpus* (hatched) and *Namacodon schinzianum* (dots).

nism not observed in *Prismatocarpus*. Thus in the middle of the very top of the ovary, six narrow, ± conical, acute processes are formed out of the septa, one on each side of them, and directed downwards (Fig. 8 B, 6 B). When the fruit ripens these processes become sclerenchymous and finally bend outwards, usu-

Fig. 10. A: *Gunillaea rhodesica,* seed, ×110. — B: ibid., testa structure, ×550. — C: *Gunillaea emirnensis,* testa structure, ×430. — D: *Namacodon schinzianum,* seed, ×55. — E—G: cross-sections of testa, ×570. — E: *Gunillaea rhodesica.* — F: *Gunillaea emirnensis.* — G: *Namacodon schinzianum.* — H: *Gunillaea rhodesica,* capsule with the pericarp partly decomposed, ×3.9. — A, B, E: Fanshawe 5950 (K), Zambia. — C: Perrier de la Bathie 6946 (P), Madagascar. — D, G: Kers 148 (M). — F: Robinson 6287 (M), Malawi. — H: Young 480 (BM), Zambia.

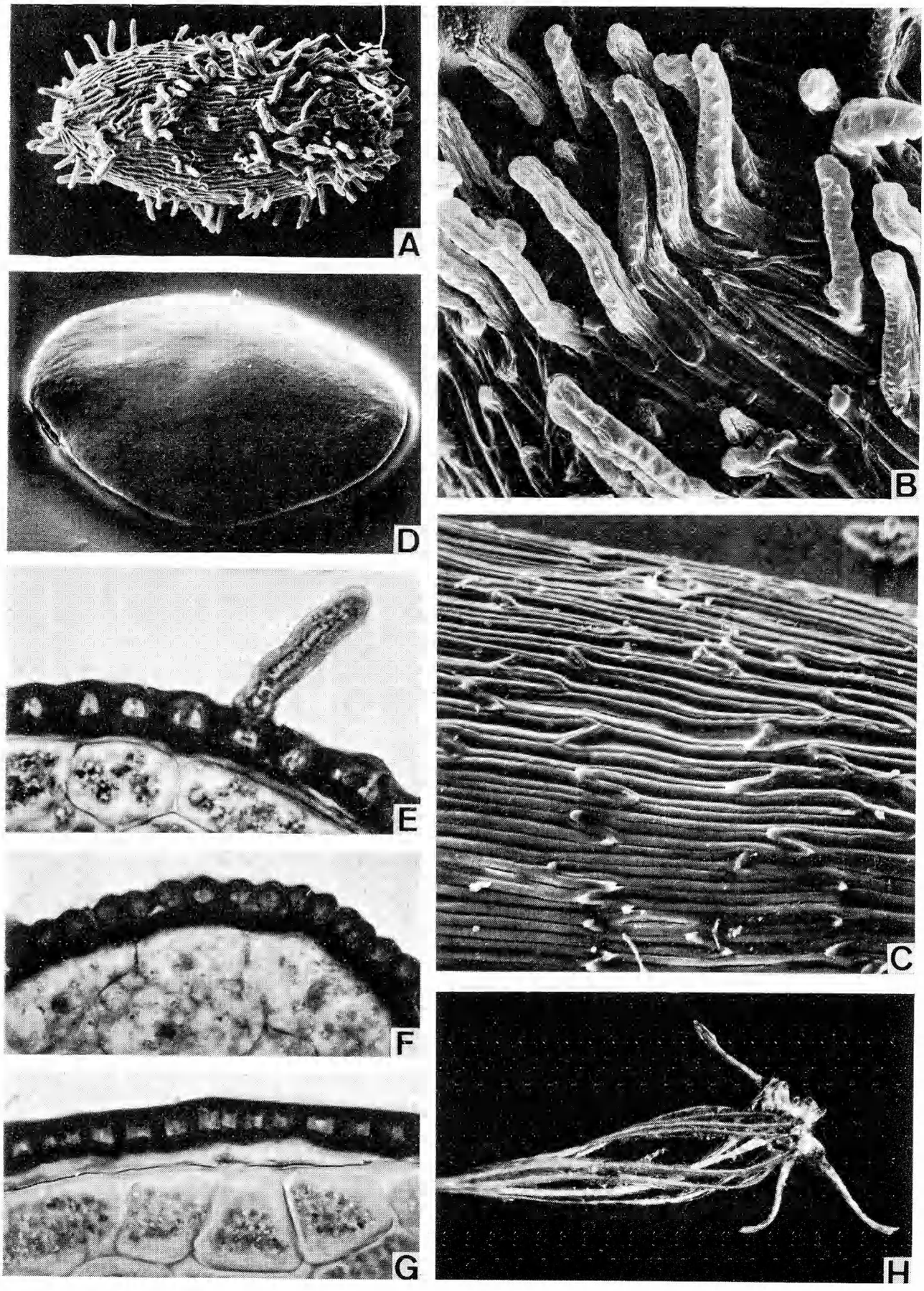


Fig. 10.

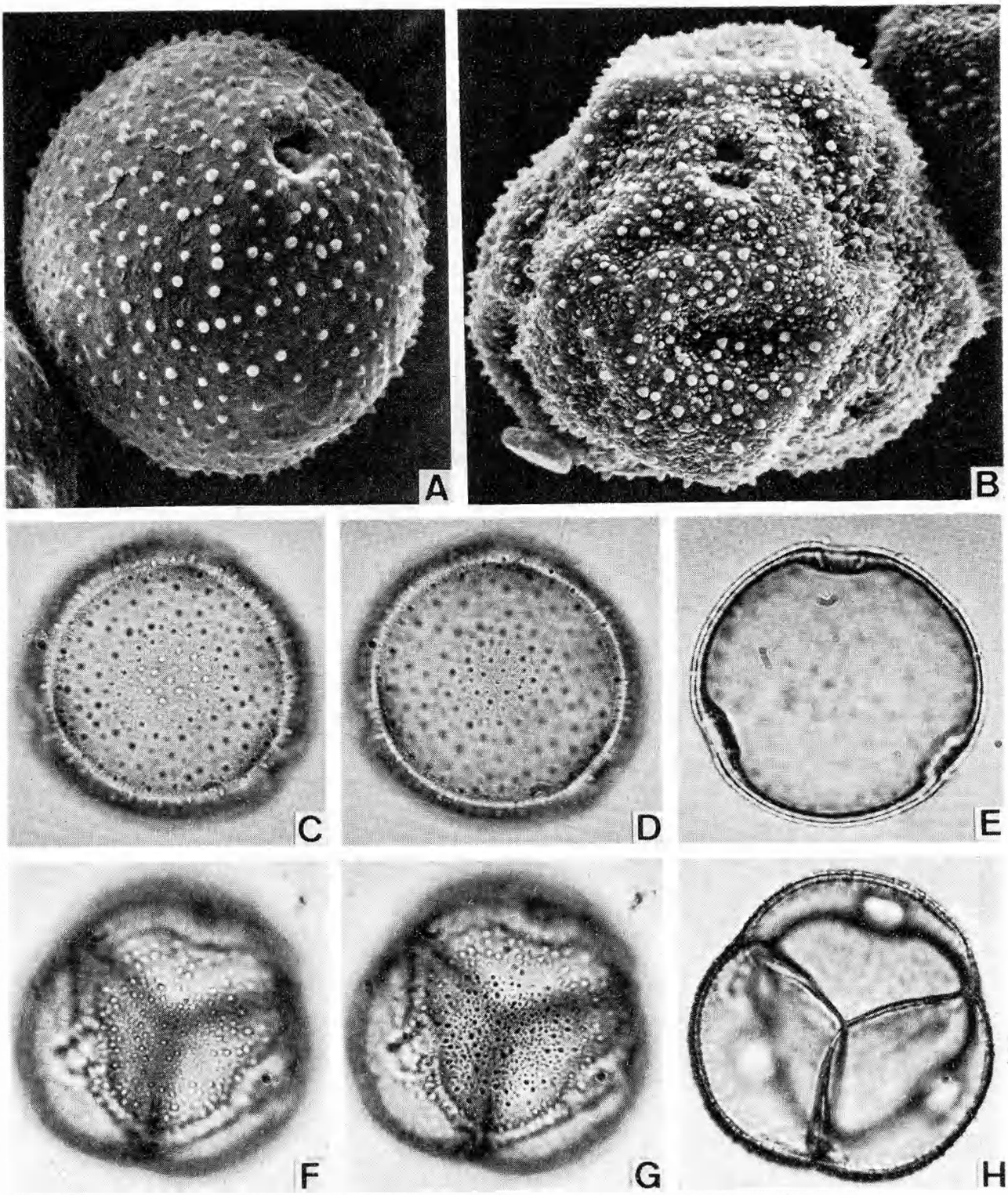


Fig. 11. Pollen grains. — A: *Gunillaea rhodesica*, ×1600. — B: *Namacodon schinzianum*, ×1050 (somewhat shrunken). — C—E: *Gunillaea rhodesica*, ×830. — F—H: *Namacodon schinzianum*, ×500. — A: ROBINSON 6751 (BR), Zambia. — B: GASSNER 87 (M). — C—E: REA 161 (K), Zambia. — F—H: v. WETTSTEIN 243 (M).

ally pairwise, one pair bending into each loculus of the capsule hereby exerting such pressure on the pericarp that it splits forming three segments. The six processes are firmly attached to the top of the ovary, which is now only fixed to the rest of

the ovary by the thin string in the middle. This soon breaks and the top of the ovary with the persistent calyx lobes and the wilted corolla drops off.

ANTHERS. The occurrence of distinct apical appendages on the connective (Fig. 7 B) is a character not known from *Prismatocarpus*. Indeed, as regards Campanulaceae, I have only seen this character previously reported from the small genus *Musschia* on Madeira (DE CANDOLLE 1830 p. 14), which has connective appendages very similar to those in *Namacodon*. The two genera are otherwise not closely related.

POLLEN. Pollen grains 3-porate, united in tetrahedral tetrads (diameter 70—85 μ). Exine generally 2.5—3.5 μ thick. Sexine thicker than nexine, which is thickened around the pores. Sexine very densely covered with small warts mixed with spinules up to 2 μ long. Fig. 11 B, F—H.

Pollen grains that are released in tetrads have not been previously reported from Campanulaceae.

POLLEN-COLLECTING HAIRS. Another observation worth mentioning concerns the pollen-collecting hairs of the style. In Campanulaceae (*Sphenoclea* excluded) these have bulbous bases which are absent in the normal hairs also present in many species, e.g. *Gunillaea rhodesica*, further down on the style (Fig. 3 D). The pollen-collecting hairs collapse after anthesis and often disappear due to invagination into the basal cavities (see CAROLIN 1960 p. 197, fig. 3 C). This is the case in *Campanula, Wahlenbergia* and *Prismatocarpus,* for example, where no pollen-collecting hairs are visible on old styles. In *Namacodon* almost the whole of the style is covered with pollen-collecting hairs (Fig. 7 A) which are also furnished with basal cavities. After anthesis these hairs collapse, but apparently never invaginate, remaining fully visible on the style even in old wilted flowers.

Phytogeography

After the transfer of *Prismatocarpus rhodesicus* and *P. schinzianus* to the new genera here proposed, *Gunillaea* and *Namacodon* respectively, the genus *Prismatocarpus,* with about 25 remaining species will be restricted to the Cape Floral Region and being an endemic Cape element (Fig. 9) as it was also considered to be by WEIMARCK (1941 p. 96).

ACKNOWLEDGEMENTS

I am indebted to Dr B. BERGH for editing the Latin descriptions, to the artist J. INDUSS for preparing Figures 1, 2 B, 5 and 6, to Prof. J. A. NANNFELDT and Dr Ö. NILSSON for advice concerning the manuscript and to Fil. lic. L. TIBELL for the scanning electronmicrographs. In particular I want to thank Dr B. JONSELL for valuable discussions and for the critical reading of the manuscript. Thanks are also due to the directors of the Herbaria listed. The work was finished with the help of grants from the Swedish Natural Science Research Council.

LITERATURE CITED

ADAMSON, R. S. 1951. A revision of the genera Prismatocarpus and Roella. — Journ. S. Afr. Bot. 17: 93—166.

— 1955. The phytogeography of Roella and Prismatocarpus. — Sv. Bot. Tidskr. 49: 24—28.

CAROLIN, R. C. 1960. The structures involved in the presentation of pollen to visiting insects in the order Campanales. — Proc. Linn. Soc. New South Wales 85: 197—207.

DE CANDOLLE, A. 1830. Monographie des Campanulées. — Paris.

— 1839. Campanulaceae. — In A. P. DE CANDOLLE, Prodromus systematis naturalis regni vegetabilis, 7. — Paris.

— 1866. Campanulacées du pays d'Angola, recueillies par M. le Dr WELWITSCH. — Ann. Sc. Nat. Bot., ser. 5, 6: 323—333.

ECKLON, C. F. & ZEYHER, C. 1837. Enumeratio plantarum africae australis extratropicae, 3. — Hamburgi.

ERDTMAN, G. 1952. Pollen morphology and plant taxonomy. Angiosperms. — Stockholm.

FEDOROV, A. A. (ed.) 1969. Chromosome numbers of flowering plants. — Leningrad.

FEER, H. 1890. Beiträge zur Systematik und Morphologie der Campanulaceen. — Engl. Bot. Jahrb. 12: 608—621.

GADELLA, TH. W. J. 1964. Cytotaxonomic studies in the genus Campanula. — Wentia 11: 1—104.

HEMSLEY, W. B. 1877. Campanulaceae. — In OLIVER, Flora of Tropical Africa, 3: 463—482. — London.

HIERN, W. P. 1898. Catalogue of the African plants collected by Dr FRIEDRICH WELWITSCH in 1853—61, 1 (3). — London.

HITCHCOCK, C. L., CRONQUIST, A., OWNBEY, M. & THOMPSON, J. W. 1959. Vascular plants of the pacific northwest, 4. — Seattle.

KUNTZE, O. 1891. Revisio generum plantarum, 2. — Würzburg.

LANJOUW, J. & STAFLEU, F. A. 1964. Index herbariorum, 1. The herbaria of the world. Ed. 5. — Regn. Veg. 31.

MARKGRAF, F. 1941. Campanuloideae. — In MILDBREAD, Beiträge zur Flora von Deutsch-Südwestafrika. — Notizbl. Bot. Gart. Berlin—Dahlem 15: 465—471.

— 1942. Campanuloideae, II. — In MILDBREAD, Beiträge zur Flora von Deutsch-Südwestafrika, III. — Notizbl. Bot. Gart. Berlin—Dahlem 15: 759—761.

— 1950. Die Campanulaceen von Südwestafrika. — Engl. Bot. Jahrb. 75: 206—220.

ROESSLER, H. 1966. Campanulaceae. — In Prodromus einer Flora von Südwestafrika, 136: 1—9. — München.

SCHINZ, H. 1900. Beiträge zur Kenntnis der Afrikanischen Flora (Neue Folge) XII. — Mém. Herb. Boissier 20: 1—36.

SCHÖNLAND, S. 1889. Campanulaceae. — In ENGLER & PRANTL, Die natürlichen Pflanzenfamilien, 4 (5): 40—70. — Berlin.

SUGIURA, T. 1942. Studies on the chromosome numbers in Campanulaceae. I. Campanuloideae—Campanuleae. — Cytologia 12: 418—434.

VATKE, W. 1874. Notulae in Campanulaceas herbarii regii berolinensis. — Linnaea 38: 699—714.

WEIMARCK, H. 1941. Phytogeographical groups, centres and intervals within the Cape flora. — Lunds Univ. Årsskr. N.F. Avd. 2, 37 (5).

Armeria L. in South America

D. M. Moore and Bronwen Yates

MOORE, D. M. & YATES, B. 1974 09 13. Armeria L. in South America. — Bot. Notiser 127: 183—192. Lund. ISSN 0006-8195.

A detailed biometrical study of 20 taxonomically important morphological characters in South American *Armeria* shows that all populations must be referred to *A. maritima* L. Despite the considerable variation, much of which is genetically determined, it is not possible to delimit major subspecific patterns within South America. Some characters, such as scape- and leaf-indumentum, scape-length and leaf-width, show a tendency towards topoclinal variation but there is little correlation between them. The austral populations, like those from North America and one circumboreal taxon, show monomorphic self-compatibility but the variation in the characters analysed was comparable to that shown by the species in the Northern Hemisphere. Consequently, no consistent difference could be found to distinguish South American and Northern Hemisphere material. Nevertheless, in view of the geographical separation and the apparently distinct evolutionary potential of the variable homogamous populations in South America they have been recognized as a distinct subspecies for which the formal combination *A. maritima* subsp. *andina* (POEPP. ex BOISS.) D. M. MOORE & YATES is made.

D. M. Moore & Bronwen Yates, Department of Botany, University of Reading, Whiteknights, Reading RG6 2AS, England.

INTRODUCTION

Armeria L. is a predominantly Northern Hemisphere genus. Most species occur in temperate Eurasia, where almost all of them exhibit a dimorphic incompatibility system (BAKER 1954, 1961, 1966), the only exception being the self-compatible, circumpolar *A. maritima* L. subsp. *sibirica* (TURCZ. ex BOISS.) NYMAN (BAKER 1953). All North American representatives of the genus have monomorphic pollen and stigma patterns and are self-compatible (BAKER 1954). They are usually included within *A. maritima* (e.g. LAWRENCE 1940), although BAKER (1966) hints that he would prefer to recognize some of the taxa as distinct species.

In the Southern Hemisphere *Armeria* is confined to South America, where it occurs in Chile southwards from c. lat. 33°S (prov. Valparaiso) and in western Argentina southwards from prov. Córdoba (lat. 31°S) to reach its southern and eastern limits in Tierra del Fuego, Isla de los Estados and the Falkland Islands (Figs. 3—4). It occurs in both coastal and inland localities and ranges from sea-level to altitudes approaching 2,500 m. near its northern limit in the Andes. As in North America, all material examined has shown monomorphic self-compatibility (BAKER 1954, 1966; MOORE 1968).

There is a considerable amount of variation in South American *Armeria,* as is attested by the number of taxa described by previous authors. Thus, no less than 13 species have been recognized at one time or another, distinguished by features of the indumentum, leaf-shape, scape-length, shape of the involucral bracts, etc. On the other hand, LAWRENCE (1940) took a rather conservative view of this variation and included all the South American material within *A. maritima,* assigning it to 5 varieties which were distinguishable by such characters as leaf-

size and -shape, shape of the involucral bracts, capitulum-size, etc. He noted that the South American plants could be differentiated from those present in the Northern Hemisphere by the minute pustular glands on the scapes and a number of less constant characters of the calyx and indumentum.

In connection with our studies on the flora of Tierra del Fuego we have had occasion to examine many collections of *Armeria* from southernmost South America and have not found any of the available taxonomic treatments to be particularly useful. Consequently we undertook a study of the variation shown throughout South America in an attempt to determine whether any pattern could be discerned and to what extent this might permit a satisfactory taxonomic treatment.

MATERIAL AND METHODS

This study is primarily based on herbarium material, which was available from most parts of the South American range of *Armeria*. Type material was included wherever possible. Northern Hemisphere material referable to *A. maritima* was examined for comparison; it included collections from Spain, France, Britain, Denmark, Sweden, Faroër Islands, Iceland and Canada. Detailed field observations to give a picture of local ecological and population patterns were made in Tierra del Fuego, while a number of the more distinctive morphological variants from southernmost South America have been in cultivation for periods of up to 7 years in order to assess the genotypic and environmentally induced components of the variation.

The morphological characters examined in detail were selected on the basis of the diagnostic features emphasized by authors describing South American taxa and also those utilized to circumscribe taxa within European *A. maritima*. Twenty vegetative and floral characters were scored (characters 1—11) or measured (characters 12—20) as follows:

1. *Leaf indumentum.* The distribution and density of hairs was classified into 3 grades: (a) glabrous; (b) ciliate margins; (c) sparsely ciliate margins and/or scattered hairs on upper surface.
2. *Leaf-outline.* (a) linear; (b) filiform.
3. *Leaf-surface.* (a) flat; (b) canaliculate; (c) convolute.
4. *Leaf-apex.* (a) acute; (b) obtuse.
5. *Scape indumentum.* The density and length of hairs was classified into 3 grades: (a) glabrous; (b) villous, the hairs long and dense; (c) pubescent, the hairs short and often sparse.
6. *Scape* arcuate or not.
7. *Apex of outer involucral bracts.* (a) acuminate; (b) acute; (c) mucronate; (d) obtuse or muticous; (e) retuse or emarginate.
8. *Calyx insertion-scar.* (a) ovate and acute; (b) orbicular; (c) ovate-oblong and truncate or obtuse.
9. *Calyx indumentum.* (a) calyx completely hairy or pubescent; (b) indumentum sparse or calyx with short hairs between the ribs; (c) calyx glabrous between the ribs; (d) hairs only on the 5 intermediate ribs ('subcostae').
10. *Stigma type.* 'Papillate' or 'cob'.
11. *Pollen type.* 'A' or 'B' as seen in genus *Limonium* (BAKER 1948).
12. *Leaf-length.*
13. *Leaf-width.*
14. *Scape-length.*
15. *Length of involucral sheath.*
16. *Diameter of capitulum.*
17. *Calyx-length.*
18. *Length of calyx-arm.*
19. *Length of outer: inner involucral bracts.*
20. *Length of spikelet-bract: length of calyx.*

The 20 characters listed above were scored in a total of 112 collections from South America and 30 collections from the Northern Hemisphere, principally western Europe.

RESULTS AND DISCUSSION

Correlation between Various Character-combinations

In order to determine to what extent morphologically recognizable entities, circumscribed by clusters of characters, could be delimited within South American *Armeria,* the data were plotted on scatter diagrams using different combinations of quantitative and qualitative characters. The only correlation in quantitative characters was shown between the length of the involucral sheath and the diameter of the capitulum, the plants with longer capitula having a longer sheath (Fig. 1). Furthermore, the greatest separation of

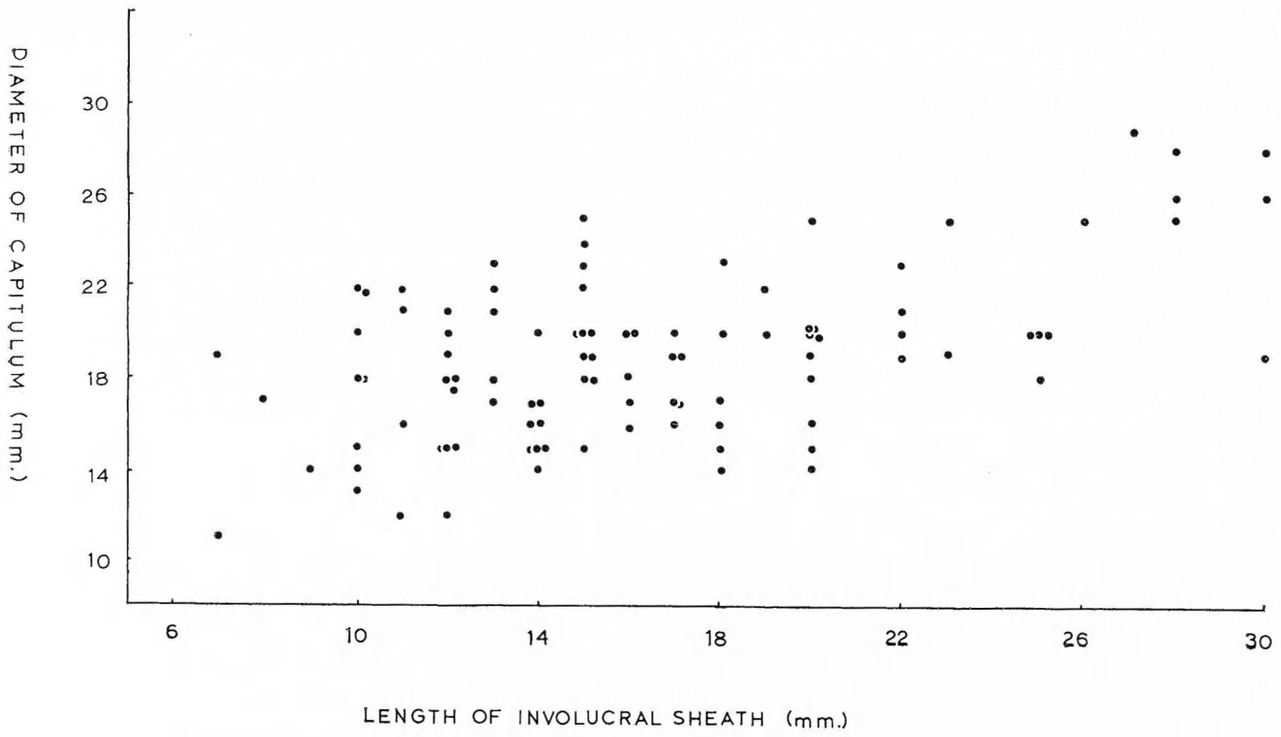


Fig. 1. Scatter diagram showing relation between capitulum-diameter and the length of the involucral sheath in South American *Armeria*.

the spots on a scatter diagram was shown by plotting the length of the involucral sheath against the leaf-width. These two characters were consequently used to provide the axes for a pictorialized scatter diagram incorporating the scape-length, shape of the calyx-insertion-scar and an estimate of the indumentum on the leaves, scape and calyx (Fig. 2).

From Fig. 2 it can be seen that there are no clear groups of correlated characters which give any basis for the recognition of taxonomic categories. After various attempts to show the character-grades pictorially it seemed that the indumentum of the scape was most likely to provide a suitable basis for examining such morphological groupings. Consequently this character was most heavily weighted in the diagram, being designated by the shape of the points plotted.

Plants with the most villous scape tend to have a short involucral sheath and scape. They have leaves of generally intermediate width but are still rather variable in this, while the other characters span the whole range of possible variation. *Armeria bella* ALBOFF, *A. chilensis* var. *brevifolia* BOISS. and *A. delfinii* PHIL. belong here.

The group of plants with glabrous scapes shows a wide range of variation. It includes the material with the widest leaves and longest scapes and much also has glabrous leaves. However, it overlaps with the preceding group in all characters and shows most of the variation possible by the system of scoring employed. *Armeria andina* POEPP. ex BOISS., *A. brachyphylla* BOISS., *A. curvifolia* BERT. and *A. macloviana* D'URV. belong in this group.

The plants in which the scape-indumentum is more or less intermediate in length and density between that of the preceding two types constitute a rather compact group which overlaps in most characters with the material having glabrous or villous scapes. They do, however, tend to have longer scapes than the villous plants and they also seem more

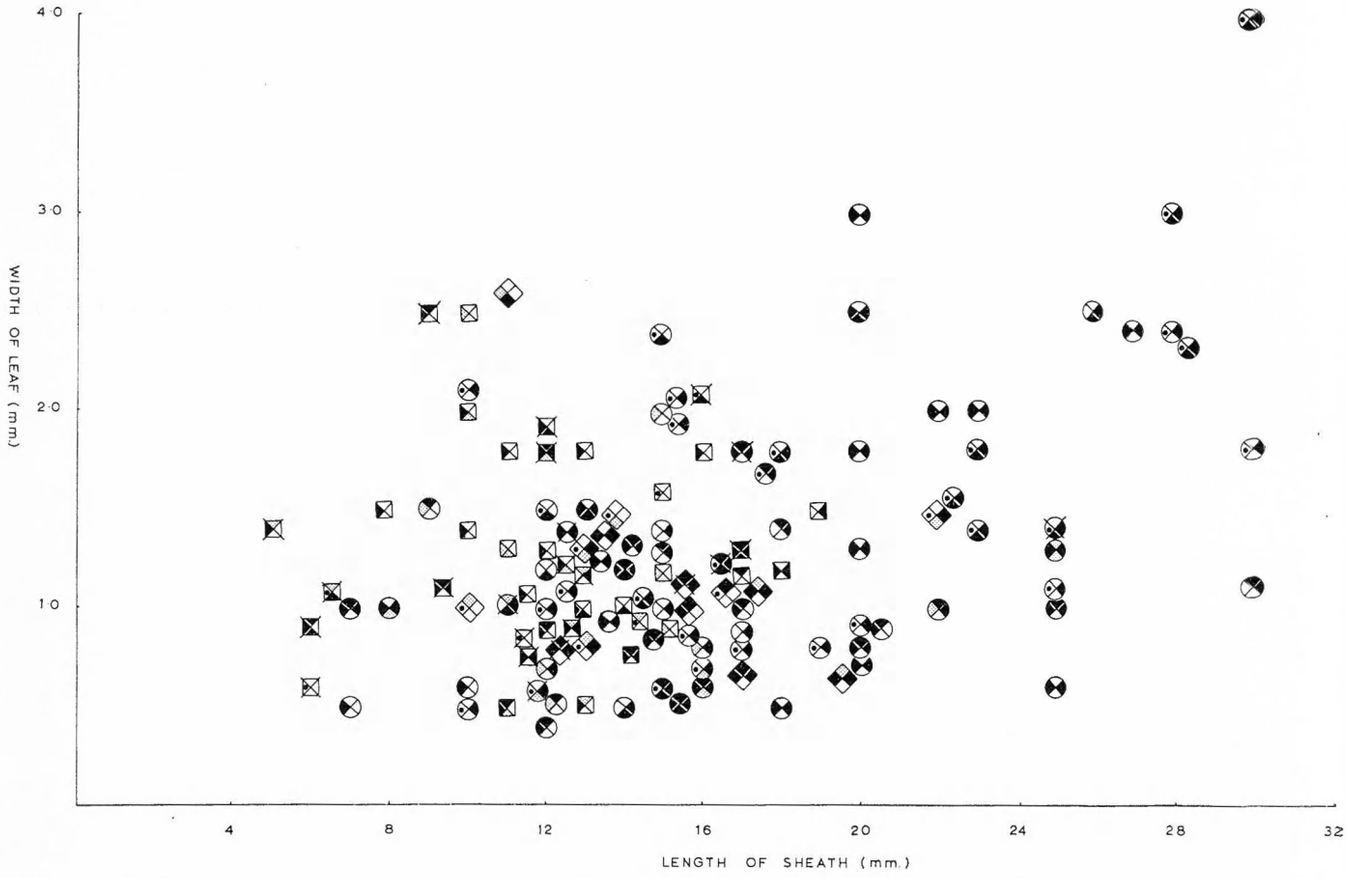


Fig. 2. Pictorialized scatter diagram showing correlation between 7 characters in samples of *Armeria maritima* from South America and the Northern Hemisphere. — Scape glabrous (○), pubescent (◇) or villous (□). — Leaf-indumentum ∨ (white=glabrous; dotted=sparsely ciliate; black=ciliate). — Scape length < (white=10 cm or less; black=more than 10 cm). — Calyx-insertion ∧ (white=ovate; dotted=truncate or obtuse; black=orbicular). Calyx-indumentum > (white=glabrous or subglabrous; dotted=with a few short hairs between ribs; black=completely hairy; white with black spot=hairs only on intermediate 'subcostae'). — Northern Hemisphere material designated by having the diagonal arms produced beyond the margin of the symbol.

likely to have intermediate nerves ('subcostae') present on the calyx. *A. chilensis* var. *magellanica* BOISS. seems to belong in this group.

The remaining small group of plants not yet mentioned are those which, having no scape, cannot be scored on scape-indumentum. There are so few of these available that it is not possible to determine the significance of their rather narrow, glabrous leaves and generally glabrous calyx. It seems probable, however, that they are merely occasional variants arising within the general pattern of variation exhibited for all other characters. *Armeria androsacea* BOISS. belongs in this group.

It seems clear from the data presented that there is no obvious correlation of characters which would give groupings recognizable as distinct species. As seen above, those species which have been recognized by earlier authors tend to be no more than occasional nodes in the general pattern of variation.

Interestingly, the Northern Hemisphere material included in these analyses generally tended to have a villous scape and it was with the group of Southern Hemisphere plants having this character that

their pattern of variation was most similar. The Northern Hemisphere plants tend to have a longer scape but they do not form a distinct group which is separable from the austral populations.

Geographical Distribution of Characters

In view of the lack of clearly correlated groups of characters within South American *Armeria* an attempt was made to plot on a map (Figs. 3—4) all the samples investigated, using the same symbols as in the scatter diagram (Fig. 2).

From Figs. 3 and 4 it is clear that some of the characters examined in this study show a marked geographical pattern. Thus, virtually all material from continental South America north of lat. c. 50°S., and all that from the Falkland Islands, has a glabrous scape. Plants with villous scapes predominate on Isla de los Estados and along the Canal Beagle, becoming less common northwards towards the Estrecho de Magallanes, and occurring only very rarely on the mainland north of the Straits. Material with an intermediate degree of scape-indumentum occupies a generally intermediate geographical area, being most common in central to northern Tierra del Fuego and the region immediately north of the Estrecho de Magallanes. Throughout this same area is also found the most intermingling of populations with villous and glabrous scape.

LEAF-INDUMENTUM. In the southern parts of Tierra del Fuego, Isla de los Estados and the Falkland Islands most plants have glabrous leaves. Further north all types occur, although pubescent or ciliate leaves predominate.

SCAPE-LENGTH. In southern Tierra del Fuego and on Isla de los Estados the majority of plants have a scape less than 150 mm long, whilst in the Falkland Islands and northwards from northern Tierra del Fuego most have a longer scape.

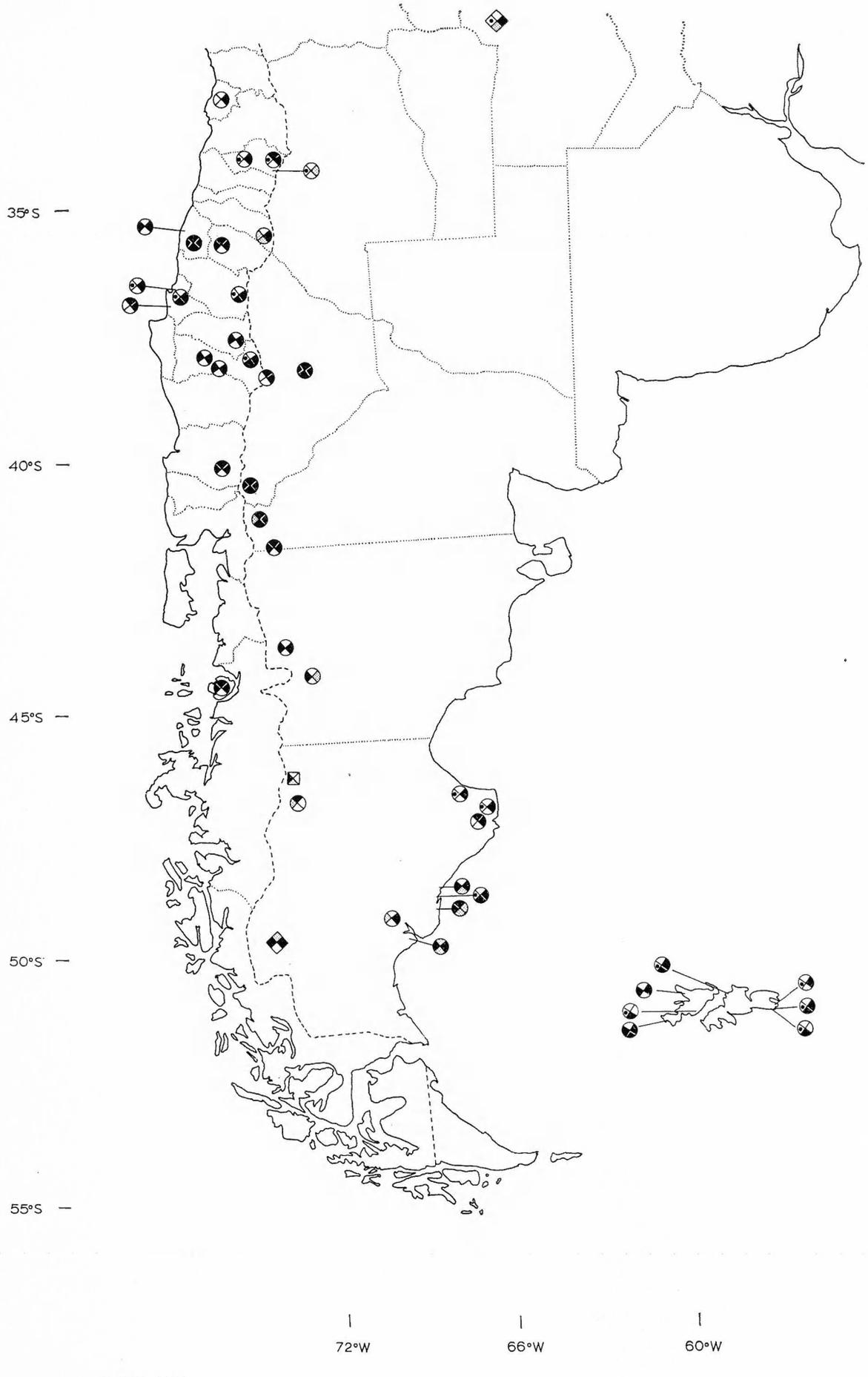
LEAF-WIDTH. This is a conspicuous character in the field, which is maintained in cultivation. The widest leaves are found in material from Central and North Chile (c. 0.9—2.0 mm) and particularly from the Falkland Islands (2.0—4.0 mm), while the narrowest leaves (0.3—1.0(—1.5)) mm occur in Patagonian populations from prov. Chubut to prov. Santa Cruz. In Tierra del Fuego and the region immediately north of the Estrecho de Magallanes there is great variation in leaf-width (0.4—2.5 mm). This shows no clear pattern, although there is some tendency for plants from the drier northern and eastern areas to have generally narrower leaves.

The distribution and density of the calyx-hairs, the shape of the calyx-insertion-scar and the length of the involucral sheath cannot be correlated with any features of the geographical distribution, although the longest sheaths occur in Falkland Islands material, which is also most likely to have the 5 intermediate nerves ('subcostae') on the calyx.

From the above observations it seems difficult to detect any convincing geographical pattern to the morphological variation. There are certainly general regional differences in the degree of expression of individual characters but these are never constantly correlated. The general pattern is rather that of uncorrelated clinal or semi-clinal variation, usually giving north—south differentiation, in some individual characters, and even more random variation in the other characters.

Taxonomic Status of South American Armeria

The absence of any constant correlation in the variation shown by the various morphological characters studied supports the unwillingness of many workers (e.g. DUSÉN 1900; SKOTTSBERG 1916; LAWRENCE 1940) to recognize the various species


35°S
40°S
45°S
50°S
55°S
72°W
66°W
60°W

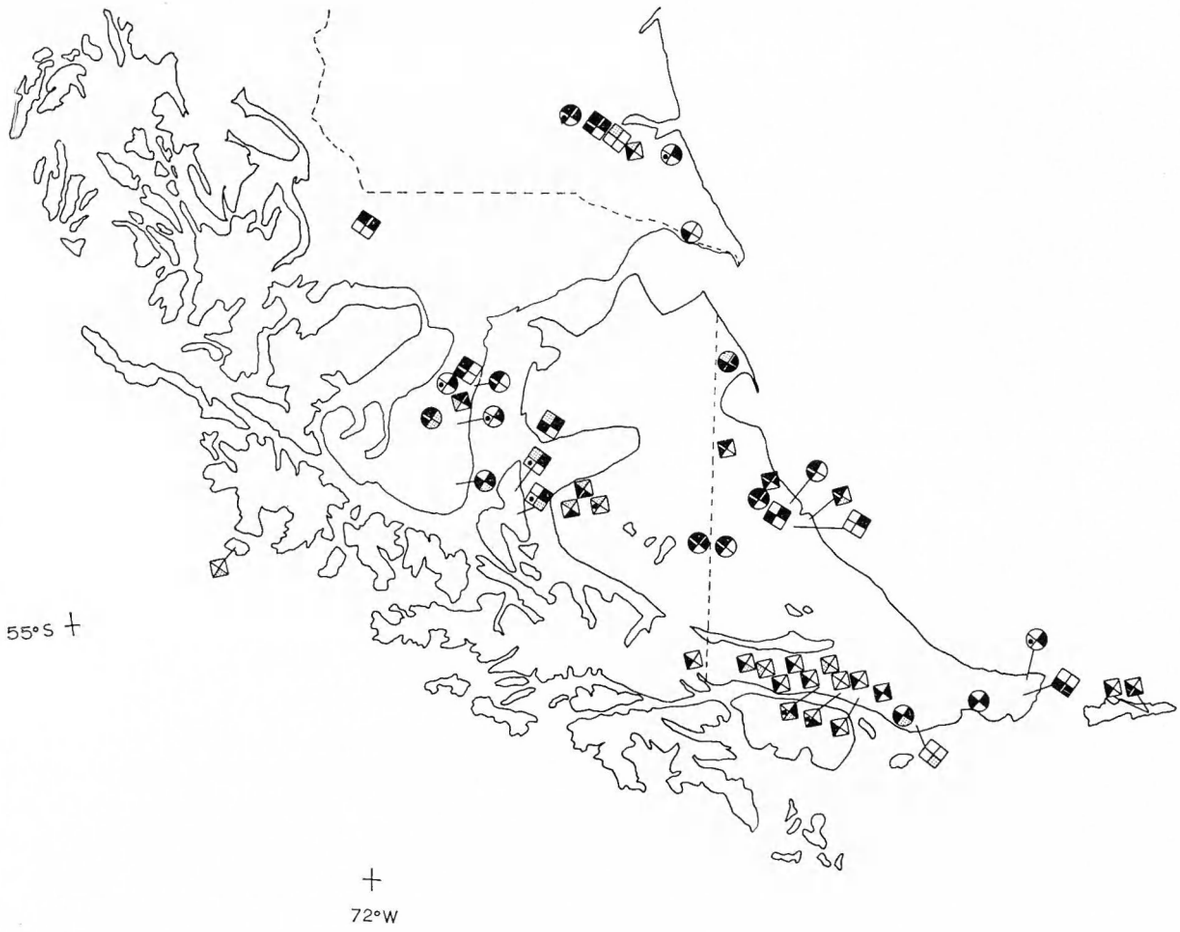


Fig. 4. Occurrence of 5 morphological characters in samples of *Armeria maritima* from Tierra del Fuego and southernmost Patagonia. Symbols as in Fig. 2.

which have been described from South America. It is equally clear from Fig. 2 and from a consideration of the expression of the characters studied that South American *Armeria* falls within the range of variation of *A. maritima* L. In consequence, two points must be considered: (a) the extent to which infra-specific categories can be recognized within South American *A. maritima;* (b) whether the austral populations are referable to the infra-specific taxa recognized in the Northern Hemisphere.

INFRA-SPECIFIC CATEGORIES IN SOUTH AMERICAN ARMERIA

Despite the wide geographical and ecological range shown by *Armeria maritima* in South America, and its extensive morphological variation, it has not proved possible to delimit infra-specific taxa in a satisfactory manner. The independent variation in several characters produces a large number of morphologically distinct entities, some of which have provided the basis for the taxa recognized by earlier workers. Clearly, although it might be appropriate to refer these taxa to varietal or even forma status, as has been done by SKOTTSBERG (1916) and LAWRENCE (1940), it seems impracticable to attempt to describe the large number of such entities which would be necessary to cover the range of morphological variants. In our present state of knowledge, such a procedure would be difficult,

Fig. 3. Geographical distribution of *Armeria maritima* showing occurrence of 5 morphological characters (Tierra del Fuego and adjacent mainland shown in Fig. 4). Symbols as in Fig. 2.

if not impossible, to carry out satisfactorily and we believe it would obscure whatever morphological patterns are currently shown. We are forced to the conclusion that at present satisfactory taxa cannot be delimited within South American material of *Armeria maritima* and that, consequently, it should be maintained as a single, very variable complex within which some clinal variation in certain characters can be discerned. Interestingly, this is almost exactly the conclusion reached by MATHIAS and CONSTANCE (1955) when considering the very widely distributed Andean species *Oreomyrrhis andicola* (KUNTH) HOOK. FIL., which shows a similarly wide variation.

AFFINITIES OF SOUTH AMERICAN AND NORTH HEMISPHERE ARMERIA MARITIMA

As mentioned earlier (p. 186) it can be seen from Fig. 2 that there is no consistent way of separating Northern and Southern Hemisphere material of *Armeria maritima* on the basis of the characters measured. Both groups of plants show a comparable range of variation and considerable overlap in all characters.

As noted earlier LAWRENCE (1940) separated the South American taxa from those in the Northern Hemisphere by the covering of minute pustular glands on their scapes. However, we have been unable to confirm this character during our examination of abundant Argentinian and Chilean material. In a number of cases we have found dense coverings of minute bodies but on close study these proved to be of fungal origin.

Armeria maritima in the Northern Hemisphere has been variously subdivided but most recent treatments (e.g. HULTÉN 1958; PINTO DA SILVA 1972) recognize up to about 7 subspecies in Eurasia, one in North America, and one common to both continents.

The major problem appears to be that the characters normally used to differentiate subspecies in Northern Hemisphere material of *Armeria maritima* show a somewhat continuous pattern of variation in South American plants which cannot be clearly separated. All the South American material is self-compatible, with monomorphic A/papillate pollen and stigma types, and consequently can be distinguished on this character from most Eurasiatic taxa, resembling only the circumboreal subsp. *sibirica,* and the North American subsp. *purpurea* and *californica.*

Even within these limits it is not possible to provide a satisfactory separation of the Southern Hemisphere populations, which overlap with, and show a greater variation than, the self-compatible populations from the north.

Here, then, one is faced with the problem of how to deal taxonomically with the South American populations of *Armeria.* They clearly belong to *A. maritima,* but cannot be satisfactorily distinguished morphologically from the northern subspecies, nor can they be assigned as varieties within any of the latter.

It seems clear that the closest relationships of the South American populations of *Armeria maritima* are with the monomorphic North American and circumboreal subspecies, which were in their turn derived from the Eurasiatic dimorphically self-incompatible populations (BAKER 1953, etc.). However, whilst the variability in these has been restricted by a combination of severe selection pressure, limited ecological tolerances and inbreeding (BAKER 1953), the South American populations seem to have escaped the limitations of the first two factors and the species is much more variable in Argentina and Chile than might be expected from experience with Northern Hemisphere self-compatible populations.

Armeria maritima in South America would appear to have a very different evolutionary potential from the Northern Hemisphere self-compatible taxa. Despite the lack of clear morphological differences this, together with the clear geo-

graphical separation and the impossibility of incorporating them into the subspecific classification in the Northern Hemisphere, leads us to believe that the only possible solution at present is to include the South American populations in *A. maritima* as a distinct subspecies. This being the case, it is necessary to select a subspecific epithet. The first names to be applied at this level to South American material were *A. chilensis* subsp. *andina* and *macloviana* (REICHE 1911). Of these two we select the former epithet and the formal combination required is as follows:

Armeria maritima subsp. **andina** (POEPP. ex BOISS.) D. M. MOORE & YATES comb. nov.

A. chilensis BOISS. subsp. *andina* (POEPP. ex BOISS.) REICHE, Fl. Chile 6: 104 (1911).
A. andina POEPP. ex BOISS. in DC., Prodr. 12: 682 (1848).
A. macloviana CHAM., Linnaea 6: 567 (1831).
A. curvifolia BERT., Merc. Chil.: 563 (1830).
A. chilensis BOISS. in DC., Prodr. 12: 681 (1848).
A. androsacea BOISS. in DC., Prodr. 12: 679 (1848).
A. brachyphylla BOISS. in DC., Prodr. 12: 682 (1848).
A. delfini PHIL., Anal. Univ. Chile. Stgo 91: 246 (1895).
A. tenuifolia PHIL., op. cit. 245 (1895).
A. patagonica PHIL., op. cit. 244 (1895).
A. exaristata PHIL., op. cit. 245 (1895).
A. aegialea PHIL., op. cit. 246 (1895).
A. bella ALBOFF, Rev. Mus. La Plata 7: 385 (1896).
Statice punicea RENDLE, J. Bot. 42: 369 (1904).
Armeria chilensis BOISS. ssp. *macloviana* (CHAM.) REICHE, Fl. Chile 6: 104 (1911).

CONCLUSIONS

The variation seen within South American *Armeria,* in which some characters tend to exhibit often uncorrelated clinal patterns and others vary in a more random fashion, is not uncommon. Indeed, such cases often parallel that in *Armeria,* with numerous taxa being initially described on the basis of scattered collections and later studies on more abundant material revealing a complex pattern of variation within which formal infra-specific categories cannot usefully be delimited.

The work described in this paper also demonstrates the often overlooked limitations of even the major infra-specific categories. Although there is no doubt that the South American *Armeria* belongs in *A. maritima,* and that its geographical separation from the rest of the species is allied to a different pattern of variation, it cannot be clearly and consistently distinguished morphologically from the taxa widely recognized in the Northern Hemisphere. In consequence, it is necessary either to adopt the procedure followed here in order to refer readily to the evolutionary distinct *A. maritima* subsp. *andina* or to abandon the characters of proven taxonomic value throughout most of the species' range in the hope that new features might allow the uniform application of a morphological subspecies concept to the species in both Northern and Southern Hemispheres. In the present state of knowledge we feel it most practicable to adopt the first alternative and draw attention to the need for much more information before it can be seen whether the second alternative is attainable in this and other cases.

ACKNOWLEDGEMENTS

This paper has arisen out of studies on the flora of Tierra del Fuego under a programme supported by the Natural Environment Research Council, to whom we are deeply indebted. We are grateful to the directors of the following herbaria for the opportunity to examine material in their care: British Museum (Natural History), London; Royal Botanic Gardens, Kew; Department of Botany, University of Leicester; Musée National d'Histoire Naturelle, Paris; University Institute of Systematic Botany, Uppsala. Mrs. F. BARNARDO kindly prepared the illustrations.

LITERATURE CITED

BAKER, H. G. 1948. Dimorphism and monomorphism in the Plumbaginaceae. I. A survey of the family. — Ann. Bot., N.S. 12: 207—219.

— 1953. Race-formation and reproductive method in flowering plants. — Symp. Soc. Exp. Biol. 7: 114—143.
— 1954. Dimorphism and incompatibility in the Plumbaginaceae. — Rapp. Comm. 8ème Congr. Int. Bot., Paris, Sect. 10: 133—134.
— 1961. Rapid speciation in relation to changes in the breeding system of plants. — In: Recent Advances in Botany, pp. 881—885. — Toronto.
— 1966. The evolution, functioning and breakdown of heteromorphic incompatibility systems. I. The Plumbaginaceae. — Evolution 20: 349—368.
DUSÉN, P. 1900. Die Gefässpflanzen der Magellansländer. — Sv. Exped. Magellansländer 3 (5): 77—266.
HULTÉN, E. 1958. The amphi-Atlantic plants and their phytogeographical connections. — K. Svenska Vetenskapsakad. Handl., Ser. 4 (7).
LAWRENCE, G. H. M. 1940. Armerias, native and cultivated. — Gentes Herbarum 4: 391—418.
MATHIAS, M. E. & CONSTANCE, L. 1955. The genus Oreomyrrhis (Umbelliferae). — Univ. Calif. Publs. Bot. 27: 347—416.
MOORE, D. M. 1968. The vascular flora of the Falkland Islands. — Brit. Antarct. Survey Sc. Rep. 60: 1—202.
PINTO DA SILVA, A. R. 1972. Armeria. — In: T. G. TUTIN, V. H. HEYWOOD, A. BURGES, D. M. MOORE, S. M. WALTERS and D. A. WEBB (eds.): Flora Europaea 3, pp. 30—38. — Cambridge.
SKOTTSBERG, C. J. F. 1916. Die Vegetationsverhältnisse längs der Cordillera de los Andes S. von 41°S. — K. Svenska Vetenskapsakad. Handl. 56 (3).

Embryology of Cynoglossum denticulatum DC.

Tasneem Fathima Khaleel

KHALEEL, T. F. 1974 09 13. Embryology of Cynoglossum denticulatum DC. — Bot. Notiser 127: 193—210. Lund. ISSN 0006-8195.

The anthers are tetrasporangiate. The anther wall develops according to the Dicotyledonous type. The tapetum is of the secretory type and its cells remain uninucleate. The microspore tetrads are of tetrahedral and decussate types. The pollen grains are dumb-bell-shaped and shed at the three-celled stage.

The ovules are anatropous with their micropyles facing the placenta. The development of the megagametophyte is according to the Polygonum type.

A tendency towards nucellar apospory has been observed. The aposporic embryo sacs rarely reach maturity.

The endosperm is of an aberrant type and does not conform to any of the deviations reported earlier in this family. It has thus been named the Cynoglossum type. The proembryonal tetrad is linear and the development of the embryo conforms to the Chenopodiad type. Rarely two embryos are seen. The pericarp shows glochidiate spinescent outgrowths. The seed coat is undifferentiated.

Tasneem Fathima Khaleel, Department of Biology, Immaculata College, Immaculata Pa 19345, U.S.A.

INTRODUCTION

GÜRKE (1897) recognized four subfamilies in the Boraginaceae, viz. Cordioideae, Ehretioideae, Heliotropioideae and Boraginoideae. The Boraginoideae are considered to be the most highly evolved, both anatomically and morphologically (LAWRENCE 1937). A review of the embryological literature on this sub-family reveals that the Boraginoideae are equally diversified and heterogeneous (FATHIMA 1969).

The genus *Cynoglossum* belonging to this sub-family, which includes about 60 species, is the most wide-spread in tropical, subtropical and temperate areas (GÜRKE 1897). In South India, it is represented by two species, viz. *C. furcatum* and *C. denticulatum* (GAMBLE 1928). The present investigation deals with the embryology of *C. denticulatum* DC. It is a part of the thesis approved by the Bangalore University for the award of a Ph. D. degree.

MATERIAL AND METHODS

Young flower buds, flowers and fruits at various stages of development were collected from round Bangalore and Bannerghatta, Mysore State, India, and fixed in formalin-acetic-alcohol. The material was infiltrated, embedded and microtomed at 5—20 μ. The sections were stained with Heidenhein's iron alum haematoxylin or Delafield's haematoxylin with fast green, orange G or eosin as counter stains. 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 strand.

OBSERVATIONS

Cynoglossum denticulatum is an erect branched herb reaching about two feet in height and flowering from March to June. The stem is woody and slightly angular with strigose villous hairs, usually with bulbous bases. The leaves are alternate and lanceolate with a thick coat of prickly hairs on the surface. The terminal leaves are almost sessile. The

inflorescence shows many branches and the flowers are arranged on long slender racemes.

Flower

The flowers are hypogynous, hermaphrodite and actinomorphic. The calyx consists of five lobes that are persistent and spread in the fruit; their outer surfaces are hairy. The corolla is pale blue in colour and consists of five imbricately aestivated petals that unite to form a corolla tube; it shows five scales at the throat. The lobes are obtuse and free above. The stamens are five in number and are inserted on the corolla tube. The filaments are short and the anthers are ovate. The gynoecium consists of a superior, bicarpellary, bilocular and syncarpous ovary which becomes quadrilocular due to the development of a false septum enclosing a single ovule in each locule. The style is gynobasic and the stigma is simple. The fruit is a depressed pyramid of four nutlets adnate to the conic-based carpophore; the nutlets are covered with glochidiate outgrowths.

The floral parts, viz., the sepals, the petals, the stamens and the carpels develop in acropetal succession.

Microsporogenesis and the Development of the Anther

Cynoglossum denticulatum is protandrous. A cross-section of a young anther shows the four-lobed condition with homogeneous cells that are bound by an epidermis. A plate of four to five archesporial cells becomes recognizable in each lobe due to their dense contents and prominent nuclei. The archesporial initials undergo periclinal divisions to form an outer layer of parietal cells and an inner layer of primary sporogenous cells (Fig. 1 A, B). The cells of the primary parietal layer undergo further divisions, both periclinal and anticlinal, and result in three layers of cells (Fig. 1 C). Thus the anther wall develops according to the Dicotyledonous type (Davis 1966) and consists of four layers of cells, viz. the epidermis, the endothecium, the middle layer and the tapetum (Fig. 1 D). The tapetum is of the secretory type and its cells are highly vacuolated and enlarged. They remain uninucleate throughout (Fig. 1 D—F, H, I, M, N). The tapetum is completely consumed during the development of the anther. A number of starch grains are found lining the inner walls of the locule and also in the tapetal cells (Fig. 1 M, N).

The endothecial cells are radially and tangentially elongated. They develop fibrillar bands of thickenings extending from their inner tangential walls, at about the time when the microspores are formed (Fig. 1 M, N). The single middle layer disintegrates during the course of development (Fig. 1 F, H, I, M).

Simultaneous with these changes the primary sporogenous cells divide further and ultimately form a group of microsporocytes (Fig. 1 B—E). The microsporocytes become rounded off before they divide meiotically (Fig. 1 E—G). The divisions are simultaneous and result in decussately and tetrahedrally arranged microspore tetrads (Fig. 1 H, I). They are enclosed by the mother wall which disorganizes before the microspore nucleus divides.

The microspores separate and develop thick walls. They become slightly elongated and dumb-bell-shaped with a median constriction (Fig. 1 J—L). The two germ pores are situated at the region of constriction. The microspore nucleus usually lies towards one side of the constricted region and sometimes in the region of constriction itself. A generative cell and a vegetative cell are formed after its division (Fig. 1 K). The generative cell divides and forms the two male cells. It is at this stage that the pollen grains are shed.

Each pollen grain measures about 7—8 $\times$3—4 μ and possesses a smooth exine.

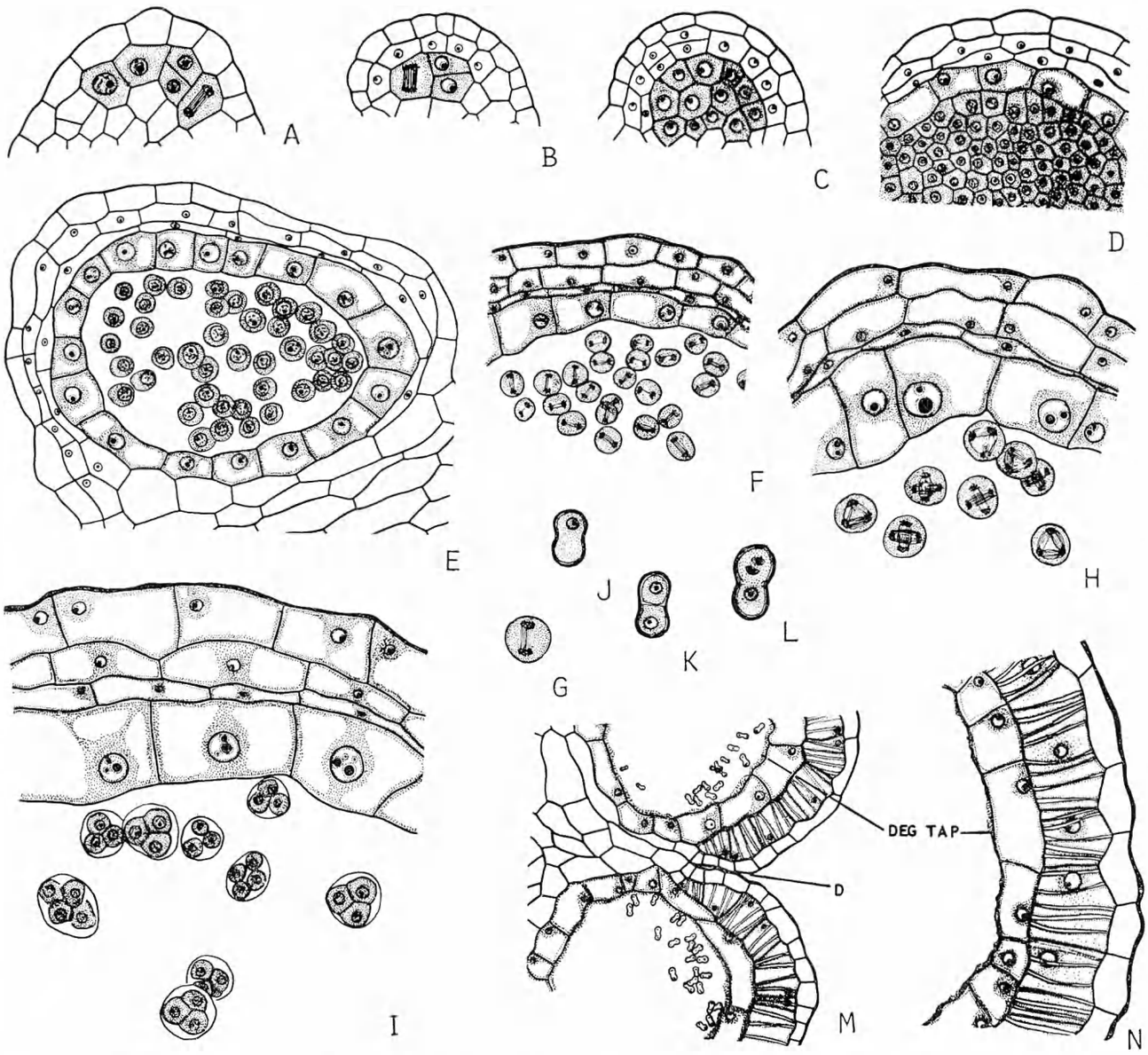


Fig. 1. Microsporogenesis and the development of anthers in *Cynoglossum denticulatum* DC. — A—D: T.S. anther lobe showing successive stages in the development of anther wall and the sporogenous tissue. — E: T.S. anther lobe showing epidermis, endothecium, middle layer, tapetal cells and microsporocytes. — F: T.S. anther lobe showing meiosis I in microsporocytes. — G: Meiosis I. — H: Meiosis II. — I: Microspore tetrads. — J—L: One-, two- and three-celled pollen grains. — M: T.S. portion of the anther showing the region of dehiscence. — N: T.S. portion of the anther wall showing epidermis, fibrillar endothecium and degenerating tapetum. — D, region of dehiscence; DEG TAP, degenerating tapetum. — A—F, H, N ×310. G, I—L ×620. M ×250.

Dehiscence of the anther occurs at the region between the two adjacent locules (Fig. 1 M). Each locule opens out independently. The endothecial cells at this region are without the fibrillar thickenings and the epidermal cells are also smaller.

Megasporogenesis and the Development of the Megagametophyte

The ovules are anatropous and due to the presence of a gynobase, they are deeply seated in the locules. The funiculus is long and the ovules are bent in such

a way that the micropyles of all the four ovules face the placenta. They are unitegminal and tenuinucellar, the integument being very massive. The ovules arise as small globular protuberances from the placenta. A rostrum-like projection is found near the micropyle and it extends up to the style. A single vascular strand enters the funiculus and branches in the integument; the branches run close to the outer epidermis of the integument (Fig. 2 J).

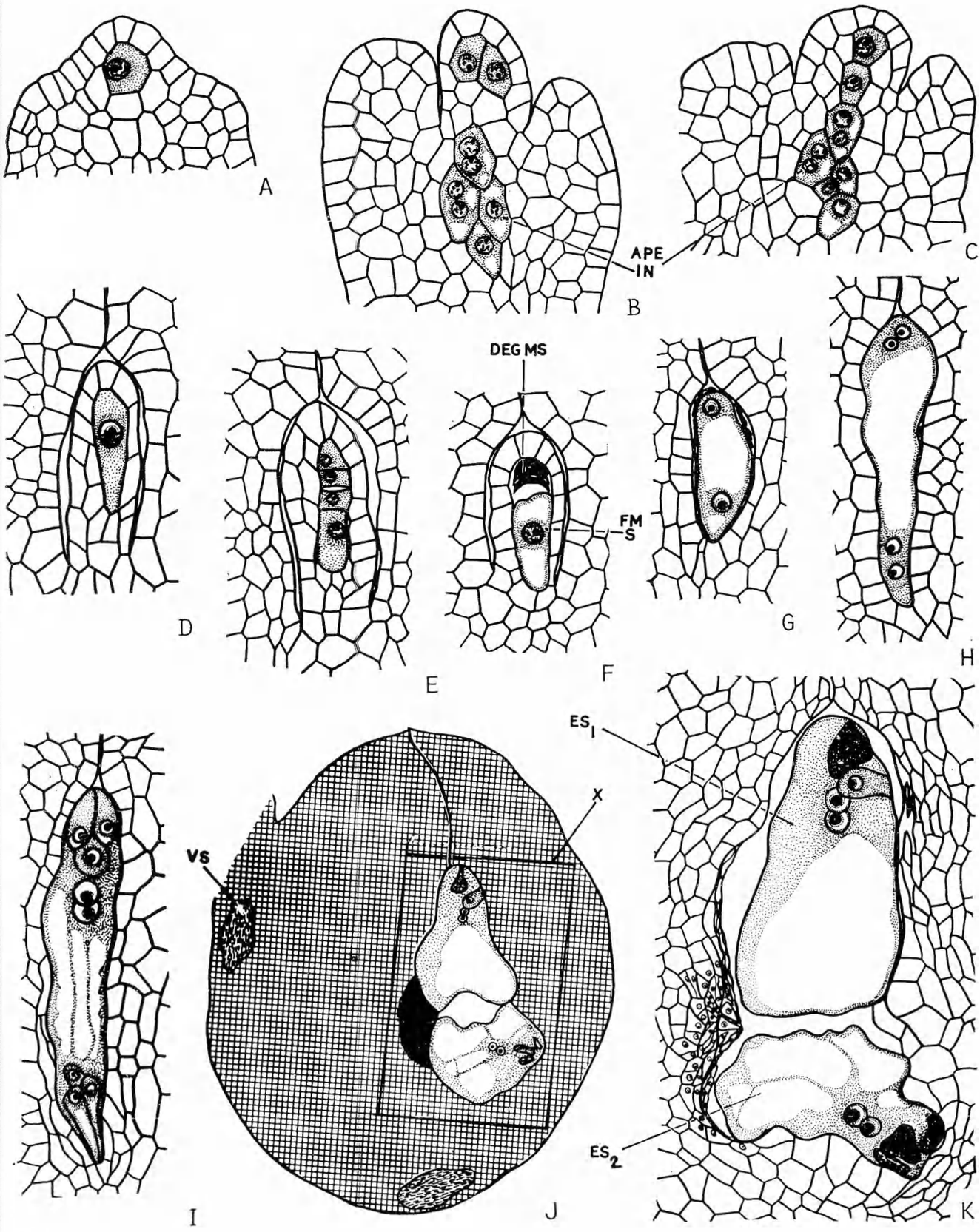
A single hypodermal archesporial initial differentiates in the nucellar dome much earlier than the initiation of the integument. It shows a conspicuous nucleus and dense cytoplasm (Fig. 2 A). Occasionally the archesporium is two-celled but only one of the cells develops further (Fig. 2 B). The functional archesporial cell enlarges and becomes the megasporocyte (Fig. 2 D). The megasporocyte undergoes meiotic divisions forming a linear megaspore tetrad (Fig. 2 E). The chalazal megaspore is larger than the other three and develops further while the three micropylar ones degenerate (Fig. 2 F). The functional megaspore enlarges and its nucleus undergoes mitosis to form a two-nucleate megagametophyte (Fig. 2 G). The two nuclei are pushed to opposite poles by the appearance of a central vacuole; there they divide to form a four-nucleate gametophyte (Fig. 2 H). At about this time, the cells of the nucellar epidermis disorganize and the surrounding nucellar cells also become crushed and degenerate. The gametophyte comes into direct contact with the innermost layer of the integument. The four-nucleate gametophyte forms the eight-nucleate gametophyte by one more nuclear division. Of the eight nuclei formed, in the micropylar region, three of them organize themselves into an egg apparatus which consists of a pair of rounded synergids and a densely cytoplasmic egg; likewise, in the chalazal region, three antipodal cells are formed. The antipodals degenerate before fertilization. The two polar nuclei lie near the egg apparatus, and fuse either during or after fertilization. Therefore the development of the gametophyte corresponds to the Polygonum type (MAHESHWARI 1950). A mature megagametophyte is longitudinally stretched; it is broader at the micropylar end and narrower at the chalazal end (Fig. 2 I).

A tendency towards nucellar apospory has been observed in this species. The aposporic embryo sac initials are four to five in number and are differentiated just below the archesporial cells. They show prominent nuclei and high vacuolation. They become binucleate and simulate two-nucleate megagametophytes (Fig. 2 B, C). However, they generally degenerate as the normal gametophyte enlarges. Rarely, one of the initials develops further along with the functional megaspore, so that a normal gametophyte and an aposporic embryo sac lie superposed in the same ovule (Fig. 2 J, K). The aposporic embryo sac degenerates after reaching the eight-nucleate condition.

Fertilization

Fertilization is porogamous. The integumentary rostrum is helpful in guiding the pollen tube to the micropyle and shortening the distance for it. One synergid is destroyed and the other persists for some time. The remnants of the pollen tube and the degenerating synergids are seen till the early stages of the endosperm development (Fig. 3 A, E). After fertilization the gametophyte enlarges considerably and the chalazal region becomes broader at about the time the first division of the

Fig. 2. Megasporogenesis and the development of the megagametophyte in *Cynoglossum denticulatum* DC. — A: L.S. nucellus showing a single archesporial initial. — B—C: L.S. nucellus showing two archesporial cells and aposporic embryo sac initials. — D: L.S. nucellus showing megasporocyte. — E: L.S. nucellus showing a linear tetrad of megaspores. — F: L.S. nucellus showing the functional megaspore and the three degenerating



ones. — G—I: Two-, four- and eight-nucleate megagametophytes. — J: L.S. ovule showing a normal megagametophyte and an aposporic embryo sac. — K: Portion marked 'x' in J enlarged. — APE IN, aposporic embryo sac initials; DEG MS, degenerating megaspores; FMS, functional megaspore; ES_1, normal megagametophyte; ES_2, aposporic embryo sac; VS, vascular strand. — A—I, K ×310. J ×135.

primary endosperm nucleus takes place (Fig. 3 A). The micropylar region of the gametophyte remains narrow.

A hypostase is formed by a few cells underlying the chalazal end of the gametophyte after fertilization. They show dense contents and thickened walls. The hypostase is persistent till the later stage of embryogeny (Fig. 3 A—G), and ultimately disorganizes along with the cells of the integument.

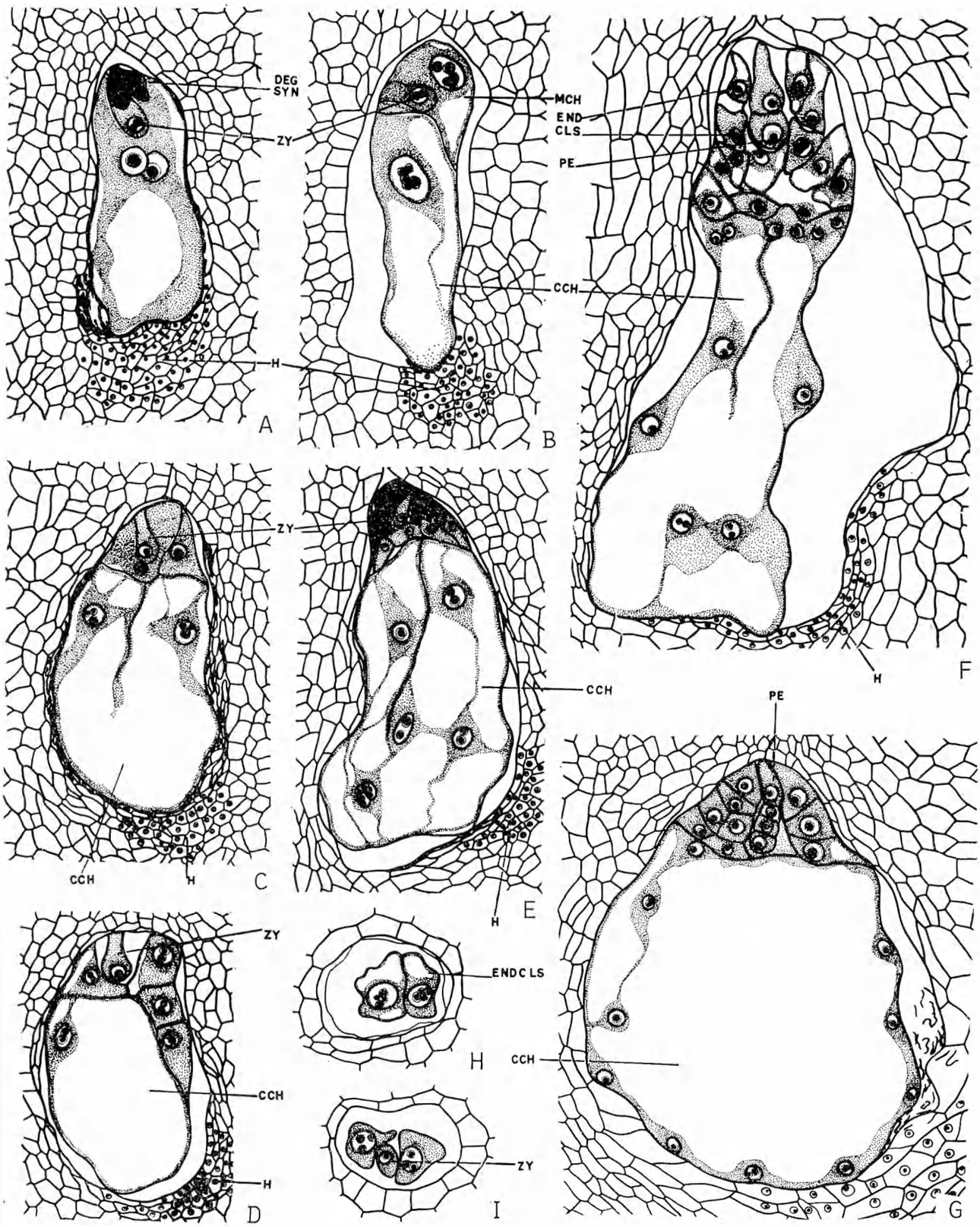
Endosperm

The development of the endosperm is of an aberrant type. The primary endosperm nucleus is generally found near the egg and its first division is accompanied by a transverse wall (Fig. 3 B). Of the two chambers formed, the chalazal chamber is almost double the size of the micropylar one. Occasionally the primary endosperm nucleus divides by an oblique wall (Fig. 3 B); in either case, the resultant cells are of unequal size; the micropylar one being invariably smaller. The next division in the micropylar chamber is accompanied by a vertical or an oblique wall (Fig. 3 C). The chalazal chamber also divides vertically, but the wall is incomplete and reaches only half the length of the cavity and ends blindly, dividing the chamber into two incomplete cells which open at the base and partially communicate with each other (Fig. 3 C). This wall disappears during the enlargement of the embryo sac. Further divisions in the micropylar chamber are always accompanied by wall formation while in the chalazal chamber they are only free-nuclear (Fig. 3 D—G; Fig. 4 A, B, D—F). There is a large central vacuole in the chalazal chamber and the nuclei are restricted to the periphery of the vacuole (Fig. 3 G). The micropylar chamber abuts upon the chalazal chamber like a mantle (Fig. 3 F, G; Fig. 4 A). The cells in the micropylar region are densely cytoplasmic and show conspicuous darkly staining nuclei (Fig. 3 H, I). The cells surrounding the zygote are elongated and simulate the zygote and the two-celled proembryo (Fig. 3 F). Even after a massive endospermal tissue has formed in the micropylar region the chalazal region shows very few nuclei (Fig. 3 D, G). Cell organization in this region takes place only at the dicot stage of the embryo (Fig. 4 C).

Embryogeny

The zygote enlarges and divides only after a group of endospermal cells has been formed (Fig. 5 A). The first division of the zygote results in a terminal cell *ca* and a basal cell *cb*. The basal cell *cb* is larger than the terminal cell *ca* and tapers towards the micropyle (Fig. 5 B). The second division in both the cells is transverse and a linear proembryonal tetrad results (Fig. 5 C), the cells of which are designated *l*, *l'* from the terminal cell *ca* and *m* and *ci* as the derivatives of the basal cell *cb*. The cells *l*, *l'* and *m* undergo vertical division (Fig. 5 E—J). The next division in these cells is also vertical but at right angles to the previous one so that each tier consists of four cells (Fig. 5 K). Periclinal divisions in these cells delimit the dermatogen (Fig. 5 L). Periblem and plerome are likewise formed by one more periclinal division (Fig. 5 M—O). The derivatives of tier *l* form the stem tip and the cotyledons and those of *l'* give rise to part of the hypocotyl. The derivatives of *m* contribute towards the remaining part

Fig. 3. Development of endosperm in *Cynoglossum denticulatum* DC. — A: L.S. ovule showing the zygote, degenerating synergids and hypostase. — B: L.S. ovule showing the zygote, hypostase and two-celled endosperm. — C: L.S. ovule showing the four-celled endosperm with incomplete wall formation. — D: L.S. ovule showing four-celled endosperm in the micropylar region and uninucleate chalazal chamber. — E: L.S. ovule showing multicellular endosperm in the micropylar region and six nuclei in the chalazal chamber with the incomplete wall. — F: L.S. ovule showing two-celled proembryo, hypostase,



multicellular endosperm in the micropylar region and multinucleate chalazal chamber with the incomplete wall. — G: L.S. ovule showing the proembryonal tetrad, multinucellar endosperm in the micropylar region and free nuclear endosperm in the chalazal region. — H, I: T.S. ovule showing two-celled endosperm at the micropylar region. — CCH, chalazal chamber; END CLS, endosperm cells; DEG SYN, degenerating synergids; H, hypostase; MCH, micropylar chamber; PE, proembryo and proembryonal tetrad; ZY, zygote. — A—C, H, I ×310. D—G ×250.

of the hypocotyl, the initials of the central cylinder of the root and the stem (Fig. 5 P, Q).

Meanwhile, the cell *ci* divides by a transverse wall resulting in *n* and *n'* (Fig. 5 D). The cell *n* undergoes a vertical division to form the root-cap; the cell *n'* forms *o* and *p* by a transverse division. The derivatives of these cells form a short suspensor of four to five cells (Fig. 5 O, P). Occasionally the suspensor cells become binucleate (Fig. 5 O). The suspensor degenerates as the embryo reaches maturity. Thus the development of the embryo corresponds to the Chenopodiad type (JOHANSEN 1950), with the embryonic formula:

$$ca = pco + pvt + \frac{1}{2}phy$$

$$ca = \frac{1}{2}phy + icc + iec + co + s.$$

Occasionally two embryos are developed in the same seed. The position of the additional embryo suggests that it can arise from the persistent synergid (Fig. 5 R, S).

Pericarp

The ovary wall is smooth and consists of undifferentiated cells before fertilization (Fig. 6 A). Later the pericarp differentiates into three zones, viz., the endocarp, the mesocarp and the epicarp.

The ovary wall consists of about eight to nine layers of parenchymatous cells before fertilization. The vascular strand traverses in the centre of these cells. After fertilization the cells of the inner epidermis become highly lignified along their inner and lateral walls and constitute the endocarp (Fig. 7 D—F). The mesocarp consists of parenchymatous cells (Fig. 7 C). The epicarp consists of the epidermis only with the glochidiate outgrowths. The cells of the epidermis become highly thickened and radially elongated. Small spinescent papillae arise on the thickened portions (Fig. 7 A—C). Some of the epidermal cells enlarge here and there and form the initials for glochidiate outgrowths which are always in pairs (Fig. 6 B). These initials enlarge further along with the neighbouring epidermal cells so that they appear as small knobs (Fig. 6 C, D). The cells of the mesocarp intrude into these knobs and elongate tangentially (Fig. 6 E). The rest of the epidermal cells become continuous with the cells lining the outgrowth. The glochidiate outgrowths are not supplied with vasculature (Fig. 6 F, G). The two terminal cells of the glochidiate outgrowths become spinescent and the epidermal cells lining the glochidiate outgrowth become highly thickened like the other cells of the epicarp (Fig. 6 F).

Seed Coat

The ovoid seed has an undifferentiated seed coat during the early stages of development. In a mature seed the seed coat is thin and papery.

The integument consists of about 18—19 layers of cells at the mature megagametophyte stage. The cells of the integument start breaking down immediately after fertilization and continue to do so till the later stages of endosperm and embryo development leaving only five to six layers in the mature seed (Fig. 4 G). Thus the testa of a mature seed consists of five to six layers of cells with the vascular strand which runs close to the epidermis (Fig. 4 A, E; Fig. 7 C). The seeds are not released from the nutlet, instead, the nutlets are dispersed as such.

DISCUSSION

The occurrence of abnormal gynoecia is a common feature in Boraginaceae. In *Cerinthe* (SVENSSON 1925), where the ovary is two-lobed, a false septum never appears, instead, there is a folding of the rachis of the carpel which grows and gets separated by a thin spongy layer, making each lobe two-celled. Abnormal gynoecia consisting of three carpels with

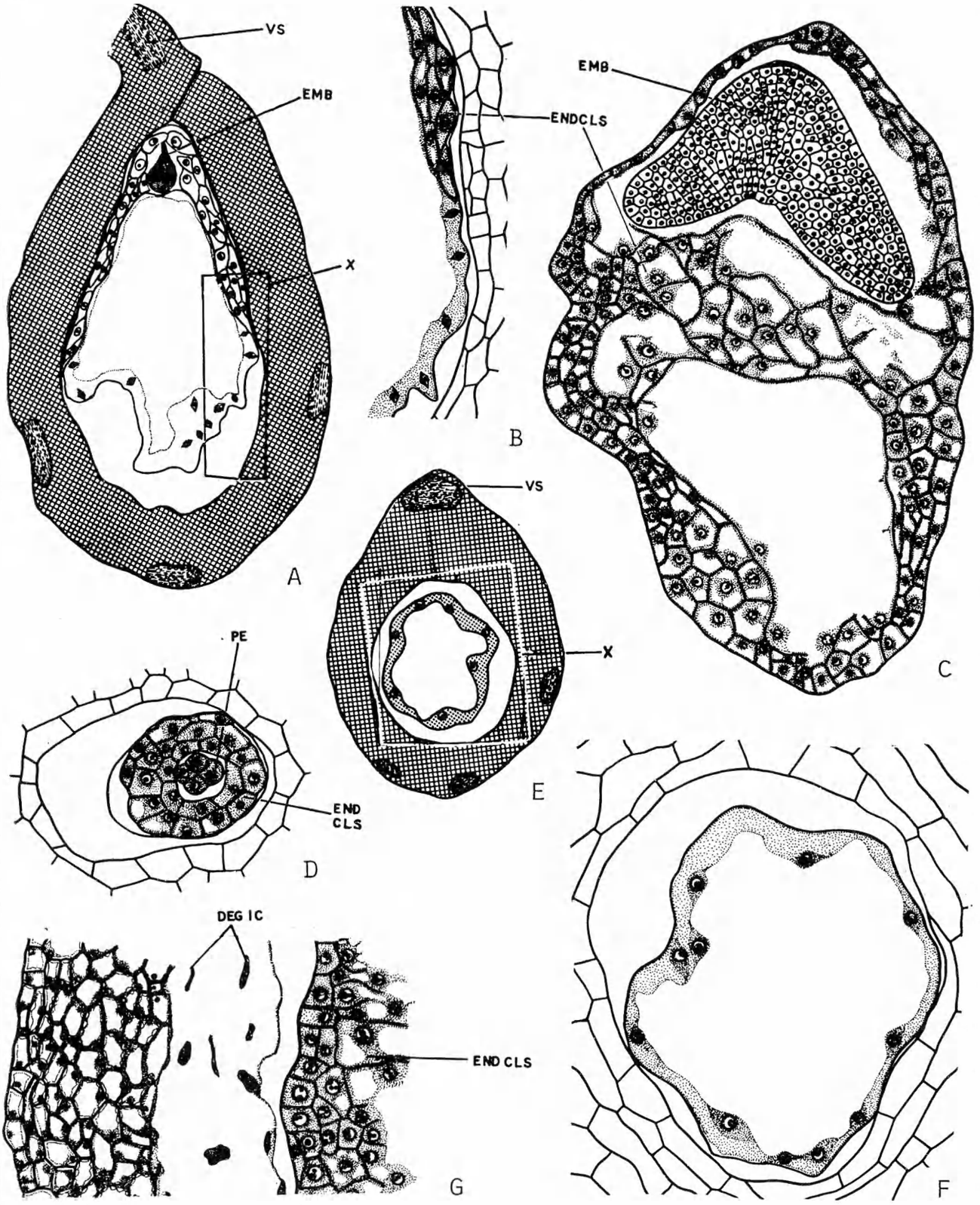


Fig. 4. Development of endosperm and seed coat in *Cynoglossum denticulatum* DC. — A: L.S. seed showing the cellular endosperm in the micropylar region and free-nuclear divisions in the chalazal region. — B: Portion marked 'x' in A enlarged. — C: L.S. seed showing mature embryo and endosperm. — D: T.S. seed in the micropylar region showing cellular endosperm. — E: T.S. seed in the chalazal region. — F: Portion marked 'x' in E enlarged to show the free nuclear endosperm. — G: L.S. portion of the seed showing the degenerating integument cells and endosperm. — END CLS, endosperm cells; DEG IC, degenerating integument cells; EMB, embryo; PE, proembryo; VS, vascular strand. — A, C, E ×135. B, D, F, G ×310.

six ovules, instead of the usual two carpels with four ovules have been reported in *Lindelofia longiflora, Cynoglossum officinale* (SVENSSON 1925) and *C. amabile* (MILLSAPS 1940). MILLSAPS (1940) is of the opinion that such a condition is indicative of a trifoliate origin. Sometimes, two well-developed carpels have been reported in a common envelope in *Symphytum tuberosum* (SVENSSON 1925). Occasionally, pistils producing five to six nutlets have been observed in *Mertensia paniculata* (KHANNA 1964 b). However, abnormal gynoecia have not been observed in *Cynoglossum denticulatum.*

Most of the Boraginoideae are characterized by a gynobasic style. *Cynoglossum* exhibits the gynobasic condition to the maximum extent. The occurrence of a gynobasic condition directly affects the nature and location of the ovules in the ovary, as a result of which the ovules are shifted to the base of the cavity. Consequently the funiculus becomes longer and the ovules make a complete turn to face the vertical axis of the carpel. The micropyle of the four ovules is turned upwards towards the placenta. This shifting of the ovules to the base of the cavity enables the pollen tube to reach the ovules more easily. In addition to this, the ovules also develop an integumentary rostrum which extends over the transmitting tissue of the style and shortens the distance for the pollen tube.

The development of the anther wall corresponds to the Dicotyledonous type (DAVIS 1966) in all the members including the present species. The tapetum is of the secretory type. The number of nuclei in the tapetal cells shows considerable variation. In most of members they are multinucleate. However, in *Cynoglossum amabile* (MILLSAPS 1940) and *Adelocaryum coelestinum* (NAGARAJ & FATHIMA 1968) the tapetal cells remain uninucleate throughout. In *Mertensia platyphylla* (KHANNA 1964 b), the tapetal cells are uninucleate at first but become multinucleate in the later stages. However, the uninucleate condition is restored due to the fusion of the nuclei to form one large polyploid nucleus in each cell. The tapetal cells are uninucleate in *C. denticulatum* as in *C. amabile* (MILLSAPS 1940) and *Adelocaryum coelestinum* (NAGARAJ & FATHIMA 1968).

The microsporocytes remain intact and are not separated till the formation of the tetrads in *Cynoglossum amabile* (MILLSAPS 1940). In *Mertensia platyphylla* and *Trichodesma amplexicaule* (KHANNA 1964 a, b) also the microsporocytes remain intact during meiosis and a special mucilaginous wall is secreted within the cytoplasm of the microsporocyte. Unlike these, in the present study the microsporocytes become rounded off during meiosis. The microspore tetrads are of tetrahedral and decussate types as in *Adelocaryum coelestinum* (NAGARAJ & FATHIMA 1968). However, only decussate tetrads have been reported in *C. amabile* (MILLSAPS 1940).

The pollen grains are of different sizes and shapes in Boraginaceae. They are spherical, triporate and show a smooth exine in *Coldenia procumbens* (VENKATESWARLU & ATCHUTARAMAMURTI 1955), *Cordia alba* (FATHIMA 1966), and *Rotula aquatica* (NAGARAJ & FATHIMA 1967). The pollen grains of *Ehretia laevis* (JOHRI & VASIL 1956) show eight prominent ridges

Fig. 5. Development of embryo in *Cynoglossum denticulatum* DC. — A: Zygote. — B: Two-celled proembryo. — C: Proembryonal tetrad. — D—Q: Stages in the development of embryo. — R: L.S. portion of the ovule showing two two-celled proembryos. — S: L.S. portion of the ovule showing two embryos. — *ca,* cell apical; *cb,* cell basal; *ci,* lower daughter cell of *cb*; EMB_1, embryo one and proembryo; EMB_2, embryo two and proembryo; END CLS, endosperm cells; *iec,* initials for root cortex; *l,* upper tier of octants; *l'*, lower tier of octants; *m,* middle cell of the 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'*; *s,* suspensor. — A—S ×310.

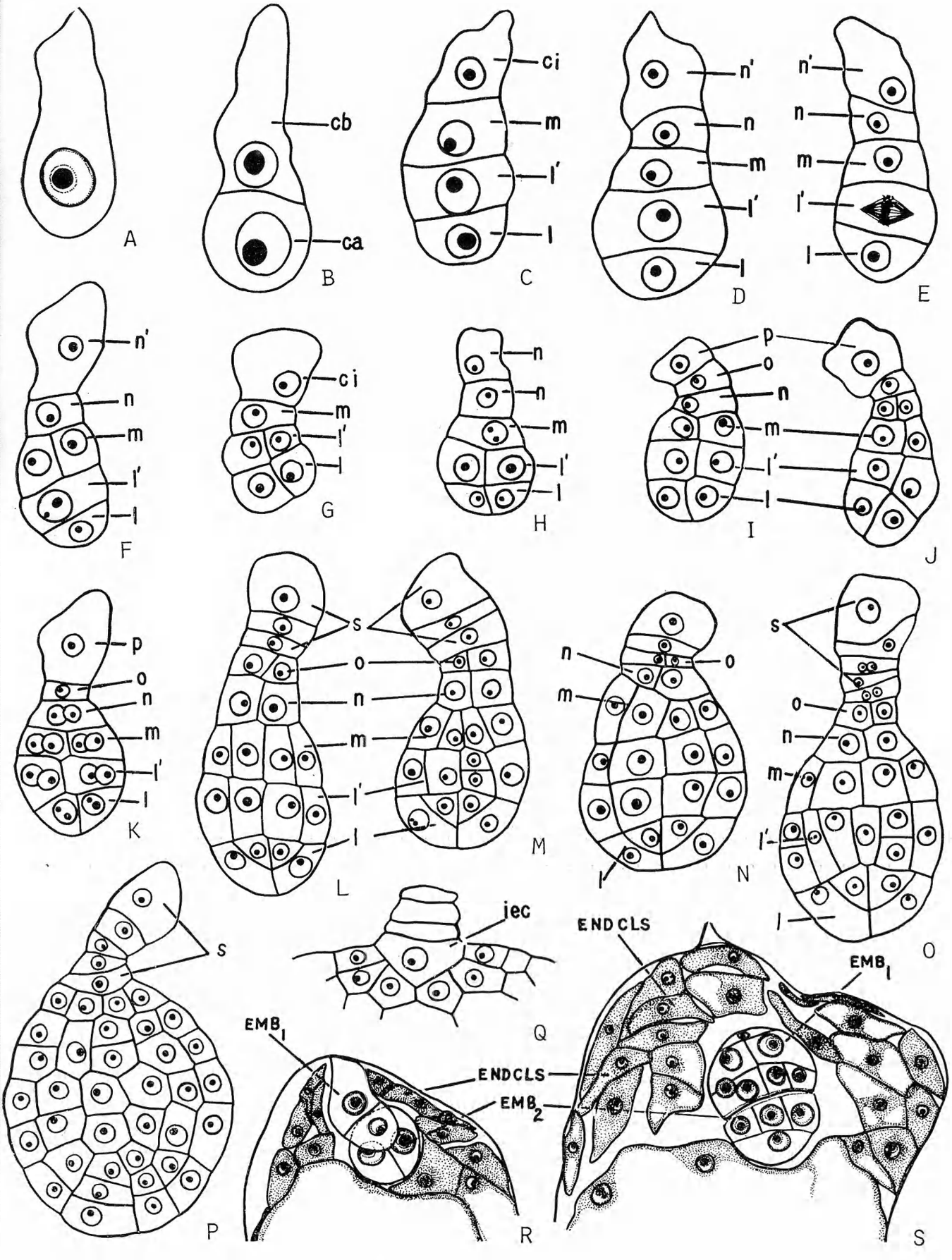

A
cb
ca
B
ci
m
l'
l
C
n'
n
m
l'
l
D
n'
n
m
l'
l
E
n'
n
m
l'
l
F
ci
m
l'
l
G
n
n
m
l'
l
H
p
o
n
m
l'
l
I
J
p
o
n
m
l'
l
K
s
o
n
m
l'
l
L
M
n
m
o
l
N
s
o
n
m
l'
l
O
P
iec
Q
EMB1
ENDCLS
EMB2
R
ENDCLS
EMB1
S

Fig. 5.

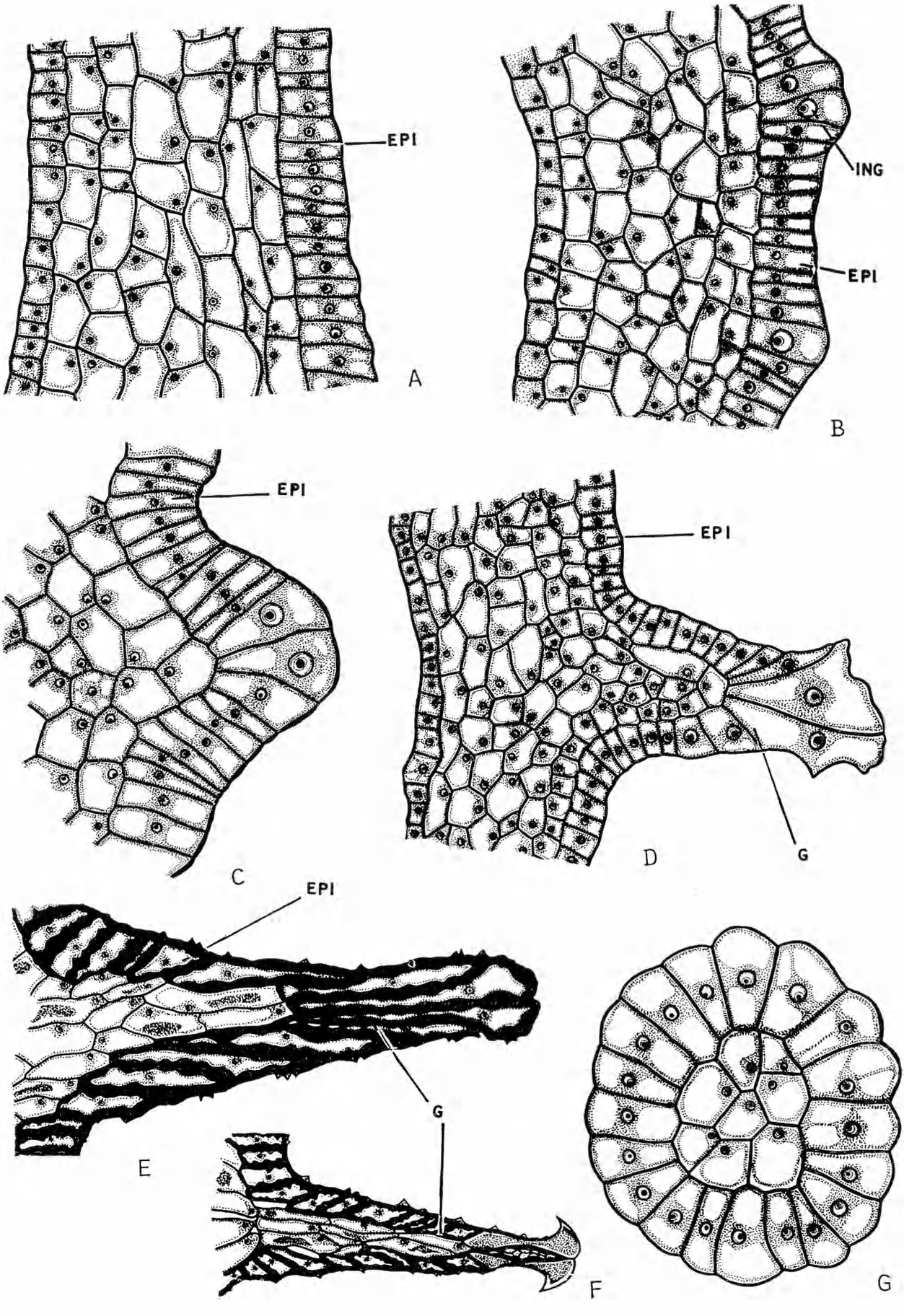


Fig. 6.

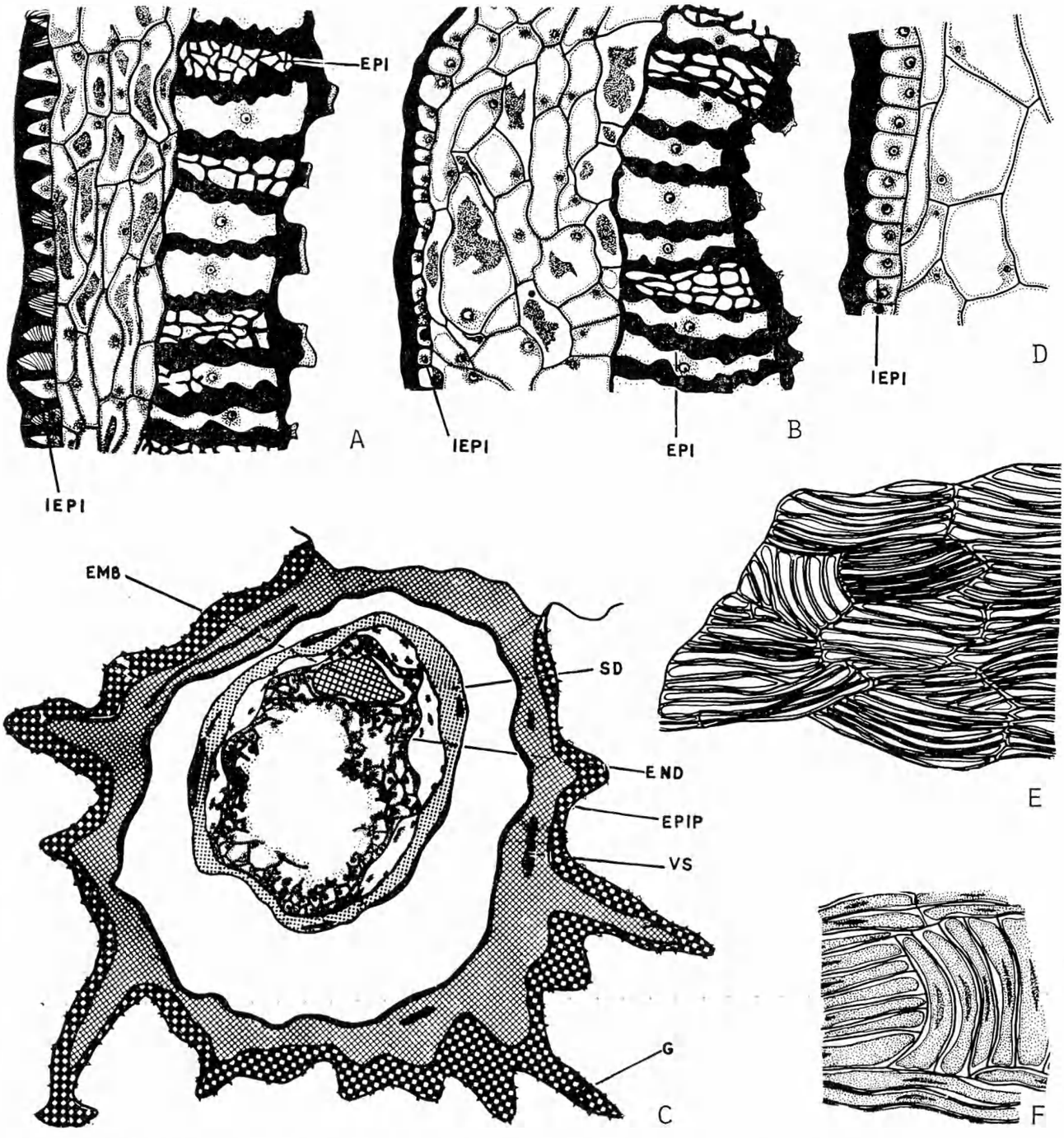


Fig. 7. Development of pericarp in *Cynoglossum denticulatum* DC. — A, B: L.S. pericarp showing the thickenings on the inner and outer epidermal layers. -- C: T.S. nutlet. — D: L.S. portion of the inner epidermis enlarged to show the thickenings on the outer tangential walls. — E: Surface view of the thickenings on the inner epidermis. — F: A portion of F enlarged. — EMB, embryo; END, endosperm; EPI, epidermis; EPIP, epicarp; G, glochidiate outgrowth; IEPI, inner epidermis; SD, seed; VS, vascular strand. — A, B, D, F ×310. C, E ×135.

Fig. 6. Development of pericarp in *Cynoglossum denticulatum* DC. — A: L.S. pericarp before the initiation of the glochidiate outgrowths. — B—E: L.S. pericarp showing stages in the development of glochidiate outgrowths. — F: L.S. glochidiate outgrowth. — G: T.S. glochidiate outgrowth. — EPI, epidermis; G, glochidiate outgrowth; ING, initials for glochidiate outgrowths. — A---G ×310.

alternating with furrows that lodge the germ pores in them. While elliptical pollen grains with reticulate exine and three colpae are seen in *Heliotropium indicum,* spherical acolpate pollen grains are characteristic of *H. curussavicum* and *H. peruvianum,* and multicolpate ones of *H. ovalifolium* (PAL 1963). Dumb-bell-shaped pollen grains with a smooth exine and two germ pores that are situated at the region of constriction are seen in *Myosotis* sp. (SVENSSON 1925), *Cynoglossum amabile* (MILLSAPS 1940), *Mertensia platyphylla* (KHANNA 1964 b) and *Adelocaryum coelestinum* (NAGARAJ & FATHIMA 1968). The pollen grains are also dumb-bell-shaped in *C. denticulatum.* The dumb-bell shape of the pollen grains facilitates dispersal according to GUÉGUEN (1902), and he is of the opinion that the constricted pollen grains have better chances of lodging between the adjoining stigmatic papillae. He further considers that the elongated, dumb-bell-shaped pollen grains are characteristic of all the members of Boraginoideae. KHANNA (1964) disagrees with GUÉGUEN's views (1902) and according to her, the dumb-bell-shaped pollen grains cannot be taken as a characteristic feature of any of the tribes of Boraginaceae. The pollen grains are spherical in *Trichodesma amplexicaule* and *Mertensia paniculata* (KHANNA 1964 a, b), both belonging to Boraginoideae.

The pollen grains in the present investigation are shed at the three-celled stage as in *Cynoglossum amabile* (MILLSAPS 1940), *Mertensia paniculata* (KHANNA 1964 b) and *Adelocaryum coelestinum* (NAGARAJ & FATHIMA 1968).

Various types of megaspore tetrads have been reported in the family Boraginaceae, a linear tetrad being more common in all the members. In *Cynoglossum officinale* (SVENSSON 1925) the megaspore tetrad is rarely T-shaped. Occasionally the upper dyad cell remains undivided and consequently the tetrad consists of three megaspore in this species. In *C. amabile* (MILLSAPS 1940) a T-shaped tetrad is of frequent occurrence. Occasionally an oblique division takes place in the dyad cells which results in a decussate arrangement of megaspores in this species. In the present investigation only a linear tetrad has been observed.

The chalazal megaspore develops into a Polygonum type of embryo sac in all the members that follow monosporic development (DAVIS 1966). However, in *Rotula aquatica* (NAGARAJ & FATHIMA 1967) any one of the remaining megaspores may enlarge simultaneously but only one of them develops into a mature gametophyte. A similar condition has been observed in *Adelocaryum coelestinum* (NAGARAJ & FATHIMA 1968) where the third or second megaspore may develop up to the two-nucleate stage in addition to the chalazal one. A bisporic type of development has also been observed in certain members of Boraginaceae. This includes *Lycopsis* and *Anchusa* sp. (SVENSSON 1925) and *Ehretia laevis* (JOHRI & VASIL 1956).

A tendency towards nucellar apospory has been observed in the present investigation. The aposporic embryo sac initials generally develop up to the two-nucleate stage but rarely reach maturity. These are seen below the normal megasporocyte, megaspore tetrad and the megagametophyte. There have been no previous reports on the occurrence of this phenomenon in the family Boraginaceae.

The megagametophyte becomes broader towards the chalazal region after fertilization in most of the Cynoglosseae including the present one. MILLSAPS (1940) concludes that such an enlargement is characteristic of Cynoglosseae while the Anchuseae have a prominent lateral diverticulum.

There is great diversity in the development of the endosperm in Boraginaceae. SVENSSON (1925) has classified the endosperm of this family in five types, viz.: the Borago type, Lycopsis type, Echium type, Lappula type and Myosotis type.

The Borago type and the Myosotis type are the two extreme types of development

in being the nuclear and *ab initio* cellular types respectively while the others are intermediate or aberrant types.

SVENSSON (1925) characterizes the Borago type as the typical free nuclear type of endosperm where wall formation sets in only in later stages. *Borago officinalis, Onosma echioides* (SVENSSON 1925), *Trichodesma amplexicaule,* and *Mertensia platyphylla* (KHANNA 1964 a, b) show this type of development.

In the Lycopsis type four free nuclei are first formed, and subsequently a small lateral cell is organized enclosing two of them the other two nuclei occupying the larger cell containing the zygote. Free-nuclear divisions occur in both the cells and wall formation sets in only in the later stages. This type of endospermal development is seen in *Lycopsis arvensis,* species of *Nonnea, Pulmonaria, Anchusa* and *Symphytum* of Anchuseae, *Cerinthe* and *Lithospermum* of Lithospermeae (SVENSSON 1925). This type of development is not seen in any other member of Boraginioideae including those in the present investigation.

SVENSSON (1925) has compared the Lycopsis type with that of the Helobial endosperm. According to SWAMY & PARAMESWARAN (1963) the Helobial endosperm is a characteristic feature of monocotyledons only. They, however, agree that the location of the primary endosperm nucleus, prior to the division and the relative size relationship of the two chambers, are in accordance with the Helobial ontogeny, but the resemblance ceases with the appearance of a wall between the two nuclei of the chalazal chamber. This feature does not occur anywhere in the monocotyledonous Helobial endosperm. Hence SWAMY & PARAMESWARAN (1963) conclude that the Lycopsis type although showing similarities to the Helobial endosperm in the early stages, actually belongs to the Nuclear-norm because of the absence of wall formation after the first division of the primary endosperm nucleus.

The third type, i.e. the Echium type is characterized by the formation of an oblique wall after the first division of the primary endosperm nucleus. The small lenticular cell cut off towards the micropylar end is lateral in position and undergoes one more division forming two cells, in each of which a few free nuclear divisions take place. The first as well as the subsequent divisions in the larger chamber are free nuclear divisions and the nuclei are embedded in the peripheral cytoplasm. This type of endosperm has so far been recorded only in *Echium plantagineum* (SVENSSON 1925) of Echieae. This type of development has not been observed in the present investigation either.

According to SVENSSON (1925) the Echium type of endosperm bears a clearer and closer similarity to the Helobial endosperm than to the Lycopsis type. SCHNARF (1929) and MAHESHWARI (1950) also consider this type of development to be a special deviation of the Helobial-norm. According to SWAMY & PARAMESWARAN (1963), there is not even a remote resemblance between the *Echium* ontogeny and the Helobial ontogeny of monocotyledons. The reverse relationship of the micropylar and the chalazal chambers is itself a feature which strongly negates any attempt to link Echium type with the monocotyledonous Helobial endosperm. Further, the first nuclear division in the lateral chamber corresponding to the micropylar chamber is followed by wall formation, which is contrary to the situation in the Helobial endosperm. Since SVENSSON (1925) himself has recorded deviations in *Echium,* SWAMY & PARAMESWARAN (1963) consider the Helobial affinity of the Echium type to be precluded.

In the fourth type of endosperm development, i.e., the Lappula type the first division of the endosperm nucleus is accompanied by a vertical wall which ends blindly in the chalazal region due to the presence of a large central vacuole. The next division is also accompanied by the formation of an incomplete vertical wall

at right angles to the previous one so that a four-celled endosperm is formed with all four cells open at the base and partially communicating. Free nuclear divisions which are eventually accompanied by wall formation take place in these cells in such a way that the endosperm becomes cellular in the micropylar region and remains free-nuclear in the chalazal region. *Lappula echinata, Asperugo procumbens* and *Krynitzkya barbigera* of the tribe Eritricheae and *Cynoglossum officinale, Omphalodes linifolia, O. verna, Lindelofia longiflora, Solenanthus apenninus* of Cynoglosseae (SVENSSON 1925) are included in this type.

SVENSSON (1925) includes *Cynoglossum officinale* and the other Cynoglosseae under the Lappula type of endosperm because he found cellular endosperm at the micropylar end and free-nuclear at the chalazal end. He was unable to get the very early stages of any of the members of Cynoglosseae and thus concludes that the endosperm development in this tribe belongs to the Lappula type. MILLSAPS (1940) agrees with SVENSSON (1925) on the basis of her observations in *C. amabile*.

The development of the endosperm in *C. denticulatum* differs considerably from the Lappula type. In this species the first division of the primary endosperm nucleus is accompanied by either an oblique or a transverse wall resulting in two unequal chambers viz., the micropylar and the chalazal. The micropylar chamber, which is smaller, always contains the zygote. Further divisions are all accompanied by wall formation in this chamber while in the chalazal chamber the first division is accompanied by an incomplete vertical wall. This wall disappears very early as the chalazal end of the embryo sac enlarges. The subsequent divisions in the chalazal chamber are all free nuclear. This type of endosperm may be considered to combine the characters of the Echium type in so far as the first division is concerned, and the Lappula type in so far as the incomplete wall is concerned provided the chalazal chamber is considered to be equivalent to the entire embryo sac cavity. Since this type of endosperm development is new to this family and has been reported for the first time in *Cynoglossum* it can be named the Cynoglossum type.

Myosotis type is the normal *ab initio* cellular type and has been reported in *Myosotis* sp. (SVENSSON 1925), *Coldenia procumbens* (VENKATESWARLU & ATCHUTARAMAMURTI 1955), *Ehretia laevis* (JOHRI & VASIL 1956), four species of *Heliotropium* (PAL, 1963) and *Rotula aquatica* (NAGARAJ & FATHIMA 1967).

There is great diversity in embryo development in Boraginaceae. The first proembryonal tetrad is either linear or T-shaped and belongs to the megarchetypes III, IV and V of the C2 series, IV of A2 series and II of the B2 series. The development conforms to either the Chenopodiad, Solanad, Onagrad or Asterad type (JOHANSEN 1950). While *Heliotropium peruvianum* (SOUÈGES 1943), *Eritrichium strictum* (CRÉTÉ 1953), *Coldenia procumbens* (VENKATESWARLU & ATCHUTARAMAMURTI 1955), *H. indicum* (PAL 1963) and *Rotula aquatica* (NAGARAJ & FATHIMA 1967) follow a Chenopodiad sequence with linear proembryonal tetrads belonging to the C2 series, *Heliotropium curassavicum* and *H. ovalifolium* (PAL 1963) show a Solanad type of development with their linear proembryonal tetrads in the megarchetype IV of the C2 series. The proembryonal tetrad is T-shaped and the development conforms to the Onagrad type in *Ehretia laevis* (JOHRI & VASIL 1956) unlike *Cynoglossum officinale* (CRÉTÉ 1955), *Omphalodes linifera* (SOUÈGES 1958) and *Trichodesma amplexicaule* (KHANNA 1964 a) where it corresponds to the Asterad type. The development of the embryo in the present investigation is of Chenopodiad type with a linear proembryonal tetrad belonging to the C2 series of the Megarchetype III

unlike the other species of *Cynoglossum* where it is T-shaped (CRÉTÉ 1955).

The structure and development of the pericarp and the seed coat in the present study are similar to that of *Cynoglossum amabile* (MILLSAPS 1940).

Taxonomically, the family Boraginaceae has been treated in various ways, the considerations being based on overlapping characters rather than clear-cut differences. CLARKE (1885) divides Boraginaceae into four tribes while GÜRKE (1897) recognises four subfamilies. The majority of systematists accept the family in a broad sense while others believe in the elevation of each of the subfamilies to family status. According to JOHNSTON (1932) Boraginaceae is a composition of several subfamilies rather than of small micro-families. LAWRENCE (1937) after an exhaustive anatomical investigation on several members of this family has concluded that the subfamilies were best treated as components of one single family. Embryological studies on *Cynoglossum denticulatum* and several other members (FATHIMA 1966, 1967, 1969; NAGARAJ & FATHIMA 1967, 1968, 1971) belonging to different subfamilies also reveal Boraginaceae to be an embryologically diversified and heterogeneous group best justified as a single family under Tubiflorae.

ACKNOWLEDGEMENTS

The author is indebted to Professor M. NAGARAJ, Bangalore University, Bangalore, India, for encouragement, guidance and facilities; to the University Grants Commission for the award of a research scholarship and to the Regional Botanist, Southern Circle, Botanical Survey of India, Coimbatore, for identification of the material.

LITERATURE CITED

CLARKE, C. B. 1885. Boragineae. — In J. D. HOOKER, Flora of British India, Vol. IV. — London.

CRÉTÉ, M. P. 1953. Embryogénie des Boragacées. Développement de l'embryon chez l'Eritrichium strictum. — C. R. Acad. Sci. Paris 236: 224—226.

— 1955. Embryogénie des Boragacées. Développement de l'embryon chez le Cynoglossum officinale. — C. R. Acad. Sci. Paris 241: 660—662.

DAVIS, G. L. 1966. The systematic Embryology of angiosperms. — New York.

FATHIMA TASNEEM 1966. Sporogenesis and the development of gametophytes in Cordia alba L. — Curr. Sci. 35: 73—74.

— 1967. Embryological studies in Trichodesma zeylanicum R. Br. — Curr. Sci. 36: 53.

— 1969. Embryological studies in Boraginaceae. — Ph. D. Thesis, Bangalore University.

GAMBLE, G. S. 1928. Flora of Presidency of Madras. Vol. II. — Reprinted by Botanical Survey of India, 1957, Calcutta.

GUÉGUEN, F. 1902. Anatomie comparée du tissu conducteur du style et du stigmate des phanérogames. — Journ. Bot. (Morot) 16: 15—30, 48—65, 138—144, 167—180, 300—313.

GÜRKE, M. 1897. Borraginaceae. — In A. ENGLER & K. PRANTL, Die natürlichen Pflanzenfamilien 4, 3a, pp. 71—131. — Leipzig.

JOHANSEN, D. A. 1950. Plant embryology. — Waltham.

JOHNSTON, I. M. 1932. Studies in the Boraginaceae, IX. — Contrib. Arnold Arb. 3.

JOHRI, B. M. & VASIL, I. K. 1956. The embryology of Ehretia laevis Roxb. — Phytomorph. 6: 134—143.

KHANNA PUSHPA 1964 a. Embryology of Trichodesma amplexicaule Roth. — Bull. Torr. Bot. Cl. 91: 105—114.

— 1964 b. Embryology of Mertensia. — J. Indian Bot. Soc. 43: 192—202.

LAWRENCE, J. R. 1937. A correlation of the taxonomy and the floral anatomy of certain of the Boraginaceae. — Amer. J. Bot. 24: 433—444.

MAHESHWARI, P. 1950. An introduction to the embryology of angiosperms. — New York.

MILLSAPS, V. 1940. Structure and development of the seed of Cynoglossum amabile Stapf & Drumm. — J. Elisha Mitchell Sci. Soc. 56: 140—164.

NAGARAJ, M. & FATHIMA TASNEEM 1967. Embryological studies in Rotula aquatica Lour. — Proc. Indian Acad. Sci (B) 66: 106—116.

— & — 1968. A note on the sporogenesis and gametogenesis in Adelocaryum. — Curr. Sci. 37: 265—267.

— & — 1971. Studies on the structure and development of pericarp and seed coat in Rotula aquatica Lour. — Proc. Indian Acad. Sci. (B) 74: 314—318.

PAL, P. K. 1963. Comparative studies in four species of Heliotropium. — Proc. Nat. Inst. Sci. India 29: 1—40.

SCHNARF, K. 1929. Embryologie der Angiospermen. — Berlin.

SOUÈGES, E. C. R. 1943. Embryogénie des Borragacées. Développement de l'embryon chez le Heliotropium peruvianum L. — C. R. Acad. Sci. Paris 217: 551—553.

— 1958. Embryogénie des Borragacées. Développement de l'embryon chez l'Omphalodes linifera Moench. — C. R. Acad. Sci. Paris 247: 249—253.

SVENSSON, H. G. 1925. Zur Embryologie der Hydrophyllaceen, Borraginaceen und Heliotropiaceen. — Uppsala Univ. Årsskr. 2.

SWAMY, B. G. L. & PARAMESWARAN, N. 1963. The Helobial endosperm. — Biol. Rev. 38: 1—50.

VENKATESWARLU, J. & ATCHUTARAMAMURTI, B. 1955. Embryological studies in Boraginaceae. 1. Coldenia procumbens L. — J. Indian Bot. Soc. 34: 235—247.

Developmental Anatomy of Seedlings of Anchoté, Coccinia abyssinica (W. & A.) Cogn. (Cucurbitaceae)

Amare Getahun

GETAHUN, A. 1974 09 13. Developmental anatomy of seedlings of anchoté, Coccinia abyssinica (W. & A.) Cogn. (Cucurbitaceae). — Bot. Notiser 127: 211—223. Lund. ISSN 0006-8195.

Anchoté is a tuberous perennial cucurbit with annual vines, unisexual flowers and small melon-like fruits cultivated in parts of Ethiopia for its edible tubers.

The primary root is tetrarch with primary tissues traceable to a common group of initials in the apical meristem. The transition zone connecting the exarch root and the endarch shoot is short and terminates below the peg. The protoxylem of the root forks by radial division and is displaced laterally to join the phloem strands. Four collateral bundles alternate with the xylem points of the root above the transition zone. They become bicollateral above the peg.

The upper part of the thick hypocotyl has six bicollateral bundles arranged in two groups of three each. These coalesce to form two plates in the intercotyledonary plane. Two strands from the ends of the plates diverge into each cotyledon and two strands, one from the central region of each plate, branch twice and constitute the six epicotylar bundles.

Mature internodes have five small and five large bicollateral bundles alternating in a single cylinder. These are bounded externally by a fibrous sheath.

Amare Getahun, College of Agriculture, Haile Sellassie I University, P.O. Box 138, Dire Dawa, Ethiopia.

INTRODUCTION

Seedling Anatomy

Except for the generalized work of ZIMMERMANN (1922) on seedlings of the family, no research on the seedlings of *Coccinia* has been located. ZIMMERMANN's account was brief and did not contain specific information on *Coccinia*. This review of the seedling will therefore concentrate on *Cucurbita* and *Citrullus*, both of which have undergone intensive investigation.

THE PRIMARY ROOT. According to WHITING (1938), JANCZEWSKI described histogens of Leguminosae and Cucurbitaceae as a type containing one generative zone from which all primary meristems of the root arose.

THE HYPOCOTYL. Hypocotyls in *Cucurbita* and *Citrullus* were highly elongated structures, and characteristically developed pegs (RUTLEDGE 1930; HUFFORD 1938; WHITING 1938). The transition zones were short and occurred at the lower part of the hypocotyls.

DESHPANDE and KASAT (1966) noted two types of transitions and described one type in which the transition zone connected the tetrarch root with six endarch bicollateral bundles that finally resolved into ten bundles in the hypocotyl. HUFFORD (1938) described a similar transition in *Citrullus*. WHITING (1938) found that the transition zone connected the tetrarch root of *Cucurbita* with eight endarch bundles in the lower hypocotyl. Further up in the hypocotyl, the two outermost bundles anastomosed reducing the number to six. Each of the fused bundles divided into three to result in ten bundles in the stem axis.

HUFFORD (1938) in *Citrullus* and WHITING (1938) in *Cucurbita* reported that each hypocotylar bundle was bicollateral and included fascicular cambium, but interfascicular cambium was absent. WHITING reported isolated phloem cells in the ground parenchyma of the hypocotyl. According to HUFFORD, the pericycle and endodermis were indistinguishable. He reported the cortex of the hypocotyl to be similar to that of the root and described the epidermis as being composed of

small, tabular, closely arranged cells. WHITING (1938) found stomata in the hypocotyls of *Cucurbita*.

Other workers who have contributed to our knowledge of the hypocotyl in other species of Cucurbitaceae are DANGEARD (1889), ZIMMERMANN (1922), HOLROYD (1924), JEAN (1926), RUTLEDGE (1930), HAYWARD (1938), HARTIG, VON MOHL, FISCHER, BRAEMER, and DE BARY according to WHITING (1938).

Peg formation and the anatomy of *Cucurbita* and *Citrullus* has been studied by WHITING (1938), HAYWARD (1938), HUFFORD (1938) and LARUE (1939).

ORIGIN OF SECONDARY ROOT. Two radically divergent opinions have been expressed concerning the origin of secondary roots in Cucurbitaceae (WHITING 1938), where according to WHITING, JANCZEWSKI found their origin involved the cortex, the pericycle and the endodermis. VAN TIEGHEM and DOULIOT (WHITING 1938) noted instead that the secondary root originated from two pericyclic layers. HUFFORD's (1938) work on *Citrullus* and WHITING's (1938) on *Cucurbita* supported JANCZEWSKI's interpretation. The secondary roots, like the primary roots, were tetrarch.

COTYLEDONS. WHITING (1938) described the cotyledons of *Cucurbita* and found that four traces diverged from the cotyledonary plate into the broad bases of the cotyledons, and vascular bundles of cotyledonary petioles were similar to those of the hypocotyl.

THE EPICOTYL. At germination, the epicotyl consisted of a small growing point overarched by a primordium of the first leaf in *Cucurbita* (WHITING 1938). The observation of embryos before germination revealed that the median trace to the first leaf was already identifiable as a procambial strand.

In the epicotyl, at the level where the first leaf diverged, there were six bundles which were branches of the six bundles of the hypocotyl in *Citrullus* (WHITING 1938). They appeared as two sets of three bundles each and one set became traces to the first leaf and the other set to the second leaf. In *Cucurbita,* according to WHITING (1938), the number of bundles and their arrangement in the first internode were variable but the second and third internodes possessed a characteristic arrangement of ten bundles.

The Shoot

THE STEM. Stem morphology of cucurbits has been studied by GHOSH (1932), BLYTH (1958), METCALFE and CHALK (1950), ZIMMERMANN (1922) and HOLROYD (1924).

Stem anatomy of cucurbits has been investigated by BLYTH (1958), HOLROYD (1924), GHOSH (1932) and FAHN (1967) using *Cucurbita* spp., *Coccinia indica,* and *Trichosanthes colabrina.*

THE VASCULAR BUNDLE. VAN TIEGEEM (BLYTH 1958 and WORSDELL 1915) described the stem of Cucurbitaceae as having ten foliar vascular strands near the exterior of the central cylinder and five strands near the centre of the cylinder. A complete vascular bundle consisted of outer phloem, outer cambium, xylem, inner cambium, and inner phloem (GHOSH 1932). ZIMMERMANN recognized three types of bundle arrangement: (1) ten bundles in two rings, (2) less than ten bundles, and (3) more than ten bundles due to accessory bundles which occurred both inside and outside the fibrous layer. CRAFTS (1932) has reviewed types of accessory bundles in the cucurbit stem. HOLROYD (1924) reviewed the literature on the internal phloem in stems, which has been extensively studied. Internal phloem was considered a well-developed anatomical specialization in Cucurbitaceae and was considered to play a prominent role in conduction (EAMES 1961; FOSTER and GIFFORD 1959).

Stems of most species studied by GHOSH (1932) had vascular bundles surrounded by thin-walled parenchyma and the pith frequently contained cavities. The inter-bundle parenchyma enlarged centrifugally so that vascular bundles became spaced further apart and, according to FAHN (1967), there was no sharp distinction between this area, the cortex and the pith.

LEAF. Leaves of *Coccinia* and their phyllotaxy have been studied by ZIMMERMANN (1922) and HAGERUP (1930). Each new leaf arose in accordance with the space-filling theory (SNOW 1965). Each developing leaf had three leaf traces which were distinct below the node.

SINGH (1942) studied the antomy of the leaf and petiole of *Zanonia indica* and reported that the petiole had an internal structure much like that of the stem. YASUDA (1901), working on wild and cultivated Japanese cucurbits, studied the anatomy of the lamina and petioles.

MATERIAL AND METHODS

Seeds were obtained from plants grown at Debre-Zeit (Shoa) and Alemaya (Harar) Agricultural Experiment Stations, Ethiopia from seeds collected in the province of Wollega. Plants used in this study were grown in pots and flats in greenhouses at the University of Florida, Gainesville, Florida.

Craf II and III were employed as fixatives for leaves, cotyledons and seedling stages. Mature stems were fixed in FAA. Other fixatives were used but with less success. Samples were dehydrated by the tertiary butyl alcohol (TBA) method, infiltrated, and embedded in "Tissumat" (SASS 1951).

Sections were cut at five, eight, ten, twelve or fifteen μ depending on the organ, its stage of development or the tissue being investigated.

Three staining techniques were employed: tannic acid, iron chloride, and safranin (FOSTER 1934); safranin and fast green (JOHANSEN 1940); and iron haematoxylin counter-stained with safranin and fast green. Temporary sections treated with phloroglucinol, Sudan III or IKI were used to supplement the permanent slide preparations.

Leaves and hypocotyls were cleared with lacto-phenol, 5 per cent aqueous NaOH or lacto-chromic acid combination. Free-hand sections were also cleared with 5 % NaOH.

Drawings were made mostly from cleared material. Kodak Panatomic-X film was used for the photomicrography.

OBSERVATIONS

Gross Morphology

Some aspects of the morphology of very young seedlings up to six days old have been reported by GETAHUN (1973). The following observations were made on seedlings one to six weeks old.

Despite the rapid growth of seedlings maturation of tissues was slow, particularly in the roots. Seedlings, except for variation in length of hypocotyl, showed a relatively high degree of morphological uniformity when subjected to the same growth conditions.

Secondary roots were initiated early in the development of primary roots and very close to the root apex. Secondary as well as tertiary roots were morphologically identical with primary roots except that they were much smaller in diameter. Table 1 shows the effect of seed position when planted on the root system after 19 days of seedling development. Primary roots were strongly leading and fewer secondary roots developed when seeds were planted vertically with the micropylar ends downwards. When seeds were planted flat, primary roots were weakly leading, and secondary roots were abundant. The outgrowth of root hairs was dense. The root-hair zone occurred 2 mm from the root tip and extended for 5 mm.

The transition zone of the hypocotyl characteristically produced four adventitious roots that were strongly developed (GETAHUN 1973 Fig. 9 B). The transition zone always measured less than 2 mm in length. The upper end of the transition zone was marked by the presence of the peg (GETAHUN 1973 Fig. 9 B). Except for its more pronounced oval outline in transverse section, the transition zone resembled the primary root in external features. The colour was dull due to the lack of cuticle and it produced hairs like those of the primary root.

The peg was variable in size and shape but was a natural and integral part of the hypocotyl. As shown in Table 1, the position of the seed during germination and thereafter greatly influenced the diameter and shape of the peg as well as the total length of the hypocotyl. Maximum peg development occurred in seeds planted flat. This position, which the seeds normally assumed as they themselves were flat, also gave rise to a large curvature of the hypocotyls. In this instance, the peg was formed like a flap on the side opposite the curvature and structurally fitted the micropylar end of the seed coat. Minimum peg development occurred in seeds planted with the micropylar ends downwards and this position of seed planting produced no hypocotylar curvature. The peg was formed as a ring. Peg development was insignificant when the seed coat was removed. Contact of seed coats was apparently instrumental in causing the curvature. The peg held the micropylar end of the seed coat as the cotyledons were being pulled out of the seed by the action of the elongating hypocotyl. The function of the peg and the size of the hypocotyl loop were both maximized by the presence of the seed coat and the flat

Table 1. Effects of position of seed in the soil on the rate of germination, hypocotyl and peg development and root system at the end of 19 days (hypocotyl length: number within brackets at the end of ten days).

Seed position	Hypocotyl			Peg	Root system	Rate of germination
	Length cm	Thickness	Shape			
Horizontal	3 (1.0)	normal	curved	large shield	main root weakly leading, profusely branched	2
Vertical with micropylar end upwards	0.5 (0.5)	thick	vertical	not apparent	much-branching	3
Vertical with micropylar end downwards	3.7 (0.8)	normal	vertical	ring	main root leading	1

position of the seed when planted. The hypocotyl became straight with subsequent seedling growth after the cotyledons had been freed from the seed coat.

The part of the hypocotyl above the peg (GETAHOUN 1973 Fig. 9) was long and slender when seeds were planted flat, and short and thick when seeds were planted vertically with the micropylar end downwards. This portion of the hypocotyl was more uniform in structure and form than the peg and transition areas. It retained its oval outline in the plane of the cotyledons except just below the cotyledonary node where it was constricted and flattened out. The portion of the hypocotyl above soil level was green and had a few stomata while the unexposed portion was devoid of chlorophyll and lacked stomata. The hypocotyl above the peg had numerous hairs and produced adventitious roots infrequently, but there was great variation between specimens. This portion of the hypocotyl had cuticle and was shiny in appearance as opposed to the primary root and the transition zone which lacked cuticle and were dull.

The thick cotyledons were green, thus probably photosynthetically important to the young seedling in the light of the slow growth of the shoot. There was a five-fold increase in length (lamina plus petiole) and a four-fold increase in breadth of the cotyledons at maturity from the initial size in the dormant embryo. Petioles remained closely appressed to the growing epicotyl but were not fused. The cotyledonary tube thus formed enclosed the shoot laterally, and the first two internodes were not visible. The first and second internodes were short and as a result the first and second leaves appeared to be inserted at the cotyledonary node. The true insertion of these leaves was apparent only upon dissection of the cotyledonary tube.

Cotyledons were smooth except at main veins and margins. Their lower surfaces were light green and displayed five to seven prominent veins. The lower epidermis had multicellular trichomes often restricted to the midrib region and to the margin and submarginal area of the lamina. There were a few stomata in the upper and lower epidermis.

Only the first four internodes of the seedling remained upright. These internodes were stout and 1 to 3 cm long. The internodes beyond these ranged from 6 to 19 cm in length. Tendrils appeared at the sixth node. The shoot became a vine after it produced lateral branches from the first few nodes.

Young stems toward the shoot apex were irregularly round as seen in transverse section. As the stems matured, they became ribbed and irregularly pentagonal

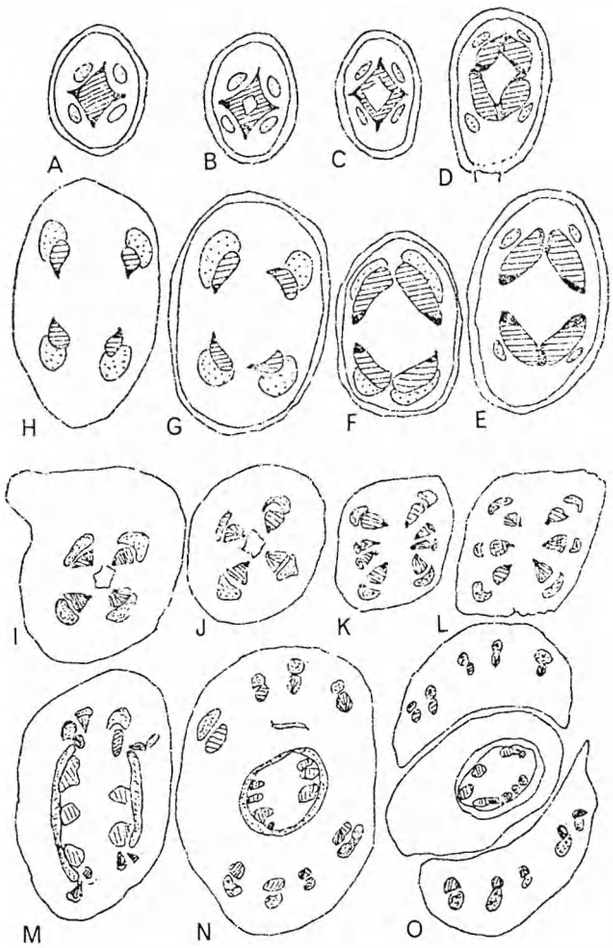


Fig. 1. *Coccinia abyssinica.* Diagrams of sequence of transverse sections of a 30-day-old seedling showing vasculation. Internal phloem in the hypocotyl and cotyledons not shown. Dotted area, phloem; solid lines, metaxylem; dark area, protoxylem. The outer double layer of A—G is endodermis; cortex and epidermis not included. A—H, 1.46 mm, 1.30 mm, 1.16 mm, 790 µ, 490 µ, 290 µ, 100 µ, and 60 µ below the peg, respectively; I, at the peg; J—L, at 408 µ, 2.23 mm and 3.42 mm above the peg; M, at the cotyledonary node; N, O, 288 µ and 568 µ above the cotyledonary node, respectively. — A—H ×4.75. I—O ×1.00.

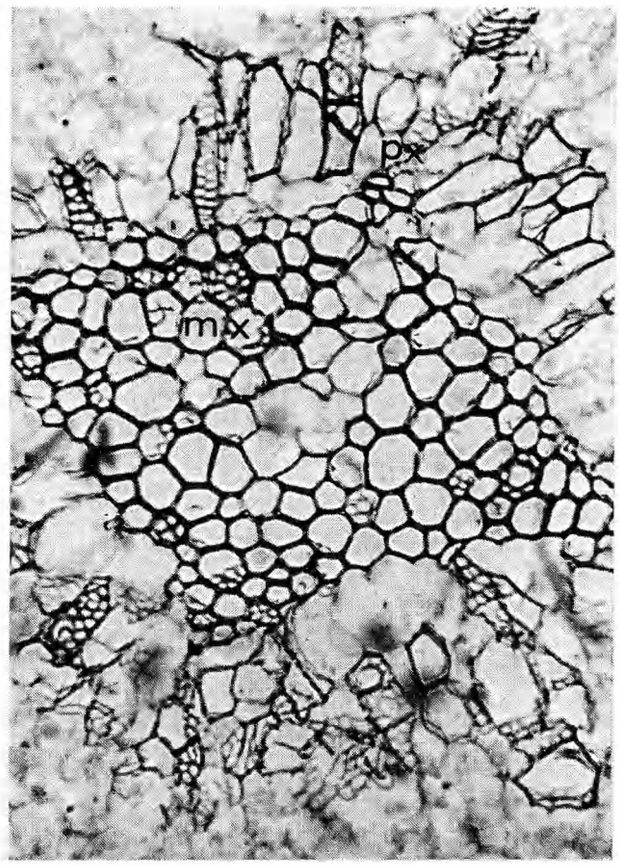


Fig. 2. *Coccinia abyssinica.* Transverse section of tetrarch xylem of a primary root at a level just below the transition zone of a 30-day-old seedling. Note pitting on end-walls of some of the metaxylem elements. Some xylary connections to the adventitious roots are visible outside the tetrarch xylem. — ×100. px: protoxylem. mx: metaxylem.

in transverse section. The epidermis had multicellular trichomes that were abundant towards the stem apex and relatively sparse in mature internodes. Hairs on younger stems were mostly glandular capitate.

Three to five strong branches were developed at the lower nodes. These as well as the primary stem had a zigzag pattern as they were bent away from the leaf at each node. The meristematic areas in the axils of cotyledons later served to produce new shoots from the tuber each growing season.

The leaves were usually heart-shaped but variable in size and shape. The first leaf above the cotyledons was always smaller than subsequent leaves at maturity. Stomata occurred in the upper and lower epidermis, and were level with the surface or slightly sunken.

Primary Root

The apical meristem of the primary root had a common group of initials from which primary meristems and the root

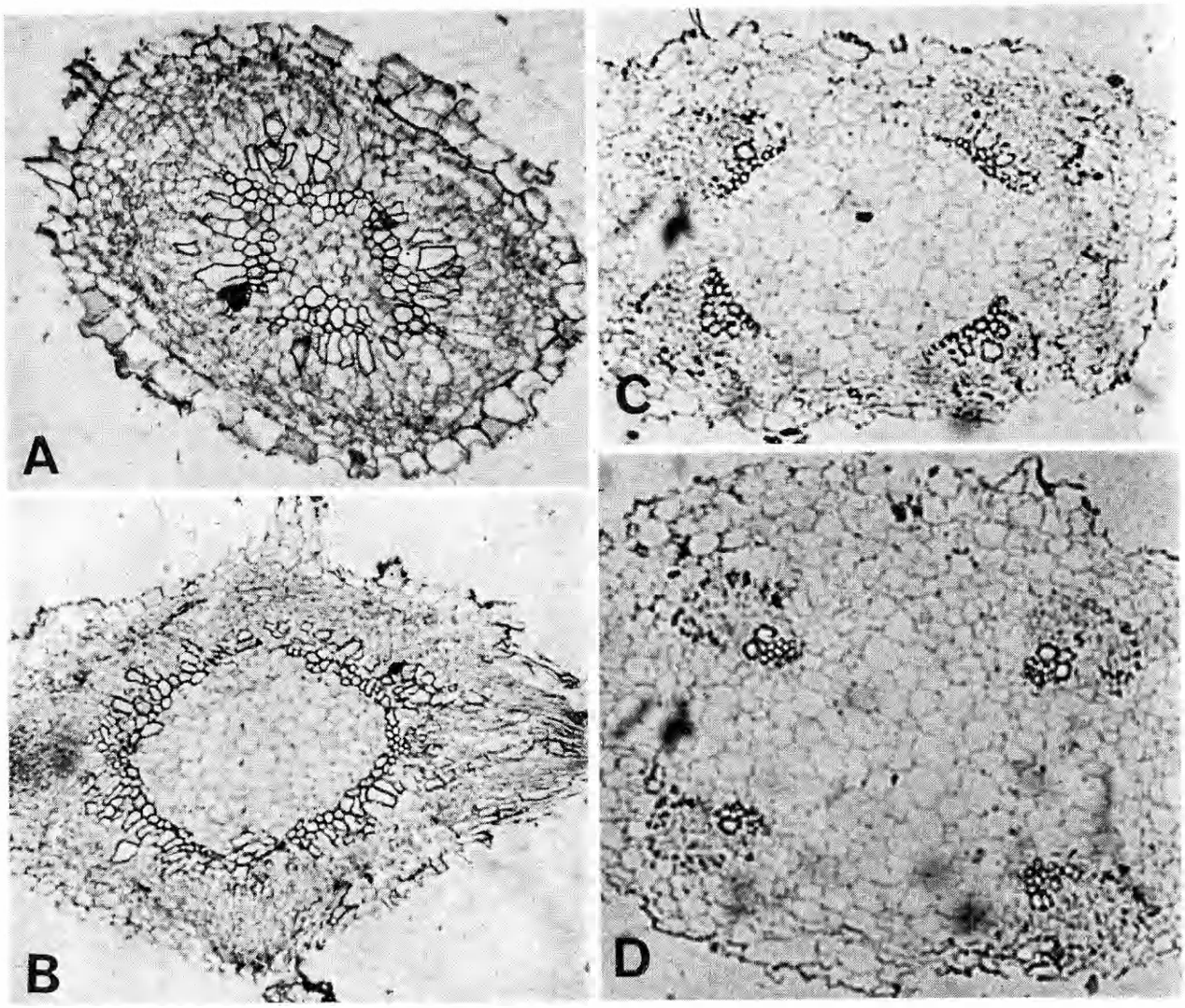


Fig. 3. *Coccinia abyssinica*. Sequence of transverse sections of the transition zone of a 30-day-old seedling. — A: 1.16 mm below peg, cortex and epidermis lost. — B: 790 μ below peg. — C: 100 μ below peg. — D: 60 μ below peg. — A ×3.2. B—D ×2.1.

cap arose. The solid vascular cylinder was the first to mature and be recognizable, and the cortex next. In transverse section, the vascular cylinder appeared as a central mass of small cells and the cortex as a uniform tissue of larger cells.

The primary root was tetrarch (Figs. 1 A, 2). Vessel members were short and broad and had scalariform perforations. The primary phloem groups were larger than the primary xylem and the pericycle was composed of a few layers of parenchyma. The endodermis was composed of a single layer of large cells with wide distinct Casparian strips on the radial walls (Fig. 3 A).

Hypocotyl

The hypocotyl was composed of a transition zone, a peg region, and an upper part above the peg. The hypocotyl, though externally simple, was structurally complex.

TRANSITION ZONE. Evidence of transition from root structure involved a change in the position of the metaxylem elements at the junction of the primary root with the hypocotyl. The central metaxylem elements diverged outwards and parenchyma appeared in the centre (Figs. 1 G, 4 B). More parenchyma appeared with the further divergence of the

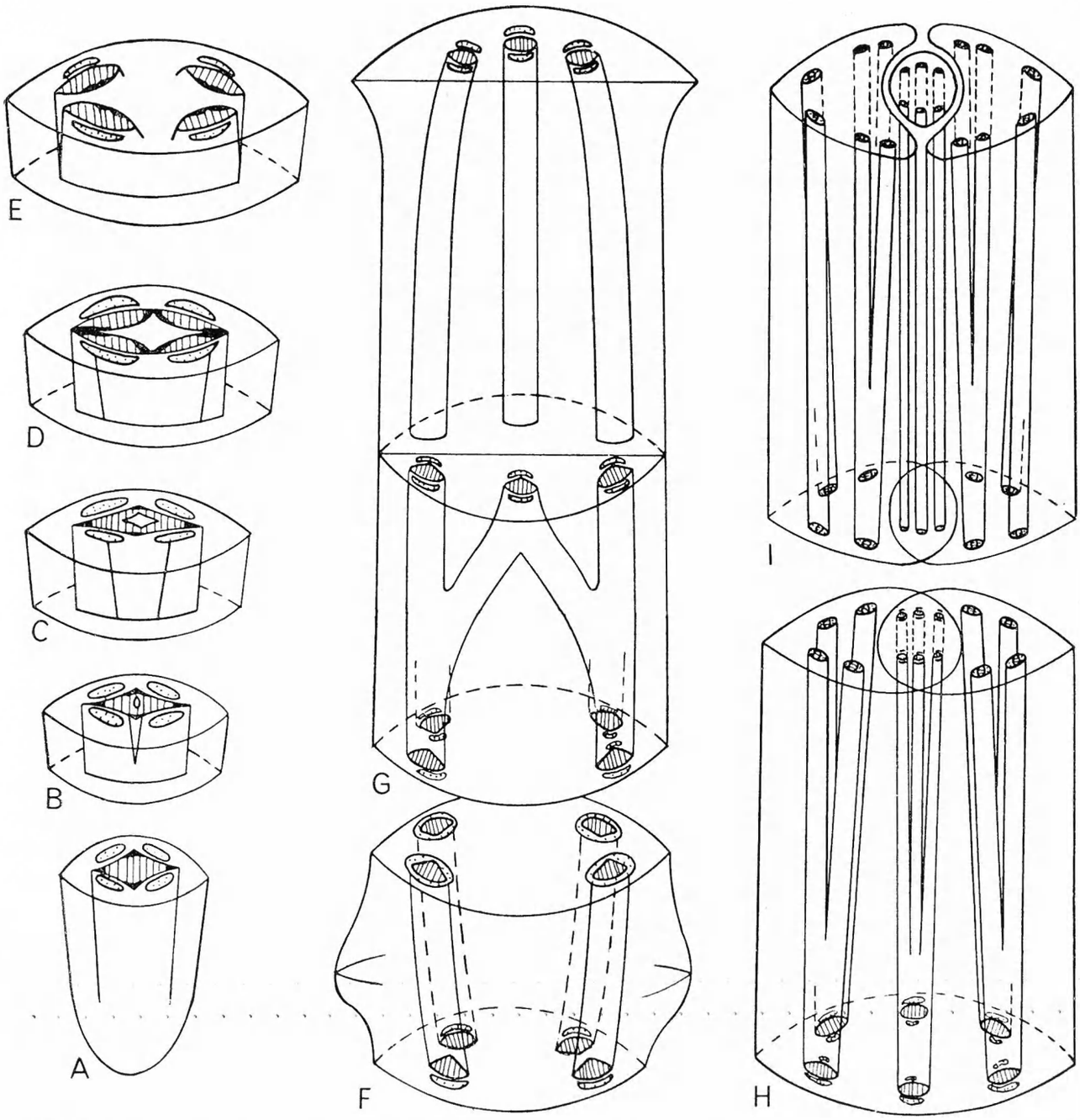


Fig. 4. *Coccinia abyssinica*. Schematic drawings showing the general plan of vascular system in seedlings. — A: primary root. — B—E: hypocotyl, lower part including transition. — F: hypocotyl at peg region. — G: upper hypocotyl. — H—I: cotyledonary petioles. — Dotted area: phloem. Dark area: protoxylem. Solid lines: metaxylem.

metaxylem elements (Figs. 1 B, C; 3 A, B; 4 C, D). Phloem groups remained in radial positions alternate with protoxylem points.

Upwards in the transition zone the metaxylem became separated at four points inwards from the protoxylem (Fig. 1 D). At this level the pith was surrounded by four areas of protoxylem and four areas became bifurcate and bent laterally upwards into eight strands located at opposite lateral edges of the four metaxylem strands (Fig. 1 E). At this level four vascular bundles were present but each had two protoxylem areas not in an exactly endarch position. Throughout the transition zone, four strands of phloem

maintained positions vertical and external to the metaxylem. The final transition involved the convergence of two protoxylem areas adjacent to each metaxylem area and the formation of four collateral bundles. Transition was completed just below the peg (Fig. 4 E). Internal phloem was absent throughout the transition zone (Fig. 4 B—E). Four endarch bundles at the end of the transition zone alternated in position with the protoxylem points of the root (Fig. 4 E). The length of the transition zone was about 1.5 mm.

The cortex and the epidermis in the transition zone were similar to the cortex and epidermis of the primary root. The endodermis was distinct but the cells were irregular in outline as seen in transverse section. Casparian strips were well developed.

The endodermis, cortex, and epidermis of the transition zone disintegrated early in the seedlings. Ten-day-old seedlings showed a disintegration of these tissues. All tissues outside the endodermis were shed before the formation of the periderm. The endodermis, because of its well-developed Casparian strips, appeared capable of restricting the radial transport of inorganic solutes and photosynthetic products and thereby possibly starving the tissues external to it. This sloughing exposed the endodermis which in turn was broken up in places due to the increase in diameter of the tissues of the stele. Meristematic action did not seem to be restricted to a cambium layer, but occurred in some cells of the pericycle and interfascicular areas. The endodermis was the outermost layer of intact cells of this zone in a 30-day-old seedling.

THE PEG AND ASSOCIATED REGION OF THE HYPOCOTYL. The peg was not anatomically discernable in the embryo and made its appearance during germination. It was produced by four-to five-fold radial elongation but retained about the same tangential dimension as the adjacent cortical cells. They measured 5×20—25 µ in transverse section.

The hypocotyl region associated with the peg had an irregularly angled central cavity. This was due to the splitting of the pith region in which only the large central cells disintegrated. The four endarch collateral bundles were surrounded by relatively homogeneous parenchymatous tissue. These bundles became bicollateral with the appearance of the internal phloem at the upper end of the peg region (Fig. 4 F). Here the phloem completely enclosed the cambium and the primary xylem. Details of the ontogeny of the internal phloem were not studied, therefore it was not possible to determine whether it resulted from a lateral extension of the outer phloem or had its own procambial origin. The internal phloem was much less than the external. The central cavity formed by the disintegration of the central pith in the lower hypocotyl was closed at the level where the internal phloem appeared lowest down.

The epidermis, cortex, and pith of a 30-day-old seedling were intact. Neither the endodermis nor the pericycle could be recognized in this region of the hypocotyl.

THE UPPER PART OF THE HYPOCOTYL. The part of the hypocotyl above the peg accounted for more than 3/5 of the total length of the hypocotyl and often attained a length of 3 cm. As seen in Fig. 4 G, this part of the hypocotyl was simple externally but its internal structure, particularly the vasculation, was relatively complex. This figure shows three distinct patterns of vasculation. Four vascular bundles above the peg were arranged in pairs and maintained their size and spatial relationship half way to the cotyledonary node. Each bundle was divided into two smaller but unequal bundles and the splitting of each of the four bundles into four smaller bundles was not simultaneous so that in transverse section one group would appear as two or three and the

other group as three or four. Above the level where the four bundles had branched the hypocotyl had a total of eight bundles for a vertical distance of 0.7 mm (Fig. 4 C). Two adjacent smaller bundles anastomosed and formed an inverted Y on the opposite side of the stele. This reduced the number of vascular bundles to six and established the beginning of the second pattern of vasculation. The six bundles in the second pattern were arranged into two groups of three each (Figs. 1, 4 G). The two bundles, each from two of the anastomosed bundles described above were smaller and lacked phloem fibres. The six vascular bundles retained their spatial and size relationships up to the cotyledonary node where they coalesced.

Origin of Secondary Roots

The origin and development of secondary roots involved the pericycle, endodermis, and cortex of primary roots. The primordium of the secondary roots developed from the pericycle perhaps from inner cells of the cortex of the primary root. The cortex of the primary root provided a small digestive pouch and the cells immediately behind the pouch were meristematic, but did not contribute cells to the secondary root.

The internal structure of mature secondary roots was similar to that of the primary root. The number of xylem points was more variable. The xylem ranged from diarch to terarch, the latter being the more common.

Adventitious Roots

Adventitious roots were observed on all three regions of the hypocotyl but none were as strongly developed as those in the transition zone of the hypocotyl. Adventitious roots from other regions of the hypocotyl were small.

Adventitious roots characteristically were initiated and developed opposite each xylem point low in the transition zone of the hypocotyl and each was ultimately connected with the xylem of the hypocotyl. The four adventitious roots were initiated at approximately the same level and were visible in the same transverse section (Fig. 3 B). Their development and structure were similar to those of secondary roots. Adventitious roots in the upper part of the hypocotyl arose from the interfascicular parenchyma. Each was connected to one of the vascular bundles of the hypocotyl.

Cotyledons

From the cotyledonary plate two vascular strands diverged towards each cotyledon and corresponded in position to the four vascular bundles of the lower hypocotyl (Fig. 4 H). Each strand was divided at the base of the cotyledonary petiole so that the proximal end of the petiole had four vascular strands (Fig. 4 H). Towards the distal end of the cotyledonary petiole, the two median strands anastomosed and concurrently the lateral strands branched and resulted in five vascular strands at the distal end of the cotyledonary petiole. The two anastomosed median strands became a conspicuous part of the midrib of the cotyledon. Anastomosis was often gradual so that in some specimens the midrib contained two parallel strands. At the proximal end of the blade of the cotyledon the two most lateral strands were divided so that seven strands constituted the main vascular system of the cotyledon. These main veins were interconnected by veinlets.

The mesophyll tissue of mature cotyledons was not discernable as palisade and spongy layers, unlike that in the dormant cotyledons in the seed. Instead, it was a loosely packed tissue with much air space. There appeared to be no increase in cell number over earlier stages as seen in transverse section. Epidermal surfaces were smooth.

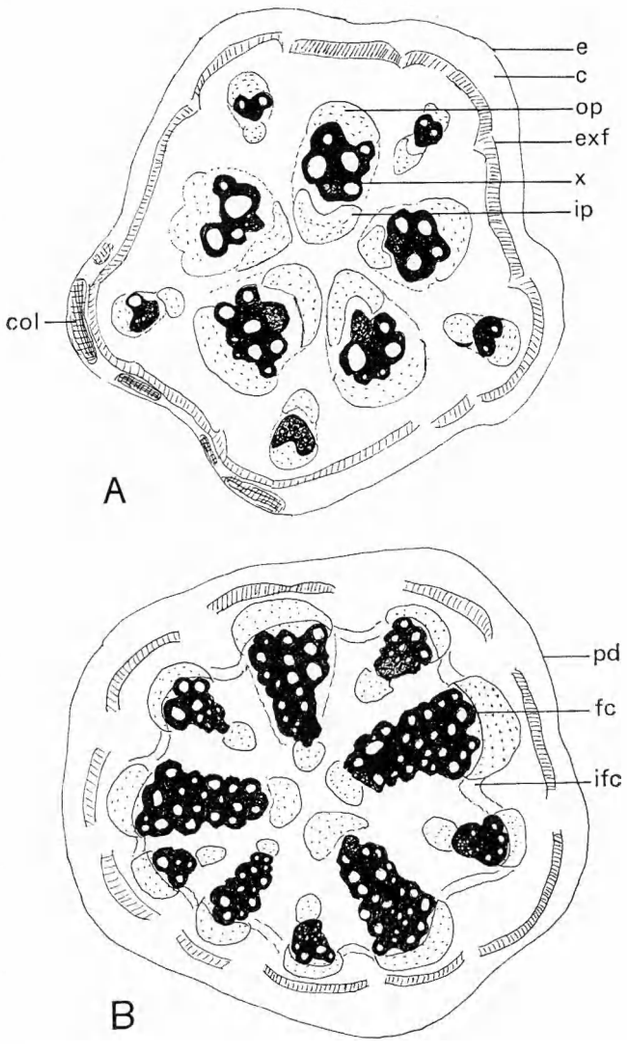


Fig. 5. *Coccinia abyssinica.* — A: Diagram of transverse section of stem showing spatial and size relationship of tissues at the tenth internode from first expanded leaf in the shoot apex. — c: cortex (parenchyma, chlorenchyma). col: collenchyma. e: epidermis. exf: extra-xylary fibre cylinder. ip: internal phloem. op: outer phloem. x: xylem. — B: Diagram of transverse section of stem showing spatial and size relationship of tissues at the twenty-third internode from first expanded leaf in the shoot apex. — fc: fascicular cambium. ifc: interfascicular cambium. pd: periderm.

The Shoot of the Seedling

There were no significant morphological changes from those described earlier for the seedling stage except for more a rapid growth in the shoot of the adult plant.

THE SHOOT APEX. The shoot apex was not studied in detail, but the corpus appeared to be enclosed by a two-layered tunica. The apical dome was small. Leaf primordia were initiated high in the apical dome. The growth of each leaf primordium overtook the shoot apex so that the apex and the leaf primordium appeared nearly equal.

In a young seedling there were six procambial strands arranged in two groups of three each above the cotyledonary plate (Fig. 4 H). The central strand in each group divided twice resulting in a total of six procambial strands (Fig. 4 H, I). A similar number of more irregularly disposed procambial strands was observed in the young internodes of the adult plant.

PRIMARY TISSUES OF THE INTERNODES. The following description of the primary tissues is largely based on the tenth and twenty-third internodes from the first expanded leaf in the shoot apex in mature plants. Figure 5 shows the location and size relationship of the primary tissues at these internodes.

The epidermis was uniseriate, more or less uniform in transverse section (Fig. 6) and composed of vertically elongated cells. The epidermis had multicellular trichomes and stomata. The guard cells had many chloroplasts.

The cortex was composed of the following zones: (1) collenchyma interrupted by chlorenchyma; (2) starchy parenchyma; (3) cylinder of fibre cells; and (4) parenchyma tissue. The collenchyma zone was discontinuous, first formed at the ridges and six to seven layers thick. This zone became continuous with age and enlarged particularly beneath the ribs. Zone two of starchy parenchyma consisted of one to three layers. Zone three, a cylinder of fibres, was uniformly thick and nearly continuous in young stems, but became discontinuous in older stems and located as caps opposite vascular bundles. It was weakly developed in the first intermode from the cotyledonary node (Fig. 6 B).

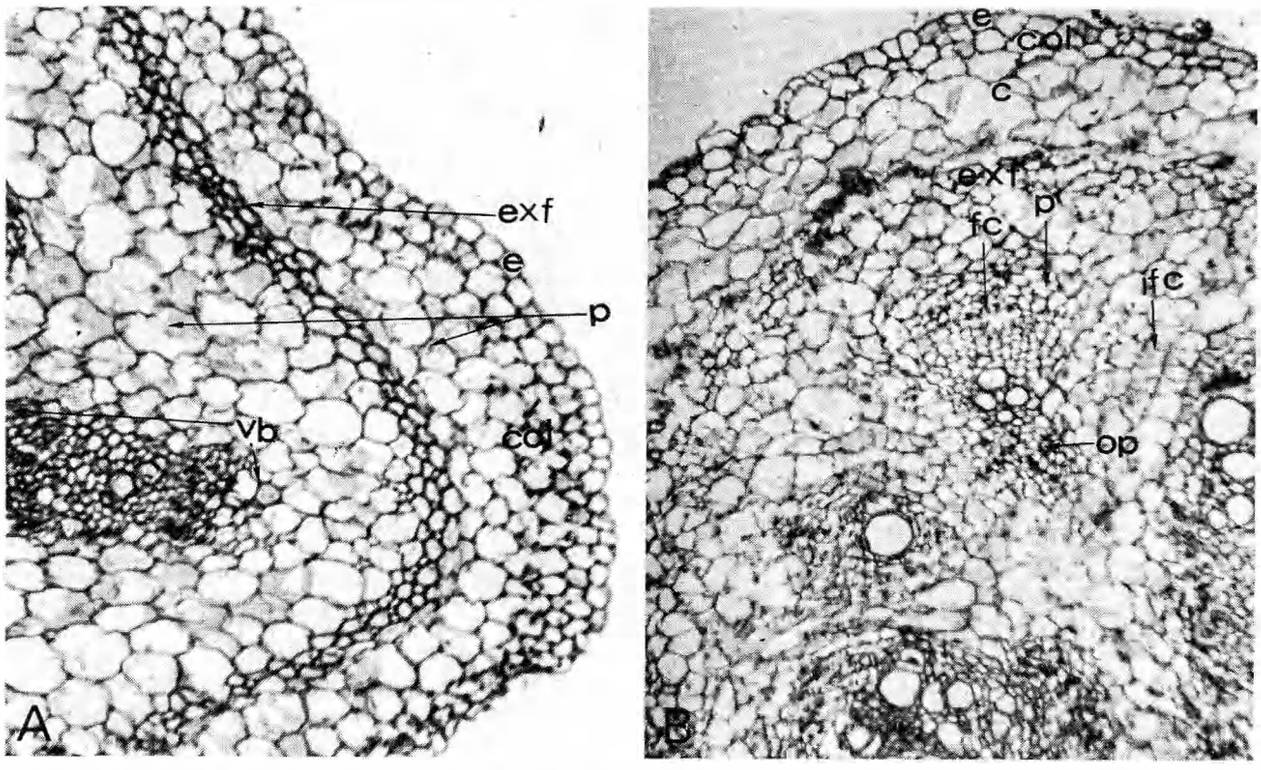


Fig. 6. *Coccinia abyssinica.* — A: Transverse section of part of a stem of an 83-day-old plant at the third internode from the cotyledonary node showing a vascular bundle and other adjacent tissues. — col: collenchyma. e: epidermis. exf: extra-xylary fibres. p: parenchyma. vb: vascular bundle. — B: Transverse section of part of a stem of a 70-day-old plant at the second internode from the cotyledonary node showing initiation of secondary tissues. — fc: fascicular cambium. ifc: interfascicular cambium. — A—B ×350.

Fibres constituting the cylinder were weakly developed and had wide lumina and uniformly thick walls in transverse section. Some retained their protoplasm and some did not have sloping end-walls. Zone four consisted of thin-walled parenchyma contiguous with the phloem and with the interfascicular areas (Fig. 6). This was the innermost zone of the cortex.

The pith collapsed in the centre of the stem. The ten prominent vascular bundles appeared to be in two series. The outer five vascular bundles were smaller and occurred opposite the ribs while the inner five vascular bundles were located opposite the furrows. The first and second internodes from the cotyledonary plate had eight or fewer vascular bundles irregularly disposed in one ring. Most vascular bundles were bicollateral, but sometimes one or two of the inner group were collateral. One of the five inner bundles was decidedly smaller than the others.

DISCUSSION

Although anchoté seedlings are similar in most features to those of *Cucurbita* (RUTLEDGE 1930; WHITING 1938), they differ in the early thickening and hairiness of the hypocotyl. The structure of the apical meristem of the primary root agrees with that reported by JANCZEWSKI (WHITING 1938), who observed a common group of initials from which all primary root tissues arose.

The transition from the exarch xylem of the root to the endarch arrangement of the shoot is not unique. It takes place by changes in the position of the protoxylem and metaxylem and by the differentiation of a central mass of paren-

chyma. Four collateral bundles above the transition zone alternate with the xylem points of the primary root unlike the condition found in *Cucurbita* (RUTLEDGE 1938) in which a doubling of the number of bundles occurs. Transition in anchoté is similar to that in *Citrullus* (HUFFORD 1938). The transition zone is unusual in that here four adventitious roots are produced. These adventitious roots develop early and complicate the structure of the transition zone.

The ruptured central portion of the pith in the peg region is limited to the larger central cells. This cavity is interpreted as the result of the stress due to increase in diameter in the peg and the unbending of the hypocotyl curvature. Stress due to the reorientation of the vascular strands can not be ruled out.

The internal phloem strands appear first just above the peg, and appear to end blindly here. The internal and external phloem are connected and encircle the primary xylem in each bundle above the peg for a very short distance. Beyond this level the hypocotyl has bicollateral bundles and the internal phloem strands remain with the hypocotylar strands as they diverge into the cotyledons. A similar arrangement of vascular tissues is seen in *Citrullus* (HUFFORD 1938) and in several other genera (FUKUDA 1967).

Unlike *Citrullus,* in which four bundles increase to six by the division of bundles at the ends of the oval (HUFFORD 1938), in anchoté all four bundles divide above the peg region. The hypocotyl of anchoté thus has eight strands for a short distance in the upper half until the adjacent daughter strands unite and reduce the number of strands to six.

DESHPANDE and KASAT (1966) reported that six bundles in the upper hypocotyl in *Coccinia* resolved into ten, of which four enter the cotyledons. In anchoté, six bundles coalesce at the cotyledonary node where the original four hypocotylar bundles or their positional equivalents each branch and diverge into the cotyledons. Concurrently, the central bundle in each bundle group of three derived from the union of the daughter bundles divide twice, resulting in six epicotylar bundles arranged in two groups of three each in the intercotyledonary plane. This arrangement is not in agreement with HUFFORD's (1938) observation on *Citrullus* in which all of the hypocotylar bundles terminated in the cotyledons.

DANGEARD (1889) described the relationship of foliar and hypocotylar bundles in the family and stated that the hypocotyledonary axis was modified later by the descent of foliar traces. In anchoté, all bundles of the hypocotyl of a mature seedling are already established as procambial strands in the dormant embryo prior to germination and long before the initiation of the leaves. Their number and arrangement as well as the general outline of the hypocotyl does not alter during subsequent stages of growth.

The first two leaves of the young shoot of the seedling each have three traces which are connected with the six bundles of the internodes above the cotyledons. This agrees with what was reported for *Citrullus* by WHITING (1938). The internodes below the first two leaves are invariably short while those above are longer and generally have less than ten vascular bundles. Similarly, the young internodes of the stem near the apex show eight or fewer procambial strands that are variable in size as seen in transverse section. This agrees with ZIMMERMANN's observations (1922) on *Coccinia engleri.*

Young and mature internodes of anchoté contain bicollateral vascular bundles which vary in size similar to that illustrated by ZIMMERMANN (1922) for *Coccinia engleri.* The irregular arrangement of bundles in the internodes of the young stem may be the result of displacement caused by leaf and branch traces. The ten vascular bundles in mature internodes are interpreted as forming only one ring. The tendency for bundles to appear in two rings is restricted to the angular young

stages. The observation of sinuous cambium in mature stems further reinforces the conclusion that the vascular bundles in the internodes of anchoté are in one cylinder. This interpretation is in agreement with POTTER's (HOLROYD 1924) earlier findings on *Cephalendra* (*Coccinia*) and HOLROYD's (1924) on *Luffa,* and disagrees with the generally accepted hypothesis that the family is characterized by two concentric rings of bicollateral bundles.

ACKNOWLEDGEMENTS

The author expresses his sincere thanks to Dr E. S. FORD for his guidance during the course of the research as well as for his help in preparing the final manuscript. Thanks are also extended to Dr MILDRED M. GRIFFITH for advice in the preparation and interpretation of material.

This article is part of a Ph. D. dissertation presented to the Graduate Council of the University of Florida, Gainesville, Florida (U.S.A.).

LITERATURE CITED

BLYTH, A. 1958. Origin of primary extraxylary stem fibers in dicotyledons. — Calif. Univ. Publ. Bot. 30: 145—231.

CRAFTS, A. S. 1932. Phloem anatomy, exudation and transport of organic nutrients in Cucurbits. — Plant Physiol. 7: 183—225.

DANGEARD, P. A. 1889. Recherches sur le mode d'union de la tige et de la racine chez les dicotylédones. — Botaniste 1: 75—125.

DESHPANDE, B. D. & KASAT, M. L. 1966. Seedling anatomy of certain members of the Cucurbitaceae. — Proc. Indian Acad. Sci. 64 (B): 62—67.

EAMES, A. J. 1961. Morphology of the angiosperms. — New York.

FAHN, A. 1967. Plant anatomy. — Oxford and New York.

FOSTER, A. S. 1934. The use of tannic acid and iron chloride for staining cell walls in meristematic tissue. — Stain Technol. 9: 91—92.

— & GIFFORD, E. M., Jr. 1959. Comparative morphology of vascular plants. — San Francisco and London.

FUKUDA, Y. 1967. Anatomical study of the internal phloem in the stems of dicotyledons with special reference to its histogenesis. — Jour. Fac. Sci., Univ. Tokyo, Sec. 3 Bot.: 314—375.

GETAHUN, A. 1973. Developmental anatomy and germination of seeds of anchoté, Coccinia abyssinica (W. & A.) Cogn. (Cucurbitaceae). — Bot. Notiser 126: 437—449.

GHOSH, E. 1932. On the microstructure of the stem of Bengal Cucurbitaceae with reference to its value in taxonomy. — J. Indian Bot. Soc. 11: 259—270.

HAGERUP, O. 1930. Vergleichende morphologische und systematische Studien über die Ranken und andere vegetative Organe der Cucurbitaceen und Passifloraceen. — Dansk Bot. Arkiv 6 (8).

HAYWARD, H. E. 1938. The structure of economic plants. — New York.

HOLROYD, R. 1924. Morphology and physiology of the axis in Cucurbitaceae. — Bot. Gaz. 78: 1—44.

HUFFORD, G. N. 1938. Development and structure of the watermelon seedling. — Bot. Gaz. 100: 100—122.

JEAN, M. 1926. Essai sur l'anatomie comparée du liber interne dans quelques familles de dicotylédones. Etude des plantules. — Botaniste 17: 225—364.

JOHANSEN, D. A. 1940. Plant microtechnique. — New York and London.

LARUE, C. D. 1939. The peg of the cucurbits: a structure induced by growth hormone? — Amer. J. Bot. 26 (suppl.): 9s—10s.

METCALFE, C. R. & CHALK, L. 1950. Anatomy of the dicotyledons. — Oxford.

RUTLEDGE, R. W. 1930. The histological anatomy of the hypocotyl of Cucurbita maxima Duchesne. — Ph. D. dissertation. Dept. of Botany, University of Chicago.

SASS, J. E. 1951. Botanical microtechnique. — Ames.

SINGH, B. 1942. The anatomy of the stem, leaf and petiole of Coccinia indica L. — J. Indian Bot. Soc. 21: 319—326.

SNOW, R. 1965. The causes of the bud eccentricity and the large divergence angles between leaves in Cucurbitaceae. — Philos. Trans. R. Soc. (Land.) B. 250. No. 762: 53—77.

WHITING, A. G. 1938. Development and anatomy of primary structures in the seedlings of Cucurbita maxima Duch. — Bot. Gaz. 99: 497—528.

WORSDELL, W. C. 1915. The origin and meaning of medullary (intraxylary) phloem in the stem of dicotyledons. 1. Cucurbitaceae. — Ann. Bot. 29: 567—590.

YASUDA, A. 1901. On the comparative anatomy of the Cucurbitaceae, wild and cultivated in Japan. — J. Col. Sci. Imp. Univ. Tokyo, Japan 18: 1—56.

ZIMMERMANN, A. 1922. Die Cucurbitaceen. Beiträge zur Anatomie, Physiologie, Morphologie, Biologie, Pathologie, und Systematik. — Jena.

Population Structures in Higher Plants as Revealed by Thin-layer Chromatographic Patterns

Gunnar Weimarck

WEIMARCK, G. 1974 09 13. Population structures in higher plants as revealed by thin-layer chromatographic patterns. — Bot. Notiser 127: 224—244. Lund. ISSN 0006-8195.

Some methods of handling and interpreting data on variation in non-identified leaf compounds separated by TLC were tested in a methodological study. *Senecio viscosus, Melandrium rubrum, Hieracium vulgatum, Gagea lutea, Cardamine bulbifera, Ranunculus ficaria, Viola mirabilis, Luzula pilosa, Thymus serpyllum, Valeriana dioica, Circaea lutetiana, C. alpina* and *C. intermedia* were chosen to represent different habits and modes of reproduction. The plants were coded, randomized and grown under uniform conditions. Variation in spot patterns was estimated by a modified hierarchical analysis of variance within extracts, between plants, between populations and, in *Circaea,* between taxa. An additional experiment with repeated sampling was performed in *Hieracium vulgatum.* Phenograms were constructed from cluster analyses. Only characters that did not vary within plants were considered reliable as a base for classification of spot phenotypes. Variation in these characters revealed genotypic variation in most taxa. Population structures were considered in relation to habit and reproduction. Some methods used in numerical chemotaxonomy were discussed.

Gunnar Weimarck, Department of Plant Taxonomy, University of Lund, Ö. Vallgatan 18—20, S-223 61 Lund, Sweden.

INTRODUCTION

Taxonomists study genetic variation at different levels, viz. between species or taxa of higher orders, between populations within one and the same taxon and between individuals within one and the same population. The hereditary variation is more or less obscured by non-hereditary variation (modification) and by experimental error.

It has long been the practice of taxonomists to draw conclusions concerning genotypic variation from variation in morphological characters. During the last 10—15 years the study of chemical characters has come to play an increasing part at each of the taxonomic levels mentioned above. In the first flush of optimism efforts were made to apply to chemical characters the type of numerical analysis earlier used for morphological characters by "numerical taxonomists". The value of this "numerical chemotaxonomy", based mainly on non-identified compounds, was soon put to question as giving no better results than numerical taxonomy based upon any other type of character. Some points of view have, for example, been forwarded by RUNEMARK (1968) and WEIMARCK (1972). Some possible sources of errors have been analysed by WEIMARCK (1970) and ADAMS (1972).

The present paper is concerned with a methodological study intended to elucidate some of the possibilities and short-comings in the use of non-identified chemical compounds as characters for an analysis of genotypic variation in higher plants. Some conceivable methods of handling and interpreting the results have been tried and will be discussed here. The study

deals with variation between populations and between individuals. Knowledge of the population structures of a plant group is often of essential interest, particularly if the group is "critical" for one reason or another. The balance between amphimixis and apomixis, allogamy and autogamy, and the presence or absence of hybridization are some of the factors reflected in population structure. It is often difficult or impossible to clarify population structure from a study of the variation displayed in morphological characters. The chromatographic technique has proved to be of value in such cases (WEIMARCK 1970, 1972).

MATERIAL

Ten taxa were selected to represent different habits and modes of reproduction. An additional three taxa forming a hybrid complex were partly accounted for by WEIMARCK (1974). The taxa are listed below and a list of localities appears in the Appendix.

Senecio viscosus L. (Asteraceae)
Melandrium rubrum (WEIG.) GARCKE (Caryophyllaceae)
Hieracium vulgatum (FR.) ALMQU. s. str. (Asteraceae)
Gagea lutea (L.) KER-G. (Liliaceae)
Cardamine bulbifera (L.) CR. (Brassicaceae)
Ranunculus ficaria L. (Ranunculaceae)
Viola mirabilis L. (Violaceae)
Luzula pilosa (L.) WILLD. (Juncaceae)
Thymus serpyllum L. (Lamiaceae)
Valeriana dioica L. (Valerianaceae)
Circaea lutetiana L. (Onagraceae)
Circaea alpina L. (Onagraceae)
Circaea intermedia EHRH. (Onagraceae)

For each taxon five collections were studied. Collection sites were chosen so as to be fairly well spaced within Skåne, southernmost Sweden.

As regards *Senecio* and *Melandrium,* achenes and seeds were sampled from mother plants taken from the whole area occupied by the population concerned. The diaspores of each mother plant were sown in separate pots in the Botanical Gardens, Lund, and one seedling per pot was allowed to grow up. Whole plants of the other taxa were taken from the entire area occupied by the population and transplanted to pots in the Gardens. In all cases not less than 10, usually about 15 plants per collection, were cultivated. Voucher specimens collected in the field are deposited at the Botanical Museum, Lund (LD).

After wintering in the Gardens, the plants were coded and randomized within each taxon. Non-random effects of possible varying environmental factors due to the position of a given collection or part of a collection in the frame were considered to have been mainly ruled out at the time of sampling.

Leaves were sampled when the plants of the taxon concerned were at flowering and early fruiting stage. The only exception was *Melandrium,* of which first-year rosette leaves were sampled. All plants of the same taxon were sampled within approximately two hours. The samples were rapidly dried between paper at a temperature not exceeding 40°C with the aid of a simplified heating fan device according to WIDDER (1970). The samples were then stored in the dark until extraction.

CHROMATOGRAPHIC METHOD

Samples for extraction were taken from 10 plants from each collection. Plants grown at the very edge of the frame were avoided as far as possible due to the possible risk of modification. Extraction was made in 0.5 or 1.0 ml of a mixture of methanol and 1-M hydrochloric acid (100:1 v/v). The amount of dry tissue used varied between taxa (25—100 mg) but was constant for all plants of the same taxon. The tissue was finely cut and left for extraction for at least 24 hours.

Separation was carried out two-dimensionally on glass plates 20×20 cm pre-coated with an Avicel cellulose layer (Merck 5716). The starting-point was in one of the corners of the plate, 3 cm from each edge. The running length was restricted in both directions to 15 cm by means of two grooves in the layer. The amount of extract applied varied between 10 and 20 µl according to the taxon so that the chromatograms would give approximately the same intensity of spot patterns, subjectively estimated, and as few spots as possible with an intensity near the threshold of perception. The amount was constant for each taxon. Two plates were processed from each extract. Identification of the plates was based on the code numbers only.

The "multiple sandwich chamber" technique described by WEIMARCK (1970) was used except that instead of using a frame padded with foam plastic the stack was sealed on three sides with broad painter's tape. Up to 24 plates could be processed simultaneously in each stack. Duplicate plates were always placed in different stacks.

Separation was made first in 200 ml distilled water: 4 ml formic acid, then in 100 ml iso-amylalcohol: 60 ml glacial acetic acid: 50 ml distilled water.

The plates were examined in UV light (Fluotest, 360 nm) after dipping them in 0.1 % diphenylboric acid ethanolamine complex (Koch-Light 2287 h) in propanol. Each spot was characterized by R_F (the distance a spot had moved on the plate relative to the solvent front) in two directions and by colour in UV light. No compound was identified chemically. Spot intensity was expressed roughly as "faintly visible" or "clearly visible".

The two plates from each extract were examined separately. This in combination with code numbering excluded the risk of subjective influence. Not until after all plates had been examined were the results decoded. The randomization had been maintained up to this point. The spots were numbered at a later stage. The numbering in each taxon was independent of that in other taxa with the exception of *Circaea,* where the spots of all three taxa were numbered collectively.

HANDLING OF DATA

Analysis of Variance of Variation in Patterns

A modified analysis of variance of a hierarchical type was made to clarify the amount of information received from the total number of spots in relation to the inevitable effects of variation due to experimental error, inconsistent estimation of spot intensity, etc. The intensity scale "not visible", "faintly visible" and "clearly visible" was expressed as 0, 2 and 3. The merits of this scale have been discussed by WEIMARCK (1970 p. 255). The separate contributions to the total variation of differences between plates of the same plant, between plants of the same collection, between collections of the same taxon, and (in *Circaea* only) between taxa were calculated.

If a collection is designated i, plant j, plate k, spot l and spot intensity X the variation between the two plates of the same plant was measured by Q_3, where

$$Q_3 = \sum_l \frac{1}{2}(X_{ij1}(l) - X_{ij2}(l))^2.$$

The variance between plates for a taxon as a whole, σ_3^2, was estimated by the mean, $\overline{Q}_3$, of all 50 Q_3's obtained.

The variation between plants within a collection was measured by Q_2, where

$$Q_2 = \sum_l \left(\frac{1}{2}(X_{ij1}(l) + X_{ij2}(l)) - \frac{1}{20} \sum_{jk} X_{ijk}(l) \right)^2.$$

The quantities Q_2 include variation arising both from real differences between plants and from experimental error. Let σ_2^2 be the variance between plants within collection for a taxon as a whole. Then σ_2^2 does not include experimental error, and to get an estimate of σ_2^2 it is necessary to subtract from Q_2 the error due to σ_3^2. Thus σ_2^2 was estimated by $\frac{10}{9}\overline{Q}_2 - \frac{1}{2}\overline{Q}_3$, where the factors $\frac{10}{9}$ and $\frac{1}{2}$ were chosen to make the estimate unbiased and $\overline{Q}_2$ is the mean of the 50 Q_2's obtained.

Variation between collections was measured by Q_1, where

$$Q_1 = \sum_l \left(\frac{1}{20} \sum_{jk} X_{ijk}(l) - \frac{1}{100} \sum_{ijk} X_{ijk}(l) \right)^2.$$

The variance between collections for a whole taxon was estimated by $\sigma_1^2 = \frac{5}{4}\overline{Q}_1 - \frac{1}{9}\overline{Q}_2$, where the factors $\frac{5}{4}$ and $\frac{1}{9}$ compensate for plant variation and variation due to experimental error, making the estimate unbiased, and $\overline{Q}_1$ is the mean of the 5 Q_1's obtained.

In *Circaea* the three different taxa were compared, making it necessary to introduce a new index h, designating the taxon.

Variation between taxa was measured by Q_0, where

$$Q_0 = \sum_l \left(\frac{1}{100} \sum_{ijk} X_{hijk}(l) - \frac{1}{300} \sum_{hijk} X_{hijk}(l) \right)^2.$$

The variance between taxa was estimated by $\sigma_0^2 = \frac{3}{2}\overline{Q}_0 - \frac{1}{4}\overline{Q}_1$. In this unbiased estimate variation within the taxa is compensated for. $\overline{Q}_0$ is the mean of the 3 Q_0's observed.

The standard error of the estimated σ_3^2 was calculated from the formula $S.E._3 = \frac{s_3}{\sqrt{50}}$, s_3 being the standard deviation of the 50 Q_3's.

The standard error of the estimated σ_2^2 was calculated from the formula

$$S.E._2 = \sqrt{\left(\frac{10}{9}\right)^2 \frac{s_2^2}{5} + \left(\frac{1}{2}\right)^2 \frac{s_3^2}{50}},$$

s_2 being the standard deviation of the mean of the Q_2's for the 5 collections.

The standard errors of the estimated σ_1^2 and σ_0^2 were not calculated.

The quantity σ_3^2 can be regarded as a measure of how well the TLC method estimates zero, since it represents the experimental error after the extraction procedure. If it is presumed that there were no differences between plants of a collection, the variation found will be due to experimental error only, and σ_2^2 would equal zero. Whether or not σ_2^2 was significantly different from zero was checked by a t-test given by

$$t = \frac{\frac{10}{9}\bar{Q}_2 - \frac{1}{2}\bar{Q}_3}{S.E._2}.$$

The t-test is valid due to the fact that the Q_2 and Q_3 values were obtained by adding a large number of measurements and thus have an approximately normal distribution, and further to the fact that the Q_2 and Q_3 values are non-correlated, regardless of whether the spots were dependent on each other or not.

The number of degrees of freedom was chosen as 4, which makes the test somewhat conservative.

Cluster Analysis of Patterns

Affinities between chromatographic patterns were illustrated by a series of cluster analyses executed by means of a centroid clustering programme, BMDP 2 M, from the University of California in Los Angeles.

The mean values of the two plates from each plant were used. Spot intensity was weighted in the same way as for the analysis of variance. Cluster analyses within each individual taxon (some of them not shown here) were made from all 50 plants, but analyses involving all three *Circaea* taxa simultaneously were made from 20 plants only per taxon due to restrictions in the number of variables accepted by the programme.

The clustering was performed in the following way (notations, see p. 226). The distance d between the plant j' in collection i' and the plant j'' in collection i'' was calculated for each pair of plants among the 50 plants of a taxon (of *Circaea*, 60 plants), where

$$d = \sqrt{\sum_l \left(\frac{1}{2}(X_{i'j'1}(l) + X_{i'j'2}(l)) - \frac{1}{2}(X_{i''j''1}(l) + X_{i''j''2}(l))\right)^2}.$$

The two plants found to be situated at the shortest distance from each other were linked up at the level determined by the distance between them. (The scale in Figs. 2 and 3 was obtained in this way.) Then the mean values of the spot intensities in the two plants were calculated. These mean values were thereafter treated as if they constituted values of one plant. The procedure was repeated for the units thus obtained until the whole material had become linked up in one single cluster.

A cluster analysis of individual plates was also carried out for the same 20 plants per taxon of *Circaea* as above.

Choice of Reliable Information

A classification of spot phenotypes in individual plants was based on the presence or absence of spots regardless of intensity. The spots were divided into three groups of which two were accepted for further study.

(1) Spots that occurred in all plants of a taxon were accepted for further study even in cases where the spot was occasionally found in only one of the two plates of the same plant. They were considered to be of general occurrence in the material concerned and thus did not carry any information on variation in population structure. They were denoted *invariable.*

(2) Spots that occurred in some but not all of the plants studied in a taxon were also accepted provided there was no inconsistency at all between plates. Such spots were denoted *consistent.* There are good reasons for regarding such observed differences in consistent spots as representing actual qualitative or quantitative differences between extracts (and, provided the extraction technique was consistent and modification due to external factors negligible, between plants also).

If for example, a given spot was found in all in two plates only of a taxon, the probability that the second one would occur in the other plate of the same plant would be $\frac{1}{99}$, provided the difference between observations was caused by random variation around the threshold of perception. (The number of plates was 100.) This also holds if a given spot is lacking in two plates only of the same plant. The probability of finding at least one such pair in any spot of a taxon by mere chance would be $1-(1-\frac{1}{99})^n$, if n is the number of spots occurring (or lacking) in exactly two plates. If a given spot was found in four plates of a taxon, the probability that they would be found in two plants only by mere chance is $\frac{3}{99 \cdot 97}$. The probability of finding in one taxon at least once in any spot four plates forming two pairs by mere chance would be $1-(1-\frac{3}{99 \cdot 97})^n$, if n is the number of spots that occurred (or were lacking) in exactly four plates in the taxon concerned. In the same way it is possible to calculate the probability of finding three, four, etc. pairs by chance. The same formulae were used for both observed and lacking spot pairs, although it could be argued that departure from randomness expressed as absence of a pair is more likely to be due to errors of extraction than departure expressed as presence of a pair.

Using a Poisson approximation an accumulated p-value was calculated. This value is given in Table 3 for the actual findings in each taxon. The distribution of consistent spots is obviously not due to any appreciable degree to random error in observation.

(3) The spots rejected were those that did not occur in all plants and that showed inconsistent variation between plates of the same plant. It would obviously be easy to overlook them on account of an intensity close to the threshold of perception or the difficulty of recognition. Such a spot could, with a rather high degree of probability, be overlooked in both plates of a plant, thus giving inadequate information. Spots of this category were denoted *inconsistent* in the sequence.

RESULTS AND DISCUSSION

The results of the analyses of variance of entire spot patterns are shown in Tables 1 and 2 and in Fig. 1. The results of the cluster analyses are shown in Figs. 2 and 3. The results of the study of variation in consistent spots were used to characterize spot phenotypes within the taxa concerned. These are summarized in Table 1 and shown in greater detail in Tables 3 and 4.

Analysis of Variance

The estimated variance between plates, σ_3^2, was highest in *Ranunculus ficaria* both in absolute terms and as calculated per spot (Table 1). In this material there

Table 1. Analysis of variance of overall spot patterns and results from information from consistent spots. Total number of spots = n.

Taxon	Analysis of variance										Number of deviating plants	Number of phenotypes
	Plate			Plant				Collection		n		
	$\sigma_3^2 = \overline{Q}_3$	S.E.$_3$	σ_3^2/n	$\overline{Q}_2$	σ_2^2	S.E.$_2$	p-value of difference between σ_2^2 and zero	$\overline{Q}_1$	σ_1^2			
Senecio viscosus	11.07	0.73	0.23	14.86	10.97	1.71	$0.001 < p < 0.01$	3.01	2.11	48	7	5
Melandrium rubrum	13.03	1.10	0.22	26.87	23.34	2.00	$p < 0.001$	3.30	1.14	60	11	5
Hieracium vulgatum	9.72	0.84	0.12	16.75	13.75	2.13	$0.001 < p < 0.01$	1.78	0.36	82	3	4
Gagea lutea	11.30	0.71	0.16	29.77	27.43	1.92	$p < 0.001$	4.37	2.16	72	10	8
Cardamine bulbifera	12.70	0.71	0.22	15.98	11.40	2.23	$0.001 < p < 0.01$	5.71	5.37	59	23	4
Ranunculus ficaria	17.90	1.18	0.30	20.16	13.45	2.16	$0.001 < p < 0.01$	4.62	3.53	60	1	2
Viola mirabilis	6.34	0.51	0.14	7.45	5.11	0.38	$p < 0.001$	2.14	1.85	45	0	1
Luzula pilosa	9.99	0.59	0.16	16.26	13.08	0.98	$p < 0.001$	1.76	0.39	64	15	4
Thymus serpyllum	15.59	0.96	0.21	24.44	19.36	1.22	$p < 0.001$	2.22	0.06	73	4	5
Valeriana dioica	7.18	0.52	0.18	8.76	6.14	0.50	$p < 0.001$	1.22	0.55	41	0	1
Circaea lutetiana	11.83	0.96	0.22	14.25	9.92	2.01	$0.001 < p < 0.01$	4.87	4.51	54	4	4
C. alpina	13.93	1.17	0.19	21.20	16.59	3.30	$0.001 < p < 0.01$	2.09	0.26	74	2	3
C. intermedia	9.34	0.68	0.15	8.31	4.57	1.36	$0.01 < p < 0.05$	1.11	0.46	62	4	4
Hieracium vulgatum ..... (additional experiment)	14.98	1.05	0.18	24.43	19.66	1.83	$p < 0.001$	14.81	15.80	81	3	3

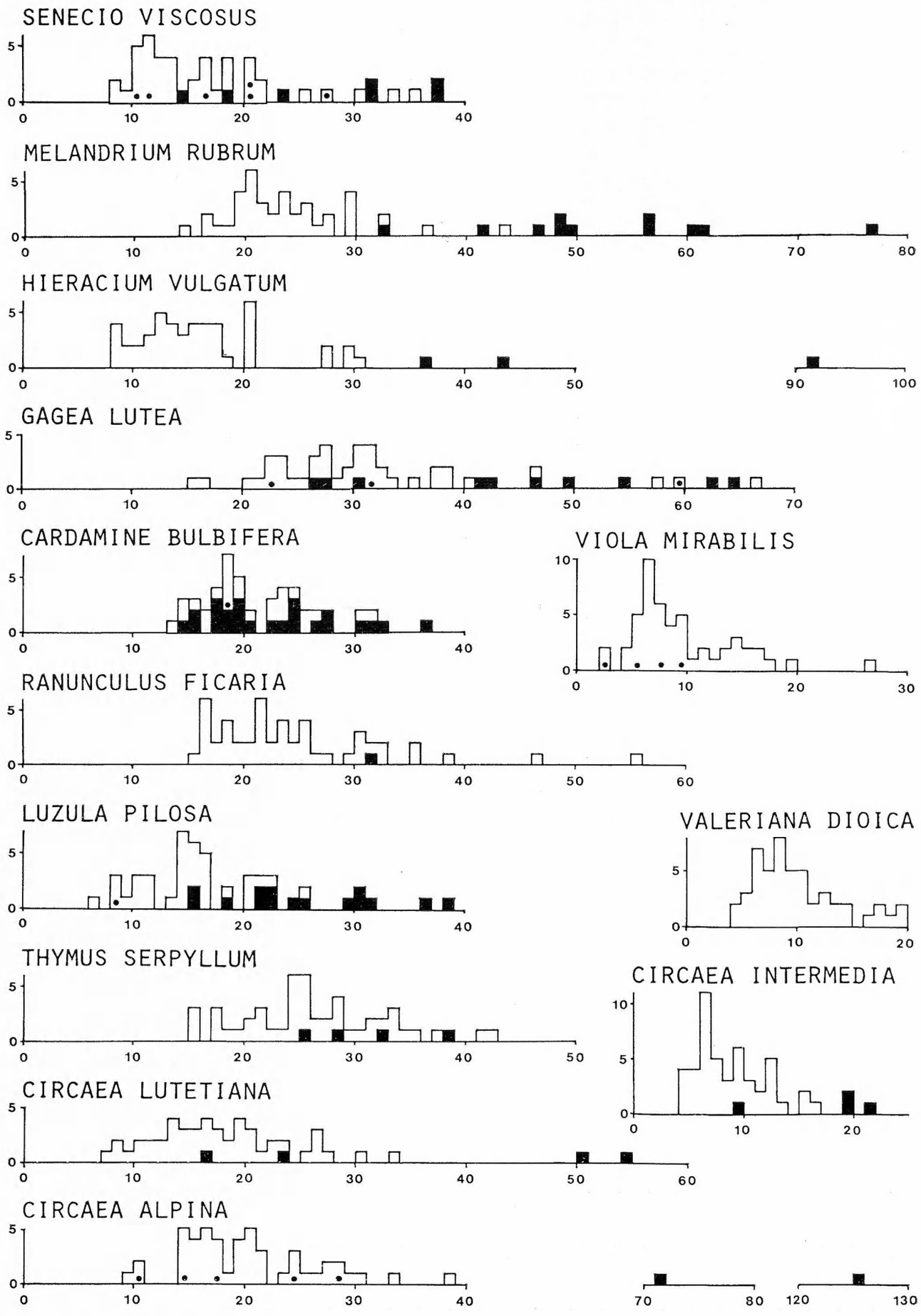

SENECIO VISCOSUS
MELANDRIUM RUBRUM
HIERACIUM VULGATUM
GAGEA LUTEA
CARDAMINE BULBIFERA
VIOLA MIRABILIS
RANUNCULUS FICARIA
LUZULA PILOSA
VALERIANA DIOICA
THYMUS SERPYLLUM
CIRCAEA INTERMEDIA
CIRCAEA LUTETIANA
CIRCAEA ALPINA

Fig. 1.

was some difficulty in analysing the patterns due to a strong tendency to tailing. Tailing presented no problems in the other taxa. In these taxa σ_3^2 is probably just an indication that the effort to avoid spots with an intensity close to the threshold of perception was not always equally successful. The correlation between σ_3^2 and the total number of spots was weakly positive, the correlation between σ_3^2/total number of spots and the total number of spots being weakly negative. It can thus hardly be argued that the number of spots found in a taxon substantially influences the precision of observation as regards each separate spot.

The estimated variance between plants within collection, σ_2^2, was highest in *Gagea lutea, Melandrium rubrum* and *Thymus serpyllum,* and lowest in *Circaea intermedia, Viola mirabilis* and *Valeriana dioica.* These results obtained from entire spot patterns do not conflict with those obtained from the analyses of spot phenotypes based on consistent spots only. σ_2^2 was statistically significant in all taxa studied. The highest p-value was found in *Circaea intermedia.*

The individual estimates of variance between plants within collection, Q_2, are shown diagrammatically in Fig. 1. They correspond rather closely to the E-values for individual plants reported by WEIMARCK (1970). The Q_2 values for plants with a deviating spot phenotype according to consistent spots are in general somewhat above the mean for the taxon as a whole, but many exceptions occur. A plant consistently deviating in one or a few spots does not necessarily display any general trend in the entire pattern. Extremely high Q_2 values as found in *Hieracium vulgatum* and *Circaea alpina* were found in single plants deviating from all the rest of the taxon in a great number of spots. But Q_2 cannot distinguish plants when they are phenotypically deviating in one or a few spots only, or when several plants deviate instead of single ones. In such cases, variation in consistent spots where adequate information is likely to be found, is masked by variation in inconsistent spots, many of which probably afford no adequate information at all at individual level (cf. WEIMARCK 1972). In *Cardamine bulbifera,* for example, where the two most frequent spot phenotypes, 1 and 2, are represented in the material by 27 and 21 plants respectively, the property of the formula for calculating Q_2 makes the individual Q_2's unusable for discriminating between them and gives all plants moderate values in spite of the distinct differences in spot phenotype obviously present in the material.

Much of the variance estimated by individual Q_2 values in the different taxa derives from inconsistent spots and therefore reflects errors in extraction. These errors are probably largely responsible for the fact that σ_2^2 differs significantly from zero.

Plants cultivated at the edges of the frame could not be completely avoided in all taxa due to shortage of material. None of these plants proved to be phenotypically deviating judged from consistent spots, nor were they represented by higher Q_2 values in general (Fig. 1). Modification due to position in the frame thus did not seem to influence the results.

The estimated variance between collections, σ_1^2, was highest in *Cardamine bulbifera,* where the frequency of spot phenotypes 1 and 2 was very different in the

Fig. 1. Diagrams of variation in the overall chromatographic pattern between plants. — Horizontal axis: individual Q_2 values. Vertical axis: number of plants. Solid squares: plants showing spot phenotypes differing from the one most frequent in the taxon (see Table 3). Dots: plants cultivated at the edge of the frame. — Unlike the Q_2 values used to calculate σ_2^2, the Q_2's shown here were not calculated within each individual collection, but for each taxon as a whole according to the formula $Q_2 = \sum_l \left(\frac{1}{2}(X_{ij1}(l) + X_{ij2}(l)) - \frac{1}{100} \sum_{ijk} X_{ijk}(l) \right)_2$.

Table 2. Contributions made by different spot categories to variation found in *Circaea*. The values have been extracted from calculations of Q_0. — Category 1: invariable spots. 2: consistent spots. 3: diagnostic spots. 4: diagnostic consistent spots. 5: partly diagnostic consistent spots. 6: partly invariable spots. 7: partly consistent spots. 8: inconsistent spots. The categories are defined in the text. — n: number of spots per category. A: contribution to Q_0. B: Contribution to Q_0, % of total Q_0. C: Contribution to Q_0 per spot in the category. D: Contribution to Q_0, % of total Q_0 per spot in the category. — $\overline{Q}_0 = 49.62$; $\sigma_0^2 = 73.75$.

Spot category	n	*Circaea lutetiana*				*C. alpina*				*C. intermedia*			
		A	B	C	D	A	B	C	D	A	B	C	D
1	7	0.38	0.66	0.05	0.09	0.27	0.44	0.04	0.06	0.15	0.51	0.02	0.07
2	6	0.02	0.03	0.00	0.00	0.09	0.15	0.02	0.03	0.04	0.12	0.01	0.02
3	9	29.82	51.50	3.31	5.72	10.78	17.44	1.20	1.94	6.44	22.09	0.72	2.45
4	4	4.12	7.12	1.03	1.78	5.07	8.20	1.27	2.05	2.56	8.80	0.64	2.20
5	2	0.60	1.04	0.30	0.52	4.62	7.48	2.31	3.74	4.00	13.73	2.00	6.87
6	18	9.13	15.77	0.51	0.88	18.93	30.61	1.05	1.70	6.26	21.50	0.35	1.19
7	4	2.52	4.36	0.63	1.09	6.09	9.85	1.52	2.46	2.14	7.35	0.54	1.84
8	35	11.31	19.53	0.32	0.56	15.96	25.82	0.46	0.74	7.55	25.91	0.22	0.74
Total ...	85	57.90	100.01			61.81	99.99			29.14	100.01		

different collections. It was also high in *Circaea lutetiana* and *Ranunculus ficaria*. σ_1^2 was very low in *Thymus serpyllum, Circaea alpina, Hieracium vulgatum, Luzula pilosa* and *Circaea intermedia*. The significance of the σ_1^2 value could not be tested statistically.

The σ_0^2 value estimated for the three *Circaea* taxa was calculated at a very high hierarchical level and thus has a very complex basis. The calculations of Q_0 were chosen for a detailed analysis that elucidated the contributions of different spots to variation at different levels.

In Table 2, the spots are grouped into categories 1—8 according to mode of variation. The contributions of (1), invariable spots (1—7), to the Q_0 value was of course extremely small. The contribution from (2), consistent spots (18, 21—24, 30), was of the same order. The contribution from (3), diagnostic spots (8—16, whose presence or absence distinguishes a taxon from the other two), which were invariable in each taxon was about 40—80 times as high. The (4) diagnostic, consistent spots (17, 20, 25, 26, considered to indicate introgression when found in plants of a taxon which in general lacked the spot concerned in the material studied) contributed to a minor extent, as did (5), spots 27 and 28, which were inconsistent in *lutetiana*, consistent in *alpina* and invariable in *intermedia*. The spots that displayed inconsistency in either one or two taxa and were invariable in the rest form a heterogeneous category (6). They are not shown in Table 3. Most of them are very weak spots probably of more or less general occurrence in the material, but which have escaped detection in some plant of one or two taxa. Some are, however, likely to belong more naturally to the diagnostic category, but have been eliminated due to inconsistency. There are a sufficient number of these to contribute substantially to the Q_0 value. The spots of category (7), viz. (19, 29, 31, 32) are consistent in one taxon, missing or inconsistent in the others. They are of variable intensity and weak in taxa where they are inconsistent. Each of them makes a considerable contribution to the Q_0 value. The last category (8) is more or less wholly inconsistent. One could have expected that it cannot reasonably yield definite information but predominantly produces "noise". Still, the contribution to the Q_0 value is considerable.

From Table 2 and the above analysis

it is evident that less than 40 % of Q_0 in *Circaea* stems from diagnostic spots and diagnostic consistent spots, more than 35 % from spots where it was doubtful if any information could be extracted and about 25 % from spots which apparently contained no analysable, adequate information at individual level. At least some of the inconsistent spots which could not be used to distinguish individual plants or populations displayed enough different mean values to make it possible to distinguish between taxa. However, I stick to the opinion earlier stated (WEIMARCK 1972) that entities distinguishable on any diagnostic character whatsoever are in general best separated without calculating any numerical index. Besides, we do not know whether the thirteen diagnostic spots found in the *Circaea* material are the result of the existence of the same number of differences in biosynthetic pathways. It cannot be taken for granted that the weighting of the difference between taxa is proportional to the number and intensity of diagnostic spots.

The analysis of variance would have been far more difficult or indeed impossible to carry out if the material had not been randomized or if the number of plants and collections per taxon had not been kept constant. The latter is of less importance when handling consistent spots only, provided there is sufficient material to keep the effects of chance within reasonable bounds.

The method used in this study requires a fixed number of populations and plants per taxon, which constitutes a serious drawback, as this is seldom possible in practical taxonomic work.

An Additional Experiment Using Hieracium vulgatum

An additional experiment was performed using collection 4 of *Hieracium vulgatum* (Tables 1, 4). The same ten plants of the collection as were used in the main study (1) were studied in a further four samples. Samples were taken: (2) from a different leaf on the same shoot as that used in the main study, sampled on July 24, 1972; (3) from a leaf of the voucher specimen collected on July 20, 1971; (4) from a leaf sampled on June 18, 1973; and (5) from a leaf sampled on September 12, 1973. These five different samples from the same collection were treated numerically in the same way as the samples from each taxon used in the main study. The σ_1^2 value, however, estimated variation due to sampling from the same collection at different times.

The overall variation of patterns as estimated by σ_2^2 was greatest in (3), the sample taken on the original site. The smallest contribution to σ_2^2 came from the sample used in the main study. Even in plants grown under "uniform" conditions the tendency to individual modification may be greater at the beginning and end of the period of vegetation, when minor differences in external factors might affect the rhythm of development more than during the time of maximum vegetative activity. It is, however, not certain that the differences in Q_2 contributed by the five samples are significant.

The greatest contribution to σ_1^2 was also given by (3). The σ_1^2 value was almost 45 times that of *Hieracium vulgatum* in the main study and about 3 times that of the highest one found in the entire main study (in *Cardamine bulbifera*). The effect of modification in the very same plants sampled on different occasions is thus impressive (cf. also the findings by WEIMARCK 1970 and ADAMS 1972). The wisdom of drawing conclusions as regards genotypic variation from overall patterns obtained from plant material that has not been grown under uniform conditions and randomized, can thus be doubted.

The results of a study of phenotypic variation in consistent spots did not differ drastically from those of the main study. Weak, inconsistent spots were probably most severely affected by sampling on different occasions, and the overall pattern

Table 3. Spot phenotypes based on information obtained from invariable and consistent spots. — Six spots in *Circaea lutetiana*, 6 in *C. alpina* and 14 in *C. intermedia* are not accounted for since they were invariably present in the taxon concerned and inconsistent in the others. Nor were they included in WEIMARCK 1974 p. 289. — – indicates inconsistency. — The probability that the variation in spot phenotype is random is given for each taxon.

Senecio viscosus $p < 1\times10^{-6}$

Population	1		2	3		4			5		
Phenotype	1	2	1	1	3	1	3	4	1	4	5
No. of plants	8	2	10	9	1	8	1	1	8	1	1
Spot											
1—12	×	×	×	×	×	×	×	×	×	×	×
13—14	·	×	·	·	·	·	·	·	·	·	×
15	·	·	·	·	×	·	×	·	·	·	×
16	·	·	·	·	·	·	·	×	·	×	·

Melandrium rubrum $p < 1\times10^{-6}$

Population	1			2		3		4				5
Phenotype	1	2	3	1	2	1	3	1	2	4	5	1
No. of plants	7	2	1	6	4	9	1	7	1	1	1	10
Spot												
1—4	×	×	×	×	×	×	×	×	×	×	×	×
5	×	·	×	×	·	×	×	×	·	×	×	×
6	·	·	×	·	·	·	×	·	·	·	·	·
7—8	·	·	·	·	·	·	·	·	·	×	·	·
9	·	·	·	·	·	·	·	·	·	×	·	·

Hieracium vulgatum $p < 1\times10^{-6}$

Population	1	2	3		4		5	
Phenotype	1	1	1	2	1	3	1	4
No. of plants	10	10	9	1	9	1	9	1
Spot								
1—31	×	×	×	×	×	×	×	×
32—34	×	×	×	·	×	×	×	×
35	×	×	×	·	×	×	×	·
36	×	×	×	·	×	·	×	×
37	×	×	×	·	×	·	×	·
38—39	·	·	·	×	·	·	·	·

Gagea lutea $p < 1\times10^{-6}$

Population	1		2		3					4				5	
Phenotype	1	2	1	3	1	3	4	5	6	1	5	7	8	1	7
No. of plants	9	1	9	1	6	1	1	1	1	7	1	1	1	9	1
Spot															
1—12	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×
13	×	×	×	×	×	×	×	×	·	×	×	×	×	×	×
14	×	×	×	×	×	×	×	·	×	×	·	×	×	×	×
15	×	×	×	·	×	·	·	×	×	×	×	×	×	×	×
16	×	·	×	·	×	·	·	×	×	×	×	×	×	×	×
17	·	×	·	·	·	·	×	·	·	·	·	×	×	·	×
18	·	·	·	·	·	·	·	·	·	·	·	·	×	·	·

Cardamine bulbifera $p < 1\times10^{-6}$

Population	1			2	3			4		5	
Phenotype	1	2	3	1	1	2	4	1	2	1	2
No. of plants	5	4	1	10	5	4	1	6	4	1	9
Spot											
1—10	×	×	×	×	×	×	×	×	×	×	×
11—12	·	×	·	·	·	×	×	·	×	·	×
13—14	·	·	×	·	·	·	·	·	·	·	·
15	·	·	·	·	·	·	×	·	·	·	·

Ranunculus ficaria $p \simeq 2\times10^{-2}$

Population	2	3	4	5		6
Phenotype	1	1	1	1	2	1
No. of plants	10	10	10	9	1	10
Spot						
1—6	×	×	×	×	×	×
7	·	·	·	·	×	·

Viola mirabilis

Population	2	4	5	6	7
Phenotype	1	1	1	1	1
Spot					
1—24	×	×	×	×	×

Luzula pilosa $p \simeq 2\times10^{-3}$

Population	1			3		4			5		6	
Phenotype	1	2	3	1	2	1	2	4	1	2	1	2
No. of plants	5	1	4	9	1	7	2	1	6	4	8	2
Spot												
1—23	×	×	×	×	×	×	×	×	×	×	×	×
24	×	×	×	×	×	×	×	·	×	×	×	×
25	×	·	×	×	·	×	·	×	×	·	×	·
26	·	·	×	·	·	·	·	·	·	·	·	·

Thymus serpyllum $p < 1\times10^{-6}$

Population	1			2		3	4	5	
Phenotype	1	2	3	1	4	1	1	1	5
No. of plants	8	1	1	9	1	10	10	9	1
Spot									
1—18	×	×	×	×	×	×	×	×	×
19	×	×	×	×	×	×	×	×	·
20	×	×	×	×	·	×	×	×	×
21	×	·	×	×	×	×	×	×	×
22	·	·	×	·	·	·	·	·	·

Valeriana dioica

Population	1	2	3	4	5
Phenotype	1	1	1	1	1
Spot					
1—17	×	×	×	×	×

Table 3 (continued).

Circaea lutetiana									$p \simeq 5\times10^{-4}$	*C. alpina*							$p < 1\times10^{-6}$	*C. intermedia*							$p \simeq 8\times10^{-4}$
Population	1	2		4			5	6		1	2	4	5				6	1		2	3	5	7		
Phenotype	1	1	2	1	3	4	1	1		5	5	5	5	6	7		5	8	9	8	8	8	8	10	11
No. of plants	10	8	2	8	1	1	10	10		10	10	10	8	1	1		10	9	1	10	10	10	7	2	1
Spot																									
1—7	×	×	×	×	×	×	×	×		×	×	×	×	×	×		×	×	×	×	×	×	×	×	×
8—14	·	·	·	·	·	·	·	·		×	×	×	×	×	×		×	×	×	×	×	×	×	×	×
15	×	×	×	×	×	×	×	×		·	·	·	·	·	·		·	×	×	×	×	×	×	×	×
16	×	×	×	×	×	×	×	×		·	·	·	·	·	·		·	·	·	·	·	·	·	·	·
17	·	·	×	·	·	·	·	·		×	×	×	×	×	×		×	×	×	×	×	×	×	×	×
18	×	×	×	×	×	·	×	×		×	×	×	×	×	×		×	×	×	×	×	×	×	×	×
19	·	·	·	·	×	×	·	·		–	–	–	–	–	–		–	–	–	–	–	–	–	–	–
20	·	·	·	·	·	·	·	·		×	×	×	×	·	×		×	×	×	×	×	×	×	×	×
21—24	·	·	·	·	·	·	·	·		·	·	·	·	×	·		·	·	·	·	·	·	·	·	·
25—26	×	×	×	×	×	×	×	×		·	·	·	·	·	×		·	×	×	×	×	×	×	×	×
27—28	–	–	–	–	–	–	–	–		·	·	·	·	·	×		·	×	×	×	×	×	×	×	×
29	–	–	–	–	–	–	–	–		×	×	×	×	×	·		×	–	–	–	–	–	–	–	–
30	×	×	×	×	×	×	×	×		×	×	×	×	×	×		×	×	×	×	×	×	×	×	·
31	·	·	·	·	·	·	·	·		–	–	–	–	–	–		–	·	·	·	·	·	·	×	·
32	–	–	–	–	–	–	–	–		–	–	–	–	–	–		–	×	·	×	×	×	×	×	×

of consistent spots was fairly constant. Still, the intensity of some of the spots (17—31) found to be invariably present in the main study was so affected in one or more of the other samples as to make the spots inconsistent, and they were therefore discarded in this experiment. One spot discarded in the main study was consistently present in the additional experiment where it was numbered 42. The way of treating the data implies that the predominant spot phenotype will be defined in another way than that in the main study. The conclusions that may be drawn from variation in spot phenotype are, however, very similar to those in the main study.

In the main study one plant in the collection deviated phenotypically in lacking spots 36 and 37 (spot phenotype 3, Table 3). This plant also consistently lacked the two spots in the additional experiment, but in some of the samples the overall intensity was affected to an extent sufficient to make variation inconsistent. The two spots were therefore not considered in this experiment. In sample (5), spot 40 characterized the same plant (spot phenotype 7, Table 4). This spot had not previously been observed in the material. Another spot not earlier observed, 41, characterized two other plants in sample (3). These plants had not been found to deviate in the main experiment. Spot 40 probably exemplifies a case where a deviating genotype was not expressed phenotypically under the conditions prevailing in the main experiment. In the case of spot 41 influence from possible heterogeneity in the environment cannot be excluded.

Cluster Analysis

The results of the cluster analyses of *Circaea* spot patterns are given in the form of phenograms (Fig. 2). They were mainly used to investigate the amount of

Table 4. Phenotypes based on information obtained from invariable and consistent spots in the additional experiment involving collection 4 of *Hieracium vulgatum*. Information on samples are given in the text. The probability that the phenotypic variation observed is random is $p \simeq 8\times10^{-4}$.

Sample	1	2	3		4	5	
Phenotype	5	5	5	6	5	5	7
No. of plants	10	10	8	2	10	9	1
Spot							
1—16, 42	×	×	×	×	×	×	×
40	·	·	·	·	·	·	×
41	·	·	·	×	·	·	·

relevant information to be found at different levels in the spot categories defined in Table 2.

The 20 plants of each taxon were selected to include those suspected of being products of introgression on the evidence of spot phenotype and pollen stainability (WEIMARCK 1974). In addition some plants showing no phenotypic deviation in consistent spots but with decreased pollen stainability were included, as well as some "normal" plants (judged by the criteria used).

Fig. 2 A is based on all spots, B on categories 1—4 (see Table 2), C on categories 5—7, and D on category 8.

In Fig. 2 A, one of the four deviating *lutetiana* plants was linked up with the others at a very high level of dissimilarity. The other three did not separate out clearly, nor did the other plants with low pollen stainability.

One of the two deviating *alpina* plants was linked up to *intermedia* and the other to the rest of *alpina* at a very high level of dissimilarity (it having four intense spots not found elsewhere). None of the other plants separated out clearly.

On the whole the spot patterns of *intermedia* were more uniform than those of the other taxa. Three of the four deviating plants formed clusters at a relatively high level of dissimilarity.

In Fig. 2 B most plants of course formed clusters at a lower level of dissimilarity. One of the two *alpina* plants mentioned above linked up to *intermedia* as in Fig. 2 A, the other one quite separately.

In Fig. 2 C the most deviating plants could still be observed. Taxa were to some extent intermingled in the clusters.

In Fig. 2 D the clustering was rather similar to that in C.

Thus, the results from the analysis of sources of Q_0 (Table 2) could be confirmed in part at least. At species level, spot categories 5—8 obviously contained a good deal of relevant information, part of which was lost when categories 6 and 8 were discarded in the study of spot phenotypes.

In the cluster analysis of individual plates (not illustrated here) 22 plants only of the 60 chosen had their plates linked up to each other before plates from other plants were included in the clusters. The affinity between patterns of individual plants in the taxa studied was evidently often of the same order as the affinity between plates of the same plant.

In the cluster analyses of taxa other than *Circaea* means for all 50 plants of each taxon were considered. Spots of different categories were not studied separately. Phenograms for four species are shown in Fig. 3.

In *Cardamine bulbifera* all plants of spot phenotype 1 were linked up in one single cluster. All but two plants of spot phenotype 2 were linked up in another cluster together with the plant representing spot phenotype 4. The plant representing spot phenotype 3 was linked up at a higher level of dissimilarity, and two remaining spot phenotype 2 plants formed a pair of their own. This fact suggests the possibility that the two last-mentioned plants

---

Fig. 2. Phenograms showing affinities between chromatographic patterns of 20 selected plants each of *Circaea lutetiana* (circles), *C. alpina* (triangles) and *C. intermedia* (squares). — A: All 85 spots considered. — B: The 26 spots of categories 1—4 considered. — C: The 24 spots of categories 5—7 considered. — D: The 35 spots of category 8 considered. — Spot phenotypes other than 1, 5 and 8 are shown for the plants concerned. Solid symbols: plants in which pollen stainability was below 65 %. The pollen stainability of some plants, including the *alpina* plant with spot phenotype 7, could not be checked. The scale units are explained in the text (p. 227). — The "reversals" occurring here and there in Figs. 2 and 3 are typical for the centroid method. They occur when the distance between centroids decreases as the groups link up. The vertical arrangement of individual plants is to some extent arbitrary.

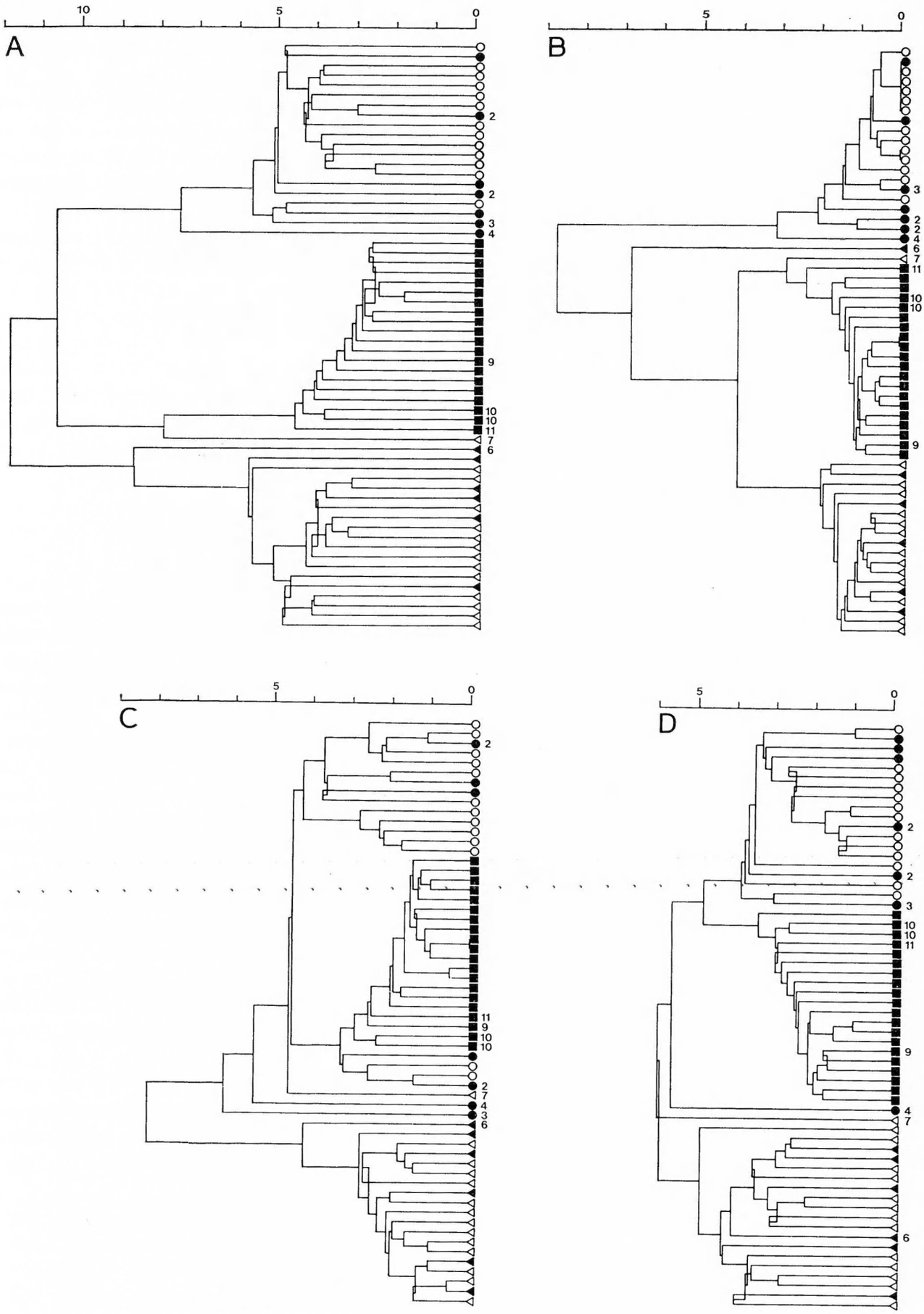

A
10
5
0
2
2
3
4
9
10
10
11
7
6
B
5
0
3
2
2
4
6
7
11
10
10
9
C
5
0
2
11
9
10
10
2
7
4
3
6
D
5
0
2
2
3
10
10
11
9
4
7
6

Fig. 2.

were actually different from the other ones classified as belonging to spot phenotype 2, but that some information had been lost when discarding non-consistent spots. The grouping shown by the phenogram is obviously not random but could not have been interpreted with any accuracy without a previous knowledge of spot phenotypes.

The phenogram of *Gagea lutea* does not make much sense. The phenotypes based on consistent spots were mixed in a way that cannot reasonably be interpreted. Although variation in consistent spots had shown that real phenotypic dissimilarities are very likely to exist in the material, this information was obviously unable to penetrate the scatter.

The three deviating spot phenotypes found in *Hieracium vulgatum* in the main study were very clearly separated out by the cluster analysis. The five different samples of the additional experiment were not separated out clearly in spite of the fact that the σ_1^2 value obtained in the analysis of variance was extremely high. Seven plants of sample (3) (voucher specimens from the original locality) were linked up separately, the remaining three were placed in various other clusters. This sample had obtained the highest Q_1 value. The high dissimilarity between plants within sample (3) was also clearly demonstrated in the phenogram. The four other samples were still more intermingled with each other. The differing spot phenotypes were not separated out. The five samples of each single plant were not in any case linked up together.

A cluster analysis demands a reasonably hierarchical structure of the material concerned to produce a meaningful phenogram. In the additional experiment with *Hieracium vulgatum* there is no such hierarchical structure. Instead, we have one grouping due to similarities between plants sampled on the same occasion and another due to similarities between samples of the same plant. Superimposed upon these two conflicting patterns is a random variation. Such a reticulate pattern of phenotypic variation is probably very common in biological material, for instance when studying parallel series of races in a number of related species. It should be borne in mind that a cluster analysis does not adequately illustrate variation in such cases.

SNEATH & JOHNSON (1972) showed that it is of advantage to include a great number of variables when studying taxa of lower organisms even if at the same time the inexactness of the information would also be increased within certain limits. The present evidence indicates that this also holds for higher plants. However, it is also evident that it does not apply at or below the population level.

Genotypic Variation

Up to this point phenotypic variation only has been discussed. Evidence obtained from the analyses of modification and error in extraction and observation indicates that the effects can be eliminated to a great extent by discarding inconsistent spots. The role of mere chance is probably extremely small. Thus, at least most of the differences in consistent spots reflect true differences between extractions. In *Hieracium vulgatum* the plants deviating from the most frequent spot phenotype in the main study deviated also in one of the samples of the additional experiment, although not in the same spot. Random variation is not very likely in this case. In *Circaea,* good agreement was shown between chromatographic evidence, pollen stainability, and leaf pubescence, all indicating introgressive traits (WEIMARCK 1974 and below). At least most differences between extractions in other taxa are in all likelihood also caused by different genotypes.

The method of discarding information derived from spots showing inconsistent variation probably, however, involves a certain loss of relevant information (see discussion on spot categories (6) and (8)

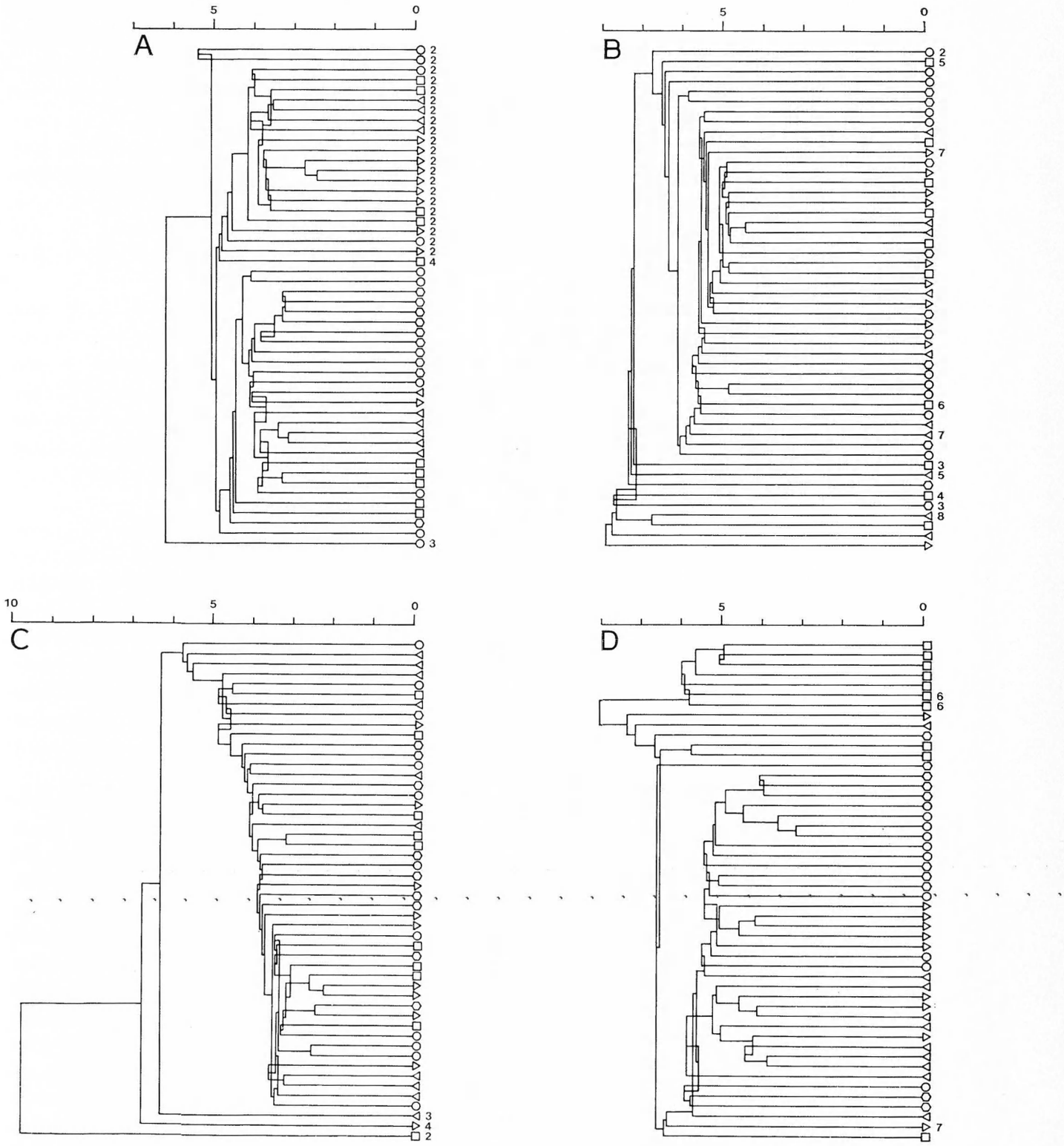


Fig. 3. A—C: Phenograms showing affinities between chromatographic patterns of 50 plants each of A: *Cardamine bulbifera,* B: *Gagea lutea* and C: *Hieracium vulgatum.* Collections 1—5 are designated by 1: circles; 2: hexagons; 3: squares; 4: triangles, one corner to the left; and 5: triangles, one corner to the right. — D: Phenogram showing affinities between chromatographic patterns of 5 samples each of 10 plants of *Hieracium vulgatum* (collection 4). Samples 1—5 are designated as collections in A—C. — Spot phenotypes other than 1 are shown for the plants concerned in A—C and spot phenotypes other than 5 in D. — See also text accompanying Fig. 2.

in the text concerning Table 2 and Figs. 2 and 3). In this connection chance may play a more important part, since a single failure in separation or observation would exclude a spot from the experiment. It is therefore hardly wise to place too much significance on failure to demonstrate variation in a taxon. Moreover, variation found in characters other than those obtained chromatographically were not taken into consideration in this study. The most conspicuous examples were flower and inflorescence characters in *Thymus serpyllum* and leaf dentation in *Hieracium vulgatum*. Distribution according to sex of plants was, however, documented in *Melandrium rubrum* and *Valeriana dioica*.

Information derived from overall spot patterns cannot be used to analyse genotypes of single individuals. One cannot assume a one-to-one correspondence between a gene and a chromatographically distinguishable "secondary" substance. There are many steps in the production of a single substance, and a single shift in the biosynthetic pathway may give rise to a group of new substances. Estimates obtained from analysis of variance, based on the overall spot pattern, are therefore not very suitable for characterizing single individuals although they give valuable information on sources of variation in the material taken as a whole. For example, the E-values for single plants presented by WEIMARCK (1970) could be used only after it had been shown that few varying spots were strongly correlated with one another; still they estimated a combination of experimental error and relevant information (discussed in WEIMARCK 1970 pp. 259—261). The technique used in that context implied that at least two plates made from each extract were examined and the maximum value of each spot was taken into account. That method of combining values from more than one observation diminished the experimental error at this level, but at the same time made it impossible to estimate the size of the error.

The disturbing effects of biochemically correlated spots is all the more serious if the effect of squaring in some formulae is not taken into account (WEIMARCK 1970 p. 255).

In the present study, the individual Q_2 values are obviously of limited interest in the analyses of genotypes. Other types of calculations based on overall spot patterns, such as those providing indices of biochemical distance, matching coefficients, coefficients of similarity and those used for making isarithm maps would probably have produced partly irrelevant groupings within the material at individual level as did those used for making phenograms (cf. above). Many spots contain predominantly nonsense information.

In my opinion variation in non-identified phenolic spots, even if they are consistent, does not provide a suitable basis for a precise gene analysis such as that described in a number of reports based on information from allozymes. Still this type of consistent spot can obviously supply fairly easily accessible additional information on population structures in plants.

A precise analysis of the genotypical constitution based on "secondary" compounds would demand identification of the substances concerned, analysis of biosynthetic pathways and a survey of the mode of inheritance by means of crossing experiments. These tasks are very laborious to carry out on the vast scale necessary to give biologically meaningful results, and they are usually not very attractive from the chemist's point of view. Much valuable information could, however, be obtained from such chemical identification, and investigations of this type are a desideratum in any taxonomic or genetic project.

Mode of Reproduction and Variation

Information on mode of reproduction and habit has, in general, been obtained

from FRYXELL (1957) and H. WEIMARCK (1953) and from personal experience.

Senecio viscosus is an annual herb held to be mostly allogamous. Some of the material studied failed to set fruit. Although this is remarkable in an annual plant, the reason has not yet been investigated. All populations but one were heterogeneous.

In *Melandrium rubrum,* a biennial or pauciennial dioecious plant, the material was too limited to permit of drawing conclusions as to a possible connection between sex and the genotypes discerned. All populations but one were heterogeneous, with up to four genotypes in one collection.

All *Hieracium* plants were determined to the microspecies *vulgatum* s.str. by an outstanding specialist, Professor E. ALMQUIST. All taxa within the group *Vulgatiformia* DAHLST. are regarded as obligate apomicts with the chromosome number 2n=27 in all cases examined. The evidence to hand indicates that a taxonomically definable microspecies does not necessarily consist of one biotype only. TURESSON (1943, 1956), who studied variation in morphology and resistance to disease in microspecies of *Alchemilla vulgaris,* arrived at a similar conclusion. SØRENSEN & GUÐJÓNSSON (1946) found a small proportion of morphologically deviating plants in microspecies of *Taraxacum.* They found that variation was associated with hypoploidy. In *Hieracium vulgatum* no cytological analysis was undertaken.

Gagea lutea propagates exclusively or almost exclusively by means of bulbil formation. To my knowledge it has not been observed to set functional seed in the region concerned. In spite of this genotypic variation is obviously considerable. The great number of genotypes observed makes the occurrence of different independent mutations seem probable, each of them giving rise to separate clones within the stands. A similar explanation was given by SUOMALAINEN and SAURA (1973) to account for the variation in allozymes found by them in parthenogenetic weevils.

Cardamine bulbifera is a perennial herb propagating by means of bulbils and rhizomes. Functional seed has seldom or never been observed in the region studied. The aberrant type (2) is very frequent in the material although not found in population 2. It is highly probable that a few genotypes propagate vegetatively side by side on the same sites.

Ranunculus ficaria showing almost no variation propagates to a great extent by means of bulbils.

Viola mirabilis has chasmogamous flowers early in spring, but these flowers generally set seed poorly. In late spring and early summer cleistogamous flowers develop and seed-setting is good. The lack of variation is not unexpected.

Luzula pilosa is a perennial chasmogamous plant forming small tufts. All populations are heterogeneous but the number of definable genotypes is moderate.

Thymus serpyllum forms small patches which often differ conspicuously in the density of inflorescences, in flowering time, frequency of abnormally developed inflorescences, colour of the flowers and leaves, habit, etc. It is polygamous and held to be capable of both autogamy and allogamy. Heterogeneity as to spot phenotype could be demonstrated in three populations. The plants were also scored as to three easily observable characters, viz. density of inflorescence, flowering time and occurrence of abnormal inflorescences. The heterogeneity in morphological characters was much greater than that in spot phenotype but also vaguer and more difficult to define in terms of genotype. No correlations with spot phenotypes could be found with certainty.

Valeriana dioica is a perennial dioecious herb. If genotypic heterogeneity exists, as could be expected, the method used was not capable of revealing it. Although

Valeriana dioica, together with *Viola mirabilis,* had the lowest total number of spots in the study the number of spots accepted for analysis of phenotypes was not exceptionally low in either of the two taxa.

Circaea lutetiana forms rather extensive stands by vegetative propagation and is likely to be predominantly allogamous (RAVEN 1963). *C. alpina* forms small patches by vegetative propagation and is likely to be predominantly autogamous (RAVEN 1963). The aberrant *alpina* and *lutetiana* plants found are probably products of introgression via *C. intermedia* which is the almost completely sterile hybrid between *alpina* and *lutetiana* evidently capable of a certain degree of back-crossing (WEIMARCK 1974). Of the *alpina* plants studied one only had sparsely pubescent leaves, viz. the plant showing spot phenotype 7. This fact gives a further indication of introgression since *alpina* normally has glabrous leaves but *intermedia* and *lutetiana* pubescent ones.

Obviously, variation in morphological characters and in spot patterns do not necessarily correspond to each other. A similar conclusion was arrived at by SELANDER & al. (1970), who showed that extreme stability over long periods of time in morphological characters of the classical phylogenetic "relic", *Limulus polyphemus,* did not imply a corresponding lack of enzymatic diversity.

The occurrence of one representative only of a deviating spot phenotype in a population was remarkably frequent in the taxa studied. It is at present impossible to judge whether this is a statistically significant phenomenon. One might argue that differing genotypes that have arisen from mutations usually tend to find difficulty in establishing themselves in great numbers due to the effects of chance and selection.

CONCLUSIONS

(1) The precision of the chromatographic separation technique and the mode of observation used is not very high. Spots with an intensity close to the threshold of perception give rise to a non-consistent variation which one has to be aware of.

Randomization of the material is very valuable for further treatment and necessary for an estimate of the probability that results obtained are due to chance or to real differences in the material.

(2) Analysis of variance makes it possible to estimate which parts of the total variation in the patterns have derived from different sources. The same plants that show the greatest amount of deviation in overall pattern do not necessarily deviate according to consistent spots, and vice versa. The accuracy of calculations based on overall patterns is reduced on account of errors in extraction, separation and observation. Phenograms constructed from overall spot patterns from the present material therefore turned out to be to some extent inadequate and misleading at individual and population levels. The failure of the clustering programme to separate out the five *Hieracium* samples in the additional experiment was especially interesting with a view to the great differences demonstrated by the analysis of variance. The same shortcomings would in all likelihood be found as regards other types of diagrams or different indices.

Variation found at infraspecific level makes comparisons between taxa based on single specimens dangerous.

With the reasonable precautions taken in experimental culture, modification of plants due to external factors is likely to play a minor part compared with technical error. Unless external factors are kept constant, however, modification can be considerable.

Problems of reproducibility and the difficulty of drawing conclusions concerning true genotypic variation from phenotypic variation are also met with when studying variation in conventional morphological characters, but are usually

more easily compensated for since we have much more experience of such characters. The need for a critical assessment of the reliability of conventional characters should also be stressed.

(3) Variation in the chromatographically obtained spot patterns can probably be best illustrated by the different phenotypes formed by combinations of consistent spots. Some information is no doubt lost when inconsistent spots are discarded but the remaining information can be regarded as fairly adequate. Most of the phenotypic variation in spots found in this study can be considered to reflect true genotypic heterogeneity. It is not possible to reach any reliable conclusions in cases when the method fails to reveal any variation in a given taxon.

(4) Phenotypic variation in spots most likely to reflect true genotypic differences could be demonstrated in all but two of the 13 taxa represented in this study. One of the two, *Valeriana dioica,* is remarkable in this respect since it is dioecious. On the other hand, *Hieracium vulgatum, Cardamine bulbifera* and *Gagea lutea* show unexpected variation, which in *Cardamine* and *Gagea* is considerable, although none of them as far as is known reproduce sexually in the geographic region concerned. These observations indicate that a further study of variation and reproduction would be worth while. For *Circaea,* further support has been obtained for the occurrence of hybridism and introgression.

I am convinced that chromatographically obtained data of the type presented here will prove to be of great value as one possible source of information when studying variation at infraspecific level, especially in taxonomically critical groups where conventional methods of analysis often fail to give results. Such data should, however, be treated with reserve and their reliability carefully checked. They should preferably be combined with other types of evidence.

ACKNOWLEDGEMENTS

Much of the laboratory work has been performed by Miss D. PERSSON. Mr H. ROOTZÉN, Institute of Mathematical Statistics, Lund, has given indispensible advice regarding statistical methods. He and Mr S. NORÉN, the Lund University Computing Centre, carried out the computer programming. Professor E. ALMQUIST, Uppsala, kindly determined the material of *Hieracium.* Professor H. RUNEMARK and Mr TH. KARLSSON, Lund, have given valuable criticism. Mrs M. GREENWOOD-PETERSSON checked the manuscript.

The work has been supported by grants from the Nilsson-Ehle Fund of the Kungl. Fysiografiska Sällskapet, Lund. Statistical aid and computer facilities were put at my disposal by the Swedish Natural Science Research Council and by the University of Lund.

LITERATURE CITED

ADAMS, R. P. 1972. Numerical analyses of some common errors in chemosystematics. — Brittonia 24: 9—21.

FRYXELL, P. A. 1957. Mode of reproduction of higher plants. — Bot. Rev. 23: 135—233.

RAVEN, P. H. 1963. Circaea in the British Isles. — Watsonia 5: 262—272.

RUNEMARK, H. 1968. Critical comments on the use of statistical methods in chemotaxonomy. — Bot. Notiser 121: 29—43.

SELANDER, R. K., YANG, S. Y., LEWONTIN, R. C. & JOHNSON, W. E. 1970. Genetic variation in the horseshoe crab (Limulus polyphemus), a phylogenetic "relic". — Evolution 24: 402—414.

SNEATH, P. H. A. & JOHNSON, R. 1972. The influence on numerical taxonomic similarities of errors in microbiological tests. — J. Gen. Microbiol. 72: 377—392.

SØRENSEN, TH. & GUÐJÓNSSON, G. 1946. Spontaneous chromosome-aberrants in apomictic Taraxaca. Morphological and cytogenetical investigations. — Biol. Skr. 4: 2. København.

SUOMALAINEN, E. & SAURA, S. 1973. Genetic polymorphism and evolution in parthenogenetic animals. I. Polyploid curculionidae. — Genetics 74: 489—508.

TURESSON, G. 1943. Variation in the apomictic microspecies of Alchemilla vulgaris L. — Bot. Notiser for 1943: 413—427.

— 1956. Variation in the apomictic microspecies of Alchemilla vulgaris L. II. Progeny tests in agamotypes with regard to morphological characters. — Ibid. 109: 400—404.

WEIMARCK, G. 1970. Spontaneous and induced variation in some chemical leaf constituents in Hierochloë (Gramineae). — Bot. Notiser 123: 231—268.
— 1972. On "numerical chemotaxonomy". — Taxon 21: 615—619.
— 1974. Population structure in Circaea lutetiana, C. alpina and C. ×intermedia (Onagraceae) as revealed by thin-layer chromatographic patterns. — In G. BENDZ, J. SANTESSON & V. RUNNSTRÖM-REIO (eds.): Chemistry in botanical classification. Nobel Symp. 25: 287—292. — Stockholm, New York and London.
WEIMARCK, H. 1963. Skånes flora. — Lund.
WIDDER, F. J. 1970. Herbartechnik (II): Die Thermostatpresse. — Phyton 14: 175—180.

APPENDIX

List of collection sites, all within the province of Skåne, southernmost Sweden.

Senecio viscosus. 1: Båstad, Kattvik, the harbour c. 500 m ESE, rubble. — 2: Vinslöv, the station c. 200 m W, railway embankment. — 3: Åhus, Ö. Täppet, refuse area by the harbour. — 4: Simris, gravelly shore by the waste-water outlet. — Vittsjö, the station c. 300 m S, railway embankment.

Melandrium rubrum. 1: Bosjökloster, the former Youth Hostel c. 50 m N, open forest. — 2: Vitaby, the built-up area c. 1,000 m N, ravine of Mölleån. — 3: Ramsåsa, the church c. 600 m SW, grove. — 4: Skepparslöv, Bjärnhult c. 500 m WSW, road-side. — 5: Baldringe, Fyledalen's brickyard c. 500 m WNW, road-side.

Hieracium vulgatum. 1: Ramsåsa, the church c. 1,000 m WSW, grove. — 2: Vittsjö, along the drive to Brahetorp, edge of forest. — 3: Röddinge, the built-up area c. 500 m SE, grove. — 4: Sibbhult, Ebbarp, edge of forest. — 5: V. Vram, Tallåsen c. 500 m SW, grove.

Gagea lutea. 1: Dalby, the built-up area c. 3,000 m NW, edge of forest. — 2: Benestad, Örup castle c. 200 m N, grove. — 3: Ramsåsa, the church c. 600 m SW, grove. — 4: Gudmuntorp, Mariannelund c. 400 m NE, edge of forest. — 5: Gudmuntorp, between Trulstorp and Lillarp, edge of forest.

Cardamine bulbifera. 1: Röddinge, Slagarp, grove. — 2: Andrarum, Breabäck, grove. — 3: Ravlunda, Dammåkra c. 1,000 m NW, grove. — 4: Kivik, the Dolmen, grove. — 5: Djurröd, Harastorp c. 600 m NE, grove.

Ranunculus ficaria. 2: Dalby, the built-up area c. 3,000 m NW, edge of forest. — 3: Benestad, Örup castle c. 200 m N, grove. — 4: Ramsåsa, the church c. 600 m SW, grove. — 5: Gudmuntorp, Mariannelund c. 400 m NE, edge of forest. — 6: Röddinge, Slagarp, grove.

Viola mirabilis. 2: N. Strö, Ekenäs, grove. — 4: Ramsåsa, the church c. 1,000 m WSW, grove. — 5: Ramsåsa, ·72 c. 300 m NW, forest. — 6: Gärdslöv, Tärnö, near Hjortholmshuset, grove. — 7: Smedstorp, Listarum, southerly esker slope, grove.

Luzula pilosa. 1: Gudmuntorp, Mariannelund c. 500 m NE, open forest. — 3: Veberöd, Kvarnbrodda c. 200 m W, edge of forest. — 4: Ravlunda, Dammåkra c. 1,000 m NW, edge of forest. — 5: Vittsjö, along the drive to Brahetorp, edge of forest. — 6: Fågeltofta, Kronovall castle c. 700 m E, open forest.

Thymus serpyllum. 1: Önnestad, Ullstorp limestone quarry c. 150 m NE, dry grassland. — 2: Åhus, Ö. Täppet, field by the harbour. — 3: Yngsjö, Gropahålet, sand dune. — 4: Gladsax, Vårhallarna, sandy beach. — 5: Tomelilla, Adelsberg, abandoned gravelpit.

Valeriana dioica. 1: Stehag, the waterworks c. 500 m S, damp forest. — 2: Djurröd, Harastorp c. 300 m NE, fen. — 3: Vittsjö, Brahetorp c. 200 m N, fen. — 4: Simris, Simrislund, fen. — 5: Tomelilla, Adelsberg, fen.

Circaea lutetiana. 1: Ramsåsa, the church c. 900 m ESE, grove. — 2: Röddinge, Slagarp c. 900 m SW, grove. — 4: Brunnby, Kockenhus c. 300 m WNW, damp forest. — 5: V. Vram, Eriksdal c. 500 m N, damp forest. — 6: Genarp, Olstorp c. 700 m ENE, edge of forest along ditch.

Circaea alpina. 1: Strövelstorp, Segahus c. 500 m S, pine forest. — 2: V. Vram, Friggestad c. 800 m SE, alder swamp. — 4: Ö. Sönnarslöv, Studabackarna c. 600 m SW, damp alder forest. — 5: Ö. Sönnarslöv, southern part of the lake Sönnarslövsjön c. 150 m S, damp alder forest. — 6: Genarp, St. Perstorp c. 400 m SE, edge of brook.

Circaea intermedia. 1: Genarp, Olstorp c. 700 m ENE, edge of forest along ditch. — 2: Genarp, Olstorp c. 300 m NNE, edge of forest along ditch. — 3: V. Vram, Skogsliden c. 500 m ESE, damp forest. — 5: Bläntarp, Elsagården c. 200 m W, damp edge of forest. — 7: Genarp, Olstorp c. 800 m ENE, edge of forest.

Contributions to the Flora and Vegetation of the Galápagos Islands

I. New Floristic Records from the Archipelago [1]

Ole Hamann

HAMANN, O. 1974 09 13. Contributions to the flora and vegetation of the Galápagos Islands. I. New floristic records from the archipelago. — Bot. Notiser 127: 245—251. Lund. ISSN 0006-8195.

Ceratophyllum llerenae FASSETT (Ceratophyllaceae), *Antigonon leptopus* HOOK. & ARN. (Polygonaceae), *Pothomorphe peltata* (L.) MIQ. (Piperaceae) and *Crescentia cujete* L. (Bignoniaceae) are reported as new to the Galápagos. *Ipomoea batatas* (L.) LAM. (Convolvulaceae) has become naturalized in the archipelago. The presence of *Histiopteris incisa* (THUNB.) J. SMITH (Polypodiaceae) is confirmed. The distribution and habitat of *Psilotum nudum* (L.) PALISOT (Psilotaceae) in the archipelago are discussed.

Ole Hamann, Institute of Systematic Botany, University of Copenhagen, 140 Gothersgade, DK-1123 Copenhagen K, Denmark.

INTRODUCTION

From December 1971 to October 1972 I worked in the Galápagos as UNESCO Associate Expert in Plant Ecology Applied to Wildlife Conservation. The main object was to start mapping the vegetation and to investigate the influence of introduced mammals on the natural vegetation. As the first of a series of publications on the flora and vegetation of the Galápagos Islands, this paper contains seven new botanical records established by my wife and myself. The collections are deposited at the Botanical Museum of the University of Copenhagen (C).

Since the species recorded as new to the islands are not included in WIGGINS & PORTER's new Flora of the Galápagos Islands (1971), short descriptions based on the specimens collected are given here. This paper will thus serve as a supplement to the Flora.

[1] The Charles Darwin Foundation Contribution no. 165.

Ceratophyllum llerenae FASSETT — Fig. 1

FASSETT 1953 p. 29.

Perennial, submerged herb. Shoots irregularly branching, with long internodes and multiple leaf-whorls. Leaves dichotomously forked 2—3 times, exstipulate, 2—3(—4) cm long; basal leaf segments (1—2 forkings) often inflated, 0.5—1 or at times up to 2 mm broad; terminal segments filiform; leaves with 10—20 or more marginal teeth; teeth about 0.1 mm long, with little or no green tissue at the base. Flowers unisexual, with a single, green perianth, solitary in the axils of leaves. Tepals (6—)9—12, about 0.6—1 mm long, linear. Fruit oblong, slightly compressed, about 3.5×1.8 mm; style persistent, up to 4 mm long; fruit marginally winged; wing about 0.1—0.3 mm broad at maturity, with 10—20 irregularly distributed marginal teeth (often lacking in immature fruits); teeth 0.5—1 or rarely up to 2.5 mm long; mature fruit an achene,

faintly and irregularly tuberculate, dark brown (Fig. 1).

Ceratophyllum llerenae is distinguished from other American species of *Ceratophyllum* by the wing and multiple teeth of the mature fruit, and by the size of the leaves. The Galápagos specimen (O. H. no. 1941) matches *Ceratophyllum cristatum* SPRUCE ex K. SCHUM. (SPRUCE no. 1583, June 1851, Brazil) in the Kew Herbarium (K). *C. cristatum* SPRUCE ex K. SCHUM. was reduced to a synonym under *C. llerenae* by FASSETT (1953). The previously described *C. cristatum* GUILL. & PERR. is an African species, differing from *C. llerenae* in having smooth leaves with very few marginal teeth and a fruit with two prominent basal horns, one descending, the other ascending (GUILLEMIN & PERROTTET 1833 p. 296). Hence *C. llerenae* is the correct name for the American species.

This is the first record of a number of the Ceratophyllaceae in the Galápagos. It was collected on Santa Cruz by a resident, Mr. ANDRÉ DEROY, in a small temporary pool near the old trail from Puerto Ayora to "La Caseta" in the tortoise reserve. The pool was covered with *Azolla microphylla* KAULF. The vegetation in the surrounding area was of the "transition-forest" type, dominated by *Pisonia floribunda* HOOK. FIL., *Psidium galapageium* HOOK. FIL., *Zanthoxylum fagara* (L.) SARG. and *Piscidia carthagenensis* JACQ. The habitat corresponds well with the habitat of the type collection from El Salvador (FASSETT no. 28553), which is described as a small pool less than 1 m deep with varying water-level (FASSETT 1953). Although a large number of small fresh-water pools on the bigger islands in the Galápagos were searched intensively for aquatic plants during our stay, no other locality for *Ceratophyllum* was found. As the collected material was fruiting abundantly the species has the potentiality for further dispersal within the islands. It appears to be either a recent natural introduction, or a species which, owing to its habitat, has been overlooked by earlier botanists.

Ceratophyllum llerenae is also known from Guatamala, El Salvador, Columbia, Trinidad, Dutch Guyana and Brazil (FASSETT 1953).

COLLECTION STUDIED. Santa Cruz. A. DEROY & M. & O. HAMANN no. 1941, pond near "La Caseta", along the old trail, about halfway from the barranco, alt. appr. 150 m, spring 1972.

Antigonon leptopus HOOK. & ARN.

HOOKER & ARNOTT 1839—40 p. 308, pl. 69.

A more or less pubescent vine with angulate branches. Leaves alternate, 5—10 cm long, ovate-cordate or broadly deltoid-cordate, deeply cordate at the base, acute or acuminate, shortly pubescent, especially along the veins and the margin. Ochreae small or reduced to a transverse line. Fascicles racemose, the rachis densely rusty-pubescent, extended into a tendril. Sepals 5, unequal, the three outer ones cordate, the two inner ones narrower; outer sepals bright rose-pink, at first 8—10 mm long, enlarging in fruit and finally about 15 mm long, with reticulate veins, slightly pubescent. Stamens 8, connate at the base; filaments glandular-pubescent. Ovary 3-angulate, styles 3. Fruit an achene, included in the calyx, 3-angulate.

The combination of cordate outer sepals and non-decurrent leaf blades separates *Antigonon leptopus* from other species of the genus.

This is the first record of the genus in the Galápagos. It was collected in the central part of the inhabited island of Santa María. The vegetation in the area was dominated by *Psidium guajava* L., which has become completely naturalized in many places in the archipelago. *Antigonon leptopus* is probably a recent introduction, but appears to be established as an escape on Santa María. Other common plants in the area included the vine *Cissus sicyoides* L. and *Salvia occidentalis*

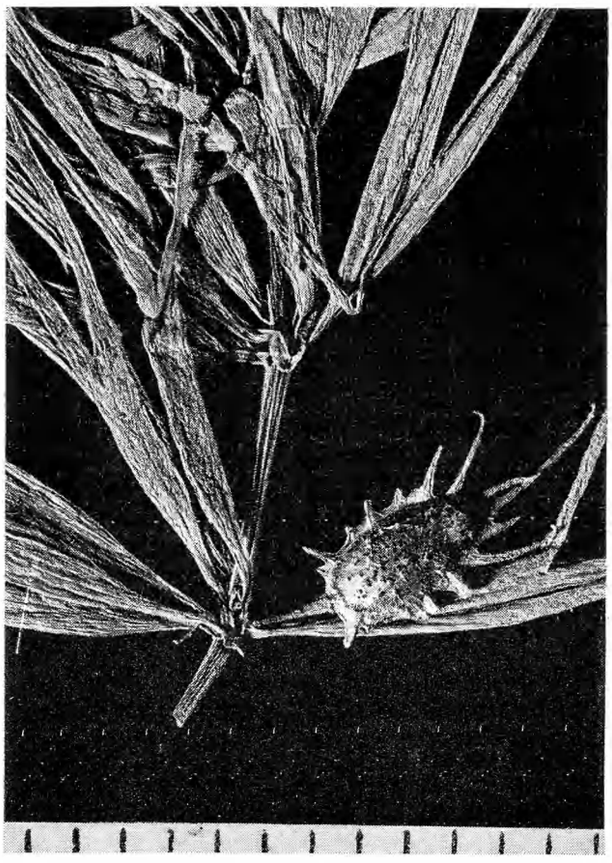


Fig. 1. *Ceratophyllum llerenae* FASSETT. Part of shoot with mature fruit; note also the inflated leaves (scale in mm). Specimen from Santa Cruz (A. DEROY & M. & O. HAMANN no. 1941). — Photo: F. SARUP.

Fig. 2. *Pothomorphe peltata* (L.) MIQ. Flowering specimen from Santa Cruz (M. & O. HAMANN no. 74). — Photo: F. SARUP.

Sw., both natural members of the mesic forest of the Galápagos.

Antigonon leptopus is a native of Mexico and Central America, but is widely cultivated as a decorative vine in South America and other tropical regions (STANDLEY & STEYERMARK 1946).

COLLECTION STUDIED. Santa María. M. & O. HAMANN no. 1413, Cerro Wittmer, south-west slope, alt. appr. 280 m, June 8, 1972.

Pothomorphe peltata (L.) MIQ. — Fig. 2

MIQUEL 1840 p. 45, pl. 4 E.

Shrub or subshrub, 1—2 m high; all vegetative parts covered with small yellow-brownish, pellucid glands. Leaves alternate, rounded-cordate, up to 18 cm long and 16 cm wide or rarely larger; apex acute, peltate at one-fourth to one-third of the length above the base; leaves long-petiolate, petiole flat and sheathing at the base. Flowering spikes umbellate at the end of a 4—7 cm long, axillary stalk. Umbel with linear-lanceolate bracts at the base of the peduncles; peduncles slender, 10—15 mm long, glabrous. Spikes several, 2—5 mm thick, 50—100 mm long, with triangular peltate, marginally fimbriate bracts. Flowers sessile, perfect. Stamens 2. Stigmas 3, small, sessile. Fruit drupaceous, small, triquetrous.

This is the first record of the genus in the Galápagos. *Pothomorphe peltata* was collected on the inhabited islands of Santa Cruz and Isabela. We found it in three localities, all in areas disturbed by farming and cattle-raising. *Pothomorphe peltata* was growing in hedges of *Jatropha curcas*

L., and at the border of pastures of *Pennisetum purpureum* L. which is widely cultivated in the islands. *Pothomorphe peltata* is a recent introduction, but appears to be naturalized and spreading rapidly.

Pothomorphe peltata is distributed throughout the West Indies and tropical America (TRELEASE & YUNCKER 1950).

COLLECTIONS STUDIED. Santa Cruz. M. & O. HAMANN nos. 74 & 1939, at path below Media Luna, south slope, alt. appr. 380 m, December 23, 1971 & July 30, 1972. — Isabela. M. HARO & M. & O. HAMANN no. 2575, Volcán Sierra Negra, south slope, near the village of Santo Tomás, alt. appr. 180 m, September 28, 1972.

Crescentia cujete L.

LINNAEUS 1753 p. 626.

A well-known, small tree, easily recognized by the flowers which have a 4—7 cm long corolla with red or purple veins, and by the large globose or ovoid fruits which have a corky pericarp, are pulpy within and have small, flattened seeds.

This is the first definite record of a member of the Bignoniaceae in the Galápagos (for further discussion see WIGGINS & PORTER 1971). *Crescentia cujete* was found on Isabela in the farming area on the south slope of Volcán Sierra Negra. The most common plants in this area are *Sapindus saponaria* L., *Coffea arabica* L., *Citrus* spp. and *Psidium guajava* together with the indigenous *Zanthoxylum fagara*. Isabela has been inhabited since 1893 (SLEVIN 1959), and the above-mentioned cultivated trees have become naturalized. *Crescentia cujete* though, was only seen in a single locality where a few trees bore mature fruits.

Crescentia cujete (calabash-tree, local name "mate") is a native of tropical America and is widely cultivated. The hard shells of the fruits are used for ornamental work, drinking cups, etc. (SANDWITH 1938).

COLLECTION STUDIED. Isabela. M. & O. HAMANN no. 2474, south slope of Volcán Sierra Negra, at Corazón Verde, alt. appr. 400 m, September 30, 1972.

Ipomoea batatas (L.) LAM.

LAMARCK 1791 p. 465.

Ipomoea batatas is easily distinguished from other species of *Ipomoea* in the archipelago by the following combination of characters: Tuberous roots, long, trailing stems which root at the nodes, and non-succulent leaves.

Ipomoea batatas (sweet potato, local name "camote") is a common cultivated plant in the Galápagos. We collected it in two localities on Santa Cruz, where it was completely naturalized. The first locality was in a forest in the tortoise reserve in the south-west part of the island. The dominant plants in this area were *Caesalpinia bonduc* (L.) ROXB., *Zanthoxylum fagara, Scalesia pedunculata* HOOK. FIL. var. *pedunculata* and *Pteridium aquilinum* (L.) KUHN var. *arachnoidum* (KAULF.) HERTER. The second locality was at Cerro Bandera in the western highlands, where the landscape is characterized by scattered trees of *Zanthoxylum fagara, Acnistus ellipticus* HOOK. FIL. and *Scalesia pedunculata* var. *pedunculata*. *Ipomoea batatas* grew in open areas between ferns and herbs such as *Pteridium aquilinum* var. *arachnoidum, Jaegeria crassa* TORRES and *Habenaria monorrhiza* (SW.) RCHB. FIL., all native Galápagos plants.

Ipomoea batatas is cultivated in the tropics all over the world. It probably originated in the American tropics (MACBRIDE 1959).

COLLECTIONS STUDIED. Santa Cruz. M. & O. HAMANN no. 1051, between El Chato and "La Caseta", south-west part of the island, alt. appr. 200 m, April 13, 1972. — M. & O. HAMANN no. 2197, Cerro Bandera, western highlands, alt. appr. 600 m, September 12, 1972.

Histiopteris incisa (THUNB.) J. SMITH

SMITH 1875 p. 294.

Rhizome long, creeping, woody, bearing linear scales. Stipes rough and muricated at the base, deep brown or stramineous glossy. Fronds distant, long stipitate, very variable in size, 10—110 cm long, membranaceous when young, becoming subcoriaceous and paler with age, oblong deltoid, tripinnate or tripinnatifid. Rhachis ± intensively stramineous glossy. Pinnae up to 21 cm long, opposite, deltoid-oblong; pinnules up to 5 cm long, sessile, opposite, apically acuminate; segments divaricate, oblong, obtuse, lowest ones often remote, these about 1 cm long; veins free or forked or irregularly anastomosing. Sori linear along the margins of the segments; indusia membranaceous, continuous or interrupted, about 0.3—0.5 mm broad. Spores about 51 µm long and 34 µm broad, roughly verrucose.

A polymorphic species, whose presence in the Galápagos was confirmed by WIGGINS & PORTER (1971) on the basis of a 1970 collection by ITOW, but no description of the species was given as the pagination had already been set.

We collected *Histiopteris incisa* on Santa Cruz and Pinta. On Santa Cruz it was found in two localities near Mount Crocker (ITOW's specimen is from the same area). It was growing in *Sphagnum* bogs and at the margins of these. The bogs are mostly situated at the bottom of small, old and eroded craters in the "fern-sedge" vegetation zone. On the inner slope of the craters the vegetation is mainly dominated by *Cyathea weatherbyana* (MORTON) MORTON, *Pernettya howellii* SLEUMER, *Pteridium aquilinum* var. *arachnoidum* and *Blechnum occidentale* L. var. *puberulum* SODIRO. On the margins of the bogs are also found *Ludwigia leptocarpa* (NUTT.) HARA, *Rhynchospora corymbosa* (L.) BRITT. and *Polygonum opelousanum* RIDDEL ex SMALL. In the *Sphagnum* bogs, which consist of *Sphagnum cuspidatum* EHRH. var. *serratulum* SCHLEIPH. and *S. erythrocalyx* HAMPE, the following species are common: *Nephrolepis cordifolia* (L.) PRESL, *Elaphoglossum glossophyllum* HIERON., *E. engellii* (KARST.) CHRIST, *Lycopodium clavatum* L., *Dicranopteris flexuosa* (SCHRAD.) UNDERW., and also *Histiopteris incisa.*

On Pinta *Histiopteris incisa* was found in a drier habitat at the summit of the island. Just below the summit the vegetation is forest-like, dominated by *Zanthoxylum fagara, Solanum erianthum* D. DON and *Tournefortia rufo-sericea* HOOK. FIL. Above this area there are dense stands of *Pteridium aquilinum* var. *arachnoidum* and scattered specimens of *Lippia rosmarinifolia* ANDERSS. var. *rosmarinifolia.* In open places in this area *Histiopteris incisa* was found growing together with *Polypodium tridens* L., *Pityrogramma calomelanos* (L.) LINK var. *calomelanos* and var. *auroflava* (HOOK.) WEATHERBY ex BAILEY, *Lycopodium cernuum* L. and *Nephrolepis biserrata* (SW.) SCHOTT.

Distribution within the archipelago, see Fig. 3.

Histiopteris incisa occurs in tropical and subtropical regions of the world (VARESCHI 1968).

COLLECTIONS STUDIED. Santa Cruz. M. & O. HAMANN no. 493, in old crater with "*Sphagnum*-bog 2", south part of Mount Crocker, alt. appr. 780 m, March 2, 1972. — M. & O. HAMANN nos. 512 & 513, in "*Sphagnum*-bog 1", south part of Mount Crocker, alt. appr. 800 m, March 3, 1972. — Pinta. M. & O. HAMANN no. 741, at the summit, central part of the island, alt. 645 m, March 22, 1972.

Psilotum nudum (L.) PALISOT

PALISOT 1805 pp. 106, 112.

Psilotum nudum was collected on Fernandina, Isabela and Santa María. Very recently WEBER (1973) published a new find of the species on Cerro Azul, Isla Isabela. However, many unpublished collections of *Psilotum nudum* have been

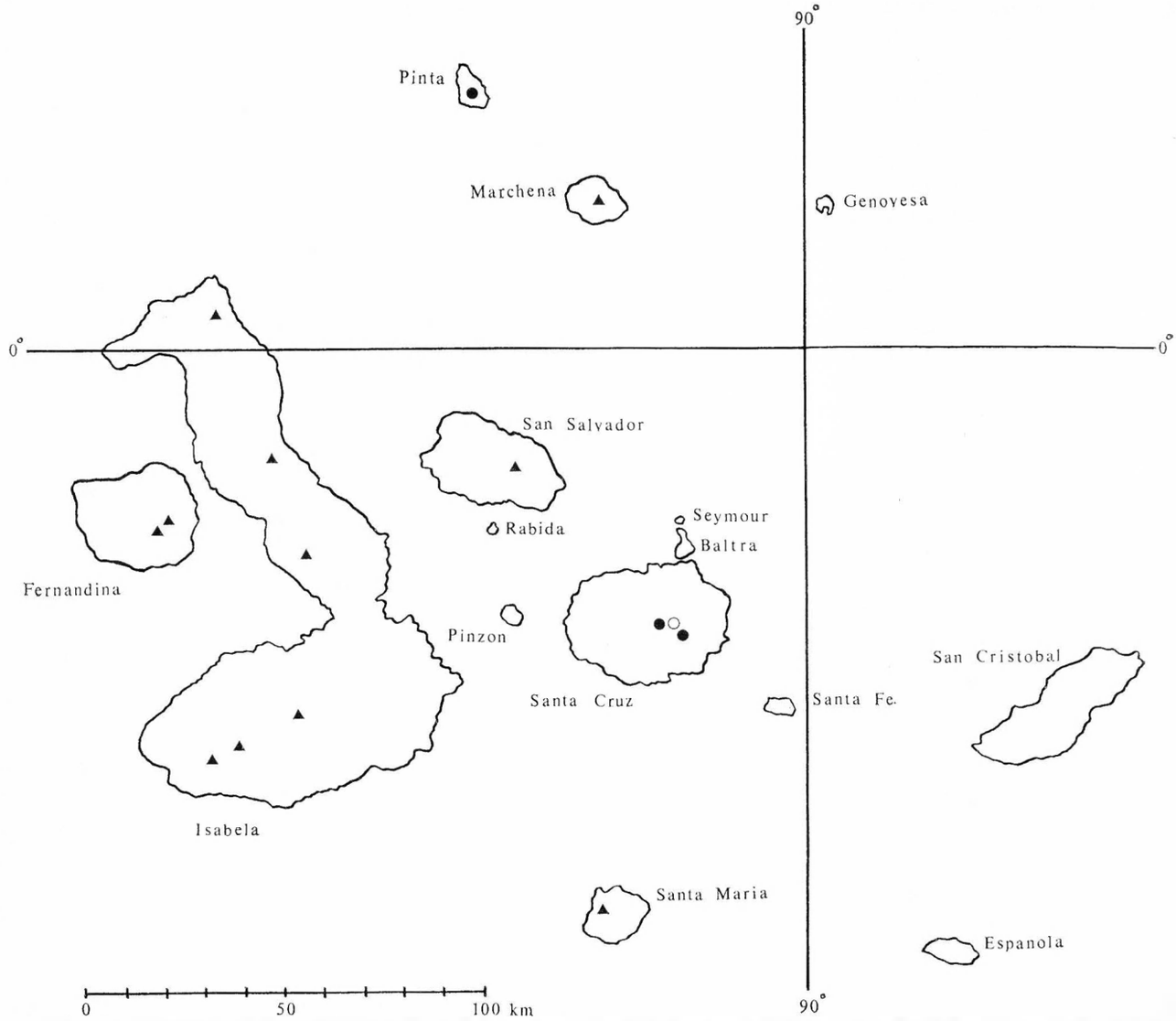


Fig. 3. Distribution of *Histiopteris incisa* (THUNB.) J. SMITH and *Psilotum nudum* (L.) PALISOT within the Galápagos Islands. — ●: *Histiopteris incisa* recorded by me in 1971—1972. ○: *Histiopteris incisa* recorded by ITOW in 1970. ▲: *Psilotum nudum* recorded in the present paper (various collectors in 1969—1972).

made in the last few years: Officials of the National Park Service of Galápagos, J. BLACK, J. VILLA and G. TORRES have reported *Psilotum* from Marchena and San Salvador (personal communication). WEBER also collected the species on Fernandina, Marchena and Volcán Darwin, Isla Isabela, and finally DE VRIES found it on Volcán Alcedo, Isla Isabela (personal communication from WEBER). These last, hitherto unpublished, records are included in the map, Fig. 3.

WIGGINS & PORTER (1971 p. 175) comment on the habitat of *Psilotum nudum:* "In moist habitats in forests or among dense shrubs, along banks of water courses, on dripping cliffs, and about bases of trees in humus and dense shade" and "It probably occurs on Isla Santa Cruz, and should be sought there in the moister, deeply shaded areas". As far as the Galápagos material is concerned this information is misleading. Apart from the Santa María collection, all known habitats of *Psilotum nudum* in the islands differ from the given description. On Fernandina, Isabela, Marchena and San Salvador *Psilotum nudum* is found in the lower

arid regions. On Fernandina and Isabela we collected *Psilotum nudum* in small cracks in the lava, where only little humus has accumulated and virtually no shade is found. It was found growing together with *Darwiniothamnus tenuifolius* (HOOK. FIL.) HARLING, *Macraea laricifolia* HOOK. FIL., *Borreria ericaefolia* HOOK. FIL. and *Polypodium tridens*. The vegetation on the lava fields, where *Psilotum nudum* is found, consists mainly of these species plus *Jasminocereus thouarsii* (WEBER) BACKBG., *Scalesia affinis* HOOK. FIL., *Cordia revoluta* HOOK. FIL., *Castela galapageia* HOOK. FIL. and *Lippia rosmarinifolia*, all regular members of the arid type of vegetation in the Galápagos. The National Park Officials have reported the same sort of habitat for *Psilotum nudum* from Marchena and San Salvador. This corresponds with RILEY, who collected *Psilotum nudum* on San Salvador; he notes on the habitat: "In fissures of lava rock". (RILEY 1925 p. 231).

Only on Santa María was *Psilotum nudum* found in a moist and shady habitat. We collected it on the south-west slope of Cerro Wittmer, among mosses and ferns in a forest-like vegetation dominated by *Psidium guajava, Tournefortia rufosericea, Zanthoxylum fagara, Croton scouleri* HOOK. FIL. and *Ctenitis sloanei* (POEPPIG) MORTON.

Whether *Psilotum nudum* in the Galápagos is represented by different ecological races is to be considered. Distribution within the archipelago, see Fig. 3.

Psilotum nudum occurs in the tropics and subtropics of the world (VARESCHI 1968).

COLLECTIONS STUDIED. Fernandina. M. & O. HAMANN no. 198, south-east slope, between Punta Mangle and the rim of the caldera, alt. 270 m, January 20, 1972. — Santa María. M. & O. HAMANN no. 1406, by the spring near the Wittmer farm, south-west slope of Cerro Wittmer, alt. 260 m, June 8, 1972. — Isabela. M. & O. HAMANN no. 2457, lava flow "El Quemado", between Cerro Azul and Volcán Sierra Negra, alt. appr. 240 —350 m, September 29, 1972.

ACKNOWLEDGEMENTS

Since this is the first publication after our stay in the Galápagos, I wish to express my gratitude to all whose help made the work possible: The World Wildlife Fund (financial support: Project no. 744), Dr PETER KRAMER, Director of the Charles Darwin Research Station, Sr JOSÉ VILLA and wardens of the National Park Service of Galápagos, and my wife MICHELLE HAMANN. I am grateful to Professor ARNE STRID for advice and help with the manuscript.

LITERATURE CITED

FASSETT, N. C. 1953. North American Ceratophyllum. — Comunic. Inst. Trop. Invest. Cient. El Salvador 2 (2): 25—45.

GUILLEMIN, J.-A. & PERROTTET, S. 1833. Florae Senegambiae Tentamen 1. — Paris.

HOOKER, W. J. & ARNOTT, G. A. W. 1839—40. The Botany of Captain Beechey's Voyage. — London.

LAMARCK, J. DE 1791. Encyclopédie méthodique. Botanique. Illustrations des genres. 1. — Paris.

LINNAEUS, C. 1753. Species Plantarum 2. — Holmiae.

MACBRIDE, J. F. 1959. Flora of Peru. Convolvulaceae. — Field Mus. Nat. Hist. Bot. Ser. 13 (5, no. 1): 487—488.

MIQUEL, F. A. 1840. Commentarii Phytographici. — Lugduni Batavorum.

PALISOT, A. M. F. J. 1805. Prodromus des cinquième et sixième familles de l'Aethéogamie. — Paris.

RILEY, L. A. M. 1925. Critical notes on Galapagos plants. — Kew Bull. for 1925: 216—231.

SANDWITH, N. Y. 1938. Bignoniaceae. — In A. PULLE, Flora of Suriname 4 (2): 82—83. — Amsterdam.

SLEVIN, J. R. 1959. The Galápagos Islands. A history of their exploration. — Occ. Papers Calif. Acad. Sci. 25: 107.

SMITH, J. 1875. Historia filicum. — London.

STANDLEY, P. C. & STEYERMARK, J. A. 1946. Flora of Guatamala 4. Polygonaceae. — Fieldiana: Botany 24 (4).

TRELEASE, W. & YUNCKER, T. G. 1950. The Piperaceae of Northern South America 2. — Urbana.

VARESCHI, V. 1968. Helechos. — In T. LASSER, Flora de Venezuela 1 (1 & 2). — Caracas.

WEBER, D. 1973. Deux orchidacées nouvelles pour la flore des îles Galapagos. — Bull. Soc. Neuchâtel. Sci. Nat. 96: 17—30.

WIGGINS, I. L. & PORTER, D. M. 1971. Flora of the Galápagos Islands. — Stanford.

Contributions to the Flora and Vegetation of the Galápagos Islands

II. A New Subspecies of Lycopodium from the Archipelago [1]

Ole Hamann

HAMANN, O. 1974 09 13. Contributions to the flora and vegetation of the Galápagos Islands. II. A new subspecies of Lycopodium from the archipelago. — Bot. Notiser 127: 252—255. Lund. ISSN 0006-8195.

Lycopodium setaceum LAM. ssp. *galapagense* O. HAM. ssp. nov. is described. It deviates from *L. setaceum* s. str. mainly by its broad sporophylls and larger spores. It is only known from Isla San Salvador, Galápagos Islands, Ecuador.

Ole Hamann, Institute of Systematic Botany, University of Copenhagen, 140 Gothersgade, DK-1123 Copenhagen K, Denmark.

INTRODUCTION

While working through the material collected in the Galápagos Islands during 1971—1972, difficulties were encountered in determining 3 specimens of *Lycopodium* not previously recorded from the archipelago. A study of the literature and of the collections of *Lycopodium* in the Botanical Museum of the University of Copenhagen (C) and in the Kew Herbarium, London, (K), has led to the conclusion that the Galápagos specimens represent an undescribed subspecies of *Lycopodium setaceum* LAM.

Lycopodium setaceum LAM. ssp. **galapagense** O. HAM. ssp. nov. — (Figs. 1 A, 2 A)

Planta epiphytica, pendula. Rami tenues, laxi, ad decies dichotomi, ad 36 cm longi, absque foliis plerumque 0.3—1.0 mm crassi, basibus foliorum decurrentibus carinati. Folia vegetativa alterna, dense congesta, plus minus adpressa, laete vel flavide viridia, plerumque 4—7 mm longa, 0.3—0.6 mm lata, plus minus recta, linearia, acuminata, margine integerrimo paululum revoluto. Rami ultimi per circiter octo partes decimas sporophyllophori, strobilis nullis formatis. Sporophylla foliis vegetativis textura et colore similia, forma breviora, manifesto latiora, 2.4—3(—4) mm longa, (0.5—)0.9—1.2 mm lata, maximam latitudinem in parte tertia basali attingentia, sporangia paulum amplectentia, adpressa, decurrentia, acuminata. Sporangia pallide mellea, reniformia sinu manifesto, 0.7—1.2 mm lata, 0.5—1.1 mm longa, pedunculata. Sporae subflavide albae, in luce transmissa colore paene nullo, plerumque 35—47 µm diam., in faciebus extrorsis convexis fossulato-foveolatae, in introrsis laeves, laesuris carinas satis manifestas efficientibus.

Holotypus die 17 mensis Augusti anni 1972 720 m supra mare in monte Cerro Espino insulae galapaganae San Salvador sub numero 2045 a M. et O. HAMANN lectus, in Museo Botanico Hauniensi (C) depositus.

Epiphytic, pendant. Branches slender, lax, up to 10 times dichotomously forked, up to 36 cm long, mostly 0.3—1.0 mm thick (exclusive leaves), ridged by the decurrent bases of leaves. Vegetative leaves alternate, closely set, ± adpressed, light green to yellow-green, mostly 4—7 mm long, 0.3—0.6 mm broad, ± straight, linear, acuminate; margin entire, slightly revolute. Sporangia not in strobili; shoot

[1] The Charles Darwin Foundation Contribution no. 166.

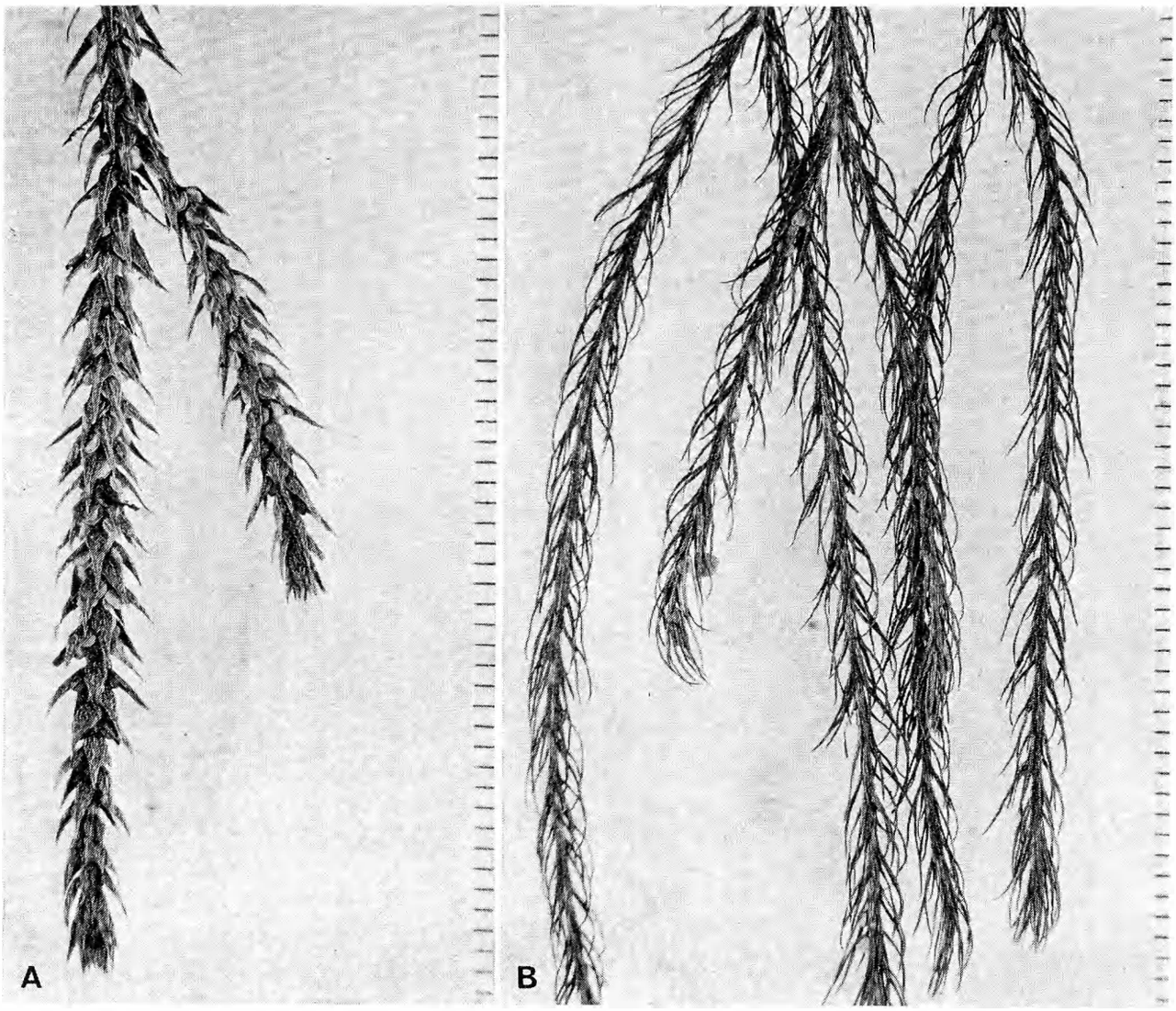


Fig. 1. A: *Lycopodium setaceum* LAM. ssp. *galapagense* O. HAM. Sporophyllous part of shoot. Holotype. — B: *Lycopodium setaceum* s. str. Sporophyllous part of shoot. Specimen from Cuba, EGGERS no. 5173, 1899, Herb. CARL CHRISTENSEN (C). — Photos: F. SARUP. Scale in mm.

sporophyllous for about 8/10 of the length. Sporophylls similar in texture and colour to vegetative leaves, but shorter and distinctly broader, 2.4—3(—4) mm long, (0.5—)0.9—1.2 mm broad, broadest in the lower third, somewhat clasping the sporangia, adpressed, decurrent, acuminate (Fig. 1 A). Sporangia pale yellow, reniform, stalked, 0.7—1.2 mm broad, 0.5—1.1 mm long, sinus distinct. Spores pale yellow-white, nearly colourless in transmitted light, mostly 35—47 µm in diameter, fossulate-foveolate on outer (distal) curved surfaces, smooth on proximal surfaces, laesurae relatively prominent as ridges (Fig. 2 A).

Type specimen: Isla San Salvador. M. & O. HAMANN no. 2045, Cerro Espino, alt. 720 m, August 17, 1972 (C holotypus).

Known only from Isla San Salvador, Galápagos Islands, Ecuador.

Lycopodium setaceum LAM. (LAMARCK 1789 p. 653) belongs to the subgenus *Urostachya* PRITZEL (1900 p. 592), which later was raised to generic rank by HERTER (1922 p. 249) as *Urostachys* HERTER and accepted as such by NESSEL

(1939) in his monograph. According to BOIVIN (1950 pp. 32—41) however, the segregation of *Urostachys* HERTER from *Lycopodium* L. is not justified. Also WILCE (1972 pp. 65—79) reaches the conclusion, that the arguments for dividing *Lycopodium* L. into separate genera are not strong enough. At present it is therefore considered best to refer the proposed new subspecies from Galápagos to the genus *Lycopodium* L.

Lycopodium setaceum LAM. has been treated as a synonym of *Urostachys verticillatus* (L. FIL.) HERTER by various authors, including NESSEL (1939). The original description of *Lycopodium verticillatum* L. FIL. was based on material from Bourbon (Réunion) (LINNAEUS FILIUS 1781 p. 448). However, as FÉE (1866 p. 130) has already pointed out, the specimens from the Antilles referred to this taxon are somewhat different. Later UNDERWOOD & LLOYD (1906 p. 108) emphasized the fact that the American plants, which differ from the Old-World specimens, are correctly placed in *Lycopodium setaceum* LAM. This has recently been followed by KRAMER (1962 p. 78), to whom the reader is referred for an extensive list of synonyms. Until the subgenus *Urostachya* PRITZEL has been subjected to a modern taxonomic treatment, I prefer to follow the above-mentioned authors in the question of nomenclature and relationship between *L. verticillatum* L. FIL. and *L. setaceum* LAM.

The subspecies *galapagense* differs from *Lycopodium setaceum* LAM. sensu KRAMER (1962) in the characters listed in Table 1. The ornamentation of the spores is essentially similar in the two taxa. In ssp. *galapagense,* the distal surfaces are nearly completely fossulate (grooved) (Fig. 2 A), whereas spores of *L. setaceum* range from foveolate (pitted) only (Fig. 2 B) to intermediate foveolate-fossulate, and to nearly completely fossulate, and thus indistinguishable from those of ssp. *galapagense.* The variation of ornamentation in *L. setaceum* does not seem to be correlated with other morphological characters. The proximal surfaces are unornamented in both taxa.

Table 1. Comparison between *Lycopodium setaceum* LAM. and *L. setaceum* LAM. ssp. *galapagense.* — The diameter of spores has been measured on samples (100 spores/specimen) taken from the 3 Galápagos specimens and from 5 representative specimens of *L. setaceum* from the Herbarium of the Botanical Museum of the University of Copenhagen (C). The spores were acetylated, mounted in glycerol jelly and measured immediately after, in order to avoid errors caused by the gradual swelling which takes place in this medium. Value within brackets according to KRAMER (1962).

L. setaceum ssp. *galapagense*	*L. setaceum*
Shoot sporophyllous for about 8/10 of the length.	Only half or less of the shoot sporophyllous.
Sporophylls 2.4—3.0, or rarely 4 mm long, 0.9—1.2, or rarely only 0.5 mm broad (Fig. 1 A)	Sporophylls 2.6—5.5 mm long, 0.3—0.7, or rarely 0.9 mm broad (Fig. 1 B)
Spore diameter 35—47 µm	Spore diameter 27—38 µm (33—36 µm)
Distribution: Isla San Salvador, Galápagos.	Distribution: West Indies & tropical America.

The spores all fall within the *Phlegmaria* type of the foveolate-fossulate group of *Lycopodium* spores described by WILCE (1972 p. 67). In this group spores of many species are almost indistinguishable (WILCE l.c.).

Lycopodium setaceum LAM. ssp. *galapagense* was collected in three localities on the upper south-west slopes of the uninhabited island of San Salvador. It was found growing on old trees of *Zanthoxylum fagara* (L.) SARG. among other epiphytes such as *Hymenophyllum polyanthos* (SW.) SW., *Polypodium lanceolatum* L. and mosses. The vegetation in the area is forest-like or scrub-like, dominated by *Zanthoxylum fagara, Acnistus ellipticus*

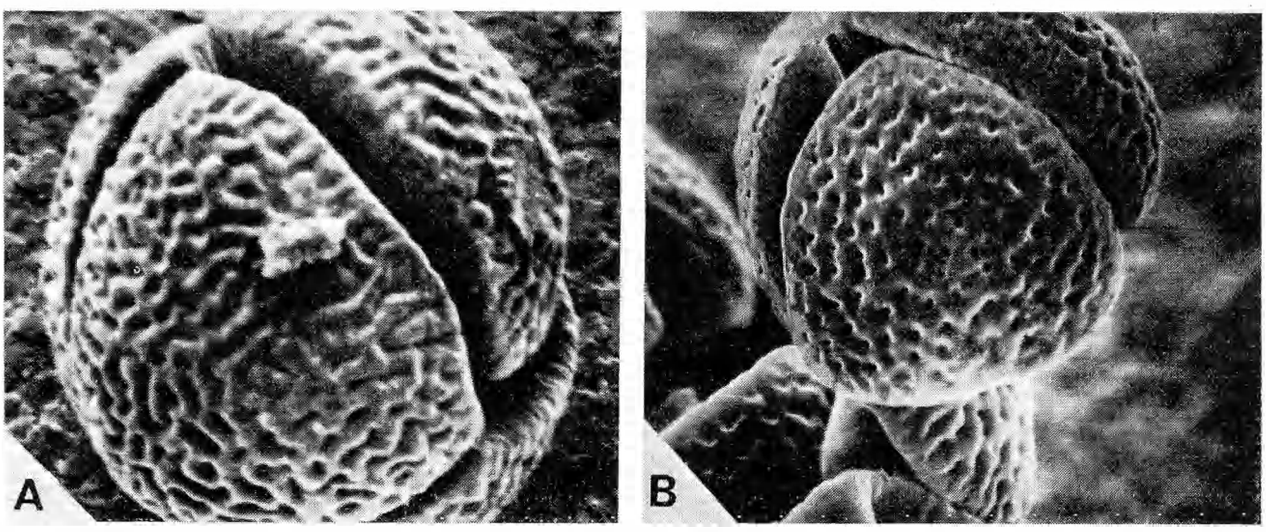


Fig. 2. SEM photographs of spores. — A: *Lycopodium setaceum* LAM. ssp. *galapagense* O. HAM., fossulate type (M. & O. H. no. 2021). — B: *Lycopodium setaceum* s. str., foveolate type (HATSCHBACH no. 19829, Rio Iguacu, Paraná, Brasil, Sept. 29, 1968). — Note also difference in size. The spore samples were mounted on SEM stubs with a little nail-polish and coated with a thin layer of carbon followed by gold. Specimens were examined with the Cambridge Stereoscan 600 at the Zoological Museum, the University of Copenhagen. — ×1,275.

HOOK. FIL., *Cordia scouleri* HOOK. FIL., *Tournefortia rufo-sericea* HOOK. FIL., *Psychotria rufipes* HOOK. FIL. and many species of ferns.

As the interior of San Salvador has previously been rather poorly investigated botanically, a week was spent in the central part of the island, but *Lycopodium setaceum* LAM. ssp. *galapagense* was found in three localities only. This restricted occurrence might explain why it has remained undiscovered until now.

COLLECTIONS STUDIED. San Salvador. M. & O. HAMANN no. 2021, east of "El Campamento Central", south of the central highlands, alt. 600 m, August 16, 1972. — No. 2045, holotype (l.c.). — No. 2107, "El Campamento Central", south of the central highlands, alt. 570 m, August 20, 1972.

ACKNOWLEDGEMENTS

I am grateful to Lektor TYGE CHRISTENSEN for the composition of the latin diagnosis and to Mr BENT W. RASMUSSEN, the Zoological Museum, Copenhagen, for his operation of the scanning electron microscope. Moreover, I am indebted to all who helped in the field work in the Galápagos.

LITERATURE CITED

BOIVIN, B. 1950. The problem of generic segregates in the form-genus Lycopodium. — Am. Fern Journ. 40: 32—41.

FÉE, A. L. A. 1866. Histoire des fougeres et des Lycopodiacées des Antilles. — In Memoires sur les Fougeres 11. — Paris.

HERTER, W. 1922. Itinara Herteriana III. — Beih. Bot. Centralb. 39 (2): 248—256.

KRAMER, K. U. 1962. Lycopodiaceae. — In A. L. STOFFERS, Flora of the Netherlands Antilles I: 78—80. — Utrecht.

LAMARCK, J. DE 1789. Encyclopédie méthodique. Botanique. 3. — Paris.

LINNAEUS, C. (filius) 1781. Supplementum plantarum. — Brunsvigae.

NESSEL, H. 1939. Die Bärlappgewächse. — Jena.

PRITZEL, E. 1900. Lycopodiaceae. — In ENGLER & PRANTL, Die natürlichen Pflanzenfamilien I (4): 563—606. — Leipzig.

UNDERWOOD, L. M. & LLOYD, F. E. 1906. The species of Lycopodium of the American tropics. — Bull. Torrey Bot. Club 33: 101—124.

WILCE, J. H. 1972. Lycopod spores, I. General spore patterns and the generic segregates of Lycopodium. — Am. Fern Journ. 62 (2): 65—79.

Cuticular and Epidermal Structures in Some Species of Eranthemum and Pseuderanthemum (Acanthaceae)

Khwaja J. Ahmad

AHMAD, K. J. 1974 09 13. Cuticular and epidermal structures in some species of Eranthemum and Pseuderanthemum (Acanthaceae). — Bot. Notiser 127: 256—266. Lund. ISSN 0006-8195.

Studies on cuticular structures in six species each of *Eranthemum* and *Pseuderanthemum* (Acanthaceae) have been carried out. The two genera were formerly treated under one genus i.e. *Eranthemum*. The most important differences in the epidermal characters of *Eranthemum* and *Pseuderanthemum* are: the presence of glandular hairs with 4-celled heads in *Eranthemum* and 4—8- (generally 8-) celled heads in *Pseuderanthemum*; the non-glandular hairs are common in *Eranthemum*, sparse and inconspicuous in *Pseuderanthemum*; double cystoliths are sparse in *Eranthemum*, but common in *Pseuderanthemum*. There are otherwise significant differences in the epidermal characters of the two genera. The present study suggests that the two genera, while showing some similarities in epidermal characters are quite distinct from each other. *Eranthemum albo-marginata* shows more similarities with the species of *Pseuderanthemum* than with *Eranthemum*. The epidermal characters support treating the genus *Daedalacanthus* as a synonym of *Eranthemum*.

Khwaja J. Ahmad, National Botanic Gardens, Lucknow-1, India.

INTRODUCTION

NEES (1847) classified the species of *Eranthemum* having sub-equal corolla lobes into two groups: (1) Grandibracteata, Old-World species with large, conspicuous bracts; (2) Parvibracteata, partly New-World and partly Old-World species with small, inconspicuous bracts. To the latter group RADLKOFER (1883) applied the generic name *Pseuderanthemum*. LINDAU (1895), who includes *Eranthemum* under the tribe Ruellieae, has created a separate tribe Pseuderanthemeae for the species included under *Pseuderanthemum*. BREMEKAMP (1965) included *Eranthemum* in the sub-tribe Ruelliinae under the tribe Ruellieae and *Pseuderanthemum* in the sub-tribe Odontoneminae (tribe Justicieae).

According to WILLIS (1966) there are 30 species of *Eranthemum* L. and 120 of *Pseuderanthemum* RADLK. distributed throughout the tropics. The present investigation which deals with the foliar cuticle and epidermis of six species each of *Eranthemum* and *Pseuderanthemum*, has been undertaken with a view to elucidating the possible taxonomic affinities between the two genera, and also to finding out the extent to which epidermal characters can be used in making inter-generic and intra-generic distinctions between *Eranthemum* and *Pseuderanthemum*.

Fig. 1. Lower and upper epidermides (lower epidermides on the left and upper on the right). — A, B: *Eranthemum albo-marginata*. — C, D: *E. capense*. — E, F: *E. nervosum*. — G, H: *E. purpurascens*. — Scale: 100 μ.

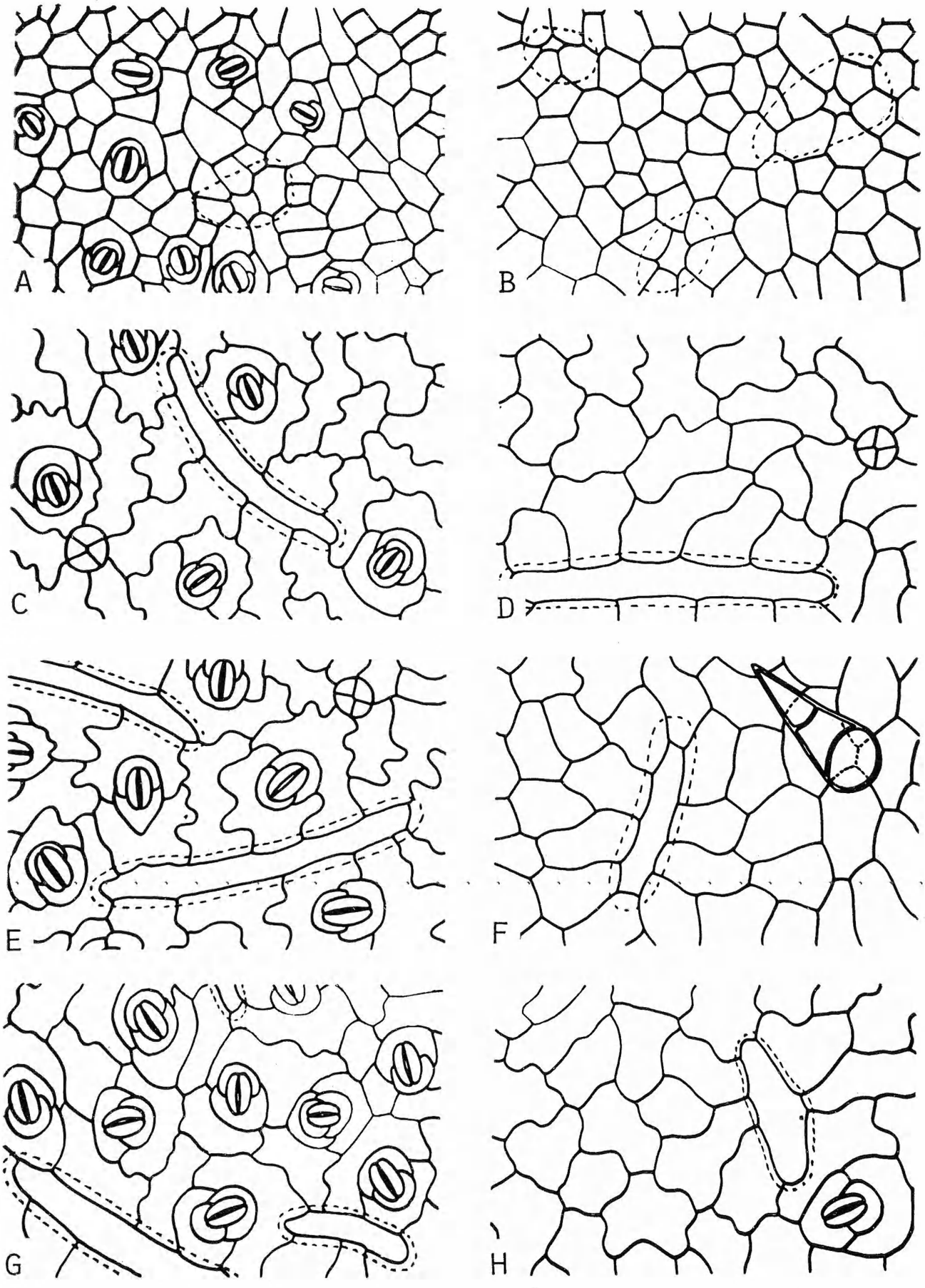


Fig. 1.

MATERIAL

The foliar material of the species listed below was either collected fresh from the living collection of the National Botanic Gardens, Lucknow (NBG) or procured as dried herbarium specimens from Dr ANIMA DE, Calcutta, India (DE); Dr K. H. KRISHNAMURTHY, Pondicherry, India (POND); Regional Botanist, Botanical Survey of India, Southern Circle, Coimbatore, India (BSI-COIMB); Dr A. N. RAO, University of Singapore (SING); and Dr K. C. CHEANG, Waterfalls Gardens, Penang, Malaysia (MALAY).

Eranthemum albo-marginata MART. (POND); *E. capense* L. (BSI-COIMB); *E. nervosum* R. BR. ex ROEM. & SCHULT. (NBG); *E. purpurascens* NEES (NBG); *E. roseum* (VAHL) R. BR. (POND); *E. wattii* STAPF. (SING); *Pseuderanthemum atropurpureum* (BULL.) BAILEY (POND); *P. bicolor* (SCHRANK) RADLK. (DE); *P. grandiflorum* DOMIN (SING); *P. kewense* BAILEY (NBG); *P. malaccense* LINDEN (MALAY); *P. variabile* (R. BR.) RADLK. (NBG).

METHODS

The cuticles were peeled from leaves or scraped off with a safety razor blade. Chemical maceration with 10—30 % nitric acid was, however, carried out on the majority of leaves, especially in cases where no fresh material was available. After removal cuticles were thoroughly washed, cleaned, and stained with 1 % aqueous safranin and mounted in pure glycerine and the coverslip was sealed with Canada balsam. In the case of dried herbarium specimens the leaf pieces were soaked and heated in water before the acid treatment. The technique is described in detail by the author elsewhere (AHMAD 1972).

The epidermal characters of six species each of *Eranthemum* and *Pseuderanthemum* are described separately under generic descriptions which embrace the characters of the species investigated. Each generic description is supplemented by the data on measurements of various epidermal characters, viz., size of intercostal epidermal cells, stomatal frequency, stomatal size, glandular hair diameter and length of the non-glandular hairs, presented in Tables 1 and 2. The stomatal frequency represents the average number of stomata per square millimeter of the intercostal areas of the lower epidermis. About 50 readings of each measurement have been taken. The length of the non-glandular hair is expressed in the tables (from left to right) as the minimum, mean and maximum length observed.

OBSERVATIONS

Eranthemum L.

LOWER EPIDERMIS. Intercostal cells irregular, with slightly sinuous or sinuous walls, in *E. capense, E. nervosum, E. purpurascens, E. roseum* and *E. wattii* (Figs. 1 C, E, G, 2 A, C); polygonal, with straight or arcuate walls in *E. albo-marginata* (Fig. 1 A). Costal cells straight-walled, elongate, arranged in rows (Fig. 4 A). Marginal cells polygonal, straight-walled, isodiametric (Fig. 4 B).

Stomata diacytic, restricted to intercostal areas. Stomata with single guard cell and stomata with both the guard cells aborted common in *E. albo-marginata* (Fig. 4 C, D).

Glandular hairs (Fig. 4 E—K) common, sub-sessile, head globular, generally 4-celled (8- or more-celled in *E. albo-marginata,* Fig. 4 I, J).

Non-glandular hairs (Fig. 4 L—V) common, generally restricted to the veins and the margin (absent in *E. albo-marginata*), 1-celled, generally conical (Fig. 4 N, P) or several-celled (usually 2—4-celled), frequently stout (Fig. 4 L, M); wall ornamented with round to elliptic tubercles (Fig. 4 W—Y); pore rim circular or polygonal; hair-base 1- to several-celled.

Cystoliths (Fig. 4 Z—II) common, simple, variously shaped; double cystoliths also present.

UPPER EPIDERMIS. Intercostal cells irregular, slightly sinuous or sinuous-walled, in *E. capense, E. purpurascens, E. roseum* and *E. wattii* (Figs. 1 D, H,

Fig. 2. Lower and upper epidermides (lower epidermides on the left and upper on the right). — A, B: *Eranthemum roseum.* — C, D: *E. wattii.* — E, F: *Pseuderanthemum atropurpureum.* — G, H: *P. bicolor.* — Scale: 100 μ.

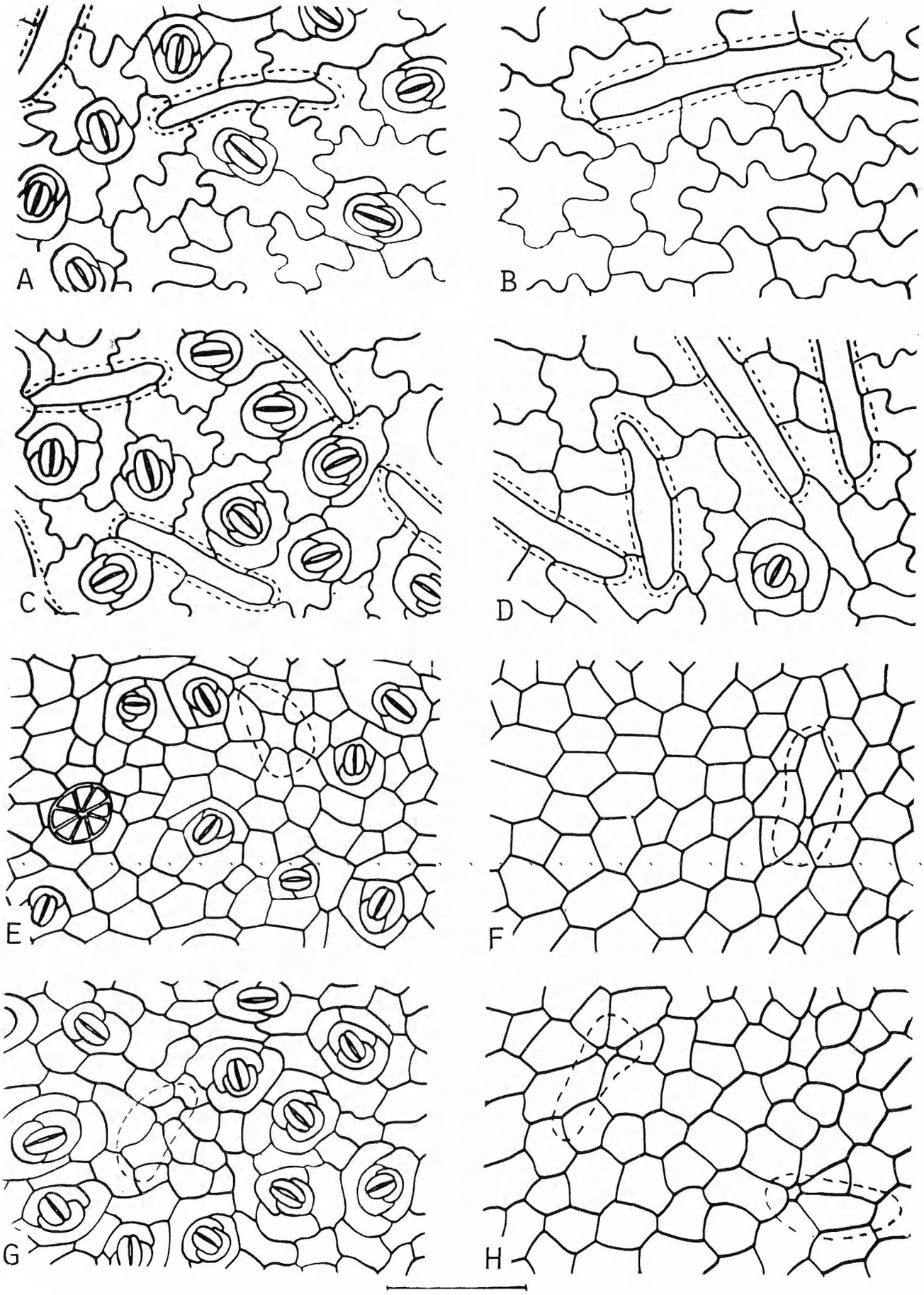


Fig. 2.

Table 1. Measurements of epidermal characters in *Eranthemum*. — A: Epidermal cell size (μ). — B: Stomatal frequency per mm². — C: Stomatal size (μ). — D: Diameter of glandular head (μ). — E: Length of non-glandular hairs (μ). — L: Lower epidermis. — U: Upper epidermis.

Species	A	B	C	D	E
E. albo-marginata	L: 35×23 U: 38×29	L: 120	21×15	30	—
E. capense	L: 75×39 U: 69×43	L: 64	22×15	25	27—70—170
E. nervosum	L: 64×31 U: 60×34	L: 106	23×13	26	22—100—235
E. purpurascens	L: 68×27 U: 79×42	L: 108	30×18	34	53—87—162
E. roseum	L: 62×41 U: 72×45	L: 83	22×15	26	57—102—195
E. wattii	L: 67×29 U: 56×35	L: 107	26×16	25	22—57—127

2 B, D); polygonal, with straight, arcuate or slightly sinuous walls, in *E. albo-marginata* and *E. nervosum* (Fig. 1 B, F). Costal and marginal cells similar to those of the lower epidermis. Stomata present, sparse in *E. nervosum, E. purpurascens* and *E. wattii*; stomata absent in *E. albo-marginata, E. capense* and *E. roseum*. Glandular hairs, non-glandular hairs and cystoliths similar to those of the lower epidermis; non-glandular hairs occur in intercostal areas also.

Pseuderanthemum RADLK.

LOWER EPIDERMIS. Intercostal cells polygonal, with straight walls, in *P. atro-purpureum* and *P. kewense* (Figs. 2 E, 3 C); polygonal, with arcuate or slightly sinuous walls, in *P. bicolor* (Fig. 2 G); irregular, with sinuous walls, in *P. grandi-florum, P. malaccense* and *P. variabile* (Fig. 3 A, E, G). Costal cells straight-walled, polygonal or elongate (Fig. 5 A), arranged in rows; costal cells generally polygonal and isodiametric, in *P. atro-purpureum, P. bicolor* and *P. kewense* (Fig. 5 B). Marginal cells straight-walled, isodiametric (Fig. 5 C).

Stomata diacytic, restricted to inter-costal areas. Abnormal stomata with single guard cell and with aborted guard cells present in *P. bicolor* and *P. kewense* (Fig. 5 D, E).

Glandular hairs (Fig. 5 F—L) common, sub-sessile, head globular, 4—8-celled (generally 8-celled).

Non-glandular hairs (Fig. 5 M—S) absent in *P. atropurpureum, P. kewense* and *P. variabile*; sparse in *P. bicolor*; common in *P. malaccense* and *P. grandiflorum*; occurring chiefly on the veins and the margin; 1- to several-celled (up to 12-celled, slender, rarely branched in *P. bicolor*, Fig. 5 M—P), uniseriate; frequently small, unicellular, conical; wall ornamented with round or oval tubercles (Fig. 5 S); pore rim circular or polygonal; hair-base 1- to several-celled.

Cystoliths (Fig. 5 T—II) common in costal and intercostal areas, simple or double, variously shaped.

Fig. 3. Lower and upper epidermides (lower epidermides on the left and upper on the right). — A, B: *Pseuderanthemum grandiflorum*. — C, D: *P. kewense*. — E, F: *P. malaccense*. — G, H: *P. variabile*. — Scale: 100 μ.

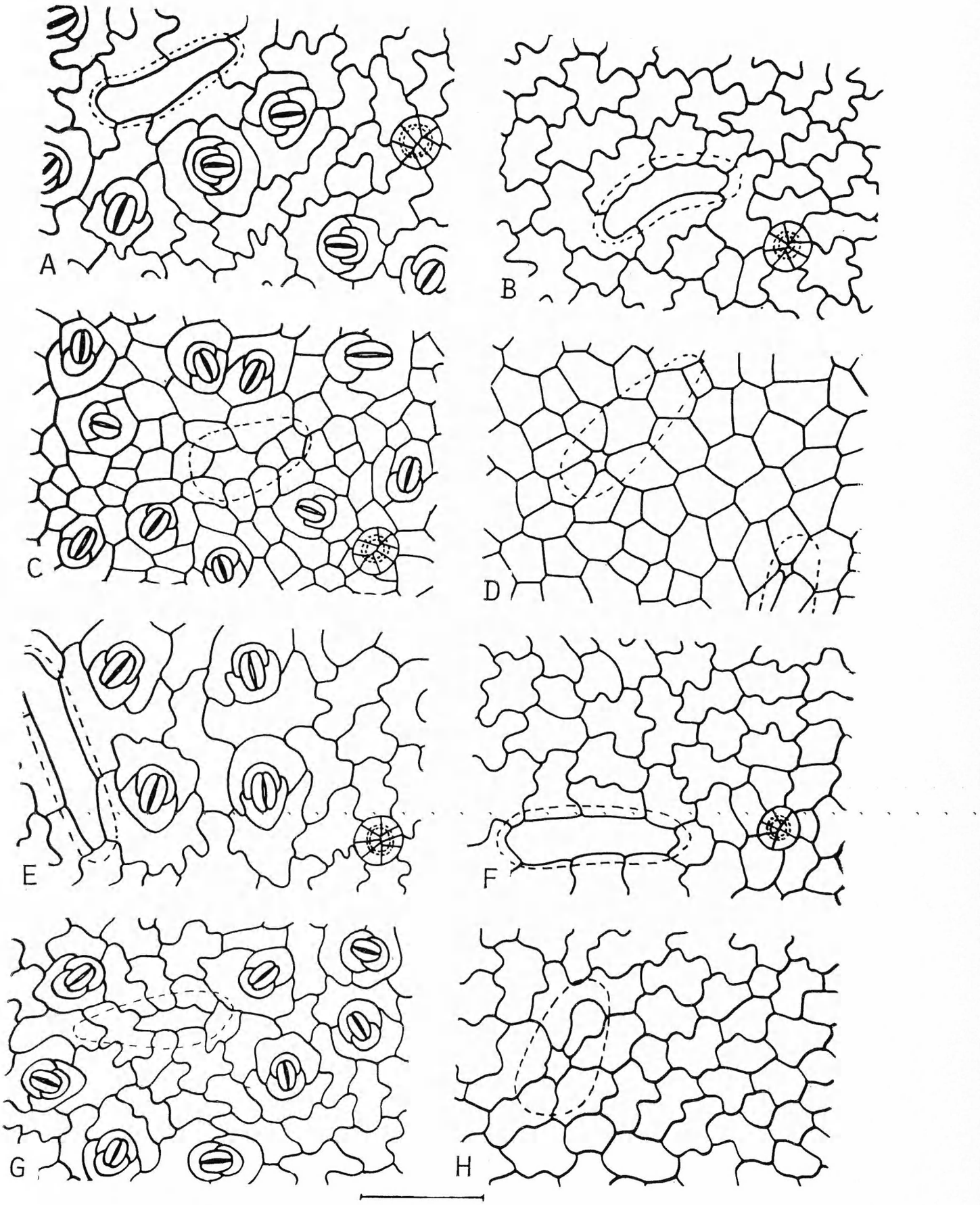


Fig. 3.

Table 2. Measurements of epidermal characters in *Pseuderanthemum*. — A: Epidermal cell size (μ). — B: Stomatal frequency per mm². — C: Stomatal size (μ). — D: Diameter of glandular head (μ). — E: Length of non-glandular hairs (μ). — L: Lower epidermis. — U: Upper epidermis.

Species	A	B	C	D	E
P. atropurpureum	L: 29×24 U: 38×31	L: 99	20×12	29	—
P. bicolor	L: 39×22 U: 41×32	L: 126	20×13	28	118—228—354
P. grandiflorum	L: 61×36 U: 58×38	L: 96	23×15	32	27—62—130
P. kewense	L: 34×21 U: 43×32	L: 124	24×14	28	—
P. malccense	L: 90×35 U: 50×30	L: 73	25×16	32	37—64—115
P. variabile	L: 42×27 U: 45×32	L: 104	20×12	27	—

UPPER EPIDERMIS. Intercostal cells polygonal, isodiametric, with straight walls in *P. atropurpureum, P. kewense* (Figs. 2 F, 3 D); polygonal, with straight or arcuate walls in *P. bicolor* (Fig. 2 H); irregular, with sinuous walls in *P. grandiflorum, P. malaccense* and *P. variabile* (Fig. 3 B, F, H). Costal cells similar to those of the lower epidermis. Stomata absent. Glandular hairs, non-glandular hairs and cystoliths similar to those of the lower epidermis.

DISCUSSION

Of the six species of *Eranthemum* investigated, all except *E. albo-marginata* show more or less uniform epidermal characters, viz., irregular, slightly sinuous or sinuous-walled epidermal cells, low stomatal frequency, glandular hairs with 4-celled heads and predominantly simple cystoliths. In *E. albo-marginata* however, the epidermal cells are very small (Table 1), polygonal in shape and straight-walled; glandular hairs have 8-celled heads, and non-glandular hairs are absent. This species appears to be closer to *Pseuderanthemum* than to *Eranthemum* as several species of *Pseuderanthemum* share these characters.

E. nervosum and *E. purpurascens* were formerly included in the genus *Daedalacanthus* (see SANTAPAU 1951). The epidermal characters of these two species are similar to those of the other species of *Eranthemum* except *E. albo-marginata*. Epidermal characters thus support RADLKOFER's (1883) treatment of the genus *Daedalacanthus* as a synonym of *Eranthemum*.

The species of *Pseuderanthemum* in-

Fig. 4. A: Costal cells of *Eranthemum roseum*. — B: Marginal cells of *E. capense*. — C: Single guard cell of *E. albo-marginata*. — D: Stoma with aborted guard cells in *E. albo-marginata*. — E—J: Sub-sessile glandular hairs of E: *E. roseum*; F: *E. capense*; G: *E. wattii*; H: *E. nervosum*; I, J: *E. albo-marginata*. — K: Sectional view of glandular hair in *E. nervosum*. — L—V: Non-glandular hairs of L—N: *E. roseum*; O—R: *E. capense*; S: *E. nervosum*; T, U: *E. wattii*; V: *E. purpurascens*. — W—Y: Portions of non-glandular hairs magnified to show wall ornamentation of W: *E. purpurascens*; X: *E. nervosum*; Y: *E. roseum*. — Z—II: Cystoliths of Z, AA: *E. wattii*; BB: *E. capense*; CC: *E. roseum*; DD—HH: *E. albo-marginata*; II: Sectional view of cystolith in *E. purpurascens*. — Left scale: 100 μ (A, B, L—V, Z—HH). Right scale: 50 μ (C—K, W—Y, II).

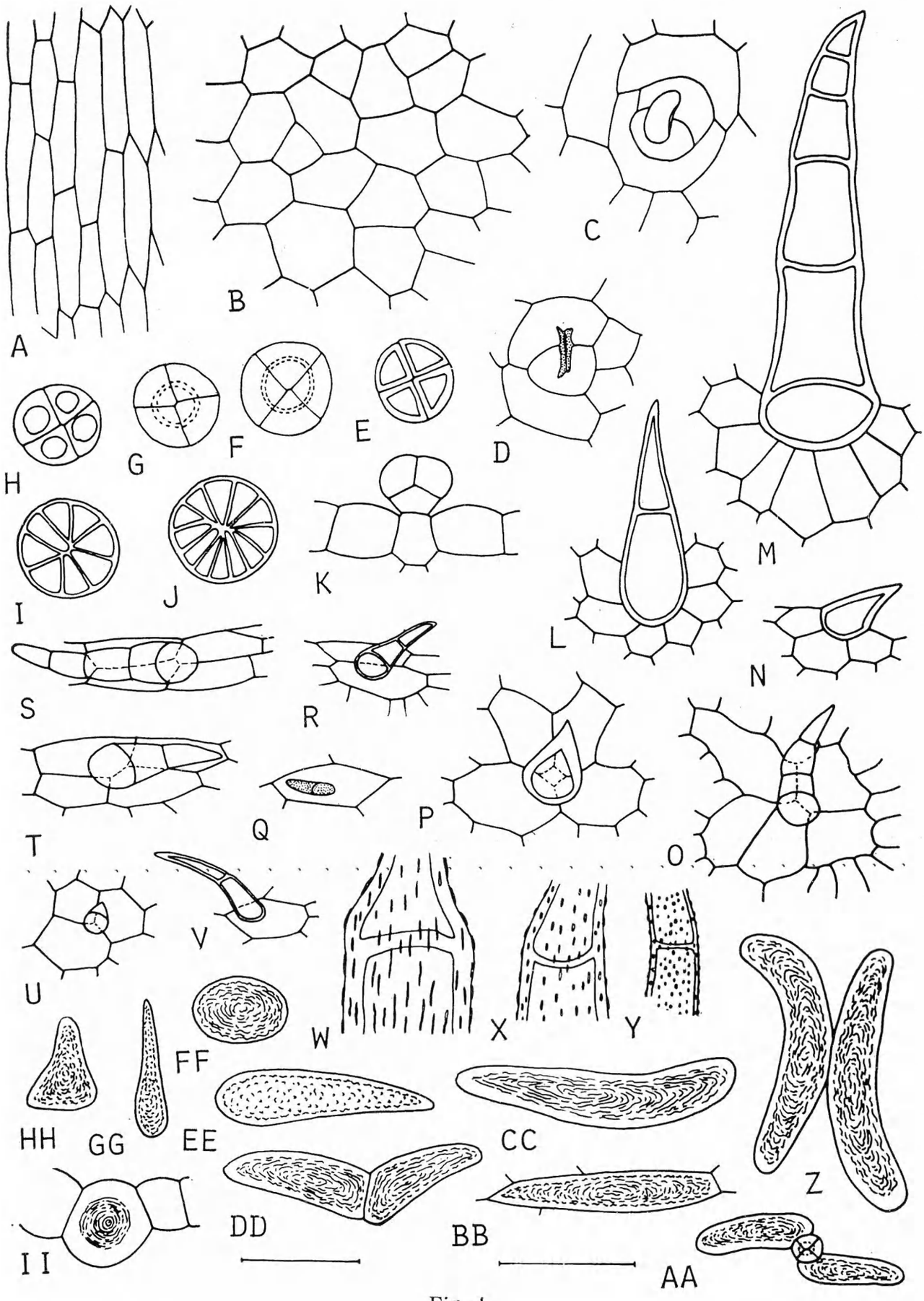


Fig. 4.

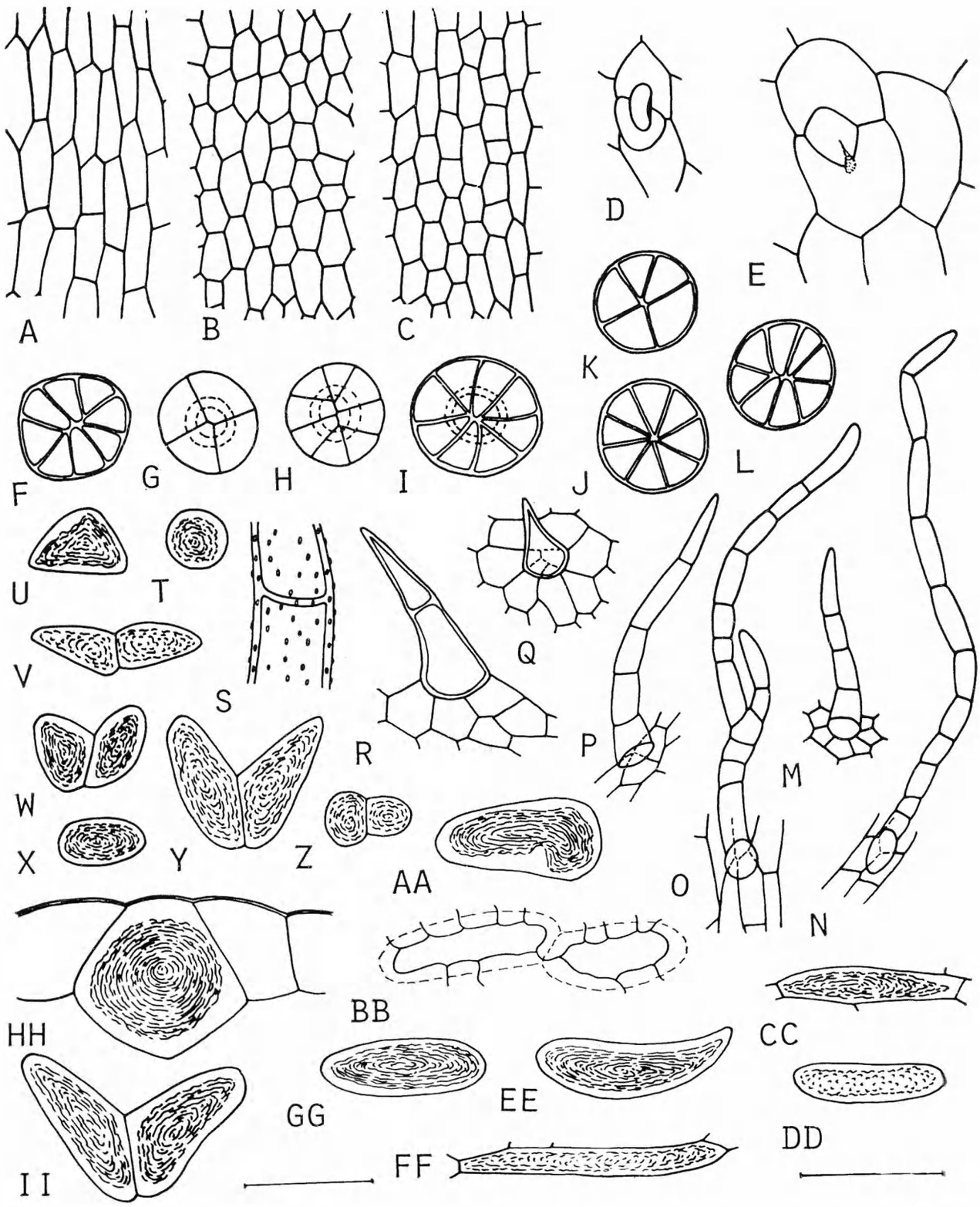


Fig. 5. A, B: Costal cells of A: *P. variabile*; B: *P. kewense*. — C: Marginal cells in *P. bicolor*. — D: Stoma with single guard cell in *P. kewense*. — E: Stoma with aborted guard cells in *P. bicolor*. — F—L: Sub-sessile glandular hairs of F: *P. variabile*; G, H: *P. bicolor*; I: *P. malaccense*; J: *P. grandiflorum*; K: *P. kewense*; L: *P. atropurpureum*. — M—S: Non-glandular hairs of M—P: *P. bicolor*; Q, R: *P. grandiflorum*; S: *P. grandiflorum*, portion of a non-glandular hair showing wall ornamentation. — T—II: Cystoliths of T—Z: *P. kewense*; AA: *P. atropurpureum*; BB—DD: *P. grandiflorum*; EE: *P. bicolor*; FF: *P. wattii*; GG: *P. malaccense*; II: *P. variabile*; HH: Sectional view of cystolith in *P. variabile*. — Left scale: 100 μ (A—C, M—R, T—GG, II). Right scale: 50 μ (D—L, S, HH).

Table 3. Comparison of epidermal characters of *Eranthemum* and *Pseuderanthemum*.

Epidermal characters	*Eranthemum*	*Pseuderanthemum*
Intercostal cells	Irregular (polygonal in *E. albo-marginata*)	Irregular in some species, polygonal in others
Costal cells	Polygonal, elongate	Polygonal, sometimes ± isodiametric
Stomata	Common in the lower epidermis, sparse or absent in the upper	Common in the lower epidermis, absent in the upper
Glandular hairs	Sub-sessile, head globular, 4-celled (8-celled in *E. albo-marginata*)	Sub-sessile, head globular, 4—8-celled, generally 8-celled
Non-glandular hairs ..	Common (absent in *E. albo-marginata*) 1- to several-celled	Common in two species, sparse or absent in the others; 1- to several-celled
Cystoliths	Common, generally simple; sometimes double	Common, both simple and double

vestigated also reveal broadly uniform epidermal characters (Table 2) such as hypostomatic leaves, low stomatal frequency, subsessile glandular hairs with 4—8- (generally 8-) celled glandular heads, and simple and double cystoliths. They can be distinguished by the shape of their epidermal cells and the presence or absence of non-glandular hairs. *P. bicolor* is characterized by its slender, sometimes branched non-glandular hairs. *P. grandiflorum* and *P. malaccense* have comparatively large epidermal cells. *P. malaccense* also has the lowest stomatal frequency among the species investigated (Table 2).

A comparison of the epidermal characters of *Eranthemum* and *Pseuderanthemum* is given in Table 3. The most important differences in the epidermal characters of *Eranthemum* and *Pseuderanthemum* are as follows: the stomata are present sparsely on the upper epidermis of some species of *Eranthemum,* but absent in *Pseuderanthemum*; the glandular hairs have 4-celled heads in *Eranthemum,* and 4—8- (generally 8-) celled heads in *Pseuderanthemum*; the non-glandular hairs are common in *Eranthemum,* sparse and inconspicuous in *Pseuderanthemum*; double cystoliths are sparse in *Eranthemum,* but common in *Pseuderanthemum*. There are no other differences between the two genera as regards epidermal characters. *E. albo-marginata* shows more similarities to the species of *Pseuderanthemum* than *Eranthemum*. VISHNU-MITTRE and SHARMA (1963) who studied the pollen morphology of eight species of *Eranthemum* and three of *Pseuderanthemum* concluded that the two genera are quite distinct from each other. Evidence from the present studies indicates differences between the genera, but the position of *E. albo-marginata* and the variation found within *Eranthemum* requires to be reconsidered.

ACKNOWLEDGEMENTS

I owe deep gratitude to Dr R. V. SITHOLEY, former Acting Director of the National Botanic Gardens, Lucknow, for his valuable guidance and advice in this work. I am grateful to Mr D. B. SHUKLA and the late Mr S. PERCY LANCASTER for helping me with the collection and identification of some of the material for this study. I wish especially to record my gratitude to Professor C. E. B. BREMEKAMP, Ustadelaan, the Netherlands, for kindly identifying the specimens which I sent him and providing me with their correct botanical names.

LITERATURE CITED

AHMAD, K. J. 1972. Cuticular studies in some Acanthaceae and Solanaceae. — Thesis, Lucknow University.

BREMEKAMP, C. E. B. 1965. Delimitation and subdivision of the Acanthaceae. — Bull. Bot. Surv. India 7: 21—30.

LINDAU, G. 1895. Acanthaceae. — In ENGLER & PRANTL, Die natürlichen Pflanzenfamilien 4: 274—354.

NEES VON ESENBECK, C. G. 1847. Acanthaceae. — In DE CANDOLLE, Prodromus systematis naturalis regni vegetabilis 11: 46—519.

RADLKOFER, L. 1883. Ueber den systematischen Werth der Pollen-beschaffenheit bei den Acanthaceen. — Sitz. K. Bayer. Akad. Wiss. 13: 256—314.

SANTAPAU, H. 1951. The Acanthaceae of Bombay. — Bot. Memoirs 2. — Bombay Univ., Bombay.

VISHNU-MITTRE & SHARMA, B. D. 1963. Contribution to the pollen morphology of the genera Eranthemum Linn. and Pseuderanthemum Radlkof. — Proc. Nat. Inst. Sci. India 29: 520—526.

WILLIS, J. C. 1966. A dictionary of the flowering plants and ferns. 7th Ed., revised by H. K. AIRY SHAW. — Cambridge.

Megasporogenesis and Megagametogenesis in Paspalum commersonii and P. longifolium at Two Polyploid Levels

Chuan-ying Chao

CHAO, C. Y. 1974 09 13. Megasporogenesis and megagametogenesis in Paspalum commersonii and P. longifolium at two polyploid levels. — Bot. Notiser 127: 267—275. Lund. ISSN 0006-8195.

Megasporogenesis and megagametogenesis were studied at two polyploid levels in three polyploids of *Paspalum commersonii* and two of *P. longifolium*. Meiosis is restitutional in the hexaploid biotype (2n=60) and induced dodecaploid (2n=120) of *P. commersonii* and tetraploid biotype (2n=40) of *P. longifolium*, but normal in the dodecaploid biotype (2n=120) of *P. commersonii* and induced octoploid (2n=80) of *P. longifolium*. As a result, the embryo sac (ES) develops mainly from an unreduced megaspore in the first three biotypes and from a reduced megaspore in the last two. Aposporic development of ES from a nucellar cell was observed in all three biotypes of *P. commersonii*, regardless of whether meiosis is restitutional or normal, to a low degree, but was not traced in the two biotypes of *P. longifolium*. In every case, the ES is 8-nucleate, of the same appearance as in the Polygonum type with the three antipodals dividing 2—3 times to form 12 or 24 binucleate or multinucleate cells in the mature ES. These results indicate that in each biotype the meiotic sequence in megasporogenesis is similar to that in microsporogenesis reported elsewhere, and that the pattern of megasporogenesis can be different at different polyploid levels of the same species, yet the type of ES is not altered by the change in the number of chromosome sets. Whether somatic apospory occurs or not in these two species seems to be species specific and will not be altered after chromosome doubling.

Chuan-ying Chao, Department of Biology, The Chinese University of Hong Kong, Hong Kong.

INTRODUCTION

Microsporogenesis at two different polyploid levels in three polyploids of *Paspalum commersonii* and two of *P. longifolium* has been reported by PI and CHAO (in press). In *P. commersonii*, the hexaploid (2n=60) and dodecaploid (2n=120) biotypes collected from the same locality are asynaptic and synaptic respectively; whereas the dodecaploid (2n=120) induced from the asynaptic hexaploid biotype by colchicine treatment is completely asynaptic. In *P. longifolium*, the tetraploid biotype (2n=40) is desynaptic, while the octoploid (2n=80) induced from the desynaptic tetraploid biotype also by colchicine treatment is synaptic. In the asynaptic and desynaptic biotypes, the first division in microsporogenesis results in the formation of a restitution nucleus. Hence each pollen mother cell (PMC) usually produces two unreduced microspores after meiosis. In the synaptic biotypes, microsporogenesis follows the normal meiotic sequence and produces four reduced microspores from each PMC, but is usually accompanied by some irregularities. These results indicate that the meiotic pattern during microsporogenesis can be different at different polyploid levels of the same species.

In order to complete the study of the

process of reproduction, the present paper deals with the megasporogenesis and megagametogenesis in the same five polyploids.

MATERIALS AND METHODS

The origin of the material used was reported previously (PI & CHAO in press). The plants were grown in the greenhouse of New Asia College, the Chinese University of Hong Kong. Spikes at stages of megasporogenesis and megagametogenesis were fixed in formalin acetic-alcohol for 24 hours. After washing in 70 % ethanol the individual ovaries were dissected out for dehydration and paraffin infiltration. Paraffin sections were cut 15 μ thick and stained with iron hematoxylin.

RESULTS

Paspalum commersonii LAMK.

HEXAPLOID BIOTYPE (2n=60)

Sections of 110 ovaries of this biotype were investigated for the development of megaspore mother cell (MMC) and meiotic division. It was found that the MMC initial elongates rapidly after it differentiates beneath the nucellar epidermis. When it has become about twice as long as broad, it undergoes megasporogenesis. At diakinesis approximately 60 univalents could be observed in the nucleus (Fig. 1 A). At metaphase I (MI) the univalents move to the equatorial plane where a restitution nucleus is later formed (Fig. 1 B, C). The second meiotic division results in the formation of two unreduced daughter nuclei (Fig. 1 D). Two types of development were observed during cytokinesis. In the one, cytokinesis results in the formation of two megaspores, the micropylar one being slightly smaller than the chalazal one. The former degenerates when the latter starts to elongate (Fig. 1 E). In the other, wall formation divides the cell into two unequal megaspores, the micropylar one being less than one half of the chalazal one in size (Fig. 1 F). The former may persist until the latter has extended to its maximum size for initiating the first mitotic division (Fig. 1 G, H). In a few cases the new cell wall is oblique (Fig. 1 I, J).

The study of the sections of 200 ovaries at different stages of megagametogenesis shows that the embryo sac (ES) that originated from the unreduced megaspore follows the normal sequence of development of most plants (Fig. 1 K—M). The maturing ES is 8-nucleate, of the same appearance as in the Polygonum type (Fig. 1 N). The three antipodals usually divide 2—3 times to form 12 or 24 binucleate antipodals in the mature ES.

In a few ovaries the division of the megasporocyte and the development of the ES follow the pattern described above, but at the same time a nucellar cell enlarges and develops into another ES (Fig. 1 O, P). The nuclei in such ES are relatively large in size.

INDUCED DODECAPLOID (2n=120)

For this taxon, which was induced from the hexaploid biotype, sections of 135 ovaries ranging from MMC initials to mature ES were examined. The results

Fig. 1. *Paspalum commersonii,* hexaploid biotype. — A: Megasporocyte at diakinesis, showing a number of univalents in the nucleus. — B: Telophase I, showing the formation of a restitution nucleus, chromosomes appearing to be stuck together. — C: A restitution nucleus. — D: Telophase II. — E: Two unreduced megaspores, the micropylar one degenerating. — F, G: Formation of two megaspores, the micropylar one being much smaller in size. — H: Uninucleate embryo sac, the micropylar megaspore still persistent. — I: Two megaspores separated by an oblique cell wall. — J: Uninucleate embryo sac and the degenerating micropylar megaspore. — K—M: Binucleate, 4-nucleate and 8-nucleate embryo sacs. — N: Maturing embryo sac of *Polygonum* type in appearance. — O: Megasporocyte at telophase II together with one binucleate embryo sac from a nucellar cell. — P: One maturing embryo sac probably from the chalazal megaspore, and one binucleate embryo sac of nucellar origin. — A—H ×750. I—P ×570.

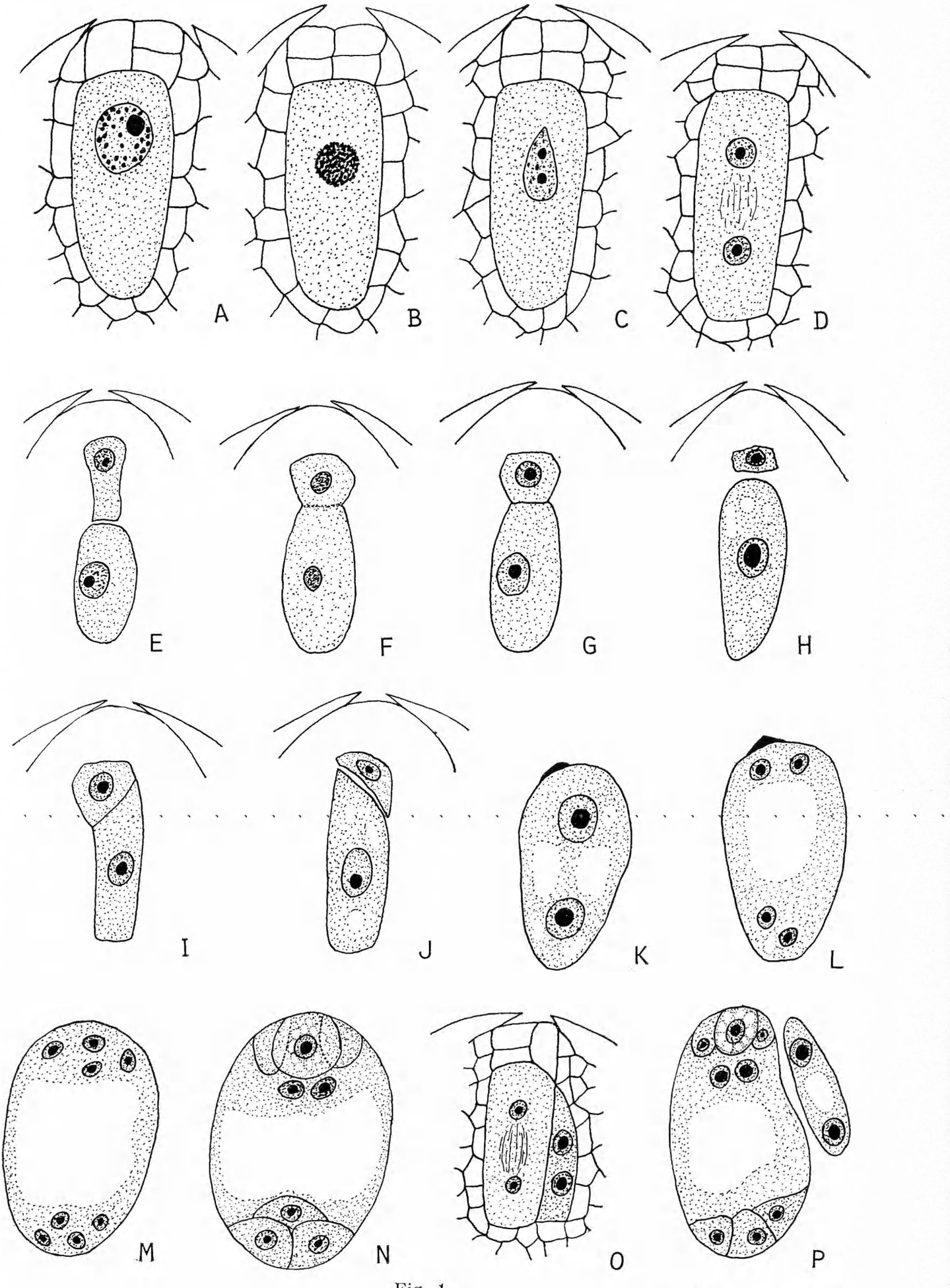


Fig. 1.

indicate that after chromosome doubling, the basic pattern of megasporogenesis and megagametogenesis was not altered as compared with its parental hexaploid biotype described in the previous section. Chromosomes are not paired at diakinesis and MI (Fig. 2 A). Two unreduced megaspores are formed from each MMC at the end of meiosis (Fig. 2 B, C). The ES is also 8-nucleate, of the same appearance as in the Polygonum type (Fig. 2 D—F). In some ovaries, simultaneous development of a nucellar cell into ES and the division of the megasporocyte was also observed (Fig. 2 G, H) as in the parental hexaploid biotype.

DODECAPLOID BIOTYPE (2n=120)

The MMC of this biotype is similar in development to that of the hexaploid biotype and the induced dodecaploid. However, it differs from them in meiotic division as revealed in the sections of 65 ovaries at this stage. In general megasporogenesis of this biotype follows the normal sequence of most plants. Chromosome pairing is normal. All the bivalents move to the equatorial plane at MI (Fig. 3 A). Two dyad cells are then formed at the end of the first division (Fig. 3 B, C), the micropylar one being smaller than the chalazal one. The second meiotic division may take place in the micropylar dyad cell as usual or fail at a certain stage of the division (Fig. 3 D), but it is normal in the chalazal one in most cases, forming two reduced megaspores (Fig. 3 D, E). Thus either tetrad or triad is formed in the ovule after meiosis (Fig. 3 E—G). Normally the innermost megaspore develops into ES (Fig. 3 E—G). There is, however, one enlarged nucellar cell situated just below the sporogenous cell or cells (Fig. 3 E, F) in a number of ovaries. It was observed in some such ovaries that when all the sporogenous cells degenerate this enlarged nucellar cell shows a tendency to develop (Fig. 3 H). But it is doubtful whether it could really form functional ES since at this stage the plants have already reached anthesis.

Sixty-eight ovaries at stages of megagametogenesis were studied. The results show that the ES of this biotype (Fig. 3 I—L) agrees with the Polygonum type, and the structure of its mature ES is quite similar to that of the hexaploid biotype although these two biotypes are different in the pattern of megasporogenesis.

From the above observations we may conclude that in *P. commersonii,* the hexaploid biotype and the induced dodecaploid exhibit meiosis characterized by the formation of a restitutional nucleus at first meiotic division (restitutional meiosis according to BATTAGLIA 1963) and ending in the formation of two unreduced megaspores, and the dodecaploid biotype has a normal sequence of megasporogenesis and produces reduced megaspores. As a result, the ES development in the former two biotypes is diplosporic, but normal in the latter one. The aposporic development of ES from a nucellar cell was observed in all three biotypes, but to a very low degree. The maturing ES, however, are all 8-nucleate, and all the mature ES contain 12 or 24 binucleate antipodals.

Paspalum longifolium ROXB.

TETRAPLOID BIOTYPE (2n=40)

Results from the examination of the sections of 73 ovaries of this biotype indicate that its MMC development and meiosis are similar to those of the hexaploid biotype of *P. commersonii.* Approximately 40 univalents could be observed at diakinesis (Fig. 4 A). A restitution nucleus is formed at the end of the first meiotic division. It then divides to form two megaspores (Fig. 4 B) with an unreduced chromosome number.

The chalazal megaspore develops into the ES (Fig. 4 C). This was invariably so in 78 ovaries studied at different stages of ES development. The formation and structure of the ES in this taxon (Fig. 4

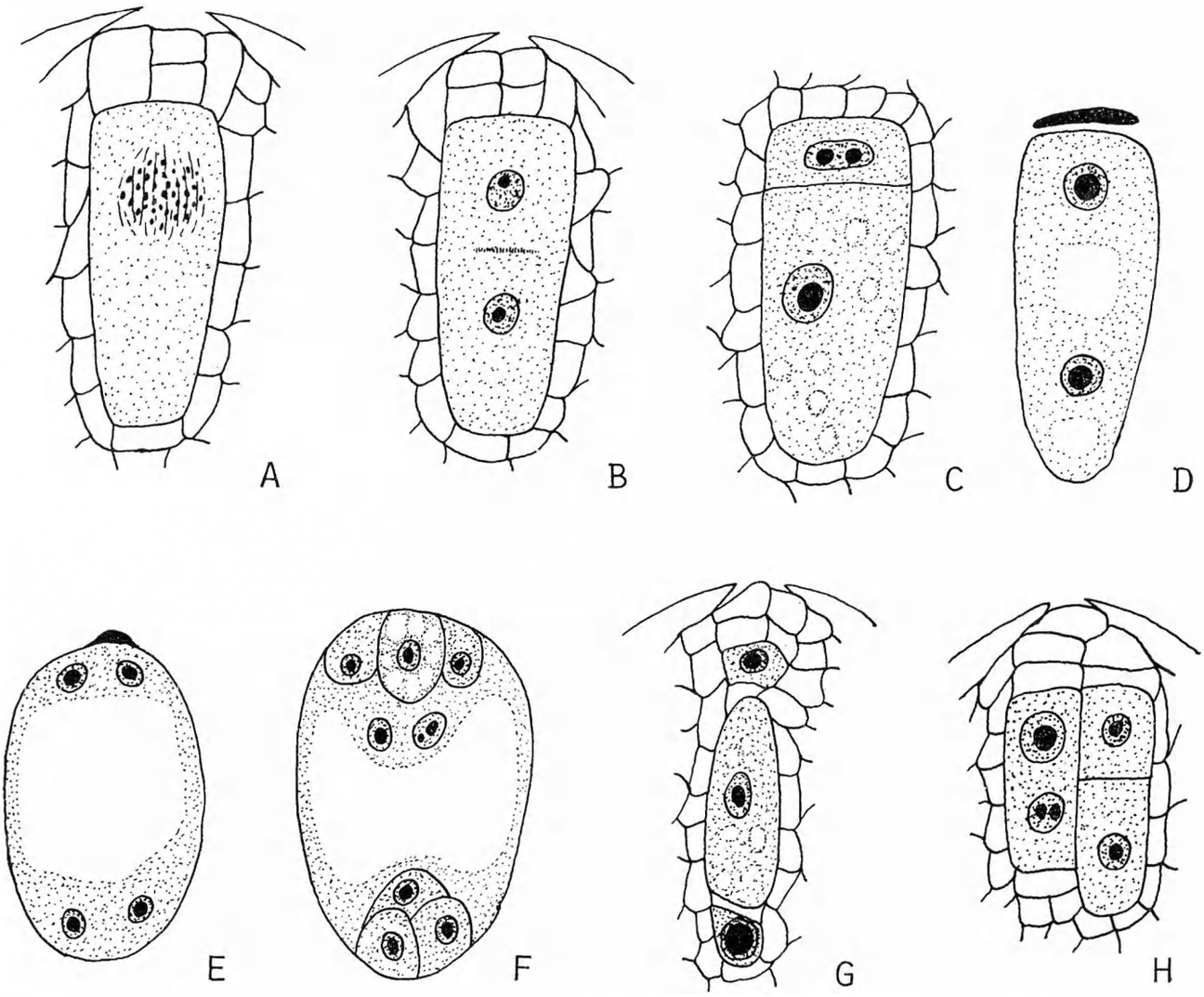


Fig. 2. *Paspalum commersonii*, induced dodecaploid. — A: Megasporocyte at prometaphase I, showing a number of univalents. — B: Telophase II. — C: Two unreduced megaspores, the chalazal one developing. — D, E: Binucleate and 4-nucleate embryo sacs. — F: Maturing embryo sac. — G: The developing and the degenerating megaspores. Notice the enlarged nucellar cell just below the developing megaspore. — H: Two megaspores divided from one megasporocyte and a binucleate embryo sac developed from a nucellar cell. — A—D ×750. E—H ×570.

D—F) are also comparable to those of the hexaploid biotype of *P. commersonii* with the exception that the antipodals of this biotype are multinucleate instead of binucleate in the mature ES.

INDUCED OCTOPLOID (2n=80)

This octoploid was induced from the tetraploid biotype by colchicine treatment. Although its MMC development is not changed after chromosome doubling, the sequence of meiotic division has been altered from desynaptic to synaptic and shows some similarities to those of the dodecaploid biotype of *P. commersonii* as revealed from sections of 85 ovaries. Chromosome pairing is quite regular and the bivalents move to the equatorial plane at MI (Fig. 5 A). Two dyad cells are formed after the first meiotic division (Fig. 5 B, C). The chalazal dyad cell divides normally to form two megaspores with the chromosome number reduced

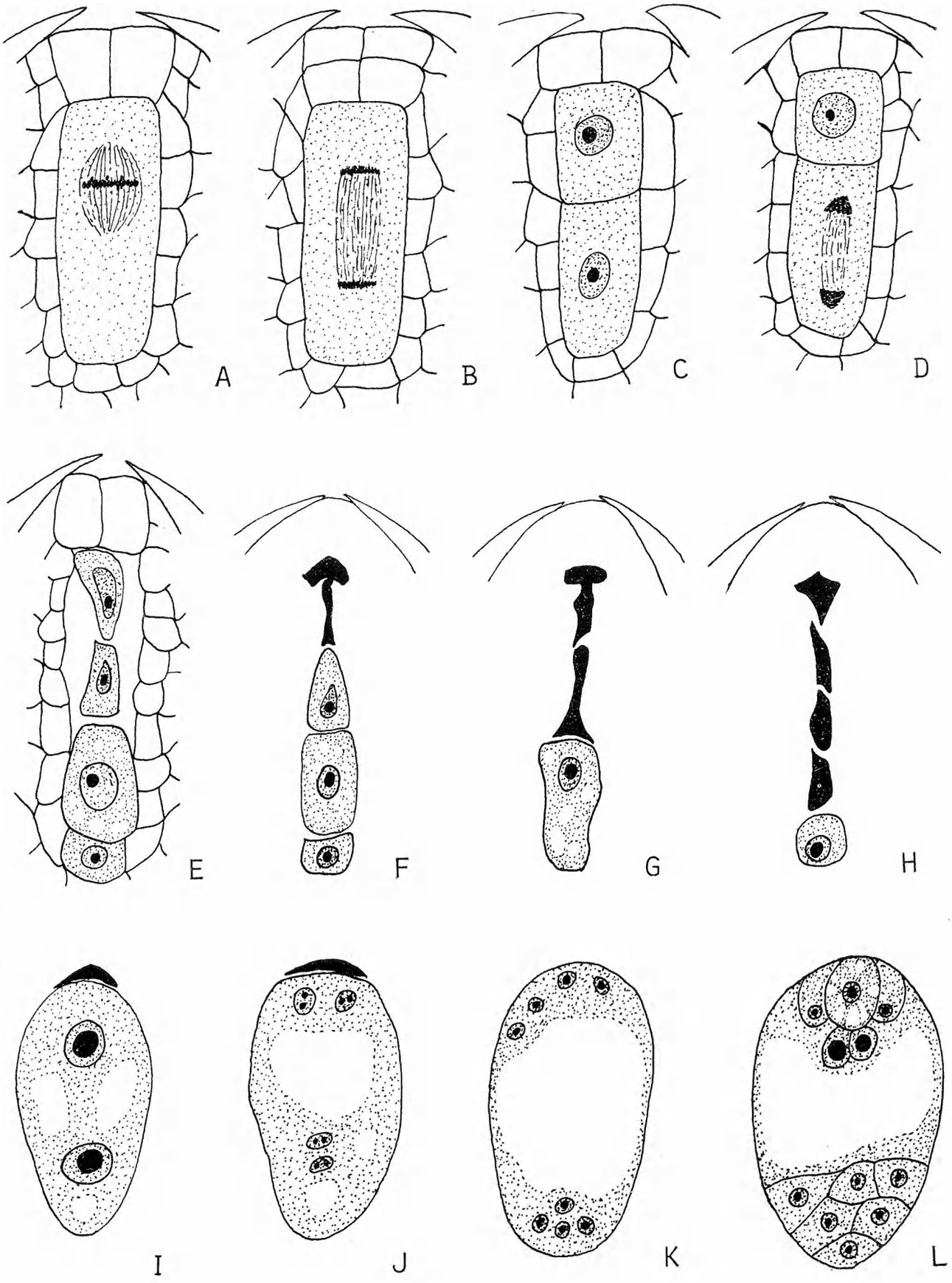


Fig. 3.

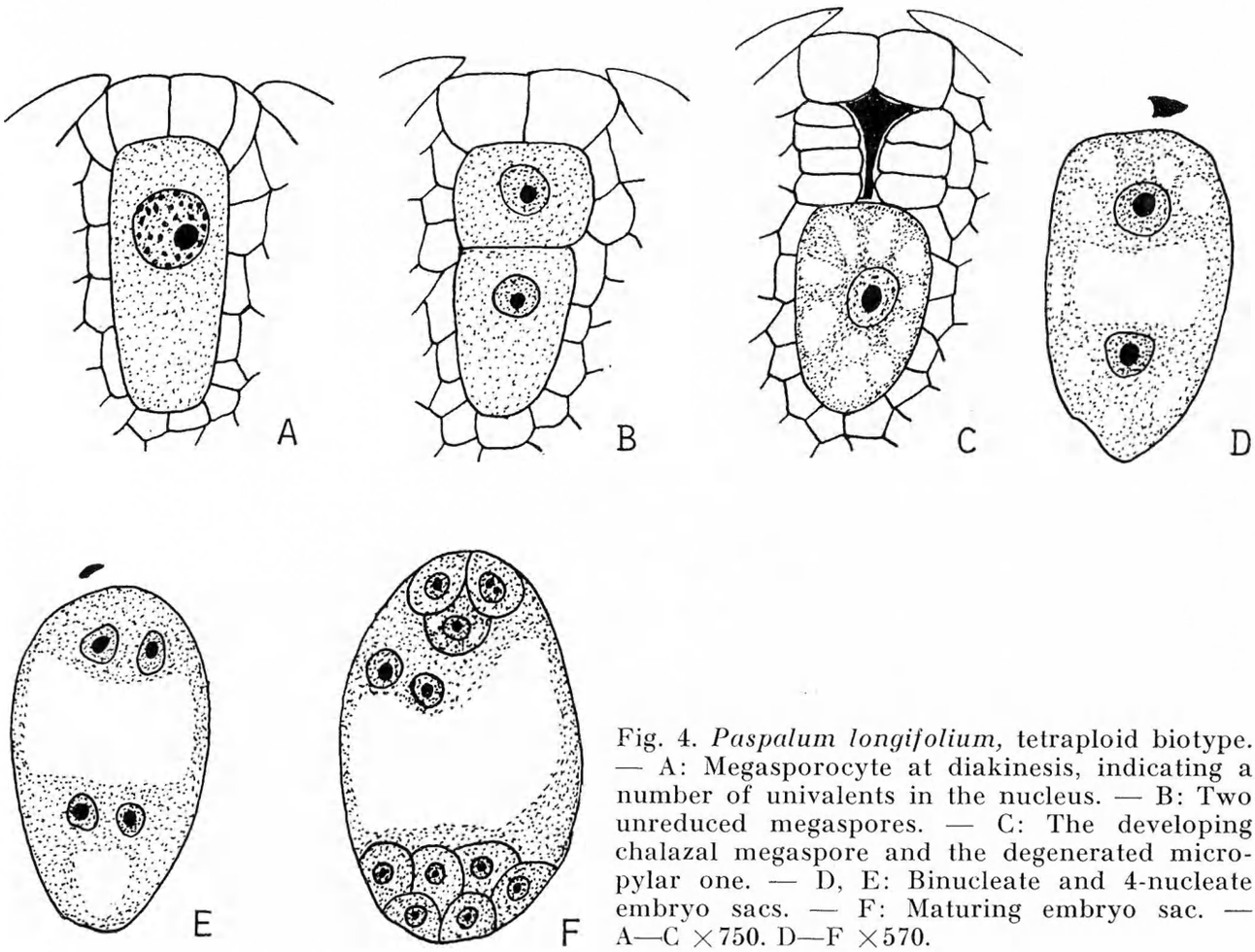


Fig. 4. *Paspalum longifolium,* tetraploid biotype. — A: Megasporocyte at diakinesis, indicating a number of univalents in the nucleus. — B: Two unreduced megaspores. — C: The developing chalazal megaspore and the degenerated micropylar one. — D, E: Binucleate and 4-nucleate embryo sacs. — F: Maturing embryo sac. — A—C ×750. D—F ×570.

to half. The second division of the micropylar one is usually delayed and incomplete (Fig. 5 D), or the spindle may not orient properly (Fig. 5 C, D). Even if two daughter nuclei are formed after division, cytokinesis may fail to take place (Fig. 5 E). As a result a triad instead of a tetrad was observed in many ovules at the end of meiosis.

Eighty-two ovaries at various stages of ES formation were examined. The innermost megaspore invariably develops into ES (Fig. 5 E—H) and the mature ES is similar to that of its parental tetraploid biotype in structure (Fig. 5 I).

From the above studies, it is concluded that in *P. longifolium* meiosis in the tetraploid biotype is restitutional while megasporogenesis in the octoploid induced from the tetraploid biotype follows the normal meiotic sequence. The development of the embryo sac is diplosporic in the tetraploid biotype but normal in the induced octoploid. The structure of the embryo sac is the same as in the Polygo-

Fig. 3. *Paspalum commersonii,* dodecaploid biotype. — A: Megasporocyte at metaphase I, showing a number of bivalents on the equatorial plane. — B: Telophase I. — C: Two dyad cells. — D: Chalazal dyad cell at telophase II, the micropylar one failing to divide. — E: Triad, the chalazal megaspore developing. Note an enlarged nucellar cell just below the developing megaspore. — F: Tetrad (or triad?), the chalazal megaspore developing, with an enlarged nucellar cell just below it. — G: Same as F, but no enlarged nucellar cell. — H: All the sporogenous cells degenerated, an enlarged nucellar cell starting to develop. — I—K: Binucleate, 4-nucleate, and 8-nucleate embryo sacs. — L: Maturing embryo sac. — A—E ×750. F—L ×570.

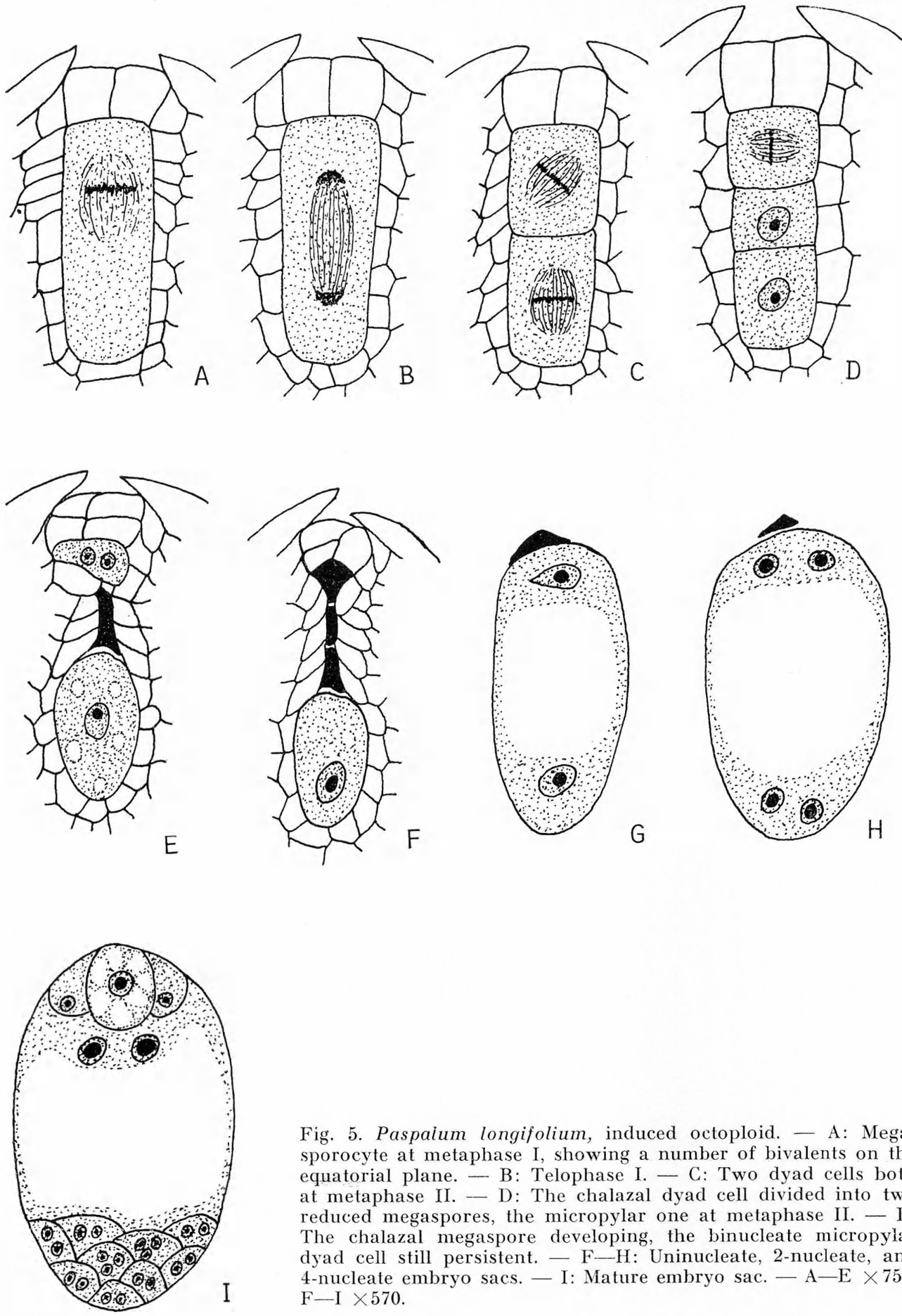


Fig. 5. *Paspalum longifolium,* induced octoploid. — A: Megasporocyte at metaphase I, showing a number of bivalents on the equatorial plane. — B: Telophase I. — C: Two dyad cells both at metaphase II. — D: The chalazal dyad cell divided into two reduced megaspores, the micropylar one at metaphase II. — E: The chalazal megaspore developing, the binucleate micropylar dyad cell still persistent. — F—H: Uninucleate, 2-nucleate, and 4-nucleate embryo sacs. — I: Mature embryo sac. — A—E ×750. F—I ×570.

num type in both biotypes. At maturity, each embryo sac contains 12 or 24 multinucleate antipodals. No aposporous development of ES was observed in either biotype studied.

DISCUSSION

Present and previous (PI & CHAO in press) results on the study of mega- and microsporogenesis respectively indicate that meiosis in each of the five polyploids of the two species, *Paspalum commersonii* and *P. longifolium,* are similar in both mega- and microsporocytes. At the end of meiosis, each of the desynaptic or asynaptic polyploids produces unreduced mega- and microspores, while each of the synaptic ones forms reduced mega- and microspores. The meiotic pattern, however, can be different at different polyploid levels in the same species. PI and CHAO (in press) proposed a mechanism of meiotic modification after chromosome doubling as due to the dosage effect of the desynaptic or asynaptic gene and its modifier(s). Similar results in meiosis in both mega- and microsporocytes in each taxon may indicate that this mechanism would operate in both sporocytes.

In this study similar sequences of ES formation and ES structure were observed in the five polyploids regardless of whether they were asynaptic or synaptic. In all cases the ES comes mainly from the chalazal megaspore, either reduced or unreduced, and is 8-nucleate, of the same appearance as in the Polygonum type. Thus, the actions of genes for the ES formation and structure are not affected by chromosome doubling in general.

After studying the ES structure of many species of the Gramineae, BROWN and EMERY (1958) concluded that, with few exceptions, diplosporic embryo sacs in Panicoideae are 4-nucleate. This may not be true in the genus *Paspalum* since the present study and previous reports (SNYDER 1957; CHAO 1964) showed that in this genus, the maturing ES of all the diplosporic taxa are 8-nucleate.

In the species *P. commersonii,* PRITCHARD (1970) reported one synaptic tetraploid biotype (2n=40) from Rhodesia. Our studies on microsporogenesis and megasporogenesis on material of this species collected in Taiwan show that the hexaploid biotype and induced dodecaploid are asynaptic, and that the dodecaploid biotype is synaptic. These results point to the fact that within the same species, the pattern of meiosis can be different at different polyploid levels. This is also true in the species *P. longifolium.* Since polyploidy is very common in many species of the genus *Paspalum,* different reproductive modes at different polyploid levels of the same species may be common in this genus. However, in *P. commersonii* the aposporic development of ES was observed in all three polyploids studied, regardless of whether they were asynaptic or synaptic although to a low degree. This is certainly not the case in the two polyploids of *P. longifolium* studied. These findings may imply that in these two species the difference in somatic apospory is species specific and would not be altered by change in the number of chromosome sets.

LITERATURE CITED

BATTAGLIA, E. 1963. Apomixis. — In P. MAHESHWARI (ed.), Recent advances in the embryology of angiosperms. — International Society of Plant Morphologists, University of Delhi, Delhi.

BROWN, W. V. & EMERY, W. H. P. 1958. Apomixis in the Gramineae: Panicoideae. — Amer. Jour. Bot. 45: 253—263.

CHAO, C. Y. 1964. Megasporogenesis, megagametogenesis and embryogeny in Paspalum orbiculare. — New Asia College Acad. Ann. 6: 15—25.

PI, P. & CHAO, C. (in press). Microsporogenesis in Paspalum longifolium and P. commersonii on two different polyploid levels. — Cytologia.

PRITCHARD, A. J. 1970. Meiosis and embryo sac development in Urochloa mosambicensis and three Paspalum species. — Aust. Jour. Agric. Res. 21: 649—652.

SNYDER, L. A. 1957. Apomixis in Paspalum secans. — Amer. Jour. Bot. 44: 318—324.

Tulipa kurdica sp. nov. from Iraq

Per Wendelbo

WENDELBO, P. 1974 09 13. Tulipa kurdica sp. nov. from Iraq. — Bot. Notiser 127: 276—277. Lund. ISSN 0006-8195.

Tulipa kurdica sp. nov. is described from the high mountains of NE Iraq. It belongs to a group of closely related species around *T. humilis* HERB.

Per Wendelbo, Department of Plant Geography, University of Göteborg, Carl Skottsbergs Gata 22, S-413 19 Göteborg, Sweden.

Tulipa kurdica WENDELBO, sp. nov.

Bulbus c. 1.5 cm longus, 1 cm latus, in tunicas brunneas inclusus, in collum distinctum productus; tunicae intus in parte superiore pilis rectis appressis antrorsis obsitae. *Caulis* 6—15 cm longus, glaber, in parte superiore brunnescenti-purpureus. *Folia* 3—4 (—5), in medio caule approximata vel per dimidium inferiorem caulis dispersa, erecta vel fortasse subfalcata, canaliculata, apice cucullata, glabra, atroviridia; folium infimum latissimum, 6—15.5 cm longum, 0.5—1.5 cm latum; folia superiora infimo circiter aequilonga sed multo angustiora. *Flos* unicus. *Tepala* inaequalia, aurantiaco-rubra, intus prope basin atro-viridimaculata, extus prope basin saepe virescenti-flavescentia; tepala exteriora 30—45 mm longa, 7—12 mm lata, anguste elliptica, basin versus attenuata, apice acuminata, glabra; tepala interiora quam exteriora breviora et latiora, 28—43 mm longa, 11—20 mm lata, elliptica, basi attenuata, ciliata, apice acuminata, subacuta. *Filamenta* subinaequalia, 7—10 mm longa, in parte superiore conica, coeruleo-violacea, pubescentia; antherae 13—14 mm longae, verisimiliter virescentes; pollen flavum. *Capsula* ignota.

Iraq. MRO: Ad nives tabescentes supra locum Sarcal dictum ad montem Helgurd (Algurd Dagh), 2420—2700 m, 5.VI. 1960, AGNEW et HADAČ leg. 2232 holotypus PRAG! isotypus E! — Algurd Dagh, 2400—3000 m, 21.V. 1951, THESIGER leg. 997 BM! — Rost, 2400—3000 m, 19.V. 1951, THESIGER 948!, 974 BM!

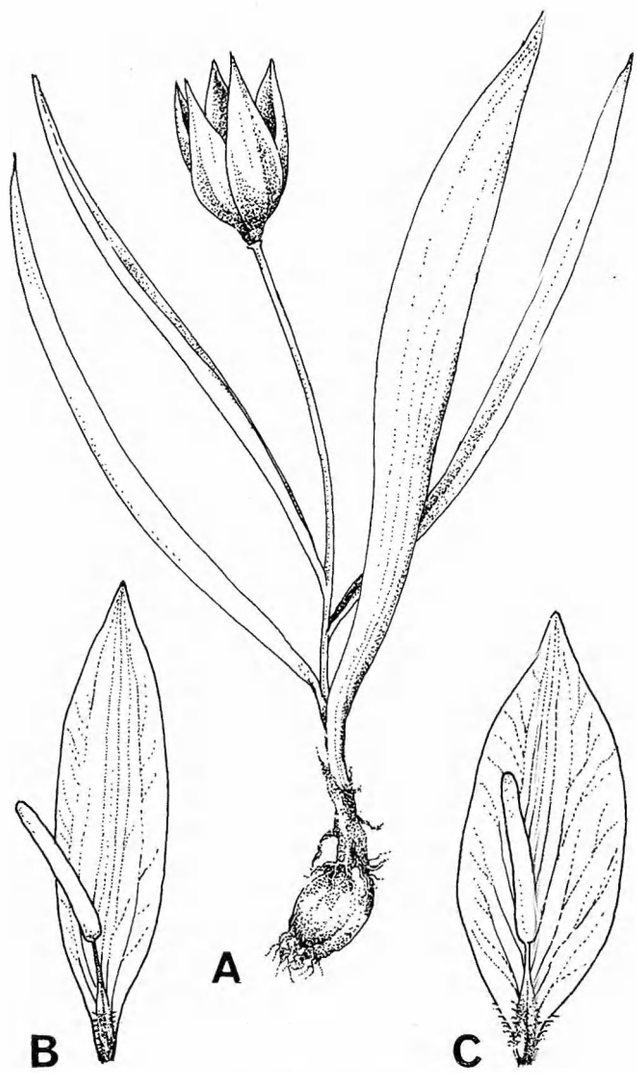


Fig. 1. *Tulipa kurdica,* sp. nov. — A: Habit, ×0.65. — B—C: Outer and inner tepal, ×1.30. — MARIANNE ERLANDSSON del.

It is with some hesitation that this taxon is described as a new species. It certainly belongs to the *Tulipa humilis*

complex and may be distinguished from the other taxa of that group mainly by the colour which is very distinct (a photograph taken at the type locality by Dr AGNEW accompanies the isotype at Edinburgh). The colour may be characterized as bright brick-red or orange-red; the tepals have a greenish-black blotch near base which is not margined by yellow or white. Species such as *T. humilis* HERB., *T. violacea* BOISS. & BUHSE, *T. pulchella* FENZL and the little-known *T. aucheriana* BAKER, are all closely related and come from the same general geographical area, E Turkey and NW Iran. They seem to be distinguished mainly on the colours of the perianth and should probably rather be treated as geographical races at subspecific level within the same species. This problem will be studied more closely in the rather extensive material now available for the "Flora Iranica" treatment.

ACKNOWLEDGEMENTS

I am indebted to Dr A. AGNEW of Aberystwyth and Professor E. HADAČ of Prague who have supplied me with information on the type collection which had been recognized by them as belonging to a new species under the provisional name *T. curdica*; and also to Professor K. H. RECHINGER of Vienna for translating my description into Latin.

Notes on Alpine and Nival Flora of the Hindu Kush, East Afghanistan[1]

Siegmar-W. Breckle

BRECKLE, S.-W. 1974 09 13. Notes on alpine and nival flora of the Hindu Kush, East Afghanistan. — Bot. Notiser 127: 278—284. Lund. ISSN 0006-8195.

The phytogeographical pattern of the lower regions is not the same as in the alpine or nival belt. The floristic relationships show close connections with Central Asia, even in eastern mountain parts. The degree of endemism decreases with increasing elevation. Plants which occur at the highest elevations have the widest geographical distribution.

Siegmar-W. Breckle, Institut für Pharmazeutische Biologie, Friedr. Wilhelms-Universität, D-5300 Bonn, Nuss-Allee 6, Bundesrepublik Deutschland.

INTRODUCTION

Afghanistan is a very mountainous country. Most of the area (60 %) is above 1,500 m. One quarter of the Afghan state is above 3,000 m (BRECKLE 1973). In most parts the vegetation exhibits distinctly semi-desert character (FREITAG 1971). The lowlands north and south of the highlands of Central Afghanistan are deserts and semi-deserts. The highlands are surrounded by fragmentary open deciduous woodlands with *Amygdalus* and *Pistacia*. Some northern slopes are covered with open juniper woodlands. The highland itself is covered mostly with spiny cushions. The climate is of mediterranean type, but considerably continental with dry, hot and long summers, and with cold, icy and sometimes snowy winters. Only in a very small region near the Pakistan border, on the south slopes of the Hindu Kush, do we have the influence of the Indian summer monsoon. Here grow the only real forests in the whole country (FISCHER 1970), consisting of evergreen sclerophyllous forests in the lower parts and coniferous forests in the upper. Above the timber line a belt of subshrubs and "krummholz" mixed with spiny cushions is found. Thus, this subalpine belt with hemicryophytic vegetation shows the same geographical pattern as do the lower vegetation regions. However, the alpine belt with its eucryophytic vegetation does not, it extends from the Western Hindu Kush in Central Afghanistan to the Eastern Hindu Kush, as far as we have seen. This might partly be explained by the fact that at this elevation the monsoon has no longer any influence. The water supply during the arid summer is derived mainly from the melting cover of winter snow. This is true for all Hindu Kush regions in the same way. As in the lower belts, the water-regime is the main factor in development of the vegetation mosaic. Only wet stands, with e.g. *Carex* and *Cobresia* meadows, show closed vegetation types, caused by allochthonous water-supply.

The timber line is observed between 3,100 m and 3,500 m, the cushion-line between 3,900 m and 4,300 m, the snow-line at about 5,000 m. In the higher Central, Northern and Eastern Hindu Kush remarkable glaciation is to be found. The altitudinal lines are given in Fig. 1.

[1] Presented at the ICSEB Congress, Boulder, Colorado; Aug., 11th, 1973.

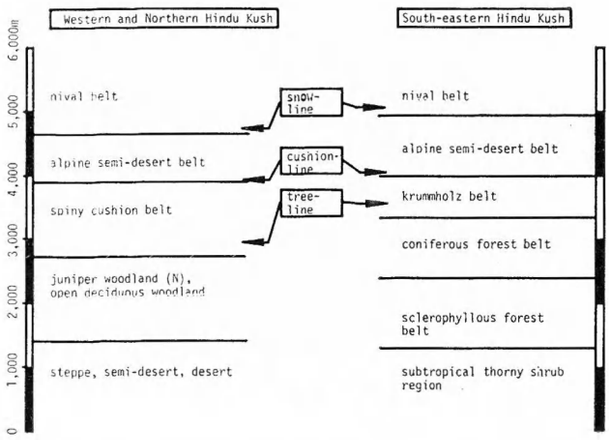


Fig. 1. Altitudinal lines of vegetation belts of the Hindu Kush.

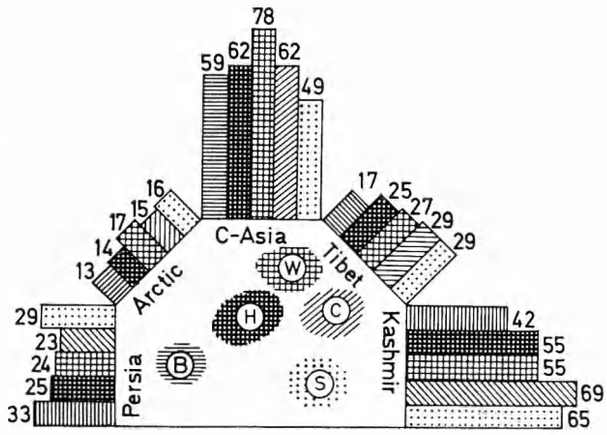


Fig. 2. The relationships of the flora of mountain parts of the Hindu Kush to the Flora of adjacent mountain regions. Included are only plant species which are known from localities at 4,000 m or higher. Within the Hindu Kush the following five mountain regions are distinguished: B: Koh-e-Baba range in Central Afghanistan; H: Western, Northern and Central Hindu Kush, main ranges; W: Wakhan range (Little Pamir) within the Afghan border; C: Chitral and Eastern Hindu Kush, on Afghan and Pakistan side; S: Safed Koh range, south of Kabul valley. — The figures indicate percentages of species in common with the following adjacent regions: Persia: Iranian highlands, Turkey, Eastern Mediterranean mountains; Arctic: Arctic and boreal elements, Siberian elements, mostly widely distributed over the Northern Hemisphere; C-Asia: Central Asiatic mountains: Pamir, Alai, Tien Shan, Tarbagatai; Tibet: Inner Asiatic mountains and highlands: Tibet, Eastern Altai; Kashmir: Western Himalayas, Karakorum.

PHYTOGEOGRAPHICAL RELATIONSHIPS

With regard to the plant species which are so far known from altitudes of 4,000 m and higher (acc. to RECHINGER, GILLI, KITAMURA etc., cf. BRECKLE et al. (1969); and own herbarium specimens), we have the following floristic relationships (see Fig. 2). It is indicated how many per cent of species the main Hindu Kush regions have in common with adjacent areas. As can easily be seen, most parts of the Hindu Kush have the strongest links with the Central Asiatic Mountains and secondly with the Western Himalayas. The closer the corresponding areas, the stronger are the floristic links. So only Chitral and Safed Koh have a higher percentage of species in common with the Western Himalayas than with Central Asia, but the difference is only slight. In this diagram (Fig. 2) out of 377 species 80 % are included. The remaining 20.2 % are endemics of the Hindu Kush, endemic to the above-mentioned five mountain regions (see Fig. 2), to which we limited this study. Those 76 taxa (20 %), which are at least known from one locality higher than 4,000 m, are partly species from the subalpine belt, which occasionally reach higher regions (see Table 1). So we have 9 *Cousinia* and 11 *Astragalus* species, the majority of which are related to the spiny cushion belt. It can therefore be said that in reality these high Hindu Kush regions have even less than 20 % of endemics. On the other hand, this list is within some plant families very incomplete and provisional and, of course, very much dependent upon the applied species concept. In Table 2 we give the number of plant species of the different plant families and their occurrence above 4,000 m, compared with figures from the Eastern Alps (Europe).

In the spiny cushion belt there are many endemic species, in some plant families (e.g. Plumbaginaceae) or genera

Table 1. Endemic species of alpine Hindu Kush regions (incl. Chitral; Afghan-Wakhan).

ALLIACEAE
Allium nuristanicum KITAM.

APIACEAE
Platytaenia lasiocarpa (BSS.) RECH. FIL. & RIEDL ssp. *lasiocarpa*
ssp. *incana* RECH. FIL. & RIEDL

ASTERACEAE
Cousinia ariana BORNM.
C. blepharobasis RECH. FIL. & GILLI
C. chionophila RECH. FIL. & KOEIE
C. carthamoides AITCH. & HEMSL.
C. kotandarica RECH. FIL. & GILLI
C. polyneura RECH. FIL.
C. scheibeana BORNM.
C. takharensis RECH. FIL.
C. trollii BORNM.
Erigeron petroiketes RECH. FIL.
Saussurea chthonocephala BORNM.
S. kerstanii (BORNM.) RECH. FIL.

BORAGINACEAE
Arnebia speciosa AITCH. & HEMSL.
A. rechingeri RIEDL
Eritrichium afghanicum RECH. FIL.
Lepichiniella albiflora RIEDL
Matthiastrum dielsii BORNM.
Omphalodes heterophylla RECH. FIL. & RIEDL
Pseudomertensia lindelofioides (RECH. FIL. & RIEDL) RIEDL
Solenanthus strictissimus BRAND
S. micranthus RIEDL
Tianshaniella wakhanica RIEDL

BRASSICACEAE
Chorispora pectinata HADAČ
Draba affghanica BSS.
Erysimum griffithii (HOOK. FIL. & THOMS.) JAFRI
Fibigia membranacea RECH. FIL.
Graellsia chitralensis O. E. SCHULZ
Gynophorea weileri GILLI
Stroganowia puberula KITAM.

CARYOPHYLLACEAE
Silene danielii HADAČ

CYPERACEAE
Carex chitralensis NELMES
C. griffithii BOOTT.

ERICACEAE
Rhododendron collettianum AITCH. & HEMSL.

FABACEAE
Astragalus ajfreidii AITCH. & BAKER
ssp. *ajfreidii*
ssp. *brevivexillatus* DEML
A. aloisii DEML
A. confertissimus KITAM.
A. gregarius DEML
A. hasarorum GILLI
A. hindukushense WDB.
A. macrostegius RECH. FIL.
A. minuti-foliolatus WDB.
A. miseriflorus SIRJ. & RECH. FIL.
A. peltatus PODL. & DEML
A. rassoulii RIEDL
Cicer nuristanicum KITAM.
C. pungens BSS.
Hedysarum minjanense RECH. FIL.
Oxytropis afghanica RECH. FIL. & KOEIE
Trigonella afghanica VASS.

FUMARIACEAE
Corydalis fedtschenkoana SCHRENK ssp. *metallica* (WDB.) WDB.

GENTIANACEAE
Gentiana micrantha AITCH. & HEMSL.

JUNCACEAE
Juncus triglumis L. ssp. *wakhaniensis* SNOG.

LAMIACEAE
Dracocephalum glechomifolium DUNN
Eremostachys calophyta HDG.
Thymus afghanicus RONN.

LILIACEAE
Gagea setifolia BAKER

PLUMBAGINACEAE
Acantholimon auganum BGE.
A. calocephalum AITCH. & HEMSL.
A. diapensioides BSS.
A. hariabense RECH. FIL. & KOEIE
A. peculiare RECH. FIL.

POACEAE
Agrostis interjacens MELDERIS
Colpodium afghanicum BOR
Festuca afghanica BOR
Oryzopsis barbellata (MEZ.) BOR
O. wendelboi BOR
Poa roemeri BOR
Psatyrostachys caduca (BSS.) MELDERIS

POLYGONACEAE
Polygonum chitralicum RECH. FIL. & SCH.-CZ.

RANUNCULACEAE
Ranunculus shaftoanus (AITCH. & HEMSL.) BSS.
Thalictrum afghanicum GILLI
Th. parvulum RECH. FIL.

ROSACEAE
Potentilla coelestis GILLI
P. collettiana AITCH. & HEMSL.
P. kurramensis TH. WOLF

SCROPHULARIACEAE
Pedicularis afghanica WDB.

Table 2. Number of plant species, reaching high elevations in the Hindu Kush, and for comparison in the European Alps.

Plant family	Hindu Kush				European Alps (E)		
	above				above		
	4,000	4,500	5,000	5,500 m	3,000	3,500	4,000 m
Alliaceae	7	2	—	—	—	—	—
Apiaceae	10	4	1	—	—	—	—
Asteraceae	37	15	5	—	11	5	—
Boraginaceae	14	4	—	—	—	—	—
Brassicaceae	38	25	8	2	9	5	1
Campanulaceae	3	1	—	—	4	2	1
Caprifoliaceae	6	3	1	—	—	—	—
Caryophyllaceae	7	4	1	—	12	3	—
Chenopodiaceae	2	—	—	—	—	—	—
Cichoriaceae	7	4	—	—	4	—	—
Crassulaceae	7	4	3	—	2	1	—
Cupressaceae	1	—	—	—	1	1	—
Cuscutaceae	1	—	—	—	—	—	—
Cyperaceae	14	4	2	—	3	1	—
Empetraceae	—	—	—	—	1	—	—
Ephedraceae	1	1	—	—	—	—	—
Ericaceae	1	—	—	—	3	—	—
Euphorbiaceae	3	1	—	—	—	—	—
Fabaceae	36	10	1	—	1	—	—
Fumariaceae	4	3	1	—	—	—	—
Gentianaceae	9	3	—	—	6	1	—
Geraniaceae	3	2	—	—	—	—	—
Grossulariaceae	3	—	—	—	—	—	—
Juncaceae	4	3	—	—	5	2	—
Lamiaceae	23	9	1	—	1	—	—
Liliaceae	8	3	—	—	1	—	—
Onagraceae	3	2	—	—	—	—	—
Papaveraceae	1	1	—	—	—	—	—
Parnassiaceae	1	—	—	—	—	—	—
Plantaginaceae	1	—	—	—	—	—	—
Plumbaginaceae	8	3	—	—	—	—	—
Poaceae	44	10	1	—	12	5	1
Polygonaceae	12	6	2	—	1	—	—
Primulaceae	9	5	2	—	4	2	1
Ranunculaceae	10	5	2	—	2	1	1
Rhamnaceae	1	—	—	—	—	—	—
Rosaceae	16	13	2	—	6	3	—
Rubiaceae	2	—	—	—	—	—	—
Salicaceae	1	—	—	—	2	—	—
Saxifragaceae	5	5	2	—	7	4	2
Scrophulariaceae	6	3	—	—	5	3	1
Tamaricaceae	2	—	—	—	—	—	—
Valerianaceae	1	1	—	—	1	—	—
Violaceae	2	1	—	—	—	—	—
Total	374	160	35	—	104	39	8
Plant families	43	32	16	—	24	15	7
Pteridophytes	3	2	1	—	1	—	—
Total	377	162	36	—	105	39	8
Bryophytes	12	8	1	—	?	?	?

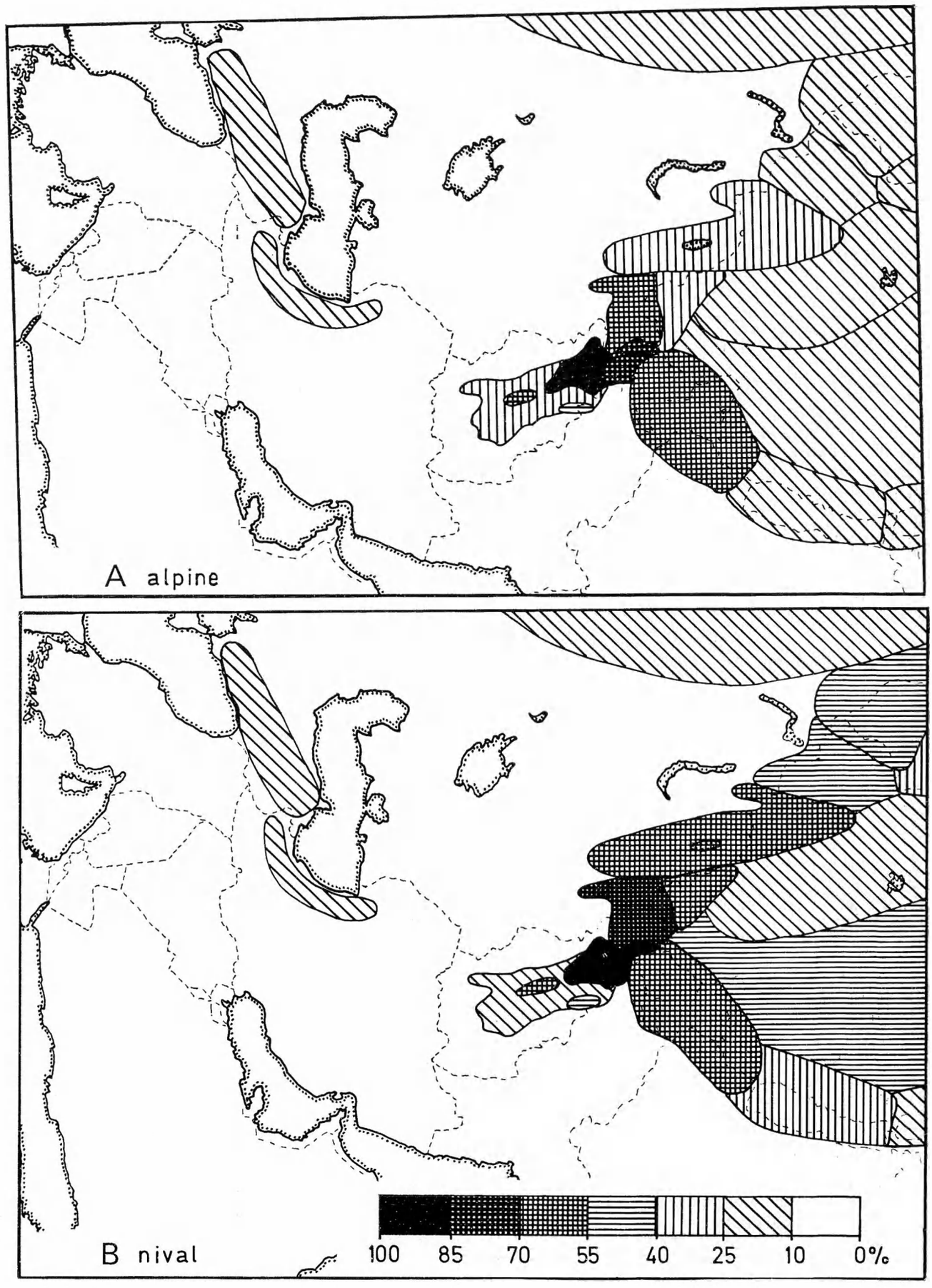


Fig. 3.

(such as *Cousinia, Acanthophyllum, Matthiastrum, Allium, Ferula, Scrophularia, Erysimum, Astragalus, Onobrychis* etc.) nearly half or more of the species are endemics. At present it is not possible to classify these endemics; even in Europe FAVARGER (1972) was unable to deal satisfactorily with montane taxa, because of too fragmentary knowledge. For Afghanistan WENDELBO (1966) and HEDGE & WENDELBO (1970) give a survey.

With regard to those taxa which reach 5,000 m and above (nival flora and hypercryophytic vegetation), we find less than 10 % endemics. By contrast, quite a remarkable number of these nival species are distributed all over the Eurasian mountains and the Arctic. As can be seen in Fig. 3, those plants which occur at the highest elevations have the widest geographical distribution. To explain this phenomenon, one must keep in mind the ecological conditions: the environment on those localities of high elevation is very similar on all mountains. The decisive factor is the microclimate, more than in lower regions, where the regional climate has an important role. The microclimate in the alpine Hindu Kush area is characterized by a long-persistent snow-cover and a short vegetation period which is usually very sunny. On the other hand most alpine species exhibit an intensive seed propagation and propagation by vegetative parts, mostly anemochorous.

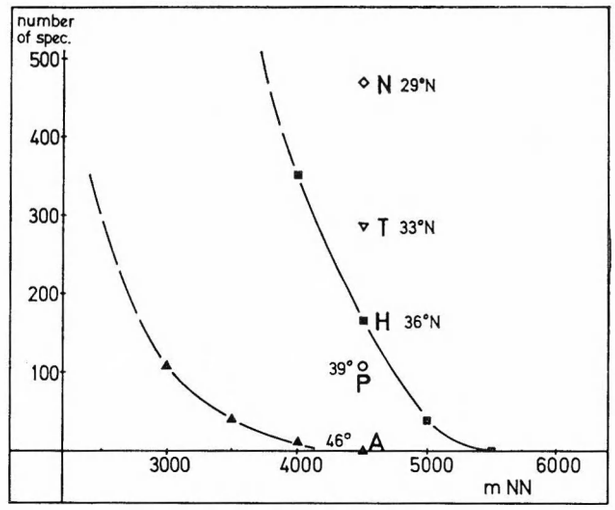


Fig. 4. The decreasing number of plant species with increasing elevation. A: East European Alps (REISSIGL & PISCHMANN 1958); H: Hindu Kush; P: Pamir (IKONNIKOV 1964); T: Tibet; N: Nepal (Himalayas). At 4,500 m the increasing number of species with decreasing latitude.

DISCUSSION

The result of the evolution of this high-alpine flora can be explained only by the major changes which took place during the glacial periods. During the Pleistocene the Central Asiatic Mountains and the Himalayas were linked with the more extended Arctic girdle. Migration of species could easily occur. The stock of species during the Tertiary, when high mountains already existed in this region and new ones had been folded up, must be regarded on the one hand as the ancestors of all the xerophytic diverse taxa and schizo-endemics. These are now developing as members of the spiny cushion belt vegetation and give rise to great taxonomic problems [*Cousinia* with about 354 species in the Flora Iranica region (RECHINGER 1972), or *Astragalus* with approx. 600 species (cf. DEML 1972, who treats two sections of the big genus)]. On the other hand, similar Tertiary ancestors must also exist for the alpine flora, and there are, as has been known for some time, floristic links across the Eurasian continent from the Pyrenees, the Alps, the Carpathians, the Caucasus to the Central Asiatic Mountains, Altai and to the Himalayas. The alpine and nival flora, however, growing today in more restricted

Fig. 3. A: Percentages of plant species of the Hindu Kush in common with adjacent regions, concerning plants growing at altitudes above 4,000 m in the Hindu Kush (alpine plant species). — B: As in A, but concerning plants growing at altitudes above 5,000 m in the Hindu Kush (nival plant species). — In both cases the number of plant species is taken as 100 % (alpine 377; nival 36).

alpine stands, has partly or totally lost the ability to, or has had too little time to differentiate. In a few examples, as for example in *Nepeta pamirense,* differentiation to microspecies (*N. leucocyanea* RECH. FIL., *N. pseudokokanica* POJARK., *N. kokanica* REGEL, etc.) seems to take place.

The exchange of floras between mountain ranges, which occurred during the glacial periods, in fluctuations, is one of the main reasons for the great similarity of the alpine and nival floras of the Asiatic mountains.

The number of species increases greatly with decreasing elevation (Fig. 4), possibly because of the very great diversity of the montane flora and the fact that the alpine and nival belts are less well known than those of the European Alps. Naturally with decreasing latitude the number of species at the same elevation (e.g. at 4,500 m, in Fig. 4) increases, corresponding to the higher level of the vegetational belts near the subtropics.

LITERATURE CITED

BRECKLE, S.-W. 1973. Mikroklimatische Messungen und ökologische Beobachtungen in der alpinen Stufe des afghanischen Hindukusch. — Bot. Jahrb. System. 93: 25—55.

— FREY, W. & HEDGE, I. C. 1969. Botanical literature of Afghanistan. — Notes R. B. Gard. Edinburgh 29: 357—371.

DEML, I. 1972. Revision der Sektionen Acanthophace Bunge und Aegacantha Bunge der Gattung Astragalus L. — Boissiera 21: 1—235.

FAVARGER, C. 1972. Endemism in the montane floras of Europe. — Taxon. phytogeogr. evol. Conf. Manchester 1971, pp. 191—204. — London.

FISCHER, D. 1970. Waldverbreitung im östlichen Afghanistan. — Afghanische Studien Bd. 2. — Meisenheim.

FREITAG, H. 1971. Die natürliche Vegetation Afghanistans. — Vegetatio 22: 285—344.

HEDGE, I. C. & WENDELBO, P. 1970. Some remarks on endemism in Afghanistan. — Israel J. Bot. 19: 401—417.

IKONNIKOV, S. S. 1964. Recent Data on the Flora of Pamir. — In V. N. SUKACHEV, Studies on the flora and vegetation of high-mountain areas, pp. 237—242. — IPST, Jerusalem.

RECHINGER, K. H. 1972. Compositae-Cynareae I: Cousinia. — Flora Iranica 90.

REISSIGL, H. & PITSCHMANN, H. 1958. Obere Grenzen von Flora und Vegetation in der Nivalstufe der Zentralen Ötztaler Alpen (Tirol). — Vegetatio 8: 93—128.

WENDELBO, P. 1966. Trekk av Afghanistans plantegeografi. — Acta Univ. Gothob., Botanica Gothob., 5: 1—20.

Botanical Literature

HUBBARD, C. E.: Gräser. Beschreibung, Verbreitung, Verwendung. Translation and revision by P. BOEKER. — Eugen Ulmer, Stuttgart. ISBN 3-8001-2430-0. 461 pp., 163 figs. Price DM 19,80.

The first edition of C. E. HUBBARD's book "Grasses. A Guide to their Structure, Identification, Uses, and Distribution in the British Isles" appeared in 1954 and was reprinted in 1959. A second edition appeared in 1968. HUBBARD's book is too well-known to warrant scrutiny here but a few points of interest as to the German edition will be touched upon.

To begin with it is most satisfactory that the book is now accessible beyond the English linguistic area. However, the German edition keeps so close to the English text that one must ask oneself what the aim of the publishers could have been. The paragraphs on distribution have been only slightly adjusted to apply to Central Europe. I have found no species added to or removed from the English edition, which specializes explicitly in the British grass flora. This point is not stated in the German title. The selection of taxa is rather poorly representative of the German flora. The *Spartina* taxa, for example, are of course highly interesting, not the least from a theoretical point of view, but can hardly be considered indispensable to a German grass flora. The same is valid for *Poa flexuosa, Poa balfouri* and some other taxa not occurring on the Continent. A number of continental, montane and alpine taxa of Central Europe are lacking. The difficulty may have been to change the illustrations, which are very informative and decorative (besides, they are of a much better quality in the German edition than in my English copy at least). However, additions to keys and text would not have been impossible to carry out. Frankly, I cannot understand why such an adaptation has not been made when such an excellent basis already existed.

In the English edition the keys are of the indented type and work fairly well, although I am personally no friend of this type of key. In the German edition the keys are not indented (for typographical reasons?) but the disposition has not been changed accordingly. This makes them extremely difficult to work with in spite of some page references given for the most difficult dichotomies (a system inherited from the English original). Non-indented keys must be built up in quite a different way if they are to be easily surveyable.

To sum up, BOEKER's edition has on the whole the same merits as HUBBARD's original and is thus without question to be recommended. I hope that Eugen Ulmer will soon have reason to publish a second edition, better adapted to the requirements of Central European botanists.

GUNNAR WEIMARCK

BIDAULT, M.: Variation et spéciation chez les végétaux supérieurs. Notions fondamentales de systématique moderne. — Doin, Paris 1971. 145 pp., 47 figs.

During the last few decades a number of text-books on the theories and methods of modern plant systematics have appeared. Among the more comprehensive ones can be mentioned those by STEBBINS (1950), DAVIS and HEYWOOD (1963) and GRANT (1971). More elementary are, for example, text-books by BRIGGS and WALTERS (1969), SOLBRIG (1970) and the book by MICHEL BIDAULT to be reviewed here.

In the first part different types of characters are presented and in the second part the causes and patterns of variation.

The third part is concerned with speciation, taxonomic units and methodology.

The limited space is used for brief surveys of most of the important disciplines within "modern" systematics. The proportions are on the whole rather reasonable although I would have preferred more space to be given to "classical" taxonomy, and find the part on numerical taxonomy in particular too comprehensive in relation to its present importance.

Moreover, I find it unfortunate to distinguish between the methods of classical taxonomy and biosystematics as sharply as is done in the methodological part. We have already had too much unfortunate experience of this sort of segregation, which often leads to neglect of one or the other of the disciplines. A synthesis is always preferable. In his own text-book the author presents examples of ignorance of nomenclatural rules. Most of the chapter on classical taxonomy (2 1/2 pages in all) is concerned with the International Code of Botanical Nomenclature. Still among the examples chosen epithets such as "ssp. *eu-glauca*", "ssp. *genuina*", "ssp. *typica*" and "ssp. *eu-laevis*" are found here and there in the text and even in the decoration on the front cover. In some cases pre-Linnean authors are cited which is also a violation of the rules. One example is *Hieracium* (TOURN.) L. instead of *Hieracium* L. (or possibly *Hieracium* TOURN. ex L.), an unfortunate mishap in a text-book that should serve as a model for students.

"Phenotype" is defined in the usual way in the glossary, but in the text on phenotypic variation the author treats it as synonymous with "modification". For example, he writes that it is not always easy to know "whether variation in a given character is purely genotypic or phenotypic or both at the same time." . . . "In *Lysimachia vulgaris,* evidence from transplantation to uniform conditions show that shade and sunshine forms, morphologically well distinct, have a purely phenotypic origin . . ." (translated from the French). To say that this is obscurely expressed is an understatement. — In another connection "phenotype" is again correctly understood.

The names of O. BJÖRKMAN, G. ERDTMAN, A. HÅKANSSON, J. HESLOP-HARRISON, A. MÜNTZING, H. NORDENSKIÖLD, A. RUTISHAUSER, M. SKALIŃSKA and N. SYLVÉN are mis-spelt in the text, some but not all of them in the bibliography, too. Moreover, Fig. 22 is upside-down. I admit that these errors are just minor details but there are too many of them and they could easily have been avoided.

I find it very regrettable that this criticism was necessary. Otherwise the book presents a stimulating selection from the vast field of plant systematics. It is a pity that the quality is so uneven that it hardly can be recommended without reserve.

GUNNAR WEIMARCK

ENCKE, F. & BUCKHEIM, G. (eds.): Zander, Handwörterbuch der Pflanzennamen. 10th ed. Verlag Eugen Ulmer, Stuttgart 1972. 744 pp. Price DM 42: — (clothbound).

Since 1927 the "ZANDER" has been known as a useful and comprehensive dictionary of families, genera and species of vascular plants. As the previous edition (1964) has been out of print for several years the present, much enlarged issue is particularly welcome. No less than c. 480 genera and c. 1100 species have been added to those listed in ed. 9.

The title of the book is not quite adequate. The book, in fact, deals mainly with cultivated plants or plants of some importance to applied botany. A choice of indigenous plants without any obvious practical or economic use have also been included.

An introductory chapter gives an abstract of the international rules of botanical nomenclature, especially of those con-

cerning cultivated plants (cf. Regnum vegetabile 64, 1969). Furthermore, we find a survey of the plant kingdom, including major divisions and families (following ENGLER's Syllabus), and a list of the families and of most genera under each family, all in alphabetical order.

The main part of this work is an alphabetical list of the genera (each with a reference to its family) and of a fairly large number of species with full authors' names. There are no descriptions, but some facts — e.g. annual, tree, climber, hybrid, greenhouse plant, poisonous plant — are indicated by means of symbols. A rich choice of synonyms is quoted with cross references.

Much attention has been paid to making the botanical nomenclature as correct as possible. A list of all specific epithets used and their meaning in German is particularly useful. The stress in all generic and specific names has been indicated. In some cases the stress differs from what is more or less common practice, e.g. *Agératum, Aíra, Balsámina, Barbárea, Cýclamen, Hydrangéa, sempérvirens, Zingíber*. These examples are evidently quite correct from a philological point of view.

The reviewer would question, however, the pronunciation *Héuchera, Kérnera,* (but *Gunnéra, Lavatéra* and *Lonicéra*!), *párkeri, spréngeri* etc. of generic names and specific epithets in the genitive case derived from family names ending in *-er*. At least in Sweden they have in general been pronounced *-éra* and *-éri*; cf. WIKÉN, Latin för botanister och zoologer (1951) p. 55. This practice is also supported by old German authorities, e.g. LEUNIS, Synopsis der Pflanzen-Kunde, ed. 3 (1886).

A biographical list of the authors following the authors' names gives a great deal of information not easily obtained from other sources.

This well-organized volume is indispensable not only to gardeners, foresters, pharmaceutists, etc. but to botanists in general, not the least on the bookshelf of an herbarium taxonomist.

OVE ALMBORN

EHRENDORFER, F.: Liste der Gefäss-Pflanzen Mitteleuropas. 2nd ed. Gustav Fischer Verlag. Stuttgart 1973. XII+318 pp. 1 map. Price DM 18:— (wrappers).

The first edition of EHRENDORFER's check-list of Central European vascular plants was published as recently as 1967. As emphasized in the preface its main purpose is to serve as a catalogue of the correct botanical names in the mapping of the Central European flora. This project, initiated by Professor EHRENDORFER (previously at Graz, now in Vienna), was presented in great detail by Dr H. NIKFELD, one of his collaborators, in an article in Taxon 20 (1971) p. 545.

The main part of this work is an alphabetical catalogue of genera (with reference to family), species and subspecies with authors' names and symbols (A, G, H, etc.) for the distribution in the countries dealt with. Each taxon has a number (e.g. *Achillea millefolium* ssp. *millefolium*=00613-1) and a code name (Achill mill (mill)). This will certainly facilitate the treatment of the material by data processing methods.

As a rule, the nomenclature used is in accordance with Flora Europaea as far as this standard work has been published to date. A good choice of synonyms is given. In many cases, critical groups have been treated as, e.g. *Agropyron junceum* agg., including two or more "Kleinarten". This is a practical arrangement pending further research. It should be emphasized, however, that these "macrospecies" and "microspecies" have no taxonomic rank under the Code of Nomenclature. Cf. Article 33, last paragraph.

"Mitteleuropa" stands for Austria, Germany (incl. Alsace), Switzerland, western Czechoslovakia, western Hungary, north-

ern Italy and northwestern Jugoslavia. It is evident, however, that this is a highly useful book even for botanists in other parts of Europe.

The present volume should be a challenge to Scandinavian botanists to prepare a similar check-list for their countries. HYLANDER, Förteckning över Nordens växter (4th ed., 1955), still frequently used, is now very out-of-date, not the least owing to the fact that the author did not accept the present rules of botanical nomenclature.

OVE ALMBORN

JALAS, J. & SUOMINEN, J. (eds.): Atlas Florae Europaeae. 1. Pteridophyta (Psilotaceae to Azollaceae), 1972. 121 pp., 150+3 maps and a folded basemap. — 2. Gymnospermae (Pinaceae to Ephedraceae), 1973. 40 pp., 50 maps. The Academic Bookstore, Helsinki. Price not indicated (wrappers).

These two volumes contain the first results of a large-scale mapping project of the areas of distribution of all vascular plants known from Europe. The need for a complete atlas of this type was discussed at an early stage of the preparation of the Flora Europaea, but whereas the Flora has been published at a good pace (3 volumes issued 1964—1972, Vol. 4 in press and the final Vol. 5 in preparation), the Atlas has progressed fairly slowly.

The pioneer work of mapping the higher plants in part of Europe was carried out by HULTÉN (Atlas of the distribution of vascular plants in NW Europe, 1950, 2nd ed. 1971). HULTÉN's important works on the amphi-Atlantic plants (1958) and the circumpolar plants (1964) should also be mentioned in this context. Basic work of this kind has been carried out in Central Europe by MEUSEL et al. (Vergleichende Chorologie der zentraleuropäischen Flora, 1965) and EHRENDORFER et al. (cf. above). In Britain the rapid development of data-processing methods has resulted in the first botanical map-work based on a standard grid system and machine-plotting of the records (PERRING & WALTERS, Atlas of the British Flora, 1962).

A Committee for the Mapping of the Flora of Europe was founded in 1965 as a separate organization in close cooperation with the staff of Flora Europaea. A secretariat was formed in Helsinki under the leadership of Dr J. SUOMINEN. The botanical members of the secretariat have, to a great extent, performed this task side by side with their main duties of teaching and other research work. A modest contribution from the Finnish Government has covered part of the administration costs of the Committee.

This small team in Helsinki has been supported by a network of collaborators and advisers all over Europe. In fact, the maps of the two present volumes have been scrutinized by more than one hundred specialists.

These maps have been produced with other techniques than in earlier works, e.g. in HULTÉN's Atlas. Following the methods developed especially by British botanists, all Europe has been covered by c. 4,400 50-km squares. The occurrence of a species or subspecies (one or several localities) within such a square has been indicated by a dot in its centre. The dots stand for native occurrences. Other symbols are used for introduced, extinct or probably extinct species. Uncertain records have been indicated by a "?" in the square in question. The age of records for introduced species, especially those with expanding tendencies, have sometimes been indicated by special symbols, e.g. before 1900, 1900—1939 and 1940 onwards.

Taxonomic concepts and nomenclature are largely the same as in Flora Europaea. Some addenda and corrigenda have been included. A choice of recent literature, mainly on cytology and distribution, has also been added under each species.

Many names may seem to be alien, at

least to Scandinavian botanists familiar with the nomenclature of HYLANDER's Flora (1953—66) and his Check-list (1955). It is to be hoped that the nomenclature of the Flora Europaea will imply an important step towards stabilization, though, in many cases, it will not represent the definite truth.

In general, the species concept used does not deviate too much from common practice. In some cases different cytotypes have been indicated by different symbols on the same map. "Progressive" botanists who would consider such taxa as species will probably find a wide field for criticism. Cf. a review by A. LÖVE in Taxon 22 (1973) p. 140.

The 200 species mapped so far are those treated in pp. 3—40 in Flora Europaea. If the entire number of species to be treated in the Flora is about 17,000, it will evidently take a very long time to complete the Atlas. However, it should be emphasized that this project, which no doubt will become one of the great milestones in phytogeography, will obtain much more support, financial as well as personal and technical, in order to ensure its development at an accelerated pace.

OVE ALMBORN

OPERA BOTANICA

Vol. 1. N. HYLANDER, I. JØRSTAD and J. A. NANNFELDT: Enumeratio Uredinearum Scandinavicarum. 1953. 102 pp. — H. HORN AF RANTZIEN: Middle Triassic Charophyta of South Sweden. 1954. 83 pp. — H. HJELMQVIST: Die älteste Geschichte der Kulturpflanzen in Schweden. 1955. 186 pp. — Price Sw. Kr. 30 (15).

Vol. 2. H. RUNEMARK: Studies in Rhizocarpon. I. Taxonomy of the Yellow Species in Europe. 1956. 152 pp. — H. RUNEMARK: Studies in Rhizocarpon. II. Distribution and Ecology of the Yellow Species in Europe. 1956. 150 pp. — G. KNABEN: On the Evolution of the Radicatum-Group of the Scapiflora Papavers as Studied in 70 and 56 Chromosome Species. A. Cytotaxonomical Aspects. 1959. 76 pp. — Price Sw. Kr. 30 (15).

Vol. 3. A. GUSTAVSSON: Studies on Nordic Peronosporas. I. Taxonomic Revision. 1959. 271 pp. — A. GUSTAVSSON: Studies on Nordic Peronosporas. II. General Account. 1959. 61 pp. — G. KNABEN: On the Evolution of the Radicatum-Group of the Scapiflora Papavers as Studied in 70 and 56 Chromosome Species. B. Experimental Studies. 1959. 96 pp. — Price Sw. Kr. 30 (15).

Vol. 4. R. DAHLGREN: Revision of the Genus Aspalathus. I. The Species with Flat Leaflets. 1960. 393 pp. — Price Sw. Kr. 30 (15).

Vol. 5. Á. LÖVE and D. LÖVE: Chromosome Numbers of Central and Northwest European Plant Species. 1961. 581 pp. — Price Sw. Kr. 40 (20), bound Sw. Kr. 48 (28).

Vol. 6. Å. PERSSON: Mire and Spring Vegetation in an Area North of Lake Torneträsk, Torne Lappmark, Sweden. I. Description of the Vegetation. 1961. 187 pp. — R. DAHLGREN: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 1—2. 1961. 120 pp. — Å. PERSSON: Mire and Spring Vegetation in an Area North of Lake Torneträsk, Torne Lappmark, Sweden. II. Habitat Conditions. 1962. 100 pp. — Price Sw. Kr. 40 (20).

Vol. 7. N. MALMER: Studies on Mire Vegetation in the Archaean Area of Southwestern Götaland (South Sweden). I. Vegetation and Habitat Conditions on the Åkhult Mire. 1962. 322 pp. — II. Distribution and Seasonal Variation in Elementary Constituents on Some Mire Sites. 1962. 67 pp. — Price Sw. Kr. 40 (20).

Vol. 8. R. DAHLGREN: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 3. 1963. 183 pp. — N. SYLVÉN: Det skandinaviska floraområdets Carices Distigmaticae. The Carices Distigmaticae of the Scandinavian Flora District. 1963. 161 pp. — C. BLIDING: A Critical Survey of European Taxa in Ulvales. I. Capsosiphon, Percursaria, Blidingia, Enteromorpha. 1963. 160 pp. — Price Sw. Kr. 40 (20).

Vol. 9. R. DAHLGREN: Studies on Aspalathus and Some Related Genera in South Africa. 1963. 301 pp. — S. O. STRANDHEDE: Chromosome Studies in Eleocharis, subser. Palustres. III. Observations on Western European Taxa. 1965. 86 pp. — Price Sw. Kr. 40 (20).

Vol. 10. R. DAHLGREN: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 4. 1965. 231 pp. — S. O. STRANDHEDE: Morphologic Variation and Taxonomy in European Eleocharis, subser. Palustres. 1966. 187 pp. — Price Sw. Kr. 40 (20).

Vol. 11. R. DAHLGREN: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 5. 1966. 266 pp. — G. NORDBORG: Sanguisorba L., Sarcopoterium Spach, and Bencomia Webb et Berth. Delimitation and Subdivision of the Genera. 1966. 103 pp. — Price Sw. Kr. 50 (30).

Vol. 12. B. E. BERGLUND: Late-Quaternary Vegetation in Eastern Blekinge, Southeastern Sweden. A Pollen-analytical Study. I. Late-Glacial Time. 1966. 180 pp. — II. Post-Glacial Time. 1966. 190 pp. — Price Sw. Kr. 70 (42).

No. 13. S. SNOGERUP: Studies in the Aegean Flora. VIII. Erysimum Sect. Cheiranthus. A. Taxonomy. 1967. 70 pp. — Price Sw. Kr. 15 (9).

No. 14. S. SNOGERUP: Studies in the Aegean Flora. IX. Erysimum Sect. Cheiranthus. B. Variation and Evolution in the Small-Population System. 1967. 86 pp. — Price Sw. Kr. 16 (9.40).

No. 15. R. DAHLGREN: Studies on Penaeaceae. I. Systematics and Gross Morphology of the Genus Stylapterus A. Juss. 1967. 40 pp. — Price Sw. Kr. 8 (4.80).

No. 16. G. NORDBORG: The Genus Sanguisorba Section Poterium. Experimental Studies and Taxonomy. 1967. 166 pp. — Price Sw. Kr. 27 (16.20).

No. 17. I. BJÖRKQVIST: Studies in Alisma L. I. Distribution, Variation and Germination. 1967. 128 pp. — Price Sw. Kr. 25 (15).

No. 18. R. DAHLGREN: Studies on Penaeaceae. II. The Genera Brachysiphon, Sonderotham-

nus and Saltera. 1968. 72 pp. — Price Sw. Kr. 13 (7.80).

No. 19. I. BJÖRKQVIST: Studies in Alisma L. II. Chromosome Studies, Crossing Experiments and Taxonomy. 1968. 138 pp. — Price Sw. Kr. 25 (15).

No. 20. B. NORDENSTAM: The Genus Euryops. I. Taxonomy. 1968. 409 pp. — Price Sw. Kr. 55 (33).

No. 21. R. DAHLGREN: Revision of the Genus Aspalathus. II. The Species with Ericoid and Pinoid Leaflets. 6. 1968. 309 pp. — Price Sw. Kr. 75 (45).

No. 22. R. DAHLGREN: Revision of the Genus Aspalathus. III. The Species with Flat and Simple Leaves. 1968. 126 pp. — Price Sw. Kr. 30 (18).

No. 23. B. NORDENSTAM: Phytogeography of the Genus Euryops (Compositae). A Contribution to the Phytogeography of Southern Africa. 1969. 77 pp. — Price Sw. Kr. 20 (12).

No. 24. T. MÖRNSJÖ: Studies on Vegetation and Development of a Peatland in Scania, South Sweden. 1969. 187 pp. — Price Sw. Kr. 50 (30).

No. 25. G. TYLER: Studies in the Ecology of Baltic Sea-Shore Meadows. II. Flora and Vegetation. 1969. 101 pp. — Price Sw. Kr. 25 (15).

No. 26. M. SONESSON: Studies on Mire Vegetation in the Torneträsk Area, Northern Sweden. III. Communities of the Poor Mires. 1970. 120 pp. — Price Sw. Kr. 30 (18).

No. 27. F. ANDERSSON: Ecological Studies in a Scanian Woodland and Meadow Area, Southern Sweden. I. Vegetational and Environmental structure. 1970. 190 pp. — Price Sw. Kr. 50 (30).

No. 28. A. STRID: Studies in the Aegean Flora. XVI. Biosystematics of the Nigella arvensis Complex. With Special Reference to the Problem of Non-adaptive Radiation. 1970. 169 pp. — Price Sw. Kr. 50 (30).

No. 29. R. DAHLGREN: Studies on Penaeaceae. VI. The Genus Penaea. 1971. 58 pp. — Price Sw. Kr. 30 (18).

No. 30. A. STRID (ed.): Evolution in the Aegean. Proceedings of a Symposium held at the Department of Plant Taxonomy, Lund, Sweden on January 22—24, 1971. 1971. 83 pp. — Price Sw. Kr. 35 (21).

No. 31. J. LUNDGREN: Revision of the Genus Anaxeton Gaertn. (Compositae). 1972. 59 pp. — Price Sw. Kr. 25 (15).

No. 32. A. K. STRID: Revision of the Genus Adenandra (Rutaceae). 1972. 112 pp. — Price Sw. Kr. 40 (24).

No. 33. A. L. STORK: Studies in the Aegean Flora. XX. Biosystematics of the Malcolmia maritima Complex. 1972. 118 pp. — Price Sw. Kr. 50 (30).

No. 34. R. VON BOTHMER: Studies in the Aegean Flora. XXI. Biosystematic Studies in the Allium ampeloprasum Complex. 1974. 104 pp. — Price Sw. Kr. 55 (33).

No. 35. K. PERSSON: Biosystematic Studies in the Artemisia maritima Complex in Europe. 1974. 188 pp. — Price Sw. Kr. 100 (60).

No. 36. U. ELIASSON: Studies in Galápagos Plants. XIV. The Genus Scalesia Arn. 1974. 117 pp. — Price Sw. Kr. 60 (36).

OPERA BOTANICA SER. B: FLORA OF ECUADOR

No. 1. G. HARLING: 216. Cyclanthaceae. 1973. 48 pp. — Price Sw. Kr. 35 (21).

No. 2. B. SPARRE: 89. Tropaeolaceae. 1973. 31 pp. — Price Sw. Kr. 25 (15).

No. 3. PH. A. MUNZ: 141. Onagraceae. 1974. 46 pp. — Price Sw. Kr. 35 (21).

Volumes in preparation. MILDRED MATHIAS and L. CONSTANCE: 145. Umbelliferae. — K. RAHN: 184. Plantaginaceae.

BOTANISKA NOTISER SUPPLEMENT

Vol. 1. S. WALDHEIM: Kleinmoosgesellschaften und Bodenverhältnisse in Schonen. 1947. 203 pp. — O. ALMBORN: Distribution and Ecology of some South Scandinavian Lichens. 1948. 254 pp. — Price Sw. Kr. 15 (10).

Vol. 2. H. HJELMQVIST: Studies on the Floral Morphology and Phylogeny of the Amentiferae. 1948. 171 pp. — O. ANDERSSON: Larger Fungi on Sandy Grass Heaths and Sand Dunes in Scandinavia. 1950. 89 pp. — A. ALME-

STRAND and A. LUNDH: Studies on the Vegetation and Hydrochemistry of Scanian Lakes. I—II. 1951. 174 pp. — Price Sw. Kr. 15 (10).

Vol. 3. A. LUNDH: Studies on the Vegetation and Hydrochemistry of Scanian Lakes. III. 1951. 138 pp. — O. HEDBERG, O. MÅRTENSSON, and S. RUDBERG: Botanical Investigations in the Pältsa Region of Northernmost Sweden. 1952. 209 pp. — K. H. RECHINGER FIL.: Monograph of the Genus Rumex in Africa. 1954. 114 pp. — Price Sw. Kr. 15 (10).

Opera Botanica (except Ser. B) is published by the Lund Botanical Society in cooperation with the Department of Plant Taxonomy, University of Lund. It consists of comprehensive papers issued at indefinite times.

Opera Botanica Ser. B, Flora of Ecuador, is published by the Department of Systematic Botany, University of Göteborg and the Section of Botany, Riksmuseum, Stockholm. This series is also issued at indefinite times.

All parts of Opera Botanica and its predecessor Botaniska Notiser Supplement are still available.

Booksellers and non-members should apply to C.W.K. Gleerup Bokförlag, Öresundsvägen 1, S-222 38 Lund, Sweden. Prices given are approximate. Members of the Lund Botanical Society receive all the three series at a reduced rate (bracketed prices). Members should apply direct to Opera Botanica, Botanical Museum, Ö. Vallgatan 18, S-223 61 Lund, Sweden.