The herbaceous members of the genus Cornus in NW North America

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The systematic relationships of the herbaceous taxa of *Cornus* (subgen. *Arctocrania*) in NW North America have been evaluated using morphological, chemical, phytogeographical and cytological evidence. *C. canadensis* L. and *C. suecica* (both 2n = 22) are distinct species. In addition two intermediate taxa occur, viz. the semi-fertile hybrid *C. canadensis* × *suecica* (2n = 22) and *C. unalaschkensis* (2n = 44), believed to be an allopolyploid derivative. *C. canadensis* occurs in inland areas, while *C. unalaschkensis* has a southern coastal, and *C. suecica* a northern coastal distribution. The diploid hybrids are found in the present overlap area between *C. canadensis* and *C. suecica*. *C. unalaschkensis* is nowadays geographically isolated from the other taxa and may represent a survivor from the Pleistocene glaciations. Eight flavonoids have been found in the taxa, quercetin 3–O gentiobioside has importance as a taxonomic and phytogeographic marker.

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Relationships within the genus *Cornus* in North America have been explored in the past (Nakai 1909, Hutchinson 1942, Hara 1948, Ferguson 1966, Jensen et al. 1975) and although all these treatments are in agreement in the segregation of the herbaceous members of the genus, either as a subgenus (subgen. *Arctocrania* Endl. ex Reichenb.) or as a genus (*Chamaepericlymenum* Hill), little work has been done to elucidate the relationships of these herbaceous taxa to one another. The present study is an attempt to fill in this gap for NW North America.

The three commonly recognized species *C. canadensis* L., *C. suecica* L. and *C. unalaschkensis* Ledeb. all occur in the British Columbia, Yukon, Alaska region. *C. unalaschkensis*, because it is morphologically intermediate between the other two species, has been considered a hybrid of the two (Hultén 1937, Olsen 1914). But as pointed out by Porsild (1939), collections have been reported from over one thousand miles from the nearest *C. suecica* location, thus casting doubt on the hybrid origin of the species.

C. canadensis is found mainly in North America, but also in NE Asia and higher altitudes in Japan (Rickett 1945, Hultén 1968). *C. suecica* is circumpolar in distribution being found disjunct on both NW and NE coasts of North America, as well as Greenland, Great Britain, Scandinavia and Siberia (Hultén 1937, 1968). *C. unalaschkensis* is found in somewhat more continental sites than *C. suecica* in NW and NE North America and Greenland (Hultén 1937, 1968).

Two chromosome numbers have been reported; a diploid number 2n = 22 and a tetraploid of 2n = 44. *C. suecica* has been reported as 2n = 22 (see Löve & Löve 1975), *C. unalaschkensis* 2n = 22 (Taylor & Brockman 1966) and 2n = 44 (Taylor & Mulligan 1968), and *C. canadensis* as 2n = 22 (Packer 1964) and 2n = 44 (Dermen 1932, Clay & Nath 1971). In the taxonomic treatment proposed by Löve & Löve

(1975) chromosome number is used as the paramount character for denoting species. Thus any tetraploid specimen is called *Chamaepericlymenum unalaschkense*. *C. canadensis* and *C. suecica* are considered strictly diploid.

The relationship of the intermediate taxon to *Cornus canadensis* and *C. suecica* is considered at present to be unclear. The morphological, phytogeographical and cytotaxonomic information so far reported is inadequate and in part contradictory.

A study of various populations of the herbaceous *Cornus* species collected throughout NW North America has been carried out using the following approaches: phytochemical data accumulated through the study of population flavonoid profiles; cytological data compiled from chromosome counts of the populations; and morphological data based on comparative population studies and hybrid indices.

Material and methods

Collections were made throughout Alberta, although primarily in the Rocky Mountain region, as well as NC British Columbia, Queen Charlotte Islands, Yukon Territory and Alaska. Living and dried material, as well as pressed specimens were obtained from most sites. Morphological variation was studied at both intraspecific and interspecific level.

Chromosome counts were made from actively growing root tips. The source of the root tips was living material transplanted from the field into 4-inch pots and grown in the greenhouse. Some root-tips were collected in the field and preserved in a solution of acetic acid and 95% ethanol (1:3). Root tips to be examined were prepared using the method of Tjio & Levan (1950). A voucher specimen for each collection is deposited at ALTA.

Guard cell length measurements were used to separate diploid and tetraploid specimens where chromosome data were unavailable. Correlation between cell size and ploidy level have previously been described by Stebbins (1971) and Sax & Sax (1937).

Preparations were made from living material by peeling the epidermis from the lower side of the leaf with a razor blade, then mounting the peel in water on a microscope slide. Length of guard cells was measured with an eyepiece micrometer at 400× using an A0 microscope.

Flavonoids. The flavonoids of various populations were analyzed using the methods of Mabry et al. (1969), Harborne (1975) and Ribéreau-Gayon (1972).

Whole plants used in flavonoid extraction were collected in the field and dried in paper bags. Only leaves and stems were used for extraction. Identification of the compounds was made for three separate populations (collection nos. 75033, 75009, 75060). Approximately 20 g of dry plant material was used in the analysis. The material was eluted in c. 300 ml of 80% ethanol and ground in an Oster blender for 15 minutes. Separation of the extract was accomplished by filtration through cheesecloth and a Buchner funnel, then Whatman no. 1 or no. 2 filter paper and a Buchner funnel.

The solution was evaporated in vacuo using a Buchler rotoevaporator until reduced to approximately 50 ml. Ten drops of the extract were spotted on each of the 32 sheets of Whatman no. 3MM chromatography paper. These were run using descending chromatography in two dimensions with two different solvents. The first dimension was run using 1-butanol:acetic acid:H_2O (BAW, 4:1:5, upper phase) and the second 15% acetic acid. The resulting spots were examined using UV light (366 nm) on untreated sheets and on sheets fumed with ammonia. Spots were also examined under visible light after they had been sprayed with ferric chloride-ferrous cyanide stain or Benedict's reagent.

Spots that overlapped on the initial chromatograph could, in most cases, be separated by eluting the spots together and streaking the mixture on full-size sheets of Whatman no. 1 paper then chromatographing in one dimension, using BAW (4:1:5 BAW; upper phase) as the solvent.

Compounds exhibiting a positive reaction with both ferric chloride-ferrous cyanide (blue) and Benedict's reagent (yellow) were cut out and eluted from unstained chromatograms in a minimum amount of spectral grade methanol. They were then analyzed using UV spectrophotometer. Scans were recorded for the methanol solution, followed by scans of the solution after the addition of sodium methoxide, anhydrous aluminum trichloride, aluminum trichloride and hydrochloric acid (N), sodium acetate, and sodium acetate and boric acid (Mabry et al. 1969 pp. 35–61) (Table 1).

To further aid identification, all pure compounds were chromatographed in one-dimension using four different solvent systems on half-sheets (23× 57 cm) of Whatman no. 1 paper. The solvent systems were: (a) 1-butanol:acetic acid:H_2O (4:1:5, upper phase); (b) saturated phenol (80% phenol:H_2O); (c) 15% acetic acid; and (d) water.

The glycosides were then hydrolyzed to aglycone and sugar constituents by refluxing in 5–7 ml of 2N HCl. Variation in the amount of HCl added occurred because of a variation in concentration of the methanol-glycoside mixture as indicated by the colour of the solution. Refluxing was carried out for fifteen minutes in a reflux condenser at 100°C. After hydrolysis the solution was cooled and partitioned against three to five ml of diethyl ether. The lower aqueous layer containing the sugars and the upper ether layer containing the aglycones were separated. After drying the aglycone and redissolving it in spectral grade methanol, part of the extract was analyzed spectrophotometrically as outlined above and the remaining solution chromatographed in one dimension using 4:1:5 BAW. Identification in all cases was made from spectral scans and supported by Rf data. The aqueous fraction, containing the sugars, was

Table 1. Spectral and chromatographic characteristics of major flavonoids isolated in *Cornus canadensis* and its relatives. – q quenching; y yellow; ygn yellow-green; BAW n-Butanol – Acetic acid – Water (4:1:5), upper phase; Ac 15% acetic acid; Ph 80% phenol; BI band I; BII band II. – Values within parentheses: inflection. – * negative values indicate a hypsochromatic shift of band I. – All Rf's given on Whatman no. 1 paper.

Compound	Colour UV/NH_3	Rf× 100				MeOH		NaoMe BI	NaoAc BII	$AlCl_3$ BI	HCl BI	$+H_3BO_3$ BI
		BAW	H_2O	Ac^-	Ph	BI	BII					
Quercetin 3-O gentiobioside	q–y	35	17	28	40	359	258 (270)	60	11	57	*–20	16
Quercetin 3-O galactoside	q–y	68	14	37	61	361 (302)	258 (268)	65	8	60	*–30	20
Quercetin 3-O sophoroside	q–y	46	28	47	37	358 (300)	270	70	8	55	*–25	22
Quercetin 3-O glucoside	q–y	60	11	29	40	361 (298)	259 (266)	50	9	41	*–29	19
Kaempferol 3-O glucoside	q–ygn	72	18	42	70	358	268	50	8	42	0	1
Kaempferol 3-O arabinoside	q–ygn	84	28	27	34	351	268	55	8	45	*– 2	0

concentrated, then spotted on half-sheets of Whatman no. 1 paper. In each case two spots of the unknown sugars were made. To one spot was added 30 μl of 0.005 M standard solution of glucose. The chromatographs were run using 80% isopropanol as the solvent. The sugars were stained using aniline hydrogen pthalate solution. Unknown sugars were identified by their Rg (distance from origin/distance of glucose from origin× 100) and by their colour after staining.

The remaining populations were analyzed chromatographically in two dimensions in a manner similar to that previously described, using a reduced amount of material. Three grams of dry plant material were eluted in 50 ml of 80% ethanol for each of the populations (a minimum of ten plants being used). Seven drops of extract were spotted on only two sheets of Whatman no. 3MM chromatography paper. No attempt was made to condense the extract by roto-evaporation. The two sheets were run chromatographically in two dimensions in the manner previously described and the chromatographic profiles were compared; but no attempt to elute the spots was made. A series of flavonoid profiles was obtained. Spots with the same Rf values were identified by comparison with the original major populations.

Pollen grain viability was ascertained by staining fresh pollen in a drop of lacto-phenol-cotton blue stain for five minutes. Pollen grains were considered viable if they took up stain and appeared a deep blue in colour at 200× magnification.

Results

Analysis of the results of this study has enabled the delimitation of four taxa: two diploid species, *Cornus canadensis* (2n= 22) and *C. suecica* (2n= 22), an amphidiploid species, *C. unalaschkensis* (2n= 44) and a diploid hybrid, *C. canadensis* × *suecica* (2n= 22). In the reporting of the results the taxa will be referred to by these four names. A discussion of this classification is given later.

Morphology

Eleven key or critical characters by which *C. canadensis* and *C. suecica* specimens could be separated were chosen. They are given in Table 2.

Initial examination of the intermediate specimens collected indicated that they exhibited many combinations of the eleven character traits of the two other species. In addition, many intermediates exhibited character states between the putative parent species.

For each of the eleven characters referred to, a numerical value was given to each of the two contrasting character states; zero for the extreme associated with *C. suecica*, and one for that associated with *C. canadensis*. For states between these two extremes, a numerical value between zero and one was given (0.25; 0.5; 0.75) which reflected which extreme the character state most clearly resembled, and to what degree. The summation of the eleven numerical values for each collection gave the collection a value expressed as a percentage of the possible total of eleven. Thus *C. canadensis* will have a numerical value approaching 100% while *C. suecica* values will approach 0%. The results are given in Table 3.

Table 2. Comparative characters used in the morphological analysis. Character states for *C. canadensis* were given numerical value 1, those of *C. suecica* 0. Character states between the extremes were given an appropriate numerical value between 0 and 1.

Character	Character state *C. canadensis*	Character state *C. suecica*
Leaf length/width ratio	> 1.50	< 1.25
Leaf arrangement	whorl in 4–6 leaves at summit	3–6 subequal pairs of leaves
Leaf shape	ovate to elliptic	lanceolate to ovate
Leaf tip	acute to shortly acuminate	broadly acute to obtuse
Leaf base	narrowed at base with distinct petiole	clasping at base
Leaf venation	2–3 veins on either side of midrib	5–7 veins arising from base of leaf
Flower number	> 25	< 15
Primary branches in cyme	4 primary branches discernible	primary branches not discernible
Sepal and hypanthium colour and pubescence	cream to green; usually ciliate	blue or purplish; ciliate with blue trichomes only at base
Petal colour	yellowish	blue or purple
Stamen length	shorter than style	longer than style

Table 3. A summary of the data given for herbaceous *Cornus*.

	C. canadensis	*C. canadensis* × *suecica*	*C. unalaschkensis*	*C. suecica*
Chromosome number (2n)	22	22	44	22
Quercetin 3-O gentiobioside	−	−	+	+
Pollen viability	≈ 98 %	≈ 52 %	≈ 98 %	≈ 98 %
Morphological index values	92 %–100 %	64 %–79 %	31 %–89 %	21 %–28 %

Morphological analysis resulted in the recognition of a key or critical character, petal colour. *C. canadensis* lacks pigment and hence is readily distinguishable from its relatives. However, *C. suecica* at times is indistinguishable from the intermediate forms on gross morphology.

Chromosome numbers

Somatic chromosome counts were determined for 48 populations. Two chromosome numbers were present among these collections: the diploid (2n = 22) and tetraploid (2n = 44) numbers described in previous publications.

Table 4 and Fig. 1 show the distribution of these two chromosome numbers, based upon collections by the authors. For some of the locations indicated on the map, chromosome number was inferred from guard cell size because plant material necessary for obtaining a chromosome count was unavailable. Information concerning guard cell size is contained in a later section.

Pollen viability

A test to determine pollen viability was carried out on those specimens which flowered under greenhouse conditions.

C. canadensis (2n = 22) exhibited pollen viabilities of 98 % (e.g. nos. 75005, 75008), *C. unalaschkensis* (2n = 44) showed 98 % viability (e.g. nos. 75024, 75035) and *C. canadensis* × *suecica* (2n = 22) exhibited a pollen viability of 52 % (e.g. nos. 75053 and 75054). *C. suecica* (2n = 22) gave results of 98 % (e.g. no. 75063).

Guard cells

Guard cell length was positively correlated with ploidy level. Diploid specimens possessed shor-

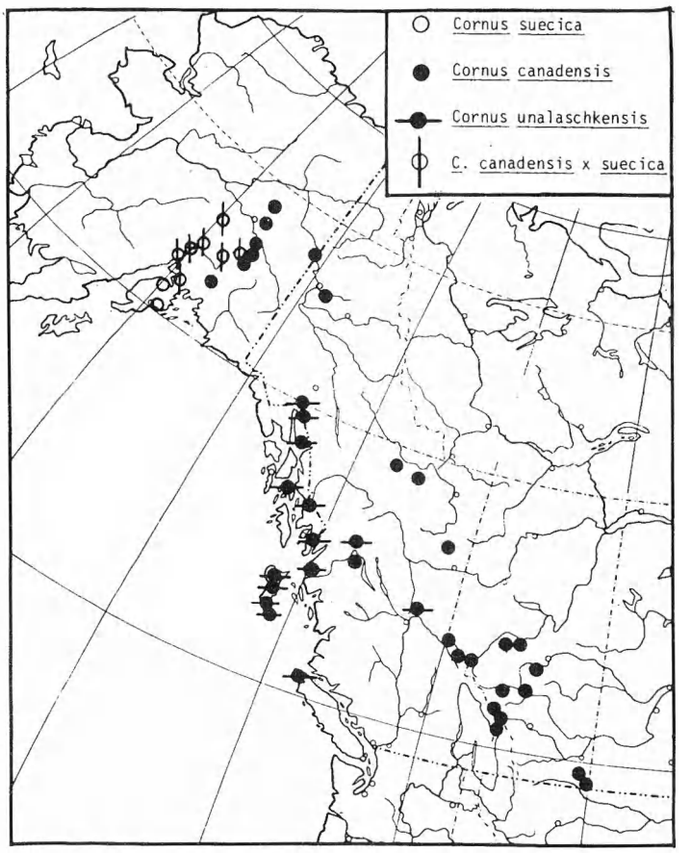

Fig. 1. Study sites of *Cornus*.

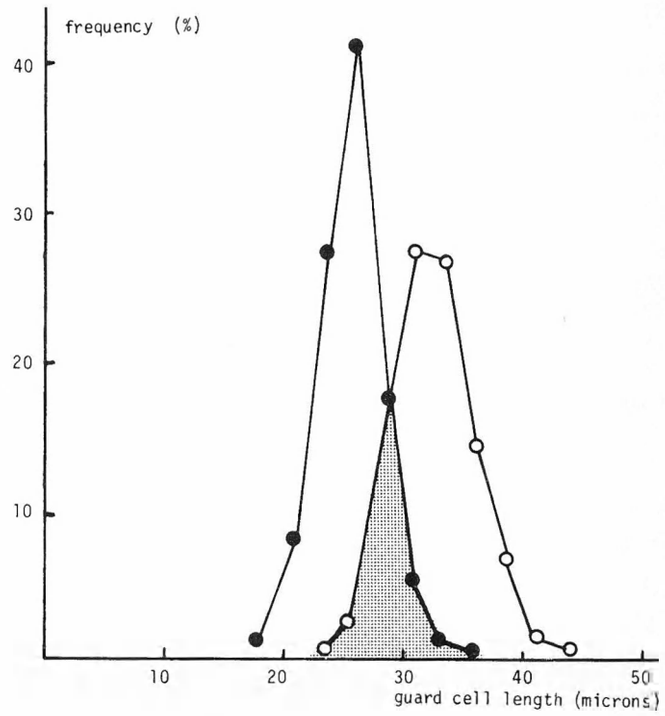

Fig. 2. Guard cell length in *Cornus*. ● diploids (1008 cells), ○ tetraploids (904 cells).

ter guard cells than tetraploid specimens. There was a significant difference between the mean guard cell sizes of the diploid ($\bar{x} = 25.20$; 1008 cells) and tetraploid ($\bar{x} = 32.05$; 904 cells) species as demonstrated by a two sample Student's t-test ($s = 1.48$, $t = 4.64$). Guard cell length of the diploids ranged from 17.9 to 38.3 μm while the guard cell length of the tetraploids ranged from 23.0 to 43.4 μm (Fig. 2). No evidence of a difference in guard cell size between different species of the same chromosome number was found.

Floral development and reproduction

No experiments were carried out to ascertain the type of breeding system found in the herbaceous *Cornus* species. However, some observations were made of the floral development of plants in the greenhouse.

At the tip of each flower bud, attached to one of the four petals is an awn-like projection which stands erect from the bud. The bud itself is similar to a small tent in structure, with the stamens bent and completely enclosed by the four petals. The whole bud springs open when the awn-like projection is touched. Simultaneously, the anthers dehisce, sending a cloud of pollen into the air. Much of the pollen lands on the flower's own stigma. Fruit very seldom developed in the greenhouse. Self-incompatibility is suspected as the means to prevent obligate selfing. The most likely means of triggering the bud opening and pollen release is the touching of the awn-like projection by an insect. The insect could act as a pollen carrier, effecting cross-pollination.

Vegetative reproduction by means of rhizomes is very commonly observed in the field.

Flavonoids

The results reported are based upon separate extracts, prepared from dried plant material from the collections by the authors (Table 4).

Glycosides of both kaempferol and quercetin were isolated from all collections examined (Table 1). The kaempferol glycosides were visible on the chromatogram as one spot but further chromatography separated the spot into two entities with a possible third compound visible. After identification of the two easily discernible spots as kaempferol 3–O glucoside and kaemp-

Table 4. Site locations used in present study. * Chromosome number determination based on guard cell measurements. – Ala Alaska, Alb Alberta, BC British Columbia.

Coll. no.		Locality
Cornus canadensis – 2n = 22		
75003	Alb	Pigeon Lake, 53°10′ N, 114°W
75004	Alb	Rocky Mountain House, 52°20′ N, 114°40′ W
75005	Alb	Rocky Mountain House, 52°30′ N, 115°30′ W
75006	Alb	Herbert Lake, 51°28′ N, 116°13′ W
75007	Alb	Lake Louise, 51°30′ N, 116°15′ W
75008	Alb	Mount Norquay, 51°15′ N, 115°35′ W
76101	Alb	Cypress Hills, Reesor Lake
76102	Alb	Cypress Hills, Spruce Coulee
75009	BC	Golden, 51°15′ N, 116°40′ W
75011	BC	Radium, 50°40′ N, 115°50′ W
75012*	BC	Altitude Creek
75013	BC	Sunshine Village
75014	BC	Lake Minnewanka, 51°15′ N, 115°30′ W
75036	BC	Smithers, 54°30′ N, 127°50′ W
75040	BC	McBride, 55 mile W of Hwy. 16
75041	BC	Jasper, 75 miles W
75073*	BC	Summit Lake
75043	Ala	N. Paxon, 64°01′ N, 145°20′ W
75044	Ala	Denali, Mile 10
75047	Ala	Denali, Mile 25
75050	Ala	McLaren River, Denali
75056	Ala	Fairbanks, 64°30′ N, 147°10′ W
75058*	Ala	Eagle, 64°10′ N, 141°15′ W
75059	Ala	Palmer, 61°55′ N, 147°20′ W
Cornus unalaschkensis – 2n = 44		
75017	BC	Moresby Lake (Queen Charlotte Islands)
75019	BC	Moresby Lake, 52°55′ N, 130°05′ W
75024	BC	West Victoria Lake (Q.C.I.)
75026	BC	Upper Victoria Lake (Q.C.I.)
75029*	BC	Graham Island
75030	BC	West Tow, 54°02′ N, 129°50′ W
75031*	BC	Tow Hill, 54°05′ N, 129°50′ W
75032	BC	Tlell River, 53°30′ N, 129°55′ W
75033	BC	Olive Lake, 54°20′ N, 130°15′ W
75035	BC	New Hazelton, 55°20′ N, 127°40′ W
75036*	BC	Smithers, 54°30′ N, 127°50′ W
75038	BC	Purden Lake, 53°55′ N, 121°55′ W
76105	Ala	Petersburg, 56°55′ N, 133°W
76110*	Ala	Chilkat Lake, Haines
76111*	Ala	Haines
Cornus suecica – 2n = 22		
75060	Ala	N. Anchorage, 61°30′ N, 149°20′ W
75063	Ala	Seward, 60°45′ N, 148°35′ W
Cornus canadensis × suecica – 2n = 22		
75046	Ala	Paxon, 63°10′ N, 145°20′ W
75048	Ala	McLaren River, Denali
75053	Ala	McKinley Park, 60°30′ N, 150°20′ W
75054	Ala	Seward, 60°10′ N, 149°30′ W
75065	Ala	Mile 12, N. Houston
75066	Ala	Mile 102, Hwy. 3

ferol 3–O arabinoside, the original large spot was hydrolyzed. The only aglycone present in the large spot was kaempferol; however, three sugars, glucose, arabinose and galactose were isolated. By inference, this third compound was identified as kaempferol 3–O galactoside. No Rf data and spectral data is present for this compound due to its low concentration.

Seven of the eight flavonols identified were present in all the collections examined, while the eighth, here named quercetin 3–O gentiobioside, was found only in *C. suecica* and *C. unalaschkensis*.

Distribution and habitats

Collections of *Cornus unalaschkensis* were made mainly along the NW coast of North America. In addition, collections from continental B. C. were made – Purden Lake (75038) and New Hazelton (75035) (Fig. 1). All collections were made from a coastal forest habitat dominated by *Picea sitchensis* (Bong.) Carv. and *Tsuga heterophylla* (Raf.) Sarg., far from the peat bogs which intersperse the coastal forest, where *Pinus contorta* Dougl. is the dominant tree species.

Cornus suecica is also restricted to a primarily coastal environment, and no significant difference between this species and *C. unalaschkensis* was found. *C. suecica* is much more northern than *C. unalaschkensis*. *C. suecica* has been reported from SE Alaska and N British Columbia (Hultén 1937, Taylor & McBryde 1977) but populations resembling *C. suecica* collected by us in these areas were all *C. unalaschkensis*. However, we have not studied all herbarium material available, so partial sympatry would still appear to be a possibility.

Cornus canadensis is more continental in our area and is thus found in an area with less rainfall than the coastal forest, in association with, e.g. *Populus tremuloides* Michx., *Picea glauca* (Moench) Voss or *Pinus contorta*.

The diploid hybrid is restricted to the present-day overlap areas of the parent species. It grows in habitats of a more continental type similar to *Cornus canadensis* at its northern limits in central Alaska.

Discussion

Flavonoid profile

The flavonoid profile of the *C. canadensis–C. suecica* complex is relatively simple. The presence of only flavonol glycosides in the complex indicates a modest chemical diversity (Harborne & Williams 1971, Rossler et al. 1966). The step from woody to herbaceous habit in plants has been shown to produce three typical changes in leaf flavonoids (Swain 1975): loss of protoanthocyanidins, loss of b-ring trihydroxylation, and replacement of flavonols by flavones. Because members of the *C. canadensis–C. suecica* complex are the only herbaceous members of an otherwise woody genus, it is therefore not surprising that they only exhibit one of these chemical changes, viz. loss of b-hydroxylation (lack of myricetin). There is no evidence of flavones replacing flavonols.

Inheritance of quercetin 3-O gentiobioside

Cornus suecica (diploid) and *C. unalaschkensis* (tetraploid) invariably have quercetin 3-O gentiobioside, while *C. canadensis* and *C. canadensis* × *suecica* (both diploids) lack this compound. If one assumes that *C. unalaschkensis* is the autotetraploid derivative of *C. suecica,* then this chemical pattern is easy to explain. However, the morphology of the tetraploids speaks against this. The presence of a diploid hybrid, morphologically intermediate between *C. suecica* and *C. canadensis*, and therefore extremely similar to *C. unalaschkensis*, strongly indicates that the latter originated by chromosome doubling in such a hybrid.

Since the diploid hybrid lacks quercetin 3-O gentiobioside, it is likely that the production of this compound is controlled by a recessive gene. In the tetraploid derivative of the diploid heterozygous hybrid, the gene will again be present in double dosage, which will lead to production of gentiobioside.

Previous classification

Previous attempts to classify these taxa have relied heavily upon morphology, which has resulted in confusion. For example, petal colour was considered by Calder & Taylor (1965) to be the diagnostic character by which *C. canadensis, C. suecica* and *C. unalaschkensis* could be separated. The petals of *C. suecica* were thought to be completely purple, those of the intermediate to be only partially purple. This was not found to be so in this study.

Another classification based strictly upon morphological characters was proposed by Lepage (1946, 1950, 1955) who described a wide range of forms, separated mainly on leaf and bract abnormalities. The results of the present study indicate that these forms are rare and are most often contained in populations of otherwise normal *C. canadensis*. These forms are, therefore, not accepted as separate taxa.

Taxonomy

The complex is most accurately treated as consisting of three morphological groups: *C. canadensis* (diploid), *C. suecica* (diploid) and an intermediate group, which can be subdivided into *C. unalaschkensis* (tetraploid) and *C. canadensis* × *suecica* (diploid). The use of all eleven morphological characters does, in most cases, give an accurate classification. *C. canadensis* is easily identified by its green flowers; all other plants have at least some purple tinge of the petals. Other identifications based on morphology are not completely reliable, so cytological and flavonoid evidence must be used.

Cornus canadensis and *C. suecica* can be separated from one another quite easily. They differ in morphology, chemistry, distribution and ecology, and their diploid hybrid is semisterile. For these reasons no change in their taxonomic status is proposed.

However, 50 % of the pollen in those specimens of the hybrid examined was viable and this leaves the possibility for introgression. No evidence of such a process has been found in the material and diploid hybrids growing beside *C. canadensis* (no. 75052, 75048, 75046) showed no evidence of interbreeding. The sterility of the hybrid has been observed in the field by Hultén (1937) and Olsen (1914).

The intermediates are, as evident from the facts presented here, the results of hybridization; the tetraploid has been derived through chromosome doubling from an initial diploid intermediate, probably closely similar to the present-day one. The wide range of the tetra-

ploid and its occurrence outside the areas of the putative parents, together with its fertility, indicates that the tetraploid represents an older cycle of hybridization than the diploid hybrids.

The allotetraploid intermediate, because it is fully fertile and reproductively isolated, is considered to be a distinct species, *Cornus unalaschkensis* Ledeb. Ledebour (1842) described this species with no knowledge of floral characters and the description of the leaf venation pattern does not fit the type specimen. We have seen the type specimen, and it clearly represents an intermediate. Examination of the guard cells of a collection from the type location (CAN 326919) suggests that it is a tetraploid.

Although morphology does not allow the easy distinction of *Cornus unalaschkensis* from the diploid hybrid, they can be separated on chromosome number, guard cell size, pollen viability, distribution and presence of quercetin 3-O gentiobioside. The formula *Cornus canadensis* × *suecica* has been chosen to delimit the diploid hybrid.

Evolution and ranges

Hybridization has occurred between the two diploid species, *Cornus canadensis* and *C. suecica*. In the earliest of the two known instances a chromosome doubling produced a fully fertile allotetraploid. This tetraploid survived the Pleistocene glaciations and climatic changes in areas where *C. suecica* failed to survive, so the present southern extremities of the distribution of the tetraploid and that of *C. suecica* are widely separate. The second instance of hybridization has occurred in more recent times resulting in formation of a diploid entity in the present overlap areas of the two species. The eventual production of the tetraploid in these overlap areas is certainly possible and would represent an example of polytopic speciation. The difference in geographic distribution between diploids and tetraploids is perhaps the result of reinvasion after glaciation. Hultén (1968) suggested that *C. suecica* once had a more southerly distribution which has been reduced due to a change in climate, whereas the tetraploid has apparently not suffered the same reduction in distribution. These climatic changes may also have changed the distribution of *C. suecica* enough to create a new "overlap area" with *C. canadensis*, and allow the process of hybridization to begin again in a new, more northern area.

The coastal areas, now occupied by the tetraploid, were all glaciated during the last advance of the ice, although various coastal refugia or unglaciated areas may have existed along the coast (Heusser 1965, Savile 1968, Randhawa & Beamish 1972). As the ice receded the areas were reinvaded by the tetraploid. The more northern areas, although also unglaciated in many parts, do not show evidence of invasion by the tetraploid, perhaps because the tetraploid race may not have existed so far north in pre-glacial times and so was not present to invade these areas.

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Key to Cornus subgen. Arctocrania in NW North America

1. Flowers greenish-white; stamens mostly shorter than the style; hypanthium hoary ..... *C. canadensis*
– Flowers purple or partly purple; stamens mostly longer than the style; hypanthium sparsely strigillose to hoary 2
2. Leaves mostly arranged in a whorl of 4–6 at the shoot apex, often with 1–2 pairs of stem leaves 4–6 cm below the whorl; leaves mostly petiolate, sometimes sessile; leaf veins arising from a distinct midrib, seldom from the leaf base 3
– Leaves mostly arranged in 3–6 subequal pairs, sometimes simulating a whorl at the shoot apex; leaves sessile to sub-sessile; leaf veins arising from the base or if from the midrib, from the basal 1/4 to 1/3 of the leaf ..... *C. suecica*
3. Distribution restricted to continental Alaska; chromosome number 2n = 22; pollen approximately 50 % inviable; quercetin 3-O gentiobioside absent ..... *C. canadensis* × *suecica*
– Distribution restricted to coastal northwestern North America (including the Aleutian Is.) and the western side of the Rocky Mountains; chromosome number 2n = 44; pollen mostly all viable; quercetin 3-O gentiobioside present ..... *C. unalaschkensis*

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International register of specialists and current research in plant systematics

The Hunt Institute for Botanical Documentation has received a grant from the U. S. National Science Foundation to produce an international register accounting for both specialists and individual research projects in systematic botany. The *Register,* to be produced in both computerized and published forms, will revive and incorporate the now dormant "Index of Current Research" previously sponsored by the American Society of Plant Taxonomists and "Register of Specialists" produced by the International Association for Plant Taxonomy. This new *Register* project is being undertaken with the endorsements and assistance of both those organizations. Financial assistance has also been received from the U. S. National Park Service, through the New York Botanical Garden.

Questionnaires and accompanying instructions (trilingual: English, French, German) will be distributed within the systematic botanical community starting in November 1978. Major means of distribution will include enclosure in individual copies of *Taxon* (first 1979 mailing) and *Systematic Botany,* and by mailing modest supplies to selected botanical institutions and academies of science. These forms have been designed to permit easy photoduplication, which is strongly encouraged. Anyone working in systematic botany (s. lat. – including its history, bibliography, art, and applications to structural, ecological and evolutionary botany) is urged to fill out and return a questionnaire by 31 August 1979. Those not receiving questionnaires directly should obtain them (or photocopies) from a convenient botanical institution or, if that is not possible, can request them by writing to: Hunt Institute, Attention Register, Carnegie-Mellon University, Pittsburgh, Pennsylvania 15213, USA. Such direct requests should be made only if the materials are unavailable through the other channels.

The first printed edition of the *Register* will be published in spring 1980. Thereafter, with adequate continuing assistance from the botanical community and its sponsors, the Institute plans to maintain the *Register* as an active computerized data base and to produce succeeding printed editions triennially. A copy of the published *Register* will be sent without charge to each questionnaire respondent as well as to relevant institutions and governmental agencies. Reasonable special query service will be available to the public at no or minimal cost upon application to the Institute. This may involve special permutations of the data, or simply requests for up-to-date information on a given topic during the periods between successive published editions.

The utility of the *Register* to both the botanical community and the general public will depend in large measure upon its comprehensiveness. To maximize coverage, the Institute requests the cooperation and active assistance of botanists and their institutions on a worldwide basis. We urge them to respond for themselves and to assist us by publicizing the project and making their copies of the questionnaire materials available for copying by others who have not received them directly. In this fashion we hope to take full advantage of the international botanical "grapevine".

Monopsis (Lobeliaceae) in tropical Africa

Mats Thulin

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Three species of the mainly S African genus *Monopsis* Salisb. (Lobeliaceae) extend into tropical Africa. For these species descriptions, synonymy and maps of distribution are given. Four lectotypes are selected. The following new combinations are proposed: *M. stellarioides* (Presl) Urb. subsp. *schimperana* (Urb.) Thulin (= *M. schimperana* Urb.), *M. decipiens* (Sond.) Thulin (= *Lobelia decipiens* Sond.) and *M. zeyheri* (Sond.) Thulin (= *Lobelia zeyheri* Sond.).

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Salisbury (1817) erected the genus *Monopsis* for two S African species of Lobeliaceae characterized by having a "nearly regular corolla of one face", as opposed to the two-lipped corolla prevailing in the related *Lobelia*. The genus remained small and was circumscribed in roughly the same way until Bentham & Hooker (1876) included it in sect. *Holopogon* of their widely circumscribed *Lobelia*. It was soon restored and redefined in a detailed study by Urban (1881), who also included in it the two small and likewise S African genera *Parastranthus* G. Don (1834) and *Dobrowskya* Presl (1836). The resulting emended *Monopsis* displays a wide variation in both vegetative and floral characters: the leaves may be alternate, opposite or verticillate, bracteoles may be present (if so they resemble small leaves) or absent, the corolla may be subregular or two-lipped and two of the petals may be almost free. Nevertheless, as demonstrated by Urban (1881), all species of *Monopsis* have in common some characteristic features of their anthers and style. These organs differ constantly from those of *Lobelia* and certainly reflect differences in the pollination mechanism, an aspect also studied by Urban on a few species cultivated in Berlin. Most easily observed on herbarium material is the style with linear, soon revolute style-lobes with a ring of pollen-collecting hairs well below them. In *Lobelia* as in almost all other genera of the family (except e.g. *Cyphia*), the style-lobes are short, broad and closely surrounded by a ring of pollen-collecting hairs. Urban (1881) also supposed all species of *Monopsis* to have non-resupinate flowers, while in *Lobelia* they are regularly resupinate, i.e. turned upside down by twisting of the pedicel. He recognized nine species in the genus, all in S Africa except for *M. schimperana* Urb. in Ethiopia, and divided the genus into two sections, *Monopsis* ("*Eumonopsis*") with subregular corolla and bracteoles absent and *Dobrowskya* with two-lipped corolla and bracteoles present. Urban's generic delimitation has been followed by most subsequent authors, notably by Wimmer (1953 b), and is also accepted in this paper. Wimmer (1953 b) recognized 18 species (still with only one in tropical Africa) placed in three sections.

In the course of a study of tropical African Lobeliaceae it has now been found necessary to transfer two more *Lobelias* to *Monopsis*. They are exceptional in the genus in that the flowers are resupinate, but in their linear style-lobes, comparatively large bracteoles resembling small leaves, and in their anther-tube with the two

lateral anthers somewhat longer than the others and with shorter hairs at the tip they agree with *Monopsis* and there is no doubt that this is where they belong. *M. decipiens* also agrees with most other species of the genus in its reticulate seeds (Fig. 1 B, E), while *M. zeyheri* deviates in having striate-verruculate seeds (Fig. 1 C). With Urban's infrageneric classification they both belong to sect. *Dobrowskya,* but with the more narrow circumscription of the sections given by Wimmer they are impossible to place satisfactorily, as they combine characters of his sections *Dobrowskya* and *Parastranthus*. Apparently both species are rather isolated in the genus and it is difficult to tell with any certainty which are their nearest relatives.

Key to Monopsis in tropical Africa

1. Leaves opposite; flowers not resupinate ..... 1. *M. stellarioides*
– Leaves alternate; flowers resupinate 2
2. Leaves linear; corolla 10 mm or more long ..... 2. *M. decipiens*
– Leaves ± elliptic; corolla 4–5 mm long ..... 3. *M. zeyheri*

1. **M. stellarioides** (Presl) Urb.

Urban 1881 p. 275; Wimmer 1953 b p. 703, Fig. 106/d. – *Dobrowskya stellarioides* Presl 1836 p. 10; Sonder 1865 p. 550. – *Parastranthus stellarioides* (Presl) Vatke 1874 p. 717, pro parte. – *Lobelia stellarioides* (Presl) Benth. & Hook. f. ex Hemsley 1877 p. 470, pro parte. – *Dortmannia stellarioides* (Presl) Kuntze 1898 p. 188. – Orig. coll.: S Africa, "Cap. b. spei", Krebs s.n. (PR holotype, not seen, B isotype).

Annual or perennial decumbent herb, often stoloniferous. *Stems* 5–60 cm, usually rooting at the lower nodes, ribbed, with harsh retrorse pubescence. *Leaves* opposite, subsessile or shortly petiolate, linear to elliptic, up to 10–35 × 2–9 mm, acute or obtuse and mucronulate at the apex, rounded to attenuate at the base, almost glabrous or usually with fine but harsh pubescence on both surfaces, usually retrorse beneath and at margin, but with forwardly directed hairs above; margin incrassate, slightly revolute, crenate or serrate; midvein prominent beneath. *Flowers* not resupinate, solitary, axillary, scattered on the stem; pedicels 8–35 mm, pubescent with retrorse hairs; bracteoles at the base of the pedicel, 6–16 mm, resembling small leaves. *Hypanthium* obconical or obovoid, ± 10-nerved, pubescent. *Calyx* lobes 2–6 mm, acute, entire, ± pubescent at the margins and on the outside, often reflexed in fruit. *Corolla* 6.5–11.5 mm, dirty yellow, dull pink, brownish purple or violet (but always ± violet when dried), with two swellings in the mouth of the tube, split on the lower side almost to the base, two-lipped with the upper lip 3-lobed and the lower lip consisting of two spathulate lobes united with the tube for 0.5–2.5 mm; short pubescent outside, often with longer hairs on the midveins of the lobes, glabrous or puberulous inside. *Filaments* free from corolla, linear, connate above, all pubescent at least on the inside above. Anther tube ± 1.6 mm, all anthers densely penicillate at the tip, otherwise glabrous. *Style* lobes ± 0.6 mm. *Capsule* ± 10-nerved, obconical to oblong-obovoid, up to 10 mm, pubescent, dehiscing by valves up to 1.5 mm long, or ± indehiscent. *Seeds* broadly elliptic or rotund in outline, compressed, ± 0.6–0.7 mm, distinctly and regularly reticulate, dark brown.

M. stellarioides subsp. **schimperana** (Urb.) Thulin, comb. et stat. nov. – Fig. 1 A, D

M. schimperana Urban 1881 p. 275, as "*schimperiana*"; Engler 1895 p. 402; Th. C. E. Fries 1923 p. 410. – *M. stellarioides* (Presl) Urb. var. *schimperana* (Urb.) Wimmer 1953 b p. 704; Hedberg 1957 p. 195, 334; Wimmer 1963 p. 315; Cufodontis 1966 p. 1061; Wimmer 1968 p. 890. – Orig. coll.: Ethiopia, near Gaffat, 23.8.1863, Schimper 1146 (B lectotype, selected here, BM, K, W isolectotypes). The specimen in B has been believed to be destroyed (Hedberg 1957), but is actually still present.

Lobelia violaceo-aurantiaca De Wildeman 1920 p. 28, 1922 p. 296. – *M. stellarioides* (Presl) Urb. f. *violaceo-aurantiaca* (De Wild.) Wimmer 1953 b p. 704. – Orig. coll.: Zaire, Ruwenzori, Butagu, 12.4.1914, Bequaert 3588 (BR holotype, UPS, W isotypes).

L. mokuluensis De Wildeman 1920 p. 26, 1922 p. 294. – Orig. coll.: Zaire, Mukule, 27.9.1914, Bequaert 5922 (BR holotype, UPS, W isotypes).

M. brevicalyx Th. C. E. Fries 1923 p. 411; Wimmer 1953 b p. 705, 1968 p. 890. – Orig. coll.: Kenya, Mt Kenya, W slope near Forest Station, 27.12.1921, Fries & Fries 387 (UPS holotype, B, BR, K, S isotypes).

M. schimperana Urb. var. *brevifolia* Chiovenda

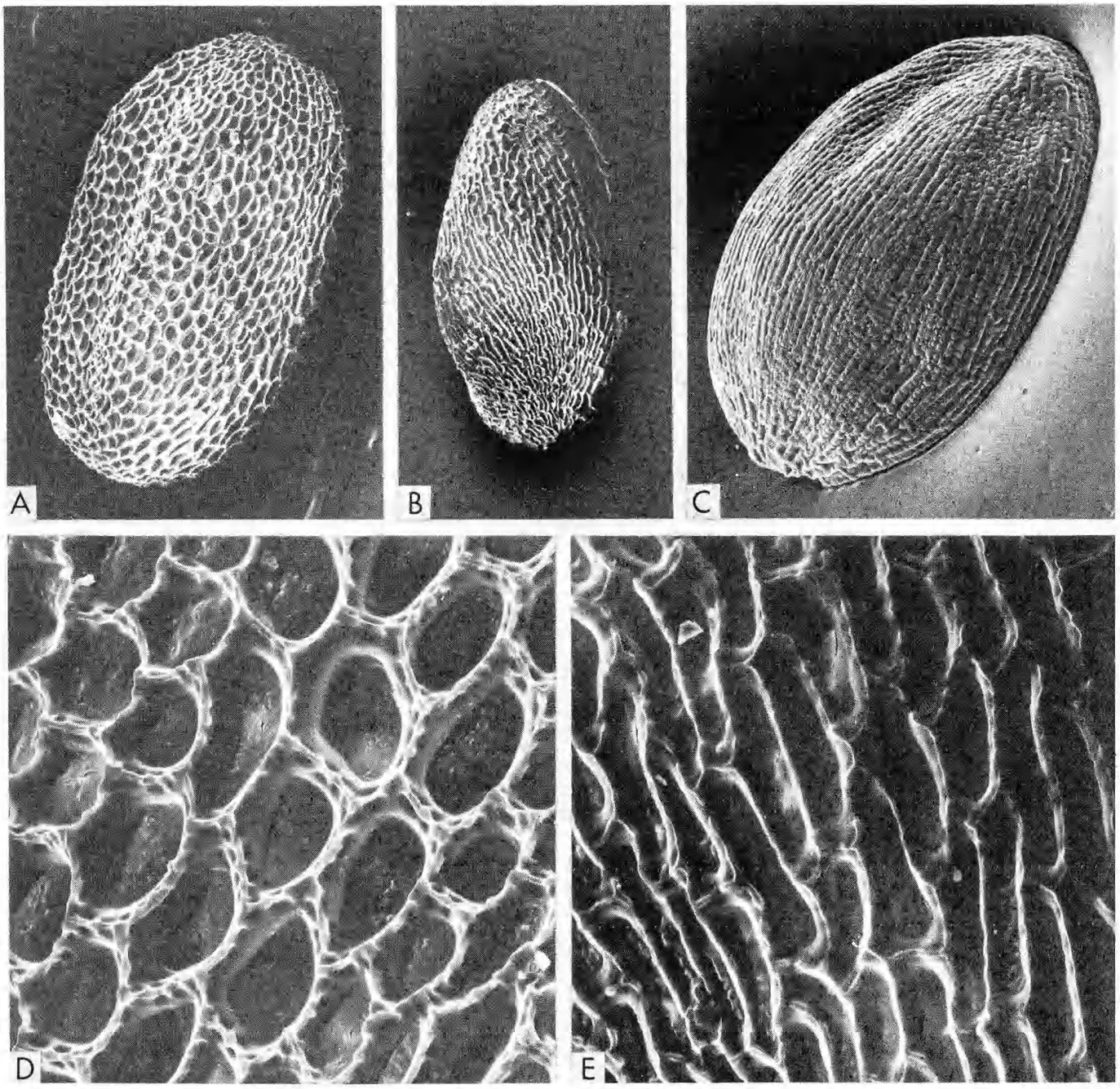

Fig. 1. Seeds (SEM). – A, D: *Monopsis stellarioides* subsp. *schimperana*, × c. 85 and c. 550. From Thulin 308 (UPS), Tanzania. – B, E: *M. decipiens*, × c. 85 and c. 550. From Mogg 6318 (UPS), Natal. – C: *M. zeyheri*, × c. 185. From Gilbert 4989 (UPS), Kenya.

1935 p. 73, synon. nov. – Orig. coll.: Mt Aberdare, Tusu, 1.12.1910, Balbo 67 (TOM holotype, not seen).

Parastranthus stellarioides sensu Vatke 1874 p. 717, pro parte, quoad specim. ex Abyssinia.

L. stellarioides sensu Hemsley 1877 p. 470, pro parte, quoad specim. ex Abyssinia.

M. stellarioides sensu Agnew 1974 p. 517, 519 (Fig.).

Corolla usually dirty yellow, dull pink or brownish purple, puberulous inside, with the two lower lobes united with the upper lip for 0.5–1.0(–1.5) mm. *Capsule* often oblong-obovoid and indehiscent, only rarely apical valves are formed.

Distribution and habitat. M. stellarioides subsp. *schimperana* is widespread in the uplands of tropical Africa with marked gaps in the Congo Basin and N Kenya. Specimens have been seen from the following countries: Ethiopia, Fernando Poo, Cameroun, Uganda, Kenya, Tanzania, Zaire, Rwanda, Burundi, Zambia, Malawi and Comoro Islands (Fig. 3 A). Growing

in upland grassland and moor, forest margins and rocky places at 1200–3600 m altitude. Subsp. *stellarioides* is distributed in E South Africa and material has been seen from Transvaal, Natal, SE Cape Province and Swaziland (Fig. 3 A).

Notes on taxonomy. It seems very appropriate to give subspecific rank to Wimmer's two varieties as they provide a good example of geographical races. The distribution and racial differentiation agree well for example with the two subspecies recognized within *Wahlenbergia krebsii* Cham. in southern and tropical Africa respectively (Thulin 1975).

Subsp. *stellarioides* is characterized by the violet corolla, often glabrous inside and with the two lower lobes united with the upper lip for c. 2–2.5 mm, and by the obovoid-obconical capsule, regularly dehiscing by apical valves. Wimmer (1953 a, b) placed the material from the Comoro Islands under his type variety, but a re-examination shows that it is no doubt subsp. *schimperana*.

I follow Hedberg (1957) in considering *M. brevicalyx* a synonym of subsp. *schimperana*. This name has been used for a form in Kenya characterized by narrow leaves, short calyx-lobes and above all, which has not been mentioned by previous authors, by the capsule often dehiscing by apical valves as is always the case in subsp. *stellarioides*. However all these characters vary ± continuously. *M. schimperana* var. *brevifolia,* also described from upland Kenya, appears from the description to be the same form.

2. **M. decipiens** (Sond.) Thulin, comb. nov. – Figs. 1 B, E, 2

Lobelia decipiens Sonder 1865 p. 540; Rolfe 1889 p. 402; Gibbs 1906 p. 451; Wimmer 1953 b p. 588. – *Dortmannia decipiens* (Sond.) Kuntze 1891 p. 972. – Orig. coll.: Transvaal, Magalisberg, Zeyher 1072 (S lectotype, selected here, BM, K, isolectotypes).

L. breynii Lam. var. *bragae* Engler 1895 p. 402. – Orig. coll.: Mozambique, Beira (locality probably erroneous), Braga 135 (B holotype).

L. dobrowskyoides Diels 1898 p. 117. – Orig. coll.: Transvaal, Quintas 216 (B holotype).

Monopsis scabra sensu Wimmer 1968 p. 891, quoad specim. ex Rhodesia.

Annual or perennial erect or ascending herb. *Stems* 5–45 cm, usually sparsely branched, ribbed, ± pubescent with upturned hairs. *Leaves* alternate, fairly numerous and densely set, ± erecto-patent, linear, up to 8–15 (–25) × 0.8–1.5 (–2.5) mm, acute at the apex, harshly strigulose mainly along margins and on the underside of the midvein; margin incrassate, entire or rarely with one pair of denticles; midvein prominent beneath. *Flowers* resupinate, solitary, axillary or apparently terminal, confined to the upper part of the plant; pedicels 15–55 mm, pubescent with forwardly directed hairs; bracteoles resembling small leaves, sometimes opposite. *Hypanthium* hemispherical or broadly obconical, ± 10-nerved, appressed pubescent. *Calyx* lobes 2–5 mm, acute, entire, strigulose on the outside, spreading. *Corolla* 10–18 mm, blue or blue and purple with yellow markings on lower lip, sometimes white or almost so, split on the upper side to ± 1 mm from the base, 2-lipped with the lower lip broadly 3-lobed and the upper lip consisting of two reflexed lobes united with the tube for most of their length; appressed pubescent outside, sparsely pubescent near the base inside. *Filaments* almost free from corolla, linear, connate above, all pubescent on the inside above. Anther tube 1.5–2.5 mm, all anthers densely penicillate at the tip, otherwise glabrous. *Capsule* ± 10-nerved, subglobose to ovoid, up to 6.5 mm, dehiscing by valves up to 2.5 mm. *Seeds* broadly elliptic in outline, compressed, 0.5–0.6 mm, reticulate, brown.

Distribution and habitat. M. decipiens is distributed in SE Africa and is known from Rhodesia, Mozambique, S Africa (Transvaal, Natal, Orange Free State, SE Cape Province), Swaziland and Lesotho (Fig. 3 C). Wimmer (1953 b) also cited a specimen from Botswana without precise locality: Holub s.n. (PR, not seen). Growing in grassland, often in seasonally wet places, at 900–2000 m altitude (in S Africa even down to 30 m).

Notes on taxonomy. Wimmer apparently had his doubts about the generic position of this plant. He noted (Wimmer 1953 b) that it has the habit and linear style-lobes of *Monopsis*, but apparently he considered the resupinate flowers decisive and nevertheless placed it in *Lobelia*. In habit it is very similar to *Monopsis scabra* (Thunb.) Urb. which was already noted by Sonder (1865).

3. **M. zeyheri** (Sond.) Thulin, comb. now. – Fig. 1 C

Lobelia zeyheri Sonder 1865 p. 539; Markgraf 1950 p. 209; Wimmer 1953 b p. 581; Roessler 1966 p. 4; Wimmer 1968 p. 871; Thulin 1975 p. 210. – Orig. coll.: Transvaal, Aapjesrivier, Zeyher 1046 (S lectotype, selected here, BM, FI, K, W, isolectotypes).

L. fonticola Engler & Gilg 1903 p. 398; Gibbs 1906 p. 452. – Orig. coll.: Angola, Chitanda R., 24.9.1899, Baum 144 (G lectotype, selected here, BM, COI, K, S,W, isolectotypes).

Cephalostigma nanellum R. E. Fries 1916 p. 315, as "*nanella*". – Orig. coll.: Rhodesia, Victoria Falls, 7.1911, R. E. Fries 193 (UPS holotype).

Slender annual erect or decumbent herb, often branched from the base. *Stems* 2–15(–28) cm, terete, somewhat ribbed, densely pubescent with spreading hairs. *Leaves* sessile, elliptic to narrowly ovate, up to 14 × 7 mm, acute at the apex, rounded or cuneate at the base, pubescent on both surfaces; margin coarsely dentate-serrate. *Flowers* resupinate, often cleistogamous, in lax racemes with leaf-like bracts diminishing in size upwards; pedicels up to 30 mm, pubescent; bracteoles at base of pedicel, resembling small leaves, 1–5 mm. *Hypanthium* broadly obconical to subglobose, ± 10-nerved, pubescent. *Calyx* lobes 0.5–1.6 mm, entire, pubescent. *Corolla* 4–5 mm, white, pale blue or pink with two yellowish swellings in the mouth of the tube, split on the back to ± 0.6 mm from the base, pubescent outside and inside on bottom of tube, 2-lipped with the lower lip 3-lobed and the upper lip consisting of 2 shorter lobes united with the tube for most of their length. *Filaments* ± attached to the corolla tube at the base, linear, scarcely connate above, all sparsely pubescent on the inside near the tip, the two anterior ones also ciliate at the base. Anther tube ± 0.6 mm, all anthers penicillate at the tip, otherwise glabrous. *Capsule* ± 10-nerved, 2–3.5 mm, pubescent; valves ± 1 mm. *Seeds* broadly elliptic in outline, strongly compressed, ± 0.35 mm, striate-verruculate, brown.

Distribution and habitat. L. zeyheri is an inconspicuous species with comparatively few and widely scattered localities in S and E tropical Africa. Material has been seen from the following countries: Kenya, first record for the country: Nairobi, Golf Range on Langata Rd., 12.2.1978, Gilbert 4989 (UPS), Tanzania, Zambia, Rhodesia, Malawi, Angola, Namibia and S Africa (Transvaal). Fig 3 B; 2 of the localities in Namibia have been taken from Wimmer (1953 b). Growing on seasonally wet ground, streambanks or shallow soils over rocks, often in sandy places, at 620–1700 m altitude.

Fig. 2. *Monopsis decipiens*, habit, × 1 and flower, × 3. From Fries, Norlindh & Weimarck 2393 (LD), Rhodesia.

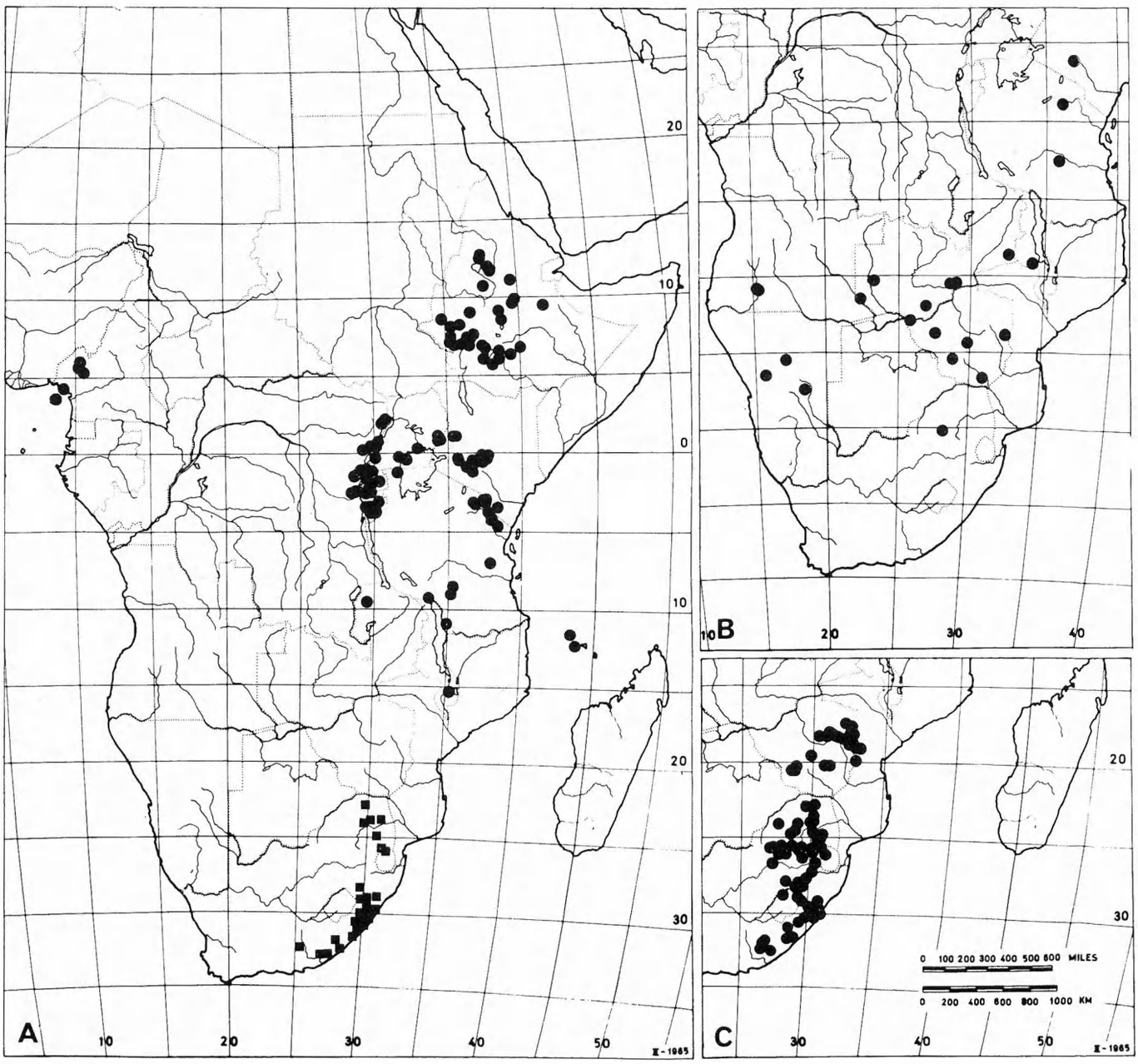

Fig. 3. Known distributions of species of *Monopsis*. – A: *M. stellarioides* subsp. *stellarioides* (■) and subsp. *schimperana* (●). – B: *M. zeyheri*. – C: *M. decipiens*.

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The Hunt Institute for Botanical Documentation announces establishment of the George H. M. Lawrence Memorial Fund, based at the Institute as a permanent Fund to honor the memory of Dr Lawrence (1910–1978), its founding Director. Income from the Fund will be used to provide an annual Award (beginning in 1979) in support of a doctoral candidate's travel for dissertation research in one or more of Dr Lawrence's fields of special interest in the plant sciences: systematic botany; horticulture; or history of botany or horticulture, including literature and exploration. An Awards Committee, comprising representatives of the Lawrence family, The Hunt Foundation, the Hunt Institute, and the botanical community, will review nominations and select recipients. Awards will be made strictly on the basis of merit – that of the proposed research, and the recipients' general scholarly promise in their fields. Notice of invitation for nominations for the first award (1979) will appear in a few months.

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Cyathus canna and its presumptive relatives (Nidulariaceae)

Harold J. Brodie

Brodie, H. J. 1979 05 15: Cyathus canna and its presumptive relatives (Nidulariaceae). *Bot. Notiser 132:* 139–143. Stockholm. ISSN 0006-8195.

The type material of *Cyathus canna* Lloyd possesses several features not recorded in the original description. The light-umber coloured fruit bodies are distinctly but faintly plicate externally and internally in most specimens and possess firm conspicuous emplacements. The small lead-coloured peridioles (1.75–2 mm) are ellipsoid in outline, have a distinctive raised rim and enclose globose spores 8–10 μm in diameter. This tropical species is recorded from Barbados, Costa Rica, Jamaica and Mauritius. Plication seems to be a less reliable character in *Cyathus* than has been assumed up to now.

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The apparent scarcity of specimens of *Cyathus canna* Lloyd in many herbaria may be the result of the species having escaped detection rather than its being of infrequent appearance or very restricted distribution. The considerable resemblance to such species as *C. earlei* Lloyd and *C. colensoi* Berkeley, especially, may well have resulted in failure of mycologists to recognize some collections from tropical regions as *C. canna*. Lloyd's description (Lloyd 1906) is not sufficiently explicit to permit recognition without difficulty; moreover, no photographs published heretofore have adequately displayed all the diagnostic features of this species. The main purpose of the present note is to provide clear photographs of Lloyd's type specimens as a possible aid in the recognition of the species and to describe features of the type material which were not reported by Lloyd. In addition, some notes concerning differences between *C. canna* and its presumptively close relatives are given, as well as comments on the few known collections and their distribution.

Published references

The specimens on which Lloyd (1906) based his description of *C. canna* are catalogued as No. 302 of the Lloyd Mycological Herbarium in the National Fungus Collections (USA) located at Beltsville, Maryland. The type material (Fig. 1 D) consists of only six specimens collected by L. Lewton-Brain, Barbados. (No date is given on any of the type labels.) Lloyd's description of this material was brief and unfortunately the photographs which accompanied it are of little value as an aid to identification.

Many years later, a second more abundant collection (No. 24877, Lloyd Herb.) of *C. canna* was commented upon by Lloyd (1925), the specimens (Fig. 1 A, B, C, E, F) having been obtained by Chas. A. O'Connor, Mauritius (no date). Again, the accompanying photograph is of very poor quality.

Writing of the Nidulariaceae of the West Indies, Brodie & Dennis (1954) included *C. canna* entirely on the basis of Lloyd's Barbados material, but these authors had no new collections to report.

The occurrence of *C. canna* in Costa Rica was recorded briefly in 1967 (Brodie 1967).

In 1968, I gave an account (Brodie 1968) of a study of pure cultures of *C. canna* which had been made in 1954 from specimens collected by C. B. Heiser in Costa Rica. The species was reported to exhibit tetrapolar sexuality, and

some observations concerning the appearance of monokaryon and dikaryon mycelia were noted.

Lloyd's name *C. canna* was incorrectly spelled as *C. cauna* in Saccardo's listing of the species (Syll. Fung. 21 p. 465, 1912).

Except for recognition and inclusion of *C. canna* in my monograph of the Nidulariaceae (Brodie 1975), there are no other references to this fungus of which I am aware.

Lloyd's description; type specimens

Lloyd's description of *C. canna* (Lloyd 1906) is reproduced herewith:

Cyathus canna (Plate 110) – Cups campanulate, rigid, 7–8 × 6–8 mm, dark brown. Externally even, scabrous with short tomentum. Internally smooth, even, white as if covered with a thin layer of whitewash. Peridioles covered on the upper side with a silvery, thin tunica. Cortex double, the outer thin, composed of small fibrils. Spores *small, globose,* 7–9 mic.

This plant grew in the earth, and is very similar to the preceding (*C. earlei*).

Lloyd was understandably pleased to recognize *C. canna* (almost twenty years after his description) in an abundant collection obtained by Chas. O'Connor in Mauritius. Lloyd's (1925), note concerning this material follows:

When we wrote our Nidulariaceae pamphlet (1906) we referred as above (*C. canna*) a collection from Barbados. It is very much the same as *Cyathus vernicosus* as to cups, but smaller, and it was based on the small globose spores, 8 mic. In all the years since, we have never received another collection and we were beginning to look on it as a lost species. This collection from Mr. O'Connor, Mauritius, appears the same but has larger cups. They resemble those of *Cyathus vernicosus* but are even and white within. The globose spores, 8 mic., are its feature. It is evidently a very rare species and we are glad it is not lost. Mr. O'Connor sends a liberal collection which grew on bare ground.

In the light of my recent study of the type specimens and those comprising the collection from Mauritius as cited above, some comments regarding Lloyd's description are in order.

(1) Words in Lloyd's description such as campanulate, rigid, even, smooth and some others are of little or no value for definition of the species at the present time. As one example, all fruit bodies of the Nidulariaceae are rigid when dry and those of *C. canna* seem neither less rigid nor more rigid than those of other species.

(2) The type specimens and the Mauritius collection both include fruit bodies that show some degree of plication externally as well as internally (Fig. 1 E), a fact not recorded by Lloyd.

(3) Fruit bodies of the type material and of the Mauritius material are wide-conic in shape, are thin-walled and have wide-flaring mouths (Fig. 1 B, C, F). These features were not noted by Lloyd in his description, though he did compare them with *C. vernicosus* (= *C. olla*) Batsch ex Pers. in his 1925 note.

(4) A very conspicuous emplacement (Fig. 1 A, D, F) to which the peridia are attached by an unusually narrow or constricted base (Fig. 1 C, E) are also features not remarked upon by Lloyd.

(5) The ellipsoidal outline of the peridioles and the conspicuous rim or ridge of each peridiole are still other characteristics of the type material which Lloyd did not include in his description.

I believe *C. canna* is a valid species. In order to facilitate its recognition, I venture to offer an expanded description of the type material now before me. The actual type from Barbados consists of only six specimens, one broken. The second collection from Mauritius and labeled by Lloyd comprises about a hundred specimens, most of which are in excellent condition. After careful comparison of the type with the Mauritius material, it is my opinion that they are taxonomically identical.

Extended description of C. canna

Fruit bodies 7–8 mm high, 8–10 mm wide at mouth, wide-obconic (Fig. 1 C, D, E) with wide flaring mouth (Fig. 1 B, C) and narrow basal attachment (Fig. 1 C, E); wall thin (c. 0.25 mm at mouth); fruit bodies fulvous to light umber in colour. External surface covered by a fine pile but also bearing irregular shaggy tufts of down-pointing hyphae (Fig. 1 A, D). Many fruit bodies plicate externally (Fig. 1 E) though some specimens lack plication (Fig. 1 C). Inner wall also showing broad transverse ridges in most specimens (Fig. 1 B, F). Emplacement very conspicuous (Fig. 1 A, D), solid, 3 mm or more wide (Fig. 1 A). Lip or mouth of fruit body unusually smooth (Fig. 1 B, C, F). Peridioles lead coloured, shiny, small, mostly ellipsoid in outline (Fig. 1 B, F), (1.75–)2–2.5 mm, flat and with

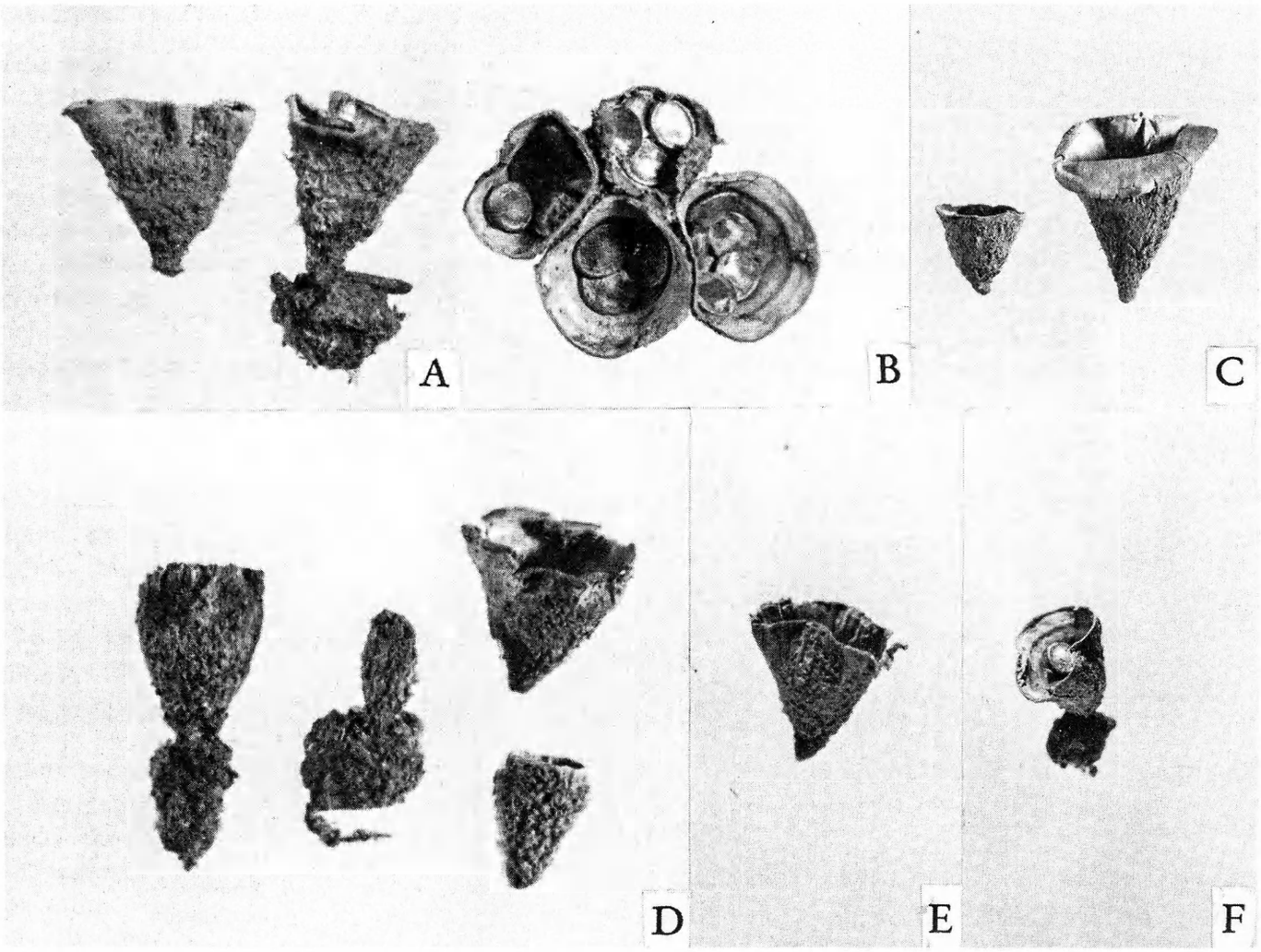

Fig. 1. *Cyathus canna*.–A–C, E, F: Lloyd Herb. No. 24877. – Note narrow attachment of peridium to large emplacement and shaggy fruit body exterior, × 3. – B: Note smooth lip of fruit body, internal ridges, ellipsoid peridioles with peripheral ridge, × 3. – C: Smallest and largest fruit bodies in the collection; note smooth inner surface of right-hand specimen, × 3. – D: Hollotype specimens, × 3. – E: Note external and internal plication, × 2. – F: Note large emplacement, smooth lip and rimmed peridioles, × 2.

conspicuous outer raised rim (Fig. 1 B); tunica present. Cortex subhomogeneous but not distinctly two-layered, 250–350 μm in overall thickness. Spores mostly globoid, 8–9 μm; a few spores ellipsoid, 8× 10 μm; spore wall 1–1.5 μm thick.

C. canna apparently belongs to the so-called *olla* group even though such affinity might seem to be questionable because of the faint plication in some specimens of the type material. In any case, *C. canna* is most likely to be confused, superficially, with *C. earlei* and *C. colensoi;* Table 1 endeavours to bring out differences as well as similarities. *C. olla* is included as the principal member of the *olla* group, although the resemblance of *C. canna* to *C. olla* is much less than to the other species; moreover, *C. olla* is essentially a species of cool regions whereas the other species are either tropical or subtropical.

It will be seen from Table 1 that *C. canna* differs from the other species mainly in the following features: (1) Peridioles small, ellipsoid in outline and with raised rim. (2) Spores small, c. 8 μm and globose. (3) Fruit bodies often faintly plicate. (4) Colour light umber.

Notes on collections examined

The notes on published references given earlier in this paper include all specimens of *C. canna* known to me with the exception of eleven packets in my personal herbarium all labeled by myself as *C. canna* before I had made the detailed study of Lloyd's type. Point-by-point

Table 1. Comparison of *Cyathus canna* (type) with related species (descriptions from Brodie 1975). Note: there is a form of *C. olla* in which the exterior is somewhat shaggy and the mouth fimbriate (Brodie 1978).

Character	*C. canna*	*C. earlei*	*C. colensoi*	*C. olla*
Fruit body				
Size	7–8 mm high, 8–10 mm wide	6–7 mm high, 8 mm wide	6–7 mm high or less, 5–6 mm wide	10–15 mm high, 8–10 mm broad
Shape	wide, with flaring mouth	wide, with flaring mouth	broad, crucible	widely conic, flared
Base	very narrow	narrow	not narrow	moderately broad
Wall	thin	thin	thick	thick
Colour	light umber	grey brown to ferrugineous	very light brown	grey to grey-fawn
Exterior				
Texture	fine pile and shaggy hairs	short hairs, slightly tufted	appressed fine hairs	fine textured, not shaggy
Plication	present or absent	absent	absent	absent
Interior				
Surface	shiny	shiny	smooth	smooth, shiny
Colour	light buff	silvery–whitish	grey-brown	lead to silvery
Plication	faint or absent	absent	absent	absent
Other	with transverse ridges	no transverse ridges	no transverse ridges	with transverse ridges
Emplacement	conspicuous, solid	conspicuous, firm	–	conspicuous
Mouth or lip	smooth	smooth	smooth	smooth
Peridioles				
Colour	lead colour	grey to brown	black	lead colour
Surface	shiny	not markedly shiny	not markedly shiny	–
Size	small: 1.75–2.5 mm	up to 2 mm	2 mm	large: to 3.5 mm
Outline	ellipsoid	irregular	irregular	irregular
Other	with raised rim	no raised rim	no raised rim	no raised rim
Cortex	subhomogeneous	two-layered	thick, one-layered	one-layered
Spores				
Shape	globoid, a few ellipsoid	ovate, ellipsoid	ellipsoid, subglobose	ovate
Size	8–10 μm	10–12 × 12–22 μm	10–12 × 8–10 μm, and subglobose, 9–12 μm	6–8 × 10–14 μm

comparison of the type with collections in my herbarium now convinces me that only five are in fact (or probably) identical with the type of *C. canna*. These are (numbers are those of my herbarium):

1236 – C. B. Heiser, Turrialba, Costa Rica, August 13, 1953.

1237 – Same data as 1236. Specimens more hairy than type; peridioles ellipsoid but without rim.

1238 – C. B. Heiser, Turrialba, Costa Rica, July 9, 1933. Somewhat darker and more hairy than type; many specimens faintly plicate.

5616 – D. A. Powell, Trelawny County, Jamaica, 1955. Agrees well with type except for slightly fimbriate mouth.

71039 – G. Guzmán, Necaxa, Pueblo, Mexico, September 4, 1966. Seems closer to the type than to any other species, but larger and darker than the type; the spores (6.5 × 8 μm) are too small for *C. earlei* which these specimens resemble somewhat and which is also known from Mexico (Brodie 1962).

The presently known distribution of *C. canna* is thus: Barbados (type), Costa Rica, Jamaica, Mauritius, Mexico.

Comments

This study was intended primarily to provide clear photographs and a detailed description of Lloyd's *Cyathus canna*. It has, however, posed a problem which may have more important implications than the mere bringing of a little-known species into sharp focus. I now suspect that plication of the fruit body is a morphological character which has been used with too great confidence for species differentiation in the past, because this is the second example of a problem involving plication to come to my attention recently.

Detailed examination of the type material of *C. triplex* Lloyd (Brodie 1979) revealed that a small proportion of the type specimens are faintly but distinctly plicate although this fact was not mentioned in the original description (Lloyd 1906) and Lloyd placed *C. triplex* in a group with *C. pallidus* which clearly has non-plicate peridia. Likewise, Lloyd did not describe *C. canna* as being even faintly plicate although many specimens of the type clearly are.

Both early monographers of the Nidulariaceae used the longitudinal plication of peridia to separate plicate species from those devoid of plication; Tulasne & Tulasne (1844), however, merely noted plication (= striae) along with other features, whereas Lloyd (1906) emphasized this feature in separating the species of *Cyathus* into groups. In my monograph I followed Lloyd here, but I did (Brodie 1975 p. 128) record a word of caution.

The strong clear plication of fruit bodies of *C. striatus* could not be overlooked by anyone, nor could anyone find longitudinal plication in fruit bodies of *C. olla*. Between these unequivocal standards there are many species (especially in the tropics) the faint plication of which may easily be overlooked. Moreover, even in those species where most fruit bodies are plicate, a few specimens may lack plication as in *C. triplex* and *C. canna*.

Clearly, it will be advisable in the future to avoid the character plication in the construction of keys for identification or at least to avoid its use in the major divarications of such keys.

Acknowledgements. I am indebted to Dr David Farr for permitting me to examine the type material cited herein and loaned by the National Fungus Collection, Beltsville, Maryland. The photographs reproduced in this paper were taken by Mr H. F. Dietrich, Department of Biology, University of Victoria, to whom I express my thanks.

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Cryptocoryne gasseri N. Jacobsen, sp. nov. (Araceae)

Niels Jacobsen

Jacobsen, N. 1979 05 15: Cryptocoryne gasseri N. Jacobsen, sp. nov. (Araceae). *Bot. Notiser 132:* 144. Stockholm. ISSN 0006-8195.

A new species of *Cryptocoryne* from Sumatra, *C. gasseri,* is described and illustrated. It is related to *C. scurrilis* De Wit.

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Cryptocoryne gasseri N. Jacobsen, sp. nov.

Holotypus: Gasser s.n., 13.4.1978, cult. ex Sumatra (C).

Folia c. 10 cm longa; laminae c. 4 × 2.5 cm, saturate viridis, manifesto bullosae, basi plus minus cordatae. Spatha c. 4 cm longa; tubus c. 2 cm; limbus brevior, flavus, reflexus, supra juxta marginem verrucis irregulariter dentiformibus armatus; collare manifestum proprio modo angustatum. Spadix c. 0.75 cm longus; stigmata ovalia; corpora olfactoria rotundata; flores masculi 30–40. Numerus chromosomatum 2n = 30.

The illustration (× 1) is drawn after colour slides of the live plant.

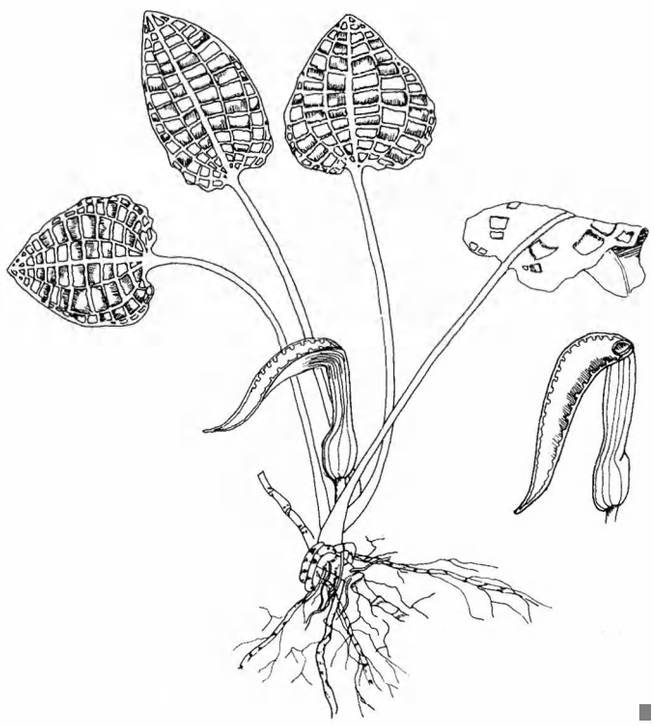
The species is related to *C. scurrilis* De Wit (2n = 60) from which it differs by the broader, more cordate, somewhat bullate leaves, by the yellow spathe with the more or less flattened denticulations along the margin, and by the chromosome number.

Nothing is known as to the exact origin of the plant; it came in a shipment of waterplants from Sumatra. The shipment also contained *C. scurrilis*.

The two species of the *C. scurrilis* group, endemic to Sumatra, are characterized by the very narrow passage through the collar, which gives the limb a peculiar look. In the *C. pontederiifolia* group, also endemic to Sumatra, the collar is broader.

The species is named in honour of R. A. Gasser, Florida, who has devoted much to the art and science of cultivating *Cryptocoryne*.

I should like to thank Tyge Christensen for the Latin description.



Embryology of Habenaria densa (Orchidaceae)

P. R. Mohana Rao and S. K. Sood

Mohana Rao, P. R. & Sood, S. K. 1979 05 15: Embryology of Habenaria densa (Orchidaceae). *Bot. Notiser 132:* 145–148. Stockholm. ISSN 000678195.

The embryology of *Habenaria densa* Wall. is described. The anther wall is initially 4-layered. The tapetal cells are uninucleate. The microspore tetrads are isobilateral, linear, T-shaped and tetrahedral. At shedding the microspores are 2-celled. The ovules are anatropous, bitegmic and tenuinucellate. The development of the female gametophyte is of the Polygonum type. Double fertilization occurs, but the primary endosperm nucleus degenerates without any division. Development of the embryo corresponds to the Onagrad type. The mature embryo is undifferentiated. The seed coat is formed entirely from the outer layer of the outer integument. The pericarp consists of 10–13 layers of parenchymatous cells.

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Habenaria densa Wall. (Orchidaceae) is common in the temperate Himalayas between 1500 and 3000 m.

Leavitt (1901) reported peculiar characteristics of the suspensor in *Habenaria tridentata* and *H. blephariglottis*. Brown (1909), Swamy (1946) and Abe (1972) recorded the Polygonum type of embryo sac and Onagrad type of embryo in different species of *Habenaria*. The embryology of *Habenaria densa* has not been investigated previously.

The material of *Habenaria densa* was collected from Faggoo, Mahasu and Simla (all Simla District) during July to September, 1977. Formalin-acetic-alcohol was used as fixative and subsequently the material was stored in 70 % ethyl alcohol. Conventional methods of microtechnique were followed. The serial sections were cut at 7–10 μm and stained with safranin-fast green. The voucher specimen (OD-7) has been deposited in the Herbarium of Botany Department, Nagarjuna University, Nagarjunanagar, India.

Microsporangium, microsporogenesis and male gametophyte. The developing anther wall consists of epidermis, endothecium, one middle layer and tapetum (Fig. 1 A, B). The tapetum is glandular and its cells are uninucleate (Fig. 1 D). At maturity the anther wall comprises epidermis and endothecium with fibrous thickenings; the middle layer and tapetum disintegrate (Fig. 1 C).

The microspore mother cells (Fig. 1 B) undergo meiotic divisions. The microspore tetrads become isobilateral, linear, T-shaped and tetrahedral (Fig. 1 E–H). The tetrads remain together as massulae (Fig. 1 C). At maturity the cytoplasm of the pollen contains starch and the microspore has divided to form a small generative and a large vegetative cell (Fig. 1 C).

Megasporangium.

At anthesis numerous ovular primordia begin to develop on the forked parietal placentae (Fig. 5 C, D). The inner integument primordium appears just after the differentiation of female archesporium (Fig. 3 C). It grows and forms the micropyle at the 2-nucleate female gametophyte stage (Fig. 2 B–E). The outer integument differentiates later and grows beyond the inner one only after fertilization (Fig. 2 B–I). Both the integuments consist of two cell layers. The mature ovule is anatropous, bitegmic and tenuinucellate (Fig. 2 H). It lacks vasculature and the cells are transparent.

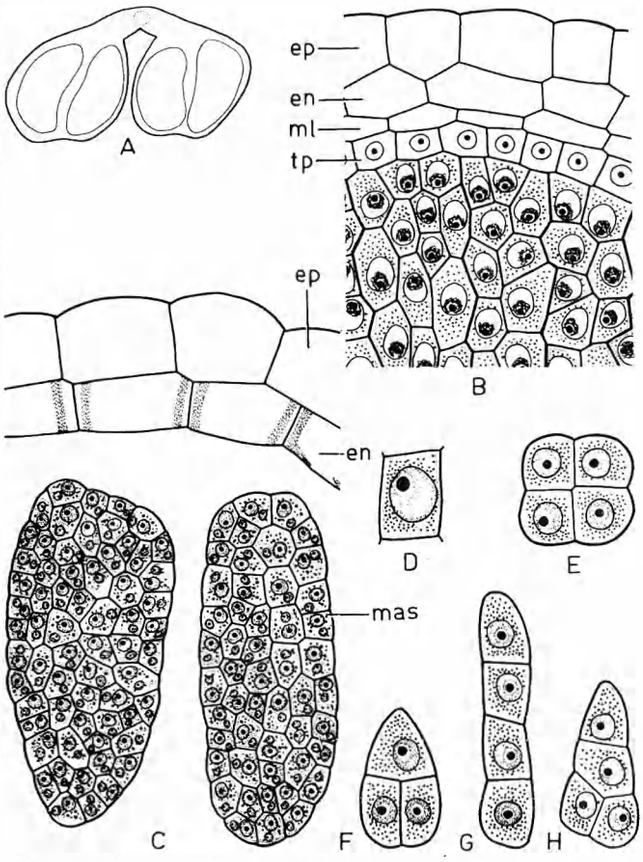

Fig. 1. Microsporangium, microsporogenesis and male gametophyte of *Habenaria densa*. – ep epidermis, en endothecium, mas massulae, ml middle layer, tp tapetum. – A: T. S. anther. – B: T. S. young microsporangium showing microspore mother cells and wall layers. – C: T. S., mature microsporangium showing massulae, fibrous endothecium and distended epidermal cells. – D: Tapetal cell. – E–H: Isobilateral, tetrahedral, linear and T-shaped tetrads. – A × 17, B, C × 180, D × 660, E–H × 410.

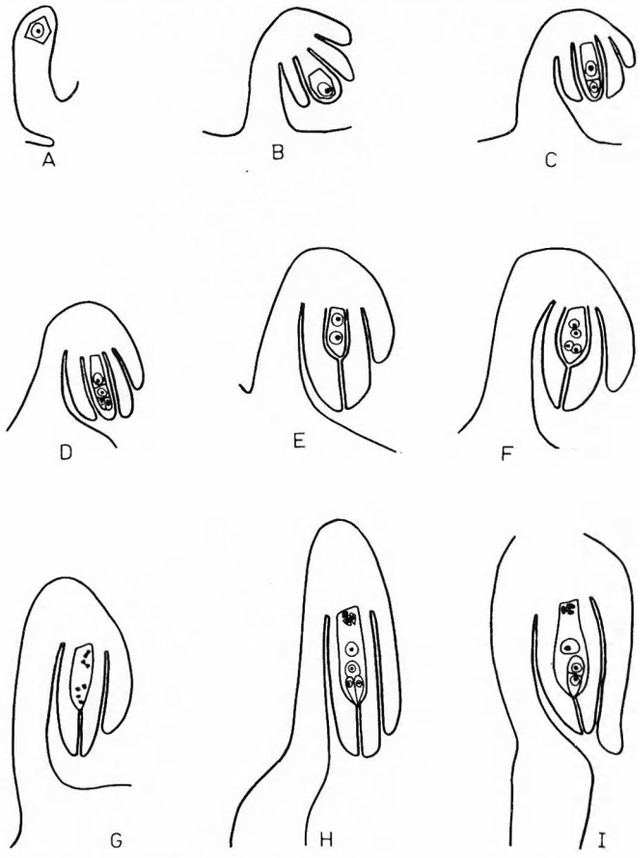

Fig. 2. L. S. ovules showing mode of curvature during growth and development of integument in *Habenaria densa*; ovule becomes completely anatropous at 2-nucleate embryo sac stage. × 150.

Megasporogenesis and megagametogenesis. The hypodermal archesporium is single-celled and functions directly as the megaspore mother cell (Fig. 3 A, C, D). However, a two-celled archesporium was once seen (Fig. 3 B). The micropylar dyad cell is smaller than the chalazal one (Fig. 3 E, F).

The chalazal dyad cell invariably undergoes the second meiotic division to give rise to two megaspores (Fig. 3 K–M). The micropylar dyad cell usually degenerates (Fig. 3 J); sometimes it undergoes the second meiotic division contributing in the formation of a T-shaped or linear tetrad (Fig. 3 H, I). Occasionally it fails to divide; thus a triad is formed of which the upper cell is diploid whereas the lower two are haploid (Fig. 3 G).

The chalazal megaspore is functional (Fig. 3 N, O). It undergoes three mitotic divisions (Fig. 3 P–S). The mature embryo sac consists of an egg apparatus, secondary nucleus and three antipodal cells (Fig. 3 T).

Fertilization and endosperm. The interval between pollination and fertilization is one to two days. The pollen tube enters the ovule through the micropyle. Double fertilization takes place (Fig. 4 A). The primary endosperm nucleus increases in size but it degenerates without any division (Fig. 4 C, E, F).

Embryo. The zygote (Fig. 4 B) divides by a transverse wall giving rise to the apical cell ca and the basal cell cb (Fig. 4 C). The cell cb divides transversely to form the middle cell m and the suspensor initial cell ci (Fig. 4 D, E). The cell ca undergoes a longitudinal division (Fig. 4 F). The proembryonal tetrad is thus T-shaped (Fig. 4 G).

The cells m and ci divide transversely to form a linear row of six or seven cells (Fig. 4 F–J). The

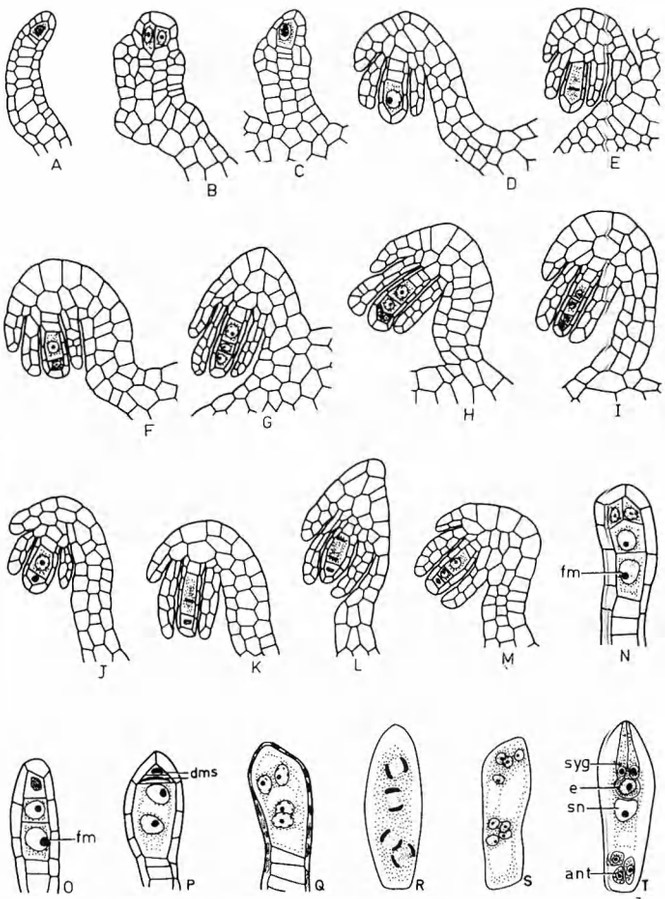

Fig. 3. Megasporogenesis and female gametophyte of *Habenaria densa*. – ant antipodals, dms degenerating megaspores, e egg, fm functional megaspore, sn secondary nucleus, syg synergid. – A, B: L. S, owular primordia showing one and two archesporial cells. –C: Enlarging megaspore mother cell. – D: Megaspore mother cell. – E: Meiosis I in megaspore mother cell. – F: Dyad with unequal cells. – G: Triad. – H, I: T-shaped and linear tetrad. – J: Dyad; note degenerated micropylar cell. – K, L: Dyad; the chalazal cell undergoing second meiotic division. – M: Triad showing two megaspores and degenerated micropylar dyad cell. – N, O: Functional megaspore. – P–S: Two-, 4- and 8-nucleate embryo sacs. – T: Mature embryo sac. – A–M × 160, N–T × 300.

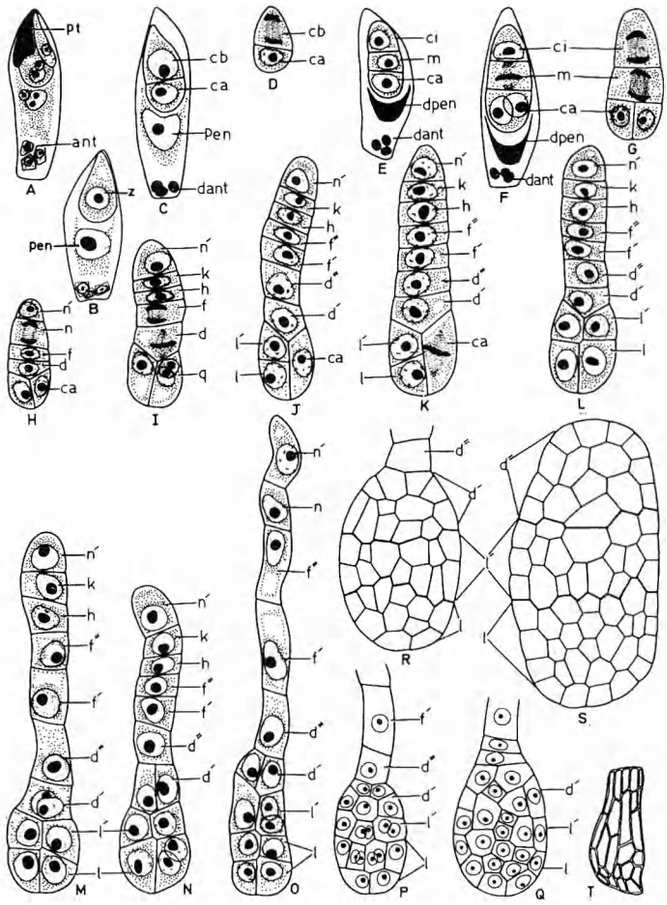

Fig. 4. Development of embryo in *Habenaria densa*. – ant antipodals, dant degenerating antipodals, dpen degenerating primary endosperm nucleus, pen primary endosperm nucleus, pt pollen tube, z zygote. – A: Double fertilization. – B: Fertilized embryo sac showing zygote and primary endosperm nucleus. – C: Two-celled proembryo. – D: Same; basal cell *cb* in division. – E: Three-celled proembryo; note the degenerating primary endosperm nucleus and degenerating antipodals. – F: Same; terminal and middle cells in division. – G: Four-celled, T-shaped embryonal tetrad with middle and suspensor initial cells in division. – H: Six-celled proembryo. – I: Nine-celled proembryo. – J–P: Stages leading to the formation of globular embryo. – Q–S: Later stages in embryogeny leading to the formation of mature embryo. – T: Mature seed. – A–O × 300, P–S × 160, T × 30.

derivative of the middle cell towards the chalaza (d) divides longitudinally to form two juxtaposed cells (Fig. 4 M, N). The two cells of ca undergo a longitudinal division at right angles to the first resulting in a quadrant q (Fig. 4 I). It divides transversely forming an octant of two tiers l and l' (Fig. 4 J–L). The cells of tier l divide transversely to form two sub-tiers (Fig. 4 N, O). Subsequently, through successive anticlinal and periclinal divisions in the cells of tier d', l' as well as in the sub-tiers of l, a globular and then a mature undifferentiated embryo results (Fig. 4 P–S). Thus, the mature embryo is formed from the derivatives of the terminal and middle cells. However, the terminal cell takes a greater share in the embryo organisation. A suspensor of five or six cells is formed from the derivatives of middle and suspensor initial cells (Fig. 4 G–J, M, O). The cells of the mature embryo contain starch.

The embryogeny in *H. densa* corresponds to the Onagrad type of Johansen (1950) or Group B

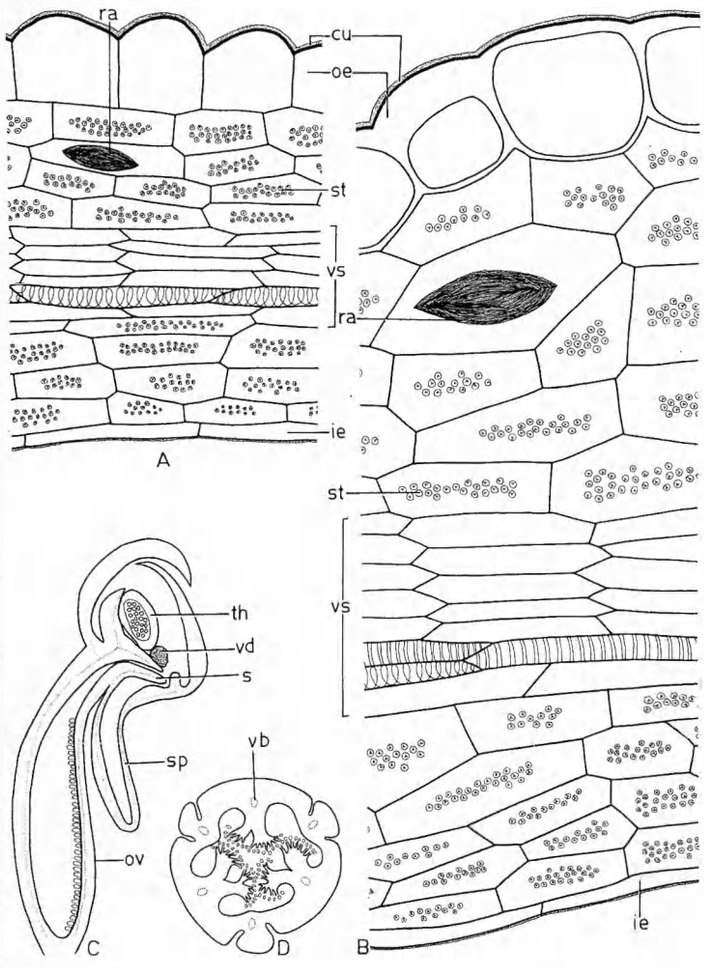

Fig. 5. Pericarp of *Habenaria densa*. – cu cuticle, ie inner epidermis, oe outer epidermis, ov ovary, ra raphides, s stigma, sp spur, st starch, th theca, vb vascular bundle, vd viscid disc, vs vascular supply. – A: L. S., ovary wall at megaspore mother cell stage. – B: L. S., pericarp of maturing fruit. – C: Median L. S. of flower. – D: T. S. ovary. – A, B × 200, C × 1, D × 20.

type of Swamy (1949). Leavitt (1901) reported in *Habenaria tridentata* and *H. blephariglottis* that from each of the six or seven suspensor cells, haustorial branches arise which elongate and embed into the tissue at the base of the funiculus. Although in *H. densa* the terminal cell of the suspensor embeds into the tissues of the funiculus, it does not seem to function as a haustorium.

Seed and seed coat. The thickened central portion of the seed (Fig. 4 T) contains the embryo. The surrounding portion of the seed is wing-like. The inner integument and the inner epidermis of the outer integument degenerate after fertilization. The mature seed coat is formed entirely by the outer epidermis of the outer integument which contains vertically elongated, thick-walled, transparent cells (Fig. 4 T).

Pericarp. The ovary wall is before fertilization made up of 10–13 layers of thin-walled parenchymatous cells with raphides and starch (Fig. 5 A). Vascular supply extends through the middle layers of the ovary. After fertilization the cells of the outer epidermis become thick-walled and strongly cutinised (Fig. 5 B).

Acknowledgements. We are greatly indebted to Professor Olov Hedberg, Uppsala, for his kind interest in this study. One of us (SKS) is grateful to the Council of Scientific and Industrial Research, New Delhi, India for financial assistance.

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A new species of Supushpa (Acanthaceae) from India

S. R. Paul

Paul, S. R. 1979 05 15: A new species of Supushpa (Acanthaceae) from India. *Bot. Notiser 132:* 149–150. Stockholm. ISSN 0006-8195.

Supushpa khoshooana Paul, sp. nov., from Netarhat, Bihar State, India, is described.

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Supushpa khoshooana Paul, sp. nov – Fig. 1

Affinis *Supushpae scrobiculatae* (Dalz. ex Clarke) Surynarayanae (plantae Ghat Occid. endemicae), sed differt foliorum ovata vel elliptici-ovata, 2.8–3.5 cm longa et 1.7–2.5 cm lata, basi paullo inaequilateralis, marginibus serratis, pagina supra obscure-viridi, hispida et ob pilorum tuberculos basilares rugosa; calyx profunde incisis, 4–8 mm longus et bracteolibus destitutis.

Typus: India, Bihar, Distr. Palaman, locis apricis Netarhat Plateau, ca. 1200 m, 19.12.1971, S. R. Paul 82317 (K holotypus CAL, LWG, PUNE isotypii).

Isophyllous, branched shrub up to 160 cm. *Stems* and branches densely villous, grey-brownish with scars of fallen leaves and branches; internodes 2.5–4 cm. *Leaves* petiolate; petioles 2.5–5 cm, terete; blade ovate to elliptic-ovate, 2.8–3.5 × 1.7–2.5 cm, base somewhat asymmetrical, apex slightly acuminate, margins serrate; upper surface dark green, hispid, rugose with tubercle-based hairs; lower surface light greenish with prominent midrib and 6–8 pairs of ascending lateral nerves. Inflorescences generally borne on the leafless parts of the stems and branches, axillary, pedunculate, of 3–6 bracteate flowers in a spike. *Bracts* 5.5–7 × 1.8–2.4 mm, dark green, persistent, densely hairy especially on the margins, with a distinct midrib one or two pairs of less conspicuous lateral nerves. Flowers generally solitary at the nodes of the rachis; bracteoles O. *Calyx* 4–8 mm, 5-partite; lobes linear with a distinct midrib, deeply incised, light greenish, densely hairy. *Corolla* 9–16 mm; tube white, 9–11 mm; throat slightly campanulate, purplish-blue, rugula 5–8 mm long; lobes 5 unequal, oval, 3–5 mm long, generally deeply grooved up to the middle of the tube, margins recurved. *Stamens* 4, didynamous, included, filaments united with the corolla tube, hairy; anthers dorsifixed, greenish-white, 1.5–2.5 mm, longitudinally dehiscent. *Pollen* ellipsoidal, c. 40 μm long, with septate bands meeting at the poles. *Ovary* glabrous, ovoid, greenish, 2-ovuled. Style 9–12 mm, greenish-white, hairy. Stigma laterally flattened, 1–1.2 mm. Mature capsule and seeds not known.

I am pleased to dedicate this species to Dr Triloki Nath Khoshoo, Lucknow, who initiated me in taxonomic research.

Acknowledgements. I am indebted to Professor C. E. B. Bremekamp, Netherlands, Dr R. K. Brummitt, Kew, England, and to Mr M. C. Suryanarayana, Poona, India, for their helpful comments. Dr A. K. Skvortsov, Moscow, prepared the Latin diagnosis.

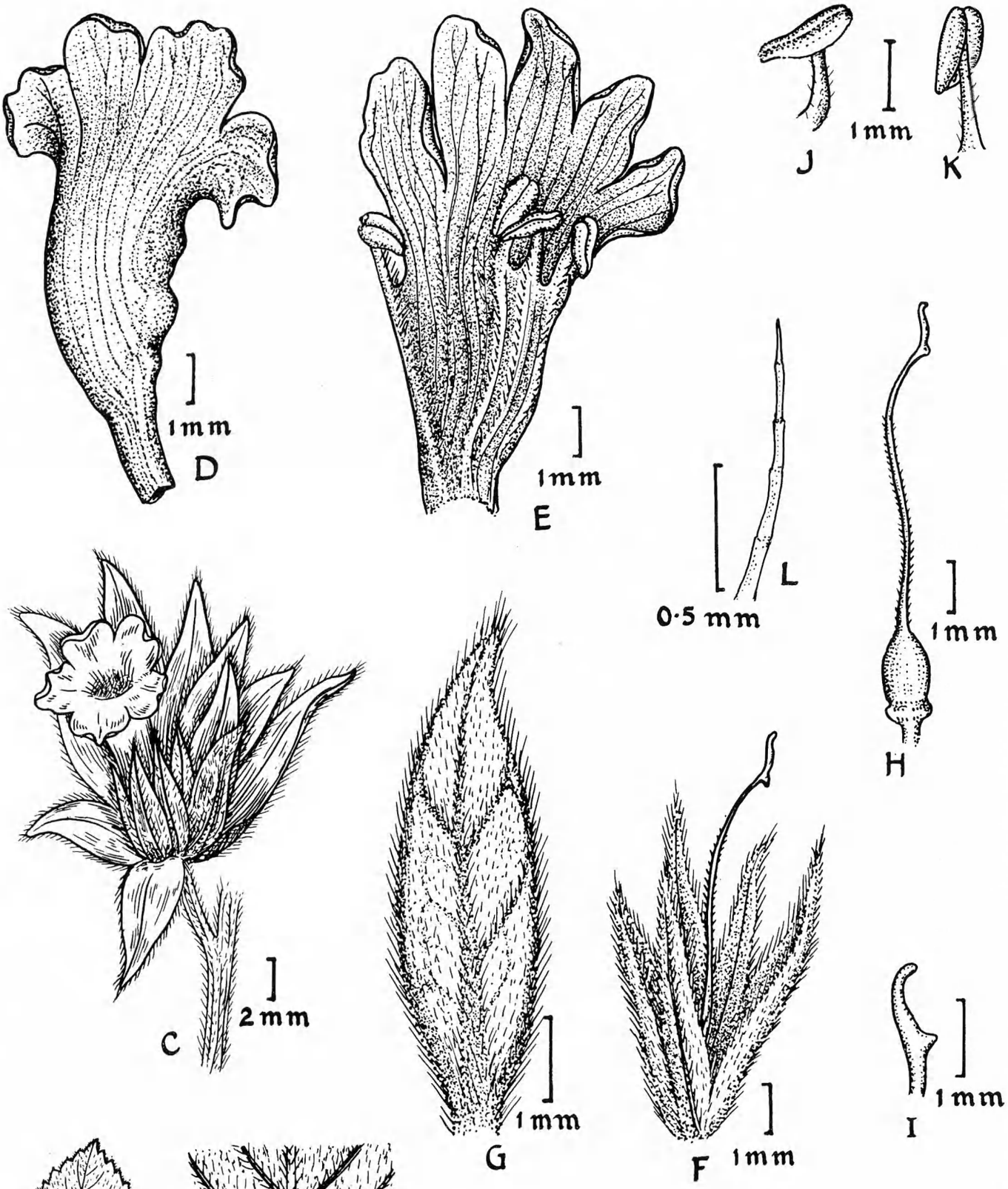

Fig. 1: *Supushpa khoshooana* Paul 82317-B (LWG). – A: Leaf. – B: Detail, lower side of leaf. – C: Portion of inflorescence. – D–E: L.S., flower. – F: Calyx. – G: Bract. – H: Pistil. – I: Stigma. – J–K: Anther. – L: Hair from bract.

Culture studies on the brown algae Halothrix lumbricalis and Elachista fucicola (Elachistaceae)

Poul Møller Pedersen

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The life history of *Halothrix lumbricalis* (Kütz.) Reinke (material from Denmark) has been investigated under various culture conditions. Swarmers from the plurilocular sporangia germinate without copulation into sterile prostrate systems from which develop new erect filaments again bearing plurilocular sporangia. Unilocular sporangia are absent both in nature and in culture. The taxonomic position is discussed with special emphasis on the idea that this species may be derived from a dictyosiphonalean type of brown alga. Several Greenland clones of *Elachista* have been studied in culture, three of them started from plants which showed the morphological features of *Elachista lubrica* Ruprecht. In all the clones swarmers from the unilocular sporangia germinate into prostrate, uniseriate, branched systems, which later under one set of culture conditions form plurilocular sporangia extensively. The morphology of this fertile prostrate system differs from that described for European *E. fucicola* (Vell.) Aresch. In spite of this the Greenland plants are considered conspecific with *E. fucicola*. Chromosome counts give an approximate number of eight.

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Halothrix lumbricalis (Kütz.) Reinke has a rather wide geographical distribution, but seems to be rare judged from the information in literature (Reinke 1889, Kuckuck 1929, Rosenvinge 1935, Hamel 1935, Taylor 1957, Parke & Dixon 1976, Rueness 1977). It occurs in the spring, most often on leaves of *Zostera*.

The life history of *H. lumbricalis* is unknown and as this species represents a somewhat aberrant type within the Elachistaceae, it is relevant to compare its morphological and developmental characters with other representatives of the family.

Elachista fucicola (Vell.) Aresch. is widely distributed and very common in the North Atlantic. *Elachista lubrica* Ruprecht, also commonly reported in the same area as an epiphyte on *Halosaccion ramentaceum,* has been considered a synonym by many authors following Rosenvinge (1893). Jaasund (1960), however, separated the two taxa at the generic level and formed the new combination, *Myriactula lubrica* (Ruprecht) Jaasund.

European isolates of *E. fucicola* have previously been studied in culture by Kylin (1937), Kornmann (1962), Blackler & Katpitia (1963), and Koeman & Cortel-Breeman (1976). The development of a North American isolate provisionally identified as *E. lubrica* was reported by Edelstein, Chen & McLachlan (1971).

In the present study the Greenland plants growing on *Chordaria flagelliformis* had typical *E. lubrica* morphology: spatula-shaped young assimilating filaments, and structures which resembled plurilocular sporangia. Further, two clones were isolated from plants growing on *Halosaccion,* and one showed none of these characters. Consequently, the material offers an opportunity for a comparison between different Greenland clones and the clones described in literature.

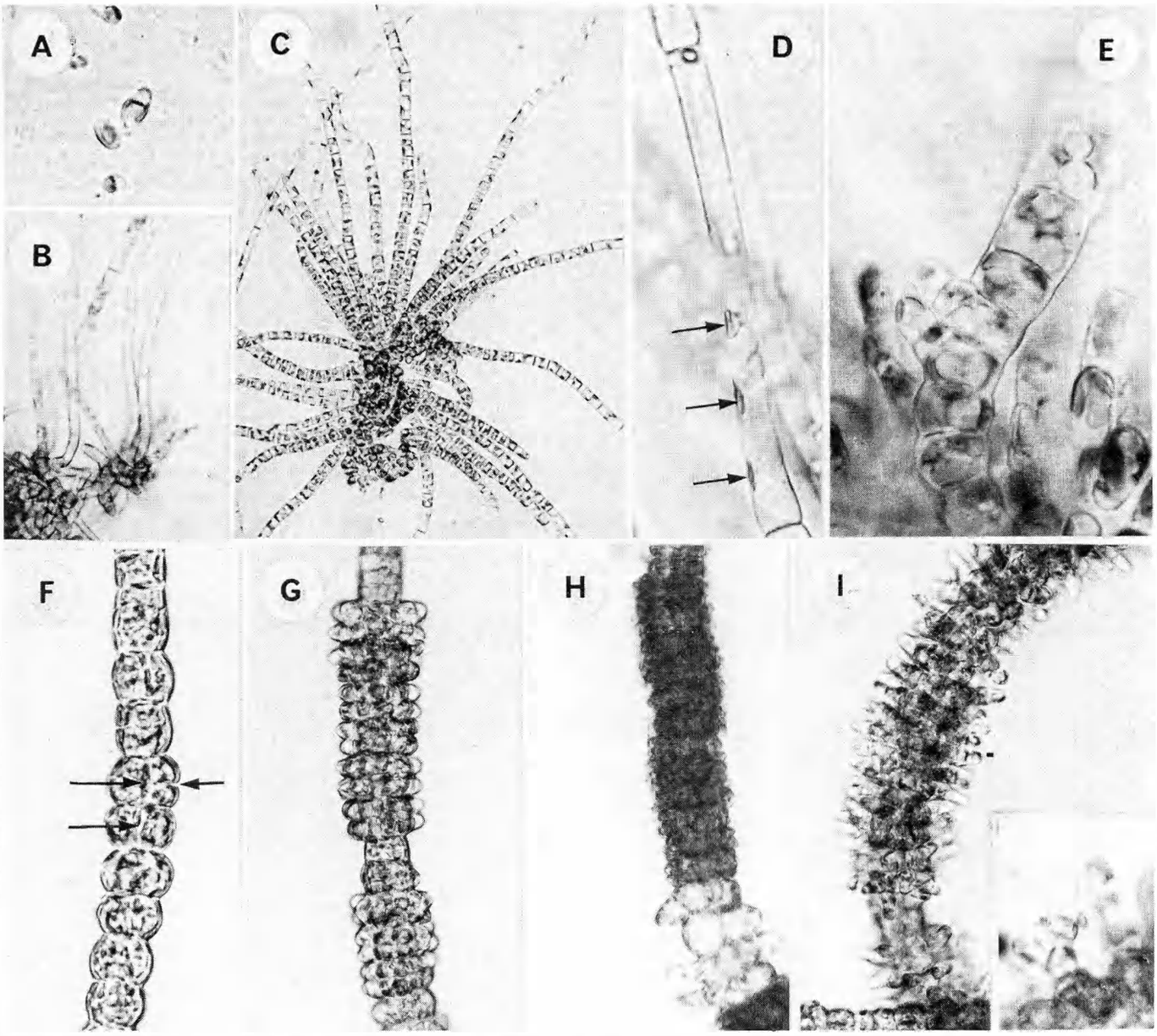

Fig. 1. *Halothrix lumbricalis* in culture. – A: Germinating swarmer. × 600. – B: Prostrate systems with erect hair-like filaments. × 200. – C: Young plant with hair-like apical parts. × 150. – D: Long, hyaline cell containing chloroplasts (arrows). × 600. – E: Basal part of erect filament with two short laterals. × 600. – F: Longitudinal and transverse divisions (arrows) are the initial stages in development of sporangia. × 500. – G: Further development of sori. × 300. – H: Sori of short sporangia like those observed in nature, separated by a sterile, parenchymatous part. × 150. – I: Sorus of long, uniseriate plurilocular sporangia. × 300. – Inserted figure: Branched sporangial branch. × 600.

Material and methods

Halothrix lumbricalis with plurilocular sporangia was found on *Zostera* leaves collected by L. Mathiesen at Skødshoved, Kalø Vig, Denmark on 22 April 1976.

Six clones of *Elachista* from Greenland have been studied. Two were established by isolating unilocular sporangia from plants growing epiphytically on *Halosaccion ramentaceum,* collected near the Fishery Station, Godthåb, on 4 August 1973. Three originate from plants growing on *Chordaria flagelliformis,* collected in a littoral pool S of the above locality on 8 August 1973, and one from a crude culture of *Rhodomela lycopodioides* collected at Apigajûp qáqâ, Kanajutsiat, Godthåb Nordland on 17 August 1973, at a depth of about 0.25 m. Unialgal cultures were obtained by pipetting germlings, and germanium dioxide added to the medium, Provasoli's ES (cf. Nielsen 1972), to prevent growth of diatoms in the initial cultures. The light source was Philips fluorescent tubes TL MF 29. For *Halothrix* the following sets of culture conditions were used: (1) 30 ‰ S, 1.7 klx, 4°C, 16 h light/8 h dark (LD); (2) 20 ‰ S, 1.7 klx, 4°C, LD; (3) 10 ‰ S, 1.7 klx, 4°C, LD; (4) 30 ‰ S, 2.5 klx, 5°C ± 2.5°C, 8 h light/16 h dark (SD); (5) 30 ‰ S, 700 lx, 15°C, LD; (6) 30 ‰ S, 2.5 klx, 15°C, LD. For *Elachista* sets 1, 4

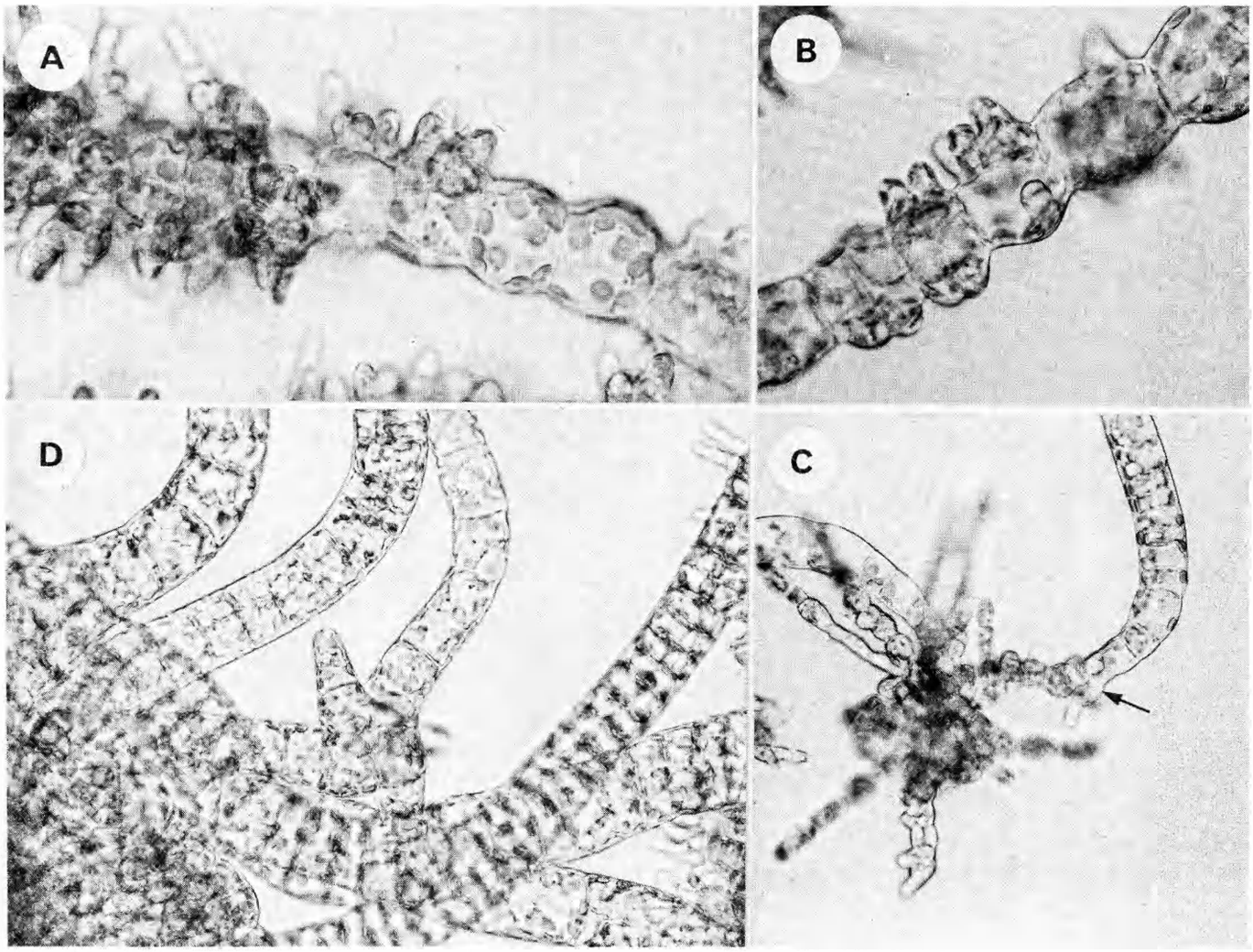

Fig. 2. *Halothrix lumbricalis* in culture. – A, B: Assimilating filaments developed under culture condition 5, showing incompletely developed sori and barrel-shaped cells. × 500. – C: Basal part of assimilating filament showing the meristem and hypomeristematic rhizoidal filament (arrow). Culture condition 5. × 300. – D: Regeneration of assimilating filaments. × 300.

and 6 were used, in set 1 with a slightly lower light intensity (1.5 klx); in addition *Elachista* cultures were subjected to (7) 30 ‰ S, 440 lx, 4°C, LD.

Culture material of *Elachista* was fixed and stained using a modified Feulgen technique devised by Olson & Fuller (1971) with the following deviations from the original description (Olson, pers. comm.): fixing for 30 min., rinsing in two changes of distilled water. After Schiff's reagent, the preparations were rinsed rapidly in 7–10 changes of deionised water instead of sulphurous acid bleach.

Preserved material of the plants is kept at the Botanical Museum (C) and the cultures are maintained at Institut for Sporeplanter.

Halothrix lumbricalis

The swarmers from the plurilocular sporangia germinate unipolarly (Fig. 1 A) and form a densely branched pseudoparenchymatous basal system, which is sterile under all conditions tested.

Erect filaments develop from several initial cells in the basal system. In crowded cultures the erect filaments consist of long hyaline cells (Fig. 1 B) which resemble hairs; Fig. 1 D shows, however, that this interpretation is incorrect as the cells contain disc-shaped chloroplasts (arrows) like normal vegetative cells. In uncrowded cultures the young erect filaments are short-celled and uniseriate, but with a tendency to form hair-like apical parts (Fig. 1 C), depending on nutritional conditions. The youngest erect thalli show diffuse, intercalary growth, and the meristem is only clearly visible at a later stage of development. Few-celled unbranched laterals from the basal part of the erect filaments (Fig. 1

Fig. 3. Part of prostrate system of *Elachista fucicola* from Greenland with empty plurilocular sporangium. Culture condition 1.

E) have been observed, but no branched structures, such as those described on material from nature. The laterals were called hypomeristematic by Kuckuck (1929), but in this investigation they developed from the meristematic cells. Before formation of sporangia the erect filaments are divided longitudinally (Fig. 1 F, arrow). The cells thus produced are further subdivided into smaller units and each cell along the surface finally functions as a sporangium mother cell. Periclinal divisions in these mother cells form collar-like sori of plurilocular sporangia separated by uniseriate or parenchymatous, sterile parts (Fig. 1 G, H). In culture the sporangia may be morphologically like those on plants from nature (Fig. 1 H), but more often they become elongated into short uniseriate filaments (Fig. 1 I), in a few cases with laterals (Fig. 1 I, inserted). The described development takes place under all conditions except 3 and 5.

The reduced light intensity of condition 5 is important in the development of the assimilating filaments (compared with condition 6). In this case the thallus consists mainly of well-developed, sterile prostrate systems. Only relatively few erect filaments are formed, and they always have an aberrant morphology. The cells are barrel-shaped and the sori incompletely developed (Fig. 2 A, B). Hypomeristematic rhizoidal branches occur (Fig. 2 C, arrow). Also in the assimilating filaments branching may occur (Fig. 2 D), probably as a result of damages, which cause regeneration of new assimilating filaments from near-by cells like in *Elachista*.

The reduction to 20 ‰ S under condition 2 had no apparent influence. Further reduction to 10 ‰ S under condition 3 caused incomplete development of the sori as under condition 5.

Elachista fucicola

Under culture conditions 1 and 7 the swarmers from the unilocular sporangia germinate into uniseriate, branched systems without hairs and with only 1–2 chloroplasts per cell. These plants develop plurilocular sporangia extensively by transformation of laterals or parts of laterals (Fig. 3, see also Pl. 4 G in Pedersen 1976). Isolation of fertile, prostrate systems resulted in new prostrate systems. Copulation of swarmers was never observed.

New assimilating filaments develop from sterile or fertile basal systems with a clear physical connection between the two phases (Fig. 4 A–C). A distinct meristem is absent in the youngest assimilating filament (Fig. 4 D), but soon becomes differentiated. Also hypomeristematic laterals are visible at an early stage of development (Fig. 4 B, arrows), and subsequent development shows these laterals to be responsible for formation of new erect filaments, paraphyses, and unilocular sporangia, the laterals now being united into the characteristic medulla.

In crowded cultures the cells in the apical parts of the assimilating filaments are rather long and hyaline, thus resembling true hairs. This similarity is, however, only superficial as the cell contain chloroplasts.

Sporangia-like structures in the assimilating filaments were not observed in culture although three clones have been started from material in which such structures were present (Fig. 5 A, B). Divisions of another type and function have, however, been observed; either a longitudinal division (Fig. 5 C); or two cells are partly separated, after which one or both regenerate

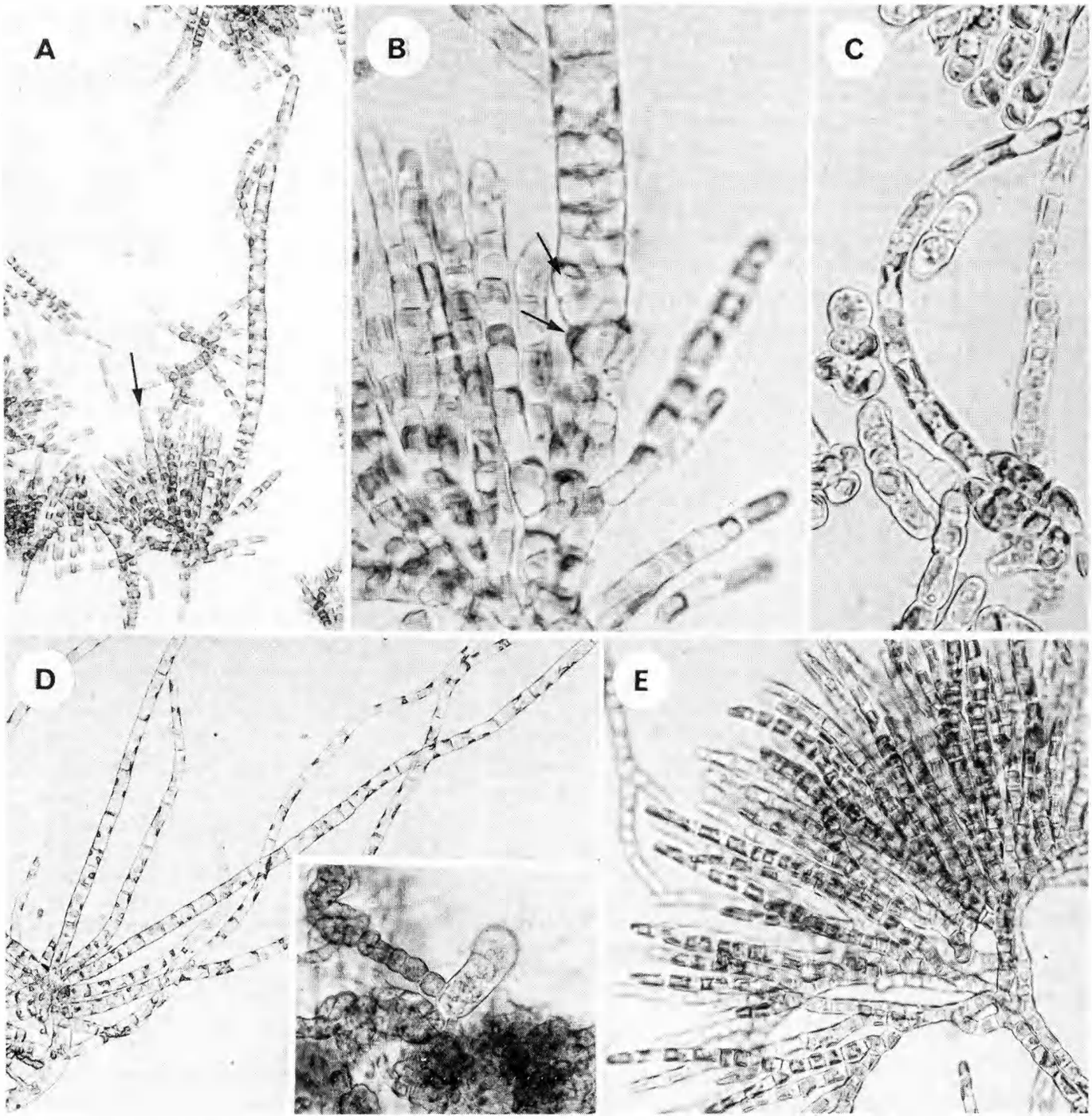

Fig. 4. *Elachista fucicola* from Greenland im culture. – A: Young assimilating filament from prostrate system with mature plurilocular sporangium (arrow). × 150. – B: The same at higher magnification showing physical connection between the two phases and the initial hypomeristematic branching (arrows). × 600. – C: Part of prostrate system with empty plurilocular sporangium and initial erect filament. × 600. – D: Young macrothallus with rather long-celled apical parts. Note that the meristem is not clearly differentiated. × 150. – Inserted figure: Unilocular sporangium or unilocular sporangium-like structure developed from pseudoparenchymatous, prostrate system under condition 6. × 300. – E: Well-developed sterile, prostrate system developed under condition 2. × 300.

new assimilating filaments (Fig. 5 C, D). These undergo the previously described differentiation and develop into young plants on the older one (Fig. 5 E).

Short day conditions, under which the species has been cultivated through a period of more than two years, have a marked effect on the development. There is no formation of plurilocular sporangia on the basal system, but vegetative growth continues, thus leading to formation of

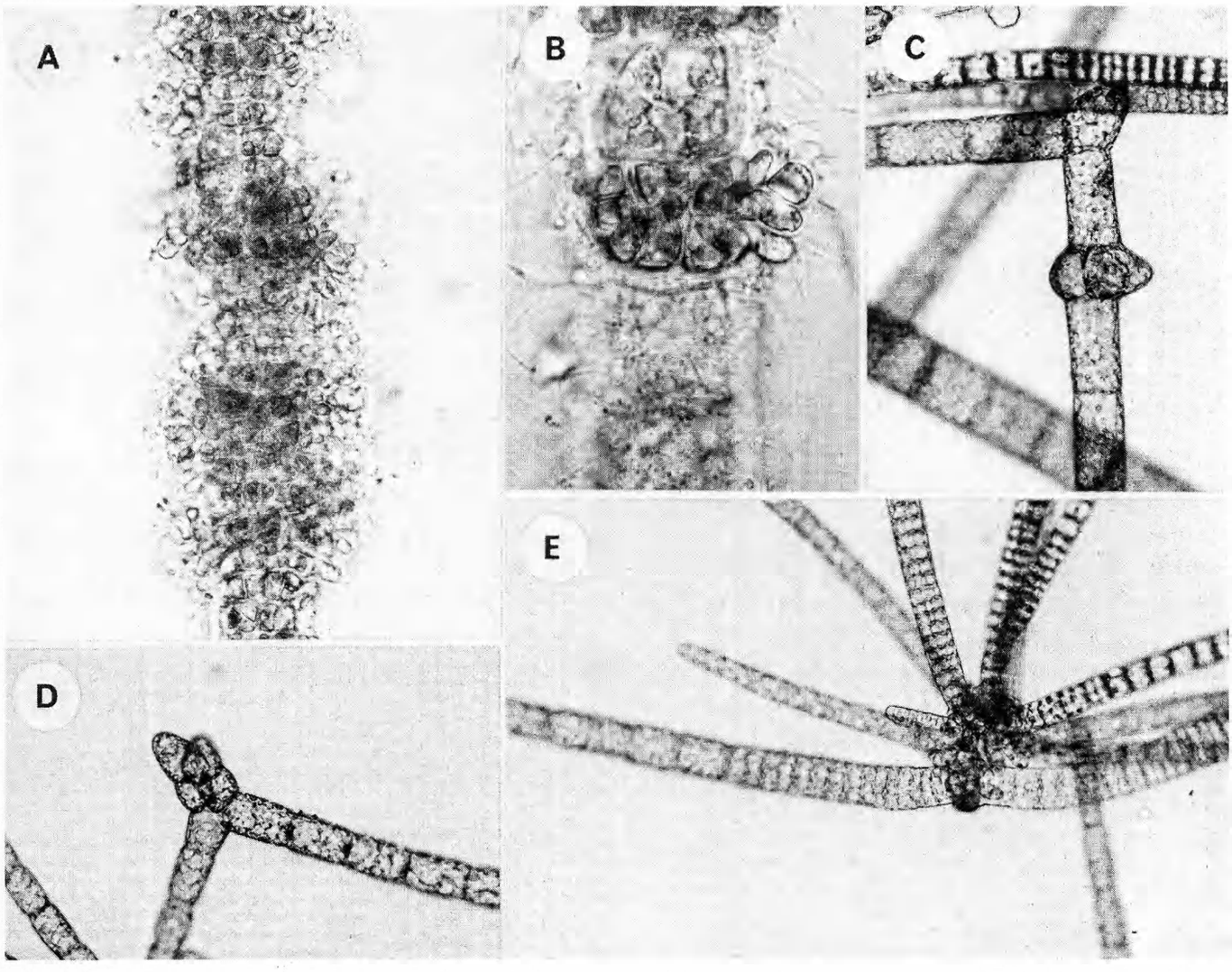

Fig. 5. *Elachista fucicola* from Greenland, in nature (A–B) and in culture (C–E). – A: Divisions in assimilating filament (often interpreted as plurilocular sporangia). × 300. – B: Similar divisions; the plant is densely covered with filamentous blue-green algae and bacteria. × 600. – C: Longitudinal division and regeneration from one of partly separated cells. × 150. – D: Regeneration of two initial filaments from partly separated cells. × 150. – E: Young plant formed by regeneration from assimilating filament. × 150.

cushion-shaped plants of uniseriate, branched filaments (Fig. 4 E). Transfer of such prostrate systems from SD to LD conditions resulted in formation of plurilocular sporangia within 26 days. A few macrothalli developed from the sterile basal systems and reached fertility, but growth was much slower than under LD conditions.

Temperature also affects the development. When prostrate systems with plurilocular sporangia were transferred from condition 1 to condition 6, swarmers from these germinated to form pseudoparenchymatous prostrate systems; when these systems grew older it became virtually impossible to discern separate filaments. Plurilocular sporangia were never found, but a few unilocular sporangia or unilocular-like structures formed by swelling and subdivision of a cell in the basal system were observed (Fig. 4 D, inserted). These cells were not seen to empty their content nor were any germlings formed in cultures under these conditions. Assimilating filaments occurred rarely and remained at an initial stage of development.

Chromosome counts have been made on cultivated plants in both the prostrate systems (cells in plurilocular sporangia), and the erect parts (cells in assimilating filaments and paraphyses). Attempts to count the chromosomes in the unilocular sporangia were unsuccessful due to density of nuclei. As usual in brown algae chromosome counts were difficult due to the

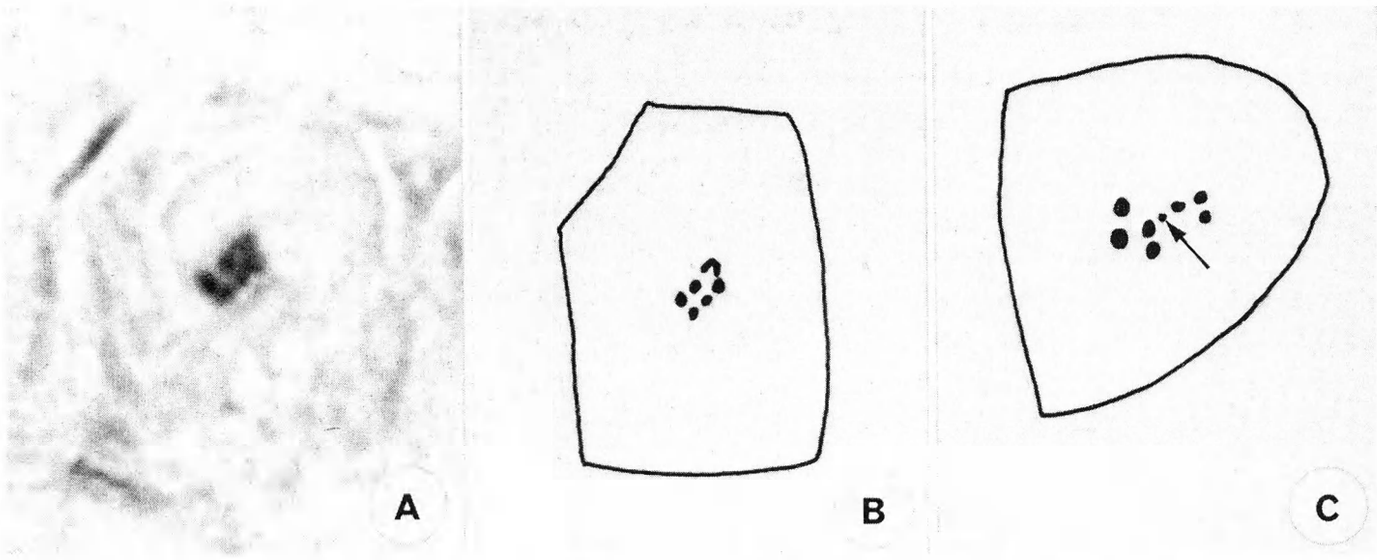

Fig. 6. Chromosomes of cultivated *Elachista* from Greenland. – A: Meristematic cell in an assimilating filament showing at least 6 chromosomes. × 3000. – B: Interpretation of the same cell. – C: Interpretation based on 5 photographs in different focal levels of an apical cell of a paraphysis showing 7–8 chromosomes. The questionable chromosome is indicated by an arrow.

small chromosomes, which are tightly packed in the metaphase. In one clone (G 115) prometaphases were found which are suitable for photographic reproduction. Fig. 6 A shows at least 6 chromosomes in a meristematic cell of an assimilating filament. Fig. 6 B is an interpretation of the same cell, while Fig. 6 C is an interpretation showing 7–8 chromosomes in an apical cell of a paraphysis. Other counts give approximately the same numbers.

Discussion

The growth and development of *Halothrix lumbricalis* under the various culture conditions used in this study show the species to be euryhaline and eurythermal, and this is in agreement with the seasonal and geographical distribution in nature. The results obtained under condition 5 suggest that the species is sensitive to reduced light intensities. This may explain why *Zostera* leaves, a relatively open habitat, is the normal substratum, while *H. lumbricalis* is absent from boulders and stones at similar depths perhaps due to increased competition for light in such places.

Within the Elachistaceae there seems to be a development away from formation of sporangia on the erect filaments, as represented by the series *Leptonematella fasciculata* – *Elachista stellaris* – *Elachista fucicola*. This runs parallel with development of a meristem and hypomeristematic branching. With regard to formation of sporangia *Halothrix* seems to find a position among unspecialized members of the family, e.g. *Leptonematella fasciculata,* being, however, more advanced in the presence of a meristem and meristematic branching. These branches remain poorly developed and a compact medulla like in *E. fucicola* is absent. That *Halothrix* is a simple elachistacean type is further supported by the fact that the erect parts are parenchymatous before sporangia formation. I have previously suggested (Pedersen 1978) that *Leptonematella* may be derived from the *Pogotrichum* type (Dictyosiphonales) of plant. I consider *Halothrix* as another example on this type of evolution.

Since they were combined by Rosenvinge (1893), *E. fucicola* and *E. lubrica* have always been regarded to be conspecific in papers on marine algae from Greenland. The treatment by authors reporting on material from other parts of the distribution area varies. Jaasund (1960) separated the two taxa at the generic level by transferring *E. lubrica* to the genus *Myriactula* because he found hairs on a myrionematoid stage which was physically connected to the macrothallus. Further differential characters were mentioned by Jaasund, the most important of which is the presence of divisions in the assimilating filaments. These have previously

Fig. 7. Map of the northern part of the Atlantic showing the total number of plants used as substratum by *E. fucicola* (upper number). The number of fucoids (lower number) is separated from the total. In E Greenland fucoids are absent in the part investigated so far.

been reported by Rosenvinge (1893), Jónsson (1904), Kuckuck (1929), Lund (1959) and Pedersen (1976), and are usually interpreted as plurilocular sporangia.

True hairs have not been observed in culture, only hair-like structures, which, however, are long-celled vegetative filaments as they contain chloroplasts (cf. Pedersen 1976, Pl. 4 I). Such filaments occur in crowded cultures, probably as a response to the nutritional conditions of the medium. Similar filaments have also been observed in other representatives of the Elachistaceae, e.g. *Halothrix* (cf. Fig. 1 C) and *Leptonematella fasciculata* (Pedersen 1978).

When Jaasund wrote his paper the presence of plurilocular sporangia on the basal system appeared a reliable character by which *E. lubrica* and *E. fucicola* could be distinguished. Kylin (1937) reported direct development of swarmers from the unilocular sporangia of *E. fucicola* without seeing sporangia on the prostrate systems. The absence of plurilocular sporangia on the plants provisionally identified as *E. lubrica* by Edelstein, Chen & McLachlan (1971) may be explained by the temperature used in their experiments (13°C). Kornmann (1962), however, showed that *E. fucicola* at low temperatures, 3–4°C, develops plurilocular sporangia on its prostrate systems, and this report was later confirmed by Koeman & Cortel-Breeman (1976) working on Dutch material. The validity of another character, the shape of the young assimilating filaments, has been questioned by Lund (1959). Divisions of some cells in the assimilating filaments in *E. lubrica* but not in *E. fucicola* is the last important distinctive feature. Such divisions have never been observed in culture, and investigations on material from nature have not shown any reproductive function, as empty cells were never seen. Lund (1959) called them abortive sporangia. The divisions seen in culture lead to formation of new assimilating filaments, and such divisions occur in nature in both European and Greenland material (Rosenvinge 1935, Lund 1959). I am not able to explain the sporangia-like divisions fully. It is, however, known that *Sarcinastrum urosporae* Lagerheim may cause aberrant divisions in *Pilayella littoralis* (L.) Kjellm. (Pedersen 1973). The filaments of *Elachista* are densely covered with bacteria and blue-green algae (cf. Fig. 5 B), one or more of which may possibly have a similar effect.

In conclusion, the major characters used to separate *E. lubrica* from *E. fucicola* seem to be of minor value. The only morphological difference concerns the basal plurilocular sporangia. In the European material these have few, large loculi, while in the material from Greenland they are siliquose with smaller loculi (compare Fig. 4 in Kornmann (1962) with Fig. 3 and Fig. 4 A, C in the present paper). This difference in loculus size results in differently sized swarmers.

Two biological differences also exist: Koeman & Cortel-Breeman (1976) found that unilocular sporangia were absent at 4°C, but present abundantly at 16°C. The material from Greenland is exactly opposite. The number of plant species used as substratum also is very different in various populations. Fig. 7 shows a decrease from 25 species of host algae (besides animals and rocks) in Greenland to 3 fucoids and more rarely two other algae in Denmark. This, together with the morphological difference of the fertile basal systems, suggests a genetic variation, but hardly justifies a separation on the species level.

A comparison of the chromosome counts on European material of *E. fucicola* and those presented here is inconclusive. Blackler & Katpitia (1963) and Russell (1971), working on

material from Britain, reported 9–10 and 24 chromosomes, respectively, in unilocular sporangia. Koeman & Cortel-Breeman (1976) in Dutch material observed 20–24 chromosomes in all structures except a few germlings developed from swarmers from a unilocular sporangium. Most of these counts are higher than in the present material. The geographical distribution of the various clones is unknown, but it is not unlikely that some overlap occurs, which may explain the low number observed by Blackler & Katpitia (1963). Variation in the ploidy level within the distribution area, but without any visible morphological effect on the sterile thallus, is also known for other marine algae, e.g. *Plumaria elegans* (Bonnem.) Schmitz (Drew 1939) and *Isthmoplea sphaerophora* (Harv.) Kjellm. (Rueness 1974, Pedersen 1975).

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Adenanthellum nom. nov. (Compositae-Anthemideae)

Bertil Nordenstam

Nordenstam, B. 1979 05 15: Adenanthellum nom. nov. (Compositae-Anthemideae). *Bot. Notiser 132:* 160. Stockholm. ISSN 0006-8195.

The new generic name *Adenanthellum* B. Nord. is proposed to replace the illegitimate *Adenanthemum* B. Nord.

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After my new South African genus *Adenanthemum* B. Nord. was published (Nordenstam 1976), I discovered the existence of an earlier generic homonym, viz. the fossil saxifragaceous genus *Adenanthemum* Conwentz (1886). The South African plant thus requires a new name. Additional studies have recently been made on plants kindly provided by Dr O. M. Hilliard, Pietermaritzburg, and grown in Stockholm. These produced long subterranean runners, which apparently provide an effective means of vegetative propagation, a hitherto unrecorded observation.

Adenanthellum B. Nord., nom. nov.

Adenanthemum B. Nordenstam 1976 p. 157, nom. illeg., non Conwentz 1886 p. 91. – Typus generis: *Adenanthellum osmitoides* (Harv.) B. Nord.

Adenanthellum osmitoides (Harv.) B. Nord., comb. nov.

Basionym: *Chrysanthemum osmitoides* Harvey 1863 p. 33 – Syn.: *Adenanthemum osmitoides* (Harv.) B. Nordenstam 1976 p. 158, nom. illeg.

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Zur Gattung Chrysolykos Mack

Arnold Nauwerck

Nauwerck, A. 1979 05 15: Zur Gattung Chrysolykos Mack. [On the genus Chrysolykos Mack.] *Bot. Notiser 132:* 161–183. Stockholm. ISSN 0006-8195.

On the basis of measurements of morphological variation and appearance at different environmental conditions, and observations of different kinds of reproduction, the genus *Chrysolykos* Mack 1951 is revised. The genus *Chrysoikos* is included in *Chrysolykos*. Members of the genus are shown to be morphologically very plastic. Environmentally induced heterauxis may be found as well as changed lorica shape in rudimentary alternation of generations. The following species and varieties are accepted: *C. skujae, C. angulatus* and *C. planctonicus* with the var. *planctonicus,* var. *recticollis,* var. *hamulatus* and var. *allabardiformis. C. calceatus* and *C. complanatus* need further investigation. They may belong to other genera.

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Aus einem Teich bei Wien beschrieb Mack (1951) eine neue Chrysomonadengattung *Chrysolykos* mit der vorläufig einzigen Art *Chrysolykos planctonicus* Mack. Einige Jahre später fand ich in nordschwedischen Hochgebirgsseen eine *Chrysolykos* ähnliche Art, die ich der Meinung meines Lehrers Heinrichs Skuja folgend zur Gattung *Diceras* Reverdin stellt und ihm zu Ehren *Diceras Skujai* Nauwerck benannte (Nauwerck 1955). Kurz nach Erscheinen der Beschreibung äusserte Kuno Thomasson (mündl.) die Ansicht, dass es sich bei der Art eigentlich eher um einen *Chrysolykos* handeln müsse. Diese Ansicht vertraten auch Juriš (1956) und Bourrelly (1957). Durch Bourrelly wurde die Art in *Chrysolykos Skujai* (Nauwerck) Bourrelly umbenannt. Skuja (1964) hingegen hielt an seiner ursprünglichen Auffassung fest und behält die Art als *Bitrichia Skujai* (Nauwerck) Skuja getrennt von *Chrysolykos* bei, während Willén (1967) die Art mit dem inzwischen von Lund (1960) beschriebenen *Chrysolykos gracilis* Lund unter dem Namen *Chrysoikos skujae* (Nauwerck) Willén zusammenzieht und mit zwei Neubeschreibungen, *Chrysoikos angulatus* und *Chrysoikos bicornis* unter dem neuen Genus *Chrysoikos* vereinigt.

Entscheidende Bedeutung misst Willén (1963) Verschiedenheiten des Gehäuses zu. Dies wird bei *Chrysolykos* als gekrümmt-tordierte, bauchig erweiterte Röhre aufgefasst, die in eine sichelförmige Spitze ausläuft und der seitlich ein mehr oder weniger grober Dorn entspringt. Bei *Chrysoikos* wird das Gehäuse als basal erweiterter Zylinder oder als Kegelstumpf verstanden, von dessen Basis zwei mehr oder weniger in der gleichen Ebene Orientierte, fast gleichlange dünne Stacheln ausgehen. Die letztere Definitionsweise gebraucht auch Lund (1960) für die Trennung seines *Chrysolykos gracilis* von *Bitrichia Skujai,* wohingegen Skuja (1964) eben diese Definitionsweise für *Bitrichia Skujai* stark betont, im Gegensatz zu meiner eigenen Beschreibung der Art (Nauwerck 1955), welche die nahe Verwandtschaft mit *Chrysolykos planctonicus* klar erkennen lässt. Bourrelly (1968) lässt zwar Willéns neue Gattung gelten, berücksichtigt aber weder Willéns frühere Vereinigung von Lunds *Chrysolykos gracilis* mit *Bitrichia Skujai* (Nauwerck) Skuja zu *Chrysoikos skujae,* noch seine eigene (Bourrelly 1957) Umstellung der ursprünglichen *Diceras Skujai* Nauwerck zu *Chrysolykos,* sondern führt Lunds Art nun zu *Chrysolykos, Chrysoikos skujae* (Nauwerck)

Willén hingegen zu *Chrysoikos*. Weitere Unklarheit enststeht, indem Bourrelly auch die letztere Einordnung wieder infrage stellt, ohne eine endgültige Meinung zu äussern. Als wesentlichen Gattungsunterschied führt Bourrelly den Plasmastiel an, mit welchem die Monade bei *Chrysoikos* am Gehäusegrund befestigt ist, ein Kennzeichen, dem allerdings Kristiansen (1969) taxonomischen Wert abspricht. Tatsächlich beschreibt bereits Mack (1951) gelegentliches Vorkommen von kontraktilen Befestigungsfäden auch bei *Chrysolykos*.

Durch Ramberg (1978) sind inzwischen drei weitere *Chrysolykos*- bzw. *Chrysoikos*-Arten beschrieben worden, nämlich *Chrysolykos hamulatus* Ramberg, *C. calceatus* Ramberg und *Chrysoikos complanatus* Ramberg. Ramberg diskutiert die phylogenetischen Beziehungen zwischen *Chrysolykos-Chrysoikos* einerseits und *Bitrichia* und *Dinobryon* andererseits. Er verzichtet jedoch auf die Erörterung der Verwandtschaftsverhältnisse zwischen *Chrysolykos* und *Chrysoikos*.

Im folgenden soll auf Basis ökologischer Beobachtungen und biometrischer Messungen gezeigt werden, dass die oben genannten Gattungen einander so nahe stehen, dass eine Aufteilung nicht berechtigt erscheint. Priorität hat also die Gattungsbezeichnung *Chrysolykos* Mack.

Bei der Darlegung der Argumente, auf die ich meine Auffassung stütze, halte ich mich, um Verwirrungen zu vermeiden, zunächst an die folgende Bezeichnungsweise: Die Gattung *Chrysoikos* mit den Arten *C. angulatus* Willén, *C. bicornis* Willén und *C. complanatus* Ramberg, und die Gattung *Chrysolykos* mit den Arten *C. planctonicus* Mack, *C. skujae* (Nauwerck) Bourrelly (= *Diceras Skujai* Nauwerck = *Bitrichia Skujai* (Nauwerck) Skuja = *Chrysoikos skujae* (Nauwerck) Willén), die ich als mit *C. gracilis* Lund identisch betrachte, sowie *Chrysolykos hamulatus* Ramberg und *C. calceatus* Ramberg.

Für Zählungen und Ausmessungen eines grossen Teils des Materiales aus dem Latnjajaure möchte ich Brita Isaksson herzlich danken.

Fundorte

Funde von *C. planctonicus* sind zuerst gemeldet worden aus Österreich (Mack 1951), Frankreich (Bourrelly 1957), der Tschechoslowakei (Juriš 1959), England (Lund 1960 = Scourfield 1930, Williams 1966), Spanien (Willén 1960), Schweden (Willén 1962), Finnland (Kristiansen 1964), Dänemark (Kristiansen 1965), Deutschland (Heynig 1965). Später erscheint die Art häufig in den Artenlisten von vor allem skandinavischen Autoren (mündl. Mitt. von G. Cronberg, P. Eloranta, S. Holmgren, L. Ramberg, G. Rosén, T. und E. Willén u.a.).

Ausser europäischen Fundangaben liegen auch einige Angaben aus Nordamerika vor, so aus Alaska (Hilliard 1966) und aus Ontario (Kling & Holmgren 1972). Selbst habe ich die Art ebenfalls in Seen Ontarios sowie in Teichen in Süddeutschland (Baar, Oberbayern) gefunden.

In den grossen Alpenrandseen und in den grossen nordamerikanischen Seen habe ich die Art nie angetroffen, dagegen und bisweilen zusammen mit *C. skujae* in grossen Seen Schwedisch-Lapplands. Auch Willén (1963) meldet gemeinsames Vorkommen beider Arten in grösseren schwedischen Seen. Im arktischen Gebiet und in hochalpinen Seen ist sie selten oder fehlt. Aus einer Anzahl Proben von grönländischen Seen, die ich G. Cronberg verdanke, konnte ich sie in einem Falle in einem Kleinsee in der Nähe von Godthåb nachweisen. Indessen habe ich sie in zahlreichen Seen der skandinavischen Gebirge, der Alpen, aber auch des Yukon, British Columbias, der kanadischen Arktis (Cornwallis Island) nicht finden können. Ebensowenig war sie in von mir untersuchten Seen Zentralafrikas (Angola bis Kenia) anzutreffen. Wenn auch ein sich ergebendes geographisches Verteilungsbild der Art mit Funden hauptsächlich aus Nord- und Zentraleuropa bis zu einem gewissen Grade eher Forschungsintressen widerspiegelt als wirkliche Ausbreitungszonen, und Angaben aus der Sowjetunion leider nicht vorliegen, spricht doch vieles dafür, dass das Kerngebiet ihrer Verbreitung in eurasisch-nördlich-zirkumpolaren Raum liegt.

Spärlicher sind die Angaben über Funde von *C. skujae*. Ausser von nordschwedischen Gebirgsseen (Nauwerck 1955, 1966) liegen Angaben aus mittel- und südschwedischen Seen vor (Willén 1963, 1969), aus Finnisch Lappland (Kristiansen 1964), aus England (Lund 1960: *C. gracilis*), aus einem See der Hohen Tatra (Juriš 1964), ferner

von Spitzbergen (Willén 1967), aus Alaska (Hilliard 1966: *C. gracilis,* Hobbie, Kalff & Holmgren 1964) und aus Ontario (Kling & Holmgren 1972). Diesen Angaben hinzuzufügen sind Beobachtungen aus südnorwegischen Gebirgsseen (mündl. Mitt. von E.-Ø. Sahlquist) sowie meine eigenen Beobachtungen aus hochgelegenen Seen des Schwarzwaldes (Feldsee, Nonnenmattweiher), aus Seen der polnischen Hohen Tatra (Morskie Oko, Szarny Staw), aus Alpenrandseen (Attersee, Wolfgangsee), aus Lake Erie und aus einem See im Material G. Cronbergs von Grönland. Erwartet aber nicht gefunden habe ich die Art dagegen in Seen des Yukongebietes, der kanadischen Arktis (Cornwallis Island), und den anderen grossen Seen der Laurenzischen Seenkette. Ebensowenig ist sie mir bisher aus Seen der Hochalpen bekannt geworden. Es ist aber deutlich, dass *C. skujae* sich hinsichtlich geographischer Verbreitung und Milieuansprüchen in kalt-oligotropher Richtung von *C. planctonicus* absetzt, d.h. seine optimalen Verhältnisse unter mehr arktisch-alpinen Bedingungen findet und im Gegansatz zu *C. planctonicus* eher in Seen als in Teichen zu finden ist.

Von den von Ramberg (1978) beschriebenen Arten sind zwei, nämlich *Chrysoikos complanatus* und *Chrysolykos hamulatus* bisher nur aus jeweils einem See im Kloten-Gebiet in Mittelschweden bekannt geworden. *C. hamulatus* wurde nur in vereinzelten Exemplaren festgestellt. Bei den Fundorten handelt es sich um relativ kleine, saure Humusseen. Ausführlichere Daten über die Seen gibt Ramberg (1976). *Chrysolykos calceatus,* den Ramberg aus zwei Seen des Sarekmassivs in Nordschweden meldet, habe ich in weiteren Seen der nordschwedischen Hochgebirge feststellen können. Auch S. Holmgren (mündl. Mitt.) hat die Art in Gebirgsseen in Jämtland wieder gefunden. Willéns (1967) *Chrysoikos*-Arten sind bisher nur aus Spitzbergen bekannt.

Jahreszeitliches Auftreten

C. planctonicus tritt in Süd- und Mitteleuropa offenbar nur als Winter- und Frühjahrsform auf. In dänischen Gewässern hat Kristiansen (1965) Jahreszyklus und ökologische Ansprüche der Art ausführlich untersucht. Weiter nördlich verschiebt sich das Maximum ihrer Häufigkeit in den Sommer und im subarktisch-arktischen Gebiet ist ihr Auftreten im wesentlichen auf den Sommer begrenzt. Während sie im Süden auf Teiche und entsprechende Kleingewässer beschränkt ist, kommt sie im Norden auch in grösseren Seen vor.

Fig. 1 zeigt das Auftreten beider Arten während einer Reihe von Jahren in zwei grösseren Seen im südlichen Schwedisch-Lappland. Näheres über die Seen gibt Rodhe (1964). Beide Arten leben in den oberen Wasserschichten, das Maximum wird gewöhnlich in 5 m Tiefe gefunden, bewegt sich aber mit zunehmender Erwärmung des Wassers von geringerer nach grösserer Tiefe. *C. skujae* beginnt seine Populationsentwicklung früher und erreicht sein Maximum in der Regel kurz nach dem Eisbruch bei 4–8°C. *C. planctonicus* erreicht sein Maximum gewöhnlich erst bei 8–12°C.

Eine weitgehende Parellelität der Entwicklung in den beiden Seen lässt gemeinsame Steuerung durch klimatologische Faktoren erkennen. Das zeitweilige Ausbleiben von *C. planctonicus* lässt darauf schliessen, dass die Art eher als *C. skujae* am Rande ihrer Ausbreitungsmöglichkeiten lebt. Im wesentlich kälteren Latnjajaure (Fig. 2) fehlt *C. planctonicus*. *C. skujae* erreicht sein Maximum meistens erst im Spätsommer und bei ähnlichen Temperaturen wie in Ransaren und Kultsjön. In kälteren Sommern bleibt auch die Entwicklung von *C. skujae* deutlich zurück.

Soweit es sich beurteilen lässt sind andere *Chrysoikos*- und *Chrysolykos*-Arten ebenfalls Frühjahrsarten in sommerwarmen Gewässern und haben ihr Maximum in relativ kälteren Gewässern später. *Chrysoikos complanatus* erscheint mit einem Maximum im Mai im Vitalampa. *C. angulatus* beschliesst seine Populationsentwicklung mit Zystenbildung bereits im Juli in spitzbergischen Gewässern. *Chrysolykos calceatus* wurde in relativ kalten Gebirgsseen zwar im August und September gefunden, jedoch wurden die betreffenden Seen auch zu keinen anderen Jahreszeiten besucht, sodass daraus keine Schlüsse gezogen werden können. Ebenso erlauben die vereinzelten Funde von *C. hamulatus* im August kaum Schlüsse über jahreszeitliche Präferenzen.

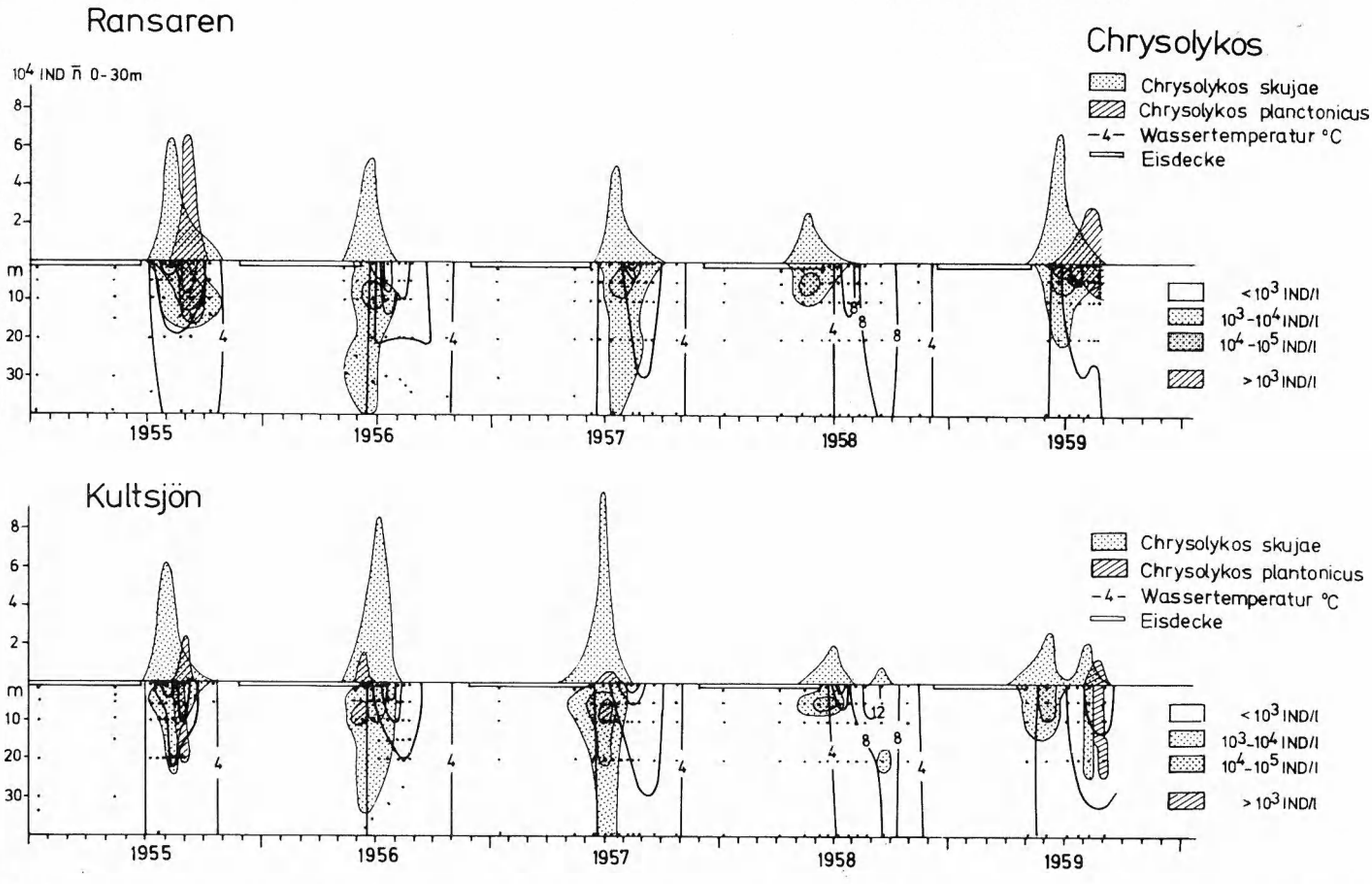


Fig. 1. Populationsentwicklung von *Chrysolykos skujae* und *C. planctonicus* in zwei Seen im südlichen Schwedisch Lappland. Mittlere Zellzahlen pro Liter, Tiefenverteilung und Wassertemperatur. Temperaturisopleten mit Interwallen von 4°C. Punkte indikieren Probeentnahmen.

Population development of *Chrysolykos skujae* and *C. planctonicus* in two lakes in southern Swedish Lapland. Average cell numbers per liter, depth distribution, and water temperature. Temperature isopletes with 4°C intervals. Plots indicating sampling points.

Chemisch-physikalische Milieuansprüche

In einem Material von ca 380 Seen aus der schwedischen Provinz Norrbotten (Stichproben, Oberfläche, Juli–August), das Seen vom Küstengebiet um den oberen Bottnischen Meerbusen bis in die Hochgebirgsregion enthält, habe ich *C. skujae* in etwa 20 % aller Seen gefunden, *C. planctonicus* in etwa 12 % aller Seen. In den Seen der Gebirge allein war *C. skujae* in etwa 70 % aller Fälle vertreten, in den Seen des Küstengebietes allein war *C. planctonicus* in etwa 20 % aller Fälle vertreten. Diese Zahlen relativer Häufigkeit geben eine Vorstellung davon, in welcher Richtung optimale Verhältnisse für die beiden Arten zu suchen sind. Für *C. skujae* dürften sie in vielen Gebirgsseen der Region gegeben sein. Für *C. planctonicus* dürften sie ausserhalb und weiter südlich von unserem Gebiet liegen. Im Gegensatz zu *C. skujae* wurde *C. planctonicus* hier nie in Mengen über 10^5 Individuen pro Liter angetroffen. Kristiansen (1965) gibt für dänische Gewässer Maximalwerte von über 10^6 Individuen pro Liter. Auch dies spricht dafür, dass die Art innerhalb unseren Gebietes nicht ihre optimalen Bedingungen findet.

Wie die Häufigkeit des Vorkommens lässt sich auch die jeweils angetroffene Populationsdichte der Arten verwenden, um ökologische Gradienten aufzustellen. In Tabelle 1 werden norrbottnische Seen nach gefundenen Populationsdichten der Algen gruppiert und die chemisch-physikalischen Bedingungen bei verschiedenen Populationsdichten verglichen.

Betreffend *C. planctonicus* zeigen die Wohngewässer mit Individuenzahlen von 10^3–10^4 pro Liter bzw. 10^4–10^5 pro Liter nur geringe Unterschiede. Eine Tendenz besteht jedoch in Richtung auf mehr eutrophe Verhältnisse in den Seen

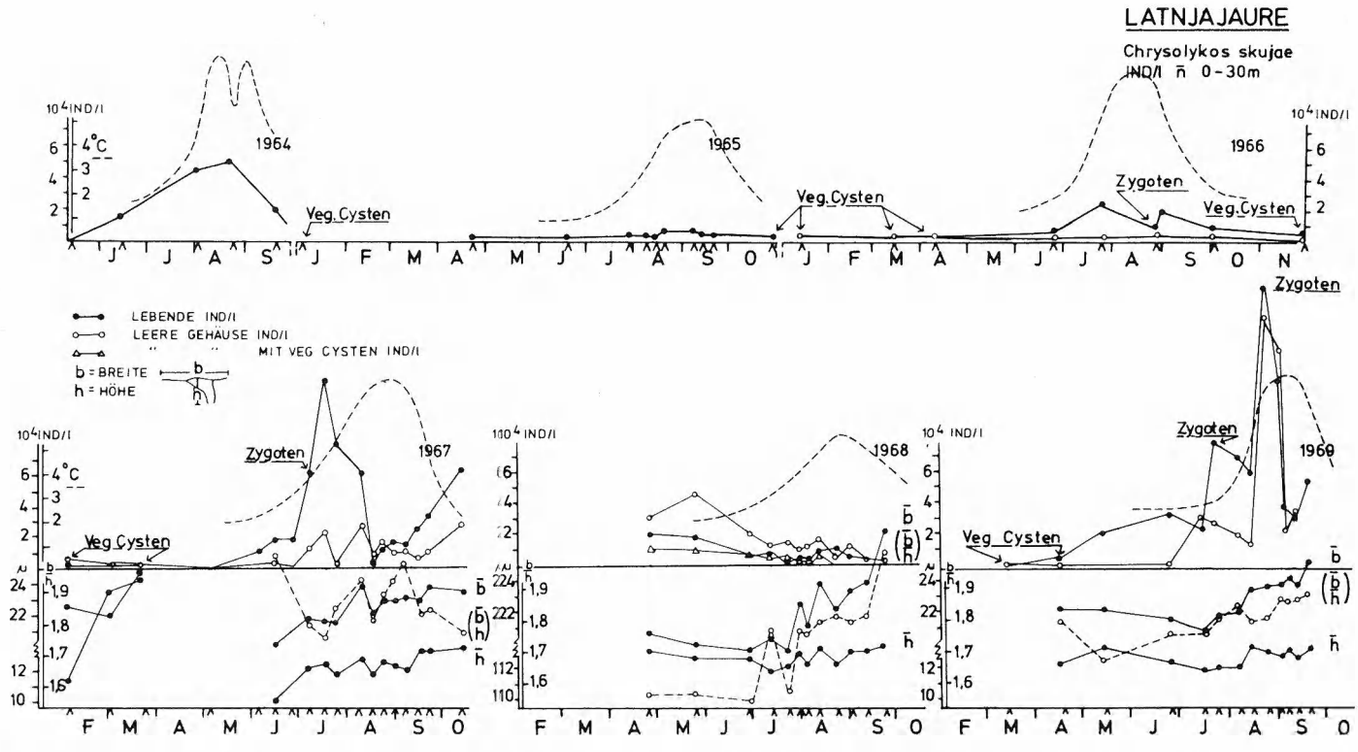


Fig. 2. Populationsentwicklung und morphologische Temporalvariation von *Chrysolykos skujae* im Latnjajaure, nördliches Schwedisch Lappland. Pfeille indikieren Zeitpunkte für Probeentnahmen. Gestrichelte Linie = Durchschnittstemperatur des Sees.

Population development and temporal variation in morphology of *Chrysolykos skujae* in the lake Latnjajaure, northern Swedish Lapland. Arrows indicate sampling occasions. Stippled line = average temperature of the lake.

mit den höheren Individuenzahlen. In den ausgesprochen eutrophen Seen des Gebietes kommt die Art jedoch offensichtlich nicht vor.

Eindeutige Unterschiede treten hervor beim Vergleich der Gewässer mit *C. skujae* und denen mit *C. planctonicus*. *C. skujae* findet sich in kalten, klaren Seen mit geringerem Einschlag an organischen Substanzen. Deutlich ist hier ein Trend zu abnehmenden pH-Werten bei höheren Individuenzahlen. Innerhalb der Gremzen allgemeiner Oligotrophie scheinen auch relativ höhere Phosphorwerte den Zuwachs von *C. skujae* zu begünstigen. Es sei hier vermerkt, dass Willén (vgl. Rodhe et al. 1962) *C. skujae* in Mengen von über 10^6 Individuen pro Liter im Stora Delsjön bei Temperaturen von 2–4°C, pH-Werten von 5,2–5,3 und Totalphosphorwerten vom 10–40 μg pro Liter gefunden hat. Nach Mitteilung von G. Rosén und E. Willén (mündl.) tritt die Art vielerorts in den versauerten Gewässern an der schwedischen Westküste auf.

Wie Willén (1962) gezeigt hat, verträgt *C. planctonicus* brackisches Wasser. Das gleiche belegt Willén (1967) für *C. skujae*, dem er zusammen mit *Chrysoikos* aus mehreren der spitzbergischen Gewässer, darunter auch dem am stärksten salzhaltigen meldet. *C. skujae* kommt in den spitzbergischen Gewässern in der Hauptsache unter den gleichen Bediungungen vor wie *Chrysoikos*, vorzugsweise aber doch in mehr seeartigen Gewässern, d.h. unter kälteren und mehr oligotrophen Verhältnissen.

Chemisch-physikalische Daten für Willéns Fundorte von Spitzbergen gibt Amrén (1964). Daten von Björnöya geben Fleetwood (1969) und Willén (1970). Unpublizierte Daten betreffend Phosphor und Stickstoff verdanke ich T. Willén. Wie Willén (1967) hervorhebt, handelt es sich um Gewässer sehr verschiedenen Typs von grossen Seen bis zu Tümpeln, elektrolytarme Binnenseen und Gewässer die auch Salzeinwirkung vom Meer ausgesetzt sein können. Die Totalphosphorwerte liegen in den meisten Gewässern unter 10 μg/l, erreichen aber in einem Fall bis zu über 60 μg/l. Die Totalstickstoffwerte variieren meistens zwischen 200 und 400 μg/l, können aber 1 mg/l überschreiten. Die Sichttiefe der grösseren Gewässer bewegt sich um 6–10 m. Die Maximaltemperaturen liegen bei ca 4°C für die Seen und bei 10–11°C für die Tümpel. Die

Tabelle 1. Milieufaktoren und quantitatives Auftreten von *Chrysolykos* in Seen in Norrbotten. – Mittelwerte und Variationsbreiten von chemisch-physikalischen Variabeln in Seen (n) wo *Chrysolykos* zu vergleichbaren Zeitpunkten in bestimmten Mengen (Ind./l) gefunden wurde. – * berechnet aus Plankton-Frischgewicht.

Variabel	*Chrysolykos planctonicus*		*Chrysolykos skujae*			
Ind./l	10^3–10^4 (n = 13)	10^4–10^5 (n = 28)	10^3–10^4 (n = 25)	10^4–10^5 (n = 25)	10^5–10^6 (n = 5)	10^6–10^7 (n = 3)
Meereshöhe (m)	227 (37–868)	245 (21–970)	819 (116–1248)	895 (282–1378)	960 (847–1178)	1335 (1310–1360)
Temperatur (°C)	16,3 (6,3–20,8)	16,6 (5,0–21,0)	8,9 (2,0–15,4)	8,6 (4,0–16,0)	7,6 (6,0–11,6)	5,9 (2,2–9,4)
Sichttiefe (m)	5,2 (1,4–12,5)	3,9 (0,9–12,7)	10,7 (6,0–15,5)	12,8 (1,7–17,2)	12–25	> 20
Farbe (mg Pt/l)	28 (5–100)	48 (< 5–150)	3 (< 5–20)	7 (< 5–60)	< 5	< 5
pH-Wert	7,1 (6,9–7,4)	7,0 (6,6–7,6)	7,1 (5,7–7,8)	7,0 (5,6–7,6)	6,2 (6,0–6,5)	5,6 (5,0–6,3)
Leitfähigkeit (mS/m)	3,1 (1,8–4,9)	3,1 (2,1–5,9)	3,3 (2,1–5,9)	3,5 (0,4–15,4)	1,1 (0,7–1,6)	2,9 (0,5–7,2)
P_{tot} (µg/l)	7 (3–11)	11 (4–28)	5 (3–11)	5 (3–17)	7 (4–9)	14 (7–19)
N_{tot} (µg/l)	297 (40–540)	277 (90–230)	120 (75–280)	154 (50–310)	68 (28–234)	72 (54–86)
NO_3-N (µg/l)	12 (< 5–46)	9 (< 5–63)	34 (< 5–83)	30 (< 5–63)	23 (16–32)	24 (12–39)
Chlorophyll a (µg/l)	2,5 (0,1–6,5)	3,3 (0,1–17,0)	0,7 (0,3–1,4)	0,9 (0,2–6,0)	0,7 (0,5–0,9)	≈ 1*

höchsten Individuenzahlen von *Chrysoikos angulatus* (maximal über $2{,}7 \cdot 10^5$ Zellen/l) werden von Anfang Juli aus Tümpeln gemeldet, d.h. bei Temperaturen um 5–6°C (Amrén 1964), jedoch bei mässigen Totalphosporgehalten. Die Leitfähigkeit variiert innerhalb weiter Grenzen zwischen 3,0 und 189 mS/m, wobei die niedersten Werte durch Schmelzwasser, die höchsten durch Salzwassereinwirkung zustande kommen. Wenn die Extremwerte ausgenommen werden, bleibt ein Mittelwert von 15–20 mS/m, also mindestens 5 mal mehr als in den norrbottnischen Wohngewässern von *Chrysolykos skujae*. Auch die Alkalinität der spitzbergischen Gewässer ist entsprechend höher und deutet auf erheblich höheren Kalkgehalt als in Norrbotten. Zwischen den Wohngewässern von *Chrysoikos angulatus* und *C. bicornis* besteht in chemisch-physikalischer Hinsicht kein Unterschied. In drei von vier Fällen meldet Willén beide Arten aus ein und denselben Gewässern.

Für die Seen des Klotengebietes gelten zur Zeit des Auftretens von *Chrysoikos complanatus* und *Chrysolykos hamulatus* nach Ramberg (1976) etwa folgende Bedingungen: Sichttiefe: 2,0–5,5 m, Wasserfarbe: 50–70 mg Pt/l, pH-Wert: 5,0–5,5, Leitfähigkeit ca. 2,0 mS/m, P_{tot}: 14–16 µg/l, N_{tot}: 200–300 µg/l, NO_3-N: 20–30 µg/l. Die Temperatur war 6–8°C im Mai im Vitalampa und ca 16°C im August im Bottjärn.

Für die Fundorte von *Chrysolykos calceatus* gilt einschliesslich der Angaben von Ramberg (1978): Temperatur 10–14°C, Sichttiefe: 7,0–15,0 m, Wasserfarbe 0–10 mg Pt/l, pH-Wert 6,5–7,4, Leitfähigkeit 1,4–3,6 mS/m, P_{tot}: 7–29 µg/l, N_{tot}: 100–220 µg/l, NO_3-N: 5 µg/l (n = 1), Chlorophyll: 0,9 µg/l (n = 1). *Chrysolykos calceatus* scheint in der Hauptsache unter Bedingungen vorzukommen die auch für *C. skujae* gelten können. Das seltene Auftreten der Art im Material aus Norrbotten und die geographische Verteilung der Fundorte kann jedoch zusammen mit den relativ höheren pH-Werten dieser Fundorte auf Bevorzugung von mehr kalkreichen Gewässern deuten.

Morphologie

Auf Fig. 3–7 werden verschiedene Formen von *Chrysolykos* und *Chrysoikos* wiedergegeben, und zwar im allgemeinen in der grössten Projektion d.h. so, wie die Algen normalerweise auf

Objektträger bzw. Zählkammerboden zu liegen kommen. Es ist also zu beachten, dass Längenmasse, vor allem der Stacheln, aufgrund der Torsion der Gehäuse nicht immer wirklichen Massen entsprechen. Neben Originalzeichnungen werden auch umgezeichnete und auf den gleichen Massstab gebrachte Figuren anderer Autoren wiedergegeben. Letzteres geschieht hauptsächlich der einfacheren Vergleichbarkeit halber, aber auch um zu zeigen, wie sehr Wiedergabetechnik und subjektive Artauffassung des Beobachters die Verständigung zwischen den gewiss um Objektivität bemühten Algologen erschweren kann.

So zeichnet z.B. Willén die Stachelenden von *Chrysoikos* mit mehr oder weniger konkav zulaufenden Linien (Fig. 6: 1–7), während ich selbst diese Linien konvex zulaufen lasse (Fig. 6:8–21). Bei selbstkritischem Nachdenken finde ich, dass ich die Details der Enden in Wirklichkeit garnicht gesehen sondern nur Gesehenes extrapoliert habe. Da man diese Details in der Lichtoptik auch garnicht sehen kann (vgl. auch Lunds (1960) Bemerkungen), spricht natürlich auch nichts dafür, dass Willéns Bilder richtiger wären. Es ist leicht zu ermessen, zu welchen Konsequenzen es führen muss, wenn solche notwendigerweise subjektiven Bilder von Autoren nachgezeichnet werden, die das Original nicht selbst gesehen haben und wenn durch successive Umbetonung der Details die ursprüngliche Botschaft zur Unkenntlichkeit entfremdet wird. Bei Skujas (1964) Wiedergabe meiner Zeichnung eines zystentragenden Gehäuses von *Chrysolykos skujae* ist reines Wunschdenken sogar nachweisbar: meine Originalzeichnung zeigte nämlich weder Porus noch abgeschlossene Stacheln. Aufgrund von Skujas Zeichnung führt Bourrelly (1968) die Art irrtümlich auch unter dem Namen *Bitrichia*.

Im übrigen habe ich gefunden, dass Grössenmassstäbe bei Zeichnungen nicht selten den Grössenangaben im Text widersprechen. Wo die letzteren fehlen, sind Zeichnungen auch aus diesem Grunde als Dokumente nur begrenzt zuverlässig.

Die Variabilität der Gehäuse von Chrysomonaden ist schon früh Gegenstand der Aufmerksamkeit der Algologen gewesen. Lemmermann (1904) beschreibt, dass die Gehäuse gewisser *Dinobryon*-Arten im Sommer länger und schlanker werden. Andere Beobachter haben nach Huber-Pestalozzi (1941) saisonmässige Veränderungen der Kolonieform notiert, die im Prinzip mit variierender Ausbildung des Fussteils der Gehäuse erklärt werden muss. In seiner Monographie der Gattung vertritt Ahlstrom (1937) zwar energisch die Ansicht, dass die verschiedenen *Dinobryon*-Arten durch sehr konstante artspezifische Merkmale unterschieden seien. Ein Vergleich von Ahlstroms Bildmaterial und Messtabellen mit Jahreszeit und Fundorten belegt gleichwohl temporale wie auch offensichtlich milieubedingte Formvariationen in weiten Grenzen. Vieles spricht dafür, dass die Vielfalt der Formen bei *Chrysolykos* zum grossen Teil Reaktionen auf spezifische Milieubedingungen widerspiegelt.

Regionale Variation

Betreffend *Chrysolykos planctonicus* fällt auf, dass Formen aus dem südlichen Ausbreitungsbereich der Art (Fig. 3:1–6) zum Teil wesentlich grösser sind als solche aus deren nördlichen Ausbreitungsbereich (Fig. 3:11–21, 24–35). Mitteleuropäische Formen erreichen Scheitelhöhen von 18–20 μm, während Formen aus Norrbotten selten grösser als 12–14 μm werden. Ferner zeichnet sich bei den nordeuropäischen Formen das Fussende des Gehäuses häufig durch Vogelkopf- oder Schnabelform aus (Fig. 3:16, 20–23, 25, 26, auch 28–30), während es bei den mitteleuropäischen Formen die typische Sichel- oder Beilform hat (Fig. 3:1–4), die freilich auch bei nördlichen Formen anzutreffen ist (Fig. 3:11–13, 19). Daneben gibt es bei den nördlichen Formen bisweilen Exemplare, denen der Seitenstachel fehlt und wo die grösste Dimension nicht die Scheitelhöhe sondern die Bogenbreite des gekrümmten Tubus sein kann (Fig. 3:28–31). Bei Formen mit nadelförmig ausgezogenem Fussende sowie mit langem, dünnen Seitenstachel (Fig. 3: 25, 26) lässt sich manchmal nicht mehr mit Sicherheit entscheiden, ob es sich ,,noch'' um *C. planctonicus* oder ,,schon'' um *C. skujae* handelt.

Eine Form mit extrem langem und geradem Halsteil und extrem breitem Stachel am kurzen, wenig gekrümmten, stumpf-konisch zulaufenden Fussteil (Fig. 3: 32–35) gibt Willén (1961, 1963) aus dem Ösbysjön, einem eutrophierten Kleinsee bei Stockholm. Einen Zwischentyp zwischen *C. planctonicus* und einer dreistacheligen *C. skujae*-Form (Fig. 4: 39–41) fand ich bei einer

Gelegenheit als dominante Form in einer Population vermischt mit *C. skujae* in dem hochalpinen Tjåmohasjaure (1045 m). Näheres über den See siehe Nauwerck & Ramberg 1979. Eine ähnliche Form aus einem anderen See (Fig. 4: 38) macht wahrscheinlich, dass sie durch Übergänge mit anderen Formen verbunden sein kann.

Bei *C. skujae* scheint der Formenreichtum etwas geringer als bei *C. planctonicus*. Eine Riesenform mit seitwärts bauchig aufgetriebenem Fussteil (Fig. 4: 3) gibt Juriš (1959) aus einem See der Hohen Tatra. Ob die Dimensionen, von denen nur die Breite des Halses auch im Text angegeben ist, richtig sind, kann hier angezweifelt werden. Indessen habe ich kleinere Typen der gleichen Form (Fig. 4: 7–8) sowohl in Seen des polnischen Teils der Hohen Tatra als auch in Voralpenseen öfters beobachtet. Bei Formen mit mehr oder weniger durchweg erweitertem Fussteil (Fig. 4: 29) ist der Übergang zu *C. planctonicus* wieder offensichtlich. Auch bei *C. skujae* kommen dreistachelige Formen (Fig. 4: 28) und Formen mit reduzierten Stacheln vor (Fig. 4: 24, 25). Die letzteren Varianten trifft man allerdings eher als teratogene Einzelfälle in grossen Populationen an, und nicht als Ökotypen unter speziellen Milieubedingungen.

Mehr bauchige und kurzstachelige Formen von *C. skujae* (Fig. 4: 10–11, 34–35) findet man öfters in alpinen Tümpeln und Kleinseen (näheres über die Gewässer siehe Eriksson & Persson 1971), während langstachelige und mehr symmetrische Formen, die als der Normaltyp von *C. skujae* gelten können (Fig. 4: 1, 2, 9, 15–20, vgl. auch Fig. 5), hauptsächlich in grösseren Seen vorkommen. Da auch bei *C. planctonicus* robuste und mehr kompakte Formen eher für Kleingewässer, grazilere Formen mit verlängerten, dünnen Fortsätzen dagegen eher für Seen typisch sind, liegt der Schlusssatz nahe, dass gegensätzliche Milieubedingungen der Biotope (z.B. in Nährstoffangebot, Wasserbewegungen, Intensität der Milieufluktuationen) zu alternativen Formbildungen führen.

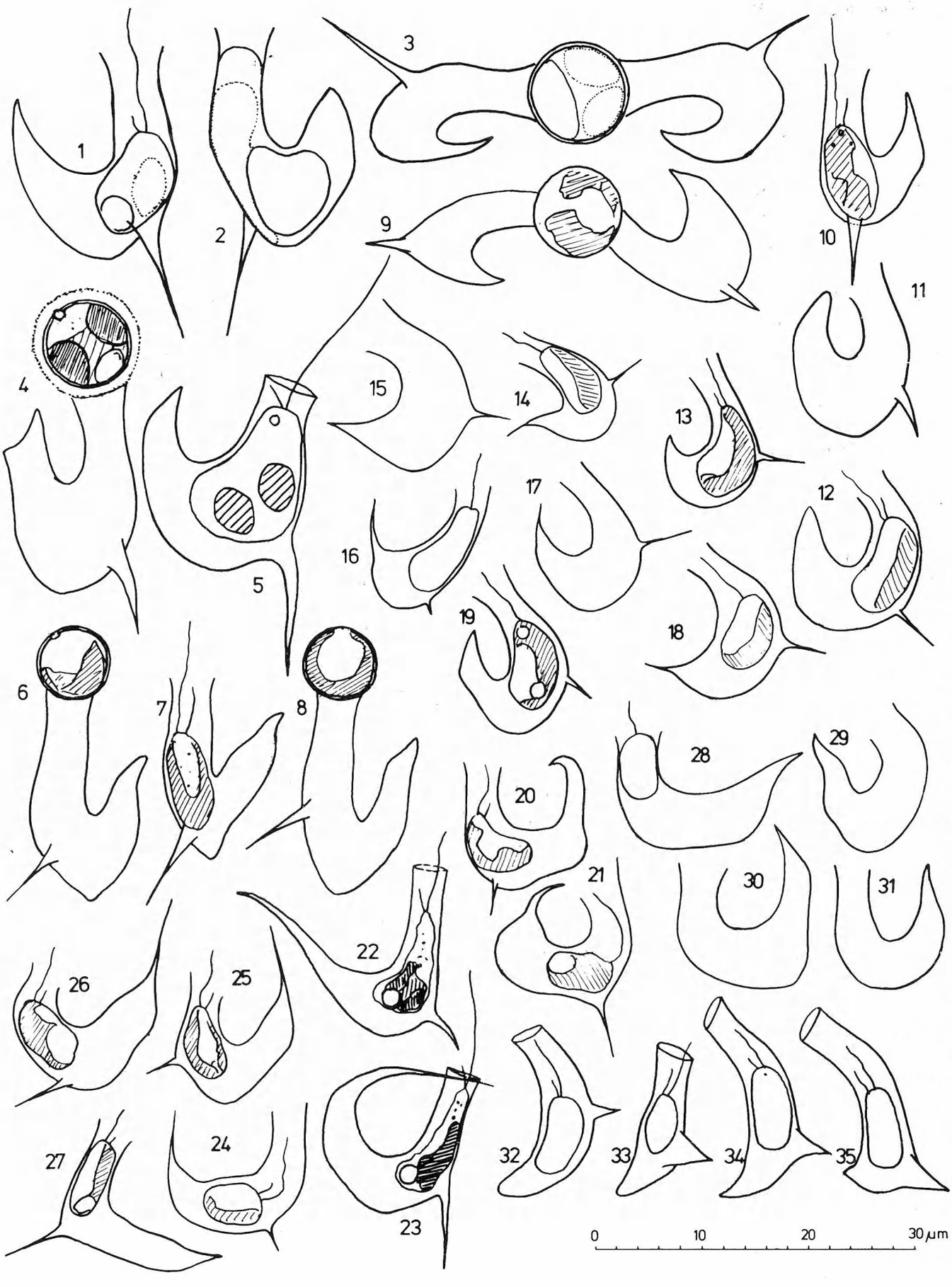
Fig. 6 und 7 zeigen verschiedene Typen von *Chrysolykos angulatus* und *Chrysoikos bicornis*. T. Willén hatte die Freundlichkeit, mir noch erhaltene Proben aus Amréns Material von Spitzbergen zur Ansicht zur Verfügung zu stellen. Wie aus den Abbildungen hervorgeht, ist der Unterschied zwischen den von Willén dargestellten Formen und den meinen zum Teil erheblich. Vor allem sind Willéns Formen fast durchweg grösser (Fig. 6: 1–6, Fig. 7: 16–19) und nur seine kleineren Typen überlappen grössenmässig mit meinen grösseren Typen.

Nach meinen Messungen (50 gemessene Exemplare) war die Halsweite beider Formen im Durchschnitt 4,4 μm (3,5–5,5 μm), die Höhe 12,0 μm (7–23 μm), die Stachellänge 3,5–15 μm und der Abstand der Stachelspitzen 7–26 μm. Die Zysten, kugelig bis oval, variierten in Form und Grösse in weiten Grenzen mit Massen von 3,5–7 × 4–11 μm, bei einen mittleren Durchmesser der reifen, d.h. soweit ersichtlich fertig ausgebildeten Zysten von 7,5–8 μm.

Es ist natürlich möglich, dass das mir vorliegende Material, das zum grössten Teil aus ausserordentlich hyalinen Gehäusen bestand, im Laufe der fast 15-jährigen Lagerung von der Fizierlösung angegriffen worden war. Wahrscheinlich ist der Grund für die Abweichungen jedoch in erster Linie in der begrenzten Anzahl und Auswahl der Proben zu suchen, die mir noch vorgelegen sind. Jedenfalls wird die bereits von Willén (1967) bemerkte grosse Variationsbreite der Formen noch um einiges erweitert.

Nicht nur durch Grössen- und Formübergänge wird die Trennung der beiden Arten infrage gestellt. Willén (1967) hat *C. bicornis* in der Regel als kleinen Einschlag in *C. angulatus*-Populationen beobachtet. Ich habe *C. bicornis*-Typen in Willéns Lokalen 25 und 85 angetroffen (Fig. 7: 25–27, 30–32), von denen Willén nur *C.*

Fig. 3. *Chrysolykos planctonicus*. – 1–3 nach Mack 1951, Heustadelwasser/Wien, Januar–Februar. – 4 nach Bourrelly 1957, Rambouillet, Frühling. – 5 nach Scourfield 1930, Epping Forest, East London. – 6–8 nach Heynig 1965, Hirschteich bei Ballenstedt/Quedlinburg, Mai. – 9–10 nach Kristiansen 1965, Veilbo Mose/Jütland, April–Mai. – 11 nach Kristiansen 1964, Kevojärvi/Finnisch Lappland, Juli. – 12 Djuptjärn (Gransjö)/Norrbotten, Juli. – 13–15, 17–19 f. *minor*, Ransaren/Schwedisch Lappland, Sommer. – 16, 20–21 f. *ornithocephala*, Ransaren, Sommer. – 22–23 nach Williams 1966, Epping Forest, East London, März. – 24–26 Zwischenformen, Kultsjön/Schwedisch Lappland, Sommer. – 27 Grenzform gegen *C. skujae* f. *tatrica*, Åträsket/Norrbotten, Juli. – 28–31 spinalose Formen, 28–30 Ransaren, Sommer, 31 Kapasjaure/Schwedisch Lappland. – 32–35 var. *recticollis*, nach Willén 1963, Ösbysjön/Stockholm, Frühling.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angulatus meldet. Darüberhinaus habe ich die charakteristischen, schlauchförmigen Ausschüben aufsitzenden Zysten, die nach Willén das eine Hauptmerkmal von *C. bicornis* ausmachen (das andere Hauptmerkmal besteht in den kürzeren Stacheln), auch bei *C. angulatus*-Typen feststellen können (Fig. 7:28–29). Runde oder längliche Zysten habe ich bei beiden Bestachelungstypen gesehen (Fig. 6: 14–16 resp. 19, 21 und Fig. 7: 20–23 resp. 26–27). In einem Fall (Fig. 6:15) wurde ein Gehäuse mit sowohl Zyste als auch Monade oder missratener Endozyste festgestellt. Was schliesslich die Stachellänge betrifft, konnte ich überhaupt keine scharfe Grenze zwischen den beiden Typen finden. Bei Willéns stets in Seitenprojektion gezeichneten Figuren von *C. bicornis* lässt sich die wirkliche Länge der Stacheln auch schlecht abschätzen. Im Material finden sich überdies gelegentlich Typen, die deutlicher an *Chrysolykos skujae* erinnern (Fig. 6: 8–12, Fig. 7: 22, 25) als der von Willén gewählte Grundtypus. Auch eine dreistachelige Form und andere abweichende Formen waren zu finden (Fig. 6: 16, 21).

Temporale Variation

Andererseits treten Formunterschiede bei *Chrysolykos skujae* z.B. im Latnjajaure auch als temporales Phänomen auf. Kurzstachelige und relativ kurzhalsige Gehäuse (Fig. 4: 26) findet man zu Beginn der Populationsentwicklung im Juni, d.h. zum Zeitpunkt des Schlüpfens aus den Zysten, hingegen langstachelige und langhalsige Gehäuse (Fig. 4: 22) gegen Höhepunkt und Ende der Populationsentwicklung. Messungen zeigen, dass Gehäusehals wie Stacheln im Laufe der Saison successiv an Länge zunehmen (Fig. 2). Da die Längenzunahme offensichtlich unabhängig von den im See dominierenden Milieufluktuationen abläuft, z.B. der Temperatur, die im August kulminiert und im Oktober bereits wieder auf Juni-Niveau gesunken ist, ist nicht auszuschliessen, dass eine echte Zyklomorphose vorliegt, d.h. von Milieubedingungen unabhängige, generationsweise Formveränderungen von Zyste zu Zyste. Dem entgegen steht wiederum die Tatsache, dass der Verlauf der allometrischen Veränderungen von Hals und Stacheln nicht von Jahr zu Jahr gleich bleibt. Im kalten Jahr 1968 werden die Stacheln absolut und relativ zur Halslänge am längsten. Eine eventuelle echte Zyklomorphose wird also auf jeden Fall von Milieueinflüssen überlagert. Milieuinduzierte Heterauxis im Sinne Jacobs (1961), wie sie bei vielen Planktontieren vorkommt und bei Planktonalgen ebenfalls zu erwarten war, dürfte also vorliegen.

Fortpflanzung

Mit seiner Erstbeschreibung hat Mack (1951) auch die isogame Zygotenbildung bei *Chrysolykos planctonicus* festgestellt (Fig. 3: 3). Zuvor war sexuelle Fortpflanzung bei Chrysomonaden nur durch Skuja (1950) bei *Dinobryon borgei* beobachtet worden, sie ist jedoch inzwischen bei weiteren Arten, besonders bei den kleinen, gehäusetragenden Formen bekannt geworden (Fott 1959 u.a.). Bei *Chrysolykos planctonicus* sind typische Kopulationsstadien später auch von Kristiansen (1965) gefunden worden (Fig. 3: 9).

Neben echten Zygoten sind für *C. planctonicus* öfters auch vegetative Zysten beschrieben worden (Bourrelly 1957, Willén 1963, Heynig 1965, Kristiansen 1965), die den Zygoten weitgehend gleichen oder sich durch etwas geringere Grösse von diesen unterscheiden (Fig. 3: 4, 6, 8). Da die Grössenangaben hier überhaupt stark variieren, darf der Grösse an sich kein allzu

Fig. 4. 1–38 *Chrysolykos skujae*. – 1 Nonnenmattweiher/Schwarzwald, Mai. – 2 Feldsee/Schwarzwald, Mai. – 3 f. *tatrica*, nach Juriš 1964, Vel'ké Hincovo Pleso/Hohe Tatra, Sommer. – 4 nach Kristiansen 1964, Kevojärvi, Juli. – 5–6 nach Holmgren 1974 und unpubliziert, Alaska, Sommer. 6 Übergangsform zur f. *tatrica*. – 7–8 f. *tatrica*. 7 Czarny Staw/Hohe Tatra, August, 8 Wolfgangsee/Salzkammergut, Mai. – 9 Lake Erie/Ontario, April. – 10–11 nach Willén 1963, Lilla Ramm (Misterhult)/Småland, April. – 12–14 nach Lund 1960 (‚*C. gracilis*'), Wie E'en Tarn/Lancashire. – 15 nach Willén 1963, Vättern. – 16–17 Kultsjön, Sommer. – 18–19 Ransaren, Sommer. – 20 Hovlössjön/Norrbotten, Juli. – 21–28 Latnjajaure/Schwedisch Lappland. 22 eine typische Sommerform, 26 eine typische Spätwinterform. – 29 Grenzform gegen *C. planctonicus*, Kapasjaure/Schwedisch Lappland, August. – 30 Tjåmohasjaure/Schwedisch Lappland, September. – 31–33 Formen die an *C. angulatus* f. *bicornis* erinnern. 31 Kleinsee nahe Råvejaure/Schwedisch Lappland, August, 32–33 Ekmanjaure/Schwedisch Lappland, Juli. – 34–35 Tümpel 1383 nahe Latnjajaure, Juli und September. – 36–37 Tarfalasjön/Schwedisch Lappland, August. – 38 dreistachelige Form, vielleicht Übergangsform zu *C. planctonicus* var. *allabardiformis*, Kuoblatjåkkojaure/Schwedisch Lappland. – 39–41 *Chrysolykos planctonicus* var. *allabardiformis*, Tjåmohasjaure, August.


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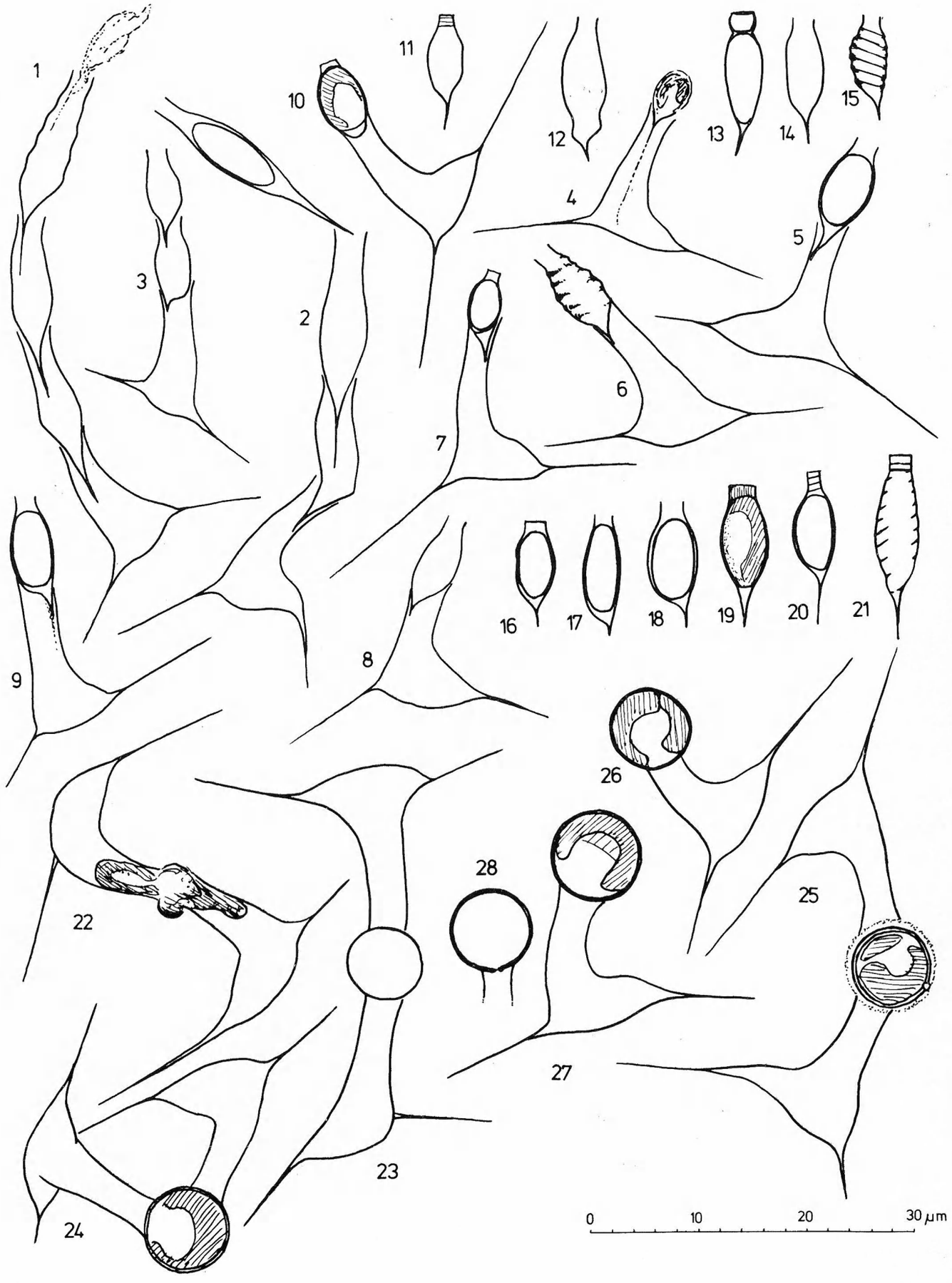
grosses Gewicht beigemessen werden. Auch Vorkommmen oder Fehlen bzw. deutliche oder nicht nachweisbare Bildung von Porus und Pfropfen sind ebenso wie eventuelle gallertige (?) Spezialhüllen keine eindeutigen Kennzeichen für den einen oder den anderen Zystentyp, wie aus den Verhältnissen bei *Chrysolykos skujae* (Fig. 5) klar hervorgeht. Heynig (1965) will nicht ausschliessen, dass es sich bei den von ihm beobachteten ,,Parthenosporen'' vielleicht doch um Zygoten handelte, denen nur noch das eine Mutterzellgehäuse anhing und das andere abgefallen war. Andererseits beschreibt Lund (1960) im Detail die Bildung der Parthenospore bei *C. skujae* (*C. gracilis*), wobei allerdings die Möglichkeit offen bleibt, dass es sich um einen durch die Behandlung des Materiales (Zentrifugierung, Deckglasbelastung, Erwärmung) provozierten, sozusagen unvollständigen Sexualakt handelt. Die Verhältnisse bei *Chrysoikos* wiederum sprechen mit hoher Wahrscheinlichkeit dafür, dass Parthenosporenbildung eine der möglichen Zystenbildungen bei *Chrysolykos* ist.

Eigentümlicherweise habe ich in dem umfassenden norrbottnischen Material nie Zysten irgendwelcher Art bei *Chrysolykos planctonicus* gefunden. Hingegen fand ich in etwa 25 % der Seen mit *C. skujae* Einzelgehäuse mit runden Zysten (Fig. 5: 26–28) und in etwa 10 % der Seen mit *C. skujae* auch die typische isogame Kopulation (Fig. 5: 22–25). Wie bei *C. planctonicus* ist die Grösse der Zygoten ziemlich variabel. Ein Porus mit Pfropfen ist oft deutlich sichtbar und befindet sich dann meistens schräg ausserhalb der Mutterzelle(n) (Fig. 5: 25). Ausnahmsweise kann er auch wie bei *Dinobryon* nach unten in den Gehäusehals gerichtet sein (Fig. 5: 28). Auch gallertige Spezialhüllen, ähnlich der Beobachtung von Bourrelly (1957) bei der Zyste von *Chrysolykos planctonicus*, wurden gefunden (Fig. 5: 5). Im häufigsten Fall waren jedoch weder Poren noch andere Spezialbildungen wahrnehmbar.

Obwohl die Einzelzysten am häufigsten zu finden sind, bin ich doch der Meinung, dass es sich dabei normalerweise um Zygoten handelt. Nichts underscheidet die beiden Zystentypen eindeutig voneinander. Einzelgehäuse mit Zysten werden auch bei Gegenwart von kopulierenden Individuen stets reichlich angetroffen. Und auch wo nur Einzelzysten zu finden sind, treten sie unter den gleichen Umständen auf, unter denen auch sexuelle Vermehrung stattfindet, nämlich im oberen Temperaturbereich des Auftretens der Art und bei verhältnismässig dichten Populationen, d.h. also wahrscheinlich auch unter günstigen Milieubedingungen. Ein entscheidender Grund für meine Meinung ist jedoch das Auftreten von gänzlich anders gearteten vegetativen Zysten in Populationen von *C. skujae* bei ins Pessimale absinkenden Milieubedingungen, wie ich sie in verschiedenen Seen im Latnjajauregebiet beobachten konnte. Fig. 2 zeigt das Auftreten solcher Zysten während Spätherbst und Winter bei langsam aussterbender Population, Zygotenbildung dagegen im Sommer bei starken und in fortgesetztem Zuwachs befindlichen Populationen.

Die vegetativen Zysten sind Endozysten, die in einem, dem Hals des ursprünglichen *Chrysolykos*-Gehäuses ansitzenden, *Dinobryon*-ähnlichen, weiteren Gehäuse gebildet werden. Solche Gehäuse (Fig. 5: 5–21) sind von extrem variierender Beschaffenheit. Als ,,Normaltyp'', wenn von einem solchen überhaupt geredet werden kann, mag der auf Fig. 5: 5, 8, 9, 18 abgebildete Typ angesehen werden. Er hat die Form eines kurzstieligen, assymetrischen *Dinobryon*-Gehäuses mit mehr oder weniger verengtem Kragen, worin die Monade sich in einer besonderen Endozyste einkapselt. Ein Pfropfen ist nicht vorhanden sondern das Gehäuse ist oben offen, was auch dafür spricht, dass es eigentlich nicht Teil der Zyste ist. Im übrigen variiert am Gehäuse fast alles, was überhaupt variieren kann: Länge, Breite, Stiellänge, Kragenweite und Kragenform, Ausbildung des Fussteils, Struktur der Schalenwand. Kurz, die markierte morphologische Flexibilität der Gattung findet hier ihren eindrucksvollsten Beweis. Zum Bau der ,,*Dinobryon*''-Gehäuse und vor der

Fig. 5. *Chrysolykos skujae*. – 1–3 mit ,,*Dinobryon*''-Bildung. 1–2 Latnjajaure, April–Mai, 3 Övre Latnjavaggejaure/Schwedisch Lappland, April. – 4–10 mit ,,*Dinobryon*''-Gehäusen und Endozysten, Latnjajaure, November–April. – 11–21 Gehäuse mit Endozysten, Latnjajaure, November–April. – 22 Kopulation, Kleinsee nahe Råvejaure, August – 22–25 Zygoten mit festhaftenden Mutterzellgehäusen, Latnjajaure, Juli–August. – 26–27 solitäre Gehäuse mit Zysten, wahrscheinlich Zygoten, Latnjajaure, Sommer. – 28 solitäres Gehäuse mit Zyste, wahrscheinlich Zygote, mit halseinwärts orientiertem Porus, Ransaren, Juli.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Bildung der eigentlichen Endozyste muss die Monade eine kürzere oder längere Zeit in einem „*Dinobryonopsis*-Stadium" gelebt haben. Zwar habe ich nur den Beginn eines solchen Stadiums direkt gesehen (Fig. 5: 4), jedoch belegen *Dinobryon*-Kolonien ähnliche Bildungen (Fig. 5: 1–3), dass dies tatsächlich der Fall gewesen sein muss. Am Rande der Existenzmöglichkeiten der Art, bei Temperaturen unter 2°C, während die Einstrahlung im eisbedeckten arktischen See gegen Null geht, mobilisiert *Chrysolykos* potentielle Eigenschaften, die unter günstigeren Lebensbedingungen nicht mehr zum Vorschein kommen. Diese sicher in der Natur mehr allgemein verbreitete Erscheinung mag Anlass zu fruchtbaren Spekulationen geben.

Was *Chrysoikos* betrifft, haben weder Willén (1967) noch ich im Material Amréns je typische Kopulationsstadien gesehen, dagegen alle möglichen Stadien der Zystenbildung ohne Partner, wobei die Zysten wiederum grosse Variation in Durchmesser wie auch Form zeigten und ein Porus bald eindeutig vorhanden, bald nicht auszumachen war. Die Bildung von Endozysten im Hals des Gehäuses hat Willén beschrieben (Fig. 6: 5). Eine Beziehung mag bestehen zwischen dem vor der Zystenbildung auswachsenden Tubus bei *Chrysoikos* (Fig. 7: 18, 19, 28, 29) und der *Dinobryopsis*-Form bei *Chrysolykos* (Fig. 5: 1–3). Solange indessen der Jahreszyklus von *Chrysoikos* nicht besser bekannt ist, kann nicht ausgeschlossen werden, dass auch hier noch weitere Vermehrungsmodi vorkommen können.

Taxonomische Revision

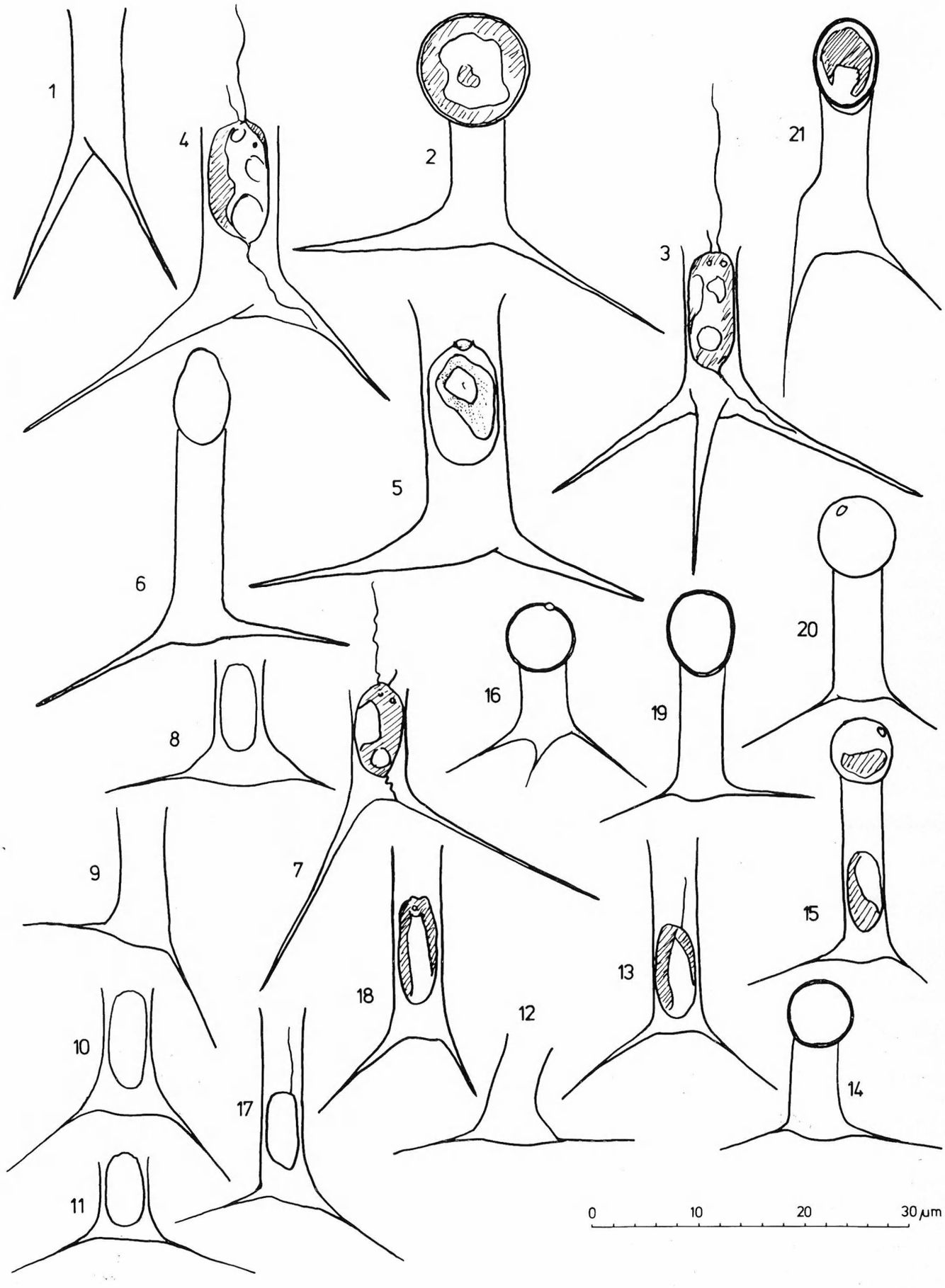
Aus dem oben Ausgeführten dürfte mit genügender Klarheit hervorgehen, dass sich eine Trennung der Gattungen *Chrysolykos* und *Chrysoikos* nicht aufrecht erhalten lässt. Die Mehrzahl der zur taxonomischen Identifikation der beiden Gattungen angeführten Merkmale hat sich nicht als spezifisch erwiesen. Die ausserordentlich grosse morphologische Variabilität der Gehäuseform erlaubt die Verwendung von Formcharakteren als Gattungs- und selbst als Artkennzeichen nur im weitesten Rahmen. Länge, Winkelung und selbst Anzahl der Stacheln, Neigung des Halsteils und Ausbildung des Kragens sind offensichtlich nur von bedingter Anwendbarkeit. Weder Anzahl und Funktionstüchtigkeit der Geisseln noch der Haftfaden, mit welchem die Zelle im Gehäusegrund befestigt sein kann, sind gute Artkennzeichen, ebensowenig Position und Raumausfüllung der Monade im Gehäuse. Wenn auch Fortpflanzungszyklus und Zyklomorphose nicht völlig aufgeklärt sind, stellt die Vielfalt der allein bei *Chrysolykos skujae* nachgewiesenen Fortpflanzungsmöglichkeiten und damit verbundene morphologische Besonderheiten auch die Anwendbarkeit solcher Eigenschaften für taxonomische Zwecke infrage. Das Beispiel von *Chrysolykos* zeigt eigentlich mit besonderer Deutlichkeit, dass man die Linnéanische Frage nach der Art garnicht stellen kann, sondern dass die Frage nur der sinnvollen Abgrenzung von Taxa, d.h. von leidlich sicher abschätzbaren Formkreisen gelten kann.

In diesem Sinne wird auch die hier vorgenommene Revision verstanden. Innerhalb der Gattung werden gut definierte Formenkreise, die sich berühren können aber sich nicht überschneiden, als Arten unterschieden. Ausgeprägte Formen werden als solche unterschieden, sind aber innerhalb des Formenkreises der Art miteinander verbunden. Der Begriff der Varietät wird für solche Formen verwendet, die einem Formenkreis nahe stehen und wo Übergänge möglich aber nicht nachgewiesen sind. Zukünftige Untersuchungen mögen sie auf den Rang von Arten erheben oder zu Formen reduzieren.

Sicher motivieren nicht die subtilen Unterschiede zwischen Lunds *Chrysolykos gracilis* und *C. skujae* die Aufstellung von verschiedenen Arten. Bei der nachgewiesenen Variabilität der *Chrysoikos*-Formen scheint mir die Unterscheidung zweier Arten ebenfalls nicht gerechtfertigt.

Von den von Ramberg (1978) beschriebenen *Chrysolykos*-Arten scheint mir nur eine, nämlich *C. hamulatus* (Fig. 7: 14, 15) eindeutig zur Gattung *Chrysolykos* gehörig. In Anbetracht der Variabilität der Gattung im allgemeinen ist es jedoch fraglich, ob die Aufstellung einer eigenen

Fig. 6. *Chrysolykos angulatus*. – 1–7 nach Willén 1967, Spitzbergen, Sommer. 2 mit sphärischer Zyste (Parthenospore), 5 mit Endozyste, 6 mit unreifer, ovaler Zyste, 3 eine dreistachelige Form. – 8–21 weitere Formen aus dem Material Willéns, eigene Beobachtungen. 8–12 Amréns Lokal 22 (Fyrsjöen), 13–16 Amréns Lokal 25, 17–21 Amréns Lokal 85 (Kongressvatnet).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Art berechtigt ist. Die von Ramberg gesehenen, wenigen Exemplare zeigen zwar einige Eigenschaften, die sie von anderen Mitgliedern der Gattung abheben. Bemerkenswert ist die grosse Länge der Hauptgeissel, die im Gegensatz zu den übrigen Arten weit über einfache Körperlänge hinausreicht. Auffällig ist auch die gleichmässige Breite des Gehäusehalses, die sonst für die Willén'schen *Chrysoikos*-Formen typisch ist. Weniger Gewicht möchte ich hingegen der starken Torsion des Gehäuses und dem verkümmerten Fussstachel beimessen. Im ganzen scheint die Form jedoch *Chrysolykos planctonicus* am nächsten zu stehen und mag bis auf weiteres als Varietät dieser Art aufgefasst werden.

Chrysolykos calceatus (Fig. 7: 1–11) ist grössenmässig stark von den anderen *Chrysolykos*-Arten verschieden. Gemeinsam mit der Gattung hat die Art die Grundform des Gehäuses. Andeutungen von Spornen finden sich, jedoch fehlen Stacheln oder Spitzenfortsätze. Wie auch bei *C. planctonicus* häufig zu beobachten, ist die Gehäusewand an Fussspitze und Fersenspitze bisweilen deutlich verdünnt. Die von mir gesehenen Exemplare (Fig. 7: 4–11) sind zum Teil etwas grösser als die von Ramberg gezeichneten. Auch gewellte Gehäuse kommen vor. Ein wichtiger Unterschied gegenüber den bekannten *Chrysolykos*-Arten scheint mir, dass jene nie Inkrustierungen oder Braunfärbungen zeigen, während die Gehäuse von *C. calceatus* in den meisten von mir gesehenen Fällen, abgesehen von einem hyalinen Kragenstück, mehr oder weniger kräftig braun gefärbt waren. Diese Eigenschaft verbindet die Art meines Erachtens eher mit dem Verwandtschaftskreis von *Pseudokephyrion,* dem auch *Dinobryon borgei, D. spirale* und *D. suecicum* aus diesem und anderen Gründen näher stehen dürften als die Eudinobryonaceen. *Chrysoikos complanatus* (Fig. 7: 12, 13) schliesslich, den auch Ramberg nur zögernd zu dieser Gattung stellt, erfüllt tatsächlich eher einige der Kriterien, die Skuja (1964) für die Hinführung von *Chrysolykos skujae* zur Gattung *Bitrichia* geltend gemacht hat. Es scheint zweifelhaft, ob diese Form überhaupt zu den Dinobryonoideae gehört. Mit der Einbeziehung von *Chrysoikos* in *Chrysolykos* muss sie jedoch einstweilen der letzteren Gattung eingereiht werden.

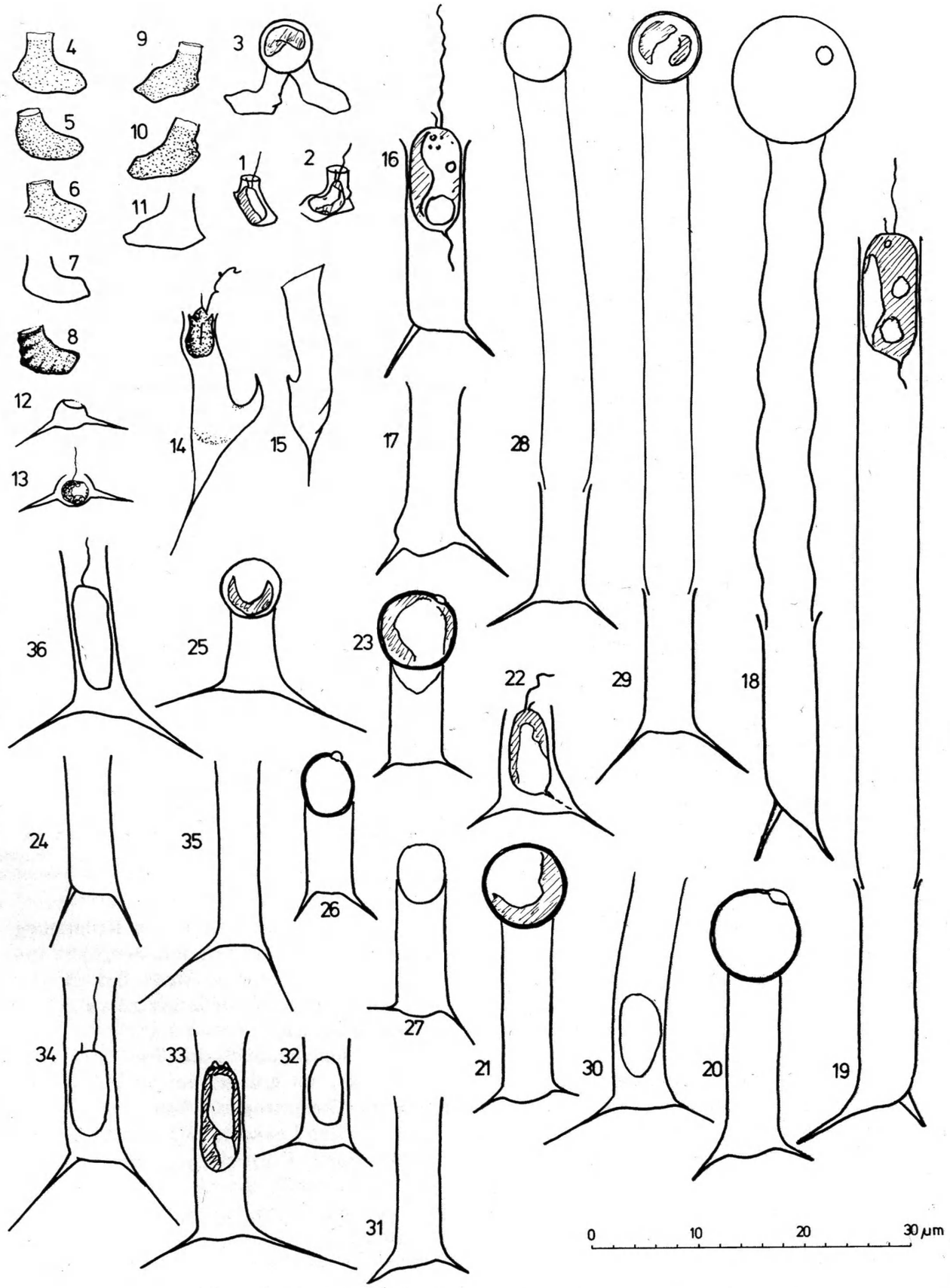
Chrysolykos Mack

Mack 1951 p. 268.
Chrysoikos Willén 1967 pp. 96–97.

Gehäusebildende Monaden der Chrysomonadales, Familie Dinobryonaceae, Unterfamilie Dinobryonoideae. Mit den eigentlichen *Dinobryon*-Arten hat *Chrysolykos* die Qualität des Gehäuses und die Parthenosporenbildung gemeinsam, mit den *Dinobryopsis*-Arten und *Pseudokephyrion* die sexuelle Vermehrung. Von beiden unterscheidet er sich durch die Form des Gehäuses. Ähnlichkeit in der Form des Gehäuses hat *Chrysolykos* mit der Gattung *Bitrichia,* jedoch ist bei *Bitrichia* der Protoplast innerhalb des Gehäuses von einer besonderen Hülle umgeben, sodass die Stacheln dem Gehäuse aufgesetzt erscheinen.

Das Gehäuse aus Zellulose hat die gleiche Wandstruktur wie das Gehäuse von *Dinobryon* (Kristiansen 1969) und ist ebenso wie jenes stark variabel. Die Grundform des Gehäuses ist zylindrisch, basal gestaucht, ± gekrümmt und tordiert und seitlich abgeplattet, der ± erweiterte Fussteil seitwärts in einen Dorn oder Stachel verjüngt und an der Krümmungsstelle mit einem in entgegengesetzte Richtung ausgezogenen Dorn oder Stachel versehen. Ein weiterer Stachel kommt manchmal vor. Sowohl zyklisch ablaufende Veränderungen der Gehäuseform als auch an gewisse Milieubedingungen gebundene Formtypen sind festgestellt worden. Allgemein werden zu Anfang der Populationsentwicklung kleinere und kompaktere Gehäuse gefunden als zum Höhepunkt derselben. Im Plankton von Seen werden schlankere Formen mit dünneren Gehäusewänden und längeren Fortsätzen ange-

Fig. 7. 1–11 *Chrysolykos calceatus*. – 1–3 nach Ramberg 1978, Kuoletisjaure/Schwedisch Lappland, September. – 4–10 Rissajaure (Sarek)/Schwedisch Lappland, August. – 11 Peuraure/Schwedisch Lappland, August. – 12–13 *Chrysolykos complanatus,* nach Ramberg 1978, Vitalampa/Bergslagen, Mai. – 14–15 *Chrysolykos planctonicus* var. *hamulatus,* nach Ramberg 1978, Bottjärn/Bergslagen, August. – 16–29 *Chrysolykos angulatus* f. *bicornis* – 16–19 nach Willén 1967, Spitzbergen, Sommer. 18–19 mit schlauchförmigem Auswuchs, 18 mit sphärischer Zyste (Parthenospore). – 20–35 weitere Formen aus dem Material Willéns, eigene Beobachtungen. 20–24 Amréns Lokal 22, 25–29 Amréns Lokal 25, 30–32 Übergangsformen zu f. *angulatus,* Amréns Lokal 85. – 33–35 *Chrysolykos angulatus* f. *angulatus,* Amréns Lokal 85.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troffen als im Plankton von Teichen, wo mehr gedrungene, oft auch grössere Formen vorherrschen.

Die ± ovale Monade hat einen parietalen Chromatophor, vor der Teilung auch zwei Chromatophoren, von hellgrün-gelblicher bis goldgelb-bräunlicher Farbe. Als Reservestoffe erscheinen feine, lichtbrechende Granula im Zytoplasma sowie ein oft relativ grosser Leukosinballen im Basalteil der Zelle. In ihrem Vorderteil sind ein oder zwei ziemlich kleine pulsierende Vakuolen beobachtet worden, in einem Fall auch ein Stigma. Am Vorderende der Zelle befinden sich die auffällig weit voneinander inserierten Geisseln, die längere meistens von wenig über oder unter Körperlänge, die kürzere viel kürzer und bisweilen ganz reduziert. Die Geisseln können auch rhizopodenähnlich verquollen und ohne Schwimmfunktion sein. Oft fehlen sie auch ganz. Wenigstens anfänglich sitzt die Monade mittels eines Plasmastranges (Epipoden) im Grunde des Gehäuses fest. Im allgemeinen sind alle diese Merkmale bei den grösseren Mitgliedern der Gattung klarer erkennbar.

Sowohl Isogamie mit Bildung verkieselter Zygoten als auch die Bildung von vegetativen Parthenosporen und Endozysten sind beobachtet worden. Die Parthenosporen können dem Hals des Gehäuses direkt aufsitzen oder, ähnlich wie bei *Dinobryon,* mit einem dem Gehäuse auswachsenden Schlauch aus diesem herausgeschoben gebildet werden. Endozysten können im Gehäuse selbst entstehen oder in vor der Enzystierung gebildeten, *Dinobryon*-ähnlichen besonderen Gehäusen.

Bestimmungsschlüssel

1. Gehäuse stark gekrümmt und ± tordiert, mit oder ohne Stacheln oder Fortsätzen 2
– Gehäuse wenig gekrümmt oder ± gerade und wenig tordiert, mit Stacheln oder Fortsätzen 3
2. Gehäuse schuh- oder fussförmig, ohne Stacheln oder Fortsätze, Sporne bisweilen angedeutet 5. *C. calceatus*
– Gehäuse sichelförmig gekrümmt, ± tordiert, basal erweitert und abgeplattet, Fussende zugespitzt oder beilförmig, am Krümmungsbogen ein kurzer, dorn- oder nadelförmiger Fortsatz, bisweilen auch fehlend ..... 1. *C. planctonicus*
3. Gehäuse gerundet und viel kürzer als die Fortsätze, Fortsätze fast gleichlang, in schwach verstellten Ebenen orientiert und wenig gegeneinander gewinkelt ..... 4. *C. complanatus*
– Gehäuse gestreckt und wenig kürzer bis viel länger als die Fortsätze 4
4. Gehäuse gerade, Halsteil relativ breit und mit fast parallelen Seiten, an der Basis kaum erweitert, wenig kürzer bis viel länger als die Stacheln, Stacheln in schwach verstellten Ebenen orientiert und ± stark gegeneinander gewinkelt ..... 3. *C. angulatus*
– Gehäuse ± gekrümmt, Halsteil ± konisch, an der Basis bauchig erweitert, wenig kürzer bis wenig länger als die Stacheln, Stacheln in ± stark verstellten Ebenen orientiert und wenig gegeneinander gewinkelt bis fast in einer Linie ..... 2. *C. skujae*

1. **Chrysolykos planctonicus** Mack var. **planctonicus**

Mack 1951 p. 268 – Typus: Mack 1951 Abb. 3: l–o (Fig. 3: 1)

Fig. 3: 1–12.

Gehäuse stark gekrümmt, im unteren Teil erweitert und seitlich abgeplattet, am Fussende tordiert-sigmoid und abgestumpft oder zugespitzt, an der Öffnung schwach eingezogen udd leicht gekragt. Im Bereich der Beugung des Gehäuses ein stachel- oder schwertförmiger Fortsatz mit räumlich verstellter Orientierung gegenüber dem Fussfortsatz. Gelegentlich kann der Fortsatz auch fehlen. Dimensionen des Gehäuses ohne Stachel von Mundöffnung bis Scheitelpunkt der Krümmung 11–20 μm (normal 12–14 μm), von Halsseite bis gegenüberliegenden Krümmungsbogen 10–14 μm. Mundöffnung 3–6,5 μm (normal 3,5–4,5 μm), engste Stelle des Halsteils 2,5–4,5 μm, breiteste Stelle bis zu ca. 12 μm, gewöhnlich 5–6 μm.

Monade länglich-oval, ca 7×4–10×6 μm, auch grösser, mit grüngelbem bis gelbbraunem parietalen Chromatophor und in der Regel grossem basalen Leukosinkorn. Längere Geissel bis etwas über Körperlänge, kürzere Geissel etwa 1/4–1/2 der längeren Geissel. Besonders bei kleineren Individuen häufig nur eine Geissel entwickelt.

Sexuelle Vermehrung durch Isogamie und Bildung kugeliger Zygoten, denen die Mutterzellgehäuse noch anhängen können. Zygoten mit oder ohne erkennbarem Porus und Pfropfen, Durch-

messer der Zygoten 8–9 μm. Daneben sind mitunter etwas kleinere, ähnliche Zysten an solitären Gehäusen beobachtet worden, 6,5–7,5 μm im Durchmesser, bei denen es sich um Parthenosporen handeln kann.

C. planctonicus ist in Europa, besonders in Nordeuropa, sowie in Nordamerika verbreitet. Im südlichen Teil ihres Ausbreitungsbereiches wird die Art hauptsächlich im Winter- und Frühjahrsplankton von Teichen gefunden, im Norden auch im Sommerplankton von grösseren Seen.

1 a. **Chrysolykos planctonicus** f. **minor** Nauwerck, f. nov.

Typus: Fig. 3: 13.

Fig. 3: 13–15, 17–19.

A forma planctonici non differtur nisi minoribus dimensionibus sine discrimine acuto.

Unterscheidet sich vom Typus lediglich durch geringere Dimensionen und ist von diesem nicht scharf abgegrenzt. Die kleinsten Formen wurden in Seen im nördlichen Teil des Ausbreitungsgebietes der Art gefunden.

1 b. **Chrysolykos planctonicus** f. **ornithocephala** Nauwerck, f. nov.

Typus: Fig. 3: 20.

Fig. 3: 20–21, auch 16, 25, 26.

Pes loricae, capiti avis similis, differt a pede forma planctonici sine discrimine acuto.

Unterscheidet sich durch die Vogelkopf-ähnliche Ausbildung des Fussteils des Gehäuses vom Typus und ist von diesem nicht scharf abgegrenzt. Diese relativ kleine Form wurde zusammen mit der f. *minor* und mit stachellosen Formen (Fig. 3: 28–31) sowie mit *Chrysolykos skujae* im Sommerplankton einiger grossen Seen in Schwedisch Lappland gefunden.

1 c. **Chrysolykos planctonicus** var. **recticollis** (Willén) Nauwerck, var. nov.

Typus: Willén 1963 Pl. 11: 7–10 (Fig. 3: 32–35).
Chrysolykos planctonicus sensu Willén 1963 p. 47.

A varietate planctonici differtur lorica, procera longitudine et curvamine minore, pede brevi hebeti, eique subiacente aculeo lato, gladii brevis forma.

Unterscheidet sich vom Typus durch langgestreckte Gehäuse mit geringer Krümmung, kurzem und stumpfem Fussteil und sehr nahe dem Fussende ausgehenden, sehr breiten Seitenfortsatz. Der Fundort der Varietät ist ein eutrophierter Kleinsee bei Stockholm.

1 d. **Chrysolykos planctonicus** var. **allabardiformis** Nauwerck, var. nov.

Typus: Fig. 4: 39.

Fig. 4: 39–41.

Differtur a varietate planctonici pede loricae, forma securiformi, cum collo angulum subrectum formante, ex hoc angulo spinam lateralem tenuem aculeiformem emittente, deinde ipsa sub angulo subrecto fracta, hoc angulo interdum in spinam secundam extracto.

Unterscheidet sich von der Art durch besonders starke Betonung der Beilform des Fussteils des Gehäuses. Dieser ist zweimal in fast rechtem Winkel zum Halsteil geknickt, an der ersten Knickstelle befindet sich der Seitendorn in Form einer dünnen Nadel, die zweite Knickstelle kann nochmals in einen Dorn ausgezogen sein. Das Gehäuse erinnert in Seitenansicht an eine Hellebarde. Diese sehr grazile Varietät wurde zusammen mit *C. skujae* in einigen hochalpinen Seen der Abiskoregion in Schwedisch Lappland beobachtet.

1 e. **Chrysolykos planctonicus** var. **hamulatus** (Ramberg) Nauwerck, comb. nov.

Basionym: *Chrysolykos hamulatus* Ramberg 1978 p. 142 – Typus: Ramberg 1978 Fig. 2 (Fig. 7:14).

Fig. 7: 14, 15.

Unterscheidet sich vom Typus durch relativ breiten, gestreckten Halsteil und stark geschraubten Basalteil mit kleinem, stark gekrümmten Fuss, der nur in einem kurzen Dorn endet. Der in Verlängerung des Halsteils orientierte Seitenstachel ist dünn-nadelförmig. Die wohl ausgebildete längere Geissel der relativ kleinen, halsständigen Monade ist von fast doppelter Körperlänge. Die Form wurde von Ramberg nur in wenigen Exemplaren in einem humösen See Mittelschwedens gefunden.

2. **Chrysolykos skujae** (Nauwerck) Bourrelly

Bourrelly 1957 p. 170 (‚*Skujai*') – *Diceras Skujai* Nauwerck 1955 p. 352 – *Bitrichia Skujai* (Nauwerck) Skuja 1964 p. 314 – *Chrysoikos skujae* (Nauwerck) Willén 1967 p. 102 – Typus: Nauwerck 1955 Abb. 1.
Chrysolykos gracilis Lund 1960 p. 102 – Typus: Lund 1960 Fig. 2 F.

Fig. 4: 1, 2, 4, 5, 9–28, 30, 34–37; 5.

Gehäuse schwach gekrümmt oder fast gerade und leicht tordiert, der Halsteil deutlich eingezogen und schief abgestutzt mit mehr oder weniger erweiterter Kragenöffnung, am Fussende gestaucht, ± konisch erweitert bzw. aufgebaucht, seitwärts in einen langen, nadelförmigen Stachel ausgezogen. Am Knickpunkt des Gehäuses gegenüber dem Basalstachel und in räumlicher Ebene gegen diesen versetzt ein zweiter nadelförmiger Seitenstachel. Basalstachel und Seitenstachel können fast in einer Linie liegen, sind jedoch stets verschieden lang und im Ansatz am Gehäuse nie völlig symmetrisch. Ausnahmsweise kann der Seitenstachel auch fehlen oder es kann noch ein weiterer Seitenstachel auftreten. Dimensionen des Gehäuses von der Mundöffnung bis zum Scheitelpunkt etwa 7–20 μm, meistens 12–14 μm, Abstand zwischen den Stachelenden 7–30 (–48) μm, meistens über 20 μm. Halsteil an der engsten Stelle 2–3 (–4) μm, Kragenweite 2,5–4 (–4,5) μm. Die Gehäuse variieren vor allem hinsichtlich Hals- und Stachellänge. Zu Beginn der Saison sind Hals und Stacheln absolut am kürzesten und die Halslänge im Verhältnis zur Stachellänge am grössten. Kurzstachelige Formen werden auch häufiger in kleinen Gewässern gefunden, während langstachelige eher in grösseren Gewässern auftreten.

Die Monade ist im Prinzip vom gleichen Bau wie bei *C. planctonicus,* ihre Dimensionen sind etwa 6 × 2,5–10 × 5 μm, die längere Geissel ist stets unter Körperlänge, die kürzere Geissel bis höchstens 1/3 der Länge der längeren Geissel und häufig fehlend bzw. nicht nachweisbar. Die Geisseln können auch rhizopodenartig verquollen und ohne Schwimmfunktion sein, auch hat die Monade öfters mehr amöboiden Charakter und kann das Gehäuse mehr oder weniger ausfüllen. Der parietale Chromatophor ist meistens schwach gelbgrün gefärbt, nur bei den grössten Formen mehr goldgelb. Ein basales Leukosinkorn kommt vor, fehlt aber meistens, und als Reservestoffe sind hauptsächlich Granula im Zytoplasma zu beobachten. Wenigstens eine pulsierende Vakuole am Vorderende ist beobachtet worden, in einem Fall auch ein Stigma.

Sexuelle Vermehrung durch Isogamie und Bildung kugeliger Zygoten wie bei *C. planctonicus.* Durchmesser der Zygoten 7–8,5 μm. Häufig werden an solitären Gehäusen kugelige Zysten des gleichen Typs beobachtet, deren Durchmesser mit 6–8 μm mitunter geringer ist als bei den Zygoten. Es ist möglich, dass es sich dabei in gewissen Fällen um Parthenosporen handelt, meistens dürften aber auch hier Zygoten vorliegen, die nur dem einen Mutterzellgehäuse verhaftet geblieben sind.

Ausser den kugeligen Zysten, die als verkieselt bezeichnet werden, kommen ovale Endozysten vor, die in besonderen Gehäusen gebildet werden (Fig. 5). Diese Gehäuse, die dem ursprünglichen Gehäuse *Dinobryon*-artig aufsitzen, zeigen mehr oder weniger typische Merkmale von *Dinobryon*-Gehäusen und sind ausserordentlich variabel in Form und Grösse. Ihre Länge, einschliesslich Basalstachel und Kragen, schwankt zwischen 8 und 22 μm, die Breite zwischen 3 und 5 μm, meistens sind sie etwa 10 μm lang, an der breitesten Stelle etwa 4 μm und an der Kragenöffnung etwa 2 μm breit. Die Gehäuse können auch unduliert sein und am Basalteil mehr oder weniger betonte Ausbuchtungen aufweisen. Der Kragen ist häufig verstärkt, manchmal mit ringförmiger oder spiraliger Struktur und bisweilen eingezogen oder röhrenförmig verlängert. Wird die Bildung von solchen Spezialgehäusen einmal eingeleitet, so kann sie offenbar einige Male wiederholt werden, ohne dass gleich Endozysten gebildet werden und es entstehen *Dinobryon*-ähnliche „Kolonien", freilich nur in einer Reihe und mit Ausnahme des letzten aus leeren Gehäusen bestehend.

C. skujae hat eine arktisch-subarktische Verbreitung und bevorzugt kalte, klare Gewässer mit niederen pH-Werten. Die Art ist hauptsächlich aus Seen der skandinavischen Gebirge bekannt, wurde aber auch aus Seen Alaskas, Grönlands, Ontarios, der Alpen, der Hohen Tatra, des Schwarzwalds sowie aus Spitzbergen gemeldet.

2 a. **Chrysolykos skujae** f. **tatrica** Nauwerck, f. nov.

Typus: Fig. 4: 7.
Chrysolykos skujae sensu Juriš 1964 p. 661.

Fig. 4: 3, 7, 8.

A forma skujae differtur loricae pede sub angulo subrecto fracta, bulbi modo inflata. Sunt transitus in forma skujae.

Unterscheidet sich vom Typus durch den fast

rechtwinkelig abgebogenen und bulbös aufgetriebenen Basalteil des Gehäuses. Die Form leitet über zur *ornithocephala*-Form von *C. planctonicus*. Juriš gibt aus einem See der Hohen Tatra eine ungewöhnlich grosse Form. Weniger als die Grösse scheint die spezielle Form des Gehäuses charakteristisch für Individuen aus Seen im südlichen Teil des Ausbreitungsgebietes der Art.

3. **Chrysolykos angulatus** (Willén) Nauwerck, comb. nov.

Basionym: *Chrysoikos angulatus* Willén 1967 p. 98 – Typus: Willén 1967 Fig. 2.

Fig. 6; 7: 33–35.

Gehäuse gerade, gleichmässig breit, wenig gekragt, am Basalteil bisweilen etwas aufgetrieben, kaum tordiert, mit zwei, selten drei, nicht gleich langen Stacheln, die im Winkel von fast 180° bis weniger als 90° gegeneinander geneigt und in etwas verschiedenen Ebenen orientiert sind. Gewöhnlich ist der eigentliche Basalstachel am breiteren Übergang zum Gehäuse erkennbar, oft erscheinen die Stacheln jedoch auch als ± gleichartig. Grösse der Gehäuse und Winkelung der Stacheln variieren stark. Dimensionen des Gehäuses von der Mundöffnung bis zum Scheitelpunkt 8–25 μm, gewöhnlich um 15–20 μm, Breite des Halsteils 4–7 μm, gewöhnlich um 5 μm. Stachellänge bis über 18 μm, gewöhnlich jedoch eher unter als über 10 μm. Grösster Abstand zwischen den Stachelspitzen weniger als 10 μm bis fast 40 μm, gewöhnlich zwischen 15 und 25 μm.

Monade ellipsoidisch, 3,5 × 6–5,5 × 13 μm mit einem parietalen Chromatophor, basalem Leukosinballen und mit Vakuole am Vorderende. Längere Geissel etwas über oder unter Körperlänge, kürzere Geissel meistens viel kürzer und selten mehr als etwa 1/5 der Länge der längeren Geissel. Der Plasmafaden, mit dem die Monade am Gehäusegrund befestigt ist, ist oft gut zu erkennen.

Kugelige oder bisweilen länglich-ellipsoidische Parthenosporen sind bekannt, ebenso Endozysten. Die ellipsoidischen Endozysten werden im Hals des Gehäuses gebildet. Die Parthenosporen, mit oder ohne erkennbare Porus und Pfropfen, sitzen der Halsöffnung auf oder werden am Ende eines schlauchförmigen Auswuchses gebildet, mit dem sich die Monade aus dem Gehäuse herausschiebt. Die Proportionen der Parthenosporen variieren in weiten Grenzen von einem Durchmesser von 6,5 μm bis zu 10 μm bzw. in Länge und Breite von 5–8 resp. 8–10 μm, jedoch dürfte es sich bei den kleineren Exemplaren auch um unreife Zysten handeln. Der dem Gehäuse entwachsende Schlauch ist zarter gebaut als dieses, mit glatter, seltener undulierter Wand, hat etwa die Breite des Gehäusehalses und ist von Längen bis zu 87 μm beobachtet worden.

Die Art ist bisher nur aus Seen und Kleingewässern Spitzbergens bekannt geworden.

3 a. **Chrysolykos angulatus** f. **bicornis** (Willén) Nauwerck, comb. nov.

Basionym: *Chrysoikos bicornis* Willén 1967 p. 100 – Typus: Willén 1967 Fig. 3.

Fig. 7: 16–32.

Unterscheidet sich vom Typus hauptsächlich durch die geringere Länge der Stacheln. Individuen mit Stachellängen unter 7 μm sind dieser Form zuzurechnen. Das von Willén ursprünglich hervorgehobene zweite Charaktermerkmal, die Bildung der schlauchförmigen Auswüchse im Zusammenhang mit der Zystenbildung kommt, wenn auch offenbar weniger häufig, auch bei *C. angulatus* selbst vor und kann nur als relatives Merkmal gelten. Unterschiede in der Form der Parthenospore sowie der Grösse des Gehäuses und der Monade, die von Willén notiert wurden, dürften innerhalb der Variabilität der Art liegen.

C. angulatus f. *bicornis* ist zusammen mit dem Typus in einigen Gewässern Spitzbergens sowie im Ellasjön auf Björnöya gefunden worden.

4. **Chrysolykos complanatus** (Ramberg) Nauwerck, comb. nov.

Basionym: *Chrysoikos complanatus* Ramberg 1978 p. 144 – Typus: Ramberg 1978 Fig. 3.

Fig. 7: 12, 13.

Gehäuse rundlich-oval, abgeplattet, ohne Kragen, mit zwei einander gegenüberstehenden, in Ebene und Winkel leicht verstellten, konischen, spitz zulaufenden Fortsätzen. Höhe des Gehäuses von Mundöffnung bis Scheitelpunkt ca. 4

μm, Breite etwa 3–4 μm, Dicke etwa 2 μm. Die ovale Öffnung ist etwa 1,5 × 1 μm gross. Monade rund mit olivgrünem Chromatophor und einer 3–5 μm langen Geissel. Die Art wurde bisher nur im Frühjahrsplankton eines humös-oligotrophen Sees in Mittelschweden gefunden.

C. complanatus unterscheidet sich in Dimensionen und Form des Gehäuses ziemlich stark von den einander klar näherstehenden Arten *C. planctonicus, C. skujae* und *C. angulatus* und erinnert in mancher Beziehung auch an *Bitrichia*. Die Stellung von *C. complanatus* muss vorläufig als unsicher gelten.

5. **Chrysolykos calceatus** Ramberg

Ramberg 1978 p. 142 – Typus: Ramberg 1978 Fig. 1.

Fig. 7: 1–11.

Das Gehäuse gleicht in der Grundform entfernt dem von *C. skujae,* hat aber keine lang ausgezogenen Stacheln oder Fortsätze, sondern höchstens angedeutete Sporne an der Gehäusebasis und an der Knickstelle des Gehäuses. In der Form erinnert es an einen Schuh oder einen Fuss. Es ist bedeutend kleiner als bei den sicheren Arten der Gattung und unterscheidet sich von diesen ferner durch braune Inkrustierung der Gehäusewand bei charakteristisch hyalin verbleibendem Kragen, wie man es bei Arten der *Pseudokephyrion*-Gruppe und *Dinobryon*-Arten der *Dinobryopsis*-Gruppe antrifft. Die Neigung des Halsteils ist auch nicht, wie bei anderen *Chrysolykos*-Arten, der Basalspitze zugewandt, sondern strebt eher von dieser weg. Bisweilen sind die Gehäuse über die Ferse mehr oder weniger deutlich unduliert. Die Höhe des Halsteils beträgt 2–5 μm, die Länge des Fussteils 4–7 μm, die ovale Halsöffnung misst etwa 2–3 μm. Der ± ovoide Protoplast passt sich der gekrümmten Gehäuseform an, ist etwa 2 × 4 μm gross und besitzt einen Chromatophoren sowie zwei wohlentwickelte, ungleich lange Geisseln, wovon die längere etwa 5 μm, die kürzere etwa 2 μm lang ist. Isogamie mit Bildung sphärischer Zygoten von etwa 5 μm Durchmesser ist beobachtet worden. Die Art ist im Sommerplankton nordskandinavischer Gebirgsseen nicht selten.

Die Eigenschaft, braun inkrustierte Gehäuse zu bilden, ist bei keiner der typischen und häufig auftretenden Arten der Gattung nachgewiesen, wenn auch Lund (1960) eine schwache Granulierung des Gehäuses von *C. skujae* (*C. gracilis*) angibt. Diese Eigenschaft verbindet *C. calceatus* so auffällig mit *Pseudokephyrion*, dass eine Zugehörigkeit zur Gattung *Chrysolykos* fraglich erscheint. Die Stellung der Art muss deshalb ebenfalls bis auf weiteres als unsicher gelten.

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Multi-layered distribution patterns and the hypothesis of rain forest refugia

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In recent years it has become a generally held opinion that the rain forests of the humid American tropics have had a much more restricted distribution during certain epochs of the Pleistocene and that these circumstances have profoundly affected speciation in rain forest organisms. The idea is put forward, that the effects of several such contractions in the forest distribution are still discernible in present-day distribution patterns and that the effects of different epochs are to be found at different taxonomic levels. The idea is elaborated using examples from the genus *Ischnosiphon* (Marantaceae), which was recently revised by the author.

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When I summed up a taxonomic revision of the genus *Ischnosiphon* (Andersson 1977), I found that the distribution patterns in that genus, as in so many other groups of rain forest organisms, were best explained by the theory of rain forest refugia. The theory assumes the existence of dry periods in the Pleistocene, during which stenotropic rain forest organisms became isolated in restricted rain forest refugia. Generally speaking, the present-day species of *Ischnosiphon* do not appear to occupy the full distribution area of their ecological potential, but have much more restricted ranges. As there are often no apparent distribution barriers, these ranges must be explained on a historical basis. Furthermore, widely distributed species like *I. leucophaeus* and *I. obliquus* are usually polymorphic, and the different forms show distinct distributional patterns coinciding with those at the species level. This pattern is common and well known by now. For a general survey of the topic, the reader should consult Prance (1973) and Simpson (1971).

Previous attempts to systematize individual distribution patterns have dealt with species and subspecies. In *Ischnosiphon* I found that groups of related species also may show distinct patterns, which led me to think that there has been not one but several refugium cycles in South America, the older ones of which have caused distributional patterns now discernible at a supraspecific level. I was strengthened in this belief by the fact that there have been several glaciations in the temperate zone and by the generally held opinion that the cold climate in the temperate zone was correlated with a dry one in the tropics. In recent years it has also been shown (van der Hammen 1974) that the Colombian Andes have been affected by numerous glaciations during the Pleistocene. It may thus be taken for granted that the climatic changes of the Pleistocene have affected also the tropics. However, very few data from the lowlands are presently available.

As I consider the number of species in *Ischnosiphon* to be too small for wide-ranging conclusions, I rather hesitated to state that "refugia . . . did not necessarily exist only once and . . . were not necessarily contemporaneous" (Andersson 1977 p. 24). Although my

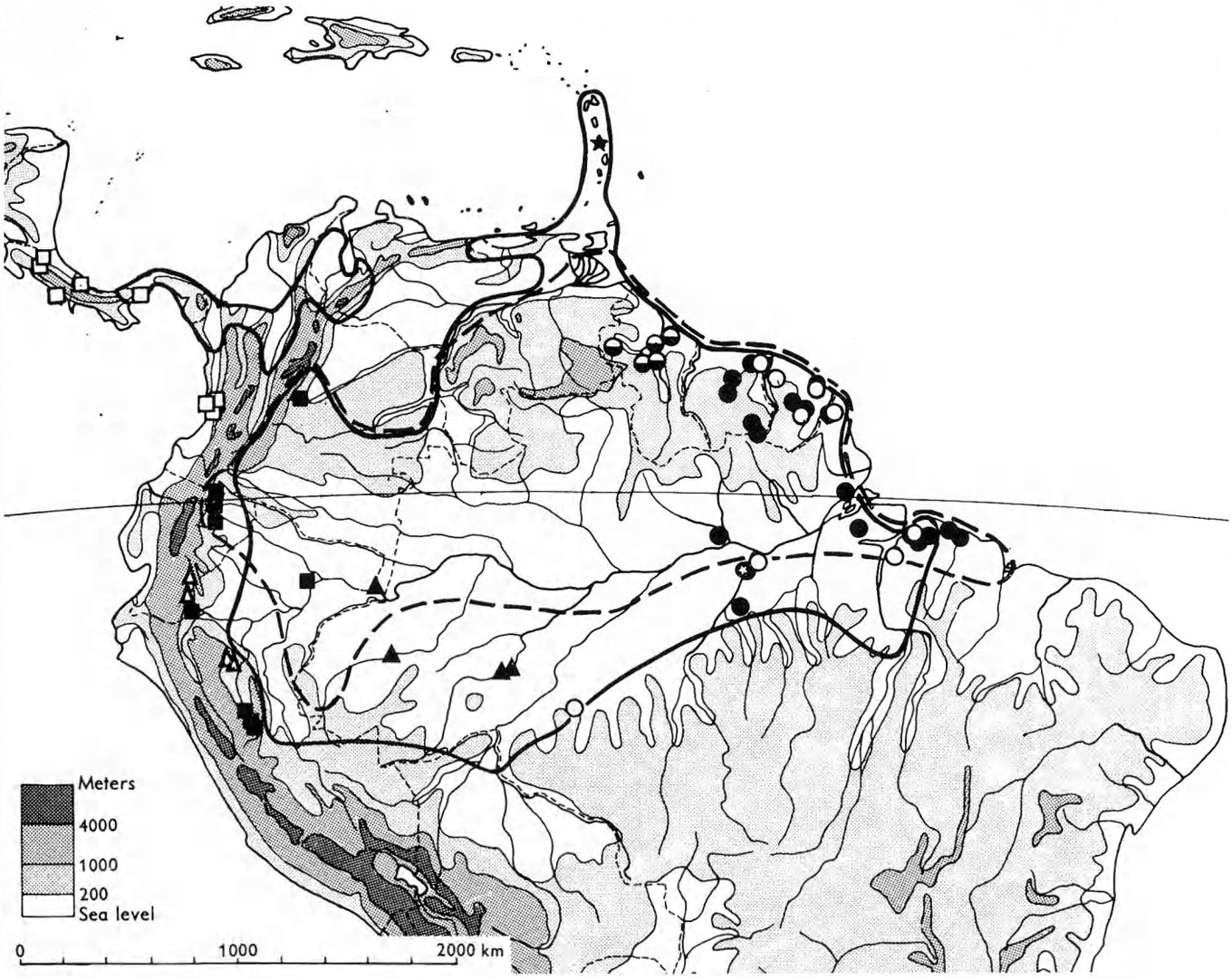

Fig. 1. Distribution patterns in *Ischnosiphon* sect. *Ischnosiphon*. Solid line: approximate range of *I. arouma*. Broken line: approximate range of *I. obliquus*. Symbols: ■ *I. cerotus*, □ *I. inflatus*, ● *I. petiolatus*, ○ *I. martianus*, ◒ *I. foliosus*, ✪ *I. paryrizinho*, △ *I. annulatus*, ▲ *I. grandibracteatus*, ★ isolated occurrence of *I. obliquus*, the spontaneity of which has been doubted. Affinity is expressed by the choice of symbols, triangular, square or circular.

factual basis has not been widened since then, a discussion with Dr G. T. Prance made me realize that my preliminary ideas might be of interest to other researchers concerned with Amazonian plants.

At this point it must be stressed that the kind of reasoning used in this paper requires a thorough understanding of the taxonomy of the group concerned. The relevant distribution patterns often turn up at different taxonomic levels in different parts of a genus and the entities which are appropriate from a phytogeographic point of view are often not practical from a taxonomic one. A person aquainted with distribution maps, but ignorant of taxonomic details might easily reach false conclusions.

Supraspecific distribution patterns in Ischnosiphon

Section Ischnosiphon (Fig. 1). Within sect. *Ischnosiphon*, comprising ten species, three groups of mutually more closely related species can be discerned, viz. *I. cerotus* and *I. inflatus; I. arouma, I. petiolatus, I. foliosus, I. paryrizinho* and *I. martianus*; *I. grandibracteatus* and *I. annulatus*. *I. obliquus*, the tenth species, is widely distributed (almost the entire Amazon Basin and the Guianas) and its taxonomic position is unclear since it shows relationships to all three groups. The taxonomical considerations are discussed in Andersson 1977 pp. 30–52. The first group, which I consider

to be the most primitive one in the genus (Andersson 1977 p. 31), has a north-western distribution, *I. inflatus* occurring in Pacific Colombia, Panama and Costa Rica and *I. cerotus* along the eastern fringe of the Andes in Peru, Ecuador and Colombia. The third group too, has a western distribution, *I. annulatus* occurring on the eastern foothills of the Andes in Peru and Ecuador and *I. grandibracteatus* in the lowlands of the western Amazonia between Rio Purus and Rio Javarí.

The second group contains one very widespread species (*I. arouma* – Amazon Basin, Guianas, Lesser Antilles, Orinoco drainage, Maracaibo Basin, Panama and Chocó), but the rest of the species are decidedly eastern. Of these eastern species *I. martianus* reaches farthest to the west and occurs in the Rio Madeira Basin. Two of the species appear to be narrow endemics, viz. *I. foliosus* in the Essequibo drainage and *I. paryrizinho* at the lower Rio Tapajós.

Within sect. *Ischnosiphon* different distribution patterns can thus be discerned at different taxonomic levels. The section is distributed over almost the entire area of the genus. At an intermediate level there is a distinction between western and eastern groups of species, and at the species level each species has its own particular distribution pattern. The specific ranges mostly center around previously hypothesized refugium areas (cf. Prance 1973). At the subspecific level, the widespread species *I. obliquus* shows a regional differentiation closely resembling that at the species level (cf. Andersson 1977 pp. 38–39). The subspecific differentiation is not into forms sufficiently discrete for taxonomical recognition.

Section Papilloderma (Fig. 2) parallels sect. *Ischnosiphon* in taxonomic and distributional differentiation, although the patterns are not equally clear. From a purely phytogeographical point of view the species could be divided into a western group and an eastern group. The former comprise *I. colombianus* (Macarena area in Amazonian Colombia), *I. elegans* (Costa Rica), *I. caudatus* (Iquitos area in Amazonian Peru) and *I. helenae* (Panama and Chocó). The latter group comprises *I. cannoideus* (central Amazon Basin between Rio Madeira and Rio Negro drainages and Rio Tapajós) and *I. ovatus* (coastal mountains of SE Brazil). *I. leucophaeus* is very widely distributed, occurring in Costa Rica, Panama, the Pacific Coast south to Guayaquil, the Maracaibo Basin, the Orinoco drainage, the Guianas and almost the entire Amazon Basin. Plants from Costa Rica, Panama, Chocó, Magdalena Valley and the Maracaibo Basin are quite distinct and have been referred to a separate subspecies (ssp. *ramosus*), while the rest is a regionally differentiated, polymorphic complex without morphologically discrete limits (cf. Andersson 1977 pp. 76–78).

The pattern of phenetic relationships within the section is a reticulate one and it is difficult to draw well-founded phylogenetic conclusions. An educated guess would be that *I. colombianus, I. elegans* and *I. caudatus,* all western species, on the one hand and *I. cannoideus, I. helenae* and perhaps *I. leucophaeus* on the other are phylogenetically more closely related to each other than to any other species of the section. *I. ovatus* resembles some forms of the polymorphic *I. leucophaeus* ssp. *leucophaeus,* but not those ones connecting with the other species of the section. I further guess that the species of sect. *Papilloderma* have arisen through the splitting up of an ancient, more or less *leucophaeus*-like species, in part perhaps as a consequence of "quantum speciation" (Grant 1971 pp. 114 ff.). These ideas have been visualized in Fig. 3.

When combining distribution data and phylogenetic speculations, one thus reaches a picture, which is similar to that of sect. *Ischnosiphon*. The section is thought to embrace three phyletic lines, viz. (1) *I. cannoideus* and *I. helenae,* (2) *I. colombianus, I. elegans* and *I. caudatus,* (3) *I. leucophaeus* and *I. ovatus*. The lines have probably arisen from a common stock, which was split up by the process of geographic speciation comparatively long ago. The lines still have faintly discernible distribution patterns, the first central Amazonian–north western, the second western, and the third uncertain, but possibly eastern. The three lines have later on become further split up and the much later origin of the present species is indicated by their distinct distribution patterns.

Section Hirsuti is rather closely related to sect. *Papilloderma*. It accommodates four closely interrelated species, viz. *I. hirsutus* (mainly from Rio Madeira-Rio Negro westwards to the Andes,

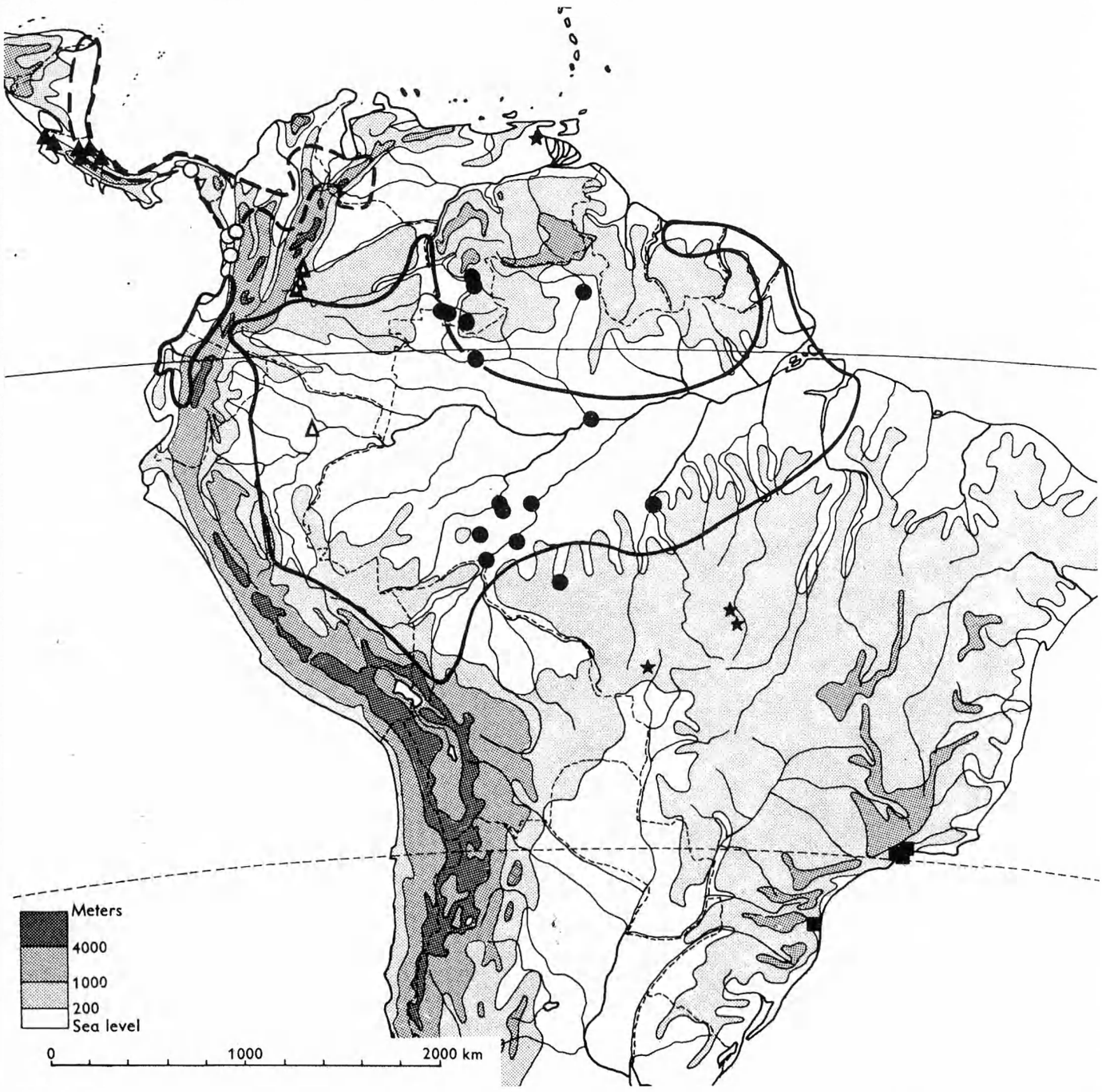

Fig. 2. Distribution patterns in *Ischnosiphon* sect. *Papilloderma*. Approximate range of *I. leucophaeus* is indicated by lines, solid line for ssp. *leucophaeus* and broken line for ssp. *ramosus*. Symbols: ● *I. cannoideus*, ○ *I. helenae*, ▲ *I. elegans*, ▲ *I. colombianus*, △ *I. caudatus*, ■ *I. ovatus*, ★ isolated occurrence of *I. leucophaeus* ssp. *leucophaeus*. Affinity is expressed by the choice of symbols, circular, triangular or square.

but also one locality at the Amazon Mouth), *I. lasiocoleus* (Amazon Basin west of Rio Madeira-Rio Negro), *I. idrobonis* (SE Amazonian Colombia) and *I. macarenae* (Cordillera de la Macarena at the eastern fringe of the Colombian Andes and Amazonian Peru E of Iquitos, a very recent collection). The entire section is thus decidedly western in distribution.

Sections Bambusastrum, Rotundifolii and Longiflori. The remaining sections are not rewarding for discerning multi-layered distribution patterns. They are widely distributed in the Amazon Basin and the Guianas. Two species, *I. puberulus* and *I. longiflorus*, are widespread and polymorphous, the others have limited ranges, centering around previously hypothesized re-

fugia, which probably existed during a comparatively recent dry period.

Discussion

From the data reviewed above, I have concluded that the taxogenesis of *Ischnosiphon* has proceeded in an unstable environment and that the diversity and differentiation is the result of a long succession of climatic events. Periods, during which suitable habitats were very restricted and widely separated, have altered with periods, during which favourable conditions were prevalent over vast continuous areas. The ancestral populations have thus become isolated and merged repeatedly. During periods of restricted distribution both natural selection and random factors may be expected to have had an increased effect on the populations making them diverge genetically, physiologically and morphologically. Also periods of confluent distributions should be expected to have had an appreciable effect, offering opportunities for new combinations of genes to arise, thus creating new material for natural selection to work on.

If, as van der Hammen's (1974) data seem to indicate, there have been as many as thirty dry periods in South America (and thus probably in all of the humid tropics), it is unlikely that we would be able to trace more than a few of the latest ones in present phytogeographic patterns. Within these limits, however, it is my conviction that much can be done comparing taxonomic and phytogeographic data. The approach is by no means new, but needs reliable taxonomic bases and has therefore been little used in the tropics. Considering the present example, the phenetic diversity pattern in *Ischnosiphon* suggests an evolution step by step. The first steps, which led to the differentiation of the sections (which perhaps are not phylogenetically comparable entities) occurred too long ago to have left still discernible distribution patterns. The differentiation of more or less distinct subgroups within the sections can still be attributed to particular although very roughly circumscribed areas. Finally the patterns are usually very clear and distinct at the species level.

The most logical explanation of the differences in distinctness of the distribution patterns at different taxonomic levels seems to be that the differentiation occurred at different times, but as a response to similar factors. It must be stressed, however, that entities of the same taxonomic rank in all probability did not all arise at the same time. I think that this will become clear as distributions in the tropics become better known.

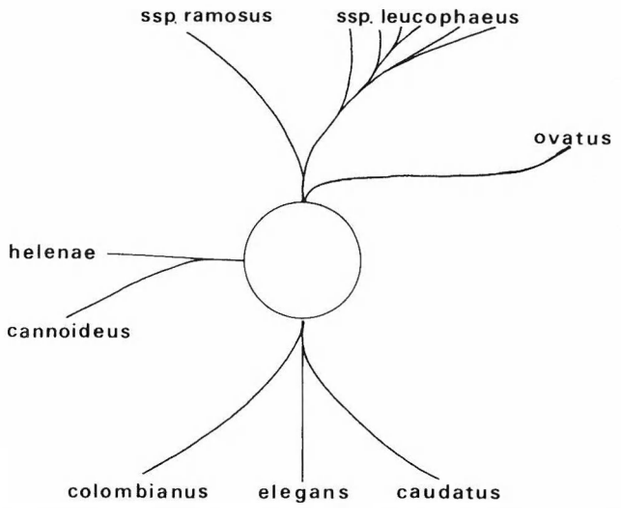

Fig. 3. Hypothesized phyletic relationships within *Ischnosiphon* sect. *Papilloderma*.

The drought periods were certainly not equally severe. Refugia, which were large and continuous during one epoch, were split up during another one. The Napo area, to take one example, has been considered to have been a vast rain forest refugium, but there are certainly variations in different parts of it. This possibly reflects, among other things, differences in biohistory. My own observations are not sufficient to elaborate this theme.

Although most hypotheses and theories dealing with tropical palaeoecology remain to be proven or consolidated, it has been clear for a number of years that the old picture of the tropics as an eternally stable biotum is rapidly falling into pieces. It is a relief to see the need for extraordinary or almost supernatural explanations of tropical taxonomic diversity disappear.

Acknowledgement. I am much indebted to Dr Ghillean T. Prance, New York Botanical Garden, for fruitful discussions and for a critical reading of the manuscript.

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The taxonomic position of Nectaroscordum koelzii (Liliaceae)

Karin Persson and Per Wendelbo

Persson, K. & Wendelbo, P. 1979: 05 15: The taxonomic position of Nectaroscordum koelzii (Liliaceae). *Bot. Notiser 132:* 191–196. Stockholm. ISSN 0006-8195.

The species *Nectaroscordum koelzii* Wendelbo has been transferred to the genus *Allium* as *A. koelzii* (Wendelbo) K. Persson & Wendelbo. As it differs from the other species of *Allium* in having several nerves in the tepals it is placed in a section of its own, *Pseudoprason* (Wendelbo) K. Persson & Wendelbo. Morphological characters clearly point to *Allium* as the right genus. The chromosome number 2n = 16, as well as details in the karyotype also favour *Allium*. True *Nectaroscordum* species have 2n = 18. In its geographical distribution *Allium koelzii* shows similarity to *Nectaroscordum tripedale*. It is endemic to the Zagros mountains of Iran, whereas *N. tripedale* has an Armeno-Kurdish pattern with a Zagros extension.

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A new species, *Nectaroscordum koelzii,* from the Zagros mountains of SW Iran was described by Wendelbo (1966). The species showed many differences from other species of the genus, and Wendelbo (1971) accordingly placed it in a section of its own, *Pseudoprason*. Already in this latter paper doubts about its true relationships were raised. More material has made it clear that the species, in spite of the several-nerved tepals, is not closely related to the true *Nectaroscordum* species and might better be placed in *Allium*. Living material also made a cytological comparison possible.

Nectaroscordum s.str. is a small genus of three or possibly four very closely related species: *N. siculum* (Ucria) Lindley in S France and S Italy; *N. bulgaricum* Janka in Roumania, Bulgaria, E Greece and adjacent parts of Turkey, and *N. tripedale* (Trautv.) Grossh. in the Transcaucasus of the USSR, NE Iraq and the Zagros mountains of Iran. Finally, the doubtful *Allium meliophilum* Juzep. from the Crimea also belongs here.

Reasons for separating *Nectaroscordum* as a genus from *Allium* are found in the several-nerved tepals, the tepals being attached to a broad, well-developed disc, in the semi-inferior ovary, and in the strongly keeled leaves of which the innermost encloses the scape for about 2/3 of its length while all the other leaves are basal. Stearn (1955) points out that *Allium* is such a variable genus that *Nectaroscordum* could well be included in it. We tend to agree but want to make further anatomical and cytological studies before we make our final conclusions.

Morphology

Nectaroscordum koelzii has several nerves in the tepals (3–7 in the outer, 1–3 in the inner ones, Fig. 1 B), which is a character not found in *Allium* to our knowledge. Thus in this respect it is similar to *Nectaroscordum* s.str. But the tepals are small (4–5 mm long; 12–20 mm in the other species) and do not have the clear distinction between the outer elliptic-oblong ones and the inner ones with a marked claw and a ± heartshaped lamina which is so characteristic of the true *Nectaroscordum* species (Fig. 2 A–C). The absence of a clearly defined disc in *N. koelzii* (Fig. 2 E, cf. D), the broad connate filaments adnate above the base of the tepals as

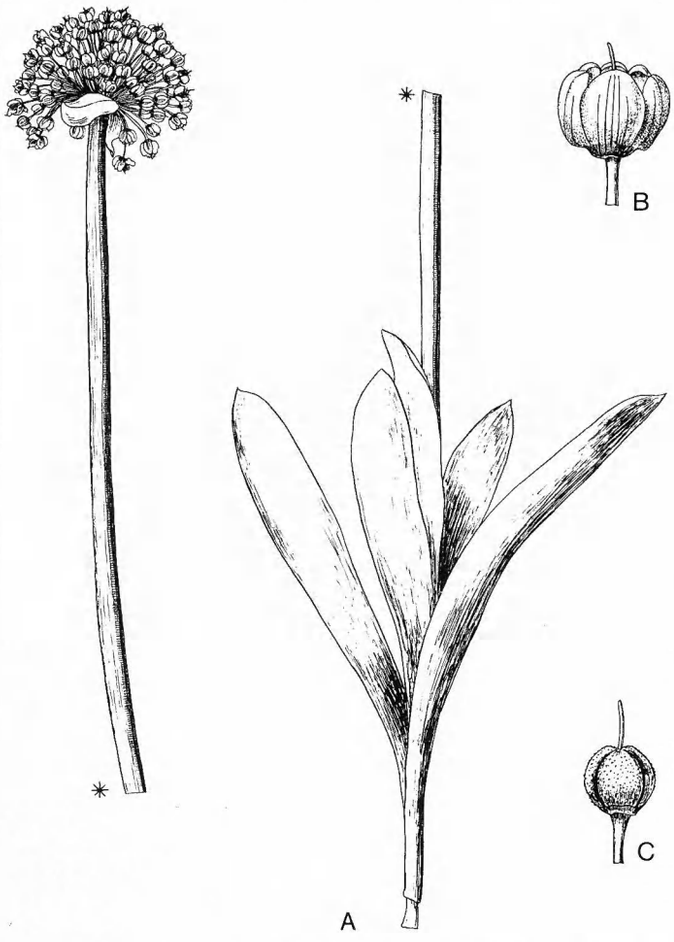

Fig. 1. *Allium koelzii* (holotype). – A: Habit, × 0.25. – B: Perianth with part of pedicel, × 2. – C: Ovary with style and part of pedicel, × 2. – Miranda Bödtker del.

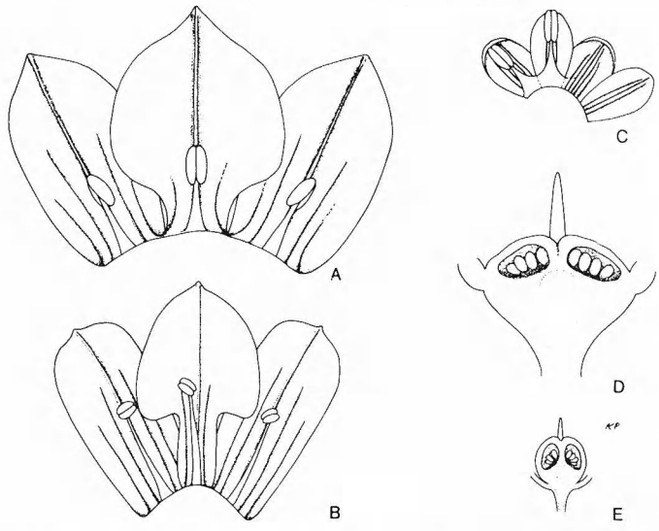

Fig. 2. Part of dissected perianths (A–C) and apex of pedicel and gynoecium in longitudinal section (D, E). – A, D: *Nectaroscordum bulgaricum* (E. B. Anderson 1942). – B: *N. tripedale* (Stapf 1986). – C, E: *Allium koelzii* (Iranshahr 8033 E). – All × 1.6.

well as the verruculose ovary (Fig. 1 C) are also characters not found in the other *Nectaroscordum* species, but common in *Allium*. All leaves are basal and unkeeled (Fig. 1 A), they look like leaves found in many species of *Allium* subgenus *Melanocrommyum* (Webb & Berth.) Wendelbo and are very different from those of *Nectaroscordum* s.str. The distinctly superior ovary contains 4–8 ovules per locule. The true *Nectaroscordum* species also have many ovules in each locule, but this is a feature shared with species of subgenus *Melanocrommyum* as well.

As regards the odour of the *Nectaroscordum* species we do not agree with Stearn (1955) and others that it is similar to that of an *Allium* or particularly "garlicky": both *N. bulgaricum* and *N. tripedale* have a very strong repugnant odour of a quite special quality, quite unlike that of *Allium* species and of *N. koelzii*.

A renewed study of the morphology of *Nectaroscordum koelzii* thus leads to the conclusion that it has more characters in common with *Allium* than with the genus in which it was placed originally.

The investigation was carried out on material of spontaneous origin (see Table 1 for localities), cultivated in the Botanical Garden, Göteborg. Material of *N. bulgaricum* (Fig. 2 A, D), obtained from the well-known British bulb grower E. B. Anderson and cultivated in Göteborg since 1942, may in fact belong to *N. siculum*. Our spontaneous material of *N. bulgaricum* from Roumania has not yet flowered and we have thus had no possibility of comparing living material. Root-tips were pretreated in a mixture of 0.6% colchicine and 2 mM 8-hydroxyquinoline and then stained and squashed according to the Feulgen method. The idiograms were based on measurements of ten good metaphase plates with about the same degree of contraction from one plant of each species. From all other plants several plates were drawn for comparison. The karyological nomenclature follows Levan et al. (1965).

Cytology

Two earlier records of *Nectaroscordum* species exist. The first is an early one (Mensinkai 1939, "*Allium siculum*"). This species was stated to have 2n = 16. Some doubts must be raised as to the accuracy of the number, however, as it was observed on metaphase plates of seemingly quite poor quality (from anther-wall cells); cf. the author's statement that "possibly one of the

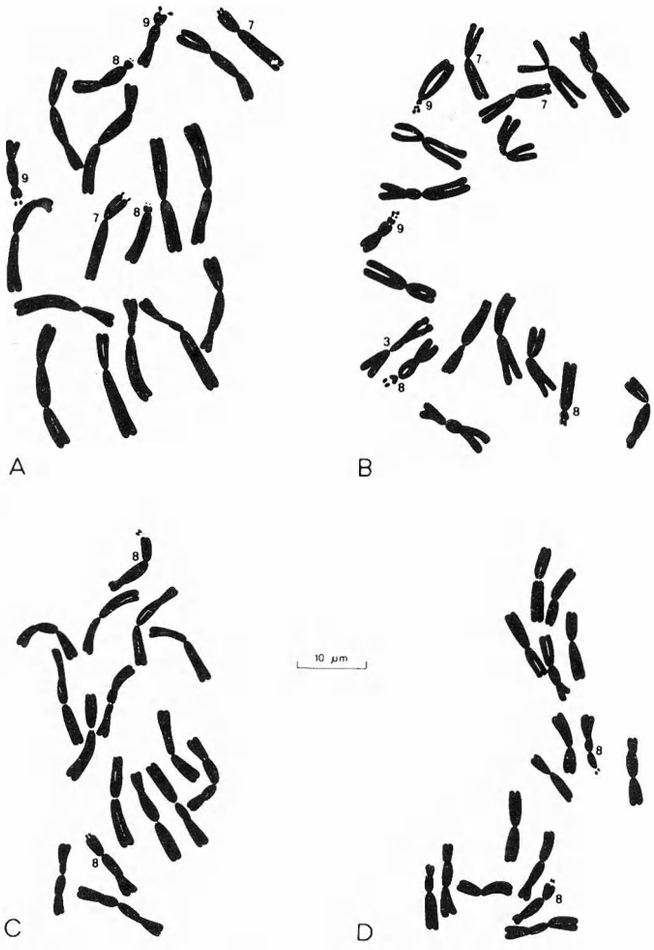

Fig. 3. Mitotic metaphases. – A: *Nectaroscordum bulgaricum* (Roumania, Babadag, leg. Forstner & Păşlăraşu). – B: *N. tripedale* (USSR, Armenia, Erevan). – C, D: *Allium koelzii* (C: Iran, Ariamehr Botanical Garden, D: Iran, Iranshahr 8033 E).

chromosomes is supplied with a satellite''. Also, there is some doubt about the true identity of the species (*N. siculum* s.str. or *N. bulgaricum*), as the investigated material was of unknown origin. The second record (Cheshmedzhiev 1971) states 2n = 18 for *N. bulgaricum* of spontaneous origin (Bulgaria). The same number was found by us (Fig. 3 A), and our idiogram for the species (Fig. 4 A) is very similar to that of the latter author. Seven of the chromosomes in the haploid set are metacentric to submetacentric, with a satellite on one of the msm chromosomes (no. 7). Chromosomes nos. 8 and 9 are considerably

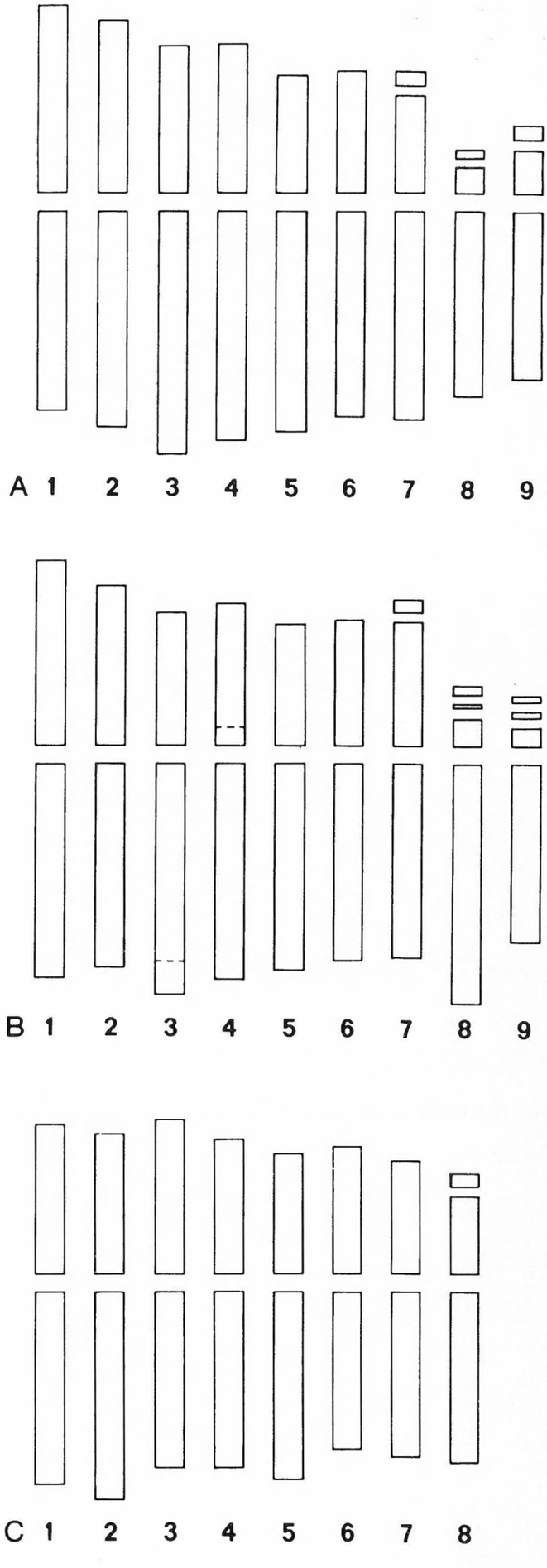

Fig. 4. Idiograms of haploid chromosome complements. – A: *Nectaroscordum bulgaricum* (Roumania, Babadag, leg. Forstner & Păşlăraşu). – B: *N. tripedale* (USSR, Armenia, Erevan). – C: *Allium koelzii* (Iran, Ariamehr Botanical Garden). – Hatched lines indicate weak secondary constrictions.

Table 1. Chromosome numbers and localities of investigated material.

2n	Collector or source	Locality
Nectaroscordum bulgaricum		
18	E. B. Anderson	
18	Dobrescu	Roumania, Deleşti, Pd. Scroafa
18	Forstner & Păşlăraşu	Roumania, Tulcea, Babadag
Nectaroscordum tripedale		
18	Erevan Bot. Gard.	USSR, Armenia, Erevan
18	Ariamehr Bot. Gard.	Iran
Allium koelzii		
16	Ariamehr Bot. Gard.	Iran
16	Iranshahr 8033 E	Iran, Arak: Golpayegan, Hendeh, 2200–2800 m

shorter than the rest, ± subtelocentric, and have a satellite of the "cepa" type (cf. Ved Brat 1965) attached to the short arm.

The karyotype of *N. tripedale* (Figs. 3 B, 4 B) is quite similar to that of *N. bulgaricum,* with only minor differences in arm index. Thus the chromosomes nos. 8 and 9 are even more asymmetric (stt) and are supplied with "tandem" satellites of a type earlier found in a few *Allium* species, also on more or less subtelocentric chromosomes, viz. in *A. cepa* (Taylor 1926), *A. validum* and *triquetrum* (Levan 1932) and *A. darwasicum* (Mensinkai 1939).

On the whole, the karyotypes of the true *Nectaroscordum* species do not deviate much from the general pattern found in *Allium*. St–t chromosomes do occur in *Allium,* though they are rare (Anderson 1931), and so do deviations from the general basic numbers x = 7 or 8 and from the usual pattern of continuous transition in size from the smallest to the largest chromosomes. In fact, these characters often coincide, e.g. in *A. karataviense,* 2n = 18 (Levan 1932) and the *A. decipiens* group, 2n = 20 (Vakhtina 1964, 1974, Pedersen & Wendelbo 1966), of the subgenus *Melanocrommyum, A. triquetrum* (Levan 1932) and *pendulinum* (Levan 1935), 2n = 18, of the subgenus *Molium,* and *A. kujukense,* 2n = 20 (Vakhtina 1964), of the subgenus *Allium*. A slight difference can be observed, however, in the symmetry of the *Nectaroscordum* karyotype as compared with *Allium:* it seems as if the mean value of the r-values for the m and sm chromosomes is somewhat higher in *Nectaroscordum* s.str. (*N. bulgaricum:* mean for nos. 1–7 is 1.55, *N. tripedale:* mean = 1.48) than in the *Allium* species described in literature up till now.

According to some authors (Levan 1932, 1935, Mensinkai 1939, Ved Brat 1965, Kollmann 1969) the reason for the linking of the characters mentioned above is to be found in the origin of the deviating higher numbers: through a probable fragmentation of a large m chromosome, possibly followed by reciprocal translocations with another chromosome of the set involved, which would result in two t or st chromosomes, respectively, from each fragmented m chromosome. This could explain the origin of the genus *Nectaroscordum* from a species or an ancestor of *Allium,* followed by further structural changes such as translocations that gave rise to the slightly more advanced state of a somewhat more asymmetrical karyotype.

On the other hand, *N. koelzii* (Figs. 3 C, D, 4 C) has a karyotype of a quite "typical" *Allium* character (besides consisting of chromosomes distinctly shorter than in *Nectaroscordum* s.str.): 2n = 16, the chromosomes are more symmetric (r is 1.1–1.6, mean 1.35, for nos. 1–7) with one chromosome having a slightly higher arm index (r = 1.9) and being supplied with a small satellite on its short arm. One pair of the latter type of chromosomes is found in many diploid species of *Allium,* especially those with 2n = 16, e.g. many species in the subgenera *Rhiziridium* (Levan 1935, Vakhtina 1965) and *Melanocrommyum* (Levan 1935, Szelubsky 1950, Vakhtina 1969, Kollmann 1970). In fact, the karyotype of *N. koelzii* looks very like that of some of the species within the subgenus *Melanocrommyum,* e.g. *A. mirum* (Pedersen & Wendelbo 1966), *A. nigrum* and *A. suworowii* (Levan 1935). The species in this subgenus generally seem to have a slightly more asymmetric karyotype (r = c. 1.0–1.6 in the m-sm chromosomes, like in *N. koelzii*) than the species in the other subgenera (corresponding arm index often only c. 1.0–1.3; cf. Levan 1935, Vakhtina 1965, 1969, Kollmann 1970, Garbari & Senatori 1975). This similarity, chiefly to the subgenus *Melanocrommyum,* is thus well in line with the results from the morphological observations. Transferring *N. koelzii* to the genus *Allium* therefore seems well

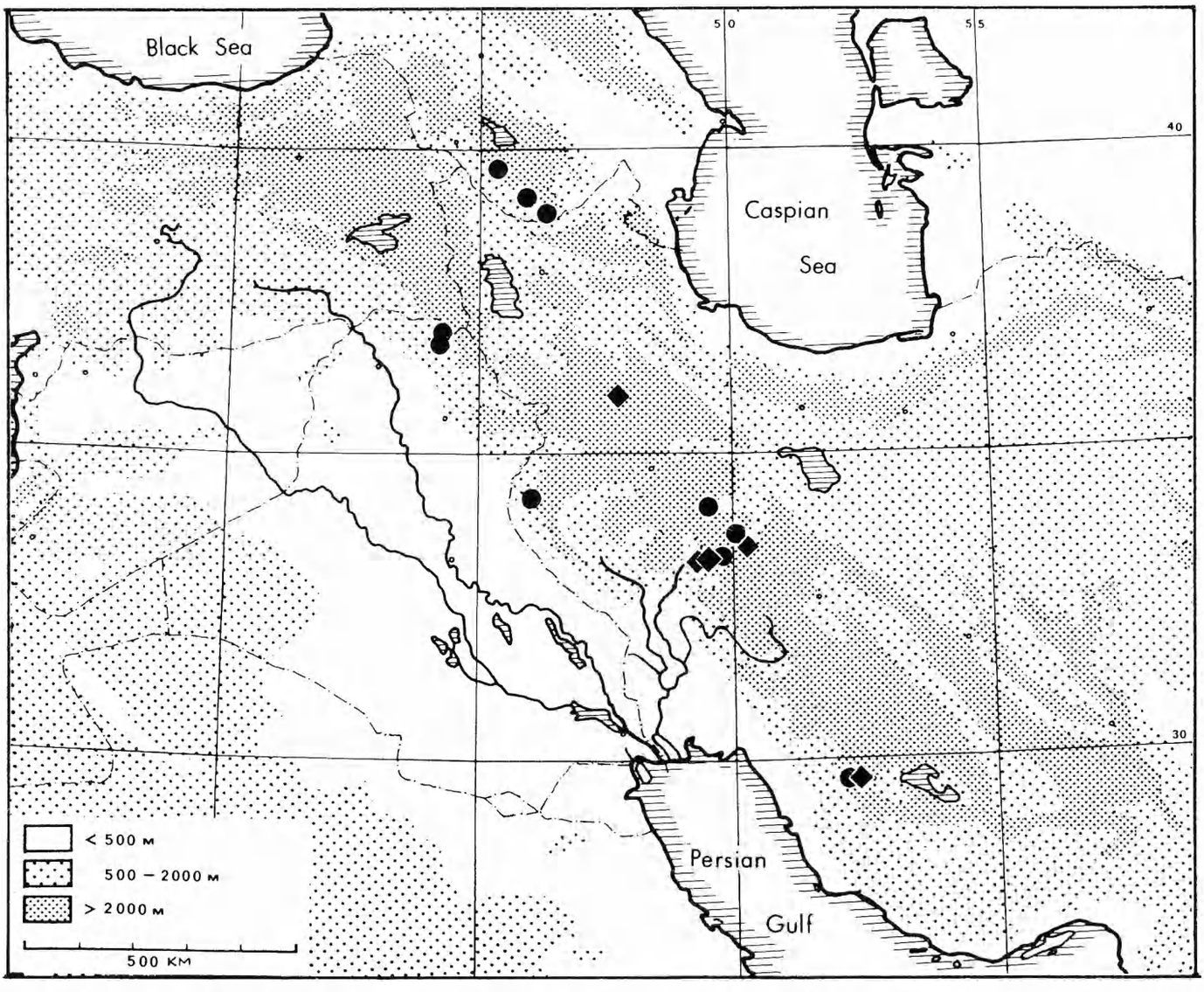

Fig. 5. Total known distribution of ◆ *Allium koelzii* and ● *Nectaroscordum tripedale* (localities in the USSR from *Flora Kavkaza 2*).

motivated. Should, after further investigations, also the other *Nectaroscordum* species be found better transferred to *Allium,* their exact taxonomic position ought to be removed from the apparently quite unrelated *N. koelzii,* preferably in a subgenus of its own.

Distribution

Oddly enough, this rather large and characteristic species is known only from rather few collections (see Wendelbo 1971, Matine 1975, 1976). No information is available about the ecological conditions under which it grows. The pattern of distribution (Fig. 5) is similar to that of the Zagros group (Hedge & Wendelbo 1978). It is endemic to the Zagros mountains. A curious fact is the striking similarity with the Iranian distribution of *Nectaroscordum tripedale* (cf. Matine 1975). But the latter species extends northwards to the Transcaucasus and is also known from NE Iraq (Fig. 5), and phytogeographically it should perhaps be placed in the Armeno-Kurdish group with a Zagros extension (Hedge & Wendelbo 1978). The other *Nectaroscordum* species are found within the Mediterranean floristic region.

Conclusions

Both from a cytological and a phytomorphological point of view, *Nectaroscordum koelzii* differs clearly from the other species of the genus and is better transferred to *Allium*. In this genus it should be placed in the subgenus *Melanocrom-*

myum, but due to the several-nerved tepals it should be kept in a section of its own.

Allium sect. **Pseudoprason** (Wendelbo) K. Persson & Wendelbo, comb. nov.

Basionym: *Nectaroscordum* sect. *Pseudoprason* Wendelbo in K. H. Rechinger, Flora Iranica Lfg. 76: 2 (1971). – Type species: *Allium koelzii* (Wendelbo) K. Persson & Wendelbo.

Allium koelzii (Wendelbo) K. Persson & Wendelbo, comb. nov.

Basionym: *Nectaroscordum koelzii* Wendelbo, Acta Horti Gotob. 28:5 (1966). – Type: Koelz 15913, W holotype.

Acknowledgement. The present study was supported by grants from the Swedish Natural Science Research Council.

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The taxonomic position of Bellevalia tabriziana (Liliaceae)

Karin Persson and Per Wendelbo

Persson, K. & Wendelbo, P. 1979 05 15: The taxonomic position of Bellevalia tabriziana (Liliaceae). *Bot. Notiser 132:* 197–200. Stockholm. ISSN 0006-8195.

Bellevalia tabriziana Turrill is in its habit not unlike *Hyacinthella* species and has formerly been treated as such. A close examination of the morphological characters shows that it should be placed in *Bellevalia* sect. *Patens* subsect. *Romana*. The karyotype (2n = 8) is typical of *Bellevalia* and quite conclusive. The idiogram is presented and discussed. New localities for the species are given; they are all situated within a small area in the central part of Azarbayejan, Iran. Phytogeographically *B. tabriziana* should be assigned to the Armeno-Kurdish element. The species which are the closest relatives have a Zagrosian distribution.

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Turrill (1929) described *Bellevalia tabriziana* with the alternative name *Hyacinthus tabrizianus* Turrill, from near Tabriz in the province of Azarbayejan, NW Iran. The new species was said to come closest to *B. micrantha* Boiss. and should thus be placed in the section *Hyacinthella*. Feinbrun (1940), in her *Bellevalia* monograph, separated *Hyacinthella* as a genus and accordingly left out also *Hyacinthella tabriziana* (Turrill) Feinbr. When Feinbrun (1961) monographed *Hyacinthella, H. tabriziana* was found after all to be a true *Bellevalia*. Still a lot of uncertainty remained.

During collecting trips to NW Iran in the springs of 1976 and 1978 one of us (P.W.) found *B. tabriziana* in 4 localities, all in central Azarbayejan. In the field this inconspicuous plant did not seem to be obviously related to any other species of *Bellevalia*. However, cytological studies showed that the plant had the very distinctive *Bellevalia* karyotype (cf. Delaunay 1922, Feinbrun 1938, Levan 1944, Garbari 1968, Pogosjan 1975). Furthermore ripe seeds had the typical smooth testa of *Bellevalia* species (Feinbrun 1940).

Bellevalia tabriziana Turrill

Turrill, Kew Bull. 1929: 234 (1929) – *Hyacinthus tabrizianus* Turrill, Kew Bull. 1929: 234 (1929), nomen alternativum – *Hyacinthella tabriziana* (Turrill) Feinbrun, Palest. Journ. Bot., Jer. Ser., 1: 405 (1940) – Orig. coll.: Hills S of Tabriz, 10.IV.1927, Gilliat-Smith 1775 (K lectotype! here selected).

Fig: 1, 2.

Bulb ovoid, c. 2 cm long, 1.3–1.5 cm broad, covered with greyish brown tunics elongated into a short neck. *Leaves* 3–4, lying ± flat on ground, exceeding inflorescence in length, up to 2.5 mm broad, canaliculate, distinctly ribbed below, greyish green, margin smooth. *Scapes* 1–3, up to 10 cm long below raceme, up to 1/2 of their length or more below ground-level. *Raceme* ellipsoid-ovoid, c. 2.5 × 1.5 cm, rather dense, 5–17-flowered. *Bracts* c. 1–1.5 mm long, truncate–unequally bilobed, gibbous at base, purplish. *Pedicels* 1–2 mm long, ascending. *Perianth* tubular-urceolate, somewhat zygomorphic, whitish to pale lilac-pink or pale blue, 6–7 mm long, split about half-way into broadly ovate lobes provided with a greenish violet raised middle nerve, at least the upper outer ones also with a distinct, oblique, crest- like

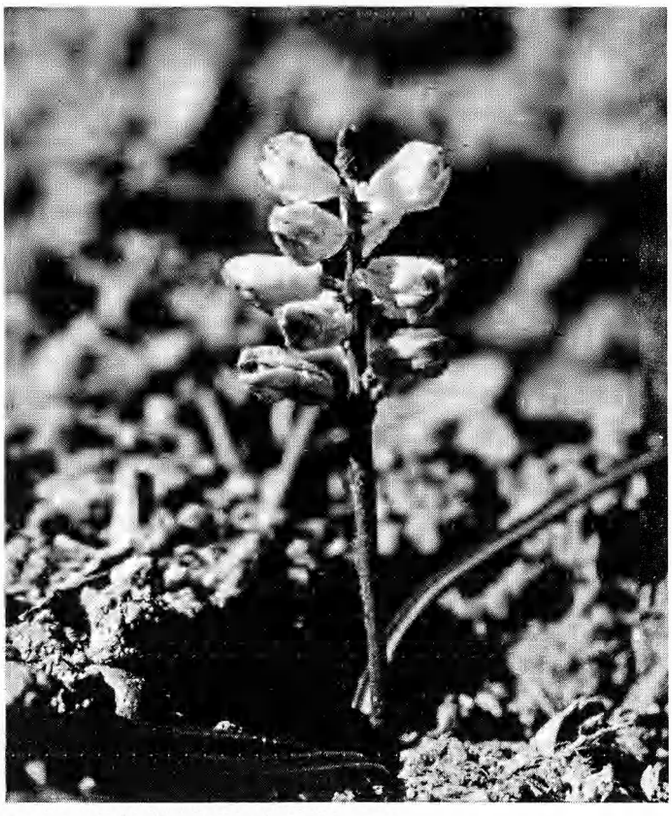

Fig. 1. *Bellevalia tabriziana,* whole plant c. 5 cm. – Wendelbo & Assadi 19209; photo PW 21.IV.1976.

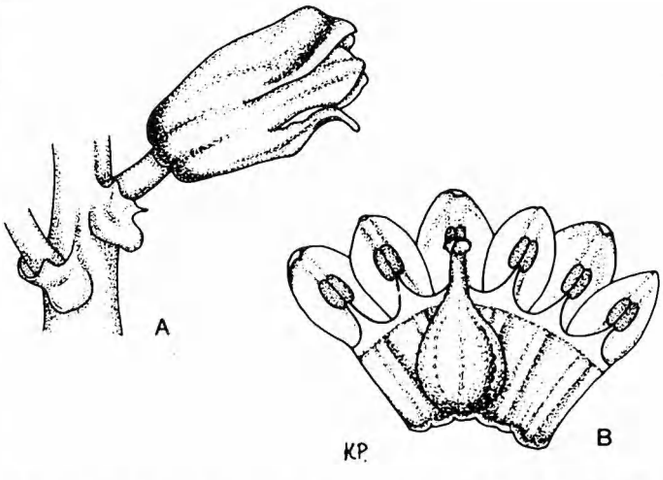

Fig. 2. *Bellevalia tabriziana* (Wendelbo & Assadi 19291). – A: Perianth with pedicel and bracts. – B: Perianth split open. – × 4.

protuberance. *Stamens* included; filaments c. 1.5 mm long, triangular, connate near base and attached just below base of perianth lobes; anthers 1–1.3 mm long, lilac. *Style* c. 1.8 mm long. *Fruiting pedicels* hardly elongated, up to 4 mm. Valves of *capsule* 8–10× 10–12 mm, suborbicular, usually somewhat broader than long,

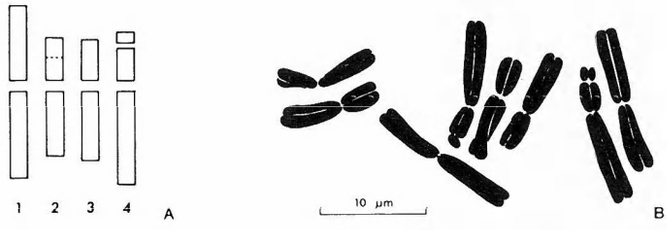

Fig. 3. Idiogram and mitotic metaphase of *Bellevalia tabriziana* (A Wendelbo & Assadi 19209, B W. & A. 19282). – Hatched line indicates a weak secondary constriction.

usually retuse at apex. *Seeds* c. 2.5 mm diam., globular, smooth with a bluish bloom.

Collections (see also type): *Iran. Azarbayejan:* Near Tabriz, 16.IV.1928, Gilliat-Smith 2211 (K!) – Near Tabriz, Egger (K!) – 23 km from Tabriz on road to Marand, 1400 m, 21.IV.1976, Wendelbo & Assadi 19209 (GB! TARI!) – 15 km NE of Shahpur on road to Sufian, 1350 m, 24.IV.1976, W. & A. 19282 (GB! TARI!) – Tabriz to Ahar, first pass, northern side, 25.IV.1976, W. & A. 19291 (GB! TARI!) – About 20 km along the Tabriz-Ahar road, 1450 m, 31.V.1978, fr., W. & A. 28018 (GB! TARI!).

Morphology

Bellevalia characters found in *B. tabriziana* are: the shape of the perianth with protuberances at least on the upper outer lobes (Fig. 2 A), the triangular, connate filaments (Fig. 2 B) attached at base of lobes (not middle of tube as stated in original description), the number of leaves (3–4), and finally the smooth seed testa. Thus only the ribbed leaves are left of what could be considered *Hyacinthella* characters. But anatomical studies are needed also of other *Bellevalia* species to check the importance of this character.

The systematic position of *B. tabriziana* within the genus must be in the section *Patens* Feinbrun subsect. *Romana* Feinbrun, but it is not obviously closely related to any of the other species. Probably *B. parva* Wendelbo, *B. decolorans* Bornm. and *B. feinbrunae* Freitag & Wendelbo are among the species that come nearest to it.

Cytology

The investigation was carried out on material collected by Wendelbo & Assadi in Iran (W. & A. 19209, 19282, 19291, see list of collections) and cultivated in the Botanical Garden, Göteborg. The root-tips were pre-

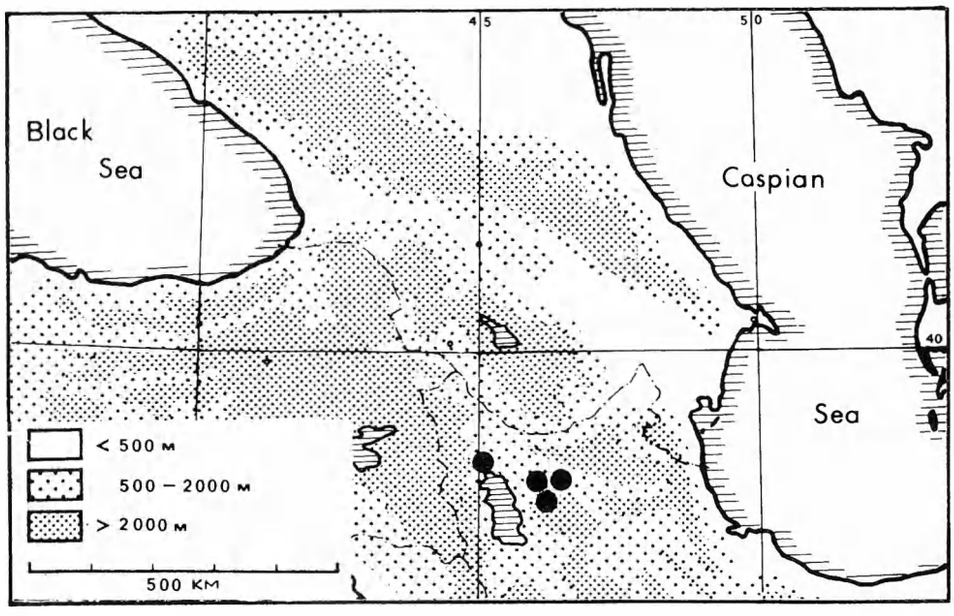

Fig. 4. Total known distribution of *Bellevalia tabriziana*.

treated in a mixture of 0.6% colchicine and 2 mM 8-hydroxyquinoline for about two hours and then stained according to the usual Feulgen squash method. The idiogram was based on measurements of ten good metaphase plates. The karyological nomenclature follows Levan et al. (1965).

B. tabriziana was found to have 2n = 8 (Fig. 3) with the basic karyotype characteristic of the genus *Bellevalia,* represented in almost all species studied, showing one large metacentric chromosome, one large and two smaller asymmetric chromosomes. The large asymmetric one is usually subtelocentric (r > 3), but in the present species it has a lower arm index (r = 2.2) and can be classified as a sm chromosome (no. 4). Such a deviation in this particular chromosome has been found also in *B. speciosa* (r = c. 1.9) of sect. *Conica* Feinbrun (Pogosjan 1975) and, interestingly enough, in *B. feinbrunae* (Bentzer et al. 1972), which belongs to the group to which *B. tabriziana* was tentatively assigned, viz., sect. *Patens* subsect. *Romana*. In *B. feinbrunae* the chromosome in question is still more symmetrical (has an almost median centromere, r = 1.05). Bentzer et al. (1972) suggest that a simple pericentric inversion may have caused the deviation, which seems plausible.

None of the other species suggested as the nearest relatives of *B. tabriziana* has been studied.

A feature apparently unknown in *Bellevalia* up till now is the large satellite observed on the short arm of the long asymmetric chromosome discussed above. Satellites in *Bellevalia* are usually (but not always) small and without exception attached to either the short arm of the large m chromosome or the long arm of the small sm-st chromosomes. In no case have satellites been observed on the large st chromosome. Heterozygosity for satellites seems to be common, however, and this is the case also in *B. tabriziana:* in the collection no. 19291 only one of the large asymmetrics had a distinct secondary constriction.

A weak secondary constriction was sometimes observed on the short arm of one of the small sm-st chromosomes (no. 2), most distinctly in coll. no. 19291.

Distribution and habitat

The known localities are situated in a small area stretching from N of the Urmia Lake to NE of Tabriz (Fig. 4). The species belongs to the Armeno-Kurdish phytogeographical element (cf. Hedge & Wendelbo 1978). Due to its small size and early flowering it has undoubtedly been overlooked in many places. There is, however, little reason to expect that new finds will change its phytogeographical status.

B. tabriziana is a plant of dry, stony slopes in hilly country, often with somewhat sandy soil. The vegetational cover is a dry, low shrub steppe. The altitudinal amplitude is between 1300 and 1650 m.

Conclusions

Typical *Bellevalia* characters of our plant are the triangular filaments attached at base of the perianth lobes and the smooth seed testa. The number and the morphology of the chromosomes leave no doubt that the species is really a *Bellevalia* in the strict sense and not a *Hyacinthella,* the examined species of which have a karyotype consisting of 2n= 18, 20, 22 or 24 definitely smaller chromosomes (Feinbrun 1961, Östergren et al. 1958, Popova 1972 and personal observations).

Acknowledgement. – The present study was supported by grants from the Swedish Natural Science Research Council.

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Alrawia, a new genus of Liliaceae-Scilloideae

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Persson, K. & Wendelbo, P. 1979 05 15: Alrawia, a new genus of Liliaceae-Scilloideae. *Bot. Notiser 132:* 201–206. Stockholm. ISSN 0006-8195.

The new genus *Alrawia* (Wendelbo) K. Persson & Wendelbo with the two species *A. nutans* (Wendelbo) K. Persson & Wendelbo and *A. bellii* (Baker) K. Persson & Wendelbo is described. Morphologically it shows similarities both to *Bellevalia* and to *Hyacinthella*. Cytologically it is clearly distinguished in its chromosome number 2n = 12. The karyotype differs much from that of *Hyacinthella* in the chromosome morphology, but is in this respect not unlike *Bellevalia*. The idiograms of the two species are presented. *A. nutans* is found in N Iraq and *A. bellii* in W Iran. They are growing in areas which might have a climax vegetation of open *Quercus* or *Pistacia-Amygdalus* forest.

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Wendelbo (1973) described a new section, *Alrawia,* of the genus *Hyacinthella* with the new species *H. nutans* as the type species. *Scilla bellii* Baker, better known under the name *Bellevalia dichroa* Hausskn. ex Bornm., was also transferred to *Hyacinthella* and placed in this section. The two species were considered to be closely related. Although they had the habit and flower colours more typical of *Bellevalia,* flower and seed characters excluded the two species from that genus. The difficulty in drawing the limits between the genera *Bellevalia, Hyacinthella* and *Muscari* as well as the possibility of solving the problems by cytological studies were pointed out.

As Dr Ali Al-Rawi of Bagdad was kind enough to supply living material of *H. nutans,* and one of us (P.W.) during a longer stay in Iran learnt to know *H. bellii* in the field and also could collect bulbs, the possibility of reevaluating the group was given.

This study of morphology and cytology has led us to raise the section *Alrawia* of *Hyacinthella* to the rank of genus.

Alrawia (Wendelbo) K. Persson & Wendelbo, gen. nov.

Hyacinthella sect. *Alrawia* Wendelbo, Kew Bull. 28: 35 (1973) – Type species: *Alrawia nutans* (Wendelbo) K. Persson & Wendelbo.

Bulb broadly ovoid; outer tunics thin, greyish, middle ones often purplish. *Leaves* 3–6, comparatively broad, cucullate and apiculate at apex. *Scape* terete. *Inflorescence* a short, several- to many-flowered raceme. *Bracts* small, bifid, lower ones gibbous at base. *Pedicels* at flowering time shorter than to about as long as perianth, recurved, becoming much elongated and thickened at fruiting stage. *Perianth* tubular-urceolate, zygomorphic, umbilicate at base, nodding, persistent during development of the fruit; tepals subequal, connate for a shorter or longer distance into a cup or tube, upper outer segments with an oblique, crest-like protuberance near apex. *Filaments* linear-cuspidate, nearly reaching apex of perianth. *Style* elongated, slender, with subcapitate stigma at level of anthers. *Ovary* with 2 ovules per locule. *Fruit* a broadly ovoid loculicidal capsule with broadly

ovate, retuse to subacute valves, suddenly narrowed at base to a short, thick foot. *Seeds* 1–2 per locule, globose to broadly ovoid, ovate-triangular in cross-section, with wrinkled surface, black, glossy.

The genus is named in honour of the Iraqi botanist Dr Ali Al-Rawi, formerly Director of Botany and Keeper of the National Herbarium of Iraq, Bagdad and collaborator of Flora of Iraq.

Key to the species

1. Leaf margin smooth; perianth in lower part tubular, tepals free for about 1/2 of their length .... 1. *A. nutans*
– Leaf margin shortly ciliate; perianth in lower part cup-shaped, tepals free for at least 3/4 of their length ..... 2. *A. bellii*

1. **Alrawia nutans** (Wendelbo) K. Persson & Wendelbo, comb. nov.

Basionym: *Hyacinthella nutans* Wendelbo, Kew Bull. 28: 33 (1973) – Orig. coll.: Iraq, 3 km S of Sinjar, Hikmat Abbas Al-Ani 9387 (K holotype!).

Fig.: Wendelbo 1973 p. 34.

Bulb 2.5–3 cm in diam. *Leaves* 3–4(–5), shorter than scape, outer broadest (1.5–3 cm), margin smooth, green. *Scape* solitary, 25–35 cm including raceme, for somewhat less than 1/2 of its length below ground-level; in fruit up to 50 cm. *Raceme* 12–35-flowered, about 3 cm long and broad, rather dense but soon elongating, rachis purplish-violet. *Pedicels* in flowering state 5–12 mm, recurved. *Perianth* 10–13 mm long with tepals connate for about 1/2 of their length; segments submucronate at apex, outer ones about 2 mm broad, elliptic-ovate, subacute, inner ones 3–4 mm broad, ± broadly obovate, retuse at apex; tube purplish-violet, segments purplish-violet with a broad white margin and greenish middle nerve. *Filaments* attached at middle of tube, white; anthers about 2–2.4 mm long, dark violet with yellowish-white pollen. *Capsules* with valves up to about 9 mm broad, on spreading pedicels up to 5 cm.

Collections (see also type): *Iraq. FAR:* Arbil, weed of rough plough in forestry enclosure, 17.III.1958, young fr., Wheeler-Haines! – *FUJ:* 5 km N of Ba'aj, Al Jazira desert, 24.III.1964, fl., Barkley & Haddad 6625! – Between Balad Sinjar and Hadhr, 18.III.1961, fl., Hadač & Agnew 3553! – Road between Tal Kotchek highway and Tal Afar, stony clay hill, 7.III.1965, fl., Hikmat Abbas Al-Ani & Kadhim Yousif 9340! – Hammam Ali, 220 m, tree plantation, 2.III.1966, fl., Anders 511! 13.III.1967, fl., Anders 1000! 2.IV.1969, young fr., Anders 2481! 26.III.1973, fl., Ali Al-Rawi! – MAM: Dohuk, 480 m, open dry rocky ground, sandstone, 8.III.1947, fl., Leatherdale 3 a! – Road to Rashid, 500 m, grain field, 19.III.1969, fl., Anders 2456! – Tigris plain, 210–300 m, corn field, 11.III.1936, fl., Low 78! – Insula Abu Saaid ad Haqlani, 10.II.1960, fl., Hadač & Hakim Al-Rawi! – *MRO:* Salah ad Din, 1000 m, 31.III.1973, fl., Ali Al-Rawi!

2. **Alrawia bellii** (Baker) K. Persson & Wendelbo, comb. nov.

Basionym: *Scilla bellii* Baker, Gard. Chron., 2nd Ser., 22: 488 (1884) – *Hyacinthella bellii* (Baker) Wendelbo, Kew Bull. 28: 35 (1973) – Orig. coll.: Persia, Lorestan, spring 1888, Mark Bell s.n. (K holotype!).

Scilla leucophylla Baker, Gard. Chron., 3rd Ser., 13: 506 (1893). – Orig. coll.: Mountains of W. Persia, cultivated, bulbs imported by Leichtlin (K holotype!).

Bellevalia dichroa Hausskn. ex Bornm., Beih. Bot. Centralbl. 24, Abt. 2: 107 (1908) – *Hyacinthus dichrous* Bornm., Beih. Bot. Centralbl. 24, Abt. 2: 107 (1908), nom. alt. – Orig. coll.: Sultanabad (Arak) in cacumine montis Mowdere, 20.IV.1889, 27.IV.1890, 11.IV.1892, Strauss (not seen).

Fig. 1.

Nomenclature. The type material of *Scilla leucophylla* Baker is of a cultivated plant. The original material was imported from "W. Persia" by the well-known German horticulturist Max Leichtlin of Baden-Baden. There is every reason to believe that Leichtlin got his bulbs, as he did in other cases, from Theodor Strauss, German consul at Arak and an ardent plant collector (Meyer 1975). In fact, there is a label with Baker's Latin description attached to the sheet Strauss no. 80 collected in 1890, and Strauss' name has been added to that of Leichtlin.

The type of *Bellevalia dichroa* must be selected among the Strauss sheets from the mountain Mowdere near Arak which probably are in the Haussknecht herbarium at Jena. The sheets from Raswend 31.IV.1890 and Girdi-Schlucht 15.IV.1890 labelled as types in the Berlin herbarium can obviously not be considered as such as they are not mentioned in the original description of the species.

The fruiting material named *Bellevalia oxycarpa* Hausskn. on labels and discussed by Bornmüller (1908) and by Feinbrun (1940) obviously belongs to *Alrawia bellii*. The name has never been validly published although it has been taken up as a "nomen" in *Index kewensis Suppl. IV.*

Bulb up to 3 cm in diam. *Leaves* 3–5(–6), shorter than scape, outer broadest (1.5–3 cm), margin

Fig. 1. *Alrawia bellii,* whole plant c. 10 cm. – Wendelbo & Assadi 16475; photo P. W. 4.V.1975.

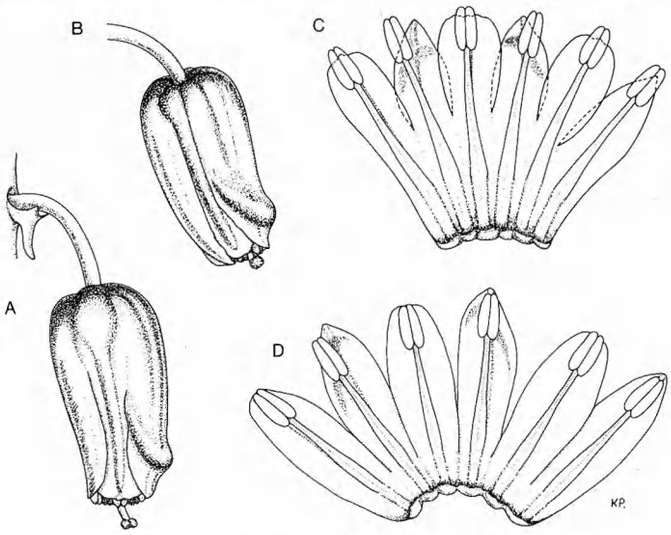

Fig. 2. Perianth with pedicel and bract (A, B) and perianth split open (C, D) – A, C: *Alrawia nutans* (Barkley & Haddad 6625). – B, D: *A. bellii* (Wendelbo & Assadi 16475). All × 2.

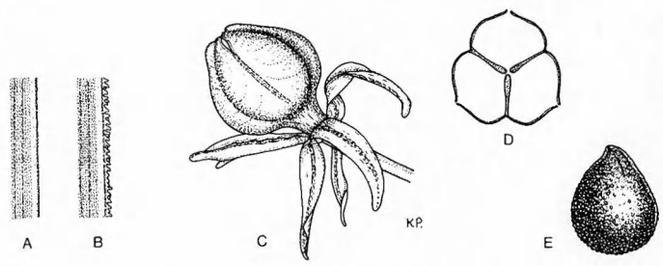

Fig. 3. A: *Alrawia nutans* (Barkley & Haddad 6625), leaf margin (× 5). – B–E: *A. bellii* (Wendelbo & Assadi 16780). – B: Leaf margin (× 5). – C: Fruit (× 1.3). – D: Cross section of fruit (× 1.3). – E: Seed (× 2.5).

shortly ciliate, greyish green. *Scape* solitary, 12–25 cm including raceme, for about 1/3 of its length below ground-level; in fruit up to 40 cm. *Raceme* 6–35-flowered, about 3 cm long and broad, rather dense but soon elongating, rachis purplish-violet. *Pedicels* in flowering state 3–6 mm, recurved. *Perianth* 8–10 mm long with tepals connate for up to 1/4 of their length; outer segments elliptic-oblong, subacute, inner ones somewhat broader than the outer, obovate, rounded at apex; cup purplish-violet, segments purplish-violet with a broad white margin in upper part and greenish middle nerve. *Filaments* attached at base of lobes, white; anthers about 2.3–2.5 mm long, dark violet with yellowish-white pollen. *Capsules* with valves up to about 9 mm broad, on spreading pedicels up to 6 cm.

Collections (see also types): *Iran. Kordestan:* Kermanshah, Tang-e Dalkushiar W of Kerend, 1450 m, shrubbery of *Quercus brantii,* limestone, 8.V.1975, young fr., Wendelbo & Assadi 16780! – Shahabad W of Kermanshah, 1100–1300 m, northern slope with sparse and damaged *Quercus persica* and low *Astragalus* shrubs, 15.IV.1963, fl., Jacobs 6626! – Kuh Sefid, SÖ von Kermanshah, 12.V.1904, fr., Strauss, n.v. – 30 km E of Harsin, weed in fallow plowed field, 7.IV.1960, fl., Bent & Wright 407–303! – Dasht-e Zaghe, about 40 km E of Sanandaj on road from Hamadan, 2000 m, margin of field, 11.V.1975, young fr., Wendelbo & Assadi 16903! – Ad austro-orientem urbis Kermanschah (10 Fars.) in alpibus Kharguschdschica, 1.V.1903, Strauss! – Akkhbolagh Morched, 60 km à l'ést de Bisar, 24.IV–10.V.1956, fl., collector unknown in Schmid 6723, 6738 G! – *Tehran:* Arak area, Kuh-e Barf Khaneh, 2300–2800 m, NE to E mountain slope with deep soil among limestone rocks, 4.V.1975, fl., Wendelbo & Assadi 16475! – Girdi-Schlucht bei Sultanabad (Arak), 15.IV.1890, fl., Strauss! – Sultanabad (Arak) in m. Raswend, 30.IV.1890, fl., Strauss 80!

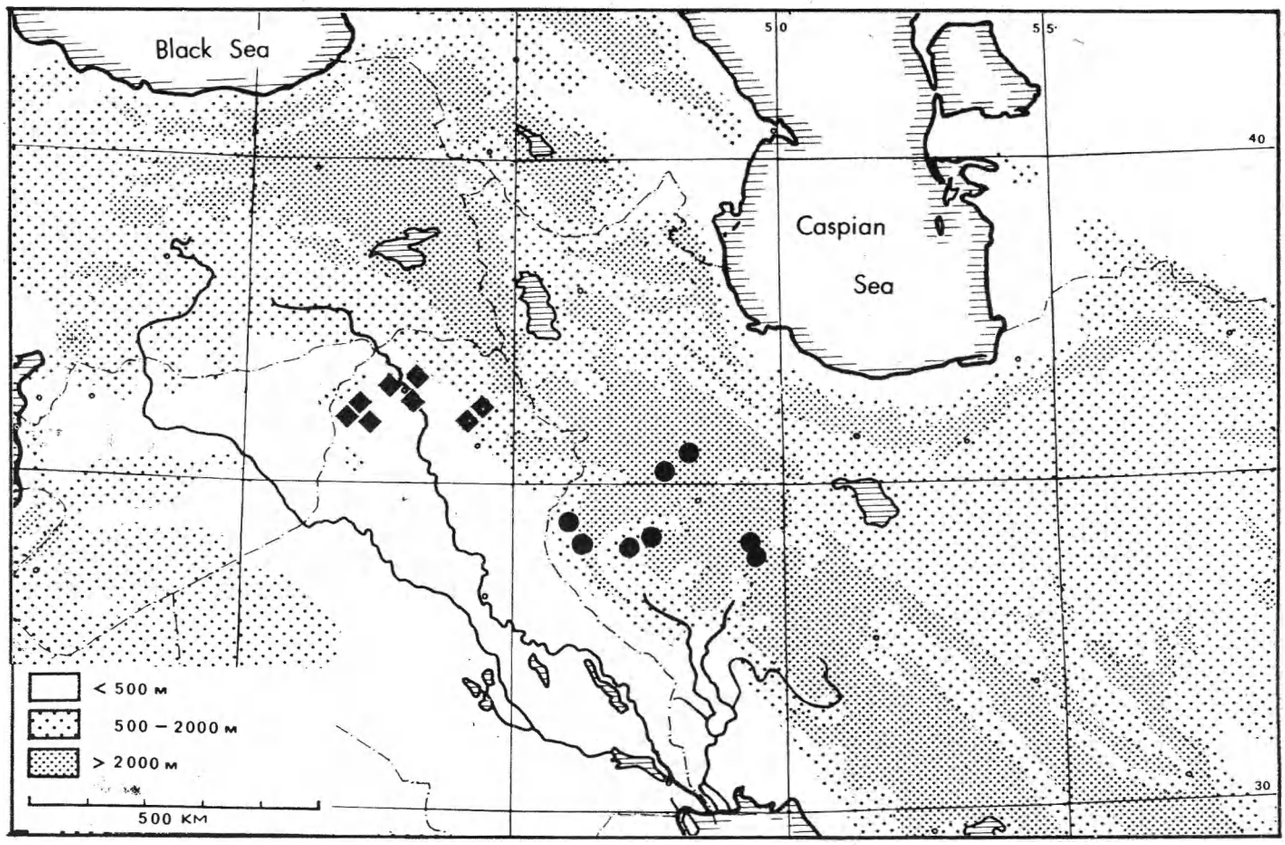

Fig. 4. Total known distribution of the genus *Alrawia* (◆ *A. nutans*, ● *A. bellii*).

Intrageneric relationships and phytogeography

There is no doubt that *A. nutans* and *A. bellii* are closely related. But the differences in leaf margin (Fig. 3 A, B) and length of corolla tube (Fig. 2 A, B) warrant specific separation. On the available material it also seems as if *A. nutans* generally has fewer leaves of a more greenish colour, and it may also be a somewhat larger plant. The distributions (Fig. 4) are clearly separated. *A. nutans* is a plant of the foothills of the Zagros mountains in N Iraq, while *A. bellii* is confined to the Zagros mountains of W Iran. There is a gap between the two areas of about 300 km. Phytogeographically the genus *Alrawia* should be assigned to the Armeno-Kurdish element.

A. nutans is in Iraq confined to what Guest (1966 p. 72, Fig. 15) called the "Moist-steppe Zone" with an annual rainfall from 350 to 500 mm and the lower part of the "Forest Zone" which has an annual rainfall from 700 upwards to 1400 mm. The vegetational climax of the former zone might well be an open savannah dominated by *Pistacia* and other trees, and the latter has a vegetation of *Quercus* forest formation (Guest 1966).

In the western part of its area (Kermanshah: annual rainfall 489 mm) *A. bellii* is found in degraded *Quercus brantii* forest, or often in fields where the climax vegetation would be a *Q. brantii* formation. Further east (rainfall about 300 mm) it grows in fields or on mountain slopes where the climax vegetation might be a *Pistacia-Amygdalus* steppe forest (cf. Zohary 1973 map 7).

Intergeneric relationships

Feinbrun (1938, 1940, 1961) has tried to clear out the morphological differences between *Bellevalia, Muscari* and *Hyacinthella*. The genus *Alrawia* differs from *Bellevalia* in the slender filaments (Fig. 2 C, D), in the corolla being persistent during ripening of the fruit (Fig. 3 C), in the valves of the fruit which are rounded on their back so that the capsule is more or less globose (Fig. 3 D), and in the seeds which are

ovate-triangular in cross-section and have a wrinkled seed coat (Fig. 3 E).

From *Hyacinthella* the new genus differs in having more than two leaves, which lack strong nerves on the under side; a bicoloured perianth which is purplish-violet and greenish-white (colours that are more like those of certain *Bellevalia* species), nodding and tubular-urceolate with crest-like protuberances (Fig. 2 A, B); a much larger fruit with a distinct foot (Fig. 3 C).

An interesting character of *Alrawia* is found in the outer, but not outermost, bulb tunics. These are sparsely to rather densely covered with a white "powder" consisting of minute needle-shaped particles. When touched the "powder" gives a soapy, talcous feeling. The same character has been noted in *Hyacinthella* species, e.g. *H. heldreichii* (Boiss.) Chouard.

The differences from *Muscari* are found in the deeply divided perianth, in the lack of a marked constriction of perianth below lobes, in the flower colour, and in the shape of the capsule.

From *Scilla* our genus differs in the short dense raceme, the shape and colour of the perianth and the connate tepals, as well as the shape and texture of the capsule.

Cytology

Material. A. nutans: Iraq, coll. Ali Al-Rawi, one of his two collections listed under the species (Dr Al-Rawi did not specify on which of the two localities he had collected the bulbs).

A. bellii: Iran, W. & A. 16475, 16903 (see under the species).

Methods. The usual squash method with Feulgen staining was used. The root-tips were pretreated in a mixture of 0.6% colchicine and 2 mM 8-hydroxyquinoline for about 2 hours. The idiograms are based on 10 good metaphase plates (with about the same degree of contraction of the chromosomes) of one individual from each species. From all other plants available several plates were drawn for comparison. The karyological terminology follows Levan et al. (1965).

Karyologically *Alrawia nutans* and *A. bellii* are very much alike (Fig. 5). Both have 2n = 12. The haploid chromosome complement consists of one long m chromosome and five considerably shorter ones, two of which are medium-sized and st, and the rest short, sm to st. All the chromosome pairs can easily be distinguished on their arm index, relative length or satellite attachments. Two of the chromosomes in the

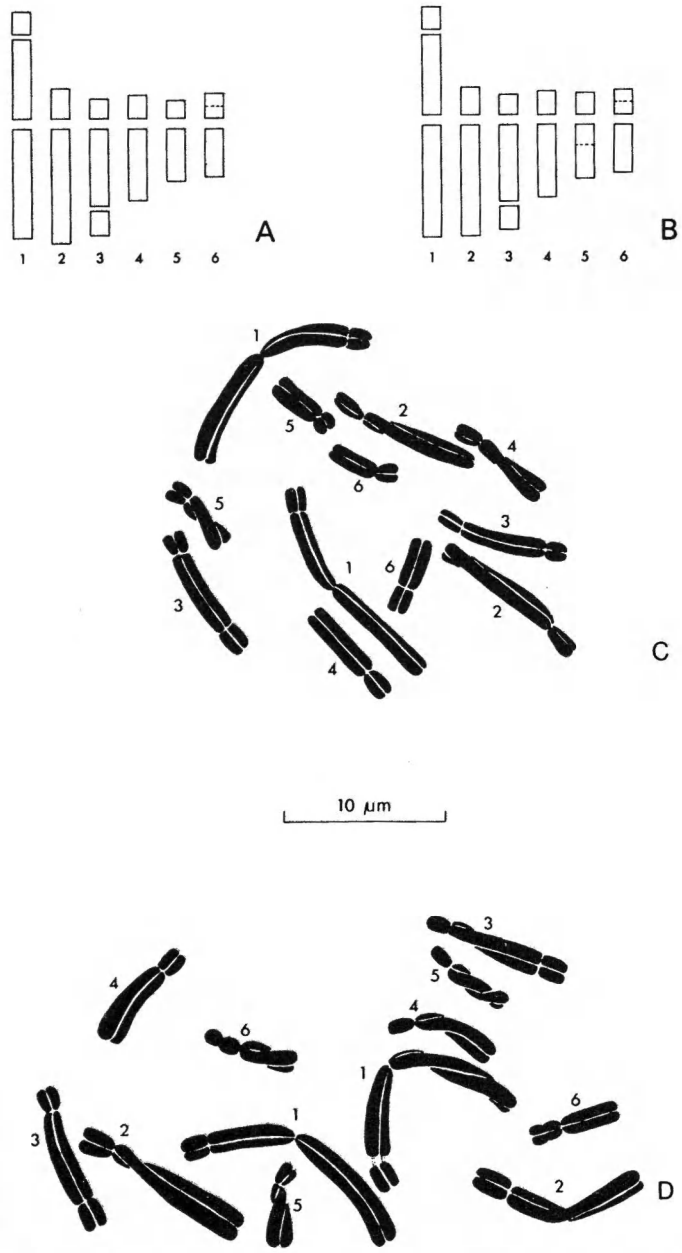

Fig. 5. Idiograms and mitotic chromosomes. – A, C: *Alrawia nutans* (Iraq, Al-Rawi). – B, D: *A. bellii* (B Wendelbo & Assadi 16903, D Wendelbo & Assadi 16475). – Hatched lines indicate the position of weak secondary constrictions.

haploid set are usually supplied with satellites, viz., no. 1 (m) which has a fairly large satellite on the shorter arm, and no. 3 (st) which has a somewhat larger satellite on its long arm (Fig. 5 A, B). Weaker secondary constrictions are to be found in the two smallest chromosomes, especially in *A. bellii,* although they are not visible in all preparations.

In its karyology the genus *Alrawia* shows certain similarities to *Bellevalia,* although in the former the chromosomes are generally (in most preparations) somewhat shorter and more slender. Both have one large metacentric chromo-

some in their haploid set, and in both the rest of the chromosomes are sm–st and shorter, although the size differences seem to be greater in *Alrawia* than in *Bellevalia*. Also, the difference in basic number is significant: all *Bellevalia* species hitherto examined (see e.g. Feinbrun 1938, Levan 1944, Bentzer et al. 1972, Pogosjan 1975) have 2n = 8 or its multiples, and the morphology of the basic set is extremely characteristic (represented in almost all species studied), all of which, together with the habit and general morphology, makes *Bellevalia* an unusually well defined genus. Certainly it might be equally relevant to point to the karyological affinities of *Alrawia* to the other genera in the *Scilloideae*. Both in *Hyacinthus* (Bentzer et al. 1974) and in certain groups of *Scilla*, e.g. the *S. hohenackeri* group (Greilhuber & Speta 1976) and the *S. liliohyacinthus* group (Giménez-Martín 1959), is to be found the same general pattern of fairly large chromosomes with one or a few long metacentric pairs and the rest distinctly shorter and more asymmetric. In the *S. liliohyacinthus* group there are even examples of the type of large satellite on the long arm of a st chromosome found in no. 3 of *Alrawia*, which is otherwise rare in the subfamily.

The affinity between *Alrawia* and *Hyacinthella* (to which *A. nutans* and *bellii* were formerly assigned) is not very obvious, however. The species of *Hyacinthella* s.str. which have been examined up till now (Östergren et al. 1958, Feinbrun 1961, Popova 1972 and personal observations) all have 2n = 18, 20, 22, or 24 and very much smaller chromosomes (generally less than 5 μm). It seems difficult to imagine a closer phylogenetic relationship between the two genera at least on the basis of the cytology, even though there are certain similarities in the reproductive organs which point to some affinity.

As a conclusion it might be said that *Alrawia* shows clear affinities in various morphological characters and in karyology both to *Bellevalia*, *Hyacinthus* and some groups of *Scilla*, and some affinity, at least morphologically, to *Hyacinthella*. The combination of morphological and cytological features is sufficiently characteristic, however, to warrant the rank of genus for *Alrawia*.

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The artificial hybrid Hyacinthus orientalis × transcaspicus (Liliaceae)

Karin Persson and Per Wendelbo

Persson, K. & Wendelbo, P. 1979 05 15: The artificial hybrid Hyacinthus orientalis × transcaspicus (Liliaceae). *Bot. Notiser 132:* 207–209. Stockholm. ISSN 0006-8195.

The myrmecochorous *Hyacinthus orientalis* (2n = 16) from Turkey has been crossed with the ballistic *H. transcaspicus* (2n = 18) from NE Iran. The karyotype of the hybrid is intermediate with 2n = 17. There is thus indication of a close relationship between the parent species. Neither morphological nor cytological characters warrant a position of *H. transcaspicus* within *Hyacinthella* as postulated by recent authors.

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In a recent paper Beljanina and Proskurjakova (1978) divided the genus *Hyacinthus* L. into three sections: *Euhyacinthus* Baker with *H. orientalis* L.; *Hyacinthella* (Schur) Baker with *H. transcaspicus* Litw., *H. leucophaeus* (C. Koch) Ledeb. and *H. pallasianus* Stev.; and *Litvinovia* Beljanina & Proskurjakova with *H. litwinowii* E. Czern.

Baranova (1965) was of the opinion that both *H. transcaspicus* and *H. litwinowii* belonged to *Hyacinthella* which she treated as a separate genus (type species: *H. leucophaea* (C. Koch) Schur). Feinbrun (1961) excluded both species from *Hyacinthella* and referred them to *Hyacinthus*.

Bentzer et al. (1974) concluded that *H. orientalis, H. transcaspicus* and *H. litwinowii* were so similar in their karyotypes that they should be treated as belonging to the same genus, *Hyacinthus*. The difference in chromosome number and morphology (*H. orientalis*: 2n = 16, four pairs of long m chromosomes; *H. transcaspicus* and *litwinowii*: 2n = 18, three pairs of long m chromosomes, Fig. 1 A, C) was explained by a change due to an unequal reciprocal translocation. In a chromosome set of the *H. transcaspicus–litwinowii* type a rearrangement may have occurred in which most of the long arm of a short sm-st chromosome changed places with a minute part of the short arm of a medium-sized sm-st chromosome. The result would be a long m chromosome and a minute chromosome consisting mostly of the region near the centromere of the original short sm-st chromosome. Provided that this region was genically inert, the minute chromosome could easily be lost. The end result, a reduction in basic number, is not a rare phenomenon in plants. Changes in basic diploid number proceed more frequently in the direction of decrease than of increase and have in some cases, e.g. in *Crepis* (Tobgy 1943, Sherman 1946), *Ixeris* (Babcock et al. 1937) and *Godetia* (Håkansson 1946), actually been shown to involve rearrangement of chromosomal segments.

A cross performed in the greenhouse of the Botanical Garden, Göteborg, between *H. orientalis* (♀) and *H. transcaspicus* (♂), gave one capsule with three seeds, one of which germinated. The resulting plant has very slowly developed into a small bulb with violet tunics and producing a few rather narrow leaves. No flowers have been produced so far. The karyotype is intermediate between the two parents with 2n = 17 (Figs. 1 B, 2) including the marker SAT-chromosomes from each of the parents (no. 4 in Fig. 1 A and C).

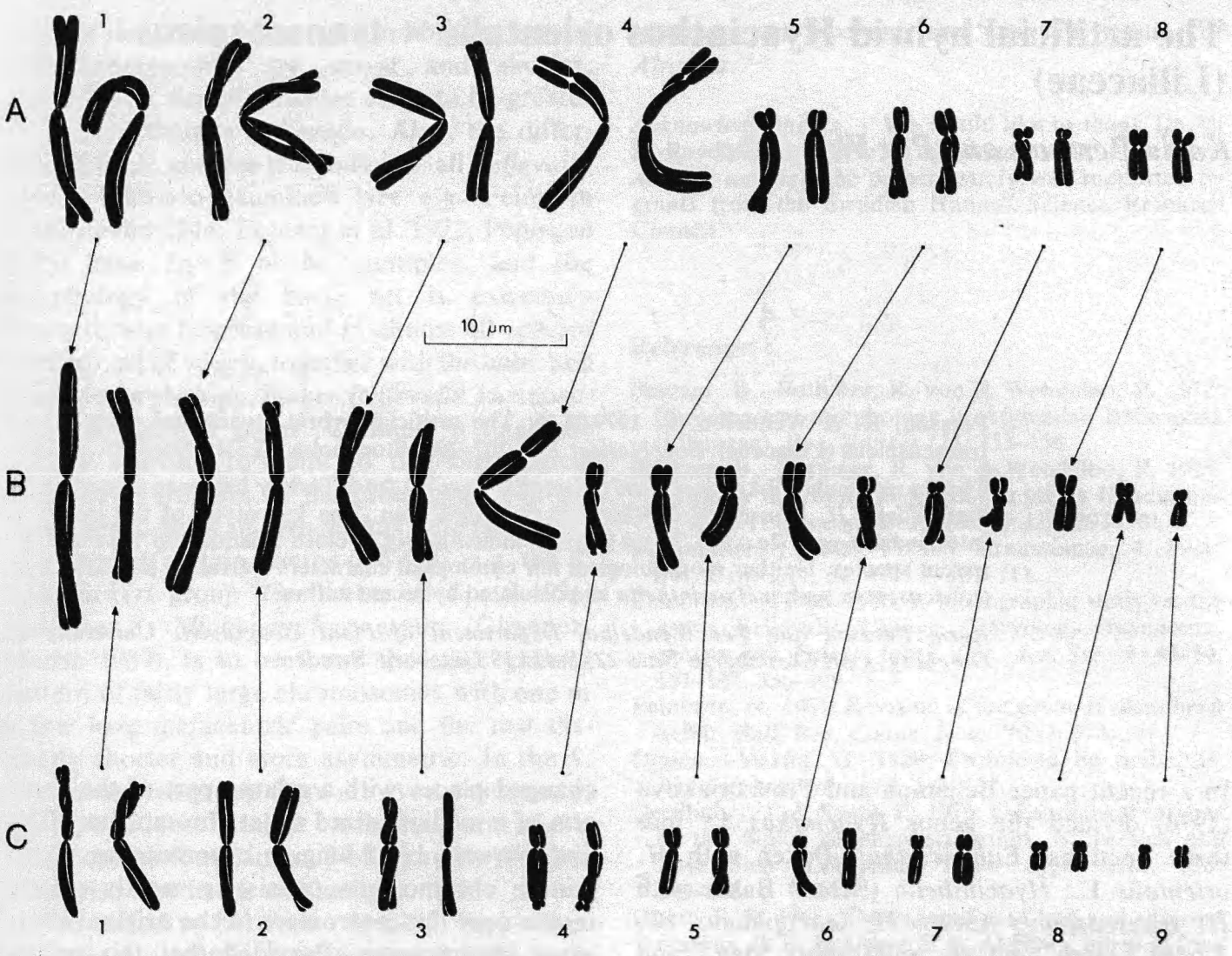

Fig. 1. Karyotypes of *Hyacinthus orientalis* (A), *H. transcaspicus* (C) and their hybrid (B). The plant used of *H. transcaspicus* has a structural heterozygosity in pair no. 6. Arrows indicate the possible origin of the hybrid chromosomes from the respective parent genomes. The marker chromosomes (4 in A and C) are both present in the hybrid.

The cytological observations were made on root tip squash preparations made according to the Feulgen staining method using a mixture of 0.6% colchicine and 2 mM 8-hydroxyquinoline as a pretreatment.

Discussion

The formation of the hybrid is an indication of the near genetical relationship between *H. orientalis* and *H. transcaspicus* postulated by Bentzer et al. (1974). Thus cytological evidence is clearly in favour of keeping the two species in the same genus. From the similarity in karyotype that exists between *H. transcaspicus* and *H. litwinowii*, the latter should follow suit.

We are not prepared to make a final decision as to whether *Hyacinthella* should be included in *Hyacinthus*, but both morphological and cytological characters indicate that the former group is probably best separated as a genus of its own. Distinguishing characters of *Hyacinthella* are: few, usually only two leaves; bracts only forming a narrow rim; perianth small, rather shortly lobed and at least some lobes provided with protuberances like in *Bellevalia;* small anthers; a much smaller capsule which seems to have a more sclerified wall. There are also differences in the karyotype, e.g. in basic number (most of the species of *Hyacinthella* s.str. have $2n = 20$, 22 or 24) and chromosome size (the longest chromosomes are generally less than 5 μm) (Östergren et al. 1958, Feinbrun 1961, Popova 1972, Persson & Wendelbo unpubl.). However, there is some morphological and cytological evidence that *Hyacinthella*, even as

circumscribed by Feinbrun (1961) may not be quite uniform. Studies on the genus are in progress.

The taxonomical conclusions that can be drawn so far are then that the three species of *Hyacinthus* s. str. are much more closely related inter se than with the species of *Hyacinthella* sensu Feinbrun.

Within *Hyacinthus* there is a clear difference between *H. orientalis* and *H. transcaspicus–litwinowii,* partly connected with different modes of seed dispersal, the first being myrmecochorous and the two others ballists. We would therefore recognize two sections within *Hyacinthus*.

Sect. *Hyacinthus*. Anthers longer than filaments. Seeds with a well developed elaiosome. 2n = 16. – *H. orientalis* L.

Sect. *Litvinovia* Beljanina & Proskurjakova. Anthers shorter than filaments. Seeds without elaiosome. 2n = 18. – *H. litwinowii* E. Czern., *H. transcaspicus* Litw.

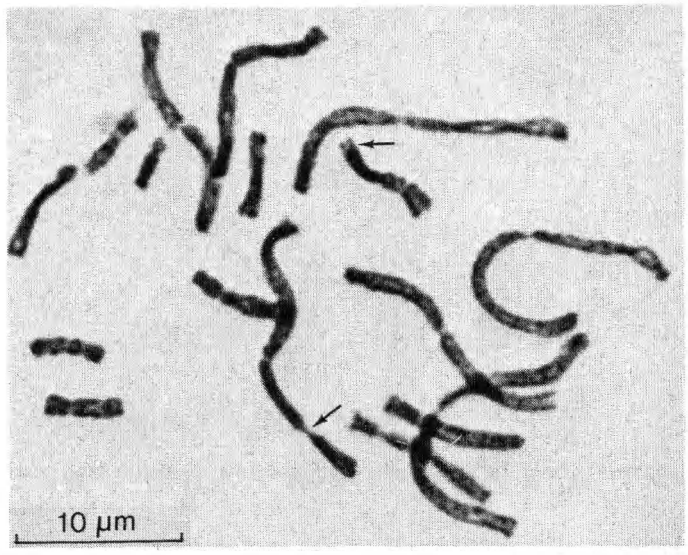

Fig. 2. Mitotic metaphase plate of *Hyacintnus orientalis* (♀) × *transcaspicus* (♂). Arrows indicate the satellited marker chromosomes.

Origin of the parent plants

Hyacinthus orientalis: Turkey, Manesa, 21 km SW of Sinderge, 430 m (Kjellquist Izmir no. 2).

H. transcaspicus: Iran, E Elburz, Gorgan to Shahrud, N of the pass (Furse 7179).

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Swedish pteridicolous Mycosphaerellae

Lennart Holm and Kerstin Holm

Holm, L. & Holm, K. 1979 05 15: Swedish pteridicolous Mycosphaerellae. *Bot. Notiser 132:* 211–219. Stockholm. ISSN 0006-8195.

The authors have revised the taxonomy and nomenclature of the *Mycosphaerella* species found on ferns in Sweden, viz. *Mycosphaerella asperulata* L. & K. Holm, sp. nova, *M. aspidii* (v. Höhn.) L. & K. Holm, comb. nova, *M. filicum* (Desm.) Starb. s. lato, *M. osmundicola* (Kirschst.) L. & K. Holm, comb. nova, and *M. pteridis* (Desm.) Schröt.

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In the course of an inventory of the Ascomycete flora on ferns in Sweden (cf. Holm & Holm 1978) it became apparent that the taxonomy and nomenclature of the pteridicolous *Mycosphaerellae* was in such a state of confusion as to necessitate a study of its own. The results of that revision are presented here. They are based largely on our own collections, in the main part from the province of Uppland, C Sweden. In addition the herbarium material in S and UPS has been revised, and some further type specimens have been obtained on loan from B and PC, which is gratefully acknowledged.

Five species have been found to occur in the country. By far most frequent is *Mycosphaerella aspidii,* a polyphagous fungus extremely common in dead fronds of various ferns. The other species are highly specialized and obviously more or less parasitic: *M. osmundicola* is confined to *Osmunda, M. pteridis* to *Pteridium,* and *M. asperulata* to *Polypodium. M. filicum,* finally, is conceived here in a broad sense, including forms on *Asplenium, Polypodium,* and *Dryopteris spinulosa.*

On the whole these fungi have not been much studied. The pioneer in the field was Desmazières (1840, 1843), who first described *M. filicum* and *M. pteridis.* Auerswald's (1869) generic monograph was to be highly influential. It included five pteridicolous taxa: Desmazières's two (partly misunderstood) species and two new ones, *Sphaerella asplenii* and *S. tirolensis* (on *Polypodium*), and finally "*Sphaerella aquilina* (Fr.) Awd." on bracken. The names introduced by Auerswald have been much employed but variously interpreted. The nomenclature confusion has been still more aggravated by mixing *Sphaeria polypodii* Rbh. (= *Glomerella polypodii* (Rbh.) L. & K. Holm) up in it. The combination *M. polypodii* (Rbh.) Lindau has been used for various pteridicolous *Mycosphaerellae.* A noteworthy article on these fungi was published by von Höhnel (1918). Based on a study of type specimens he correctly interpreted *Sphaeria filicum* and *S. polypodii.* By far the most thorough study devoted to any pteridicolous fungus is the investigation by Aggéry (1935) on the life history of "*Sphaerella subostiolicola*".

Artificial key

1. Ascocarps clothed with asperulate hyphae. On *Polypodium* ..... 1. *M. asperulata*
– Ascocarps with ± sparse, smooth hyphae 2

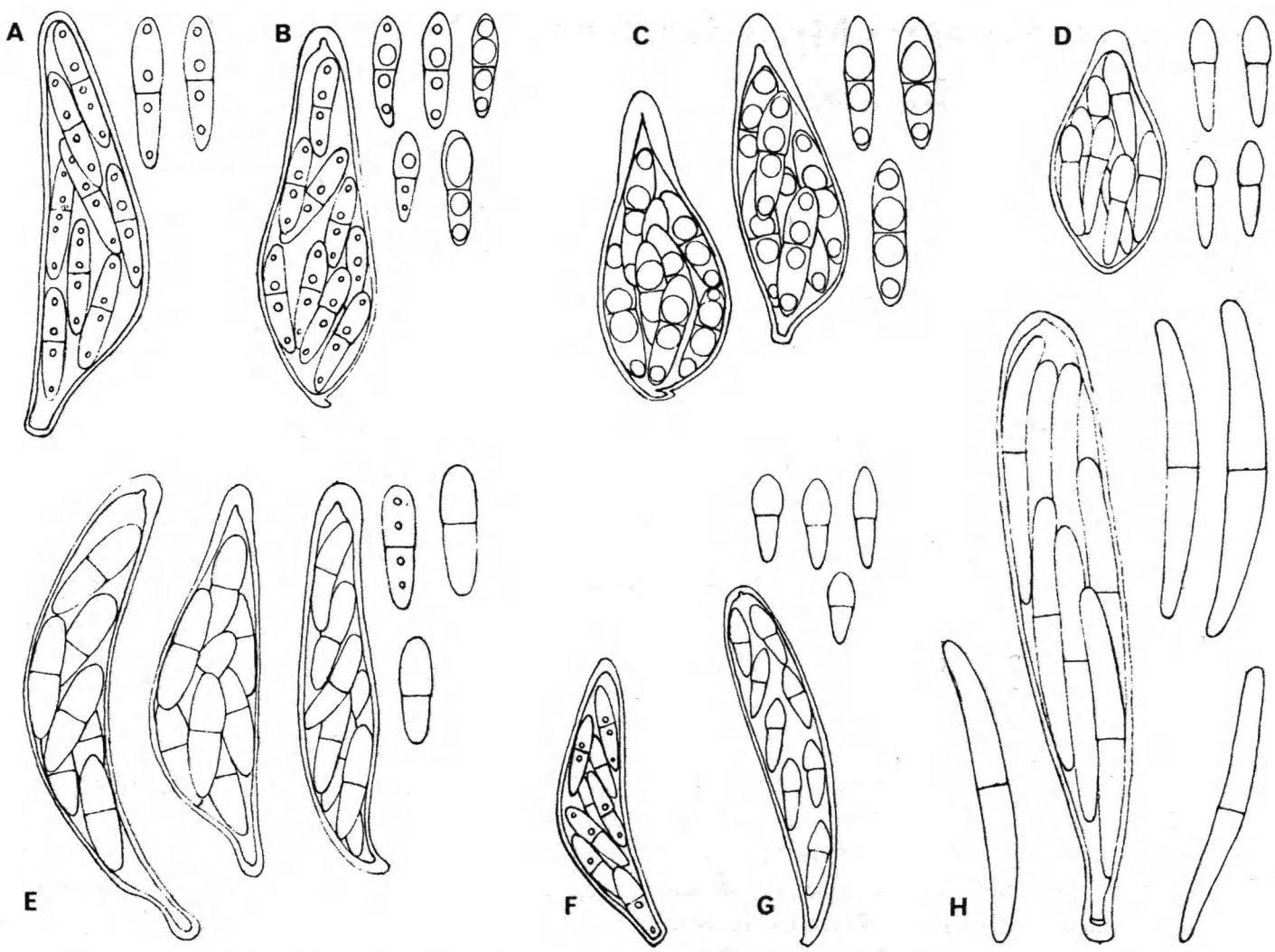

Fig. 1. Asci and spores. – A: *Mycosphaerella filicum* on *Asplenium adiantum-nigrum* (Jaap, F. sel. 617). – B: Ditto, on *Dryopteris spinulosa:* ascus (Lind), mature spores (Holm 350 a). – C: Ditto, on *Polypodium vulgare* (Holm 925 a). – D: *M. osmundicola*. – E: *M. asperulata*. – F: *M. aspidii* on *Polypodium vulgare*. – G: Ditto, on *Dryopteris filix-mas*. – H: *M. pteridis*. – All × 1000.

2. Spores cylindrical, > 25 μm. On *Pteridium* ..... 5. *M. pteridis*
– Spores fusiform, cuneate, or oblong, < 20 μm 3
3. Spores with a supramedian septum. On *Osmunda* ..... 4. *M. osmundicola*
– Spores with a median septum 4
4. Saprobic. Ascocarps scattered, spores without or with indistinct guttules ..... 2. *M. aspidii*
– Parasitic. Ascocarps mostly grouped. Spores with very distinct guttules ..... 3. *M. filicum*

1. **Mycosphaerella asperulata** L. & K. Holm, sp. nova

Typus: Suecia, Uplandia, par. Dalby, "Jerusalem", in frondibus languescentibus Polypodii vulgaris, 29.VII.1978, K. & L. Holm 1469 (UPS holotypus).

?*Sphaerella subostiolicola* Aggéry, Bull. Soc. Hist. Nat. Toulouse 68: 72 (1935) – Type: France, Pyrénées Orient., Molitg-les-Bains, "sur les feuilles vivantes de *Polypodium vulgare* L., *P. vulgare* var. *serratum* D. C. et *P. cambricum* L." (n.v.).

Exs.: Karst., F. fenn. 669 ('*Sphaeria Polypodii*', UPS).

Fig. 1 E, 2.

Species inter Mycosphaerellas mycelio profuso asperulato perdistincta.

Ascocarps gregarious in *hypophyllous* spots, piercing the epidermis with a minute papilla, ± globose, 80–140 μm diam., clothed by a dark grey asperulate tomentum. *Peridium* 15–20 μm of 2–3 layers of ± flattened cells, up to 12 μm. *Asci* rather numerous in a fascicle, oblong to slightly ventricose, 40–50 × 10–12 μm, 8-spored. *Spores* oblong, with obtuse ends and a ± median septum, generally 12–15 × 4–4.5 μm,

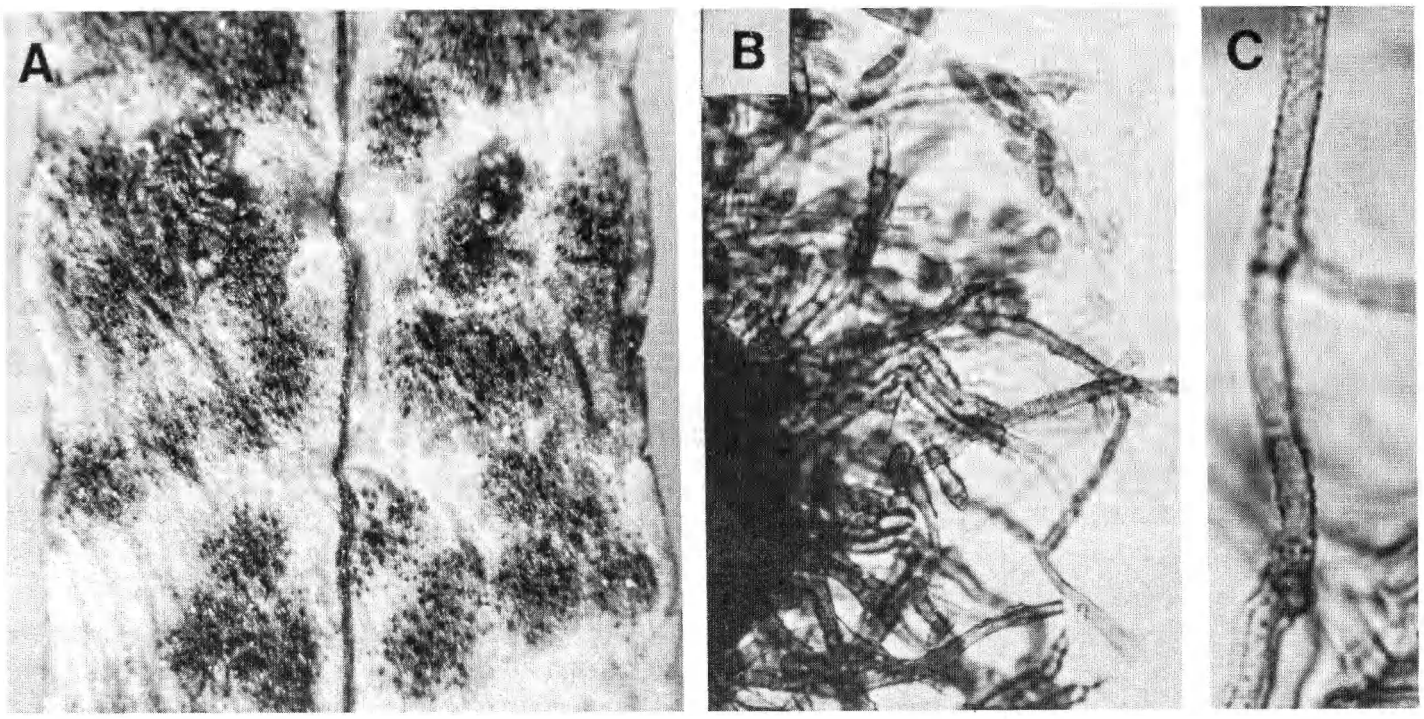

Fig. 2. *Mycosphaerella asperulata*. – A: Groups of ascocarps, × 8. – B: Hairs, × 530. – C: Hair, × 1300.

hyaline, when fully mature with a granular plasma.

Parasitic–saprobic in the fronds of *Polypodium vulgare*.

Mycosphaerella asperulata is a most characteristic fungus, which generally can be identified with the naked eye. Infested leaflets turn brownish and their underside is spotted by numerous, indefinite dark patches, 1–2 mm large, caused by the clustered tomentose ascocarps. The profuse mycelium is distinctly asperulate, hence the specific epithet. We do not know of any other species of *Mycosphaerella* with this type of mycelium, and possibly it is not well accommodated in the genus. It is rather strange that this most distinctive species has been largely overlooked. Possibly *Sphaerella subostiolicola* Aggéry might be identical; its hypophyllous habit is suggestive. Unfortunately, it has been impossible to trace any material of that species (according to kind information from Dr J. Fayret, Toulouse).

Munk (1957 p. 312) recorded a fungus on *Polypodium* under the name of *''Mycosphaerella* cfr. *filicum''*; judging from the description it probably was *M. asperulata*.

It is possible that *M. asperulata* is less common than the other fungi forming leaf-spots on *Polypodium,* i.e. *Glomerella polypodii* and *M. filicum,* but it is certainly not rare in Scandinavia. Besides the type we have seen the following material:

Sweden: Uppland, Dalby, ''Jerusalem'', 27.VII.1978, Holm 1468 a; 300 m ESE of ''Jerusalem'', 9.XI.1978, Holm 1524; 400 m SSW of ''Jerusalem'', 7.VII.1976, Holm 885 b. – Häggeby, Skadevi, VII.1888, C. W. Broström (S). – *Södermanland,* Mariefred, 7.VI.1938, Th. Arwidsson (S). – *Västmanland,* Nora, Kerstinbo, 21.V.1975, Holm 571 a.

Finland: Tavastland, Mustiala (= Karst., F. fenn. 669). – Häämenlinna, Aulanko, 27.VI.1968, P. Alanko 6836 (H). – Elimäki, 19.VI.1971, P. Alanko 16889 (H).

2. **Mycosphaerella aspidii** (von Höhnel) L. & K. Holm, comb. nova

Carlia Aspidii v. Höhnel, Ann. Mycol. 16: 62 (1918) – Lectotype: Austria, Schladming, *Dryopteris filix-mas,* VIII.1908, v. Höhnel (= Rehm, Asc. 1809, sub nom. *Myc. Asplenii* var. *Aspidii,* S!)

[*Mycosphaerella filicum* sensu auct. plur., non sensu orig.]

[*Mycosphaerella aquilina* sensu auct. plur., non sensu orig., vide infra.]

Mycosphaerella aquilina f. Aspidiorum (Sacc.) Jaap, F. sel. exs. 615 in sched. (1913) – *Sphaerella aquilina* f. *Aspidiorum* Saccardo, Ann. Mycol. 7: 435 (1909) – Type: Germany, pr. Werneuchen, *D. filix-mas,* 30.V.1909, H. Sydow (= Syd., Myc. germ. 784, UPS isotype!)

Exs.: On *Dryopteris filix-mas:* Fckl, F. rhen. 854 (*'Sphaeria Polypodii* Rabh. f. *Aspidii'*) (S) – Jaap, F. sel. 615 (*'Myc. aquilina* f. *aspidiorum'*) (S) – Krieg., F.

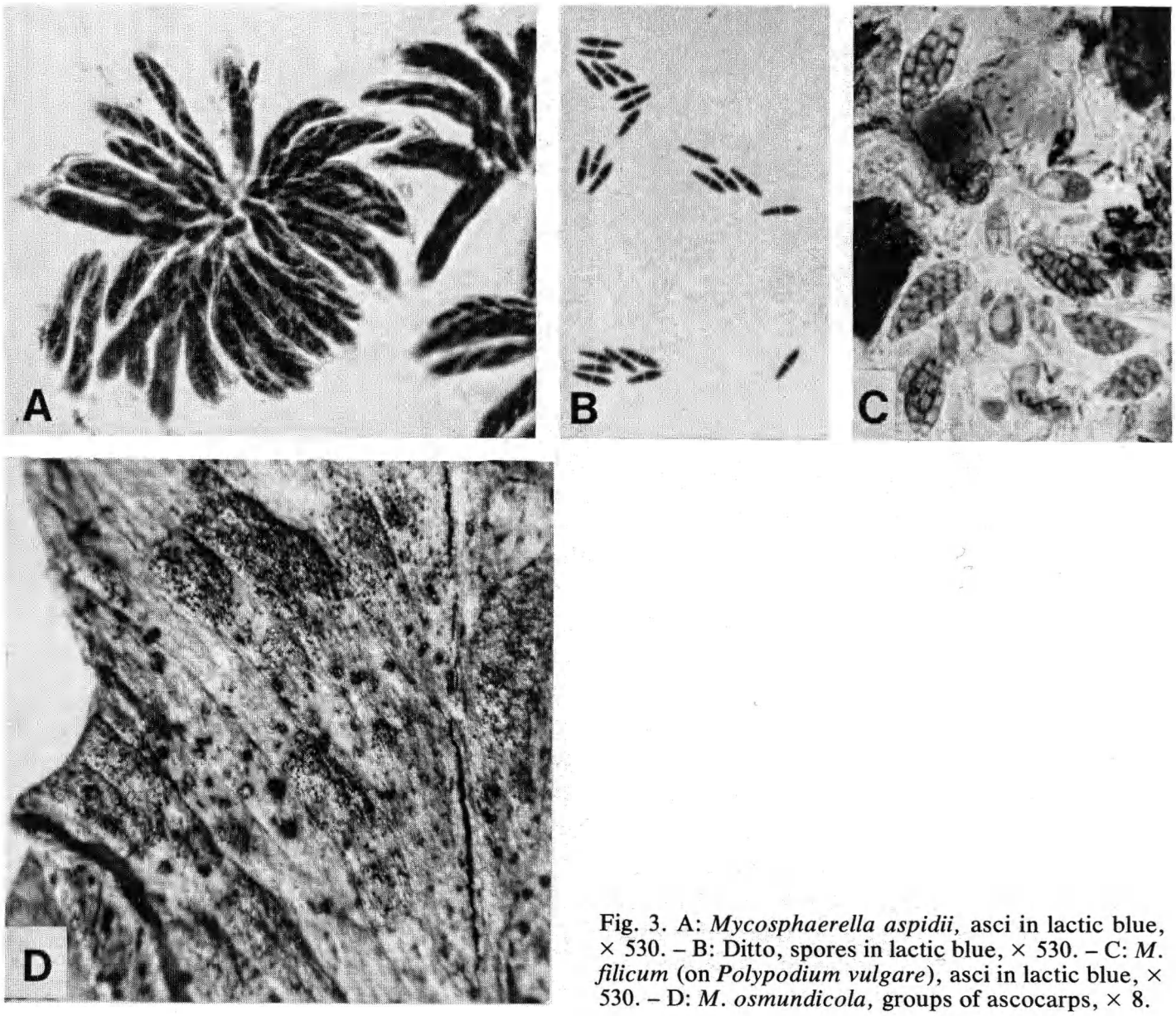

Fig. 3. A: *Mycosphaerella aspidii,* asci in lactic blue, × 530. – B: Ditto, spores in lactic blue, × 530. – C: *M. filicum* (on *Polypodium vulgare*), asci in lactic blue, × 530. – D: *M. osmundicola,* groups of ascocarps, × 8.

sax. 2063 ('*M. aquilina*') (S) – Lundell & Nannf., F. exs. suec. 2270 ('*M. filicum*') (S, UPS) – Petr., Fl. Bohem. Mor. II:1:778 ('*M. aquilina* f. *Aspidiorum*') (S) – Rehm, Asc. 1809 ('*M. Asplenii* v. *Aspidii*') (S) – Syd., Myc. germ. 784, 1334 ('*Sphaerella aquilina* f. *Aspidiorum*') (S, UPS).

On *Pteridium aquilinum:* Rbh., F. eur. 1728 ('*Sphaerella aquilina*') (S, UPS).

Fig. 1 F, G, 3 A, B, 4 A.

Ascocarps amphigenous, mostly in dead fronds, generally scattered, ± sparsely connected by hyphae, subglobose, immersed, piercing the epidermis with the bluntly conical apex, 50–80 (–100) μm diam. *Peridium* c. 10 μm broad, of 2–3 layers of ± flattened cells up to 25 μm large. *Asci* generally numerous in a fascicle, oblong-clavate or ± saccate, c. 35–40 × 7–8 μm, very briefly stipitate. *Spores* ± distichous, somewhat cuneate, 8–11 × 2.5–3.5 μm, with a median septum, hyaline, generally eguttulate but on some hosts with indistinct oil droplets, cf. below.

Mycosphaerella aspidii is probably the most frequent of all pteridicolous ascomycetes. It is apparently polyphagous, and we have found it on a number of ferns: *Athyrium alpestre* (= *A. distentifolium*), *A. filix-femina, Cystopteris fragilis, C. montana, Dryopteris cristata, D. filix-mas, D. dilatata* coll., *D. spinulosa, Lastrea dryopteris, L. phegopteris, Matteuccia struthiopteris, Osmunda regalis, Polypodium vulgare,* and *Pteridium aquilinum*. It is extremely common and is hardly ever absent from dead fronds of e.g. *Athyrium* and *Dryopteris* spp. The fructifying mycelium is generally saprobic, but

may exceptionally be parasitic, as is evident from Fckl., F. rhen. 854, with ascocarps in spotted green leaves of *Dryopteris filix-mas*. This widespread fungus seems on the whole to be but little variable, though special biotypes may occur on *Polypodium* and *Pteridium*. On these hosts it is always found with indistinctly guttulate spores, a condition otherwise only rarely met with in this species. The form on *Polypodium* moreover seems to deviate by fewer and more saccate asci (cf. Fig. 1 F). It has sometimes been identified with *Mycosphaerella tyrolensis,* see under *M. filicum* whilst the form on bracken has passed as *M. aquilina,* see below.

The nomenclature is rather complicated. Surprising as it is, this most common among fern fungi had to wait long for a name of its own. This delay was due to the common belief that the fungus was identical with *M. filicum*. Apparently von Höhnel (in Rehm 1909 p. 136) was the first one to break with this bad tradition, and later on (von Höhnel 1918 p. 61) he introduced the substitute name "*Carlia Aspidii* (Fuckel) von Höhnel". The reference to Fuckel is not correct, though, as the implied basionym, "*Sphaeria Polypodii* f. *Aspidii* Fuckel", is a nomen nudum. However, von Höhnel himself supplied a short description, sufficient to validate the name *Carlia aspidii,* which should be ascribed to von Höhnel alone. But the typification is somewhat problematic. Selecting Fuckel, F. rhen. 854, as the collection first cited by Höhnel, would seem fairly reasonable. However, von Höhnel's description was evidently not based on this material, which he stated to be "ganz unreif, ohne Schläuche" (von Höhnel 1918 p. 62). He cited several other exsiccata, too, among others Rehm, Asc. 1809, which seems to be an appropriate lectotype. It is moreover the type of *M. asplenii* var. *aspidii* von Höhnel, Ann. Mycol. 7: 136 (1909).

Another name which has been much used for this species is *Mycosphaerella (Sphaerella) aquilina,* cf. the list of exsiccata. The nomenclator is as follows: *Xyloma aquilinum* Fries, Obs. Mycol. 2: 362 (1818) – *Sphaeria aquilina* Fries, Syst. Mycol. 2: 522 (1823) – *Sphaerella aquilina* Auerswald, Mycol. Eur. 5/6: 20 (1869) – *Mycosphaerella aquilina* Schröter, Pilze Schlesiens 2: 341 (1894). – Following Schröter most authors have applied this name to the small-spored *Mycosphaerella* on bracken. Nannfeldt, on the contrary, in Lundell & Nannfeldt (1954 p. 32) used it for the long-spored one, i.e. *M. pteridis,* on the basis of Vestergren's (1897 p. 266) report that Fries's "type specimen" represented the latter form. As a matter of fact, this material contains a mixture of both species. However, Fries's *Sphaeria aquilina* surely was neither of them. The fungus was originally referred to *Xyloma,* a name which Fries certainly would not have employed for a sphaerellaceous species. In Systema Mycologicum it is listed between *Sphaeria empetri* (= *Duplicaria empetri*) and *Sphaeria artocreas* (= *Discosia artocreas*). This company, as well as Fries's description certainly will exclude the fungus from *Mycosphaerella*. The original material in UPS, referred to by Vestergren, is labelled "*Sphaeria aquilina* Fr. Femsjö" in Fries's characteristic handwriting, and might be considered "type material". Besides numerous ascocarps of *Mycosphaerella aspidii* and *M. pteridis,* there are some dark spots on the fronds, which could well be the Friesian *Sphaeria aquilina*. These spots are indeterminable remnants of dead fruit bodies. Von Höhnel (1919 p. 74) interpreted *Sphaeria aquilina* Fr. as identical with a fungus which occurs intermixed in Thüm., Myc. univ. 73 ('*Hysterium aquilinum*') and Rehm, Asc. 270 ('*Hypoderma aquilinum*'). Von Höhnel named this fungus "*Placostroma aquilinum* (Fr.) v. Höhn". This identification is fairly reasonable. However, the old name *Sphaeria aquilina* has been conceived in still another sense, as referring to a species of *Leptopeltis,* viz. the so-called "*Leptopeltis aquilina* (Fr.) Petr.", i.e. *L. pteridis* (Mouton) v. Höhn. (cf. Holm & Holm 1977 p. 220). This species is present, too, in the cited exsiccata, and is certainly the fungus which Thümen and Rehm had in mind. In any case, it seems strongly advisable to drop the name *Sphaeria aquilina* wholly, in view of the various interpretations of the name and of the bad condition of the original material. *Sphaeria aquilina* sensu von Höhnel was recently described by us as *Monographos minor* (Holm & Holm 1978 p. 106).

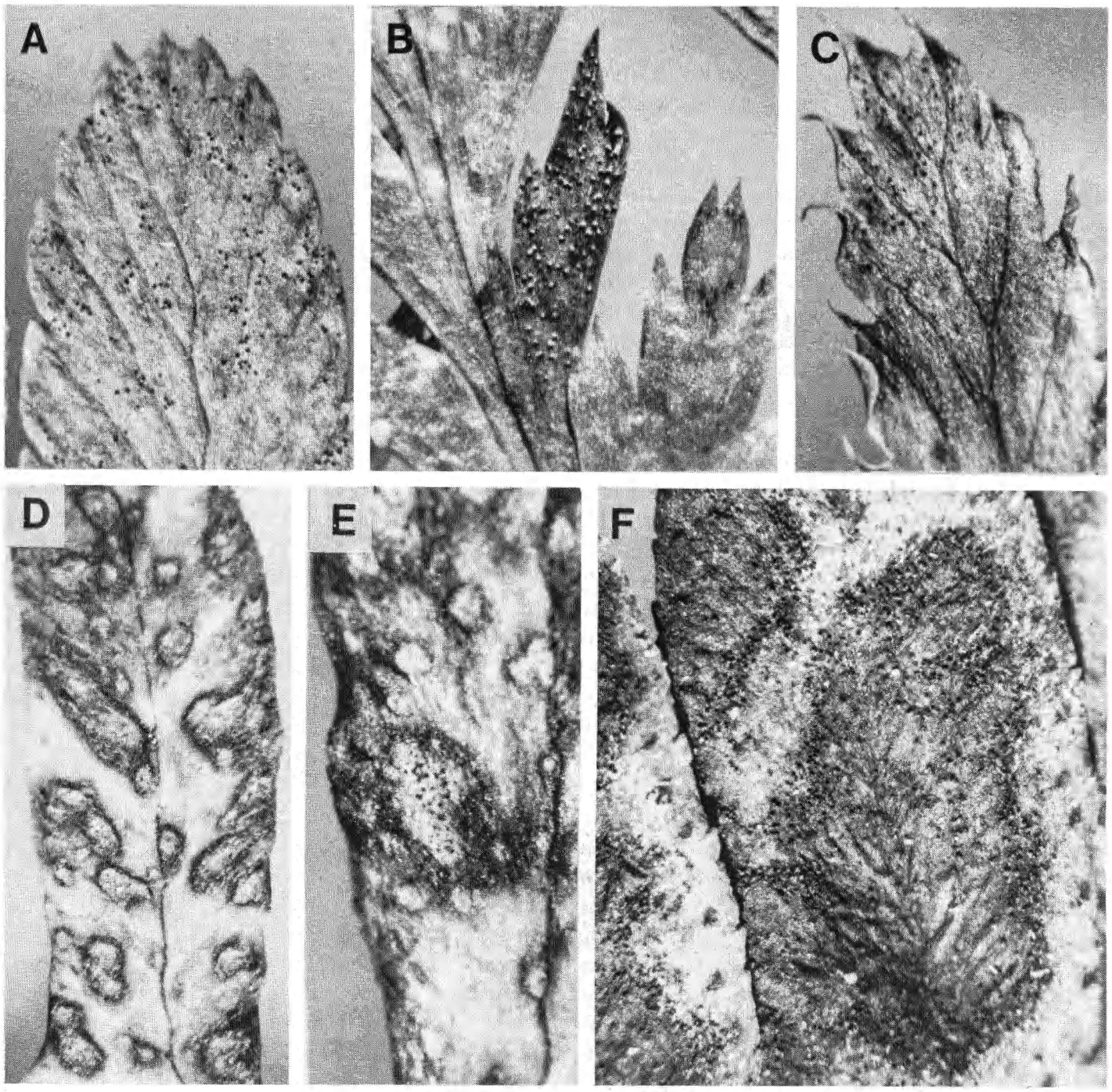

Fig. 4. Ascocarps. – A: *Mycosphaerella aspidii,* × 8. – B: *M. filicum* on *Asplenium adiantum-nigrum,* × 8. – C: *M. filicum* on *Dryopteris spinulosa,* × 8. – D–F: *M. filicum* on *Polypodium vulgare*. – D: Young spots in living leaves, × 4. – E: Detail of D, × 8. – F: Elderly spot in dead leaflet, × 8.

3. **Mycosphaerella filicum** (Desm.) Starbäck, s. lato

Starbäck, Bihang K. Sv. Vet.-Akad. Handl. 15:3:2:9 (1889) – *Sphaeria Filicum* Desmazières, Pl. Crypt. France ed. 1: 983 (1839); Ann. Sci. Nat. Bot. ser. 2. 13; 187 (1840) – *Sphaerella filicum* (Desm.) Auerswald in Mycol. Eur. 5/6: 20 (1869) – Type: France, *Asplenium adiantum-nigrum* (PC!).

Mycosphaerella asplenii (Awd) Lindau in Engler-Prantl, Nat. Pflanzenfam. 1:1:426 (1897) – *Sphaerella Asplenii* Rbh. ex Auerswald, Mycol. Eur. 5/6: 20 (1869) ; Rbh. ex Niessl, Verhandl. Naturforsch. Ver. Brünn. 3: 178 (1864), nom. nud. – Type: "Auf allen Theilen abgestorbener Wedel von *Asplenium septentrionale*" (n.v.).

?*Mycosphaerella tirolensis* (Awd) Magnus in Dalla Torre & Sarnthein, Fl. Tirol, Vorarlberg und Liechtenstein 3: 463 (1905) – *Sphaerella tirolensis* Auerswald, Mycol. Eur. 5/6: 20 (1869) – Type: "Lebt auf abgestorbenen Wedeln von *Polypodium vulgare*" (n.v.).

Fig. 1 A–C, 3 C, 4 B–F.

Mycosphaerella filicum is used here as a comprehensive name for some closely related forms, which start their development as true parasites but which apparently will not reach full maturity until the host tissue is dead. They can be characterized as follows:

Ascocarps generally densely grouped in brownish spots in living fronds, immersed, piercing the epidermis with a bluntly conical apex, subglobose, (50–)60–80 μm diam., connected by olivaceous hyphae. *Asci* few, mostly 10–15, finally pyriform, 25–40 × 10–14 μm. *Spores* oblong, (11–)13–15(–18) × 3.5–4.5 μm, with a median septum, slightly greenish, in each cell with 2 very distinct oil globules, which finally fuse.

M. filicum is distinctive owing to the parasitic habit, the saccate asci and the strongly guttulate spores. Since it forms leaf spots it catches the eye and has been relatively much collected, unfortunately generally in an unripe condition. It is possible that the ascocarps do not reach full maturity until the infested fronds are dead. As understood here, *M. filicum* will comprise forms on *Asplenium* spp., on *Polypodium vulgare,* and on *Dryopteris spinulosa,* which will be discussed separately. Unfortunately the nomenclature has been much confused, as the name *Mycosphaerella (Sphaerella) filicum* has been widely employed for *M. aspidii*. This practice was introduced by Auerswald (1869) and perpetuated by many authors, i.a. Starbäck who made the combination in *Mycosphaerella*.

Our treatment of *M. filicum* is admittedly preliminary. The taxonomy of these forms can probably not be definitely settled without extensive cultivation experiments, which are outside the scope of this study.

On Asplenium species

Exs.: On *A. adiantum-nigrum:* Desm., Pl. Cr. Fr. 983 (PC) – Fuckel, F. rhen. 831 (S) – Jaap, F. sel. 617 (S), 710 a, b (S) – Rehm, Asc. 1571 (S).

On *A. septentrionale:* Jaap, F. sel. 616 (S) – Petr., Fl. Bohem. Mor. II:1:2481 (S); Myc. gen. 327 (UPS) – Rbh., F. eur. 2438 (S) – Rehm, Asc. 1570 (S).

On *A. trichomanes:* Thüm., F. austr. 243 (UPS).

Fig. 1 A, 4 B.

Particularly when growing on *A. adiantum-nigrum* the fungus is quite conspicuous owing to the ± discoloured leaves; often a large part of the lamina turns brownish, beginning at the margins (Fig. 4 B). The clustered ascocarps are generally epiphyllous, but hypophyllous groups of ascocarps are not at all rare. Almost all herbarium material seen by us is more or less immature. However, we can find no support for distinguishing between the forms on different species of *Asplenium,* as some authors have tried. We thus include *Mycosphaerella asplenii* in *M. filicum*. (We have not seen any authentic material of *Sphaerella asplenii,* but there can be no doubt about the identity of Auerswald's fungus; particularly convincing is his drawing of the spores with oil globules.)

Mycosphaerella filicum is probably rather common on *Asplenium* spp., though it catches the eye only on *A. adiantum-nigrum*. We have seen material from Sweden, Denmark, France, Germany, Switzerland, Austria, Hungary, and Yugoslavia. So far only three Scandinavian collections are known:

Sweden: Uppland, Dalby, Löjhällen, *A. septentrionale,* 7.VI.1976, Holm 831b. – Ännesta, *A. s.,* 4.XI.1978, Holm 1523.

Denmark: Bornholm, Hammershus, *A. adiantum-nigrum,* 8.VIII.1922, J. Lagerkranz (UPS).

On Dryopteris spinulosa

Exs.: Eriksson, F. par. 196 (S, UPS) – Rbh., Herb. Mycol. II:534 (S) – Vgr., Micr. 1080 (S, UPS).

Fig. 1 B, 4 C.

This form is very noteworthy because of the *hypophyllous* ascocarps; otherwise it agrees well with the forms on *Asplenium* and *Polypodium*. Possibly it also has somewhat smaller spores. Anyway we do not feel justified in describing it as a new taxon, as we have seen only one fully mature collection (Holm 350).

It is indeed amazing that this form seems to be restricted to *Dryopteris spinulosa* or in any case to have a marked preference for this particular species. We have searched for it in vain in the Scandinavian collections of *D. dilatata* s.lat. in UPS whilst scrutinizing the material of *D. spinulosa* resulted in one find (Umeå, cf. below). If the fungus will discriminate between those closely related species it must be ranked as a skilful taxonomist.

On account of the leaf spots the fungus is rather conspicuous, and has been noticed by several collectors and throughout identified as

Mycosphaerella (Sphaeria, Sphaerella) filicum. Besides the above-mentioned exsiccata we have seen the following material:

Sweden: Småland, Ö. Torsås, Sunnansjö, 16.VIII.1883, C. J. Johanson (S). – *Dalarna,* Garpenberg, Realsbo, 29.VIII.1974, Holm 350 a. – *Västerbotten.* Umeå, X.1919, V. Ålund (UPS).

Denmark: Sealand, Slangerup, 20.X.1907, J. Lind (S).

Germany: Brandenburg, pr. Buckow, 20.X.1917, P. Vogel (S). – *Saxony,* Schandau, Hort. Bot., VIII.1903, P. Sydow (S).

On Polypodium vulgare

Exs.: 0. (Roumeg., F. gall. 2935 sub nom. *Sphaerella tyrolensis* is quite immature and indeterminable, at least in UPS – Vgr, Micr. rar. sel. 1489 sub nom. *M. tyrolensis* is *Glomerella polypodii,* UPS.)

Fig. 1 C, 3 C, 4 D–F.

Generally forming very distinct necrotic leaf spots, first in live, then in dying fronds; the patches are first whitish with a few epiphyllous ascocarps (Fig. 4 D, E) and later turn brown with many crowded fruit bodies (Fig. 4 F). At a late saprobic stage scattered ascocarps also occur, outside the spots, even in the underside of the leaves. Those ascocarps may grow intermixed with fruit bodies of *M. aspidii,* which are very similar.

It is possible and perhaps probable that Auerswald's *Sphaerella tirolensis* belongs here. Unfortunately we have not been able to trace any authentic material (there is none in B, nor in K). Anyway this fungus has been little collected. Nevertheless it seems to be common around Uppsala. It should not be confused with "*Mycosphaerella polypodii*", i.e. *Glomerella polypodii,* cf. Holm & Holm (1978 p. 102) which is superficially similar.

4. **Mycosphaerella osmundicola** (Kirschst.) L. & K. Holm, comb. nova

Sphaerella osmundicola Kirschstein, Hedw. 81: 194 (1944) – Type: Germany, Olpe, in dead leaves of *Osmunda regalis,* 23.VI.1940, leg. A. Ludwig (B!).

Fig. 1 D, 3 D.

Ascocarps amphigenous, densely crowded, immersed in the leaf tissue, subglobose, c. 50 μm diam., connected by a ± profuse, dark intramatrical mycelium. *Asci* few, c. 10, pyriform, 25–30 × 10–12 μm, sessile, 8-spored. *Spores* conglobate, ± cuneiform, 10–13(–15) × 2.5–3 μm, hyaline, with a supramedian septum.

This species seems very distinctive, in aspect as well as microscopically: the groups of ascocarps appear as dark spots, c. 5 mm long; the spores are characterized by the supramedian septum. It has so far been known only from two German collections, cf. Kirschstein (1944). Possibly Schröter's (1894 p. 342) record of "*Mycosphaerella filicum*" on *Osmunda* actually refers to this species.

Sweden: Småland, Femsjö, Älmås, in last year's leaves of *Osmunda regalis,* 13.VII.1929, Nannfeldt 2416 (UPS).

5. **Mycosphaerella pteridis** (Desm.) Schröter

Schröter, Pilze Schlesiens 2: 341 (1894) – *Sphaerella pteridis* (Desm.) De Notaris, Sfer. ital. 87 (1863), non *Sphaerella pteridis* Cooke, J. Bot. 4: 250 (1866) quod est *Didymella prominula* – *Sphaeria pteridis* Desmazières, Pl. Crypt. Fr. ed. 1: 1295; Ann. Sci. Nat. Bot. sér. 2. 19: 359 (1843) – Type: France, *Pteridium aquilinum* (P C!). [? *Sphaeria punctiformis* b. *Pteridis* Fries, Syst. Mycol. 2: 525 (1823), nom. nud.]

Sphaerella indistincta Peck, Ann. Rept N. Y. State Mus. 28:81 (1877) – Type: USA, N. Y., Albany, *Pteridium aquilinum,* VI.1876, leg. Peck (= Thüm., Myc. univ. 759, UPS isotype!).

Exs.: Desm., Pl. Crypt. Fr. I:1295 (PC) – ? Fr., Scl. suec. 86 ('*Sphaeria punctiformis*', UPS) – Fckl, F. rhen. 852 ('*Sphaeria aquilina*', S) – Krieg., F. sax. 129 (S) – Lundell & Nannf., F. suec. 2268 ('*M. aquilina*', S, UPS) – Rbh., F. eur. 249 (S) – Rehm, Asc. 443, 837 ('*Sphaerella aquilina*', S) – Syd., Myc. germ. 3311 (S, UPS); Myc. march. 1072 (?), 1973 ('*Sphaerella aquilina*', S, UPS) – Thüm., Myc. univ. 759 ('*Sphaerella indistincta*', UPS), 1841 (UPS).

Fig. 1 H.

Ascocarps epiphyllous, scattered or often rather densely grouped, subglobose, 100–130 μm diam., immersed, piercing the epidermis with a blunt apex. *Peridium* up to 30 μm broad, of textura angularis. *Asci* rather numerous, ± oblong, 60–70 × 12 μm, with a brief but distinct pedicel, 8-spored. *Spores* ± parallel, cylindric-fusiform with obtuse ends, often arcuate, (25–) 30–38 × 4–5 μm, without (or with indistinct) guttules, hyaline, with a median or slightly supramedian septum.

In dead fronds of *Pteridium aquilinum.*

This species is easily distinguished from the other Nordic pteridicolous *Mycosphaerellae* by its long and narrow spores. It can also be

identified under the binocular fairly safely because of the relatively large ascocarps, grouped in the upper leaf side. It is very common and apparently confined to *Pteridium,* often found intermixed with *Mycosphaerella aspidii.*

We concur here in a widely accepted tradition when identifying this fungus with Desmazières's *Sphaeria pteridis*. His original material (PC!) is quite immature, but agrees well in appearance with *M. pteridis* as understood here, and as nothing forbids the supposed identity, we think it appropriate to follow the tradition from De Notaris, Winter and Schröter. In his protologue Desmazières cited *Sphaeria punctiformis* b. *Pteridis* Fr. as a synonym with explicit reference to Fr., Scl. suec. 86. (It is uncertain whether this means the first or the second edition.) The identification may be correct: the material at UPS of ed. 1, No. 86 is immature but could well be Desmazières's species. In any case the epithet *''pteridis''* should be credited to Desmazières alone, as *''Sphaeria punctiformis* b. *Pteridis* Fr.'' is a nomen nudum.

Sphaerella pteridis Cooke is quite different. Cooke referred to Desmazières but as is evident from his description and illustration his fungus is the so-called *Didymella prominula* (Speg.) Piroz. & Morgan-Jones (possibly a form of *Scirrhia aspidiorum?).*

Finally it is worth mentioning that Desmazières's description contains a remarkable passage: ''ascis clavatis e duplici membrana compositis'' (Desmazières 1843 p. 359). This may be the first record in the literature of a bitunicate ascus!

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Species concept in Anthracoidea (Ustilaginales) and some new species

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Criteria for the species delimitation and the relation of the taxonomy of *Anthracoidea* to that of the host plants are discussed. Five new species are described: *A. baldensis, A. michelii, A. pilosae, A. sempervirentis* and *A. tomentosae*. Two species are transferred from *Cintractia* to *Anthracoidea,* viz. *A. carphae* and *A. schoenus,* based on *Ustilago carphae* Speg. and *Cintractia schoenus* G. H. Cunn., respectively. *Cintractia waiouru* G. H. Cunn. is synonymous with *A. carphae*.

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The genus *Anthracoidea* was erected by Brefeld (1895) for the black ovariicolous smuts on *Carex* (lectotype *A. caricis* (Pers.) Bref. on *Carex pilulifera* L.), based on the fact that the promycelia are two-celled, whereas those of *Ustilago* are four-celled. Cornu (1883) described the genus *Cintractia* for Berkeley's *Ustilago axicola,* parasitic on *Fimbristylis diphylla* (Retz.) Vahl. The sori of this species are formed on the inflorescence axis and in the inflorescence. The host tissues are covered by a thick layer of sterile hyphae to form a stroma (with U-shaped formations), in which the spores are formed. A sterile stroma or hyphal strands lack in the ovariicolous *Anthracoidea* sorus. Magnus (1896) used the name *Cintractia* for the ovariicolous smuts on *Carex*. After Magnus, the majority of the authors treated *Cintractia* and *Anthracoidea* together under the older name *Cintractia*. Kukkonen (1963) demonstrated the necessity of reestablishing the genus *Anthracoidea*.

Species of the genus *Anthracoidea* parasitize members of *Carex, Carpha, Kobresia, Schoenus, Trichophorum* and *Uncinia* (for *Carpha* and *Schoenus* see *Two new combinations* below). The infection is a local, floral infection produced by germinated sporidium (basidiospores) or also by the imperfect *Crotalia* stage (Kukkonen & Vatanen 1968). Whereas most species belonging to the Ustilaginales are heterothallic, the species of *Anthracoidea* are (apparently) homothallic or pseudo-homothallic (Kukkonen & Rautakoski 1964), since no fusion between sporidia or promycelial cells has been seen. The absence of cross-fertilisation greatly reduces the possibility of producing new varieties and explains the observation that there is a close relation between the species of *Anthracoidea* and their hosts. The homothallism in *Anthracoidea* smuts limits their variability and their ability to attack more than one or a few host species. In the papers by Savile & Calder (1953), Nannfeldt & Lindeberg (1957, 1965), Kukkonen (1961, 1963, 1964 a) and Nannfeldt (1977) there is extensive evidence for a close connection between the species of *Anthracoidea* and their host (or hosts), and for a phylogenetic co-evolution of the parasite with its host. Some workers admit only a few, morphologically very different species. Others recognize many narrowly circumscribed species restricted to a certain host. Savile (1952) used the rank of variety for some of the 'smaller' taxa. His varieties and species are generally confined to a particular species or section of *Carex* but he also often assigns smuts on less closely related hosts to the same species or variety.

The evolution within *Anthracoidea* has in

many cases reached the *species* level when the parallel evolution of the host has reached the level of *section*. This is easily demonstrated when there are clear morphological differences between the species (e.g. in the sorus characteristics, in the spore size, colour and shape, in the spore wall thickness, thickenings, gelatinous coat, light-refractive areas and internal swellings, surface ornamentation, in spore germination, promycelia and sporidia characteristics etc.). For instance, there are four very distinct *Anthracoidea* species which parasitise different members of sect. *Acutae* (subgen. *Carex*): *A. echinospora* (Lehtola) Kukk. (small spores with truncate spines), *A. heterospora* (B. Lindeb.) Kukk. (small, only faintly verruculose spores), *A. bigelowii* Nannf. (medium-sized spores with small but distinct warts) and *A. liroi* (Lehtola) Nannf. (large, only faintly verruculose spores). On sect. *Paludosae* (subgen. *Carex*) there are at least five morphologically well differentiated species: *A. americana* (Nannf. & B. Lindeb.) Kukk., *A. angulata* (H. Syd.) Boidol & Poelt, *A. inclusa* Bref., *A. lasiocarpae* B. Lindeb., *A. subinclusa* (Körn.) Bref., and one intermediate: *A. intercedens* Nannf. It is more difficult to find the species limits when the morphological differences are not so clear. In contrast to other smuts, *Anthracoidea* is split up into a large number of distinct, genetically isolated but morphologically often only little different 'small' species. On this basis more than 20 species have been described in the last 20 years by Kukkonen, Lindeberg, Nannfeldt, Savile and others. As the morphological characteristics are few and the variability has its limits, the number of possible character combinations is not very large. This means that (1) it is difficult to have many morphologically well differentiated species, and that (2) theoretically the possibility exists that there are two or more species with the same (or nearly the same) morphology, but nevertheless difficult to distinguish at least with the present methods. In this latter case the taxonomic position (section!) of the host may be of value in the delimitation of species. And in fact, a thorough examination of the spores of a large number of different provenances may show small but constant differences between the spores of *Anthracoidea* parasitising *Carex* or *Kobresia* species belonging to different, not closely related sections. And, inversely, the knowledge of the *Anthracoidea* species may be of value for the classification of *Carex* or *Kobresia* species as to section, as well as in the phylogenetical investigations (used i.a. by Savile & Calder 1953).

The difficulties are made even greater by the greater or smaller variation of the spore characteristics within a given species. For instance a species with medium-sized spores may also have a certain number of small and large spores. Therefore it is insufficient to give only the limits of the spore measurements. It is more relevant to present 'normal' values together with the extreme ones in brackets; and still better would be to give the percentage distribution of the spore measurements in a diagram. However, such diagrams may show considerable differences, sometimes even when the measurements were made on one and the same material. A more correct characterisation of the spore dimensions would be to give the area or, even better, the volume of 100 spores, but this is impossible in actual practice. Furthermore, it is clearly impossible to express *all* morphological characteristics by percentages with today's investigation routines. However, with a certain experience, it is nevertheless possible to distinguish even closely related (and inadequately described) species by careful comparison of microscopical preparations.

The identification of *Anthracoidea* species is complicated by the presence of 'accidental infections' by 'accessory parasites' beside the 'principal parasite' (or parasites) of *Anthracoidea*, typical for a given host species or section.

In this paper five new species are described according to these principles. Several authors (e.g. Kukkonen 1963 p. 84, Kochman & Majewski 1973 p. 103 and Braun & Hirsch 1978 p. 58 and Tomková-Součková 1960 p. 164) have already drawn attention to the fact that these smuts do not agree with previously known species of *Anthracoidea*.

Material and methods

For measurement, the spores were suspended in lactophenol, heated to the boiling point and then cooled. The measurements of one hundred spores for each species were made by an oil-immersion lens at 1000 times magnification.

The abbreviations of herbaria follow Index Herbariorum (Holmgren & Keuken 1974). The following personal herbaria have also been checked:

HBr: Herb. W. Brandenburger, Inst. für Pharmazeutische Biologie der Universität Bonn, Nussallee 6, D-5300 Bonn 1, W. Germany.
HDö: Herb. P. Döbbeler, Botanische Staatssammlung, Menzinger Str. 67, D-8000 München, W. Germany.
HUV: Herb. Ustilag. Vánky, K. Vánky, Kyrkbyn 44, S-780 41 Gagnef, Sweden.
HZogg: Herb. prof. H. Zogg, Eidg. Forschungsanstalt für Landw. Pflanzenbau, Zürich-Reckenholz, Postfach, CH-8046 Zürich, Switzerland.

Smuts on Carex curvula and baldensis

Carex sect. *Curvulae* and sect. *Baldenses,* both monotypic, are of uncertain taxonomic position. They are tristigmatic, but nevertheless Kükenthal (1909) included them in the subgenus *Vignea*! However, he suggested affinities with the subgenus *Carex,* viz. with *Frigidae* for *Carex curvula* and with *Pallescentes* for *C. baldensis*.

Both *C. curvula* and *C. baldensis* are parasitised by *Anthracoidea* species. Dr I. Kukkonen (pers. comm.) intends to describe the *C. curvula* smut as a separate species. The *C. baldensis* smut is described here. It is not related to any known *Vignea* smut, but may be identical with one of the three undescribed species on *C. pallescens* mentioned by Nannfeldt (1979).

Anthracoidea baldensis Vánky, sp. nov.

Typus: *Carex baldensis;* Helvetia: Graubünden, Ofenberg, ob Wegerhaus, 26.7.1906, H. C. Schellenberg (Herb. Vánky holotypus (HUV 7609), UPS, ZT isotypi).

Sori in ovariis sicut corpuscula nigra, globulosa usque ovoidea, 2–3.5 mm longa, primo membrana tenui, cinerascenti induta et utriculis obtecta, in statu maturo utriculi longitudinaliter scissi, membrana cinerascens lacerata et massa sporarum nigra gradatim dissoluta. *Sporae* magnitudine mediocres, deplanatae, visu plano ovoideae, rotundato-polyangulare usque irregulares, 13.5–20× 17–21.5(–23) μm diam. (M= 17.5–20 μm longae), latere visu elongatae, c. 9.5–12 μm crassae, mediocriter rubrobrunneae; *pariete* inaequaliter, 1.2–2 μm crasso, in angulis usque ad 3.5 μm incrassato, saepe maculis refractivis, nonnunquam etiam 1–2 gibberulis parvis internis instructo, verruculis deplanatis, interdum partim confluentibus et saepe in seriebus brevibus vel catervulis ordinatis ornato, huis convenienter linea extrema fere undulatae. Superficies sporarum sub SEM verrucis obtusis, 0.2–0.6 μm diam. vel confusione majoribus et c. 0.3–0.4 μm altis instructa. Germinatio sporarum non observata.

Sori in the ovaries as black, globulose to ovoidal, 2–3.5 mm long bodies, at first covered by a thin, greyish membrane and hidden by the utricles. When mature the utricles split longitudinally, the greyish membrane flakes away and the black spore mass becomes exposed. *Spores* (Fig. 3 C) medium-sized, flattened, in plan view ovoidal, rounded–polyangular to irregular, 13.5–20× 17–21.5(–23) μm in diameter (M= 17.5–20 μm long), in side view elongated, c. 9.5–12 μm thick, medium reddish-brown. *Spore wall* unevenly thickened, 1.2–2 μm thick, at the angles up to 3.5 μm, light-refractive spots often present, sometimes 1–2 weak internal swellings; surface provided with low warts, sometimes partly fusing and often arranged into short rows or groups, making the spore profile to appear just wavy. In SEM (Fig. 3 D) surface provided with blunt, rounded warts 0.2–0.6 μm in diameter, or bigger if confluent, 0.3–0.4 μm high; rests of a thin gelatinous coat often present. Germination unknown. Matrix: *Carex baldensis* L. (sect. *Baldenses*).

Specimens examined: Switzerland. Graubünden: 25.7.1906, O. Appel (ZT) – Engadine, Grisons, 12.8.1916, L. Guyot (HZogg) – (see also type).

Smuts on Carex sect. Rhomboidales

The European members of *Carex* subgen. *Carex* sect. *Rhomboidales* Kük. are parasitised by at least two morphologically different species of *Anthracoidea* previously included in *A. caricis*. The one on *Carex michelii* is characterized by very irregular spores provided with prominent warts. The other, on *C. pilosa,* has larger, more regular and finely verruculose spores. Both species are here described as new.

Anthracoidea michelii Vánky, sp. nov.

Typus: *Carex michelii;* Hungaria, in declivibus supra pag. Solymár, c. 15 km NW Budapest, 3.6.1917, A. Degen (Herb. Vánky holotypus (HUV 122), BP isotypus).

Sori in ovariis. *Sporae* forma valde variae, parum complanatae, superne visu angulares vel irregulares, 13–20× 14–24(–30) μm diam., e latere elongatae, 10–13 μm crassae, mediocriter vel ± atre rufobrunneae; *pariete* superne visu distincte verruculoso, verruculis ± aequaliter dispersis, e latere distincte papillato vel serratulato, non aequaliter, 1–3(–5) μm crasso, in angulis crassissimo, regulariter areis refractivis saepe abundantibus, 1–2 gibberis internis nonnunquam praesentibus. Superficies sporarum sub SEM verrucis aliquid irregulariter dispersis, densiuscule dispositis, rotundatis, magnitudine variis: 0.2–0.6 μm diam. et 0.15–0.5 μm altis instructa.

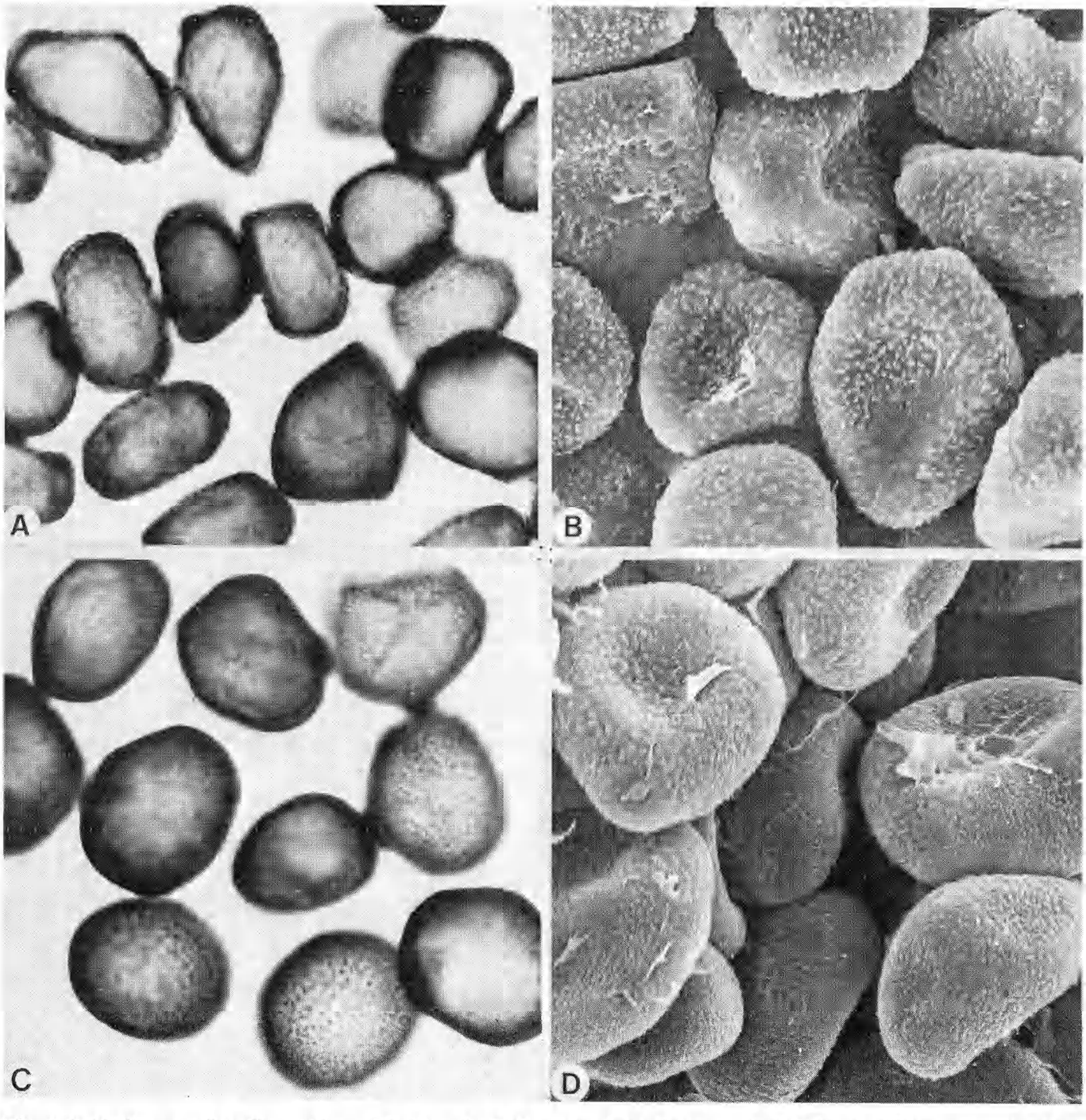

Fig. 1 A, B: Spores of *Anthracoidea michelii*. – C, D: Spores of *A. pilosae*. – A, C: LM, c. 1000 ×. – B, D: SEM, c. 1800 ×. – Photos K. Vánky.

Sori in the ovaries. *Spores* (Fig. 1 A) variable in form, moderately flattened, in plan view angular–irregular, 13–20 × 14–24(–30) μm in diameter, in side view elongated, 10–13 μm thick, medium to dark reddish-brown. *Wall* in face view distinctly verruculose, warts more or less evenly dispersed over the whole spore surface, in side view clearly papillate to serratulate, of uneven thickness, 1–3(–5) μm wide, thickest at the angles, light-refractive areas common, often abundant, 1–2 internal swellings sometimes present. Surface by SEM (Fig. 1 B) with moderately densely, somewhat irregularly dispersed, rounded warts of different size, 0.2–0.6 μm in diameter and 0.15–0.5 μm in height. Germination not studied. Matrix: *Carex michelii* Host (sect. *Rhomboidales*).

Specimens examined: Austria. Nieder-Österreich: Am Hintel, 4.1879, G. Beck (HUV) – *Czechoslovakia. Moravia:* Brno (Brünn), G. Niessl (M) – *Slovakia:*

Trentschin, mt. Turecko, 5.1883, L. Holuby, in Linh. fgi. hung. 102, sub *Ustilago caricis,* together with *Anthracoidea caryophyllea* Kukk. on *Carex caryophyllea* Latourr. (H, HUV, M); Bohuslavice (Bosác), 15.5.1895, L. Holuby (BP, HUV) – *Hungary. Pest:* pr. Budapest, mt. Hárshegy, 6.1882, Gy. Szépligeti (BP, UPS) – Budakeszi, 6.1882, Gy. Szépligeti (BP) – Szentendre, 20.5.1907, G. Lengyel (HUV) – Farkasvölgy, 7.6.1910, G. Moesz (BP) – (see also type) – *Baranya:* mt. Mecsek pr. urbem Pécs, 11.6.1911, G. Lengyel (BP) – *Veszprém:* mt. Bakony, Hódoséri hegy, 30.5.1902, Pilliz (BP, HUV) – *Poland:* Dźvinogŕod-Podde, 3.6.1933, R. Piech (WA) – *Romania. Muntenia:* Filipeşti de Pădure, pr. Ploieşti, 25.6.1955, I. Şerbănescu (BUCM, HUV) – *Transylvania:* Valea Lungă (Hosszúaszó), W oppid. Mediaş (Medgyes), 19.6.1919, A. Benedek (BP) – *Soviet Union. Ukraine* (formerly Poland): Na Kryszczatku nad Dniestrem na Podolu bukowińskiem, A. Wróblewski, in Racib. Mycoth. pol. 114, sub *Anthracoidea caricis* (HUV, M, WA) – Podole Ścianski n. Dniestrem, 4.6.1933, W. Zablocka (WA) – Zaleszczyki nad Dniestrem, 6.6.1933, W. Zablocka (WA).

Some samples of *Carex michelii* from Hungary (mt. Hárshegy pr. Budapest, 6.1908, Gy. Szépligeti (BP, HUV) contain, besides sori of *A. michelii,* also sori of an *Anthracoidea* species characterised by elongated, only finely verruculose and light-coloured spores. More material is needed to judge whether it is a new species or only an accidental infection by a previously described *Anthracoidea* species.

Anthracoidea pilosae Vánky, sp. nov.

Typus: *Carex pilosa;* Hungaria, comit. Nógrád, mons Börzsöny pr. pag. Diósjenö, 12.6.1955, L. Baksay (Herb. Vánky holotypus (HUV 134), BP isotypus).

Sori in ovariis. *Sporae* forma et magnitudine parum variae, plano visu polyedricae vel irregulares, 15–22 × 20–28(–32) μm diam. (M = 22–26 μm longae), latere visu parum depressae, 12–15 μm crassae, rufobrunneae; *pariete* 1–4 μm crasso, in angulis saepe incrassato, a fronte visu tenuiter vel mediocriter, ± uniformiter verruculoso, a latere visu leviter, papillato vel serratulato, nonnunquam et areis refractivis et gibberis internis vix conspicuis parvis instructo. Sub SEM paries ± uniformiter denseque verruculosus, verruculis 0.2–0.7 μm diam. et 0.1–0.5 μm altis. Areae inter verrucula subtilissime verruculosae. Germinatio sporarum non observata.

Sori in the ovaries. *Spores* (Fig. 1 C) moderately variable in form and size, in plan view polyhedral to irregular, 15–22 × 20–28(–32) μm in diameter (M = 22–26 μm long), in side view moderately flattened, 12–15 μm thick, reddish-brown. *Wall* 1–4 μm thick, often thickest at the angles, in face view finely to moderately, more or less uniformly verruculose, in side view finely papillate–serratulate, light-refractive areas and weak, hardly visible internal swellings sometimes present. Surface by SEM (Fig. 1 D) more or less uniformly and densely verruculose; warts 0.2–0.7 μm in diameter and 0.1–0.5 μm in height. The space between the warts are extremely finely verruculose. Germination not studied. Matrix: *Carex pilosa* Scop. (sect. *Rhomboidales*).

Specimens examined: Austria. Nieder-Österreich: Gaaden, Palla, in Fl. exs. Austro-hung. 3173/II, sub *Cintractia caricis* (BP, H, HUV) – Kuhberge pr. Pottenstein, 5.1879, G. Beck (HUV) – *Czechoslovakia. Moravia:* Blansko, 29.6.1927, R. Picbauer (BRNM) – M.-Weisskirchen, Ribar, 6.1938, F. Petrak (M) – *Slovakia:* Bratislava (Pozsony, Pressburg), 18.6.1887, 6.1889 & 8.1892, J. A. Bäumler (BP, HUV) – Banská Stiavnica (Selmecbánya, Schemnitz), mt. Sytno, 2.8.1887 & 2.8.1892, A. Kmeť (BP, HUV, S, UPS) – *Hungary:* (see type) – *Soviet Union:* 25 km NW Moskow, Stepankowo, 5.1874, Fischer v. Waldheim, in Rbh. fgi. eur. 2397, sub *Ustilago urceolorum* f. *caricis sylvaticae* (BP, HUV, M, S) – *Switzerland. Aargau:* Baden, 9.6.1861, A. Geheeb, in Wartmann & Schenk, schweiz. krypt. 501/b, sub *Ustilago urceolorum* (HUV) – *Zürich:* Mt. Zürichberg pr. Zürich, 8.1880, G. Winter, in Winter, fgi. helv. suppl. 3, sub *Ustilago caricis* (UPS) – Kachberg pr. Ellikon a. Rhein, 3.7.1934, W. Koch (UPS).

Anthracoidea sempervirentis Vánky, sp. nov.

Typus: *Carex sempervirens;* Romania, Transylvania (olim Hungaria), in alpibus Rodnei, mt. Koronjis, ultimo Iuliae, 1883, legit Gy. Linhart, in Linh. fgi. hung. 204, sub *Ustilago caricis,* in *Carex tristis* (Herb. Vánky holotype (HUV 164), BP, M, S, UPS isotypi).

[?*Ustilago caricis* (Pers.) Tul. c *C. mielichoferi* Fuss 1878 p. 446 nom. nud.]

[?*Ustilago caricis* (Pers.) Tul. d *C. sempervirentis* Fuss 1878 p. 446, nom. nud.]

Sori in ovariis sicut corpuscula nigra, globulosa vel ovoidea, 2–3.5 mm longa, dura, carbonacea, glumis partim obtecta, in superficie pulverulenta. *Sporae* magnitudine mediocrae, parum et irregulariter complanatae, in visu plano rotundatae, plerumque parum polyedricae vel irregulares, 14–22 × (16–)19–24(–27) μm diam. (M = 20–22 μm longae), latere visu elongatae, c. 12–15 μm crassae, fusco-rufobrunneae vel atrobrunneae; *pariete* inaequaliter, 1.5–2.5 μm crasso, in angulis usque ad 4 μm incrassato, in areis incrassatis nonnunquam maculis refractivis, sine gibberis internis, fronte visu obscure vel conspicue maculoso, latere visu fere levi vel leviter verrucoso, margine tenuiter serratulato. Superficies sporarum sub SEM a parum aspera et nodulis c. 0.1–0.2 μm altis sparse dispositis ornata usque ad verrucis usque 0.5 μm altis, dispersis denseque dispositis, irregularibus, rotundatis, saepe confluentibus instructa. Germinatio sporarum (in

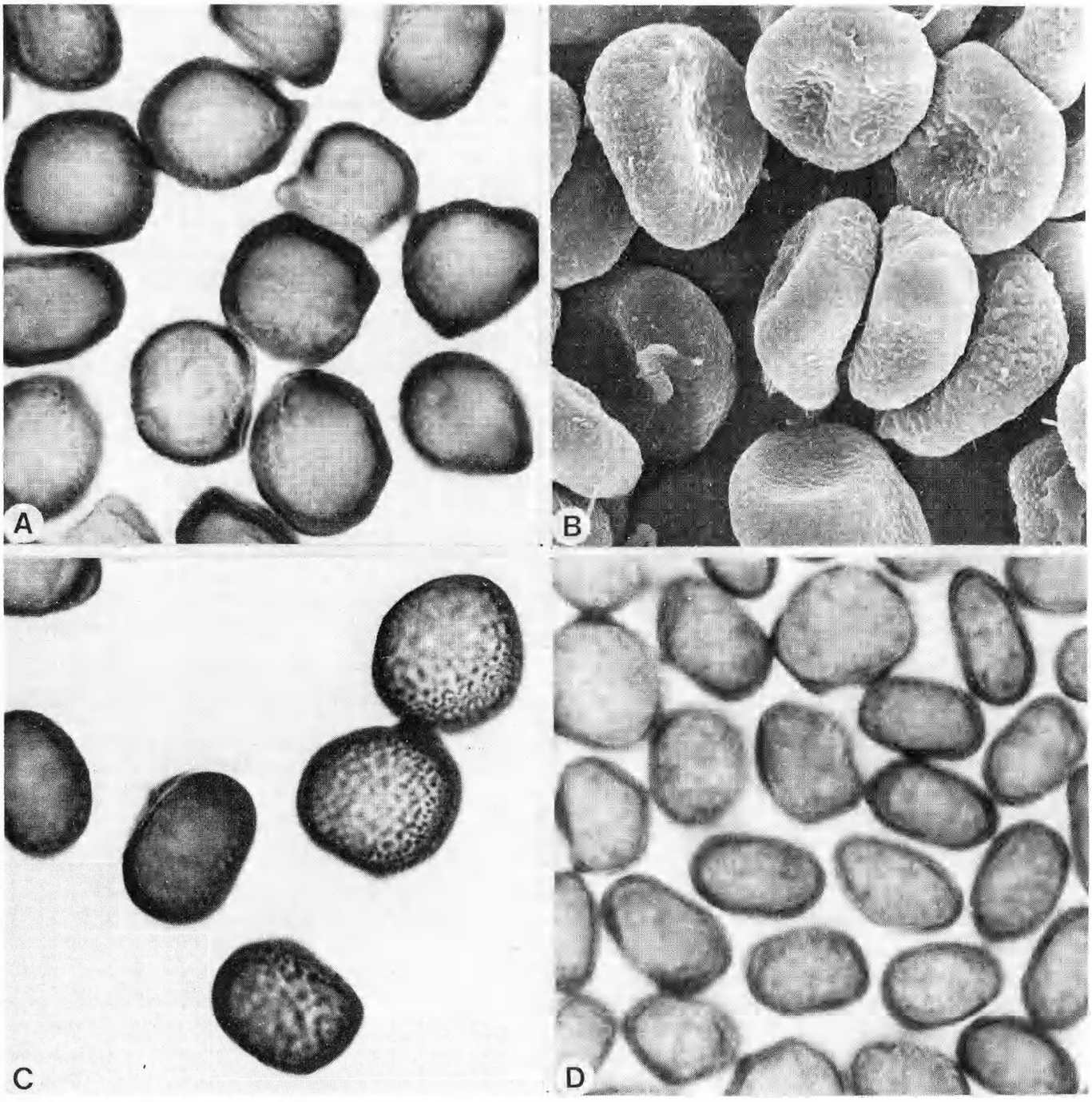

Fig. 2 A, B: Spores of *Anthracoidea sempervirentis*. – C: Spores of *A. misandrae*. – D: Spores of *A. altera*. A, C, D: LM, c. 1000 ×. – B: SEM, c. 1800 ×. – Photos K. Vánky.

Carex firma) ad exemplar schemae "Euanthracoidea". *Crotalia* status non observata.

Sori in the ovaries as black, globulose to ovoidal, 2–3.5 mm long, hard, carbonaceous bodies, partially hidden by the glumes, powdery on the surface. *Spores* (Fig. 2 A) medium-sized, slightly and irregularly flattened, in plan view rounded, usually moderately polyangular to irregular, 14–22 × (16–)19–24(–27) μm in diameter (M = 20–22 μm long), in side view elongated, c. 12–15 μm thick, dark reddish-brown to black-brown. *Wall* unevenly thickened, 1.5–2.5 μm thick, thickest at the angles (up to 4 μm), sometimes with light-refractive spots in the thickest area, without internal swellings, in face view obscurely to clearly dotted, in side view nearly smooth to finely verrucose, spore profile therefore appearing finely serratulate. Surface by SEM (Fig. 2 B) partly with sparse, 0.1–0.2 μm high knobs, partly with abundant and dense, up to 0.5 μm high,

irregular, often confluent, rounded warts. Germination (on *Carex firma*) after "Euanthracoidea" scheme (Boidol & Poelt 1963). *Crotalia* stage not observed. *Matrix: Carex brachystachys* Schrank, *C. ferruginea* Scop., *C. fimbriata* Schkuhr, *C. firma* Host, *C. kitaibeliana* Degen, *C. mucronata* All. and *C. sempervirens* Vill. (the principal host) (sect. *Frigidae*).

A small proportion of larger (16–24 × 19–32 μm), thick-walled spores (2–4, at the angles up to 7 μm) with well-developed light-refractive areas was found in the following specimens: On *Carex ferruginea:* Switzerland, Graubünden, Fürstenalp, 10.8.1906, A. Volkart (UPS) – On *C. fimbriata:* France, Hautes-Alpes, col du Lautaret, 2000 m, 22.9.1954, Ruffier-Lanche (UPS) – On *C. firma:* Italy, Valle di Cei, 1891, Gelmi (UPS).

Exsiccatae (as *Ustilago* or *Cintractia caricis*, or *U. urceolorum*): On *Carex ferruginea:* All. & Schn., Fgi. bavarici 2 (BP, HUV, M, S) – Crypt. exs. Vindob. 4401 (BP, GZU, H, HUV, M, S) – Rbh. Fgi. eur. 2296 (BP, HUV, M, S). – On *Carex firma:* All. & Schn. Fgi. bavarici 101 (HUV, M, S, UPS). – On *Carex kitaibeliana:* Syd. Ustil. 360 (BP, HUV, M, S) – Syd. Ustil. 412 (BP, HUV, M, S). – On *Carex sempervirens:* Crypt. exs. Vindob. 4502 (H, HUV, S) – Herb. mycol. roman. 464 (BP, BUCM, M, S) – Kze. Fgi. sel. exs. 305 (BP, H, HUV, M, S) – Linh. Fgi. hung. 204 (BP, HUV, M, S, UPS) – Syd. Ustil. 176 (HUV, M, S) – Syd. Ustil. 263 (HUV, M, S) – Zillig, Ustil. Eur. 75 (BP, HUV, M, S).

Cintractia caricis on *Carex firma* in Syd. Ustil. 175 is *Anthracoidea caryophylleae* Kukk. on *Carex caryophyllea* (at least the copies in H, HUV, M and S).

Specimens examined: In all 196 collections have been examined from the following countries: Austria (44), Bulgaria (4), Czechoslovakia (9), France (2), Germany (54), Greece (1), Italy (7), Poland (2), Romania (10), Spain (2), Switzerland (52) and Yugoslavia (9). The most common host is *Carex sempervirens* (123) followed by *C. ferruginea* (33), *C. firma* (21), *C. kitaibeliana* (12), *C. mucronata* (5), *C. brachystachys* (1) and *C. fimbriata* (1). (A complete list can be obtained from the Swedish Museum of Natural History, S-104 05 Stockholm, Sweden, or directly from the author.)

Note. Two other species of *Anthracoidea* parasitize members of sect. *Frigidae*, viz. *A. misandrae* Kukk. and *A. altera* Nannf.

A. misandrae (Fig. 2 C) differs from *A. sempervirentis* by having lighter, larger, more regular, round-ellipsoidal spores with thinner wall (1–1.5 μm) and by germination after the Proceres scheme. It is known from *C. atrofusca* Schkuhr and *C. misandra* R. Br. (N Europe and N America), and occasionally from *C. ferruginea, C. firma* and *C. fuliginosa* Schkuhr in C Europe.

A. altera (Fig. 2 D) is similar to *A. misandrae* but the spores are smaller (15–18 × 16–21 μm) and are provided with low internal swellings. Spore wall c. 1 μm thick. Germination after Euanthracoidea scheme. It is known only from N Finland (Lapponia Enontekiensis, Mt. Saana) on *Carex misandra*. *A. sempervirentis* differs from *A. altera* by much thicker spore wall and by more irregular and darker spores.

Anthracoidea tomentosae Vánky, sp. nov.

Typus: *Carex tomentosa;* Romania: Transylvania, prope urbem Cluj (Kolozsvár, Clausenburg), loco dicto Făget (Bükk), c. 600 m, 16.7.1978, G. Negrean & K. Vánky (Herb. Vánky holotypus (HUV 7478), isotypi in BUCM et in Vánky: Ustilaginales exs. 261).

Sori in ovariis. *Sporae* magnae, visu plano (12–)13.5–23 × (18–)20–26(–28) μm diam. (M = 21–24 μm longae), rotundae angulares vel irregulares, parum complanatae (13–16 μm diam.), rufobrunneae; *pariete* (1.5–3(–4) μm crasso, parum inaequaliter incrassato, maxime ad angulos et ad partes protuberantes, raro areis refractivis, 1–3 gibberis internis humilibus; superficie a fronto visu tenuiter denseque maculosa, a latere paene laevi vel leviter verruculosa, margine subtiliter serratulata. Superficies sporarum sub SEM verrucis a rare usque dense dispositis, saepe confluentibus depressisque, rotundatis, 0.3–1.2 μm diam. et 0.1–0.7 μm altis instructa. Spatium inter verrucas lenissime verruculosum.

Sori in the ovaries. *Spores* (Fig. 3 A) large, in plan view (12–)13.5–23 × (18–)20–26(–28) μm in diameter (M = 21–24 μm long), rounded angular to irregular, slightly flattened (13–16 μm thick), reddish-brown. *Wall* moderately unevenly thickened, thickest at the angles and protuberances, 1.5–3(–4) μm thick, rarely with light-refractive spots, 1–3 low internal swellings; surface in face view finely and densely dotted, in side view nearly smooth to finely verruculose, giving a finely serratulate aspect to the spore margin. Surface by SEM (Fig. 3 B) provided with sparse–dense, often confluent and flattened, rounded warts, 0.3–1.2 μm in diameter and 0.1–0.7 μm height. The space between the warts are extremely finely and densely verruculose. Germination unknown but on the basis of the spore morphology the species belongs to subgenus *Proceres* (Kukkonen 1963). Matrix: *Carex tomentosa* L. (sect. *Montanae*).

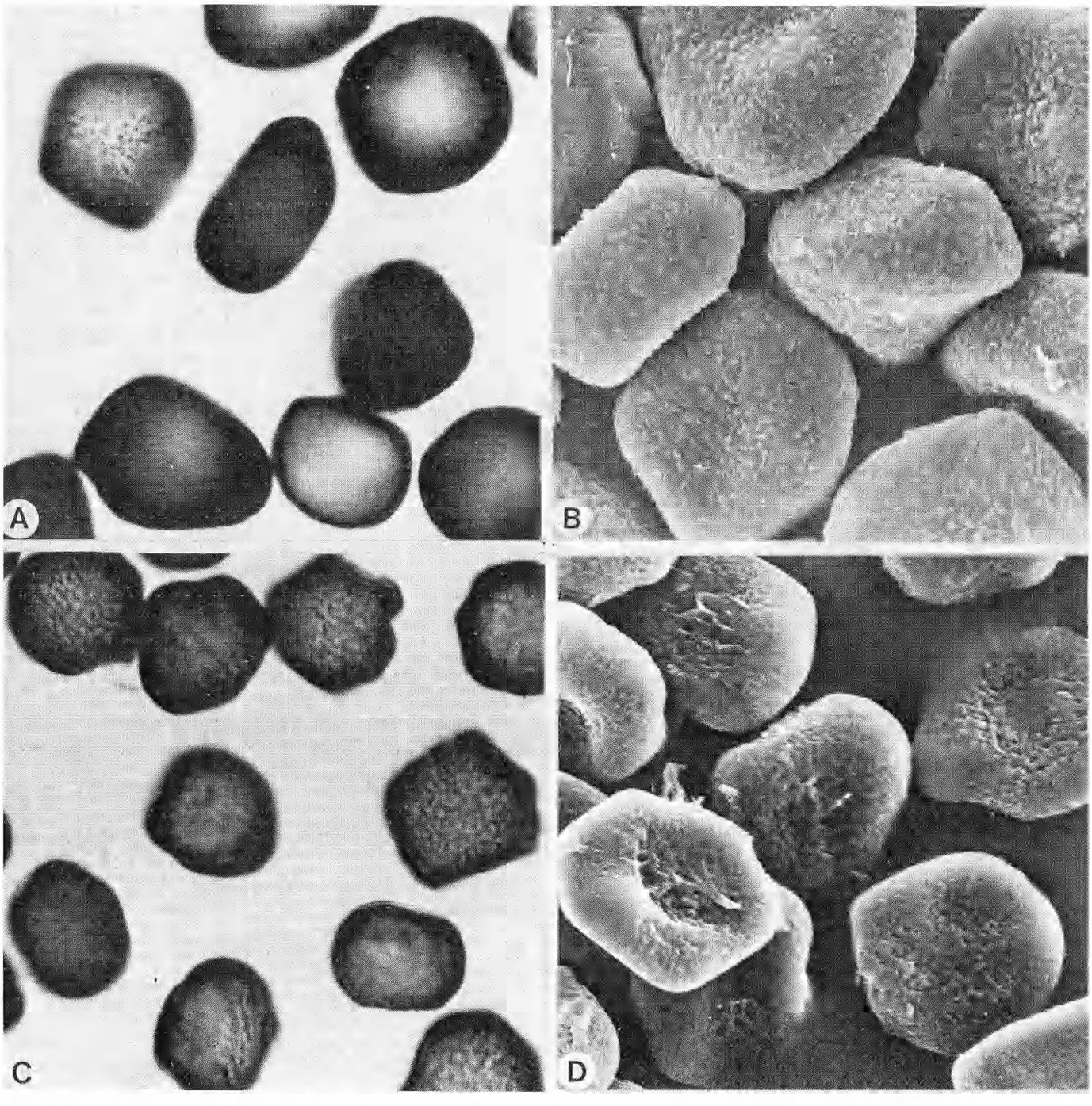

Fig. 3 A, B: Spores of *Anthracoidea tomentosae*. – C, D: Spores of *A. baldensis*. – A, C: LM, c. 1000 ×. – B, D: SEM, c. 1800 ×. – Photos K. Vánky.

Specimens examined: Hungary. Mt. Bükk, 26.7.1909, J. Budai (BP) – *Poland*. Kielce, 29.5.1918, G. Moesz (BP, BUCM, HUV) – *Romania*. *Oltenia:* E Buneşti, 18.6.1961, Ş. & N. Roman (HUV) – *Transylvania* (see also type): – Pr. Arad, pag. Şiria (Világos), 26.7.1887, L. Simonkai (HUV) – Pr. Cluj (Kolozsvár), La Fînaţe (Szénafüvek), 450 m, 11.6.1923, E. I. Nyárády, in Fl. Roman. exs. 1121, sub *Cintractia caricis* (H, HUV); 17.7. 1978, G. Negrean & K. Vánky (BUCM, HUV) – Mociu (Mocs), 15.6.1962, Ş. Roman (HUV) – Sărmăşel (Kissármás), 14.6.1962, N. Roman (HUV) – *Muntenia:* Pr. Piteşti, Ştefăneşti, 5.1944 (BUCM) – *Sweden*. *Gotland:* Slite, 21.7.1968, P. Alanko (HUV) – Gothemhammar, 23.7.1968, P. Alanko (HUV) – Sproge, 27.7. 1968, P. Alanko (HUV).

Notes. One, rather rich collection of *Carex tomentosa* (HUV 5725, Romania, Transylvania, Borsec, 20.7.1965, K. Vánky) was slightly infected by *Anthracoidea irregularis* (''accidental infection''). On the same place *Carex ornithopoda* Willd., heavily infected by the same smut, was abundant.

Species of *Carex* sect. *Montanae* are the hosts of

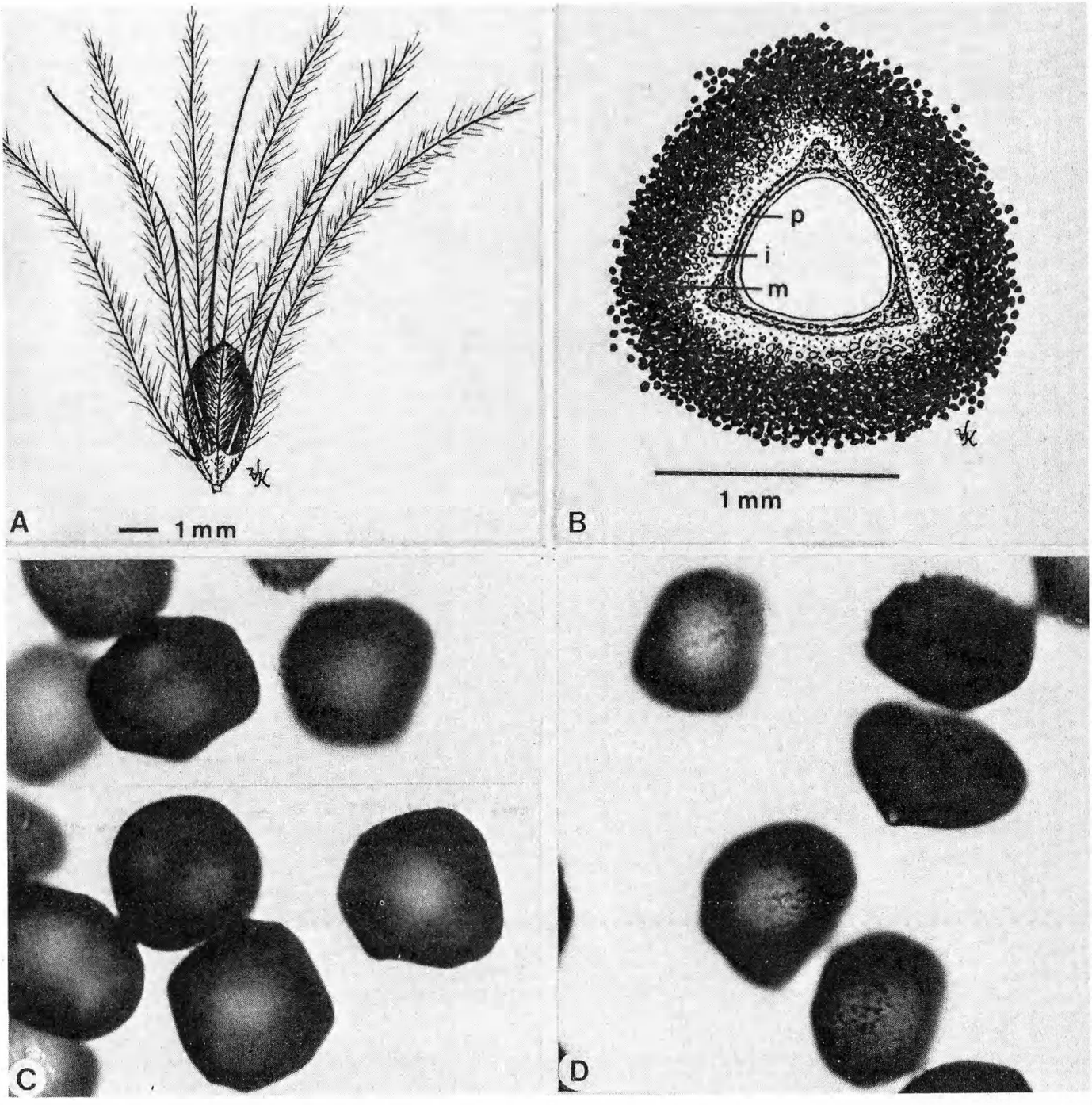

Fig. 4 A: Flower of *Carpha alpina* with a sorus of *Anthracoidea carphae*. – B: T.s., sorus of *A. carphae*. p pericarp, i immature spores, m mature spores. – C: Spores of *A. carphae*. – D: Spores of *A. schoenus*. – C, D: LM, c. 1000 ×. – Photos K. Vánky.

three species of *Anthracoidea*, all belonging to subgen. *Anthracoidea*, viz. (1) *A. caricis* (Pers.) Bref. on *C. montana* L. and *C. pilulifera* L. (spores M = 18–22.5 μm long); (2) *A. caryophylleae* Kukk. on *C. caryophyllea* Latourr. and *C. ericetorum* Poll. (spores M = 16.5–20.5 μm long); and (3) *A. globularis* Kukk. on *C. globularis* L. (spores M = 19.5–23 μm long). *A. tomentosae* differs from these species i.a. by having large spores. Furthermore, it belongs to subgen. *Proceres*.

Two new combinations

A study of the sorus structure and spore morphology of *Cintractia schoenus* G. H. Cunn. on *Schoenus pauciflorus* Hook. (Cyperaceae-Rhynchosporoideae), and *Cintractia waiouru* G.

H. Cunn. on *Carpha alpina* R. Br. (Cyperaceae-Scirpoideae), both from New Zealand, reveals typical *Anthracoidea* characteristics (Fig. 4), which justify their transfer to this genus, even if the spore germination characteristics are still unknown. The fact that often only scattered ovaries are infected in the spike, speaks for a local, floral infection, probably in the same way as for *Anthracoidea* on *Carex*.

Anthracoidea carphae (Speg.) Vánky, comb. nov.

Basionym: *Ustilago carphae* Spegazzini 1887 p. 178 – *Cintractia carphae* (Speg.) Hirschhorn 1936 p. 109 – Type: *Carpha alpina;* Argentina, Tierra del Fuego, Isla de los Estados, near Port Cook, 3.1882, C. Spegazzini (LPS 3134 holotype).

Cintractia waiouru G. H. Cunningham 1945 p. 335 – Type: New Zealand, Auckland, Waihouhounu Stream, National Park, 4.1945, J. M. Dingley (n.v.).

Sori in (scattered) ovaries as black, ovoidal–elongated, 2.5–3.5 × 1.5–2 mm, hard, carbonaceous bodies, partially hidden by the glumes, first covered by a thin greyish membrane which flakes away, exposing the powdery surface. *Spores* (Fig. 4 C) reddish-brown, in plan view 15–20 × 17–25(–27) μm, subcircular, ovoidal, rounded polyangular to moderately irregular, in side view flattened, 12–14 μm thick. *Wall* evenly thickened (1–1.5 μm), sometimes (when the spores are angular) thicker at the angles (up to 3 μm), light-refractive areas sparsely present, no internal swellings; surface finely, densely and uniformly verruculose; profile smooth, finely wavy or finely serratulate. Matrix: *Carpha alpina* R. Br. (*C. schoenoides* Banks & Soland.)

The description above was made up from the type material of *U. carphae* and from material from New Zealand. An examination of the type material of *C. carphae* shows that *C. carphae* and *C. waiouru* are conspecific. The reason for the slight differences between the original descriptions concerning spore size and sculpturing is probably that the optical equipment was more primitive in Spegazzini's time. The species is known from S Argentina and New Zealand.

Specimens examined: Argentina (see holotype) – *New Zealand:* Canterbury, Arthur's Pass, Margaret's Tarn, 15.1.1956, J. M. Dingley (PDD 15796, HUV 7517).

Anthracoidea schoenus (G. H. Cunn.) Vánky, comb. nov.

Basionym: *Cintractia schoenus* G. H. Cunningham 1928 p. 503 – Type: *Schoenus pauciflorus;* New Zealand, Canterbury, Cook Range, 700 m, 1.1928, G. H. Cunningham (n.v.).
Known only from New Zealand.

Specimens examined: New Zealand. Otago, Greenstone Valley, 2.1948, J. M. Dingley (PDD 6126, HUV 7515) – Canterbury, Arthur's Pass, 2700 ft, 18.1.1956, J. M. Dingley (PDD 15794, HUV 7516).

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New species of Calceolaria (Scrophulariaceae) from northern Peru

Ulf Molau

Molau, U. 1979 05 15: New species of Calceolaria (Scrophulariaceae) from northern Peru. *Bot. Notiser 132:* 233–238. Stockholm. ISSN 0006-8195.

Five species of *Calceolaria* L. (Scrophulariaceae) from the Andes of northern Peru are described as new, viz. *C. densiflora, C. discotheca, C. flacca, C. gaultherioides* and *C. oreophila*. They are all restricted to an area just S of the Piura Divide, a deep valley of phytogeographical importance.

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The genus *Calceolaria* probably reaches its highest species diversity in the mountains of S Ecuador and N Peru. The area is divided into two floristically distinct parts by a deep depression in the Andean cordillera, the Piura Divide, the phytogeographical importance of which has been pointed out by several authors (e.g. Pennell 1945, Simpson 1975, Molau 1978 a). In my studies of *Calceolaria* in South America (Molau 1978 a–b, 1979) the Piura Divide (also known as the Huancabamba Deflection or the Porculla Pass) has been chosen as the southern limit of the investigated area. However, the isolation is not complete, and there are a few species known to overbridge the break. On the other hand, the number of vicarious taxa occurring on either sides of the divide is much greater. Thus, the Piura Divide usually acts as a distributional limit at the species level, but is of no significance as to the distribution areas of the sections. It seems likely that the importance of the Piura Divide as a phytogeographical border-line has increased relatively recently when regarding the phylogenetics of *Calceolaria* as a whole.

The presence of continuously distributed species and ± closely related vicarious taxa of *Calceolaria* in N Peru made it necessary for me to consider also the species appearing immediately S of the Piura Divide, and a large number of collections from the departments of Lambayeque, Cajamarca and Amazonas have been studied. Although a lot of N Peruvian taxa were described by Edwin (1970), there are still some species which require recognition. Five species are described as new in this paper.

Calceolaria oreophila Molau, sp. nov.

Orig. coll.: Sandeman 4201 (K holotype, OXF).

Illustrations. Fig. 1A–B.

Frutex, c. 0.5 m altus; tota planta glabra et glutinosa. Folia coriacea, decussata, ± fasciculata, 2.7–4.0× 0.7–1.0 cm, lanceolata sive elliptica, acuta, ad basin attenuata; supra atrovirentia, rugosa; infra albescentia, costa elevata, cetera nervatura inconspicua; margines revoluti. Petioli indistincti, 2–5 mm. Inflorescentia ± diffusa, terminalis vel subterminalis, 1–2 paria cymarum 2–4 florum complectens. Bracteae cymarum adsunt. Sepala pallide flavovirentia, ovata, acuta sive acuminata, 7.5–9.0× 5.5–7.0 mm in anthesi. Corolla citrea vel flava, labio superiore arcuato, c. 5× 5 mm, labio inferiore procurrente, 16–18× 11–13 mm, media fere longitudine saccato. Antherae flavo-albescentes, 2.2–2.4 mm, totae dehiscentes; thecae leviter deflexae, aequales. Filamenta 1.0–1.5 mm. Stylus rectus, c. 2.0 mm. Capsula anguste ovoides, leviter acuminata, c. 7 mm longa.

Subshrub, c. 0.5 m high, the whole plant glabrous and strongly glutinous. *Leaves* decussate, coriaceous, ± fasciculate, lanceolate or elliptic, 2.7–4.0× 0.7–1.0 cm, subacute, attenuate at base; above dark green and slightly rugose;

beneath whitish, midrib raised, other venation obsolete; margins revolute, appearing entire. Petioles ill-defined, 2–5 mm. *Inflorescence* ± diffuse, terminal or intercalary and subterminal, comprising 1–2 pairs of 2–4-flowered cymes on primary peduncles 0.5–1.3 cm long. Cyme bracts present. Pedicels 0.8–2.0 cm. *Sepals* light yellow-green, ovate, acute or slightly acuminate, 7.5–9.0 × 5.5–7.0 mm at anthesis. *Corolla* lemon yellow or bright yellow; upper lip arched, c. 5 × 5 mm; lower lip projecting, distally upcurved, 16–18 × 11–13 mm, saccate in about 1/2 of its length. *Anthers* yellowish white, 2.2–2.4 mm, opening throughout; thecae somewhat deflexed, equal. *Filaments* 1.0–1.5 mm. *Style* straight, c. 2.0 mm. *Capsule* narrowly ovoid, slightly acuminate, c. 7 mm long.

Remarks. Calceolaria oreophila is known only from the mountains of the province of Cutervo, department of Cajamarca, where collected twice in the vicinity of Llama. It belongs to sect. *Thamnobia* and is probably most closely related to *C. helianthemoides,* a species of S Ecuador. The unique leaf venation along with large sepals and other floral characters (e.g. anthers opening throughout) justify recognition of *C. oreophila* as a distinct taxon.

Specimens studied. Peru. Cajamarca: Llama, prov. Cutervo, growing among grass and scrub, 2300 m, VII.1943, Sandeman 4201 (K, OXF), 4203 (K).

Calceolaria densiflora Molau, sp. nov.

Orig. coll.: Sandeman 4101 (K holotype, OXF).

Illustrations. Fig. 1C–D.

Herba robusta, minimum 0.5 m alta. Plantae dense villosae sive hispidae, pilis albidis vel cremeis, eglandulatis. Folia herbacea, decussata, sessilia, ovata, 3.0–5.0 × 2.3–3.0 cm, acuta, ad basin cordata; supra chlorascentia, hispida, rugosa; infra pallidiora, nervis primariis et secundariis elevatis et strigosis–villosis, interstitiis pilosis et glandulis sessilibus obsitis; margines acute serrati. Inflorescentia terminalis, 2–4 paria cymarum 16–28 florum complectens. Bracteae cymarum adsunt. Sepala viridula, ovata, 3.0–4.3 × 2.4–3.4 mm in anthesi, intus glabra, marginibus ciliatis. Corolla citrea collo macula rubenti praedito, labio superiore deminuto, 1–2 × 2–3 mm, labio inferiore ascendente, tertia fere parte longitudinis saccato, parte ascendente 6–10 × 5–7 mm. Antherae fuscae, 1.3–1.5 mm, totae dehiscentes; thecae divaricatae, aequales. Filamenta 0.8–1.0 mm. Stylus curvatus, 1.5–2.0 mm. Capsula ovoides, dense glandulosus, minimum 3 mm longa.

Stout *herb,* at least 0.5 m high, sparsely branched. Inflorescence and distal parts of stems densely villous or hispid with ascending whitish or buffish gland-less hairs. *Leaves* decussate, herbaceous, sessile, ovate, 3.0–5.0 × 2.3–3.0 cm, acute, cordate at base; above dull green, hispid, rugose; beneath paler, primary and secondary veins raised and strigose to villous, interspaces pilose and sparsely beset with small sessile yellowish glands; margins sharply and somewhat irregularly serrate. *Inflorescence* terminal, comprising 2–4 pairs of dense 16–28-flowered cymes on primary peduncles 0.6–3.5 cm long. Cyme bracts present (sometimes rudimentary in upper cymes). Pedicels 0.5–1.2 cm. *Sepals* light green, ovate, subacute, 3.0–4.3 × 2.4–3.4 mm at anthesis, externally strigose and glandular, internally glabrous, margins short-ciliate. *Corolla* lemon yellow with a reddish spot in the throat; upper lip reduced, 1–2 × 2–3 mm; lower lip strongly upcurved, saccate in about 1/3 of its length, upcurved portion 6–10 × 5–7 mm. *Anthers* brown, 1.3–1.5 mm, opening throughout; thecae divaricate, equal. *Filaments* 0.8–1.0 mm. *Style* curved, 1.5–2.0 mm. *Capsule* ovoid, densely glandular, at least 3 mm long.

Remarks. Calceolaria densiflora is a most typical species of sect. *Anacyrta,* which reaches its highest diversity in N Peru and S Ecuador. This species is probably restricted to the mountains of the department of Cajamarca, collected twice in the vicinity of Llama, prov. Cutervo. It is distinct from other species of the section by the coarse pubescence and the deeply serrate leaf-margins, although it shows certain affinities to the Central Ecuadorean *C. serrata* Lam. in shape and arrangement of the leaves.

Specimens studied. Peru. Cajamarca: Bank above Llama, 2200–2300 m, 17.VII.1948, Pennell 15920 (PH) – Llama, prov. Cutervo, 2300 m, VII.1943, Sandeman 4101 (K, OXF).

Calceolaria gaultherioides Molau, sp. nov.

Orig. coll.: Edwin & Schunke 3639 (F holotype, NY).

Illustrations. Fig. 1E–F.

Frutex, usque ad 1 m altus. Plantae dense hispidae vel velutinae, pilis luteo-ferrugineis. Folia coriacea, decussata, petiolata, ovata sive elliptica, 2.2–2.8 × 1.1–1.4 cm, acuta, ad basin rotundata; supra atrovirentia, hispida, rugosa; infra pallide viridia, pinnato-venosa, costa velutina pilis aureis, interstitiis pilosis; margines

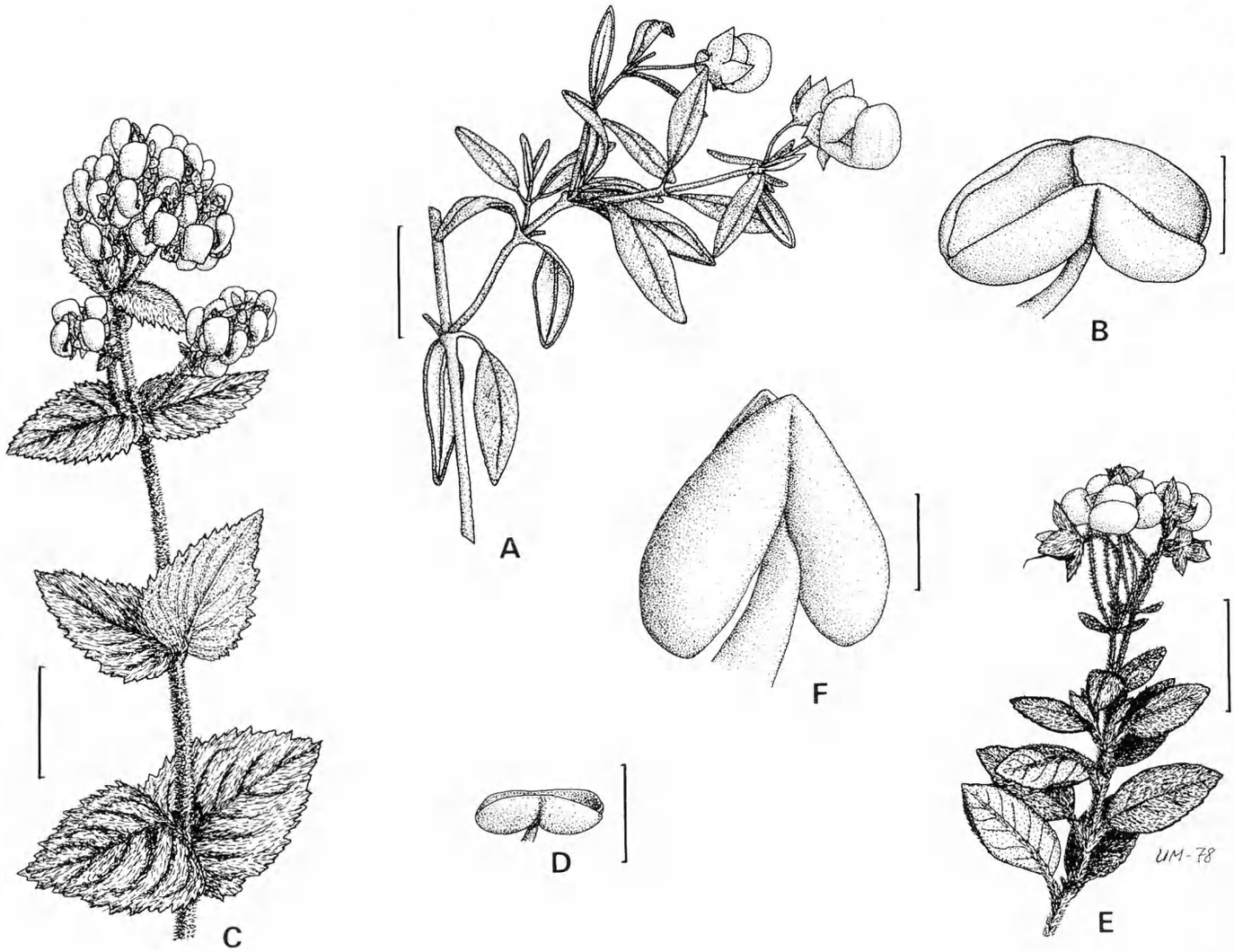

Fig. 1. A–B: *Calceolaria oreophila* (Sandeman 4201). – A: Flowering branch. – B: Stamen. – C–D: *C. densiflora* (Sandeman 4101). – C: Flowering branch. – D: Stamen. – E–F: *C. gaultherioides* (Edwin & Schunke 3639). – E: Flowering branch. – F: Stamen. – All drawings made from herbarium material. – Scales: A, C, E 2 cm, B, D, F 1 mm.

leviter crenati, deflexi. Petioli 5–7 mm. Inflorescentia terminalis, singula paria cymarum 4–8 florum complectens. Bracteae cymarum adsunt. Sepala brunnescentia, ovata, acuta, 5.0–6.4× 4.0–4.8 mm in anthesi, extra breviter pilosa vel hispida, intus glabra, excepta vitta breviter tomentosa iuxta marginem. Corolla flava, labiis fere aequalibus, labio superiore cucullato, c. 7× 8 mm, labio inferiore protrudente, c. 8× 9 mm, ad dimidiam fere partem longitudinis saccato. Antherae atro-fuscae, 2.3–2.8 mm latae, totae dehiscentes; thecae 2.5–3.0 mm longae, valide deflexae, aequales. Filamenta 1.5–2.0 mm. Stylus paene rectus, 4.5–5.6 mm. Capsula ovoides, leviter acuminata, 4–6 mm longa.

Shrub, to c. 1 m high. Inflorescence and distal parts of stems densely hispid with yellow-brown or ferrugineous hairs. *Leaves* decussate, coriaceous, petiolate, ovate or elliptic, 2.2–2.8× 1.1–1.4 cm, acute, rounded at base; above dark green, hispid, rugose; beneath light green, pinnate-venose, velutinous with golden yellow hairs on the midrib, interspaces pilose; margins crenulate, deflexed or slightly revolute. Petioles velutinous, 5–7 mm. *Inflorescence* terminal, comprising 1 pair of 4–8-flowered cymes on primary peduncles 1.0–3.5 cm long. Cyme bracts present, small or rudimentary. Pedicels 0.8–2.2 cm. *Sepals* brownish, ovate, acute, 5.0–6.4× 4.0–4.8 mm at anthesis, externally shortly pilose or hispid, internally glabrous except of a short-tomentose border along the margin. *Corolla* yellow, lips about equal-sized; upper lip hooded, c. 7× 8 mm, concealing the anthers; lower lip projecting, c. 8× 9 mm, saccate in 1/2 of its length. *Anthers* dark brown, 2.3–2.8 mm wide, opening throughout; thecae 2.5–3.0 mm,

strongly deflexed, equal. *Filaments* 1.5–2.0 mm. *Style* almost straight, 4.5–5.6 mm. *Capsule* ovoid, slightly acuminate, 4–6 mm long, sparsely hirsute with gland-tipped hairs.

Remarks. This handsome species is unique in its dense bright yellow-brown pubescence. In vegetative morphology it resembles some of the Andean species of the genus *Gaultheria* (Ericaceae). It is probably endemic to the mountains of northern Peru, known only from a single collection from the department of Amazonas.

Calceolaria gaultherioides certainly belongs to sect. *Phaeanthera,* which is known to comprise a few species from N Peru to S Colombia. Reliable section characters are brownish pubescence, tomentose border on the inner sepal surface, equal-sized corolla lips and brown anthers with deflexed thecae.

Specimens studied. Peru. Amazonas: E slope of Cerro Calla-Calla, prov. Chachapoyas, growing in rocky cliff above road, c. 3000 m, 2.VI.1966, Edwin & Schunke 3639 (F, NY).

Calceolaria discotheca Molau, sp. nov.

Orig. coll.: Wurdack 849 (F holotype).

Illustrations. Fig. 2A–C.

Frutex scandens 2–4 m longus; ramis patentibus. Plantae minute puberulae, pilis purpurascentibus. Folia herbacea, decussata, petiolata, lanceata, 4.8–6.0× 1.3–1.8 cm, acuta, ad basin attenuata, utrimque puberula et parvis glandulis obsita; supra chlorascentia; infra pallide viridia, reticulato-venosa; margines serrati. Petioli 3–8 mm. Inflorescentia diffusa subterminalis, 1–3 paria cymarum 1–4 florum complectens. Bracteae cymarum adsunt. Sepala inaequalia, subtilia, sepalo dorsali maximo, cordiformi, acuminato, 10.3–12.5× 9.2–10.8 mm in anthesi. Corolla flava, extra glandulosa, labio superiore arcuato, 4–6× 12–18 mm, labio inferiore protrudente, 16–17× 17–18 mm, ad duas quintas partes longitudinis saccato. Antherae atro-fuscae, 2.5–3.3 mm, totae dehiscentes; thecae divaricatae, aequales, discoïdes. Filamenta 1.8–2.0 mm. Stylus paene rectus, 3.1–3.3 mm. Capsulam maturam non vidi.

Vine, climbing 2–4 m, branches divaricately spreading. Inflorescence and distal parts of stems minutely puberulous with purplish hairs. *Leaves* decussate, herbaceous, petiolate, lanceate, 4.8–6.0× 1.3–1.8 cm, acute, attenuate at base, on both surfaces puberulous and beset with minute hyaline glands; above dull green; beneath pale green, reticulate-venose; margins serrate. Petioles puberulous, 3–8 mm. *Inflorescence* diffuse, intercalary and subterminal, comprising 1–3 pairs of 1–4-flowered cymes on primary peduncles 0.8–3.2 cm long. Cyme bracts present. Pedicels 1.1–2.0 cm. *Sepals* unequal, thin, turning red, minutely puberulous on both surfaces; dorsal sepal the largest one, cordiform, slightly acuminate, 10.3–12.5× 9.2–10.8 mm at anthesis; the others somewhat shorter and much narrower, the ventral one almost lanceate. *Corolla* yellow, externally densely beset with small yellowish stalked or sessile glands, proximally finely puberulous on both lips; upper lip arched, 4–6× 12–18 mm; lower lip projecting, distally upcurved, inflated, 16–17× 17–18 mm, saccate in about 2/5 of its length. *Anthers* dark brown, 2.5–3.3 mm, opening throughout; thecae divaricate, equal, flattened (whence name). *Filaments* 1.8–2.0 mm. *Style* almost straight, 3.1–3.3 mm. Mature *capsule* not seen.

Remarks. The unusual calyx morphology together with branching angles and stem pubescence make *Calceolaria discotheca* a typical member of sect. *Polyclada*. It is closely related to *C. brachiata* Sodiro from Ecuador, the type species of the section, but differs in foliage and floral characters. *C. discotheca* is known only from a single collection from the mountains of the Bongará province, department of Amazonas. However, this area is floristically almost unknown, and a wider distribution than indicated by the single collection cited below is probable.

Specimen studied. Peru. Amazonas: Montane rainforest 2–4 km WSW of Pomacocha, prov. Bongará, occasional at forest edge, 2200–2400 m, 16.VI.1962, Wurdack 849 (F).

Calceolaria flacca Molau, sp. nov.

Orig. coll.: Ferreyra 15499 (UC holotype).

Illustrations. Fig. 2D–E.

Frutex flaccidus, 1–1.5 m altus. Plantae tomentosae pilis ferruginosis. Folia herbacea, decussata, petiolata, ovata, 1.8–2.6× 1.0–1.3 cm, acuta, ad basin cuneata vel rotundata; supra obscure atro-virentia, breviter hirsuta glandulis in brevibus stipitibus sitis obsita; infra pallide viridia, pinnato-venosa, in nervis tomentosa, interstitiis glandulis stipitatis obsitis; margines leviter serrati vel crenati. Petioli 5–12 mm. Inflorescentia terminalis, 2–4 paria cymarum 4–6 florum complectens. Bracteae cymarum adsunt. Sepala brunneo-viridia, ovata vel lanceata, acuminata, 4.1–5.8× 2.2–3.2 mm in anthesi, extra breviter hirsuta pilis glanduliferis, intus puberula. Corolla flava, labio

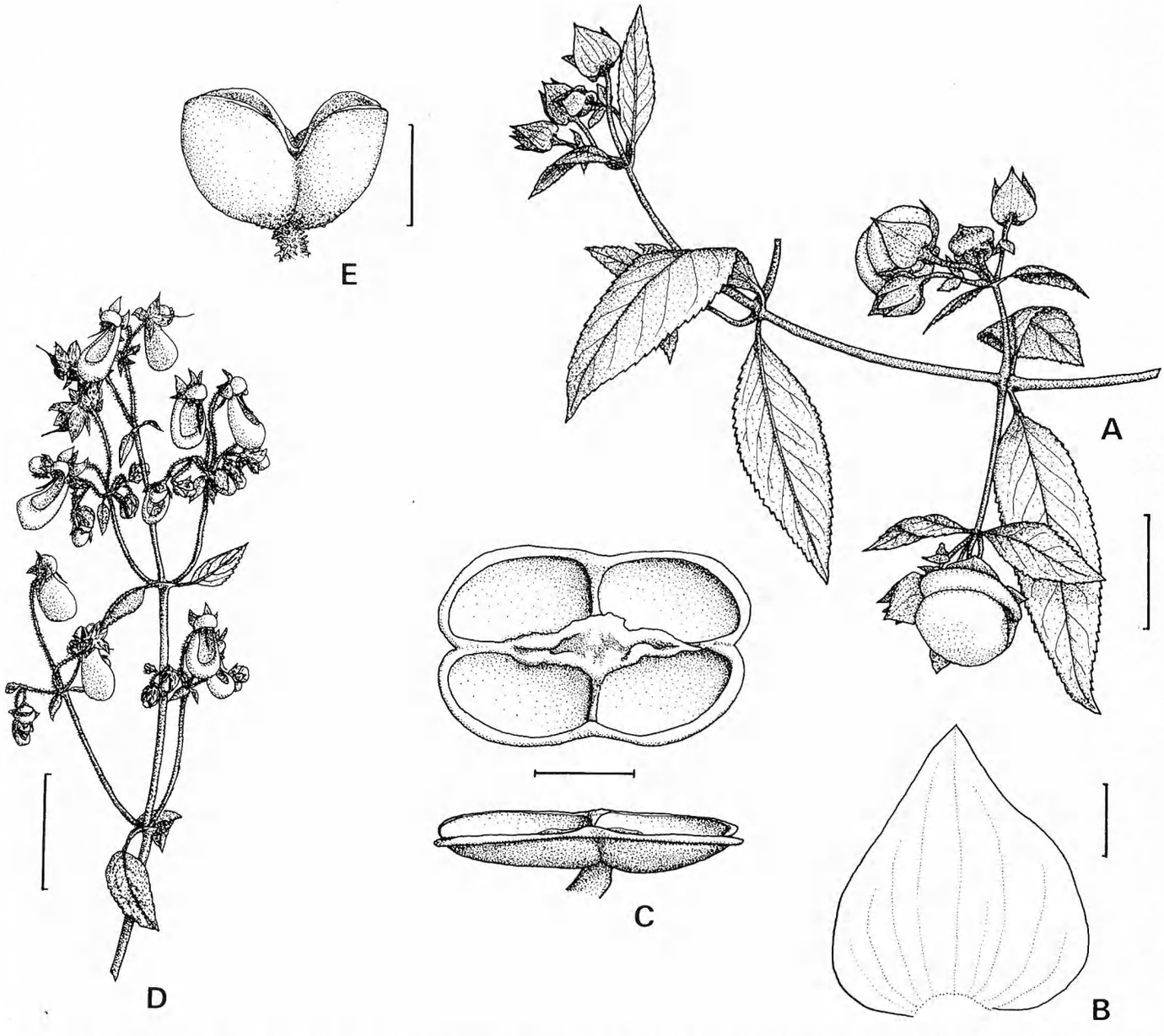

Fig. 2. A–C: *Calceolaria discotheca* (Wurdack 849). – A: Flowering branch. – B: Dorsal sepal. – C: Stamen. – D–E: *C. flacca* (Ferreyra 15499). – D: Flowering branch. – E: Stamen. – All drawings made from herbarium material. – Scales: A, D 2 cm, B 3 mm, C, E 1 mm.

superiore extra hirsuto, arcuato, 2–3 × 3–4 mm, labio inferiore ± pendente, 10–17 × 7–10 mm, ad quartam vel tertiam partem longitudinis saccato. Antherae fuscae, 2.0–2.3 mm latae, totae dehiscentes; thecae ascendentes, 1.3–1.5 mm longae, aequales. Filamenta 1.0–1.2 mm. Stylus rectus, 4.0–6.2 mm. Capsulam maturam non vidi.

Subshrub, 1–1.5 m high. Inflorescence and distal parts of stems tomentose with short red-brown hairs. *Leaves* decussate, herbaceous, petiolate, ovate, 1.8–2.6 × 1.0–1.3 cm, acute, rounded or cuneate at base; above dull dark green, densely short-hirsute with gland-less hairs intermingled with stalked glands; beneath pale green, pinnate-venose, veins brownish tomentose, interspaces beset with stalked yellowish glands; margins shallowly serrate or crenate, slightly deflexed. Petioles densely tomentose, 5–12 mm. *Inflorescence* terminal, comprising 2–4 pairs of 4–6-flowered cymes on primary peduncles 1.5–2.8 cm long. Cyme bracts present. Pedicels 0.8–2.5 cm. *Sepals* dark brownish-green, ovate or lanceate, 4.1–5.8 × 2.2–3.2 mm at anthesis, slightly acuminate, externally shortly glandular-hirsute, internally puberulous (most densely so towards the margins). *Corolla* bright yellow; upper lip externally

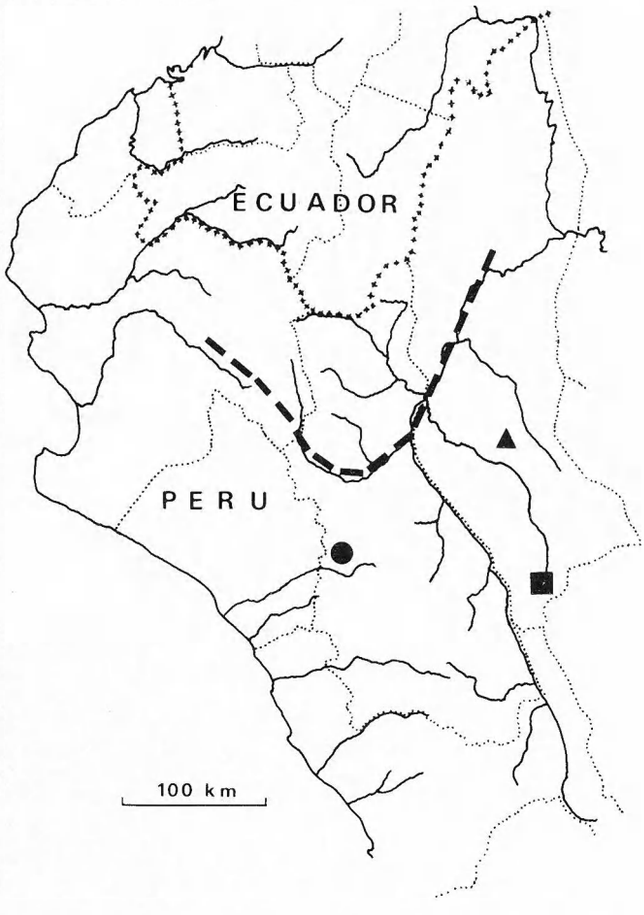

Fig. 3. Type localities of *Calceolaria oreophila* and *C. densiflora* (●), *C. gaultherioides* and *C. flacca* (■), and *C. discotheca* (▲). The Piura Divide is indicated by the dashed line.

hirsute, arched, subglobose, 2–3 × 3–4 mm, not concealing the anthers; lower lip externally sparsely pilose, pendent, 10–17 × 7–10 mm, saccate in only 1/4–1/3 of its length, orifice exposed. *Anthers* brown, 2.0–2.3 mm wide, opening throughout; thecae ascending, 1.3–1.5 mm long, equal. *Filaments* 1.0–1.2 mm. *Style* straight, 4.0–6.2 mm. Mature *capsule* not seen.

Remarks. This species is remarkable by its combination of brownish pubescence, very open flowers, ascending thecae and long style. *Calceolaria flacca* is known only from two collections from the southernmost part of the department of Amazonas, and probably has a very restricted distribution. Its closest relatives are possibly to find in sect. *Urticopsis*, but it deviates greatly from the species of that section in pubescence as well as in floral characters. A complete revision of the Peruvian species of *Calceolaria* is required to elucidate the systematic position of *C. flacca*.

Specimens studied. Peru. Amazonas: Near Leimebamba, prov. Chachapoyas, 3400–3500 m, 17.IV.1964, Ferreyra 15499 (UC) – Barro Negro, Leimebamba–Abra road, prov. Chachapoyas, cloud forest, 3000–3200 m, 27.II.1976, Plowman 5578 (GH).

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The lichen genus Coccocarpia in New Zealand

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Three species of *Coccocarpia* Pers. are recognized in the New Zealand flora, viz. *C. erythroxyli* (Spreng.) Swinsc. & Krog, *C. palmicola* (Spreng.) Arvidss. & D. Gall., comb. nov., and *C. pellita* (Ach.) Müll. Arg. *Vischia coccocarpoides* Dodge (type species of the genus *Vischia* Dodge) is reduced to synonymy with *C. palmicola*. A key to the species is given together with details of their morphology, habitats and distribution.

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The genus *Coccocarpia* was described by Persoon (1826) to comprise five tropical species (*C. molybdaea* Pers., *C. incisa* Pers., *C. polyphylla* Pers., *C. smaragdina* Pers. and *C. viridescens* Pers.) having a ± radiating, lobate thallus of a characteristic lead-grey colour and with adnate, convex, brown-red apothecia resembling insects of the genus *Coccus* L., from which Persoon derived the name *Coccocarpia*.

Material of the genus first collected in New Zealand by William Colenso and Joseph Hooker was published as *Solorina aurantiaca* Hook. f. & Tayl. and *Parmelia plumbea* Ach. (Hooker & Taylor 1844), taxa now referable to *Coccocarpia erythroxyli* (Spreng.) Swinsc. & Krog and *C. palmicola* (Spreng.) Arvidss. & D. Gall. (Taylor later wrote to Hooker (letter dated 31.3.1845, preserved at Kew) "I find by Sir William's specimens that our *Solorina aurantiaca* is a *Coccocarpia* Pers., but I believe none of the described species, I am too imperfectly acquainted with the characters of *Coccocarpia* to say it is a genus that should be adopted, although I own our species has not the habit of the other Solorinae".) Raoul (1846) used Hooker and Taylor's names. The first detailed account of the New Zealand lichen flora was that of Babington (1855) and in it he recorded two species of *Coccocarpia: C. smaragdina* (= *C. erythroxyli*) and *C. pulchella* (= *Normandina pulchella*). He also listed *Parmelia plumbea* (= *C. palmicola*).

Hooker (1867) lists *C. molybdaea* var. *plumbea* Nyl. However, Hooker's description of this plant accommodates both *C. erythroxyli* and *C. palmicola*. Nylander's (1869) account of *Coccocarpia* included the following from New Zealand: *C. gayana* (Mont.) Nyl., *C. molybdaea* and *C. smaragdina*, the latter two names being referable to *C. erythroxyli*. Knight (1875) described *Pannaria periptera*, and later Nylander (1888) placed this species in *Coccocarpia*, including also *C. gayana* (and var. *melaclina* Nyl.), *C. aurantiaca* (Hook. f. & Tayl.) Nyl. and *C. smaragdina*. *C. periptera* cannot be placed in *Coccocarpia*, and Hooker's (1867) description of *Pannaria gayana* covers two distinct species to be referred to a genus of its own (Arvidsson & Galloway in prep.). Nylander's arrangement was largely adopted by Hue (1892), while Müller Argoviensis (1894) recorded *C. pellita* var. *smaragdina* Müll. Arg., *C. aurantiaca*, *Pannaria periptera* and *Parmeliella gayana* (Mont.) Müll. Arg. from New Zealand. Hellbom's (1896) account of Berggren's New Zealand lichens contained *C. smaragdina*.

The following species of *Coccocarpia* have

thus been reported from 19th century New Zealand collections of Hooker, Colenso, Knight and Berggren: *C. erythroxyli, C. gayana, C. palmicola, C. pellita* and *C. periptera*. However, in our opinion *C. gayana* and *C. periptera* do not belong to *Coccocarpia* and they are omitted here.

In the present century, although H. H. Allan collected *C. palmicola* from several localities prior to 1925 (Galloway 1976), it was not until 1926–27 that the New Zealand lichen flora was investigated in any depth. The inspiration for this came from the visit of G. Einar Du Rietz and his wife Greta Sernander-Du Rietz and in their large collections of New Zealand lichens (at present at UPSV) *C. erythroxyli, C. palmicola* and *C. pellita* are represented. Zahlbruckner (1941) lists *C. cronia* (= *C. palmicola*) with the vars. *furfuracea* and *primaria,* while Martin's (1966) catalogue records *C. cronia* vars. *aurantiaca, furfuracea* and *primaria,* and *C. pellita* and var. *smaragdina*. Dodge (1970) described two new lichens from New Zealand, *Coccocarpia fineranii* Dodge (type not seen) which is probably a species of *Pannaria* close to *P. immixta,* and a new genus *Vischia,* typified by *V. coccocarpoides* Dodge, which is a synonym of *C. palmicola*.

Material

In the present account, most of the published taxa relating to *Coccocarpia* in New Zealand have been re-examined. All relevant 19th century collections from New Zealand were checked, and numerous collections made from 1925 to the present were investigated. Material was obtained from BM, CANU, CHR, H–NYL, OTA, UPS, UPSV, W, WELT, and from the personal herbaria of J. Bartlett (Auckland) and G. Degelius (Askim).

General information on the genus

Morphology and anatomy: Thalli of *Coccocarpia* are foliose, heteromerous, dorsiventral, ± orbicular in outline and rarely more than 10 cm in diam. The lobes are adjacent or imbricate, broadly cuneate to flabellate, the margins usually slightly thickened and curled downwards. Some larger species are conspicuously ridged above, the ridges being arranged in curved concentric lines parallel with the lobe apices and reflecting the attachment of rhizines on the lower surface. The upper surface is glabrous, smooth and often shining, or minutely wrinkled or scabrid, colour usually ± leaden grey but sometimes brownish-grey, bluish or almost black. The upper cortex is paraplectenchymatous, and the cells are arranged in ± parallel lines radiating along the lobes from the centre to the periphery, giving rise to faint striae in larger species (Fig. 1 F; a diagnostic character, use × 10 lens).

The phycobiont is referable to *Scytonema* (Ahmadjian 1967). Medulla of thin-walled, periclinal hyphae overlaying usually two rows of thick-walled lower cortical cells. Lower surface corticate, often densely covered with long silky rhizines which may be pale, white or grey to dark bluish-black or black with white tips. Such variation in rhizine colour are often seen in a single specimen and have no taxonomic significance.

Isidia occur on the upper surfaces of *C. palmicola* and *C. pellita*. In *C. erythroxyli* small foliate lobules or phyllidia, distinct from isidia, are often seen in older parts of the thallus. Soralia are lacking in all species known.

In all species of *Coccocarpia* the apothecia are biatorine (Henssen & Jahns 1973), adnate, and lack a prominent proper margin. Ascogones are formed in association with isodiametric cells in the primordium, and Henssen (1963) used this character to establish the family Coccocarpiaceae which includes *Coccocarpia* and *Spilonema*. Spores of *Coccocarpia* are simple, ellipsoidal, colourless, eight per ascus although some species (not represented in New Zealand) may have globose spores. Swinscow & Krog (1976) reported that occasionally some spores may have a septum but we have not seen this in any New Zealand material. However, many spores of both *C. palmicola* and *C. erythroxyli* have two oil droplets, and the plasma interspace between these could be mistaken for a septum. Pycnidia may be found in warts on fertile specimens (Fig. 1 F); conidia are rod-shaped.

Chemistry. Hot acetone extracts of all specimens of *Coccocarpia* investigated were analysed by the TLC procedure of Culberson & Kristinsson (1970). No substances of taxonomic value were detected.

Taxonomy. *Coccocarpia,* comprising some 30 species of mainly tropical or subtropical origin, appears to have two centres of speciation, one in

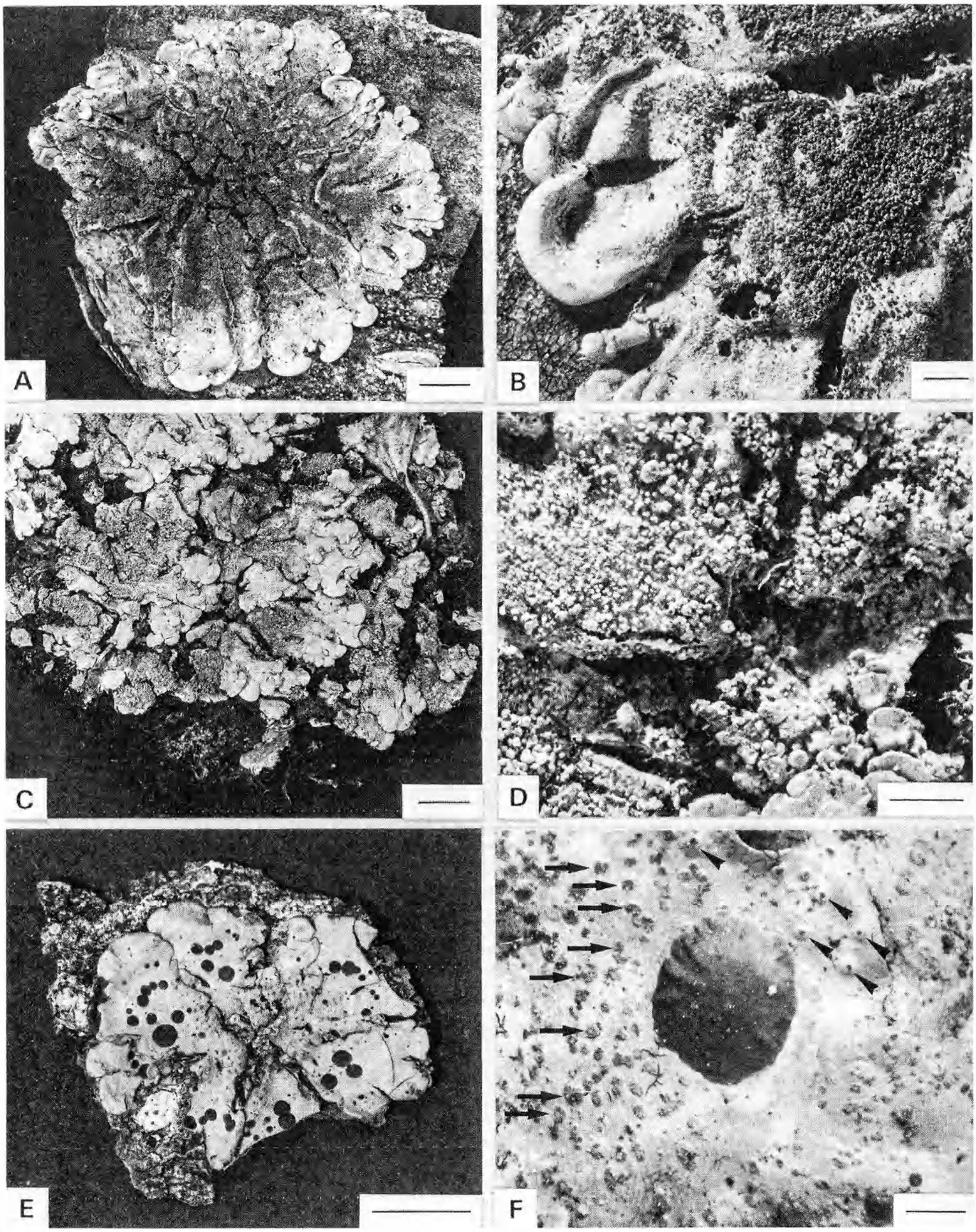

Fig. 1. A–B: *Coccocarpia palmicola,* Southland, Longwood Range, J. S. Thomson (CHR 162996). Note terete isidia. – C–D: *C. pellita,* South Auckland, Rangitoto Island, H. H. Allan (CHR 264069). Note squamulose isidia. – E: *C. erythroxyli,* South Auckland, Red Mercury Island, B. W. & G. C. Hayward (CHR). – F: *C. erythroxyli,* South Auckland, Mangaotaki River, Galloway (CHR). Ascocarp; small, dark, wartlike ascocarp initials (arrows); and pycnidia (arrowheads). Note the faint striae of the cortex. – Scales: A, C, E 5 mm, B, D, F 1 mm.

the northern part of S America, and one in Indonesia. About ten species are restricted to each of these two centres, and three species, viz. *C. erythroxyli, C. palmicola* and *C. pellita* are of wide distribution.

Many subspecific taxa have been described in *Coccocarpia,* and most of these are poorly understood. Stable characters are few and great variation is encountered in the width of lobes and in the colour of rhizines as well as the apothecial disc. Chemistry is of little use since most species lack lichen products. At present *Coccocarpia* is the subject of a monographic revision by Arvidsson.

Key to Coccocarpia in New Zealand

1. Thallus isidiate, rarely fertile 2
– Thallus not isidiate, frequently fertile ..... *C. erythroxyli*
2. Isidia terete, simple or branched ..... *C. palmicola*
– Isidia ± strongly flattened, squamulose ..... *C. pellita*

Coccocarpia erythroxyli (Spreng.) Swinsc. & Krog

Swinscow & Krog 1976 p. 256; for synonymy, see the same paper.

The specific epithet was wrongly spelt *'erythroxili'* by Swinscow & Krog. In the original paper by Sprengel, the basionym reads *'Lecidea Erythroxyli'* (= growing on *Erythroxylon,* derived from *xylos,* wood).

Thallus ± orbicular, to 8 cm in diam. Lobes 0.3–0.7(–1.0) cm wide, adjacent and often imbricate, broadly cuneate to flabellate; apices rotund. Upper surface smooth, matt or shining, without isidia. Lobes sometimes with transverse, concentric ridges. Rhizines numerous, pale to bluish black (then often white-tipped), sometimes projecting beyond lobe margins. Apothecia ± frequent, ± adnate, to 0.6 cm in diam., orbicular at first, becoming irregular with age; disc pale brown-red to black. Short white hairs, projecting from the margins of the disc, may be present. Spores 9–12 × 3–5 μm.

Affinity and variation. The ± wide lobes (often ridged) and the large, irregular, adnate apothecia (Fig. 1 E) are characteristic of *C. erythroxyli* and the lack of isidia distinguishes it from both *C. palmicola* and *C. pellita.* There is considerable variation in the colour of the apothecial disc and the rhizines, but apart from this the New Zealand populations are uniform. In older thalli, small regenerating lobules or phyllidia are commonly seen. In some specimens apothecial initials are observed as small wart-like protuberances (Fig. 1 F), often with projecting hyphae (trichogynes?).

Habitats and distribution. C. erythroxyli is widely distributed in tropical and subtropical areas (Swinscow & Krog 1976) and occurs also in Europe (Portugal; Tavares 1960). In New Zealand it has a distribution similar to that of *C. pellita* (Fig. 2). It is characteristic of warm, humid habitats, and although once collected from rock on the Three Kings Islands, it is mainly an epiphyte of twigs or small branches and is also frequently collected from the bark of *Leptospermum ericoides, L. scoparium* and *Metrosideros excelsa.* It is commonly found in association with *Collema* spp., *Erioderma* cf. *chilense, E. sorediatum, Lobaria scrobiculata, Normandina pulchella, Parmeliella amphibola, P. pycnophora, Pannaria fulvescens, Physma chilense, Polychidium contortum, Pseudocyphellaria aurata, P. carpoloma, P. hookeri, P. intricata, Psoroma durietzii, P. euphyllum, P. pallidum, P. leprolomum* and *Usnea* cf. *rubescens. C. erythroxyli* has been found from sea level to 1000 m.

Specimens examined. North Auckland: Three Kings Islands, Galloway (CHR) – Radar Bush, J. Bartlett (CHR) – Rangitoto Island, G. E. & G. Du Rietz 2670:13 (UPSV); H. H. Allan (CHR 264081) – *South Auckland:* Red Mercury Island, B. W. & G. C. Hayward (CHR) – Penguin Island, B. W. & G. C. Hayward (CHR) – Mangaotaki River, Galloway (CHR) – Waimeha Stream, J. Bartlett (CHR) – *Nelson:* Anatoki River, M. M. Davidson (CHR) –Cobb Ridge, J. Bartlett (CHR) – St. Arnaud Range, Lake Rotoiti, Galloway (CHR) – *Canterbury:* Hope River near Lewis Pass, Galloway (CHR).

Coccocarpia palmicola (Spreng.) Arvidss. & D. Gall., comb. nov.

Basionym: *Lecidea palmicola* Sprengel 1820 p. 46 – Orig. coll.: Guadeloupe, in cortice *Cocos nucifera,*

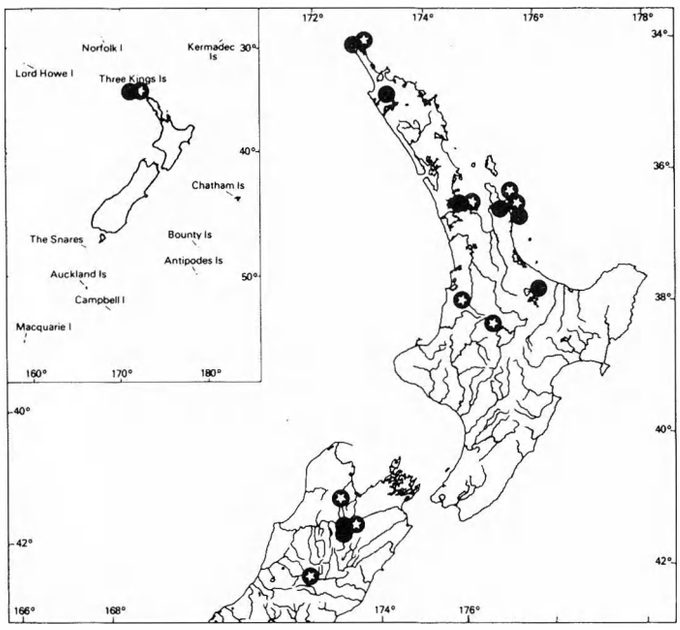

Fig. 2 (left). Known New Zealand distribution of *Coccocarpia erythroxyli* (dots with a star) and *C. pellita* (dots).

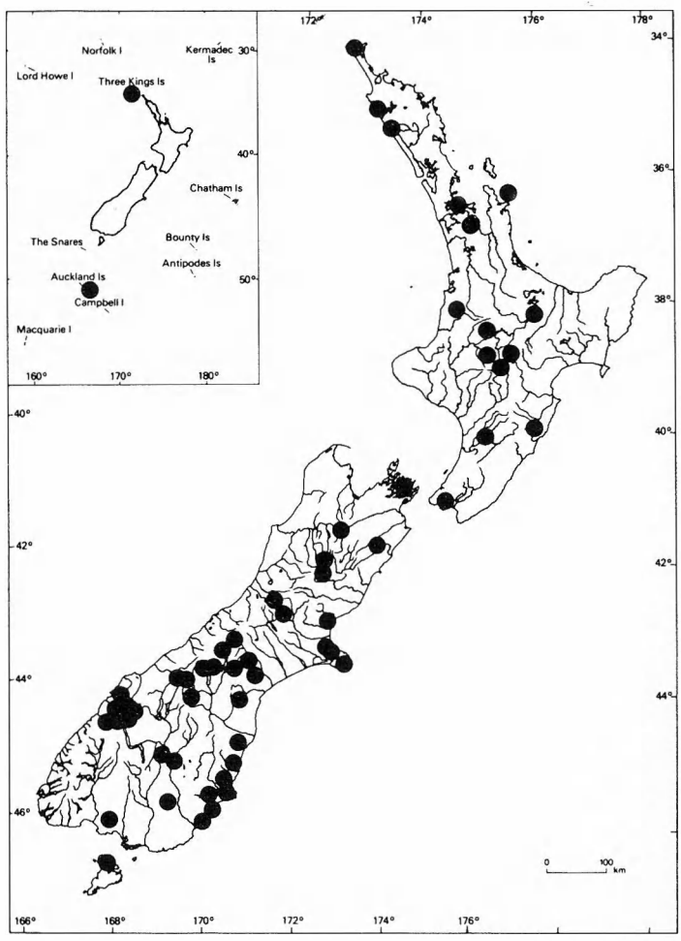

Fig. 3 (right). Known New Zealand distribution of *C. palmicola*.

1817 (TO! lectotype, here designated; photo Tavares 1960 Pl. 3 fig. 1).

Parmelia cronia Tuckerman 1848 p. 228 – *Coccocarpia cronia* (Tuck.) Vainio 1915 p. 103 – Orig. coll.: Massachussets, Lynn Hills, on mossy rocks, Tuckerman, Nov. 1843 (FH! lectotype, here designated).

Vischia coccocarpoides Dodge 1970 p. 467 – Orig. coll.: New Zealand, South Island, Canterbury, Sugerloaf, muscicole, L. Visch C 19, May 1958 (CANU! holotype).

Additional synonymy, see Swinscow & Krog 1976 p. 253.

Thallus ± orbicular, to 8 cm in diam. Lobes 0.2–0.6(−1.0) cm wide, adjacent to imbricate, broadly cuneate to flabellate; apices rotund. Upper surface rather variable in texture, smooth, matt or slightly shining to ± wrinkled, scabrid, isidiate, often also with transverse, concentric ridges. Isidia concolorous with thallus or darker, terete, nodular when young, becoming coralloid, sparse or forming a dense, ± areolate crust at centre of thallus. Rhizines dense, colour variable, pale to dark bluish black (then often white-tipped), sometimes projecting beyond lobe margins. Apothecia adnate, to 0.4 cm in diam., orbicular at first, becoming irregular with age, disc pale brown-red to black (apothecia of lectotype are black). Spores (lectotype) 9–11 × 3–5 μm. Only 3 specimens out of 110 examined from New Zealand were fertile and the spores of these agree well with those of the type.

Nomenclature. Tavares (1960) first drew attention to the fact that the type of *Lecidea palmicola* Spreng. in TO consists of two seemingly discordant elements. These, however, are not two distinct entities as Tavares suggested but belong to the same taxon (Swinscow & Krog 1976). The right-hand fragment has terete isidia while on the fertile, left-hand specimen the isidia are mostly broken off. Thus *L. palmicola* does not lack isidia as reported by Tavares. The authenticity of Sprengel's material was checked by Tavares in a comparison of the handwriting on the TO label with a known example of Sprengel's handwriting in a letter to Elias Fries. The asterisk that in the original label follows the specific epithet is further evidence of authenticity. A similar mark has been printed with the names of the new species described by Sprengel (1820).

The type material of *Parmelia cronia* in FH consists of specimens collected by Tuckerman from three different localities in Massachussetts. The protologue

says: "common on the coast of Massachussetts." All specimens belong to the same taxon and they fit well with the original description. We have chosen the specimens from Lynn Hills as lectotype. The material agrees in every respect with the type material of *L. palmicola*.

Affinity and variation. Coccocarpia palmicola is a very variable species closely related to *C. pellita* (see under that species) but separated from it by the morphology of the isidia. The texture and colour of the upper thallus surface of *C. palmicola* are variable and appears to be modified by microhabitat and/or microclimate. For example, exposed muscicolous or terricolous collections are dark greyish or black with a thick, leathery, rather scabrid thallus, while specimens from more protected, subalpine or alpine sites are conspicuously blue-grey (particularly at the lobe margins), with a rather thin, delicate, friable thallus.

Isidia (Fig. 1 B) may be sparse or dense, forming a ± areolate or dense crust, and may be simple or coralloid, even on the same thallus. The colour of the rhizines varies continuously from dark bluish or black to pale, sometimes in one specimen. The colour of the disc may vary from pale brown to dark reddish-brown or blackish within the same apothecium.

Habitats and distribution. C. palmicola is a widely distributed tropical–subtropical species; it is the most widespread and frequently collected species of *Coccocarpia* in New Zealand (Fig. 3). It colonises a wide range of substrates and is known as an epihyte of trees and shrubs from coastal broadleaf forests as well as from *Nothofagus* forests. It also occurs on clay banks, on bryophyte cushions in subalpine grasslands and on rocks in alpine fell-field. It ranges from sea level to 2500 m.

When growing as an epiphyte in forest it is often associated with species of *Hypogymnia, Leptogium, Menegazzia, Nephroma, Pannoparmelia, Parmelia, Pseudocyphellaria, Psoroma, Sphaerophorus, Sticta, Thysanophoron* and *Usnea*. As a coloniser of soil on roadside cuttings or on consolidated river gravels it is associated with *Baeomyces heteromorphus, B. fungoides* and rarely *B. absolutus,* and with species of *Placopsis;* in alpine sites it grows with *Siphula decumbens* and *Toninia bullata*. From alpine fell-fields it is associated with *Hypogymnia inflata, H. lugubris, Menegazzia aeneofusca,* species of *Placopsis, Psoroma, Steinera, Stereocaulon, Thamnolia vermicularis* and *Usnea contexta*.

Representative specimens. North Auckland: Three Kings Islands, Galloway (CHR) – Rangitoto Island, H. H. Allan (CHR 162996) – Kawerua, B. W. & G. C. Hayward (CHR) – *South Auckland:* Waipakahi Valley, A. J. Dakin (CHR) – Kaingaroa Plains, K. W. Allison (CHR 264064) – Mangaotaki Valley, Galloway (CHR) – *Wellington:* Whariti Peak, Ruahine Range, Galloway (CHR) – York Bay, G. E. & G. Du Rietz 1149 (UPSV) – *Marlborough:* Mt. Fyffe, D. Given (CHR 162623) – Mt. Tapuaenuku, Inland Kaikoura Range, J. S. Thomson (CHR 264071) – *Nelson:* St. Arnaud Range, Galloway (CHR) – *Canterbury:* Boundary Stream, North Canterbury, B. P. J. Molloy (CHR) – Port Hills, H. H. Allan (CHR 264061) – Te Huruhuru, Hunters Hills, Galloway (CHR) – Governor's Bush, Mt. Cook, H. D. Wilson (CHR) – *Westland:* Arthur's Pass, G. Degelius NZ 275 (herb. Degel.) – Mt Brewster, Haast Pass, P. W. James 480/2 (BM) – *Otago:* Mt. Maungatua, J. Murray (OTA) – Kakanui Range, B. W. Campbell (OTA) – Lake Harris Saddle, Galloway (CHR) – Alexandra, W. Martin A 571 (CHR) – Bold Peak, Lake Wakatipu, G. E. & G. Du Rietz 1878:5 (UPSV) – *Southland:* Milford Sound, G. Degelius NZ 415 (herb. Degel.) – Black Gully, Blue Mountains, W. Martin (CHR) – Longwood Range, J. S. Thomson (CHR 162996) – *Stewart Island:* Mt. Anglem, Galloway (CHR) – *Auckland Islands:* Ross Bay, Laurie Harbour, P. W. James 1002/2 (BM).

Coccocarpia pellita (Ach.) Müll. Arg. emend. Santesson

Santesson 1952 p. 420.
For synonymy, see Swinscow & Krog 1976 p. 258.

Thallus ± orbicular, to 6 cm in diam. Lobes 0.3–0.6 cm wide, adjacent to somewhat imbricate, broadly cuneate to flabellate, rotund at apices. Upper surface isidiate, often also with transverse, concentric ridges. Isidia flattened, squamulose, marginal or laminal. Rhizines pale, forming a ± dense matt on lower surface. Apothecia not seen in New Zealand material.

Affinity and variation. C. pellita is characterised by flattened, squamulose isidia (Fig. 1 D). Santesson (1952) claimed that a thin thallus is another characteristic of the species but Swinscow & Krog (1976) stated that this character is as variable as it is difficult to measure precisely. In New Zealand material we have not found *C. pellita* to have a thinner thallus than either *C. palmicola* or *C. erythroxyli*. Swinscow & Krog discussed the difficulties in separating *C. pellita* from specimens of *C. palmicola* having terete to

squamulose isidia, and record the existence of many intermediate forms in African populations of *Coccocarpia*. Further, they record the possible effect of environmental modifications influencing the morphology of isidia in this species, with specimens having a thin thallus and squamulose isidia being found in moist, shady habitats and plants with a thicker thallus and terete, coralloid isidia occuring in open, drier habitats.

Material of *C. pellita* from New Zealand is still very scanty. In a collection from Penguin Island (B. W. & G. C. Hayward, CHR) both terete and flattened isidia are found on the same specimen, but in collections from other localities the strongly flattened isidia characteristic of *C. pellita* are seen. Only field observations will prove if *C. pellita* is a good species or merely a shade or moisture form of *C. palmicola*. However, sympatric populations of typical *C. pellita* and typical *C. palmicola* have been observed by one of us (L.A.) in the Andes of Ecuador, and Swinscow & Krog (1976) recorded altitudinal differences in their distribution in East Africa. For these reasons, we keep them separate.

Habitats and distribution. C. pellita is a widely distributed tropical species. It seems to be rare in New Zealand, and to be characteristic of warm, humid habitats in moderate shade where it is found in association with *Pannaria fulvescens, Parmotrema cristiferum, Pseudocyphellaria episticta, Heterodermia* cf. *japonica, Parmotrema reticulatum* and *Leptogium* spp. It is an epiphyte of coastal broad-leaved forest trees and shrubs in N New Zealand though specimens are also known from Lake Rotoiti in North Island and from near Lake Rotoiti in Nelson Lakes National Park in South Island (Galloway & Simpson 1978). It has been collected from sea level up to 400 m.

Specimens examined. North Auckland: Three Kings Islands, Galloway (CHR) – Pandora, J. Bartlett (CHR) – Kaitaia, J. Bartlett (CHR) – Rangitoto Island, H. H. Allan (CHR 264069) – *South Auckland:* Penguin Island, B. W. & G. C. Hayward (CHR) – Shoe Island, B. W. & G. C. Hayward (CHR) – Hinehopu, Lake Rotoiti, A. E. Wade 373 (BM) – Mt Mangatawhiri, Coromandel Peninsula, B. W. & G. C. Hayward (CHR) – *Nelson:* West Bay, Lake Rotoiti, Galloway (CHR) – Black Hill, Lake Rotoiti, Galloway (CHR).

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Botanical literature

Acocks, J. P. H. 1975: *Veld types of South Africa*. Second edition. Memoirs of the Botanical Survey of South Africa 40. Botanical Research Institute, Pretoria. ISBN 0 621 02256 X. Price in South Africa R. 8,60, other countries R. 10,75.

Acocks' *Veld types* of 1953, already a classic, has been out of print for some time, and a revised text is not yet ready for print. In the meantime a second edition has now been made available, which certainly fulfills a need. The book is widely-used by ecologists, phytogeographers and taxonomists, as well as by agronomists.

The text of the new edition is unchanged, but plant names have been brought up to date. Otherwise the main new feature is the inclusion of a large number of photographs of the different veld types described. They add considerably to the usefulness and informative value of the book. An enlarged format, a better quality of paper and a more varied typography also contribute to improve the appearance of the second edition.

Bertil Nordenstam

Dyer, R. A.: *The genera of Southern African flowering plants*. Vol. 1, Dicotyledons. Vol. 2, Gymnosperms and monocotyledons. Pretoria 1975, 1976. ISBN 0 621 02854 1 and 0 621 02863 0, respectively. Price in South Africa R. 11,00 + 8,00, other countries R. 14,00 + 10,00.

Dyer's *Genera* is not merely a revised edition of Phillips' well-known *Genera* of 1951, but an entirely new publication. The sequence and numbering of the genera still follow De Dalla Torre and Harms, and genera described after 1909 are given a letter in addition to the number of the closest genus. Genera which have now been transferred from one family to another are also similarly re-numbered. Such recent transfers include e.g. *Heteropyxis* to Myrtaceae, *Oftia* to Scrophulariaceae, *Pauridia* to Hypoxidaceae, and *Lanaria* to Haemodoraceae. The grasses are arranged in a new sequence, according to the Kew system, with their former numbers shown in brackets. The generic descriptions are entirely new, and Phillips' awkward double descriptions have been discarded.

The number of genera has increased considerably, due to several factors. Firstly, weedy and naturalized genera are now included, and this is a welcome and useful addition. Secondly, many new generic records have been added, following the recent exploration of northernmost South West Africa, northern Natal and the Transvaal Lowveld. Finally, changes in generic concepts have led to many additions, especially perhaps within the Gramineae and the Mesembryanthemaceae. The new generic records include many aquatics, the distributions of which have only recently been satisfactorily investigated in Southern Africa, e.g. the Lemnaceae have been increased from two to six genera and the Pontederiaceae from one to three.

The Iridaceae have been dealt with by P. Goldblatt, who introduces a new numbering of the genera described after 1909. He also provides a much improved generic key and very accurate descriptions.

The controversial families included in the Centrospermae have suffered much shuffling about during the intervening years. Dyer prefers to include the Molluginaceae and the Tetragoniaceae in the Aizoaceae, but he recognizes the Mesembryanthemaceae as a sepa-

rate family. The treatment of the 'Mesems' in Phillips was so provisional as to be practically useless. The great advances in our knowledge of the family made during the past few decades permit a much more complete survey, with adequate generic descriptions, to be given now.

All references to the relevant literature are now found directly after each genus, being thus much more readily available than in Phillips' edition. Some omissions and minor mistakes are inevitable, such as the erroneous quotation of Norlindh's Calenduleae monograph (Lund 1943) as *Sv. Bot. Tidskr.* or even *'Tidsch'*.

The tribal system adopted for the Compositae is unnecessarily old-fashioned and rather odd, as are the spelling conventions (''Vernoneae'', ''Eupatoreae'', ''Mutisiaceae'' etc.). A tribe called ''Gorterieae'' has been separated off from the Arctotideae which, however, still retains the anomalous genus *Ursinia*.

Hertia Neck. is an invalid name and ought to have been replaced by *Hertia* Less., which is not even cited as a synonym, and nor is *Othonnopsis* Jaub. & Spach.

Many more minor criticisms could be made, but the main impression given remains nevertheless favourable. Here is a new and indispensible standard work on the South African flora, and it is unfortunate that the binding (at least of vol. 1) will no doubt prove far too weak to withstand the frequent handling which the book will receive.

Bertil Nordenstam

Heywood, V. H., Harborne, J. B., & Turner, B. L. (eds.) 1978: *The biology and chemistry of the Compositae*. 2 vols. 1189 pp. Academic Press, London. Price £ 55:–.

In July 1975 a symposium on *The biology and chemistry of the Compositae* took place at Reading near London. It was organized by V. H. Heywood, J. B. Harborne, and B. L. Turner, the editors of these two expensive symposium volumes, which were published at the beginning of 1978, not 1977 as stated on the title-pages. The title is somewhat misleading; *The taxonomy and chemistry of the Compositae* would have been a more adequate description of the contents.

The books are introduced with a survey of the contents written by the editors. This introduction has replaced the symposium opening lecture, given by A. Cronquist, who refused to adjust his contribution according to the editors' suggestions. The curious reader will find Cronquist's introduction in *Brittonia 29:* 137–153 (1977).

Most of the first volume contains chapters on various aspects of the family as a whole, fossil history and geography, aspects of diversification in the capitulum, evolution of capitulum types in the light of insect–flower interaction, developmental and comparative anatomy, microcharacters in the ligules, pollen morphology (with an extensive bibliography), chromosomal cytology and evolution, and pharmaceutical and economic uses.

Many contributors consider the origin of the Compositae and families such as Calyceraceae (similar pollen and inflorescences) and Umbelliferae (similar polyacetylenes and sesquiterpene lactones) are discussed as possible relatives. Relationship or not is often vaguely inferred from overall similarities or dissimilarities rather than from an evaluation of jointly possessed, uniquely derived features, indicating common ancestry. With the latter, phylogenetic approach the classical view of Compositae and Campanulaceae as sister groups, both possessing inulins, seems valid.

It is a widely held view that the ancestral stock of the Compositae were yellow-flowered shrubs, similar to some allegedly primitive members of the Heliantheae. The specialist on this tribe, T. F. Stuessy, takes another position, however, and maintains that both ancestral Compositae and the tribe Heliantheae may have been originally herbaceous. C. Jeffrey presents the new hypothesis that the ancestral corolla type in the Compositae was zygomorphic bilabiate and one implication is that the Mutisieae should be regarded as the most primitive tribe, at least with respect to corolla morphology.

The most significant feature of these two volumes is the reviews of the tribes. For each tribe there is a systematic report with a complete list of accepted genera with information on approximate number of species, general distribution, known chromosome numbers, and important references. There is also a description and a general discussion of each tribe and some contributors have provided new subtribal classifications. Except for short notes on habit there

is unfortunately little or no information on the morphology of genera belonging to the larger tribes, however. No doubt the tribal reviewers have laid down much work on their reports and it would certainly be too much to ask for generic descriptions. But a lot of genera are distinguished by a single or a few technical characters only, certainly well-known to the reviewers in many cases, and if such information had been included, no matter how inconsistently or unevenly, it would have considerably enhanced the usefulness of the tribal systematic reports.

Many pages are devoted to chemistry. There are chapters on sesquiterpene lactones, flavonoids, and polyacetylenes as well as chemical reviews of each tribe (except Liabeae and Mutisieae). The terpenoid-based sesquiterpene lactones (the bitter taste in e.g. *Artemisia absinthium*), the fatty acid derived polyacetylenes, and the polysaccharide fructans (inulins; the sweet taste of artichoke, *Cynara scolymus*) are characteristic constituents of the Compositae. Senecioneae (s.str.), having pyrrolizidine alkaloids and a special type of sesquiterpene lactones but lacking most polyacetylenes, is remarkably different from the other tribes.

Tribal classification became the main theme of the symposium and so it has remained in the books. The editors adopted G. Bentham's over 100 years old system as a frame for the symposium tribal reviews. Except for his tribe Helenieae, "a hotchpotch of chaffless taxa" dismantled by Turner and A. M. Powell, they conclude that "Bentham's tribal classification has stood the test of time". This may be partly true but the preconceived adoption of Bentham's system has indeed hampered the presentation and possibly also the acceptance of relevant changes. There is no summary or list of proposed, accepted, or discussed tribes. An enumeration of tribes runs as follows: Eupatorieae, Vernonieae, Astereae, Inuleae, Heliantheae, Helenieae (now abolished), Coreopsideae, Tageteae, Liabeae, Senecioneae, "Arniceae" (not formally recognized), Anthemideae, Arctoteae, Calenduleae, Cardueae, Carlineae, Echinopeae, and Lactuceae.

Eupatorieae was and is a tribe much in need of a review. Almost 100 eupatorioid new genera have been proposed by R. M. King and H. Robinson in a flood of papers during the past ten years. And obviously there is more to come; Robinson states that there are about 100 described species not yet assigned to genera.

Turner and Powell venture to dismount Helenieae, generally regarded as polyphyletic. A number of subtribes are transferred to Heliantheae, where they have been accepted by Stuessy. One subtribe is proposed as a new tribe, Coreopsideae, by Turner and Powell but it is not recognized by Stuessy, who considers it a subtribe of Heliantheae. The *Arnica* group of genera and four other subtribes of Helenieae, Turner and Powell wish to transfer to Senecioneae but the reviewer of that tribe, B. Nordenstam, flatly refuses to accept them. An alternative position is within the Heliantheae but Stuessy supports Turner's and Powell's proposed rearrangements. The question of the arnicoid genera became a major controversy at the symposium and it is repeatedly referred to in the books. Nordenstam lists 18 points of difference between *Arnica* and Senecioneae, and concludes that the affinities of *Arnica* and related genera are with the Heliantheae. Turner and Powell state that they have attempted to relate helenoid entities such as the *Arnica* group "back to existing tribes from which they might have evolved". They consider this philosophy "the most phylogenetic" and they are certainly right that any group, no matter how isolated or "alien", should be classified with its phylogenetically closest relative. From the majority of evidence presented not only by Nordenstam but also by other authors it appears, however, that the *Arnica* group phylogenetically belongs with or within the Heliantheae. Nordenstam also mentions the possibility of creating a new tribe, "Arniceae", but this is not formally proposed.

Tageteae and Liabeae are two revived tribes, presented by J. L. Strother and Nordenstam, respectively. These two tribes seem to be generally accepted but M. Dittrich's splitting of the Cynareae (an illegitimate name) into three tribes is apparently considered unnecessary at least by some contributors.

The Compositae is indeed a large family. The estimated number of known species, summarized by Turner in the last chapter, is c. 21889 (in the preface the figure is 13000, a misprint?). In his review of Lactuceae A. S. Tomb reports 60 for *Taraxacum* and 1000 for *Hieracium*.

Apparently the "agamospecies" of *Hieracium* are included but those of *Taraxacum* excluded. Excluding all "agamospecies" the number of known Compositae species should thus be estimated to close to 21000. The number of accepted genera approaches 1300.

The two volumes contain a wealth of information and an array of viewpoints; no doubt they will become the synantherologist's standard books of reference for a long time to come and the editors and authors are congratulated to their achievement.

Kåre Bremer

Irvine, D. E. G. & Price, J. H. (eds.) 1978: *Modern approaches to the taxonomy of red and brown algae*. The systematics association special vol. 10. 484 pp. Academic Press, London. ISBN 0-12-374050-9. Price £ 26.20.

In the spring of 1978 a symposium was held at the Polytechnic of North London on taxonomy of red and brown algae. The comprehensive proceedings of this symposium have been published within a remarkable short period of time compared with other proceedings referred to in some of the papers.

The book contains 18 papers with a broad range of topics, e.g. the taxonomic value of haemagglutinins, the use of immunochemistry in classifying polysaccharides, the rôle of TEM and SEM in the taxonomy of red algae, and the rôle of computers in either identification or taxonomy of brown algae. Some of the papers are reviews, mainly important in collecting extensive information and references.

The reviewer is mainly interested in brown algal taxonomy, and shall therefore concentrate on this subject. Phycologists seem to have found a new toy, the computer. This has been used to compile diagnostic keys and in numerical taxonomy studies. I do not quite see the advantage of computer-generated keys, as the light microscope is a pre-requisite in all cases, which means that the skilled phycologist can answer much faster than the computer. Further, the keys naturally depend on the input the machine receives. This has lead to an almost meaningless keying out of *Phaeostroma pustulosum*, "thallus a pseudodisc, periclinal cell divisions of prostrate vegetative system present". The thallus of this alga is not always a pseudodisc, and a more obvious feature than periclinal cell divisions, the characteristic morphology of the hairs, is not mentioned. The numerical taxonomy study by Russell & Garbary published earlier in 1978 (some of the dendrograms are modified to greater clarity in this book) has shown that the genera of the brown algal family, Ectocarpaceae, are not clearly circumscribed. On this basis they have suggested to reduce the many genera, generally accepted in this family, to one. Numerical taxonomy is a typical man-made pragmatic system, which seems to ignore phylogeny. In the present case it leads to peculiar groupings. *Polytretus reinboldii, Sorocarpus micromorus* and *Giffordia fenestrata* are therefore placed together mainly because they have only plurilocular sporangia as reproductive structures. From a phylogenetic point of view these plants seem to have little to do with each other. Further, it is also known that members of the Dictyosiphonales have basal systems, which under certain environmental conditions may exist alone in the fertile condition, and thus may be identified as belonging to the genus *Streblonema*. Numerical taxonomy says nothing of that kind.

The micrographs are rather bad or badly reproduced in some cases. Some figures appear almost black and others grey with little contrast. The first is the case with Fig. 4 A–B on p. 270, where one of the arrows points to something hardly visible. Some figures in the paper on Ralfsiaceae also lack contrast, and I am unable to identify a hair on a seven-day-old germling (Fig. 25), as stated in the legend to be present.

These, however, are minor flaws in a contribution which gives very valuable information on recent results in the taxonomy of red and brown algae, and the book is highly recommended.

Poul Møller Pedersen

Kennedy, H. 1978: *Systematics and pollination of the "closed-flowered" species of Calathea (Marantaceae)*. 90 pp. + 20 plates, 17 figs, 9 tables. University of California Press. ISBN 0-520-09572-3 (paper). Price not indicated.

In spite of being both common and easily discovered, the Scitaminae (Zingiberales) are very

poorly known, both taxonomically, morphologically and biologically (except for the economically important genus *Musa*). Collectors dismiss them because they are bulky and difficult to dry and taxonomists dislike them because they are poorly and fragmentarily preserved in the herbarium. It is therefore with satisfaction we can now note an increased interest in these plants.

In the New World tropics, *Calathea* is probably the largest scitaminean genus with something like 150 species. The latest monograph came in 1902 and for a long time it has been impossible to reliably identify specimens of this genus, the more recent floras being so full of mistakes and confusion that they are quite useless. In the late sixties Helen Kennedy began to work on this difficult task, one of the results being the present volume dealing with a Middle American group of the genus.

The species dealt with are characterized by having flowers, which do not open spontaneously. The structurally very complex pollination mechanism is worked by Euglossine bees, which forcibly open the flowers in their search for nectar. The paper is based on an extensive field study carried out during several years and on a large number of localities in S and C America. The observations do not only concern floral morphology and pollinator behaviour but also phenology, ecology, distribution, germination etc. The morphological observations on which the taxonomic part is based were also mainly made on live plants in the field. Two introductory chapters deal with floral and vegetative morphology. They are illustrated by very instructive plates. The pollination chapter contributes a surprising wealth of information on structure and behaviour of flowers and pollinators. The pollination sequence is further illustrated by a number of excellent photographs.

Each species of *Calathea* has a very limited number of legitimate pollinator species, but nectar robbing is quite frequent. A bee acting as pollinator in one species of *Calathea* acts as robber in another one, depending on the relationship between length of the floral tube and proboscis length. These relations and the ecological demands of various species, plants as well as bees, are important isolating factors. As nectar thieves often fail to trig the pollination mechanism, a flower which has been robbed can later be worked by a legitimate pollinator. From the point of view of the pollinator, however, these visits are in vain as there is very little nectar left in the flower. Dr Kennedy suggests that the closed-flowered but allogamous habit has evolved as a response to the tendency of the pollinators to favour very young flowers where the probability of finding abundant nectar is highest. She supports this view with observations on open-flowered species, where pollinators have been observed to open nearly mature buds.

The taxonomical part contains very detailed descriptions of 15 species, four of which are described as new. The morphological descriptions give much information on habit, structural details and colours of live plants, most of it not previously described. A great number of taxonomical and nomenclatural problems are clarified and ecological, phenological and distributional data are given for each species. There is also a key to the species and a discussion of species relationships and the subdivision of the genus. The taxonomic decisions give the impression of being sound and well supported.

The strength of this paper is the large amount of careful observations supplied in a plain and easily comprehensible language. The arrangement of the text is exemplary. Information compiled from the literature, on the other hand, sometimes gives the impression of being a bit undigested. When the author states, for example, that a careful ontogenetic study is needed to solve the problematic interpretation of the inflorescence, she disregards the fact that such studies were carried out by Eichler and by Thompson many years ago and published in beautifully illustrated works, which she refers to in other contexts. Their studies did not render definite explanations, however.

In emphasizing the importance of field observations, Dr Kennedy tends to underestimate the significance of studies made in herbaria and laboratories. Herbaria will continue to provide information on regional differentiation and variation patterns in all foreseeable future, aspects which I think are essential for the taxonomic evaluation of organisms. The problem is thus not to become independent of herbaria, but to learn to make optimal use of them. Field studies and herbarium investigations are not mutually exclu-

sive but complementary. Well knowing that many potentially useful characters are not preserved in ordinary herbarium material, I am nevertheless a bit disappointed to note that Dr Kennedy's keys and descriptions are of relatively little use in herbaria. Her polemic attitude to indoor botany is not very fruitful.

Although this paper presents a large amount of invaluable and highly interesting observations, there are rather few conclusions and few hypotheses are made. In this respect I think that Dr Kennedy is not making full use of her fine material.

As I do not want to let a critical word to be the last one, I should like to underline once again the great importance of Dr Kennedy's contribution, which has few equals in tropical botany.

Lennart Andersson

Wickens, G. E. 1976: *The flora of Jebel Marra (Sudan Republic) and its geographical affinities*. 368 pp., 208 maps and 34 figs. Kew Bull. Additional Series V. Her Majesty's Stationary Office, London. ISBN 0-11-241100-2. Price £ 25 (wrappers).

Probable even people with quite a good knowledge of African geography would be unable to place Jebel Marra on the map. It is a volcanic massif, rising to just above 3000 m, situated in westernmost Sudan, in Darfur province, near the Chad border, virtually in the centre of the African continent if distance from the sea is used as criterion. It first became known to Europeans in 1917. This lack of knowledge was not entirely due to its geographical remoteness. Political events, notably the Mahdi revolts in the Sudan, prevented European access to the area before World War I, except for a few years during the 1870's.

Man, however, has profoundly influenced the area for a long time. It has been cultivated for at least 2000 years and abandoned terraces exist on the hill-slopes up to 2750 m. Jebel Marra formed part of successive N African kingdoms, including the mighty Bornu empire of years ago. Important trade and pilgrim routes have crossed the area for centuries.

In the fascinating introductory chapters of his monograph of the Jebel Marra, Dr G. E. Wickens, the Sudan expert at Kew, emphasizes these facts, which are of basic importance to an understanding of the vegetation and floristics of the area. Jebel Marra is situated close to the border between semi-desert conditions to the north and the savanna in the south. The lowland parts are covered with thorn savanna, scrub and deciduous savanna woodland, with montane vegetation above ca 2000 m. Wickens was the first botanist to explore the area intensively and he records nearly 1000 species of vascular plants. The primary aim of his monograph is to elucidate the phytogeographical connections of that flora, its history and immigration routes.

Fundamental for the theories presented are a series of highly informative and well-disposed chapters about the Jebel Marra in particular (geology, geomorphology, soils, vegetation) and on Africa in general (phytogeographical divisions, geomorphological history and continental drift, conditions on the continent during the Quaternary period).

The chapter on the vegetation is enhanced by a number of schematic vegetation diagrams. The true gallery forests of the deep river gorges, enclaves of an equatorial vegetation with Guineo-Congolian rain-forest species, represent a feature of special interest. There is a surprising number of associations of savanna and grassland vegetation, related to the varied soil conditions (volcanic soils, clays, sands, soils of the basement complex) and altitudinal range.

The phytogeographical chapter provides a broad and critical review of the recent literature dealing with Africa. As a basis he ,es White's divisions, now well-known and widely accepted. These are carefully defined by Wickens, probably in more detail than ever before. He readjusts White's regions on some points, notably in creating a separate Sahelian Domain in the Sudano-Zambesian Region, for the strip of land south of the Sahara affected by the Pleistocene sand invasions. The term 'Afroriental' is adopted for White's 'Oriental Domain' in order to avoid confusion with the Near East. Maps and climatic diagrams support the text. This chapter should not be neglected by anyone concerned with African botany.

A chronological tabular survey of African geomorphological history is included in the following chapter, but the author is anxious to stress that his review may soon be outdated.

This is a rapidly advancing field of research. Of even more direct interest to botanists is his account of the Quaternary period. He provides parallel chronologies for various parts of Africa and for Europe. The evidence for an alternation of pluvial and dry periods is well-presented and an account is given of Quézel's studies on the Sahara region during the Pleistocene, together with a map. The probable vegetation of the Sudan 10,000 years ago is shown on another map, although he emphasizes how insufficient and conflicting the available evidence still is.

The phytogeographical analysis of the savanna flora shows that its closest connections are with the east and south-east. An almost insuperable boundary seems to have existed with the flora west of the Chad area, explicable in terms of Pleistocene history. A detailed analysis is given of the 106 entirely montane taxa. This is of particular interest, since the Jebel Marra is well-placed to throw light upon the interplay between tropical and temperate floras in Africa. The overall distributions of these taxa have been clarified and by sound, critical use of a computer they have been grouped together according to their geographical affinities. Their connections with Ethiopia and the E African mountains are particularly strong. The temperate element, notably Mediterranean, is well represented. It apparently immigrated from the east, via the Red Sea Hills. A number of maps show hypothetical migration routes for the Jebel Marra montane flora. The floristic connections between the Jebel Marra and the Sahelian mountains, e.g. Tibesti are surprisingly weak. There are only four exclusively Saharo-Montane taxa. The number of endemic taxa for the Jebel Marra area as a whole is only 11 (1.2% of the total), none of which is montane. The formation of the Jebel Marra is considered to be more or less contemporary with the E African mountains, i.e. Pliocene to early Pleistocene, and much younger than the Ethiopian highlands.

A check-list of all taxa, with relevant synonymy and exhaustive citation of the literature is given. It is complemented by dot maps of the African (plus Arabian and Mediterranean) distributions of no less than 208 of these taxa, virtually all mapped for the first time. The largest families are the Gramineae (205 species), the Leguminosae (108) and the Compositae (76). Genera with more than 10 taxa include *Brachiaria*, *Eragrostis* and *Hyparrhenia*, *Acacia* and *Crotalaria*, *Ipomoea* and *Cyperus*.

My only major criticism of this book concerns its title, which gives no real idea of how much it contains of general phytogeographical interest. It is my fond hope that reviews, such as this one, will help to make this clear to all concerned. It is an indispensible book for anyone working on the flora of Africa.

Bengt Jonsell

Ross, J. H. (ed.): *Flora of Southern Africa. Vol. 16.* Part 1, Mimosoideae (by J. H. Ross), 1975. ISBN 0-621-02263-2. Price in South Africa R. 13,50, other countries R. 16,75. – Part 2, Caesalpinioideae (by J. H. Ross), 1977. ISBN 0-621-03832-6. Price in South Africa R. 16,00, other countries R. 20,00. – Botanical Research Institute (Pretoria).

The fourth and fifth parts of the *Flora of Southern Africa* to appear, deal with the subfamilies Mimosoideae and Caesalpinioideae of the Leguminosae. These contributions are notable for several reasons. Members of these subfamilies form important and conspicuous constituents of various types of vegetation. Thus several of Acocks' veld types are dominated by species of *Acacia*, by races of *Dichrostachys cinerea*, or by stand-forming species such as Mopane (*Colophospermum mopane*). Others are valuable timber trees (e.g. *Burkea africana*, *Baikiaea plurijuga*). Furthermore, some naturalized *Acacia* species are among the most aggressive invaders of the fynbos vegetation of the Cape Province.

No fewer than 68 species are dealt with under the largest genus, *Acacia*, 47 of which are indigenous. Many of these are already familiar to both learned and lay botanists alike, such as the most widespread of them all, *A. karroo*, commonly known as 'Sweet Thorn' or 'Soetdoring'. Another is the 'Ana Tree', *A. albida*, which holds a taxonomically isolated position among the African acacias and which, especially by French botanists, is sometimes separated off as the monotypic genus, *Faidherbia*. The equally well-known 'Camel Thorn', or 'Kameeldoring', can unfortunately no longer retain its familiar name, *A. giraffae* Willd., but has had to be

re-named *A. erioloba* E. Mey. The most recently recognized species is *A. redacta* Ross. It is the smallest shrub and also has the narrowest range, inhabiting a small area of the inhospitable Richtersveld in NW Cape Province.

The cultivated and naturalized acacias include some economically important species, e.g. the 'Black Wattle' (*A. mearnsii,* previously often wrongly-named *A. mollissima*) and the 'Blackwood' (*A. melanoxylon*). The latter species, and especially the 'Port Jackson Willow' (*A. saligna*) and the 'Rooikrans' (*A. cyclops*), have become serious threats to the natural vegetation of many areas.

Naturalized species are also recorded in some related genera, e.g. *Leucaena* and *Albizia*. The latter, with 11 indigenous species, is an important genus in Southern Africa, as is the phytogeographically-significant genus *Elephantorrhiza,* the nine described species of which all occur within the territory covered by the Flora.

There are quite lengthy, but valuable discussions on taxonomic matters. Typification of all the taxa dealt with has been attempted, though not always entirely successfully. For example, all attempts to trace the type of *Schotia cuneifolia* Gand. are said to have failed, and the identity of the taxon has therefore remained somewhat doubtful. However, a fine sheet of the type collection, Penther 2516, exists in Stockholm (S); the specimen clearly belongs to *S. latifolia*. One wonders whether the possible existence of a holotype in Lyon (LY) has really been properly investigated.

The monographic approach, with ample comments on taxonomy, variation and ecology, may be justified by the particular importance of these two subfamilies. Alternative keys are provided for flowering and fruiting material. Even three alternative keys are provided for *Acacia*. Further help in identification can be gained from the illustrations, e.g. drawings of seed pods, seeds and petiolar glands. There are also many fine full-page drawings by various artists. Some of the illustrations have been published previously elsewhere (*Flora zambesiaca, Flora of Tropical East Africa*).

However, the ambitious format of the Flora raises some doubts about hopes of its eventual completion. In the present two parts, fewer than 200 species are dealt with in about 300 pages. Given equivalent space, the total vascular plant flora of South Africa will require something like thirty-thousand pages, and assuming a similar speed of publication the final volume would not appear before the year 2150! Obviously a more effective approach is needed, and some modifications have already been proposed for forthcoming parts, such as much shorter descriptions, less bibliographic information, and minimal citation of specimens. Even so, the production of this Flora represents an enormous task, which will necessitate both national devotion and international cooperation.

Bertil Nordenstam

Rechinger, K. H. (ed.): *Flora iranica*. Lfg. 111–114 (1975), 115–121 (1976), 122–125 (1977), 126–138 (1978). Akademische Druck- und Verlagsanstalt, Graz.

Since the time of my last review of this outstanding flora (*Bot. Notiser 129:* 217) a further 28 parts have appeared. These range in size from the single-page on the Goodeniaceae to the 560-page volume on the Compositae-Lactuceae. The latter naturally attracts the most attention, being the first tribe of that huge family to be completed for the Flora. Rechinger himself is responsible for the main body of data, but substantial contributions are also provided by H. W. Lack (*Picris, Chondrilla, Hieracium* p.p.) and J. L. v. Soest (*Taraxacum*), together with a few minor contributions by other authors.

Among the larger genera within the Lactuceae, *Scorzonera* deserves special mention, with no fewer than 68 species occurring in the area, more than 50% of which are endemics. It should be noted, however, that the 'narrow' species concept, as found for example in the *Flora of the USSR,* has been adopted here for this particularly difficult genus. A similar treatment applies to *Tragopogon,* another genus which shows a high degree of endemism and having a marked centre of variation within the area.

In dealing with *Picris,* H. W. Lack naturally follows his own generic delimitation, presented a few years ago in his doctoral thesis. This means that the genus *Helminthotheca,* typified by *Picris echioides* L., is separated off as a distinct

genus. This apparently well-founded taxonomic decision has not as yet found its way into European floras.

The crucial genera *Hieracium* and *Taraxacum* are very differently represented within the area covered by the Flora. The former genus extends only into the temperate north, and by a small number of species. The provisional treatment is admittedly orthodox, being based on Zahn's largely outdated work, with its much too broad species concept.

Taraxacum, on the other hand, is richly represented, with as many as 17 sections, about a half of which have their phytogeographical centres within the area. van Soest recognizes 91 species, but remarks that further species can be expected in the future, as a result of further collecting forays. The closely-related, endemic and monotypic genus *Wendelboa* v. S. is also of great phytogeographical interest. Another interesting monotypic genus from West Pakistan, *Spiroseris* Rech. f., is here described for the first time. It is allied to the Sino-Himalayan genus *Dubyaea,* but is nevertheless distinct, especially in its achene and floret morphology.

The impressive Lactuceae volume is concluded by 208 pages of illustrations, mostly photographs of dried specimens, but which are sometimes supplemented by drawings of achenes or other floral details.

Numerous smaller families are also dealt with in other parts of the Flora, e.g. Berberidaceae and Rhamnaceae (by K. Browicz and J. Zieliński), Nyctaginaceae and Polygalaceae (by J. Chrtek and B. Křisa), Callitrichaceae (by H. D. Schotsman), and Cucurbitaceae (by J. S. Andersen). In the Malvaceae (by I. Riedl) the genus *Alcea* is noteworthy for its high degree of endemism (34 species out of a total of 56, i.e. 61%).

The Iridaceae, a fine volume, has been written jointly by P. Wendelbo and B. Mathew. The text is accompanied by instructive drawings and more than fifty excellent colour photographs, some from nature, others of plants in cultivation. Such illustrations are particularly useful for these plants, which generally tend to lose their flower shape and colour on drying. *Iris* is the largest genus, especially since the bulbous species have not been split off from the genus, as done in recent Russian floras. This is a difficult genus for a number of reasons. Most species show a great deal of infraspecific variation, especially in flower colour, and the available herbarium material is often of poor quality. The occurrence of subspontaneous or escaped garden forms further complicates the picture, as does hybridization and the fact that some taxa seem to be still in process of evolution. Taxonomically isolated endemic species also occur, however, such as *I. cycloglossa* Wendelbo and *I. microglossa* Wendelbo.

The Orchidaceae volume, by J. Renz, is equally or even more impressive, being lavishly illustrated with 117 magnificent colour photographs, in addition to a number of the usual black-and-white photographs of herbarium specimens. Orchids are sparsely represented in the area, and only terrestrial species are known. Most of the 66 recorded taxa occur in the western and north-western mountainous districts, the remainder mainly in the easternmost corner of the area. The majority are familiar to European botanists, only four species being endemic to the region. The author has carried out extensive field studies in the area covered by the *Flora iranica* and his thorough knowledge is made evident throughout the text, which is full of pertinent observations and taxonomic discussion. As for the Iridaceae, identification keys in both English and Latin are provided. To facilitate use of the text even further, the descriptions as well are given in both English and Latin. This exception to the general editorial policy is certainly justified by the great interest in orchids taken by amateur and professional botanists alike.

Bertil Nordenstam