

Phloem ultrastructure and systematic position of Gyrostemonaceae

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The three species of Gyrostemonaceae investigated contain S-type sieve-element plastids. Starch grain morphology and occurrence was tentatively compared with data from sieve-element plastids of other members of Capparales. Similarities were found in Bataceae and Salvadoraceae. The companion cells of *Gyrostemon ramulosus* regularly include protein-containing vacuoles which by their development and contents are comparable with dilated ER-cisternae of Brassicaceae and Capparaceae. The results exclude the family from Phytolaccaceae and Centrospermae as a whole and support a position close to Capparales.

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The small family Gyrostemonaceae (5 genera, 17 species), until quite recently, has almost unanimously been allied with Centrospermae, where it was either included in Phytolaccaceae or recognized as a separate family. Early doubts with regard to the position of Gyrostemonaceae came from studies of their pollen grains which are unique among Centrospermae but in some features resembled those of Bataceae, a family also doubtfully allied with Centrospermae (Erdtman 1952, Prijanto 1970 a, b). Flower morphology also provided data emphasizing the isolated position of Gyrostemonaceae: centripetal development of stamens is not found elsewhere in Centrospermae, while the presence of rudimentary glandular stipules again finds a parallel in Bataceae (Eckardt 1971, cf. Eckardt 1976). Then, a survey on the chromosome numbers of Gyrostemonaceae established their base number to be $n = 14$ (Keighery 1975) which is uncommon in Centrospermae thus implying their separation from both Phytolaccaceae and the order Centrospermae as a whole.

Recently, Goldblatt et al. (1976) considered results from palynology, cytology, chemical analysis and ultrastructure of sieve-element

plastids and concluded that the family should be removed from Centrospermae. The presence of glucosinolates suggested a relationship with Capparales. After carefully weighing morphological, chemical and other characters Dahlgren (1975) also favoured an inclusion of Gyrostemonaceae in Capparales or, alternatively, its placing in a closely related separate order.

Details of phloem ultrastructure have proved useful in providing additional criteria for the circumscription of higher taxa in angiosperms (Behnke 1972, 1977). In this investigation two features have been tested with regard to their possible evidence for the assignment of Gyrostemonaceae to Capparales (s.l.): (1) S-type sieve-element plastids (recorded in part by Goldblatt et al. 1976), and (2) the occurrence of dilated cisternae. The presence of glucosinolates in Capparales generally coincides with the presence of so-called myrosin cells, usually idioblasts, the vacuoles of which give a positive reaction to protein staining. In addition, dilated cisternae of endoplasmic reticulum are described for a great number of taxa from Brassicaceae and Capparaceae (Iversen 1970, Behn-

ke 1977). Dilated cisternae occur in a few different cell types among which the most prominent are phloem-parenchyma cells and, as can be demonstrated with the transmission electron microscope, always contain protein material. Myrosin cells and dilated cisternae have both been regarded as potential sites of glucosinolate and/or myrosinase (glucosinolate-hydrolyzing enzyme) activity in capparalean plants. As glucosinolates have been recorded for Gyrostemonaceae it is appropriate to screen their phloem parenchyma for the presence of dilated cisternae.

Material and methods

Material. Gyrostemonaceae: *Codonocarpus cotinifolius* (Desf.) F. Muell., *Didymotheca tepperi* F. Muell. ex Walter (both collected in Northern Territory, Australia, by J. R. Maconochie) and *Gyrostemon ramulosus* Desf. (raised from seeds at the Botanical Garden, Copenhagen, 1976/276).

Bataceae: *Batis maritima* L. (one plant shipped from Texas and then grown at the Zoologisches Institut, Universität Heidelberg).

Salvadoraceae: *Azima tetracantha* Lam. and *Salvadora persica* L. (both from the Botanical Garden, Copenhagen).

Capparaceae: *Cleome spinosa* Jacq. (from the Botanical Garden, Bonn).

Brassicaceae: *Alyssum saxatile* L. (from the Botanical Garden, Bonn) and *Peltaria alliacea* Jacq. (from the Botanical Garden, Heidelberg).

Methods. Stem parts of the taxa mentioned were cut into longitudinal sections by hand and were immediately immersed into a fixing fluid containing a combination of formaldehyde and glutaraldehyde. Postfixation with osmic acid, dehydration with acetone, embedding and polymerisation in epoxy resins were carried out according to standard procedures. Ultrathin sections of phloem-containing parts were examined and photographed with a Siemens Elmiskop 101.

Plastids

The sieve-element plastids of the three species of Gyrostemonaceae examined are clearly of the starch-storing S-type. No protein accumulations have been detected. Every sieve-element plastid contains several roughly spherical starch grains of different size (Fig. 1 A–D). The grains are completely surrounded by a small coat of particulate, darkly stained material. There is usually a narrow light zone between the starch grain and the coat (Fig. 1 A–D, arrows). As in other plants investigated in this respect, the matrix contents of the sieve-element plastids are gradu-

ally reduced during the development of the sieve elements, to judge from their stainability properties: compare Fig. 1 A and B (young cells) with Fig. 1 D (a so-called mature sieve-element).

The species investigated (25) from other families within Capparales (sensu Dahlgren 1975) except for *Brassica chinensis* (Favali & Gerola 1968) and *Capparis cyanophallophora* (with P-type plastids) also contain S-type sieve-element plastids. However, starch grains very similar to those recorded in Gyrostemonaceae have hitherto only been found in Bataceae and Salvadoraceae (*Azima*, *Salvadora*) (Fig. 1 E, F). In *Azima* at least (Fig. 1 F, arrows), the light zone separating the coat can be seen. Among the other Capparales investigated the starch grains are predominantly ovoid and variable in size (Fig. 1 G–I). They are often accompanied by or disintegrated into small particles.

Protein-containing vacuoles

The stem phloem of *Gyrostemon ramulosus* has been carefully screened for the presence of dilated cisternae of ER. No inclusions of the type seen in Brassicaceae and Capparaceae have been detected. However, protein-containing vacuoles were found to be a regular component of companion cells of *Gyrostemon* sieve tubes. These vacuoles are derived from cisternal ER which contains some amorphous material and is almost agranulate when extending (Fig. 2 A, B). As soon as it has widened up to a vacuole-like compartment it already contains distinct protein filaments (Fig. 2 C). Finally the protein-containing vacuole extends considerably, parallel to the longitudinal axis of the companion cell: lengths of over 20 μm have been measured while their diameter is only 1–2 μm (Fig. 2 D). The protein filaments are orientated roughly longitudinally inside the vacuole. Their over-all diameter is about 50 nm; due to their bent course, their length is not possible to determine. The 50 nm filaments (Figs. 2 D, 3, double arrows) look like being composed of helically arranged subunits (Fig. 3, boldface arrow). The subunits probably first assemble into smaller, 20–25 nm broad entities (Fig. 3, arrow) before combining to form the 50 nm filaments. The membrane surrounding the entire organelle is completely devoid of ribosomes; it obviously corresponds to a normal tonoplast (Fig. 3, T).

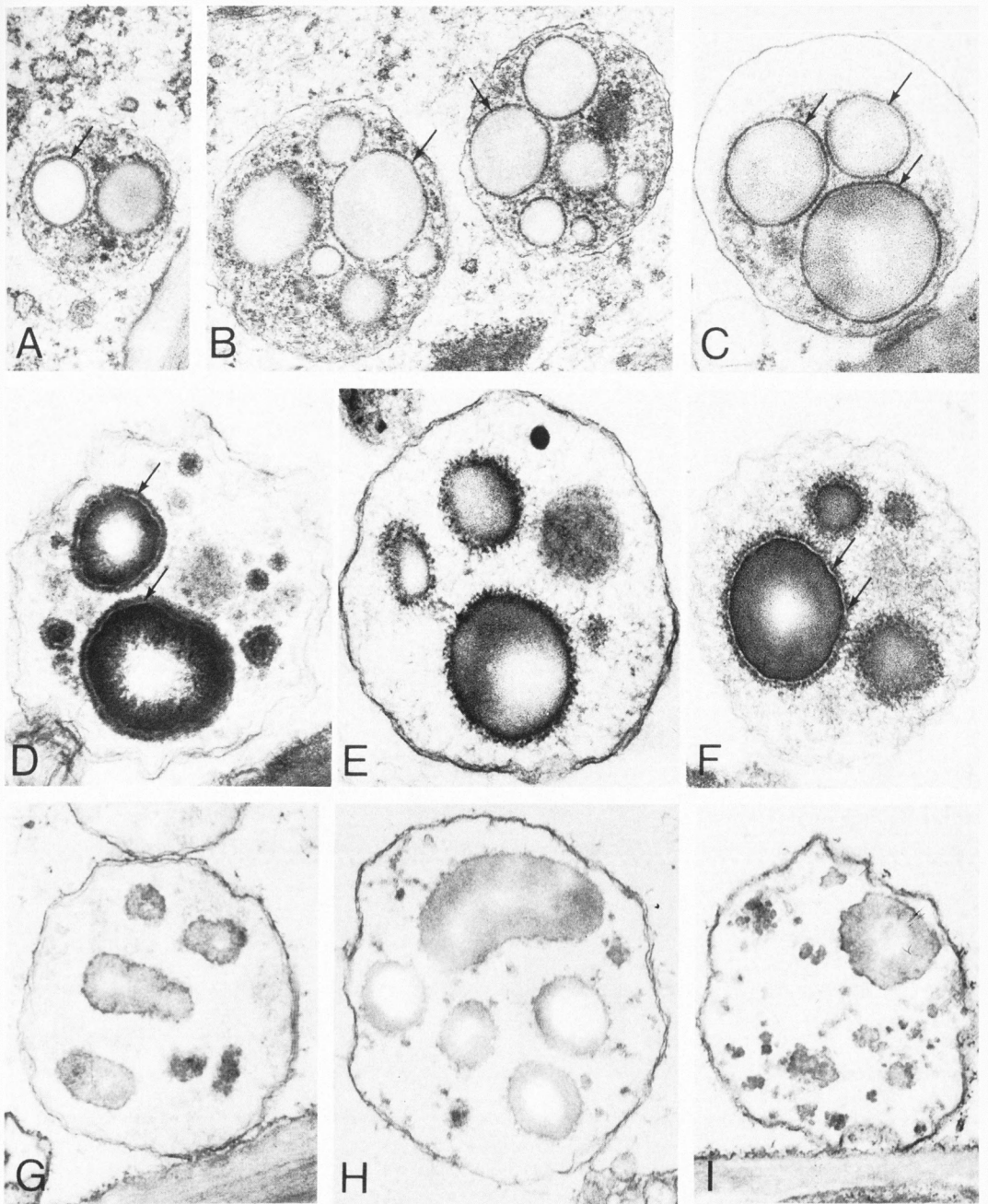
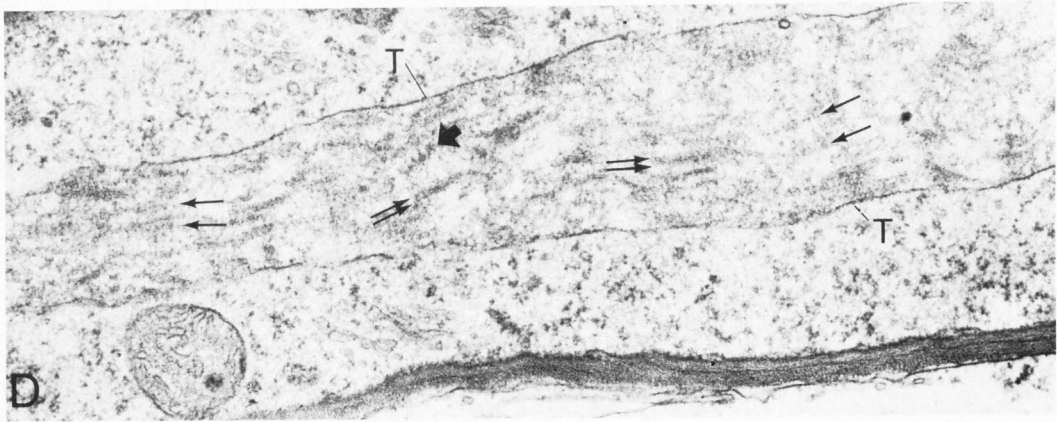
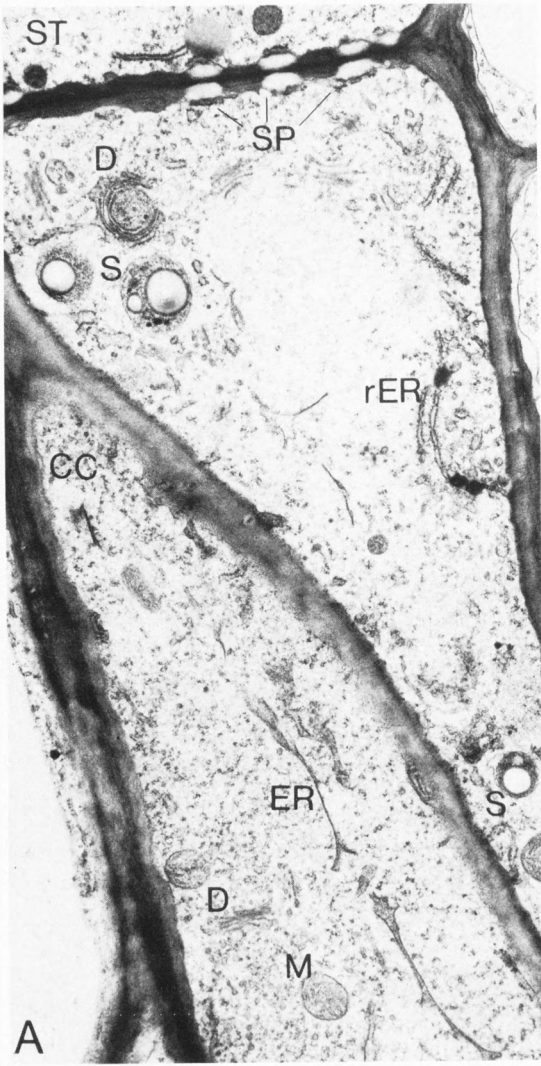


Fig. 1. S-type sieve-element plastids of Gyrostemonaceae and other members of Capparales (s.l.). - A: *Gyrostemon ramulosus* (Gyrostemonaceae). $\times 30,000$. - B, C: *Didymothecha tepperi* (Gyrostemonaceae). Young sieve-element in B, plastid of mature sieve-element with dislocated envelope, due to aberrant fixation procedures, in C. Both $\times 30,000$. - D: *Codonocarpus cotinifolius* (Gyrostemonaceae). $\times 40,000$. - E: *Batis maritima* (Bataceae). $\times 40,000$. - F: *Azima tetracantha* (Salvadoraceae). $\times 40,000$. - G: *Alyssum saxatile* (Brassicaceae). $\times 40,000$. - H: *Peltaria alliacea* (Brassicaceae). $\times 30,000$. - I: *Cleome spinosa* (Capparaceae). $\times 30,000$. - Arrows point to light zone between starch grain and surface coat.



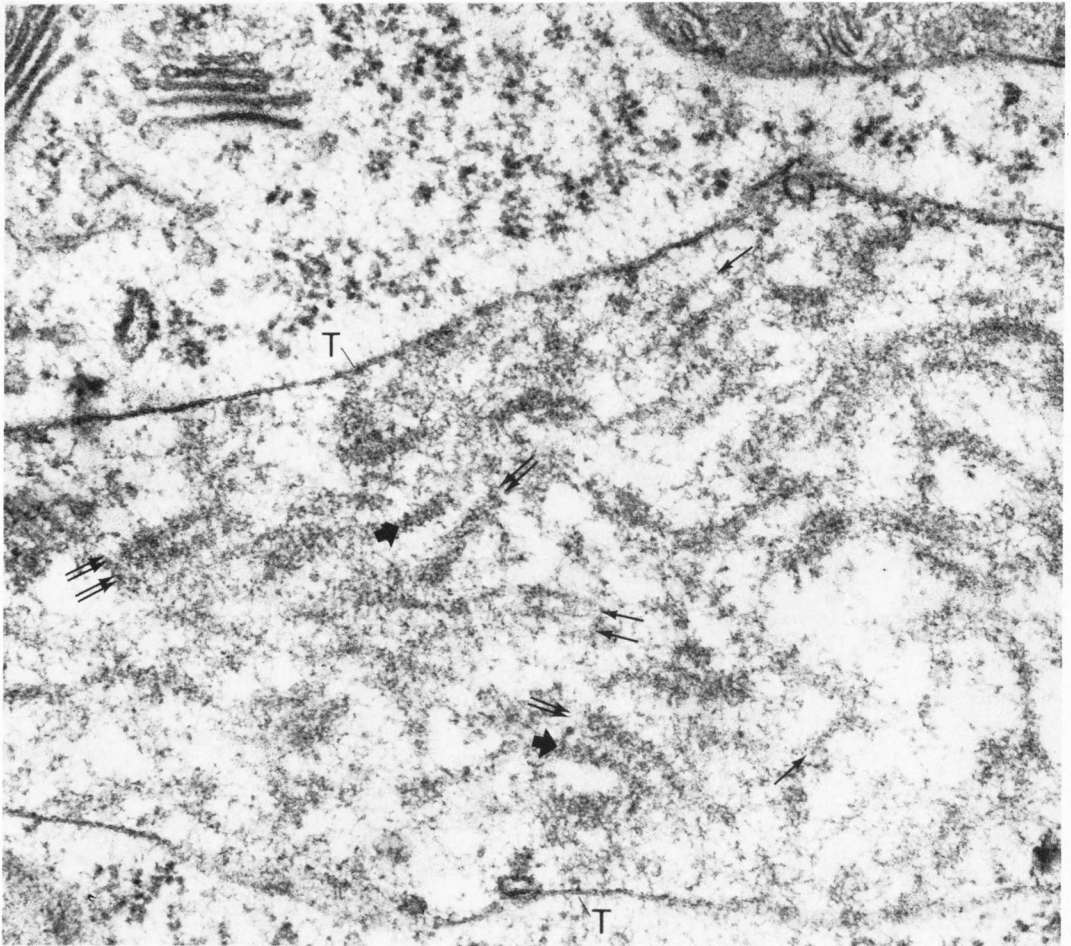


Fig. 3. Part of a protein-containing vacuole from companion-cell cytoplasm of *Gyrostemon ramulosus*. Vacuole surrounded by tonoplast (T) contains protein filaments (double arrows, diameter about 50 nm) which sometimes show composition of helically arranged subunits (boldface arrows); single arrows point to smaller (about 25 nm) filaments. $\times 50,000$.

Discussion

The presence of S-type sieve-element plastids clearly distinguishes *Gyrostemonaceae* from the P-type containing order *Centrospermae* and is

strong evidence against its inclusion in *Phytolaccaceae* (Behnke 1976). The more general use of S-type plastids as positive markers for the alignment of a taxon has still to be achieved since no reliable criteria which enable a general

Fig. 2. Protein-containing vacuoles in companion cells of *Gyrostemon ramulosus*. - A: Longitudinal section of stem phloem with sieve-tube (ST) and companion cell (CC). D dictyosome, ER agranular ER in companion cell, rER granular ER in sieve tube, M mitochondrium, S S-type plastid, SP sieve plate pores. $\times 12,000$. - B: Agranular, slightly dilated ER of companion cell. $\times 25,000$. - C: Companion cell with protein-containing vacuole (V) and granular ER (rER). $\times 25,000$. - D: Protein-containing vacuole of companion cell surrounded by tonoplast (T) and including small (single arrows) and broad filaments (double arrows), partly showing helical arrangement of subunits (boldface arrow). $\times 25,000$.

subclassification of this plastid-type, have as yet been worked out. It can be assumed, however, that, apart from ontogenetic changes, the phenotype of starch grains is genetically fixed like that of protein deposits. A first attempt at using the morphology of starch grains from sieve-element plastids as a taxon-specific feature has been undertaken by Behnke (1974) who found that the starch grains in Gymnospermae were usually club-shaped. The present comparison of starch-grain morphology and occurrence in sieve-element plastids of Capparales (s.l.) may perhaps lead towards further investigations. There seems to be a close similarity between Gyrostemonaceae, Bataceae and Salvadoraceae, whereas the core families Brassicaceae, Capparaceae, and Resedaceae stand somewhat apart.

The protein-containing vacuoles in the companion cells of *Gyrostemon ramulosus* find their counterpart in the dilated cisternae of Brassicaceae and Capparaceae. Although on superficial inspection they look quite different, they have some attributes in common: (1) they occur in phloem-parenchyma, (2) derive from endoplasmic reticulum, and (3) contain morphologically defined protein material. Therefore, both organelles may be interpreted as being the quantitative variations of one pattern, e.g. the exclusion of (enzyme?) proteins from its reaction site. The vacuoles in the companion cells of *Gyrostemon*, still of a limited size, would thus represent an intermediate between dilated cisternae of Brassicaceae and the protein-containing vacuoles of the glucosinolate species *Drypetes roxburghii*, which extend over almost the entire lumen of the phloem-parenchyma cell (Jørgensen et al. in prep.). From these results the conclusion can be drawn that Gyrostemonaceae are close to but not within the core-group families of Capparales.

To summarize: data from phloem ultrastructure favour considerations to include Gyrostemonaceae and other glucosinolate-containing families peripheral to Capparales (s. str.) in a separate but closely related order (see e.g. Dahlgren 1975).

Acknowledgements. The author is extremely grateful to J. R. Maconochie, Alice Springs, Australia, who several times collected material of the three Gyrostemonaceae species and also fixed some specimens at their natural habitat. Without his generous help this

study would not have been possible. T. J. Mabry, Austin, sent a potted *Batis maritima* from the Gulf coast; R. Dahlgren, Copenhagen, gave permission to use a seedling of *Gyrostemon ramulosus* raised for his studies; L. B. Jørgensen, Copenhagen, helped to find species of interest for this study in the Botanical Garden, Copenhagen and assisted during their fixation; Mrs E. Grünbacher took care of the *Batis* plant in Heidelberg; Miss B. Schmidt, Miss A. Rüsken and Mrs D. Laupp gave technical assistance and conducted the photographic work. I would like to express my sincere thanks to all these people. The work was supported by grants from the Deutsche Forschungsgemeinschaft.

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A new *Tribulus* species with winged carpels

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Hosni, H. A. 1977 09 15: A new *Tribulus* species with winged carpels. *Bot. Notiser* 130: 261-262. Stockholm. ISSN 0006-8195.

Tribulus arabicus H. Hosni sp. nov. is described and illustrated. It is distinguished from the other *Tribulus* species with winged carpels by its larger flowers and fruits. It is believed to be endemic in S Arabia.

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Up to now, four species of *Tribulus* with winged carpels have been known, viz. *T. longipetalus* Viv., *T. bimucronatus* Viv., *T. pterocarpus* Ehrenb. and *T. pterophorus* Presl. The first three seem to be confined to the arid zones in N Africa and eastwards in Palestine, Iraq, Arabia, Iran and India. *T. pterophorus* is only known from Arabia and S Africa.

The author is preparing a thesis under the

title "A revision of the *Tribulus* species with winged carpels in the Old World" under the supervision of Professor M. N. El Hadidi. During the revision of the material in BM, CAI, CAIM and K, a new species was recognized. It is described here as *T. arabicus*. The differences between the species of *Tribulus* with winged carpels can be summarized as follows.

Key to *Tribulus* species with winged carpels

- | | |
|--|------------------------|
| 1. Fruit over 5 mm diameter | 2 |
| - Fruit less than 5 mm diameter | <i>T. bimucronatus</i> |
| 2. Flower 2-2.5 cm diameter | 3 |
| - Flower 0.8-1 cm diameter | 4 |
| 3. Carpels with hairy dentate wings | <i>T. arabicus</i> |
| - Carpels with glabrous entire wings | <i>T. pterophorus</i> |
| 4. Carpels with hairy dentate wings | <i>T. longipetalus</i> |
| - Carpels with glabrous entire wings | <i>T. pterocarpus</i> |

Tribulus arabicus H. Hosni sp. nov. - Fig. 1

Frutex erectus, ad 100 cm altus omnino dense hirsutus, cinerascens; internodia 7-25 mm longa. *Folia* paripinnata, 4-7-jugata, 8-35 mm longa, foliola oblonga 5-7 mm longa, 3-4 mm lata; stipulae basi ovatae superne acuminatae 6 mm longae, 4 mm latae. *Flos* magnus 2.5 cm diam. *Pedicellus* 15 mm longus. *Sepala* lanceolata 7 mm longa, 2 mm lata. *Petala* flava obovata sepalis multo longiora 15 mm longa, 10 mm lata. *Stamina* 10, petalis breviora 5-8 mm longa. *Ovarium* 2 mm diam.; stylus brevis 1 mm longus, stigma gracile 3 mm longum. *Fructus* ellipticus 9 mm longus 7 mm latus, dense hirsutus. *Carpella* postice punctata

9 mm longa 1.5 mm lata, alis 2 cristatis 2.5 mm latis striatis trapeziformibus margine dentatis basi interruptis munita.

Holotypus: Yemen, Lower Wadi Najran (18°30'N, 45°0'E), 16.7. 1962, Zeller s.n. (BM).

Woody erect shrub up to 100 cm high, densely hairy, greyish-green; internodes 7-25 mm long. *Leaves* paripinnate, 8-35 mm long with 4-7 pairs of leaflets; leaflets 5-7 mm long and 3-4 mm broad, oblong; stipules ovate at the base, lanceolate above, 6 mm long and 4 mm broad.

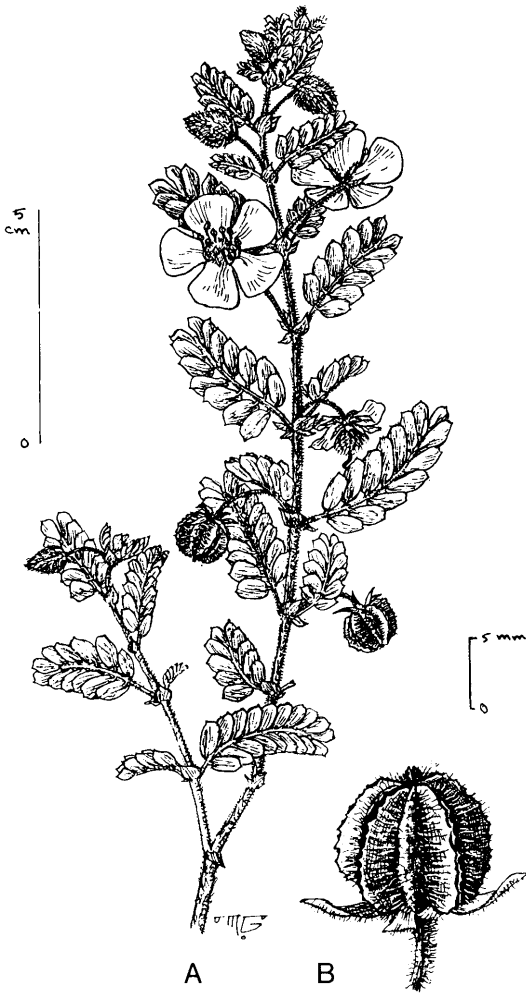


Fig. 1. *Tribulus arabicus*. - A: Flowering branch. - B: Fruit.

Flowers large, 2.5 cm across. Pedicels 15 mm long. Sepals 7 mm long and 2 mm broad. Petals yellow, obovate, longer than the sepals, 15 mm long and 10 mm broad. Stamens 10, shorter than the petals, 5-8 mm long. Ovary spherical, 2 mm broad; style short, 1 mm long, stigma slender, 3 mm long. Fruit elliptic, 9 mm

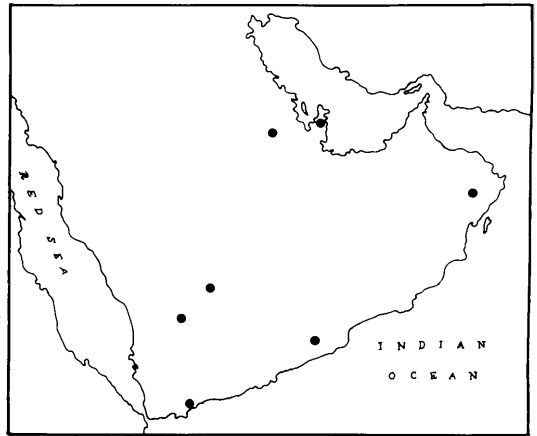


Fig. 2. *Tribulus arabicus*. Known distribution.

long and 7 mm broad, densely hirsute. Carpels dorsally punctate, 9 mm long, 1.5 mm broad, with two marginal wings 2.5 mm broad, crusted, striate, trapeziform, margins dentate, interrupted at the base.

Distribution: Endemic in S Arabia: Rub El Khali, Yemen, Hadramout, Oman and Qatar (Fig. 2).

Collections: Saudi Arabia. Nefud Dahi, 12. 1951, Popov 503 (BM, K) - Rub El Khali, 12. 1946, Zeller (BM) - Rub El Khali, Arq Artha, 2. 1952, Popov, Tilin & Gililand 4158 (K).

Arab Republic of Yemen: Lower Wadi Najran, 7. 1962, Zeller (BM holotype, CAI).

Democratic Republic of Yemen: Aden, W of Wadi Mitani, 5. 1962, Stewart 689 (K) - Hadramout, 3. 1938, Feild 8A (K) - Hadramout, Adraj, 1939, Philpy (BM) - 100 m NE of Zumukh, Hadramout, 10. 1950, Guichard & Had 412 (BM, CAI).

Oman: Oman, 1. 1952, Lee (BM).

Qatar: Umm Bab, 4. 1975, Obeid 156 (CAI).

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Karyotypes of some *Iris* taxa

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Chromosome numbers of 16 *Iris* taxa of the subgenera *Limniris*, *Scorpiris* and *Susiana* are reported. Their karyotypes are presented and illustrated.

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The classification problems within the genus *Iris* are becoming increasingly complex with each new taxonomic and/or cytologic report e.g. Rodionenko (1961), Weymouth & Chaudhary (1974), Gustafsson & Wendelbo (1975), Chaudhary et al. (1976). The accumulation of such data eventually, however, should lead to a more widely acceptable and rational classification of the genus. The present study is a continuation of an effort to investigate cytological characteristics of *Iris* taxa.

Methods

The cytological observations were made from root-tip squashes following the usual propionic-carmin staining technique after pretreatment with 0.002 mol/lit 8-hydroxyquinoline solution for 2–3 hours at c. 15°C. As many dividing cells as possible were studied for karyotype analyses, never less than 10 cells per taxon. The karyological nomenclature proposed by Levan et al. (1965) has been followed and the four groups of chromosomes referred to according to their *r* values: *m* (*r* = 1.0–1.7), *sm* (*r* = 1.7–3.0), *st* (*r* = 3.0–7.0) and *t* (*r* > 7.0).

Subgenus *Limniris* Tausch ex Spach

I. melanosticta Bornmüller

Material. S Syria, between Gezira and Daraa, Chaudhary & Kirkwood s.n. (BEI).

Chromosome number and karyotype. $2n = 24$ (Fig. 1 A). *m*-chromosomes: 5 pairs, I, VI, VII, IX and XI (*r* = 1.0, 1.4, 1.3, 1.7 and 1.7, respectively). *sm*-chromosomes: five pairs, II, V, VIII, X and XII (*r* = 1.8, 2.7, 2.3, 1.9 and 2.0, respectively). *st*-chromosomes: two pairs, III and IV (*r* = 3.5 and 3.6, respectively). The members of pairs II, III, IV and VIII have short and/or long arms of unequal length. These inequalities in pairs III and VIII do not interfere with their separation into chromosome groups but the members of pairs II and IV are so unequal (*r* = 1.4 and 2.2 for II and 2.8 and 4.2 for IV) that they could be placed into different groups. Satellites are found on pairs IV and XII.

Previous report. $2n = 24$ (Simonet 1952).

Subgenus *Scorpiris* Spach

I. aucheri (Baker) Sealy

I. fumosa Boiss. & Hausskn. in Post & Dinsmore 1934 and Mouterde 1966. – *I. sindjarensis* Boiss. & Hausskn. in Post & Dinsmore 1934 and Mouterde 1966.

Material. N Syria, Qilaat Simaan, Chaudhary s.n. (BEI); Bishmishly, Chaudhary & Kirkwood s.n. (BEI).

Chromosome number and karyotype. $2n = 24$

(Fig. 1 B). m-chromosomes: four pairs, I, II, IV and VIII ($r=1.0, 1.1, 1.3$ and 1.4 , respectively). sm-chromosomes: four pairs, III, V, VI and XI ($r=1.9, 2.0, 2.0$ and 2.0 , respectively). st-chromosomes: four pairs, VII, IX, X and XII ($r=5.0, 3.3, 3.6$ and 3.0 , respectively). Satellites are found on pair X.

***I. nusairiensis* Mouterde**

Material. Syrian desert, 32 km E of Homs, Chaudhary & R. A. Shad s.n. (BEI).

Chromosome number and karyotype. $2n=20$ (Fig. 1 C). m-chromosomes: two pairs, I and II ($r=1.5$ for each). sm-chromosomes: three pairs, III, VIII and X ($r=1.8, 2.6$ and 2.6 , respectively). st-chromosomes: five pairs, IV, V, VI, VII and IX ($r=4.1, 3.7, 7.0, 3.3$ and 3.8 , respectively). No satellites could be observed.

***I. postii* Mouterde**

Material. Syrian desert, near Ayn-al-Baida, Chaudhary & A. R. Shad s.n. (BEI).

Chromosome number and karyotype. $2n=20$ (Fig. 1 D). m-chromosomes: nine pairs, I-IX ($r=1.0, 1.0, 1.1, 1.2, 1.4, 1.0, 1.4, 1.1$ and 1.1 , respectively). st-chromosomes: one pair, X ($r=5.0$). Prominent satellites are found on pair X.

***I. palaestina* (Boiss.) Klatt**

Material. Lebanon, along Sidon highway near Khaldeh, S. & Z. Chaudhary s.n. (BEI).

Chromosome number and karyotype. $2n=24$ (Fig. 1 E). m-chromosomes: four pairs, I, II, XI and XII ($r=1.2, 1.1, 1.4$ and 1.5 , respectively). st-chromosomes: eight pairs, III-X ($r=5.5, 6.3, 6.0, 5.8, 6.8, 6.0, 5.6$, and 5.2 , respectively). Prominent satellites are found on pair IV.

Previous report. $2n=24$ (Simonet, unpublished?, as cited by Werckmeister 1967).

Subgenus *Susiana* Spach

The investigated species in this group have exclusively t-chromosomes.

***I. bismarckiana* Damman & Sprenger**

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. $2n=20$ (Fig. 1 F). The chromosomes can be divided into two groups, one consisting of four large chromosome pairs and the other of six small, the latter gradually decreasing in length. Satellites are found on two pairs of the "small" group.

***I. hermona* Dinsmore**

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. $2n=20$ (Fig. 1 G). As in *I. bismarckiana*, the chromosomes can be divided into two groups of four and six pairs, respectively. Satellites are found on two pairs of the "small" group.

Previous report. $2n=20$ (Simonet 1952).

***I. antilibanotica* Dinsmore**

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. $2n=20$ (Fig. 1 H). The chromosome pairs constitute the usual two length-groups but because of the relatively small difference between pairs IV and V there is no sharp discontinuity between the two groups. Satellites are found on one pair in the "small" group.

Previous report. $2n=20$ (Simonet 1952).

***I. damascena* Mouterde**

Material. Syria, Jabl Qasyoun (type locality), A. Khateeb 27-75 (BEI).

Chromosome number and karyotype. $2n=20$ (Fig. 1 I). Two length-groups which are not very well defined, just as in *I. libanotica*. Satellites are found on one pair in the "small" group.

***I. susiana* Linnaeus**

Material. The material was obtained from Mr W. P. van Eeden, Noodwijk, Holland.

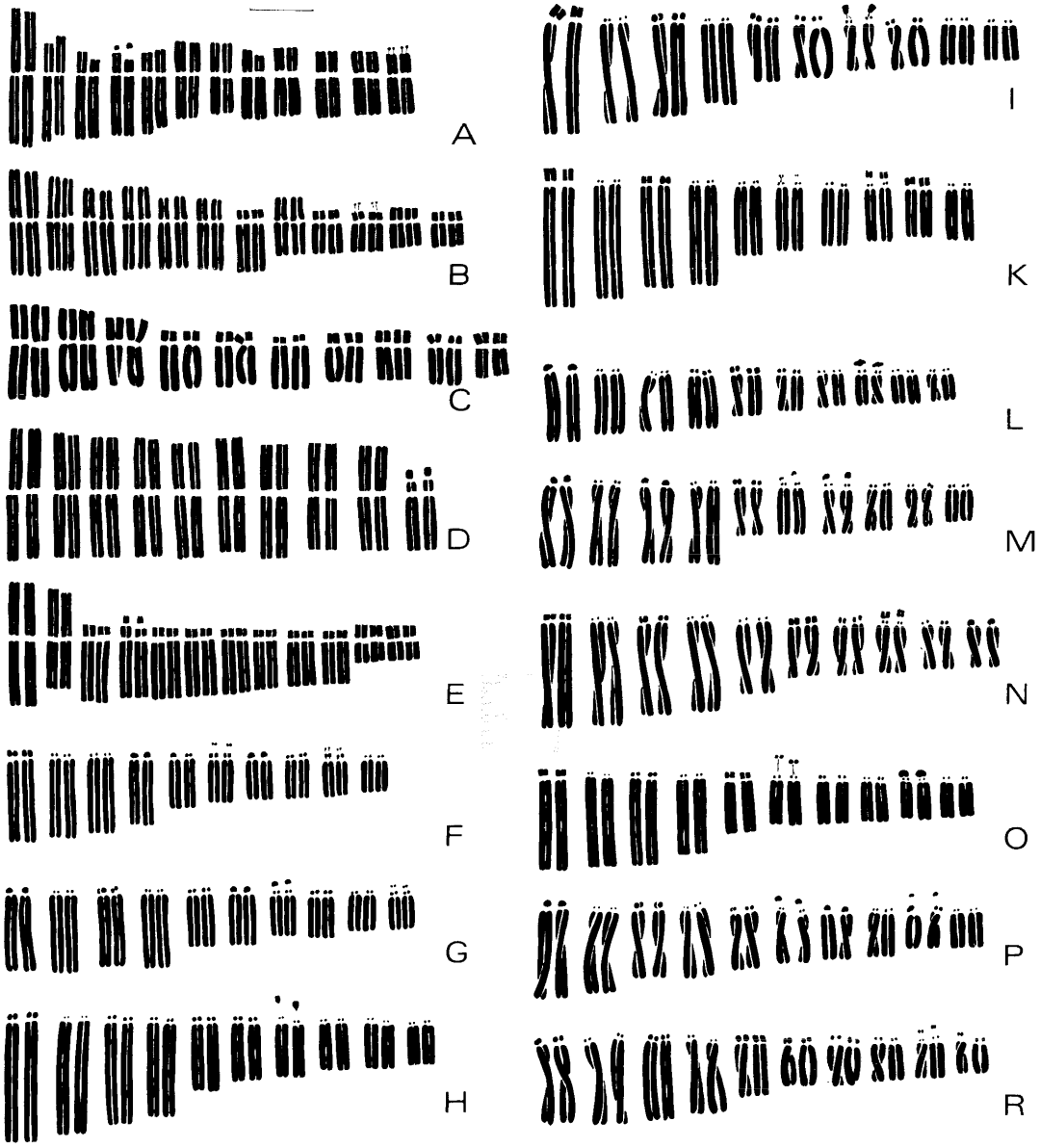


Fig. 1. Karyotypes of *Iris*. - A: *I. melanosticta*. - B: *I. aucheri*. - C: *I. nusairiensis*. - D: *I. postii*. - E: *I. palaestina*. - F: *I. bismarckiana*. - G: *I. hermona*. - H: *I. antilibanotica*. - I: *I. damascena*. - K: *I. susiana*. - L: *I. samariae*. - M: *I. haynei*. - N: *I. petrana*. - O: *I. nigricans*. - P: *I. paradoxa*. - R: *I. sp.* - Scale 5 μ m.

Chromosome number and karyotype. $2n=20, 21$ (Fig. 1 K). Two well defined length-groups as in *I. bismarckiana*. Satellites are found on two pairs of the "small" group.

In some of the material investigated, an additional chromosome was found, with the same size and morphology as the members of the smallest pair. This taxon has been under cultivation for a long time and its origin is controversial. The karyotype, however, is of the Sofarana type of Weymouth & Chaudhary (1974). van Eeden, who supplied the material, comments that "it seems *Iris susiana* (material) is all imported (into Holland) from Turkey, each year."

Previous reports. $2n=20$ (Simonet 1932, Mitra 1956).

I. samariae Dinsmore

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. $2n=20$ (Fig. 1 L). The chromosome pairs do not fall into different length-groups, instead there is a continuous decrease in size. Prominent satellites are found on one of the smaller pairs.

Previous report. $2n=20$ (Simonet 1952).

I. haynei (Baker) Mallett

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. $2n=20$ (Fig. 1 M). Two distinct length-groups as in *I. bismarckiana*. Satellites are found on two pairs of the "small" group.

I. petrana Dinsmore

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. $2n=20$ (Fig. 1 N). As in *I. libanotica* the dividing line between the two length-groups is not very sharp. Satellites are found on one pair of the "small" group.

I. nigricans Dinsmore

Material. Jordan, between Karak and Madaba, 1975, R. Avolizzi (BEI).

Chromosome number and karyotype. $2n=20$ (Fig. 1 O). Two not very well defined length-groups as in *I. libanotica*. Satellites are found on two pairs of the "small" group.

Previous report. $2n=20$ (Simonet 1952).

I. paradoxa Steven

Material. The material was obtained from the Aril Society International.

Chromosome number and karyotype. $2n=20$ (Fig. 1 P). Two not very well defined length-groups as in *I. libanotica*. Satellites are found on two pairs of the "small" group.

Previous reports. $2n=20$ (Delaunay 1928, Simonet 1934).

Iris sp.

Iris heylandiana in Chaudhary et al. (1976).

Material. The material was obtained from the Aril Society International, collected by Dr Barkouda of Damascus University near Ras-al-Ain in NE Syria.

Chromosome number and karyotype. $2n=20$ (Fig. 1 R). Two not very well defined length-groups as in *I. libanotica*. Satellites are found on one pair of the "small" group.

Comments

The karyotypes presented in this report show that the variation in chromosome morphology of the species in subgenus *Scorpiris* is rather large as compared to the variation of the species in subgenus *Susiana*. In the former subgenus the karyotypes vary from predominantly symmetrical to predominantly asymmetrical while *Susiana* is characterized by an asymmetrical karyotype.

Acknowledgements. The authors want to express their sincere thanks to the Aril Society International, USA, and particularly its members Mr Herbert McKusick, Mr Clay Osborne and Mr Thomas Wilkes who have helped in the procurement of research material and in arranging grants for the study.

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The *Festuca brachyphylla* group in Greenland

Signe Frederiksen

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The *Festuca brachyphylla* group consists of non-viviparous species especially characterized by very short anthers (less than 1.3 mm). In Greenland three species are recognized within this group, viz. *F. brachyphylla* Schult. & Schult. ($2n=42$), *F. baffinensis* Polun. ($2n=28$), and *F. hyperborea* Holmen ex Frederiksen ($2n=28$). The latter species is validated and typified. The taxonomy and distribution of the species is discussed, and dot maps are presented for Greenland.

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In Greenland all native species of *Festuca* belong to sect. *Ovinae* Fr. The following species have been reported: *F. rubra* L. s.l., *F. vivipara* (L.) Sm., *F. brachyphylla* Schult. & Schult., *F. baffinensis* Polun., and *F. hyperborea* Holmen ex Frederiksen. In this paper the three latter species, all characterized by the very short anthers, are treated.

Collections from BM, C, DAO, GH and O have been studied.

Spikelets were always measured in the middle of the panicle. The measurements refer to the length of the glumes and the three lowest lemmas excluding the arista.

Cross-sections of the leaves were prepared according to Frederiksen (1974).

Only synonyms published on material from Greenland have been listed.

Lists of specimens examined of *F. brachyphylla* var. *groenlandica*, *F. baffinensis*, and *F. hyperborea* will be sent on request.

Festuca brachyphylla Schult. & Schult.

Scholander 1934 p. 69 p.p.; Seidenfaden & Sørensen 1937 p. 92 p.p.; Böcher 1938 p. 210; Sørensen 1943 p. 48; Holmen 1952 p. 28; Jørgensen et al. 1958 p. 29; Raup 1965 p. 16; Böcher et al. 1968 p. 256. – Type: Edwards, Melville Island 1819–20 (BM lectotype, selected here).

F. brevifolia R. Br. non Mühlenberg, nom. illeg. – Lange 1857 p. 115 quoad Vahl, Godthåbs Fj. (Baals

Ravier); Vahl, Upernaviarsuk; non quoad Vahl, Umanak 1836; Rink, Qaersut (Karsuk); Devold & Scholander 1933 p. 138.

F. ovina L. ssp. *brevifolia* Hack. – Ostenfeld & Lundager 1910 p. 15 p.p.

F. ovina L. var. *brevifolia* (R. Br.) S. Wats. – Sørensen 1933 p. 137 p.p.

F. ovina L. var. *alpina* (Gaud.) Koch f. *subspicata* Lange 1887 p. 302. – Type: Warming & Holm, Ikertôq, 13.VII. 1884; Warming & Holm, Kangerdluarssuk tugdleq, 5.VIII. 1884 (C syntypes).

F. ovina L. var. *borealis* Lange 1880; basionym *F. brevifolia* R. Br. non Mühlenberg.

F. ovina L. var. *alpina* (Gaud.) Koch sensu Lange 1880 p. 179 non (Gaud.) Koch.

F. ovina L. var. *tenuifolia* (Sibth.) Sm. sensu Lange 1880 p. 179 non (Sibth.) Sm.

Until 1940, when *F. baffinensis* was established by Polunin, the taxa now known as *F. brachyphylla*, *F. baffinensis*, and *F. hyperborea* were treated as one species only. This was first known as *F. brevifolia* R. Br. (Brown 1823) but as that name turned out to be a later homonym for *F. brevifolia* Mühlenberg 1817, it was changed by Schultes & Schultes, who referred to the description of Brown (Schultes & Schultes 1827). The types of *F. brevifolia* R. Br. and *F. brachyphylla* Schult. & Schult. are consequently identical. It was collected on Melville Island during Captain Parry's first voyage in 1819–20; at least two specimens were collected,

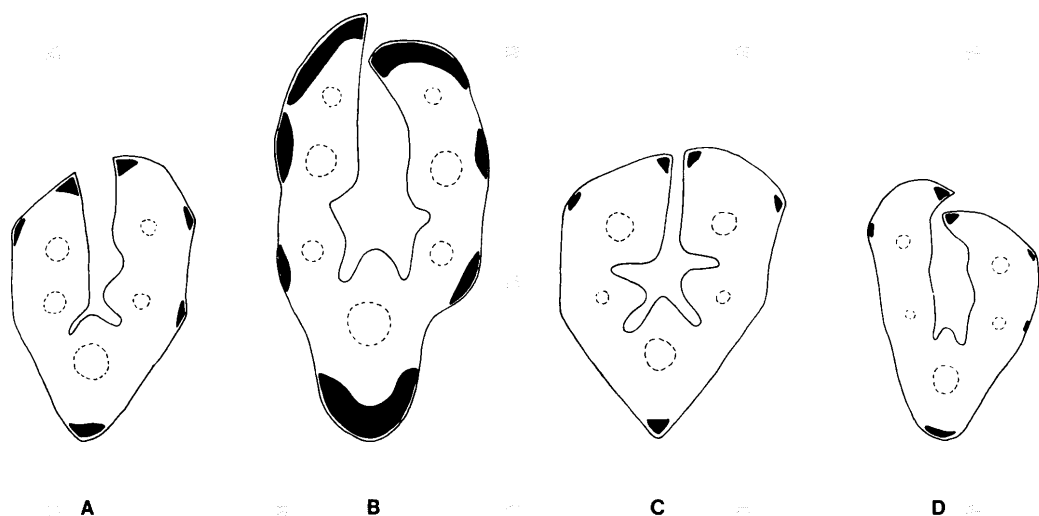


Fig. 1. Cross-sections of leaves, mechanical tissue black. – A: *F. brachyphylla* var. *brachyphylla*. – B: *F. brachyphylla* var. *groenlandica*. – C: *F. baffinensis*. – D: *F. hyperborea*. – $\times 60$.

one by Ross and one by Edwards, and both were later studied by Brown. In the opinion of Schultes & Schultes the Ross collection hardly agreed with Brown's description, as the basal leaves were smaller, and the sheath of the upper culm leaf was comparatively long (Schultes & Schultes 1827). It is thus in agreement with Schultes & Schultes to choose the other collection, that of Edwards, as the lectotype of *F. brachyphylla*. The collection of Ross belongs to *F. hyperborea*, described below. However, it is a poorly developed specimen with an exceptionally short culm.

In the Arctic area there is some variation within *F. brachyphylla*, but apparently one chromosome number only, viz. $2n=42$ (Hedberg 1967, Holmen 1952, 1964, Johnson & Packer 1968, Jørgensen et al. 1958, Mosquin & Hayley 1966, Packer & McPherson 1974, Žukova 1965 a, 1965 b, Žukova & Tichonova 1973, Žukova et al. 1973, Frederiksen unpubl.). The few counts on $2n=28$ reported for *F. brachyphylla*, are most likely to be referred to material of *F. hyperborea* or *F. baffinensis* (Flovik 1938, Mosquin & Hayley 1966, Žukova 1965 a). The specimen (M & M-6458) cited by Mosquin & Hayley (1966), has been determined by me as *F. hyperborea*.

F. brachyphylla normally has a very weak mechanical tissue in the basal leaves (Fig. 1 A), but in the southern parts of Greenland a morphologically not quite distinct form appears, characteristically with strongly developed mechanical tissue; this form is quite different from var. *groenlandica* discussed below.

Outside the Arctic, in high-alpine areas in Colorado and neighbouring states, there are forms of *F. brachyphylla* with smaller spikelets and a very slender habit. In such plants $2n=28$ has been counted (Holmen 1964, Mosquin & Hayley 1966).

The distribution of *F. brachyphylla* is circum-polar. On the American continent it extends as far as Colorado, following the Rocky Mountains. In the Flora Arctica URSS (Tolmačev 1964) *F. brachyphylla* also comprises *F. baffinensis* and *F. hyperborea*; I have only seen *F. brachyphylla* s.str. from Novaja Zemlja, but it has been reported from several places in the Sovjet Union (Žukova & Petrovskij 1972, Žukova & Tichonova 1973, Žukova et al. 1973). In Greenland it is widespread, though apparently rare in the northern and south-eastern parts (Fig. 2).

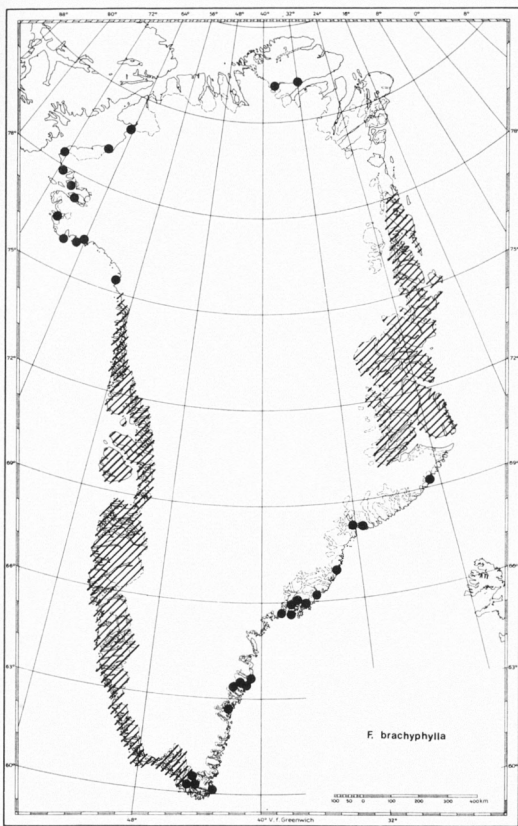


Fig. 2. Known distribution of *F. brachyphylla* in Greenland.

***Festuca brachyphylla* var. *groenlandica* Schol.**

Scholander 1934 p. 69; Böcher 1938 p. 210; Böcher et al. 1968 p. 258. – Type: Devold & Scholander, Greenland, Eqalungmiut (Dr. Maries Dal), 24.VII. 1932 (C holotype); 12.VIII. 1932 (O syntype); Devold & Scholander, Greenland, Finnsbu 24.VII. 1932 (O syntype); 14.VIII. 1932 (C, O syntypes).

As stated by Scholander (1934), this variety deviates in several characters from var. *brachyphylla* (Table 1). The most obvious are the very dense panicle, with smaller and broader spikelets, and the shorter, somewhat curved arista (Fig. 3). The mechanical tissue of the basal leaves is well developed in var. *groenlandica* (Fig. 1 B). The taxonomical value of this character has been judged very differently; among others Hackel (1882), Saint-Yves (1925) and Komarov (1934) regarded it as being a very



Fig. 3. Spikelets. – A: *F. brachyphylla* var. *brachyphylla*. – B: *F. brachyphylla* var. *groenlandica*. – Both Astrup et al. GBU 865, Skjoldungen Distr., Eqalungmiut, 1970 (C). – ×8.

important character. Studies by Bidault (1963) seem to show that it is to some extent independent of the environment, whereas Kjellquist (1961) came to the conclusion that it could not be used within his material of *F. rubra*. In my opinion the character is important but has to be used with great care. In var. *groenlandica* nearly all specimens studied show a distinctly stronger development of the mechanical tissue than is normally seen in var. *brachyphylla*. Nevertheless, as there seem to be some transitions, and since the distribution of var. *groenlandica* lies within that of var. *brachyphylla*, it is reasonable to keep the taxon on varietal level.

F. brachyphylla var. *groenlandica* seems to be restricted to Greenland, where it is found especially on the east coast (Fig. 4).

***Festuca baffinensis* Polun.**

Holmen 1952 p. 26; Holmen 1957 p. 120; Jørgensen et al. 1958 p. 29; Raup 1965 p. 17; Fredskild 1966 p. 20; Böcher et al. 1968 p. 256. – Type: Polunin 706, Baffin Island, 12.IX. 1934 (GH holotype not seen, disappeared? CAN, BM isotypes).

F. brachyphylla Schult. & Schult. sensu Scholander 1934 p. 69 p.p.

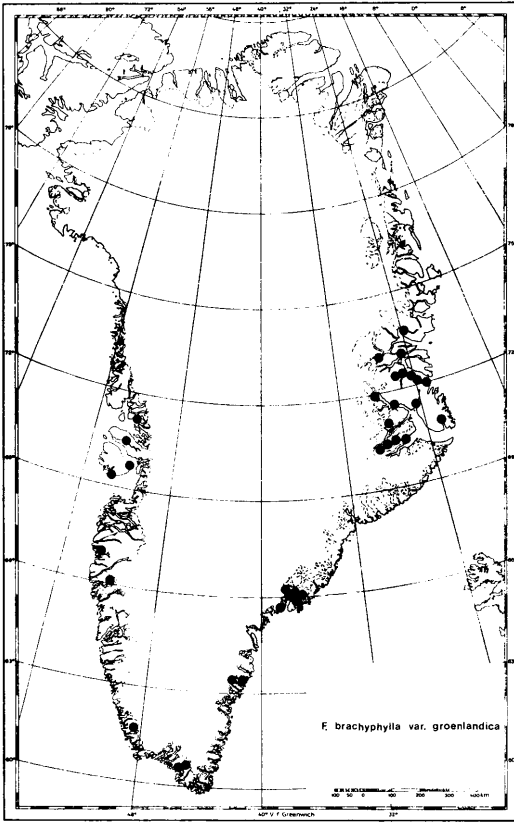


Fig. 4. Known distribution of *F. brachyphylla* var. *groenlandica*.

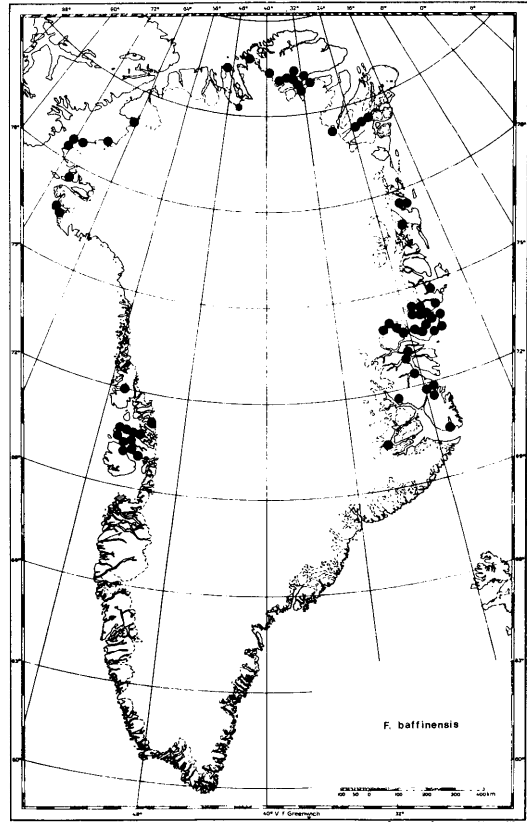


Fig. 5. Known distribution of *F. baffinensis* in Greenland.

F. brevifolia R. Br. non Mühlenberg, nom. illeg. sensu Lange 1857 p. 115 quoad Vahl, Umanak 1836; Rink, Qaersut (Karsuk); non quoad Vahl, Godthåbs Fj. (Baals Revier); Vahl, Upernaviarsuk.

F. ovina L. ssp. *brevifolia* Hack. sensu Ostenfeld & Lundager 1910 p. 15 p.p.

F. ovina L. var. *brevifolia* (R. Br.) S. Wats. – Ostenfeld 1923 p. 230 quoad Th. Wulff, Gunnar Anderson Dal, 11.VII. 1917; Th. Wulff, I. P. Koch Fj., 20.VI. 1917; Sørensen 1933 p. 137 p.p.

F. ovina L. var. *borealis* Lange 1880 p. 179 quoad Rink, Niaqornat (Niakornak); Rink, Qaersut (Karsuk); Vahl, Umanak, 1836; Copeland & Pansch, Jackson Isl.; Lange 1871 Tab. 2706.

Lange regarded *F. brevifolia* R. Br. as a synonym to *F. ovina* L. var. *borealis* but added that he had never seen the specimens of Brown (Lange 1871); nearly all the specimens determined by him as *F. brevifolia* (1857) or *F.*

ovina var. *borealis* (1880) belong in fact to *F. baffinensis*.

F. baffinensis is normally very easy to recognize because of its hairy upper culm and its short, broad panicle of glossy spikelets (Table 1). A few specimens have been seen in which the culm is very sparsely hairy, and these may form transitions between *F. baffinensis* and *F. brachyphylla* or *F. hyperborea*. As in *F. brachyphylla* the mechanical tissue in the basal leaves is very poorly developed (Fig. 1 C).

The distribution seems to be circumpolar, arctic-alpine. In America it is found as far south in the Rocky Mountains as Colorado (Weber 1961). In Eurasia the distribution is not known in detail but I have seen specimens from Svalbard and Novaja Zemlja, and it has been

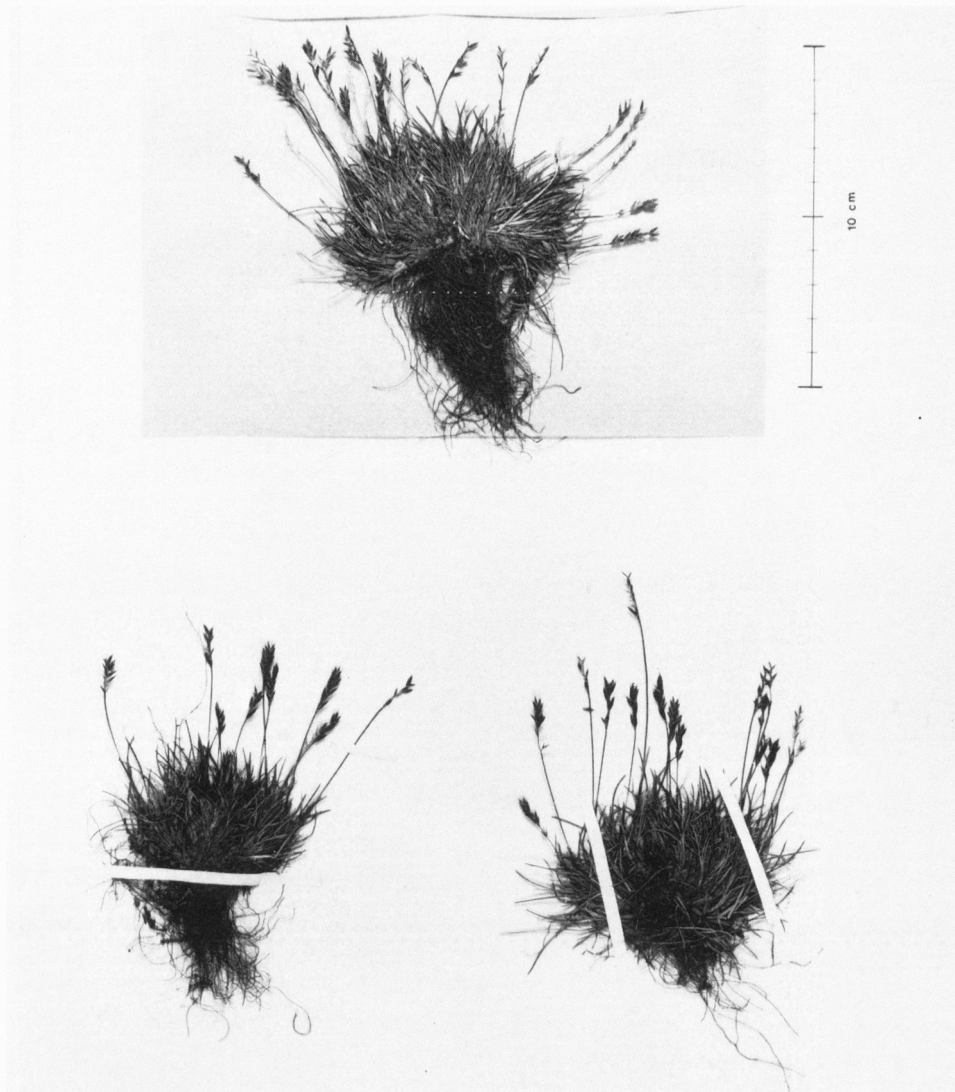


Fig. 6. Type specimen of *F. hyperborea*.

mentioned from the island of Wrangel (Žukova 1965 b), and the province of Chukotsk (Žukova & Tichonova 1973). In Greenland it is restricted to the northern areas with relatively basic rocks (Fig. 5).

***Festuca hyperborea* Holmen ex Frederiksen**

Holmen 1952 p. 28; Holmen 1957 p. 120; Jørgensen et al. 1958 p. 29; Fredskild 1966 p. 20; Böcher et al.

1968 p. 258. – *Type*: Holmen 8078, Greenland, Jørgen Brøndlund Fj., 28.VII. 1950 (C holotype).

F. brachyphylla Schult. & Schult. sensu Scholander 1934 p. 69 p.p.

F. ovina L. var. *brevifolia* (R. Br.) S. Wats. – Ostenfeld 1923 p. 230 quoad Th. Wulff, Black Cape, 4.VI. 1917; Th. Wulff, I. P. Koch Fj., 20.VI. 1917; Th. Wulff, Cape Salor, 29.VI. 1917; Th. Wulff, John Murray Isl., 3.VII. 1917; Th. Wulff, Sommerdal, 14.VII. 1917; Th. Wulff, Dragon Point, 19.VII. 1917; non quoad Th. Wulff, Gunnar Anderson Dal, 11.VII. 1917; Th. Wulff, I. P. Koch Fj., 20.VI. 1917.



Fig. 7. *F. hyperborea*. Detail of the panicle of the type specimen. $\times 2$.

F. ovina L. var. *supina* (Schur) Hack. sensu Sørensen 1933 p. 137 non (Schur) Hack.; Böcher 1938 p. 211.

F. hyperborea was recognized by Holmen (1952), but the name was never validly published; nevertheless the species has been accepted by most botanists working on the Arctic flora. The following description of *F. hyperborea* is based on the type pointed out by Holmen (1952), and the material in C determined by him. Holmen (1952) supposed that *F. hyperborea* is identical to *F. ovina* L. var. *supina* (Schur) Hack. sensu Sørensen (1933), which is undoubtedly correct. In fact the Arctic collections of Sørensen have nothing to do with *F. ovina* var. *supina*, which is known to occur in Central Europe (Schur 1866), where *F. brachyphylla* and its allies have never been found.

Gramen perenne, laxe caespitosum, glaucum, pruinatum, opacum. Culmi 5–15 cm alti, omnes vel saltem

exteriores caespitum majorum geniculati vel procumbentes. Folia basalia 2–5 cm longa, curva, breviter acuta, sclerenchymate satis debile. Foliolum superius culmi lamina brevi, raro plus quam 5 mm longa, saepe omnino deficiente, vagina paulum inflata. Panicle brevis vix ultra 20 mm longus, subfusiformi-ovoides, plerumque primarios solum ramos formans, e paucis spiculis compositus. Lemma lanceolato-ovale, violaceum, ad apicem versus scaberulum. Arista brevis, saepe curva, subterminalis. Anthera 0.4–0.7 mm longa. Numerus chromosomatum $2n = 28$.

Illustrations: Figs. 6, 7.

Perennial grass. Loosely tufted, at least the outer culms of large tufts geniculate or prostrate. The plant glaucous, pruinose, opaque. Culms rarely exceeding 15 cm. Basal leaves rarely more than 5 cm, recurved, quickly tapering. Mechanical tissue in the leaf blade very weak (Fig. 1 D). Upper culm leaf with or without a very short blade (5 mm), the sheath somewhat inflated. Panicle short, rarely exceeding 20 mm, normally simply branched, with few spikelets. When measured after the method given in the introduction, spikelets are 4.4–6.8 mm; third lemma in these spikelets 3.0–4.4 mm, lanceolate-ovate, purple, scabrous towards the tip. Arista short, on the third lemma 1.4–2.0 mm, often curved or geniculate, subterminal. Anthers 0.4–0.7(–0.8) mm. Chromosome number $2n = 28$ (Holmen 1952).

As mentioned by Holmen (1952, 1957), *F. hyperborea* is very closely related to *F. brachyphylla*, while *F. baffinensis* is more isolated. There are some intermediates between *F. brachyphylla* and *F. hyperborea*, but nevertheless it seems reasonable to keep them as separate species, partly because of the morphological differences and the difference in chromosome number, and partly because of differences in distribution.

The difference in chromosome numbers between *F. brachyphylla* s.str. and *F. hyperborea* must impose a strong reproductive isolation, and there is nothing to suggest that hybridization takes place. The tetraploid specimens of *F. brachyphylla* reported from Colorado (cf. above) obviously have nothing to do with *F. hyperborea*.

The distribution is characteristically high-arctic, and the species seems to be restricted to areas with relatively basic rocks. The distribution outside Greenland is not known in detail, but the species has been mentioned from Svalbard (Rønning 1961), Iceland (Löve & Löve

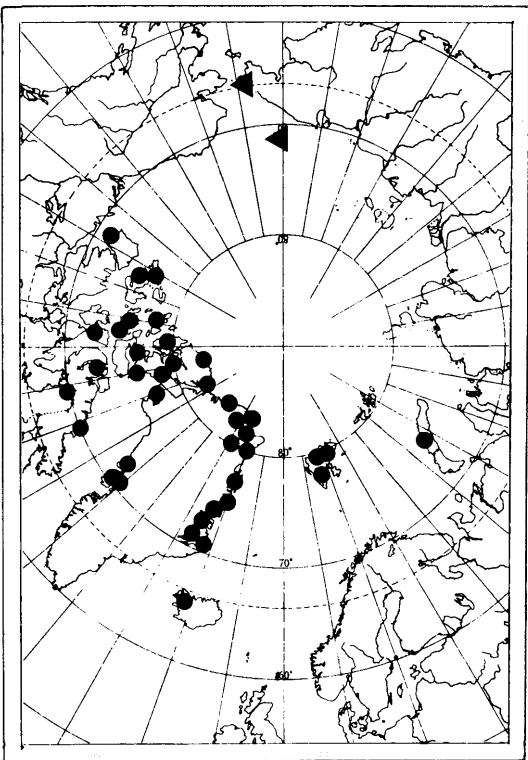


Fig. 8. Known distribution of *F. hyperborea*. ● specimens examined, ▲ references from the literature.

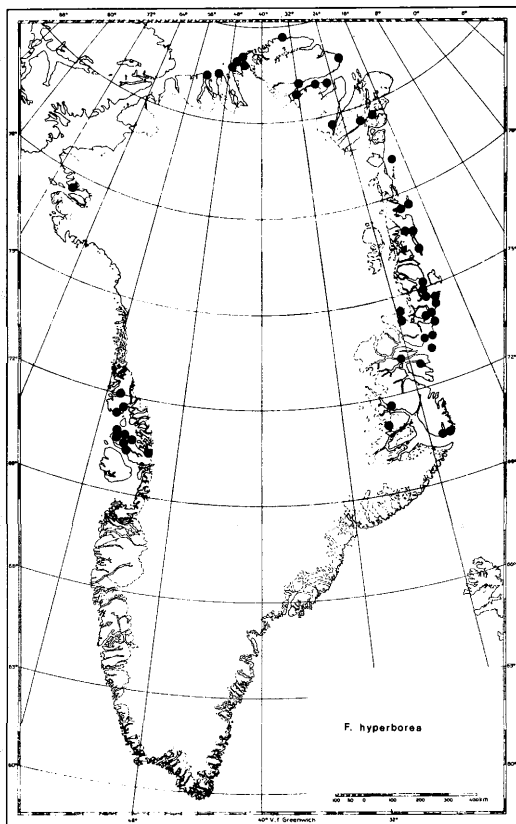


Fig. 9. Known distribution of *F. hyperborea* in Greenland.

1956), arctic America (Hedberg 1967), and from the province of Chukotsk and the island of Wrangel in USSR (Žukova & Petrovskij 1972, Žukova & Tichonova 1973, Žukova et al. 1973). It is not known from the American mainland and only from a few places on the Eurasian mainland (Fig. 8). In Greenland it has nearly the same distribution as *F. baffinensis*, and is thus restricted to areas with basic rocks (Fig. 9).

Final remarks

In addition to the species found in Greenland there seems to be only one more North American species in the group treated here. This is *F. saximontana* Rydb. from the northern parts of America, which is similar to *F. brachyphylla* and like the latter has $2n=42$ (Bowden 1960). *F. saximontana* differs from *F. brachyphylla*, for instance, by having strong mechan-

ical tissue (Saint-Yves 1925). I have not studied the type specimen of Rydberg but neither the description (Rydberg 1909), nor the specimens in C, suggest that *F. saximontana* should be conspecific to any of the taxa treated here. Contrary to *F. brachyphylla* var. *groenlandica* it has an open panicle with fewer and larger spikelets, and a long and erect arista.

The viviparous taxa of *Festuca* occurring in the Arctic have sometimes been regarded as being closely related to the group treated here (cf. Ostenfeld & Lundager 1910, Ostenfeld 1923, Sørensen 1933, Holmen 1964). However, the former always have higher chromosome numbers, viz. $2n=49$, 56, and 63 (Jørgensen et al. 1958, Holmen 1964, Johnson et al. 1968, Frederiksen unpubl.). Normally they have no flowers, but when anthers are occasionally

Table 1. Summary of characters in the species of the *Festuca brachyphylla* group in Greenland.

<i>F. brachyphylla</i> var. <i>brachyphylla</i>	<i>F. brachyphylla</i> var. <i>groenlandica</i>	<i>F. baffinensis</i>	<i>F. hyperborea</i>
Densely tufted	Densely tufted	Densely tufted	Loosely tufted
Plant normally fresh green, more or less shining	Plant fresh green to glaucous	Plant fresh green, normally shining	Plant glaucous, pruinose, often opaque
Basal leaves 5–10 cm, straight or almost so, long tapering	Basal leaves 6–15 cm, straight, long tapering	Basal leaves 3–10(–14) cm, straight or almost so, long tapering	Basal leaves 2–5 cm, recurved, short tapering
Mechanical tissue in basal leaves normally weak	Mechanical tissue in basal leaves well developed	Mechanical tissue in basal leaves weak	Mechanical tissue in basal leaves weak
Culm 10–30 cm, glabrous or almost so	Culm 14–37 cm, glabrous or almost so	Culm 5–20(–30) cm, in its upper half densely tomentose of short curved hairs	Culm 5–15 cm, glabrous or almost so
Culms erect	Culms erect	Culms erect	Culms often prostrate or geniculate
Upper culm leaf normally about 10 mm. Sheaths not inflated	Upper culm leaf with a relatively long blade (10–50 mm). Sheaths not inflated	Upper culm leaf with a blade normally exceeding 10 mm. Sheaths inflated	Upper culm leaf with an extremely short blade 0–5(–15) mm. Sheaths inflated
Panicle with few or more spikelets, (15–)30–50 mm, often branched, open, lanceolate, green or purple	Panicle with many spikelets, 20–50 mm, always branched, lanceolate, green or purple	Panicle normally with few spikelets, dense, 15–35 mm, often branched, broadly ovate, dark purple	Panicle with few spikelets, seldom exceeding 20 mm, normally simple, lanceolate-ovate, normally purple
Spikelets 5.0–6.6 mm	Spikelets 4.2–5.6 mm	Spikelets 6.2–7.5 mm	Spikelets 4.4–6.8 mm
Lemma almost glabrous or scabrous towards the tip. Third lemma 3.3–4.6 mm	Lemma almost glabrous or scabrous towards the tip. Third lemma 2.9–3.4(–3.7) mm	Lemma almost glabrous, glossy. Third lemma 3.7–5.0 mm	Lemma scabrous towards the tip. Third lemma 3.0–4.4 mm
4–8 flowers in the spikelets	3–5 flowers in the spikelets	3–6 flowers in the spikelets	3–6 flowers in the spikelets
Arista erect or almost so, terminal. Arista on the third lemma (1.2–)2.1–2.5 mm	Arista more or less curved. Arista on the third lemma (0–)0.8–2.1 mm	Arista erect, terminal. Arista on the third lemma 1.7–3.3 mm	Arista curved or geniculate, subterminal. Arista on the third lemma 1.4–2.0 mm
Anther (0.6–)0.7–1.1 mm	Anther 0.8–1.3 mm	Anther 0.4–0.7(–0.8) mm	Anther 0.4–0.7(–0.8) mm
2n = 42	2n unknown	2n = 28	2n = 28

developed these are 1.6–2.1 mm long, i.e. distinctly longer than in *F. brachyphylla* and its allies (Table 1).

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A review of the Andean genus *Cacosmia* H.B.K. (Compositae–Liabeae)

Bertil Nordenstam

Nordenstam, B. 1977 09 15: A review of the Andean genus *Cacosmia* H.B.K. (Compositae–Liabeae). *Bot. Notiser* 130: 279–286. Stockholm. ISSN 0006-8195.

The small genus *Cacosmia* H.B.K. is restricted to the Andes of Ecuador and Peru. Three species are recognized, one of which is described as new, viz. *C. harlingii* B. Nord. In the type species, *C. rugosa* H.B.K., three varieties are distinguished.

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Cacosmia H.B.K. was established in 1818 as a monotypic genus of the Heliantheae (Humboldt, Bonpland & Kunth 1820; text available in 1818). Cassini (1828, 1830) more aptly associated the genus with *Liabum* and its allies in the subtribe “Liabeae” of the Vernonieae. Lessing (1831, 1832) and De Candolle (1836) treated *Cacosmia* in the same taxonomic context. The latter also simultaneously described *Clairvillea quinquenervia* DC. as a new monotypic genus of the subtribe “Flaverieae” (= Flaveriinae) of the Senecioneae. De Candolle soon realized that his *Clairvillea* was merely a synonym of *Cacosmia* (De Candolle 1838 p. 265). He noted, however, that *Clairvillea quinquenervia* differed somewhat from *Cacosmia rugosa*, mainly in pubescence, and he added, “An var.? An species propria?” (1838 p. 266). Steudel (1840) formally transferred De Candolle’s species to *Cacosmia*. The two taxa are now treated as varieties of *C. rugosa*.

Bentham (in Bentham & Hooker 1873) violated Cassini’s natural arrangement by removing the Liabeae from the Vernonieae to the Senecioneae, except for *Cacosmia*, which he assigned a position in the heterogeneous tribe Helenieae. He admitted, however, that it was “somewhat anomalous” there (Bentham 1873 p. 381). Hoffmann (1890) followed Bentham, and the systematic position of *Cacosmia*

remained obscure for some time. Cabrera (1954) re-established the connection to the *Liabum* group, and further evidence to the same effect was presented by Skvarla & Turner (1966 a, b). The Liabeae are now recognized as a separate tribe closest to the Vernonieae (Robinson & Brettell 1974, Nordenstam in print). The closest relative of *Cacosmia* appears to be the recently described genus *Ferreyranthus* Robinson & Brettell, which also has a similar distribution.

There is a range of similarities between *Cacosmia* and *Ferreyranthus* extending from gross morphological features like habit, leaf shape and tomentum, to micromorphological characters like stylar pubescence and achenial wall crystals. The latter are elongate and rod-shaped in contrast to the short prismatic crystals of, e.g., the genus *Liabum* sensu stricto (Fig. 1). *Ferreyranthus* is significantly distinct, however, in a number of important characters, e.g. the setose and pappose achenes.

Until recently *Cacosmia* was generally regarded as monotypic, although considerable variability was noted by several authors, and Bentham (in Bentham & Hooker 1873 p. 396) wrote, “Species 2 v. 3”. The polymorphism first received taxonomic recognition with Hieronymus (1901), who distinguished three varieties. A study of the genus was recently taken

up independently by the present author and Robinson, who published a new species and a new variety (Robinson 1976).

The present revision is based on herbarium material in BM, GB, K, P, S and US (abbreviations according to Holmgren & Keuken 1974). A third species is added, and the genus now comprises altogether five taxa.

Cacosmia H.B.K.

Humboldt, Bonpland & Kunth 1820 p. 289; Kunth 1823 p. 509; Sprengel 1826 p. 588; Lessing 1829 p. 338, 1831 p. 705, 1832 p. 152; De Candolle 1836 p. 98; Jameson 1865 p. 72; Bentham in Bentham & Hooker 1873 p. 396; Hoffmann 1890 p. 252.

Clairvillea De Candolle 1836 p. 636, 1838 p. 265.

Erect branching shrubs. *Stems* and branches laxly lanate and/or hirsute with articulated hairs. *Leaves* opposite, shortly petiolate or subsessile with stem-sheathing connate 'semi-stipules', flat, ovate-lanceolate; upper surface bullate-rugose, green, glabrous or setose; lower surface densely tomentose. *Capitula* several-many in terminal corymbose-paniculate inflorescences, heterogamous, radiate. *Involucre* narrowly oblong-ovoid. Involucral bracts ca 20-25, imbricated in 5-6 series, ovate-lanceolate, somewhat coriaceous, green, brown or purplish,

obtuse (outer) to acute (inner), glandular or subglabrous. Receptacle flat-convex, alveolate. *Corolla glands* stipitate-subsessile, with a stalk of two cell-rows and a larger, thick-walled terminal cell. *Corolla hairs*, if present, thin, flexuous, consisting of a single cell-row. *Ray-florets* usually 5, female, ligulate, yellow or greenish yellow to dirty white or orange-coloured. *Style* filiform, bilobed, hispidulous from about the middle or subglabrous, basally glabrous. *Disc-florets* usually 6, perfect. Corolla funnel-shaped, 5-lobed, yellow to greenish white. *Anthers* dorsifixed (filament inserted slightly below the middle of the theca), basally obtuse-subacute, ecaudate; apical appendage ovate, obtuse. Endothecial cells shortly oblong or almost isodiametric, with few thickenings mainly on horizontal walls. *Style* filiform-cylindric with a dilated base on a short nectary, densely hispidulous in the distal half or more, bilobed, with continuous stigmatic surfaces on the inside of the branches. *Achenes* oblong, somewhat compressed or subtriquetrous, subhomomorphic (those of the disc less compressed and more 4-5-angular), glabrous, faintly ribbed, 8-10-veined, with numerous elongate prismatic wall crystals. *Pappus* 0.

Species 3, Ecuador, Peru. Type: *C. rugosa* H.B.K.

Key to the species and varieties of *Cacosmia*

1. Involucre predominantly green or yellowish. Leaf-margins distinctly denticulate (1. *C. rugosa*) 2
- Involucre predominantly brown or purple. Leaf-margins indistinctly denticulate 4
2. Upper leaf surface \pm glabrous (softly pubescent along veins, rarely sparsely setose) 3
- Upper leaf surface evenly and \pm densely setose 1 c. *C. rugosa* var. *kingii*
3. Stem pubescence mainly hirsute with numerous articulated hairs 1 a. *C. rugosa* var. *rugosa*
- Stem pubescence white-lanate-floccose without coarser articulated hairs 1 b. *C. rugosa* var. *nivea*
4. Involucre \pm purple, 5-6 mm long. Rays orange-coloured. Corollas without long hairs 2. *C. harlingii*
- Involucre dark brown-purplish brown, 7-8 mm long. Rays yellow. Disc corollas villous with conspicuous long hairs 3. *C. hieronymi*

1. *C. rugosa* H.B.K.

Humboldt, Bonpland & Kunth 1820 p. 290. - *Orig. coll.*: Humboldt & Bonpland no. 3312, Ecuador, Saraguro (P holotype, isotypes in B: herb. Willdenow and P: ex herb. Bonpland et ex herb. Schultz Bip.).

Clairvillea quinquenervia De Candolle 1836 p. 636. - *Cacosmia quinquenervia* (DC.) Steudel 1840 p. 377. - *Orig. coll.*: Dombey s.n., Peru (P holotype, prob. isotypes in P: Dombey 255, ex herb. Schultz Bip. et ex herb. Drake).

According to information kindly submitted by Dr A. Lourteig, the number 3312 in the journal of Hum-

boldt and Bonpland has a description written by Bonpland and the name "*Cacosmia rugosa* n. sp." added by Kunth. The matching specimen in the Humboldt and Bonpland herbarium is the holotype, also named by Kunth. I have seen this specimen only in microfiche. There is an isotype in Willdenow's herbarium in B, another in P from Bonpland's herbarium, and in P also a fragment from the Willdenow specimen.

A further specimen in Bonpland's herbarium (P) represents a different collection from Gonzanamá in Ecuador. In the present taxonomy it belongs to var. *nivea* (q.v.).

Erect-ascending shrubs 1-4(-5) m tall. *Stems* white- or grey-lanate and often also hirsute with coarser, distinctly articulated hairs, sometimes glabrescent with age. *Leaves* shortly petiolate or sessile, ovate or narrowly ovate, 1-9 cm long, 0.5-4 cm wide, acute-acuminate, with 3 or 5 main longitudinal veins and a finer reticulate venation pattern; margins laxly serrulate or callos-denticulate; upper side \pm glossy green, setose or subglabrous; lower side densely white- or grey-tomentose. *Capitula* numerous in somewhat lax to fairly compact synflorescences, with rich or golden yellow florets (in one collection said to be greenish white). *Involucre* 5-7 mm long, 2.5-4 mm wide. Involucral bracts pale-dull green, sometimes with darker green or slightly brownish tips or margins; outer phyllaries ovate, obtuse, eglandular; inner phyllaries lanceolate, 5-6 mm long, acute, glandular on the lower half, with somewhat fimbriate-ciliate margins. *Ray-florets* (4-)5. Tube subcylindric, narrowest basally, 2-3.5 mm long, glandular with sessile and stipitate glands. Lamina concave or flat, elliptic-oblong, 3-7 mm long, 2-4 mm wide, 4-veined, abaxially glandular, apically trifid. *Style* branches subulate-filiform, 2.5-3.5 mm long, with shortly hispidulous outsides. *Achenes* oblong, 1.5-2 mm long, 0.6-0.9 mm wide, somewhat compressed-triangular with distinct lateral ribs and fainter ribs ad- and abaxially, brown. Disc-floret corolla 5-6 mm long, glandular with subsessile and stipitate glands and sometimes also a few (rarely many) apically thinner flexuous hairs; corolla lobes lanceolate, 2-2.5 mm long, acute, becoming rolled back. *Anthers* 2-2.7 mm long incl. appendage; base obtuse-subacute without distinct papillae. *Style* branches 0.5-1.2 mm long, semiterete, obtuse; style narrowly cylindrical, thickest about the middle, densely hispidulous on the distal 1/2 or 2/3. *Achenes* as in ray-florets, but less compressed, somewhat 4- or 5-angled, 4-5-ribbed.

On the basis of stem and leaf pubescence three varieties of *C. rugosa* can be distinguished. They are quite characteristic and easily recognized (cf. the key), and transitional forms seem to be rare. Eglandular corolla hairs may be present in varying quantity, but never as copiously as in *C. hieronymi* (cf. Fig. 2 D, Fig. 3 H, I).

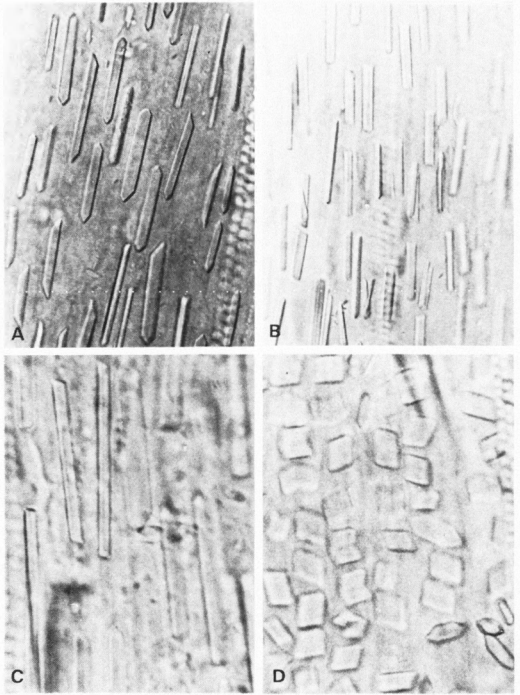


Fig. 1. Achenial wall crystals in the Liabaeae. - A: *Cacosmia harlingii* (Harling 6050). - B: *C. hieronymi* (Asplund 17770). - C: *Ferreyranthus excelsus* (Hutchison & Wright 3854). - D: *Liabum wrightii* (Ekman 9253). - Photomicrographs by the author, $\times c. 500$.

1 a. *C. rugosa* var. *rugosa*

Illustr.: Humboldt, Bonpland & Kunth 1820 Plate 404; Lessing 1829 Plate 2 Figs. 31, 53-56; Hoffmann 1890 Fig. 122 A; Fig. 2 A-D.

Stems densely lanate and hirsute, the interwoven white hairs mixed with coarser, often brown- or purple-articulated hairs. Leaves acute; upper surface glabrous or nearly so, somewhat glossy green; lower surface densely white- or grey-tomentose.

Ecuador. Prov. Imbabura: S of Gonzales, 2700-3000 m, 1952, Fagerlind & Wibom 1293 (S) - Cajas, 3000 m, 1955, Asplund 17052 (S, US). - *Prov. Pichincha*: Prope Pifo, Sodiro (P) - Prope Pifo, 1897, Mille 582 (US). - *Prov. Chimborazo*: Vicinity of Huigra, mostly on the Hacienda de Licay, 1918, Rose 22204 (US) - Cañon of the Río Chanchán, ca 5 km N of Huigra, 5000-6500 ft, 1945, Camp E-3323 (K, P, US), Camp E-3454 (S) - Above Chunchí on road to Hacienda

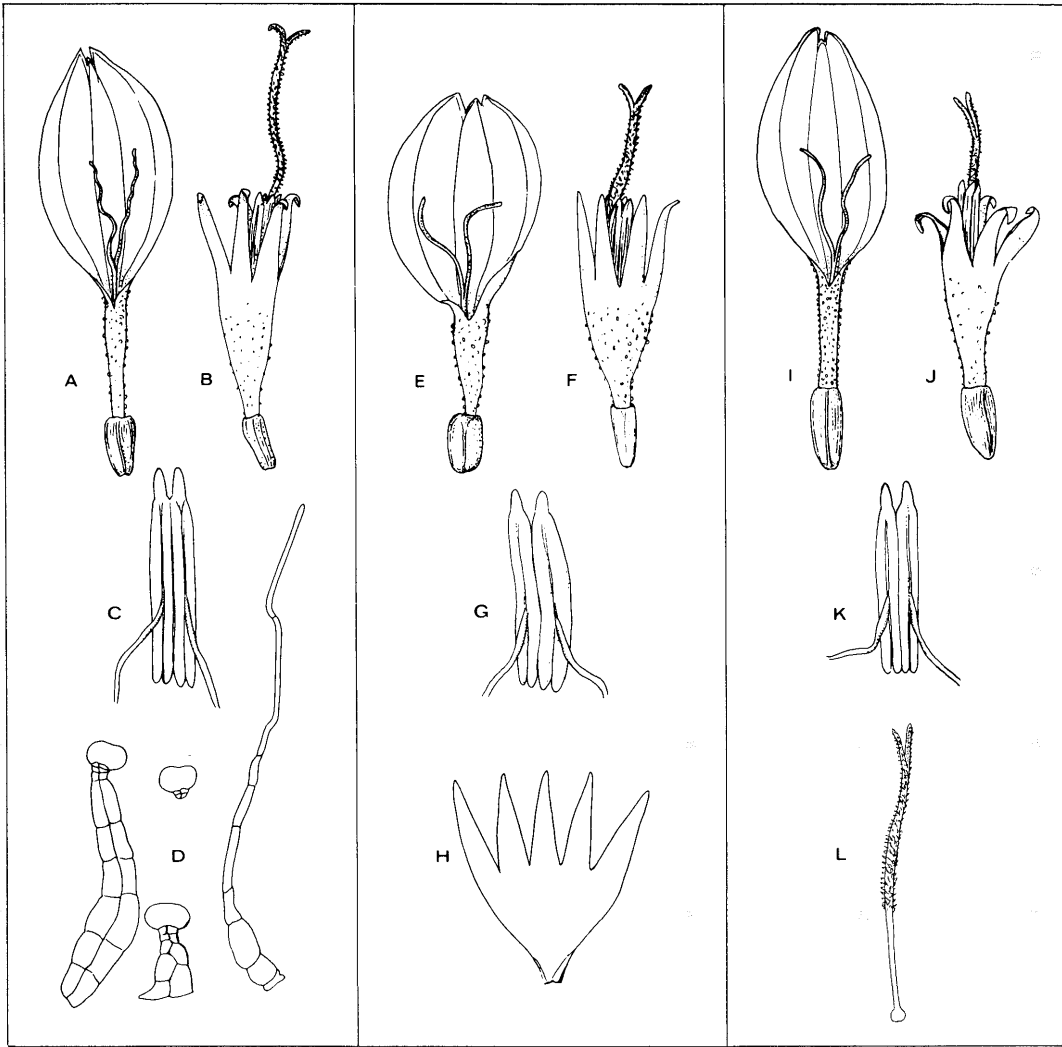


Fig. 2. *Cacosmia rugosa* var. *rugosa* (A-D), var. *nivea* (E-H) and var. *kingii* (I-L). - A, E, I: Ray-floret, $\times 6$. - B, F, J: Disc-floret, $\times 6$. - C, G, K: Anthers, $\times 12$. - D: Corolla glands and hairs, $\times 100$. - H: Corolla of disc-floret, laid out, $\times 6$. - L: Style of disc-floret, $\times 6$. - A-C: Harling & Andersson 14079, D: Hutchison & Wright 5031, E-H: Harling & Andersson 13467, I-L: Asplund 17938. - Del. auct.

Magna, Páramo de Cacheaco, 2500-3000 m, 1959, Barclay & Juajibioy 8305 (US). - *Prov. Cañar*: Between El Tambo and highest point on road from Cañar to Chunchí, 3100 m, 1959, Barclay & Juajibioy 8728 (US). - *Prov. Azuay*: Victoria de Portete, between division of road, SW of Cuenca, and Girón, 2820-2950 m, 1959, Barclay & Juajibioy 8339 (US). - *Prov. Loja*: Saraguro, Humboldt & Bonpland 3312 (P), herb. Willdenow 16749 (B non vidi, P fragment) - Vicinity of Saraguro, 1918, Rose 23135 (US) - Road from Loja to San Lucas, km 25, 2200 m, 1961,

Dodson & Thien 568 (S, US) - Road Loja-Zaruma, near Chinchos, 2400 m, 1974, Harling & Andersson 14079 (GB, S).

Peru. Dep. Piura. Prov. Huancabamba: W slope of Paso de San Cristobal, between Canchaqui and Huancabamba, 2800 m, 1947, Fosberg 27676 (US) - Abra de Porculla, entre Olmos y Jaén, 2000 m, 1959, Ferreyra 13738 (US). - *Dep. and Prov. Cajamarca*: Ca 1 km above and NE San Pablo, 2630 m, 1964, Hutchison & Wright 5031 (US). - *Dep. Libertad. Prov. Otuzco*: Usquil, 3000-3100 m, 1950, Ferreyra

7639 (US). – *Dep. Amazonas. Prov. Bongará*: Yambrasbamba–Pomacocha trail between Yambrasbamba and Yanayacu, 1900–2200 m, 1962, Wurdack 1016 (US).

Sine loco. “Peru”, herb. Ruiz & Pavón (BM), “Huayaquil”, Ruiz & Pavón (BM).

1 b. *C. rugosa* var. *nivea* Hieron.

Hieronymus 1901 p. 619. – *Orig. coll.*: Dombey s.n., Peru (holotype not traced; isotypes in P).

Clairvillea quinquenervia DC. – *Cacosmia quinquenervia* (DC.) Steud. – See under the species.

Illustr.: Fig. 2 E–H.

Stems and branches white-lanate without coarser articulated hairs, glabrescent with age. Leaves acute–acuminate; upper surface subglabrous and \pm glossy green; lower surface densely white-tomentose.

Ecuador. Prov. Loja: Gonzanamá, Bonpland (P) – Summit and upper slopes of Cerro Villonaco, 2600–2750 m, 1974, Harling & Andersson 13467 (GB, S) – Road Loja–Zaruma, between Chinchas and Sambí, 1700–2400 m, 1974, Harling & Andersson 14255 (GB, S).

Peru. Dep. Amazonas: Chachapoyas, 1840, Mathews 3075 (BM, K). – *Dep. Cajamarca. Prov. Chota*: Huambos, 2000 m, 1956, Soukup 4540 (US). – *Dep. Libertad*: Sunchubamba, upper Chicama Valley, 3100 m, 1957, Ellenberg 1765 (US). – *Dep. Huánuco. Prov. Huánuco*: Huánuco, hills, 1863, Pearce 62 (K) – Mito, 3000 m, 1922, Macbride & Featherstone 1386 (US) – Huallaga, by Chaglla (Dep.?) 3000 m, 1909–14, Weberbauer 6708 (US) – Mitotambo, arriba de Mito, 3000–3100 m, 1950, Ferreyra 6668 (US), Ferreyra 6901 (US) – Yanano, 2000 m, 1923, Macbride 4941 (S, US) – *Prov. Pachitea*: Panoa, 2500 m, 1940, Asplund 13576 (S, US).

Sine loco. Peru, herb. Pavón (P), Peru, Pavón, ex herb. Schultz Bip. (P), “Huayaquil”, Ruiz & Pavón (BM) – Peru, Dombey 255 (P), Dombey s.n. (P), Dombey s.n., ex herb. Schultz Bip. (P).

1 c. *C. rugosa* var. *kingii* H. Robinson

Robinson 1976 p. 48. – *Orig. coll.*: Fosberg 27777, Peru, Dep. Cajamarca, Prov. Jaén, Tabaconas, on Río Tabaconas, 20 km ESE Huancabamba, 1900 m, 11.VI. 1947 (US holotype).

Illustr.: Robinson 1976 p. 51–52: Fig. 2 I–L.

Stem pubescence as in var. *rugosa*. Leaves acute; upper surface \pm densely setose, green; lower surface densely grey-tomentose.

Usually of a lower stature than the other varieties, normally about one metre tall. The presence of milky sap has been recorded from

this taxon, but the distribution of this character in the genus needs further investigation, as pointed out by Robinson (1976).

Ecuador. Prov. Loja: Mountains of Cuenca and Loxa, Jameson (US, wrongly cited as *C. hieronymi* in Robinson 1976); sine loco, Jameson (S) – Loja, 2200 m, 1947, Harling 1596 (S) – Loja, S of the town, 2350 m, 1955, Asplund 17938 (S) – Loja, road to La Toma, 1958, 2400 m, Harling 5749 (S) – Cerro Villonaco, 20 km W of Loja along the road to Catomayo, 2200 m, 1967, Sparre 16259 (S) – Nudo de Cajanuma, 6 km S of Loja, 2400 m, 1967, Sparre 16573 (S) – Along the road to Zamora, ca 2 km E of Loja, 7000 ft, 1976, King & Garvey 6913 (US).

Peru. Dep. Amazonas. Prov. Chachapoyas: 1838, Mathews (K, P). – *Dep. Cajamarca, Prov. Jaén*: Above Tabaconas, 2300 m, 1912, Weberbauer 6304 (US) – Tabaconas, on Río Tabaconas, 20 km ESE Huancabamba, 1900 m, 1947, Fosberg 27777 (US).

2. *C. harlingii* B. Nord. sp. nov.

Orig. coll.: Harling 6050, Ecuador, Prov. Loja, Cariamanga, road to Amaluza, km 15, 22.VII. 1959 (S holotype, GB isotype).

Illustr.: Fig. 3 A–G.

A. C. rugosa H.B.K. foliis non manifeste denticulatis, involucris partim purpureis, a *C. hieronymi* H. Robinson foliis majoribus, tomento caulium pilis articulis intermixto, corollis pubescentia carentibus, ab ambabus ligulis aurantiacis differt.

A sparingly branching shrub ca 1 m high. Stems floccose-lanate with white interwoven hairs mixed with brownish articulated coarser hairs, becoming glabrescent with age, striate and brownish-purplish. Leaves in distant pairs, sessile, ovate, up to 6.5 cm long and 3 cm broad, acute–acuminate, with three main longitudinal veins and a fine reticulate venation pattern; upper side green and glabrous except for some tomentum along the impressed veins; lower side white-tomentose; leaf-margin finely crenulate-serrulate without distinct teeth. Capitula rather densely corymbose-paniculate. Involucre 5–6 mm long, 2.5–3 mm wide, subglabrous, somewhat 5-angular with 20–25 phyllaries in 5 vertical rows, coriaceous-subscarious, faintly mid-veined, fimbriate-ciliate-margined; outer ones small, ca 1 mm long and wide, ovate with rounded tip; middle ones 2.5–3.5 mm long and 1.5 mm wide, ovate-oblong; inner ones ca 5 mm long and 1 mm wide, oblong-lanceolate, acute, densely glandular on the proximal half. Ray-florets 5, orange-

coloured. Tube 2–2.5 mm long, narrowly cylindrical, occasionally split almost to the base, glandular, but without hairs. Lamina elliptic-oblong, 3.5–5 mm long, 1.5–2.3 mm wide, 4-veined, abaxially glandular, apically minutely trifid. *Disc-florets* 6. Corolla 4.5–5 mm long, glandular with scattered subsessile glands; lobes lanceolate, 1.5–2 mm long, 0.5 mm wide, without midvein, becoming recurved. *Anthers* 2 mm long incl. appendage, basally glabrous or minutely papillate, obtuse. *Style* densely hispidulous from about the middle; style branches 0.6–0.8 mm long, obtuse. *Achenes* (immature) oblong, somewhat flattened-triangular (esp. in the ray-florets) with 2 lateral ribs and 1 adaxial rib, glabrous, brown, apically truncate, ca 2 mm long and 1 mm wide, 10-veined.

The new species is named in honour of its collector, Professor Gunnar Harling, leader of the 'Flora of Ecuador' project. Distinctive features are the purplish involucre, the orange-coloured rays, and the absence of corolla hairs. The small size of capitula and rays is also noteworthy, especially in comparison to *C. hieronymi*.

Ecuador. Prov. Loja: Cariamanga, road to Amaluza, km 15, 1959, Harling 6050 (GB, S).

3. *C. hieronymi* H. Robinson

Robinson 1976 p. 46. – *Orig. coll.:* King 6702, Ecuador, Prov. Azuay, along the road to Loja, ca 6 km SE of Cumbe, 9600 ft, 4.II. 1974 (US holotype).

C. rugosa var. *arachnoidea* Hieronymus 1901 p. 601. – *Orig. coll.:* Lehmann nos. 5213 (isosyntype in K) and 7957 (isosyntype in US).

Illustr.: Robinson 1976 p. 50, 52; Fig. 3 H–M.

Much-branched shrubs 1–2 m high. *Stems* and branches floccose-lanate with a white–grey tomentum, with age glabrescent, striate, brownish. Internodes usually 1–4 cm long. *Leaves* shortly petiolate, narrowly ovate–lanceolate, acute, 1.5–5 cm long, 0.5–1.7 cm wide, green and glabrous above (except for some tomentum along the main veins), densely grey-tomentose below; margins bullate-crenulate without distinct teeth. *Capitula* ± densely corymbose-paniculate. *Involucral bracts* ca 25, ovate–oblong–lanceolate, up to ca 8 mm long and 2 mm wide (outer gradually smaller, to ca 1 mm), dark or purplish brown at least apically, faintly 1–3-veined, laxly tomentose – somewhat villous

or subglabrous, with scattered dark glands on the outer ones and more densely set light glands basally on inner phyllaries; margins somewhat ciliate-villous. *Ray-florets* yellow or sulphur yellow. Tube cylindrical, 2–5 mm long, glandular and laxly villous. Lamina elliptic-oblong, 5–8 mm long, 3–5 mm wide, 4–7-veined, apically tridentate. *Style* branches subulate, ca 2.5 mm long, minutely puberulous or subglabrous. *Disc-floret* corolla yellow or greenish yellow, 5–7 mm long, villous with thin flexuous hairs; lobes lanceolate, 2–2.5 mm long and ca 0.5 mm wide, rolled back. *Anthers* 2–2.5 mm long incl. appendage; base obtuse–subacute, distinctly papillate. *Style* densely hispidulous above the middle; style branches 0.4–0.6 mm long, obtuse. *Achenes* oblong, somewhat compressed-triangular (ray-florets) or somewhat 4–5-angular (disc-florets), 1.5–2 mm long, glabrous, faintly ribbed, brown.

This taxon was independently recognized as a distinct species by Dr H. Robinson and myself. It differs from other taxa of the genus by the smaller leaves without obvious marginal teeth, the more or less brown involucre, the condensed inflorescences, and the rich corolla pubescence. Apparently the species is restricted to southern Ecuador, which is obviously the centre of variation in the genus.

Ecuador. Prov. Cañar: Vicinity of Santa Rosa de Cañar, 1918, Rose 22666 (US) – N of Biblián, 2900–3200 m, 1974, Harling & Andersson 13246 (GB, S). – *Prov. Azuay:* About Cuenca, Jameson (?), ex herb. Hooker (K) – Supra Quinjed in Andibus mediis cuencanis, 2800–3200 m, Lehmann 5213 (K, wrongly labelled as Colombia, Popayán) – Prope Mariviña in prov. Cuenca, 2800–3200 m, Lehmann 7957 (US) – Páramo Alpacada, along Pan-American Highway 82 km S of Cuenca, 9500 ft, 1944, Wiggins 10810 (US) – Along Río Tarqui, 4–18 km S of Cuenca, 8300–9000 ft, 1945, Camp E-1890 (US) – Vicinity of Cuenca, near union of Ríos Tarqui and Yanuncay, 8200–8900 ft, 1945, Camp E-2635 leg. Prieto (K) – Cuenca, Cumbe, 3000 m, 1947, Harling 822 (GB, S) – Hacienda Pizhin on road from Cuenca to Oña, 2800 m, 1955, Asplund 17770 (GB, S) – Between Cumbe (2704 m) and ca 2800 m on southbound road, 1959, Barclay & Juajibioy 8435 (US) – S of Cumbe, 2700 m, 1968, Harling, Storm & Ström 8697 (GB, S) – Ca 6 km SE of Cumbe along the road to Loja, 9600 ft, 1974, King 6702 (US) – Road Cuenca–Loja, upper N slopes of Valle del Río León and S parts of Páramo de Tinajillas, 2800–3200 m, 1974, Harling & Andersson 14514 (GB) – Ca 39 km SE of Cumbe along the road to Loja, 10200 ft, 1976, King 6903 (US). – *Prov. Loja:* Between

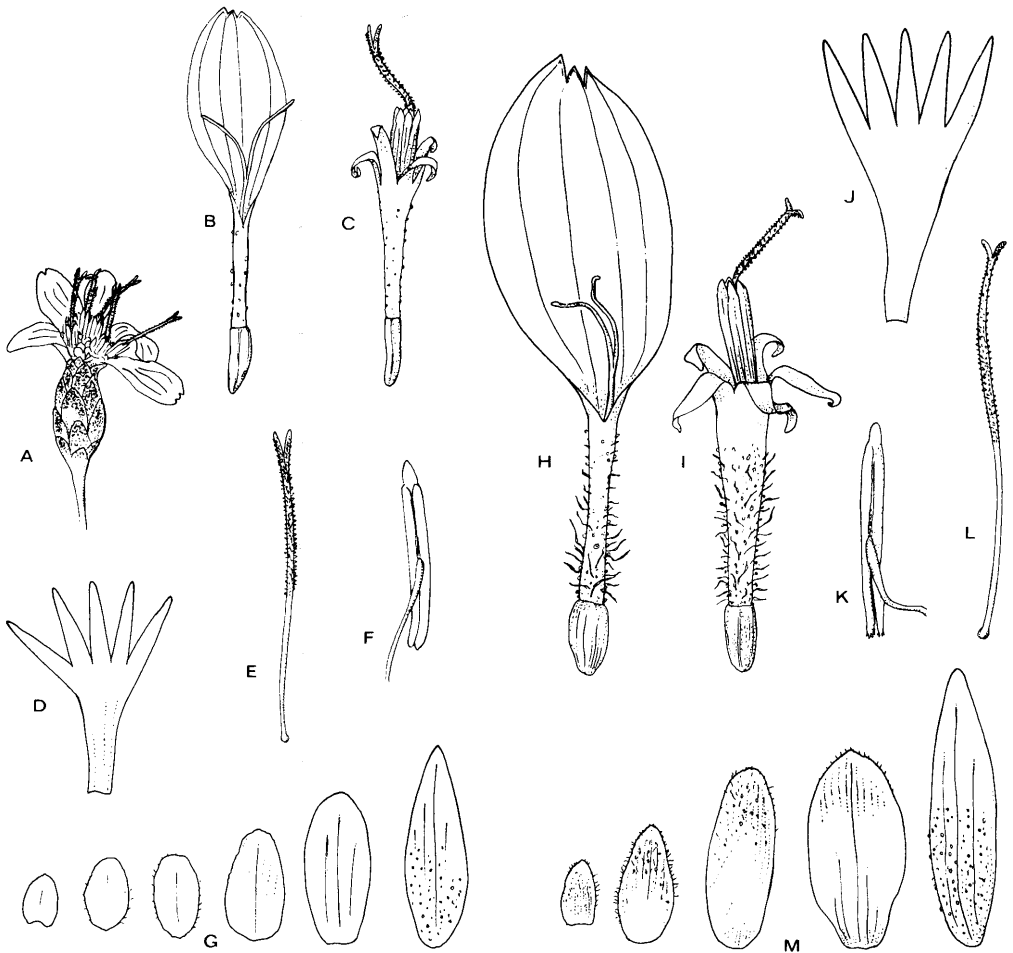


Fig. 3. *Cacosmia harlingii* (A-G: Harling 6050) and *C. hieronymi* (H-M: Asplund 17770). - A: Capitulum, $\times 3$. - B, H: Ray-floret, $\times 6$. - C, I: Disc-floret, $\times 6$. - D, J: Corolla of disc-floret, laid out, $\times 6$. - E, L: Style of disc-floret, $\times 6$. - F, K: Anther, $\times 12$. - G, M: Series of involucral bracts, $\times 6$. - Del. auct.

San Lucas and Oña, 2200-3100 m, 1923, Hitchcock 21569 (US) - On road from Loja to Cuenca, 2900 m, 1961, Dodson & Thien 854 (S, US).

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Some Bothnian subspecies in the *Ranunculus auricomus* complex: origin and dispersal

Erik Julin

Julin, E. 1977 09 15: Some Bothnian subspecies in the *Ranunculus auricomus* complex: origin and dispersal. *Bot. Notiser* 130: 287–302. Stockholm. ISSN 0006-8195.

Ranunculus auricomus ssp. *dactylophyllus* Julin ssp. nov. and ssp. *pectinifolius* Julin ssp. nov. are described and illustrated. Distribution maps of these and seven other subspecies are given. *R. monophyllus* ssp. *neumanii* has a western Bothnian distribution and seems to be of preglacial origin. *R. auricomus* ssp. *crassiusculus* and ssp. *inconspectus* are amphi-Bothnian and perhaps of preglacial origin. *R. auricomus* ssp. *holanthus*, ssp. *pectinifolius*, ssp. *rotundellus* and perhaps ssp. *dactylophyllus* seem to be indigenous and to have originated in the western Bothnian area in postglacial times. *R. auricomus* ssp. *obscurans* is eastern Bothnian and seems to be of postglacial origin. *R. auricomus* ssp. *oligandrus* seems to have spread from Estonia to Finland and thence to Sweden. Dispersal in hay and manure and, over longer distances, by shipping and road and railway traffic have all been important. All taxa are hemerophilous and some may be in danger of extinction due to reduction of suitable habitats.

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When it became clear in the 1930's that the *Ranunculus auricomus* group consists of apomictic (pseudogamous) microspecies, extensive collecting was started, by Gunnar Marklund in Finland and by John Axel Nannfeldt in Sweden, in order to describe the microspecies and establish their distributions. The basic material is still insufficient; nevertheless an analysis of the regions of origin and the migration routes of some biotypes is now possible.

Unfortunately little or nothing has been published on the taxonomy and distribution of the *R. auricomus* complex in Norway, Denmark or the southern part of the Baltic area.

The phytogeographically most interesting microspecies are those with comparatively large distribution areas and particularly those showing disjunctions. Some such microspecies, whose distribution areas at least in places reach the Gulf of Bothnia, are discussed in this paper.

The same terminology which was proposed in a previous paper (Julin 1967) has been used here: viz. *gynoclinium* is used for the pistil-bed and *androclinium* for the stamen-bed. *Interval* is that part of the recep-

tacle which lies between the androclinium and the gynoclinium. The stipe of an individual carpel is called a *carpellophore*.

In Figs. 4 and 10, the oldest leaf is shown at top left-hand, the youngest at bottom right-hand side. Since the whole leaf series is rarely present on a single specimen, the leaves drawn are derived from several plants in the type collection.

Localities already published can be found in the references given under each subspecies. A complete list of all new localities has been deposited at the Museum of Natural History, Section for Botany, S-104 05 Stockholm 50, Sweden, and copies will be sent on request. The abbreviations of province names follow Hylander (1953), except that 'Klm' has been included in 'Sm' and 'Gbg' in 'Vg'.

R. auricomus L. ssp. *crassiusculus* Markl.

Marklund 1961 p. 37.

Localities: Ahti & Hämet-Ahti 1971, Julin & Nannfeldt 1966 (the information concerning Gstr is erroneous), Malmgren 1970, Marklund 1961. – *New localities*: Sweden: Srm 2, Upl 4, Gstr 2, Hls 6, Mdp 5, Hrj 4, Ång 12, Jmt 7, Vb 6, ÅsL 3, LyL 5, PL 2, LL 1. Norway: STrd 1.

This subspecies often occurs in damp places. It has a wide distribution on both sides of the

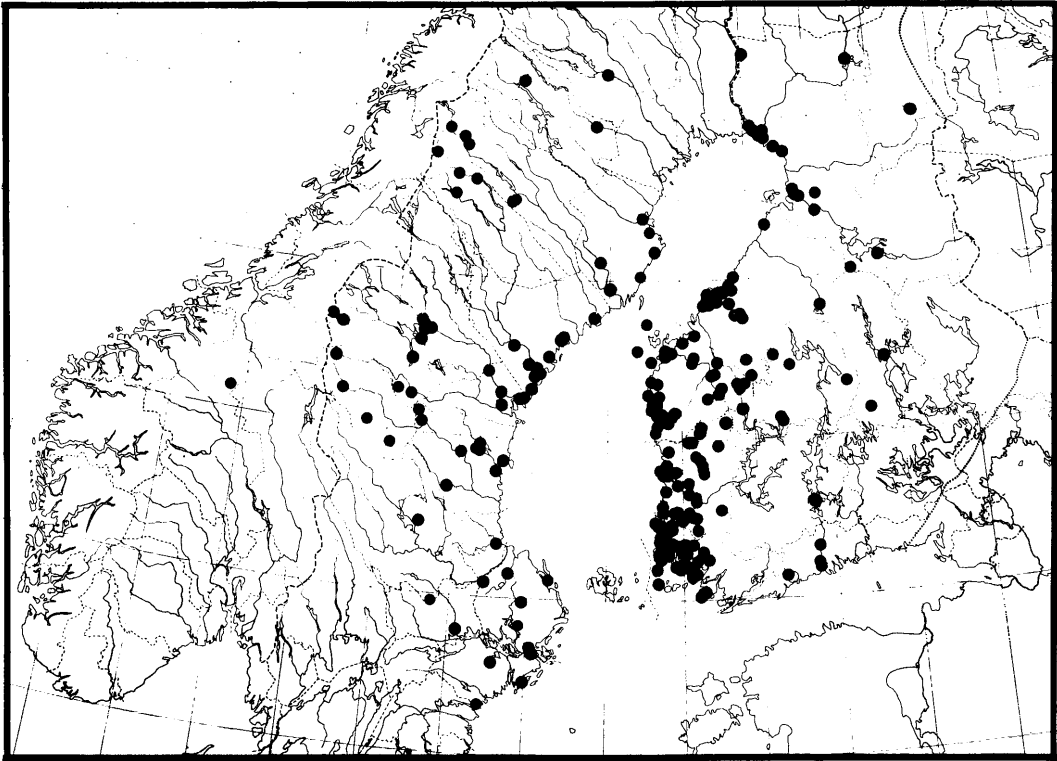


Fig. 1. Known distribution of *R. auricomus* ssp. *crassiusculus*.

Bothnian Gulf (Fig. 1). In Finland it is most common in the west. The occurrence of this subspecies is better known in Finland than in Sweden, which may explain the apparent difference in frequency in the two countries. In Sweden there are many inland localities near the mountains. However, these localities seem to be very much associated with human activities. With some hesitation, I consider this subspecies to be of preglacial origin.

R. auricomus* L. ssp. *dactylophyllus

Julin ssp. nov.

Holotypus: Suecia, Vestrobothnia, Vännäs, Vännfors, in prato ripario secus flumen Vindelälven 1.7. 1966 Julin (UPS).

Localities: Sweden: Srm 1, Upl 1, Gstr 1, Hls 8, Mdp 15, Hrj 1, Ång 20, Vb 13, PL 1. Finland: Ob 2.

Planta mediocriter alta vel parva, sat gracilis. *Caules* erecti, inferne violacei, ramum infimum sub angulo c. 45° emittentes. *Folia* rosularia ambitu semi-

orbicularia, basi plerumque lineam fere rectam formante. *Folia* exteriora multilobata, lobis lanceolatis, plerumque integerrimis. *Folia* intermedia et interiora multipartita, segmentis lanceolatis, acutis, integerrimis vel parce acuti-dentatis. *Folia* aestivalia multivel trilobata vel fere indivisa, acute triangulariter dentata. *Laciniae* foliorum caulinarum sat anguste lanceolati-lineares, integerrimae. *Flores* vel imperfecti, petalis omnibus abortivis, vel – saepissime – perfecti, ad 18 mm diametro. *Sepala* pallida. *Stamina* numerosa capitulum pistillorum rotundum superantia. *Torus* obovate oblongus, albidus, dense pilosus, pilis disparibus, non eadem longitudine. *Carpellophora* apice mediocriter longa, basi brevia. *Androclinium* intervallo perbrevis aliquanto crassius.

A medium-sized, rather slender plant, with erect stems which are violet basally. The lowermost branch emerges at an angle of c. 45°. *Basal leaves* semiorbicular in outline. Exterior basal leaves multilobate, their lobes lanceolate, usually entire. Central and inner leaves multipartite, their parts lanceolate, acuminate, entire or with a few acuminate teeth. Summer leaves mul-

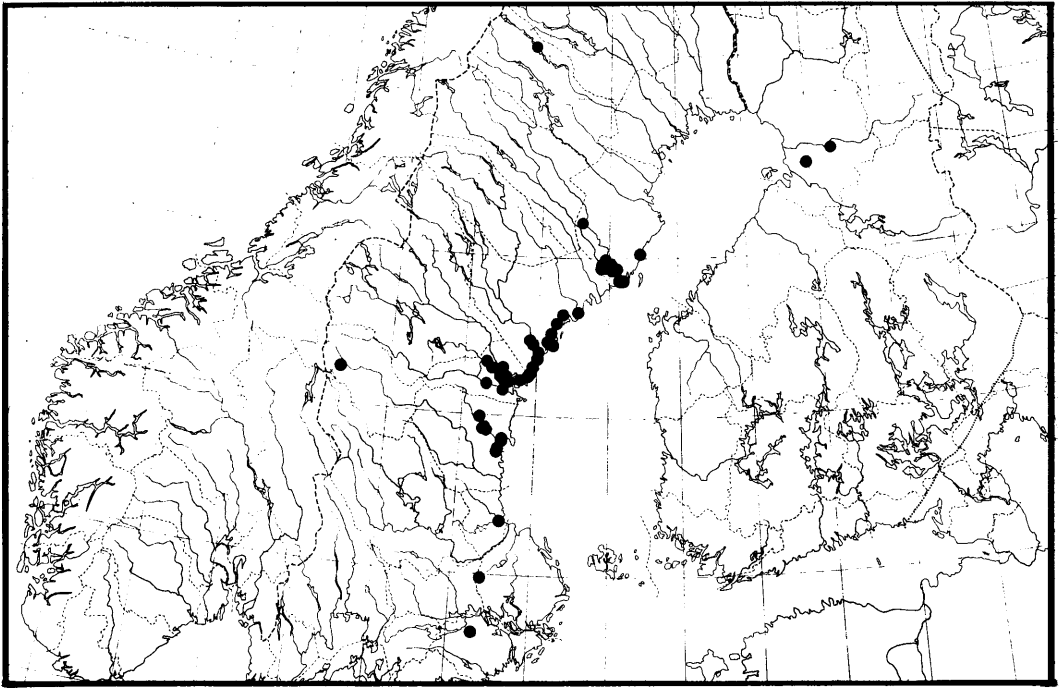


Fig. 2. Known distribution of *R. auricomus* ssp. *dactylophyllus*.

tilobate, trilobate or almost entire, with acuminate, triangular teeth. Segments of cauline leaves rather narrow, lanceolate-linear, entire. Flowers either imperfect, with all petals abortive or, most frequently, perfect, up to 18 mm in diameter. Sepals pale. Stamens numerous, overtopping the rounded head of pistils. Receptacle obovate-oblong, densely pubescent, whitish. Upper carpellophores of the receptacle of medium length, lower carpellophores short. Androclinium somewhat thicker than the interval, which is very short.

Some features of ssp. *dactylophyllus* are reminiscent of *R. monophyllus*, e.g. the intermixture of short hairs among the long ones on the receptacle and the shape of the basal leaves. Whether or not bladeless sheaths are present basally is uncertain. Such sheaths are characteristic for *R. monophyllus*, but usually disappear during anthesis and can only be studied on young, fresh material. The 'species' limits within the *R. auricomus* complex are vague (Marklund 1954, 1961, Marklund & Rousi 1961, Julin & Nannfeldt 1966). However, in our

present state of knowledge, e.g. the hairs on the ripe carpels are denser and somewhat longer than in *R. monophyllus*, this subspecies should be included in *R. auricomus*.

This subspecies occurs in e.g. alder fens, valley bottoms, relatively damp pastures and paddocks, and in more or less natural, damp meadows. Its continuous distribution is confined to a small part of the W coast of the Bothnian Gulf (Fig. 2), where it may have originated in postglacial time (cf. ssp. *holanthus* and ssp. *pectinifolius*). According to this hypothesis, however, the outlying localities present difficulties, especially since some of them, e.g. that in Härjedalen, seem to be spontaneous. Together with the morphological similarity with *R. monophyllus* this may indicate that ssp. *dactylophyllus* is nevertheless of preglacial origin.

***R. auricomus* L. ssp. *holanthus* Markl.**

Marklund 1964 p. 22.

Localities: Marklund 1964. – *New localities*: Sweden: Gstr 14, Hls 6, Mdp 13, Ång 35, Jmt 1, Vb 11. Finland: Ab 1. Norway: Nrd 1.



Fig. 3. *R. auricomus* ssp. *dactylophyllus*. Holotype. – Below right: Receptacle, $\times 20$.

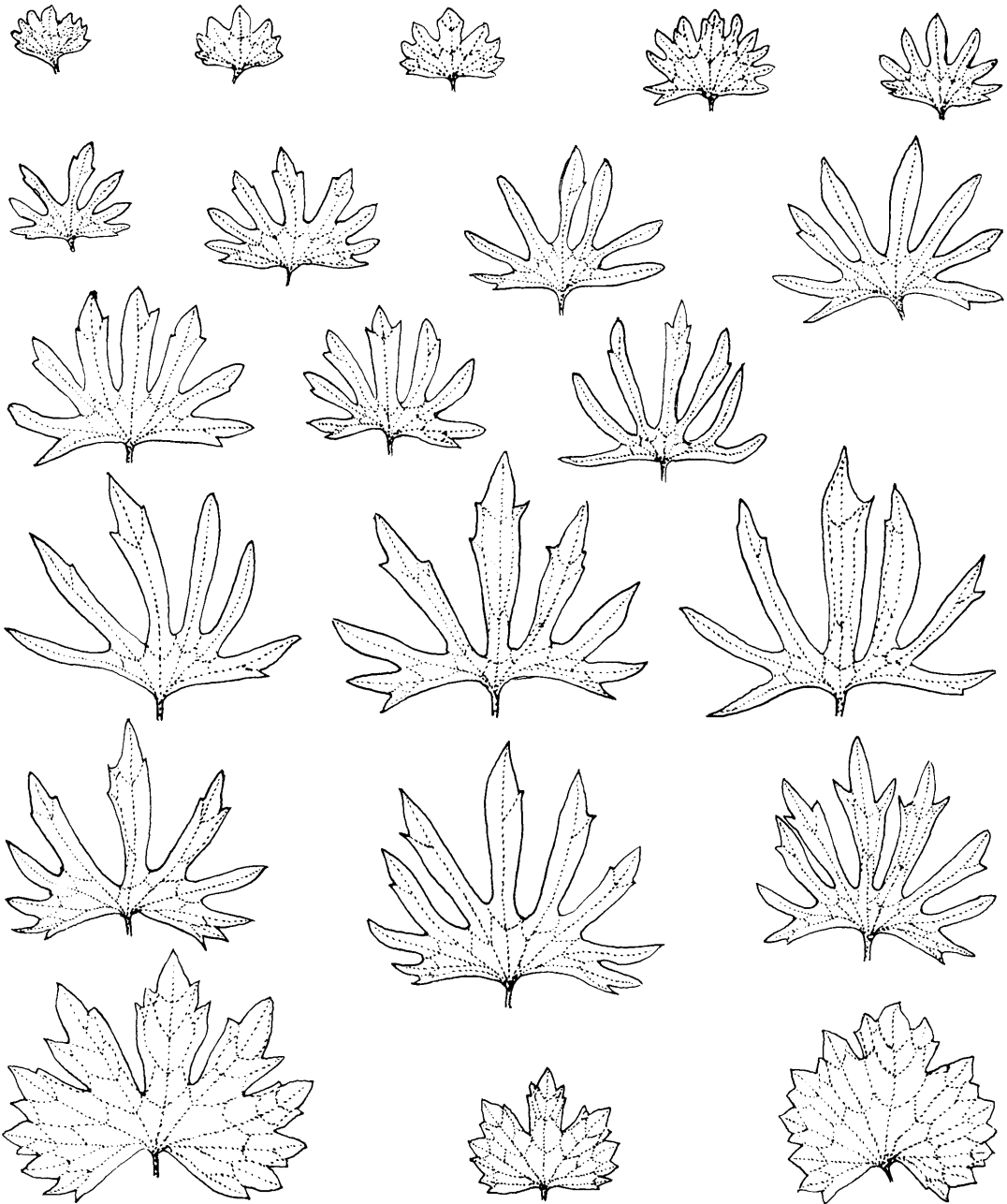


Fig. 4. *R. auricomus* ssp. *dactylophyllus*. Basal leaves of the type collection.

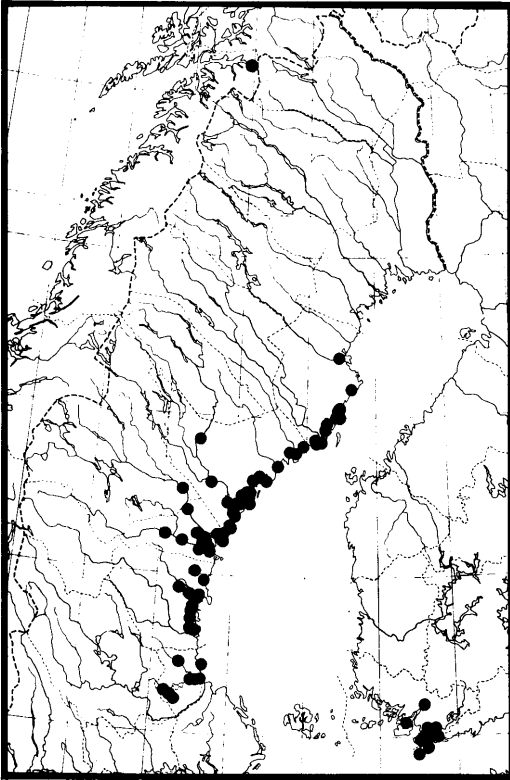


Fig. 5. Known distribution of *R. auricomus* ssp. *holanthus*.

The main Swedish distribution of this subspecies lies within a narrow belt along the W coast of the Bothnian Gulf (Fig. 5). It has almost certainly evolved within this area, and is consequently of postglacial origin. The many coastal localities indicate that dispersal by shipping, and by traffic along the old coastal road, has been important.

The Finnish localities are the result of an introduction from Sweden (Marklund 1964). In the middle of the thirteenth century the south coast of Finland was colonized from Sweden. The settlers came partly from the area around the lake Mälaren and partly from the coastal region of S Norrland. *R. auricomus* ssp. *holanthus* is restricted to those areas where Swedish is spoken; it does not occur in the adjacent Finnish-speaking parishes.

The Norwegian find was made by the present author on 14.7. 1965. The locality was on an

abandoned farm near the railway station of Katterat, in the innermost part of the Rombakfjord just where a stream flows into the fjord. In the same locality ssp. *pectinifolius* was also found. The two subspecies occurred near each other, in patches covering 20–30 m² each. The occurrences of both these subspecies so far away from their main areas of distribution is most likely due to dispersal by railway traffic. In view of the size of the clusters, the occurrences are not very recent and may well date back to the construction of the Kiruna–Narvik railway-line which was opened for provisional traffic in 1902. Close to the locality there was a stable for the horses which were used when the railway was under construction. Some of the hay for the horses was imported from Sweden, most probably by rail from the eastern part of Medelpad province where both subspecies are common.

Assuming that ssp. *holanthus* colonised its Norwegian locality when the railway was under construction, the annual increase can be estimated as being 0.7 m². If only local dissemination has occurred this rate of spread seems reasonable. The increase of its area in Finland has been much more rapid. Here it is a question of a rural landscape, where the activities of the peasants and of their domestic animals have greatly facilitated dispersal.

R. auricomus L. ssp. *inconspectus* Markl.

Marklund 1961 p. 63.

Localities: Ahti & Hämet-Ahti 1971, Marklund 1961, Olofsson 1961. – *New localities*: Sweden: Sm 1, Srm 2, Nrk 1, Vrm 2, Upl 5, Dir 1, Hls 2, Mdp 1, Hlj 1, Ång 3, Jmt 5, Vb 6, LyL 2.

Like ssp. *crassiusculus*, this subspecies often occurs in very damp places, has a wide distribution on both sides of the Bothnian Gulf (Fig. 6), and is predominantly western in Finland. The apparent differences in frequency between Finland and Sweden are probably due to the same cause as mentioned under ssp. *crassiusculus*.

With some hesitation I consider ssp. *inconspectus* to be of preglacial origin.

R. auricomus L. ssp. *obscurans* Markl.

Marklund 1961 p. 83.

Localities: Julin & Nannfeldt 1966, Marklund 1961,

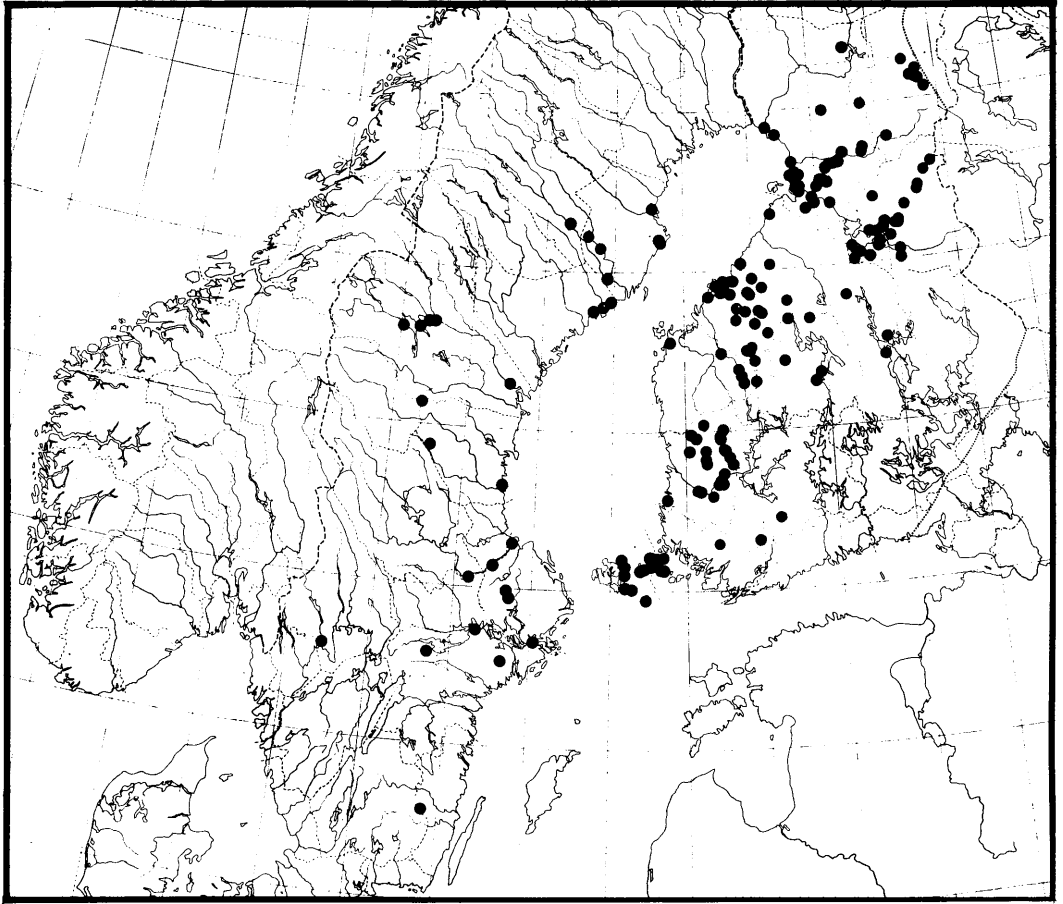


Fig. 6. Known distribution of *R. auricomus* ssp. *inconspectus*.

Olofsson 1961. – *New localities*: Sweden: Sk 2, Sm 1, Ög 1, Vg 1, Srm 3, Upl 2, Ång 3, Vb 13, LyL 2. Finland: Al 1.

This subspecies is very common on the Åland Islands and on the SW coast of the Finnish mainland, and probably originated there in post-glacial times (Fig. 7). In Sweden, scattered occurrences are found from the province of Uppland southwards to Skåne, with an outlying, more concentrated area around the town of Umeå and along the valleys of the rivers Umeälven and Vindelälven in Västerbotten province, where it probably arrived by shipping from Finland.

***R. auricomus* L. ssp. *oligandrus* Markl.**

Marklund 1961 p. 88.

Localities: Julin 1964 a, Marklund 1961, Olofsson 1961. – *New localities*: Sweden: Ög 6, Srm 7, Nr 3, Upl 2, Vrm 1, Gstr 1, Hls 1, Mdp 7, Ång 6, Vb 4, Nb 36, LL 2, TL 4. Finland: Sa 1. USSR: Estonia 16, Latvia 2.

This subspecies has an eminent capacity for colonising man-made habitats and for otherwise benefiting from human activities in nature (Marklund 1954, 1961). This is especially clear for the N Swedish occurrences, e.g. around the town of Haparanda ssp. *oligandrus* is one of the most troublesome of garden weeds and between

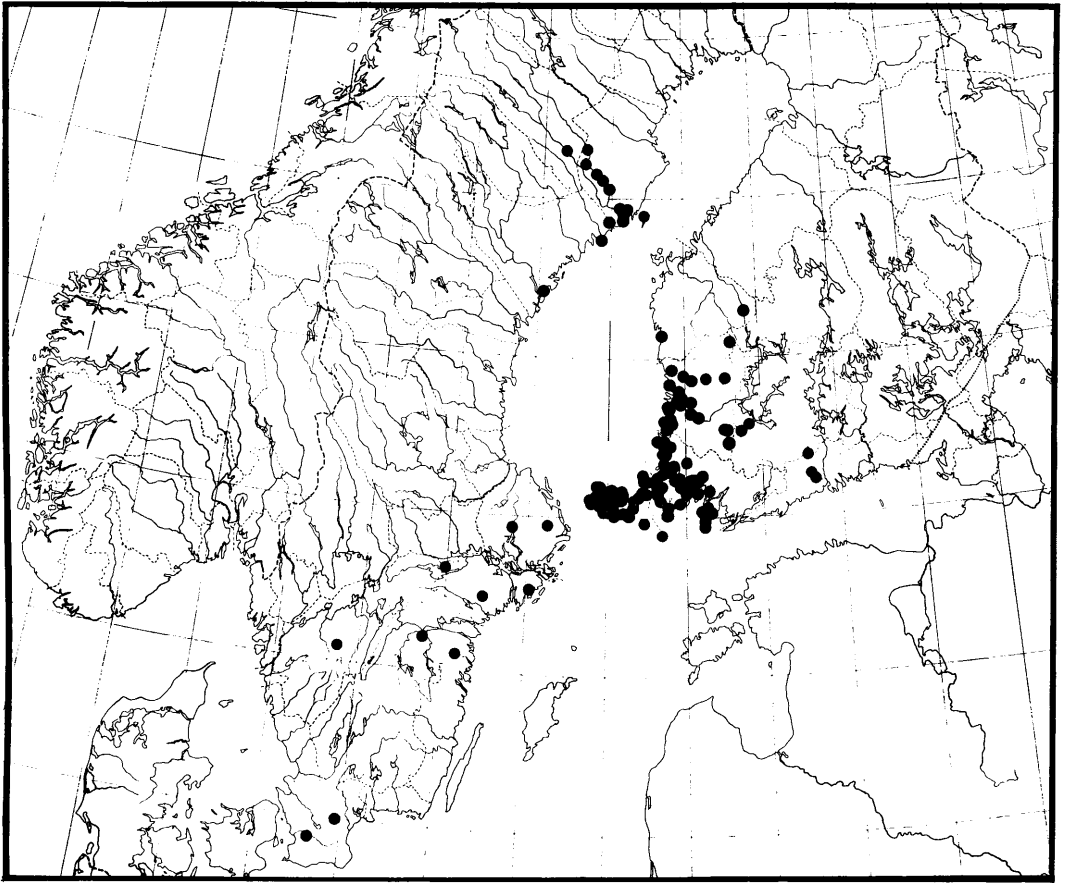


Fig. 7. Known distribution of *R. auricomus* ssp. *obscurans*.

Piteå and Älvsby it can be found at even the smallest of railway stations. Most of the inland localities in N Sweden have originated by dispersal along the railways.

A prime reason for the extensive distribution of this subspecies may be its capacity of growing vigorously in man-made habitats. It has the most extensive distribution area of all our subspecies of Goldilocks. There are also some records from Estonia and Latvia, many more than could be expected considering the low number of collections of *R. auricomus* available from these areas. The subspecies may in fact be very common there.

Judging from the map (Fig. 8) ssp. *oligandrus* would appear to have originated in postglacial times in S Finland, since it seems to be most

common there nowadays. However, considering its rapid spread in recent times, its close connection with man-made habitats, and its discontinuous range, especially in Sweden but also in W Finland, I consider it more probable that ssp. *oligandrus* migrated into Finland from the SE during the postglacial and thence spread to Sweden.

***R. auricomus* L. ssp. *pectinifolius* Julin ssp. nov.**

Holotypus: Suecia, Medelpadia, Selånger, Solbacken in pascuo betuloso 22.6. 1962 Julin (UPS).

Localities: Sweden: Hls 1, Mdp 21, Ång 12, Vb 1. Norway: Nrd 1.

Planta mediocriter alta. *Caules* plerumque curvati, graciles, inferne violacei, ramos sub angulo angusto emittentes; caules laterales subtus pilosi. *Folia* rosu-

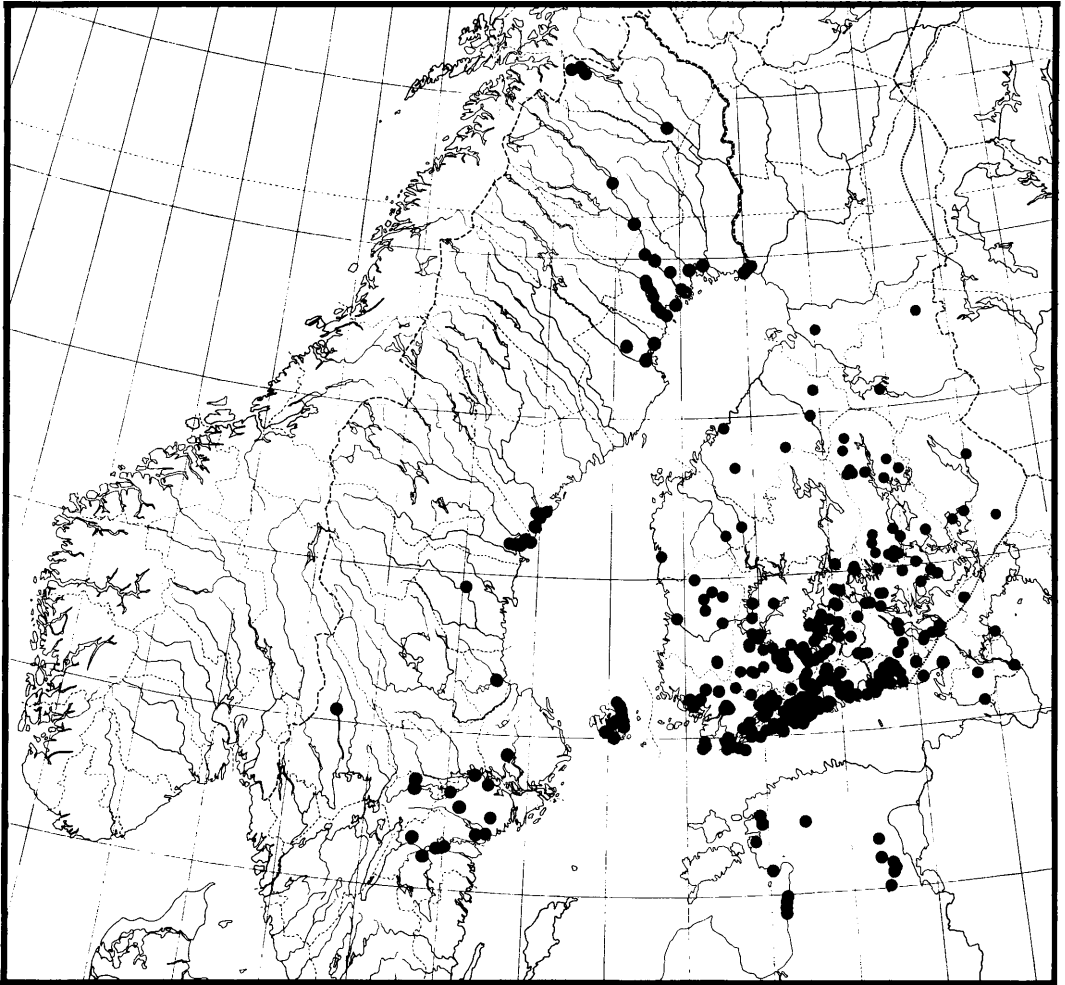


Fig. 8. Known distribution of *R. auricomus* ssp. *oligandrus*.

laria exteriora parva, reniformia, indivisa, obtusate crenata. Folia sequentia ambitu reniformia, multilobata, lobis apice dilatatis, crenatis vel integerrimis. Folia intermedia ambitu fere orbicularia, multipartita, segmento medio \pm late cuneato, dente apicali lato, obtuso et dentibus lateralibus minoribus praedito, vel indiviso vel profunde trilacinulato et petiolulato, segmentis lateralibus cuneatis. Folium sequens multipartitum, segmentis anguste lanceolatis, petiolulatis, integerrimis vel parce dentatis vel lacinulatis, sinu basali peraperto. Folia interiora multipartita, segmentis lanceolatis vel lanceolati-cuneatis, acutis, acute dentatis vel lobulatis. Folia aestivalia reniformia, trilobata, lobo medio rotundate cuneato, lobis lateralibus latis, leviter lobulatis vel indivisis, lobis (lobulis) late breviterque acute mammiformi-dentatis, sinu basali fere 90° . Laciniae foliorum caulinarum medio-

eres ad sat longae, lineari-lanceolatae, obtusulae, integerrimae vel - validiores folii infimi - interdum dente vel lacinula una alterave praeditae. Flores vel valde imperfecti, petalis omnibus vel plurimis abortivis vel interdum perfecti, petalis bene evolutis, c. 20 mm diametro. Sepala apice rubro-violacea. Stamina numerosa apicem capituli pistillorum superantia. Torus parvus, breviter obovatus ad ovatus, glaber; carpellophora mediocriter longa; intervallum breve.

A medium-sized plant with generally curved, slender stems, which are violet basally. The branches emerge at an acute angle. Lateral stems pubescent basally. Exterior *basal leaves* small, reniform, entire, truncately crenate. Sub-



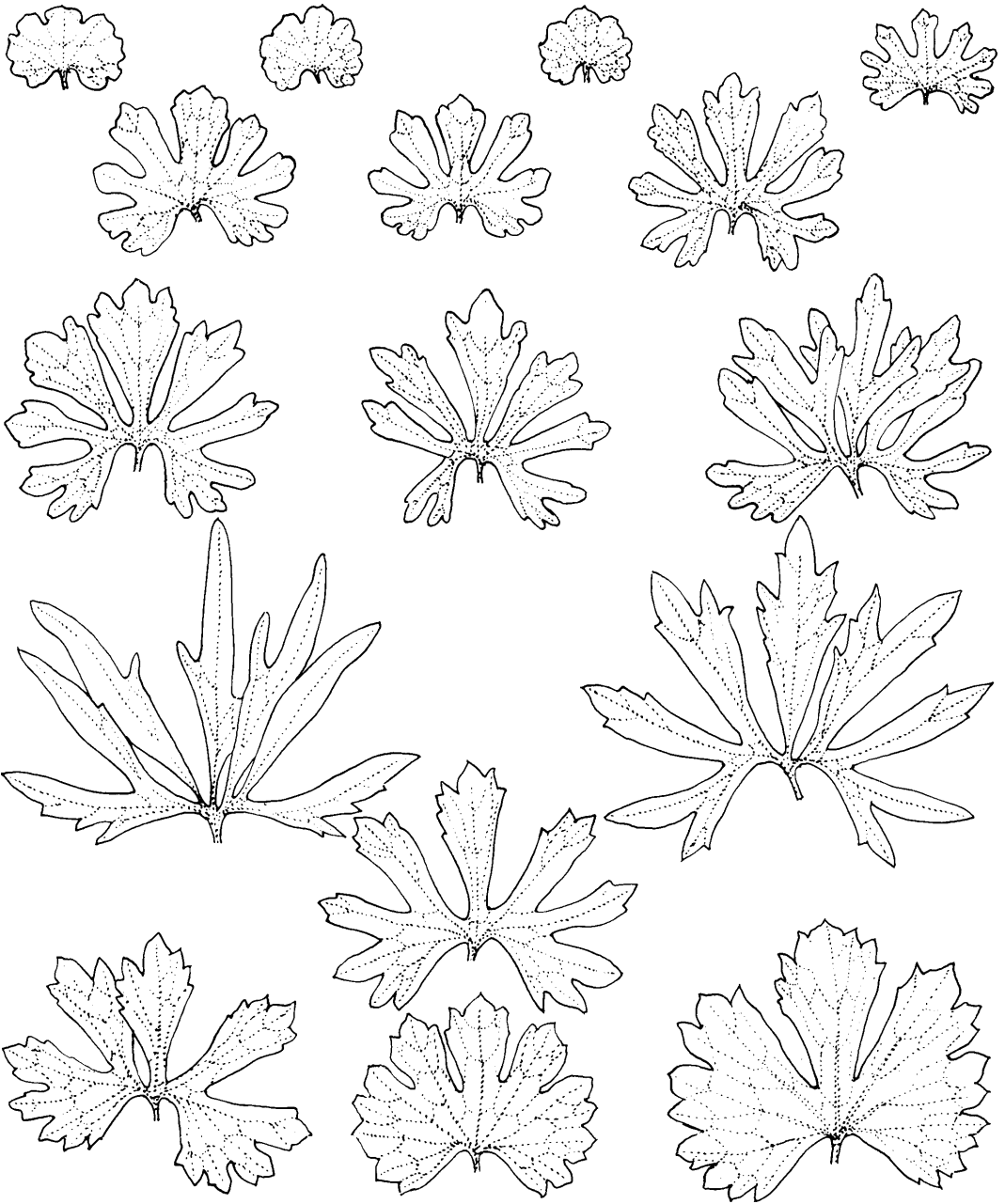


Fig. 10. *R. auricomus* ssp. *pectinifolius*. Basal leaves of the type collection.

Fig. 9. *R. auricomus* ssp. *pectinifolius*. Holotype. – Below right: Receptacle, $\times 20$.

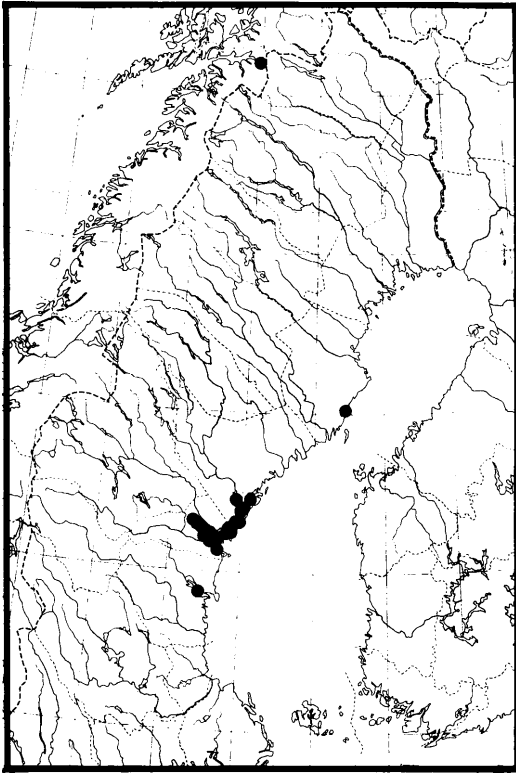


Fig. 11. Known distribution of *R. auricomus* ssp. *pectinifolius*.

sequent leaves reniform in outline, multilobate, lobes broader above, crenate or entire. Central leaves nearly orbicular in outline, multipartite, their median part more or less broadly cuneate with a broad, obtuse terminal tooth and smaller lateral teeth, either entire or more or less deeply trisected, shortly petiolulate, their lateral parts cuneate. The subsequent leaf multipartite, its parts narrowly lanceolate, petiolulate, entire or sparsely toothed or lacinate, the basal angle very open. Interior leaves multipartite, their parts lanceolate or lanceolate-cuneate, acuminate, acuminately toothed or lobulate. Summer leaves reniform, trilobate, median lobe roundly cuneate, lateral lobes broad, slightly lobulate or undivided, lobes (lobules) broad and short, with acuminate, nipple-shaped teeth, basal angle c. 90°. Segments of the cauline leaves moderately to fairly long, linear-lanceolate, a little obtuse, entire or – the most vigorous segments of the lowest leaf – some-

times possessing a few teeth or slender lobes. *Flowers* either imperfect, with all or most petals abortive, or sometimes perfect, with well-developed petals, c. 20 mm in diameter. Sepals purple apically. Stamens numerous, overtopping the head of pistils. Receptacle small, shortly obovate to ovate, glabrous; carpellophores moderately long; interval short.

This subspecies occurs in e.g. pastures and paddocks, relatively dry meadows, roadsides, lake- and sea-shore meadows, valley bottoms, alder fens and alder woods. Its main distribution area is a narrow belt along the W coast of the Bothnian Gulf (Fig. 11), where it almost certainly originated in postglacial times. There is also an extremely disjunct occurrence in N Norway, obviously the result of recent long-distance dispersal (cf. the discussion under ssp. *holanthus*, which has a very similar distribution).

R. auricomus L. ssp. *rotundellus* Markl.

Marklund 1961 p. 109.

Localities: Julin & Nannfeldt 1966, Malmgren 1970, Marklund 1961, Olofsson 1961. – *New localities*: Sweden: Vg 1, Srm 4, Upl 32, Vsm 2, Gstr 1.

This subspecies probably originated in the W part of the central postglacial area of evolution of the *R. auricomus* group (Fig. 12). It has probably been spread by shipping to Finland as well as to some of its more peripheral localities in Sweden. The Swedish W coast locality is in the Göteborg Botanical Gardens (a single plant).

R. monophyllus Ovcz. ssp. *neumanii* Julin

Julin 1964 b p. 487.

Localities: Julin 1964 b. – *New localities*: Sweden: Vg 4, Dlr 3, Hls 1, Mdp 19, Ång 6, Jmt 9, Vb 2, LyL 1, LL 1. Norway: Opl 7, STRd 8.

The discovery of these new localities (Fig. 13) has altered the picture presented by my previous map of this taxon (Julin 1964 b). My impression that ssp. *neumanii* has a preglacial origin has been strengthened. The localities in Falbygden (Västergötland province) may date back to the Middle Ages, since the mediaeval pack-way between Norway and Denmark passed

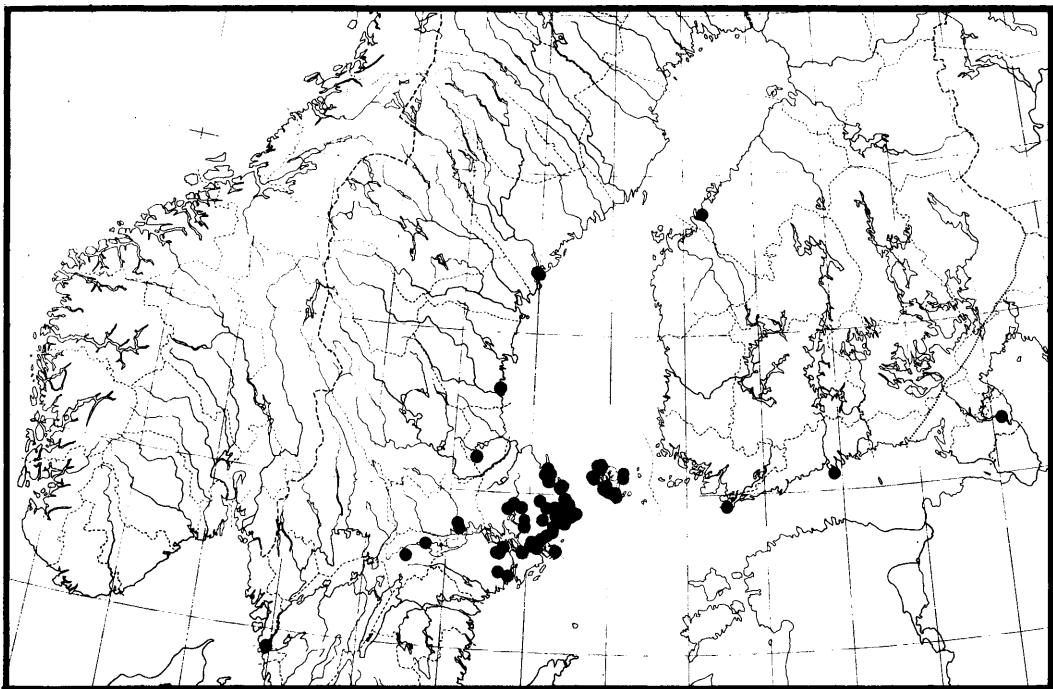


Fig. 12. Known distribution of *R. auricomus* ssp. *rotundellus*.

through this area (Nannfeldt, pers. comm.). The four northernmost Swedish localities are at railway stations and thus probably of later date.

The collective species *R. monophyllus* Ovcz. seems to comprise a number of fairly old, arctic subspecies. Its preglacial area, perhaps like that of *R. auricomus* var. *glabratus* Lyngé (*R. lyngéi* H. Sm.; Marklund & Rousi 1961), may have been extensive. Marklund (1965) considers that the subspecies of *R. monophyllus* reached Finland from the east. Without taking sides, I would like to draw attention to another possibility. A migration route southwards from the northern Norwegian ice-free refugia was already open by 8000 B.C., whereas immigration from the east seems to have been impossible for a long period of time because of formerly greater extent of the present White Sea (see e.g. Hultén 1971 p. 36). For ssp. *parvulifrons* Markl. and ssp. *boreigenus* Markl. at least, an immigration from the north appears to be the most probable alternative. I imagine

that Marklund had something like that in mind when he gave the latter subspecies its name.

The general lack of knowledge of the detailed distributions of the various subspecies of *R. monophyllus* in N Finland presents a great difficulty. Further collecting is urgently needed before the phytogeographical problems connected with this taxon can be finally solved.

Possible means of dispersal

Goldilocks have no specialized means for dispersal. Their diaspores are small, relatively heavy and normally fall to the ground when ripe. They are viable only for a short period after ripening.

Dispersal by water seems to be of little importance. Fresh, fully ripe nutlets sink at once. Ripe nutlets, kept in a herbarium for some years, sank after few hours when put in water. To the best of my knowledge, Hesselman's (1897 p. 99) observation is the only report of the dispersal

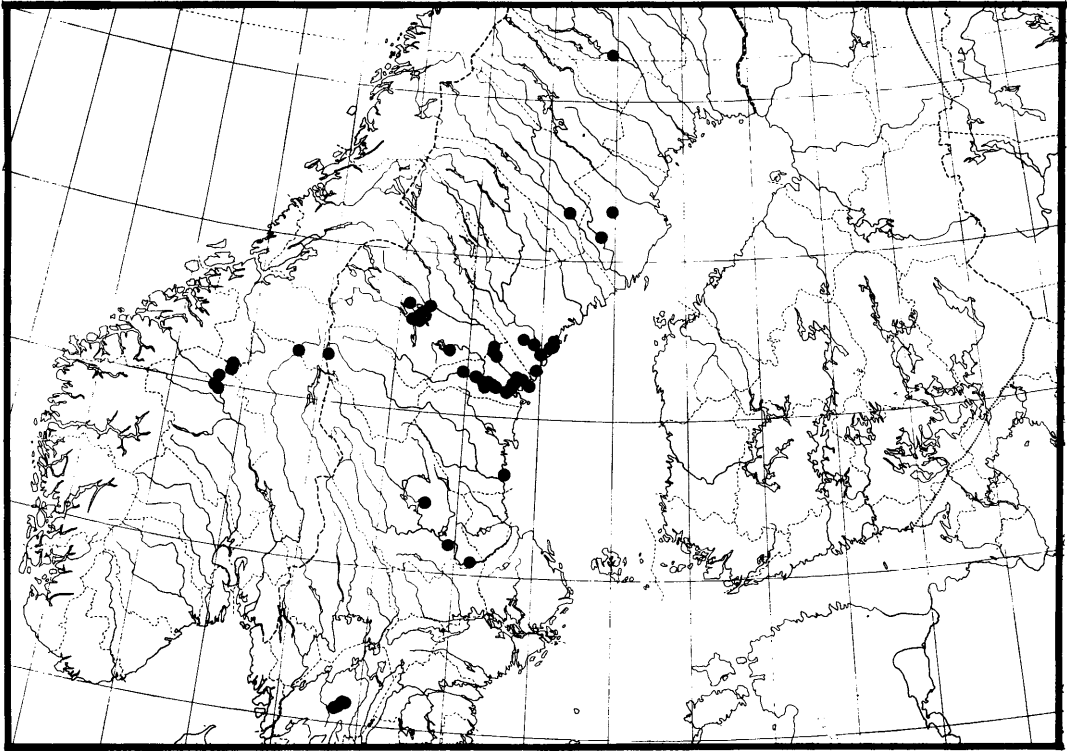


Fig. 13. Known distribution of *R. monophyllus ssp. neumanii*.

of Goldilocks by water. Only a single nutlet was caught in a drag-net after rowing c. 250 km. Water dispersal can only be of importance along fairly rapidly-flowing water-courses.

Dispersal with imported grass-seed (like *Hieracium*; Hylander 1943) has not been demonstrated, but should not be discounted (Julin 1965 p. 30).

Dispersal with manure. Goldilocks are not as acrid and poisonous as some other *Ranunculus* species. Nevertheless they are avoided by grazing animals, especially when they grow in pure stands. Therefore they are usually only swallowed by accident. As far as I know, the germination ability of nutlets, after passing through the alimentary canal of animals, has not been experimentally investigated. However, Paul Olofsson, who has a long experience as a farmer, emphatically claims that Goldilocks can be spread with manure, partly via the droppings of grazing animals, partly via the manure spread

on natural meadows, which was at least formerly common on Vårdö, Åland (Olofsson 1961).

Rasch (1970), working on material from Gotland, also considered grazing animals to be of importance for the dispersal of Goldilocks, but apparently thought dispersal to be synzoochoric.

Before the activities of man and his domestic animals provided a means of dispersal for the Goldilocks, dispersal by wild animals, perhaps by the reindeer in particular, must have formed one of the most important factors.

Dispersal with hay. This was particularly important in the past, when a lot of the hay crop came from "natural" meadows (Olofsson 1961). In N Finland and Sweden, where Goldilocks are generally rather rare, they often occur near hay-barns.

Around Swedish country churches various subspecies of *R. auricomus*, derived from different parts of the parish, can often be found.

These accumulations may well date back to the days when people travelled to church by horse and carriage. The Goldilocks may have been introduced in the hay brought as fodder for the horses, or in the horse droppings.

Dispersal by shipping. For long periods of time shipping on the Gulf of Bothnia was subject to two special circumstances: viz. the Bothnian trade restrictions and the fishery along the coast of C Norrland carried on by fishermen from towns in C Sweden.

The Bothnian trade restrictions date back to the Middle Ages and were abolished in 1765. They imposed a ban on the ports of the Gulf of Bothnia to trade with any other place than Stockholm. Ballast for the return journey, when the cargo as a rule was lighter, was thus obtained from within the area of vigorous postglacial evolution of new taxa of Goldilocks, viz. the provinces of Södermanland, Uppland, the Åland archipelago and SW Finland.

The organized Bothnian coast fishery also started in the Middle Ages; in 1646 authorised fishing-vessels were sent northwards from the towns of Gävle, Öregrund, Strängnäs, Nyköping, Södertälje and Stockholm. Later several other towns were granted the same privilege. Along the coast of Norrland these fishermen established seasonal habitations to which they brought their goats and sometimes a few cows, and also hay for fodder. This type of fishery gradually came to an end in the late nineteenth century (Vedin 1939, Frödin 1958).

These two conditions may have contributed to the relatively richer flora of Goldilocks found along the SW part of the Bothnian coast, as compared with the NW part.

Dispersal by road and rail traffic. Dispersal along roads occurred in connection with the transport of hay, and also via horse droppings. The old coastal road along the Swedish side of the Gulf of Bothnia, as well as the roads leading inland up the large valleys in Norrland must have been of great importance.

Hay transport was also an important factor where dispersal by railway traffic was concerned, e.g. see *R. auricomus* ssp. *oligandrus*.

Hemerophily and survival

Most taxa in the *Ranunculus auricomus* complex are more or less hemerophilous. Never-

theless, all the subspecies treated here, with the possible exception of ssp. *oligandrus*, seem to be indigenous. The hemerophilous habit is more marked in the northern parts of the distribution areas and in the extreme north all occurrences are on man-made habitats.

Olofsson (1961) has described the ecological conditions for the rich flora of Goldilocks on the Åland Islands and pointed out that the number of suitable habitats has been gradually reduced, especially by the ploughing-up of natural meadows. However, he considered that local, man-made habitats, or new coastal habitats created by natural processes such as land uplift, may help to conserve the diversity of the *Ranunculus auricomus* flora.

Olofsson's reasoning may hold true for Swedish conditions too. Nevertheless, the future for the Goldilocks seems uncertain. Large-scale dispersal in hay and manure no longer occurs. Chemical weed control damages the existing populations. Hay-fields and pastures, preferred habitats for the Goldilocks, are being transformed into arable land, or afforested. When grazing and mowing cease, the Goldilocks become crowded out by more competitive species.

Apomictic taxa have fewer possibilities of adapting to changing ecological conditions than do sexually-reproducing taxa. When the changes in their habitats have reached a certain limit they will disappear. With their small distribution areas and their dependence on former agricultural practices, many of the subspecies in the *R. auricomus* complex are therefore probably now threatened with extinction.

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Cerastium alpinum and C. arcticum, a mature polyploid complex

Tyge W. Böcher

Böcher, T. W. 1977 09 15: *Cerastium alpinum* and *C. arcticum*, a mature polyploid complex. *Bot. Notiser* 130: 303–309. Stockholm. ISSN 0006-8195.

Cerastium alpinum ($2n=72, 144$) and *C. arcticum* ($2n=54, 108$) together constitute a polyploid complex which has now reached the mature stage and is exclusively composed of high polyploids. Some deviating numbers are probably derived from the euploid series. The nature of the intergradation and diversity in the complex and the role of hybridization are discussed. Two new subspecies are proposed to cover the truly arctic representatives of the *C. arcticum* group. *C. arcticum* ssp. *procerum* (Lange) Böcher comb. nov. seems to be restricted to Greenland and W Spitzbergen, while *C. arcticum* ssp. *hyperboreum* (Tolm.) Böcher comb. nov. extends from NE Canada to Novaya Zemlya but does not occur in Scandinavia. *C. arcticum* ssp. *arcticum* is atlantic-montane centering in the Faeroes and radiating to Scotland, Scandinavia, Iceland and southernmost Greenland.

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Hultén (1956) treated the *Cerastium alpinum* complex as a “case of worldwide introgressive hybridization”. Without denying hybridization to be fundamental for the understanding of the structure and origin of the complex it may be advantageous to visualize this taxonomically troublesome group as a polyploid complex. It is not the intention to unravel the *C. alpinum*–*C. arcticum* complex in detail, but to discuss it in the light of experiences gained from other polyploid complexes.

The classical polyploid pillar complex comprises basic diploid taxa, which are morphologically distinct and reproductively separated, and polyploids which intergrade and form series of poorly defined entities. This model is impossible to transfer directly to the situation in the *C. alpinum*–*C. arcticum* complex. This complex has reached a level higher than tetraploidy, and clearly belongs to the category of mature complexes. Stebbins (1971) assumes that such complexes originated during Pleistocene and Pliocene.

Polyploid complexes contain at the higher

ploidy levels entities which cannot be regarded as species in the traditional sense. These entities are neither uniform, nor well demarcated. On the other hand they may represent characteristic, perhaps common character combinations which are either resulting from a preference to certain environmental conditions or are due to historical events (survival and isolation in refugia, changes in biotype contents during migrations). Taxonomists would, in such cases, have to use their experience by estimating which characters they would prefer when they have to draw more or less artificial demarcation lines between the entities. In a case like *C. alpinum*–*C. arcticum* ecological and geographical evidence should be considered together with the morphological and cytological facts.

Hybridization

The *Cerastium alpinum*–*C. arcticum* complex falls naturally into two groups, the *C. arcticum*

group with $2n = 54, 108$ and the *C. alpinum* group with $2n = 72, 144$.

Asplund (1918) discusses the possibility of hybridization between *C. alpinum* and *C. arcticum*. He says that although hybrids have been recorded from Scandinavia it is doubtful whether intermediate specimens in the high Arctic should be evaluated as hybrids. Here the species are autogamous and the intermediate specimens do not produce bad pollen which is the case with Scandinavian hybrids. According to Warming (1920) *C. alpinum* and *C. arcticum* ("*C. latifolium*") from Dovre, Norway, are usually self-pollinating or, where the plants locally are gynomonocious, the female plants are probably pollinated by insects. Judging from the available chromosome counts crossing may be difficult. *C. alpinum* seems to consist mainly of octoploids ($2n = 72$) while *C. arcticum* is most often dodecaploid ($2n = 108$). Fertilization between gametes with $n = 36$ and $n = 54$ may not be easy and no plants with $2n = 90$ have been recorded.

Possible origins of *Cerastium arcticum*

In the *Cerastium alpinum*–*C. arcticum* complex no diploid original species have been recorded. But it seems justified to discuss the alpine *C. latifolium* group as a relatively original and perhaps ancient group. According to counts by Favarger & Söllner (1949) and Söllner (1952, 1953) the *C. latifolium* group consists of tetraploids ($2n = 36$). The species (*C. latifolium*, *C. uniflorum* and *C. pedunculatum*) vary a great deal and intermediates have been described, but according to Merxmüller (1950) the many forms may largely be modifications and not species hybrids. The species of the *C. latifolium* group resemble members of the *C. arcticum* group to such an extent that they can be thought of as possible ancestors of *C. arcticum* s.l.

Söllner (1953) was the first who discussed the evolution of the polyploidy in the *C. arcticum* group. He suggested that *C. arcticum* ssp. *arcticum* ("*C. edmondstonii*") with $2n = 108$ might have arisen after chromosome doubling in a theoretical hexaploid, which might in turn be the result of a cross between *C. alpinum* ($2n = 72$) and *C. latifolium* ($2n = 36$). It is not unlikely that *C. latifolium* s.l. is one of the ancestors of the *C. arcticum* group, but it is difficult to

imagine that *C. alpinum* could have contributed with as much as two genomes each with 18 chromosomes. Anyway, the type of pubescence of *C. arcticum* ssp. *arcticum* is very unlike that of *C. alpinum*. It is probably impossible to point out a recent taxon which could have been the other ancestor.

As the first step in the evolution one should perhaps suggest the formation of a triploid hybrid between a species related to *C. latifolium* ($2n = 36$) and an extinct, diploid "*pre-alpinum*" ($2n = 18$). The hybrid ($2n = 27$) would probably be sterile and by doubling give an allohexaploid, fertile entity with $2n = 54$. Again this might, after a second doubling, give rise to plants with $2n = 108$. If two allohexaploids of slightly different origin and genetical constitution were joined, the final step would result in double allo-dodecaploids. According to this scheme *C. arcticum* might be polyphyletic, a possibility which would fit in with the taxonomic subdivision of the species given below.

Although most of the counts referable to *Cerastium arcticum* s.l. are dodecaploid ($2n = 108$), two hexaploid counts ($2n = 54$) are mentioned by Löve & Löve (1975), one from Greenland (Böcher & Larsen 1950) and one from Mt Chibiny (Kola Peninsula) by Sokolovskaja & Strelkova (1960). Both counts are listed under *C. hyperboreum* Tolm. by Löve & Löve (1975), presumably since Böcher et al. (1968) mentioned $2n = 54$ for *C. arcticum* var. *vestitum* Hult. which was listed as a synonym for *C. hyperboreum* by Hultén (1956).

With regard to the material from Kola very little information is given by Sokolovskaja & Strelkova (1960). They refer their plant to *C. alpinum*. The material from Greenland is discussed under *C. arcticum* ssp. *procerum* below.

Cerastium arcticum Lange ssp. *arcticum*

C. edmondstonii (Wats.) Murbeck & Ostenfeld in Bot. Notiser 1898 p. 246 (1898) – *C. arcticum* ssp. *edmondstonii* (Wats.) Löve & Löve in Acta Horti Gotoburgensis 20 p. 110 (1956).

It seems impossible to maintain ssp. *edmondstonii* as a separate entity because the type of *C. arcticum* from S Greenland and Iceland is almost identical to material from Iceland and the Faeroes referred to *C. edmondstonii* (Fig. 1).

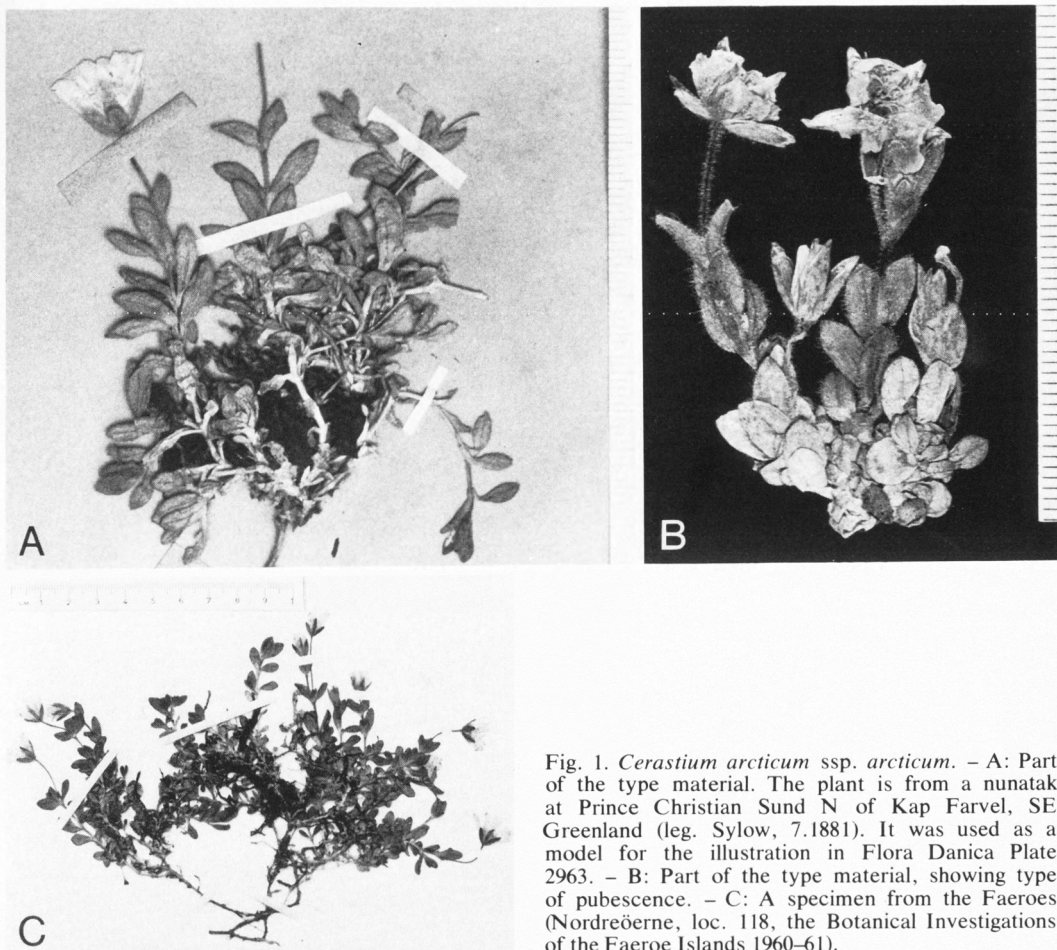


Fig. 1. *Cerastium arcticum* ssp. *arcticum*. – A: Part of the type material. The plant is from a nunatak at Prince Christian Sund N of Kap Farvel, SE Greenland (leg. Sylow, 7.1881). It was used as a model for the illustration in Flora Danica Plate 2963. – B: Part of the type material, showing type of pubescence. – C: A specimen from the Faeroes (Nordreöerne, loc. 118, the Botanical Investigations of the Faeroe Islands 1960–61).

Thus, according to the rules, the name *C. arcticum* has to cover plants which originate from environments which are not typically arctic, e.g. the Faeroes, the Shetlands, Scotland and the Kap Farvel area in S Greenland. *C. arcticum* is very typical and very uniform in the Faeroes. According to Ostenfeld "*C. edmondstonii*" is "pretty distinct from the alpine *C. latifolium* but verges towards another alpine species *C. uniflorum*". He concludes that the Faeroese plant belongs to a small north-Atlantic group of species (e.g. *Alchemilla faeroensis*) which is common all over the Faeroes but otherwise has a limited distribution. This view was also held by Simmons (1906) who doubts that the true "*C. edmond-*

stonii" is present on Greenland. After having studied the rich material labelled *C. edmondstonii* in C I have come to a similar conclusion. This taxon appears to be very distinct. It is common on all the islands but less frequent in the lowlands (Hansen 1966 map p. 49, "*C. arcticum*"). From this centre it radiates towards Iceland and the coastal mountains in S Greenland, Scandinavia and Scotland, but many populations found in these areas are less typical, perhaps because they have undergone introgression from other dodecaploids which they have met. Icelandic specimens referred to *C. arcticum* var. *vestitum* are clearly intermediate.

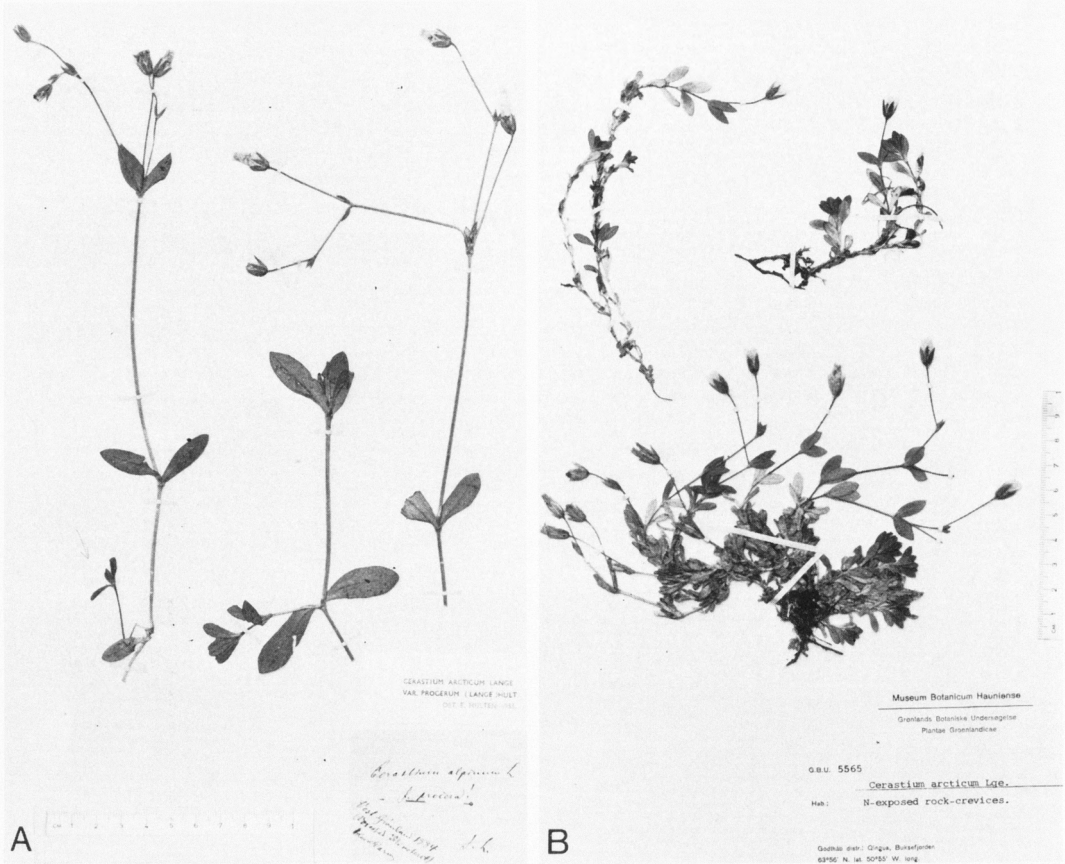


Fig. 2. *Cerastium arcticum* ssp. *procerum*. – A: The type material, from W Greenland (Holm & Warming 1884). – B: Specimens from the head of the Buksefjord, Greenland, 53° 56' N (leg. Jon Feilberg, G.B.U. 5565). It has grown in north-exposed rock-crevices. Note reduced number of flowers but long internodia.

The number $2n=108$ was attached to *C. arcticum* Lange by Löve & Löve (1975). However, in their paper on the Icelandic flora (Löve & Löve 1956) they say that Icelandic material of two types which they call ssp. *arcticum* and ssp. *edmondstonii* as well as plants which appear to be fertile hybrids between them have $2n=108$. The same chromosome number was given for “ssp. *edmondstonii*” from the Shetlands (Söllner 1953) and Scotland (Brett 1954).

Brett (1954) reports formation of multivalents in *C. arcticum* from Scotland but adds that the disjunction of the chromosomes appeared to be regular. However, in a flower bud from Snowden, meiosis was highly deviating with unpaired

chromosomes, laggards, bridges and fragments in every PMC. A few seedlings had $2n=c. 126$ which might be explained as the results of hybridization.

***Cerastium arcticum* ssp. *hyperboreum* (Tolm.) Böcher comb. nov.**

Basionym: *C. hyperboreum* Tolmatchev in Skr. Svalbard Ishavet 34 p. 6, Plate I Fig. 1 (1930) – *C. arcticum* var. *sordidum* Hultén in Svensk Bot. Tidskr. 50 p. 456 (1956) – *C. arcticum* var. *vestitum* Hultén in Svensk Bot. Tidskr. 50 p. 453 (1956).

Hultén (1956) did not accept Tolmatchev's *C. hyperboreum* as a distinct species. Instead, he referred the material to his two varieties *C.*

arcticum var. *sordidum* and var. *vestitum*. The two varieties are not well separated morphologically, although I prefer to keep var. *sordidum* as a variety under this subspecies.

C. arcticum ssp. *hyperboreum* seems to be well circumscribed ecologically and geographically, being typically arctic, ranging from NE America and Greenland to Spitzbergen and Novaya Zemlya. It does not reach Scandinavia. Areas where ssp. *hyperboreum* and ssp. *arcticum* overlap are W Spitzbergen, N Iceland, middle Greenland, NE Labrador and S Baffin. This area needs to be investigated more carefully. My impression is that the occurrence of ssp. *procerum* in Greenland and W Spitzbergen complicates the matter, at least as far as Greenland is concerned.

The chromosome number $2n=108$ has been reported for material that clearly belongs to this subspecies. Holmen (1952) states this number for plants collected by him in Peary Land, and the material from this area belongs almost exclusively to var. *sordidum*. Holmen's count was referred to in Böcher et al. (1968 p. 129).

The material with $2n=108$ ($n=54$) from Clavinger Island in NE Greenland (Jørgensen et al. 1958 p. 57, Fig. 85) also probably belongs to var. *sordidum* or var. *vestitum* which are abundant on that island. However, there are no specimens bearing indication regarding the chromosome numbers.

Cerastium arcticum ssp. *procerum* (Lange)

Böcher comb. nov.

Basionym: *C. alpinum* γ *procerum* Lange in Meddel. Grønland 3 p. 245 (1887) – *C. arcticum* var. *procerum* (Lange) Hultén in Svensk Bot. Tidskr. 50 p. 451, Plate III Fig. 1 (1956).

There is no doubt about the existence in Greenland of a coarse and tall, not densely tufted entity which has a type of pubescence reminiscent of that in *C. arcticum* ssp. *arcticum* but which is very different in other respects. Lange (1887) draws attention to the divaricate cymes and the long pedicels, characters that seem to be very useful. I prefer to evaluate the taxon as a subspecies mainly because it seems to cross occasionally with other members of the 108 chromosome group. The material to be regarded as the type was collected in W Greenland in 1884 by Holm and Warming (Fig. 2 A).

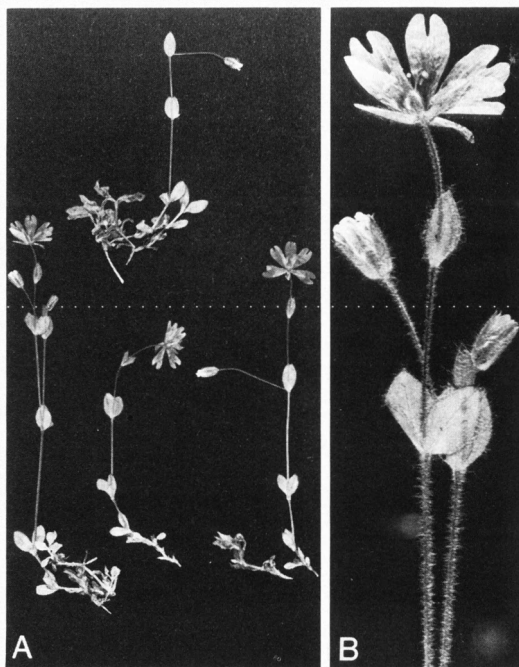


Fig. 3. *Cerastium arcticum* ssp. *procerum*. – A: Material grown from seeds from Fredskild 797. – B: Detail.

In 1957 Bent Fredskild collected a very vigorous, 30 cm tall, loosely tufted plant at Sermermiut S of Jakobshavn, W Greenland. The plant (Fredskild 797) grew in manured soil. Plants grown from seed had $2n=108$ and were lower and had shorter leaves (Fig. 3). The original plants as well as the offspring had green, pubescent leaves but no *alpinum* hairs. They clearly belong to ssp. *procerum*. Fredskild 5659, Perdlertutkuat, $69^{\circ}58'$ lat. N, Nordfjord, Disko Island is very similar, being about 30 cm, loosely tufted with 6–7 cm long pedicels and ripe capsules measuring up to 2 cm. It is also green, not lanate, and has long and narrow, tapering-pointed sepals. It grew in a south-exposed knee-high *Salix* shrub, in other words under favourable conditions. Another specimen from a moss-marsh by a brook in the same locality reached a height of 16 cm and had smaller leaves, but the same long pedicels and capsules. Here the cymes are reduced to one flower on a long, often projecting pedicel, cf. similar specimen from Buksefjord (Fig. 2 B).

A hexaploid collection ($2n=54$) mentioned by

Böcher & Larsen (1950) was originally referred to var. *vestitum* due to its type of pubescence. However, considering the habit and leaf size it is clearly more suitably accommodated in ssp. *procerum*. The plants (Jakobsen 882, 2.9. 1947, Niaqornat, 70°47' lat. N, 53°40' long.) seem to have been loosely tufted with 8–12 cm long stems and cymes of (1)–2(–4) flowers. The sepals are tapering with scarious margins and acute apices. The petals are twice as long as the sepals. Leaves, stems and pedicels are pubescent with long, light yellowish hairs and short glandular ones particularly on the stems and pedicels. The pedicel of the lowermost flower in a cyme of three often projects at almost right angles to the stem below.

Both hexaploids and dodecaploids have thus been found in ssp. *procerum*. The principle of including races with different chromosome numbers under the same name has been used in other polyploid complexes, e.g. the *Phacelia magellanica* complex (Heckard 1960) or the *Campanula rotundifolia* complex (Böcher 1960).

The *Cerastium alpinum* group

The many counts cited in Löve & Löve (1975) show that most plants of this group are octoploids ($2n=72$). However, Brett (1954) found $2n=c. 144$ in material of "*C. alpinum*" from Abisko in N Sweden.

Among the octoploids are *C. alpinum* ssp. *alpinum* and ssp. *lanatum* (Lam.) Simk., *C. glabratum* Hartm. (*C. alpinum* ssp. *glabratum* (Hartm.) Löve & Löve), *C. regelii* Ostenf. and *C. beeringianum* Cham. & Schlecht.

Some additional records are mentioned below together with a few remarks.

C. alpinum ssp. *lanatum*. – Angmagssalik, E Greenland (coll. T. Hatting 1958). B 29. $2n=72$, $n=36$ – Disko, Lyngmarksfjeldet, 300 m (coll. TWB). B 21. $2n=72$ – Qapiarfik N of Jakobshavn, W Greenland (coll. TWB). B 32. $2n=72$, $n=36$. During anaphase I some bridges were observed while acentric fragments could not be detected. – Kangarsuneq S of Christianshåb, W Greenland (coll. TWB). B 35. $2n=72$ – Hasselsfeld, Søndre Strømfjord, W Greenland. B 4832. $n=36$. During anaphase I a number of univalents were observed lagging. $n=36$ was counted at anaphase II which appeared almost normal – Akureyri, Iceland. B 38. $2n=72$. The cultivated plants had small leaves with densely spaced long white hairs.

C. glabratum. – Ankerlien, Kåfjorddalen, Troms,

Norway (coll. G. Halliday). $2n=72$ was counted in plants raised from seeds.

C. regelii or perhaps *C. arcticum* × *regelii*. – Ny-Ålesund, W Spitzbergen (coll. N. Foged 1958). $2n=82-86$. A few seedlings gave rise to plants which were close to *C. regelii*. They died before a close study was possible.

C. beeringianum ssp. *terrae-novae* (Fern. & Wieg.) Hult. – Montreal. Counts of root-tip mitoses resulted in a number lower than 72 (perhaps 68). The plants grew perfectly well and resembled those pictured by Hultén (1956 Plate V).

Discussion

The *Cerastium alpinum*–*C. arcticum* complex is a mature high polyploid complex, but following the thoughts of Stebbins (1971 p. 169) it has to be considered as being among the declining complexes where the diploid ancestors have become extinct. However, although being mature and without ample possibilities of further increase in ploidy the complex is not evolutionarily stagnant. Jørgensen et al. (1958) discuss hybrids between entities belonging to the two euploid series (*C. alpinum* and *C. arcticum*), thereby approaching the views advanced by Hultén (1956). Also the deviating numbers found by Brett (1954) and by me (in a plant related to *C. regelii*) suggest that crossing can still take place even at a high polyploid level and in spite of most entities usually being autogamous.

However, crossing between recent high polyploids is probably of secondary importance for the understanding of the intergradation and variation in the complex. Allopolyploid evolution involving crossing between genomes of 9 or 18 chromosomes and doubling of the hybrid products has probably taken place as repeated cycles two or three times in both groups. The resulting entities which we see today may be composed of up to 12 or 16 genomes each with 9 chromosomes. The genomes have different, although related, genetic constitutions and usually many genomic parts are present 2–8 or more times enabling permanent heterozygosity for several alleles of the same genes, which serves as a buffer against genetic change. High polyploid entities thereby have firmly incorporated a great ecological versatility but have not lost the possibility of gene exchange. In our case where the various genomes probably contain considerable genetic material in common with the original now extinct diploids we may

set up a model according to which each specimen (biotype) is composed of different numbers of modified (genetically changed) basal genomes which we might call "latifolium", "lanatum", "alpinum", "glabratum" and "regelii". A low number of such modified *alpinum* genomes and a higher number from *latifolium* might give *C. arcticum* ssp. *arcticum*, while ssp. *procerum* might contain modified *latifolium*, *alpinum* and *glabratum* genomes and ssp. *hyperboreum* would perhaps mainly involve modified *latifolium* and *lanatum* genomes.

The great ecological amplitude in the *arcticum* group enables it to find suitable ecological niches from the maritime foggy and subarctic Faeroe mountains (ssp. *arcticum*) to the deserts of high arctic Peary Land (ssp. *hyperboreum*). But at the same time we find a more or less clinal transition from green subglabrous rather loosely tufted small-leaved biotypes to grizzled, hairy, more densely tufted or pulvinate ones. As we proceed to low-arctic middle W Greenland we gradually find relatively high-growing, loosely tufted, subglabrous, rather large-leaved biotypes. These transitions suggest that a selection is taking place or has taken place among the multitude of available combinations in the complex. Therefore the transitional types should not be regarded merely as hybrids between well circumscribed taxa. They may largely be due to long-time selection of the best adapted combinations within this wide-ranging polyploid complex.

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Studies in African Cyperaceae XVI

New taxa of *Isolepis* R. Br.

Kåre Arnstein Lye and Richard Wheeler Haines

Lye, K. A. & Haines, R. W. 1977 09 15: Studies in African Cyperaceae XVI. New taxa of *Isolepis* R. Br. *Bot. Notiser* 130: 311–313. Stockholm. ISSN 0006-8195.

Isolepis meruensis R. Haines & K. Lye sp. nov. and *I. setacea* (L.) R. Br. var. *aberdarica* R. Haines & K. Lye var. nov. are described and illustrated from East African material. *I. meruensis* is related to *I. cernua* (Vahl) Roem. & Schult., but has larger spikelets, glumes, crested anthers and a different nutlet. *I. setacea* var. *aberdarica* differs from var. *setacea* in the culm-base and has more reduced leaves. One new combination is made, viz. *I. trollii* (Kükenth.) K. Lye comb. nov.

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Isolepis meruensis R. Haines & K. Lye sp. nov. – Fig. 1

Herbae annuae, glabrescentes. *Culmus* 1–15 cm altus et 0.2–0.4 mm latus. *Folia* ad vaginas reducta. *Anthela* simplex, 1–2-spiculosa. *Spiculae* 2.5–5.0 mm longae et 1.5–2.0 mm latae, 15–25-florae. *Squamae* dense imbricatae, ovatae, obtusae, fuscae, 1.2–1.4 mm longae; *carina* viridis. *Stamina* 3. *Stylus* trifidus. *Nux* 0.7–0.8 mm longa et 0.7–0.8 mm lata, globosa, conspicue apiculata, brunnea, minute punctulata.

Typus speciei: Vesey-FitzGerald 6295, 3.VI. 1969. Tanzania, Arusha National Park, Meru Crater, Njeku gorge, 8400 ft (EA holotype).

A slender annual with 5–15 cm long and 2–4 mm thick culms and rather conspicuous brown or purple leaf-sheaths. *Leaf-blades* absent or consisting of an up to 1 mm long limb; very rarely an up to 2 cm long leaf-blade is found. *Inflorescence* a terminal spike, or very rarely with two spikes. Major inflorescence-bract glume-like, but with a short leafy limb, not overtopping the spikelet except in immature spikelets. *Spikelets* ovate to conic, 2.5–5.0 mm long and 1.5–2.0 mm wide, 15–25-flowered. *Glumes* 1.2–1.4 mm long, light to dark reddish-brown, broadly ovate with a rounded apex, a green midrib which ends below the apex, and several

minor lateral nerves; marginal uncoloured border present. *Stamens* 3; anthers with a prominent projection. *Style* short but with 3 long branches. *Nutlet* 0.7–0.8 mm long and 0.7–0.8 mm wide, triangular, rounded in outline and with a short apiculus; surface brown, minutely punctate.

In edge of muddy pool, 2560 m (8400 ft). Only known from the type collection.

This species is somewhat similar to *I. cernua* (Vahl) Roem. & Schult., but has larger spikelets and glumes, apiculate anthers and a different nutlet.

Isolepis setacea (L.) R. Br. var. *aberdarica* R. Haines & K. Lye var. nov. – Fig. 2

Herbae perennes, glabrescentes. *Rhizoma* erecta. *Culmus* 3–10 cm altus et 0.3–0.6 mm latus. *Folia* bis 2 cm longa vel ad vaginas reducta. *Anthela* simplex, 1–2-spiculosa. *Spiculae* 3–5 mm longae et 1.5–2.5 mm latae, ovatae, fuscae, 10–15-florae. *Squamae* dense imbricatae, 1.5–1.8 mm longae, ovatae, brunneae vel fuscae; *carina* viridis. *Stamina* 3. *Stylus* trifidus. *Nux* 0.8–1.0 mm longa et 0.7–0.8 mm lata, obovata, striatula, conspicue apiculata.

Typus speciei: Lye 74/86, 1974. Kenya, Aberdares Mts, near the road on the West Escarpment, just outside Mt Aberdares National Park (EA holotype).

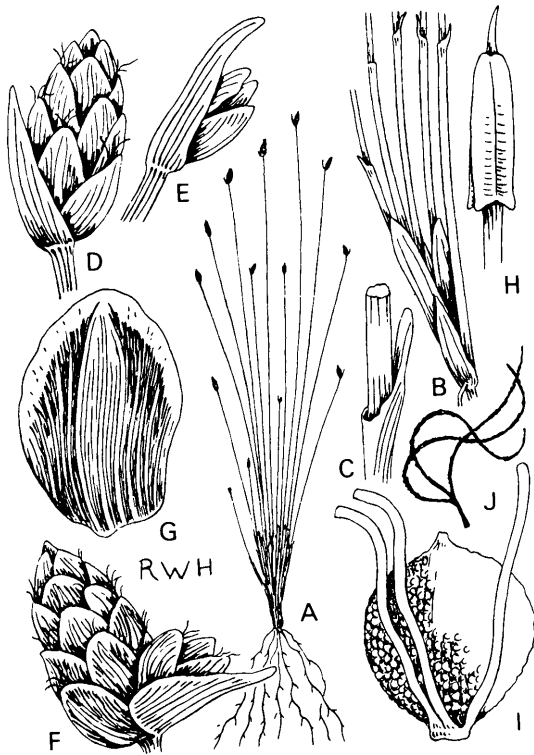


Fig. 1. *Isolepis meruensis*. - A: Habit, $\times 0.5$. - B: Shoot-base, magnified. - C: Detail from culm showing throat of leaf-sheath. - D, E: Mature and young spikelet with bract. - F: Atypical inflorescence with 2 spikelets. - G: Glume. - H: Crested anther. - I: Achene with 3 filaments. - J: Style with 3 long branches. - Drawn from the holotype.

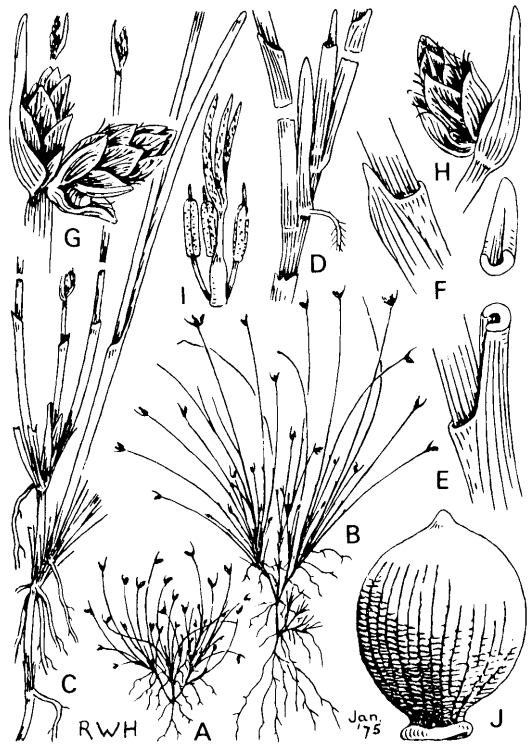


Fig. 2. *Isolepis setacea* var. *aberdarica*. - A, B: Habit, $\times 0.5$. - C, D: Shoot-bases, magnified. - E: Detail from culm showing throat of leaf-sheath with leaf-blade. - F: Detail from culm showing throat of leaf-sheath without leaf-blade. - G, H: Inflorescences consisting of 2 and 1 spikes respectively. - I: Flower consisting of 3 stamens and a gynoecium with 3-branched style. - J: Mature achene. - Drawn from the holotype.

A low perennial forming flat and rounded tussocks 8–15 cm in diameter; the centre of the tussock consisting of numerous crowded slender and branched rhizomes, rooting at the nodes. *Branches* extra-axillary in origin, each branch ending in a group of curved culms. *Culms* 3–10 cm long and 0.3–0.6 mm thick, somewhat flattened, glabrous. Earlier culms with several nodes and bearing leaves with grey to brown sheaths and long green channelled limbs, later with only two nodes, one at the base of the bud-subtending prophyll, the other at the base of a tubular limbless sterile sheath. *Inflorescence*

a solitary spikelet or an anthela consisting of two sessile spikelets. Inflorescence-bracts glume-like, but the excurrent green midrib sometimes longer than the spikelet. *Spikelets* 3–5 mm long and 1.5–2.5 mm wide, ovate, brown, 10–15-flowered. *Glumes* 1.5–1.8 mm long, oval, concave, light to dark brown with usually shortly excurrent green midribs, all fertile. *Stamens* 3. *Style* with 3 branches. *Nutlet* 0.8–1.0 mm long and 0.7–0.9 mm wide, grey, triangular, obovate to almost rounded in outline, and with a short apiculus; surface longitudinally ridged with transverse bars, shiny.

In mountain-moorland, on soil newly laid bare. Only recorded from Aberdares Mountains in Kenya.

This variety differs from var. *setacea* in having a different culm base, shorter bracts and more reduced leaves.

***Isolepis trollii* (Kükenth.) K.** Lye comb. nov.

Basionym: *Scirpus trollii* Kükenth. in Feddes Repert. 53 p. 72 (1944).

The type is from the Uluguru Mountains in Tanzania (Troll 4916; B).

Fragilaria lata, a new diatom species

Ingemar Renberg

Renberg, I. 1977 09 15: *Fragilaria lata*, a new diatom species. *Bot. Notiser* 130: 315–318 Stockholm. ISSN 0006-8195.

Fragilaria lata (Cleve-Euler) Renberg comb. nov. is described and illustrated with light and scanning electron micrographs. It is compared with *Synedra parasitica*, *F. construens* and *F. constricta*.

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In the palaeolimnological investigation of the lake Prästsjön, province of Västerbotten, northern Sweden, a rich material of a number of *Fragilaria* species was obtained (Renberg 1976). One of these, at that time simply called *Fragilaria* sp. a, is here described as *Fragilaria lata*, and four subspecific taxa of *Synedra parasitica* (W. Sm.) Hust. and one of *Fragilaria construens* (Ehr.) Grun. published by Cleve-Euler (1953) are shown to be synonymous with *F. lata*.

Material and methods

The museum slides studied (from S and S-PA) are those present in A. Cleve-Euler's and Å. Berg's collections which are labelled with the names of lakes cited by Cleve-Euler (1953) as the localities for the subspecific taxa of *S. parasitica* and *F. construens* in question. A number of slides in R. W. Kolbe's collection (S-PA) have also been examined.

My own collections, from a number of lakes in Västerbotten and Lapland, consist of subfossil material from sediment cores, recent material from surface sediments and samples of the epiphytic and planktic diatom floras.

The description is based on specimens collected in the lakes Prästsjön and Lillträsket in the province of Västerbotten. In certain samples in the sediment core from Prästsjön, valves of *Fragilaria lata* comprise about 5 % of the total number of diatom valves found (Renberg 1976). The type material, on the other hand, as well as the other museum material examined, contains only single valves.

The light micrographs show specimens taken from

core samples from Prästsjön and surface sediment samples from Lillträsket. The valves were cleaned with hydrogen peroxide, embedded in Hyrax and photographed under a Wild M20 microscope using a Photo-Automatic camera and Agfa Gevaert Pan AHI film. The scanning electron micrographs were taken with a Cambridge Stereoscan S4 and a Jeol JSM-P15 microscope. The counts of striae were made on light micrograph prints at 5000 × magnification.

***Fragilaria lata* (Cleve-Euler) Renberg**
comb. nov.

Basionym: *Synedra parasitica* (W. Sm.) Hust. var. *parasitica* ("var. *genuina* Mayer") f. *lata* Cleve-Euler 1953 in K. Sven. Vetenskapsakad. Handl. Ser. 4, Bd. 4, No. 1, p. 56, fig. 372 a, e (S-PA).

Synedra parasitica var. *intermedia* Cleve-Euler 1953 p. 57, fig. 372 f.

Synedra parasitica var. *subconstricta* sensu Cleve-Euler 1953 p. 57, fig. 372 h, non Grunow 1880–1881 in Van Heurck, Syn. T. 45, fig. 29.

Synedra parasitica "var. *genuina* × var. *subconstricta*" Cleve-Euler 1953 fig. 372 i.

Fragilaria construens (Ehr.) Grun. var. *binodis* (Ehr.) Grun. f. *bigibba* (Cleve-Euler) Cleve-Euler 1953 p. 35, pro parte, fig. 346 x, y, non fig. 346 w = var. *bigibba* A. Cleve 1895 p. 35, fig. 28, which probably is the true *F. construens* var. *binodis*.

Cells in ribbon-like colonies or solitary. Frustules in girdle-view narrowly rectangular, girdle very narrow. Length of perivalvar axis ca 4–5 μm. Valve mantle striated. Small forms, especially, often with short striae, of only a few

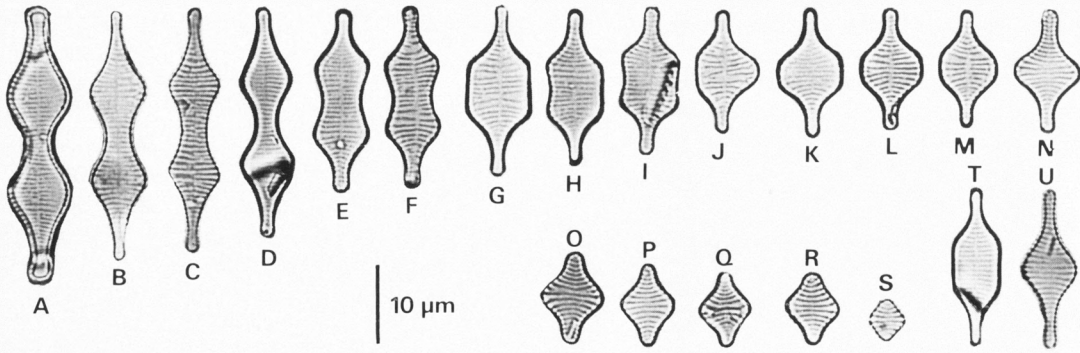


Fig. 1. Light micrographs of *Fragilaria lata* ($\times 1000$); T and U are two unusual forms.

puncta, on valve mantle between ordinary continuous striae. Valve face flat, bilaterally symmetrical. Valve mantle almost perpendicular to valve face.

Valve shape very variable. Large forms narrowly oblong, deeply constricted medially and with elongated apices, sometimes slightly capitate. Intermediate forms oblong, sometimes square, often slightly constricted medially and with elongated apices, occasionally slightly capitate. Small forms either rhombic or almost circular, or rhombic or circular with elongated apices.

Length of apical axis $4\text{--}35\ \mu\text{m}$, of transapical axis $3\text{--}9\ \mu\text{m}$. A very narrow axial area often present, but sometimes lacking. Striae punctate, ca 50 puncta per $10\ \mu\text{m}$, radiate, in the middle of the valve face in larger forms, parallel. $15\text{--}17$ striae per $10\ \mu\text{m}$ (mean 16) along the margin of the valve face, generally one more when measured along the axial area. No ocellus has been observed. Linking spines present on the margin of the valve face, even at the apices.

Ecology. In acidic lakes (pH 5–6), probably non-planktic.

Slides examined. Norway. Hordaland. Lindås par., Gåsetjønn, PEK No. 8, surface sediment, water depth 10–12 m, leg. Kaland, coll. Aasheim, Bergen, det. Renberg.

Sweden. Södermanland (all leg. Silfversparre, coll. Kolbe (S-PA), det. Renberg). – Nacka par., Ulvsjön, No. VIII. 40, bottom sample, water depth 4.2 m, 23.III.1948 – Tyresö par., Långsjön 2, No. VIII. 37, bottom sample, water depth 2.4 m, 20.III.1948 – Tyresö par., Trehörningen I, No. VIII. 58, core sample from 2 m, II.1948 – Österhaninge par., Bylsjön, No.

VIII. 20, bottom sample, water depth 2 m, 18.I.1948.

Västmanland. Ölsjön, bottom sediment near the shore, water depth 0.7 m, 4.IX.1941, coll. et det. Cleve-Euler (S).

Västerbotten (all leg., coll. (UME) et det. Renberg). – Umeå par., Prästsjön 142, subfossil sediment, 14.IV.1972 – Umeå par., Lill-Tavelsjöavan, surface sediment, 28.II.1974 – Sävar par., Svartjärn, surface sediment, 12.III.1974 – Degerfors par., Lillträsket 430, surface sediment, 15.III.1972.

Åsele lappmark (all leg. et coll. Berg (S-PA), det. Cleve-Euler). – Örträsk par., Örträsk 11:1 (right-hand coverslip), 1922 – Örträsk par., Örträsk 8:2 E and 8:3 E, 1923 – Örträsk par., Örträsk 8:4 E, 1923 (lectotype).

Discussion

Since most of the material of *Fragilaria lata* is subfossil it has been difficult to decide whether this species forms any kind of colonies, or only occurs as solitary cells. Colonies, or even two valves belonging to different frustules yet attached together, have never been observed in any of the cleaned material which has been studied. When sediment samples suspended in a drop of water were examined, colonies composed of a few cells, joined together valve-to-valve, were found, indicating that *Fragilaria lata* does form ribbon-like colonies. These are obviously readily disrupted, as for instance during routine cleaning processes.

This species is probably often overlooked because of its small size and its superficial resemblance to *Fragilaria construens* and its varieties, *F. constricta* and *Synedra parasitica* under the light microscope. The characters observable under the scanning electron microscope, however, quite easily differentiate it from

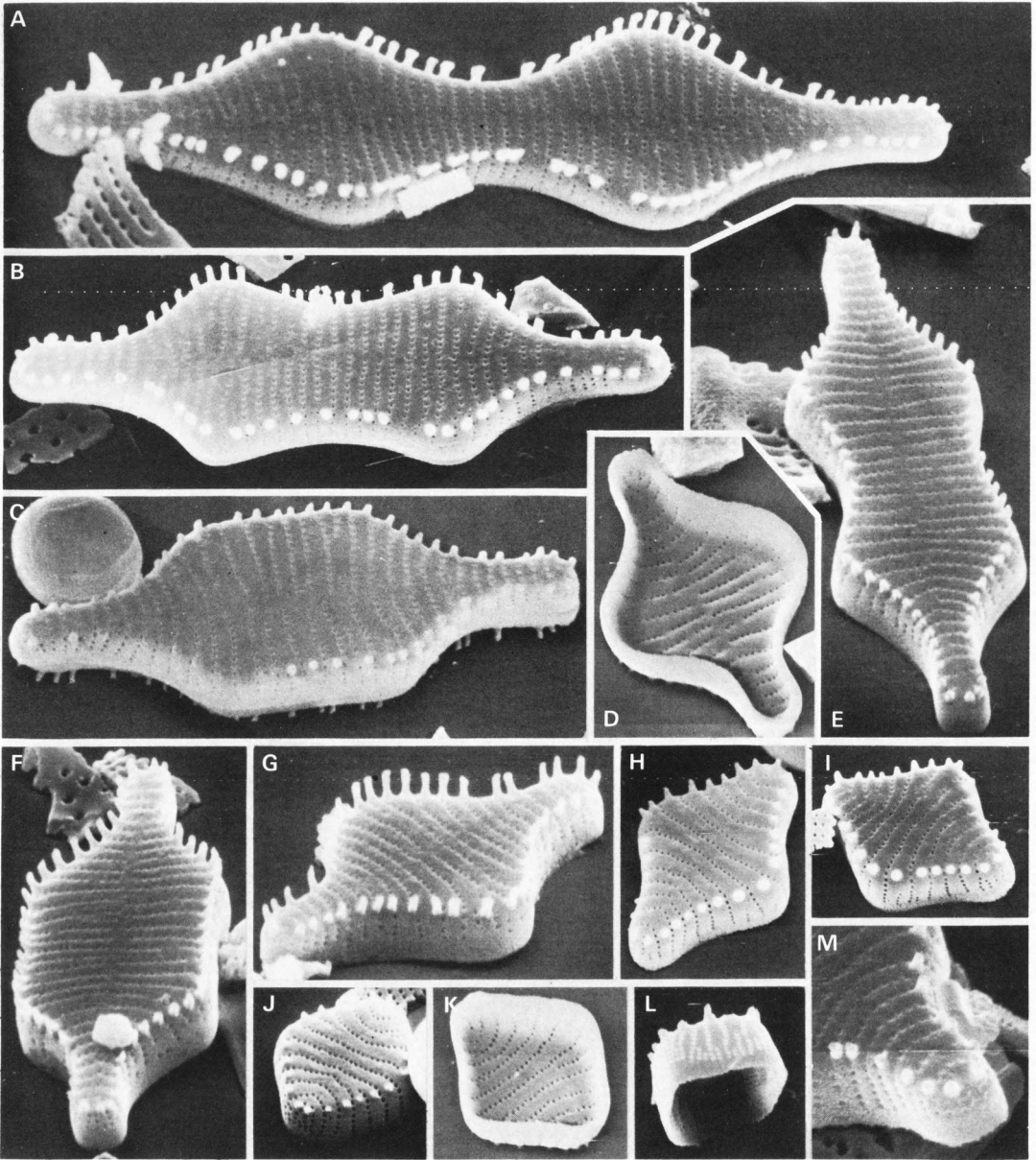


Fig. 2. Scanning electron micrographs of *Fragilaria lata*. - A-L $\times c. 4000$, M $\times c. 6000$.

these species (Fig. 3), but there are also distinct differences which can be seen under the light microscope. *S. parasitica* has marginal striae, *F. construens* has a large axial area and *F. constricta* is generally larger and has a different valve outline. Certain forms of *F. lata* may

also be confused with *F. hungarica* var. *tumida* Cleve-Euler (1953 p. 40, fig. 349 n), see also Renberg (1976 p. 148, fig. 5), which, however, has an ocellus and is more densely striated.

The external shape of *Fragilaria lata* is variable. Its fine structure, however, is not.

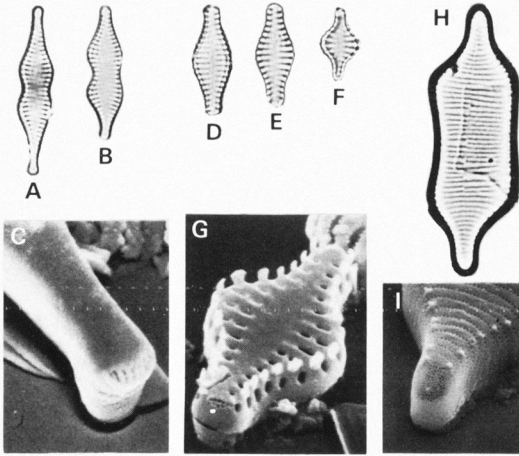


Fig. 3. A, B: Light micrographs of *Synedra parasitica* ($\times 1000$). – C: Scanning electron micrograph showing the apical ocellus of *S. parasitica* ($\times 8000$). – D–F and G: Light and scanning electron micrographs of *Fragilaria construens* ($\times 1000$ and $\times 3750$ respectively). – H: Light micrograph of *F. constricta* ($\times 1000$). – I: Scanning electron micrograph showing the largest ocellus of *F. constricta* ($\times 2400$).

Irrespective of size, all valves have about the same number of striae and puncta per $10\ \mu\text{m}$. Small and intermediate forms were commoner than the large forms in the present material. Valves of abnormal shapes and striation patterns were occasionally encountered.

The variation in external shape exhibited by *Fragilaria lata* is quite reasonable since valve shape in diatoms becomes gradually simplified in the course of successive cell divisions (Geitler 1932). There is one fact, however, which in-

dicates that the observed variation is not continuous. The micrographs (Fig. 1) and a statistical treatment of all available data show that valve width (length of transapical axis) of small and intermediate forms is not less than that of large forms, but more commonly the reverse is true. It is therefore uncertain whether the largest forms (Fig. 1 A–F) are capable of yielding the whole spectrum of forms which have been observed, even though it is a well-known fact (Geitler 1932) that the relative valve width of pennate diatom species may diminish to a lesser degree than would be expected in the course of repeated cell divisions.

The investigations carried out up to now are too limited to substantiate whether or not the observed range of variation is environmentally induced and ecologically significant, or genetically fixed, i.e. whether a separation of sub-specific taxa would be justified within *Fragilaria lata*.

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A note on *Fuirena ciliaris* (Cyperaceae) and related species

R. Wingfield

Wingfield, R. 1977 09 15: A note on *Fuirena ciliaris* (Cyperaceae) and related species. *Bot. Notiser* 130: 319–320. Stockholm. ISSN 0006-8195.

Fuirena ciliaris (L.) Roxb. var. *apetala* Wingfield var. nov. is described from Tanzania and differences between it and similar 'apetalous' varieties of related African species are pointed out. Additional localities are given for *F. microcarpa* K. Lye and *F. zambeziaca* K. Lye.

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***Fuirena ciliaris* (L.) Roxb. var. *apetala* Wingfield var. nov.**

Orig. coll.: Tanzania, 5 km S of Tanga, 1.1. 1970, Botany students in DSM 1501 (DSM holotype, EA, K isotypes).

A var. *ciliaris* squamis hypogynis absentibus differt.

Var. *ciliaris* is much commoner in the area than is var. *apetala*. I have seen intermediates in only one locality (Wingfield 2039). The intermediate plants have some fruits with no hypogynous scales, and others, sometimes in the same head, with one or rarely two scales of normal *F. ciliaris* appearance. The scales are fully developed when present.

The intermediate plants were growing mixed with both varieties, the ratio of var. *ciliaris* to var. *apetala* (including intermediates) being about 15:1. The intermediates are less frequent than var. *apetala* but I give no ratio, since in order to be sure a plant is not intermediate, one would have to examine every flower, which is impracticable. Out of about 300 plants from this site, examined quickly, I found only four intermediates.

The new variety is readily distinguishable from *F. microcarpa* K. Lye on fruit characters (the character states of *F. microcarpa* are given within parentheses): fruit 0.7–0.8 × 0.5 mm, c. 3/4 as wide as long (0.5 × 0.3 mm, c. 1/2 as wide

as long), opaque (translucent), brown when ripe (pale green), with more prominent angles, the faces of the fruit being more or less flat in T. S. (markedly convex); also, the mature spikelets are larger, at least 5 × 1.7 mm, disregarding the bristles and the part where the glumes have fallen off (up to 4 × 1.5 mm).

It is less easy to distinguish the new variety from *F. leptostachya* Oliv. var. *nudiflora* C. B. Cl. and from corresponding, theoretically possible but still unknown, 'apetalous' varieties of *F. angolensis* (Schinz) K. Lye and *F. sagittata* K. Lye.

In *F. leptostachya* and *F. angolensis* the ligule is hairy, whereas in *F. ciliaris* it is nearly or quite glabrous (sometimes minutely ciliate). The fruit of *F. leptostachya* is smaller (c. 0.5 × 0.4 mm) than in *F. ciliaris*, with the sides frequently more convex (seen from top of fruit), the fruit of *F. sagittata* is larger (0.9–1.1 × 0.5–0.6 mm according to Lye) than in *F. ciliaris*.

F. leptostachya, *F. angolensis* and *F. sagittata* are not known to be sympatric with the new variety, their nearest known populations being as follows: *F. leptostachya* var. *leptostachya*, 40 km W of Dar es Salaam, lowest altitude 130 m; *F. leptostachya* var. *nudiflora*, 560 km W of Dar es Salaam at 1320 m; *F. angolensis*, 500 km WSW of Dar es Salaam (Ruaha National Park) and 330 km WNW of Tanga

(Tarangire National Park), lowest altitude 850 m; *F. sagittata*, 380 km W of Dar es Salaam, lowest altitude 1080 m. *F. ciliaris* var. *apetala* grows between 0 and 40 m.

Additional collections: Tanzania, 7 km SW of Dar es Salaam, Kilwani Pond by Pugu Road, 40 m, 17.7. 1971, Wingfield 1692 (DSM, K) – 28 km NNW of Dar es Salaam, 200 m S of Log Cabins, 15.7. 1972, Wingfield 2039 (DSM, K); only the intermediates from this collection were kept).

Fuirena microcarpa K. Lye

K. Lye in Bot. Notiser 127: 111 (1974).

The holotype of this species is really Wingfield 2100 (not 1638 as stated by Lye), the data Lye gives being from 2100. The holotype is at DSM, isotypes at C, EA, K, NU, MO. No. 1638, which I did not send to Lye, but which was mentioned on the label of 2100, is the same species but from 4 km further west, at Dar es Salaam University campus, 14.7. 1971 (DSM, EA, K).

The fruit is relatively narrower than those of *F. leptostachya* and *F. ciliaris* (both of which have varieties without hypogynous scales), being about 1/2 as wide as long (not 3/4 as in the latter species), and is pale green in life when shed. The fruit-wall is rather translucent and glassy-looking (not brown and opaque as in the latter two species).

F. microcarpa ranges in height from 5 to 30

cm. It grows mixed with *F. ciliaris* var. *ciliaris* (3–66 cm tall), but I have found no intermediates although I have examined several hundred plants from mixed populations.

The known altitudinal range of *F. microcarpa* is 30–910 m.

Additional collections: Tanzania, Selous Game Reserve, 8°38'S, 38°29'E, c. 175 m, 15.8. 1976, K. Vollesen in MRC 3936 (DSM, EA, K) – Mozambique, Bandula, 910 m, 6.4. 1952, Chase 4548 (BM).

Fuirena zambesiaca K. Lye

K. Lye in Bot. Notiser 127: 109 (1974)

This species was recorded from Mozambique and SE Tanzania by Lye. The two collections cited below extend its known range: 0°49'S to 14°50'S, altitude 0–850 m.

A search at several relevant herbaria (BM, BR, DSM, EA, MO, NA, WAG) by me in Dec. 1975–Jan. 1976 revealed no further collections of this species, or of *F. microcarpa*. The only other collection of either found at K (S. Hooper in letter, June 1973) was one of *F. zambesiaca* by Schlieben from near Madaba, near Kilwa in SE Tanzania, which is presumably the one referred to by Lye.

Additional collections: NE Tanzania, 25 km NNW of Dar es Salaam, sea-level, 15.7.1972, Wingfield 2041 (DSM, EA, K, MO, NU) – Kenya, Tana River, Seven Forks, 850 m, 3.3. 1974, S. A. Robertson 206 A (DSM, EA, MO: mixed with *F. angolensis* 206 B).

Notes on the genus *Epidendrum* (Orchidaceae) in Ecuador

Bernt Løjtant

Løjtant, B. 1977 09 15: Notes on the genus *Epidendrum* (Orchidaceae) in Ecuador. *Bot. Notiser* 130: 321–328. Stockholm. ISSN 0006-8195.

One new species, *Epidendrum echinatum* Løjtant, is described, and the new combinations *E. garayii* Løjtant (based on *Pleuranthium cardiochilum* Garay) and *E. suavis* (Rchb. f. & Warsz.) Løjtant are made. *E. isomerum* is reported for the first time from S America and the following species are reported for the first time from Ecuador: *E. aggregatum*, *E. anthoceros*, *E. anthropophorum*, *E. carnosiflorum*, *E. cornanthera*, *E. densifolium*, *E. elleanthoides*, *E. evectum*, *E. funckii*, *E. ionodesme*, *E. jajense*, *E. lacustre*, *E. macbridei*, *E. pachyphyton*, *E. rolfeanum*, *E. sertorum*, *E. suaveolens* and *E. suavis*.

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The taxonomic decisions presented are a result of determining the orchids collected by the 1st and 2nd Danish Botanical Expeditions to Ecuador (Holm-Nielsen & Jeppesen 1968, Holm-Nielsen et al. 1975).

The drawings of flowers and floral parts are made from material preserved in FAA.

Epidendrum aggregatum Lindley

Lindl. in Hooker, J. Bot. 3: 84, 1841.

This rare and conspicuous species, which can grow more than 2 m tall and have the appearance of a small tree, has hitherto only been known from very few collections from Peru.

Schweinfurth (1959) cites a specimen collected in Colombia, distr. Cauca (von Sneidern 855) under the name of *E. aggregatum*, but a study of this specimen at AMES has shown that it hardly belongs to *E. aggregatum* because the lateral sepals are acute and not spatulate and the floral segments are too large (lateral sepals 15 × 4 mm, petals 14 × 2 mm). Furthermore, the leaves are broader (up to 2.7 cm in contrast to 1.7 cm in the type of *E. aggregatum*).

Ecuador, prov. Zamora-Chinchipe, road Loja-Zamora, km 33, dry rocky slopes with grass and scattered shrubs, 1800–1850 m (79°04' W, 3°59' S), 21.4.1973, Holm-Nielsen et al. 4148 (AAU).

Epidendrum anthoceros Linden & Reichenbach f.

Lind. & Rchb. f. in Bonpl. 2: 281, 1854.

Epidendrum anthoceros has hitherto only been reported from Venezuela, Colombia (type) and Peru (Schweinfurth 1959, Foldats 1970, Dunster-ville & Garay 1976).

Ecuador, prov. Napo, between Cuyuja and Papallacta, 10 km E of Papallacta on road to Baeza, rocky slope along the road, 2800–2900 m (78°01' W, 0°21' S), 5.6.1973, Holm-Nielsen et al. 6858 (AAU).

Epidendrum anthropophorum Reichenbach f.

Rchb. f. in Bonpl. 4: 215, 1856.

This species, the description of which is based upon material of uncertain origin collected by Ruiz and Pavón, can now be reported from Ecuador. Although also known from Colombia (Leslie A. Garay, pers. comm.), the only sample

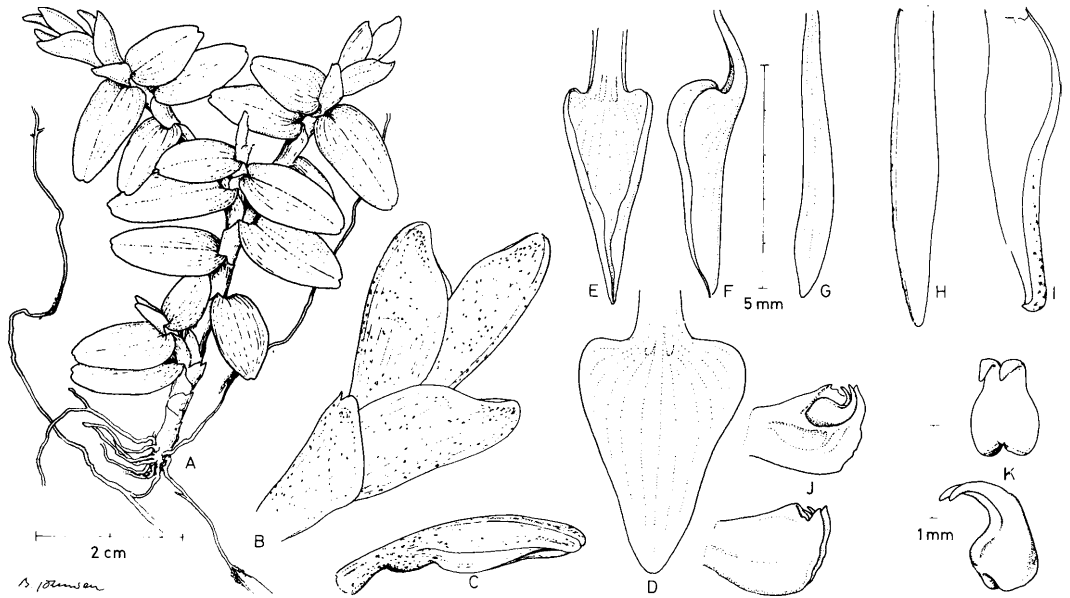


Fig. 1. *Epidendrum cornanthera*. Holm-Nielsen et al. 7026 (AAU). – A: Habit. – B: Inflorescence showing the lepidote bracts. – C: Bud (lepidote). – D: Lip, spread out. – E–F: Lip. – G: Petal. – H: Dorsal sepal. – I: Lateral sepal. – J: Column. – K: Anther.

of this species in AMES is Barclay & Juajibioy 8074 which, like our collection, comes from the surroundings of Pilaló.

Ecuador, prov. Cotopaxi, around Pilaló, 2400 m (79°02' W, 0°57' S), 1.7.1968, Holm-Nielsen & Jepsen 1130 (AAU).

Epidendrum carnosiflorum C. Schweinfurth

C. Schweinf. in Bot. Mus. Leaflet 11: 87, 1943.

This species has so far only been reported from the type locality in Peru.

Ecuador, prov. Zamora-Chinipe, road Loja–Zamora, c. 2300 m, 17.4.1973, Holm-Nielsen et al. 3753 (AAU).

Epidendrum cornanthera Lehmann & Kränzlin—Fig. 1

Lehm. & Kränzlin in Engl. Bot. Jahrb. 26: 463, 1899.

This poorly known species of *Epidendrum* has only been known previously from Colombia. It is not very rare but has seldom been collected,

no doubt due to the fact that it is tiny and inconspicuous. It is closely related to the widespread neotropical *E. strobiliferum* and to the Venezuelan *E. strobiloides* Garay & Dunsterv., but it is distinguished from them by e.g. the form of the anther (see Fig. 1 and Dunsterville & Garay 1966).

Ecuador, prov. Pichincha, "Finca Carlita", at km 13 on road Santo Domingo de los Colorados–Chone, secondary rain forest and slopes with secondary herb vegetation, 550 m (79°14' W, 0°15' S), 10.6.1973, Holm-Nielsen et al. 7026 (AAU).

Epidendrum densifolium Kränzlin

Kränzlin in Feddes Rep. 1: 186, 1905.

Evidently, this species has so far only been known from Peru (Schweinfurth 1944, 1959).

Ecuador, prov. Azuay, km 85 on Pan American Highway N of Loja, dry low scrub vegetation, more humid in small hollows and valleys 2850–2950 m (79°11' W, 3°35' S), 3.5.1973, Holm-Nielsen et al. 4813 (AAU).

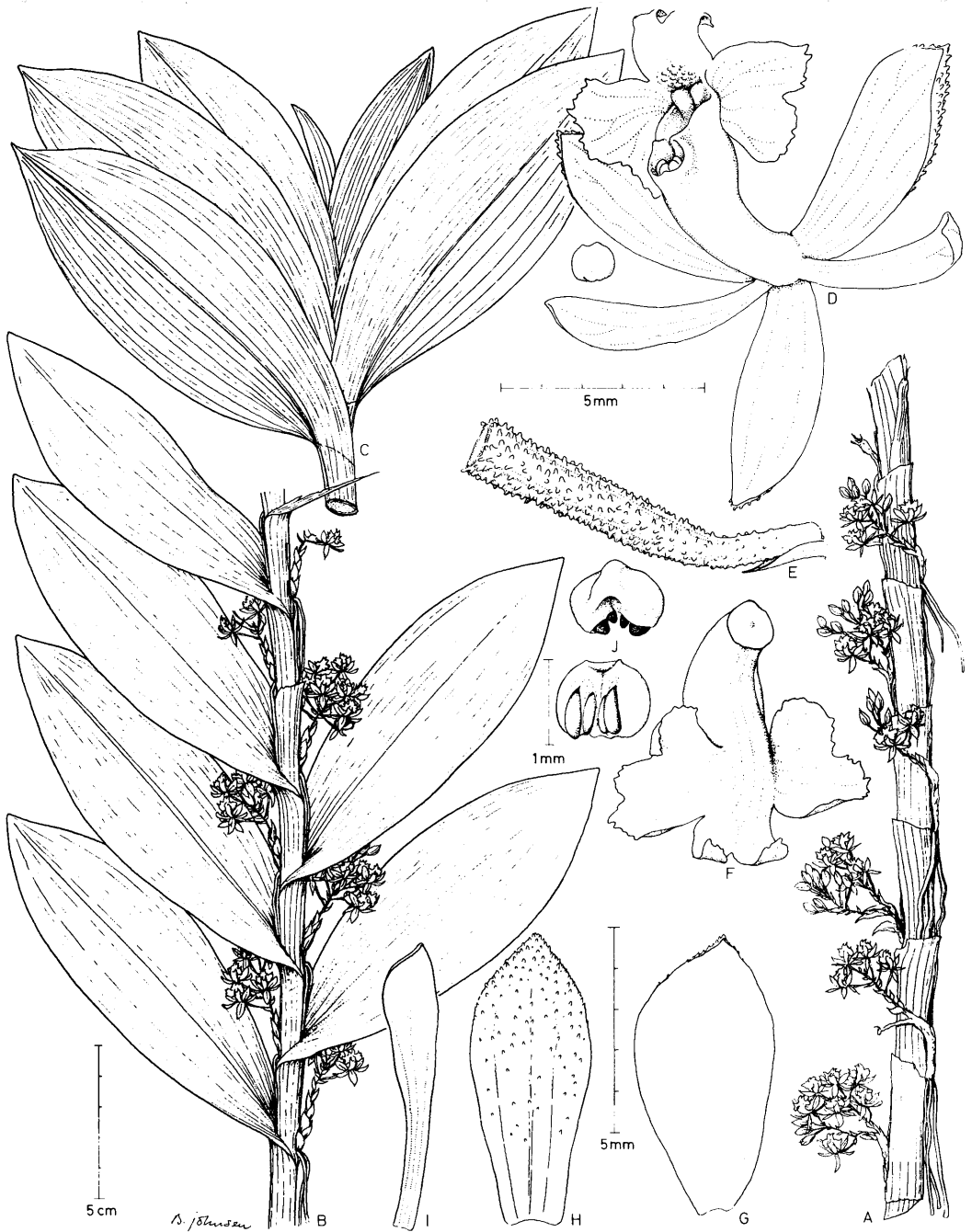


Fig. 2. *Epidendrum echinatum*. Holm-Nielsen, Jeppesen, Løjtant & Øllgaard 3001 (AAU holotype). - A-C: Lower, middle, and upper part of the stem. - D: Flower. - E: Bract, pedicel, and ovary. - F: Lip, seen from behind. - G: Lateral sepal. - H: Dorsal sepal. - I: Petal. - J: Anther.

***Epidendrum echinatum* Løjtnant sp. nov. –**

Fig. 2

Orig. coll.: Ecuador, prov. Cotopaxi, Quevedo-Latacunga road, rocky slopes with rain forest, c. 800–950 m (79°10' W, 0°55' S), 5.4.1973, Holm-Nielsen, Jeppesen, Løjtnant & Øllgaard 3001. 1.5 m high tufted shrub. Terrestrial on wet cliff in the rain forest. Flowers greenish white, sometimes violet tinged (AAU holotype).

Terrestris, caespitosis, usque ad 1.5 m alta; *rhizomate* valde abbreviato; *radicibus* fasciculatis, carnosis, glabris; *caulibus* erectis, simplicibus, dense foliosis, inferne denudatis, vaginis adpressis obtectis; *foliis* distichis, anguste obovatis, acutis, basin versus sensim angustatis, sessilibus, usque ad 15 cm longis, 4.5 cm latis; *inflorescentiis* caulinis, foliis oppositis, brachycladis vel simplicibus, patentibus; *pedunculo* vaginis obtecto, usque ad 3.5 cm longo; *rhacide* brevi, satis dense multifloro; *bracteis* ovatis, acutis vel subacuminatis usque ad 2 mm longis; *ovario* pedicellato, echinato, usque ad 1 cm longo; *sepalo* postico obovato, obtuso, extus echinato, usque ad 7 mm longo, 3 mm lato; *sepalis lateralibus* oblique obovatis, obtusis, extus echinatis, usque ad 7 mm longis, 3.5 mm latis; *petalis* lineari-oblancoelatis, obtusis, margine supra erosulo, usque ad 7 mm longis, 1.3 mm latis; *labello* e basi cordata, 3-lobo, lobis lateralibus dolabriformibus vel transverse reniformibus, plus minusque lobulatis, margine erosulo, 2.5 mm longis, lobo intermedio subquadrato, bilobato, margine erosulo, 2 mm longo latoque; disco incrassato, basin bicalloso; *columna* clavata, arcuata, 5 mm longa.

This new species belongs to sect. *Pleuranthium* Rehb. f. It is distinguished from all other known species of that section by the relatively short, narrowly obovate leaves and the densely echinate petioles, ovaries and sepals.

The specific name is descriptive of the echinate petioles, ovaries and sepals, echinatus meaning prickly.

***Epidendrum elleanthoides* Schlechter**

Schltr. in Feddes Rep. Beih. 7: 132, 1920.

Originally described from Colombia, this species is now reported from Ecuador, close to the Peruvian border.

Ecuador, prov. Zamora-Chinchipec, road Loja-Zamora, km 14, mountain ridges with elfin forest and open bogs, 2750–2770 m (79°09' W, 4°S), 19–20.4.1973, Holm-Nielsen et al. 3837 (AAU).

***Epidendrum evectum* Hooker**

Hook. in Bot. Mag. 97: t. 5902, 1871.

Epidendrum evectum, presumably described on material from Colombia, is usually included in the polymorphic *E. elongatum* Jacq. However, it should be regarded as a distinct species, since it has considerably larger and brighter purple flowers, thicker, succulent leaves and more robust stems. The collections below are apparently the first records of *E. evectum* from Ecuador.

Ecuador, prov. Pichincha, road Santo Domingo de los Colorados–Quito, above Tandapi (Cornejo Astorga), montane forest, river beds and roadsides, 2300–2450 m (78°43' W, 0°27' S), 12.6.1973, Holm-Nielsen et al. 7105, 7109, 7111, 7112 (AAU). – Prov. Cotopaxi, Quevedo–Latacunga road, 2–5 km W of Pilaló, steep rocky slopes in montane forest, 2200–2350 m (79° W, 0°55' S), 8.4.1973, Holm-Nielsen et al. 3199 (AAU).

***Epidendrum funkii* Reichenbach f.**

Rehb. f. in Linnaea 22: 839, 1849.

E. brachycladium Lindl., Fol. Orch. Epidendrum 60, no. 186A, 1853.

E. brachycladium Lindl. β *crassipes* Lindl., Fol. Orch. Epidendrum 60, no. 186B, 1853. – *E. crassipes* (Lindl.) Kränzl. in Engl. Bot. Jahrb. 54, Beibl. 117: 25, 1916. – *E. crassipes* (Lindl.) Schltr. in Feddes Rep. Beih. 6: 69, 1919.

Epidendrum funkii has been reported from Peru, Bolivia, Colombia (type) and Venezuela (Lindley 1853, Schlechter 1919, Schweinfurth 1956, 1959). However, until now it has not been reported from Ecuador. *E. funkii* is unlikely to be rare in Ecuador, but it has often been confused with forms belonging to the polymorphic *E. elongatum* Jacq. (*E. secundum* auct. non Jacq.).

The specific epithet is normally spelled “*funkii*”, but as the taxon is named in honour of its first collector, Nicholas Funck, it should be spelled as above. Schlechter (1919) based his superfluous combination *E. crassipes* on *E. brachycladium* Lindl. var. *crassipes* Lindl. but cited Reichenbach f. as the author of var. *crassipes*. Accordingly there has been confusion

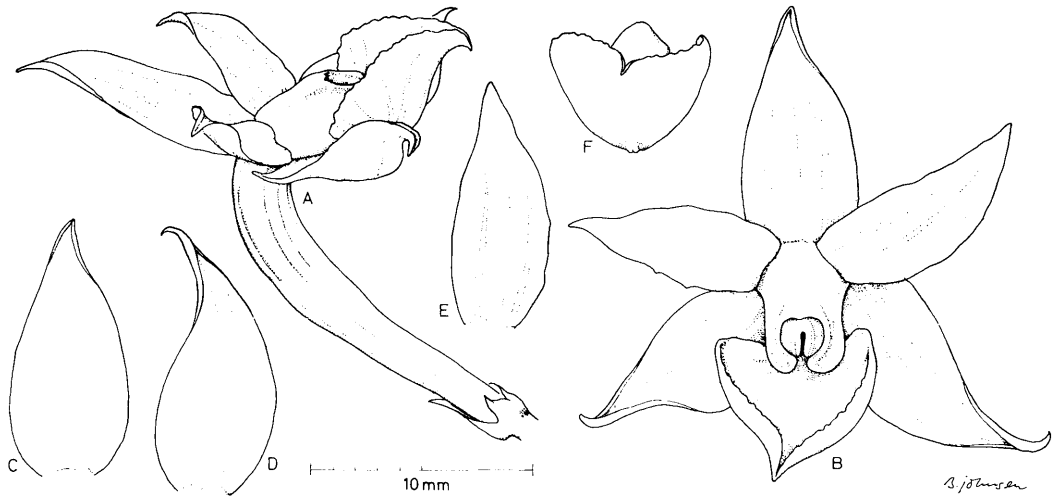


Fig. 3. *Epidendrum garayii*. Holm-Nielsen et al. 6477 (AAU). – A–B: Flower. – C: Dorsal sepal. – D: Lateral sepal. – E: Petal. – F: Lip.

concerning the synonymy of *E. funckii*. The full synonymy is therefore given above.

Ecuador, prov. Carchi, Valle de Maldonado, km 71 on road Tulcán-Maldonado, steep forested slopes, 2100–2200 m (78°06' W, 0°54' N), 20.5.1973, Holm-Nielsen et al. 6052 (AAU). – Prov. Pichincha, km 40–51 on road Santo Domingo de los Colorados–Quito, forested slopes along Río Pilatón, 1100–1400 m (78°55' W, 0°22' S), 14.6.1973, Holm-Nielsen et al. 7175 (AAU).

Epidendrum garayii Løjtnant comb. et nom. nov. – Fig. 3

Based on: *Pleuranthium cardiochilum* Garay in Arquiv. Jard. Bot. 12: 181, 1952.

A study of the collection mentioned below, which is referable to *Pleuranthium cardiochilum* Garay, has revealed that the flowers are terminal and not axillary. Hence the species should be excluded from *Pleuranthium*. Moreover, in my opinion *Pleuranthium* (Rchb. f.) Benth. can easily be accommodated in *Epidendrum*; see Reichenbach (1849), Lindley (1853), Bentham (1881), Bentham & Hooker (1883), Williams (1952) and Garay (1956).

Since the binomial *Epidendrum cardiochilum* L. O. Wms. (in Am. Orch. Soc. Bull. 9: 4, 1940) is already published the new name given above has been adopted.

P. cardiochilum was described from Ecuador: Ost-Cordillera von Riobamba, 3200 m (not 300 m as stated in the original description), coll. Rimbach 801! (S). This is evidently the second record for this species.

Ecuador, prov. Imbabura, timberline vegetation on Hacienda Yura Cruz, 10 km N of Ibarra, 3700–3800 m (78°05' W, 0°22' N), 25.5.1973, Holm-Nielsen et al. 6477 (AAU).

Epidendrum ionodesme Schlechter

Schltr. in Feddes Rep. Beih. 7: 134, 1920.

In most publications *E. ionodesme* is considered to be conspecific with *E. paniculatum* Ruiz & Pavón. However, it differs considerably from the type of *E. paniculatum* both in habit and in the form of the lip and in my opinion should be treated as a separate species.

Because this species has previously been included in *E. paniculatum* it is difficult to give distributional data for it. However, it seems only to have been reported from Colombia previously.

Ecuador, prov. Carchi, Valle de Maldonado, km 60 on road Tulcán-Maldonado, cleared slopes along the road and denser cloud forest, 2700 m (78°04' W, 0°51' N), 18.5.1973, Holm-Nielsen et al. 5693; also at 2600 m, 21.5.1973, no. 6216 (AAU).

***Epidendrum isomerum* Schlechter**

Schltr. in Feddes Rep. 2: 132, 1906.

The collections cited below are the first reports of *E. isomerum* from S America. The species is previously known from Mexico, Guatemala (type), British Honduras, Costa Rica and Panama.

Ecuador, prov. Pichincha, "Finca Carlita", at km 13 on road Santo Domingo de los Colorados-Chone, secondary rain forest and slopes with secondary herb vegetation, 550 m (79° 14' W, 0° 15' S), 10.6.1973, Holm-Nielsen et al. 7032, 7038 (AAU).

***Epidendrum jajense* Reichenbach f.**

Rchb. f. in Bonpl. 2: 20, 1854.

This rare species has hitherto been reported from Peru, Colombia and Venezuela (type) (Garay 1972).

Ecuador, prov. Pichincha, "Finca Carlita", at km 13 on road Santo Domingo de los Colorados-Chone, secondary rain forest and slopes with secondary herb vegetation, 550 m (79° 14' W, 0° 15' S), 10.6.1973, Holm-Nielsen et al. 7042 (AAU).

***Epidendrum lacustre* Lindley**

Lindl., Fol. Orch. Epidendrum 50, no. 157, 1853.

Contrary to the opinion of Ames (1924), this species does seem to occur throughout the American tropics; it is previously known from Nicaragua, Costa Rica, Venezuela (type), Colombia and Peru. It seems to be uncommon in the Andean regions, however, since it has not been reported from Ecuador previously and since it was unknown also from Peru until recently (Schweinfurth 1970).

Epidendrum obessum Ames, conspecific with *E. lacustre*, was reported from prov. Chimborazo in Ecuador by Wiggins (1950). However, the collection cited in Wiggins's report belongs to *E. spectatissimum* Rchb. f. (Leslie A. Garay, pers. comm.).

Ecuador, prov. Zamora-Chinchipe, road Loja-Zamora, km 24-25, steep rocky slopes covered with scrub, 1950-2100 m (79° 05' W, 3° 59' S), 15.4.1973, Holm-Nielsen et al. 3475 (AAU).

***Epidendrum macbridei* C. Schweinfurth**

C. Schweinf. in Bot. Mus. Leaflet 11: 94, 1943.

Epidendrum macbridei, described from Peru, has apparently not been reported from elsewhere until now.

Ecuador, prov. Morona-Santiago, Pachicutza, at "Escuela Fiscomisional Cardinal Döpfner", km 140 on road Loja-Gualaquiza, tropical rain forest with cleared areas along Río Zamora and along the road, 900-1000 m (78° 34' W, 3° 37' S), 26-27.4.1973, Holm-Nielsen et al. 4594 (AAU).

***Epidendrum pachyphyton* Garay**

Garay in Orquideologia 8: 182, 1973.

This species, described from Colombia in 1973 and found in Venezuela in 1974 (Dunsterville & Garay 1976), is now reported from Ecuador.

Ecuador, prov. Zamora-Chinchipe, road Loja-Zamora, km 33, dry rocky slopes with grass and scattered shrubs, 1800-1850 m (79° 04' W, 3° 59' S), 21.4.1973, Holm-Nielsen et al. 4126 (AAU).

***Epidendrum rolfeanum* Lehmann & Kränzlin**

Lehm. & Kränzlin in Engl. Bot. Jahrb. 26: 468, 1899.

Up to now, this species has apparently been known only from Colombia.

Ecuador, prov. Napo, 1 km E of the oil pump station on road Papallacta-Baeza, gallery vegetation along Río Papallacta, 2050 m (78° W, 0° 21' S), 6.6.1973, Holm-Nielsen et al. 6979 (AAU).

***Epidendrum sertorum* Garay & Dunsterville**

Garay & Dunsterville, Venz. Orch. Ill. 5: 100, 1972.

Epidendrum sertorum, closely related to the variable and widely distributed *E. diffforme* Jacq. and recently described from Venezuela, is now reported from Ecuador.

Ecuador, prov. Morona-Santiago, Misión Bomboiza, rain forest, c. 800 m (78° 34' W, 3° 29' S), 23.4.1973, Holm-Nielsen et al. 4248 (AAU).

***Epidendrum suaveolens* Ames**

Ames in Sched. Orch. 1: 21, 1922.

This conspicuous species, closely related to *E. mojanidae* Schltr., *E. pichincae* Schltr.,

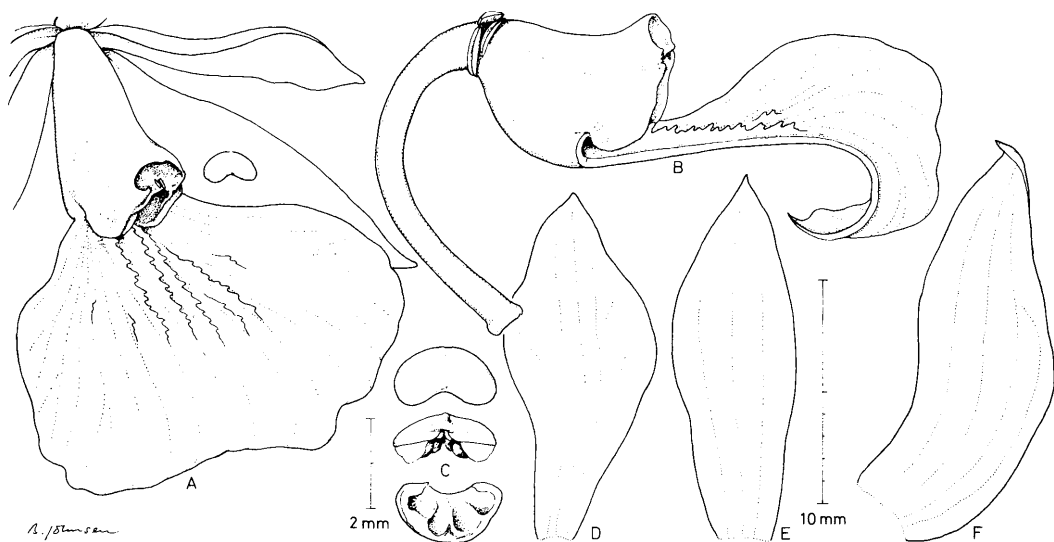


Fig. 4. *Epidendrum suavis*. Holm-Nielsen et al. 3205 (AAU). – A: Lip and gynostemium. – B: Gynostemium and the lip in bisection, showing that the claw of the lip is adnate to the face of the column. – C: Anther. – D: Petal. – E: Dorsal sepal. – F: Lateral sepal.

E. torquatum Lindl. (types from Ecuador) and *E. pastoense* Schltr. (type from Colombia) has hitherto only been reported from Colombia (type) and Venezuela (Dunsterville & Garay 1975, Garay 1975).

Ecuador, prov. Napo, between Cuyuja and Papallacta, 10 km E of Papallacta on road to Baeza, rocky slope along the road, 2800–2900 m (78°01' W, 0°21' S), 5.6. 1973, Holm-Nielsen et al. 6855 (AAU).

Epidendrum suavis (Reichenbach f. & Warscewicz) Løjtnant comb. nov. – Fig. 4

Basionym: *Diothonea suavis* Rchb. f. & Warsc. in Bonpl. 2: 112, 1854.

Epidendrum suavis, like *E. diothoneoides* Schltr. (type from Ecuador), has the general appearance of a *Diothonea*. A study of the type of *D. suavis* from the Reichenbach Herbarium in Vienna, however, revealed that the claw of the lip is adnate to the face of the gynostemium and that the labellum and gynostemium therefore do not meet at an angle as they do in *Diothonea* (Fig. 4). For this reason the species is here transferred to *Epidendrum*.

Epidendrum suavis, although a spectacular

species, is rarely collected. It was described from Peru and is now, for the first time, recorded outside that country.

Ecuador, prov. Cotopaxi, Quevedo–Latacunga road, 2–5 km W of Pilaló, steep rocky slopes in montane forest, 2200–2350 m (79° W, 0°55' S), 8.4. 1973, Holm-Nielsen et al. 3205; also at the timberline, 3450–3500 m (78°56' W, 0°58' S), 8.4.1973, no. 3301 (AAU).

Acknowledgements. I am greatly indebted to Dr Leslie A. Garay, Harvard, who guided my work with unfailing interest and gave me invaluable help during my stay at his laboratory. Thanks are also due to Miss Laura J. Pieters, Professor Kai Larsen, Dr Ivan Nielsen and Mr Peter Wagner for criticism of the manuscript. Economic support was given by the Botanical Institute, University of Aarhus, Aarhus Universitets Jubilæumsfond, and the Arnedst, Filtenborg and Højgaard foundations.

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Seedling morphology and iridoid occurrence in *Montinia caryophyllacea* (Montiniaceae)

Rolf Dahlgren, Søren Rosendal Jensen and Bent Juhl Nielsen

Dahlgren, R., Jensen, S. R. & Nielsen, B. J. 1977 09 15: Seedling morphology and iridoid occurrence in *Montinia caryophyllacea* (Montiniaceae). *Bot. Notiser* 130: 329–332. Stockholm. ISSN 0006-8195.

The cotyledons of *Montinia caryophyllacea* Thunb. are unusual in possessing fused petioles. The plumule breaks through laterally and gradually forces the fused petioles aside. Dried leaf material of full-grown plants was found to contain a previously unknown iridoid gentiobioside, here named montinoside, structurally related to compounds usually found in *Deutzia*, *Viburnum* and members of Valerianaceae. The available evidence suggests a peripheral position for Montiniaceae in Cornales, or close-by.

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The family Montiniaceae consists of two or three genera, viz. *Montinia*, *Grevea* and probably also *Kaliphora*. *Montinia* is monotypic: the single species *M. caryophyllacea* extends from the Cape Province of South Africa to northern Namibia. *Grevea* has two species in East Africa (Tanzania and Kenya) and one species on Madagascar (Milne-Redhead 1955). *Kaliphora* is monotypic: *K. madagascariensis* is endemic on Madagascar. The latter species has usually been placed in Cornaceae, but a probable affinity to Montiniaceae is suggested by Capuron (1969), Airy Shaw (1973) and Krach (1976). Pollen morphology also supports this assignation (Hideux 1972).

According to Gibbs (1974) the family Montiniaceae has been described as new three times: by Kerner (1891), Nakai (1943) and Milne-Redhead (1955). Its ultimate taxonomic position has remained uncertain. Kerner (1891) placed it in Myrtiflorae and Milne-Redhead in Myrtales, a logical position judging from its epigynous tetramerous flowers and the sometimes opposite leaves. In fact, *Montinia* has been placed as an anomalous genus at the end of Onagraceae already by Bentham & Hooker (1862) and

Baillon (1877). Airy Shaw (1973) pointed out possible connections with such divergent families as Celastraceae, Cucurbitaceae, Onagraceae and Escalloniaceae, which clearly demonstrates the great taxonomic problems involved. Although Dahlgren (1975) included the family in Celastrales, the most commonly proposed affinity of *Montinia* or Montiniaceae as a whole is with Saxifragaceae s.lat., particularly with Escalloniaceae, into which the genus was included by Hutchinson (1973). Takhtajan (1969) accepted the family as such and placed it in Saxifragales, while Schulze-Menz (1964), Cronquist (1968) and Thorne (1968) included *Montinia* (and *Grevea*) in Saxifragaceae s.lat.

Raven (1975) and Goldblatt (1976) report a chromosome number for *Montinia* of $n=34$, a relatively high number. Krach (1976) shows that the main features of the seeds of *Montinia* and *Grevea* agree, but deviate so much from those of the genera of Escalloniaceae that familial separation is justified. The embryo was found to be small-celled and the cotyledons 4 times as long as the hypocotyl. The endosperm lumen accumulates fatty oils and protein and the testa was found to be 3-layered. According to

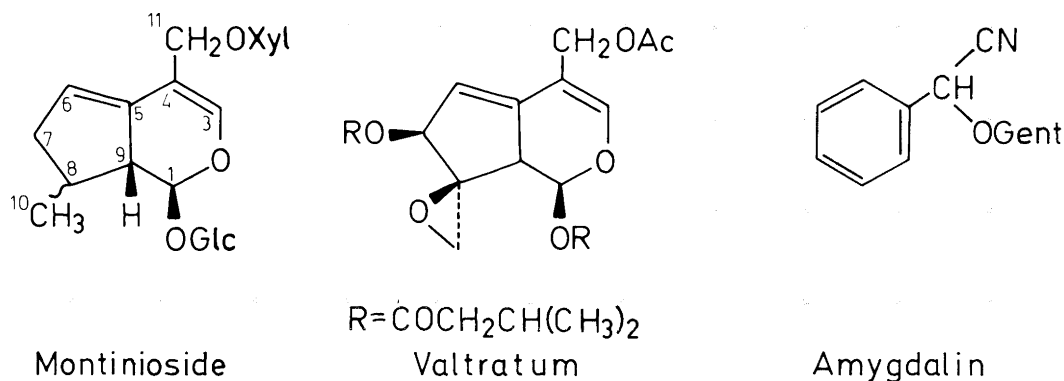


Fig. 1. Montinioside, an iridoid found in *Montinia caryophyllacea*, and two model compounds mentioned in the text.

Schulze-Menz (1964) the members of Montiniaceae have unitegmic ovules. Metcalfe (1955), who studied the anatomy of *Montinia* and *Grevea*, found that great differences exist between the genera. However, neither possessed intraxylary phloem, which is noteworthy since Milne-Redhead regarded them as Myrtalean.

In view of these facts and the common opinion that Montiniaceae is a woody member of the former Saxifragaceae s.lat. – and one with unitegmic ovules like Hydrangeaceae and Escalloniaceae – its likely affinity is Cornalean. As most of the families included by Dahlgren (1975) in Cornales often contain iridoids, a test for these compounds in *Montinia caryophyllacea* was considered relevant.

Occurrence of iridoid glycosides

A synonym of *Montinia caryophyllacea* is *M. acris* L. fil., referring to the sharp taste of its leaves. This might suggest the presence of glucosinolates. However, preliminary tests on the seeds by M. G. Etlinger and E. Asmussen at the Ørsted Institute, Copenhagen, gave no indication of the presence of a thioglucosidase that hydrolyzes glucosinolates.

Dry leaf and stem material, kindly supplied by Dr J. Rourke, Compton Herbarium, Kirstenbosch Botanic Gardens, South Africa, was examined for iridoids. It yielded a new gentiobioside, which we have named montinioside.

Ground material (19 g) was extracted with ethyl acetate in a Soxhlet apparatus yielding 1.5 g of crude glycosides. These were dissolved in water and the

solute passed through neutral alumina. This gave a syrup containing 1.3 g (7%) of montinioside. The data after silica gel (CHCl_3 -MeOH; 3:1) chromatography are: $[\alpha]_D^{20} - 14^\circ$ (c 0.6 in MeOH) – $\lambda_{\text{max}}^{\text{MeOH}} = 251 \text{ nm}$ (log ϵ 3.83) – $^1\text{H NMR}$ spectrum (90 MHz, D_2O , DSS): 6.61 ppm (br. s, H-3); 5.70 ppm (br. d, $J = 1 \text{ Hz}$, H-6); 5.15 ppm (d, $J = 9 \text{ Hz}$, H-1); 4.36 ppm (m, 3 H, 11- CH_2 -O-Xyl and H-1'); 1.18 ppm (d, $J = 6 \text{ Hz}$, 10- CH_3) – $^{13}\text{C NMR}$ spectrum (22.63 MHz, D_2O , diox.): 145.0 ppm (d, $J = 191 \text{ Hz}$, C-3); 135.3 ppm (s, C-5); 123.1 ppm (d, $J = 164 \text{ Hz}$, C-6); 110.2 ppm (s, C-4); 103.6 ppm (d, $J = 170 \text{ Hz}$, C-1); 102.3 ppm (d, $J = 160$, C-1'); 99.5 ppm (d, $J = 163 \text{ Hz}$, C-1'); 76.7 (1C), 76.4 (2C), 73.4 (2C) and 70.1 (2C) ppm (d's, C-5', C-3, C-2 and C-4 of the two glycosyl units, respectively); 67.4 ppm (t, $J = 150 \text{ Hz}$, C-11); 65.7 ppm (dd, $J = 142/152 \text{ Hz}$, C-5''); 61.3 ppm (t, $J = 146 \text{ Hz}$, C-6'); 53.1 ppm (d, $J = 131 \text{ Hz}$, C-9); 40.7 ppm (t, $J = \text{ca } 135 \text{ Hz}$, C-7); 38.1 ppm (d, $J = 128 \text{ Hz}$, C-8); 19.3 ppm (q, $J = 126 \text{ Hz}$, C-10). After boiling with mineral acid for 2 h, glucose and xylose was detected in the hydrolysate, using TLC and authentic compounds.

A provisional structure for montinioside is shown in Fig. 1. Comparison with the model compounds valtratrum (Thies 1968, Thies et al. 1973) and methyl xyloside gave satisfactory correspondence with the appropriate functionalities in ^1H and ^{13}C NMR, respectively, viz. the ^1H NMR signals of H-3 and H-6 of valtratrum are found at 6.72 and 5.86 ppm, compared to 6.61 and 5.70 ppm for montinioside. With the exception of C-1', all the ^{13}C NMR absorption arising from the glucosyl and xylosyl moieties of montinioside fall within a range of 0.7 ppm of the corresponding signals from those of other iridoid glucosides and methyl β -xyloside, respectively. The coupling constant $J_{1,9} = 9 \text{ Hz}$ points to the *trans* relationship of H-1 and H-9, leaving only

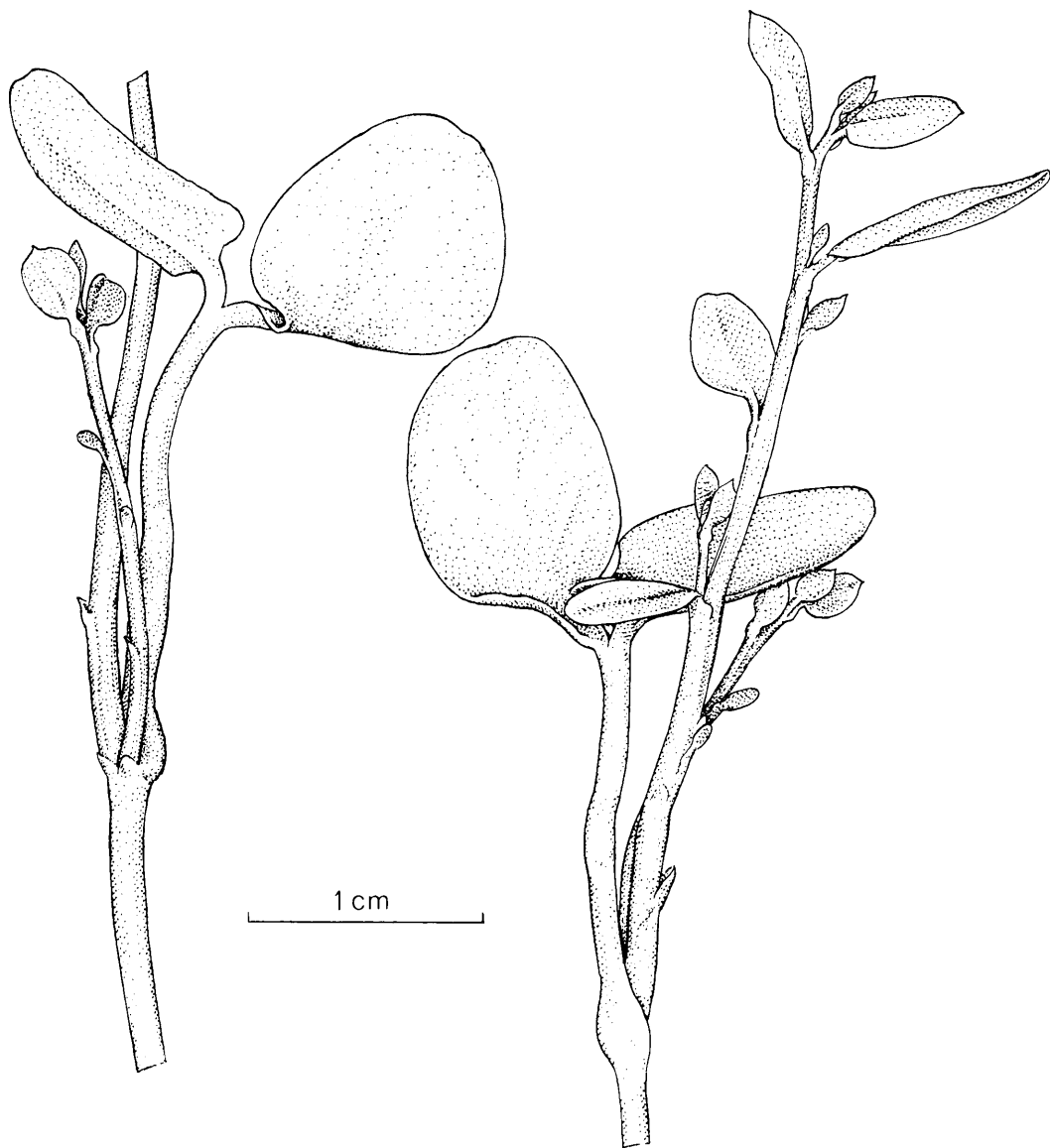


Fig. 2. Seedling of *Montinia caryophyllacea*.

the stereochemistry at C-8 to be determined. Finally, the UV-spectrum of montinioside corresponds to that of valtratum ($\lambda_{\text{max}}^{\text{MeOH}} = 256 \text{ nm}$; $\log \epsilon 4.04$).

The presence of a 5,6-double bond and an 11- CH_2OH group is a combination that has so far only been found in *Valeriana* iridoids. This is the first example of an iridoid containing a sugar different from glucose.

Work on the elucidation of the full structure of montinioside is in progress and will be reported elsewhere.

Seedling morphology

The unusual cotyledons of *Montinia* had already been observed by one of us (Dahlgren) and by Dr B. Peterson, Gothenburg, in 1957, although

the observations were neither documented nor reported at that time. The present material was grown from seed (kindly supplied by Dr J. Rourke, South Africa) in the Botanic Garden of the University of Copenhagen.

Very young seedlings have a normal appearance. The elliptic-ovate cotyledons, with a somewhat truncate apex, seem to be sessile, or have petioles which are less than one mm in length. However, the plumule, when breaking through, appears laterally some 10–15 mm below the bases of the cotyledon laminae, indicating that in fact the petioles of the cotyledons are connate. The stem (Fig. 2) on and above the level of the base of the cotyledon petiole, bears a number of small, scale-like leaves. Lateral branches develop in the axils of some of these and even – as seen in Fig. 2 – in the axil of the first leaf which develops above the cotyledons. In the material studied the first leaves following the cotyledons were constantly alternate. The leaf base is conspicuously pulvinous.

Conclusion

The assembled morphological evidence, including the presence of unitegmic ovules and the lack of intraxylary phloem, in combination with the presence and kind of iridoids, indicate a possible position of Montiniaceae in the order Cornales or close-by. The iridoids agree most closely with those found in *Deutzia* (Hydrangeaceae), *Viburnum* (Sambucaceae) and Valerianaceae of the orders Cornales and Dipsacales (Jensen et al. 1975). Iridoids have not been recorded in members of Celastrales, Myrtales or Saxifragales, in so far as these orders are circumscribed by Dahlgren (1975). The assignment of Montiniaceae to any of these orders, therefore, is not supported by the present results.

The fused petioles of the cotyledons in *Montinia caryophyllacea* is a peculiarity that should be looked out for in possibly-related genera.

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An unusual flowering strategy and new species in *Calathea*

Helen Kennedy

Kennedy, H. 1977 09 15: An unusual flowering strategy and new species in *Calathea*. *Bot. Notiser* 130:333-339. Stockholm. ISSN 0006-8195.

Two new species of *Calathea* (Marantaceae) are described: *C. gymnocarpa* from Panama and Costa Rica and *C. verecunda* from Panama. *C. gymnocarpa* exhibits a type of mass flowering, a phenomenon previously unknown in *Calathea*, which is accompanied by the disintegration of the bracts and prophylls.

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Calathea gymnocarpa Kennedy sp. nov. – Fig. 1, 2 A, B

Planta ad 1.4 m alta. Folia rosulata, petioli parte superiori glabra; lamina supra glabra, inferne minutissime tomentosa, trichomis uncinatis, statu juvenili, ovata acuminata supra viridia striata, lineis parallelis geminatis rubris vel albidis, inferne purpurea; lamina, statu maturo, elliptica vel oblongo-elliptica supra viridia, inferne griseo-viridia. Bracteolae mesophyllaque nulla. Bractea prophylla que fugacia. Florescentia circa una hebdomas.

Perennial rosulate herb, 0.8–1.5 m high, bearing 4–8 leaves. The inflorescence is terminal on the leafy shoot and is subtended by a bladeless sheath. *Cataphylls* rotting away, usually absent on flowering individuals, narrowly ovate, apex mucronulate, green abaxially in adults, purple in juveniles, minutely tomentose. *Leaf blade* leathery, tough, elliptic to oblong-elliptic, apex broadly obtuse to rounded, occasionally with an acumen, base unequal, rounded, abruptly shortly acuminate at the junction of the blade to the pulvinus, the midrib depression extending into the upper part of the pulvinus, 22–62 cm long and 16–35 cm wide in innermost leaf, 58–84 cm long and 30–43 cm wide in others. Leaf blade in juveniles shiny, dark green above with single or paired pink or white lines paralleling the lateral veins; dark red-purple below. Subadult leaf blade green above with two broad,

longitudinal yellow-green bands (one on either side of the midrib); grey-green tinged purple below. Adult leaf blade deep green above, shiny in young leaves, dulling with age, glabrous, midrib yellow-green, glabrous, toward leaf base subglabrous; blade dull grey-green below, minutely tomentose (hairs recurved, occasionally straight, less than 0.3 mm) mainly along veins and midrib, midrib yellow-green. *Pulvinus* broadly elliptic in cross-section, dark olive-green to yellow-green, glabrous, often acuminately extended along the upper side of the petiole, confluent with the petiole, (1.2–)4–7.5 cm long in innermost leaf, 5.3–9(–12) cm long in others. *Petiole* green, sparsely minute tomentose (hairs mostly straight, less than 0.3 mm), occasionally absent, when present up to 18 cm long. *Leaf sheath* not auriculate, membranaceous, the margins rapidly disintegrating, green to dark green, minutely tomentose (hairs straight, less than 0.3 mm), (3.1–)22–50(–66) cm long. *Stem* green, minutely tomentose (hairs straight or bifurcate), internode between bladeless sheath and innermost leaf up to 55 cm.

Inflorescence terminal, the scape bearing 2, occasionally 1, bladeless sheaths below the inflorescence, the bladeless sheath subtending the inflorescence often similar to the bracts, caducous, densely minute appressed tomentose, 6–18 cm long. Inflorescence 1 per shoot, ovoid, (8–)

9–15 cm high and 6–10 cm in diameter. *Bracts* numerous (over 30), membranaceous, spirally arranged, lower bracts ovate, middle and upper bracts narrowly ovate, apex somewhat eccentric, sub-obtuse to acute in lowermost bracts, acute to acuminate in upper ones, 3.5–5.1 cm high and (0.8–)1.1–1.8(–2.1) cm wide. Outer surface of bract pale green basally in very young bracts, the bracts quickly dying, turning a pale tan to cream-yellow, somewhat translucent at apex and margins, densely puberulent; inner surface glabrous. Each bract subtending up to 5 potential flower pairs, usually only 3 actually mature. *Prophyll* membranaceous, not truly bicarinate, the “carina” represented by two somewhat raised areas, ovate to narrowly elliptic, apex acute, translucent tan, densely minute puberulent; glabrous within, 2.3–3.5 cm high and 0.95–1.4 cm wide. *Secondary bracts* absent. *Bracteoles* absent. The common pedicel of the flowers cream, densely appressed tomentose, 2.5–4 mm long in flower, in fruit up to 1.3 cm, individual pedicels subequal, 1.5–3 mm long.

Sepals fugacious, membranaceous, often wrinkled at base, narrowly elliptic to narrowly ovate-elliptic, apex acute to acuminate, translucent tan, lower half sparsely pilose, upper half appressed pilose, (2.1–)2.4–2.9 cm long and (0.4–)0.5–0.85 cm wide. *Corolla tube* cream to pale yellowish, appressed pilose (hairs to 1 mm), 1.5–2.3 cm long, staminal tube 0.8–1.2 cm long; corolla lobes subequal, elliptic, slightly sigmoidal, apex acute, pale cream, sparsely minute pilose (hairs less than 0.3 mm), 2.6–3.8 cm long and (0.5–)0.7–0.95 cm wide. *Outer staminode* obovate, apex obtuse, faintly orange to apricot-colored, paler at margins, (1.8–)2–2.6 cm long and 1–1.4 cm wide. *Callose staminode* elliptic to broadly rhombic-obovate, petaloid, apical half reflexed, apex retuse, cream at base, pale orange above, darker centrally, (1.6–)1.9–2.8 cm long and 1.1–1.75 cm wide. *Cucullate staminode* cream apically, basal portion apricot, 0.8–0.9 cm long and 0.5–0.8 cm wide, provided with a subterminal filiform appendage. *Filament* with lateral petaloid appendage c. 1 mm; anther

free, 3–4 mm long. Style and stigma golden. *Ovary* cream-tan, densely villous (hairs tan), 2.5–3 mm high and 3–3.5 mm in diameter. *Capsule* fleshy, rough, obconoid, pale tan turning orange to red-orange at maturity, 1.3–1.4 cm high and c. 1.8 cm wide, occasionally the basal 1–3 mm of the shriveled sepals remains attached. *Seeds* usually 3 per capsule, smooth, subtrigonus to rotund, dark blue, 6–9 mm high and c. 6–7 mm in diameter, bearing a basal white aril to 2.5 mm high.

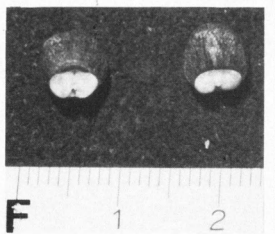
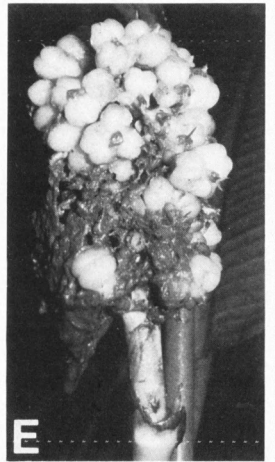
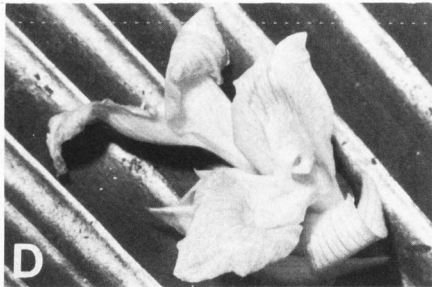
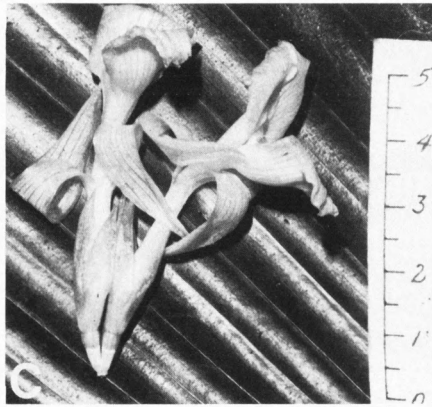
Type. Panama. Prov. Colón, Río Guanache, c. 1.5 miles upstream from the bridge, 10–20 m, wet lowland evergreen forest, 4.9.1974, Kennedy, Maas, Dressler & Toft 3393 (holotype F 1790971 and 1790970, isotypes F, GH, MO, U, US).

Other collections. Panama. Prov. Bocas del Toro, Almirante, Filo de Almirante, 1.12.1971, Kennedy & Dressler 1313 (F) – Costa Rica. Prov. Puntarenas, 10 km in on Pacific trail from Rincón, Osa Productos Forestales land, Osa Peninsula, 200 m, 2.3.1965, Lent 442 (F) – Prov. Heredia, original wet forest and cocoa plantation on the property of Dr L. Holdridge, c. 2 km upstream on the Río Puerto Viejo, c. 100 m, 10°23' N, 83°59' W, 5–6.1.1967, Burger & Matta U. (F) – Cultivated. Flowered at Kew 1914, Sander 485 (K) from material of Forget (Forget 2).

Calathea gymnocarpa flowers mainly during the rainy season, July through December. A fruiting specimen has been collected as late as early March. It occurs in the lowland evergreen wet forest and is found within the forest, in moderate to deep shade, as scattered individuals though occasionally it is locally abundant. It occurs in the wetter forests along the Atlantic lowlands of Costa Rica and Panama and the wet forests around the Golfo Dulce, Costa Rica, on the Pacific coast.

Calathea gymnocarpa can readily be distinguished from all other Central American Marantaceae by the distinctive pattern on the juvenile foliage. The upper leaf surface is dark green with pink or white lines paralleling the lateral veins; the lower leaf surface is red-purple. As a flowering individual, this species is distinguished by its capitate inflorescence, short flowering period (c. 1 week), the absence of secondary bracts (interphylls) and bracteoles,

Fig. 1. *Calathea gymnocarpa*. A: Habit. – B: Inflorescence in flower. – C: Flowers on upper surface of leaf. – D: Tripped flower showing shape of callose and outer staminodes; note pollen in the stigma. – E: Inflorescence in fruit; note the disintegrating bracts at left. – F: Seeds. – Scale in cm.



the rapidly disintegrating bracts and prophylls and the resultant cluster of exposed maturing capsules. These latter adult characteristics also distinguish this species from the related South American *Calatheas* which exhibit the same juvenile foliage pattern. The recurved hairs on the underside of the leaf distinguish the juveniles of *C. gymnocarpa* from other similarly patterned juveniles. There is a gradual transition in leaf pattern from the striped juvenile through the subadult pattern to the loss of the pattern altogether in the adult. The pattern on any given leaf is fixed, the type of pattern depends largely on the size (food reserves?) of the plant when that leaf was produced. If the rhizome of a mature plant is divided into small pieces, the new shoots will bear juvenile foliage, whereas if the rhizome is divided into a couple of moderate-sized pieces the new shoots will exhibit subadult foliage patterns.

The specific epithet *gymnocarpa* refers to the exposed position of the capsules after the covering bracts have rotted away. This species was observed to be pollinated by *Eulaema speciosa* at the type locality.

Flowering and fruiting in *Calathea gymnocarpa*

The flowering period of a single individual of *Calathea gymnocarpa* is quite short, probably lasting only a week or so. All the bracts in the lower third to half of the inflorescence bear flowers the first day. By the second or third day all the bracts in the inflorescence bear mature flowers. The time between the anthesis of the first pair of flowers and second pair of flowers within a bract is very short. During flowering, the bracts begin to disintegrate and, within a week or so, both the bracts and prophylls have rotted off, revealing the cluster of developing capsules. This short flowering time is quite unusual in the Marantaceae. Though mass flowering is known for a number of tropical trees and shrubs (Janzen 1967, Gentry 1974), it has not been reported in *Calathea* and is not known in any other species of Central American Marantaceae. In the majority of

Calatheas, only a few flowers are produced each day over a long (over 2 months) period; both mature capsules and flowers can be found together on the same inflorescence.

Another unusual aspect of the reproductive biology of *Calathea gymnocarpa* is the rapid disintegration of the bracts and prophylls which begins during flowering. In this species, both the secondary bracts (interphylls) and the bracteoles have been lost, whereas the secondary bracts (and usually bracteoles as well) are present in related species. However, in the most closely related species, *C. inocephala* (O. Ktze) Kennedy & Nicolson, the bracteoles are also absent. The bracts also die back shortly after the initiation of flowering in the related species *C. inocephala*, *C. altissima* (P. & E.) Koernicke and *C. grandis* Petersen, but in these species the bracts, or remnants thereof, remain on the inflorescence.

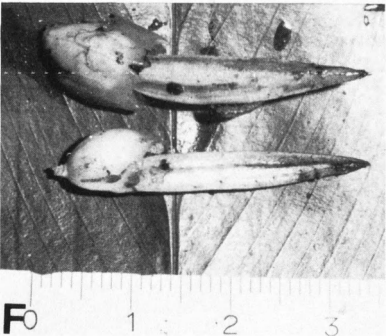
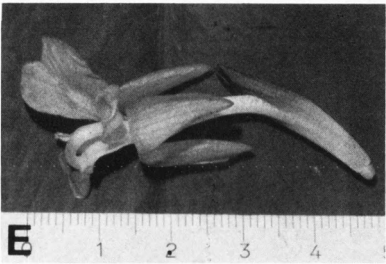
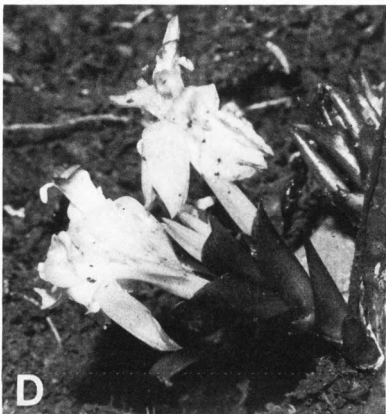
The bracts of a *Heliconia* which occurs with *C. gymnocarpa* at the Río Guanche locality also disintegrate completely and leave a cluster of capsules closely resembling that of *C. gymnocarpa*. In the *Heliconia* the capsules are red rather than orange or red-orange. The habit of the *Heliconia* is likewise similar to *C. gymnocarpa* and is rather atypical for *Heliconia*. The convergence in inflorescence position and manner of fruit presentation suggests that there has been selection for utilization by both species of a common dispersal agent, most probably a bird. Clearly a detailed study of the biology of both the *Calathea* and *Heliconia* is needed to understand the evolutionary significance of the striking similarity between them.

Calathea verecunda Kennedy sp. nov. –

Fig. 2 C–F

Planta ad 70 cm alta. Folia 1–2, raro 3–4; lamina, pulvino, petiolo et vagina utrinque glabra. Spica e rhizomate; bracteis 6–15 glabris, extus atropurpureis, intus viridibus; paria florum bracteolis 4 comitata; prophyllis bicarinatis ad 1.6 cm longis, ovoides ellipticisve, glabris, apice rotundata; corollae tubo ad 3.1 cm longo, albo; staminodiis exterioribus et callosis pallide purpureis.

Fig. 2. A–B: *Calathea gymnocarpa*. A: Juvenile foliage. – B: Subadult foliage. – C–F: *Calathea verecunda*. C: Habit. – D: Inflorescence. – E: Flower on upper surface of leaf. – F: Capsule with persistent calyx on leaf. – Scale in cm.



Perennial, rhizomatous herb, 30–70 cm high. *Rhizome* 0.3–0.8 cm in diameter. Shoots bearing 1–2, rarely 3 or 4 leaves. *Cataphylls* thin, papery, narrowly ovate, apex obtuse, mucronulate, green when young, often dried up on mature individuals, glabrous; innermost cataphyll 13–28 cm long. *Leaf blade* pliable, somewhat leathery, narrowly ovate, apex caudate-acuminate, base obtuse to rounded, junction of blade to pulvinus abruptly shortly acuminate, 15–31 cm long and (4–)5–8 cm wide. Leaf blade above dark green, glabrous, midrib lighter green, glabrous; leaf surface below slightly lighter, almost concolorous, glabrous. *Pulvinus* oval in cross-section, strongly curved, olive-green, glabrous, articulate with petiole, 0.5–1(–1.5) cm long. *Petiole* round in cross-section, deep green, glabrous, 17–47 cm long. *Leaf sheath* not auriculate, dark green, darker at base with slight purplish tinge, glabrous, (3.5–)7–23 cm long; base of sheath swollen, pale white-tan or pinkish. *Stem* tan, tinged pinkish.

Inflorescences one to two associated with a leafy shoot, arising directly from the rhizome, ovoid, bracts imbricate, 2.5–4.2 cm high and 1.7–2.2 cm in diameter. *Peduncle* purple, glabrous, 0.9–4.5 cm long. *Bracts* 6–12(–15) in number, herbaceous, spirally arranged, ovate to narrowly ovate, apex acute to acuminate, upper bracts longer and narrower than basal ones, apex subpatent, 1.9–2.5 cm high and 1.2–1.7 cm wide. Outer surface of bract red-purple at the very base, the rest dark purple, glabrous; inner surface green, glabrous; each bract subtending 2 or more flower pairs. *Bicarinat* *prophyll* membranaceous, narrowly ovate, apex acute, translucent faint greenish, tinged purple apically, glabrous, 1.5–2 cm high and 0.5–0.6 cm wide, carina to carina, 0.8–1 cm wide, total width. *Secondary bracts* membranaceous, ovate to elliptic, apex rounded, translucent faint greenish, tinged purple apically, glabrous, 1.2–1.6 cm high and 0.4–0.8 cm wide. *Bracteoles* 4 per flower pair, 2 lateral, channeled, and 2 central, channeled, faint greenish to transparent below, apex tinged purple, glabrous, 0.9–1.8 cm high and 0.2–0.6 cm wide, the lateral ones longer and wider than the central ones.

Sepals herbaceous, narrowly obovate, apex acute to obtuse, lower 1/2 white, green above, apical margin tinged purple, glabrous, 2.3–2.4

cm long and 0.3–0.45 cm wide. *Corolla* tube white, glabrous, 3–3.1 cm long; corolla lobes subequal, ovate-elliptic, apex obtuse, the margins inrolled appearing acute, white, occasionally tinged purple at the apex, glabrous, 1.7–1.8 cm long and 0.6–0.8 cm wide. *Outer staminode* transverse broadly elliptic, clawed at base, apex emarginate, lavender, the basal portion white, 1.4–1.6 cm long and 1.3–1.5 cm wide. *Callose staminode* almost totally fleshy, apex obtuse to irregular, white below, apex light to dark purple, 1–1.1 cm long. *Cucullate staminode* white, 0.6–0.7 cm long and 0.5–0.6 cm wide, provided with a subterminal filiform appendage. *Filament* white with lateral white petaloid appendage to 1.5 mm wide; anther white, 2 mm long. Style and stigma white. *Ovary* cream-white, smooth, glabrous, 2.5–3 mm high and c. 2 mm wide. *Capsule* obconoid, trigonous, apical edge of one face irregularly tridentate, white to light green, 1–1.1 cm high and 0.8–0.9 cm wide; crowned by a persistent, live, enlarged calyx. *Seeds* usually 3 per capsule, trigonous, rugose on the outer surface.

Type. Panama. Prov. Panamá, La Eneida, region of Cerro Jefe, 3.3.1973, Dressler 4285 (holotype F 1790790, isotypes MO, US).

Other collections. Panama. Prov. Panamá, km 20 on the El Llano–Carti road, 22.2.1973, Kennedy & Dressler 2575 (DUKE, PMA); km 12–13 on the El Llano–Carti road, evergreen wet forest, 380–420 m, 25.2.1976, Kennedy & Dressler 3517 (F).

This species flowers mainly in the dry season, February through May. It occurs in moderate to deep shade within the forest on well-drained slopes, often near the base of large trees.

Calathea verecunda is distinguished from other Central American species by the inflorescence borne on a separate shoot directly from the rhizome (not terminating a leafy shoot); by the glabrous leaf blade, pulvinus, petiole and sheath; by the 6–15 dark purple, glabrous bracts and almost totally fleshy callose staminode. It is similar to *C. bachemiana* E. Morren in aspect but differs in having a plain green rather than a patterned leaf, a shorter (1.6 versus 2.3 cm) outer staminode, a callose staminode dissimilar in shape to the outer staminode and a lavender rather than a white flower. *Calathea verecunda* differs from the other species of *Calathea* which have the inflorescence(s) borne

on a separate leafless shoot by the following characters: the absence of clavicate bracteoles, the narrowly ovate leaf, and the glabrous bracts and pulvinus.

This species was referred to for several years as *Calathea* "unknown", as numerous seedlings and vegetative individuals were found but flowering individuals were still unknown, hence the epithet *verecunda*, meaning modest, shy or bashful.

Acknowledgements. I wish to thank Dr Robert Dressler for making possible the collection of these species in the field and Dr John Fay for his help with the Latin descriptions.

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Botanical literature

Gams, W. 1971: *Cephalosporium-artige Schimmelpilze (Hyphomycetes)*. X + 262 pp., 137 figs., 3 plates. Gustav Fischer Verlag, Stuttgart. Price (bound) 86 DM.

A great number of exceedingly different fungi have been placed in the genus *Cephalosporium* Corda (1839). Most of them are mould-like Hyphomycetes, which produce simple or ramified, sometimes synnematous, usually hyaline conidiophores with phialides and dry, one-celled conidia in chains, or slimy conidia in heads. The difficulty in circumscribing *Cephalosporium* and "allied" genera, such as *Acremonium*, *Paecilomyces*, and *Verticillium*, has resulted in numerous transfers of species between these and other genera. In spite of the recent studies published by several authors, no overall survey of these fungi was available. This is what Gams has tried to provide, and his task has not been easy. Not least the perusal of the literature must have been laborious, since accounts of the species have appeared in many different kinds of publications.

The general part of the monograph includes sections on methods, morphology, history, unaccepted genera, correlated Ascomycete genera, a full bibliography, and a key to all *Cephalosporium*-like genera in the widest sense. The special part contains descriptions, nomenclature, keys to and illustrations of the taxa, lists of cultures and of the herbarium specimens studied, and a list of excluded species (not complete). A third part provides surveys of certain ecological groups (species present in soil, on plants, chitin, animals, fungi, man, and antibiotic-producing species). The work ends with a glossary, an English translation of all keys, and an index.

The imperfect genera dealt with are: *Acre-*

monium (82 species), *Tilachlidium* (1), *Septofusidium* gen. nov. (1), *Monocillium* (13), *Verticillium* (20, light-coloured species only), and *Aphanocladium* gen. nov. (2). Unnamed conidial states of *Emericellopsis* (5), *Calonectria* (1), *Wallrothiella* (1), and some marginal species are also included. Two genera, 39 species, 3 sections, 5 "series", one name, and some 70 combinations are new, the last-mentioned mostly in *Acremonium*. *Cephalosporium* itself, however, is excluded because its original species are probably Phycomycetes of the genus *Mortierella*.

Gams uses a special terminology, which is partly his own, to describe different modes of growth on agar, the ramifications of the conidiophores, the position of the phialides, and the shape of the conidia. Notwithstanding, most of these terms seem superfluous. 'Ellipsoidal', for example, tells as much about the conidial form as "homopolar-polysymmetrisch" (p. 9), a term borrowed from palynology. To distinguish between synnema and coremium (p. 6) also goes against current practice. The author's ambition is understandable, however, bearing in mind the difficulties in finding diagnostic characters for these organisms.

In the discussion, some phenomena of taxonomic importance are pointed out. A catenate or capitate arrangement of the conidia seems to be specific characters only or even modifications strongly influenced by different substrates and moisture conditions. Substrate type and the age of the colonies govern the form and size (length) of the conidia. Not even the pigmentation and ornamentation of the conidia and conidiophores appear to be useful as generic characters.

These aspects have led Gams to adopt a wide generic concept, as is manifested by his

treatment of i.a. *Acremonium* and *Verticillium*. The former genus has conidial states in several Ascomycete families, and has devoured the whole of *Gliomastix* (as a section) and some species of *Paecilomyces*. Many *Nectria* imperfects form another section. This is disputable taxonomically, but is dictated for practical reasons. The dilemma lies in the acceptance of form-genera, which conflicts with a striving towards natural groups correlated with possible perfect states. It is the reviewer's opinion that if the *Nectria* imperfects be recognized as a section, one might just as well separate them at generic level, and, if not, then the section would be better deleted.

In *Gliomastix* s.str. the species possess pigmented conidia, but are related to hyaline-spored species, all of which have "chondroid" hyphae with thick, light-refractive walls. It would perhaps have been preferable to have kept *Gliomastix* at generic level in the one or the other sense. *Verticillium* has also become an unwieldy genus by the inclusion of species from both the Hypocreaceae and Clavicipitaceae. In other cases the classification adopted is simpler. *Monocillium*, for example, is easily defined in morphological terms, and, besides, belongs to only one perfect genus, *Niesslia*.

There are some nomenclatural errors. *Acremonium* sect. *Simplex* contains the type of the generic name and must thus bear the name *Acremonium*. The five "series" in *Gliomastix* are not validly described and series *Murorum* shall be named *Gliomastix*. *Acremonium* sect. *Nectrioidea* has not been typified and is accordingly illegitimate. Nor is it clearly indicated whether the types of all the new specific names are based on dried or living specimens. The present rules do not permit typifications based on living cultures, a clause laid down already in the 1966 Code of Nomenclature.

The author has been painstaking with the type investigations, but in many cases there was simply no material available. He has been very restrictive in his use of old names if there were any doubts attached, and he has also adopted a fairly narrow species concept. It is easy to sympathize with his motives here, but a number of name changes will certainly follow when the older type collections are eventually traced. Gams founds his descriptions mainly on living cultures (in Baarn), and has evidently

revised only a few samples in other herbaria.

The present monograph is on the whole very impressive. One must appreciate this serious effort to bring order and system into such a difficult group of fungi. Gams has also arranged the text in a very straightforward manner, to which e.g. the synoptic key to *Acremonium*, the ecological surveys, and the translations for English-speaking readers bear witness. The author is to be congratulated on having produced a work of lasting value.

Nils Lundqvist

Gottschalk, W. 1976: *Die Bedeutung der Polyploidie für die Evolution der Pflanzen*. Fortschritte der Evolutionsforschung, Band 7. 511 pp., numerous figs. Gustav Fischer Verlag, Stuttgart. ISBN 3-437-30221-3. Price DM 210:.-

Discovery is a cumulative process, which includes not only the important phase of collecting and describing data of objective facts, but perhaps still more the philosophical evaluation that places new observations into their reasonable perspective. Because of the great importance of the latter, every scientific approach is, at a certain stage, in need of a basic synthesis of what has become known by aid of the descriptive and comparative methods. If that synthesis is comprehensive enough, then, at least for a time, a periodical upgrading through partial reviews is usually satisfactory, until adjustments in the general philosophical position require a new and extensive reevaluation. This is true in all branches of knowledge, but it is perhaps most important in the disciplines related to organic evolution, the correct explanation of which is basic to most of the biological sciences and their practical application.

To paraphrase Kipling, there may be nine and sixty ways in which the evolution of life has proceeded. Extensive investigations of the part of this event that has been called speciation indicate that it may not be a continuous process as frequently suggested but a stratified stability of ladderlike advances, each step of which apparently being protected from oblivion by something called reproductive isolation. Numerous studies of many plants seem to indicate that the complex phenomenon of poly-

ploidy may have been the most important of these processes in eukaryotic plants with a localized centromere. Since no other genetical incident has been as widely investigated by population geneticists, its relative significance may, of course, be somewhat overrated; but that does not diminish the fact that polyploidy is a very important evolutionary process.

An issue so significant and so extensively studied must be reviewed and synthesized regularly so that its implication can be appraised and its progress directed into areas of possible neglect. Such reviews have, indeed, been published a few times for certain aspects of polyploidy, although still nobody seems to have attempted to compile a comprehensive philosophical and interpretative synthesis that could help to find its exact place in the modern understanding of life and thus clarify many observations that still appear to be ambiguous.

The main reason for the lack of a general synthesis of our present knowledge of polyploidy is probably the magnitude of the task, because few biologists have the energy or even ability for a detailed scrutiny, digestion and philosophical evaluation of more than ten thousand reports and books in which polyploidy has been described and discussed during the past three quarters of a century. Perhaps the solution lies in an organized division of the work between carefully selected members of a team of conscientious and energetic specialists who afterwards could together compose, as a kind of a conclusion, a comprehensive philosophical summary on basis of the more special reviews. At present such a team seems to be nonexistent, or perhaps its possible organizer and leader is nodding?

The most extensive digest of any part of the polyploid process has just become available in a book on the significance of polyploidy for the evolution of plants, written by Professor Werner Gottschalk of the University of Bonn, who is also the author of a synopsis of the evolutionary significance of gene mutations. After having examined a substantial part of the tremendous literature on the subject, he places the main emphasis on a survey of the characteristics of experimentally produced polyploids because he is of the opinion that this is necessary for establishing a firm basis for the identification of natural polyploids. Even that is a gargantuan

task. Although the author has avoided the much needed philosophical part of the explanation, and the importance of polyploidy for speciation by forming an effective reproductive barrier between gene pools in which its fundamentality for evolution is most significant, and, therefore, limited his search to a single, albeit important, area of the subject, he has, in the view of this reviewer, succeeded amazingly well in writing a synopsis of considerable weight.

Professor Gottschalk divides his treatment into eighteen chapters. The essential chapters discuss experimental and natural polyploids, anorthoploids, aneuploids, and the distribution of polyploids, with an emphasis on means to identify and distinguish autopolloids and allopolloids in nature. Of course, some of the chapters are more detailed than others, for various reasons, and some are by necessity shallow for lack of information. It is a pity that the introductory chapter, on theoretical viewpoints for the evaluation of polyploid plants, is rather incomplete and philosophically weak, as are some conclusions regarding certain other basic phenomena elsewhere in the synopsis, but weaknesses of that kind are amply compensated for by the genuine thoroughness of the descriptive chapters that form the bulk of the book.

In such a large text all geneticists will find a wealth of important observations gathered from many sources. It is, however, inevitable that some specialists may join issue on various conclusions or even question the wisdom of the selection of references by the exclusion of others, and the size of the work makes it ideal for nitpickers. The present reviewer would have liked to see a more solid evaluation of the differences between various kinds of polyploids based on their assumed origin and later evolution and a more advanced classification into groups than is met with in the system adopted, which is essentially that of Stebbins in 1938, when less than one-fifth of the literature on the subject had been published. It could also have been emphasized more strongly that most of the knowledge of the physiology of polyploids is based on much too few and much too preliminary investigations published a generation ago so that the field is actually widely open for a modern and extensive attack which could benefit immensely from being connected with sound ecological observations. From the point

of view of some readers, it may seem unfortunate that the author apparently follows the 18th century philosophy of nominalism in his weak concept of the taxonomic categories, as is prevalent among many modern botanists but certainly contrary to all genetical and evolutionary concepts that are strictly empirical and materialistic. Furthermore, the author tends to accept uncritically most original reports, even when later papers, which he frequently ignores, have corrected their mistakes. Therefore, some of his conclusions and a few of the most elaborate tables must be taken with a grain of salt. This is, for instance, the case with Tables 6 and 7 which are characterized by the inclusion of many old and very doubtful examples of so-called "intra-specific polyploidy", which itself is an idea that may look as a nominalistic anachronism in a book on evolution. Actually, much too many of the almost 200 examples of such "species" are worthless because they were originally based on direct misidentification, downright misunderstanding, or lack of taxonomic skill by the original authors so that a more critical scrutiny would have reduced them to perhaps a handful of still doubtful cases. But a strict adherence to the uncritical principle adopted ought to have increased such "examples" manifold because even the so-called scientific literature abounds in superficial observations.

In the important discussion on the frequency of autopolyploids and allopolyploids it is, correctly, pointed out that the great majority of such plants are intermediate, whereas pure autopolyploids and strict allopolyploids are claimed to be rare. I am in no doubt that this is correct as far as their success and natural occurrence is concerned. However, I would like to add the observation, based on numerous studies of large samples of germinating seeds of many species of gymnosperms, monocots and dicots, that strict autopolyploids seem to be formed in a low permille frequency in all plants of which large samples have been studied, and perhaps in all populations of all plants; but if a seed gives rise to an autopolyploid individual, this plant is likely to be weak and soon selected away, which may be the reason for that such polyploids are rare under natural conditions. Likewise, a special emphasis could have been given the important remark by Müntzing and only hinted at in the

book, that strict allopolyploids, produced from completely sterile hybrids between unrelated species, are likely to be entirely missing and to occur only in theory except after a thorough secondary differentiation of intermediate polyploids has taken place, for the simple reason that species with fully unrelated chromosomes cannot hybridize. Such minor remarks that could be made also on some other questions demonstrate the difficulties that any scientist must inevitably encounter when attempting such a wide synthesis, but small inaccuracies of fact and especially of judgement are human and cannot be escaped even by the most careful of compilers. And none of the more or less trite comments above can lessen the fact that the author has succeeded unusually well in his difficult task.

As a conclusion it is only fair to admit that it is the nature of most synoptic work not to be complete or even exact, although this text is unusually thorough and inclusive in the fields it covers. It was planned to embrace only some of the literature on the significance of polyploidy in evolution. For practical reasons the author shuns all discussion on the more general significance of polyploidy that some readers might have preferred. Therefore, the book may fall short of satisfying the need for an interpretative synthesis of polyploidy as a whole, but its virtue lies in its comprehensiveness rather than in its completeness in the areas it wants to cover. There has apparently been some difficulty in composing the bibliography of about 2500 titles, because some papers mentioned in the text are missing. The register is hardly sufficient for a work of this magnitude, and a few but insignificant printing errors will probably please those who find such matters to be important. But since this is by far the most important review of polyploidy ever published, it must be highly recommended to all botanists and geneticists interested in population biology, basic or applied, and, especially, to those working in the fields of evolutionary botany.

Åskell Löve

Lundqvist, J. et al. 1974: *Survey of the vegetation conditions in the catchment area of river*

Vindelälven, northern Sweden. 332 pp., 10 figs., 37 plates and 10 tables. SNV PM 409. Statens Naturvårdsverk, Stockholm.

Lundqvist, J. & Wistrand, G. 1976: *Riverside vascular flora in the upper and middle catchment area of the river Skellefteälven, northern Sweden*. 175 pp., 19 figs., 3 maps and 8 tables. Växtekologiska Studier 9. Uppsala. ISBN 91-7210-806-6.

From times immemorial human progress has depended upon the wise and effective exploitation of natural resources. Until the scientific method was invented, attempts to regulate even simple phenomena were frequently so groping that success was easily replaced by disaster. This is amply documented by history even from Scandinavia, when great lakes or rivers were tampered with through mistaken foresight. Even during recent times technological advance without scientific planning has sometimes caused unexpected harm so that unwarranted pollution or other disturbances by technologically desirable projects has endangered animals and plants and even human habitations over large areas, though such difficulties are frequently counteracted by natural regulation when time passes.

A continued but scientifically guided regulation of natural phenomena is certainly required for the improving of the conditions of life even for others than the fortunate few in all parts of the world. Of these conditions, the harnessing of energy seems to be the most widely discussed at present, not least because it is frequently connected with dangerous pollution or disturbance of other vitally important natural resources or with the impairing or destruction of ecosystems that may be essential for present or future production of food, maintenance of health, or simply for the well-being of human beings who still do not live on bread alone.

Sweden, which leads the development of the welfare state that the entire world will hopefully enjoy in the centuries to come, also stands in the front in the exploitation of water power which forms one of the essential pillars of its industrial strength. During the past generation, most of the large Swedish rivers have been thoroughly developed for hydroelectric power by aid of artificial reservoirs that sometimes have caused the transformation or even extinction of irreplaceable vegetation at the

same time as it has led to the quieting of some of the most beautiful waterfalls in the world. In most cases this technological progress has been preceded by some biological investigations on which were based recommendations for modifications that favorably counteracted some of the negative effects of the technologically desirable projects and, sometimes, even led to their rejection.

Two recent publications demonstrate the approaches and methods of Swedish botanists studying the ecosystems of large river valleys before and after the technologists exploit them for much needed electrical power. The first of these, which is a survey of the condition of the vegetation in the catchment area of the river system Vindelälven in northern Sweden, is a 1974 report of a detailed floristic and ecological study that was initiated by the great late ecologist Professor G. Einar Du Rietz in 1961 and carried out by several well qualified botanists under the able leadership of Dr Jim Lundqvist, who compiled the report. This river is in its lowest parts confluent with the river Umeälven, which was heavily exploited during the past two decades, whereas Vindelälven remains largely unregulated so that it is a worthy object for vegetation studies of a resource prior to technological progress. The second book is a similar study of the river Skellefteälven, which is one of the most thoroughly exploited river systems in northern Scandinavia. Several ecologists have investigated this area in cooperation with the authors of the report, Dr Jim Lundqvist and Dr Gunnar Wistrand, who claim in the introduction that the regulation of this river system, made mainly during the past 15 years, has been so severe that a considerable part of the original ecosystems may be regarded as totally destroyed. In other words, the two publications describe a boreal ecosystem before and after a severe and perhaps disastrous exploitation.

The Vindelälven book begins with an historical review of botanical studies of this large area, which was visited by Linnaeus in 1732 and by some later botanists, although more extensive observations on the flora were hardly made until during the present project. The topographical and geological conditions are summarily described, as are also the effects and characteristics of various human activities since

the colonization of the area began in the 18th century. The bulk of the book, however, reviews the zonation and floristic composition of the vegetation of the river banks and valleys which reach from the spruce forests of the lowlands through the pine forests and mixed forests of the montane areas to the birch forests and tundra zones of the subalpine and alpine regions. The floristic composition at numerous sites has been analysed exactly and in great detail both qualitatively and quantitatively to demonstrate the wide variation and extreme richness of the vegetation. It is a pity that the magnitude of the task has not yet allowed a detailed phytosociological analysis of all sites studied, because that would evidently also have shown an unusual assemblage of plant associations at various stages of development. The floristic review concludes with a survey, by Gunnar Wisstrand, of the distribution and lower limits of the alpine plants and a review of some of the rare species met with in the area, and a chapter, by Sten Nordenstam, on the many species of the apomictic genus *Hieracium* that are characteristic of this part of northern Sweden. Then come a few conclusions concerning nature protection, by Jim Lundqvist. There is an index of species mentioned in the text, and the book ends with 37 excellent photographs.

The Skellefteälven text reviews first the geography of the area and surveys the exploitation of this large river valley as explained by aid of an impressive map of the extensive regulation of the river, before delving into a discussion of the flora of the region as influenced by the recent technological advance. As could be expected, the vegetation near still undeveloped tributaries and on the mostly unaffected mountains remains conspicuously rich in species, and the plant associations in these places are undisturbed, whereas the flora of the riverbanks within the regulated area has been drastically reduced so that many of the lowland species seem to have been exterminated and most of the associations deranged beyond recognition. Fortunately, there have been left some pockets of less disturbed forests rich in species from where some plant associations might perhaps disperse for a partial recovery of the area when the artificial situation has stabilized, although complete recovery may require considerable and expensive human

assistance. The destruction could, of course, have been minimized and the recovery simplified if a study like that of the Vindelälven had preceded the technical exploitation and been used as a basis for the selection of protected areas from where vegetation could invade the affected grounds, without restraining the certainly necessary technical development.

The investigations of these large river systems and the vegetation that is dependent upon them could be used as models for the planning of extensive exploitation in other parts of the world. They clearly show that even modest floristic-ecological studies by taxonomically competent ecologists are of the greatest importance in planning large technological projects in such a way that even drastic engineering projects could avoid disastrous effects on other natural resources. It is evident that the vegetation near Skellefteälven has been seriously though hardly irreparably hurt because the mistaken but well-intentioned eagerness of the technologists blinded their foresight and even the biologists may have been sleeping on their guard. Similar mistakes caused by a lack of proper safety measures are still being made in connection with mining and industrialization in many parts of the world, especially where the supply of conscientious and properly competent floristic ecologists is scarce or where their rare existence is ignored by technologists and bureaucrats who themselves may have little understanding for the need for an environmental protection so they are satisfied by only paying for so-called environmental impact studies that are worthless because they were made without honest qualifications that border to fraudulence. These superb Swedish studies could not have been done by ecologists without a profound floristic training, and they would also have been impossible if the flora of Scandinavia had not been thoroughly covered by critical and modern flora manuals, which are the most important tools of botanists of either basic or applied learning.

The energy requirements of the industrial welfare state seem to increase exponentially as long as the population explosion is not effectively restrained. Since hydroelectric power evidently is less expensive and less polluting than other presently available energy, it is understandable that those who are responsible

for industrial progress find it desirable to utilize every available river to the utmost. Presently, all but four large Swedish rivers have been ultimately harnessed, and the time is rapidly nearing when those that are left also have to be utilized. Perhaps it is permissible to suggest, however, that the politicians and technologists look into the hardly unreasonable wish that these rivers could for ever be left untouched by developers so that unborn generations will be able to enjoy limited recreation in the pristine surroundings of great Scandinavian waterways and to profit from the natural beauty that always has stimulated the creative minds of poets and thinkers. The Vindelälven area seems to be a most ideal Scandinavian reservate for a total protection against all so-called developments, at the same time as the present study could serve as the first step towards an extended and detailed biological and geographical research and restricted experimentation. Perhaps most of all, a strict but scientifically guided conservation of such an area could create a northern Scandinavian enclave for effective conservation of the natural genetical diversity of the biota and thus become the first and most essential step towards establishing a worldwide network for the protection of the gene-pools which form the basis for life on planet earth.

Åskell Löve

Tzvelev, N. N. 1976: *Zlaki SSSR-Poaceae USSR*. 788 pp., 9 figs., 16 tables with drawings. Nauka, Leningrad. Price 5.26 rubel.

Until recently, the classification of grasses into genera and species has been based largely on the structure and arrangement of their spikelets. Emphasis on such characteristics led to some very artificial groupings so that natural genera were split and unrelated groups united. During the past four to five decades, beginning with the extensive review of the cytology of grasses by Avdulov, increasing attention has been devoted to evolutionary and anatomical aspects. These studies have yielded much evidence of relationship and resulted in a more natural classification, although further investigations and experiments are still needed before all genera and species of grasses can be satis-

factorily circumscribed and placed logically in the new evolutionary system.

A critical review of all the grasses of the world has never been compiled, and most of the available manuals are largely outdated because they were either published before or ignored the recent revolution in grass systematics. Therefore, a modern manual of the many grasses of the Soviet Union, by N. N. Tzvelev, is highly welcome, and hopefully it will soon lead to similar manuals for other large areas.

The book includes a considerable proportion of the species and genera of this large family, which has been estimated to comprise perhaps 500 genera and about 8000 biological species. It first reviews the history of exploration of the flora and especially the grasses of this region, and then explains the modern background of the revision in great detail on more than 40 pages. Since this is the most concentrated and comprehensive review of the principles of modern grass systematics available in any language, it is to be hoped that the author soon will find it possible to publish it separately in English or German to make it available to others working with the classification of grasses. The bulk of the text is devoted to the taxonomic part, which begins with a description of the family Poaceae and a sixteen pages long key to the 177 genera that are included in the book. The genera are grouped into 28 tribes and numerous subtribes.

Every genus is given its valid Latin name, with proper references to authors and synonyms, if any, and then described in detail. Types or lectotypes are listed for each genus and a mention made of the diversity and of the general distribution of the taxon as a whole. When more than a single species are met with, a comprehensive key follows, aided by some good drawings of taxonomically important details. Thereafter, sections, if any, are concisely described, often with types or lectotypes mentioned, before each species is listed without description except in keys but with proper nomenclatural references, information on flowering times, distribution, the somatic chromosome number if known, and certain other pertinent information when available.

The classification at the generic level reflects the modern idea that all the species of a good genus must be related through a linear-branched

evolution from a common ancestor. Although other characters are utilized for their identification, the author puts a strong emphasis on basic chromosome number and karyotypes to delimit the higher categories down to the generic level. The common basic numbers in grasses are $x=5, 7$ and 9 , but the highest number is $x=12$ and the lowest $x=2$, which is represented in the Soviet Union by the genera *Colpodium* s.str., *Molineriella* and *Zingeria*. Most of the generic names are, naturally, familiar to botanists elsewhere although some have been little used, but many are circumscribed more exactly than has been customary, and others are new because the more precise concept requires splitting of collective units or the lumping of others that have been found to be biologically similar.

One of the more important groups for which a new and improved classification is presented is the tribe Triticeae, which is subdivided into three subtribes and seventeen genera on basis of recent experimental and karyological evidence. The subtribe Triticinae comprises the genera *Elymus* s.str., *Elytrigia*, *Agropyron* s.str., *Eremopyrum*, *Heterantherium*, *Amblyopyrum*, *Aegilops*, *Triticum*, *Dasypyrum* and *Secale*. The subtribe Hordeinae includes the genera *Hystrix*, *Leymus*, *Psathyrostachys*, *Hordeum*, *Hordelymus* and *Taeniatherum*, whereas the subtribe Henrardiinae contains only the genus *Henrardia*. This is a great improvement from the conventional treatment of these taxa as a few unnatural and collective genera some of which combining genera here grouped into different subtribes, although one may wonder why a part of *Aegilops* as here defined has not been transferred to *Triticum*, and why the perennial genus *Critesion* has been left as a subgenus of the otherwise annual *Hordeum* s.str. with which it can hardly be hybridized experimentally. Since some of the genera cross occasionally, the author accepts a few hybrid genera to accommodate these ephemeral taxa of the tribe. Although the present reviewer agrees with this treatment, he believes that the author is biologically and nomenclaturally mistaken when among these hybrid groups are listed the experimentally produced allopolyploid species of *Triticale*, which are, indeed, of hybrid origin as are all allopolyploids, but certainly not hybrids in the correct sense of the term; these species

may either be logically classified in the genus *Triticum* as the species *T. aestivosecale* and *T. turgidosecale* as proposed by Mac Key, or as these two species in the genus *Triticale* as described by von Tschermak, not Müntzing, whereas the name of the primary hybrid seems to be *Triticosecale* Wittm.

Other remarkable improvements are too numerous to be mentioned. A few perhaps illogical conclusions have, however, not been avoided, as, e.g., the incomplete splitting of the genera *Briza* and *Brachypodium*, and the acceptance as distinct genera of some groups that cross easily, as, e.g., *Danthonia* and *Sieglingia*, *Phippsia* and *Puccinellia*, and *Calamagrostis* and *Ammophila*, and the sinking of the recently described genus *Arctopoa* in *Poa*. One may even question why the author refrains from transferring the subgenus *Schedonorus* from *Festuca* to *Lolium*, as is supported by extensive experimental evidence, or from separating the other subgenera of *Festuca* as genera in their own right, since their species never cross. There are a few genera that remain collective as indicated by two or more basic chromosome numbers referred to in the book, but the author has apparently preferred to be cautious in dividing them for some reasons not stated. But perhaps it is not fair to even hope that a specialist as thoroughly consistent as the author of this book never will fail in following strictly the same exact biological definition when treating so many critical genera.

Although the very advanced generic concept may disturb some agrostologists who have neglected the recent revolution in grass systematics, the species concept of the author is not likely to strike botanists from northern and central Europe as being unduly advanced, since he follows the Linnaean and biological concepts that Scandinavian botanists of note have adopted for two centuries, defining this category mainly by aid of its reproductive barrier but describing it morphologically. This is a great deviation from the Wettstein-Komarov species concept of the Flora SSSR. However, since the author apparently has a limited understanding of the significance of certain cytological characteristics as strong indicators of the occurrence of reproductive barriers, he sometimes fails to recognize the fact that it is illogical to include units separated by such characteristics

as geographical races only. Therefore, he sometimes reduces morphologically, geographically and cytologically well defined species to the rank of subspecies. But perhaps some lack of logic is excusable in the light of the generally high biological quality of this immense work – even Homer sometimes nodded.

The book about the grasses of the Soviet Union is a work of a magnitude that very few botanists could have undertaken. There is no book like it in any language. It seems to have been printed in only 2900 copies. Perhaps one may conclude with the wish that the able author could spend his time in composing a similar text for all the grasses of the world so that we may at long last get a modern and complete manual of these most important of plants.

Åskell Löve

Stafleu, F. A. & Cowan, R. S. 1976: *Taxonomic literature*. A selective guide to botanical publications and collections with dates, commentaries and types. 2nd ed. Vol. 1: A–G. XL + 1136 pp. Regnum vegetabile Vol. 94. Bohn, Scheltema & Holkema, Utrecht. ISBN 90 313 0225 2. Price (bound) Dfl 275.

The publication of Stafleu, *Taxonomic literature*, in 1967 was a great event in the history of botanical documentation (cf. review in *Bot. Notiser* 122 (1969) p. 146). In his preface Stafleu stressed the words “selective guide” in the subtitle. As a rule only major works were recorded, not papers printed in periodicals. There was a preponderance of literature from Central and Western Europe as well as of literature on phanerogams. Cryptogams and paleobotany were treated briefly, a great number of important authors and works being omitted.

Less than ten years later the first volume of a much enlarged new edition of the same work has appeared. Dr Cowan (Washington, D.C.) has joined Dr Stafleu (Utrecht) as co-author. Stafleu has organized a group working on “Taxonomic documentation” at Utrecht. A similar team is working with Cowan at the Smithsonian Institution. With this broad background, including much aid from libraries and

private botanists all over the world, it will hopefully be possible to complete two further volumes and a supplement (with addenda and indices) within the next eight years.

To judge from the present volume the coverage of the vast field of taxonomic botany is at least six times as much in ed. 2 as in the previous version. The temporal coverage is more or less defined by the years 1753 and 1940 with a special emphasis on the period between 1870 and 1914, in which descriptive plant taxonomy reached its highest achievements. A few earlier authors, e.g., Bauhin, C. and J., Boerhaave and Dillenius, have been included. This is important from a nomenclatural point of view as their works were often quoted by Linnaeus. The Swedish reader, especially if he is a cryptogamist, will notice that C. Agardh, J. G. Agardh, E. Fries, Th. M. Fries and others have now been treated in detail.

The presentation of the material follows, as a rule, the same principles as in ed. 1. However, the entries on collections, biography and bibliography contain much richer information. As stated in the preface, the work has now become a “bibliography of bibliographies”. Additions are handwriting (references to published examples of an author’s handwriting) and eponymy (i.e. information on the use of authors’ names for generic names of plants or for titles of journals).

Other interesting news proposed standard abbreviations of authors’ names and of book-titles. It is a well-known fact that authors’ names have been abbreviated in very different ways, cf. the often diverse usage in *Flora Europaea* and in the International Code of Botanical Nomenclature. Admittedly, the choice proposed here is subjective and it may be difficult to be consistent. The four Swedish botanists mentioned above are cited as C. Agardh, J. Agardh, Fr. and Th. Fr. in the present work. The Frieses have mostly been abbreviated in this way, at least by Swedish authors, whereas the short forms proposed for the Agardhs conflict with common international usage (though this is not quite uniform) Ag. and J. Ag. (or J. G. Ag.) among phycologists.

This volume concludes with two useful indexes, one to titles of the works cited (with the author’s name in brackets), another to names of authors, collectors, botanical artists, etc.

and to generic names of plants derived from personal names. Complete cumulative indices will follow in the supplement.

It is unavoidable that a few misprints (for instance in Swedish book titles) and other shortcomings can be found in the enormous material presented here. The reviewer will restrict himself to some minor remarks.

The destruction of the greater part of the Berlin Herbarium in 1943 is characterized as "one of the greatest catastrophes ever suffered by plant taxonomy". Under several German botanists (e.g. Engler) we read "Herbarium and types B (mostly destroyed)". However, according to recent information from staff members of the Berlin Herbarium, the catastrophe was not quite so total as has been believed. In many cases it has been possible to restore plant material saved. Hence a plant taxonomist searching for types presumably located at Berlin before 1943 should inquire at Berlin before writing B† in his monograph.

Types and collections of bryologists are sometimes (e.g. under Dusén) reported as located at

the Section for Paleobotany, Natural History Museum, Stockholm (S-PA). In fact, all collections of recent plants (including bryophytes and pteridophytes) were transferred to the Section for Botany (S) at the beginning of the 1970's. S-PA has now collections of fossil plants only.

The only botanist still alive recorded in this volume is Gunnar Degelius (b. 1903). However, the statement "Herbarium and Types UPSV" is not correct. His collections (mainly lichens) were housed there earlier, but since the beginning of the 1960's they are in his home at Askim, near Göteborg, Sweden. The Botanical Museum at Göteborg (GB) can also arrange loans from his private herbarium.

Searching for an envoi to conclude this article the reviewer finds words such as "comprehensive", "indispensable", etc. to be not strong enough. It can suffice to state that taxonomic botanists all over the world eagerly await the forthcoming volumes of this standard work.

Ove Almborn