

The genus *Rosenia* (Compositae)

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Rosenia Thunb. emend. Bremer (Compositae-Inuleae) is a genus of shrubs from southern Africa. In this revision the circumscription is extended to include some *Nestlera* species. Four species are recognized, but the taxonomic treatment on the species level is regarded as preliminary. New combinations are *R. humilis* (Less.) Bremer and *R. oppositifolia* (DC.) Bremer. Chromosome numbers reported are $2n=14$, $c. 28$ and $c. 56$ for *R. humilis* and $2n=c. 28$ for *R. oppositifolia*.

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Rosenia Thunb. emend. Bremer is a genus of shrubs from southern Africa's karoo areas. It belongs to the Compositae-Inuleae. The circumscription is here extended to include the remaining species of the genus *Nestlera*, the major part of which was recently transferred to *Relhania* (Bremer 1976). This study has been carried out in close connection with the revision of *Relhania* and the acknowledgements and methods in the latter work being applicable here, too. The methods do not differ from those commonly employed in taxonomic revisions mainly based on herbarium material. In addition to the limited living material studied in the field and in cultivation, I have examined collections from the following herbaria: B (only microfiches), BM, BOL, C, FI, G, G-DC (only microfiches), GRA, K, L, LD, LD-RETZ (herbarium Retzius at LD), LINN, M, NBG, NUH, P, PE, PRE, RUH, S, SAM, SBT-BERG (Herbarium Bergius at SBT), STE, TCD, UPS, UPS-THUNB (Herbarium Thunberg at UPS), W and Z (abbreviations according to Holmgren & Keuken 1974). The overwhelming majority of the material is at the Botanical Research Institute in Pretoria (PRE). A list of examined specimens is kept at the Museum of Natural History, Section for Botany, Stockholm.

The genus *Rosenia* is well-defined and homogeneous in its proposed circumscription, but the species are more difficult to distinguish. I have adopted a rather wide species concept based on morphology. The taxonomic treatment on the species level must be regarded as preliminary, awaiting future research including extensive field studies and karyological investigations.

History and generic delimitation

On his travel to Roggeveld Thunberg collected a plant, which he later (1800 p. 161) described as the new genus *Rosenia* with the species *R. glandulosa*. The genus was named in honour of two Swedish physicians, Nils Rosén von Rosenstein and his brother Eberhard Rosenblad. It was characterized by a paleate receptacle and a double pappus of scales and a few bristles. Lessing (1832 pp. 371–372) described other species, lacking both paleae and bristles. These had to be placed in other genera, viz. *Nestlera*, with an epaleate receptacle and a crownlike pappus of connate scales and no bristles as defined by Lessing, and the new genus *Polychaetia*, also with an epaleate receptacle, but with a pappus of several free scales and no bristles. In "Flora capensis" Harvey (1865 p.

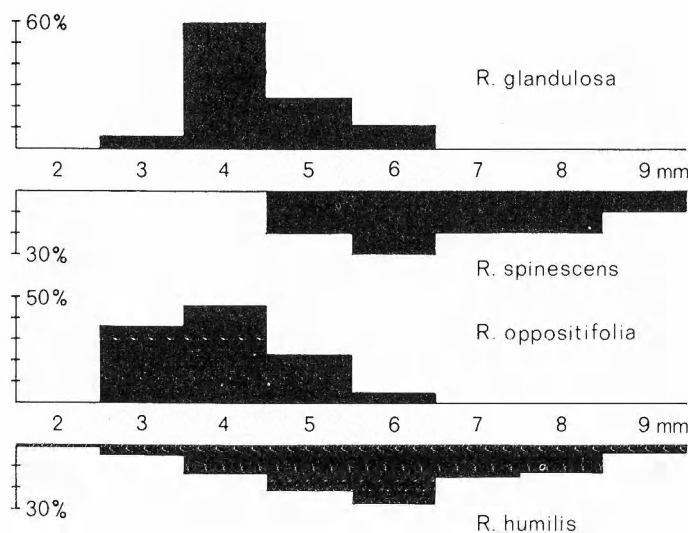


Fig. 1. Variation in leaf-length of *Rosenia*-collections, expressed by bar diagrams showing percentage of examined collections with 2, 3, 4 9 mm long leaves (arithmetic means), respectively. Variation is greatest in *R. humilis*; coefficient of variation (= $100 \times$ standard deviation/arithmetic mean for all collections of one species) for *R. glandulosa* 17%, *R. spinescens* 19%, *R. oppositifolia* 21% and *R. humilis* 25%. — The number of collections measured are for *R. glandulosa* 17, *R. spinescens* 10, *R. oppositifolia* 22 and *R. humilis* 225.

295) reduced *Polychaetia* to a section under *Nestlera*. De Candolle (1838 pp. 280, 283–285), who had material from the rich collections by Burchell, Drège, Ecklon and Zeyher, added several new species of the genera here discussed. Many of these are here united under the polymorphic species *Rosenia humilis*.

Later authors have not questioned the generic delimitation between *Rosenia*, *Nestlera* and the related genus *Relhania*, which was defined by a paleate receptacle and a pappus of scales and no bristles. The loss of receptacular paleae and pappus bristles has occurred several times, even within species as is shown below. This has led to some confusion. Specimens with pappus bristles, but without paleae, would not match the description of any of the three genera. Such specimens have been named *Nestlera rosenioides* Hutchinson ex Compton or *Rosenia nestleroides* Compton (1931 p. 318). A plant without pappus bristles, but with paleae, was described as a *Relhania*, viz. *R. lanata* Compton (1942 p. 267).

Phillips (1951 p. 802) knew that pappus bristles may develop occasionally in the closely related genus *Relhania*, so that he reduced *Rosenia* to

a synonym of *Relhania*. However, *Rosenia* is a quite distinct genus of shrubs with lateral brachyblasts. *Relhania* differs in habit and other characters; lateral brachyblasts having evolved independently in two species only. The genera have approximately vicarious distributions; *Rosenia* covers the inner karoo areas, whereas *Relhania* occurs in the more or less mountainous areas around the coast of South Africa. The generic delimitation is further discussed in my revision of *Relhania* (Bremer 1976 p. 9). The absence of receptacular paleae and pappus bristles, diagnostic characters of the third genus *Nestlera*, are not sufficient for generic distinction and in my revision most species of *Nestlera*, including the type species, were referred to *Relhania* L'Hérit. emend. Bremer. The remaining species are here included in *Rosenia* Thunb. emend. Bremer.

Morphological aspects

Habit. *Rosenia* comprises woody karoo shrubs with crowded leaves on lateral brachyblasts. The ramification is variable from lax to dense. In the latter, compact forms, the leaves are crowded and brachyblasts cannot be distinguished from the long shoots. The branches are sometimes rather stiff and subspinescent. In *R. spinescens* spines of a special type are developed by the upper branches. These grow out to leafless spines, from which leaves and axillary shoots later develop, thus continuing vegetative growth.

Foliage. The leaves are always entire, but variable in size and shape. The variation is great even within the species, as expressed by the diagram of leaf-length in Fig. 1. Much of this variation is due to environmental modifications. I have moved specimens of *Rosenia* from the field into greenhouses, where they develop considerably longer and often narrower leaves. In *R. humilis*, if not in all species, leaf variation is also genetically controlled (to be discussed under the next heading).

The leaves are glabrous or laxly–densely tomentose. The indumentum is more dense on the ventral side of the often somewhat canaliculate leaves. These characters are important for the position of *Rosenia* in the *Relhania* group of genera (Bremer 1976 p. 9). The hairs con-

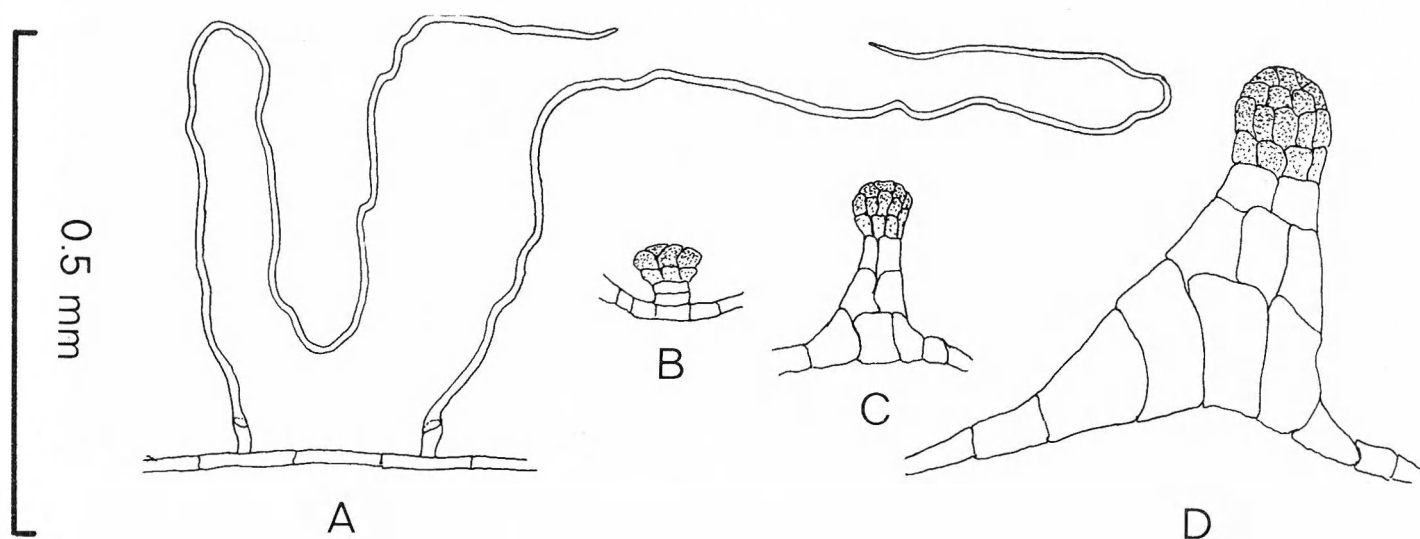


Fig. 2. Leaf hairs (A) and glands (B–D), drawn from whole mounts of epidermis and cross-sections of leaves. – A, C: *R. humilis*, Bremer 164 (S). – B: *R. oppositifolia*, Nordenstam & Lundgren 2077 a (S). – D: *R. spinescens*, Acocks 19012 (PRE).

sist of a basal cell and an apical, long, curled cell (Fig. 2A). Glands are often present. These have a multicellular head on a multicellular, short or long stalk (Fig. 2B–D). In *R. oppositifolia* the glands are shortly stalked, whereas the other species often, but not always, have longer, conspicuous glands.

Involucre. The involucre bracts are firm basally and often brown apically (Fig. 3A–F). In *R. glandulosa* the brown middle stripe with the pale margins (Fig. 3A) gives the involucre a brown-and-white-striped appearance, possibly with a signalling effect. In some collections of *R. humilis* the bracts are laxly tomentose dorsally, otherwise completely glabrous, but with occasional glands.

R. humilis and to a lesser extent *R. spinescens* generally have involucre bracts, which keep together, enclosing the achenes after flowering. Thus persistent capitula with ripe achenes may remain on the plant for several years before fruit dispersal. *R. glandulosa* and *R. oppositifolia* have rather loose bracts and the achenes are usually released after flowering.

Receptacle. Paleate versus epaleate receptacle has sometimes been used as a diagnostic character distinguishing genera. As such it has often turned out to be useless and in *Rosenia* both conditions occur within the species. *R. glandulosa* has paleae, which sometimes are absent from the central part of the receptacle. The

shape of the paleae is variable from flat and narrow to oblong and canaliculate (Fig. 3G–I). The other species are almost always without paleae, but often with a squamose receptacle; the scales may be reduced paleae or outgrowths from the receptacle.

Floral morphology. Apart from differences in size and number of florets, there is little variation in floral morphology. Florets and floral parts are shown in Fig. 4. The corollas are yellow, but there is usually a dorsal, brownish purple stripe on the ray-floret lamina. This occurs in other genera too, e.g. *Relhania* (Bremer 1976 p. 19). Glands (Fig. 4I) are sometimes present, mainly on the floret tubes.

The oblong achenes are smooth or, especially in *R. humilis*, rugose basally. In this species they are generally enclosed in the closely appressed bracts and may not be released for several years. Then they are often dispersed together (synaptospermy). Thus a shrub of *R. humilis* often consists of several individuals, developed from the achenes of one capitulum. The achenes are often glabrous or laxly pilose, especially ray-floret achenes. The hairs are of the tricellular type (Fig. 4Q), widespread in the Compositae (Hess 1938). *R. humilis* has a basal tuft of these achene hairs (Fig. 5C).

The pappus consists of scales and often a few bristles (Fig. 5A, B). The scales are probably outgrowths from the apical rim of the ovary. There are all transitions from free to more

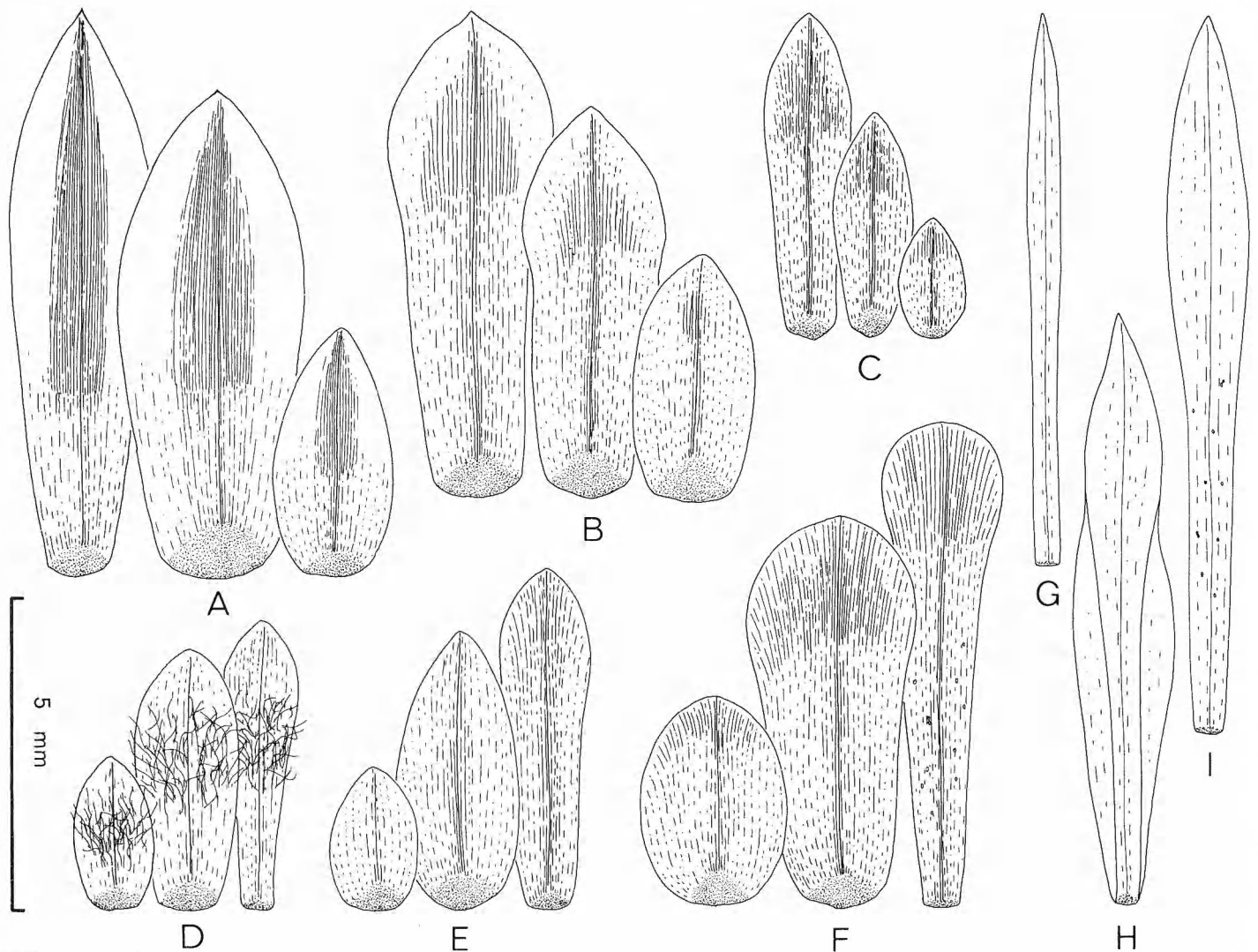


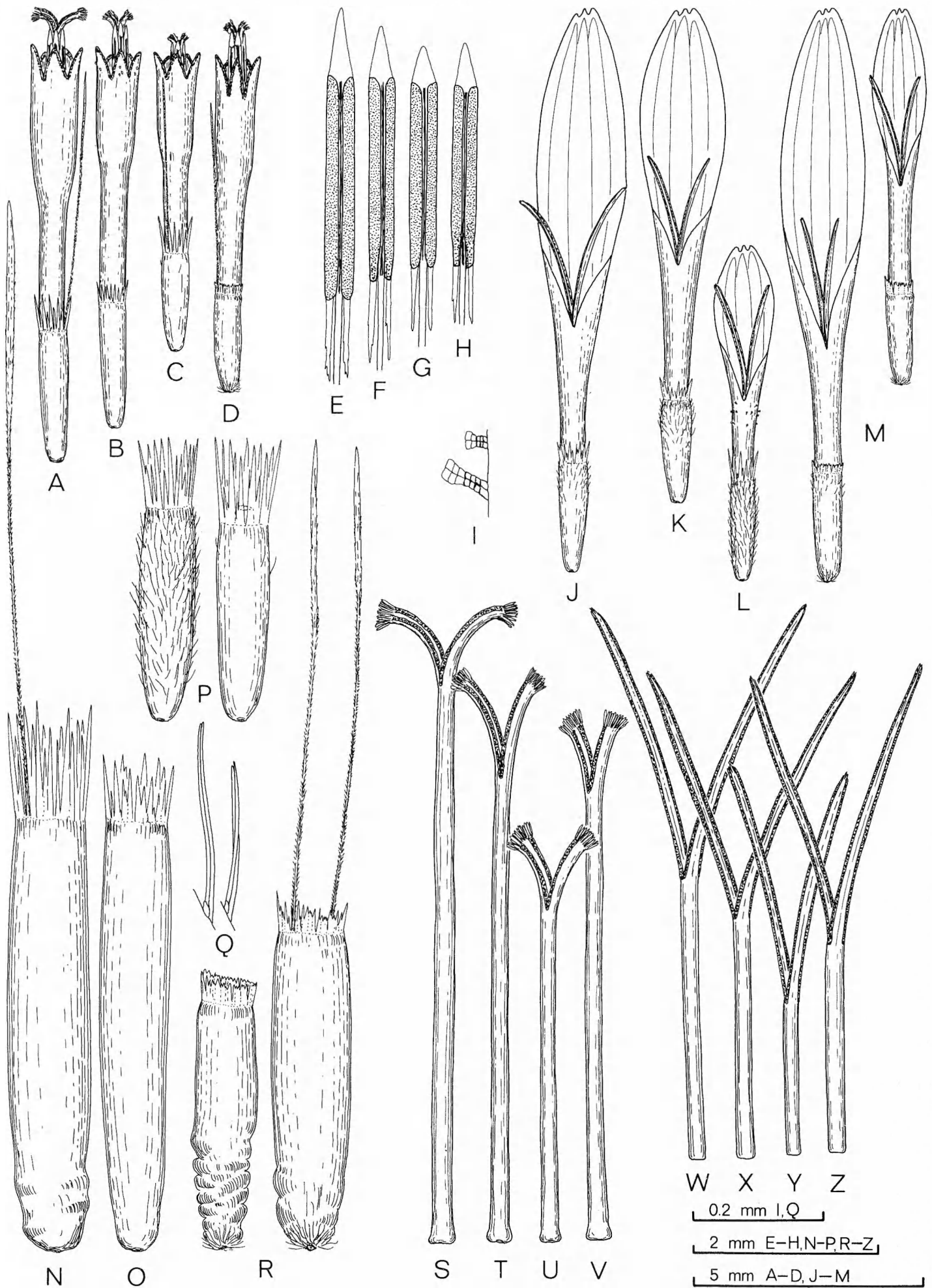
Fig. 3. Involucral bracts (A-F) and paleae (G-I). - A, G-I: *R. glandulosa*. - B: *R. spinescens*. - C: *R. oppositifolia*. - D-F: *R. humilis*. - A, G: Bremer 301 (S). - B: Esterhuysen 2752 (BOL). - C: Bremer 280 (S). - D: Wall, N of Vosberg (S). - E: Bremer 302 (S). - F: Bremer 164 (S). - H: Maguire 1966 (NBG). - I: Whitlock 597 (PRE).

connate scales, forming a crownlike cup. The latter condition is common in *R. humilis*. The pappus bristles are scabrid to barbellate, flattened and smoother at the tip. Although generally present, they are lost in many specimens. Bristles develop only occasionally in *Relbania*, whereas they are present in all other related genera (Bremer 1976 p. 9).

Embryology. The suspicion that *Rosenia* may be agamospermous (see below) led me to investigate the embryology of the genus. This was

possible, when plants of *R. humilis*, raised from seeds of one collection (Bremer 436, kept in S), flowered in cultivation after several years. However, no embryos developed in the capitula of these plants. Thus agamospermy could not be detected, nor were any pollen tubes or normal fertilization observed. After flowering the embryo sac degenerates, but the ovule and the fruit develop further, giving the impression of a mature achene with a seed. The latter is, however, only the enlarged, hollow ovule without any embryo.

Fig. 4. Florets and floral parts. - A-D: Disc-florets. - E-H: Stamens. - I: Floret tube glands. - J-M: Ray-florets. - N-P, R: Achenes. - Q: Achene hairs. - S-V: Styles of disc-florets. - W-Z: Styles of ray-florets. - A, E, J, N, S, W: *R. glandulosa*. - B, F, K, O, T, X: *R. spinescens*. - C, G, I, L, P, Q, U, Y: *R. oppositifolia*. - D, H, M, R, V, Z: *R. humilis*. - A, E, J, S, W: Acocks 14351 (PRE). - B, F, K, O, T, X: Esterhuysen 2752 (BOL). - C, G, I, L, P, Q, U, Y: Bremer 280 (S). - D, H, M (left ray-floret), V, Z: Bremer 198 (S). - M (right ray-floret): Bremer 302 (S). - N: Bremer 301 (S). - R (left achene): Henderson 22 (PRE). - R (right achene): Compton 3952 (NBG).



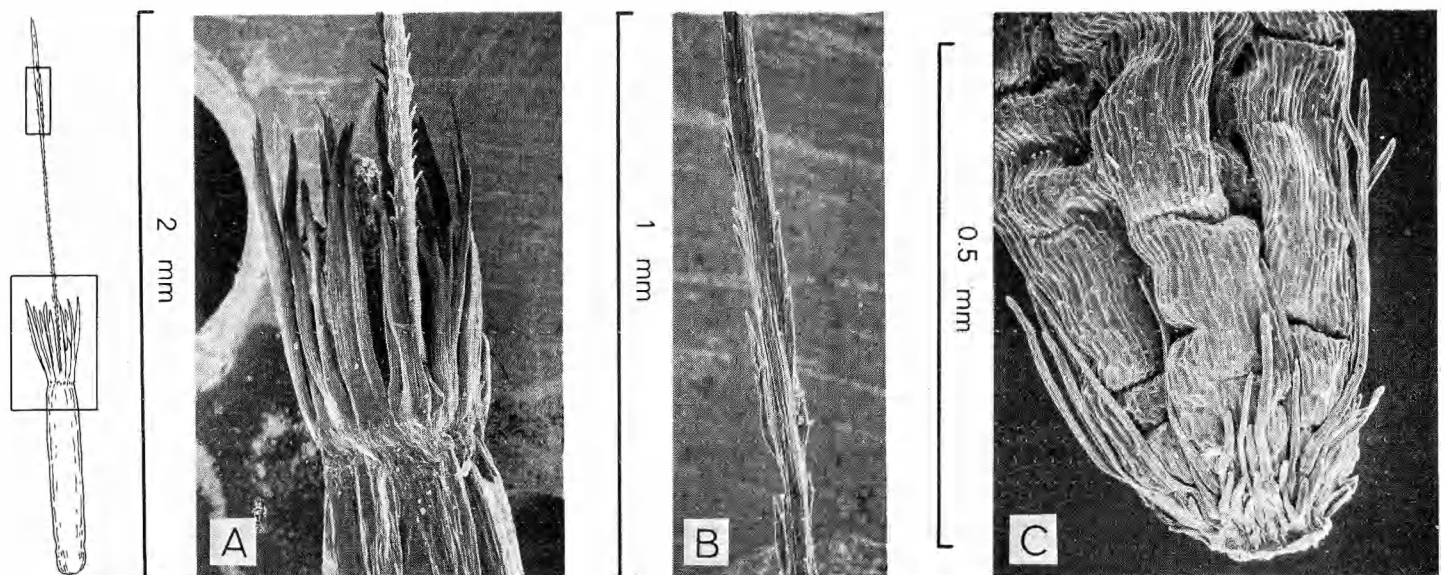


Fig. 5. Pappus and achene hairs (electrosan-photomicrographs). – A, B: *R. glandulosa* with pappus of scales and one bristle. – C: *R. humilis* with basal tuft of achene hairs. – A, B: Bremer 301 (S). – C: Bremer 645 (S).

In the few cases observed, the embryo sac development is monosporic and of the 8-nucleate, *Polygonum* type. An ovule with a mature embryo sac is shown in Fig. 6. During maturation of the embryo sac a hypostase-like tissue (see Maheshwari 1950 pp. 65–67) of larger cells with irregular nuclei develops in the chalazal region and around the embryo sac.

The capitula studied were fixed in FAA, microtome-cut and stained in Heidenhain's iron hematoxylin, safranin and light green.

Pollen morphology. This has been investigated for *Rosenia* and allied genera by Besold (1971 pp. 17–18). The pollen of *R. humilis* (syn. *Nestlera minuta* auct.) was described. I have examined material from all species of *Rosenia*, and it fits both Besold's description and my own of *Relhania* pollen (Bremer 1976 p. 22). It is unnecessary to give any third description here, although pollen size and number of spines in *Rosenia* is somewhat greater, but in agreement with the upper half of the range of variation in *Relhania*.

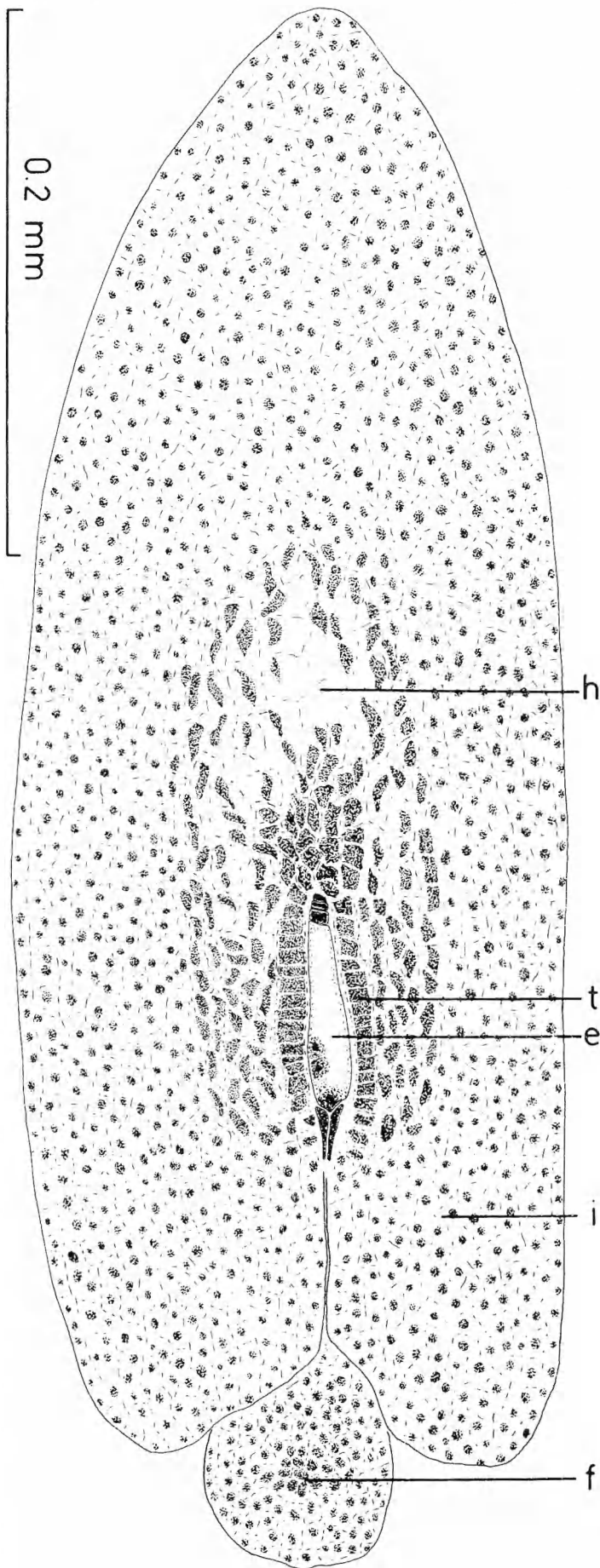
Chromosome number. Somatic chromosome numbers have been investigated for 2 species. The results are given in Table 1. Apparently polyploidy is important in this genus, with tetraploids and an octoploid so far known in addition to the diploids. Further levels of polyploidy are likely to be revealed by future

investigations. The basic number, $x=7$, is the same as in the related genus *Relhania* (Bremer 1976 p. 22). The chromosomes are c. 2–5 μ long.

The counts were made from microtome-cut sections of root-tips fixed in Navashin-Karpechenko and stained in crystal violet or from squashed root-tips fixed in Carnoy and stained in aceto-orcein. The voucher specimens are kept at S.

Table 1. Chromosome numbers in *Rosenia*.

Voucher specimen	2n
<i>Rosenia oppositifolia</i>	
Bremer 269, Roggeveld, Cape Province	c. 28
<i>Rosenia humilis</i>	
Bremer, s.n., 3 km W Springfontein, Orange Free State	14
Bremer 302, E Great Karoo, Cape Province	14
Bremer 429, South West Africa	14
Bremer 436, South West Africa	14
Bremer 645, Little Karoo, Cape Province	14
Bremer 198, Little Karoo, Cape Province	c. 28
Bremer 164, SW Great Karoo, Cape Province	c. 56



Discussion

In this revision *Rosenia* comprises 4 species. *R. glandulosa*, *R. spinescens* and *R. oppositifolia* are fairly constant and fit the morphological species concept commonly used in taxonomic revisions. Maybe the variation in *R. spinescens* is somewhat discontinuous, but I have only seen 10 collections of this species. More material might bridge the gaps.

The fourth species, *R. humilis*, is extremely variable and it might seem, as if I had applied a much too wide species concept. *R. humilis* consists of several different form series, varying in many characters. Variation in leaf-length is diagrammatically illustrated in Fig. 1. A similar picture could be derived from measurements of other characters. Differences in involucre bracts, ray-florets, achenes and habit are shown in Figs. 3D-F, 4M, R and 9. In the field two or three quite different forms are often found growing side by side. They must differ genetically and be reproductively isolated from each other. However, considering all of the almost 300 collections, it becomes impossible to distinguish any well-defined forms within *R. humilis*. This is no "dustbin species", where the difficult collections have been assembled. There are characters, such as the basal tuft of achene hairs, which define *R. humilis* from the three other species.

I have obtained a few chromosome numbers in *Rosenia* (Table 1). There are both diploids and polyploids in the genus. The diploids are from different form series within *R. humilis*. Consequently there are probably several diploid, reproductively isolated entities. Possibly these are outcrossing, thus constituting biological species. Outcrossing is the more common breeding system in perennials and the diploid plant, the embryology of which was investigated (see above), was not self-fertilized. Hybridization between these biological species can produce allopolyploids and the morphological discontinuities between the original species will be

Fig. 6. Section through ovule with mature embryo sac of *R. humilis* (Bremer 436, kept in S). - h: Hypostase-like tissue. - t: Integumentary tapetum. - e: Embryo sac with egg apparatus of egg and two synergids, two polar nuclei and three antipodes. - i: Integument. - f: Funiculus.

obscured. The result is a polyploid complex (Grant 1971 pp. 300–304). I believe this is the situation in *Rosenia*.

High polyploids in polyploid complexes are likely to be agamospermous, as shown e.g. by Babcock and Stebbins (1938) in the *Crepis occidentalis* group. In such cases we have an agamic complex superimposed on the polyploid complex (Grant 1971 p. 297). This has not been shown in *Rosenia*. The plant of *R. humilis* investigated embryologically (see above) is diploid and not agamospermous. However, the variation pattern within *R. humilis* is suggestive of an agamic complex. The individuals growing close together due to synaptospermy are identical, so there seems to be little or no genetical variation between the progeny from different seeds in one capitulum. This is expected, if the plant is agamospermous. If reproduction is sexual, then the plants must be homozygous to a great extent.

In summary the occurrence of polyploidy and the pattern of variation indicate a polyploid complex in *Rosenia*. Whether this is combined with agamospermy is an open question. It should be evident from the discussion above, that, at the present state of knowledge, it is justified to recognize only four species in *Rosenia*. Herbarium taxonomy has its limits and I believe, that the recognition of numerous morphological forms without knowledge of their chromosome number and reproductive system would do no service to taxonomy.

Suggestions for future research. The species situation in *Rosenia* furnishes a challenging and interesting problem for a future taxonomist or geneticist. Much weight must be laid on field studies of the populations, their distribution and ecology. Extensive karyological investigations are necessary in order to reveal the structure of the polyploid complex. The reproductive systems should be investigated and the possibility of agamospermy observed.

TAXONOMY

Rosenia Thunb. emend. Bremer, emend. nov.

Thunberg 1800 p. 161; Lessing 1832 p. 369; De Candolle 1838 p. 280; Harvey 1865 p. 294; Bentham &

Hooker 1873 p. 327; Hoffmann 1890 p. 198. – Type species: *R. glandulosa* Thunb.

Nestlera auct. (non Spreng. 1818 p. 568, nec Willd. ex Steud. 1841 p. 192, nec E. Mey. ex Walp. 1852 p. 856), p. p. excl. typus; Lessing 1832 p. 372; De Candolle 1838 p. 283; Harvey 1865 p. 295; Bentham & Hooker 1873 p. 325; Hoffmann 1890 p. 197; Phillips 1951 p. 800; Merxmüller 1967 p. 112.

Polychaetia Less. (non Tausch ex Less. 1832 p. 129); Lessing 1832 p. 371; De Candolle 1838 p. 284. – Type species: *P. relhanioides* Less. (= *Rosenia humilis* (Less.) Bremer).

Densely–moderately branched, compact–diffuse, sometimes spiny shrubs. Stems prostrate–ascending–erect, glabrous or laxly tomentose, leafy and with lateral brachyblasts with crowded leaves, becoming glabrous and beset with basal, stem-clasping part of leaves or marked with scars from leaves and brachyblasts. Cortex brown, becoming grey with age. *Leaves* decussate or sometimes alternate, laxly–densely set, crowded on brachyblasts, semiamplexicaul, sessile, entire, mid-ribbed, glabrous or tomentose, usually glandular with stalked glands.

Capitula heterogamous, solitary, sessile, terminal on stems and brachyblasts, often in the fork of two branches. *Involucre* urceolate–cyathiform–campanulate. Involucral bracts 3–10-seriate, imbricated, entire, basally firm, apically spreading and scarious and sometimes brown with pale margins, otherwise yellowish, glabrous or seldom dorsally tomentose, often glandular. *Receptacle* flat, paleate or epaleate, sometimes shortly squamose. Paleae, if present, subtending all or occasionally most disc-florets, flat or canaliculate, usually entire, glabrous, dorsally often glandular.

Ray-florets female, fertile. Tube cylindrical–funnel-shaped, sometimes glandular. Lamina spreading, elliptic, yellow and sometimes dorsally with a brownish purple stripe, usually 4-veined, apically minutely 3-lobed. Style terete, bifid; style-branches spreading–revolute, semiterete, linear, glabrous or minutely penicillate apically, obtuse; stylopodium 0 or indistinct.

Disc-florets perfect. Corolla indistinctly divided into a lower cylindrical tube and an upper cyathiform limb, yellow, 5-lobed; corolla lobes spreading, ovate-triangular, marginally thickened, dorsally usually gland-dotted. Style terete, bifid; style-branches spreading–revolute, semiterete, narrowly oblong, apically penicillate and truncate; stylopodium \pm distinct, conical–

terete. Anthers linear, with a sterile, flat, ovate, apical appendage and sterile, subulate, entire or slightly branched tails; filaments filiform.

Achenes terete or angular, ± narrowly oblong,

glabrous or pilose, always more densely in ray-florets; pappus crownlike, scarious, of many ± connate scales, often also with 1–4, barbellate, apically slightly flattened bristles.

Key to the species

- 1. Upper branches transformed into straight, rigid, leafless spines 2. *R. spinescens*
Unarmed or subspinescent, but not with leafless spines 2
- 2. Involucre brown and white; displayed part of bracts thin and papery, with a dark brown middle stripe and wide, pale, scarious margins 1. *R. glandulosa*
Involucre yellowish brown mainly basally; bracts firm and yellowish brown, but inner bracts often apically brown with scarious margins 3
- 3. Involucre ≤ 6 mm wide, narrowly cyathiform–campanulate, with loose, apically brown bracts 3. *R. oppositifolia*
Involucre often > 6 mm wide, if narrower then urceolate with yellowish brown, appressed bracts 4. *R. humilis*

1. *Rosenia glandulosa* Thunb.

Thunberg 1800 p. 161; Lessing 1832 p. 370; De Candolle 1838 p. 280; Harvey 1865 p. 294; Oliver 1892 plate 2228. – Orig. coll.: Thunberg, Herb. No. 20091 (UPS-THUNB lectotype, SBT-BERG).

Illustrations. Figs. 3 A, G–I, 4 A, E, J, N, S, W, 7. – Oliver loc.cit.

Moderately and often subdichotomously branched, sometimes subspinescent shrubs. *Leaves* flat–somewhat triquetrous, mid-ribbed, linear–narrowly elliptic-oblong, 2–10 mm long, 0.5–2.5 mm wide, tomentose and often glandular with stalked glands, greyish green.

Involucre campanulate, 3–15 mm wide. Involucral bracts 25–50, outer ovate-oblong, inner gradually longer and oblong-obovate, basally firm and yellowish brown, upper displayed part spreading, thin and papery, with a dark brown middle stripe and wide, pale, scarious margins, up to 12 mm long, up to 4 mm wide. *Receptacle* paleate and sometimes also shortly squamose. Paleae subtending all or occasionally only outer disc-florets, subulate–linear–narrowly spatulate and flat or oblong and canaliculate and almost embracing disc-floret basally, entire or apically irregularly serrate–laciniate, 7–12 mm long, 0.3–2 mm wide.

Ray-florets 5–18. Lamina elliptic, 5.5–12 mm long. Style 5–8 mm long. *Disc-florets* 12–55. Corolla 4.5–6.8 mm long. Style 5.5–9 mm long. Anthers 3.3–5 mm long; tails c. 1/4 of the length of the anther. *Achenes* terete or somewhat angular, narrowly oblong, 3.5–5.5 mm long, 0.7–1.2 mm wide, glabrous or mainly apically pilose, smooth or basally transversely rugose;

pappus crownlike, of ± connate scales, up to 2 mm long, almost always also with 1–4, 4.5–7 mm long, barbellate bristles.

Flowering period mainly August–September.

This species is characterized by its involucre with thin and papery, brown and white bracts (see key and description). The receptacle is generally furnished with narrow–wide paleae, whereas it is almost always epaleate in the other species. *R. glandulosa* is possibly most closely related to *R. spinescens*. Apart from the spines in the latter species, they are similar in habit and they have vicarious distributions. Starved specimens with small capitula look similar to *R. oppositifolia*, but they can nevertheless be distinguished by the above mentioned characters.

Distribution. Fig. 7. *R. glandulosa* is not uncommon in the Nieuwveld and Roggeveld mountain ranges up to Calvinia and just north from there. It grows in often stony karoo veld on lower mountain slopes. 21 collections have been examined.

2. *Rosenia spinescens* DC.

De Candolle 1838 p. 280. – *Nestlera Dregeana* Harv., nom. superfl.; Harvey 1865 p. 296. – *Nestlera spinescens* (DC.) Druce 1917 p. 638. – Orig. coll.: Drège, Nieuwveld, between Rhinosterkop and Ganzefontein, 3500–4500 ft. (G-DC holotype, BM, G, P, S, W).

Relhania lanata Compton 1942 p. 267. – Orig. coll.: Compton 9246, Laingsburg, Ngaap Kop, 1100 m, 1940 (NBG holotype, BOL, PRE).

Illustrations. Figs. 3 B, 4 B, F, K, O, T, X, 7.

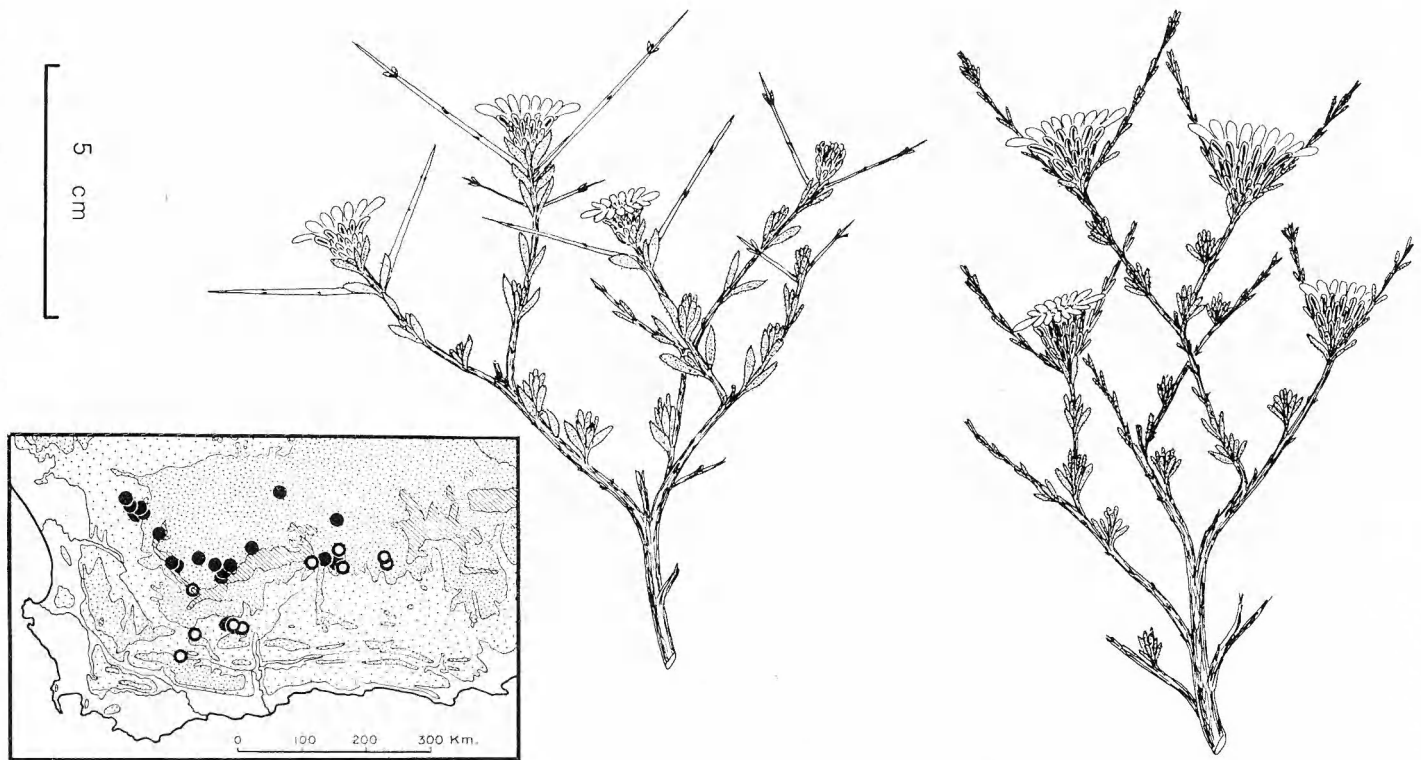


Fig. 7. Distribution and portion of plant of *Rosenia glandulosa* (right, ●) and *Rosenia spinescens* (left, ○). – *R. glandulosa*: Maguire 1940 (NBG). – *R. spinescens*: Esterhuysen 2752 (BOL).

Moderately and often subdichotomously branched, spiny shrubs; upper branches transformed into straight, rigid 1–5 cm long, leafless spines. *Leaves* flat or somewhat canaliculate, mid-ribbed, narrowly obovate-oblong–spatulate, 3–15 mm long, 1–4.5 mm wide, ± tomentose and often glandular with stalked glands mainly marginally and on mid-rib dorsally, greyish green.

Involucre widely cyathiform–campanulate, 4–14 mm wide. Involucral bracts 35–60, outer ovate-oblong, inner gradually longer and obovate-oblong–spatulate, apically spreading and brownish with scarious margins, up to 10 mm long, up to 3.5 mm wide. *Receptacle* epaleate, but sometimes shortly squamose or occasionally paleate with linear, up to 4.5 mm long paleae.

Ray-florets 12–25. Lamina elliptic, 5.5–12 mm long. Style 5–8 mm long. *Disc-florets* 25–75. Corolla 4.5–6.8 mm long. Style 5.5–9 mm long. Anthers 3.3–5 mm long; tails c. 1/4 of the length of the anther. *Achenes* terete or somewhat angular, narrowly oblong, 4–6 mm long, 0.6–1 mm wide, glabrous or mainly apically pilose, almost smooth; pappus crownlike, of ± connate scales,

up to 0.9 mm long, often also with 1–2, up to 7 mm long, barbellate bristles.

Flowering period mainly August–September.

This spiny species is easily recognized. The upper branches beneath a capitulum grow out in pairs to leafless spines. Thereafter leaves develop and vegetative growth is continued by axillary shoots near the spine-tips. *R. spinescens* is probably related to *R. glandulosa* (see discussion under this species).

Variation. The collections of *R. spinescens* are variable in size of leaves and capitula. Furthermore some specimens are vigorous with thick spines, while others are much more slender. The southernmost collection from Jakkalsfontein in the Little Karoo (van Breda 990, PRE) has less developed spines and small capitula. It is here provisionally included in *R. spinescens*.

Distribution. Fig. 7. *R. spinescens* mainly occurs in the Great Karoo from Whitehill to Murraysburg south of and in the southern parts of the Nieuwveld range. It grows in stony or rocky

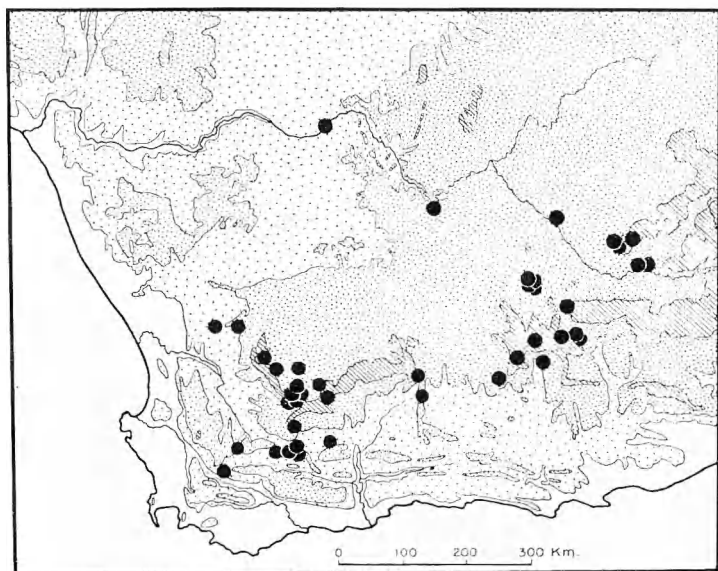


Fig. 8. Distribution and portion of plant of *Rosenia oppositifolia*. – Bremer 280 (S).

karoo veld (fide coll.). 10 collections have been examined.

3. *Rosenia oppositifolia* (DC.) Bremer, comb. nov.

Basionym: *Polychaetia oppositifolia* De Candolle 1838 p. 285. – *Nestlera prostrata* Harvey 1865 p. 296. – Orig. coll.: Drège, Sneeuwbergen, 4000–5000 ft. (G-DC holotype, BM, G, K, L, LD, P, S, SAM, STE, TCD, W).

Rosenia angustifolia Compton 1932 p. 337. – Orig. coll.: Compton 3775, in the karoo association at Jandebos, 2800 ft., 1931 (BOL holotype).

Nestlera Levynsae Hutchinson 1946 p. 140. – Orig. coll.: Levyns 1649, top of Verlaten Kloof, c. 5400 ft., 1926 (K holotype).

Illustrations. Figs. 3C, 4C, G, L, P, U, Y, 8.

Moderately branched, sometimes prostrate shrubs. *Leaves* triquetrous with projecting mid-rib dorsally, linear, 1.5–12 mm long, 0.4–0.8 mm wide, tomentose on both sides between margins and mid-rib, dark greyish green.

Involucre narrowly cyathiform–campanulate, 2–6 mm wide. Involucral bracts 12–45, outer elliptic, inner gradually longer and obovate-oblong to narrowly obovate, apically spreading and brown with scarious margins, up to 7 mm long, up to 2 mm wide. *Receptacle* minute, epaleate, but shortly squamose.

Ray-florets 3–8. Lamina elliptic, 3–4.5 mm long. Style 3.6–5 mm long. *Disc-florets* 5–15. *Corolla* 4–5.3 mm long. Style 4.2–5.5 mm long.

Anthers 2.5–3.5 mm long; tails c. 1/4 of the length of the anther. *Achenes* somewhat triquetrous, oblong, 2–3.3 mm long, 0.4–0.7 mm wide, glabrous or mainly apically pilose; pappus crownlike, of \pm connate scales, up to 1.3 mm long, often also with 1–2, up to 4 mm long, barbellate bristles.

Flowering period mainly September–October.

This is a fairly constant species with always linear, greyish-green leaves and generally numerous, small, few-flowered capitula with loose, apically brown bracts. The branching is somewhat diffuse and not subdichotomous as often as in the other species. It might look similar to some specimens of *R. glandulosa* (see discussion under this species).

Distribution. Fig. 8. *R. oppositifolia* is rather common south of and in the Roggeveld and Nieuwveld mountain ranges, as well as in the Sneeuwbergen area between Murraysburg and Middelburg. It is rather widespread and known from several other parts of the inner Cape Province and the southern Orange Free State. It grows in shaly, sandy or stony karoo veld. *R. oppositifolia* (syn. *Nestlera prostrata* Harv.) is one of a dozen species, which, according to Acocks (1953 in index) are undesirable for grazing and should be eradicated. 57 collections have been examined.

4. *Rosenia humilis* (Less.) Bremer, comb. nov.

Basionym: *Nestlera humilis* Lessing 1832 p. 372; De Candolle 1838 p. 283; Harvey 1865 p. 297. – *Relhania dichotoma* Willd. ex Less., pro syn.; Lessing 1832 p. 372. – Orig. coll.: Herb. Willdenow No. 16149 (B holotype).

Polychaetia relhanioides Lessing 1832 p. 371; De Candolle 1838 p. 285. – *Relhania linifolia* Willd. ex Less., pro syn.; Lessing 1832 p. 371. – Orig. coll.: Herb. Willdenow No. 16150 (B holotype).

Nestlera minuta auct. (excl. *Pteronia minuta* Linné f. 1781 p. 357 = *Asaemia axillaris* (Thunb.) Harv.); De Candolle 1838 p. 283; Merxmüller 1967 p. 113.

Nestlera oppositifolia De Candolle 1838 p. 283; Harvey 1865 p. 298. – Orig. coll.: Drège, Swartberg (G-DC holotype).

Nestlera rigida De Candolle 1838 p. 284. – Orig. coll.: Ecklon, Uitenhage (G-DC lectotype).

Nestlera muriculata De Candolle 1838 p. 284; Harvey 1865 p. 297. – Orig. coll.: Drège, Swarttruggens (G-DC holotype).

Nestlera conferta De Candolle 1838 p. 284; Harvey 1865 p. 297; Merxmüller 1967 p. 113. – *Relhania dumosa* E. Mey. ex DC., pro syn.; De Candolle 1838 p. 284. – Orig. coll.: Drège, Karoo (G-DC lectotype).

Nestlera Dinteri Muschl. ex Dinter, nom. nud.; Dinter 1924 p. 316. – Orig. coll.: Dinter 1210, Zachanabis, not traced, destroyed?

Rosenia nestleroides Compton 1931 p. 318. – Orig. coll.: Compton 2948, Karoo Garden, Whitehill, 1924 (BOL lectotype, NBG).

Nestlera rosenioides Hutchinson ex Compt., pro syn. sub *Nestlera oppositifolia* DC.; Compton 1931 p. 318. – Orig. coll.: Bolus 12089, Swartberg, near Cango Caves, 1905 (BOL holotype, BM, GRA, K, PRE).

Nestlera incana Dinter ex Merxm., nom. nud., pro syn. sub *Nestlera humilis* Less.; Merxmüller 1952 p. 158. – Orig. coll.: Dinter 8280, Jakkalskuppe, 1934 (M lectotype, BM, BOL, G, K, PRE, S, Z).

Illustrations. Figs. 3D–F, 4D, H, M, R, V, Z, 5C, 9.

Nomenclatural note. In "Supplementum plantarum" *Pteronia minuta* was described by Linné f. (1781 p. 357) on material from Herbarium Bäck. An account of this herbarium, as well as of those specimens of Bäck used by Linné f., has been given by Juel (1924) and Exell (1931), respectively. These specimens should now be in Smith's herbarium at the Linnean Society in London. However, the type of *Pteronia minuta* is missing.

Thunberg collected the South African plants in Bäck's herbarium. According to Lessing (1832 p. 264) *Pteronia minuta* L. f. is conspecific with Thunberg's *Tanacetum axillare*, at present known as *Asaemia axillaris* (Thunb.) Harv. There are specimens of Thunberg's original collection of this plant at Uppsala

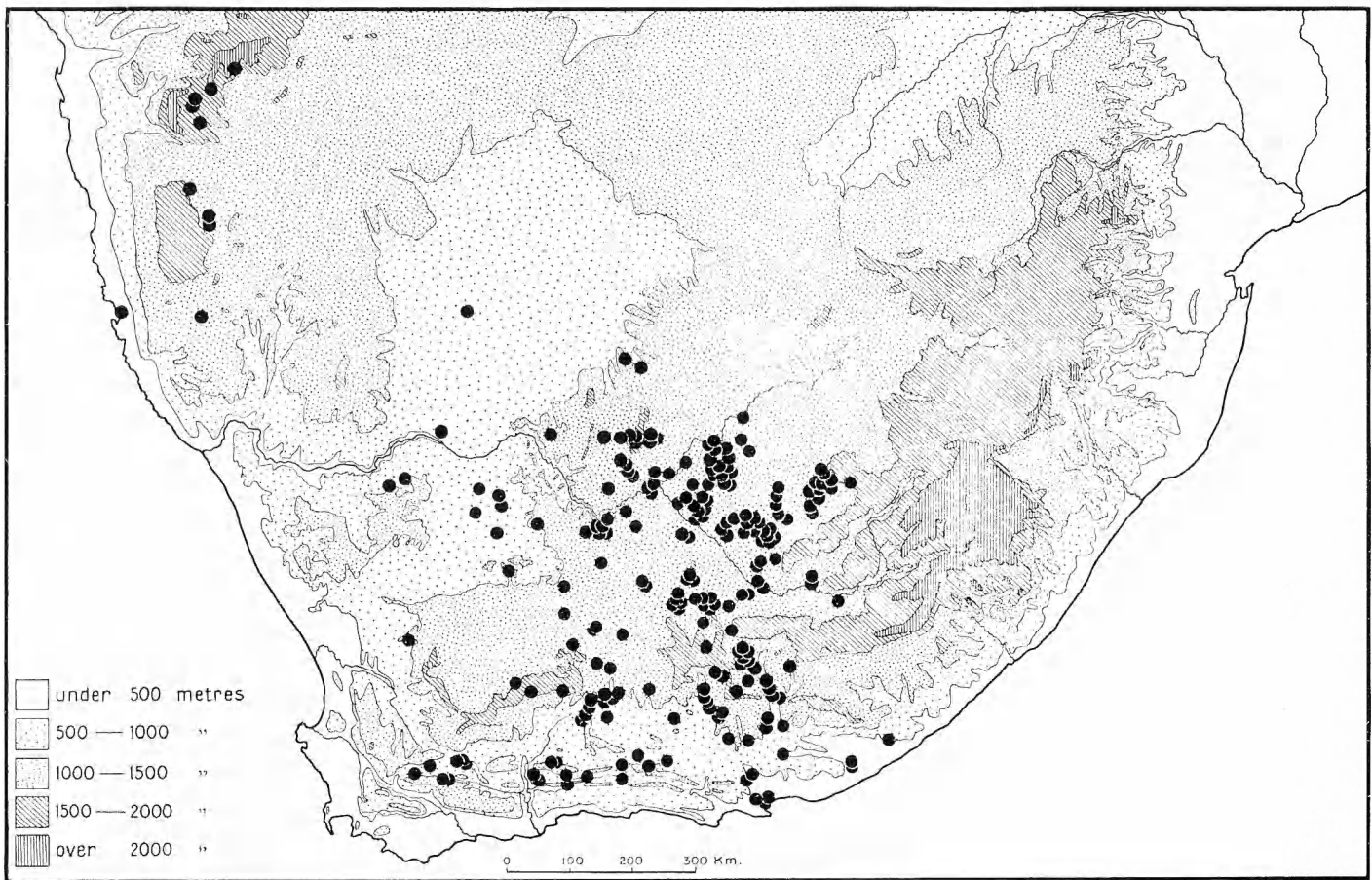
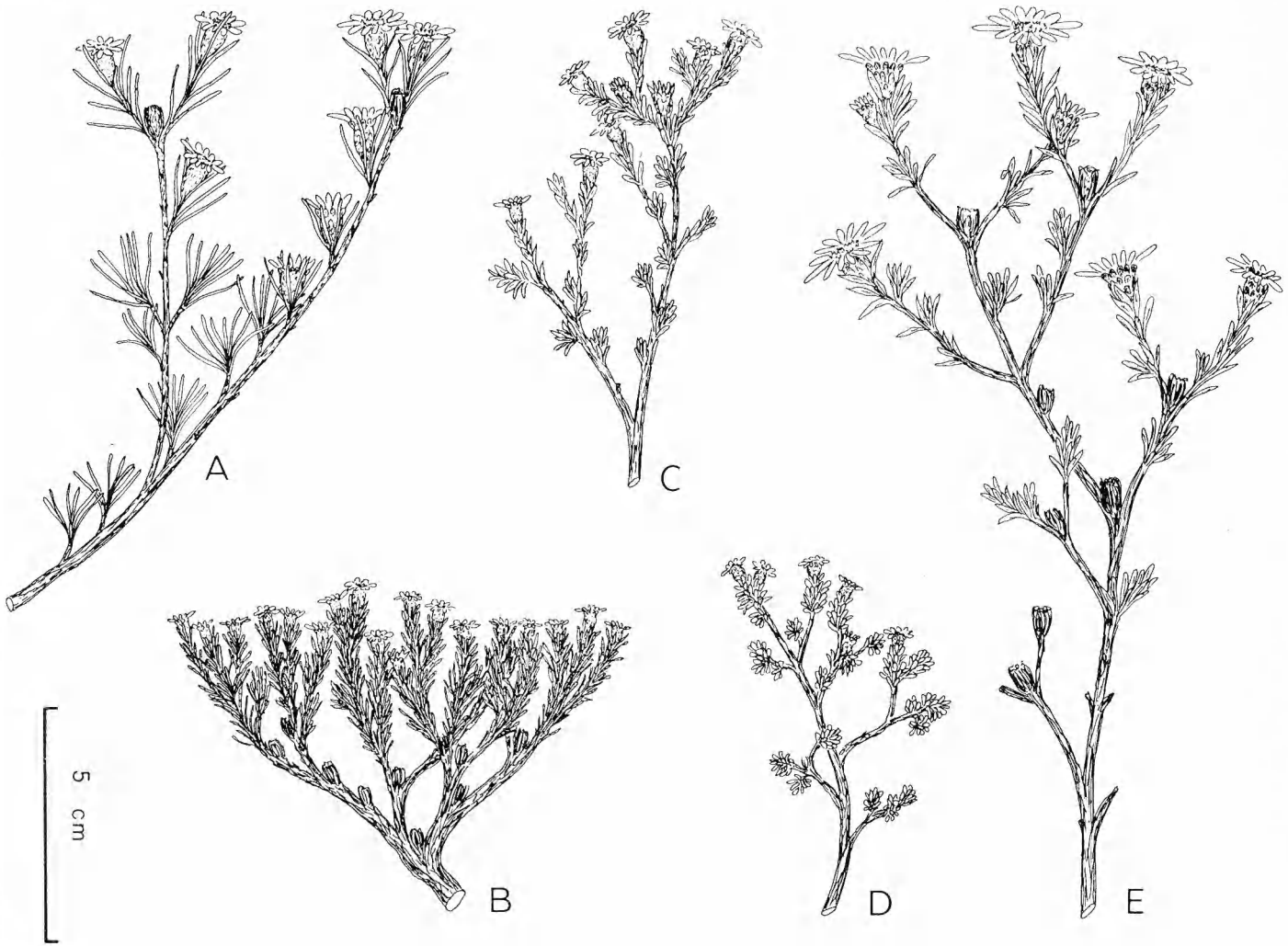
(UPS-THUNB), Stockholm (S), Copenhagen (C) and in the Linnaean herbarium in London (LINN, Herb. No. 980:6, left specimen). Some of these have been annotated "*Pteronia minuta*" or even "*Pteronia minuta nova*" and I believe the species of Thunberg and Linné f., respectively, are based on the same collection. Consequently, *Nestlera minuta* (L. f.) DC. goes into synonymy under *Asaemia*, although De Candolle (1838 p. 283) and later authors have used this name for specimens of *Rosenia humilis*.

Densely–moderately and generally subdichotomously branched, compact–diffuse, occasionally somewhat spiny, often vigorous shrubs, very variable in habit. *Leaves* variable, flat–semiterete–triquetrous with margins sometimes involute, mid-ribbed, linear–narrowly elliptic–obovate, 1–20 mm long, 0.4–2 mm wide, quite glabrous and bright green with young leaves often deciduously tomentose mainly above to densely tomentose and greyish–green–grey on both sides, often glandular with stalked glands.

Involucre urceolate–cyathiform–campanulate, 2–11 mm wide. Involucral bracts 10–55, outer ovate, inner gradually longer and oblong–spatulate, apically scarious and spreading and sometimes brownish, up to 9 mm long, up to 3 mm wide, glabrous or seldom dorsally tomentose and whitish. *Receptacle* epaleate or occasionally paleate with linear–narrowly spatulate, up to 8 mm long paleae, subtending all or most disc-florets.

Ray-florets 5–22. Lamina elliptic, 3.5–13 mm long. Style 3.5–7 mm long. *Disc-florets* 5–40. Corolla 3.6–7.3 mm long. Style 3.5–8 mm long. Anthers 2.3–4.5 mm long; tails c. 1/5 of the length of the anther. *Achenes* almost terete, oblong, 2–4.8 mm long, 0.5–1.2 mm wide, always with a basal tuft of hairs, otherwise glabrous or ± sparsely pilose, basally transversely conspicuously rugose and brown, apically smooth and light yellowish (ripe achenes only), often with a thickened rim apically below pappus; pappus crownlike, irregularly and minutely toothed, of connate, short scales, up to 1.5 mm long, often also with 1–3, up to 6 mm long, smooth or barbellate bristles.

Fig. 9. Distribution and portions of plant of *Rosenia humilis*. – A: Henrici 3987 (PRE), leaves glabrous, green. – B: Nordenstam & Lundgren 2102 (S), leaves glabrous, bright green (formerly known as *Nestlera conferta* DC.). – C: Nordenstam & Lundgren 2103 (S), leaves tomentose, greyish. – D: Wall, N of Vosberg (S), leaves tomentose, greyish. – E: Bremer 164 (S), leaves tomentose, greyish–green (formerly known as *Nestlera humilis* Less.).



Flowering period mainly August–October.

Vernacular names. “Bekkerbos(sie), Gemsbok-karoo, Perdebossie, –karoo, –kool, Springbok-karoo, Volstruisbossie, –karoo, Blouperde-karoo, Hartebeeskaroo” (Smith 1966 p. 615).

R. humilis is a very variable species, consisting of several form series. Different levels of polyploidy are known. The chromosome numbers and the species situation have been discussed above. Specimens of *R. humilis* are not difficult to distinguish from the three other species, usually very characteristic (see discussions of these species). In doubtful cases the achenes should be examined. In all collections of *R. humilis* that I have seen, these are furnished with a basal tuft of hairs (Fig. 5C), which is lacking in the other species. Furthermore the achenes are often rugose basally in this species and the pappus scales are shorter and more connate.

Variation. Formerly there were two species recognized, viz. *Nestlera humilis* Less. (syn. *Nestlera minuta* auct.) and *Nestlera conferta* DC. The former species comprised more or less laxly branched shrubs with tomentose, greyish-green leaves, whereas the latter species included more or less compact, low shrubs with linear, glabrous, bright green leaves and small capitula. Much of the material of *Rosenia humilis* will fit into these two form series. However, there are many other forms in addition, viz. densely–moderately branched, compact–diffuse shrubs with linear or narrowly elliptic–obovate, glabrous or tomentose leaves and small, slender or wide capitula. Some of these are shown in Fig. 9. The variation is further treated under Morphological aspects and Discussion above.

Distribution. Fig. 9. The distribution of *R. humilis* approximately covers that of the genus as a whole. It occurs in South West Africa south of Windhoek, in the karoo areas of the Cape Province and the southern Orange Free State. It is not reported from Botswana, but is likely to occur in the southern or southwestern part. *R. humilis* often grows in heavier soil than the three other species. Although it often grows in stony ground, it is usually found on sandy, shaly or clayey karoo flats. It sometimes grows in partially moist, partially dried-up areas, i.e.

vleis and pans. *R. humilis* is listed under several of Acocks' (1953) karoo veld types. 296 collections have been examined.

Taxa to be excluded

- Nestlera acerosa* (DC.) Harvey 1865 p. 296 = *Relhania acerosa* (DC.) Bremer
Nestlera angusta Compton 1949 p. 107 = *Relhania tricephala* (DC.) Bremer
Nestlera biennis (Jacq.) Sprengel 1818 p. 568 = *Relhania biennis* (Jacq.) Bremer
Nestlera consimilis S. Moore 1917 p. 105 = *Relhania relhanioides* (Schltr) Bremer
Nestlera corymbosa Bolus in Oliver 1894 plate 2324 = *Relhania corymbosa* (Bolus) Bremer
Nestlera Dieterlenii Phillips 1917 p. 344 = *Relhania dieterlenii* (Phillips) Bremer
Nestlera Garnotii (Less.) Harvey 1865 p. 296 = *Relhania garnotii* (Less.) Bremer
Nestlera minuta (L. f.) DC. (excl. descr.); De Candolle 1838 p. 283 = *Asaemia axillaris* (Thunb.) Harv.
Nestlera reflexa (Thunb.) De Candolle 1838 p. 283 = *Relhania biennis* (Jacq.) Bremer
Nestlera relhanioides Schlechter 1899 p. 205 = *Relhania relhanioides* (Schltr) Bremer
Nestlera tenuifolia De Candolle 1838 p. 284 = *Relhania garnotii* (Less.) Bremer
Nestlera tricephala (DC.) Harvey 1865 p. 297 = *Relhania tricephala* (DC.) Bremer
Nestlera virgata N. E. Brown 1895 p. 25 = *Relhania tuberosa* Bremer
Polychaetia acerosa De Candolle 1838 p. 285 = *Relhania acerosa* (DC.) Bremer
Polychaetia brevifolia De Candolle loc.cit. = *Geigeria brevifolia* (DC.) Harv.
Polychaetia Garnotii Lessing 1832 p. 372 = *Relhania garnotii* (Less.) Bremer
Polychaetia passerinoides auct. (excl. *Relhania passerinoides* L'Hérit.); De Candolle 1838 p. 285 = *Geigeria ornativa* O. Hoffm.
Polychaetia passerinoides (L'Hérit.) De Candolle loc.cit. = *Relhania genistifolia* (L.) L'Hérit.
Polychaetia pectidea De Candolle loc.cit. = *Geigeria pectidea* (DC.) Harv.
Polychaetia tricephala De Candolle loc. cit. = *Relhania tricephala* (DC.) Bremer
Polychaetia triflora De Candolle 1838 p. 287 = *Relhania tricephala* (DC.) Bremer

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Ombrophytum peruvianum (Balanophoraceae) found in the Galápagos Islands

Henning Adersen

Adersen, H. 1976 06 30: *Ombrophytum peruvianum* (Balanophoraceae) found in the Galápagos Islands. [Contribution no. 195 from the Charles Darwin Foundation for the Galápagos Islands.] Bot. Notiser 129: 113–117. Stockholm. ISSN 006-8195.

Ombrophytum peruvianum Poeppig & Endlicher, a subterranean root parasite, is reported as new to the Galápagos Islands. It is previously known from sub-Andean areas in the South American continent. A detailed description is given, with notes on the phenology, habitat and distribution.

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This paper is the first of a series of scientific reports based on my work as a Unesco Associate Expert in plant ecology at the Charles Darwin Research Station, Isla Santa Cruz, Islas Galápagos, Ecuador, from February 1974 to February 1975. The main aims were: to map the flora and vegetation, to study succession (especially in relation to the impact of introduced plants and animals), and to aid in the establishment of a Herbarium at the Charles Darwin Research Station (CDS). Duplicates of my collections are deposited at the Botanical Museum, Copenhagen (C).

Fig. 2 A and B have been transferred from Kodachrome 2 diapositive colour slides. The author has several colour dias.

Ombrophytum peruvianum Poeppig & Endlicher 1838 has been collected on Isla Santa Cruz, Galápagos. No previous reports of Balanophoraceae has been published from the archipelago. The existing description of the taxon is incomplete and based on specimens from sub-Andean environments in Peru. Therefore a detailed description based only on Galápagos material is submitted.

Description

Herbaceous, fleshy root parasites, devoid of chlorophyll and roots. At point of contact with host root a subspherical to cordiform faintly verrucous yellowish tuber (in our specimens up to 10 cm in diameter at the most). Stems 1–5 appearing successively from tuber, developed endogenously, at base surrounded by short-lobed sheath, 1–4 cm high to point of lobes; these deltoid, 0.5–2 cm high. Stems 3–20 cm high from tuber, 0–5 cm appearing above ground, pushing up small heaps of soil. Stems cylindrical to clavicate; diameter at base from 1.5–2.5 cm, midway 1.5–7 cm; rounded towards apex, white to yellowish. Lower quarter or so of stems sterile, sometimes with caducous peltate fleshy leaves, approx. 1 cm in diameter, with 2–4 upright lobes; upper part forming a spadix-like inflorescence crowded with secondary branches. Each secondary branch supported by an early caducous bract. Outer peltate part of branches atrophying particularly on female branches.

Male branches 0.5–1 cm long 0.8–1 cm thick, cylindrical to conical; peltately widened distal part up to 1.5 cm in diameter. Female branches 0.5–1.5 cm long, 0.4–0.8 cm in diameter, prismatic to cylindrical to obconical, peltate distal part 0.4–0.8 cm in diameter.

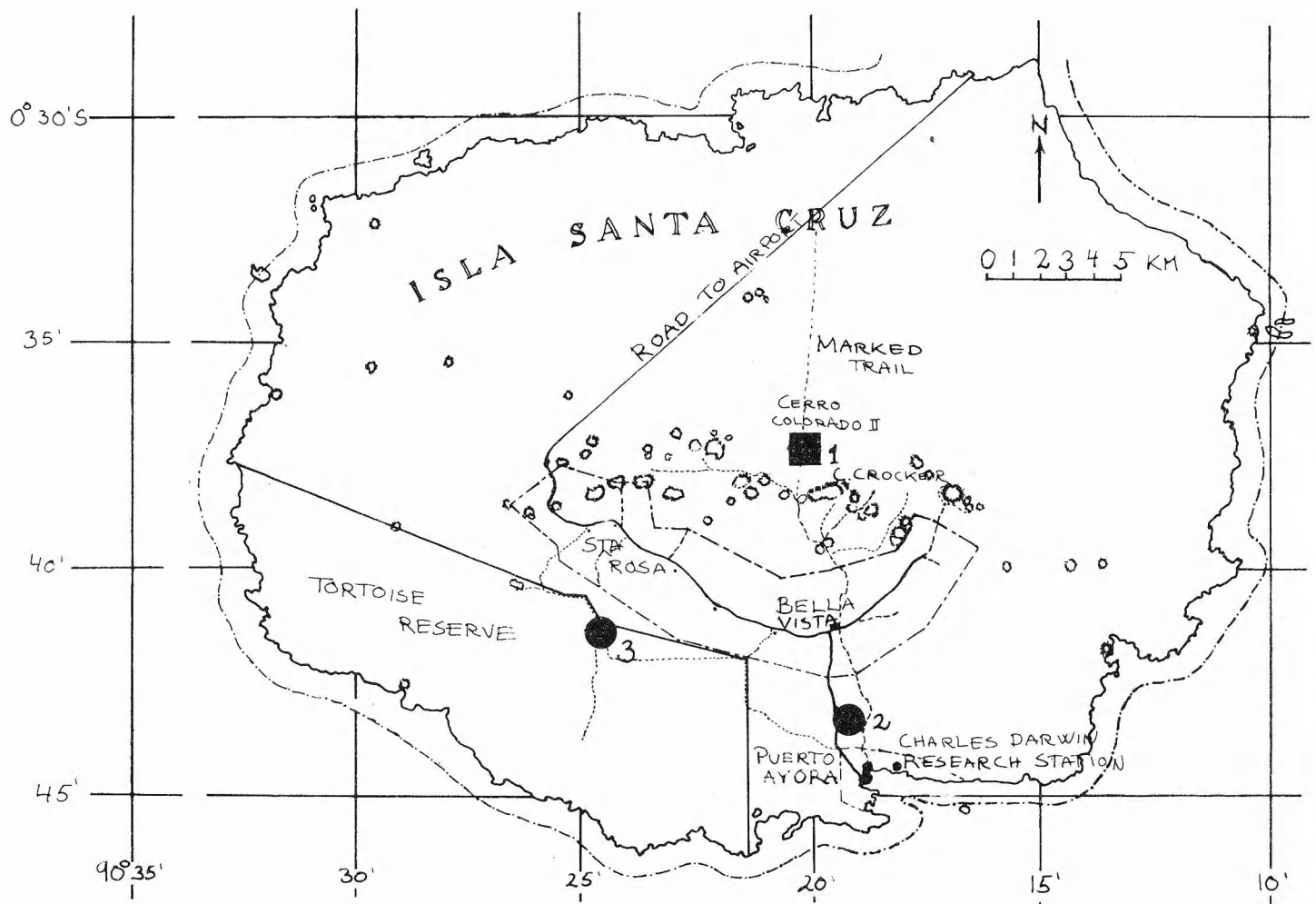


Fig. 1. Localities of *Ombrophytum peruvianum* on Isla Santa Cruz, Galápagos. - 1: Area described in this paper. - 2: Finds reported by A. Kastdalen (pers. comm.) around 1955. - 3: Finds reported by W. G. Reeder in August 1970, C. MacFarland (pers. comm.).

Male flowers on and between the male branches, without perianth, consisting of 1-2 stamens inserted in the fissures between small mamilliform violet protrusions 1-2 mm high, 3-4 mm broad (primordia or rudimentary flowers?). Filaments free, stout, filiform, 1.2-2 mm long, anthers basifixed, 1.5-2 mm long, dark violet, elliptic to oblong, 2-locular, opening by a longitudinal slit. No mature pollen observed.

Female flowers on female branches, without perianth, ovary obovoid to prismatic, 3-4 mm long, greatest diameter about 2 mm, red-violet, styles 2 (rarely 3) inserted at inverted margin of flowers, length about 1 mm, divergent, colourless; stigma capitate, violet.

There is no external difference between female flowers and fruits. The latter are one-seeded berries persisting when the inflorescence decays.

Identification

A revision of American Balanophoraceae by Dr Bertel Hansen, Botanical Museum, Copenhagen, is in progress. Only four specimens of *Ombrophytum peruvianum* have been found in 31 of the major herbaria of South American material: Harling et al 7026 from Prov. Napo, Ecuador, 1968; Prance et al 7664 from State of Acre, Brazil, 1968; Schunke 3953 from Dep. San Martin, 1970; and Ule s.n. from Alto Acre, Brazil, 1911. The type specimen collected by Poeppig in Cuchero, Peru, around 1830 and presumably kept in W is no longer extant. However, Poeppig's description (Poeppig & Endlicher 1838 p. 40) is detailed and is accompanied by a drawing (pl. 155). The Galápagos material agrees quite well with Poeppig's description and drawing apart from the tuber and sheath. The original description and drawing of these organs

are not clear and are probably erroneous, due to poor preservation and to the lapse of time between collection and the description of the specimens.

Phenology

The first collections were made on April 22, 1974 and May 6, 1974, at the end of the hot season (see Wiggins & Porter 1971 pp. 13–30). The specimens collected represented all stages of development from a spherical tuber 1.5 cm in diameter to dead specimens in advanced stages of decay. In spite of an exhaustive search only a few specimens were found and no dry dead specimens. At the time there was a relatively dense herb cover indicating that the soil had just previously been wet through. Thus soil-water saturation may initiate stem development as suggested by Poeppig or accelerate decay. In the following months till December, when we last visited the locality, the vegetation gradually became drier and the temperature fell. During this period stems were fairly abundant and it was always possible to find dry dead specimens. The specimens seen and collected in the later part of the period were smaller and more sclerotic.

Habitat

The collections were made along and approximately 20 m to each side of a trail from Cerro Puntudo northwards. We marked the trail for every 100 m, and the collection area is between the 2100 m and 2600 m mark, on the gentle northwestern slope of Cerro Colorado II at altitudes of 610 to 650 m.

On this short stretch of the trail a very marked change in the vegetation occurs reflecting the climatic conditions. It can be regarded as the upper part of the main slope of the island and here the wet upland climate changes to an arid north slope-lowland climate. In the hot season from approximately January to June precipitation in both areas is in the form of infrequent heavy showers sufficient to wet the soil. In the cold season (the garua season), from June to January, there is very little precipitation on the north slope whereas the upland regions are enveloped in more or less continual fog (garua), sufficient to keep the vegetation wet but not

wetting the soil to more than 1–2 cm. This abrupt line of contrast (the garua limit) is encountered within the collecting area.

Soil conditions also change along this stretch. In the upland region the finer soil particles originating from weathering and pyroclastic material are protected from erosion and leaching by the denser evergreen plant cover, whereas on the typical north slope and lowland localities there is virtually no visible soil, the plants (mostly deciduous) being rooted in pockets of soil between the lava boulders at a depth of 1–2 m. The soil of the sample area is largely of upland type and is red to brown, probably due to the influence of lava or ash from Cerro Colorado II (i.e. the Red Mountain). The following edaphic factors were measured for a soil sample: pH of fresh soil 7.5–8; humus content (Walkley-Black) 20%; sulphuric acid extracted P 223 ppm P; cation exchange capacity 50 mval/100 g; NH_4Ac -exchangeable ions: Ca 38.7; Mg 8.46; Na 0.4; K 1.22 mval/100 g; base saturation 97%.

The vegetation comprises a closed evergreen forest dominated by *Scalesia pedunculata*, rich in epiphytes, with a continuous crown layer at 5–8 m above ground level, a shrub layer closed to variable extent and a sparse and ephemeral herb layer. There is a thin layer of litter.

In the collecting area the following species were noted: Trees: *Scalesia pedunculata* (forming more than 80% of the crown canopy), *Psidium galapageium*, *Pisonia floribunda* and *Zanthoxylum fagara*. Shrubs: *Psychotria rufipes*, *Chiococca alba*, *Tournefortia pubescens*, *T. psilostachya*, *Cordia anderssonii*, *Plumbago scandens*, *Castela galapageia* and *Capsicum frutescens*. Herbs: *Alternanthera halimifolia*, *Bidens pilosa*, *Paspalum conjugatum*, *Blechnum brownei*, *Doryopteris pedata*, *Acalypha sericea*, *Abutilon depauperatum* and *Solanum nodiflorum*.

Root samples from the woody plants occurring in the area were compared under the microscope and the host root was identified as *Scalesia pedunculata*. This genus is endemic to Galápagos, so a host-specific relationship is highly unlikely and co-introduction to the archipelago is impossible.

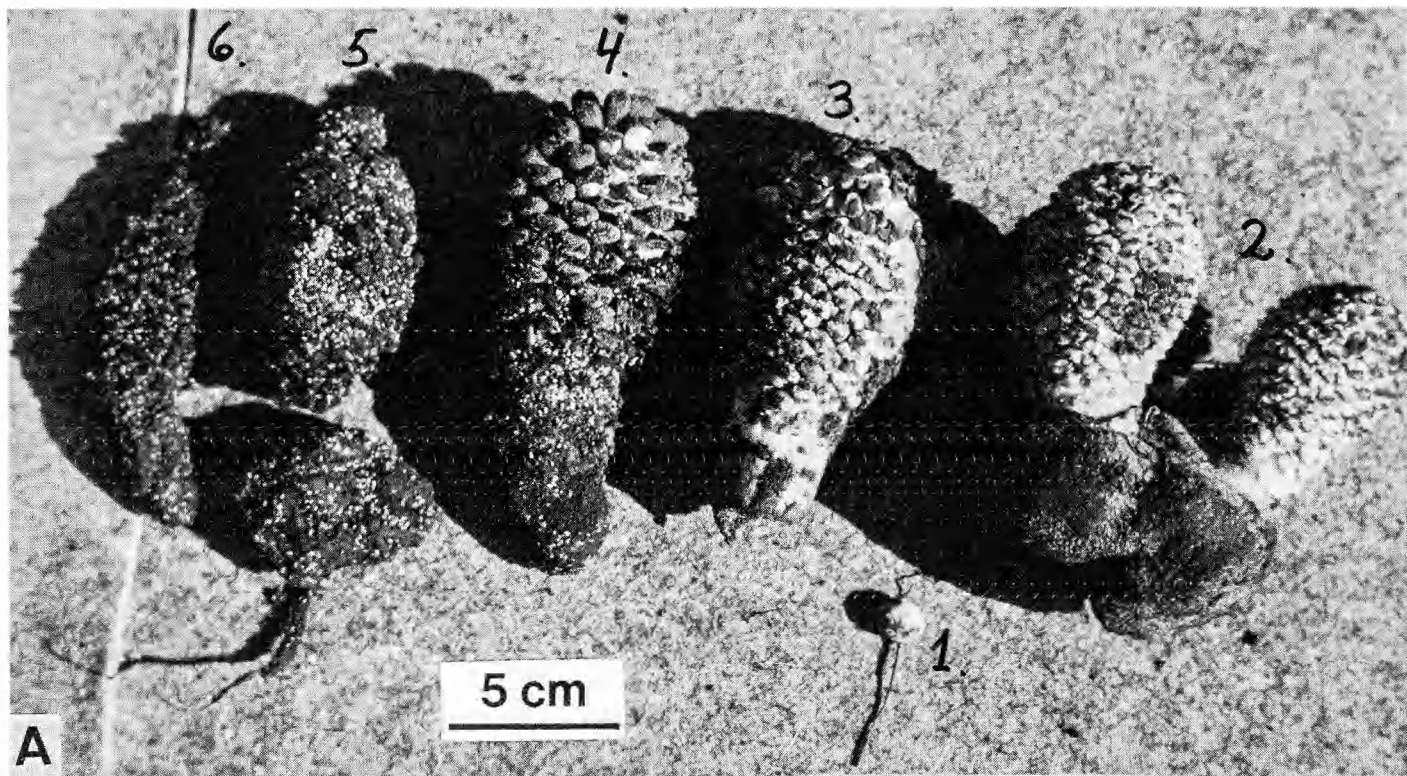


Fig. 2. *Ombrophytum peruvianum*. - A: A. & H. Adersen 244, photographed immediately before preserving in FAA. - 1: Very young tuber developing on root. - 2: Tuber with 5 young successively developed inflorescences. - 3: Flowering stage. - 4: Fruiting stage. Atrophying of the distal peltate part of the branches has occurred. - 5, 6: Stages of decay. Note that the fruits persist in the decaying tissue. - B: A. & H. Adersen 243, photographed in the field. Note the difference between the male upper part of the inflorescence and the female lower part.

Distribution

The occurrence of a subterranean parasitic plant on Isla Santa Cruz has been known for some time. A. Kastdalen and C. MacFarland have informed me of the previous finds as indicated on the map. It is interesting that both records are from areas where the upland *Scalesia* forest is gradually replaced by dry lowland deciduous forest. The specimens from these localities were lost and never identified but doubtless belonged to the species which has now been found.

Ombrophytum peruvianum has previously only been recorded from sub-Andean environments in Peru, Ecuador and Brazil (MacBride 1937 p. 429, B. Hansen pers. comm.). The finds in Galápagos are a remarkable extension of the area of distribution which gives rise to interesting questions of means of dispersal. The fruits lack adhesive agents and are apparently spread mostly by ants or other invertebrates of the soil. Furthermore most of the fruits are deposited below soil surface. Short-distance dispersal may also occur by means of rats since the marks of rats' teeth were observed on some tubers.

The lack of perfect pollen may indicate that the plant is, in fact, parthenogenetic which may facilitate survival of populations originating from one diaspore.

Acknowledgements

Special thanks should be directed to Dr Craig MacFarland, director of the Station, Drs Tjitte de

Vries, H. van der Werff and Sr Camilo Calapucho for field company. I also thank the officials of the National Park of Galápagos for help and advice and permission to work in the National Park.

I am very much indebted to Dr Bertel Hansen, Botanical Museum of Copenhagen, who identified the plant and guided me in the literature on Balanophoraceae, and to Mrs Cherry Nielsen, B.Sc., who helped with the translation.

Last but not least special thanks to Dr Guy Coppois, who shared struggles and pleasures with my wife and me on most field trips, and whose interest in snails literally drew my attention to the soil where *Ombrophytum* grows.

Specimens studied

Galápagos: Isla Santa Cruz, Cerro Colorado II, A. & H. Adersen 243, 6.5. 1974 (C); 244, 22.4. 1974 (C); 1323, 5.12. 1974 (C); Coppois s.n. 9.9. 1974; van der Werff 597, 8. 1974 – *Ecuador*: Prov. Napo, Hacienda Cotapino (Concepción), Harling, Storm & Ström 7026, 19–20.2. 1968 (GB) – *Peru*: Prov. Mariscal Caceres, Dpto. San Martin, northwest of the nursery of the Instituto Agropecuario de Tocache, Schunke V. 3943, 18.4. 1970 (F) – *Brazil*: Seringal S. Francisco, Ule s.n., 9. 1911 (B) – State of Acre, Mun. of Sena Madureira, road Sena Madureira to Rio Branco, Prance, Coelho, Ramos & Farias 7664, 29.9. 1968 (INPA).

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Urocystis poae-palustris Vánky, sp. nov.

Kálmán Vánky

Vánky, K. 1976 06 30: *Urocystis poae-palustris* Vánky, sp. nov. *Bot. Notiser* 129: 119–121. Stockholm. ISSN 0006-8195.

A new species of *Urocystis* (Ustilaginales, Tilletiaceae) on *Poa palustris* L. is described from Transylvania.

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In Transylvania (Rumania) the writer collected several samples of *Poa palustris* L. heavily infested with a species of *Urocystis* which cannot be identified with any earlier known *Urocystis* species on *Poa*. It is therefore described here as a new species: *Urocystis poae-palustris* Vánky.

Sori in culmis, foliis vaginisque, elongato-linearibus. initio plumbeis, epidermide tectis, dein longitudinaliter erumpentibus, nigris, granuloso-pulverulentis. *Glomerulis* \pm globosis vel irregularibus, 15–40 μm diam., e 1–5 sporis centralibus fertilibus et numerosis cellulis exterioribus sterilibus, stratum discontinuum vel continuum efformantibus. *Sporis* subglobosis,

ovoideis, irregularis vel polygonalibus, dilute brunneis, 9.6–13.6(–15.2) \times 12–17.6(–19.2) μm diam., episporio levi, 0.8–1 μm crasso. *Cellulis sterilibus* subglobosis, ovoideis, elongatis vel irregularis, 4.8–9.6 \times 5.6–13.6 μm diam., dilute flavo-brunneis, episporio levi, 0.8–1.4 μm crasso. Habit. in *Poa palustris* L. – Rumania, Transylvania, pr. oppid. Toplița, 11.VII.1965, leg. K. Vánky. Holotypus depositus in S.

Sori (Fig. 1 A) in the culms, leaves and sheaths as small, long streaks between the veins, lead-coloured, first covered by the epidermis which ruptures longitudinally disclosing the black, granular-powdery mass of spore balls. The

Table 1. Differences between *Urocystis* species on *Poa*.

Character	<i>U. poae-palustris</i> (type)	<i>U. agropyri</i> (K. V. Ust. 13)	<i>U. occulta</i> (H: Cegléd, 1930, Husz)	<i>U. poae</i> (type)
Sori	long, narrow streaks	long, somewhat wider streaks	long, narrow streaks	long, somewhat wider streaks
Spore mass	black	dark brown	black	dark brown
Spore balls composed of	1–5 spores (1=33%, 2=46.5%, 3=14.5%, 4=4%, 5=2%)	1–3(–4) spores (1=66%, 2=28%, 3=5.5%, 4=0.5%)	1–4(–5) spores (1=49.5%, 2=35%, 3=13%, 4=2%, 5=0.5%)	1–3(–4) spores (1=67%, 2=31%, 3=1.75%, 4=0.25%)
The sterile cells form	\pm continuous layer	\pm continuous layer	discontinuous layer	continuous layer
The plants attacked	flower sometimes	do not flower	flower often	do not flower



leaves often rupture longitudinally. *Spore balls* (Fig. 2 A) globose, ovoidal to irregular, 15–40 μm in diameter composed of 1–5 central spores surrounded by a discontinuous to continuous layer of peripheral sterile cells. *Spores* subglobose, ovoidal, irregular or polyhedral, light brown, 9.6–13.6(–15.2) \times 12–17.6(–19.2) μm in diameter, with smooth wall 0.8–1 μm thick. *Sterile cells* subglobose, ovoidal to oblong or irregular, 4.8–9.6 \times 5.6–13.6 μm in diameter, light yellowish-brown, with smooth wall 0.8–1.4 μm thick. On *Poa palustris* L. (det. C. Zahariadi), Rumania: Transylvania, near the town Toplița, 46.56 N, 25.50 E, c. 700 m, 11.VII.1965, coll. K. Vánky (1196). Holotype deposited in S, isotypes in BP, BPI, IMI, UPS and in the author's private herbarium.

Discussion

Three species of *Urocystis* have so far been reported on *Poa*: (1) *U. agropyri* (Preuss) Fisch. v. Waldh., (type on "Queckengrass" (*Elytrigia repens* (L.) Nevski), Germany, Saxony, Hoyerswerda, C. G. T. Preuss); (2) *U. occulta* (Wallr.) Rbh., (type on *Secale cereale* L., Germany, Thuringia, F. G. Wallroth); and (3) *U. poae* (Liro) Padw. & Khan, (type on *Poa pratensis* L., Sweden, Gotland, Bro par., Eriks, VII.1898).

The main characteristics distinguishing these species and *U. poae-palustris* are given in Table 1.

Two conclusions can be drawn:

(1) *Urocystis poae-palustris* cannot be identified with any earlier known *Urocystis* species on *Poa*.

(2) *U. poae* (the type) and *U. agropyri* (on *Elytrigia repens*, in K. Vánky: Ustilag. No. 13) are very closely related.

Acknowledgement. The author is grateful to Dr Lennart Holm (Uppsala) for critically reading the manuscript.

Fig. 1. A: *Urocystis poae-palustris* Vánky on *Poa palustris* L. – B: *U. poae* (Liro) Padw. & Khan on *Poa pratensis* L.

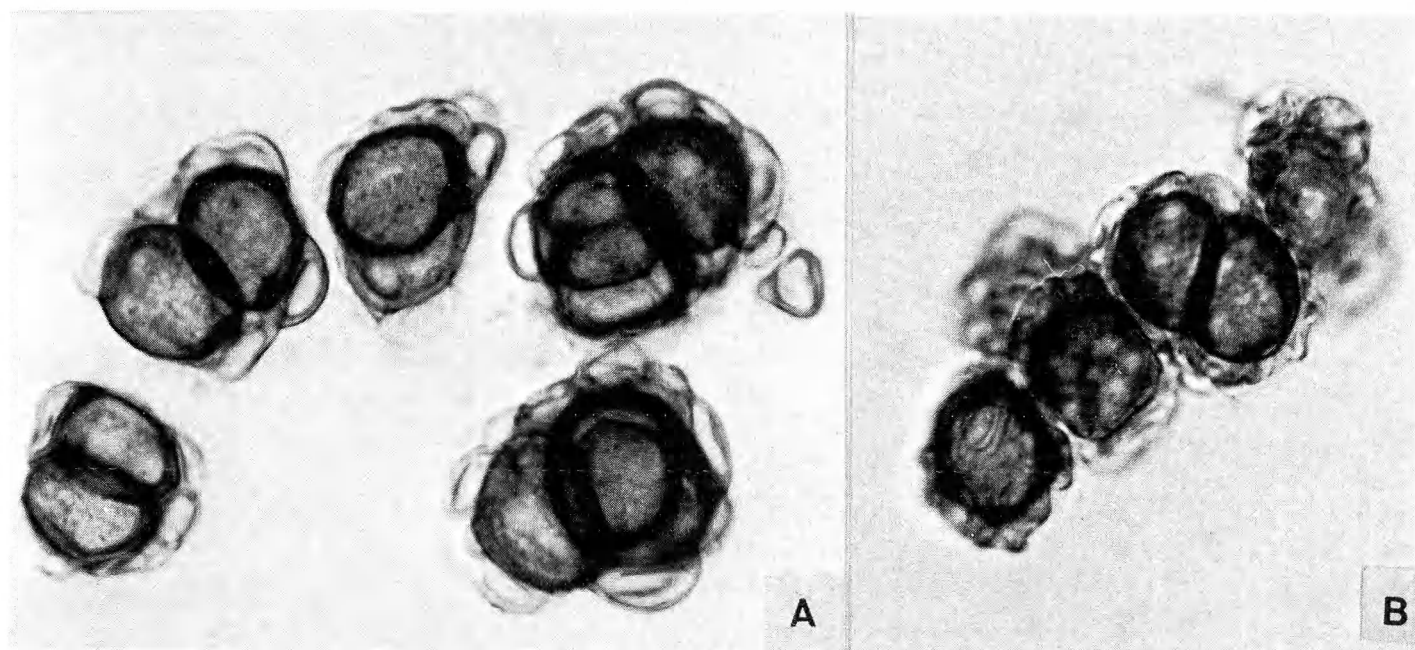


Fig. 2. A: Spore balls of *Urocystis poae-palustris* Vánky. – B: Spore balls of *U. poae* (Liro) Padw. & Khan (type). – c. 695 ×.

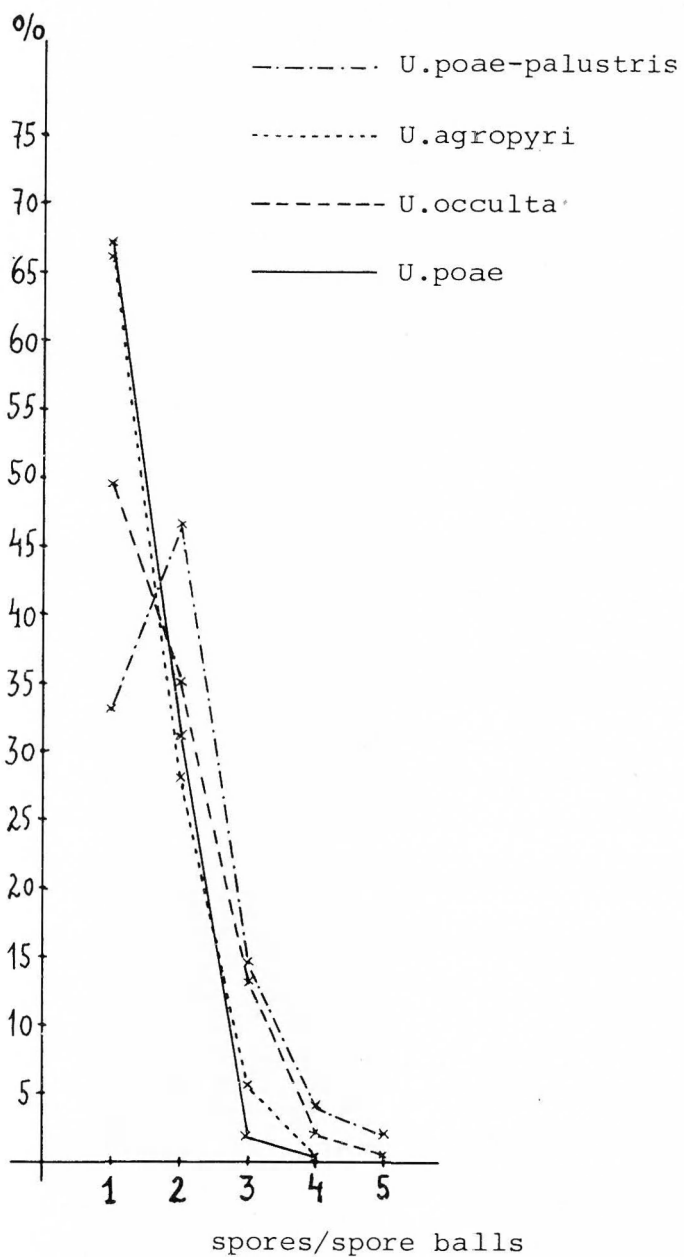


Fig. 3. Frequency of different kinds of spore balls in *Urocystis* species on *Poa*.

Some tropical African Cruciferae

Chromosome numbers and taxonomic comments

Bengt Jonsell

Jonsell, B. 1976 06 30: Some tropical African Cruciferae. Chromosome numbers and taxonomic comments. – *Bot. Notiser* 129: 123–130. Stockholm. ISSN 0006-8195.

Chromosome numbers with comments are presented for 17 species of Cruciferae. The material originates from Ethiopia, Kenya and Tanzania. For 6 species (*Cardamine obliqua*, *Erucastrum arabicum*, *E. pachypodum*, *Oreophyton falcatum*, *Sisymbrium erysimoides* and *Thlaspi alliaceum*) no chromosome numbers have previously been reported, for 2 species (*Cardamine trichocarpa*, *Crambe hispanica*) numbers differing from previous reports are given. A polyploid series combined with aneuploidy seems to occur within *Cardamine obliqua*. The *Erucastrum arabicum* complex is interpreted as consisting of 3 species, two diploids and one tetraploid. For one of the former the new combination *E. pachypodum* (Chiov.) Jonsell is published.

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In the course of revisional work on tropical African Cruciferae, primarily aiming at a presentation for the Flora of Tropical East Africa edited by the Royal Botanic Gardens, Kew, seed samples of several species have been obtained from various parts of E Africa and Ethiopia. This has made possible the determination of chromosome numbers, which are presented here with short taxonomic comments. These are in the main preliminary pointing to problems rather than suggesting solutions. As regards *Crambe* I have taken the opportunity to discuss the nomenclature to be employed in the Flora. Two genera, *Rorippa* and *Lepidium*, have been treated in separate papers (Jonsell 1974, 1975).

The chromosome numbers are in many cases the first reported for the species, and with one or two exceptions the first from their E African areas of distribution. Voucher specimens of all counts will be deposited at UPS. The determinations were made from root tips, usually fixed in chrome-acetic formalin (Müntzing 1933), stained in gentian violet, embedded in paraffin and sectioned. In these crucifers at least squashes usually give inferior results but were sometimes successful (pretreatment in α -monobromonaphthalene, fixation in Östergren &

Heneen's (1962) agency, staining according to the Feulgen method). I have found it superfluous to cite all previously published counts, especially those of widespread species, but refer to the lists by Fedorov (1969) and Moore (1973, 1974). No critical estimate of older, sometimes dubious, counts has been made.

In tropical E Africa (Kenya, Uganda, Tanzania) about 60 species of Cruciferae are to be found. Most of them belong to the Afro-montane or Afro-alpine phytogeographical regions (cf. White 1965), many of the rest being introduced weeds. In Ethiopia there are in addition very approximately c. 20 species, most of which belong to the arid areas (Sudano-Zambesian phytogeographical region). Only c. 5 E African species of Crucifers are unknown from Ethiopia. Nearly all species included in this study are Afro-montane or -alpine plants or alien weeds, while there are no species from the arid area.

Arabidopsis thaliana (L.) Heynh.

$2n = 10$. Ethiopia, Tigre-Begemdir, Simien, Geech, 3700 m, Hedberg s.n. 16.10. 1973 – Ethiopia, Tigre-Begemdir, Simien, Mt Buahit, 4225 m, Hedberg 5433.

This chromosome number has been repeatedly reported for *A. thaliana* (Fedorov 1969). The montane African *A. thaliana* is usually low, richly branched from the base and rather compact, and has on these grounds often been regarded as var. *pusilla* (A. Rich.) O. E. Schulz (basonym: *Cardamine pusilla* A. Rich.). Hedberg (1964) showed that for plants from a Kenyan population these characters are largely maintained in cultivation. On the other hand there are herbarium specimens from montane Ethiopia (Simien) closely approaching the normal European plant. The cultivated specimens cited above are about intermediate in this respect. Like Hedberg (1957) I find it therefore impossible to make a subdivision for African material of this species.

Arabis alpina L.

2n = 16. Ethiopia, Tigre-Begemdir, Simien, Mt Buahit, 4225 m, Hedberg 5431 – Ethiopia, Arussi, Chilalo awraja, Mt Chilalo, 3500 m, Thulin 1660 – Ethiopia, Bale, Bale Mts, Tullu Deemtu, 4000 m, Hedberg s.n. 2.11. 1973 – Kenya, Central Prov., Mt Kenya, Teleki Valley, 3900 m, Ryman 152 – Tanzania, Arusha Prov., Mt Meru, E slope, 2800 m, Jonsell 2178.

Hedberg (1957) demonstrated that the Afro-alpine population of *A. alpina* in various ways combines features regarded as characteristic of *A. alpina*, "*A. albida*" Stev. (= *A. caucasica* Willd.) and *A. cuneifolia* Hochst. ex A. Rich., names that have all been used for the African plant. Crossing experiments (Hedberg 1962 a) supported the view that the African *Arabis* is conspecific with the northern *A. alpina*, while *A. caucasica* s. str. seemed to be isolated. Sebald (1969), however, still reported the species under the name of *A. cuneifolia*. Hedberg (1962 a) counted 2n = 16 in a strain from Mt Kenya, a number repeatedly reported from northern areas (Fedorov 1969).

Capsella bursa-pastoris (L.) Medik.

2n = 32. Kenya, Central Prov., Mt Kenya, W slope, 2450 m, v. Hofsten 512.

In E Africa and probably also in Ethiopia the species is an introduced weed. Curiously enough Franchetti (1958) redetermined all *C. bursa-*

pastoris from Ethiopia as *C. rubella* Reut. She drew attention to the concave lateral margins of the siliculae, a constant character in *C. rubella* but sometimes also present in *C. bursa-pastoris*, for example in the Kenyan plant cited above. Specific *C. rubella* characters, such as the very short petals tinged to varying degrees with red, are not found in the African material which I include without any doubt in *C. bursa-pastoris*.

2n = 32 is the chromosome number repeatedly reported for *C. bursa-pastoris*. *C. rubella* is a diploid with 2n = 16 (Fedorov 1969).

Cardamine africana L.

2n = 16. Tanzania, Arusha Prov., Mt Meru, E slope, 2700 m, Hedberg 4741 – Tanzania, Arusha Prov., Ngurdoto Crater Rim, 1600 m, Jonsell 2146.

In Africa, where it consistently has tripartite leaves, *C. africana* is only slightly variable. *C. holtziana* Engl. & Schulz in Schulz (1903) from the Usambara Mountains in Tanzania, distinguished on its larger flowers and longer petioles, falls within a continuous variation range and cannot be upheld at any taxonomic rank. *C. africana*, which is widely distributed in montane tropical areas of the Old and New World, is in S America more variable and approaches *C. jamesonii* Hook. and the *C. obliqua* complex (cf. below). In a study on S American *Cardamine* Sjöstedt (1975) circumscribed *C. africana* much too widely, as he included within it even the African *C. obliqua*.

2n = 16 was also reported by Morton (1972), probably in material from the Cameroons.

Cardamine hirsuta L. – Fig. 1 A

2n = 16. Ethiopia, Tigre-Begemdir, Simien, Geech, Sacha, 3750 m, Hedberg 5395.

In Africa the species is represented by a form which in cultivation was shown to be strictly annual with an extremely rapid development from germination to ripe seeds. This is in contrast to the form native to N Europe, which goes through a stage as a leaf rosette (winter annual or strictly biennial) before flowering. In many parts of the world the annual form is a weed, but the many montane and alpine African

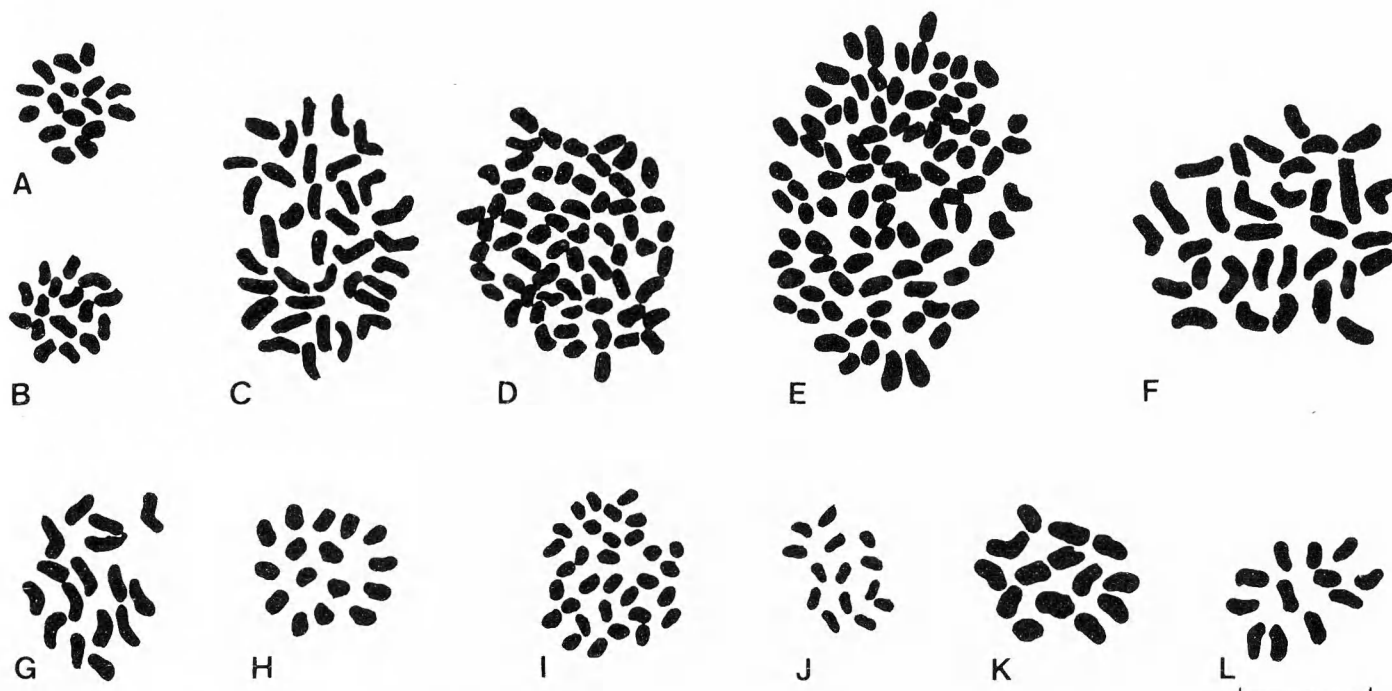


Fig. 1. Mitotic metaphase plates in root tips drawn from micrographs. – A: *Cardamine hirsuta*, $2n = 16$ (Hedberg 5395). – B: *C. trichocarpa*, $2n = 16$ (Hedberg 5327). – C: *C. obliqua*, $2n = 36$ (Thulin 1019). – D: *C. obliqua*, $2n = 62$ (Hedberg 5348 b). – E: *Crambe hispanica*, $2n = 90$ (Thulin 1594). – F: *Erucastrum abyssinicum*, $2n = 32$ (Jonsell 3087). – G: *E. arabicum*, $2n = 16$ (Ryman 3.2.1972). – H: *E. pachypodum*, $2n = 16$ (Thulin 1373). – I: *Oreophyton falcatum*, $2n = 32$ (Hedberg 5435). – J: *Sisymbrium erysimoides*, $2n = 14$ (Thulin 1372). – K: *Thlaspi alliaceum*, $2n = 14$ (Lundqvist 7752). – L: *Turritis glabra*, $2n = 12$ (Ryman 222). – The scale unit is equal to 5μ .

localities give the impression of being natural, although the taxon may well be a fairly recent immigrant.

$2n = 16$ is the only reliable chromosome number previously reported for *C. hirsuta*.

Cardamine obliqua Hochst. ex A. Rich. –

Fig. 1 C, D

$2n = 36$. Tanzania, Eastern Prov., Morogoro Distr., Uluguru Mts, Lukwangulu Plateau, 2400 m, Thulin 1019.

$2n = 56$. Tanzania Northern Prov., Mt Kilimandjaro, W slope, 2500 m, Jonsell 2086.

$2n = 62$. Ethiopia, Tigre-Begemdir, Simien, Geech, 3600 m, Hedberg 5348 b.

$2n = c. 64$. Ethiopia, Bale Prov., Bale Mts, Garba-Goracha Camp, 4000 m, Hedberg 5553.

$2n = 72$. Kenya, Central Prov., Mt Kenya, W slope, 3250 m, Jonsell 2209 – Tanzania, Northern Prov., Arusha Distr., Mt Meru, 2900 m, Hedberg 4742.

The *C. obliqua* complex displays one of the most intricate variation patterns among Afro-montane plants, both morphologically (Hedberg 1957) and cytologically. The very limited cytological evidence available to date (the above list)

suggests a situation that may resemble that in the *Cardamine pratensis* complex (Lövkvist 1956), in which a long polyploid series with considerable aneuploidy is partly correlated with morphological differentiation. The two species complexes are no doubt very closely related. The *C. obliqua* complex occurs in montane-alpine Ethiopia and E Africa, and very similar forms in some montane parts of C and tropical S America. The interrelationships of these populations remain to be clarified as is their distinction from *C. africana*. A separate paper on *C. obliqua* is in preparation.

Cardamine trichocarpa Hochst. ex A. Rich. –

Fig. 1 B

$2n = 16$. Ethiopia, Tigre-Begemdir, Simien, Sankobar, 3100 m, Hedberg 5327 – Kenya, Central Prov., Mt Kenya, W slope, 2400 m, Jonsell 2213 – Tanzania, Northern Prov., Arusha Distr., Mt Meru, 2500 m, Hedberg 4940 – Tanzania, Tanga Prov., near Amani, Marvera tea estate, Hedberg 4795.

C. talamontiana Chiovenda (1911) and a number of infraspecific taxa not meriting recognition

(Schulz 1903) fall within this fairly homogeneous species, distributed in montane areas from the Cameroons to Tanzania and Ethiopia and recurring in India. *C. trichocarpa* is apparently gaining foothold as a weed in E Africa.

Morton (1972) reported $2n = 32$ for *C. trichocarpa*, probably from the Cameroons which indicates the presence of two cytotypes in the species.

***Crambe hispanica* L. – Fig. 1 E**

$2n = 90$. Ethiopia, Arussi Prov., Chilalo awraja, Chebbi (c. 20 km N of Asella), 1800 m, Thulin 1594.

$2n = c. 90$. USSR, Moldavia, cultivated form; seeds received from Botanical Garden, Leningrad, Jonsell 2469.

The taxonomy and nomenclature of this species has become rather confused. The main area of distribution of *C. hispanica* is the Mediterranean region and the Near East extending eastwards to Iran (Hedge & Rechinger 1968). In Ethiopia and N Kenya there is an outlying area. This population was regarded by the 19th century authors as conspecific with the Mediterranean plant, although Hochstetter distributed it in an exsiccate as *C. abyssinica*. This name was validated independently by both Fries (1914) and Schulz (1916). Schulz used it for the Ethiopian plant with smooth fruits and comparatively long petals, which was the one distributed by Hochstetter and here regarded as conspecific with *C. hispanica*. Fries, whose validation has priority, confused two species. In the description he cited Hochstetter's specimen (Schimper II; 1249) as well as others of that species, but the specimen designated as the type and with which the description agrees belongs to another very distinct species which Schulz (1916) described as *C. kilimandscharica*. It has reticulate or rugose fruits and petals not longer than the sepals. Schulz's name has generally been used for this species, although it could hardly be in doubt that *C. abyssinica* would be its correct name if the circumstances related below did not disqualify it. Type and description plainly refer to this species. Agnew (1974) used *C. abyssinica* in this sense.

The name *C. abyssinica* has, however, much oftener been used in quite another sense, viz. not only for the wild Ethiopian population with

smooth fruits but also for the forms of that species cultivated as an oil-seed crop. The cultivation was apparently initiated in the USSR (Vaughan 1957, Cornelius & Simmons 1969) and followed up by trials in a number of countries. The place of origin of the cultivated form is not clear but it is undoubtedly conspecific with *C. hispanica* L., which is thus its correct name. Accordingly, since the name *C. abyssinica* has been and is still being used commercially for one species, and is employed in a flora (Agnew 1974) and in other taxonomic literature for another species, it should be abandoned as being a "nomen ambiguum" (I. C. 1972, Article 69). The two above-mentioned species from tropical Africa should thus be called *C. hispanica* L. and *C. kilimandscharica* Schulz respectively.

In S Ethiopia–N Uganda a third species is found, also an annual, *C. sinuato-dentata* Petri in Schweinf. which has been little collected but is clearly distinct. Rechinger (in Hedge & Rechinger 1968) suggested that infraspecific taxa may be distinguishable within *C. hispanica*. The Ethiopian population deviates somewhat from that in the Mediterranean area in leaf-shape but does not merit taxonomic recognition.

As noted the same chromosome number probably exists in the wild Ethiopian population and in the cultivated form. There is an old report of $2n = 60$ for cultivated "*C. abyssinica*" (Manton 1932), but it is not possible to decide to what plant it actually refers.

***Erophila verna* (L.) F. Chev. s. lat.**

$2n = c. 60$. Ethiopia, Bale Prov., Bale Mts, Garba-Goracha Camp, 3950 m, Hedberg 5550.

The genus *Erophila* was only recently discovered in tropical Africa, by Sebald (1969) in the Simian Mountains in N Ethiopia at c. 4200 m altitude. This plant has very short obovoid siliculae ($3-3.5 \times 2-2.5$ mm) and was mainly for that reason, but also because of the type of indumentum, attributed to subsp. *spathulata* (Láng) Walters (cf. Tutin et al. 1964). Because of the markedly larger seeds (0.55–0.85 mm compared with a maximum length of 0.5 mm in *E. verna* in general) Sebald (1969) distinguished it as var. *macrocarpa*. In 1973 O. Hedberg discovered *Erophila* in two montane areas of

Ethiopia, in Simien rather close to Sebald's locality and in the Bale Mountains in S Ethiopia. Both collections display the same characteristics as Sebald's plants, even when raised from seed in the greenhouse. The plants did not all die after flowering, some leaf rosettes persisting. They have, however, not flowered a second time. We obviously have an indigenous high-montane *Erophila* in Ethiopia, probably more widely distributed than the scattered finds reveal. With regard to the complicated and special modes of differentiation in *Erophila* it can be suspected that the similarity between subsp. *spathulata* from Europe and the Ethiopian form is wholly superficial. Its relation to the E Mediterranean-Iranian *E. minima* C. A. Mey., which has similar siliculae but fewer and still larger seeds (c. 1.0 mm long) and linear leaves, remains to be clarified. In both *E. minima* and the Ethiopian form the number of ovules is less than is generally found in *E. verna* (10–15, and more than 20 resp.) but the Ethiopian form and *E. verna* s. str. share the character of spatulate leaves. *E. minima* seems to show little variation and with our present knowledge the Ethiopian form should preferably be included in the variable *E. verna* s. lat. Only a detailed study of *Erophila* can elucidate its proper taxonomic position.

The chromosome number reported indicates an approximately octoploid level for the Ethiopian *E. verna*, a species in which a range from diploids to dodecaploids is known (Winge 1940).

The *Erucastrum arabicum* complex

***Erucastrum abyssinicum* (A. Rich.) O. E. Schulz**
– Fig. 1 F

2n = 32. Ethiopia, Arussi Prov., Kulurusa, 2200 m, Fröman s.n. (Jonsell 3601) – Plants raised from seed from the Botanical Garden, Copenhagen (origin unknown), comm. from Prof. Gómez-Campo, Madrid (GC No. 0430-66), Jonsell 3087.

***Erucastrum arabicum* Fisch. & Mey.** – Fig. 1 G

2n = 16. Ethiopia, Arussi Prov., Langano area, 1600 m, Fröman s.n. (Jonsell 3602) – Kenya, Eastern Prov., Machakos Distr., Mombasa Road, 1400 m, Ryman s.n. 3.2. 1972 – Kenya, Central Prov., Nairobi, Ryman 5 – Tanzania, Tanga Prov., Lushoto Distr., Amani, Hedberg 4781.

***Erucastrum pachypodum* (Chiov.) Jonsell, comb. nov.** – Fig. 1 H

Basionym: *Sisymbrium pachypodum* Chiovenda in Ann. Bot. Roma 9: 52 (1911).

2n = 16. Ethiopia, Tigre-Begemdir, Simien, 3 km S of Chenek, 3550 m, Hedberg 5479 – Ethiopia, Arussi Prov., Chilalo awraja, near Bejoki, 2700 m, Thulin 1373, and Fröman s.n. (Jonsell 3600) – Ethiopia, Bale Prov., Bale National Park, Head Quarter, 3200 m, Hedberg s.n. 28.10. 1973.

Within this complex ("species collectiva" in Schulz 1919, p. 96) only tetraploids (2n = 32) have previously been reported (Harberd 1972). All these counts were made on material from botanical gardens and cannot now be fully verified. The tetraploid J 3087 (obviously the same strain was also studied by Harberd 1972) agrees morphologically with the Ethiopian tetraploid J 3601. Many herbarium specimens from the Ethiopian highlands are of this type, *E. abyssinicum* s. str., which is in many respects intermediate between two other types, both known to be diploid. One is *E. arabicum*, widespread in Africa and Arabia and in E Africa spreading as a weed. Herbarium material corresponding to the other diploid has usually been included in *E. abyssinicum* but can be identified with a plant described as *Sisymbrium pachypodum* Chiov. (*E. abyssinicum* var. *pachypodum* (Chiov.) O. E. Schulz), known only from elevated areas of the Ethiopian highlands. The characters distinguishing these taxa are listed in Table 1. Evidence that the three entities are distinct and merit recognition as separate species will be presented in a coming paper.

***Oreophyton falcatum* (A. Rich.) O. E. Schulz**
– Fig. 1 I

2n = 32. Ethiopia, Tigre-Begemdir, Simien, Mt Buahit, 4225 m, Hedberg 5435.

O. falcatum, a perennial, usually acaulescent rosette plant, adapted to an Afro-alpine environment at c. 4000–4900 m (Hedberg 1957, 1964) is the most remarkable crucifer from tropical Africa. Schulz (1924) established a monotypic genus for this species, endemic to the high mountains of Ethiopia and E Africa (Mt Elgon, Mt Kenya, Mt Aberdare, Kilimanjaro). Its taxonomic position is not obvious. The species was

Table 1. Principal diagnostic characters for the species of the *Erucastrum arabicum* complex.

Character	<i>E. arabicum</i>	<i>E. abyssinicum</i>	<i>E. pachypodum</i>
Length of siliqua rostrum (mm)	1.5–4.5	1.0–4.0	0–1.0
Pedicel length (mm)	5–c. 20	2–c. 20	0–1
Occurrence of bracts in the inflorescence	ebracteate (rarely with bracts at lowest pedicels)	bracteate at least below	bracteate
Leaf shape	sinuate, repand or serrate	pinnatifid or sinuate	pinnatifid
Stem habit	erect	twining (rarely erect)	twining

originally described within *Arabis* (Richard 1847) and has also been included in *Sisymbrium* (Fournier 1865) and other genera. It seems reasonable to assume that it has derived from one of the larger comparatively unspecialized genera within Arabideae or Sisymbrieae, *Arabis*, *Rorippa* or *Sisymbrium*.

In *Oreophyton* the cotyledons are broadly elliptic, obtuse, attenuating into a petiole of about the same length as the lamina, and glabrous, a type often found within the above genera. The occurrence of forked and stellate hairs on the leaves makes an affinity with *Rorippa*, in which only simple hairs are known, scarcely probable. The nectaries of *Oreophyton* practically surround the lateral stamens and proceed as marked ridges outside each pair of median stamens. This is in contrast with *Arabis* in which the lateral nectaries are usually not closed as rings and the median ones are only

slightly developed, a close affinity with this genus being thus unlikely. In both *Rorippa* and *Arabis* the cotyledons are, as far as is known, accumbent in the embryos, while in *Oreophyton* and usually in *Sisymbrium* they are incumbent. The last-mentioned genus also agrees with *Oreophyton* with respect to the indumentum and the arrangement of the nectaries. The seeds of *Oreophyton* deviate from the type common in *Sisymbrium* (Vaughan & Whitehouse 1971) in not being mucilaginous and in having a palisade layer with the radial and inner tangential walls thickened (Fig. 2). The epidermis cells peel off early and only the central cylindrical solid columns standing on the palisade layer are left.

The sum of the evidence indicates a position for *Oreophyton* closer to *Sisymbrium* than to the other two genera. One discrepancy is the basic chromosome number $x = 8$, constant in *Rorippa*, by far the most common in *Arabis*, but very rarely reported in *Sisymbrium* in which $x = 7$ is normal. From other high mountainous areas there are biological counterparts to *Oreophyton* in the family, isolated forms seemingly adapted to rigorous environmental conditions (cf. Hara 1974). Since *Oreophyton* cannot with complete certainty be associated with any other genus and since the generic concept in Cruciferae is on the whole narrow, it should in my opinion be upheld as a genus.

Variation has been observed within *O. falcatum*, and has even led to taxonomic subdivision (Schulz 1924, Franchetti 1958) but it may be largely modificative. Of greater interest is the occurrence of forms with entire instead of pinnatifid leaves (Sebald 1969).

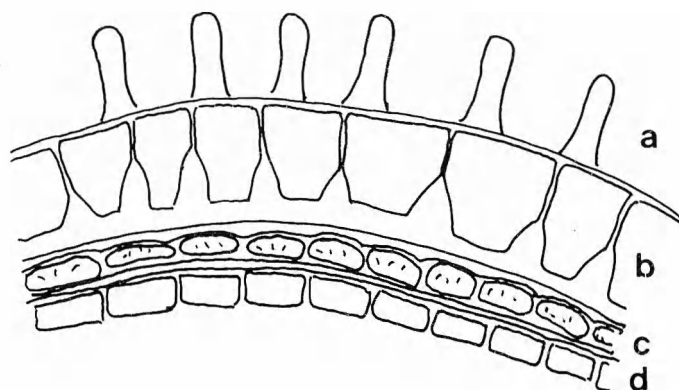


Fig. 2. *Oreophyton falcatum* (Hedberg 5435). Diagram of testa in cross-section. a epidermis, b palisade layer, c pigment layer, d aleuron layer. — C. $\times 510$.

Sisymbrium erysimoides Desf. – Fig. 1 J

2n = 14. Ethiopia, Arussi Prov., Chilalo awraja, near Bejoki (60 km S of Asella), 2700 m, Thulin 1372 – Tanzania, Northern Prov., Mt Kilimanjaro, W slope E of Lemosho Glades, 2400 m, Jonsell 2090.

S. erysimoides shows little variation but is widely distributed from the Canary Islands over the Mediterranean area to Iran and Arabia, and in N E Africa southwards to N Tanzania. *S. pinnatifidum* Forsk., which grows in Yemen, Sudan, Ethiopia and Somalia is a closely related but apparently distinct species.

This is the first report of a chromosome number for *S. erysimoides*.

Subularia monticola A. Br. ex Schweinf.

2n = 28. Tanzania, Northern Prov., Mt Kilimanjaro, Shira Plateau, 3600 m, Jonsell 2101.

Hedberg (1957) reported the same chromosome number for two collections from Mt Kenya. *Subularia* comprises only two species, *S. aquatica* L., widespread in the north temperate region, and *S. monticola*, endemic to the Ethiopian and E African mountains (cf. map in Hedberg 1962 b). Both have the same chromosome number. Mulligan & Calder (1964) reaffirmed the status of *S. monticola* as a separate species. The strain cited above was cultivated in a greenhouse at depths of water varying from 0–80 cm (level of stem bases). Even the most deeply submerged plants showed the thicker stems and leaves that distinguish *S. monticola* from *S. aquatica*, although they were markedly elongated. This confirms the suggestions by Hedberg (1957 p. 272) founded upon field observations. Further ecological observations are to be found in Hedberg (1964, 1971).

Thlaspi alliaceum L. – Fig. 1 K

2n = 14. Ethiopia, Tigre-Begemdir, Simien, Mt Buahit, 4225 m, Hedberg 5427 – (Yugoslavia, Croatia, near Bresha-Greda 15 km S of Zagreb, Lundqvist 7752).

T. alliaceum, which is a distinct species and by some authors regarded as constituting a section of its own, *Chaunothlaspi* Schulz 1936 (cf. also Meyer 1973) grows in two restricted, widely

disjunct areas, viz. C to S Europe and the Ethiopian and E African mountains (Simien, Bale, Mt Elgon, the Cherangani Hills, Mt Kenya, Mt Aberdare and some lower hills in N Tanzania). The African plant was described as *T. oliveri* Engler (1892) but there are no constant differences between African and European specimens. It is true that some African specimens from high altitudes (c. 4000 m) are low, compact and decumbent, characters that do not seem wholly the result of external factors. In cultivation the Ethiopian plants were low and ascending, while the ones from Yugoslavia grew much taller and were erect. But African specimens from lower altitudes agree completely with many European ones, although among the latter extremes with much taller stems and longer pedicels can be found. Not even the difference in hairiness of the stem bases (Hedberg 1957) holds good in the more extensive material now available. The odour of garlic, unique for this species of *Thlaspi*, occurs in both African and European plants.

This is the first report of chromosome numbers for *T. alliaceum*.

Turritis glabra L. – Fig. 1 L

2n = 12. Kenya, Rift Valley Prov., Kajiado Distr., Ngong Hills, 2200 m, Ryman 222.

T. glabra occurs locally in mountainous parts of E Africa but has not been found in Ethiopia. The African specimens agree completely with those from Europe. The situation and in some cases the age of the African finds make the introduction by human agency of *T. glabra*, not a particularly aggressive weed, less probable. 2n = 12 has been repeatedly reported for *T. glabra* (Fedorov 1969).

Acknowledgements

My thanks are due to Professor O. Hedberg, who has generously put his extensive material consisting of collections of seeds and specimens of Cruciferae from Ethiopia and E Africa at my disposal, to Mr B. von Hofsten, Mr B. Fröman, Mr S. Ryman and Dr M. Thulin who have all contributed seed samples, and to Mrs Karin Ryman for her skilful and patient preparatory work. The study was supported by the Swedish Natural Science Research Council grant No. 2588-012.

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Calicium denigratum (Vain.) L. Tibell, comb. nov.

Leif Tibell

Tibell, L. 1976 06 30: *Calicium denigratum* (Vain.) L. Tibell, comb. nov. [Notes on Caliciales 3.] *Bot. Notiser* 129: 131–136. Stockholm. ISSN 0006-8195.

Calicium denigratum (Vain.) L. Tibell, comb. nov. is described and compared with the morphologically similar species *C. abietinum* Pers. and *C. glaucellum* Ach. Simple statistical methods have been employed in an effort to standardize the measurement of spore sizes. *C. denigratum* occurs on lignum in the Southern to Northern Boreal Zone in the Scandinavian countries and is also reported from the Upper Oroboral Zone in the Alps.

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Since the time of Persoon and Acharius the name *Calicium abietinum* Pers. (or *C. curtum* Turn. & Borr.) has been used without discrimination by most lichenologists for some morphologically similar species. In a recent paper (Tibell 1975) *C. abietinum* was lectotypified and compared with the similar *C. glaucellum* Ach. and *C. parvum* L. Tibell. All these species occur in Europe but distribution and ecology differ (Tibell 1975). *C. abietinum* and *C. parvum* occur in the Hemiboreal and Temperate Zones in Northern and Northwestern Europe (vegetation zone system of Ahti, Hämet-Ahti & Jalas 1968), and corresponding Oroboral zones in other parts of Europe. *C. glaucellum* has a wider distribution, also occurring in the Southern Boreal and Middle Boreal Zone.

During a field trip to Dalarna, Sweden, in 1969 I noticed the sometimes abundant occurrence of a species slightly similar to *C. glaucellum*. Later on I found it in several provinces of middle and northern Sweden, and it was also present in herbarium material investigated. I have also recently received material of this species from the Alps collected by Dr K. Kalb. Investigations in the Vainio herbarium in Turku revealed that this species had been described by Vainio as *Calicium curtum* v. *denigratum*. This species is described below and compared with

the morphologically similar species *C. abietinum* and *C. glaucellum*.

Methods

Some efforts have been made to standardize the measurement of spore size. In a mazaedium a large number of spores of different age are available. The selection of mature spores is difficult, and discrepancies in results are probably mainly due to inadequate limitation of the class "mature spores". For the spore measurements recorded a rather high coefficient of variation has been met with. Whether this is a real feature of the population or due to inadequate limitation of the class "mature spores" during sampling is not evident. Spores with fully developed ornamentation and thickened, dark brown walls were considered mature. Measurements have been made on material stained in Lactic Blue.

Abbreviations used: N = total sample size, \bar{X} = arithmetic mean of the variate, $\bar{X}_1 = \bar{X}$ for length of spore, $\bar{X}_w = \bar{X}$ for width of spore, s_1 = sample estimate of standard deviation of spore length, s_w = ditto of spore width, V_1 = coefficient of variation of spore length. In the text spore measurements have been given as $\bar{X} \pm 1 s$, since this seems to correspond fairly well to values stated in various taxonomic treatments of *Calicium*.

Herbaria are abbreviated according to Index Herbariorum (1974), and material from the following Herbaria has been investigated: C, H, LD, S, TUR and UPS. Material from Dr K. Kalb's herbarium is cited as "Kalb", and from my own herbarium as "Tib."

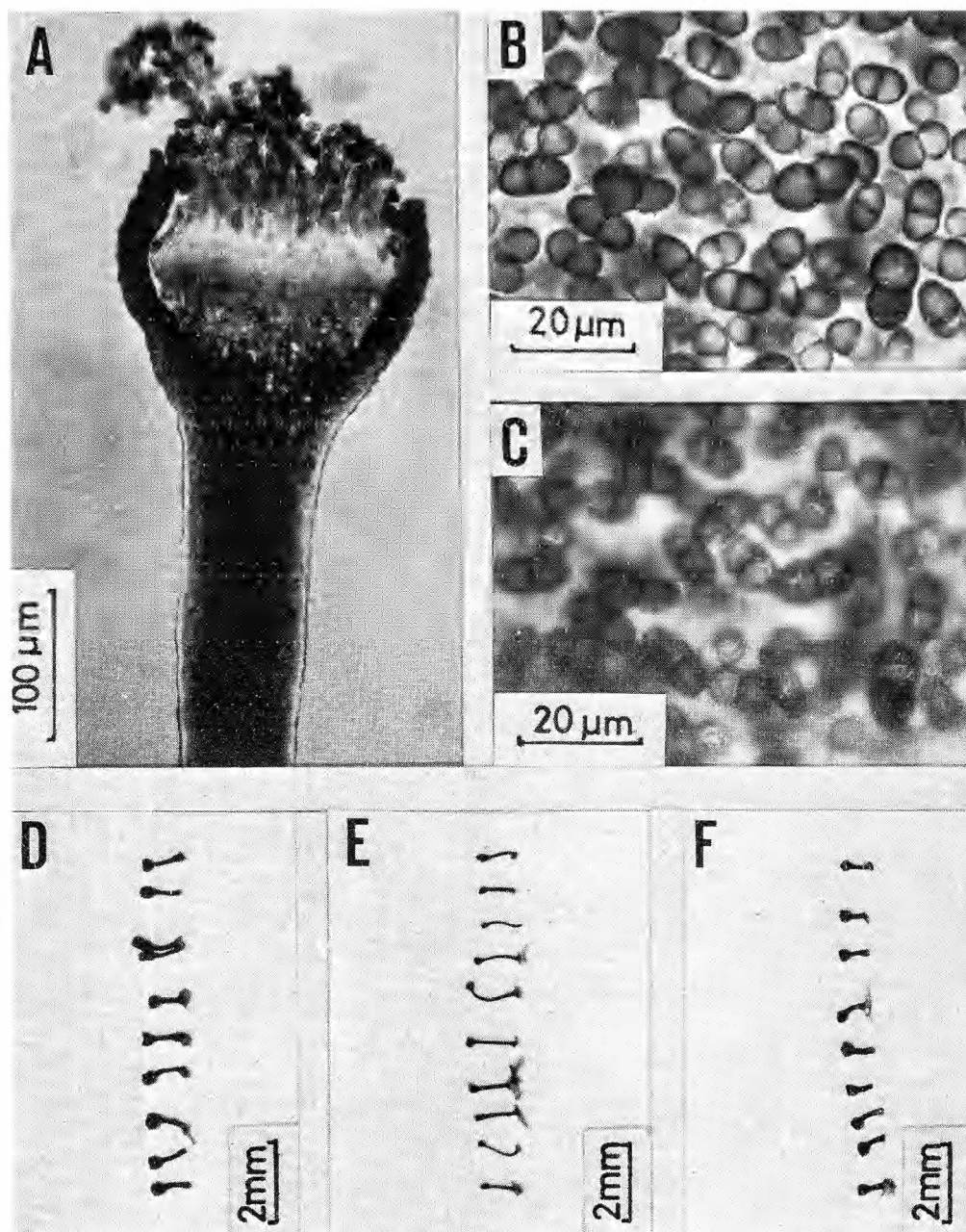


Fig. 1. A–C, E: *Calicium denigratum*. – A: Longitudinal section of apothecium. Note the thin hyaline envelope surrounding the stalk. – B, C: Mature spores. In C (focusing the surface of the spores) the irregular areolate-cracked ornamentation is seen. – E: Apothecia. – D: *Calicium abietinum*, apothecia. – F: *Calicium glaucellum*, apothecia. – A: Laurila s.n., Kitisnvaara (H) – B–C: Tibell 3881 (Tib.) – D: Tibell 5570 (Tib.) – E: Tibell 3872 (Tib.) – F: Tibell 3756 (Tib.).

***Calicium denigratum* (Vain.) L. Tibell, comb. nov.**

Calicium curtum Borr. v. *denigratum* Vain. 1881: 95. – Holotype: Finland, Ostrobothnia kajanensis, Kuhmo, Lentiira, on tree trunk in transition between heath forest and raised bog, 1877 Vainio, Herb. Vain. 29,378 "specim. orig." (TUR). Isotypes: Vainio, Herb. Vain. 29,377 and 29,379 (both TUR).

Calicium abietinum Pers. v. *meizopus* Vain. 1927: 43. Holotype: Finland, Savonia borealis, Kuopio, Enonlahti, Enonmäki, on decaying tree trunk, 1909 Linkola, Herb. Vain. 29,389 (TUR).

Thallus immersed. *Apothecia* 0.7–1.3 mm high (protruding part of mazaedium not included), often flexuous and with slightly bell-shaped capi-

tulum. All parts of apothecium shining black and without pruina. More rarely the stalk has a slightly brownish tinge. Middle part of stalk 0.07–0.10 mm in diam. Ratio height of apothecium/diameter of stalk: 10–14 (cf. Fig. 3). Stalk consisting of dark brown, sclerotized hyphae, and surrounded by a distinct hyaline envelope of prosoplectenchymateous tissue 4–17 μm thick (Fig. 1A). Walls of capitulum consisting of tissue similar to that of stalk. *Hymenium* 27–40 μm high. *Hypothecium* with flat surface, 55–70 μm high, in lower part confluent with stalk. *Mazaedium* of very variable thickness, though usually not protruding very far beyond edge of excipulum. *Asci* cylindrical, 38–48 \times 4–5 μm . *Spores*

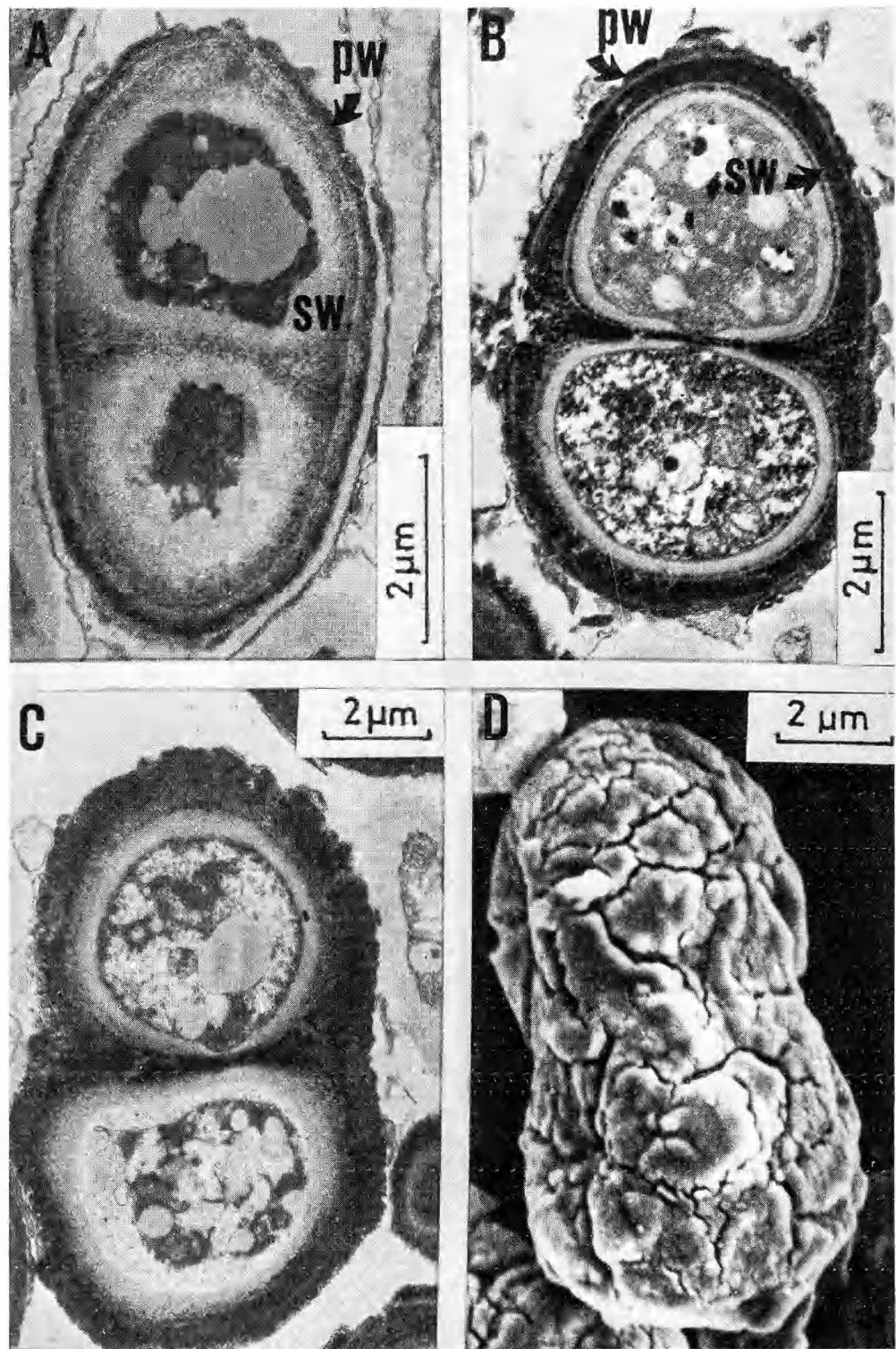


Fig. 2. *Calicium denigratum*.
 – A: Young spore with distinct primary wall (pw) and developing secondary wall (sw). – B: Semi-mature spore. Primary wall (pw) still distinct though irregular in outline. Secondary wall (sw) more electron-dense than in A. – C: Mature spore. No distinct difference between primary and secondary wall. Some furrows in the outermost part of the wall are seen. – D: Mature spore with distinct ornamentation of furrows surrounding irregular areolae. – Tibell 5484 (Tib.).

uniseriate, 8/ascus. Mature spores dark brown, with more or less distinct incision at septum, $11.1\text{--}13.6 \times 6.2\text{--}7.6 \mu\text{m}$ (9 collections, $N = 168$, $\bar{X}_1 = 12.36 \mu\text{m}$, $s_1 = 1.21 \mu\text{m}$, $\bar{X}_w = 6.94 \mu\text{m}$, $s_w = 0.70 \mu\text{m}$, $V_1 = 10.9$). Ratio spore length/spore width in mature spores: 1.7–1.9 (cf. Fig. 3). Under the light microscope (LM) mature spores show an irregular, coarsely cracked-areolate ornamentation (Fig. 1C). In young and semi-

mature spores no ornamentation is seen. Studies by transmission electron microscopy (TEM) show the young spores with a very distinct primary wall (Fig. 2A, cf. Tibell 1975), which is also clearly visible in semi-mature spores (Fig. 2B), though at this stage it becomes somewhat irregular. In mature spores the primary wall is not clearly distinguishable from the secondary wall, which now makes up the major

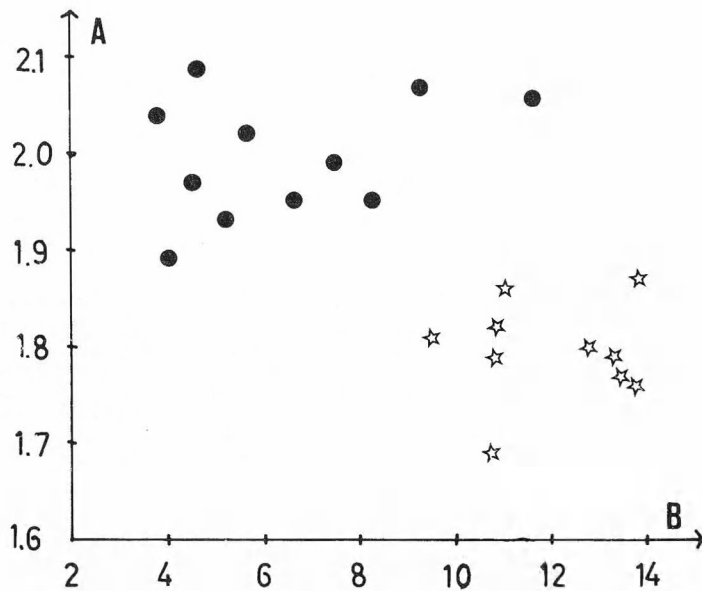


Fig. 3. Ratio spore length/spore width (A) and ratio height of apothecium/diameter of stalk (B) in *Calicium denigratum* (stars) and *C. glaucellum* (dots).

part of the spore wall (Fig. 2C). Under the scanning electron microscope (SEM) mature spores show a coarsely areolate surface (Fig. 2D).

Distribution and ecology

Calicium denigratum is so far known from the Southern Boreal to the Northern Boreal Zone in the Scandinavian countries (including Finland), and (presumably) the Upper Oroboral Zone in the Alps. In some parts of Sweden (Northern Dalarna, Härjedalen and Jämtland) it is at least locally the most frequently occurring species of *Calicium* on lignum along with *C. trabinellum*.

C. denigratum has been found on lignum only, primarily on decorticated trunks and stumps of still standing *Pinus sylvestris*. This wood is hard and dry. In the Alps it occurs on decorticated stumps of *Pinus cembra*. In one case it has also been recorded from lignum of *Larix*. In the Scandinavian countries it is usually found in open situations, along mires and in open forest stands at moderate altitudes (up to 800 m). In the Alps it has been recorded from 1800–2100 m.

Taxonomic remarks

Calicium denigratum is similar to *C. glaucellum* and *C. abietinum*. Like these species it is ligni-

colous and has a totally immersed thallus. It differs, however, in a number of respects and the differences in geographical distribution have already been pointed out above.

Calicium denigratum differs from *C. glaucellum* in having completely epruinose apothecia with a more bell-shaped capitulum and longer and slenderer stalks. The height of the apothecia in *C. glaucellum* is 0.45–0.85 mm, the diameter of the middle part of the stalk 0.09–0.14 mm. The ratio height of apothecium/diameter of stalk is 4–8, only in some rare instances exceeding 10 (cf. Figs. 1 E, F). The spores are rather similar in size in *C. denigratum* and *C. glaucellum* ($10.4\text{--}12.8 \times 5.1\text{--}6.5 \mu\text{m}$, 11 collections, $N=210$, $\bar{X}_1 = 11.61 \mu\text{m}$, $s_1 = 1.22 \mu\text{m}$, $\bar{X}_w = 5.80 \mu\text{m}$, $s_w = 0.71 \mu\text{m}$, $V_1 = 10.6$), but there is some difference in form – the spores of *C. denigratum* being comparatively broader. The ratio spore length/spore width in *C. glaucellum* is 1.9–2.1. An illustration of these differences is presented in Fig. 3. The hyaline layer surrounding the stalk is much thinner in *C. denigratum* than in *C. glaucellum* (c. 20–35 μm), see Tibell 1975 Fig. 16 a and this paper, Fig. 1 A.

These species also differ in spore ontogeny. Young and semi-mature spores in *C. glaucellum* have an ornamentation consisting of minute, irregular ridges mainly orientated parallel with the long axis of the spore (cf. Tibell 1975 Fig. 16 d). The young and semi-mature spores of *C. denigratum* appear smooth in LM, and in TEM the primary wall is homogeneous without the distinct, electron-lucent areas present in *C. glaucellum* (Tibell 1975 Fig. 18 b). The mature spores also differ in ornamentation, *C. glaucellum* having a more or less distorted pattern of ridges and irregular cracks (Tibell 1975 Fig. 20), while *C. denigratum* has an areolate ornamentation without ridge elements (Figs. 1 C, 2 D). In mature spores of *C. glaucellum* the primary wall is quite distinct, forming the surface ornamentation, whereas in *C. denigratum* the structure of the primary and secondary wall is very similar in mature spores, and the two walls are not easily distinguished.

In many respects *C. denigratum* more closely resembles *C. abietinum* than *C. glaucellum*. They both lack pruina and have shining stalks, though the stalk of *C. abietinum* is intermediate to *C. denigratum* and *C. glaucellum* as to ratio height of apothecium/diameter of stalk

Table 1. Diagnostic features of *Calicium abietinum*, *C. denigratum* and *C. glaucellum*.

Features	<i>C. abietinum</i>	<i>C. denigratum</i>	<i>C. glaucellum</i>
Whitish pruina below capitulum	absent	absent	present
Colour of apothecia	black to brownish	black	black
Ratio height of apothecium/diameter of central part of stalk	6–11	10–14	4–8
Spore size (μm)	12.4–15.1 \times 5.5–7.1	11.1–13.6 \times 6.2–7.6	10.4–12.8 \times 5.1–6.5
Ratio spore length/spore width	2.0–2.4	1.7–1.9	1.9–2.1
Ornamentation in mature spores (LM)	minute warts	coarsely and irregularly areolate	minute ridges and irregular cracks

(6–11) and though the apothecia (0.55–0.85 mm) are only slightly longer than in *C. glaucellum* (cf. Fig. 1D–F). The hyaline layer surrounding the stalk in *C. abietinum* is intermediate in size between those of *C. denigratum* and *C. glaucellum*. The spores in *C. abietinum* measure 12.4–15.1 \times 5.5–7.1 μm (6 collections, $N = 99$, $\bar{X}_1 = 13.77 \mu\text{m}$, $s_1 = 1.35 \mu\text{m}$, $\bar{X}_w = 6.27 \mu\text{m}$, $s_w = 0.83 \mu\text{m}$, $V_1 = 9.9$), thus overlapping in size with the spores of *C. denigratum* and *C. glaucellum*. With respect to ratio spore length/spore width (2.0–2.4) *C. abietinum* is closer to *C. glaucellum* than *C. denigratum*. The mature spores of *C. abietinum* have an ornamentation of minute warts (cf. Tibell 1975 Figs. 7d, 9b, c) as compared with the coarsely and irregularly areolate ornamentation of *C. denigratum*. TEM studies (cf. Tibell 1975 Figs. 8, 9) show that the ontogeny of the spores is rather similar to that of *C. glaucellum*, though resulting in a different ornamentation pattern. In semi-mature spores of *C. abietinum* electron-lucent parts are seen regularly distributed in the primary wall, and the electron-dense parts of the primary wall later on form the minute warts of the surface. Thus the difference between the primary and the secondary wall remains distinct in the mature spores of *C. abietinum* as it does in those of *C. glaucellum*. A comparison of diagnostic features of *C. abietinum*, *denigratum* and *glaucellum* is given in Table 1.

Collections

Exsiccata examined: Räsänen, Herb. Lich. Fenn. 539 (C, H, LD, TUR, UPS), 847 (C, H, LD, UPS).

Austria: Tirol, Ötztaler Alpen, Leierstal, N-Hang, alt. 1880–2030 m, 1966 Kalb (four collections, Kalb); Do., Ötztal, in the vicinity of Umhausen, alt. 1850–2000 m, 1966 Kalb (two collections, Kalb); Do., Leierstal Alm, alt. 1800 m, 1965 Kalb (Kalb).

Finland: Karelia borealis, Pielisjärvi par., Kitsinvaara, Ylinen-Pitkäjärvi, 1936 Laurila (H) – Tomajärvi par., 5 km SE of Onkamo railway station, 1939 Ahlner (S) – *Kuusamo*, Kuusamo par., by river Oulanjoki, Taivaalköngäs, 1939 Laurila (Räsänen, Herb. Lich. Fenn. 847) – *Lapponia kemensis*, Muonio, 1867 Norrlin (H) – Sodankylä par., Pyhäntunturi, 1878 Vainio, Herb. Vain. 29,380 (TUR) – *Ostrobotnia borealis*, Rovaniemi, 1921 Räsänen (TUR, UPS) – *Ostrobotnia kajanensis*, Kuhmo par., Lentiira (holotype and two isotypes, cf. above) – *Savonia borealis*, Kuopio par., Enonlahti, Enonmäki, 1909 Linkola (holotype of *Calicium abietinum* v. *meizopus*, cf. above); Kumpusaari, 1909 Linkola Herb. Vain. 29,385 (TUR) – *Tavastia australis*, Tammela par., Mustiala, 1867 Kullhem (H).

Sweden: Ångermanland, Anundsjö par., vicinity of point 296 S of the railway station, 1951 Ahlner (S) – *Dalarna*, Älvdalen par., Hållstugan, 1891 Hedlund (S) – Hamra par., Hamra National Park, 1932 Malme (S), 1973 Tibell 5455 (Tib.) – Idre par., 1.5–3 km W of point 1130.9 of Mt Städdjan, 1969 Tibell 3872, 3881 (Tib.); 5 km NE of Idre, Himmeråsen, 1969 Tibell 3844 (Tib.); Burusjön, 1.3 km SW of Nipvallen, 1969 Tibell 3891 (Tib.) – *Hälsingland*, Bergsjö par., Slavattenberget, 1961 Ahlner (S) – Los par., 12 km NW of Los, Riberget, 1973 Tibell 5442 (Tib.) – Ramsjö par., 2 km SE of Tallnäs, 1944 Hasselrot (S) – *Härjedalen*, Hede par., Sånfjället National Park, by river Valmán, Lars-Larskojan, 1973 Tibell 5484 (Tib.) – *Jämtland*, Åre par., 1.5 km SSW of point 707 of Täljstensberget, 1967 Tibell 3102 (Tib.) – Offerdal

par., 46 km NNE of Åre, Åkroken, 1975 Tibell 6297 (Tib.) – Revsund par., Grötingen, 1946, 1951 Ahlner (S); Laxsjöbäcken, 1951 Ahlner (S) – *Lycksele lappmark*, Stensele par., Kyrkberget, 1924 Magnusson 7862 a (UPS); Sandvik, 1924 Magnusson 7902 a (UPS) – *Pite lappmark*, Arjeplog, Sommerfelt (UPS) – *Värmland*, Ransäter par., Gäddtjärns mossen, 1946 Hedlund (S).

U.S.S.R.: *Karelia ladogensis*, Suistamo par., Loimola, 1939 Ahlner (S) – *Kuusamo*, Salla par., Kutsajoki, Sieminkijoki, 1937 Laurila (H) – *Lapponia petsamoënsis*, Petsamo par., between Nilijärvi and Karablekk, 1938 Räsänen (Räsänen, Lich. Fenn. exs. 539); Kalkuovi, 1938 Räsänen (H); Kuvernöörinkoski, 1931 Räsänen (H) – *Siberia*, Amski, 1880 Vainio, Herb. Vain. 29.387, 29.388 (TUR).

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Appendix: Collections measured

To construct Fig. 3, 20–25 mature spores from at least two apothecia and 10–15 apothecia from each collection were measured.

C. denigratum. *Finland*: *Ostrobothnia borealis*, Rovaniemi, 1921 Räsänen (TUR). – *Sweden*: *Dalarna*, Tibell 3844, 3872, 3881, 5455 (Tib.). *Hälsingland*, Tibell 5442 (Tib.). *Härjedalen*, Tibell 5484 (Tib.). *Jämtland*, Tibell 3102 (Tib.). *Lycksele lappmark*, Magnusson 7862 a (UPS). – *U.S.S.R.*: *Lapponia petsamoënsis*, Räsänen, Herb. Lich. Fenn. 539 (TUR).

C. glaucellum. *Finland*: *Alandia*, Tibell 4392 (Tib.). – *Norway*: *Hedmark*, Tibell 5534 (Tib.). – *Sweden*: *Dalarna*, Tibell 5421 (Tib.). *Uppland*, Tibell 3756, 4564 (Tib.). *Västergötland*, Tibell 10 (Tib.). *Västmanland*, Tibell 3831 (Tib.). – *Switzerland*: *Neuchâtel*, Tibell 4351 (Tib.). – *Canada*: *British Columbia*, Tibell 4984, 4957, 5180 (Tib.).

Re-classification of *Chrysanthemum* L. in South Africa

Bertil Nordenstam

Nordenstam, B. 1976 06 30: Re-classification of *Chrysanthemum* L. in South Africa. *Bot. Notiser* 129: 137–165. Stockholm. ISSN 0006-8195.

The South African taxa hitherto treated in *Chrysanthemum* L. are revised. Nine species are recognized and referred to five new genera, viz. *Adenoglossa* B. Nord., *Leucoptera* B. Nord., *Scyphopappus* B. Nord., *Cymbopappus* B. Nord., and *Adenanthemum* B. Nord., all belonging to the Compositae-Anthemideae. New species are *Leucoptera oppositifolia* B. Nord., *L. subcarnosa* B. Nord., and *Cymbopappus hilliardiae* B. Nord. The new classification is based on an array of macro- and micro-morphological characters, including pollen morphology. The pollen grains of *Adenanthemum* are hexa-panto-colporate and thus deviate in aperture number and arrangement from the usual pattern in the Compositae. The chromosome number $2n=18$ is reported for *Leucoptera subcarnosa* B. Nord.

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The genus *Chrysanthemum* L. (Compositae-Anthemideae) is generally believed to have a few representatives in South Africa. Harvey (1865) recognized four indigenous species, and the number was raised to five in Hutchinson's revision (1917). A sixth species was added later (Hutchinson 1936). There is a widely accepted opinion that these South African taxa are nearest related to the Macaronesian group of *Chrysanthemum*, known as *Argyranthemum* (as section, subgenus or genus, cf. Humphries 1976).

In the present study these conceptions are shown to be erroneous. The South African taxa are regarded as not closely related to *Chrysanthemum*, even if the latter is defined broadly (as e.g. in Bentham 1873). Furthermore, they form a heterogeneous assemblage of species, which have to be re-arranged in five different genera. However, they all belong to the tribe Anthemideae.

The study is based to some extent on the author's field work in South Africa in 1962–64 and 1974 and on herbarium material mainly from the following herbaria, BM, BOL, E, G, K, L, NBG, S, SAM (abbreviations in accordance with Holmgren & Keuken 1974) and

UPS-THUNB (herb. Thunberg, Uppsala). Specimens from herb. De Candolle (G-DC) have only been seen in microfiche. In the locality lists N. stands for B. Nordenstam and N. & L. for B. Nordenstam & J. Lundgren.

Acetolysed pollen preparations have been studied of all species except *Leucoptera nodosa* and *Cymbopappus lasiopodus*.

Adenoglossa B. Nord., gen. nov.

Typus: *A. decurrens* (Hutch.) B. Nord.

Herba annua erecta, praeter internodium caulis primum ciliatum glabra. *Folia* opposita vel alterna integra anguste linearia carnosae. *Pedunculi* terminales nudi monocephali. *Capitula* heterogama, flosculis marginalibus femineis ligulatis fertilibus, flosculis disci hermaphroditis fertilibus. *Involucri bractae* imbricatae latae apice rotundatae. *Receptaculum* conicum nudum. *Flores radii* pauci lutei, tubo leviter complanato glanduloso, lamina brevi demum reflexa. *Flores disci* lutei; corolla superne campanulata quinquelobata zygomorpha, lobis adaxialibus brevibus lineis resinosis notatis. *Antherae* appendix glande aurantiaca instructa. *Achaenia* homomorpha complanata bialata, facie abaxiali madefacta mucosa, alis lateralibus latis hyalinis. *Pappi squamae* 5–6 scariosae, quarum 3 adaxiales rotundatae–obovatae imbricatae, 2–3 abaxiales minores discretatae.

Erect annual herb, glabrous except for the ciliate first stem internode. *Leaves* opposite or alternate, narrowly linear, entire, fleshy, semiterete or subterete, apically obtuse and apiculate. *Peduncles* terminal, solitary, nude, monocephalous. Heads heterogamous, radiate.

Involucre broadly campanulate-hemispherical. Involucral bracts imbricated, broad and rounded, with many resiniferous veins, herbaceous. *Receptacle* conical, naked.

Rays few, yellow, fertile. Tube short, somewhat compressed, sparsely glandular. Lamina short, oblong-obovate, usually 4-veined and reflexed, smooth, glabrous, 3-fid at the apex. Style branches oblong, truncate.

Disc-florets yellow. Corolla zygomorphic, 5-lobed, with shorter lobes and distinct resin canals on the adaxial side; limb campanulate; tube somewhat compressed, glandular. *Anther* appendage ovate, obtuse, with a distinct orange-yellow resin gland. Endothelial cells with thickenings partly on horizontal walls (polarized tissue), partly on vertical walls (non-polarized tissue). Filament collar oblong-cylindric, of subequal cells. Style fertile with truncate branches; base distinctly swollen, placed on top of a narrower, conical-oblong, distinct nectary.

Achenes homomorphic, dorsiventrally strongly compressed and laterally amply winged, with 3 veins and 2 resin ducts, adaxially smooth and with a faint midrib, abaxially with closely set longitudinal striae, ending in hair-like apical projections and becoming mucilaginous when soaked; wings hyaline, apically auriculate. Ovary wall crystals elongate. *Pappus* of 5-6 scales; 1 median adaxial scale, semicircular, opaque, white with brown base; 2 lateral scales, subhyaline, folded laterally, oblong-obovate; 2-3 smaller abaxial discrete scales, spatulate-narrowly oblong, subhyaline.

Corolla glands multicellular, columnar.

Pollen grains isopolar, radially symmetrical, oblate-spheroidal, tectate, crassisexinous, 3-colporate. Infratectal bacula vestigial, leaving a conspicuous interspace between sexine and the underlying nexine.

Species 1, northwestern Cape Province.

1. *Adenoglossa decurrens* (Hutch.) B. Nord., comb. nov.

Chrysanthemum decurrens Hutchinson 1917 p. 116. — Orig. coll.: Bolus 9571, L. Namaqualand Div., in

dry places between Port Nolloth and Oograbies, ca. 300 ft, VIII. 1883 (K holotype, BOL isotype).

Illustr.: Fig. 1. — Map 1.

Erect annual, 4-20 cm high; stem simple basally, repeatedly branching above; first stem internode ciliate with 1-2 mm long, thin, white, spreading hairs, disappearing with age. *Leaves* opposite or (upper ones) often alternate, rather crowded on young branches, 2-3(-5) cm long, 1-1.5 mm wide, slightly glaucous, with somewhat decurrent base. *Peduncles* often numerous due to dense branching, 2-15 cm long, slender, up to ca 1 mm thick, flexuous and often nodding before and after anthesis.

Involucre 6-10(-12) mm wide. Involucral bracts 11-20, all with very obtuse-rounded apex; outer involucral bracts elliptic-oblong, 2.5-4 mm long, 2-3 mm wide, with 4-7 resiniferous veins; middle bracts elliptic-oblong-obovate, 4-5 mm long, 2.5-4 mm wide, 4-11-veined; inner bracts not distinctly smaller, broadly oblong-obovate-spathulate, 4-5 mm long, 2-4 mm wide, subhyaline, indistinctly veined. *Receptacle* conical or at least convex with a central conical projection, nude, irregularly warty.

Rays usually 4-5 (3-8), yellow, 2.5-4 mm long. Tube 1-1.5 mm long, somewhat compressed, with distinct veins and resin canals. Lamina 1.5-2.5 mm long and wide, with 4 main veins and 0-3 incomplete vestigial veins, apically \pm truncate and shallowly 3-lobed. Style terete with somewhat swollen base, placed on a short nectary.

Disc-florets 15-25. Corolla 2-2.5 mm long; tube 0.7-1 mm long; limb 1-1.5 mm long; lobes triangular-ovate, acute, 0.5-0.7 mm long (adaxial lobes shortest and provided with marginal resin canals). Style 1.6-1.8 mm long; branches 0.3-0.4 mm long, truncate or slightly convex at the apex; nectary ca 0.2 mm high and broad. *Anthers* 0.6-0.7 mm long incl. appendage.

Achenes obovate in outline, 2-2.5 mm long (excl. pappus), 2.5-3.5 mm wide (incl. wings); adaxial side smooth, glossy, faintly midribbed basally; abaxial myxogenic striae ca 18-21, alate and transversely striate; lateral wings hyaline, 0.5-1 mm broad, transversely finely striate, apically with a flaplike projection. *Pappus* of 5-6 scales; adaxial median scale 1-1.5 mm long and wide, scarious; lateral scales 1.5 mm long and 1 mm wide, light brownish, laterally folded

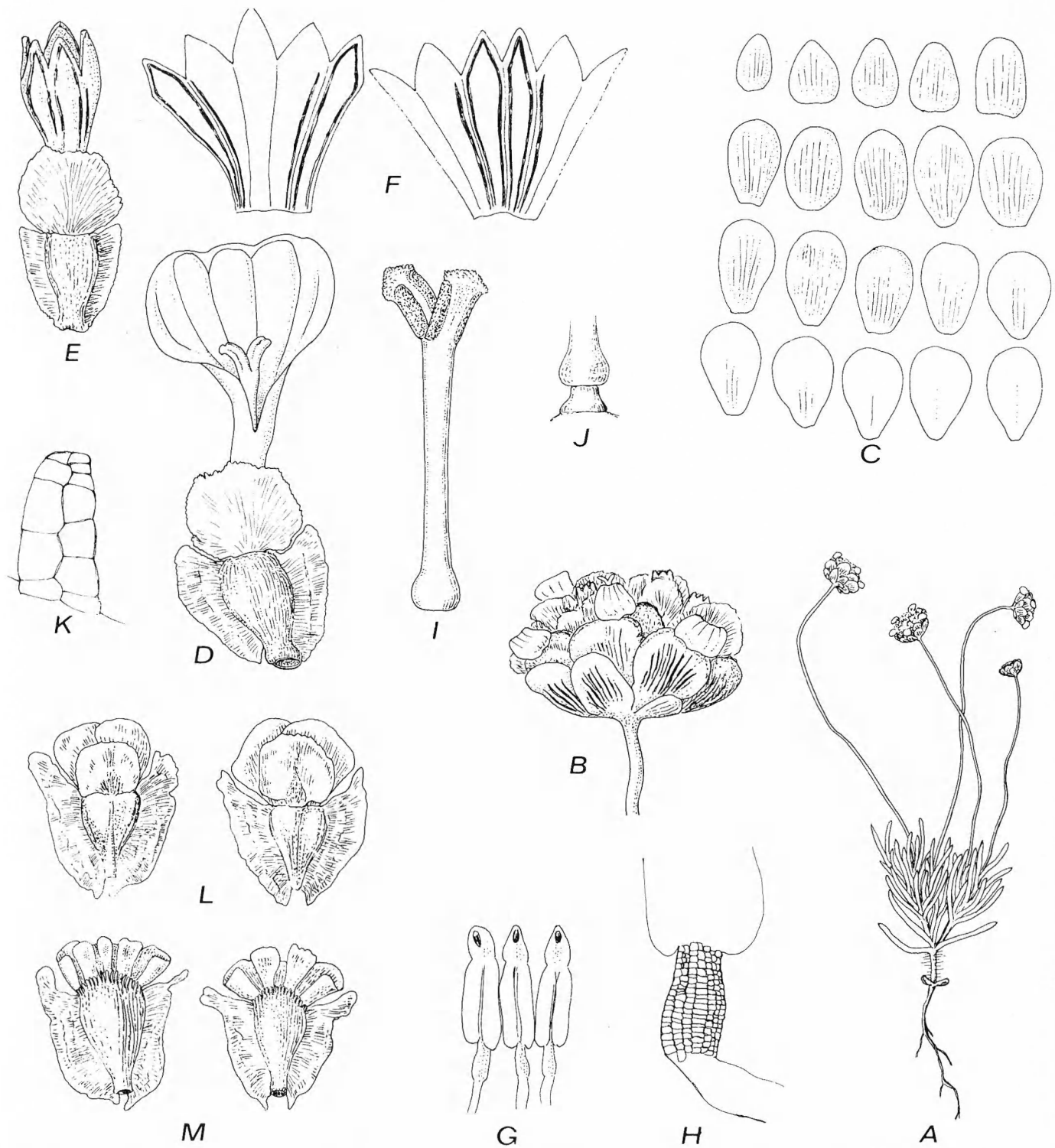


Fig. 1. *Adenoglossa decurrens*. - A: Habit, $\times 0.5$. - B: Capitulum, $\times 3$. - C: Series of involucre bracts from one capitulum (outer: upper left; inner: lower right), $\times 3$. - D: Ray-floret, $\times 12.5$. - E: Disc-floret, adaxial side, $\times 12.5$. - F: Corollas of disc-florets laid out, opened with an adaxial slit (left) and an abaxial slit (right); note resin ducts and shorter lobes on adaxial side, $\times 12.5$. - G: Anthers, $\times 25$. - H: Filament collar, $\times 100$. - I: Style of disc-floret, $\times 25$. - J: Style base and nectary of disc-floret, $\times 25$. - K: Corolla gland, $\times 250$. - L: Achenes, adaxial side, $\times 6$. - M: Achenes, abaxial side, $\times 6$. - A: N. 1810. - B: N. 1259. - C, H, J, K: N. 1606. - D-G, I, L, M: N. 1784.

with a small abaxial portion; abaxial smaller scales up to 1 mm long, 0.2–0.5 mm wide, light brownish.

Pollen grains ca $41 \times 43 \mu$ (spines included). Exine ca 11μ thick. Supratectal spines 2.5–3 μ high, pointed with solid tips superimposed upon a minute spheroidal hole. Total number of spines in one grain 45–50 (ca 12 in one mesocolpium), spaced approximately 7–9 μ from each other. Tectum continuous, undulated, 1–2 μ thick, with minute intratectal bacula, below spines bulging and forming a supratectal spiny unit 4–4.5 μ high and wide. Infratectal bacula reduced, leaving a distinct interspace between sexine and underlying nexine, esp. at the poles. Nexine comparatively thick and compact, ca 1.5 μ thick. Colpi ca $15 \times 5 \mu$ with somewhat acute ends. Ora somewhat lalongate, ca $4 \times 5 \mu$.

Flowering period: August–November.

Cape Province. L. Namaqualand Div.: Between Port Nolloth and Oograbies, 1883, Bolus 9571 (BOL, K) – Gembokvlei, 17 miles from Port Nolloth on Steinkopf road, 1961, Hardy 664 (G, K) – 2 miles S of Stinkfontein, 1962, N. 1223 (BOL, K, M, S) – 3 miles SW of Brakfontein, 1962, N. 1259 (S) – Oograbies Poort, 1962, N. 1267 (M, S) – 27 miles W of Steinkopf on Port Nolloth road, 1962, N. 1597 (K, M, MO, S) – 39 miles W of Steinkopf and 1 mile W of the road, 1962, N. 1603 (S) – 22 miles E of Port Nolloth, mtn 1.5 mile S of the road, 1962, N. 1606 (K, M, MO, NBG, S) – 9 miles E of Arrisdrift, 1962, N. 1691 (M, S) – Anniskop, 2 miles NW of Annisfontein on Bloudrif track, 1962, N. 1700 (NBG, S) – 3 miles N of Annisfontein, 1962, N. 1709 (M, S) – 7 miles N of Annisfontein on Sendelingsdrift track, 1962, N. 1721 (S) – 9 miles N of Annisfontein, 1962, N. 1728 (M, S) – Mtn between Numees and Hellskloof, 1962, N. 1764 (BM, M, S) – Granite Boss, S of Kuboos, 1962, N. 1784 (MO, S) – 10 miles NW of Brakfontein on Kuboos track, 1962, N. 1797 (K, M, S) – 3 miles SW of Brakfontein, 1962, N. 1798 (S) – 2 miles NE of Lekkersing on Stinkfontein road, 1962, N. 1810 (S) – 5 miles E of Stinkfontein on road to Klein Hellskloof and Violsdrift, 1962, N. 1865 (S) – 10 miles E of Stinkfontein, 1962, N. 1867 (S).

Adenoglossa decurrens is a small annual herb, easily recognized on the short yellow rays and the conspicuous glands on the anther appendages (which have inspired the generic name). Until now this taxon has been insufficiently known. Even important characters of gross morphology like the annual habit and the yellow rays have remained unrecorded. In involucre and to some extent achene morphology the new

genus recalls *Leucoptera* B. Nord., which is no doubt the most closely related genus. For generic distinction, see Discussion and Table 1.

This interesting taxon is restricted to the north-western corner of the Cape Province, which is a desolate and inhospitable area known as the Richtersveld. The plant seems to grow only in favourable years and had been collected only twice before 1962, when I found it in many places all over the Richtersveld (see Map 1). The species has not yet been found in South West Africa, but can be expected there, since the Orange River is no phytogeographical barrier for arid karroo elements. Phytogeographically the species belongs to the Gariiep element within the Karroo-Namib floral region (cf. Nordenstam 1966 p. 484, 1969 p. 48).

Leucoptera B. Nord., gen. nov.

Typus: *L. nodosa* (Thunb.) B. Nord.

Fruticuli erecti–decumbentes glabri. Folia alterna aut opposita angusta teretia–applanata subcarnosa vel coriacea nunc integra nunc lobata. *Pedunculi* terminales nudi monocephali. *Capitula* heterogama, flosculis marginalibus femineis ligulatis fertilibus, flosculis disci hermaphroditis fertilibus. *Involucrum bractearum* imbricatae latae apice rotundatae, intimae minores \pm oblongae submembranaceae. *Receptaculum* convexum nudum. *Flores* radii c. 8 (usque ad 13), tubo leviter complanato glanduloso, lamina 4–7-nervia alba demum erubescens reflexa. *Flores disci* lutei; corolla superne campanulata quinquelobata actinomorpha. *Achaenia* complanata bialata eburnea, facie abaxiali madefacta mucosa, alis lateralibus scariosis opacis. *Pappi* squamae 3 adaxiales scariosae albae opacae, quarum 1 mediana \pm rotundata, 2 sublaterales minores oblongae–rotundatae.

Erect or decumbent glabrous shrublets. *Leaves* alternate or opposite, filiform–linear or oblanceolate, entire or lobed, terete or flattened, usually somewhat carnosose or coriaceous, apically \pm obtuse and often apiculate. *Peduncles* terminal, solitary, erect, nude, monocephalous. *Capitula* heterogamous, radiate.

Involucre broadly campanulate–hemispherical. Involucral bracts imbricated, broad, ovate–oblong–obovate with very obtuse or rounded tips, many-veined, herbaceous, with membranous margins; innermost bracts somewhat shorter, \pm oblong, submembranous, \pm truncate. *Receptacle* convex, nude.

Rays usually ca 8, sometimes up to 13, white, often becoming pink–reddish and revolute. Tube somewhat compressed, glandular. Lamina 4–7–

veined, with a smooth surface, apically 3-toothed or subentire. Style branches oblong, truncate or somewhat emarginate.

Disc-florets actinomorphic, yellow. Tube broadly cylindrical, glandular. Limb campanulate, 5-lobed. *Anther* appendage \pm ovate, obtuse. Endothelial cells with thickenings mainly on horizontal walls (polarized tissue). Filament collar subcylindrical with subequal cells. Style branches oblong, truncate; style base partly immersed in the broad and distinct nectary.

Achenes homomorphic, dorsiventrally strongly compressed, laterally winged, white, with 3 veins and 2 sometimes indistinct resin ducts; adaxial side smooth and with a faint midrib; abaxial side with longitudinal myxogenic striae apically ending in a fringe of fused projections; lateral wings scarious, white, opaque. Ovary wall crystals small, \pm isodiametric, rounded or star-shaped. *Pappus* of 3 adaxial white scarious scales; 1 larger rounded median scale, and 2 sublateral oblong-rounded smaller scales.

Corolla glands multicellular, columnar.

Pollen grains isopolar, radially symmetrical, usually oblate-spheroidal to spheroidal, tectate, crassisexinous, 3-colporate. Infratectal bacula well developed, sometimes detached from the nexine, leaving there free interspaces esp. at the poles.

Species 3, western Cape Province.

1. *Leucoptera nodosa* (Thunb.) B. Nord., comb. nov.

Arctotis nodosa Thunberg 1823 p. 711. – *Pinardia nodosa* (Thunb.) Lessing 1831 p. 169. – *Ismelia nodosa* (Thunb.) Lessing 1832 p. 255. – *Chrysanthemum nodosum* (Thunb.) De Candolle 1837 p. 65; Harvey 1865 p. 162; Hutchinson 1917 p. 116. – Orig. coll.: Herb. Thunberg no. 20785, Patryberg, Oct., Thunberg (UPS-THUNB holotype).

Chrysanthemum leptophyllum DC. (incl. *α. trisetum* DC.); De Candolle 1837 p. 65. – Orig. coll.: Drège 6028, Olifantrivier (G-DC lectotype).

Illustr.: Fig. 2. – Map 2.

An erect slender glabrous shrublet up to ca 0.5 m high, moderately branching mainly in the upper parts; stems and branches becoming nude and knotty with old leaf-bases. *Leaves* alternate, closely set, suberect-erecto-patent, filiform, some entire and some 3-forked above the middle

or pinnatipartite with 2 pairs of segments, 1–4 cm long, ca 0.5 mm wide, herbaceous or subcoriaceous, subterete-slightly flattened, minutely mucronate. Leaf-base somewhat decurrent, swollen, firm, yellowish, up to 1 mm wide, persistent. *Peduncle* erect, 5–20 cm long, 0.5–1.2 mm thick, faintly striate.

Involucre 1–1.5 cm wide; outermost involucre bracts ovate or broadly ovate, many-veined, with narrow membranous margins; inner bracts oblong-obovate with membranous margins and tips, up to 1 cm long and 0.5(–0.7) cm wide, with obtuse-rounded tips; innermost bracts smaller. *Receptacle* convex, nude.

Ray-florets 8–13, white. Tube ca 2.5–3 mm long, somewhat compressed, glandular especially in the upper half. Lamina elliptic-oblong, 9–12 mm long, 3–4.5 mm wide, (4–)7-veined, apically shallowly 3-toothed. Style branches flattened, oblong, with a central resin excretion.

Disc-florets numerous. Corolla 3–4 mm long. Tube subcylindrical, 1.2–2 mm long, densely glandular-hirsute in the upper half. Limb campanulate, 1.8–2 mm long; lobes triangular-ovate, 0.7–0.8 mm long, with a distinct resin gland near the apex. *Anthers* 1.5–1.7 mm long incl. the broadly oblong-ovate obtuse appendage. Style branches 0.6–0.8 mm long, flattened, truncate.

Achenes oblong-obovate, 2.5–4 mm long and 2–3 mm broad, creamy white; lateral wings 0.2–0.5 mm broad. Median *pappus* scale 1–2 mm long, 1–1.5 mm wide, glossy white with light brownish tinge; sublateral scales ca 0.5 mm long with often premorse apex.

Flowering period: July–September.

Cape Province. L. Namaqualand Div.: Between Hondekliip Bay and Zwartlinter River, 1924, Pillans (BOL) – 6 miles ESE of Hondekliip Bay, 1963, Acocks 23323 (K) – *Vanrhynsdorp Div.*: Ebenezer, Drège, α , a (K) – Wind Hoek, 1896, Schlechter 8353 (BOL, G, K, L, S) – *Clanwilliam Div.*: Patryberg, Thunberg (UPS-THUNB) – Between Langevalei and Heerenlogement, Drège, α , b (G, K, L, S, SAM); Olifantrivier, Drège 6028 (G-DC) – Lamberts Bay, 1925, flowered in Mrs. le Roux's garden 1926, Herb. Bolus. 18528 (K) – Lamberts Bay Road, cult. in Kirstenbosch, NBG 578/26 (BOL, NBG) – Sandveld near Clanwilliam, 1941, Leipoldt 3577 (BOL, K, NBG, SAM).

De Candolle knew Thunberg's *Arctotis nodosa* only from description, which explains why he could describe the same species anew as *Chry-*

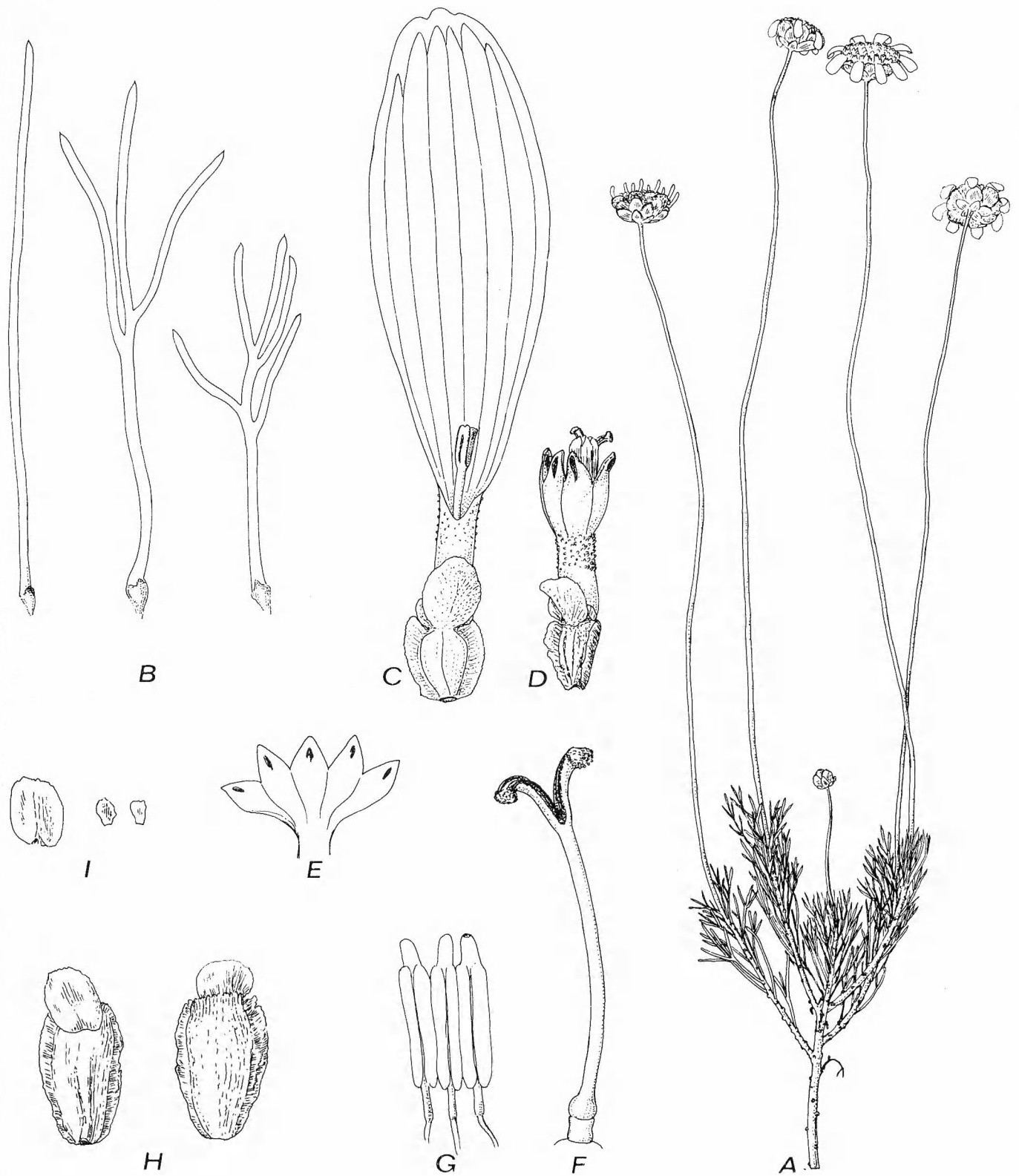


Fig. 2. *Leucoptera nodosa*. - A: Portion of plant, $\times 0.5$. - B: Leaves, $\times 3$. - C: Ray-floret, $\times 6$. - D: Disc-floret, $\times 6$. - E: Corolla of disc-floret laid out, $\times 6$. - F: Style of disc-floret, $\times 12.5$. - G: Anthers, $\times 12.5$. - H: Achene, adaxial side (left) and abaxial side (right), $\times 6$. - I: Pappus scales, $\times 6$. - H, I: Schlechter 8353, otherwise Leipoldt 3577.

santhemum leptophyllum and place it in a different section from *C. nodosum*.

De Candolle's *β. indivisum* is a different species, which has repeatedly (Harvey, Hutchinson) been confused with *C. nodosum*. It is described below as *Leucoptera subcarnosa* B. Nord.

Leucoptera nodosa can be recognized by its non-fleshy, narrow, alternate leaves, many of which are trifid or pinnatifid, and the persistent knot-like leaf-bases. The rays are comparatively large, and the corolla lobes of the disc-florets have a central resin gland (a character also occurring in *L. oppositifolia*).

In contrast to its congeners *L. nodosa* grows in sandveld. It has been recorded from Clanwilliam, Vanrhynsdorp and L. Namaqualand Divisions, and the range more or less surrounds the areas of the two other species, which are confined to quartzite outcrops in Vanrhynsdorp Division.

2. *Leucoptera oppositifolia* B. Nord., sp. nov.

Orig. coll.: N. & L. 1738, Vanrhynsdorp Div., 1 km NE of Kerskloof (=ca 10 km NW of farm Komkans), quartzite outcrop, 8. IX. 1974 (S holotype, BM, BOL, C, E, G, K, LE, M, MO, NBG, PRE, W isotypes).

Illustr.: Fig. 3. – Map 2.

Fruticulus ramosus erectus vel ascendens glaber. *Folia* plerumque opposita linearia-oblongata vulgo integra leviter complanata coriacea obtusa. *Pedunculi* ± erecti nudi usque ad 18 cm longi. *Involucrum* late campanulatum; involucri bracteae c. 16–18 imbricatae late ovatae-elliptico-oblongae herbaceae, margine et apice membranaceae, intimae breviores ± oblongae submembranaceae truncatae vel emarginatae. *Flores radii* c. 8 (6–11) albi erubescens, lamina obovato-oblonga-elliptico-oblonga usque ad 7 mm longa et 3.5 mm lata 5–7-nervia apice tridentata. *Flores disci* lutei, corolla superne campanulata, lobis deltoideo-ovatis glande resinosa subapicali instructis. *Achaenia* valde complanata bialata ambitu late oblongo-obovata, facie adaxiali laevi leviter costata, facie abaxiali striata, madefacta valde mucosa. *Pappi* squamae 3 adaxiales albae scariosae, quarum 1 mediana rotundata-ovata usque ad 2 mm longa et 1.5 mm lata, 2 sublaterales oblongae minores.

Erect or ascending shrublets 2–6 dm high, moderately to richly branched. *Leaves* opposite (rarely some subopposite or alternate), rather laxly set (internodes mostly 0.5–1 cm, sometimes up to 2 cm long), linear-oblongate, 0.5–2(–2.5) cm long, 1–2(–3) mm thick, somewhat narrowed towards the base, usually entire,

seldom 3(–4)-lobed below the middle, somewhat flattened, leathery, greyish green, obtuse. *Peduncles* erect, often flexuous when young, 5–18 cm long, 0.6–1 mm thick, faintly striate.

Involucre 0.6–1.3 cm wide. Outer (visible) involucre bracts ca 12, broadly ovate to elliptic-oblong, with 5–7 faint resiniferous veins, herbaceous, with brownish membranous margins and obtuse-rounded tips. Innermost involucre bracts 4–5, shorter than the largest outer ones, ± oblong, truncate-emarginate, submembranous. *Receptacle* convex-hemispherical, nude.

Ray-florets ca 8 (6–11). Tube 1–1.3 mm long, somewhat compressed, glandular in the upper part. Lamina oblong-obovate-elliptic-oblong, 3–7 mm long, 2.5–3.5 mm wide, 5–7-veined, apically shallowly 3-lobed, white, becoming pink-reddish and reflexed when old. Style branches 0.3–0.5 mm long, oblong, slightly emarginate, with a central resin excretion.

Disc-florets 25–50. Corolla 2.4–2.8 mm long. Tube 1–1.3 mm long, broadly cylindrical, glandular-hirsute in the upper part. Limb campanulate, ca 1.5 mm long; lobes deltoid-ovate, 0.5–0.7 mm long, with a small resin dot near the tip (rarely 2–3 dots). *Anthers* ca 1 mm long incl. the ovate-triangular obtuse-subacute appendage. Style branches ca 0.5 mm long, with a central resin excretion, truncate.

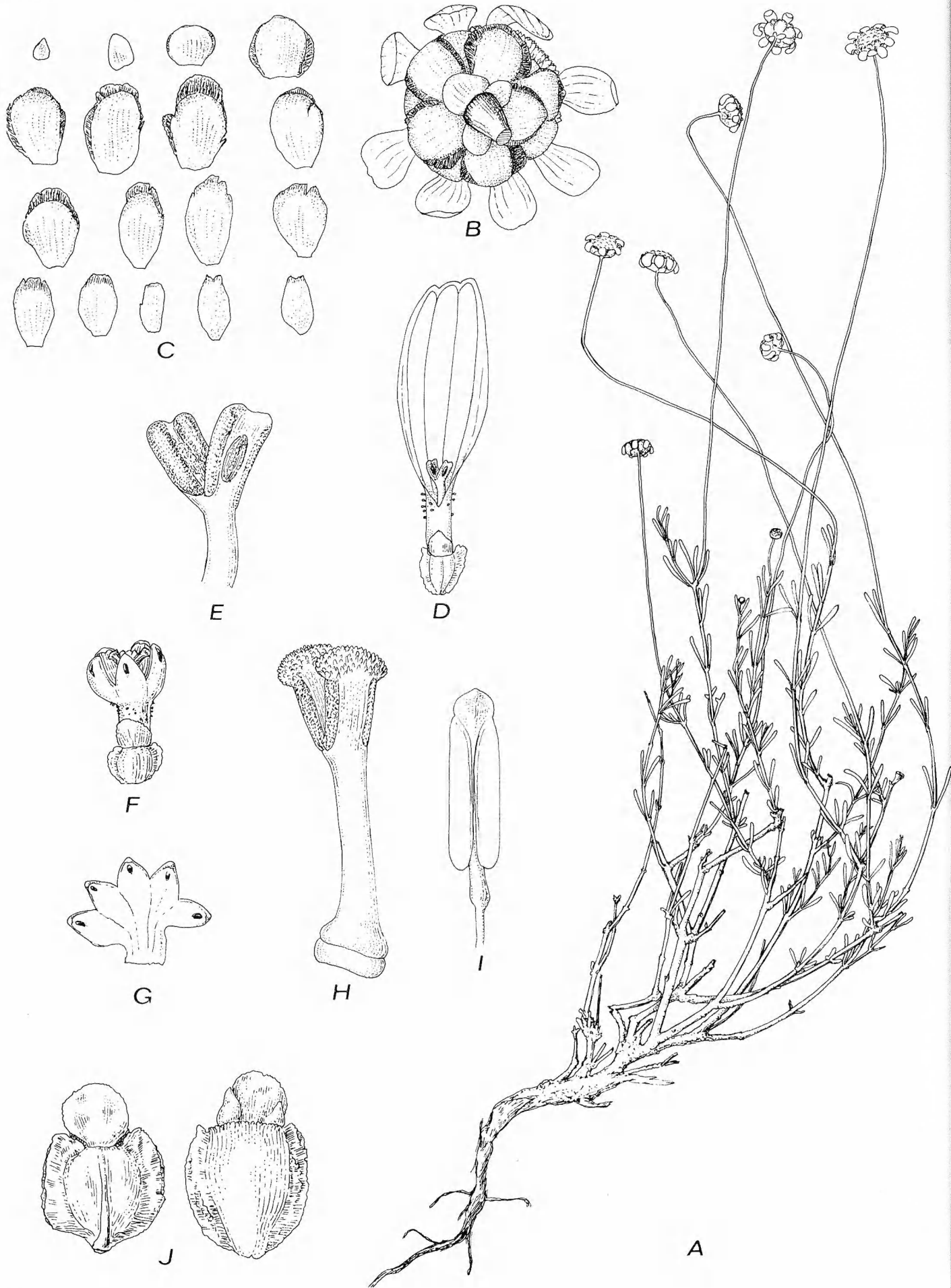
Achenes broadly oblong-obovate, 2.5–3.5 mm long, 2–3 mm wide, with 3 veins and 2 incomplete resin canals, glossy white-bone-white; lateral wings ca 0.5 mm broad. Median *pappus* scale rounded-ovate, white, 1–2 mm long, 1–1.5 mm wide. Sublateral pappus scales oblong, 0.7–1 mm long, 0.5–0.8 mm wide.

Pollen grains ca 37×39 μ (spines included). Total number of spines in one pollen grain ca 38. Exine as in *L. subcarnosa*.

Flowering period: August–September.

Cape Province. Vanrhynsdorp Div.: 2 miles S of Komkans station, quartzite area W of the road, 1962, N. 952 (E, K, M, S) – Komkans station, at the river, quartzite area E of the road, 1962, N. 977 (BM, S) – 1 km NE of Kerskloof (=ca 10 km NW of farm Komkans), 1974, N. & L. 1738 (BM, BOL, C, E, G, K, LE, M, MO, NBG, PRE, S, W).

This new species is distinguished i.a. by its opposite, non-fleshy leaves, and the resin glands in the corolla lobes. The latter character recurs in *L. nodosa*, which, however, has alternate,



filiform, often trifid leaves with a distinctly swollen base, and larger florets.

L. oppositifolia is only known from my own collections near Komkans in the northwestern corner of the Kners Vlakte region. Like *L. subcarnosa* it is apparently confined to quartzite outcrops.

3. *Leucoptera subcarnosa* B. Nord., sp. nov.

Orig. coll.: Nordenstam 796, Vanrhynsdorp Div., 6 km N of Holriver station, quartzite outcrops near Moedverloor, 28. VII. 1962 (S holotype, BM, E, K, M, NBG isotypes).

Chrysanthemum leptophyllum DC. β *indivisum* DC.; De Candolle 1837 p. 65. – Orig. coll.: Drège 2831, Klein Namaqualand (G-DC holotype).

Illustr.: Figs. 4, 5. – Map 2.

Fruticulus humilis glaber. *Folia* alterna linearia–oblanceolata integra vel 2–3-fida subcarnosa teretia vel complanata, apice obtusa plerumque minute apiculata. *Pedunculi* erecti nudi usque ad 30 cm longi. *Involucrum* late campanulatum; involucri bracteae c. 16–18 imbricatae late ovatae–ellipticae herbaceae, margine et apice membranaceae, intimae breviores \pm oblongae submembranaceae truncatae. *Flores radii* plerumque 8 (6–11) albi erubescetes, lamina elliptico-oblonga–oblongo-obovata usque ad 1 cm longa et 0.5 cm lata 4(–7)-nervia, apice tridentata vel subintegra, demum reflexa. *Flores disci* lutei, corolla superne campanulata, lobis triangulari-ovatis sine canali resinifero vel glande resinosa. *Achaenia* valde complanata bialata ambitu oblongo-obovata–elliptico-rotundata, facie adaxiali laevi leviter costata, facie abaxiali striata, madefacta valde mucosa. *Pappi* squamae 3 adaxiales albae scariosae, quarum 1 mediana rotundata–late obovata usque ad 2.5 mm longa et lata, 2 sublaterales oblongae–rotundatae minores.

A low shrublet; stems and branches short, often decumbent, up to 10 cm long or seldom longer. *Leaves* alternate (or rarely subopposite), rather closely set on young branches, more scattered on older branches, linear–oblanceolate, somewhat narrowed towards the base, 0.5–3(–4) cm long, 1–2.5(–4) mm wide, entire or some 2–3(–4)-toothed or -lobed above the middle, somewhat fleshy, terete or flattened, slightly greyish green, smooth, mostly obtuse and minutely apiculate, sometimes with rounded tips. *Peduncles* erect, 5–30 cm long, terete, smooth or faintly striate.

Involucre 1–1.5 cm wide, consisting of 8–9 outer and 8–9 inner involucral bracts. Outer involucral bracts broadly ovate–rounded-elliptic with obtuse–rounded tips, 2.5–8 mm long, 3–5 mm wide, indistinctly many-veined, herbaceous with membranous margins and tips. Inner involucral bracts shorter than the largest outer ones, submembranous, \pm oblong, truncate or pre-morse. *Receptacle* convex, nude.

Ray-florets usually ca 8 (6–11). Tube ca 1.5 mm long, somewhat flattened, sparsely glandular. Lamina elliptic-oblong–oblong-obovate, 4–10 mm long, 2.5–5 mm wide, usually with 4 main veins and 0–3 additional \pm incomplete veins, white, eventually often pink or reddish and revolute, apically 3-toothed or subentire. Style branches oblong, flattened, somewhat emarginate, with an elongated central resin excretion.

Disc-florets 20–50. Corolla 3.5–4 mm long. Tube 1.5–2 mm long, subcylindrical, glandular. Limb campanulate, ca 2 mm long; lobes triangular-ovate, ca 1 mm long, without midvein or resin gland. *Anthers* 1.2–1.3 mm long incl. the ovate-cordate or broadly triangular-ovate obtuse appendage. Style branches ca 0.7 mm long, oblong, with a central resin excretion, truncate.

Achenes oblong-obovate–elliptic-rounded in outline, 3–4 mm long, 2–3.5 mm wide, glossy white or bone-white, with 2 incomplete resin ducts. Median *pappus* scale orbicular–broadly obovate, 1.5–2.5 mm long and wide, white, sometimes with a light purplish tinge. Sublateral *pappus* scales oblong-rounded, 0.7–1.5 mm long and wide.

Pollen grains ca $40 \times 43 \mu$ (spines included). Exine ca 11μ thick, usually equally thick at poles and equator. Supratectal spines ca 3μ long, pointed with solid tips superimposed upon a minute spheroidal hole. Total number of spines in one pollen grain ca 40 (10–12 in one mesocolpium), spaced approximately 8–9 μ from each other. Tectum continuous, undulated, slightly less than 1μ thick, consisting of minute intratectal bacula faintly discernible in optical cross-section. Tectum bulging below spiny processes, amalgamating with the latter to a supratectal

Fig. 3. *Leucoptera oppositifolia*. – A: Habit, $\times 0.5$. – B: Capitulum from below, $\times 3$. – C: Series of involucral bracts from one capitulum, $\times 3$. – D: Ray-floret, $\times 6$. – E: Style branches from ray-floret, $\times 25$. – F: Disc-floret, $\times 6$. – G: Corolla of disc-floret laid out, $\times 6$. – H: Style of disc-floret, $\times 25$. – I: Anther, $\times 25$. – J: Achene, adaxial side (left) and abaxial side (right), $\times 6$. – A, D–I: N. 952. – B, C, J: N. & L. 1738.

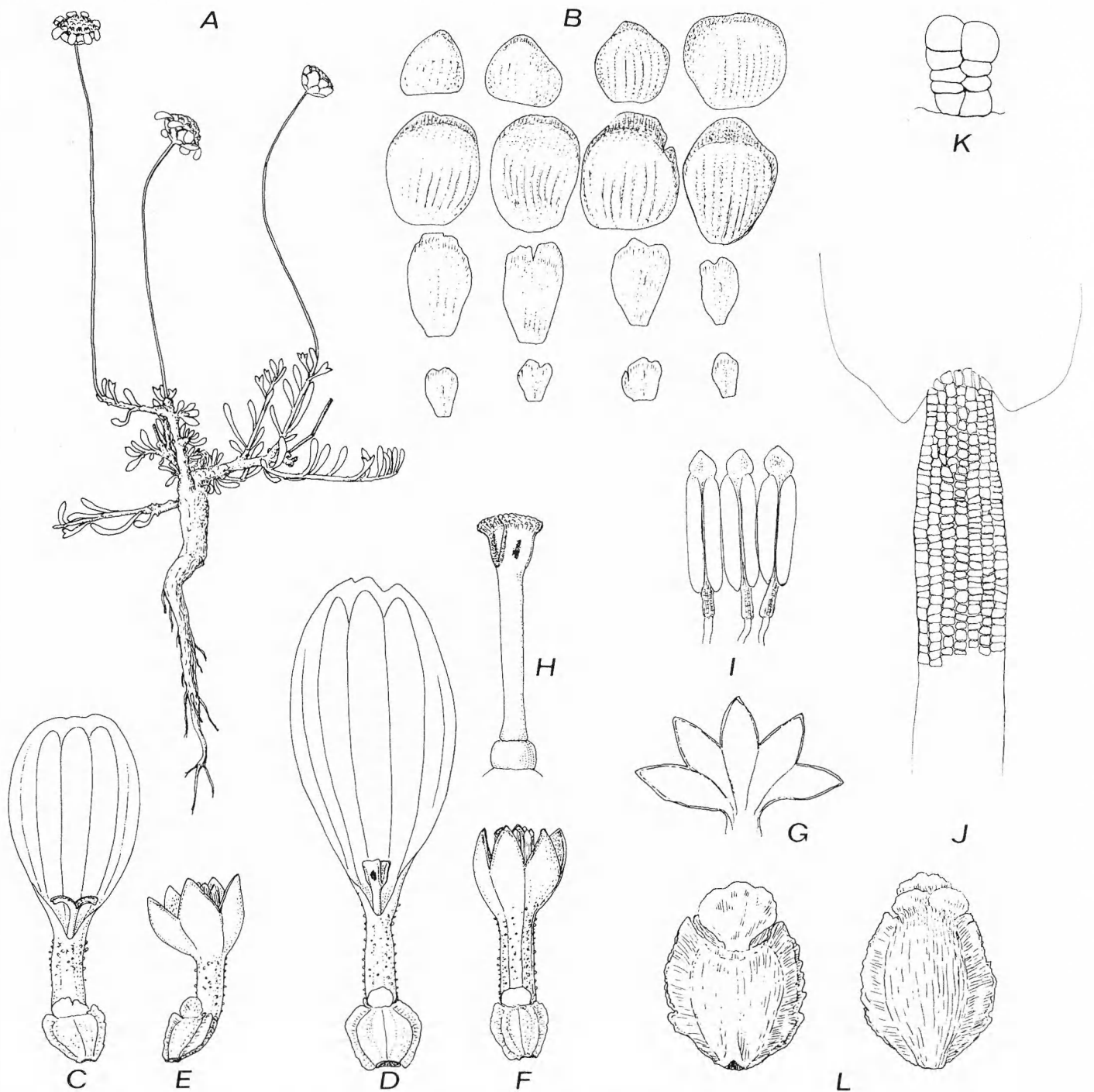


Fig. 4. *Leucoptera subcarnosa*. - A: Habit, $\times 0.5$. - B: Series of involucral bracts from one capitulum, $\times 3$. - C, D: Ray-florets, $\times 6$. - E, F: Disc-florets, $\times 6$. - G: Corolla of disc-floret laid out, $\times 6$. H: Style of disc-floret, $\times 12.5$. - I: Anthers, $\times 12.5$. - J: Filament collar, $\times 100$. - K: Floral gland, $\times 250$. - L: Achene, adaxial side (left) and abaxial side (right), $\times 6$. - A, L: N. 1025. - B, C, E: N. & L. 1418. - D, F-K: N. 796.

spiny unit ca 5μ high and 5μ wide at the base. Infratectal bacula $2-4 \mu$ long, usually branched distally, occasionally detached from the underlying nexine. Nexine compact, ca 1μ thick, slightly thicker in the apertural areas. Colpi ca $13 \times 5 \mu$ with somewhat acute ends. Ora lalongate, $3 \times 6 \mu$, to slightly lolongate, $5 \times 3 \mu$.

Chromosome number: $2n = 18$. (Counted in root tip mitoses from six plants, grown from seeds of N. 2930; paraffin method, Navashin-Karpechenko fixative, crystal violet staining.)

Flowering period: July-September.

Cape Province. Vanrhynsdorp Div.: Between Zwart Doorn River and Groen River, Drège, β , a (G, K, L); Klein Namaqualand, Drège 2831 (G-DC) – Bitterfontein, 1897, Schlechter 11034 (BOL, G, K, L, S) – Knechts vlakte, 1941, Bond 1114 (NBG), Esterhuysen 5396 (BOL, K) – 6 km N of Holriver station, near Moedverloor, 1962, N. 796 (BM, E, K, M, NBG, S), N. 895 (S), 1963, N. 2930 (S), 1970, Hall 3689 (K), 1974, N. & L. 1581 (K, LD, MO, S), N. & L. 1615 (BM, S) – 4 miles N of Koekenaap, kopje W of the road, 1962, N. 1025 (BOL, E, K, M, S) – 6 miles N of Koekenaap, quartzite area E of the road, 1962, N. 936 (E, K, S) – 4 km N of Koekenaap, 1.5 km E of the road, 1974, N. & L. 1662 (BM, K, MO, NBG, S); between the road and the railway, 1974, N. & L. 1685 (S) – 8 km E on Kliprand road from road junction 4 km N of Bitterfontein, 1974, N. & L. 1418 (BM, BOL, E, K, MO, S) – 6 km E on Kliprand road from road junction 4 km N of Bitterfontein, 1974, N. & L. 1458 (M, NBG, S).

L. subcarnosa was first described by De Candolle as a variety of *Chrysanthemum leptophyllum* DC., which is a synonym of *L. nodosa*. It has ever since been confused with the latter species, and only scanty material has been available until recently.

L. subcarnosa is characterized, i.a., by the short stems, rather densely set and somewhat fleshy leaves, and the absence of resin glands in the corolla lobes. It is a quite variable species, in spite of its restricted range in quartzite areas of Vanrhynsdorp Division. The small local populations may differ in habit, leaf shape, length of peduncles and rays, etc.

The Moedverloor populations have entire, almost terete and rather long leaves (ca 2 cm) and sometimes very long peduncles (20 cm or more). A very similar type grows 6 miles N of Koekenaap (N. 936), but this has on an average shorter rays. The other Koekenaap populations have shorter leaves (usually about 1 cm), which are more flattened and frequently 2–3-lobed above the middle, and generally shorter peduncles. The populations NE of Bitterfontein have a similar habit, but most leaves are apically 3–4-toothed and not distinctly apiculate. Finally, two collections without precise locality (Bond 1114, Esterhuysen 5396) and Schlechter 11034 from Bitterfontein differ from all others by the more elongate and laxly foliated branches and the unusually large rays (Fig. 5).

Although the differences mentioned are regarded as insufficient for taxonomic recognition, they are nevertheless interesting from an evolutionary point of view. Possibly they represent

local non-adaptive variations, which have become fixed in the populations by means of genetic drift. Like many other taxa in the Kners Vlakte area of Vanrhynsdorp Division, the local populations are confined to quartzite outcrops, which are often separated by large tracts of sand with a very different vegetation. The population size may be very small, especially in dry years, which are indeed prevalent in this region. Many local endemics of this area are well nigh impossible to find for periods of several years, until they suddenly flourish again in favourable years like 1962 and 1974. Such climatic fluctuations, which reduce population sizes drastically, may favour an evolution by random fixation of non-adaptive mutations in these isolated populations.

Scyphopappus B. Nord., gen. nov.

Typus: *S. frutescens* (Less.) B. Nord.

Fruticulus erectus glaber. *Folia* alterna angusta trilobata vel pinnatipartita applanata coriacea. *Pedunculi* terminales monocephali subnudi, bracteis paucis instructi. *Capitula* heterogama, flosculis marginalibus femineis ligulatis fertilibus, flosculis disci hermaphroditis fertilibus. *Involucri bractee* imbricatae ovatae-oblongae, margine membranaceae, apice appendice scariosa dilatata ornatae. *Receptaculum* conicum nudum. *Flosculi radii* 8–13 albi, tubo leviter complanato glanduloso, lamina 5–7-nervia. *Achaenia* complanata trialata glabra eglandulosa fusca, alis duabus lateralibus, una adaxiali. *Pappus* oblique cyathiformis. *Flosculi disci* actinomorphi, tubo glanduloso, limbo campanulato quinquelobato. *Achaenia* subangulata anguste trialata glabra eglandulosa, *pappo* oblique cyathiformi coronata.

Erect glabrous shrublet. *Leaves* alternate, trilobate or pinnatipartite with linear segments, coriaceous, flattened, apically obtuse and apiculate. *Peduncles* terminal, solitary, monocephalous, with a few small bract-like leaves.

Capitula heterogamous, radiate. Involucre broadly campanulate. *Involucral bracts* imbricated, ovate-oblong, indistinctly veined, herbaceous-subcoriaceous with membranous margins and a dilated scarious apical appendage. *Receptacle* conical, naked. *Achenes* heteromorphic.

Ray-florets 8–13. Tube subcompressed, glandular. Lamina 5–7-veined, obtuse, entire; upper surface colliculate, lower surface smooth. Style branches oblong, truncate. *Achenes* dorsiventrally compressed, 3-winged with 2 lateral wings

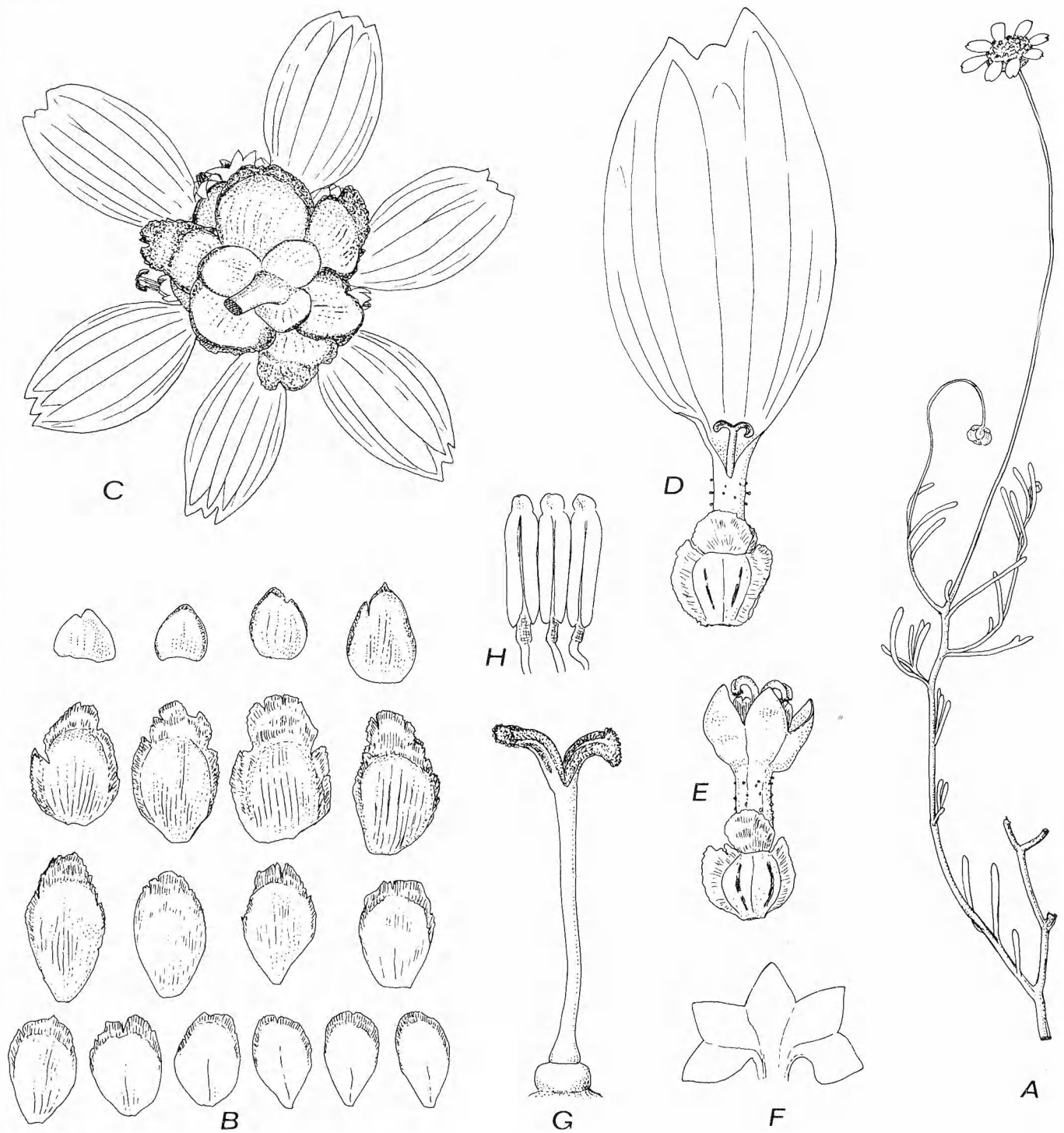


Fig. 5. *Leucoptera subcarnosa*, erect, laxly leafy, large-flowered form. – A: Habit, $\times 0.5$. – B: Series of involucre bracts from one capitulum, $\times 3$. – C: Capitulum from below, $\times 3$. – D: Ray-floret, $\times 6$. – E: Disc-floret, $\times 6$. – F: Corolla of disc-floret laid out, $\times 6$. – G: Style of disc-floret, $\times 12.5$. – H: Anthers, $\times 12.5$. – Esterhuysen 5396.

and 1 adaxial wing, glabrous, eglandular, brown. *Pappus* obliquely cup-shaped, abaxially emarginate.

Disc-florets \pm actinomorphic, with a glandular cylindrical tube and a campanulate 5-lobed limb. *Anthers* with a triangular-ovate subacute apical

appendage. Endothelial cells with thickenings on vertical walls (non-polarized tissue). Filament collar basally dilated with larger cells. Style branches truncate; style base slightly swollen, partly immersed in a short, broadly cylindrical nectary. *Achenes* turbinate-oblong,

somewhat angular, narrowly and obscurely 3-winged, ca 5-veined, glabrous, eglandular, abaxially ribbed. *Pappus* as in ray-florets.

Corolla glands stipitate, multicellular, with a large terminal cell.

Pollen grains isopolar, radially symmetrical, \pm spheroidal, distinctly 3-lobed in polar view, tectate, crassisexinous, 3-colporate. Infratectal bacula very distinct.

Species 1, Cape Province.

1. *Scyphopappus frutescens* (Less.) B. Nord.,
comb. nov.

Pinardia frutescens Lessing 1831 p. 168. – *Ismelia frutescens* (Less.) Lessing 1832 p. 255. – *Chrysanthemum carnosulum* DC., nom. illeg.; De Candolle 1837 p. 65, quoad syn. sed excl. descr. et specim. – *C. thunbergii* Harvey 1865 p. 162, nom. illeg.; Hutchinson 1917 p. 116. – Orig. coll.: Herb. Thunberg no. 20183, "Pyrethrum frutescens 2, e Cap. b. spei", Thunberg (UPS-THUNB holotype).

C. frutescens auct. non L.: Thunberg 1823 p. 693 p.p.

Illustr.: Fig. 6.

A moderately branching shrublet, a few dm high. *Leaves* often crowded on brachyblasts, linear, some 3-lobed above the middle, others pinnatifid with usually 2 pairs of lobes, 0.5–2.5 cm long, apiculate with an eventually firm point; leaf segments 0.5–1 mm wide. *Peduncles* erect, naked except for 1 or 2 small bracts in the lower half, 7–15 cm long, 0.5–1 mm thick, striate.

Involucre 8–12 mm wide, 5–7 mm high; involucre bracts with brown membranous margins and a scarious, subpellucid, somewhat lacerated, pale brownish and glossy appendage; appendage of innermost bracts largest, much dilated, ca 3 mm long and 5 mm wide.

Ray-florets probably white. Tube 1.5–2 mm long. Lamina narrowly elliptic-oblong, ca 10 mm long and 2 mm wide. Style branches flattened, oblong, truncate. *Achene* (immature) broadly oblong in outline, with a convex abaxial side, triolate with firm brown wings. *Pappus* an oblique firm cup, adaxially 1–1.5 mm long, truncate, abaxially deeply emarginate and only ca 0.5 mm long or less.

Disc-florets probably yellow. *Corolla* 2.5–2.8 mm long. Tube 1–1.3 mm long. Limb campanulate, ca 1.5 mm long; lobes deltoid, ca 0.5 mm long, without midvein and resin ducts. *Anthers* 1.3–1.5 mm long incl. appendage. Style branches

ca 0.5 mm long. *Achene* (immature) somewhat angular and obscurely triolate, 5–6-ribbed abaxially, without myxogenic cells. *Pappus* as in ray-florets.

Pollen grains spheroidal to prolate-spheroidal, ca 32×30 – 32μ (spinules included). Exine at equator (centre of mesocolpia) 8–10 μ , at poles ca 6 μ thick. Supratectal spinules finely pointed with solid tips, 2.5–3 μ high, spaced 6–7 μ from each other. Total number of spinules in one pollen grain ca 28–30 (ca 12 in one mesocolpium). Tectum continuous, undulated, slightly less than 1 μ thick, with minute intratectal bacula visible in optical cross-section. Infratectal bacula well developed, 2–3 μ long, branched distally. Nexine compact, ca 1 μ thick. Colpi with acuminate ends, ca $19 \times 5 \mu$. Ora somewhat rounded, ca $5 \times 5 \mu$.

Flowering period: Not known.

Sine loco. Cap. b. spei, Thunberg, Herb. Thunberg no. 20183 (UPS-THUNB).

The exact geographical origin of this interesting taxon is unfortunately not known. In general appearance and especially in involucre the plant looks very much like an *Ursinia*, but the achenes and pappus are very different.

The species has only been collected once, viz. by Thunberg, who confused it with another species (*Cymbopappus adenosolen*, cf. below) and misidentified it as *Chrysanthemum frutescens* L. (= *Argyranthemum frutescens* (L.) Sch. Bip., Canary Islands). Lessing realized the mix-up and described the species as *Pinardia frutescens* Less. However, the confusion was perpetuated by De Candolle, who introduced the name *Chrysanthemum carnosulum* DC., citing *Pinardia frutescens* Less. as a synonym. De Candolle's epithet becomes nomenclaturally a synonym to our species, although his description and specimen citations apply to the other Thunbergian species (*Cymbopappus adenosolen*). Harvey re-named our species *Chrysanthemum thunbergii* Harv., also a superfluous name according to the present rules of nomenclature. See further Nomenclatural note under *Cymbopappus adenosolen*.

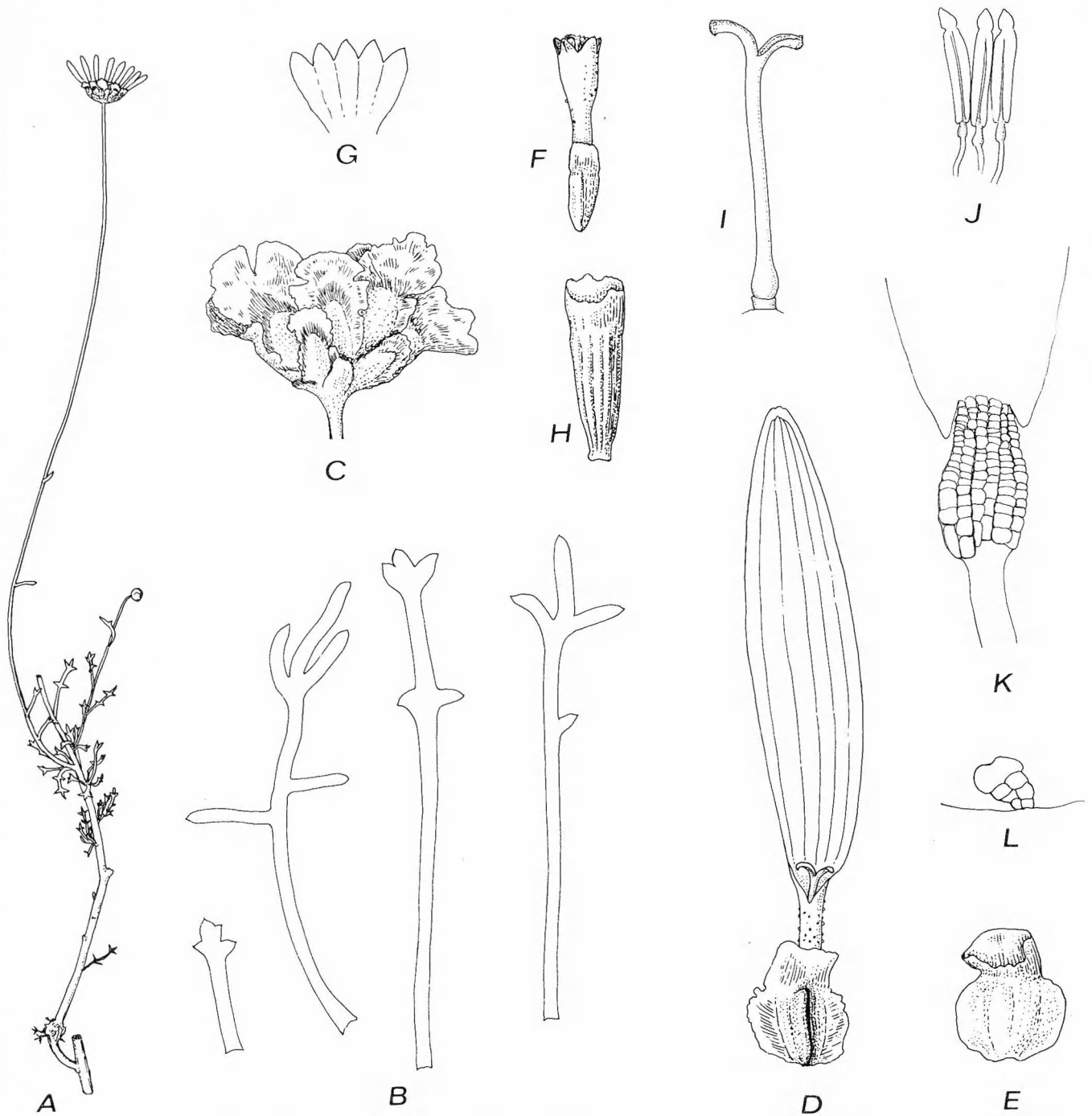


Fig. 6. *Scyphopappus frutescens*. – A: Portion of plant, $\times 0.5$. – B: Leaves, $\times 3$. – C: Involucre, $\times 3$. – D: Ray-floret, $\times 6$. – E: Achene of ray-floret, abaxial side, $\times 6$. – F: Disc-floret, $\times 6$. – G: Corolla of disc-floret laid out, $\times 6$. – H: Achene of disc-floret, abaxial side, $\times 12.5$. – I: Style of disc-floret, $\times 12.5$. – J: Anthers, $\times 12.5$. – K: Filament collar, $\times 100$. – L: Corolla gland, $\times 100$. – Herb. Thunberg 20183, Typus.

Cymbopappus B. Nord., gen. nov.

Typus: *C. lasiopus* (Hutch.) B. Nord.

Frutices erecti glabrescentes–subglabri aut *caudex subterraneus* lignosus caules lanatos glandulosos edens. *Folia* alterna anguste integra vel lobata–pinnatipartita subteretia–complanata herbacea–coriacea pubescentia–glabrescentia impressa glandulosa. *Pedunculi* terminales monocephali breves aut longi. *Capitula* heterogama, flosculis marginalibus femineis ligulatis fertilibus, flosculis disci hermaphroditis fertilibus.

Involucri bracteae imbricatae ovatae–lanceolatae vel oblongae–spathulatae coriaceae glandulosae pubescentes–glabrescentes, margine et apice membranaceae. *Receptaculum* convexum nudum. *Flosculi* radii 9–21 albi vel erubescens, tubo leviter complanato glanduloso, lamina 4(–5)-nervia subtus glandulosa. *Flosculi disci* numerosi, corolla lutea subtubulosa, tubo paulum spongioso glanduloso, limbo angusto quinquelobato. *Achaenia* oblonga exalata costata plerumque quinquenervia glandulosa, madefacta plus minusve mucosa. *Pappus* oblique cyathiformis.

Erect much-branched shrubs, or caudex subterranean, lignified, emitting herbaceous or suffruticose aerial stems; woolly or glabrescent or nearly glabrous. *Leaves* alternate, closely set, linear-filiform, entire or lobed-pinnatifid, sometimes with additional lobes from the leaf-base ("pseudostipules"), subterete-flattened, herbaceous-coriaceous, pubescent-glabrescent, with impressed glands in hollows or furrows, apically obtuse, mucronate or acuminate. *Peduncles* terminal, solitary, monocephalous, nude, but sometimes very short.

Capitula heterogamous, radiate. Involucre hemispherical-cup-shaped. *Involucral bracts* imbricated, ovate-oblong-lanceolate or spatulate, coriaceous with brownish membranous margins and tips, glandular and floccose-woolly or glabrescent. *Receptacle* convex-hemispherical or subconical, nude.

Ray-florets 9-21, fertile, white-pinkish. Tube somewhat compressed, glandular. Lamina 4(-5)-veined, with upper surface colliculate and lower surface smooth and laxly glandular, apically 3-fid. Style branches oblong, truncate. *Achenes* oblong, terete or angular, usually 5-ribbed and 5-veined (sometimes with vestigial additional veins), glandular with broad sessile glands, with myxogenic cell layers especially abaxially. *Pappus* obliquely cup-shaped, abaxially emarginate, white, scarious, opaque.

Disc-florets numerous, yellow. Corolla \pm actinomorphic with a somewhat spongy glandular tube and a narrow 5-lobed limb. *Anthers* with ovate-oblong obtuse-subtruncate apical appendage. Endothelial cells elongate with numerous thickenings on vertical walls. Anther base obtuse. Filament collar oblong, of subequal cells. Style fertile with truncate branches; base not much swollen, partly immersed in the short and sometimes indistinct nectary. *Achenes* and pappus as in ray-florets, but pappus often shorter.

Corolla glands large, sessile, consisting of one broad cell and a double foot-cell.

Pollen grains isopolar, radially symmetrical, spheroidal to oblate-spheroidal, tectate, crassisexinous, 3-colporate. Infratectal bacula very distinct.

Species 3, Cape Province, Transkei and Transvaal.

1. *Cymbopappus lasiopodus* (Hutch.) B. Nord., comb. nov.

Chrysanthemum lasiopodum Hutchinson 1936 p. 84. - Orig. coll.: Schlechter 3846, Transvaal, Lydenburg Div., in cliv. mont. Elandspruitbergen, 7600 ft, 3.XII. 1893 (K holotype).

Illustr.: Fig. 7. - Map 3.

Caudex subterranean, woody, \pm rounded or oblong, 1-3 cm in diam., crowned with greyish-brown dense wool. *Stems* erect, herbaceous or suffrutescent, up to 40 cm high, monopodial with several suberect lateral branches, ca 2 mm thick, distinctly ribbed-striate, laxly woolly and glandular with sessile rounded light-yellow glands. *Leaves* alternate, closely set, imbricated on young shoots, suberect and somewhat incurved, pinnatifid with 2-5 pairs of lobes and some additional \pm reflexed or recurved lobes from the leaf-base, 0.5-1.5 cm long, sparsely setose or subglabrous, distinctly gland-dotted; rachis 0.5-1 mm broad, distinctly midribbed basally on the abaxial side; leaf lobes filiform-subulate, 1-4 mm long, 0.2-0.5 mm thick, acuminate-mucronate with elongated thin tips. *Peduncles* terminal, solitary, simple, (5-)10-20 cm long, laxly leafy in the lower part, otherwise nude, ribbed-striate, laxly woolly and glandular.

Involucre broadly and shallowly cup-shaped, ca 1.5 cm wide. *Involucral bracts* imbricated, ca 20-30, lanceolate-oblong, coriaceous with brown membranous margins and tips, glabrous or subglabrous with scattered wool hairs, gland-dotted, obtuse; outer bracts ca 3-4 mm long and 1 mm wide, inner bracts ca 6-8 mm long and 3-4 mm wide. *Receptacle* convex, nude.

Ray-florets ca 13, white. Tube 1-1.5 mm long, glandular. Lamina 7-10 mm long, 1.5-2 mm wide, narrowly oblong, 4-veined, with a papillate upper surface and smooth lower surface, 3-toothed at the apex. Style branches ca 0.4 mm long, truncate. *Achene* narrowly oblong, subterete, glabrous, apically glandular, 5-ribbed. *Pappus* obliquely cupshaped, 1-2.5 mm long, much emarginate abaxially, truncate, opaque, white.

Disc-florets yellow. Corolla 2.5-3 mm long. Tube 0.8-1.2 mm long, glandular with scattered, broadly oblong-rounded glands. Limb narrowly campanulate, 1.5-1.8 mm long; lobes narrowly triangular-ovate, 0.5-0.7 mm long, papillate

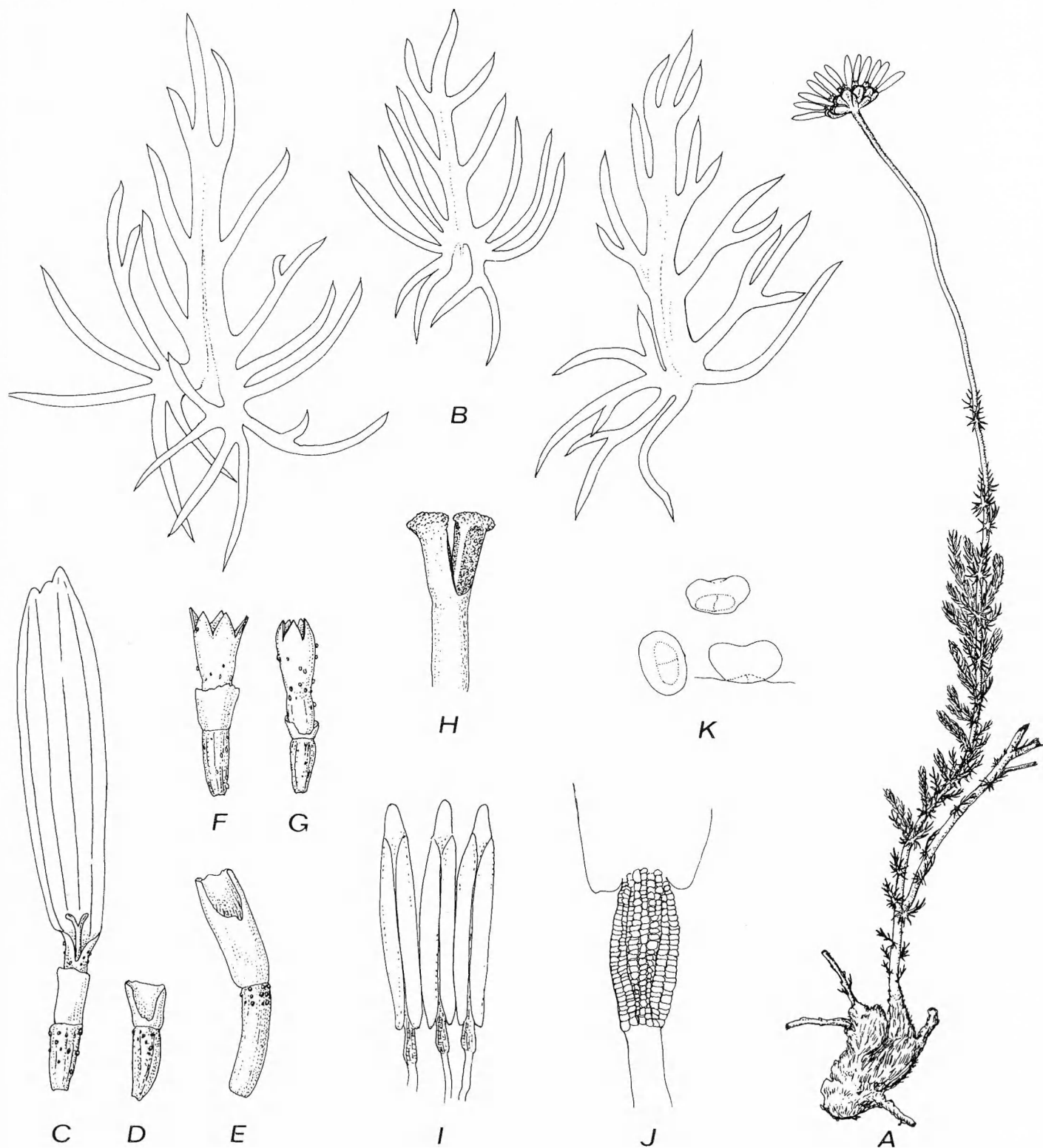


Fig. 7. *Cymbopappus lasiopodus*. - A: Habit, $\times 0.5$. - B: Leaves, $\times 6$. - C: Ray-floret, $\times 6$. - D, E: Ray-floret achenes, abaxial side, $\times 6$. - F: Disc-floret, adaxial side, $\times 6$. - G: Disc-floret, abaxial side, $\times 6$. - H: Style branches from disc-floret, $\times 25$. - I: Anthers, $\times 25$. - J: Filament collar, $\times 100$. - K: Floral glands, $\times 100$. - A, C, D, F-K: Codd & De Winter 3285. - B, E: Prosser 1507.

towards the acute and somewhat cucullate apex. *Anthers* 1-1.2 mm long incl. the ovate-oblong obtuse-subtruncate appendage. Endothelial cells elongate with numerous thickenings on vertical walls. Anther base obtuse. Filament

collar distinct, of transversely rectangular \pm uniform cells. Style terete with slightly swollen base, placed on and partly immersed in a broadly oblong nectary; style branches 0.4-0.5 mm long, truncate. *Achene* subterete, 5-ribbed,

narrowly oblong, glabrous, apically glandular. *Pappus* obliquely cupshaped, 0.8–1.5 mm long, truncate, whitish, deeply–completely emarginate on the abaxial side.

Flowering period: October–December.

Transvaal. Lydenburg Div.: Elandspruitbergen, 1893, Schlechter 3846 (K) – 8 miles E of Lydenburg on road to Sabie, 1947, Codd & De Winter 3285 (K) – 12 miles E of Lydenburg, 1952, Codd 7600 (K) – 19 miles W of Lydenburg, 1953, Codd 8046 (K, L) – *Belfast Div.*: Near Belfast, near railway line, 1950, Prosser 1507 (K).

C. lasiopodus has the characteristic “pyrophytic” lifeform of many grassland species, viz. a subterranean lignified caudex, from which new shoots easily generate especially after fires. In habit, ecology and distribution the species is strikingly different from *C. adenosolen*, which is a shrublet from southern Cape, and from the densely shrubby *C. hilliardiae*, which inhabits rocky mountain slopes of the Transkei.

The tendency in the genus to develop “pseudo-stipules” is most pronounced in *C. lasiopodus*, the leaves of which are provided with several more or less reflexed lobes from the base.

The species is confined to mountain grassland (“sourveld”) in a small area around Lydenburg in the eastern Transvaal.

2. *Cymbopappus hilliardiae* B. Nord., sp. nov.

Orig. coll.: Hilliard & Burt 7289, Transkei, Mt. Ayliff Div., Mt. Insiswa, 17.XI. 1973 (E holotype).

Illustr.: Fig. 8. – Map 3.

Frutex erectus ramosus, rami floccoso-lanati dense foliati, vetusti nudi cinerei cicatricosi. *Folia* alterna ± patentia filiformia usque ad 4 cm longa plerumque supra medium trisecta, aliquot integra vel pinnatipartita, parce lanata apice obtusa, basi dilatata triangulari nodosa post defoliationem persistente. *Pedunculi* erecti parce lanati glandulosi subnudi, foliis basalibus paucis simplicibus instructi. *Involucrum* late campanulatum; involucri bracteae c. 30–35 imbricatae glandulosae parce lanatae glabrescentes lanceolatae-oblongae-spathulatae carinatae, apice appendice membranacea hyalina-brunneola ornatae, intimae minores submembranaceae. *Flores radii* 13–21 albi vel erubescens, lamina elliptico-oblonga usque ad 8 mm longa et 4 mm lata 4(–5)-nervia, apice tridentata, subtus sparsim glandulosa. *Flores disci* numerosi; corolla lutea, apice saepe rubella, glandulosa, superne anguste campanulata, lobis deltoideis. *Achaenia* ± oblonga costata exalata glandulosa, facie abaxiale madefacta

paulum mucosa. *Pappus* oblique cyathiformis scariosus albus.

Dense rounded erect shrubs, repeatedly branching in a somewhat di- to polychotomous fashion; young branches floccose-woolly, densely leafy, becoming nude with age and marked with persistent leaf-bases. *Leaves* alternate, closely set, ± spreading, filiform, 2–4 cm long, ca 0.5 mm wide, mostly trisect above the middle, often some simple or pinnatipartite, laxly woolly and somewhat glabrescent, impressed-glandular, apically obtuse; leaf-base slightly dilated and almost half-clasping, with a central hunch, persistent as a triangular scale after abscission of the leaf. *Peduncles* terminal, solitary, nude, except for a few scattered simple basal leaves, 5–15 cm long, ca 1 mm thick, ribbed, laxly woolly and glandular.

Involucre widely campanulate, 0.8–1.2 cm in diam. *Involucral bracts* ca 30–35, imbricated in about 3–4 series, glandular, laxly floccose-woolly and ± glabrescent; outer bracts narrowly oblong-lanceolate, 2–4 mm long and 0.5–1.2 mm wide, keeled and coriaceous in the middle; margins thinner, membranous, colourless or brownish; tips membranous, short, truncate or premorse; inner bracts oblong-spathulate, 5–6 mm long, 1.5–2 mm wide, coriaceous and keeled in the middle, with thin, often brownish margins and a somewhat dilated, membranous, light brownish or silvery, apical appendage, 2–3 mm long and wide; innermost bracts smaller, narrowly oblong-spathulate, 3–4 mm long, ca 0.5 mm wide basally, widening to 1–1.5 mm wide apically, submembranous with membranous tips. *Receptacle* convex, nude.

Ray-florets 13–21, white–pinkish. Tube 1–1.5 mm long, slightly compressed. Lamina elliptic-oblong, 7–8 mm long, 2.5–4 mm wide, 4(–5)-veined; upper surface densely colliculate; lower surface smooth, sparsely glandular; apex 3-fid. Style branches ca 0.5 mm long, truncate-emarginate; nectary short and indistinct. *Staminodes* usually present. *Achenes* ± oblong, ribbed, glandular, with mucilaginous cell layers (when soaked) especially on the abaxial side. *Pappus* cup-shaped, 1.5–2 mm long, white, opaque, apically premorse-truncate, abaxially emarginate (0.5–1 mm long).

Disc-florets numerous (up to 200–300), yellow with often reddish tips. Corolla 2.5–3 mm long,

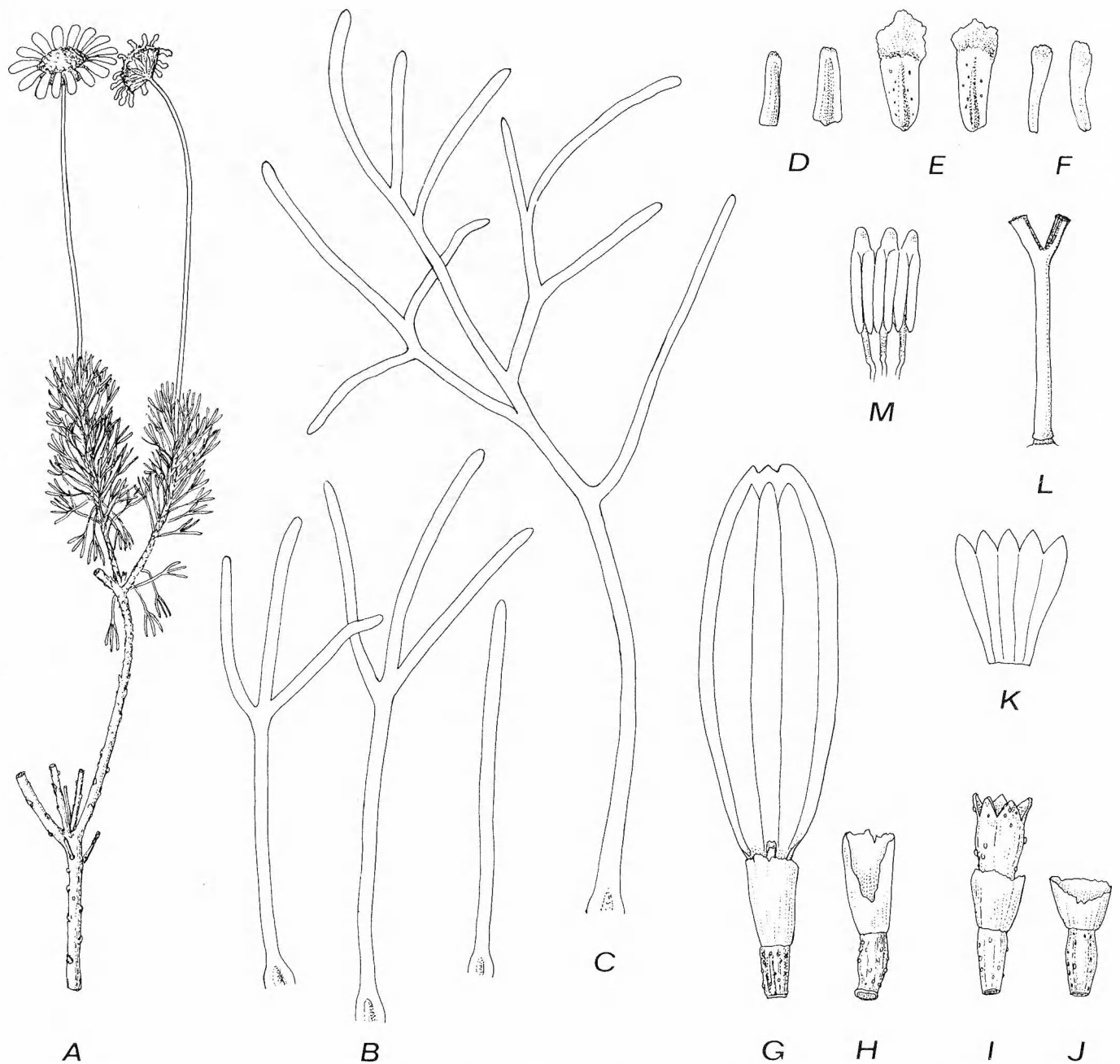


Fig. 8. *Cymbopappus hilliardiae*. - A: Portion of plant, $\times 0.5$. - B: Leaves, $\times 3$. - C: Exceptionally much-lobed leaf, $\times 3$. - D: Outer; E: inner; and F: innermost involucral bracts, $\times 3$. - G: Ray-floret, $\times 6$. - H: Ray-floret achene, abaxial side, $\times 6$. - I: Disc-floret, $\times 6$. - J: Disc-floret achene, abaxial side, $\times 6$. - K: Corolla of disc-floret laid out, $\times 6$. - L: Style of disc-floret, $\times 12.5$. - M: Anthers, $\times 12.5$. - A: Hilliard & Burt 7289. - B, D-M: Hilliard & Burt 6540. - C: Schlechter 6458.

glandular. Tube ca $\frac{1}{2}$ corolla length, subcylindrical or subangular, somewhat spongy. Limb narrowly campanulate, not much thicker than the tube; lobes deltoid, ca 0.5 mm long. *Anthers* 1-1.2 mm long incl. the broadly ovate-oblong, obtuse-subtruncate, somewhat keeled apical appendage; anther base obtuse; filament collar uniformly thick, of \pm equal subquadratic cells. Style branches 0.4-0.5 mm long, truncate. *Achenes* as in ray-florets, but pappus shorter,

0.6-1.5 mm long, abaxially somewhat emarginate.

Pollen grains spheroidal to oblate-spheroidal, ca $28 \times 30 \mu$ (incl. spinules). Exine at equator (centre of mesocolpia) ca 7μ , at poles ca 5μ thick. Sexine (incl. spinules) ca 5μ thick. Supratectal spinules finely pointed with solid tips, ca 2μ long, spaced approximately 5μ from each other. Their total number in one pollen grain 30-35 (ca 12 spinules in one mesocolpium).

Tectum continuous, undulated, slightly less than $1\ \mu$ thick, with minute intratectal bacula, distinct in optical cross-section. Infratectal bacula well developed, $1\text{--}2\ \mu$ long, usually branched distally. Nexine compact, uniform in thickness, ca $1\ \mu$ thick. Colpi with acute ends, ca $15 \times 3\ \mu$. Ora lalongate, ca $3 \times 8\ \mu$.

Flowering period: November–February.

Transkei. Mt. Ayliff Div.: Mt Insiswa, 6500 ft, 1895, Schlechter 6458 (E fragment, L); 4800 ft, 1971, Hilliard & Burt 6540 (E); 1973, Hilliard & Burt 7289 (E).

I have pleasure in naming this new species for Mrs Olive Hilliard, eminent South African botanist and especially synantherologist. Jointly with Mr B. L. Burt she has collected the species twice.

The leaves of *C. hilliardiae* are narrow and densely set and, especially when young, greyish from the somewhat deciduous tomentum. Most leaves are tripartite above the middle, but simple as well as more lobed leaves occur on the same specimens. The impressed glands on the leaves are sometimes barely discernible, being hidden in furrows and wrinkles of the leaf surface.

The single locality so far known is a mountain in the northern Transkei, where the plants form rounded shrubs on rocky slopes together with *Proteas* and other shrubby growth.

3. *Cymbopappus adenosolen* (Harv.) B. Nord., comb. nov.

Marasmodes adenosolen Harvey 1865 p. 175. – Orig. coll.: Ecklon & Zeyher, Caledon Div., mts. at Caledon and Genadendal (S holotype).

Chrysanthemum carnosulum auct. non DC.; De Candolle 1837 p. 65, quoad descr. et specim. cit., non quoad syn.; Harvey 1865 p. 162; Hutchinson 1917 p. 117.

C. carnosulum DC. var. *filifolium* Harvey 1865 p. 163; Hutchinson 1917 p. 117. – Orig. coll.: Pappe, Swellendam (TCD lectotype fide Hutchinson l.c., non vidi; K, S isotypes).

Illustr.: Fig. 9. – Map 3.

Nomenclatural note. The nomenclatural history of this species is somewhat entangled. It is commonly known under the name *Chrysanthemum carnosulum*, but it appears that this epithet cannot be used. The species, let us call it A, was first collected by Thunberg, who confused it with another species, B, and misapplied the Linnaean name *Chrysanthemum frutescens* on this mixture. Lessing (1831) described species B as *Pinardia frutescens* Less. and soon

afterwards transferred it to *Ismelia* (Lessing 1832). Up to now it has been known as *Chrysanthemum thunbergii* Harv., but is in the present paper named *Scyphopappus frutescens* (cf. above). Species A remained unnamed for some time, although it was found by several of the early collectors, viz. Burchell, Drège, Ecklon & Zeyher. De Candolle had thus ample material, which he named *Chrysanthemum carnosulum* DC. (1837). His description and specimens leave no doubt that species A is intended, but he incorrectly identified it with Lessing's *Pinardia frutescens*. Had the latter epithet not been preoccupied in *Chrysanthemum*, De Candolle would certainly have used it. Instead he introduced the new name *carnosulum*, which becomes a nomenclatural synonym of *Pinardia frutescens* Less. Under *Chrysanthemum* it would be the correct name for species B, but it now goes into the synonymy of *Scyphopappus frutescens*.

An available epithet for species A was found from a quite unexpected source, viz. the genus *Marasmodes*. When describing *M. adenosolen* Harvey (1865) misinterpreted the pappus as consisting of five separate scales and the capitula as being homogamous. By careful examination of the single flower-head of the type specimen I could establish the presence of ray-florets as well as a coroniform, though sometimes deeply lobed pappus. The specimen agrees well with slender-leaved forms of species A, named *C. carnosulum* var. *filifolium*. For example, Schlechter 7591 is a perfect match of the type of *M. adenosolen* and originates from the same area in Caledon Division. The coroniform pappus of *C. adenosolen* is often lobed and in extreme cases may appear to consist of 3–5 discrete scales.

The species hitherto known as *M. adenosolen* (e.g. Schlechter 7899 from Piketberg, cited in Hutchinson 1916) is a true member of *Marasmodes* and obviously requires a new name. This matter will be dealt with in a forthcoming paper.

A glabrous or glabrescent, much-branched, sometimes almost divaricate, erect shrub, 2–6 dm high, with a woody taproot; branches ribbed-striate, often laxly puberulous when young; old stems up to 5 mm thick and strongly woody, nude, ash-grey. *Leaves* closely set on the upper branches, alternate, erecto-patent–spreading, 3–20(–30) mm long, linear–filiform, 3–5-lobed above the middle with often spreading or recurved tips, or some or all entire; rachis and lobes 0.5–1 mm wide, somewhat flattened or subterete, punctate with impressed glands, obtuse and mucronate; leaf-base often with short lateral lobes.

Capitula sessile or shortly pedunculate, solitary, often somewhat nodding. *Involucre* shallowly cup-shaped–broadly campanulate, 5–10 mm wide. *Involucral bracts* ca 15–22, imbricated, lanceolate–ovate–oblong, subcoria-

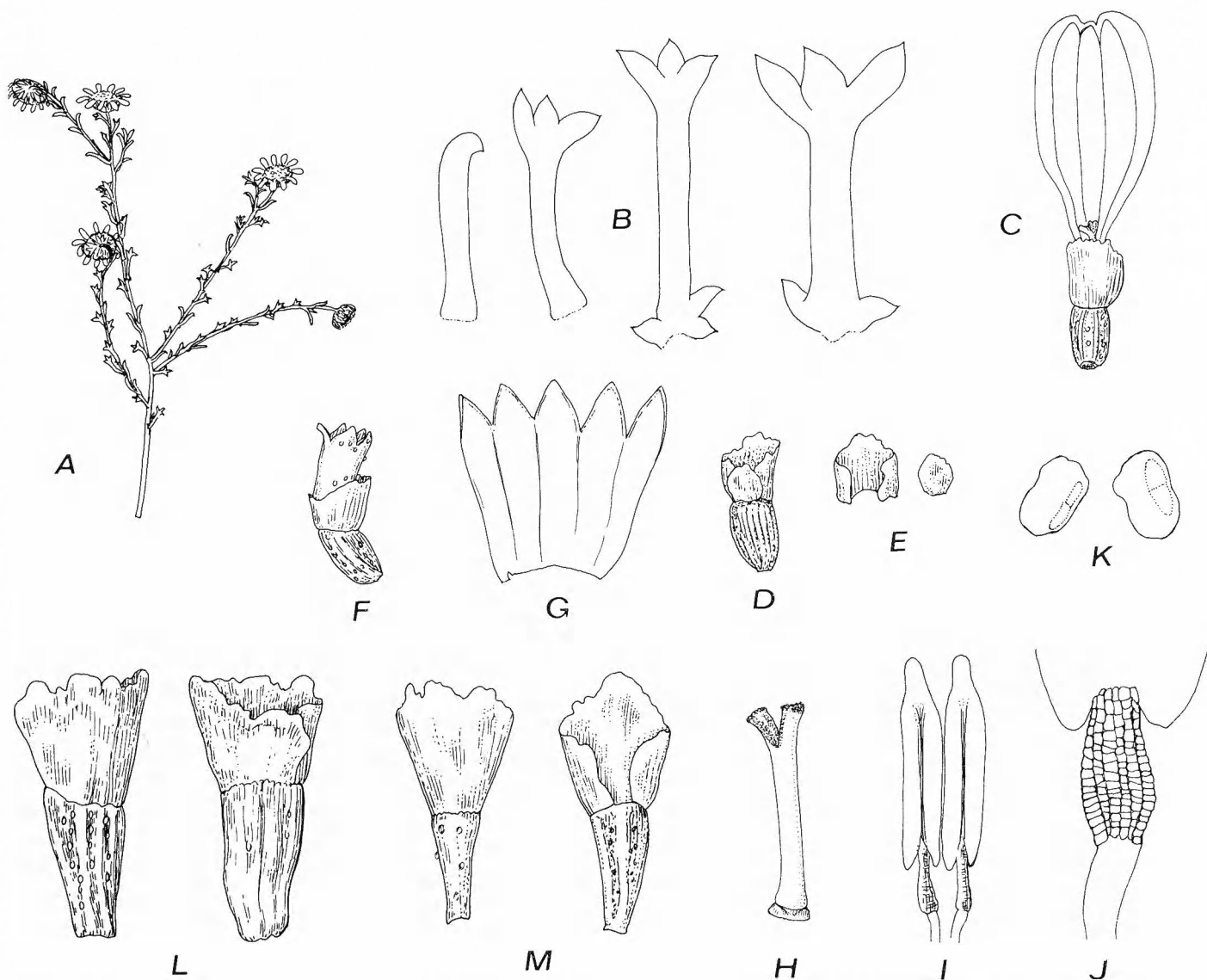


Fig. 9. *Cymbopappus adenosolen*. - A: Portion of plant, $\times 0.5$. - B: Leaves, $\times 6$. - C: Ray-floret, $\times 6$. - D: Ray-floret achene (with an extra abaxial pappus scale), abaxial side, $\times 6$. - E: Pappus scales from ray-floret, $\times 6$. - F: Disc-floret, lateral view, $\times 6$. - G: Corolla of disc-floret laid out, $\times 12.5$. - H: Style of disc-floret, $\times 12.5$. - I: Anthers, $\times 25$. - J: Filament collar, $\times 100$. - K: Floral glands, $\times 100$. - L: Ray-floret achene, adaxial side (left) and abaxial side (right), $\times 12.5$. - M: Disc-floret achene, adaxial side (left) and abaxial side (right), $\times 12.5$. - A, B: Schlechter 1793. - C-M: Schlechter 10539.

ceous with membranous, somewhat glossy, whitish-pinkish margins and tips, with rounded-convex or almost keeled back and obtuse tip; inner bracts up to 4-6 mm long and 2-3 mm wide, outer smaller. *Receptacle* obtusely conical-hemispherical, glabrous, somewhat tuberculate.

Ray-florets 9-13, white. Tube somewhat compressed, elliptic-oblong, 0.5-1 mm long and wide, glandular. Lamina \pm oblong, 3-6 mm long, 1.5-3 mm wide, 4(-5)-veined, \pm reflexed after anthesis, marginal veins often with one lateral branch each, apex 2-3-toothed or -lobed, upper

side colliculate, lower side smooth and sparsely glandular. Style terete with little swollen base; nectary short, indistinct; style branches 0.3-0.4 mm long, truncate.

Disc hemispherical with ca 70-100 florets. Corolla tubular, yellow with sometimes purplish tips, 1.5-2.5 mm long. Tube thickish and spongy, ca 1 mm long. Limb narrow, not distinctly campanulate; lobes triangular-ovate, 0.3-0.6 mm long. *Anthers* 0.8-1.2 mm long incl. the oblong subtruncate appendage. Endothelial cells elongate, with numerous thickenings on vertical walls. Filament collar distinct, of \pm uniform,

broadly rectangular-subquadratic cells. Style branches 0.2–0.4 mm long, truncate; nectary short and sometimes indistinct.

Achenes 0.7–1 mm long, oblong, subquadrangular, 5-ribbed, glandular with broad sessile glands, abaxial side flattish and faintly striate with a myxogenic cell layer. *Pappus* obliquely cup-shaped, scarious, white, 0.5–1.2 mm long, \pm truncate or premorse, abaxially deeply or sometimes completely emarginate, occasionally deeply 3–5-lobed, rarely with an additional small adaxial scale (in ray-florets).

Pollen grains spheroidal, diameter ca 22 μ (incl. spinules). Exine at equator ca 8 μ thick. Supratectal spinules totally ca 36–40. Exine otherwise as in *C. hilliardiae*. Colpi with acuminate ends, ca 13 \times 3 μ . Ora alongate, ca 2 \times 4 μ .

Flowering period: September–January, April, July.

Cape Province. Ceres Div.: Koude Bokkeveld, Klyn Vley, 1897, Schlechter 10216 (G, K, L, S) – *Caledon Div.*: Mts. at Caledon and Genadendal, Ecklon & Zeyher, 81. (S) – Near Caledon Springs, 1892, Bolus 7464 (K) – Bot River, 1896, Schlechter 7591 (G, K) – Hillside in front of Caledon Hospital, 1933, Herb. Bolus. 20542 leg. L. Bolus (K) – *Bredasdorp Div.*: Zeekoevley, 1897, Schlechter 10539 (G, K, L, S) – Bredasdorp, 1931, Galpin 11236 (K) – Between Struis Bay and Bredasdorp, 1931, Levyns 3090 (K) – Near Bredasdorp, 1933, Herb. Bolus. 20543 leg. L. Bolus (K) – 6 miles N of Struis Bay, 1933, Salter 4147 (K) – *Swellendam Div.*: Between Swellendam and Breede River, 1815, Burchell 7450 (K) – Near Breede River, 1815, Burchell 7461 (K) – Swellendam, Pappe (S, sub nom. *Adenachaena leptophylla*) – Rietcuyl, Ecklon (S) – Between Rietkuil and Buffeljagdsrivier, Zeyher 2831 (S) – Between Rietkuil and Hemelen-Aarde, on the Kenko River, Zeyher 2831 (K) – “Swellendam and Georg”, Ecklon & Zeyher, 91., leg. Mundt (G-DC) – “Swellendam” (prob. at Karmelksrivier), Drège 5953 (G-DC) – 7 miles N of Storms Vlei, 1933, Salter 3105 (K) – Between Storms Vlei and Swellendam, 1937, Wall (S, sub nom. *Phymaspermum leptophyllum* and mixed with *Pentzia* sp.) – Ca 36 miles NNE of Bredasdorp, 1948, Acocks 14588 (K, LD) – *Riversdale Div.*: Near Zoetemelks River, 1814, Burchell 6741 (K) – Between Great Valsch River and Zoetemelks River, 1814, Burchell 6578 (G-DC, K) – Gouritz River, Pappe (K) – Near Riversdale, 1892, Schlechter 1793 (G, K, S) – Gouritzriver, 1894, Penther 1163 (S, sub nom. *Phymaspermum leptophyllum*).

Cymbopappus adenosolen differs from its congeners by the absence of a distinct pedunculoid portion on the flowering branches. Thus the capitula appear sessile or nearly so.

There is much variation in leaf-shape within the species, from lobed and short leaves (less than 1 cm long) to simple and filiform leaves (more than 2 cm long). The latter types have been distinguished as var. *filifolium*, but I could find no discontinuity in this variation or correlation with other characters. The variation in pappus is discussed above under Nomenclatural note.

Apart from an outlying locality in the Cold Bokkeveld, *C. adenosolen* is restricted to the southern Cape, ranging from Caledon eastwards to the Gouritz River. Although this region is known as the most extensive limestone area of the Cape, this species seems to have no special preference for such a substrate. It probably grows in mainly arid vegetation types like rhenosterveld. The shrubs have a somewhat karroid appearance, resembling e.g. shrubby species of *Pentzia*, and in herbaria they are sometimes also confused with *Phymaspermum leptophyllum* (DC.) Bth.

Adenanthemum B. Nord., gen. nov.

Typus: *A. osmitoides* (Harv.) B. Nord.

Caudex subterraneus lignosus sericeo-villosus caules herbaceos setosos edens. *Folia* alterna sessilia plana herbacea lanceolata-ovata-elliptica pubescentia vel glabrescentia margine serrata. *Capitula* terminalia solitaria vel laxe corymbosa heterogama, flosculis marginalibus femineis fertilibus ligulatis, flosculis disci hermaphroditis fertilibus. *Involucri bractearum* imbricatae lanceolatae-anguste obovatae herbaceae acutae, margine et apice membranaceae. *Receptaculum* leviter convexum nudum. *Flosculi radii* numerosi; corolla sine tubo distincto, lamina alba multinervia subtus glandulosa apice bifida vel subintegra. *Achaenia radii* oblonga subcomplanata glandulosa 10-costata, nervis 10 et item canalibus resiniferis 10. *Pappus* nullus. *Flosculi disci* numerosi, corolla tubulosa actinomorpha quinquelobata glandulosa. *Achaenia disci* epapposa, radii similia sed minus complanata subteretia.

Caudex subterranean, woody, with dense hair tufts, emitting herbaceous simple or little-branched stems; stems and branches \pm setose. *Leaves* alternate, sessile, lanceolate-ovate-elliptic, flat, herbaceous, midveined, pubescent-glabrescent, with serrate margins.

Capitula heterogamous, radiate, terminal, solitary or laxly corymbose on more or less distinctly pedunculoid branch ends. Involucre broadly campanulate. *Involucral bracts* imbric-

cated, lanceolate-oblong-narrowly obovate, herbaceous, acute, with membranous margins and tips. *Receptacle* somewhat convex, nude.

Ray-florets numerous, fertile, white, without a distinct tube; lamina many-veined, apically bifid or subentire, with a densely colliculate upper surface and a glandular smooth lower surface. *Achenes* oblong, somewhat compressed, with 10 ribs, 10 veins and 10 associated resin canals, glandular, without myxogenic cell layers. *Pappus* 0.

Disc-florets numerous, yellow. Corolla tubular, \pm actinomorphic, 5-lobed, glandular. *Anthers* with a broadly ovate-oblong obtuse-rounded appendage. Endothelial cells with numerous thickenings on vertical walls. Anther base obtuse, ecaudate. Filament collar oblong, of subequal cells. Style fertile with truncate branches, style base swollen, placed on top of and partly immersed in a short and broad nectary. *Achenes* similar to those of the ray-florets, but less compressed. *Pappus* 0.

Corolla glands sessile, consisting of one large broad cell on a double foot-cell.

Pollen grains apolar, spheroidal, tectate, crassisexinous, 6-panto-colporate.

Species 1, Transvaal, Natal, Swaziland.

1. *Adenanthemum osmitoides* (Harv.) B. Nord., comb. nov.

Chrysanthemum osmitoides Harvey 1863 p. 33; Harvey 1865 p. 163; Hutchinson 1917 p. 117. - Orig. coll.: Gerrard 1026, Natal, Omgati (TCD holotype, non vidi; K isotype).

Illustr.: Harvey 1863 Plate 152; Fig. 10. - Map 1.

Subterranean caudex rounded-oblong, ca 1-2 cm thick, apically with dense silky-villous brown tufts. *Stems* erect, simple or little-branched, 25-60 cm long, up to 3-5 mm thick basally, apically narrower (1-2 mm wide below the capitulum) and subpedunculoid with reduced leaves, ribbed-sulcate, densely to sparsely setose with long appressed or patent thick-based hairs (apical thin portion often falling off). *Leaves* scattered-subimbricate, suberect-erecto-patent, lanceolate-narrowly ovate or elliptic-ovate-elliptic, 1-4(-5) cm long, 0.2-1.5 cm wide, green, ciliate-setose or glabrescent, midveined and with a faint reticulate venation, sharply serrate; teeth 2-9 on each side, up to 5 mm long and

2 mm wide, acuminate-mucronate; uppermost leaves smaller, often entire, acuminate.

Involucre 1.5-2 cm wide. *Involucral bracts* ca 30-40, imbricated in 3-4 series, obscurely midveined, green with brownish tips, herbaceous, glabrous; outer bracts ovate-lanceolate, 5-7 mm long and 1-2 mm wide, acute-acuminate, with or without narrow membranous margins and tips; inner bracts narrowly oblong-obovate or subspathulate, 7-10 mm long and 2-4 mm wide, acute, with membranous, somewhat fringed or lacerate margins and tips.

Ray-florets ca 16-25 (often 21), white or creamy white. Corolla continuous with the ovary; lamina narrowly oblong-obovate, 1-2.5 cm long, 2.5-5 mm wide, many(6-9)-veined with branching marginal veins. Style base not much swollen; nectary indistinct; style branches oblong, truncate, ca 0.5 mm long. *Achenes* compressed, 3-4 mm long, ca 1.5 mm wide.

Disc-florets ca 250. Corolla tubular without a distinct campanulate upper portion, 2.5-4 mm long; lobes deltoid-ovate, 0.5-0.7 mm long, apically subcucullate. *Anthers* 1.3-2 mm long incl. appendage. Style branches 0.3-0.4 mm long. *Achenes* oblong, somewhat compressed or subquadrangular, ca 2-3 mm long and 1 mm wide, sparsely glandular, 10-ribbed.

Pollen grains ca 45 μ (incl. spinules). Exine at centre of the area between the apertures ca 10 μ thick. Sexine 8-9 μ thick (incl. spinules). Supratectal spinules finely pointed with solid tips, 3-4 μ long, spaced approximately 6 μ from each other. Their total number in one pollen grain 55-65 (14-16 in one exine area encompassed by the colpi). Tectum continuous, undulated, slightly less than 1 μ thick, with minute intratectal bacula distinct in optical cross-section. Infratectal bacula very distinct, 1-2 μ long, branched distally. Nexine compact, uniform in thickness, ca 1 μ thick. Colpi with acute ends, 18 \times 5 μ . Ora lalongate, 3 \times 5 μ .

Flowering period: October-February.

Transvaal. Middelburg Div.: Near Middelburg, 1916, Scott Elliot 1531 (E) - *Barberton Div.*: Hills above Barberton, 1889, Medley-Wood 5729 leg. Thorncroft (K) - Saddleback Range, 1889, Galpin 685 (K) - Barberton, Rogers 18216 (G, S p.p., mixed with *Inezia integrifolia*) - Road to Lomati Falls from Barberton, 1929, Hutchinson 2501 (K) - 10 miles SE of Barberton on road to Havelock, 1953, Codd 8170 (K) - *Ermelo Div.*: 9 miles Warburton P. O. on Mbabane road, 1968, Hilliard 4779 (E, K) - *Amersfort Div.*: Wakker-

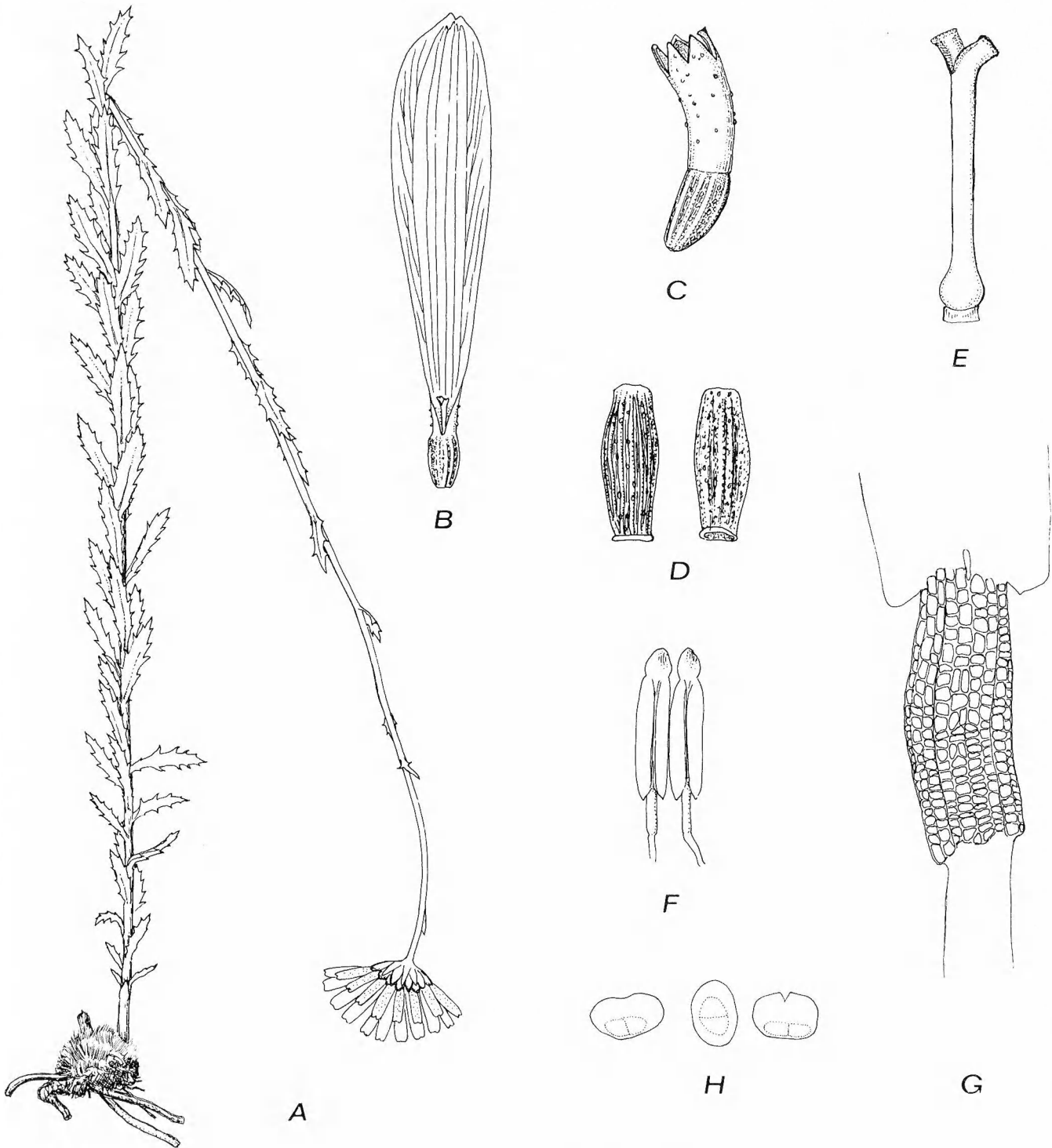


Fig. 10. *Adenanthemum osmitoides*. - A: Habit, $\times 0.5$. - B: Ray-floret, $\times 3$. - C: Disc-floret, $\times 3$. - D: Achene, adaxial side (left) and abaxial side (right), $\times 6$. - E: Style of disc-floret, $\times 12.5$. - F: Anthers, $\times 12.5$. - G: Filament collar, $\times 100$. - H: Floral glands, $\times 100$. - A: Buehrmann 24. - B-H: Sidey 1962.

stroom, Groothoek, 1969, Buehrmann 24 (K) - *Piet Retief Div.*: Iswepe, 1949, Sidey 1962 (S).

Natal. Omgati, Gerrard 1026 (K) - *Utrecht Div.*: 2 miles Kemp's Lust road, off Utrecht-Wakkerstroom road, 1963, Hilliard 2214 (E) - *Vryheid Div.*: 15 miles E of Vryheid on road to Enyati, 1969, Hilliard & Burt 5867 (E) - *Ngotshe Div.*: Ngome, along forest road, 1969, Strey 9427 (K).

Swaziland: Black Mbuluze River Valley, "The

Caves" near Mbabane, 1965, Hilliard 3087 (E) - Mbabane side of the Komati Valley en route to Pigg's Peak, 1966, Hilliard & Burt 3571 (E).

Adenanthemum osmitoides is a characteristic taxon with flat serrate leaves and large capitula with numerous tube-less rays, which are conspicuously gland-dotted below. The life-form is

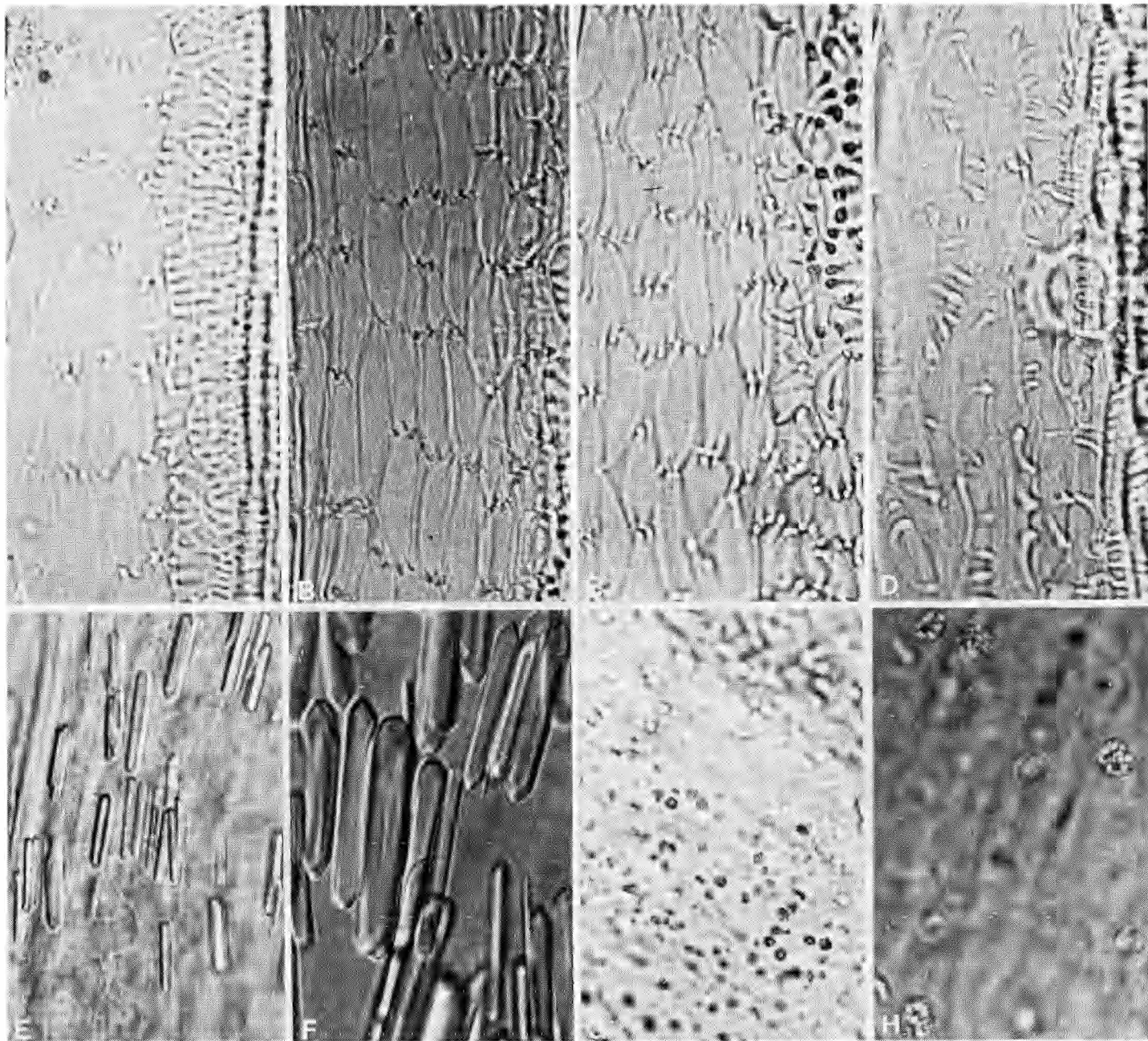


Fig. 11. Endothelial tissue (A–D) and ovary crystals (E–H). – A: Partly polarized tissue of *Adenoglossa decurrens* (N. 1784). – B: Mainly polarized tissue of *Leucoptera nodosa* (Schlechter 8353). – C: Mainly polarized tissue of *L. oppositifolia* (N. & L. 1738). – D: Non-polarized tissue of *Cymbopappus hilliardiae* (Hilliard & Burt 7289). – E, F: Ovary crystals of *Adenoglossa decurrens* (E: N. 1606, F: N. 1784). – G, H: Ovary crystals of *Leucoptera subcarnosa* (G: N. & L. 1418, H: N. 796). – Preparations mounted in Hoyer's solution; F, H \times c. 1200, otherwise \times c. 450. Photomicrographs by the author.

similar to that of *Cymbopappus lasiopodus* and many other grassland species of eastern Transvaal and adjacent areas of Natal and Swaziland.

The species is quite variable in its vegetative parts. The stems are typically erect and simple, but sometimes they are apically branched. The leaves vary considerably in size, especially in width, and in number of teeth. The

pubescence on stems and leaves may be rather dense, but is sometimes almost absent.

Discussion

The new taxonomy presented above is founded on a combination of morphological characters, perhaps with special emphasis on achene and pappus morphology. Supplementary evidence is

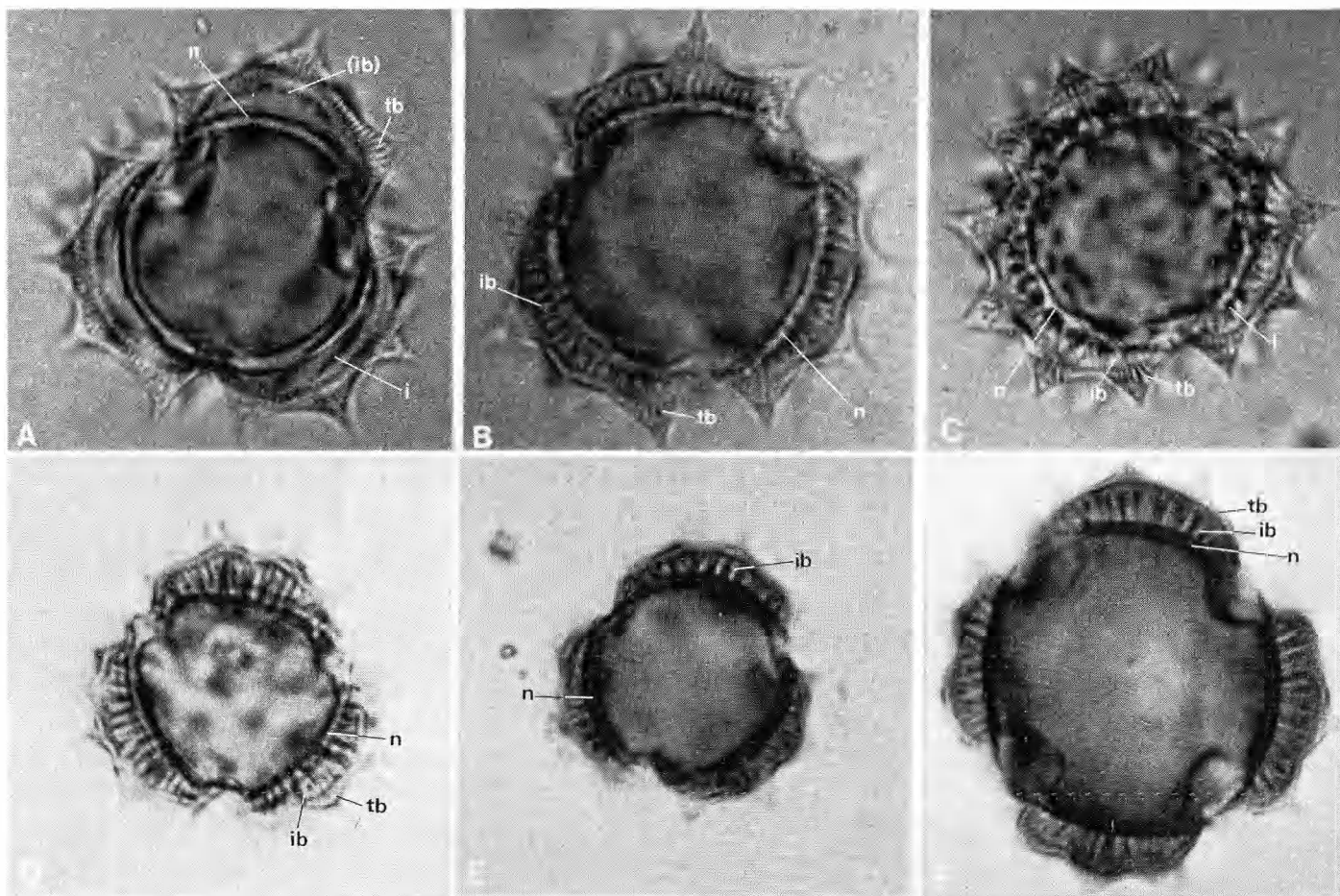


Fig. 12. Acetolysed pollen grains in optical transect. – A–E: 3-colporate pollen grains in polar view. – F: 6-colporate pollen grain, 4 apertures visible. – tb intratectal bacula, ib infratectal bacula, l lacunae in between infratectal bacula, i interspace between sexine and nexine, n nexine. – A: *Adenoglossa decurrens* (N. 1797). – B: *Leucoptera subcarnosa* (N. 2930). – C: *L. oppositifolia* (N. 952). – D: *Scyphopappus frutescens* (Herb. Thunberg no. 20183). – E: *Cymbopappus hilliardiae* (Hilliard & Burt 7289). – F: *Adenanthemum osmitoides* (Sidey 1962). – $\times 1100$ – 1300 . Photomicrographs by the author.

derived from micro-morphological characters of, e.g., anther appendages, endothelial tissue, filament collars, ligule epidermis, floral glands, and pollen grains. The most significant generic characteristics are summarized in Table 1.

The endothelial cells of the anthers are said to form a polarized tissue, when the wall thickenings are restricted to the horizontal walls. If the thickenings are distributed along the vertical walls as well, the tissue is described as non-polarized (cf. Fig. 11). As a rule the endothelial tissue in the Anthemideae is non-polarized, but some cases of polarized tissue have been observed in addition to *Adenoglossa* and *Leucoptera*, e.g. *Ursinia* and *Lasiospermum*. In my opinion the latter two genera are related and clearly belong to this tribe.

The affinities of the new genera are not with the north hemispherical *Chrysanthemum* com-

plex, but rather with various South African genera of the Anthemideae. The numerous representatives of this tribe in the southern hemisphere are still insufficiently studied, however, and the boundaries and affinities of many genera need further investigation. Nevertheless, some suggestions regarding the relationships of the five new genera may be made.

Adenoglossa and *Leucoptera* are no doubt closely allied and may be conceived as sister groups derived from a common ancestor. Both have broad involucre scales, smooth rays, strongly compressed achenes with lateral wings and with similar venation and myxogenic tissue, discrete pappus scales, more or less polarized endothelial tissue, and similar pollen. If the annual *Adenoglossa* was thought to have evolved directly from the shrubby *Leucoptera*, a case could possibly be made for referring them

Table 1. Morphological characteristics of the five new genera.

<i>Adenoglossa</i>	<i>Leucoptera</i>	<i>Scyphopappus</i>	<i>Cymbopappus</i>	<i>Adenanthemum</i>
Annual herb	Shrublets	Shrublets	Shrubs, or caudex woody, subterranean	Caudex woody, subterranean
Leaves narrowly linear, sub- or semi-terete, entire	Leaves linear-filiform, terete-flattened, entire-lobed	Leaves linear, flattened, lobed	Leaves linear-filiform, subterete-flattened, entire-lobed, with impressed glands	Leaves flat, serrate
Peduncles long, nude	Peduncles long, nude	Peduncles long, with a few bractlike leaves	Peduncles long or short, nude or leafy	Peduncles indistinct, leafy
Involucral bracts broad with rounded tips, many-veined	Involucral bracts broad with rounded tips, many-veined	Involucral bracts narrow, indistinctly veined, with conspicuous apical scarious appendage	Involucral bracts narrow, indistinctly veined or keeled, with membranous margins	Involucral bracts \pm ovate-oblong, flat, acute, midveined, with membranous margins
Rays yellow	Rays white-pink	Rays white	Rays white-pink	Rays white-creamy white
Tube of ray-floret distinct	Tube of ray-floret distinct	Tube of ray-floret distinct	Tube of ray-floret distinct	Ray-floret without distinct tube
Ligule usually 4-veined, smooth, eglandular, apically 3-fid	Ligule 4-7-veined, smooth, eglandular, apically 3-fid	Ligule 5-7-veined, colliculate above, eglandular, apically \pm entire	Ligule usually 4-veined, colliculate above, glandular below, apically 3-fid	Ligule many-veined with branching marginal veins, colliculate above, glandular below, apically bifid
Corolla glands multicellular, columnar	Corolla glands multicellular, columnar	Corolla glands multicellular, stipitate	Corolla glands large, unicellular, sessile	Corolla glands large, unicellular, sessile
Disc-floret corolla zygomorphic, campanulate above, with adaxial resin ducts	Disc-floret corolla actinomorphic, campanulate above, without resin ducts	Disc-floret corolla campanulate above	Disc-floret corolla subtubular, with spongy tube	Disc-floret corolla tubular, tube not spongy
Anther appendage with resin gland, obtuse	Anther appendage without resin gland, obtuse	Anther appendage without gland, subacute	Anther appendage without gland, obtuse-subtruncate	Anther appendage without gland, obtuse-rounded
Endothelial tissue partly polarized (Fig. 11 A)	Endothelial tissue mainly polarized (Fig. 11 B, C)	Endothelial tissue non-polarized	Endothelial tissue non-polarized (Fig. 11 D)	Endothelial tissue non-polarized
Filament collar with subequal cells	Filament collar with subequal cells	Filament collar with larger basal cells	Filament collar with subequal cells	Filament collar with subequal cells
Style base on top of a narrower nectary	Style base partly immersed in a broader nectary	Style base partly immersed in a broad short nectary	Style base partly immersed in a short or indistinct nectary	Style base partly immersed in a short nectary
Achenes homomorphic, strongly compressed	Achenes homomorphic, strongly compressed	Achenes heteromorphic, compressed	Achenes homomorphic, not compressed	Achenes subheteromorphic, somewhat compressed
Achenes amply 2-winged with thin wings	Achenes amply 2-winged with thin wings	Achenes 3-winged with firm thickish wings	Achenes not winged	Achenes not winged
Achenes with 3 veins and 2 resin ducts	Achenes with 3 veins and 2 resin ducts	Achenes with ca 5 veins and 5-6 ribs	Achenes with usually 5 veins and 5 ribs	Achenes with 10 veins, 10 resin ducts and 10 ribs
Achenes eglandular	Achenes eglandular	Achenes eglandular	Achenes glandular	Achenes glandular
Achenes with myxogenic tissue	Achenes with myxogenic tissue	Achenes without myxogenic tissue	Achenes with myxogenic tissue	Achenes without myxogenic tissue
Ovary crystals elongate, prismatic (Fig. 11 E, F)	Ovary crystals minute, \pm isodiametric (Fig. 11 G, H)	Ovary crystals minute, \pm isodiametric	Ovary crystals minute, \pm isodiametric	Ovary crystals minute, \pm isodiametric

Table 1 (cont.).

<i>Adenoglossa</i>	<i>Leucoptera</i>	<i>Scyphopappus</i>	<i>Cymbopappus</i>	<i>Adenanthemum</i>
Pappus of 5-6 ab- and adaxial scales	Pappus of 3 adaxial scales	Pappus cup-shaped	Pappus cup-shaped	Pappus 0
Pollen grains isopolar, 3-colporate; infratectal bacula vestigial, sexine \pm separated from nexine (Fig. 12 A)	Pollen grains isopolar, 3-colporate, infratectal bacula well developed, sometimes detached from nexine (Fig. 12 B, C)	Pollen grains isopolar, 3-colporate, conspicuously 3-lobed in polar view; infratectal bacula very distinct (Fig. 12D)	Pollen grains isopolar, 3-colporate; infratectal bacula very distinct (Fig. 12 E)	Pollen grains apolar, 6-panto-colporate; infratectal bacula very distinct (Fig. 12F)

to the same genus. In several respects like life form, floral symmetry, leaf texture, and pollen morphology, *Adenoglossa* certainly appears more advanced than *Leucoptera*, but on the other hand the number and arrangement of the pappus elements rather indicate a more primitive condition. The generic distinction is supported by additional diagnostic features of ray-floret colour, anther glands and ovary crystals. The affinities of *Leucoptera* and *Adenoglossa* are probably with the *Cotula* complex. In the latter we can find broad involucre bracts, similar corolla glands, resin ducts in corollas and achenes, and strongly compressed, few-veined and sometimes winged achenes.

Scyphopappus and *Cymbopappus* have a somewhat similar pappus, but they are in other respects very different. The former is distinguished i.a. by the heteromorphic, three-winged achenes, campanulate disc corollas, stipitate floral glands, and amply appendaged involucre bracts. The latter character recalls species of *Ursinia*, but other facts speak against a near relationship.

Cymbopappus has homomorphic, exalate achenes, subtubular disc corollas with a somewhat spongy tube, involucre bracts without conspicuous appendage, and large sessile floral glands. This type of corolla gland is widely spread in the tribe and occurs also in *Adenanthemum*, and in the much debated genus *Ursinia*. The affinities of *Cymbopappus* may be sought in genera like *Pentzia* and *Marasmodes*. Both of these have homogamous capitula, but otherwise share many characters with *Cymbopappus*. Some species of *Pentzia* are strongly reminiscent of *Cymbopappus* in involucre, receptacle, corolla shape, floral glands, achenes and pappus. The South African species referred to *Matricaria*

present special problems still unsolved. The annual species must be considered in context with *Pentzia*, but two unrelated elements can be excluded, viz. *M. nigellifolia*, which can be treated as a monotypic genus, *Sphaeroclinium* (cf. Mitsouka & Ehrendorfer 1972), and *M. zuurbergensis* (cf. below).

The genus *Adenanthemum*, finally, has some very distinctive features, like the absence of a corolla tube in the rays, the branching venation of the ligules, the absence of a pappus, and the hexa-panto-colporate pollen grains. The pollen type is unique in the tribe and most unusual in the family. The genus may have some affinity to *Inezia*, which is similar in habit, hair types and glands, ray-floret shape and ligule epidermis. Furthermore, the pappus of *Inezia* is much reduced, and the achenes are exalate and ribbed. On the other hand there are significant differences like the ciliate hairs on ray-floret achenes and corollas, and the four-lobed disc-florets of *Inezia*. Another, possibly related taxon is the above-mentioned *Matricaria zuurbergensis*, the taxonomic status of which deserves further attention.

Acknowledgements. My thanks are due to Dr J. Praglowski for valuable advice on palynological matters, and to Dr T. Nyholm, who kindly checked the Latin descriptions.

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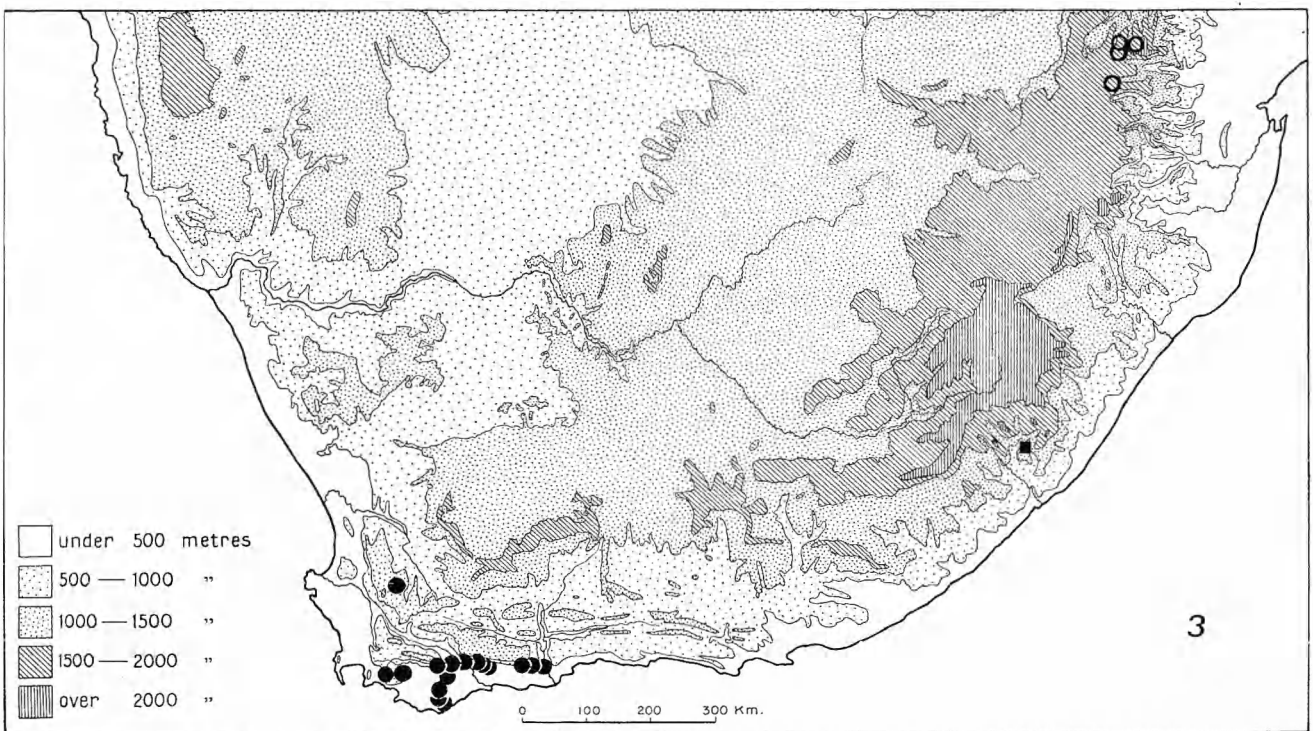
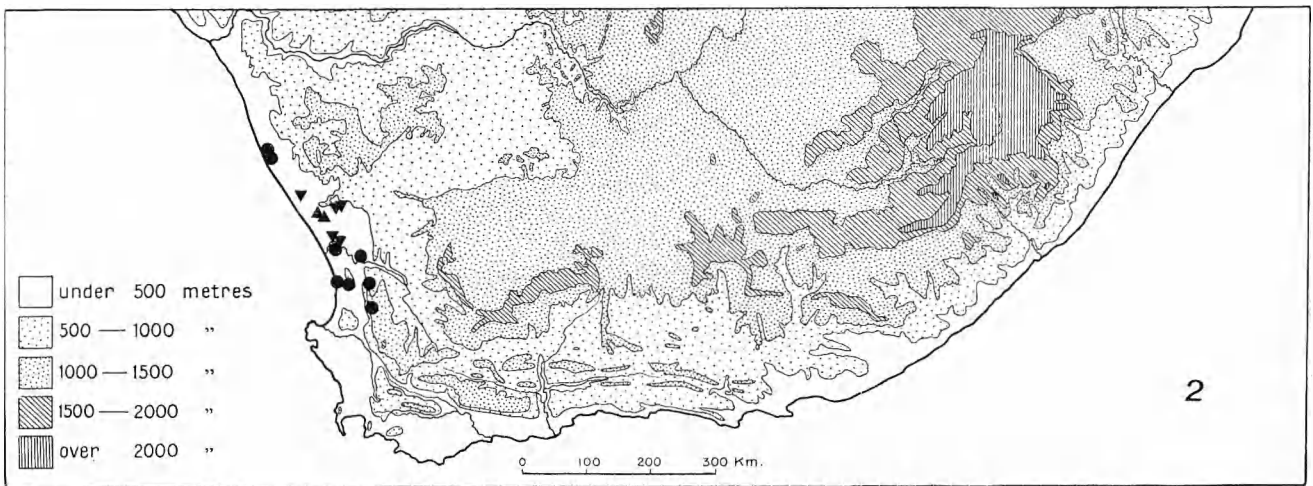
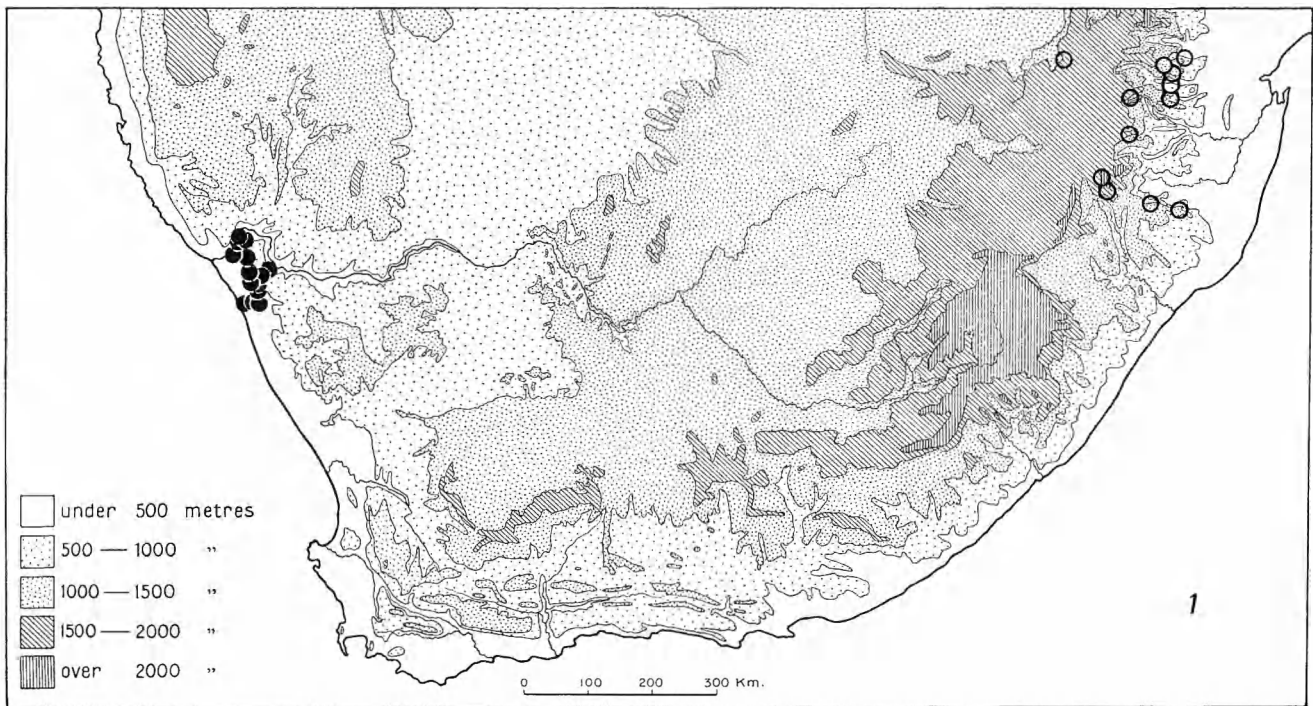
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Map 1. *Adenoglossa decurrens* (●) and *Adenanthemum osmitoides* (○).

Map 2. *Leucoptera nodosa* (●), *L. oppositifolia* (▲), and *L. subcarnosa* (▼).

Map 3. *Cymbopappus lasiopodus* (○), *C. hilliardiae* (■), and *C. adenosolen* (●).



Two new species of *Trifolium* from Ethiopia

Mats Thulin

Thulin, M. 1976 06 30: Two new species of *Trifolium* from Ethiopia. *Bot. Notiser* 129: 167–171. Stockholm. ISSN 0006-8195.

The two new species *Trifolium spananthum* Thulin and *T. chilaloense* Thulin are described from the Ethiopian highlands. They are both placed in section *Amoria*, *T. spananthum* in subsection *Amoria* and *T. chilaloense* in subsection *Loxospermum*. $2n = 16$ is reported for them and for *T. tembense* and *T. multinerve*.

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Ethiopia has by far the most species of *Trifolium* of any tropical African country. Some 30 species have hitherto been recorded, 8 or 9 of which are endemic. Five sections of the genus are represented (see Gillett 1952), but all Ethiopian endemics belong to section *Amoria* (Presl) Lojac. In this paper two more apparently endemic species in this section are described on the basis of recent collections.

A revision of the genus *Trifolium* is in preparation by Zohary and Heller (see e.g. Zohary 1972). Their work has given rise to considerable changes in the subdivision of the genus, but as only a small part of this new classification has as yet been published in detail I have kept to the subdivision used by Gillett (1952, 1971) which mainly follows Taubert (1893).

***Trifolium spananthum* Thulin, sp. nov. –**

Fig. 1 A–E

Orig. coll.: Thulin 1355, Ethiopia, Arussi Region, Chilalo awraja, near Bekoji, c. 60 km S of Asella, 5.X. 1971 (UPS holotype, BR, EA, ETH, FI, HUI, K, MO, WAG).

Species nova ab affini *T. tembense* Fresen. habitu perenni, omnibus petiolis ex parte liberis, inflorescentiis floribus 1–6, tubo calycis plerumque 9- vel 10-nervi et vexillo obovato supra medium latissimo diversa.

Perennial, often mat-forming glabrous herb, with usually many prostrate or ascending stems up to

2.5–20 cm long, from a tap root. Stipules up to 15 mm long, \pm ovate, attached to petioles for most of their length, often strongly reddish-veined, with the free part abruptly contracted to a fine point. Petioles up to 4 cm long, always distinct to the top of the plant and never entirely fused with the stipules. Leaflets 3, elliptic or obovate, cuneate at the base, acute, rounded, truncate or slightly emarginate at the apex, up to 19 mm long and 8 mm wide, but usually much smaller; margin dentate or serrate except for the proximal part; main nerves 6–11 on each side, at angles of 40° – 60° to the midrib. Inflorescences usually many, 1–6-flowered; peduncle up to 3 cm long; bracts c. 1 mm long, usually bifid; pedicels up to c. 1.5 mm long. Calyx tube 2.4–3.2 mm long, 9–10(–13)-nerved, splitting down the vexillary side in fruit, thinly puberulous on inside, glabrous on outside; lobes 1.8–3.2 mm long, about as long as the tube or somewhat shorter, \pm 1–1.2 mm wide at the base, \pm narrowly triangular with scarious sparsely hairy margins and \pm subulate tips. Corolla purple (standard mauve, keel violet according to Mooney 6119); standard obovate, broadest above the middle, 6–11 mm long; wings and keel \pm shorter than standard, attached to the filament tube in the lower part. Stamens \pm 5–7.5 mm long. Ovary sparsely hairy or papillose, 4–5-ovulate. Pod glabrous, with uneven somewhat thickened

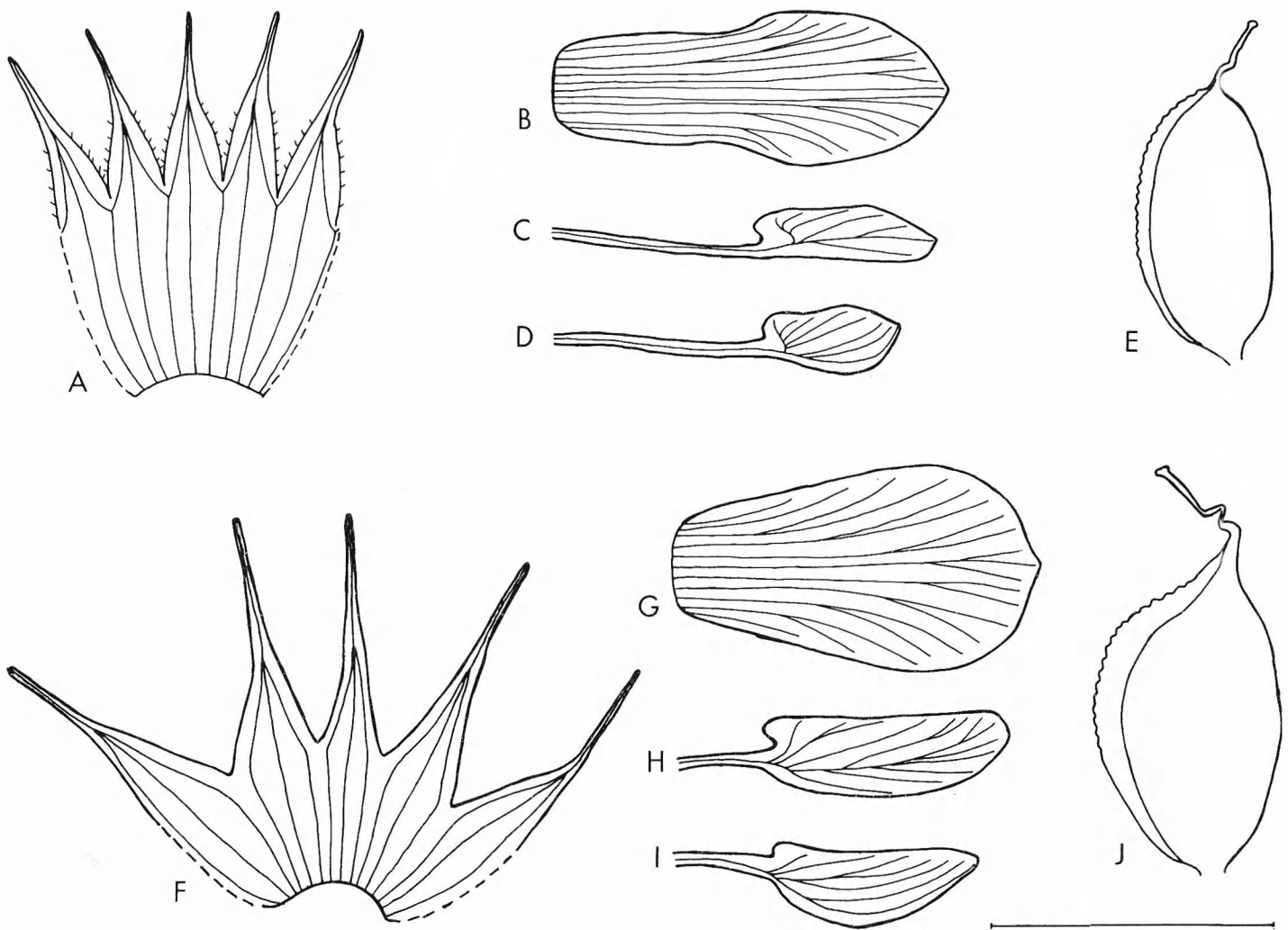


Fig. 1. A-E: *Trifolium spananthum*, drawn from Thulin 1355. - A: Calyx, cut open along the single vexillary commissural nerve. - B: Standard. - C: Wing. - D: Keel. - E: Pod. - F-J: *Trifolium chilaloense*, drawn from Thulin 1642. - F: Calyx, cut open between the vexillary commissural nerves. - G: Standard. - H: Wing. - I: Keel. - J: Pod. - Scale 5 mm.

vexillary margin, 4-6.5 by 2.5-3 mm. Seeds usually 3-5, brown usually mottled with purple, smooth, oval, \pm 1.6 by 1.2 mm; hilum at end. $2n=16$.

Habitat and distribution. Grassland, often in heavily grazed pastures or on disturbed or bare ground along tracks, etc. at 2300-3900 m in the SC Ethiopian highlands. Owing to its resistance to grazing and trampling *T. spananthum* seems to be a valuable constituent of the pastures in this area despite its small size.

Discussion. *T. spananthum* is closely related to the sympatric *T. tembense* Fresen., a widespread E African species in subsection *Amoria*. This subsection is characterized by having the petioles free for most of their length, at least in

lower leaves, less than 15-nerved calyx tube and 2-9-ovulate ovaries.

In contrast to the annual *T. tembense*, *T. spananthum* is a perennial, often mat-forming herb, very variable especially in size, habit and shape of the leaflets. This variation is apparently largely environmentally conditioned. Small plants with \pm prostrate stems are generally found in places exposed to grazing or trampling (e.g. Thulin 1354), while larger ascending plants are developed in more protected places (e.g. Thulin 1355). The size and shape of the leaflets and the number of flowers per inflorescence vary accordingly. Small obovate, apically rounded or truncate leaflets and few-flowered inflorescences are characteristic of plants from exposed places, while larger, elliptic, acute

leaflets and up to 6-flowered inflorescences tend to predominate in more protected habitats. Seeds from the collection Thulin 1552, which consists of rather stunted individuals with small, mostly obovate, apically rounded leaflets and 1–2-flowered inflorescences produced a progeny in greenhouses at the Uppsala Botanical Garden of rather erect plants with elliptic, acute leaflets up to 15 by 5 mm, and up to 6-flowered inflorescences.

The petioles of *T. spananthum* are distinct and partly free from the stipules in all leaves, while in *T. tembense* the petioles of the upper leaves are often entirely fused to the stipules. The inflorescences are 1–6-flowered (in *T. tembense* 3–16-flowered), and the calyx tube is usually 9- or 10-nerved, while in *T. tembense* the number of nerves is usually 11.

There are many species within subsection *Amoria* with 11-nerved calyx tubes. The eleventh nerve is formed by the division of the vexillary commissural nerve into two. Between these two vexillary nerves the calyx tube splits as the pod ripens. This condition seems to be rather stable in *T. tembense* and only once have I seen a calyx with 12 nerves. In this case another of the commissural nerves had also divided into two.

In *T. spananthum* the vexillary commissural nerve is normally either undivided (Fig. 1A) or entirely lacking, thus giving a total of 10 or 9 nerves respectively. With the limited material available it is difficult to say which is the commonest number. Furthermore, in Mooney 6119, where the calyx tube is usually 10-nerved, calyces with up to three of the commissural nerves divided from the base also occur making up to 13 nerves in all.

The shape of the standard differs markedly in *T. spananthum* and *T. tembense*. In *T. tembense* it is abruptly narrowed above the middle into a characteristic, oblong, truncate, downward-curved tip. In *T. spananthum*, on the other hand, it is broadest above the middle (Fig. 1B), and not downward-curved at the tip. The size of the standard and other floral parts is rather variable within *T. spananthum*. The standard is mostly ± 7 mm long but in Mooney 6119 it is up to 11 mm.

$2n=16$ was counted in both *T. spananthum* (progeny of Thulin 1552) and *T. tembense* (progeny of Thulin 1568 from Ethiopia, between

Sagure and Bekoji, c. 50 km S of Asella). Root tips fixed in Navashin-Karpeschenko and stained with crystal violet were used.

Collections

Ethiopia. Kaffa region, Deccano, Soddu road, NE slopes of Mt Maigudo, 22.X. 1954, Mooney 6119 (K) – *Arussi region*, Chilalo awraja, near Bekoji, c. 60 km S of Asella, 5.X. 1971, Thulin 1354 (EA, ETH, K, UPS), 1355 (BR, EA, ETH, FI, HUI, K, MO, UPS, WAG); Ticho awraja, between Siré and Robi, 25.X. 1971, Thulin 1552 (EA, ETH, K, UPS) – *Bale region*, S part of Bale National Park, 6°57' N, 39°40' E, 6.XI. 1971, S. Gilbert 73 (UPS); Bale National Park, between Garba Goracha and Little Batu camps, 3.XI. 1973, Hedberg 5662 (UPS); *ibid.*, near Little Batu camp, 3.XI. 1973, Hedberg 5678 (UPS).

Trifolium chilaloense Thulin, sp. nov. –

Fig. 1 F–J, 2

Orig. coll.: Thulin 1642, Ethiopia, Arussi Region, Chilalo awraja, near Kersa, c. 50 km SW of Asella, 12.XI. 1971 (UPS holotype, BR, EA, ETH, FI, HUI, K, MO, WAG).

Species nova ab affini *T. multinerve* A. Rich. inflorescentiis paucis floribus 5–12, calyce tubo 15(–18)-nervi, 2–2.5 mm longo, lobis tubo circa duplo longioribus glabris vel subglabris, ovario 4-ovulato et seminibus verruculosus diversa.

Annual, erect herb up to 12 cm high. Stem with few spreading branches, glabrous or sparsely pilose below the upper nodes. Stipules 1–2 cm long, attached to the petiole for about two-thirds to three-quarters of their length, strongly reddish-veined, tapering into long filiform tips. Petioles up to 4 cm long, glabrous or weakly pilose. Leaflets oblanceolate to very narrowly elliptic, acute at the apex, up to 25 mm long and 7 mm wide, \pm weakly pilose at the margins near the base and on petiolules, otherwise glabrous; margin finely serrate in the distal half; main nerves 7–10 on each side, often branched, at an angle of c. 20° to the midrib. Inflorescences few, up to 5 in number, 5–12-flowered; peduncle up to 4 cm long, weakly pilose, but more densely so at the tip; bracts minute, pedicels 0.5–1.2 mm long. Calyx tube 2–2.5 mm long, 15(–18)-nerved, splitting down the vexillary side in fruit, thinly puberulous on inside, glabrous on outside; lobes 3.5–4.5 mm long, usually about twice as long as the tube, narrowly triangular with subulate tips, glabrous or with a few hairs at the margin. Corolla

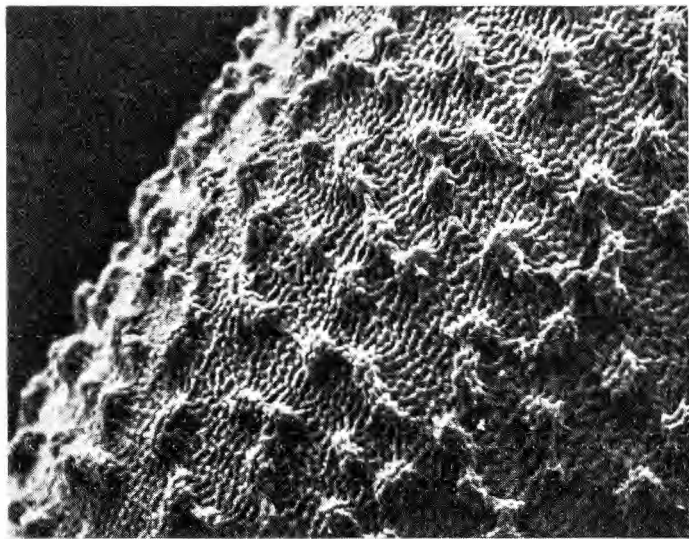


Fig. 2. Detail of seed of *Trifolium chilaloense* showing sculpturing of the testa (SEM). – From Thulin 1642, c. $\times 110$.

purplish-red; standard obovate, ± 7 mm long, wings of about the same length, keel somewhat shorter; wings and keel attached to the filament tube in the lower part. Ovary sparsely papillose, 4-ovulate. Pod glabrous, beaked, with uneven thickened upper margin up to c. 5 by 3 mm. Seeds usually 3–4, brown mottled with black, finely warty, oval, ± 1.6 by 1.2 mm; hilum at end. $2n=16$.

Habitat and distribution. In grassland patches in *Hagenia* forest at c. 2900 m. Only known from the type collection from the SC Ethiopian highlands.

Discussion. *T. chilaloense* belongs to subsection *Loxospermum* (Hochst.) Celak. within section *Amoria*. This subsection is restricted to E and NE tropical Africa and comprised four species in Gillett's revision of the *Trifolium*s in S Arabia and Africa S of the Sahara (Gillett 1952). Of these *T. decorum* Chiov. and *T. schimperi* (Hochst.) A. Rich. are Ethiopian endemics, *T. elgonense* Gillett is known from Mt Elgon and Ethiopia (previously known only from S Ethiopia, but recently collected also in Simien by Hedberg & Aweke), while *T. multinerve* A. Rich. is widespread in E tropical Africa from Eritrea in the N to E Zaïre in the S. The species of subsection *Loxospermum* are annuals with the petioles free for most of their length, calyx tube with 15–30 nerves and somewhat inflated

in fruit, 1–15-flowered inflorescences, and 3–12-ovulate ovaries.

T. elgonense is procumbent with only 1 or 2 flowers in the leaf axils and *T. schimperi* is distinguished by its few large flowers with standard over 15 mm long and calyx lobes about 10 mm long. *T. decorum* is similar to *T. chilaloense* in its comparatively many-flowered inflorescences (up to 15-flowered), but the flowers are much larger with the calyx only half as long as the corolla or less, and the leaves are broadly elliptic.

The nearest ally of *T. chilaloense* seems to be the sympatric *T. multinerve*, and although these species differ in many ways it is not easy to find really clear-cut differences between them.

Few, usually only one to three per plant, about 10-flowered inflorescences are characteristic of *T. chilaloense*, but the number of flowers is occasionally only 5 per inflorescence. *T. multinerve* usually has numerous inflorescences per plant, with 1–6, occasionally up to 8, flowers each. The stipules are usually larger in *T. chilaloense* (up to 2 cm long), while they scarcely exceed 1 cm in *T. multinerve*. The leaflets are of similar shape in the two species but are slightly larger in *T. chilaloense*, where they are also weakly pilose at the base.

The calyx tube is 2–2.5 mm long and normally 15-nerved (Fig. 1 F) in *T. chilaloense* and only occasionally a few more weak nerves were observed. The calyx tube is 3–4 mm long in *T. multinerve*, and Gillett (1971 p. 1034) gives the number of nerves as 15–30. I was not able to verify this and only saw calyces with more than 20 nerves, and if 15-nerved calyces do occur in *T. multinerve* it is certainly not common. The calyx lobes in *T. chilaloense* are about twice as long as the tube, although sometimes shorter, and are glabrous or have only a few hairs at the margin. In *T. multinerve*, however, they are as long as or slightly longer than the tube and have pilose margins. The number of ovules in *T. chilaloense* was 4 in all ovaries studied, while *T. multinerve* has 5–9 ovules.

Finally a good distinguishing character is found in the seeds. In *T. chilaloense* these are brown, mottled with black and distinctly warty (Fig. 2). The warts can also be seen in unripe seeds. In material of the other species in subsection *Loxospermum* (except perhaps in *T. deco-*

rum of which no fruiting material was available) the seeds were found to be smooth.

Both *T. chilaloense* (seeds from the type collection) and *T. multinerve* (seeds from Thulin 1450, Ethiopia, Arussi Region, 3 km S of Asella) have been kept in cultivation in greenhouses in Uppsala, but only the latter flowered. The *T. chilaloense* plants became much etiolated and were up to 40 cm high. However, the size of leaves and stipules agreed with the herbarium material. The plants of *T. multinerve* were similar in size to the corresponding herbarium material. From this it can be presumed that under favourable conditions plants of *T. chilaloense* may attain to a much larger size than that given in the description.

$2n=16$ was counted in both *T. chilaloense* and *T. multinerve* (same plants as mentioned above). The number for *T. multinerve* agrees with a previous count on material from Kenya (Thulin 1970 p. 489).

Previous records

T. spananthum and *T. chilaloense* have been mentioned earlier by me as *T. sp. A* and *T. sp. B* respectively in a stencilled report (Thulin 1972) and the same designations are used by Fröman (1975), where *T. spananthum* is illustrated by photographs. Fröman's illustration of *T. chilaloense* (as *T. sp. B*), however, is hardly of this species, but presumably of *T.*

steudneri Schweinf. In an agro-botanical study by Håkansson (1968) *T. spananthum* is mentioned as *T. sp. near elgonense*.

Acknowledgements. I am indebted to Dr L. Holm for editing the Latin diagnoses, to Dr L. Tibell for the scanning electron micrograph and to Mrs K. Ryman for technical assistance.

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Radiigera Zeller, a genus of Gasteromycetes new to Europe

Lars E. Kers

Kers, L. E. 1976 06 30: *Radiigera* Zeller, a genus of Gasteromycetes new to Europe. *Bot. Notiser* 129: 173–178. Stockholm. ISSN 0006-8195.

Radiigera atrogleba Zeller is reported from the E part of central Sweden. This is the first European record of *Radiigera*, hitherto known only from America. The Swedish material is described and its characteristic features are illustrated. The species can easily be mistaken for an unopened *Geastrum*. It is suggested that the genus might better be placed in Geastraceae than in Mesophelliaceae.

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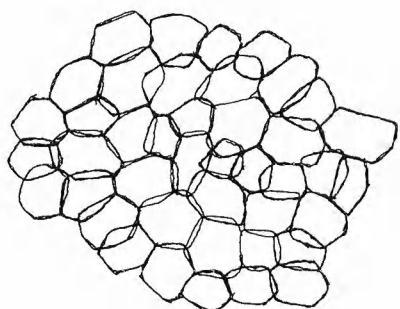
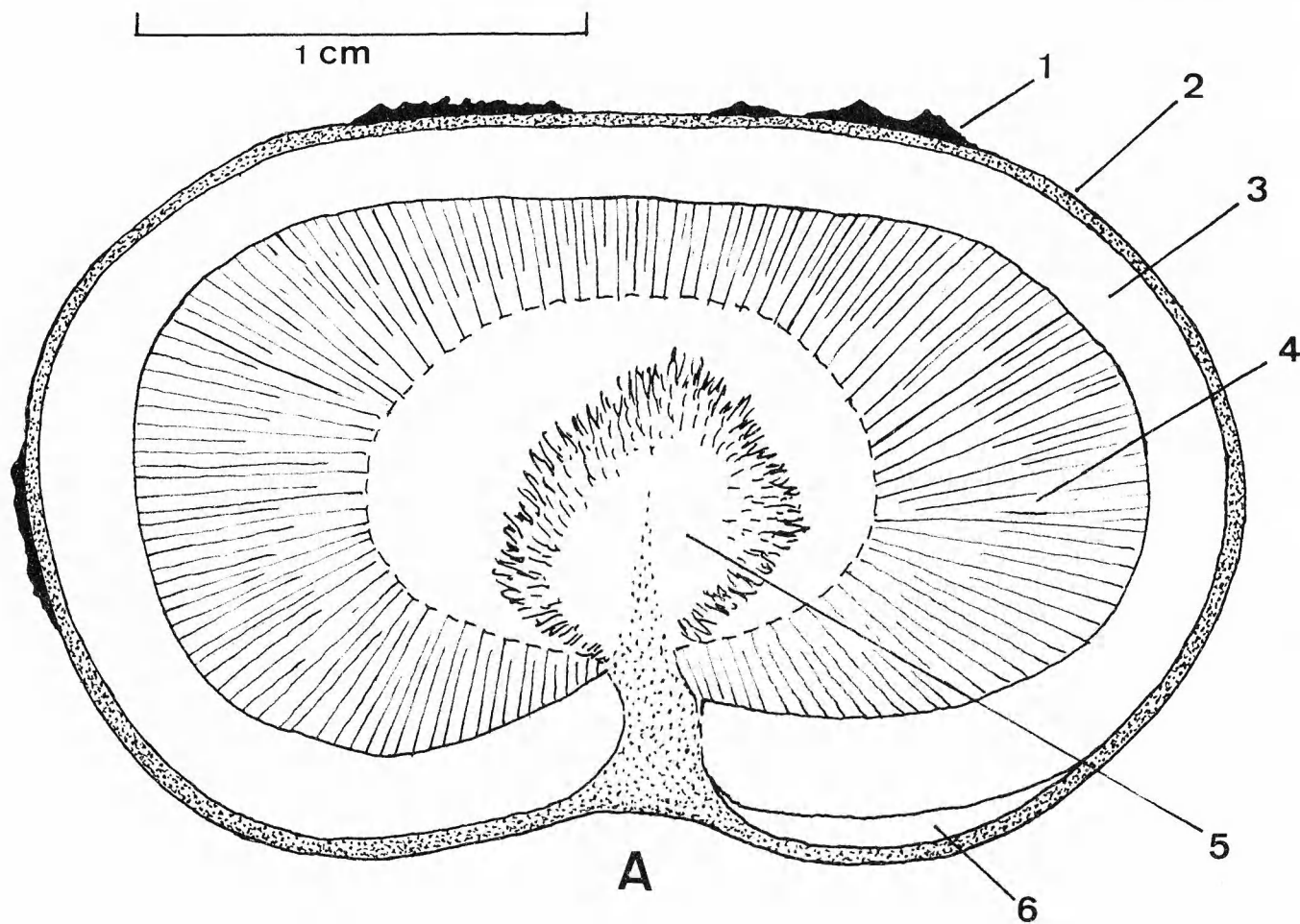
Late in 1974 when I visited the small island Röllingen in the lake Mälaren about 40 km W of Stockholm, I came across a peculiar Gasteromycete that was more or less hypogeous. At first sight I thought the specimens were phalloid eggs. When opened up, however, no receptacle was seen and the gleba was pulverulent and gave off a distinct odour resembling that of ink. This made me presume that I had found a "truffle", unknown to me. When the opened sporocarps were examined in detail I found that the fundamental construction was much the same as that of an unopened *Geastrum* or *Trichaster*, and thus in no way resembling a "truffle".

A study of the literature has revealed that this Gasteromycete species belongs to the genus *Radiigera* Zeller (1944). The Swedish material has been determined as *R. atrogleba* Zeller. This species has previously been recorded from North America (Oregon, Idaho) and Mexico (Zeller 1944, Guzmán 1971).

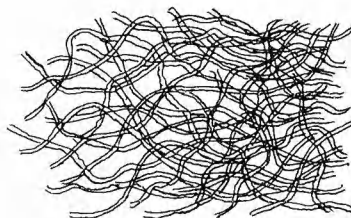
Description of the Swedish material

Sporocarps hypogeous and erumpent, growing more or less clustered in small groups from a white, conspicuous mycelium, sporocarps depressed globose to irregularly rounded, often oblong, 2.5–4 cm long and 1.5–3 cm high, white when fresh, later turning pale brownish, erum-

pent specimens with a thin mycelial layer covering the basal half, this layer being more or less lost from the upper exposed portions, basal portion of sporocarp provided with a few, delicate and soon evanescent mycelial cords, no stipe-like extension of the sporocarp base. *Mycelium* conspicuously developed as a white felt, densely binding together the upper mull soil, forming irregular "fairy rings" which are clearly visible when the leaf litter has been removed. *Peridium* consisting of two main layers and with a mycelial covering. *The mycelial layer* white, thin and flocculent, with adhering soil, usually lacking on the exposed parts of the erumpent sporocarps. *Exoperidium* separated into two distinct strata. *Outer layer* white, about 1 mm thick when fresh, tough, consisting of densely packed hyphae running mostly parallel to each other, this layer readily separable from the inner peridial layer, dehiscing by irregular rupture in apical portions forming a few irregular lobes, drying to a thin, papery, sac-like remnant very pliable when wet, rather resistant to weathering. *Inner pseudoparenchymatous layer* white to pale yellowish, about 3 mm thick when fresh, brittle, juicy when broken, consisting of cells that are about isodiametric, of same thickness all around, as a rule not breaking up together with the outer peridial layer, sometimes dehiscing by a few accidental ruptures, with age

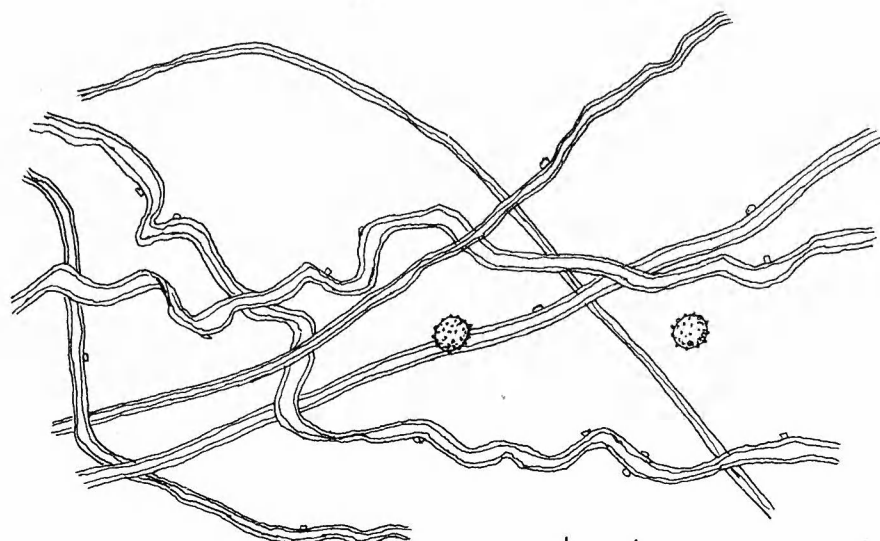


B



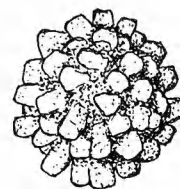
C

25 μ



D

10 μ



E

5 μ

usually disappearing by deliquescence, with the gleba adhering to the inner surface. *Endoperidium* not developed. *Pseudocolumella* developed as in a *Geastrum*, projecting to about the centre of the sporocarp body, borne from the outer peridial layer, but clearly separated from the inner, pseudoparenchymatous layer, in the ripe sporocarps collapsing and becoming free of the gleba, forming a thin, plug-shaped structure in the spherical sporocarps, laterally flattened and keel-like in the oblong sporocarps, evanescent with age. *Gleba* organized into a radiating manner between the peridium and the pseudocolumella, composed of densely packed spore-filled tubes of delicate fascicles of hyaline remnants of sterile gleba and of capillitium, readily disintegrating into a black, pulverulent mass, odour resembling that of ink, gleba adhering to the inner peridial surface in the ripe sporocarps but torn free of the collapsing pseudocolumella. *Capillitium* few-branched, thin-walled, 2–6 μ in diameter, hyaline to pale brown, often weak and contorted, with minute debris adhering. *Spores* spherical, 4–6 μ in diameter (inclusive of ornamentation), distinctly verrucose, with a minute pedicel stump or pedicel scar, dark brown under the microscope, black in mass.

Material: Sweden, Uppland, Torsvi parish (Enköping district), island of Röllingen in the lake Mälaren. In a valley on the northern side of the island. On soil under deciduous trees, mainly *Fraxinus excelsior*. – Kers 4548, 16.9. 1974 (S, UPS); Kers 4549, 2.10. 1975 (S).

Field notes. The valley is small, running north leading down to Mälaren. On both sides is an old, undisturbed and moss-rich coniferous forest (mainly *Picea abies*). In the south the head of the valley is in steep bedrock slopes with scattered stands of *Pinus sylvestris*. Ruins of a small homestead can be seen in the lower part of the valley. Soil: sandy to gravelly, rather dry, rich in mull in the upper layers, surface covered with a loose layer of leaves (*Fraxinus excelsior*, *Acer platanoides*, *Quercus robur*) and twigs

from deciduous trees. Vegetation: a dense stand of old *Fraxinus* trees with numerous *Fraxinus* plants 3–4 dm high on the ground between the trees. Almost no herbs (seen in autumn only). The locality is much shaded due to the north-facing situation and the dense canopy of trees.

In 1974 (16.9. and 24.9.) the fungus was quite abundant here, but only within a limited upper part of the valley. All specimens were ripe with collapsed pseudocolumellae. In 1975 (2.10.) very few sporocarps were to be found and these were almost completely obliterated. The sparse occurrence in 1975 may have been partly the result of the preceding dry summer and autumn, partly of the late date. The odour of the gleba was very distinct and has been appropriately described as "metallic and resembling that of actual ink" (Zeller 1944 p. 635). This odour is in 1976 still clearly discernable from some dry specimens that have been kept in a closed glass jar since 1974.

This fungus is difficult to find. In the Swedish locality it must be looked for before the first frost. Later the sporocarps are completely hidden by a cover of ash leaves. Unlike *Geastrum* the fungus does not leave long persistent and easily identified "mummies", just insignificant, sac-like brown remnants consisting solely of the thin outer peridial layer.

Discussion

The Swedish material does not differ essentially from the descriptions of *R. atrogleba* (Zeller 1944, Guzmán 1971). It can be identified on sight from the instructive photos published by Zeller (Zeller 1944 p. 632).

Radiigera fuscogleba and *R. cinnamomea* have a brown gleba (black in *R. atrogleba*) and they also differ in microscopic characters. *Radiigera atrogleba* differs from *R. taylorii* and *R. paulensis* in having much bigger spores (about 2.5–3.7 μ in the latter).

Owing to the limited material so far collected and the limited field studies carried out on these

Fig. 1. *Radiigera atrogleba*. – A: Ripe sporocarp in transverse section. 1 Remnants of mycelial covering (black); 2 outer layer of exoperidium; 3 pseudoparenchymatous layer of exoperidium; 4 gleba; 5 collapsed pseudocolumella; 6 air space, showing separation of exoperidial layers. – B: Texture of pseudoparenchymatous peridial layer. – C: Texture of outer peridial layer. – D: Capillitium and spores. – E: Spore drawn from a SEM photo. – Kers 4548 (S).

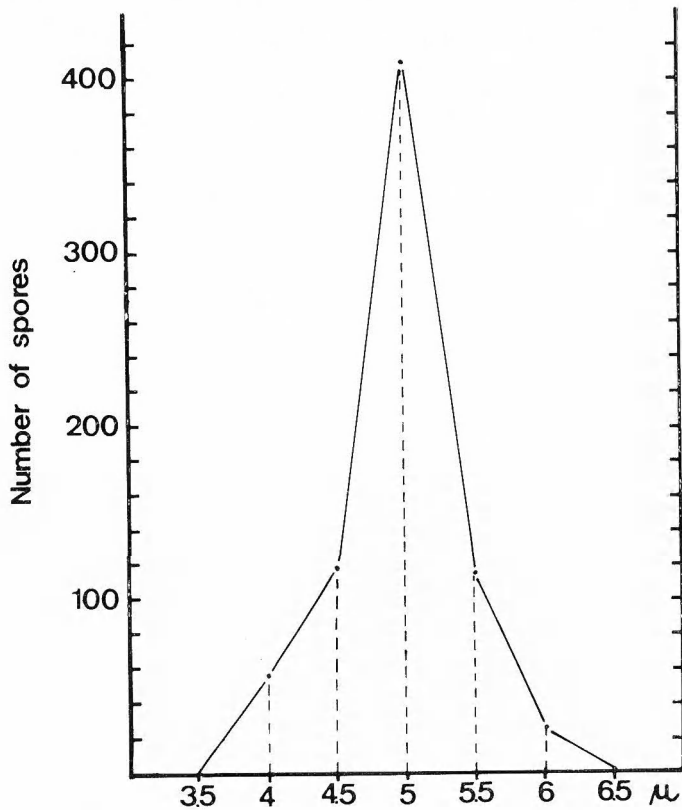


Fig. 2. Spore size diagram in *Radiigera atrogleba*. Measurements from dry spores mounted in water. Ornamentation included. — Kers 4548 (S).

species the full extent of their morphological variation is not yet known (cf. Guzmán 1971). The discrepancies between the descriptions of *R. atrogleba* and the Swedish material are without doubt due to variable features in this species. The mycelial covering of the sporocarps is stated by Zeller to be distinctly developed but is less obvious in the Swedish material. This layer, however, is more apparent in hypogeous specimens than it is in erumpent ones (cf. Zeller 1944 p. 635). The inner peridial layer is said by Zeller to become hard on drying, whereas it is clearly deliquescent in the samples seen by me. I think these differences are mainly due to different ontogenetic stages of the material. The American sporocarps were certainly not as ripe as the Swedish ones and they may also have been dried more quickly. The sporocarps illustrated by Zeller are definitely younger than those found by me (Zeller 1944 p. 632, Fig. 1:5).

It is well known that some Gasteromycete genera and species were originally described on unopened specimens of *Geastrum* and *Astraeus*. In most cases this mistake is obvious

to modern taxonomists. In some other cases it is less evident and any rejection of a taxon must be left to the revising botanist. From my first acquaintance with this fungus, I was quite convinced that it neither represented an unopened *Geastrum* nor a *Trichaster*. The morphology was too different in many important details. Neither could any dry remnants of a *Geastrum* (viz. from 1973) be found in association with the fresh sporocarps of *Radiigera* in 1974. On the other hand, a few much-weathered remnants of *Radiigera* were found, apparently from 1973. To make sure the locality was revisited in 1975. Only typical *Radiigera* specimens were found — no sporocarps of *Geastrum*. It is of interest to note that while the summer and autumn of 1974 had been unusually wet, the same periods in 1975 were very dry. These observations mean that only typical *Radiigera* sporocarps developed in this locality during the three years 1973–1975, irrespective of the extremely variable weather conditions.

Radiigera atrogleba is readily distinguished from *Geastrum* by lack of an endoperidium, by the white, depressed globose and erumpent sporocarps, the readily separable outer peridial layer, the odour and the mode of dehiscence (irregularly dehiscent outer peridial layer, deliquescent pseudoparenchymatous layer). The radiating gleba which adheres to the pseudoparenchymatous peridial layer is another difference from *Geastrum*. In all these characters *R. atrogleba* also differs from *Trichaster*. *Trichaster* is distinguished from *Geastrum* by means of its compact pseudocolumella and its vestigial endoperidium, which does not normally separate from the inner exoperidial surface. Moreover, the spore mass is enclosed within a “puff ball” in *Geastrum*, whereas it is freely exposed in a ripe *Trichaster*. Consequently there is a considerable difference between *Radiigera* and *Trichaster*.

Lloyd seems to have been the first to realize that specimens now referred to this genus could not be interpreted as unopened specimens of *Geastrum* (Lloyd 1924 p. 1305). Lloyd tentatively placed his North American species (now known as *Radiigera taylorii*) in *Mesophellia*, but pointed out its anomalous position in this Australian genus. Lloyd suggested that the species, when better known, might better be placed in a separate genus.

Lloyd's suspicion was confirmed by Zeller (1944). He proposed the genus *Radiigera* for three species: *R. taylorii* (Lloyd) Zeller, *R. atrogleba* Zeller and *R. fuscogleba* Zeller (*typus generis*). All these species were described on North American material. Two species have later been added to this genus: *R. cinnamomea* Zeller (1948 p. 652) and *R. paulensis* Singer, Wright & Horak (1963 p. 600). One species previously treated in *Radiigera* has been transferred to *Morganella* as *M. puiggarii* (Speg.) Kreisel & Dring (1967 p. 116).

Guzmán has shown that some of the North American species extend their areas to comprise Mexico, viz. *R. fuscogleba*, *R. atrogleba* and tentatively also *R. taylorii* (Guzmán 1971, 1973 p. 1325). The genus has not yet been reported outside the American continent.

Mainly following Cunningham's interpretation of the Australian Lycoperdaceae, Zeller proposed the family Mesophelliaceae in which he included *Mesophellia*, *Castoreum* (both with elliptic spores), *Abstoma* and *Radiigera* (with spherical spores) (Cunningham 1932 p. 315, Zeller 1944 p. 631). A recent addition to Mesophelliaceae is *Mesophelliopsis*, a monotypic genus described from South America (Batista & Vital 1957 p. 14). The inclusion of *Radiigera* in Mesophelliaceae has been followed by other authors (Singer et al. 1963, Guzmán 1971, 1973, Dring 1973 p. 463).

Mesophelliaceae may have been too widely circumscribed by Zeller (1944). Its genera are little known, especially as regards the fundamental construction of the peridium and the pseudocolumella. A comparative morphological study of the genera is much needed. In my opinion it seems quite clear that *Radiigera* has more characters in common with *Geastrum* and *Trichaster* (Geastraceae) than with *Mesophellia* and *Castoreum* (Mesophelliaceae s. str.). Whether *Abstoma* also shows a "Geastrum-like" peridial construction cannot be clearly read from the available descriptions but it seems unlikely (cf. Cunningham 1944 p. 133 and Plate XVII). The spore characters of *Abstoma reticulatum* G. H. Cunn. point to closer affinities with Lycoperdaceae than with Geastraceae (Bronchart & Demoulin 1973 p. 272).

The mutual relationships of *Radiigera*, *Trichaster* and *Geastrum* are very close and obvious. Of these three genera *Radiigera* shows

the simplest organization of the sporocarps. In *Radiigera* the process of differentiation has largely remained at the simple level found in young *Geastrum* and *Trichaster*.

The deliquescent pseudoparenchymatous peridial layer of *Radiigera* (*atrogleba*) and the distinct odour, correlated with an irregular and often accidental dehiscence of the sporocarps, are characters which are clear biological adaptations to the more or less hypogean mode of growth. The presence of these "new" characters, which would be meaningless in *Geastrum* or *Trichaster*, clearly indicates that *Radiigera* is not an abnormality sometimes to be found in *Geastrum* or *Trichaster*.

It would be quite natural to transfer *Radiigera* from Mesophelliaceae to Geastraceae. Geastraceae is, however, by tradition and convenience circumscribed to include genera with stellate dehiscence. But just as *Astraeus* (very *Geastrum*-like and with stellate dehiscence) has been separated from Geastraceae on microscopic characters, *Radiigera* (not with stellate dehiscence) could be included in Geastraceae on the general organization of its sporocarp.

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Notes on *Cryptocoryne* of Sri Lanka (Ceylon)

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Fourteen species of *Cryptocoryne* (Araceae), all endemic are known from Sri Lanka. The investigation of herbarium material at Peradeniya (PDA) and material available in Europe has led to the revision of the interpretation of *C. nevillii* Trim. ex Hook. f., *C. willisii* Reitz and *C. undulata* Wendt. Karyologically the species fall into two groups, one with $2n=28$ or 42 and the other with $2n=36$. A taxonomic grouping of the species is suggested, and the evolutionary aspects are briefly discussed.

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Species of *Cryptocoryne* from Sri Lanka have been popular in Europe as aquarium plants for the past 70 years, and there is an ever-increasing demand for new plants for cultivation. The identification of these imported plants has always been problematic. Herbarium specimens of *Cryptocoryne* are few and are often in poor condition. Plants were exported to Europe and cultivated, sometimes for a period of years, before it was realized that they represented new species. For instance, the importation of two Sri Lanka species, *C. willisii* Reitz and *C. undulata* Wendt, to Germany around 1905 caused considerable confusion as they later proved to be new species. The number of species known to Sri Lanka continued to increase considerably in the course of the years. Schott (1857) described the first two species: *C. walkeri* and *C. thwaitesii*. Thwaites (1864) recognized two species: *C. spiralis* and *C. thwaitesii*. Hooker (1898) in Trimen, Handbook of the Flora of Ceylon, mentioned five species: *C. spiralis*, *thwaitesii*, *nevillii*, *walkeri*, and *beckettii*. In 1908 Reitz described *C. willisii* Reitz, a name that antedates the widely used *C. willisii* Engl. ex Baum (1909). The latter is in actual fact conspecific with *C. undulata* Wendt. Engler's conspectus in Das Pflanzenreich (1920) includes

four species from Sri Lanka: *C. thwaitesii*, *walkeri*, *beckettii*, and *nevillii*. His descriptions of the last three species are based on plants cultivated at Peradeniya (RBGP). Engler's descriptions can only be interpreted with difficulty, but I am of the opinion that the plants described as *C. beckettii* and *C. nevillii* are in actual fact *C. undulata* and *C. willisii* Reitz respectively, whereas I am not able to refer the description of *C. walkeri* to any species I know. It is almost certain that the two species cultivated in the Botanical Garden in Berlin-Dahlem after 1905 (e.g. Baum 1909 b), viz. *C. willisii* Reitz and *C. undulata*, were collected by Engler on his travels in Asia in 1905. Petch (1928) treated the Sri Lanka species on the basis of live material seen by him. He was able to establish that five, possibly six, species had recently been collected, but found it difficult, with the exception of *C. thwaitesii*, to assign them to species previously described from the island. Alston (1931) described two new species, *C. petchii* and *C. lutea*, and one variety, *C. lutea* var. *minor*. Wendt (1955 a) described *C. undulata*. De Wit described five species during the period 1958–1975: *C. lucens*, *parva*, *wendtii*, *legroi*, and *alba*. De Wit 1971 is illustrated with drawings of all the species of *Cryptocoryne* rec-

ognized by him. Rataj (1975 a) revised the genus *Cryptocoryne* and described *C. bogneri* and four varieties of *C. wendtii*. Unfortunately he did not see the type material at Peradeniya. Rataj's statement that *C. walkeri*, *beckettii*, and *nevillei* were described on the basis of plants cultivated at Peradeniya is based on an incorrect translation of Engler's notes in Das Pflanzenreich. In all, 14 species and 5 varieties have been described from Sri Lanka.

During a stay in Sri Lanka in March, 1975, the author collected live specimens of *Cryptocoryne* and also studied the material in the Herbarium at Peradeniya (PDA). This, together with observations on material available in Europe, led to some nomenclatural and taxonomic revisions.

Data on each species are presented below in order of publication.

Cytological preparations were made from root tips according to Jacobsen (1957).

Voucher specimens of the chromosome counts are deposited at C. Photographs of the Peradeniya plants are also at C.

***Cryptocoryne walkeri* Schott – Fig. 3 B**

Schott, Bonplandia 5: 221 (1857). Holotype: Walker 288 (K). Drawing at W.

C. lutea Alston var. *minor* Alston in Trimen, Handb. Fl. Ceyl. 6: 293 (1931. Type: Silva, Halloluwa 18.2. 1925 (PDA, 3 sheets).

The holotype of *C. walkeri* consists of a single spathe which is somewhat folded. Unless this is dissected it will not be possible to establish with certainty whether the interpretation by Petch (1928 p. 22, and pl. IV. fig. 5–8) and De Wit (1971 p. 202, Abb. 69 r) as well as in this paper is indeed correct. When describing *C. lutea* Alston apparently had not seen the type of *C. walkeri*. His concept of *C. walkeri* (Alston 1931, 1938) is based on one of his own collections (Alston no. 1386) which is actually *C. undulata*.

Rataj (1975 a) reduced *C. lutea* and *C. legroi* to varieties under *C. walkeri*. Obviously *C. lutea* and *C. legroi* are very close, whereas I believe that *C. walkeri* is more distantly related to these two. The collar of the spathe is small, distinct, and swollen in *C. lutea* and *C. legroi*, but there is a large and indistinct collar zone in *C. walkeri*. The type of *C. lutea* var. *minor* agrees with *C. walkeri* in this respect. When illuminated with

ultraviolet light at 350 μm the broad collar zone of *C. walkeri* shows a dark, reddish-brown colour and the limb is yellowish. In *C. lutea* the collar and the limb show the same yellowish colour when illuminated with ultraviolet light at 350 μm .

The chromosome number is $2n=28$ (vouchers: P 1965/337 cult.; NJ 2913 cult.).

***Cryptocoryne thwaitesii* Schott – Fig. 3 E**

Schott, Bonplandia 5: 221 (1857). Holotype: Ceylon Plants (C.P.) 3464, sine loc. (K). Drawing at W. Two isotypes at PDA, one of them marked: C.P. 3464, May 1855, Singhe Raja Forest.

There are two other collections at PDA: Kottawa Forest, near Galle, April 1884; Alston, Kottawa Forest Reserve 17.8. 1926.

The interpretation of Petch (1928) and De Wit (1971) [excl. *C. dalzelii* Schott] is no doubt correct. De Wit (1971) and Sadilek (1969) show the limb as upright whereas in the plants I collected at Kottawa the limb was bent forward at an angle of 90° or more so that the tip reached the ground. Plants from Kottawa grown in Copenhagen sometimes developed spathes that failed to bend, curving only slightly like the one illustrated by De Wit. Rataj (1975 a, c) illustrates a spathe with an upright limb and twisted differently in the throat region and with far fewer red spots than in the plants from Kottawa. Rataj's specimen may in actual fact not belong to *C. thwaitesii* s. str. At Kottawa *C. thwaitesii* grew emerged along a small stream in deep shade.

Rataj's statement (1975 a, pp. 57–58) that *C. thwaitesii* is related to the Malaysian species is ill founded. There is a superficial resemblance to *C. johorensis* Engl. and *C. longicauda* Becc. ex Engl. (?=*C. caudata* N. E. Brown), but the texture of the leaf is quite different and the collar is lacking in *C. thwaitesii*. The chromosome number for *C. thwaitesii* is $2n=36$ (voucher: NJ 14-1 Kottawa), the same as for *C. bogneri* and *C. alba*, whereas the Malaysian species probably belong to the $2n=34$ group.

***Cryptocoryne beckettii* Thw. ex Trim. – Fig. 2 E**

Trimen, Journ. Bot. 23 p. 269 (1885). Holotype: Beckett, Matale East, Feb. 1865. C.P. 3868, number not Beckett's (PDA).

There are 10 other sheets at PDA: Kailla 1.6. 1866; van Buuren, Gangaruwa Village 24.3. 1919 (maybe duplicate at K); RBGP 21.9. 1921 a. Gangaruwa "A", b. Heedeniya "A"; Silva, Gangaruwa 29.1. 1925 (two sheets); Petch, brought from Gangaruwa "A" 11.2. 1925, cult. RBGP; Silva, Halloluwa 18.2. 1925; Alston 1384, brought from Halloluwa by H. L. van Buuren, cult. RBGP 5.10. 1925; Alston 1385, brought from Gangaruwa "A", cult. RBGP 11.5. 1926; Silva 206, Gangaruwa 3.12. 1927 (dupl. at K). Another sheet at PDA labelled *C. "beckettii"*, Kahata-ata-hela, Jan. 1888 is *C. wendtii*.

The interpretation of the holotype, one immature spathe, and one mature kettle, presents considerable difficulties. The leaves are large and of a kind which I have only seen in plants matching *C. beckettii* sensu Petch (1928). Petch's study was partly based on live material and his interpretation of *C. beckettii*, which was followed by Wendt (1953 b, 1955 b), De Wit (1971), and Rataj (1975 a), is probably correct.

The shape of the limb varies to some extent, as do the leaves cf. *C. petchii*.

I have found this species at Kegalla and Halloluwa and in both places it grew in shady, sheltered places along the river.

The chromosome number is $2n=28$ (vouchers: NJ 23-19 Halloluwa; Jayasuriya 2246, Menik-Ganga, Ruhuna National Park).

Cryptocoryne nevillei Trim. ex Hook. f. – Fig. 1

Hook. f. in Trimen, Handb. Fl. Ceylon 4 pp. 346–347 (1898). Holotype: Grukamana Tank, Wawinni, Nov. 1885 (PDA). A fragment of the type is at K.

The holotype is a rather poor specimen with only a few leaves although four mature spathes exist. I have seen only one other specimen which I assign to this species: Kundu & Balakrishnan 185, Batticaloa 11.10. 1970 (PDA, US). Other specimens cited in various publications are mostly *C. willisii* Reitz, *C. parva* and *C. lucens*. The localities given by Rataj (1975 a) are thus erroneous. *C. nevillei* has only been found in the Eastern Province and has not yet been cultivated in Europe.

Two species of *Cryptocoryne* were brought from Sri Lanka to Europe around 1905 and have been cultivated ever since. Reitz (1908) referred one of them to *C. beckettii* and described the other as a new species, *C. willisii* Reitz. Baum (1909 a, b), who had probably seen the same material, unfortunately switched the names. Wendt (1958) does mention that Baum switched the names, but he is not aware of the publication

of *C. willisii* Reitz. Unfortunately Reitz's publication was overlooked, and *C. willisii* Engl. ex Baum became established as the name of the species which must be called *C. undulata* Wendt. Later on *C. willisii* Reitz (*C. beckettii* sensu Baum 1909 a, b) was referred to *C. nevillei* (Böhmer 1935, Wendt 1953 a, De Wit 1971 and Rataj 1975 a). A comparison between these "European *C. nevillei*" and the type of *C. nevillei* Trim. ex Hook. f. in PDA showed that they are different species. Petch (1928 p. 238) may partly be held responsible for the establishment of the erroneous interpretation of the cultivated plants. He illustrated some plants collected at Yatiellagala (=Kulugamman) and Halloluwa (Pl. V), and referred them to *C. nevillei*, later (p. 25), however, adding that "until the type has been matched by fresh specimens it is not certain that the recent Yatiellagala plant is *C. nevillei*". Petch did not succeed in obtaining fresh specimens from the type locality.

The material illustrated by Petch (1928 Pl. V) is heterogeneous. The specimens in Fig. 7 and 11 are apparently *C. parva* and those in Fig. 9 and 10 probably *C. willisii* Reitz or *C. lucens*.

The following description of *C. nevillei* Trim. ex Hook. f. is based on Kundu & Balakrishnan 185: Rhizome stout, branched, stolons absent in the herbarium specimens. Leaves 15–20 cm, green, apparently without purple; lamina up to 7×1.5 cm, lanceolate, broadest below the middle or obovate and then shorter; margin with a border of hyaline cells; petiole up to 10 cm, rather broad, flat, and whitish. Spathe very long, up to 23 cm; tube narrow, whitish; limb 3 cm, purple, bent somewhat backwards, more or less smooth; collar very prominent, 0.5 mm high, dark purple; kettle without alveolae in the wall. The exact shape and colour of the limb are difficult to ascertain. Male flowers 80–100, smooth. Female flowers 5–6, small, slender, with divergent ovate stigmas which are rather flat and not sunken in the centre.

The plant is characterized by the lanceolate leaves the lower ones of which are obovate, and by the spathe which far exceeds the leaves. The herbarium specimens suggest that the whole petiole has been subterranean. It is possible that this species withers during the dry Yala season (April–September) to emerge again and flower when the rains come. This may be the reason for the poor state of the holotype, which

may have been collected just at the beginning of the season when only a few leaves and some spathes had emerged. The note by Trimen cited by Hooker (1898 p. 347) "Only the tip of the spathe protruded above ground" may be entirely correct.

Professor De Wit, Wageningen, who has kindly read the manuscript, is of the opinion that *C. nevillii* Trim. ex Hook. f. and *C. willisii* Reitz are conspecific, and that the latter is a synonym of the former. At the present state of knowledge I believe, however, that they are best retained as separate species.

***Cryptocoryne willisii* Reitz non Engl. ex Baum – Fig. 2 A**

Reitz, Wochenschrift für Aquarien- und Terrarienkunde, Sept. 29th 1908, p. 523. The name is typified by the description and the photograph on p. 523 and Fig. 4 left.

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

There are two other sheets at PDA which may represent this species but they are sterile: van Buuren, Kulugammana no. 2 (Yatiellagala) 18.2. 1925; Silva, brought from Kulugammana (no. 2), cult. RBGP 10.10. 1925.

C. willisii Reitz has been cultivated in Europe under various names, and for the last 25 years as *C. nevillii* auct.

The following description is based on a plant received from Dansk Akvarieforening in 1914 and cultivated in the Botanical Garden in Copenhagen since then (P 1914/114): Leaves up to 20 cm long, lamina green, acutely ovate to lanceolate, 3–7 cm long and 1.0–1.5 cm wide; veins not prominent; petiole 6–12 cm long, green, often somewhat purple-brown at the base. Spathe 5–10 cm, densely speckled-blotched with red-brown; kettle 1 cm, mostly whitish; limb c. 2 cm, purple, papillose, upright and slightly twisted above; collar present, yellowish with a more or less purplish rim, towards the throat abruptly changing to purple. The yellowish collar can sometimes be purplish. Male flowers 40–60. Female flowers c. 5; stigma oval, sunken in the centre. Kettle wall alveolar in the upper half.

This is the same species as De Wit's (1971) illustrations and which he describes as *C. nevillii*.

The chromosome number is $2n=28$ (vouchers: P1914/114 cult.; P 1966/353 cult.).

***Cryptocoryne lutea* Alston – Fig. 3 A**

Alston in Trimen, Handb. Fl. Ceylon 6 p. 293 (1931). Lectotype (selected here): Silva, Kulugammana (Yatiellagala) no. 1, 2.10. 1925 (PDA).

At PDA there are five other specimens: van Buuren, Kulugammana no. 1, 18.2. 1925 (sterile); Silva, brought from Kulugammana no. 1, 5.10. 1925; Alston 1703, cult. RBGP 21.2. 1928; Alston 253, brought from Kulugammana no. 1, cult. RBGP 29.3. 1926 (dupl. at K) – erroneously indicated as isotype by Rataj (1975 a); RBGP cult. 18.1. 1928.

Alston (?) marked two sheets (PDA) *C. lutea* var. *minor*: Silva, Halloluwa 18.2. 1925. There is no doubt that these two sheets are part of the collection labelled *C. walkeri* by Petch (1928) and illustrated. One other sheet from the same collection, also labelled by Petch, has not been marked in any way by Alston. All three sheets are *C. walkeri*.

I do not share Rataj's opinion that *C. lutea* is a variety of *C. walkeri*. I have seen some specimens of *C. lutea* with a yellow limb and some with a green limb, and the tube can be yellow or densely purple-spotted.

This species grows along the river at Halloluwa in open sunny places as well as in shade, well sheltered from strong currents.

The chromosome number is $2n=28$ (vouchers: NJ 2767 cult.; 1963/629 cult.; NJ 23-1 Halloluwa; NJ 23-6 Halloluwa).

***Cryptocoryne petchii* Alston – Fig. 2 F**

Alston in Trimen, Handb. Fl. Ceylon 6 p. 293–294 (1931). Holotype: Petch, brought from Ratnapura by H. L. van Buuren, cult. RBGP 31.1. 1925 (PDA).

There are three other sheets at PDA: Alston 1387, brought from Ratnapura, cult. RBGP 2.2. 1926 (?); Alston 1388, brought from Ratnapura, cult. RBGP 29.3. 1926; Alston 1684, Hakkinda 14.11. 1927.

The plant described by Petch (1928 p. 22) as *Cryptocoryne* sp. was later established as a new species, *C. petchii*, by Alston.

This species is very variable and is at times difficult to separate from *C. beckettii*. I do not consider that the distinguishing characters between *C. beckettii* and *C. petchii* are constant. The colour of the limb varies from brown to green, and the denticulations at the edge are often lacking. The collar varies in shape from oval to round and in colour from light purple to blackish-purple. The leaves are also very

variable. Some forms of *C. petchii* flower often, others rarely.

C. petchii is probably best regarded as a triploid of *C. beckettii*, and I assume that the *beckettii-petchii* relationship is analogous to that between diploids and triploids in *C. wendtii* coll. In *C. wendtii* diploids and triploids are also found and in my experience the greatest variation seems to be found in the triploids.

The chromosome number is $2n=42$ (vouchers: P 1963/631 cult.; NJ 2847 cult.).

Cryptocoryne undulata Wendt – Fig. 2 I

Wendt, Aquarienpflanzen in Wort und Bild, Lieferung 14, leaf 267/269 (1955). The name is typified by the photographs and the protologue.

C. willisii Engl. ex Baum, Gartenwelt 13: 5–7 (1909), nom. illeg.; *C. willisii* Engl. ex Baum, Blätter für Aquarien- und Terrarienkunde 20: 7 (1909), nom. illeg.; *C. axelrodii* Rataj, Revision of the genus *Cryptocoryne* 69–70 (1975), nom. illeg.

There are three sheets of this species at PDA: By the Mahaweli River, Gatembe, June 1888; Alston 1386, brought from Ganaruwa B (?). This latter sheet is probably responsible for Alston's establishment of *C. lutea*, as it was his interpretation of *C. walkeri* (Alston 1931, 1938). Another sheet (sterile) from Ganaruwa, 9.1. 1925 may be Alston's original collection of no. 1386.

The name *C. willisii* Engl. ex Baum has been used in many years for this species, but has proved to be a later homonym of *C. willisii* Reitz which is a different species.

In 1955 Wendt described *C. undulata* as a new species, differing from *C. willisii* Engl. ex Baum as interpreted by him. Wendt's descriptions are difficult to interpret but I am quite sure that *C. undulata* is conspecific with *C. willisii* Engl. ex Baum (not sensu Wendt, 1958).

At the Botanisches Museum, Berlin-Dahlem, there is a pickled specimen of *C. undulata*, no. 286, Cult., Hort. Berol. Another specimen *C. cf. cordata* Griff. no. 288, leg. A. Engler has the date January 1906, which implies that *C. undulata*, no. 286 was also preserved around 1906. There is also a pickled specimen of *C. undulata* (P 1911/59) at C, received from Akvarieforeningen, Copenhagen, in 1911 and cultivated in the Botanical Garden. The plants, which in illustrations by Reitz (1908) and Baum (1909 a, b) were called *C. beckettii* and *C. willisii* Engl. ex Baum, respectively, are probably from the

same stock as the above-mentioned no. 286 and the specimen at C probably also comes from the same source.

If new evidence some day proves that *C. willisii* Engl. ex Baum and *C. undulata* are two different taxa this would invalidate the latter, as Wendt cited *C. willisii* Engl. ex Baum as a synonym of *C. undulata*, even though he later (1955 a, 1958) added "Dem Verfasser ist ebenfalls ein Irrtum unterlaufen . . .". We would then be faced with the situation of having two taxa and no legitimate names, *C. axelrodii* Rataj being a nomen ambiguum.

I consider that the plant illustrated by Wendt (1958) as *C. willisii* Engl. ex Baum is a different species which has not yet been named. It may be conspecific with a plant I have received from Kew (K.E. no. 305–70.03945) but until I have seen more material in flower I hesitate to describe it as a new species.

De Wit (1971 p. 206) was neither able to get material of *C. undulata* nor of *C. willisii* Engl. ex Baum from Wendt and is of the opinion that *C. undulata* is conspecific with *C. willisii* Engl. ex Baum.

Rataj (1975 a p. 69) is of the opinion that *C. willisii* Engl. ex Baum and *C. undulata* Wendt are not correctly described according to the International Code of Botanical Nomenclature, and proposed a new name, *C. axelrodii* Rataj. In a short paper Rataj (1975 b) gives the reasons for considering the two names illegitimate, but does not mention the fact that *C. willisii* Reitz antedates *C. willisii* Engl. ex Baum. However, none of the arguments are correct as they are based on misinterpretations and misquotations of the Code.

I have seen *C. undulata* growing in three places west of Kandy: at Kandekenna, where it grew submersed in a very small stream; at Udamulle where in one place it had purple leaves and grew submersed sheltered between rocks in a small stream, and in another emerged below a tree and exposed to currents at high water; and at Halloluwa where it also grew below a tree and exposed to currents at high water.

The chromosome number is $2n=28$ (vouchers: NJ 22-1 Udamulle E of Kegalla, Mana Oya; Kandekenna, 7°23'N, 80°25'E; NJ 23-2 Halloluwa; NJ 2825 cult.).

Cryptocoryne wendtii De Wit – Fig. 2 G, H

De Wit, Meded. Bot. T. Belmonte Arb. II, 4 pp. 97–101 (1958). Holotype: H. G. D. Zewald s. n., 20.9. 1958 (WAG).

At PDA there is one sterile sheet which undoubtedly belongs to this species: Kahata-ata-hela, near Nilgala, Uva, Jan. 1888. This specimen was referred to *C. beckettii* by Hooker (1898), Petch (1928) and Rataj (1975 a).

There is no doubt that this species is from Sri Lanka although it was originally described as coming from Thailand (cf. Rataj 1975 a).

The description is quite unambiguous despite the variability of the species. The colour of the limb varies from shades of light brown to red-brown, and the twist of the limb may also vary, partly in response to environmental conditions. These characters are difficult to describe in morphological terms.

Rataj (1975 a) distinguished five varieties of *C. wendtii*. The species is certainly very variable but the varieties are poorly defined and a much more detailed investigation is needed.

Two chromosome numbers have been found, $2n=28$ and 42. There is much more variation in the triploids than in the diploids. I consider that the occurrence of two chromosome numbers and the variation within this species is analogous to the relationship between *C. beckettii* and *C. petchii* and between *C. lutea* and *C. legroi*. Vouchers of $2n=28$: P 1964/281 cult.; P 1961/342 cult.; NJ 2779 cult. Vouchers of $2n=42$: 1671/11a Mahauswera, Mi Oya, 19.2. 1973, Leg. Winde-løv; NJ 2849 cult.; NJ 2855 cult.

Cryptocoryne lucens De Wit – Fig. 2 B

De Wit, Meded. Bot. T. Belmonte Arb. VI, 4 p. 92–94 (1962). Holotype: De Wit s. n., Martii 1959 (WAG).

This species was described as being dioecious, a feature not found in the plants I collected at Halloluwa. Apparently, both monoecious and dioecious plants occur, resembling the situation found in *Arisaema*, e.g. van Steenis (1948) found different ratios between male and female flowers.

The illustration in Petch (1928 Pl. V, Fig. 9 and 10) may represent this species. The plant illustrated by Wendt (1953 a, 153/2) represents *C. lucens*.

Several of my collections from Halloluwa, provisionally referred to *C. lucens*, approach *C. willisii* Reitz, and further collections may show that it is not possible to distinguish these two species.

At Halloluwa this species occurs in more sheltered places than *C. parva*.

The chromosome number is $2n=28$ (vouchers: NJ 23-4 Halloluwa; NJ 24-4 Peradeniya).

Cryptocoryne parva De Wit – Fig. 2 C

De Wit, Belmontia IV, 13 p. 279 (1970). Holotype: J. Schulze, 20.2. 1967 (WAG).

There are four sheets of this species at PDA: Silva, Halloluwa 18.2. 1925; Alston 1389, brought from Halloluwa 2.5. 1926; Alston 1390, Urugala 7.9. 1926; RBGP 18.1. 1928.

C. parva is very distinct morphologically and ecologically even though it certainly is related to *C. willisii* Reitz and *C. lucens*. It prefers somewhat exposed but stable river banks below the high-water mark, often between the roots of trees.

This species is illustrated in Petch (1928 Pl. V, Fig. 7 and 11) as *C. nevillei*.

The chromosome number is $2n=28$ (vouchers: P 1974/23 Halloluwa; NJ 22-4 Hiriwadunna, NE of Kegalla).

Cryptocoryne legroi De Wit – Fig. 3 C

De Wit, Belmontia IV, 13 p. 279 (1970). Holotype: R. A. H. Legro (WAG).

The species is closely related to *C. lutea*, but differs in the much larger, brownish leaves, and the spathe which is greenish, rugulose-verruculose. The relation between *C. lutea* and *C. legroi* (diploid and triploid respectively) is probably parallel to that between *C. beckettii* and *C. petchii* and between cytotypes of *C. wendtii* coll.

The specimen illustrated by Sadilek (1972) is probably *C. walkeri*.

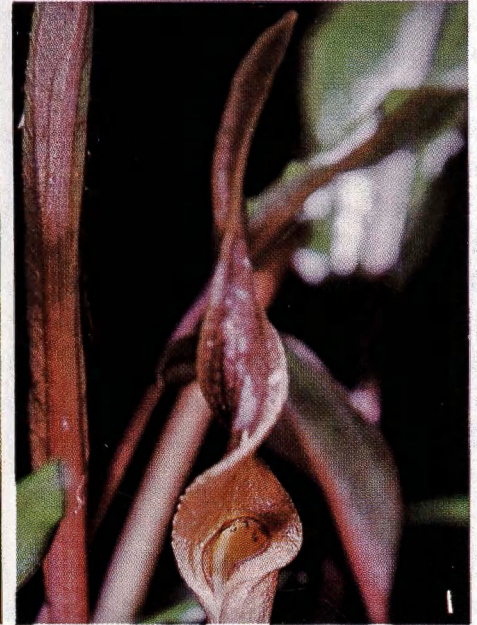
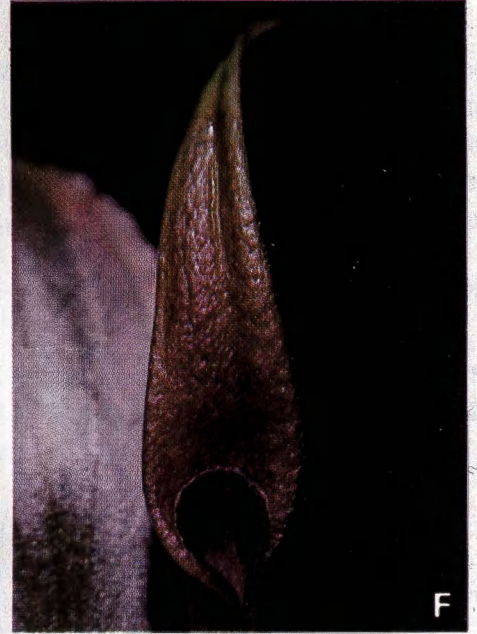
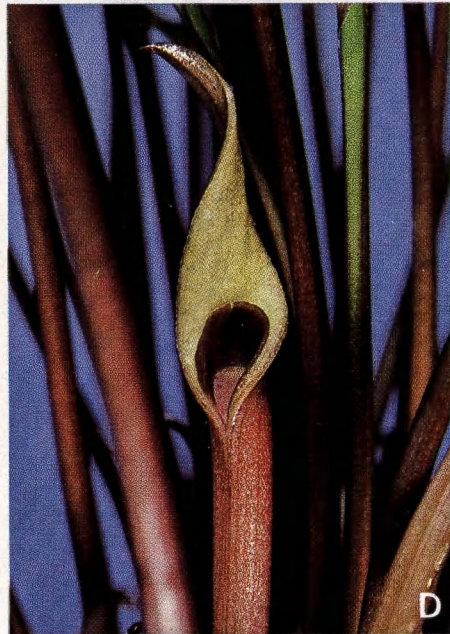
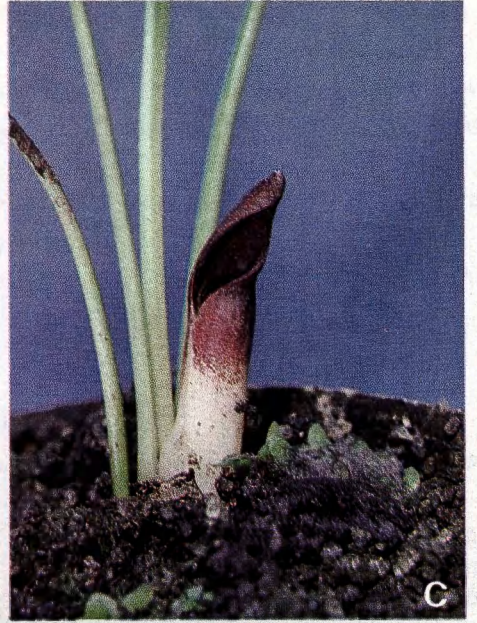
The chromosome number is $2n=42$ counted by Dr Legro (De Wit 1971).

Cryptocoryne bogneri Rataj – Fig. 4 A

Rataj, Revision of the Genus *Cryptocoryne*, ČSAV studie, č 3 p. 100 (May 1975). Holotype: Bogner 484, Atweltota (M).



Fig. 1. *Cryptocoryne nevillei* Trimen ex Hook. f. Plant drawn from Kundu & Balakrishnan 185, Batticaloa (US). – A: Habit. – B: Lower leaf with small lamina and broad sheathing petiole. – C: Limb showing the very prominent collar. – D: Kettle with part of wall removed. – E: Enlarged female flowers showing the stalked stigmas.



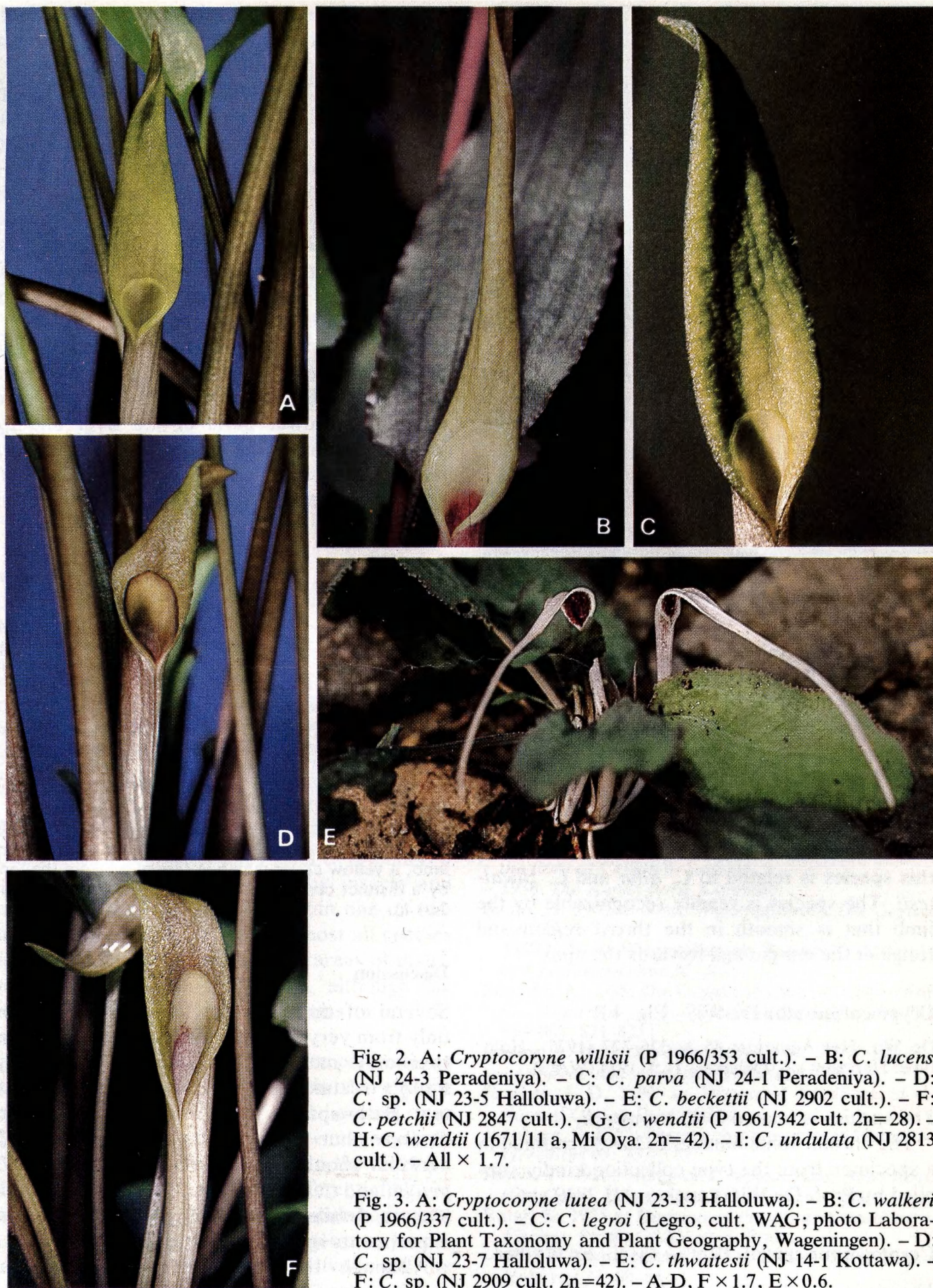


Fig. 2. A: *Cryptocoryne willisii* (P 1966/353 cult.). - B: *C. lucens* (NJ 24-3 Peradeniya). - C: *C. parva* (NJ 24-1 Peradeniya). - D: *C. sp.* (NJ 23-5 Halloluwa). - E: *C. beckettii* (NJ 2902 cult.). - F: *C. petchii* (NJ 2847 cult.). - G: *C. wendtii* (P 1961/342 cult. $2n=28$). - H: *C. wendtii* (1671/11 a, Mi Oya. $2n=42$). - I: *C. undulata* (NJ 2813 cult.). - All $\times 1.7$.

Fig. 3. A: *Cryptocoryne lutea* (NJ 23-13 Halloluwa). - B: *C. walkeri* (P 1966/337 cult.). - C: *C. legroi* (Legro, cult. WAG; photo Laboratory for Plant Taxonomy and Plant Geography, Wageningen). - D: *C. sp.* (NJ 23-7 Halloluwa). - E: *C. thwaitesii* (NJ 14-1 Kottawa). - F: *C. sp.* (NJ 2909 cult. $2n=42$). - A-D, F $\times 1.7$, E $\times 0.6$.

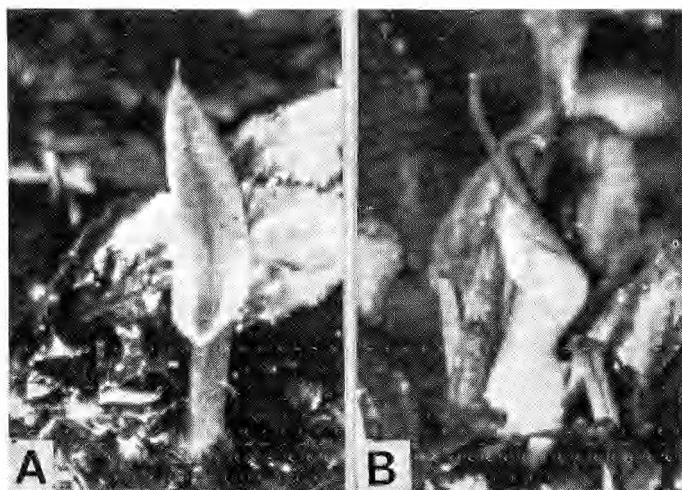


Fig. 4. A: *Cryptocoryne bogneri* (Bogner 484, Atweltota; photo J. Bogner, Botanische Garten, München). – B: *C. alba* (Hermsen s.n., Dehiwala; photo Laboratory for Plant Taxonomy and Plant Geography, Wageningen). – A \times 1.0, B \times 1.2.

C. bogneri De Wit, Het Aquarium 45: 326–327 (June 1975, issued July ?). Holotype: Bogner 484, Atweltota (WAG, isotype M).

Rataj published his description a few months before De Wit. Both descriptions were based on the same collection. The drawing in De Wit is very good.

Rataj's conclusion on p. 100 that *C. bogneri* belongs to sect. *Auriculatae* is rather doubtful as is the connection with *C. walkeri*. There is no doubt that even on morphological grounds, but particularly in view of the chromosome number $2n=36$ (vouchers: NJ 2917 cult.; NJ 2934 cult.) this species is related to *C. alba* and *C. thwaitesii*. The species is readily recognizable by the limb that is smooth in the throat region and rough at the margin and towards the apex.

Cryptocoryne alba De Wit – Fig. 4 B

De Wit, Het Aquarium 45 p. 326–327 (1975). Holotype: Hermsen s.n. Dehiwala 11.9. 1974 (WAG).

The species is related to *C. thwaitesii*.

The chromosome number is $2n=36$ counted in a specimen from the type collection kindly supplied by Prof. De Wit (voucher: NJ 2949 at C).

Cryptocoryne spiralis (Retz.) Fisch. ex Wydler

The species was reported from Sri Lanka by Thwaites (1864 p. 334). The report was based on

a specimen collected by Walker, without doubt the same which had previously been described as *C. walkeri* Schott. An isotype of Koenig's collection of *C. spiralis* at BM bears the inscription "Ceylon" while the holotype at LD and the isotypes at C bear the inscription "Tranquebar" as does the protologue.

Mrs Walker (1840 p. 229) reported *Arum spirale* as frequent on the banks of the Ginderah River (Gin Ganga) south of Hiniduma, and Alston (1931 p. 294) assumed that the plant in question was the same as that collected by Walker and later described as *C. walkeri*. I think it is more probable that the plant in question is *Lagenandra ovata* (L.) Thw. or maybe *L. thwaitesii* Engl., the former being very common in the lower parts of the river and the latter common in the upper parts. *C. walkeri* probably does not occur in the southwestern lowlands. The true *C. spiralis* does not occur in Sri Lanka.

Additional collections

At Halloluwa I made two collections which do not match any of the species described, but a closer study of more material is needed. Both collections have $2n=28$, and are as follows: NJ 23-5 (Fig. 2D) is similar to *C. lucens*, but the leaves are longer and wider and have a purple border. The collar is purple and the limb is greenish with small purple warts. NJ 23-7 (Fig. 3D) is similar to *C. lutea*, but has a brown ring at the edge of the collar which fades towards the centre; the limb is brownish-yellow.

A plant cultivated in Copenhagen NJ 2909 (Fig. 3 F) resembles *C. lutea*. It has a brownish-yellow, recurved limb, a yellow collar which is separated from the limb by a distinct brown line, and a purple-spotted throat. $2n=42$.

Discussion

Several of the Sri Lanka species are known only from very few gatherings, and their present taxonomy must be regarded as preliminary. Rataj's treatment (1975 a) is somewhat inconsistent. He lumps together *C. walkeri*, *C. lutea* and *C. legroi* but following the same principles *C. beckettii* should also have been placed with *C. petchii* and *C. willisii* with *C. lucens*. Obviously a more detailed study by means of cultivation experiments is much needed.

Although the taxonomic status of some species is uncertain, the following grouping can be made (the chromosome number of *C. nevillei*

is unknown, but the species is placed in the first group for morphological reasons).

2n=28, 42

C. nevillei

C. willisii

C. lucens

C. parva

C. undulata

C. wendtii

C. beckettii

C. petchii

C. lutea

C. legroi

C. walkeri

2n=36

C. thwaitesii

C. alba

C. bogneri

It is a remarkable fact that in the Halloluwa locality at least five species grow in places within sight of one another. I made 22 collections of live plants in this locality. There are obvious niche preferences among the species even in this very limited area. There may also be differences in the flowering periods and in the type of insect visitor. It is interesting to note that the species smell quite differently.

The evolutionary situation in *Cryptocoryne* differs in several respects from that commonly found in aquatic plants. Species of *Cryptocoryne* are amphibious, are pollinated by insects and have seeds which germinate within one or two days and die if they dry out. Almost all species of *Cryptocoryne* have very small areas of distribution. Even within Sri Lanka, although the material is very limited, there seems to be definite patterns of distribution.

In the mountainous southwestern part with its radiating system of rivers, and in the eastern and northern parts with hills and isolated river systems, a genus like *Cryptocoryne* may undergo evolutionary radiation, adapting to the different local conditions and also differentiating at random. Well-adapted local populations can further become established by vegetative propagation. As the seeds are short-lived and the pollinating insects (mostly small flies) unable to travel over long distances gene exchange be-

tween populations of different river valleys is rare. Moreover, owing to the highly varied environmental conditions two separate populations are seldom in flower at the same time.

Ecological specialization and evolutionary radiation in small populations will thus produce a large number of local populations that differ slightly morphologically. A broad species concept may prove to be the most suitable in this situation but experimental studies at population level are badly needed.

Acknowledgements

My visit to Sri Lanka in March 1975 was supported by Vingresor, Arntstedt's Foundation and P. C. N. Friderichsen's Foundation, which is gratefully acknowledged. Mindelegatet for Brygger J. C. Jacobsen and Marcus Lorenzen's Foundation have most kindly made the printing of colour plates possible. Thanks are due to many colleagues for their help and for their interest in my work, to H. C. D. de Wit, Wageningen and to J. Bogner, München, for valuable discussions and information and for letting me publish their pictures of *C. alba*, *C. legroi* and *C. bogneri* and to A. Strid for critical comments on the manuscript. H. Windeløv kindly placed his large collection of *Cryptocoryne* at my disposal. I am also indebted to the Director and staff of the Herbarium, the Botanic Garden, Peradeniya. The Botanical Garden of the University of Copenhagen placed facilities at my disposal for the cultivation of *Cryptocoryne* species in the experimental hothouse.

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Hedyotis erecta Manilal & Sivarajan (Rubiaceae), a new species from S India

K. S. Manilal and V. V. Sivarajan

Manilal, K. S. & Sivarajan, V. V. 1976 06 30: *Hedyotis erecta* Manilal & Sivarajan (Rubiaceae), a new species from S India. Bot. Notiser 129: 191–192. Stockholm. ISSN 0006-8195.

A new species of *Hedyotis*, *H. erecta* collected from Calicut, Kerala, India is described and illustrated. This is related to *H. corymbosa* L. but differs from it in several important characters.

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V. V. Sivarajan, Department of Botany, Kirori Mal College, University Enclave, Delhi, India.

During a study of the medicinal plants of Malabar, the authors came across a species which resembles *Hedyotis corymbosa* L. to some extent but differs from all other known species of *Hedyotis* (cf. Backer & Bakhuizen 1965, Rao & Hemadri 1973). It is reported here as a new species, *Hedyotis erecta* Manilal & Sivarajan sp. nov.

Hedyotis erecta Manilal & Sivarajan sp. nov. insignis, *H. corymbosae* L. arcte affinis, sed differt caule erecto et ramis fastigiatis, stipulis in fimbriis 2 vel 3 productis et cellulis testae parietibus rectis instructis.

Herba annua. Caulis erectus, 17–25 cm longus; rami pauci ad nodos solitarii et ad partem inferiorem caulis restricti; caulis ramique glabri, pars superior internodiorum distincte quadricostata. Folia anguste lanceolata, apice acuta vel mucronata, usque ad 2 cm longa et 0.5 cm lata, supra omnino glabra, subtus parce hirtella, margine recurvata, parum scabridula, costa basin versus impressa, venis lateralibus obscuris; stipulae glabrae, fimbriis 2 vel 3 filiformibus, 1.0–1.5 mm longis instructae. Inflorescentiae nunc cymae 2-florae vel rare 3-florae, nunc ad florem solitarium, ad apicem pedunculi insertum reductae; pedunculus et pedicelli filiformes; pedunculus usque ad 1.5 cm longus, patens; pedicelli multo breviores, i.e. 3–4 mm longi. Flores isostyli; ovarium glabri sub anthesi 1 mm altum, post anthesin usque ad 2 mm expansum; lobi calycis lanceolati, 1 mm longi, margine parum scabriduli; corolla rosea, tubo tereti 1 mm longo, i.e., longitudine lobos calycis fere aequante, in fauce annulo pilorum pellucidorum instructa, lobis ovatis, acutis, 0.5 mm longis, patentibus; antherae sessiles, paulum supra medium tubum insertae, oblongae; stylus 1 mm longus, glaber; lobi stigmatis clavati,

papilloso. Capsula compressa, 2 mm diametro, apice parum producta, ab apice loculicida. Semina multa; cellulae testae fere rectangulares, parietibus rectis instructae, laeves.

Typus (Sivarajan 491) in declivo lateritico prope locum Idimuzhikkal collectus, circ. 5 km a campo Universitatis Calicutensis (Kerala) remotum, in herbario Lucknowensi (LWG) conservatus.

Hedyotis erecta Manilal & Sivarajan, sp. nov. differs from the closely related *H. corymbosa* L. in its invariably erect main shoot with fastigiate branches, stipules with 2 or 3 filiform appendages and testa cells with straight walls.

Annual herb. Stem erect, 17–25 cm long; branches few, solitary at the nodes and confined to the lower part of the stem, fastigiate; stem and branches glabrous; the upper part of the internodes distinctly four-ribbed. Leaves narrowly lanceolate, acute or mucronate at the top, up to 2 cm long and 0.5 cm wide, on the upper side entirely glabrous, on the lower one sparsely hirtellous; margin recurved and slightly scabridulous; midrib towards the base impressed; lateral nerves inconspicuous; stipules glabrous, provided with 2 or 3 bristles, 1.0 to 1.5 mm long. Inflorescence either in the form of a 2- or, rarely, 3-flowered cyme or reduced to a single flower at the top of the peduncle; peduncle and pedicels filiform; peduncle up to 1.5 cm long, spreading; pedicels much shorter, viz. 3–4 mm long. Flowers isostylus; ovary

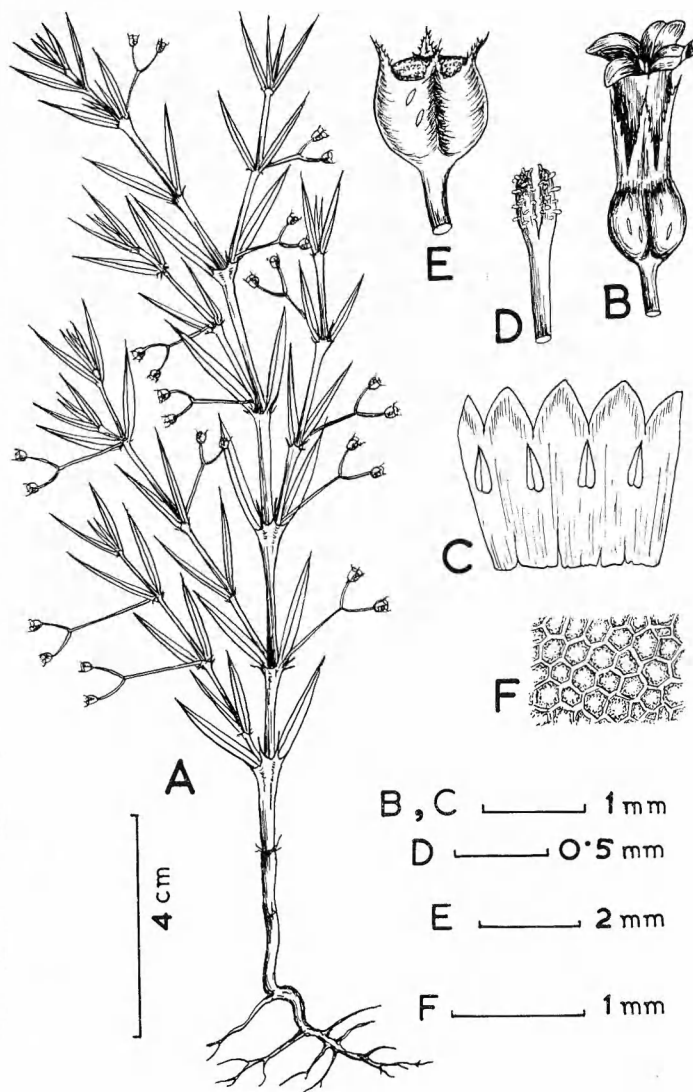


Fig. 1. *Hedyotis erecta* sp. nov. - A: Habit. - B: Flower. - C: Corolla spread open. - D: Stigma. - E: Fruit. - F: Testa cells showing straight walls.

glabrous, in the flowering stage 1 mm, in the fruiting stage up to 2 mm long; calyx lobes lanceolate, 1 mm long, with slightly scabridulous margin; corolla pink; tube terete, 1 mm long, i.e. almost as long as the calyx lobes, on the inside in the throat with a ring of hyaline hairs; lobes ovate, acute, 0.5 mm long, spreading; anthers sessile, inserted slightly above the middle of the corolla tube, oblong; style 1 mm long, glabrous; stigma lobes clavate, papillose, capsule compressed, 2 mm in diam., at the top slightly beaked, loculicidal from the tip. Seeds many; testa cells almost rectangular, with straight walls, smooth. Fig. 1.

The type specimen (Sivarajan 491) was collected from the laterite slopes at Idimuzhikkal, about 5 km from the Calicut University Campus in Kerala, and is deposited at LWG.

Acknowledgements. We are very grateful to Dr C. E. B. Bremekamp for rendering the Latin description and for other kind assistance.

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Drawings of Scandinavian plants 113–114

Epilobium L. sect. Epilobium

Alf Oredsson and Sven Snogerup

Oredsson, A. & Snogerup, S. 1976 06 30: Drawings of Scandinavian plants 113–114. *Epilobium* L. sect. *Epilobium*. *Bot. Notiser* 129: 193–197. Stockholm. ISSN 0006-8195.

Drawings and descriptions are given for *E. lamyi* F. Schultz and *E. tetragonum* L. The taxonomic treatment of these species is discussed.

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These two species are very similar, and have often been confused even by otherwise reliable collectors and authors of floras. Despite their similar habit, they display a series of distinguishing characters, e.g. shape and margin of leaves, size of bracts, hairiness of midrib of upper leaves, length of capsule stalks, length and branching of inflorescence and size of seeds. According to Raven (1968), they are connected by numerous fertile intermediates. This is not the case in Scandinavia and not in the limited European material studied by us. The intermediates observed are very few, but seed setting is on the average c. 80%. Thus the distinction between these two species is probably mainly upheld because of predominant autogamy.

113. *Epilobium lamyi* F. Schultz 1844

Perennial herb, (15–)40–75(–110) cm high. Stem usually densely branched in upper half only, rarely from the base. Late in the autumn often forming adventitious shoots within the inflorescence with leaves similar to basal or lower cauline ones. Stem usually with 8–12 pairs of leaves below the inflorescence, leaves longer than the internodes, producing several or rarely one (5–)10–15-flowered inflorescences, inflorescence region often repeatedly branched and rather dense. Stolons subterranean, densely

rooted, up to 10 mm, formed late in the autumn. Turions formed at ends of stolons as loose epigeal rosettes of 10–15 light green, spatulate to narrowly obovate, glabrous, obtuse, subentire leaves (15–)25–70(–90) mm long. Glandular hairs never found on any part of the plant.

Stem (1–)2–3(–5) mm thick, almost square in transection or in old, thick parts terete, with 4 usually conspicuous raised lines below the leaf margins, those from opposite leaves not uniting but separate for entire length of internode. Stem sparsely hairy below, mainly along the lines and below the midribs, above more evenly moderately to densely hairy, hairs 0.1–0.3(–0.5) mm, incurved to adpressed.

Most leaves opposite, usually only the bracts alternate, petioles winged and the leaf margin often narrowly decurrent on the lines, leaf bases not united. Basal leaves 10–30(–50) mm long, with petioles up to 5(–15) mm long, spatulate to lanceolate, obtuse, subentire. Middle cauline leaves (15–)30–60(–90) mm long, 5–12(–20) mm broad, sessile or with a petiole up to 2 mm long, very narrowly ovate or rarely lanceolate to linear, acute to obtuse, regularly serrate with several forward-pointing but usually not hooked teeth up to 0.5 mm high. Upper leaves considerably smaller, narrowly ovate, acute. Basal and middle cauline leaves subglabrous to sparsely hairy chiefly on the margin, bracts moderately to densely hairy on the abaxial

side of the midrib and the margin, hairs like those of the stem.

Pedicels first erect, in fruit erectopatent. Buds ovoidal, with a distinct conical tip. Sepals 4.5–6.5 mm, connate to 1–1.5 mm at base, narrowly ovate, green when young, later often reddish, densely hairy on the connate part, moderately so above. Petals (4.5–)7–8 mm, notched to 1–2 mm, rather dark purplish-pink or rarely light reddish-pink. Anthers (0.75–)0.85–1.0 mm, long filaments 3.0–4.5 mm, short filaments 1.8–2.5 mm. Style about equalling the long stamens, stigma capitate.

Capsule stalk (5–)7–12(–20) mm. Capsule (55–)65–80(–95) mm, densely and evenly hairy, hairs like those of the stem. Seeds (0.85–)0.9–1.0 mm long, 0.45–0.5 mm broad, narrowly obovoidal, flattened and deeply furrowed ventrally, broadly obtuse apically, obtuse to subacute basally, without a neck, surface with distinct papillae c. 0.03 mm high in rather distinct rows, chalazal hairs usually 40–50, 6–7.5 mm long. Flower homogamous, at least in small-flowered types sometimes cleistogamic.

E. lamyi has a rather uneven distribution in Scandinavia, with concentrations in the Stockholm area and some areas of SE Sweden and S Denmark. It is chiefly found along ditches and in other man-made habitats, so that it is a debatable point to what extent its present distribution is the result of introductions.

It is probably indigenous along the W Baltic coastal areas to SW Finland. In many places in S. Sweden and Denmark it is obviously introduced.

E. lamyi occurs in Europe, Asia Minor and Madeira.

Known hybrids: with *E. collinum*, *hirsutum*, *montanum*, *parviflorum*, *roseum* and *tetragonum*.

114. *Epilobium tetragonum* L. 1753

Perennial herb, (15–)60–80(–110) cm high. Small specimens often simple, large ones moderately to densely branched in middle and upper part, or rarely from the base. Stem usually with 6–10

pairs of leaves below the inflorescence, leaves longer than the internodes, producing several or in small specimens only one (5–)15–25(–35)-flowered inflorescence. Stolons, when present, less than 10 mm long, subterranean, densely rooted. Turions formed in the autumn, sessile or at the end of the stolons, as loose epigeal rosettes of light green, spatulate to lanceolate, glabrous, obtuse or acute, weakly serrate or subentire leaves (10–)50–100 mm long. Glandular hairs never found on any part of the plant.

Stem (1–)3–5(–7) mm thick, almost square in transection or old, thick parts terete, with 4 usually conspicuous raised lines below the leaf margins, those from opposite leaves usually not uniting but separated for the entire length of internode. Stem subglabrous below, sparsely hairy above, denser along the lines and below the midribs, hairs 0.1–0.2(–0.3) mm, incurved to adpressed.

Most leaves opposite, usually only the upper bracts alternate, petioles, when present winged and the leaf margin somewhat decurrent on the lines of the stem. Basal leaves 20–55 mm long, with petioles up to 10(–15) mm long, spatulate to lanceolate, obtuse, weakly and irregularly serrate, often with bases uniting around the stem. Middle cauline leaves (25–)40–80(–95) mm long, (5–)7–15(–22) mm broad, always sessile, not uniting around the stem, very narrowly ovate to almost linear, acute, regularly serrate with several forward-pointing and often hook-shaped teeth up to 1 mm high. Upper leaves smaller, but even the bracts comparatively large, in small specimens in particular often some flowers present even in the axils of middle cauline leaves. Leaves all subglabrous or the upper ones sparsely hairy chiefly at the margin, midribs with few hairs only, hairs like those of the stem.

Pedicels first erect, in fruit erectopatent. Buds ovoidal, with a distinct conical tip. Sepals 4.0–5.5(–6.0) mm, connate to 1–1.5 mm at base, narrowly ovate, apiculate, green when young, later sometimes reddish, densely hairy on the connate part, moderately so above. Petals (4.5–)5–6.5(–7.5) mm, notched to 1–1.5 mm, usually rather dark purplish-pink but sometimes

Fig. 113. *Epilobium lamyi* F. Schultz. – A: Habit, $\times 1/3$. – B: Turions, $\times 1/2$. – C: Stem node, $\times 2.5$. – D: Cauline leaves, $\times 1$. – E: Upper leaves, $\times 1$. – F: Upper stem part and leaves, $\times 2.5$. – G: Buds, $\times 1$. – H: Flower, $\times 1$. – J: Apical part of capsules, $\times 2.5$. – K: Style, $\times 1$. – L: Petal, $\times 1$. – M: Sepals, $\times 2.5$.



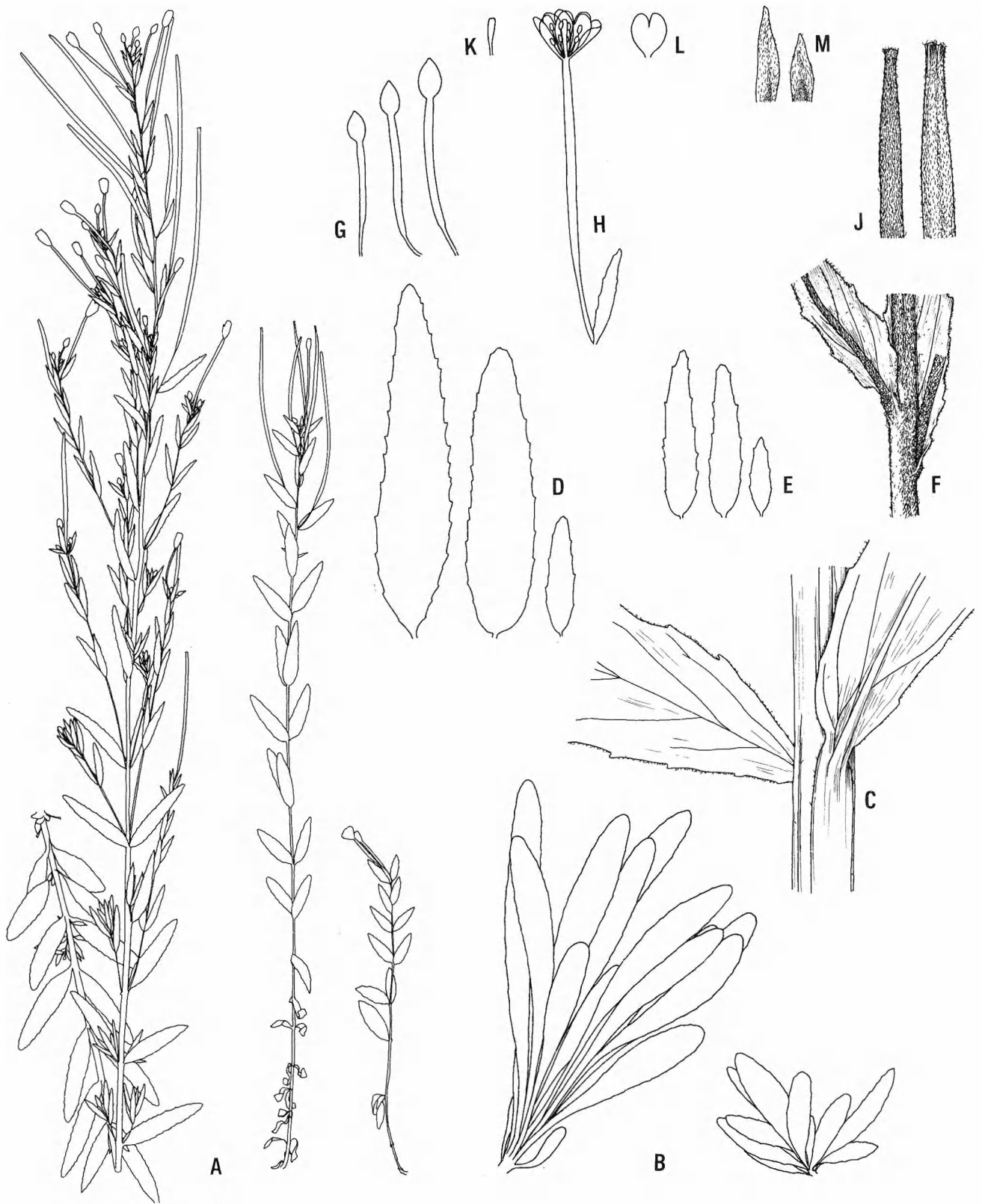


Fig. 114. *Epilobium tetragonum* L. - A: Habit, $\times 1/3$. - B: Turions, $\times 1/2$. - C: Stem node, $\times 2.5$. - D: Culine leaves, $\times 1$. - E: Upper leaves, $\times 1$. - F: Upper stem part and leaves, $\times 2.5$. - G: Buds, $\times 1$. - H: Flower, $\times 1$. - J: Apical part of capsules, $\times 2.5$. - K: Style, $\times 1$. - L: Petal, $\times 1$. - M: Sepals, $\times 2.5$.

light. Anthers 0.7-0.9 mm, long filaments 2.5-3.5 mm, short filaments 1.5-2 mm. Style equaling or slightly longer than the long stamens, stigma capitate.

Capsule stalk (10-)15-25(-40) mm. Capsule (55-)70-85(-95) mm, young ovary usually densely hairy, ripe capsules sparsely to moderately so, hairs like those of the stem. Seeds (0.9-)1.0-1.1 mm long, 0.4-0.5 mm broad, narrowly obovoidal, flattened and deeply furrowed ventrally, broadly obtuse apically, acute basally, without a neck, surface with distinct papillae 0.02-0.03 mm high in distinct rows, chalazal hairs usually 35-40, 6.5-7.5 mm long. Flower homogamous, sometimes some flowers at least cleistogamic.

E. tetragonum is probably indigenous in parts of S Scandinavia such as S Denmark, Skåne,

Öland and Gotland, mainly occurring at the margins of watercourses. Most of the present-day localities are, however, in ditches of cultivated areas and in ruderal localities. It is thus difficult to decide how much of its present distribution is the result of introductions. It occurs rather frequently in the above-mentioned areas and with scattered localities in other parts of S Sweden and in a few localities in SE Norway and SW Finland.

E. tetragonum occurs in Europe and W Asia.

Known hybrids: with *E. lamyi*, *montanum*, *palustre*, *parviflorum* and *roseum*.

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Phleospora idahoensis and Didymella festucae from Gotland, Sweden

J. Drew Smith

Smith, J. Drew 1976 06 30: *Phleospora idahoensis* and *Didymella festucae* from Gotland, Sweden. *Bot. Notiser* 129: 199–200. Stockholm. ISSN 0006-8195.

Phleospora idahoensis Sprague is reported as new to Sweden. Measurements of conidia and of ascospores of its associated perfect state, *Didymella festucae* (Weg.) Holm are presented.

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Eriksson (1967) reported that pycnidia with worm-like conidia were present with *Didymella festucae* (Weg.) Holm (syn. *Didymosphaeria festucae* Weg.) of *Festuca rubra* L. in a Swedish collection made by T. Vestergren in Bro parish on the island of Gotland on 17 June 1920. The original determination of *D. festucae* was made by Dr Lennart Holm (1953) on 17 June 1953. Eriksson (1967) did not connect the conidia with the *Didymella* perfect state because he knew of no such imperfect state in *Didymosphaeria* or *Didymella*. The collection already referred to, and another, also made by T. Vestergren on 22 June 1920 on *Avena pubescens* Huds. from Brissund on Gotland (S), were examined and spores measured after treating the material with warm 3% potassium hydroxide solution (Table 1).

No pycnidia or conidia were found in the Brissund sample. The identification of the grass host as *Avena pubescens* appears incorrect in this case. A single flower with ripe seed remaining attached in a portion of inflorescence had no awn on the outer palea, a characteristic of this species. There was no indication that an awn had ever been present there or in a detached flower where the length/width ratio of the ripe (germinated) caryopsis was 2:1 approximately. In *A. pubescens* (= *Helictotrichon pubescens* (Huds.) Pilger) the latter ratio is 6:1 approximately (Hubbard 1968). No reliable identifica-

tion is possible with the amount of material available.

The range of length of ascospores, 21–43 μ for the two Swedish collections falls within that found by Smith & Shoemaker (1974) for many collections of *D. festucae* from North America. Width ranges also concurred. The maximum length was slightly greater than for Norwegian material (Smith 1976). Perithecia, asci and ascospores were typical of the Swiss

Table 1. Measurements of ascospores of *D. festucae* and associated conidia in microns (50 measurements).

Measure- ment	Range	Mean	Median	Mode
Bro on F. rubra				
<i>Ascospores</i>				
Length	21–38	29	30	25
Width	4.5–7.8	6.8	6.2	6.7
<i>Conidia</i>				
Length	28–73	46	51	45, 50
Width	2.2–5.6	3.9	3.9	3.4
Brissund on A. pubescens				
<i>Ascospores</i>				
Length	25–43	32	34	31
Width	5.6–8.9	7.3	7.2	6.7

type of Rehm Ascomyceten No. 1240 (Smith & Shoemaker 1974). The non-septate, vermiform conidia were typical of *Phleospora idahoensis* Sprague which was shown to be the imperfect state of *D. festucae* in North America (Smith 1971). The two states were also found associated in the Swiss type, and Norwegian material. Conidia were similar in length and width to those from the latter. Apparently this fungus, which is endemic on native fescues in North America and highly destructive in seed crops of *F. rubra* in northwestern Canada has a wide arctic/alpine distribution in the northern hemisphere. Although the fungus does not seem to have been found in the USSR (Personal communication Dr V. A. Melnik, Komarov Botanical Institute, Leningrad, 20 July 1975) its occurrence there is highly probable.

I am indebted to the Curator, Botanical Museum, Stockholm and Dr Ove Eriksson of Umeå University for the opportunity to examine the material.

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Gyrostemonaceae: status and affinity

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Pollen structure and chromosome cytology of the Gyrostemonaceae strongly support the recognition of this family as distinct from Phytolaccaceae. Presence of S-type plastids suggests, in addition, that the family is not related to the order Centrospermae. Betalains and anthocyanin pigments were not detected in two genera of the family, *Gyrostemon* and *Codonocarpus*, that were examined for these substances. However, an earlier report of the isolation of an isothiocyanate from *Codonocarpus cotinifolius* taken together with the recent discovery of a glucosinolate in *Batis maritima* and the pollen similarity between *Batis* and members of the Gyrostemonaceae, suggest that both the Bataceae and Gyrostemonaceae should be removed from the Centrospermae. Chemical evidence supports their inclusion in the Capparales.

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The family Gyrostemonaceae consists of 5 genera and 17 species (Willis 1973). The distinctness of the family was recognized as early as 1840 by Endlicher (1836–1840) who included the genera *Gyrostemon* Desf. and *Codonocarpus* A. Cunn. ex Hook. Later, Endlicher (1850) added also *Didymotheca* Hook. f. Moquin-Tandon (1849) treated these three genera as tribe Gyrostemoneae of the Phytolaccaceae and established a new genus, *Tersonia* Moq., which he also included in Phytolaccaceae as tribe Tersonieae. Most subsequent authors treated these genera as members of the Phytolaccaceae (Bentham & Hooker 1880, Heimerl 1889, Engler & Gilg 1912, Wettstein 1935). *Cypselocarpus* F. Muell. had a more varied taxonomic history. It was originally described as *Threlkeldia haloragoides* F. Muell. ex Benth. and placed in the Chenopodiaceae (Bentham 1870), but was subsequently referred to the Phytolaccaceae by

Mueller (1873) as a new genus. Bentham & Hooker (1880) accepted the genus but moved it back to the Chenopodiaceae where it was considered as of doubtful position by Volkens (1892). Finally, Stapf (1915) recognized its relationship to *Tersonia* and placed the genus in the tribe Gyrostemoneae of the Phytolaccaceae.

Cronquist (1968) includes Gyrostemonaceae in the Phytolaccaceae, while most other recent authors recognize it as a separate family (Heimerl 1934, Gundersen 1950, Eckardt 1964, Takhtajan 1969, Thorne 1968, Dahlgren 1975). Of particular interest in connection with our studies is Dahlgren's (1975) inclusion of Gyrostemonaceae in the Capparales, together with Bataceae, a small family also previously allied with the Centrospermae.

Recently, several independent lines of study have provided evidence not only of the validity of Gyrostemonaceae, but have focused doubt

on the ordinal position of the family. Ultrastructural data from pollen exine and sieve-element plastids and chemical evidence, already proven to be useful for the clarification of systematic problems in the Centrospermae (Hunziker et al. 1974, Behnke et al. 1974, Mabry and Behnke 1976, Nowicke 1976), as well as chromosome cytology, are presented below as results of a collaborative investigation of the systematic position and affinities of the Gyrostemonaceae.

Ultrastructure of sieve-element plastids

Transmission electron microscope studies were made of *Codonocarpus cotinifolius* (Desf.) F. Muell. and *Didymotheca tepperi* F. Muell. ex Walter. Their sieve-elements have been demonstrated to contain starch-storing S-type plastids (Behnke 1975, a micrograph is published in Behnke 1976). This is in contrast to all families of the order Centrospermae, including Phytolaccaceae, which are characterized by distinctive P-type sieve-element plastids, but corresponds with S-type sieve-element plastids of Bataceae, another family of doubtful alliance to Centrospermae (Behnke 1972, 1976). The micromorphological differences between these P-type plastids and the S-type found in *Codonocarpus* and *Didymotheca* thus seem adequate to propose the exclusion of Gyrostemonaceae from Centrospermae (Behnke 1975).

Palynology

Species examined: *Codonocarpus cotinifolius* F. Muell. (Everist 2734 US); *Didymotheca pleiococca* F. Muell. (French s.n. US); *Gyrostemon australasicus* (Moq.) Heim. (Perry 2471 US); *G. ramulosus* Desf. (Pritzel 384 US); *Tersonia brevipes* Moq. (Pritzel 793 US).

All taxa examined in this study and previously (Nowicke 1976) had grains which were medium-sized, more or less prolate, 3-colpate, and with a psilate or slightly scabrate ectexine (Fig. 1 A, B). Prijanto (1970 a) in a study of the Gyrostemonaceae for the World Pollen Flora, examined all genera and 14 of the 17 species;

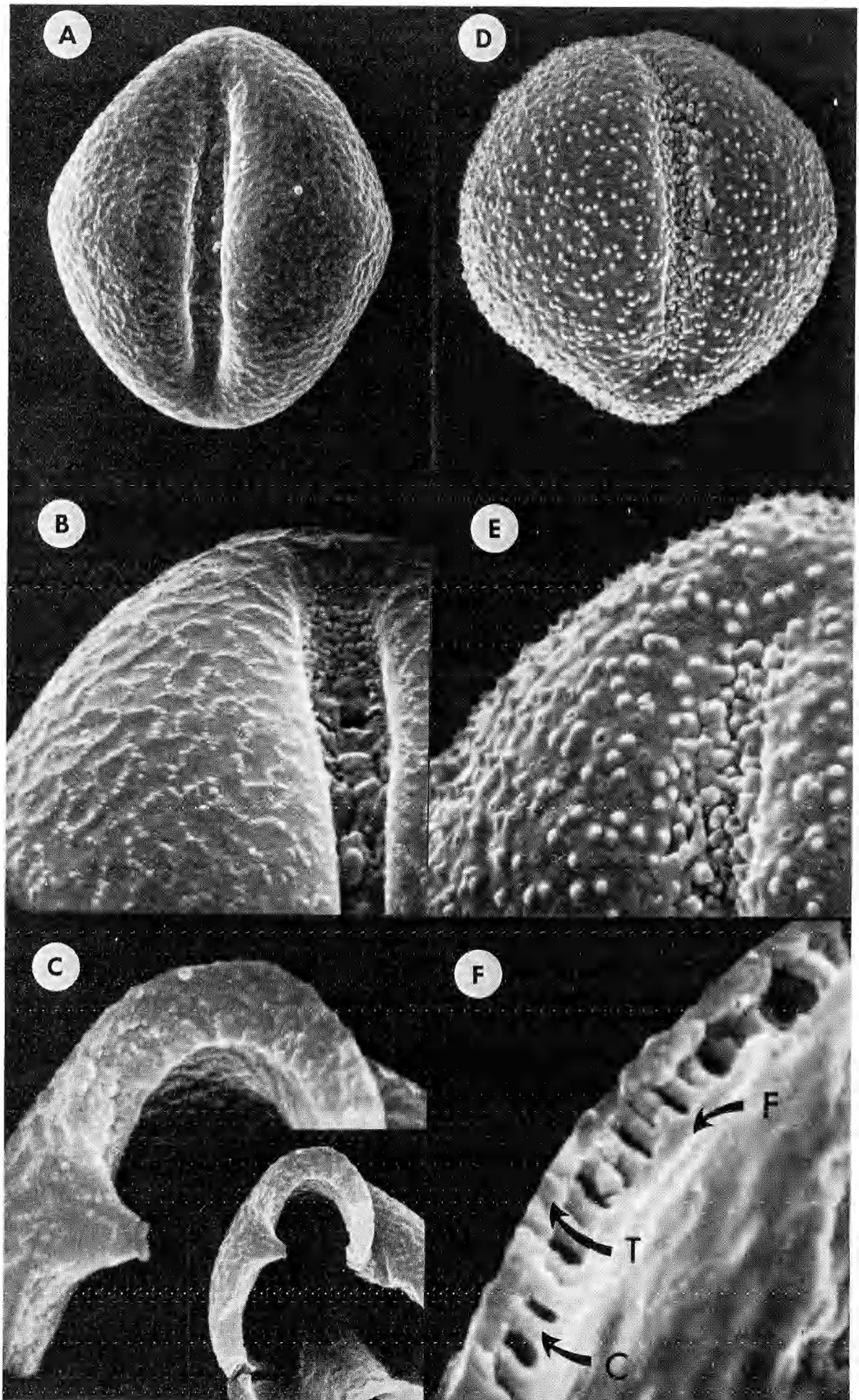
detailed measurements and descriptions are given in this study. In an earlier study of the Centrospermae (Nowicke 1976), almost 85% (151 of 177) of the species examined in the betalain families and the Caryophyllaceae and Molluginaceae had grains with an ectexine pattern which was described as spinulose and tubuliferous-punctate (Fig. 1 D, E). Moreover, these centrospermous grains have an exine which typically consists of a foot layer, columellae, and tectum (Fig. 1 F). This type of exine structure is not found in the Gyrostemonaceae. In light microscopy the exine appears solid, and to consist of a very thin nexine and a very thick sexine. For scanning electron microscopy, acetolyzed grains were mechanically broken, and in cross-section also appeared solid (Fig. 1 C), the exine not differentiated into the three layers mentioned above.

The ectexine pattern and the internal structure of the exine make the pollen grains of the Gyrostemonaceae distinct from the most common type found in the Centrospermae. In fact, none of the taxa examined in either the betalain families or the Caryophyllaceae and Molluginaceae had pollen grains similar to those of the Gyrostemonaceae (Nowicke 1976). Notably, however, *Batis maritima* has pollen grains very closely resembling those of Gyrostemonaceae (Prijanto 1970 b) and in view of the very unusual nature of these grains it seems likely that these two families may be related.

Chemistry

Using standard procedures all organs of the available plant samples of *Gyrostemon* and *Codonocarpus* were examined for the presence of the characteristic anthocyanins or betalains, since betalains are unique to nine and anthocyanins occur in two of the eleven centrospermous core families (Mabry 1976). However, not even trace amounts of either type of these red-violet pigments were detected. Thus these chemical data do not clarify the position of the Gyrostemonaceae with respect to either the betalain-

Fig. 1. Scanning electron micrographs of pollen. – A–C: *Codonocarpus cotinifolius* (Gyrostemonaceae). – D–F: *Phytolacca americana* (Phytolaccaceae). – A: Equatorial view, $\times 2350$. – B: Ektexine, $\times 5250$. – C: Cross-section, mesocolpial region, $\times 6300$; inset, fractured grain from which the enlargement was taken, $\times 2275$. – D: Equatorial view, $\times 2200$. – E: Ektexine, $\times 5250$. – F: Cross-section from fractured grain, illustrating foot layer (F), columellae (C), and tectum (T), $\times 10,500$.



or anthocyanin-producing centrospermous families. However, in view of the pollen similarity between members of the Bataceae and the Gyrostemonaceae, it is significant that a glucosinolate was recently detected in *Batis maritima* (M. G. Ettliger unpubl. mscr.), thus linking this family to the other glucosinolate families (e.g. Cruciferae, Capparidaceae, etc.); Ettliger also (see Ettliger & Kjaer 1968) pointed out that the previous report of an isothiocyanate (a compound derived by hydrolysis of a glucosinolate) from *Codonocarpus cotinifolius* (Bottomley & White 1950) indicates that the Gyrostemonaceae also belongs with these same families.

Chromosome cytology

Material: *Gyrostemon ramulosus* Desf. $2n = 28$ (30). Australia, W. Australia, seeds obtained from King's Park Botanic Garden, cultivated at Missouri Botanical Garden, P. Goldblatt 3400 (MO).

At the time that the chromosomes of *Gyrostemon ramulosus* were under investigation, the cytology of the family was unknown, and a chromosome number of $2n = 28-30$ was obtained from mitotic studies of root tips of germinated seedlings, and this was provisionally reported in Raven's (1975) review of the cytology of the angiosperms. A recent and more thorough cytological survey of the Gyrostemonaceae by Keighery (1975) has established the chromosome number of the family to be $n = 14$ in four of the five genera, including *G. ramulosus*, investigated mitotically here.

The chromosome number of $n = 14$ in the Gyrostemonaceae confirms the validity of the segregation of Gyrostemonaceae from Phytolaccaceae, all species of the latter having chromosome numbers based on $x = 9$. The base number of $n = 14$ suggests not only that the family is unrelated to Phytolaccaceae, but reinforces the phytochemical and ultrastructural data in inferring that the placement of Gyrostemonaceae in the order Centrospermae is incorrect. Most families of the Centrospermae are characterized by a basic chromosome number of $x \times 9$, although other numbers are recorded, with $x = 11$ in Cactaceae, $x = 12$, 11 in Basellaceae, $x = 7, 8, 9, 10, 11, 12, 13$ in Caryophyllaceae, while abundant aneuploidy is found in Portulacaceae, Nyctaginaceae and

Amaranthaceae (Raven 1975), making it difficult to determine base numbers in these. Chromosome numbers of $n = 14$ are, however, very uncommon throughout the order, and occur only in occasional polyploids in a few families, while this number is fundamental in Gyrostemonaceae.

Discussion

The ultrastructural evidence presented here alone is of such fundamental nature as to form the basis for the exclusion of Gyrostemonaceae from the Centrospermae. In this light, the inability to detect the presence of anthocyanins and betalains may be taken as support of the exclusion of Gyrostemonaceae from the Centrospermae and the previous report of the isolation of an isothiocyanate indicates, as suggested by Ettliger to us, alignment with the glucosinolate families.

The pollen morphology of the Gyrostemonaceae serves not only to emphasize the close relationship of the five genera in the family but, more importantly, supports its familial status as distinct from the Phytolaccaceae and its removal from the order Centrospermae. Palynologically, the Gyrostemonaceae appear most closely related to the Bataceae (Priyanto 1970 a, b), a small family also often placed in Centrospermae. In a recent paper, Walker & Skvarla (1975) indicated that columellaless pollen is a condition associated for the most part with members of the Magnoliales, which suggests that the Gyrostemonaceae may be more primitive than previously thought. Columellaless pollen has not been reported from the Capparales, s. s.

Recently, Dahlgren (1975) being aware of the glucosinolate results and views of Ettliger, placed Gyrostemonaceae in Capparales with Bataceae amongst other families, commenting, however, that Gyrostemonaceae and Bataceae might be grouped in a separate order of his Violanae. Similarity of the pollen of Gyrostemonaceae and *Batis* is remarkable and consistent with this treatment and, in view of the previous isolation of an isothiocyanate from *Codonocarpus cotinifolius* and the recent detection by Ettliger of benzylglucosinolate in *Batis maritima*, we favor the placement of the Gyrostemonaceae along with the Bataceae in or near

the Capparales. Differences in basic chromosome number between Gyrostemonaceae with $n = 14$ and Bataceae with $n = 11$ (Fulcher 1972, Goldblatt 1976) (a report of $n = 9$ for *Batis maritima* (Engel & Schmidt 1972) is probably erroneous) suggest, however, that the relationship between these two families may not be close.

It is hoped that this study will stimulate further morphological, anatomical and chemical research on the affinities of Gyrostemonaceae (for example; verification of glucosinolates in Gyrostemonaceae is desired).

Acknowledgements

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Iridoid compounds in Fouquieriaceae and notes on its possible affinities

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The presence of iridoid glucosides in three species of the monogeneric family Fouquieriaceae is reported. The compounds adoxoside and loganin as well as a few other related iridoids have been identified. Tentative structures are given for the compounds.

A list of characters is presented. The family is compared in particular with families of the orders Tamaricales, Ericales, Cornales and Solanales, sensu Dahlgren 1975. It is concluded that *Fouquieria* is more closely allied to taxa of Ericales than of the other orders. It should perhaps be placed in a separate order in the Cornanae near Ericales and Cornales. A close affinity between Fouquieriaceae and Polemoniaceae, which has previously been suggested, is considered but is not found particularly convincing.

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Fouquieriaceae is monogeneric and, according to Henrickson (1972), contains 11 species. It consists of shrubs, small ("candelabra") trees or bizarre succulents native to Mexico and the arid southwestern parts of USA. The family has been studied in detail and revised by Henrickson (1967, 1968, 1969 a, b, c, 1972 and 1973), but the characters have not pointed to any definite affinities. Conventionally the family is still often placed with Tamaricaceae and Frankeniaceae and other families in orders with parietal placentation (Parietales, Violales, Guttiferales, Cistales, etc.), as it has been in many systems from Endlicher 1836–40 up to Cronquist 1968 and Hutchinson 1973. (For further references see Gibbs 1974.) Less conventional positions have been: in or near Crassulaceae, in Euphorbiales, Ebenales, Primulales and by Skottsberg (1940), Melchior (1964) and recently by Thorne (1968) near Polemoniaceae (in Solanales), and by one of us (Dahlgren 1975) in Saxifragales. In none of these families or orders have any iridoid compounds been found.

An interesting position was given to Fouquieriaceae by Dumortier (1829), viz. in what is equivalent to Ericales.

The presence of various "groups" of iridoids among the dicotyledons was given in Jensen et al. 1975, where it was shown that iridoids of the same kinds as reported below in Fouquieriaceae are also found, for example, in Ericales and Cornales as defined by Dahlgren 1975.

Iridoid compounds in Fouquieriaceae

A reference, Bate-Smith 1964, indicating the presence of an iridoid compound, "asperocotillin", in *Fouquieria splendens* was regrettably omitted in our paper, Jensen et al. 1975. Since then we have investigated material of three species of the genus for the presence of iridoids and can confirm that several iridoid compounds are present in *Fouquieria*.

Our preliminary results are shown in Fig. 1.

The acetates of adoxoside (V) and loganin (VI) have been compared (NMR, melting point and mixed melt-

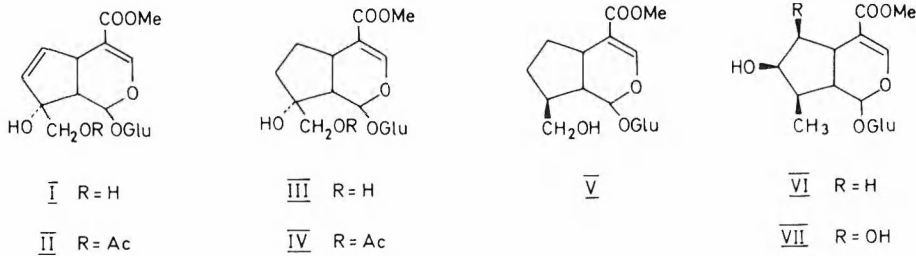


Fig. 1. Iridoid compounds found in *Fouquieria*. – I, II, III, IV and two unknown iridoids are present in *F. diguetii* (subg. *Fouquieria*). – I, III, V and two unknown iridoids are present in *F. splendens* (subg. *Fouquieria*). – The substances VI and VII were found in *F. columnaris* (subg. *Idria*).

ing point) with the authentic compounds. The structures of compounds I–IV and VII are tentative (^1H and ^{13}C NMR data).

A full account of these investigations will be given elsewhere when completed.

Discussion

In Table 1, selected characters of Fouquieriaceae are given (mainly according to Henrickson 1967–73). Some of the properties mentioned are deserving of comment (the numerals refer to the characters in Table 1).

Special attention will be paid to *Tamaricales*: Tamaricaceae, Frankeniaceae; to *Ericales*: Actinidiaceae, Clethraceae, Cyrillaceae, Roridulaceae, Ericaceae, Monotropaceae, Pyrolaceae, Epacridaceae, Diapensiaceae, Empetraceae (Byblidaceae and Grubbiaceae should perhaps be treated here, too); to *Cornales*: Garryaceae, Alangiaceae, Cornaceae, Davidiaceae, Nyssaceae, Icacinaceae, Escalloniaceae, Columelliaceae, Stylidiaceae, Hydrangeaceae, Alseuosmiaceae, Sambucaceae and Adoxaceae; and finally, to *Solanales*: Solanaceae, Goetzeaceae, Nolanaceae, Convolvulaceae, Cuscutaceae, Cardiopterygiaceae, Cobaeaceae, Polemoniaceae, Hydrophyllaceae, Ehretiaceae, Boraginaceae, Wellstediaceae, Lennoaceae and Hoplestigmataceae. The orders are according to Dahlgren 1975. – Within Solanales, Polemoniaceae in particular will be considered in the following discussion.

Simple leaves (1) are found in Ericales and Cornales as well as in Solanales and Tamaricales. They are also usually spirally set (2) in these orders, and stipules (4) are also largely or entirely absent. The occurrence of short shoots (2), the thorny branches (5), and the specialized structures for water and starch storage (6) are probably ecological adaptations of restricted phylogenetic importance.

Inflorescence characters (7) agree well with Cornales. The same type is probably also basic in Ericales, where indeterminate inflorescences, however, prevail. Inflorescence types

similar to those in Fouquieriaceae are also found in Solanales.

Pentamerous (10), and hypogynous (9) flowers are common in all the orders considered here. Free (11), spirally set (12) sepals occur, e.g. in Ericales. Unlike in Fouquieriaceae (14), corolla aestivation is contorted in Polemoniaceae.

The marked sympetaly (13) is a noteworthy character in *Fouquieria*. Its combination with stamens borne on the receptacle, thus being free from the corolla tube (16), is common in Ericales as well as, for example, in Escalloniaceae within Cornales, while in Solanales the filaments are oftener but not always inserted in the corolla tube.

The stamen number varies in *Fouquieria*; 10 stamens are found in most species and this is also the commonest (“basic”) number in Ericales. In Solanales the stamens (15) are as a rule not more than 5 in number. Apiculate (or cuspidate) anther apices (17) occur in various angiosperms and are found in Ericaceae and Tamaricaceae, but are rare in Solanales and do not occur in Polemoniaceae. Dorsifixed (18) anthers are common in all the orders concerned. In Ericales anther appendages as well as anther dehiscence by means of pores are common but these features are by no means constant. Thus characters (18)–(21) do not yield conclusive information on possible affinities, nor does the tapetum (22) which is said to vary in *Fouquieria*.

Syncarpy (23) is a common character in these groups, but the 3-carpellate state (25), common in Ericales and Tamaricales and also found in many Cornales, should be noted. In Solanales the carpels are generally 2 only, though 3-carpellate ovaries occur, e.g., in Solanaceae. A character which has probably been over-emphasized in Fouquieriaceae is the unilocular ovary with parietal placentae (26). In actual fact

Table 1. Selected characters of Fouquieriaceae.

Vegetative characters

- (1) leaves simple
- (2) leaves spirally set in 2:5 phyllotaxis, on long and short shoots
- (3) leaf bases decurrent
- (4) stipules absent
- (5) stems thorny
- (6) specialized structures for water and starch storage in the stem

Inflorescence

- (7) basically determinate in the sense that a terminal flower is present; mostly a panicle varying from compound and drupiform or corymbiform to simple ("raceme with an apical flower")
- (8) bracteose

Floral characters

- (9) flowers hypogynous
- (10) flowers pentamerous
- (11) sepals free
- (12) sepals imbricate, in 2:5 phyllotaxy
- (13) petals united to a tube
- (14) petal lobes imbricate
- (15) stamens 10 (basic condition; in seven species) or 14-18 (in four species)
- (16) stamens borne on the receptacle in a single whorl
- (17) anthers cuspidate at apex
- (18) anthers dorsifixed
- (19) anthers tetrasporangiate
- (20) anthers without appendages
- (21) anthers dehiscent introrsely by longitudinal slits
- (22) tapetum glandular or secretory
- (23) ovary syncarpous
- (24) ovary base nectariferous
- (25) ovary 3-carpellate
- (26) ovary one-locular, with parietal, septiform placentae, but in the lower portion 3-locular, with central marginal placentae
- (27) ovules variable in number, mostly 14-20

Embryology

- (28) ovules anatropous
- (29) ovules tenuinucellate (archesporial cell functioning directly as the megaspore mother cell)
- (30) ovules bitegmic
- (31) inner integument protruding beyond outer and forming micropyle
- (32) Polygonum type of embryo sac
- (33) epistase cap-like, distinct
- (34) endosperm formation cellular
- (35) prominent (lateral) haustorium formed at least from the chalazal end of the endosperm
- (36) embryogeny of the Asterad type

Fruit, seeds

- (37) fruit a dry, loculicidal capsule
- (38) seeds broad, winged; the wings made up of unicellular trichomes derived from epidermis of outer integument
- (39) embryo small, with well-developed cotyledons
- (40) endosperm present as a thin layer

Pollen grains

Mainly after Henrickson 1973.

- (41) tricolporate
- (42) elliptical in outline
- (43) semitectate, eurenticulate, with lumina 0.5-5 μm wide
- (44) with simple baculae
- (45) binucleate (Brewbaker 1967)
- (46) associated with yellowish oils

Anatomy

See also above; mainly from Henrickson 1969a.

- (47) periderm layered, of two cell types: suberized and fibrous
- (48) cortex with a thick layer of sclereid nests (water and starch storage tissues see above)
- (49) vessel ends with mostly simple perforation
- (50) calcium oxalate crystals present (but raphides lacking)
- (51) mucilage cells present
- (52) stomata anomocytic

Chromosome number

- (53) $2n=24$ (diploids), 48 (tetraploids), or 72 (hexaploids)

Chemistry

- (54) waxes ("ocotillo-wax") triterpenes and triterpene saponins present (Hegnauer 1966)
- (55) steroidal saponins and/or saponogenins present (Gibbs 1974)
- (56) tannins probably present (Gibbs 1974)
- (57) ellagic acid present (Bate-Smith 1964)
- (58) also caffeic acid, quercetin, kempferol, leucocyanidin and other phenolic compounds present (Bate-Smith 1964)
- (59) iridoid compounds present (see above)
- (60) coumarins present
- (61) seeds containing fatty oils (c. 18%, found in *Fouquieria splendens*). Further information, e.g., in Gibbs 1974 and Hegnauer 1966.

the ovary is basally 3-locular (see Henrickson 1972 Fig. 7 b) with central, marginal placentae in this part; thus these conditions should not be referred to as more closely resembling the parietal types in Tamaricales than to the central-marginal types in the other orders concerned. The ovule number (27) varies in the four orders.

In *Fouquieria* the micropyle of the ovules is downwardly directed (pendulous, apotropous; see Johansen 1936; Mauritzon 1936 p. 94) as in most families of Solanales (except Hydrophyllaceae and Boraginaceae). The ovules are bitegmic (30) as in Tamaricales but unlike those in practically all members of Ericales, Cornales and Solanales. This is of note since nearly all other iridoid-containing families have unitegmic ovules (exceptions in addition to *Fouquieria* are *Liquidambar* and *Daphniphyllum*). However, the ovules in *Fouquieria* are tenuinucellate (29) as in most taxa of the three orders mentioned, and moreover the endosperm formation is cellular (34) as in nearly all Ericales, Cornales and most Solanales (not nuclear as in Tamaricales and in some families of Solanales such as Convolvulaceae and Polemoniaceae).

A prominent haustorium formed by at least the chalazal part of the endosperm (35) is probably of some taxonomic significance. Endosperm haustoria are common in Ericales and Cornales but lacking in Solanales and Tamaricales.

Dry, loculicidal capsules (37) are also found in Tamaricales and in several families of Ericales (e.g. Clethraceae, Pyrolaceae, Monotropaceae, many Ericaceae and Diapensiaceae), but more seldom in Cornales. They are also found in Polemoniaceae, Hydrophyllaceae and other families in Solanales. The broad seed wings (38) of the particular kind found in Fouquieriaceae do not seem to be matched in the other orders. There is no evidence that the seed hairs in Tamaricales are homologous to the wings in *Fouquieria*, nor has it been demonstrated that the seed wings often found in Ericales (e.g. Pyrolaceae, Monotropaceae) or in Solanales (e.g. *Cobaea*) correspond to those occurring in *Fouquieria*.

The mature *Fouquieria* seeds have a thinner layer of endosperm (containing oil) than have practically all Ericales and Cornales and many Solanales (e.g. most Polemoniaceae). The embryo of *Fouquieria* is as a consequence also

better developed with proportionately larger cotyledons.

Tricolporate pollen grains (41) are also found in Ericales, Cornales and Solanales, but not in Tamaricales where the pollen grains are colpate. In Polemoniaceae, which is often compared with Fouquieriaceae, the pollen grains are mainly porate. The other details of the pollen wall (Henrickson 1973) need to be compared in greater detail with that of the orders concerned. The pollen grains are dispersed as tetrads in many Ericales, but as simple grains (as in Fouquieriaceae) in other groups of this order. Binucleate grains (45) prevail in the four orders discussed except in Cornales where trinucleate grains are quite common.

The anatomical characters in *Fouquieria* are of great interest and evidently represent xeromorphic specializations. The perforations in the end walls of the vessels are simple while in Ericales they are mainly scalariform. This, however, may be an adaptation to the rapid water uptake often found in desert plants. Anomocytic stomata are common and prevail in all four orders discussed here.

The chromosome numbers (53), $2n=24, 48$ and 72 , denote a basic number of 12 or 6. This agrees with Tamaricaceae ($x=12$) but not with Frankeniaceae. It agrees well with several families of Ericales, for which Raven (1975) suggests an original basic number of $x=6$; " $x=12$ being present in the common ancestor of Ericaceae, Pyrolaceae and Monotropaceae"; Diapensiaceae and Epacridaceae also seem to have $x=6$; Empetraceae (like *Sarracenia*) has $x=13$. In Cornales $x=12$ is found within Escalloniaceae and Icacinaceae and $x=11$ and 13 are common. However, in Solanales $x=12$ is also found, for example in Nolanaceae, some Convolvulaceae, etc., whereas $x=9$ is dominant in Polemoniaceae. In the case of Fouquieriaceae the chromosome number itself probably contributes little to the phylogenetic discussion.

More indicative are perhaps the chemical characters. *Fouquieria* contains iridoids (59), and ellagic acid (57) has been detected in hydrolyzed extracts (cf. Bate-Smith 1964). Each of these compounds occur restrictedly and rather specifically in the angiosperms. In addition to *Fouquieria* the occurrence together of these compounds is restricted to *Liquidambar* (Hamamelidales) and some families in Ericales

and Cornales. This was discussed by Bate-Smith (1972) who considered these plants to "occupy key positions in dicotyledonous phylogeny". It is noteworthy that the iridoids found in these plants are not of the "advanced" types (Jensen et al. 1975).

The iridoid compounds found in *Fouquieria* which can be currently used for systematic considerations are adoxoside (V) and monotropein methyl ester (II). Adoxoside has so far only been found in Cornales (*Adoxa*, *Viburnum*), whereas monotropein is common in Ericales but occurs sporadically in other orders.

In the four orders discussed here, iridoids (Jensen et al. 1975) are restricted to Ericales and Cornales and are not registered in any member of Solanales or Tamaricales. Triterpenes are found in many plant groups such as Ericaceae, and triterpene saponins are similarly widely distributed among the dicotyledons. Steroidal saponins reported in *Fouquieria* subgenus *Idria* (Gibbs 1974) are more restricted, but found, for example, in some Solanaceae.

Conclusions

The above comparison between *Fouquieriaceae* and the four orders Tamaricales, Ericales, Cornales and Solanales represents only a limited survey of the possible affinities in the angiosperm system.

Fouquieriaceae has commonly been placed in Tamaricales by virtue of its shrubby habit, sympetalous corolla, diplostemonous flowers, and, in particular parietal placentation and septicidal capsules with seeds, the wings of which may have been thought to correspond to the seed hairs found in Tamaricaceae and Frankeniaceae. Apart from the bitegmic ovules the embryological characters in particular differ widely, however.

Solanales might seem to offer more similarities. However, the unitegmic ovules, the haplostemonous flowers, the nonapiculate anthers, the predominantly bicarpellate pistil, the often nucellar endosperm formation, the lack of endosperm haustoria, the complete absence of iridoids and the absence of such polyphenolics as ellagic acid together constitute strong evidence that *Fouquieria* should *not* be placed here. In certain characters Solanaceae shows greater similarity to *Fouquieria* than does Polemoni-

aceae (three carpels, tricolporate pollen grains, cellular endosperm formation, occasional occurrence of steroidal saponins), but differs more in other characters (having, for example, intraxylary phloem and tropane alkaloids). The obviously great similarity in floral and other structures between *Fouquieriaceae* and Polemoniaceae is probably the result of convergent evolution caused by common environmental conditions and common pollinators.

Fouquieria certainly does not seem to fit in better in this order than in or, preferably, next to Ericales and the related Cornales in the superorder Cornanae. However some reservations must be made: the specialized anatomy including the simple perforation of the vessels, the bitegmic ovules, and the better-developed embryos surrounded by a correspondingly thinner endosperm. What may support a possible connection with the orders of Cornanae is the embryology (apart from the two integuments), the whole floral structure including the tricarpellate capsules, and the chemical properties.

It is suggested that *Fouquieriaceae*, like *Saracenaceae*, should be placed in an order of its own, *Fouquieriales*, near Ericales and Cornales in the superorder Cornanae (see Dahlgren 1975). The evidence for placing it in Saxifragales, as was done with hesitation in Dahlgren 1975, is supported by a number of characters and should also be considered, though the presence of iridoids favours the above-mentioned alternative.

Acknowledgements. The authors are very grateful to the staff of the Botanical Garden, Copenhagen, for material of *Fouquieria diguetii* and *F. columnaris* and to Dr Tom J. Mabry, University of Texas, for abundant material of *F. splendens*. We thank Drs E. C. Bate-Smith and B. Hansen for reading the manuscript critically. We are also grateful for criticism received from Dr R. F. Thorne who does not share our conclusions, however. The English text has been revised by Mrs Margaret Greenwood Petersson.

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Botanical literature

Radford, A. E., Dickison, W. C., Massey, J. R. & Bell, C. R. 1974: *Vascular plant systematics*. 891 pp. Harper & Row, New York, Evanston, San Francisco, London. ISBN 06-045308-7 (clothbound); 06-045309-5 (paperback). Price US \$ 19.95 (clothbound); 9.95 (paperback).

The reviewer of scientific literature is rarely at ease with his task – negative criticism all too often takes a leading place so that enthusiasm is killed. "Vascular Plant Systematics", however, has been a real pleasure to study and I shall return to it frequently. It is intended as a reference text for introductory courses and as a source book of information, procedures and literature, but also serves as a comprehensive compendium for students and teachers for recurrent use at different levels, and for research workers. It is also within reach of the ambitious amateur. The volume is not intended to be read and mastered as a single block. On the contrary it will be most effective if integrated into the educational system according to the particular requirements of the student and teacher. The student is stimulated to make intelligent use of the exercise material, to solve problems, write summaries, etc.

Theory and practice are combined in a very fruitful manner. Say we are faced with the task of describing a plant. We then look up "Description and Descriptive Format" and "Plant Identification". Under the first heading we find an introduction presenting the demands of descriptive writing, suggestions for the format of keys and descriptions, recommendations for manuscript order with several examples adopted from a modern Flora, excerpts from a Guide for Contributors dealing with taxonomic philosophy, concepts and policies in a given Flora, a

practical exercise and references to literature. Under "Plant Identification" the concepts of identification and classification are presented, suggestions made for the use of and construction of keys including examples of different types of keys, other methods of identification are outlined and discussed, a practical exercise is suggested and another very comprehensive list of recommended literature is given.

The same essential organization of information, discussion, practical advice and suggested further activity is met with whatever subject is looked up: nomenclature, cytological evidence, structural evolution and phylogeny, herbarium facilities, etc. The various aspects of systematics are so extensively covered in the thirty-six chapters and more than twenty glossaries and special indexes that it is hardly possible to imagine what more could be added. I am particularly pleased that the planning of research including the collection, analysis and documentation of data is so well treated. Lack of adequate instruction has forced all too many of us to start our career as research worker without satisfactorily planning our research. An improvement on this point at an early stage would effect a considerable increase in efficiency.

The book is clearly written for use primarily in the eastern parts of the United States. Many examples and illustrations require a knowledge of or material from this vegetation and flora. Some of the terms in the glossaries are also unfamiliar to a botanist whose knowledge has been mainly derived from British or German textbooks. References to European literature are less frequent than I could have wished and Scandinavian orthography in particular is often mishandled in the lists of literature. But these few adverse comments are of minor significance in a consideration of this stimulating and excellent

textbook. The price is ridiculously low, especially for the paperback edition which, moreover, seems to be surprisingly well bound. If relevant parts of this book were to be studied by all students of vascular plant systematics our discipline would gain immensely in richness of ideas and in efficiency.

Gunnar Weimarck

Ellenberg, H., Esser, K., Merxmüller, H., Schnepf, E. & Ziegler, H. (eds.) 1975: *Progress in botany/Fortschritte der Botanik*. Vol. 37/Band 73. xvii + 402 pp., 1 table, 20 figs. Springer Verlag, Berlin, Heidelberg, New York. ISBN 3-540-07504-6. Price (cloth) DM 120.—, US \$ 49.20.

There is no point in presenting an ordinary review of a volume of *Fortschritte der Botanik*. Every botanist who has had occasion to use one is familiar with the style and contents. Those who haven't should acquaint themselves with it as soon as possible. The scientific standard is invariably excellent, the coverage fair, and the reviewers are scientists in whom one can have full confidence.

There are regrettably other points, which, perhaps, impress themselves more strongly upon the reader/reviewer when turning the leaves of this volume. There is the technical standard. Not many years ago, this publication came in beautiful hot-metal printing on fine paper. Technically the work is still almost perfect, but how the offset printing and the offset paper lower the standard! On the other hand, one may say that a publication like this is by nature ephemeral, and therefore we must accept the second-rate quality.

Far worse is the general lack of erudition that has forced that change-over (so far only partial) to another language. Belonging to a generation and a nation for whom a reasonable command of the three major European languages in addition to one's own was considered a prerequisite for scientific work, one shudders at the thought of these modern science-workers from the big nations who are simply too lazy to learn any language (frequently not even their own), and who by weight of number and pur-

chasing power force fine, old journals with long and honorable traditions in science to become plastic-age supermarket goods. This volume is not worst – it is bad enough.

Reviewing journals are almost as old as science itself. Today there are all types, from the esoteric to the catholic, from red-hot ones that present the abstracts almost before the papers themselves are out, to more leisurely ones. Do review journals in the classical sense, such as this one, still serve a useful purpose; can they rightfully claim a place in the world of scientific writing?

To my mind, yes. They can treat themselves and their readers to a few small luxuries which the more high-powered abstract journal or the information services cannot afford. They can be selective. Reviewers have not only the right to avoid trivia, too often the despair of the abstracter, it is their duty to do so. The reviewer can be critical – how often the abstracter is unhappy over the material he must disseminate. The reviewer can evaluate, and if what has happened in the field since the latest issue is of no importance, there is no obligation for him to write about it.

The review journal is no alternative to the abstract journal, it is a complement. To read only one of them would be bad policy. The effect of the style adopted in *Fortschritte der Botanik* is that the articles that are most rewarding are those that are not in, but very close to one's own speciality. Articles further removed are less useful, the presentation is too succinct to be followed without previous experience in the field. And about half-way out one is better served by a modern handbook plus picking a colleague's brain.

A consequence of the editorial policy of having independent reviewers in different fields is a certain redundancy: topics and publications can, and do, appear in various places. It does no harm and safeguards against important items being lost or forgotten.

I have one serious complaint: The lack of titles of publications in the list of references. The references are not quite useless as they are, for with the help of other works of reference and the university library one can usually find out about them. If a journal is not available locally, and not all of them are, the title of a paper makes such a difference to the decision of getting

hold of it or not. It costs so little to give the titles; it makes such a difference to the usefulness. Why not do it?

Knut Fægri

Hegi, G. *Illustrierte Flora von Mittel-Europa*. Band III. Teil 3. Zweite, völlig neubearbeitete Auflage, herausgegeben von Prof. Dr. Karl-Heinz Rechinger (Lieferung 1) und Prof. Dr. Jürgen Damboldt (Lieferung 2 ff.). 1. Lieferung S. 1–80, Juli 1965; 2./3. Lieferung S. 81–240, Februar 1974; 4./5. Lieferung S. 241–356, März 1974. Carl Hanser Verlag, München. ISBN 3-446-10432-1. Price DM 148.—.

The publication of another volume of Hegi is an important event for European taxonomists. The present volume comprises the families once known collectively as Polycarpicaceae (Nymphaeaceae, Ceratophyllaceae, Magnoliaceae, Paeoniaceae, and Ranunculaceae). Four out of the five fascicles making up the present volume were edited by J. Damboldt (Berlin), who also undertook the heavy task of writing the account of the largest genus, *Ranunculus*. Other important contributors are H. Meusel (Halle), H. Mühlberg (Halle), and W. Zimmermann (Tübingen). The first fascicle (pp. 1–80) was edited by K. H. Rechinger (Vienna).

The sheer weight of information makes Hegi more of an encyclopedia than a flora. In this respect it is truly unique. No other flora includes such detailed and authoritative accounts on morphology, chemistry, ecology, cultivation, pathology, etc., in addition to the more familiar information on taxonomy, nomenclature and distribution. Bibliographies are generally extensive and up to date. There is a great variety of illustrations including colour plates, photographs and line drawings, covering everything from pollen and anatomical details to floral diagrams and habitat. Some 25 distribution maps, mostly taken from Meusel, Jäger & Weinert, are reproduced.

Whereas the amount and diversity of information greatly exceeds that normally found in floras, it is not always in an easily digested form. Long solid paragraphs in small type make

for difficult reading. The quality of the illustrations is somewhat uneven, and a more systematic selection would have facilitated comparison.

There is a comprehensive account (pp. 53–76) of general morphology and anatomy in Ranunculaceae written by Zimmermann who is a distinguished expert in this field. Ranunculaceae provides many lucid examples of evolution from primitive to advanced types with respect to floral morphology and pollination ecology. Detailed descriptions are often found under the respective genera and species. Gregory's classical scheme of karyotype relationships within the family is reproduced (p. 75).

Hegi has never indulged in the excessive splitting that characterized (and to some extent still characterizes) the analytical tradition of central and eastern Europe. In the present edition as well as in the first there is only one subspecific category, the subspecies, and taxonomic treatment is generally somewhat conservative. Microspecies in apomictic groups are omitted. The *Ranunculus auricomus* complex, for instance, is divided into three species (*R. auricomus*, *cassubicus* and *fallax*). The reproductive system is described, but the reader who wishes to ramble in the bewildering jungle of microspecies and subspecies is referred to papers cited in the extensive bibliography. Similarly, *Caltha palustris* is divided into five subspecies and *Ranunculus ficaria* into three.

The genus *Ranunculus* is taken in a broad sense to include *Batrachium*, *Ficaria* and *Ceratocephalus*. Fortunately there are recent biosystematic studies of two of the most difficult groups, subgenus *Batrachium* and the *Ranunculus montanus* group (by Cook and Landoldt, respectively). Similar studies are wanting in other groups (e.g., *Thalictrum minus* and the *Ranunculus acris* complex), but the treatment in Hegi generally seems to give a sound representation of our present knowledge.

It should be pointed out that there is an up-to-date revision of the difficult annual species of *Adonis*, largely based on a paper by Steinberg (1971). This treatment includes a nomenclatural error, however. Under *A. annua* L. ssp. *cupaniana* (Guss.) Steinberg 1971 the following comment appears: "Zur subsp. *cupaniana* ist auch die subsp. *carinata* Vierhapper 1935 ... aus Südeuropa zu rechnen, obwohl sie nur einen kleinen Teil der Unterart umfasst". Con-

sequently the subspecific epithet should be *carinata*.

The cover flaps list the parts that have appeared so far. It is a slightly confusing array of editions, reprints, volumes and fascicles, confirming the impression that Hegi is a goldmine of information that is not always presented in the most easily available form.

Arne Strid

King, R. M. & Dawson, H. W. (eds.) 1975: *Cassini on Compositae*. Collected from the *Dictionnaire des Sciences Naturelles*. 3 volumes, xl + 1963 + xxxvii pp. Oriole Editions, New York. Price US \$ 100.- (cloth).

Comparatively little is known of the life of the greatest of all synantherologists, Henri Cassini (1781–1832). Suffering from poor health he died at the age of 50, the last of a famous French family. Cassini was a modest man who only reluctantly entered on a successful legal career. Although he ended up as a peer he led a simple and secluded life devoted to the study of law and, above all, of plants of the order Compositae.

Cassini is rightly known as the founder of synantherology, but his writings have often been neglected, no doubt because of a considerable degree of inaccessibility. The bulk of his synantherological contributions appeared in Cuvier's *Dictionnaire des Sciences Naturelles*. No less than 898 entries are scattered throughout 60 volumes published between 1816 and 1830. Furthermore, of necessity though often somewhat arbitrarily, Cassini included information under rather inappropriate headings during the course of the publication of the encyclopaedia. For example, a summary of the family appears under "*Zoegea*", a generic table of *Astereae* under "*Paquerolle*" (the French name for *Bellium*) and a table of *Coreopsidinae* under the heading "*Zinnia*".

All these entries have now been collected in a single publication, which in addition has the great advantage of being provided with a complete generic index with references to all relevant passages. With this meticulously prepared work Robert M. King and Helen W. Dawson

have presented the world's synantherologists with an indispensable tool.

Cassini distinguished 20 tribes, nearly all of which are still recognized as systematic units with only minor modifications in circumscription or rank. It is highly remarkable that Cassini's system has stood the test of 150 years of expanding taxonomic research where new tools such as cytology, palynology and chemotaxonomy have been employed. The various modifications of the Cassinian system by Lessing, De Candolle and Bentham and Hoffman introduced only minor improvements which sometimes implied no progress at all. Cassini was without doubt a genius with unsurpassed analytical skill and powers of perception, as well as being a master of description.

The latest landmark in synantherology was an international symposium on "The Biology and Chemistry of the Compositae", held at Reading in July 1975. The resulting two-volume publication will include systematic surveys that attempt to classify all described genera into well-defined tribes. Numerous large and small changes in tribal circumscription will be suggested. In spite of the wealth of basic information now available a significant feature of the symposium was the lack of unanimity on some crucial issues such as the disposition of many members of the artificial tribe *Helenieae*. Such difficulties are mainly due to divergent opinions on the delimitation of the large tribes *Heliantheae* and *Senectioneae*.

Another obvious trend in this most recent classification of the Compositae is the return to many of Cassini's original ideas and the revival of a number of long-forgotten Cassinian genera. Synantherologists all over the world will have to continue consulting Cassini as a source of ideas and information. We are all grateful to Dr King and his collaborator for facilitating this in such a remarkable way. The three substantial volumes are certainly worth the price.

Bertil Nordenstam

Rechinger, K. H. (ed.) 1974: *Flora Iranica*. Lfg. 101–110. Akademische Druck- und Verlagsanstalt, Graz.

The most recent fascicles of *Flora Iranica* cover ten fairly small families. By far the most substantial volume treats the Plumbaginaceae (by K. H. Rechinger and H. Schiman-Czeika). This family is of special importance in the 'Flora Iranica' area because of the pronounced endemism there. The largest genus is *Acantholimon* with 165 species in the area 139 of which are endemic. After *Astragalus* and *Cousinia* it is the largest genus of flowering plants in this region. No less than 70 species have been described by Rechinger (with or without co-authors). *Acantholimon* has a very pronounced centre in the Iranian highlands and in this respect resembles several other genera, e.g. *Eremurus*, *Eremostachys*, *Dionysia* and *Cousinia*. Unlike these, however, the genus extends westwards into Europe with a single representative. The phytogeographical significance of *Acantholimon* in the 'Flora Iranica' area is further enhanced by the predominance of several species in various arid vegetation types.

Two new genera of Plumbaginaceae are distinguished, viz. *Dictyolimon* Rech. f. and *Aeoniopsis* Rech. f. The former has two species in the area and also occurs in India. The latter is monotypic and endemic to Afghanistan and West Pakistan.

The Plumbaginaceae volume is richly illustrated with black-and-white photographs, drawings and a selection of fine colour photographs mainly depicting species of *Acantholimon* in their natural habitats.

The other families treated are Podophyllaceae and Araliaceae (K. Browicz), Urticaceae (J. Chrtek), Fumariaceae and Dioscoreaceae (P. Wendelbo), and Apocynaceae, Linaceae, Burseraceae and Moringaceae (all by K. H. Rechinger).

The format of this outstanding flora has been presented in previous reviews in this journal. Since publication started in 1963 there has been a considerable and commendable increase in taxonomic commentaries and illustrations. The latter are always very useful, but Tab. 4 in the Urticaceae fascicle is somewhat cryptic. The plate probably consists of diagrams of *Urtica* achenes but there is no explanation except for

the names of taxa involved. These include *U. dubia* Forsk., which is nowhere mentioned in the text. The latter species is also represented by leaf silhouettes in Tab. 3, together with *U. angustifolia* Fisch., for example, which likewise does not appear elsewhere in the fascicle.

The Fumariaceae fascicle is particularly well illustrated with eight full-page colour photographs in addition to drawings and black-and-white photographs. The taxonomically intricate genus *Corydalis* has 27 species in the area, but the author (Wendelbo) admits the treatment is provisional pending more detailed biosystematic investigations.

Each new fascicle of this important flora adds valuable information and increases optimism as regards its eventual completion.

Bertil Nordenstam

Foster, A. S. & Gifford, E. M. Jr 1974: *Comparative morphology of vascular plants*. Ed. 2. 751 pp. and numerous illustrations. Freeman, San Francisco. ISBN 0-7167-0712-8. Price \$17.—.

The new edition of Foster & Gifford has been extended considerably. While the first edition is a modest book of 555 pp. the second comprises 751 pp. which are, moreover, two-columned and considerably larger. The text has been improved and extended and there are far more drawings and photographs, many produced with the help of microscopic, electron microscopic and scanning techniques. The result is impressive, and the new edition stands out as one of the most attractive, informative and up-to-date textbooks on the subject. New data have been added, especially on ultra-structure, morphogenesis and palaeontology. Compared with the first edition this edition seems to me to be more advanced. However, the titles of chapters are more or less the same. According to the authors the aim is also the same: to provide a textbook on the subject "for upper-division and graduate-level college students".

The approach of the book is comparative rather than typological, which is a guarantee that the reader will not drown in a multitude of detail. The authors have also chosen not to relate the amount of text to the number of

species or to the economic importance of the groups, but to give one or a few examples from each of the higher categories from Rhyniopsida up to the angiosperms. These examples are presented in relatively great detail and are accompanied by many excellent illustrations. Some readers may look in vain for information on the frequency or approximate occurrence of one or the other state of a character among the families or orders among the angiosperms in particular, but information of this type probably has to be left out of a textbook where the stress

is not on taxonomy. I notice with great satisfaction the many short but well-balanced discussions on the evolutionary significance of various characters, for example on types of endosperm formation, pollen grains and vascular elements.

Foster & Gifford's new textbook is to be strongly recommended for the more advanced students at Scandinavian universities. It is one of the best, if not the very best, in this field and scope.

Rolf Dahlgren

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