Drawings of Scandinavian Plants 105–108

Epilobium L. Sect. Epilobium

Alf Oredsson and Sven Snogerup

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Drawings and descriptions are given for *E. alsinifolium* VILL., *E. hornemannii* REICHENB., *E. lactiflorum* HAUSSKN. and *E. anagallidifolium* LAM.

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The four species nos. 105—108 are without doubt closely related. They all occur mainly in the arctic areas, in the mountain chain and by springs and cold streams in the northern lowlands. The group is recognized by a usually simple inflorescence, two lines of hairs on the stem and the lack of or scarcity of eglandular hairs on the capsules.

There are some fully fertile populations that are difficult to determine but most of the material can without any difficulty be referred to one of the species. Some of the extreme measurements in our descriptions may refer to introgressive populations but we have avoided specimens which are obviously intermediate in several characters. The nature and significance of hybridization in the group is in need of further experimental investigation. Morphological variation in populations from the northern part of Scandinavia has been treated in detail by KYTÖVUORI (1972).

In the case of the seed surface structure, there is an apparent contradiction between the descriptions given by KYTÖVUORI (1972) and those by SKVORTSOV and RUSANOVITCH (1974) and BERGGREN (1974) founded on scanning electron microscopy. In reality, the fresh seeds have papillae, but these collapse on hard drying. The preparation technique for scanning microscopy will cause all or most papillae to collapse, resulting in a pitted structure.

105. **Epilobium alsinifolium** VILLARS 1779

Perennial herb, (10—)15—30(—50) cm high, often forming dense stands. Stem more branching than in related species, sometimes forming adventitious stems or green, epigean runners from the basal nodes, usually with more or less stunted branches in the axils of middle cauline leaves, producing one (1—)2—5(—8)-flowered inflorescence or sometimes also a few smaller lateral ones. Stolons formed from basal nodes, subterranean or occurring deep down in floating vegetation, 2—10 cm long, 1—2 mm thick, pale, with long internodes and scale-like leaves 2—5 mm long. Turions formed at the ends of the stolons, compact, c. 10 mm long and 5 mm thick, with blunt, fleshy leaves.

Stem 1—3(—4) mm thick, terete, at least in the basal part with 4 weak ridges or lines below midribs and leaf margins. Two rows of hairs below the leaf margins, rarely also more uniformly hairy in upper part, hairs 0.1—0.3 mm, usually all recurved, rarely also some glandular, erect ones on upper part.

Most leaves opposite, usually only upper

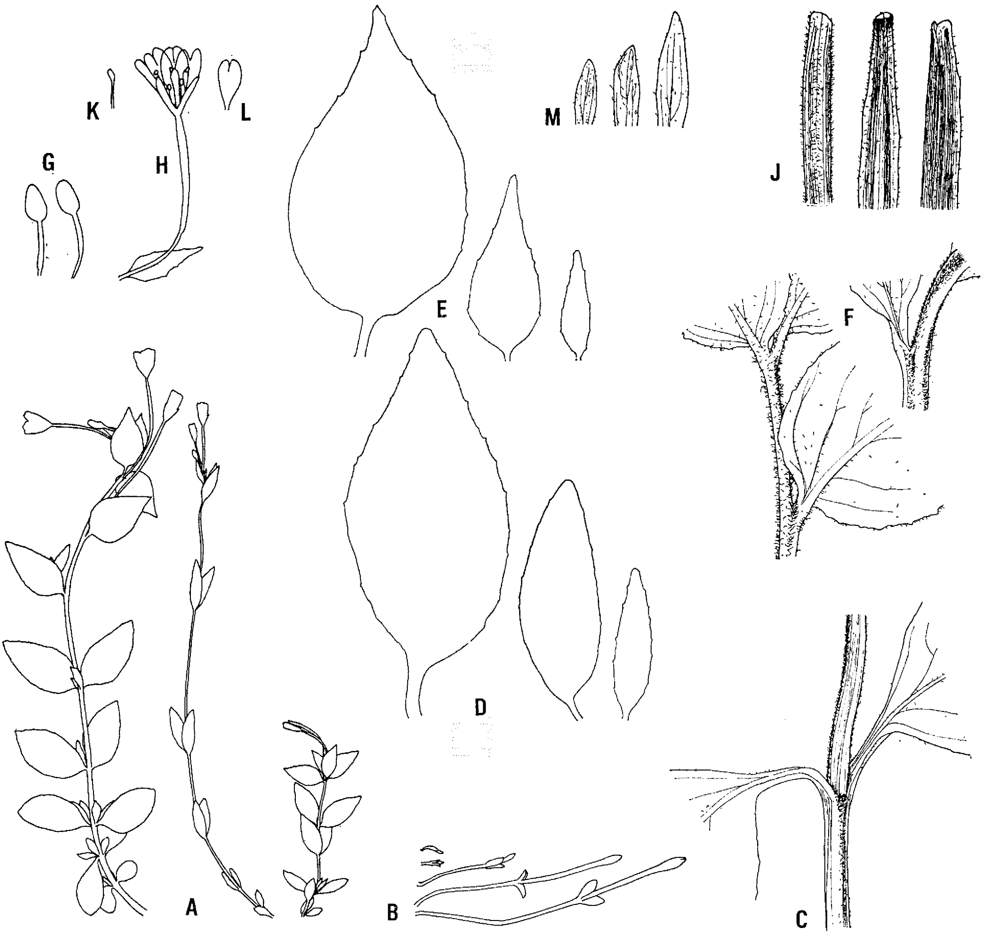

Fig. 105. *Epilobium alsinifolium* VILL. — A: Habit, ×1/3. — B: Stolons, ×1/2. — C: Stem node, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem parts with leaves, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

bracts alternate, all petiolate, petiole 0.5—3(—7) mm, longest in lower and middle parts, leaf bases united around the stem but never decurrent. Basal leaves smaller, on the lowest part of the stem in mud or dense vegetation often scale-like, higher up obovate to elliptical, obtuse. Middle and upper leaves (10—)20—35(—60) mm long, (5—)10—18(—25) mm broad, all ovate or rarely some of the lower ones elliptical, middle ones tapering to an obtuse apex, upper ones acute, serrate with small, usually up to 0.3 mm high teeth evenly distributed or denser towards apex. Bracts broader than in related species, even the upper ones large, often concealing the buds. Leaves subglabrous, sparsely hairy only on adaxial side of midrib, hairs like those of the stem. Inflorescense almost erect even when young, though often bent in dried material. Pedicels erect to erecto-patent in all stages. Buds ovoidal to ellipsoidal, blunt or with a minute mucro. Sepals (4.5—)6—7(—7.5) mm, connate to 0.8—2 mm at base, narrowly ovate, acute or rarely obtuse, reddish or rarely pure green, sparsely glandular-hairy. Petals (6—)9—12(—13) mm, notched to 1—1.5 mm, reddish-violet, very rarely purplish-pink or white. Anthers 0.7—0.9 mm, long filaments (4.5—)5—6.5 mm, short filaments (3.5—)4—4.5 mm. Style equalling or shorter than the long stamens, stigma capitate.

Capsule stalk (10—)15—30(—50) mm. Capsule 40—60(—70) mm, young ovary rather densely glandular-hairy, with a few eglandular hairs on the ridges, hairs like those of the stem, ripe capsules usually subglabrous. Seeds narrowly obovoidal, with one markedly flattened side, (1.1—)1.4—1.8 mm long, (0.35—)0.45—0.55 mm broad, with an acutely tapering base and a blunt apex, neck (0.05—)0.1—0.15 mm, surface with many rows of low papillae, chalazal hairs 50—60, 4.5—7 mm long. Flower homogamous.

E. alsinifolium occurs almost exclusively by springs and along watercourses, often in water, rarely in other wet places. It is commonest below the timberline, in the north it is found up to 700 m, to c. 1300 m in the S part of the mountain chain. It is at least slightly calcicole.

E. alsinifolium is an European endemic occurring on most mountains except in the extreme south. In Scandinavia it occurs in the entire mountain chain, in the arctic and subarctic parts and with scattered localities in the lowlands of Sweden southwards to c. 61° N and in Finland to 64° N.

Known hybrids: with *E. hornemannii*, *lactiflorum* and *palustre*.

106. **Epilobium hornemannii** REICHENBACH 1824

Perennial herb, (10—)15—30(—40) cm high. Stem usually simple, rarely forming some adventitious stems or creeping branches up to 5 cm long from the lower nodes, usually lacking branches in the axils of cauline leaves, producing one 2—8(—10)-flowered inflorescence or rarely also a few smaller lateral ones. Stolons often lacking, if present green, epigean, usually erect to erecto-patent, 5—20(—50) mm long, c. 1 mm thick, with small, opposite leaves. Turions formed at the end of the stolons as loose rosettes of green leaves 1.5—10 mm long.

Stem 1—2(—3) mm thick, terete, its basal part often pale, with small leaves, at least in its lower part with 4 weak ridges or lines below midribs and leaf margins. Two rows of hairs below the leaf margins, hairs 0.1—0.3 mm, usually all eglandular, incurved, rarely also few to many glandular, erect ones on upper part.

Most leaves opposite, only some upper ones alternate, all petiolate, petioles 1—5(—10) mm, longest in lower and middle leaves, bases uniting around the stem but never decurrent. Basal leaves smaller, obovate to elliptical, often some of the lowest ones scale-like. Middle and upper leaves (10—)20—30(—50) mm long, (5—)8—15(—25) mm broad, all ovate or some of the lower ones elliptical, tapering to an obtuse to acute apex, upper ones always acute. Leaves serrate with teeth usually less than 0.5 mm, denser on upper part of margin or evenly distributed. Leaves subglabrous, usually sparsely hairy only on the adaxial side of the midrib, hairs like those of the stem.

Inflorescence almost erect even when young, though often bent in dried material. Pedicels erect to erecto-patent in all stages. Buds broadly ellipsoidal to subglobose, obtuse. Sepals (3—)4.5—5.5 mm long, connate to c. 1.5 mm, narrowly ovate, acute or obtuse, always reddish, sparsely glandular-hairy. Petals (4.5—)5—7(—8.5) mm, notched to 1—1.5 mm, reddish or pinkish-purple, very rarely white. Anthers 0.4—0.5(—0.85) mm, long filaments 4.5—5 mm, short filaments 3—3.5 mm. Style shorter than the long stamens, stigma capitate.

Fig. 106. *Epilobium hornemannii* Reichenb. — A: Habit, ×1/3. — B: Stolons and winter buds, ×1/2. — C: Stem node, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem part with leaves, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

Capsule stalk (10—)15—30(—40) mm. Capsule (35—)40—50(—55) mm, young ovary densely or moderately glandular-hairy, ripe capsules usually subglabrous, hairs 0.1—0.2 mm, erect. Seeds narrowly obovoidal, with one markedly flattened side, 1.0—1.25(—1.4) mm long, 0.35—0.45 mm broad, with an acutely tapering base and a blunt apex, neck 0.05—0.15 mm, surface with many rows of more or less conical papillae, chalazal hairs 45—50, 3.5—5.5 mm long. Flower homogamous.

E. hornemannii grows by springs and watercourses but also in fens and meadows and along ditches, both in the lower alpine zone and in the woodland, up to 1100 m in the north, to 1500 m in the southern mountains.

E. hornemannii has a discontinuous circumpolar distribution. In Scandinavia it is fairly common in the mountains and in the arctic and subarctic parts, with scattered occurrences in the lowlands of Sweden southwards to 60.5° N and in Finland to 63° N.

Known hybrids: with *E. alsinifolium, anagallidifolium, lactiflorum* and *palustre.*

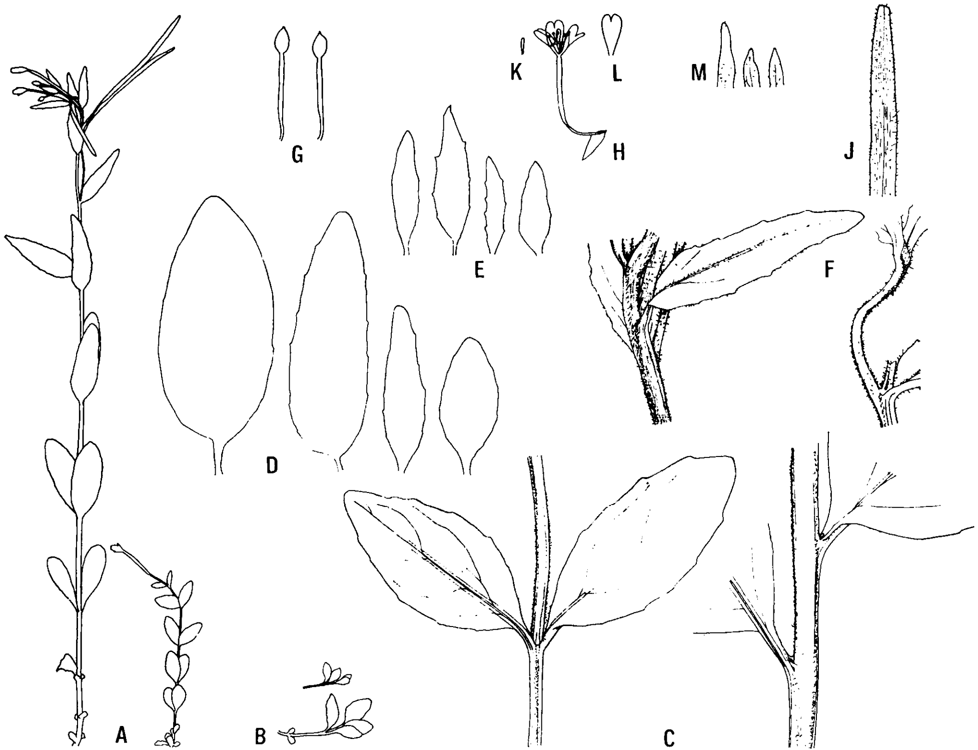

Fig. 107. *Epilobium lactiflorum* HAUSSKN. — A: Habit, ×1/3. — B: Stolons, ×1/2. — C: Stem nodes, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem parts with leaves, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsule, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

107. **Epilobium lactiflorum** HAUSSKNECHT 1879

Perennial herb, (5—)15—30(—40) cm high. Stem usually simple, without branches in the axils of cauline leaves, producing one (1—)2—6(—8)-flowered inflorescence. Stolons often lacking, if present very short or up to 10 mm long, 0.5—1 mm thick, pale or green, epigean, with a few small, usually scale-like leaves. Turions formed at the ends of stolons or apparently directly in the axils of basal leaves, as loose rosettes of leaves 2—10 mm long. Specimens sometimes apparently branched basally because of the proliferation of several turions from the same old stem base.

Stem 1—2 mm thick, terete, at least in the lower part with 4 weak ridges or lines below midribs and leaf margins. Two rows of hairs below the leaf margins, hairs 0.1—0.3 mm, usually all eglandular, incurved, rarely some erect, glandular ones in the upper part.

Most leaves usually opposite, upper ones alternate, all petiolate, petioles 0.5—4(—8) mm, longest in lower cauline leaves, bases uniting around the stem but never decurrent. Basal leaves smaller, spathulate to obovate or elliptical. Middle and upper leaves (10—)15—35(—40) mm long, (3—)5—12(—15) mm broad, all ovate or often some middle ones elliptical, uppermost ones ovate to narrowly ovate, middle ones usually broadly obtuse, upper ones acute. Bracts smaller than the other leaves, upper ones often very small, not con-

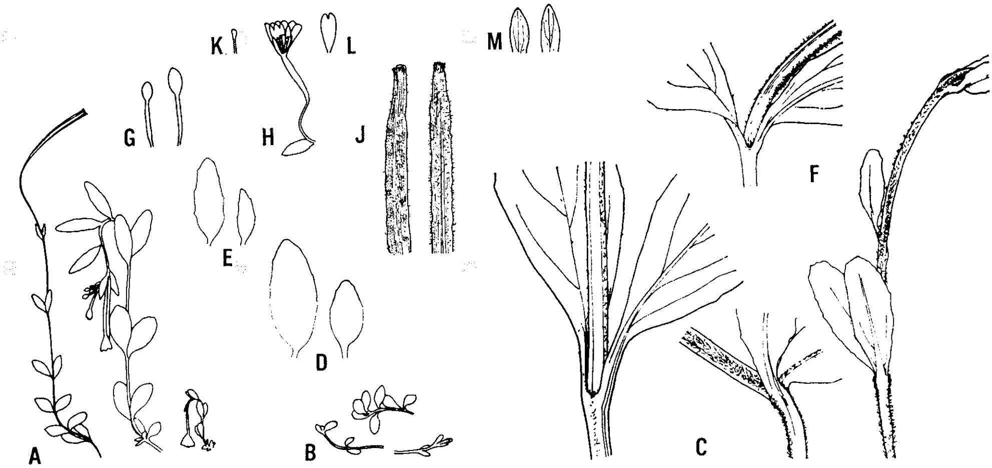

Fig. 108. *Epilobium anagallidifolium* LAM. — A: Habit, ×1/3. — B: Stolons, ×1/2. — C: Stem nodes, ×2.5. — D: Cauline leaves, ×1. — E: Upper leaves, ×1. — F: Upper stem parts with leaves, ×2.5. — G: Buds, ×1. — H: Flower, ×1. — J: Apical part of capsules, ×2.5. — K: Style, ×1. — L: Petal, ×1. — M: Sepals, ×2.5.

cealing the buds. Lower and middle leaves subentire or serrate with small teeth more numerous in the middle part of the margin or uniformly distributed, upper leaves always serrate. Leaves subglabrous, hairy only on adaxial side of the midrib and on the margin, hairs like those of the stem though smaller.

Inflorescence almost erect even when young, though often bent in dried material. Pedicels erect to erecto-patent in relation to axis in all stages, or often the young capsule ± pendent due to bending of the pedicel. Buds subglobose, with a distinct, blunt tip. Sepals (2.8—)3.5—4.5(—5) mm, connate to 1—1.5 mm, narrowly ovate, acute or rarely obtuse, pure green or more or less reddish, sparsely glandular-hairy. Petals (3—)4.5—5.5(—7) mm, notched to c. 1 mm, white, pinkish-white or rarely pinkish violet. Anthers 0.45—0.55 mm, long filaments 2.5—3.5 mm, short filaments 1.5—2.5 mm. Style equalling or shorter than the long stamens, stigma capitate.

Capsule stalk (10—)15—30(—40) mm. Capsule 35—50(—60) mm, young ovary sparsely to densely glandular-hairy, hairs erect, 0.1—0.2 mm. Seeds narrowly obovoidal with one markedly flattened side, (1—)1.2—1.35(—1.4) mm long, 0.35—0.45 mm broad, with an acutely tapering base and a blunt apex, neck 0.05—0.15 mm, surface with many rows of very flat papillae, thus often apparently smooth, chalazal hairs c. 40, 7—9 mm long. Flower homogamous.

E. lactiflorum occurs in wet meadows and fens, rarely along watercourses. It is found up to 1600 m in the southern part of the mountains, to 900 m in the north.

E. lactiflorum has a discontinuous circumpolar distribution. It is rather common in the mountains and in the arctic parts of Scandinavia, with isolated occurrences in the lowlands southwards to 60.5° N in Sweden, in Finland only occurring in the extreme north.

Known hybrids: with *E. alsinifolium, anagallidifolium, davuricum, hornemannii, montanum* and *palustre.*

108. **Epilobium anagallidifolium** LAMARCK 1786

Perennial herb, (2—)5—15(—20) cm high. Stem unbranched, producing one 1—3-flowered inflorescence. Stolons usually present, epigean, 5—20(—50) mm long, c. 0.5 mm thick, rarely branching, with opposite, widely spaced leaves 2—10 mm long. Turions formed at the end of the stolons as loose rosettes of green leaves 2—10 mm long.

Stem terete, 0.5—1(—1.5) mm thick, in the basal part with 4 low ridges or lines below midribs and leaf margins. Two rows of hairs below leaf margins, especially in the upper part, hairs 0.1—0.3 mm, all eglandular, recurved, or also some erect, glandular ones within the inflorescence.

Basal and middle leaves opposite, upper ones alternate, all petiolate, 0.5—3(—10) mm, longest in the middle leaves, bases uniting around the stem, but never decurrent. Basal leaves smaller, obovate to spathulate. Middle and upper leaves 5—20(—25) mm long, 2—5(—10) mm broad, ovate to elliptic, all obtuse or the upper ones acute, lower ones subentire, upper ones serrate with few, short, irregular teeth. Bracts usually smaller than the middle leaves, not concealing the buds. Basal and middle leaves glabrous to subglabrous, upper ones sparsely hairy on adaxial side of midrib and the margin, hairs usually less than 0.15 mm, mostly eglandular, recurved, rarely also a few erect, glandular ones.

Inflorescence characteristically nodding when young, in fruit strictly erect. Pedicels erect in relation to the axis in all stages. Buds broadly ellipsoidal to ovoidal, obtuse. Sepals 3—4 mm, connate to c. 1 mm, narrowly ovate, acute, reddish, sparsely glandular-hairy. Petals 3.5—6 mm, notched to 0.5—1 mm, reddish or pinkish-purple. Anthers 0.3—0.4(—0.5) mm, long filaments 2.5—3 mm, short filaments 2—2.5 mm. Style equalling or slightly exceeding the long stamens, stigma capitate.

Capsule stalk (6—)20—40(—50) mm. Capsule 20—30(—35) mm, young ovary sparsely hairy, with both glandular hairs and basally some eglandular, incurved ones, hairs 0.1—0.2 mm, ripe capsule subglabrous. Seeds narrowly obovoidal, with one markedly flattened side, 0.8—1.1 mm long, 0.35—0.4(—0.5) mm broad, with an acutely tapering base and a blunt apex, neck c. 0.5 mm, surface with many rows of small, flat papillae, chalazal hairs 40—50, 3—4 mm long. Flower homogamous.

E. anagallidifolium occurs on the banks of watercourses, on wet slopes, meadows and snow-beds. Mainly in the alpine and arctic zones, to 1750 m in the S mountains, to 1100 m in the north.

E. anagallidifolium has an arctic-alpine circumpolar distribution. In Scandinavia it is rather common throughout the mountain chain and in the arctic coastal areas, with only few, scattered localities along watercourses in the northern lowlands.

Known hybrids: with *E. hornemannii, lactiflorum* and *palustre.*

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Interrelationships of the Subfamilies of the Ericaceae and Derivation of the Monotropoideae

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WALLACE, G. D. 1976 02 09. Interrelationships of the subfamilies of the Ericaceae and derivation of the Monotropoideae. — Bot. Notiser 128: 286—298. Lund. ISSN 0006-8195.

The mycoparasitic Monotropoideae and other subfamilies of the Ericaceae were examined to clarify the position of the former in this family. There are few, if any, absolutely distinctive characteristics in any of the subfamilies. Excluding the features associated with mycoparasitism, the Monotropoideae have features found among other members of the Ericaceae. Based on their floral biology, nature of the stamens and particularly anthers, embryology, phytochemistry and other features, the Monotropoideae are most closely allied to the Arbuteae of STEVENS' (1971) Vaccinioideae. STEVENS' concept of the Vaccinioideae (i.e. including Vaccinieae and Arbuteae) is accepted here.

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The aim of this paper is to clarify the taxonomic position of the Monotropoideae with respect to the rest ot the Ericaceae. The possibility of derivation of the subfamily from other groups of the Ericaceae will be discussed. The Monotropoideae and Pyroloideae are usually placed in or near the Ericaceae and close to one another. There remains, then, to be determined how much taxonomic divergence, in this case, is allowable to a subfamily and how much is allowable before a subfamily should be elevated to familial status. A newly erected family would, of course, be closely allied to the family from which it is segregated since the mere act of separation of two taxa should not inherently alter the taxonomic distance which precipitated the division. The greater the number of characteristics common to the Monotropoideae and the other members of the Ericaceae, the closer the two groups should be placed to one another and the less tenable would be a shift to a different status. This assumes the use of taxonomically relevant characters. Many of the earlier classifications of the Monotropoideae were either based upon incomplete information or incorrect interpretations of available data. Rarely has adequate material of all the species been available for study. Even though most classifications have put the Monotropoideae close to the Pyroloideae, there is no particular reason to believe that they were derived from the Pyroloideae. The Pyroloideae may represent quite a different line of the Ericaceae. Comparative data for each of the six subfamilies THORNE (1968) recognized in the Ericaceae are given in Table 1.

The mycotrophic, achlorophyllous species which comprise the Monotropoideae have usually been considered saprophytes. More recent studies (BJÖRKMAN 1960, FURMAN & TRAPPE 1971) have shown evidence of the existence of fungal bridges between the mycotrophs and the host species. This habit could be termed mycoparasitism to differentiate it from other forms of parasitism and to draw attention to the integral role played by the mycorrhizae. The 12 species of the Monotropoideae are distributed among 10 genera. This may be compared with the nearly 40 species in three (two to four) genera of the Pyroloideae and the approximately 100 genera and 2,500 species of the rest of the Ericaceae. A description of the Monotropoideae and one for each of the included species has been provided in another paper (WALLACE in press). Any study to determine the relationships of the Monotropoideae must take into account those characteristics related to their mycoparasitic habit. Such features could be expected to be interrelated. There is no reason to doubt that there have been normal evolutionary pressures upon pollination mechanisms and propagule dispersal systems of the Monotropoideae.

There are a few other families in which there are mycoparasites. A rather complete list of the genera, by family, was given in FURMAN and TRAPPE (1971). In each of the families considered, except the Triuridaceae, the majority of the species are chlorophyllous. The mycoparasitic *Epirixanthes* BLUME differs from autotrophic *Salomonia* LOUR., both of the Polygalaceae, only in habit (KENG 1969). The former genus is the only case of mycoparasitism in the Polygalaceae. WILLIS (1973) combined the two genera in *Salomonia*. *Petrosavia* BECC. is the only mycoparasitic genus placed in the Liliaceae by THORNE (1968) and FURMAN and TRAPPE (1971). *Protolirion* RIDL., listed by the latter authors, is synonymous with *Petrosavia*. WILLIS (1973) considered the genus a monotypic family. There are about 200 species among the mycoparasitic genera of the Orchidaceae noted by FURMAN and TRAPPE (1971). They also list six genera of the Gentianaceae which include over 50 mycoparasites. The Triuridaceae is the only family composed entirely of mycoparasitic species. STANT (1970) stated that she would have no objections to placement of *Petrosavia* in the Triuridaceae on the basis of anatomical evidence. This could be a case of convergence of habit. The family Burmanniaceae is interesting in that mycoparasitic species outnumber autotrophic species. There are about 14 genera of mycoparasites and only *Burmannia* has chlorophyllous and achlorophyllous species. In *Burmannia*, JONKER (1938) treated 23 of the 57 species as saprophytic, here termed mycoparasitic. Only the Triuridaceae have apparently diverged too far to be allied with any close autotrophic relatives.

PREVIOUS TAXONOMIC TREATMENT

The members of the Monotropoideae, historically, have been placed in several taxonomic positions close to the Ericaceae. NUTTALL (1818) was one of the first botanists to unify the known genera of the Monotropoideae. He erected a separate family, his "natural order", the Monotropeae (sic). NUTTALL noted the similarities among the seeds of *Monotropa* L., *Hypopithys* SCOP., and *Pterospora* NUTT., the genera he knew and accepted, and those of *Pyrola* L. He considered the form and distribution of the anthers of the three genera sufficiently different, however, to warrant their separation from *Pyrola* as a family. NUTTALL claimed that *Monotropa* had a "monopetalous" corolla that was separate to the base, which appeared then as separate petals. The petals are, in fact, entirely separate in *Monotropa*. DESVAUX (1827) treated the Monotropoideae as a family, the Semicirculaceae, apart from the Ericaceae. *Monotropa hypopithys* L. was the only member of the family. LINDLEY (1836) elevated both the Pyroloideae and Monotropoideae to separate families. His Monotropaceae differed from the Pyrolaceae in that its members had straight styles, longitudinally dehiscent anther sacs, leafless stems, apparently sympetalous corollas, and were parasitic plants. DE CANDOLLE (1839) reasoned the group to be a segregate family, pointing out the lack of terminal pores in anthers and the difference in

Table 1. Comparative data on the Monotropoideae and other subfamilies of the Ericaceae. The subfamilies are those recognized by THORNE (1968). Data are drawn from the descriptions of over 100 genera, many of which were assigned to subfamilies by STEVENS (1971); additional genera were assigned by the author. The Vaccinioideae s. str. indicates my view that the Arbutoideae should be included in the Vaccinioideae as the Arbuteae. Most data on the Monotropoideae were obtained from studies of the group by the author. Data in Table 1 were also obtained from the following sources: ABRAMS 1951, ANDERSON 1959, BAKER & OLIVER 1967, BOLUS, GUTHRIE & BROWN 1909, BULLOCK 1954, BUSH 1967, DAVIS 1966, ERDTMAN 1952, HITCHCOCK, CRONQUIST & OWNBEY 1959. HOOKER 1882, HULTÉN 1968, MACBRIDE 1959, MARLOTH 1932, MEISNER 1863, MUNZ 1974, MUNZ & KECK 1959, OHWI 1965, OLIVER 1877, PALSER 1954, 1958, SLEUMER 1966, SMITH 1932, 1933, STANDLEY & WILLIAMS 1966, STEARN 1972, WEBB 1972, WOOD 1961.

Pyroloideae	Monotropoideae	Arbutoideae	Vaccinioideae s. str.	Rhododendroideae	Ericoideae
DISTRIBUTION					
N temp.: Euras. N & C Am.; W.I.	N temp. or mont. zones of N trop. Am., espec. W Am.; Eur.; E & S As.	N circumpolar; temp. N,C, & S Am.; E & S As. Himal., Malesia; Circumpacific, Tasm., N.Z., Galap. IS, Falk., W As., Eur., Med.	temp. Am. & mont. zones of trop. N, C, & S Am., Andes, W.I.; SE As., N. Gu., Malaya; S Afr., Madag.; Qld., Fiji; some Pac. Is; arctic	N circumpolar; temp. & trop. As. & Am.; S & E As., Himal.; N. Gu. & other Pac. Is; Atl. Eur., Azores; Austr.	S Afr., Madag., trop. Afr.; Med. Eur., some Atl. Is; As. Min., Syria; (Atl. N Am.).
HABIT					
per., herb to slightly woody, evergr. rarely achlorophyllous herbs with creeping rhizomes, terr. Lvs. alt., or whorl.; coriaceous or thin marg. ent. to dent. or ser.; oblan., ellip. or ovate; petiolate; us. glab	per., herb., achlorophyllous herbs; roots creeping to variously clustered. Lvs. absent, axill. appendages are sterile bracts. Inflor. annual & the only above ground parts	per., woody, evergr. (—decid.) erect to prostr. subshrubs to sm. trees, rarely lian.; oft. thin exfol. bark; occas. bog or epiphy. pls. Lvs. alt., opp. or whorl.; coriaceous or thin & decid.; marg. ent., ser. or cren. oft. revol. linear to ovate, ellip.; petiolate, occas. sessile; oft. glab.; winter buds scaled	per., woody, evergr. (—decid.) erect to prostr. shrubs to sm. trees, oft. epiphy., occas. stolonif. Lvs. alt.; oft. small; coriaceous, occas. thin; marg. ent., ser., or cren.; oblan. to ovate etc.; petiolate, occas. sessile; oft. gland. pubes. winter buds scaled	per., woody, evergr. to decid. erect to prostr. shrubs to sm. trees rarely epiphy. Lvs. alt., opp., or whorl.; coriaceous or thin & decid.; marg. ent. to revol.; oval, obovate, ellip., to narrow; petiolate rarely sessile; some gland. pubes.; winter buds scaled	per., woody, evergr., erect to prostr. shrubs. Lvs. us. whorl., rarely opp.; coriaceous; marg. revol. or channeled; back convex; mostly narrow; short petiolate; no winter buds formed
INFLORESCENCE					
racem. to corymb.; one- to several-fl.; bracteate; term.	racem., occas. condensed or scapose; one- to few- or many-fl.; bracteate	racem., panic., or corymb. rarely fascic.; one- to several- or many-fl.; oft. bracteate; term. occas. axil.; rarely perulate	racem., corymb., or panic.; one- to few- (or many-) fl.; some bracteate; us. axil. some term.; some perulate	racem., corymb. or panic., one to several fl.; bracteate; term. occas. axil.; some perulate	variously clust.; oft. one to few fl. per head, racem. or panic.; some bracteate; term., axil., or variable; not perulate

Table 1 (continued).

Pyroloideae	Monotropoideae	Arbutoideae	Vaccinioideae s. str.	Rhododendroideae	Ericoideae
FLOWER					
actino. to zygo.; med.-sized; pedicel.; ebracteolate; bisex.	actino.; med. to sm.; pedicel.; rarely bracteolate; bisex.	actino.; rather sm.; pedicel.; us. bracteolate; bisex. *Pernettya mucronata* funct. dioecious	actino.; oft. sm. to med.; pedicel., oft. articulate; bracteolate; bisex	actino. to zygo.; lg. to sm.; oft pedicel.; us. bisex. *Epigaea* funct. dioecious. us. bracteolate	us. actino.; sm. to larger; us. pedicel.; some bracteolate; bisex.
PERIANTH					
5-merous; calyx of persist. coriaceous, basally unit. sepals; imbric. in bud. Corolla of sep. concave petals; saucer-shaped to shallow campan.; us. decid.	5 (3—6)-merous; calyx of persist. coriaceous or thin, decid. sepals; imbric. in bud. Corolla of sep. or unit. petals; open campan., cylind. or urceo.; decid. or persist.	5, rarely 4—8-merous; calyx of persist. us. coriaceous, us. unit. sepals; Imbric., valv. or quin. in bud; some accrescent in fruit. Corolla of unit. petals; urceo., campan., ovoid or cylind. persist. or decid.	5, seldom 4-merous; calyx occas. winged, of persist. us. coriaceous, unit. sepals; campan. or cup-shaped; occas. adnate to ovary, some angled. Corolla of unit. petals; ovoid, urceo., tub.or campan.; rarely angled; decid. or perist.	5, 4 (6—8)-merous; calyx us. of persist., coriaceous, sep. to unit. sepals; us. imbric. in bud. Corolla of unit. or sep. petals; saucer shaped, campan., rotate, occas. tub. or urceo.; decid. or perist.	4 (3)-merous; calyx us. of persist., coriaceous, unit. occas. sep. sepals; campan. to tub.; oft. one sepal larger; oft. 4-angled. Corolla of unit. (occas. sep.) petals; campan., urceo. or variable; persist. (or decid.)
ANDROECIUM					
stam. 10; us. incl.; hypog. Fil. free or not; glab. or pubes.; oft. incl. to one side of fl.; some dilated at base; gen. flat.	stam. 10 (6) or irreg. more; incl.; hypog.; oft. of alt. uneq. lengths. Fil. free; pubes. or glab.; some dilated at base; terete to flat.	stam. 10, rarely 8; incl.; hypog. rarely basally epi. Fil. free; us. pubes. & dilated at base; terete to flat.; some geniculate	stam. 10 (8) rarely 4, 12; incl.; hypog. or basally epi.; some of alt. uneq. lengths. Fil. free or con.; glab. to pubes.; some dilated at base; terete to flat; some geniculate	stam. 10—(5, 8), rarely 4—25; incl. to exser.; us. hypog.; oft. of alt. uneq.lengths. Fil. free; glab. to cil.; some dilated at base; some incl. to one side	stam. 4, 8, occas. 3—6; us. incl.; us. hypog. Fil. free to variously con.; us. glab.; some geniculate
ANTHER					
oblong, elong.; awnless; dehis. by pores, dist. occas. horned or short-tubed	glob. to linear; rarely awned; dehis. by term. or oblique gaping slits or longi.	oblong to oval; oft. awned; dehis. by pores, occas. slits, these oblique-term.; some with tubules	oblong to oval; occas. awned; dehis. by term. clefts, pores or short slits; tubules present	ellip., oval to linear; awnless; dehis. by term. or lat. longi. slits, or term. pores	oblong to elong.; awned or not; dehis. by slits, term. or lat. pores; sacs free or con.
POLLEN					
tetrads, rarely monads; no "viscin" strands	monads; no "viscin" strands	tetrads; no "viscin" strands	tetrads; no "viscin" strands. *Enkianthus* monad	tetrads; us. "viscin" strands present	tetrads, rarely monads; no "viscin" strands

Table 1 (continued).

Pyroloideae	Monotropoideae	Arbutoideae	Vaccinioideae s. str.	Rhododendroideae	Ericoideae
GYNOECIUM					
ov. sup.; us glab.; 5 loc.; plac. axile may appear pariet. above; style straight or declined to one side, apex upturned; stigma peltate or lob. Nect. pres. or not	ov. sup.; pubes. to glab.; 1, 5, 4 (6) loc.; plac. axile or "intruded" pariet.; style straight, elong. to column., incl.; stigma disc. to funnel-formed. Nect. pres. lob. or low ridges	ov. sup., rarely half infer.; 5 (4—10) loc.; plac. axile, apical or pendulous; style straight, elong., some exser.; stigma minute, simple, truncate or obtuse. Nect. oft. pres.	ov. infer.; 5 (3 or falsely 8—10) loc.; plac. axile or cent. etc.; style filiform, straight, us. incl.; stigma truncate to obtuse. Nect. pres.	ov. sup., rarely emmersed; 4—5 (2—7) loc.; plac. us. axile; style oft. straight, short to long, some declined to one side; stigma cap., glob. or obscur. lobed. Nect. pres.	ov. sup. rarely half infer.; 2—4 (1, 8) loc.; rarely stipitate; plac. oft. cent.; style straight oft. exser.; stigma simple, peltate, rarely 4-fid or cap. Nect. oft.pres.
OVULE					
numer. per loc.; anatrop.; unitegmic; tenuinucellar	numer. per loc.; anatrop.; unitegmic; tenuinucellar	one to numer. per loc.; anatrop. to campy.; unitegmic; tenuinucellar	one to several per loc.; anatrop. to campy.; unitegmic; tenuinucellar	us. numer. per loc.; anatrop.; unitegmic; tenuinucellar	one to several per loc.; us. pendul.; unitegmic; tenuinucellar
FRUIT					
capsular, loc. dehis.; cent. column persist. Seeds minute, spindle-shaped	baccate & indehis. or capsular & loc. dehis., us thin-walled; gen. glob. to elong. Seeds minute, ovoid to spindle-shaped; winged or not	capsular, loc. dehis., some thin-walled or baccate to drupaceous & indehis.; some glob. Seeds small, ovoid to elong., winged or not; variously aggregated nutlets	baccate (or drupaceous), indehis. Seeds small ellips. to lentic. not winged	capsular, sept. dehis.; oft. elong. Seeds minute, ovoid to linear, winged or not	capsular, loc. dehis.; rarely somewhat fleshy; *Calluna* sept. Seeds minute, ellips. rarely lentic.; rarely winged

numbers of perianth segments in terminal versus lateral flowers. He inferred relationships among his Monotropaceae, *Pyrola aphylla* SMITH in REES, and *Cladothamnus* BONG. BENTHAM and HOOKER (1876) elevated the Monotropoideae, but not the Pyroloideae, to familial status. They supposed the Monotropoideae to be root parasites. They also recognized a link among their Monotropeae, Ericaceae, and Pyroloideae through *Pyrola aphylla.* The Monotropaceae of SMALL (1914) were noted to possess simple pollen grains. He judged the members to be saprophytes and that their ovaries were either 1- or 4—6-celled. The baccate fruits of some of the members were still poorly known at that time and SMALL noted that the fruits of some were merely somewhat fleshy. Recently CRONQUIST (1968) also recognized Monotropaceae. He lists lack of chlorophyll, lack of leaves, presence of longitudinally dehiscent anthers, monad pollen, and variable placentation as differentiating characteristics. EICHLER (1875) was the only author to treat the Monotropoideae as a subfamily of the Hypopityaceae (sic). Similarly ROUY (1897) considered the Pyroloideae and Monotropoideae subfamilies of his Monotropaceae. The Monotropoideae was considered a tribe of the Ericaceae by D. DON (1834). He characterized the group as having unilocular anthers, peltate seeds, and as being leafless, parasitic herbs. BAILLON (1891) separated the genera which make up the Monotropoideae into two series, the Monotropées and the Pterosporées which he subordinated to the Ericaceae. The two series were distinguished by whether or not the corolla was sympetalous.

Usually the Monotropoideae is placed as a subfamily of the Pyrolaceae or Ericaceae. DRUDE (1889) put the subfamily into the Pyrolaceae. He noted that the Pyroloideae had reflexed anthers with apical dehiscence at anthesis and pollen in tetrads. His Monotropoideae had erect anthers with united, ring-shaped or hippocrepiform slits and monad pollen. DRUDE's treatment was used by SCHULTZE-MOTEL (1964). LAWRENCE (1951) stated that the Pyrolaceae, in which he included the Monotropoideae and Pyroloideae, differed from the Ericaceae by their herbaceous habit, corolla of distinct petals, and loculicidally dehiscent capsule. There are some exceptions to each of these characteristics. *Chimaphila umbellata* (L.) BART. and *C. maculata* (L.) PURSH are somewhat woody; *Hemitomes* GRAY, *Monotropsis* SCHW. in ELL., *Pterospora,* and *Sarcodes* TORR. have sympetalous corollas; and *Cheilotheca* HOOK. FIL., *Hemitomes, Monotropastrum* H. ANDRES, *Monotropsis, Pityopus* SMALL, and *Pleuricospora* GRAY have baccate fruits. The author has considered the Monotropoideae a subfamily of the Ericaceae in a previous paper (WALLACE in press). This position had also been taken by several earlier authors (HENDERSON 1919, COPELAND 1939, 1941, 1947, THORNE 1968, STEVENS 1971). HENDERSON (1919) allied the Monotropoideae and Pyroloideae to the Ericaceae in a series characterized by increasing saprophytism. This increasing saprophytism was accompanied by anatomical and morphological change. She noted that except for their saprophytism, the supposed differences among the Monotropoideae, Pyroloideae and Ericaceae broke down when viewed carefully. COPELAND (1939) followed JEPSON (1925) in placing the Monotropoideae and Pyroloideae in the Ericaceae, admitting his uncertainty of their true relationships. In two later papers COPELAND (1941, 1947) maintained this position but gave reasons for treating the two subfamilies as tribes of the Arbutoideae of the Ericaceae. THORNE (1968) did not elaborate on his reasons for placement of the Pyroloideae and Monotropoideae in the Ericaceae. STEVENS (1971) stated that in placing the two subfamilies in the Ericaceae he followed COPELAND (1941, 1947) and HENDERSON (1919). He asserted that several characteristics and observations utilized by DRUDE (1889) in his classification of the groups were incorrect.

DISCUSSION

The subfamily Monotropoideae has usually been considered to be close to the Ericaceae. The question is whether they should be included in the Ericaceae. The following will include a discussion of some of the information provided in Table 1. Other data, whose presentation is not enhanced by a tabular format, and a brief discussion on the acceptability of some of the other subfamilies and their members will be included.

The Pyroloideae and Monotropoideae are restricted to the Northern Hemisphere. The Ericoideae, apparently indigenous only in the Old World, has the Cape Province of Africa as its center of diversity and is infrequently represented outside Africa in comparison. The Rhododendroideae, Vaccinioideae, and Arbutoideae are also probably of northern origin but are widespread in the New and Old Worlds. The center of diversity for the Monotropoideae is western North America. Five genera are restricted to this area and two of the other five are found there. Some of the species are seldom collected.

Many modifications of the Monotropoideae are related to their mycoparasitic habit. These include reduced herbaceous habit, presence of nonphotosynthetic sterile bracts instead of leaves and associated features, and lack of above ground vegetative buds. The only above ground portions of the species are the annual inflorescences. These reproductive structures represent the most noticeable portions, and not surprisingly the major source of taxonomic data of the species. SLEUMER (1966) pointed out that sterile material of any members of the Ericaceae is of little value because the most useful information is to be found in the characteristics of the reproductive structures. WATSON (1965) based some suggested taxonomic alterations within the Ericaceae upon stomatal characters and few other features. Some of his other data do not seem to support changes suggested by his stomatal data, particularly in the case of removal of the Phyllodoceae from the Rhododendroideae (HARBORNE & WILLIAMS 1973, IKUSE 1954).

Floral Biology

Several features utilized in taxonomic delimitations of members of the Ericaceae may be directly related to specialized pollen presentation mechanisms. Awned, shaker-type anthers; narrow orificed, urceolate corollas; and pollen lacking "viscin" (sporopollenin) strands are found primarily in the Ericoideae and Arbutoideae. The constricted mouth of the corolla with awned anthers presented just below its narrowest portion may be selective for particular insects or may spatially restrict entry so pollen will not be wasted. The anthers are disturbed, in their pendulous position, when the insect visitor pushes on the anthers or awns trying to reach the nectar at the base of the flowers. Pollen will normally be shaken out at this time. Autogamy, usually effected in later stages of anthesis, has been described for some species in the Ericaceae with pollen presentation mechanisms of this type (HAGERUP 1954, KERNER VON MARILAUN, 1894—95). The more flaring flowers of the Rhododendroideae have awnless anthers and "viscin" strands among the pollen grains. The pollen thus held in aggregates may become tangled in the feet or other body parts of insects and transferred to the sticky stigma. The comparisons noted in Table 1 reflect characteristics of extant members of the Ericaceae and include data on specialized features of the above types. These specializations may hinder any attempt at erecting a natural arrangement of the Ericaceae. For this reason care must be taken to consider data from many potentially useful features before tentative lines of development are drawn.

Stamens

The range of characters associated with the androecium and anthers of the Monotropoideae may usually be found among the other subfamilies of the Ericaceae as well. Anther dehiscence varies greatly in most of the subfamilies. Monad pollen occurs in five genera of the Ericoideae, one of the Vaccinioideae, one of the Pyroloideae, and all ten genera of the Monotropoideae. Characteristics of anthers are of particular taxonomic value in the Ericaceae. These may exhibit a wide range of forms depending upon the pollen presentation mechanism peculiar to the taxon concerned. The general form of the ericaceous stamen is, however, relatively uniform. MATTHEWS and KNOX (1926) noted that the stamens, of members of the Ericaceae, have a single trace which usually curves from the connective toward the distal portion of the anther, whether or not it is termed the apex or base of the anther. They chose the latter term. In most of the stamens they depicted, the trace was unbranched and generally occupied the most massive or isolated areas of sterile tissue in the anthers. In *Daboecia polifolia* D. DON, as might be expected, the much elongate anther sacs are provided with a trace between them, which MATTHEWS and KNOX termed a subsidiary trace. This strand is found toward the porous end of the anther. This would be consistent with CARLQUIST's (1970) emphasis on the probability that relative size and duration of the stamen determine the amount of vascularization. In many cases in the Ericaceae, the anthers at maturity are positioned with their distal portions directed toward the base of the ovary on the adaxial sides of the staminal filaments. COPELAND (1943) noted that the anthers of the members of the Rhododendroideae were developed in, rather than moved to, the position described above. The anthers of *Erica hirtiflora* CURT. were described by MATTHEWS and TAYLOR (1926) as developing with their distal portion directed toward the base of the ovary. These do not undergo late anther inversion. In this respect they are similar to the anthers of the Rhododendroideae described by COPELAND (1943). This is the most frequently encountered situation among the other members of the Ericaceae. Flowers of some members of the Arbutoideae mentioned by MATTHEWS and KNOX (1926) develop with the distal portions of the anthers directed toward the still closed floral orifice and invert during the latter stages of their development to attain the same positions as the anthers of other Ericaceae. COPELAND (1943) mentioned species of *Pyrola* and *Arctostaphylos* ADANS. whose staminal development would conform to this description.

There are several types of stamens found among the members of the Monotropoideae. *Cheilotheca, Hemitomes, Monotropa hypopithys, Pityopus, Pleuricospora,* and *Sarcodes* have straight filaments topped by erect, linear or hippocrepiform anthers which undergo no movements like those described above. *Allotropa* TORR. & GRAY ex GRAY in NEWBERRY, *Monotropa uniflora* L., *Monotropastrum, Monotropsis,* and *Pterospora* have relatively straight filaments topped by globose or variously shaped anthers, but these are not linear. The distal portions of these anthers are horizontally directed toward the style. During their maturation, the distal portions of the anthers may bend downward slightly, but usually less than 90° from the horizontal, so that it approaches a position more directed toward the floral base. The inversion in these species of the Monotropoideae is not considerable and in some cases may be achieved by the reflection of the stamens allowed by the expansion of the corolla at anthesis. The ovaries of *Allotropa, Monotropa uniflora, Monotropastrum, Monotropsis,* and *Pterospora* are rather globose or oblate spheroidal. In bud, the anthers usually occupy the space in the angle between the apex of the ovary and the straight style. In most of the other species of the Monotropoideae the ovaries are more elongate and the stamens lie along side of and parallel to the style. This latter condition is found in many members of the Ericaceae in which there is little or no movement of the anther in relation to the mature expanded filament. The movement is more pronounced in some species of the Pyroloideae. In *Moneses* SALISB. the angle through wich the anther must deflex is greater than that encountered in any species of the Monotropoideae. The anthers of *Moneses* are also provided with short tube-like channels. Movement of the maturing anthers atop the filaments may serve to orient the extending awns, possessed by many of the species, to a position where the awns are against the corolla. The slight movement of some of the anthers of the Monotropoideae is all that is required to orient the dehiscence openings of those species. Many species with urceolate corollas do not have anthers which undergo any degree of inversion. These are most frequent among members of the Vaccinioideae. In these, the anthers are provided with elongate dehiscence tubules which would, in most cases, spatially preclude any inversion movements of the anthers. The inversion would be detrimental anyway since the apparent purpose is to align the dehiscence openings of the anthers toward the floral orifice. MATTHEWS and KNOX (1926) further noted that many taxa in the Vaccinioideae have, in addition to the tubules, appendages on either their filaments or anthers. These appendages are of variable position, and would serve to orient the anthers. In the Ericoideae, some species with included stamens but awnless anthers have filaments that are curved to make contact with the corolla and thus provide the necessary support for the orientation of the anthers. STEVENS (1970) reported the presence of curved filaments, which he called geniculate, in several genera of the Andromedeae. These were also noted in a later paper (STEVENS 1971). The stamens and anthers of the Monotropoideae seem to be most closely allied to those of the Arbutoideae. Among the members of the Monotropoideae only *Pterospora* has an urceolate corolla and awned anthers.

Pollen

The distribution of bi- and trinucleate pollen grains among the mycoparasites and other angiosperms is of interest but of uncertain significance. BREWBAKER (1967) included a long list of taxa and their type of pollen. He considered trinucleate pollen grains the advanced type. Binucleate pollen grains predominate in the angiosperms and among mycoparasitic genera. BREWBAKER listed *Neottia* GUET. of the Orchidaceae, *Salomonia* LOUR. of the Polygalaceae, and the Monotropoideae and Pyroloideae of the Ericaceae as having binucleate pollen grains. The Triuridaceae, as well as *Apteria* NUTT. (Burmanniaceae) and two chlorophyllous species of *Burmannia* L., are trinucleate. He listed two mycoparasitic species of *Burmannia* as binucleate. BREWBAKER's list included relatively few genera of these families so the prevalence of either type of pollen is unknown. This would be necessary for proper comparisons in light of other taxonomic evidence to determine the significance of this type of information. *Enkianthus* LOUR. is the only genus of the Ericaceae known to possess trinucleate pollen grains.

Embryology

All the features associated with the gynoecia of members of the Monotropoideae may be found elsewhere in the Ericaceae. Characteristics of the ovules are almost uniform throughout the Ericaceae. On the basis of her embryological work DAVIS (1966) separated the Monotropaceae and Pyrolaceae from the Ericaceae. For the purpose of this discussion data for her three families will be considered as though it were for a united family, the Ericaceae.

DAVIS noted several embryological characteristics. The ovules are anatropous, unitegmic, and tenuinucellate except in some of her Ericaceae where the ovule may be nearly campylotropous. The archesporial cell functions directly as the megaspore mother cell and cytokinesis accompanies meiosis. Some members of DAVIS's Ericaceae vary in the latter characteristic. The chalazal megaspore of a usually linear tetrad develops into a *Polygonum*-type embryo sac. Endosperm formation is *ab initio* cellular in almost all cases. Embryogeny is of the caryophyllad type in DAVIS's Pyrolaceae and Monotropaceae but of the solanad type in the Ericaceae. The difference may represent a reduction of the embryo from the solanad type in which the basal cell forms a suspensor for two or more cells, to the caryophyllad type in which the basal cell undergoes no further divisions (MAHESHWARI 1950).

Data from GANAPATHY and PALSER (1964) and STUSHNOFF and PALSER (1969) indicate that the embryos of members of the Ericaceae, except for the Pyroloideae and Monotropoideae, are linear and have two short cotyledons. COPELAND (1947) stated that the embryos of the genera he put in the Pyroleae (*Pyrola, Chimaphila* PURSH, and *Moneses*) failed to form any distinct parts. According to JOHANSEN (1950), the mature embryo of *Monotropa hypopithys* consists of about nine cells. TEREKHIN (1963) claimed that the embryo and endosperm in the Pyroleae and Pterosporeae consisted of about 30—40 cells. Embryos of species of the Pyrolaceae (including *Monotropa*) studied by PYYKKÖ (1968) were reportedly undifferentiated and embedded in endosperm. COPELAND (1947) had reported that the embryos absorbed most of the endosperm. The reduction of the embryos of the Monotropoideae and Pyroloideae is in keeping with their reduced stature and habit. It seems likely that in both subfamilies infection by the mycorrhizal fungi occurs soon after the seeds are shed. This may alleviate the necessity for abundant endosperm. MAHESHWARI (1950) provided a list of embryological features common to the Ericales. PALSER (1961) expanded this list. There are some minor exceptions to some of the noted features in her list.

Phytochemistry

HEGNAUER (1966 a) recorded the occurrence of several compounds among the members of the Ericaceae. The diterpenes are the toxic constituent of the Ericaceae. Andromedotoxin, one of these, has been isolated from members of the Rhododendroideae and Arbutoideae but was not found among the few species of the Ericoideae, Vaccinioideae, and Pyroloideae investigated. It was, however, found in *Monotropa uniflora*, the only member of the Monotropoideae investigated. HEGNAUER (1966 b) mentioned the presence of arbutin in *Arbutus* L., *Arctostaphylos, Pyrola,* and *Vaccinium* L. All members of the Pyroloideae and Monotropoideae were said to possess monotropeoside.

Gossypetin was recognized as a useful taxonomic marker by HARBORNE and WILLIAMS (1973). This compound was noted by them primarily in the Rhodoreae and Phyllodoceae of the Rhododendroideae but was also found in *Erica* L. (some species) of the Ericoideae; *Comarostaphylis* ZUCC. of the Arbutoideae; and *Harrimanella, Chamaedaphne* KUNTZE, and *Oxydendrum* DC. of the Vaccinioideae. Hydroquinone was found in all members of the Arbutoideae examined, *Pyrola,* and *Chimaphila* as well as some species of *Pernettya* GAUDICH and *Vaccinium* (HARBORNE & WILLIAMS 1973). They also noted the occurrence of the monomethyl ether of hydroquinone in *Pyrola* and *Vaccinium*. Ursolic acid, β-sitosterol, and p-coumaric acid have been reported from *Monotropa uniflora* by BOBBITT et al. (1966). HEGNAUER (1966 a) reported ursolic acid from each of the other subfamilies of the Ericaceae. He mentioned the occurrence of β-sitosterin in *Befaria*

MUTIS ex L., *Lyonia* REICHB., and *Pyrola*. HARBORNE and WILLIAMS (1973) state that the Pyroloideae and Monotropoideae fit into the Ericaceae based upon their chemistry and suggest that the Vaccinioideae is similar.

The tribes and most of the subfamilies of the Ericaceae are fairly distinct but have been subjected to various taxonomic combinations. For the purposes of this brief discussion of the other subfamilies of the Ericaceae, STEVENS' (1971) classification is the most useful. The presence of gossypetin and pollen grains with "viscin" strands, among the taxa of the Phyllodoceae and Rhodoreae enforce STEVENS' treatment of the Rhododendroideae. The Ericoideae is relatively distinct in most of its features. STEVENS placed the Arbutoideae as a tribe of the Vaccinioideae. His classification has many merits, however, the Arbutoideae is separated in the present work in an attempt to allow comparison of the two groups. I would have to agree with STEVENS (1971), however, and unite the Arbutoideae with the Vaccinioideae. Several characters associated with pollen presentation mechanisms were found to be common between the two groups. These mechanisms were not correlated by STEVENS. Some of the characters which are interrelated include the shape of the corolla, presence or absence of "viscin" strands, presence or absence of anther tubules, and inversion of anthers.

CONCLUSIONS

Data in Table 1 clearly indicate the close relationship of the Monotropoideae to the other members of the Ericaceae. Most features found among the members of the Monotropoideae may be found in some other members of the Ericaceae. The mycoparasitic habit of the subfamily is the most distinguishing feature of the group. Several characteristics are associated with this habit. Among these are reduced habit and embryological features, as well as changes in gross morphology, anatomy, physiology, and pollen presentation mechanisms. The Monotropoideae appear to be most closely allied to the Arbuteae of STEVENS' (1971) Vaccinioideae. In addition to evidence from Table 1 there are other shared characteristics. Anthers of some members of the Monotropoideae undergo a modified form of anther inversion, a feature noted in the Arbuteae and Pyroloideae. The Monotropoideae and Arbuteae possess a similar range of floral characteristics. Chemical evidence also indicates a close relationship among the tribes of the Vaccinioideae and the subfamily Monotropoideae. The case against maintainence of the Pyrolaceae is also apparent from data in Table 1. They, like the Monotropoideae, possess no features unique among Ericaceae, except possibly mycoparasitism.

The Pyroloideae form a rather uniform subfamily which should be placed near the Monotropoideae. The Monotropoideae and Pyroloideae were probably derived from the vaccinioid line, but in both cases the separation was some time ago and extant members have diverged to a great extent. There is no reason to belive that the Monotropoideae were dervided from the Pyroloideae, even though one or more species of *Pyrola* are occasionally leafless and so perhaps mycoparasitic, and *Pyrola secunda* L. has monad pollen. This probably represents similar levels of specialization. The subfamily Arbutoideae is recognized in Table 1 following THORNE (1968). This greatly simplified presentation of the data and provided an opportunity to examine STEVENS' placement of the Arbuteae with the Vaccinioideae. STEVENS' combination does, as expected, seem quite reasonable. THORNE proposes to follow this view in the future (THORNE, pers. comm.). The recognized subfamilies of the Ericaceae would then be as follows: Rhododendroideae, Ericoideae, Vaccinioideae, Pyroloideae, and Monotropoideae. The taxa of each of these are aligned as in STEVENS (1971). WILLIS (1973) tentatively placed *Wittsteinia* F. MUELL. of

STEVENS' Wittsteinioideae in the Epacridaceae. Since no new evidence on the placement of this controversial genus (STEVENS 1971) could be provided, it was not treated in this paper.

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Contribution à l'étude cytotaxonomique de quelques Angiospermes de l'Iran

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ARYAVAND, A. 1976 02 09. Contribution à l'étude cytotaxonomique de quelques angiospermes de l'Iran. — Bot. Notiser 128: 299—311. Lund. ISSN 0006-8195.

Chromosome numbers are given for 41 species of angiosperms from Iran belonging to 33 genera and 12 families. The chromosome numbers of 27 species and six genera (*Lepyrodiclis* FENZL ex ENDL., *Pseudofortuynia* HEDGE, *Robeschia* HOCHST. ex FOURN., *Straussiella* HAUSSKN., *Lepechiniella* M. POP. and *Hymenocrater* FISCH. & MEY.) are published for the first time. The chromosome numbers of three species differ from those given by other authors. Chromosome races have been found in *Arabidopsis pumila* (STEPH.) N. BUSCH, *Primula auriculata* LAM. and *Senecio coronopifolius* DESF.

In *Clypeola aspera* (GRAUER) TURRILL a cytotype with n = 13 was found. It probably originated from material with n = 14 by means of one unequal translocation.

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Dans le cadre de nos recherches cytotaxonomiques sur la flore de l'Iran (ARYAVAND 1975 a, b), nous présentons dans ce travail les résultats concernant 42 espèces appartenant à 12 familles et 33 genres différents. Pour environ deux tiers de ces taxons les nombres chromosomiques sont rapportés pour la première fois.

MATÉRIEL ET MÉTHODES

La plus grande partie de notre matériel consiste en boutons floraux que nous avons récoltés et fixés sur le terrain en Iran, à l'alcool-acétique (3: 1). Seul le matériel de *Cousinia tenella* ainsi qu'un échantillon de *Lepyrodiclis holosteoides* proviennent de graines reçues respectivement des jardins botaniques de Taschkent et de Versailles. Ces graines ont été cultivées dans le jardin botanique de l'Institut de Botanique de l'Université de Neuchâtel. Les boutons ont été fixés par le Professeur C. FAVARGER. Pour chacun des taxons étudiés, un témoin a été séché; ces témoins seront conservés dans l'herbier de la Faculté des Sciences de l'Université d'Esfahan (Iran). La technique utilisée a été celle des écrasements au carmin acétique. Les familles ont été classées suivant la classification du Syllabus der Pflanzenfamilien de ENGLER-DIELS (DIELS 1936) et dans chaque famille les genres et les espèces sont présentés par ordre alphabétique. Nous n'avons figuré ici que les images cytologiques se rapportant à des plantes qui n'avaient pas encore été étudiées à ce point de vue ou qui présentaient un intérêt particulier.

Tous nos comptages concernant la méiose sont effectués sur les cellules-mères du pollen.

LILIACEAE

Allium ascalonicum L. — n = 8

LOCALITÉ. Esfahan: Khunsar, Golestan kuh, 2400 m (74-165).

Ce nombre a été trouvé par plusieurs auteurs chez cette espèce sur des provenances différentes (in BOLKHOSKIKH et al. 1969) et cela indique, pour le moment, que le nombre chromosomique de cette espèce est constant. Les chromosomes ont une taille assez grande.

Allium stamineum BOISS. — 2n=16

LOCALITÉ. Fars: Ali abad-e Kamin, 1600 m (74-206).

Notre résultat concorde avec celui de FEINBRUN (in BOLKHOSKIKH op. cit.) sur du matériel de Palestine. Les chromosomes sont grands. Chacun d'eux mesure environ 13 microns à l'anaphase de la mitose somatique de l'ovaire.

Bellevalia glauca (LINDL.) KUNTH — n=4 (Fig. 1 A)

LOCALITÉ. Esfahan: Damaneh, 2100 m (74-163).

Cette espèce n'a pas fait l'objet d'un comptage chromosomique. Mais le nombre de base x=4 est très fréquent chez le genre *Bellevalia.* PODLECH et BADER (1974) ont trouvé chez *Bellevalia saviczii* WORON. le nombre 2n=24 (hexaploïde) sur un matériel d'Afghanistan. *B. glauca* a été subordonné par BOISSIER (1884) à *B. ciliata* (CYRILL) NEES. Ce dernier taxon possède aussi 2n=8.

Eremurus persicus JAUB. & SPACH — 2n=14 (Fig. 1 B)

LOCALITÉ. Esfahan: Ghameshlou, 2050 m (74-149).

Cette espèce n'a pas été étudiée auparavant à notre connaissance. Mais toutes les espèces du genre *Eremurus* qui ont été étudiées jusqu'à maintenant possèdent le nombre chromosomique 2n=14. Donc au point de vue du nombre chromosomique ce genre semble être très uniforme.

CARYOPHYLLACEAE

Lepyrodiclis holosteoides C. A. MEY. — n=17, 2n=34 (Fig. 2 A)

LOCALITÉS. Esfahan: Nadjaf abad, 1550 m (74-130) — Iran (récolté par le jardin bot. de Versailles) (71-988).

Aucun représentant du genre *Lepyrodiclis* FENZL ex ENDL. n'a fait à notre connaissance l'objet d'un comptage chromosomique. Nous avons étudié deux spécimens différents, l'un récolté directement dans la nature (Nadjaf-Abad à 20 km W d'Esfahan) et l'autre, également originaire de l'Iran, provenant du jardin botanique de Versailles.

Dans les deux cas, nous avons obtenu le nombre n=17. Ce nombre se rencontre également dans certains genres de la famille des Caryophyllacées, comme *Honkenya* EHRH., *Gypsophila* L. et surtout *Cerastium* L. Il existe certaines affinités morphologiques entre ce dernier et le genre *Lepyrodiclis.*

PAPAVERACEAE

Hypecoum pendulum L. — 2n=16 (Fig. 2 B)

LOCALITÉ. Esfahan: Cité Universitaire, 1600 m (74-22).

Cette espèce n'a jamais fait l'objet d'un comptage chromosomique. SMITH (1935—1936) et SUGIURA (1937) (in BOLKHOSKIKH et al. 1969) ont trouvé chez *Hypecoum procumbens* respectivement les nombres 2n=12 et 16?. MĚSICEK et SOJAK (in MOORE 1973) ont compté chez *Hypecoum erectum* L. 2n=16 sur du matériel de

Fig. 1. A: *Bellevalia glauca,* mitose pollinique, n=4. — B: *Eremurus persicus,* mitose somatique de l'ovaire, 2n=14. — C: *Clypeola aspera,* métaphase I, n=13. — D: *Clypeola aspera,* mitose de la racine, 2n=26. — E: *Nonnea caspica,* métaphase I, n=22. — F: *Nonnea persica,* diacinèse, n=16 (14 bivalents et 1 tétravalent). — G: *Cousinia pugionifera,* prophase de la mitose somatique de l'ovaire, 2n=24.


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Mongolie. En plus CHOUKSANOVA (in BOLKHOSKIKH op. cit.) a trouvé chez *Hypecoum trilobum* TRAUTV. 2n = 32. Ces résultats montrent que le nombre de base chez le genre *Hypecoum* L. est probablement 8.

Papaver tenuifolium BOISS. — n = 7 (Fig. 2 C)

LOCALITÉ. Esfahan: Ghameshlou, 2050 m (74-134).

Cette espèce n'a pas été étudiée auparavant à notre connaissance. Mais dans le genre *Papaver* L., le nombre chromosomique 2n = 14 est le plus répandu.

BRASSICACEAE

Arabidopsis pumila (STEPH.) N. BUSCH — n = 8 (Fig. 2 D)

LOCALITÉ. Esfahan: Mt Homayoun shahr, 1700 m (74-56).

MANTON (1932) a compté sur un spécimen du SW de l'Asie le nombre chromosomique 2n = 32. Donc, notre échantillon qui provient de la région d'Esfahan (Iran) est un diploïde (n = 8). Mais malheureusement MANTON n'a pas indiqué la localité précise de son échantillon. Il faut mentionner que *Arabidopsis wallichii* (HOOK. FIL. & THOMS.) N. BUSCH possède aussi le nombre chromosomique 2n = 16 (PODLECH & BADER 1974).

Arabidopsis pumila avec une aire de distribution assez vaste (Russie centrale et méridionale et Asie centrale et austro-occidentale) possède de nombreuses variétés (SCHULTZ 1924). De toute façon, nos observations montrent que cette espèce a au moin deux races chromosomiques, l'une diploïde (Iran: Esfahan) et l'autre tétraploïde (SW Asie).

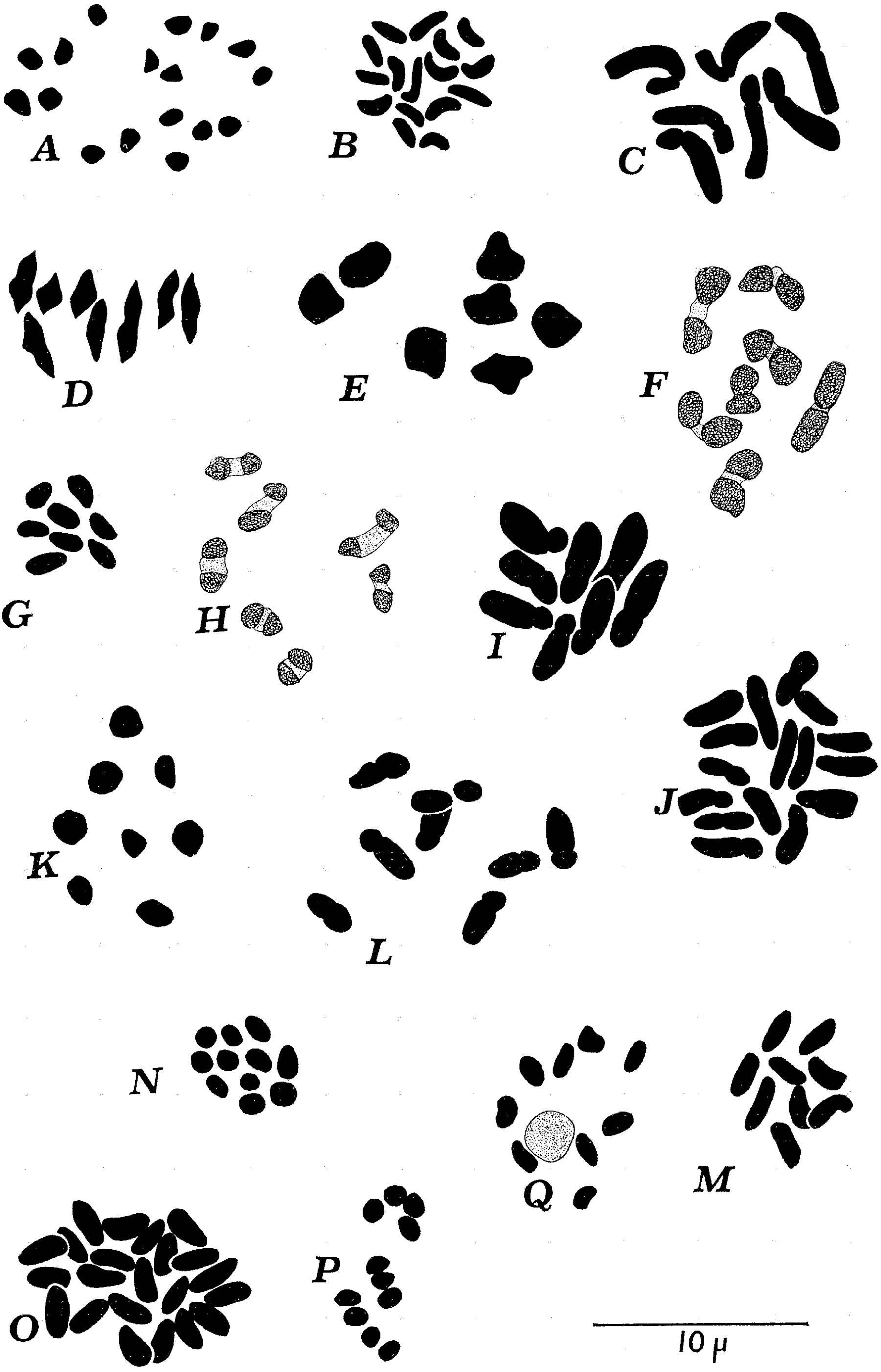
Clypeola aspera (GRAUER) TURRILL — n = 13, 2n = 26 (Fig. 1 C, D)

LOCALITÉS. Esfahan: Mt Kolah-ghazi, 1800 m (75-534) — Fars: Kazeroun, Komaradj, 1100 m (75-569).

D'après nos recherches antérieures (ARYAVAND 1975 a), il existe chez cette espèce deux nombres chromosomiques différents: n = 7 et n = 14. Depuis lors, nous avons observé chez deux individus de provenances différentes le nombre chromosomique n = 13 et 2n = 26. Dans les mitoses somatiques de la racine, on aperçoit 12 chromosomes avec constriction dans la région médiane, 12 chromosomes à constriction submédiane et 2 chromosomes dont la taille est environ deux fois plus grande que celle des autres et possèdant une constriction submédiane. A la métaphase I des cellules-mères de pollen, nous avons observé 12 bivalents de taille normale et 1 bivalent beaucoup plus grand que les autres et en forme d'anneau à deux chiasmas. Il semble bien que le type à n = 13 dérive du type à n = 14 par fusion de deux chromosomes entre eux à la suite sans doute de translocations inégales (cf. SWANSON 1960 p. 397). Jusqu'à présent nous n'avons pu déceler de différences morphologiques entre les plantes à n = 14 et à n = 13, mais ce point exigera encore d'autres investigations.

Ce phénomène de fusion des chromosomes n'est pas comparable au phénomène Robertsonien, souvent observé dans le

Fig. 2. A: *Lepyrodiclis holosteoides,* anaphase I, n=17. — B: *Hypecoum pendulum,* mitose somatique de l'ovaire, 2n=16. — C: *Papaver tenuifolium,* mitose pollinique, n=7. — D: *Arabidopsis pumila,* métaphase I, n=8. — E: *Clypeola dichotoma,* anaphase I, n=7. — F: *Pseudofortuynia esfandiarii,* diacinèse, n=7. — G: *Robeschia schimperi,* mitose pollinique, n=8. — H: *Sisymbrium septulatum,* diacinèse, n=7. — I: *Straussiella purpurea,* mitose pollinique, n=8. — J: *Astragalus bachtiaricus,* mitose somatique de l'ovaire, 2n=16. — K: *Astragalus candolleanus,* mitose pollinique, n=8. — L: *Astragalus fragiferus,* mitose pollinique, n=8. — M: *Sophora griffithii* ssp. *hortensis,* mitose pollinique, n=9. — N: *Primula auriculata,* métaphase II, n=11. — O: *Arnebia decumbens,* mitose somatique de l'ovaire, 2n=22. — P: *Lepechiniella persica,* anaphase I, n=11. — Q: *Hymenocrater bituminosus,* anaphase I, n=9.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règne animal et rarement chez les plantes supérieures (KOLLMANN 1969), puisque dans ce cas ce sont des chromosomes télocentriques qui se soudent entre eux pour donner par exemple des chromosomes méta- ou submétacentriques, le nombre total des bras restant identique. Tandis que dans notre cas, il ne s'agit pas de chromosomes télocentriques mais plutôt de chromosomes à constriction médiane ou submédiane ou enfin subterminale qui se soudent entre eux pour donner un nouveau chromosome. Il semble bien cependant que la masse totale de la chromatine reste à peu près identique.

Clypeola dichotoma BOISS. — n=7 (Fig. 2 E)

LOCALITÉ. Esfahan: Mouteh, 2000 m (74-194).

Nous avons compté (ARYAVAND 1975 a) le nombre chromosomique des *Clypeola microcarpa* et *C. aspera* appartenant respectivement aux sections *Jonthlaspi* (ADANS.) DC. et *Bergeretia* DC. L'espèce *C. dichotoma* BOISS. appartient à la section *Pseudanastatica* BOISS. Dans l'état actuel de nos connaissances, le nombre x=8 est particulier à la section *Jonthlaspi* et x=7 aux sections *Bergeretia* et *Pseudanastatica.*

Conringia persica BOISS. — 2n=14

LOCALITÉ. Esfahan: Mt Homayoun shahr, 1700 m (74-55).

Notre résultat concorde avec le comptage effectué par PODLECH et DIETERLE (1969) sur du matériel d'Afghanistan. Ce nombre a été trouvé chez deux autres espèces du genre *Conringia* (cf. BOLKHOSKIKH op. cit.) et on peut dire pour le moment que le nombre de base chez le genre *Conringia* est x=7.

Pseudofortuynia esfandiarii HEDGE — n=7 (Fig. 2 F)

LOCALITÉ. Esfahan: Ghameshlou, 2050 m (74-151).

Pseudofortuynia HEDGE est un genre monotypique, endémique des provinces de Fars et d'Esfahan de l'Iran. Ce genre, découvert récemment par HEDGE (HEDGE & RECHINGER 1968), ne comporte qu'une seule espèce *P. esfandiarii* HEDGE. Notre échantillon provient de la région de Ghameshlou à environ 60 km au NW d'Esfahan. C'est une nouvelle localité pour cette espèce. C'est la première fois qu'un comptage chromosomique a été effectué dans ce genre. D'après HEDGE (HEDGE & RECHINGER op. cit.), le genre *Pseudofortuynia* appartient à la tribu Brassiceae et à la sous-tribu Moricandiinae. Or, dans cette sous-tribu on connaît les nombres chromosomique des trois genres: *Conringia, Moricandia* et *Orychophragmus.* Chez ce dernier genre, le nombre chromosomique de *O. violaceus* (L.) O. E. SCHULZ a été déterminé par MANTON (1932): 2n=24, nombre dont nous ne pouvons pas tirer de conclusion. Comme nous l'avons expliqué plus haut, chez le genre *Conringia,* le nombre de base est 7. Quant au genre *Moricandia,* on connaît à l'heure actuelle, les nombres chromosomiques de quatre espèces. Tous ces comptages, à l'exception d'un comptage effectué par QUÉZEL (1955) sur *M. arvensis* (L.) DC. 2n=24, ont donné comme nombre chromosomique 2n=28 (in BOLKHOSKIKH op. cit. et MOORE 1973). Toutes ces observations montrent que le nombre n=7 de *Pseudofortuynia esfandiarii* HEDGE justifie la situation taxonomique de ce taxon.

Robeschia schimperi (BOISS.) O. E. SCHULZ — n=8 (Fig. 2 G)

LOCALITÉ. Esfahan: Mouteh, 2000 m (74-192).

Le genre *Robeschia* HOCHST. ex FOURN. ne comporte qu'une seule espèce dans le monde: *R. schimperi* (BOISS.) O. E. SCHULZ (SCHULZ 1924). Cette espèce se trouve au Sinai, en Syrie, en Iran et au Pakistan. Cette plante n'a pas été étudiée auparavant à notre connaissance.

Sisymbrium septulatum DC. — n=7, 2n=14 (Fig. 2 H)

LOCALITÉ. Esfahan: Mt Kolah-ghazi, 1800 m (74-67).

Cette espèce, non plus, n'a pas été étudiée auparavant. Mais le nombre 2n=14 est très fréquent chez le genre *Sisymbrium*. Le nombre chromosomique 2n=28 a été trouvé chez *S. irio* L. par PODLECH et DIETERLE (1969) sur du matériel d'Afghanistan, et par AMIN (in LÖVE 1973) sur du matériel d'Egypte.

D'après SCHULZ (1924), notre espèce appartient à la section *Pachypodium* (WEBB & BERTH.) FOURN. dont deux autres représentants (à savoir *S. altissimum* L. et *S. orientale* L.) ont un nombre chromosomique de 2n=14 (in BOLKHOSKIKH op. cit.). Il faut ajouter que la section *Pachypodium* est tout à fait proche de la section *Irio* DC. dont fait partie l'espèce *S. irio* L.

Straussiella purpurea (BGE.) HAUSSKN. — n=8 (Fig. 2 I)

LOCALITÉ. Esfahan: Mouteh, 2000 m (74-186).

C'est à notre avis le premier comptage publié sur le genre *Straussiella* HAUSSKN. *Straussiella purpurea* est une plante vivace, endémique de l'ouest et du centre de l'Iran. Le genre *Straussiella* appartient à la tribu *Alysseae* dans laquelle un certain nombre de genres comme *Alyssum, Fibigia, Clypeola* (pro parte) etc. présentent aussi le nombre chromosomique x=8.

Torularia aculeolata (BOISS.) O. E. SCHULZ — n=7

LOCALITÉ. Esfahan: Mt Homayoun shahr, 1700 m (74-43).

Dans un travail antérieur (ARYAVAND 1975 a), nous avons publié pour la première fois le nombre chromosomique (2n=14) pour cette espèce. Notre comptage sur un spécimen d'une autre localité donne le même resultat.

FABACEAE

Astragalus bachtiaricus BGE. — 2n=16 (Fig. 2 J)

LOCALITÉ. Esfahan: Ghameshlou, 2050 m (74-159).

Cette espèce n'a pas été étudiée auparavant. Mais le nombre 2n=16 est très fréquent chez le genre *Astragalus*.

Astragalus candolleanus BOISS. — n=8 (Fig. 2 K)

LOCALITÉ. Esfahan: Kuf-e Sofeh, 1700 m (74-75).

Cette espèce non plus, n'a jamais fait l'objet d'un comptage chromosomique. Nous avons observé quelques phénomènes anormaux dans la mitose pollinique des échantillons que nous avons étudiés (ARYAVAND, en cours de publication).

Astragalus fragiferus BGE. — n=8 (Fig. 2 L)

LOCALITÉ. Esfahan: Mt Kolah-ghazi, 1800 m (74-88).

Cette espèce n'a pas, non plus, été étudiée auparavant. A la métaphase de la première mitose pollinique le chromosome paranucléolaire présente une constriction assez grande.

Melilotus officinalis (L.) MED. — n=8

LOCALITÉ. Teheran: Ab-e ali, 2400 m (74-277).

Notre résultat concorde avec celui de nombreux auteurs sur des matériels de provenances différentes (cf. BOLKHOSKIKH op. cit. et MOORE 1973). Il faut noter que le nombre chromosomique 2n=32 pour cette espèce (LESINS 1952) correspond à une race artificielle obtenue par l'utilisation de colchicine.

Sophora griffithii STOCHS ssp. **hortensis** (BOISS. & BUHSE) YAKOVL. — n=9 (Fig. 2 M)

LOCALITÉ. Esfahan: Cité Universitaire, 1600 m (74-24).

Ce taxon n'a pas été étudié auparavant.

Mais le nombre x=9 est très fréquent chez le genre *Sophora*. C'est un arbuste ornemental à fleurs jaunes qui a été multiplié ces dernières années à Esfahan.

Vicia sativa L. — 2n=12

LOCALITÉ. Khuzistan: Ahvaz, Hamidyieh, 150 m (74-15).

Beaucoup de comptages chromosomiques ont été effectués sur cette espèce. Trois nombres chromosomiques ont été notés: 2n=10, 12, 14. Le nombre 2n=12 est signalé le plus souvent.

GERANIACEAE

Erodium cicutarium (L.) L'HÉRIT. ex AITON — 2n=40

LOCALITÉ. Esfahan, Mt Kolah-ghazi, 1800 m (74-33).

Cette espèce collective a été beaucoup étudiée par différents auteurs. Les résultats montrent qu'il existe en général deux nombres de base différents x=9 et x=10. Le nombre x=10 est de beaucoup le plus fréquent. La plupart des auteurs semblent être d'accord pour la dérivation du nombre x=9 à partir de x=10. PODLECH et DIETERLE (1969) ont trouvé le nombre 2n=36 sur du matériel d'Afghanistan.

Comme le type à 2n=18 n'a jamais été rencontré jusqu'a l'heure actuelle chez cette espèce, il semble bien que le type à 2n=20 a donné naissance au type 2n=40 et celui-ci, dans certaines régions de l'aire de distribution de l'espèce a donné naissance au type à 2n=36 par un phénomène d'aneuploïdie.

Il faut ajouter que PODLECH et DIETERLE (1969) ont rapporté d'après ROTTGARDT (1956) le nombre 2n=18 pour le var. *immaculatum* et 2n=20 pour le var. *pimpinellifolium*. Il s'agit sans doute d'une erreur typographique car les nombres publiés par ROTTGARDT sont respectivement n=18 et n=20.

ZYGOPHYLLACEAE

Peganum harmala L. — n=12

LOCALITÉ. Esfahan: Mt Kolah-ghazi, 1800 m (74-122).

Si l'on fait abstraction d'une numération assez ancienne de NEGODI (1937 in BOLKHOSKIKH op. cit.): 2n=22, notre comptage est identique aux résultats obtenus par plusieurs auteurs (in BOLKHOSKIKH op. cit. et MOORE 1973) sur des plantes de provenances différentes. Il faut noter que récemment HANLET (in LÖVE 1973) a trouvé une race tétraploïde (n=24) de cette espèce en Mongolie dans des peuplements de *Lasiagrostis*, influencés par l'homme.

PRIMULACEAE

Primula auriculata LAM. — n=11 (Fig. 2 N)

LOCALITÉ. Esfahan: Khunsar, Golestan kuh, 2500 m (74-166).

Le premier comptage effectué chez cette espèce date de 1920 (MARCHAL): 2n=54, résultat qui nous paraît erroné. SOKOLOVSKAJA et STRELKOVA (1940, 1948, in BOLKHOSKIKH op. cit.) ont trouvé 2n=45 sur du matériel du Caucase. TUMAJANOV et BERIDZE (1970) ont compté 2n=44 sur du matériel de l'Ossètie (Géorgie). Enfin KRESS (1969) a compté sur un matériel du jardin botanique de Münich le nombre chromosomique 2n=44. Cette plante avait été récoltée lors d'une expédition anglaise (Bowles-Expedition), et c'est M. le Dr B. MATHEW qui nous a aimablement communiqué l'endroit précis de sa récolte. Il s'agit de la région Khoy, à 2000 m alt. à l'extrême Nord-ouest de l'Iran, à environ 70 km de la frontière de l'URSS.

L'état actuel des connaissances cytologiques sur cette espèce peut se résumer ainsi:

Race tétraploïde
  2n=45 (Caucase)
  2n=44 (Géorgie)
  2n=44 (Khoy, NW de l'Iran)

race diploïde
2n=22 (Golestan kuh, Khunsar, environ à 130 km NW d'Esfahan), le présent auteur.

Au point de vue taxonomique SCHWARZ (1968) divise ce taxon en deux espèces différentes. D'après cet auteur les plantes de l'Iran peuvent être considérées comme étant le *P. auriculata* LAM. (au sens strict), et les spécimens du Caucase, de la Transcaucasie et de l'Asie Mineure comme appartenant à *P. glacialis* ADAM. ex WILLD. Comme, nous venons de l'expliquer, les limites des races chromosomiques ne coïncident pas parfaitement avec la proposition de SCHWARZ. Dans l'état actuel de nos connaissances, nous pouvons dire que la partie sud de l'aire de distribution de cette espéce est occupée par la race primitive diploïde. Cette race diploïde a donné naissance vers le NW à une race tétraploïde qui occupe actuellement le NW de l'Iran et le Caucase et probablement l'Asie Mineure. Une étude biosystématique plus complète serait d'un grand intérêt pour distinguer les limites précises de ces deux races.

BORAGINACEAE

Arnebia decumbens (VENT.) COSS. & KRAL. — n=11, 2n=22 (Fig. 2 O)

LOCALITÉ. Esfahan: Mouteh, 2000 m (74-182).

Notre résultat sur cette espèce ne concorde pas avec les résultats obtenus par MATVEJEVA et TIKANOVA (en cours de publication) (in BOLKHOSKIKH op. cit.). En effet les auteurs russes ont compté le nombre 2n=8 sur un matériel provenant probablement de l'URSS. D'après RIEDL (1967), cette espèce comprend deux sous-espèces dans le territoire couvert par «Flora Iranica». Notre échantillon appartient probablement au ssp. *decumbens,* mais en l'absence de fruits nous ne pouvons pas l'assurer.

Lepechiniella persica (BOISS.) H. RIEDL — n=11 (Fig. 2 P)

LOCALITÉ. Tehran: Plour, 2300 m (74-273).

A notre connaissance, aucun représentant du genre *Lepechiniella* M. POP. n'a fait l'objet d'un comptage chromosomique. *Lepechiniella persica* (BOISS.) H. RIEDL est une espèce vivace, endémique du nord de l'Iran.

Nonnea caspica (WILLD.) G. DON — n=22, 2n=44 (Fig. 1 E)

LOCALITÉ. Esfahan: Cité Universitaire, 1600 m (74-20).

Notre résultat ne concorde pas avec ceux obtenus par PODLECH et BADER (1974) sur cette espèce. En effet les auteurs allemands ont compté 2n=28 sur du matériel de l'Afghanistan. Cette espèce selon RIEDL (op. cit.) possède dans le territoire couvert par «Flora Iranica» quatre sous-espèces différentes. L'avenir dira si la différence de nombre chromosomique coïncide ou non avec les limites de ces sous-espèces.

A noter que VASUDEVAN (à l'impression) a compté n=8 chez un *Nonnea caspica* du Tangmarg (Kashmir). Si la plante a été correctement déterminée, cela signifie qu'il y a des races de cette espèce possédant n=14 et n=8, ce qui permettrait de comprendre l'existence d'un nombre n=22.

Nonnea persica BOISS. — n=16 (Fig. 1 F)

LOCALITÉ. Esfahan: Ghameshlou, 2050 m (74-153).

Cette espèce n'a pas été étudiée auparavant à notre connaissance. Mais plusieurs auteurs ont trouvé le nombre 2n=16 chez *N. rosea* LINK (in BOLKHOSKIKH op. cit.). Il faut noter que *N. persica* appartient à la section *Nonnea,* tandis que *N. rosea* appartient à la section *Orthocaryum* DC.

Il faut ajouter que, à la diacinèse nous avons observé 14 bivalents et 1 tétravalent. La présence d'un tétravalent laisse supposer qu'il s'agit peut-être d'un autotétraploïde.

LAMIACEAE

Eremostachys adenantha Jaub. & Spach — n=11 (Fig. 3 A)

LOCALITÉ. Esfahan: Mouteh, 2000 m (74-195).

C'est à notre avis le premier comptage publié sur cette espèce. Le nombre chromosomique 2n=22 est déjà connu pour six autres espèces du genre *Eremostachys* (cf. Bolkhoskikh op. cit. et Moore 1973). A la métaphase de la première mitose pollinique un des chromosomes possède un satellite.

Hymenocrater bituminosus Fisch. & Mey. — n=9 (Fig. 2 Q)

LOCALITÉ. Esfahan: Mt Kolah-ghazi, 1800 m (74-81).

Aucun représentant du genre *Hymenocrater* n'a été étudié auparavant à notre connaissance. Le nombre chromosomique n=9 est assez répandu dans la famille des Labiées.

Nepeta racemosa Lam. s. l. — n=18 (Fig. 3 B)

LOCALITÉ. Tehran: Plour, 2300 m (74-274).

Cette espèce n'a pas été étudiée auparavant. Il s'agit probablement d'une espèce tétraploïde avec le nombre de base x=9. Or, ce dernier nombre est très fréquent chez le genre *Nepeta* L.

Nepeta schiraziana Boiss. — n=8 (Fig. 3 C)

LOCALITÉ. Shahr-e Kord: Kuh-rang, 2350 m (74-259).

Cette espèce du genre *Nepeta* n'a pas, non plus, fait l'objet d'un comptage chromosomique. Mais le nombre chromosomique 2n=16 a été trouvé chez *N. teydea* Webb et Berth. par plusieurs auteurs (cf. Bolkhoskikh op. cit. et Moore 1973).

SCROPHULARIACEAE

Veronica farinosa Hausskn. — 2n=16 (Fig. 3 D)

LOCALITÉ. Esfahan: Damaneh, 2100 m (74-161).

Cette espèce n'a pas été étudié auparavant. Elle appartient au groupe *Orientalis* (Römpp 1928). Comme Fischer (1970), en particulier, l'a montré, le nombre de base dans ce groupe est x=8 avec des taxons diploïdes (comme *V. farinosa* Hausskn.), tétraploïdes (comme *V. microcarpa* Boiss.), hexaploïdes (comme *V. multifida* Benth.) et octoploïdes (*V. elmaliensis* M. Fischer).

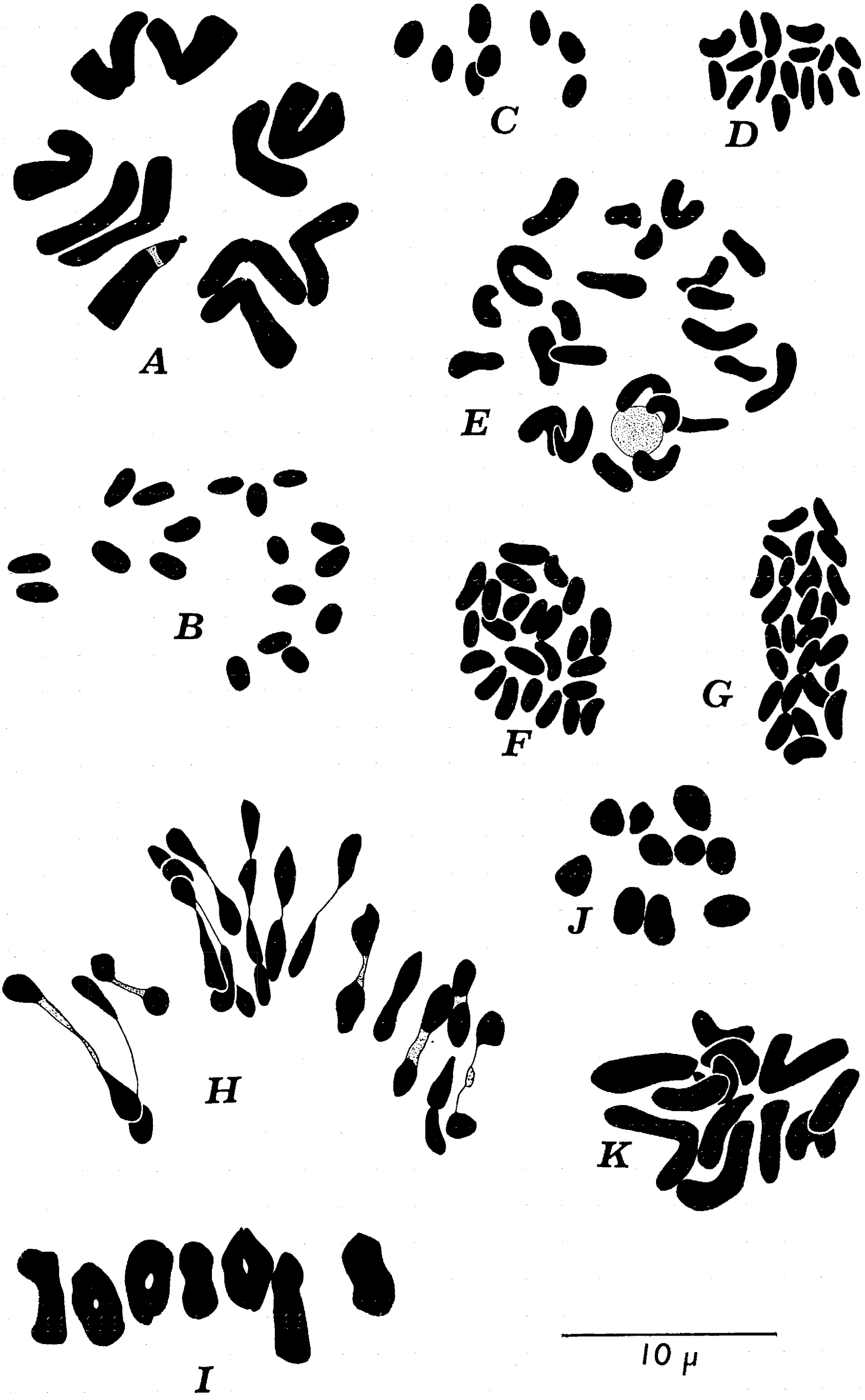
ASTERACEAE

Cousinia congesta Bge. — 2n=24 (Fig. 3 E)

LOCALITÉ. Esfahan: 25 km S Delidjan, 2100 m (74-263).

Notre résultat ne concorde pas avec le comptage effectué par Chouksanova (non publié, in Bolkhoskikh op. cit.) sur du matériel probablement originaire de Turkmenistan. En effet, l'auteur russe a trouvé le nombre chromosomique 2n=26. C'est une espèce vivace de la section *Congestae* Bge. qui se trouve dans le nord de l'Iran, le Turkmenistan et l'Afghanistan.

Fig. 3. A: *Eremostachys adenantha,* mitose pollinique, n=11. — B: *Nepeta racemosa,* anaphase I, n=18. — C: *Nepeta schiraziana,* métaphase II, n=8. — D: *Veronica farinosa,* mitose somatique de l'ovaire, 2n=16. — E: *Cousinia congesta,* prophase de la mitose somatique de l'ovaire, 2n=24. — F: *Cousinia kornhuberi,* mitose somatique de l'ovaire, 2n=24. — G: *Cousinia tenella,* mitose somatique de l'ovaire, 2n=26. — H: *Onopordon heteracanthum,* métaphase I, n=17. — I: *Scorzonera picridioides,* métaphase I, n=7. — J: *Senecio coronopifolius,* anaphase I, n=10. — K: *Tragopogon straussii,* mitose somatique de l'ovaire, 2n=12.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Cousinia kornhuberi HEIMERL — 2n=24 (Fig. 3 F)

LOCALITÉ. Hamadan, Barrage de Shahnaz, 2000 m (74-232).

C'est à notre avis le premier comptage publié sur cette espèce vivace, endémique de la province d'Hamadan située à l'ouest de l'Iran.

Cousinia pugionifera JAUB. & SPACH — 2n=24 (Fig. 1 G)

LOCALITÉ. Esfahan: 10 km N Meymeh, 2100 m (74-245).

Cette espèce non plus n'a pas été étudiée auparavant. C'est une espèce bisannuelle ou vivace de la section *Pugioniferae* BGE., endémique de la région d'Esfahan.

Cousinia tenella FISCH. & C. A. MEY. — 2n=26 (Fig. 3 G)

LOCALITÉ. Récolté par le jardin bot. de Tashkent (74-220).

L'échantillon que nous avons étudié provient du jardin botanique de Taschkent; il a donc probablement été récolté dans le Turkmenistan ou l'Asie centrale. Cette espèce se trouve en Iran dans les provinces Azerbaidjan, Gorgan, Tehran et Khorassan. Ce taxon annuel de la section *Tenellae* BGE. n'a pas fait non plus l'objet d'un comptage chromosomique.

Le genre *Cousinia* est bien représenté dans la flore de l'Iran. Il prend le deuxième rang au point de vue du nombre d'espèces après le genre *Astragalus*. Heureusement, ce genre a été le sujet d'un remarquable volume de la «Flora Iranica» traité avec beaucoup de mérite par le Professeur Dr RECHINGER (1972). Il possède 354 espèces dont la plupart endémiques. Mais au contraire, peu d'études cytotaxonomiques ont été consacrées à ce genre. Les nombres chromosomiques connus jusqu'à présent chez 24 espèces dans l'ensemble du genre sont 2n=18, 20, 24, 26 et 36. Il est encore trop tôt pour avoir une idée générale sur la cytotaxonomie de ce genre. Mais nous espérons continuer son étude cytotaxonomique au fur et à mesure de nos possibilités.

Onopordon heteracanthum C. A. MEY. — n=17 (Fig. 3 H)

LOCALITÉ. Esfahan: Djargouyeh, 1550 m (74-261).

Cette espèce, non plus, n'a jamais fait l'objet d'un comptage chromosomique. Mais, il semble bien que le nombre 2n=34 soit pour le moment le seul nombre chromosomique connu chez le genre *Onopordon*.

Scorzonera picridioides BOISS. — n=7 (Fig. 3 I)

LOCALITÉS. Esfahan: Mt Kolah-ghazi, 1800 m (74-30) — Esfahan: Ghameshlou, 2000 m (74-132).

Cette espèce non plus n'a pas été étudiée auparavant. Mais dans le genre *Scorzonera*, le nombre chromosomique n=7 est le plus répandu.

Senecio coronopifolius DESF. — n=10 (Fig. 3 J)

LOCALITÉ. Luristan: Tangueh Malavi, 850 m (74-13).

Nous avons compté le nombre chromosomique n=10 sur un matériel provenant de Tangueh-Malavi (Luristan), localité située à l'ouest des chaînes de montagnes Zagros.

MEHRA et RAMANANDAN (in LÖVE 1969) ont rapporté pour cette même espèce le nombre n=20 trouvé sur un matériel de Simla (dans l'Himalaya occidental). Donc, il existe probablement chez cette espèce annuelle et polymorphe (BOISSIER 1875), au moins deux races chromosomique différentes; l'une diploïde (n=10) (ouest de l'Iran) et l'autre, tétraploïde (Himalaya occidental). Il serait très intéressant de déterminer les limites géographiques de ces deux races, ainsi que leurs différences morphologiques.

Tragopogon straussii BORNM. — $2n=12$ (Fig. 3 K)

LOCALITÉ. Arak: 35 km W de la ville Arak, 2000 m (74-241).

C'est à notre avis le premier comptage publié sur cette espèce. Le nombre chromosomique $2n=12$ est le plus fréquent chez le genre *Tragopogon*.

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Notes on Central American Marantaceae II

New Species from Panamá and Costa Rica

Helen Kennedy

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Three new species of *Calathea* (Marantaceae) are described: *Calathea portobelensis* and *C. robin-fosteri* from Panamá and *C. similis* from Panamá and Costa Rica. A new record, *Calathea guzmanioides,* previously known only from Colombia is noted for Panamá.

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The Marantaceae is a family of herbaceous monocots, including forest floor species 15 cm high as well as clambering liana-like species of 7—8 m. It is a prominent element in the moist to wet tropics below 1500 m elevation. The majority of species occur in the Neo-tropics, especially near the equator.

As an outgrowth of pollination studies of this family in Central America (KENNEDY 1974) a revision of the Marantaceous flora of Panamá was undertaken. Although the number of species of Marantaceae known from Panamá has significantly increased in the past 5—6 years, it continues to be a rich source of unreported and undescribed species. In his comments on the coverage of families treated in the early parts of WOODSON and SCHERY's Flora of Panama (1945), DRESSLER (1972 p. 184) noted 35 species of Marantaceae as occurring in Panamá, a sizable increase over the 23 species listed in the flora. Since then the number of species known from Panamá in this family has risen to 49. In *Calathea,* the largest and most diverse genus of the family, an additional 23 species have been found since the original treatment, an increase of 164 %. In the family as a whole the percent increase is 110.

Much of the wet forest area near the continental divide and on the Atlantic slope of Panamá remains inadequately explored botanically. This is indicated by the number of new species in the Portobelo area (Colón Province) and in the recently accessible forest along the El Llano-Carti road (km 12—17) in the Cordillera de San Blas. A total of 17 species is known from this latter area of which 7 (6 *Calatheae* and 1 *Ischnosphon*) were new records for Panamá as well as new species. Of the 15 species known from the Río Guanche site (near Portobelo, Colón Prov.), 6 were new records for Panamá, 5 of which were also new species. Out of the 13 species at Cerro Jefe (Panamá Prov.) 5 were new records and 3 new species. Seven species were common to both Cerro Jefe and the Carti road area, 5 species in common between Cerro Jefe and Río Guanche and 5 between the Carti road and Río Guanche. The degree of species overlap between these relatively rich wet forest areas is only about 1/3. Many of these species are known from only a few individuals or small, very localized, populations. This low population density and sporadic occurrence is most common in species of the wetter forest habitats growing within the forest rather than at an edge or in disturbed situations. Because of the distributional patterns of these species the problem of adequately sampling an area such as the Atlantic slope becomes a challenge indeed, especially considering the lack of roads. Of the 26 species of *Calathea* discovered since 1945 in Panamá, 15 are known from only a single locality within Panamá. Probably a few of these species are indeed narrow endemics. However, more extensive collecting in Panamá, Costa Rica and the Chocó region of Colombia will quite likely show these species to have a wider distribution, though not necessarily a wider habitat tolerance. Six of the 15 Calatheas mentioned above have been collected in Costa Rica and 3 in Colombia. The claviculate bracteoles which are so characteristic of inflorescences in the majority of South American Calatheas, though rare in Central American ones, occur in 8 species from eastern Panamá (east of the Canal Zone) but in none from western Panamá, indicating their South American affinities. With continued exploration of the wet forest areas of Panamá the Marantaceous flora for this area will probably reach 60—70 species.

Calathea portobelensis KENNEDY sp. nov. — Fig. 1

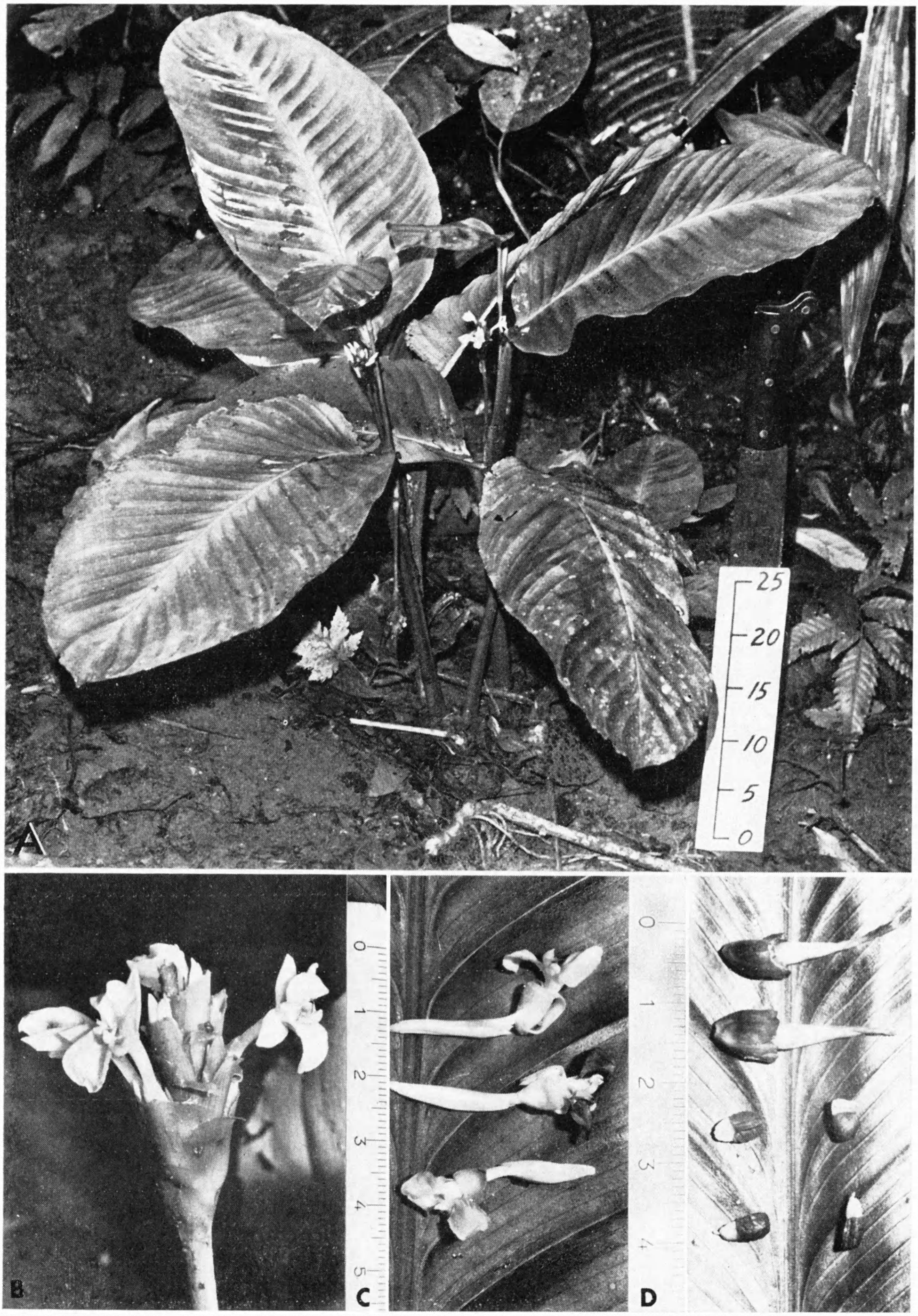
Planta ad 1.1 m alta vulgo ramificans. Petioli supra sulcati, parte superiore ad 2 cm longa callosa supra tomentosa; lamina elliptica supra smaragdina secus parte centrale pallidior. Spicae plures raro solitariae cylindricae, pedunculo ad basim tumido albo demum deflexo; bracteae dilute virides; omnis par florum bracteolis indurato-claviculatis comitatum; corollae albae vel violaceo-suffusae tubo ad 2.6 cm longo.

Caulescent herb, 0.4—1.1 m high. An individual plant usually has one or more branch shoots arising in the axils of the lowermost leaves, though generally only one shoot per leaf axil. In older plants branch shoots often arise in the axil of the leaf subtending the inflorescence. Rhizome ca 6—10 mm in diameter, internodes 3—9 mm, roots occasionally bearing swollen tubers. Cataphylls herbaceous, narrowly ovate, apex mucronulate, green, minutely appressed puberulent (14×). Leaf blade herbaceous, surface shallowly undulate, elliptic, apex of larger leaves rounded with an acumen, acuminate in smaller leaves, base rounded, shortly and abruptly acuminate at the junction with the pulvinus, 5—30 cm wide and 9—61.5 cm long. Leaf surface above semilustrous grass-green with a jagged-edged light green pattern along the midrib (ca 1/6 the width of the leaf), glabrous, occasionally minutely puberulent along major veins (14×), not visible to naked eye, midrib minutely tomentose, more densely so near apex. The lower surface dull grey-green, midrib and veins minutely tomentose, and glabrous between the veins. Pulvinus round in cross section, slightly larger in diameter than petiole, light green, glabrous to subglabrous, minutely tomentose along upper side, 0.35—2 cm long. Petiole bearing a shallow groove along the upper side, grass-green, minutely tomentose, 0.6—24 cm long, occasionally absent altogether. Leaf sheath herbaceous, grass-green, minutely puberulent (14×) to subglabrous in upper portion, the basalmost portion (1—2 cm) pink, dense appressed tomentose, 4—45 cm long. Stem grass-green, minutely puberulent (14×). The first inflorescence is terminal on the shoot, additional inflorescences with their concomitant bicarinate prophylls are borne in the axil of the leaf subtending the first inflorescence. In addition, a leafy branch shoot may also be formed in the axil of the subtending leaf and likewise bear 1 or more inflorescences. Bicarinate prophylls subtending axillary inflorescences or shoots green, minutely puberulent, 1.8—7.8 cm long. Peduncle green, subglabrous to minutely tomentose basally, (3) 5.5—28 cm long, the basal 1 cm pale green to whitish, swollen, with age the peduncle bends in this area reflexing the inflorescence downward. Inflorescences usually several. 1—4 (7) per leafy shoot, cylindric to fusiform, (2) 3—7.5 cm long and 0.8—2.3 cm wide. Bracts (3) 6—15(18) imbricate, spirally arranged, herbaceous, apex erect or occasionally slightly spreading, broadly elliptic to obtrullate in upper bracts, apex acuminate to subacute, lowermost bract occasionally broadly transverse ovate, 1.6—2.2 cm high and 0.8—2 cm wide; each subtending up to 8 flower pairs. Outer bract surface wholly light green or pale whitish-tan with margins tinged purplish, minutely tomentose; within, light green above, paler toward base or white, glabrous. Bicarinate prophyll membranaceous, elliptic to ovate-elliptic, rounded to obtuse, translucent pale green or pale tan, minutely puberulent at apex, 1.3—1.8 cm high and 0.8—1.2 cm wide. Mesophyll membranaceous, narrowly ovate to ovate, obtuse to rounded, translucent pale green or pale tannish, minutely puberulent (14×) at apex, 1.45—1.8 cm high and 0.7—0.8 cm wide. Bracteoles subtending individual flowers, 2 per flower pair, membranaceous, translucent chartreuse or faint tan, glabrous, 1.25—1.9 cm long, 0.3—0.45 cm wide. Each flower pair is provided with an indurate claviculate bracteole, 1.7—2.1 cm long, the lower half translucent white, the upper half stiff, cream-yellow. The flower opens spontaneously. Sepals thin, herbaceous, narrowly obovate-elliptic, acute, white, glabrous, 1.5—1.9 (2.1) cm long and 0.25—0.4 cm wide. Corolla tube white, glabrous, 2.2—2.6 cm long, additionally a staminal tube 3—4 mm long is usually present. Corolla lobes ovate to elliptic, obtuse, white or light purple, 0.8—1.1 cm long and (3.5) 4—6 (7) mm wide. Outer staminode broadly transverse elliptical, circular or broadly elliptical, apex rounded or shallowly retuse, very shortly clawed at the base, white or purple, 0.9—1.2 cm long and 0.7—1 cm wide. Callose staminode spatulate, apical portion petaloid, broadly transverse elliptic, emarginate, lower portion callose, white or marked with purple, 1—1.2 cm long and 0.7—1 cm wide. Cucullate staminode white or purple, 0.45—0.5 cm long and 0.35—0.5 cm wide, provided with a subterminal filiform appendage. Filament white or purple, bearing a lateral petaloid appendage to 2.5 mm wide; anther 2 mm long. Ovary white, glabrous, 1—1.5 mm long. Style and stigma white. Capsule obovoid, trigonous, semitranslucent light green, glabrous with fleshy slightly raised apical rim, 8—9 mm high and 5.5—7 mm wide, crowned by a live expanded persistent calyx, 6.5—7 mm wide. Seeds usually 3, trigonous, rugose on the outer surface, red-brown, 3—4 mm high and 3—4 mm in diameter with a basal white aril 2.5—3 mm high.

TYPE. Panamá: Prov. Colón, Río Guanche, ca 1.5 mi. upstream from the bridge, lowland wet forest, ca 10 m, 23 Aug. 1972, H. KENNEDY and R.L. DRESSLER 1500 (holotype US, isotypes BM, COL, DAV, DUKE, F, GH, K, MO, NY, PMA, U, W).

OTHER COLLECTIONS. Panamá: Prov. Colón, semi-swampy flood plain near bridge over Río Buenaventura, near Portobelo, 4 April 1970, R.B. FOSTER 1689; near Portobelo at the bridge over the Río Buenaventura, 14 Aug. 1970, H. KENNEDY & R. B. FOSTER 445 (B, DUKE, LE, MEXU, MO, P, VEN); semi-inundated forest and tierra firma, 27 Aug. 1970, H. KENNEDY 467 (DAV, MICH, S, UC, US); Río Guanche, 2 mi. upstream from the bridge, mature forest, 17 July 1971, H. KENNEDY, R. B. FOSTER & R. L. DRESSLER 1095 (MO); ca 1.5 mi. upstream from the bridge, 10—20 m, wet lowland evergreen forest, 4 Sept. 1974, H. KENNEDY, R. L. DRESSLER, P. J. M. MAAS & C. TOFT 3383 (BM, BR, GOET, H, M, U); along Río Guanche, 6 km S of Portobelo 1—3.5 km E of Portobelo-Puerto Pilon road bridge, 0—10 m, tropical wet forest, 10 Dec. 1973, M. NEE & A.

Fig. 1. *Calathea portobelensis*. A: Habit. — B: Inflorescence with untripped flowers. — C: Flowers on upper leaf surface, callose and outer staminodes of middle flower purple, white in the others. — D: Capsules with persistent sepals and arillate seeds on upper leaf surface. — Scale in cm.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GENTRY 8689; Río Boqueron ca 6 km upstream from Peluca Hydrographic station, 7 April 1974, R. L. DRESSLER 4651 (US); 6—8 km from Peluca Hydrographic station on the road to Nombre de Dios, 29 Aug. 1974, H. KENNEDY & R. L. DRESSLER 3333 (US). Province unknown, 1911, H. PITTIER 4214 (F).

Flowering mainly during the rainy season, May through December. However, in the Portobelo area a few individuals may be found in flower at almost any time during the year. Occurring along stream banks, in run-off channels and in the sandy soil of old stream beds, or on slopes above the stream. This species differs from other Panamanian and Costa Rican Calatheas by the claviculate bracteoles, pale green irregular pattern along the midrib, the several (rarely 1) small inflorescences of light green or tannish white bracts, and the characteristic tendency toward branching. It is distinguished from the South American *Calathea lietzei* MORREN and *C. lousiae* GAGNAPAIN by its less defined color pattern on the leaf and possession of claviculate bracteoles. The claviculate bracteoles bear an extra-floral nectary subterminally which accounts for the common occurrence of ants on the inflorescences of this species.

The specific epithet refers to its discovery and prevalence in the forested region near Portobelo, Panamá.

Calathea robin-fosteri KENNEDY sp. nov. — Fig. 2

Planta ultra metralis. Folia solitaria longissime petiolata; petioli atrovirides glabri, parte superiore ad 3.2 cm valde conspicue callosa glabra; lamina anguste elliptica apice acuminato vel obtuso base acuta, supra ad medium minutissime puberula, subtus dilute viridis glabra ad medium rubra raro flavo-virens, vagina haud conspicua. Spica e rhizomate ellipsoidea, pedunculo ad 8.6 cm longo subglabro; bracteae spiraliter dispositae minute puberulae; omnis par florum bracteolis indurato-claviculatis comitata; sepala ultra 2.3 cm longa glabra; corollae glabrae; ovarium glabrum.

Herb 1.1—1.65 (1.8) m high, aerial adult shoots bearing a single leaf, rarely two, the several leaves (shoots) connected by a common rhizome. Juvenile shoots bearing several leaves. Rhizome to 1.5 cm in diameter, internodes 0.2—1.2 cm in length. Cataphylls 5—6 per shoot, fleshy toward base, above subcoriaceous, ovate to narrowly ovate-triangular, acute to obtuse in lower ones, purple or green tinged with purple, subglabrous to minutely puberulent, innermost one up to 71 cm long. Leaf blade semi-coriaceous, slightly oblique, narrowly elliptic, apex broadly acute to obtuse, base acute, 36.3—85.5 cm long and 10.1—20.7 cm wide. Leaf surface above green, opaque, glabrous, proximal half of midrib subglabrous, distal half puberulent especially at apex; leaf below light green (in juvenile plants dark purple) dull, midrib red, occasionally yellow-green. Pulvinus glabrous, dark green with red-purple tinge, or reddish-brown, 1.3—3.2 cm long, articulate with petiole, junction on upper side, acuminate. Petiole dark green tinged slightly with purple-brown, glabrous, 32—80 cm long, most commonly 40—55 cm long. Leaf sheath inconspicuous, margins fleshy, highly reduced, to 7.8 (11.7) cm, the basal portion conspicuously swollen, bright pink in young leaves turning pale green to tan with age, 2—3.5 cm long, the outer cells becoming corky. Inflorescence arising directly from the rhizome, shoot bearing the inflorescence is provided with up to 7 bladeless sheaths. Sheaths ovate to narrowly ovate, obtuse to acute, purple, minutely pubescent, the base and the internode of the rhizome below sericeous. Scape dark purple to

Fig. 2. *Calathea robin-fosteri.* A: Habit. Note inflorescence at base of plant. — B: Inflorescence on separate shoot from the rhizome. Note pale needle-like claviculate bracteoles protruding from the bracts. — C: Untripped flower showing shape of callose and outer staminodes. — D: Flower on lower leaf surface. — E: Capsules with persistent sepals and arillate seeds on upper leaf surface. — Scale in cm.

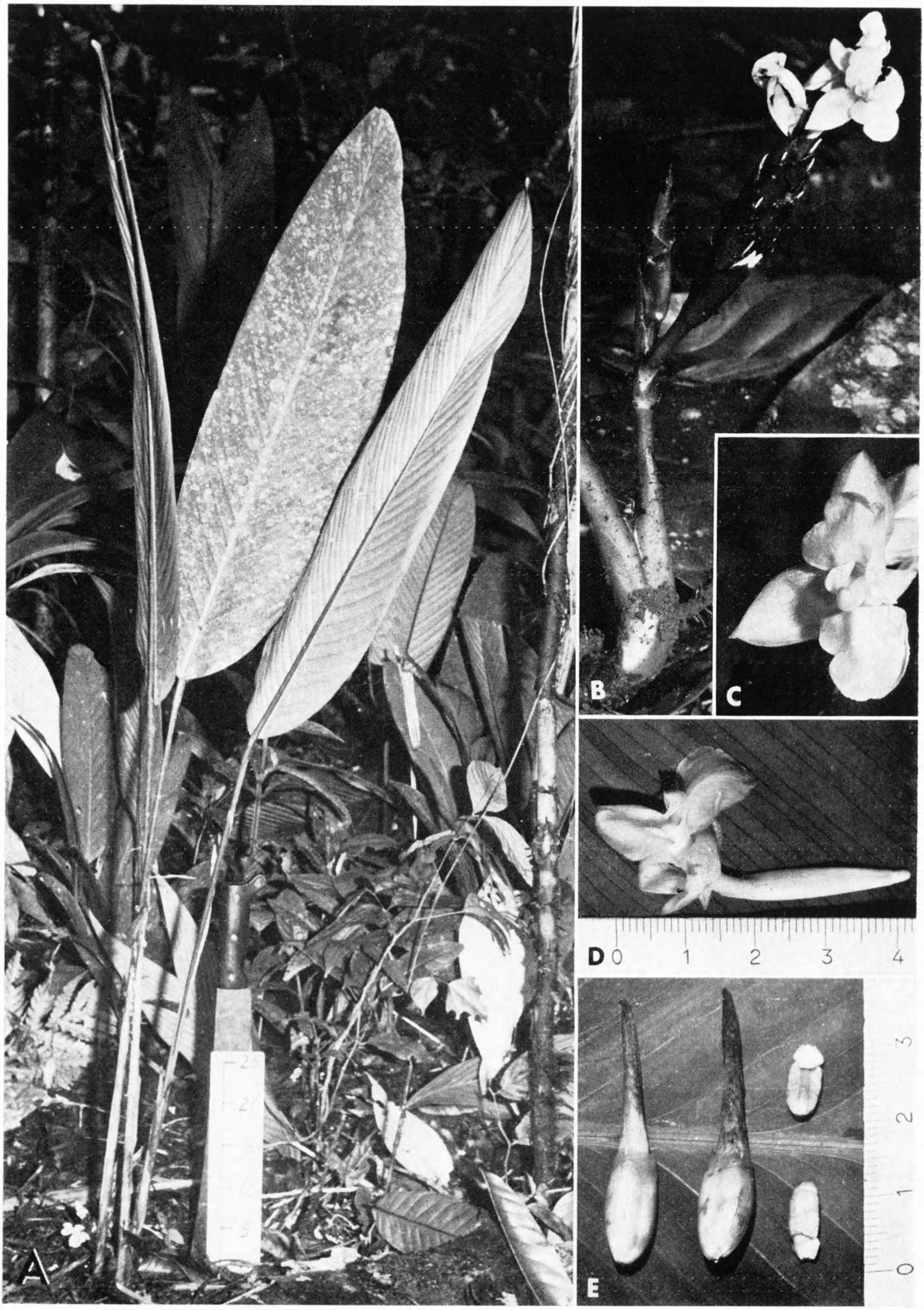

Fig. 2.

purple-brown, subglabrous, 2.2—8.6 cm long, bearing a narrowly ovate, acute sterile purple bract which subtends 2 inflorescences, one borne terminally, the second arising in the axil of this bract separated from the first by a bicarinate prophyll and subtended by a reduced leafless sheath, these last two structures always shorter than the sterile bract. Occasionally only the terminal inflorescence subtended by the sterile bract is developed. Inflorescence spiciform, narrowly ellipsoid-fusiform to subcylindrical, 4.5—7 cm long, 1.3—2.2 cm wide. Peduncle subglabrous, dark purple, 1.1—7 cm long, the terminal one longer. Bracts 9—13, spirally arranged, imbricate, herbaceous to subcoriaceous, dark red-purple to brownish-purple, minutely tomentose, hairs less than 0.3 mm, not visible to the naked eye, mitre shaped, acute, rarely obtuse, 2.3—2.8 cm high and 1.2—1.8 cm wide, each subtending 2 or more flower pairs. Bicarinate prophyll membranaceous, narrowly ovate, acute, margins and apex puberulent, 2—2.5 cm high and ca 0.8—0.9 cm wide. Mesophyll membranaceous, narrowly ovate, acute, apical 1/3 puberulent (14×), 2.4—2.6 cm high and 0.9—1.1 cm wide. Bracteoles subtending individual flowers two per flower pair, membranaceous, narrowly ovate, puberulent at apex, 2.3—2.5 cm long and 5—6.5 mm wide. Each flower pair is accompanied by an indurate claviculate bracteole 2.5—3.1 cm long, yellow-tan apically, tinged purple below. Sepals oblong to narrowly subobovate, acute, glabrous, entirely white or with apical half faintly tinged pink, 2.3—2.6 cm long and 0.4—0.55 cm wide. Corolla tube glabrous, white, (2.3) 2.5—3.0 cm long; lobes subequal, shallowly concave, elliptical acute to obtuse, apical margins incurved, glabrous, entirely white or with the distal half tinged pale pink, 1.5—1.6 cm long and 0.8—1 cm wide. Outer staminode broadly elliptic to suborbicular, apex rounded, irregular, shallowly emarginate, white, 1.25—1.4 cm long and 1.1—1.2 cm wide. Callose staminode petaloid apically, upper half depressed elliptical, apex emarginate, white, 1.5—1.6 cm long and 1.35—1.45 cm wide. Cucullate staminode white, 0.5—0.6 cm long and ca 0.55 cm wide, bearing a subterminal filiform appendage 2—2.5 mm long. Stamen with lateral petaloid appendage to 1.5 mm wide narrowing above, anther ca 2 mm long, apical 1/3 free. Style and stigma white. Ovary white, glabrous, ca 3 mm long and ca 2 mm in diameter. Capsule smooth, fleshy, ellipsoidal, with slight constriction subterminally, with a thickened, raised, apical rim, the apical margin of each valve tridentate, crowned by a persistent calyx. Seeds usually three per capsule, trigonous, rugose on outer surface, brown, 6—7.5 mm long and 3.5—4.5 mm in diameter, provided with a basal white aril ca 3 mm high.

TYPE. Panamá: Prov. Colón, Río Guanche ca 1.5 mi. upstream from bridge, mature forest, 10 m elev., 1 Nov. 1971, H. KENNEDY 1235 (holotype US, isotypes F, MO).

OTHER COLLECTIONS. Panamá: Prov. Colón, Río Guanche, 2 mi. upstream from the bridge, mature forest, 17 July 1971, H. KENNEDY, R. B. FOSTER & R. L. DRESSLER 1083 (GH, K, NY); ca 1.5 mi. upstream from the bridge, mature forest, 10 Aug. 1971, H. KENNEDY, R. L. DRESSLER & H. WIEHLER 1106 (US); lowland wet forest, ca 10 m, 23 Aug. 1972, H. KENNEDY & R. L. DRESSLER 1499 (DUKE, PMA, U); Río Iguanita, ca 1 mi. upstream, lowland wet forest, elev. ca 10 m, 27 Mar. 1975, H. KENNEDY & R. L. DRESSLER 3474 (F).

This species was also found in the Río Boqueron drainage, 6—8 km beyond the Peluca Hydrographic station on the road to Nombre de Dios, Colón Province, Panamá.

Flowering mainly during the rainy season, April to November. However, along the Río Iguanita plants were in flower in March. It occurs in moderate to deep shade on well drained sites not subject to flooding.

It is easily distinguished from other Central American Calatheas by possessing a single leaf per shoot and the inflorescence borne on a separate shoot, imbricate bracts, claviculate bracteoles, and a corolla tube shorter than 3.2 cm. Vegetatively it closely resembles the often cultivated

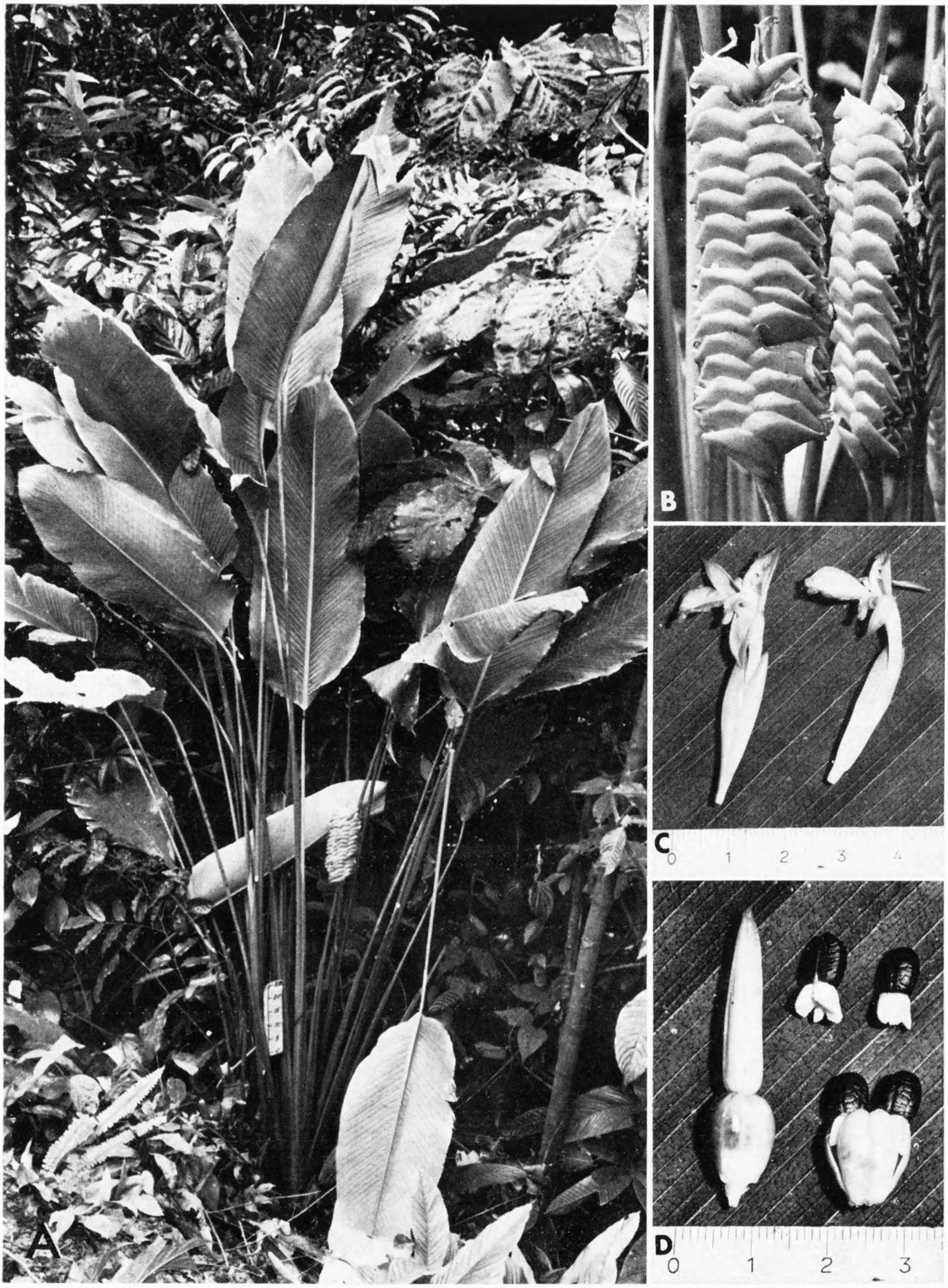

Fig. 3. *Calathea similis.* A: Habit. — B: Inflorescences. — C: Tripped flowers on upper surface of leaf. — D: Capsules with persistent calyx, dehisced capsule with emerging seeds and arillate seeds on upper leaf surface. — Scale in cm.

C. variens KOERNICKE and is distinguished from that species by the glabrous, solid-colored petiole. It differs from other species having separate floral and single-leaved vegetative shoots (*Calathea* Series *Rhizanthe,* SCHUMANN 1902 p. 70) by the imbricate bracts, indurate claviculate bracteoles, acute leaf base and leaf width greater than 10 cm.

This species is named in honor of Dr ROBIN FOSTER whose help and logistic support has greatly aided this study and whose fascination with tropical forests led to his investigation of the Río Guanche area and hence the discovery of this, as well as other new species.

Calathea similis H. KENNEDY sp. nov. — Fig. 3

Planta 1.7—3.2 m alta. Petioli villosi vel glabri, folia ovata acuminata vel subuncinata base obtusa vel rotundata supra dense villosa subtus pars marginalis sparsim villosa ceterum glabra. Spicae ad 24 cm longae folio comitata pedunculis ad 70 cm longis villosis vel glabris; bracteae distichae apice emarginato aureae unctuosae ad marginem villosae valde suaveolentes; paria florum ad 6; sepala ad 2.5 cm longa; corollae aureae tubo ad 3 cm longo.

Caulescent herb 1.7—3.2 m high, shoots bearing 5—8 leaves, 4—7 arising basally, the uppermost leaf which subtends the inflorescences is borne above an elongated stem internode up to 1.3 m long. Rhizome fibrous, semi-woody. Cataphylls usually dead, partially rotted on mature flowering shoots, narrowly ovate, obtuse, mucronulate, abaxially grass-green, villose, especially basally and centrally, innermost cataphyll 40—115 cm long. Leaf blade semi-leathery, pliable, apex acuminate to uncinate, base obtuse to rounded, 80—91 cm long and 32—39 cm wide in subtending leaves, others 75—105 cm long and 25—38 cm wide. Leaf blade above grass-green to dark green, densely villose (hairs ca 2 mm long), midrib yellow-green, villose; leaf surface below light green to glaucous, glabrous, occasionally sparsely villose. Pulvinus round in cross section, olive-green, glabrous, articulate with petiole, the junction light yellow-green, 10.3—12.5 (14) cm long in the subtending leaf, 7.5—16 cm in others. Petiole grass-green to deep green, glabrous to villose, 51—74 cm long in subtending leaf, 45—120 cm in others. Leaf sheath not auriculate, grass-green to deep green, villose throughout or the margins densely villose with the central abaxial portion partially or entirely glabrous; pale green glabrous within, 33—56 cm long in subtending leaves, 60—120 cm in others. Stem grass-green to deep green, subglabrous to villose; puberulent to subglabrous where covered by the leaf sheaths. Inflorescences 2—4 per shoot depending on age, commonly 2, the first one terminal, the second arising in the axil of the subtending leaf with accompanying bicarinate prophylls and bladeless sheaths, rectangular, compressed, 20—24 cm high and (6.5) 7—8 cm across. The subtending bicarinate prophylls yellow-green, villose along the carina. Peduncle grass-green to deep green, villose (21) 40—72 cm long, the peduncle of the first inflorescence longer than the rest. Bracts 26—34 in number, leathery, distichously arranged, reniform, conduplicately folded, apex emarginate, 3.8— 4.1 cm high and 6.8—7.8 cm wide, unfolded, with a strong sweet, fruity fragrance, each subtending 6 or more flower pairs. Abaxial surface of bract shiny, oily in appearance, deep golden yellow to yellow-orange, lower bracts villose with scattered hairs, upper ones more sparsely so; adaxial surface yellow-orange, very shiny with a marked oily appearance, glabrous. Bicarinate prophyll membranaceous, broadly ovate, apex obtuse to slightly rounded, translucent to subopaque orange, abaxial surface of carina villose, the rest glabrous; within glabrous, 2.4—2.8 cm high, 1.1—1.5 cm wide carina to carina, and 1.8—2.4 cm total width. Mesophyll membranaceous, broadly ovate, apex rounded, translucent to subopaque orange, glabrous, occasionally bearing a few hairs at the apex, 2.5—2.7 cm high and 2.1—2.8 cm wide. Bracteoles subtending individual flowers 1 per flower pair, membranaceous below, apically thickened, stiff, obovate-elliptic, orange, glabrous, 2.4—2.6 cm long and 0.3—0.5 cm wide. Sepals channeled, narrowly obovate, apex acute, translucent cream below, apical 1/3 yellow-orange, occasionally tinged with green, glabrous, 2.2—2.55 cm long and 0.5—0.6 cm wide. Corolla tube light yellow-orange, glabrous, 2.8—3 cm long; staminal tube 2—3 mm long; corolla lobes subequal, narrowly obovate-elliptic, apex obtuse, margins infolded, appearing acute, bright yellow, apical portion yellow-orange, glabrous, 1.3—1.5 cm long and 0.35—0.5 cm wide. Outer staminode broadly elliptic very shortly clawed at the base, apex rounded, bright yellow-orange, 1.1—1.2 cm long and 0.7—0.9 cm wide. Callose staminode rectangular, apical portion petaloid, deeply bifid into two unequal appendages, yellow-orange to dark gold, 1.2—1.4 cm long. Cucullate staminode yellow-orange, 0.55—0.7 cm long and 3.5—4 mm wide provided with a subterminal filiform appendage. Stamen with lateral yellow-orange petaloid appendage to 1.5 mm wide, extending halfway up the anther; anther 3 mm long. Style and stigma golden orange. Ovary cream-colored with faint greenish tinge, glabrous, 2.5—3 mm high. Capsule thin, smooth, obovoid, apex rounded, straw-colored to orange-yellow, 1.1—1.3 cm high and 0.8—0.9 cm wide, crowned by a persistent live, expanded, bright orange calyx. Seeds usually 3 per capsule, trigonous, dark blue, 6—7 mm high and ca 5 mm in diameter bearing a basal white aril 4—5 mm high.

TYPE. Panamá: Prov. Colón. Santa Rita Ridge below the rain gauge, 13 Aug. 1971, H. KENNEDY, R. L. DRESSLER & H. WIEHLER 1127 (holotype US, isotypes F, MO).

OTHER COLLECTIONS. Panamá: Prov. Colón, Santa Rita Ridge road past Santa Rita, 10 July 1969, H. KENNEDY, R. L. DRESSLER & N. H. WILLIAMS 298 (PMA). Prov. Panamá, km 10—12 on the road to Carti, 18 Sept. 1974, H. KENNEDY, P. J. MAAS, R. L. DRESSLER & C. TOFT 3400 (F). Prov. Veraguas, Río Primero Braso, 2.5 km beyond Agriculture School Alto Piedra, near Santa Fe, 700—750 m, 24 July 1974, T. CROAT 25498 (MO). Prov. Bocas del Toro, Punta Peña, vicinity of Chiriquicito, ca 1000 ft, rain forest, 7 June 1967, W. LEWIS et al. (SCZ, UC). — Costa Rica: Prov. Heredia, small hills of cleared agricultural land and areas of remnant original forest now being logged at 150—250 m, near Tirimbina E of the Río Sarapiqui, 10° 24′ N, 84° 7′ W, 12—15 Aug. 1971, W. C. BURGER & M. BURGER 8141 (F); La Selva OTS field station on Río Puerto Viejo, near Pto. Viejo, 27 May 1969, H. KENNEDY 263 (MO); 15 July 1970, H. KENNEDY 405A (CR).

Flowering May to November during the rainy season. Occurring in evergreen wet forests usually at the forest edge and frequently in disturbed areas with full sun in association with second growth species. It appears to be rather shade intolerant. It is most closely related to *Calathea insignis* PETERSEN (with which it has been confused) and *C. trinitensis* BRITTON. It is easily distinguished from other distichously bracted species by the villose upper surface of the leaf, its relatively large size (usually over 2 m), the sparsely, not densely villose bright yellow-orange, unctuose bracts and the absence of claviculate bracteoles. The distinct fragrance of the bracts is sufficient to distinguish it from all other species in the field and might act as a signal to pollinators as it is strongest in young inflorescences. The degree of pubescence varies between populations. The peduncle, petiole and leaf sheath are densely villose throughout in the Panamanian specimens while the petiole, upper portion of the peduncles and the central abaxial portion of the leaf sheath are glabrous in the Costa Rica material.

The specific epithet is from the Latin adjective *similis*, referring to the similarity of its laterally compressed inflorescence with that of *C. insignis* PETERSEN.

Calathea guzmanioides SMITH & IDROBO

SMITH & IDROBO in Caldasia 5: 47 (1948).

This species, previously known only from Colombia in the Departments of Chocó and El Valle, has recently been found in the Atlantic lowlands of Panamá.

Specimens from Panamá (DRESSLER 4214) were compared with the type (KILLIP & CUATRECASAS 38748, US) and clearly represent this species.

Panamá: Prov. Colón, along tributary between Caño Rey and San Lucas, S of Coclé del Norte, 19 Aug. 1972, R. L. DRESSLER 4214 (F, US).

This species is most closely related to an as yet undescribed species from Panamá and Costa Rica and slightly less so to *Calathea allenii* WOODSON, all having a similar inflorescence structure. It is easily distinguished from *C. allenii* by its larger size (up to 2.5 m versus 1.4 m), the non-plicate leaf (*C. allenii* is strongly plicate) and the bract margin entire rather than deeply emarginate. *Calathea guzmanioides* differs from the undescribed species by the entire, instead of emarginate, lower bracts and the seeds oblong-elliptic rather than circular in outline.

ACKNOWLEDGEMENTS

The author acknowledges the invaluable assistance of Dr ROBERT L. DRESSLER during her field studies in Panamá and wishes to thank Dr ROBIN FOSTER for introducing her to the Río Guanche area and Dr WILLIAM C. BURGER for reading the manuscript.

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Lamprocephalus B. Nord., a New Senecioid Genus from South Africa

Bertil Nordenstam

NORDENSTAM, B. 1976 02 09. Lamprocephalus B. Nord., a new senecioid genus from South Africa. — Bot. Notiser 128: 323—326. Lund. ISSN 0006-8195.

Lamprocephalus montanus B. NORD. is described as a new monotypic genus of the Compositae-Senecioneae. It is a shrublet with solitary, discoid capitula and a curiously appendaged style, which is unique in the tribe. The distribution is confined to some mountains of the western Cape Province.

Bertil Nordenstam, Section for Botany, Swedish Museum of Natural History, S-104 05 Stockholm 50, Sweden.

Lamprocephalus montanus B. NORD., gen. et sp. nov. (Compositae—Senecioneae)

Orig. coll.: SCHLECHTER 10119, Cape Province, Ceres Div., Koude Bokkeveld, in montibus pone Tweefontein, 5500 ft., 24.III.1897 (S holotype; BM, BOL, K isotypes).

Fruticulus erectus vel adscendens, glaber praeter axillas et dorsa foliorum araneoso-tomentosa. *Folia* alterna sessilia simplicia integerrima imbricata linearia subtriquetra apice mucronata basi semiamplexicaulia. *Pedunculi* terminales solitarii elongati scaposi monocephali. *Involucrum* campanulatum basi truncatum, *bracteis* 11—13 uniseriatis liberis lineari-lanceolatis. *Receptaculum* planum nudum. *Capitulum* homogamum discoideum. *Corolla* tubulosa glabra; lobi triangulares canali resinifero mediano instructi. *Styli* rami dilatati glabri intra area stigmatica continua vestiti, apice appendice oblongo-triangulari minute papillosa et protuberationibus tribus dorsalibus ornati. *Antherae* basi breviter sagittatae apice appendice plana anguste triangulari acuta coronatae. *Achaenia* oblonga truncata demum nigra obscure quinquangulata albopapillata. *Pappi* setae copiosae albae persistentes corolla breviores.

Erect or ascending shrublet, 0.2—0.5 m high, branching basally, glabrous except for a loose cobwebby tomentum in leaf-axils and on adaxial sides of young leaves. Branches becoming nude with age and lepidote with persistent leaf-bases.

Leaves alternate, sessile, simple, imbricated, linear from a broader half-clasping base, (0.5—)1—2(—3) cm long, 1—1.5 (—2) mm wide, suberect—erecto-patent and somewhat curved, more spreading with age, subtriquetrous with flattish or slightly concave adaxial side, abaxially obscurely keeled especially basally, subcarnose or coriaceous, mucronate.

Peduncles terminal, solitary, simple, scapose, 3—25 cm long, ca 1.5 mm thick, with 3—7 scattered filiform-subulate reduced leaves up to 1 cm long.

Involucre cupuliform—narrowly campanulate with a truncate base, 1.5—2 cm high, 1—1.5 cm wide, basally only 3—5 mm wide. Involucral bracts uniseriate, 11—13, equal, free from the base, linear-lanceolate, 1.2—1.8 cm long, 1—2 mm wide, 2—3-veined, coriaceous in the centre and with thinner margins, apically acuminate.

Receptacle flat, nude.

Capitula homogamous, discoid, ca 15—30-flowered. Corolla tubular, 10—14 mm long, probably red with yellowish base, glabrous; lobes narrowly triangular, 1—1.3 mm long, with a distinct resiniferous midvein, thickish, with involute margins and subcucullate tips. Style terete, basally swollen; style branches distinctly broader than

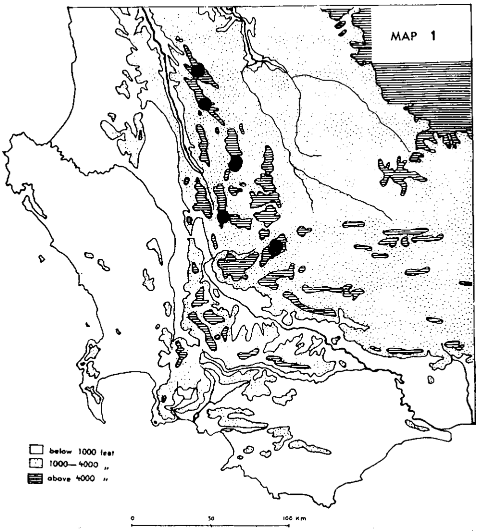

Fig. 1. Distribution of *Lamprocephalus montanus* B. NORD.

the shaft, 4—5 mm long, glabrous, inside with continuous stigmatic areas, outside faintly 3—4-ribbed, apically with a 1—1.5 mm long oblong-triangular obtuse—subacute minutely papillate dorsally 3(—4)-hunched appendage. Anthers 4—4.5 mm long incl. the flat and acute narrowly triangular appendage, basally minutely sagittate; endothecial cells with laxly set thickenings on longitudinal and transverse walls; filament collar ca 1 mm long, basally dilated with somewhat larger cells, broader than the filament.

Achenes narrowly oblong, 6—9 mm long, 1.5—2 mm broad, with rather truncate ends, obscurely 5-angular, brown, eventually black, covered with small whitish mucilaginous papilliform duplex hairs arranged in five longitudinal fields. Pappus bristles copious, pluriseriate, 9—11 mm long, persistent, laxly and minutely serrulate, glossy white.

Flowering period: Dec.—April.

CAPE PROVINCE. Clanwilliam Div.: Cedarberg Mts, Pk S of Sneeuwkop, SW slopes, shale band, 5000 ft, I. 1942, ESTERHUYSEN 7591 (BOL) — S Cedarberg, Apollo Pk, slopes, 4000—5000 ft, III. 1956, ESTERHUYSEN 25526 (BOL). — Ceres Div.: In clivis saxosis montium Skurfdebergen prope Gydouw, 5400 ft, XII. 1891, H. BOLUS 7551 leg. A. BODKIN (BOL, K) — Koude Bokkeveld, in montibus pone Tweefontein, 5500 ft, III. 1897, SCHLECHTER 10119 (BM, BOL, K, S) — Schurweberg Pk, betw. Bokkeveld Sneeukop and Bokkeveld Tafelberg, stony slopes, S aspect, 4500 ft, I. 1962, ESTERHUYSEN 29435 (BOL, S). — Worcester Div.: Plateau betw. Matroosberg and Sonklip, 6000 ft, IV. 1958, ESTERHUYSEN 27679 (BOL) — Matroosberg, shale band, 6500—7000 ft, I. 1959, ESTERHUYSEN s.n. (BOL).

This remarkable new taxon was first collected in 1891 by BODKIN and six years later by SCHLECHTER, who distributed it as "*Senecio lamprocephalus* SCHLTR n. sp." This name was never validly published, although it has been used in herbaria as well as in literature (MUSCHLER 1909 p. 56). It therefore seems appropriate to adopt SCHLECHTER's epithet as a generic name.

In gross morphology the new taxon resembles some *Senecio* species (e.g. those of sect. *Pinifolii*). The peculiar style is very different from anything known in *Senecio*, however. The style branches are unusually stout and crowned by a large sterile appendage. Sweeping-hairs are completely lacking, but the appendage has a papillate surface and a few dorsal hunches near the base. The stigmatic areas are continuous, covering the whole of the inside of the style branches except for the tip of the apical appendage (Fig. 2 C, D). This type of style is quite unique in the tribe Senecioneae. The sterile tips of the style branches in e.g. *Gynura* are very differently shaped. The typical *Senecio* style has discrete stigmatic areas and a terminal brush of sweeping-hairs.

Other characteristics of the new genus are the scapose peduncles with (probably) red-flowered discoid capitula, the uniseriate involucre without a calyculus, and the acute anther appendages. The achenial wall is very firm, and the five veins are best seen after dissection.

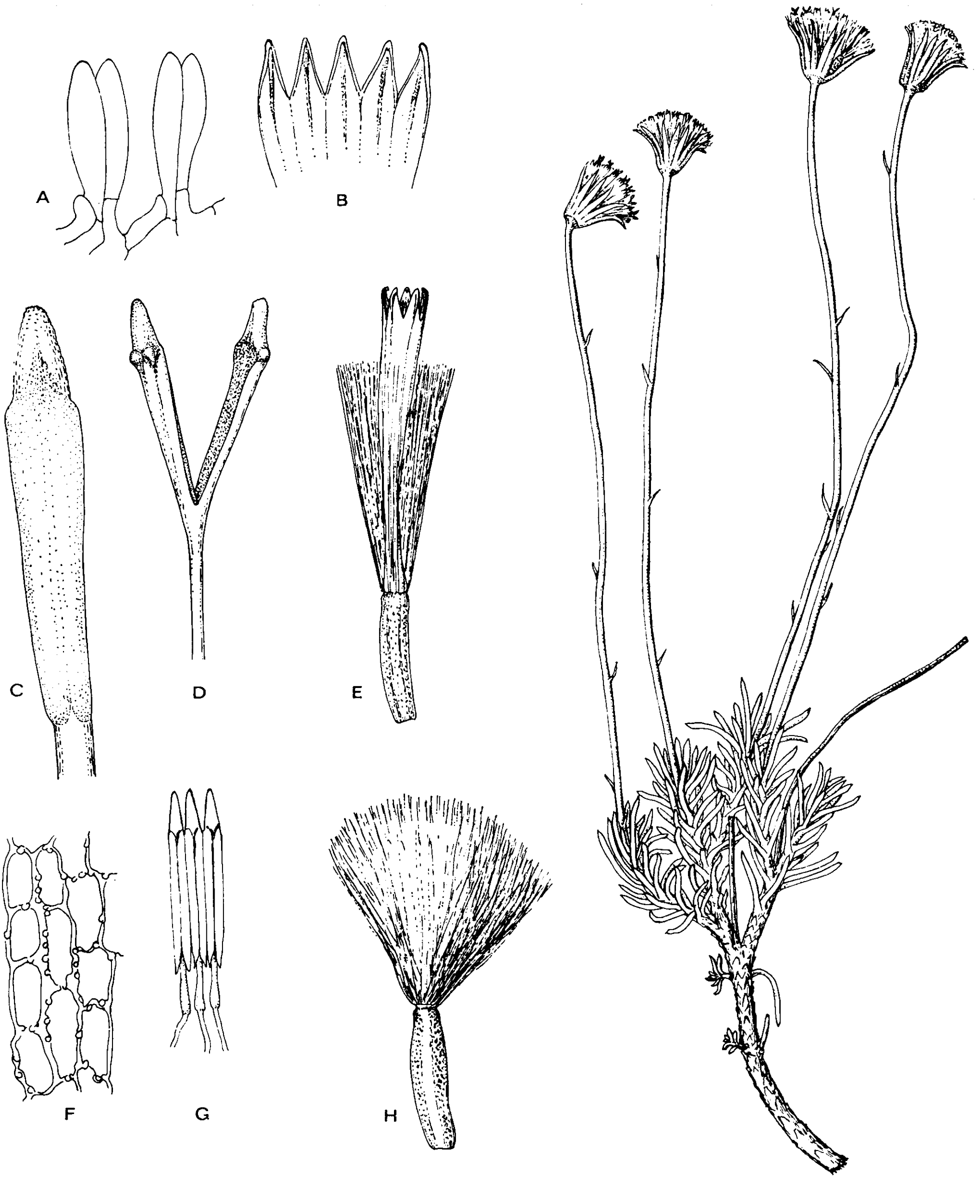

Fig. 2. *Lamprocephalus montanus* B. NORD. (SCHLECHTER 10119, typus). — A: Achenial hair, ×150. — B: Corolla lobes, laid out, ×6. — C: Style branch, inside, ×12. — D: Style branches, ×6. — E: Floret, ×3. — F: Endothecial cells, ×75. — G: Anthers, ×6. — H: Achene, ×3. — Right: Habit, $\times{}^{1}/_{2}$. — Del. auct.

The distribution of the monotypic genus is limited to some western Cape mountains, from the Cedarbergen in the north to the Matroosberg in the south (Fig. 1). In the phytogeographical groupings of the Cape floristic element (WEIMARCK 1941, NORDENSTAM 1969) the taxon belongs to the Northwestern Endemics. The apparently rare species seems to favour stony slopes with a southerly or south-westerly aspect at altitudes of between 1200 and 2100 metres.

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A Comparative Study on the Cambial Structure of Some Arid Zone Species of Acacia and Prosopis

A. K. M. Ghouse and Muhammad Iqbal

GHOUSE, A. K. M. & IQBAL, M. 1976 02 09. A comparative study on the cambial structure of some arid zone species of Acacia and Prosopis. — Bot. Notiser 128: 327—331. Lund. ISSN 0006-8195.

The cambial constituents in the different species of *Acacia* and *Prosopis* differ in size, relative number, and extent of area occupied in the cambial zone. The cambium is stratified in *A. catechu* and non-stratified in others. Among the latter, Indian species are characterized by tall, broad, multi-seriate ray initial units with a relatively high proportion of ray initials, while the exotics possess short and narrow ray initial units with a relatively low proportion of ray initials.

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The present report, dealing primarily with the cambial structure of some *Acacia* and *Prosopis* species, forms part of the programme of this laboratory investigating the structure and behaviour of the vascular cambium in tropical trees. It is hoped that the information thus obtained will make it possible to recognize the trends of specialization, if any, in cambia of tropical trees.

MATERIAL AND METHODS

Cambial samples (20—24 for each species) along with some sapwood and inner phloem were collected in September 1973 (2 cm square blocks) from the main trunks of adult trees of *Acacia* and *Prosopis* species, viz. *Acacia catechu* WILLD., *A. farnesiana* WILLD., *A. melanoxylon* R. BR., *A. nilotica* (L.) WILLD. var. *cupressiformis* STEWART (Ramkanta or Ramkati babul), *A. nilotica* var. *telia* TROUP (Godi babul), *A. nilotica* var. *vediana* COOKE (Kauria babul), and *Prosopis spicigera* L., growing in or around Aligarh within a radius of 16 km, and fixed on the spot in FAA. The samples were aspirated for the free access of the fixative into the deeply situated cambial tissue and after five days were preserved in 70 % ethanol. Two- to three-year-old twigs were also collected, fixed, and preserved as above. Transverse and tangential sections through the cambial zone were made from all collections on a sliding microtome at a thickness of 10—12 μ, and stained with tannic acid-ferric chloride (FOSTER 1949) and Heidenhain's haematoxylin. They were mounted in Canada balsam after dehydration in the ethanol series (SASS 1958).

To calculate the area occupied by different types of initials camera lucida drawings were made on tracing paper. Portions of the drawings containing the ray initials were carefully removed and weighed on an electrically operated microbalance. The pieces of paper bearing only fusiform initials (after the removal of the drawings of ray initials) were also weighed separately. The proportion of one type of element to the other in the cambial strip was then calculated per unit area on the basis of the weights thus obtained. To confirm the accuracy the results were compared with those obtained by direct calculation based on the measurements of the size of initials as described by GHOUSE and YUNUS (1974 a).

OBSERVATIONS

The vascular cambium in aerial axes of all the species investigated in the present study appears as a cylinder between the xylem and phloem, and consists

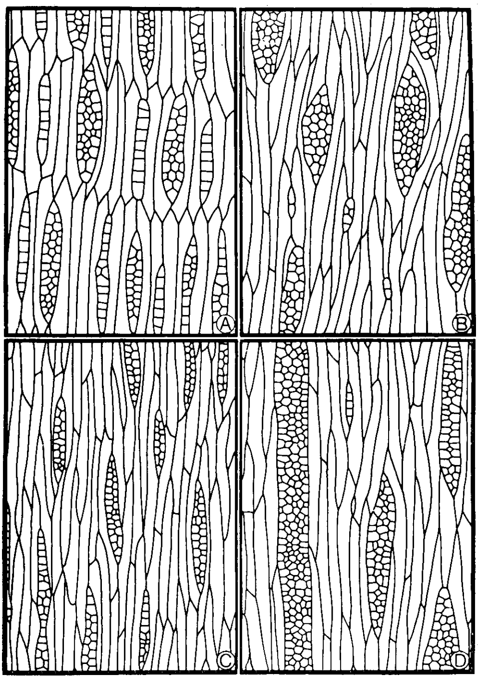

Fig. 1. Camera lucida drawings of the cambial strips of *Acacia* and *Prosopis* as seen in tangential sections. — A: *A. catechu.* — B: *A. farnesiana.* — C: *A. melanoxylon.* — D: *P. spicigera* (all ×30).

of elongated fusiform cells as well as the ray initials. Fusiform cells, in all species except *A. catechu*, are roughly hexangular with long parallel sides and narrow pointed ends which overlap and elongate apically (Figs. 1 B—D, 2). In *A. catechu* on the other hand, fusiform cells, which show no overlapping and apical elongation, remain comparatively short (Fig. 1 A), the cambium stratified.

The length of fusiform cells varies in the different species, ranging from 190—360 μ in *Acacia* species, and 200—320 μ in *Prosopis*. End walls of these cells measure from 10—170 μ in *Acacia* and 45—120 μ in *Prosopis* (Table 1). In all the species studied, the fusiform cells were found to be shorter in younger axes than in the older ones.

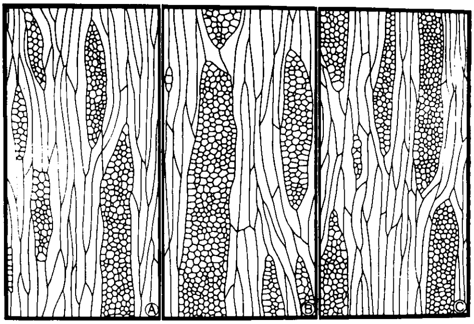

Fig. 2. Camera lucida drawings of the cambial strips of three varieties of *Acacia nilotica* as seen in tangential sections. — A: var. *vediana.* — B: var. *telia.* — C: var. *cupressiformis* (all ×20).

Ray initials aggregate frequently to form fusiform units of varying magnitude in all the species. Often two or more such units unite to form complex bodies running to a greater depth, covering the length of two or more fusiform cells (Figs. 1 D, 2). They form very tall structures in *A. nilotica* and *P. spicigera,* comprising over 70 cells. In *A. catechu,* 98 % of the ray initial units are short (1—15 cells) while in *A. farnesiana* and *A. melanoxylon,* up to 68 % and 80 % respectively are short. In the remaining species about 50 % of the ray units are short, except in the variety *cupressiformis* of *A. nilotica* in which only 27 % of the ray initials units fall within this category (Fig. 3).

Like the depth, the width of ray initial units also differs markedly in the different species studied. In *A. nilotica,* 60—78 % of the ray units are multiseriate (4—9 cells), while in others such broad units are either absent (*A. melanoxylon*) or considerably less in number. *A. catechu, A. melanoxylon,* and *P. spicigera* show the maximum of uni-, bi- and triseriate ray initial units respectively (Fig. 4).

Fig. 5 indicates the relative proportions of fusiform and ray initials in the species investigated. Fusiform initials constitute about 82 % of the cambial zone

Table 1. Anatomical data on the variation of cambial cell size and structure in *Acacia* and *Prosopis*. The mean is based on three thousand independent measurements taken at random. Range within parentheses.

Species	Fusiform initials			Ray initials		Ray initials units	
	Mean length (μ)	Mean width (μ)	Mean length of gabled or tapering end (μ)	Tangential diameter (μ)	Radial diameter (μ)	Height (no. of cells)	Width (no. of cells)
Acacia catechu	237 (190—271)	16 (13—17)	30 (10—50)	15 (10—20)	15 (9—18)	12 (3—19)	2 (1—4)
A. farnesiana	290 (230—320)	18 (15—25)	95 (60—170)	18 (10—30)	13 (5—20)	11 (1—32)	4 (1—8)
A. melanoxylon	288 (200—360)	15 (10—20)	63 (30—130)	14 (10—20)	10 (9—15)	11 (1—32)	2 (1—3)
A. nilotica var. *cupressiformis*	280 (220—350)	18 (15—20)	66 (30—100)	15 (7—20)	12 (7—18)	25 (6—62)	4 (2—7)
A. nilotica var. *telia*	274 (200—350)	16 (10—20)	70 (30—100)	15 (10—20)	15 (10—20)	20 (5—70)	5 (1—9)
A. nilotica var. *vediana*	237 (230—360)	16 (10—20)	81 (30—170)	18 (12—23)	15 (7—23)	17 (2—70)	4 (1—8)
Prosopis spicigera	263 (200—320)	20 (15—25)	77 (45—120)	18 (15—20)	17 (10—20)	17 (2—65)	3 (1—4)

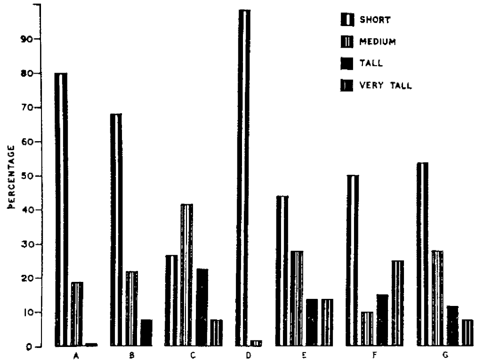

Fig. 3. Histograms showing the frequency of ray initial units of varying height in the cambial zone of *Acacia* and *Prosopis*. — A: *A. melanoxylon*. — B: *A. farnesiana*. — C: *A. nilotica* var. *cupressiformis*. — D: *A. catechu*. — E: *P. spicigera*. — F: *A. nilotica* var. *telia*. — G: *A. nilotica* var. *vediana*. — Short: 1—15 cells. Medium: 16—30 cells. Tall: 31—45 cells. Very tall: 46—70 cells.

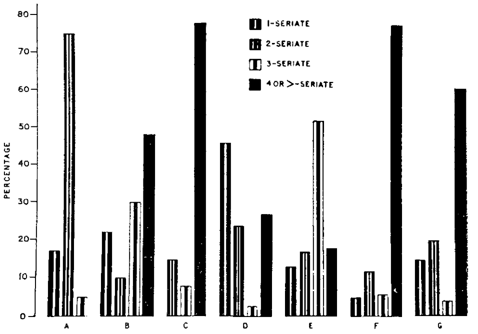

Fig. 4. Histograms showing the frequency of ray initial units of varying width in the cambial zone of *Acacia* and *Prosopis*. — A: *A. melanoxylon*. — B: *A. farnesiana*. — C: *A. nilotica* var. *cupressiformis*. — D: *A. catechu*. — E: *P. spicigera*. — F: *A. nilotica* var. *telia*. — G: *A. nilotica* var. *vediana*.

in *A. melanoxylon*, 78 % in *A. farnesiana*, 70 % in *A. catechu*, 63 % in *P. spicigera* and 57—75 % in *A. nilotica*.

DISCUSSION

Although the cambial components are the same in all species investigated, their composition appears to be species specific. The mode of aggregation and the extent of multiplication of ray initials differ in the different species. Ray initials, for instance, invariably form short and uniseriate structures in *A. catechu*, and mostly tall and broad bodies in *A. nilotica* and *P. spicigera*. It is also worth noting that in *A. farnesiana* and *A. melanoxylon* (both exotics) ray initials from short narrow units, while in rest of the species (all indigenous) tall to very tall and broad multiseriate ray units characterize the cambium (except in *A. catechu*). *A. catechu* having stratified cambium (Ghouse & Yunus 1974 b) enjoys a phylogenetically advanced position among other species of the genus *Acacia* in the opinion of Bailey (1923) and Metcalfe and Chalk (1950).

The present findings on the proportions of fusiform cells and ray initials are in opposition to the widely accepted view that fusiform cells constitute about 90 %

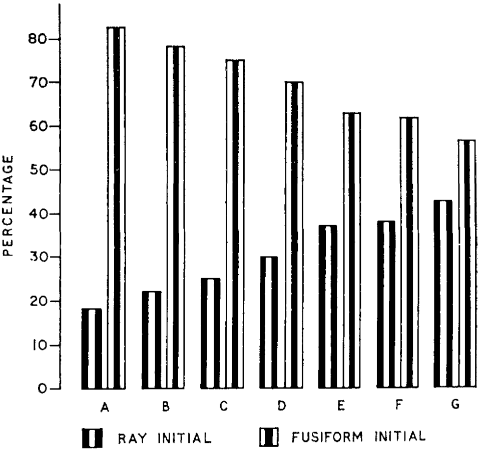

Fig. 5. Histograms showing the proportion of fusiform and ray initials in the cambial zone of *Acacia* and *Prosopis*. — A: *A. melanoxylon*. — B: *A. farnesiana*. — C: *A. nilotica* var. *cupressiformis*. — D: *A. catechu*. — E: *P. spicigera*. — F: *A. nilotica* var. *telia*. — G: *A. nilotica* var. *vediana*.

or more of the cambial zone in different plants or plant groups (BAILEY 1923, WILSON 1963, 1964, KOZLOWSKI 1971, BUTTERFIELD 1972), at the same time confirming the earlier findings made in this laboratory on various tropical trees (GHOUSE & YUNUS 1974 a, c).

The length of fusiform initials varies in different positions within the tree. It gradually increases with the increasing age of the axis till the fusiform cells attain the adult state. Thus the present observations run parallel to those of BAILEY (1923), BANNAN (1962), CARLQUIST (1962), EVERT (1961) and GHOUSE and YUNUS (1973) on some conifers and dicotyledons.

ACKNOWLEDGEMENTS

The authors are grateful to Professor R. KHAN, Head of the Department of Botany, Aligarh Muslim University, Aligarh for providing laboratory facilities. The second author (M. I.) is grateful to the C.S.I.R., New Delhi, for the award of a fellowship. The help rendered by Mr M. YUNUS in preparing the text figures is also gratefully acknowledged.

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Embryo Sac of Hydrobryopsis sessilis (Podostemaceae) – Origin, Organization and Significance

Govindappa D. Arekal and C. R. Nagendran

AREKAL, G. D. & NAGENDRAN, C. R. 1976 02 09. Embryo sac of Hydrobryopsis sessilis (Podostemaceae) — origin, organization and significance. — Bot. Notiser 128: 332—338. Lund. ISSN 0006-8195.

Both Podostemum and Dicraea embryo sac types have been recorded in a single taxon, *Hydrobryopsis sessilis* (Podostemaceae), for the first time. The Dicraea type is reinterpreted. The presence of antipodal cells in the family is refuted. Interrelationships between the Podostemum and Dicraea types are discussed.

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BATTAGLIA (1971) reviewed the existing literature on the embryo sac development in members of Podostemaceae and recognized three major types, viz. (A) the Apinagia type found in the majority of taxa investigated, (B) the Dicraea type confined to the genus *Dicraea* (now *Polypleurum* (TAYL. ex TUL.) WARMING; see HALL 1971) and (C) the Podostemum type the occurrence of which was considered doubtful.

Attempts have been made in this laboratory to understand the development of the female gametophyte in all the Indian genera of Podostemaceae (NAGENDRAN 1974, AREKAL & NAGENDRAN 1975, NAGENDRAN et al. 1976). Since there is no embryological report on *Hydrobryopsis sessilis* (WILLIS) ENGLER — a monotypic genus endemic to South India — the development of the embryo sac has been investigated and its significance presented.

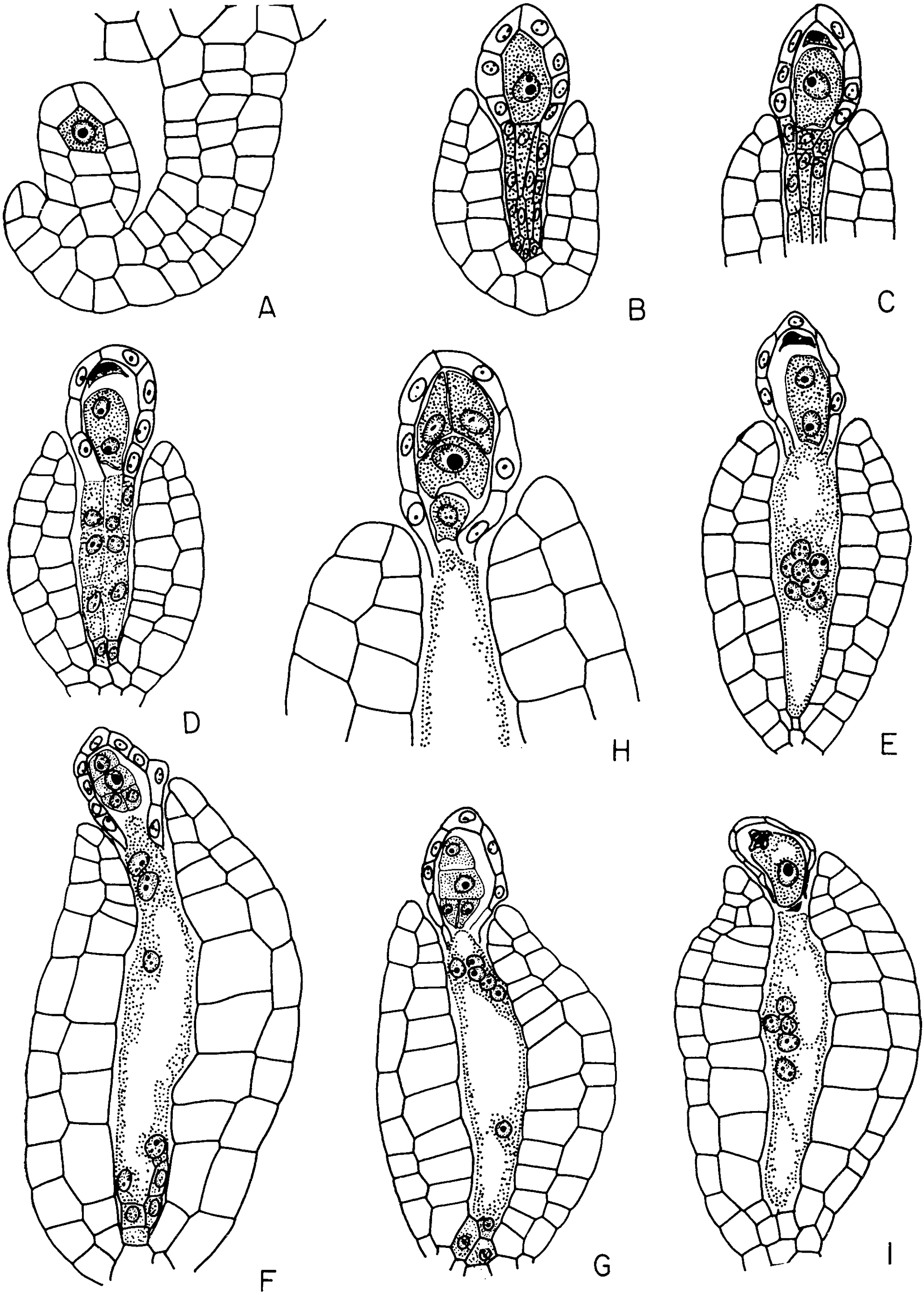
MATERIAL AND METHODS

Material of *Hydrobryopsis sessilis* was collected in formalin/acetic acid/alcohol (FAA) from streams in the South Canara and Chikmagalur districts of Karanataka during January, 1973. Customary methods of dehydration and embedding were employed. Sections were cut on a microtome at 6—10 microns and stained with Heidenhain's Iron alum-Haematoxylin, using erythrosin in clove oil as counter stain.

OBSERVATIONS

The thalloid plant body is pinnately branched and closely appressed to rocks. The flowers are enclosed in 5—7 sessile bracts, only the stamens and stigmas projecting. Each flower has 2 long stamens and 2 staminodes. The pollen is shed as dyads. The ovary is superior, bicarpellary, syncarpous and bilocular with a number of ovules on a massive

Fig. 1. Development of embryo sac in *Hydrobryopsis sessilis.* — A: Ovular primordium with archesporial cell. — B: Megaspore mother cell: outer integument not shown. — C: Functional dyad cell; note degenerated micropylar dyad cell. — D: Two-nucleate embryo sac, just prior to the organization of nucellar plasmodium. — E: Two-nucleate embryo sac; after formation of nucellar plasmodium. — F—G: Organized embryo sacs each with two juxtaposed chalazal synergids, an egg and a micropylar polar cell. — H: Organized embryo sac with two synergids at the micropylar end, an egg below and a chalazal polar cell. — I: Zygote in contact with nucellar plasmodium. — A—B, D—G, I ×640; C ×700; H ×1180.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axile placenta. The fruit is a smooth, subsessile, loculicidal capsule.

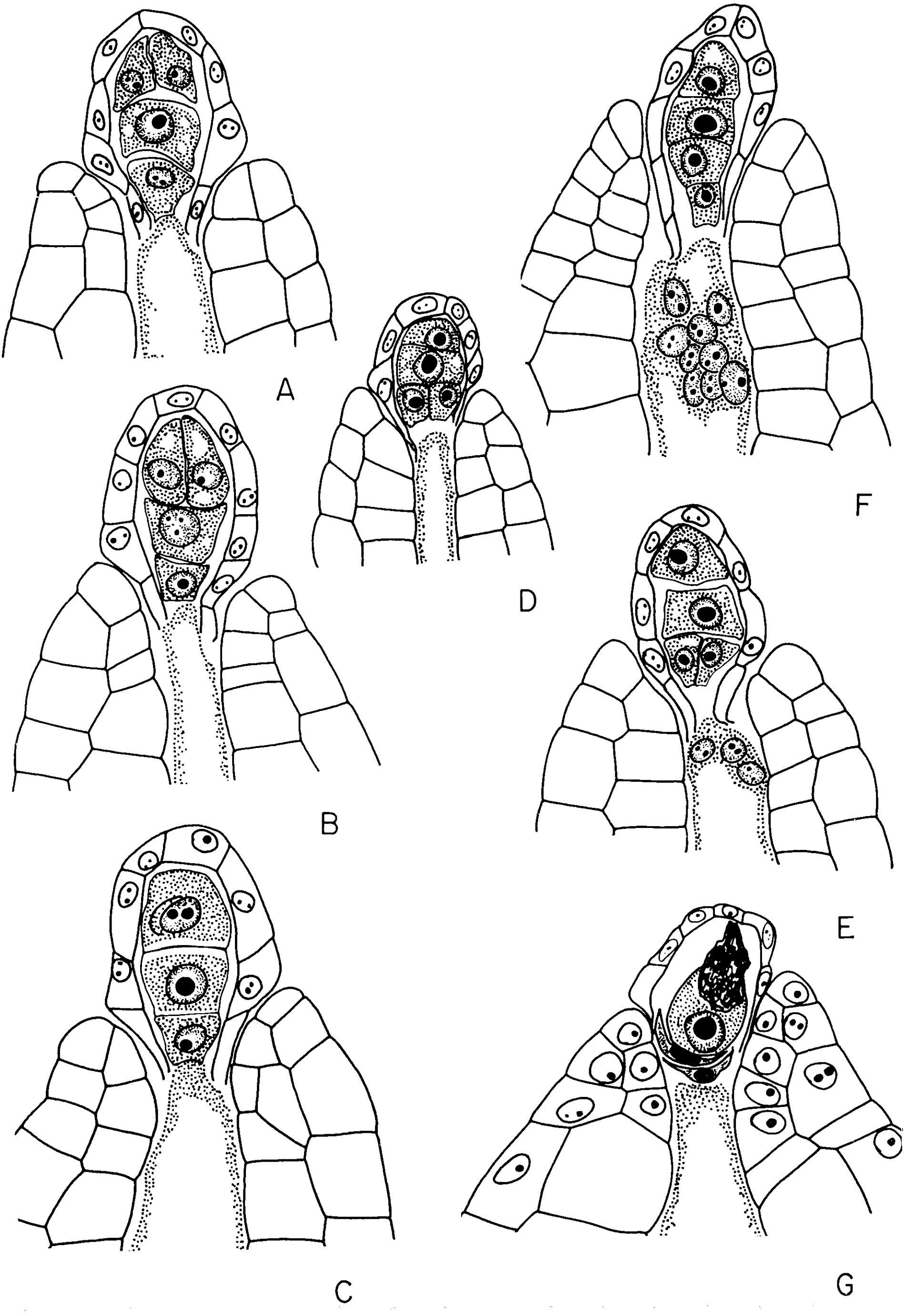
The ovules are anatropous, tenuinucellate and bitegmic. The inner integument is short, the outer alone forming the micropyle. A hypodermal archesporial cell organizes very early in the ovular primordium (Fig. 1 A) and directly functions as megaspore mother cell (Fig. 1 B). It has dense cytoplasm and a large nucleus. The first meiotic division in the megaspore mother cell results in two unequal dyad cells. The smaller micropylar dyad cell soon degenerates and is recognized as a crescent-shaped cap (Fig. 1 C). The nucleus of the lower dyad cell completes the second meiotic division and a two-nucleate embryo sac results (Fig. 1 D—E). The two nuclei move apart and after a simultaneous mitotic division produce four daughter nuclei which contribute to the organization of the embryo sac. In almost 30 % of the ovules the spindles of the two dividing nuclei are disposed in a T-shaped manner. In these ovules, the organized embryo sac has two juxtaposed, pear-shaped synergids at the micropylar end, an egg below them and a polar cell beneath the egg — conforming to the Podostemum type (Figs. 1 H, 2 A—C). On the other hand in 70 % of the ovules the spindles of the two dividing nuclei are oriented in an inverted T-shaped manner. The organized embryo sac consists of two small juxtaposed cells at the narrow chalazal end of the embryo sac, a conspicuous egg above them and a large cell at the broad micropylar end — an embryo sac conforming to the so-called Dicraea type (Figs. 1 F—G, 2 D—E). Occasionally in these embryo sacs, the two smaller chalazal cells may be obliquely disposed or placed one above the other (Fig. 2 F) depending upon available space and the orientation of the spindles of the dividing chalazal nucleus of the two-nucleate embryo sac.

Meanwhile, the nucellar cells situated below the developing megaspore mother cell elongate and become densely protoplasmic (Fig. 1 B). When the embryo sac attains the two-nucleate stage, these cells lose their walls and organize a multinucleate protoplast in which the nuclei are usually situated at one end (Fig. 1 D—I). This is the nucellar plasmodium (AREKAL & NAGENDRAN 1975) that nourishes the future embryo (Fig. 2 G).

DISCUSSION AND CONCLUSIONS

The occurrence of a bisporic tetranucleate embryo sac of the Podostemum type such as noted in the present study was reported by MAGNUS (1913) in *Podostemum subulatus* GARDN., *Farmeria metzgerioides* (TRIMEN) WILLIS and *Zeylanidium olivaceum* (GARDN.) ENGL. Subsequently CHIARUGI (1933) reported a similar type of embryo sac in *Weddellina squamulosa* TUL. However, HAMMOND (1937) who examined *Podostemum ceratophyllum* MICHAUX reported a bisporic five-nucleate embryo sac in which the chalazal nucleus degenerates at the two-nucleate stage (=Apinagia type of BATTAGLIA 1971). A reinvestigation of *Zeylanidium olivaceum* by RAZI (1955) revealed that the embryo sac development conformed to Apinagia type and not to the Podostemum type as stated by MAGNUS (1913). Further, the very existence of the Podostemum type in the family itself has been doubted time and again (P. MAHESHWARI 1937, 1941, 1947, S. C. MAHESHWARI 1955, BATTAGLIA 1971, AREKAL & NAGENDRAN 1975). Nevertheless, the present study has revealed beyond all doubt the existence of the Podostemum type in nearly 30 % of the ovules. The

Fig. 2. Development of embryo sac in *Hydrobryopsis sessilis*. — A—C: Organized embryo sacs with two micropylar synergids, an egg below and a chalazal polar cell. — D—E: Organized embryo sacs with two juxtaposed chalazal synergids, an egg above and a micropylar polar cell. — F: Organized embryo sac with two synergids placed one above the other at chalazal end. — G: Zygote; note degenerated chalazal synergids. — All ×1180.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Podostemum type of embryo sac is simpler than the Apinagia type and closely related to it. Here, the nucleus which would later degenerate and which represents the remnants of the disappearing chalazal quartet of nuclei of an Allium type of embryo sac is not produced at all. The embryo sac is therefore bisporic and tetranucleate, all the four nuclei belonging to the micropylar quartet. Although this type of embryo sac is designated the Podostemum type, its validity could be admitted only when it is consistently found in the genus *Podostemum* MICHAUX. A careful investigation of all species of *Podostemum* would clarify the position.

The occurrence of a bisporic tetranucleate embryo sac of the Dicraea type with two small chalazal cells designated antipodal cells, egg and a single micropylar synergid, both considered as sisters, and without a polar cell, has been reported in *Dicraea elongata* TUL. (MAGNUS 1913), *D. stylosa* WIGHT (MUKKADA 1962, 1964) and *D. agharkarii* NANDI (RAZI 1966). This type has hitherto been regarded as exclusive to the genus *Dicraea*. Its occurrence along with the Podostemum type in ovules of the same ovary in the present study makes it revealing. Actually the Dicraea type presents an inverted image of the Podostemum type and this disposition has neither altered the location nor the size of the egg. The large pear-shaped synergids noted at the micropylar end of the Podostemum type have become much smaller in size with sparse contents and are confined to the narrow region of the embryo sac. There is no doubt that the narrow lower end of the embryo sac is responsible for the smaller size of the cells and their occasional oblique or superposed disposition is due to the orientation of spindles of the dividing nucleus of the lower chalazal zone. Further, these cells can never be regarded as antipodal cells, on the grounds that in the family Podostemaceae itself there is an unmistakable trend towards the elimination of the antipodal complements through the "Strike" phenomenon exhibited by the chalazal nucleus of the two-nucleate embryo sac leading towards simplification in both size and structure. In *Indotristicha ramosissima* (WIGHT) VAN ROYEN (CHOPRA & MUKKADA 1966, and our own observations), the disappearance of the primary chalazal nucleus occurs about the time of the organization of the embryo sac, while in *Farmeria indica* WILLIS emend. AREKAL & NAGENDRAN (AREKAL & NAGENDRAN 1974, 1975) it occurs much earlier. In the Podostemum type, the "Strike" phenomenon is complete and the nucleus which would later degenerate is not produced at all. Thus the Dicraea type of embryo sac is nothing but an inverted Podostemum type and need not be considered unique as in the following description: ". . . the peculiar egg apparatus with a single synergid and egg, the absence of polar nuclei and the presence of two (occasionally only one) antipodal cells are a rare combination of characters not found in any other angiosperm — not even in any other member of the Podostemaceae" (MUKKADA 1964 p. 291). According to our interpretation the organization of the embryo sac in the genera *Dicraea* and *Hydrobryopsis* falls into line with other angiosperms in not having the synergid and egg as sister cells.

As there is only syngamy and no endosperm in the family (BATTAGLIA 1971, NAGENDRAN et al. 1976), the haploid polar cell in members so far investigated appears to have lost its functional significance. While in the Apinagia and Podostemum types of embryo sacs the position of the polar cell is chalazal, in the Dicraea type it is located at the micropylar end. The so-called single synergid reported as sister to the egg (MUKKADA 1964) is therefore nothing but the polar cell hitherto regarded as being absent. This shift in position does not alter the location of the egg which has remained in the middle of the embryo sac whether it is of the Podostemum or the Dicraea type. Further, the nucellar plasmodium that nourishes the developing embryo has factors for influencing the fertilized egg to extend towards it, irrespective of the disposition of other complements of the embryo sac.

WILLIS (1902) in his taxonomic monograph on the Podostemaceae of India and Ceylon described a new species in the genus *Hydrobryum* ENDL., under the name *H. sessile* WILLIS, from the collections of C. A. BARBER for the South Indian Flora made at Beltangadi, South Canara district in Karnataka State (No. 2520). ENGLER (1930) referred this taxon to a new monotypic genus under the name of *Hydrobryopsis sessilis* (WILLIS) ENGLER, based on fruit characters. The mode of embryo sac development noted in the present study lends support to ENGLER, since it is of the Apinagia type in *Hydrobryum* (NAGENDRAN et al. 1976) and is of both Dicraea and Podostemum types in *Hydrobryopsis*.

SUBRAMANYAM (1962) in his account on aquatic angiosperms inadvertently cited the present taxon as *Hydrobryopsis sessile* (WILLIS) ENGL. But the correct name remains *Hydrobryopsis sessilis* (WILLIS) ENGL. Further, SUBRAMANYAM & SREEMADHAVAN (1969) while providing a key to the Indian genera of Podostemaceae state that the pollen in the present taxon is shed as monads. But in the present study it has been consistently observed that the pollen, as in all other genera of Indian Podostemoideae, is shed as dyads.

Hydrobryopsis sessilis is an interesting taxon which unites several Indian genera of Podostemaceae. It resembles *Zeylanidium* TUL. in vegetative characters, *Dicraea* TUL. and *Podostemum* MICH. in embryo sac types and *Griffithella* WARM. in the smooth, spherical capsule.

ACKNOWLEDGEMENT

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Der Arillus der Gattung Musa

Walter L. Friedrich und Friedrich Strauch

FRIEDRICH, W. L. & STRAUCH, F. 1976 02 09. Der Arillus der Gattung Musa. — Bot. Notiser 128: 339—349. Lund. ISSN 0006-8195.

Arils are found in wild seeded bananas and cultivated edible forms which develop some ovules. The aril consists of simple trichomes embedded in mucilage, arising from the funiculi and surrounding the ovules and younger seeds. The aril and the mucilage begin to disappear in edible and wild bananas when the growth of the pulp starts. In mature fruits of seeded bananas only vestiges of the aril can be recognized in the neighbourhood of the funiculi. In mature edible fruits the mucilage together with the trichomes of the aril are visible as a yellowish mass in which the degenerated ovules are embedded.

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Die Erhaltung von Arillus bei Pflanzenfossilien konnte erstmalig an der fossilen *Spirematospermum wetzleri* (HEER) CHANDLER (Monocotyledones) aus dem Tertiär nachgewiesen werden (FRIEDRICH & KOCH 1972). Dieses Pflanzenfossil ließ sich u. A. auf Grund des trilokularen Aufbaus der Frucht und der arillaten Samen mit Sicherheit zu den Zingiberaceen stellen. *Spirematospermum*, aus 130 Fundstellen aus Eurasien bekannt, ist fast identisch mit dem heute in Indochina vorkommenden *Cenolophon oxymitrum* (SCHUMANN) HOLTTUM (FRIEDRICH & KOCH 1970, KOCH & FRIEDRICH 1971).

Spirematospermum zeigt auch erstaunliche Ähnlichkeiten zu den samenbildenden Musaceen und auch zu der fossilen *Musa cardiosperma* JAIN aus dem Tertiär von Indien. In der Morphologie der trilokularen Früchte und im Bauplan der Samen ist auch die Beziehung zu den samenbildenden Bananen besonders augenfällig.

Die rezenten Zingiberales (=Scitamineae) sind (bis auf wenige allerdings noch ungeklärten Ausnahmen) arillat (Tabelle 1); sie wurden deshalb früher bereits als „Arillatae" bezeichnet (PFEIFFER 1891, ENGLER & GILG 1924 S. 163).

Eine nahe Beziehung zwischen rezenten Zingiberaceen und Musaceen hatte MAURITZON (1935 S. 30) bereits festgestellt; auch MCGAHAN (1961 S. 237) beobachtete ähnliche Bildungen im Bau der Samen bei den beiden Familien.

Der Nachweis des Arillus bei einer fossilen Zingiberacee aus dem Tertiär bestätigt die Theorie von CORNER (1953 S. 469), „The Durian Theory", zumindest in dem Punkt, daß der Prototyp der Zingiberales (=Scitamineae) arillat sei; und zeigt zudem, daß die Reduktion des Arillus bei einigen rezenten Formen als Progression zu deuten ist (FRIEDRICH & KOCH 1972 S. 58). Nach HUMPHREY (1896 S. 34) sind arillare Strukturen besonders häufig bei dehiszenten Früchten, während sie bei indehiszenten nicht anzutreffen sind.

Der Vergleich von *Spirematospermum* mit den rezenten Vertretern der Zingiberales zeigt, daß sich die karpologischen Merkmale in dieser Gruppe, von einigen Progressionen abgesehen, kaum geändert haben. Auffällig ist indessen, daß bei

Musa und *Heliconia* kein Arillus vorhanden sein soll, wie man aus der betreffenden Literatur schließen könnte. WINKLER (1930 S. 526) schreibt: „Niemals besitzen die Samen in der Gattung *Musa* einen Arillus", und auch in A. ENGLER's „Syllabus der Pflanzenfamilien" (POTZTAL 1964) heißt es bei der Unterfamilie Musoideae „Samen ohne Arillus".

MATERIAL UND METHODE

Bei der vorliegenden Untersuchung wurden hauptsächlich Früchte und Samen aus der Sammlung des Botanischen Museums in Kopenhagen verwandt, die unter den Thai-Dänischen Expeditionen der letzten Jahrzehnte eingesammelt worden waren. Außerdem wurde auch Material aus den Botanischen Gärten Köln, Tübingen, Århus, Kew Gardens und Kopenhagen untersucht. Die Früchte und Samen aus dem Botanischen Museum in Kopenhagen waren nur in wenigen Fällen artlich bestimmt; es kann daher bei dem hier besprochenen Material nur eine grobe Einteilung in die beiden Fruchttypen *Musa balbisiana* COLLA (4 Samenreihen pro Kammer) und *Musa acuminata* COLLA (2 Samenreihen pro Kammer) gegeben werden.

Außer samenbildenden, wilden Bananen-Früchten wurden auch Kulturformen in die Untersuchung einbezogen: Pisang aus Java, *paradisiaca*-Typen und gewöhnliche Eßbananen.

Die Früchte wurden in der üblichen Weise über die Alkohol-Reihe entwässert, in Paraffin eingebettet und auf einem Schlittenmikrotom geschnitten. Zur Färbung wurde Toluidin und in einigen Fällen auch Hämatoxylin-Eosin benutzt. Zur Herstellung von Ultradünnschnitten wurde Durcupan als Einbettungsmittel verwandt. Die Präparate wurden mit Glasmessern auf einem Ultramikrotom der Firma Reichert geschnitten. Besonders kontrastarme Strukturen in den Präparaten wurden mit einer Interferenz-Kontrast-Einrichtung nach Nomarski der Firma Zeiss fotografiert.

Das in der vorliegenden Arbeit beschriebene Material wird im Botanischen Museum in Kopenhagen (C) und im Herbarium Jutlandicum Aarhus (AAU) aufbewahrt. Nachstehend einige Angaben zu den abgebildeten Stücken:

MUSA SP. AUS THAILAND: K. LARSEN, S. S. LARSEN, I. NIELSEN & T. SANTISUK 31040, peninsula between Takupah and Surat Thani, limestone area, 6 m high, leaves glaucous underneath, 8° 59 N, 98° 48 E, 200 m, 16.7. 1972 (AAU). TH. SØRENSEN, K. LARSEN & B. HANSEN 4772 (Copenhagen spir. coll: 6627), Wang Tao, common by a small stream, 6.9. 1958 (C). FLOTO 7650, (Copenh. spir. coll. 6628), 12 km from Ban Mussoe, 400 m, 22.7. 1959 (C). TH. SØRENSEN, K. LARSEN & B. HANSEN 4773 (Copenhagen spir. coll. 6630), Wang Tao, common by a small stream, 6.9. 1959 (C).

MUSA SP. AUS JAVA: H. JENSEN s.n. (Copenh. spir. coll. 4243-I), Java, Buitenzorg, 1905 (C).

ENSETE AUS THAILAND: *Ensete* sp. (Syn. *Musa glauca*) K. LARSEN 10000 (Copenhagen spir. coll. 6629) Soi Dao, old clearing near village, 200 m, 11.6. 1963 (C).

HISTOLOGISCHE BEFUNDE

Das Untersuchungsmaterial wurde so ausgewählt, daß die verschiedenen samenbildenden Grundtypen *Musa balbisiana* COLLA (mit 4 Samenreihen pro Kammer) und *Musa acuminata* COLLA (mit 2 Samenreihen pro Kammer), sowie eßbare nicht samenbildende Bananen gleichmäßig repräsentiert sind.

Die Definition des Arillus, die besonders in der älteren Literatur unterschiedlich gehandhabt wird (PLANCHON 1845, WETTSTEIN 1935), ist zumindest in Bezug auf die Zingiberales (Scitamineae) eindeutig; hier faßt man die vom Funikulus ausgehenden und den Samen mehr oder weniger einhüllenden Bildungen als Arillus auf (HUMPHREY 1896, MAURITZON 1935 S. 22). VAN DER PIJL (1955 S. 307) gibt folgende allgemeine Definition: „A postfloral outgrowth from the top of the funicle (the hilum region) covering the seed more or less".

Der Musa acuminata Fruchttyp

Der *Musa acuminata* „Fruchttyp" mit 2 Samenreihen pro Lokulus wurde in verschiedenen Wachstumsstadien untersucht. Im juvenilen Stadium (Fig. 1 A, B) erkennt man deutlich bereits makroskopisch die drei Kammern, in denen die Samen als dunkle Flecke von einer gelblichen, gallertartigen Masse umgeben sind. Diese Masse entspringt von den Funikuli

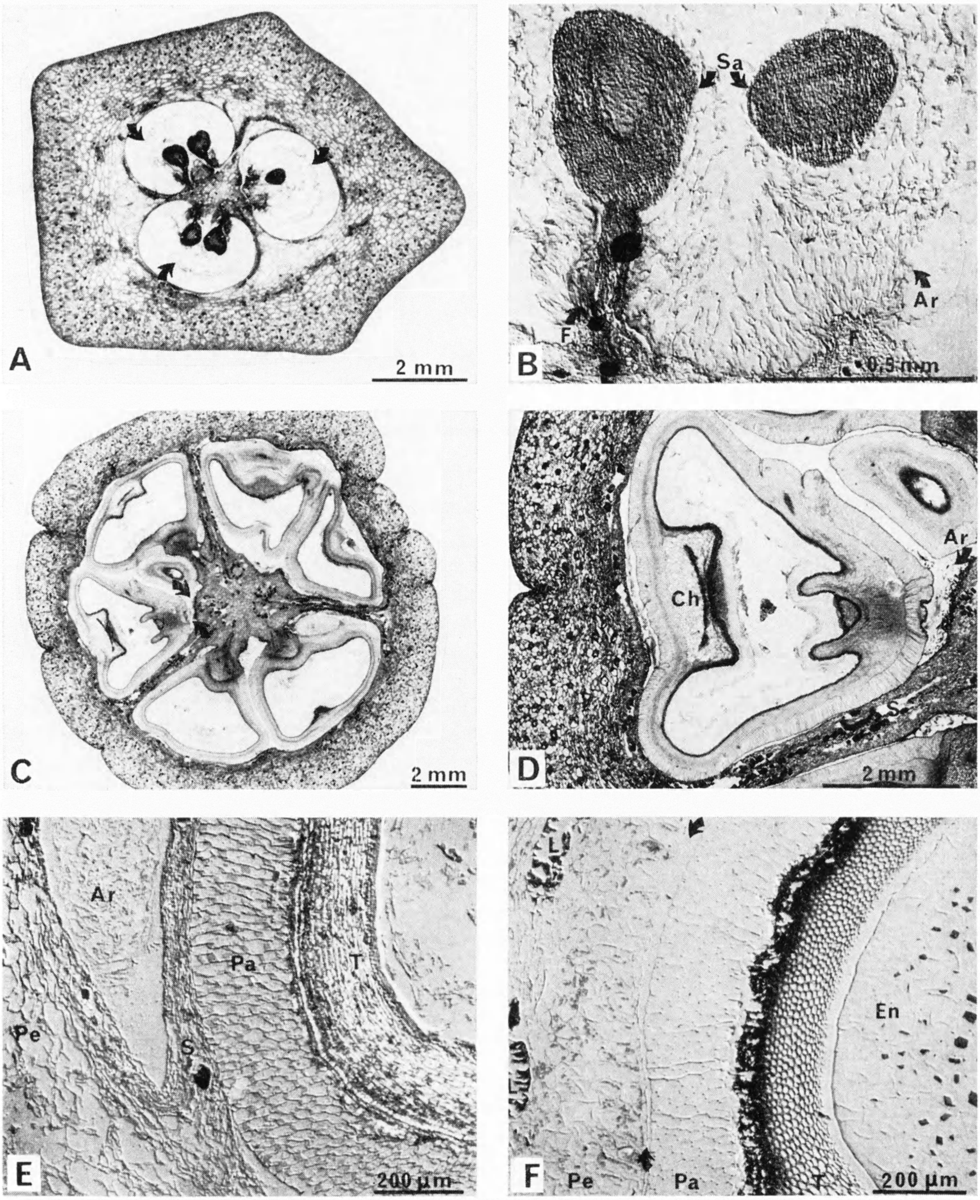

Fig. 1. *Musa* sp. aus Thailand. *M. acuminata* „Fruchttyp" mit zwei Samenreihen pro Lokulus. — A: Nr. 6627, Querschnitt, juveniles Exemplar, Arillus die Samenanlagen umgebend (Pfeile). — B: Gleiches Stück wie A. Arillushaare von den Funikuli ausgehend, die Samenanlagen umgebend. — C: Nr. 6630, Querschnitt, fast ausgereifte Samen, Arillusrelikte nur an den Funikuli (Pfeile). — D: Vergrößerter Ausschnitt aus C. — E: Nr. 31040, Querschnitt durch Teil einer Frucht; fehlgeschlagene Kammer mit Arillus gefüllt. — F: Gleiche Frucht wie E. Kein Arillus zwischen Perikarp und Palisadenzellen des Samens. — B, E, F: Differential-Interferenzkontrast. — Abkürzungen: Ar Arillus. F Funikulus. Ch Chalaza. En Endosperm. Pa Palisadenzellen. Pe Perikarp. Sa Samenanlagen. T Testa. L Latexgefässe. S Septum.

der Samenlagen und füllt die Kammern fast vollständig aus. Bei stärkerer Vergrößerung (Fig. 1 B) lassen sich in dieser Masse offenbar einzellige Trichome erkennen, die aus den Funikuli auswachsen. Nach der Definition handelt es sich um den Arillus. In der Nähe des Funikulus sind sie noch straff geordnet; im distalen Bereich liegen sie unregelmäßig und befinden sich bereits unter Auflösung. Eine Pulpabildung ist in diesem Stadium noch nicht feststellbar, die ja später besonders von der Innenseite des Perikarps einsetzt.

Im fortgeschrittenen Wachstumsstadium (Fig. 1 C, D) füllen die noch unreifen Samen bereits die drei Kammern vollständig aus. Die gallertartige Arillusmasse ist bis auf einige Trichomfragmente in der Nähe der Funikuli und am Hilum, zurückgedrängt. In einer abortierten Kammer ist der fehlgeschlagene Bereich noch von Arillus gefüllt, während in der normal entwickelten Kammer Arillusbildungen nicht mehr feststellbar sind (Fig. 1 E).

Ausgereifte Samen, an der Verfestigung der Testa erkennbar, haben keine Arillusbildungen mehr. Die äußerste Schicht der Testa wird hier von langgestreckten Palisadenzellen gebildet, die direkt an die Innenseite des Perikarpes anliegen. In diesem Wachstumsstadium beobachtet man kleine Stärkekörner in den Parenchymzellen des Perikarps, die die beginnende Pulpabildung anzeigen.

Der Musa balbisiana Fruchttyp

Bei diesem Fruchttyp sind 4 unregelmäßige Samenreihen pro Lokulus entwickelt. Bei juvenilen Früchten sind die Kammern von der gallertartigen Arillusmasse ausgefüllt, in der die Samenanlagen eingebettet sind (Fig. 2). Die Trichome wachsen strahlenförmig aus den Funikuli aus und sind nur in direkter Nähe der Austrittsstellen als Haare zu erkennen. Mit zunehmender Entfernung von den Funikuli gehen sie mehr und mehr in eine formlose Substanz über. Bei diesem Fruchttyp sind Arillusbildungen solange feststellbar, bis die Samen die Kammern vollständig ausgefüllt haben, erst dann setzt die Pulpabildung von der Innenseite des Perikarpes ein und drängt sich zwischen die einzelnen Samen, wie bei einer ausgereiften Frucht von *Musa* sp. (Nr. 31040) aus Thailand beobachtet werden konnte.

Musa sp., Pisang gabu, aus Buitenzorg, Java

Die Früchte dieser Hybride vereinigen Merkmale des *balbisiana* und des *acuminata* „Fruchttypes" (Fig. 3). Unter dem uns vorliegenden Material befindet sich eine Frucht mit drei regelmäßig ausgebildeten Kammern, die jeweils 2 Samenreihen enthalten (Fig. 3 B) und ein Exemplar mit 4 Kammern mit wenigen abortierten Samenlagen (Fig. 3 A, C). In allen Fällen sind die nicht entwickelten Samenanlagen von Arillus umgeben. Makroskopisch erkennt man an Querschnitten durch diesen Fruchttyp drei (seltener 4) halbmondförmige Bereiche, die von einer gelblichen gallertartigen Masse ausgefüllt sind, die sich bei stärkerer Vergrößerung in den Dünnschnitten als Arillusbildung erweist. Bei diesen Früchten ist eine starke Anhäufung der Latexgefäße feststellbar, besonders an der Innenseite des Perikarpes und an den Septen. Im zentralen Bereich der Frucht umgeben sie die Leitungsstränge, so daß sie im Querschnitt ein kreisförmiges Punktmuster ergeben. Von der Innenseite des Perikarpes und der Septen wachsen weitmaschige Parenchymzellen in die Kammern hinein. Sie enthalten Stärkekörner, während die Trichome des Arillus keine Stärkekörner enthalten (Fig. 3 D).

Musa sp.

Die gewöhnliche Eßbanane leitet sich von den beiden Wildformen *Musa balbisiana* und *Musa acuminata* her (SIMMONDS 1962 S. 130). Im Querschnitt durch eine Eßbanane lassen sich makroskopisch nur

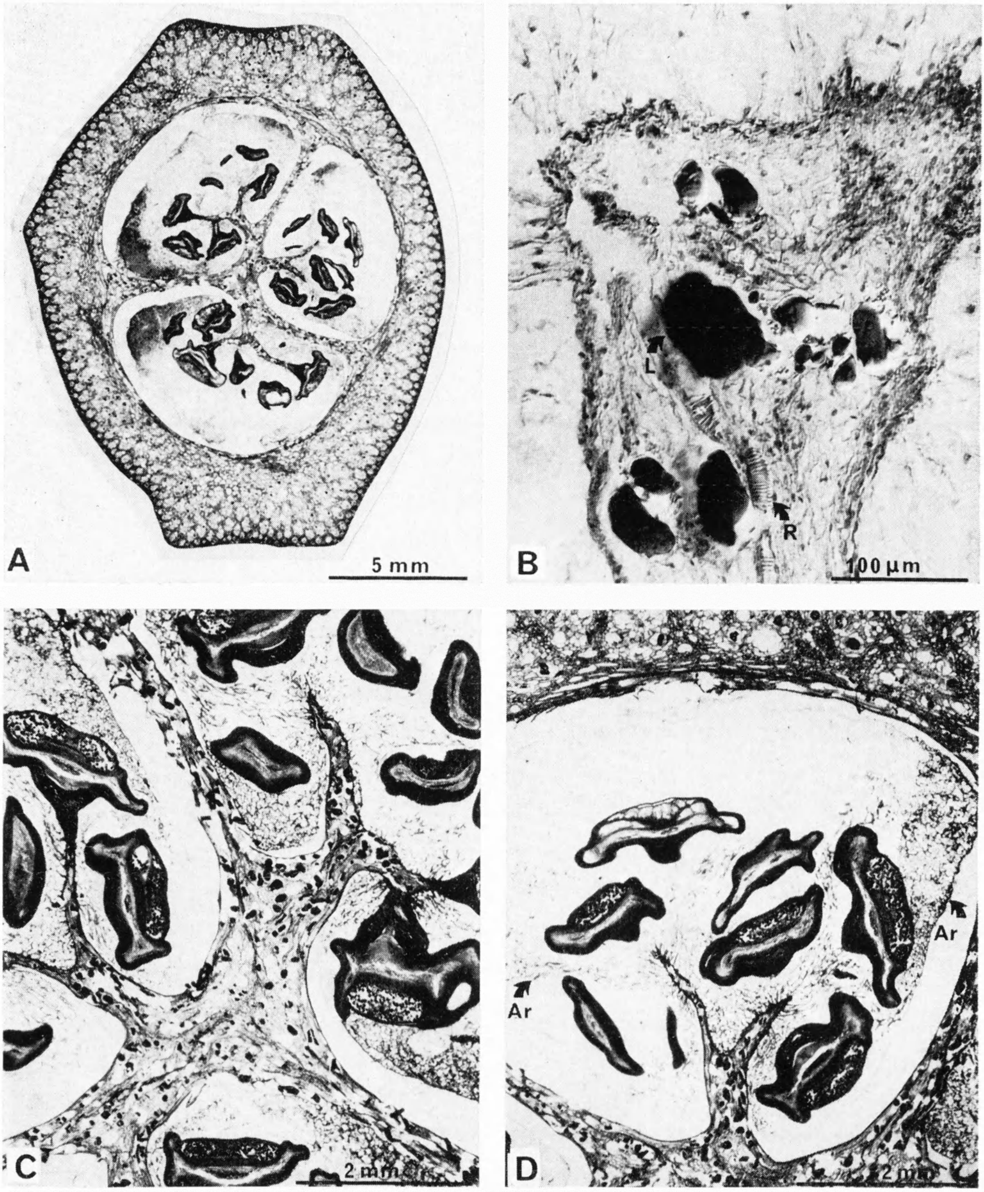

Fig. 2. *Musa* sp., Nr. 6628 aus Thailand. *M. balbisiana* „Fruchttyp“ mit vier unregelmäßigen Samenreihen. — A: Juvenile Frucht, Querschnitt. Die Samenanlagen sind von Arillusbildungen umgeben, die von den Funikuli ausgehen und die Kammern fast ausfüllen. — B: Gleiches Präparat wie A. Funikulus mit Raphe und Latexgefäßen aus dem Arillus-Trichome auswachsen. — C, D: Vergrößerte Ausschnitte aus A. — Differential-Interferenzkontrast. — Abkürzungen: Ar Arillus. L Latexgefässe. R Raphe.

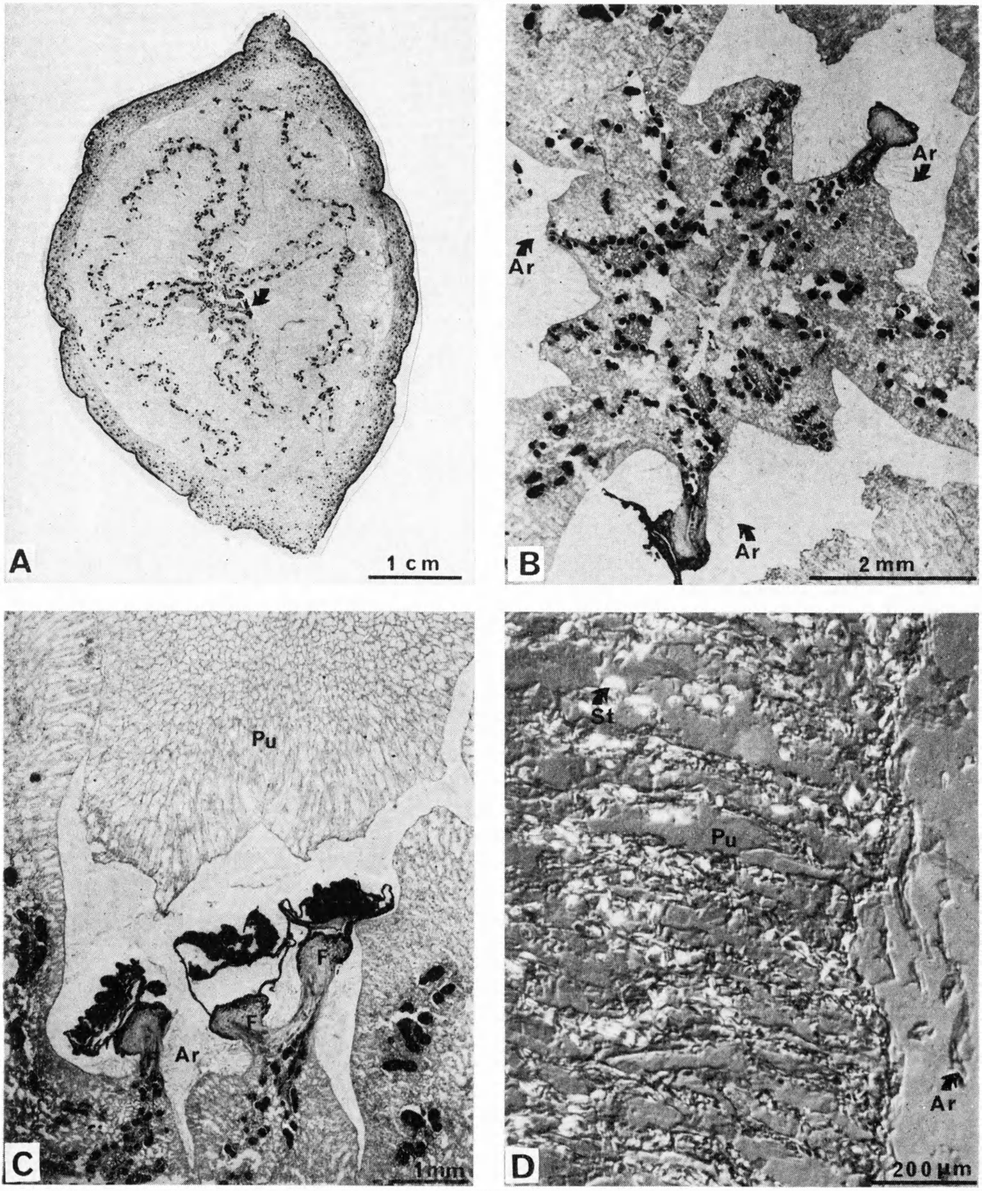

Fig. 3. *Musa* sp. „Pisang gabu". Nr. 4243-I aus Buitenzorg, Java. — A: Frucht mit vier Kammern, Querschnitt. Pfeil zeigt auf den in C vergrößerten Ausschnitt. — B: Zentraler Teil einer trilokularen Frucht mit je zwei Samenreihen pro Lokulus, Querschnitt. Arillusbildungen an den Funikuli (Pfeile). — C: Vergrößerter Ausschnitt aus A. Drei rudimentäre Samenanlagen sind von Arillusbildungen umgeben. Von den Septen und von der Innenseite des Perikarpes wächst Pulpagewebe in die Kammer und verdrängt den Arillus. — D: Ausschnitt aus B. Pulpagewebe mit Stärkekörnern (helle Punkte) angrenzend an Arillus-Trichomen (ohne Stärkekörner). Differential-Interferenzkontrast. — Abkürzungen: Ar Arillus. F Funikulus. Pu Pulpa. St Stärkekörner.

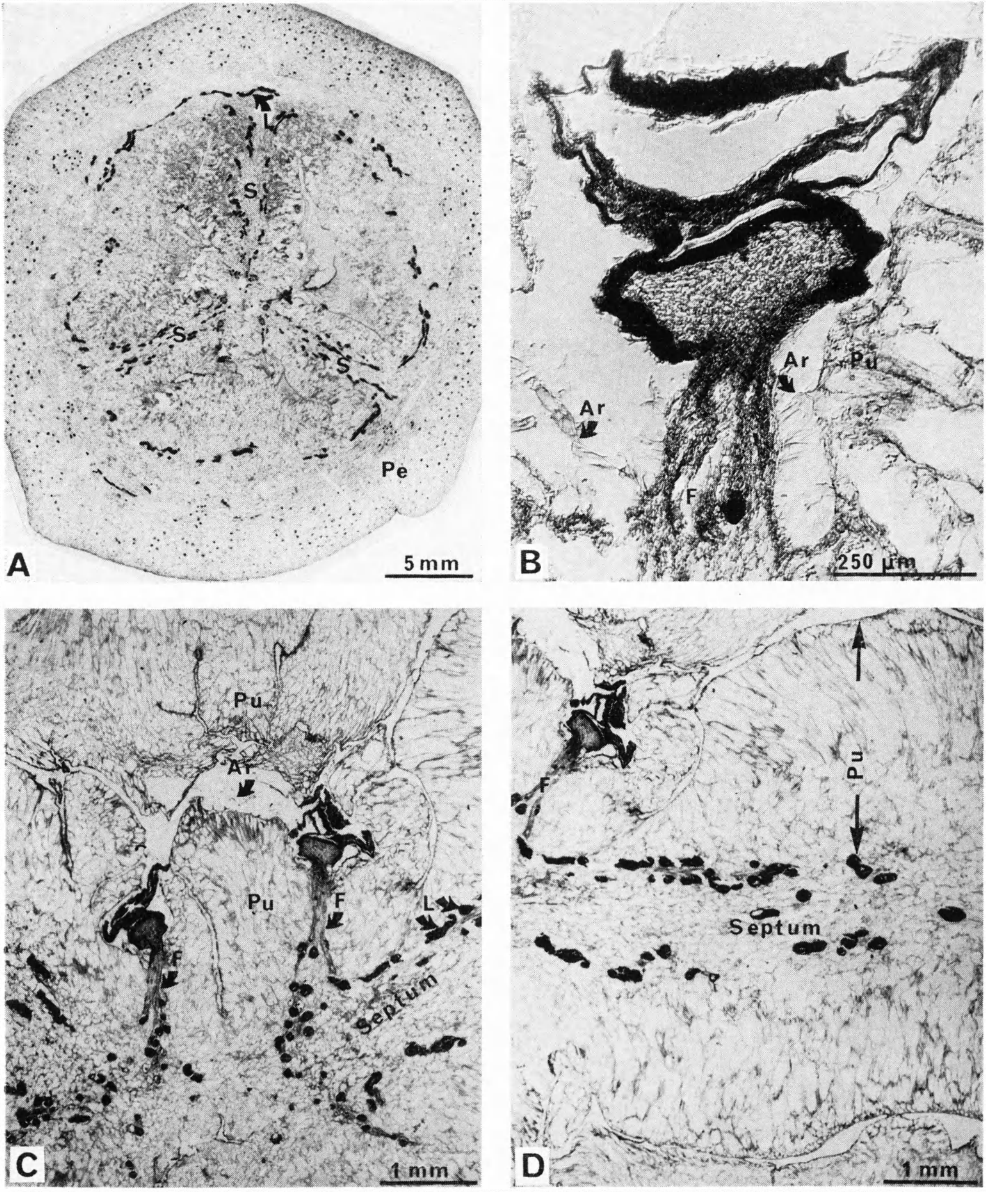

Fig. 4. *Musa* sp. — A: Querschnitt, Eßbanane mit drei Septen. — B: Ausschnitt aus A. Abortierte Samenanlage, umgeben von Arillus-Trichomen, die am Funikulus auswachsen. Differential-Interferenzkontrast. — C: Gleiches Präparat wie A. Zentraler Teil einer Frucht, Querschnitt. Zwei abortierte Samenanlagen in einer Kammer. Pulpabildungen an den Septen, den Funikuli und der Innenseite des Perikarpes verdrängen die Relikte des Arillus. — D: Gleiches Präparat wie A. Querschnitt durch ein Septum mit Latexgefäßen (schwarze Flecke) und abortierte Samenanlage. Starke Pulpabildung am Septum. — Abkürzungen: Ar Arillus. F Funikulus. L Latexgefässe. Pe Perikarp. Pu Pulpa. S Septum.

noch wenige Relikte dieser beiden Stammformen erkennen (Fig. 4 B—D). Die Latexgefäße markieren den Grenzbereich Perikarp zu den mit Pulpa gefüllten Kammern und zeigen die Lage der drei Septen an. Verkümmerte Samenanlagen sind nur selten zwischen den Pulpawucherungen zu finden. Untersucht man die abortierten Samenanlagen, so findet man im Bereich der Plazenten Arillusbildungen in Form von 0,025 mm dicken Trichomen, die aus den Funikuli auswachsen. Mit zunehmender Reife der Frucht werden sie von der Pulpa verdrängt und gehen mehr und mehr in Auflösung.

DISKUSSION DER ERGEBNISSE

Bereits in der älteren Literatur stellte man Haarbildungen im Bereich der Plazenten bei *Musa* fest. WITTMACK (1868 Tafel III, Fig. 25), der eine Beschreibung von *M. ensete* gibt (heute wird *Ensete* als eigene Gattung aufgefaßt), bildet einen Querschnitt von *M. rosea* ab und bezeichnet die Haare an den Samenanlagen als Plazentahaare. HUMPHREY (1896 S. 28), der ebenfalls Samenanlagen und junge Samen von *M. rosea* untersuchte, konstatiert: „The ovule presents nothing noteworthy, except a dense felt of long simple trichomes arising from the sides of the funiculus. No trace of these remains in the seed. As compared with the ovule, the seed shows great lateral extension, so the embryonal cavity is much shorter than broad. The trace of the micropylar opening can still be recognized, and, as might be expected from the indehiscent fruit, no aril is developed."

Sowohl WITTMACK's (1868) als auch HUMPHREY's (1896) Ergebnisse werden von späteren Bearbeitern erwähnt. So benutzt JÄHKEL (1909 S. 23) den Begriff „Plazentahaare" von WITTMACK (1868) und D'ANGREMOND (1915 S. 74) beobachtet: „Die Samenknospen der Bananen sind in einer durchscheinenden Gallerte eingebettet und von vielen Zellfäden umgeben, die aus dem Fuß des Funikulus ihren Ursprung nehmen". Was die Gallerte angeht, so bezieht er sich in einer Fußnote auf JÄHKEL (1909). MAURITZON (1935), der eine umfassende Übersicht über „Samenbau und Embryologie einiger Scitamineen" gibt, erwähnt unter Musaceae nur die Gattungen *Heliconia* und *Strelitzia* und verweist bezüglich der Gattung *Musa* auf frühere Untersuchungen (1935 S. 3). Es ist daher nicht erstaunlich, daß WINKLER (1930 S. 526) in ENGLER-PRANTL behauptet: „Niemals besitzen die Samen in der Gattung *Musa* einen Arillus". Auch in neueren Arbeiten liest man (SIMMONDS 1953 S. 89): „Each loculus bears two rows of ovules embedded (or nearly so) in a strip of mucilage which is pervaded at its axial face by numerous hair-like cells emergent from the axis especially in the neighbourhood of the ovules". Im gleichen Zusammenhang erwähnt er: „The number of hair-like cells in the mucilage seems to increase for the first week or two, but later all traces of them disappears as the mucilage goes". In ähnlicher Weise gibt SIMMONDS diesen Sachverhalt in späteren Arbeiten wieder (SIMMONDS 1959 S. 29 und 1962 S. 78). Es ist daher auch nicht verwunderlich, daß in Übersichtwerken wie A. ENGLER's „Syllabus der Pflanzenfamilien" (POTZTAL 1964 S. 609) unter der Unterfamilie Musoideae erwähnt wird: „Samen ohne Arillus".

Unter Berücksichtigung der bereits oben zitierten Beobachtungen früherer Bearbeiter und unserer eigenen Feststellungen kann zusammenfassend folgendes über den Arillus bei der Gattung *Musa* L. gesagt werden: Bei allen von uns untersuchten *Musa*-Früchten ist in juvenilen Stadien ein Arillus entwickelt. Er besteht aus einfachen Trichomen, die von den Funikuli ausgehen und die Samenanlagen umgeben.

Bei fortschreitender Maturität der Samen wird der Arillus zurückgebildet. Die Auflösung des Arillus erfolgt zu dem Zeitpunkt, wo die Bildung der Pulpa beginnt. Bei reifen Samen ist der Arillus nur noch in Relikten an den Funikuli vorhanden.

Tabelle 1. Karpologische Merkmale der Zingiberales (Scitamineae). Verändert und ergänzt nach KOCH & FRIEDRICH 1971.

Familie	Zingiberaceae				Costaceae	Marantaceae	Cannaceae	Musaceae		Heliconiaceae	Strelitziaceae			Lowiaceae
Genus	Spirematospermum	Cenolophon	Hedychium	Globba	Costus	Maranta	Canna	Musa	Musa	Heliconia	Phenacospermum	Ravenala	Strelitzia	Lowia
fossil/rezent	fossil	rezent	rezent	rezent	rezent	rezent	rezent	fossil	rezent	rezent	rezent	rezent	rezent	rezent
Frucht	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel beerenartig	Kapsel	Kapsel	Kapsel	Kapsel	Kapsel
Zahl d. Lokuli	3	3	3	1	3	1	3	3	3	3	3	3	3	3
Dehiszenz	indehiszent?	indehiszent?	lokulizid	unregelmässig	dehiszent	indehiszent	zuweilen indehisz.	unbekannt	meist indehiszent	septizid	lokulizid	lokulizid	lokulizid	
Plazenten	zentralwinkelständig	zentralwinkelständig	zentralwinkelständig	parietal	zentralwinkelständig		zentralwinkelständig	zentralwinkelständig	zentralwinkelständig	basal	zentralwinkelständig	zentralwinkelständig	zentralwinkelständig	zentralwinkelständig
Samenreihen pro Lokulus	2	2	4		2	nur ein Same	2	1	2 und mehr	1 Same pro Fach	4 und mehr	2	2	2
Deckel	+	+	+		+	+		+	+	+		—		
Arillus	+	+	+	+	+	+ basal	+	vermutlich	+	homolog. Gewebe	+	+	+	+
Mikropylarkragen	+	+			+	+	+	+	+				+	

An Querschnitten von *Ensete* sp. aus Thailand (LARSEN 10 000) waren an den Funikuli der fast reifen Samen keine Arillusbildungen feststellbar; ein abortierter Same in der selben Frucht war jedoch von Arillustrichomen umgeben. Offenbar gilt bei der Gattung *Ensete* in Bezug auf den Arillus derselbe Sachverhalt wie bei *Musa,* nämlich daß der Arillus in juvenilen Früchten entwickelt ist und mit zunehmender Reifung zurückgebildet wird.

Über die biologische Funktion des Arillus bei den Zingiberales haben sich zahlreiche Autoren geäußert. Allgemein nimmt man an, daß er eine Rolle bei der Dehiszenz der Früchte (PFEIFFER 1891) und bei der Verbreitung der Samen durch Tiere spielt. Bei *Musa* sind die Früchte beerenartig und meist indehiszent. Der Arillus hat hier seine Funktion in Folge der Progression verloren. Die Rolle als Lockmittel für Tiere, die die Samen verbreiten, wird von der Pulpa übernommen, die offenbar als Ersatz für den funktionslosen Arillus entwickelt wurde. Pulpabildung tritt ja bekanntlich nicht nur bei Kulturformen sondern auch bei wilden Bananen auf.

Die Entdeckung des Arillus bei der fossilen *Spirematospermum wetzleri* (Zingiberaceae), die sehr nahe verwandt ist mit der rezenten *Cenolophon oxymitrum* und auch in vielen morphologischen und anatomischen Einzelheiten den wilden rezenten Bananen nahe steht, zeigt, daß der Arillus ein sehr altes Element der Zingiberales ist (Tabelle 1). Die gut erhaltenen fossilen Bananenfrüchte aus dem Paleogen von Indien waren unserer Meinung nach wahrscheinlich ebenfalls arillat, da JAIN (1964 S. 46) beobachtet: „The seeds, though filling each locule, show no sign of compression and the space left between the seeds is filled with a non-cellular matrix“. Auch die Verdickung der Testa im Bereich des Hilum bei den fossilen *Musa*-Samen spricht für die Existenz eines Arillus, wie JAIN (1964 S. 53) übrigens selbst feststellt, später aber wieder verwirft.

DANK

Für wichtige Hinweise und die freundliche Überlassung des Untersuchungsmateriales möchten wir Dr. B. HANSEN (Kopenhagen) und Professor K. LARSEN (Aarhus) danken. Zahlreiche Anregungen und Diskussionsbemerkungen verdanken wir Lektor B. E. KOCH (Aarhus) und Dr. H. KOCH (Köln). Zu Dank verpflichtet sind wir auch L. THAMDRUP und D. HUNDTOFTE für die Herstellung der Präparate, J. SOMMER für die Fotoarbeiten und A. M. KRISTENSEN für die Reinschrift des Manuskriptes. Finanzielle Unterstützung erhielten wir von Statens naturvidenskabelige Forskningsråd.

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Campanula keniensis Thulin sp. nov., and Notes on Allied Species

Mats Thulin

THULIN, M. 1976 02 09. Campanula keniensis Thulin sp. nov., and notes on allied species. — Bot. Notiser 128: 350—356. Lund. ISSN 0006-8195.

Campanula keniensis THULIN sp. nov., is described from Kenya. Although an annual its nearest ally is believed to be the perennial *C. edulis* FORSK. Crossing experiments between *C. keniensis* and *C. edulis* gave highly sterile offspring. The synonymy of *C. edulis* is given and all names are typified. Crossings between a large-flowered and a small-flowered strain of *C. edulis* yielded an intermediate offspring with no reduction of fertility. Chromosome numbers are reported for *C. afra* ($2n=24$), *C. dichotoma* ($2n=24$), *C. edulis* ($2n=56$), *C. kremeri* ($2n=24$) and *C. keniensis* ($2n=54$). *Wahlenbergia tenuiloba* THULIN nom. nov., is proposed for the illegitimate *W. congesta* THULIN.

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Campanula keniensis THULIN sp. nov.
(Figs. 1 A, 2 A, D)

ORIG. COLL.: MOBERG 1415, Kenya, Kaijado Distr., Ngong Hills, south of highest part, along the path to the top, 3.I. 1971 (UPS holotype).

Species nova ab affini *C. edulis* FORSK. habitu erecto annuo, corolla cylindrica 6—8 mm longa lobis erectis 1—1.6 mm longis extus dense puberula, stylo tubo corollae breviore, floribus breviter pedicellatis vix nutantibus et chromosomatum numero $2n=54$ diversa.

Annual ± stiffly erect herb, up to 35 cm tall. Stem branched mainly in the upper part, strongly ribbed, hirsute with mixed hairs of very variable length. Leaves sessile, narrowly ovate to ovate above, elliptic to oblanceolate or narrowly ovate towards the base, up to 10—25 mm long, 5—10 mm wide, acute or subacute with truncate, or, at least in the upper leaves, cordate base, hirsute with hairs often bulbous at the base; margin cartilaginous, ± undulate-crenate; midvein and lateral veins prominent beneath. Inflorescence lax with marked overtopping of the terminal flower giving a dichotomous appearance; pedicels short, elongating up to 10 mm in fruit. Hypanthium broadly obconical, with 5 distinct nerves and up to 5 additional ± weak nerves in between them, shortly and densely pubescent but with long hairs on the nerves. Calyx-lobes narrowly triangular, 4—7 mm long, acute, with long hairs at margins and on midvein outside, otherwise shortly and densely pubescent on both sides; calyx-appendages ovate, 1.5—2.5 mm long, reflexed, ± obtuse. Corolla blue or mauve with whitish base, cylindrical, 6—8 mm long, with erect apiculate lobes 1—1.6 mm long; midveins of petals distinct with ± long hairs, corolla otherwise densely puberulous outside, glabrous inside. Stamens with ovate, shortly ciliate filament-bases; anthers 1.3—2.0 mm long. Ovary 3-locular, inferior; style much shorter than the corolla-tube, 3-lobed, with pollen-collecting hairs along most of its length, but with normal hairs at the base. Capsule 3-locular, dehiscing by basal valves. Seeds numerous, elliptic-oblong in outline, compressed, ± 0.6 mm long, almost smooth, yellowish-brown. $2n=54$.

Table 1. Chromosome numbers of some species of *Campanula*. Voucher specimens in UPS. *C. afra* and *C. kremeri* are regarded as distinct species for the sake of convenience (see text).

Taxon	Voucher	Origin of material	2n
C. afra	RYMAN 1340	Canary Is., Tenerife	24
C. dichotoma	THULIN 2410	Algeria, El Milia	24
	THULIN 2414 b	Algeria, El Milia	24
	BARKOUDAH s.n.	Algeria, Tizi Ouzou	24
C. edulis	THULIN 1367	Ethiopia, Asella	56
	BJÖRNSTAD 1575	Tanzania, Ngorongoro	56
C. keniensis ..	MOBERG 1415	Kenya, Ngong Hills	54
C. kremeri ...	THULIN 2302	Algeria, Oran	24

C. keniensis is only known from the Ngong Hills, just south of Nairobi in Kenya, where it has been collected in grassland on the summit ridge and along the western slopes at altitudes of between 2150 and 2430 m.

COLLECTIONS. Kenya: Kaijado Distr., Ngong Hills, XII. 1954 BALLY 9889 (K), XI. 1966 ARCHER 528 (EA), XI. 1967 AGNEW 9681 (NAI), I. 1971 MOBERG 1415 (UPS).

DISCUSSION

AGNEW (1974 p. 509) was the first to pay attention to *C. keniensis*. He called it *Campanula* sp. A and pointed to its annual habit and densely pubescent corolla as characters distinguishing it from *C. rigidipila* (=*C. edulis,* see below).

The species shows a striking similarity to, among annual species, the mainly Mediterranean *C. dichotoma* group (*C. dichotoma* L., *C. afra* CAV., *C. kremeri* BOISS. & REUT., *C. semisecta* MURB., etc.) and *C. balfourii* WAGN. & VIERH. on Socotra, which perhaps belongs to the same group. The taxonomic treatment of these species varies considerably (see e.g. MURBECK 1897 p. 115—119, QUÉZEL 1953) and most of them have at times been regarded as subspecies or forms of *C. dichotoma*. The perennial *C. edulis* in eastern tropical Africa and Yemen is also very close to *C. keniensis*. All these species mentioned have calyx-appendages, capsules dehiscing by basal valves or pores, 3-merous gynoecia and are placed in *Campanula* sect. *Medium* A. DC. The only previously known chromosome number among them is 2n=24, reported from Italian *C. dichotoma* by GADELLA (1964 p. 14). 2n=34 in *C. sarmentosa* (a synonym of *C. edulis,* see below) was reported by SUGIURA (1942 p. 431). It is presumably erroneous like many other of his counts (see GADELLA 1964 p. 43). Chromosome numbers obtained by the present author are summarized in Table 1 (see also Fig. 2 A—C).

The subdivisions of the genus *Campanula* by DE CANDOLLE (1830), BOISSIER (1875) and FEDOROV (1957) were reviewed by GADELLA (1964), who considered them all more or less unnatural and proposed a provisional subdivision into seven groups where much importance was ascribed to cytological data. *C. dichotoma* was placed on its own in Group V, but it was presumed that many other annual appendiculate species belonged there although chromosome data were lacking. *C. kremeri,* as could be expected, fits into the same group. The chromosome number 2n=54 in *C. keniensis,* however, cannot easily be derived from 2n=24. Furthermore, the chromosomes of *C. keniensis* are smaller (c. 1—1.5 µm) than in *C. dichotoma* and *C. kremeri* (c. 1.5—2 µm). A close affinity between *C. keniensis* and the *C. dichotoma* group is therefore im-

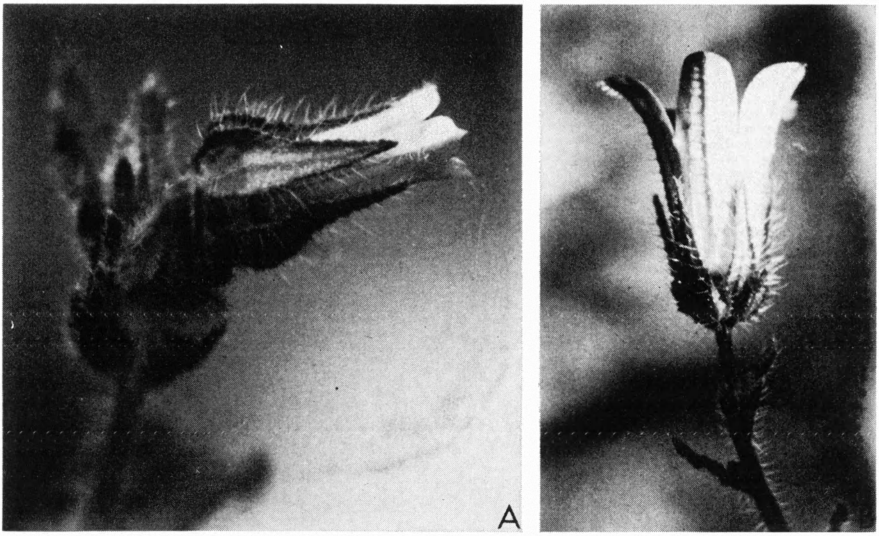
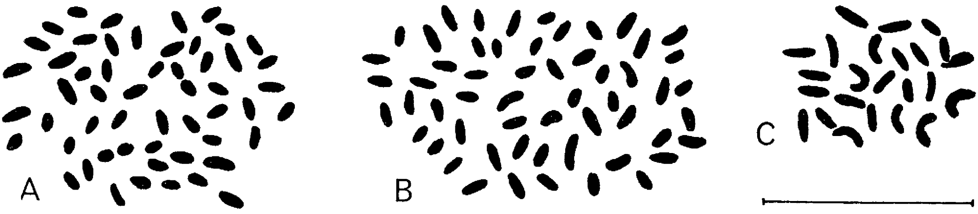


Fig. 1. Flowers of cultivated specimens. — A: *Campanula keniensis,* progeny of Moberg 1415, ×4.5. — B: *C. edulis,* progeny of a cross between the small-flowered strain Thulin 1367 and the large-flowered strain Björnstad 1575, ×2.5.

probable. *C. keniensis* is morphologically distinguishable from this group mainly by its cylindrical corolla with very short and erect lobes (Fig. 1 A). In the *C. dichotoma* group the corolla is ± funnel-shaped with longer lobes, which are spreading to almost perpendicular to the tube (however, in herbarium material this may be difficult to see). The hairiness of the corolla varies within the *C. dichotoma* group, and plants with the outer surface of the corolla densely puberulous as in *C. keniensis* also occur.

The plant described as *C. balfourii* by Wagner & Vierhapper (in Vierhapper 1906 p. 301, see also Vierhapper 1907 p. 474—476) was previously thought by Balfour (1888 p. 148) to be a form of *C. dichotoma.* As distinguishing features Vierhapper (1907 p. 475) mainly mentioned the smaller corolla and shorter calyx-lobes and appendages. Compared with *C. balfourii, C. keniensis* seems to be a somewhat more robust plant. Longer hairs such as are present on the midveins of the petals in *C. keniensis* can hardly be seen in *C. balfourii.* The midveins themselves are also more inconspicuous in this species. The corolla is of a more campanulate shape in *C. balfourii* (otherwise the corolla is of a similar size and is also densely puberulous outside in both these species). Further, the hypanthium usually has more than 5, often c. 10 nerves in *C. keniensis* (5 in *C. balfourii*), the additional nerves being ± weak. The best distinguishing character for *C. keniensis* is its short comparatively stout style, usually much shorter than the corolla-tube, versus the slender style, as long as or longer than the corolla-tube in *C. balfourii.* Calyx-lobes and appendices, seeds and pollen grains (3-porate, 30—35 µm in equatorial diameter, and with densely and finely spinular exine) are similar in all essentials in the two species. Until the chromosome number of *C. balfourii* is known it can hardly be determined with certainty whether its nearest affinity is with *C. dichotoma* or with *C. keniensis,* although the former alternative seems most probable.



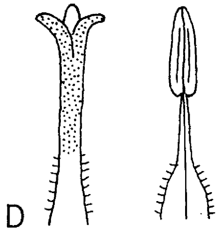


Fig. 2. A—C. Somatic metaphase plates. — A: *Campanula keniensis,* MOBERG 1415 ($2n=54$). — B: *C. edulis,* THULIN 1367 ($2n=56$). — C: *C. kremeri,* THULIN 2302 ($2n=24$). — Scale = 10 µm. — D: Semi-diagrammatic drawing of style and stamen in *C. keniensis.* The dotted area of the style indicates distribution of pollen-collecting hairs. From MOBERG 1415, ×8.

Apart from *C. keniensis, C. edulis* is the only native *Campanula* in Kenya and these two virtually are the only representatives of the genus south of the equator. It is distributed from Yemen, Sudan and Ethiopia in the north to eastern Zaïre and northern Tanzania in the south. In Kenya it seems to be rare and is not known from the Ngong Hills. The nearest localities are in the Aberdares and the Chyulu Hills.

As opposed to the stiffly erect, annual *C. keniensis*, *C. edulis* is usually a decumbent or ascending perennial with a thick, soon lignified tap-root (however, in cultivation it flowers even during the first year while the tap-root is still very thin). The corolla is usually larger in *C. edulis* and campanulate (Fig. 1 B), but forms with a corolla comparable in size and shape to that in *C. keniensis* also occur. However, the corolla is glabrous or has long hairs on the midveins of the petals only, and is devoid of the dense short pubescence of *C. keniensis.* The style is rather short and stout in *C. edulis* and much shorter than the corolla as in *C. keniensis,* but as this is usually ± deeply lobed the style is often as long as the corolla-tube. The hypanthium is usually more than 5-nerved in both species. The pedicels are up to 5 cm long in *C. edulis* and usually much longer than in *C. keniensis.* The marked nodding of the capsules in *C. edulis* is much less pronounced, if occurring at all, in *C. keniensis.* The basal part of the style below the pollen collecting hairs is glabrous in *C. edulis* but hairy in *C. keniensis* (Fig. 2 D). The leaf shape is very variable in *C. edulis,* and although often having narrower, ± oblanceolate or almost spathulate leaves no clear distinction can be made using this character.

The chromosome number of *C. keniensis,* $2n=54$, is most easily explained as a result of a reduction from $2n=56$, and probably the species is closely related to and possibly derived from *C. edulis.* The chromosomes are also of a similar size in these two species (1—1.5 µm, Fig. 2 A, B).

Crossing experiments performed between offspring of the holotype of *C. keniensis* and a strain of *C. edulis* (offspring of THULIN 1367, Asella, Ethiopia) resulted in seed formation in 10 out of 16 pollinated flowers. Vigorous hybrids, intermediate in all respects and with 2n=55, were obtained from all successful crossings. They behaved as annuals, although more long-lived than the parental *C. keniensis*. The pollen fertility of the parents, obtained by counting the percentage of lactic blue staining pollen in a sample of 200 grains, was found to be 95—100 %. In 18 hybrid specimens studied the pollen fertility varied between 10 and 40 % (mean value 30 %). In the parental plants seeds were formed abundantly by autogamy. In the hybrids, however, not a single seed was formed, not even after artificial self-pollination. Thus a strong genetic barrier exists between these species, probably mainly owing to the difference in chromosome number.

C. keniensis and *C. edulis* are not easily placed in any of the groups proposed for the genus by GADELLA. 2n=56 has previously been reported only from *C. vidalii* (sometimes placed in the monotypic genus *Azorina* FEER) on the Azores, which is totally unrelated to *C. edulis* and 2n=54 is a new number for the genus. Group VI includes species with 2n=28, but these are all devoid of calyx-appendages. Obviously the chromosomal diversity and the relationships within the genus are still more complicated than is revealed by GADELLA's work.

The wide variation present in *C. edulis* has given rise to a rather extensive synonymy which is summarized below. All lectotypes have been chosen by the present author.

Campanula edulis FORSKÅL

FORSKÅL 1775 p. 44. — Orig. coll.: FORSKÅL s.n., Yemen, Kurma (C lectotype).

There are three sheets in FORSKÅL's herbarium in C, two of which are without locality. The third specimen, the lectotype, consists of two individuals and apart from the specific name has the locality "ad Kurma" written in FORSKÅL's handwriting. There is also a specimen in Stockholm (S) collected by FORSKÅL and with the locality "ad Hadje". This was originally sent to MONTIN by VAHL in 1780. Hadje is the second locality cited by FORSKÅL (1775 p. 44) for *C. edulis*. Also a specimen without collector and locality in Herb. Thunberg (UPS) was probably distributed by VAHL.

C. esculenta RICHARD 1851 p. 4. — *C. rigidipila* STEUD. & HOCHST. ex A. RICH. var. *esculenta* (A. RICH.) DI CAPUA 1904 p. 236. — Orig. coll.: QUARTIN DILLON & PETIT s.n., Ethiopia, Tigre, Ouodgerate (P lectotype).

C. quartiniana RICHARD 1851 p. 5. — *C. schimperi* VATKE var. *quartiniana* (A. RICH.) VATKE 1876 p. 201, nom. illegit. — *C. rigidipila* STEUD. & HOCHST. ex A. RICH. var. *quartiniana* (A. RICH.) ENGLER 1892 p. 410. — Orig. coll.: QUARTIN DILLON & PETIT s.n., Ethiopia, Tigre, Memsah 8.IX. 1839 (P holotype).

RICHARD cites a QUARTIN DILLON specimen collected in Memsah in September as the type of *C. quartiniana*. The only specimen in Herb. RICHARD with this data has no specific name written on it, but as the specimen agrees very well with the original description there is no reason for doubting that it is the specimen used by RICHARD.

C. rigidipila STEUD. & HOCHST. ex RICHARD 1851 p. 3. — *C. schimperi* VATKE 1874 p. 712, nom. nov. superfl. pro *C. sarmentosa* et *C. rigidipila* (type as for *C. rigidipila*, see ENGLER 1892 p. 410). — *C. schimperi* VATKE var. *rigidipila* (STEUD. & HOCHST. ex A. RICH.) VATKE 1876 p. 201, nom. illegit. — Orig. coll.: QUARTIN DILLON & PETIT s.n., Ethiopia, Tigre, Ouodgerate (P lectotype).

C. sarmentosa HOCHST. ex RICHARD 1851 p. 4. — *C. schimperi* VATKE var. *sarmentosa* (A. RICH.) VATKE 1876 p. 201, nom. illegit. — *C. rigidipila* STEUD. & HOCHST. ex A. RICH. var. *sarmentosa* (HOCHST. ex A. RICH.) ENGLER 1892 p. 410. — Orig. coll.: QUARTIN DILLON & PETIT s.n., Ethiopia, Choa (P lectotype).

Campanula bordesiana MAIRE (1929 p. 188) described from Ahaggar and also reported from Tibesti, is probably also conspecific with *C. edulis*. However, I have seen too little material yet to formally reduce it to a synonym. The area of distribution of *C. edulis* may thus be extended to southern Algeria in the west.

DISCUSSION

C. esculenta was said by RICHARD to differ from *C. edulis* in having a glabrous corolla (however, a few hairs are present near the apex of the corolla-lobes in the syntypes) and obovate-oblong, subspathulate, not lanceolate leaves. It was distinguished from *C. rigidipila* by its leaf-shape and shorter calyx-lobes and appendages.

C. quartiniana was characterized by long, upright, striate and hispid stems with scattered leaves, and by having hairy midveins on the petals.

C. sarmentosa was said to differ from *C. rigidipila* in having thinner and decumbent stems and larger, obovate and obtuse leaves.

The name *C. edulis* in the literature was apparently first used for African material by SCHWARTZ (1939 p. 270). He cited *C. rigidipila* as a synonym. *C. rigidipila* in its turn had long been in use for *C. edulis* in Yemen. CUFODONTIS (1965 p. 1052) cited *C. esculenta, C. sarmentosa* and *C. rigidipila* as synonyms of *C. edulis,* but regarded *C. quartiniana* as distinct, though with hesitation. I agree that this is a rather characteristic form because of the long upright stems (± decumbent at the base, however) and branches, but there are numerous intermediates and I prefer to regard them all as a single polymorphic species.

The most conspicuous variation in *C. edulis* is to be found in the size of the flowers. The corolla ranges from 7 to 25 or occasionally 30 mm in length. However, the variation is continuous, even though large-flowered forms predominate on certain mountains, for instance Mount Moroto in Uganda, Mount Hanang and Ngorongoro Crater in Tanzania, and some others in Ethiopia.

Crossing experiments were performed between the two strains of *C. edulis* cited in Table 1. THULIN 1367 from Ethiopia is a typical "*quartiniana*" form with an 8—9 mm long corolla while BJÖRNSTAD 1575 from Tanzania is closest to a "*sarmentosa*" form with corollas 15 to 20 mm long. Seeds were formed in five out of eight crosses attempted. From all successful crossings hybrids intermediate in corolla length were obtained (Fig. 1 B). Pollen fertility was investigated in 23 specimens of the F1 generation and was found to range from 96 to 100 %. Numerous seeds were formed by autogamy in all of them and an F2 generation was raised without difficulty. No genetic barriers thus exist between these two rather dissimilar strains from quite different parts of the area of distribution of the species. These results strongly support the wide circumscription of the species given here.

ADDENDUM

Wahlenbergia tenuiloba THULIN nom. nov.

Syn. *W. congesta* THULIN 1975 p. 209, nom. illegit. [non *W. congesta* (CHEESM.) N. E. BROWN 1913 p. 336].

Unfortunately N. E. BROWN's combination, which refers to a species in New Zealand, was overlooked in my recent study of tropical African *Wahlenbergia*. *W. tenuiloba* is endemic in Zaïre and only known from the type collection. The new specific epithet refers to the very narrow calyx-lobes of the species.

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The Total Range of Euphrasia

Eric Hultén

HULTÉN, E. 1976 02 09. The total range of Euphrasia. — Bot. Notiser 128: 357—364. Lund. ISSN 0006-8195.

A new map of the total range of the genus *Euphrasia* L. (Scrophulariaceae) is presented, as well as a more detailed one of its distribution in the Northern Hemisphere. A third map shows the ranges of *E. tatarica, E. frigida* and *E. mollis*. The connection between the ranges in the Old and New Worlds is over the Aleutian Islands.

A few comments on the complicated taxonomy within the genus and on the occurrences in the Southern Hemisphere are made. No attempt is made to outline the history of the genus.

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In connection with the study of the total ranges of Scandinavian plants I became interested in the total area of distribution of the genus *Euphrasia,* and tried to improve earlier maps of the genus. The result of this study is presented here (Figs. 1, 2).

The following maps, at least, of the genus *Euphrasia* have been published: WETTSTEIN (1896 Karte 1); IRMSCHER (1922 Figs. 2, 3); DU RIETZ (1940 p. 224); CROISAT (1952 Figs. 7, 11); BURBIDGE (1960 p. 180); VAN STEENIS (1962 p. 260, 1964 Fig. 7, 1971 Map 2, 1972 p. 285); VAN STEENIS & BALGOOY (1966 p. 97); SCHMITHÜSEN (1968 p. 113); SCHNELL (1970 Fig. 58); HARTL in HEGI (1972 p. 338); THORNE (1972 p. 379).

At least as far as the range in the Northern Hemisphere is concerned they are all based on WETTSTEIN's very schematical map, but since 1896 our knowledge of the distribution of plants has increased very considerably, and none of the above-enumerated maps are sufficiently detailed to give a reasonable idea of the actual conditions. Since WETTSTEIN's map was completed a number of works including the following have appeared, allowing a far more detailed map to be made of the range of the genus in the Northern Hemisphere: FERNALD & WIEGAND (1915); HULTÉN (1930 pp. 107, 290; 1937 pp. 294, 376; 1950 Maps 1568—1580; 1958 Map 32; 1968 p. 814); JØRGENSEN (1919); KARAMYSCHEVA & RACHKOVSKAYA (1973 p. 111); KRYLOV (1939 pp. 2474—87); LI (1953); POPOV (1959 p. 664); PAVLOV (1965 pp. 102—109); SELL & YEO (1970); YAMAZAKI (1963).

The maps presented here are based on information found in these works as well as on that in the about 1,400 taxonomic works enumerated in my work on the circumpolar plants (HULTÉN 1971 pp. 405—446). The herbarium and collection of distributional maps at the Natural History Museum of Stockholm (Riksmuseum) has also been used.

In Ann. Jard. Bot. Madrid 1(17), 1959 pp. 452—458, six species of *Euphrasia* are reported from Peru. Acc. to EDWIN 1971 p. 671 only two of them possibly belong to that genus — and only *E. pubescens* R. & P. is supposed to occur in Peru. The report is based on an old collection kept in the Paris herbarium. No special locality is given and the report most probably is erroneous. Peru is therefore not marked on the map presented here.

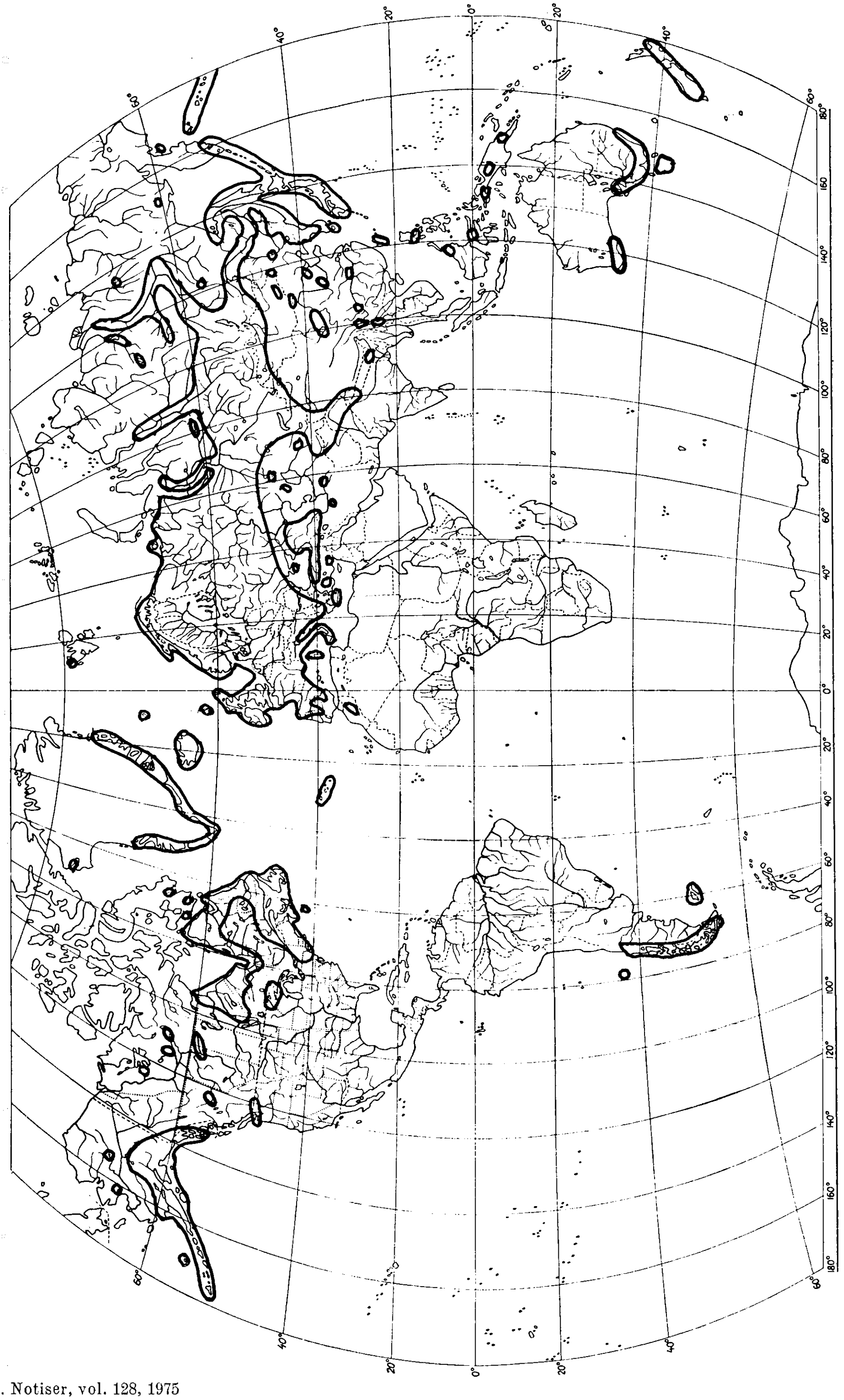

Fig. 1. Total range of the genus *Euphrasia*.

Fig. 2. Total range of the genus *Euphrasia* in the Northern Hemisphere.

COMMENTS ON THE RANGE

The genus *Euphrasia* occupies a circumpolar area in the Northern Hemisphere, but reappears in western South America and on the Falkland Islands and also in New Zealand and Australia with a few intermediate stations, for example on Formosa, Borneo, Celebes and New Guinea. In Africa it only occurs in Morocco.

In the Himalayas *Euphrasia* specimens have been collected above 4000 m, in China up to 4450 m (Li 1953). It is very remarkable that practically all localities in North America are situated on land that was glaciated during the Pleistocene. The genus does not occur in the unglaciated inner parts of Alaska and Yukon. It is especially common in the once inundated areas around southern Hudson Bay, but apparently avoids inner Labrador.

Euphrasia taxa are easily spread, for instance together with hay, and it is therefore not always possible to state their natural range. The isolated occurrences at Thule in N Greenland and on Spitzbergen (at a hot spring) could be taken as being anthropochorous, but the occurrence on the rarely visited Jan Mayen may cast doubt on this.

The genus is lacking in northeastern Siberia, and in northern Siberia it seems only to occur washed down along the large rivers. The connection between Asia and America is formed by a single, fairly characteristic microspecies, *E. mollis* Ledeb., with an almost linear area from southern Alaska over the Aleutian Islands and southern Kamchatka to northern Japan, but lacking in the Bering Strait area (Fig. 3). It is not out of the question that a connection over Bering Sound has existed in earlier warmer periods.

EUPHRASIA IN THE NORTHERN HEMISPHERE

Wettstein (1896) divided the genus into 87 taxa which he gave the status of species, while 22 are regarded as hybrids. He admits that he uses the term species merely for convenience. It must be remembered that Wettstein's admirable study was made before Mendel's hereditary laws had been rediscovered. His concept of hybridization and its consequences must therefore have been very unclear. However, even later authors, for instance Karlsson (1974), admit that hybridization seems to play a great part in the variation within the genus.

Since Wettstein's monograph appeared a great number of new taxa ("species") have been described, and Wettstein's concepts and the limitations of many of his species have been changed. Thus, for instance, in the Soviet Union 62 "species" are now recognized in the Flora URSS (Juzepchuk 1955 a), and new ones with smaller and smaller ranges are still being described by practically everyone dealing with the genus in restricted areas. Thus, for instance, Juzepchuk (1955 b) described 22 new species from the Soviet Union, most of them with very limited areas of distribution. Altogether about 500 taxa given the status of species have been described. In other words, in this respect the genus *Euphrasia* behaves in the same way as a number of other complexes, the members of which are sometimes taken as single collective species, though usually as a conglomerate of "microspecies", e.g. *Betula, Thymus serpyllum* s. lat., *Trapa natans* s. lat., *Polygonum aviculare,* the *Poa pratensis* group and still others. The seasonal dimorphism as well as the fact that *Euphrasia* taxa are hemiparasites contribute to complicate the picture.

In the Northern Hemisphere the genus *Euphrasia* behaves as a complex species, *E. officinalis* s. lat., with the exception of the Azorean and some of the Japanese taxa which are essentially different. It consists of a highly variable circumpolar lowland population, and superimposed on this and poorly differentiated from it a group of arctic-montane taxa (*E. fri-*

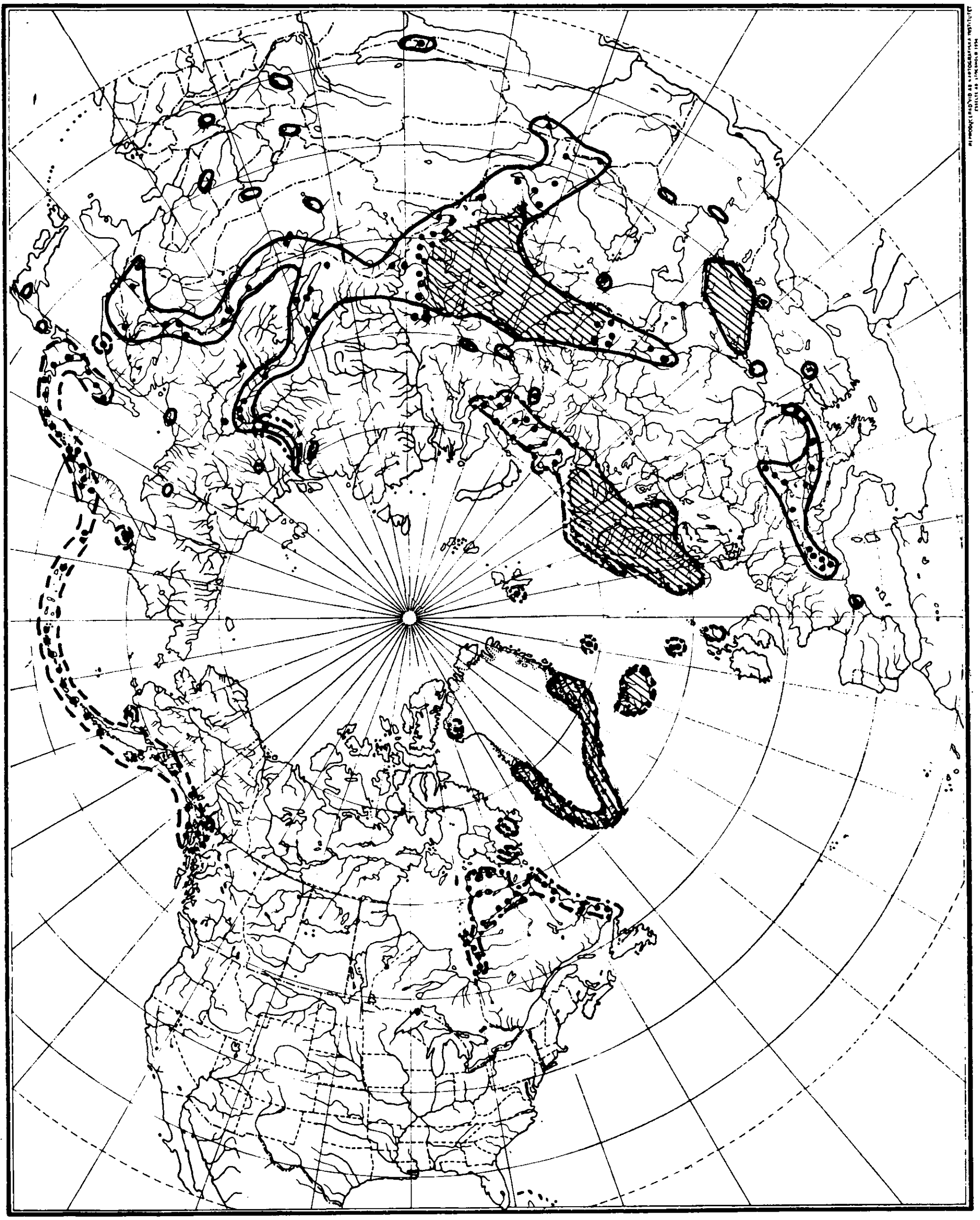

Fig. 3. Range of three remarkable *Euphrasia* taxa. — Unbroken outline: *E. tatarica*. — Outline with dashes and dots: *E. frigida* (including *E. subarctica* JUZ. along the Lena River. *E. frigida* occurs according to YEO 1972 doubtfully in C Europe.) — Broken outline: *E. mollis* (including *E. pseudomollis* JUZ.).

gida—minima, E. salisburgensis—lapponica). Many of the lowland taxa are sympatric, often even occurring together in the same population, and they are often connected by dubious forms.

Northern and boreal plants, chiefly occurring in areas that were glaciated during the Pleistocene, are replaced south of their ranges by closely related preglacial counterparts. When the ice retreated biotypes or fragments of this southern population, well adapted to the new climatic and ecological conditions, spread northwards into the new land laid bare by the melting ice. They formed the basis of the present boreal species.

In the case of *Euphrasia* one of these southern taxa is what passes for *E. tatarica* FISCHER ex SPRENG. It occurs in Europe and Asia (Fig. 3), and by FERNALD & WIEGAND (1915 p. 198) was even accepted as occurring in eastern America under the name of *E. stricta* var. *tatarica*. *E. tatarica* is, however, not sharply differentiated from the northern population, especially not from *E. stricta*. Outside the area marked in Fig. 3 it may occur on Sakhalin and in Japan. In Flora Europaea (YEO 1972) part of *E. tatarica* is included in *E. stricta*, the rest in *E. pectinata* TEN. In other respects also *E. officinalis* s. lat. shows great similarity to other complex species. For instance, a number of related but more highly differentiated, isolated taxa occur along the southernmost rim of the whole complex. These taxa are so distinct that they could be regarded as species even using the normal species concept. One such taxon is, for instance, *E. pectinata* which, however, also presents forms that are intermediate between this and the more northern populations.

EUPHRASIA IN THE SOUTHERN HEMISPHERE

Very few plant taxa have a range similar to that of *Euphrasia*, and it can therefore be of interest to discuss this point in greater detail.

Quite a number of taxa with their main range in the Northern Hemisphere reappear in a more or less identical form in southern S America. Some of these have been discussed by ROIVAINEN (1954), others by CONSTANCE et al. (1963). Examples are *Carex pyrenaica* and *C. magellanica*, the genera *Ribes, Empetrum, Sanicula* and *Saxifraga*, as well as a number of western American taxa belonging to the genera *Phacelia, Nama, Agoseris, Microseris, Osmorrhiza* and *Bowlesia*. Some, for instance *Carex macloviana*, the *Phacelia magellanica* complex and the genus *Saxifraga* occur in intermediate stations along the Andes indicating the route of migration.

One species, *Trisetum spicatum* L. s. lat., has a range similar to that of the genus *Euphrasia* with intermediate stations both in eastern Asia and Central and South America. This has been discussed in detail by the author (HULTÉN 1959). In this case the migrational routes seem to have been very well established.

Another plant, *Fimbristylis annua* (DEL.) ROEM. & SCHULT. s. lat., distributed from the hot springs of Kamchatka over Japan, Korea, China and Polynesia to Australia and also occurring in Mexico and S America, may in this connection be worth closer study, as it probably occupies a chain of localities in both hemispheres.

As regards the taxa of the Southern Hemisphere, WETTSTEIN referred those from S America to a separate section, *Trifidae*, on their three-cleft leaves, while those of southeastern Asia, New Zealand and Australia were regarded as a subsection of the section *Euphrasia*, and thus more closely related to the *Euphrasias* of the Northern Hemisphere.

It is therefore extremely remarkable that SKOTTSBERG (1922) described a new perennial species of *Euphrasia* with entire leaves and large flowers from Masafuera off the Chilean coast not belonging to the section *Trifidae*, but showing close affinities to the New Zealand—Australian group of *Euphrasia* taxa. It is very rarely that taxa which in South America only occur on Juan Fernandez reappear on the other side of the Pacific. Such cases are, according to information received from BENKT SPARRE, for example the following: *Arthopteris altescandens* (COLLA) J. SM. reappearing in Polynesia, Australia and Africa; *Histiopteris incisa* (THUNB.) J. SM. reappearing in Australia, Tasmania and S Africa (introduced in the province of Magellanes); *Santalum fernandezianum* T. PHIL. now extinct, the genus reappearing in Hawaii and E Asia; *Halorrhagis,* four endemic species on Juan Fernandez, the genus reappearing in Polynesia and Australia; *Coprosma,* two endemic species on Juan Fernandez, numerous species in Polynesia and Australia.

Very few phytogeographers today would agree with the conclusion with which DU RIETZ (1940 p. 272) sums up his discussion of the bipolar problem: "To explain the facts of bipolar plant distribution is seems necessary to look for epeirogenetic transtropical highland bridges older than the mountain chains of the Alpine Orogen. Such highland bridges may have existed not only in Africa, but also bordering Alpine geosynclines (i.e. the Andean and Malaysian geosynclines), partly passing over present deep sea bottom."

The old concept of land bridges between continents must be revised in the light of the theory of plate tectonics that is becoming more and more accepted. To what extent this theory can be applied to the history of the genus *Euphrasia* depends on judgements concerning the age of the genus and the time scale of the presumed plate movements.

It seems premature to attempt a sketch of the development of the genus from its presumably Asiatic origin to the present peculiar worldwide range. Knowledge of the present conditions is, however, essential as a base for furthermore discussion.

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Studies on the Flora of Jordan

1. Diplotaxis villosa sp. nov. (Cruciferae)

Loutfy Boulos and Walid Jallad

BOULOS, L. & JALLAD, W. 1976 02 09. Studies on the flora of Jordan. 1. Diplotaxis villosa sp. nov. (Cruciferae). — Bot. Notiser 128: 365—367. Lund. ISSN 0006-8195.

Diplotaxis villosa BOULOS & JALLAD sp. nov. is described from the southern desert of Jordan. The new species seems to represent a unique group within the genus *Diplotaxis* DC. and does not fit into any of the four sections of the genus. A key is given to separate *Diplotaxis villosa* from the four previously known species of *Diplotaxis* in Jordan. A drawing of the plant and a map are presented.

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The genus *Diplotaxis* DC. in Jordan is represented by four species, viz. *Diplotaxis harra* (FORSSK.) BOISS., *D. acris* (FORSSK.) BOISS., *D. erucoides* (L.) DC. and *D. viminea* (L.) DC. (POST & DINSMORE 1932 pp. 118—120, ZOHARY 1966 pp. 305—308, pl. 453—456, JALLAD 1975). The present paper reports the discovery of a new species in the southern desert of Jordan.

Our new species is collected from an area which seems to have been very rarely visited by botanists or has never even been explored botanically. The occurrence of this remarkable new species within a vast area stretching over a few square kilometres, with thousands of individuals almost in pure stands, may draw attention to the need to carry on further floristic studies, as the area may include some other interesting elements which still await discovery. The site where our new species was collected is about 40 kilometres northeast of El-Jafr in the upper course of Wadi Shaumari, a fairly long wadi stretching northwards from El-Jafr for about 60 kilometres.

Diplotaxis villosa sp. nov. seems to constitute a distinct group within the genus *Diplotaxis*. It does not fit into any of the four sections given by SCHULZ (1919) viz. *Hesperidium* O. E. SCHULZ, *Catocarpum*

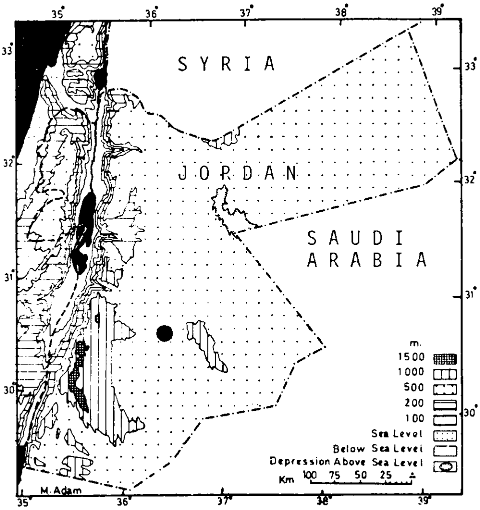

Fig. 1. Distribution of *Diplotaxis villosa*.

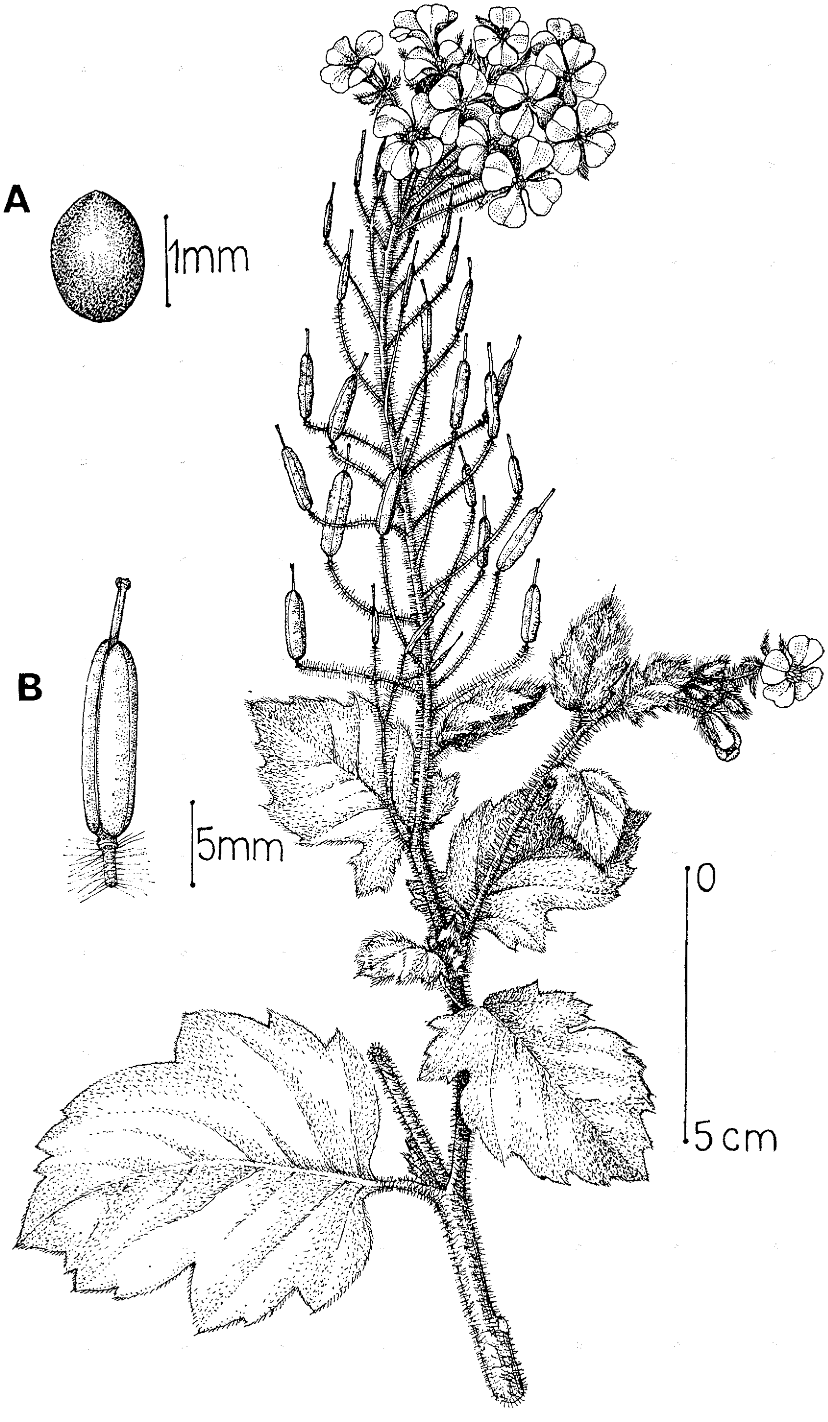

Fig. 2. *Diplotaxis villosa.* — A: Seed. — B: Fruit.

DC., *Rhynchocarpum* PRANTL and *Anocarpum* DC.

We propose to name this species *Diplotaxis villosa* due to the most characteristic white villous hairs which densely cover most of the plant parts. It may be described as follows:

Diplotaxis villosa BOULOS & JALLAD, sp. nov. — Fig. 2

Annua, albo-villosa, 5—60 cm alta, plerumque valde ramosa. Folia petiolata, sinuato-dentata usque lyrata, inferiora sparse pilosa, superiora dense villosa. Inflorescentia racemosa, multiflora, usque 30 cm longa. Flores laete flavi, 1.2—1.5 cm diametro, pedicellis 1—1.5 cm longis adscendentibus usque patentibus. Sepala 5—7 mm longa, villosa, sub anthesi patentia. Petala (unguiculo incluso) 1—1.2 cm longa. Stamina longiora exserta, filamentis anguste alatis. Pedicelli sub fructu 1.5—2.5 cm, adscendentes, villosi. Fructus 13—17 mm, erectus, cylindricus, glabrescens; valvae uninerves, sutura prominenter carinata. Stylus 2—3 mm longus, glaber. Semina 1×1.2 mm, numerosa, in quoque loculo biseriata, brunnea, late elliptica, glabra, rugulosa.

HOLOTYPE: Wadi Shaumari, upstream, c. 40 kms northeast of El-Jafr. 9 April 1975. BOULOS & JALLAD 7994. University of Jordan Herbarium, Amman. Isotypes: BM! CAI! G! K! LD! RNG! S!

Annual, white-villous, 5—60 cm high. Stem erect or ascending, usually richly branched. Cauline leaves petiolate, petiole 1—2.5 cm long, blade 4—7×3.5—7 cm, sinuate-dentate to lyrate, sparsely hairy on both surfaces; upper leaves short-petioled, blade 1.5—3×1—2.5 cm, densely villous. Inflorescence a many-flowered raceme, up to 30 cm long. Flowers bright yellow, becoming orange-yellow when dry, 1.2—1.5 cm in diameter; flowering pedicels 1—1.5 cm long, ascending to spreading, narrowly cylindrical, villous. Sepals 5—7 mm long, villous, yellowish-green in bud, green and spreading during anthesis, lanceolate to ovate-lanceolate. Petals 1—1.2 cm long including the claw, limb obovate, veined. Long stamens exserted; filaments narrowly winged. Fruiting pedicels 1.5—2.5 cm long, ascending, villous. Fruit 13—17×3—5 mm, erect, cylindrical, glabrescent; beak seedless, valves uninerved, with a prominent ridge along the suture; replum membranous. Style 2—3 mm long, glabrous; stigma bilobed; gynophore very short. Seeds 1×1.2 mm, numerous, in two rows in each cell, brown, broadly elliptic, glabrous, rugulose.

KEY TO THE DIPLOTAXIS SPECIES KNOWN FROM JORDAN

1. Flowers yellow
    2. Biennials or perennials, fruit deflexed .... *D. harra*
    2. Annuals, fruit erect to ascending
        3. Plants densely white-villous, fruit cylindrical .... *D. villosa*
        3. Plants glabrous or glabrescent, fruit compressed .... *D. viminea*
1. Flowers white, pink or violet
    4. Flowers pink or violet, over 16 mm long .... *D. acris*
    4. Flowers white, up to 16 mm long .... *D. erucoides*

ACKNOWLEDGEMENTS

We wish to thank Mr H. K. AIRY SHAW, The Herbarium, Royal Botanic Gardens, Kew, for his kind help with the Latin diagnosis. Thanks are also due to UNESCO and to the Jordan Research Council, Amman, for providing facilities and financial support.

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Studies on the Flora of Jordan

2. Seven Species New to the Flora of Jordan

Loutfy Boulos, Walid Jallad and Jamil Lahham

BOULOS, L., JALLAD, W. & LAHHAM, J. 1976 02 09. Studies on the flora of Jordan. 2. Seven species new to the flora of Jordan. — Bot. Notiser 128: 368—370. Lund. ISSN 0006-8195.

Seven species are recorded as new to Jordan: *Papaver glaucum* BOISS. & HAUSSKN. (Papaveraceae), *Hypericum olivieri* (SPACH) BOISS. (Guttiferae), *Linum corymbulosum* Reichb. (Linaceae), *Allium sindjarense* BOISS. & HAUSSKN. (Alliaceae), *Colchicum crocifolium* BOISS. (Liliaceae), *Consolida tomentosa* (AUCHER) SCHRÖD. subsp. *oligantha* (BOISS.) DAVIS (Ranunculaceae) and *Thalictrum isopyroides* C. A. MEY. (Ranunculaceae). The genus *Thalictrum* L. has not previously been known from Jordan.

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The present paper reports seven species new to the flora of Jordan. Specimens of these species are deposited at the University of Jordan Herbarium, Amman.

Papaver glaucum BOISS. & HAUSSKN. in BOISS.

This species is not among the six species enumerated by ZOHARY (1966) from Jordan. CULLEN (1965) gives the following distribution for *P. glaucum*: Turkey (eastern Anatolia), the Syrian desert, northern Iraq and western Iran; Irano-Turanian element. According to MOUTERDE (1970) the geographical distribution is: Turkey, Syria, Iraq and Iran.

Specimens collected from Jordan: c. 30 km northeast of H-4, 9 April 1974 (fl., fr.) BOULOS, JALLAD & LAHHAM 6861. — Wadi Ruweishid, 12 km east of H-4, 11 April 1974 (fl.) BOULOS, JALLAD & LAHHAM 6918. — 9 km north of Aqaba, 5 April 1974 (fl., fr.) BOULOS, JALLAD & LAHHAM 6671. — Wadi Yutum, upper stream, 15 km north of Aqaba, 21 March 1975 (fr.) BOULOS, JALLAD, LAHHAM & ABU-HMAIDAN 7476. — 4 km south of Rum Rest House, along the road to Rum Police Station, 23 March 1975 (fr.) BOULOS, JALLAD, LAHHAM & ABU-HMAIDAN 7674.

Hypericum olivieri (SPACH) BOISS.

The specimens were determined by N. K. B. ROBSON. Dr ROBSON (verbal comm.) did not see any material of this species from Jordan during his many years of research on the genus *Hypericum* L. ROBSON (1967) refers to this species as being from Turkey, the Syrian desert and western Iran. MOUTERDE (1970) gives the following geographical distribution for *H. olivieri*: "Turquie, Syrie, presque sûrement Iraq et Transjordanie, W. de l'Iran." This shows that he suspected its presence in Jordan; however, he did not give enough evidence of its occurrence. There is no mention of this species in ZOHARY 1966.

Specimens collected from Jordan: Hussein Housing District, Amman, 10 June 1974 (fl.) S. ORAN s.n. — University Campus, Al-Jubaiha, near Amman, 22 July 1974 (fr.) BOULOS 7286. — Duplicates of both specimens in BM!

Linum corymbulosum REICHB.

POST and DINSMORE (1932) as well as ZOHARY (1972) recorded this species from Palestine but not from Jordan. Davis (1967) gives the general distribution of *L. corymbulosum* as follows: South Europe, Crimea, Southwest Asia, East Africa; Mediterranean element. He gives no details about any particular countries in Southwest Asia.

Specimen collected from Jordan: 12 km north of Irbid (3 km north of Sal), 26 April 1975 (fl., fr.) Boulos, Jallad & Lahham 8173.

Allium sindjarense Boiss. & Hausskn.

According to Mouterde (1966) this species is known from southern Turkey, Iraq and Syria. Post & Dinsmore (1932) report its occurrence in Syria. Our find from Jordan comes from a locality very close to the Syrian border.

Specimen collected from Jordan: 80 km northeast of H-4, near the Syrian border, 10 April 1974 (fl.) Boulos, Jallad & Lahham 6881.

Colchicum crocifolium Boiss.

Post & Dinsmore (1933) do not mention this species in their treatment of the genus *Colchicum* L. However, Mouterde (1966) gives the following geographical distribution for *C. crocifolium*: Syria, Turkey, Iraq and Iran.

Specimen collected from Jordan: 35 km northeast of H-4, 11 April 1974 (fr.) Boulos, Jallad & Lahham 6952.

Consolida tomentosa (Aucher) Schrödgr. subsp. **oligantha** (Boiss.) Davis

Zohary (1966) enumerates three species of *Consolida* (DC.) S. F. Gray from Jordan. Our species is not among these three. Davis (1965) reports on the geographical distribution of our species as follows: Turkey, North Iraq and the Syrian Desert? Irano-Turanian element. He adds: "Some Syrian specimens are intermediate between subsp. *oligantha* and subsp. *tomentosa* (Syrian Desert and N. Iraq) . . . its presence in Turkey remains in doubt."

Our find represents an extreme southern extension in the geographical range of the species (Fig. 2).

Specimen collected from Jordan: 5 km south of Shaubak, 29 June (fl., fr.) Jallad, Lahham & Hanania 616.

Thalictrum isopyroides C. A. Mey.

According to Davis et al. (1965) the geographical distribution of *Thalictrum isopyroides* is as follows: Soviet Armenia, Northern Iraq, Turkey (scattered mainly in eastern Anatolia), the Syrian Desert, Iran, Afghanistan and Altai; mainly in the Irano-Turanian region. Mouterde (1970) gives a more or less similar distribution for the same species. Lecoyer (1885) already gave an almost identical distribution for *T. isopyroides* in his monographic treatment of the genus *Thalictrum*. The plant grows in mountainous regions (Lecoyer 1885) among volcanic rocks (Post & Dinsmore 1932).

Thalictrum isopyroides was collected in southern Jordan, 1—3 km south of Ras en Naqb, 30°01′N and 35°28′E. This locality represents the extreme southwestern limit of the geographical range of the species. Djebel Druz, southern Syria, was the southwestern limit before the discovery at Ras en Naqb, Jordan. The genus *Thalictrum* L. is entirely new to the flora of Jordan.

The presence of *Thalictrum isopyroides* as far south as Ras en Naqb, about 90 kilometres northeast of the Gulf of Aqaba, the Red Sea, is probably due to the high altitude of this area (c. 1400 m). Moreover, the plants were collected on the western slopes of the Ras en Naqb escarpment, which may provide a milder microclimate within that area.

Among the rare and interesting species collected by the authors at Ras en Naqb are: *Biebersteinia multifida* DC., *Tulipa polychroma* Stapf, *Iris palaestina* Boiss.

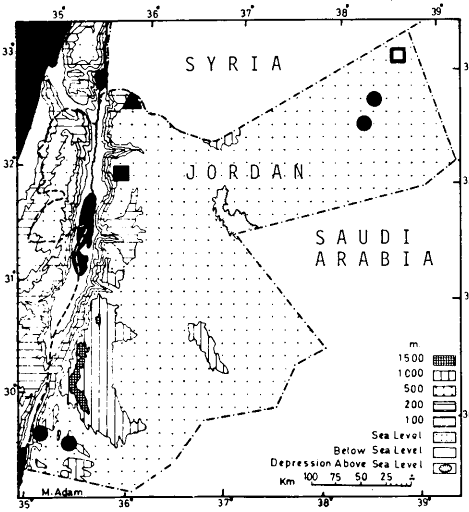

Fig. 1. The distribution within Jordan of *Papaver glaucum* (dots), *Hypericum olivieri* (filled square), *Linum corymbulosum* (triangle), and *Allium sindjarense* (unfilled square).

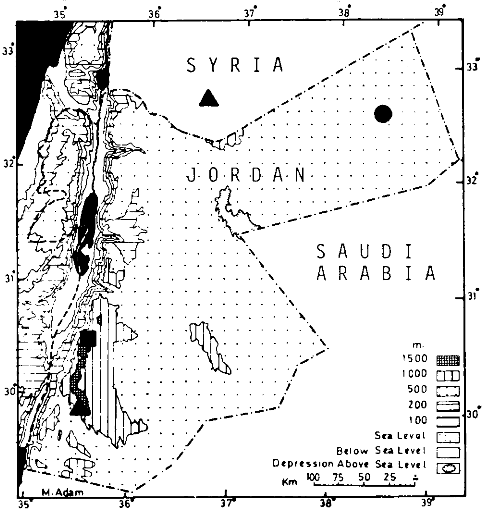

Fig. 2. The distribution within Jordan of *Colchicum crocifolium* (dot), *Consolida tomentosa* subsp. *oligantha* (square), and *Thalictrum isopyroides* (triangles). For *T. isopyroides* the southwesternmost Syrian locality (Djebel Druz) is also shown.

and *Pyrethrum santolinoides* DC. In Jordan these species and probably others are almost restricted to Ras en Naqb and hardly exist outside this area.

Specimens collected from Jordan: 1—3 km south of Ras en Naqb, 12 March 1974 (fl. buds) Boulos, Al-Eisawi & Jallad 5997. — 1—4 km south of Ras en Naqb, 19 March 1975 (fl.) Boulos & Jallad 7353. — 1—2 km south of Ras en Naqb, 4 April 1975 (fr.) Boulos & Jallad 7803.

ACKNOWLEDGEMENTS

The authors are indebted to the Director, Deputy Director and Staff of the Herbarium and Library, Royal Botanic Gardens, Kew for the facilities and help they were afforded during the preparation of this work. Thanks are also due to the Salén Foundation, Sweden and the Jordan Research Council for their financial support. The facilities offered by UNESCO and the University of Jordan during the field trips are much appreciated.

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Botanical Literature

Miège, J. & Stork, Adélaïde L. (eds): Origines des flores africaines et malgaches. Nature-speciation. Comptes rendus de la VIIIe réunion de l'AETFAT, Vol. 1. — Boissiera 24 a. Genève 1975. 422 pp.

Since its first meeting in Brussels in 1951 the "Association pour l'Etude Taxonomique de la Flore d'Afrique Tropicale" (AETFAT) has organized eight conferences at various institutions involved in the study of African flora and vegetation. The latest conference took place at the Conservatoire et Jardin Botanique de la Ville de Genève in September 1974 and was attended by more than a hundred botanists from a wide range of European and African countries.

It has been the general practice at the AETFAT meetings to devote the main part of the conference to papers relating to a selected topic of general interest. At the 1974 meeting the topic was "The Origin of the Floras of Africa and Madagascar and the Nature of Speciation". Papers on a number of other subjects within AETFAT's sphere of research were also read, including progress reports on expedition activities, and progress in the publication of distribution and vegetation maps, recurrent subjects at AETFAT meetings. A total of more than 70 papers was read at the Geneva meeting. The present Volume 1 of the "Comptes-rendus" comprises 47 papers, mainly those with themes relating to the main topic of the meeting. The remaining papers, including the progress reports and a number of papers on nature conservation, will appear in a forthcoming volume.

The 47 papers in Volume 1 are grouped around a number of themes: Records of fossil pollen; changes in floras and vegetation during the Pleistocene; microevolution in mountain habitats; distribution maps of Sahelian plants; phytogeographical papers on local endemism and on the relation between the floras of Madagascar and of tropical East Africa; taxonomic, morphological and phylogenetic papers on various African genera and families; phytochemistry, mainly of the genera *Acacia* and *Adansonia*; numerical taxonomy and biometry of the grass genera *Aristida* and *Panicum*; computerization of herbaria with important collections of African plants. It is very difficult to select any of the papers for reviewing in detail.

The general impression one receives from the papers as a whole is that of a very rich and many-faceted research activity. The present volume, and indeed all the volumes from the AETFAT meetings, is indispensable to students of the flora of Africa as the proceedings represent up-to-date cross-sections of the many themes of African botany at present under study in European and African herbaria and universities. But the disjointed nature of the contents of the papers also clearly indicates how far there is still to go before reaching the goal suggested by the main topic of the meeting: an exhaustive description and explanation of the origin of the floras of Africa and Madagascar.

Ib Friis

Boney, A. D.: Phytoplankton. Studies in Biology 52. Edited by the Institute of Biology. — Edward Arnold Ltd. London 1975. 116 pp. Price £ 3.80 (boards); 1.90 (paperback).

The phytoplankton, the most important vegetation in about 73 % of the earth's surface area, is the subject of this book.

Both marine and freshwater phytoplankton are dealt with in the 116 pages. It, however, concentrates mostly on the marine organisms. The title "Phytoplankton" indicates that no attempt has been made to restrict this enormous subject and the impression remains after reading the book. It must, however, be stated that the author has succeeded in giving information on much of the subject "phytoplankton".

The three major chapters deal with the organisms, factors affecting their growth and their succession. Briefer accounts treat buoyancy, interactions with other organisms, biomass, production, pollution and other effects made by man.

In my opinion the chapter on the organisms gives too short an introduction to each of the taxonomic groups of the phytoplankton. It would have been to advantage if the classes had been subdivided into orders as well. The chapter "Factors Affecting Phytoplankton Growth" treats light, temperature and nutrients in a way easy to survey for a beginner in the study of phytoplankton. Part of the chapter takes up the important tool of phytoplankton studies — culture techniques.

The succession of phytoplankton is a subject which has interested many scientists and a great deal of work has been done. General conclusions are very difficult to draw, but those which exist are dealt with in an interesting way.

In the chapter on the buoyancy of phytoplankton aspects of outgrowths on the cell, physiological regulations and the importance of water movement are summarized. Recent authors seem to consider that water movement is the determining factor, which is stated by the author. More stress could have been laid on this.

The book ends up with a short chapter on man-made effects, giving very brief accounts of a number of effects. This part can be looked upon as a stimulus to further reading.

My only objection is the lack of references in the text or at least after each chapter. This I consider necessary in a small book like this covering such an extensive subject.

LARS EDLER

SCHUSTER, RUDOLF M.: The Hepaticae and Anthocerotae of North America East of the Hundredth Meridian. Vol. III. XIV+880 pp. 475 figures. "1974" (in fact published on April 24, 1975). — Columbia University Press, New York and London. Price £ 12.50 (cloth).

The third volume of this work maintains the same high standard of print and illustrations found in the previous two issues (Vols. I, 1966, and II, 1970). These were reviewed in Bot. Notiser 124 (1971) pp. 176—178. The appreciative summary "This work is much more than a flora of North American liverworts, it is a treasure of information in all fields of this topic" may just as aptly be attributed to the present volume.

Vol. III treats a major portion of the order Jungermanniales, i.e., the four families Gymnomitriaceae (primarily, also in Vol. I p. 386, known as Marsupellaceae; the change has been necessary under the Code of Nomenclature), Scapaniaceae, Antheliaceae and Cephaloziaceae and ends with the genus *Odontoschisma*. Particularly the first two have undergone extensive and complex speciation in the Arctic. Dr SCHUSTER has spent four full summers in Ellesmere Island and Greenland; this has given him the unique opportunity to study several critical taxa under very extreme conditions. His discussions on the differentiation within a species are based largely on study of living specimens rather than of herbarium material.

The infraspecific variation and its response to environmental conditions is treated in great detail. In some cases, "phenotypes which are so far out of the normal range exhibited that I assume they represent genetic variants" have been described as forms. The modificative variation has often been recorded with terms like "mod. *colorata, parvifolia, integrifolia*" which have no status under the Code of Nomenclature.

The author has restricted himself to conditions seen in nature. He has not tried to make a "biosystematic" analysis of the variation. Hence it must remain as an open question how the taxonomic characters can be modified under varied climatic conditions (under cultivation) such as light and humidity. Recent research of this kind has shown an unexpectedly high variability within otherwise well-known "species" or "varieties" of bryophytes. Cf., e.g., KAI WIGH, "Studies on the Moss Family Brachytheciaceae with Special Reference to the Genus *Brachythecium*". (Thesis, Department of Plant Taxonomy, University of Gothenburg, 1975).

In his preface Dr SCHUSTER declares that he takes a "conservative" attitude to nomenclature. "Consideration of whether *Scapania nemorosa* should be called *S. nemorea* is a waste of valuable intellectual energy." The critical reader can easily find several cases to discuss. *Gymnomitrion* "Sect. 4. *Corallodes* SCHUST., sect. n." is recorded (p. 147) without a description. In the Index it is met with as "*coralloides.*" *Gymnomitrion* Sect. "*Apiculatae*" should be *Apiculata*, and *Odontoschisma* Sect. "*Denudatae*" should be "*Denudata*" (both neuter plural; cf. Code of Nomenclature, Art. 21). *Odontoschisma* "Sect. *Macouniae*" founded on *O. macounii* is inadmissible under the Code.

In Vol. I (1966) this work was projected to comprise 3 volumes. It is evident that its scope has been changed to some extent during the past ten years. The sequence of families has sometimes been altered when one compares with the classification proposed in Vol. I. As several large groups remain to be treated we may expect one, perhaps two, further volumes in order to complete this monumental treatise.

OVE ALMBORN