Drawings of Scandinavian Plants 50–54

Juncus L.

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Subgen. **Genuini** BUCHENAU 1875

Perennials, moderately tall or up to 2 m high, with a strong rhizome carrying flowering stems and specialized shortshoots with one large, stemlike leaf. Leaves of adult specimens terete, nonseptate, stemlike. Central part of stems and leaves filled with an aerenchymatic medulla of asterisciform cells or more irregular, rounded cells with thin connecting rays. Vascular bundles all situated in the surrounding parenchymatic layer. Lowest bract of inflorescence ± large, forming an apparent prolongation of the stem. Flowers single, though often crowded, each with usually 2 enclosing bracteols. Seeds usually lacking appendages. Chromosomes very small, known basic numbers x = 20, 21.

Subgen. *Genuini* has a worldwide distribution. In Scandinavia it is represented by 6 species. Interspecific hybridization is common and several hybrids show great vegetative vigour. The species and 4 hybrids will be illustrated as nos. 50—59.

50. **Juncus effusus** L. 1753

Perennial, densely caespitose. Stems 50—150 cm, basal sheaths of varying colour, usually reddish brown, the uppermost often with a tiny lamina. Stems and leaves smooth or inconspicuously striate, with 40—70 weak subepidermal sclerenchyma strands not oriented outside the largest vascular bundles. Epidermis uniform. Largest vascular bundles often forming inward projections from the parenchymatic cylinder. Medulla continuous, its cells asterisciform. Lowest bract long, with a narrow sheath, the stem often obviously contracted below the inflorescence. Inflorescence manyflowered, usually lax, rarely compact. Tepals 2—3 mm, ovate to narrowly ovate, acuminate, outer ones slightly longer. Stamens 3 or rarely 4—6, 1/2—3/4 as long as the tepals, anthers equalling the filaments, 0.6—0.8 mm. Style very short, stigmata 0.6—1 mm long. Capsule ovoidal to sphaeroidal, apically trigonous, with an obtuse or usually ± flat top, not or slightly retuse, usually without projection at the style base, usually shorter than the tepals, rarely equalling them or longer. Seeds c. 0.5 mm, obliquely ovoidal, reticulate. 2n = 42.

The above description of the capsule form does not apply to specimens from other areas. In material of E. Mediterranean and Oriental origin the capsule is often retuse and usually has a substylar

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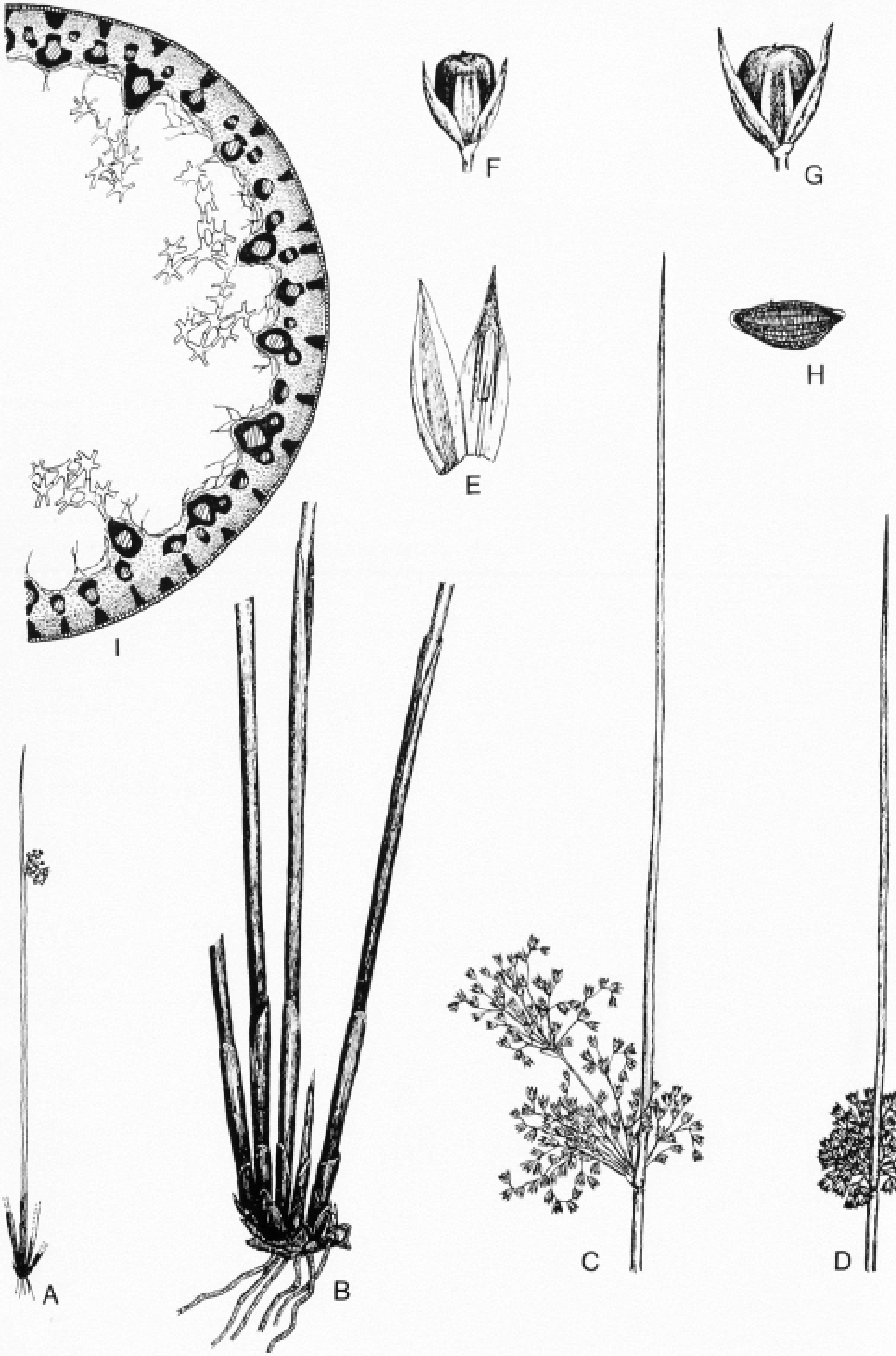
[1] NILSSON is responsible for the drawings and SNOGERUP for the text.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projection. *J. effusus* is a plant of fens, meadows, pastures, and shores, but it usually does not grow in heaths. It is widely distributed throughout Europe, W. and C. Asia, Africa, and temperate N. America, and has also been introduced in many other areas. In Scandinavia it is very common in the southern lowlands up to about 60° N and along the Norwegian coast, with scattered localities up to c. 65° N.

51. **Juncus conglomeratus** L. 1753

Perennial, densely caespitose. Stems 40—100 cm, their basal sheaths of varying colour, usually light brown, ± reddish, the uppermost often with a tiny lamina. Stem below the inflorescence conspicuously longitudinally striate from 12—30 strong subepidermal sclerenchyma strands oriented outside the largest vascular bundles. In thicker parts of stems and leaves more or less conspicuous ridges. Epidermis cells of the ridges enlarged with a thick cuticula. Medulla continuous, its cells asterisciform. Lowest bract long, with a wide sheath. Inflorescence manyflowered, usually compact, rarely composed of several clusters or lax. Tepals (2—) 2.5—4 mm, ovate or narrowly ovate, acuminate, outer ones slightly longer. Stamens 3, rarely 4—6, 1/2—2/3 as long as the tepals, anthers 0.4—0.7 mm, usually shorter than the filaments. Style very short, stigmata 0.6—1 mm long. Capsule ovoidal to sphaeroidal, apically trigonous, obtuse or usually ± markedly retuse, with a conical projection below the style base, shorter to equalling or rarely slightly exceeding the tepals. Seeds c. 0.5 mm long, obliquely ovoidal, reticulate. $2n=42$.

J. conglomeratus occurs in habitats similar to those of *J. effusus*, with which it often occurs together, but it also occurs in poorer fens, in heaths, and in drier grassland. It is also more common than *J. effusus* on open sand and gravel. Its distribution area includes Europe, NW. Africa, W. and SW. Asia and a few localities in N. America. In Scandinavia it extends further north than *J. effusus*, in Finland as far as the northern end of the Bothnian Gulf, and along the Norwegian coast to the Lofoten Islands.

52. **Juncus inflexus** L. 1753

Perennial, densely caespitose. Stems 50—120 cm, their basal sheaths usually chestnut-coloured, glossy, rarely dark brown or reddish. Stems below the inflorescence conspicuously longitudinally striate from 10—20 strong subepidermal sclerenchyma strands oriented outside and often connected to the largest vascular bundles. Also thicker parts of stems and leaves with few and pronounced ridges. Epidermal cells outside the ridges enlarged, with a thick cuticula. Medulla interrupted by empty parts of various length, its cells asterisciform. Lowest bract long, with a narrow sheath. Inflorescence manyflowered, in Scandinavian specimens always lax. Tepals (2.5—) 3—4 mm, narrowly ovate, acuminate, outer ones longer. Stamens 6, about 1/2 as long as tepals, anthers 0.8—1 mm, 1—1.5 times as long as filaments. Style c. 0.5 mm, stigmata 0.8—1.5 mm long. Capsule 3—4 mm, exceeding the tepals, trigono-ovoidal to trigono-ellipsoidal, mucronate, usually dark brown to chestnut, glossy. Seeds c. 0.5 mm, obliquely ovoidal, reticulate. $2n=40$.

J. inflexus grows in fens and meadows, and on wet, open soil. In Scandinavia it is restricted to soils rich in lime. It occurs in Europe, N., E. and S. Africa, and SW. to C. Asia. It has also been found as introduced or causual in most other temperate areas. In Scandinavia it is indige-

Fig. 50. *Juncus effusus* L. — A: Habit, ×0.05. — B: Basal part, ×0.5. — C: Common type of inflorescence, ×0.5. — D: Rare form of inflorescence, ×0.5. — E: Tepals and stamen, ×10. — F—G: Capsules, ×6. — H: Seed, ×25. — I: Transect of stem below inflorescence, ×30.

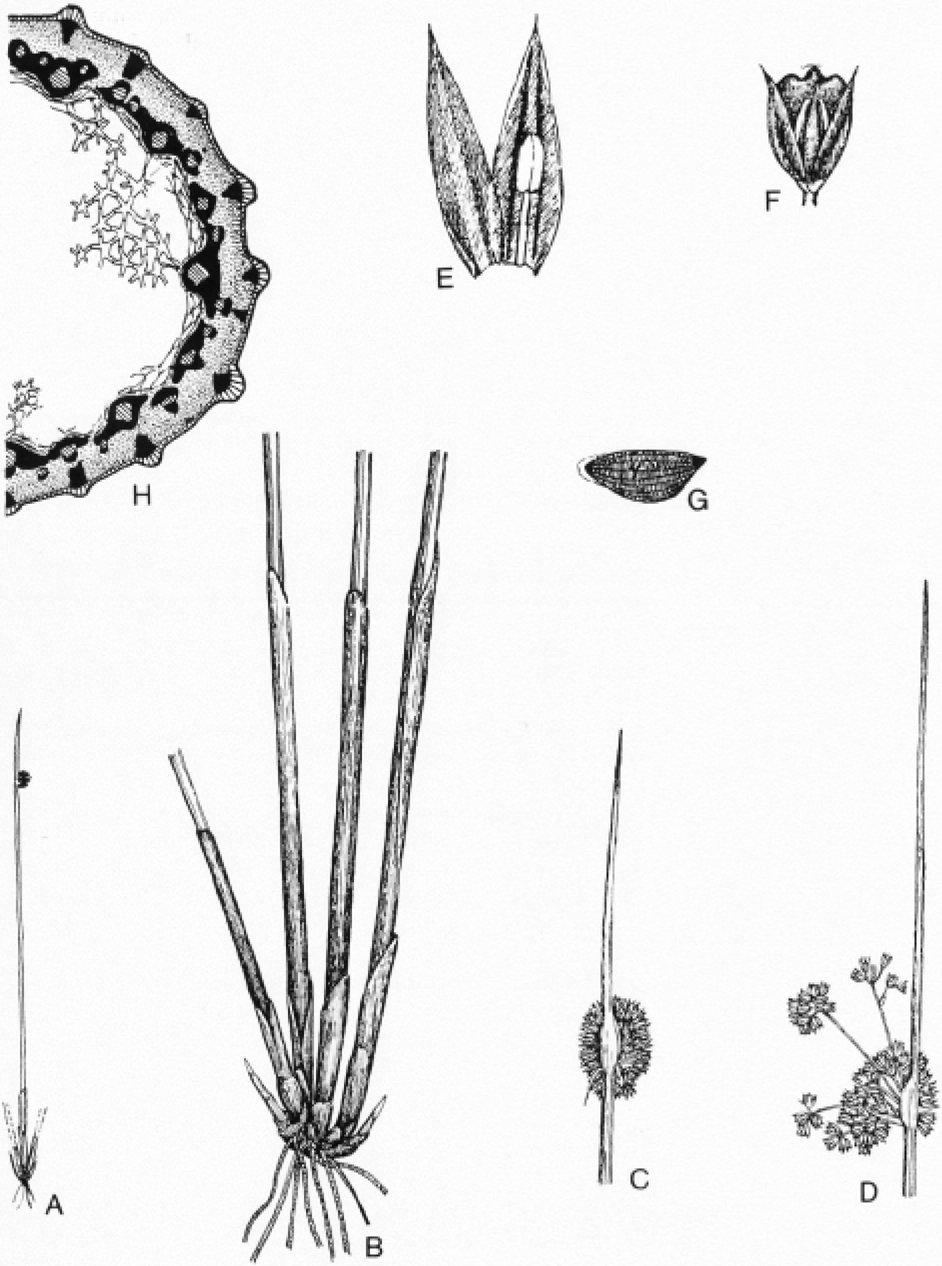

Fig. 51. *Juncus conglomeratus* L. — A: Habit, ×0.05. — B: Basal part, ×0.5. — C: Common type of inflorescence, ×0.5. — D: Rare form of inflorescence, ×0.5. — E: Tepals and stamen, ×10. — F: Capsule, ×6. — G: Seed, ×25. — H: Transect of stem below inflorescence, ×30.

Fig. 52. *Juncus inflexus* L. — A: Habit, ×0.05. — B: Basal part, ×0.5. — C: Inflorescence, ×0.5. — D: Tepals and stamens, ×10. — E: Capsule, ×6. — F: Seeds, ×25. — G: Transect of stem below inflorescence, ×30.

nous only in Denmark, Skåne, Öland and Gotland, but has been introduced in some localities further north.

53. **Juncus effusus** L. × **inflexus** L.

This hybrid is most similar to *J. inflexus* in habit, though usually taller and

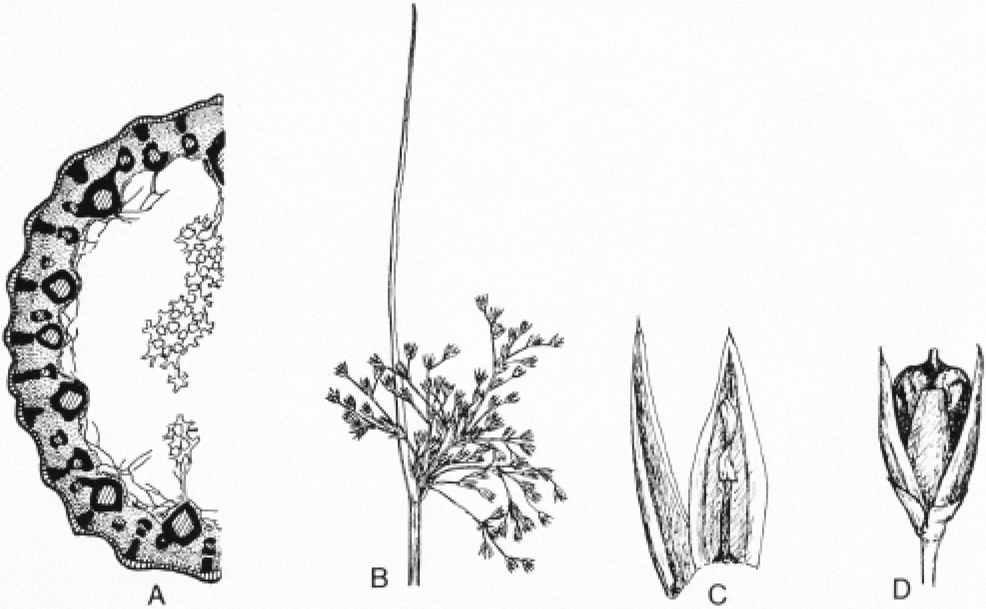

Fig. 53. *Juncus effusus* × *inflexus*. — A: Transect of stem below inflorescence, ×30. — B: Inflorescence, ×0.5. — C: Tepals and stamen, ×10. — D: Capsule, ×6.

more light green. It continues flowering until late autumn, when the parents are already in fruit. The anthers are usually poorly developed. The capsule is very variously developed; usually it degenerates early but in some cases it may be rather well developed, though not producing viable seeds. In stem and leaf anatomy the hybrid is intermediate. The largest subepidermal sclerenchyma strands are rather strong, with ± enlarged epidermis cells outside, but most of them are not oriented outside the largest vascular bundles. These are projecting somewhat inwards like in *J. effusus*. Some smaller bundles are connected outwards like in *J. effusus*.

J. effusus × *inflexus* occurs rather often where the parents meet, and once formed in a locality it persists because of its vegetative vigour. There are, however, many misdeterminations of *J. inflexus*, because the seed setting of this species is often disturbed by fungi or bad weather in the northern part of its area. The stem anatomy is very helpful for the determination in critical cases.

54. **Juncus conglomeratus** L. × **effusus** L.

This hybrid is usually most similar to *J. conglomeratus* in its inflorescence and capsule form, but in the stem anatomy it usually resembles *J. effusus* by a comparatively uniform epidermis and vascular bundles projecting inwards. Many of the largest sclerenchyma strands are, however, oriented as in *J. conglomeratus* and have a somewhat thickened cuticula outside. This hybrid seems to be ± completely seed sterile; the capsules are developed but only rarely contain seeds.

J. conglomeratus × *effusus* is very rare in Scandinavia. I have seen material only from a few localities in Skåne. The scarcity of the hybrid may partly depend on

Fig. 54. *Juncus conglomeratus* × *effusus*. — A: Transect of stem below inflorescence, ×30. — B—C: Inflorescences, ×0.5. — D: Tepals and stamen, ×10. — E: Capsule, ×6.

the fact that the flowering times of the parental species do only partly overlap in most localities. *J. conglomeratus* starts flowering earlier than *J. effusus*. In contradiction to these observations there are reports from Czechoslovakia by Křísa (1962) and from Britain by Agnew (1968), who state the hybrid to be both more common and more fertile. Křísa even maintains that there is so much introgression that the specific distinction between *J. effusus* and *J. conglomeratus* is obscured. My own studies of continental herbarium material have, however, given quite contradictory results on that point. I think the material can without difficulty be identified to the species in almost 100 % of the cases. Yet there may be differences in interfertility between different populations of the parental species, and their flowering times may also coincide to a greater extent in some localities. Further studies, preferably crossing experiments, are needed.

LITERATURE CITED

AGNEW, A. D. Q. 1968. The interspecific relationships of Juncus effusus and J. conglomeratus in Britain. — Watsonia 6: 377—388.

KŘÍSA, B. 1962. Relations of the ecologico-phenological observations to the taxonomy of the species Juncus effusus L. s. l. — Preslia 34: 114—126.

Studies in Montia L., Claytonia L. and Allied Genera VI

The Genera Limnalsine Rydb. and Maxia Ö. Nilss.

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ABSTRACT

Nilsson, Ö. 1971. Studies in Montia L., Claytonia L. and allied genera VI. The genera Limnalsine Rydb. and Maxia Ö. Nilss. — Bot. Notiser 124: 187—207.*

The genera *Limnalsine* Rydb. and *Maxia* Ö. Nilss. (subfam. Montioideae, Portulacaceae) are circumscribed and their relations to allied genera discussed. On account of floral and inflorescence characters and pollen morphology the two genera are placed in the *Montia* group of the subfamily. Their relations to remaining genera of the group are uncertain. The two genera are monotypic.

Limnalsine diffusa (Nutt.) Rydb. is a moderate-sized, annual herb characterized by the petiolate, ovate to cordate leaves. The inflorescence is pedunculate with an elongate common axis and normally one bract at the lowest flower. The involucre is shorter than the tepals but equalling the capsule. The seeds are not keeled and have a long, tap-shaped strophiole. Particular attention has been paid to branching habit, leaf morphology and anatomy, and seeds and dispersal. The relation of *L. diffusa* to the annual *Montiastrum* species is discussed. It grows in woods and some of its characteristics seem to be correlated with its ecology.

Maxia howellii (S. Wats.) Ö. Nilss. is a dwarfish, annual herb with decumbent stems and branches. The flowers are very reduced and the involucre is longer than the tepals. The inflorescence is fasciculate and has been interpreted as a reduced scorpioid cyme that lacks peduncle and common axis. The stamens are usually three. The seeds are keeled and the strophiole is very minute. The deviating branching habit and the reduction of inflorescence and flowers are discussed with regard to the predominant autogamy of the species. The species is compared to the annual *Montia* species and their relations are considered. *Maxia howellii* grows in open, moist habitats.

Limnalsine and *Maxia* are sympatric and occur in a narrow, humid zone along the Pacific coast of North America from Southern British Columbia to Northern California. The two species are little variable.

INTRODUCTION

This paper is a contribution to the author's series on the taxonomy of the *Montia*—*Claytonia* complex in the subfamily Montioideae sensu Pax & Hoffmann (1934) of Portulacaceae (Nilsson 1967, 1970, 1971). The complex was divided into two groups by Nilsson (1970 p. 120), the *Montia* and the *Claytonia* groups. The genera *Limnalsine* and *Maxia* are placed in the former group because of some common characters in inflorescences, flowers, stem and leaf anatomy, and pollen grains. The two genera are monotypic. *Limnalsine* was established by Rydberg (1932) and *Maxia* by Nilsson (1967). The author has favoured a splitting of the *Montia* group into eight genera which constitute natural units with defined circumscriptions. The splitting may seem far-reaching, but is a

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natural way to bring order to the taxonomy of the complex and elucidate its evolution.

Although distinct, *Limnalsine* and *Maxia* have connections to the remaining genera of the group, but the relationships are uncertain. Some indications point to an affinity between *Maxia* and *Montia,* and there are also a few which show a connection between *Maxia* and *Limnalsine*.

The two genera are sympatric with a distribution in the Pacific States of North America. Their distribution falls somewhat outside that of other North American genera of the group, and it seems reasonable to assume that this isolation has contributed to their present distinctness. *Limnalsine* and *Maxia* have different ecology and many of their characteristics seem to be correlated with this.

MATERIAL AND METHODS

Only herbarium material has been available for this study. Material from the following herbaria has been studied: BM, CAN, E*, F, GB, GH*, JEPS*, K*, LA*, MO, NY*, ORE*, OSC*, S*, UBC*, UC, V*, WS*, WTU* (in herbaria marked with * the entire *Limnalsine* and *Maxia* material has been examined; the abbreviations follow Index Herbariorum, Ed. 5, 1964). Experience from investigations on living material of related genera is considered.

Anatomical and palynological preparations have been made from herbarium specimens. Some pollen preparations according to the acetolysis method were made at the Palynological Laboratory, Solna, Sweden.

Some illustrations of organ details are camera lucida drawings made from preparations in which the vascular system was stained with safranin. The surrounding tissue was usually made transparent with lactic acid. Dry material was soaked in water before the treatment. Some illustrations, e.g., those of branching habit and inflorescences are diagrammatic. The maps are based on herbarium material only.

KEY TO THE GENERA

1. Leaf blade ovate to cordate, distinctly petiolate, flat and thin, basal leaves rosulate. Inflorescence with axis and peduncle. Involucre shorter than the tepals. Stamens five Style longer than the ovary. Seeds not keeled, with a long, tap-shaped strophiole .... 1. *Limnalsine* p. 188
2. Leaves linear to linear-spathulate, not distinctly petiolate. Inflorescence without axis and peduncle. Involucre longer than the tepals. Stamens usually three. Style branches almost sessile. Seeds keeled with a minute, not protruding strophiole .... 2. *Maxia* p. 198

1. LIMNALSINE Rydberg, N. American Flora 21 (4): 295 (1932).

Claytonia L. § *Naiocrene* Torrey & Gray 1838 pp. 201—202 p.p.; *Claytonia* § *Limnia* **** *Montiastrum* Gray 1887 pp. 280—283 p.p.; *Claytonia* sect. *Montiopsis* v. Poellnitz 1932 p. 281.

Montia L. p.p. in Greene 1891 p. 181; *Montia* [sect.] *Montiastrum* (Gray) Robinson in Gray 1897 p. 276 p.p.; *Montia* sect. *Limnalsine* (Rydb.) Pax & Hoffmann 1934 p. 259; ditto sensu Swanson 1966 p. 232.

The genus is monotypic; for description, see under the species.

Type species: *Limnalsine diffusa* (Nutt.) Rydb. (cf. Rydberg l.c.).

Limnalsine diffusa (Nutt.) Rydberg, N. American Flora 21 (4): 295 (1932).

Claytonia diffusa Nuttall in Torrey & Gray 1838 p. 202; *Montia diffusa* (Nutt.) Greene 1891 p. 181.

[Non *Claytonia diffusa* (Gill.) O. Kuntze 1891 p. 57 = *Calandrinia diffusa* Gill.].

ORIGINAL COLLECTION: [USA, Washington] Oregon (Nuttall; K lectotype, isotypes in NY and probably in GH, K; cf. Piper 1906 p. 251; "Type locality: In pine woods, a few miles above Fort Vancouver. Collected by Nuttall.")

Some specimens of the original collection are labelled "Oregon, woods" (GH, K, NY). Nuttall was probably irresolute about the name of this species. The specimens from GH and K were called *Claytonia* * *procumbens.* This name was deleted in the NY specimen and replaced by *diffusa*. In the lectotype only the name *C. diffusa* is given.

Annual, glabrous, small to moderate-sized herb. Primary root rather thin, persistent with fibrous, lateral branches (Fig. 1 A). *Stem* almost terete, ± sappy, sometimes (in sunny sites) turning reddish, 4—24 cm high (usually 8—15 cm), 0.8—3.5 mm thick, erect to ascending, usually much branched, branches ascending or diffusely spreading, main stem often not distinct (Figs. 1 A; 2 A); basal internodes very short, up to c. 3 mm, upper internodes 1—8 cm long (usually 2—5 cm). *Leaves* simple, entire, usually numerous on flowering plants, alternate, at the stem-base in a many-leaved rosette persistent till anthesis, flat and thin, distinctly petiolate; leaf-base slightly dilated and somewhat clasping; petioles flattened, often narrowly winged and sometimes triple-ribbed almost to the base (Fig. 3 A); blade with a reticulate veining and a distinct, often dark hydathode at the apex; rosette-leaves 1.5—7 cm long (usually 3—5.5 cm), petiole somewhat longer than the blade (usually 1.1—1.7 times longer), 0.8—4.3 cm long, blade 0.6—3.5 cm long and 0.5—2.7 cm broad, broadly ovate to almost cordate, base truncate to subcordate, apex ± obtuse; cauline leaves 0.8—6.5 cm long, in succession smaller upwards, petiole of upper leaves usually somewhat shorter than the blade, blade 0.5—3.0 cm long and 0.3—2.2 cm broad, cordate to ovate or broadly lanceolate, with a subcordate, truncate or cuneate base, sometimes with unequal lobes, apex acute to subacute (Fig. 1 C). *Stomata* very numerous on both sides of the leaf, irregularly spaced, slightly sunken on the adaxial side; subsidiary cells lacking; guard cells with distinct outer and inner ledges, the inner minute (Fig. 1 D); leaf epidermis very thin, cells rounded to oblong with ± undulating side walls, cuticle thin and smooth. *Inflorescences* usually several, 7—45 (occasionally 3 or up to 140) per plant, pseudolateral or very occasionally terminal scorpioid cymes, axis normally elongate (Fig. 3 A), 0.5—2.5 cm, sometimes with one or few internodes not developing (Fig. 3 B—G); flowers 2—10 (usually 4—7) per inflorescence, usually one in anthesis per day, homogamic, allogamous or autogamous. *Peduncle* ± erect, elongate, 0.7—3.6 cm (usually 1.5—2.5 cm). *Bract* normally one, opposite the lowest pedicel (sometimes one or two additional), 3.0—8.0 mm long, 1.8—3.8 mm broad (usually 3.5—5 ×2.2—3.0 mm), usually ovate, half-clasping at the base, acute to obtuse and sometimes apiculate, green and papery, sometimes with very narrow, white margins towards the top (Fig. 1 B). *Pedicels* erect and 0.3—0.7 cm long at anthesis, after anthesis usually sharply reflexed from the base, growing up to 0.9—1.8 cm, erect at maturity. *Involucral leaves* two, opposite, almost equal or the outer slightly longer than the inner, the outer laterally clasping the inner at least at the base, very thin, persistent, broadly obovate, truncate or often obtuse and apiculate, at anthesis 1.8—2.4 mm long, after anthesis growing to 2.1—3.6 mm long (usually 3.0—3.5 mm), and 2.3—3.2 mm broad, usually as long as the capsule or slightly shorter, green with a very narrow white margin (Fig. 2 B, C). *Tepals* five, almost equal in size and shape, obovate to broadly oblong, 3.3—4.5 mm long, 1.5—2.2 mm broad, usually twice as long as the involucre, ascending at anthesis, obtuse to truncate or slightly emarginate, usually distinctly petiolate, petiole 0.5—1.0 mm, all at the base laterally shortly connate in a length of 0.1—0.2 mm, pink to almost white; veins in the tepal blade undulating; tepals often persistent (Fig. 2 D). *Stamens* five, equal, opposite the tepals, 2.4—3.3 mm long, about 3/5 of the tepal length, free from each other but filaments dilated at the base and adnate to the tepal for 0.4—0.7 mm; anther 0.3—0.5 mm long and 0.3—0.5 mm broad, ovoid to globose, medifixed, not versatile, laterorse, white to yellowish (Fig. 2 D). *Ovary* obovoid, 0.7—1.0 mm long, 0.4—0.7 mm broad, with three ovules. *Style* about twice as long as the ovary, 1.9—2.2 mm, sharply set off from the ovary and falling off from a distinct point after anthesis. *Style branches* three, comparatively long, 1.0—1.3 mm, slightly diverging at anthesis, with very closely set, long papillae on the adaxial face (Fig. 2 E). *Capsule* obovoid or sometimes pear-shaped, with a distinct apical point formed by the style base, somewhat triangular, 2.3—3.0 mm long, 1.8—2.2 mm broad, slightly trisulcate at the base (Fig. 2 F). *Seeds* obovate, somewhat flattened, 1.3—1.5 mm long, 1.0—1.2 mm broad, 0.5—0.7 mm thick, not keeled, attachment plate in a depression; strophiole comparatively large, protruding, tap-shaped, 0.3—0.5 mm long, white; testa slightly colliculate to almost smooth, with distinct cells in regular, concentric rows, black, dull to somewhat glittering (Fig. 2 G). *Pollen grains* spherical, 42—44 µ in diameter, pantocolpate, usually with 21—24 colpi, 10—12 µ long; sexine tectate, with sparsely set small spinulae, punctate or scrobiculate, yellowish white (cf. NILSSON 1967 p. 352).

HISTORICAL SURVEY

Claytonia diffusa was described by NUTTALL (in TORREY & GRAY 1838 pp. 201—202), and the species was together with some others placed in the "section" *Naiocrene*. After the description NUTTALL added, "A very remarkable species with much of the habit and appearance of *Stellaria media*, except that the leaves are alternate." In 1887 GRAY transferred *C. diffusa* to the "section" *Montiastrum* (HOLM 1913), where it was placed together with *C. linearis* and *C. dichotoma* (cf. NILSSON 1971 p. 90). In 1932 v. POELLNITZ established the new, monotypic section *Montiopsis* for *C. diffusa*. GREENE (1891 p. 181) transferred the species to the genus *Montia*. The new genus *Limnalsine*, with the one species *L. diffusa*, was established by RYDBERG in 1932. His generic concept has been followed here.

PAX & HOFFMANN (1934 p. 259) and later SWANSON (1966 p. 232) applied the name *Limnalsine* for the section of *Montia* in which they placed *M. diffusa*. However, this is inadmissible because of the older section name *Montiopsis* (see above), which ought to have been adopted according to the 'International Code' Art. 54.

STEM AND BRANCHING HABIT

The development of the main shoot is slow or suppressed in the autumn which results in short basal internodes and crowded leaves. At the nodes in this rosette some lateral branches develop, the number depends on the stature of the plant. In the next spring the main shoot and the lateral branches grow rapidly and the internodes become very elongate. In this stage further branching is sparse. The main stem turns erect and the branches become ascending to erect. The main stem and the branches often have the same size and thus the position of the main stem is often obscure. The branching is not restricted to any specific part of the plant although it is sparse towards the base and often very rich in the inflorescence region. Lateral branches may develop at every node (Fig. 2 A).

The branching is usually very regular and follows a system diagrammatically illustrated in Fig. 2 A. The system has a pseudodichotomous appearance, and several similarities to that of *Montiastrum dichotomum* (NILSSON 1971 p. 95). A regu-

Fig. 1. *Limnalsine diffusa*. — A: Habit, * marks the first inflorescence of the main stem, o marks accessory shoots. — B: Four bracts, showing variation. — C: Leaf series (not complete), the left leaf from the rosette, the remainder in succession from the base to the top of a branch. — D: Leaf epidermis with stomata, from adaxial side. — E: Stem stele in cross-section, simplified, somewhat above the middle of an internode, at the node above one inflorescence, one leaf and an accessory shoot; 1) endodermis, 2) xylem, 3) hollow of pith, 4) cells with thickened walls. — F: Stem epidermis in cross-section.

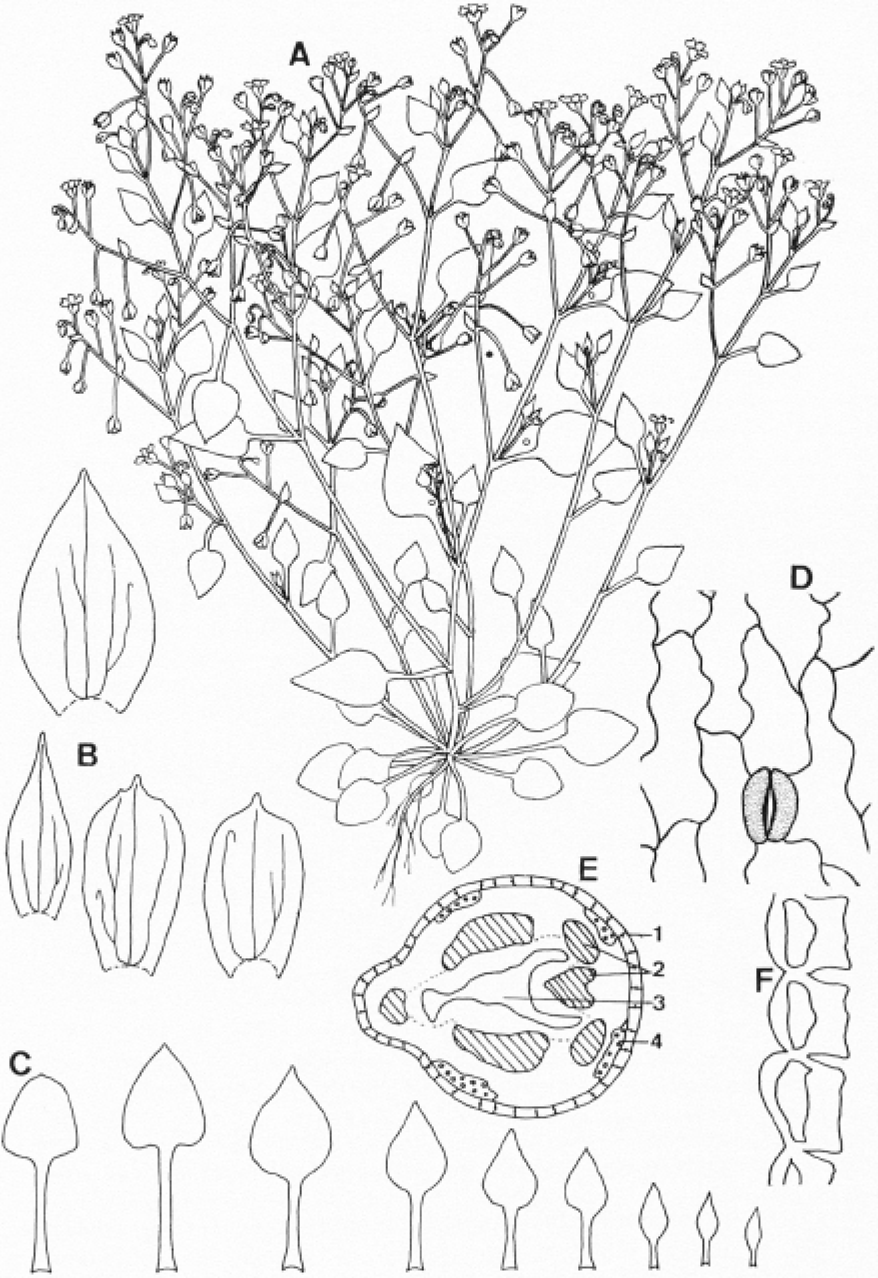

Fig. 1.

lar feature in the branching is that the internode of the primary shoot is shorter than that of the lateral branch, often only half as long.

Each shoot is terminated by an inflorescence (HOLM 1913 p. 8) and the growth is continued by lateral branches in a sympodial manner. In the sympodium the inflorescences have a pseudolateral position and develop successively with one at each node arranged in a 2/5 spiral. The growth of the sympodium continues in such a way that true terminal inflorescences are very rare and appear only when the growth of the plant ceases and further lateral branches fail to develop.

The plants often become very richly branched and numerous inflorescences develop. The branching is sometimes further increased by means of accessory shoots. These develop in or usually below the inflorescence region, and are axillary. Often they are somewhat weaker than the ordinary shoot, but inflorescence-bearing. There is never more than one accessory shoot at each node. In the inflorescence region the branching is restricted to the system described above and accessory shoots seem to be the only way to increase the branching and the number of inflorescences beyond the initial limit. Accessory shoots are rare in the group, and *Limnalsine diffusa* is the only species in which they are commonly occurring.

SWANSON (1966 p. 230) illustrates the branching habit of *Limnalsine*, but some features of the diagram show that it has been misinterpreted.

The stem anatomy of *L. diffusa* has some deviating features but is in general similar to that of other genera of the *Montia* group. The epidermis cells are longitudinally elongate and are characterized by their thickened inner wall. The stomata are sparse. The cuticle is very thick and particularly thickened laterally, and its surface is smooth (Fig. 1 F). The cortex is comparatively thick, sappy, open and assimilatory, and consists of large, in cross-section rounded cells. The endodermis is rather distinct but with hardly discernable Casparian dots. Near the stem base the xylem usually forms a continuous ring in cross-section, but in the inflorescence region it is split up into separate elements by several gaps. There is a wide leaf gap and three almost equal vascular bundles of the leaf trace. The pith is usually widely hollow. A characteristic of the stele is the poorly developed thick-walled, fibre-like cells (pericycle) inside the endodermis. Sometimes they are completely lacking but usually they occur in some small, scattered groups (Fig. 1 E).

LEAVES

The leaves of *L. diffusa* alternate in a 2/5 spiral. The plant is a winter annual which hibernates as a hemicryptophyte in a rosulate stage, and at least some of the rosette leaves persist until flowering. The leaves of different parts of the plant vary in size and shape. A leaf series is shown in Fig. 1 C (some leaves omitted).

The veining of the blade can be characterized as reticulate. The midvein ends near the leaf apex in a very distinct, more or less swollen hydathode that darkens on dry specimens.

The nature of the petiole is somewhat uncertain. Usually it has three distinct veins from the base and is flattened and often somewhat winged. The leaf base is only slightly dilated and is not sheathing as in most other genera of the group (SWANSON 1966 p. 232). The vascular bundles to the leaf are usually free almost from the next lower node and marked on the stem as a usually distinct ridge below the leaf. Thus it seems that the petiole consists of a free part and a part coalescent with the stem (Fig. 3 A).

The epidermis is very thin. The cells have more or less strongly undulating side walls and are variable in size and shape. The cuticle is thin and smooth. On the blade the stomata are irregularly spaced but on the petiole they often occur in distinct rows. The mesophyll is differentiated

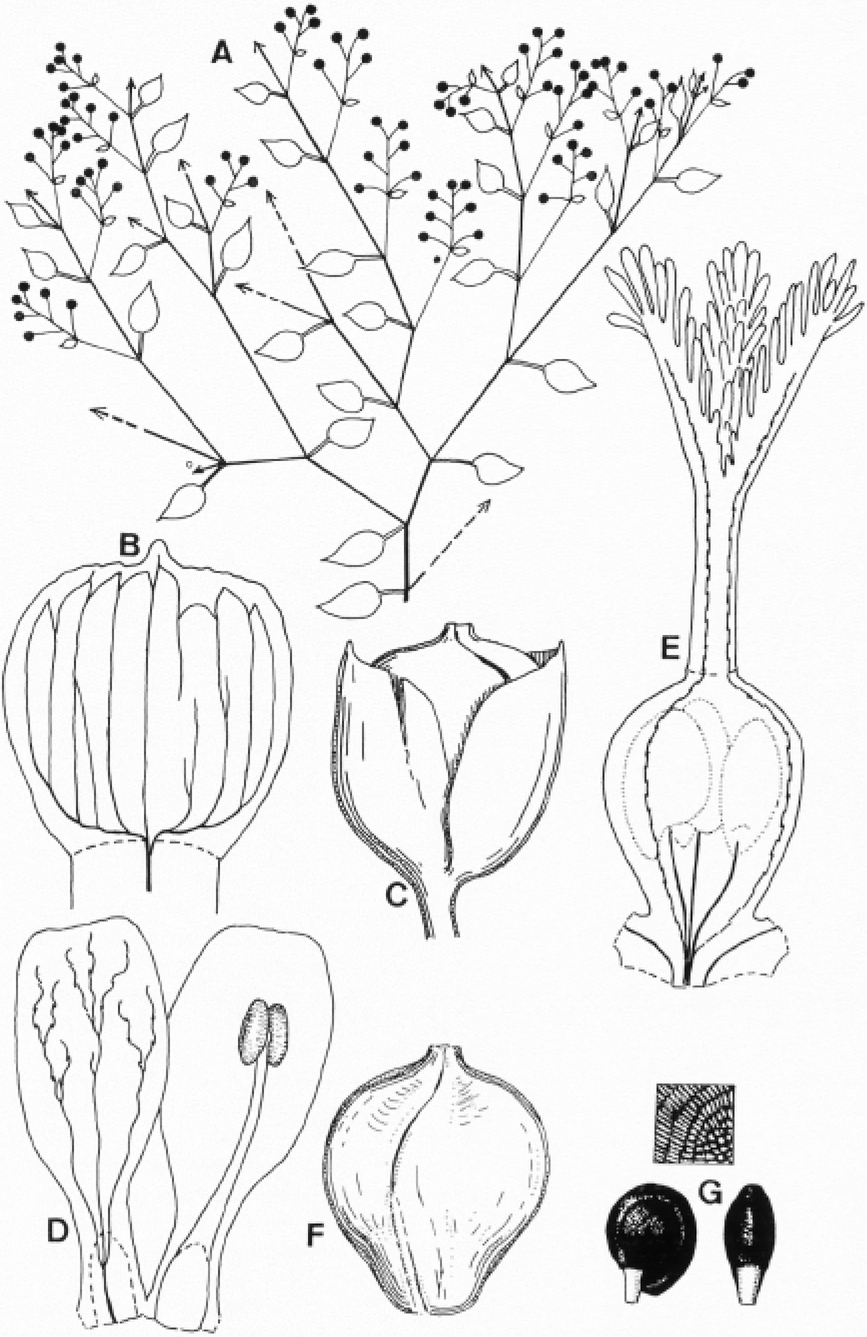

Fig. 2. *Limnalsine diffusa.* — A: Diagrammatic drawing of a part of a plant, showing the type of branching, broken lines indicate omitted branches, arrows lateral shoots, * and o see Fig. 1 A. — B: Outer involucral leaf. — C: Involucre and capsule. — D: Part of the perianth with stamen. — E: Pistil. — F: Capsule. — G: Seeds, the left in lateral view, and a part of the testa in the square.

in a rather compact, adaxial palisade parenchyma and a lower, very open, spongy parenchyma. No mechanical tissue occurs in the very thin leaves.

L. diffusa grows in woods, and several features of the leaf, e.g., shape, horizontal direction, texture, and anatomy, seem to have evolved as adaptations for a life in the shade. Occasionally plants grow, e.g., in wood clearings; such plants are generally more small-leaved and often turn reddish.

INFLORESCENCES

The number of inflorescences varies with the development of the plant. In the upper part of the plant there is usually one inflorescence at every node (Fig. 2 A). Normally a lateral branch opposite the inflorescence continues the growth of the shoot. The first inflorescence of the main shoot flowers simultanously with the lower ones of the lateral branches.

The inflorescence is a several-flowered scorpioid cyme of the type that prevails in in the *Montia* group. It is always pedunculate and the peduncle spreads opposite a leaf (Fig. 3 A). In bud the inflorescence is apically coiled, but becomes straight and ascending to erect at anthesis. Opposite the base of the lowest pedicel there is a thin, green and papery bract, resembling the leaves in texture. The bract is usually 3-nerved, but the nerves are not always distinct; its shape varies (Fig. 1 B). According to Holm (1913 p. 8), the bract has the same shape as the ordinary leaves which is a much misleading statement.

Fig. 3 B illustrates diagrammatically the usual type of inflorescence of *L. diffusa*. However, some divergent types (Fig. 3 C—G) occur and additional bracts are rather common particularly in the terminal part of the inflorescence. Sometimes one or a few internodes of the common axis (especially the basal) do not develop or occasionally all fail to develop (Fig. 3 D). Similar divergences occur in *Crunocallis* (Nilsson 1970 pp. 134—135) and *Montiastrum* (Nilsson 1971 p. 107).

The involucre equals the capsule in length and is many-ribbed (Fig. 2 B, C). It is very thin and perishable (often ruptured in dry material) and not as persistent as in other genera of the group.

FLOWERS AND POLLINATION

Anthesis occurs in one or very rarely two flowers per inflorescence per day. At anthesis the pedicel is erect and thus the flower is directed upwards. After anthesis the pedicel reflexes, usually sharply, from the base and elongates, and at maturity it is again erect.

The flowers are up to about 4.5 mm in diameter and pink to almost white. Their individual attraction value seems almost insignificant, but on the same plant there are usually several flowers in anthesis simultaneously, which may increase the attraction. Very minute nectaries occur at the ovary base. After fading, the tepals are often persistent, sometimes till maturity.

The five stamens are all perfect; no flowers with three stamens seem to occur. The filaments are ascending at anthesis and do not curve inwards. In five examined flowers there was an average pollen production of 320 grains. The divergence of the style branches takes place simultaneously with the dehiscence of the anthers. In the expanded flower the anthers do not come in contact with the stigmas.

Morphologically, the flower of *L. diffusa* belongs to the allogamous type described by Nilsson (1971 p. 110). However, the flowers have some characteristics which do not fit entirely with that type, e.g., their small size, the non-versatile anthers, and the homogamy. In these features the flower forms a transition to the autogamous type. No cleistogamous flowers occur, but bud-pollination seems to be rather frequent which is indicated by the anthers which often dehisce in the bud and by the fact that almost all examined open flowers were pollinated. The nearly always perfect seed set also shows that autogamy must prevail. Only in a few cap-

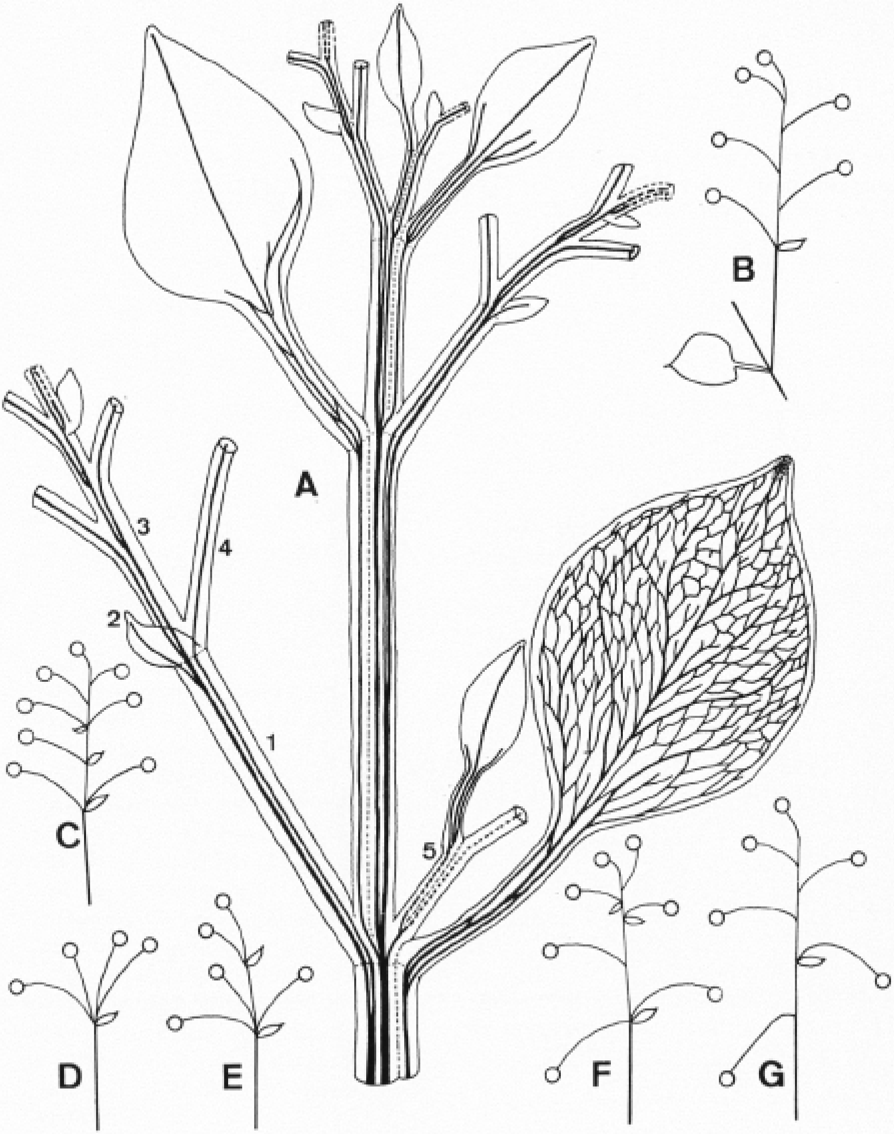

Fig. 3. *Limnalsine diffusa.* — A: Part of stem, inflorescences, and leaves, showing branching and vascular system, 1) peduncle, 2) bract, 3) axis, 4) pedicel, 5) accessory shoot (somewhat simplified). — B—G: Inflorescences, highly simplified, showing variation. — B: The normal type. — C: Additional bracts. — D: Reduction of the axis. — E—F: Reduction of some internodes of the axis and additional bracts. — G: Bract in coalescence with the axis over one internode.

sules less than three seeds were found. Although self-pollination seems to be predominant, cross-pollination very probably occurs, but its extent must be determined by field studies and experiments.

The pollen morphological relations between *Limnalsine* and *Montiastrum* were discussed by NILSSON (1971 p. 111).

SEEDS, DISPERSAL AND REPRODUCTION

The most conspicuous feature of the seed is the long, protruding, white and tap-shaped strophiole (cf. below). The testa is usually dull and its cells are distinct and vaulted. Those of the central parts are rounded while the lateral ones are somewhat elongate (Fig. 2 G). The cell surface is provided with minute processes. The cotyledons have an oblique position in the seed.

In the ovary there are three almost complete septa which may be persistent almost until flowering. Fragments of them often remain as a small tap at the top of the valves. In other genera of the *Montia* group the septa decline very early in ontogeny and no fragments remain at maturity.

The capsule opens with three valves which split to the top of the capsule grooves. In *Limnalsine* the valves are never as strongly reflexed and involute as in the other genera in the group (NILSSON 1971 p. 113). The lignified elements in the epidermis cell walls of the valves are slender and the epidermis is comparatively thin. The active seed dispersal mechanism is of the same type as in the rest of the group, but seems less effective.

L. diffusa is the only forest plant of the *Montia* group, and like other such spring-blooming plants its seeds are provided with a large strophiole. Ants often play an important rôle in the dispersal of such seeds. It is possible that *L. diffusa* is myrmechorous too, which may compensate for the reduced function of its own dispersal mechanism. Some *Claytonia* species are also forest plants, and they have almost as large a strophiole as *Limnalsine*.

Well-developed specimens of *L. diffusa* have a very large seed production per plant, the largest in the *Montia* group. An ordinary plant may produce about 600—700 seeds annually; in an exceptionally well developed plant the number was c. 2500. In spite of this large seed production the species never seems to be abundant in its natural habitats. Its ecological demands are probably very special. "Only a few individuals" is an often occurring note on the labels.

The collections of this species usually consist of a few specimens only, and thus it is difficult to determine the variation within the populations. However, a few collections are rich and morphologically very homogeneous.

VARIATION AND RELATIONS

L. diffusa is a rather uniform species; most of the variation in the material seems to be modificative and concerns mainly plant size. However, some genetic variation occurs, which is indicated by some differences between the collections, e.g., in leaf shape and flower colour. A few collections, e.g. SHARSMITH 4858 and ROSE 42068 (cf. Appendix), are characterized by rather deep pink flowers, whereas they are white in most other collections. The local populations seem to be uniform.

Limnalsine and the annual *Montiastrum* species have some characters in common. The resemblance in the branching habit is of particular interest. Both also have alternating leaves and similar inflorescences. *Limnalsine* differs from the annual *Montiastrum* species in the following characters: leaf shape and anatomy, stomata lacking subsidiary cells, postanthesial pedicel direction, involucre shape, size and texture, 5-staminate flowers, and morphology of seeds and pollen grains.

The difference between the two genera is more obvious if the perennial *Montiastrum* species are included in the com-

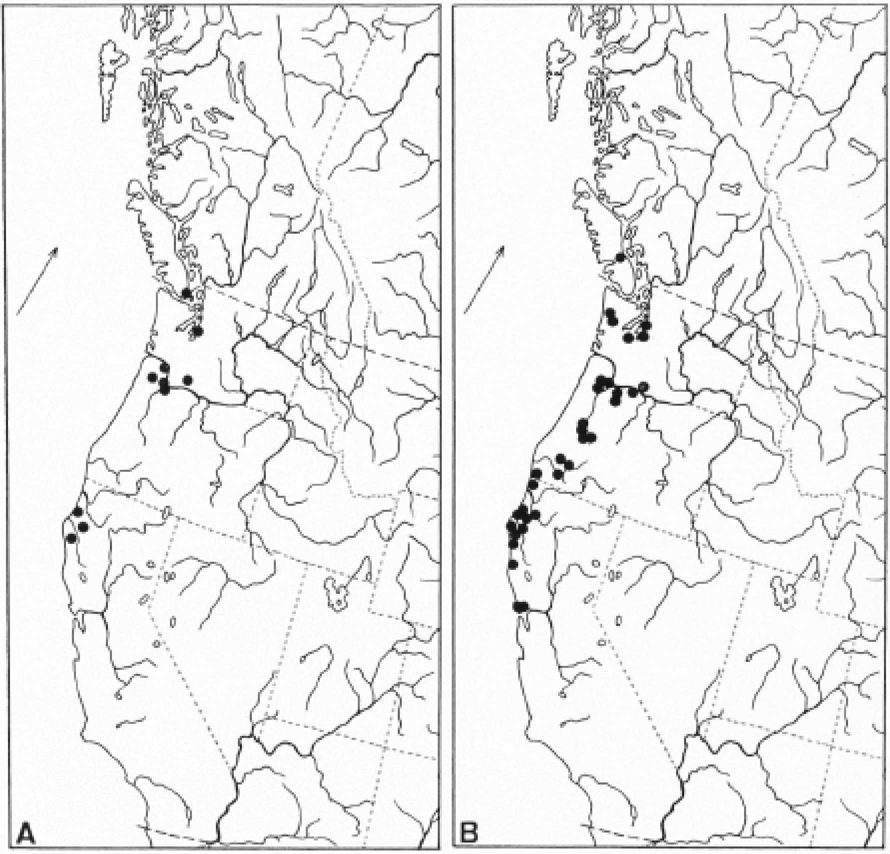

Fig. 4. The distribution in western North America of A: *Maxia howellii*, and B: *Limnalsine diffusa*.

parison. The above characters and others give the genus *Limnalsine* a very distinct and natural circumscription. Some of the most conspicuous external chareceristics seem to be correlated with its deviating ecology. A few characters in leaf anatomy and seed morphology and the similar distribution may indicate an affinity between *Limnalsine* and *Maxia*. The other genera of the group, e.g., *Montia, Naiocrene, Neopaxia,* and *Mona* are more deviating.

DISTRIBUTION AND HABITAT

Limnalsine diffusa occurs along the Pacific Coast of North America from Vancouver Island to San Francisco Bay. The distribution covers mainly the Coast Ranges and the western slopes of the Cascades. The species is restricted to a rather narrow area along the coast and reaches its easternmost localities in the valley of the lower Columbia River. The distribution is almost continuous and centres in northern California in the counties of Humboldt, Mendocino and Del Norte. The species occurs in the following states: California, Oregon, and Washington in USA and British Columbia in Canada (cf. RYDBERG 1932 p. 295, ABRAMS 1964 p. 124, HITCHCOCK et al. 1964 p. 239; Appendix and Fig. 4 B).

Maxia has a similar but more restricted distribution and seems to have a more northern centre (cf. p. 205 and Fig. 4 A). *Limnalsine diffusa* is a rather rare species and recent collections are sparse. It occurs in the Humid Transition to Transition Zones from near sea level to an elevation of c. 1000 m.

L. diffusa is a forest plant, occurring mainly in shady places in moist and cool coniferous woods, often with Douglas fir and redwood. More occasionally it has been collected in open sites, e.g., cut or burnt places in the woods. In northern California the species may occur in the shade of, e.g., *Pseudotsuga menziesii, Umbellularia californica, Alnus* spp., *Cornus* spp., *Fraxinus oregona, Quercus chrysolepsis, Sambucus* spp., and *Sequoia sempervirens.* SWANSON (1966 p. 239) supposed that the species was more widely distributed in the late tertiary, when the coastal coniferous forests were more extensive in western United States.

FLOWERING PERIOD: (April—) May to July.

2. MAXIA Ö. NILSSON, Grana Palynol. 7 (2): 359—360 (1967).

Montia L. p.p. sensu S. WATSON 1882 p. 191; *Montia* [sect.] *Montiastrum* (GRAY) ROBINSON in GRAY 1897 p. 276 p.p.; *Montia* sect. *Montiastrum* (GRAY) PAX & HOFFMANN 1934 p. 259 p.p.; *Montia* sect. *Montia* sensu SWANSON 1966 p. 232 p.p.

Claytonia § *Limnia* **** *Montiastrum* GRAY 1887 p. 283 p.p.; *Claytonia* L. p.p. sensu PIPER 1906 p. 251; *Claytonia* sect. *Pseudo-Claytonia* v. POELLNITZ 1932 pp. 281—282 p.p.

Montiastrum (GRAY) RYDB. p.p. in RYDBERG 1932 pp. 295—296.

The genus is monotypic; for description, see under the species.

Type species: *Maxia howellii* (S. WATS.) Ö. NILSS. (cf. NILSSON 1967 l.c.).

Maxia howellii (S. WATS.) Ö. NILSSON, Grana Palynol. 7 (2): 360 (1967).

Montia Howellii S. WATSON 1882 pp. 191—192; *Claytonia dichotoma* NUTT. p.p. in GRAY 1887 p. 284; *Claytonia Howellii* (S. WATS.) PIPER 1906 p. 251; *Montiastrum Howellii* (S. WATS.) RYDBERG 1932 p. 296.

ORIGINAL COLLECTION: [USA] Oregon, Sauvie's Island, May 1883, J. & T. J. HOWELL (K lectotype; cf. PIPER 1906 p. 251; "Type locality: On Sauvies Island, in the Willamette River, Oregon. Collected by Howell").

There are several specimens of this species in different herbaria (CAN, F, GH, K, NY, ORE, WS; cf. Appendix p. 207) collected in the same locality, Sauvie's Island, by J. and T. J. HOWELL, either by both together or singly, from 1882 to 1886. The specimens of these collections are all similar, e.g., in development and size, and might have been collected at the same time. My previous choice of lectotype (NILSSON 1967 p. 360) must be rejected because it was preceded by the one stated above.

Annual, glabrous, dwarfish and very slender herb, often forming small, loose mats (Fig. 5 A). Primary root thin, with fibrous branches, soon replaced by adventitious roots from the basal parts of stem and branches. *Stem* terete, 1.0—9.5 cm long (usually 3—6 cm), 0.3—0.7 mm thick,

Fig. 5. *Maxia howellii.* — A: Habit, * marks the first inflorescence of the main stem. — B: Diagrammatic drawing of A, showing branching habit, * see A; arrows indicate lateral shoots. — C: Part of the stem with leaves and inflorescences showing the branching and the vascular system, 1—4 = pedicels in order after development (somewhat simplified). — D—E: Inflorescences, highly simplified; D, the normal type; E, the lower pedunculate. — F: Bract. — G: Leaf margin in cross-section (simplified). — H: Epidermis of the adaxial leaf side, guard cells spotted, subsidiary cells hatched. — I: Stomata and leaf epidermis in cross-section. — J: Stem epidermis cells in cross-section. — K: Stem stele in cross-section, somewhat above the middle of an internode, at the node above one inflorescence and one leaf (simplified), explanation in Fig. 1 E.

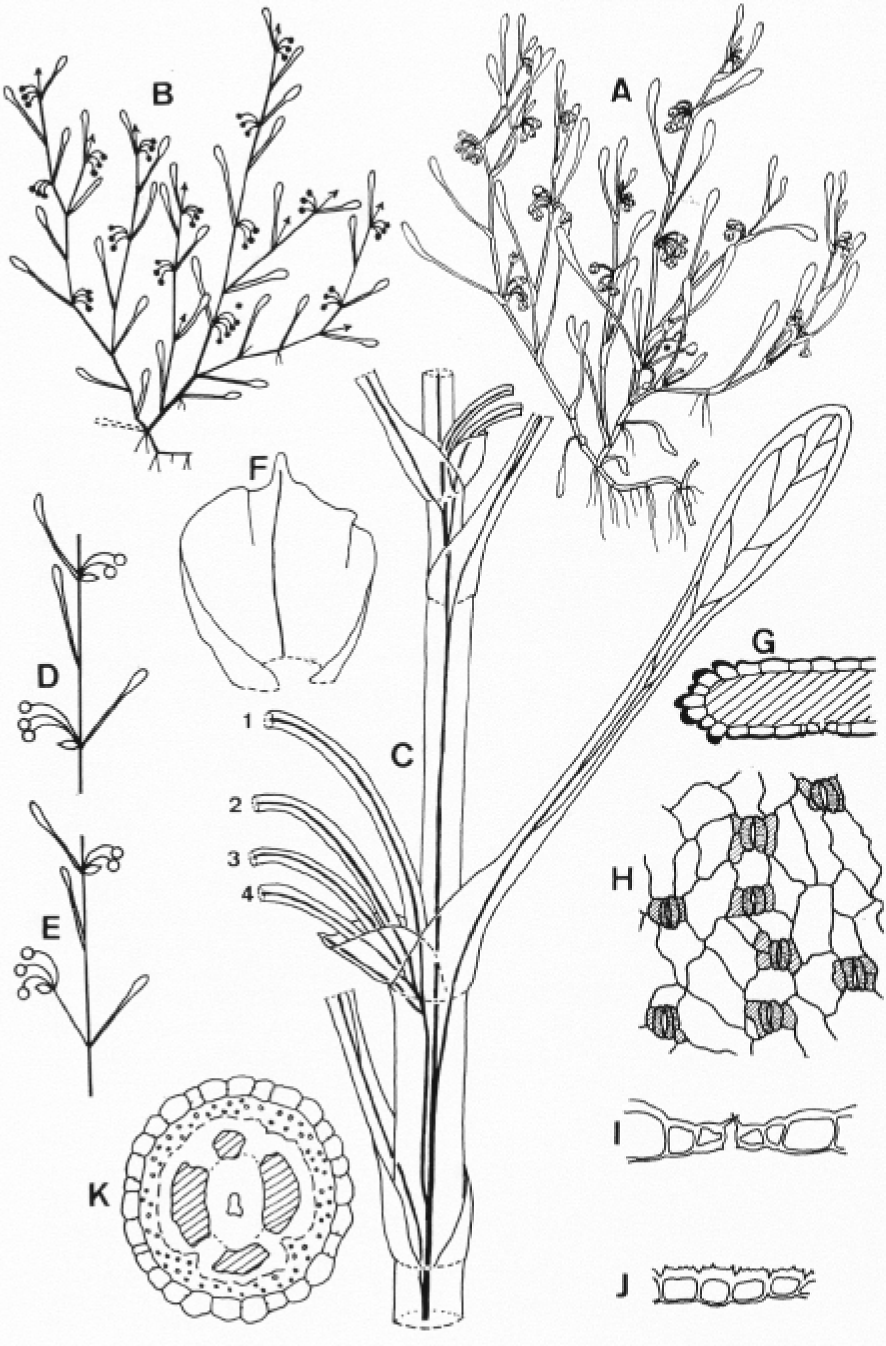

Fig. 5.

erect to ascending or decumbent, moderately branched; branches sometimes secondarily branched, basal parts of the stem and branches often creeping, basal internodes rather short, 2—6 mm, the upper ones somewhat longer, 2—14 mm (usually 7—10 mm; Fig. 5 B). *Leaves* simple, entire, usually rather numerous on flowering plants, soon withering in the basal part of the stem, alternate, often erect to ascending, rather thin and flat, linear-spathulate to almost linear, indistinctly petiolate, 0.5—2.5 cm long (usually 1—2 cm), 0.3—1.8 mm broad; "blade" 2—9 mm long, 3-ribbed with a narrowly cuneate base and an obtuse apex without a distinct hydathode; "petiole" very narrow; leaf base much dilated with broad, very thin, hyaline margins, almost perfectly amplexicaul, forming a sheath about 2—5 mm long. *Stomata* on both sides of the leaf, sparser on the abaxial face, somewhat sunken; subsidiary cells usually distinct, 2—4, lateral (Fig. 5 H); guard cells with a distinct, broad but thin external ledge, the internal very minute (Fig. 5 I); leaf epidermis thin, cells oblong to square in outline with almost straight side walls, along the leaf margins with a group of elevated, distinct cells (Fig. 5 G); cuticle smooth, rather thick, particularly on the marginal cells. *Inflorescences* usually 2—12 per plant, pseudolateral or very occasionally truly terminal; flowers 1—6 (usually 3—5) per inflorescence in fasciculate, reduced cymes opposite a leaf (Fig. 5 C, D); axis and peduncle normally lacking. *Bract* one, at the base of the inflorescence, hyaline, very thin, 0.6—1.6 mm long, 0.8—1.7 mm broad, clasping at the base, very broadly ovate, obtuse to almost truncate, apiculate. *Pedicels* usually recurved like a bow, or hooked before, at and after anthesis, at maturity and rarely at anthesis ± erect, at anthesis 0.5—2.5 mm long, after anthesis growing up to 3—10 mm. *Flowers* homogamic, obligately autogamous, mainly cleistogamous and very reduced. *Involucral leaves* two, opposite, almost equal, the outer only very briefly clasping the inner at the base (Fig. 6 E, F), thin, green, persistent, ovate to broadly ovate, obtuse to acute, at anthesis 0.4—0.8 mm long, at maturity 0.8—1.2 mm long, 0.8—1.1 mm broad, distinctly shorter than the capsule (Fig. 6 E). *Tepals* five or sometimes two, when five those opposite the stamens smaller, when two those opposite the stamens lacking, larger tepals 0.5—0.7 mm long, 0.2—0.4 mm broad, smaller tepals c. 0.4 mm long and 0.15 mm broad, tepals laterally connate at the base for c. 0.2 mm, obovate, obtuse, somewhat shorter than the involucre, whitish (Fig. 6 A, B); sometimes a deep slit between two of the staminate tepals. *Stamens* normally three, very rarely five, equal, opposite the tepals, 0.4—0.5 mm long, free from each other but filaments dilated at the base and adnate to the tepals for c. 0.2 mm; anthers c. 0.1 mm long and c. 0.2 mm broad, very broadly ovoidal, medifixed, not versatile, laterorse to almost introrse, pink (Fig. 6 A, B). *Ovary* broadly obovoid, 0.4 mm long, with three ovules. *Style branches* short, c. 0.1—0.2 mm long, diverging, almost sessile with small, sparsely set papillae mainly on the adaxial face (Fig. 6 C). *Capsule* very broadly obovoid, 0.9—1.2 mm long, 1.0—1.3 mm wide, slightly depressed at the top, somewhat triangular, distinctly trisulcate at the base and with a small bulge at the top of each groove (Fig. 6 D). *Seeds* obovoid, flattened, 0.8—0.9 mm long, 0.6—0.7 mm wide, and 0.4 mm thick, with a rather distinct, low keel almost all around; attachment plate in a depression, strophiole minute, scarsely protruding, whitish (Fig. 6 G); testa smooth, cells almost indiscernable, oblong, in concentric rows, chestnut black, very shining. *Pollen grains* spherical, 22—25 µ in diameter, pantocolpate, usually with 12 colpi, tectate with 1.2—2.1 µ high verruccae, puncta lacking, sexine of a uniform thickness, pink (cf. NILSSON 1967 p. 254).

HISTORICAL SURVEY

In 1882 *Montia howellii* was described by WATSON. GRAY (1887) confused this

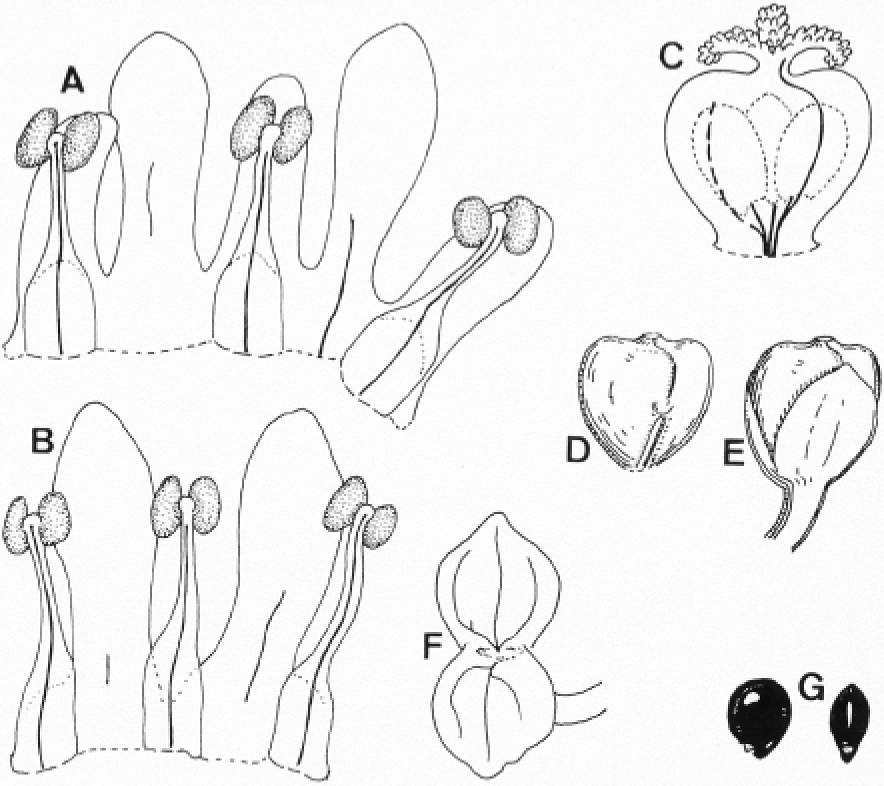

Fig. 6. *Maxia howellii.* — A—B: Perianth with stamens, in B the tepals opposite the stamens are reduced. — C: Pistil. — D: Capsule. — E: Involucre and capsule. — F: Involucre, the lower leaf is the inner. — G: Seeds, the left in lateral view.

species with small forms of *Claytonia dichotoma,* which was placed in the "section" *Montiastrum* of *Claytonia* (cf. NILSSON 1971 p. 90). As a separate species of the genus *Montia, M. howellii* was retained in the section *Montiastrum* together with *M. linearis* and *M. dichotoma* by ROBINSON in GRAY (1897 p. 276) and by PAX & HOFFMANN (1934 p. 259). These three species were placed in the section *Pseudo-Claytonia* of *Claytonia* by v. POELLNITZ in 1932. The genus *Montiastrum* was established by RYDBERG in 1917 and in that he placed *M. howellii* in 1932.

SWANSON (1966 p. 232) restricted the section *Montiastrum* (of *Montia*) to include *M. linearis* and *M. dichotoma,* and transferred *M. howellii* to the section *Montia.* In this section it was placed together with *M. fontana* L. s. lat., *M. australasica* (HOOK. f.) PAX & HOFFM., and *M. chamissoi* (LEDEB.) GREENE. The circumscription of the section *Montia* seems rather diffuse and it conglomerates species which have very vague characters in common and do not show any evident relations.

For *M. howellii* the genus *Maxia* was established in 1967 by NILSSON.

In general habit *M. howellii* is rather similar to some annual *Montia* species. This resemblance was pointed out already by WATSON, and JEPSON (1917) emphasized the similarity and supposed *M. howelli* to be an alternate-leaved variety of *M. fontana.*

STEM AND BRANCHING HABIT

The stem of *Maxia howellii* is usually much branched and the branches are not confined to any distinct region of the plant, although basal branching is sometimes predominant. The main stem and the branches may often be repent in their basal parts and adventitious roots develop particularly at the nodes. The mode of branching of the plant indicates that it is a winter annual. The lowest internodes are very short, the development of the main stem is suppressed, and the basal leaves are withered at the anthesis. The branching development is similar to that of some winter annual *Montia* species and to *Montiastrum dichotomum* (Nilsson 1971 p. 104).

In the spring, the main shoot is soon terminated by an inflorescence and the continued growth is by lateral branches which usually constitute the main part of the plant. The branching is sympodial and diagrammatically illustrated in Fig. 5 B. In the sympodium the terminal inflorescences become pseudolateral, because they are overtopped by lateral branches; only very occasionally the inflorescences have a truly terminal position. In the upper part of the plant the branching is usually very regular with an inflorescence at every second node. This type of branching is different from that of any other genus of the *Montia* group. In the other genera with alternate leaves, e.g., *Limnalsine* and *Montiastrum*, inflorescences may develop at every node.

The stem anatomy is similar to that of other genera of the *Montia* group. The epidermis has a rather thick cuticle which is wrinkled (Fig. 5 J). The cells are long with straight side walls and a thin inner wall. The cortex is very open and assimilatory, and consists of comparatively large cells. Its innermost part is differentiated as an endodermis of large cells with rather distinct Casparian dots. Immediately inside the epidermis is a rather thick continuous layer of thick-walled fibre-like cells (pericycle). The xylem part of the stele forms in transection a ring which, however, is split by a wide leaf gap below the nodes (Fig. 5 K). The number of vascular bundles of the leaf trace is uncertain. The centre of the pith is usually narrowly hollow. The stem withers soon after fruiting.

LEAVES

The leaves alternate in a 2/5 spiral. In the basal part of the stem a few may be somewhat crowded. According to Swanson (1966 p. 234) *M. howellii* is "fundamentally opposite-leaved" as, e.g., *Montia fontana* L., although he describes it as alternate-leaved. These statements are conflicting and seem to be caused by the leaf opposite the bract (interpreted as a small leaf) at the inflorescence. However, Swanson has not realized the sympodial branching of the plant and the reduced peduncle of the inflorescence which causes the bract to be opposite the leaf of the lateral branch (Fig. 5 C). At a pseudolateral inflorescence of *Montia* there are two leaves and one bract, the bract in the axil of the leaf opposite that of the lateral branch. Such a position of the bract does not occur in *Maxia howellii* and also conflicts due to the fact that branches may develop at the node under the inflorescence (Fig. 5 B).

The leaves are ascending or at the top of the branches almost erect in a very characteristic fashion. The veining of the blade may be described as camptodrome. The hydathode at the end of the midrib, occurring in most genera of the *Montia* group is lacking in *Maxia*.

The leaf is rather thin and flat and not as succulent as in *Montia* or *Montiastrum*. Along the margins of the blade there is a group of cells which are distinctly elevated and have a thickened culticle. A similar type of large marginal cells occurs in *Naiocrene*, but is unknown from other genera of the group. The cuticle of the leaf is with the exception of the marginal cells thin, particularly on the abaxial side. The mesophyll is almost homogeneous and no mechanical tissue occurs. The vascular bundles are surrounded by a distinct endodermis.

INFLORESCENCES

In the sympodium the inflorescences usually have a pseudolateral position, often at every second node (p. 202); sometimes when further branching occurs the inflorescences may be separated by two nodes. The flower emerges in the axil of a very thin, hyaline but often green-tipped, half-clasping bract with usually only one median vein (Fig. 5 F). The bract encloses the inflorescence during its early development. The first developing flower is opposite and farthest from the bract, and the last one next to it. The development of the flowers and the vascular system of the inflorescence (Fig. 5 C) show that it can be regarded as a reduced scorpioid cyme of the same type that prevails in the *Montia* group. (The hypothetical original inflorescence of *Neopaxia* was described by NILSSON 1971 p. 107).

The reduction involves a loss of the peduncle and the common axis (cf. NILSSON 1970 p. 134) which causes the flowers to be fasciculate in the axil of the bract in a position opposite a leaf. This interpretation is further supported by the fact that a developed peduncle has once been observed (Fig. 5 E).

A similar type of reduction of the inflorescence occurs in some autogamous *Montia* species but in no other genus of the group. In *Montia* the peduncle is usually lacking but an axis sometimes develops. It is possible that the reduced inflorescence is an adaptation connected with the predominant autogamy. Another feature which seems to be connected with the autogamy is the pedicels which usually do not become erect at the anthesis but remain recurved until maturity. Thus the flowers never become exposed upwards. At maturity the pedicels become straight and upright which makes seed dispersal more effective. In other taxa of the *Montia* group, the pedicels always turn erect at anthesis. The inflorescence is very uniform in *M. howellii*.

FLOWERS AND POLLINATION

The flowers are of the autogamous type described by NILSSON (1971 p. 110). The tepals are normally distinctly shorter than the involucre. The occurrence of five or two tepals in the flowers is not consistent; the same plant can have both types.

Between the two proximate staminate tepals there is often a distinct deep slit almost to their base. A similar slit occurs in the flowers of most *Montia* species, and in *Mona meridensis*.

The stamens are very minute and normally three, only once a 5-staminate flower has been seen, and in this the accessory stamens were dwarfed and without pollen. The anthers have a very low pollen production, often only about 60 grains per flower (three flowers examined). At anthesis the filaments curve somewhat inwards and bring the anthers in contact with the stigmas.

The perfect seed-set, three seeds in all examined capsules, and the floral morphology indicate an almost obligate autogamy. The flowers are homogamic and probably exclusively cleistogamous, only a few have been seen which appeared to be somewhat open. The attraction value of the flowers is low and is further reduced by their recurved position at anthesis. In the inflorescence only one flower is daily in anthesis. No nectaries occur.

With regard to its floral reductions *Maxia* is one of the extremes in the group. Similar reductions are only known in a few annual North American *Montia* species, e.g., *M. dipetala* RYDB.

The anthers are pinkish in colour because of the translucent pink pollen. Pink pollen grains are very rare in Montioideae and in the *Montia* group only known in *Maxia;* the other genera have pale yellow to white pollen.

SEEDS, DISPERSAL, AND REPRODUCTION

The small seeds of *Maxia* are similar to those of *Montiastrum* in being keeled and having the attachment plate in a depression and a very minute strophiole. In *Montia* they are not keeled and the attachment plate is elevated. Like in *Montiastrum* the testa is smooth and very shining with hardly discernible cells. The testa cells lack the minute processes which occur on most *Montia* seeds. The cotyledons have an oblique position in the seed.

The capsule which at maturity is somewhat longer than the persistent involucre dehisces with three valves which split to the grooves of the capsule and become reflexed and strongly involute. The seed dispersal mechanism is of the type that prevails in the subfamily (p. 196). The seeds are actively thrown away from the plant. At maturity the pedicels, which grow somewhat after anthesis, become erect. The seeds ripen very rapidly; mature capsules and flowers sometimes occur in the same inflorescence.

A high and safe annual seed production is an essential quality in *Maxia,* as in most annuals, and this is safeguarded by an effective self-pollination (cf. NILSSON 1971 p. 117).

The almost obligate autogamy must result in inbreeding; the populations become poor in biotypes and the genetic variation is insignificant. This is reflected in the collections studied, which consist of very similar specimens. The loss of genetic variation is partly compensated by the great plasticity of the plants, which modify particularly with the access of water from being "tall-grown" in moist habitats to very minute in dry.

This annual plant has radiating repent branches. This is not actually vegetative reproduction, but facilitates the growth of the individual plant and results in larger specimens. Although to a limited extent it makes it possible for the plant to reach an environment which may be more favourable than the original. It is also a safeguard if some part of the plant should be injured.

VARIATION AND RELATIONS

Maxia howellii is a uniform species and no significant variation occurs apart from that caused by modification.

The species has often been regarded as related to the genera *Montia* and *Montiastrum.* In particular its relationship to the annual *Montia* species and to *Montiastrum dichotomum* has been emphasized.

The annual *Montia* species and *Maxia howellii* are similar in habit and in having similar types of reductions in flowers and inflorescences, and the pollen grains are 12-pantocolpate. *Maxia* differs in the following characters: the branching habit; the leaves which are alternate with a broad sheathing base, flat and thin with particular marginal cells; the stomata which occur on both leaf sides and have distinct subsidiary cells; the pedicel which is evenly curved; the anthers which are two-celled; the seeds which are keeled with the attachment plate in a depression, have smooth testa and oblique cotyledons; the pollen grains which are pink and very small and verrucate with a sexine of uniform thickness.

Montiastrum dichotomum and *Maxia* agree in being alternate-leaved with sheathing leaf bases, in stomata characters, in similar floral reductions and in seeds. *Maxia* differs in the following characters: the mode of branching; the leaves which are thin and differentiated in blade and petiole, lack a hydathode and have particular marginal cells; the few-flowered inflorescence lacking peduncle and axis; the involucre which is shorter than the capsule and lacks a distinct parallel veining; the style branches which are almost sessile; the cotyledons which are oblique in the seeds; the pollen grains which are not tholate.

In the above comparison one finds *Maxia howellii* similar to both genera mentioned — in particular the similarity in floral morphology is obvious. However, all these species are predominantly autogamous and the floral similarities may be due to convergent evolution. *Maxia* differs in several more or less important characters, of which the branching habit is emphasized, and together these give the genus a distinct and natural circumscription.

The similarity between *Maxia* and *Montiastrum* is rather superficial whereas the agreement with the annual *Montia* species may be more far-reaching, indicating an affinity. However, the relations between *Maxia* and *Montia* are still uncertain. The position of *Maxia* in the *Montia* group seems to be rather independent. Although at present very distinct, there are some indications of an affinity between *Maxia* and *Montia*, but there are also indications pointing to a relation between *Maxia* and *Limnalsine*. These two genera are almost sympatric but ecologically isolated which may have caused the divergent evolution.

DISTRIBUTION AND HABITAT

Maxia howellii occurs in a narrow area along the Pacific Coast of North America from southern Vancouver Island in the north to northern California. It occurs west of the Cascades and in the Coast Ranges. The area is not continuous, a gap occurring between the localities along the lower Columbia River and those of northern California. Most collections of the species originate from localities along the lower Columbia River, and it is possible that the species is centred in this area. The species occurs in the following states: California, Oregon, Washington, and in British Columbia (cf. RYDBERG 1932, ABRAMS 1964, and HITCHCOCK et al. 1964; Fig. 4 A and Appendix p. 207).

The distribution of *Maxia* agrees in several respects with that of *Limnalsine* but is different from that of other North American genera of Montioideae. *Maxia* and *Limnalsine* are both confined to the humid coastal areas, but the area of *Maxia* is smaller and does not reach as far south (p. 198). Collections of recent date are very sparse and seem to be entirely lacking after 1939. However, this small-sized, early deciduous species may easily be overlooked, and the distribution gaps are perhaps not real.

M. howellii occurs within the Humid Transition Zone from about sea level up to an elevation of about 200—250 m. There is very scanty and mostly incomplete information on its ecology. It occurs in wet or at least temporarily wet habitats, e.g., borders of ponds, moist meadows, and fields. The vegetation of these localities is sparse, open, and lowgrown. The species has been collected together with, e.g., *Montia* spp. and *Callitriche* spp.

FLOWERING PERIOD: (March—) April to May (—June).

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LIST OF MATERIAL EXAMINED

Limnalsine diffusa

CANADA, BRITISH COLUMBIA

Cameron Lake, 1899 J. R. Anderson 935 (V, WS). — Vancouver Island, Port Alberni, 1916 J. K. Henry (V).

USA, CALIFORNIA

1868—69 A. Kellog & W. G. W. Harford 98 (GH, NY). — Marin Co., Lagunitas, 1878 H. Edwards (NY). — Humboldt Bay, 1878 V. Rattan (GH). — Mendocino Co., near Mendocino, 1898 H. E. Brown 775 (F, NY, UC). — Marin Co., Mill Valley, 1901 A. Eastwood (NY, UC). — Humboldt Co., Redwood Belt, 500 feet, 1901 H. P. Chandler 1271 (NY, UC). — Mendocino Co., Kaisen District, 1903 J. Mc Murphy 238 (E, NY). — Mt. Tamalpais, 1905 P. A. Rydberg 6243 (NY). — Humboldt Co., near Hangley's Mill, Kneeland Prairie, 2000 feet, 1906 J. P. Tracy 2487 (UC). — Humboldt Co., Opposite Bucke Mt., valley of Van Duzen River, 1908 J. P. Tracy 2725 (UC). — Humboldt Co., 3 miles NW of junction of Willow Creek with Trinity River and near Beebe's Ranch, 1911 J. P. Tracy 3404 (UC). — Humboldt Co., Kneeland Prairie, 2500 feet, 1930 J. P. Tracy 9165 (GH, JEPS, WS). — Del Norte Co., Shelley Creek, near Monumental, 2300 feet, 1936 H. E. Parks & J. P. Tracy 11340 (UC). — Humboldt Co., Four-Mile Creek W of the mouth of south fork of Trinity, 1937 J. P. Tracy 15379 (NY). — Humboldt Co., above Van Duzen River 1 mile below Dinsmore's., 2500 feet, 1940 L. Constance & A. A. Beetle 2615 (GH, JEPS, K, NY, S, WS). — Marin Co., Cascade Canyon Mill Valley, 100 feet, 1942 L. S. Rose 42068 (GH, NY). — Humboldt Co., valley of South Yager Creek, head of valley, 2500 feet, 1950 J. P. Tracy 18652 (UC). — Humboldt Co., Brush Mt., 3.5 miles SW of Willow Creek, 2800 feet, 1957 D. Hagar 59 (LA, UC). — Mendocino Co., E shore of South Fork of Eel River, from confluence with Elder Creek to about 25 miles downstream, 1961 H. K. Sharsmith 4858 (UC).

OREGON

Nuttall (K). — "Woods", Nuttall (GH, K, NY). — Salem, O. B. Johnsen (WTU). — Near Willamette Slough, 1875 J. & T. J. Howell (WS). — Near Portland, 1875, 1876 J. Howell (F). — Willamette Sloughs, 1876 J. Howell (WS). — Multnomah Co., 1877 T. J. Howell 56 (GH). — About Hood River, 1880 L. F. Henderson (ORE). — Howell's Pacific Coast Plants, 1880, 1881 T. J. Howell (F, GB, NY, ORE, WTU). — La Camas, 1884 L. F. Henderson 132 (UC). — Near Portland, 1887 T. Howell (NY); 1888 (ORE). — Sauvie's Island, 1887 T. Howell (OSC). — Sykes Creek, 1892 E. W. Hammond 49 (ORE). — Jackson Co., Winner, 1893 E. W. Hammond 54 (NY). — Gale's Peak, Forest Grove, 1893 F. E. Lloyd (NY, UC); 1894 (NY); 1895 (NY). — Portland, Willamette Hts, 1902 E. P. Sheldon 10289 (F, GH, NY, ORE, UC, WS). — N end of Rocky Butte, near Sand Road, Portland, 1910 M. A. Flinn (ORE). — Illuhe, 1917 J. C. Nelson 1421 (GH). — Clackamas Co., N side of Oswego Lake, 1919 J. C. Nelson 2557 (GH). — Oswego Lake, 1919 M. W. Gorman 4496 (WS). — Curry Co., along Chetco River, 2 miles above Harbor, 1919 M. E. Peck 8898 (GH). — Along Scroggins Creek, 6 miles NW of Gaston, 1927 M. E. Peck 14815 (WTU). — Douglas Co., South Umpqua, above Tiller, 1930 L. F. Henderson 13162 (ORE). — Lane Co., near the top of Spencer Butte, 1933 R. Brown 341 (ORE). — Lane Co., grade S of Box Canyon Meadows, 3500 feet, 1934 L. F. Henderson 16678 (ORE). — Lane Co., Gt. Oakridge and bridge over Willamette River, 1934 L. F. Henderson 16104 (ORE). — Lane Co., Clark Butte Way, Big Fall Creek, 1938 L. F. Henderson 18546 (ORE).

WASHINGTON

Seattle, C. V. Piper 471 (WTU). — Klickitat Co., near the mouth of the Lann River, 1883 W. N. Suksdorf 468 (BM, F, GH, WS). — Klickitat Co., Bingen, 1891 W. N. Suksdorf

3383 (WS). — Tront Lake, 1892 F. Liddelle (F). — About Olympia, 1892 L. F. Henderson (WTU). — Seattle, 1892 E. A. Shumway 1112 (WTU). — Klickitat Co., on Bingen Mt., 1896 W. N. Suksdorf 3725 (UC, WS). — Gig Harbor, near Tacoma, 1895 J. B. Flett (WS); 1896 (WS). — Tacoma, 1897 J. B. Flett (WTU). — Klickitat Co., Bingen Mt., at Bingen, 1900 W. N. Suksdorf 3996 (WS). — Olympic peninsula, Hurricane Ridge, 3500 feet, 1931 G. N. Jones 3334 (WTU). — Jefferson Co., Olympic Mts., along the Dosewallops River, 500 feet, 1931 J. W. Thompson 6571 (GH, K, WTU). — Jefferson Co., Constance Ridge, 500 feet, 1931 J. W. Thompson (OSC).

Maxia howellii

CANADA, BRITISH COLUMBIA

Near Victoria, 1885 Fletcher (GH). — Vicinity of Victoria, 1893 J. Macoun (BM, MO, NY). — Ten Mile Point, Victoria, 1939 J. W. Eastham (UBC).

USA, CALIFORNIA

Humboldt Co., Eureka, 1904 J. P. Tracy 2018 (GH); 1909 J. P. Tracy 2956, 2947 (JEPS, K, WS); 1916 J. P. Tracy 4686 (JEPS). — Humboldt Co., Phillipville Flat, south fork of Eel River, 300 feet, 1921 J. P. Tracy 5431 (JEPS). — Humboldt Co., Bridgeville, 250 feet, 1933 J. P. Tracy 12526 (NY).

OREGON

Sauvie's Island, T. Howell (ORE). — Sauvie's Island, 1882 L. F. Henderson (ORE). — Along the Willamette River, 1882 L. F. Henderson 139 (OSC); 1884 (WS). — Sauvie's Island, 1882, 1883, 1884 J. Howell (CAN, GH, WS); 1883 J. & T. J. Howell (K); 1884 (F); 1884 T. Howell (NY, ORE); 1886 (BM, NY). — Along the Willamette R., below Portland, 1884 L. F. Henderson (ORE). — Washington Co., Forest Grove, 1894 F. E. Lloyd (NY). — Columbia Co., St. Helens, 1895 W. N. Suksdorf 2373 (GH, WS). — Sauvie's Island, 1902 M. W. Gorman 10338 (ORE).

WASHINGTON

Seattle, 1888 C. V. Piper (WS); 1889 C. V. Piper 241 (GH, S, WTU). — Klickitat Co., Bingen, 1902 W. N. Suksdorf 3998 (WS).

Monsonia parvifolia Schinz (Geraniaceae), a Species with Concealed Spurs

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ABSTRACT

Kers, L. E. 1971. Monsonia parvifolia Schinz (Geraniaceae), a species with concealed spurs. — Bot. Notiser 124: 208—212.

Monsonia parvifolia Schinz has often been confused with *M. umbellata* Harv. and *M. namaensis* Dinter. The sepals have a concealed spur, as in *Pelargonium*, which is a new feature to be reported for *Monsonia*. The petals vary in colour from pink with purple stripes to yellow and even white. The triangular shape of the sepal mucro is shown to be an essential character. The species is confined to the Namaqualand Region of South Africa and S.W. Africa.

Monsonia parvifolia Schinz

Schinz, Verh. Bot. Ver. Brandenb. 29: 61 (1888).

TYPUS SPECIEI: Steingröver 106, s. dat. Orangefluss. Südgrenze von Lüderitzland (Holotype Z).

SYN.: *Monsonia senegalensis* Guill. & Perr. var. *hirsutissima* Harv. in Fl. Cap. II, (1862), Suppl. p. 591. Typus: Atherstone. Sandy flats near the Orange River (non vidi); Wyley. Sandy flats near the Orange River (SAM).

"*Monsonia leucotricha*" Schlechter in sched. Nomen illeg. Collection: Schlechter 51, 1897, Great Buschmanland, Regio namaquensis, Naroep (BOL, S, Z).

LITT.: Dinter 1921 p. 32; Dinter 1923 p. 237; Erdtman 1966 p. 186 sub *M. leucotricha;* Knuth 1912 p. 307; Merxmüller & Schreiber 1966 p. 5; Range 1932 pp. 139, 145.

ICON.: Fig. 1.

DISTRIB.: Fig. 2.

Annual or short-lived perennial *herb*. *Branches* up to 50 cm long, prostrate; axillary branches usually very short; internodes 14—40 (—65) mm long, often reddish brown, pilose with spreading white hairs, which are up to 3 mm long. *Leaves* opposite, unequal, the smaller about 1/3—1/2 as large as the opposite; petioles (4—) 11—42 mm long, rather stiff, brownish, provided with subsessile glands and pilose with spreading, up to 2 mm long, white hairs; lamina broadly cordate, nearly as broad as long, usually from 9×9 to 22×22 mm, often rich in subsessile glands between the nerves; indumentum variable, margin ciliate, faintly serrate—dentate to almost entire. *Stipules* approx. 2 mm long, pilose—ciliate along the margin. *Peduncles* 1—3 (—4)-flowered, 10—44 (—55) mm long, usually shorter than the leaves, rather stiffly erect, brownish, pilose with up to 2 mm long hairs. *Floral bracts* 2—4 mm long, triangular to narrowly ovate, ciliate, brown. *Pedicels* usually shorter than the peduncle, 6—21 mm, often gently curved in a S-shaped way below the fruit, indumentum as on the peduncle. *Sepals* 6—8 mm long and 3—4 mm broad, oblong, green, flushed with purple, with ± hyaline margins, pilose on the back, adaxial face glabrous; each sepal provided at the base with a concealed, approx. 1 mm long sac-like spur which is connate to the pedicel axis; sepal mucro reflexed, triangular in lateral view, flattened from the sides, 2—4 mm long, pilose—ciliate. *Petals* 1.2—2 cm long and 0.6—1.1 cm broad, about twice as long as the sepals, spatulate to narrowly obcordate, apex bilobed—notched, colour variable, "white", "pale yellowish", "primrose yellow" or pink with 3—4 dark violet stripes, claw ciliate, adaxial face of the limb glabrous, abaxial side puberulent (Fig. 1 A). *Stamens* 15, in five almost free groups; filaments in each group fused in their basal 1/2—2/3, 10—13 mm long, pale yellowish, puberulent in their lower portions. *Anthers* 2—2.5 mm long, yellow. *Stigma lobes* 2—3.5 mm long, yellow. *Fruits* 50—65 mm long when ripe; deliberated beaks plumose; fruitlets 3—5 mm long and c. 2 mm broad, densely covered with short, brown, stiff, patent hairs.

Some specimens have rather large pink flowers with purplish stripes and thus do not fit the available keys and descriptions. One such collection (GIESS, VOLK & BLEISSNER 5490) was listed under *Monsonia umbellata* HARV. by MERXMÜLLER and SCHREIBER (1966 p. 5), but in the author's opinion (cf. KERS 1968 p. 46) it represents a pinkflowered form of *Monsonia parvifolia*.

Monsonia parvifolia has some features in common with *M. drudeana* SCHINZ, e.g. the white petals which fade to yellow and have red stripes. The two species can hardly be confused, however; *M. drudeana* has up to 27 mm long petals, the petal apex is blunt and the red stripes are confined to the abaxial side of the petal limb and near its apex (MERXMÜLLER & SCHREIBER 1965 pp. 556, 561).

In *M. parvifolia* certain morphological features are of particular interest to distinguish this species from its allies. These features are: the shape of sepal mucro, the (variable) petal colour, the concealed spurs and the few-flowered peduncles.

1. SHAPE OF SEPAL MUCRO (Fig. 1 D, E, J)

In *M. parvifolia* the sepal mucro is triangular in lateral view, and laterally compressed. In *M. umbellata* and allied species the mucro is filiform. The shape of the mucro is characteristically developed already in young buds.

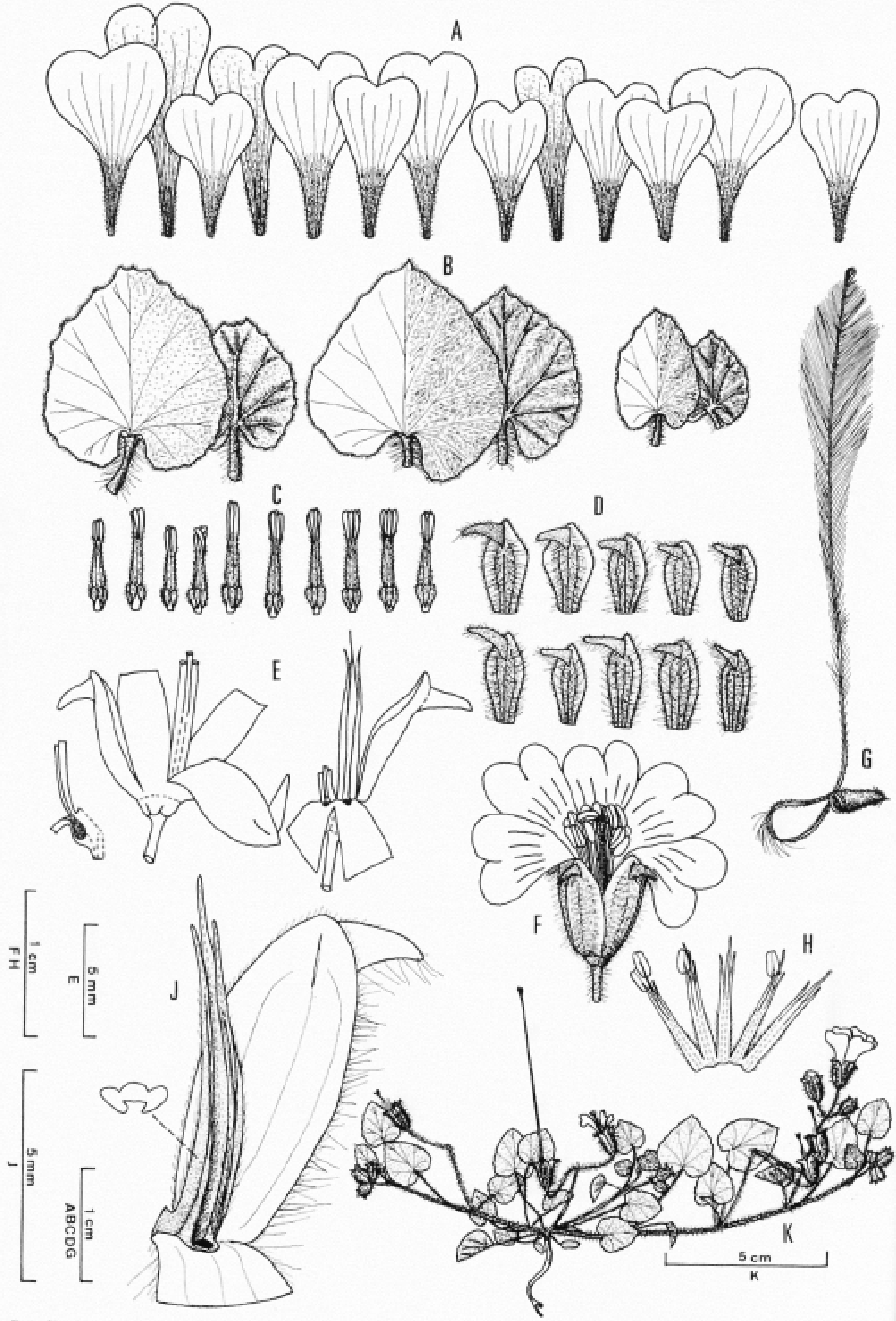
2. PETAL COLOUR

The petals vary much in colour from pink with purplish stripes to yellow or white, but the original colour is often difficult to determine from herbarium material. There are notes about white, yellow or pink petals on a few sheets. Pink flowers are verified also by DINTER's name (in sched.) "*Monsonia rosea*", which was given to the pink-coloured form of *M. parvifolia* (DINTER 1191, SAM!).

The type of *M. parvifolia* was stated to have yellowish white flowers with red stripes, a character that also KNUTH mentioned in his description of this species (SCHINZ 1888 p. 61; KNUTH 1912 p. 309). MERXMÜLLER & SCHREIBER stated the petals to be yellow (MERXMÜLLER & SCHREIBER 1966 p. 3). The original flower colour, in so far as it can be judged, has been given in the list of the collections studied.

3. SEPAL SPURS (Fig. 1 E, J)

The spurs have the same construction as in *Pelargonium*, but in *Monsonia parvifolia* all five sepals are spurred. The spur is a minute, pouch-like cavity concealed at the pedicel apex and at the base of the sepals. Each spur opens by a small pore on the adaxial side of the base just where the stamen groups are inserted (Fig. 1 E, J). The inner surface of the spur is densely papillated. Together with the corresponding stamen group, the spur forms a nectary apparatus. Thus, at the base of the abaxial side of the stamen groups, the filaments form a narrow channel which


A
B
C
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1 cm
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J
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5 cm
K

leads down to the spur opening. This longitudinal channel is covered with numerous ascending hairs. In *M. umbellata* s. str. the spurs are hardly discernable, and the flowers are inconspicuous, always white and without colour markings. The flowers are seldom if ever fully expanded and the anthers and the stigma lobes are very small. Contrary to *M. parvifolia,* therefore, *M. umbellata* s. str. is probably mainly self-pollinated.

4. NUMBER OF FLOWERS

In *M. parvifolia* the peduncles are 1—3 (—4)-flowered and shorter than or equalling the subtending leaf. In *M. umbellata* and allied species they are normally 5—10-flowered and longer than the leaf.

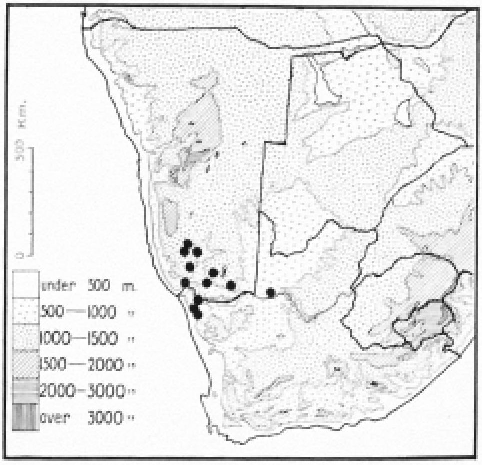

Fig. 2. The distribution of *Monsonia parvifolia* SCHINZ based on material from the following herbaria: BOL, NBG, S, SAM, UPS, Z.

COMMENTS ON KNUTH'S DRAWING OF MONSONIA PARVIFOLIA

In KNUTH's monograph of Geraniaceae there is an illustration which is said to represent *M. parvifolia* (KNUTH 1912 p. 2308, Fig. 38 C). The drawing deviates in several important characteristics from KNUTH's description of *M. parvifolia,* however, and SUESSENGUTH (1950 p. 48) suggested that it represented a species which he described as *M. rehmii.* Supposedly *M. rehmii* is synonymous with *M. umbellata* s. str. sensu KERS (cf. also MERXMÜLLER & SCHREIBER 1966 p. 5).

In the opinion of the author, KNUTH's drawing of *M. parvifolia* gives an almost perfect representation of *M. namaensis* DINTER (Type: DINTER 2040, SAM!). This species is closely allied to *M. umbellata* and differs from *M. parvifolia* in the manyflowered and long peduncles, the thread-like sepal mucro, the serrate—dentate leaf-margin, the larger leaves etc. Only white flowers are known so far from *M. namaensis.*

Fig. 1. *Monsonia parvifolia* SCHINZ. — A: Petal variation. Adaxial side except nrs. 2, 4 and 9. — B: Leaf variation. The left leaf in each pair shows the upper surface. — C: Pistils. — D: Sepals showing the shape of the sepal mucro. — E: Drawings illustrating the concealed spurs. Left: Spur in longitudinal section with portions of the stamen filaments and the sepal. Central: Flower in lateral view showing the spurs at the base of the sepals. Right: The opening to the spurs are situated at the base of each stamen group (cf. J). — F: General aspect of flower. A pink flowered specimen with violet stripes. — G: Fruit with the plumose beak. — H: Androecium dissected to show the five stamen groups. Only four anthers drawn. — J: Stamen group in abaxial view showing the position of the small opening (black) leading down to the spur. Left: Cross section. — K: General aspect of plant. — A: From left: BARNARD 36107, GIESS, VOLK & BLEISSNER 5490, MARTIN 501, GIESS 10312, FLECK 229 a, THORNE 51580, MARTIN 501, PILLANS 6437, NORDENSTAM 2193, TAYLOR 1187, DINTER 5015, BAYLISS & LEACH 13084, SCHLECHTER 51. — B: Left: GIESS 10312. Central: SCHLECHTER 51. Right: BARNARD 36107. — C—D: Drawn from different collections. — E: THORNE 51580. — F, H, K: NORDENSTAM 2193. — J: BAYLISS & LEACH 13084.

Material studied of Monsonia parvifolia

(Petal colour: w=white, y=yellow, p=pink with purple stripes, ?y=probably yellow, ?p=probably pink, ?=not determinable.)

SOUTH AFRICA, CAPE PROVINCE

Upington distr.: BARNARD 36107, VI. 1925, Reimvastmaak (SAM) ? p. — Namaqualand distr.: MARTIN 501, 7. IX 1950, Namaqualand, Ratel Kraal (NBG) w; SCHLECHTER 51, 14. X 1897, Great Buschmanland, Regio namaquensis, Naroep (BOL, S, Z) ?; TAYLOR 1187, 7. X 1935, S. Vioolsdrift (SAM) y; THORNE 51580, III. 1935, 6 miles S of Vioolsdrift (SAM) y. — Without precise locality or locality not identified: FLECK 229 a, V. 1891, Cape Colony (Z) ?; WYLEY s. n. (14521), s. dat., Sandy flats near the Orange River. Type of *Monsonia senegalensis* GUILL. & PERR. var. *hirsutissima* HARV. (SAM) ? y.

SOUTH WEST AFRICA

Lüderitz distr.: STEINGRÖVER 106, s. dat., Orangefluss. Südgrenze von Lüderitzland. Type of *Monsonia parvifolia* SCHINZ (Z) "y". — Bethanie distr.: DINTER 1191, 1900, Sandverhaar (SAM) p; DINTER 8269, 24. III 1934, Buchholtzbrunn (BOL, S, Z) ?; GIESS 10312, s. dat., Farm Umub 42, 8 Meilen nördlich Bethanie (S) p; GIESS, VOLK & BLEISSNER 5490, 25. II 1963, Farm Schwartzkuppe 39 (S) p; NORDENSTAM 2193, 14. IV 1963, 9.3 miles W of Koniep on Lüderitz road (S) p; RANGE 710, VIII, 1909, Nuichas (BOL, SAM) ? p. — Warmbad distr.: DINTER 5015, 11. X 1923, Garius (BOL, SAM, Z) p. — Keetmanshoop distr.: BAYLISS & LEACH 13084, 31. VII 1965, 26 miles E of Karasberg (NBG) y; A. ÖRTENDAHL s. n., 1925, Klein Karas (UPS) p. — Locality not identified: PILLANS 6437 and 6452, IX. 1931, S.W.A. Between Modder Drift and Sjambok River (BOL) y.

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Chromosome Numbers in Some Swedish and Danish Mosses

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ABSTRACT

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Chromosome numbers are reported from 149 populations belonging to the families Bryaceae (1 species), Mniaceae (6 species), Thuidiaceae (2 species), Lembophyllaceae (1 species), Brachytheciaceae (10 species), Hypnaceae (4 species), and Polytrichaceae (8 species).

A survey of earlier Scandinavian investigations on moss cytology is given, and it is also referred to other, extra-Scandinavian reports on chromosome numbers published previously for the species treated. The methods used for cultivation, pretreatments, and staining are discussed.

The chromosome number of *Abietinella abietina* (Hedw.) Fleisch. (n=11) is reported for the first time. New chromosome numbers are given for *Brachythecium reflexum* (Starke) B.S.G. (n=11), and for *Homalothecium lutescens* (Hedw.) Robins. (n=10).

INTRODUCTION

Chromosome studies on Scandinavian mosses were carried out by Vaarama (1949, 1950a, 1950b, 1953, 1954a, 1954b, 1955, 1968) on Finnish mosses, and by Holmen (1955, 1958) on mosses from Denmark and Sweden. From Sweden Holmen studied *Sphagnum* species only.

The reports on chromosome numbers show by comparison often struggling discrepancies, and the rule seems to be that aneuploids, often corresponding to taxa or infraspecific races, exist in genera and species of mosses.

It is a rather unique condition to find euploid series. Modern investigations have shown that such euploid series occur, e.g., in the family Polytrichaceae (n=7, 14, 21), and in the family Thuidiaceae where most species have n=11, but where species occur also with n=22. In *Philonotis* (family Batramiaceae) only two chromosome numbers are known which, however, also form an euploid series, viz. n=6 and n=12.

The main purpose of our investigations is to study the infraspecific chromosomal conditions in Scandinavian populations. The studies will later be concentrated to a few groups. One of these is *Brachythecium* which is investigated by the junior author, Mr. K. Wigh M. Sc., who has also made the main part of the preparations for the present paper.

METHODS

When chromosome counts are made on meiotic stages, there are often difficulties in determining the chromosome numbers defini-

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tely, especially in late metaphases and in early anaphases, and when the meioses are cytologically disturbed. To avoid these difficulties mitoses of gametophytes or, in a few cases, of sporophytes were studied.

The mosses were cultivated in glass pots with a cover of polythene. No substratum was used in most cases. The pots were kept in a greenhouse during the initial stages of our studies. The conditions of light and temperature became, however, unsuitable for several mosses during the summers. The cultures were then moved into a constant room where the temperature was kept at 15°C and the light at 4000—5000 lux for 14 hours followed by 10 hours of darkness.

Several pretreatments were tried for better separation of chromosomes. Cold treatment contracts the chromosomes and spreads them in the cell. The whole pots were placed in a refrigerator at 2°C for 15—24 hours, or the shoot tips only were placed in water at the same temperature for 5 hours. The first method gave good results in e.g. Brachytheciaceae and the second was the best one for Polytrichaceae and *Pleurozium*.

Better spreading of the chromosomes and an accumulation of metaphases were obtained by soaking the shoot tips in 8-hydroxyquinoline (at 7°C), colchicine (at 7°C) or in acenaphtalene (at 25°C). The acenaphtalene gave good results in *Mnium*.

The shoot tips were fixed in Farmer's solution 3 : 1 (3 parts absolute alcohol, and 1 part glacial acetic acid) or in Carnoy's solution 6 : 3 : 1 (6 parts absolute alcohol, 3 parts chloroform, and 1 part glacial acetic acid). The shoot tips were mostly fixed during 24 hours, but they were sometimes kept fixed for a month without any negative results.

The tips were as a rule stained according to Feulgen's staining schedule somewhat modified: hydrolysis in 1-normal HCl at 60°C for 8 minutes, staining in Schiff's reagent (leuco-basic fuchsin) for 2—4 hours at 20°C, soaking in pectinase (5 %) for 15—60 minutes.

The meristematic zone of the shoot tips was dissected and squashed on a slide in 45 % acetic acid under a cover slip of vipolon. After 2 hours the slides were put into aceton overnight and then mounted.

Some genera, e.g. *Homalothecium*, did not stain satisfactorily with this technique. In such cases the shoot tips were stained in aceto-orcein (1 %) for 2—3 hours at 45°C.

KEY TO INFORMATION AND RESULT

The information given in the first line is always obtained in the present studies: the haploid chromosome numbers counted, and the pictures of mitotic metaphases in the gametophytes.

The numbers of populations studied and the names of the original localities are then given. Abbreviations are used for localities referred to more than twice. The numbers in parentheses refer to the voucher specimens kept at the Botanical Museum, University of Göteborg (GB). The authors are the collectors if nothing else is mentioned.

Abbreviations used for localities:

Gt = Gotland, Sweden
Hl = Halland, Sweden
J = Jylland, Denmark
Öl = Öland, Sweden
Sk = Skåne, Sweden
Sm = Småland, Sweden
Vg = Västergötland, Sweden

I = J, Hörning, Sindal, Slotved Skov
II = J, Ålborg, Årestrup, Nörlund Savverk
III = J, Hjörring, Tornby, Kærsgård Klit
IV = Sk, Knislinge
V = Sk, Knislinge, Vanås
VI = Sk, Billinge, Stockamöllan
VII = Sk, Ivetofta, Valje
VIII = Sk, Ivetofta, Ryssberget, Leingaryd
IX = Sk, Ivetofta, Edenryd
X = Sk, Ivetofta, Grundsjön
XI = Sk, S. Rörum, Linderödsåsen
XII = Sk, Röstånga, Odensjön
XIII = Sk, V. Sönnarslöv, Söderåsen, Klöva hallar
XIV = Sk, Tåssjö, Rössjöholm
XV = Sk, Stenestad, Dragesholm
XVI = Sm, Växjö, Lövsjön
XVII = Sm, Växjö, Hinnsjön
XVIII = Vg, Partille, Uddared
XIX = Vg, Göteborg, Botaniska trädgårdens naturpark
XX = Hl, Lindome, Sandsjön

INFORMATION AND RESULT

Family Bryaceae

Bryum pseudotriquetrum (HEDW.) SCHWAEGR. — n = 10 (Fig. 1)

1 population: XVI (68—516).

Chromosome counts published previously:

n = 10: HEITZ (1928), SMITH & NEWTON (1968) — 3 populations.
n = 11: STEERE (1954), STEERE et al. (1954).
n = 20: ANDERSON & CRUM (1958).

One of the ten chromosomes is markedly longer than the others. The observation agrees with SMITH and NEWTON who noted one large bivalent in meiotic metaphase.

STEERE et al. observed a minute bivalent in addition to the other ten.

Family Mniaceae

Mnium affine BLAND. — n=6 (Figs. 2, 3, 38)

6 populations: J, Viborg, Nr. Vinge, Vinge Mölle (68—431); IV (69—15); VI (69—70); XVI (68—474, 68—492); Sm, Stenbrohult (68—504).

Chromosome counts published previously:

n=6: LOWRY (1948) — 3 populations, SINOIR (1950), HOLMEN (1958).

Mnium is the only genus in which the authors have observed centromeric constrictions. The chromosome idiogram is shown in Fig. 3. All the chromosomes are rather similar in size.

Mnium cinclidioides HÜB. — n=6 (Fig. 4)

1 population: Vg, Björketorp, Hindås (69—95).

Chromosome counts published previously:

n=6: LOWRY (1948).

The population studied by LOWRY had one chromosome noticeably longer than the others. In the Swedish population there is no long chromosome.

Mnium cuspidatum HEDW. — n=12 (Fig. 5)

3 populations: I (68—280); VII (69—39, 69—40).

Chromosome counts published previously:

n= 6: HEITZ (1942), LOWRY (1948).

n=12: HEITZ (1942), LOWRY (1948) — 2 populations, HOLMEN (1958), LAZARENKO & VYSOTSKAYA (1965), VYSOTSKAYA (1967), SMITH & NEWTON (1968) — 2 populations, BOWERS (1968) — 2 populations.

LOWRY described the population with n=6 as small-growing, with small leaves, and small cells (2881 cells per square mm) as compared to the populations with n=12 (1885 cells per square mm).

The leaves are less stongly decurrent as compared with the n=12 cytotype. The taxonomical status of the two cytotypes is, however, not clear.

Mnium hornum HEDW. — n=6 (Figs. 6, 39)

18 populations: J, Skanderborg, Sdr. Vissing, Addit Skov (68—229); I (68—267); II (68—303); V (69—13, 69—19); VI (69—73); VIII (69—26); XI (69—1, 69—2); XII (69—57); XIII (69—63); XVII (68—495); Sm, Växjö, SW Lövsjön (68—469, 68—509); XVIII (68—542, 68—546); XIX (69—93); Vg, Mölndal, Toltorpsdalen (69—89).

Chromosome counts published previously:

n= 6: WILSON (1909), MARCHAL & MARCHAL (1911), HEITZ (1928), JACHIMSKY (1935), LOWRY (1948), HAMANT (1950), LEWIS (1957), SMITH & NEWTON (1967) — 4 populations, RAMSAY (1969) — 4 populations.

n= 7: TATUNO & ONO (1966), ONO (1967).

n=12: HOLMEN (1958).

The karyotypes found in the 18 populations studied by the present authors agree closely with LOWRY's drawing.

The cytotype with n=7 reported by TATUNO and ONO has 6 large chromosomes and one of minute size. According to ONO (1967), the n=7 cytotype has structurally recognizable sex-chromosomes. The Y-chromosome has a larger quantity of heterochromatine than the X-chromosome.

RAMSAY studied mitoses of male and female gametophytes in four populations, all of the n=6 cytotype. She could not find any cytological differences between the sexes of this cytotype.

The cytotype with n=12 has only been

Figs. 1—17. Gamophytic mitoses. — 1: *Bryum pseudotriquetrum*, n=10. — 2: *Mnium affine*, n=6 (cf. Fig. 38). — 3: *M. affine*, idiogram. — 4: *M. cinclidioides*, n=6. — 5: *M. cuspidatum*, n=12. — 6: *M. hornum*, n=6 (cf. Fig. 39). — 7: *M. seligeri*, n=6. — 8: *M. undulatum*, n=6 (cf. Fig. 40). — 9: *M. undulatum*, idiogram. — 10: *M. undulatum*, n=7 (cf. Fig. 43). — 11: *Abetinella abietina*, n=11 (cf. Fig. 51). — 12: *Thuidium tamariscinum*, n=11 (cf. Fig. 54). — 13: *Isothecium myurum*, n=11. — 14: *Brachythecium albicans*, n=7 (cf. Fig. 45). — 15: *B. plumosum*, n=11. — 16: *B. plumosum*, n=10 (cf. Fig. 46). — 17: *B. populeum*, n=10.

reported once from a natural population. MARCHAL and MARCHAL have produced plants with n=12 experimentally from the somatic tissue of sporophytes.

Mnium seligeri (JUR. ex LINDB.) LIMPR. — n=6 (Fig. 7)

1 population: III (68—335).

Chromosome counts published previously:

n=6: HEITZ (1942), HOLMEN (1958) — 2 populations.

The centromeric regions are clearly seen in the contracted chromosomes. The centromeres are median to submedian.

Mnium undulatum HEDW. — n=6 (Figs. 8, 9, 40); n=7 (Figs. 10, 43)

n=6: 11 populations: I (68—264); III (68—345); VI (69—71); VII (69—35); IX (68—464); XIV (68—459); Sk, V. Vram, Sätaröd (69—46); Sk, Lund (69—49); XVI (68—490); XVIII (68—536, 68—555).

n=7: 1 population: VI (69—74).

Chromosome counts published previously:

n=6: HEITZ (1942), HAMANT (1950, 1954), HOLMEN (1958), VYSOTSKAYA (1967), SMITH & NEWTON (1968), RAMSAY (1969).
n=7: TATUNO & ONO (1966).
n=8: MAZZEO (1941).

This species is one of the most extensively studied in the genus. The centromeres are easily observable in the metaphase stage. One chromosome has a secondary constriction near the end of the arm. Two other chromosomes have negative heteropycnotic end segments (Fig. 40.)

It is obviously correct that two chromosome races occur in the species: n=6 and n=7. The cytotype n=6 seems to be the most common.

According to recent Japanese studies, the n=7 cytotype observed in several species of *Mnium* consists of 6 large chromosomes and one minute chromosome. The n=7 cytotype reported from one population by the present authors consists also of 6 large chromosomes and one minute, rather faintly stained chromosome (Fig. 43). It cannot be excluded that this minute chromosome has sometimes been overlooked in previous counts where n=6 were reported.

The first chromosome number reported in the species, n=8, has not been verified by any other author and may be a mistake.

Family Thuidiaceae

Abietinella abietina (HEDW.) FLEISCH. — n=11 (Figs. 11, 51)

2 populations: Öl, Alböke, Bruddesta (69—103, coll. S. SUNHEDE); Öl, Borgholm (69—106, coll. S. SUNHEDE).

No chromosome counts have previously been reported. In both populations 3 large chromosomes, 7 small, and 1 minute are found. This agree well with INOUE's results in several other genera in Thuidiaceae from which he reported quite the same karyotype (INOUE 1965 b).

Abietinella is closely related to *Thuidium* and many authors do not distinguish between these two genera.

Thuidium tamariscinum (HEDW.) B.S.G. — n=11 (Figs. 12, 54)

1 population: Sk, Gödelöv, Björnstorp (68—446).

Chromosome counts published previously:

n=11: SMITH & NEWTON (1966, 1968) — 7 populations, RAMSAY (1969) — 4 populations.

In recent studies on this genus, all species are reported to have 11 chromosomes. In some older investigations, *Thuidium* was reported to have only 10. The minute chromosome was probably overlooked previously.

The karyotype is similar to that of *Abietinella abietina* and many other genera in Thuidiaceae, viz. 3 large, 7 small, and one minute chromosomes. The same

Figs. 18—37. Gamophytic mitoses. — 18: *Brachythecium reflexum*, n=11 (cf. Fig. 41). — 19: *B. rivulare*, n=6 (cf. Fig. 42). — 20: *B. rivulare*, n=12 (cf. Fig. 47). — 21: *B. rutabulum*, n=12 (cf. Fig. 53). — 22: *B. velutinum*, n=10 (cf. Fig. 52). — 23: *Eurhynchium striatum*, n=11 (cf. Fig. 50). — 24: *Homalothecium lutescens*, n=10. — 25: *H. sericeum*, n=11 (cf. Fig. 44). — 26: *Pleurozium schreberi*, n=5 (cf. Fig. 49). — 27: *Rhytidiadelphus loreus*, n=5. — 28: *R. squarrosus*, n=10. — 29: *R. triquetrus*, n=6. — 30: *Atrichum undulatum*, n=21. — 31: *Pogonatum aloides*, n=7. — 32: *P. urnigerum*, n=7. — 33: *Polytrichum commune*, n=7. — 34: *P. formosum*, n=7. — 35: *P. juniperinum*, n=7. — 36: *P. longisetum*, n=7. — 37: *P. piliferum*, n=7 (cf. Fig. 48).

karyotype was reported by INOUE (1965 b). No centromeres could be seen by the present authors, but INOUE observed three chromosomes with subterminal centromeres. RAMSAY reported four chromosomes with subterminal (or nearly terminal) centromeres.

Family Lembophyllaceae

Isothecium myurum (BRID.) BRID. — n=11 (Fig. 13)

1 population: Sm, Stenbrohult (68—505).

Chromosome counts published previously:

n=10: LAZARENKO & VYSOTSKAYA (1964), VYSOTSKAYA (1967).
n=11: VYSOTSKAYA & FETISOVA (1969).
n=11+m: SMITH & NEWTON (1966) — 5 populations, VYSOTSKAYA (1970).

The population studied here has one chromosome larger than the others. This observation agrees with the results of SMITH and NEWTON in other species of the genus, where n=11 has been found, e.g. *I. myosuroides* (BRID.) BRID. (SMITH & NEWTON 1966; VAARAMA 1968), and *I. subdiverseforme* BROTH. (INOUE 1965 a).

SMITH and NEWTON reported 5 populations of *I. myosuroides* with n=11, but 4 populations with n=11+m. It is obvious that populations with and without the very small m-chromosome exist in *Isothecium*.

Family Brachytheciaceae

Brachythecium albicans (HEDW.) B.S.G. — n=7 (Figs. 14, 45)

6 populations: XI (69—8); Sk, Riseberga, Ljungbyhed, Bonnarp (69—87); Sk, Barsebäck (69—47); Sk, Gladsax, Vårhallarna (68—449); Vg, Björketorp, Hindås (69—88); XX (69—98).

Chromosome counts published previously:

n=6 or 7: HOLMEN (1958).
n=9: VAARAMA (1950a), HO (1956).

HOLMEN counted n=6 in meiotic preparations of a Danish population, but in some of the sporocytes studied, an additional minute chromosome configuration could be observed. HOLMEN was uncertain if the population had n=6 or n=7.

In all populations studied here, 4 long chromosomes, 2 medium, and 1 small chromosomes are observable. The conditions agree rather well with HOLMEN's results.

Brachythecium plumosum (HEDW.) B.S.G. — n=10 (Figs. 16, 46); n=11 (Fig. 15)

n=10: 1 population: VIII (69—44).
n=11: 1 population: XX (69—101).

Chromosome counts published previously:

n=10: IRELAND (1965), SMITH & NEWTON (1967) — 14 populations, VYSOTSKAYA (1967).
n=10+m: ANDERSON & AL-AISH (1963), CHOPRA & KUMAR (1967).
n=11: INOUE (1967).

In both populations studied, one chromosome is markedly longer than the others, and three other chromosomes are of intermediate size. A minute chromosome is the cytologicaly observable difference between the two cytotypes.

The n=11 karyotype agrees well with the one found by INOUE.

Brachythecium populeum (HEDW.) B.S.G. — n=10 (Fig. 17)

1 population: XII (69—86).

Chromosome counts published previously:

n= 9: VAARAMA (1950 a).
n=10: VAARAMA (1950 a), YANO (1955), SMITH & NEWTON (1967) — 10 populations, VYSOTKAYA (1967) — 5 populations, VYSOTSKAYA & FETISOVA (1969).
n=11: INOUE (1964, 1967), CHOPRA & KUMAR (1967).

The population studied by the present authors have 1 long + 3 medium + 6 short chromosomes. The markedly long chromosome was observed also by SMITH and NEWTON as a large bivalent. The relative sizes of the chromosomes of the Swedish population are similar to those found by YANO and by INOUE.

The two cytotypes reported by VAARAMA represent populations of two ecological races. The n=9 populations is xerophilous, and the n=10 population is mesophilous.

Brachythecium reflexum (STARKE) B.S.G. — n=11 (Figs. 18, 41)

2 populations: XI (69—10); XIX (69—97).

Chromosome counts published previously:

n=20: LAZARENKO et al. (1970).

Two long chromosomes are easily recognizable; the other 9 chromosomes are more difficult to identify as the differences between them are small.

Brachythecium rivulare B.S.G. — n=6 (Figs. 19, 42); n=12 (Figs. 20, 47)

n=6: 1 population: II (68—304).

n=12: 2 populations: II (68—327); Sm, Växjö, SW Lövsjön (68—507).

Chromosome counts published previously:

n= 6: HOLMEN (1958), SMITH & NEWTON (1968), VYSOTSKAYA & FETISOVA (1969).
n=11: INOUE (1967).
n=13: VYSOTSKAYA (1967, 1970).
n=16: ANDERSON & BRYAN (1958).

At least two chromosome races exist in Scandinavia. In the n=6 cytotype all the chromosomes are of the same size which agrees with HOLMEN's drawing. In the population with n=12, all the chromosomes are also of about the same size.

It has not yet been studied if there are any morphological differences between the two cytotypes.

Brachythecium rutabulum (HEDW.) B.S.G. — n=12 (Figs. 21, 53)

7 populations: IV (69—16); XI (69—7); XII (69—84); XIII (69—80); Sk, Gödelöv, Björnstorp (68—445); Sk, N. Sandby (69—21); XVIII (68—549).

Chromosome counts published previously:

n= 5: HOLMEN (1958).
n=10: MOUTSCHEN (1955), HOLMEN (1958).
n=11: SINOIR (1952), CHOPRA & KUMAR (1967).
n=12: WILSON & BURNETT (1959), SMITH & NEWTON (1967) — 12 populations, RAMSAY (1969), VYSOTSKAYA & FETISOVA (1969), VYSOTSKAYA (1970) — 2 populations.
n=13: VYSOTSKAYA (1967).
n=20: RAMSAY (1969) — 2 populations.

The populations studied by HOLMEN probably belong to two different taxa within the *Brachythecium rutabulum* complex. The one with n=10 is closely related to *B. curtum* (LINDB.) LIMPR. and is autoicous while the population with n=5 is probably diocious. These two taxa are morphologically distinguished by the cell structure, the spore size, the setae, and the capsules.

B. rutabulum is morphologically markedly polymorphous, and meiotic irregularities are also common. The failure of chromosome pairing, and the occurrence of lagging chromosomes, bridges, fragments, and other cytological irregularities make it difficult to analyse the meiotic metaphases and to count chromosome numbers in meiotic stages.

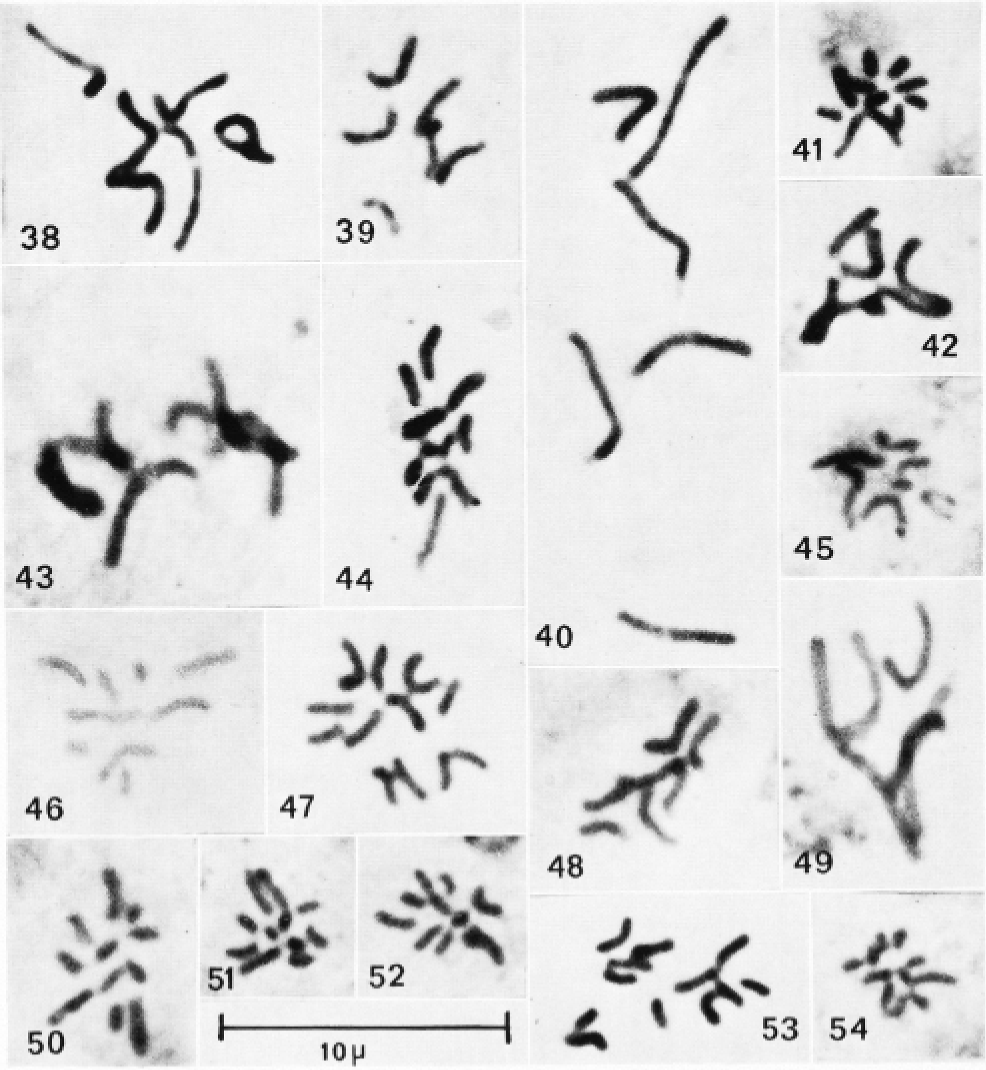
WILSON and BURNETT suggested that the n=12 cytotype might be an autopolyploid strain, but SMITH and NEWTON object to this conclusion as they neither found any haploid population, nor trivalents or quadrivalents in meiotic studies of the n=12 cytotype.

Brachythecium velutinum (HEDW.) B.S.G. — n=10 (Figs. 22, 52)

1 population: IV (69—17).

Chromosome counts published previously:

n=10: MARCHAL & MARCHAL (1911), HO (1956) — 2 populations, LAZARENKO & VYSOTSKAYA (1954), VYSOTSKAYA (1967) — 3 populations, SMITH & NEWTON (1968).



Figs. 38—54. Photomicrographs of gamophytic mitoses drawn in previous pictures. — 38: *Mnium affine*, n=6 (cf. Fig. 2). — 39: *M. hornum*, n=6 (cf. Fig. 6). — 40: *M. undulatum*, n=6 (cf. Fig. 8). — 41: *Brachythecium reflexum*, n=11 (cf. Fig. 18). — 42: *B. rivulare*, n=6 (cf. Fig. 19). — 43: *Mnium undulatum*, n=7 (cf. Fig. 10). — 44: *Homalothecium sericeum*, n=11 (cf. Fig. 25). — 45: *Brachythecium albicans*, n=7 (cf. Fig. 14). — 46: *B. plumosum*, n=10 (cf. Fig. 16). — 47: *B. rivulare*, n=12 (cf. Fig. 20). — 48: *Polytrichum piliferum*, n=7 (cf. Fig. 37). — 49: *Pleurozium schreberi*, n=5 (cf. Fig. 26). — 50: *Eurhynchium striatum*, n=11 (cf. Fig. 23). — 51: *Abietinella abietina*, n=11 (cf. Fig. 11). — 52: *Brachythecium velutinum*, n=10 (cf. Fig. 22). — 53: *B. rutabulum*, n=12 (cf. Fig. 21). — 54: *Thuidium tamariscinum*, n=11 (cf. Fig. 12).

n=11: Vaarama (1950a).
n=12: Smith & Newton (1968).

The population studied has 4 long, 2 medium, and 4 short chromosomes.

Meiotic irregularities make it difficult to count the chromosomes in meiotic stages (Smith & Newton).

Eurhynchium striatum (Hedw.) Schimp. — n=11 (Figs. 23, 50)

2 populations: XIV (68—461); XVII (68—513).

Chromosome counts published previously:

n= 6: Holmen (1958).
n=11: Ho (1956), Smith & Newton (1967) — 8 populations.
n=12: Vysotskaya (1967).

Except 8 chromosomes difficult to classify, there are 3 large chromosomes in the two populations studied here. This corresponds to the findings by Ho and by Smith and Newton who could recognize 3 large bivalents in their material.

Homalothecium lutescens (Hedw.) Robins. — n=10 (Fig. 24)

2 populations: IX (69—83): Gt, Rute, Storungs (69—105, coll. S. Sunhede).

Chromosome counts published previously:

n= 8: Holmen (1958).
n=11: Smith & Newton (1968).
n=12: Lazarenko & Lesnyak (1966), Vysotskaya (1967).
n=14: Ho (1956).

The two populations studied have 2 long + 2 medium + 5 short + 1 minute chromosomes.

Homalothecium sericeum (Hedw.) B.S.G. — n=11 (Figs. 25, 44)

2 populations: VII (69—43); Sk, Gumlösa (69—81).

Chromosome counts published previously:

n=8: Holmen (1958), Smith & Newton (1968) — 9 populations, Vysotskaya & Fetisova (1969).
n= 9: Smith & Newton (1968).
n=10: Ramsay (1969).
n=10+m: Smith & Newton (1968); as n=10+?, Ramsay (1969).
n=11: Smith & Newton (1968) — 2 populations.
n=11+m: Smith & Newton (1968).
n=12+2m: Ramsay (1969).

It has been difficult to get a good contrast between the chromosomes and the cytoplasm, and to make correct chromosome counts in mitotic metaphases of this species.

According to Smith and Newton it is also very difficult to determine the chromosome number in meiotic metaphases as a result of occurring cytological irregularities as univalents, trivalents, pentavalents, bridges, fragments, etc.

Family Hypnaceae

Pleurozium schreberi (Brid.) Mitt. — n=5 (Figs. 26, 49)

17 populations: IV (69—11); V (69—12); VII (69—34); X (69—30); XII (69—76); XIII (69—65); Sk, Fulltofta, Ludvigsborg (68—442); Sk, Gualöv (69—18); Sk, V. Vram, Linderödsåsen, Sätaröd (69—45); XVI (68—482, 68—511); XVII (68—502); XVIII (68—519, 68—529, 68—532); XIX (69—94); Öl, Högby, Lindnabben (69—104, coll. S. Sunhede).

Chromosome counts published previously:

n=5: Vaarama (1954a), Holmen (1958), Lazarenko & Vysotskaya (1965), Vysotskaya (1967) — 2 populations, Smith & Newton (1968), Yano (1968) — older counts corrected, Ramsay (1969) — 2 populations, Vysotskaya & Fetisova (1969).

The mitotic metaphases always consist of 1 long and 4 medium sized chromosomes. This karyotype is similar to the one shown in drawings by Vaarama, whos paper on this species is a pioneer work on the centromeric conditions of mosses.

Rhytidiadelphus loreus (Hedw.) Warnst. — n=5 (Fig. 27)

1 population: XVII (68—479).

Chromosome counts published previously:

n=5: IRELAND (1965) — 2 populations, SMITH & NEWTON (1967) — 2 populations.

It is often difficult to get good preparations of the mitotic metaphases as the chromosomes of *Rhytidiadelphus* are insufficiently spread. The five chromosomes of *R. loreus* are rather large and all of about the same size.

Rhytidiadelphus squarrosus (HEDW.) WARNST. — n=10 (Fig. 28)

2 populations: III (68—356); Sk, Brunnby, Lerhamn (68—443).

Chromosome counts published previously:

n= 6—8: HEITZ (1928).

n= 8: VAARAMA (1968).

n=10: LAZARENKO & VYSOTSKAYA (1965), VYSOTSKAYA (1967).

The chromosomes are all much shorter than those of *R. loreus*. Five chromosomes are of about half the length of the longest chromosomes.

It should be remarked that YANO (1950, 1951, 1952, 1963) published n=10 for *R. calvescens* (WILS.) BROTH., taxinomically regarded as closely related to *R. squarrosus*.

Rhytidiadelphus triquetrus (HEDW.) WARNST. — n=6 (Fig. 29)

1 population: XVII (68—501).

Chromosome counts published previously:

n=5: YANO (1950).

n=6: IRELAND (1967), YANO (1951, 1952, 1963), HOLMEN (1958), SMITH & NEWTON (1967) — 2 populations, VYSOTSKAYA (1967).

The chromosomes are all of about the same size, similar to the longest chromosome of *R. squarrosus*.

Family Polytrichaceae

Atrichum undulatum (HEDW). P. BEAUV. — n=21 (Fig. 30)

10 populations: V (69—20); VI (69—77); VII (69—38); XI (69—6); XII (69—54); XIII (69—67); XV (69—52); XVII (68—496, 68—499); XVIII (68—543).

Chromosome counts published previously:

n= 7: KURITA (1950), TATUNO (1953), LOWRY (1954), KHANNA (1967), SMITH & NEWTON (1968) — 2 populations.

n=14: LOWRY (1954), LAZARENKO & VYSOTSKAYA (1965), SMITH & NEWTON (1966) — 4 populations, TATUNO & KISE (1970).

n=21: KURITA (1937), TATUNO (1953), LEWIS (1957), LAZARENKO & VYSOTSKAYA (1964, 1965), SMITH & NEWTON (1966, 1968) — 13 populations, VYSOTSKAYA (1966, 1967, 1970), VYSOTSKAYA & FETISOVA (1969), FETISOVA & VYSOTSKAYA (1970).

More approximative counts have also been published:

n=14—16: HEITZ (1926, 1928).

n=20—22: HEITZ (1926, 1928).

2n c. 42: HOLMEN (1958).

It is hardly possible to distinguish different size classes among the chromosomes though the longest ones are about twice as long as the shortest chromosome.

Pogonatum aloides (HEDW.) P. BEAUV. — n=7 (Fig. 31)

1 population: XVI (68—486).

Chromosome counts published previously:

n=7: HOLMEN (1958), GANGULEE & CHATTERJEE (1960, 1962), SHARMA (1960, 1963), LAZARENKO et al. (1967), SMITH & NEWTON (1967) — 3 populations, VYSOTSKAYA (1967), RAMSAY (1969) — 2 populations.

One of the chromosomes is markedly longer than the other ones, which are all of medium size.

Pogonatum urnigerum (HEDW.) P. BEAUV. — n=7 (Fig. 32)

5 populations: V (69—23); XII (69—58, 69—78); XIII (69—68); XVI (68—488).

Chromosome counts published previously:

n=6—7: Heitz (1928).

n=7: Kurita (1937), Yano (1954), Smith & Newton (1966) — 2 populations, Ireland (1967), Vysotskaya (1967).

The relative lengths of the chromosomes in this species are rather similar to those of *P. aloides*.

Structural sex-chromosomes have been reported by Yano in this species.

Polytrichum commune Hedw. — n=7 (Fig. 33)

10 populations: V (69—25); X (69—31); XII (69—56); XV (69—50); XVI (68—477, 68—493); XVIII (68—525, 68—531); Vg, Mölndal, Toltorpsdalen (69—90); XX (69—100).

Chromosome counts published previously:

n=7: Jachimsky (1935), Kurita (1937), Vaarama (1950a, 1956, 1964), Yano (1953), Lazarenko & Vysotskaya (1965), Smith & Newton (1967) — 2 populations, Vysotskaya (1967), Ramsay (1969) — 2 populations.

n=14: Kurita (1937).

In *Polytrichum* as also in *Pogonatum*, it is difficult to get the chromosomes spread. This problem may be an explanation of an older report of n=6, which obviously is an incorrect count.

One long and one short chromosome are easily recognizable in the karyotype. As will be discussed under *P. formosum*, these two chromosomes have been regarded as sex-chromosomes by some authors.

Polytrichum formosum Hedw. — n=7 (Fig. 34)

19 populations: IV (69—14); V (69—22); VI (69—75); VII (69—33); VIII (69—27); X (69—29); XI (69—5); XII (69—59; 69—60); XIII (69—62, 69—64); XIV (68—460); XVII (68—480, 68—500); XVIII (68—521, 68—524, 68—533, 68—535, 68—540).

Chromosome counts published previously:

n= 7: Schimotomai & Kimura (1934, 1936), Yano (1953), Lewis (1957), Holmen (1958), Smith & Newton (1967), Vysotskaya (1967), Ramsay (1969) — 4 populations.

n=14: Kurita (1937), Lazarenko & Vysotskaya (1965), Vysotskaya (1967) — 2 populations.

It is possible to recognize one long chromosome also in this species, but any markedly short chromosome can hardly be distinguished.

According to Shimotomai and Kimura, the longest chromosome in this species is a female sex-chromosome, but the male sex-chromosome is one of the shortest chromosomes.

The same system of sex-chromosomes was described by Shimotomai and Koyama (1932) in *Pogonatum inflexum* (Lindb.) Lac. According to Yano (1953, 1954), the sex-chromosomes are the two longest chromosomes in *Polytrichum* as well as in *Pogonatum*.

Polytrichum juniperinum Hedw. — n=7 (Fig. 35)

3 populations: X (69—32); XV (69—53); XVIII (68—534).

Chromosome counts published previously:

n=6: Arens (1907), J. & W. Leeuwen-Reijnvaan (1907, 1908), Allen (1912), Vandendries (1912).

n=7: Heitz (1928) as n=(6)—7, Kurita (1937), Vaarama (1950a), Yano (1953), Lewis (1957), Anderson & Crum (1958) — 2 populations, Smith & Newton (1967) — 3 populations, Ono (1968), Ramsay (1969) — 2 populations.

The karyotype of this species is similar to those of other *Polytrichum* species: one long and one short chromosome are here again easily recognizable.

The first reports on the chromosome number of *P. juniperinum* are all different from later reports. The chromosome number $n=6$ is obviously incorrect and may be a result of improper methods.

Polytrichum longisetum Sw. ex. Brid. — $n=7$ (Fig. 36)

1 population: VII (69—37).

Chromosome counts published previously:

$n=7$: Vysotskaya (1967).
$n=12$—14: Heitz (1928).
$n=14$: Vaarama (1953), Holmen (1958).

The karyotype is similar to that one observed in some other *Polytrichum* species: one long and one short chromosome are easily recognizable.

Heitz' report of $n=12$—14 seems to indicate uncertainty rather than a cytological variation.

Polytrichum piliferum Hedw. — $n=7$ (Figs. 37, 48)

5 populations: Sk, Brunnby, Krapperup (68—444); Sk, Riseberga, Ljungbyhed, Bonnarp (69—61); XVIII (68—530, 68—547); XX (69—99).

Chromosome counts published previously:

$n=6$: J. & W. Leeuwen-Reijnvaan (1907, 1908), Vandendries (1912).
$n=7$: Heitz (1928), Vaarama (1905a), Yano (1953), Anderson & Crum (1958), Smith & Newton (1967) — 2 populations, Ono (1968), Ramsay (1969).

The karyotype is rather similar to that one found in some other *Polytrichum* species, though it is more difficult to recognize any markedly long chromosome.

According to Yano, the two longest chromosomes are heterochromosomes of sex-character. Anderson and Crum could, however, not find any heterochromosomes when they studied a population from the Canadian Rocky Mountains.

The old reports of $n=6$ are probably incorrect.

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A Contribution to the Bryophytic Flora of Attica and Peloponnese

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ABSTRACT

RUNGBY, S. 1971. A contribution to the bryophytic flora of Attica and Peloponnese. — Bot. Notiser 124: 228—230.

Some hepaticae and musci collected in Attica and Peloponnese are recorded. The specimens are preserved in the Botanical Museum, Copenhagen.

The present list enumerates some hepaticae and musci collected in March—April 1969 and February 1970 in Attica and Peloponnese for the areas of which, as well as for the Greek mainland on the whole, the knowledge of mosses is scarce.

Notable are 2 papers by COPPEY (1907, 1909), which — on the basis of previous literature and contemporary collections from some localities scattered all over the territory — draw up catalogues on the species found up to that time and include some remarks about ecology and distribution.

Somewhat better is the situation about the Aegean islands. RECHINGER (1943) names the species found on the islands before Flora Aegaea was written, CIFERRI (1944 pp. 137—139) gives a list concerning the islands once occupied by Italy, DÜLL (1966) gives a comprehensive account of mosses from Crete, and RUNGBY (1966, 1967) adds some species from Rhodes and Crete not previously recorded.

The available material, as expected, seems to confirm that the Greek moss-flora is in accordance with that of the rest of the Mediterranean area.

All species stated in the present list, except *Barbula revoluta*, are stated from Crete in DÜLL's paper, which also gives information on the ecological conditions of the species.

These conditions are the same as generally are valid for the whole Mediterranean area, and as the species in the present list also were found growing in the same way, only exceptionally remarks on ecology are given.

The samples are kept in the Botanical Museum, Copenhagen (C).

The localities are: Agora in Athens, Lykabettos, Hymettos, Pentelikon opposite Kiphisia, Pentelikon opposite Penteli, Parnes: *Abies cephalonica*-forest near the summit, Perama, Dafni, Eleusis, Marathon, Sounio, Salamis, Aegina, Corinth: the ancient town, Mycenae, Sparta.

For some of the localities are applied abbreviations, which easily are to be understood.

Targionia hypophylla L. — Kor.

Lunularia cruciata (L.) DUM. — Agora — Hym. — Dafni.

Frullania dilatata (L.) DUM. — Parnes, on *Abies cephalonica*.

Bartramia stricta BRID. — Agora — Pent. P. — Aeg. — Kor.

Bryum torquescens BR. EUR. — c.fr. Hym.

— c.fr. Pent. K. — c.fr. Sounio — Kor. — c.fr. Sparta.

Bryum bicolor Dicks. — Lyk. — Hym. — Pent. K.

Bryum caespiticium Hedw. var. *comense* (Schpr.) Husn. — Lyk.

Funaria hygrometrica Hedw. — c.fr. Pent. K. — c.fr. Parnes.

Funaria mediterranea Lindb. — c.fr. Lyk.

Encalypta vulgaris Hedw. — c.fr. Lyk.

Tortula intermedia (Brid.) De Not. — Lyk. — c.fr. Hym. — Pent. P. — c.fr. Parnes — Dafni — Sparta.

Tortula atrovirens (Sm.) Lindb. — c.fr. Lyk.

Tortula marginata (Br. eur.) Spruce — c.fr. Agora.

Tortula muralis Hedw. — Agora — Lyk. — Pent. K. — Pent. P. — Aeg. — Sparta — all c.fr.

Crossidium squamigerum (Viv.) Jur. — Lyk. — Hym. — Eleu. — Aeg. — all c.fr.

Crossidium chloronotos (Brid.) Limpr. — Lyk.

Aloina ambigua (Br. eur.) Limpr. — Agora — Lyk. — Hym. — Perama — Dafni — Sounio — Salamis — Aeg. — Kor. — all c.fr.

Pottia starkeana (Hedw.) C. Müll. — Lyk. — Pent. K. — Mar. — all c.fr.

Timmiella barbuloides (Brid.) Mönkem. — c.fr. Agora — Hym. — c.fr. Aeg. — c.fr. Kor.

Pleurochaete squarrosa (Brid.) Lindb. — Agora — Lyk. — Hym. — Dafni.

Tortella tortuosa (Hedw.) Limpr. — Lyk. — Hym. — Parnes.

Tortella flavovirens (Bruch) Broth. — c.fr. Sounio.

Trichostomum crispulum Bruch — Hym. — Pent. K. — Parnes — Sounio — Aeg.

Trichostomum mutabile Bruch — Hym. — Dafni.

Trichostomum mutabile Bruch var. *densum* Schpr. — Sounio.

Gymnostomum aeruginosum Sm. — Agora — Lyk.

Gyroweisia reflexa Schpr. — Hym.

Barbula convoluta Hedw. — Agora — Hym. — Pent. K. — Pent. P. — Aeg. — Kor.

Barbula unguiculata Hedw. — c.fr. Agora — c.fr. Lyk. — c.fr. Hym. — Pent. K. — Parnes — c.fr. Mar. — c.fr. Sounio.

Barbula revoluta (Schrad.) Brid. — Eleu. — Sounio — Kor.

Barbula hornschuchiana Schultz — c.fr. Agora — Hym. — Salamis — Kor.

Barbula rigidula (Hedw.) Mitt. — c.fr. Agora — c.fr. Lyk. — Hym. — Pent. K. — Pent. P. — c.fr. Perama — Dafni — Eleu. — Mar. — c.fr. Sounio — Aeg. — Kor. — Mycenae.

Barbula trifaria (Hedw.) Mitt. — Pent. K.

Barbula tophacea (Brid.) Mitt. — Lyk. — Hym. — Salamis — Mar.

Barbula tophacea (Brid.) Mitt. f. *acutifolia* (Schpr.) Mönkem. — c.fr. Hym. — c.fr. Pent. K. — Dafni — c.fr. Sounio.

Barbula tophacea (Brid.) Mitt. f. *humilis* (Schpr.) Mönkem. — Hym. — Pent. P.

Barbula cylindrica (Tayl.) Schimp. — Hym. — Parnes.

Grimmia trichophylla Grev. — Parnes.

Grimmia pulvinata (Hedw.) Sm. — c.fr. Lyk. — c.fr. Hym. — Pent. K. — c.fr. Pent. P. — c.fr. Dafni — c.fr. Parnes.

Amisothecium varium (Hedw.) Mitt. — Lyk. — Hym. — Mar.

Orthotrichum cupulatum Brid. — c.fr. Parnes, on calcareous walls near Haghia Triada.

Orthotrichum lyellii Hook. & Tayl. — Parnes, on *Abies cephalonica.*

Leucodon sciuroides (Hedw.) Schwaegr. var. *morensis* (Hedw.) Sm. — Parnes, on rocks and *Abies cephalonica.*

Pterogonium gracile (Hedw.) Br. eur. — Parnes, extensive mats on rocks and *Abies cephalonica.*

Leptodon smithii (Dicks.) Mohr — Parnes, on rocks and *Abies cephalonica.*

Neckera menziesii Hook. — Parnes, on rocks and *Abies cephalonica.*

Homalothecium sericeum (Hedw.) Br. & Sch. — Lyk. — Hym. — Pent. K. — Parnes — Dafni.

Scleropodium tourettii (Brid.) L. Koch — Hym. — Kor.

Scorpiurium circinatum (Brid.) Flschr. & Loeske — Lyk. — Sparta.

Rhynchostegium megapolitanum (Bland.) Br. & Sch. — Lyk. — c.fr. Hym. — Parnes.

Hypnum cupressiforme Hedw. — Hym. — Parnes — Pent. K.

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Past and Present Distribution of Nigella arvensis L. ssp. arvensis in Europe

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ABSTRACT

Strid, A. 1971. Past and present distribution of Nigella arvensis L. ssp. arvensis in Europe. — Bot. Notiser 124: 231—236.

Nigella arvensis L. ssp. *arvensis*, formerly a widely distributed weed of cultivated fields in most of continental Europe, has decreased considerably in frequency during this century, especially in the northern and atlantic parts of the continent. Three maps show its distribution 1) before 1890, 2) 1890—1929, and 3) 1930—1969, according to material preserved in c. 30 major European herbaria.

Three main reasons for the decrease in frequency are suggested: 1) early harvesting, 2) improved purification of seed, and 3) use of herbicides.

INTRODUCTION

The total distribution area of *Nigella arvensis* L. includes continental Europe (except the Iberian Peninsula), North Africa, Asia Minor, and the Middle East as far as Persia and the Caucasus (cf. Meusel, Jäger & Weinert 1965 a pp. 311, 485; 1965 b p. 156).

N. arvensis ssp. *arvensis* occurs in continental Europe and western North Africa. In central and southern Greece (approximately south of the 40th parallel) it is replaced by ssp. *aristata* (Sibth. & Sm.) Nym., and in Turkey by ssp. *glauca* (Boiss.) Terracc. Closely related endemic species and subspecies occur on the Aegean islands (cf. Strid 1970).

The eastern Mediterranean taxa grow in natural or semi-natural habitats (phrygana, sea-shores, abandoned fields etc.), whereas *N. arvensis* ssp. *arvensis* is a weed of cultivated fields.

When scanning the *Nigella* material of some major European herbaria it became evident that in large parts of its distribution area *N. arvensis* ssp. *arvensis* had been collected much less over the past few decades than previously. To obtain some, admittedly rough, idea of its past and present distribution, three maps were designed indicating collections made 1) before 1890 (mainly 1850—1889), 2) during the period 1890—1929, and 3) after 1929. The maps were based on material from the following herbaria (abbreviations according to Lanjouw & Stafleu (1964): B, BM, BR, BRSL, C, CL, E, FI, G, GB, HBG, JE, K, KRA, KRAM, LD, LE, LY, M, MA, P, POZ, PRC, S, SARA, SO, UPS, W, WA, WU, ZA.

Outside Europe, *N. arvensis* ssp. *arvensis* is known also from Morocco, Algeria, and Tunisia. The records are not sufficient for conclusions about possible changes in distribution and have been excluded from the maps.

OBSERVATIONS

Before 1890, *Nigella arvensis* appears to have been widely and evenly distri-

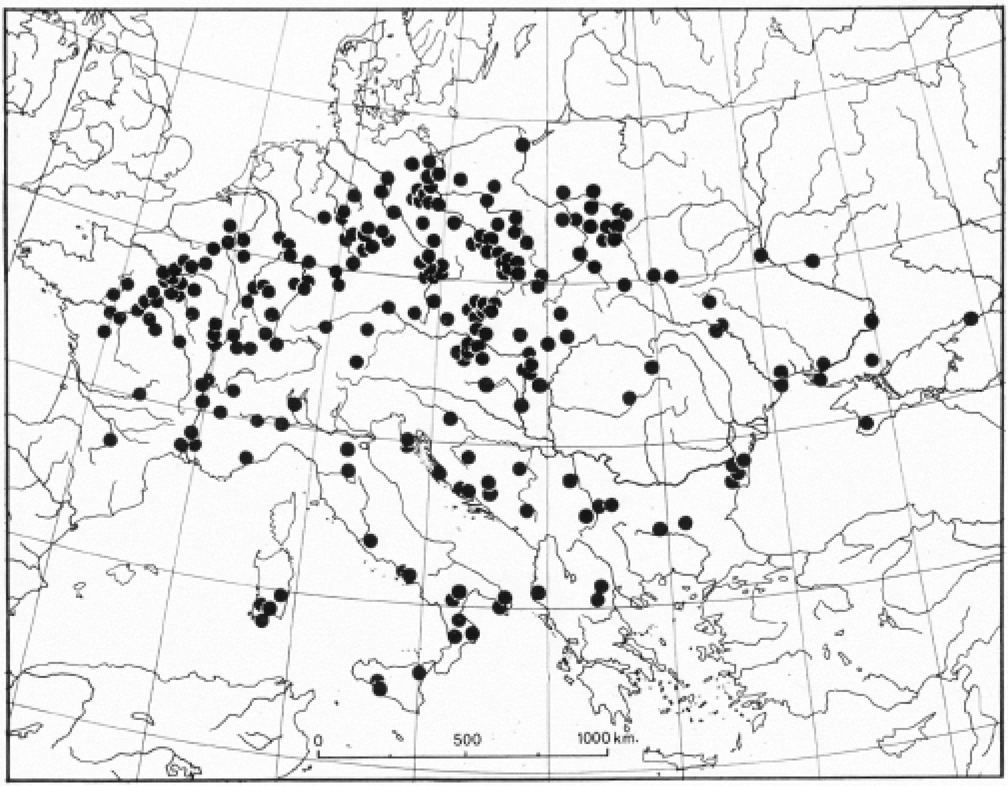

Fig. 1. *Nigella arvensis* L. ssp. *arvensis*. Collections made before 1890 (mainly 1850—1889).

buted in most of continental Europe except the Iberian Peninsula (where it is replaced by *N. hispanica* L.) and the more atlantic parts of France, Belgium, Holland, and Germany (Fig. 1). According to the usually scanty information on herbarium labels it occurred in a wide variety of disturbed habitats, but mainly as a weed among cereals on calciferous soils and rarely at altitudes above 500 m. On the Balkan Peninsula, where it may occur at higher altitudes (up to c. 1400 m in the southern part), it was no doubt more common than indicated by the map. There are surprisingly few records from Italy except in the extreme south. In the north of the continent it reached the Baltic Sea in eastern Germany and Poland, but seems never to have been collected in Scandinavia. In Holland, Belgium, and the lowlands of northern and north-western Germany (Schleswig-Holstein, Mecklenburg, Pommern) it is only recorded as a casual (cf. Ascherson & Graebner 1929 p. 616; Hegi 1912 p. 475). In Switzerland it has apparently always been rare and is only known from the northern and western parts.

During the period 1890—1929 (Fig. 2) the species decreased markedly in the northern and atlantic parts of the continent, but was still fairly widespread. In parts of Poland, Czechoslovakia, Hungary, and Austria a similar but much less pronounced tendency may be observed, although there are still areas, like Bohemia and Moravia, where no actual decrease seems to have occurred. In general

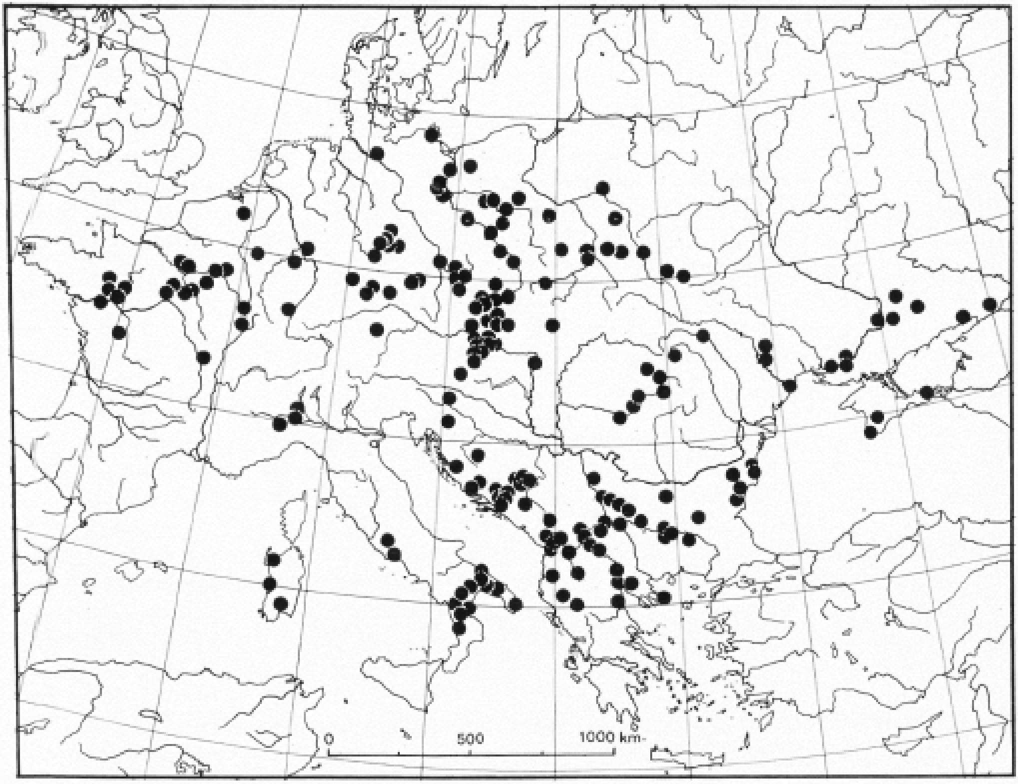

Fig. 2. *Nigella arvensis* L. ssp. *arvensis*. Collections made 1890—1929.

the species tended to withdraw to more continental areas. On most of the Balkan Peninsula as well as in southernmost Italy it was apparently common.

Over the past 40 years there has been a continued decrease in the frequency of *Nigella arvensis* throughout most of the European continent (Fig. 3). The species now appears to be fairly comon only on the Balkan Peninsula, especially in the southern parts. Locally it has been rather well collected as late as the 1960:s in parts of Czechoslovakia and Poland with scattered localities also in Hungary, Romania, and Ukraine. After 1950 there are only a few records from Italy, France, and E. Germany (DDR). In Switzerland, Austria, and W. Germany (BRD) it is very rare and possibly extinct.

The view obtained from herbarium material is supported by personal communications with botanists in several European countries, as shown in the following quotations:

"*Nigella arvensis* kam in unserer Gegend seit eh und je selten vor. Etwa seit 1950 ist sie aus der mir genauesten bekannten Gegend (ca 50 km Umkreis Stuttgart) praktisch völlig verschwunden. In diesem Bereich habe ich die Pflanze zum letzten Male 1949 gesehen . . . ." (Prof. Dr. D. AICHELE, Ehningen).

". . . dass *Nigella* bei uns in Oberösterreich eine grosse Rarität geworden ist; noch vor 50 Jahren als Ackerunkraut nicht gar so selten, ist sie jetzt . . . fast gänzlich verschwunden." (Dr. H. H. F. HAMANN, Linz).

". . . the distribution of *Nigella arvensis* in Poland decreases markedly." (Dr. L. Frey, Kraków).

"Je doute que l'on puisse récolter des graines de *Nigella arvensis* aux environs de Genève où l'espèce est pour aini dire inconnue." (Dr. R. Weibel, Geneva).

"*Nigella arvensis* kam in unseren Getreidefeldern früher sehr wenig vor, heute gar nicht mehr . . ." (Prof. Dr. M. Welten, Bern).

"Je ne connais pas actuellement aux environs de Paris, ni dans aucune des localités que je fréquente, un seul *Nigella arvensis*." (Dr. P. Joret, Paris).

". . . son existence dans notre région est menacée par l'emploi des hormones pour le désherbages des champs de blé." (Directeur, Jardin Botanique, Lyon).

Schubert and Hilbig (1969 pp. 189—191) made a detailed collocation of past and recent records of *Nigella arvensis* in the mapping area of 'Arbeitsgemeinschaft mitteldeutscher Floristen', i.e., southern DDR and adjacent parts of BRD, Czechoslovakia and Poland. Formerly widely distributed on loess and other calciferous soils in cultivated areas, especially in Thüringen and on the southern and eastern foothills of Harz, it has decreased markedly in frequency and is now restricted to a few localities in the drier and more continental parts of the region. Among species showing a similar tendency are *Bupleurum rotundifolium* L., *Caucalis latifolia* L., *Orlaya grandiflora* (L.) Hoffm., and *Adonis flammea* Jacq., whereas *Legousia hybrida* (L.) Del. is becoming restricted to the more atlantic parts of the mapping area in accordance with its general distribution (Schubert & Hilbig op. cit.).

DISCUSSION

Nigella arvensis ssp. *arvensis* is likely to have originated in the southern part of the Balkan Peninsula or in adjacent areas of north-western Anatolia, where it occurs in more or less natural habitats. Spreading into the European continent presumably took place with the introduction of agriculture. The species is recorded as early as the 9th century from a monastery in Switzerland (Hegi 1912 p. 476).

Fig. 1 can be supposed to correspond to its maximum distribution. In some areas, e.g., the northern and atlantic parts of France and Germany, regression seems to have started with the turn of the century or possibly even earlier. More continental areas were affected somewhat later.

Obvious shortcomings in the present mapping technique arise from the facts that 1) some areas have been more visited by collecting botanists than others, and 2) collecting activity has varied a great deal during different periods of time. Thus in Fig. 1 there are numerous records around cities like Vienna, Wroclaw, Berlin, and Paris, whereas the Balkan Peninsula and Russia are most probably undercollected. In Fig. 3, on the other hand, there is no doubt an unproportionally great number of records from northern Greece, which has recently been subject to a more detailed scanning (cf. Strid 1970 pp. 34, 47).

Considering these difficulties it has only been possible to observe prolonged general trends in the material. More sophisticated studies must be restricted to limited areas where herbarium material and literature records are extensive. Excellent examples are provided by the maps prepared by the Halle group of phytogeographists (cf. Meusel, Jäger & Weinert 1965 b, Schubert & Hilbig 1969).

The main reason for the decrease in the frequency of *Nigella arvensis* is no doubt the modern methods of agriculture. Three factors may be emphasized:

1. Early harvesting, a distinctive feature of modern agriculture resulting from improved early varieties of cereals. *Nigella arvensis* flowers in the late summer and often does not produce ripe seeds

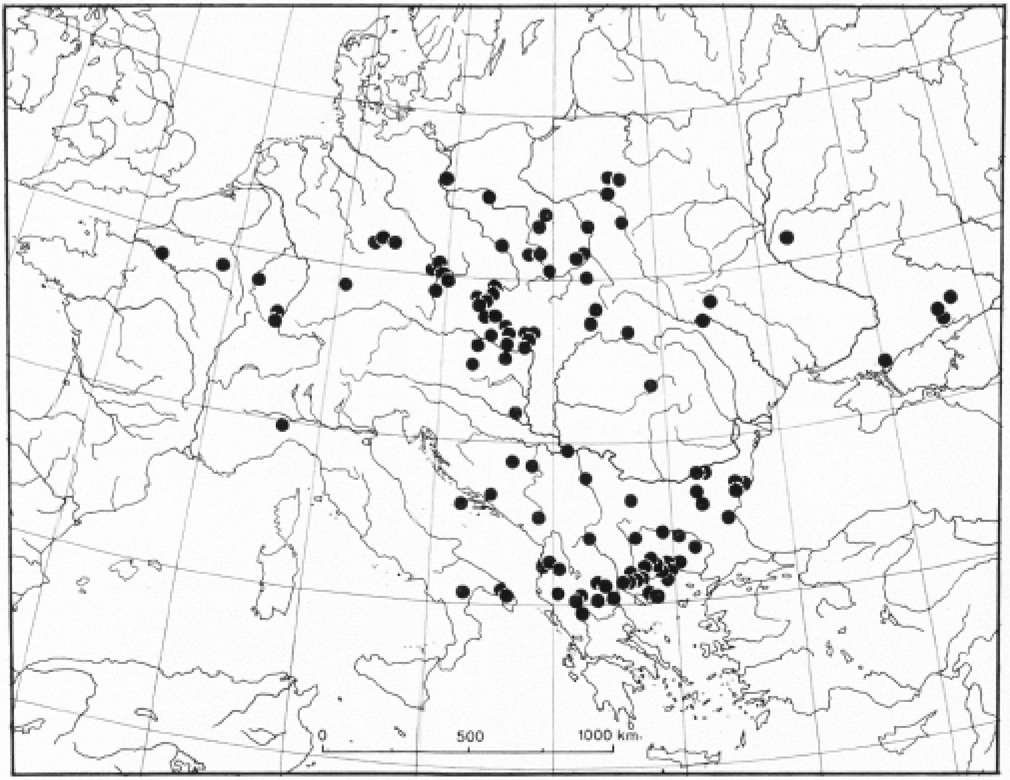

Fig. 3. *Nigella arvensis* L. ssp. *arvensis*. Collections made 1930—1969.

until September. When growing among cereals it thus runs a considerable risk of being cut before seed-setting.

2. Improved threshing methods and purification of seed material. Until recently this was probably the main factor involved.

3. Use of herbicides, a factor of increasing importance during the last few decades.

The combined effect appears to be a gradual extinction of *Nigella arvensis* from all areas where it has not become established in semi-natural habitats. The only region in central Europe where it still seems to be fairly common (although decreasing) is parts of Bohemia and Moravia. In these areas, as well as locally in Poland, it occurs not only among cereals but also to some extent in xerothermic communities on loess. Nevertheless, it is reasonable to assume that the species will eventually become restricted to its original area in the eastern Mediterranean.

ACKNOWLEDGEMENTS

I am indebted to several botanists who have supplied information about the occurrence of *Nigella arvensis* in various parts of Europe. In addition to those quoted in the text I should like to mention Prof. R. Corti (Florence), Prof. Dr. R. Domac (Zagreb), Dr. W. Hilbig (Halle), Dr. P. Lanzara (Rome), Mme A. Lourteig (Paris), Dr. J. Měšíček (Pruhonice), Dr. P. Müller-Schneider (Chur), Mrs H. Ritter (Sarajevo), and Dr. K. Rostański (Kraków). Thanks are also due to the directors and curators of the herbaria listed in the introduction who have sent their *Nigella* material on loan.

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Contribution to the Embryology of Scoparia dulcis L.

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ABSTRACT

Arekal, D., Rajeshwari, S. & Swamy, S. N. R. 1971. Contribution to the embryology of Scoparia dulcis L. — Bot. Notiser 124: 237—248.

The development of the ovary, ovules, male and female gametophytes, endosperm and embryo of *Scoparia dulcis* L. has been studied.

The microsporangium wall consists of an epidermis, endothecium, middle layer, and glandular tapetum. The tapetal cells become binucleate and the endothecial cells develop fibrous thickenings in later stages. Quadripartition of microspore mother cells is simultaneous. At shedding the pollen grains are two-celled and tricolpate.

Development of female gametophyte is of the Polygonum type. The synergids are hooked. An endothecium surrounds the middle part of the mature embryosac.

The endosperm is *ab initio* cellular. The chalazal haustorium consists of two long uninucleate cells. The micropylar haustorium has four such cells. The haustorial cells do not fuse together but degenerate as such. The organization of a quadriseriate chalazal part of the endosperm proper and the development of a secondary haustorium are noteworthy features.

Development of the embryo is of the Crucifer type. The cell *d* functions as the hypophysis.

The embryological data obtained in the study have been evaluated in the light of previous work in the tribe Digitaleae. The genus *Scoparia* appears to be nearer to the tribe Gratioleae than to the Digitaleae in which it is placed by Bentham (1846) and Wettstein (1897).

INTRODUCTION

The family Scrophulariaceae has attracted the attention of several embryologists from time to time because of the interesting diversity in structure and organization of endosperm haustoria. The publications of Crété (1953), Yamazaki (1953, 1954, 1957), Banerji (1961), Arekal (1963, 1964, 1965, 1966) and Tiagi (1965, 1966), summarize the embryological work on the family.

Embryology has long been recognized as one of the tools in correlating relationships among the taxa. In his recent publication on the Scrophulariaceae Arekal (1966) has pointed out its bearing on intra- and intertribal relationships within the family.

The genus *Scoparia* with which this paper deals has been placed under Digitaleae by Bentham (1846) and Wettstein (1893). Pennel (1935), on the other hand, places it under the Gratioleae which he regards as the most primitive tribe in the family Scrophulariaceae. The present investigation dealing with the development of male and female gametophytes, endosperm, embryo and seed coat structure of *Scoparia dulcis*, collected from Srirangapatna, was undertaken because of partial and inadequate earlier account furnished by Raghavan and Srinivasan (1941) on the species and also to elucidate its tribal position based on embryology.

OBSERVATIONS

Microsporangium and Male Gametophyte

In transverse section, the very young anther is four-lobed (Fig. 1 A). Each lobe contains a plate of 5—6 large-nucleated densely cytoplasmic hypodermal archesporial cells (Fig. 1 B). Periclinal divisions of the archesporial cells give rise to the outer primary parietal and the inner primary sporogenous layers. The primary parietal layer after a similar division produces two rows of cells, the inner of which functions directly as the glandular tapetum and the outer ultimately gives rise to the endothecium and middle layer (Fig. 1 C—D). The tapetal cells enlarge in size and elongate radially. After a free nuclear division each cell becomes binucleate (Fig. 1 E—F). It is of interest to note that the tapetal cells on the connective side are more often two-layered and they are sparsely cytoplasmic including only small nuclei (Fig. 1 D—F). During later stages of sporangium development the middle layer is crushed and absorbed and the endothecial cells become larger in size and acquire characteristic fibrous thickenings. Meanwhile the tapetal cells become consumed by the developing microspores and the pollen grains. The scanty remains of the tapetum are left near the inner tangential walls of the endothecial cells within the microsporangium (Fig. 1 N).

The cells of the primary sporogenous layer in the meantime undergo anticlinal and periclinal divisions producing a sporogenous tissue (Fig. 1 C—D). The microspore mother cells derived from the sporogenous tissue round up and undergo the usual meiotic divisions (Fig. 1 E—K). Meiosis I is not followed by a cell wall (Fig. 1 G). The two resulting dyad nuclei undergo a simultaneous division. The orientation of the spindles of the dividing nuclei is such that the resulting four daughter nuclei after meiosis II become disposed in a tetrahedral manner within the cytoplasm (Fig. 1 H—I). Quadripartition of spore mother cells is simultaneous. The microspore tetrad is of the tetrahedral type (Fig. 1 K). It should be pointed out here that the wall of the microspore mother cell becomes a thick homogeneous layer around the cytoplasm during meiosis and the layer continues to surround the microspore tetrad (Fig. 1 G—K). Soon the microspores of the tetrad enlarge in size and their cytoplasm acquires small vacuoles (Fig. 1 L). The remains of the wall of microspore mother cells disappear by now. Division of the microspore results in the genesis of a generative cell and a tube cell. The generative cell is very much smaller in size compared to the tube cell but its cytoplasm is denser and finer. The mature pollen grain is almost spherical with a thin intine and a thick exine bearing three colpae. The generative cell is embedded in the cytoplasm of the tube cell. At pollen-shedding the adjacent microsporangia coalesce due to the breakdown of the separating layer of cells between the sporangia. The grains of both sporangia are therefore released through a single opening.

Megasporangium and Female Gametophyte

A long section of a very young ovary presents two massive hump-like placentae (Fig. 2 A). Each of them later organizes on the surface a large number of small finger-like ovular primordia (Fig. 2 B—C). These give rise to unitegmic, tenuinucellate and anatropous ovules (Fig. 2 C, E, K).

A large, densely protoplasmic hypodermal archesporial cell appears very early in the ovular primordium (Fig. 2 C). It elongates and directly functions as the megaspore mother cell (Fig. 2 D). After the first nuclear division during meiosis two superposed dyad cells are formed (Fig. 2 E—H). The nuclei of the dyad cells undergo a simultaneous division. Followed by trans-

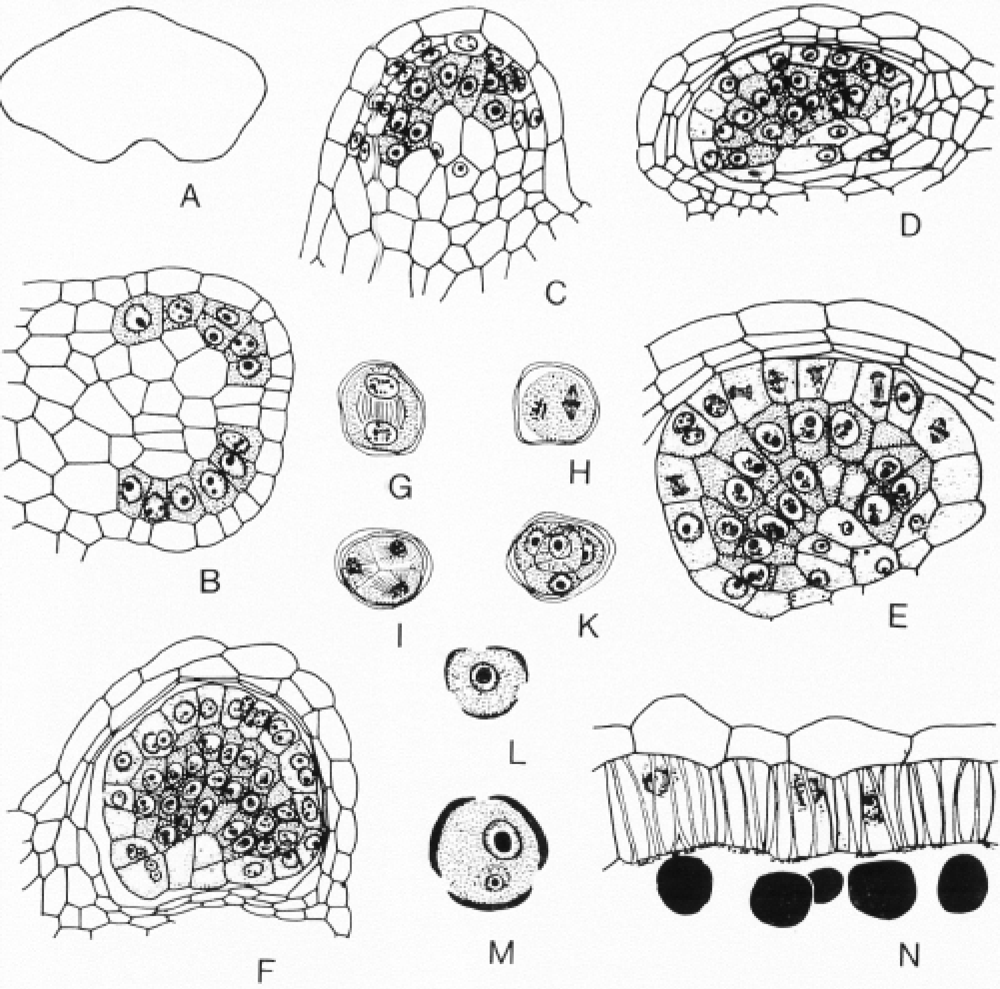


Fig. 1. Microsporangium and male gametopyte of *Scoparia dulcis*. — A: Transverse section of very young anther. — B: T.s. two adjacent microsporangial primordia lodging hypodermal archesporial cells. — C: T.s. of young microsporangium showing division in primary parietal and primary sporogenous layers. — D: T.s. microsporangium with a four-layered wall enclosing the sporogenous tissue; note more than one layer of tapetal cells on the connective side. — E: T.s. part of microsporangium showing nuclear divisions in tapetal cells. — F: T.s. microsporangium at the binucleate stage of tapetal cells. — G—K: Development of tetrahedral type of microspore tetrad from a mother cell. — L: A uninucleate pollen grain. — M: A mature pollen grain. — N: Part of t.s. of anther wall at pollen shedding showing fibrous thickenings of the endothecium. — A ×340, B—C ×780, D ×560, E ×780, F ×560, G—M ×1570, N ×560.

verse walls a linear tetrad of megaspores is formed (Fig. 2 I). Usually the three micropylar megaspores degenerate and the chalazal one functions (Fig. 2 L). Rarely a second megaspore in a tetrad shows signs of further development (Fig. 2 K). The functional megaspore enlarges in size and the vacuoles in its cytoplasm become conspicuous (Fig. 2 M). Division of the megaspore nucleus is not followed by a cell wall. The resulting daughter nuclei move apart to the opposite ends as a large central vacuole organizes between them (Fig. 2 N). The two-nucleate embryosac elongates further and enlarges in size crushing and absorbing the surrounding nucellar cells (Fig. 2 N—O). The two-nucleate sac become four-nucleate by a free nuclear division (Fig. 2 O). It is now in direct contact with the inner epidermis of the integument. The epidermal cells around its enlarging micropylar part degenerate (Fig. 2 O). The four-nucleate embryosac becomes eight-nucleate after another simultaneous free nuclear division. The eight nuclei are disposed in two groups of four each. Organization of the female gametophyte commences soon (Fig. 2 P). An egg apparatus of two synergids and an egg and a micropylar polar nucleus arise from the micropylar quartet. Three small antipodal cells and a chalazal polar nucleus are organized from the chalazal quartet. The two polar nuclei increase in volume and move towards each other meeting near the middle region of the embryosac (Fig. 2 Q).

The mature female gametophyte is spindle-shaped with a broader micropylar part. The egg apparatus is conspicuous and consists of two large posteriorly vacuolate hooked synergids and a prominent egg. The polar nuclei fuse together and the large secondary nucleus becomes located near the egg apparatus. The three small antipodal cells show signs of degeneration. An endothelium surrounds the comparatively narrow cylindrical middle region of the female gametophyte (Fig. 2 R).

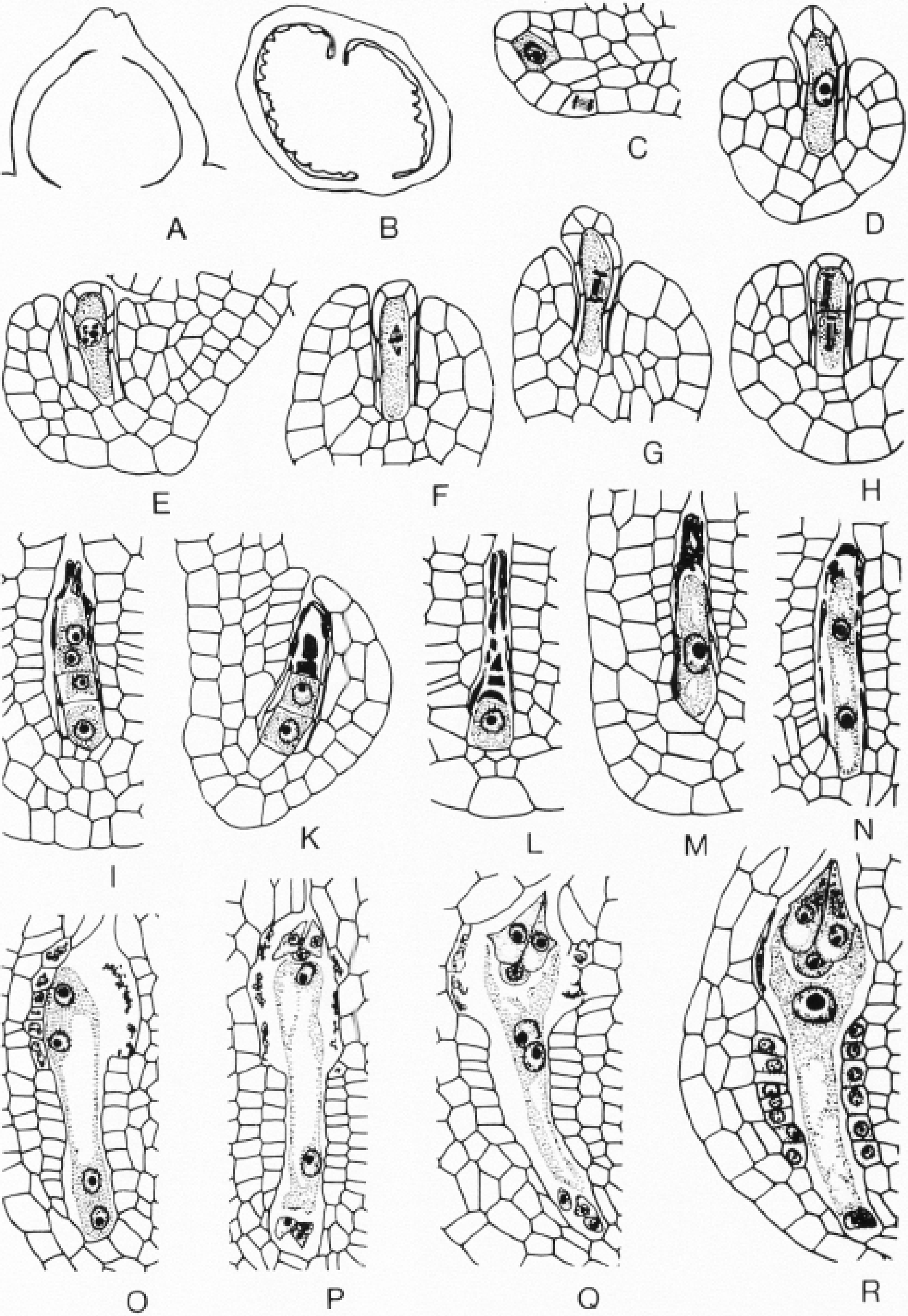
Endosperm

The division of the endosperm mother cell occurs much earlier to that of the zygote. The first division is transverse and it initiates the two primary endosperm chambers. Both of them soon undergo a vertical division and produce two tiers of two cells each. The chalazal tier directly develops into the chalazal haustorium of two uninucleate cells. The two cells of the micropylar tier undergo a vertical division at right angles to the previous one forming four circumaxial cells. These divide transversely organizing two tiers of four cells each. The upper tier develops into the micropylar haustorium and the lower includes the initials of the endosperm proper. Diagrammatic figure 3 A depicts the initial sequence of divisions in the endosperm mother cell. This sequence is exactly similar to the sequence given in the earlier account by Raghavan and Srinivasan (1941).

The two uninucleate cells of the chalazal haustorium during seed development elongate and enlarge as their nuclei increase in volume (Fig. 3 B—C). They do not fuse together during their period of activity and finally degenerate as such earlier to that of the micropylar haustorium (Figs. 3 F, 4 A—C).

The four uninucleate micropylar haustorial cells enlarge in size and extend into the micropylar canal of the developing seed breaking down the surrounding cells of the integument (Figs. 3 B, D; 4 B). Their nuclei increase in size and become prominent as the cytoplasm becomes denser (Fig. 4 B). The micropylar haustorium stays active for a long time during seed development and appears to play a more significant role in the nutrition of

Fig. 2. Megasporangium and female gametophyte of *Scoparia dulcis*. — A: Longitudinal section of a very young ovary. — B: Transverse section of a slightly older ovary showing initiation of ovular primordia. — C: Ovular primoridium with a hypodermal archesporial cell. — D: A megaspore mother cell. — E—I: Development of a linear tetrad of megaspores from a mother cell. — K: Two megaspores of tetrad showing signs of further development. — L: Functional megaspore. — M—Q: Development of embryosac from functional megaspore. — R: A mature embryosac. — A—B ×1120, C—R ×900.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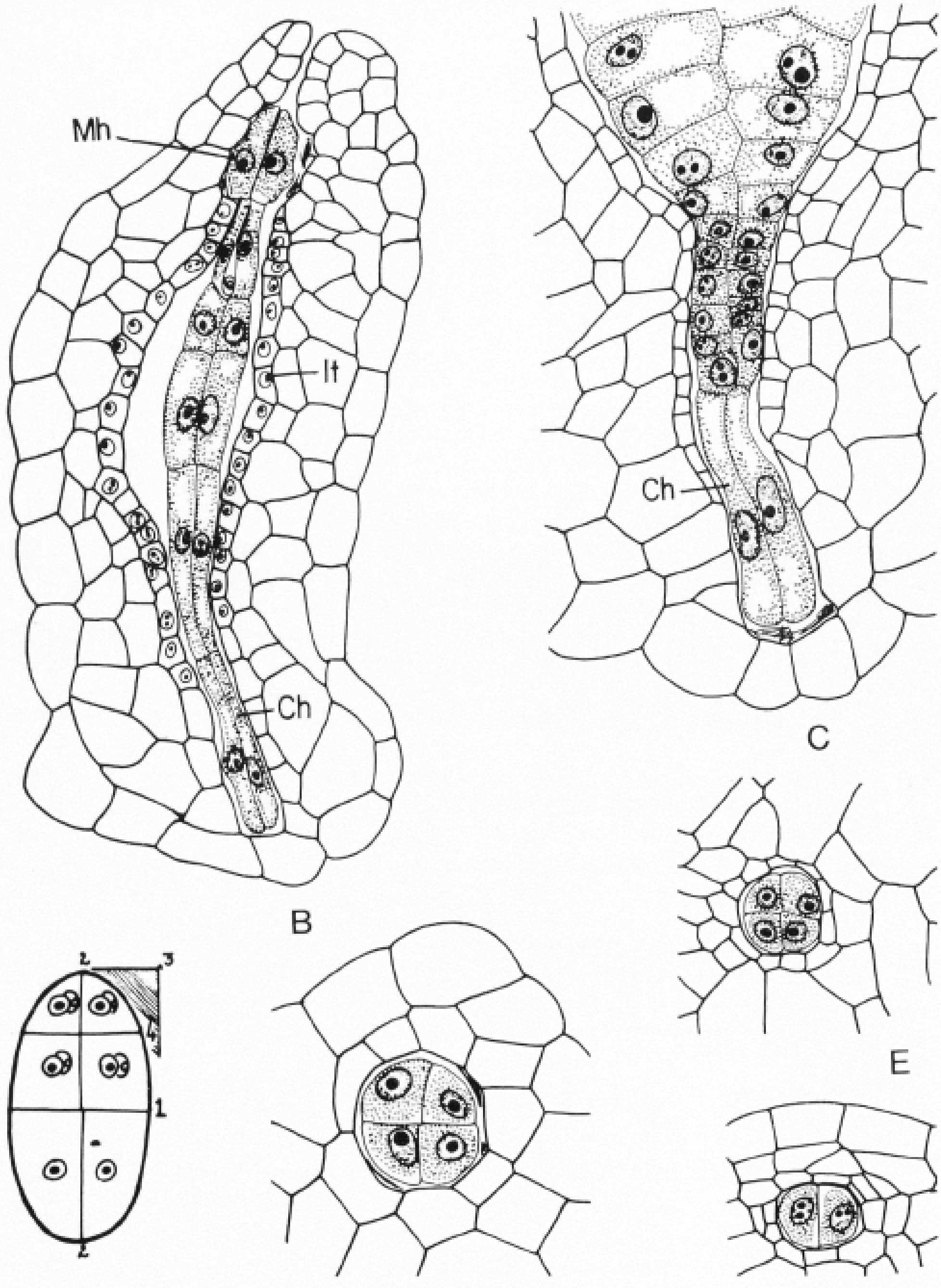
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the embryosac than the chalazal haustorium.

Meanwhile, the initials of the endosperm proper undergo a series of transverse divisions producing a long quadriseriate row of cells (Fig. 3 B—C, E). A few tiers of these cells located above the chalazal haustorium do not increase in size but become densely protoplasmic, while cells of the other tiers, further above, enlarge in size and become conspicuously vacuolate (Fig. 3 C). By transverse and vertical divisions these large cells give rise to the bulk of the endosperm tissue into which the developing embryo thrusts itself (Fig. 4 A—C).

The most noteworthy feature in the endosperm proper is that the cells of the quadriseriate lower part undergo only transverse divisions increasing the number of small densely protoplasmic cell-tiers. This region extends further towards the chalazal end as the cells of the chalazal haustorium break down. Very frequently it is observed that the four cells of lowermost tier of the endosperm proper enlarge in size and act as a secondary haustorium (Fig. 4 A, C).

As the endosperm tissue increases in bulk in the upper part of the embryosac the surrounding endothelial cells become stretched, accommodating to the increase in volume of tissue (Fig. 4 B—C). A greater part of the central core of endosperm tissue is consumed by the developing embryo. In the ripe seed the surviving endosperm cells acquire deep staining granular reserve food material. The outer tangential walls of the outermost layer of endosperm cells acquire heavy lamellated thickenings (Fig. 4 D—F). The seed coat consists of the outer epidermis of the integument and the crushed remains of the endothecium.

Embryo

The zygote elongates during the initial development of endosperm and divides transversely forming the terminal cell *ca* and the basal cell *cb* (Fig. 5 A—B). The shorter terminal cell enlarges in size and undergoes a vertical division while the longer basal cell divides transversely giving rise to cells *m* and *ci* (Fig. 5 D). The first four cells of the proembryo are therefore arranged in a T-shaped manner and the proembryonal tetrad consequently belongs to the A_2 category (Souèges 1921). The two juxtaposed cells derived from *ca* give rise to the quadrants, *q*, after another vertical division at right angles to the first (Fig. 5 E). Transverse division of the quadrants initiates the octants disposed in two superposed tiers of four cells each, the upper tier being designated as *l* and the lower as *l′* (Fig. 5 F—H). Meanwhile, the lowermost cell of the proembryonal tetrad, cell *ci*, gives rise to *n* and *n′* after a transverse division (Fig. 5 G—H, L, N). Only occasionally it does not divide (Fig. 5 I—K). The middle cell *m* produces cells *d* and *f* after a similar division (Fig. 5 H—I). Periclinal divisions in the octants delimit the dermatogen, *de*, from an inner group of cells (Fig. 5 I). The inner cells of tier *l′* give rise to the periblem, *pe*, and plerome, *pl*, after periclinal division (Fig. 5 K). Further divisions in tier *l* form the stem apex, *pvt*, and cotyledons, *cot*, of the embryo, while divisions in *l′* form the hypocotyl, *phy* (Fig. 5 L, Q). Cell *d* functions as the hypophysis. After a transverse division it gives rise to two superposed cells (Fig. 5 K). The upper lenticular cell functions as the initial of the root cortex, *iec*, and the lower acts as the initial of the root cap, *ico*. Usually these cells produce

Fig. 3. Endosperm in *Scoparia dulcis* (*Ch*=Chalazal haustorium, *It*=Integumentary tapetum, *Mh*=Micropylar haustorium). — A: Diagrammatic representation showing sequence of initial divisions in endosperm mother cell. — B: L.s. young seed. — C: L.s. chalazal part of endosperm; note narrow part of endosperm proper above the chalazal haustorium. — D: T.s. micropylar haustorium. — E: T.s. through the narrow chalazal part of endosperm proper revealing quadriseriate nature of the region. — F: T.s. chalazal haustorium. — B ×560, C ×780, D ×1120, E—F ×780.

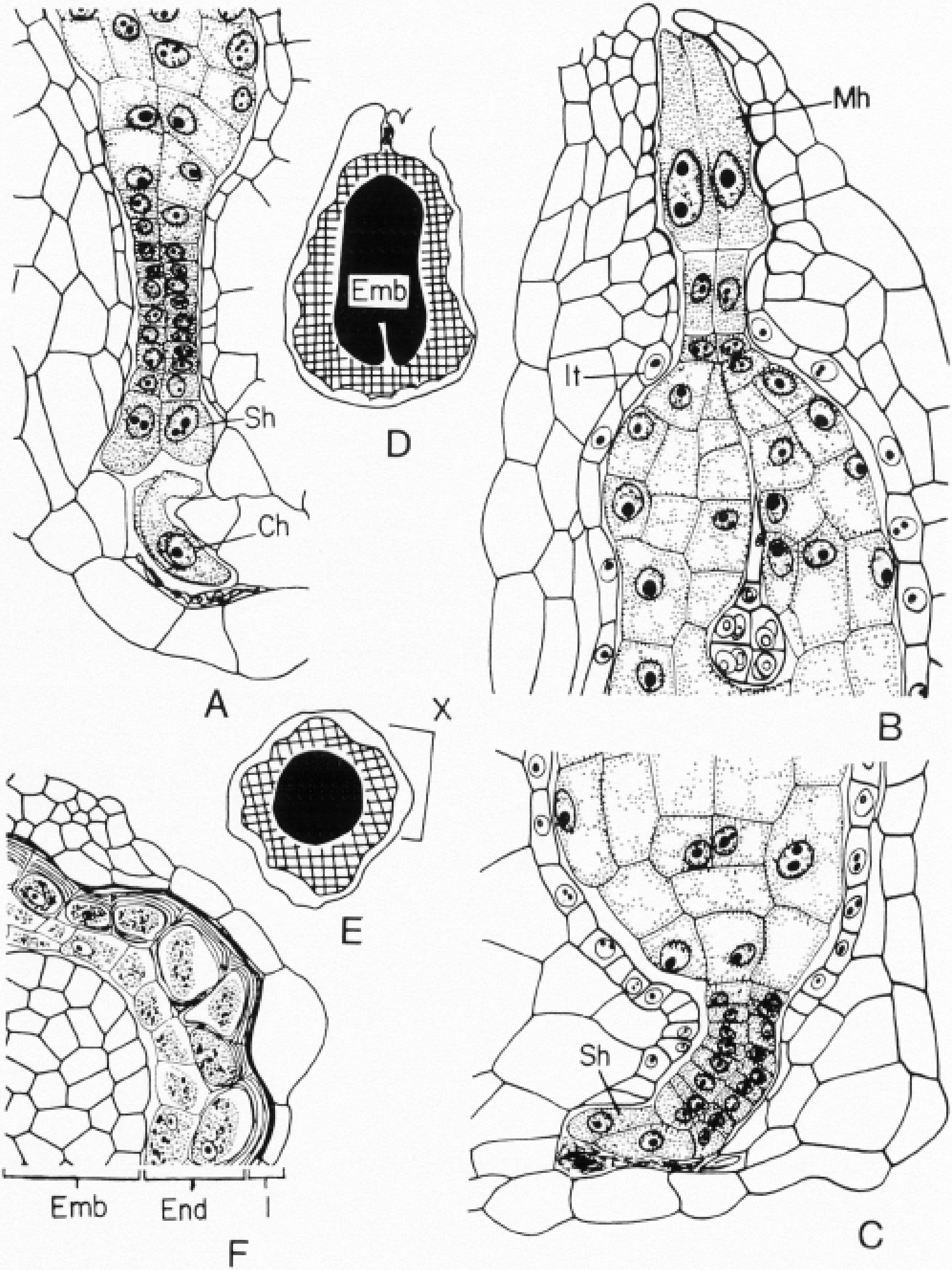

Fig. 4. Endosperm haustorium and seed in *Scoparia dulcis*. (*Ch*=Chalazal haustorium, *Emb*=Embryo, *End*=Endosperm, *I*=Integument serving as seed coat, *It*=Integumentary tapetum, *Sh*=Secondary endosperm haustorium). — A: L.s. Chalazal part of endosperm;

two plates of four cells each as a consequence of two vertical divisions at right angles to each other (Fig. 5 L, O). Further divisions lead to the organization of the root cortex and root cap, *co* (Fig. 5 P—Q). The short uniseriate suspensor consisting of cells *f*, *n* and n' degenerates as the embryo matures. The embryo in the ripe seed is comparatively massive. It has shorter cotyledons, stouter hypocotyl and a radical (Fig. 5 Q).

DISCUSSION

The development of the microsporangium in the present study is essentially similar to that of the investigated Digitaleae. Nevertheless, the occurrence of more than one layer of tapetal cells on the connective side noted in *Scoparia dulcis* has not been recorded in any other member of the tribe. The two-celled condition of the pollen grains at shedding appears to be a general feature within the tribe.

The female gametophyte development of *Scoparia dulcis* conforms to the Polygonum type (Maheshwari 1950) as in other species of Digitaleae so far studied. The mature embryosac has a broad micropylar part and a narrow chalazal region. The two polar nuclei fuse together forming a secondary nucleus as in many species of *Veronica* (Jönsson 1879—80, Gscheidle 1924, Weiss 1932, Varghese 1963, Arekal 1966), *Digitalis purpurea*, *D. ambigua* (Schmid 1906), *Isoplexis canariensis*, *Rehmannia angulata* (Krishna Iyengar 1939, 1942) and *Erinus alpinus* (Crété 1954). On the contrary, in a few species of *Veronica* Schmid (1906) has recorded the absence of fusion of polar nuclei before fertilization. This character was considered by him as quite important and he used it in grouping of species within that genus.

The three antipodal cells of *Scoparia dulcis* are ephemeral as in the other Digitaleae although in *Veronica alpina* (Weiss 1932) they appear to persists even during the initial development of endosperm.

The endosperm is *ab initio* cellular. The first division of the endosperm mother cell is transverse and initiates the two primary endosperm chambers. The second is vertical as in the other investigated Digitaleae. The earlier reports on the occurrence of a transverse division in the primary micropylar endosperm chamber leading to the development of a uniseriate row of three cells in a few species of *Veronica* (Hofmeister 1859, Buscalioni 1893, Schmid 1906, Weiss 1932) have been corrected subsequently (Meunier 1897, Gscheidle 1924, Yamazaki 1957), the division being vertical instead of transverse. The primary chalazal chamber always contributes only to the chalazal haustorium while the primary micropylar chamber gives rise to both the micropylar haustorium and the endosperm proper.

The mode of delimitation of the micropylar haustorium and the initials of the endosperm proper in *Scoparia dulcis* is similar to that of *Digitalis* and *Erinus* (Crété 1953, 1954).

The two uninucleate cells constituting the chalazal haustorium such as observed in the present species have also been recorded in *Veronica alpina*, *V. aphylla* (Weiss 1932), *V. nipponica* and *V. onoei* (Yamazaki 1957). In a large majority of *Veronica* (Meunier 1897, Schmid 1906, Gscheidle 1924, Weiss 1932, Yamazaki 1957, Varghese 1963, Arekal 1966) and in *Rehmannia angulata* (Krishna Iyengar 1942) the chalazal haustorium is unicellular and binucleate. *Veronica ponae* (Gscheidle 1924), on the other hand, usually has unicellular binucleate chalazal

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note the organization of secondary haustorium. — B: L.s. micropylar half of developing seed. — C: L.s. chalazal part of seed; note complete degeneration of chalazal haustorium and development of secondary endosperm haustorium. — D: Diagramatic l.s. of ripe seed. — E: T.s. ripe seed. — F: Sector marked X in C enlarged to show details of endosperm and seed coat. — A—C ×780, D—E ×160, F ×560.

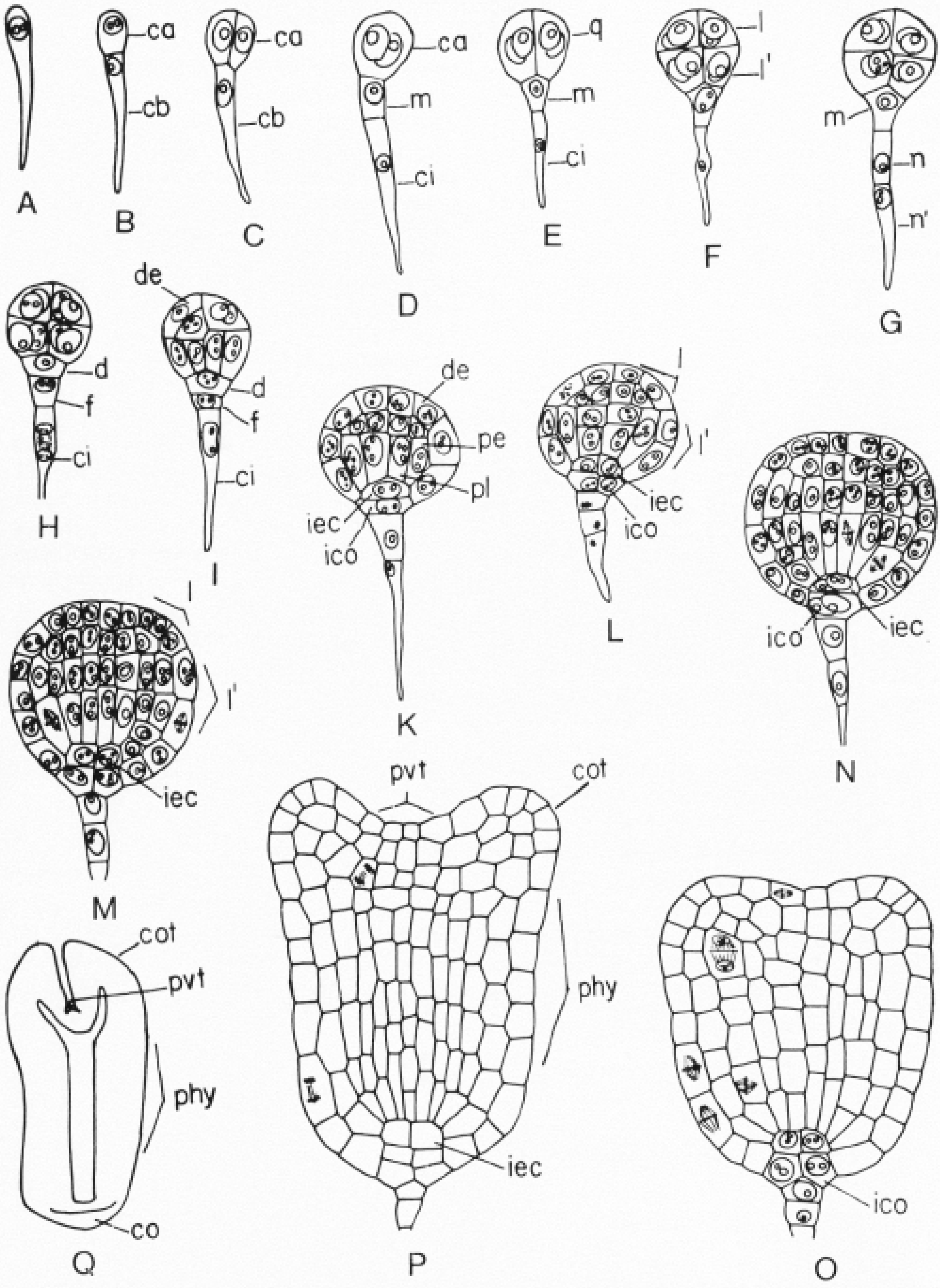

Fig. 5. Development of embryo in *Scoparia dulcis*. — A—P ×780, Q ×340. For abbreviations see text.

haustorium but occasionally a complete vertical wall develops between the two nuclei. Further, in a few species of *Veronica* (GSCHEIDLE 1924, WEISS 1932, YAMAZAKI 1957), *Isoplexis canariensis* (KRISHNA IYENGAR 1939), *Digitalis purpurea* and *Erinus alpinus* (CRÉTÉ 1953, 1954) the chalazal haustorium consists of four uninucleate cells. The four-celled chalazal haustorium is generally considered as a primitive state and the binucleate unicellular condition advanced, brought about by progressive reduction and simplification.

Scoparia dulcis is more like *Digitalis purpurea* (CRÉTÉ 1953) in possessing four uninucleate cells in the micropylar haustorium disposed in a single tier. Although the micropylar haustorium of *Veronica virginica, V. longifolia* (GSCHEIDLE 1924), *Veronicastrum sibiricum* var. *japonicum, V. axillare* and *Wulfenia carninthiaca* (YAMAZAKI 1957) is four-celled, the cells are disposed in two tiers of two cells each unlike in the present study. In many species of *Veronica* (MEUNIER 1897, GSCHEIDLE 1924, WEISS 1932, YAMAZAKI 1957, VARGHESE 1963, AREKAL 1966) two juxtaposed binucleate cells constitute the micropylar haustorium and these cells usually fuse together forming a four-nucleate body.

A remarkable feature observed in the development of endosperm of *Scoparia dulcis* is the organization of a narrow quadriseriate chalazal part of the endosperm proper, located immediately above the chalazal haustorium. Further, the four densely cytoplasmic cells of the lowermost tier of this quadriseriate part enlarge in size and together function as a secondary haustorium. SCHMID (1906) who studied *Veronica chamaedrys* also observed the cells of the endosperm proper at the chalazal end enlarging and penetrating into the surrounding tissue functioning as secondary haustorium soon after the degeneration of the chalazal haustorium.

The development of the embryo in the present species conforms to the Crucifer type as in the other Digitaleae. The progress of segmentation in the apical cell of the two-celled proembryo is very much faster than the basal cell. The cell *d* functions as the hypophysis as in *Digitalis purpurea, Erinus alpinus* (CRÉTÉ 1953, 1954), *Veronica hederifolia* and *V. maritima* (YAMAZAKI 1957). On the other hand in *V. arvensis* (SOUÈGES 1921), *V. persica* (YAMAZAKI 1957) and *V. agrestis* (VARGHESE 1963) it undergoes further transverse division and the uppermost derivative acts as the hypophysis. However, the subsequent behaviour of the hypophyseal cell is similar in all species of the tribe Digitaleae studied.

As for the tribe of *Scoparia dulcis* is concerned, it should be pointed out that the embryology of the different tribes of the Scrophulariaceae is closely similar. Nonetheless, the mode of delimitation of the endosperm haustoria and the number, structure and behaviour of haustorial cells appear to provide clues on the relationships within the family.

Although the development of endosperm of *Scoparia dulcis* begins as in *Digitalis* and *Erinus* (CRÉTÉ 1953, 1954) its final organization, with a four-celled single-tiered micropylar haustorium and a chalazal haustorium of two juxtaposed uninucleate cells, is different. Further, none of the Digitaleae so far studied has an endosperm organization similar to the one noted in the present study. On the other hand, genera such as *Ilysanthes* and *Lindernia* (YAMAZAKI 1954) included under the tribe Gratioleae possess an endosperm which is essentially similar in development and final organization such as noted in *Scoparia dulcis*. Apparently *Scoparia dulcis* seems to be nearer to the Gratioleae than to the Digitaleae. Therefore the present study justifies PENNEL's (1935) inclusion of the genus *Scoparia* in the tribe Gratioleae.

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Studies on the Flora of the Balearic Islands I

Chromosome Numbers in Balearic Angiosperms

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ABSTRACT

Dahlgren, R., Karlsson, Th., and Lassen, P. 1971. Studies on the flora of the Balearic Islands I. Chromosome numbers in Balearic angiosperms. — Bot. Notiser 124: 249—269.

Somatic chromosome numbers for 197 taxa of angiosperms from the islands of Mallorca and Menorca have been determined. As far as the authors are aware, 21 of the taxa have not previously been studied cytologically. 21 counts differ from earlier records. Comments are made on some interesting points. The new chromosome numbers occur within the following genera: *Ajuga, Alkanna, Allium, Althaea, Anthyllis, Arisarum, Arum, Asteriscus, Asterolinum, Astragalus, Brassica, Carduus, Clematis, Cneorum, Cymbalaria, Echium, Fumana, Launaea, Lavatera, Linaria, Lotus, Melica, Merendera, Micromeria, Ophrys, Parietaria, Plantago, Polycarpon, Polygala, Ranunculus, Reseda, Rubia, Ruta, Salvia, Silene, Stipa, Valerianella, Viola, Vulpia.*

INTRODUCTION

The authors have undertaken a cytological investigation of material collected on the Balearic Islands in 1969. The present account represents a preliminary step in a project involving the flora of the western Mediterranean, with the main emphasis on the flora of northern Morocco.

MATERIAL AND METHODS

The material used in this investigation was collected in May, 1969, during a botanical tour on the islands of Mallorca and Menorca. Seeds were collected in nature and also from the dried specimens collected for the Lund Herbarium. In some cases the plants were raised from bulbs or other subterranean parts. The collecting sites of the material investigated are listed in Table 2. The approximate locations of these sites are shown in Fig. 5.

The chromosome counts were made in root-tips of plants cultivated in the experimental greenhouses of the Lund Botanical Garden. The young plants were cooled overnight at a temperature of +2—4°C to contract the chromosomes. Root-tips were taken in the morning and fixed in Navashin-Karpechenko fixative according to the Svalöf modification, cut with a microtome, and stained with crystal violet.

When sufficiently developed to be identifiable with accuracy — generally in the flowering or fruiting stage — the cultivated plants were dried and pressed and are now preserved as voucher specimens at the Botanical Museum, Lund (LD). Since the plants from which the seeds were originally collected, were usually also dried, there is mostly double reference material.

The material in culture was so comprehensive that not all plants could be observed individually. Consequently, refixing was generally not possible when preparations from the first fixing were not satisfactory. In this paper, however, approximate counts are given only when they are considered to be of special interest.

RESULTS

The chromosome numbers found are presented in Table 1 together with the collection numbers (= the voucher numbers). These bear the designation MMF when seeds were collected, and MMK when bulbs or other subterranean parts were taken.

In order to avoid extensive citations from literature, reference is made to Fedorov 1969 (abbreviated F) and Regnum Vegetabile, 50, 55, 59 (1967, 1968, 1969; ed. Ornduff) and 68 (1970; ed. Moore) — abbreviated RV 50, RV 55, RV 59, and RV 68. These should be consulted for further reference. The chromosome numbers given in these works are listed in Table 1 in order to put the present counts in relation to what was previously known. However, the authors are fully aware of the fact that the chromosome numbers given in the works mentioned are frequently not relevant for the taxa owing to mis-determinations, divergent opinions on the circumscription of taxa, unstable nomenclature, etc. Additional references, not included in these works, are given separately in the table.

New counts are marked in the table with an asterisk in the column for references. Further comments have been made on some of the counts obtained. Camera lucida drawings, all of the same magnification, are given in Figs. 1—4 for almost all the new counts.

Table 1. Chromosome numbers of the species from the Balearic Islands studied cytologically, with reference to the collection number and to the results of previous investigations.

Taxon	Coll. no	2n	Previous counts and references
APIACEAE			
Bupleurum semicompositum L.	MMF 859	16	16 F
Conium maculatum L.	MMF 143	22	16 F 22 F, RV 59
Ferula communis L.	MMF 721	22, [23]	22 F, RV 68, Engstrand 1970
Scandix pecten-veneris L.	MMF 140	26	16 F, RV 59, RV 68
	MMF 1032	26	26 F, Fl. Eur. II (1968)
Torilis nodosa (L.) Gaertner	MMF 39	24	22 F
	MMF 417	24	24 Engstrand 1970
	MMF 1048	24	
	MMF 1911	24	
ARACEAE			
Arisarum vulgare Targ.-Tozz.	MMF 1904	c. 55 (Fig. 1 A)	52 F
Arum italicum Miller	MMF 235	28	64, 84 F
	MMF 2012	28 (Fig. 1 B)	
ASTERACEAE			
Aetheorrhiza bulbosa (L.) Cass. [= *Crepis bulbosa* (L.) Tausch]	MMF 206	18	18, 32 F
Anthemis arvensis L.	MMF 55	18	18 F
	MMF 468	18	
	MMF 902	18	
	MMF 1024	18	
Asteriscus aquaticus (L.) Less.	MMF 863	14 (Fig. 1 C)	*
Bellium bellidioides L.	MMF 2102	18	18 F
Calendula arvensis L.	MMF 1909	44	36, 44 F
	MMF 1910	44	

Taxon	Coll. no	2n	Previous counts and references
Carduus pycnocephalus L.	MMF 2003	62—64	54 F
Centaurea melitensis L.	MMF 36	24	22 F 24 F, Björkqvist et al. 1969 36 F
Cirsium syriacum (L.) Gaertner [=*Notobasis syriaca* (L.) Cass.]	MMF 1041	34	34 F
Crepis vesicaria L.	MMF 170	16	8, 9, 9—12, 16 F
Crupina crupinastrum (Moris) Vis.	MMF 83	28	28 F
Filago pyramidata L. [=*F. spathulata* C. Presl]	MMF 1026	28	28 F
Galactites tomentosa (L.) Moench	MMF 14	22	22 F
Hedypnois spp.	MMF 48	8	The genus:
	MMF 89	8	8, 12, 12+1, 16, 54 F
	MMF 137	8	
	MMF 869	8	
	MMF 146	13	
Hyoseris radiata L.	MMF 164	16	12 F
	MMF 632	16	16 F, Björkqvist et al. 1969
	MMF 683	16	
	MMF 865	16	
Hyoseris scabra L.	MMF 88	16	16 F
Hypochoeris achyrophorus L. [=*H. aetnensis* (L.) Ball] ..	MMF 50	12	12 F
	MMF 406	12	
Launaea cervicornis (Boiss.) Font-Quer & Rothm.	MMF 827	18 (Fig. 1 D)	*
Phagnalon rupestre (L.) DC. ..	MMF 61	18	18 F
	MMF 103	18	
	MMF 391	18	
Phagnalon saxatile (L.) DC. ..	MMF 32	18	18 F, Björkqvist et al. 1969
	MMF 730	18	
	MMF 1025	18	
Reichardia picroides (L.) Roth ssp. *picroides*	MMF 19	14	14 F
	MMF 418	14	
	MMF 651	14	
Reichardia tingitana (L.) Roth ssp. *orientalis* (L.) Maire ...	MFF 866	16	16 F
Rhagadiolus stellatus (L.) Gaertner	MMF 128	10	10 F
Senecio linifolius L.	MMF 341	40	40 F
	MMF 2013	c. 40	
Senecio rodriguezii Willk.	MMF 232	20	20 RV 59
	MMF 636	20	
	MMF 854	20	
Silybum marianum (L.) Gaertner	MMF 897	34	34 F, Björkqvist et al. 1969
Sonchus oleraceus L.	MMF 277	32	16 F
	MMF 839	32	32 F, RV 68
	MMF 2004	32	
Tragopogon porrifolius L.	MMF 34	12	12 F
Urospermum dalechampii (L.) F. W. Schmidt	MMF 363	14	14 F
	MMF 2051	14	

Taxon	Coll. no	2n	Previous counts and references
Urospermum picroides (L.) F. W. Schmidt	MMF 150	10	8, 10 F
	MMF 834	10	
BORAGINACEAE			
Alkanna lutea (DC.) Moris	MMF 288	28 (Fig. 1 E)	*
	MMF 336	28	
Echium parviflorum Moench ..	MMF 259	16 (Fig. 1 F)	*
	MMF 1021	16	
Lithospermum apulum (L.) Vahl	MMF 364	28	28 F
BRASSICACEAE			
Brassica balearica Pers.	MMF 544	32 (Fig. 1 G)	18 F
Cardamine hirsuta L.	MMF 459	16	16 F, RV 59, RV 68
	MMF 537	16	32 F
Eruca vesicaria (L.) Cav. ssp. *sativa* (Miller) Thell.	MMF 2105	22	22 F
Hornungia petraea (L.) Reichenb. [=*Hutchinsia petraea* (L.) R. Br.]	MMF 318	12	12 F
	MMF 526	12	
Matthiola incana (L.) R. Br. ssp. *incana*	MMF 165	14	14, 14+1−2 B F
Raphanus raphanistrum L. ssp. *landra* (DC.) Bonnier & Layens	MMF 175	18	18 F
CARYOPHYLLACEAE			
Arenaria balearica L.	MMF 511	18	18 F
	MMF 534	18	
Polycarpon polycarpoides (Biv.) Zodda	MMF 872	48 (Fig. 1 H)	*
Silene gallica L.	MMF 209	24	24 F, RV 68, Björkqvist et al. 1969
	MMF 225	24	
	MMF 695	24	
Silene nocturna L.	MMF 67	24	24 F
	MMF 404	24	
	MMF 426	24 (Fig. 1 I)	
	MMF 719	24	
	MMF 916	24	
Silene pseudatocion Desf.	MMF 1029	24 (Fig. 1 J)	*
Silene rubella L. ssp. *rubella* ...	MMF 66	24	24 F
Silene secundiflora Otth	MMF 965	24	24 RV 55
	MMF 973	24	
	MMF 1017	24	
Silene sedoides Poiret	MMF 873	24	24 F
Spergularia bocconii (Scheele) Ascherson & Graebner	MMF 3 a	36	36 F
	MMF 376	36	
Spergularia heldreichii E. Simon-secundus & P. Monnier	MMF 1	36	36 F
Spergularia media (L.) C. Presl [=*S. marginata* Kittel]	MMF 198	18	18 F, Björkqvist et al. 1969, 36 F
CHENOPODIACEAE			
Chenopodium murale L.	MMF 342	18	18 F, RV 59
Halimione portulacoides (L.) Aellen	MMK 2011 c	36	36 F

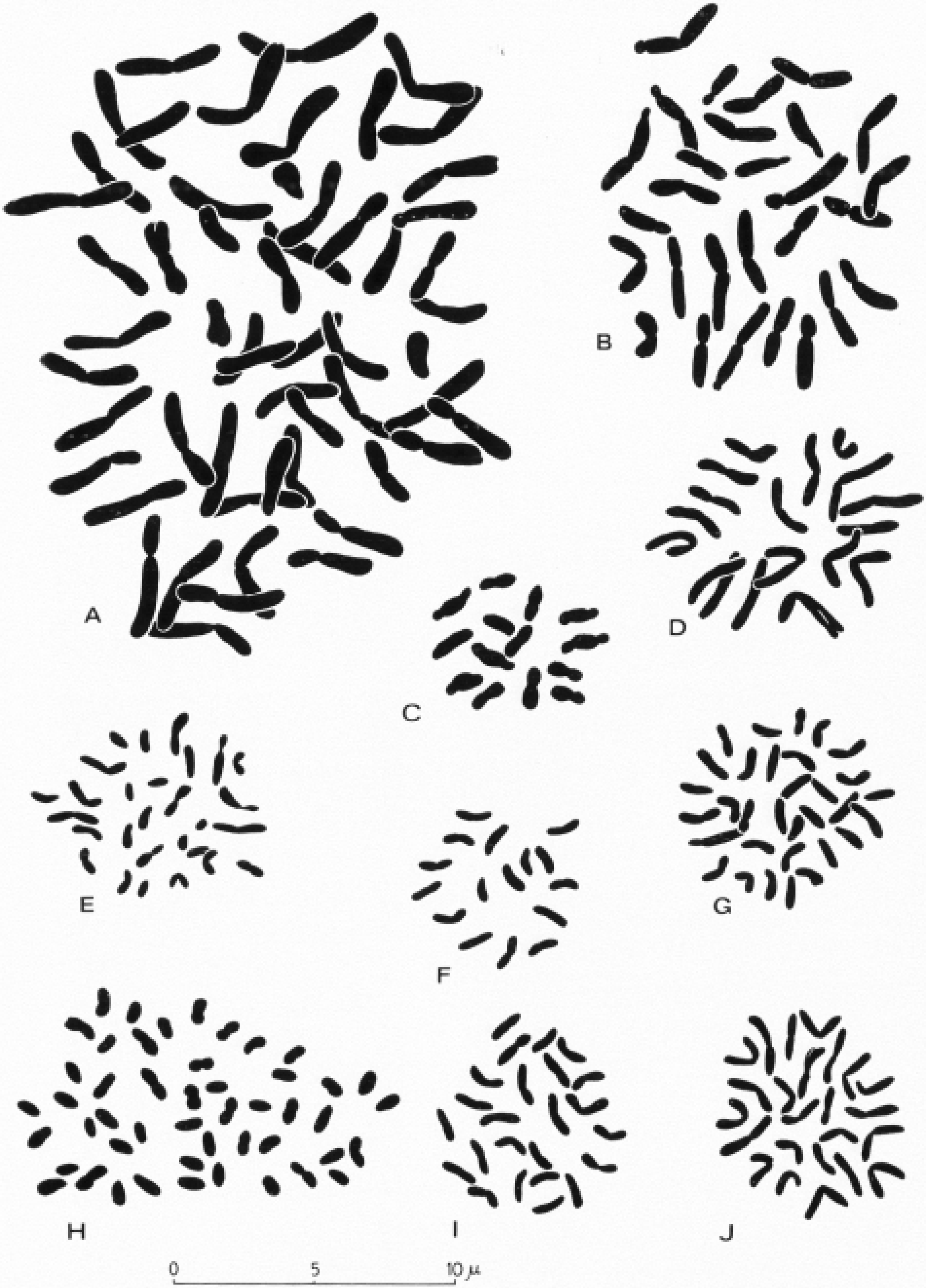
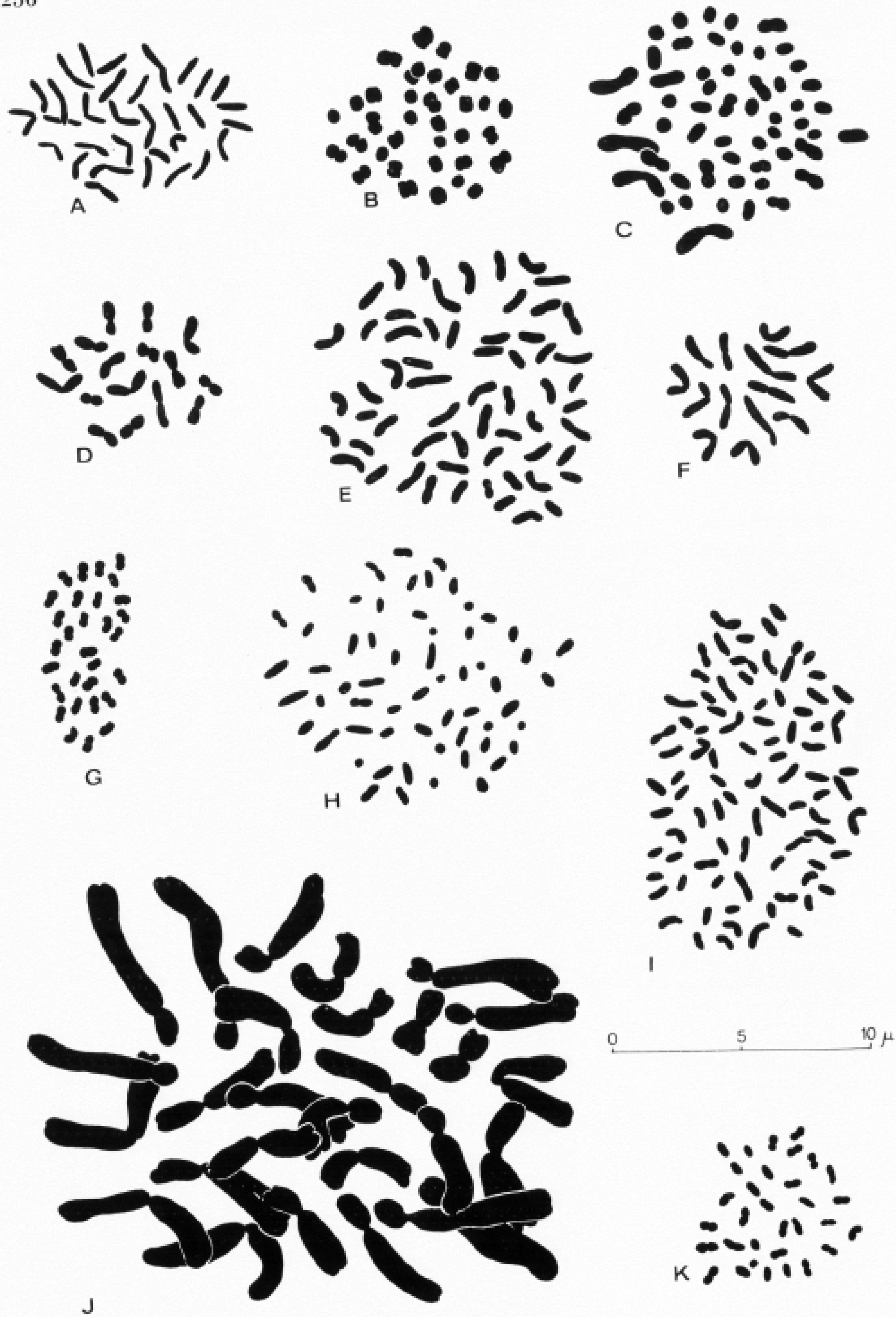


Fig. 1. Somatic metaphases in root-tips of Balearic angiosperms. — A: MMF 1904 *Arisarum vulgare*, 2n=c. 55. — B: MMF 2012 *Arum italicum*, 2n=28. — C: MMF 863 *Asteriscus aquaticus*, 2n=14. — D: MMF 827 *Launaea cervicornis*, 2n=18. — E: MMF 288 *Alkanna lutea*, 2n=28. — F: MMF 259 *Echium parviflorum*, 2n=16. — G: MMF 544 *Brassica balearica*, 2n=32. — H: MMF 872 *Polycarpon polycarpoides*, 2n=48. — I: MMF 426 *Silene nocturna*, 2n=24. — J: MMF 1029 *Silene pseudatocion*, 2n=24.

Taxon	Coll. no	2n	Previous counts and references
CISTACEAE			
Cistus albidus L.	MMF 1906	18	18 F
Cistus clusii Dunal in DC. [=*C. libanotis* auct.]	MMF 626	18	18 F
Cistus salvifolius L.	MMF 627	18	18 F
Fumana ericoides (Cav.) Gand. in Magnier	MMF 970	32 (Fig. 2 A)	*
Fumana thymifolia (L.) Spach ex Webb	MMF 75	32	32 F
Tuberaria guttata (L.) Fourr.	MMF 959	c. 24	24, 36, 48 F
CNEORACEAE			
Cneorum tricoccon L.	MMF 344	36 (Fig. 2 B)	*
CONVOLVULACEAE			
Convolvulus siculus L. ssp. *siculus*	MMF 1018	44	22 F 44 F, RV 59
DIOSCOREACEAE			
Tamus communis L.	MMF 598	48	48 F
EUPHORBIACEAE			
Euphorbia characias L. ssp. *characias*	MMF 251	c. 20	20 F, RV 68
Euphorbia exigua L.	MMF 40	24	16, 24, 28 F
Euphorbia peplus L.	MMF 70	16	16 F, RV 68, Björkqvist et al. 1969
	MMF 319	16	
	MMF 851	16	
Euphorbia segetalis L.	MMF 809	16	16 F
Euphorbia terracina L.	MMF 163	18	18, 36 F
Mercurialis annua L.	MMF 1036	48	12, 14, 16, 32, 48, 64, 80, 96, 112 F
FABACEAE			
Anthyllis tetraphylla L.	MMF 677	16	16 F
Anthyllis vulneraria L. ssp. *praepropera* (A. Kerner) Bornm.	MMF 860	12	*Anthyllis vulneraria* s. lat.:
	MMF 934	12	12 F, RV 59, RV 68
Astragalus epiglottis L. ssp. *epiglottis*	MMF 76	16 (Fig. 2 D)	*
Hedysarum spinosissimum L.	MMF 354	16	16 F
Hippocrepis ciliata Willd.	MMF 42	14	14 Guern & Gorenflot 1966
	MMF 962	14	
Lathyrus sphaericus Retz.	MMF 974	14	14 F, RV 50
Lotus cytisoides L.	MMF 861	14	14 F, RV 59 28 RV 59
Lotus edulis L.	MMF 704	14	14 F
Lotus ornithopodioides L.	MMF 616	14	14 F
	MMF 688	14	
Lotus parviflorus Desf.	MMF 818	12	12 F
Lotus tetraphyllus L.	MMF 837	14 (Fig. 2 F)	*
Medicago littoralis Loisel.	MMF 169	16	16 F, RV 59, RV 68, Björkqvist et al. 1969
	MMF 181	16	
	MMF 321	16	
Medicago minima (L.) Bartal.	MMF 289	16	16 F, RV 59
	MMF 438	16	
	MMF 1032 a	16	

Taxon	Coll. no	2n	Previous counts and references
Medicago orbicularis (L.) BARTAL.	MMF 686	16	16 F, RV 59 32 F
Medicago polymorpha L.	MMF 52	14	14 F, RV 59
	MMF 63	14	16 F
	MMF 139	14	
Medicago scutellata (L.) MILLER	MMF 64	32	32 F, RV 59
	MMF 141	32	
Medicago truncatula GAERTNER	MMF 51	16	16 F, RV 59
	MMF 62	16	
Medicago turbinata (L.) ALL. [= *M. tuberculata* (RETZ.) WILLD.]	MMF 135	16	14, 16 F, 16 RV 59
Melilotus messanensis (L.) ALL.	MMF 223	16	16 F
Melilotus segetalis (BROT.) SER. in DC.	MMF 215	16	16 F
	MMF 2011 h	16	
Melilotus sulcata DESF.	MMF 71	16	16 F
	MMF 668	16	
Ononis minutissima L.	MMF 411	30	30 Fl. Eur. II (1968)
	MMF 430	30	
Ononis reclinata L.	MMF 415	c. 60	60, 64 F
	MMF 703	60 (Fig. 2 E)	
	MMF 867	60	
Trifolium campestre SCHREBER	MMF 54	14	14 F, RV 68
Trifolium cherleri L.	MMF 707 a	10	10 RV 59
Trifolium glomeratum L.	MMF 782	16	14, 16 F
Trifolium scabrum L.	MMF 991	10	10 F, RV 68
	MMF 1905	10	16 F
Trifolium squamosum L. [= *T. maritimum* HUDSON]	MMF 757	16	16 F
Trifolium tomentosum L.	MMF 360	16	16 F
Vicia bithynica (L.) L.	MMF 690	14	14 F, RV 59
	MMF 698	14	
	MMF 702	14	
	MMF 946	14	
	MMF 1040	14	
Vicia pubescens (DC.) LINK	MMF 940	14, [28]	14 RV 59
Vicia sativa L.	MMF 46	12	The species complex:
	MMF 436	12	10 F
	MMF 705	12	12 F, RV 59, RV 68
	MMF 2053 d	10	14 F
Vicia tetrasperma (L.) SCHREBER	MMF 405	14	14, 28 F
FRANKENIACEAE			
Frankenia pulverulenta L.	MMF 3 b	20	20 F
	MMF 891	20	
GENTIANACEAE			
Centaurium pulchellum (SCHWARTZ) DRUCE	MMF 158	36	20, c. 34, 36, c. 38, 40, 42, 54, 56 F
	MMF 659	36	
GERANIACEAE			
Erodium cicutarium (L.) L'HER.	MMF 581	40	20, 36, 40, 48, 54, (56) F
Geranium rotundifolium L.	MMF 607	26	26 F
JUNCAGINACEAE			
Triglochin bulbosa L. ssp. *barrelieri* (LOISEL.) KONY	MMF 226 b	32	30, 32 F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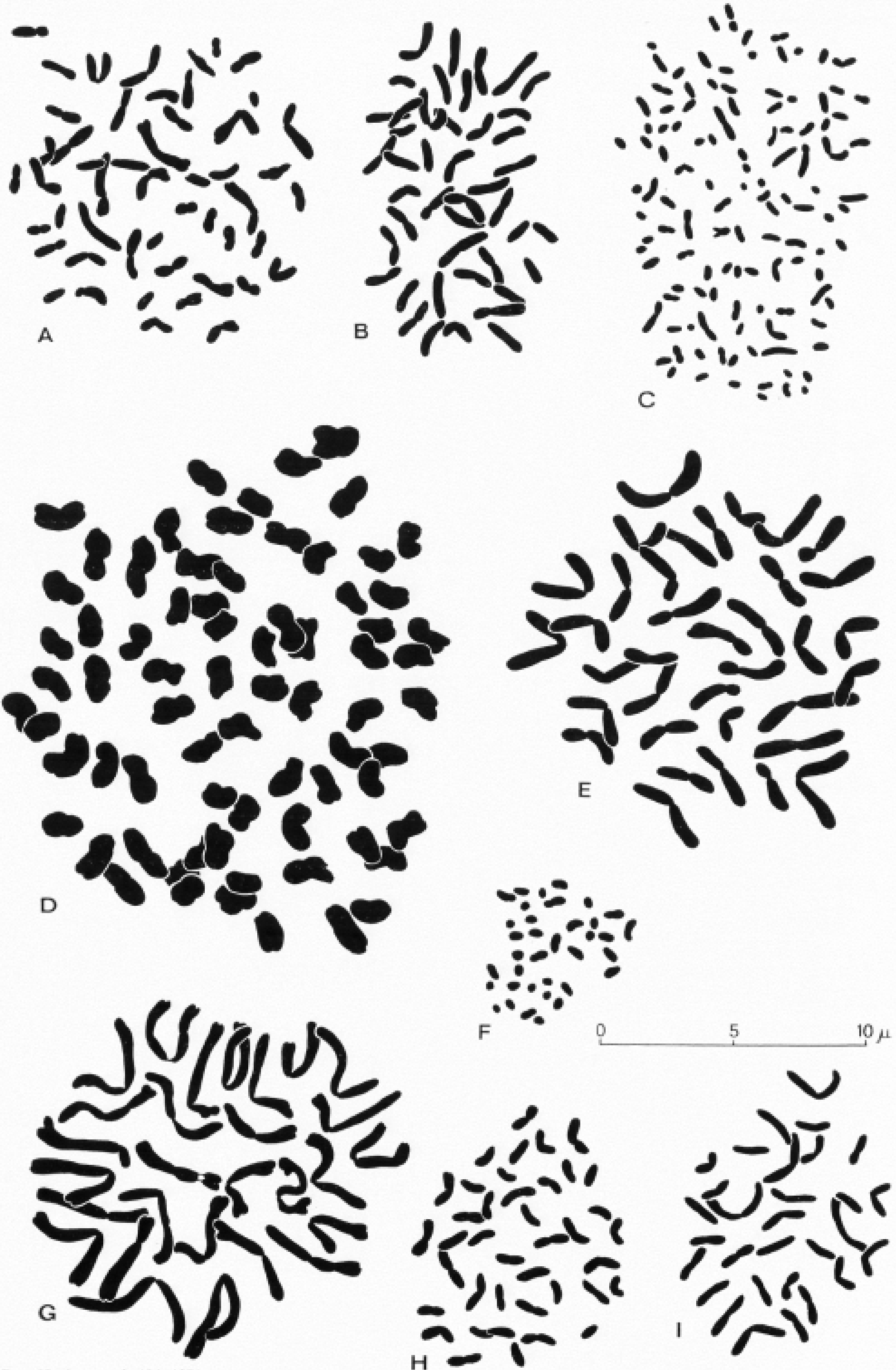
Taxon	Coll. no	2n	Previous counts and references
LAMIACEAE			
Ajuga iva (L.) Schreber	MMF 90	c. 86 (Fig. 2 I)	*
Lamium amplexicaule L.	MMF 77	18	18 F, RV 59
	MMF 907 b	18	
Mentha rotundifolia (L.) Huds.	MMK 775	36	24, 36 F, RV 68 54 F
Micromeria filiformis (Aiton) Benth.	MMF 302	30 (Fig. 2 G)	*
	MMF 924	30, 60	
	MMF 1004	30	
Salvia verbenaca L.	MMF 119	c. 60	42, 54 F
	MMF 676	60 (Fig. 2 H)	c. 58 Björkqvist et al. 1969
	MMF 870	c. 60	59 RV 59 64 F, RV 59
Sideritis romana L.	MMF 1001	28	28 Björkqvist et al. 1969
Stachys ocymastrum (L.) Briq. [=*S. hirta* L.]	MMF 15	18	18 F, Björkqvist et al. 1969
Teucrium chamaedrys L.	MMF 449	62—64	32, 60, 64 F 60—64 RV 68
LILIACEAE			
Allium roseum L.	MMF 384	32	32, 48 F 40 RV 59
Allium subhirsutum L.	MMF 374	14	14 F, RV 59
	MMK 540	28	
	MMF 1014	28 (Fig. 2 J)	
Allium triquetrum L.	MMF 373	18	18 F, RV 59
	MMF 2011 i	18	
Asphodelus fistulosus L.	MMF 85	56	28 F, RV 55 56 F, Björkqvist et al. 1969
Asphodelus microcarpus Salzm. & Viv. in Viv.	MMF 1908	28	The species complex: 28, 52, 56 F (*A. ramosus* L.) 26, 28, 56 F, RV 59 (*A. albus* L.)
Leopoldia comosa (L.) Parl. [=*Muscari comosum* (L.) Miller]	MMK 2001	18	18 F, RV 55, RV 68, Bentzer 1969
Merendera filifolia Camb.	MMK 2020	54 (Fig. 2 C)	*
LINACEAE			
Linum bienne Miller [=*L. angustifolium* Hudson]	MMF 641	32 (Fig. 2 K)	30, 32 F
Linum strictum L.	MMF 640	18	18 F, RV 68
Linum trigynum L. [=*L. gallicum* L.]	MMF 639	20	20 F

Fig. 2. Somatic metaphases in root-tips of Balearic angiosperms. — A: MMF 970 *Fumana ericoides*, 2n=32. — B: MMF 344 *Cneorum tricoccon*, 2n=36. — C: MMK 2020 *Merendera filifolia*, 2n=54. — D: MMF 76 *Astragalus epiglottis* ssp. *epiglottis*, 2n=16. — E: MMF 703 *Ononis reclinata*, 2n=60. — F: MMF 837 *Lotus tetraphyllus*, 2n=14. — G: MMF 302 *Micromeria filiformis*, 2n=30. — H: MMF 676 *Salvia verbenaca*, 2n=60. — I: MMF 90 *Ajuga iva*, 2n=c. 86. — J: MMF 1014 *Allium subhirsutum*, 2n=28. — K: MMF 641 *Linum bienne*, 2n=32.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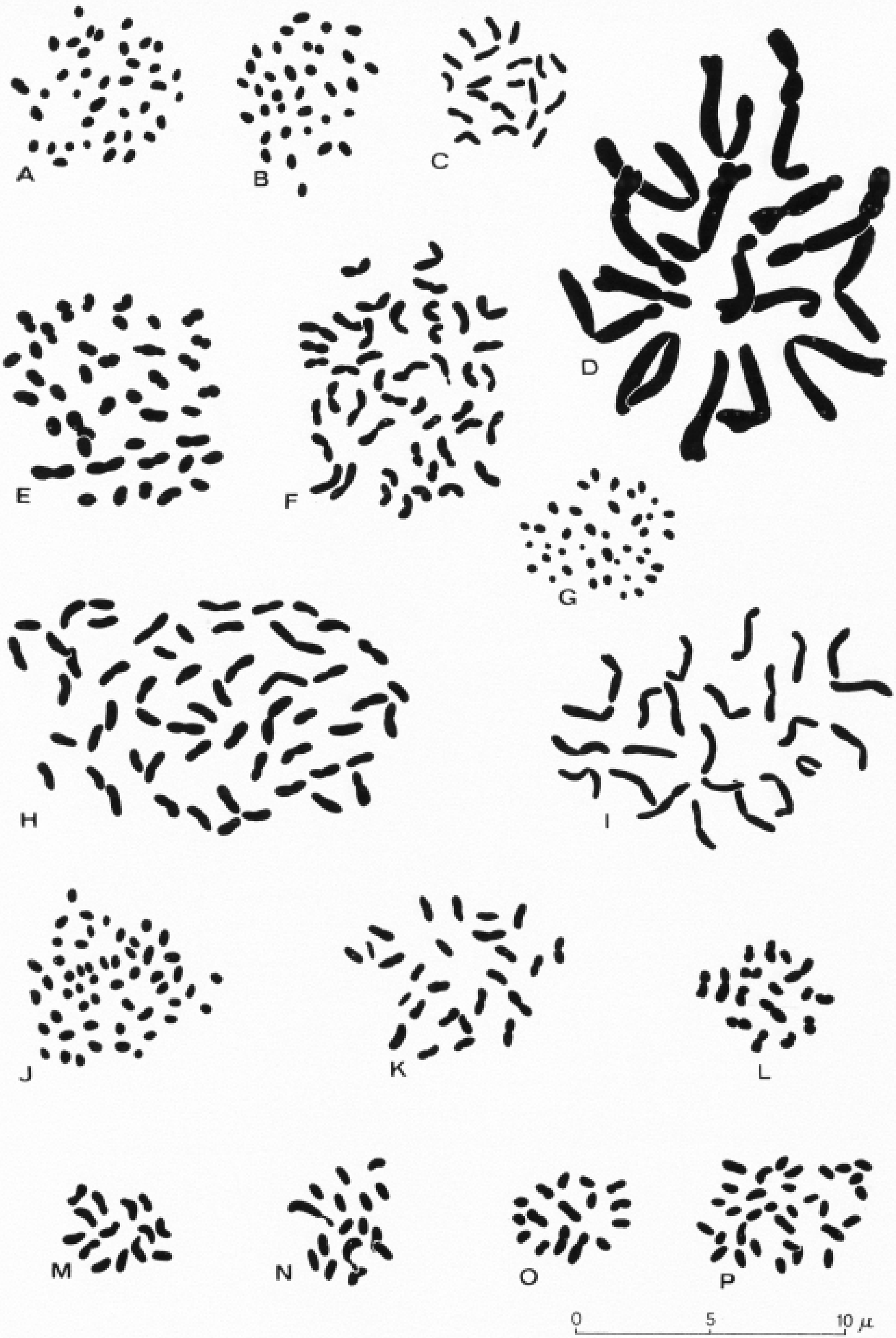
Taxon	Coll. no	2n	Previous counts and references
MALVACEAE			
Althaea hirsuta L.	MMF 396	c. 50 (Fig. 3 A)	*
Lavatera cretica L.	MMF 898	118—120 (Fig. 3 C)	40—44, c. 112 F
Lavatera maritima Gouan	MMF 1008	44 (Fig. 3 B)	*
ORCHIDACEAE			
Ophrys fusca Link	MMK 358	c. 73 (Fig. 3 D)	36 F
PLANTAGINACEAE			
Plantago bellardii All.	MMF 707 b	10	10 F, RV 55, RV 59
Plantago crassifolia Forsk.	MMF 160	20	20, 24 F
Plantago lanceolata L.	MMF 35	12	12 F, RV 59, RV 68 13, 24, 96 F
Plantago macrorrhiza Poiret	MMF 653	30 (Fig. 3 I)	10 F
Plantago psyllium L.	MMF 12	12	12 F, RV 55, RV 59
	MMF 420	12	
POACEAE			
Aegilops ovata L.	MMF 81	28	28 F, RV 50
	MMF 120	28	
	MMF 879	28	
Aegilops ventricosa Tausch	MMF 1034	28	28 F
Aira elegans Willd. in Gaudin	MMF 770	14	14 F, RV 68
Avena alba Vahl [=*A. barbata* Pott.]	MMF 114 a	28	14 F
	MMF 114 b	28	28 F, RV 55, RV 68 32 F
Avena sterilis L.	MMF 114 c	42	28, 42, 44 F
	MMF 148	42	
	MMF 2056	42	
Briza maxima L.	MMF 441	14	14 F
	MMF 724	14	
Briza minor L.	MMF 204	10	10, 14 F
Bromus madritensis L.	MMF 31	28	14 F
	MMF 100	28	28 F, Ovadiahu-Yavin 1969
	MMF 101	28	
	MMF 130	28	42 F
	MMF 815	28	
Bromus rigidus Roth ssp. *gussonei* (Parl.) Maire	MMF 145	56	28 F 56 F, Ovadiahu-Yavin 1969
Bromus rubens L.	MMF 102	28	28 F, Björkqvist et al. 1969, Ovadiahu-Yavin 1969
Cutandia maritima (L.) Benth.	MMF 159	14	14 F
Hordeum leporinum Link	MMF 9	28	14, 28, 42 F
	MMF 86	28	
	MMF 121	28	

Fig. 3. Somatic metaphases in root-tips of Balearic angiosperms. — A: MMF 396 *Althaea hirsuta*, 2n=c. 50. — B: MMF 1008 *Lavatera maritima*, 2n=44. — C: MMF 898 *Lavatera cretica*, 2n=c. 118. — D: MMK 358 *Ophrys fusca*, 2n=c. 73. — E: MMF 774 *Melica minuta*, 2n=36. — F: MMF 8 *Stipa capensis*, 2n=36. — G: MMF 224 *Vulpia membranacea*, 2n=28. — H: MMF 78 *Rumex pulcher*, 2n=40. — I: MMF 653 *Plantago macrorrhiza*, 2n=30.

Taxon	2n	Coll. no	Previous counts and references
Hordeum marinum Hudson	MMF 845	14	14, 28 F
Lamarckia aurea Moench	MMF 312	14	14 F
Lolium rigidum Gaudin	MMF 762	14	14 F, RV 55 14+1–2 B F
Lolium temulentum L.	MMF 123	14	14 F, RV 55, RV 68 28 F
Melica minuta L.	MMF 255	18	18 F
	MMF 774	36 (Fig. 3 E)	
Polypogon maritimus Willd. ssp. *subspathaceus* (Req.) Ascherson & Graebner	MMF 161	14	14, 28 F
Scleropoa rigida (L.) Griseb.	MMF 53	14	14 F
Stipa capensis Thunb. [=*S. retorta* Cav.]	MMF 8	36 (Fig. 3 F)	c.34 F
Vulpia membranacea (L.) Link	MMF 224	28 (Fig. 3 G)	14, 42 F
POLYGALACEAE			
Polygala rupestris Pourret	MMF 74	38	28 Björkqvist et al. 1969
	MMF 350	38	
	MMF 429	38 (Fig. 4 A)	
	MMF 975	34 (Fig. 4 B)	
POLYGONACEAE			
Rumex pulcher L.	MMF 78	40 (Fig. 3 H)	20 F, RV 59 40 F
PRIMULACEAE			
Anagallis arvensis L.	MMF 858	40	40 F, RV 59 80 RV 59
Asterolinum linum-stellatum (L.) Duby	MMF 308	20 (Fig. 4 C)	40 F
	MMF 583 a	20	
	MMF 952	20	
RANUNCULACEAE			
Clematis cirrhosa L.	MMF 413	16	*
Ranunculus bulbosus L.	MMF 1047	16	14 F 16 F, RV 59, RV 68
Ranunculus macrophyllus Desf.	MMF 700	16 (Fig. 4 D)	28 F
Ranunculus sardous Crantz	MMF 187	16	16 F, RV 68 18, 47, 48 F
RESEDACEAE			
Reseda alba L.	MMF 628	40 (Fig. 4 E)	20 F
ROSACEAE			
Sanguisorba minor Scop. ssp. *magnolii* (Spach) Briq.	MMF 586	28	28 Nordborg 1967

Fig. 4. Somatic metaphases in root-tips of Balearic angiosperms. — A: MMF 429 *Polygala rupestris*, 2n=38. — B: MMF 975 *Polygala rupestris*, 2n=34. — C: MMF 308 *Asterolinum linum-stellatum*, 2n=20. — D: MMF 700 *Ranunculus macrophyllus*, 2n=16. — E: MMF 628 *Reseda alba*, 2n=40. — F: MMF 673 *Rubia peregrina*, 2n=44. — G: MMF 905 *Ruta angustifolia*, 2n=40. — H: MMF 264 *Cymbalaria aequitriloba*, 2n=56. — I: MMF 813 *Linaria pelisseriana*, 2n=24. — J: MMF 352 *Viola arborescens*, 2n=52. — K: MMF 144 *Parietaria diffusa*, 2n=26. — L: MMF 311 *Parietaria lusitanica*, 2n=16. — M: MMF 1901 *Valerianella coronata*, 2n=14. — N: MMF 947 *Valerianella eriocarpa*, 2n=16. — O: MMF 99 *Valerianella microcarpa*, 2n=16. — P: MMF 99 *Valerianella microcarpa*, 2n=32. From same plant as Fig. 4 O.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Taxon	Coll. no	2n	Previous counts and references
Sanguisorba minor Scop. ssp. *muricata* (Spach) Nordborg	MMF 389	56	28, 56 Nordborg 1967
RUBIACEAE			
Crucianella latifolia L.	MMF 443	44	22, 44 F
Galium murale All.	MMF 346	44	44 F
Galium parisiense L.	MMF 273	c. 66	22, 44, 55, 66 F
	MMF 402	c. 66	
	MMF 403	64—66	
Galium setaceum Lam.	MMF 450	22	22, 44 F
Rubia peregrina L.	MMF 673	44 (Fig. 4 F)	66, 132 F
Sherardia arvensis L.	MMF 45	22	22 F, RV 68
	MMF 2006	22	
Valantia hispida L.	MMF 73	18	18 F
Valantia muralis L.	MMF 254	18	18 F
	MMF 956	18	
	MMF 2008	18	
RUTACEAE			
Ruta angustifolia Pers.	MMF 905	40 (Fig. 4 G)	*
SCROPHULARIACEAE			
Cymbalaria aequitriloba (Viv.) A. Chevalier	MMF 264	56 (Fig. 4 H)	42 F
Linaria pelisseriana (L.) Miller	MMF 813	24, [48] (Fig. 4 I)	*
Sibthorpia africana L.	MMF 322	20	20 F
	MMF 1000	20	
Veronica arvensis L.	MMF 593	16	14 F 16 F, RV 59, RV 68 16—18 F
Veronica polita Fries	MMF 604	14	14 F
	MMF 2007 x	14	
SOLANACEAE			
Hyoscyamus albus L.	MMF 853	68	34, 68 F
Solanum nigrum L.	MMF 238	72	24 F, RV 59, RV 68
	MMF 335	48	36, 40 F 48 F, RV 59, RV 68 72 F, RV 59 96, 144 F
THELIGONACEAE			
Theligonum cynocrambe L.	MMF 256 a	20	20 F
URTICACEAE			
Parietaria diffusa Mert. & Koch in Röhling	MMF 144	26 (Fig. 4 K)	*
	MMF 379	26	
	MMF 795	26	
	MMF 1020	26	
Parietaria lusitanica L. ssp. *lusitanica*	MMF 311	16 (Fig. 4 L)	*
	MMF 326	16	
	MMF 331	16	
Urtica dubia Forsk. [=*U. caudata* Vahl, *U. membranacea* Poiret]	MMF 240	22	22, 24 F

Taxon	Coll. no	2n	Previous counts and references
VALERIANACEAE			
Centranthus calcitrapa (L.) Dufr.	MMF 262	32	32 F
	MMF 579 a	32	
	MMF 788	32	
	MMF 817	32	
Centranthus macrosiphon Boiss.	MMF 43	32	32 F
Valerianella coronata (L.) DC.	MMF 80	14	14 F
	MMF 1901	14 (Fig. 4 M)	
Valerianella eriocarpa Desv.	MMF 457	16	14 F
	MMF 575	32	
	MMF 947	16 (Fig. 4 N)	
Valerianella microcarpa Loisel.	MMF 99	16 [32] (Fig. 4 O, P)	14 F
VIOLACEAE			
Viola arborescens L.	MMF 352	52 (Fig. 4 J)	c. 140 Fl. Eur. II (1968)

Table 2. Collecting sites of the cytologically investigated material reported here. The collections were all made in May, 1969 on the islands of Mallorca (Mall.) and Menorca (Men.).

Coll. no MMF/MMK	Locality	Date	No. on map Fig. 5
1	Mall. Can Pastilla. In sand on the shore	25	1
3 a, 3 b	Mall. San Telmo. Weeds near the harbour	25	2
8 — 55	Mall. Top of the pass between San Telmo and S'Arraco, ca. 2 km E of San Telmo. Garigue and olive yard	25	3
61 — 103	Mall. Top of the pass 2 km S of Andraitx. Garigue and olive plantation, terraces with weed vegetation	25	4
114 — 150	Mall. Along the road Palma—Inca, a few km SE of Inca. Cultivated fields and roadside	26	5
158 — 181	Mall. Just NW of Alcudia. Sandy beach	26	6
187 — 226 b	Mall. 1 km NW of Alcudia. Salt marshes and the adjacent sandy and weedy fields	26	7
232	Mall. Cabo Formentor. Cliffs by the lighthouse	26	8
235 — 240	Mall. Formentor Peninsula, 1—2 km SW of the lighthouse. Rocky ground	26	9
251 — 254	Same as 232	26	8
255 — 264	Same as 235—240	26	9
273 — 277	Mall. Formentor Peninsula, Cala Figuera. Along the road	26	9
288 — 289	Mall. Isla Dragonera, northern part. Rocky ground facing SE, near sea level	27	10
302 — 308	Mall. Isla Dragonera, central part. Slopes facing SE, ca. 150—225 m above sea level	27	11
311 — 335	Mall. Isla Dragonera, central part, near the summit. Slopes and cliffs ca. 250—315 m above sea level	27	11
336 — 342	Mall. Isla Dragonera, central part, between the peaks. Slope facing SW, ca. 200 m above sea level. Garigue and cliffs	27	11
344	Mall. Isla Dragonera, central part, SE side. 40 m above sea level, near the road	27	11
346 — 350	Mall. Isla Dragonera, central part, SE side. Ravine near the sea	27	11
352 — 358	Mall. W side of the pass between San Telmo and S'Arraco	27	3
360 — 364	Mall. 1 km W of Paguera	27	12
373 — 374	Mall. Pass S of Soller, slope towards Soller, facing N	28	13

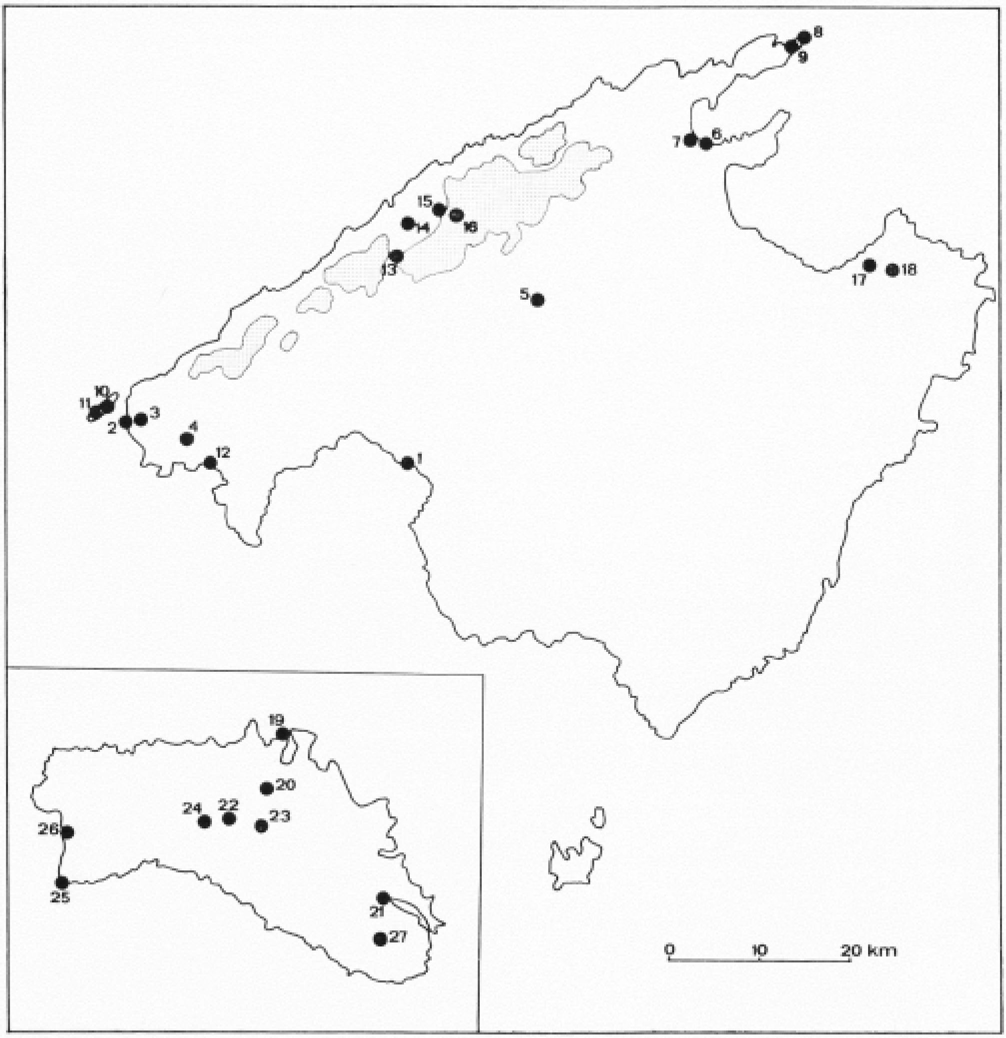

Fig. 5. Map of the islands of Mallorca and Menorca showing the location of collecting sites for material reported in the present paper. Owing to the small scale, the dots often represent two or more adjacent collecting sites.

Coll. no MMF/MMK	Locality	Date	No. on map Fig. 5
376 — 379	Mall. Soller, weeds near the railway station	28	14
384 — 420	Mall. Pass between Soller and Puig Major, 480 m above sea level. Roadside, olive terraces	28	15
426 — 450	Mall. By the road Soller—Puig Major, 560 m above sea level. Vegetation with *Ampelodesma mauritanicum*	28	15
457 — 468	Mall. Mount Tossals, W slopes facing Puig Major, 680—1000 m above sea level. Scrub grazed by sheep	28	16

Coll. no MMF/MMK	Locality	Date	No. on map Fig. 5
511 — 583 a	Mall. Mount Tossals. Cliff and scrub around the summit, 900—1000 m above sea level	28	16
586 — 616	Mall. Pass S of Soller, facing N. Shady places	28	13
626 — 628	Mall. Can Pastilla. Sandy ground under *Pinus halepensis*	28	1
632 — 659	Men. Cabo Fornells. Rocks and gravel by the sea	29	19
668 — 707 b	Men. 4 km N of Mercadal. Pasture	29	20
719	Men. Mahon, weedy ground near the harbour	30	21
721	Men. 3 km W of Mercadal. Roadside	30	22
724 — 730	Men. Roca. Scrub by a quarry	30	23
757	Men. Roca, by a quarry. Moist places at foot of rocks	30	23
762	Same as 724—730	30	23
770 — 818	Men. 1 km E of Ferrerias. Wood (*Olea, Quercus ilex, Cercis*) and by the roadside	30	24
827 — 879	Men. Cabo Dartuch. Exposed rocky ground by the sea, scrub of *Pistacia lentiscus* and *Juniperus phoenicea*. Including some moister ground	30	25
891	Men. Cala de Santandria. Horizontal rocks and stony ground by the sea	30	26
897 — 902	Men. Mahon, at the airport	30	27
905 — 907 b	Mall. Can Pastilla. Sandy places in the town	31	1
916 —1004	Mall. Eremita de Betlem (Artà), 2 km ESE of the monastery. Heavily grazed and burnt rocky ground with *Chamaerops*	31	17
1008 —1041	Mall. Eremita de Betlem (Artà). Cliffs and scrub by the monastery, facing N	31	17
1047 —1048	Mall. Border of cultivated field at the road junction Eremita—Morey—Artà	31	18
1901 —1906	Same as 8—55	25	3
1908 —1911	Same as 61—103	25	4
2001 —2007 x	Same as 114—150	26	5
2008	Same as 235—240	26	9
2011 a—2011 i	Same as 187—226 b	26	7
2012	Same as 311—335	27	11
2013	Same as 346—350	27	11
2020	Same as 511—583 a	28	16
2050	Same as 632—659	29	19
2051 —2053 d	Same as 668—707 b	29	20
2056	Same as 897—902	30	27
2102	Mall. Eremita de Betlem (Artà). Well near the monastery	31	17
2105	Same as 905—907 b	31	1

COMMENTS

APIACEAE

Ferula communis. — The chromosome numbers of the two plants studied was 2n=22 and 2n=23, respectively. The latter most probably represents a casual aberration only, as the number 2n=22 is reported several times for *Ferula communis* and other *Ferula* species. It is the only number known in the genus.

Torilis nodosa. — Our counts, 2n=24, agree with those of Engstrand (1970) from the Aegean region.

ARACEAE

Arisarum vulgare. — There is some uncertainty as to the exact chromosome number in our count, but it must lie around 2n=54—56. There is only one previous record for the species, 2n=52 (Jones 1952, cited from Fedorov 1969).

Arum italicum. — 2n=28 is previously known for other *Arum* species, but there are no earlier records of *A. italicum* on this low ploidy level; it is repeatedly reported to have 2n=64 or 2n=84.

ASTERACEAE

Carduus pycnocephalus. — The chromosome number for the collection MMF 2003 lies in the region of 2n=62—64. The only record prior to this is 2n=54 (MOORE & FRANKTON 1962), the highest chromosome number previously known in the genus.

Hedypnois. — The 2n=13 collection (MMF 146) is very distinct from the 2n=8 collections in having claviform peduncles and glabrous involucral scales. The peduncles of the 2n=8 collections are only slightly thickened towards the apex, and the involucral scales are ciliate to hispid.

BRASSICACEAE

Brassica balearica. — 2n=32 was obtained from the two individuals studied. MANTON (1932) reports 2n=18 for spontaneous material from Sicily. However, *B. balearica* is only known from Mallorca. MANTON's count therefore very probably refers to some other species of *Brassica.*

EUPHORBIACEAE

Euphorbia peplus. — 2n=16. The collection MMF 319 corresponds to *E. peploides* GOUAN [=*E. peplus* f. *peploides* (GOUAN) KNOCHE], with smaller leaves, and smaller seeds with fewer pits than *E. peplus* in the narrow sense. In cultivation, growth was luxuriant, but the morphological characteristics mentioned remained constant.

FABACEAE

Vicia pubescens. — 2n=14. Endopolyploidy was found in one of the root-tips, single cells having 2n=28.

Vicia sativa. — The 2n=10 collection (MMF 2053 d) belongs to ssp. *cordata* (WULFEN ex HOPPE) ASCHERSON & GRAEBNER, and the 2n=12 collection MMF 46 to ssp. *nigra* (L.) EHRH. [=*Vicia angustifolia* L.]. This agrees with the results of METTIN and HANELT (1964), who found the different chromosome numbers in the *Vicia sativa* complex to be correlated with different morphological types. — The two collections MMF 436 and MMF 705 could not with absolute certainty be referred to subspecies.

LAMIACEAE

Ajuga iva. — Our count, 2n=86 is approximate but obtained from two plants. *A. iva* thus seems to exhibit pronounced polyploidy. There are no previous counts in the genus higher than 2n=32.

Micromeria filiformis. — 2n=30. Of the two specimens studied among the progeny of the collection MMF 924, one was diploid (2n=30), and the other tetraploid (2n=60). In this case, the tetraploid may represent a chance aberration, and it remains to be proved if polyploid plants of *M. filiformis* occur in nature. The variation within the taxon on the Balearic Islands is rather wide, especially in the size of the vegetative parts, characters often reported to be influenced by polyploidy.

LILIACEAE

Allium subhirsutum. — Out of three collections of this species, MMF 374 proved to be diploid (2n=14), while the other two are tetraploid (2n=28). The tetraploid number was obtained both from material collected as bulbs (MMK 540) and from plants grown from seeds (MMF 1014). The tetraploid number has not previously been reported for *A. subhirsutum*, but intraspecific polyploidy is not a rare phenomenon in *Allium* (see, e.g. VON BOTHMER 1970).

LINACEAE

Linum bienne. — The chromosome number 2n=32 was found in all three individuals studied in the progeny of MMF 641. Several very distinct metaphase plates were seen. Many authors have reported 2n=30 for the species; there is only one previous record of 2n =32 (Martzenitzina 1927, cited from Fedorov 1969).

ORCHIDACEAE

Ophrys fusca. — 2n=c. 73. This seems to be the first record of such a high ploidy level in *Ophrys*. The plant was collected as a bulb; consequently, the genotype had been successfully established in nature. As there were cell divisions in only one of the fixed root-tips, the possibility that it is merely a case of endopolyploidy can not be ruled out. The flowers are typical of *O. fusca*.

PLANTAGINACEAE

Plantago crassifolia. — The chromosome number for this species was first reported as 2n=24 by McCullagh (1934; cited from Böcher et al. 1955). Our count, 2n=20, agrees with the basic number (x=5) for the *Plantago coronopus* group (i.e. the species with winged adaxial sepals) of sect. *Coronopus*, and with one previous count by Böcher et al. (1955).

Plantago macrorrhiza. — One plant was collected on Menorca and could only be determined with some difficulty. It is characterized by an appressed rosette of thick, fleshy, rigid and hirsute leaves which are linear-spathulate with c. 4 pairs of short ovate lobes (c. 5 mm) in the upper half; the rachis is 4—5 mm broad. The peduncles are many, decumbent, stout, longer than the leaves, and the spikes are 5 mm thick, dense, c. 5 cm long. The bracts are long-acuminate and about as long as the calyx. The abaxial sepals are 3 mm long, with the hairy carina broader than the membranous ciliate margins. The adaxial sepals are 3.5 mm long, with a conspicuous, ciliate, membranous, c. 0.5 mm broad wing on the back. The seeds are light brown, 1.0 —1.5 mm.

Seeds from this plant gave rise to two plants cultivated in the greenhouse. They turned out to be hexaploid (2n=30). They are strongly modified and deviate markedly from the mother plant by the ascending leaves which are glabrescent, narrowly oblanceolate and remotely dentate in upper 1/3, up to 1 cm broad excluding teeth. In floral characteristics, however, they agree closely with the mother plant. All three plants flowered in their first year. It has not been possible to refer them with any certainty to any of Pilger's (1937) three subspecies.

Following Böcher et al. (1955) the mother plant should be referred to ssp. *occidentalis* Pilger, and the progeny rather to ssp. *macrorrhiza*. The *Plantago coronopus* complex has been treated from a cytological point of view by several authors in recent years (see Böcher et al. 1955; Runemark 1967), but further work seems to be needed, especially in the western Mediterranean.

POACEAE

Melica minuta. — The occurrence of polyploidy in the *Melica minuta* complex does not seem to have been reported previously. The collection MMF 255 (2n =18) corresponds to ssp. *minuta* in having densely fasciculate, 1—2 dm tall, slender culms, entirely convolute, glaucescent leaves which are villous on the upper side, and a long ligule. The collection MMF 774 (2n=36) corrensponds to ssp. *major* (Parl.) Trabut. It is considerably taller, the culms are stout and not fasciculate, the leaves are glabrous, pure green, not convolute, and the ligule is shorter and truncate. In cultivation the leaves of ssp. *minuta* were not convolute, but still considerably narrower than those of ssp. *major*. The rest of the morphological characteristics mentioned proved stable.

POLYGALACEAE

Polygala rupestris. — 2n=34 and 2n=38 were unambiguously counted in different collections. Björkqvist et al. (1969) report 2n=28 from Spain. More counts of the species are needed before anything can be said about the variation pattern of the chromosome number. Glendinning (1955, cited from Larsen 1959) found different chromosome numbers in different strains of *Polygala chamaebuxus* L.

RANUNCULACEAE

Ranunculus macrophyllus. — 2n=16. Langlet (1936) counted 2n=28 in *R. macrophyllus* obtained from Oslo (probably cultivated). It is doubtful whether Langlet's material really belonged to the true *R. macrophyllus* Desf.

RUTACEAE

Ruta angustifolia. — The species has not previously been studied cytologically. The number 2n=40 was obtained from both specimens studied. It deviates from earlier counts of *Ruta* species, which are multiples of x=9 (2n=18, 36, 72, 81). Further studies of the genus would be desirable.

SCROPHULARIACEAE

Linaria pelisseriana. — 2n=24. In a segment of one root-tip, cells with 2n=48 were noted.

SOLANACEAE

Solanum nigrum. — The two collections studied differ in some respects. MMF 238 (2n=72) has cuneate leaf-bases and pure white flowers, whereas MMF 335 (2n=48) has truncate leaf-bases and veins of the corolla striated with violet. These characters proved to be constant in cultivation. Both collections are perennial, and woody below. The plants grew on rather exposed rocky ground facing the sea.

VALERIANACEAE

Valerianella. — Our counts, 2n=14, in *Valerianella coronata* confirm the counts of Elvers (1932). Elvers also gave 2n=14 for, among others, *V. eriocarpa* and *V. microcarpa*. In material of these two species from the Balearic Islands, we have clearly counted 2n=16, or in the *V. eriocarpa* collection MMF 575, 2n=32. In the only *V. microcarpa* collection studied, MMF 99, there were polyploid segments (2n=32; Fig. 4 P) in several of the root-tips.

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Chromosome Numbers of Vascular Plants from Austria, Mallorca and Yugoslavia

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ABSTRACT

Nilsson, Ö. and Lassen, P. 1971. Chromosome numbers of vascular plants from Austria, Mallorca and Yugoslavia. — Bot. Notiser 124: 270—276.

Somatic chromosome numbers of 108 taxa of vascular plants from Austria, Mallorca, and Yugoslavia are reported. The chromosome numbers of 24 taxa are new or deviate from previously published counts.

MATERIAL AND METHODS

The material studied from Austria and Yugoslavia was collected by Ö. Nilsson in July, 1969, and the material from Mallorca by Mr. J. Kraft during two botanical tours, the first in November, 1969, and the second in April, 1970. The collections consisted either of living plants or seeds. Plants (usually five per collection) were raised from the seeds in greenhouses in the Botanical Garden, Lund.

The chromosome counts were made on sectioned root tips, treated according to the paraffine method (fixative: the Svalöv modification of Navashin-Karpechenko; stain: crystal violet and aniline).

The chromosome counts have been made by Ö. Nilsson who also determined the material from Austria and Yugoslavia. The Mallorcan plants have been determined by P. Lassen.

RESULTS

The somatic chromosome numbers obtained are presented in the Table below. New counts are marked with an asterisk in front of the taxonomic epithet. The origin of the collections are given in the central column of the table. Voucher specimens are preserved in the Lund Botanical Museum (LD). The designation ÖN refers to material collected by Nilsson and JK-M to collections by Mr. Kraft (nr. 1—260 first tour, 300—350 second tour). Uncertain counts are marked with c. in front of the chromosome number.

In the right column of the Table previously chromosome numbers are cited; the abbreviations BGMZ 1969, Fl. E., and Regn. Veg. 68, refer to Bolkhovskikh et al. (1969), Flora Europaea edited by Tutin et al. (1964, 1968), and Regnum Vegetabile 68 (1970), respectively; cf. Literature cited. For the case of brevity the papers in which the chromosome numbers were originally published are not cited if they are not further discussed.

The taxa are presented in alphabetical order. The nomenclature is according to Flora Europaea in its present extension and for the remaining taxa other standard floras of the areas have been consulted.

DISCUSSION

Vascular plants of 108 taxa have been studied as to their chromosome numbers, 12 from Austria (one locality), 32 from Yugoslavia (three localities), and 65 from Mallorca. Eleven counts represent new, additional numbers for the respective taxa,

Taxon	Voucher	Origin	2n	Previous counts
AIZOACEAE				
Mesembryanthemum crystallinum L.	JK-M 321 A	Mallorca; San Vicente	18	18; BGMZ 1969
ANACARDIACEAE				
Pistacia lentiscus L.	JK-M 130	Mallorca	24	24; BGMZ 1969
APIACEAE				
Foeniculum vulgare Mill. ssp. *piperitum* (Ucria) Coutinho	JK-M 140	Mallorca; Palma	22	22; BGMZ 1969
Kundmannia sicula DC.	JK-M 253	Mallorca	22	22; BGMZ 1969
Orlaya grandiflora (L.) Hoffm.	ÖN 48	Yugoslavia; Croatia, Novi Vinodolski	20	20; BGMZ 1969
**Pastinaca lucida* L.	JK-M 9	Mallorca; Palma	22	
ARACEAE				
**Arum italicum* Mill.	JK-M 42	Mallorca	28	64, 84; BGMZ 1969
ASTERACEAE				
Bellium bellidioides L.	JK-M 330	Mallorca; San Vicente	18	18; BGMZ 1969
Buphthalmum salicifolium L.	ÖN 68	Yugoslavia; Slovenia, 2 km S of Pivka	20	20; BGMZ 1969
**Centaurea dichroantha* A. Kerner	ÖN 54	Same locality	20	
**Centaurea rupestris* L.	ÖN 36	Yugoslavia; Croatia, Novi Vinodolski	20	24; BGMZ 1969
**Centaurea splendens* L.	ÖN 40	Same locality	20	
Cichorium intybus L.	JK-M 102	Mallorca; Genova	18	18; BGMZ 1969
Cirsium canum (L.) All.	ÖN 50	Yugoslavia; Slovenia, 2 km S of Pivka	34	34; BGMZ 1969
Erigeron bonariense L.	JK-M 114	Mallorca; Palma	54	54; BGMZ 1969
Helichrysum italicum (Roth) G. Don	ÖN 37	Yugoslavia; Croatia, Novi Vinodolski	28	28; BGMZ 1969
Hyoseris radiata L.	JK-M 37	Mallorca	16	16; BGMZ 1969
Inula graveolens (L.) Desf.	JK-M 113	Mallorca; Palma	20+0—2 B	20; Björkqvist et al. 1970
Inula spiraeifolia L.	ÖN 31	Yugoslavia; Croatia, Novi Vinodolski	16	16; Reg. Veg. 68
Inula viscosa (L.) Ait.	JK-M 115	Mallorca	18	18; BGMZ 1969
Leontodon hispidus L.	ÖN 75	Austria; Saltzburg, Klammstein	14	14; BGMZ 1969
Phagnalon rupestre (L.) DC.	JK-M 121	Mallorca	18	18; BGMZ 1969
Reichardia picroides (L.) Roth ssp. *picroides*	JK-M 36	Mallorca	14	14; BGMZ 1969

Taxon	Voucher	Origin	2n	Previous counts
BRASSICACEAE				
Arabis alpina L.	ÖN 77	Austria; Saltzburg, Klammstein	16	16; BGMZ 1969, 32; Fl. E. 1964
Arabis hirsuta (L.) Scop.	ÖN 30	Yugoslavia; Croatia, Novi Vinodolski	32	8, 16, 32, 64; BGMZ 1969
Carrichtera annua (L.) DC.	JK-M 313	Mallorca; Cala Mayor	16	16, 32; BGMZ 1969
**Erophila verna* (L.) E. Mey. ssp. *praecox* (Steven) Walters	JK-M 304	Mallorca; Tossals	32	
Erysimum helveticum (Jacq.) DC.	ÖN 62	Austria; Saltzburg, Klammstein	c. 56	14, 28, 48, 56; BGMZ 1969
Hornungia petraea (L.) Rchb.	JK-M 303	Mallorca; Tossals	12	12; BGMZ 1969
**Lepidium graminifolium* L. ssp. *suffruticosum* (L.) P. Monts.	JK-M 137	Mallorca	48	
Moricandia arvensis (L.) DC.	JK-M 336	Mallorca; Palma	28	26, 28; BGMZ 1969
CAMPANULACEAE				
Campanula bononiensis L.	ÖN 71	Yugoslavia; Slovenia, 2 km S of Pivka	34	34; BGMZ 1969
Campanula cochlearifolia Lam.	ÖN 78	Austria; Saltzburg, Klammstein	34	34, 35, 37, 68; BGMZ 1969
Campanula erinus L.	JK-M 1 B	Mallorca	28	28; BGMZ 1969
Phyteuma orbiculare L.	ÖN 65	Austria; Saltzburg, Klammstein	24	22, 24, 26; BGMZ 1969
CARYOPHYLLACEAE				
Dianthus silvestris Wulf. ssp. *tergestinus* (Rchb.) Hayek	ÖN 22	Yugoslavia; Croatia, Novi Vinodolski	30	30; BGMZ 1969
Gypsophila repens L.	ÖN 72	Austria; Saltzburg, Klammstein	34	34, 35, 36; BGMZ 1969
CHENOPODIACEAE				
Kochia scoparia (L.) Schrad.	JK-M 146	Mallorca	18	18; BGMZ 1969
**Arthrocnemum fruticosum* (L.) Moq.	JK-M 252	Mallorca; Palma Nova	72	54; Regn. Veg. 68
CISTACEAE				
Cistus albidus L.	JK-M 27	Mallorca	18	18; BGMZ 1969
Cistus monspeliensis L.	JK-M 17	Mallorca	18	18; BGMZ 1969
Cistus salvifolius L.	JK-M 250	Mallorca	18	18; BGMZ 1969
**Fumana ericoides* (Cav.) Gand.	JK-M 128	Mallorca; Illetos	32	
Fumana procumbens (Dunal) Gren. & Godr.	ÖN 46	Yugoslavia; Croatia, Novi Vinodolski	32	32; BGMZ 1969
Fumana thymifolia (L.) Spach	JK-M 124	Mallorca	32	32; BGMZ 1969

**Hypericum balearicum* L.	JK-M 138	Mallorca; Palma	24	
	JK-M 139	Mallorca; Genova	24	
Hypericum perforatum L.	JK-M 147	Mallorca	32	32, 36; BGMZ 1969
CRASSULACEAE				
**Sedum sediforme* (JACQ.) PAU	JK-M 38	Mallorca	c. 64	32; Fl. E. 1968
Sedum sexangulare L.	ÖN 32	Yugoslavia; Slovenia, Loibl Pass	74	74, 108; BGMZ 1969
EUPHORBIACEAE				
Euphorbia exigua L.	JK-M 320	Mallorca; San Vicente	24	16, 24, 28; BGMZ 1969
Euphorbia segetalis L.	JK-M 43—45	Mallorca	16	16; BGMZ 1969
FABACEAE				
Chamaecytisus supinus (L.) LINK.	ÖN 53	Yugoslavia; Slovenia, 2 km S of Pivka	48	48, 96; BGMZ 1969
Chamaespartium sagittale (L.) P. GIBBS	ÖN 55	Same locality	48	44, c. 46, 48; BGMZ 1969
**Dorycnium pentaphyllum* SCOP. ssp. *germanicum* (GREMLI) GAMS	ÖN 35	Yugoslavia; Croatia, Novi Vinodolski	14	
Hippocrepis balearica JACQ.	JK-M 144	Mallorca; Puerto de Soller	14	14; BGMZ 1969
Lembotropis nigricans (L.) GRIESEB.	ÖN 13	Yugoslavia; Croatia, Novi Vinodolski	48	48, 96; BGMZ 1969
Medicago littoralis ROHDE	JK-M 327	Mallorca; Palma Nova	16	16; BGMZ 1969
Medicago minima (L.) BARTAL.	JK-M 328	Same locality	16	16; BGMZ 1969
Medicago prostrata JACQ.	ÖN 26	Yugoslavia; Croatia, Novi Vinodolski	16	16, 32; BGMZ 1969
Medicago scutellata (L.) MILL.	JK-M 314	Mallorca; Cala Mayor	32	32; BGMZ 1969
Ononis minutissima L.	JK-M 150	Mallorca; Palma Nova	30	30; Fl. E. 1968
Ononis pusilla L.	ÖN 18	Yugoslavia; Croatia, Novi Vinodolski	30	30; BGMZ 1969
Trifolium lappaceum L.	ÖN 33	Same locality	16	16; BGMZ 1969
Trifolium medium L.	ÖN 25	Same locality	c. 76	c. 80, 80, c. 84, c. 96—98, c. 126; BGMZ 1969
Trifolium rubens L.	ÖN 59	Yugoslavia; Slovenia, 2 km S of Pivka	16	16; BGMZ 1969
Vicia cassubica L.	ÖN 61	Same locality	14	12, 14; BGMZ 1969
GLOBULARIACEAE				
**Globularia alypum* L.	JK-M 119	Mallorca	16	32; BGMZ 1969
Globularia willkommii NYM.	ÖN 34	Yugoslavia; Croatia, Novi Vinodolski	16	16; BGMZ 1969
IRIDACEAE				
**Crocus minimus* DC. var. *cambessedesii* (GAY) KNOCHE	JK-M 70—75	Mallorca; San Vicente	16	[24; BGMZ 1969]

Taxon	Voucher	Origin	2n	Previous counts
Gladiolus illyricus KOCH	JK-M 67—68, 100	Mallorca; Palma Nova	60	60, 90; BGMZ 1969
LAMIACEAE				
**Calamintha ascendens* JORD.	JK-M 11—12, 149	Mallorca	48	
**Lavandula dentata* L.	JK-M 58	Mallorca	44	45; BGMZ 1969
Rosmarinus officinalis L.	JK-M 52	Mallorca	24	24; BGMZ 1969
Stachys recta L.	ÖN 29	Yugoslavia; Croatia, Novi Vinodolski	c. 34	32, 34, 48; BGMZ 1969
**Teucrium chamaedrys* L.	JK-M 57	Mallorca	64	32, 60, 64; BGMZ 1969
	ÖN 19	Yugoslavia; Croatia, Novi Vinodolski	c. 80	
Teucrium montanum L.	ÖN 9	Same locality	30	16, 30, 60; BGMZ 1969
LILIACEAE				
Allium carinatum L.	ÖN 52 A	Yugoslavia; Slovenia, 2 km S of Pivka	24	16, 24, 25, 26; BGMZ 1969
Allium sphaerocephalum L.	ÖN 43	Same locality	16	16, 32; BGMZ 1969
Asphodelus fistulosus L.	JK-M 13—16	Mallorca; Palma	56	28, 56; BGMZ 1969
**Asphodelus microcarpus* VIV.	JK-M 1	Same locality	28	
Urginea maritima (L.) BAKER	JK-M 5	Mallorca	30	12, 30, 40, 60; BGMZ 1969
	JK-M 7, 41	Mallorca	40	
LINACEAE				
Linum strictum L.	JK-M 321	Mallorca; San Vicente	18	18; BGMZ 1969
Linum tenuifolium L.	ÖN 38, 42	Yugoslavia; Croatia, Novi Vinodolski	18	16, 18; BGMZ 1969
MYRTACEAE				
Myrtus communis L.	JK-M 101	Mallorca; Aubarca	22	22; BGMZ 1969
PLUMBAGINACEAE				
**Limonium virgatum* (WILLD.) KUNTZE	JK-M 132	Mallorca; Palma Nova	36	
POACEAE				
**Ampelodesma mauritanicum* (POIR.) DUR. & SCHINZ	JK-M 19—20, 106	Mallorca; Palma Nova	48	96; BGMZ 1969
Stipa juncea L.	JK-M 240	Mallorca; Genova	44	44; BGMZ 1969
POLYPODIACEAE				
Polypodium australe FÉE	JK-M 30	Mallorca	c. 70	74; Fl. E. 1964

PRIMULACEAE				
Anagallis arvensis L.	JK-M 39	Mallorca	40	40; BGMZ 1969
ROSACEAE				
**Potentilla caulescens* L.	ÖN 73	Austria; Saltzburg, Klammstein	42	14; BGMZ 1969
RUBIACEAE				
Valantia muralis L.	JK-M 309	Mallorca; Genova	18	18; BGMZ 1969
**Rubia peregrina* L.	JK-M 152	Same locality	44	66, c. 132; BGMZ 1969
SAXIFRAGACEAE				
Saxifraga aizoides L.	ÖN 69	Austria; Saltzburg, Klammstein	26	26; BGMZ 1969
Saxifraga aizoon JACQ.	ÖN 1	Same locality	28	28; BGMZ 1969
SCROPHULARIACEAE				
Chaenorrhinum littorale (WILLD.) FRITSCH	ÖN 10	Yugoslavia; Croatia, Novi Vinodolski	14	14, 42; BGMZ 1969
Verbascum sinuatum L.	JK-M 46	Mallorca; Palma	30	30; BGMZ 1969
Veronica arvensis L.	JK-M 337	Same locality	16	14, 16, 16—18; BGMZ 1969
Veronica cymbalaria BODARD	JK-M 315	Mallorca; Cala Mayor	18	18, 36, 54; BGMZ 1969
Veronica spicata L.	ÖN 20	Yugoslavia; Croatia, Novi Vinodolski	68	34, 35, 36, 64—70, c. 68, 68; BGMZ 1969
Veronica urticaefolia JACQ.	ÖN 67	Austria; Saltzburg, Klammstein	64	64, 128; BGMZ 1969
SOLANACEAE				
Solanum nigrum L.	JK-M 122	Mallorca; Palma	48	24, 36, 40, 48, 72, 96, 144; BGMZ 1969
THELIGONACEAE				
Theligonum cynocrambe L.	JK-M 306	Mallorca; Tossals	20	20; BGMZ 1969
URTICACEAE				
**Parietaria lusitanica* L. ssp. *lusitanica*	JK-M 307	Mallorca; Tossals	16	
**Urtica dubia* FORSK.	JK-M 117	Mallorca; Palma	26	22; BGMZ 1969
VALERIANACEAE				
Valeriana montana L.	ÖN 76 A	Austria; Saltzburg, Klammstein	32	32; BGMZ 1969
Valeriana saxatilis L.	ÖN 76 B	Same locality	24	24; BGMZ 1969
Valerianella coronata (L.) DC.	JK-M 319	Mallorca; San Vicente	14	14; BGMZ 1969

and 13 of the taxa have not, to our knowledge, been cytologically investigated before.

New ploidy levels are found or indicated by our numbers of the following taxa: *Ampelodesma mauritanicum, Arthrochnemum fruticosum, Arum italicum, Globularia alypum, Lepidium graminifolium* ssp. *suffruticosum, Potentilla caulescens, Rubia peregrina,* and *Sedum sediforme.* Octoploidy (2n=72) has not previously been reported in the *Arthrochnemum-Salicornia* complex. *Lepidium graminifolium* ssp. *graminifolium* is reported to be diploid, but our count on ssp. *suffruticosum* indicates hexaploidy, which is not previously known in the genus.

Our count (2n=32) on *Erophila verna* ssp. *praecox* seems to be the first of this subspecies, but agrees with some counts reported for this species complex. The chromosome number of *Crocus minimus* var. *cambessedesii* (2n=16), an endemic of the Balearic islands, deviates from that reported for *C. minimus* by other authors. The karyotype is characterized by two pairs of chromosomes which are considerably larger than the remainder. In *Kochia scoparia,* endopolyploidal (2n=36 and 72) segments of cells in the root tips were remarkably common.

The two collections of *Teucrium chamaedrys* were different, in particular with regard to indumentum, the Yugoslavian being more pubescent.

Centaurea scabiosa and *C. rupestris* belong to the same section, *Acrocentron* (CASS.) DC. of the genus. According to FRITSCH (1935) the two species have 2n=24. Later, several authors have counted 2n=20 for *C. scabiosa.* We have found the same number (2n=20) in *C. rupestris. C. dichroantha* appears to be intermediate between the two species mentioned. According to HEGI (1929) *C. dichroantha* has often been mistaken as the hybrid *C. rupestris×scabiosa.* The chromosome number of *C. dichroantha* (2n=20) is not conflicting against the supposed hybrid origin of the species.

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A Bifurcate Frond of Laminaria digitata from Sweden

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ABSTRACT

SUNESON, S. 1971. A bifurcate frond of Laminaria digitata from Sweden. — Bot. Notiser 124: 277—279.

An abnormal frond of *Laminaria digitata* (HUDS.) LAMOUR. with a bifurcate stipe and two separate blades is reported from the West Coast of Sweden. The abnormality is believed to be due to a deep splitting of the frond into the meristematic tissue, situated between lamina and stipe, and not to a coalescence of two individuals. References are made to some examples of coalescence in *Laminaria* species, reported from Japan, and to several examples of abnormal branching, due to splitting of the meristem. The abnormality seems to be rare on the Swedish West Coast, possibly due to the fact that the *Laminaria* associations are never laid bare at low water in Sweden.

When collecting material of *Laminaria digitata* (HUDS.) LAMOUR. for school herbaria I found an abnormal specimen, provided with a forked stipe and two separate blades. The plant was collected in July 1959 in the vicinity of the Zoological station Kristineberg on the West Coast of Sweden. It grew near the rocky shore at a depth of 1.5 m in a moderately exposed place.

The laminae were unequal in size. The total length of the plant was 66 cm, the old blade at the top of the larger lamina included. After photographing the fresh specimen (Fig. 1), the basal part (holdfast and branched stipe) was preserved in alcohol. This material has later been soaked in water, photographed (Fig. 2) and examined more closely. The holdfast was quite normal and the basal part of the stipe was round and smooth. The abnormal frond can therefore hardly be due to coalescence of two plants. Nor did longitudinal sections through the stipe in the region of the branching point show any trace of such a process. Three examples of coalescence of fronds in Laminariales have been reported from Japan, one concerning *Laminaria fragilis* MIYABE (HASEGAWA & FUKUHARA 1956), another *L. japonica* ARESCH. (TOKIDA & OHMI 1956). The third example is a chimaera of two plants, belonging to different genera, viz. *Alaria* and *Laminaria* (TOKIDA, OHMI & IMASHIMA 1958). In these cases the laminae of two individuals have fused. Their margins are thought to have been damaged in the transition zone, where the meristematic tissue is situated in all Laminariales.

The actual abnormal frond of *Laminaria digitata* seems to be due to a deep longitudinal splitting into the meristem of the plant. A parallel may be drawn to the genera of the family Lessoniaceae of the Laminariales (e.g. *Lessonia* and *Macrocystis*). The elaborate fronds of these Laminariales are due to a process of splitting, which extends into the transition zone, so that the secondary blades are each provided with a part of the original meristem and can thus develop secondary stipes of their own (cf. FRITSCH 1952 pp. 203, 219). In the family Lami-

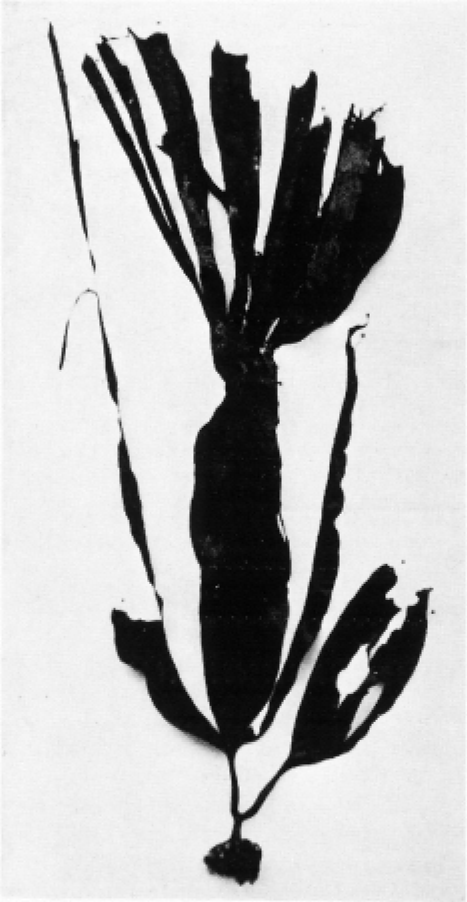

Fig. 1. *Laminaria digitata,* bifurcate frond. ×c. 1/8. Photo: the author.

Fig. 2. *Laminaria digitata,* basal part of bifurcate frond. Slightly reduced. Photo: S. NYGREN.

nariaceae some members (e.g. *Laminaria saccharina*) have an undivided lamina, while in other species (e.g. *L. digitata*) the blade is divided by longitudinal splitting into several segments. However, in this family the splitting of the lamina does not usually extend into the transition zone between stipe and lamina. The meristem therefore remains a single entity. In the bifurcate specimen of *L. digitata,* reported here, the splitting of the primary blade has probably extended into the meristem, with a resulting segregation of it into two separate entities. As may be seen from Fig. 2, the secondary stipes were slightly flattened in their upper parts.

Several examples of branching in *Laminaria* have been reported in the literature. SETCHELL (1905 pp. 141—148) studied the "periodic physiological regeneration" (i.e. the normal renewal of the blade) and the "restorative regeneration" in *Laminaria,* especially in the Pacific species *L. Sinclairii* (HARV.) FARL. The habitats of this species are extremely exposed to the waves, and many specimens, branched in different ways, were found. In all cases where the cause of the abnormality could be traced, it was due to wounds in the superficial layers. Vertical wounds at the top of the stipe, caused by a continued splitting of the blade into the meristematic zone, may according to SETCHELL result in a bifurcation of the stipe. SETCHELL (1905 p. 149) also mentions a bifurcate specimen of *L. digitata* (preserved in Herb. FARLOW). SAUVAGEAU (1918 p. 138, Fig. 47) describes a specimen of *L. digitata* (by the name of *L. flexicaulis*) with a branched stipe, collected in Roscoff (France). He also mentions that he had found three other branched specimens of the same species, without having looked for them. Furthermore he mentions several specimens of *L. Cloustoni* EDM. with branched stipe, collected by LE JOLIS.

From the Swedish West Coast no finds of branched *Laminaria* fronds have, as far as I know, been reported before. The abnormality therefore seems to be rare on this coast, which might be connected with the fact that the *Laminaria* associations are never laid bare here at low water. The tidal range does not exceed 30 cm (KYLIN 1918 p. 68; GILLNER 1965 p. 97; SÖDERSTRÖM 1965 p. 85). The fluctuations in water level due to weather conditions are more marked especially during the winter. During late winter and spring there are usually long periods of comparatively low water. According to KYLIN (l.c.) the water level at Kristineberg can be pressed down to about 60 cm (in extreme cases even to 87 cm) below the medium water-line. These periods of low water often coincide with severe frost, which can kill off emerged algae of frost sensitive species, like young *Laminaria* plants (KYLIN 1918 pp. 86—87). Therefore, associations of *Laminaria digitata* and *L. saccharina* do not occur above a depth of c. 1 m at the Swedish West Coast. *L. Cloustoni* only occurs at depths of c. 10—20 metres (KYLIN 1947 p. 81).

ACKNOWLEDGEMENTS

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Studies in African Cyperaceae II

The Genus Oxycaryum Nees

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ABSTRACT

Lye, K. A. 1971. Studies in African Cyperaceae II. The genus Oxycaryum Nees. — Bot. Notiser 124: 280—286.

The monotypic genus *Oxycaryum* Nees is regarded as distinct from *Scripus*, its relationship being with the tribe Cypereae rather than with Scirpeae. A new combination, *Oxycaryum cubense* (Poep. & Kunth) K. Lye, is made.

The relationship between the two tribes Scirpeae and Cypereae is discussed, and it is concluded that all genera of Scirpeae with a *Cyperus*-type embryo should be transferred to Cypereae.

GENERIC CIRCUMSCRIPTIONS IN SCIRPEAE AND CYPEREAE

It is well known that the genus *Scirpus*, as interpreted by Linnaeus (1753 pp. 47—52), and accepted with some alterations by later authors (cf. Clarke 1894, 1902, Phillips 1926, 1951, Shishkin 1935, Hutchinson & Dalziel 1936, Fernald 1950, Gleason 1952, Munz 1959, Fournier 1961, Lid 1963, Steyermark 1963, Ohwi 1965, Schultze-Motel 1966, Hultén 1968, and Hitchcock et al. 1969), is a very heterogeneous assemblage of species (cf. Kern 1962). Since 1753 *Scirpus* sensu L. has been split into numerous smaller genera, viz. *Abildgaardia* (Vahl 1806 p. 296), *Actinoschoenus* (Bentham 1881 p. 33), *Baeothryon* (Ehrhart 1789 p. 147 — nomen nudum), *Blysmus* (Roemer & Schultes 1824 p. 41), *Bulbostylis* (Clarke 1894 p. 651), *Desmoschoenus* (Hooker 1855 p. 271), *Dichostylis* (Beauvois in Lestiboudois 1819 p. 39), *Eleocharis* (Brown 1810 p. 224), *Eleogiton* (Link 1827 p. 284), *Ficinia* (Schrader 1832 p. 43), *Fimbristylis* (Vahl 1806 p. 285), *Fuirena* (Rottböll 1773 p. 70), *Hemichlaena* (Schrader 1821 p. 2066), *Holoschoenus* (Link 1827 p. 293), *Isolepis* (Brown 1810 p. 221), *Nelmesia* (van der Veken 1955 p. 143), *Nemum* (Desv. in Hamilton 1825 p. 13), *Oxycaryum* (Nees 1842 p. 90), *Pterolepis* (Schrader 1821 p. 2071), *Schoenoplectus* (Palla 1888 b p. 298), and *Trichophorum* (Persoon 1805 p. 69), as well as three genera which are interpreted as belonging to Cypereae by some authors (cf. Koyama 1961) and to Scirpeae by others (cf. Kern 1962), viz. *Ascolepis* (Steudel 1855 p. 105), *Lipocarpha* (R. Brown in Tuckey 1818 p. 459), and *Hemicarpha* (Nees in Walker-Arnott 1834 p. 263). In addition to the genera mentioned above, a large number of other now abandoned genera has been described (cf. Koyama 1958).

The treatment of this complex of genera has varied from author to author. While most have accepted such genera as *Eleocharis, Fimbristylis, Fuirena, Ascolepis* and *Lipocarpha*, Clapham et al. (1962) are among the few recent authors who have also accepted *Isolepis* and *Schoenoplectus*. HESS et al. (1957) have accepted *Schoenoplectus* but included *Isolepis* in this genus. Although morphologically similar these last two genera are not closely related since their embryos differ (cf. VAN DER VEKEN 1965). The classification of the Scirpeae is difficult because there are often small morphological differences between genera which are phylogenetically widely separated. KOYAMA (1958) therefore united *Fuirena* (described in 1773) and *Eriophorum* (which even LINNAEUS in 1753 kept as a separate genus) with *Scirpus*, and later he even went as far as to include *Lipocarpha* in *Cyperus* while *Hemicarpha* was still retained in *Scirpus* (KOYAMA 1961). KERN (1962) speaks strongly against placing *Lipocarpha* in *Cyperus*. A later paper in this series will show that *Lipocarpha* is in fact closely related to the genus *Cyperus*, and that *Hemicarpha* may have to be included in *Lipocarpha*. KOYAMA (1961) also included *Bulbostylis* in *Fimbristylis*, and LYE (1971) accepted this union if the classical concept of the genus *Bulbostylis* is followed, but recent research seems to show that with a new generic circumscription *Bulbostylis* and *Fimbristylis* are not very closely related (cf. VAN DER VEKEN 1965, LYE 1971). On the other hand, *Bulbostylis* may eventually have to be included in *Abildgaardia*.

Because of this very confusing generic concept in the tribe Scirpeae (and partly Cypereae) recent embryographical studies are of the utmost importance. VAN DER VEKEN (1965) following up SCHNEIDER's (1932) results, found that the genus *Scirpus* s. lat. has embryo types characteristic of *Cyperus, Carex, Bulbostylis, Fimbristylis, Schoenus* and *Schoenoplectus* (the last is the *Scirpus* type of VAN DER VEKEN). VAN DER VEKEN believed that the genera he investigated should be so circumscribed as to include only one embryo type, but did not think that the embryo types were important for the classification of genera into tribes or higher units. VAN DER VEKEN may have been at least partly wrong in this last statement, his embryographic results being more important for the classification of the Cyperaceae than he himself claimed. Working in Uganda, and without knowledge of VAN DER VEKEN's paper, we came to the conclusion that the genera *Eleogiton, Isolepis, Scirpus* section *Microstyli* (excluding *Scirpus isolepis* and *S. micranthus*, which are both *Lipocarpha*) and *Scirpus* section *Micheliani* (both sections of CLARKE 1902 p. 448) are related closely to the genera *Ascolepis* and *Lipocarpha* (including *Hemicarpha*), which are again closely related to the genus *Cyperus* s. lat. These groups all have a *Cyperus*-type embryo. The remaining groups of *Scirpus* s. lat. with a *Cyperus*-type embryo are the sections *Holoschoenus, Oxycaryum* and *Desmoschoenus*, which have all at one time been regarded as separate genera. We believe that even these three sections of the genus *Scirpus* can be transferred from Scirpeae to Cypereae as distinct genera. *Desmoschoenus* consists of a single species, viz. *D. spiralis* HOOK. F. (syn. *Scirpus frondosus* BOECK.). This genus is rather distinct and its relationship is likely to be with Cypereae rather than Scirpeae. *Holoschoenus* consists of a rather heterogeneous group of species, the type species of which is *H. vulgaris* LINK (syn. *Scirpus holoschoenus* L.). Other species investigated by VAN DER VEKEN and regarded by him as belonging to *Scirpus* section *Holoschoenus* included *Scirpus nodosus* ROTTB., *S. membranaceus* THUNB., *S. beccarii* BOECK., and *S. prolifer* ROTTB. At the moment we will not discuss the relationship of these species, but it is very likely that even these species belong to Cypereae, although they cannot all be included in *Holoschoenus*.

The Genus Oxycaryum NEES V. ESENBECK (1842 p. 90)

The type species is *O. cubense* (POEP. & KUNTH) K. LYE comb. nov.; syn. *O. schomburgkianum* NEES V. ESENBECK in MART. Fl. Bras. 2 (1): 90 (NEES 1842) and *Scirpus* *cubensis* Poep. & Kunth in Enum. 2: 172 (Kunth 1837).

Other names given to this plant are *Isolepis echinocephala* Oliv. (Oliver 1875) and *Anosporum cubense* (Kunth) Boeck. (Boeckeler 1870). The genus *Anosporum* is actually older than *Oxycaryum* (cf. Nees 1835), but its type species is *Anosporum monocephalum*, which is based on *Cyperus monocephalus* Roxb. (cf. Roxburgh 1820) and regarded as a synonym for *Cyperus cephalotes* Vahl by Boeckeler (1870 p. 411) and Clarke (1894 p. 597). It is possible that *Oxycaryum cubense* is related closely to *Cyperus cephalotes* Vahl, and if they are regarded as belonging to the same genus, this species will have to be renamed *Anosporum cubense* (Kunth) Boeck. or possibly *Cyperus cubensis* (combination not published). We, however, regard *Oxycaryum* as being generically distinct from *Anosporum* and *Cyperus*, differing in its fruit and spirally arranged glumes, as well as in habit and anatomical characters. Another generic name sometimes connected with *Scirpus cubensis* Kunth is *Atomostylis*. *Atomostylis* was described by Steudel (1855 p. 315) and its type species is either *A. flavescens* Steud. or *A. cyperiformis* Steud.; both are synonyms of *Cyperus nudicaulis* L. (cf. Fig. 2). Although *Oxycaryum cubense* is more closely related to *Cyperus* than to *Scirpus*, we do not think it is related closely to *Cyperus nudicaulis*.

Koyama (1958 p. 290) writes about his section 11. *Oxycaryum:* "Though this group has traditionally been placed in *Euscirpus* because of its gramineous leaves and bracts, it may possibly be better regarded as one closer to the so-called *Isolepis* group than to *Euscirpus;* its relatively large achenes (1.5—3 mm long) and nodeless culms show somewhat Isolepisoid features". Koyama (1958) includes *Scirpus cubensis* Poep. & Kunth, *S. schaffneri* Boeck. and *S. orbicephalus* Beetle in his section *Oxycaryum*, but Koyama and McVaugh (1963) transferred *S. orbicephalus* Beetle to the genus *Cyperus*, and *S. schaffneri* Boeck. sensu Beetle was regarded as a synonym of *S. orbicephalus*. The only species remaining in *Oxycaryum* Nees is then the type species itself, viz. *Oxycaryum cubense* (Poep. & Kunth) K. Lye.

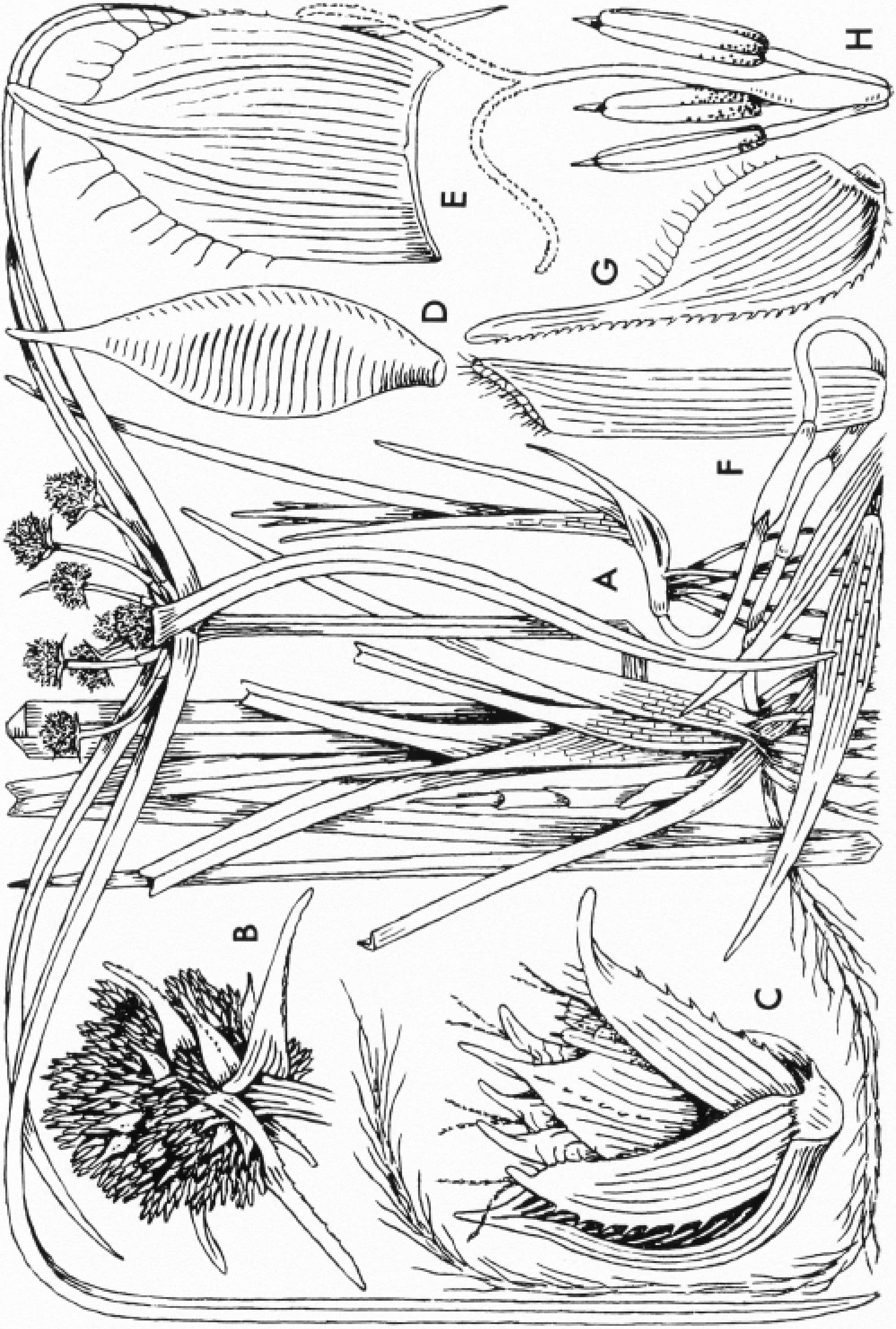
SCIRPEAE VERSUS CYPEREAE

The main difference between the two tribes Scirpeae and Cypereae has traditionally been that Scirpeae has spirally arranged glumes while in Cypereae they are two-ranked. This difference is not very clear-cut because in *Cyperus* section *Dichostylis* the glumes are irregularly spirally ranked, while in some species of *Scirpus* sections *Isolepis* and *Actaeogeton* (cf. Koyama & McVaugh 1963) they are conspicuously two-ranked. Koyama (1961) found that a more useful point of difference between the two tribes is that Cypereae always has a strongly metamorphosed two-keeled and usually empty scale (prophyll) at the base of the spikelet, while in Scirpeae all floral scales are alike and supporting flowers. This is not always true, however, since in species of *Eleocharis* and *Bulbostylis* the lower scales are frequently not supporting flowers. We believe the two tribes can best be separated on their embryo types. In Cypereae the embryo is cylindric-ellipsoid to ellipsoid with basal micropyle and lateral funiculus (cf. descriptions and figures in van der Veken 1965). In Scirpeae the embryos are of various types but never as in Cypereae.

Oxycaryum cubense (Poep. & Kunth) K. Lye — Fig. 1.

A robust stoloniferous floating perennial with long hanging roots and scaly stolons. Stolons 5—20 cm long and 2—3 mm wide

Fig. 1. *Oxycaryum cubense* (Poep. & Kunth) K. Lye. — A: Habit-drawing. — B: Inflorescence-head. — C: Spikelet. — D: Achene. — E: Glume. — F: Tubular prophyll from base of peduncle. — G: Bract. — H: Flower. — Drawn from Haines 4113, collected at Bugiri, Busoga, Uganda. Original by Richard Wheeler Haines.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with 2—3 cm long blackish scales, rooting at the nodes, spreading horizontally and producing new plants at their apices. Stem 45—70 cm long and 3—5 mm thick, sharply triangular, smooth. Leaves all basal or nearly so, 40—90 cm long and 4—10 mm wide, usually much longer than the culms, often purple and strongly V-shaped below, flat above; midrib protuding below, longitudinal ridges narrow; margin and midrib with minute spine-like teeth (i.e. scabrid); lower leaf-sheaths inflated with longitudinal veins and some cross-veins (only conspicuous from outside); ligule a low rim with densely set hairs on the margin.

Inflorescence of 3—10 subumbellately arranged heads and with peduncles of usually variable length. Inflorescence-bracts leafy, the longest 30—60 cm long and 4—9 mm wide; each bract subtending one inflorescence-head. Peduncles 1—35 mm long and 0.6—1.8 mm thick, set in a purple-stained tubular prophyll with ciliate margin. Inflorescence-heads 5—15 mm across, globose or hemispheric (rarely triangular in outline), with numerous closely packed spikelets. Spikelets 3.5—6.0 mm long and 2.5—3.5 mm wide, subtended by scale-like bracts with short leafy apices, but with no prophylls. Glumes about 3.5 mm long, very stiff, reddish-brown but sometimes with a paler greenish midrib; longitudinal "nerves" indistinct, uncoloured and not protruding; keel of the midrib glabrous or set with spine-like teeth; margin with long ciliate hairs; apex very thick, acuminate. Stamens 3. Style-branches 2. Nutlet 2.6—3.0 mm long (including a 0.7 mm long beak) and 0.6—0.8 mm wide, elongate with cuneate base and ending in a long beak, glabrous, yellowish but brown at the base and in the centre (cf. also CHERMEZON 1924). This description is based on Ugandan material only.

It is found floating in lake-edges and in open water in permanent marshes or in slow-flowing rivers, more rarely attached to wet soil in swamps.

Oxycaryum cubense is widespread but uncommon throughout tropical Africa. In East Africa it is known from the Sudan, Uganda, Tanzania, Zambia, Malawi, and Rhodesia. In West Africa it is known from Senegal, Ghana, Nigeria, Upper Volta, Cameroun, the Congo, and Angola (cf. also HUTCHINSON & DALZIEL 1936). *O. cubense* is fairly widespread in South and Central America. It is not known from Asia, Australia or Europe.

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Fig. 2. *Cyperus nudicaulis* POIR., the type species of the genus *Atomostylis* STEUDEL. — A: Habit-drawing. — B: Inflorescence-heads. — C: Spikelet. — D: Glume and young flower with 3 stamens and 3-branched style. — E: Achene with persistent filaments. — F: Upper part of leaf-sheath. — Original by RICHARD WHEELER HAINES.


B
C
F
A
D
E
RWH

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Studies in African Cyperaceae III

A New Species of Schoenoplectus and some New Combinations

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ABSTRACT

Lye, K. A. 1971. Studies in African Cyperaceae III. A new species of Schoenoplectus and some new combinations. — Bot. Notiser 124: 287—291.

Schoenoplectus microglumis K. Lye, sp. nov. is described from Central Uganda. This species is easily distinguished from all other species of *Schoenoplectus* on its minute glumes.

The genus *Schoenoplectus* Palla is regarded as being generically distinct from *Scirpus* L., *Isolepis* R. Br. and *Eleogiton* Link, but not from *Bolboschoenus* (Aschers.) Palla.

Eight new combinations of East African species of *Schoenoplectus* are made, viz. *Schoenoplectus brachyceras* (A. Rich.) K. Lye, *S. confusus* (N. E. Br.) K. Lye, *S. inclinatus* (Del.) K. Lye, *S. jacobi* (Fischer) K. Lye, *S. lateriflorus* (Gmel.) K. Lye, *S. rogersii* (N. E. Br.) K. Lye, *S. roylei* (Nees) K. Lye, and *S. subulatus* (Vahl) K. Lye.

During the revision of East African Cyperaceae for a book "The Sedges and Rushes of Uganda" one undescribed species of *Schoenoplectus* turned up.

Schoenoplectus microglumis K. Lye, sp. nov.

Herbae annuae, glabrescentes minutae. *Culmus* 4—15 cm altus et 0.6—0.8 mm latus. *Folium* breve vel ad vaginam reductum. *Inflorescentia* lateralis capitata. *Spiculae* 3—15, 3—5 mm longae et 1.5—2.0 mm latae, multiflorae. *Squamae* ovatae, 1.3—1.6 mm longae, rufae. *Perigonium* nullum. *Stamina* 3. *Nux* obovata, 0.7—0.8 mm longa et 0.5—0.6 mm lata, castaneo-brunnea vel nigra.

TYPUS SPECIEI: Langdale—Brown 2323, 12. VIII. 1957. Uganda, Busoga U 3, Bugabula county, near Ndolva, 1050 m (KAW holotype, MHU isotype).

Schoenoplectus microglumis K. Lye is a tufted glabrous annual with shallow root-system. Stems few or numerous, 4—15 cm long (excluding the stem-like bract above the inflorescence, or total length 10—30 cm when including the bract) and 0.6—0.8 mm thick, terete with rounded ridges. Leaf-blade absent or very short; leaf-sheath pale, ending in a 1—5 mm long linear lobe.

Inflorescence consisting of 3—15 sessile or subsessile apparently lateral spikelets in a dense headlike cluster (rarely with a few sessile spikelets on an up to 5 mm long stalk). Main inflorescence-bract stem-like, 4—16 cm long and 0.6—0.9 mm wide, slightly flattened with longitudinal ridges, usually about as long as the stem. Spikelets 3—5 mm long and 1.5—2.0 mm wide, variegated reddish-brown to straw-coloured, slightly "spiny" with the acute spreading glumes. Glumes 1.3—1.6 mm long, ovate, reddish-brown with pale greenish midrib and pale non-ciliate margin; midrib protruding above and ex-current in a short mucro. Perianth-segments absent. Stamens 3. Style-branches 3. Nutlet 0.7—0.8 mm long and 0.5—0.6 mm wide, obovate, bluntly triangular, with transverse frills, pale brown as young, dark brown to blackish when ripe.

In seasonal swamp grassland with *Eleocharis atropurpurea* (Retz.) Presl, 1050 m (3500 ft.). Very rare or overlooked. Only recorded from the type locality, viz. near Ndolva, Busoga, Uganda.

This species is easily recognized on its minute reddish-brown glabrous glumes, only 1.3—1.6 mm long. It is possibly most closely related to *Schoenoplectus lateriflorus* (Gmel.) K. Lye, which is, however, a larger plant with larger glumes with ciliate margin.

History of Schoenoplectus

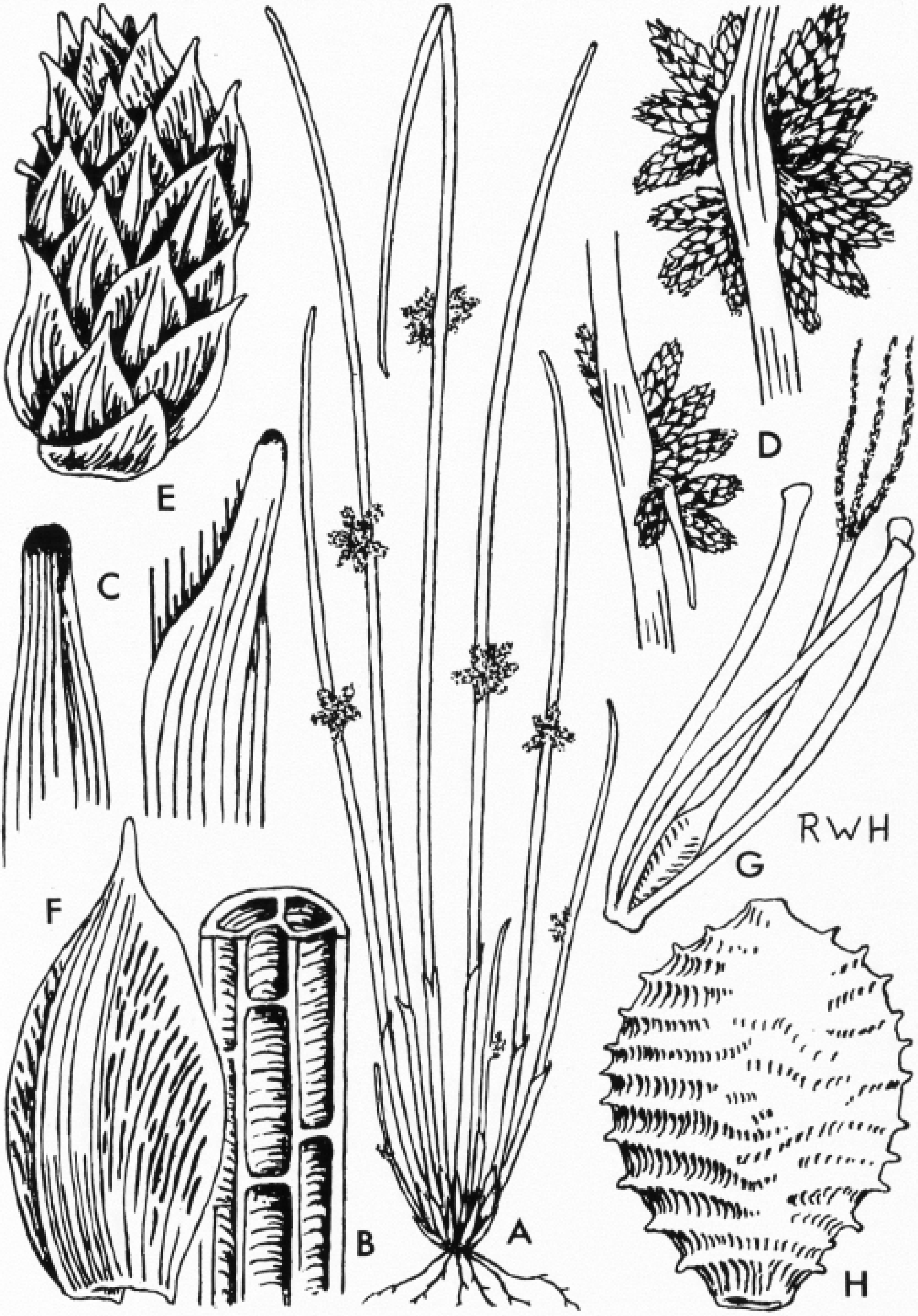
The genus *Schoenoplectus* was described by Palla (1888 b p. 298), and he regarded this genus as being synonymous with *Scirpus* subgen. *Schoenoplectus* Reichenbach (1846 p. 40). This genus has been conserved over the older genera *Heleophylax* Beauvois ex Lestiboudois Ess. Cyp. 41 (1819), *Hymenochaeta* Beauvois ex Lestiboudois Ess. Cyp. 43 (1819), and *Elytrospermum* C. A. Meyer Mém. Sav. Étr. Pétersb. 1: 200 (1831). Another older name is *Pterolepis* Schrader Goett. Gel. Anzeig. 3: 2071 (1821) based on *Scirpus littoralis* Schrad., but *Pterolepis* (A. P. De Candolle) Miquel Comm. Phytogr. 2: 72 (1839) based on species in the Melastomataceae, has been conserved over the older *Pterolepis* Schrad. Another generic name is *Malacochaete* Nees (Nees 1835 p. 292) based on the following species: "*M. latora* N. et Meyen, *riparia* N. et Meyen, *littoralis* (*Scirpus littoralis* Schrad.), *pectinata* (*Scirpus pectinatus* Roxb.), *Pterolepis* (*Pterolepis scirpoides* Schrad.)". *Malacochaete* Nees was, however, nomenclaturally superfluous when published since *Pterolepis* Schrad. was cited as synonym. In 1905 Palla (in Hallier 1905 p. 2531) described a new genus *Bolboschoenus* (Aschers.) Palla based on *Scirpus maritimus* L. (cf. Lye 1971). An earlier name, *Reigera* Opiz Seznam rostlin květeny české 83 (1852) is also based on *Scirpus maritimus* L., but was published as a nomen nudum.

Palla (1888 b p. 299), when describing the genus, made the following new combinations of *Schoenoplectus* (not all of which are cited in Index Kewensis): *S. lacustris* (L.) Palla, *S. carinatus* (Sm.) Palla, *S. Tabernaemontani* (Gm.) Palla, *S. triqueter* (L.) Palla, *S. littoralis* (Schrad.) Palla, *S. pungens* (Vahl) Palla, *S. mucronatus* (L.) Palla, *S. supinus* (L.) Palla, *S. javanicus* (Nees) Palla, *S. quinquefarius* (Hamilton) Palla, *S. articulatus* (L.) Palla, *S. juncoides* (Roxb.) Palla, *S. senegalensis* (Hochst.) Palla, *S. paludicola* (Kunth) Palla, *S. olneyi* (Gray) Palla, *S. Tatora* (Kunth) Palla, and *S. riparius* (Vahl) Palla. The type species of this genus is *Scoenoplectus lacustris* (L.) Palla (cf. Lanjouw 1966).

Some years later Palla (in Hallier 1905) changed his concept of the genus *Schoenoplectus*, and included *Scirpus fluitans* L. and *Scirpus setaceus* L. in *Schoenoplectus*. *Scirpus setaceus* L. is the type species of the genus *Isolepis* (Brown 1810 p. 221) and *S. fluitans* L. is the type species of *Eleogiton* (Link 1827 p. 284). If these species are included in *Schoenoplectus*, this genus is of no value, but the embryographical studies by van der Veken (1965) has clearly shown that *Scirpus fluitans* and *S. setaceus* are not closely related to *Schoenoplectus*.

Our present-day knowledge of *Schoeno-*

Fig. 1. *Schoenoplectus microglumis* K. Lye, sp. nov. Drawn from the holotype (Langdale—Brown 2323). — A: Habit, ×1. — B: Longitudinal section of culm. — C: Upper part of leaf-sheath showing short leaf-blade. — D: Inflorescence-heads. — E: Spikelet. — F: Glume. — G: Flower consisting of 3 filaments and ovary with 3-branched style. — H: Nutlet. — Original by Richard Wheeler Haines.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plectus is much increased due to van der Veken's embryographical results. We believe that *Schoenoplectus* should include the following sections of *Scirpus* (sensu van der Veken 1965): 3. sect. *Actaeogeton* Reichenb.; 4. sect. *Pterolepis* (Schrad.) Aschers. & Graebn.; and 5. sect. *Bolboschoenus* Aschers. — all having a "mushroom"-type of embryo with lateral micropyle and funiculus. Section 1. *Actinoscirpus* Ohwi, based on *Scirpus grossus* L. f., and section 2. *Pseudoschoenus* C. B. Cl., based on *Scirpus inanis* (Thunb.) Steudel, which both have a similar embryo but with a rather different morphology, can either be placed in *Schoenoplectus* as two new subgenera or regarded as distinct genera. If this classification system is accepted, *Schoenoplectus* comes out as a very natural genus, easily characterized by its mushroom-like embryo.

Schoenoplectus versus Scirpus and Isolepis

There has been much disagreement among botanists as to the status of the genus *Schoenoplectus* Palla. Clapham et al. (1962) are among the few recent authors who have accepted the genus *Schoenoplectus* as separate from *Isolepis*, while Hess et al. (1967) have accepted *Schoenoplectus* but included *Isolepis* in this genus. Although superficially similar in morphological characters, the genera *Schoenoplectus* and *Isolepis* are not related closely as is shown by van der Veken's embryographical studies (van der Veken 1965). His work has also shown that *Schoenoplectus* Palla is not related closely to *Scirpus* L. emend. Palla (type species of this genus is *Scirpus sylvaticus* L.), but that it is related closely to *Bolboschoenus* (Aschers.) Palla. We believe that *Bolboschoenus* can be kept separate from *Schoenoplectus* on a sectional or possibly subgeneric level only.

New Combinations

The following new combinations of *Schoenoplectus* are needed for "The Sedges and Rushes of Uganda":

1. *Schoenoplectus brachyceras* (A. Rich.) K. Lye, comb. nov.; syn. *Scirpus brachyceras* Hochst. ex A. Rich. Tent. Fl. Abyss. 2: 496 (1851).
2. *Schoenoplectus confusus* (N. E. Br.) K. Lye, comb. nov.; syn. *Scirpus confusus* N. E. Br. Kew Bull 1921: 300 (1921).
3. *Schoenoplectus inclinatus* (Del.) K. Lye, comb. nov.; syn. *Isolepis inclinata* Del. Fl. Aegypt. Illustr. 50 (1812).
4. *Schoenoplectus jacobi* (Fischer) K. Lye, comb. nov.; syn. *Scirpus jacobi* C. E. C. Fischer in Kew Bull. 1931: 103 (1931).
5. *Schoenoplectus lateriflorus* (Gmel.) K. Lye, comb. nov.; syn. *Scirpus lateriflorus* J. F. Gmel. Syst. Nat. 2: 127 (1791).
6. *Schoenoplectus rogersii* (N. E. Br.) K. Lye, comb. nov.; syn. *Scirpus Rogersii* N. E. Br. Kew Bull. 1921: 301 (1921).
7. *Schoenoplectus roylei* (Nees) K. Lye, comb. nov.; syn. *Isolepis Roylei* Nees in Wight Contrib. 107 (1834).
8. *Schoenoplectus subulatus* (Vahl) K. Lye, comb. nov.; syn. *Scirpus subulatus* Vahl Enum. plant. 2: 268 (1806).

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Current Topics

Multiple Similarity of Leaf between Two Genera of Cape Plants, Cliffortia L. (Rosaceae) and Aspalathus L. (Fabaceae)

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ABSTRACT

Dahlgren, R. 1971. Current topics. Multiple similarity of leaf between two genera of Cape plants, Cliffortia L. (Rosaceae) and Aspalathus L. (Fabaceae). — Bot. Notiser 124: 292—304.

A great number of species in *Cliffortia* with different leaf types show correspondence with species of *Aspalathus* in the shape, venation, texture, and arrangement of the leaves. Branches of 19 pairs of species in the two genera are compared by photographs. The rôle of climatic and edaphic factors in the evolution of the leaf types is stressed. The differentiation of the leaves, with possible courses of evolution in each genus, is outlined, and it is discussed whether the leaves in the two genera have had some particular quality in common that can account for the peculiar similarities. Similar features of differentiation could be demonstrated in other genera of Cape plants, e.g. in Asteraceae, Campanulaceae, Polygalaceae, Proteaceae, Rubiaceae, and Rutaceae, but probably not as pronounced as in the *Cliffortia - Aspalathus* case.

INTRODUCTION

A botanist working in South Africa or in any region with a Mediterranean climate is struck by the similarity in the shape and arrangement of leaves in various groups of systematically very remote families. This is not unique, however, because in desert areas corresponding similarities are found in succulence of stem and leaves in various groups, and in tropical rain forests similar large-sized leaves will be found in various families of dicotyledons. Very well-known and often cited in textbooks are the convergence in evolution of the succulent "cactus stem" in the Cactaceae, Euphorbiaceae, and Asclepiadaceae, as well as the similarity of pitcher-like leaves in Nepenthaceae, Sarraceniaceae, and Cephalotaceae.

The present case of similarity between two systematically remote groups is in many respects very striking. Because of the monographic works on *Cliffortia* by H. Weimarck and on *Aspalathus* by myself, there is an exceptional opportunity of presenting adequately chosen material of the genera. From the beginning it should be stressed that the material compared here is chosen by tendentious selection from a rich variety of leaf types in both genera. Beside the species compared, there are several other pairs of species with almost equally striking similarities, but each genus also contains leaf types not matched in the other genus.

PRESENTATION OF THE GENERA

Cliffortia

This genus, of tribe Poterieae, Rosaceae, consists of at least 110 species of dioecious or monoecious shrubs or shrublets with trifoliolate, bifoliolate, or simple leaves, sometimes with a relatively short petiole but generally sessile, and always with a stipulate leaf base grasping the stem. The flowers are unisexual and have a simple perianth of 3 or seldom 4 sepals. Petals are absent. The stamens vary greatly in number, and the pistils are solitary or seldom two in each flower, enclosed by a receptacle with various texture and surface patterns.

The genus is concentrated to the south-western parts of the Cape Province, with about 30 species on the Cape Peninsula. Some species are found outside the Cape Province in the north-east, and one species even occurs in central East Africa.

A monograph on *Cliffortia* was presented in 1934 by H. WEIMARCK, who also added a complementary survey of the genus in 1948.

Cliffortia, thus concentrated to South Africa, has its counterpart in *Acaena, Margyricarpus, Tetraglochin,* and *Polylepis* found mostly in southern and western South America, and in *Sanguisorba, Sarcopoterium,* and *Bencomia* of the Mediterranean regions, the Canary Islands, Madeira, etc.

Hagenia, occurring from Abyssinia to Nyasaland, and *Leucosidea,* in Rhodesia and South Africa, deviate from the genera mentioned in having petals. In this respect they probably represent an "ancestral" group within the tribe Poterieae. The origin of the markedly southerly centres in the tribe has been discussed by several botanists.

Aspalathus

Aspalathus, tribe Genisteae, Fabaceae, consists of about 255 species of shrubs or shrublets with sessile, exstipulate, and either trifoliolate or simple leaves. The leaflets are flat or more often narrow and linear, i.e. "ericoid" or "pinoid". In many species they are furnished with apical, pungent spinelets. The flowers are typically papilionaceous and of varying size, usually with yellow petals. The fruits are few- or seldom many-seeded legumes.

Like *Cliffortia, Aspalathus* is concentrated to the south-western divisions of the Cape Province, but has a smaller total distribution range. It is limited to the Cape Province with the exception of a few species, which occur in part of Natal.

Aspalathus has been monographically treated in "Revision of the genus Aspalathus", published mainly in Opera Botanica.

Its relatives are to be found mainly among the South African genera *Wiborgia, Lebeckia, Rafnia,* etc., in which stipules are rudimentary or wanting, and perhaps *Buchenroedera,* where stipules are usually well-developed. A couple of genera in South America are referred to the same group of genera within the tribe Genisteae as the South African genera mentioned.

In the Mediterranean regions, *Genisteae* is represented by several genera, most of which are not particularly closely allied to the South African. Other groups of genera within the tribe attain a particularly rich differentiation in Australia.

CLIMATICAL AND ECOLOGICAL CONDITIONS IN THE REGIONS OF THE "CAPE MACCHIA"

The genera compared here belong to the "Cape macchia" (or "Cape fynbos" or "Cape sclerophyll scrub"). In its principal features of the plants it resembles the Mediterranean vegetation.

It is largely confined to the regions of southernmost South Africa with a mean annual rainfall of at least 250 mm (see DAHLGREN 1963 b p. 434) and with the greater part of this precipitation (or in the eastern parts about 50 %) concentrated to the cooler half of the year, the winter.

Beside great differences in rainfall between different areas of the southern Cape, there are differences in moisture conditions due to temporary mists in the mountains or in certain coastal areas.

There are also great differences in temperature, wind, and amount of sunshine over short distances depending on altitude and exposition of slopes, which causes great local variation in the composition and type of the flora. This is easily seen in certain mountains of Little Karroo, where the northern slopes exposed to the sun are covered with succulent Karroo vegetation, while the southern, more shady slopes are covered with "Cape macchia" vegetation.

Grazing has probably with time favoured selection of species with spiny-tipped leaves in certain regions (see DAHLGREN 1970). The complex topography and geology of the country in general account for small plant populations. In these the chances that mutations will be established are comparatively great. In small populations of allogamous, variable species there are likewise great chances for rapid changes to occur in the proportion of different biotypes. Evolution can therefore be expected to be relatively rapid.

These conditions all contribute to the rich diversity of the flora in the regions concerned. The flora is considered to be "old" in the sense that it is not known to have been erased by any major catastrophies at least since the Cretaceous Period.

LEAF VARIATION IN THE TWO GENERA

Cliffortia

The great variation of the leaves in *Cliffortia* fascinated A. P. DE CANDOLLE as early as 1824: "Le feuillage des jolis arbustes du cap de Bonne-Espérance, auxquels Linné a donné le nom de *Cliffortia,* présente des bizarreries remarquable . . . . .". DE CANDOLLE in his article gave the first survey and interpretations of leaf types in *Cliffortia.*

In WEIMARCK's monograph on *Cliffortia* (1934) leaf shape was of fundamental importance for the division into sections of the larger of the two subgenera, *Monographidium* (=subgenus *Cliffortia*).

Sect. *Petiolatae* thus is characterized by trifoliolate, petiolate leaves; sect. *Costatae, Alatae,* and *Arboreae* by trifoliolate sessile leaves; sect. *Bifoliolatae* by mainly bifoliolate, sessile leaves; sect. *Multinerviae* (=sect. *Cliffortia*) by simple, flat leaves with several more or less parallel nerves arising from the base; and sect. *Simplices* by simple (=unifoliolate), variously shaped leaves with a basally simple vein.

The *Cliffortia* leaf is accordingly tri- or bifoliolate or simple. In most other genera of the tribe Poterieae they are imparipinnate with few to many pairs of leaflets dispersed on a long rhachis. The latter type of leaf is probably the more primitive one, from which the *Cliffortia* leaf has developed by reduction.

The leaf types shown in Fig. 5 B—K are found in particular species of *Cliffortia.* They are naturally not links in a phylogenetic evolutional system. However, they represent distinct levels of organization, each with particular characteristics and possibilities in a country with varying humidity, light, grazing conditions, wind, etc. at different times of the year. Each kind is dependent on density of arrangement on the shoots, epidermal structures, presence or absence of pubescence and spines, etc. When the actual examples are disregarded and the figures conceived as types, the arrows in Fig. 5 may indicate possible courses of evolution, but other alternatives than those presented are feasible.

The initial stage in Fig. 5 is represented by an imparipinnate leaf with few pairs of leaflets and with well-developed sheath and stipules (Fig. 5 A). Such a leaf would connect the trifoliolate, petiolate leaves of some *Cliffortia* species with the common, imparipinnate leaves with several to numerous leaflets found in most other genera of Poterieae. Though *Leucosidea,* a petaliferous South African genus of the tribe, has been chosen to illustrate this stage, other groups may correspond better to the ancesteral forms in leaf shape, perhaps certain species of *Acaena.*

To regard the imparipinnate leaf as the original type is to conclude that the petiolate leaf would have preceded the sessile (Fig. 5 B—D). The weak, rather mesophilous, and serrate leaflet type is found in the majority of the genera of Poterieae (and in some species of *Cliffortia,* Fig. 5 B) and is likely to be the original type in *Cliffortia,* and a type from which the entire, myrtiform and the narrow, linear, ericoid or pinoid leaflet types have evolved.

It is most probable that the bifoliolate leaves of sect. *Bifoliolatae* (Fig. 5 F) have evolved from a sessile or subsessile trifoliolate type, and in *Cliffortia varians* Weim., Weimarck (1948 p. 190) in fact found that the leaves varied between tri- and bifoliolate.

Furthermore, it is plausible that the simple leaves have evolved either by reduction from the trifoliolate leaves (and then have probably followed more than one line of evolution, such as indicated in Fig. 5 C and G), or by "fusion" (i. e. inhibited division of the embryonal tissue) of the three leaflets. The latter course was considered by Weimarck to be the most likely for the leaf types of Fig. 5 I—K.

The unifoliolate leaf type shown in Fig. 5 G has probably evolved from a flat type judging from the canaliculate upper side.

The occurrence in *Cliffortia multiformis* Weim. of trifoliolate, variously tripartite, and simple and 3-nerved leaves on the same shoots was referred to by Weimarck to support that the simple leaves in sect. *Multinerviae* (Fig. 5 I—K) could

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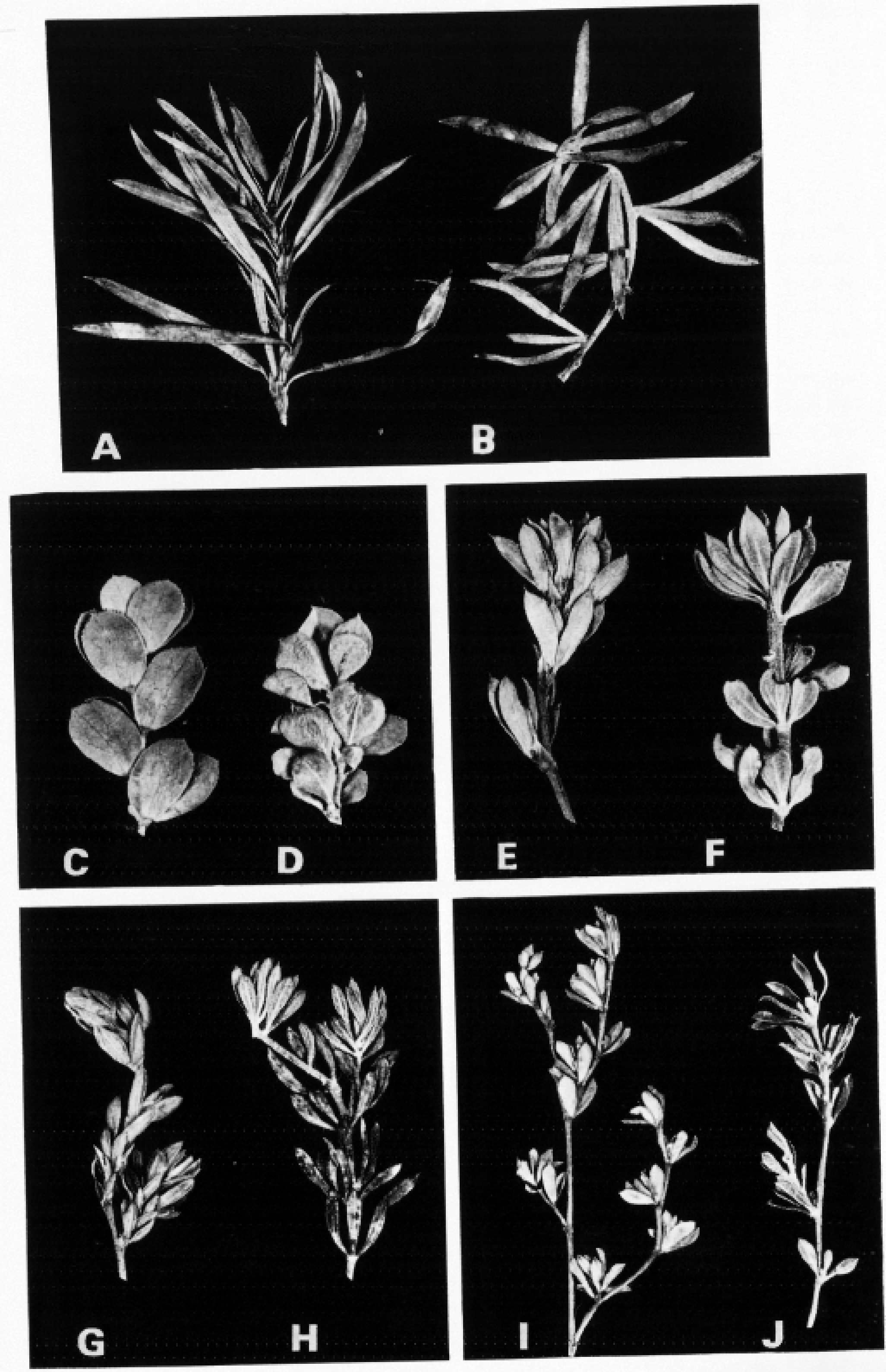
Legend. Figures on following two pages.

Fig. 1. Species of *Cliffortia* and *Aspalathus* compared. — A: *Cliffortia strobilifera* Murr.; Fries, Norlindh, & Weimarck 666 from near Port Elizabeth. — B: *Aspalathus rugosa* Thunb. ssp. *linearifolia* (DC.) R. Dahlgr.; Dahlgren & Peterson 793 from French Hoek Valley, Paarl Div. — C: *Cliff. mirabilis* Weim.; Esterhuysen 19654 from near Keeromsberg, Worcester Div. — D: *Asp. orbiculata* Benth.; Esterhuysen 28612 from Matroosberg, Worcester Div. — E: *Cliff. drepanoides* Eckl. & Zeyh.; Esterhuysen 27969 from Kouga Mts, Uniondale Div. — F: *Asp. securifolia* Eckl. & Zeyh.; Esterhuysen 29060 from Langeberg Mts, Robertson Div. — G: *Cliff. polygonifolia* L.; Loseby 2197 from Gordon's Bay, Somerset West Div. — H: *Asp. stenophylla* Eckl. & Zeyh. ssp. *colorata* R. Dahlgr.; Dahlgren & Strid 4360 from near Grabouw, Caledon Div. — I: *Cliff.* sp. near *C. geniculata* Weim.; Esterhuysen 24851 from Meiring's Poort, Oudtshoorn Div. — J: *Asp. esterhuyseniae* R. Dahlgr.; Esterhuysen 27025 from Great Winterhoek Mts, Tulbagh Div.

Fig. 2. Species of *Cliffortia* and *Aspalathus* compared. — A: *Cliffortia robusta* Weim.; Stokoe, SAM 58298 from Swartberg Pass, Prince Albert Div. — B: *Aspalathus acanthes* Eckl. & Zeyh.; Lewis 5408 from Berg Kloof, Mossel Bay Div. — C: *Cliff. neglecta* Weim.; Esterhuysen 27785 from Matroosberg, Worcester Div. — D: *Asp. hirta* E. Mey. ssp. *hirta*; Dahlgren & Strid 2681 from Langeberg Mts, Riversdale Div. — E: *Cliff. subsetacea* (Eckl. & Zeyh.) Diels; Esterhuysen 13695 from near Palmiet River Mouth, Caledon Div. — F: *Asp. acutiflora* R. Dahlgr.; Dahlgren & Strid 4627 from Blombos, Riversdale Div. — G: *Cliff. setifolia* Weim.; Esterhuysen 26774 from Swartberg Mts, Ladismith Div. — H: *Asp. hypnoides* R. Dahlgr.; Esterhuysen 27887 from Langeberg Mts, Swellendam Div. — I: *Cliff. linearifolia* Eckl. & Zeyh.; Esterhuysen 27470 from east of Joubertina, Uniondale Div. — J: *Asp. wittebergensis* Compt. & Barnes; Dahlgren & Strid 4434 from Cedarberg Tafelberg, Clanwilliam Div. — K: *Cliff. polita* Weim.; Esterhuysen 16459 from Kamanassie Mts, Uniondale Div. — L: *Asp. pedicellata* Harv.; Esterhuysen 29452 from Schurweberg, Cold Bokkeveld, Ceres Div.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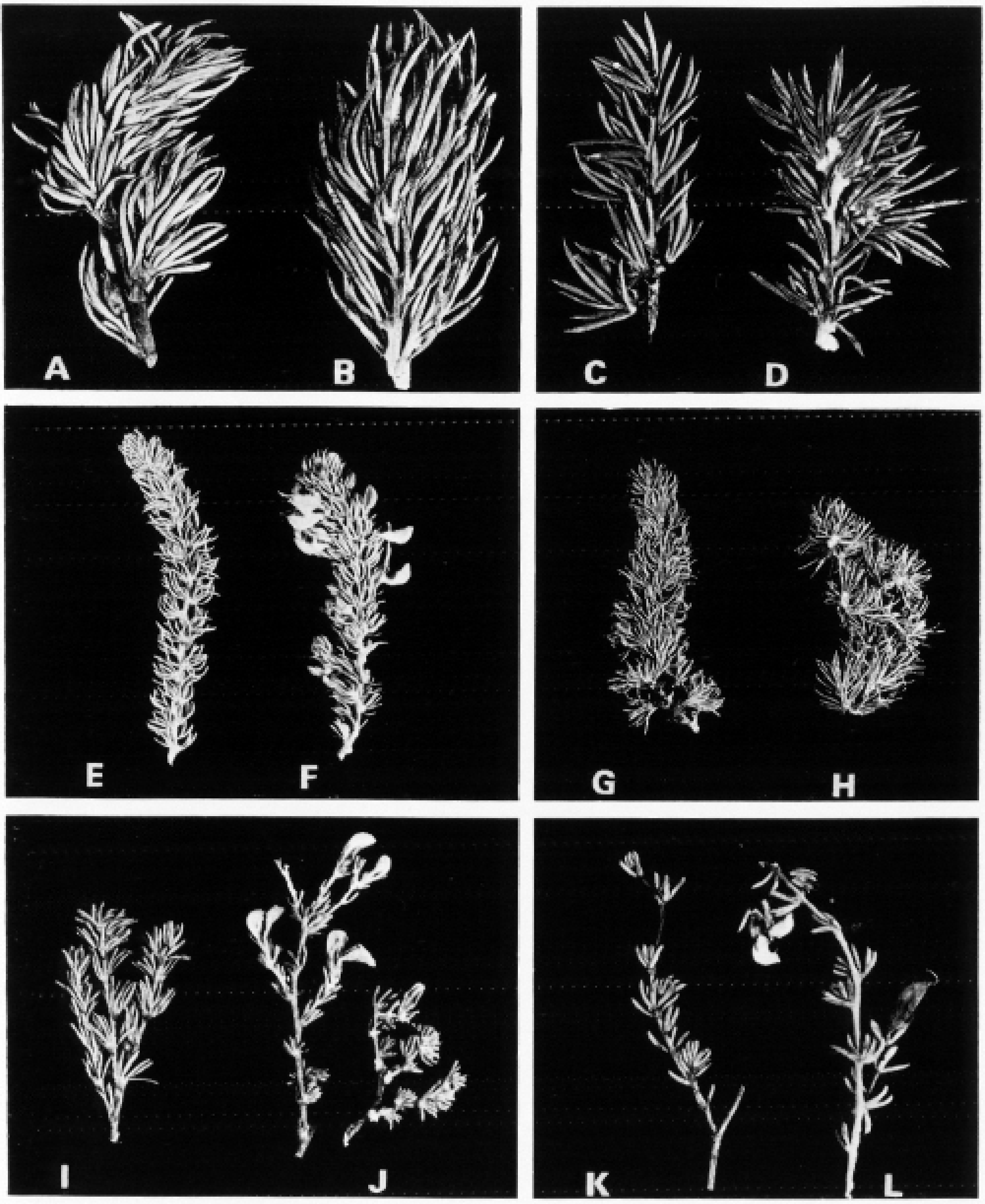

Fig. 2.

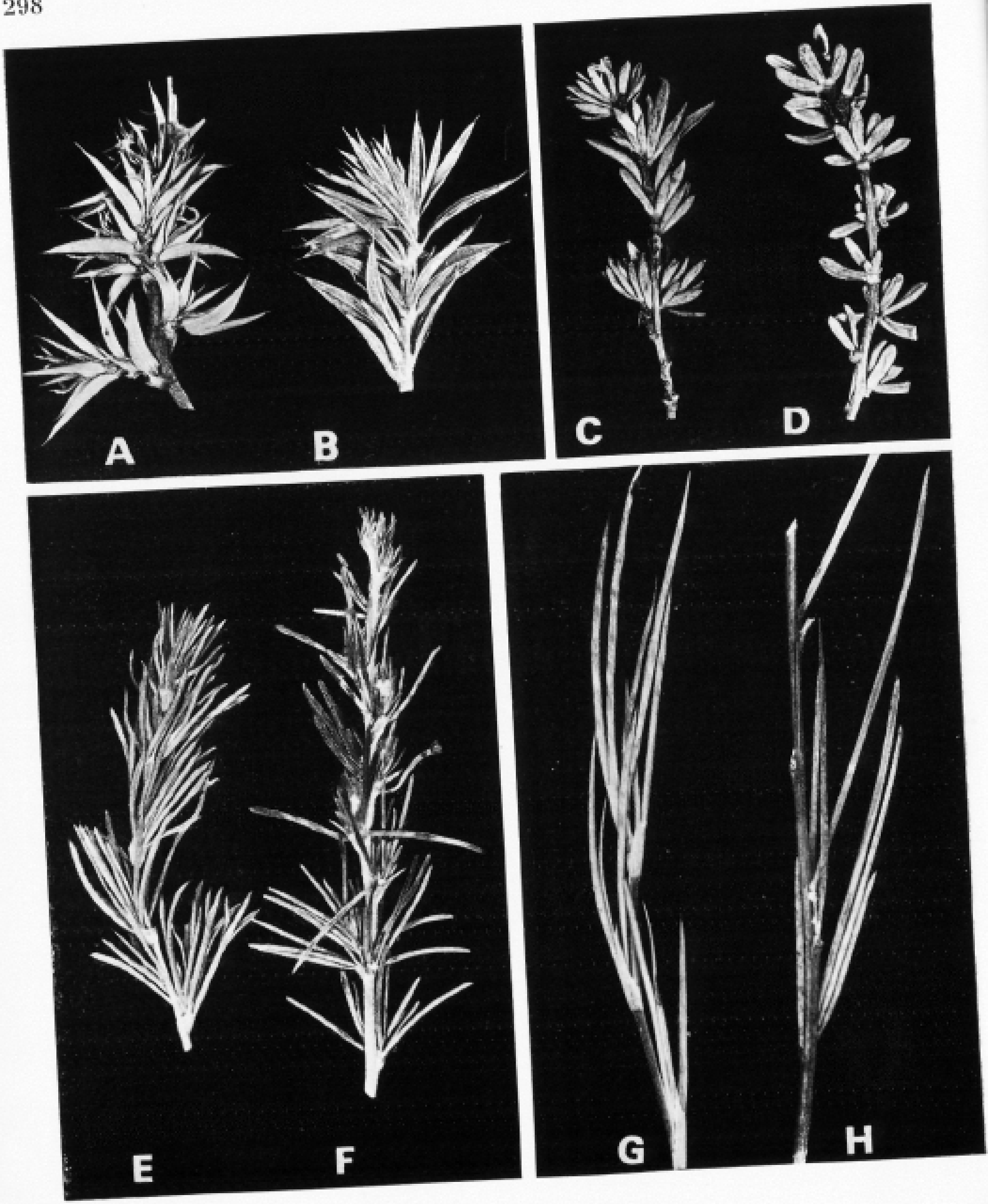

Fig. 3.

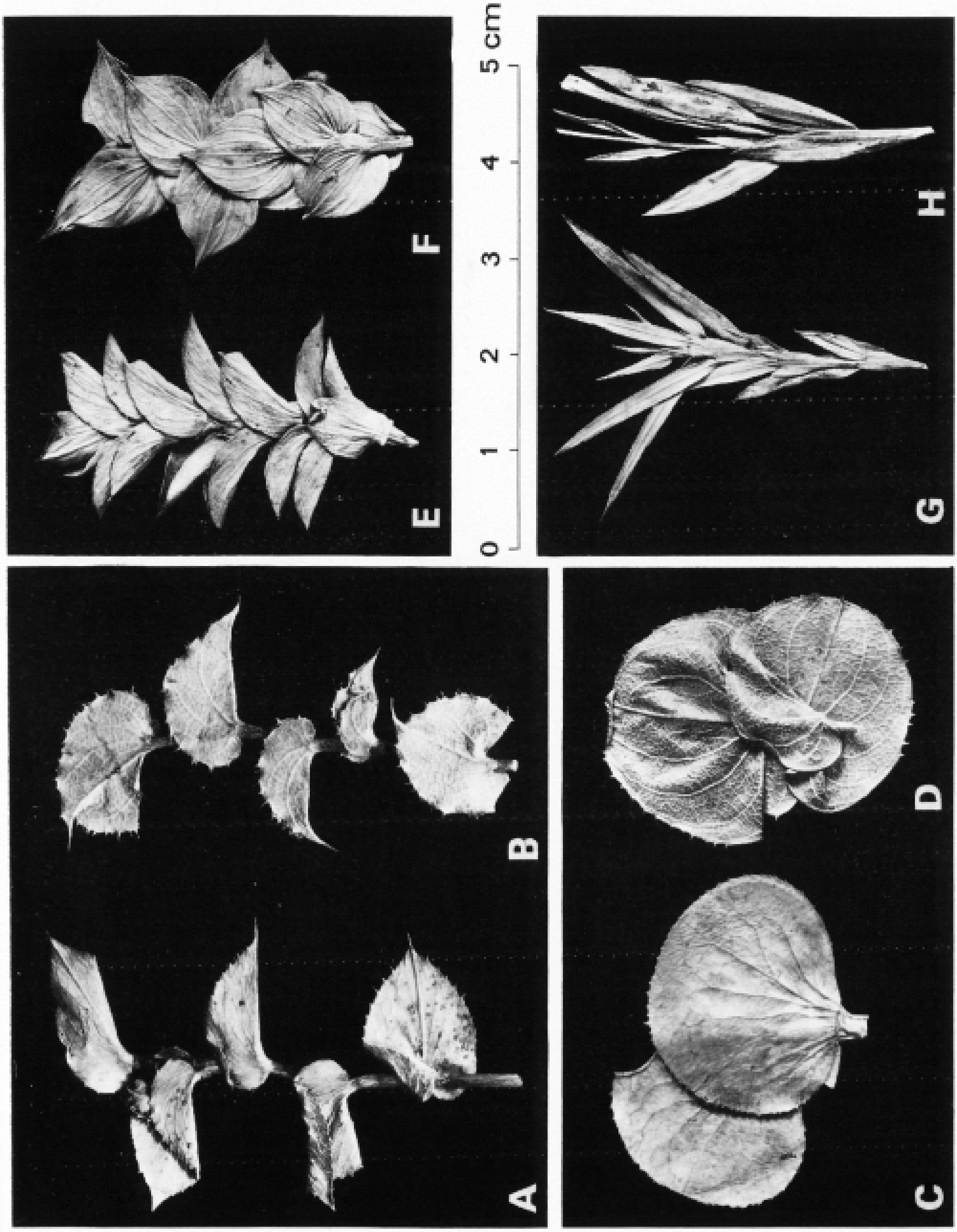

Fig. 4.

be derived from trifoliolate types by "fusion". Another possible support for that hypothesis are the apically tricuspidate, many-nerved leaves of, e.g., *C. intermedia* Eckl. & Zeyh. A reduction of the lateral leaflets would also be possible, because each of the leaflets in the section *Bifoliolatae* is basally more than one-nerved.

Aspalathus

The differentiation of the leaves in *Aspalathus* has been described in the different parts of the revision of the genus and also in Dahlgren 1963 a and 1970. In the latter work it was pointed out that there is probability for simple leaves in different groups of species to have evolved by parallelism from trifoliolate ones.

The simple, flat leaves with several nerves arising from the base (cf. *Cliffortia* sect. *Multinerviae*) was a basic character of *Borbonia* as a genus, until it was included in *Aspalathus* for reasons given, for example, in the two above-mentioned articles.

In *Aspalathus* the leaves are almost invariably sessile, exstipulate and trifoliolate or simple, and when simple probably unifoliolate.

In most other genera of the tribe Genisteae which are particularly similar to *Aspalathus*, the leaves are petiolately trifoliolate. Stipules are present in several of the genera. In *Aspalathus* subgen. *Nortieria* very small stipular teeth are occasionally seen. It is probable that the *Aspalathus* leaf once evolved from a trifoliolate petiolate leaf with stipules. This leaf might have been similar to the hypothetical leaf in Fig. 6 A. Similar leaves occur in *Lebeckia*, a genus closely similar

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Legend. Figures on previous two pages.

Fig. 3. Species of *Cliffortia* and *Aspalathus* compared. — A: *Cliffortia cymbifolia* Weim.; Levyns 10429 from near Pringle Bay, Caledon Div. — B: *Aspalathus acidota* Garab. ex R. Dahlgr.; Dahlgren & Strid 3219 from Dasklip (=Kardouw) Pass, Piketberg-Clanwilliam Div. border. — C: *Cliff. semiteres* Weim.; Esterhuysen 25977 from Anysberg, Ladismith Div. — D: *Asp. fusca* Thunb.; Dahlgren & Strid 3414 from Koueberg Mts, Bredasdorp Div. — E: *Cliff. burchellii* Stapf; Esterhuysen sine no. from Zizikamma Mts, Uniondale Div. — F: *Asp. uniflora* L. ssp. *uniflora;* Dahlgren & Strid 2433 from Bain's Kloof, Paarl Div. — G: *Cliff. aculeata* Weim.; Stokoe 8606 from Swartberg Pass, Prince Albert Div. — H: *Asp. linearis* (Burm. fil.) R. Dahlgr. ssp. *linearis*; Dahlgren & Peterson 1014 from Olifant River Mts, Clanwilliam Div.

Fig. 4. Species of *Cliffortia* and *Aspalathus* compared. — A: *Cliffortia virgata* Weim.; Esterhuysen 16158 from Twenty-Four River Mts, Piketberg Div. — B: *Aspalathus perfoliata* (Lam.) R. Dahlgr. ssp. *phillipsii* R. Dahlgr.; Dahlgren & Strid 2550 from mountains east of Citrusdal, Clanwilliam Div. — C: *Cliff. crenata* L. fil.; Esterhuysen 27596 from Hex River Valley, Worcester Div. — D: *Asp. perfoliata* (Lam.) R. Dahlgr. ssp. *perfoliata*; Dahlgren & Strid 4080 from Jonkershoek Valley, Stellenbosch Div. — E: *Cliff. integerrima* Weim.; Levyns 5277 from Smitswinkel Bay, Cape Peninsula. — F: *Asp. crenata* (L.) R. Dahlgr.; Dahlgren & Strid 3983 from Gydo Pass, Ceres Div. — G: *Cliff. graminea* L. fil. var. *elegans* Weim.; Esterhuysen 2646 from Rooskraalberg, Caledon Div. — H: *Asp. lanceifolia* R. Dahlgr.; Dahlgren & Strid 3810 from near Riversonderend, Caledon Div.

Opposite.

Fig. 5. Examples of leaf types in *Leucosidea* (A) and *Cliffortia* (B—K), somewhat simplified, without regard to scale. All details, except A, F, and K, are redrawn after Weimarck 1934 and 1948. The leaf types are represented in the following species: A: *Leucosidea sericea* Eckl. & Zeyh. — B: *Cliffortia pedunculata* Schltr — C: *C. discolor* Weim. — D: *C. drepanoides* Eckl. & Zeyh. — E: *C. geniculata* Weim. — F: *C. varians* Weim. — G: *C. neglecta* Schltr — H: *C. burchellii* Stapf — I: *C: theodori-friesii* Weim. — J: *C. virgata* Weim. — K: *C. graminea* L. fil. var. *elegans* Weim. — If the figures are looked upon as organization levels and the taxa represented are neglected, the plate shows possible evolution courses, which are likely to have proceeded in the direction of the arrows.

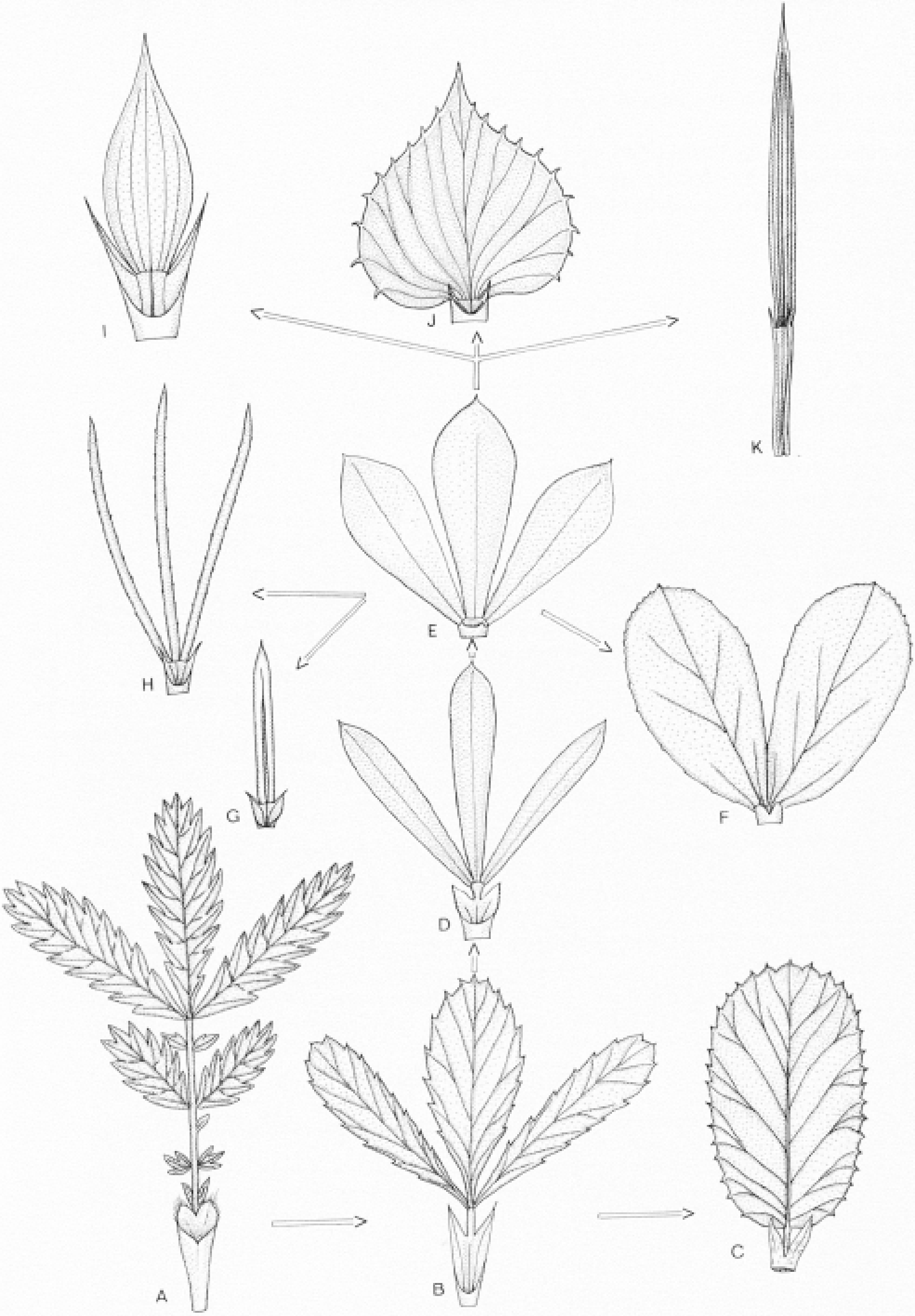

Fig. 5.

to *Aspalathus* in floral characters, but in *Lebeckia* stipules are usually wanting. In *Buchenroedera,* which likewise has flowers similar to those in some *Aspalathus* species, the leaves are petiolate and generally provided with well-developed stipules.

Fig. 6 B shows a leaf type common in *Aspalathus*. The simple (unifoliolate) leaf of *A. sericea* BERG., shown in Fig. 6 C, almost certainly originated from a leaf of this type, such as in the florally very similar *A. radiata* GARAB. ex R. DAHLGR. (see DAHLGREN 1970).

It is plausible that the carnosely linear leaf types represented by Fig. 6 D and F originally evolved from types with flat leaflets, an evolution which has possibly occurred along more than one line. Whether the simple leaf of *A. linearis* (BURM. FIL.) R. DAHLGR. (Fig. 6 E) is unifoliolate and has evolved from a type with three linear leaflets or not is most uncertain, however.

The leaf of the trifoliolate kind shown in Fig. 6 G is in principle very similar to that in Fig. 6 B. It is found in a couple of species, however, which are very similar in inflorescence, flower and fruit characters to a number of species with simple leaves of the types seen in Fig. 6 H—J. These leaves have several more or less parallel veins which arise from the leaf base. They have probably become simple by reduction of the lateral leaflets in a trifoliolate leaf of the type shown in Fig. 6 G, and would then be unifoliolate (see DAHLGREN 1970).

As pointed out for *Cliffortia* in Fig. 5, one must not look upon Fig. 6 as a phylogenetic tree. On one hand it shows examples of existing leaf types in *Aspalathus* (B—J), and on the other — when disregarding the actual examples and regarding the figures as leaf types — it illustrates possible pathways of evolution.

DISCUSSION AND CONCLUSIONS

The leaf types occurring in *Cliffortia* (Fig. 5 B—K) and in *Aspalathus* (Fig. 6 B—J) show great similarities. The agreement demonstrated in Figs. 1—4 is also striking.

Variation due to chance alone is not likely to provide the reason for this extensive similarity.

Climatic conditions have certainly been of decisive importance, the very particular selection affecting the plants in this part of South Africa having favoured some kinds of leaves (leaflets), especially the "ericoid" and "pinoid" types, but also the *Myrtus-* and *Ruscus*-like types.

It is important to stress once again that conditions under which the "Cape macchia" grows vary greatly over short distances. Leaf types of a rather mesophilous character, as in Fig. 1 A—B, occur in areas with relatively high humidity and in topographically protected positions. *Myrtus-* and *Ruscus*-like types become increasingly hard or coriaceous in successively drier habitats. The grass-like leaf shape in *Cliffortia graminea* and *Aspalathus monosperma* (Figs. 5 K, 6 J, and 4 G—H) is restricted to relatively moist, protected areas in the southern regions. Hard, pinoid, and often spiny-tipped leaves generally (but not always) occur in somewhat drier, more exposed regions. Closely contracted, linear and terete, often weak

Fig. 6. Examples of leaf types in *Aspalathus* (B—J) and a leaf type representative of its group in the Genisteae (A). The details are somewhat simplified and drawn without regard to scale. The leaf types are represented in the following species: B: *Aspalathus securifolia* ECKL. & ZEYH. — C: *A. sericea* BERG. — D: *A. uniflora* L. — E: *A. linearis* (BURM. FIL.) R. DAHLGR. — *A. hirta* E. MEY. — G: *A. lanata* E. MEY. — H: *A. cordata* (L.) R. DAHLGR. — I: *A. perfoliata* (LAM.) R. DAHLGR. — J: *A. monosperma* (DC.) R. DAHLGR. — If the figures are looked upon as organization levels and the taxa represented are neglected, the plate shows possible evolution courses, which are likely to have proceeded in the direction of the arrows.

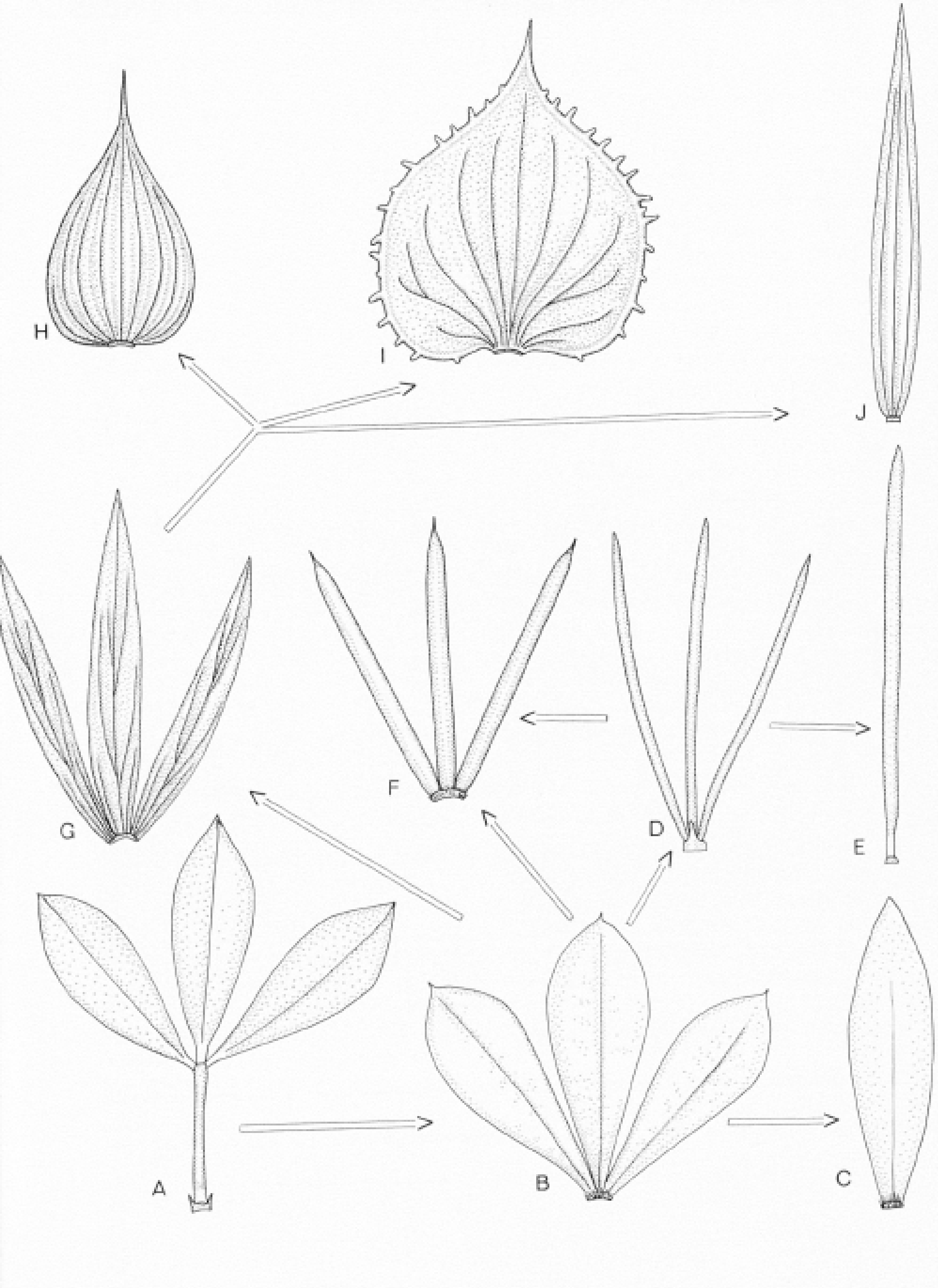

Fig. 6.

leaves are often found in alpine, exposed habitats.

If one compares the two genera further, the question will arise as to whether there are other reasons that would account for the particular similarity between the genera. In the South American flora, the genus *Marggricarpus* has — possibly under similar ecological pressure — developed leaves with prevailingly similar, ericoid leaflets as found in *Cliffortia* and *Aspalathus*, but within an imparipinnate leaf with several to many leaflets. Within the Mediterranean flora the multipinnate leaf type with flat leaflets dominates in the tribe Poterieae.

In the case of *Cliffortia*, the differentiation has occurred at a more or less irreversibly attained trifoliolate level, from which possibilities for further differentiation are similar to those in the trifoliolate *Aspalathus* leaf. Another feature common to *Aspalathus* and a great part of *Cliffortia* is that the petiole has been lost, probably at an early stage. As in *Aspalathus*, the leaflets in the primitive forms were doubtless flat, and a differentiation in both genera has proceeded towards narrow, subterete or terete stages favoured by pronounced selection. A reduction in leaflet number in connection with increased breadth of the leaves (Figs. 5 I—K and 6 H—J) is a well-known phenomenon and has occurred in species of both genera, but in both genera there is, besides, reduction in leaflet number in species with narrow leaves. Finally, both genera consist of shrubs and shrublets with similar types of growth and a common tendency to develop short shoots. The ecological tolerance has become about equal in the two genera.

Consider the similarities mentioned, some of which cannot be due to chance, and the fact that both genera have attained a great measure of differentiation over a long period — they now comprise c. 110 and c. 255 species respectively, evolved under the same ecological conditions. Seen in this light, the extent of the similarity between so many pairs of species of the two genera as demonstrated in Figs. 1—4 is perhaps not so difficult to comprehend.

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Botanical Literature

Elsa Nyholm: Illustrated Moss Flora of Fennoscandia. II: 6. — C. W. K. Gleerup, Lund 1969. 152 pp. Price 25 Sw.Kr.

With the 6th part this gigantic work by Mrs. Nyholm has now been completed (cf. the review of part I, Bot. Notiser 1955 p. 430). Having had the pleasure to comment on all the previous parts, I am happy to tend my sincerest congratulations.

Part 6 comprises mainly the whole subclasses Sphagnales and Andreaeales and of subclass Bryales the following families: Buxbaumiaceae, Tetraphidaceae and Polytrichaceae. A summary of the systematic arrangement of the whole series is given on p. 766, and distinctive features for families and higher categories are listed on p. 767. The book ends up with a comprehensive list of names, including synonymes. The Latin nomenclature is now consistent with the revised nomenclature of the Index Muscorum 1959—1967. A list of those names in the earlier parts of the author's Flora which deviate from the Index Muscorum is found on pp. 774—776.

The nomenclature question is a difficult one in all botanic literature. Let us take for instance a common species like *Dicranum undulatum* Ehrh. This Latin name has been in use in Europe since the beginning of the 19th century. For a short period of time the name *D. rugosum* Brid. was considered more correct (in Scandinavia) and was introduced in the Nyholm Flora part I (1954 p. 63). Now there has been a new change and the species is named according to the Swedish bryologist Olof Swartz *D. polysetum*. The name *D. undulatum*, however, is not at all out of use; it shall be inherited by the species which for the last 165 years has been called *D. bergeri* Bland. (This is, of course, no criticism against the Flora — it is merely a comment on the risks of confusion!)

The illustrations in part 6 are extraordinarily distinct. The exquisite illustrations of the Sphagna are of special merit. The originals, however, (in the Swedish Riksmuseum, Stockholm) are works of art in comparison to which the reproductions in the Flora are less striking. The artist's name is Sylvia Kasubski. Together with A.-L. Nilsson, Sylvia Kasubski seems to have illustrated also part 5, although she alone has done *Sphagnum*.

The family Polytrichaceae holds numerous species of sociological and ecological importance. It is said of *Atrichum tenellum* that it is "widespread . . . in the south and central part . . ., rare towards the North and in the mountains". But nowhere in Sweden does it grow as abundantly as in the coastal regions of Västerbotten, where the sandy soil on river banks etc. offers the best possible ground.

In the genus *Polytrichum, P. gracile* Menz. has been renamed *P. longisetum* Sw. ex Brid., and *P. swartzii* and *P. jensenii* have been reduced to varieties of *P. commune*. I have no particular opinion on *P. jensenii*, but it is quite possible to distinguish *P. swartzii* from *P. commune* both morphologically (shorter and straighter leaves) and ecologically. In Upland *P. swartzii* belongs mainly to rich fens, *P. commune* to poor fens and moist soil in pine forests.

This is, however, more acceptable than the treatment of *P. strictum* Menz. (=*P. affine* Funck) which has been made a variety of *P. juniperinum* in spite of the fact that it is easily recognised both morphologically and ecologically. The pictures on p. 687 of *P. juniperinum* and "var. *gracilius*" are certainly very similar, but misleading. In reality the latter has much shorter and differently shaped leaves.

The illustrations of *Diphysicum* and *Buxbaumia* (pp. 649 and 650) are richer in details than in any other European Flora I have seen and give the reader an instant idea of the appearance of those not too uncommon species (the colour of the capsules, which is important, is described in the text).

Within the genus *Andreaea* I am happy to state that *A. obovata,* easily recognisable and robust, is considered a species on its own. I am not familiar with the two Norwegian species *A. alpina* and *A. frigida,* but as far as the Swedish species are concerned it seems to me that this Flora thanks to the excellent illustrations will be of invaluable help to bryologists of all categories. There are many discussions on species and evaluation of species, not least in plants with leaf-veins. The problem whether *A. crassinervia* differs sufficiently from *A. rothii* is difficult to solve, and the genus must still be considered crucial.

The Sphagnaceae are treated specially by Mrs. BODIL LANGE, Copenhagen.

There is no doubt that this fully illustrated Moss Flora will for considerable time meet with the old need of botanists. Not only in Scandinavia but in all other temperate parts of the Northern Hemisphere with a similar or partly similar stock of moss species this Flora will be of great importance. Together with other works it has also earned the author an honorary Ph.D. at the University of Lund.

EDVARD VON KRUSENSTJERNA

To have the genus *Sphagnum* duely fitted into a general moss flora has always been a problem. ELSA NYHOLM has succeded in having also this intricate genus comprehensively treated.

The illustrations are of genuine quality, better then most others in the flora thanks to the excellent style of the artist, SYLVIA KASUBSKI. Especially the figures of the habit of the plants are both delicate and true, even if certain details have been lost in the printing process. The original plates are in colour.

There is an ample selection of figures of details. Here, as in the work as a whole, the magnification is not given, and here and there some details of natural importance have been omitted, such as the papillae from branch leaves in face view for *S. papillosum.* However, in general also the figures of details are very good, even if they cannot cover the broad amplitude of variation for the individual species. This applies probably still more to the illustrations of habit which is extremely variable within most species.

The illustrations in this last part of the six sections ought to have had their own legend of signatures. There is a long way back to part 1 page 12, and a few new abbreviations have sneaked in as unaccounted for.

There is a good key to the sections of the genus, and then to the individual species. In the key to the sections, page references would have made life easier.

The taxonomic division and the selection of names is naturally not revolutionary, in places slightly oldfashioned, as for instance in the section names, where it would have been reasonable to adopt the corrections proposed by ISOVIITA in his theses from 1966. Same applies to some minor points in the species concept, e.g. the establishing of *S. subtile* as a species. But here is of course room for personal opinion.

The notes on the individual species are quite ample, also the small hints, so useful for those who really want to use the text.

The indications of distribution in world scale are probably somewhat fragmentary, but this could hardly be otherwise, and the occurrence in Fennoscandia is well accounted for in general. Maybe the problems of the occurrence and variability of the species in the far northern regions have been handled with less precision than the similar problems in more southern areas. Thus, information is lacking on the special arctic and subarctic forms of *S. squarrosum* and *S. fimbriatum*.

The difficult problem of the species concept has been solved with what could be called a moderate conservatism. Thus both *S. angustifolium* and *S. flexuosum* are referred to *S. fallax*. Personally I cannot follow ANDREWS that far. The species are difficult to keep apart in the laboratory, much easier so in the field.

A difficult — even very difficult — task has been solved with diligence and skill. A Fennoscandian *Sphagnum* flora completes the comprehensive work. We sphagnologists shall certainly appreciate this contribution and our criticisms will be much smaller than our thanks to the author.

BODIL LANGE

PRESTON, R. D. (ed.): Advances in Botanical Research, vol. 3. — Academic Press Inc., London 1970. xi+309 pp. Price 95 shillings.

This volume contains four articles covering very different fields of botany. A paper by P. B. TOMLINSON entitled "Monocotyledons — Towards an Understanding of their Morphology and Anatomy" (pp. 207—292) is of particular interest to taxonomists.

TOMLINSON argues that a change in our approach to the study of monocotyledons ("in many respects a neglected group") is needed. More attention should be focused on ontogenetic changes, and greater familiarity with arborescent tropical forms is necessary. It is particularly unfortunate that plants presented to students as "typical" monocotyledons, such as grasses, sedges, and lilies, are in many respects highly specialized.

It is stated that the importance of growth habit and other vegetative characteristics has generally been underestimated by morphologists. The development of the vascular cambium of monocots is discussed at some length with special reference to the "palm-type" of vascular construction.

Putative evolutionary trends in the genus *Tillandsia* are described and attractively illustrated on pp. 224—229. For a non-specialist it is difficult to appreciate that the familiar "Spanish Moss", *T. usneoides,* is a member of Bromeliaceae, where most species are broad-leaved tank-epiphytes with a pineapple-like habit. The probable phylogenetic development from "normal" tank-epiphytes to root-less, reduced dew-epiphytes is interpreted as a progressive delay in geotropic response accompanied by progressive reduction of the inflorescence. Adult plants of *T. usneoides* have many features in common with seedlings of less specialized species.

Although many of the families and genera mentioned are no doubt unfamiliar to most European botanists, the problems discussed are of fundamental importance and presented in a lucid, non-technical way. The illustrations are of high quality. The article should not be overlooked by taxonomists interested in the morphology and evolution of monocotyledons.

The other articles in this volume are: L. ANDREW STAEHELIN and M. C. PROBINE: Structural Aspects of Cell Membranes (pp. 1—52); W. KREUTZ: X-ray Structure Research on the Photosynthetic Membrane (pp. 53—169); and P. E. WEATHERLEY: Some Aspects of Water Relations (pp. 171—206).

THE EDITOR

STEBBINS, G. L.: Chromosomal Evolution in Higher Plants. In E. J. W. BARRINGTON and A. J. WILLIS: Contemporary Biology. — Edw. Arnold Ltd., London 1971. 216 pp., 88 illustrations. Price £4. net (boards).

A new textbook by the indefatigable G. L. STEBBINS is a major event for students of plant cytology and evolution. According to the preface this book "should not be regarded as a general textbook in the field" nor "as an exhaustive treatment of the subject for research workers."

Nevertheless it is a lucid digest of a rapidly developing branch of study with some 250 carefully selected references to original research papers, some of them published as late as 1969.

Although the book is not primarily concerned with ultrastructure the account is naturally influenced by the discoveries of DNA structure and function which, since about 1953, have revolutionized life science. Chapter 1 thus describes the elementa of DNA replication and gene action. The other five chapters are entitled: Chromosomal Organization in Relation to Gene Action; Variation in Size and Organization of the Chromosomes; Chromosomal Changes, Genetic Recombination, and Speciation; The Morphological, Physiological, and Cytogenetic Significance of Polyploidy; and Polyploidy, Plant Geography, and Major Trends of Evolution.

Many of the fundamental problems of chromosome function and evolution are still unsolved and thus even a textbook of this kind will inevitably be controversial at some points, although the author has in such cases endeavoured to present both sides of the picture. Personally I find it hard to support, for instance, the rather categoric statement (originally derived from LEVITSKY) that "there is a predominant trend in flowering plants towards increasing asymmetry of the karyotype." This is somewhat contradictory to the common assumption (see, e.g. STEBBINS' textbook of 1950) that centric fusion producing one pair of metacentric chromosomes from two pairs of acrocentrics is a frequent phenomenon in karyotype evolution. The supporting example of putative evolutionary trends in Ranunculaceae tribe Helleboreae is not well chosen. It is stated that "the highly asymmetrical karyotypes found in *Delphinium* and *Aconitum* are associated with highly specialized zygomorphic flowers, while genera of this tribe having less asymmetrical karyotypes, such as *Caltha, Trollius, Cimicifuga,* and *Nigella,* also have less specialized flowers." The karyotype of *Nigella* is indeed asymmetrical (five pairs of large metacentrics, one pair of small acrocentrics) and the flowers, albeit actinomorphic, are in other respects highly specialized (complicated nectaries, elaborate pollination mechanism, etc).

Karyotype morphology as an aid in taxonomy, plant geography, and ecology is discussed with special emphasis on meiotic pairing in interspecific hybrids. It is pointed out that the distinction between genic and chromosomal sterility frequently made in previous literature breaks down when recent discoveries about gene action are taken into consideration.

Nearly half of the book is devoted to a thorough and up-to-date account of polyploidy. This subject was also extensively treated in the author's classical "Variation and Evolution in Plants" where most of the basic facts can be found, but the present text has been rewritten and profoundly modernized. Special attention has been paid to polyploid complexes and to the relationship between polyploidy and apomixis. Reference is also made to the peculiar case of *Claytonia virginica* where regulatory mechanisms have apparently broken down and somatic numbers form an aneuploid series ranging from 12 to c. 191. In general, most of the examples are taken from North American plant groups, which should not discourage European botanists from getting acquainted with this very useful survey of an intricate subject. The book can be recommended without reserve to biosystematists and research students in plant evolution.

THE EDITOR

KUNKEL, G.: Helechos cultivados. — Ediciones del Exmo. Cabildo Insular de Gran Canaria. IV. Ciencias. 3. Las Palmas 1967. 175 pp., 44 figures in text, 24 plates illustrating 40 species. Price 250 pesetas (wrappers).

Dr. G. KUNKEL, a former German botanist, has travelled in many parts of the world, i.a. with Professor C. SKOTTSBERG in South America and the Pacific. In 1965 he settled in Gran Canaria, where he founded a private botanical garden, in the first hand devoted to ferns, at Tafira Alta near Las Palmas. This modest garden was later moved to new localities at Santa Lucia de Tirajana in the same island. Here he is gradually building a botanical centre including a fairly large botanical garden "Llano de la Piedra", herbarium and library. He is also the editor of "Cuadernos de Botanica Canaria" (12 volumes since 1967) mainly containing short contributions to the flora of the Canary Islands, and "Monographiae Biologicae Canarienses" (since 1970) for the publication of major monographic treatises.

As a result of his fern studies Dr. KUNKEL has published a volume "Helechos Cultivados" (=Cultivated Ferns). A selection of 40 species from all parts of the world have been treated in detail. Many of them are not too difficult to cultivate, at least in greenhouses, also in a temperate climate. Though written in Spanish this book is fairly easy to understand especially owing to the introductory chapter on terminology and the numerous drawings in the text. Unfortunately, some of the photographs (black-and-white) in the plates are too dark and give little help with identification. We also find a considerable amount of information how to cultivate these ferns and a chapter on parasites affecting ferns.

OVE ALMBORN

KUNKEL, G.: Arboles Exóticos. Los arboles cultivados en Gran Canaria I. — Ediciones del Exmo. Cabildo Insular de Gran Canaria. IV. Ciencias 5. Las Palmas 1969. 245 pp., 100 plates. Price 300 pesetas (wrappers).

In the last few decades the Canary Islands have attached a considerable interest to a wide public mainly induced by sheap charter flights. An increasing number of botanists have also visited these "Lucky Islands". The splendid wealth of ornamental plants often flowering in our winter time, are mostly the same species as occur in all tropical or subtropical areas. The highly interesting indigenous Canary flora containing a considerable number of endemic species is somewhat hidden among all these introduced plants.

The need for a modern flora of the Canary Islands has been felt for many years. The classical work WEBB & BERTHELOT, Phytographia canariensis (1836—1850) was followed by a comprehensive flora of "Les Iles Canaries" by PITARD & PROUST (1908). Important contributions mainly founded on material from German expeditions were published by SCHENK (1907, the Valdivia Expedition) and LINDINGER (1926). The Danish botanist BÖRGESEN issued "Contributions to the knowledge of the vegetation of the Canary Islands" (1924). A modern guide illustrated with coloured plates is SCHAEFFER, Pflanzen der Kanarischen Inseln (1963, also with English text). This work, however, treats only a limited selection of plants, mainly trees and shrubs. Swedish visitors will find some information, easily written and illustrated with drawings in black-and-white, in a small volume by ULLA BEYRON, "Kyskhetsträd och änglatrumpet" (=Chastity tree and Angle trumpet) (1969).

Dr. G. KUNKEL has published a volume describing and illustrating 100 species of ornamental trees and shrubs cultivated in Gran Canaria. They represent 72 genera and 42 families, Dicotyledons only. As the Canary flora has a total of some 250 species of cultivated trees and shrubs we may look forward to a second volume. It is an interesting fact that the number of indigenous trees and shrubs is small, only some 30 species.

Each species is described, in fair detail, in Spanish. We also find short notes on names in English, German or French, etymology of Latin names, medical or other practical uses and origin of the species in question. Opposite each text page there is a drawing in black-and-white (by Mrs

Mary Anne Kunkel) showing flowers, fruits, leaves and other essential details. Mrs Kunkel is a good artist, and, in the reviewer's opinion, her illustrations are highly useful for the identification of the species treated.

It should be added that Dr. Kunkel is preparing an Atlas on the flora of Gran Canaria with colour drawings by Mrs Kunkel. The first set (some 50—70 species) will probably be issued in the beginning of 1972.

Ove Almborn

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