Drawings of Scandinavian Plants 17—44

Key to Rubus L. Subgen. Rubus

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ABSTRACT

OREDSSON, A.: Drawings of Scandinavian Plants 17—44. *Rubus* L. Subgen. *Rubus*. — Bot. Notiser 122: 1—8, 153—159, 315—321, 449—456; 123: 1—7, 213—219, 363—370, 447—454. Lund.

Rubus L. subgen. *Rubus* is in Europe represented by sect. *Rubus* containing 3000 named blackberries. In Scandinavia, HYLANDER (1955) recognized 78 species, 30 of them within the *corylifolius* agg.

The current series deals with 28 taxa — namely, according to the division into subsections by FOCKE (1914), 8 from *Suberecti*, 17 from *Senticosi*, 1 from *Glandulosi*, and 2 from *Caesii* (*R. caesius* and *R. corylifolius* agg.). A list of the taxa considered is presented (p. 452).

Ten corresponding morphological characters of each taxon are illustrated.

Each taxon is briefly described using nine recurring characters, as well as a varying number of other characters useful within smaller groups of taxa. The descriptions are based on vegetative and floral characters in the upper half of the first and second year growths, respectively. Distributions of taxa are included.

Finally, a key to 26 of the treated Scandinavian *Rubi* is presented (pp. 447—451).

KEY TO 26 SCANDINAVIAN TAXA OF RUBUS SUBGEN. RUBUS

Perennial plants with herbaceous biennial shoots. First-year growth from buds at the ground level. Second-year growth from buds in the leaf axils. Stem 0.5—5 m long, erect, arched, or procumbent, equipped with prickles. Leaves alternate, ternate, digitate, or pedate, with serrate leaflets. Leaflets 3—7 (5-digitate leaves with the terminal leaflet ternate). Inflorescence, always from second-year growth, racemose or paniculate. Flowers bisexual, actinomorphic. Sepals 5, green—grey,

with a white-felted border. Petals 5 (—8), free, white, or pink. Stamens numerous. Carpels numerous. Fruit a drupe, deep red, black, dull black, or pruinose, consisting of 1-seeded, coherent druplets and the conical or cylindrical receptacle.

Flowering period: June—August.

The key presupposes the availability of two specimens from the same shrub — namely, one specimen from the upper half of the primocane (first-year growth), with two or three well-developed leaves, and another specimen from the top of the floricane (second-year growth) in flower or in fruit.

Unless an explicit exception is made, *prickles* and *leaves* belong to the middle of the stem; *bristle* and *bristle-like prickle* are used synonymously; *gland* signifies stalked gland; and the *disposition of the sepals* refers to the sepals of the immature fruit.

Some of the botanical terms used in the key are illustrated in Fig. 2.

1 a. Stipules broadly lanceolate. Fruit pruinose (dewberry). — Stem creeping, terete, pruinose. Prickles 1—3 mm long, recurved. Leaves 3-foliolate. Sepals long-acuminate. **Plate 44** ..... *R. caesius*

1 b. Stipules narrowly lanceolate—linear. Fruit deep red—black (blackberry) 2

2 a. Stem upright—high-arched. Glands absent from both the stem and the inflorescence. Terminal leaflet cordate or ovate (oblong in *R. nitidus*). Sepals, except the white-felted border, green—greyish green. (Subsect. *Suberecti* FOCKE) 3

2 b. Stem high-arched—procumbent (recurved in *R. thyrsanthus*). Glands absent or present. Terminal leaflet of varying shapes. Sepals, except the white-felted border, greyish green—grey 8

3 a. Flowers 2.5—3.5 cm across. Petals broadly obovate. Filaments 5—6 mm long 4

3 b. Flowers up to 2.5 cm across. Petals narrowly obovate or obovate. Filaments 2—5 mm long 7

4 a. Prickles of the stem 2—5 mm long. — Stem terete. Leaves thin, glabrescent. Inflorescence short, leafy. **Plates 17—18** ..... *R. nessensis*

4 b. Prickles of the stem 7—10 long 5

5 a. Basal leaflets with at least 2 mm long petiolules. — Stem erect, slightly recurved. Prickles with a broad base. Prickles of the inflorescence few and small. **Plate 21** ..... *R. sulcatus*

5 b. Basal leaflets sessile or with short petiolules 6

6 a. Prickles of the inflorescence large, hooked. — Leaves hairy beneath. Terminal leaflet oblong. Sepals with numerous prickles. **Plate 23** .. *R. nitidus*

6 b. Prickles of the inflorescence long, straight. — Leaves densely hairy beneath, sometimes grey-tomentose. Terminal leaflet cordate, acuminate. Sepals with some prickles at the base. **Plate 24** ..... *R. affinis*

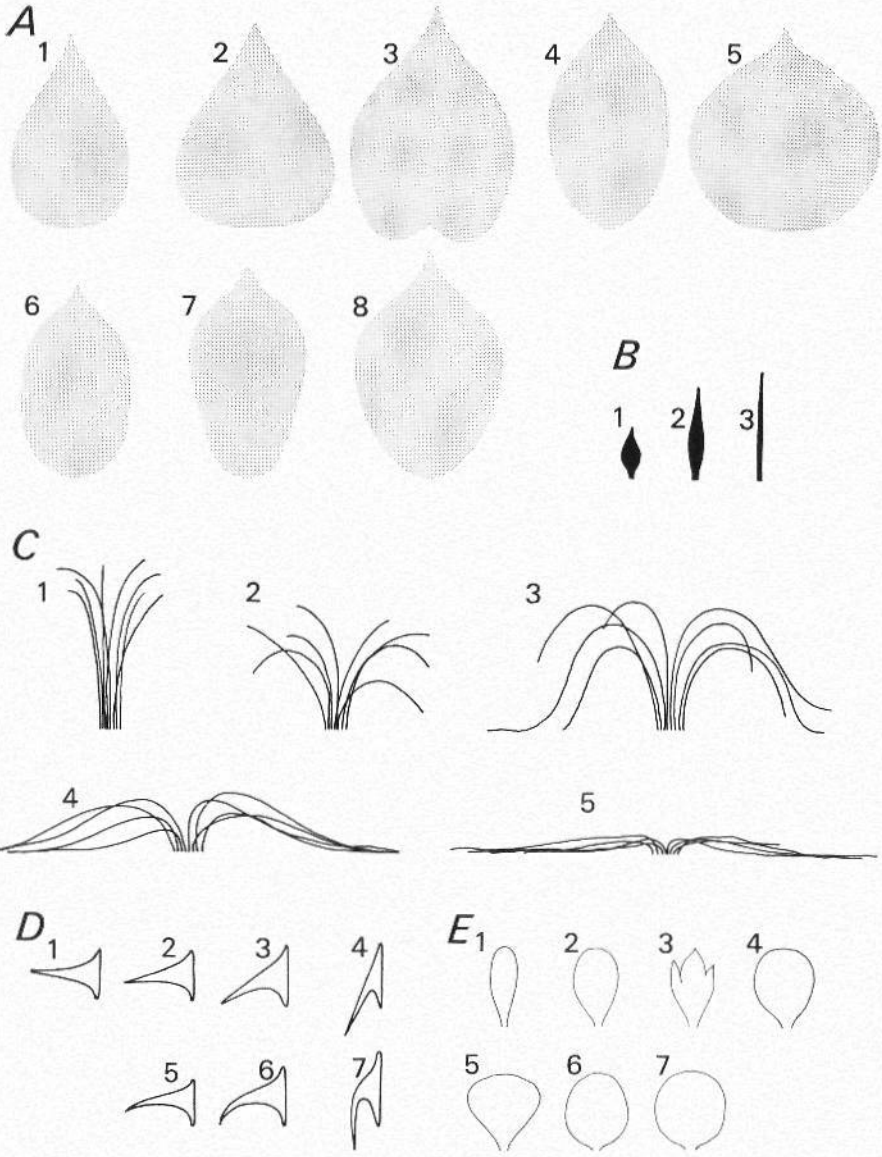

Fig. 2. — A. *Terminal leaflet* (petiolule downwards): 1. ovate, 2. broadly ovate, 3. cordate, 4. elliptic, 5. orbicular (orbiculate), 6. oblong, 7. obovate, 8. broadly obovate. — B. *Stipule:* 1. broadly lanceolate, 2. narrowly lanceolate, 3. linear. — C. *Stem:* 1. upright (erect), slightly recurved, 2. recurved, 3. high-arched, 4. low-arched, 5. creeping (procumbent). — D. *Prickle:* 1. patent, 2. slightly (somewhat) recurved, 3. recurved, 4. retrorse, 5. slightly bent (slightly curved), 6. falcate, 7. hooked. — E. *Petal*: 1. narrowly obovate, spathulate, 2. obovate, 3. irregularly incised at the apex, 4. broadly obovate, 5. cuneate, 6. broadly elliptic, 7. orbicular (circular).

7 a. Prickles of the stem 2.5—5 mm long. — Prickles of the stem numerous, straight or slightly recurved, subulate. Leaves 5—7-foliolate. Petals white. **Plates 19—20** ..... *R. scissus*

7 b. Prickles of the stem 5—8 mm long. — Prickles of the stem falcate. Leaves 5-foliolate. Petals pink—white. **Plate 22** ..... *R. plicatus*

8 a. Petiolules of the lower pair of leaflets about 1 mm long or lacking. Stipules narrowly lanceolate. Fruit dull black, pulpy. — Stem terete—angular, with 3—6 mm long, patent or somewhat recurved prickles. Leaves 5 (3—7)-foliolate. Sepals short-tipped. **Plate 43** .... *R. corylifolius* agg.

8 b. Petiolules of the lower pair of leaflets at least 2 mm long (sessile in *R. vestervicensis*, 1—2 mm long in *R. taeniarum*). Stipules linear. Fruit black, firm 9

9 a. Glands absent from both the stem and the inflorescence 10

9 b. Glands of the stem none—numerous. Glands of the inflorescence few—numerous 15

10 a. Leaflets 5, divided into pairs of laciniated segments. — Sepals grey tomentose with long, green tips, often also with numerous prickles. Petals irregularly incised at the apex, obovate when entire. **Plate 25** .. *R. laciniatus*

10 b. Leaflets (3—) 5, serrated 11

11 a. Stem hairy—rather densely hairy. Leaves green—grey tomentose beneath 12

11 b. Stem glabrous—sparsely hairy. Leaves grey—white tomentose beneath 14

12 a. Petals deep pink. — Terminal leaflet broadly ovate—elliptic. Prickles at the apex of the inflorescence long and subulate. Flowers about 3 cm across. **Plate 31** ..... *R. insularis*

12 b. Petals white 13

13 a. Terminal leaflet orbiculate. — Leaves quite green beneath, softly hairy. Prickles of the inflorescence recurved—hooked. Petals broadly obovate—circular. **Plate 29** ..... *R. scheutzii*

13 b. Terminal leaflet obovate. — Leaves green—grey tomentose beneath, softly pubescent. Prickles of the inflorescence hooked. Petals obovate. **Plate 33** ..... *R. lindebergii*

14 a. Prickles of the stem about 10 mm long. — Stem robust, arching, with patent or slightly bent prickles. Terminal leaflet broadly obovate—orbicular. Flowers about 3 cm across. **Plate 34** ..... *R. armeniacus*

14 b. Prickles of the stem 4—7 mm long. — Stem 0.5—2 m long, recurved, with recurved prickles. Terminal leaflet ovate. Flowers 2—2.5 cm across. **Plate 35** ..... *R. thyrsanthus*

15 a. Glands absent from the stem (by *R. pyramidalis* and *R. vestitus* few or none). Stem without bristles (*R. vestitus* normally almost bristle-less) 16

15 b. Glands on the stem few—numerous. Stem with bristles (few or none by *R. vestervicensis* and *R. fuscus*) 21

16 a. Stem densely hairy. Leaves rather hairy above. — Prickles of the stem 6—9 mm long, patent. Prickles in the apex of the inflorescence long and subulate, slightly recurved. **Plate 37** ..... *R. vestitus*

16 b. Stem sparsely hairy—hairy. Leaves glabrous—sparsely hairy above .. 17
17 a. Leaves 3—5-foliolate. Sepals loosely clasping the fruit 18
17 b. Leaves 5 (—7)-foliolate. Sepals deflexed 19
18 a. Petals bright rose-pink, obovate. Filaments about 4 mm long. — Leaves bright green beneath, hairy. Terminal leaflet elliptic—obovate, acuminate. Prickles of the inflorescence hooked. **Plate 27** ..... *R. sprengelii*
18 b. Petals light pink, orbicular. Filaments about 2.5 mm long. — Leaves sparsely hairy beneath. Terminal leaflet orbiculate, subcordate. Prickles of the inflorescence straight or slightly curved. **Plate 28** ..... *R. axillaris*
19 a. Leaves with shiny, rather rigid hairs beneath, seldom also greyish tomentose. — Prickles of the stem relatively weak, with a narrow base. Prickles of the inflorescence long, subulate. Sepals with glands and prickles. **Plate 30** ..... *R. pyramidalis*
19 b. Leaves green—grey tomentose beneath 20
20 a. Prickles of the inflorescence rather numerous, strong, falcate. — Stem ridged, with falcate or patent prickles. Inflorescence long and broad, dense, leafy. **Plate 26** ..... *R. selmeri*
20 b. Prickles at the apex of the inflorescence few, small, straight. — Stem terete—angled, with straight, somewhat recurved prickles. Inflorescence long, dense, leafless. **Plate 32** ..... *R. polyanthemus*
21 a. Glands of the stem few or scattered 22
21 b. Stem glandular or with numerous glands 24
22 a. Petals narrowly obovate—spathulate. — Stem with few hairs. Basal leaflets sessile. Prickles of the inflorescence few, small, straight. **Plate 36** ..... *R. vestervicensis*
22 b. Petals cuneate—broadly elliptic 23
23 a. Stem hairy. — Stem angled—furrowed. Petiolules of the lower pair of leaflets 0.1—0.2 cm long. Inflorescense with bristles and rather strong, flat, falcate, or hooked prickles. **Plate 39** ..... *R. taeniarum*
23 b. Stem densely hairy. — Stem terete—angled. Petiolules of the lower pair of leaflets about 0.4 cm long. Prickles of the inflorescence recurved—reflexed and straight. **Plate 40** ..... *R. fuscus*
24 a. Larger prickles of the stem 2—5 mm long. (Subsect. *Glandulosi* FOCKE) — Larger prickles of the stem retrorse, straight. Leaves 3-foliolate, green, somewhat scabrous beneath. Petals narrowly obovate. **Plate 42** ..... *R. bellardii*
24 b. Larger prickles of the stem 5—8 mm long 25
25 a. Stem sparsely hairy. — Prickles at the apex of the inflorescence straight, patent or slightly recurved. Sepals devoid of prickles. **Plate 38** ..... *R. radula*
25 b. Stem densely hairy. — Larger prickles of the inflorescence recurved or hooked. Sepals with numerous prickles. **Plate 41** ..... *R. hartmani*

SURVEY OF TREATED TAXA

Plate	*Rubus*	Bot. Notiser vol.	Plate, page	Text, page(s)
17	*nessensis* var. *nessensis*	122 (1969)	3	4
18	*nessensis* var. *armatus*		5	4
19	*scissus*		6	4—8
20	*scissus* var.?		7	8
21	*sulcatus*		154	153
22	*plicatus*		155	155—158
23	*nitidus*		156	158
24	*affinis*		157	158
25	*laciniatus*		316	315
26	*selmeri*		317	315—320
27	*sprengelii*		318	320
28	*axillaris*		319	320
29	*scheutzii*		450	449
30	*pyramidalis*		451	454
31	*insularis*		452	454
32	*polyanthemus*		453	455
33	*lindebergii*	123 (1970)	2	1
34	*armeniacus*		3	1—6
35	*thyrsanthus*		4	6
36	*vestervicensis*		5	6—7
37	*vestitus*		214	213
38	*radula*		215	213—216
39	*taeniarum*		217	216—217
40	*fuscus*		218	217—219
41	*hartmani*		364	363
42	*bellardii*		365	363—368
43	*corylifolius* agg.		366	368—369
44	*caesius*		367	369—370

TAXA NOT INCLUDED

Because of insufficient data at present, I have decided not to treat 22 species as recognized by HYLANDER (1955) belonging to *Rubus* subgen. *Rubus* (but not to *R. corylifolius* agg.) with Scandinavian distributions restricted to Denmark. Of these, referring to FRIDERICHSEN (1922), 13 species do not occur outside southern Jylland, Als, Fyen, and Langeland, whereas only three species occur on Sjælland.

Rubus dasyphyllus ROGERS, occurring on northernmost Jylland (Fredrikshavn) and, since 1942, extinct in south-eastern Skåne (Kivik).

Rubus langei G. JENSEN, known from Sønderjylland, but recently found at Ystad in southern Skåne (OREDSSON 1966).

Two hybrids, recognized by HYLANDER (1955), within *Rubus* subgen.

Rubus, namely, *R. plicatus*×*R. sulcatus*, very rare in Denmark and Sweden and *R. sprengelii*×*R. wahlbergii* (within the *R. corylifolius* agg.), very rare in Sweden.

Aberrant blackberry shrubs, rare in nature, for example, *R. plicatus*, *R. selmeri*, or *R. radula* with markedly reduced leaf size, and *R. plicatus* or *R. thyrsanthus* with incised leaflets.

CHROMOSOME NUMBERS

The great majority of the European species investigated within *Rubus* subgen. *Rubus* are tetraploids with 2n=28. Five of the twenty-eight taxa treated in the current contribution to "Drawings of Scandinavian Plants" have deviating chromosome numbers. Two of these are triploids with 2n=21, namely, *R. nitidus* and *R. thyrsanthus*; another two are pentaploids with 2n=35, namely, *R. vestervicensis* and *R. bellardii*, whereas tetra-, penta-, as well as hexaploid specimens have been found within the *R. corylifolius* agg. (GUSTAFSSON 1943 pp. 90—97).

ADDITIONAL REMARKS

With this survey, I have endeavoured to preserve something of the tradition of Scandinavian *Rubi* as upheld by pioneers like FRIDERICHSEN, GUSTAFSSON, and LIDFORSS. Unfortunately, the oral communication that was of such importance for discrimination among the *Rubus corylifolius* agg. seems now to have ceased.

Instead of the promised discussion here, I would like to have personal communication with all who have information to offer concerning *Rubus* subgen. *Rubus*, no matter what aspect or geographical region.

ERRATA

Bot. Notiser 122 (1969) p. 449 (*Rubus scheutzii*). — . . . the basal leaflets have 2.5 cm long petiolules. — Should be: . . . the basal leaflets have 2.5 mm long petiolules.

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Morphology and Embryology of Mimusops elengi L.

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ABSTRACT

BHATNAGAR, S. P. & GUPTA, M.: Morphology and Embryology of Mimusops elengi L. — Bot. Notiser 123: 455—473, Lund.

The flowers arise in pairs or fascicles in the axil of leaf. They are bracteate, tetramerous, bisexual and rusty tomentose. There are eight sepals arranged in two whorls of four each. Each lobe out of eight constituting gamopetalous corolla bears two dorsal appendages. The androecium comprises an outer whorl of eight alternisepalous stamens and two inner whorls of eight alternipetalous, petaliferous and hairy staminodes. Both stamens and staminodes are epipetalous. The ovary is pubescent, superior and octalocular. Each locule has a single basal ovule. The entire flower (except corolla) is covered by thick-walled, two-armed hairs.

The anther wall comprises epidermis, fibrous endothecium, three or four ephemeral middle layers and secretory polyploid tapetum. Anomocytic stomata are found on the anther. Cytokinesis is simultaneous resulting in tetrahedral, decussate or isobilateral tetrads. The pollen grains are bi-, tri- or tetracolporate and are shed at two-celled stage.

The ovules are anatropous, unitegmic and tenuinucellate. The archesporium is single-celled and functions directly as the megaspore mother cell. The development of embryo sac conforms to the Polygonum type. The synergids have a distinct filiform apparatus. The chalazal end of the embryo sac develops into a finger-like projection. Endothelium and hypostase are not organized.

The endosperm is Nuclear. The primary endosperm nucleus divides before the division of zygote. More than a thousand nuclei are formed before the endosperm becomes cellular.

The embryo has a massive and multicellular suspensor. The cells are of various sizes, bloated and uninucleate. Cotyledons are foliaceous and show reticulate venation.

Testa is completely sclerified; the sclereids have tannin deposited in lumen. Thus the seed coat is hard and dark. There is a basal scar on the seed.

The fruit is a one-seeded berry with leathery sclerified outer zone, slightly pulpy middle zone traversed by a number of laticiferous ducts, and innermost zone of compactly arranged cells.

INTRODUCTION

Mimusops belongs to the family *Sapotaceae* which comprises about 35—75 ill defined genera and 800 species (WAGENITZ 1964; WILLIS 1966). *Mimusops* is a heterogeneous taxon (see MEEUSE 1960) and in its limited sense consists of 57 species (WILLIS 1966).

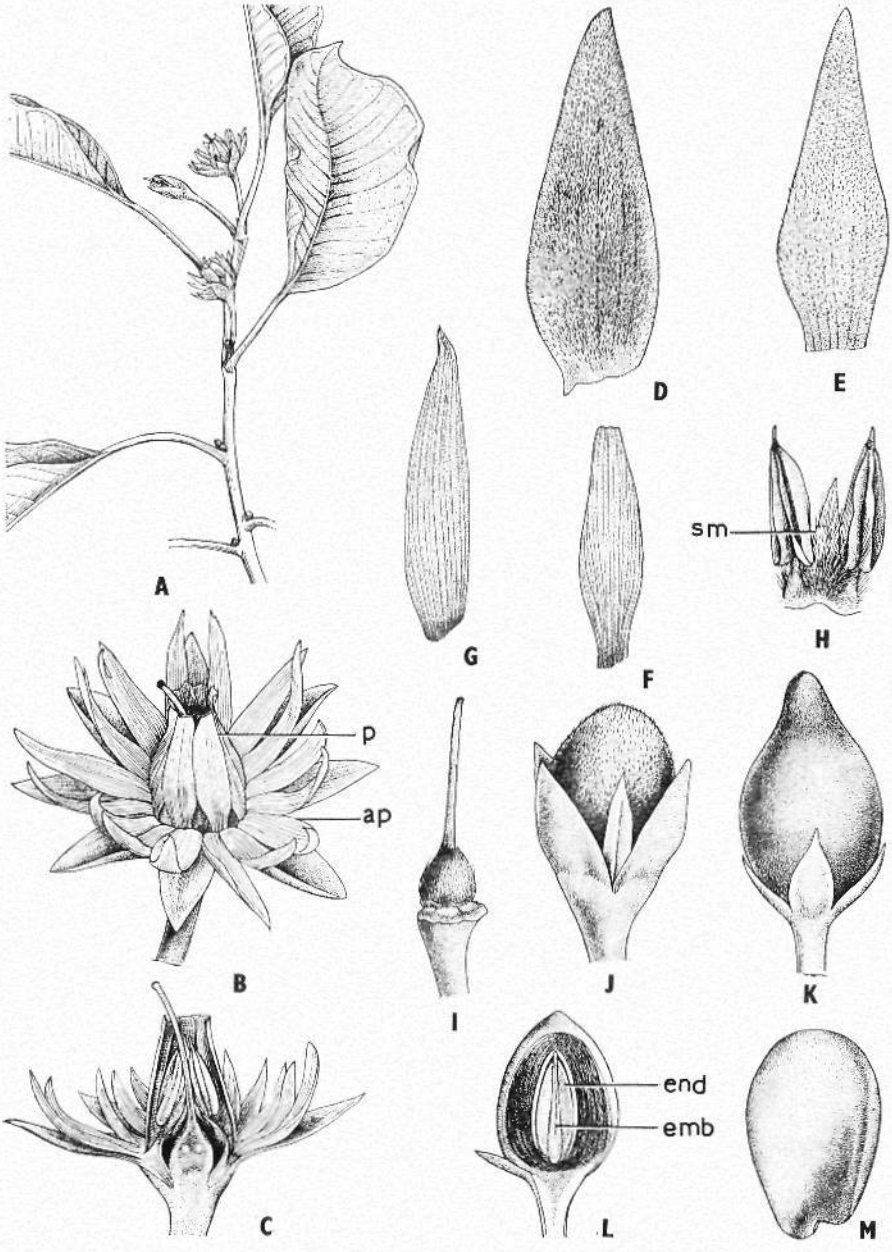
Sapotaceae is a tropical family and consists of shrubs and trees (HOOKER 1879; HUTCHINSON 1959; MEEUSE 1960). The plants belonging to this family yield besides timber, a variety of useful products like edible fruits, oil seeds, gutta-percha, balata and chicle.

Mimusops elengi is distributed in the Deccan Peninsula and Andaman islands and is cultivated throughout India for its timber, fragrant flowers, edible fruits, oil seeds and astringent bark (CHOPRA 1958; WILLIS 1966). WARMING (1913) and SAUNDERS (1934) have studied the floral anatomy of *Mimusops*. Except for megasporogenesis and female gametophyte (MURTHY 1941) there is no work on other aspects of embryology of this plant. Therefore, the present investigation on the morphology and embryology of *Mimusops* was undertaken with a view to furnish more information.

MATERIAL AND METHODS

The buds, flowers and fruits of *Mimusops elengi* were collected from trees growing in the campus of University of Delhi. These were fixed in formalin-acetic-alcohol, acetic alcohol, Carnoy's fluid and Bouin's fluid, and later stored in 70 per cent ethanol. At the time of fixation buds, carpels, fruits and seeds were trimmed on two sides. The different whorls of flower, except corolla, are covered with thick-walled hairs which presented difficulty in microtomy. In order to facilitate sectioning several methods were tried. Dissolving the hairs by dipping each bud or carpel in concentrated sulphuric acid for 20 to 30 seconds and then washing under running water was found to be most satisfactory. By rubbing with fingers, the stubs of burnt hairs were removed. The material was dehydrated in tertiary-butyl alcohol—ethanol series and embedded in paraffin. The embedded material was partially exposed and soaked

Fig. 1. *Mimusops elengi* (*ap*, appendage; *emb*, embryo; *end*, endosperm; *p*, petal; *sm*, staminode). — A: Portion of flowering twig. — B: Single flower showing corolla with dorsal appendages. — C: Longisection of flower to show epipetalous stamens. — D: Sepal of outer whorl. — E: Sepal of inner whorl. — F: Corolla lobe. — G: Appendage. — H: Stamens with alternating staminode. — I: Carpel showing pubescent ovary. — J: Young fruit with persistent calyx. — K: Mature fruit. — L: Longisection of mature fruit showing copious endosperm and embryo. — M: Seed showing basal seed scar. — A×0.8, B—C×3.2, D—G×5, H—J×3.4, K×1.7, L×2.3, M×1.7.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in water and Gifford's solution (GIFFORD 1950) for five or six days. The sections were cut between 5 and 16 microns and stained in Heidenhain's iron-alum haematoxylin or safranin and counterstained with fast green or erythrosin.

Development of endosperm and embryo was followed from dissections and cleared whole mounts. Acetocarmine squashes of anthers were prepared to study the microsporogenesis. Pollen grains were acetolyzed to study their exine structure.

OBSERVATIONS

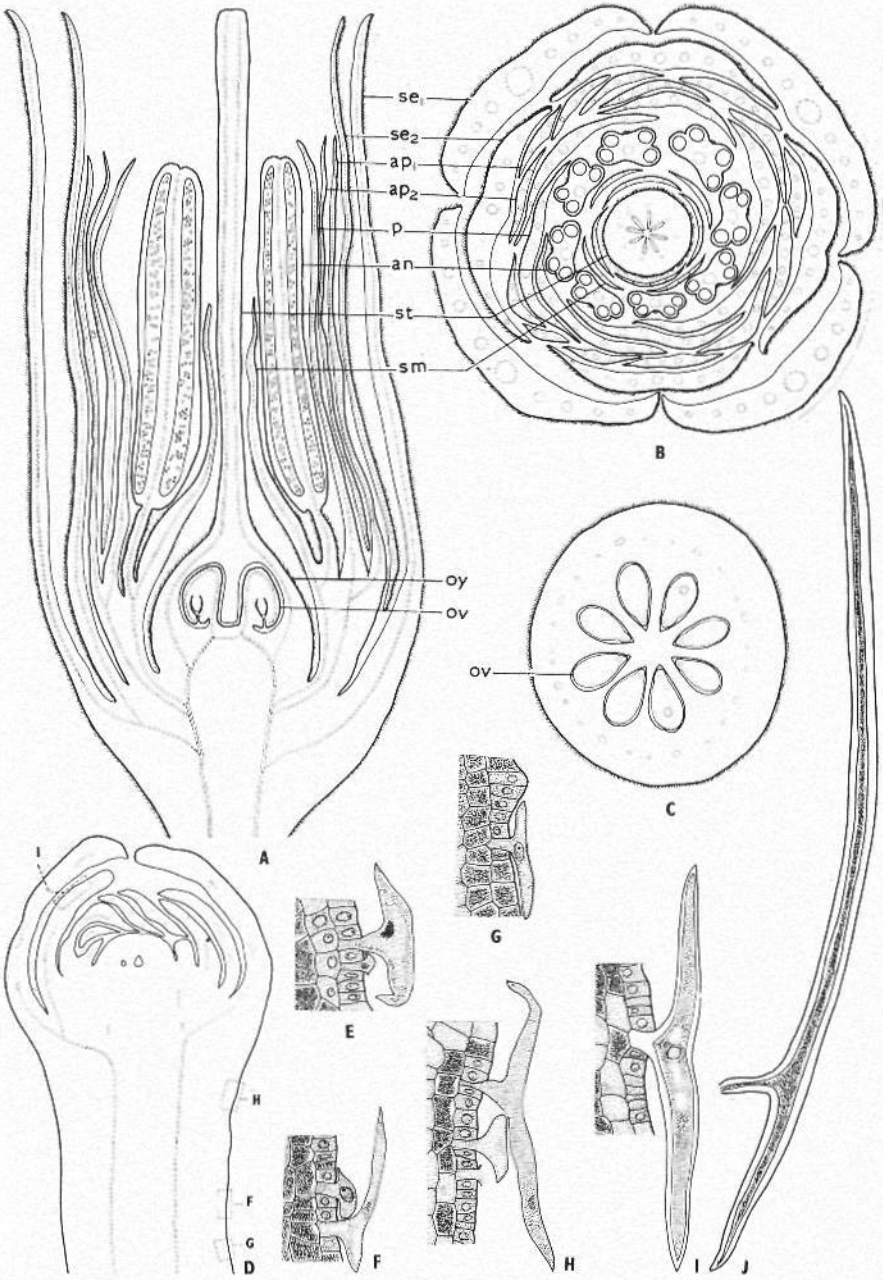
External Morphology

Mimusops elengi is a tree. The young leaves have hairy surface and entire margin. Older leaves, however, have shiny and coriaceous surface with undulate margin (Fig. 1 A). Stomata on leaf are anisocytic and undergo syndetocheilic type of development (BHATNAGAR & GUPTA, 1969). The plant starts flowering in May and June and continues to do so, though sporadically, up to February. Occasionally, some plants may come to bloom in December and January and fruit in April and May. The flowers are white and arise in pairs or fascicles in the axil of leaf (Fig. 1 A). The flowers are protogynous. They are erect but become pendulous during dehiscence of anther and always face the dorsal surface of leaves (Fig. 1 A). The only insect observed to be active in pollination is bee. It takes almost an year for a bud primordium to develop into a mature fruit. The flower is actinomorphic, tetramerous, bisexual and rusty tomentose (Fig. 1 B). There are eight long, elliptic and acute sepals (Fig. 1 D, E) arranged in two whorls of four each (Fig. 2 A, B).

The corolla is gamopetalous (Fig. 1 C) with eight white, lanceolate lobes (Fig. 1 F). Each lobe has a pair of dorsal appendages (Figs. 1 B, 2 A) which except for their acute apex are almost similar to the lobe itself (Fig. 1 F, G).

The androecium consists of an outer whorl of eight alternisepalous

Fig. 2. *Mimusops elengi* (*an*, anther; ap_1, ap_2, appendages; *ov*, ovule, *oy*, ovary; *p*, petal; se_1, se_2, sepals of outer and inner whorl, respectively; *sm*, staminode; *st*, style). — A: Longisection of flower to show vascular supply to various floral whorls. — B: Transection of flower showing disposition of floral parts. — C: Transection of ovary to show its chambered nature. — D: Longisection of bud; outline diagram for F—I. — E—I: Progressive stages in the development of hair. — J: Whole mount of a hair on ovary; the arms are unequal. — A×13, B—C×26, D×31, E—I×300, J×135.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stamens (Fig. 2 B) and inner two whorls of eight alternipetalous staminodes (Fig. 2 B). Both stamens and staminodes are epipetalous (Fig. 1 C). Numerous hairs are present on the filament, connective and staminode (Fig. 1 H).

The gynoecium is octacarpellary, syncarpous with a long style terminating in a capitellate stigma (Fig. 1 I). The ovary is pubescent, superior, octalocular with axile placentation (Fig. 2 C). Each locule has a single basally affixed ovule (Fig. 2 A). There are eight stylar canals at the base of the style which continue upwards into the stigma and downwards into the locules. Each canal is lined by a single layer of transmitting tissue whose cells are rectangular, densely cytoplasmic with conspicuous nuclei. These cells in the region of the stigma become papillate and are directed upwards.

The fruit is a one- (rarely two) seeded berry (Fig. 1 L) with persistent calyx (Fig. 1 J, K). The ellipsoidal and compressed seed has a small, circular basal seed scar (Fig. 1 M). The endosperm is copious (Fig. 1 L). The flat foliaceous cotyledons are as wide as the seed.

Abundance of thick-walled, unicellular two-armed hairs on all the floral parts, except corolla, is a constant feature of this plant (Fig. 2 D—J).

Development of Hair

The hair is epidermal in origin. As growth proceeds the outer wall of the epidermal cell elongates and bifurcates near the outer tangential wall (Fig. 2 E). The arms elongate parallel to the epidermis (Fig. 2 F). The length of the two arms may vary. The hairs on the ovary are characteristic as they have one arm much longer than the other (Fig. 2 J). Meanwhile the hair stalk increases in length after which a thick secondary wall is deposited. The nucleus usually degenerates by this time. While this hair is developing another cell in its vicinity may act as hair initial (Fig. 2 E, F). Such a condition results in the formation of sheets of hairs — arms of old hairs overlapping those of young hairs (Fig. 2 H). In older fruits the hairs formed later are comparatively smaller in size.

Microsporangium

In a young anther, which is somewhat rectangular in cross section (Fig. 3 A), a plate of hypodermal cells differentiates as archesporial cells. Each archesporial cell divides into a primary parietal cell and a

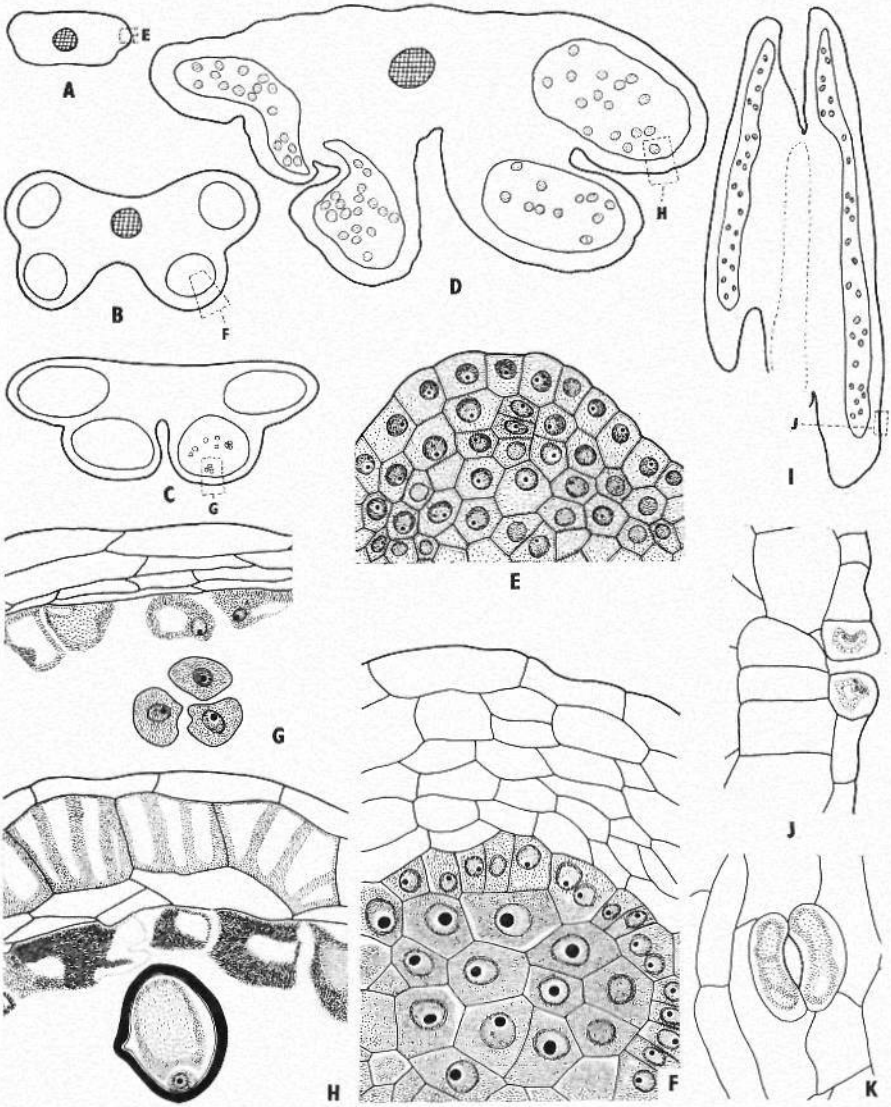

Fig. 3. *Mimusops elengi*. — A—D: Transections of anther at different stages of development. — E: Magnified view of sector *E* in A to show primary parietal cell and primary sporogenous cell. — F—G: Enlarged view of portions *F* and *G* in B and C showing wall layers at microspore mother cell and tetrad stages, respectively. — H: Portion *H* enlarged from D to show flattened epidermis, fibrous endothecium and degenerating middle layers, and tapetum. — I: Longisection of anther; outline diagram for J. — J: Enlarged view of sector *J* in I to show stoma on anther lobe. — K: Surface view of stoma on anther connective. — A—D×70, E—H×700, I×35, J—K×700.

primary sporogenous cell (Fig. 3 E). The former further divides periclinally and gives rise to the wall of the anther, whereas the latter undergoes a few divisions in various planes to form microspore mother cells (Fig. 3 B, F).

Initially the epidermis keeps pace with the growth of inner tissue but later its cells become vacuolated and tangentially compressed. Fibrous thickenings develop in the endothecial cells at two-celled stage of pollen grains (Fig. 3 H); similar thickenings may also develop in the connective cells lying adjacent to the endothecium. The middle layers begin to degenerate before fibrous thickenings develop in the endothecium (Fig. 3 C, G) but their remnants persist in the ripe anthers (Fig. 3 D, H).

At microspore mother cell stage the tapetal cells become bi- (Fig. 3 F) or tetranucleate (Fig. 4 A—C); the nuclei fuse to form polyploid masses (Fig. 4 D). The tapetal cells remain healthy till microspores separate but degenerate *in situ* by the time the pollen grains become 2-celled (Fig. 3 H). Thus, the tapetum is of the secretory type. Occasionally in some anthers when microspore tetrads are formed a few of the tapetal cells enlarge from 10 μ×20 μ to 105 μ×53 μ. (Fig. 4 E, F) with the result that the tetrads get crushed. The hypertrophied tapetal cells show larger nuclei and vacuolated cytoplasm. The number of nuclei varies from two to seven. Such anthers are sterile.

The epidermis shows the presence of anomocytic stomata both on anther lobes (Fig. 3 I, J) and connective (Fig. 3 K).

Microsporogenesis and Male Gametophyte

The reduction divisions in the microspore mother cells are normal (Fig. 4 G—M) and nonsynchronous. The cytokinesis is simultaneous resulting in tetrahedral (Fig. 4 O, Q), decussate (Fig. 4 N, P) or more commonly isobilateral tetrads. The nucleus of uninucleate pollen grains, after moving towards the periphery (Fig. 4 R), divides to form a large vegetative and a small generative cell (Fig. 4 S). The pollen grains are shed at 2-celled stage. They are of various sizes and may be bi-, tri- or tetracolporate with a thick, slightly reticulate exine and a thin intine (Fig. 4 T).

Megasporangium

The ovule is anatropous, unitegmic and tenuinucellate (Fig. 5 F). It develops as a small protuberance on the placenta (Fig. 5 A) and begins

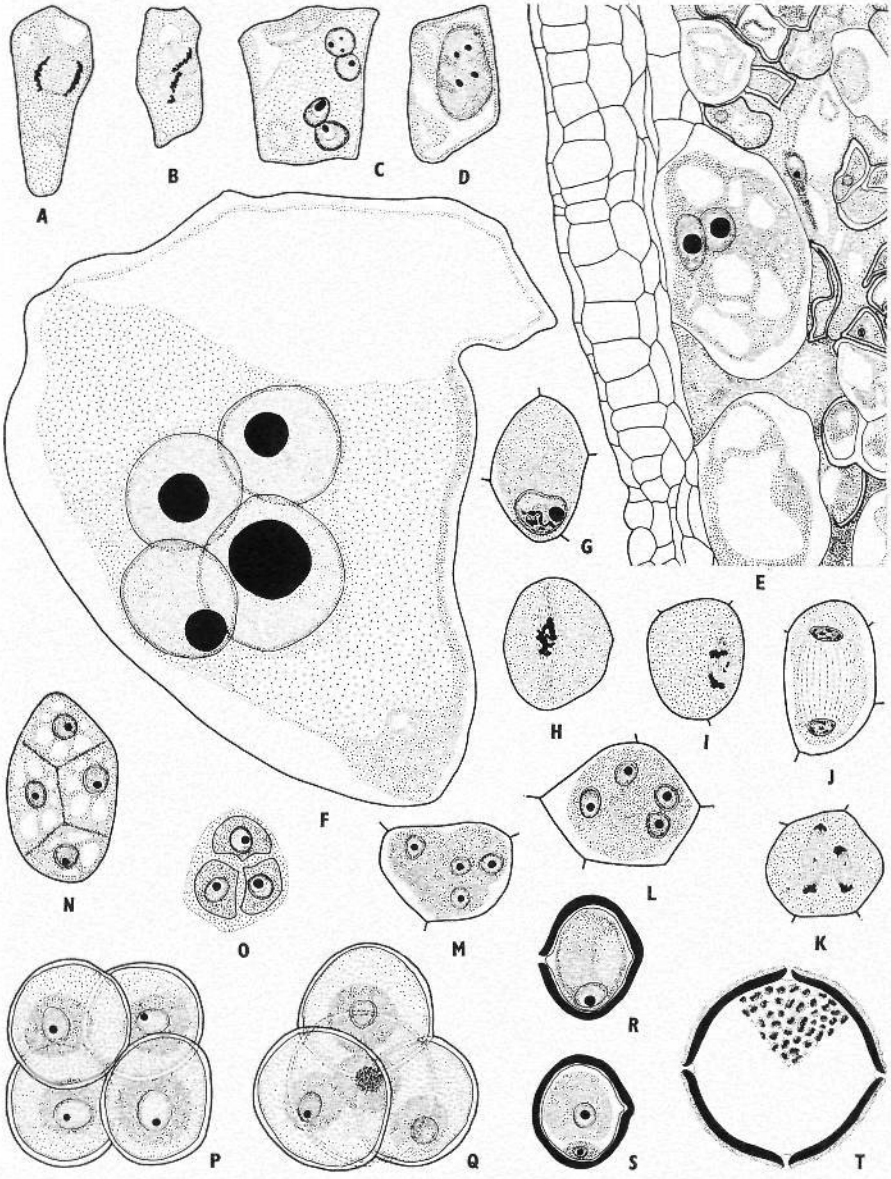

Fig. 4. *Mimusops elengi*. — A—D: Tapetal cells showing mitosis and polyploid nucleus. — E: Portion of longisection of anther to show hypertrophied tapetal cells and crushed microspore tetrads. — F: A hypertrophied tapetal cell. — G—M: Meiosis I and II. — N: Initiation of cytokinesis to form decussate tetrad. — O: Tetrahedral tetrad. — P—Q: Decussate and tetrahedral tetrads prior to liberation of microspores. — R: Uninucleate pollen grain. — S: Two-celled pollen grain. — T: Acetolyzed pollen to show reticulate exine. — A—D×1035, E×345, F×1035, G—T×670.

to curve at an early stage (Fig. 5 B) until it becomes anatropous (Fig. 5 C, D). The integumentary primordium starts developing after the differentiation of archesporial cell (Fig. 5 C) and envelops the nucellus at the megaspore mother cell stage forming a long and narrow micropyle (Fig. 5 E). The ovule rotates further so that the micropyle faces the funiculus. During rotation the micropyle becomes obliquely oriented (Fig. 5 F). The vascular trace to the ovule enters the funiculus and reaches almost the tip of the integument (Fig. 5 F).

The integumentary cells lining the embryo sac may become filled with tannin-like substance. An endothelium is not organized (Fig. 7 A, B). In some of the ovules, below the chalazal region of embryo sac, appears a strip of radially elongated cells. These are sparsely cytoplasmic, and can hardly be compared to a hypostase.

Megasporogenesis and Female Gametophyte

A single hypodermal cell acts as the archesporial initial (Fig. 5 G) which functions directly as the megaspore mother cell (Fig. 5 H). For a considerable time meiosis is not initiated in the megaspore mother cell, during which it increases in size (Fig. 5 I). Through meiosis (Fig. 5 J) it produces a T-shaped tetrad of megaspores (Fig. 5 K). The three micropylar megaspores are non-functional and degenerate. The nucleus of the functional megaspore undergoes three successive divisions (Fig. 5 L—N) to produce an eight-nucleate embryo sac. The development thus conforms to the Polygonum type. Sometimes the eight-nucleate embryo sac may show 2+6 arrangement of nuclei. The mature gametophyte shows two hooked and beaked synergids possessing filiform apparatus which becomes conspicuous when egg and polars are enlarging (Fig. 5 O), an egg, two polars and three ephemeral antipodal cells arranged linearly in the chalazal projection of the embryo sac (Fig. 5 N). Just beneath the egg, the polars fuse to form secondary

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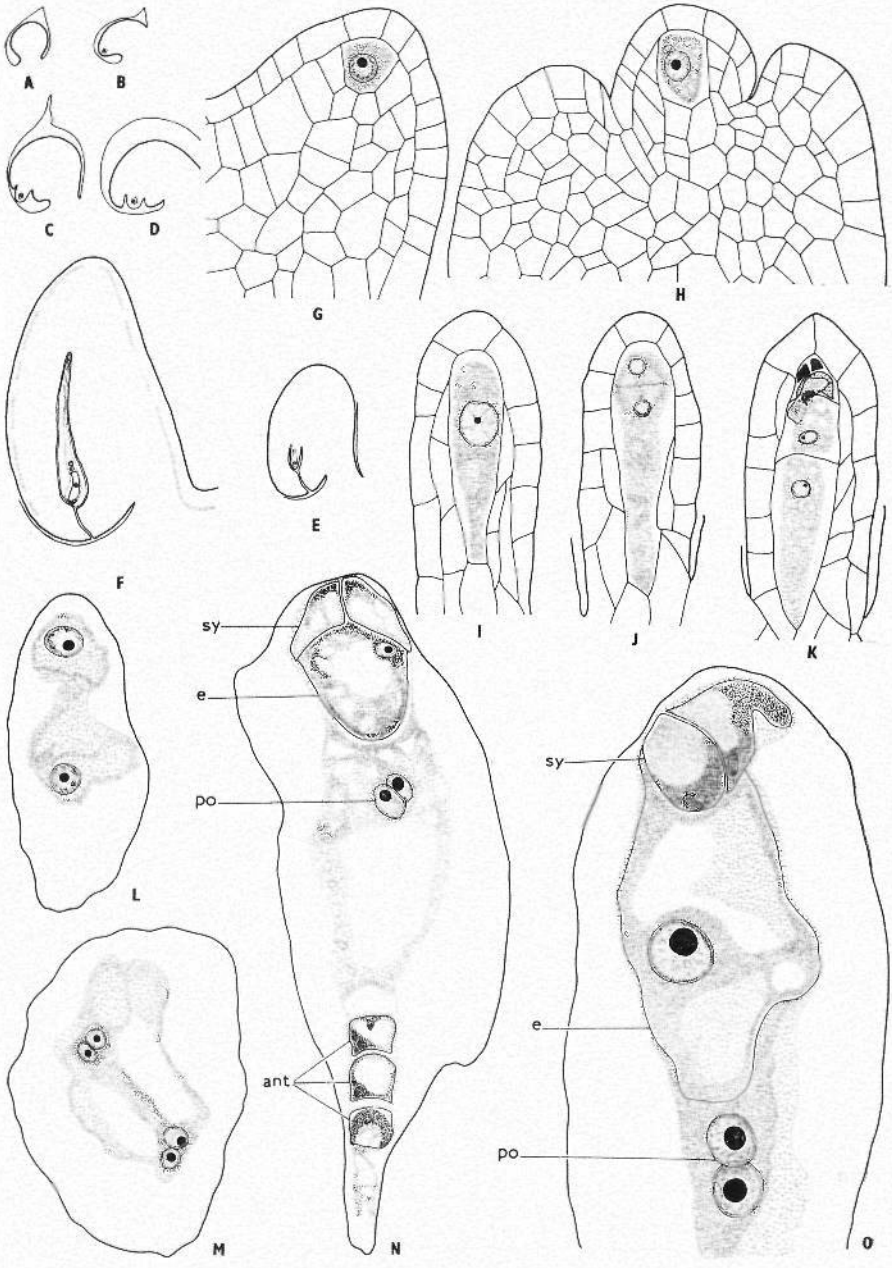
Fig. 5. *Mimusops elengi* (*ant*, antipodal cells; *e*, egg; *po*, polars; *sy*, synergid). — A—F: Progressive stages in development and curvature of ovule. Vascular supply to integument reaches almost up to the tip (F). — G: Longisection of part of ovule showing a single hypodermal archesporial cell. — H—I: Megaspore mother cells. — J—K: Megaspore dyad and tetrad, respectively. — L—M: Two and 4-nucleate embryo sacs. — N: Organized embryo sac. — O: Micropylar portion of mature embryo sac to show filiform apparatus in synergids, enlarged egg and polars. — A—F×60, G—O×555.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nucleus, the latter maintaining the same position till fertilization. After fertilization the synergids usually become displaced.

Endosperm

The primary endosperm nucleus divides earlier than the zygote (Fig. 6 A). The division of the endosperm nucleus is not followed by wall formation (Fig. 6 A—D). Thus the development is Nuclear. The divisions of endosperm nuclei are non-synchronous and produce more than a thousand nuclei. At this stage, cytoplasm starts aggregating around the peripheral nuclei present at the micropylar end. The cell formation is centripetal and begins from micropylar to chalazal end. Ultimately, the entire endosperm becomes cellular (Fig. 6 E). The endosperm cells are small towards the periphery but large in centre. These cells accumulate fat as reserve food material (Fig. 6 F).

Embryology

There is a time lapse between fertilization and division of the zygote. The zygote divides later than the division of the primary endosperm nucleus (Fig. 6 A).

The earliest stage available was an eight-celled proembryo (Fig. 6 C, G). It undergoes both anti- and periclinal divisions (Fig. 6 H) resulting in a large globular embryo (Fig. 6 I). Localized meristematic activity at two points in the apical region of globular embryo (Fig. 6 J) results in the formation of a heart-shaped embryo (Fig. 6 K). Further activity gives rise to 2 cotyledons (Fig. 6 L). The embryo has a large massive suspensor (Fig. 6 I—L). The cells of the suspensor are bloated, uninucleate and of various sizes. As the cotyledons enlarge the suspensor degenerates (Fig. 6 M). The mature cotyledons are flat, folia-

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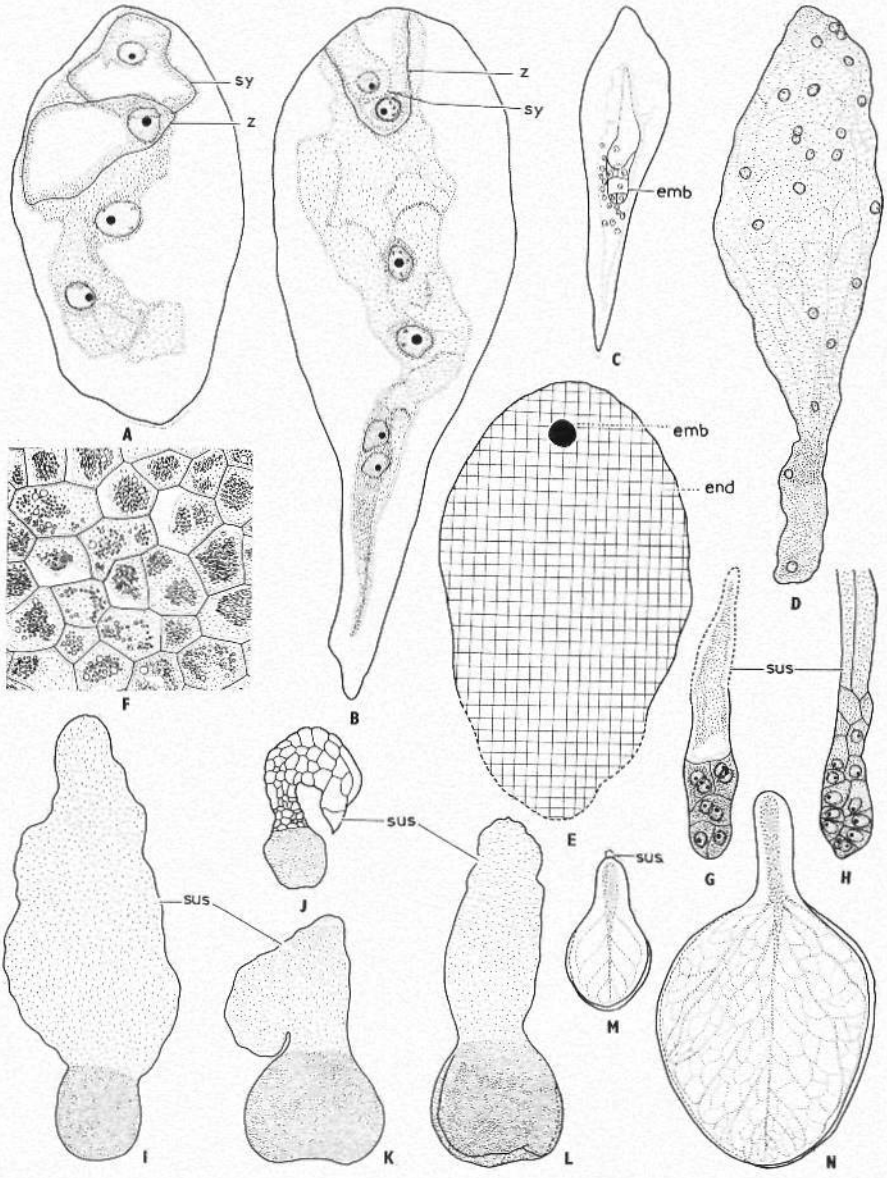
Fig. 6. *Mimusops elengi* (D—E, I, K—N are from whole mounts, rest from microtome sections. *emb*, embryo; *end*, endosperm; *sus*, suspensor; *sy*, synergid; *z*, zygote). — A: Two-nucleate endosperm, one of the persistent synergids seen. — B: Four-nucleate endosperm. — C: Longisection of young seed at 16-nucleate endosperm stage. — D: Free nuclear endosperm; embryo was probably lost during dissection. — E: Cellular endosperm with globular embryo. — F: A few endosperm cells enlarged to show oil globules. — G—H: Young proembryos. — I—L: Globular, heart-shaped and dicotyledonous embryos; note massive suspensor. — M—N: Young and mature dicotyledonous embryos showing vasculature. — A—B×565, C—D×130, E×30, F×130, H×270, I—L×60, M—N×6.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ceous with reticulate venation (Fig. 6 N). A small root cap protects the radicle. Plumule is very small and is present inbetween the two cotyledons. The cells of cotyledons accumulate fat though its amount is lesser than that in the endosperm. A para-cotyledonary section of a mature seed reveals an embryo almost reaching the expanse of seed and surrounded by endosperm. The short radicle fits into the narrow groove of copious endosperm.

Testa

At the mature embryo sac stage, the integument is about 15-layered (Fig. 7 A, B). A few cells in the chalazal region, just below the epidermis, show accumulation of tannin. By this time nucellus is completely consumed.

At free-nuclear stage of endosperm, the testa becomes nearly 25 to 30-layered. About six layers of cells accumulate tannin (Fig. 7 C). The accumulation starts from chalazal to micropylar region.

As the seed matures, the tannin-filled cells are transformed into sclereids (Fig. 7 D) which have characteristic thick and lignified walls with branched pit canals and narrow lumen. The lumen is completely filled with tannin. Meanwhile, tannin continues to accumulate in the inner layers followed by their gradual sclerification. Finally, when the seed is mature, the entire integument becomes sclerified.

Pericarp

The ovary wall, at mature embryo sac stage, comprises about 25 to 35 layers of compactly arranged parenchymatous cells. Numerous latex sacs and tannin-filled cells are interspersed in parenchymatous tissue. Tannin may completely fill the cells of outer and inner epidermis (Fig. 8 A).

At preglobular stage of embryo, the pericarp shows increased number of layers. The parenchyma cells undergo divisions in various planes to form 35 to 40-layered tissue (Fig. 8 B). About seven layers subjacent to the inner epidermis, have a characteristic tiered arrangement of cells. Also, about five rows underlying outer epidermis consist of compactly arranged cells which simulate cork (see RENDLE 1925). At places alternate rows of these cells accumulate tannin. As the embryo becomes globular 2 or 3 layers inner to 'cork' enlarge (Fig. 8 C). Cytoplasm starts receding from walls but nuclei remain conspicuous. As a result

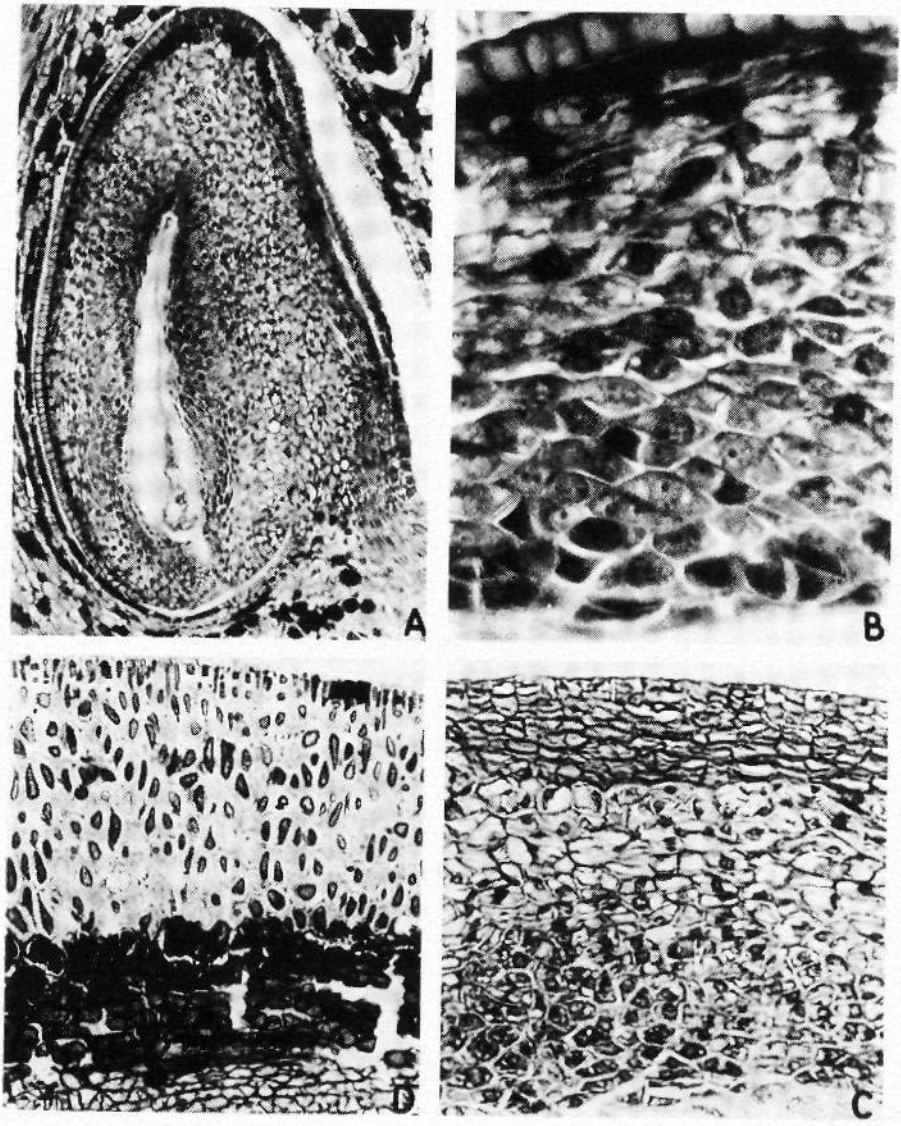

Fig. 7. *Mimusops elengi* (Photomicrographs) — A: Longisection of ovule at mature embryo sac stage. — B: Portion of integument from A enlarged, innermost layer is not organized into endothelium. — C: Same at free nuclear stage of endosperm to show a few of the outer layers filled with tannin. — D: Portion of longisection of seed at cellular stage of endosperm showing outer zone of sclerified cells, middle zone of tannin-filled cells and innermost zone of parenchymatous cells. — A×93, B×716, C×233, D×92.

of enlarging of these cells, the inner cells get crushed. Sclerification starts first in cells which are at the base of the fruit. At the late globular stage of embryo, rows of sclereids are formed (Fig. 8 D). Sclereids are thick-walled with branched pit canals and narrow lumen. A few layers internal to the inner epidermis get crushed.

When the embryo has become dicotyledonous a very thick cuticle is deposited throughout the surface of fruit. 'Cork' layers accumulate more tannin and about 15 underlying layers become sclerified. Parenchyma cells increase in size.

Thus the fruit has three zones: (a) the outermost zone consists of an outer epidermis, 'cork' and sclereids, (b) the middle zone of parenchymatous tissue, and (c) innermost zone of inner epidermis and some subjacent layers.

DISCUSSION

The available morphological and embryological data on the family *Sapotaceae* are discussed in the light of present observations on *Mimusops elengi*.

The corolla of *Sapotaceae* is gamopetalous consisting of a corolla tube and one or two whorls of 2—5 or more lobes. In several genera each lobe bears a pair of lateral or dorsal appendages. The appendages in *Mimusops elengi* have been described as dorsal by RENDLE (1925), LAM (1941) and WILLIS (1966), and lateral by MEEUSE (1960). However, the present observations on this plant support the former view. The vascular supply to the corolla lobe branches near its base. One of the branches enters the lobe, whereas the other bifurcates, one trace entering each appendage.

The ovules may be anatropous or hemianatropous (WARMING 1913; MURTHY 1941) and obliquely oriented, or orthotropous (WARMING 1913). The single vascular bundle in the raphe gives off branches which supply the thick integument. The ovules in *Mimusops elengi* are anatropous with obliquely oriented micropyle. The vascular supply to the ovule does not stop at chalaza but reaches almost up to the tip of the integument.

According to MURTHY (1941) in *Achras sapota* L. and *Manilkara hexandra* (ROXB.) DUB. there is no endothelium but in *Madhuca indica* GMEL., (*Bassia latifolia* ROXB.) and *Mimusops elengi* there is a tendency towards its differentiation. The integumentary tapetum is normally

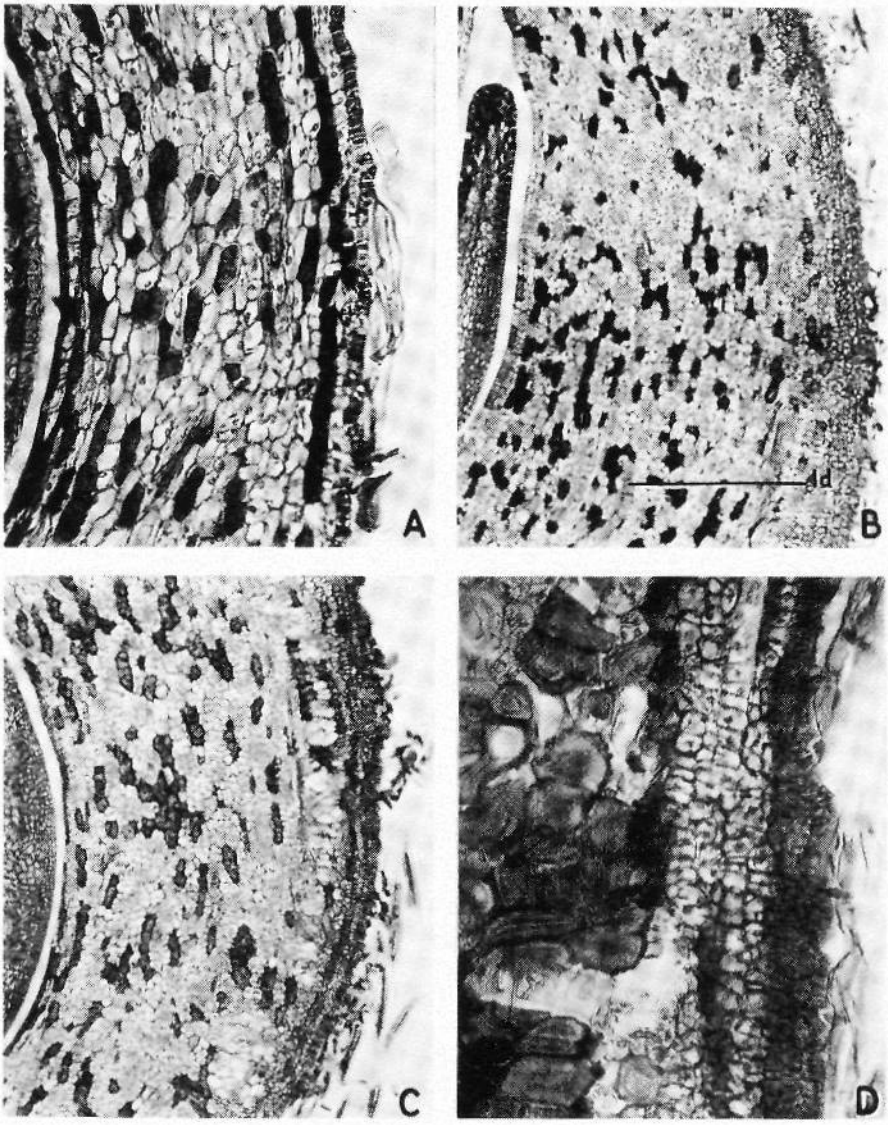

Fig. 8. *Mimusops elengi* (Photomicrographs, *ld*, laticiferous duct). — A: Portion of ovary wall (longisection) at mature embryo sac stage. — B: Same at a slightly older stage to show 'cork' and laticiferous ducts. — C: Pericarp at globular stage of embryo to show enlarged cells beneath 'cork'. — D: Outer zone of pericarp showing 'cork' and sclereids. — A×118, B—C×61, D×274.

characterized by radially elongated, densely cytoplasmic cells with prominent nuclei. Since in *Mimusops elengi* the innermost layer of integument lacks all these features, it would be incorrect to call this layer as endothelium.

MURTHY (1941) observed a distinct hypostase in *Madhuca indica* and *Mimusops elengi*, and a poorly developed hypostase in *Achras sapota*. In *Manilkara hexandra* he found that the cells at the chalazal end become loose and large after fertilization and probably have a nutritive role. In *Mimusops* we have observed in some ovules a strip of cells below the embryo sac. These cells are radially elongated and sparsely cytoplasmic. Since this is not a regular feature of the plant, this mass of cells need not be designated as hypostase.

In *Achras*, *Madhuca*, *Manilkara* and *Mimusops* the antipodal nuclei have been reported to disappear before the organization of the embryo sac (MURTHY 1941). However, we find that, although ephemeral, the antipodal cells are organized and are linearly arranged at the chalazal end.

MURTHY (1941) reported the absence of filiform apparatus in synergids of *Madhuca*. The present work, however, reveals its presence. It is likely that on reinvestigation other genera may also show filiform apparatus. According to MURTHY (1941), in *Achras sapota* the division of the primary endosperm nucleus takes place later than that of the zygote. On the other hand, our observations show that in *Mimusops* primary endosperm nucleus divides earlier than the zygote. The endosperm is Nuclear and wall formation is much delayed. Nearly a thousand nuclei are formed before walls are laid down.

Members of *Sapotaceae* are economically important, and unfortunately, there is not much work on the morphology and embryology of these plants. Although the plants flower profusely, seed set is relatively low. Detailed studies leading to a fuller understanding of the embryology and seed formation in these plants should prove very rewarding.

ACKNOWLEDGEMENTS

We are grateful to Professor B. M. JOHRI for his keen interest and constant encouragement. To Dr. N. N. BHANDARI we are obliged for his valuable suggestions.

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Miscellaneous Notes on Algal Taxonomy and Nomenclature III

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ABSTRACT

DIXON, P. S. and IRVINE, L. M.: Miscellaneous Notes on Algal Taxonomy and Nomenclature III. — Bot. Notiser 123: 474—487. Lund.

1. Typification of the genus *Scinaia* BIVONA shows that the correct name for the type species of the genus is *S. forcellata* BIV.
2. The conservation of *Grateloupia* C. AGARDH (1822) [*Cryptonemiales*] against *Grateloupia* BONNEMAISON (1822) [*Ceramiales*] is proposed.
3. The typification of *Halymenia latifolia* CROUAN FRAT. ex KÜTZ. is discussed.
4. The use of the generic name *Polysiphonia* by SPRENGEL (1827) is discussed in detail.
5. The correct name for *Dasya pedicellata* (C. AG.) C. AG. is shown to be *D. baillouviana* (GMEL.) MONT.
6. A possible record of the occurrence of *Dasya baillouviana* in Britain is rejected and the time at which the immigration of this species into Europe occurred is considered.

INTRODUCTION

The following notes refer to further taxonomic and nomenclatural problems detected during preliminary work for the forthcoming "Flora of British Marine Algae".

THE TYPIFICATION OF THE GENUS SCINAIA BIVONA

The genus *Scinaia* was first described by Baron A. BIVONA-BERNARDI in 1822. Contrary to the remark by SETCHELL (1914 p. 80) that no diagnosis or discussion of *Scinaia* as a genus is given, BIVONA does in fact say "Scinaia, algarum marinarum novum genus. Tubi extus glabri, intus filamentosi, gelatina solidiuscula repleti, filamentis centro intertextis

in funiculum axiforme. Capsulae tuborum parieti interno adhaerentes." BIVONA then proceeds to describe the single species which he referred to the genus: *Scinaia forcellata*. The specific epithet is taken from IMPERATO's "*Forcellata*", (1599 p. 736) and from his *Fucus forcellata*, "Cup. Pamph. 3 t. 105". This latter publication has not been located. The name is spelled *forcellata* throughout the paper and has no connexion with TURNER's *Ulva furcellata* (TURNER 1801), despite the fact that the two entities are conspecific. Consequently, it cannot be accepted that BIVONA made the combination *Scinaia furcellata* (TURN.) BIV. as has been generally assumed.

J. AGARDH (1852), quoting both *Ulva furcellata* TURN. and *Scinaia forcellata* BIV., made the combination *Scinaia furcellata* (TURN.) J. AG. The epithets *forcellata* and *furcellata*, however, have the same derivation and ought, therefore, to be treated as mere orthographic variants. [In fact BIVONA's *forcellata* is usually mis-spelled *furcellata* in the literature and the epithets have been the source of much confusion.] In this case *Scinaia furcellata* (TURN.) J. AG. must be rejected as a later homonym of *Scinaia forcellata* BIV., based upon a different type. The correct name of the type species of the genus *Scinaia* is thus *S. forcellata* BIV., not *S. furcellata* (TURN.) J. AG. as is given by SCHMITZ (1889) and KYLIN (1956). The type of *Scinaia forcellata* is BIVONA's materials, the localities for which he gives as "ad litora maris ab undis rejecta hiem et vere prope Panormum et Neapolim reperitur." The whereabouts of BIVONA's material is not at present known, but his illustration is reasonably good and can be taken as typifying the species, at least temporarily.

Two species of *Scinaia* have been reported in Europe, *S. turgida* CHEMIN and *S. furcellata* (TURN.) J. AG., and it is essential to determine to which of these entities *S. forcellata* BIV. refers. The figure given by BIVONA is a representation at natural size of his plant, with some anatomical details at a slight magnification. On the basis of the height of the plant, the breadth of the axes, the orientation of branch insertion, the frequency of branching and the infrequency of carposporophytes it can be stated that *S. forcellata* BIV. is conspecific with the plant known previously as *S. furcellata* (TURN.) J. AG.

CONSERVATION OF GRATELOUPIA

C. AGARDH established a new genus in 1822, naming it in honour of the French botanist J. P. A. G. GRATELOUP, and this has been accepted

by all subsequent workers. Three species were referred to the genus in the initial treatment: *Grateloupia ornata*, *G. hystrix* and *G. filicina*. Of these, only the last is retained in the genus today, *G. ornata* having been referred to *Chaetangium* (PAPENFUSS 1951) and *Grateloupia* transferred to *Gigartina* (SETCHELL & GARDNER 1933). Unfortunately, in the same year as C. AGARDH established his genus, BONNEMAISON described a second genus naming it *Grateloupia* also.

The dating of the various parts of the 'Species algarum' of the elder AGARDH is complex. NORDSTEDT (1914) showed that the first part of volume I was not issued until late 1820 in Lund, a second issue with new title page appearing in the following year in Greifswald, but he gave no information on the dating of the second part of that volume, the portion relevant to the present discussion. Although evidence is by no means complete, the second part appears not to have been issued prior to late 1822 in Lund. No reference to this part prior to December 1822 has been discovered personally in the literature or in AGARDH's correspondence. According to STAFLEU (1967), the second part was issued in two portions, with pages 169 to 398 appearing probably in November 1822 and pages 399 to 531 in 1823. In addition to the Lund issue, there was a re-issue with new title-page from Greifswald in 1823.

The dating of BONNEMAISON's publication is much easier. The paper appeared in two parts of which the second, containing the description of *Grateloupia* BONNEMAISON, was published in the issue of the 'Journal de Physique' for the month of April 1822, and was acquired by the Library of the Academy of Sciences between June 17th and 24th, 1822 (see P. V. Acad. Sci. Paris 7 p. 339).

There seems little doubt that *Grateloupia* BONNEMAISON antedates *Grateloupia* C. AGARDH. Since the former is a name never used except by its originator, whilst the latter is a well-known name for a widely distributed genus of some commercial importance, after which a family has been established, conservation of *Grateloupia* C. AG. is, therefore, fully warranted.

BONNEMAISON typified his new genus with *Conferva arbuscula* DILLW. Although the two treatments by DILLWYN (1807, 1809) confused representatives of the genera *Callithamnion* and *Dasya* (cf. DIXON 1960, 1964) and it has been shown that the epithet *arbuscula* must be applied to the former, BONNEMAISON's account clearly indicates that his description is based upon the *Dasya* component of DILLWYN's treatment. *Grateloupia* BONNEMAISON (1822) antedates *Dasya* C. AGARDH (1824) nom. cons. [T.: *D. pedicellata* (C. AGARDH) C. AGARDH] and should be

added as a nomen rejiciendum as it is a taxonomic synonym based on a different type [T.: *G. arbuscula* BONNEMAISON (*Conferva arbuscula* DILLWYN pro parte, quoad Suppl. pl. G)].

THE TYPIFICATON OF HALYMENIA LATIFOLIA

The alga now known as *Haymenia latifolia* was first recognized in northwest France by H. M. and P. L. CROUAN. Although a species of relatively rare occurrence, it was collected in sufficient quantity for specimens to be distributed in November 1849 under that name, as number 191 of the exsiccata 'Algues de l'Ouest de la France' of JAMES LLOYD (see DIXON 1967). Unfortunately no description was provided so that the binomial is used there as a nomen nudum. Despite this, the name is usually attributed to the CROUANS, the exsiccatum being cited as the place of publication (e. g. DE TONI 1905). Although a description was published eventually by the brothers CROUAN (1867), this is antedated by the one which appeared in the preceding year (KÜTZING 1866) validating the binomial. KÜTZING (1866 Pl. 96) indicated that his description was based upon a specimen of LLOYD's exsiccatum in SONDER's herbarium. In view of the confusion which prevails regarding many of the flat, membranaceous members of the *Rhodophyta,* location of the original specimen examined by KÜTZING was obviously essential. This proved to be extremely troublesome and it was finally found in that part of SONDER's herbarium which was acquired by F. VON MUELLER during the nineteenth century and taken to Australia where it passed eventually to the National Herbarium of Victoria at Melbourne (MEL). Examination of collections there disclosed the presence of a specimen (MEL 10332) which, apart from the loss of about 5 cm of material from one axis, is a perfect mirror-image of KÜTZING's illustration (see Fig. 1). The locality from which the specimen was collected is cited by KÜTZING as "Brest"; the annotation on the specimen gives this more precisely as the "Anse du Dondic".

KÜTZING's illustration of the microscopic structure of this specimen, the holotype of *Halymenia latifolia* CROUAN FRAT. ex KÜTZ., though difficult to interpret, shows what appears to be a section of a carposporophyte surrounded by an internal pericarp, a feature typical of the genus *Halymenia* and distinguishing it from *Halarachnion* in which the carposporophytes are not invested in this way. In Britain, broad forms of the erect phase of *Halarachnion ligulatum* (WOODW.) KÜTZ.

have been confused with *Halymenia latifolia*, but can be distinguished by this feature since even small erect thalli of the former almost invariably bear carposporophytes.

SPRENGEL'S USE OF THE GENERIC NAME POLYSIPHONIA

Polysiphonia is a generic name first used by GREVILLE (1823) as an avowed substitute for *Hutchinsia* C. AGARDH (1817) non *Hutchinsia* R. BR. (in AITON 1812). The name is currently conserved against *Vertebrata* S. F. GRAY (1821), *Grammita* BONNEMAISON (1822) and *Grateloupella* BORY (1823). When he first used the name, GREVILLE transferred only one species to the genus, although in the following year (1824) he made further transfers. It is obvious from his comments that he planned to produce a work on the filamentous, or 'articulated', algae equivalent to his 'Algae Britannicae' (GREVILLE 1830), but this was never completed. No manuscript is known to exist, although acknowledgement was given to GREVILLE when further transfers of species to *Polysiphonia* were made by HARVEY (1833). Many of these and other later transfers are antedated by the work of SPRENGEL (1827) who was the first author to adopt the name *Polysiphonia* for the majority of the species placed by C. AGARDH in his genus *Hutchinsia* in 1824. SPRENGEL referred 27 species to *Polysiphonia*, of which 22 were new combinations: these are reprinted here, in alphabetical order, together with their present attribution if synonyms.

P. badia (DILLW.) SPRENG.
= *P. nigra* (HUDS.) BATT.

P. brodiaei (DILLW.) SPRENG.

P. coccinea (DILLW.) SPRENG.
= *Heterosiphonia plumosa* (ELLIS) BATT.

P. complanata (C. AG.) SPRENG.
= *P. virgata* (C. AG.) SPRENG. [non *P. complanata* (CLEM.) J. AG. (1863), nom. illeg. = *Pterosiphonia complanta* (CLEM.) FALKENB.]

P. deusta (ROTH) SPRENG.

P. discolor (C. AG.) SPRENG.

P. divaricata (C. AG.) SPRENG.
= *P. violacea* (ROTH) SPRENG.

P. elongata (HUDS.) SPRENG.

P. fibrillosa (DILLW.) SPRENG.

P. filamentosa (WULF.) SPRING.
= *Spyridia filamentosa* (WULF.) HARV. in HOOK.

P. foeniculacea (C. AG.) SPRENG.

P. fruticulosa (WULF.) SPRENG.

P. glomerulata (C. AG.) SPRENG.
= *Tolypiocladia glomerulata* (C. AG.) SCHMITZ in ENGLER et PRANTL

P. lepadicola (LYNGB.) SPRENG.
= *P. urceolata* (DILLW.) GREV.

P. macrocarpa (C. AG.) SPRENG.
[non *P. macrocarpa* HARV. in MACKAY (1836), nom. illeg.] This plant is of unknown attribution (cf. J. AGARDH 1863).

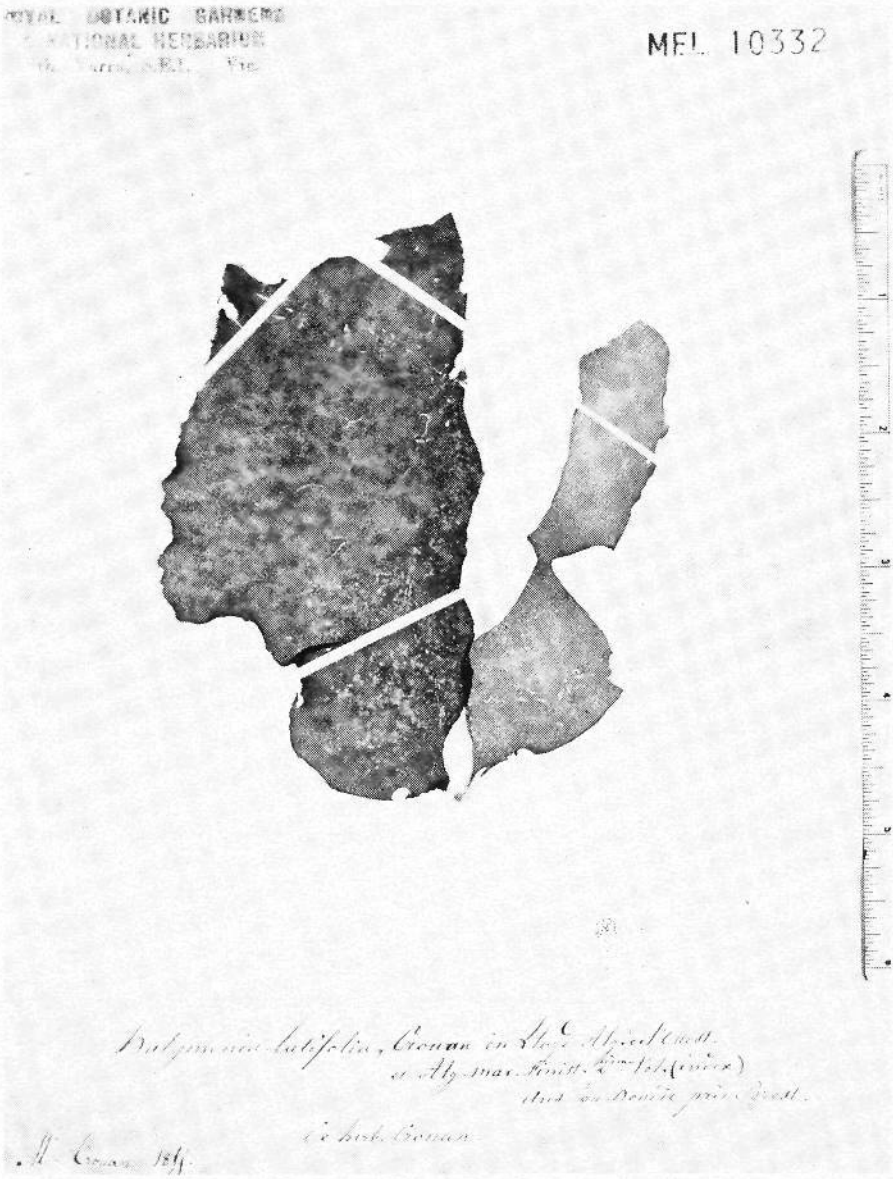

Fig. 1. The specimen of *Halymenia latifolia* used by KÜTZING for his illustration (Tab. phyc., vol. 16, pl. 96). Reduced.

P. moestingii (LYNGB.) SPRENG.
= *Pterosiphonia parasitica* (HUDS.) FALKENB.

P. penicillata (C. AG.) SPRENG.
= *P. brodiaei* (DILLW.) SPRENG.

P. pulvinata (ROTH) SPRENG.
Attribution uncertain, see comments under *Polysiphonia macrocarpa* HARV. in MACKAY (1836), below.

P. ramulosa (C. AG.) SPRENG.
= *P. opaca* (C. AG.) SPRENG. [non *P. ramulosa* HARVEY (in HOOKER 1853), nom. illeg.]

P. recurva (C. AG.) SPRENG.
The identity of *Hutchinsia recurva* C. AGARDH (1824), the basionym, is unknown. It does not appear to have been reconsidered either by the original or any other author except SPRENGEL. From the diagnosis it seems likely to be referable to *P. urceolata* (DILLW.) GREV.

P. violacea (ROTH) SPRENG.

P. virgata (C. AG.) SPRENG.

Fortunately, the data given above raise no difficulties except in connection with the name of the alga currently listed (PARKE & DIXON 1964, 1968) as *Polysiphonia macrocarpa* HARV. in MACKAY. The latter appears to be a distinct species, readily identifiable in British waters, although there have been various opinions as to the correct name which should be applied to it (cf. HARVEY 1847; BORNET 1892; DE TONI 1903), even before the discovery that its currently accepted name is illegitimate. Selection of the correct name awaits critical analysis and typification of various entities, in particular *Conferva pulvinata* ROTH (1797) and *Ceramium sertularioides* GRATELOUP (1807).

THE CORRECT NAME FOR DASYA PEDICELLATA

Dasya pedicellata, which has also been known as *D. elegans,* is widely distributed in the Mediterranean and on the Atlantic Coast of North America and there have been several recent reports of its arrival and spread in northern Europe. The alga is of very characteristic and spectacular appearance, markedly different at different stages of development. The thallus measures up to 50 cm in length and may be simple or branched. The thalli develop in the spring and early summer, during which time the axes are densely clothed with lateral filaments of limited growth. These fall away acropetally together with any tetrasporangial or spermatangial stichidia so that in the autumn the axes are naked. In female plants the developing carposporophyte induces secondary development, the resulting stalked "cystocarps" being a very prominent feature of such carpogonial material in the autumn. The superficial similarity between such a plant and a terete member of the *Gigartinales*

explains why C. AGARDH (1822) assigned such material to the genus *Sphaerococcus*.

The original treatment of *S. pedicellatus* (C. AGARDH 1822 p. 321) is based on material collected by JOHN TORREY "ad litus Noveboracense [=New York] Americae Borealis". The AGARDH Herbarium, at the Botanical Museum, Lund, now contains the following specimens received from TORREY:

(1) 44128, labelled "Hutchinsia villosa Ag. Ceramio Ocellato Gratel. Journ. de Medec. prox quod 5 plo minus Torrey misit e N. York", in C. AGARDH's hand.
(2) 44131, labelled "Torrey misit N. York", in C. AGARDH's hand.
(3) 44132, labelled "Sphaeroc. Torreyi Ag. New York misit Torrey", in pencil and "D" in ink, both in C. AGARDH's hand.

Of these three, the first (44128) is probably the best choice to serve as lectotype.

The annotation on the third specimen provides the explanation of a problem which has existed for many years. C. AGARDH received many specimens from TORREY prior to the publication of the first volume of his "Species Algarum" and one of the species described therein was named *Sphaerococcus torreyi*. The description is extremely brief and no specimens appear to have been distributed either by C. A. AGARDH or his son. As a consequence, the application of the name has been doubtful although *S. torreyi* is generally accepted as a species of *Gymnogongrus*. On the basis of his examination of a fragment in the TORREY Herbarium, however, BAILEY (1848 p. 39) claimed that *Sphaerococcus torreyi* was based on a battered specimen of the *Dasya* under consideration, a suggestion dismissed by FARLOW (1879) as "singular". SETCHELL (1905) made the first attempt to solve the problem by typification and showed that the AGARDH Herbarium contained several specimens filed at 24119 which appear to represent type material. As indicated by SETCHELL, these are annotated "New York. Torrey, in Hb. C. Agardh", in J. G. AGARDH's hand. It therefore appears that *Sphaerococcus torreyi* was based on a mixture of two components, one referable to *Dasya* and the other, as indicated by SETCHELL, to *Ahnfeldtia*.

AGARDH (1824) subsequently erected the genus *Dasya* (as *Dasia*) to receive his previously described *Sphaerococcus pedicellatus*. Three years later, MARTENS (1827) published independently a description of the taxon under the name *Rhodonema elegans*. It is not known why AGARDH should later (1828) have adopted this epithet in preference

to his own earlier *pedicellatus*, but it is as *Dasya elegans* that the species was known for many years before the priority of the earlier epithet was accepted.

There is, however, a much earlier epithet available. GRISELLINI (1750) provided an excellent pre-Linnean description of the alga under discussion as "La Baillouviana": his figure shows that there can be no question as to its identity. His publication is of such extreme rarity that a reproduction of the figure seemed desirable here (Fig. 2). ADANSON (1763) made this figure the basis for his genus *Baillouviana*, which antedates *Dasya* C. AGARDH: the latter has been conserved against *Baillouviana* (cf. SILVA 1952). S. G. GMELIN (1768 p. 165), however, referred the entity to the genus *Fucus*, as *F. baillouviana*, thus providing the earliest valid epithet for the alga. This epithet was transferred to *Dasya* by MONTAGNE (1841 p. 164) so that the correct name and authority for the species is *D. baillouviana* (GMEL.) MONT. There is no known material surviving and it would seem best to select GRISELLINI's plate as the lectotype.

DASYA BAILLOUVIANA IN NORTHERN EUROPE

There have been several reports of the naturalization and spread of this species of *Dasya* in Holland and Sweden (KOSTER 1952; DEN HARTOG 1964) which suggest that it is a potential addition to the British flora. The species has been reported from water which is shallow and somewhat foul, conditions likely to be met with in estuarine areas of the east and south coasts of England, but so far, despite searches, it has not yet been discovered. It has been assumed that the introduction into European waters occurred recently, although there are several older references in the literature, largely ignored, which report the species as having been collected in Northern Europe. These reports clearly require scrutiny, because if they are correct, they suggest that either the initial entry took place very much earlier than assumed at present or that several immigrations have occurred of which only the last has been particularly successful.

HOLMES (1883), in a discussion of Essex algae, stated that he had observed a specimen of DAVID LANDSBOROUGH's labelled "Thames River February", but commented "whether it was found on the Essex coast or not was not mentioned". By this, HOLMES implied that the material had been collected in England but questioned "is it a native

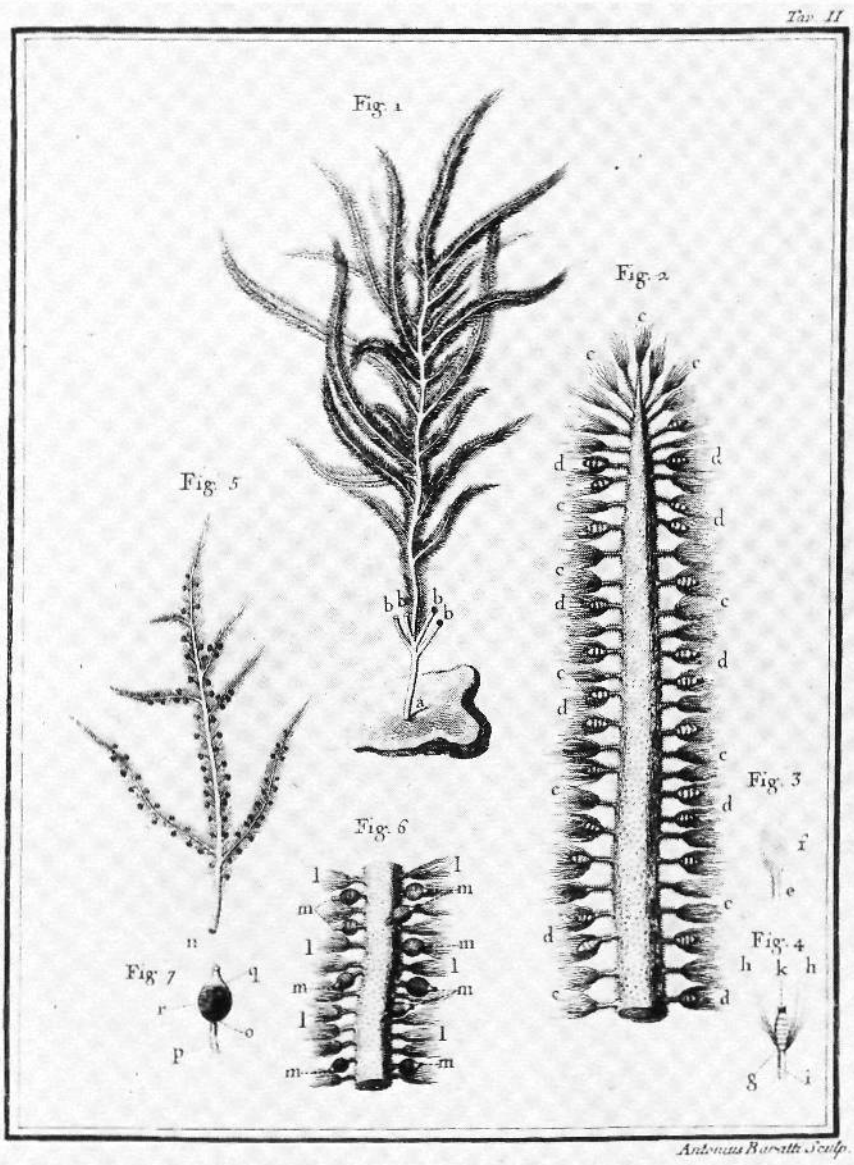

Fig. 2. The illustration of "La Baillouviana" given by GRISELLINI (1750). Slightly reduced.

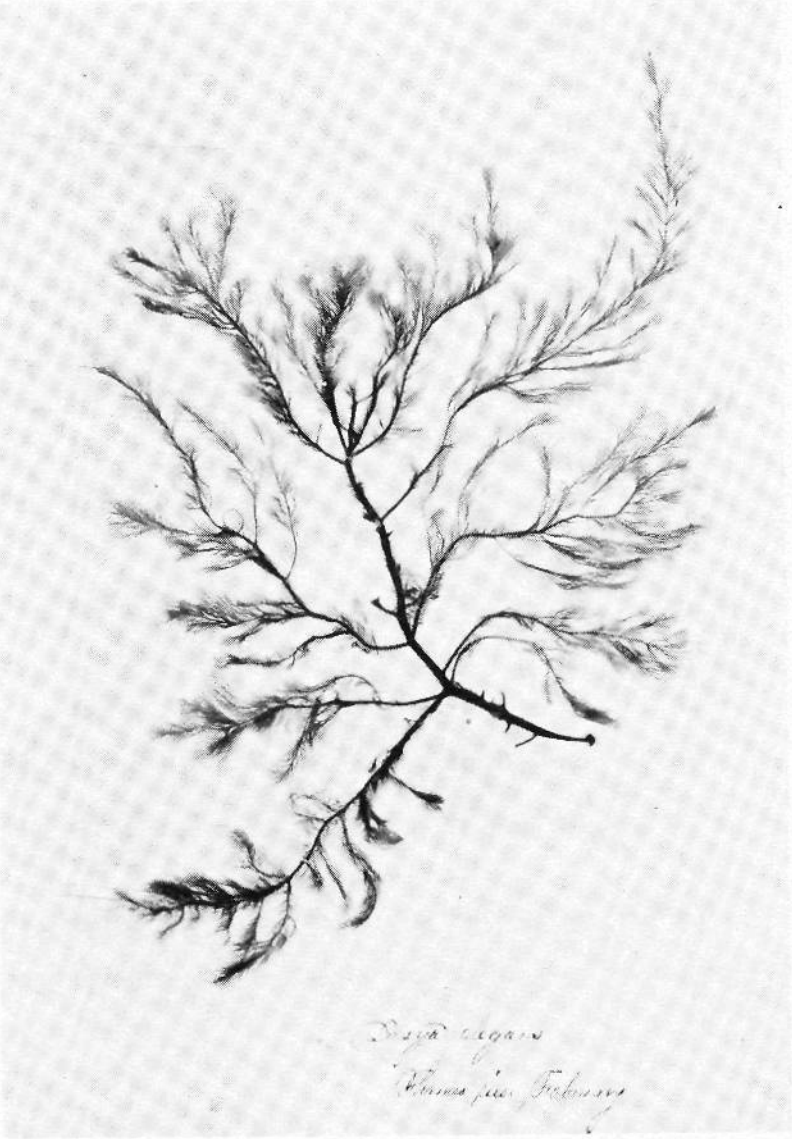

Fig. 3. The LANDSBOROUGH specimen of *Dasya baillouviana*. Natural size.

of Britain or was it merely brought here attached to a vessel". A bound volume of LANDSBOROUGH's specimens has been discovered in the Herbarium of the Royal Botanic Garden, Edinburgh. This contains a specimen of the species under consideration which is probably that mentioned by HOLMES. The annotation is difficult to decipher, but is either "Thames River February", as indicated by HOLMES, or "Thames Pier February", in an unknown hand, not that of LANDSBOROUGH (Fig. 3). The most probable explanation is that this is not a British specimen at all, but was obtained from the estuary of the Thames River, Connecticut, U. S. A., for which state the species has been collected frequently (HYLANDER 1928).

In Holland, SURINGAR (1858) reported the species from Boxmeer "In aliis Algis, Zandvoort. Jan. 1844; legit Buse". LUCAS (1950) stated that a specimen of this species of *Dasya,* attached to a fragment of *Himanthalia,* which corresponds with SURINGAR's published comments, is now preserved in the Rijksherbarium, Leiden. This specimen (Herb. Lugd. Bat. 939.69.1214) has been examined, and although filed under *Dasya pedicellata,* it is misidentified, being referable not to the entity under consideration, but to another species of the genus.

ACKNOWLEDGEMENTS

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Chromosome Numbers of Some Vascular Plants from East Africa

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ABSTRACT

THULIN, M.: Chromosome Numbers of Some Vascular Plants from East Africa. — Bot. Notiser 123: 488—494, Lund.

Somatic chromosome numbers are reported for 33 taxa of vascular plants from Cherangani Hills in Kenya. 23 of these do not seem to have been recorded previously. The counts on *Cynorkis* (*Orchidaceae*), *Sebaea* (*Gentianaceae*) and *Uebelinia* (*Caryophyllaceae*) are new generic reports.

MATERIAL AND METHODS

The material used was collected by the author and Mr. Å. TIDIGS during a collecting trip in Cherangani Hills in western Kenya in August 1968, while with the Brathay Exploration Group. Cherangani Hills is a mountain of Precambrian origin with the highest summits reaching about 3400 m. The collecting was done preferably in the upper parts of the Montane Forest Belt and in the Ericaceous Belt (HEDBERG 1951). The fixations were made in the field, utilizing chromo-acetic formalin. The counts were made on metaphase plates in paraffin sectioned root tips, stained with crystal violet and embedded in Depex. A number of metaphase plates are illustrated by camera lucida drawings.

RESULTS

The somatic chromosome numbers obtained are presented in the Table below. New counts are marked with an asterisk. Voucher specimens are preserved in the Botanical Museum, Uppsala (UPS). Further sets of most of the specimens are in the Museum of Natural History, Stockholm (S), the Kew Herbarium, London (K) and the East African Herbarium, Nairobi (EAH). The plants are collected on four different localities. The positions of these localities are respectively: Chepkotet, c. 1°15′N, 35°26′E; Kaibwibich, c. 1°13′N, 35°17′E; Kapseis, c. 1°13′N, 35°24′E; Labot, c. 1°6′N, 35°25′E.

Taxon	Voucher THULIN & TIDIGS No	2n	Locality and Altitude
RANUNCULACEAE			
**Ranunculus multifidus* FORSK.	78	32	Kapseis, 2850 m s.m.
Ranunculus oreophytus DEL.	87	32	Kapseis, 2850 m s.m.
Ranunculus volkensii ENGL.	194	80	Kaibwibich, 2550 m s.m.
FUMARIACEAE			
**Corydalis mildbraedii* FEDDE	235	16	Chepkotet, 3150 m s.m.
CARYOPHYLLACEAE			
**Stellaria sennii* CHIOV.	238	c.52	Chepkotet, 3150 m s.m.
**Uebelinia crassifolia* T. C. E. FRIES	232	c.48	Chepkotet, 3150 m s.m.
LEGUMINOSAE			
Indigofera arrecta A. RICH.	261	16	Kaibwibich, 2650 m s.m.
**Trifolium multinerve* A. RICH.	83	16	Kapseis, 2850 m s.m.
CRASSULACEAE			
**Crassula granvikii* MILDBR.	179	32	Kaibwibich, 2500 m s.m.
COMPOSITAE			
**Anthemis tigreensis* A. RICH.	203	18	Chepkotet, 3150 m s.m.
**Conyza subscaposa* O. HOFFM.	147	18	Kaibwibich, 2700 m s.m.
**Guizotia reptans* HUTCH.	68	c.60	Kapseis, 2850 m s.m.
**Haplocarpha rueppellii* (SCH. BIP.) BEAUVERD	67	30	Kapseis, 2850 m s.m.
**Helichrysum globosum* SCH. BIP.	104	14	Kaibwibich, 2650 m s.m.
**Senecio cheranganiensis* COTTON & BLAKELOCK	145	c.80	Kaibwibich, 2700 m s.m.
**Senecio hochstetteri* SCH. BIP.	195	20	Kaibwibich, 2600 m s.m.
**Senecio* sp.	217	20	Chepkotet, 3300 m s.m.
CAMPANULACEAE			
**Lobelia aberdarica* R. E. & T. C. E. FRIES	105	28	Labot, 2850 m s.m.
**Lobelia* cf. *duriprati* T. C. E. FRIES	220	26	Chepkotet, 3300 m s.m.
**Lobelia nannae* T. C. E. FRIES	198	14	Chepkotet, 3150 m s.m.
PRIMULACEAE			
Anagallis serpens DC. ssp. *meyeri-johannis* (ENGL.) P. TAYL.	221	22	Chepkotet, 3300 m s.m.
**Lysimachia ruhmeriana* VATKE	259	24	Chepkotet, 3150 m s.m.
GENTIANACEAE			
**Sebaea brachyphylla* GRISEB.	218	22	Chepkotet, 3150 m s.m.
Swertia crassiuscula GILG	206	20	Chepkotet, 3150 m s.m.
**Swertia kilimandscharica* ENGL.	91	26	Labot, 2850 m s.m.

Taxon	Voucher Thulin & Tidigs No	2n	Locality and Altitude
ORCHIDACEAE			
**Cynorkis anacamptoides* Kraenzl. ...	190	14	Kaibwibich, 2550 m s.m.
IRIDACEAE			
Dierama pendulum (L. f.) Bak.	207	20	Chepkotet, 3240 m s.m.
XYRIDACEAE			
Xyris capensis Thunb.	111	34	Labot, 2850 m s.m.
COMMELINACEAE			
Cyanotis barbata D. Don	219	20	Chepkotet, 3300 m s.m.
GRAMINEAE			
Exotheca abyssinica (A. Rich.) Anderss.	278	20	Kaibwibich, 2650 m s.m.
Koeleria capensis (Steud.) Nees	249	14	Chepkotet, 3250 m s.m
**Pennisetum schimperi* A. Rich.	277	18	Kaibwibich, 2600 m s.m.
**Sporobolus olivaceus* Napper	253	24	Chepkotet, 3300 m s.m.

DISCUSSION

Ranunculaceae

The chromosome number of *Ranunculus oreophytus* has previously been reported to 2n = c. 32 and 2n = c. 30 (Hedberg 1957). The number 2n = 32 was now obtained both for this species and *R. multifidus*. These species are closely allied, and introgressive hybridization between them has also been suspected (Hedberg 1957). On this locality they were, however, apparently keeping apart.

An approximate number 2n = c. 64 of *R. volkensii* is also reported by Hedberg (1957). My material turned out to have 2n = 80. The most common basic number in *Ranunculus* is x = 8, so the plant apparently represents a decaploid level in the polyploidy series with that basic number.

Leguminosae

The somatic number 2n = 16 for *Indigofera arrecta* has been reported several times previously (Darlington & Wylie 1955; Frahm-Leliveld 1957, 1960).

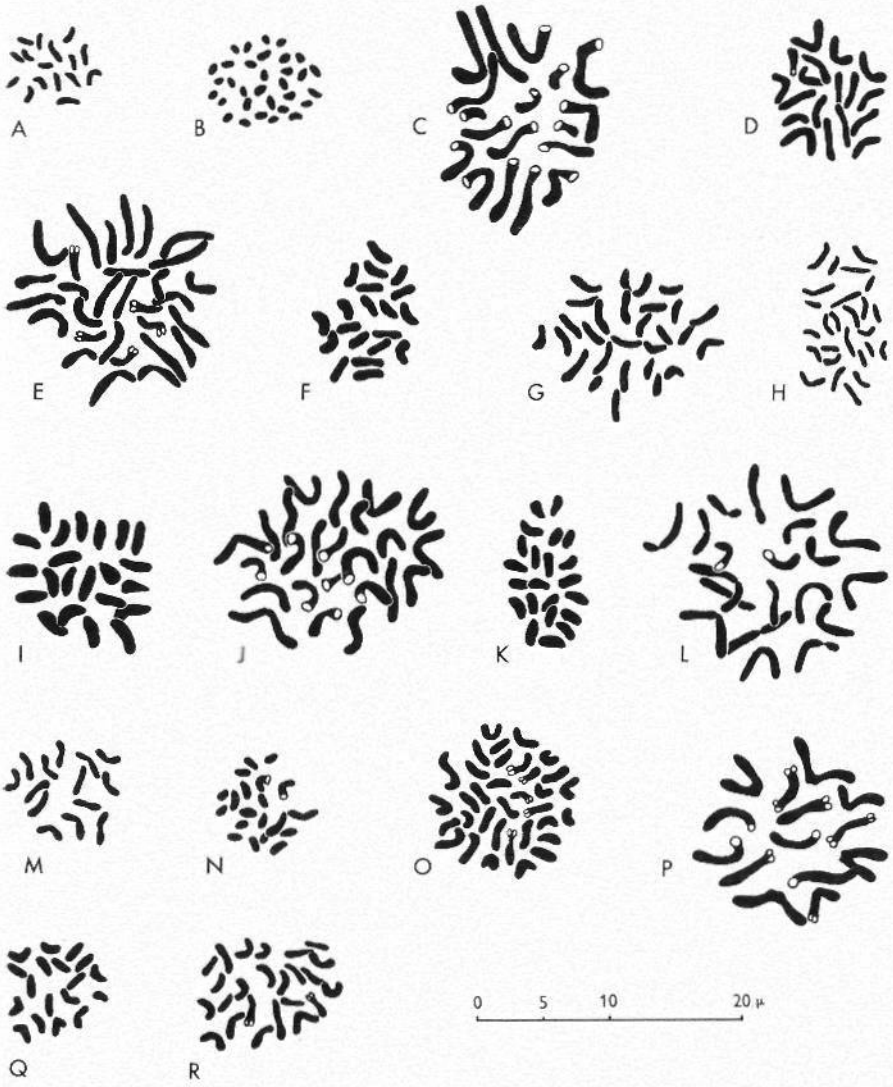

Fig. 1. Somatic metaphase plates of East African vascular plants. — A: *Corydalis mildbraedii* (2n=16). — B: *Crassula granvikii* (2n=32). — C: *Anthemis tigreensis* (2n=18). — D: *Conyza subscaposa* (2n=18). — E: *Haplocarpha rueppellii* (2n=30). — F: *Senecio* sp. (2n=20). — G: *Lobelia aberdarica* (2n=28). — H: *Lobelia* cf. *duriprati* (2n=26). — I: *Anagallis serpens* ssp. *meyeri-johannis* (2n=22). — J: *Lysimachia ruhmeriana* (2n=24). — K: *Sebaea brachyphylla* (2n=22). — L: *Swertia crassiuscula* (2n=20). — M: *Cynorkis anacamptoides* (2n=14). — N: *Dierama pendulum* (2n=20). — O: *Xyris capensis* (2n=34). — P: *Koeleria capensis* (2n=14). — Q: *Pennisetum schimperi* (2n=18). — R: *Sporobolus olivaceus* (2n=24).

Compositae

The only chromosome number previously reported from the genus *Guizotia* seems to be 2n=30 for *G. abyssinica* (L. f.) Cass. (Darlington & Wylie 1955).

The gamophytic number n=9 for *Haplocarpha scaposa* Harv. is the only one known from the genus before (Turner & Lewis 1965). The count 2n=30 for *H. rueppellii* adds a new basic number for the genus viz. x=15.

No exact count exists for the East African giant Senecios. Hedberg has estimated 2n=c. 80 for *Senecio barbatipes* Hedb. (Hedberg unpubl.), and this material of *S. cheranganiensis* does not permit a more definite count.

Campanulaceae

The count 2n=28 for *Lobelia aberdarica* is in agreement with the numbers of some other African giant Lobelias (Hedberg 1957).

The chromosome number of *Lobelia* cf. *duripratii* was clearly counted to 2n=26. The genus *Lobelia* otherwise seems to have a very constant basic number of x=7, and the somatic number 26 has probably arisen through secondary reduction. A similar case has recently been reported to occur on diploid level, where 2n=12 was recorded for *L. coronopifolia* L. (Nordenstam 1969).

Primulaceae

The very variable taxon *Anagallis serpens* ssp. *meyeri-johannis* apparently contains a number of different chromosomal strains (Hedberg 1957). He reports the numbers 2n=c. 20, 2n=20, 2n=22, 2n=c. 60–64 and 2n=c. 66.

Gentianaceae

The number 2n=20 for *Swertia crassiuscula* is in agreement with a previous count (Hedberg 1957).

Orchidaceae

2n=14 for *Cynorkis anacamptoides* is a new generic report. The number does not seem to be known for any orchids before, even if x=(7), 14 is the basic number of several other genera.

Iridaceae

2n=20 for *Dierama pendulum* is a confirmation of an earlier count (DARLINGTON & WYLIE 1955).

Xyridaceae

Xyris capensis THUNB. var. *schoenoides* (MART.) NIELSSON has previously been cytologically studied on material from Thailand (LARSSEN 1963). This African material of *X. capensis* shows the same chromosome number, 2n=34.

Commelinaceae

Cyanotis barbata seems to be cytologically heterogeneous. One report gives the number 2n=24 (SHARMA & SHARMA 1958) and another the gamophytic number n=11 (LEWIS 1964).

Gramineae

2n=20 for *Exotheca abyssinica* is in agreement with a previous count (TATEOKA 1965).

The somatic number 14 has previously been recorded for *Koeleria capensis*=*K. convoluta* STEUD.=*K. gracilis* PERS. var. *convoluta* (STEUD.) HEDB. (HEDBERG 1957; TATEOKA 1965).

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Apomixis and Sexuality in Hierochloë alpina (Gramineae) from Finland and Greenland and in H. monticola from Greenland

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ABSTRACT

WEIMARCK, G.: Apomixis and Sexuality in Hierochloë (Gramineae) from Finland and Greenland and in H. monticola from Greenland. — Bot. Notiser 123: 495—504. Lund.

Hierochloë alpina (SWARTZ) ROEMER & SCHULTES 2n=66 from Northern Finland developed eight-nucleate embryo sacs from unreduced initials, presumably both aposporous and diplosporous. A megaspore mother cell could be present but rarely divided. The possible development and functioning of reduced embryo sacs could, however, be inferred from both embryological evidence and earlier thin-layer chromatographical observations. — Abnormal or degenerating embryo sacs were frequent. One egg-like antipodal and one antipodal embryo were observed. Embryo sacs were very frequent in some anthers. — Additional observations were made in *H. alpina* 2n=56 and in *H. monticola* (BIGELOW) LÖVE & LÖVE, both from Greenland.

INTRODUCTION

Apomictic seed-setting has been found in the diploid *Hierochloë australis* (SCHRADER) ROEMER & SCHULTES (WEIMARCK 1967 a), in hexa- and octoploid *H. odorata* (L.) WAHLENBERG (NORSTOG 1963; WEIMARCK 1967 a), and in *H. monticola* (BIGELOW) LÖVE & LÖVE (WEIMARCK 1967 b). Tetraploid *H. odorata* has been found to set seed sexually (WEIMARCK 1967 a).

JØRGENSEN, SØRENSEN and WESTERGAARD (1958 p. 12) observed almost normal male meiosis in Greenlandic specimens of *Hierochloë alpina* (SWARTZ) ROEMER & SCHULTES. Therefore they did not assume this taxon to be apomictic, as they did in the case of *H. monticola* because of its abnormal or abortive pollen formation and its uneven chromosome number.

Hierochloë alpina and *H. monticola* resemble each other but can be differentiated by a number of morphological characters (cf. SØRENSEN 1954 pp. 6—7). *H. alpina* is reported to have the chromosome number 2n=56 by BOW-

DEN (1960 p. 551), FLOVIK (1938 p. 301), HEDBERG (1967 p. 310), JOHNSON and PACKER (1968 p. 414), JØRGENSEN, SØRENSEN and WESTERGAARD (1958 p. 12), KNABEN and ENGELSKJÖN (1967 p. 15), LÖVE and RITCHIE (1966 p. 432), SOKOLOVSKAJA (1960 p. 44; 1963 p. 49), SOKOLOVSKAJA and STRELKOVA (1960 p. 373), TATEOKA (1954 p. 46), WEIMARCK (1970 a) and ZHUKOVA (1967 p. 984). The number 2n=66 was found by WEIMARCK (1970 a), and various collections from Northern Sweden, Norway and Finland have somatic numbers from c. 56 to about 70 (WEIMARCK unpubl.). *H. monticola* is reported to have the chromosome number 2n=63 by JØRGENSEN, SØRENSEN and WESTERGAARD (1958 p. 12), LÖVE and LÖVE (in LÖVE & SOLBRIG 1964 p. 201), and WEIMARCK (1967 b, 1970 a).

AIMS, METHODS, AND GENERAL OBSERVATIONS

The purpose of this work was to investigate the embryo sac formation of *Hierochloë alpina* and to make complementary investigations on the embryo sac formation of *H. monticola* previously treated by WEIMARCK (1967 b).

Hierochloë alpina plants from Sweden, Norway and Finland were transplanted to the Botanical Gardens, Lund, in 1964. Voucher specimens have been preserved at the Department. However, the plants did not flower in culture and within a few years all had died. FLOVIK, who transplanted *H. alpina* from Spitsbergen to Tromsö, has reported similar difficulties (1938 p. 272). Early in May 1967 I therefore transplanted 18 new plants in a frozen condition from Markkina, Enontekiö parish, Finland (locality B D R, 2n=66, cf. WEIMARCK 1970 a), placing some in the Gardens in Lund, and some in the Arktisk Hus in Copenhagen where the conditions are more favourable to arctic plants. Flower buds that had been dormant since the preceding year developed in an apparently normal manner in both places and were fixed in the way described by WEIMARCK (1967 a p. 210). Seventy-one well-stained and well-orientated spikelets could be used. Additional fixations were made in the Arktisk Hus in 1968, giving another 210 spikelets. In Lund no plants survived the first winter.

Some fixations were also made in the Arktisk Hus in 1969 and 1970 from Greenlandic *Hierochloë alpina* 2n=56 plants collected in 1968 in Godthåb (locality B G A) and in the Søndre Strømfjord area (localities B G D, B G F, B G H, B G K, and B G M), giving a total of 93 well-stained and well-orientated spikelets.

As a complement to the study of apomixis in *Hierochloë monticola* from the USA (WEIMARCK 1967 b), flower buds were fixed from speci-

mens of Greenlandic *H. monticola* 2n=63 plants collected in 1968 in Narssarssuaq (locality B F B) and in the Fredrikshåb area (localities B F D, B F F, B F M, B F N, B F O, B F P, and B F R), giving a total of 66 well-stained and well-orientated spikelets.

The illustrations were made with the help of an Abbe camera lucida on a Leitz microscope. In this paper as in previous ones the micropylar part of the nucellus is directed upwards.

The structure of the spikelet and of the ovule agreed in general with that of *Hierochloë* species previously studied (cf. WEIMARCK 1967 a p. 211; 1967 b p. 449). For exceptions see pp. 498, 501, 502.

HIEROCHLOË ALPINA

Collection B D R, 2n=66

One or more (up to 3) megaspore mother cells (MMC) were found in 4 (10 %) of 41 young nucelli studied (Fig. 1 *A*, *B*; Table 1). In three of these cases no embryo sac initial (EI) was present. In addition there were some cases of a degenerated remnant among the EI, indicating the possibility of an MMC that had been superseded at a very early stage. The other nucelli had one or more (up to 5) initials and uninucleate embryo sacs (ES; Fig. 1 *D*) arranged in the same way as in *Hierochloë monticola* (WEIMARCK 1967 b p. 449).

One distinctly abnormal anaphase II (Fig. 1 *C*) and one apparently normal tetrad were observed. Clear instances of further development were not seen. It is possible that some ES with nuclei with a flattened or elongated shape and a higher number of nucleoli per nucleus (Fig 1 *E*, *H*) were unreduced, in contrast to those with typically rounded nuclei and fewer nucleoli per nucleus (Fig. 1 *F*, *G*). The last-mentioned ones were less frequent and clearly distinguishable (cf. also WEIMARCK 1967 a p. 226; 1967 b pp. 449—450). — A mature ES is illustrated in Fig. 1 *I*.

As in *Hierochloë monticola* (WEIMARCK 1967 b p. 450) the secondary nucleus divided before the egg in some cases, the egg before the secondary nucleus in others. In *H. odorata* only the first-mentioned alternative was observed (WEIMARCK 1967 a p. 231).

In some cases when either the embryo or endosperm had reached a very advanced state without any division of the other nucleus occurring, an abnormal course of development was strongly indicated.

The material did not permit an estimation of the rate of development into an eight-nucleate ES as could be done for *Hierochloë australis*, *H. odorata* and *H. monticola* (WEIMARCK 1967 a, b), since the conditions of culture were different and male meiosis often too irregular to be suitable as the starting-point of measuring the lapse of time. In one of the plants in Lund, however, eight-nucleate ES were developed within 14 days after the plant had been cut out from the frozen ground. At the time of collection the top of the panicles were already some 20—30 mm above the surface of the ground, protruding into the melting snow. The property of having young flower buds remaining dormant throughout the winter is shared with many other arctic plants, and was earlier noted by HODGSON (1966) in both *Hierochloë alpina* and *H. odorata*.

Out of a total of 149 nucelli studied at stages corresponding to the development from binucleate to mature ES, 56 (38 %) contained only degenerating or wholly abnormal ES or merely degenerative traces. The value for 91 nucelli at stages corresponding to young embryos was 11 (12 %). The numbers from 1967 were unfortunately too small to permit comparisons between plants grown in the open and in the Arktisk Hus. — Germination tests have not been made.

An egg-like antipodal of the type found in *Hierochloë monticola* (WEIMARCK 1967 b p. 450) was found in one ES with an undivided egg and a four-nucleate endosperm. In another ES both the egg and one antipodal had developed into embryos.

Aberrations in the structure of the spikelet occurred in the *Hierochloë alpina* collection B D R. Normally the uppermost floret only is hermaphrodite. One case was found where all three florets were hermaphrodite and a few cases where the two upper ones were hermaphrodite and the lowermost one male.

Male meiosis was observed in plants which had been placed in the Arktisk Hus. Division was badly disturbed. In many cases no meiosis at all occurred, and the contents of the anthers was found to be degenerating. In the anthers of some plants up to four-nucleate ES were observed in great numbers. They appeared to have originated from the archesporium, thus being diplosporous.

Fig. 1. *Hierochloë alpina*, coll. B D R. — *A*: 1 MMC, prophase. — *B*: 3 MMC, prophase; 1 unreduced uninucleate ES. — *C*: anaphase II, disturbed. — *D*: 1 unreduced uninucleate ES. — *E*: 2 binucleate ES, presumably unreduced. — *F*: 1 four-nucleate ES, presumably reduced. — *G*: 2 eight-nucleate ES, presumably reduced. — *H*: 1 eight-nucleate ES, presumably unreduced. — *I*: 1 mature ES.

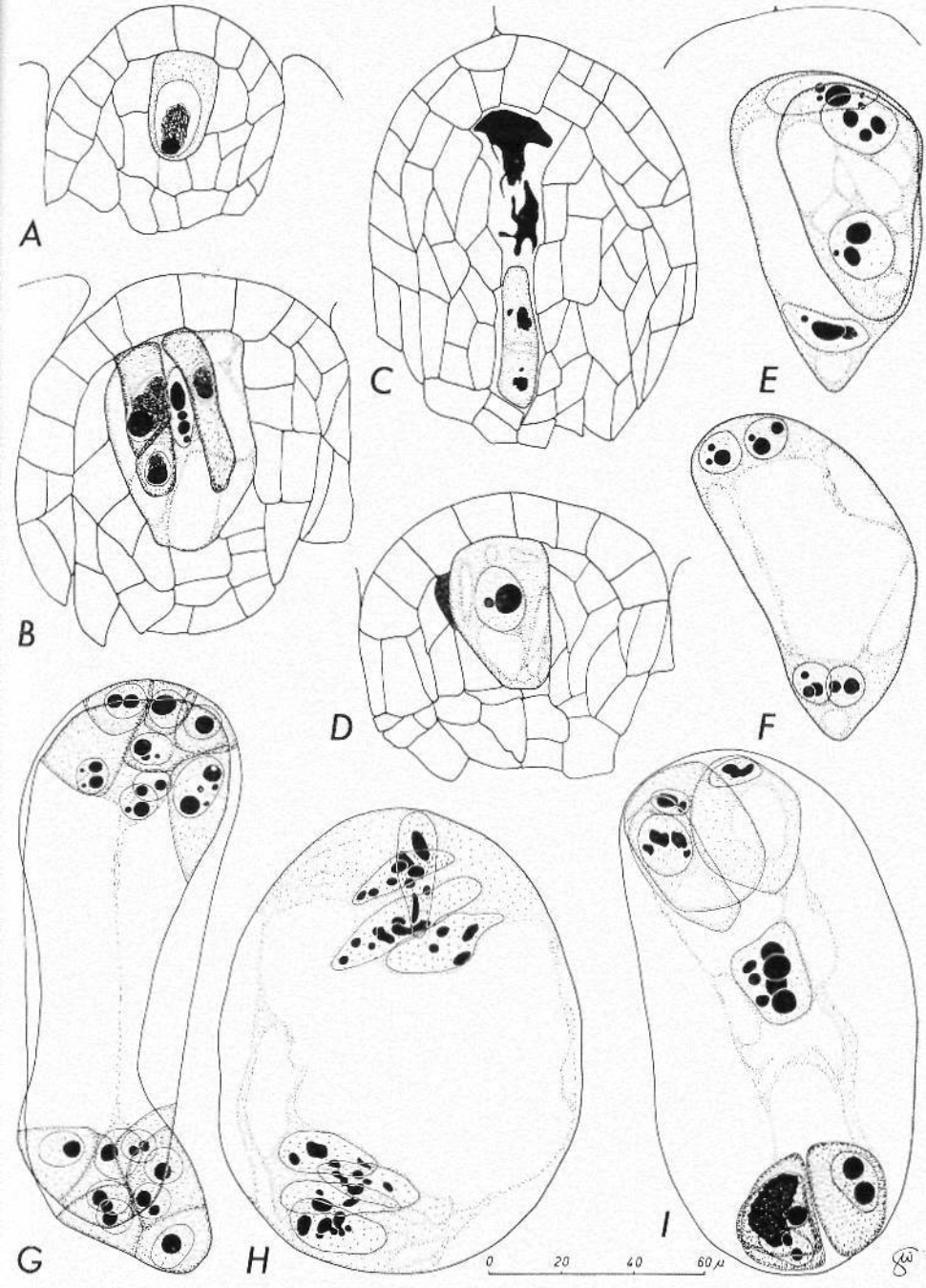
A
B
C
D
E
F
G
H
I
0 20 40 60 μ

Table 1. Occurrence of one or a few MMC in young nucelli.

a: Number of young nucelli studied
b: Number of young nucelli with one or a few MMC
c: b in percents of a

Collection	a	b	c	Collection	a	b	c
H. alpina 2n=66				*H. monticola* 2n=63			
B D R	41	4	10	B F D	5	3	60
	41	4	10	B F M	13	3	23
H. alpina 2n=56				B F N	5	0	0
B G A	6	1	17	B F P	2	0	0
B G D	4	1	26	B F R	9	1	11
B G F	16	6	38		34	7	21
B G H	4	0	0				
B G K	11	2	18				
B G M	10	0	0				
	51	10	20				

Collections B G A, B G D, B G F, B G H, B G K, and B G M, 2n=56

The *Hierochloë alpina* collections from Greenland which were studied usually consisted of only 1—2 plants due to inevitable lack of space during cultivation in the Arktisk Hus. Furthermore, each panicle yielded only 6—11 (—14) spikelets (each with one hermaphrodite flower), and many plants produced no panicles at all. In addition, there was the normal wastage due to unfavourable sectioning, etc. The results from the 2n=56 collections in Table 1 and 2, although accounted for separately for each collection, could preferably be put together.

In some of the Greenlandic plants it seems possible to discern a somewhat higher rate of occurrence of one (rarely more than one) MMC or derivative thereof than in collection B D R. However, differences between collections were high (Table 1).

The material points to a certain difference between 2n=66 and 2n=56 collections as to degenerative frequency in late stages (Table 2). ES development was of the same type as that described for collection B D R.

Male meiosis was badly disturbed in all collections studied. Some fixations contained apparently no viable pollen at all. Other plants did complete divisions although often irregularly. The frequency of ES in anthers was very high, especially in some plants.

Table 2. Occurrence of degenerating nucelli at different stages of development.

A: Stages corresponding to the series from binucleate to mature ES
B: Stages corresponding to young embryos
a: Number of nucelli studied
b: Number of nucelli with degenerating or collapsed contents
c: b in percents of a

Collection	A			B		
	a	b	c	a	b	c
H. alpina 2n=66						
B D R	149	56	38	91	11	12
	149	56	38	91	11	12
H. alpina 2n=56						
B G F	·	·	·	20	10	50
B G M	15	4	27	7	4	57
	15	4	27	27	14	52
H. monticola 2n=63						
B F B	7	5	71			
B F F	7	2	29			
B F N	9	8	89			
B F O	9	3	33			
	32	18	56			

HIEROCHLOË MONTICOLA

Collections B F B, B F D, B F F, B F M, B F N, B F O, B F P, and B F R, 2n=63

The Greenlandic *Hierochloë monticola* material was limited for the same reasons as that of *H. alpina* (Tables 1 and 2).

The percentage of occurrence of one MMC or derivatives thereof was about as high as that previously found in material studied from the USA (WEIMARCK 1967 b p. 449). The development of the ES was also in agreement with the results obtained earlier.

Abnormal or wholly abortive male meiosis was fairly common. ES formation in anthers were rare.

Three spikelets having two hermaphrodite flowers each were detected.

DISCUSSION

The collections of *Hierochloë alpina* and *H. monticola* studied in this paper and of *H. monticola* (WEIMARCK 1967 b) have many embryological features in common. The frequencies of degeneration and of the

existence of an MMC are not very different. Egg-like antipodals have been observed in both.

The actual functioning of reduced ES in competition with unreduced ones can only be uncertainly inferred by means of embryological methods (cf. p. 497 and WEIMARCK 1967 a pp. 214, 226; 1967 b p. 449).

A numerical analysis of thin-layer chromatographically obtained results made population studies possible in some collections of *Hierochloë australis*, *H. odorata* and *H. alpina* (WEIMARCK 1970 b). Both *H. australis* and *H. alpina* were shown not only to form clones within one locality but in some instances to form genetically heterogeneous populations. These observations strengthen the assumption that reduced ES occur and may be functioning. Unfortunately, *H. monticola* could not at that time be studied chromatographically in this respect.

In *Hierochloë alpina* EI can often be found in such a position as to suggest they are homologous with archesporial cells. They should thus be classified as diplosporous rather than aposporous. Diplospory was suspected to occur in *H. australis* and *H. monticola*, possibly also in octoploid *H. odorata* (WEIMARCK 1967 a pp. 214, 227, 228; 1967 b p. 449).

I have not observed in other species of *Hierochloë* such an apogamous development of an antipodal as found in *H. alpina*, collection B D R. NORSTOG who studied twinning in North American *H. odorata* 2n=56 found it to be due solely to the occurrence of more than one ES per nucellus, not to the development of embryos from other cells in the ES besides the egg (1960 b p. 364; 1963 p. 820).

Two aberrations in the structure of the spikelet had been found in specimens of *Hierochloë odorata* studied previously (one in collection A H B, 2n=28, one in collection A H E, 2n=42). In both, the two upper florets were hermaphrodite, the lowermost one male. — Another type of aberration was described by NORSTOG (1960 a), who found some Icelandic *H. odorata* plants with spikelets containing four florets, the upper ones being hermaphrodite. I have found a similar type of spikelets in some *H. alpina* specimens from Alaska.

Male meiosis is evidently much more abnormal in the plants studied by me than in those Greenlandic ones studied by JØRGENSEN, SØRENSEN and WESTERGAARD (1958 p. 12). I am not inclined to ascribe this amount of disturbance merely to the fact that the plants in question were kept in culture, nor is there any reason to assume the female development to be appreciably influenced. Conditions in the Arktisk Hus fairly well resemble natural conditions. Anyhow, the latent capacity to produce

abnormalities does exist in my material. It is still unknown whether other *Hierochloë alpina* biotypes which show better male meiosis are amphimictic or not.

The *Hierochloë alpina* plants studied have the highest frequency of ES formation in anthers of the *Hierochloë* collections in my work. The abnormal tendency to develop ES in anthers is apparently common for a number of taxa within the genus, as is the apomictic potentiality in general.

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The European Species of Scaligeria (Umbelliferae)

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ABSTRACT

ENGSTRAND, L.: The European Species of Scaligeria (Umbelliferae). — Bot. Notiser 123: 505—511, Lund.

A new species, *Scaligeria moreana* from Peloponnisos, Greece is described. Variation and taxonomic problems in *S. napiformis* and *S. halophila* are briefly discussed. Maps and key to the three European species are presented.

INTRODUCTION

Scaligeria is mainly an Asiatic genus. In Flora U.S.S.R. (KOROVIN 1950) there are 19 species representing the subgenera *Elaeostica* KOROVIN and *Chaerophylloides* KOROVIN. In Europe the genus is represented by three species, *S. napiformis* (SPRENGEL) GRANDE, *S. halophila* (RECH.F.) RECH.F. and *S. moreana* ENGSTR. sp. nov., all in the subgenus *Pimpinelloides* KOROVIN.

MATERIAL

Material from the following herbaria has been studied (abbreviations according to LANJOUW and STAFLEU 1964): BM, FI, G, K, LD, LY, M, S, UPS, WU. I am most indebted to the directors and curators of these institutes. I am also grateful to Dr. O. ALMBORN for helping me with the Latin diagnosis.

The following abbreviationes of collectors names are used: BE = B. BENTZER, B = R. VON BOTHMER, N = B. NORDENSTAM, P = J. PERSSON, R = H. RUNEMARK, S = S. SNOGERUP, ST = A. STRID.

THE EUROPEAN SPECIES

Key to the European Species of Scaligeria

1. Basal leaves lanceolate in outline, fruit ellipsoid ..... *S. moreana*
1. Basal leaves triangular in outline, fruit with cordate base 2
2. Leaves fleshy, fruit c. 2.5 mm long ..... *S. halophila*
2. Leaves not fleshy, fruit c. 1.5 mm long ..... *S. napiformis*

Scaligeria napiformis (SPRENGEL) GRANDE

GRANDE, Bull. Orto Bot. Napoli 4: 188 (1914). — *Bunium napiforme* WILLD. ex. SPRENGEL, Spec. Umbellif.: 95 (1818).

ORIG. COLL.: A specimen in Herb. GUNDELSHEIMER in Herb. WILLDENOW (B).

Scaligeria cretica (URV.) BOISSIER, Diagn. Pl. Or. Nov. 2(10): 52 (1849). *Scaligeria cretica* (URV.) VISIANI, Fl. Dalm. 3: 70 (1850—1852). — *Bunium creticum* D'URVILLE, Mém. Soc. Linn. Paris 1: 287 (1822).

Scaligeria cretica (MILLER) BOISS., incorrectly established by TUTIN in Fl. Europ. 2: 328 (1968). — *Bunium creticum* MILLER, Gard. Dict. ed. 8 (1768).

The correct name of this species was reestablished by GREUTER and RECHINGER (1967).

Glabrous biennial 10—50 cm high, with tuberous root. *Stem* slender with ± straight branches. *Basal leaves* triangular in outline with rombic-ovate lobes. *Uppermost leaves* entire or only consisting of a sheath. *Terminal umbel* with 5—20 rays. *Bracts* missing, *bractlets* few, lanceolate to narrow elliptic. *Fruit* ovoid with cordate base. *Stylopodium* conic-cylindric.

S. napiformis is a highly variable species especially with respect to the shape of the basal leaves, number and length of the rays, number of bractlets, and length of the stem. A small form is common on the Cycladic islands. It is 10—15 cm high with 5—7 rays in the terminal umbel. The basal leaves are dark-green to reddish-green. This form does not seem to be an altitudinal modification since it is distributed from c. 100 to 850 m s.m. Sometimes it is also found on the mainland, and since tall-grown mainland forms occur also on the islands, it has not been possible to establish any geographically circumscribed pattern of variation within the species. Furthermore there are also gracile, divaricately branched plants (especially on Euboea and the Sporades), while others are stout and erect.

Some variation is found also in the fruits. Mostly they have slender

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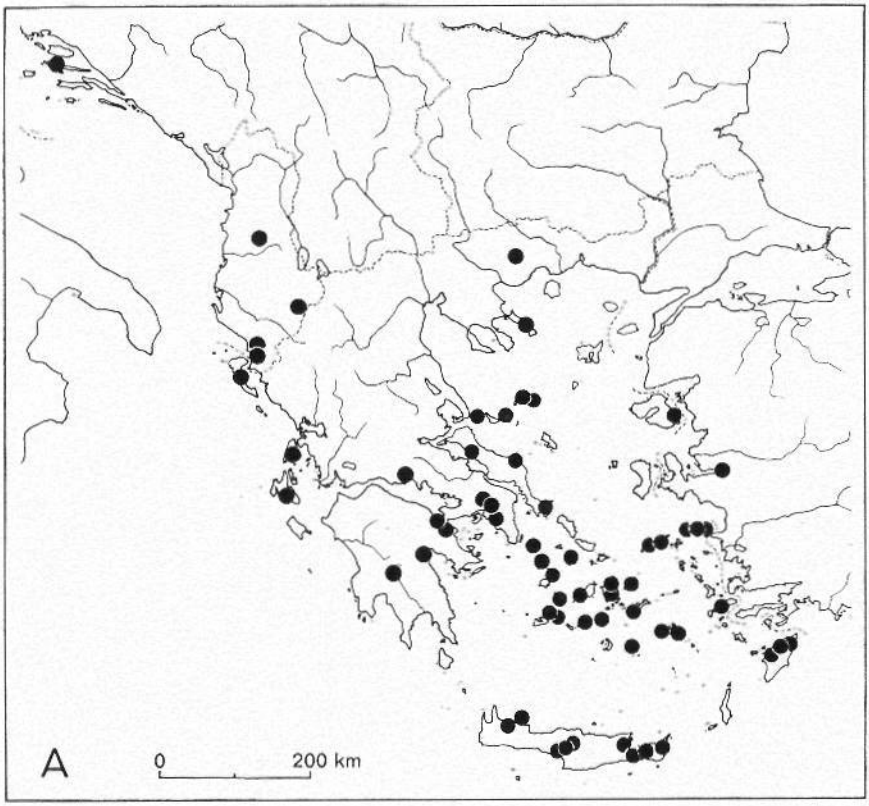
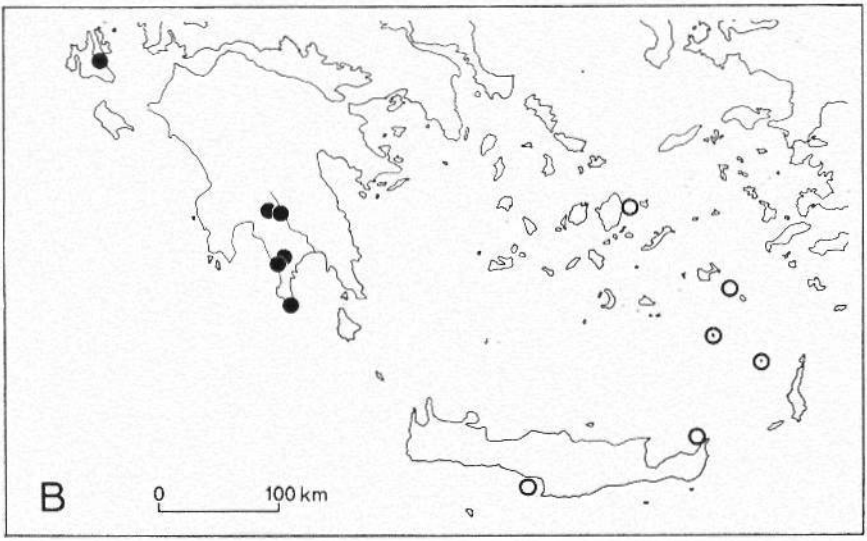
Fig. 1. A: Distribution of *Scaligeria napiformis* according to investigated herbarium material. Outside the map *S. napiformis* is distributed in Turkey, Cyprus, Syria, Lebanon, Israel and Libya. — B: Distribution of *Scaligeria moreana* (dots) and *Scaligeria halophila* (rings).


A
0
200 km


B
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100 km

inconspicuous ridges, but sometimes the ridges are prominent in the upper part of the fruit. Small vestiges of sepals are sometimes found, for instance, in a specimen from Cyrenaica, which is otherwise similar to mainland forms from the Balcan peninsula.

DISTRIBUTION (Fig. 1 A). *S. napiformis* is common in Greece and Albany. The only Yugoslavian material seen by the author is from the Dalmatian island of Hvar (Lesina), where the species has been collected several times. Outside Europe it occurs in Turkey, Cyprus, Syria, Lebanon and Israel. Two specimens from Cyrenaica have been seen, but the species is not known from Egypt. This is not an unusual distribution for an east Mediterranean species (cf. RECHINGER 1950).

Scaligeria halophila (RECH.F.) RECH.F.

RECHINGER, Österr. Bot. Zeitschr. 112: 186—187 (1965). *S. cretica* (URV.) VIS. ssp. *halophila* RECH.F., Denkschr. Akad. Wiss. Wien 105: 102 (1943).

ORIG. COLL.: Crete: Dionysades: In fissuris rupium calc. litoris insulae Dragonara, 13.5 1942. RECHINGER 12921 (W).

Illustration: ENGSTRAND 1970 Fig. 2.

S. halophila is very closely related to *S. napiformis*, and has possibly originated as an ecotype of the latter. The chromosomes of *S. halophila* are indistinguishable from those of *S. napiformis*. The chromosome number is 2n=20 in both (ENGSTRAND 1970), and no differences have been found in the pollen morphology.

S. halophila occurs only on small islands. It grows in limestone cliffs and open phrygana from the spray-zone up to 100 m s.m. The plant is 15—35 cm high with slightly curved branches. The stem is stout compared with that of *S. napiformis*. The number of rays in the terminal umbel is 6—9. The basal leaves are broadly triangular in outline, whereas the uppermost only consist of a sheath. All leaves are fleshy with a light-green colour. The lobes are always larger than those of *S. napiformis*. The fruit is similar to that of *S. napiformis* but larger (c. 2.5 mm long).

A specimen from one of the Makares islands near Naxos has a more slender stem than plants from other localities. The fruits are smaller and the leaves are more purely green.

DISTRIBUTION (Fig. 1 B). *S. halophila* is distributed on small islands in the southern Aegean and on Paximadhia south of Crete.

LOCALITY LIST: Greece. Dodecanesos. Dio Adelphi, the W-island, R & N 14161 (LD), R & N 14192 (LD), R & P 22296 (LD). — Dodecanesos. Stakida, R & S 7583 (LD), R & S 7473 (LD), R & Be 28391 (LD). — Dodecanesos. Safrania (Safrano, Safora). In saxosis calc litoreis, Rechinger 7638 (W), Safora. NE of the harbour bay, R & S 7172 (LD), R & S 7173 (LD), Safora, the NW part of the island, R & S 7208 (LD), Safora, between the cistern and the highest peak, R & Be 28172 (LD), Safora, the island of Makri Safora, R & Be 28236 (LD), Safora, Mikro Safora, R & P 22577 (LD). — Cyclades. Makares, Strongylo, R & S 10384 (LD), R & S 10344 (LD). — Crete. Ag. Vasilis. Insel Paximadhia, Dörfler 1114 (WU), Paximadhia, the W-island S, St & B 20920 (LD). — Crete. Dionysades, insulae Dragonara, Rechinger 12921 (W).

Scaligeria moreana Engstr., spec. nov.

Similis *Scaligeriae napiformi* (Sprengel) Grande, sed foliis basalibus lanceolatis, lobis acute acuminatis. Fructus ellipsoideus vel parum ovoideus, 1.5—2.5 mm longus, jugis primariis prominentibus. Vittae 2—4 inter jugos, irregulariter distributae. Commisura lata.

ORIG. COLL.: Greece, Laconia, in the valley W of Mirsini, 7—8 km ENE of Areopolis, 20.5 1964. Runemark & Snogerup (R & S 22019), in Herb. Bot. Lund (LD).

Illustration: Fig. 2.

Glabrous biennial, 40—60 cm high with tuberous root. *Stem* erect with many straight branches. *Basal leaves* lanceolate in outline, 2(—3)-pinnate, lobes acute to acuminate. Basal lobes of the primary segments situated very close to the rachis. *Uppermost leaves* entire or only consisting of a 1—4 cm long sheath. Umbels up to 15. *Terminal umbel* with 5—8 rays, the *lateral umbels* with up to 15 rays. *Bracts* usually missing, *bractlets* 5—10, lanceolate to narrow elliptic. Flowers hermaphrodite. *Sepals* small conspicuos. *Petals* white with a reddish-brown mid-rib, obcordate with inflexed apex. *Fruit* ellipsoid, 1.5—2.5 mm long with prominent ridges. *Vittae* 2—4 per interval, irregularly distributed. *Commisure* wide. *Stylopodium* 1/4—1/3 as long as the fruit, conic-cylindric with 1.2—2.5 mm long, slender styles.

Unfortunately available seeds did not germinate, and consequently nothing is known about the seedlings and the chromosomes.

The species is named after Morea an old name for Peloponnisos.

In habit *S. moreana* is rather similar to *S. napiformis*. However, it is easily distinguished by the lanceolate basal leaves with acuminate lobes.

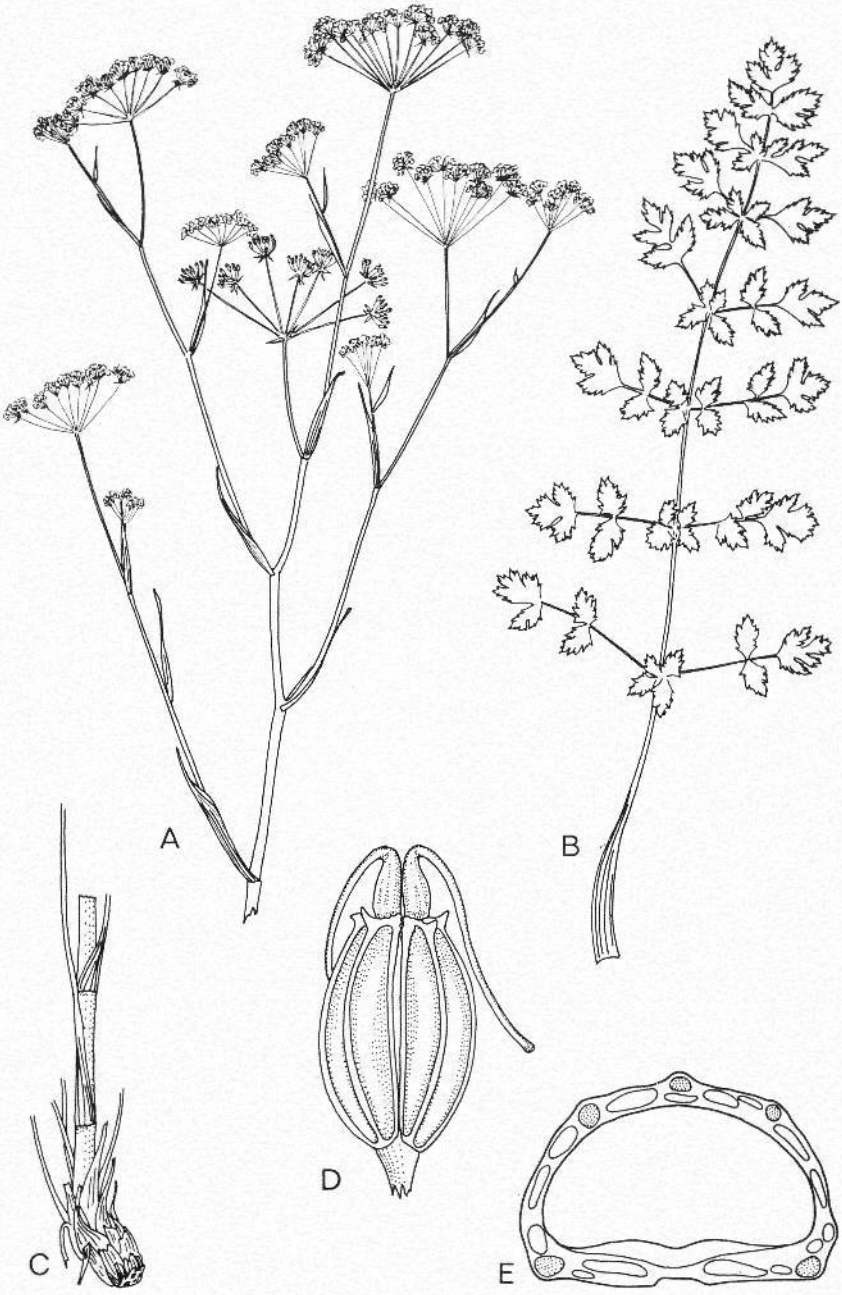

Fig. 2. *Scaligeria moreana* ENGSTR. — A: Upper part of stem (×0.5). — B: Basal leaf (×0.5). — C: Basal part of stem (×0.5). — D: Lateral view of fruit (×12.5). — E: Transverse section of mericarp (×37).

The fruits are ellipsoid or slightly ovoid but never with a cordate base as in *S. napiformis*. The ridges are visible as light-brown lines running from the top to the base of the fruit. The vestiges of the sepals can easily be seen in small magnification.

In the diagnosis of the subgenus *Pimpinelloides*, KOROVIN (1928) writes "folia ternata". This should disqualify *S. moreana* for the subgenus. However, on the basis of the shape of the stylopodium, the shape of the petals, and the great similarities in habitus, I believe that it is correct to place the three European species in the same subgenus.

DISTRIBUTION (Fig. 1 B). *S. moreana* is distributed in the southern part of Peloponnisos and on the adjacent island of Kephallenia.

LOCALITY LIST: Greece. Laconia. 7—8 km ENE of Areopolis. 20.5 1964, R & S 22019 (LD). — Gr. Lac. 2 km N of Areopolis. 22.5 1964, R & S 20727 (LD). — Gr. Lac. Penins. Mani, supra porto Kalion. 10.6 1958, RECHINGER 20136 (M). — Gr. Lac. m. Taygeti borealis, in distr. Alagonia. 27.5 1900, HELDREICH Herb. Gr. Norm. 1637 (FI). — Gr. Lac. Mistrà, 1844, HELDR. 242 (FI). — Gr. Kephallenia, above Sami. 9.6 1966, S 23614 (LD).

S. moreana grows in open phrygana vegetation with limestone blocks and cliffs. This type of biotope is not uncommon in the area, and probably the species is undercollected.

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The Genus Zaluzianskya F. W. Schmidt (Scrophulariaceae) Found in Tropical East Africa

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ABSTRACT

HEDBERG, O.: The Genus Zaluzianskya F. W. Schmidt (Scrophulariaceae) Found in Tropical East Africa. — Bot. Notiser 123: 512—518, Lund.

A new annual species of the genus *Zaluzianskya* F. W. SCHMIDT (*Scrophulariaceae*), *Z. elgonensis* HEDB., is described from the afroalpine belt on Mt Elgon in Uganda. This northern outpost of the mainly South African genus is believed to have arisen through long distance dispersal.

The genus *Zaluzianskya* F. W. SCHMIDT (*Scrophulariaceae*) has its main distribution in South Africa — 32 species were recorded in Flora Capensis (HIERN 1904; cf. PHILLIPS 1926) and 5 species occur on the Cape Peninsula (ADAMSON & SALTER 1950). It is still well represented in the Drakensberg, where the Cathedral Peak area harbours 7 species (KILLICK 1963), and reaches its northernmost earlier known outpost in Rhodesia, where 2 species are known from the Inyanga district (GOODIER & PHIPPS 1961).

During a collecting trip on the Uganda side of Mt Elgon I found in December 1967 a small annual species of this genus growing on rocky ground with thin soil cover in the alpine belt, which means a northwards extension of its area by some 2200 km (see map Fig. 1). My Elgon collection was later compared to the material of the genus available at Kew, but it could not be matched to any South African species, nor could it be identified with any description found in the literature. Consequently it is here described as a new species.

Zaluzianskya elgonensis HEDB., n. sp.

Z. gilioidi SCHLECHT. affinis a qua foliorum marginibus integris, inflorescentiis abbreviatis subcapitatis, corollis brevioribus extus fuscopurpureis, stylisque maturitate manifeste exsertis differt A *Z. pusillae* (BENTH.) WALP.

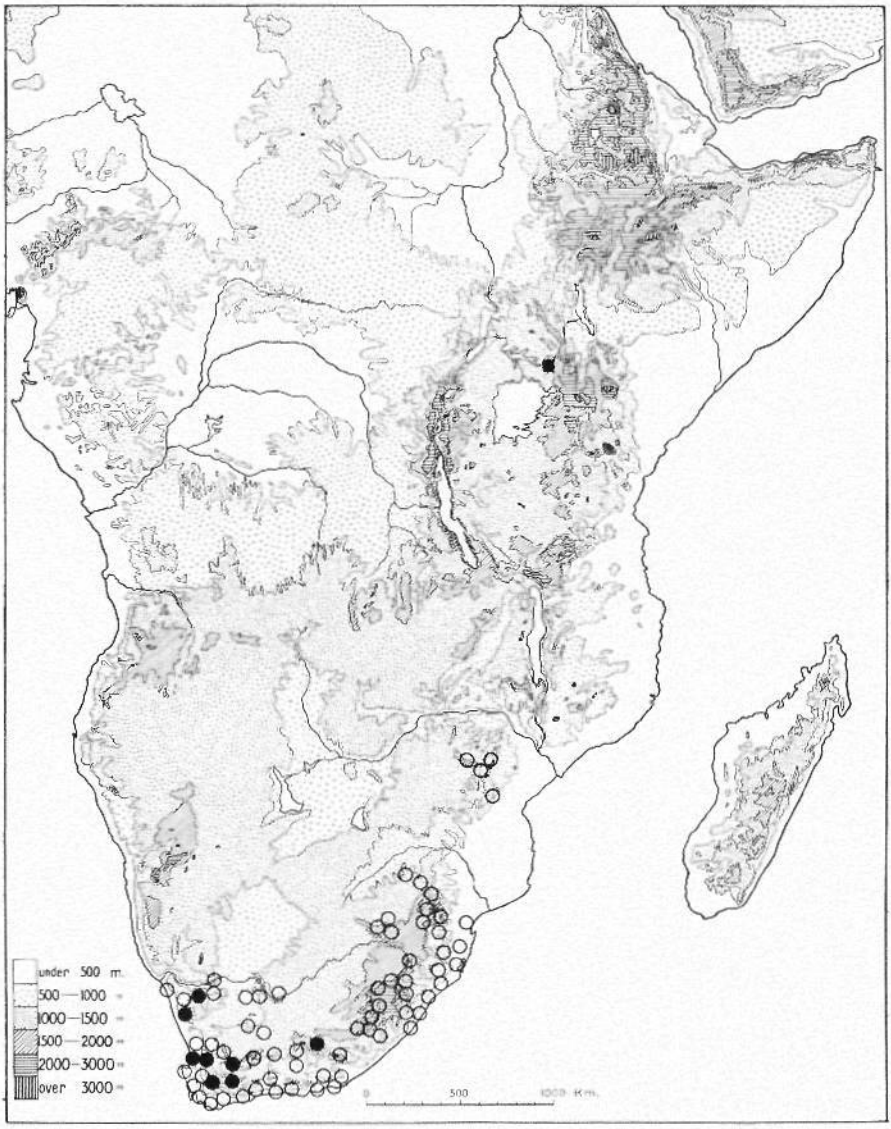


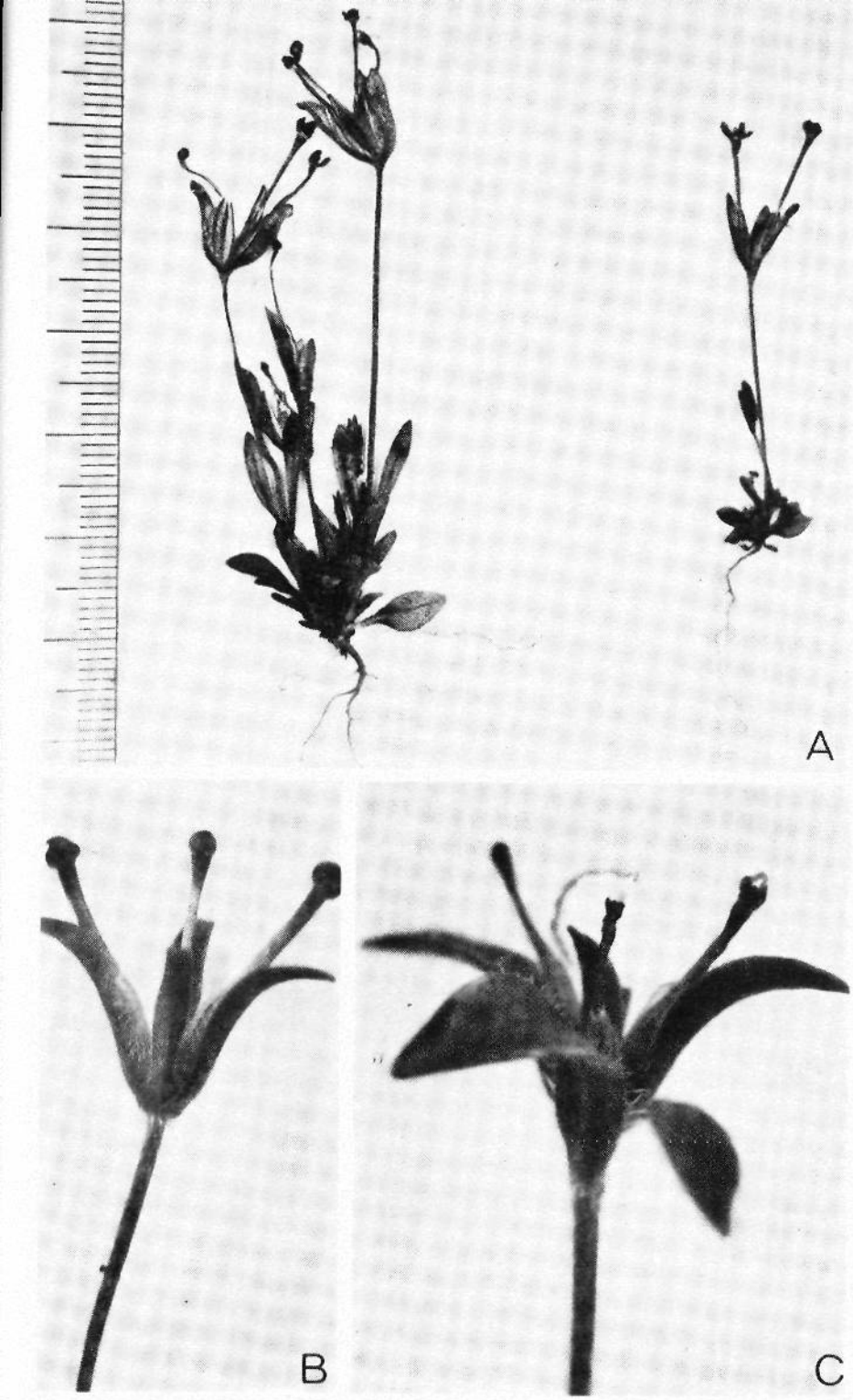
Fig. 1. Map of the total known distribution of the genus *Zaluzianskya* F. W. SCHMIDT, based on the material available in the Kew Herbarium. The black square marks the type locality for the new species *Z. elgonensis* HEDB. described in this paper, the black dots refer to localities for *Z. gilioides* SCHLECHT. and *Z. pusilla* (BENTH.) WALP., and the open circles represent localities for other species of the genus.

caulibus subscaposis, inflorescentiis subcapitatis, colore corollae, antheribusque inferis inclusis facile diagnoscenda.

Planta parva, annua, subscaposa, sparse puberula. *Caulis* 2—7 cm altus, e basi ramosus, teres. *Folia* opposita, integra, obtusa, 4—15×1.5—5 mm, basalia oblato-lanceolata petiolata, supera lanceolata sessilia. *Inflorescentia* subcapitata floribus 1—6 dense aggregatis. *Calyx* ovoideo-tubulosus c. 5 mm longus. *Corolla* tubulosa extus fuscopurpurea, intus cremea, tubo 10—12 mm longo 0.7 mm diametiente, lobis oblongis integris 1.5—2 mm longis. *Stamina* 4, didynama, antheris 0.5 mm longis, 2 anticis tubo superantibus, 2 posticis inclusis. *Stylus* filiformis maturitate exsertus.

Small annual herb about 2—7 cm high, in cultivation up to 15 cm. *Stem* usually branched from the base with 2—5 ascending—erect scape-like branches, one or two of which are often more powerful than the rest, terete with lax pubescence of patent to reflexed soft hairs. *Leaves* opposite, entire, crowded towards the base and usually absent from the upper half or two thirds of the stem, sparsely pubescent, especially along the margins, 4—15 mm long and 1.5—5 mm wide, the lower ones petiolate, ovate to lanceolate with cuneate base and obtuse apex, the upper ones sessile, lanceolate. *Inflorescence* terminal, subcapitate with usually (1—) 2—4 (—6) densely crowded flowers. *Bracts* sessile, erect, elliptic-lanceolate, 7—11 mm long and 1—2.5 mm wide with obtuse apex, thinly pilose. *Calyx* c. 5 mm long, ovoid-tubular with 5 distinct purplish (or, in cultivated specimens grown in shadow, green) pubescent ribs, separated by thin, hyaline portions, 5-toothed with teeth about 1 mm long, indistinctly bilabiate, asymmetrical because the ribs and lobes are turned towards the adaxial side, the abaxial side being largely hyaline and connate with the bract for half of its length. *Corolla* about 12—14 mm long, purplish brown outside and cream-coloured inside with 5 orange-coloured spots round the throat; tube slender, 10—12 mm long and about 0.7 mm wide, purplish-streaked and glandular-pubescent outside, entirely glabrous inside; limb cup-shaped and symmetrical with 5 oblong lobes 1.5—2 mm long with entire, rounded apex. *Stamens* 4, didynamous, the outer two reaching above the mouth of the corolla tube, the inner two included in the tube; anthers about 0.5 mm long, the upper ones transversely oriented, the lower ones parallel to the tube.

Fig. 2. — A: Photograph of two specimens of *Zaluzianskya elgonensis* HEDB. from the type collection. The scale to the left gives (cm and) mm. — B—C: *Z. elgonensis* HEDB. Close-up of two inflorescences of living specimens, raised in a greenhouse in Uppsala from seeds of the type collection. Note the subcapitate inflorescence and almost closed corolla limb in the young inflorescence (B), and the exserted styles in two older flowers of the inflorescence (C).


A
B
C

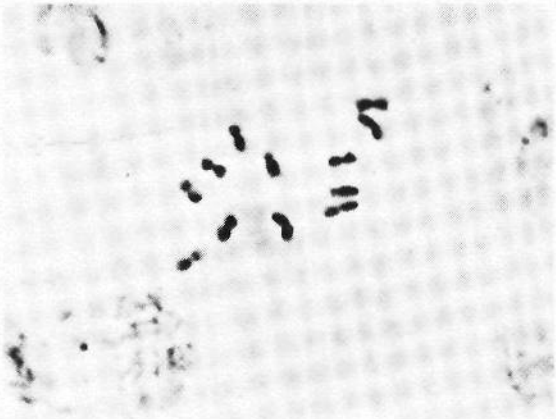


Fig. 3. *Zaluzianskya elgonensis* HEDB. Photomicrograph of mitotic metaphase from root tip of offspring plant from type collection, grown in a greenhouse in Uppsala. Preparation and microphoto by Dr. I. HEDBERG.

Style in mature flowers distinctly exserted (2—3 mm or more), its upper part flattened and more or less spirally coiled with a strip of stigmatic tissue along the margins. Self-pollination seems to occur regularly in bud. *Fruit* a two-roomed septicidal capsule about 6 mm long. *Seeds* irregularly prismatic, about 0.4—0.5 mm in diameter, light brown. Somatic chromosome number 2n=12. — Figs. 2—3.

TYPE: Uganda, Bugishu Distr., Mt Elgon, W. slope above Butadiri, along the track via Mudangi through the Caldera, on rocky ground with thin soil cover in the alpine belt, 3800 m, 5.12 1967, O. HEDBERG 4478 (EA, K, MHU, PRE, UPS, holotype).

From a phytogeographical point of view this new discovery is very interesting. Together with the recently described *Wurmbea hamiltonii* (WENDELBO 1968) the new species forms a remarkable addition to the South African (or perhaps Cape) element in the afroalpine flora (cf. HEDBERG 1965). The taxonomy of the genus *Zaluzianskya* is far from sufficiently known, but the closest relatives of the new species seem to be restricted to the Cape Province (cf. map Fig. 1). The wide geographic disjunction between the new species and the South African center of diversity of the genus makes it probable that the northern outpost has been recruited through long-distance dispersal. This may have been facilitated by the fact that *Z. elgonensis* is at least facultatively autogamous — its flowers seem to remain mostly closed, and the anthers

open and effect pollination already in bud. A single seed might therefore have been sufficient for effective dispersal. Establishment on Mt Elgon may have been facilitated by the comparatively low degree of competition obtaining on the rocky ground with thin soil cover where the plant occurs. Its mode of dispersal from South Africa to Mt Elgon can of course only be guessed at — the most likely vector may be migrant birds, but anemochoric dispersal cannot be excluded (cf., e.g., RIDLEY 1930, LIBEN 1962, HEDBERG 1969, 1970).

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Cytological Studies in Allium I. Chromosome Numbers and Morphology in Allium Sect. Allium from Greece

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ABSTRACT

BOTHMER, R. VON: Cytological Studies in Allium I. Chromosome Numbers and Morphology in Allium Sect. Allium from Greece. — Bot. Notiser 123: 518—550, Lund.

Five species of *Allium* sect. *Allium* from Greece have been cytologically investigated. Three species of the "*ampeloprasum* complex", viz., *A. ampeloprasum* L. (4×, 5×, 6×), *A. bimetrale* GANDOG. (2×, 3×, 4×), and *A. bourgaei* RECH. FIL. (2×, 3×, 4×) have been studied as well as two species, which do not belong to this complex, viz., *A. sphaerocephalum* L. (2×), and *A. descendens* L. (2×, 3×, 4×). Chromosome numbers have been determined in 147 populations.

A general survey of the karyotype in *Allium* is presented. Eight populations in the *ampeloprasum* complex have been studied in detail; idiograms have been worked out and the variation in marker chromosomes has been studied. In general the differences are small and not obviously correlated with taxonomic categories. Some sources of error in karyotype analysis are discussed.

INTRODUCTION

Since 1964 the author has been studying the *Allium ampeloprasum* complex in the Aegean area. The purpose is partly a taxonomic revision of the group but mainly a study of variation and evolution at the population level. In this type of investigation karyotype analysis may serve as a valuable instrument. The polymorphism of *A. ampeloprasum* s. str. and its relationship to *A. porrum* (the leek) may be better understood through cytological studies of populations from the entire range of the species (FEINBRUN 1943, JONES & MANN 1963, KOUL & GOHIL 1970).

This publication is the first in a planned series of papers on cytological problems in the *Allium ampeloprasum* complex. In the present

paper, a general survey of chromosome numbers and chromosome morphology will be given as well as some comparisons between taxa. At the end of the paper the forthcoming cytological work will be outlined.

MATERIAL

Allium sect. *Allium* has its distribution centre in the eastern Mediterranean. Apart from *A. ampeloprasum* L. s. str., two endemic species of the *ampeloprasum* complex are frequent in the Aegean area, viz., *A. bourgaei* RECH. FIL. and *A. bimetrale* GANDOG. The latter occurs in Crete, and on small, pronouncedly maritime islands in the Kikladhes, SE Dodekanisos, Ionian islands, and Northern Sporades. *A. bourgaei* is a chasmophytic plant growing in E Crete, on the larger of the Kikladhian islands, on Ikaria, and on some islands in SE Dodekanisos. Two species that do not belong to the *ampeloprasum* complex in its narrower sense have also been included in the investigation, viz., *A. sphaerocephalum* L. (C Europe and Mediterranean area) and *A. descendens* L. (E Mediterranean). Both species are in need of revision.

As the taxonomic and nomenclatorial results are hitherto unpublished, in this paper I will follow RECHINGER's Flora Aegaea (1943), even if this means that the names of some taxa must subsequently be changed. The only exception from Flora Aegaea is *Allium bimetrale*, which was treated as a subspecies of *A. ampeloprasum* by RECHINGER, but is here kept as a separate species.

The cultivated material was collected in Greece and Turkey during journeys in 1964—1969. The plants were grown from bulbs (in some cases from seeds) and cultivated in the greenhouses and outdoors in the Botanical Garden of Lund. In all cultivated material the chromosome numbers were determined. One population of each taxon was studied in detail. In some cases idiograms were constructed from populations of different ploidy levels within a species.

The following material was studied in detail:

Allium bimetrale: B 22—25, Nomos Piraeus, Kithera, NW the town of Kithera, c. 150 m s.m. 25.5 1964 coll. BOTHMER; B 524, Nomos Euboea, Skiros, large vertical rocks facing NE just E the town of Skiros, 80—100 m s.m. 21.7 1966 coll. STRID; B 764, Nomos Kikladhes, Mikonos, Prassiounisi, the eastern island. 15.5 1968 coll. RUNEMARK & ENGSTRAND; B 770*, Nomos Kikladhes, Tinos, Panormos. 22.5 1968 coll. RUNEMARK & ENGSTRAND; B 771, Nomos Kikladhes, Tinos, the islet of Dragonisi. 22.5 1968 coll. RUNEMARK & ENGSTRAND; B 780*, Nomos Kephallinia, Kephallinia, in scopulis ad insulam, in saxosis calc. 7.6 1969 coll. PHITOS.

A. bourgaei: B 408, Nomos Dodekanisos, Karpathos, 6 km NW Pigadhia, limestone rocks, c. 160 m s.m. 9.7 1966 coll. BOTHMER & MELLQUIST; B 475*, Nomos Dodekanisos, Kasos, Plato Nisia, the eastern island, limestone rocks, c. 5 m s.m. 23.7 1966 coll. BOTHMER; B 530, Nomos Kikladhes, Tinos, 2 km ENE Kardiani, schist cliffs, c. 600 m s.m. 12.6 1964 coll. SNOGERUP; B 533, Nomos Kikladhes, Ios, 3 km N the town of Ios, small limestone rock, 250 m s.m. 21.6 1964 coll. SNOGERUP; B 774, Nomos Kikladhes, Siros, Ag. Varvaras. 30.5 1968 coll. RUNEMARK & BOTHMER.

A. ampeloprasum: B 773, Nomos Kikladhes, Tinos, Ag. Ioannis Ormos, field. 29.5 1968 coll. RUNEMARK & ENGSTRAND.

A. sphaerocephalum: B 526, Nomos Arkadhia, large vertical rocks facing NW, 3 km ENE Agiorgitika (c. 15 km E Tripolis), 820—860 m s.m. 12.7 1966 coll. STRID; B 747, Nomos Kikladhes, Kea, SE of the village of Kea, c. 400 m s.m. 1.6 1968 coll. SNOGERUP & BOTHMER.

A. descendens: B 7, Nomos Lakonias, 1—2 km ENE Areopolis, NW-exposed limestone cliffs, 700—750 m s.m. 21.5 1964 coll. BOTHMER.

Populations marked with an asterisk have been used in this paper for illustrations.

METHODS

Technique used in the Cytological Investigation

Vigorous root tips from young bulbs were treated according to a modification of the technique described by ÖSTERGREN and HENEEN (1962):
1. Plants of about three weeks age were well watered with fertilizer added and kept in strong light the day before fixation. *2.* Pretreatment of excised roots in a mixture of 0.3 % colchicine and 1 mM 8-hydroxyquinoline for three hours. *3.* Fixation in acetic alcohol (1 : 3). *4.* Staining in the Feulgen reagent for 2—3 hours after hydrolization in 1 N HCl for 8 min. *5.* Treatment in 5 % pectinase for 2—3 hours to dissolve the middle lamellae of the cell walls and facilitate squashing. The enzyme treatment also decolourises the cytoplasm. *6.* Squashing in 45 % acetic acid under a vipolon plastic cover slip, which is subsequently dissolved in acetone. *7.* Mounting in Permount after rinsing in acetone : xylene (1 : 1) and pure xylene.

Chromosome Measurements and Construction of Idiograms

Ten good metaphase plates with about the same degree of contraction were selected from each population, and drawn with the aid of a camera lucida at a constant magnification of 4770 diameters. Measurements were taken from the drawings.

The ordinary r-index (long arm/short arm ratio) was calculated for

Table 1. Nomenclature recommended for centromeric position by LEVAN et al. (1965), compared to terminology suggested by BATTAGLIA (1955).

Term	Location	r-value	Classification sensu BATTAGLIA (1955)
M	median point	1.0	isobrachial chromosome
m	median region	1.0—1.7	heterobrachial chromosome
sm	submedian region	1.7—3.0	heterobrachial chromosome
st	subterminal region	3.0—7.0	hyper-heterobrachial chromosome — monobrachial chromosome
t	terminal region	7.0—∞	hyper-heterobrachial chromosome — monobrachial chromosome
T	terminal point	∞	hyper-heterobrachial chromosome — monobrachial chromosome

each chromosome in each drawing, and the mean values for the population were worked out. In satellited chromosomes the length of the satellite, but not of the interspace, was added to the length of the arm. The length of an individual chromosome was expressed as a percentage of the total length of the haploid complement to allow comparisons between populations at different ploidy levels. Accessory chromosomes, when present, were not included in the complement, but their length was calculated as a percentage of the haploid complement.

Centromeric positions were described as recommended by LEVAN, FREDGA and SANDBERG (1965); see Table 1. In chromosomes with distal linear satellites (p. 526), a *satellite index* was calculated (SAT-i=distal portion/proximal portion ratio). This index was also used to describe the positions of weaker, "tertiary" constrictions (BURNHAM & HAGBERG 1956) indicated by dotted lines in the idiograms. A similar index was used in *Allium sativum* by BATTAGLIA (1963) to compare the typical "*sativum* satellite" (p. 526) with the long chromosome arm (long arm/linear satellite ratio).

The chromosomes have been classified into groups by means of r-index values and arranged according to decreasing relative length values within each group. With the exception of *A. descendens*, four such groups were recognized. The groups were given Roman numbers (I—IV), and the chromosome pairs Arabic numbers (1—8). Nos. (6—)7—8 are marker chromosomes, i.e., they can be unambiguously identified and have therefore been used for statistical calculations.

SOURCES OF ERROR IN KARYOTYPE ANALYSIS

Different authors have described the karyotypes in the closely related species *Allium cepa*, *A. fistulosum* and *A. ascalonicum* variously, but in

the opinion of BATTAGLIA (1957) "— — — all disagreements are due to different cytological techniques, to the use of varying terminologies, and to the little attention paid to the variability of chromosome length." This statement is important, since results obtained by different investigators in the same or similar materials ought to be directly comparable. Thus, the different sources of error in the determination of chromosome lengths should be taken into consideration as far as possible.

There is contradictory information as to the uniformity of contraction during the course of mitosis. SVÄRDSON (1945) found in *Salmonidae* and WICKBOM (1949) in Amphibian material that there was a positive correlation between length of arms and degree of shortening from early metaphase to anaphase, but BAJER (1959) could not find any differences in spiralization rate during the mitotic cycle in *Haemanthus* and *Leucojum*. However, this problem is likely to be small in a karyotype analysis compared with the errors arising in the technical procedure.

In the handling of chromosomes, especially the pre-treatments with colchicine, 8-hydroxyquinoline and other substances affect mitosis. SASAKI (1961) found in his studies of colchicine influence on mammalian chromosomes that "— — — in a given cell longer chromosomes tend to be more contracted than shorter ones" and "— — — a significant tendency for the centromere generally to be located in a more median position in the more highly contracted chromosome". As far as I know, no plants have been investigated in a similar way, but it seems reasonable to presume a similar tendency. In plants with undifferentiated and symmetrical karyotypes like *Allium* the effect is likely to be smaller than in species with highly differentiated chromosomes.

During the whole technical procedure for making slides there are many occasions when artifacts may occur, both mechanically, e.g., uneven squashing causing stretching of constrictions or chromosome segments, closely studied by SYBENGA (1959), and through the influence of chemical substances. When the measurements are taken other difficulties arise, e.g., how to estimate chromosome overlapping, vertical rises in the chromosomes etc. (SYBENGA 1959, LEWITSKY 1931, SIMAK 1962).

In *m* chromosomes with low r-values and no secondary constrictions, confusion or "reversal of arms" is possible. SIMAK (1962) calculated that in *Larix* the arm lengths must differ by more than 12 % (corresponding to r=1.27) to assure certain identification, but according to MATÉRN and SIMAK (1968) "the risk cannot be disregarded if the average

Table 2. A. Deviations from mean values of r- and SAT-indices in marker chromosomes in studies of ten cells from the same plant (*Allium bimetrale*, population B 524). Mean values for chromosome no. 7: r-index 1.63 (I), SAT-index 5.05 (IV); chromosome no. 8: r-index 2.57 (II), SAT-index 1.02 (III). B. Differences of r- and SAT-indices between homologous chromosomes in each of the ten investigated cells.

	I		II		III			IV	
	A	B	A	B	A	B		A	B
≤0.05	8	3	7	3	8	2	≤0.25	6	0
0.06—0.10	5	3	3	2	4	5	0.26—0.50	3	3
0.11—0.15	4	1	2	0	6	0	0.51—0.75	5	2
0.16—0.20	1	0	1	1	0	1	0.76—1.00	1	3
0.21—0.25	2	0	2	1	0	0	1.01—1.25	1	2
0.26—0.30	0	1	4	2	1	0	1.26—1.50	3	0
>0.30	0	2	1	1	1	2			

difference is less than 20 %" (corresponding to r=1.50). The error of reversal of arms will result in too high r-values, which is illustrated by chromosome no. 8 B in *Allium descendens* (Table 7). The presence of a secondary constriction made an unambiguous identification of arms possible. The r-value was 0.98. If the arms had not been identifiable the estimated r-value would have been 1.07.

The contraction of the individual chromosomes in a plate may not always be wholly synchronized, and in such cases identification of homologues based on relative length may lead to misidentification, "reversal of orders". In a polyploid or a species with minute size differences between the chromosomes, more than two chromosomes may be involved in the reversal.

Reversal of orders and arm reversals will both decrease the variance, which tends to confirm non-existent differences between chromosomes. The errors of reversals have been studied in detail by Essad et al. (1966) and Matérn and Simak (1968, 1969). They have suggested statistical methods based on variance analysis for avoiding reversals.

In *Allium*, with its very undifferentiated karyotype, the possibilities of errors being caused by reversals are extremely great and closer study of the whole chromosome complement is impossible with the usual methods. Investigations must consequently be restricted to a few marker chromosomes, i.e., in the present study nos. 7 and 8 and in some cases no. 6.

Due to the different kinds of sources of error outlined above, the present study must be regarded as a survey of the different chromosome types present, and the histograms constructed as partly "apparent idiograms" (Matérn & Simak 1968).

In order to elucidate the variation in the present material, deviations from mean values and differences between homologues in r- and SAT-indices for marker chromosomes of ten cells in one plant of *Allium bimetrale* are shown in Table 2 (cf. BENTZER 1969).

THE KARYOTYPE IN ALLIUM

Chromosome Numbers

About 300 out of the more than 500 *Allium* species are known with respect to chromosome numbers (cf. FEDOROV 1969). The basic numbers are 7, 8 and 9, 8 being by far the most common. For discussion concerning evolution of basic numbers see LEVAN (1935) and VED BRAT (1965 a). The frequencies of infraspecific polyploidy and aneuploidy are shown in Table 3.

A deviating chromosome number was reported by PEDERSEN and WENDELBO (1966 Fig. 1 C, p. 309), who found in *Allium chelotum* from Iran 2n=20 and with no telocentric chromosomes present; hence the karyotype had not evolved by misdivision of metacentric chromosomes. A similar karyotype was reported in two Russian species, *A. kujukense* and *A. decipiens* (VAKHTINA 1964 a). In *A. decipiens*, however, MENSINKAI (1939) counted 2n=16. Whether these three species really have a deviating basic number ($\times=10$) or if only a few individuals deviating from a "normal" basic number have been studied should be investigated more closely.

Polyploidy is a common phenomenon and polyploid series are often found. In *Allium neapolitanum*, for instance, 14-, 21-, 28- and 35-chromosomic plants are known (HATTERSLEY-SMITH 1956). In *A. nutans* all levels from di- to octoploids are reported, as well as aneuploids (LEVAN 1936 a), and this species also has the highest chromosome number in *Allium* known to the author, 2n=108=13×+4 (LEVAN op. cit.). Polyploidy above the hexaploid level, however, is very rare in the genus.

Table 3. Frequence of different chromosome numbers within the genus *Allium* (from FEDOROV 1969).

2n	14	16	17	18	20	24	28	32	Intraspecific polyploidy	Aneuploids	Σ
Number of species	48	122	1	6	1	1	4	23	47	18	271

Disturbances during meiosis giving rise to unbalanced gametes are known, e.g., in *Allium odorum*, *A. bakeri* (KATAYAMA 1936), and *A. paniculatum* (VED BRAT 1967), and some of the reported aneuploids may have originated in this way. In the normally 16- and 24-chromosomic *A. carinatum*, TSCHERMAK-WOESS (1947) found a huge hypertriploid clone with 2n=25 and some populations with 2n=26. Aneuploid individuals with 17 chromosomes in populations with normally 2n=16 are also found, e.g., in *A. pulchellum* (TSCHERMAK-WOESS & SCHIMAN 1960), *A. caspium* (VAKHTINA 1964 b), and *A. cardiostemon* (PEDERSEN & WENDELBO 1966). In *A. ochroleucum*, KHOSHOO and SHARMA (1959 b) found one population with 2n=19 beside the normal chromosome numbers 16 and 32.

New chromosome numbers may be formed by splitting of a metacentric chromosome into two telocentrics, which is not a rare phenomenon, studied, e.g., in *Allium rubellum* by VED BRAT (1967). KOLLMAN (1969) reported a good example in the *A. erdelii* group in sect. *Molium* from the Near East with ×=7 (partly outlined by FEINBRUN 1950, and EID 1963, 1964). In this group *A. qasyunense* was found to have 2n=14 (all *m*), *A. erdelii* 2n=16 (12 *m* and 4 *t*), and *A. negevense* 2n=20 (8 *m* and 12 *t*). *A. condensatum* 2n=17 (15 *m* and 2 *t*) has evolved in the same way (SATO 1942).

In sect. *Allium* the basic number is ×=8 with di- and tetraploid levels most frequent. Hexaploids are also present, as well as tri- and pentaploids.

Chromosome Morphology

In *Liliaceae* several genera have highly differentiated karyotypes, e.g., *Polygonatum* (THERMAN 1953), *Ornithogalum* (CULLEN & RATTER 1967), and *Leopoldia* (GARBARI 1968, 1969, and BENTZER 1969). As pointed out by several authors, e.g., LEVAN (1935), VAKHTINA (1964 b, 1965, and 1969), and VED BRAT (1965 a, b), there is no such structural variation in the genus *Allium*. The chromosomes are ± symmetrical (*msm* types) and *stt* chromosomes are rare (ANDERSON 1931). There is usually continuous transition from the biggest to the smallest chromosomes in an idiogram (SHOPOVA 1966, TSCHERMAK-WOESS 1947, and TSCHERMAK-WOESS & SCHIMAN 1960). Exceptions are *A. triquetrum*, *A. zebdanense*, *A. macranthum*, and *A. bidwelliae*, where the longest chromosomes are more than twice as long as the shortest ones (LEVAN 1932, 1935, and MENSINKAI 1939).

Satellites are found in one or two chromosomes in most species, and are nearly always attached to the short arm. The most frequent satellite type is the classical one in the sense of NAVASHIN (1912), small distal bodies connected to the arm by a thin thread ("*paniculatum*-type" sensu VED BRAT 1965 a). This type does not occur in sect. *Allium*. In the *ampeloprasum* group the following kinds of satellites are found:

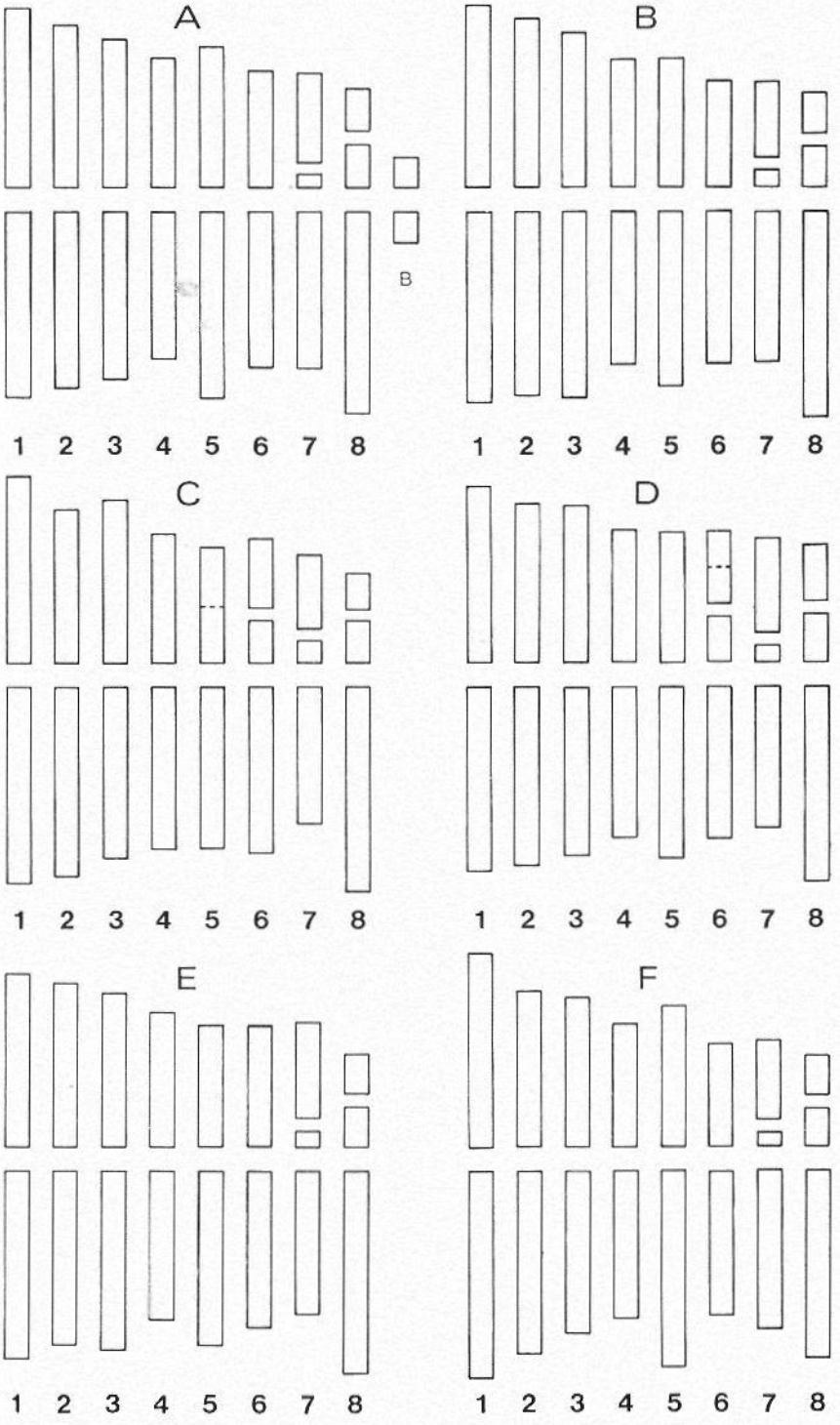
a. "*scorodoprasum*-type": the short arm of the chromosome has a ± median constriction (SAT-index = c. 1.0). This type is probably identical with the tandem satellites described by TAYLOR (1926) in *Allium cepa* or the tandem trabants in *Aucuba japonica* (MEURMAN 1929). In the *ampeloprasum* group this type of secondary constriction is found in chromosome no. 8 (r-index > 1.80). In some populations chromosome no. 6 has a similar secondary constriction, but can be distinguished from no. 8 by its lower relative length value and lower r-index.

b. "*sativum*-type": the short chromosome arm has a constriction near to the centromere region. In the *ampeloprasum* group chromosome no. 7 is of this type.

In both chromosome types the distal part of the short arm is a linear satellite sensu BATTAGLIA (1955). In *Allium porrum*, KURITA (1955) and KADRY and KAMEL (1955) reported both types of satellites. Surveys of satellite types in *Allium* have been made by LEVAN (1935) and VED BRAT (1965 a).

In vegetatively reproducing species cytological aberrations may easily become established. Many authors have reported variation in the marker chromosomes of *Allium* (cf. DYER 1963). Structural heterozygosity in satellited chromosomes is reported in several species, e.g., in *A. triquetrum*, *A. wakegi*, *A. schoenoprasum*, *A. ammophilum*, *A. paniculatum*, and *A. pallens* (KURITA 1953, 1958, LEVAN 1935, 1936 b, and VED BRAT 1965 a, 1966). EID (1956) found several inversions in *A. myrianthum*, partly identified in marker chromosomes, and KATO (1956) reported deficiency of the satellite in a commercial variety of *A. fistulosum*. KHOSHOO and SHARMA (1959 a) found, in a triploid population of *A.*

Fig. 1. Idiograms in the *Allium ampeloprasum* group. — A—B: *A. bimetrale;* A: population B 761, B: Pop. B 524; — C—E: *A. bourgaei;* C: Pop. B 408; D: Pop. B 533; E: Pop. B 530; — F. *A. ampeloprasum;* Pop. B 773.


A
B
1 2 3 4 5 6 7 8
B
1 2 3 4 5 6 7 8
C
1 2 3 4 5 6 7 8
D
1 2 3 4 5 6 7 8
E
1 2 3 4 5 6 7 8
F
1 2 3 4 5 6 7 8

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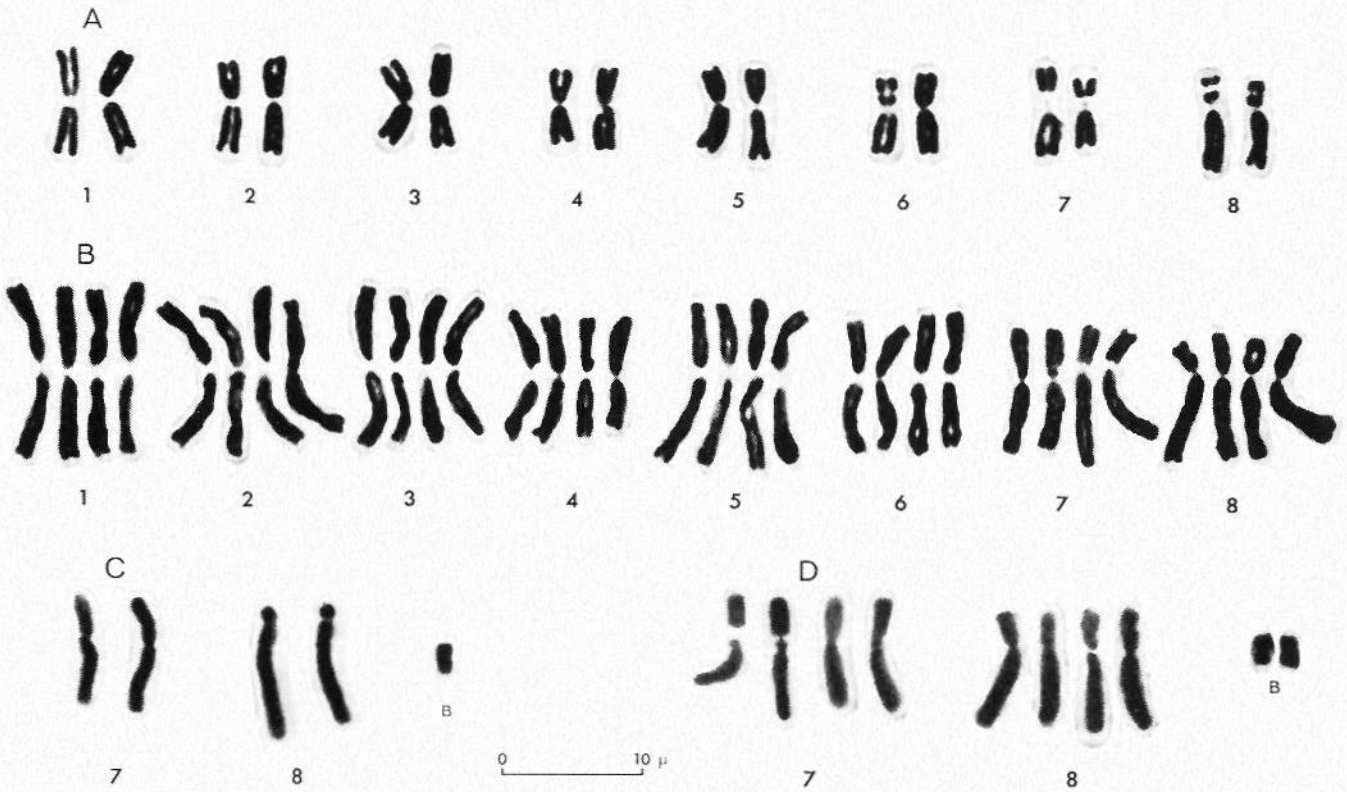

Fig. 2. Karyotypes from root-tip mitosis in *Allium bimetrale*. — A: Population B 780 (2×). — B: Pop. B 771 (4×). — C: Marker and accessory chromosomes Pop. B 770 (2× + B). — D: Pop. B 764 (4×+2B).

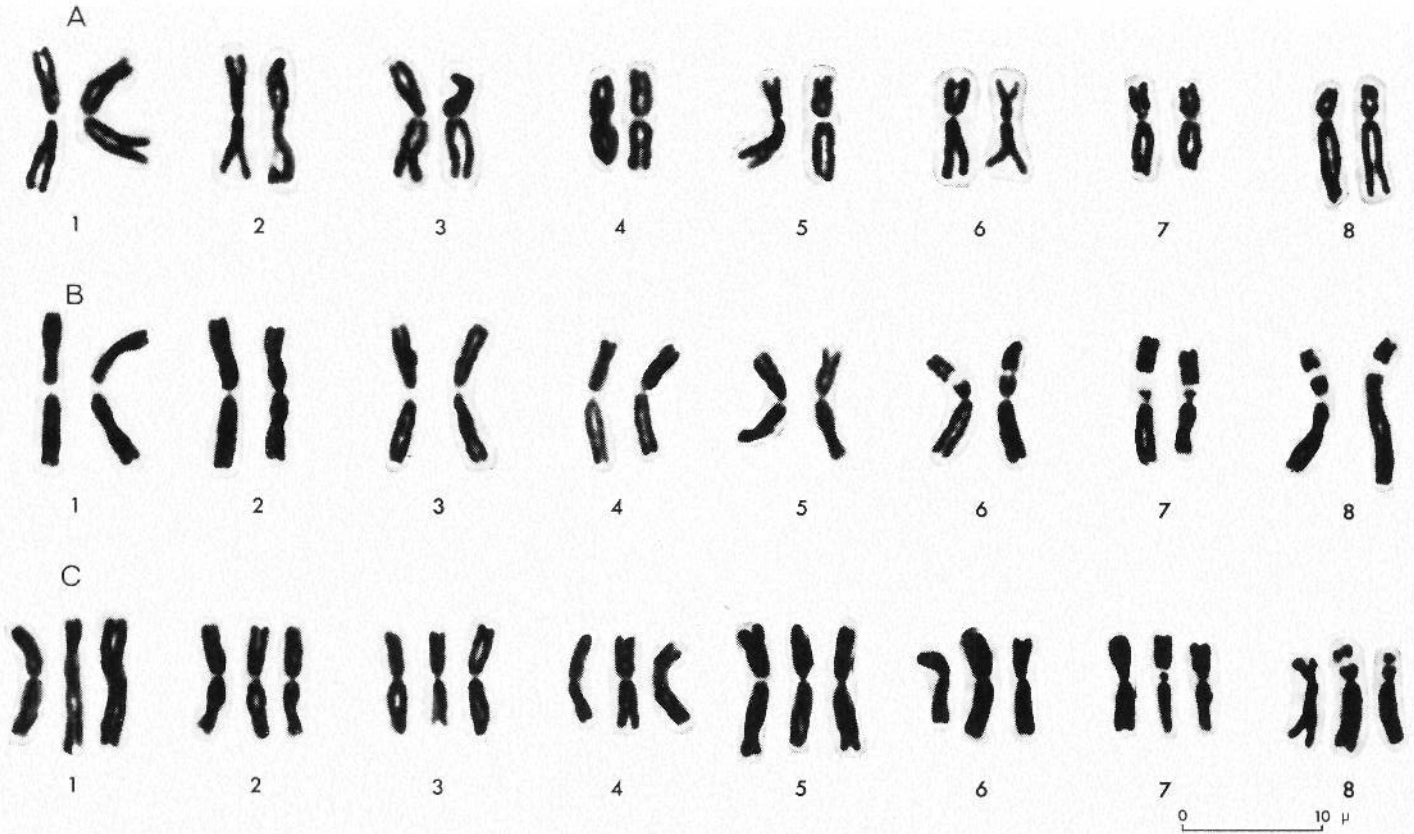

Fig. 3. Karyotypes from root tip mitosis in *Allium bourgaei*. — A: Population B 475 (2×). — B: Pop. B 533 (2×). — C: Pop. B 530 (3×).

Table 4. r- and SAT-index values for investigated populations of the *Allium ampeloprasum* complex and *Allium sphaerocephalum*. Concerning the grouping of chromosomes see pp. 521, 532 and 534.

Chromosome group no.		I					II		III		IV	
Chromosome no.		1	2	3	4	5	6		7		8	
							r	SAT-i	r	SAT-i	r	SAT-i
A. bimetrale	B 764 (4×)	1.05	1.08	1.13	1.14	1.31	1.34	—	1.53 ± 0.02	7.03 ± 0.18	2.37 ± 0.05	0.99 ± 0.03
	B 524 (2×)	1.05	1.09	1.21	1.19	1.36	1.43	—	1.63 ± 0.02	4.56 ± 0.18	2.57 ± 0.05	0.98 ± 0.04
	B 22—25 (2×)	1.10	1.05	1.22	1.21	1.30	1.47	—	1.54 ± 0.03	4.91 ± 0.18	2.89 ± 0.09	0.72 ± 0.02
A. bourgaei	B 408 (2×)	1.05	1.24	1.05	1.27	1.37	1.51 ± 0.01	1.63 ± 0.05	1.42 ± 0.01	3.42 ± 0.16	2.60 ± 0.04	0.85 ± 0.02
	B 533 (2×)	1.05	1.13	1.07	1.14	1.32	1.29 ± 0.02	1.63 ± 0.04	1.29 ± 0.02	5.76 ± 0.20	1.88 ± 0.03	1.17 ± 0.02
	B 530 (3×)	1.05	1.26	1.08	1.09	1.39	1.31	—	1.28 ± 0.02	6.69 ± 0.20	2.39 ± 0.05	0.98 ± 0.03
	B 774 (3×)	1.08	1.06	1.17	1.10	1.43	1.29	—	1.29 ± 0.02	5.99 ± 0.23	2.56 ± 0.05	0.98 ± 0.02
A. ampeloprasum	B 773 (4×)	1.06	1.18	1.08	1.19	1.39	1.40	—	1.71 ± 0.05	5.79 ± 0.23	2.45 ± 0.07	1.05 ± 0.03
A. porrum f. *elefant* (4×) (after MURIN 1964)		1.00	1.00	1.22	1.00	1.43	1.67	—	2.11	8.00	2.05	1.00
A. sphaero-cephalum	B 526 (2×)	1.10	1.09	1.11	1.11	1.23	1.25	—	1.05	13.93	1.48	—
	B 747 (2×)	1.07	1.11	1.06	1.10	1.26	1.35	—	1.70	5.32	1.29	1.83

Table 5. Relative length values for investigated populations of the *Allium ampeloprasum* complex and *Allium sphaerocephalum*. Concerning the grouping of chromosomes see pp. 521, 532 and 534.

Chromosome group no.		I				II		III	IV
Chromosome no.		1	2	3	4	5	6	7	8
A. bimetrale	B 761 (4×)	14.95	13.86	12.93	11.31	13.39	11.17	10.60 ± 0.10	11.79 ± 0.11
	B 524 (2×)	15.29	14.49	13.98	11.52	12.40	10.60	9.94 ± 0.14	11.78 ± 0.09
	B 22—25 (2×)	16.04	14.20	13.80	12.46	11.58	10.68	9.76 ± 0.07	11.44 ± 0.14
A. bourgaei	B 408 (2×)	15.75	14.10	13.70	12.00	11.39	11.53 ± 0.21	9.63 ± 0.13	11.75 ± 0.18
	B 533 (2×)	14.83	13.89	13.36	11.65	12.44	11.16 ± 0.22	10.39 ± 0.12	12.29 ± 0.12
	B 530 (3×)	14.82	14.74	13.42	11.39	12.62	11.16	10.56 ± 0.10	11.25 ± 0.13
	B 774 (3×)	14.93	13.96	13.71	11.66	12.21	11.42	10.49 ± 0.09	11.57 ± 0.14
A. porrum f. *elefant*	(4×) (4×)	18.84	14.13	12.87	9.42	14.13	10.20	10.38 ± 0.20	10.91 ± 0.24
A. porrum f. elefant (after MURIN 1964)	(4×)	18.84	14.13	12.87	9.42	14.13	11.30	8.79	10.52
A. sphaero-cephalum	B 526 (2×)	14.07	13.06	12.03	11.08	12.74	11.17	13.71	12.16
	B 747 (2×)	15.16	14.33	13.28	11.41	12.18	10.28	12.11	11.20

rubellum, structural heterozygosity in six marker chromosomes, the satellites of which were all dissimilar. On the basis of structural heterozygosity in satellited chromosomes, TSCHERMAK-WOESS (1947, 1964) and TSCHERMAK-WOESS and SCHIMAN (1960) could recognize different clones of *A. carinatum* and *A. pulchellum*. Concerning the cytological variation in *A. cepa*, *A. fistulosum* and *A. ascalonicum* see p. 521.

Accessory Chromosomes

Several species of *Allium* are known to have accessory chromosomes (partly reviewed by SHOPOVA 1966, cf. also FEDOROV 1969). They occur in most sections of the genus and may be differently shaped, but two types seem to be most common: 1) rather large subtelocentrics [seldom telocentrics, *stt* r≥(2.5—) 3.0] equal to or exceeding half the length of the normal chromosomes, e.g., in *A. angulosum*, *A. nutans*, *A. senescens* (SHOPOVA 1966), *A. pulchellum* (TSCHERMAK-WOESS & SCHIMAN 1960), *A. sphaerocephalum* (KURITA 1956, see p. 535), and *A. paniculatum* (VED BRAT 1965 a). 2) minute bodies with different centromeric positions, mostly *sm* and *st*, e.g., in *A. cernuum* (GRUN 1959), *A. stracheyi* (SHARMA & AIYANGAR 1961), and *A. porrum* (LEVAN 1940, NYBOM 1947, VOSA 1966). In *A. porrum*, VOSA (op. cit.) described subtelocentric B-chromosomes arisen by deletion of a part of the shorter arm in the normally submetacentric B-chromosomes. This derivative was present in nearly all investigated varieties of the species.

Accessory chromosomes of type no. 1 occur in low numbers (often single) when present in a specimen. Type no. 2 is more numerous (e.g., 2—10 in *Allium stracheyi* and up to 5 in *A. porrum*).

Both types of B-chromosomes are present in sect. *Allium*, no 1 in *A. sphaerocephalum* (p. 535), and no. 2 in *A. porrum* and *A. bimetrale* (p. 533).

RESULTS

CYTOLOGIC OBSERVATIONS IN THE ALLIUM AMPELOPRASUM COMPLEX

The following four chromosome groups are recognized:

group no. I: chromosome no. 1—4; r=c. 1.00—1.30 (*m*).

— II: chromosome no. 5—6; r=c. 1.30—1.50 (*m*); in some populations chromosome no. 6 has a linear satellite of "*scorodoprasum*-type".

group no. III: chromosome no. 7; r=c. 1.25—1.75 (*msm*), with a linear satellite of "*sativum*-type".

— IV: chromosome no. 8; r=c. 1.80—2.90 (*sm*), with a linear satellite of "*scorodoprasum*-type".

1. **Allium bimetrale** Gandog.

2n=16 (2×) was found in 14 populations, 2n=24 (3×) in 4 populations, and 2n=32 (4×) in 34 populations. Five populations were mixed and had clones with different chromosome numbers. The distribution of populations investigated as to chromosome numbers is shown in Fig. 7. The number of accessory chromosomes found varied between 0 and 4, usually 2 with a median centromere. No chromosome counts have been reported previously.

Populations studied in detail: B 764 (4×), B 524 (2×), and B 22—25 (2×). Figs. 1 A—B, 2. Tables 4—5.

2. **Allium bourgaei** Rech. fil.

2n=16 (2×) was found in 28 populations, 2n=24 (3×) in 6 populations, 2n=32 (4×) in 1 population, and mixed numbers in 2 populations (2× and 3× in one, and 2× and 4× in the other). The distribution of investigated populations is shown in Fig. 6 A, and the distribution of different chromosome numbers on the island of Siros in Fig. 6 B. No chromosome counts have been reported previously.

Populations studied in detail: B 408 (2×), B 533 (2×), B 530 (3×), and B 774 (3×). Figs. 1 C—E, 3. Tables 4—5.

The two diploid populations were both found to have linear satellites in chromosome no. 6. Population B 408 had a tertiary constriction in chromosome no. 5 (SAT-index c. 1.0) and B 533 in the linear satellite of chromosome no. 6 (SAT-index c. 1.2).

3. **Allium ampeloprasum** L.

2n=32 (4×) was found in 18 populations, 2n=40 (5×) in 7 populations, and 2n=48 (6×) in 12 populations. No accessory chromosomes were found.

Previous reports: 2n=16 Renzoni (1964). — 2n=32 Maude (1940),

VED BRAT (1965 a, b), KOUL & GOHIL (1970). — 2n=48 KHOSHOO et al. (1960), VED BRAT (1965 a).

Population studied in detail: B 773 (4×). Figs. 1 F, 4. Tables 4—5.

MURIN (1964) made a cytological investigation of *Allium porrum* forma *elefant* from Czechoslovakia. He applied an inverted arm index value (r=s/l instead of r=l/s) and also used a different method to represent the length of the chromosomes. As the cultivated leek is closely related to the investigated complex and esp. to *A. ampeloprasum* s. str., a comparison has been made between the present material and the cultivated Czechoslovakian form of *A. porrum*. From the figures given by MURIN comparable index values and relative length values have been calculated (Tables 4, 5). The karyotypes are remarkably similar and all chromosome groups in the *ampeloprasum* group can be distinguished also in the leek.

In their investigation of a cultivated, tetraploid form of *Allium ampeloprasum*, KOUL and GOHIL (1970) recognized 8 chromosomes with secondary constrictions and the same type of linear satellites as found in the present study, but a closer comparison is unfortunately impossible since no quantitative data (r-index and rel. lengths) were given. However, it appears from the picture (op. cit. p. 14. Fig. 2) that all four chromosome groups recognized in the present study are represented. These authors also described structural heterozygosity in all chromosome pairs but, as outlined in the discussion of sources of error (p. 521), closer studies in non-marker chromosomes must be very uncertain and dubious.

CYTOLOGIC OBSERVATIONS IN ALLIUM SPHAEROCEPHALUM L.

2n=16 (2×) was found in 10 populations. Previous reports: 2n=16: LEVAN (1930, 1931, 1935), TSCHERMAK-WOESS (1947), FERNANDES (1950), DIANNELIDIS (1951), KURITA (1956, see below). — 2n=32: MARTINOLI (1955).

4 chromosome groups were recognized:

group no. I: chromosome no. 1—4; r=c. 1.00—1.15 (*m*).
— II: chromosome no. 5—6; r=c. 1.20—1.35 (*m*).
— III: chromosome no. 7; r=c. 1.00—1.70 (*msm*), with a linear satellite of "*sativum*-type".
— IV: chromosome no. 8; r=c. 1.25—1.50 (*m*), 1 population with a linear satellite of "*scorodoprasum*-type".

Fig. 4. Marker chromosomes from root-tip mitosis in *Allium ampeloprasum*. Upper row: chromosome no. 7; lower row, chromosome no. 8.

Populations studied in detail: B 526 (2×) and B 747 (2×). Fig. 5 A—B, D. Tables 4—5.

In B 747 a *sm* accessory chromosome was found. In material from Portugal KURITA (1956) found ×=9 and reported this as a new basic number for *Allium sphaerocephalum*. The 9th chromosome identified by KURITA in the haploid set corresponds to the B-chromosome found in B 747. The arm index and relative length values in B 747 are 2.62 and 2.41, respectively, and in KURITA's material 3.25 and c. 2.30, respectively. He also found four marker chromosomes in the Portuguese material, viz., two with satellites of "*scorodoprasum*-type" (e and h), one with a satellite of "*sativum*-type" (f), and one with a secondary constriction in the long arm (g, SAT-index c. 1.0). In karyotypes published by other authors two chromosomes in the haploid set have secondary constrictions, but the linear satellites seem to vary in size. In the present material two marker chromosomes in the haploid set occurred in one population (B 747), but only one in the other (B 526).

CYTOLOGIC OBSERVATIONS IN ALLIUM DESCENDENS L.

2n=16 (2×) was found in 4 populations, 2n=24 (3×) in 1 population, and 2n=32 (4×) in 1 population. No chromosome numbers have been reported previously.

Population studied in detail: B 7 (2×). Fig. 5 C, E. Table 6.

The idiogram for *Allium descendens* differs remarkably both from the *ampeloprasum* group and from *A. sphaerocephalum*. Chromosomes nos. 6—8 were found to have satellites of "*sativum*-type" and the investigated population was structurally heterozygous in chromosome pair no. 8.

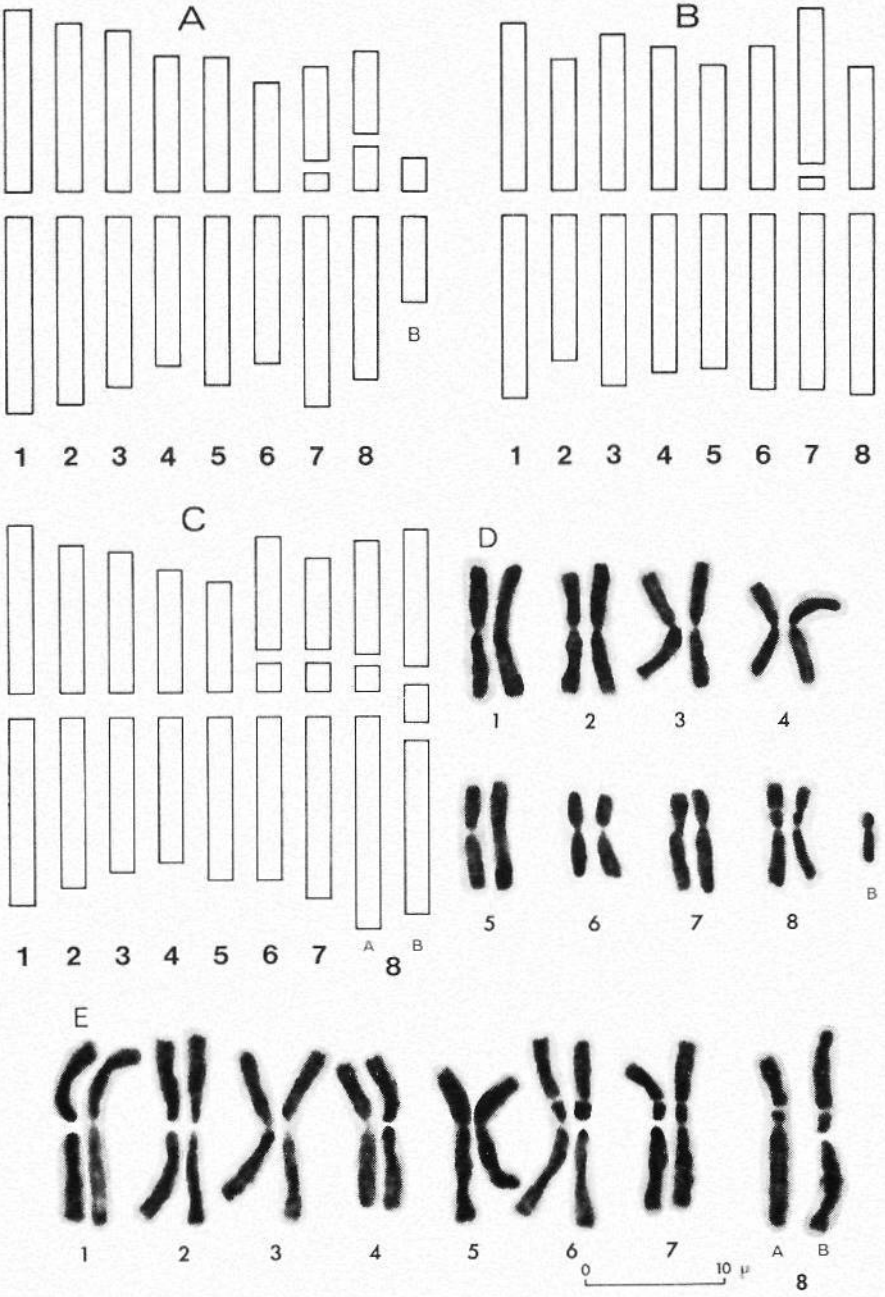

Fig. 5. Karyotypes from root-tip mitosis and idiograms in *Allium sphaerocephalum* (A, B, D) and *Allium descendens* (C, E). — A, D: Population B 717 (2×+B). — B. Pop. B 526 (2×). — C, E. Pop. B 7.

Table 6. Relative length (B), r- and SAT-index values (A) for one population (B 7) of *Allium descendens*.

Chromosome no.	1	2	3	4	5	6		7		8 A		8 B	
						r	SAT	r	SAT	r	SAT	r	SAT
A	1.11	1.16	1.09	1.19	1.49	1.15	3.86	1.52	3.19	1.52	4.48	1.52	4.42

Chromosome no.	1	2	3	4	5	6	7	8
B	14.28	12.79	11.89	10.77	11.51	12.28	12.18	14.13

The homologous chromosomes in the 8th pair had the same length but differed with respect to the short arm. In 8 A the intercalary segment, i.e., the segment between the centromere and secondary constriction, clearly belonged to the shorter arm, but in 8 B it was impossible to distinguish between the centromere and the secondary constriction. If the intercalary segment was referred to the longer arm, about the same r- and SAT-indices were obtained as in 8 A, even if the arms and satellites were of different lengths (Fig. 5 C, E). If the intercalary segment was referred to the shorter arm quite different indices were obtained, and the r value varied around 1.00 (Table 7).

Table 7. A comparison between different r- and SAT-indices in chromosome 8 B in populations B 7 of *Allium descendens* (three plants) obtained when the intercalary segment is referred to A) the long chromosome arm, and B) the short chromosome arm. Within brackets the values obtained if no constriction had been present between the segment satellite and the short chromosome arm.

r-index			SAT-index	
A	B		A	B
1.60	1.02	(1.02)	4.61	3.50
1.36	0.88	(1.13)	4.37	3.95
1.46	0.96	(1.04)	4.77	3.95
1.59	1.04	(1.04)	4.95	3.74
1.45	1.04	(1.04)	4.11	4.89
1.95	1.09	(1.09)	3.70	2.41
1.53	1.02	(1.02)	5.05	3.95
1.35	0.81	(1.23)	3.50	—
1.47	1.00	(1.00)	5.22	4.22
1.47	0.94	(1.07)	4.53	3.62
M 1.52	0.98	(1.07)	M 4.42	3.80

Table 8. t-values obtained by comparing arm indices for chromosome no. 7 in different populations of the *Allium ampeloprasum*-complex.

		B 764	B 524	B 22—25	B 408	B 533	B 530	B 774	B 773
A. bimetrale	B 764	—							
	B 524	3.54**							
	B 22—25	0.28	2.50*						
A. bourgaei	B 408	4.20***	9.39***	3.80**					
	B 533	8.49***	12.02***	6.93***	5.81***				
	B 530	8.84***	12.38***	7.21***	6.26***	0.35			
	B 774	8.49***	12.02***	6.93***	5.81***	0.00	0.35		
A. ampelo-prasum	B 773	3.31**	1.49	2.92**	5.69***	7.80***	7.99***	7.80***	—

Table 9. t-values obtained by comparing SAT-indices for chromosome no. 7 in different populations of the *Allium ampeloprasum*-complex.

		B 764	B 524	B 22—25	B 408	B 533	B 530	B 774	B 773
A. bimetrale	B 764	—							
	B 524	9.70***							
	B 22—25	8.33***	1.38						
A. bourgaei	B 408	14.99***	4.73***	6.19***					
	B 533	4.72***	4.46***	3.16**	9.14***				
	B 530	1.26	8.92***	6.62***	12.77***	3.29**			
	B 774	3.56**	4.90***	3.70**	9.17***	0.76	2.30*		
A. ampelo-prasum	B 773	4.25***	4.21***	3.01**	8.46***	0.10	2.95*	0.62	—

Table 10. t-values obtained by comparing relative length values for chromosome no. 7 in different populations of the *Allium ampeloprasum*-complex.

		B 764	B 524	B 22—25	B 408	B 533	B 530	B 774	B 773
A. bimetrale	B 764	—							
	B 524	3.84***							
	B 22—25	6.88***	1.15						
A. bourgaei	B 408	5.91***	1.62	0.88					
	B 533	1.34	2.44*	4.54***	4.30***				
	B 530	0.89	3.60**	6.55***	5.67***	1.09			
	B 774	0.82	3.31**	6.40***	5.44***	0.67	0.52		
A. ampelo-prasum	B 773	0.98	1.80	2.93**	3.14**	0.04	0.81	0.50	—

Table 11. t-values obtained by comparing arm indices for chromosome no. 8 in different populations of the *Allium ampeloprasum*-complex.

		B 764	B 524	B 22—25	B 408	B 533	B 530	B 774	B 773
A. bimetrale	B 764	—							
	B 524	2.83*							
	B 22—25	5.05***	3.10**						
A. bourgaei	B 408	3.59**	0.47	2.94**					
	B 533	8.40***	11.83***	10.65***	11.40***				
	B 530	0.28	2.55*	4.86***	3.28**	8.75***			
	B 774	2.69*	0.14	3.21**	0.63	11.66***	2.40*		
A. ampelo-prasum	B 773	0.93	1.40	3.86**	1.86	7.48***	0.70	1.27	—

Table 12. t-values obtained by comparing SAT-indices for chromosome no. 8 in different populations of the *Allium ampeloprasum*-complex.

		B 764	B 524	B 22—25	B 408	B 533	B 530	B 774	B 773
A. bimetrale	B 764	—							
	B 524	0.20							
	B 22—25	7.49***	5.81***						
A. bourgaei	B 408	3.88**	2.91**	4.60***					
	B 533	4.99***	4.25***	15.91***	11.32***				
	B 530	0.24	0.00	7.21***	3.61**	5.27***			
	B 774	0.28	0.00	9.19***	4.60***	6.72***	0.00		
A. ampelo-prasum	B 773	1.41	1.40	9.15***	5.55***	3.33**	1.65	1.94	—

Table 13. t-values obtained by comparing relative length values for chromosome no. 8 in different populations of the *Allium ampeloprasum*-complex.

		B 761	B 524	B 22—25	B 408	B 533	B 530	B 774	B 773
A. bimetrale	B 764	—							
	B 524	0.07							
	B 22—25	1.97	2.04						
A. bourgaei	B 408	0.19	0.15	1.36					
	B 533	3.07**	3.40**	4.61***	2.50*				
	B 530	3.17**	3.35**	1.00	2.25*	5.88***			
	B 774	1.24	1.26	0.66	0.79	3.91**	1.68		
A. ampelo-prasum	B 773	3.33**	3.39**	1.91	2.80*	5.14***	1.25	2.38*	—

COMPARISON BETWEEN POPULATIONS IN THE ALLIUM AMPELOPRASUM COMPLEX

In the eight populations which were investigated in detail the marker chromosomes were compared with respect to arm index (r), SAT-index, and relative length. t-tests were carried out for chromosomes nos. 7 and 8, and in two populations (B 408 and B 533) also for chromosome no. 6. The t-values obtained by comparing the respective mean values for homologous chromosomes are presented in Tables 8—14. In many cases the differences between populations are highly significant (one, two, and three asterisks indicate significances at the 5 %, 1 %, and 0.1 % levels, respectively), and t-values >10 occur, esp. for B 533, indicating greater differences between compared populations. The differences between B 530, B 774, and B 773 are minute, though the last-mentioned population belongs to *Allium ampeloprasum* and the other two to *A. bourgaei*.

From the data presented in Table 8—15 some conclusions can be drawn about the material investigated: *1.* variation in chromosome no. 7 is greater than in no. 8. *2.* Variation in r- and SAT-indices are of about the same magnitude and greater than in rel. length. *3.* Populations B 22—25, B 408, and B 533 show the biggest cytological deviations from the rest of the populations. In B 533, and probably also in B 408, the cytological differences are correlated with morphological ones (BOTHMER unpublished), and those two populations both have the constricted chromosome no. 6, which is lacking in the rest of the material.

DISCUSSION

Reproduction

The evolutionary pattern in *Allium is* complicated and partly dependent on the different modes of reproduction in the genus. A characteristic feature is the high rate of asexual reproduction including agamospermy (HÅKANSSON 1951). VED BRAT (1965 b) reported that c. 60 % of the species in the genus reproduce vegetatively. Meiosis and even flowering is absent in some species, e.g., *A. rubellum* (KHOSHOO & SHARMA 1959 a), *A. nipponicum* and *A. bakeri* (KATAYAMA 1936). These species must of course be regarded as evolutionary blind alleys but may in a stable environment be theoretically immortal. Such examples from other plant groups are, e.g., *Salix*, *Quercus* and *Arctostaphylos*, which sprout from roots and may have a life span approaching that of the plant community

Table 14. t-values obtained by comparing: A. r-index, B. SAT-index, and C. Rel. length values for chromosome no. 6 in two populations of *Allium bourgaei*.

		B 408
B 533	A.	9.84***
	B.	0.00
	C.	1.22

Table 15. A survey of significances in the Tables 8—13. In the three figure combination the first figure indicates number of significances at the 0.1 % level, the second figure number of significances at the 1 % level, and the third figure number of significances at the 5 % level.

		B 764	B 524	B 22—25	B 408	B 533	B 530	B 774	B 773
A. bimetrale	B 764	—							
	B 524	2–1–1							
	B 22—25	4–0–0	1–1–1						
A. bourgaei	B 408	3–2–0	2–1–0	2–2–0					
	B 533	4–1–0	4–1–1	5–1–0	5–0–1				
	B 530	1–1–0	2–2–1	5–0–0	3–2–1	3–1–0			
	B 774	1–1–1	2–1–0	3–2–0	4–0–0	2–1–0	0–0–2		
A. ampeloprasum	B 773	1–2–0	1–1–0	1–4–0	3–1–1	3–1–0	1–0–1	1–0–1	—

itself (STEBBINS 1950). The different modes of asexual reproduction, however, preserve a genetic stability which is not desirable from an evolutionary point of view. The genetic variations obtained are gene mutations, structural changes in the chromosomes, and changes in chromosome numbers through non-disjunction or polyploidisation. An example of the last-mentioned phenomenon was found in *A. stracheyi*, which in cultivation very rapidly (within a month) converted mitotically from di- to tetraploid level (SHARMA & AIYANGAR 1961). In a huge clone of *A. myrianthum* EID (1956) found 2n=33 formed by non-disjunction.

Most species of *Allium* have a ± normal sexual reproduction beside formation of bulbils. This increases the genetic variability and hence the evolutionary fitness of the species. Sexual reproduction will also increase cytological polymorphism, and aberrations arisen in this way may well be established in a population and increase in numbers by clonation.

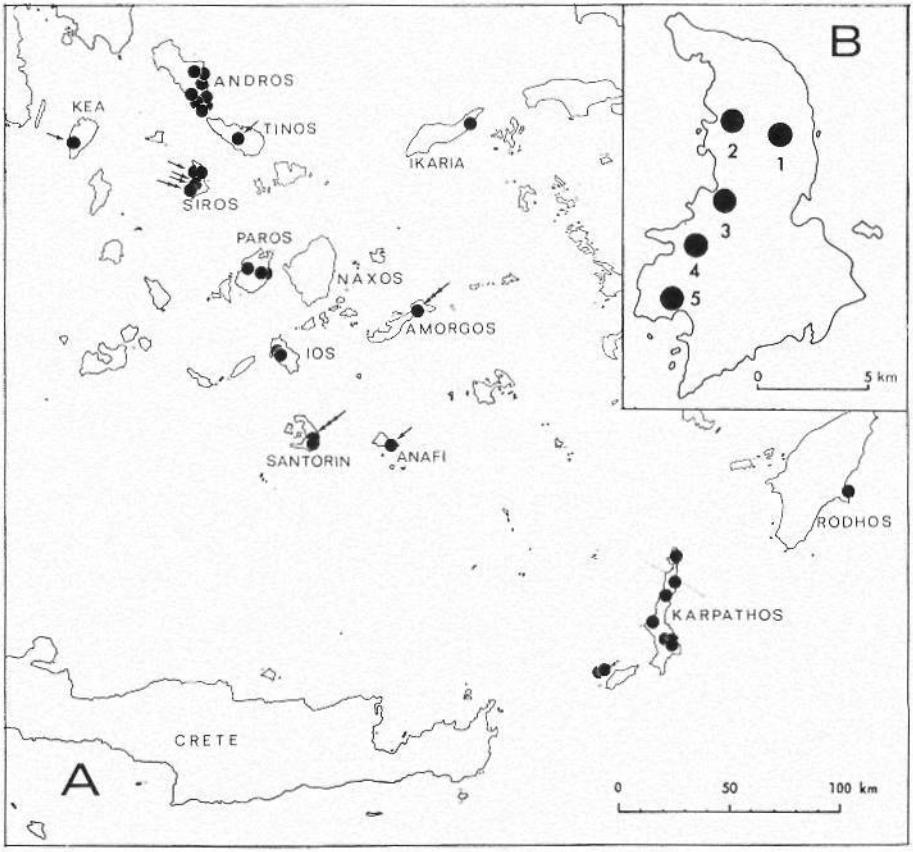

Fig. 6. *Allium bourgaei*. A: Distribution of different chromosome numbers. 2×: dots without arrows, 3×: single arrows, 4×: double arrow, mixed populations: three double arrows. — B: Distribution of different chromosome numbers in the island of Siros. 2×: no. 1, 3×: nos. 2—4, 4×: no. 5.

Chromosome Numbers

The basic chromosome number in the whole sect. *Allium* is ×=8. In *A. bourgaei* only diploid plants were found in the SE Aegean form series (Fig. 6). In the Kikladhian form series triploid plants occurred frequently in two centres (Siros-Tinos-Kea and Amorgos-Santorin-Anafi, Fig. 6 A). On Siros (Fig. 6 B) one di- and one tetraploid population were found on different sides of the island and three triploid populations were discovered in the area between them, suggesting hybridization between the two different ploidy levels. A similar case was reported by KURITA

and KUROKI (1964) in *A. gray* from Japan, where pentaploids occurred in the region between tetra- and hexaploid populations.

If the triploid populations of *Allium bourgaei* in the Kikladhes consist of one or a few clones they must be old relicts, since there has been no land connection between most of the islands at least since the Riss glaciation (SNOGERUP 1967) and recent long distance migration is highly improbable. It seems more likely that the deviating populations have originated separately with the exception of some triploids on Siros, which might be members of a larger clone.

Allium bimetrale shows a more scattered picture as to chromosome numbers than *A. bourgaei*. The tetraploid level is the most common but neither di- nor triploids are rare. The diploids have two distribution centres, one in southwestern Kikladhes (Fig. 7), where six populations were found, and one around the island of Skiros in the Northern Sporades, where three diploid populations have been discovered. One islet close to Skiros has a triploid population, another a mixed one with all three (2×, 3× and 4×) ploidy levels present, but no pure tetraploid populations have been found in this area. With the exceptions of the two diploid centres the distribution of 2×, 3× and mixed populations are ± at random in the Aegean.

In *Allium bimetrale* the evolutionary pattern appears to be more complicated than in *A. bourgaei*, partly owing to the biotope. As already mentioned (p. 519), *A. bimetrale* grows mainly on minute islands poor in species. These species are subject to "reproductive drift" and distributed more or less at random (RUNEMARK 1969). In *A. bimetrale* big, two-coated bulbils are frequently formed, which are able to survive in water for a long time (unpublished experimental data) and may be hydrochorously dispersed between islands. The big and vigorous bulbils are likely to establish themselves relatively easily in new communities and may subsequently compete successfully with other species. Several islets have been found crowded with flowering specimens and millions of bulbs of *A. bimetrale* and none or very few individuals of other species. It is an aggressive species only in its special environment and is remarkably rare on bigger islands.

Allium ampeloprasum is a weedy plant in its entire distribution range and has reached the tetra- (penta-) and hexaploid levels. It differs markedly in the asexual reproduction from the other two species in the group by the extreme formation rate of bulbils, which is at least three times as high as in *A. bourgaei* and *A. bimetrale* (GALIL 1965 a, b, and BOTHMER unpublished). This gives *A. ampeloprasum* an advantage in the

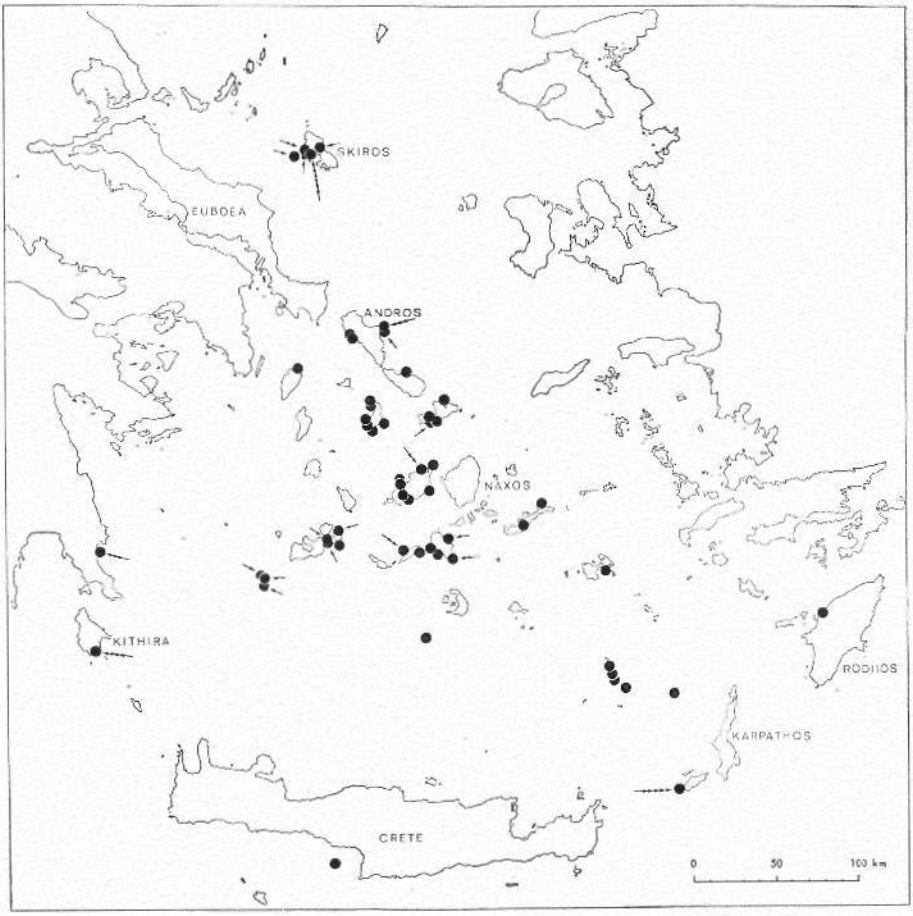

Fig. 7. *Allium bimetrale*. Distribution of different chromosome numbers. 4×: dots without arrows, 2×: single arrows, 3×: double arrows; mixed populations: 2× and 3×: three double arrows, 2× and 4×: four double arrows, 3× and 4×: five double arrows, 2×, 3×, and 4×: six double arrow.

competition with other species in invading disturbed or open habitats.

Populations with unbalanced chromosome numbers are a common feature in many species in *Allium* (p. 525), and in the present group triploids (and pentaploids) appear ± regularly. Triploid individuals may originate in two different ways: *1.* fusion of one normal haploid and one unreduced gamete. *2.* hybridization between diploid and tetraploid

individuals. The tetraploid level can be reached by fusion of two unreduced gametes or by somatic autotetraploidization.

The three species in the *ampeloprasum* complex in the Aegean have attained different frequencies of polyploidy and may represent different "evolutional levels". Primarily all of them must have been diploid. This is still the normal condition in *Allium bourgaei* but some populations have higher chromosome numbers (3× and 4×), which may indicate an incipient evolutional process. In *A. bimetrale* this process is almost finished as the tetraploid level is ± regularly established. *A. ampeloprasum* reached the tetraploid level long ago and is now evolving towards higher polyploidy. If this hypothesis is correct the *ampeloprasum* complex is well suited for a study of a plant group in active evolution.

The reasons for such polyploidisation processes are two: *1.* random fixation in course of time 2. The polyploid condition has evolved on the basis of a higher selective value. An indication for a selective advantage with a higher polyploid level is possibly found in *A. bourgaei*, where some populations with higher chromosome numbers occur, not in the closed chasmophytic community, where they normally belong, but in ± open habitats, e.g. rocky phrygana vegetation and terraces (± weedy), where other competition factors are present. TSCHERMAK-WOESS (1964) found in *A. carinatum* that triploid populations occurred in disturbed habitats and diploids in natural ones.

The diploid condition in *Allium sphaerocephalum*, and possibly also in *A. descendens*, appears to be more stable than in the *ampeloprasum* group, and evolution in these species proceeds in other ways.

Chromosome Morphology

DIANNELIDIS (1951) considered on the basis of similarities in SAT-chromosomes that *Allium margaritaceum* and *A. sphaerocephalum*, though morphologically rather dissimilar, are closely related. In genera like *Allium*, with its extremely stable karyotype any conclusions of relationships based on chromosome similarities on the species level must be very uncertain (cf. SZELUBSKY 1950, and KHOSHOO & SHARMA 1959 a).

The present investigation shows that groups of species in the genus have similar chromosome morphology. Minute differences occur but these may be of the same magnitude between different populations within one species as between species in the group (cf. Tables 4—5).

In *Allium descendens* the chromosome morphology deviates markedly from other species in the section. It is often referred to as a subspecies of *A. sphaerocephalum* but considering the karyological stability in the genus it is probably more distantly related. Morphological data also indicate that *A. descendens* is more isolated, and possibly distantly related to *A. chamaespathum* BOISS.

In most species of *Allium* marker chromosomes are present (p. 526), and in the *ampeloprasum* group two (or sometimes three) secondarily constricted chromosomes occur with linear satellites of "*sativum*" and "*scorodoprasum*-type". Minute though significant differences have been found between different populations and in the further cytological work only the variation in chromosomes nos. (6—) 7—8 will be studied. Variation in the rest of the chromosome complement certainly exists but is impossible to detect with the method used (see p. 522). The three characters r-index, SAT-index and rel. length appear to be useful for cytological work on the population level. The karyological variation within as well as between populations and variation in frequency of accessory chromosomes will be studied in combination with investigations of morphological and possibly also chemical variation.

The main aim of further investigations will be to clarify the structure of populations and rate of clonation, especially in *Allium bimetrale*, where it can be assumed that several clones are widespread in the archipelago.

ACKNOWLEDGEMENTS

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Current Topics

Parallelism, Convergence, and Analogy in Some South African Genera of Leguminosae

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ABSTRACT

DAHLGREN, R.: Current Topics. Parallelism, Convergence, and Analogy in Some South African Genera of Leguminosae. — Bot. Notiser 123: 551—568, Lund.

The article was inspired by the fact that in J. HUTCHINSON, The Genera of Flowering Plants, the three genera *Borbonia*, *Euchlora*, and *Rafnia* were placed together to form a separate tribe, the *Borbonieae*. Evidence is presented to show that this tribe is more probably artifical. The "primitively simple leaves", the most important diagnostic character of *Borbonieae*, 1) are presumably secondarily simple, and 2) have attained the simple form in different ways and along different lines of evolution.

The conception of the *Borbonieae* as a tribe is therefore dismissed, but can be regarded as a good example of *convergence* in evolution. Another presumable case of convergence with regard to leaf development is shown in the genus *Lebeckia*. The occurrence in the genus *Aspalathus* of simple leaves within two entirely different groups of species is presented as an example of *parallelism*. Evolutional *analogy* is demonstrated by the different kinds of spine protection in *Aspalathus*, the spines being leaflet apices, protracted leaf bases, short lateral (branchlet) thorns, and terminal (branch) thorns.

The genera *Lebeckia*, *Wiborgia*, *Rafnia*, and *Aspalathus* (including *Borbonia*) are believed to be closely allied genera, which should be placed in the same tribe whatever its extent. Beside certain floral similarities, such as the shape of petals and staminal tube, and the absence of strophiole on seeds, these genera have in common the absence or poor development of stipules and the prevailing chromosome number 2n = 16 or 18. The group is chiefly found in south-western South Africa.

INTRODUCTION

In the following pages the terms homology, analogy, convergence, and parallelism will be used.

Structures are *homologous* when they have originated from the same parts of the plant, which means that their evolution when traced backwards leads to the same original structure. Whether they are similar or dissimilar, or have the same function or not is irrelevant.

Analogy is more or less the opposite of homology, because stress is laid entirely on similarity of function, i.e. on the ecological-biological result. The similarities are not necessarily referable to a common ancestry.

This division into homologous and analogous structures should be kept separate from the following, in which is expressed the trends of evolution in two or more lineages compared.

When the evolution of an original organ or of two similar organs results in considerable difference in appearance or function it is classified as *divergence*.

When an essentially similar evolutionary trend has developed independently in two or more lineages where originally similar organs were involved, to give rise to homologous, ecologically and (or) typologically similar structures, the adequate term is *parallelism*.

Convergence, finally, is the term used when more or less dissimilar organs become similar and/or ecologically equivalent along independent evolutionary lines. Convergence is not necessarily related to homology. The resultant organs, as in the case of the simple leaves in *Lebeckia* described below, may have in common nothing or very little of the original structures, even where these have once been homologous.

As a preliminary step in the present discussion, let us examine a systematic group, the tribe *Borbonieae*, presented some years ago together with many other tribes of *Fabaceae* in HUTCHINSON's "The Genera of Flowering Plants. Dicotyledones. I" (1964 p. 345).

The tribe was characterized as follows.

"Shrubs, shrublets, or perennial herbs; *leaves primitively simple*; *stipules and stipels absent*; flowers solitary to racemose or subcapitate, terminal or leaf-opposed; calyx-lobes subequal or not; corolla papilionaceous; stamens *all connate into a sheath or tube* split above (adaxially); *anthers dimorphic*, alternately basifixed and dorsifixed and versatile; style *glabrous*; fruit 2-valved, continuous inside; seeds estrophiolate."

The tribe consisted of three genera, *Borbonia* L., *Rafnia* THUNB., and *Euchlora* ECKL. & ZEYH.

Of the italicized characters, the presence of a single split in the staminal tube, the glabrous styles, and the anther characters are also common to several genera in the much larger tribe *Lotononideae* similarly distinguished by HUTCHINSON. Hence, the single important diagnostic character of *Borbonieae* is the simple exstipulate leaves. Whether the leaves should be designated as *primitively simple* or not will be analyzed below.

EUCHLORA. A CASE OF PREDOMINANT SUPPRESSION OF LEAF DIFFERENTIATION (Fig. 1)

One of the genera with "primitively simple" leaves (HUTCHINSON, loc. cit.) is *Euchlora* ECKL. & ZEYH. An account of the single species was given in DAHLGREN 1964, but a brief review will be given here in conjunction with **Fig. 1.**

There are numerous marked similarities between *Euchlora* and several species of the genus *Lotononis* ECKL. & ZEYH. The similarities pertain to practically all characters except in the leaf, viz. habit, pubescence, inflorescence, bracts, bracteoles, calyx, petals (including details like pattern of wrinkles on wings, claw length, general shape of each petal), staminal sheath, anthers, pistil, and fruit.

Let us compare in particular the fruit shape in *Euchlora* and a species of *Lotononis*, e.g. *L. azurea* (ECKL. & ZEYH.) BENTH. (Fig. 1, below). The upper edge of the somewhat inflated, smooth, and hard legume is furnished with a row of very characteristic, obtuse, peg-like teeth or spines. Precisely the same striking qualities are found in the legume of *Euchlora* (Fig. 1, bottom right). Now, the acquisition of such a legume shape by convergence is theoretically feasible. However, in the light of the numerous *other* similarities mentioned here the probability for this is negligible, and it must be suggested that the species are descendents from very closely related ancestors.

The remaining differences between *Euchlora* and *Lotononis* would then be restricted to the leaves. The results of a recent study of regional variation in *Euchlora* now come into the picture (see Fig. 1, top). In one sample from the northern extremity of the area of distribution, it was found that the leaves on one and the same shrub varied from simple to *petiolately trifoliolate with well developed stipules*, i.e. to a shape exactly like that of the leaves of those *Lotononis* species that show a marked similarity to *Euchlora* in floral and other characters. —

In a few other plants from a more southern population, the leaves were sometimes trilobate or had two lateral lobes (corresponding to lateral folioles) and one separate central foliole.

To judge from the above evidence, it seems highly improbable that *Euchlora* would *not* be very closely allied to species of *Lotononis*.

The close similarity of all characters of *Euchlora*, including leaf characters, to those of a number of particular species of *Lotononis* makes it justifiable to include *Euchlora* in the larger genus *Lotononis*, as done by DAHLGREN 1964.

In the majority of the species of *Lotononis* (including *Euchlora*) and in allied genera the leaves are trifoliolate and petiolate with stipules. A mechanism partially blocking leaf differentiation has obviously developed in *Euchlora*. Thus the simple leaf corresponds to an entire, undifferentiated leaf, which cannot be classified as phyllodinous nor as homologous with a foliole.

PARALLELISM WITH REGARD TO LEAF DIFFERENTIATION IN ASPALATHUS (Fig. 2)

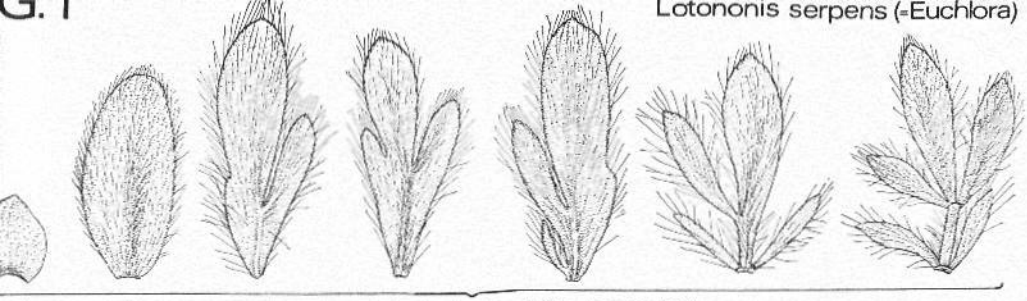
In its present scope *Aspalathus* L. comprises ca 240 species with trifoliolate (and sessile, exstipulate) leaves and 21 species with simple leaves. In three of the latter, representing the subgenera *Nortieria* and *Rafnioides*, there is some doubt about the morphological nature of the simple leaves. These species will not be discussed here.

In three cases there are similarities in practically all respects between species with trifoliolate leaves on the one hand and simple, apparently unifoliolate, leaves on the other. Two of the cases are presented in **Fig. 2.** A third and parallel case, comprising *A. oblongifolia* R. DAHLGR. with trifoliolate leaves and *A. caledonensis* R. DAHLGR. with simple leaves, is entirely comparable.

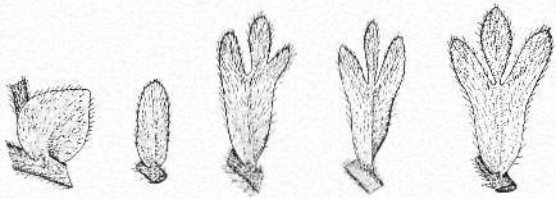
In the upper half of Fig. 2, *A. radiata* GARAB. ex R. DAHLGR. represents the trifoliolate condition and *A. sericea* BERG. the simple one. A close examination has shown similarity between the two species in all other characters, such as habit, mode of branching, inflorescence, bracts, bracteoles, calyx, details of petals and stamens, ovary pubescence, number of ovules, and fruit shape — characters which are otherwise highly variable in the genus. There is also similarity in the pubescence of the floral parts. The illustrated form of *A. sericea* shows a more sericeous

G. 1

Lotononis serpens (=Euchlora)

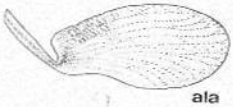


Leaf variation in sample ×



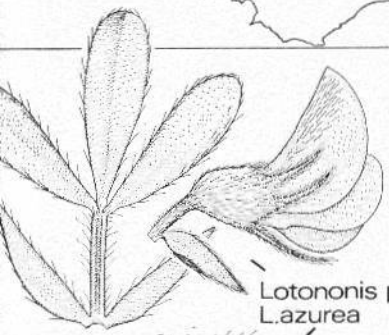
Leaf variation in the population marked with circles

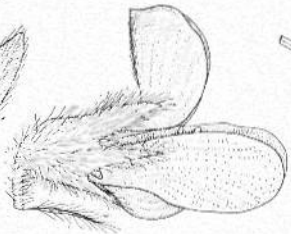
vexillum



ala

carina petal

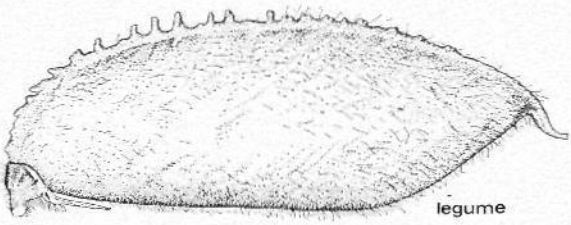




pistil

Lotononis peduncularis
L.azurea

legume



legume

form of pubescence than does *A. radiata*, but variation is great in both species.

There is accordingly significant evidence that the similarity indicates close relationship. As there is no tendency to fusion in leaflets in this group of species, and as the leaf of *A. sericea* agrees in shape and venation with a leaflet in *A. radiata* and similar species, the simple leaf is presumed to be equivalent to a leaflet. — The simple leaves of *A. sericea* have also been observed by previous botanists, none of whom have proposed that the species should be placed in a separate genus.

The lower half of Fig. 2 shows another, entirely different pair of species that can likewise be compared with each other, viz. *A. lanata* E. MEY., which has trifoliolate leaves, and *A. lanifera* R. DAHLGR. with simple leaves. The two species occur on shaley ground in partly the same mountainous regions, mainly the Clanwilliam—Ceres Divisions. The plants are low and have the same mode of branching. As seen in Fig. 2 the branch terminates in an inflorescence, but a strongly developed branch in the axil of the uppermost vegetative leaf pushes the inflorescence aside into a pseudo-lateral, leaf-opposed position. The bracts, bracteoles, calyx, corolla, and stamens are so similar in both species that it may be difficult for even a specialist to distinguish them without having recourse to the leaf. The legumes differ somewhat, but fruit shape normally varies greatly within this group, and the *lanata* type of legume is more common among simple-leafed species related to *A. lanifera* than among the trifoliolate-leafed species.

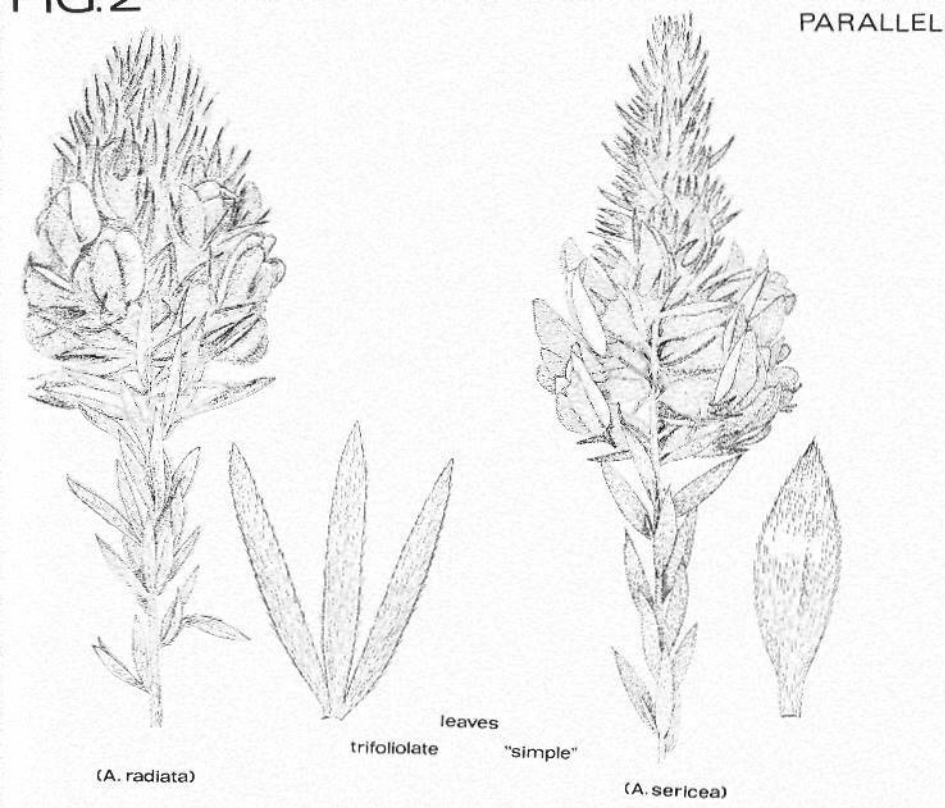
There is strong evidence to support the theory that *A. lanata* and *lanifera* are very closely related in the same way as are *A. radiata* and *sericea*.

On the other hand, *A. lanifera* is related to a number of other species with simple leaves. These species with simple leaves have previously been grouped together as a separate genus, *Borbonia*. However, there is greater similarity between the representatives of "*Borbonia*" (i.e. *A. lanifera*) and of *Aspalathus* s. str. (i.e. *A. lanata*) compared here, than between many closely related species of *Aspalathus* s. str.

Thus, *A. lanata* E. MEY., *A. latifolia* BOL., *A. bracteata* THUNB. (these three with trifoliolate leaves), *A. lanifera* R. DAHLGR., *A. compacta* R. DAHLGR., and *A. alpestris* (BENTH.) R. DAHLGR. (the latter three species with simple leaves, and members of "*Borbonia*") show more striking similarities among themselves than do many comparable series of species within the large genus *Aspalathus* in the strict sense, or than do all the "*Borbonia*" species among

FIG.2

PARALLELISM

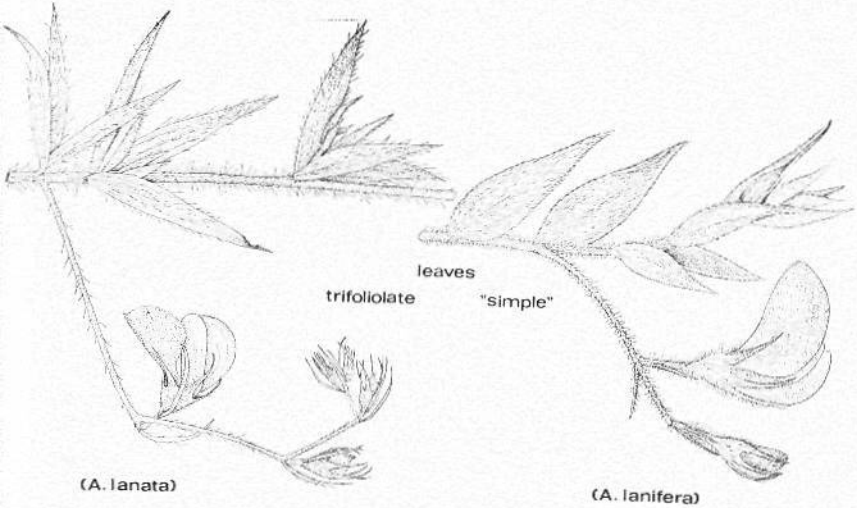


leaves

trifoliolate "simple"

(A. radiata)

(A. sericea)

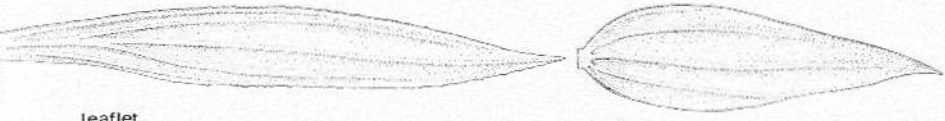


leaves

trifoliolate "simple"

(A. lanata)

(A. lanifera)



leaflet

leaf

(indumentum omitted)

themselves. The trifoliolate species of *Aspalathus* do not constitute an entirely homogeneous or easily definable group of species, as might have been suggested by their common leaf character (see the diverse parts of Revision of the Genus Aspalathus, DAHLGREN 1960—68).

Consequently, there are good reasons for incorporating *Borbonia* in *Aspalathus* (DAHLGREN 1963 B).

Just as in the pair *Lotononis-Euchlora*, it is likely that the simple leaves concerned with here have been derived from trifoliolate (but sessile and stipuleless) ones.

In Fig. 2 below, one leaflet, the central one, of *A. lanata* and a leaf of *A. lanifera* are compared to show the similar venation. It is most probable that they correspond to each other, i.e. the leaf in *A. lanifera* is homologous with a leaflet in *A. lanata*.

If the above points are accepted, the *Aspalathus radiata—A. sericea* and *A. lanata—A. lanifera* cases together represent a case of parallelism. The similarity of the simple leaves in this case expresses homology.

CONVERGENT EVOLUTION WITH RESPECT TO LEAF DIFFERENTIATION IN LEBECKIA (Figs. 3—4)

The genus *Lebeckia* THUNB. does not include as many species as *Aspalathus*, but it has a wider distribution. It differs from *Aspalathus* primarily in having usually petiolate leaves and long and many-seeded legumes, the latter feature a very rare one in *Aspalathus*. *Lebeckia* is a variable, but probably natural group. It is in great need of systematic revision. The names used here must therefore be regarded as preliminary.

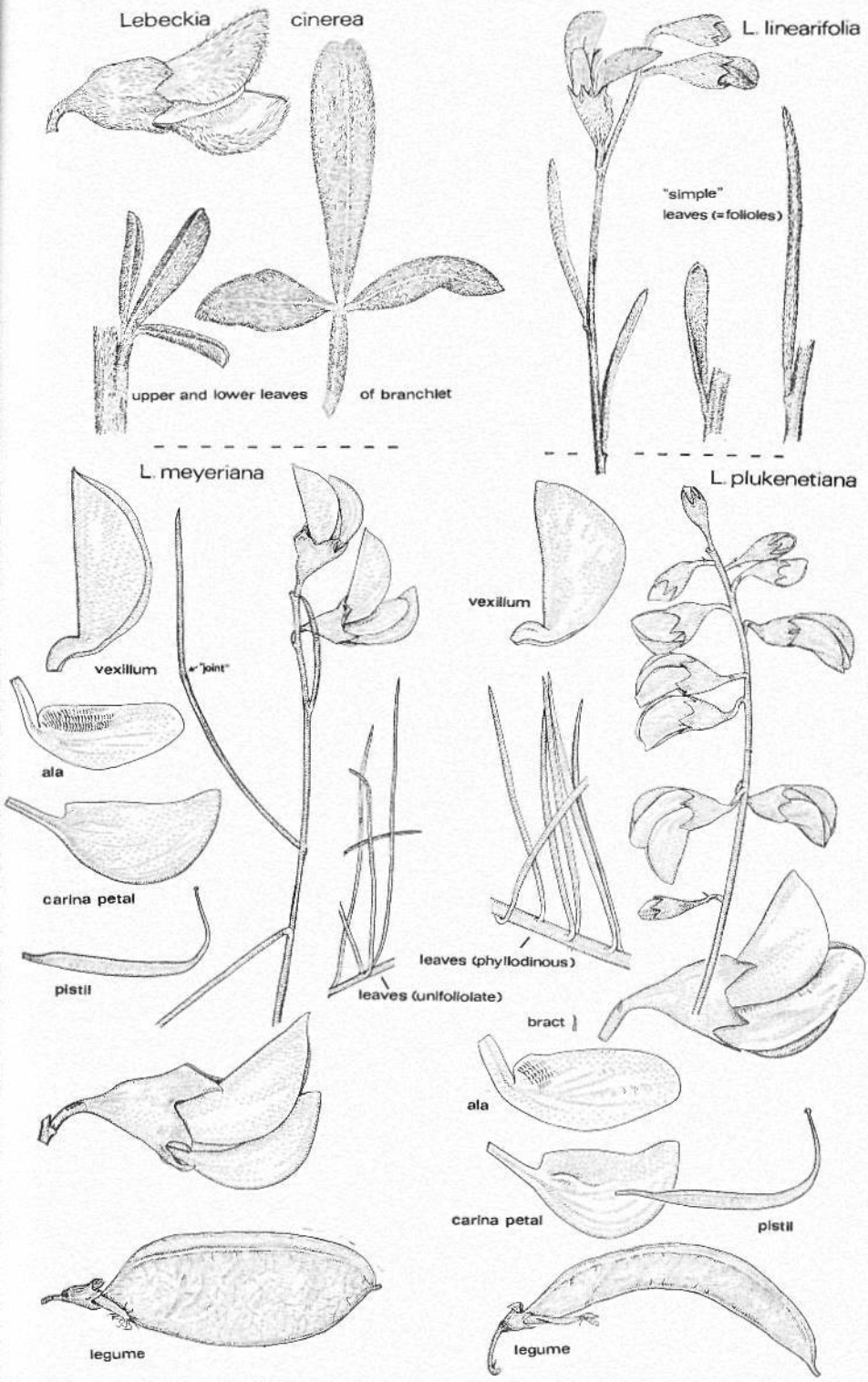
Let us consider two of several species with simple leaves, each very similar to species with trifoliolate-petiolate and unifoliolate-petiolate leaves respectively (see **Fig. 3**).

Lebeckia cinerea E. MEY. belongs to a group of species found chiefly in the north-western part of the Cape Province and extending into South West Africa. It is pubescent on the vegetative parts and also has a pubescent standard and keel, the latter being longer than the wings. The leaf petioles tend to be very short towards the ends of the branchlets, where the lateral leaflets are also smaller than the central ones.

In *L. linearifolia* E. MEY. the leaves are simple, but in other respects the species shows so many similarities to *L. cinerea* that a close relationship seems probable. The simple leaves are sometimes narrowly

FIG.3

ANALOGY by CONVERGENCE



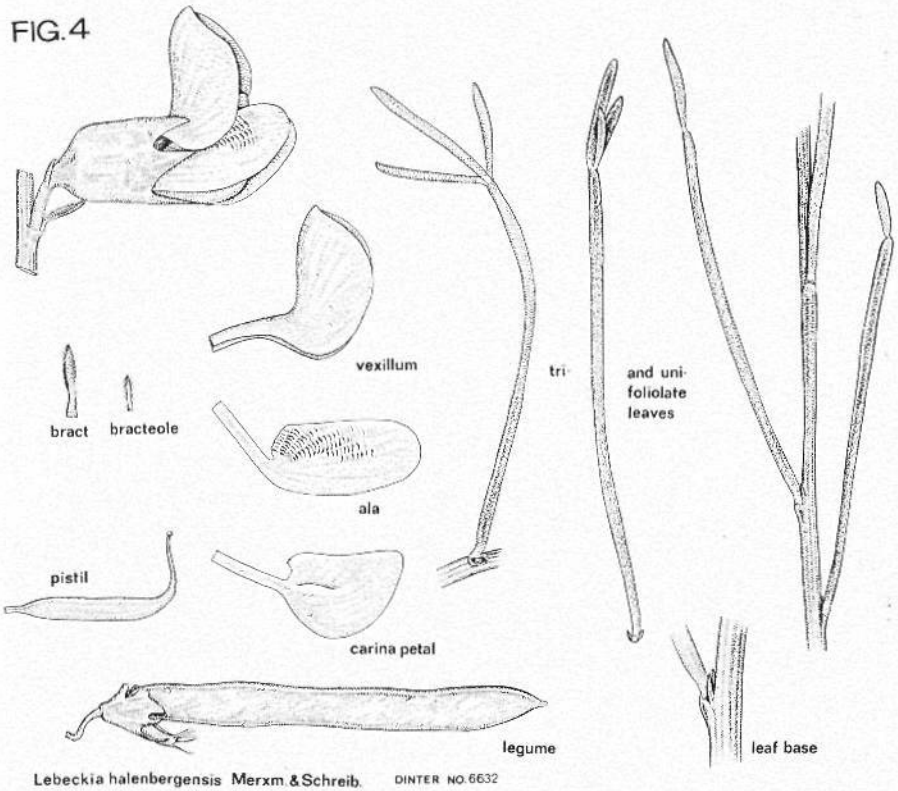
linear, but more commonly flat (or with involute margins) and narrowly spathulate, resembling strongly the central leaflets in *L. cinerea*. It seems most likely that the leaf of *L. linearifolia* has arisen from a trifoliolate leaf of the *L. cinerea* type through the suppression of the petiole and lateral leaflets.

Such simple leaves, although usually broader, are also found in the related section *Stiza* (E. MEY.) BENTH., where the flowers are very similar to those of the two above-mentioned species. In *L. pungens* THUNB. the seedlings have trifoliolate petiolate leaves and the older branches unifoliolate petioleless (i.e. simple) leaves. Transitional forms, e.g. with short petiole and one leaflet, are found on the young plant (see DAHLGREN 1967 p. 155, Fig. 2 A).

The other pair of species (Fig. 3 below) belongs to a more southern group of *Lebeckia*. It consists of *L. meyeriana* ECKL. & ZEYH. and *L. plukenetiana* E. MEY. The former has linear leaves with a "joint" somewhat above the middle, representing the junction between the petiole and a solitary leaflet (compare *L. halenbergensis* below). The leaf is jointless in *L. plukenetiana*, which therefore has simple leaves. It can be seen that the floral characters agree well between the two species. The legume in *L. meyeriana* is broader than in *L. plukenetiana*, but both are somewhat flat and have a wing-like upper margin. There is no tendency in the unifoliolate linear leaves of *L. meyeriana* and similar species towards a reduction of the petiole, and the colourless basal part of the petiole of the unifoliolate leaf resembles that of the simple leaf in *L. plukenetiana*. Hence, the latter type of leaf is probably phyllodinous in nature, i.e. it consists of the petiole only. — Sections through the petiole and leaflet portion respectively, of species of *Lebeckia* with linear, "jointed" leaves do not show any particular anatomical difference that can give more definite proof of the nature of the entirely simple leaves of similar species.

In a species from South West Africa, *L. halenbergensis* MERXM. & SCHREIB., the leaves vary from trifoliolate to unifoliolate, which may indicate the way in which the linear, "jointed" leaves of more southern species have originally evolved (see **Fig. 4**).

The two cases described above represent *convergence* rather than parallelism. The resultant simple leaves are not homologous, as they probably do not represent the same parts of the original trifoliolate leaf, but convergence, in this case, has resulted in analogy.



The species of *Lebeckia* illustrated in Fig. 3 below show considerable similarities to certain species of *Rafnia*, the third genus included by HUTCHINSON in the tribe *Borbonieae*. The reader may notice the similarity between these *Lebeckia* species and the *Rafnia* species shown in Fig. 5. My observations favour the hypothesis that these groups may have a common ancestry, and, in addition, that the leaf of *Rafnia* is of a phyllodinous nature.

TRIBUS BORBONIEAE, AN ARTIFICIAL GROUP CHARACTERIZED BY SECONDARILY SIMPLE NON-HOMOLOGOUS LEAVES DEVELOPED BY CONVERGENCE (Fig. 5)

In the tribe *Borbonieae* three genera have been discussed, viz. *Euchlora*, *Borbonia*, and *Rafnia*, each in conjunction with the groups outside the tribe that are morphologically most closely allied to it. None of them show marked similarity with the other genera of the tribe, except in that they have simple leaves. The group is accordingly artificial, the

three genera probably representing the end points of three distinct lines of evolution (see Fig. 5), the resultant species sharing an incidental common likeness with regard to one conspicuous leaf character.

The simple leaves in different groups of *Borbonieae* are not homologous but in all probability correspond to:

1) a leaflet (*Borbonia*)
2) a leaf petiole (*Rafnia*)
3) an undifferentiated entire leaf of other type (*Euchlora*).

The simple leaves have presumably been derived from diversely trifoliolate ancestors (which are probably not identical with any of the trifoliolately leafed present species mentioned) along three different lines of evolution. Tribus *Borbonieae* thus represents an excellent example of convergence with respect to the simple leaves. This is schematically illustrated in **Fig. 5,** which is necessarily somewhat hypothetical.

In the evolutionary branch of *Aspalathus* (including *Borbonia*), each terminal branchlet is intended to represent a particular species. Due to lack of space, only a fraction of the whole genus *Aspalathus* is illustrated. The two branchlets terminating closest to the circumference of the circle on either side represent *A. lanata* E. MEY. and *A. lanifera* R. DAHLGR. respectively; the branchlet with a lobate transection outside the circle represents *A. bracteata* THUNB.

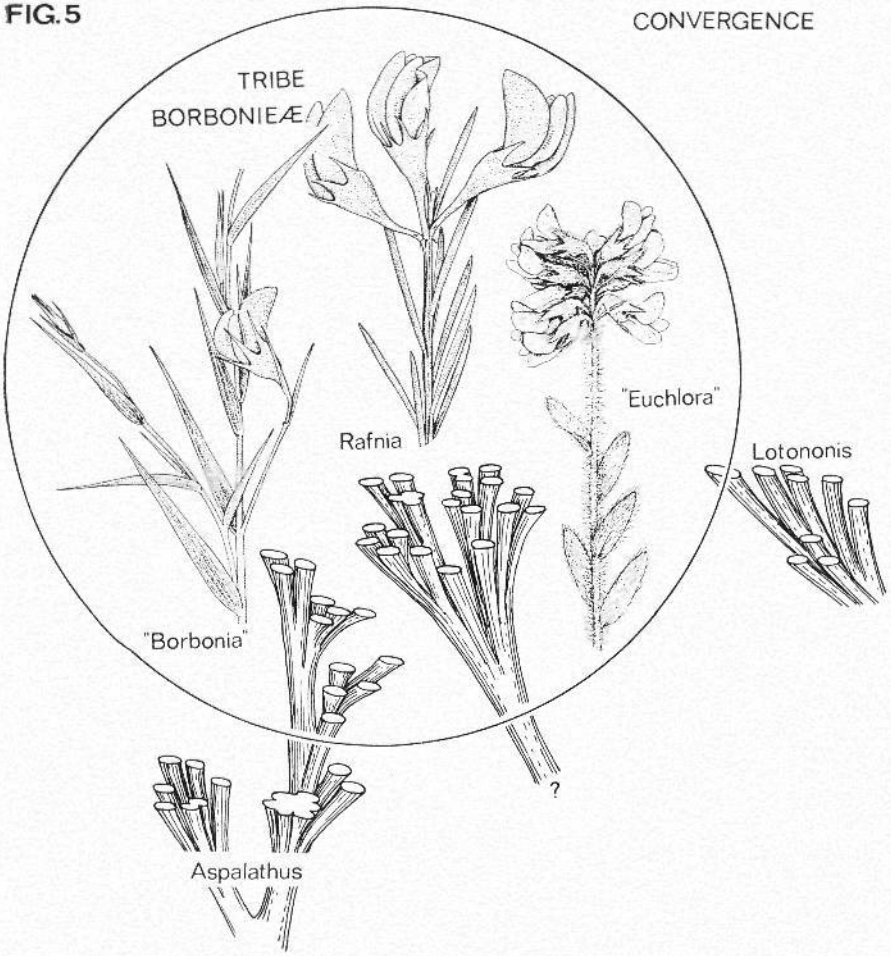
With regard to *Rafnia* a revision of the species is desirable, and the branched tree within the circle is entirely symbolic. In fact, it should probably have been shown as even more branched and complex.

"*Euchlora*" represents a shoot of the *Lotononis* branch of evolution. To judge from morphological and, fragmentary, cytological indications, *Lotononis* is probably rather distantly related to the other genera mentioned here. The *Lotononis* branch of evolution in Fig. 5 represents a purely symbolic fraction of that genus.

The genera *Lebeckia, Wiborgia, Rafnia,* and *Aspalathus* (including *Borbonia*) are believed to be closely allied genera, which should be placed in the same tribe whatever its extent. Beside certain floral similarities, such as the shape of petals and stamens, and the absence of strophiole on the seeds, these genera have in common the absence or poor development of stipules and the prevailing chromosome number $2n = 16$ or 18.

Several other groups of species within the *Leguminosae*, where compound leaves are predominant, display this tendency to evolve simple leaves. Illustrations could also be taken from the *Crotalaria* L. (see e.g. POLHILL 1968), and a striking case in point can be found among a few representatives of *Aeschynomene* in Rhodesia (WILD 1953).

FIG.5



The present example will also serve to illustrate a tendency among botanists to rely on single "key characters". The importance of single conspicuous "diagnostic" characters, in this case trifoliolate versus simple leaves, can easily be over-estimated. HUTCHINSON is by no means more prone than many other botanical authorities to over-emphasize a single striking feature. It is purely incidental that his tribe *Borbonieae* illustrates this point.

ANALOGY IN THE EVOLUTION OF DIVERSE TYPES OF SPINES IN ASPALATHUS (Fig. 6)

In the flora of South Africa, *spines* — pungent, rigid processes of any kind whatsoever — have doubtless evolved in response to ecological pressure in the form of grazing animals. This spine protection has apparently been of

decisive importance as a selective factor in the genus *Aspalathus*, because it is found in about 35 per cent of the more than 260 species. In many cases where species of *Aspalathus* lack protective spines or thorns, other characters may have contributed as "protection" against grazing, for example, dense pubescence, a low matted habit, and the presence of aromatic substances, characters that have probably been established, primarily or in part, as a response to other ecological factors.

There is a tendency in *Aspalathus* for lowland species to be more effectively armed, especially by means of branch or branchlet thorns, than are mountain species. It is possible that during the time the species were evolving natural grazing was more intense in the lowlands than in the mountains. The difference is not great, however, and many mountain species have leaflets with spiny tips.

Some types of spine protection in *Aspalathus* are presented in **Fig. 6.** They fall into the following categories:

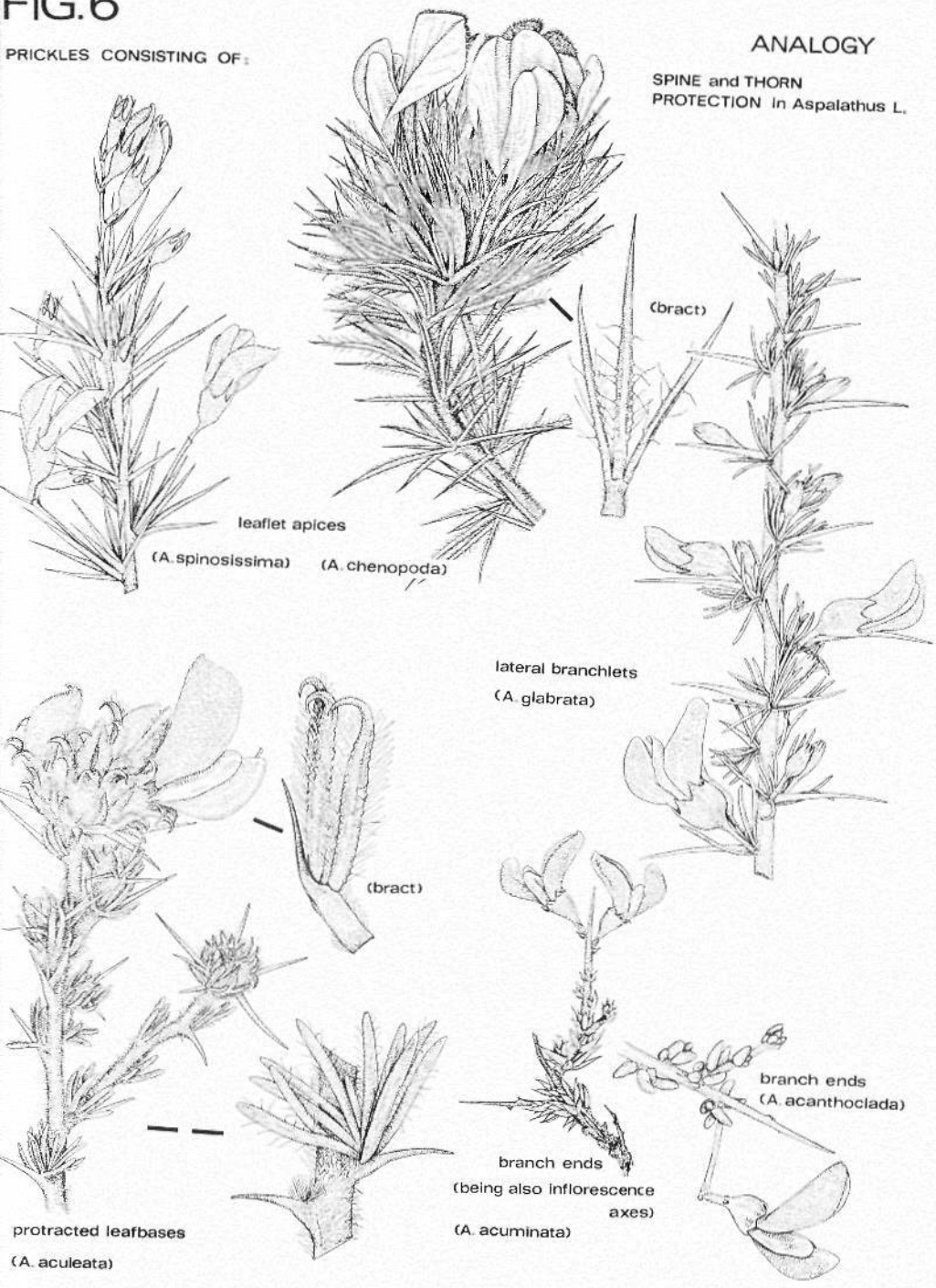
1) *Leaflet apices*, which are very often developed as spines of varying length and sharpness, from short, mucros, to long, hard, and with needle-like points. This type of spine is by far the commonest in *Aspalathus*, and has probably evolved independently along many lines. Spine-like tips occur in species with flat as well as subterete leaflets, and in species with simple leaves (see Fig. 5, "Borbonia") as well as with trifoliolate leaves.

2) *Leaf-base processes*. Spines developed from the leaf-base (other than paired stipules) are unique, and — as far as I know — are limited to a number of species in *Aspalathus*. In *A. aculeata* THUNB. (Fig. 6) the spines, which are of this type, are long and well developed, but they are also conspicuous in species as widely different as *A. tridentata* L. (where lateral processes from the spine base may occur), *A. desertorum* BOL., *A. rycroftii* R. DAHLGR., and *A. uniflora* L. Similar spur-like processes from the leaf-base also occur in some other species.

Leaf-base spines seldom occur in combination with other kinds of spines, and we may notice that *A. chenopoda* L. and *A. aculeata* THUNB., both in Fig. 6, have very similar floral and inflorescence characters and, for example, trifoliolate outer bracts. In *A. chenopoda*, which is a mountain species, the leaflets are armed with spine-tipped apices; in *A. aculeata*, which grows on the south-western lowlands and has unarmed and weak leaflets, the spines consist of the protracted leaf-bases.

3) *Branch thorns and branchlet thorns*. In several species, often very dissimilar with regard to floral morphology, the branches take on the shape of more or less sharp, rigid thorns. These thorns have probably evolved along several lines, and may provide good examples of parallelism in evolution. In species with the inflorescence located at the end

FIG.6


PRICKLES CONSISTING OF:
ANALOGY
SPINE and THORN
PROTECTION In Aspalathus L.
(bract)
leaflet apices
(A. spinosissima)
(A. chenopoda)
lateral branchlets
(A. glabrata)
(bract)
branch ends
(A. acanthoclada)
branch ends
(being also inflorescence
axes)
(A. acuminata)
protracted leafbases
(A. aculeata)

of the main branch, the thorn serves at the same time as an inflorescence axis, as in *A. acuminata* LAM. (Fig. 6). In other thorny species, the flowers are concentrated to lateral branchlets, which are often developed as short shoots or are sometimes peduncle-like, as in *A. acantholada* R. DAHLGR. (Fig. 6). In *A. spinosa* L. there is great variation in the thorns. In some populations the main branches as well as lateral branchlets of varying length develop into thorns, but in most forms the thorns consist of relatively short, hook-like, and leafless branchlets, a condition also found in the similar species *A. glabrata* R. DAHLGR. (Fig. 6).

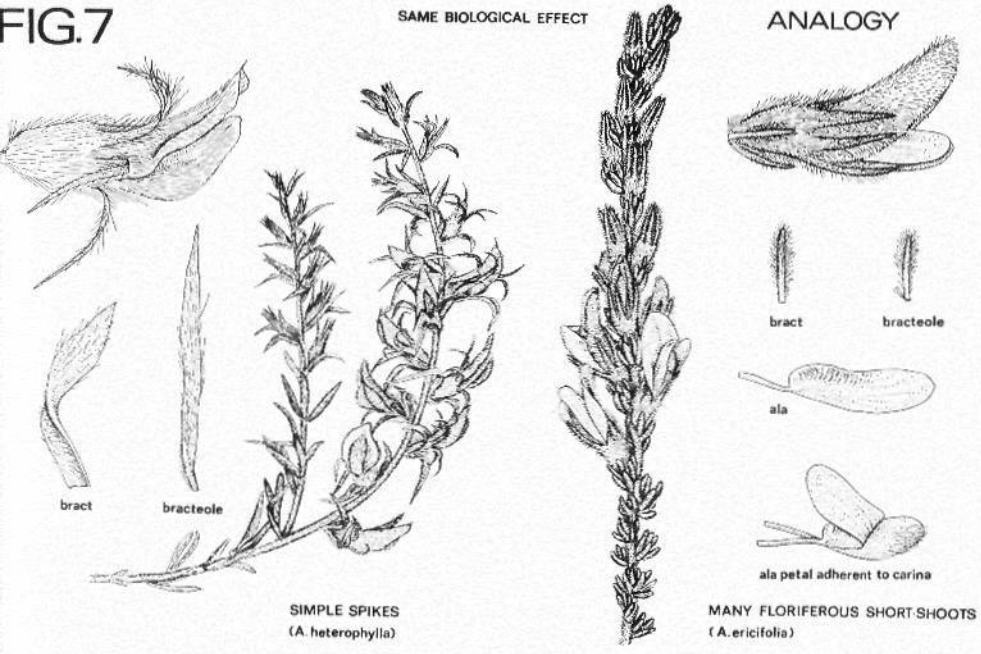
There are accordingly three main types of spine protection in the genus, and these are by no means homologous. They represent a *functional similarity* not related to the origin of the structure, and thus may serve as an example of *analogy*.

ANALOGY IN THE DISTRIBUTION OF FLOWERS (Fig. 7)

The mode of distribution of flowers on the plant in an allogamous species is of decisive importance for pollination. In some groups of species in *Aspalathus* the flowers are assembled in terminal multiflorous spikes, heads, or racemes, which in themselves exert sufficient attraction on insects. An elongated spike of *A. heterophylla* L. FIL. is seen to the left in **Fig. 7.**

In other groups of species the inflorescences are few- or one-flowered and located on lateral branchlets. The flowers, especially when rather small, need to be aggregated in order to be sufficiently conspicuous to the insects. This state has been obtained in a great number of *Aspalathus* species by the concentration of branchlets to dense (floriferous) short shoots. The spike-like pseudo-inflorescence in *A. ericifolia* L., shown to the right in Fig. 7, represents this type. It is probably a derived state in relation to a single many-flowered inflorescence of the kind mentioned above.

In several species of *Aspalathus* the flowers are borne on peduncles, a condition which in certain cases may be of selective advantage, as the flowers are more effectively displayed. These peduncles are of different types, however (see DAHLGREN 1963 A p. 59, Fig. 3). In species like *A. lanata* E. MEY., *A. lanifera* R. DAHLGR. (both in Fig. 2), and *A. alpestris* (BENTH.) R. DAHLGR. ("Borbonia" in Fig. 5) the peduncle



represents the internode just below a pauciflorous inflorescence at the end of a branch in a sympodial system. In *A. serpens* R. DAHLGR. and several other species the peduncle consists of the uppermost internode below a usually unifloral inflorescence of a lateral branchlet. In *A. retroflexa* L., *A. longipes* HARV., and several other species it is a prolonged internode (other than the uppermost) of such a lateral branchlet. The effect is principally the same in relation to the pollinating insects. Moreover, botanists have usually been taken in, having supposed a close systematic affinity between all the pedunculiferous species (cf. HARVEY's section "*Pedunculares*"; HARVEY 1862 p. 139).

Dense inflorescences and pedunculate flowers both represent adaptations to insect pollination. Such adaptations may be attained along different phyletic lines in response to a common selective pressure.

ACKNOWLEDGEMENTS

I wish to thank several of my colleagues who have stimulated me greatly with ideas and criticism. The English text has been improved by Mrs. MARGARET PETERSSON, Lund.

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Botanical Literature

Botanisk litteratur

Wild Flowers of Greece, painted by NIKI A. GOULANDRIS, text by CONSTANTINE N. GOULIMIS, edited by W. T. STEARN. Publication of the Goulandris Botanical Museum, Kifissia, Athens 1968. 214 pp., 119 coloured plates, linen bound, 38×28 cm. Price (prepublication) US $40.

This book, which is intended as no. 1 in a series of publications from the Goulandris Botanical Museum, is an outstanding contribution to Greek botany and to the art of botanical illustration. It contains 119 life-size illustrations of Greek plant species painted in water-colours by Mrs. NIKI GOULANDRIS and printed in six-colour litho-offset by J. MARKIS S.A. of Athens. The accompanying descriptive text is written by the late Dr. C. N. GOULIMIS of Athens and by Dr. W. T. STEARN of the British Museum. A foreword is provided by Sir GEORGE TAYLOR, Kew.

The Goulandris Botanical Museum, in Kifissia near Athens, was established in 1963 to house the important collections of C. N. GOULIMIS and to stimulate research on the Greek flora. The herbarium has subsequently been augmented by the extensive collections of NIKI GOULANDRIS and co-workers, and now comprises approximately 100,000 sheets. It has developed into a centre of increasing importance to students of Greek botany.

CONSTANTINE GOULIMIS was born in Athens in 1886. After receiving the degree of Doctor of Laws at the University of Athens, he served for a period of forty-four years as the legal adviser to the British Embassy in Athens. His botanical interest was aroused while in exile in South Africa as legal adviser to the Greek Government during the Second World War. After returning to Greece, he devoted much of his time between 1946 and his unfortunate death in 1963 to the exploration of the Greek flora, especially the plants of the high mountains. He gathered a rich herbarium and discovered no less than 230 species hitherto not recorded from Greece, several of them new to science. Part of his material was revised by Professor K. H. RECHINGER of Vienna, Dr. W. MÖSCHL of Graz, as well as other botanists. His name is commemorated in such species as *Campanula goulimi*, *Linum goulimi*, and *Stachys goulimi*.

Mrs. NIKI GOULANDRIS is a well-known artist from Athens. Her paintings in oils and water-colours have been shown at separate exhibitions in Athens, and are represented in many public and private galleries in Europe. In associa-

tion with GOULIMIS she took interest in botany and commenced to paint Greek wild flowers in 1956. Some 800 paintings have now been completed.

The present volume is the most spectacular sign of the activity of the Goulandris Botanical Museum. No doubt it will principally be remembered for its illustrations combining great artistry with faithful botanical accuracy. The accompanying text contains synonyms, brief descriptions of the plants, citations of specimens, details on distributions, and Greek vernacular names. Since most readers are no doubt unfamiliar with the Greek language, some etymological comments would have been desirable.

Some of the illustrated species, for example, *Coronilla emerus*, *Styrax officinalis*, *Lavandula stoechas*, *Asphodeline lutea*, and *Ornithogalum nutans*, are well-known and widespread Mediterranean plants likely to be seen by the ordinary traveller. Others, such as *Pancratium maritimum* and *Colchicum* spp., are widespread but flower at times when most botanists have finished their field work and returned to indoor activities; thus, the illustrations of such taxa are particularly welcome. Among the selection of plants are several rare or endemic species, some of which have never been illustrated before. Recherché mountain plants as *Sempervivum reginae-amaliae* and *Viola delphinantha* may be mentioned. There is also an exceptionally fine and well-illustrated specimen of *Haberlea rhodopensis*, an endemic to eastern Macedonia and Bulgaria belonging to the same family (*Gesneriaceae*) as the more famous *Jankea heldreichii* of Mt. Olympus. Special interest has been devoted to the monocots, notably the orchids and genera such as *Crocus* and *Fritillaria*, whose delicate beauty is depicted with skill and artistic feeling.

The artist and students of the Greek flora are to be congratulated for the work so fortunately commenced with the present volume. If continued along the same lines, it will develop into a worthy successor to SIBTHORP and SMITH' *Flora Graeca* — the greatest of all illustrated floras — from the beginning of the 19th century.

ARNE STRID

BJÖRKQVIST, I. 1967—1968. Studies in Alisma L. I. Distribution, variation and germination. — Opera Botanica 17. II. Chromosome studies, crossing experiments and taxonomy. — Opera Botanica 19.

The two papers are a brief survey of the investigation of the genus *Alisma* L.

The total distribution of the genus is regarded as spontaneous on the whole. Some groups of species can be distinguished in regard to the geographical distribution. *1.* Species with wide European distribution: *Alisma plantago-aquatica* and *A. lanceolatum*. — 2. Species with rather wide American distribution: *A. subcordatum* and *A. triviale*. — *3.* Species with rather wide European-American distribution: *A. gramineum*. — *4.* Species with restricted Scandinavian distribution: *A. wahlenbergii*. — *5.* Species with restricted Asiatic distribution: *A. orientale*, *A. rariflorum*, and *A. canaliculatum*.

All species are fresh-water plants and reach their most normal development in moderately eutrophic water.

The morphological variation within the population is normally small. De-

tailed accounts are provided of the morphology, germination and seedling development of the various species. Information is also given on modification experiments carried out to elucidate the effect of varying environmental conditions.

The leaf morphology is highly modifiable and influenced by the water depth and connected factors.

The chromosomes have been extensively studied and the evolution of some taxa, especially the tetraploids and hexaploids, is discussed.

The basic number of the genus is 7, and the genus consists of diploid, tetraploid and hexaploid species. Furthermore there is one aneuploid number, 2n=26, on the tetraploid level. Karyologically the genus is rather uniform, but quite different from the related genera. The genomes of the different species exhibit great similarities and the chromosomes can be separated into two groups. The first comprises five large chromosome pairs with median or submedian centromeres, whereas the second group contains two small pairs with ± subterminal constrictions. One of these pairs has satellites and is the nucleolar organisers.

Some natural hybrids are recorded, including *A. lanceolatum* (2n=28)× *A. plantago-aquatica*. The cytotype with 2n=26 has not been found to hybridise with *A. plantago-aquatica* in the wild. In the Swedish province of Gotland a plant found with 2n=27 is probably the putative hybrid *A. lanceolatum* (2n=28)×*A. lanceolatum* (2n=26).

A large series of crossing experiments has been made with material from all taxa of the genus as well as from the related genera. The result indicates ± clear sterility barriers between the species and shows that the genus *Alisma* seems to be genetically isolated from the other genera of the family. The genetic isolation of taxa seems to be rather effective but of different degrees. In all cases the F_1-hybrids obtained have a considerably reduced fruitsetting and germination.

The spontaneous and the artificial hybrids are very much alike.

No sterility barrier is demonstrated between the different populations of the taxa.

Based upon the investigations a taxonomic evaluation of the genus is made. Descriptions of the various taxa is provided, together with synonymy and a key to their identification. The following nine taxa are upheld. No taxonomical rang is given to the two cytotypes of *A. lanceolatum*.

A. plantago-aquatica L. 1753	2n 14	*A. lanceolatum* With. 1796	2n 26, 28
A. orientale (Sam.) Juz. 1934	2n 14	*A. rariflorum* Sam. 1932	2n 26
A. gramineum Lej. 1811	2n 14	*A. triviale* Pursh 1814	2n 28
A. wahlenbergii (Holmberg) Juz. 1934	2n 14	*A. canaliculatum* A. Braun et Bouché 1862	2n 42
A. subcordatum Rafin. 1808	2n 14		

The editor

TYLER, G. 1969. Studies in the ecology of Baltic sea-shore meadows II. Flora and vegetation. — Opera Botanica 25.

The paper is a descriptive study on flora and vegetation of Baltic sea-shore meadows in the provinces of Södermanland and Östergötland, south-central Sweden. The vegetation is described in terms of comprehensive associations and subassociations, characterized floristically by groups of characteristic and differential species.

Continuously submerged vegetation is only discussed briefly. Two associations of the Ruppion maritimae, the Najadetum marinae and the Potamogeto filiformis - Charetum asperae, are described. The hydrolitoral is occupied by primary Phragmition vegetation, distinguished as Phragmito-Scirpetum maritimi, though sometimes replaced by a secondary Eleocharetum parvulae. The vegetation of the geolitoral is distinctly girdled. The lower part of this belt is occupied by an Eleocharetum uniglumis, typically an Eleocharetosum uniglumis, in sheltered sites often replaced by a Caricetosum mackenziei. The middle and upper geolitoral is covered by a Juncetum gerardi with three zonally arranged subassociations. On shores rich in gravel or superficial bedrock it is mostly replaced by a Caricetum pulchellae with three subassociations.

In and around shallow depressions zonations of secondary communities are developed in the geolitoral. An Agrostis stolonifera - Triglochin palustre community, floristically related to the Eleocharetum uniglumis, is the most common unit but sometimes replaced by an open Sperguletum salinae.

Some attention is also given to the vegetation of drift litter and the main vegetation of the epilitoral. In a final chapter the present and earlier use of sea-shore meadows, as well as the effects of grazing are discussed.

THE EDITOR

Announcement

First International Mycological Congress 1971

The First International Mycological Congress will be held at the University of Exeter, Devon, England, from Tuesday 7th September to Thursday 16th September, 1971. President: Professor C. T. INGOLD. Secretary: Professor JOHN WEBSTER.

There will be seven concurrent symposia each day. These will be grouped into seven sections as follows: 1. Structure and Morphogenesis. 2. Cytology and Genetics. 3. Taxonomy. 4. Physiology and Biochemistry. 5. Industrial and Applied Mycology. 6. Ecology. 7. Symbiosis and Pathogenicity.

Meetings on the Organisation of Mycology will cover Nomenclature, Herbaria and Culture Collections, Mycological Education, Mycological Publications and Information, Mapping Schemes.

Exhibitions and Demonstrations will include an exhibition of Ultrastructure Photographs. Teaching Techniques and Material, etc.

Forays. The British Mycological Society as well as The British Lichen Society wellcome Congress Members to Congress forays. If there is sufficient support it is hoped to arrange a post-Congress Foray of interest to specialists in microfungi.

Preliminary registration card can be received from Dr. ROLF SANTESSON, Institute of Systematic Botany, P.O. Box 123, S-751 04 Uppsala, Sweden.

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