Drawings of Scandinavian Plants 11–12

Eleocharis R. Br.

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Eleocharis uniglumis (Link) Schult.

[*Scirpus uniglumis* Link, *S. palustris* L. sensu ampl. p.p. (=var. β in Fl. lapp. 1737), *E. palustris* ssp. *uniglumis* (Link) Hartm., *S. palustris* ssp. *uniglumis* (Link) Syme]

Rhizomes often more slender than in E. palustris but, as in that species, the second internode of the shoot generations of about the same length as the first internode of the next, axillary shoot generation accreted to it. Basal sheaths of the culms normally *lustrously red to blackish red* or greenish (especially in the northern part of Scandinavia); orifice straight or somewhat oblique, often with a marked margin.

Culms less variable in length than in *E. palustris*, usually shorter than 70 cm, not easily compressed and extreme water modifications absent; the anatomy of the culms similar to that of *E. palustris*; subpopulations often with different colour of the culms, varying from yellowish green to olive green and bluish green.

The single sterile basal glume of the spike amplexicaul, shorter than half the spike. Fertile glumes variable and normally differing somewhat in the two subspecies, commonly *shining blackish red* with (or often without) a narrow midrib and in certain infraspecific taxa and subpopulations with ± hyaline margins during prefloral and floral stages, when older increasingly membranaceous. Receptacle density 20—39 fruits per cm of the rachis.

Thecae pure yellow and more than 1.9 mm in length. Shape of the pollen grains markedly sector- or sack-shaped; size different in the two subspecies.

Achene shape obovoid to pyriform with a slight difference between

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[1] Strandhede is responsible for the text and Dahlgren for the drawings.

infraspecific taxa; length 1.1—2.0 mm, width 1.0—1.6 mm with differences between subpopulations and strains; colour ranging through various shades of yellow, especially in coastal subpopulations, or brown in inland subpopulations; *surface ± markedly reticulate. Style bases* prominently developed, *necked*; shape variable, length (0.3—) 0.4—0.7 (—0.9) mm, width 0.5—1.0 mm. Bristles varying in number, shape, and length, often lacking in ssp. *uniglumis*; barbs retrorse, of varying lengths.

Chromosome number different in the two subspecies.

E. uniglumis is especially common along the coasts of Scandinavia. Though it tolerates at least temporarily the influence of salt water, *it prefers brackish water and eutrophic wet meadows along the coasts as well as inland*. It is rare in oligotrophic areas, where it occurs most frequently in localities with only slightly acidic or neutral water or with the influence of fertilizing substances. *E. uniglumis* is more competitive and more tolerant of grazing than *E. mamillata* and *E. palustris*.

E. uniglumis has a wide, ± circumboreal distribution and constitutes a series of ± distinct subpopulations distinguished in minor morphologic characters and ecologic preferences, but mainly in geographical distribution. Some of the most distinct subpopulations have been described as taxa, often as species. The results of cytological, genetical, and morphological studies have, however, shown that several of them can be most adequately regarded as infraspecific taxa. Thus two interfertile subspecies with different chromosome numbers and three varieties with the same chromosome number as the main population have been distinguished in Scandinavia.

E. uniglumis (LINK) SCHULT. ssp. **uniglumis**

[*E. polycaula* WENDEROTH, *E. sareptana* ZINSERL., *E. multiseta* ZINSERL., *E. paucidentata* ZINSERL., *E. transcaucasica* ZINSERL.]

This subspecies is distinguished from the subsequent one in the following characters:

Colour of the culms variable in different subpopulations. *Stomatal length* (40—) *50—63* (—76) µ.

Basal glumes and fertile glumes variable in length, shape, and colour, *hyaline margins commonly ± narrow or lacking, often some-*

what yellowish during prefloral and floral stages. Receptacle density 20—39 fruits per cm of the rachis.

Theca length 2.0—2.7 mm. Pollen length (36—) *39—53* (—58) μ, width (26—) 31—40 (—45) μ.

Achene shape, size, and colour variable between different subpopulations and strains, *often with a dark, reddish or brownish, open and irregular venation on the surface,* quite independent of the reticulation of the surface. Style bases variable in form and size. *Bristles 0—4* (—*8*) *of variable length and appearance, often ± reduced or lacking*; barbs retrorse and variable in size.

Chromosome number 2n=46 (heteroploid chromosome numbers occur).

The following regional and ecological races in Scandinavia are treated as varieties:

E. uniglumis (LINK) SCHULT. ssp. **uniglumis** var. **uniglumis**
[*E. sareptana* ZINSERL.]

According to the nomenclatural type specimen [cf. Opera Bot. **10** (2) p. 125] this variety corresponds to meadow strains of ssp. *uniglumis* which are rather common in inland localities in Scandinavia.

Rhizomes slender; basal sheaths normally lustrous, ± dark red.

Culms 20—60 cm long, normally slender (diameter ≤ 1 mm), midgreen and remaining green also when dried.

Spikes variable, often rather short.

Achenes brownish, size and form varying between different strains. *Bristles ≤ 4, generally well developed,* sometimes lacking.

This variety is *rather common in ± eutrophic inland localities* in Norway as well as in Sweden and Denmark [cf. Opera Bot. 10 (2) pp. 127—128]. It also occurs in calcareous fens on Öland and Gotland, where it forms hybrids with *E. uniglumis* ssp. *sterneri.*

The total distribution of this variety is incompletely known. It occurs in Central Europe and also Russia where it has been described as a species of its own (*E. sareptana* ZINSERL.). Several of the meadow strains investigated from Central Europe are, however, hyperploids with 2n=48—51 and morphologically slightly different from the Scandinavian strains. The taxonomical value of those hyperploids is still uncertain.

E. uniglumis (LINK) SCHULT. ssp. **uniglumis** var. **fennica** (PALLA) HYL.
[*E. fennica* PALLA in KNEUCKER]

This variety is characterized by the following features:

Rhizomes slender; basal sheaths normally lustrous, ± dark red.

Culms 5—20 (—50) cm *long, slender (diameter ≤ 1 mm), ± greyish green.*

Spikes variable, *normally rather short and with rather few flowers* (< 20).

Achenes brownish, length usually ≤ 1.5 mm, width usually ≤ 1.3 mm. Bristles normally lacking, rarely ± developed.

This variety, which is morphologically rather similar to the first mentioned variety, *is the dominant form of E. uniglumis along the shores of the Gulf of Bothnia,* where it occurs in a zone landwards of *E. palustris* ssp. *palustris* var. *lindbergii* (cf. Bot. Notiser 121 p. 9). Around Åland (Alandia), along the south coast of Finland and also from Gästrikland southwards around the Baltic Sea, var. *fennica* is gradually replaced by var. *vestergrenii* (cf. below). Intermediates and other segregates between the two varieties are common.

E. uniglumis (LINK) SCHULT. ssp. **uniglumis** var. **vestergrenii** HYL.

[*E. eu-uniglumis* ZINSERL., "*S. uniglumis* ssp. *fennica*" (PALLA) VESTERGREN sensu VESTERGREN in LINDM., "*S. uniglumis* var. *fennica*" (PALLA) HOLMB. sensu VESTERGREN in LINDM.]

This variety is characterized by the following features:

Rhizomes rather coarse; basal sheaths lustrous, ± dark red to blackish red.

Culms stout, normally ≥ 30 cm with diameter ≥ 1 mm, ± yellowish green, normally becoming yellowish when dried.

Spikes stout, often with a considerable number of flowers (> 20). *Fertile glumes lustrously dark, sometimes with narrow, yellowish hyaline margins* during prefloral and floral stages.

Achenes yellowish to light brown, usually large (length 1.5—2.0 mm, width 1.3—1.5 mm). Style bases low and broad. *Bristles normally lacking,* rarely ± developed.

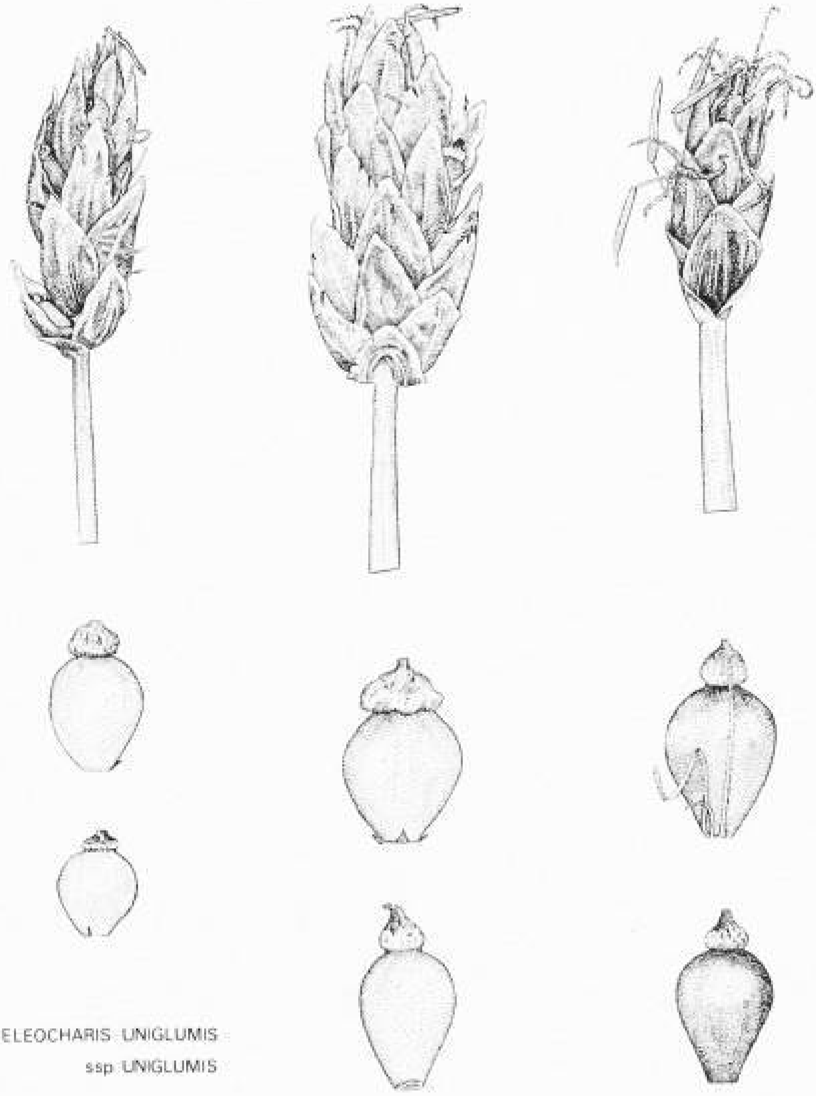
This variety is *the dominant form of E. uniglumis along the shores of the Baltic Sea south of Åland.* The regional difference between var. *vestergrenii* and var. *fennica* is not absolute, but there are also ecologic and physiologic differences. Var. *vestergrenii* prefers localities richer in nutriment than var. *fennica,* and var. *vestergrenii* developes to fruit ripeness somewhat slower than var. *fennica.*

In the straits of Öresund (the Sound) and the Belts, var. *vestergrenii* is gradually replaced by another coastal form of *E. uniglumis,* which occurs along the west coast of Sweden and Norway. This west coast form has never been described as a taxon of its own.

E. uniglumis (LINK) SCHULT. ssp. **uniglumis** var. **septentrionalis** (ZINSERL.) STRANDH.

[*E. septentrionalis* ZINSERL.]

This variety is characterized by the following features:



ELEOCHARIS UNIGLUMIS
ssp UNIGLUMIS

var. FENNICA

var VESTERGRENII

var SEPTENTRIONALIS

Rhizomes stout; basal sheaths normally pale or greenish, rarely reddish. *Culms stout but extremely variable in length*, from 5 to c. 6 cm, *dark green, normally becoming yellowish when dried.*

Spikes stout but often ± reduced in extreme localities. *Fertile glumes lustrously blackish* with narrow or no hyaline margins.

Achenes brown, usually large, 1.5—2.0 mm, width ≧ 1.3 mm. Bristles usually well developed, but occasionally lacking.

This variety occurs *along the coasts of the northernmost parts of Fennoscandia. It grows in wet meadows and shallow water at the mouths of rivers and brooklets.* It is described as a species of its own by ZINSERLING in Flora SSSR from the island of Solovetsk in the White Sea.

From Nordland in Norway and southwards it is gradually replaced by the "west coast form" of *E. uniglumis* mentioned above.

E. uniglumis (LINK) SCHULT. ssp. **sterneri** STRANDH.

This subspecies is distinguished from ssp. *uniglumis* in the following characters:

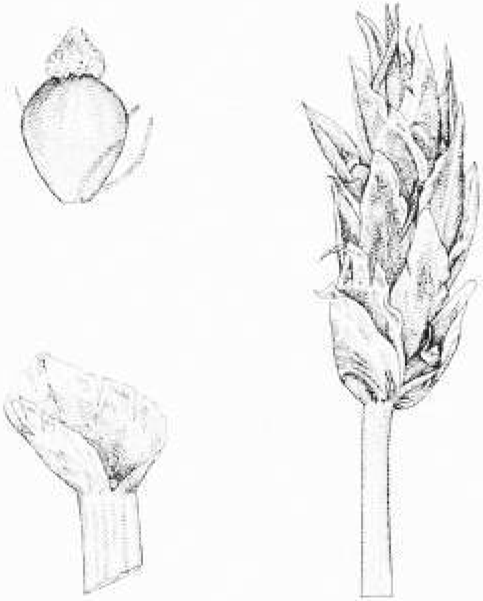
Colour of the culms bluish green to green. *Stomatal length* (52—) *63—78* (—85) μ.

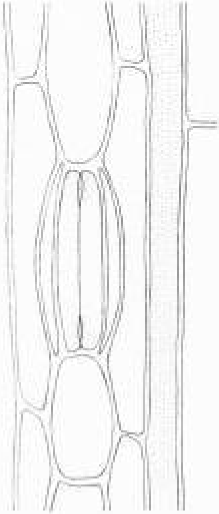
Basal glumes of the spikes with a markedly broad, silvery hyaline margin; fertile glumes longer than 3.5 mm, blackish and with conspicuously broad, silvery hyaline margins in the basal part of the spike during prefloral and floral stages. Receptacle density normally < 32 fruits per cm of the rachis.

Theca length 2.0—3.5 mm. Pollen length (43—) *47—62* (—70) μ, width (33—) 35—38 (—45) μ. Achene shape intermediate or obovoid, length commonly > 1.5 mm, width commonly > 1.3 mm; *colour brown, veins invisible*; surface markedly reticulate. Style bases commonly large and broader than high. *Bristles 4, rather coarse and longer than half the achenes*; barbs retrorse and well developed.

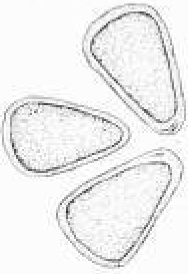
Chromosome number $2n=74$—82, varying from plant to plant in the localities.

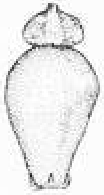
The known distribution of E. uniglumis ssp. sterneri is restricted to the islands of Öland and Gotland in the Baltic Sea where it is common in the small, shallow, ± ephemeric waters called "vätar", and in calcareous fens. It is never observed along the seashores or on the mainland of Scandinavia. Similar high polyploid populations of *E. uniglumis* occur, however, in Central Europe, viz. in Austria, Switzerland, France,



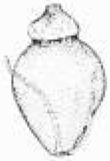


ELEOCHARIS UNIGLUMIS
ssp STERNERI

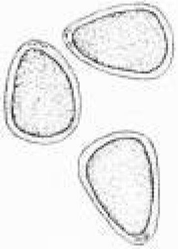




transitional form
within ssp uniglumis



ssp UNIGLUMIS
var UNIGLUMIS



and England [cf. Opera Bot. 9 (2), p. 57, and Ibid. 10 (2) pp. 140—142].

Ssp. *sterneri* often occurs intermingled with the meadow form of ssp. *uniglumis*, called var. *uniglumis*, and fertile hybrids with intermediate chromosome numbers and hybrid segregates have been observed.

Stable Telocentric Chromosomes Formed by Spontaneous Misdivision in Nigella doerfleri (Ranunculaceae)

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ABSTRACT

The normal chromosome number of *Nigella doerfleri* is 2n=12. In a population originating from the island of Ios, Kikladhes (Greece) about half of the individuals were found to have 2n=14. Karyotype analysis indicated that a certain chromosome pair had been broken transversely in the centromere, the arms appearing as separate chromosomes.

Thirteen-chromosomic hybrids were produced by crossing 12- and 14-chromosomic individuals. All three cytotypes possessed normal fertility and were morphologically indistinguishable. In progeny of self-fertilized 13-chromosomic plants, 12-, 13- and 14-chromosomic individuals were distributed according to a 1 : 2 : 1 ratio.

The mechanism of centromeric breakage is briefly discussed, and some of the literature is reviewed.

INTRODUCTION

Nigella doerfleri VIERH. is endemic to Greece, where it is distributed on the Kikladhian islands and Kriti. It is a small annual inhabiting open patches between shrubs in dry garigue vegetation. It flowers in April and May, i.e. considerably earlier than related species occurring in the same area, and is easily distinguished from them, e.g., by its small flowers. Seed setting takes place rapidly after flowering, and the plants survive the hottest period of the year as seeds.

VIERHAPPER (1926) described two species of *Nigella*, *N. doerfleri* and *N. degenii*. The former was recorded from the small island of Paximadhia S. of Central Kriti, and the latter from the islands of Naxos, Mikonos, and Tinos in the group of the Kikladhes. Unfortunately, the names were used in an incorrect sense by subsequent authors, and *N. doerfleri* VIERH. from the Kikladhes became known as *N. degenii* VIERH. (cf. RECHINGER 1943, TUTIN in Flora Europaea 1964, DAVIS 1965). Comparison between the type specimen of *N. doerfleri* (DÖRFLER It. cret. 1904, no. 998) and Kikladhian material determined as *N. degenii*, e.g. by RECHINGER, shows without doubt that they are conspecific. The type material of *N. degenii* is distinct from *N. doerfleri*, and is probably conspecific with *N. huthii* BRAND.

All species of *Nigella* hitherto investigated, including *N. doerfleri*, have the chromosome number 2n=12, and their karyotypes are similar. Five pairs of chromosomes have median to submedian centromeres and are about 8—10 μ long. The remaining pair has an almost terminal centromere and is only slightly more than half as long.

CYTOLOGICAL TECHNIQUE

The preparations were made according to a modification of the method described by ÖSTERGREN and HENEEN (1962). Excised roots were pretreated in a 0.3 % aqueous solution of colchicin for 2—3 hours and fixed in Carnoy (3 parts absolute alcohol: 1 part glacial acetic acid). After hydrolysis for ca. 8 minutes in 1-N HCl at 60° C they were stained with Feulgen. The roots were softened in 5 % pectinase for 2—3 hours, and transferred to 50 % acetic acid for 10—20 minutes. The meristematic regions were disintegrated in a droplet of 50 % acetic acid on a slide, and squashed under a cover slip of Astralon (Vipolon) plastic. The preparations were sealed by means of a frame of rubber solution, and the cover slip was dissolved in acetone. Finally, after transfer to acetone + xylene and pure xylene, the preparations were mounted in Permount, using an ordinary cover slip of glass.

Preparations of young anthers for the study of meiosis in PMC:s were produced in a similar way. However, the pretreatment was omitted, and the flower buds were fixed in Carnoy with chloroform (6 parts absolute alcohol: 3 parts chloroform: 1 part glacial acetic acid). After 48 hours they were transferred to 70 % alcohol, where they can be kept for several weeks without any deleterious effects. Pectinase treatment was made with a 2 % solution for 1—2 hours.

OBSERVATIONS

The karyotype consisting of five pairs of metacentric to submetacentric chromosomes and one pair of subtelocentric chromosomes was constantly found in numerous populations of *Nigella doerfleri* originating from different Kikladhian islands. During cytological routine work, however, a deviating chromosome number (2n=14) was found in some of the plants raised from seeds collected on the island of Ios ("Along a stonewall between fields, ca. 2 km N. the harbour of Ios, ca. 70 m s.m. A. STRID, 5.7.1966"). Several individuals (probably about 50), distributed over a small area and forming a continuous natural population, were represented in the seed collection. Comparison with

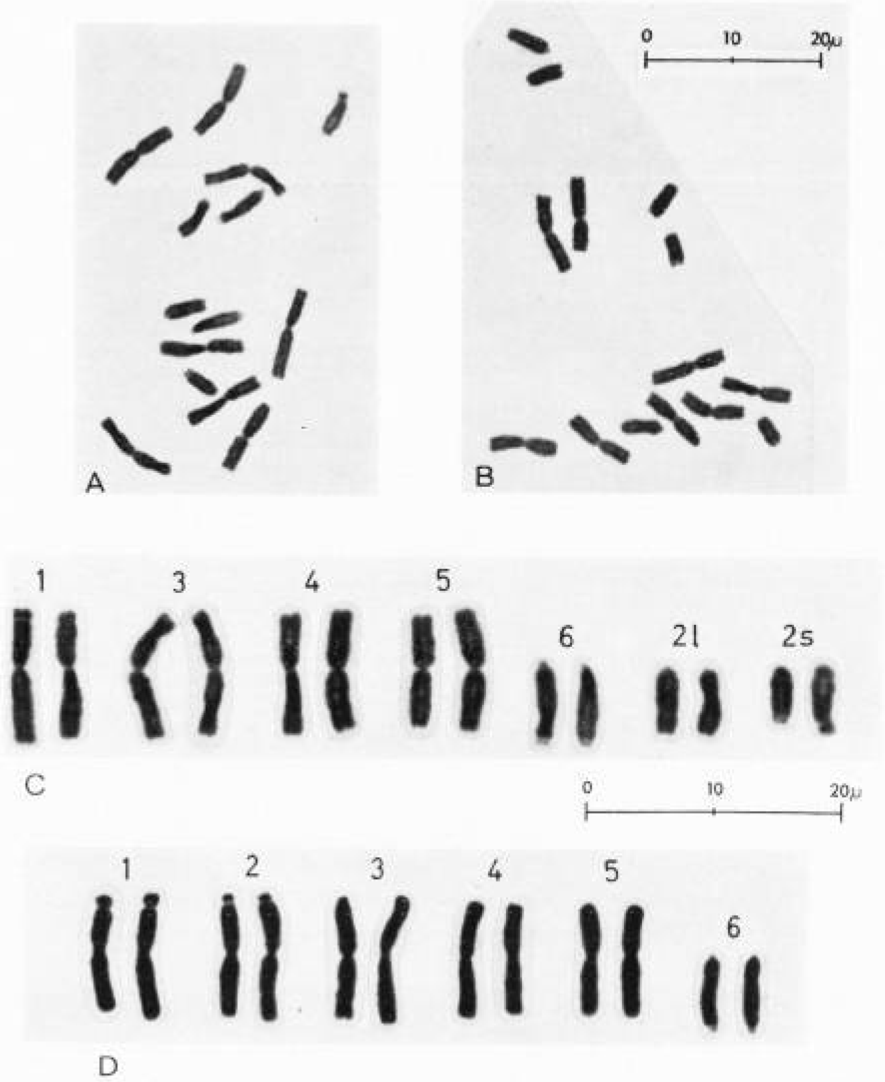

Fig. 1 A—B. Metaphase plates from root tips of 14-chromosomic individuals. Note the presence of six small chromosomes; C. The chromosome complement in A arranged as karyotype. The long and short arms of chromosome no. 2 are indicated by 2l and 2s, respectively; D. Normal 12-chromosomic karyotype from an individual in the same population.

the normal karyotype from individuals in the same population indicated that a certain chromosome pair had been broken tranversely in the centromere region, the arms appearing as separate chromosomes.

Out of 26 individuals, 11 were found to have 2n=14 while 15 had the normal chromosome number 2n=12.

The 12-chromosomic karyotype may be described as follows:

Chromosome no. 1: Submedian centromere. Large satellite attached to the short arm.

Chromosome no. 2: Submedian centromere. Small satellite attached to the short arm.

Chromosomes nos. 3—5: Median to submedian centromeres. No satellites.

Chromosome no. 6: Subterminal centromere. Minute satellite attached to the long arm.

In preparations from 14-chromosomic individuals the four arms of chromosome pair no. 2 appear as separate chromosomes. The short arms can be identified by means of their satellites. Metaphase plates from root tip preparations as well as karyotypes of 12- and 14-chromosomic cells are shown in Fig. 1 A—D. Thus the 14-chromosomic plants have four pairs of chromosomes with more or less median centromeres (nos. 1, 3, 4, and 5), one pair with a subterminal centromere (no. 6), and two pairs with truly terminal centromeres (the arms of no. 2). At the tapering centromeric ends of the latter, faint knobs or chromomeres may sometimes be seen, probably belonging to the broken centromere. There is no indication of instability of the telocentric chromosomes in somatic cells. Apparently they are able to carry out replication and anaphase movement in a normal way, and the chromosome number 2n=14 is constantly found in all cells.

Meiosis was studied in PMC:s of young anthers. Twelve-chromosomic plants form 6 bivalents at M I, one of which is smaller than the others and derived from the subtelocentric chromosomes of pair no. 6. Fourteen-chromosomic plants form 7 bivalents at M I, 3 of which are smaller than the others and derived from pair no. 6 and the respective homologous arms of the broken chromosome no. 2 (see Fig. 2).

Chromosome pairing and separation occur in a regular manner in both types of individuals, the gametes receiving 6 and 7 chromosomes, respectively, and being identical with respect to their chromatin content. Thus the broken centromeres are also efficient in the meiotic division cycle.

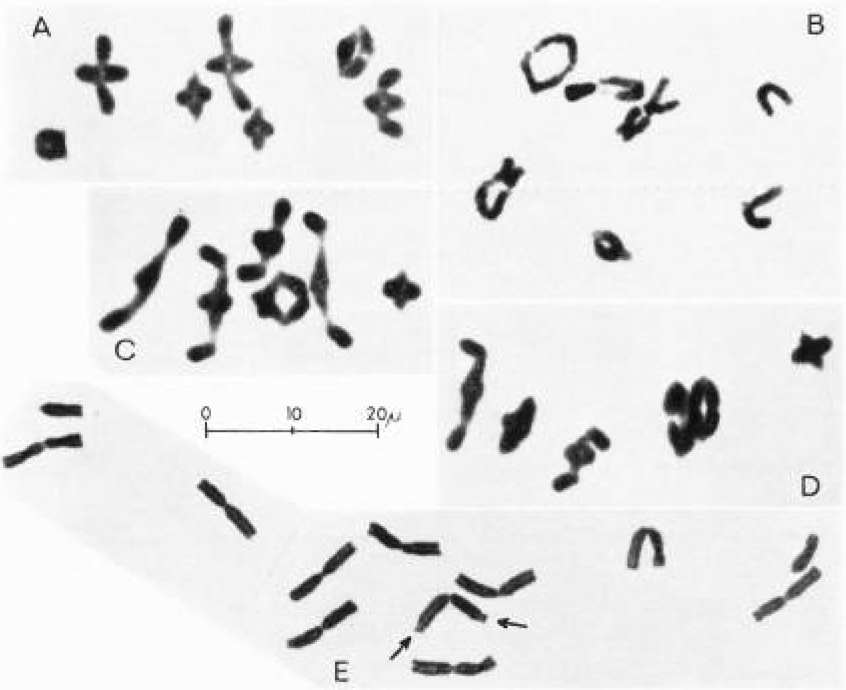

Fig. 2 A—B. Metaphase I and diakinesis, respectively, in PMC:s of 14-chromosomic individuals. Note four large and three small bivalents; C—D. Metaphase I in PMC:s of 12-chromosomic individuals from the same population. Note five large and one small bivalent; E. Metaphase plate from root tip of *Nigella hathii*. A chromosome with two identical arms is indicated by arrows.

The percentage of morphologically good pollen (determined by staining in cotton blue) is high in both 12- and 14-chromosomic individuals (mean values 96.3 ± 0.4 and 93.9 ± 1.3, respectively; $t = 1.76$; $10\,\% > P > 5\,\%$). Seed setting is invariably high, and no differences could be observed between the cytotypes, which are also morphologically indistinguishable.

CROSSES BETWEEN 12- AND 14-CHROMOSOMIC INDIVIDUALS

Several crosses were made in both directions between 12- and 14-chromosomic individuals. As expected, the resulting hybrids were found to have 13 chromosomes. With respect to morphology, pollen fertility and seed setting they are indistinguishable from the parents.

Table 1. Distribution of different chromosome number in F_1 after self-fertilization of three 13-chromosomic plants.

	2n=12	2n=13	2n=14	Total
Plant no. 1	13	22	16	51
Plant no. 2	12	22	6	40
Plant no. 3	11	21	18	50
Total	36	65	40	141

$\chi^2_1=1.59$; fg=2; 95 % $>$ P $>$ 10 %. $\chi^2_2=2.4$; fg=2; 95 % $>$ P $>$ 10 %. $\chi^2_3=3.24$; fg=2; 95 % $>$ P $>$ 10 %. $\chi^2_{\text{total}}=0.92$; fg=2; 95 % $>$ P $>$ 10 %.

The same results were obtained regardless of the direction of pollen transfer (12 → 14 or 14 → 12). The 13-chromosomic individuals have one normal submetacentric chromosome no. 2, and two small telocentric chromosomes, each of which is identical in appearance with one arm of chromosome no. 2.

At meiosis five bivalents and one trivalent are regularly found. The latter results from the pairing of the two telocentric chromosomes with the respective arms of the normal submetacentric chromosome no. 2. Because of the close pairing of homologous segments, the trivalent is indistinguishable from a normal bivalent at late prophase and M I, and the cells appear to have six bivalents like those of 12-chromosomic individuals. The true nature of the trivalent is revealed at A I, however, when seven chromosomes, two of which are telocentric, move to one pole, and six chromosomes, including the normal no. 2, move to the other. The resulting daughter nuclei are identical with respect to their chromatin content. Anaphase separation seems to occur in a very regular manner, preventing the formation of genetically unbalanced gametes.

Thirteen-chromosomic plants were self-fertilized, and the distribution of different chromosome numbers in the progeny was checked. As shown in table 1, the numbers do not differ significantly from the expected 1 : 2 : 1 ratio for 12-, 13-, and 14-chromosomic plants, respectively. Hence, fertilization brings about random fusion of 6- and 7-chromosomic gametes formed in equal numbers.

DISCUSSION

The fact that 12- and 14-chromosomic plants but no 13-chromosomic ones were found in the original population indicates that *Nigella doerfleri* is being exclusively or predominantly self-fertilized. Misdivi-

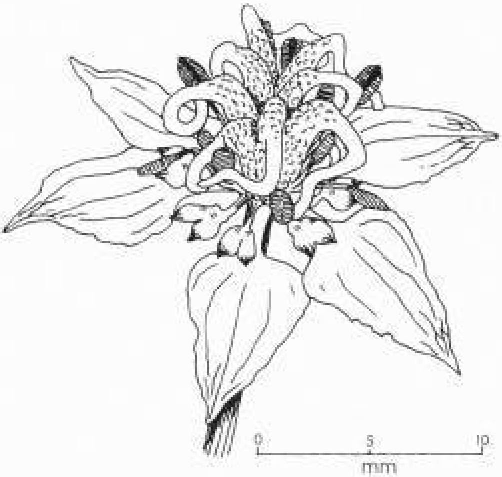

Fig. 3. Flower of *Nigella doerfleri*. The follicle beaks become twisted around the anthers. Further explanation in the text.

sion is very unlikely to have occurred simultaneously in two homologous chromosomes. The original 13-chromosomic plants have most probably been converted into 12- and 14-chromosomic ones as a consequence of successive inbreeding. *Nigella doerfleri* is easily self-fertilized even when individual flowers are isolated in pergamine bags. In spite of the fact that the anthers are extrorse and situated at some distance below the receptive adaxial surface of the follicle beaks, self-fertilization occurs by means of a particular mechanism. The slender beaks of the follicles, which are straight and erect in bud stage become strongly recurved, finally reaching the anthers and becoming loosely twisted around them as the pollen is shed (cf. Fig. 3). This precise movement of the stigmatic parts of the follicles along with simultaneous movement of the stamens has been observed also in other species of *Nigella* (cf. KNUTH 1898, TROLL 1922, KUGLER 1955). In *Nigella doerfleri* the mechanism is very effective and, even under green-house conditions in the absence of pollinating insects and with very little turbulence in the air, seed setting is constantly very high. As a high and regular seed setting is essential to an annual with a rapid life cycle such a mechanism is no doubt beneficial, although inbreeding might be deleterious in the long run.

Several authors have expressed disbelief as to the existence of strictly telocentric chromosomes (NAVASHIN 1916, LEWITSKY 1931, MULLER 1940). Others accept the occasional occurrence of such chromosomes.

but conclude that they are unstable and hence do not survive in nature (DARLINGTON 1939, RHOADES 1940, WHITE 1954).

SANCHEZ-MONGE (1951) suggested that there are two types of telocentric chromosomes: the stable telocentrics which arise through whole arm deletions and thus have complete centromeres and the unstable ones which are produced by misdivision and can secondarily be transformed into isochromosomes. SANCHEZ-MONGE (op. cit.) visualized the formation of these two types of telocentrics in accordance with the observations of TJIO and LEVAN (1950) that the centromere normally consists of four chromomeres. The present observations seem to prove, however, that telocentric chromosomes formed by misdivision may also be perfectly stable.

LIMA-DE-FARIA (1949, 1956) distinguished three regions within the centromere, an exterior, faintly staining region, a chromomere region, and an internal region which may or may not contain chromomeres. The structure is duplicated and forms a "reversed repeat". Telocentric chromosomes may originate by transverse division through the internal region. This possibility was considered in the thoroughly investigated case of *Notoscordum*, where different numbers of telocentric chromosomes were found in different strains (ANDERSON 1931, BEAL 1932, LEVAN & EMSWELLER 1938, SATO 1942, KURITA 1953). MATTSSON (1963) found 12 metacentric and four telocentric chromosomes in a strain of *Tradescantia commelinoides*, in disagreement with previous records of 14 metacentric chromosomes, and concluded that one pair had most probably undergone transverse breakage in the centromere.

Evidence of the formation of stable telocentrics in plants following breakage within the centromere was given by DARLINGTON and LA COUR (1950) and MARKS (1957 a, b).

The existence of stable truly telocentric chromosomes was unambiguously demonstrated by JOHN and HEWITT (1966) in the locust, *Locusta migratoria*. The telocentric chromosomes have a centric organisation equivalent to one half of that present in the metacentric elements, thus giving support to LIMA-DE-FARIA's interpretation of the centromere structure.

In materials where telocentric or subtelocentric chromosomes occur, and the chromosome numbers of related taxa form an aneuploid series, the highest number is usually regarded as primitive, and the lower numbers are interpreted as the results of successive centric fusions (i.e. translocations followed by the elimination of minute centric fragments). However, the series need not necessarily be read in this

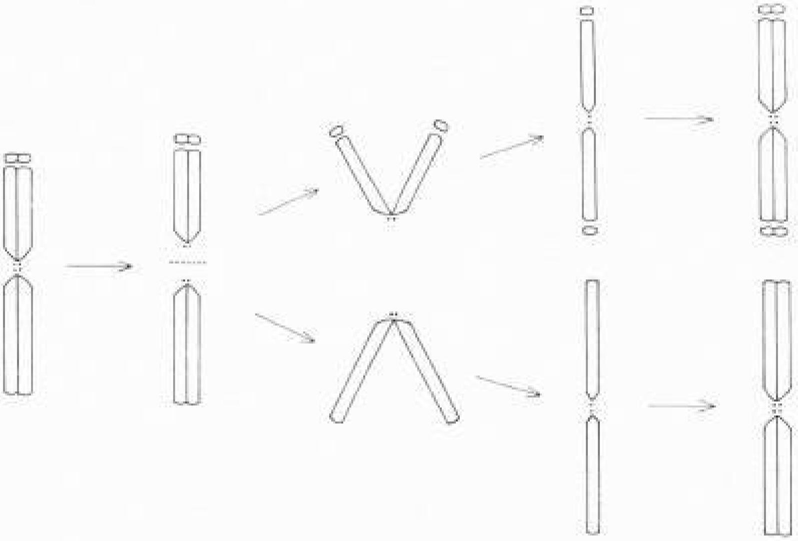

Fig. 4. Diagrammatic representation of centromeric breakage giving rise to telocentric chromosomes and/or isochromosomes.

direction. The present observations on *Nigella doerfleri* strongly indicate that new karyotypes may indeed be produced by transverse division of the centromere of a metacentric chromosome.

It is generally believed that ordinary chromosome or chromatid breaks caused, e.g., by radiation or chemical agents may be followed by reunion of the freshly broken ends, and thus escape detection. It remains to be convincingly demonstrated, however, whether two telocentrics formed by misdivision through the internal region of the centromere in a metacentric chromosome can fuse by their centromeric ends to reestablish the metacentric. Ordinary chromosome ends have properties distinctive from those of a freshly formed surface, and are defined as telomeres (MULLER 1940). The terminal centromeres formed by misdivision must be capable of functioning as telomeres as well, and it might be assumed that they undergo rapid, irreversible chemical changes preventing their reunion. However, there is certain evidence that a spontaneous interchange heterozygote in *Triticum aestivum* was formed by simultaneous misdivision of two non-homologous chromosomes followed by illegitimate reunion (MORRISON 1954). Certain induced translocations in barley involve rearrangement of a whole chromosome arm following a break within the centromere (RAMAGE, BURNHAM & HAGBERG 1961; HAGBERG, PERSSON & WIBERG 1963).

> "The translocation T 6—7 d has one of the breaks in the centromere of chromosome 7, and the other break is in the short arm of chromosome 6, rather close to the secondary constriction. This gives a very short chromosome with two satellites and a very long chromosome with two centromeres; one normal centromere (the one from chromosome $6 = c^6$), and the other which is a part of the centromere from chromosome 7 ($= c^{7/2}$). Both function as centromeres but the normal c^6 is always stronger than the $c^{7/2}$. The remaining part of c^7 functions very well as it is the only centromere present in the new, very short chromosome." (HAGBERG, PERSSON & WIBERG op. cit.).

The fact that a part of a centromere functions normally in barley is an interesting parallel to the *Nigella* case described in the present paper. The centromere is obviously divisible into smaller elements capable of preforming the function of the whole centromere.

The possible origin of telocentric chromosomes and isochromosomes by misdivision of the centromere is shown diagrammatically in Fig. 4. The existence of a probable isochromosome was observed in a single mitotic metaphase plate from a species related to *Nigella doerfleri* (*N. huthii* BRAND from the Marmaris peninsula, W. Turkey). In Fig. 2 E a chromosome with two equal satellited arms is indicated by arrows.

Nigella doerfleri apparently provides an example of a population containing individuals with telocentric chromosomes formed by misdivision together with individuals with a normal karyotype. This observation supports LIMA-DE-FARIA's conception of centromere structure but contradicts WHITE's view that stable telocentric chromosomes do not exist in nature (WHITE 1954, 1957, 1965).

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Revision of the Genus Aspalathus. II

The Species with Ericoid and Pinoid Leaflets. 7
Subgenus Nortieria. With Remarks on Rooibos Tea Cultivation

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ABSTRACT

The two species *Aspalathus linearis* (BURM. FIL.) R. DAHLGR. and *A. pendula* R. DAHLGR., which make up subgenus *Nortieria* R. DAHLGR., are studied in this paper. The placing of the species in *Aspalathus* is considered appropriate because the proper morphological characteristics, except for the simple leaves, are in evidence. (In most of the other *Aspalathus* species the leaves are trifoliolate.) The leaves in *Nortieria* are most probably unifoliolate although it is also conceivable that they may be phyllodinous in which case a close affinity to *Lebeckia* is probable. Anatomical details do not settle the nature of the leaves.

Within *A. linearis* three subspecies are distinguished. The nomenclature, characteristics, natural variation, ecology, distribution, and other particulars of these subspecies are outlined, and the related species, *A. pendula*, is similarly described.

A. linearis ssp. *linearis* is the commonest of the subspecies, and was described and illustrated by PLUKENET about the year 1700. This subspecies, which includes the forms used for "tea", has a very great variation in total size, leaf length and coarseness, leaf colour, floral size, petal colour, etc. The leaves of the southernmost, relatively pubescent forms lack the ability of forming the aroma and colour typical of certain northern populations. Extremely small-flowered populations occur in certain relatively southern regions (especially the Paarl and Worcester Divisions). There is great variation within the populations in the Cedarberg and Olifants River Mountains. The fermented and dried leaves of particular forms from these regions are used as "Rooibos Tea". The cultivated biotypes yield a commercial product, now known as "Rooi Tea", which is becoming increasingly popular in South Africa. Until recently, certain types of Rooibos Tea was also made from wild forms. Wild populations which possibly correspond to these tea types are discussed. A preliminary thin layer chromatographic test shows that there are special differences between the tea types mentioned with regard to phenolic compounds.

The cultivated biotype material of ssp. *linearis* is quite variable and indicates predominant allogamy. This variation may be observed in total size, density of branching, stiffness of branches, number and distribution of flowers on the branches, development of short-shoots, flowering time, etc. Some of these factors are of great moment in the Rooi Tea industry. The cultivation and processing of the Rooi Tea are described.

INTRODUCTION

The subgenus *Nortieria* was described in DAHLGREN 1963 A; it contains two species: *Aspalathus linearis* (BURM. FIL.) R. DAHLGR. and *A. pendula* R. DAHLGR. Certain forms of *A. linearis* are the source of the Rooibos Tea or the "Rooi Tea" as the cultivated product is now named. The name of the subgenus, *Nortieria*, was given after Dr. P. LE F. NORTIER, the chief pioneer in the cultivation of the species.

The present article forms part of the series "Revision of the Genus Aspalathus" which is continuously being published in Opera Botanica and Botaniska Notiser. The order, the abbreviations and the methods used in this article follow this series and the reader is referred to previous parts of this work for further particulars.

A. pendula and the wild forms of *A. linearis* have been studied during two periods of field work in South Africa (1956—57 and 1965—66), when also the Rooibos Tea Centre at Clanwilliam was visited. My own collections are indicated with an exclamation mark (e.g. ! no. 1000).

In DAHLGREN 1963 A has previously been discussed the treatment of the two species, *A. pendula* and particularly *A. linearis*, in previous literature (pp. 19, 23), the systematic position (p. 50), the morphology (pp. 61, 71, 72, 73, 93, 94), the trichomes (pp. 227, 228), the chromosomes (pp. 231, 232), and the cultivation of *A. linearis* (pp. 233, 234). The subgenus and its species were described and illustrated in this work on pp. 213—216, and the Latin diagnoses and nomenclature concerning the subspecies of *A. linearis* as well as *A. pendula* are found on pp. 283 and 285 respectively. Distribution and features of variation were mentioned briefly in DAHLGREN 1963 B on pp. 443, 452, and 461. Finally, the rather intricate nomenclature of *A. linearis* and its synonyms was treated in DAHLGREN 1964.

The wild forms of *Aspalathus linearis* and *pendula* have been studied and collected in the field in 1956—57 and 1965—66. Herbarium material has been studied from the following herbaria, abbreviated according to LANJOUW & STAFLEU 1964 (Index Herbariorum): B, BM, BOL, C, CT, G, GB, GH, GRA, HBG, K, L, LD, LINN, M, NBG, NH, P, PR, PRC, PRE, S, SAM, STE, UPS, W, and Z. Cultivated material has been studied on farms in the Clanwilliam

Division, and the Rooibos Tea Industry at Clanwilliam was visited in 1965, when also certain shrub material (Fig. 10) in comparative cultivation was studied. Seeds have been sown in greenhouses in Lund and seedling collections of wild forms (in this case particularly of *A. l.* ssp. *latipetala*) have been in cultivation in the National Botanic Gardens, Kirstenbosch. For cytological investigations, root-tips of *A. linearis* have been fixed in Navashin-Karpechenko and stained in crystal violet with the addition of aniline. Measurements of floral parts have been made on herbarium material quickly soaked in water. Chromosomes and anatomical details have been drawn by the camera lucida method and the other parts with the help of a fine scale ruler.

SYSTEMATIC POSITION

The two species of subgenus *Nortieria* have most features in common with the other groups of *Aspalathus*. They do not differ from the rest of the genus in any floral details, and, notably, the shape and structure of the pod is quite similar, being narrowly and obliquely lanceolate and few-seeded, not linear and many-seeded as in most species of *Lebeckia*, a genus otherwise most similar to subgenus *Nortieria* in leaf characters and sometimes also in habit and certain floral details. However, the branches are not green and assimilating in subgenus *Nortieria* as they are in most forms of the *Lebeckia* species with a comparable leaf shape, and the latter *Lebeckia* species also have long, linear, and many-seeded legumes.

Accordingly, it is only in the leaf character that subgenus *Nortieria* differs greatly from the other groups of *Aspalathus*, resembling certain species of *Lebeckia*. The reader is referred to the rather detailed discussion of the leaves in *Aspalathus* and *Lebeckia*, given in DAHLGREN 1963 A on pp. 61—73 and 255—263, respectively. Whether the pale, narrow portion at the base of the leaf in subgenus *Nortieria* should be classified as a "pulvinus" or a pale short petiole cannot be settled. The main question is whether the main green part of the *Nortieria* leaf represents a single leaflet (the leaf being unifoliolate and subsessile) or a petiole (the leaf being phyllodinous). Already the leaves immediately following the cotyledons are of the same simple linear shape as the later developed ones and thus cannot settle this question (as in, e.g., *Lebeckia pungens* THUNB. described in DAHLGREN 1967, pp. 153 and 155).

In those species of *Lebeckia* which have "jointed" linear leaves the petiole and the solitary leaflet are of the same linear, green, and subterete appearance: the anatomical details of the transversal sections of petiole and leaflet are also so similar that a distinction between them is not possible (see DAHLGREN 1963 A p. 258). The transversal section of the *Nortieria* leaf is similar, and the anatomy of the leaf can accordingly not settle the question as to the phyllodinous or unifoliolate nature.

A basal "pulvinus" somewhat similar to that in subgenus *Nortieria* occurs on the base of the leaves in certain *Lebeckia* species, but it cannot be stated whether this denotes a common background. *L. linearifolia* E. MEY., illustrated in DAHLGREN 1963 A, Fig. 77 K—M, belongs to the *Lebeckia* species which are most similar to subgenus *Nortieria* in floral characters. It belongs to a group of frequently quite pubescent species, chiefly with trifoliolate leaves with relatively long petioles. The leaves in *L. linearifolia* are simple and flat and seem to be phyllodinous (which is indicated by comparison with similar species which have long-petiolate leaves with ± rudimentary folioles). In this and related species, however, there are conspicuous differences from *A. linearis*, e.g., in the pods, which are long, linear, and many-seeded, and the similarities in flowers and leaves may have been achieved by convergent evolution.

Aspalathus and *Lebeckia* largely agree in chromosome number and this gives no indication on the relationship. Most *Aspalathus* species and the four species of *Lebeckia* investigated have $2n=18$, which number is also found in *Nortieria* (see Fig. 1 I—L and DAHLGREN 1967).

The *Nortieria* leaf apparently represents an advanced type; within *Aspalathus* and *Lebeckia* "simple leaves" may have evolved along different lines from a trifoliolate precursor, without and with petiole respectively, the result being functionally and anatomically equal. Therefore, it is still uncertain in a group like *Nortieria* to which category the leaf belongs. In the present paper the two species are placed in *Aspalathus*, where they have generally been treated, but as a morphologically marginal group.

PREVIOUS TAXONOMIC TREATMENT

The species now known as *Aspalathus linearis* appeared early in botanical literature. Perhaps it was the species described by RAY in Historia plantarum (1686 p. 104) as "*Genista Africana frutescens, foliis Linariae angustioribus glaucis, flore lutea* D. Sherard"; on the other hand this may also have represented a species of *Lebeckia*. It is more likely that the present species is that illustrated on Plate 412: 5 in PLUKENET's Phytographia plantarum (1691—96) and later described by PLUKENET (1700 p. 82) as "*Galega affinis Malabarica arborescens siliquis majoribus articulatis*". A specimen in SLOANE's herbarium (BM), vol. 92, p. 72, seems to correspond well with this illustration.

The species was first validly described in 1768 by N. L. BURMAN in his Florae Capensis prodromus on p. 22, viz. as *Psoralia (linearis)* — *foliis simpli-*

bus linearibus cum acumine, floribus terminalibus ternis (see DAHLGREN 1964 Fig. 2). The later homonym *Psoralea linearis* THUNB. is a different species and has a phrase name different from that of BURMAN's species, which THUNBERG did not quote. *P. linearis* THUNB. is probably a synonym of *Psoralea axillaris* L. FIL.

Psoralea linearis BURM. FIL. represents the basionym of the correct name *Aspalathus linearis* (BURM. FIL.) R. DAHLGR., a combination not made until 1963 (DAHLGREN 1963 A p. 284; see also DAHLGREN 1964 pp. 188—191).

In 1771 (p. 268), LINNAEUS described a species called *Spartium contaminatum*, which represents, in fact, a species of *Lebeckia* according to present concepts. This species was placed by THUNBERG (1800 A p. 122; 1800 B p. 139) in *Lebeckia*, but according to the specimens in THUNBERG's herbarium (UPS) the name was then used for the present *A. linearis*, although LINNAEUS' *Spartium contaminatum* was quoted. This concept of the name was noted in HARVEY 1862. DRUCE in 1917, p. 606, made the combination *Aspalathus contaminata* referring to THUNBERG's *Lebeckia contaminata* only, and apparently meant for the present *A. linearis*. In this sense the name has also been used in several later publications. (See DAHLGREN 1964.)

Aspalathus linearis was also described as *A. tenuifolia* by DE CANDOLLE in 1825 (p. 143) and as *A. corymbosa* E. MEY. in MEYER 1832 (p. 159), ECKLON & ZEYHER 1836 (p. 104), BENTHAM 1848 (p. 653), HARVEY 1862 (p. 139), MARLOTH 1925 (p. 77), and in several other works. It was also described as *A. cognata* by PRESL in 1845 (p. 556) and as *Borbonia pinifolia* by MARLOTH in 1912 (p. 238).

Aspalathus pendula, the second species of the group, was incorrectly named *A. tenuifolia* DC. by MEYER in 1836 (p. 65). It was described under the present name as late as 1963 (DAHLGREN 1963 A p. 285 and p. 214 with Fig. 69).

MARLOTH, who described *Borbonia pinifolia* in 1912, was one of the first botanists to identify the species as the source of a "bush tea". He wrote (M. 1912 p. 239): 'The plant is of special interest, as it supplies the "rooibosh-tea", which is now so largely used in South Africa either under this name or as "naald-thee" or "koopmans-thee". The shrublet occurs apparently only on the Cedar Mountains near Clanwilliam and Wupperthal'. Nevertheless, the particular branch on which *B. pinifolia* is typified does not correspond to those forms which are at present being cultivated.

In 1951 KIES gave an account of the species under the name *Aspalathus contaminatus* in her revision of the genus *Cyclopia*. Several species of *Cyclopia* were likewise used as "bush tea".

BOLUS & WOLLEY-DOD identified the species (under the name *A. corymbosa*) as a member of the Cape Peninsula flora in 1913, and SALTER (in ADAMSON & SALTER 1950 pp. 474, 484), who called the species *A. contaminatus* (THUNB.) DRUCE, noted that its leaves are simple and that "this species has affinities with the genus *Lebeckia*, with which it seems to be somewhat intermediate".

Recently, in connection with its cultivation, *A. linearis* has been carefully investigated with regard to the chemical constituents of the fermented leaves (articles by W. H. K. COETZEE & al. 1944 and 1953) and in connection with the "tea" industry.

SUBGENUS NORTIERIA R. DAHLGR. 1963 A

Shrubs (prostrate—) decumbent—erect, up to > 2 m tall. Branches short-pubescent—subglabrous. *Leaves simple*, long, *linear, subterete or slightly flattened*, sometimes with longitudinal shallow grooves; *in the basal part with a constricted*, often short-pubescent *segment*; leaf-base below this part broadening and occasionally with very short stipular teeth. Flowers solitary or more often several together in a corymb or raceme. *Bracts and bracteoles small, simple*, triangular or *subulate*. Pedicel often relatively long, usually sparsely or closely puberulous. Calyx on outer side usually adpressedly puberulous, rarely glabrous; calyx lobes triangular—broadly subulate, lowest lobe somewhat narrower and often slightly longer than the upper; lower sinuses of calyx also not as deep as the upper. *Petals pale or bright yellow* or in the wild forms often partly purplish (especially on vexillum back and carina bottom); vexillum usually ovate, pubescent on part of back side; alae glabrous or almost so, elongate, the blades with some rows of minute folds on the upper basal parts; carina lunate, glabrous or usually short-sericeous on the lower parts. *Ovary mostly sericeous, with 2 (—4) ovules; stigma small, capitate. Pod* relatively large, *obliquely lanceolate*, opening when ripe, generally with one seed only. Seed usually pale brownish-pink.

Type species: *Aspalathus linearis* (BURM. FIL.) R. DAHLGR.; DAHLGREN 1963, p. 213.

Aspalathus linearis (Burm. fil.) R. Dahlgr.

Nomenclature, literature, etc., see under the subspecies.

Shrublets or shrubs, varying from decumbent or depressed to ascending or erect, and from quite low to about 2 m high. Branches usually slender, sparingly or rather closely branched; bark usually grey on (> 1 1/2 year) old parts, but commonly ferruginous, dark-red or purplish on younger parts; young branches usually sparsely and shortly sericeous, seldom subglabrous. — *Leaves* (interpretation see above and in DAHLGREN 1963 C p. 71 ff.) simple, narrowly linear; generally 15—60 mm long and 0.4— > 1.0 mm broad; straight (or slightly incurved); acute, acuminate or mucronulate-apiculate; subterete or slightly flattened; often (especially when dry) longitudinally rugose; somewhat rigid; pale, bright or sombre green (or glaucous), seldom light green; when dry often becoming ± ferruginous; glabrous or shortly and adpressedly puberulous. Leafbase with a ca. 0.4—1.2 mm long and narrow, only ca. 0.2—0.4 mm thick segment pale (sometimes purplish) in colour and generally distinctly pilose; leaf base below this part with a wider, ± brownish basal plate occasionally bearing < 0.3 mm long stipular tips or teeth on its sides. — *Flowers* solitary or several, occasionally up to > 10, in corymbs or short or seldom elongate racemes on the branch tips, often also solitary or few together on short shoots along the branch ends. — *Bract*, emerging at pedicel base, subulate or narrowly triangular, usually 0.3—1.5 mm long, acute, puberulous on inner side, glabrous or puberulous on outer side, often shed at an early stage. — *Pedicel* narrow, usually 1.5—4.0 mm long (in ssp. *latipetala* up to > 6.5 mm long), sparsely or closely short-sericeous, seldom glabrous. — *Bracteoles* similar to bract, 0.2—0.8 mm long. — *Calyx* tube infundibuliform or openly campanulate, shorter on upper than on lower side (and as a result appearing oblique), glabrous or very shortly sericeous. Lobes deltoid—broadly subulate, glabrous or short-sericeous; upper lobes 0.5—2.0 (—3.5) mm and lower 1.0—3.2 (—4.5) mm long. — *Petals* pale—bright yellow or often with sombre-violet shades on vexillum back and carina bottom, occasionally dark violet on most parts. — *Vexillum* blade circular or broadly obovate or ovate, 4.2—7.5×3.0—8.0 mm large, acute—obtuse (or retuse) at apex, usually short-sericeous on most of back side, glabrous on front side except for a basal hair tuft. Claw only ca. 0.5—1.2 mm long. — *Ala* blades narrowly elliptic-oblong or obovate, 2.8—5.3×1.0—2.0 mm large, glabrous or with few hairs, with (2—) 3—5 rows of minute depressions on basal upper parts. Claws 1.3—2.3 mm long. — *Carina* blades lunate, 3.1—6.0×2.0—3.6 mm large, obtuse or occasionally (in ssp. *pinifolia*) with an acuminate process below apex, glabrous (in ssp. *latipetala*) or usually short-sericeous at least on lower apical parts. Claws 1.5—2.7 mm long. — *Pistil* with short stipe; ovary elongate, with 2 (rarely 3—4) ovules, short-sericeous on most parts (usually ± glabrous below); style often ± sericeous on basal parts. — *Pod* narrowly and obliquely lanceolate, (10.5—) 12.5—17×3—4.2 mm large, sparsely short-sericeous in young stages, generally glabrescent, in ripe stage brown, bright-ferruginous or reddish.

The species has a mainly western-southwestern distribution and ranges from the Cape Peninsula to the Calvinia and Vanrhynsdorp Divisions in the northwest and to the Swellendam Division in the southeast. It comprises a multitude of populations, and is divisible into three form groups which are here given subspecies rank.

KEY TO THE SUBSPECIES

1 A. Carina ± pubescent, at least on lower apical parts.
  2 A. Carina without a pointed tooth below the apex .... ssp. *linearis*
  2 B. Carina with a prominent, pointed, toothlike process below the apex .. .. ssp. *pinifolia*
1 B. Carina glabrous .... ssp. *latipetala*

Aspalathus linearis (Burm. fil.) R. Dahlgr. ssp. linearis

Dahlgren 1963 A p. 283; 1964 p. 180 ff. — *Psoralea linearis* Burm. fil.; N. L. Burman 1768 p. 22. — *Lebeckia linearis* (Burm. fil.) DC.; de Candolle 1825 p. 137 ("L. ? *linearis*"). — Original specimen: "*Psoralea linearis*" in Burman's herbarium (G, lectotype; see Dahlgren 1964 Fig. 2).

"*Aspalathus contaminata* (Thunb.) Druce" sensu Druce 1917 p. 606, non *Spartium contaminatum* Linnaeus 1771 p. 268, nec *Lebeckia contaminata* (L.) Thunberg 1800 B p. 140. See the discussion above on p. 169 and in Dahlgren 1964. Druce's concept of *Aspalathus contaminata* has been adopted in various later botanical works. *Aspalathus contaminata* (L.) Druce is to be typified by a *Lebeckia* specimen.

Aspalathus tenuifolia DC., de Candolle 1825 p. 143. — Original specimen: "Lambert 1816" in de Candolle's herbarium (G-DC, lectotype). — In Meyer 1836 p. 65, Bentham 1848 p. 653, Harvey 1862 p. 139, and Kies 1951 p. 170 the name was used for *A. pendula* R. Dahlgr. (see below).

Aspalathus corymbosa E. Mey.; Meyer 1832 p. 159; 1836 p. 61; Ecklon & Zeyher 1836 p. 204; Bentham 1848 p. 653; Harvey 1862 p. 139; Bolus & Wolley-Dod 1903 p. 254; Marloth 1925 p. 77; etc. — Original collection: "Auf dem Tafelberge." Ecklon (S, lectotype).

Aspalathus cognata Presl; Presl 1845 p. 556. — Original collection: "Cederbergen". Drège: "*A. corymbosa* c" (K, L, P; syntypes).

Shrublet or shrub, varying from decumbent or depressed to erect, and from quite low to ca. 2 m tall. — *Leaves* generally 1.5—6 cm long and 0.4— > 1 mm broad; terete or slightly depressed; glabrous or pale—bright green, turning greyish—bright ferruginous when dried; glabrous or sparsely short-sericeous. Leafy short-shoots often developed in leaf axils. — *Flowers*, variable in size, few or several in corymb-like racemules on branch tips, but commonly also distributed, 1—2 (seldom more) together, on short-shoots along the branches. — *Bract* usually subulate and 0.3—1.0 mm long. — *Pedicel* (1.3—) 1.7—3.0 (—3.7) mm long, usually short-sericeous, more seldom glabrous. — *Bracteoles* 0.3—0.8 mm long. — *Calyx* tube glabrous or very slightly sericeous; lobes (0.7—) 1.0—2.2 (—2.6) mm long, linear, acute, lowest lobe longer than the upper. — *Petals* usually pale—bright yellow on most parts, but often with violet tinge on vexillum back; sometimes ± dark violet on most parts of vexillum and carina and on part of alae. — *Vexillum* blade usually ovate, (4.2—) 4.6—6.5 (—7.4) × (3.8—) 4.0—5.6 mm large, acute (or obtuse), closely (or occasionally sparsely) sericeous on half or 3/4 of back side. Claw 0.6—1.2 mm long. — *Ala* blades (2.8—) 3.2—4.8 (— 5.3) × (1.0—) 1.2—2.0 mm large. Claws 1.3—2.1 (—2.3) mm long. — *Carina* blades lunate, (3.1—) 4.0—5.6 × (2.2—) 2.5—3.3 mm large, obtuse, lacking apical process, with straight or often slightly concave (seldom slightly convex) upper margins, and with sericeous pubescence at least on lower parts of apical half. Claws 1.8—2.7 mm long. — *Ovary* ± sericeous; ovules 2 (very rarely 3 or 4). — *Pod* usually 12—17 × 3.3—4.2 mm large. 2n = 18.

DISTRIBUTION. Western, ranging from the southern part of the Cape Peninsula and the Cape Hangklip region in the south to the Nieuwoudtville region, Calvinia Division, in the north. There seems to be — if not an actual gap — at least a region of low frequency between the Paarl and the Porterville regions, although undisputed, indigenous forms are recorded at least in the Bosjesveld and Witzenberg Mountains. The spontaneous distribution is at present somewhat obscured by escapes from the rooibos tea plantations, although such forms are usually easily recognizable by their appearance. Map on p. 185, Fig. 5 A.

COLLECTIONS (samples certainly cultivated not included)

Simonstown Div.: Nr. Cape Point. 1939, Lewis no. 493 (SAM). — Smitswinkel Berg. 1896, Wolley-Dod no. 767 (BM). — Klaver Valley. 1924, Moss no. 7741 (LD); 1927, Salter (BM); 1936, Salter no. 5804 (SAM). — Simonsberg. 1896, Wolley-Dod no. 284 (K). — Mt. slope 2 miles SE of Simonstown. 1965, ! no. 4046 (LD). — Foot of mts. nr. Simonstown. 1880, H. Bolus no. 3815 (K). — Mts. nr. Simonstown; ca. 300 m. 1892, Schlechter no. 308 (BM, GRA, P).

Wynberg Div.: Chapmans Peak. 1940, Compton no. 8483 (NBG); 1943, Compton no. 15407 (NBG). — Chapmans Peak, N slopes. 1943, Compton no. 14467 (NBG). — Noord Hoek Mt. 1939, Salter no. 7999 (CT). — Vlaggeberg. 1896, Wolley-Dod no. 720 (BM, K, PRE); 1913, Kensit (CT); 1931, Salter no. 1906 (SAM). — Slopes above Constantia Nek Waterworks. 1934, Acocks no. 3895 (S). — Orange Kloof. 1956, Salter no. 9790 (BM).

Cape Town Div.: Llandudno. 1928, Compton (CT). — Blinkwater ravine; 200 m. 1929, Levyns (CT). — Camps Bay, lower Blinkwater. 1956, Cassidy no. 109 (NBG). — (Above) Camps Bay. Zeyher no. 4823 (SAM); 1927, Young (PRE); 1934, Hafström (GH, S); 1957, ! no. 1744 (LD). —

Slopes above Victoria Rd. nr. Oudekraal. 1932, ACOCKS no. 1085 (S); 1956, ! no. 606 (LD). — Along rd. to Kloof Nek. 1938, WALL (S). — Foot of Table Mt. ("Prope urbem.") 1929, DRÈGE (P). — Table Mt. 1846, PRIOR (K, PRE). — Slopes of Table Mt. 1924, MOSS no. 9121 (BM). — Foot of Table Mt. 1833, PAPPE (S). — Table Mt. 1844, PAPPE (S). — Table Mt., edge of plantations below Saddle, N side. 1952, ESTERHUYSEN no. 20841 (PRE). — Saddle and Contour Path, Table Mt. 1937, PENFOLD, SAM no. 52752 (SAM). — N foot of Table Mt.; ca. 300 m. 1882, MAC OWAN, Herb. Norm. Austr. Afr. no. 59 (BM, BOL, G, K, NH, P, SAM, W). — N slope of Table Mt. 1827, ECKLON (U. I.) no. 56 (M, P, PR, S, W); ECKLON & ZEYHER no. 1396 p.p. (G, K, L, M, P, PR, S, SAM, W). — N side of Table Mt. 1934, HAFSTRÖM (GH, LD, S). — N slope of Table Mt., Contour Path. 1922, MOSS no. 77561 (LD). — Between Cape Town and Table Mt. 1811, BURCHELL no. 917 (K). — Slopes E of Cape Town. 1927, YOUNG no. 317 (LD, PRE). — Devils Peak. REHMANN (BM).

Somerset W Div.: Hottentotsholland. ZEYHER (S). — Kogelberg; ca. 80 m. 1946, COMPTON no. 18948 (NBG). — Slope above Kogel Bay. 1947, REHM (M). — Rooi Els. 1947, STOKOE, SAM no. 61793 (SAM). — Between Stenbras River and Kogel Bay. 1936, GILLETT no. 1485 (SAM). — Stenbras River Mouth. 1966, ! no. 3881 (LD, NBG). — Just S of Stenbras River Mouth. 1957, ! no. 1766 (LD). — Ca. 1 mile N of Gordon's Bay along rd. to Sir Lowry's Pass. 1957, ! no. 1801 (LD). — Sir Lowry's Pass. 1896, SCHLECHTER no. 7201 (BM, G, GRA, K, L, P, PR, PRE, S, W); 1933, MEEBOLD no. 16778 (M); 1957, ! no. 1757 (LD). — Below Sir Lowry's Pass, W side. 1934, HAFSTRÖM (S); 1965, ! no. 4351 (LD, NBG). — Below Sir Lowry's Pass, along rd. to Strand. 1956, ! no. 1299 (LD). — Somerset West. 1941, PARKER no. 3631 (GH, K, NBG).

Caledon Div: "Nieuw Kloof", Houw Hoek Mts. 1815, BURCHELL no. 8128 (GH, K).

Stellenbosch Div.: Bottelary. 1942, COMPTON no. 12924 (NBG). — Stellenbosch Flats. 1925, DUTHIE no. 1651 p.p. (STE). — Lower slopes of Botmanskop. 1922, DUTHIE (STE).

Paarl Div.: S slope of low hill NE of Klapmuts. 1935, ACOCKS no. 4145 (S). — Slope ca. $^1/_2$ mile N of top of French Hoek Pass. 1965, ! no. 4008 (LD). — French Hoek Pass. 1948, COMPTON no. 20481 (NBG). — French Hoek; ca. 500 m. 1895, BOLUS (NBG). — Klein Vallei Farms, French Hoek. 1964, KLEIN (NBG). — Paarl ("Bergrivier nr. Paarl"). 1828, DRÈGE (G, K, L, P, S, W).

Worcester Div.: Bosjesveld Mts., Villiersdorp side. 1940, STOKOE, SAM no. 56000 (SAM). — Nr. Worcester. 1947, VAN BREDA no. 5 (PRE). — Mts. nr. Groot Kloof, De Doorns. 1948, STOKOE, SAM no. 61829 (SAM). — 1 mile N of Darling Bridge, roadside. 1957, ! no. 1777 (cult. escapes?; LD).

Tulbagh Div.: Mts. nr. Tulbagh. ECKLON & ZEYHER no. 1396 p.p. (see Table Mt. above).

Piketberg Div.: Porterville Mts.; 1000—1300 m. 1952, TAYLOR no. 371 (? cult.; NBG).

Ceres Div.: Roadside ca. 2 miles N of Gydo Pass, Koude Bokkeveld. 1965, ! no. 4398 (sterile; ssp. somewhat uncertain; LD). — Witzenberg range; nr. and on top of Old Witzenberg Pass. 1965, ! no. 4378 (LD, NBG). — Top of Witzenberg range just N of Inkruip. 1956, ! no. 1179 (LD).

Clanwilliam Div.: Just E of top of Grey's Pass, nr. turn-off to Warmbad. 1956, ! 993 (LD); 1965, ! no. 2524 (LD). — Top of Grey's Pass. 1965, ! no. 2516 (LD, NBG). — Grey's Pass, 4 miles SW of Citrusdal. 1956, ! no. 901 (LD). — 7 miles S of Modderfontein, NW slopes of Olifants River Mts., rd. to Warmbad. 1956, ! no. 1014 (LD). — Olifants River Mts. MARLOTH no. 7369 (PRE). — 5 miles ESE of Citrusdal; 450 m. 1965, ! no. 2542 (LD, NBG). — Skurfteberge, E of Citrusdal. 1928, PRIMOS, SAM no. 45695 (SAM). — Upper slopes of hill behind "Kromme Rivier" homestead, Cedarberge. 1934, ACOCKS no. 3122 (S). — "Cedar Mts."; 1000 m. 1911, MARLOTH no. 4728 (GH, NBG). — Cedarberg Mts. 1917, (Forester) BATH (GH, PRE). — Cedarberge (Blaauwberg). DRÈGE (GH, K, L, P). — Olifants River Valley, ca. 3 miles S of Kriedouwkrans. 1965, ! no. 4443 (LD, NBG). — W slope, Alpha. 1963, BARKER no. 9911 (LD, NBG). — Ca. 1 mile SW of Kriedouwkrans nr. Olifants River. 1966, ! no. 5017 (LD, NBG). — 5 miles E of Kriedouwkrans on rd. to Algeria. 1956, ! no. 933 (LD). — 6 miles E of Kriedouwkrans. 1956, ! no. 936 (LD). — Nieuwoudt Pass, E of Kriedouwkrans. 1941, BOND no. 1318 (NBG). — Nieuwoudt Pass; 500 m. 1965, ! no. 3248 (LD, NBG). — W end of Algeria Valley; 590 m. 1965, ! nos. 3251 and 3254—3255 (LD, NBG). — 2 miles W of Algeria Forest Stn. 1956, ! 942 A (LD); 1965, ! no. 4274 (LD, NBG). — Ca. 1 mile W of Algeria Forest Stn. 1965, ! no. 4271 (LD, NBG). — Algeria. (Forest Officer) SAM no. 52347 (SAM). — Boskloof, ca. 4 miles NW of Algeria. 1965 ! no. 4480 (LD, NBG). — Cedarberge nr. Clanwilliam; 500 m. 1897, BODKIN, BOL no. 8978 (BOL, K). — 9 miles W of Clanwilliam along rd. to Van Puttens Vlei. 1956, ! nos. 1002 and 1004 (LD). — Pakhuis Pass. 1934, COMPTON nos. 4759 and 4774 (NBG); 1948, ACOCKS no. 15029 (K). — S slope of Pakhuis Pass. 1934, SALTER no. 5045 (BM, K, SAM). — Pakhuis Mt., ca. 1/2 mile W of summit of Pakhuis Pass. 1956, ! no. 892 (LD). — Pakhuis. 1941, ESTERHUYSEN no. 7420 (PRE). — 6 miles from Pakhuis along rd. to Calvinia, ca. 1 mile from Travellers' Rest. 1965, ! no. 3283 (LD, NBG).

Calvinia Div.: Elandsfontein. 1940, HENRICI no. 3413 (LD, PRE). — Lokenburg, 21 miles S of Niewoudtville. 1953, STORY no. 4729 (GRA, K, PRE). — Lokenburg, arid fynbos of T.M.S. ridges. 1953, ACOCKS no. 17365 (K). — Arendsdal Farm nr. Nieuwoudtville. 1962, BARKER no. 9772 (cult. escapes?; LD, NBG). — Onder-Bokkeveld; ca. 800 m (between Grasberg River and Waterval). 1830, DRÈGE (P).

Vanrhynsdorp Div.: Giftberg, steep middle slopes. 1961, BARKER no. 9599 (LD, NBG).

ECOLOGY. Ssp. *linearis* (contrary to ssp. *latipetala*) grows mainly in sand, often among sandstone rocks in mountains of the Table Mountain series. In exceptional cases (e.g. in the Algeria Valley) the soil may be clayey.

In the southern divisions (with higher humidity and precipitation) it often grows at low altitudes, sometimes near sea level, in the Cedarberge and other mountains in the north it is usually found at altitudes of ca. 500 m or more. The seedlings are sensitive to snow and frost whereas the adult shrubs are resistent in that respect (cf. the methods in germinating the "tea" plants). The annual rainfall required is reported to be between 350 and 650 mm, although humidity of the air, dew, and general evaporation conditions should also play a great role.

The special requirements of the species make it unsuitable for greenhouse culture and of the originally numerous plants cultivated by me in the Lund greenhouses 1966—67 most have died off gradually and none have yet flowered.

VARIATION IN THE WILD FORMS

Cape Peninsula. The Peninsula forms (Figs. 1 A—H, 2 A, and 3 A) are normally decumbent or somewhat ascending shrublets with branches of up to > 50 cm long but normally not > 30 cm in height. The ascending branchlets are covered with a close, whitish indumentum of short adpressed hairs (Fig. 1 M—N) on the youngest parts. The leaves are ascending, straight, and relatively coarse for the species, generally ca. 0.7 mm, but occasionally up to > 1.0 mm broad (thick) and they may be up to ca. 5 cm long. They are subterete or slightly flattened and are commonly puberulous on the basal parts; the basal constricted portion is constantly short-pubescent. The flowers are generally clustered, often 3—6 (—10) together, in a condensed cyme or umbel on the branch tips, but sometimes also assembled few together on short-shoots below the branch tips. The bracts are shortly subulate, the bracteoles narrowly triangular, and the pedicel closely white-puberulous. The calyx is shortly adpressed-puberulous and has triangular, 0.6—1.6 mm long, often slightly upcurved upper lobes, and somewhat longer and narrower lower lobes. The petals are relatively small and pale-yellow in colour although the vexillum often has a darkish, violet tinge. The vexillum is closely short-sericeous on the back side and usually 4.5—5.5×3.6—5.0 mm large. The ala blades are usually 3.0—4.0×1.1—1.7 mm large, and the quite strongly upcurved, obtuse carina blades are 3.5—4.5×2.4—3.1 mm large. The ripe pods are ca. 14—15×3.4—4.0 mm large. — In these forms the leaves do not turn ferruginous when crushed and dried and do not seem to get the aroma of the northern forms. They keep their pale greyish-green colour or may, at the most, turn greyish or dark-brown.

On the whole the variation of the subspecies is remarkably restricted on the Peninsula, and there is no correspondence to the great differences seen between different shrubs in, e.g., the Algeria Valley or the Pakhuis region in the Cedarberge. Due to the small variation between different shrubs one might suppose the fertilization to be autogamous in this region.

The Stellenbosch, Somerset West, and Caledon Divisions. Forms similar to those on the Cape Peninsula also occur on the Hottentots Holland Mountains in the Gordons Bay area (e.g., DAHLGREN & PETERSON nos. 1757 and 1801), but the variation in that region is considerable. In a form from the Kogelberg (COMPTON no. 18948) the leaves are slenderer and glabrous (also on the con-

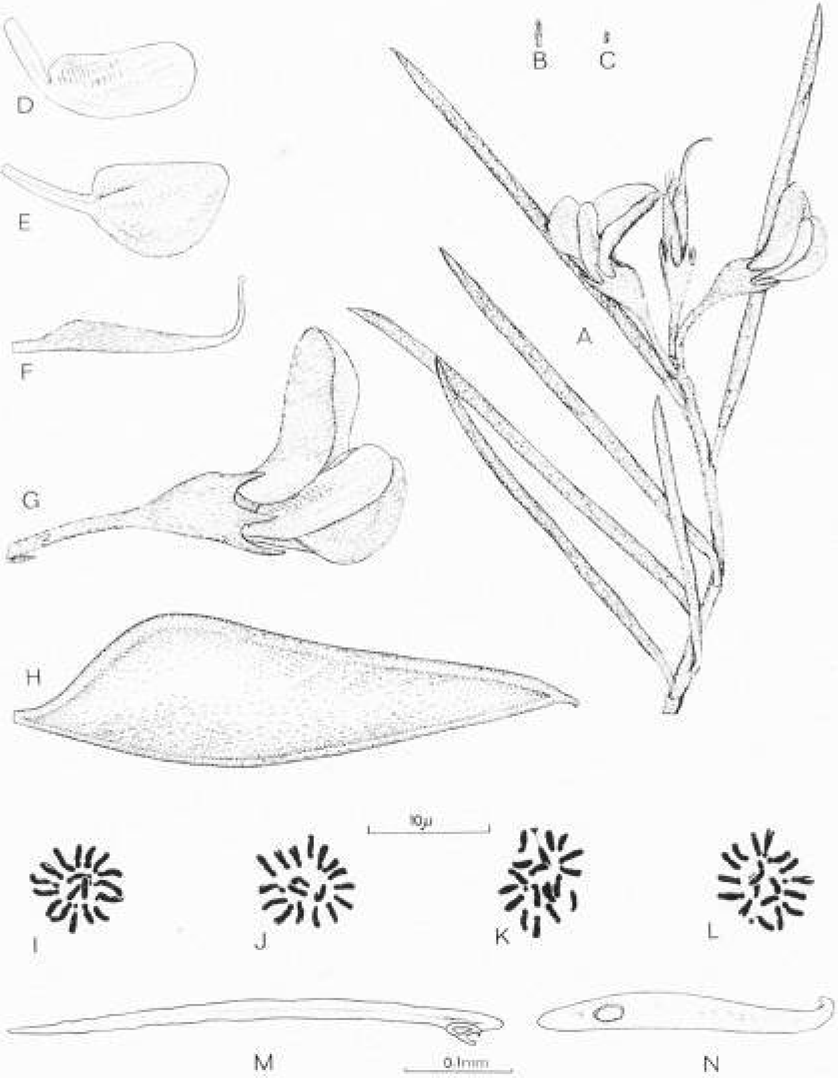

Fig. 1. — *Aspalathus linearis* ssp. *linearis*; A—G: DAHLGREN & PETERSON no. 606 from the coastal mountain slopes south of Camps Bay, Cape Peninsula; H: Pod of D. & P. no. 1744 from the same region; I—L: Root tip mitoses of cultivated forms of "Rooibos Tea", seeds obtained from the Clanwilliam Tea Industry; M—N: Trichomes of D. & P. no. 606 (see above). — A: Branchlet tip with inflorescence. — B: Bract. — C: Bracteole. — D: Ala petal. — E: Carina petal. — F: Pistil. — G: Flower. — A ×2.5; B—H ×5; I—L and M—N according to scales given.

stricted basal part) and turn more distinctly reddish than in any form of the Peninsula population. Similar, relatively slender-leaved forms are also recorded from the Somerset West region (e.g., PARKER no. 3631). The flower size in these forms is comparable to that in the Peninsula population; however, a very small-flowered plant, GILLETT no. 1485, has been collected in the Kogel Bay area.

The Paarl and Worcester Divisions. In these divisions the species is known only from a limited number of localities. Forms in the French Hoek Mountains (Fig. 3 B) resemble the Peninsula forms, but they have slenderer and less pubescent leaves with a pronounced tendency of turning brownish when dried. Their flowers, as in most Peninsula forms, are concentrated chiefly to corymb-like groups on the branch tips, and are of about the same appearance as in these, and of the same size or slightly smaller. The shrubs are low, ascending or decumbent.

In two collections from the Bosjesveld Mountains (south of Worcester) and from the Kawadouw Mountains (northeast of Worcester) the flowers are smaller than in any other population of the species (see Figs. 2 B and 3 C). In the former collection the calyx lobes are only ca. 0.5 mm long, and the vexillum, ala, and carina blades only ca. 4.0×3.0, 2.4×1.0, and 3.0×1.7 mm large, respectively; in the latter collection they are somewhat larger. Their leaves are straight, ca. 3 cm long, more glabrous and slenderer than in the Peninsula population (i.e., similar to those in the French Hoek region) and have a red-brown, dark, glossy surface when dried. A similar, decumbent form (DAHLGREN & PETERSON no. 1777; Fig. 3 D) but with thicker, pale green leaves was collected by the author on the sand flats near Breede River south of Wolseley. However, in the vicinity there was at that time a Rooibos Tea plantation, the plants of which were more erect and had larger flowers and somewhat slenderer and brighter green leaves. Whether the mentioned collection was influenced from the plantation or not is uncertain.

In the afore mentioned forms in the Paarl and Worcester Divisions the calyx lobes are always relatively short (cf. below). There is still an obvious similarity in the flower appearance between the Peninsula forms and the population in the French Hoek area, whereas those in the Worcester Division are distinctly small-flowered. The leaves in the latter forms are slenderer, less pubescent, and when fresh usually more clearly green (when dry more distinctly brown) than in the average Peninsula forms.

A form recorded from the Porterville mountains shows certain similarities to cultivated forms and may be an escape from cultivation.

The Ceres Division. The forms seen in the Ceres Division, i.e. in the Witzenberg Mountains and the Koude Bokkeveld area, are all decumbent and low, with ascending and often closely leafy branchlets. The leaves are slender and often slightly incurved (Fig. 3 E). The petals resemble those of ssp. *pinifolia* in their proportions (cf. the distribution of this subspecies): the carina is relatively large and violet on most parts as in this subspecies; the prominent "tip" however is lacking.

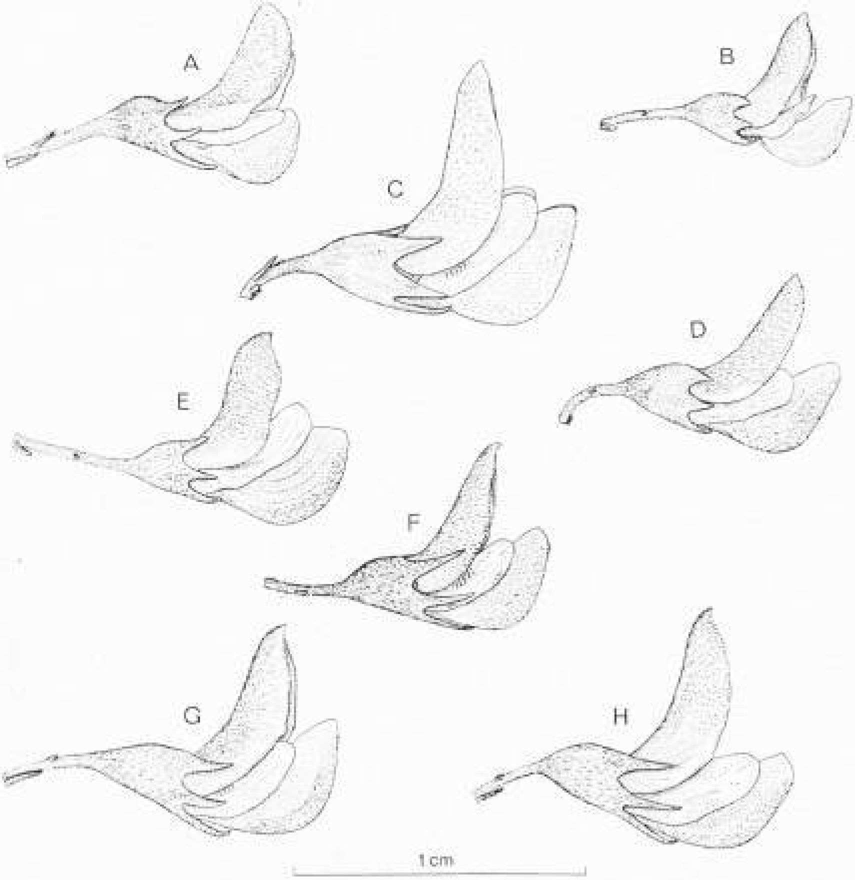

Fig. 2. *Aspalathus linearis* ssp. *linearis*; comparison of flowers from different populations. — A: Dahlgren & Peterson no. 606 from the Cape Peninsula (petals pale yellow). — B: Stokoe, SAM no. 56000 from the Bosjesveld Mts., Worcester Division (petals mainly yellow). — C: D. & P. no. 901 from Grey's Pass, Olifants River Mts., Clanwilliam Division (petals yellow). — D: Dahlgren & Strid from the Kriedouwkrans region, western bank of Olifants River, Clanwilliam Division (vexillum and carina somewhat violet). — E: D. & P. no. 892 from rocky slopes of Pakhuis Mt., northern Cedarberge, Clanwilliam Division (vexillum back rather violet, carina dark violet on most parts). — F: D. & S. no. 3255 from the Algeria Valley, Central Cedarberg Mts., Clanwilliam Division (petals rather bright yellow). — G: D. & S. no. 4480 from Boskloof, Central—Northern Cedarberge (petals bright yellow). — H: Cultivated form from plantation of the Clanwilliam Rooi Tea Industry, sample 14 (corresponds to Fig. 9 E; petals bright yellow). — All ×4.

The Clanwilliam Division and the northern outposts. In the Clanwilliam Division we find the greatest variation within the species with regard to practically all features. The flowers are constantly larger than in the Paarl-Worcester Divisions, and generally larger than on the Cape Peninsula. The calyx is sparsely puberulous or glabrous on the outer side, its lobes are medium-sized or often relatively long, and the petals vary from entirely and rather bright yellow to a pattern of pale-yellow and violet in variable proportions. Prostrate and decumbent forms are not rare in the mountains, but there are also forms with an erect and rigid stature, 2 m or more in height. In the coarseness and colour of the leaves the variation is likewise great and, beside the forms with relatively slender and bright green leaves, there are others with pronouncedly greyish or even glaucous leaves which in some cases are as thick as those in the Cape Peninsula population. On the other hand the leaves in the northern forms are usually glabrous; and in most, though not all, forms from the Cedarberg Mountains the leaves turn ferruginous or brownish when dried (especially after being crushed as in a plant press or in the processing of the "tea"). Certain features of variation can be recognized, although the documented material is sometimes too limited for generalizations, especially as the variation is generally great within the populations.

In the mountain and sandy valley of the Olifants River practically all wild forms seen are erect shrubs varying in height from < 1 to ca. 2 m tall. The branches are generally straight and slender, but often rather rigid, the short-shoots often poorly developed, and the leaves generally sparse, ca. 3—5 cm long, up to 1 mm thick, stiff, straight, greyish-green, and when dry often greyish-brown in colour. These forms are doubtless unsuitable for Rooibos Tea, although some of the forms may have contributed in yielding the "Vaal Tea" (see p. 196). Relatively large-flowered forms occur in Grey's Pass, but the flowers vary in size and are not always as large as in DAHLGREN & PETERSON no. 901 which is illustrated in Figs. 2 C and 3 F. In this collection the calyx lobes are 1.7—2.2 mm long, and the vexillum, ala, and carina blades are ca. 6.8—7.5 × 4.5 mm, ca. 4.7 × 1.7 mm, and ca. 5.2 × 3.0 mm large, respectively. Thus they are larger than in practically all other wild forms and larger than in most cultivated ones, too. The calyx outside and part of the pedicel are glabrous in this form, and the vexillum back and carina bottom are only sparsely

Fig. 3. *Aspalathus linearis* ssp. *linearis*; comparison of branches from different wild populations in same scale. — A: DAHLGREN & PETERSON no. 606 from the Cape Peninsula. — B: KLEIN, from the French Hoek region, Paarl Division. — C: STOKOE, SAM no. 56000, from the Bosjesveld Mts., Worcester Division. — D: D. & P. no. 1777, from the sandy part of Breede River Valley east of Bain's Kloof, Worcester Division. — E: DAHLGREN & STRID no. 4378 from the Witzenberg Mt., Ceres Division. — F: D. & P. no. 901, from the top of Grey's Pass, Olifants River Mts., Clanwilliam Division. — G: D. & S. no. 4480 from Boskloof, Central—Northern Cedarberg Mts., same division. — H: D. & P. no. 892, from rocky slopes of Pakhuis Mt., Northern Cedarberge, same division. — I: D. & S. no. 5017, from the Olifants River Valley near Kriedouwkrans, same division.

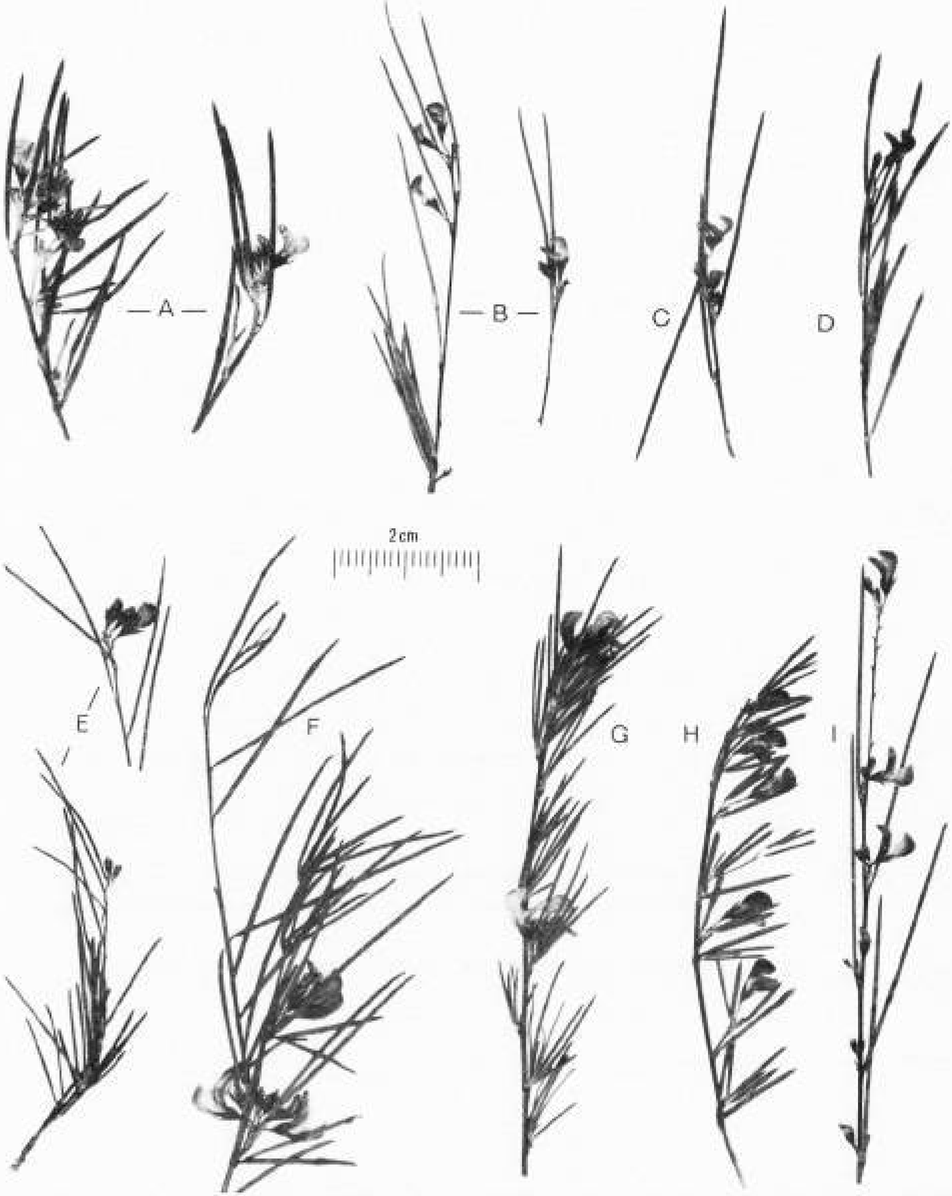

Fig. 3.

sericeous, but — like the flower size — the pubescence is also variable in this area.

Similar, tall-grown forms occur east of Citrusdal and further to the north in the Olifants River Valley. Shrubs up to 2 m tall with greyish-green leaves, and often with late and poor development of the axillary short-shoots occur in the Kriedouwkrans area half-way between Citrusdal and Clanwilliam. Such a form is seen in Figs. 2 D and 3 I; it has smaller flowers than in the Grey's Pass area and an exceptionally long axis of the apical inflorescence.

In the Cedarberg Mountains there is great variation in most features of the plants, and, e.g., in the Algeria region (east of Kriedouwkrans) in Central Cedarberg Mountains no two shrubs seem to match each other exactly, but differ in size, habit, and details of leaves and flowers, thus performing a typical allogamous pattern.

The height of the shrublets in the mountainous populations in this region is usually less than one metre. Depressed shrublets (like DAHLGREN & PETERSON no. 936) and ascending ones, almost 1 m tall (like DAHLGREN & STRID no. 3254) may occur in practically the same place. On the average, the leaves are somewhat smaller and especially slenderer than in the forms of the Olifants River Valley and Mountains, and may be constantly as short as ca. 1 cm on certain shrubs (as in DAHLGREN & STRID no. 3251). Also their thickness varies, and the colour may range from almost glaucous (as in D. & P. no. 936 and D. & S. no. 3248) to bright green, which colour is more common. When dried the leaves usually become reddish (sometimes, perhaps, blackish), and no doubt most forms can be used for "Rooibos Tea" although the quality would be most uneven. The flowers (Fig. 2 F) are variable but generally smaller than in the forms in Grey's Pass, and of about the same size or slightly smaller than in most cultivated forms. They resemble the cultivated forms in the usually sparsely puberulous calyx with relatively long, broadly subulate lobes, and in the often rather bright yellow petals.

Wild forms representig the original material for cultivation are reported to derive mainly from the Pakhuis Mountains in the northern Cedarberge. Among the wild forms seen by me, one collection from Boskloof (Figs. 2 G and 3 G), between Algeria and Clanwilliam, somewhat south of Pakhuis Pass, seems to match very closely the cultivated forms regarded as favourable for tea. The leaves are relatively light green and turn reddish when dried; the ripe pods

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Fig. 4. *Aspalathus linearis* ssp. *linearis*; A—H: DAHLGREN & PETERSON no. 1778, form cultivated in 1957 on a field south of Wolseley, near Breede River, "Darling Bridge" area, representing an inferior biotype (possibly with introgression of wild forms in the area) compared to those cultivated today (cf. Fig. 2 H); I—N: D. & P. no. 892, a wild form from the rocky slopes of Pakhuis Mt. (see also Figs. 2 E and 3 H), Clanwilliam Division. — A and I: Parts of branches; notice the difference in distribution of flowers. — B: Leaf base. — C and J: Bracts. — D: Bracteole. — E and K: Vexillum petals. — F and L: Ala petals. — G and M: Carina petals. — H and N: Pistils. — A and I ×2.5; B ×10; C—H and J—N ×5.

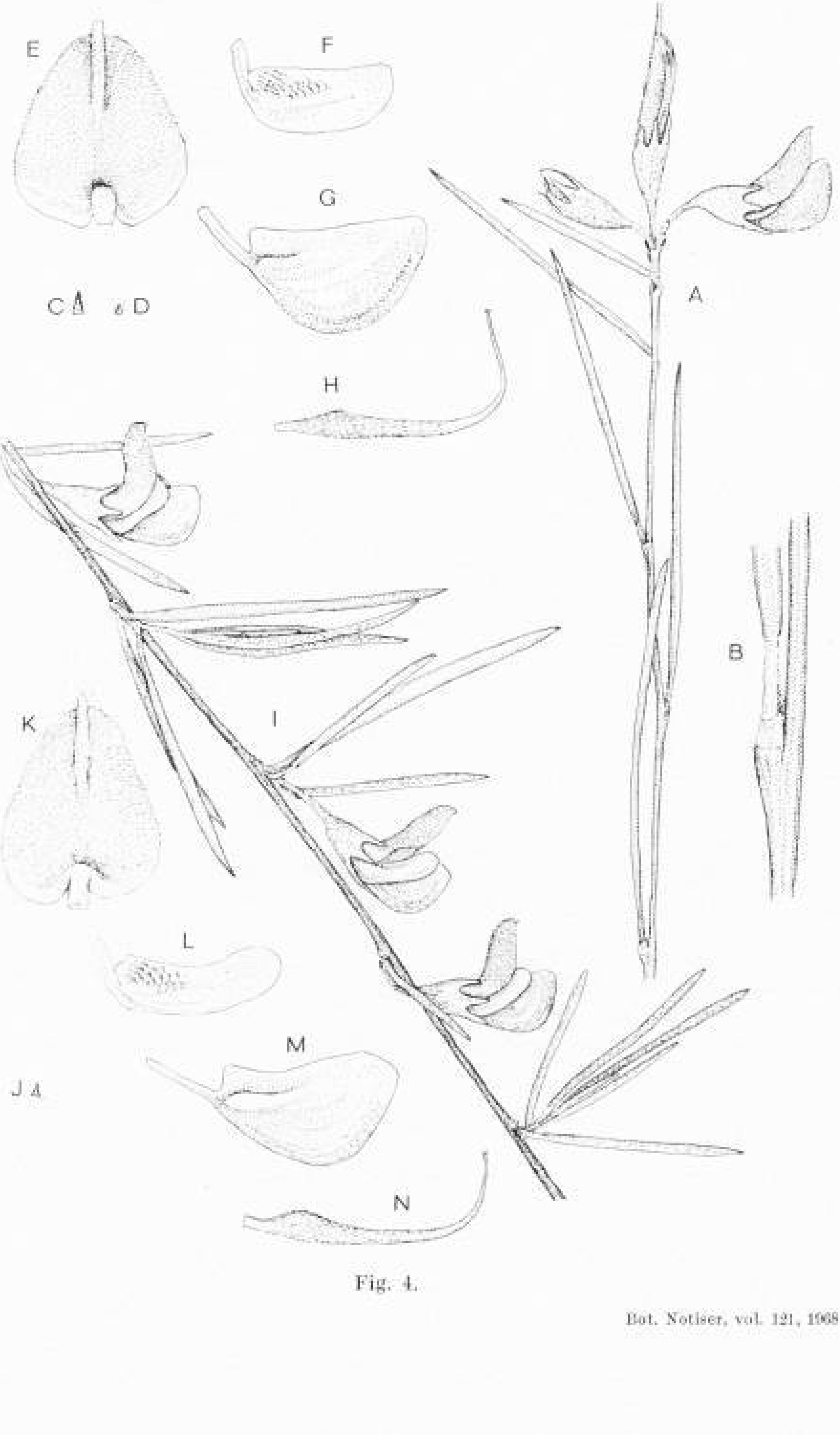

Fig. 4.

are bright ferruginous; and the flowers (details in Fig. 2 G) have bright yellow petals.

Some presumably wild forms collected in the Pakhuis Pass area (e.g., COMPTON nos. 4759, 4774) seem to be similar to cultivated ones, but since there are plantations in this area (e.g., at Klein Kliphuis, from the neighbourhood of which the original material for cultivation is sometimes said to have been collected) there are difficulties in distinguishing indigenous forms from cultivation escapes.

A form very different from the cultivated ones, growing on the rocky slopes of the Pakhuis Mountain, is illustrated in Figs. 2 E, 3 H, and 4 I—N. It is decumbent, the leaves are coarse (ca. 1 mm thick), and the flowers have short calyx lobes, a relatively small vexillum violet on the back side, and a relatively large, obtuse carina, dark violet on most parts. The forms yielding the "Swart Tea" probably correspond to similar mountainous biotypes.

On the hills and plateaus west of Clanwilliam, rather low forms with sparsely puberulous and greyish-green leaves have been collected (D. & P. nos. 1002 and 1004) and a similar subprostrate form with relatively small flowers has been collected on the Giftberg, Vanrhynsdorp Division.

On the sandy plateaus of the low mountains east of Pakhuis, towards the Gamka River, the subspecies is represented by erect forms up to 2 m tall with straight, ascending, rather slender, green leaves. These, which seem to be rather dominant locally in the area, resemble in habit the forms of the Olifants River Valley.

Decumbent as well as almost erect, slender-leaved forms with relatively small flowers are known from the Nieuwoudtville area (BARKER nos. 9772 and 9775). Whether they are indigenous in the region or derive from escapes of Rooibos Tea cultivation is uncertain, however.

FLOWERING PERIOD. Mainly August—December.

Aspalathus linearis (Burm. fil.) R. Dahlgr. ssp. pinifolia (Marl.) R. Dahlgr.

DAHLGREN 1963 A pp. 93, 94, 213, 215, *283*; 1963 B p. 461. — *Borbonia pinifolia* MARL.; MARLOTH 1912 p. 288. — Original collection: "Cedar Mts." MARLOTH no. 4728 (SAM, lectotype). — Illustrations: Fig. 6; DAHLGREN 1963 A Fig. 14 C p. 94 (carina petal). — Map: Fig. 5 B (■).

A decumbent or ascending, sparingly branched shrublet of moderate size; branches usually 30—60 cm long, grey on lower parts, dark-red and from very sparsely to rather closely, shortly and adpressedly puberulous on upper parts. — *Leaves* usually 2—3.5 cm long, 0.5—0.7 mm thick, subterete, straight or usually slightly incurved near apex, glabrous or almost so, dull green, becoming greyish or reddish brown when dried; near base with a short-pubescent, constricted, < 0.5 mm thick portion of ca. 1 mm length; base below this part abruptly broadened

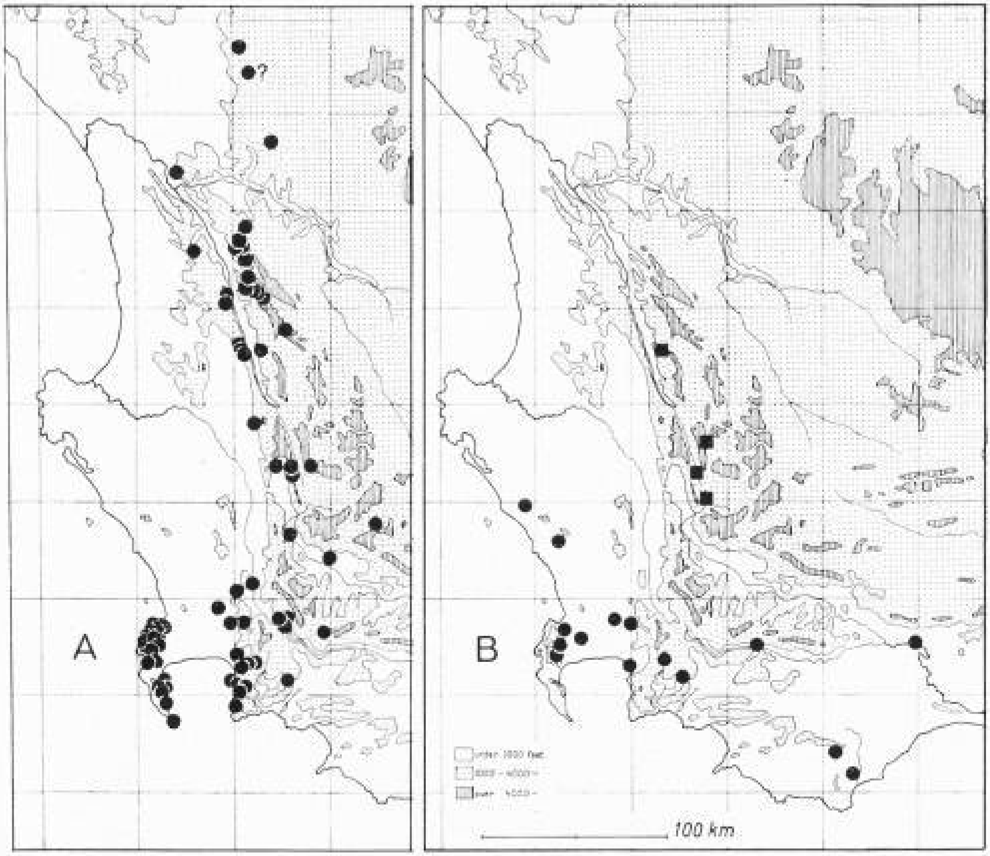

Fig. 5. Distributions of wild forms of the subspecies in *Aspalathus linearis* as documented by collected material. — A: Ssp. *linearis*. — B: Ssp. *pinifolia* (squares) and ssp. *latipetala* (dots).

into a shield- or platelike leaf-foot. — *Inflorescence* a 2—5-flowered apical racemule, but flowers usually also situated solitarily or in pairs on very short lateral branchlets (sometimes developed as brachyblasts) below the branch tips, sometimes along 10 cm or more of the branch ends. — *Bract* broadly subulate or narrowly triangular, usually 0.3—1.0 mm long, short pubescent at least on the inner side and margins. — *Pedicel* slender, usually only 0.2—0.3 mm thick, but 1.5—2.5 mm long, short-sericeous. — *Bracteoles* similar to the bract but smaller, 0.2—0.6 mm long. — *Calyx* variably sparsely short-sericeous on outer side; tube infundibular-campanulate, longer than the lobes; upper lobes triangular or subulate-triangular, 0.7—1.1 mm long; lower lobes subulate-linear, 1.2—2.0 mm long. — *Petals* partly pale-yellow but violet at least on lower parts of the carina and usually also on apical parts of vexillum back. — *Vexillum* blade constantly shorter than carina blades, ovate, usually 4.3—5.3×3.2—4.5 mm large, acuminate (often with a short tip), short-sericeous on most of back, the sides often incurved in the flowering stage. Claw ca. 0.8 mm long. — *Ala* blades narrowly oblong, usually 3.5—4.2×1.0—1.7 mm large, glabrous, with 1—2 (—3) rows of distinct lamellalike transverse folds on upper basal parts. Claws ca. 1.4—1.8 mm long. — *Carina* blades lunate, usually 5.0—5.7×2.2—2.8 mm large, with straight or slightly curved upper margins, and with a distinct, up to 0.8 mm long, forwardly directed, pointed tooth (Fig. 6 H); lower apical parts short-sericeous. Claws 1.8—2.3 mm long. — *Pistil* shortly stipitate; ovary short-sericeous on most parts, 2-ovulate; style sericeous on base and upper basal parts. — *Pod* lanceolate, usually 10.5—13.5×3.0—4.0 mm large, sparsely and very shortly sericeous.

DISTRIBUTION. Mountains and flats, probably mostly on sandy ground, among the mountains in the Ceres Division and in the southern part of the Cedarberg range, Clanwilliam Division. (Certain, rather similar forms of *A. linearis* in the Witzenberg range which lack the tooth on the carina apex are referred to ssp. *linearis*.)

COLLECTIONS

Ceres Div.: Flats nr. Ceres; 600 m. 1883, H. Bolus no. 5320 (BOL). — Witzenberg Vlei. 1938, Thorne, SAM no. 52774 (SAM). — Kloof from Citrusdal to Ceres. 1936, Gillett no. 3492 (SAM). — Koude Bokkeveld, in sand nr. Klyn Vlei; 1300 m. 1897, Schlechter no. 10065 (BM, G, GRA, K, L, LD, P, PR, PRE, S, W).

Clanwilliam Div.: "Cedar Mts."; 1000 m. 1911, Marloth no. 4728 (SAM). — Elandskloof. 1951, Compton no. 22687 (LD, NBG).

COMMENTS. Ssp. *pinifolia* apparently represents a geographically defined race of the species. Its variation is limited although the development of the short-shoots varies to a great extent. The most conspicuous characteristic is the apical carina process, but the systematic value of this is difficult to estimate. This character is combined with others which are also found in certain populations of ssp. *linearis*.

There are no reports indicating that ssp. *pinifolia* has been used for "tea".

FLOWERING PERIOD. Mainly October—January (—March).

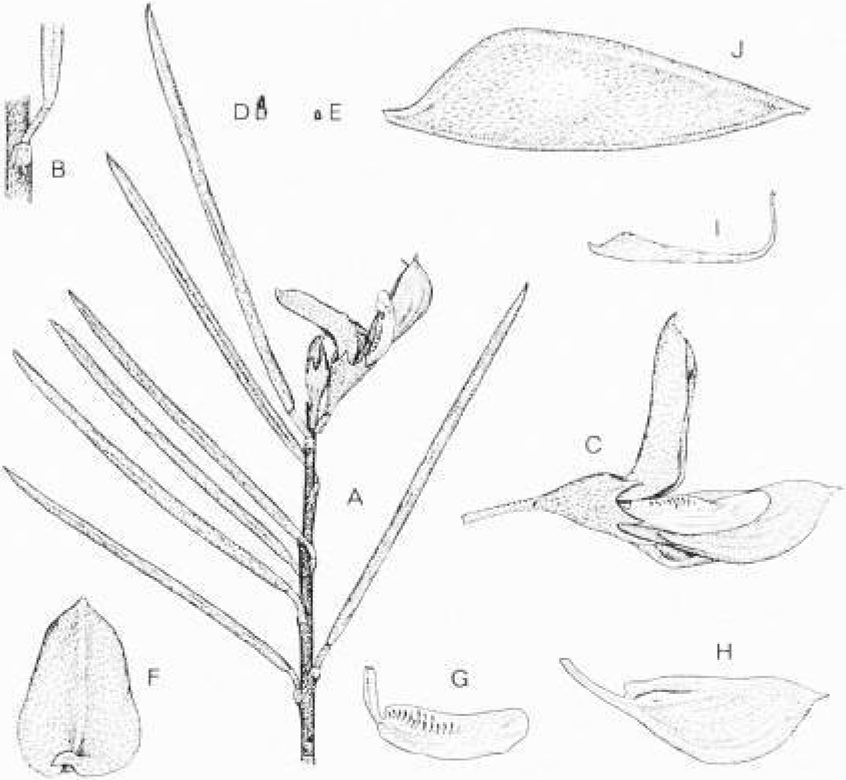

Fig. 6. *Aspalathus linearis* ssp. *pinifolia*; THORNE, SAM no. 52774, from "Witzenberg Vlei", Ceres Division. — A: Branch end with inflorescence (the flowers are often distributed on short-shoots along the branches in this subspecies). — B: Leaf base. — C: Flower. — D: Bract. — E: Bracteole. — F: Vexillum petal, back side. — G: Ala petal. — H: Carina petal. — I: Pistil. — J: Pod. — A ×2.5; B—J ×5.

Aspalathus linearis (Burm. fil.) R. Dahlgr. ssp. latipetala R. Dahlgr.

DAHLGREN 1963 A pp. 94, 213, 215, *283*; 1963 B p. 461. — Original collection: COMPTON no. 22625 (BOL; NBG, holotype). — Illustration: Fig. 7; DAHLGREN 1963 A Fig. 14 A on p. 94. — Map: Fig. 5 B (●).

A procumbent—decumbent (—ascending) shrublet. Branches usually 30—70 cm long, sparingly (seldom rather closely) branched, bowing-ascending, covered with grey bark on lower parts. Young branches and branchlets longitudinally striated, usually dark-purplish and sparsely and very shortly sericeous. — *Leaves* usually 2.5—4.5 cm long and 0.7—1.1 mm thick, tapering, mucronulate—apiculate, usually ± curved near apex, otherwise often straight, subterete or slightly depressed, pale or dull green, glabrous or with sparse adpressed hairs; constricted part near base usually short-sericeous; base below this part widened, glabrous on outer side, without distinct stipular teeth. — *Flowers* solitary or several (up to 5) on the branch tips or solitary or in pairs on lateral branchlets or short-shoots (often at several successive nodes) in leaf axils below branch tips, when several situated in a corymblike racemule. — *Bract* narrowly triangular—broadly subulate, usually 0.6—1.3× 0.25—0.4 mm large, puberulous at least on inner side and margins, often also on outer side. — *Pedicel* 1.6—5 (in fruit stage up to > 6.5) mm long, slender, subglabrous or usually with short sparse adpressed hairs, gradually widening into the calyx base. — *Bracteoles*, on lower half of pedicel, narrowly triangular, 0.2—0.6 (—0.8)×0.1—0.25 mm large, similar to bract. — *Calyx* shortly (sometimes very shortly) and usually rather sparsely sericeous; tube infundibular-campanulate, smooth or prominently veined, longer than the lobes; upper lobes triangular, acuminate, (0.5—) 0.7—1.2 mm long; lower lobes narrowly triangular or broadly subulate, usually 1.0—2.6 mm long. — *Vexillum* blade circular or broadly obovate, obtuse or retuse (but commonly with a little tip), 5.0—7.0 (—7.5)×5.0—7.0 (—8.0) mm large, yellowish but as a rule with sombre-violet tinge, short-sericeous on most of back side, glabrous on front side. Claw 0.7—1.2 mm long. — *Ala* blades elliptic-oblong (often broadest near apex), often slightly upcurved, (3.8—) 4.0—5.3×1.4—1.8 (—2.0) mm large, glabrous, pale-yellow, of shape seen in Fig. 7 E. Claws 1.4—2.2 mm long. — *Carina* blades lunate, 4.8—5.8× (2.7—) 2.9—3.6 mm large, glabrous, obtuse, with convex upper margins (Fig. 7 F); truncate or sometimes auriculate at upper part of base; pale-yellow but often ± violet on lower parts. Claws 1.8—2.6 (—3) mm long. — *Anthers*: four elongate, 0.8—1.3 mm long; five short, ca. 0.35—0.45 mm long; one ca. 0.5—0.6 mm long. — *Pistil* very shortly stipitate; ovary 2 (—3)-ovulate, sericeous on most (upper and apical) parts; style sericeous on base and upper-basal parts. — *Pod* ca. 15.5—16.5×3.2—3.6 mm large, of shape seen in Fig. 7 H.

DISTRIBUTION. Lowlands in the southwestern divisions between the Malmesbury Division in the northwest and the Swellendam Division in the east.

COLLECTIONS

Swellendam Div.: Bontbok National Park, ca. 2 miles S of Swellendam. 1962, LIBENBERG no. 6677 (STE); 1965, ! no. 4563 (LD, NBG).

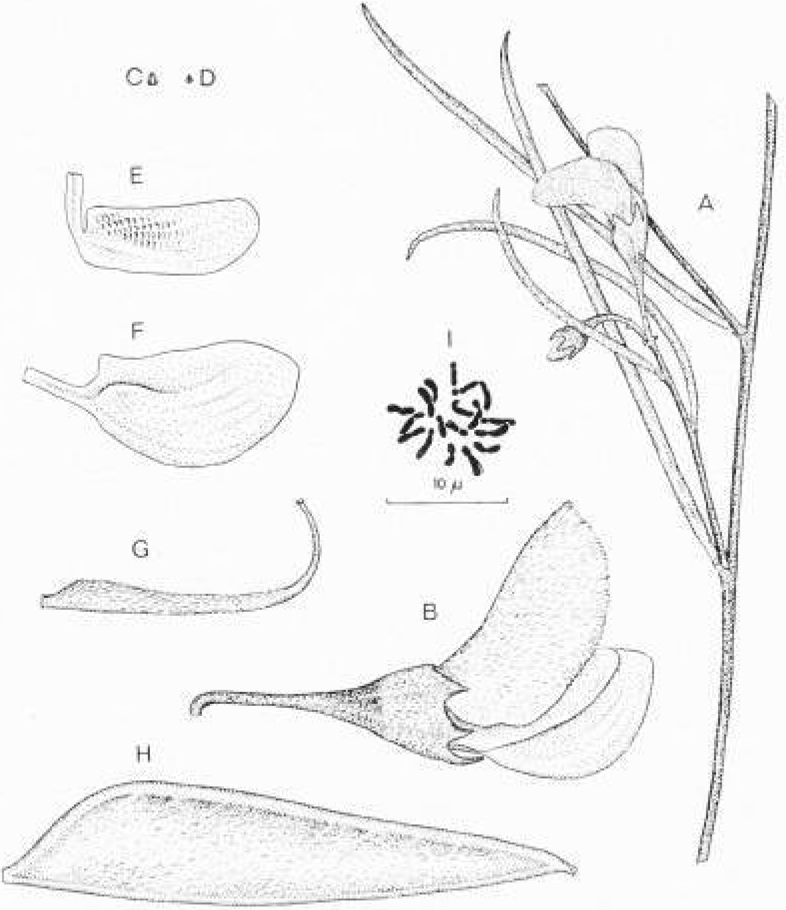

Fig. 7. *Aspalathus linearis* ssp. *latipetala*; A—H: Compton no. 22625, from the lowlands northeast of Cape Agulhas, Bredasdorp Division; I: Root tip mitosis of Dahlgren & Strid no. 4563, collected south of Swellendam. — A: Part of branch with a lateral floriferous branchlet. — B: Flower. — C: Bract. — D: Bracteole. — E: Ala petal. — F: Carina petal. — G: Pistil. — H: Pod. — A ×2.5; B—H ×5; I according to scale given.

Bredasdorp Div.: Bontbok Park (the old park). 1951, Compton no. 22625 (BOL, NBG). — Meierskraal nr. Elim. 1938, Wall (S).

Caledon Div.: S of Genadendal nr. Greyton—Caledon rd. 1966, ! no. 4980 (LD, NBG). — Viljoens Pass; 80 m. Rogers no. 28835 (NBG). — Houw Hoek; 250 m. 1892, Guthrie no. 2244 (NBG).

Somerset W Div.: Between Strand and Gordon's Bay: flats ca. 500 m from sea coast. 1957, ! no. 1792 (LD).

Stellenbosch Div.: Golf Course, Stellenbosch. 1925, Duthie no. 1651 p.p. (STE).

Bellville Div.: Between Bottelary Rd. and Main Line. 1932, Acocks no. 54 (S). — N of Bottelary Rd. 1932, Acocks no. 1175 (S).

Wynberg Div.: Steenberg. 1938, Salter no. 7933 (CT). — Klipfontein. Zeyher no. 440 (K, P, S, SAM, W). — Kenilworth Race Course. 1937, Levyns no. 6402 (CT); 1937, Salter no. 7139 (NBG); 1937, Salter no. 7907 (NBG). — Cape Flats, Mowbray. 1889, Guthrie no. 319 (CT).

Malmesbury Div.: Mamre Flats. 1940, Penfold no. 246 (NBG). — Darling Flora Reserve. 1956, Rycroft no. 2014 (NBG).

ECOLOGY. The subspecies seems to grow mainly on clayey flats, but may also be found in sand. Thus in the easternmost locality known, near Swellendam (! no. 4563), it grows on clayey as well as sandy substrate, and on the flats near Strand (! no. 1792) and south of Genadendal (! no. 4980) it grows in clayey soil together with *Aspalathus recurva* Benth. and *A. biflora* E. Mey. respectively.

VARIATION. The peripheral forms in the Malmesbury and Swellendam Divisions, seem to have slightly smaller flowers than the others, whereas those on the Cape Flats (e.g., on the Kenilworth Race Course) but also in the Viljoens Pass have relatively large flowers. The leaves are relatively (> 1 mm) thick in Guthrie no. 2244 from Houw Hoek Pass, relatively slender in the population of the Bredasdorp Division. However, the subspecies varies relatively little, and especially the carina shape (and its lack of pubescence), the long pedicels, and the rather constantly decumbent habit are quite characteristic. Other details, like the density of pubescence, the leaf length, and the size of the floral parts vary within certain limits. The size of the shrubs is usually modified by grazing animals.

Ssp. *latipetala* and ssp. *linearis* are rather distinctly demarcated from each other, and it might even be justifiable to give them specific status.

To the author's knowledge, ssp. *latipetala* has never been used for "tea".

FLOWERING PERIOD. November—March (most flowering material has been collected in February).

Aspalathus pendula R. Dahlgr.

Dahlgren 1963 A pp. 213—215, *285*; 1963 B p. 447. — Original collection: Dahlgren & Peterson no. 930 (LD, holotype; BOL, NBG, PRE, S). — Illustrations: Fig. 8. — Dahlgren 1963 A Fig. 69 on p. 214. — Map: Fig. 8 M.

"*Aspalathus tenuifolia*" auct. non DC. in MEYER 1836 p. 65, BENTHAM 1848 p. 653, HARVEY 1862 p. 139, KIES 1951 p. 170, etc.

A large shrub or, usually, a small tree 1.5—5 m tall generally with an unbranched trunk about half as long as the total height and 3—7 cm thick at base. Stem and branches rather smooth, light or dark grey on thicker parts. Branches dark grey on thinner parts but often reddish on youngest parts, sparingly ramified, very slender, lax, pendulous, longitudinally striated or sulcate, with sparse, short and adpressed hairs on youngest parts. — *Leaves* linear, straight (or slightly curved near apex), slender, (2.5—) 4—7 cm long and 0.4—0.7 mm thick, acuminate, subterete or slightly depressed, glabrous (but in young stage sparsely and shortly puberulous), lissom, rather rigid, sombre green, often with a slightly constricted, reddish or pale-yellow segment at base, below this with a widening leaf-base with a couple of ± indistinct, short and narrow, lateral, acuminate stipular teeth (Fig. 8 C). Leaves primarily simple, but because of the frequently occurring brachyblasts often appearing "fasciculate". — *Inflorescence* a sparse, lax, elongate raceme, usually with 3—7 flowers situated at intervals of 3—10 mm from each other on a sparsely short-sericeous axis. — *Bract* subulate, caducous, 1.5—3 mm long, acuminate, glabrous on outer side, short-pubescent on margins and inner side, usually shed in flowering stage. — *Pedicel* usually 4.5—6 mm long, shortly silky-sericeous, merging into the calyx. — *Bracteoles* subulate, ca. 0.8—1.2×0.25—0.35 mm large, glabrous on outer side, puberulous on inner side. — *Calyx*: tube obliquely campanulate (shortest above), 4—5 mm long, from sparsely and very minutely sericeous to subglabrous on outer side; lobes triangular or deltoid, 0.8—1.2 mm long, acute—acuminate, subglabrous on outer side. — *Petals* pale yellow but with violet shade on middle parts of vexillum back and sometimes on lower parts of carina. — *Vexillum* blade broadly ovate, usually 8.5—9.5×8.5—9 mm large, obtuse, short-sericeous on most of back (but glabrous on its lateral basal parts), glabrous on the front except for some pubescence on the base. Claw 1.5—2.5 mm long. — *Ala* blades narrowly elliptic-oblong, usually 7.5—9×ca. 3 mm large, obtuse, glabrous, with about 5—6 rows of small lunulate folds on upper basal parts. Claws 3.5—5 mm long, glabrous, relatively broad. — *Carina* blades lunate, about 6.5—7×4 mm large, short-sericeous on lower parts, with almost straight or slightly concave upper margins, and with a distinct basal bulge on each side. Claws 4—5 mm long, glabrous, rather broad. — *Pistil* with a short glabrous stipe; ovary sericeous on most parts (occasionally subglabrous on lower side), 2—4-ovulate; style upcurved, sericeous on basal parts, otherwise glabrous; stigma capitate, almost regular. — *Pod* lanceolate, about 20—22 × 4.7—5.5 mm large, sparsely sericeous in early stage, when ripe mainly glabrous and brownish.

DISTRIBUTION. The Piketberg Mountain complex (Piketberg Division) and the central part of the Cedarberg range (Clanwilliam Division).

COLLECTIONS

Piketberg Div.: Piketberg, rocky humid places; 260 m. 1828, DRÈGE no. 1425 ("*Aspalathus tenuifolia* DC.") (BOL, G, GH, K, L, P, PRE, PR, S, W). — Piketberg; ca. 400 m. 1892, GUTHRIE no. 2592 (SAM). — Slopes of Piketberg. 1892, H. BOLUS no. 7526 (BOL, NBG, PRE, Z). — Hills nr. Piketberg. 1913, MARLOTH no. 5361 (BOL, GRA, LD, PRE, SAM). — Piketberg, hill W of village; 250 m. 1922, MARLOTH no. 11063 (GH, PRE). — Piketberg. EDWARDS no. 221 (BOL, PRE, Z). — Just below middle of Versfeld Pass and nearby. 1965, ! no. 2479 (LD, NBG). — Versfeld Pass, below middle of slopes. 1965, ! no. 3855 (LD, NBG). — Just W of Stawelklip, Piketberg Mt. plateau. 1956, ! no. 986 (LD). — Between Stawel Klip and Kaffers Kloof. 1965, ! no. 4256 (LD). — Hills NW of Moutons Vlei, Piketberg. 1934, PILLANS no. 7316 (BOL, K, PRE). — Heuningberg, hill slope. Above old house of farm "Vrede"; 200—350 m. 1963, TAYLOR no. 5562 (LD, PRE, STE).

Clanwilliam Div.: Cedarberg Mts., Niewoudt Pass, W side. 1948, ESTERHUYSEN no. 14348 (BOL, K, PRE). — Niewoudt Pass, 5 miles from Kriedouwkrans along rd. to Algeria, rocky slopes; 550 m. 1956, ! no. 930 (BOL, LD, NBG, PRE, S); 1965, ! no. 3247 (LD).

ECOLOGY. *A. pendula* grows mainly on sandy substrate. It is found in sand on rocky mountain slopes at an altitude of ca. 550 m in the Nieuwoudt Pass on the western slopes of Central Cedarberge west of Algeria. In this area the trees vary between 2 and 5 m in height. On the eastern slopes of the Piketberg Mountain, in the Versfeld Pass area, it grows in an often reddish, sandy substrate. On the middle—upper slopes north of the pass it was observed in 1965, forming a small "wood" comprising about a hundred trees. In this place it is associated

Fig. 8. *Aspalathus pendula*; A—L: DAHLGREN & PETERSON no. 930, from the Central Cedarberg Mts., in the upper part of Niewoudt Pass, west of Algeria. — A: Branchlet. — B: Inflorescence. — C: Leaf-base (lateral short-shoot developed). — D: Transversal section of leaf at middle. — E: Bract. — F: Bracteole. — G: Base of pedicel. — H: Calyx, upper two lobes to the right in the figure. — I: Ala petal. — J: Carina petal. — K: Pistil. — L: Pod. — M: Map showing verified distribution. — A ×0.8; B ×2; C and G ×8; E—F and H—K ×4; D and M according to the scales given.

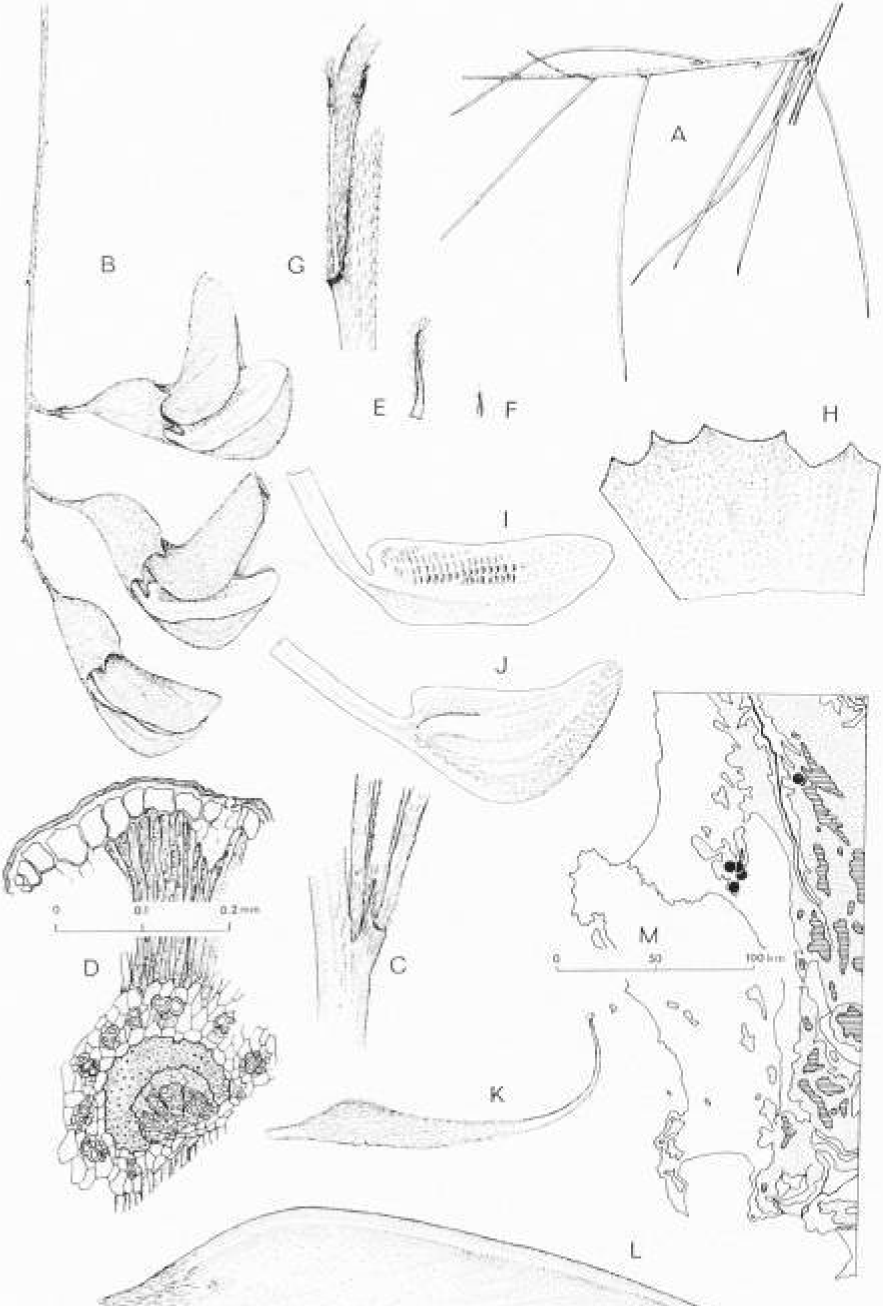

Fig. 8.

with *Euryops speciosissimus* DC. and *Serruria aitonii* R. BR. among *Passerina* scrub. The height of the *A. pendula* trees in this place usually varied between 2 and 4 m. Single specimens of the species also occur in the central parts of the Piketberg Mountain plateau.

REMARKS. The species is distinct. It differs from *A. linearis* by its trunk (=treelike growth), size, pendulous branches, larger flowers, and the long but narrow leaves.

MARLOTH remarked on the label of M. no. 5361 from the Piketberg, that this plant was the source of "Naaldthee". His note was mentioned by KIES (1951 p. 170), who thought that this species (called *A. tenuifolia*) was endemic on the Piketberg. The statement that *A. pendula* gave the "Naald tea" should not be accepted without caution, because certain forms of *A. linearis* have quite similar (although generally thicker) leaves.

FLOWERING PERIOD. Mainly October—November.

APPENDIX. ROOIBOS TEA CULTIVATION AND INDUSTRY

History of Cultivation

Already in the 19th Century (or possibly earlier), the coloured people knew how to use the wild forms of *Aspalathus linearis* for a "tea". With fine axes they chopped the branches of the wild shrubs in the mountains, bruised the harvest with wooden hammers, and placed it in heaps to ferment. In about 1905, BENJAMIN GINSBERG started to buy, pack, and trade such "tea" collected in the mountains by the coloured people, but it was not until about 1930 that Dr. P. LE F. NORTIER, a medical practioner, started some research on how to collect the seeds efficiently, how to improve germination, and how to handle the seedlings and grow the shrubs in plantations. His experience was shared with some farmers, who started to produce the tea on a relatively large scale. The first plantations were situated in the Pakhuis Mountains, Northern Cedarberge, on the farms "Teevlak" and "Varkensfontein" of OLOFF BERGH and "Klein Kliphuis" of WILLIAM RIORDAN.

The firm of B. GINSBERG marketed this tea, which was bought at that time from the farmers at a price of approx. 50 cents (=2 1/2 shillings, English currency) per kg. However, the seeds were expensive and difficult to collect. After a steady increase, the Rooibos Tea market underwent a servere crisis after the Second World War (about 1947), and the Clanwilliam Tea Cooperative was established in 1948 to rescue the interests of the tea producers. A later crisis, in about 1953—54, was due to over-production and a weak market; however after the establishment of the Rooibos Tea Control Board in 1954, the market of the tea increased, doubtless due to the improvement of the sorts cultivated, the control and classification of the tea marketed, and advertising promotion. The improved product is derived exclusively from cultivated, selected biotypes of the so-called Nortier Type and is called Rooi Tea. Rooi Tea has not yet been exported in any appreciable degree. (See BERGH and SAAYMAN 1965.)

Types of Rooibos Tea

The professional producers of "tea" from *A. linearis* distinguish between the main types mentioned below. Although all types of Rooibos Tea were still commercially available only a few years ago, only Rooi Tea is available today. The other types originated from wild forms which are only fragmentarily known even among the tea producers and buyers at Clanwilliam, and this knowledge will probably fade rapidly as the types are disappearing altogether. The facts (and to some extent conjecture), stated below, are based on correspondence and discussion with persons of the Rooibos Tea Centre at Clanwilliam and partly on comparisons between the wild (and pressed) material and the appearance of the tea itself. (Samples of the tea types are in the author's possession by the courtesy of the Clanwilliam packing centre.)

In populations where short-shoots (with several—many leaves) tend to be delayed in development or poorly developed on the whole, the amount of leaves will be small in relation to stem material, giving a tea rich in "stems and coarse material". The samples of wild forms, examined by COETZEE & al. 1949, were selected at random and are perhaps not representative in this respect, although it is significant that the "Dark Grey Cedarberg" and "Greyish Black Sandveld" samples which partly may correspond to Vaal (Grey) Tea (see below) have a high percentage (> 30 per cent) of such material. On the other hand a comparable amount was also found in the sample named "Reddish Brown Nortiers".

ROOI (RED) TEA TYPES

NORTIER TYPE. This is obtained from cultivated, successively selected biotypes which originally derive from wild forms, mainly found in the northern part of the Cedarberg Mountain range (at least partly in the Pakhuis Pass area). The cultivated forms selected have fresh-green (not pale or bluish green), relatively slender leaves, erect growth, and a leafy habit. The flowers which are relatively bright yellow are more thoroughly described below. The plants are no doubt predominantly allogamous and the wild as well as cultivated material varies greatly in a number of respects. Selection and breeding work is still in progress. The tea, obtained according to the procedure described below, is reddish and has a mild aroma.

CEDARBERG TYPE. This is obtained from the wild forms out of which the cultivated Nortier Type has been selected. These forms occur mainly in the Pakhuis Mountains (northern part of the Cedarberg range) and also to some extent in the mountains in the Citrusdal area (and possibly in the Olifants River Mountains). Some of these forms may derive from cultivation escapes. Because of the broader variety of biotypes, this tea has a somewhat inferior quality compared to the Nortier Type, although the colour and the aroma is similar.

ROOI-BRUIN (RED-BROWN) TEA TYPE

This was obtained from wild plants reported to grow mainly on the sand flats in the northern regions of the distribution area, especially in the lowlands from Pakhuis (Clanwilliam Division) northeastwards into the Calvinia Division and northwards into the Vanrhynsdorp Division, but the range of these wild forms are not known in detail. Wild forms, seen e.g. on the sand plateaus in the Traveller's Rest area between Pakhuis and Doringbos, might belong to populations yielding this type. They are erect, with a height of 1.5—2 m, and have relatively long leaves. The tea produced is reddish-brown and not or only slightly coarser than the Rooi Tea; the flavour is not very different.

VAAL (GREY) TEA TYPE

This was obtained from wild forms in the mountains chiefly of the Cedarberg (but probably also the Olifants River) Mountain range in the Clanwilliam Division. The variation of the species in the Cedarberg Mountains is very great (see above), and most forms have more pale or greyish green and often coarser leaves than the cultivated ones. The forms which yielded the Vaal Tea, according to available sources at the Rooibos Tea Centre in Clanwilliam, are thought to occur in the relatively dry and sandy parts of the mountains, perhaps mainly on the lower sand slopes in the Olifants River Valley and the lower slopes of the Cedarberg. The leaves of the forms yielding this tea type are rather pale and greyish green, and the tea obtained is also more greyish in colour. The tea is considered to have a somewhat undesirable honey aroma.

SWART (BLACK) TEA TYPE

Similarly, this type is said to have been obtained from forms chiefly growing in the Cedarberg Mountains, but different from those yielding the Vaal and Rooi Tea. According to information from the professional Rooibos Tea producers at Clanwilliam, the forms yielding the Swart Tea occur in rocky regions of the Cedarberg Mountains. They may possibly correspond to the plant illustrated in Fig. 3 H, from rocks in the Pakhuis Mountains. The tea is distinctly darker in colour than the Vaal Tea and has an aroma markedly different from all the other tea types. This type of tea was the first to be discontinued on a commercial basis.

Thin-Layer Chromatography of Rooibos Tea Types

Extracts were made of 0.05 g dry, crushed tea in 1 ml methanol (with an addition of HCl); 10 μl of the extract was used in each case. Smooth glass plates 16×12 cm large were covered with an even, thin layer of cellulose (Merk Avicel 2330). The solvents used in the first direction was formic acid (1 ml conc. formic acid per 50 ml H_2O) and in the second direction amyl alcohol, acetic acid, and water in the proportions 22: 11: 13 ml respectively. The glass plates were examined under ultra violet light, before spraying, after spraying with 1 % $AlCl_3$ (solved in methanol and propanol, 1: 1), and after spraying with 1 % NaOH (solved in methanol) as well. Five parallel tests of each tea type were made.

Before examining the results, the following points should be considered. The tea in each test is composed of 3—ca. 6 small pieces of leaves doubless from equally many specimens; small amounts of tea being taken out of large boxes of commercial tea. *Each chromatogram accordingly represents more than one specimen out of a population or possibly more than one population.* Moreover, the tea has undergone fermentation (see below) whereby changes of the chemical constitution of some of the compounds possibly have occurred. The leaves are also of different age, which is known to be combined with biochemical differences. The comparison between the tea types will accordingly have a somewhat limited but still great interest.

Results. — 1. The pattern of spots shows great agreement between the 5 different chromatograms for each tea type. Differences with regard to certain spots occur only ocasionally and then only very faintly discernible ones are normally involved. — 2. There are differences between all four tea types. — 3. There is otherwise rather great agreement betwen Rooi Tea (cultivated) and Rooi-Bruin Tea, but these differ clearly from Swart Tea and Vaal Tea which show mutual resemblance. — 4. The quantity of phenolic compounds as estimated from the intensity of the spots is markedly greater in Rooi Tea and Rooi-Bruin Tea than in the other two tea types.

The scope of the investigation does not justify any statistical treatment or tabulation of R_f-values. However, accumulative chromatograms of the tea types are illustrated in Fig. 9 without and with double spraying (see above).

It is not known whether the tea used of each of the three types which derive from wild forms, is a mixture of tea from different populations or originates only from a limited population. However, it is probable that at least the Vaal and Swart Tea samples derive from a larger area, because the wild forms are rarely abundant in the field. As the Rooi and Rooi-Bruin Tea types, which yield an acceptable beverage, have certain features in common with regard to the pattern of spots, it seems probable that there is a certain co-variation in the selection of phenolic compounds and the compounds decisive for the tea aroma, although these are probably not identical. Therefore, a routine chromatographic test of fermented (most probably also unfermented) leaves might give indications on whether or not a plant is suitable for tea, notably if it shows resemblance to the Rooi Tea Type in regard to the spot pattern.

Characteristics and Variation of Cultivated Rooi Tea Plants

It is obvious from the above that the variation in the wild forms of *A. linearis* ssp. *linearis* is very wide. The habit varies from subprostrate or decumbent to erect and 2-m-high, the leaves from slender to quite thick and from pale or bright green to glaucous. The flowers may be concentrated on the branch tips or dispersed along the distal parts of the branches and vary greatly in size and colour.

In the cultivated biotypes recombination and selection has resulted in patterns of characteristics which are rarely found in nature.

Certain wild forms in the Pakhius Mountains are said to represent the most important base material for the cultivated forms, and occasional collections from this region may be difficult to distinguish from cultivated biotypes of the Nortier Type. Such a collection is ! no. 4480 from Boskloof (between Clanwilliam and Algeria) illustrated in Figs. 2 G and 3 G.

The cultivated biotypes are characterized morphologically by the following combination of characters. The shrubs are erect (or ascending by "topping") and usually 70—180 cm tall; the branches are relatively straight and slender; the leaves are rather slender and light—bright green, not pale greyish green or glaucous, and turn markedly reddish

Fig. 9. Comparison of chromatograms of samples of the four main types of Rooibos Tea. Spots of phenolic compounds visible in ultra violet light. Upper row: without spraying. Bottom row: after spraying with solutions of $AlCl_3$ and NaOH. Spots ± faintly visible drawn with broken lines. Unless given a number, the spots were represented in all the five tests of each tea type. The figures accompanying some spots denote the number of tests in which the spots were represented. — The differences between the tea types is, perhaps, most conspicuous before spraying. Colour of spots: yellow |; black —, and blue /.

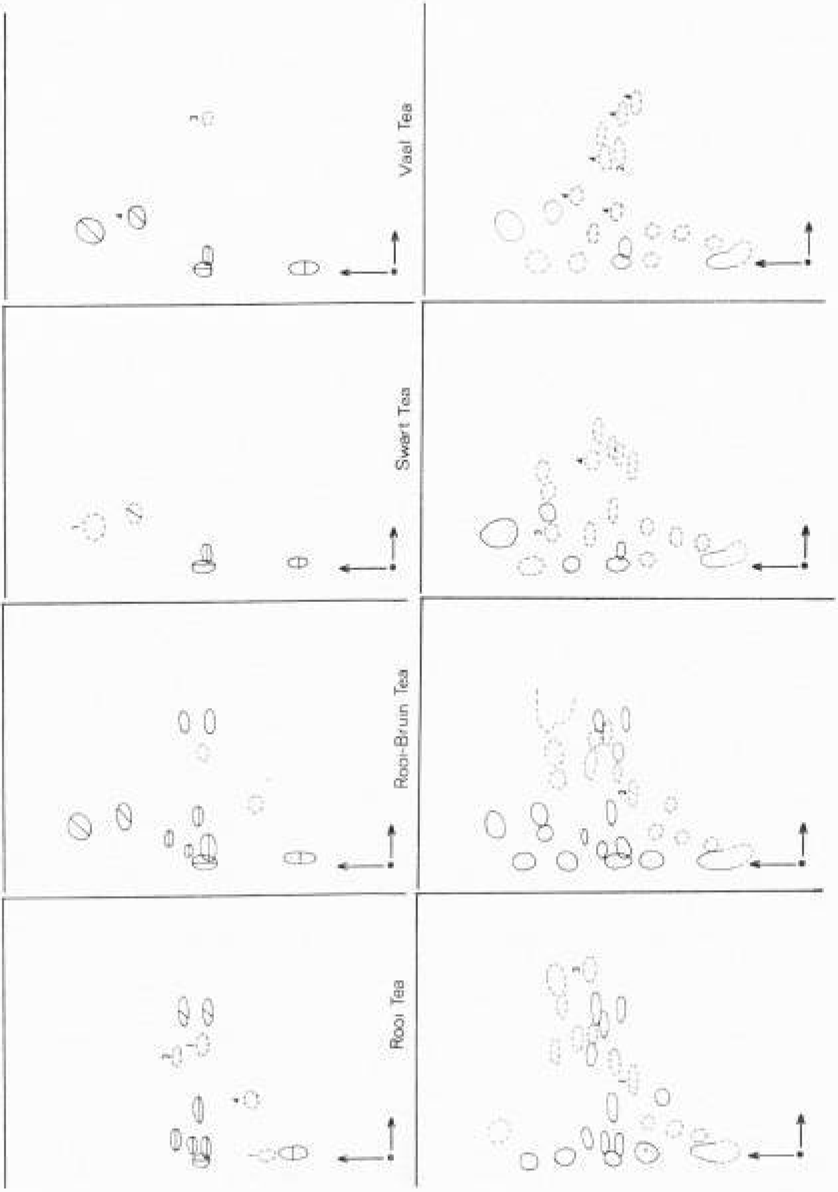

Fig. 9.

when bruised and dried; the flowers are relatively large on the average and have more brightly yellow petals than average wild forms, lacking as a rule the common violet shades on the vexillum back and carina bottom. Thus, the cultivated forms have a more spectacular blossom than the wild ones, although this is not necessarily combined with a larger number of flowers (cf. below). The pedicel is usually short-sericeous and the calyx adpressedly and very sparsely short-puberulous on the outer side. The calyx lobes in the presently cultivated forms are usually subulate and 2—3 mm long. The vexillum blade is, on the average, about 6.5×5 mm large and rather pointed (there is some variation in size); the ala blades are ca. 4.2—4.5 mm long, and the generally somewhat acute and tapering carina blades are ca. 5.0 mm long and pubescent on the lower parts. The flower in Fig. 2 H represents an average biotype of the cultivated "Rooi Tea" shrubs (in Fig. 2 G is seen a corresponding wild form).

Within this general appearance, however, there is great variation which is to some extent illustrated in Fig. 10. The size and density of branches are quite variable. Thus two specimens, illustrated in Figs. 1—2 in COETZEE, VAN DER MERWE, & BURGER 1953, have perhaps a ratio of 20:1 with respect to their amount of foliage. The variation pattern indicates predominant cross-fertilization, no two shrubs having the same appearance.

A good shrub should be wide, with many branches and a rounded shape; the branches should be ascending or erect and not bowing or pendulous; they should also be closely leafy with relatively short internodes and possess many leaves (which are not too short) and developed on short-shoots in leaf axils along the branches. Flowers should not occur in too large an amount. Most important are of course the features of the leaves which should be rather bright green and, when bruised after cutting, rather brightly reddish and with a pleasent aroma.

Fig. 10 illustrates branch ends from different shrubs grown under uniform conditions at the Rooibos Tea Centre at Clanwilliam. They were all of the same age, when collected (on September 4, 1965).

Fig. 10. Branches of selected, cultivated, equally old shrubs of *Aspalathus linearis* ssp. *linearis*, used for "Rooi Tea" (Nortier Type), studied on the same day and in the same place with the same substrate (sand) on the grounds of the Rooibos Tea Centre at Clanwilliam. See comments in the text. (Of the samples collected on this occasion the illustrated ones represent, A: no. 13; B: no. 11 (superior biotype); C: no. 6; D: no. 1; E: no. 14; and F: no. 4.) All on the same scale.

Fig. 10.

The branches of **A** derive from a ca. 90 cm tall, erect, rather sparingly branched shrub with erect branches and rather short leaves. This biotype flowers exceptionally late. — The branches of **B** were picked from a shrub regarded as superior in most respects. It was ca. 180 cm tall, widely branched, and had rather stiff ascending branches with rich foliage, the brachyblasts being rather closely set each with several leaves. It flowers relatively late and sparsely. — The branch of **C** was from a rather richly branched, ca. 1.8 m tall shrub with erect branches flowering somewhat earlier than A and B. The flowers are mainly situated on lateral short-shoots. — The **D** branch derives from a relatively sparingly branched shrub, ca. 1 m tall, with ascending branches. In this biotype the flowers are mainly concentrated to the branchlet tips, and the brachyblasts are poorly developed on the young branches with regard to foliage as well as flowers. — The branches in **E** come from an erect, rather rigid but sparingly branched shrub ca. 85 cm tall. It is rich-flowered, and the leaves are relatively short but closely set. — In **F**, finally, the branches derive from a ca. 1.4 m tall, much-branched, wide shrub with weak, bowing branches and rich blossom but rather sparse foliage. Flowering occurs relatively early.

Beside the variation in the mentioned characters there are doubtless also differences between the specimens in the texture, colour, and aroma of the leaves after processing. Closeness of flowers is generally not combined with rich foliage. In the cultivated Rooi Tea a great proportion of shrubs are doubtless too rich-flowered for an optimal tea production (Fig. 10 F). The percentage of such plants will, of course, increase if seeds are collected at random from the cultivated bushes, rich-flowered biotypes yielding a larger amount of seeds. Therefore, in seed harvesting the selected, more sparsely pod-bearing shrubs should be favoured, provided that they are favourable with regard to the other characteristics.

Mountain plantations used for seed harvesting must also be well isolated from wild forms in the adjacent fynbos to prevent the introduction of unfavourable gene material by illegitimate pollination. (Cf. below.)

Controlled artificial pollination is cumbersome and could hardly be used in any but purely scientific scale. The concentration of a relatively large number of shrubs, all selected as "superior" with regard to most of the properties for the tea, in places suitable for a favourable pollination during blossom, with subsequent seed harvest, and selection of the offspring, repeated for several generations, seems a feasible way of improving the biotype selection further.

In this connection, it may seem appropriate to make some comments on the cultivated forms which I have collected at times in places other than Clanwilliam.

In a sand field near the Breede River south of Romans River (W part of the Worcester Div.), there was a Rooibos Tea cultivation in 1956—57. In spite of considerable variation the shrubs agree largely with the present Nortier Type. However, the flowers of the two collections (! no. 702 and 1778; see Fig. 4 A—H) made here are distinctly smaller than in any of the biotypes studied in the above-mentioned Clanwilliam plantation in 1965. A possibly wild, decumbent, even much more small-flowered form with relatively coarse leaves was collected close to the plantation, (! no. 1777); it is described among the wild forms on p. 178.

Plants occurring on a field in the Citrusdal region (! nos. 1026—1032) were also studied in 1956. Some specimens of these collections show characteristics not matched by any of the biotypes in the Clanwilliam plantation. Thus, one shrub (! no. 1028) is closely similar to the *wild* forms found in this region (near Grey's Pass) the leaves being long, coarse and greyish green, and short-shoots being absent in the leaf axils of young branches. In this case the wild forms in the area have either spread to the plantation, or have been adopted among the biotypes selected. The plant may also be a "crossing" product between wild forms on the mountain slopes and the cultivated ones. Other biotypes, cultivated in the same field, correspond more closely to the forms described above from Clanwilliam.

Odd random samples, taken in 1965 from fields in the Citrusdal area (! no. 3278) as well as in the Nieuwoudtville area (! no. 3289), correspond largely to biotypes in the assortment at Clanwilliam.

Cultivation

Seeds are most easily obtained by harvesting the greenish half-ripe pods and placing them in bags to dry and ripen, whereby the pods burst open and the seeds assemble on the bottom of the bag.

Before sowing the seeds are scarified (e.g. by rubbing with sand) or treated with acids. If this is omitted the germination proceeds slowly and only a fraction of the seeds germinate promptly. With these methods germination is reported to vary from < 60 to > 90 per cent in different plantations (cf. Farmer's Weekly, Aug. 10, 1960, p. 25), probably depending on treatment before sowing, method of seed harvesting, and seed bed conditions. The seeds are placed in warm water for ca. 12 hours before sowing.

Sowing usually takes place between January and March. The seeds are usually sown in rows ca. 10 cm apart at a depth 1—1.5 cm in specially prepared nursery beds with deep, well drained, slightly acid sand soil. No or only slight manuring should be used for the nursery beds. The depressions where the seeds are placed are sometimes covered with white river sand to facilitate the penetration of the soil by the seedlings. After sowing the nursery beds are well watered and often covered with reeds for the first days to decrease evaporation. The cotyledons are elliptic and the next leaves to develop have a simple linear shape.

After the first winter rains, 3—4 months after sowing, and usually in May—June, the young plants are 10—15 cm high and can be transported to the plantations which are usually situated in the mountains or on the mountain plateaus at altitudes of ca. 500 m or more above sea level. These plantations generally rest on sand weathered from sandstone (of the Table Mountain Series) and the reaction is somewhat acid. A rainfall of at least 300—350 mm per annum is considered necessary for the Rooi Tea. The rain falls mainly in the winter with showers also in late autumn and early summer. The winter is rather cold with occasional snow and frost, and the summer is hot, occasionally up to 40°C. This great fluctuation in temperature is endured by the adult shrubs, but the seedlings are more sensitive.

Virgin land to be planted with the Rooi Tea is favoured by cultivation of cereals (wheat, oats, corn) for 1—2 years before the tea is planted. In April—May, before planting, the soil should be fertilized and ploughed. A relatively rich addition of phosphate and potash is needed, but no nitrogen, as the plants have bacteria nodules on the roots capable of utilizing free nitrogen from the air.

The plants are put in rows with a distance of ca. 1 1/2 m between the rows as well as between the shrubs in each row. At an age of 10—12 months the shrublets are topped at a height of 25—40 cm, whereby apical growth of the main shoots is prevented and laterals develop which give the shrubs a more rounded and "bushy" shape, and involves the formation of a greater amount of foliage.

Two years after planting the shrubs may offer their first profitable harvest. Harvesting is made in late summer (about February). Three years after planting the shrubs are in full production. The yield of each shrub is extremely variable depending on the genetic constitution, but good adult shrubs (ca. 4—5 years old) give an amount of ca. 1/2 kg dry tea per year. The maximum age of the shrubs is said to be 6—18 years depending on soil, climate, genetic constitution of the plant, etc., but after the 7th season the shrubs are usually not economically profitable. Dead bushes in the plantation are pulled up and substituted with young ones.

The Rooi Tea plantations are concentrated in the Clanwilliam Division. The crops of 1964—66 were produced according to the following percentages in the Divisions of Clanwilliam, Vanrhynsdorp, Calvinia, and Piketberg:

Division of	Per cent of total Rooi Tea crop		
	1964	1965	1966
Clanwilliam	83.9	85.2	83.7
Vanrhynsdorp	7.5	7.6	8.5
Calvinia	7.2	5.1	4.7
Piketberg	1.4	2.0	3.0

Totally, about 1,430,000 kg of tea were produced in 1964 and 1,350,000 kg in 1966.

Processing of the Rooi Tea

In short, the procedure is the following. The leafy branch ends are harvested by cutting and when brought to the fermentation yard cut again finely to a length of ca. 1/2 cm, moistened, bruised (e.g. with wooden hammers), and placed in heaps to ferment. Then the material is spread open in the sun and stirred intermittently until dry. After drying it is sifted, classified, and packed.

A uniform and standardized procedure of processing the tea has not yet evolved. Each producer has his own method or modification of a method, which varies according to the experience of the farmer, the location (i.e. local climate) of the farm, the weather, and other circumstances. (Cf. COETZEE, VAN DER MERWE, & BURGER 1953).

Harvesting is generally made in summer and early autumn (according to COETZEE et al., op. cit., in January—March) by cutting the branch ends 25—50 cm in length depending on the shape of the bush, and by reducing the shrubs to about 2/3 of their length. The cutting is made with sickles. The branches are brought in bundles to the processing yard within 24 hours and are cut by (tobacco, hay, or special) cutting machines into pieces somewhat more than 1/2 cm in length. The cut product is dampened with clean water; ca. 6 l being used for 100 kg of green tea. This is bruised under tractor wheels, in machines with steel rollers, or in other ways, whereby the sap of the leaves is partly released. The bruised product, now reddish in colour, is piled in low heaps, ca. 10—15 cm thick and covered with bags to ferment for 8—24 hours, depending mainly on the temperature and the degree of bruising. During fermentation the pH of the tea increases successively, ammonia (NH_3) being formed from the proteins (see COETZEE et al., op. cit.). The heaps are turned over some times during the fermentation.

After fermentation the tea is spread out in a layer only ca. 2 cm thick on concrete yards to dry in the sun and is stirred intermittently. When dry, after 1—3 days, it is bagged and delivered to the Board where it is graded according to special agreements and stifted in special machines whereby dust and sticks are removed. After this the tea is ready for packing and marketing.

The reddish colour of the Rooi Tea is mainly achieved during the bruising process. There is some diversity of opinion about the extent of bruising in order to produce the most favourable tea. Removal of hard branch pieces before bruising seems to be desirable. The fermentation time depends on the degree of bruising (shorter with extensive bruising) and temperature; temperatures somewhere between 35 and 50°C are regarded suitable for the process. Fermentation at a high temperature probably requires a shorter time than fermentation at a low temperature. According to COETZEE, VAN DER MERWE, & BURGER 1953, the drying conditions are of importance for the flavour. The desirable flavour constituents are volatile in hot air, and therefore drying in the open air in the sun seems preferable. It may be added that none of the *A. linearis* forms in the southern divisions turn reddish to such an extent as the cultivated forms in the Clanwilliam Division nor do they achieve such a flavour.

Contents of the Rooibos Tea

With regard to the major contents of the Rooibos Tea reference is made to the publications of REYNEKE, COETZEE, & BESTER 1949 and COETZEE, VAN DER MERWE, & BURGER 1953. In these articles chemical analyses are considered to be of no decisive value in the grading of the tea, i.e. for determining the quality. Instead, the grades must be judged by colour, flavour, moisture, and by the absence of dust and stem contents in the tea. The average percentage of water in the tea is usually 9.5—11; harvested tea, withered before bruising and processing, has a lower water content than if bruised in fresh condition. Protein and tannin compounds occur approximately at 5—6 per cent and ca. 3 per cent, respectively; these values are quite low in relation to ordinary Ceylonese Tea. Alcaloids, like caffeine or theine, are absent or negligible. A considerable amount of vitamin C is found, however. The phenolic constituents of Rooibos Tea have been studied extensively by B. H. KOEPPEN, Stellenbosch, in a number of papers.

Preparation of the Beverage

The Rooi Tea is prepared like ordinary Ceylonese Tea. The colour of the beverage is orange-red. Rooi Tea may be blended with Ceylonese Tea. Sugar, milk, or lemon may be added according to taste; and the drink may be served cooled, preferably with ice and lemon. The leaves can be used repeatedly without disadvantage for the aroma, the low content of tannin being a definite advantage. The aroma and colour are also retained for several days when the drink is stored in a refrigerator.

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Thanks are also due to the directors and staffs of the herbaria from which material has kindly been supplied for the studies, to Dr. HANS RUNEMARK and Mr. ARNE STRID for reading the manuscript critically, to Mr. GUNNAR WEIMARCK, for advice in the cromatographic work, and to Mr. HAROLD M. KOCH for revising the English.

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The Genus Euryops

Part II. Aspects of Morphology and Cytology

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CONTENTS

ABSTRACT

Morphology. The flowering shoot system of *Euryops* is a polytelic trunk synflorescence with simple, one-headed peduncles in a lateral or pseudo-terminal position. The most primitive condition is found in species of sect. *Angustifoliae* with lateral peduncles basally provided with two well-developed leaves. More commonly the peduncular leaves are rudimentary or lacking altogether. In sect. *Euryops, Chrysops, Brachypus,* and *Psilosteum* the peduncles are pseudo-terminal. Umbellately disposed pseudo-terminal peduncles (e.g. in *E. linearis*) have a sympodial character and may be derived from a shoot system with solitary pseudo-terminal peduncles.

The uniseriate involucre is derived from a spiral arrangement, and the numbers of phyllaries often conform with the denominators of the lower Fibonacci fractions (5, 8, 13, and 21).

The leaf trichomes are either simple or branching and variously shaped. Glandular hairs are rare. The stellate trichomes of *E. anthemoides* ssp. *astrotrichus* may be derived from more simple or cross-wise branching hair types found in other species.

The achene hairs are usually tricellular with a small basal cell and two larger parallel cells with mucilaginous properties when soaked. Several species have non-mucilaginous, often multicellular achene hairs, which are clearly homologous with the former type.

Several evolutionary trends in morphological features, e.g. development of disc-floret (♀)sterility and loss of pappus, have occurred independently in different sections of the genus.

The pollen grains are morphologically uniform throughout the genus. The pollen type found in *Euryops* and related genera comes close to the Senecio type.

Cytology. Mitotic chromosome numbers for 36 taxa are presented. The basic number is $x=10$. Polyploids occur especially in some widely distributed karroo species of sect. *Angustifoliae*. Tetraploids ($2n=40$) were found in *E. lateriflorus, oligoglossus, subcarnosus,* and *glutinosus*. *E. cuneatus* proved to be hexaploid ($2n=60$). Accessory chromosomes occur in variable numbers (1—11) in several species.

I. INTRODUCTION

The present part of my study of the genus *Euryops* (*Compositae—Senecioneae—Othonninae*) deals with some morphological and cytological aspects. The phytogeographical study of the genus has expanded to a general treatise on South African phytogeography and will be published as a separate volume.

The reader is referred to Part I (Nordenstam 1968) for taxonomic matters, locality lists, as well as acknowledgements. The latter shall be supplemented here with a word of thanks to the Head of the Palynological Laboratory, Solna, Sweden, for kindly supplying me with acetolysed pollen preparations of *Euryops* and related genera.

II. MORPHOLOGY

A brief survey of the morphological characters of taxonomic importance in *Euryops* was presented in Nordenstam 1968 (Chapter III). Some morphological aspects of special interest will be further discussed below.

Organization and Evolution of the Synflorescence

The organization of the capitulous branches in the shoot system was given much weight in the taxonomic considerations in Nordenstam 1968, especially for distinction of sections within the genus. The large section *Angustifoliae* is characterized by lateral peduncles, which are always simple and terminated by a single capitulum. In Troll's terminology the flowering shoot may be described as a polytelic "Rumpfsynfloreszenz", i.e., the main axis lacks a terminal inflorescence (TROLL 1964 b, p. 157). *Trunk synflorescence* may be suggested as an English equivalent of the German term ("trunk" in this connection meaning a body without a head). This type of synflorescence is no doubt derived from the complete polytelic synflorescence characterizing most *Compositae*. The derived 'truncated' type is probably uncommon in the family, but TROLL (1962, p. 122; 1964 a, p. 127) mentions some examples from *Hieracium*, *Andryala*, *Aster*, *Espeletia*, *Euryops*, a.o.

In most species of *Euryops* sect. *Angustifoliae* the peduncles are quite devoid of leaves. They are always axillary and subtended by a single normal leaf. In several species, however, two lateral leaves occur at the very peduncle-base. These leaves are usually distinctly smaller than the normal leaves, sometimes only 1—2 mm long and subulate, but in a few cases they are well developed and more or less equalling the normal leaves in size and shape (e.g. *E. pinifolius*, *antinorii*, *jacksonii*). The latter type may be regarded as the most primitive in the genus, and from this type a reduction series within sect. *Angustifoliae* may be seen, ending in complete loss of the basal peduncular leaves (cf. Fig. 1 C—E).

A hypothetical ancestor of *Euryops* is outlined in Fig. 1 B. Its floral region is a racemose arrangement of axillary leafy shoots with single terminal capitula. The main axis lacks a terminal flowerhead, and the flowering sequence is acropetal. The derivation of this type may be imagined as a loss of the terminal top inflorescence in combination with a reversal of the order of development in a complete synflorescence of the type shown in Fig. 1 K. The latter is found in species of *Othonna* (a genus related to *Euryops* but with truly terminal capitula), and its connection with other types found in that genus is intimated in Fig. 1 I—J. From the hypothetical *Euryops* ancestor the organization in sect. *Angustifoliae* is easily derived through a basipetal displacement of the peduncular leaves or, in other words, a 'reduction' of the basal, foliate portion of the peduncles.

Most species of sect. *Angustifoliae* have comparatively small or medium-sized capitula, but this feature is often compensated by the large numbers of capitula in the floral regions. Often the peduncles are racemose (Fig. 1 E) but not infrequently more corymbose, by elongation of the lower peduncles (Fig. 1 F). There is, of course, no significant difference or distinct limit between these two types.

Prolification is a common phenomenon in sect. *Angustifoliae*, i.e. the shoot apex resumes its vegetative growth after flowering. After some time of vegetative growth a new floral region is developed (Fig. 2 C). The time interval between two subsequent flowering periods may be one year (e.g. in areas with a regular winter rainfall), but often it is shorter, due to external factors (e.g. sporadic precipitation).

The sections *Euryops*, *Chrysops*, *Brachypus*, and *Psilosteum* are all characterized by seemingly terminal peduncles, which are either borne singly or sometimes two or several together. Since they are always simple and leafless and do not have the appearance of being direct continuations of a main axis, it seems reasonable to assume that they are not truly terminal but derived from the lateral condition. Thus these peduncles may be designated as *pseudo-terminal* (cf. NORDENSTAM 1968, p. 23). In sect. *Brachypus* the pseudo-terminal peduncles are reduced, sometimes to the extent that the capitula appear sessile (Fig. 1 H).

In Fig. 1 the derivation of the pseudo-terminal peduncle arrangement is indicated simply with an arrow from the racemose condition (Fig. 1 E, G). The steps in this process of terminalization are less obvious, however. The solitary pseudo-terminal peduncle may just as well be derived more directly from the hypothetical ancestor in Fig. 1 B. More likely, however, the process has been more complicated. A closer examination reveals that the pseudo-terminal peduncle in many cases emerges from an assemblage of two or three leaves (e.g. in sect. *Euryops*), in other cases only one leaf, or sometimes only from a tuft of wool. This seems to indicate a reduction series from a basal leaf

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Fig. 1. Development of synflorescence types in *Euryops*, diagrammatic. — A: Primitive composite type with single terminal head. — B: Hypothetical ancestor of *Euryops*. Main axis without terminal head (trunk synflorescence). Lateral capitulous branches leafy, with single capitula. Flowering sequence acropetal. — C: *E. pinifolius* a.o. Peduncles lateral, simple, nude, with two well-developed basal leaves in the axil. — D: *E. floribundus* a.o. Similar to C but basal peduncular leaves rudimentary. — E: *E. spathaceus* a.o. Peduncles without basal leaves, lateral, racemose. — F: *E. rehmannii* a.o. Similar to E but lower peduncles elongated; corymbose arrangement. — G: Sect. *Euryops* a.o. Solitary pseudo-terminal peduncle, derived from a lateral position. — H: Sect. *Brachypus*. Solitary sessile head. Similar to G but peduncle reduced. — I—K: Some synflorescence types found in *Othonna*. — I: Solitary terminal capitulum (*O. ciliata*). Cf. A! — J: Complete synflorescence with terminal head on main axis and lateral capitulous branches of first and second order (*O. parviflora*). — K: Complete synflorescence with lateral capitulous branches of first order only (*O. coronopifolia*). If truncated, this type comes close to B.

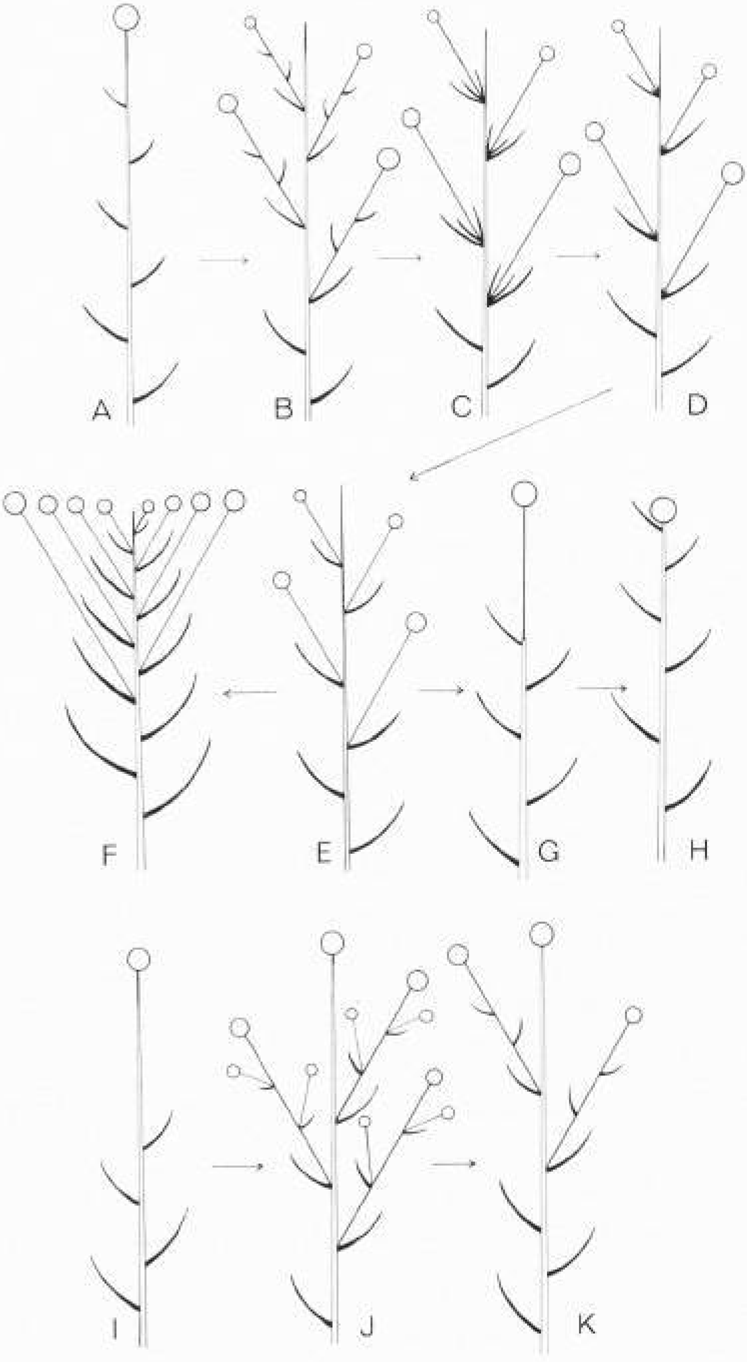

Fig. 1.

cluster and gives a hint at the possible course in the terminalization process. With Fig. 1 E as a starting-point the process may have involved three steps: (i) a shortening of the axis to a brachyblast, (ii) a reduction in number of peduncles to ultimately one, and (iii) a vertical orientation of the solitary peduncle and the remaining basal leaf cluster to a pseudo-terminal position. Some evidence in support of this hypothesis can be had from sect. *Angustifoliae*. Within this section a reduction of flowering shoots to brachyblasts is observable in many species (nos. 41—51 in NORDENSTAM 1968). In its most reduced forms these brachyblasts consist of only a leaf cluster of a few leaves and sometimes only one peduncle, which thus has a subterminal position on the reduced shoot (e.g. *E. asparagoides, microphyllus*).

The explanation suggested above could account for the variation in number of the pseudo-terminal peduncles (from 1 to 3 or sometimes more in the same specimen). However, the terminal umbel found in e.g. *E. linearis* (Fig. 2 H) cannot be derived simply by a contraction of a racemose synflorescence (Fig. 1 E). The flowering sequence within the umbel is more or less distinctly centrifugal with the central capitulum developing first, suggesting a sympodial origin of the synflorescence. The most likely derivation is by contraction of a sympodially branching shoot system with solitary pseudo-terminal peduncles (Fig. 2 D, cf. also A). Such a condensation is found in some forms of *E. pedunculatus* with apically closely branching shoots suggesting an umbellate arrangement at a superficial glance (Fig. 2 G). A similar process may account for the usually ternate pseudo-terminal peduncles in *E. chrysanthemoides* (Fig. 2 B) and similar arrangements with varying numbers of peduncles in several other species. The central

Fig. 2. Diagrams of flowering shoots in *Euryops*. — A: Pseudo-terminal solitary peduncles in a sympodially branching shoot system (*E. brevilobus* a.o.). — B: Pseudo-terminal ternate peduncles (*E. chrysanthemoides* a.o.). — C: Prolification in synflorescence with lateral peduncles (*E. lateriflorus* a.o.). The shoot apices resume vegetative growth after flowering, resulting in alternating floral and vegetative regions on each shoot. — D: Pseudo-terminal solitary peduncles in a sympodially branching shoot system (*E. abrotanifolius* a.o.). — E: Tendency towards monopodial mode of growth in *E. polytrichoides* through suppression of all but one branch, which continues its growth in a vertical direction. — F: Similar growth in *E. hypnoides* with usually two peduncles close together. — G: Condensed apical branching in forms of *E. pedunculatus*, combined with a reduction in the time interval between subsequent floral regions. — H: Umbellate synflorescence of pseudo-terminal peduncles in *E. linearis*. Note flowering sequence with central head developing first.

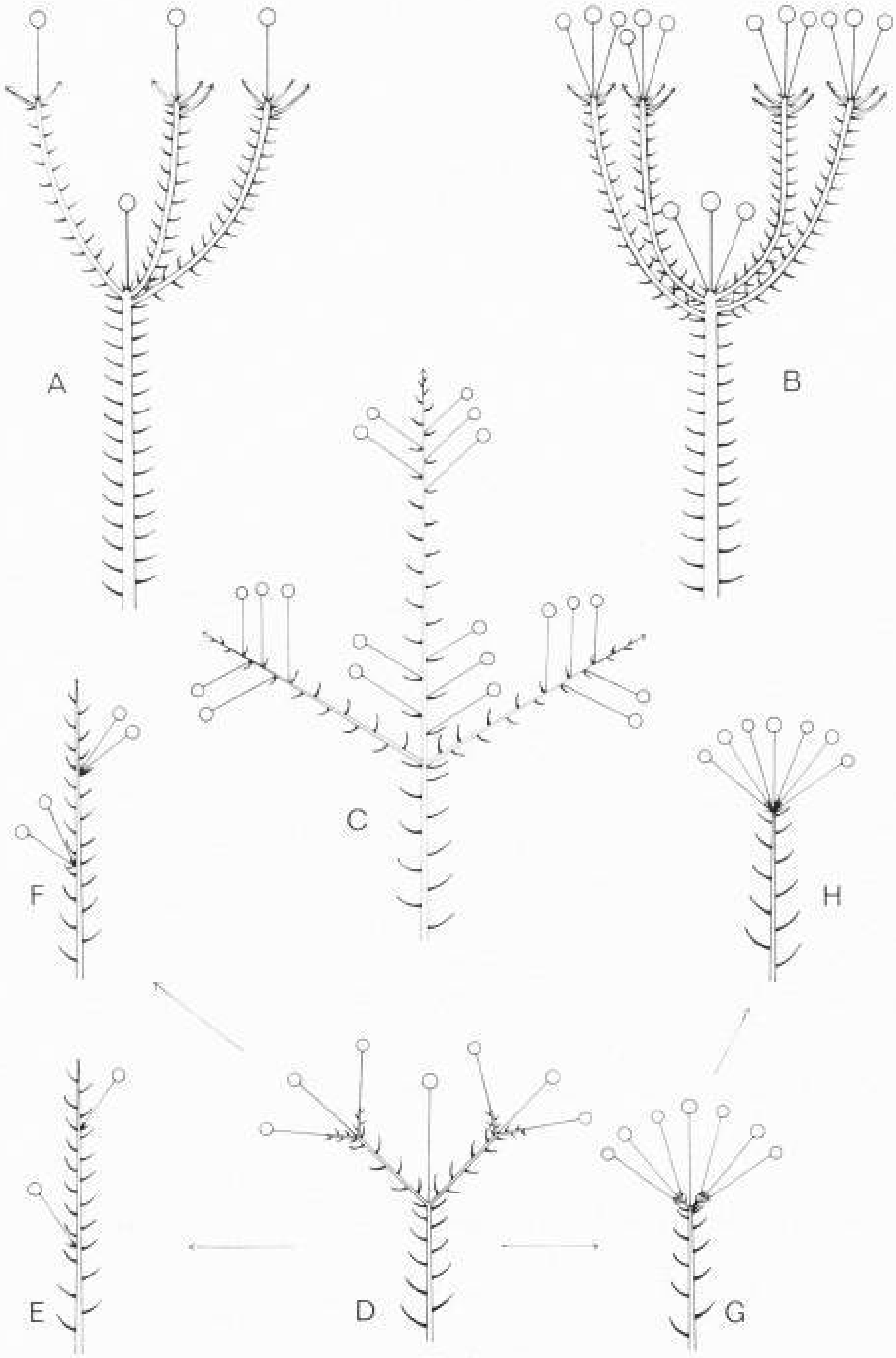

Fig. 2.

peduncle develops first and is usually devoid of basal leaves, whereas the peripheral peduncles usually have each a subtending leaf.

In the species with pseudo-terminal peduncles the shoot apex ceases its growth with the development of the floral region. Prolification does not occur, and the shoot systems are thus more strictly sympodial than in sect. *Angustifoliae*. A few species show some tendency towards a monopodial mode of growth, which is achieved by a suppression of all but one branch at a ramification. The favoured branch continues its growth more or less in the direction of the main axis (rectascendence) and the peduncles (1 or 2 in number) become somewhat lateralized (Fig. 2 E, F).

Involucre

As a consequence of the peduncle arrangement described above, transitions between ordinary leaves and involucral bracts do not occur in *Euryops*. The involucral bracts are usually uniseriate, i.e. set in one row, and more or less connate at least by their lower margins. Strictly speaking the arrangement is spiral, which is most easily observed in species with little connate phyllaries and especially in young stages. During the course of anthesis the spiral arrangement usually develops towards a more distinctly uniseriate condition, and in species with much connate phyllaries the spiral arrangement may be completely obliterated. Sometimes the involucral bracts are so distinctly overlapping as to be described as biseriate or in vague terms (subbiseriate, subuniseriate) indicating intermediate conditions.

Certain mathematical regularities in the number of phyllaries were observed. In many species the number is almost invariably 5, in others normally 8, and in still others there is a maximum around 13. A few species with a large number of phyllaries seem to have a maximum around or near 21. These figures are immediately recognizable as denominators in the Fibonacci fractions, well-known to students of phyllotaxy. Obviously the predominance of these phyllary numbers is intimately connected with the originally spiral organization of the involucre. It is noteworthy that in *E. abrotanifolius*, which is variable in number of phyllaries (10—22), there is a distinct maximum around 13, and a local race from Caledon Division has a maximum near 21 (cf. NORDENSTAM 1968, p. 281 f.) A somewhat similar variation is found in *E. tenuissimus* (op. cit., Fig. 5, p. 81).

Similar mathematical regularities may also be found in the number

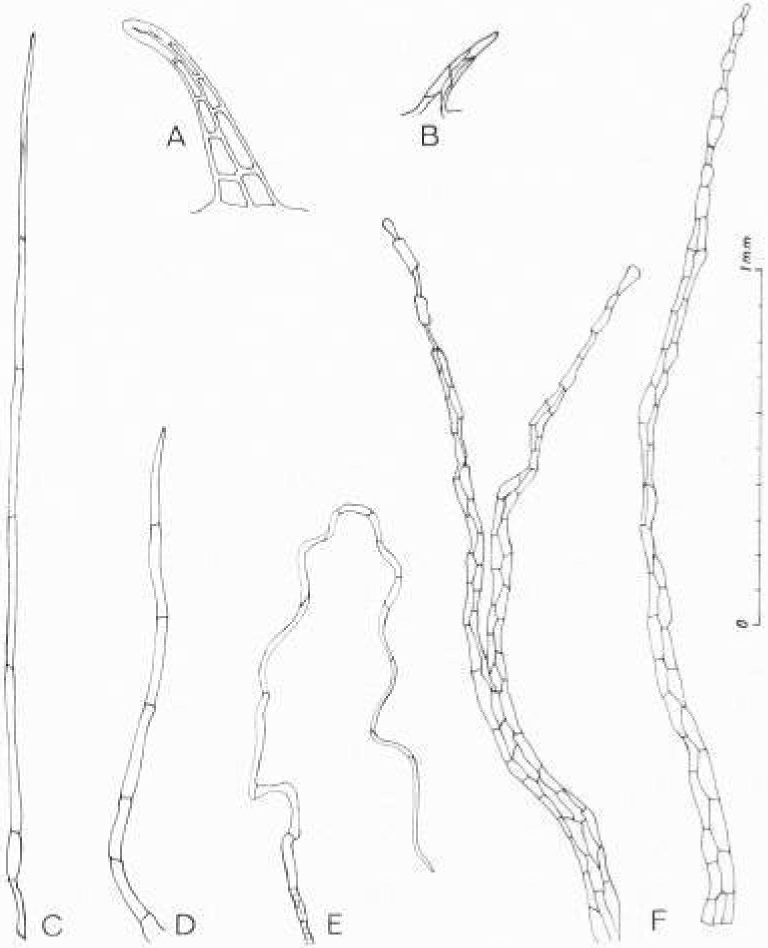

Fig. 3. Leaf hairs in *Euryops*. — A: *E. gilfillanii*, setiform hair from leaf-margin. — B: *E. mirus*, setiform hair. — C: *E. gilfillanii*, trichoid hair from leaf-base. — D: *E. mirus*, trichoid hair. — E: *E. brachypodus*, trichoid hair from leaf-base. Note numerous small basal cells. — F: *E. hebecarpus*, branching and simple multicellular hairs.

of florets in the capitula. Few-flowered capitula often prove to have 5, 8, or 13 disc-florets and 5 or 8 ray-florets, but in many-flowered capitula there seem to be more frequent deviations from the ideal numbers, which may be influenced by limiting factors like space and nutrition supply.

Leaf Hairs

Only few species of *Euryops* are conspicuously pubescent on stems and leaves, the most striking examples being *E. dregeanus* (sect. *Angustifoliae*), and *E. pectinatus, othonnoides* and *tagetoides* (sect. *Euryops*). All these species are densely and appressedly tomentose on the vegetative parts. A laxer and less conspicuous hair-covering is found in several other species (e.g. *E. tenuissimus, rehmannii, hebecarpus, mirus, anthemoides*), especially on the young leaves. In some species the pubescence is restricted to more limited portions of the plants, e.g. leaf-margins (*E. elgonensis*), leaf midvein (*E. thunbergii*), leaf-base (several species), or peduncles (*E. brownei, elgonensis*).

On closer examination very few species turn out to be completely glabrous. Scattered trichomes may occur along the basal leaf-margins, and especially the young leaf-axils are usually provided with some lax and entangled wool.

The most frequent type of leaf trichome is long and slender, flexuous, and composed of a single row of elongated cells with straight or somewhat oblique walls (Fig. 3 C—E). Sometimes numerous smaller basal cells occur (Fig. 3 E). This type, which may be called *trichoid*, is white, due to the thin cell walls and practically empty cells. *Setiform* hairs are likewise multicellular but have more than one row of cells with some contents and thicker walls (Fig. 3 A—B). Large multicellular simple or sometimes branching hairs occur in *E. hebecarpus* (Fig. 3 F).

Some other hair types are illustrated in Fig. 4. The stellate hairs of *E. anthemoides* ssp. *astrotrichus* call for some comments. This trichome type is stellately branched and provided with a basal cell or sometimes sessile (Fig. 4 H, J). It would be surprising to find such a unique hair type only in one single taxon in the genus. A closer examination reveals the existence of similar types in other taxa as well, although the stellate character is usually less obvious. In *E. dregeanus* the trichomes are branching cross-wise in close sequence (Fig. 4 K) and sometimes much-

Fig. 4. Leaf hairs in *Euryops* (continued). — A: *E. tagetoides*, branching stellate trichome with basal cell. — B—D: *E. pectinatus*, branching and simple trichomes with basal cell. — E: *E. othonnoides*, branching multicellular trichome. — F: *E. tenuissimus*, much-branched multicellular trichome. — G: *E. anthemoides* ssp. *anthemoides*, multicellular trichome. — H: *E. anthemoides* ssp. *astrotrichus*, stellate hairs, basal cell visible in the left figure. — I: *E. virgineus*, glands from leaf-margin. — J: *E. anthemoides* ssp. *astrotrichus*, stellate hair in higher magnification, basal cell distinct. — K: *E. dregeanus*, cross-wise branching substellate hairs. — (The lower scale applies to J and K only.)

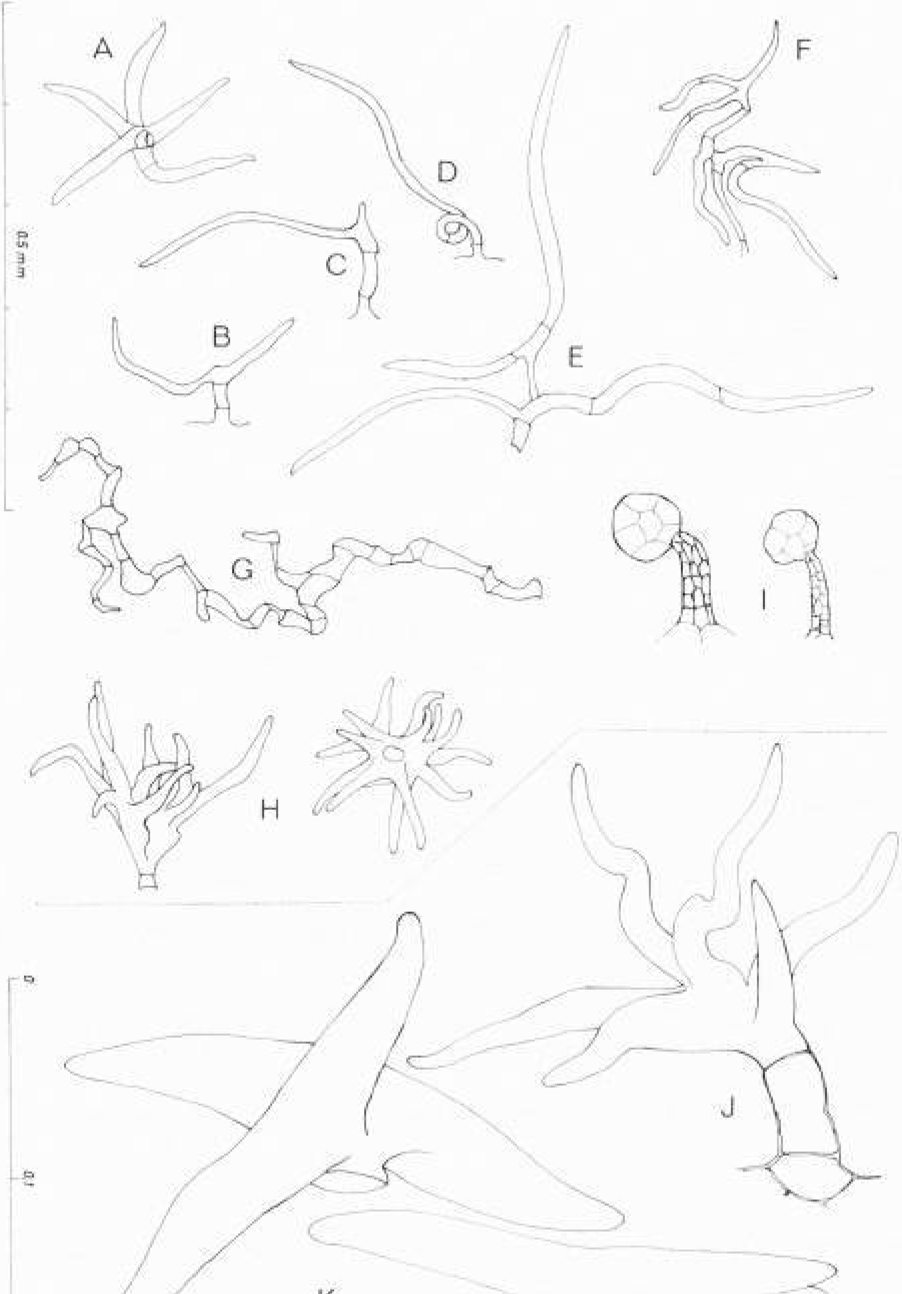

Fig. 4.

branched in a stellate manner. Similar but less regularly branching trichomes are found in *E. tagetoides* (Fig. 4 A). The derivation of these hairs from more simple trichomes is comprehensible on comparison with the types found in *E. pectinatus* (Fig. 4 B—D). The latter have a basal cell and the subsequent cell is simple or forking. From such types may be derived more loosely branching hairs (Fig. 4 E—G) as well as the more compact stellate hairs of *E. anthemoides* ssp. *astrotrichus*.

Scattered glandular hairs occur along the leaf-margins of some species. They are easily overlooked but fairly distinct in, e.g., *E. virgineus* and *algoënsis*. The glands have a multicellular stalk and a globular multicellular head (Fig. 4 I).

Achene Hairs

More than half the number of species of *Euryops* have some indumentum on the achenes. In the majority of these species the achene hairs become strongly mucilaginous when soaked in water, wheras others lack this property. This character was found to be of some use in the taxonomy and called for a closer examination.

Most achene hairs in *Euryops* have a uniform and very special organization. They consist of two parallel cells and one smaller basal cell in a somewhat lateral position (Fig. 5, especially A—B). The two large cells have some contents with the appearance of an amorphous mass with a coiled internal structure. In water the cells burst, usually apically or sometimes in other parts of the cells, and mucilaginous tubes or threads grow out to considerable length, forming a thick slimy cover around the achene (cf. Fig. 5 H—I). Fig. 5 illustrates the variation in the mucilaginous hairs found in the genus. There is considerable variation in length and thickness of the two main cells, and also the basal cell is variable in size, but the uniformity in the fundamental organization is obvious.

Also the non-mucilaginous hairs (Fig. 6) are referable to the same basic type. There is no fundamental difference between the two types of hairs, and some taxa are indeed transitional. E.g., in *E. rehmannii*

Fig. 5. Mucilaginous achene hairs in *Euryops*. — A: *E. marlothii*. — B: *E. virgatus*. — C: *E. transvaalensis* ssp. *setilobus*. — D: *E. pedunculatus*. — E: *E. laxus*. — F: *E. floribundus*. — G: *E. rehmannii*. — H—I: *E. arabicus*, extrusion of mucus of achene hairs soaked in water. — J: *E. tagetoides*. — K: *E. othonnoides*. — L: *E. tenuissimus* ssp. *tenuissimus*. — M: *E. annuus*. — N: *E. rupestris* var. *dasycarpus*. — O: *E. namibensis*. — P: *E. lateriflorus*. — R—U: *E. subcarnosus*. R: ssp. *subcarnosus*. S: ssp. *vulgaris*. T: ssp. *foetidus*. U: ssp. *minor*.

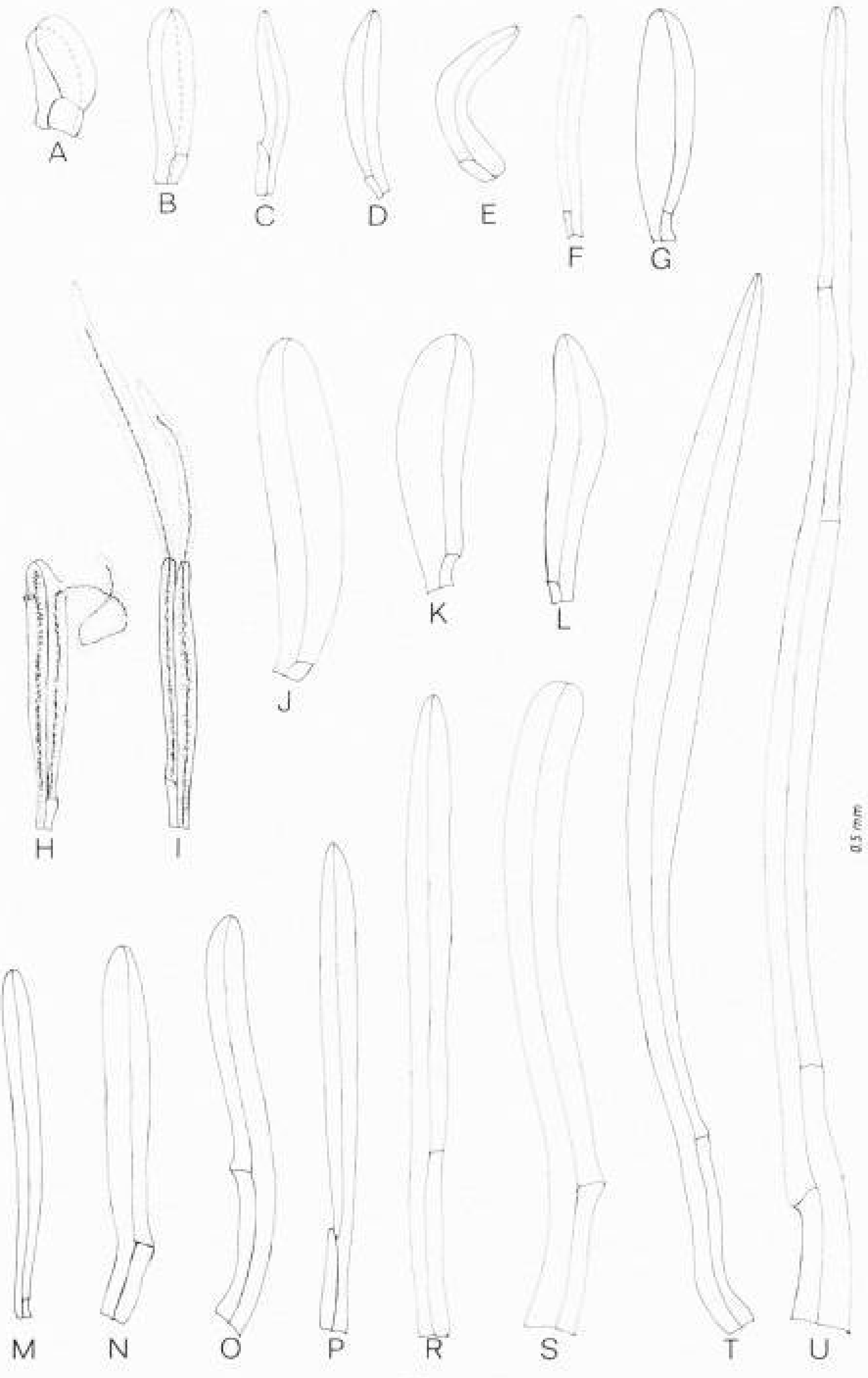

Fig. 5.

the achenes do not become distinctly mucilaginous when soaked (in contrast to *E. tenuissimus*, cf. NORDENSTAM 1968, p. 68), but the mucilaginous character is revealed on examination of individual achene hairs under the microscope. The types found in *E. subcarnosus* are also illuminating. Ssp. *minor* differs from the other subspecies by the less mucilaginous character of the achenes (op. cit., p. 210). Its achene hairs were found to be multicellular (Fig. 5 U) with some mucilaginous properties remaining in the basal cells. This type forms a transition to the multicellular non-mucilaginous hairs found in, e.g., the related species *E. trifidus, multifidus,* and *cuneatus* (Fig. 6 J—L). These species have long and slender multicellular achene hairs, which elongate considerably in the fruiting stage.

Other modifications of the original design include an increase in the number of basal cells (Fig. 6 A, F, G) and a thickening of the cell walls in the almost papilliform hairs of *E. hebecarpus* (Fig. 6 B). It is noteworthy that the latter species is the only representative of sect. *Psilosteum* with achene hairs of this type. The achene papillae of some other species in this section consist of excrescences from the epidermis, either formed by one or several protruding cells (*E. hypnoides, leiocarpus*) or consisting of elongated projections of the outer wall of single epidermis cells (*E. ericifolius*, Fig. 6 C).

The peculiar mucilaginous achene hairs may have a biological function, enabling the achene to utilize a limited amount of water for germination. Several other genera of *Compositae* have achenes with similar qualities, but it remains to investigate if their achene hairs are morphologically similar to those found in *Euryops*. The same hair type has been found in *Senecio*, however, by DRURY & WATSON (1965), but these authors mention nothing of the mucilaginous character.

Pollen Morphology

The pollen grains are of little help in the infrageneric taxonomy of *Euryops*, except for the usefulness of size measurements in connection with polyploidy (cf. NORDENSTAM 1968, under *E. oligoglossus, lateriflorus, subcarnosus* et al.). The pollen grains are morphologically

Fig. 6. Non-mucilaginous achene hairs in *Euryops*. — A: *E. brownei*. Basal cells 2 and 3, resp. — B: *E. hebecarpus*. Note small basal cell and thickened cell walls of main cells. — C: *E. ericifolius*, epidermal papillae. — D: *E. decumbens*. — E: *E. brevipapposus*. — F—G: *E. mirus*. Note variation in number of basal cells. — H: *E. evansii* ssp. *dendroides*. — I: *E. trilobus*. — J: *E. trifidus*. — K: *E. multifidus*, long multicellular hair. — L: *E. cuneatus*, very long multicellular hair.

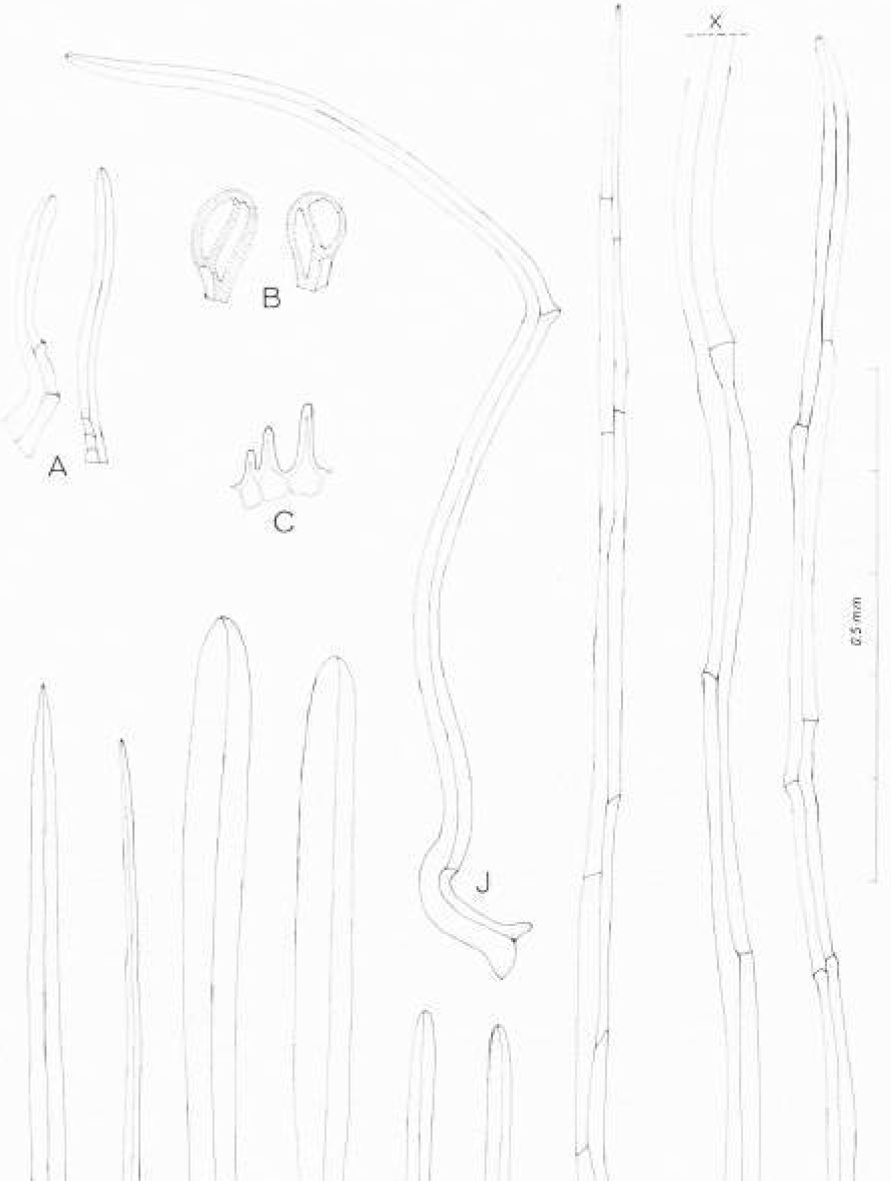

Fig. 6.

comes closest to the 'Senecio type' distinguished by STIX (1960) for species of *Ligularia, Neurolaena, Schistocarpha, Senecio,* and *Werneria.* The 'Euryops type' differs from the 'Senecio type' chiefly by the more pointed spines and by the greater part taken by the tegillum in forma- remarkably uniform throughout the genus. The type found in *Euryops* tion of the spines.

A description of the 'Euryops type' is given below, based on measurements of acetolysed material of selected taxa from all sections. The preparation method is described by ERDTMAN 1952 (pp. 7—9). The pollen slides were prepared at the Palynological Laboratory, Solna, where one set of slides is kept. A duplicate set is preserved in the Botanical Museum, Lund. (The taxa investigated are nos. 1, 3, 12 b, 24, 44, 48 a, 49, 53, 56, 62, 66, 77, 81, 84, 92, 95, and 97, following the taxonomic sequence of NORDENSTAM 1968). The diagnosis has been brought into conformity with those of STIX (1960), for easier comparison with the various pollen types in *Compositae* distinguished by her.

Pollen grains tricolporate, prolate-spheroidal, c. 25—34 µ×18—25 µ incl. sexine, c. 23—32 µ×17—22 µ excl. sexine. Colpi 13—21×2—5 µ, with acute—acuminate ends. Ora lalongate, c. 4—8 µ long at the outer margin, 1.6—4 µ long at the inner margin, 5—12 µ broad, with acute ends. Mesocolpia in equatorial plane with 13—21 spines.

Exine 4.8—8 µ thick incl. spines. Sexine usually separated from the nexine by a narrow cavity (c. 1—1.5 µ thick). Sexine tegillate, with spines, and perhaps sometimes with infrategillar bacula. Tegillum c. 0.8—1.2 µ thick between the spines and 2—2.5 µ thick below the spines, baculate, with a thin homogeneous outer layer and a thin or sometimes thickened homogeneous inner layer. Spines 2.4—4.8 µ high, with a median distance of 4.5—5.6 µ, sharply pointed (acuminate—mucronate or sharply acute), with a small and sometimes hardly observable cavity in the solid tip, basally formed by the protruding baculate tegillum. Nexine c. 1—1.5 µ thick.

The diagnosis does not cover the variation in quantitative characters in the genus, but it may be generally valid in the main morphological features. It is noteworthy that the related genera *Othonna, Gymnodiscus,* and *Steirodiscus* seem to have pollen grains closely similar to those of *Euryops.* All of these have distinctly pointed spines and a more or less well developed tegillum. Apart from these deviations from the 'Senecio type', the tribe (except *Liabinae,* cf. STIX 1960, pp. 70, 98) is remarkably uniform in pollen morphology.

Evolutionary Trends in Euryops

Some trends in the organization of the synflorescence were discussed earlier in this chapter, and it appeared with reasonable probability that an evolution from lateral to pseudo-terminal peduncles has taken place in the genus. It may be tempting to summarize some other trends from a 'primitive' towards a more 'advanced' condition. The following suggestions can be made, borne in mind their highly speculative nature and the numerous pitfalls involved, like cases of parallel or convergent evolution.

Table 1. Evolutionary Trends in Euryops.

	Primitive characters		*Advanced characters*
A	Habit fruticose	a	Caudex subterranean
B	Perennial	b	Annual
C	Shoots long	c	Brachyblasts
D	Leaves narrow	d	Leaves broad
E	Leaves simple	e	Leaves divided
F	Basal peduncular leaves present	f	Basal peduncular leaves 0
G	Peduncles lateral	g	Peduncles pseudo-terminal
H	Peduncles well-developed	h	Peduncles reduced
I	Involucral bracts connate only basally	i	Involucral bracts connate high up
J	Ray-florets present	j	Ray-florets reduced or 0
K	Disc-florets fertile	k	Disc-florets sterile
L	Pappus present	l	Pappus 0
M	Achene hairs mucilaginous	m	Achene hairs non-mucilaginous
N	Achenes pubescent	n	Achenes glabrous
O	Diploidy	o	Polyploidy

Some of these trends may be regarded as reasonably well documented, but others are more open to criticism. Nevertheless, it may be illuminating to analyse the distribution of these characters in the various sections (Table 2).

Table 2. Distribution of Primitive and Advanced Characters in the Sections of Euryops.

Section	Primitive characters															Advanced characters														
	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o
Angustifoliae	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	.	×	×	×	×	.	.	×	×	×	.	×	×	×
Euryops	×	×	×	×	×	.	.	×	×	×	×	×	×	×	×	.	.	.	×	×	×	×	.	×	.	.	.	.	×	.
Chrysops	×	×	×	×	×	.	.	×	×	×	×	×	×	×	×	×	.	.	×	×	×	×	.	×	×	×	×	×	×	.
Brachypus	×	×	×	×	×	.	.	.	.	×	×	×	.	×	×	.	.	×	×	×	×	×	×	×	.	×	.	×	×	.
Psilosteum	×	×	×	×	×	.	.	×	×	×	×	.	.	×	×	.	.	.	×	×	×	×	×	×	.	×	×	×	×	.
Leptorrhiza	.	.	.	×	.	.	×	×	.	×	×	×	×	×	?	.	×	.	.	×	×	.	.	×	.	.	.	.	.	?

From Table 2 it appears that sect. *Angustifoliae* is the only section where all supposedly primitive characters are represented, but also that a considerable number of the advanced features have developed within the section. This is the only section with polyploidy as far as is known.

If the sections represent natural (i.e. monophyletic) groups it follows that several of the characters regarded as advanced have been independently developed within different sections of the genus. There is no evidence against the assumption that, e.g., disc sterility, loss of pappus, high connation of phyllaries, and loss of achene hairs present such cases of parallel evolution in the genus.

The geographical distribution of primitive and advanced characters within a genus or taxon of higher rank has often led to speculations about the origin and subsequent migrations of the taxon. An often quoted example is the tribe *Stapelieae* of *Asclepiadaceae* (cf. Good 1952; 1964, p. 170 ff.). In *Euryops* most of the advanced features are assembled in South Africa, where also the maximum concentration of species is found. The comparatively few East and North African species possess several primitive and few advanced characters and belong to sect. *Angustifoliae* with one notable exception. The Ethiopian species *E. prostratus* is a remarkable northern outpost of sect. *Brachypus*, a section with many advanced features. The interpretation of these and other distributional data will be spared to the phytogeographical treatise. I shall here only conclude with the remark that the history of the genus probably traces back to ages too remote to allow any speculations on its ultimate origin.

III. CYTOLOGY

Chromosome Numbers

Only four chromosome counts of *Euryops* species have been reported by previous authors. These counts are listed in Table 3 below.

Table 3. Previous Chromosome Counts in Euryops.

Species	Chromosome number	Author	Voucher
E. brownei	2n=c. 20—22	Hedberg 1957, p. 246	Hedberg 1550
E. speciosissimus (as *E. athanasiae*)	n=10	Ornduff et al. 1963, p. 132	Raven 13872
E. pectinatus	n=10	,,	Raven 13870
E. chrysanthemoides (as *Gamolepis chrysanthemoides*)	n=10	,,	Raven 13864

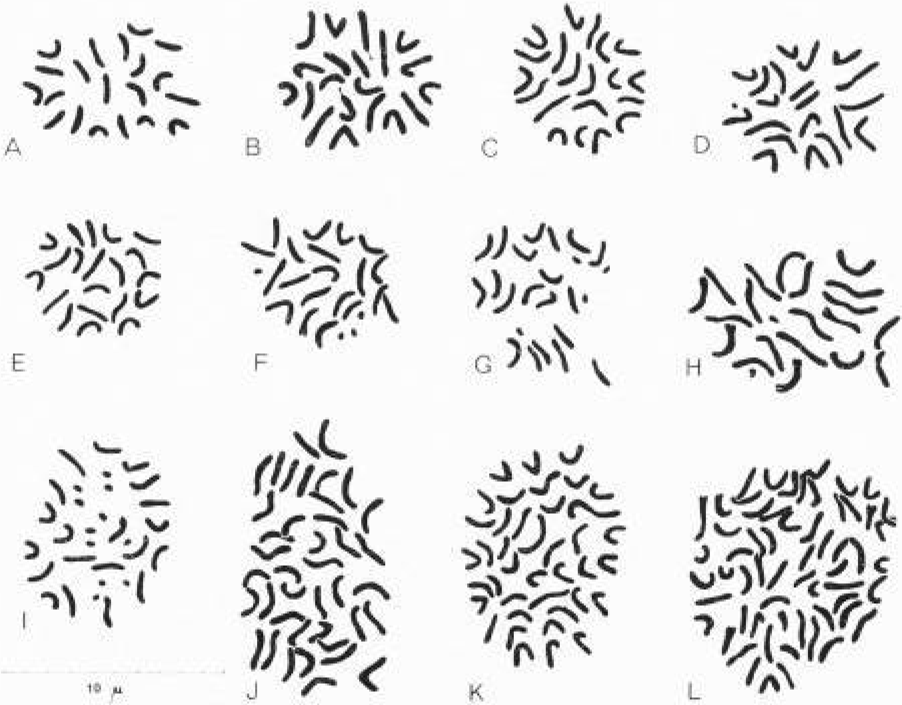

Fig. 7. Somatic metaphase plates of *Euryops* species. — A: *E. pinnatipartitus*, 2n=20 (Dahlgren & Strid 4892-3). — B: *E. chrysanthemoides*, 2n=20 (Nordenstam 2143-3). Note minute satellites. — C—D: *E. decumbens*, 2n=20 (Nordenstam 2110-3). In D an accessory chromosome is visible. Both plates are from the same root. — E: *E. othonnoides*, 2n=20 (Dahlgren & Strid 4717-3). — F: *E. othonnoides*, 2n=20+4 B (Dahlgren & Strid 4717-16). — G: *E. rehmannii*, 2n=20+4 B (Nordenstam 1916-5). — H: *E. spathaceus*, 2n=20+2 B (Nordenstam 3138-1). — I: *E. abrotanifolius*, 2n=20+11 B (Dahlgren & Strid 4073-4). — J: *E. subcarnosus* ssp. *vulgaris*, 2n=40 (Nordenstam 1773-3). — K: *E. glutinosus*, 2n=40 (Nordenstam 1910-5). — L: *E. cuneatus*, 2n=60 (Nordenstam 3534-1).

All voucher specimens have been seen by me. It should be noted that Raven 13870 (in LD) is not a pure *E. pectinatus* but its hybrid with *E. chrysanthemoides* (cf. Nordenstam 1968, pp. 372—374). There is no reason to doubt that the count was made on true *pectinatus*, however. Probably the hybrid arose in the garden among the parents and was later collected and distributed as a voucher specimen.

In the present investigation the somatic chromosome numbers of 248 individuals representing 36 different taxa were determined. The counts were made in sections of root tips from young plants grown from seeds

Table 4. Chromosome Numbers in Euryops.

Taxon	Collection no. (N.=NORDENSTAM D. & S.=DAHLGREN & STRID)	Chromosome number (2n)	No. of individuals studied	Remarks (B=accessory chromosomes)
abrotanifolius	N. s.n., Bains kloof	20	4	—
,,	D. & S. 4343	20	6	—
,,	D. & S. 4755	20	3	—
,,	D. & S. 4073	20	5	1 plant had 4—11 B
annae	N. 1948	20	1	—
,,	N. 1982	20	1	—
brachypodus	D. & S. 4806	20	10	—
brevilobus	N. 3230	20	4	—
candollei	N. 2041	20	1	—
chrysanthemoides	N. 2143	20	6	—
,,	N. 2143 (F_1)	20	5	—
chrysanthemoides ×*euryopoides*	N. 2143×N. 251	20	2	Artificial hybrid, produced in Lund Bot. Garden
cuneatus	N. 3534	60	3	—
decumbens	N. 2110	20	5	In 1 specimen some plates had 1 B
empetrifolius	N. 3207	20	5	—
euryopoides	N. 251	20	1	—
floribundus	N. 1949	20	1	—
galpinii	N. 1985	20	5	—
glutinosus	N. 1910	40	5	—
imbricatus	N. 3588	20	5	—
indecorus	N. 3347	20	6	—
lateriflorus	N. 1123	20	2	—
,,	N. 3022	40	5	—
latifolius	N. 266	20	1	—
linearis	D. & S. 4915	20	6	1 plant had an occasional cell with $2n=40$
marlothii	N. 3596	20	5	1 plant had an occasional cell with $2n=40$
,,	N. 3527	20	5	—
,,	N. 3635	20	2	1 plant had 2 B
multifidus	N. 3504	20	3	—
oligoglossus ssp. *oligoglossus*	N. 1941	20	5	—
ssp. *racemosus*	N. 3600	40	4	—
othonnoides	D. & S. 4717	20	18	1 individual had 2 or 4 B
		(30)	1	An occasional triploid
pectinatus ssp. *pectinatus*	D. & S. 4757	20	1	—
,, ,,	D. & S. s.n. Table Mtn.	20	6	—

Taxon	Collection no. (N. = NORDENSTAM D. & S. = DAHLGREN & STRID)	Chromosome number (2n)	No. of individuals studied	Remarks (B = accessory chromosomes)
pinnatipartitus	D. & S. 4883	20	1	—
„	D. & S. 4892	20	4	—
rehmannii	N. 3213	c. 20	1	—
„	N. 1916	20	4	1 plant without B 2 plants with 2—4 B 1 plant with 2—3 B
„	N. 3455	20	1	—
„	N. 3475	20	3	—
rupestris var. *dasycarpus*	N. 3325	20	4	—
spathaceus	N. 2875	c. 20	1	—
„	N. 3138	20	2	1 plant with 1 B, 1 plant with 2 B
speciosissimus	N. s.n. Piketberg, Versveld Pass	20	13	—
„	D. & S. 4447	20	10	—
„	D. & S. 4716	20	6	—
„	D. & S. 4724	20	6	—
subcarnosus ssp. *vulgaris*	N. 3653	20	1	—
„ „	N. 1773	40	5	—
sulcatus	N. 3518	20	5	—
tenuissimus ssp. *tenuissimus*	N. 1863	20	1	—
„ „	N. 1889	20	5	—
„ „	N. 3419	20	3	—
ssp. *trifurcatus*	N. 3310	20	5	1 plant with 2 B
trifidus	N. 3528	20	5	—
„	N. 3592	20	6	—
virgineus	D. & S. s.n. Kirstenbosch	20	4	—
wageneri	D. & S. 4725	20	4	—

in greenhouses in the Botanical Garden, Lund. The Svalöv modification of the Navashin fixative was used. In several cases the plants were kept overnight in a refrigerator (+2—4°C) before fixation for better contraction of the chromosomes. After embedding in paraffin the preparations were microtome-cut (10—12 μ) and stained in crystal violet, sometimes with an addition of aniline.

The results are presented in Table 4. The chromosome numbers were included without particulars in the taxonomic chapter in NORDENSTAM 1968. The reader is referred to the same work for original localities of the cultivated material and taxonomic discussions. Voucher specimens are preserved in the Botanical Museum, Lund (LD).

The basic numer in *Euryops* is x=10, and most species investigated are diploid. The chromosomes vary between 1 and 3 μ in length. The small size and the methods employed did not permit further interpretations of chromosome morphology. Satellites and constrictions were observable only in occasional good preparations. Accessory chromosomes were found in a number of species (see further below).

Polyploidy

Species of all sections except sect. *Leptorrhiza* were cytologically investigated, but only in sect. *Angustifoliae* polyploidy was found. Tetraploids (2n=40) occurred in four species. Of these, *E. glutinosus* is a local endemic of the Klein Zwartbergen mountain range. It is a distinct and little variable species and very likely constantly tetraploid. The other three species, viz. *E. lateriflorus*, *oligoglossus*, and *subcarnosus*, are widespread and highly variable karroo species comprising diploid as well as tetraploid cytotypes. These are distinguishable on quantitative morphological characters, e.g. size of pollen grains, but when a large material was examined the discontinuities observed were not distinct enough to permit a taxonomic separation of the cytotypes, except in *oligoglossus* (cf. NORDENSTAM 1968). Further investigations are needed to establish the distribution and morphological variation of the cytotypes in *E. lateriflorus* and *E. subcarnosus*. The latter species belongs to a taxonomically intricate group of taxa. The variation in pollen grain size in this group (cf. Fig. 26 a in NORDENSTAM 1968) indicates that polyploidy may have played an important role in the differentiation within the complex. There are some indications that the polyploids may be more widely distributed in the most arid parts of the distribution ranges. If so, parallels may be drawn with the often discussed results obtained by HAGERUP (1932) from a cytological study of the desert flora of Timbuktu, where the polyploids (e.g. in *Eragrostis*) favoured the most arid localities. DE WINTER's (1965, p. 306 f.) study of *Stipagrostis* may also be mentioned. This genus consists of mainly deserticolous species (e.g. in South West Africa), most of which are tetraploids.

The single hexaploid found (2n=60) also belongs to the *E. subcarnosus* complex but is distinguished as a separate species, *E. cuneatus*.

Accessory Chromosomes

Small stainable bodies, probably accessory chromosomes were found in seven species. With the cytological methods employed it was not possible to deduce if they are heterochromatic or not, and their behaviour at meiosis is still unknown. The accessory chromosomes were observed in varying numbers (1—11) in occasional specimens. They are not constant in number within the local populations or even in individual specimens. They seem to have no taxonomic (evolutionary) significance and are probably easily eliminated in some specimens and, up to point, enriched in others. No harmful effects on the vitality of the plants were observed. When occurring in larger numbers they may prove to have some effect on the pollen fertility, but too few of the plants have flowered in cultivation to allow any conclusions on this matter.

Comparison with Related Genera

The chromosome numbers obtained in *Euryops* may seem to confirm the assumption by ORNDUFF et al. (1963, 1967), that x = 10 is the original basic number in the *Senecioneae*. Other authors (e.g. AFZELIUS 1949, DARLINGTON & WYLIE 1955, TURNER & LEWIS 1965) have assumed an original number of x = 5, which is supported by the occurrence of the diploid number 2n = 10 in *Emilia* and occasional species of *Senecio*. Whatever the original basic number of the tribe may be, x = 10 is by far the most common basic number in the genera hitherto investigated. Some genera have deviating numbers, however, especially in the subtribe *Liabinae*, which may be incorrectly referred to the tribe. An aneuploid series of high numbers is known in the genus *Werneria*. Some genera with x = 9 probably ought to be transferred to other tribes (*Crocidium*, *Mallotopus*, cf. ORNDUFF et al. 1967), but a truly senecionid genus with x = 9 is *Gymnodiscus* (NORDENSTAM 1967 b). This small genus of annual species is probably a derivative of *Othonna*, a large genus of perennials with x = 10 (NORDENSTAM 1967 a). *Othonna* is karyologically similar to *Euryops* in several respects: (i) most species are diploid but tetraploids and hexaploids are known, (ii) infraspecific polyploidy occurs, and (iii) accessory chromosomes occur in low numbers in occasional specimens.

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Studies in the Aegean Flora XIII
Tordylium L. (Umbelliferae)

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ABSTRACT

Tordylium officinale L., *T. pestalozzae* BOISS., *T. aegaeum* RUN. sp. nov., and *T. hirtocarpum* CAND. have previously been much confused in spite of conspicuous differences in number and length of umbel rays, shape of bracts and bractlets, size of radiating petals, hair types and distribution of vittae in the mericarps. The variation of these species as well as *T. apulum* L. is discussed. Pollen grains of the Aegean species have been investigated. All species can be distinguished on details in pollen morphology, such as the degree of thickenings of the exine in the equatorial zone, and the shape of the apertures. Chromosome numbers, and to a certain extent chromosome morphology, have been investigated in the following species: *T. apulum* ($2n=20$), *T. officinale* ($2n=18$), *T. pestalozzae* ($2n=20$), *T. aegaeum* ($2n=20$), *T. hirtocarpum* ($2n=8$), and *T. maximum* L. ($2n=20$). The only species previously investigated cytologically is *T. maximum* for which the number $2n=22$ has been reported. Maps of the total distribution are given for *T. pestalozzae*, *T. aegaeum*, and *T. hirtocarpum*, as well as a map showing the Aegean distribution for *T. apulum*. A key to all species recorded in the Aegean (i.e., all European species) has been prepared. Descriptions are given of *T. apulum*, *T. officinale*, *T. pestalozzae*, *T. aegaeum*, and *T. hirtocarpum*.

MATERIAL

The study is based on the following material: (1) ca. 130 herbarium collections from the Aegean by the author, SVEN SNOGERUP, BERTIL NORDENSTAM, ARNE STRID, ROLAND VON BOTHMER, JIMMY PERSSON, and BENGT BENTZER in 1957—1967, (2) ca. 60 herbarium collections in the Botanical Museum (LD), Lund, and (3) 27 samples (each of 3—6 individuals) cultivated in the greenhouses of the Botanical Garden, Lund.

MORPHOLOGY

Tordylium apulum

Tordylium apulum is an isolated member of the genus, usually referred to a section of its own [*Condylocarpus* (HOFFM.) DC.]. It is characterized, e.g., by single, radiating, deeply and ± equally lobed petals in the outer flowers of peripheral umbellulae and by a high number (7—13) of vittae on the dorsal face of the mericarps.

The material from the southern and central Aegean (ca. 75 collections) has been compared with herbarium material from the mainland of the Balcan Peninsula, Italy, and North Africa (ca. 40 collections). The following observations are worth mentioning.

HABIT. The Aegean material is usually only 10—20 cm high. Material from the Aegean cultivated in greenhouses is considerably taller, but not as tall and stout as herbarium material from other localities, which is usually 40—60 cm high.

LEAVES. The number of leaflet pairs in basal and lower cauline leaves varies between 1 and 4 (M 2.5) in the Aegean material and in other collections between 2 and 5 (M 3.5). The parents from the field of three Aegean samples had 2, 2, and 3 pairs, respectively, while the progeny in the greenhouses had 3, 3—4, and 4.

UMBELS. The number of rays in well developed umbels varies in Aegean material between 2 and 7 (M 3.5) and in other collections between 3 and 10 (M 5.9). The parents from the field of three Aegean samples had 2, 2, and 4 rays, respectively, while the progeny in the greenhouses had 4—6, 6 and 6.

FLOWERS. The length of radiating petals varies between 2.5 and 6.5 mm (M 4.4) in Aegean material, while other collections varied between 4.5 and 9.5 mm (M 6.8). Cultivated Aegean samples had 5.0—7.0 mm long, radiating petals.

MERICARPS. The size of the mericarps varies very much within, as well as between, different umbels. The size of the largest mericarps of each collection has been measured. In Aegean material the length varies between 5 and 10 mm (M 7.6) and in other collections between 6 and 10 mm (M 8.9). The parents from the field of three Aegean samples had 6, 8, and 8 mm long mericarps, respectively, while the progeny had 8, 8, and 10 mm long ones. Extremely small mericarps (ca. 5 mm long) have been found in a few Aegean collections from very small islands (Kikladhes: Gaidaronisi, Anidros).

The number of vittae on the dorsal face varies between 7 and 13 (9 and 11 predominate, M 9.6). No distinct differences were found in comparisons between Aegean material and other collections.

The dorsal face of the mericarps has ± numerous hairs (cf. Fig. 2 I). In the Aegean material these hairs are strictly vesicular. However, in a few collections (Kikladhes: Naxos, Makares, and Anidros) the vesiculum is born on a long, tubular process. The collections from areas outside the Aegean always have such tubular hairs with a vesicular apex. Rarely also strictly tubular hairs have been observed (e.g., from Attica).

DISCUSSION. Deviations in the material from the southern and central Aegean compared to other collections investigated can be summarized as follows: The individuals are smaller and more slender, have smaller leaves with fewer pairs of leaflets, fewer inflorescences, umbels with fewer rays, and smaller, radiating petals. In all these characters there is, however, great variation. Aegean material cultivated in greenhouses under rather optimal conditions is larger in all mentioned characters, but in most of them not comparable to herbarium material from the mainland of the Balcan Peninsula and Italy.

The data presented show that individuals from the Aegean have considerably lower production of organic matter than those from other areas. This may be explained as a result of selection of genotypes, which respond on the actual climate (usually no rainfall in May—August) by producing rapidly growing, "dwarf" individuals.

The Tordylium officinale Complex

The *Tordylium officinale* complex is represented by four taxa in the Aegean, viz. *T. officinale* L., *T. pestalozzae* BOISS., *T. aegaeum* RUN., and *T. hirtocarpum* CAND. The morphological investigation below is based on ca. 70 herbarium collections and 21 cultivated samples.

HABIT. The size of the plants is very variable depending on the ecological conditions. All species produce dwarf individuals under arid conditions. When cultivated under rather humid conditions in greenhouses *T. officinale*, *T. pestalozzae*, and *T. aegaeum* are normally 40—80 cm high and very similar in habit. *T. hirtocarpum* is considerably smaller and more slender.

LEAVES. Simple as well as pinnate basal and lower cauline leaves occur in all species. In cultivation the individuals of all species have 1—4 pairs of leaflets and a large terminal leaflet. The leaflets are sessile or shortly petiolate. In the field small individuals usually have simple leaves, while well developed plants have pinnate ones.

The terminal leaflet and simple leaves are ovate or rounded, crenate, and often basally ± lobed. Lateral leaflets are rounded to shortly ovate and crenate. Upper cauline leaves are normally simple, lanceolate, dentate, and often basally lobed.

All species are softly hairy at least on part of the lamina, but especially on veins and petioles. *T. hirtocarpum* has only short hairs (0.15—0.30 mm) on the petioles, while *T. officinale*, *T. pestalozzae*, and *T. aegaeum* also have ± numerous, long ones (0.6—1.2 mm).

The size, but also the shape of the leaves, is apparently highly modifiable in all four species. In comparative cultivation the leaves of *T. officinale*, *T. pestalozzae*, and *T. aegaeum* are indistinguishable. *T. hirtocarpum* has distinctly smaller leaves and leaflets.

UMBELS. The number of rays varies considerably. In well developed inflorescences *T. officinale* has 8—14 rays, *T. pestalozzae* 5—10, *T. aegaeum* 5—12, and *T. hirtocarpum* 2—3 (exceptionally 4—5). In poorly developed individuals and in accessory inflorescences the number may be smaller.

The rays of the marginal umbellulae are much longer than the central ones in *T. officinale* and *T. aegaeum*, while they are equal or subequal in length in *T. pestalozzae* and *T. hirtocarpum* (Fig. 2 L—O). In *T. officinale* the marginal rays are 4—8 times as long as ripe mericarps, in *T. pestalozzae* 3—5, in *T. aegaeum* 1.5—3, and in *T. hirtocarpum* 1—1.5.

The inflorescence is flat-topped in *T. officinale*, *T. aegaeum*, and *T. hirtocarpum* during anthesis, while it is ± hemispherical in *T. pestalozzae*. In fruit stage the marginal rays are ascending in *T. officinale*, *T. pestalozzae*, and *T. aegaeum*, while they are ± spreading or erecto-patent and straight in *T. hirtocarpum* (Fig. 2 L—O).

The rays of all species have stiff, spreading or erecto-patent hairs. The size of the hairs is rather variable, sometimes also within the same ray. In *T. officinale* they are slender, slightly ascending and 0.3—0.7 (—1.0) mm long, in *T. pestalozzae* also rather slender and 0.1—0.3 mm, in *T. aegaeum* stout, usually basally thickened and 0.15—0.5 mm, and in *T. hirtocarpum* almost conical and 0.1—0.2 mm.

BRACTS AND BRACTLETS. The number of bracts is usually the same as the number of rays. The bracts are deflexed already in anthesis in *T. officinale*, *T. pestalozzae*, and *T. aegaeum*, while they are constantly spreading in *T. hirtocarpum*. In *T. officinale* they are subulate, 10—20 mm long and 0.3—0.6 mm broad, in *T. aegaeum* subulate or narrowly lanceolate and cuspidate, 8—15 mm long and 0.5—1 mm broad, in *T. pestalozzae* broadly lanceolate and cuspidate (sometimes narrowly triangular), 8—16 mm long and 2—3 mm broad, and in *T. hirtocarpum* broadly lanceolate and cuspidate, 3—7 mm long and 1—1.5 mm broad. The bracts have a single vein, though occasionally 3-veined, very broad bracts may occur. All species have a white margin on the bracts. In *T. officinale* and *T. aegaeum* it is inconspicuous, while it is broad and distinct in *T. pestalozzae* and *T. hirtocarpum*. The margin of the bracts is ciliate of erecto-patent to patent hairs. In *T. officinale* the hairs are stiff and slender, 0.4—0.7 mm long, in *T. pestalozzae* weak and 0.2—0.5 mm, in *T. aegaeum* stout and 0.15—0.5 mm, and in *T. hirtocarpum* weak, almost conical and 0.1—0.2 mm. The abaxial face of the bracts are evenly puberulous in *T. hirtocarpum* and *T. pestalozzae*, while hairs are mostly restricted to the vein in *T. officinale* and *T. aegaeum*.

The number of bractlets in an umbellula varies between 3 and 5 in all species. If 5 bractlets are present, two are normally considerably smaller. There are conspicuous differences in the shape of the bractlets in the species (Fig. 2 E—H). In *T. officinale* the bractlets are slender, subulate and 10—15 mm long, in *T. aegaeum* stiff, stout, subulate and 8—15 mm long, in *T. pestalozzae* weak, lanceolate to broadly lanceolate and cuspidate, 5—12 mm long and 1—3 mm broad, in *T. hirtocarpum* broadly lanceolate and cuspidate, and 5—7 mm long and 1.5—2 mm broad. The bractlets of *T. pestalozzae* and *T. hirtocarpum* have conspicuous white margins. In pubescence the bractlets coincide with the bracts.

The differences in shape and pubescence of bracts and bractlets described above on herbarium material are maintained in cultivated material.

FLOWERS. The petals are often ± yellowish or rarely reddish in bud. During anthesis they are, however, purely white. Dried material usually turns ± yellowish, which is especially conspicuous in *T. officinale*.

The two outer petals of marginal flowers in peripheral umbellulae are much larger than the inner ones. They are divided into one large and one very small lobe. Some differences in shape and size of the large lobes have been observed. Thus, *T. officinale* has broadly obovate to broadly elliptical, radiating petals, 6—10 mm long and 4—7 mm broad, *T. pestalozzae* also has obovate to broadly elliptical ones, ca. 5 mm long and 3 mm broad. In *T. aegaeum* the main material (from the Naxos area, the east Aegean islands, and western Anatolia) has obovate to narrowly obovate petals, 5—8 mm long and 2.5—3 mm broad. The material from the Astipalea area and one collection from Naxos deviate in having broadly elliptic, radiating petals, 3.5—5 mm long and 2.5—3 mm broad. In this material the petal shape and size much remind of *T. pestalozzae*. *T. hirtocarpum* has the smallest radiating petals, 1—2

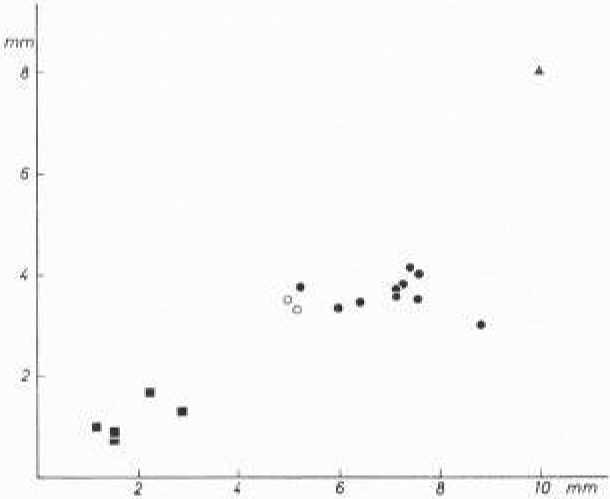

Fig. 1. Length (horizontal axis) and breadth (vertical axis) of radiating petals in cultivated material of *Tordylium hirtocarpum* (squares), *T. pestalozzae* (rings), *T. aegaeum* (dots), and *T. officinale* (triangle).

mm long and 0.8—1.4 mm broad. In poorly developed umbels of this species the radiating petals are scarcely distinguishable from normal ones.

The differences discussed above are based on investigations of herbarium material. In material cultivated in greenhouses the petals of all species are usually somewhat larger, but the differences between the species are maintained (Fig. 1).

MERICARPS. The mericarps have a thickened, moniliform-crenate margin in all four species. The dorsal face has three, inconspicuous ridges and the commissural face has one central ridge. The outline of the mericarps is broadly elliptical to ovate, in *T. officinale* also often roundedly triangular (Fig. 2 A—D). In *T. officinale* the mericarps are 3—4 mm long, in *T. pestalozzae* 6—7.5 mm, in *T. aegaeum* 5—8 mm,

Fig. 2. A—D. Dorsal face (above) and commisural face (below) of mericarps. The vittae are indicated as black structures. A: *Tordylium officinale*, B: *T. hirtocarpum*, C: *T. aegaeum*, D: *T. pestalozzae*. — E—H. Bractlets (the vein is indicated as a black structure). E: *T. officinale*, F: *T. aegaeum*, G: *T. pestalozzae*, H: *T. hirtocarpum*. — I—K. Hair types on the dorsal face of the mericarps. I: *T. apulum*, J: *T. aegaeum*, *T. pestalozzae*, and *T. officinale*, K: *T. hirtocarpum*. — L—O. Schematic drawings of umbels during anthesis (above) and in fruit stage (below). L: *T. officinale*, M: *T. aegaeum*, N: *T. pestalozzae*, and O: *T. hirtocarpum*.

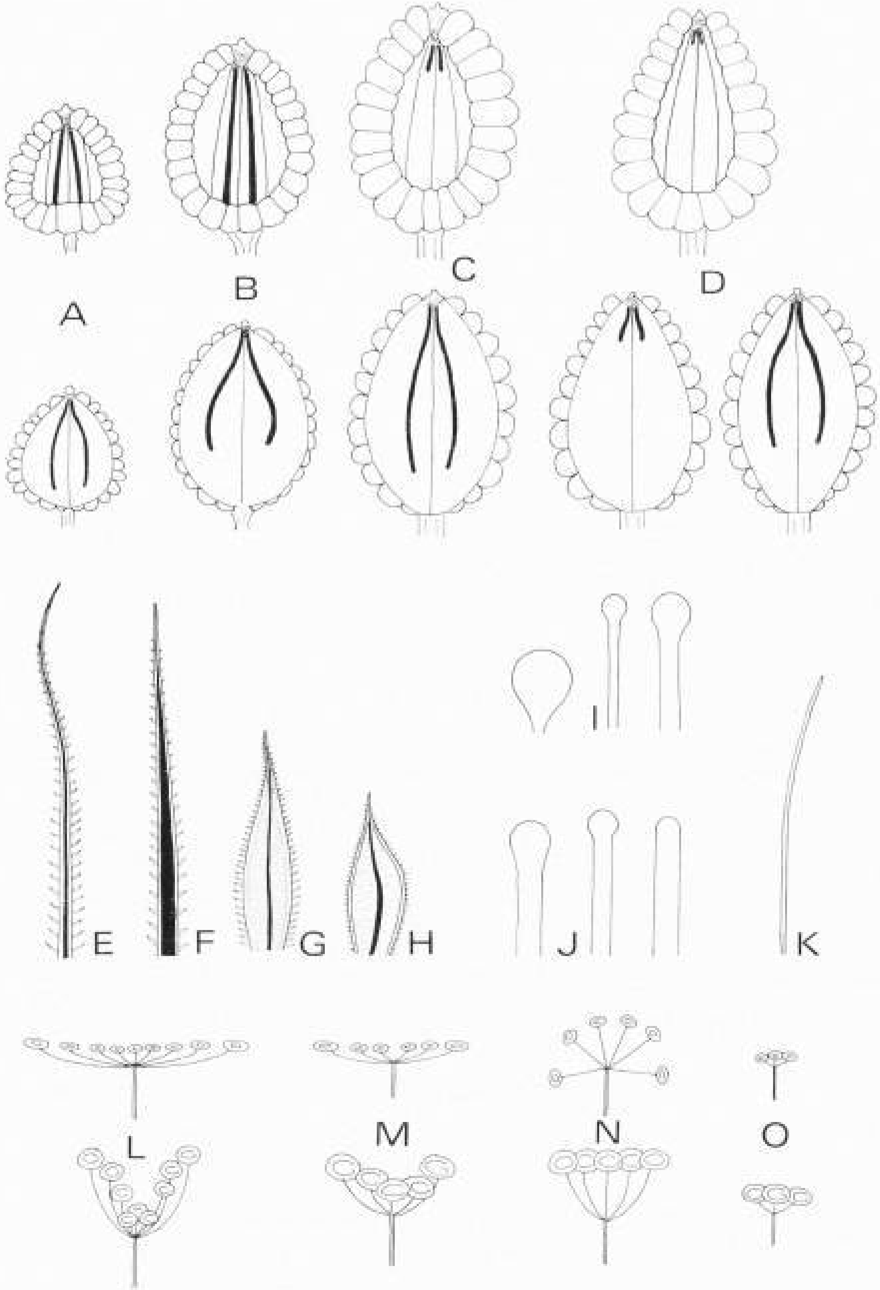

Fig. 2.

and in *T. hirtocarpum* 5—6 mm. Material of *T. aegaeum* from Naxos and adjacent islands usually has 7—8 mm long mericarps, while material from the Astipalea area usually has only 5—6 mm long mericarps. The material from the east Aegean islands is intermediate in this respect. Material cultivated in greenhouses usually has somewhat larger mericarps than the herbarium material discussed above.

All four species have two lateral vittae, concealed by the thickened margin. *T. officinale* and *T. hirtocarpum* have two ± straight, prominent vittae reaching all over the dorsal face (Fig. 2 A—B). *T. aegaeum* and *T. pestalozzae* have no dorsal vittae or very short ones, in length up to 1/4 of the mericarp (Fig. 2 C—D). On the commissural face *T. officinale, T. aegaeum,* and *T. hirtocarpum* have two vittae, which do not reach the base of the mericarp (Fig. 2 A—C). In *T. pestalozzae* there is considerable variation. The commisural vittae may be very short and indistinct or they may be as long as in the other species (Fig. 2 D).

On the dorsal face of the mericarps all species have thin-walled hairs, which often have collapsed in dried material. In *T. officinale, T. pestalozzae,* and *T. aegaeum* they are erect, tubular, usually inflated at the apex and up to 0.5 mm long (Fig. 2 J). In *T. hirtocarpum* they are extremely thin, with a ± acute apex, slightly curved and directed in various angles (Fig. 2 K). In dried material they are curled, forming a villous pubescence.

POLLEN MORPHOLOGY

Pollen grains have been investigated in herbarium material as well as in living material cultivated in the greenhouses at the Botanical Garden, Lund. When analysed they have been kept in a medium of glycerine and gelatine.

The size of the pollen grains is similar in *Tordylium apulum, T. officinale, T. pestalozzae,* and *T. hirtocarpum,* while it is slightly larger in *T. aegaeum* (Fig. 3 A—D). The absolute size of pollen grains taken from herbarium material (the mean of measurements of 20 pollen

Fig. 3. Length (horizontal axis) and breadth (vertical axis) of pollen grains. Each symbol represents the mean of measurements of 20 pollen grains. — A: Herbarium material of *T. hirtocarpum* (triangles), *T. pestalozzae* (ring), and *T. aegaeum* (dots). — B: Cultivated material (fresh pollen grains) of *T. hirtocarpum* (triangles), *T. pestalozzae* (rings), and *T. aegaeum* (dots). — C: *T. officinale;* fresh pollen grains (ring) and pollen grains from herbarium material (dots). — D: *T. apulum*; fresh pollen grains (rings) and pollen grains from herbarium material (dots).

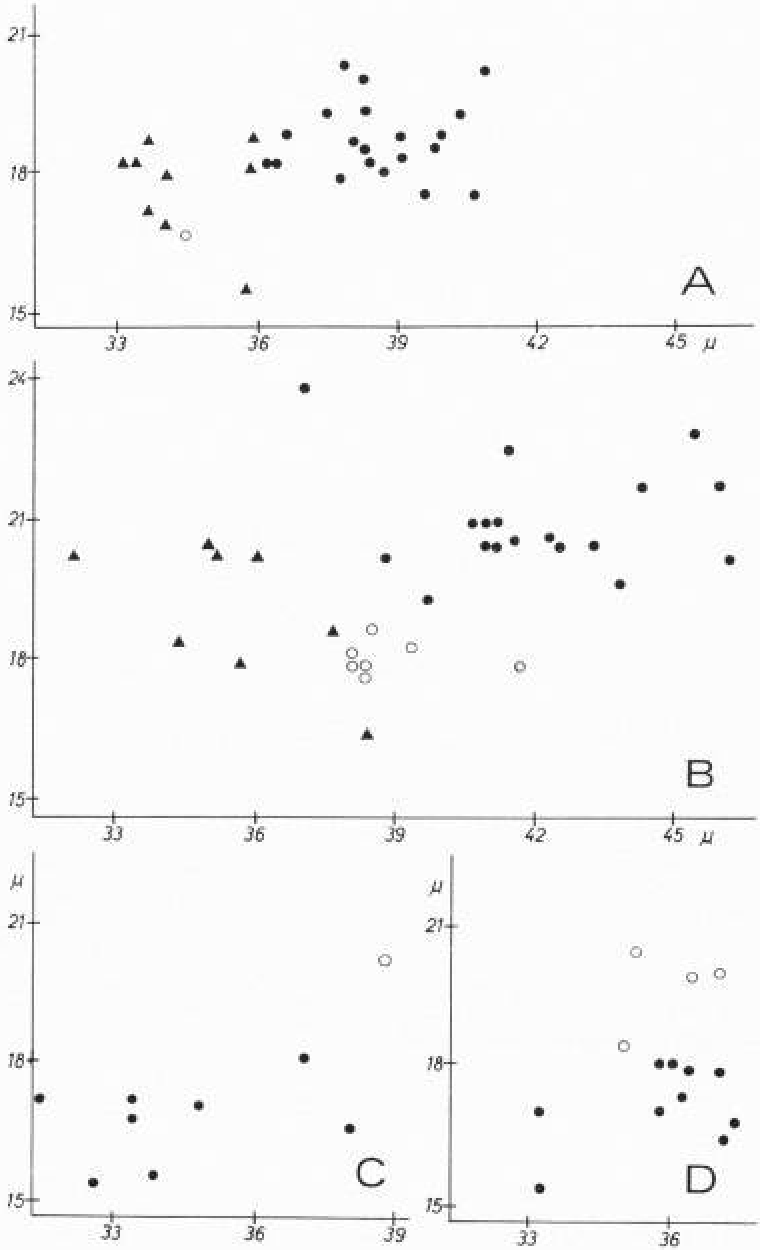
A
21
18
15
33
36
39
42
45
μ
B
24
21
18
15
33
36
39
42
45
μ
C
μ
21
18
15
33
36
39
D
μ
21
18
15
33
36

Fig. 3.

grains from each individual) is 33—38×15—18 μ in *T. apulum*, 31—38×15—20 μ in *T. officinale*, ca. 35×17 μ in *T. pestalozzae*, 33—36×15—19 μ in *T. hirtocarpum*, and 36—41×17—20 μ in *T. aegaeum*. Fresh pollen grains taken from cultivated material are usually considerably larger (Fig. 3 B—D).

The pollen grains are 3-colporate, isopolar to slightly subisopolar, in polar view roundedly triangular, in lateral view broadly oblong, sometimes with a slight equatorial constriction.

The sexine is tectate and thick. The nexine is thin and inconspicuous. The sexine but also the nexine are distinctly thickened in the equatorial zone (Fig. 4 A—E). The sexine thickenings are very prominent in *T. apulum* and *T. aegaeum*, while *T. hirtocarpum* has relatively slight thickenings.

There are considerable differences between the species in the shape of the apertures (Fig. 4 A—E). Thus, in *T. apulum* exoapertures are lanceolate, while they have a rounded or roundedly square-formed central part in *T. aegaeum*, *T. hirtocarpum*, and *T. officinale*. In *T. pestalozzae* the exoaperture may be similar to the last mentioned species having a prominent, rounded central part. In other collections it may be just a rounded structure. The aperture may in this case be described as a pore. Similar conditions have been reported by CERCEAU-LARRIVAL (1962) for *Tordylium syriacum* L. The occurrence of pore-like apertures does not seem to have been reported for other genera in *Umbelliferae*. The endoapertures are ± rounded in *T. pestalozzae*, while they are broadly and transversely elliptical in *T. hirtocarpum*, *T. aegaeum*, and *T. officinale*. In *T. apulum* they are narrowly and transversely elliptical to oblong with a distinctly double wall structure.

All 5 Aegean species investigated seem to be recognizable on features of the pollen grains, like the equatorial exine thickenings and the shape of the apertures.

CYTOLOGY

Chromosome studies have been performed in root-tip sections of material cultivated in the greenhouses at the Botanical Garden, Lund.

Fig. 4. A—E. Pollen grains in lateral and polar view. A: *Tordylium apulum*, B: *T. hirtocarpum*, C: *T. officinale*, D: *T. aegaeum*, and E: *T. pestalozzae*. — F—K. Metaphase plates. F: *T. hirtocarpum* (2n=8), G: *T. officinale* (2n=18), H: *T. pestalozzae* (2n=20), I: *T. aegaeum* (2n=20), J: *T. apulum* (2n=20), and K: *T. maximum* (2n=20).

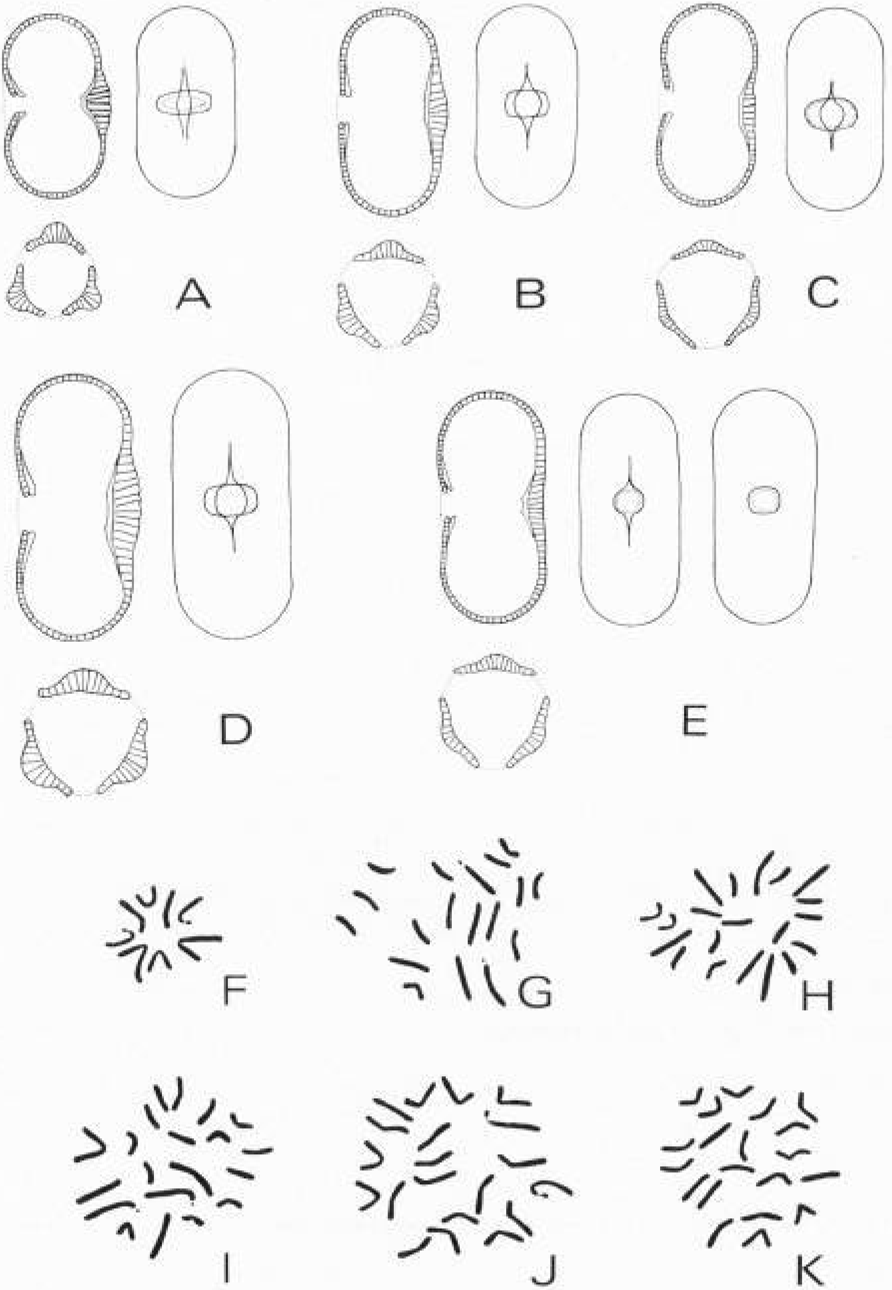

Fig. 4.

The material was fixed in the Svalöf modification of Navashin-Karpeschenko and stained in crystal violet. 3—6 individuals of each collection have been studied. For details concerning material the reader is referred to the Appendix (cf. also Figs. 5—8).

The following chromosome numbers have been found (Fig. 4 F—J):

Tordylium apulum 2n=20 (5 collections studied)
T. pestalozzae 2n=20 (3 collections studied)
T. aegaeum 2n=20 (12 collections studied)
T. officinale 2n=18 (1 collection studied)
T. hirtocarpum 2n=8 (6 collections studied)

As far as I know, none of these species have been cytologically investigated previously.

Besides, one collection of *T. maximum* L. from France has been investigated. The somatic chromosome number was 2n=20 (Fig. 4 K), which does not coincide with the single previous record, 2n=22 by TAMAMSCHJAN (1933).

The occurrence of 2n=20 in so widely different species as *T. syriacum* L., *T. cordatum* (L. f.) POIR. (GARDÉ & MALHEIRO-GARDÉ 1954), *T. maximum*, *T. apulum*, *T. pestalozzae*, and *T. aegaeum* gives the impression, that the basic number in the genus is x=10.

Aneuploids are common in many genera of *Umbelliferae*. Therefore 2n=18 found in *T. officinale* is in no way remarkable. The number 2n=8 in *T. hirtocarpum* seems more difficult to explain. The number is the lowest ever recorded in the family. A possible explanation is the occurrence of an original basic number x=5 in *Tordylium*. Then all examined species, except *T. hirtocarpum*, would be tetraploids. In this species an original chromosome number 2n=10 may have been reduced to 8 by reciprocal translocations, resulting in a very large chromosome and a small, inert one (which has been eliminated). Such an explanation is to some extent supported by the occurrence of one pair of very large chromosomes in *T. hirtocarpum* (Fig. 4 F). If this interpretation is correct, *Tordylium* is one of the few genera in *Umbelliferae*, in which polyploidy has played an important role during the evolution.

The chromosomes are 2—4 μ long. Detailed karyologic studies are difficult to perform on sectioned material. Further studies using squash technique are therefore planned. Some details concerning the karyotypes may, however, be given.

T. hirtocarpum (2n=8) has one pair of very long chromosomes with slightly submedian centromeres. The other three pairs are comparatively similar in length. One pair has median centromeres, and two pairs distinctly submedian centromeres. One of the last mentioned pairs has large satellites.

T. aegaeum (2n=20) has 3 pairs of long chromosomes and 7 pairs of relatively short ones. The small pairs are relatively similar and have ± median centromeres. One of the large pairs, with slightly submedian centromeres, has small satellites.

T. pestalozzae (2n=20) seems to have chromosomes rather similar to those of *T. aegaeum*, but no satellites have been observed.

The restricted material studied of *T. officinale* (2n=18) has been rather difficult to analyse. The species may have 3 pairs of long chromosomes, 2 pairs of intermediate and 4 pairs of relatively small chromosomes with median centromeres. One of the large pairs has small satellites.

In *T. apulum* (2n=20) all chromosomes are of relatively similar length. One pair with distinctly submedian centromeres, has rather large satellites.

T. maximum (2n=20) has chromosomes similar to those of *T. apulum*, but no satellites have been observed.

VARIABILITY

The species treated, viz., *Tordylium apulum, T. officinale, T. pestalozzae, T. aegaeum*, and *T. hirtocarpum* are all stenotypic. Normally they have not developed local morphological variants even in spatially isolated areas. The only exceptions are *T. apulum*, which apparently has developed a low, rapidly growing ecotype in the central and southern Aegean, and *T. aegaeum*, which is mainly represented by populations with small mericarps, short bractlets and short radiating petals in the Astipalea area. The very small spatial differentiation within the *Tordylium* species in the Aegean is a striking contrast to the conditions in several other genera of annuals, e.g., *Nigella* and *Malcolmia*.

DISTRIBUTION AREAS

Tordylium apulum is a Mediterranean species distributed from southern France and Sicily to Turkey and Syria. It is also reported from a few localities in Algeria. In the Aegean it is very common and seems to be evenly distributed over all island complexes (Fig. 5). It is

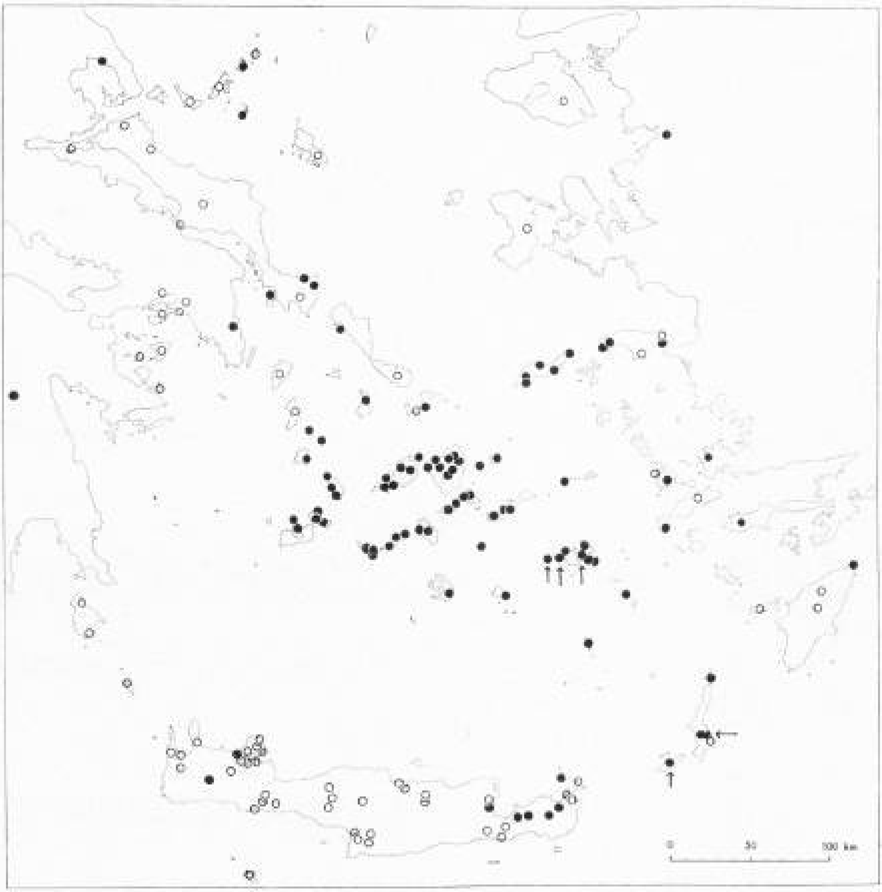

Fig. 5. The distribution of *Tordylium apulum* in the Aegean (dots=herbarium material seen and my own field annotations; rings=literature records). — The arrows show cytologically investigated material.

only lacking in some of the smallest, isolated islands. It grows in garigue, fields and other localities strongly influenced by human activity.

Tordylium officinale occurs in Italy and the Mediterranean parts of the Balcan peninsula. In the Aegean it probably only occurs in western Crete (Fig. 6). The records in Rechinger (1943) from the Kikladhes and the east Aegean islands have probably all to be transferred to *T. aegaeum*. *T. officinale* grows in garigue, abandoned fields and other localities with naked soil.

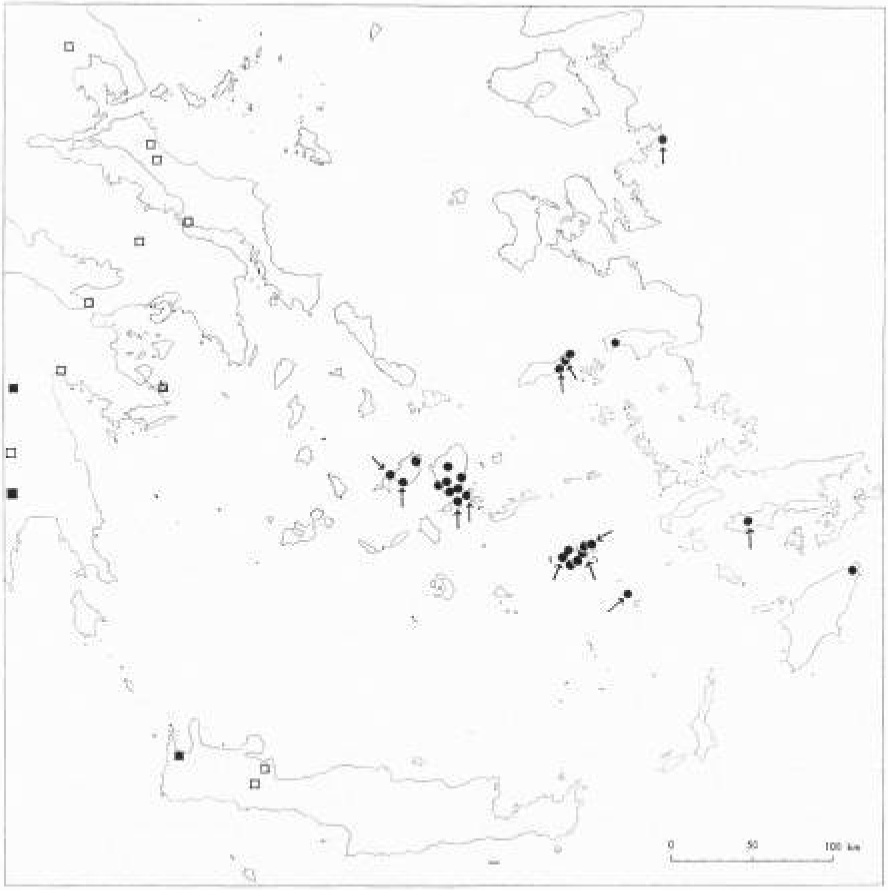

Fig. 6. The known distribution of *Tordylium aegaeum* (dots = herbarium material seen). — Besides the distribution of *T. officinale* in eastern Greece is indicated (black squares = herbarium material seen; open squares = literature records). — The arrows show cytologically investigated material.

Tordylium pestalozzae is known from a few localities in southwestern Turkey (Caria and Lycia) and from a single locality in Rodos (Fig. 8). The distribution in Turkey is insufficiently known and probably the range of the species will be widened in the future. The species seems to be restricted to scree below limestone cliffs.

Tordylium aegaeum occurs in the Kikladhes, the east Aegean islands, and along the western coast of Anatolia (Fig. 6). The western boundary of the species given in Fig. 6 is probably correct as the species has been searched for in vain by me in Karpathos, eastern Crete and the western islands of the Kikladhes. The distribution in the Kikladhes given is certainly correct, i.e., the species is restricted to Naxos-Paros and the Astipalea areas. Most probably *T. aegaeum* is more common than indicated on the map on the east Aegean islands and along the western coast of Anatolia. The species grows in garigue, abandoned fields and other localities with naked soil.

Tordylium hirtocarpum is known from the Kikladhes, the east Aegean islands and Karpathos. The western boundary given in Fig. 7 is probably correct as the species has been searched for in vain by me in eastern Crete and the western islands of the Kikladhes. The map gives most probably the total distribution within the Kikladhes (the Naxos, the Anafi, and the Ios-Sikinos areas). On the east Aegean islands the species is most probably more common than indicated on the map. It also ought to be searched for along the western coast of Anatolia. *T. hirtocarpum* is restricted to scree below high limestone cliffs.

The distribution areas for *T. aegaeum* and *T. hirtocarpum* are remarkable. Both species probably have their main distribution on the east Aegean islands and at least for *T. aegaeum* also along the western coast of Anatolia. Besides both occur in the Kikladhes and *T. hirtocarpum* also in Karpathos. Thus, they are distributed on both sides of the phytogeographical boundary between Greek (European) and Anatolian flora (cf. Fig. 7) stressed by RECHINGER (1950).

There is little reason to believe in a long distance migration of *T. hirtocarpum* over this boundary, as the species is restricted to scree below high limestone cliffs, a relatively rare and spatially very restricted habitat. As *T. aegaeum* sometimes grows in abandoned fields and other localities with naked soil a relatively recent introduction by man cannot wholly be excluded. However, the occurrence of a local, morphologically deviating population complex in the Astipalea area does not favour such an explanation. Also the recent distribution in the Kikladhes, where both species are abundant in certain areas but wholly absent in others, does not give an impression of an ability for long distance migration for any of the species.

T. aegaeum and *T. hirtocarpum* may very well be old, rigid species, already established before the Aegean land was split into a great number of islands in the beginning of the Quaternary. The present, restricted areas for both species in the Kikladhes may be regarded as refugia, in

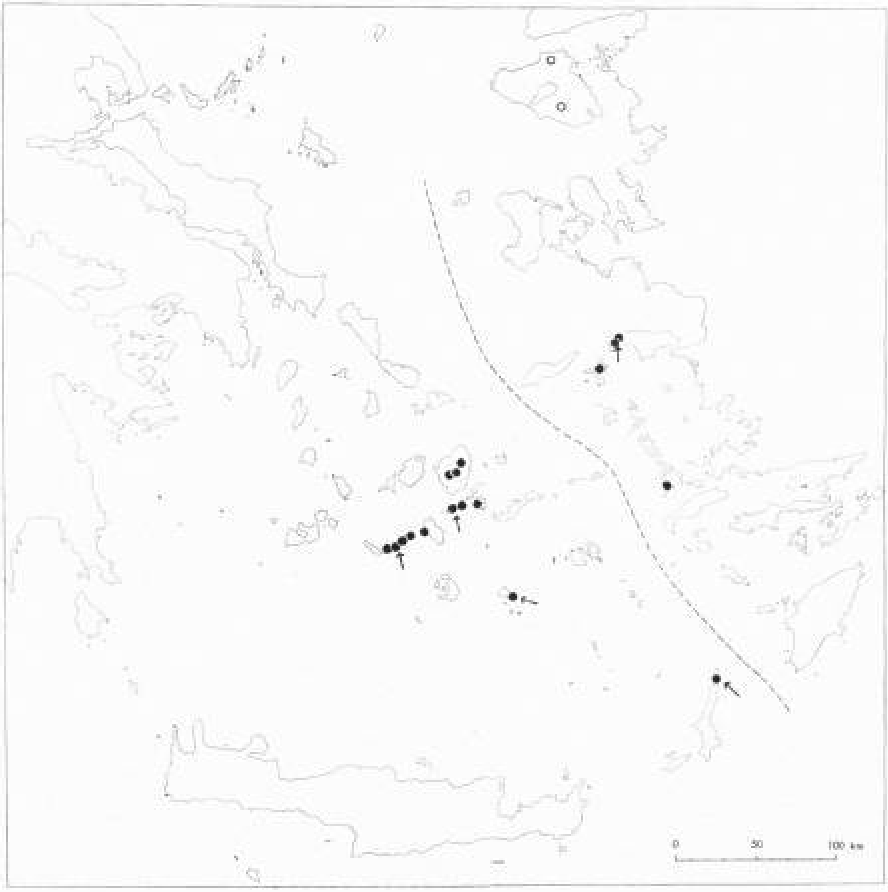

Fig. 7. The known distribution of *Tordylium hirtocarpum* (black dots=herbarium material seen; rings=literature records). — The arrows show cytologically investigated material. — The broken line indicates the phytogeographical boundary between the Anatolian and Greek flora (cf. RECHINGER 1950).

which they have been able to survive during Quaternary climatic fluctuations. Many otherwise common species in the Aegean have similarly split distribution areas in the Kikladhes, e.g. *Quercus coccifera* L., *Euphorbia acanthothamnos* HELDR. & SART., and *Phlomis fruticosa* L., which can only be explained as a result of extinction in some islands during Quaternary climatic fluctuations.

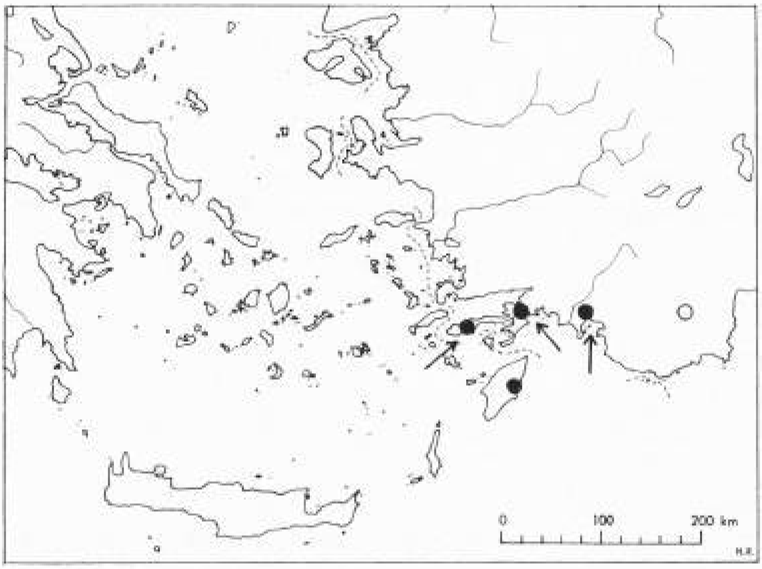

Fig. 8. The known distribution of *Tordylium pestalozzae* (dots = herbarium material seen; ring = the type locality). — The arrows show cytologically investigated material.

TAXONOMY

In previous literature *Tordylium officinale* L., *T. pestalozzae* Boiss., *T. hirtocarpum* Cand., and *T. aegaeum* Run. have been confused in the Aegean.

T. maximum L. has been reported from Crete by Belli (1594—1596) according to Raulin (1869). This single record for the species from the Aegean is probably incorrect. *T. byzantinum* (Azn.) Hay. has been reported from western Crete by Gandoger according to Rechinger (1943). The phytogeographically remarkable record is possibly due to misidentification of flowering individuals of *T. officinale,* which is known from the actual area. Recently *T. byzantinum* has also been reported from the Northern Sporades by Phitos (1967). As I have seen no material from the Aegean of *T. maximum* and *T. byzantinum*, they are only included in the key, but no descriptions are given.

The descriptions and the key are based on investigations of herbarium material taken from the field. The terminology mostly follows Lawrence (1951).

Key to the Aegean species (i.e., to all European species).

1. Mericarps with thickened moniliform-crenate margins.
    2. Radiating petals divided into two ± equal lobes. Vittae 7—13 on the dorsal face of the mericarps .... *T. apulum*
    2. Radiating petals divided into very unequal lobes. Vittae 0 or 2 on the dorsal face of the mericarps.
        3. Bractlets subulate, stiffly ciliate. Inner rays much shorter than the peripheral ones.
            4. Mericarps 5—8 mm long. Dorsal vittae 0 or 2 very short ones. Marginal hairs of bracts and bractlets stout .... *T. aegaeum*
            4. Mericarps 3—4 mm long. Dorsal vittae 2, as long as the dorsal face. Marginal hairs of bracts and bractlets slender .... *T. officinale*
        3. Bractlets lanceolate, with softly ciliate white margins. All rays of equal or subequal length.
            5. Mericarps villous of very thin, acute hairs. Dorsal vittae 2, as long as the dorsal face. Radiating petals 1—2 mm .... *T. hirtocarpum*
            5. Mericarps with thick, erect, tubular hairs, vesicular or obtuse at the apex. Dorsal vittae 0 or 2 very short ones. Radiating petals ca. 5 mm .... *T. pestalozzae*
1. Mericarps with thickened, smooth margins.
    6. Mericarps ca. 3 mm, with soft tubular or vesicular hairs on the dorsal face .... *T. byzantinum*
    6. Mericarps 5—8 mm, with stiff, acute hairs on the dorsal face and on the thickened margins .... *T. maximum*

Tordylium apulum L.

Softly hairy, usually much branched annuals, 10—60 cm high. Basal and lower cauline leaves pinnate, with 1—5 pairs of rounded to ovate, crenate leaflets. Upper cauline leaves with lanceolate or linear lobes. Umbel of 2—10 umbellulae, ± hemispherical during anthesis. Rays equal or subequal in length, ± ascending in fruit stage, 2—5 times as long as the ripe mericarps, and with short erecto-patent hairs. Bracts and bractlets 5—10 mm long and 1—2 mm broad, spreading or slightly reflexed, lanceolate, shortly ciliate in the margins. Abaxial side of bracts and bractlets glabrous or with short hairs on the vein. Outer flowers of peripheral umbellulae with one radiating, ± equally and deeply 2-lobed petal, 2.5—9 mm long. Mericarps 5—10 mm long, broadly elliptical to round in outline, with moniliform-crenate margins. Dorsal face with weak, vesicular or tubular hairs with a vesicular or rarely obtuse apex. Vittae 7—13 on the dorsal face, ca. 10 on the commissural face. Pollen grains 33—36×15—18 μ, exine much thickened in the equatorial zone, exoapertures lanceolate, endoapertures narrowly and transversely elliptical to oblong. Chromosome number $2n = 20$.

ECOLOGY. Garigue, fields and other naked soil.

DISTRIBUTION. The Mediterranean, from southern France and Sicily to Turkey and Syria; Algeria. Very common in the Aegean.

VARIABILITY. In the central and southern Aegean the species is mainly represented by a 10—20 cm high, rapidly developing ecotype.

Tordylium officinale L.

Softly hairy, usually branched annuals, 20—50 cm high. Basal and lower cauline leaves simple, ovate, crenate or pinnate, with 1—2 pairs of ovate to rounded, crenate leaflets. Upper cauline leaves usually simple, lanceolate, dentate, often basally lobed. Umbel of 8—14 umbellulae, flat-topped during anthesis. Peripheral rays during anthesis ± spreading, in fruit stage ascending, with slender, erecto-patent hairs. Peripheral rays 3—6 times, inner ones 1—2 times as long as the ripe mericarps. Bracts and bractlets 10—20 mm long, subulate, deflexed, stiffly ciliate of slender, erecto-patent, 0.4—0.7 mm long hairs. Abaxial side of bracts and bractlets usually only sparsely hairy on the vein. Outer flowers of peripheral umbellulae with two radiating, very unequally 2-lobed petals, 6—10 mm long and 4—7 mm broad. Mericarps 3—4 mm long, broadly elliptical, ovate or roundedly triangular in outline, with moniliform-crenate margins. Dorsal face with thick, weak, tubular hairs with a vesicular or obtuse apex. Vittae 2 on the dorsal face and 2 on the commissural face. Pollen grains $31—38 \times 15—20$ μ, exine moderately thickened in the equatorial zone, exoapertures with a prominent rounded central part, endoapertures transversely and broadly elliptical. Chromosome number $2n=18$.

ECOLOGY. Garigue, abandoned fields and other naked soil.

DISTRIBUTION. Italy, Mediterranean parts of the Balcan Peninsula, western Crete. The records in RECHINGER (1943) from the Aegean islands Mytilene, Chios, Ikaria, and Paros probably have all to be transferred to *T. aegaeum*.

VARIABILITY. The material studied by me from Istria, Dalmatia, the Greek mainland, and Crete is very homogeneous.

Tordylium pestalozzae Boiss.

Softly hairy, branched annuals, 10—50 cm high. Basal and lower cauline leaves simple, ovate, crenate, sometimes with a cordate base or pinnate, with 1—2 pairs of ovate to rounded, crenate leaflets. Upper cauline leaves usually simple, ovate to lanceolate, dentate, often lobed.

Umbel of 5—10 umbellulae, ± hemispherical during anthesis. Peripheral rays during anthesis spreading, in fruit stage ascending, with short, erecto-patent hairs. All rays of equal or subequal length, 3—5 times as long as the ripe mericarps. Bracts deflexed, broadly lanceolate, cuspidate to narrowly triangular with a prominent white margin, 8—16 mm long and 2—3 mm broad. Bractlets deflexed, lanceolate to broadly lanceolate, 5—12 mm long and 1—3 mm broad. Bracts and bractlets with ciliate margins of erecto-patent, weak hairs, 0.2—0.5 mm long. Abaxial side of bracts and bractlets evenly pubescent of weak, short, almost conical hairs. Outer flowers of peripheral umbellulae with two radiating, very unequally 2-lobed petals, ca. 5 mm long and 3 mm broad. Mericarps 6—7.5 mm long, broadly elliptical to ovate in outline, with moniliform-crenate margins. Dorsal face with thick, weak, tubular hairs, vesicular or obtuse at the apex. Vittae 0, or 2 very short ones on the dorsal face, and 2 very short or rather long ones on the commissural face. Pollen grains ca. $35 \times 17\ \mu$, exine moderately thickened, exoaperture a colpus with a prominent rounded central part or a rounded pore, endoaperture ± rounded. Chromosome number $2n=20$.

ECOLOGY. In scree below limestone cliffs.

DISTRIBUTION. South-western Turkey, Rodos.

REMARKS. The species was described by BOISSIER (1849) on material from Elmalu in Lycia. The detailed description gives no doubt that the material collected by me and my collaborators in Caria and Rodos is conspecific. In Flora orientalis (1872) BOISSIER also included a collection from Rodos (BORGEAU 59) and one from Izmir in the species. I have examined a duplicate of the collection from Rodos, which has to be transferred to *T. aegaeum*. For phytogeographical reasons it is probable that also the Izmir collection belongs to *T. aegaeum*. The records in RECHINGER (1943) of *T. pestalozzae* from the Aegean have probably all to be transferred to *T. aegaeum* and *T. hirtocarpum*, possibly with the exception of some records from Rodos.

Tordylium aegaeum Run. sp. nov.

DIAGNOSIS. Species *Tordylio pestalozzae* similis, sed bracteolis subulatis et ramis umbellularum centralium iis marginalium multo brevioribus ab eo differt. — Graeca. Astipalea, Maltesana. 11.5 1960. RUNEMARK & NORDENSTAM 13542 (Holotypus in LD).

Softly hairy, branched annuals, 10—40 cm high. Basal and lower cauline leaves simple, ovate, crenate or pinnate, with 1—2 pairs of ovate to rounded, crenate leaflets. Upper cauline leaves usually simple, lanceolate, dentate, often basally lobed. Umbel of 5—12 umbellulae, flat-topped during anthesis. Peripheral rays during anthesis ± spreading, in fruit stage ascending, with erecto-patent hairs, 0.15—0.5 mm long. Peripheral rays 1.5—4 times and inner ones 0.5—1 times as long as the ripe mericarps. Bracts deflexed, subulate to narrowly lanceolate and cuspidate, 8—15 mm long and 0.5—1 mm broad. Bractlets ± deflexed, stiff, stout in fruit stage, subulate, 8—12 mm long and 0.5—1 mm broad. Bracts and bractlets with ciliate margins of erecto-patent, stout hairs, 0.15—0.5 mm long. Abaxial side of bracts and bractlets with short, stiff hairs, mainly on the veins. Outer flowers of peripheral umbellulae with 2 radiating, very unequally 2-lobed petals, 5—8 mm long and 3—4 mm broad. Mericarps 5—8 mm long, broadly elliptical to ovate in outline, with moniliform-crenate margins. Dorsal face with weak, tubular hairs, vesicular or obtuse at the apex. Vittae 0, or 2 very short ones on the dorsal face, and 2 long ones on the commissural face. Pollen grains 36—41×17—20 μ, exine much thickened in the equatorial zone, exoapertures with a prominent rounded central part, endoapertures transversely and broadly elliptical. Chromosome number $2n=20$.

ECOLOGY. Garigue, abandoned fields and other naked soil.

DISTRIBUTION. Kikladhes, east Aegean islands, westernmost Anatolia.

VARIABILITY. The species is relatively invariable. However, most material from the Astipalea area has short petals, short bractlets, and small mericarps.

REMARKS. In some respects *T. aegaeum* is morphologically intermediate between *T. pestalozzae* and *T. officinale*. Previously material of *T. aegaeum* has been referred to either of these species.

Tordylium hirtocarpum Cand.

Softly hairy, branched annuals, 10—25 cm high. Basal and lower cauline leaves simple, ovate, crenate or pinnate, with 1—3 pairs of ovate to rounded, crenate leaflets. Upper cauline leaflets simple, lanceolate, dentate, sometimes basally lobed. Umbel of 2—3, exceptionally 4—5 umbellulae. Rays erecto-patent in anthesis and in fruit stage, with ± erecto-patent, 0.1—0.2 mm long hairs. All rays of equal or subequal length, about as long as the ripe mericarps. Bracts patent or slightly reflexed, broadly lanceolate, cuspidate, 3—7 mm long and 1—1.5 mm broad. Bractlets patent or slightly reflexed, broadly lanceolate, cuspidate, 5—7 mm long, and 1.5—2 mm broad. Bracts and bractlets with ciliate margins of weak, 0.1—0.2 mm long hairs. Abaxial side of bracts and bractlets evenly pubescent of short, weak hairs. Outer flowers of peripheral umbellulae with two radiating, very unequally 2-lobed petals, 1—2 mm long and 0.8—1.4 mm broad. Mericarps 5—6 mm long, broadly elliptical to ovate, with moniliform-crenate margins. Dorsal face villous of very thin, ± acute hairs, up to 1 mm long. Vittae 2 on the dorsal face (easily observed as brownish red strips) and 2 on the commissural face. Pollen grains 33—36×15—19 μ, exine slightly thickened in the equatorial zone, exoapertures with a prominent rounded central part, endoapertures broadly and transversely elliptical. Chromosome number $2n=8$.

ECOLOGY. In scree below high limestone cliffs.

DISTRIBUTION. Kikladhes, Karpathos, east Aegean islands.

VARIABILITY. The material seen is very homogeneous.

REMARKS. *T. hirtocarpum* was described from Mytilene by CANDARGY (1897) together with ca. 60 other new species. These new species have mostly been regarded as superfluous or at least dubious. *T. hirtocarpum* is one of the few good species. It was distinctly described with stress on, i.a., the villous pubescence of the mericarps and the small, radiating petals. The drawing of *T. pestalozzae* in RECHINGER (1943, Tafel 5: 1) has to be referred to *T. hirtocarpum*.

APPENDIX

All verified localities are listed for *T. aegaeum*, *T. hirtocarpum*, and *T. pestalozzae*. Only localities of cytologically investigated material are given for *T. officinale*, *T. apulum*, and *T. maximum*.

Localities from which material has been cultivated and cytologically investigated are indicated by an asterisk after the collection number. Voucher specimens of cytologically investigated material are preserved in the Botanical Museum, Lund.

The names of the localities have been taken from the detailed sea charts of the British Admirality (cf. also the maps in RUNEMARK et al. 1960). The following abbreviations have been used for the names of the collectors: B, ROLAND VON BOTHMER; Be, BENGT BENTZER; N, BERTIL NORDENSTAM; P, JIMMY PERSSON; R, HANS RUNEMARK; S, SVEN SNOGERUP.

Tordylium aegaeum

(All verified localities)

Greece.

Kikladhes. Paros: 1—3 km S of Naoussa (R & Be 29299)*, the bay E of Akr. Makria (R & Be 30897)*, Antiparos, the island of Dhiplo (R & Be 30799)*. — Naxos: 2 km SSE of Sangri, 200 m s.m. (S 20191), Akr. Ag. Ioannis (R 1809, R 1859), Ormos Agiasou (R & S 10079), N of Ormos Agiasou (R & S 10139), N of Ormos Kalantou (R & S 10219), N of Panormo (R & S 10751), W of Psiliammos (R & S 10681), the island of Skinousa, N and NW of Psiliammo (R & N 15983), Kato Koufonisi, the E part of the island (R & N 15875)*. — Astipalea: W of the town (Rechinger 7588, LD), Maltesana (R & N 13542, R & P 22737)*, between Maltesana and Vriseu Punda (R & N 13461)*, Panormos (R & P 22756), S of Baia della Sabbia (R & N 15107), between Vathi and Baia di Zofiri (R & N 15178), the island of Pontikoutha (R & N 13896)*. — Sirina: the valley N of the village (R & S 7414), the NE-part (R & Be 28474)*, the central part (R & N 14473)*, N of Ag. Ioannis Ormos (R & S 7269, R & P 22360).

East Aegean islands. Samos: the valley and the shore at Ag. Kiriaki (R & S 19791). — Ikaria: Ag. Kirikos (R-1297)*, Pharos (R & S 12488)*, SSE of Ormos Yero (R & S 6598). — Rodos, Bastida (Borgeau 59, LD).

Turkey.

Izmir distr., 1 km S of Galtidere (leg. R. von Bothmer, R-3903)*.

Mugla distr., 0—1 km SSW of the village of Datça (leg. R. von Bothmer, R-3905)*.

Tordylium hirtocarpum

(All verified localities)

Greece.

Kikladhes. Naxos: NW of the peak of Oros Zeus, 600—800 m s.m. (R & S 5825), near the peak of Ammomachis Oros, 850—880 m s.m. (S 20218), NE of Apiranthos, 600 m s.m. (R 2754), 3 km SSW of Filoti (R 980), the island of Iraklia: Ormos Pegadi (R & S 5305), between the harbour and "Spilea Cove" (R & N 13257), 1—2 km W of Chora (R & N 13305)*, the island of Skinousa, between the village and the harbour (R 4408), the island of Keros (Karos), Andreas (R & S 10898). — Ios, N of the harbour, 250 m s.m. (R 2333). — Sikinos: the E-promontory (R & Be 24793), between Skala and Kastro (R & Be 24888), S-slope of the highest peak (R & Be 24932, 24966) W of Kara (R-3737)*, the island of Kardiotissa (R & N 14553). — Anafi, Kalamos (R & N 14890)*.

Karpathos area. Saria, Ormos Armyro (R & S 7534, 7685).

East Aegean islands. Mytilene: Olympos Paleokastron (Candargy, not seen), Petrovouni (Candargy, not seen). — Samos. Mt. Kerki: the valley of Leka 200—400 m s.m. (R & S 18849), the peak area 800—1000 m s.m. (R & S 19705), N of Ag. Kiriaki (R & S 19555), the SW-slope 400—800 m s.m. (R & S

19586)*, 1—3 km W of Maratokampos 250—350 m s.m. (R & S 19185)*, 3—4 km W of Maratokampos 350—400 m s.m. (R & S 19062)*. — Fourni, Thimena, Selada (RECHINGER 4694, LD). — Kalimnos, at the monastery 3 km SW of the town (R & P 22279).

Tordylium pestalozzae

(All verified localities)

Greece.

East Aegean islands. Rodos, 2.5 km S of Kalatos, 200 m s.m. (S 22117).

Turkey.

Muğla distr., 7 km WSW of Datça, 200—300 m s.m. (leg. R. VON BOTHMER, R-3904)*, 8 km NW of Marmaris, 50 m s.m. (R & Be 29418)*, Göçek (20 km NW of Fethiye), 100 m s.m. (R-4109)*.

Tordylium officinale

(Cytologically investigated material)

Greece. Ionian islands. Kefallinia, W of Poros (S 23799)*.

Tordylium apulum

(Cytologically investigated material)

Greece.

Kikladhes. Astipalea: Maltesana (R & N 13374)*, the island of Pontikoutha (R & N 13958)*, the island of Ofidousa (R & N 13814)*.

Karpathos area. Kasos, Ophris (B 23205)*. — Karpathos, 5.5 km NE of Mesochorio (leg. R. VON BOTHMER, R-4322)*.

Tordylium maximum

(Cytologically investigated material)

France.

Ardèche. Les Ollières (received by seed exchange, R-3914)*.

ACKNOWLEDGEMENTS

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Studies on Penaeaceae V
The Vascular Anatomy of the Flower of Glischrocolla formosa

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ABSTRACT

The vascular anatomy of the flower of *Glischrocolla formosa* (THUNB.) R. DAHLGR. is described in detail. The perianth is interpreted as a corolla, and there is no evidence to consider it a calyx. The placentation is axile, with the ventral bundles of the carpels branching and supplying the ovules. The morphology of the gynoecium shows a number of interesting features. The carpellary dorsal bundles send small branches into the perianth just beneath the base of the gynophore (stipe). The dorsal bundles are small and it is the septal bundles alternating with them that are continued prominently into the stigma. The four lobes of the stigma are in commissural positions.

INTRODUCTION

The morphology of *Glischrocolla formosa* (THUNB.) R. DAHLGR. has been described in DAHLGREN 1967. For convenience in following the anatomical features, a brief account of the floral organization would not be out of place here. The pedicel has two opposite bracteoles in lateral positions. The perianth is monochlamydeous and gamophyllous, with the long tubular portion ending in four lobes. The stamens are four, epiphyllous, alternating with the perianth lobes, and inserted just beneath the sinuses of the perianth. The anthers are subbasifixed. The ovary, which is superior, has a prominent stipe (gynophore). The gynoecium is syncarpous, four-carpellary, four-locular, and almost square in transverse section, with two pendulous and two ascending ovules arising from an axile position near about the middle of the length of the ovary. The style is long and ends in a small, capitate, indistinctly four-lobed stigma.

ANATOMY

The *pedicel* has a continuous, thick vascular cylinder (Fig. 1 A), which becomes elliptic in transverse section, and usually divides into eight bundles (Fig. 1 B). Two of these, at the narrow end of the ellipse, pass out as the *bracteole* traces. These branch in their outward transit (Fig. 1 C), and further branching occurs within the bracteoles (Fig. 1 D). Although rudimentary and sometimes not even seen externally, each bracteole has a minute vestigial bud with a vascular supply, in its axil. It consists of two traces arising one on either side of the bracteole trace gap (Fig. 1 C). These are somewhat arc-shaped in section. Their outer margins are often connected with the edges of the bracteole trace for a short distance.

Above the insertion of the bracteoles, the pedicel contains six bundles of which the anterior and the posterior ones are smaller than the rest (Fig. 1 D). Through a division of two of the larger strands the number of bundles is increased to eight, with four small bundles alternating with four larger ones (Fig. 1 E). The bundles fuse laterally, however, and give rise to a continuous cylinder from which emerge eight traces (Fig. 1 F). Four of these are perianth-carpellary dorsal cords which divide in their outward transit into a *perianth* midrib trace (C) and a dorsal bundle (D) of a carpel (see Fig. 1 G). Of these four bundles two are in the median (anterior and posterior) and two in lateral positions. The alternating four bundles are conjoined perianth-commissural—staminal cords. These enter the perianth and run unbranched within it upto a little beneath the level of insertion of the stamens.

Just beneath the level of separation of the perianth tube from the stipe (gynophore) the dorsal bundles of the carpels bear small laterally outward traces which enter the perianth tube and run within it as minor lateral bundles (Fig. 1 H and J). Occasionally these minor laterals are derived as laterally arising and inwardly moving branches of the perianth-commissural—stamen cords (Fig. 1 I).

The origin of the eight traces referred to above results in the formation of gaps and a ring of eight bundles in the central zone (Fig. 1 G). By a fusion in pairs, these give rise to four arc-shaped strands in diagonal position (Fig. 1 H). In the basal region of the stipe itself the dorsal bundles (D) of the *carpels* bear lateral branches which divide further. The stipe of the ovary thus has a ring of small bundles in the periphery, of which four, in the median (anterior and posterior) and lateral positions, are the dorsal bundles of the carpels, while the others are lateral branches of these. In the centre there is a ring of four arc-shaped bundles on radii alternating with those of the dorsal bundles (Fig. 1 J). These bundles in the centre fuse by their margins for a

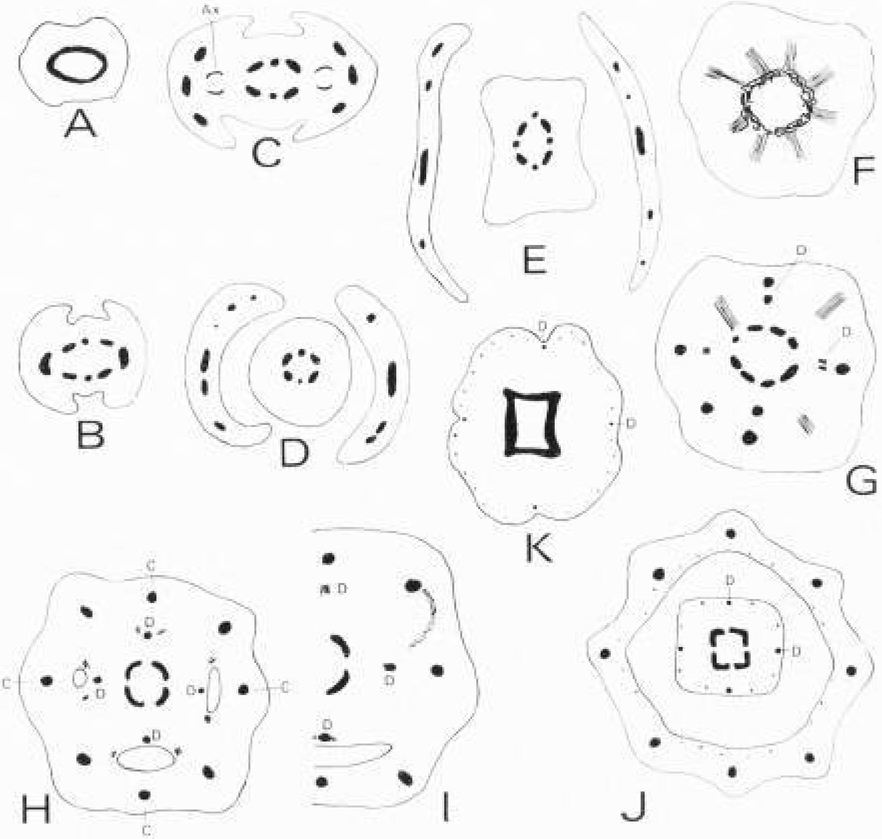

Fig. 1. Transversal sections through the basal part of the flower in *Glischrocolla formosa*. — A: T. S. of pedicel. — B: Origin of bracteole traces. — C: Shows traces for the rudimentary axillary structures in the axils of the bracteoles. — D—E: T. S. above the level of the detachment of the bracteoles. — F: Origin of eight traces from the vascular cylinder. — G: Division of four out of the eight traces into an inner dorsal bundle of a carpel and an outer perianth midrib trace. — H: The carpellary dorsals are seen to send branches towards the perianth tube. — I: Occasional origin of a lateral bundle of the perianth as a branch of a perianth commissural bundle. — J: T. S. above separation of the gynophore (stipe) from the perianth. — *Abbreviations used in the illustrations:* Ax: Traces for the rudimentary axillary bud of the bracteole. — C: Perianth midrib trace. — D: Dorsal bundle of a carpel. — PL: Placental supply. — S: 'Septal' bundles alternating in position with the carpellary dorsals. — V: Ventral bundles of carpels.

short distance giving a prominently quadrangular structure, its angles corresponding in position to the septal radii (Fig. 1 K).

Near the level of the *base of the loculi*, this angular vascular cylinder divides into: (*1*) four pairs of ventral (placental) bundles (v) which run opposite the loculi, and (2) four much larger radially flattened bundles (s) opposite the septa (Fig. 2 A). These latter bear outward branches into the ovary wall on either side almost throughout the length of the ovary (Fig. 2 A—D). Each of the loculi has four *ovules* arising from a knob-like projection from the so-called axile zone into the loculus near the middle of the length of the ovary (Fig. 2 S). Two of the ovules are ascending and side by side in position; the other two are descending and also collateral in relation to each other. The two ascending ovules arise just above the position of the two descending ones. The knob on which they are placed is the placenta, although it differs in appearance from the placentas in most other families. The two ventral bundles of each carpel run into the placenta and each of them divides into an upper and a lower branch which enter the ascending and the descending ovules respectively on the same side (Fig. 2 C—D and S). Above the level of the placentas, the four radially flattened 'septal' bundles fuse by their inner margins giving rise to an almost complete vascular cylinder. From this, outward extensions develop opposite the loculi (Fig. 2 E). However, they contain very few xylem elements as compared with the 'septal' bundles. The vascular cylinder thus becomes deeply fluted, with eight outwardly extending ridges, four of them (which are opposite the loculi) being deficient in xylem (Fig. 2 E).

The ovary throughout its length is prominently squarish or "diamond"-shaped in section, with the dorsal bundles running in the angles. Opposite each dorsal bundle the ovary surface has a narrow, shallow, longitudinal furrow, which extends throughout the length of the style

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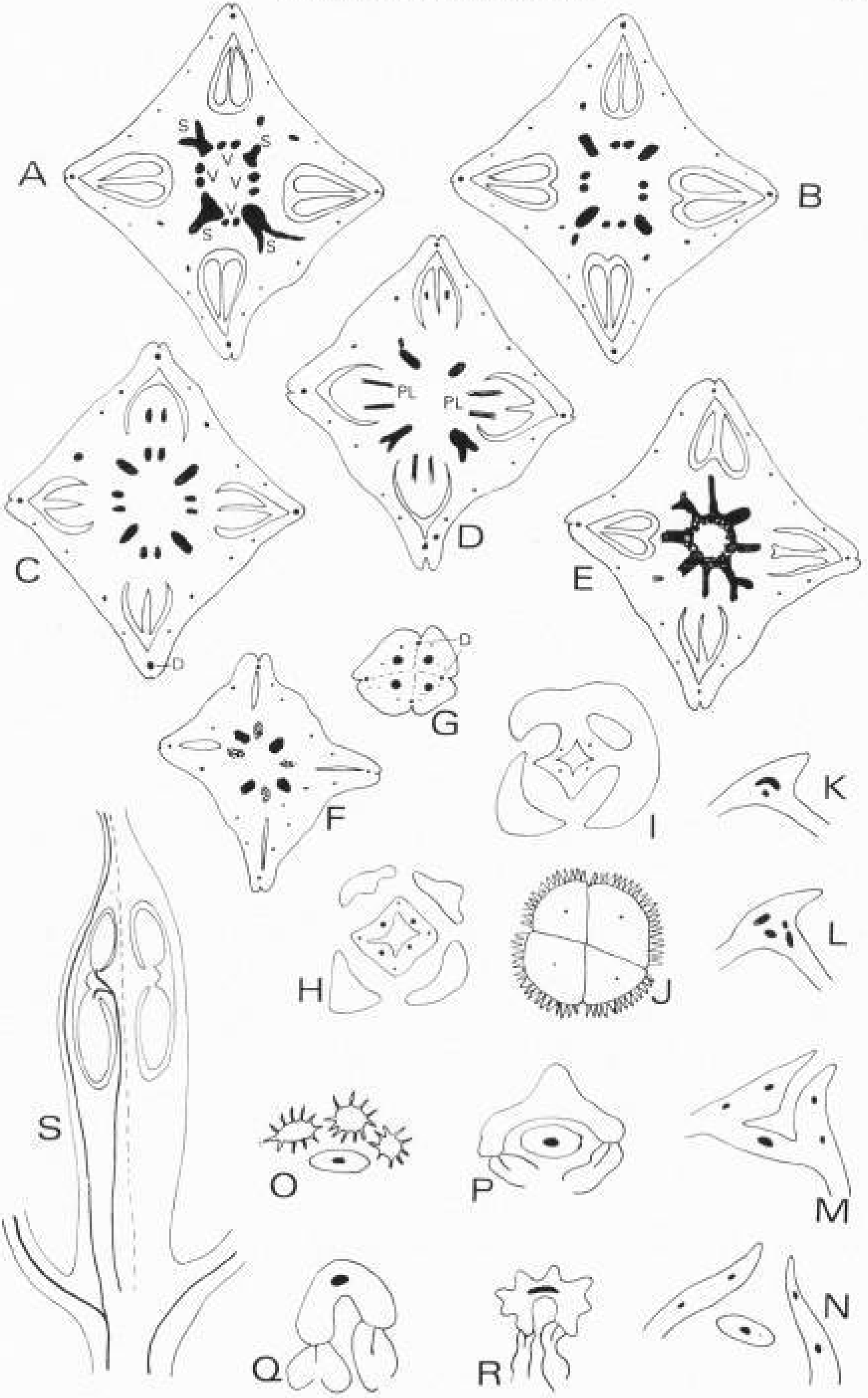
Fig. 2. Transversal and longitudinal (S) sections through flower of *Glischrocolla formosa*. — A—B: T.S. of ovary showing the dorsal bundles, lateral bundles, pairs of ventral bundles, and the 'septal' bundles. — C—D: T.S. at higher levels, showing placental supply. — E: T.S. through upper part of ovary showing strongly fluted vascular cylinder. — F: T.S. near apex of ovary. — G: T.S. of style. — H—J: T.S. of stigma through successively higher levels. — K—N: T.S. through part of perianth tube showing separation of stamen from it. — O—R: T.S. of anther at successively higher levels. — S: Diagrammatic longitudinal section of ovary showing placentation and vascular supply to two ovules. — Abbreviations as used in Fig. 1.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as well (Fig. 2 A—G). The *style* thus has a four-lobed appearance in transverse section, although on an external examination this is not obvious. The carpellary dorsals are small throughout.

Towards the top of the ovary the loculi become reduced to narrow radial slits, which still higher up appear as four radial lines opposite the dorsal bundles (Fig. 2 F). The fluted vascular cylinder gets divided into eight bundles of which four are opposite the dorsal bundles and are less prominent than the others on account of the insignificant amount of xylem present in them. In the basal part of the style they get reduced to a group of deep-staining cells, while the bundles on the septal radii are prominent and continue into the stigmatic region along with a few small other bundles of the ovary wall. Even within the ovary, the dorsal bundles (D) are small, and in the style they become smaller (Fig. 2 G). Within the greater part of the style a faint line runs from the dorsal bundle towards the centre. These lines, together with the furrows on the surface of the style opposite the dorsal bundles, make the style transection appear four-lobate. These lobes, however, do not correspond to the carpels, as they alternate with the dorsal bundles (Fig. 2 G). The septal bundles run in a reduced state into the *stigma*, while the other small laterals as well as the dorsal bundles disappear gradually beneath the stigmatic level. Although not visible externally, the stigma is obscurely four-lobed, with each lobe protracting slightly downwards (Fig. 2 H—J). *The stigmatic lobes are in commissural position and are not above the carpellary midribs.*

The *perianth tube* receives the four midrib bundles, four perianth-commissural—stamen strands, and a number of minute lateral bundles. Higher up, a prominent ridge (see DAHLGREN 1967, Fig. 2), indicative of fused margins of adjacent perianth members, is formed towards the outside opposite the perianth-commissural—stamen bundles. These bundles divide into an inner staminal trace and an outer arc-shaped bundle (Fig. 2 K) that divides further and supplies the margins of adjacent perianth members (Fig. 2 K—N). The *filament* is attached for a short distance to the adjacent margins below the point of detachment (Fig. 2 M—N). The perianth midribs also bear lateral branches.

The filament is clearly attached to the inner surface of the basal region of the *connective* which is flattened and concave (Fig. 2 P—Q). The latter has three short, downwardly directed projections (Fig. 2 O). The vascular bundle of the filament enters the connective and runs upto its tip.

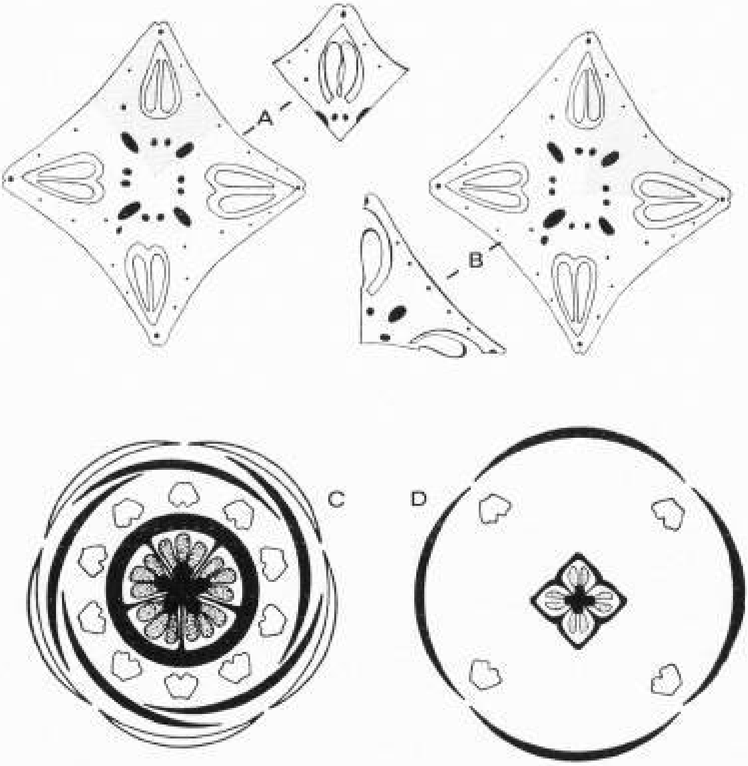

Fig. 3. A—B: Interpretation of carpels in the ovary of *Penaeaceae* applied on Fig. 2 B; A according to generally accepted views; B according to the views of BAILLON (see further in the text). — C—D: Flower diagrams in *Melastomataceae* (C) and *Penaeaceae* (D), C according to MORLEY 1953 Fig. 6, D as constructed from the present results.

DISCUSSION

Previous Aspects and Interpretations

According to A. DE JUSSIEU 1846, DE CANDOLLE 1856, VAN TIEGHEM 1893, and others, the flower in *Penaeaceae* consists of a gamosepalous, four-lobed calyx, four stamens alternating with these lobes and attached along the main filamental region to the inner side of the calyx tube, and four carpels. Each of the carpels encloses its own loculus, with the 2—4 ovules emerging from a placenta located at the inner fused margins of the carpels, i.e. in marginal position. The carpels alternate with the stamens and are opposite the calyx lobes.

An entirely divergent opinion was held by BAILLON (1876 pp. 93—97), who regarded the flower tube to be of receptacular nature, bearing the (undefined) perianth lobes, and the alternating stamens, at its top. What is especially divergent is, however, BAILLON's interpretation of the pistil (BAILLON op cit., flower diagram in Fig. 60), which he considered made up of four carpels standing *opposite the stamens* and each consisting of a wall with a central septum protruding to the centre of the pistil and bearing two placentae, one on the inner margin of each of two adjacent loculi. Such an interpretation accordingly would correspond to Fig. 3 B. BAILLON's interpretation of the pistil in *Penaeaceae* is almost of the same type as SAUNDER's views which appeared later and for other groups (and according to her it would be classified as a case of "fertile semi-solid carpels"). For several reasons it cannot be accepted.

Present Interpretation and Comparison to Other Groups

The perianth of *Penaeaceae* accordingly has usually been referred to as the calyx, the flower being regarded as apetalous. The family was supposed to be related to *Thymelaeaceae*, in which the calyx is corolla-like, and in which petals or petaloid scales are frequently inserted near the mouth of the calyx tube. The stamens in *Thymelaeaceae* are mostly of the same number as the calyx lobes and are situated *opposite* them. When a second series of stamens is present, its members alternate with those of the outer series and the calyx lobes. — The vascular anatomy of *Glischrocolla* gives no convincing evidence for the calyx nature of the perianth. On the other hand, even the occurrence of stamens in positions alternating with the perianth lobes indicates that it corresponds to a corolla and not to a calyx (see also below). If it is regarded as a calyx, one has to imagine an ancesteral condition with two whorls of stamens of which the outer is 'normal' in position, opposite the sepals, and that the corolla as well as the whorl of antesepalous stamens have disappeared, because then only could the condition seen in *Glischrocolla* result. It is simpler and more logical to assume that a calyx with its vasculature is not developed, and that the perianth represents the corolla. The stamens alternate with the petals as they normally should.

A derivation of the penaeaceous flower from a pentacyclic one is accordingly by no means the only possibility conceivable. However, as there are obvious similarities in anatomical, palynological, and vegetative-morphological features, in connective structure, etc., between

Penaeaceae and, e.g., *Melastomataceae* (see DAHLGREN 1968 p. 24), a comparison between the whorls in the flowers of these families will be justified. — Accepting that each loculus of the ovary corresponds to one carpel, we find in *Penaeaceae* that the carpels alternate with the stamens, and correspond in position to the inner whorl of stamens in *Melastomataceae* (see Fig. 3 A, C, and D). Similarly the stamens alternate with the perianth members in *Penaeaceae*, whereby in position they would correspond to the *petal* whorl in *Melastomataceae*, an aspect worth notifying against the background of previous, purely typological interpretations (see above) that the perianth represents a calyx. In *Penaeaceae* there are no traces of a second whorl of stamens.

Each perianth member in *Glischrocolla* receives a 3-trace supply, with the marginal traces of adjacent members fused mutually and also with the staminal trace. A 3-trace supply is said to be typical of a sepal, and a 1-trace supply characteristic of a petal. But there are so many exceptions to this that such a vasculature cannot be taken as a diagnostic criterion. There are many species of different families in which sepals receive a single trace, just as there are also cases in which a petal receives three traces. HEINIG (1951) contradicted the supposed relationship of *Thymelaeaceae* to *Elaegnaceae*, *Proteaceae*, and *Nyctaginaceae*. A relationship of *Thymelaeaceae* to *Penaeaceae* also seems very doubtful.

An adnation of petal traces with carpellary dorsals is seen in a number of families, but *Glischrocolla* is peculiar in that the carpellary dorsal bundles send minor lateral branches for the perianth.

In *Thymelaeaceae* a hypogynous disc is present, while in *Glischrocolla* such a structure is not noticeable, but a gynophore or stipe is a common feature. The ovules are solitary in each loculus of *Thymelaeaceae*, whereas *Glischrocolla* has four ovules per loculus, arising from a knob-like placenta on the inner angle of each loculus near the middle of the length of the ovary. The placentation is thus to be called axile.

The smallness of the dorsal bundles of the carpels is commensurate with the loculicidal dehiscence of the capsule. It is the septal bundles which are large and run into the style. An important feature shown by the anatomical method is that the stigmatic lobes are above the lines of junction of the carpels, and hence comparable to what is called commissural stigmas in some other famiiles. Whether the stigma in *Glischrocolla* is to be called commissural or not is a matter of opinion, but may be justified when comparing with the condition in, e.g., *Penaea* where the stigmatic areas are separated by prominent non-stigmatic lobes. One can say that in *Glischrocolla* it is due to a minor bifurcation of the carpellary tip, with adjacent branches of different carpels fusing to form a stigmatic lobe in commissural position.

A further discussion of these and other points should await a closer examination of the other genera of the family.

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Some New Species of Allium (Liliaceae) from Afghanistan

Studies in the Flora of Afghanistan 9

By Per Wendelbo
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ABSTRACT

Five new species of *Allium* are described: *A. bracteolatum* WENDELBO (C. Afghanistan) and *A. ionandrum* WENDELBO (S. Afghanistan) of the section *Haemoprason*; *A. longicollum* WENDELBO (S. Afghanistan) of section *Allium*; *A. protensum* WENDELBO (C. Afghanistan and possibly also adjacent parts of the USSR) and *A. caroli-henrici* WENDELBO (SE. Afghanistan) of section *Melanocrommyum*.

INTRODUCTION

In the material of *Allium* collected by Professor K. H. RECHINGER in 1967 during his third journey to Afghanistan three new and distinct species were revealed. Also in the material that IAN HEDGE and I collected in 1962 there were still another two undescribed species.

I am much indebted to Professor RECHINGER for sending me this material for identification as well as for translating my descriptions into Latin.

Allium bracteolatum WENDELBO, sp. nov. (Fig. 1 A)

Sect. *Haemoprason* HERM.

Bulbus solitarius, ovoideus, 0.75—1.3 cm diametro; tunicae exteriores cinerascenti-brunneae, papyraceae, ± distincte nervosae, interiores purpureo-violaceae usque albae. *Scapus* solitarius, 12—30 cm altus, basi ± curvatus, usque ad 1/3—2/5 vaginis foliorum glabris tectus. *Folia* 2, distantia, quam scapus breviora, 0.5—2 mm diametro, filiformia, cylindrica, fistulosa, florendi tempore ± emarcida. *Spatha* c. 5 mm longa, 2-valvis, hyalina, purpureo-nervosa. *Umbella* fasciculata usque hemisphaerica, pauci- usque multiflora, densa; pedicelli inaequales, 5—10 mm longi, crassiusculi, basi bracteolis bene evolutis usque ad 4 mm longis provisi. *Perigonium* campanulatum, umbilicatum, album, nervis virescenti-purpurascentibus usque purpureis; tepala 6—8 mm longa, elliptica, apice cucullata, exteriora quam interiora paulo breviora. *Filamenta* c. 3/4 petalorum longitudinis aequantia, inaequalia, per c. 1.5 mm inter se connata et basi tepalorum adnata; exteriora linearia, quam interiora triangularia subbreviora; antherae 1.2—1.4 mm longae, flavae. *Stylus* brevis crassus; stigma subcapitatum. *Capsula* c. 3.5 mm diametro, subsphaerica, perigonio persistente cincta.

A. bracteolatum in affinitatem *A. rubelli* M.B. spectat; differt a speciebus huius gregis imprimis bracteolis bene evolutis; differt ab *A. rubello* M.B. perigonio majore albo, ab *A. umbilicato* Boiss. perigonio albo et foliorum vaginis laevibus, ab *A. fibroso* Regel perigonio multo majore, ab *A. griffithiano* Boiss. tepalis subaequalibus quorum interiores basi saccata manifeste carent.

Afghanistan. Kabul: Unai, near village, dry slopes, 3000 m, 25.VI.1962, Hedge and Wendelbo 4548, holotype BG, isotype E. — Ghazni: Ad lacum Sabzab, inter Okak et Behzud, 2800 m, 6.VII.1962, Rechinger 17849 W. — Bamian: Darrah Kalu, 2800 m, dry slopes, 27.VI.1962, Hedge and Wendelbo 4677 BG; Bamian near the hotel, 2500 m, 26.VI.1962, Hedge and Wendelbo 4654 BG; Bulola, 2550 m, 12.VII.1967, Rechinger 36969 W; Darrah-i Shikari, inter Doab et Bulola, 1600—2000 m, Rechinger 16720 W.

Allium ionandrum Wendelbo, sp. nov. (Fig. 2 C, D)

Sect. *Haemoprason* Herm.

Bulbus ovatus usque ad 2 cm diametro; tunicae exteriores crassae durae diffractae atro-brunneae, interiores numerosae brunnescentes usque griseae reticulato—fibrosae. *Scapus* solitarius vel scapi bini e bulbis separatis tunica communi tectis, 20—30 cm alti, 1—2.5 mm diametro, ± curvati, in sicco costati, ± purpureo-suffusi, in quarta circiter parte inferiore vaginis foliorum approximatis glabris tecti. *Folia* 2, subopposita, scapum subaequantia vel eo manifeste breviora, 1—2 mm lata, cylindrica, apice canaliculata, longitudinaliter costata, solida, glabra, margine laevia. *Spatha* 8—12 mm longa, 4-loba, distincte rostrata, albo-hyalina, purpureo-nervosa, demum reflexa. *Umbella* hemisphaerica, 2.5—5 cm diametro, multiflora, densa; pedicelli usque ad 2.5 cm longi, tenues, infra perigonium incrassati, ebracteolati. *Perigonium* campanulato-urceolatum, in sicco album, tepalis apice purpurascentibus, nervis virescenti-purpureis; tepala inaequalia

Fig. 1. A: *Allium bracteolatum* sp. nov. (HEDGE & WENDELBO 4548, holotype BG); B—C: *Allium longicollum* sp. nov., B: RECHINGER 34761, holotype W, C: RECHINGER 34823, W. Photo H. RASPER.

nervo basin versus valde incrassato, exteriora c. 3.2 mm longa, elliptica, apice rotundata, interiora c. 3.5 mm longa, anguste elliptica, attenuata, obtusa. *Filamenta* inaequalia, filiformia, inter se connata et tepalis per c. 3/4 mm adnata; exteriora vix 4 mm longa, basi utrinque denticulo provisa vel edenticulata; interiora quam exteriora sublongiora, utrinque prope basin dente majore provisa; antherae c. 1 mm longae, atroviolaceae. *Ovarium* nectariis distinctis provisum, laeve. *Stylus* filiformis, exsertus; stigma capitulatum. *Capsula* valvis 3 mm longis latiuscule obcordatis provisa, tepalis persistentibus inclusa.

Species nova valde distincta facile recognoscenda *A. lamondiae* WENDELBO similis, a quo manifeste differt tunicis reticulato-fibrosis, floribus minoribus, filamentis filiformibus, antheris exsertis atroviolaceis.

Afghanistan. Urgun: 35 km NW Urgun (32°52'N, 69°07'E) versus Surmat (33°27'N, 69°02'E), 2200—2400 m, 10.VI.1967, RECHINGER 35915, holotype W.

Allium longicollum WENDELBO, sp. nov. (Fig. 1 B, C)

Sect. *Allium*

Bulbus unicus vel bini, interdum plures, 1.5—2 cm diam., ovoidei, tunicis crassis brunneis reticulato-fibrosis longicollis inclusi. *Scapus* 16—30 cm longus, ± curvatus, costatus, juventute secus costas tenuiter puberulus, usque ad tertiam partem inferiorem foliorum vaginis ± pubescentibus tectus. *Folia* 3, approximata, quam scapus breviora, 1—3 mm diametro, semicylindrica, secus costas indistinctas ± pilosa. *Spatha* c. 7 mm longa, valvis 2—3 acuminatis, hyalina, viridi-nervosa. *Umbella* hemisphaerica usque subsphaerica, multiflora, densa; pedicelli subaequales, usque ad 10 mm longi, basi bracteolati. *Perigonium* campanulatum, album, viridi-nervosum, umbilicatum; tepala c. 4 mm longa, apice cucullata, exteriora elliptico-oblonga usque oblonga, cymbiformia, dorso omnino vel secus nervos tantum scabrido-papillosa, interiora oblonga usque oblongo-spathulata, dorso laevia. *Filamenta* 3—3.5 mm longa, inter se connata et usque paulo supra basin tepalis adnata; exteriora e basi anguste ovato-triangulari subulata; interiora quam exteriora duplo latiora et quam tepala basi latiora, tricuspidata, cuspide mediana antherifera dimidium basis latae et dimidium cuspidum lateralium filiformium longitudinis aequante. *Stylus* 1.5 mm longus; stigma capitatum. *Capsula* valvis 4.5 mm latis vix 4 mm longis emarginatis, perigonio persistente cincta.

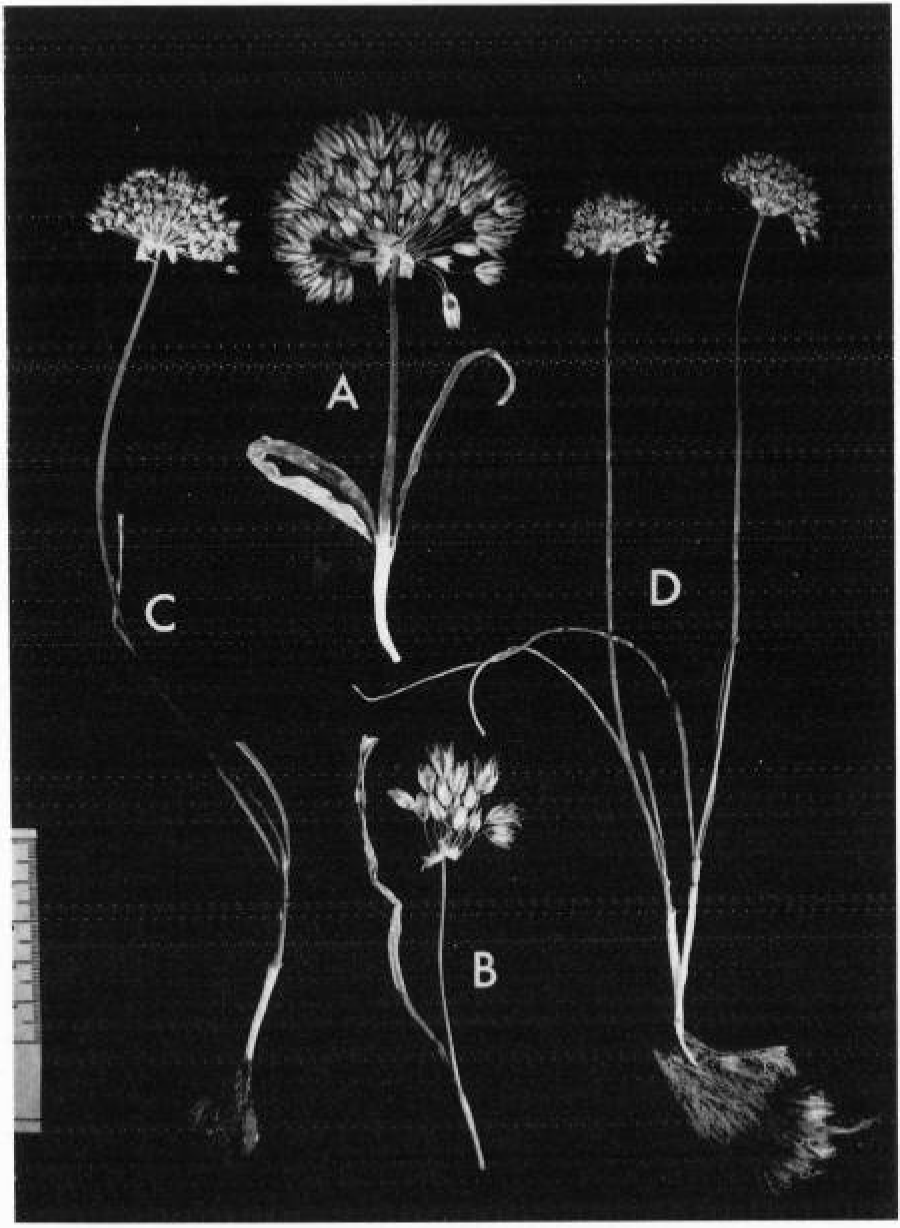

Fig. 2. A—B: *Allium caroli-henrici* sp. nov. (RECHINGER 35053, W), A: holotype; C—D: *Allium ionandrum* sp. nov. (RECHINGER 35915, W), C: holotype. Photo H. RASPER.

A. longicollum, *A. dictyoscordo* VVEDENSKY et *A. filidenti* REGEL proximum. Species nova ab ambabus differt foliorum vaginis et foliis pubescentibus et scapo juventute quidem pubescente; ab *A. dictyoscordo* insuper differt statura minore, foliis angustioribus et perigonio minore; ab *A. filidente* insuper differt foliis non fistulosis et tepalis scabridis vel scabride nervosis.

Afghanistan. Farah: inter Farah Rud et Dilaram, 27 km SE Farah Rud, 900 m, 24.IV.1967, RECHINGER 33444 W, — Kandahar: in collibus saxosis 44 km NE Qala Bist, 900 m, 21.V.67, RECHINGER 34761, holotype W; 30 km E Dilaram versus Girishk, 1050 m, 24.IV.1967, RECHINGER 33532 W; in saxosis aridis 80 km W Kandahar, versus Girishk, 1100 m, 21.V. 1967, RECHINGER 34823 W; ad lacum artificiale "Arghandab Reservoir", c. 50 km N Kandahar, 1200 m, 23.V.1967, RECHINGER 34936 W; 34 km N Kandahar versus "Arghandab Reservoir", 1100—1200 m, 22—23.V.1967, RECHINGER 34866 W; in lapidosis 10—20 km NE Kandahar, 1100 m, 26.V.1967, RECHINGER 35249 W; in monte 15 km SW Kandahar, 1100 m, 22.V.1967, FREYTAG in RECHINGER 34837 W. — Tirin: 20—25 km S Tirin, versus Kandahar, 1800 m, 23.V.1967, RECHINGER 35117 W.

A. caroli-henrici WENDELBO, sp. nov. (Fig. 2 A, B)

Sect. *Melanocrommyum* WEBB et BERTH.

Bulbus sphaericus, 1.5—2 cm diametro; tunicae exteriores coriaceae, nigrescentes, interiores tenuiores, pallide brunneae, dense tenuiter nervosae, longitudinaliter fissae; bulbilli 1.5 cm longi, cymbiformes, rostrati, flavi, nitentes. *Scapus* 8—12.5 cm longus, 1.5—3 mm diametro, leviter curvatus, in sicco distincte costatus, ± purpureo-suffusus. *Folia* 1—2, quam scapus longiora, 4—9 mm lata, margine minute scabrida. *Spatha* 1.5 cm longa, 4-loba. *Umbella* hemisphaerica usque fasciculato—hemisphaerica, ± multiflora, densiuscula; pedicelli inaequales, usque ad 3 cm longi, tenues. *Perigonium* campanulatum, in sicco in parte inferiore pallide brunnescenti—flavidum, in parte superiore purpurascens et atrius nervosum; tepala subinaequalia, c. 10 mm longa, exteriora 3.5 mm lata, elliptica, obtusa, interiora aliquantum breviora, 4.5 mm lata, ovata, obtusa. *Filamenta* subinaequalia, dimidium circiter tepalorum longitudinis aequantia, per c. 1.5 mm inter se connata et tepalis adnata, exteriora e basi latiore subulata, interiora sublongiora et duplo latiora; antherae 2 mm longae, oblongae, flavae. *Ovarium* ovoideo-cylindricum, viride, angulis indistincte verruculosis, loculis 4-ovulatis. *Stylus* c. 2 mm longus, subulatus; stigma punctiforme. *Capsula* ignota.

Fig. 3. *Allium protensum* sp. nov. (HEDGE & WENDELBO 4815, holotype BG). Photo H. RASPER.

A. caroli-henrici sine dubio *A. cucullato* WENDELBO affine sed ab eo tepalis majoribus inaequalibus, tribus interioribus ovatis, colore magis purpurascente et filamentis dimidium tantum tepalorum longitudinis aequantibus differt. In *A. cucullato* inflorescentia magis sphaerica et pedicelli magis inaequales videntur.

Afghanistan. Tirin: 42 km S Tirin (32°40′N, 65°50′E), versus Kandahar 31°36′N, 65°47′E), 1800 m, 23.V.1967, RECHINGER 35053, holotype W. — Orozgan: Inter Tirin et Orozgan (33°00′N, 66°40′E), 24.V.1967, RECHINGER 35150 W.

The new species is named in honour of the editor of "Flora iranica", the infatiguable collector professor KARL-HEINZ RECHINGER who has during his travels discovered many new *Allium* species.

Allium protensum WENDELBO, sp. nov. (Fig. 3)

Sect. *Melanocrommyum* WEBB et BERTH.

Bulbus sphaericus, 2—3 cm diametro; tunicae coriaceae, apice in fibras fissae, exteriores nigrae, sequentes purpurascentes. *Scapus* 10—25 cm altus, crassus, apice plerumque crassissimus (usque ad 1.7 cm), basin versus sensim attenuatus. *Folia* 3, quam scapus longiora, 1.5 cm lata, plana, margine minute scabrida. *Spatha* c. 2 cm longa, acuminata, 3-valvis. *Umbella* sphaerica, multiflora, laxa (aperta); pedicelli valde inaequales, longissimi, ei florum sterilium 6—16 cm longi, quam ei florum fertilium circiter duplo longiores, apice clavato-incrassati. *Perigonium* late campanulatum, in vivo pallide brunnescens nervis atrioribus, in sicco sordide album nervis purpurascentibus; tepala 7—8 (—10) mm longa, lineari-lanceolata usque lanceolata, obtusa usque subobtusa, apice leviter involuta, post florendum erecta, nervo centrali non valde incrassato. *Filamenta* c. 2/3—3/4 tepalorum longitudinis aequantia, e basi triangulari subulata; filamenta basi alternatim latiora inter se per 1—1.5 mm connata et basi perigonii adnata. *Stylus* non exsertus, filiformis. *Ovarium* florum fertilium sphaericum, verruculosum, stipitatum. *Capsula* c. 4 mm diametro, stipitata.

Allio schubertii ZUCC. similis sed scapo humiliore, floribus pallide brunnescentibus et ovario verrucoso ab eo diversum.

Afghanistan. Bamian: E of Nayek on road from Band-e Amir to Panjao, dry stony slopes, 2800 m, 30.VI.1962, HEDGE and WENDELBO W. 4815, holotype BG, isotype E.

The new species is closely related to *A. schubertii* ZUCC. which occurs in Libya, Israel, and Syria and is a much coarser plant with scape

30 to 60 cm high and with much longer leaves. Judging from cultivated material *A. protensum* has a pale brown flower whereas it is purplish violet in *A. schubertii*; the latter also has an ovary with a wrinkled-reticulate surface while it is verruculose in the former. Admittedly the two species are very close to each other morphologically, and it is thus interesting to note that they are very widely separated geographically. Records of *A. schubertii* from Iran and Iraq are based on wrong determinations.

Material from the Central Asiatic part of USSR most probably belongs to the new species. I have only seen one sheet from Tien Shan (Alejmtau, leg. BONDARENKO & BUTKOV) which seems to be identical with my Afghan specimens.

A New Species of Corydalis Sect. Oocapnos (Fumariaceae) from Tibet

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ABSTRACT

Corydalis retingensis LUDLOW, a fifth species of sect. *Oocapnos* M. POPOV, is described from Reting, 96 km north of Lhasa, southeastern Tibet.

INTRODUCTION

The section *Oocapnos* M. POPOV (1937) of *Corydalis* L. differs from the other Asiatic sections of this large and intricate genus in having an inflated capsule, a feature which led FEDDE to give it independent generic rank as *Cysticorydalis*. WENDELBO (1966) recognized four species as belonging to this section, i.e. *C. crassifolia* ROYLE of the Kumaun Himalaya, *C. crassissima* CAMB. of the northwestern Himalaya, Karakoram and north-eastern Hindukush, *C. fedtschenkoana* REGEL of the Tien Shan and Pamir-Alai in central Asia and *C. metallica* WENDELBO of the north-eastern Hindukush, and he provided a key to these. Whilst working in the Herbarium of the British Museum (Natural History), London, on the rich material of *Corydalis* assembled here from the Himalaya and Tibet I recognized as a fifth and hitherto undescribed member of the section a species which GEORGE SHERRIFF and I had collected in 1944 at Reting north of Lhasa. This extends the range of the section to southeastern Tibet. The material available is admittedly far from perfect but, since Tibet is no longer accessible to botanists, it seems desirable to publish a description of this new species.

Corydalis retingensis LUDLOW, sp. nov.: *C. crassifoliae* ROYLE ut videtur affinis sed foliorum pinnis regulariter profunde pinnatilobis, lobis obovatis apice rotundatis, distinguitur.

Rhizoma ramosum, apice petiolorum cauliumque vetustorum basibus instructum. *Caulis* erectus, simplex, c. 15 cm altus, basi juxta rhizoma

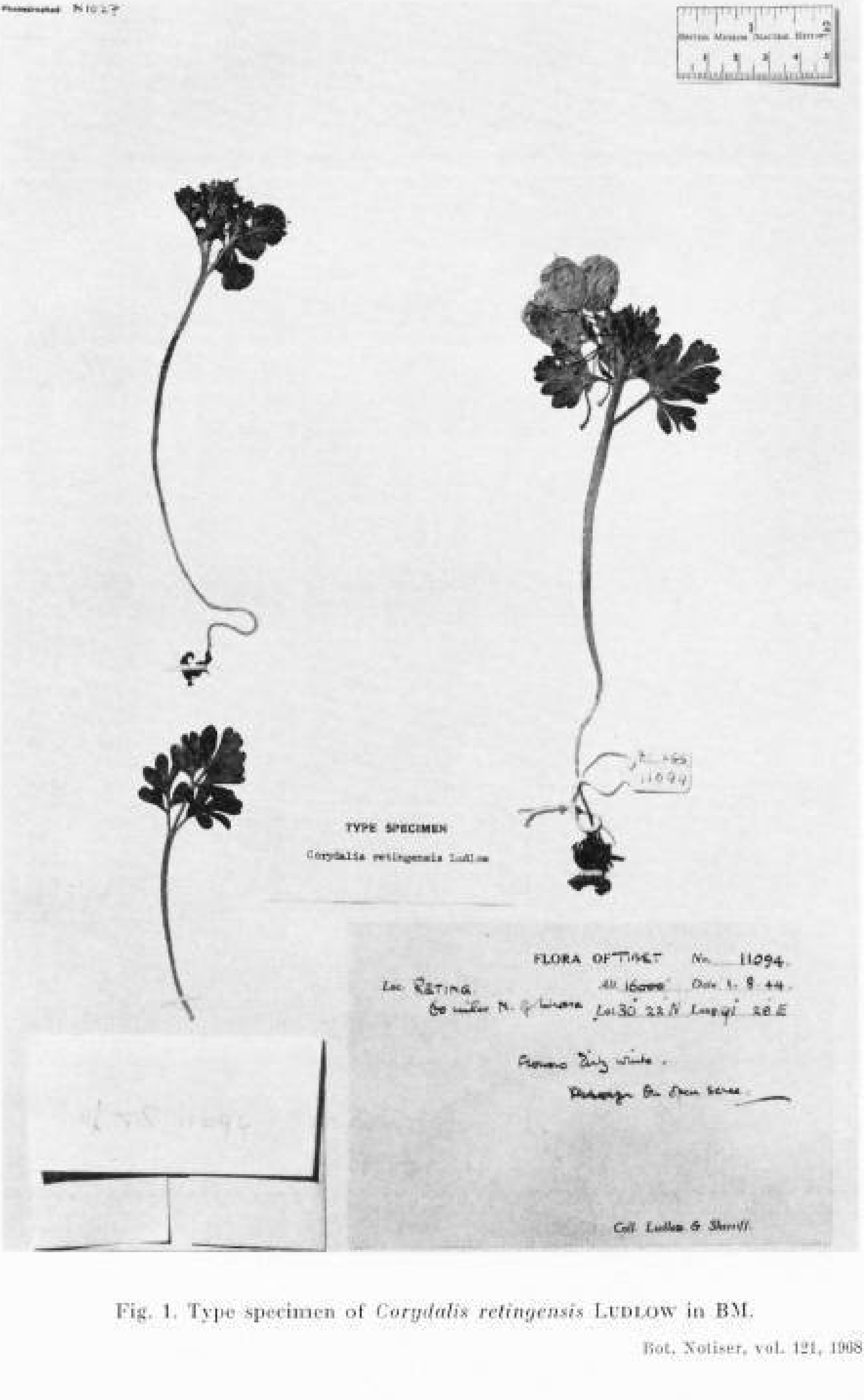

Fig. 1. Type specimen of *Corydalis retingensis* LUDLOW in BM.

1 mm diam. sed apicem versus incrassatus 4 mm diam. *Folia radicalia* (unum solum visum) pinnata, 9—10 cm longa petiolo 6—7 cm longo incluso; pinnae 5, eae jugi inferioris c. 3 cm longae petiolulo 7—8 mm longo incluso, regulariter profunde pinnatilobae, lobis ad 10 mm longis et 5 mm latis obovatis apice rotundatis; pinnae jugi superioris c. 2 cm longae, inferioribus similes sed subsessiles lobis paucioribus; pinna terminalis his similis sed petiolulo 4 mm longo. *Folia caulina* quam radicalis breviora sed similiter lobata, infimum c. 4 cm longum petiolo 1.75 cm longo incluso, pinnis subsessilibus; folia superiora cum bracteis minora. *Inflorescentia* terminalis, brevis, densa; flores 10—12, albi pedicellis c. 2.5 cm longis apicem versus valde incrassatis. *Sepala* non visa. *Petalum posticum* ad 17 mm longum calcare 3.5 mm longo incluso; petala cetera non visa. *Staminum* phalanx postica 9 mm longa. *Stylus* 2—2.5 mm longus, paulo attenuatus, persistens; stigma transverse quadrangulum, 8-papillosum. *Capsula* subglobosa, c. 2 cm diam.; semina 8—10, nigra, nitida, rotundata, 1.5 mm diam.

Tibet. Reting, ca. 96 km N. of Lhasa (30°22′N., 91°28′E.), 4,800 m, on open scree, "flowers dirty white", 1 Aug. 1944, LUDLOW & SHERRIFF 11094 (BM, holotype).

The material available is scanty, consisting of two specimens in fruit, a basal leaf and the spurred petal of a flower with its attached staminal phalange. The plant is, however, obviously distinct in foliage from other species of the section. Only *C. crassifolia* ROYLE s.str. has foliage bearing any resemblance, but the coarse irregular lobing of the pinnate leaves of *C. crassifolia* contrasts markedly with the regular lobing of the pinnae in the Tibetan plant. Moreover in *C. retingensis* the spur is shorter than in any other species of the section, being approximately one-fifth of the total length of the corolla. The quadrangular shape of the stigma and the number of papillae agree with those of the other species and, like them, *C. retingensis* inhabits alpine scree.

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Placentation in Relation to Anatomy

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ABSTRACT

Puri (1952) tries to interpret and redefine axile and parietal placentations on an anatomical basis. This, however, introduces complications and solves no problem; in fact it introduces a problem where there is none. The placentation in *Burmannia pusilla* in relation to the anatomical aspects proves the superiority of the classical definitions of axile and parietal placentations.

Ever since Puri's (1952) publication of his paper on placentation, a tendency is noticeable among some authors to mix up placentation on a purely topographical basis with what is just an interpretation of placentation on anatomical grounds. This has sometimes gone to such an extent as to describe placentation purely on an anatomical basis. For a taxonomist or general botanist it is quite enough, and it should be so, if in a multilocular ovary the ovules are arising from a central column of tissue, to call it as axile placentation. The orientation of the ventral bundles is immaterial to him. Similarly, if in a syncarpous unilocular ovary, the ovules arise along the lines of junction of the carpels, or from the inner margins of incomplete, inwardly projecting septa, he would call it as parietal placentation, irrespective of the position and orientation of the ventral bundles.

According to Puri's (1952) definitions, in axile placentation, the gynoecium is multicarpellary, syncarpous and multilocular; the placentae are borne on the fused margins of the same carpel; the placentae derive their vascular supply from the ventrals of the same carpel; and the ventral bundles are inversely oriented with reference to the floral axis and lie almost on the same radii as the dorsals. In parietal placentation, the gynoecium is multicarpellary, syncarpous and unilocular; the placentae are borne on the fused margins of different carpels; the placentae derive their vascular supply from ventrals of different carpels; and the ventral bundles are normally oriented with reference to the floral axis and lie on different radii from those of the dorsals. From the above, the points which have to be discussed are only those relating to the position and orientation of the ventral bundles.

Let us now examine the condition in *Burmannia pusilla*, a plant which attracted the author's attention on noticing a number of errors of observation in a recently published paper on its floral anatomy. PAI (1966) states that "although the ovary at the base is trilocular and the placentation apparently axile, still it is fundamentally parietal, the trilocular nature being merely a result of the intruding placentae meeting in the centre. . . . The orientation and behaviour of the carpellary ventrals is significant in this context. They are *normally oriented*, and the ventrals of adjacent carpels fuse to form the compact placental bundles — a situation characteristic of parietal placentation (cf. PURI, 1952)." This is the exact opposite of the unpublished observations of the present author on a very large number of flowers of *B. pusilla* collected from Karjat and Khandala. The ventral bundles in this species do not have the normal orientation at all, but they show a very clear, unmistakable, inverse orientation (Fig. 1, A and B). I sent a slide to Prof. PURI for confirmation of my observation and he agreed that the ventral strands here are definitely with an inverse orientation. He also pointed out that more or less similar conditions were found by him in *Cucurbitaceae*. Wrong observations have a tendency for being perpetuated in literature and are not congenial for the development of correct scientific interpretations. It is likely that PAI merely inferred, without a close examination, that the ventral bundles might have a normal orientation and reported it as a statement of fact, just because in the upper part of the ovary there is a clear parietal placentation. In fact, he quotes PURI's paper quite irreleventlly. The ovary, as in a number of other families, is trilocular in the basal part and unilocular above, no doubt, but the ventral bundles are inversely oriented.

In this connection, it is necessary to mention the condition in *Cucurbitaceae*. The morphology of the inferior ovary of this family is too well known to be repeated here. PURI (1954) found that in most members of this family, the vascular bundle in the inner angle of the placental ridge is inversely oriented. This is the bundle which was called the "internal bundle" in his descriptions. He discussed the "internal

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Fig. 1. Photomicrographs of transversal section through ovary of *Burmannia pusilla*, showing inverse orientation of the ventral bundles of the carpels. A: Low magnification; B: High magnification. The arrow points to the xylem.

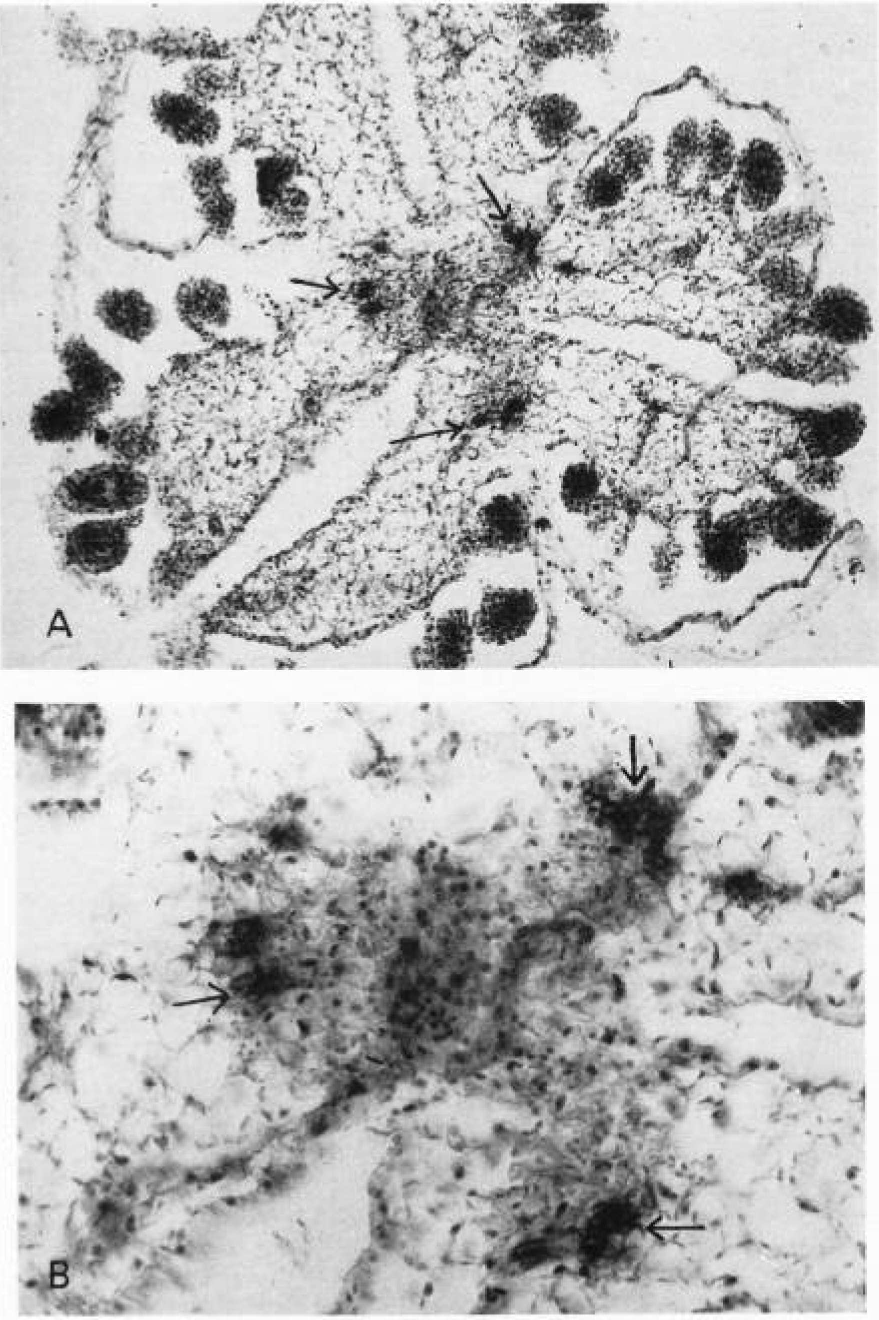

Fig. 1.

bundles" in detail and correctly interpreted them as ventral bundles occurring on septal radii. The placentation was regarded by him as parietal in spite of the inverse orientation of those bundles, because they are present on radii different from those of the dorsal bundles. Also in *Cruciferae, Capparidaceae, Papavaraceae, Moringaceae* and *Passifloraceae* the placentation is parietal, but the ventral bundles are inverted, a feature said by him to be characteristic of axile placentation. PURI interpreted that a change occurred from an ancestral axile placentation to the parietal type, and that the inversion is a relic of past history somehow retained.

It must be mentioned at the outset that PAI did not refer to PURI's paper on *Cucurbitaceae* or to his accounts of the other families mentioned above. He consulted PURI's paper on placentation (1952) and although this paper contains the necessary information about *Cucurbitaceae*, no notice was taken of it for comparison. The condition in *Burmannia pusilla* is somewhat similar to that in *Cucurbitaceae* as pointed out by PURI in a personal communication. In this species, the 'placentas' are borne on inwardly projecting septa formed by carpellary margins. Towards the inner ends of the septa are the inversely oriented ventral bundles. Although PURI emphasizes that the orientation of the ventral bundles is a very important feature, still in many families like *Cucurbitaceae*, it is the position on the septal radii that made him decide the type of placentation as parietal. It may be recalled that in his definitions (PURI 1952) normal orientation of the ventral bundles is given as characteristic of parietal placentation, and the inverse orientation as typical of axile placentation, but apparently, where it did not suit his interpretation in any family, he ignored the emphasis on orientation.

It should be perfectly acceptable to call the placentation in the lower part of the ovary of *B. pusilla* as axile irrespective of considerations like the method of formation of the loculi, and the placentation in the upper part where the ovary becomes unilocular, as parietal without going into the question of the orientation of the ventral bundles. The latter point might be useful in speculations on the phylogeny of placentations but introduces a confusion in plain descriptions of placentation on topographical grounds. Even in typical cases of axile placentation all possible types of fusions of ventral bundles are seen in many families — (*1*) the two ventral bundles of each carpel remaining separate, (*2*) their fusion into a single strand that lies on the same radius as the dorsal bundle, (*3*) fusion in pairs of adjacent ventral bundles of different carpels, (4) fusion of the ventral bundles of all the carpels into a hollow cylinder, and (5) the division of the ventral strands into a varying number of bundles. It is not essential that in axile placentation the ovules are always supplied by ventral bundles of the same carpel. Sometimes in one and the same ovary we get different types of arrangements at different levels. PURI's circumscription of axile and parietal placentations introduces the nature of the vascular bundles, and in doing so, confusion as well. As shown by the example of *Burmannia pusilla*, some workers assume either inversion or normal orientation and draw diagrams accordingly to fit in their material with PURI's definitions. It is not in every plant that the orientation of the ventral bundles is clearly seen, but in such a case it would be better if workers refrain from reporting assumptions as facts. SWAMY and PERIASAMY (1964), who do not attach any special importance to the inverse orientation of ventral bundles, are correct in saying that "the morphological compactness of the vascular strands of a carpel and their delimitation from the surrounding tissues vary widely with the type of material under study. - - - there are numerous examples where either the primary xylem or primary phloem components are not only less compact and more diffuse but also their limits more or less merge with the surrounding tissues. Under such conditions, the determination of the xylem-phloem axis in relation to orientation becomes a matter of subjective and biassed judgement." *Burmannia pusilla*, however, fortunately is not such a plant, and shows a very definite inverse orientation as shown in the 'untouched' photographs (Fig. 1). It is really a surprise how PAI calls them as normally oriented.

PURI (1952) states that if the multilocular condition is brought about by fusion of placental regions only and not by fusion of carpellary margins, we are justified in interpreting the placentation as parietal. But it is not always possible to distinguish between placental tissue and carpellary tissue. There are many plants in which one cannot be certain where one ends and the other begins. PURI's assumption that the ventral bundle marks the limit of the carpellary tissue cannot be correct, because then one has to assume that the ventral bundle runs at the extreme margin of a carpel and that there is no carpellary tissue beyond it. The ventral bundles do not run at the extreme margin of the carpel. They are more or less intramarginal and at least some carpellary tissue must exist beyond it. The term placenta has been indiscriminately used by many authors. EAMES (1961 p. 205) is of the opinion that the term placenta should be loosely used for the fertile area of a carpel or of united carpels, and he defines placentation as the pattern of ovule arrangement on the carpel.

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Inventering av Blekinges flora 1958–1968 – resultat och metodik

(Investigation of the Flora in the Province of Blekinge 1958–68 – Results and Methods)

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ABSTRACT

In the year of 1958 "Sektionen Blekinges Flora" was started within the Lund Botanical Society. The purpose of this Section is to investigate the distribution of the vascular plants and their communities in the province of Blekinge, southeastern Sweden. The investigation units are parishes which are divided into sections with an area of 2 to 3 square kilometres. The botanical activity by the participants in this team-work is shown with a map, where shaded areas indicate where investigations are going on. The mapping result for a plant (*Stellaria holostea*) whose frequencies (three grades are used) within each section are noted during the field work is shown. About 60 species of plant geographical interest are being mapped in this way. The results of the field work will be published successively in a series started in 1962 (Bot. Notiser 115).

Våren 1958 bildades »Sektionen Blekinges Flora» inom Lunds Botaniska Förening med uppgift att leda utforskandet av den blekingska kärlväxtfloran (se Bot. Notiser 1958 sid. 479—481). Ett decennium har förflutit sedan dess, varför det finns anledning att redogöra för arbetet under denna tidsperiod.

Aktiviteten inom sektionen intensifierades först i början av 1960-talet. Bidragande orsak härtill var anordnandet av diskussionssammanträden under vinterhalvåret, varvid särskilt fältmetodik men även taxonomiska problem togs upp till behandling. För att upprätthålla kontakt mellan inventerarna under det än viktigare sommarhalvåret har exkursioner företagits varje år sedan 1961 i olika delar av landskapet. Även då har metodfrågorna spelat en stor roll, eftersom en enhetlig fältmetodik ansetts vara av största betydelse för en inventering av detta slag. Under de senaste fem åren har botaniska inventeringar pågått i ett 20-tal socknar av ett motsvarande antal botanister, flertalet knutna till Lunds universitet men några boende i Blekinge. De områden, i vilka undersökningar är påbörjade resp. avslutade, redovisas på kartan fig. 1. Av denna framgår att mycket små områden är slutinventerade, vilket får ses mot bakgrunden av att flertalet botanister har blekingeinventeringen som en hobby vid sidan av andra kanske mera betydelsefulla sommararbeten.

Publiceringsverksamheten har nått och jämnt kommit igång. Då sektionen bildades föreslogs, att inventeringsresultaten skulle samlas i en serie, »Bidrag till Blekinges flora». I denna har hitintills endast utkommit nr. 1—3, B. E. BERGLUND: Vegetation på ön Senoren I—III (Bot. Notiser 115—116, 1962—1963). Under de senaste åren har stor osäkerhet rått beträffande lämpligt publiceringsforum. Eftersom floristiska beskrivningar av denna art bör ingå i någon svenskspråkig publikation torde den omredigerade Fauna och Flora, Svensk Botanisk Tidskrift eller en planerad naturvårdsårsbok, Blekinges Natur, vara lämpliga för sektionens behov.

Fältarbetet har fått ekonomiskt stöd genom i allmänhet årliga anslag från Kungl. Fysiografiska Sällskapet. Sektionen har även fått anslag för sin verksamhet från Hierta-Retzius stipendiefond och från Fonderna för blekingsk hembygdsforskning.

Inventeringsmetodik

Eftersom fältmetodiken skiljer sig något från den som används vid inventeringar i Skåne kommer den här att beskrivas i korthet (den avviker också från det första arbetsprogrammet publicerat i Bot. Notiser 1958). En utförligare handledning finns stencilerad och tillhandahålles av sektionen. Metodiken är ett gemensamt resultat av blekingebotanisternas diskussioner under 1960-talets början, och den har nu prövats i fält under ett flertal år. Främst skiljer den sig från den skånska metodiken genom inventeringssektionernas mindre storlek och genom att frekvenser beräknas för en grupp växtgeografiskt intressanta arter. Inventeringen har till syfte att kartera dels de enskilda arternas förekomster, dels olika växtsamhällens utbredning (översiktliga vegetationskarteringar är önskvärda). Det förhållandet, att Blekinge utgör ett gränsområde mellan ett sydligt ädellövskogsområde och ett nordligt barrskogsområde, understryker betydelsen av denna dubbelsidiga inventering. Härigenom bör också resultaten få större dokumentariskt värde, vilket är av största betydelse i en tid, då landskapet håller på att omvandlas.

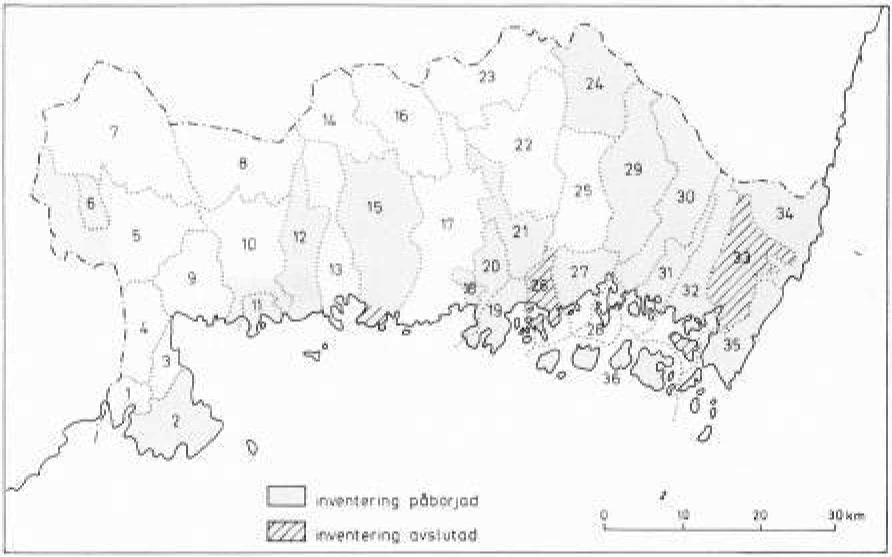

Fig. 1. Blekinge indelat i 36 inventeringsenheter. Områdenas namn, areal och inventerare anges nedan.

1 Sölvesborg (25 km²)	—
2 Mjällby (77 km²)	Elma och Torgny von Wachenfeldt, Lund
3 Ysane (26 km²)	—
4 Gammalstorp (56 km²)	—
5 Jämshög (159 km²)	Kurt Lindberg, Lund
6 Olofström (27 km²)	Densamme
7 Kyrkhult (215 km²)	—
8 Ringamåla (125 km²)	—
9 Mörrum med Elleholm (77 km²)	—
10 Asarum (112 km²)	Jane Nilsson, Enskede
11 Karlshamn (16 km²)	Densamma
12 Hällaryd (76 km²)	Lennart Månsson, Asarum
13 Äryd (91 km²)	Ingvar Nordin, Uppsala (skärgården)
14 Öljehult (73 km²)	—
15 Bräkne-Hoby (173 km²)	Carl-Erik Nylander, Ronneby och Ronnie Liljegren, Lund
16 Backaryd (102 km²)	—
17 Ronneby lfs (171 km²)	—
18 Ronneby stad (14 km²)	Ove Almborn, Lund
19 Listerby (43 km²)	Hans Wachtmeister, Wambåsa
20 Edestad (33 km²)	Densamme
21 Hjortsberga (65 km²)	Densamme
22 Tving (146 km²)	—
23 Eringsboda (121 km²)	—
24 Sillhövda (101 km²)	Sten Rundgren, Lund
25 Fridlevstad (102 km²)	—
26 Förkärla (31 km²)	Hans Wachtmeister, Wambåsa
27 Nättraby (44 km²)	Mats Sonesson, Lund och Bengt Lundberg, Strängnäs
28 Karlskrona (30 km²)	Lennart Mattsson, Karlskrona
29 Rödeby (129 km²)	Bo Hammar, Lund
30 Augerum (110 km²)	Lennart Mattsson, Karlskrona
31 Lösen (40 km²)	Karin Brunsberg, Lund
32 Ramdala (83 km²)	Björn Berglund, Lund
33 Jämjö (88 km²)	Karin Brunsberg, Lund
34 Kristianopel (92 km²)	Marianne Olsson, Jämjö och Bo Svensson, Lund
35 Torhamn (66 km²)	Björn Berglund, Lund
36 Karlskrona skärgård: Sturkö, Hasslö, Aspö, Tjurkö (42 km²)	Hans Runemark, Lund (Sturkö) och Björn Berglund, Lund (övrigt)

Socknarna används som grund för den första indelningen av landskapet; vissa smärre socknar i skärgården har dock slagits samman. Landskapet kommer därigenom att omfatta 36 inventeringsenheter. På grund av dessas storlek måste de emellertid indelas i sektioner med en areal av 2—3 km². Sektionsstorleken är vald så, att en »lokal» (=en prick) på en utbredningskarta för hela landskapet i skala 1 : 500 000 skall ungefärligen motsvara en sektion. Varje sektion bör inom sig rymma så många vegetationstyper som möjligt men ej innehålla alltför skarpa naturgeografiska kontraster. Sektionsindelningen granskas och godkännes av sekreteraren i Sektionen Blekinges Flora. Fullständiga artlistor upprättas för varje inom sektionen förekommande växtsamhälle och kompletteras efter »finkamning» av sektionen med lokalangivelser för tillkommande enskilda arter. Positioner anges så exakt som möjligt och hänföres alltid till topografiska kartan i skala 1 :50 000, som finns utgiven för hela landskapet.

Eftersom frekvensskillnader i en arts utbredning är minst lika viktiga som den absoluta utbredningsgränsen har ett 60-tal växtgeografiskt intressanta arter utvalts, för vilka frekvenser beräknas. Bland dessa arter finns representanter för nordliga, västliga, sydliga och sydöstliga floraelement jämte arter karakteristiska för urbergsterräng (större delen av Blekinge) och kalkområden (Listerhalvön). Artlistan har följande utseende.

Boreala arter med i allmänhet nordlig utbredning i Blekinge: *Carex magellanica*, *C. pauciflora*, *Equisetum silvaticum*, *Geranium silvaticum*, *Lycopodium annotinum*, *Melampyrum silvaticum*, *Linnaea borealis*, *Parnassia palustris*, *Ramischia secunda*, *Rubus chamaemorus*, *Scheuchzeria palustris* och *Trollius europaeus*.

Atlantiska arter med västlig utbredning: *Galium hercynicum*, *Juncus squarrosus* och *Narthecium ossifragum*.

Subatlantiska arter med sydlig utbredning: *Allium scorodoprasum*, *A. vineale*, *Cardamine hirsuta*, *Corynephorus canescens*, *Euonymus europaeus*, *Geranium lucidum*, *Hedera helix*, *Hypericum humifusum*, *Lonicera periclymenum*, *Melica uniflora*, *Ononis repens*, *Orchis morio*, *Serratula tinctoria*, *Teesdalia nudicaulis* och *Trifolium striatum*.

Allmänt sydliga arter: *Allium oleraceum*, *Anemone ranunculoides*, *Arnica montana*, *Cardamine amara*, *Carex paniculata*, *Chaerophyllum temulum*, *Dentaria bulbifera*, *Eupatorium cannabinum*, *Gagea spathacea*, *Galium odoratum*, *Geranium sanguineum*, *Lamium galeobdolon*, *Lathyrus niger*, *Mercurialis perennis*, *Orchis mascula*, *Prunus spinosa*, *Spergula vernalis* och *Stellaria holostea*.

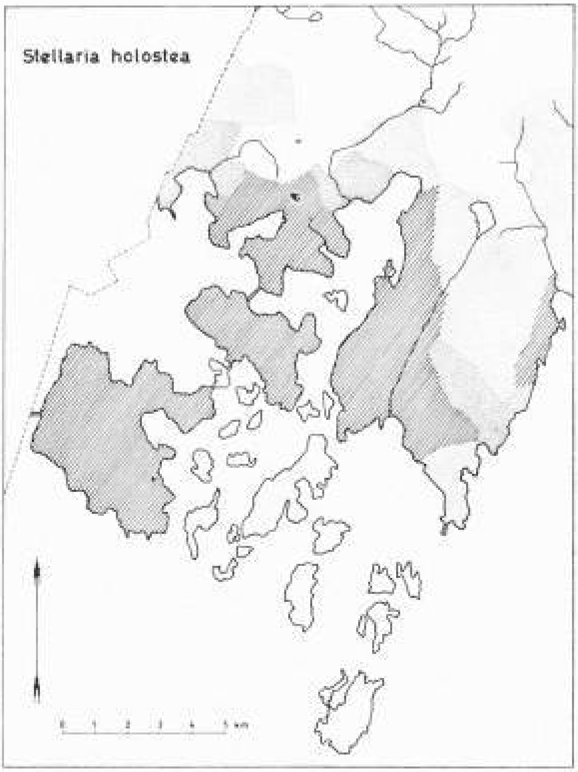

Fig. 2. Utbredningen av *Stellaria holostea* i sydöstra Blekinge (södra delen av Jämjö kommun) enligt en preliminär inventering med användning av frekvensskala. Inom streckat område är arten allmän, inom grovprickat tämligen allmän och inom finprickat sällsynt. Genom denna karteringsmetod framträder artens koncentration till den lövskogsrika kustbygden tydligare än vad som skulle skett vid vanlig kartering.

Kontinentala arter med sydlig-sydöstlig utbredning: *Cirsium acaule, Cynanchum vincetoxicum, Gagea minima, Gypsophila muralis, Helichrysum arenarium, Melampyrum nemorosum, Scorzonera humilis, Veronica spicata* och *Vicia cassubica.*

Övriga arter: *Carex pseudocyperus, Dactylorchis sambucina, D. incarnata, Drosera intermedia, Sedum annuum* och *Viscaria alpina.*

Den använda frekvensskalan grundar sig på följande definition av växtlokal: en lokal skall anses ha en radie av 200 m och följaktligen vara mer än 400 m åtskild från en annan lokal.

1—2 lokaler: sällsynt
3—4 lokaler: tämligen allmän
$\geq$5 lokaler: allmän.

Resultatet av en frekvenskartering av *Stellaria holostea* illustreras i Fig. 2.

I handledningen för inventeringar understrykes också värdet av dokumentation genom beläggexemplar och foton av växtsamhällen. Inom vissa områden (Jämjö, Senoren i Ramdala, Järnaviksområdet i Bräkne-Hoby) har översiktliga vegetationskarteringar utförts i samband med det floristiska fältarbetet. Dessa har ett särskilt stort dokumentariskt värde.

Inventeringsresultaten överföres av varje botanist från fältboken till ett register med tryckta kort för varje socken. Särskilda regler finns för denna registrering. Kortlådorna kommer senare att sammanföras till ett centralt kartotek med utbredningskartor.

Naturligt nog har de botaniska inventeringarna fått stor betydelse för länets naturvårdsverksamhet. Sektionens sakkunskap har av länsstyrelsen tagits i anspråk vid upprättandet av en »Fredningsplan» för Blekinge (sammanställd av lantmätare DAVID ÅBERG 1966). Flera av botanisterna har haft personliga naturvårdsuppdrag, bl.a. inventeringar i samband med utredningar för bildande av naturreservat. Vegetationskarteringar har därvid synnerligen stort värde.

Brief Articles and Reports

Nya fynd av Alchemilla cymatophylla Juz.

(New Records of Alchemilla cymatophylla Juz. in Sweden)

ABSTRACT. — *Alchemilla cymatophylla* Juz., which in Sweden has its main distribution area in the Province of Hälsingland, is reported from other localities: near Stockholm and near the town of Boden in N. Sweden. It has also been collected near the town of Kiruna and in the Ruskola Valley and at Armasjärvi in the Övertorneå region in northernmost Sweden and in the town of Ludvika, Dalecarlia.

För några år sedan meddelade jag (Hylander 1961) ett par fynd av *Alchemilla cymatophylla*, som jag gjort i Stockholms-trakten, alltså inom ett område, varifrån arten ej tidigare var känd. Fastän jag sedan dess inte haft tillfälle att systematiskt efterforska den inom nämnda trakt, kunde jag dock vid exkursioner där under åren 1962 och 1963 finna den på tre nya lokaler, alla (liksom den 1961 nämnda Fagersjö-lokalen) inom nuvarande Farsta församling, nämligen nära Fagersjövägen mellan Fagersjö och Hökarängen, vid Farsta gård och slutligen på motsatta sidan av Magelungen V om Ågestabron. Detta kan knappast tydas annorlunda än att arten i trakten kring Magelungen (dit även min Huddinge-lokal hör) har ett litet stabiliserat förekomstområde, vars ålder ej nu kan bedömas och vars utsträckning återstår att utforska. Avståndet mellan de yttersta av mina fyndplatser är ej mer än c. 4 km.

Artens rikaste förekomstområde var enligt Samuelssons framställning Hälsingland, och artens stora frekvens där har blivit ännu mera påtaglig genom de i Riksmuseet (S) liggande stora insamlingar, som M. Engstedt gjorde där 1943—1950. Utom en ofantlig skörd från Delsbo samt talrika kollekter från de redan i Samuelssons förteckning upptagna socknarna Norrbo, Bjuråker, Hassela, Forsa samt Hudiksvalls stad innehålla Engstedts samlingar arten från Loos, Järvsö, Ljusdal och Färila. Ökningen av antalet lokaler framgår vid en jämförelse mellan Samuelssons karta (1943) och Hulténs (1950).

I sina huvuddrag stämma dock de båda kartorna överens; vad som tillkommit efter 1943 är blott en utfyllnad inom förut kända centra. På samma sätt har den västra av de båda jämtländska lokalgrupperna i någon mån vidgats genom insamlingar av H. Smith på några närliggande lokaler vid Enafors.

Något utanför denna räjong faller ett fynd i Föllinge: Skärvängens by, belagt med ett ex. i S, samlat av L. Strindberg 1943. Från Dalarna, där Samuelsson endast kände den från Ore, nära Hälsinge-gränsen, ha Almquist & Björkman senare publicerat en av den sistnämnde gjord och bestämd kollekt från Ludvika stad.

Vid ett besök i Boden vid midsommar 1966 fann jag vid en liten promenad kring järnvägsstationen på en föga naturlig ängsmark en vacker grupp av *A. cymatophylla*, växande i sällskap med bl.a. *A. micans* och *A. Wichurae*. Denna från först nämnda utbredningsområden långt avlägsna lokal är emellertid inte artens nordligaste. I sin uppsats om floran i Övertorneå-trakten i Norrbotten meddelade nämligen Lönnqvist (1964) ett fynd av arten i Övertorneå, i Ruskola-dalen »rätt nära en kallkälla i lundartad skog». I en samling av Alchemillae, som Lönnqvist sänt mig men som jag först nyligen haft tid att genomgå, fann jag ännu en kollekt från samma socken: Armasjärvi, landsvägsdiket vid Lugnets gård, 13.VI.1960.

Arten har dock, enligt belägg i S, redan tidigare samlats ännu längre norrut: där ligga nämligen två vackra insamlingar, gjorda av E. Asplund 1949 och 1952, från Kiruna: Konduktörsgatan, ruderatmark, resp. gräsmatta. Förekomstsättet erinrar alltså mycket om det vid Boden, och i båda fallen ligger det närmast att tänka på järnvägen som förmedlare, direkt eller indirekt, av spridningen. Den nyss nämnda Ruskola-kollekten kan ju å andra sidan tyckas tala för en »naturlig» förekomst; även *A. micans* nämns emellertid av Lönnqvist l.c. från likartad (samma?) lokal i Ruskola-dalen, och denna art kan ju över huvud taget inte räknas som indigen hos oss. Säkerligen gäller detta även *A. cymatophylla*, så som även Samuelsson ansåg; men uppenbarligen är det för tidigt att söka fastställa dennas spridningsvägar och spridningshistoria hos oss. Av allt att döma skall den visa sig finnas på åtskilligt flera platser än hittills känt och inom vitt skilda områden. En närmare undersökning av Norrbottens kustland synes t.ex. över huvud kunna ge en hel del i fråga om *Alchemilla*-floran — ytterst litet är här samlat, och redan den lilla glimt jag fick av den vid Boden syntes mycket lovande.

Högst sannolikt står *A. cymatophylla* att finna även i Finland; möjligen höra hit ett par exemplar som jag sett men funnit för ofullständiga för en säker bestämning. Arten är emellertid enligt Juzepczuk 1959 funnen i nordligaste Ryska Karelen (Kk) på ett par ställen vid mynningen av Kandalaksjaviken. För övrigt har den helt nyligen (Fröhner 1967) rapporterats som ny för Tyskland (Crottendorf i Erzgebirge).

Jag kan till sist i detta sammanhang nämna, att bland Lönnqvists hittills obestämda samlingar från Övertorneå fanns även en kollekt från Matarengi (14.VI.1960), som jag ej tvekar om att föra till *A. propinqua*. Denna är i Sverige förut ej känd nordligare än Jämtland (där den traktvis är vanlig!) och Ångermanland — med undantag för en lokal i Torne Lappmark; liksom *A. cymatophylla* är den nämligen (enligt Samuelsson) samlad på en gräslinda vid en station, i detta fall Vassijaure. Riksgränsbanans stationer skulle antagligen bjuda på flera överraskningar i *Alchemilla*-väg om ej deras gräsmattor sloges så tidigt som åtminstone varit fallet, när jag velat pröva min lycka där. Även denna art är enligt Juzepczuk funnen vid Kandalaksjaviken, vid själva polcirkeln, alltså långt från de av SAMUELSSON kända östligaste lokalerna på Karelska näset. Efter hans tid ha emellertid åtskilliga fynd av arten gjorts även i Finland, särskilt i Kajanska Österbotten (Kainu; se JALAS 1965).

ZUSAMMENFASSUNG. — Die zuerst von SAMUELSSON für Schweden nachgewiesene Art *Alchemilla cymatophylla* hat dort, wie er schon feststellte, ihre Hauptverbreitung in der südnorrländischen Provinz Hälsingland, was durch grosse Einsammlungen von M. ENGSTEDT in den Jahren 1943—50 noch mehr hervorgehoben wurde; vgl. die Karten bei SAMUELSSON 1943 und HULTÉN 1950. Ausserhalb dieses Gebietes kannte SAMUELSSON diese Art von einer Lokalität in der Provinz Dalarna (Ore, nahe der Grenze von Hälsingland) sowie aus verstreuten Standorten in den Provinzen Närke, Västmanland, Medelpad, Ångermanland und Jämtland. Ein paar von mir in der Stockholmer Gegend gefundene Lokalen habe ich im Jahre 1961 publiziert, und hier habe ich später diese Art noch in ein paar benachbarten Lokalitäten gefunden. Während eines Aufenthaltes im Sommer 1966 in der Stadt Boden in Norrbotten, der nordöstlichsten Provinz Schwedens, fand ich einen kleinen aber wohlentwickelten Bestand von *A. cymatophylla,* also weit von den nördlichsten von SAMUELSSON genannten Fundorten. Später hat es sich aber gezeigt, dass die Art schon 1949 und 1952 in der Nähe der Eisenbahnstation der Stadt Kiruna in Torne Lappmark (c. 67° 50′ n.Br.) von E. ASPLUND gesammelt wurde; überdies ist die Art aus Norrbotten von einem sehr nördlichen Standort (Ruskola in Kirchspiel Övertorneå, c. 66° 20′ n.Br.) von O. LÖNNQVIST 1964 publiziert worden, und aus demselben Kirchspiel liegt noch ein nicht früher veröffentlichter Fund (aus Armasjärvi) desselben Sammlers vor. Weiter südlich wurde die Art in Dalarna, in der Stadt Ludvika, von G. BJÖRKMAN gefunden (ALMQUIST & BJÖRKMAN 1960). Die Art ist noch nicht in Finnland festgestellt worden. Dagegen sind von JUZEPCZUK aus dem nördlichsten Teile von Russisch Karelen (bei dem Kandalakscha-Busen des Weissen Meeres) ein paar Funde publiziert worden.

Zu den Arten, die JUZEPCZUK aus dieser Gegend mitgeteilt hat, gehört auch *Alchemilla propinqua.* Diese Art wurde in den letzten Jahren an mehreren Orten im inneren Finnland (Provinz Ostrobottnia kajanensis) gefunden (s. Karte bei JALAS 1965) also weit von den östlichsten von den SAMUELSSON bekannten fennoskandischen Fundorten. In Schweden ist diese Art in Jämtland ziemlich häufig, übrigens war sie aber nur aus verstreuten Lokalitäten in Mittelschweden (s. Karte bei SAMUELSSON 1943) und einem einzigen Lokal im nördlichsten Torne Lappmark (Station Vassijaure bei der norwegischen Grenze) bekannt. Neulich fand ich sie aber unter unbestimmtem *Alchemilla*-Material, das O. LÖNNQVIST bei Matarengi in Övertorneå, Norrbotten, gesammelt hat. — *A. cymatophylla* und *A. propinqua* dürften im nördlichsten Schweden eine grössere Verbreitung haben als bisher bekannt ist.

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Nils Hylander

En ny lokal för Veronica praecox i Skåne

(A New Find of Veronica praecox All. in Scania, South Sweden)

ABSTRACT. — *Veronica praecox* All. is reported from the Parish of V. Karaby in Scania, South Sweden.

Veronica praecox All. har under vår tid rapporterats från Gotland av Hylander (1941), från Öland av Albertson (1944) och Sterner (1946) och från Skåne av Merker (1959). Medan arten på Gotland och Öland är funnen på alvarmark, är den i Skåne ett åkerogräs. Merker fann den på två lokaler, Stävie sn, Lundåker och V. Karaby sn, Jonstorp.

Tillsammans med professor Nils Hylander studerade jag den 12 maj 1968 den från *Veronica hederifolia* nyss utspaltade *V. sublobata*. Båda arterna förekom flerstädes rikligt. Vid ett stopp för att inventera floran i ett rågfält på mycket lätt sand i V. Karaby sn, 100 m öster om gamla E4-vägen på Björnstorps gård, fanns förutom nyssnämnda arter även *V. triphylla* rikligt och till vår stora överraskning även ett tiotal välutvecklade 10—15 cm höga plantor av den sällan funna *Veronica praecox*. Denna nya lokal ligger ca 3 km väster om Merkers från samma socken.

Andra ogräs i samma rågåker var bl.a. *Saxifraga tridactylites*, *Camelina microcarpa*, *Veronica persica*, *V. agrestis* och *V. arvensis*. Anmärkningsvärt är att såväl på Öland som även på växtens enstaka fyndplatser i England *Saxifraga tridactylites* och *Veronica triphylla* uppges som följearter.

Detta fynd verifierar Merkers uppfattning att *Veronica praecox* har ett vidare utbredningsområde på lätta sandjordar i västra och södra Skåne. Artens tidiga och korta utvecklingsperiod försvårar upptäckt och identifikation. Den är även svår att återfinna på tidigare lokaler.

Citerad litteratur

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BERTIL HYLMÖ

Botanisk litteratur
(Botanical Literature)

HUIKARI, O. and PAARLAHTI, K.: Results of Field Experiments on the Ecology of Pine, Spruce and Birch. — Communicationes Instituti Forestalis Fenniae 64.1, 135 pp.

Peatland drainage is an activity of great importance for Finland's economy. A large part of the resources available for silvicultural improvement will be used on the peatlands and a considerable part of future forest yields will be taken from these areas. It is thus not surprising that research into problems pertaining to plant growth on peatlands, both drained and undrained, is very active in Finland. Much of the earlier work has been reviewed by HEIKURAINEN 1964 (in International Review of Forestry Research, Vol. 1) but the highly practical scope of much of the peatland expermentation may lead many ecologists to overlook the reports on Finnish peatland research as sources of basic ecologcial information. One example of this type of research is HEIKURAINEN's elegant investigation of the water consumption of tree-stands on peatlands, by following the daily fluctuations in ground water level (Acta Forest. Fenn. 76, 5—16, 1963). Another and more comprehensive study is the paper presented in the headline above. This paper reports extensive series of ecological experiments mainly carried out in 1962, 1963 and 1964 within two different areas, Vilppula in southern Finland (62° lat. N) and Kivalo in northern Finland, not far from the Arctic Circle. The studies were carried out in pine, spruce, and birch stands established on peatlands drained earlier.

The following ecological factors were varied: ground water level (at 10, 30, 50, and 70 cm below soil surface), soil temperature (by cooling the ground, see below), air temperature (by inclosing whole trees in plastic tents) and nutrient level (by adding a NPK fertiliser at a suitable rate). In addition to these experimental changes, various climatic and other factors were recorded. Height growth and stem growth were measured at close intervals, the stem growth measurements by dendrometer tapes.

Cooling the ground sounds difficult, but the authors have tackled the problem in an interesting way. After preliminary experiments with various cover materials, they found that the most efficient way of cooling was to remove the snow in the winter so as to let the winter cold penetrate deep into the soil. Then, in late winter, cover material such as straw or low humified *Sphagnum* peat was applied over the ground, retarding the melting of the snow considerably in the spring. Soil frost disappeared one to three months later on the cooled ground than on the control plots. Of course there may be effects of the covering other than on the soil temperatures and therefore the authors laid out separate controls with the same cover material, but applied in autumn before snow fall. In this way they claim to have separated the mulching effect from the effect on soil temperature.

The results of the investigation are presented partly in tables and partly in diagrams. In this review only a few items of particular ecological interest can be mentioned. One such observation is that the soil temperature seemed to have rather little effect on tree growth, while an increase in air temperature speeded up the growth-rate considerably in the early stages — although growth began almost simultaneously outside the plastic tents. The trees in tent ceased growth earlier and their total growth was not very different. Precipitation and air humidity had a measurable positive effect on growth, although weaker than that of temperature. Dry periods decreased the rate of diameter growth, even on plots where the ground water level was 10 cm below soil surface. The authors discuss the technical difficulties of separating growth from swelling of the trunk and seem to be of the opinion that drought really affected growth. Of the various ground water levels, 30 and 50 cm appear to be optimum on fertilized plots, while 70 cm plots often showed a lower growth than plots with somewhat higher ground water level. Nutrient application was tested on the poorer pine sites and always had a favourable influence on growth; fertilized trees appeared to be less sensitive to adverse effects of other factors, such as high ground water level and drought.

It is the reviewer's hope that these short remarks have indicated the unusual character of this paper, in which the effect of climatic and edaphic factors was studied by direct experiment in the field. The report gives all essential facts about the experiments but it is not always easy to follow the authors' text, mainly because of the richness of data. In fact this is the one of the very few cases where the reviewer would have preferred a somewhat longer text. The present 135 pages do not allow full discussion of all the interesting ecological relations dealt with.

There is not much to criticise in the report; the authors are very critical in their conclusions. It is somewhat surprising that no text reference is made to the extensive investigations by MORK and co-workers in Norway on the influence of air temperature on extension growth (although one of MORK's papers is quoted in the reference list). Some of the growth comparisons would certainly have been easier, if the diagrams had presented relative growth, as in MORK's papers. Most of the statistical treatment is very satisfactory, with an effective use of earlier diameter widths as concomitant measurements in analyses of covariance. However, in some of the significance tests the authors apparently use each sample tree as an independent measuring unit. The high statistical significances obtained in this way concern differences between plots, not necessarily between treatments. Most of the experiments are laid out without more than one plot treated similarly in all respects. There are then no "degrees of freedom" left for computation of the variation between plots within treatments, which would provide the correct variance estimate to compare with that between treatments. However, in the reviewer's opinion, no great mistakes have been made. On the contrary, he recommends the present paper to all ecologists interested in problems connected with growth-limiting factors in natural and semi-natural vegetation.

C. O. Tamm

EN BOKANMÄLAN

Överstelöjtnant K. Hasselrots »Västergötlands flora» (Lund 1967) har mötts av delvis självförvållad hård kritik. Boken verkar slarvigt hopkommen, med flera felstavade växtnamn och många tryckfel i övrigt, vårdslös interpunktion, stor brist på konsekvens, diverse dubbelföringar, en ofullständig litteraturförteckning osv. Korrekturgranskningen tycks ha varit minimal. En huvudorsak till bristerna synes vara, att förf. haft för bråttom både med utarbetningen och tryckningen. Man tycker dock att han i förväg borde ha kunnat eliminera de flesta skönhetsfläckarna.

Kritiken har begripligtvis skjutit in sig på dessa men inte mycket berört själva sakinnehållet, vilket såvitt jag kan se står på betydligt högre plan. Visst lider också texten av nämnda svagheter, även oklarheter och småfel av olika slag. Men intet grövre sakfel har hittills påtalats, och jag tror ej att man skall hitta många sådana.

Detta inlägg föranledes av den recension, som Örjan Nilsson i Bot. Notiser 1967 ägnat Hasselrots flora. Slarvigt utförd liksom denna är den dessutom helt negativ och så rik på missförstånd, överdrifter och småaktigheter, att ett genmäle tarvas. — Emedan jag rådfrågats av KH i vissa stycken och hjälpt honom med en del formuleringar, nödgas jag tala något i egen sak. Nämnas bör att jag också hade sett hans manus och tillrått en grundlig justering före tryckningen.

Nu till recensionen. Strax i början läses: »Avsikten synes ha varit att revidera och komplettera A. Rudbergs Förteckning . . . (1902)». Ja, därom behöver ÖN inte tveka, revideringen är nöjaktig och tillökningen ansenlig. (Litet längre fram nämnes, att »boken innehåller flera arter och nyare lokaluppgifter än R:s förteckning», vilket — eo ipso självklart — utgör ÖN:s enda positiva erkännande.) Faktiskt har KH ett 70-tal ± bofasta arter som hos R. saknas (el. stå med ?), ca 220 nya »finstilsarter» (adventiva el. förvildade), en mängd (± säkra) nya hybrider samt ett mångdubblat lokalantal inkl. 1000-tals nya fynd av KH och hans medhjälpare. Nog borde detta kunna mätta »ett ackumulerat behov av nya floristiska uppgifter», varom ÖN ordar.

Floran inledes med N. Albertsons utmärkta skildring »Västergötlands växtvärld» (Natur i Vg). Med förläggarens medgivande har KH däri gjort nödiga smäändringar och — mest i det sista avsnittet — några tillägg, som borde ha fått en egen underrubrik. Alltså skjuter ÖN, siktande på KH, men träffar mest N. Albertson, som ju svarar för den »ofta» missvisande rubriceringen och skrivit »den för södra Sverige unika fjällarven» — ett uttryck som ÖN kallar en »ganska överraskande upplysning». Som sådan räknar han även en utsaga om *Betula nana*, där »södra» framför Sverige fallit bort (vilket en vettig läsare genast inser), ävensom KH:s uppräkning av bl.a. *Epipactis palustris* och *helleborine* i kalkkärr etc. Själv har jag utan förvåning sett båda sida vid sida, den ena växande mellan, den andra ovanpå tuvorna.

Källcitat är en svår sak, kraven på korthet och precision tyvärr oförenliga. Man kan med ÖN beklaga, att inte KH citerat varje källskrift för sig utan endast författaren, även om denne skrivit mer än *ett* arbete. Månget citat är likväl mera preciserat (med årtal). Dessvärre går det ej att i större skala förfara så. I stort sett synes mig KH ha gjort det enda praktiskt möjliga, fast han måste tillvitas en rätt stor nonchalans i sitt sätt att citera. Att som ÖN påstå: »för att finna citatet får man leta genom 11, 15, resp. 15 arbeten», är ju rent nonsens. En klok läsare bedömer av titeln, var han bör söka, och hittar oftast citatet i skrift n:r 1 el. 2 (el. 3). Kanske får han i värsta fall söka förgäves, det må gälla en opublicerad uppgift el. någon gång ett felcitat, vilket förekommer i de bästa skrifter.

I ett längre stycke nagelfar ÖN bl.a. valet av stilsort, vissa uteslutningar m.m. och vill ha »förklaring» el. »motivering» för åtskilligt, som helt enkelt beror på slarvig redigering! Delvis gäller det också rena smakfrågor ss. uteslutningen av snödroppe, pärlhyacint och en »ofta förvildad» lilja kallad *Lilium flavum* (månne *Hemerocallis flava*?). För ÖN, som tycks likställa »förvildad» med »tillfällig», ter det sig inkonsekvent att sätta *Lilium bulbiferum* och *martagon* med fetstil (i motsats till västgötsk *Tulipa* m.fl.); han förstår därvid ej, att så skett just för att markera dem som icke tillfälliga (jfr Hylanders flora!). I allmänhet har KH gjort lämpligt stilval, även t.ex. för *Koeleria pyramidata* (god motivering i citerade källor!). — Det är förståeligt att synonymer nämnas utan auktor av KH, som oftast anfört dem blott för lättare jämförelse med Rudberg, där auktorsbeteckningar helt saknas. — En »besynnerlig» sådan tror sig ÖN ha funnit vid *Erophila* (skall vara *Euphrasia*) *brevipila v. procumbens*, men där står blott ett årtal jämte finnaren. — Den enligt ÖN »tämligen fullständiga» artförteckningen saknar mig veterligt ett enda taxon av betydelse, *Phleum pratense* ssp. *nodosum*. Men ÖN efterlyser i stället de från Angered och/el. Nödinge kända *Rumex sanguineus* och *Gagea spathacea*; han tycks ej ha läst KH:s motivering för uteslutningen av dessa 2 socknar, som förut redovisats i H. Fries' Bohusflora. Vidare saknar ÖN »den mera tillfälliga *Leonurus marrubiastrum* (belägg i LM)». Den är funnen just i dessa socknar (Bot. Notiser 1945 sid. 451 o. 460) men kan ju möjligen också tillhöra de många växtgeografiska missfoster, som genom snedvridet intresse hos hrr Thedenius m.fl. kommit att belasta Vg-floran, men som KH dessbättre satt inom klammer. — Att ytterligare påtala frånvaron av så föga kända taxa som *Rosa Sherardii* (se nedan), *Ranunculus aquatilis* (s.str.) och *Callitriche platycarpa*, vittnar ej om gott omdöme, då väl ingen enda säker uppgift från Vg förelegat. — Större fog har ÖN:s påpekande, att okontrollerade herbarie- och andra uppgifter tydligen ofta godtagits. En del felbestämningar (särskilt betr. hybrider) måste dock anses ofrånkomliga i ett så stort och heterogent material. Blott ett exempel anför dock ÖN: *Epipactis atrorubens* från Kinnekulle (N. Sylvén), enligt ÖN = *E. helleborine*. Då t.o.m. en framstående kännare av svensk flora råkat göra denna ej ovanliga förväxling, bör KH ursäktas. »I kritiska släkten kan exemplen mångfaldigas» tillägger sedan ÖN (efter stickprov i Lunda-museet). Nå, en mångfald av 1 är kanske ej så stor, och då brist ju råder på kunniga specialister, bleve man ÖN särdeles tacksam för de rättelser han kan göra. Även museet finge gagn därav. Som varje fackman vet, äro felbestämningar i offentliga museisamlingar legio.

För en lekman som KH har nog detta stått mindre klart. Man finner dock flera befogade ? även i Vg-floran. — Vidare läses, att ÖN skulle »välkomnat uppgifter om florans nuvarande utseende i provinsen». Man tror knappt sina ögon. Just detta har ju KH sökt belysa, med massor av ± färska årtal, talrika »utg.» el. »ej återf.» osv. Efter blandat klander nås omsider det långa styckets slut, där ÖN häcklar diverse »lätt misstolkade eller otympliga formuleringar». Hans idoga felsökande tycks menligt ha påverkat förmågan att läsa innantill. Ett av citaten (om *Gentianella*) är falskt, ett annat (om *Hedera*) lättbegripligt i sitt sammanhang. Och visst kan man tillåtas en språklig frihet som »sällan långlivad» (*Digitalis*); ej ens ÖN lär väl tro, att uttrycket åsyftar individerna.

Ansvaret för uteslutningen av *Rosa Sherardii* (förut kallad *R. tomentosa*) påvilar mig, liksom en lapsus betr. *Rosa*-hybriderna. Det föll sig enklast att nyttja de citerade källornas benämningar, men de borde ju haft cit.-tecken (»*R. coriifolia*×*mollis*» resp. »*R. glauca*×*mollis*»). Av alla uppgifter om *R. tomentosa* i Vg återstår i HULTÉNs atlas en enda prick (nära Mariestad), vilken jag ej hann utreda. Enligt ÖN har arten »sedan gammalt kända lokaler i Skövdetrakten». Om dessa tiger all mig bekant litteratur. Inte kan väl ÖN, själv västgöte, ha förväxlat Mariestad med Skövde? Det återstår då att förklara, hur han kunde negligera de påstådda förekomsterna, när han ett halvår tidigare skrev om *R. Sherardii* (Bot. Notiser 1967). I denna f.ö. välkomna utredning saknas all antydan om inlandsfyndorter.

Riktig är också recensionen i mångt och mycket, som väl är. Men den ger genom sin osaklighet och negativitet en skev och orättvis föreställning om vår nya Vg-flora. Rättvisligen måste sägas, att KH:s bok har ett mycket stort värde som växttopografisk orientering. Att denna måste nyttjas med kritik, inser utan svårighet varje fackman liksom övriga i ämnet bevandrade. Trots allt erbjuder den en systematiskt nästan fullständig och geografiskt ganska fyllig bearbetning av ett hittills ytterligt splittrat material rörande Vg:s nutida flora. Den bör därför oaktat sina formella brister uppskattas av de botanistgenerationer, som utan KH:s insats torde fått vänta till döddagar på den välbehövliga sammanställningen. Till förtjänsterna hör också, att KH lyckats mobilisera en reserv av delvis mycket kunniga blomstervänner, som utan att själv skriva tillfört floran många värdefulla rön och upptäckter av intresse. Man önskar livligt, att KH:s arbete närmast må stimulera till fortsatt amatörbotanisk livaktighet.

ERIK ALMQUIST

ETT GENMÄLE

I min recension av KARL HASSELROTS (KH) Vg-flora uppehöll jag mig främst vid det slarv den formella utformningen vittnade om, då det kunde befaras att detta även kommit sakinnehållet till del. Det gläder mig därför att floran tycks ha flera förtjänster än vad jag lät påskina. I fråga om den formella utformningen var dock min negativa inställning till boken befogad. I min recension påpekades att en redaktör (eller granskare) skulle kunnat eliminera åtskilligt av det som nu drar ned intrycket av boken. I den mån min kritik sålunda drabbat även bokens granskare vill jag beklaga att det myckna arbete dessa osjälviskt nedlagt på att förbättra KH:s arbete i så ringa mån beaktats av denne. Granskarnas rättelser och påpekanden har ej sällan betraktats som petitesser och ignorerats av KH, ett förfaringssätt som talar för sig själv.

Det framfördes ej enbart anmärkningar av formell karaktär i min recension. Där påpekades att meddelade växtfynd och herbarieuppgifter godtagits utan närmare kontroll. Vad detta kan leda till är självklart! Att sätta ett ? efter en tveksam uppgift är ett bekvämt sätt att undandraga sig besväret att kontrollera. I LD har endast herbarieetiketterna avskrivits utan att ansvar tagits för bestämningen, vilket meddelades KH. Registreringen av Vg-materialet i LD var ofullständig. Detta kallar jag ett okritiskt utnyttjande av ett tillgängligt material. Något tillskott skulle Vg-floran fått om detta material brukats till fullo, t.ex. en notis om *Empetrum hermaphroditum* från Kinnekulle. Felaktigheter skulle kunna ha undvikits. Här skall nämnas ytterligare *ett* exempel från företagna »stickprov». I Vg-floran finns sex lokaluppgifter för *Fragaria viridis*, som grundar sig på material i LD. Samtliga är *F. moschata*. Jag ställer mig tveksam inför accepterandet av många hybrider i floran, t.ex. i *Salix*. I detta släkte är 29 hybrider medtagna av vilka 6 saknas i Hylanders flora (1966), vilket borde varit en anledning till kontroll. Jag framhöll också att samarbetet mellan de i Vg verksamma botanisterna tycks ha brustit. Säkert skulle L. Fridén och Bengt M. P. Larsson kunnat bidraga med åtskilliga lokaler till floran. Båda saknades i listan över insamlare och meddelare. Inte på något ställe i boken nämns om KH el. hans medarbetare samlat ett beläggmaterial för sina fynd, var detta ev. material finns, el. om det granskats.

Till slut ett bemötande till några av de anmärkningar prof. Almquist gör på min recension. Jag vill härvid beklaga de två felaktiga växtnamn, som förekom i min recension, vilket var slarv. — Det står i KHs bok »den för södra Sverige unika fjällarven», och »södra» framför Sverige (om *Betula nana*) har fallit bort. I regel förekommer ej *Epipactis palustris* och *helleborine* »sida vid sida» i kalkkärr. — Det ackumulerade behovet av floristiska uppgifter från Vg kan anses mättat vad det beträffar »nytillkomna» arter (flera publicerade tidigare). När det gäller lokaluppgifter saknas däremot ännu mycket. Endast omkr. hälften av landskapets socknar är inventerade. Vissa delar är mycket översiktligt inventerade och åtskilliga inventeringar börjar bli ålderstigna. — Sättet att citera källmaterial i floran är otillfredsställande. KH har i floran ej enbart tagit upp den eller de arter som eventuellt figurerar i ett arbetes titel. Man kan tvingas att söka igenom alla arbeten under en citerad uppgiftslämnare. Man kan också få leta förgäves eftersom ej åtskillnad gjorts på publicerade och opublicerade uppgifter. Med hänsyn till källförteckningens form och ofullständighet finner jag inget förmildrande i KHs sätt att behandla originaluppgifter. Det är inte ens praktiskt.

En förklaring till valet av stilsorter i artnamnen efterlystes därför att det på grund av en slarvig redigering ofta ej var möjligt att avgöra vad de olika stilsorterna innebar. Av vad som framgår ur citerade källor är det ej möjligt att avgöra om *Koeleria pyramidat*a skall betraktas som stationär el. tillfällig på sin Kållandslokal. Skårman såg den 1921 och 1924. KH anger inte om den finns kvar. Arten är indigen i Danmark vilket motiverar Hylanders (1953) stilval. — Att utelämna auktorer på synonymer må vara tillåtet i en bok av denna typ. En missledande konsekvens kan det få, vilket tydligt framgår av behandlingen av *Rosa*-hybriderna. Många anmärkningar kan i övrigt göras mot auktorsbeteckningarna i boken av vilka flera är så grava att de kan betraktas som sakfel, t.ex. »*Salix daphnoides* L.», »*Rumex aquaticus* RECH. FIL.» och »*Galium verum* L. ssp. *euverum* L.» — Auktorsbeteckningarna på »*Potentilla anserina* ssp. *euanserina* (HYL)» och »*Euphrasia brevipila* BURN & GREMLI v. *procumbens*» är besynnerliga. — Arturvalet till en bok av denna typ kan diskuteras. Vissa kritiska taxa kan med fördel uteslutas. Man förvånas då av den inkonsekvens som föreligger i Vg-floran härvidlag. Sålunda är kritiska taxa som *Carex Bergrothii* och *tumidicarpa* och *Dactylorchis Fuchsii* medtagna. Med tanke på de upplysningar man i dessa fall kan hämta ur floran hade det nog varit förnuftigt att dylika taxa utelämnats helt.

Andra exempel nämnde jag för att belysa den inkonsekvens som förelåg i boken, där de båda socknarna Angered och Nödinge dels var med å kartan över området och dels i förteckningen över områdets kommuner och socknar, men i övrigt uteslutna. Min anmärkning gentemot »uppgifter om florans nuvarande utseende» gällde främst sällsyntare arter, jfr *Koeleria pyramidata* ovan. I övrigt har KH givit många värdefulla upplysningar i detta avseende. — Mitt citat om *Gentianella campestris* är rätt. För att belysa den otympliga formuleringen återges hela meningen. »Det mesta säges vara v. *suecica* FROEL. (SKÅ, KJ, S&S), likväl uppges v. *germanica* FROEL. »som vanligt i Vg» ensam sedd i Dala (ALB) o. på Falbygdens berg (SKÅ).» — I LD finns material av *Rosa Sherardii* från Vg, bl.a. Skövde. I mitt arbete över de skandinaviska rosorna (Bot. Notiser 1967) angavs för många arter inte utbredningarna i detalj.

Nog ordat om detaljer. Min negativt hållna recension av Vg-floran var ett uttryck för besvikelsen över att floran inte uppfyllde de högt ställda förväntningarna på en modern och kritisk flora över landskapet. Flera kollegor har omvittnat liknande reaktioner. Floran saknar givetvis inte sitt värde, men de uppenbara bristerna i källkritik, materialutnyttjande, konsekvens och noggrannhet framstår fortfarande som beklagliga.

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