Drawings of Scandinavian Plants 3–4
Rosa L.

By *Örjan Nilsson*

Institute of Systematic Botany
University of Lund

Rosa canina L. em. CRÉP.

(*R. dumetorum* THUILL.)

Shrub, 2—4 m tall, with arching, erect or sometimes climbing stems; young stems green or reddish green. *Prickles* rather stout (up to 10 mm long); *curved or hooked* with rather broad bases, usually all similar, rather sparse on young stems. *Leaflets* 5—7, ovate, elliptic or broadly lanceolate (15—40×10—20 mm), usually acute or acuminate; the terminal one the largest; glabrous or less frequently pubescent beneath, eglandular or occasionally with a few glands below on the main veins, or on rachis; *simply* or occasionally doubly *serrate*, teeth rather long, acute, straight or curved inwards; stipules usually narrow, often minutely glandular- serrate, auricles long, acute. Bracteoles rather narrow, acute, usually shorter than the pedicels. *Pedicels comparatively long*, 1—2.5 cm (of about the same length as the hips or usually somewhat longer), usually glabrous, erect. Flowers solitary or a few (2—4) together, white or pink. *Sepals usually reflexed* and *falling soon after flowering*; outer 3 pinnatifid, *their lobes narrow*, usually *entire* and sometimes glandular-margined. Stamens falling soon after flowering. *Styles* long, rather *few, usually glabrous or sparsely villous; stigmas in a loose, diffuse, globose or conoidal head; disc 4.5—5.5 mm,±conoidal, orifice 0.5—1 mm. Hip* 1—2 cm long, ovoid or ellipsoid, *usually smooth, hard and leathery, ripening late*, in S. Scandinavia in the beginning of October. June—July. 2n=35.

Native. Scrub on sunny and dry hill slopes, open woods, and shores. *R. canina* is widely distributed in Europe (except for the N. parts) and SE. Asia, and is very common in the lowlands of C. and W. Europe. In Denmark *R. canina* is the commonest rose, occurring on the islands and

in SE. Jutland (particularly common is var. *canina*, cf. below) but it is
rare or absent in W. and N. Jutland (mainly var. *canina*); in Norway it
occurs only in the coastal districts between Sogn and Rogaland and
along the coast of Skagerak (both varieties); in Sweden it is the com-
monest rose in most of the southern coastal districts (mainly var.
canina), reaching northwards to Bohuslän and Uppland, less abundant
in the inland, locally rare or absent (in Norrland as escapes from cul-
tivation); in Finland it is rather common in the "skärgård" of Åland.

R. *canina* is very variable (like the dog, hence the specific epithet) in
Scandinavia. Two form groups may be distinguished, here treated as
varieties. Several intermediate forms are found.

Var. *canina*, the first group, is distinguished by glabrous leaves and
styles (the variety here illustrated).

Var. *dumetorum* (THUILL.) MERT. & KOCH, the second group, has ±
pubescent leaves and usually villous styles.

These two groups have often been treated as separate species. In
Scandinavia the two form groups have the same distribution areas, only
locally one or the other may be absent. However, on the whole var.
dumetorum seems to be less common than var. *canina*. Many attempts
have been made to make further divisions of the two groups, e.g., by
CRÉPIN who distinguished 6 form series within var. *canina*, primarily
according to the serration of the leaflets, secondarily according to
presence versus absense of glands on the pedicels. Var. *dumetorum* was
divided after the same characters. Later authors have divided the taxa
even more, until almost every single collection got its own name in the
rank of, e.g., subforma.

In Scandinavia R. *canina* is known to form hybrids with R. *sherardii*,
R. *villosa*, and R. *rubiginosa*. Several forms intermediate between R.
canina and R. *dumalis* are also found, see below.

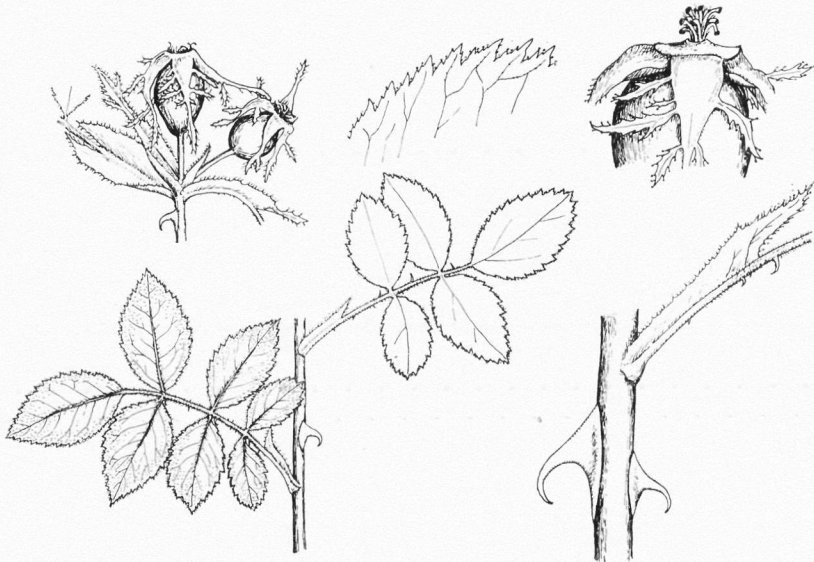## R. obtusifolia DESV.

(*R. tomentella* LÉMAN, *R. sclerophylla* SCHEUTZ)

Similar to R. *canina* but stems up to about 2.5 m tall, young stems
green; *prickles* stout (up to about 15 mm long), *strongly hooked with
broad bases*; *leaflets broadly ovate or oval* (15—35 × 15—25 mm), more
rounded in outline and less acute or *often obtuse, usually doubly
glandular-serrate* or occasionally simply serrate, teeth broadly triangu-
lar, acuminate, with glands, upper side softly pubescent or sometimes
glabrous, lower side pubescent all over or sometimes only on the veins,

R. CANINA

R. OBTUSIFOLIA

usually glandular on the main veins, sometimes eglandular, or occasionally glandular all over; stipules rather narrow, ± pubescent, often reddish; rachis densely pubescent, glandular, with crowded, minute acicles and sparse prickles; *pedicels rather short*, 0.5—1.5 mm, *glabrous*; flowers white or pale pink; *sepals* rather short, *deflexed and falling soon after flowering*, eglandular, *outer 3 distinctly pinnatifid, their lobes broad, deeply glandular-dentate or lobed*; *styles* rather long, *subglabrous or thinly pilose, stigmas in a rather loose, ± globose head; disc rather broad, about 5 mm, flat or often somewhat conoidal, orifice 0.5—1.0 mm wide*; *hips* 1—2 cm long, ovoid or globose, *glabrous, hard, red, ripening* almost as *late* as those of *R. canina*. June—July. 2n=35.

Native. In localities of the same type as *R. canina*. *R. obtusifolia* seems to have a western, suboceanic distribution in Europe. In Scandinavia it is a rather rare plant, occurring only in the southern parts; in Denmark it is common only on the island of Bornholm, but there are also a few localities on some of the other islands and in SE. Jutland; in Sweden it is rare in the southern coastal districts, on the west coast occurring northwards to Bohuslän, on the east coast to N. Småland and on the islands of Öland and Gotland.

Within this area *R. obtusifolia* seems to be rather uniform. A few varieties may be distinguished, the commonest form is that illustrated here, var. *sclerophylla* (SCHEUTZ) CHRIST, which is distinguished by glabrous pedicels. Other varieties with glandular pedicels and sepals are very rare in Scandinavia. Probably *R. obtusifolia* is closely related to *R. canina*, particularly to its var. *dumetorum*. Intermediate forms between these two species have been reported from Gotland. Morphologically *R. obtusifolia* has a transitional position between *R. canina* and *R. rubiginosa*.

R. dumalis BECHST.

(*R. afzeliana* FR., *R. coriifolia* FR., *R. glauca* VILL. non POURR., *R. reuteri* GODRON, *R. subcanina* CHRIST, *R. subcollina* (CHRIST) DALLA TORRE & SARNTHEIN, *R. vosagiaca* DESPORTES)

Similar to *R. canina* but stems up to 2.5 m tall, erect, young stems often pruinose or green; *prickles* usually *smaller* (up to about 7 mm long), *constricted, with narrow bases*, usually only slightly curved, more crowded on young stems; *leaflets* ovate, obovate, or elliptic (20—45×15—25 mm), usually acute, glabrous or pubescent, sometimes
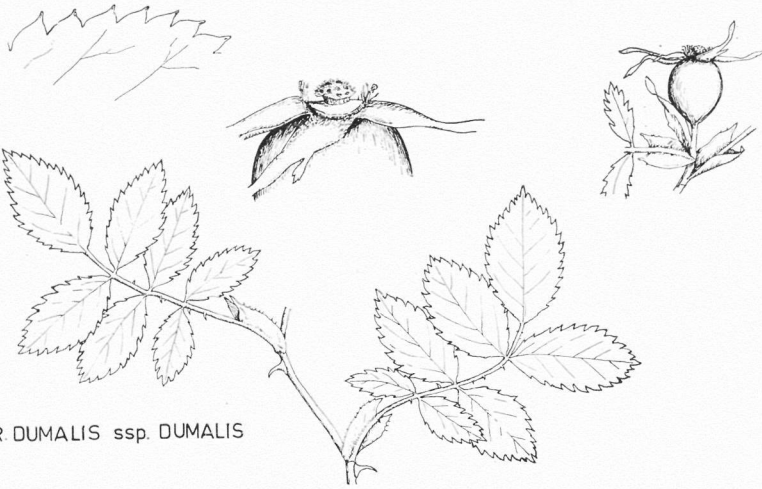
R. DUMALIS ssp. DUMALIS
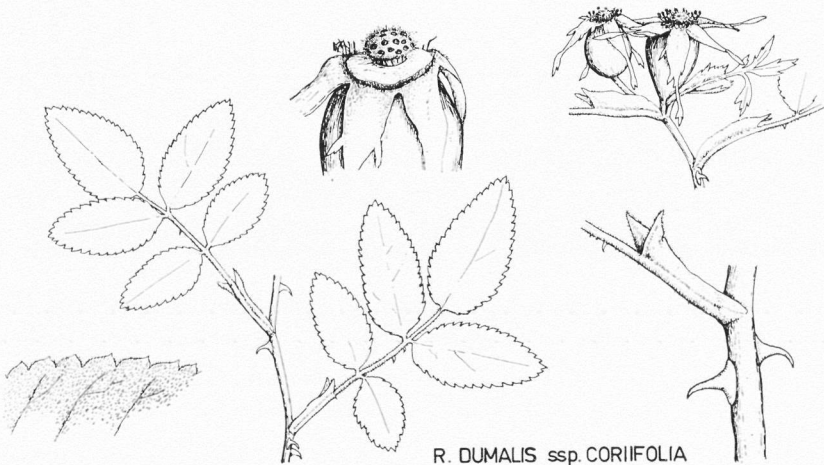
R. DUMALIS ssp. CORIIFOLIA

densely pubescent or tomentose and often glaucous beneath and occa-
sionally with a few glands, *usually simply* but sometimes doubly *serrate*,
teeth rather short, acuminate or long and acute; stipules comparatively
broad, often red tinged, auricles rather short, acute; bracteoles broad,
longer than the pedicels; *pedicels relatively short*, 0.5—1.0 (—1.5) cm,
shorter than the hips, glabrous or sometimes stipitate-glandular;
flowers usually deep pink; *sepals usually erect or ascending*, sometimes
patent or reflexed after flowering, *persistent at least till the hip reddens*;
stamens persistent till the hip ripens; *styles* rather *short, villous, stigmas
in a dense, cushioned, flattened head, concealing the disc, disc rather
small, about 4 mm wide, flat or concave, orifice 2—2.5 mm; hip 1.5—
2.5 cm, globose, ellipsoid, sometimes pyriform (the central in most
inflorescences), smooth, rather soft, deep red* (as young often pruinose),
ripening 2—4 weeks *earlier than R. canina* in S. Scandinavia. June—
July. 2n=35.

Native, occasionally cultivated. Scrub, hedges, and open woods. *R.
dumalis* has a mainly N. and C. European distribution with a boreal-
montane tendency. In Scandinavia it is almost as common as, and locally
commoner than, *R. canina*; in Denmark it is common in almost the
whole country but seems to be less abundant on the southern islands,
Lolland and Falster, and on the southern part of Sealand, and becomes
more rare in W. Jutland where it is only locally common [both
subspecies (see below) have about the same distributions and seem to be
equally common]; in Norway it is common in the coastal districts ex-
tending northwards to the northern part of Nordland, reaching to an
altitude of 800 m, and is in Sydland and Ostland the commonest rose;
in Sweden it occurs in the north to Bohuslän, Dalecarlia, and extends
along the east coast to Ångermanland (next to *R. canina* it is the com-
monest rose in the coastal districts), becoming very rare in the inland
of the southern parts, e.g., in the lake district and in the southern,
central highland [both subspecies are common and seem to have almost
the same distribution, but ssp. *coriifolia* seems to be commoner in the
eastern parts (however, their distributions are imperfectly known)]; in
Finland it is rather common in the SW. parts and in Åland, and follows
the north coast of the Finnish Bay to SW. Karelia.

R. dumalis, if possible, seems to be still more variable than *R. canina*.
Both vary after almost the same pattern. Two distinct form groups may
be distinguished. They are treated here as subspecies, because their

characters seem to be rather constant, intermediates between them are rather rare, and the distributions as mentioned tend to be different.

1. Ssp. *dumalis* (*R. glauca*, *R. afzeliana*, *R. vosagiaca*), the first group, is distinguished by stems with long internodes that are pruinose like the unripe hips, and glabrous leaflets with a distinct serration with long acute teeth, and the sepals are usually erect; in this group forms ± intermediate to *R. canina* are found [var. *subcanina* (CHRIST) H. BR.].

2. Ssp. *coriifolia* (FR.) A. PEDERS. (*R. coriifolia*), the second group, is distinguished by leaflets that are pubescent or tomentose at least on the lower side and with relatively shorter teeth, the stems are green and have short internodes, the sepals are usually ascending or patent; in this group forms ± transitional to *R. canina* are met with [var. *subcollina* CHRIST]. Both subspecies are illustrated here.

The two subspecies and the two varieties have all been treated as separate species. Several attempts to further divisions have been made; each of the infraspecific taxa mentioned here has been divided into four form series according to the serration of the leaflets, the shape of the leaflets, and the glabrous or glandular pedicel (sometimes these divisions have been made according to very unusual taxonomical systems, cf. S. ALMQUIST 1916 and 1919, and C. A. M. LINDMAN 1918, with e.g., α and β species). There seems to be no obvious ecological difference between the two subspecies.

In Scandinavia *R. dumalis* is known to form hybrids with *R. elliptica*, *R. rubiginosa*, *R. sherardii*, and *R. villosa*. As was mentioned above, intermediate forms between *R. canina* and *R. dumalis* are often met with. Sometimes it may be very difficult to find a distinct limit between these two species.

A New Dionysia (Primulaceae) from the Bakhtiari Mountains of Iran

By Per Wendelbo

Botanical Garden, Gothenburg

ABSTRACT

The violet-flowered *Dionysia archibaldii* is described. All other species of sect. *Anacamptophyllum* have yellow flowers. The species was collected at 4150 m altitude which is the highest recorded for any species of the genus. The genus now consists of 35 species.

Mr. J. C. Archibald of Dorset, England collected extensively in Iran during 1966. His main purpose was to bring new and attractive plants into cultivation. He took special interest in the genus *Dionysia* (*Primulaceae*) and collected many species mostly in their known localities. In the Bakhtiari Mts., however, Mr. Archibald came across a distinct new species which is described below and named in honour of its discoverer.

The altitude, 4000—4150 m a.s.l., at which the new species was found is remarkable. *D. curviflora* Bge is the only other species recorded to reach the 4000 m level, next comes *D. rhaptodes* Bge (up to 3800 m). As appears from Mr. Archibald's photograph (Fig. 1) of the locality it looks very desolate with bare rocks and snow in the bottom of the gorge as late as in August.

Dionysia archibaldii Wendelbo, sp. nov. (Figs. 2 and 3).

Sect. *Anacamptophyllum* Melchior subsect. *Revolutae* Wendelbo

Fruticulosa, laxe caespitosa, foliis emarcidis in glomerulis secus surculos persistentibus, ± dense lanato-farinosa vel fere efarinosa. *Folia* 4—7,5 mm longa, oblongo-elliptica vel oblonga, margine revoluto integro vel valde indistincte crenulato, glanduloso-pubescentia, glandulis 0,05—0,15 mm longis capitatis, stipite articulato; folia surculorum juvenilium usque ad 10 mm longa, anguste elliptica, marginibus planis. *Inflorescentia* singuliflora, sessilis. *Bracteae* 2, inaequales, 3—4 × 0,4—0,7 mm, lineari-oblongae, acutae, pubescentes, pilis usque ad 0,5 mm longis. *Flos* sessilis. *Calyx* 4—5 mm longus,

Fig. 1. Tang-i-Sirdan, Bakhtiari country, 4100 m alt. Type locality of *Dionysia archibaldii*. Note snow in bottom of the gorge. — J. C. ARCHIBALD photo 7.8.1966.

campanulatus, in segmenta lineari-oblonga, acuta, 3—3,5 mm longa, extra pubescentia et glandulosa, intra glandulosa fissus. *Corollae* dimorphae, violaceae; limbus lobis 4 mm longis, anguste obcordatis; tubus 12—14 mm longus, extra glaber. *Antherae* c. 1,2 mm longae; filamenta in floribus brevistylis c. 3 mm infra faucem affixa, in floribus longistylis c. 7 mm infra faucem affixa. *Stylus* florum brevistylorum 3,5 mm, florum longistylorum c. 7 mm longus; stigma capitatum. *Capsula* subsphaerica, seminibus 5—10.

IRAN. Bakhtiari: Tang-i Sirdan, between Kuh Rang and Bazuft valleys, 4000—4150 m, 7. VIII. 1966, J. ARCHIBALD 3053 Holotypus GB; Zardeh Kuh, 4150 m, 5. VIII. 1965, J. ARCHIBALD 3010 GB.

The violet-flowered *Dionysia archibaldii* belongs to sect. *Anacamptophyllum* subsect. *Revolutae*, but is distinguished in the flower colour from all the other species which are yellow-flowered. The only other species of *Revolutae* with entire leaves is the densely tufted and much more small-leaved *D. rhaptodes* BGE from the Kerman area. In its growth *D. archibaldii* is similar to other loose-tufted species of *Revolutae* like *D. leucotricha* BORNM. and also *D. revoluta* BOISS. The number of young seeds was 5 in a capsule from a long-styled flower and c. 10 in one from a short-styled flower. This points to a stronger reduc-
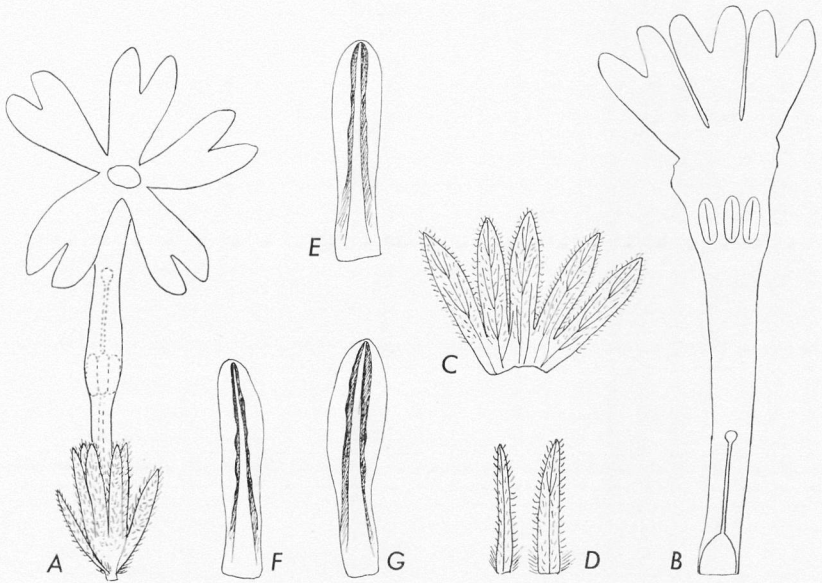
Fig. 2. *Dionysia archibaldii* sp. nov. — A. Long-styled flower with bracts; B—D. Short-styled flower; B. Dissected corolla; C. Dissected calyx; D. Bracts; E—G. Normal revolute-margined leaves from below, glands not drawn. (×4.)

tion in number of seeds than found in *D. revoluta, D. leucotricha* and *D. aretioides* (LEHM.) BOISS., but the number is higher than that found in *D. oreodoxa* BORNM. and *D. rhaptodes*. In my scheme of evolution and relationship within the genus *Dionysia* (WENDELBO 1961, Fig. 9; 1964, Fig. 12) *D. archibaldii* fits in well, above *D. leucotricha* and *D. aretioides* on the transition between stages II and III.

It is interesting to note that this is the first species to be described of sect. *Anacamptophyllum* with violet flowers. Phylogenetically yellow may be older than violet within the genus, but violet obviously has appeared several times in different evolutionary lines. Of the 35 known species, 11 now are known to have a violet (or pink?) flower colour, the rest have shades of yellow.

In the monograph of the genus (WENDELBO 1961) 28 species were treated. Six new species were added from Afghanistan (WENDELBO 1964), and thus with *D. archibaldii* the number of *Dionysia* species has been raised to 35. There is every reason to expect that more species will be found both in Iran and Afghanistan. It should also be noted that several species have been found only once or only in their type locality.

Fig. 3. *Dionysia archibaldii* sp. nov. — Habit. Upper two branches with large flat-margined young leaves, from plants probably growing in shade. Lower 3 branches from plants with normal revolute-margined leaves. (Nat. size.)

LITERATURE CITED

WENDELBO, P. 1961. Studies in Primulaceae 1. A monograph of the genus Dionysia. — Acta Univ. Bergensis. Ser. Math. Nat. 1961 No. 3. 83 pp.
— 1964. Studies in Primulaceae 4. The genus Dionysia in Afghanistan with descriptions of 6 new species. — Ibid. 1963 No. 19. 28 pp.

Chromosome Numbers in Some South African Genera of the Tribe Genisteae s. lat. (Leguminosae)

By Rolf Dahlgren

Institute of Systematic Botany
University of Lund

ABSTRACT

The following chromosome numbers are reported:

Priestleya laevigata (L.) DRUCE 2n = 18
— undescribed species 2n = 18
Amphithalea intermedia ECKL. & ZEYH. 2n = 18
— *ericifolia* (L.) ECKL. & ZEYH. 2n = 18
Lebeckia pungens THUNB. 2n = 18
— *pauciflora* ECKL. & ZEYH. 2n = 18
— *sepiaria* (L.) THUNB. 2n = 18
— *capensis* (L.) DRUCE 2n = 18
Wiborgia obcordata THUNB. 2n = 18
— *armata* THUNB. 2n = 18

Wiborgia, undescribed taxon near *W. sericea* THUNB. 2n = 18
Aspalathus macrantha HARV. 2n = 16
— *uniflora* L. 2n = 16
— *lanata* E. MEY. 2n = 18
— *lanifera* R. DAHLGR. 2n = 18
— *perfoliata* LAM. 2n = 18
Rafnia elliptica THUNB. 2n = 16
Lotononis involucrata (L. fil.) BENTH. 2n = 28

Discussions on taxonomy and morphology are given for most of these species.

INTRODUCTION

During a period of field work in South Africa lasting between August 1965 and March 1966 I had the opportunity of making a number of seed collections of *Aspalathus* and *Wiborgia*, and also some other genera of *Leguminosae*. The chromosome conditions in the former two genera will be more extensively investigated and presented later.

Very little is known about the chromosome numbers of South African *Leguminosae*. Except for *Aspalathus* (see DAHLGREN 1963 b, 1963 c, 1965 a, 1966, 1967) none of the genera dealt with here have been investigated cytologically. Among the South African *Genisteae* s. lat., *Melolobium* has the somatic number of 18 (RILEY 1963 p. 32). *Crotalaria* is known to have 2n = 14, 16, and 32.

MATERIAL AND METHODS

Most of the material investigated was raised from seeds collected in the field in South Africa and sown in Lund in April 1966. Root tips were fixed in the Svalöv modification of Navashin-Karpechenko after the plants had been kept over night at a temperature of 2—4 centigrades. The preparations were stained in crystal violet with an addition of anilin. Each seed collection is accompanied by a matching dried specimen preserved at present in Lund.

Some of the counts were made from root-tip fixations of seedlings kept in cultivation in the National Botanic Gardens, Kirstenbosch, South Africa. The seedlings were collected, together with the adult plants, in the field, and brought in pots into the nursery garden. They were not cooled before fixation (but DAHLGREN & STRID no. 4145 was treated in 8-hydroxyquinoline) and thus the chromosomes (Fig. 1 L—N) seem to be less contracted than those fixed in Lund. Navashin-Karpechenko was used as a fixative in Kirstenbosch.

GENERA REPRESENTED AND THEIR POSITION ACCORDING TO SOME STANDARD WORKS

Priestleya and *Amphithalea* differ from the other four genera especially in the presence of a conspicuous caruncle on the seeds. According to BENTHAM & HOOKER (1880), TAUBERT (1894), and other works they belong to tribus *Genisteae* subtribus *Lipariinae*, according to HUTCHINSON (1964) to tribus *Liparieae*.

Aspalathus (and *Borbonia*), *Lebeckia*, *Wiborgia*, *Rafnia*, and *Lotononis* according to the former two works mentioned belong to tribus *Genisteae* subtribus *Crotalariinae*. According to HUTCHINSON (1964) they belong to tribus *Lotononideae*, except for *Rafnia* and *Borbonia* which together with *Euchlora* compose the separate tribus of *Borbonieae*, characterized by "primitively" simple leaves. This was discussed in DAHLGREN 1965 b p. 270. *Borbonia* was incorporated into *Aspalathus* in DAHLGREN 1963 a and *Euchlora* into *Lotononis* in DAHLGREN 1964. Thus there are strong reasons against HUTCHINSON's division on this point.

PRIESTLEYA

This genus consists of about 20 species or less, with alternate, simple, entire leaves and yellow flowers. It has previously been divided into two groups of species, *Isothea* and *Anisothea*, the former with involute calyx base, the latter with normal subcampanulate calyx tube. These groups are sharply delimited from each other. The two species repre-
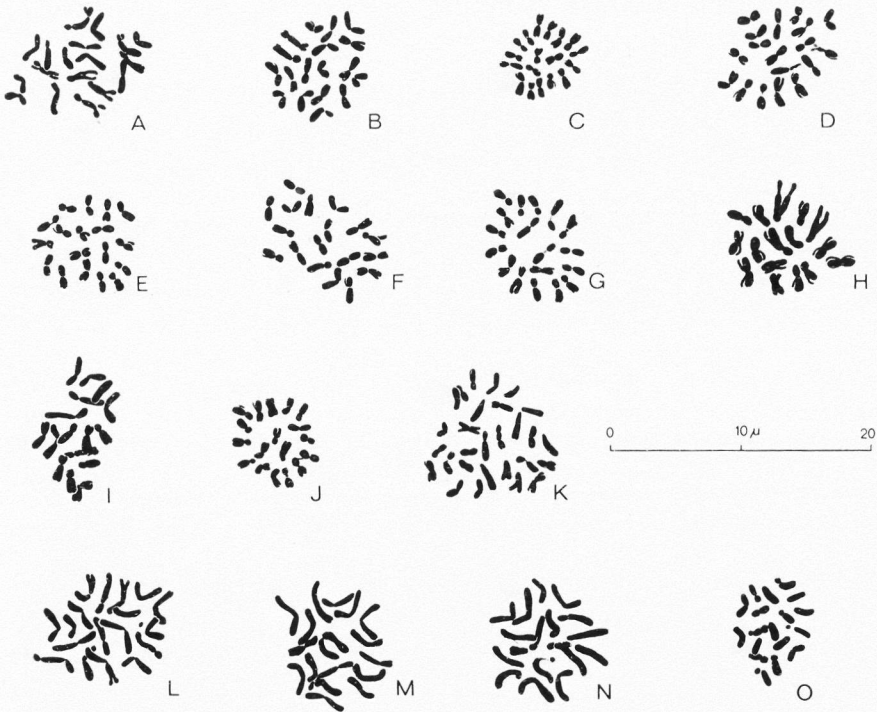
Fig. 1. Chromosome plates of South African *Genisteae*. — A: *Priestleya laevigata*; DAHLGREN & STRID no. 4160. — B: *Amphithalea intermedia*; D. & S. no. 3955. — C: *Lebeckia pungens*; D. & S. no. 4853. — D: *Lebeckia pauciflora*; Algeria Valley, 1965, without no. — E: *Wiborgia obcordata*; D. & S. no. 4953. — F: *W. armata*; D. & S. no. 4408. — G: *Wiborgia* sp. aff. *W. sericea*; D. & S. no. 4335 a. — H: *Aspalathus macrantha*; Wynberg Hill, 1965, without no. — I: *A. uniflora* ssp. *willdenowiana*; D. & S. no. 4418. — J: *A. perfoliata*; D. & S. no. 4441. — K: *Lotononis involucrata*; D. & S. no. 4104. — L: *Priestleya* sp. aff. *P. tomentosa*; D. & S. no. 4217. — M: *Lebeckia sepiaria*; D. & S. no. 4665. — N: *Aspalathus lanata*; D. & S. no. 4275. — O: *A. lanifera*; D. & S. no. 4145. — A—K grown in greenhouse culture in Lund, L—O grown in National Botanic Gardens, Kirstenbosch. The scale is the same for all plates.

sented below belong to each of these groups. Some species of the genus are up to 2 m tall or more and may have a treelike habit, others are small undershrubs. — 2n=18.

Priestleya laevigata (L.) DRUCE

DAHLGREN & STRID no. 4160, Somerset W. Division: Kloof between Somerset Sneeuwkop and Landdrostkop Peaks, alt. c. 600 m. 5.11. 1965. — [Matching

collection in flower: D & S. no. 4983 from the same area, but higher up, at about 1000 m. 22.2.1966 (LD).]

The collection studied belongs to a population of shrubs 2—3 m tall. On the slopes at about 900—1000 m altitude the species forms a miniature wood. Like *Protea cynaroides*, growing on the same slope, the species is visited by sunbirds which may play some role in its pollination.

Cultivated in Lund. 2n=18. Fig. 1 A.

The seedlings have densely woolly branches and also young branches are villous, but the older branches are glabrous. The calyx is velutinous-lanate, but the lobes and the lower side of the bracts are partly glabrous, and the pubescence seems to flake off gradually. As much of the systematics on species level is based on calyx and branch pubescence (cf. the key in HARVEY 1862 p. 16) the distinctness of some of the species is questionable, and the genus is in urgent need of revision. *P. myrtifolia* (THUNB.) DC., *latifolia* BENTH., and *leiocarpa* ECKL. & ZEYH. are doubtless very closely allied to, some probably conspecific with, the present species.

Priestleya sp. near *P. tomentosa* (L.) DRUCE

DAHLGREN & STRID no. 4217, Bredasdorp Division: Lower NW. slope of Elim Hill. Low shrublets, in sand. 16.11.1965.

Cultivated in the Kirstenbosch Botanic Gardens. 2n=18. Fig. 1 L.

This form differs from the forms of *P. tomentosa* seen, in the much smaller total size (it is a shrublet only c. 15 cm tall), and the smaller calyx with much narrower lobes, the upper two of which are connate except for one apical mm. As petals are lacking in the material I refrain from describing the species at present.

AMPHITHALEA

A genus of about 16 species, usually with rose petals and (like *Priestleya*) diadelphous stamens. The leaves are entire, simple, alternate, and usually sericeous. The genus is apparently closely related to *Coelidium*, which has monadelphous stamens, however, and was placed by HUTCHINSON (1964) in *Bossiaeae*, a tribus otherwise restricted to Australia. — For *Amphithalea*: 2n=18.

Amphithalea intermedia ECKL. & ZEYH.

DAHLGREN & STRID no. 3955, Swellendam Division: Tradu Pass, S. part, c. 1 mile N. of bridge. Moist ground on steep rocky slope. 1.11.1965.

Cultivated in Lund. 2n=18. Fig. 1 B.

A. intermedia is a variable (possibly heterogeneous) species which deserves a close study. The form examined has a relatively tall virgate growth in relation to certain other forms of the species. There is only one ovule in each ovary.

Amphithalea ericifolia (L.) ECKL. & ZEYH.

DAHLGREN & STRID no. 3558, Caledon Division: 3 miles N. of Mossel Rivier. In sand among rocks, alt. about 220 m. 7.10.1965.

Erect shrublets 30—40 cm tall, with linear leaves glabrous on the upper side and with revolute margins partly enclosing the lower pubescent side. *A. ericifolia* is the commonest and, perhaps, the most variable species in the genus.

Cultivated in Lund. 2n=18.

LEBECKIA

This is a relatively large genus of about 50—60 species. Contrary to the previous two genera, but like the following ones, it lacks strophioles on the seeds. The genus has a most variable leaf shape (see DAHLGREN 1963 c pp. 225—263). It was divided by BENTHAM (1844) into five sections, three of which are represented below. — 2n=18.

Lebeckia pungens THUNB.

DAHLGREN & STRID no. 4853, Uniondale Division: About 2 miles SW. of Uniondale. 11.2.1966 (fruit stage). — Matching collection from same area, 5 ¹/₂ miles SW. of Uniondale. D. & S. no. 3003, 9.9.1965 (flowering stage; LD).

Cultivated in Lund. 2n=18. Fig. 1 C.

L. pungens is one of the three species of *Lebeckia* which was placed by BENTHAM (1844) in section *Stiza* (a former genus of ECKLON & ZEYHER 1836). This section is characterized by the pungent branch ends and the sparse, flat, unifoliolate leaves. However, the seedlings have trifoliolate leaves, which has not been recorded before; Fig. 2 A. The legumes are flattened and curved (Fig. 2 B) and the carina is relatively long.

The present species has puberulous branches and villous pods. The specimens studied were about 40—70 cm tall and closely branched, and had spreading sharp thorns. They grew in a mixed rhenosterveld-karroo vegetation on clayey ground.

Lebeckia pauciflora ECKL. & ZEYH.

Seed collection from the Clanwilliam Division: Cedarberg Mountains, Algeria Valley, W. part. 9.12.1965. — Matching collections from same area: DAHLGREN & STRID no. 3258, 21.9.1965 (LD), and D. & S. no. 4276, 20.11.1965 (LD).

Cultivated in Lund. 2n=18. Fig. 1 D.

This rather common species belongs to section *Eulebeckia* sensu BENTHAM (1844) and HARVEY (1862), which should be sect. *Lebeckia* according to present nomenclatural rules. This section is characterized by linear leaves with a middle "joint", i.e., unifoliolate leaves with stalk and leaflet of similar structure and shape (see DAHLGREN 1963 c. pp. 225—263), by acute rather long carina, and narrow long legumes which in *L. pauciflora* are falcate and ± constricted between the relatively few and sparse seeds.

11

Lebeckia sepiaria (L.) THUNB.

Seedlings collected; DAHLGREN & STRID no. 4665, Knysna Division: Brenton, opposite Knysna. Hill near lagoon, on sandy cleared patches. 18.12.1965.

Cultivated in the Kirstenbosch Botanic Gardens 1965—66. 2n=18. Fig. 1 M.

Like *L. pauciflora*, this species belongs to section *Lebeckia* ("*Eulebeckia*") (being, in fact, the type species of the genus). It is characterized by its sub-rostrate carina, small flowers, and decumbent—ascending growth. The plants with which the seedlings were collected were 25—30 cm tall.

Lebeckia capensis (L.) DRUCE

DAHLGREN & STRID no. 4453, Piketberg Division: W. base of Grey's Pass, in sand. 9.12.1965.

The shrubs in this place were 1.5—2 m tall, with long narrow legumes, each with numerous small seeds.

Cultivated in Lund. 2n=18.

L. capensis (synonym: *L. cytisoides* THUNB.) is a rather widely distributed species with large flowers and rather large, petiolate and trifoliolate, leaves with linear or oblanceolate leaflets. It belongs to the section *Calobota* according to BENTHAM 1844 and is commented on in DAHLGREN 1963 c p. 256.

WIBORGIA

This genus contains only about 8 species occurring mainly in the lowlands of western Cape. They are morphologically similar to certain species treated in *Lebeckia* sect. *Wiborgioides*, e.g., *L. sessilifolia* (ECKL. & ZEYH.) BENTH. (see discussion in DAHLGREN 1963 c pp. 261—263), but differ in the few-ovulate ovary and the short, broad, and flat pod always with a marked wing on the upper side.

Several collections of this genus are at present in cultivation in Lund. All seem to have the chromosome number 2n=18. Three examples are selected here.

Wiborgia obcordata THUNB.

DAHLGREN & STRID no. 4953, Bellville Division: About 4 miles E. of Ascot, Cape Flats. 20.2.1966 (LD).

Cultivated in Lund. 2n=18. Fig. 1 E.

W. obcordata (see DAHLGREN 1963 c Fig. 79 p. 264) differs from most of the *Wiborgia* species in having rather narrow wings on the pod (Fig. 2 C). It is a slender-branched shrub up to > 2 m tall, usually growing on sandy substrate. It occurs from the Cape Peninsula in the south to at least the Van-rhynsdorp Division in the north.

Wiborgia armata THUNB.

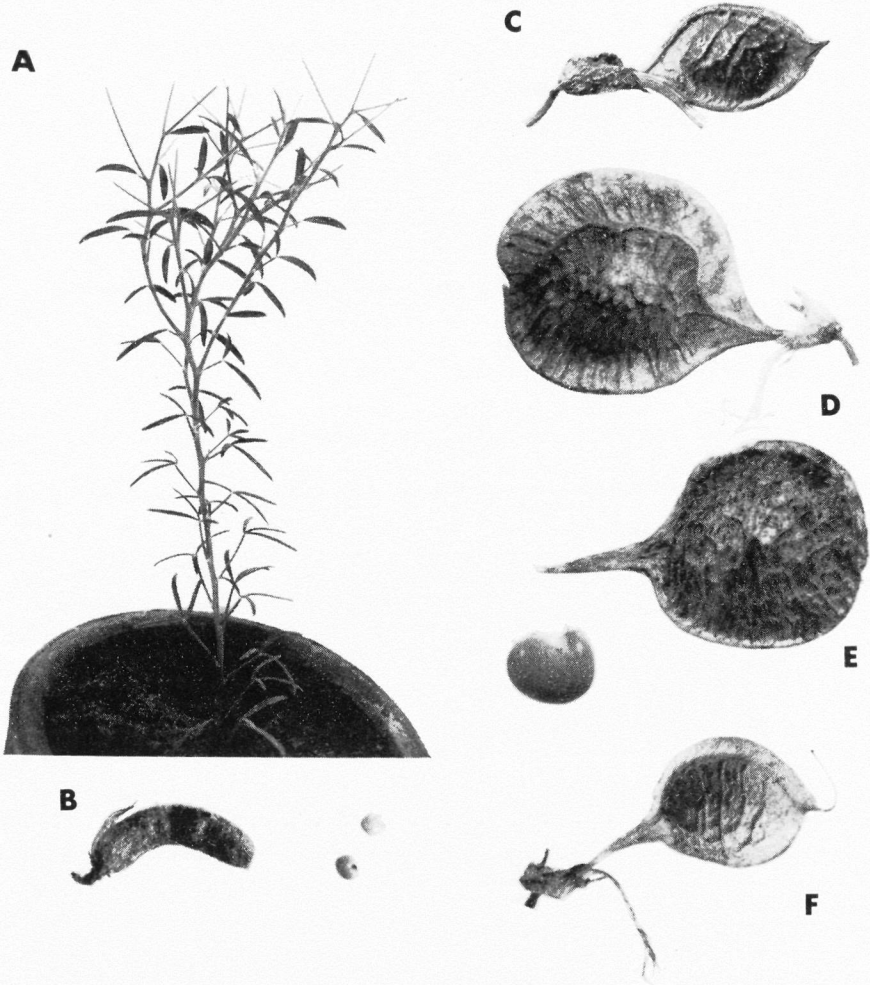DAHLGREN & STRID no. 4408, Robertson Division: Halfway between Mac Gregor and Bushmanpas. Dry sandy area. 5.12.1965.

Fig. 2. — A—B: *Lebeckia pungens*; DAHLGREN & STRID no. 4853; seedling, legume, and seeds. Notice that the lower leaves of the seedling are trifoliolate. (A approx. ×2; B ×1.3.) — C: Pod of *Wiborgia obcordata*; D. & S. no. 4953 from Cape Flats (×2.8). — D: Pod of *W. armata*; D. & S. no. 4408 from the Robertson Division (×3). — E: Pod and seed of *Wiborgia* sp. near *W. sericea*; D. & S. no. 4335 a from hills north of Mamre (×3). — F: Young pod of same population as E; D. & S. no. 2794 (×2.5).

Cultivated in Lund. 2n=18. Fig. 1 F.

W. *armata* (Fig. 2 D) ranges from this region through the Worcester Division as far, at least, as the Clanwilliam Division, where it is locally very com-

mon and even dominant in certain areas, e.g. in the Olifant River Valley and north of Pakhuis. It is an erect, spreading shrub 0.8—2 m tall or more, with thorny branches. It occurs in relatively dry areas where most of the typical fynbos species are eliminated from the vegetation.

Because of the difficulties in combining fruit and flower material with each other, the systematics on the species level has been very confused in *Wiborgia*, and a revision is needed.

Wiborgia sp. close to *W. sericea* THUNB.

Seeds from DAHLGREN & STRID no. 4335 a, collected in the Malmesbury Division: About 2.5 miles from Mamre along the road to Darling. Hills with red, clayey soil. 28.11.1965. — Other collection from the same area: D. & S. no. 2794, 30.8.1965 (LD, Fig. 2 F).

Cultivated in Lund. 2n = 18. Figs. 1 G and 2 E.

This population north of Mamre has somewhat variable pod shape (cf. Fig. 2 E—F), which at least partly depends on the stage. However, the pods constantly have narrower wings than the more northern *W. sericea* s. str., and the Mamre population probably represents a separate taxon which is apparently not yet named. One representative was treated under the name *W. sericea* (litt. b) by MEYER (1836 p. 30).

ASPALATHUS

A great number of the about 250 species of *Aspalathus* have been cultivated in the Kirstenbosch Botanic Gardens during 1965—66 and in Lund 1966—67. This material is not yet fully investigated. The results will be presented later. Some observations may be of particular interest, however, and therefore a few species are selected for a preliminary report here.

The commonest chromosome number in the genus seems to be 2n = 18, but several species have 2n = 16. The number 2n = 14 was found in *A. uniflora* L. (see DAHLGREN 1963 c Fig. 74 p. 232), but has not been verified again in the later, and richer, material investigated of the same species. Two species are mentioned below (also some others have been cytologically examined) which belong to the former genus *Borbonia*, included into *Aspalathus* in DAHLGREN 1963 a.

Aspalathus macrantha HARV.

Seeds from plants growing on the plot of Mr. H. HALL on Wynberg Hill, Wynberg Division. Collected 11.11.1965. About *A. macrantha*, see DAHLGREN 1965 a p. 76.

Cultivated in Lund. 2n = 16, a number not recorded with certainty in the genus previously. Fig. 1 H.

Aspalathus uniflora L. ssp. *willdenowiana* (BENTH.) R. DAHLGR.

Seeds from DAHLGREN & STRID no. 4418, collected in the Paarl Division: Middle part of French Hoek Pass. 5.12.1965. — Matching collection from same place also D. & S. no. 4005. 4.11.1965 (LD).

Cultivated in Lund. 2n=16. Fig. 1 I.

For the particulars of this species see DAHLGREN 1965 a p. 81.

Aspalathus lanata E. MEY.

Seedlings collected with DAHLGREN & STRID no. 4275 growing in the Clanwilliam Division: Cedarberg Mountains, Algeria Valley, c. 2 miles W. of Algeria Forest Station. 20.11.1965.

Cultivated in the Kirstenbosch Botanic Gardens. 2n=18. Fig. 1 N. One pair of the chromosomes is satellited.

This species, treated in DAHLGREN 1960 p. 336 and 1963 a p. 188, is the one which connects most closely the species of the former *Borbonia* with *Aspalathus* in the former narrow sense. Except for the trifoliolate contra unifoliolate leaves, there are very inconspicuous differences between *A. lanata* and forms of *A. lanifera* R. DAHLGR. (see below).

Aspalathus lanifera R. DAHLGR.

Seedlings collected with DAHLGREN & STRID no. 4145 in the Ceres Division: Witzenberg Vlakte between Witzenberg and Schurfteberg Mountains, halfway between Slagboom and Old Witzenberg Pass. Prostrate, matlike, on clay. 14.11. 1965.

Cultivated in the Kirstenbosch Botanic Gardens. 2n=18. The root tips were pretreated in 8-hydroxyquinoline before fixation. (Notice the two satellited chromosomes.) Fig. 1 O.

This species is the one within the former *Borbonia* which is morphologically most similar to any other *Aspalathus* species, particularly to *A. lanata*. *A. lanifera* is very variable, and the form studied cytologically is more large-flowered than, for example, the type (cf. DAHLGREN 1963 a Fig. 3 p. 190).

Aspalathus perfoliata (LAM.) R. DAHLGR. ssp. *phillipsii* R. DAHLGR.

DAHLGREN & STRID no. 4441, Clanwilliam Division: Cedarberg Mountains, just W. of the top of Nieuwoudt Pass, W. of the W. end of Algeria Valley. 9.12.1965 (LD).

Cultivated in Lund. 2n=18. Fig. 1 J.

This species (DAHLGREN 1963 c Fig. 66 p. 208) is one of the common ones in the group previously treated in *Borbonia*. It has a rather extreme leaf shape.

RAFNIA

A genus of about 30—35 species concentrated in the southwestern parts of the Cape Province. It is characterized, within subtribus *Crotalariinae*, by the combination of simple, entire, and usually smooth leaves.

the absence of indumentum, and the yellow or ± reddish petals (which usually tend to become black when dried). See also comments in DAHL-GREN 1963 c p. 266. — 2n=16.

Rafnia elliptica THUNB.

DAHLGREN & STRID no. 4871, George Division: 31 miles WSW. of Uniondale along the road to George, N. side of Outeniqua Mountains. Rhenosterveld—fynbos transition. 12.2.1966.

The species in this place was up to about 70 cm tall, with several or numerous branches ascending from the base. *R. elliptica* is one of the common and variable species of the genus.

Cultivated in Lund. 2n=16. No chromosomes were satellited and no distinct secondary constrictions were observed.

LOTONONIS

A large genus of more than a hundred species. It is characterized by the (1—) 3 (—5)-foliolate, petiolate leaves with 1—2 (sometimes more) stipules. The pods are often rather inflated and frequently have ± prominent projections along the upper suture (see, e.g., DAHLGREN 1964 Fig. 6). *Lotononis* is widely distributed but has a centre in South Africa. The only species represented here belongs to a group (section *Polylobium* according to BENTHAM 1843) concentrated in southwestern Cape.

Lotononis involucrata (L. fil.) BENTH.

Seeds from DAHLGREN & STRID no. 4104 collected in the Malmesbury Division: Paardeberg, NE. part, above the farm Nooitgedacht. Alt. c. 360 m. In sand on granite outcrop; prostrate. 13.11.1965.

Cultivated in Lund. 2n=28. Fig. 1 K.

L. involucrata is variable in pubescence, leaf and flower size, and length of the internodes below the flower heads. The collection D. & S. no. 4104, unlike many other forms, does not have any peduncle-like internodes below the inflorescences.

CONCLUSIONS

In *Priestleya* and *Amphithalea* the chromosome numbers counted are 2n=18. These genera of subtribus *Lipariinae* are very dissimilar to the remaining genera studied, and the fact that the number is most often 18 also in the latter does not necessarily imply that the two groups of genera are closely allied.

In one species of *Lotononis*, — contrary to all the material investigated of *Aspalathus* (incl. *Borbonia*), *Lebeckia*, and *Wiborgia*, — the number

was found to be 2n=28, which, if it proves to be common or constant in the genus, indicates a more separate position in relation to the other genera mentioned (where the number is 16 or 18).

In somes species of *Lebeckia* and *Wiborgia* and a great number of species of *Aspalathus* (incl. *Borbonia*) the chromosome number is 2n= 18, and in several *Aspalathus* species and the single *Rafnia* species investigated the number is known to be 2n=16.

Within the species studied of the former genus *Borbonia* (*A. lanifera*, *perfoliata*, and some species not inclued in the present paper) the number is 2n=18, which agrees with the numbers in the most similar species of *Aspalathus* in the previous narrow sense, and thus the present results do not contradict the inclusion of *Borbonia* in *Aspalathus*.

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Studies in the Aegean Flora XII
Cytologic and Morphologic Investigations in Centaurea

By Hans Runemark

Institute of Systematic Botany
University of Lund

ABSTRACT

The morphologic variation within *Centaurea argentea* L., *spinosa* L., and *urvillei* DC. is briefly discussed. The *Centaurea raphanina* complex is treated in detail. Two morphologically well distinguished form series in *C. raphanina* S. & S. are recognized, *viz.* ssp. *raphanina* restricted to Crete and Karpathos and ssp. *mixta* (DC.) RUN. stat. nov. occurring in the Greek mainland. In the Cyclades apparently a large scale introgression has taken place between the subspecies, resulting in an almost chaotic morphologic variation. A hybrid between *C. oliveriana* DC. and *C. raphanina* S. & S. has been obtained in cultivated material and a hybrid swarm has been observed in the field in Naxos. *C. halacsyi* DÖRFL. and *C. nigrotriangulata* RECH. f., are both interpreted as hybrids between *C. oliveriana* DC. and *C. raphanina* S. & S. A new species, *C. scyria* RUN. sp. nov., is described. It is endemic to Skiros and possibly related to *C. oliveriana* DC. Chromosome counts of 11 species are presented. Of these species *C. solstitialis* L. is the only one previously cytologically investigated. The chromosome numbers found are as follows:

C. argentea L.	$2n=18$	*C. scyria* RUN.	$2n=20$
C. spinosa L.	$2n=36$	*C. oliveriana* DC.	$2n=22$
C. solstitialis L.	$2n=16$	*C. oliveriana* DC. ✕ *raphanina*	
C. cretica (BOISS. & HELDR.)		S. & S.	$2n=21$
NYM.	$2n=22$	*C. raphanina* S. & S.	
C. exscapa URV.	$2n=20$	ssp. *raphanina*	$2n=20$
C. redempta HELDR.	$2n=20$	ssp. *mixta* (DC.) RUN.	$2n=20$
C. spruneri BOISS. & HELDR.		*C. urvillei* DC.	$2n=40$
ssp. *guicciardii* (BOISS.)			
HAY.	$2n=20$		

INTRODUCTION

The morphologic analyses are mainly based on the extensive material collected by HANS RUNEMARK, SVEN SNOGERUP, BERTIL NORDENSTAM, ARNE STRID, ROLAND VON BOTHMER, and JIMMY PERSSON during field investigations in 1957—1966.

The cytologically investigated individuals have been obtained from seeds of spontaneous material collected in the field. In most cases 4—6 individuals of each collection have been analysed. Cytologic observations have been made on root-tip sections (fixation in the Svalöf modification of Navashin-Karpechenko and staining in crystal violet, in some cases with the addition of aniline).

The material investigated and in most cases also the parents collected in the field have been dried and are preserved in the Botanical Museum, Lund, Sweden. The names of the exact localities have been taken from the detailed sea charts of the British Admirality (cf. also maps in RUNEMARK et al. 1960).

Centaurea argentea L. [sect. *Acrolophus* (CASS.) DC.]

2n = 18 (Fig. 2 A)
Crete. Sfakia, 1—2 km N of the village of Sfakia 50—250 m SNOGERUP (R-3894).
    Sitia, 1 km SE of Kavousi 300 m SNOGERUP (R-3895).

The chromosomes are very dissimilar to those of other Aegean *Centaurea* species investigated. A difference in the structure of one of the satellited chromosome pairs seems to exist between the two collections studied.

C. argentea is an obligate chasmophyte, endemic to the southern Aegean. It is known from c. 20 localities in eastern and western Crete, but in 1964 it was also discovered in the island of Kithera, S of Peloponnisos (RUNEMARK & SNOGERUP 20822). *C. argentea* is extremely variable in habit, leaf shape and shape of the apical part of the involucral scales (Fig. 1 A—F). The variation is probably the result of genetic drift in small, isolated cliff populations.

A detailed study of the morphologic variation within and between the populations and a thorough investigation of the chromosome morphology is planned.

Centaurea spinosa L. [sect. *Acrolophus* (CASS.) DC.]

2n = 36 (Fig. 2 B)
East-Aegean islands. Ikaria, Pharos RUNEMARK & SNOGERUP (R-1260, 1712).
Cyclades. Naxos, 2 km N of Mitria RUNEMARK & SNOGERUP (R-1511).
    ,, , 3 km S of Axapsis 30 m RUNEMARK & SNOGERUP (R-1545).
    Paros, 2 km N of the peak of Prof. Elias 450 m RUNEMARK & SNOGERUP (R-1711).
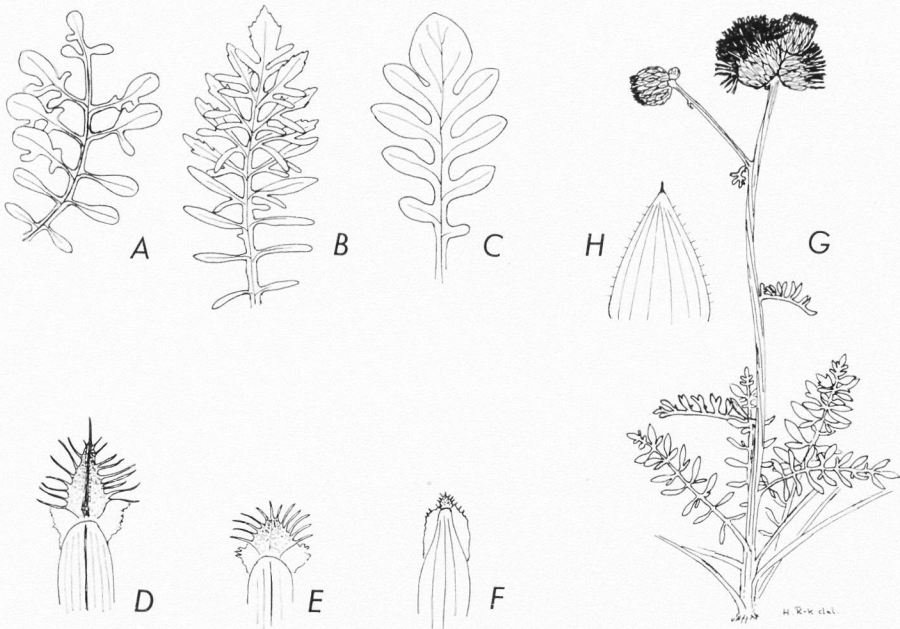
Fig. 1. A—F. *Centaurea argentea*. A—C leaves, D—E involucral scales from different populations (A and D: Crete, Sitia, Leopetra, B and E: Crete, Sfakia, C: Crete, Sitia, Kavousi, F: Kithera, near the town). — G, H. *Centaurea scyria*. G: a whole individual (only the petioles of the lowermost leaves are indicated), H: an involucral scale.

C. spinosa is a maritime, spinose shrub, endemic to the Aegean. It is a rather common species recorded from all parts of the Aegean (cf. map in RECHINGER 1947). It is very variable in leaf shape, pubescence and colour of the florets. Such differences observed in the field are maintained in cultivated material.

HAYEK (1928) and RECHINGER (1943) subdivided *C. spinosa* into two geographically vicarious subspecies: ssp. *tomentosa* (HAL.) HAY. with densely tomentose, silvery leaves and reddish florets and ssp. *cycladum* (HELDR.) HAY. with almost glabrous, green leaves and yellowish florets. During the investigation of the material collected by me and my collaborators the following was found:

1. The subspecies described merely represent extreme forms within an apparently continuous variation series.

2. Material, which must be referred to ssp. *cycladum*, has been outside the Cyclades (e.g. in Ikaria).

3. Material, which must be referred to ssp. *tomentosa,* is common in the Cyclades.

4. Material referable to ssp. *tomentosa* and ssp. *cycladum* have the same chromosome number (2n=36).

A subdivision into geographically vicarious subspecies does not seem to be justified.

C. spinosa is rarely found in non-maritime localities (e.g., in the central part of Paros 450 m above sea level, RUNEMARK & SNOGERUP 12692). A closely related taxon, *C. tragacanthoides* RECH. f., occurs on loose schists above the timber line (1000—1200 m) on the mountain of Kerki, Samos. It is characterized by somewhat smaller capitula, weaker spines and dark purple florets. Possibly it ought to be included into *C. spinosa* as a distinct mountain ecotype.

Centaurea solstitialis L. [sect. *Mesocentron* (CASS.) DC.]

2n=16 (Fig. 2 C)

Cyclades. Naxos, the chapel N of Zeus Oros 600 m RUNEMARK (R-1484).

The same chromosome number (2n=16) has been reported by GUINOCHET (1957) from North Africa and by HEISER and WHITAKER (1948) on introduced material from California.

C. solstitialis is widely distributed in the Mediterranean and in western and central Europe. In the Cyclades it is rare and probably occurs as an introduced weed only.

Centaurea cretica (BOISS. & HELDR.) NYM. [sect. *Aegialophila* (BOISS. & HELDR.) HAY.]

2n=22 (Fig. 2 D)

Crete. Sitia, Cape Sidero SNOGERUP (R-3901).

C. cretica and the closely related *C. pumila* L. are both psammophytes occurring along the East-Mediterranean sea from Crete and Cyrenaica to Israel (cf. map in RECHINGER 1947). Because of the unique pappus structure the two species have been referred to a genus of its own, *Aegialophila* BOISS. & HELDR. WAGENITZ (1955) pointed out that in other morphologic characteristics (e.g. the shape of the involucral scales) they are similar to sect. *Acrocentron* in *Centaurea.* He also showed that they have the same pollen type (the *scabiosa* type) as in *Acrocentron.* He therefore referred them to a section within *Centaurea,* closely related to *Acrocentron.*
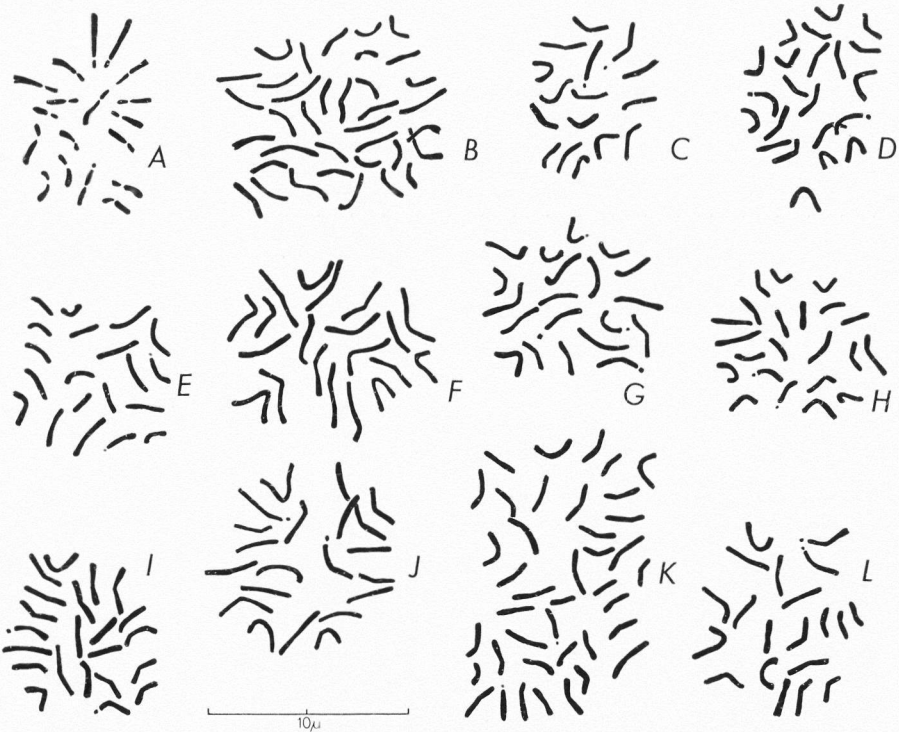
Fig. 2. Chromosome (somatic metaphase plates) in Aegean material of *Centaurea*. — A: *C. argentea* (2n=18). — B: *C. spinosa* (2n=36). — C: *C. solstitialis* (2=16). — D: *C. cretica* (2n=22). — E: *C. exscapa* (2n=20). — F: *C. redempta* (2n=20). — G: *C. spruneri* ssp. *guicciardii* (2n=20). — H: *C. scyria* (2n=22). — I: *C. oliveriana* (2n=22). — J: *C. oliveriana*×*raphanina* (2n=21). — K: *C. urvillei* (2n=40). — L: *C. raphanina* ssp. *raphanina* (2n=20).

The chromosome morphology of *C. cretica* is similar to that found in Aegean *Acrocentron* species. Besides, the same chromosome number (2n=22) has been found in two Aegean *Acrocentron* species (*C. oliveriana* DC. and *C. scyria* Run.).

Centaurea exscapa Urv. [sect. *Acrocentron* (Cass.) DC.]

2n=20 (Fig. 2 E)

East-Aegean islands. Simi, Nano Bay Bothmer (R-3910).

C. exscapa is a mostly chasmophytic species, endemic to the islands along the Anatolian westcoast. It is closely related to the Anatolian species *C. chrysoleuca* Boiss. and *C. eriophylla* Boiss. & Bal. and to *C. acicularis* S. & S. from Cyprus.

Centaurea redempta HELDR. [sect. *Acrocentron* (CASS.) DC.]

2n=20 (Fig. 2 F)

Crete. Kissamos, 9 km SSE of Kastello, SE of Rocco 150 m SNOGERUP
(R-3892).

C. redempta is a chasmophyte, endemic to western Crete. Besides
the locality discovered by SNOGERUP the species has only been recorded
from two localities. Together with *C. laconia* BOISS. (*C. subarachnoidea*
BOISS. & HELDR.), a chasmophyte in central Peloponnisos, and a newly
discovered chasmophytic species in the island of Kithera (RECHINGER,
unpublished), it constitutes a small group of vicarious taxa without ob-
vious affinities to other species in the section *Acrocentron*.

Centaurea spruneri BOISS. & HELDR. ssp. **guicciardii** (BOISS.) HAY.
[sect. *Acrocentron* (CASS.) DC.]

2n=20 (Fig. 2 G)

Cyclades. Sifnos, Cape Khondropo RUNEMARK & SNOGERUP (R-1713).
Andros, 2 km SSE of Batsi SNOGERUP (R-3893).

The *C. spruneri* complex, occurring in the southern part of the Greek
mainland, the western Cyclades, and Crete, is in urgent need of revi-
sion. The Cycladian material, usually treated as v. *lineariloba* (HAY. &
DÖRFL.) HAY., occurs in natural habitats (garigue and rocky slopes)
and seems rather distinct. The form series occurring as weeds in fields
and vineyards in the Greek mainland are, however, extremely variable,
e.g., in habit, leaf shape, and the development of involucral spines.

Centaurea scyria RUN. sp. nov. [sect. *Acrocentron* (CASS.) DC.]

2n=22 (Fig. 2 H)

Skiros, Exo Diavathi RUNEMARK & NORDENSTAM (R-3705).

DIAGNOSIS. Habitu *Centaurea ragusinae* L. similis, sed differt involucrae
squamae in mucrone brevi attenuatae et flores fusci purpurei. — Graecia.
Skiros (Skyros), in insula Exo Diavathi 26.7 1960 RUNEMARK et NORDENSTAM
16842 (Holotypus in Herb. Bot. Lund).

DESCRIPTION (cf. Fig. 1 H, G). 30—60 cm high, basally lignified,
adpressedly tomentose, wholly white perennial. Leaves pinnatisect to
bipinnatisect, (in juvenile plants entire, ovate); segments broadly lanceo-
late. Stem 5—10 mm in diam., striate, in upper part sometimes
branched. Capitula sessile, 2—5 together, 1.5—2.5 cm in diam. Invo-

lucral scales greenish yellow, with indistinct parallel nerves, tapering from a rounded base into a c. 1 mm long, brownish red mucro, and in the margins with sparse c. 0.5 mm long, stiff, brownish red hairs. Florets brownish purple. Pollen of *scabiosa*-type (cf. WAGENITZ 1955). Achenes c. 5 mm, greyish brown with long, silky hairs. Pappus c. 5 mm with numerous setae of varying length.

ECOLOGY. In maritime limestone cliffs, c. 20 m above sea level.

DISTRIBUTION. Only known from a single collection on the small island of Exo Diavathi, W of Skiros in the northern Aegean.

AFFINITIES. *C. scyria* seems to be an isolated member of sect. *Acro-centron*. In habit it is similar to *C. ragusina* L. from the Dalmatian coast. It is, however, questionable if *C. scyria* is in fact related to this species, which has yellow florets and a very different type of invo-lucral scales, with pectinately ciliate apex. *C. scyria* is similar to *C. oliveriana* DC. from the central Cyclades in the shape of the involucral scales, and also in the very special colour of the flowers (brownish purple) not found in any other Greek *Centaurea* species.

Centaurea oliveriana DC. [sect. *Acrocentron* (CASS.) DC.]

2n=22 (Fig. 2 I)

Cyclades. Naxos, Mavrianos 200 m RUNEMARK & SNOGERUP (R-1211, R-1707).
    „ , W-slope of Fanari Oros 750 m RUNEMARK & SNOGERUP (R-1320, R-1710).
    „ , 2 km W of Hypsiliammos 240 m RUNEMARK & SNOGERUP (R-1449, R-1704).
    „ , 2 km S of Ammomachis Oros 300 m RUNEMARK & SNOGE-RUP (R-1708).
Amorgos, 1 km S of Panagia 250 m BOTHMER (R-3907).

Centaurea oliveriana is a very characteristic, relatively invariable chasmophyte, endemic to the central Cyclades (see map in RUNEMARK et al. 1960). It has been regarded as an isolated member of sect. *Acro-centron*. Possibly it is related to the newly discovered *C. scyria* RUN., a chasmophyte from Skiros in the northern part of the Aegean. It also shows some similarities to *C. lactucaefolia* BOISS., another isolated spe-cies usually referred to sect. *Phalolepis* (CASS.) DC., which is a chasmo-phyte endemic to Rhodos and adjacent islands. — *C. oliveriana* and *C. scyria* are the only species within sect. *Acrocentron* known to have 2n=22. Also in chromosome morphology they are similar (Fig. 2 I, H).

Centaurea oliveriana DC.×**C. raphanina** S. & S. [sect. *Acrocentron* (CASS.) DC.]

2n=21 (Fig. 2 J)

Cyclades. Naxos, 2 km W of Hypsiliammos 240 m RUNEMARK & SNOGERUP (R-1708-5).

This unexpected hybrid between the giant species *C. oliveriana* and the small acaulescent *C. raphanina* was obtained from a seed collection of *C. oliveriana*. The hybrid individual seems to be completely sterile.

When comparing herbarium material it became evident that *C. nigrotriangulata* RECH. f. and *C. halacsyi* DÖRFL., both known from a single collection in the Cycladian island of Amorgos, belong to this hybrid.

In material of *C. nigrotriangulata* from the original locality Panagia Chozoviotissa in Amorgos collected by SNOGERUP in 1964 a few relatively well developed seeds were found. One of these seeds germinated, but the seedling died after 10 days.

In Naxos, 2 km WSW of Liona (RUNEMARK & SNOGERUP 9130, 9148) a variable hybrid swarm between *C. oliveriana* and *C. raphanina* consisting of 10—20 individuals (Fig. 3) has been found. At least part of the material represents backcrossings to the parents.

Centaurea raphanina S. & S. [sect. *Acrocentron* (CASS.) DC.]

Ssp. **raphanina**

2n=20 (Fig. 2 L)

Crete. Sitia, S of Turloti 300 m RUNEMARK & SNOGERUP (R-3889).
Sitia, the valley W of Maronia 400 m RUNEMARK & SNOGERUP (R-3890).

Ssp. **mixta** (DC.) RUN.

2n=20

Attica. Porto Rafti 100 m SNOGERUP (R-3897).
Euboea. 3 km WSW of Akr. Kafirevs RUNEMARK & SNOGERUP (R-1705).
East-Aegean islands. Ikaria, Cape Papas RUNEMARK & SNOGERUP (R-1334).

Intergrades between ssp. **raphanina and** ssp. **mixta**

2n=20

Cyclades. Koufonisi, the islet of Kopria RUNEMARK & SNOGERUP (R-1706).
Naxos, Stavros Keramotis 600 m RUNEMARK (R-33, 74).
Naxos, Akr. Ag. Ioannis RUNEMARK (R-1143).

Fig. 3. Some individuals of the hybrid swarm between *C. oliveriana* and *C. raphanina* found in Naxos. The largest individual is similar to that in cultivation (×0.4).

Fig. 3.

As far as can be observed in chromosome plates obtained in root-tip sections no differences in chromosome structure occur between ssp. *raphanina* and ssp. *mixta*.

Within the *raphanina* complex six species have been described, viz. *C. raphanina* S. & S. (1817), *C. mixta* DC. (1837) = *C. hellenica* BOISS. (1843), and the four endemic, Cycladian species: *C. myconia* BOISS. & SART. (1859), *C. halacsyi* DÖRFL. (1901), *C. eriopoda* RECH. f. (1934) and *C. nigrotriangulata* RECH. f. (1934). RECHINGER (1943) showed that the endemic, Cycladian species do not occupy different geographic areas, and that intermediates between them are very common, and therefore reduced them to varieties of *C. mixta*. RECHINGER later (1947 and 1950) drew attention to the chaotic variability of *C. mixta* in the Cyclades, according to him partly caused by ecologic differentiation (chasmophytic and colline series).

According to RECHINGER (1950) two well delimited, strictly vicarious species of the *raphanina* complex occur in the Aegean, viz. *C. mixta* on the Greek mainland and in the central Aegean islands, *C. raphanina* in Crete and Karpathos, both replaced by *C. urvillei* in the East-Aegean islands. According to him the boundaries between the species wholly coincide to the oldest fault zones in the Aegean area.

A renewed analysis, also including cultivated material, can now be carried out as extensive collections have been made in southern Greece (mainly in the Cyclades) by the author and his collaborators in 1957 —1966.

MORPHOLOGIC ANALYSIS

As mentioned already by RECHINGER (1943) the material of *C. mixta* from the Greek mainland is fairly homogeneous. A morphologic analysis of *C. raphanina* from Crete and Karpathos has shown that also this material is relatively invariable. A comparison between material of *C. mixta* from the Greek mainland and *C. raphanina* revealed a number of differences (cf. Fig. 4).

1. Pronounced differences

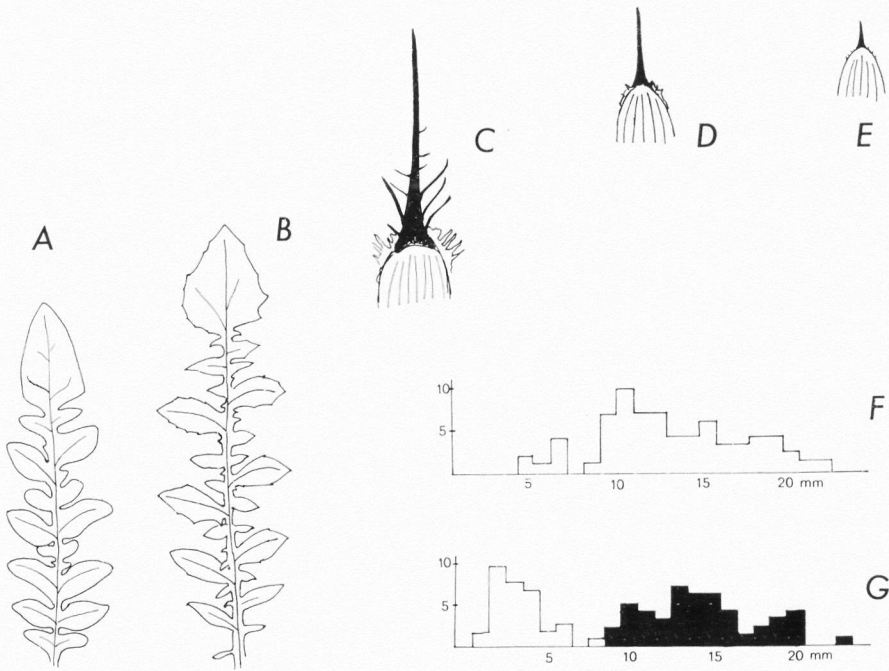| *mixta*	*raphanina*
At least largest leaf segments with scattered, small teeth.	All leaf segments lacking teeth.
Small, stiff hairs in leaf margin, but no hairs on leaf surface.	Small stiff hairs in leaf margin and on leaf surface.
Leaves glossy on upper side.	Leaves matt on upper side.
Longest spines of involucre 10—20 mm.	Longest spines of involucre 2—8 mm.

Fig. 4. *Centaurea raphanina*. — A: leaf of ssp. *raphanina*, B: leaf of ssp. *mixta*, C: involucral scale of ssp. *mixta*, D, E: involucral scales of ssp. *raphanina*. — F, G. The length of the longest spine in a capitulum. The number of individuals is indicated on the vertical axis, the length of the spine on the horizontal one. F: Cycladian material, G: ssp. *raphanina* from Crete (white) and ssp. *mixta* from the Greek mainland (black).

Thin, lateral spinelets on lower part of spine.	No thin, lateral spinelets on lower part of spine.
Involucral scales rather broad, with rounded apex.	Involucral scales narrow, with tapering apex.
Capitula rounded, with truncate base.	Capitula elongated, with tapering base.

2. Less pronounced differences

mixta	*raphanina*
Leaves dark green, of firm texture.	Leaves light green to green, rather soft.
Terminal lobe of leaf normally small.	Terminal lobe of leaf large.
Flowering stem very short.	Flowering stem often elongated (5—20 cm).

An analysis of the material from the Cyclades gave the following result (cf. Fig. 5).

Table 1. *Centaurea raphanina.* — The frequences (in %) of ssp. *raphanina* and ssp. *mixta* characteristics in 6 populations in the Astipalea area in the south-eastern Cyclades. In the comparisons made the *mixta* characteristics are placed to the left. — The material from Ofidousa coincides in all respects with ssp. *mixta* from the Greek mainland. — The analyses were made in the field in 1966.

	Leaves				Involucral spines					number of individuals
	glabrous	hairy	dentate	non-dentate	long	inter-mediate	short	lateral spinelets present	absent	
Astipalea										
Maltesana ...	85	15	30	70	5	30	65	70	30	20
Panermo	60	40	55	45	35	55	10	80	20	20
Kounoupia ..	90	10	60	40	85	15	—	90	10	20
Sirina	6	94	12	88	48	52	—	55	45	33
Levitha	90	10	40	60	50	50	—	45	55	20
Ofidousa	100	—	100	—	100	—	—	100	—	c. 50

A. Material in all details coinciding with *C. mixta* from the Greek mainland occurs sparingly in the whole area. It is remarkable that in the SE Cyclades it is found exclusively on small, isolated islands (Anidros, Ofidousa and Levitha).

B. Material in all details coinciding with *C. raphanina* is found on some islands south of Naxos (Ios, Iraklia, Koufonisi). Only certain individuals within a population coincide completely with *C. raphanina*. It is doubtful whether populations exist, in which all individuals are of the *raphanina* type.

C. Material showing a mixture of morphologic characteristics from *C. raphanina* and the mainland form of *C. mixta* constitutes the main part of the collections from the central, south-western and south-eastern Cyclades. However, two characteristics (the narrow involucral scales and the small spines) occur only in the area (Iraklia, Koufonisi, Ios) where individuals indistinguishable from *C. raphanina* have been found. Other *raphanina* characteristics, such as narrow capitula with a tapering base, lack of lateral spinelets, hairy surface of the leaves and non-dentate leaves seem to be evenly distributed over the area. In the characteristics mentioned there is a wide variation within most populations. Single individuals within a population can thus be characterized by 1, 2, 3 or more of the *raphanina* characteristics. Also morphologically transitional forms occur, e.g., in leaf-shape and shape of the involucral spines (cf. Fig. 4 F, G). — Population analyses from the Astipalea area in the south-eastern Cyclades are presented in Tab. 1.

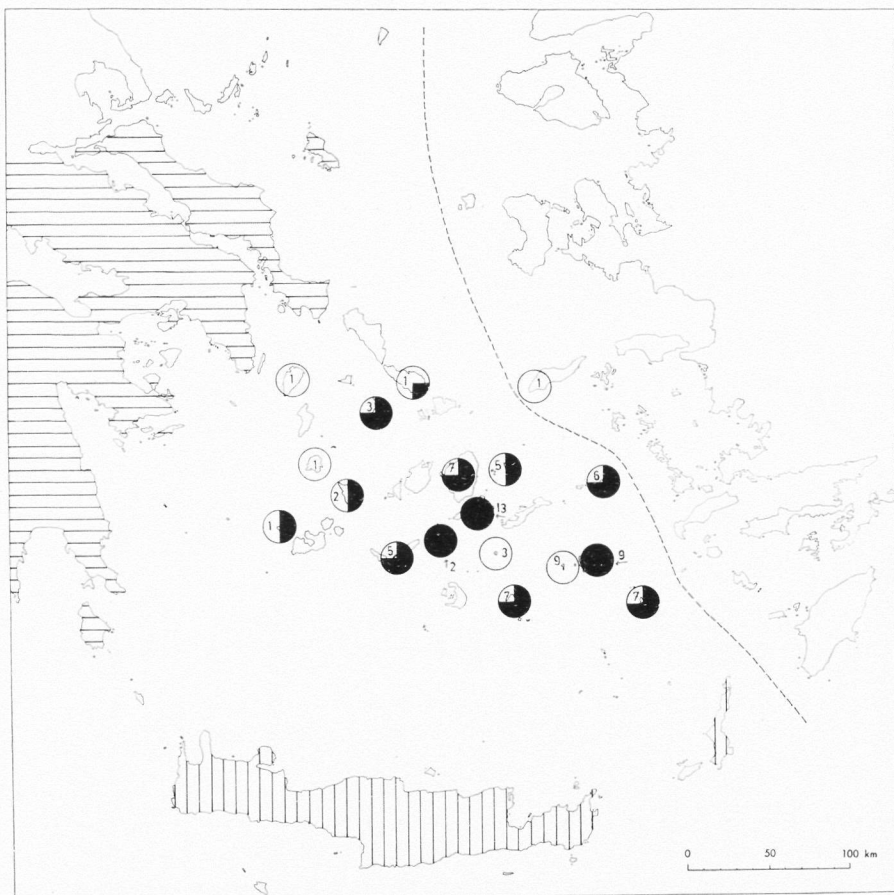Intermediate forms from the Cyclades have been cultivated by the

Fig. 5. The distribution in the Aegean of *C. raphanina* ssp. *raphanina* (vertical lines) and *C. raphanina* ssp. *mixta* (horizontal lines and open circles). — The solid circles indicate that intermediates have been found in the area covered by the circle, having 1, 2, 3 or 4 (wholly black circles) of the following ssp. *raphanina* characteristics: (A) spines less than 8 mm, (B) no lateral spinelets, (C) leaf surface hairy, and (D) leaf segments non-dentate. — The figures given are the numbers of collections (usually of 2—10 individuals) studied.

author for several years. The morphologic characteristics discussed do not seem to be influenced by the environment. Individuals originating from the same collection show different combinations of *raphanina* characters.

It is hardly possible that the *raphanina*-like material from the islands S of Naxos has developed from *C. mixta* by convergent evolution, as

it coincides with Cretan material of *C. raphanina* in a considerable number of morphologic characteristics.

Apparently a large scale introgression between *C. mixta* and *C. raphanina* has taken place in the Cyclades. Such an introgression will be a natural explanation for the non-regular combination of characteristics in the Cycladian material observed already by RECHINGER. As the typical mainland form of *C. mixta* is still found on small isolated islands in the SE Cyclades, it seems probable that the introgression has not taken place until *C. mixta* was established all over the Cyclades.

A case which is in some respects parallel occurs in *Phagnalon*. *Ph. graecum* BOISS. et HELDR. is distributed all over the Aegean. The closely related *Ph. rupestre* L. (West- and East-Mediterranean with a gap in the Aegean) is found in its typical form on a few, small, isolated islands (e.g., Anidros). The main part of the material from the southern Cyclades is, however, intermediate between *Ph. rupestre* and *Ph. graecum*.

As most of the material from the Cyclades is intermediate in one or several characteristics it seems inappropriate to keep *C. mixta* and *C. raphanina* as separate species. As they are vicarious to a large extent they will, in accordance with GUGLER (1909), be treated as subspecies.

TAXONOMIC TREATMENT

Centaurea raphanina SIBTHORP and SMITH 1813

C. myconia BOISSIER & SARTOR in BOISSIER 1859. — *C. hellenica* BOISSIER & SARTOR, in BOISSIER 1845, nom. illeg. — *C. mixta* DE CANDOLLE 1837 p.p. — *C. eriopoda* RECHINGER f. 1934.

Perennial herb with a fleshy taproot, 1—2 cm in diam. stem very short (0.5—5 cm). Leaves rosulate, pinnatisect, with small, rounded, oblong or broady lanceolate segments with stiff hairs in the margins. Capitula ± sessile, 1—4 together, rounded or elongated, 1—2 cm in diam. Involucral scales elliptic or broadly lanceolate with an apical spine, 2—25 mm long. Florets red.

Ssp. *raphanina*

C. mixta ssp. *raphanina* (S. & S.) GUGLER 1909, nomen illeg.

Leaves with a matt, hairy surface, segments non-dentate, usually oblong. Capitula elongate with a tapering base. Involucral scales broadly lanceolate, tapering towards the apex. Apical spine simple, 2—8 mm. Chromosome number $2n = 20$.

DISTRIBUTION. Crete, Karpathos.

Ssp. *mixta* (DC.) RUN. stat. nov.

C. *mixta* DC. 1837 — C. *mixta* ssp. *eu-mixta* GUGLER 1909, nomen illeg.

Leaves glossy, glabrous except in margins, at least large segments dentate. Capitula rounded, with a truncate base. Involucral scales elliptic with a rounded apex. Apical spine 10—25 mm, in lower part with lateral spinelets. Chromosome number 2n=20.

DISTRIBUTION. Southern Greece, Kerkira (Corfu), Skiros, Ikaria and scattered localities in the Cyclades.

Intergrades between ssp. *raphanina* and ssp. *mixta*

DISTRIBUTION. Central, south-western and south-eastern Cyclades.

Taxa described in the *C. raphanina* complex.

1. *C. myconia* BOISS. et SART. is a form of *mixta* with long spines. The species was reduced to synonymy already by BOISSIER in Flora Orientalis (1875).

2. *C. hellenica* BOISS. The material mentioned in the original description of *C. mixta* includes both Greek plants (=*mixta* in present sense) and plants from Turkey (=*C. urvillei*). Because of the heterogeneity of the original material BOISSIER withdrew the name *mixta,* which was substituted by *hellenica.* According to the present code of nomenclature such a treatment is incorrect.

3. *C. eriopoda* RECH. f. The species is based on material from Siros in the Cyclades, belonging to intergrades between ssp. *raphanina* and ssp. *mixta.* It is characterized mainly by its elongated capitula and relatively small spines. Its resemblance to *C. raphanina* from Crete was noticed already by RECHINGER.

4. *C. halacsyi* DÖRFL. The type material is a hybrid between *C. oliveriana* and *raphanina,* cf. p. 168.

5. *C. nigrotriangulata* RECH. f. The type material is a hybrid between *C. oliveriana* and *C. raphanina,* cf. p. 168.

PLANTGEOGRAPHIC NOTE

The perfect coincidence between the oldest fault zones in the Aegean and the distribution of *C. urvillei, C. raphanina* ssp. *raphanina* and ssp. *mixta* stressed by RECHINGER (1950) is now somewhat obscured, because of the introgression in the Cyclades between ssp. *raphanina* and ssp. *mixta* and by the discovery of ssp. *mixta* in an East-Aegean island (Ikaria, Cape Papas RUNEMARK & SNOGERUP 11034).

Centaurea urvillei DC. [sect. *Acrocentron* (CASS.) DC.]

2n=40 (Fig. 2 K)

East-Aegean islands. Rhodos, 5 km E of Ag. Issidoros 450 m BOTHMER (R-3909).

C. urvillei is similar to *C. raphanina* S. & S. and replaces it in the East-Aegean area. It is most easily distinguished from *C. raphanina* by the occurrence of an arachnoid indumentum on stems and young leaves.

Within the *urvillei* complex at least 5 species have been described, viz. *C. urvillei* DC., *C. lydia* Boiss., *C. chiosicola* Beauv., *C. czezottae* Hay. and *Aegialophila longispina* Cand. Rechinger (1943, 1947, 1950) treated *C. chiosicola* and *Aegialophila longispina* as merely synonyms to *C. urvillei*. He also drew attention to the close relationship between *C. urvillei* and other Anatolian species, especially *C. lydia* and *C. czezottae*. Bornmüller (1944) stressed the extreme variability of *C. urvillei* and mentioned the difficulty of a subdivision as different morphologic forms often are found growing together. He also questioned the separation of *C. czezottae* from *C. urvillei*. Meikle (1954) presented the hypothesis, that the small-headed material from Chios "may be at least locally distinct variants of the variable *C. urvillei*". However, small-headed specimens, comparable to those from Chios, have also been collected in Paphlagonia on the northern coast of Turkey.

The cytologically investigated material from Rhodos has very large capitula, large leaves and stout, 10—20 cm long flowering stems. Besides the normally developed achenes, very narrow, cylindric ones were found in the same capitulum. However, these achenes did not germinate.

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Morphological Studies
on Histiopteris and Hypolepis

By B. K. Nayar, Surjit Kaur and Nisha Bajpai

National Botanic Gardens
Lucknow, India

ABSTRACT

Morphology of the sporophyte and gametophyte of *Histiopteris incisa* and *Hypolepis punctata* is described. Both are terrestrial ferns with long creeping, branched rhizome clothed with elongated, stiff, non-glandular, acicular hairs. The hairs are uniseriate, except at the base where they are multiseriate. The ground tissue of the rhizome is parenchymatous, but a few layers of cells next to both the epidermis and endodermis are thick-walled. The vascular cylinder of the rhizome at the internodal region is a hollow cylinder with corrugated surfaces. Towards the leaf base it becomes gutter-like (by developing a dorsal median slit) and directly enters the leaf as a large gutter-like leaf trace. In *Histiopteris* the vascular cylinder, before entering the leaf base, becomes dissected into 5 ribbon-like strands (one broad ventral strand, a pair of large lateral strands towards the dorsal surface, and pair of narrow lateral ones next to the abaxial strand).

At the base the leaf in both the genera bears two or more alternately placed lateral branches. The branch trace is gutter-like at origin and is associated with a short branch gap. Soon it becomes tube-like resembling the main rhizome, and like it, ends in a leaf trace. The vascular bundle in the stipe and rachis is gutter-like with flattened base and nearly perpendicular sides, each having a prominent broad longitudinal invagination close to the basal region. In *Histiopteris* it is dissected to form a pair of large curved adaxial strands, a pair of narrow lateral ones and a broad corrugated ventral strand. Vascular connection to lateral branches of the rachis are paired strands originating intramarginally from the gutter-like vascular strand of the rhizome (one from near the adaxial margin and the other from near the flattened basal region). The leaf lamina is tripinnate-quadripinnatifid, herbaceous and with undifferentiated mesophyll tissue. The venation of the ultimate pinnae is characteristically reticulate in *Histiopteris* but free in *Hypolepis*.

Elongated acicular hairs occur on both surfaces of the lamina as well as on the stipe and rachis. The sorus is submarginal in both the genera. In *Histiopteris* it is elongated, extending along an intramarginal vein connecting the vein-tips; in *Hypolepis* sori are circular, discrete and subapical on the veins. In both, the sorus is protected by the infolded margin of the leaf.

Sporangia are mixed with filamentous paraphyses and are of the common leptosporangiate-type but with the annulus slightly tilted to one side at the base; the stalk is 2 cells thick except at the capsule base where a 3rd row is developed secondarily as a downward protrusion of a basal wall cell of the capsule. Spores are monolete, bilateral, devoid of perine and with the exine bearing tubercle-like excrescences in *Histiopteris* and spine-like ones in *Hypolepis*. The prothallus in both the species is of the common cordate type, naked, and developing from a uniseriate, short germ filament in the usual manner (by the formation of an apical obconical meristematic cell which is later replaced by multicellular meristem). Sex organs are of the common type found in advanced ferns.

INTRODUCTION

Among the fern genera included by COPELAND (1947) in the *Pteridaceae,* the Chaetopterid ferns (CHRISTENSEN 1938) have proved themselves phyletically most controversial. Recently MEHRA (1961) has suggested, on cytological grounds, the separation of these ferns along with *Histiopteris* as a distinct family *Hypolepidaceae*. This suggestion seems to be well substantiated by cytology, all these genera of tropical ferns being characterised by chromosome numbers based on $x = 13$. A study of comparative spore-morphology of Indian ferns recently undertaken by us (NAYAR and DEVI 1966) supports this suggestion based on cytology. This has prompted us to undertake a morphological study of some of the little known genera belonging to the group, so that the phylogeny and relationships of these ferns may be better judged from total morphological comparisons. This communication deals with the morphology of two of these genera, *Histiopteris* (AG.) J. SM. and *Hypolepis* BERNH. The significance of the observations recorded here will be discussed later, when the morphology of other genera of the Hypolepidoid ferns are presented.

Both *Histiopteris* and *Hypolepis* are pantropic terrestrial ferns, represented in the Indian flora. *Hypolepis* is a large genus with over 45 species; *Histiopteris* includes one wide-spread species, *H. incisa*, and seven other local oriental species (COPELAND 1947). *Hypolepis* is regarded as a Dennstaedtioid derivative by most pteridologists (BOWER 1928, COPELAND 1947, HOLTTUM 1947) whereas *Histiopteris* is considered a relative of *Pteris*. According to COPELAND both genera may be derived from different elements in *Dennstaedtia*, along with *Microlepia*, *Paesia* and *Pteridium*. Commenting on *Histiopteris* he assumes that "if its direct affinity to any Dennstaedtioid fern is established, it would fix the place of *Pteris*, but any such affinity is an assumption rather than an established fact" (COPELAND 1947 p. 80). HOLTTUM (1947) postulates that

one of the main lines of evolution from the primitive Dennstaedtioid stock has been "by way of *Hypolepis* to *Pteridium* and *Pteris*" (HOLT-TUM 1947 p. 134). PICHI-SERMOLLI (1958, 1959) regards *Histiopteris* and *Hypolepis* as belonging to the *Dennstaedtiaceae*, phyletically distinct from *Pteris* and its allies. He however regards both the Dennstaedtioid and Pteroid lines of descent (the *Dicksoniales* and *Pteridales* respectively) to have originated from a Schizaeoid ancestor.

Morphological information on both the genera discussed here, is limited. Details of organisation of the vascular cylinder of the rhizome are reported by TANSLEY & LULHAM (1902) and TANSLEY (1908) in the case of *Histiopteris* and GWYNE-VAUGHAN (1903) in the case of *Hypolepis*. Spore-morphology of some species of both the genera is described by NAYAR & DEVI (1966). Cytology of *Hypolepis punctata* (MANTON 1954, MANTON & SLEDGE 1954, MEHRA & VERMA 1960) and *Histiopteris incisa* (BROWNLIE 1954, 1961, MANTON & SLEDGE 1954) is studied by various workers from different parts of the world. Both genera are based on the monoploid number $x=13$, *Histiopteris incisa* ranging from $n=96—104$. Polyploid races occur in *Hypolepis punctata,* plants from most regions studied having $n=104$ as the chromosome number; the Malayan and Ceylonese plants are reported to have a chromosome number $n=51—53$ (MANTON 1954, MANTON & SLEDGE 1954).

For this study *Hypolepis punctata* was collected from Western Ghats of South India and *Histiopteris incisa* from Garo Hills as well as K. & J. Hills of Assam. Fresh spores collected in the field were cultured in the laboratory on sterile nutrient agar medium (NAYAR 1962) maintained at a light intensity of 600 ft-c., and temperature range of $24 \pm 2°C$. All observations on the development, etc., of the prothalli are based on these cultures. For study of spores, the common acetolysis technique (ERDTMAN 1952) is used and comparison is made to fresh spores mounted directly in glycerine jelly. Technique of study and spore-descriptions are after NAYAR (1964). For study of sporophyte morphology, material preserved in F.A.A. and stored in 70 % alcohol is used. Study of the organisation of the vascular system is based on serial transverse sections as well as cleared material, as described in earlier communications (NAYAR 1963, NAYAR & KAUR 1965).

RHIZOME

The rhizome in both the genera is long creeping, profusely branched, cylindrical and clothed with dark-brown, stiff, acicular, hairs. The

hairs are cylindrical and composed of elongated, rather thick-walled, barrel-shaped cells with stiff transverse walls. The basal portion of many of the hairs is broadened and composed of many rows of small cells; beyond this basal region the hairs are uniseriate. The base of such hairs is conical and 2 or 3 cells thick in *Hypolepis* (Fig. 1 D), whereas it is dorsiventrally flattened and usually only one cell thick in *Histiopteris* (Fig. 1 A). The terminal cell of the hair (Fig. 1 B, C) is elongated, tapered upwards, non-glandular and stout. The hairs are brittle when old and are generally shed in the older regions of the rhizome, except at the axils of branches and leaves.

The rhizome is parenchymatous, the ground tissue consisting of narrow, thin-walled cells, rather elongated along the longitudinal axis of the rhizome and having dense starch deposits. The epidermis is thin walled while a few (4 or 5) layers of hypodermal cells are thick walled and dark brown, the thickening of the wall being progressively less prominent in the inner layers so that the hypodermal sheath merges imperceptibly with the cortical parenchyma. An irregular sheath of thick-walled cells, similar to the hypodermal sheath, occurs around the vascular cylinder on both the surfaces; the sclerenchymatous sheath on the inner surface of the stelar cylinder (facing the pith) is sometimes interrupted irregularly and occasional strands of cells with comparatively thicker walls occur in between.

The vascular cylinder of the rhizome (Fig. 1 E, F) is siphonostelic in both the species and possesses irregular longitudinal corrugations. In *Histiopteris* it appears polycyclic in some regions, due to the characteristic nature of the branch- and leaf-traces. In both the genera the vascular cylinder of each internode apparently ends in a median leaf trace (Fig. 1 E, F-*lt*). This leaf trace, before it enters the leaf base, gives off two or more branch traces laterally. The branches of the rhizome in their turn terminate in leaf traces and the process is repeated. Externally the leaf base and the rhizome (as well as its branches) are similar. All are borne in the same plane (parallel to the substratum), but soon after the separation of the branches the leaf base curves sharply upwards, making the stipe vertical (with its grooved 'adaxial' surface facing the earlier node). Roots are borne profusely on the ventral surface of the leaf base as well as on the base of the branches. The vascular cylinder at the internodal regions is an intact cylinder devoid of any gaps in both genera.

In *Hypolepis* it opens up towards the anterior end of the internode by a dorsal longitudinal slit, thus becoming gutter-shaped. It then di-
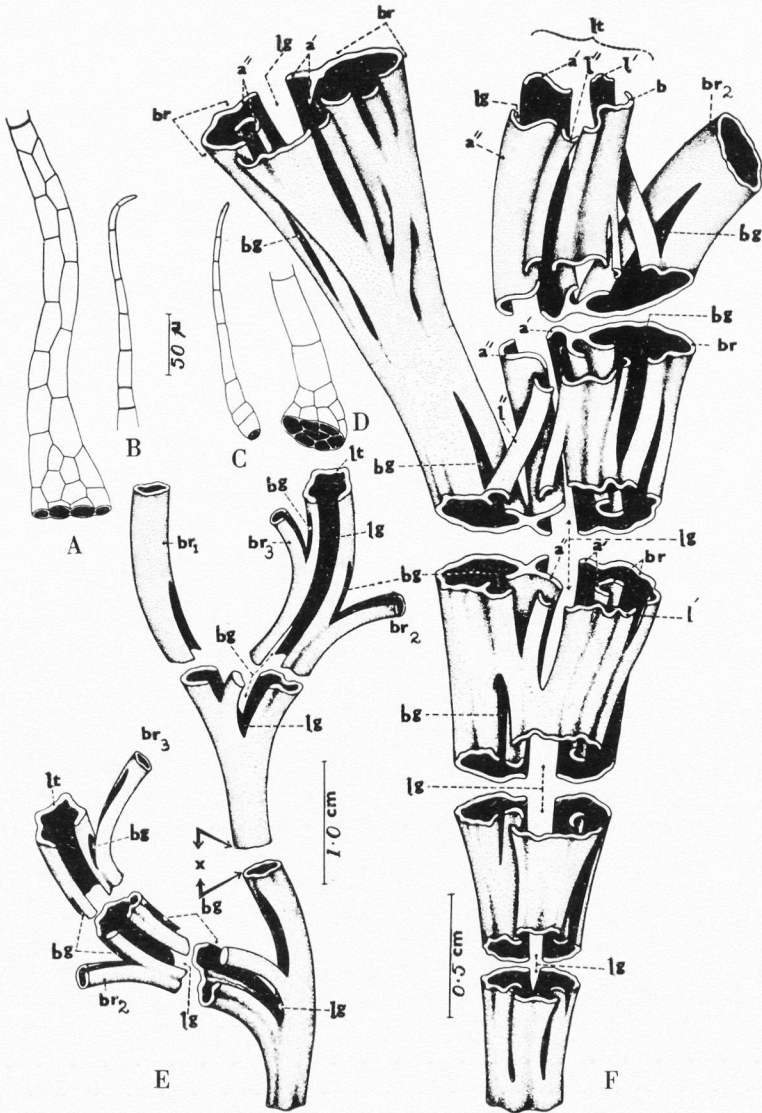
Fig. 1. Morphology of the rhizome (a', a'': the first and second adaxial vascular strand of leaf trace, b: abaxial vascular strand of the leaf trace, bg: branch gap, br_1, br_2, br_3: successive shoots in their order of development, l', l'': lateral vascular strands of the leaf trace, lg: leaf gap, lt: leaf trace, x: A portion, 3 cm. long, of the stelar cylinder omitted in the drawing). — A: Basal portion of a large trichome on the rhizome of *Histiopteris incisa*. B: Apical portion of the same. C: A small trichome on the rhizome of *Hypolepis punctata*. D: Basal portion of a large trichome on the same. E: Vascular cylinder of portions of the rhizome (roots omitted) showing the origion of the branches and leaf-traces in *Hypolepis punctata*. F: Same in *Histiopteris incisa*.

rectly enters the leaf base as a gutter-shaped, corrugated bundle. Vascular connections to two or generally three branches (Fig. 1 E-*br*) are regularly given off laterally by this gutter-shaped strand before it enters the stipe. Each branch trace is associated with an adaxial branch gap which is generally short and narrow (Fig. 1 E-*bg*). The branch trace is gutter-like at origin, but soon becomes siphonostelic by the fusion of its free margins. The branch formed first is usually more prominent than the other branches, and during growth often appears as a direct continuation of the rhizome. In successive leaves such basal branches are on opposite sides so that the rhizome appears to be sympodial with leaves borne alternately on either side. The branches associated with each leaf are alternate on either side of the leaf base. The gutter-shaped vascular bundle of the leaf base of *Hypolepis* is intact. The basal region is nearly flat and the sides are nearly perpendicular to it but with a prominent longitudinal invagination laterally towards the abaxial side.

The stelar cylinder of the rhizome (Fig. 1 F) of *Histiopteris* differs from that of *Hypolepis* in that it becomes dissected into three main strands and two subsidiary strands before it enters the leaf base. Also, generally there are only two branches associated with each leaf base. The branches often appear opposite to and directed away from each other, so that the rhizome appears to fork into two with a prominent leaf located between the two branches. Contrary to the condition in *Hypolepis*, the lateral accessory bundles of the leaf trace (Fig. 1 F-*l'*, *l''*) are often fused with the outer margins of the branch trace at the base. The leaf trace of *Histiopteris* at the base of the stipe is gutter-shaped, with the lateral sides conspicuously invaginated, margins incurved and the basal portion nearly flat except for a broad median invagination (so that there are three longitudinal bulges facing the centre of the stipe, two of them lateral and one basal). Further, it is dissected by conspicuous lateral lacunae, into three main bundles and two or sometimes more smaller bundles. The three main bundles are the transversely placed, broad basal one (constituting the base of the gutter, Fig. 1 F-*b*) and a pair of ribbon-like lateral adaxial strands (Fig. 1 F-*a'*, *a''*) perpendicular to it on either side (constituting the margins of the gutter). Between the adaxial bundles and the basal strand are a pair of narrow curved strands, one on either side (Fig. 1 F-*l'*, *l''*). These are sometimes further dissected, forming a reticulum in the larger leaves. The lacunae separating the adaxial strands from the abaxial one extend far back into the stelar cylinder of the internode, whereas the lacunae separating the

lateral minor strands from the abaxial one extend usually only to the leaf base. The basal vascular strand of the leaf trace separates from the stelar cylinder of the internode (on its ventral surface) much before the leaf gap opens up the stelar cylinder on the dorsal surface. Vascular connection to the branches associated with each leaf originates from the adaxial strands of the leaf trace.

Thus, the siphonostelic stelar cylinder of the internodal region in *Histiopteris incisa* splits into three large vascular strands before entering the leaf base. Of these three strands the ventral one is often further dissected by elongated lacunae and establishes one or two marginal vascular commissures with the lateral strands on either side. The lateral strands curve markedly and give off a branch trace each, accompanied by a narrow, short, branch gap. The branch trace at origin is laterally fused with the adaxial bundles. This results in the vascular cylinder appearing polycyclic at the region where the branch trace originates.

LEAF

In both the genera, the stipe is continuous with the rhizome, and hardly differentiated from it at the base. It is grooved on the dorsal surface, and is either cylindrical as in *Histiopteris* or tetragonal as in *Hypolepis*. In *Histiopteris* the dorsal groove is faint and discernible only towards the base. However, it extends a short distance on to the rhizome. In *Hypolepis* the groove is prominent all along the length of the stipe and continues on to the rachis and its branches. Lateral aerenchyma bands are conspicuous in both the genera. At the base, the stipe is oriented in the same plane as the main rhizome (parallel to the substratum) in both the genera. Soon, however, it curves upwards (perpendicular to the substratum), becoming vertical so that the dorsal surface of the stipe faces the posterior end of the rhizome. When young, the stipe bears hairs similar to those on the rhizome. On older stipes the hairs are shed, sometimes leaving prominent scars (which make the surface of the stipe muricate in *Histiopteris*).

The stipe is hard in both the genera. The vascular bundle of the stipe is gutter-shaped with conspicuously broadened, nearly flat, basal region and nearly vertical or slightly divergent sides with incurved free margins. There is a prominent lateral longitudinal invagination on either side towards the flattened gutter base. The vascular bundle of the stipe is intact (not perforated) in *Hypolepis punctata*, but is dissected usually by 4 longitudinal, elongated, narrow lacunae in *Histiopteris incisa*.

Also, it is more convoluted in the latter. The lacunae are lateral, cutting off the lateral invaginated region on either side of the vascular strand into small strap-shaped bundles. Thus, in a t.s. of the stipe there are usually 5 ribbon-like vascular strands (see Fig. 2) in *Histiopteris* (a large, broad, often corrugated, abaxial strand; a pair of large broad adaxial strands perpendicular to the basal strand and with incurved adaxial margins; a pair of narrow, curved lateral strands, one on either side of the abaxial strand and between it and the adaxial strand on that side). In the larger stipes the lateral strands are further dissected by narrow short lacunae, into a loose reticulum. The ground tissue of the stipe is parenchymatous in both the genera. In *Histiopteris* a few layers of the peripheral cells are thick walled, the thickening progressively becoming more prominent in the outer layers; the epidermal cells are also thick walled like the hypodermal cells. In *Hypolepis* there is a distinct cortical sheath of sclerenchyma (8—12 cells broad) sharply delimited from the inner ground tissue. The cells of the sclerenchyma sheath possess conspicuously thickened, lamellated and pitted walls.

The rachis and its branches are similar to the stipe in structure. They are cylindrical and devoid of any dorsal groove in *Histiopteris incisa* but prominently grooved in *Hypolepis punctata*. The groove in *Hypolepis* is continuous on the primary and secondary rachises, being markedly broad at the regions of the branches. In *Hypolepis* the rachises are profusely hairy. The hairs are of the uniseriate type, similar to those on the rhizome, but light yellowish in colour and not stiff. In *Histiopteris* the hairs are usually shed early, except those at the bases of the rachis branches. The vascular bundle of the rachis is nearly similar in shape to that of the stipe, but more or less compressed dorsiventrally (omega-shaped in a t.s.). Vascular connection to the branches of the rachis originates extra-marginally from the gutter-shaped vascular bundle of the rachis. In *Hypolepis,* to supply the branch rachis, the vascular bundle of the main rachis develops a hollow lateral bulge towards the flattened basal region (Fig. 2 O) next to its lateral invagination (i.e. at the corner of the rachis bundle, where the flattened basal region merges with the vertical lateral side). The inner margins of the bulged out portion come close to each other and merge (Fig. 2 P), so that the bulged region becomes tube-like, including a central cylindrical shaft of parenchyma. Meanwhile the adaxial margin of the rachis bundle curves towards the bulged region on that side and fuses with it at a point a little below the free margin. The bulged out region, along with a portion of the margin with which it is united, now becomes
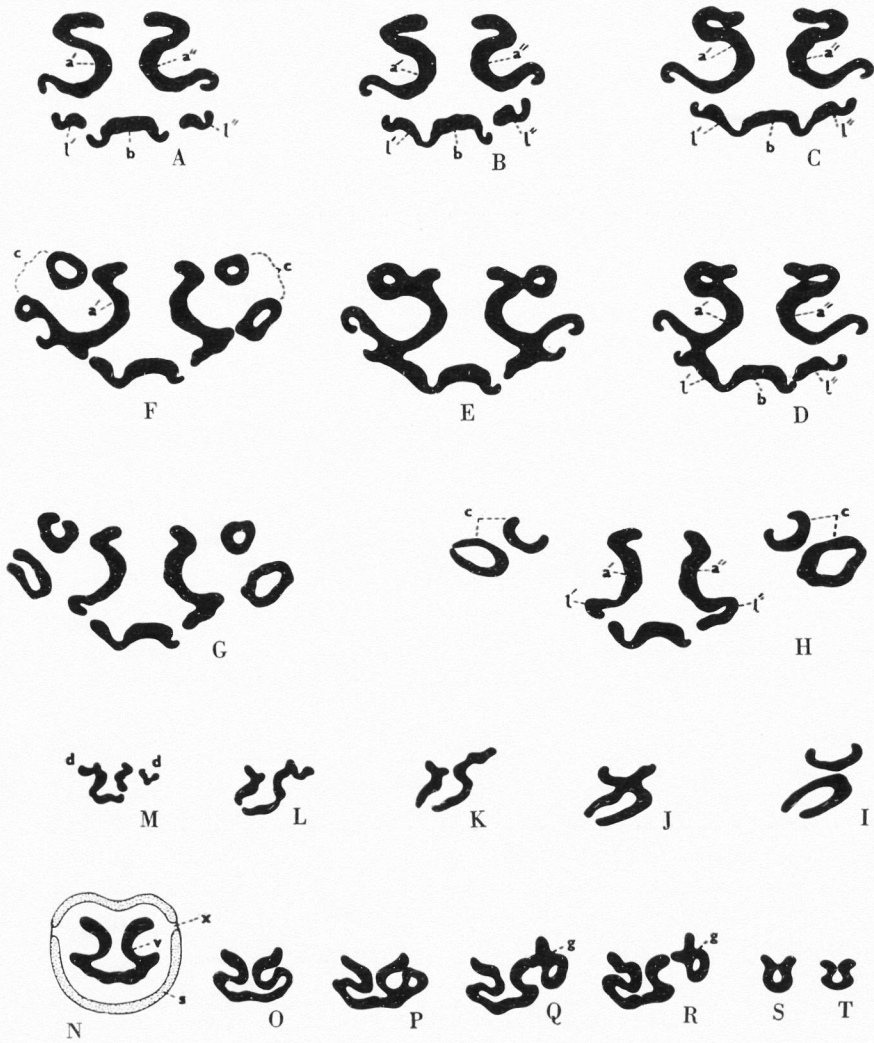
Fig. 2. Vascular structure of the stipe and rachis (*a'*, *a"*: adaxial bundles: *b*: abaxial bundle, *c*: vascular supply to the primary branch, *d*: vascular supply to the pinna, *g*: vascular supply to primary branch of rachis, *l'*, *l"*: lateral bundles, *s*: sclerenchyma tissue, *v*: vascular strand, *x*: aerating tissue). — A—H: Series of t.s. of the vascular supply of the rachis (adaxial side above) showing the origin of vascular supply to the primary branches of the rachis in *Histiopteris incisa*. I—M: Serial t.s. of the vascular supply at the base of a primary branch of the rachis of *Histiopteris incisa*, showing origin of vascular supply to the pinna. N: Transection of the stipe of *Hypolepis punctata* showing vascular strand. O—R: Serial t.s. of vascular supply of rachis of *Hypolepis punctata*. S, T: Transection of vascular supply at the base of primary branch of the rachis in *Hypolepis punctata*.

free of the main rachis bundle (Fig. 2 Q, R-g) and proceeds to curve off towards the branch base. This vascular strand (Fig. 2 S) consists of a hollow cylindrical ventral half bearing a pair of divergent dorsal flaps. The ventral half soon opens up by a longitudinal dorsal slit (between the two dorsal flanges), thus becoming gutter-shaped (Fig. 2 T). Rarely (in larger leaves) the cylindrical abaxial region of the vascular supply to the branch rachis becomes separated from the vascular strand of the main rachis before it fuses with the margin of the strand.

In *Histiopteris* the nature of the vascular supply to the branch rachises is similar to that of *Hypolepis* but a little more complex owing to the complex nature of the vascular supply of the main rachis. Both the dorsal and ventral halves of the branch supply originate independently as hollow cylindrical bundles. Of these the dorsal one is formed as a sub-marginal bulge developed on the ribbon-like adaxial vascular strand of the rachis supply (the bundles marked a', a'' in Fig. 2). The margins of this bulge come together and unite (Fig. 2 D) to form a hollow cylinder which later separates from the main strand (Fig. 2 E, F). Meanwhile the abaxial margin of the main strand, along with the adjacent margin of the lateral strand, similarly cuts off the ventral half of the branch supply (Fig. 2 A—F). Soon after separation from the vascular supply of the rachis, the two cylindrical branch bundles open up on the side facing away from each other, thus forming a pair of gutter-like strands, one above the other and with their convex surfaces facing each other (Fig. 2 G—I). Later they come together and fuse by their convex surfaces (Fig. 2 J), thus forming a 4-flanged strand (having a pair of adaxial flanges formed by the margins of the dorsal gutter-shaped strand, and a pair of abaxial ones formed by the margins of the ventral gutter-shaped strand). Soon this 4-flanged strand splits longitudinally in the middle (Fig. 2 K) to form two corrugated ribbon-like strands placed side by side (each formed by half of the original dorsal gutter-like bundle and half of the ventral one). The ventral margin of one of the ribbon-like strands curves towards the other and is later cut off to form a flat ventral strand (Fig. 2 L, M). The 3 ribbon-like strands thus formed (one ventral and a pair of lateral ribbon-like strands) enter the branch base, assuming the characteristic shape and orientation of the vascular supply of the main rachis. Vascular supply to the pinnae are simple gutter-like strands given off marginally by the vascular supply of the branch rachis (Fig. 2 M-d).

The leaf lamina in both the species is tripinnate-quadripinnatifid. The ultimate divisions are elongate-oblong in shape and gradually

tapered to a rounded apex. The margin is lobed, being pinnatifid in *Hypolepis punctata,* the resultant segments being ovate with serrate or lobed ultimate margin. The basal pair of lateral pinnae are different from the others in *Histiopteris,* forming pinnatifid or pinnate stipule-like outgrowths at the base of the ultimate branches. The midrib of the leaf segments is grooved on the upper surface in both species. It bears pinnately arranged lateral veins which are forked. The venation is free in *Hypolepis punctata.* In *Histiopteris incisa* the venation is reticulate, having a row of costal areoles extending from one main lateral vein to the other, and several rows of smaller areoles beyond them (Fig. 3 A); the areoles are devoid of included veinlets. The leaf lamina is herbaceous with thin-walled epidermal cells and a few rows of prominently armed undifferentiated parenchyma cells forming the mesophyll. Stomata are restricted to the lower epidermis, and in *Hypolepis* the subsidiary epidermal cell of the stoma surrounds nearly $^2/_3$ the circumference of the stoma. The lamina is profusely hairy in *Hypolepis punctata,* the hairs being of the elongated acicular type as on other parts of the plant: the hairs are more profuse over the veins and those on the larger veins and midrib are conspicuously larger in size.

SPORANGIA AND SPORES

The fertile leaves are similar to the sterile ones in both the species. In *Histiopteris* sporangia are borne towards the margin of the lamina, at the tips of the veins as well as on an intramarginal vascular commissure connecting the tips of the veins (forming a continuous, elongated sorus parallel to the margin): the sorus is protected by the infolded margin of the lamina beyond the veins. In *Hypolepis* the sori are discrete, and borne submarginally towards the tips of the veinlets: the extreme tip of the vein is often sterile, extending beyond the sorus. The sorus is protected by a reflexed, marginal, tooth-like protrusion of the lamina. The placenta is slightly elongated along the vein and raised. Often the sorus is restricted to the anterior branch of each of the forked lateral veins, except in the case of basal lateral veins of the pinnae which bear sori on both the branches.

Sporangia are mixed with filamentous paraphyses having swollen, probably glandular, terminal cells; in *Hypolepis* the paraphyses are small and usually only 3 or 4 cells long. Sporangia are of the common lepto-sporangiate type, with an elongated stalk bearing a lens-shaped capsule. The annulus is nearly vertical, except at the capsule-base where it is slightly tilted towards one side (so that the stalk appears partially on

one side) with the ends of the annular ring close to each other, though not contiguous (Fig. 3 F—J). The capsule wall is composed of a few large thin-walled cells. Annulus is composed of 14—18 thick-walled cells. The stomium is well developed, continuous with the annulus and composed of 8—10 transversely elongated thin-walled cells, of which the middle ones are prominent and lip-like. The stalk is commonly 2 cells thick, except at the capsule base (Fig. 3 E, I). In very young sporangia the stalk is two cells thick throughout. In *Hypolepis* the two rows of stalk cells are contiguous with either lateral side of the capsule (the two placed one lateral to the other). In *Histiopteris,* on the other hand, the rows are parallel to the annular ring and each continuous with one side of the sporangial capsule (the two rows placed anteroposteriorly). In both, a 3rd row of stalk cells is formed secondarily during sporangial development. It develops as a downward protrusion of one of the basal wall cells of the sporangial capsule, usually the wall cell next to the stomial end of the annular ring. The secondary row of stalk cells appears as a continuation of the stomium in *Hypolepis* (Fig. 3 E-x) whereas in *Histiopteris* it masks the ends of the annular ring. The 3rd row sometimes extends to the base of the sporangial stalk but in *Hypolepis* it is commonly short and tapered at the base. The sporangial stalk in many cases is more than 3 cells thick (Fig. 3 F, H) in *Histiopteris.* In such cases more than one basal wall cell of the sporangial capsule produce secondary rows of stalk cells during sporangial development.

The spores (Fig. 4 A) of both *Histiopteris incisa* and *Hypolepis punctata* are of the monolete bilateral type with the laesural margins faintly thickened. They are planoconvex in lateral view and oblong in polar view. In *Histiopteris* they measure on an average 24×40 μ (P×E), but commonly vary from 20×30 μ to 30×50 μ, and swell to 30×48 μ on acetolysis. In *Hypolepis* the spores are about 25×35 μ, swelling slightly on acetolysis and varying from 20×32 μ to 28×40 μ in size. The exine is about 3 μ thick and light yellowish-brown in both the species. In *Histiopteris* the exine is densely tuberculate with the tubercles progressively less prominent on the proximal than on the distal surface (nearly absent around the laesura). The tubercles are irregular in shape and crowded; sometimes the nearby ones are coalesced to form large rugulae with undulate sides and surface. The exine surface is densely and uniformly spinulose in *Hypolepis punctata.* The spines are about 5 μ tall, 3 μ thick at the base and sometimes rather flattened. Fresh spores contain many small, light-green plastids and prominently
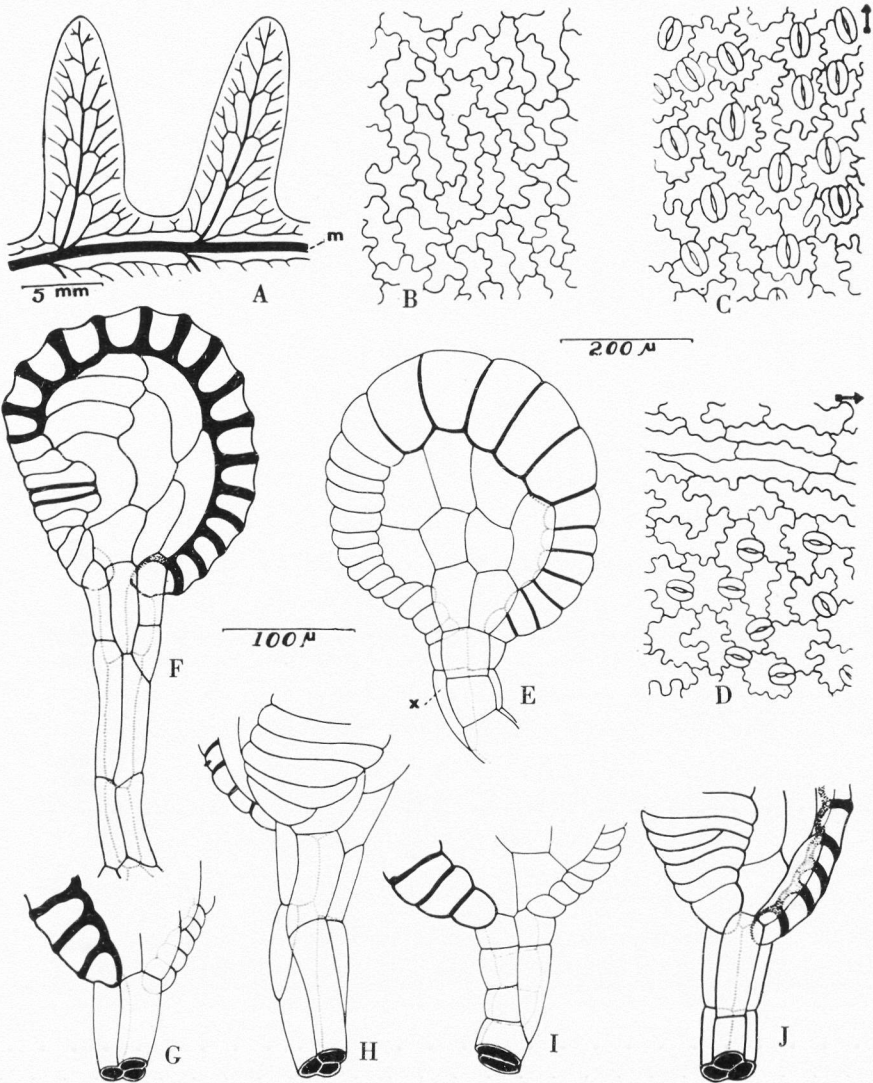
Fig. 3. Morphology of the leaf and sporangia (*m*: midrib, *x*: secondary row of stalk cells). — A: Portion of the pinna of *Histiopteris incisa* showing venation. B, C: Upper and lower foliar epidermis of *Hypolepis punctata* (the arrow points to the margin of the leaf). D: Lower foliar epidermis of *Histiopteris incisa*. E: Young sporangium of *Hypolepis punctata*. F: Mature sporangium of *Histiopteris incisa* with the stalk 5 cells thick above. G—J: Base of the sporangial capsule of *Histiopteris incisa* in different views, showing attachment of the stalk to the capsule.

vacuolated protoplasm. Several abnormal spores, some of them ill-developed or aborted and others excessively large, occur in all samples of *Histiopteris incisa* examined.

PROTHALLUS

On sowing the spores of both the species germinate in about a week. The spore swells, the plastids become deeper green and the oil globules usually merge into a large droplet. The exine opens up at the laesura, and the first rhizoid emerges at the proximal pole, soon followed by the deep green germ filament, lateral to it. Successive transverse divisions followed by elongation of daughter cells produce a 3 or 4 cells long germ filament within 2 or 3 days of spore germination (Fig. 4 B). The cells of the germ filament are usually broader than long, and all except the terminal cell contain yellowish oil droplets. The basal cell is hemispherical in *Histiopteris,* and slightly elongated in *Hypolepis;* it bears one or two rhizoids and is usually surrounded by the spore coat. The anterior region of the germ filament broadens, and the formation of a prothallial plate is initiated in about a week after spore germination (when the germ filaments are 4—6 cells long). The terminal cell divides longitudinally into two daughter cells, of which one enlarges more markedly than the other and soon divides by a wall oblique to the vertical wall separating the two daughter cells. This delimits an obconical apical meristematic cell (Fig. 4 C). Meanwhile the penultimate cell of the germ filament divides longitudinally and the anterior cells on either side of the meristematic cell undergo transverse divisions (Fig. 4 D). The anterior region of the prothallial plate thus formed expands and soon the plate is ovate (Fig. 4 E, F). The differentiation of meristematic cell may in some cases be delayed; in such cases the terminal and the penultimate cells of the germ filament divide longitudinally and the daughter cells undergo one or two further longitudinal divisions, resulting in an ovate, expanded, ameristic prothallial plate (Fig. 4 G, H). Some of the germ filaments may form such ameristic plates when they are only 2 or 3 cells long. Soon a meristematic cell may be differentiated by an oblique wall in an anterior cell, or the prothallial plate may continue ameristic growth (Fig. 4 I—M) till a multicellular apical meristem is differentiated directly from the anterior marginal cells. The basal cell of the germ filament remains uniseriate in all cases.

Young prothalli of *Histiopteris* grow rapidly; in about 10 days of germination (Fig. 4 N) they may become 5—6 cells broad at the ante-
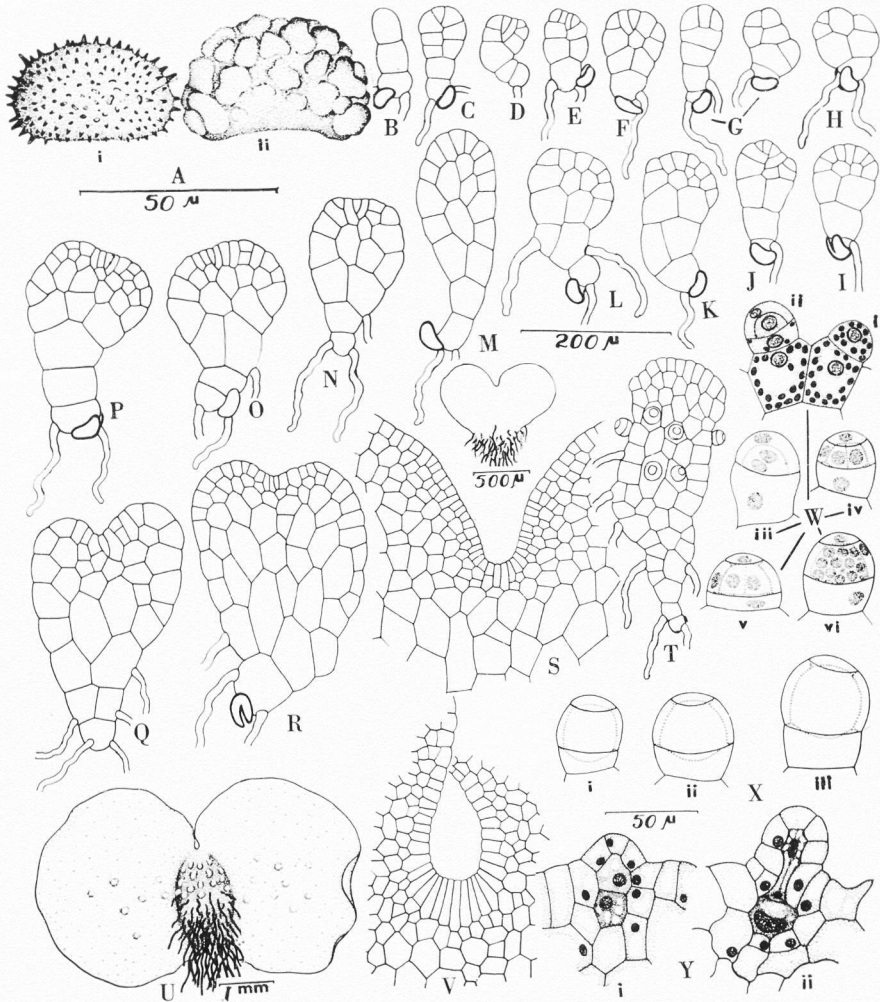
Fig. 4. Gametophyte of *Histiopteris incisa* (A$_{ii}$, B—L, N—P, R—U & Y) and *Hypolepis punctata* (A$_i$, M, Q, & V—X). — A: Lateral view of spore (i: *Hypolepis*, ii: *Histiopteris*). B: Germ filament. C—F: Formation of a prothallial plate and establishment of apical meristematic cell in young prothalli. G: Initiation of ameristic prothallial plate. H—M: Development of ameristic prothallial plate. N—Q: Stages in development of young prothallus by the activity of an apical meristematic cell. R: Young prothallus showing formation of multicellular meristem. S: Young cordate prothallus and its apical region showing cellular organization. T: An antheridial thallus. U: Mature prothallus. V: Apical portion of mature prothallus of the same. W: Stages (i—vi) in the development of antheridium. X: Mature antheridia (i—iii). Y: L.s. of archegonium (i: young archegonium, ii: mature archegonium).

rior end (the cells being progressively smaller towards the anterior end). Marginal cells of the posterior half develop rhizoids. Growth is comparatively slow in *Hypolepis,* the prothallus taking about 3 weeks to become 5 or 6 cells broad. In either case, the young thallus soon becomes obovate (Fig. 4 N—P). In *Histiopteris* the meristematic cell is replaced by a multicellular meristem in the usual way when the thalli are 15—20 days old and when the apical region of the thallus is still flat or convex. Later, the apex of the thallus becomes notched, and finally cordate. In *Hypolepis* the apical region of the prothallus becomes notched, with the meristematic cell located at the bottom of the notch (Fig. 4 Q). A distinctly cordate apex is developed when the thalli are about 2 months old; the meristematic cell is then replaced by a multicellular meristem. Many of the young ameristic thalli, however, are comparatively sluggish and often become rather elongated and sometimes irregular in shape instead of developing into the usual cordate form (Fig. 4 T). These thalli produce crops of antheridia both superficially and marginally. The antheridia are often profuse and produced in successive crops. Those prothalli which develop a meristem, soon become cordate with a distinct apical notch at the bottom of which the meristem is located.

Cordate thalli about 2 mm. broad and bearing a few superficial rhizoids on the posterior half (in addition to many marginal rhizoids) are produced in cultures in about 3 weeks after spore-germination in *Histiopteris* and about 2 months after spore-germination in *Hypolepis.* Formation of a median midrib is initiated in the cordate prothalli when they are about a month old in *Histiopteris* and about 3 months old in *Hypolepis.* Archegonia are formed soon after initiation of a midrib and are developed close to the apical meristem on the lower surface of the midrib. The prothalli of *Histiopteris* become fully grown in about 2 months from spore-germination; in *Hypolepis* it takes 4—5 months for the thalli to become full grown. Generally the cordate thalli are strictly archegonial (under cultural conditions). The ameristic antheridial thalli remain small and do not become cordate or develop a midrib. However, in some cases both sex organs are borne on the cordate thallus, the antheridia being mostly restricted to the wings (Fig. 4 U). The adult prothallus is cordate, 5—7 mm. broad, slightly less long, naked and with a deeply notched anterior end beyond which the wings overlap (Fig. 4 U). The midrib is broad and 5—8 cells thick. The wings are spread-out and not sharply delimited from the midrib. The wing cells are densely chlorophyllous and uniformly thin walled in *Histio-*

pteris: in *Hypolepis* the corners of the wing cells possess faint collen-chyma-like thickenings. The meristem consists of a row of many nar-row, rather elongated cells (Fig. 4 V).

Sex Organs

The antheridia (Fig. 4 X) are small, sub-globose or often slightly elongated, and having the usual structure as found in advanced lepto-sporangiate ferns. The basal cell is short and often barrel-shaped or sometimes saucer-shaped, the upper wall being either nearly flat (as usually in *Histiopteris*) or very slightly arched downwards (as com-monly in *Hypolepis*). Rarely the basal cell of the antheridium is slightly elongated, and then sometimes divided transversely so that the anthe-ridium is 'stalked'. To produce an antheridium the nucleus of a pro-thallial cell divides and one of the daughter nuclei thus formed moves near to a peripheral wall which soon bulges outwards. The transverse wall developed between the two daughter nuclei cuts off the bulged out region as the antheridial initial (Fig. 4 W-*i*). The initial is densely chlorophyllous like its sister cell, develops dense cytoplasmic contents and enlarges to become hemispherical. The nucleus of the antheridial initial divides soon and the daughter nuclei are separated by a trans-verse wall cutting off a small discoid basal cell and a large hemispheri-cal anterior cell. Chloroplasts are comparatively few in the anterior cell and, later during development, disintegrate. The nucleus of the hemispherical anterior cell now enlarges markedly and divides, result-ing in a larger lower daughter nucleus and a slightly smaller anterior one close to the anterior end. The wall separating these daughter nuclei is dome-like (periclinal) touching the upper wall of the disk-like basal cell all around; it thus cuts off a central hemispheral cell from a dome-shaped peripheral cell (Fig. 4 W-*iii*). The nucleus of the peri-pheral cell now divides and the wall formed between the daughter nuclei touches the anterior end of the dome-shaped wall of the central cell, thus delimiting an opercular cell from the annular cell (Fig. 4 W-*iv, v*). Meanwhile the central androgonial cell enlarges and its nucleus divides repeatedly to form about 32 sperm initials (Fig. 4 W-*iii-vi*), which later metamorphose into characteristic corkscrew-shaped spermatozoids.

Archegonia are restricted to the lower surface of the midrib of the cordate thalli. Their structure and development are of the usual type in advanced leptosporangiate ferns (Fig. 4 Y). The archegonial neck is elongated and curved away from the growing apex of the prothallus.

The neck is comparatively shorter in *Histiopteris* than in *Hypolepis*, mainly because the neck cells in the former are shorter. Usually 4 tiers. each consisting of 4 or 5 cells, constitute the neck. The ventral canal cell is ephemeral. At maturity the neck canal cell is binucleate; it is conspicuously swollen at the apex in *Hypolepis*.

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New Species of Felicia and Pentzia (Compositae) from the Brandberg, South West Africa

By Bertil Nordenstam

Institute of Systematic Botany
University of Lund

ABSTRACT

Felicia gunillae B. NORD. and *Pentzia tomentosa* B. NORD. are described from the Brandberg, South West Africa, on material collected by the author in 1963.

INTRODUCTION

The highest mountain of South West Africa, the isolated and almost inaccessible Brandberg massif, is botanically still very insufficiently known. Apart from Mr. H. J. WISS, who joined a mainly archaeological expedition to the Brandberg in 1955 and collected a number of plants (WISS 1957), the present author is the only botanist who has explored the upper regions of that mountain. An account of its flora is under preparation.

In this paper two new species of *Compositae* are described, both confined to the upper parts of the mountain. The uppermost zone, from c. 1800 m to the top of the highest peaks (2500-2600 m), is characterized by a flora, which is rather distinct from that of the lower areas. Some other plants only known from this zone are *Plumbago wissii* FRIEDR., *Othonna brandbergensis* B. NORD., and a peculiar pillar-shaped species of *Euphorbia* allied to *E. monteiroi* HOOK. fil.

Felicia gunillae B. NORD. sp. nov. (Fig. 1)

Holotype: NORDENSTAM 2803 (LD).

Suffrutex erectus ramosus scabrido-echinatus glandulosus flavovirens. *Folia* alterna patentia spathulata—oblanceolata basi linearia apice dilatata rotundata —elliptica 5—7-lobata, superiora cuneata paucilobata ad fere linearia integra. *Capitula* terminalia solitaria radiata. *Involucri bracteae* imbricatae lanceolatae acutae glandulosae et parce setosae, interiores margine membranaceae
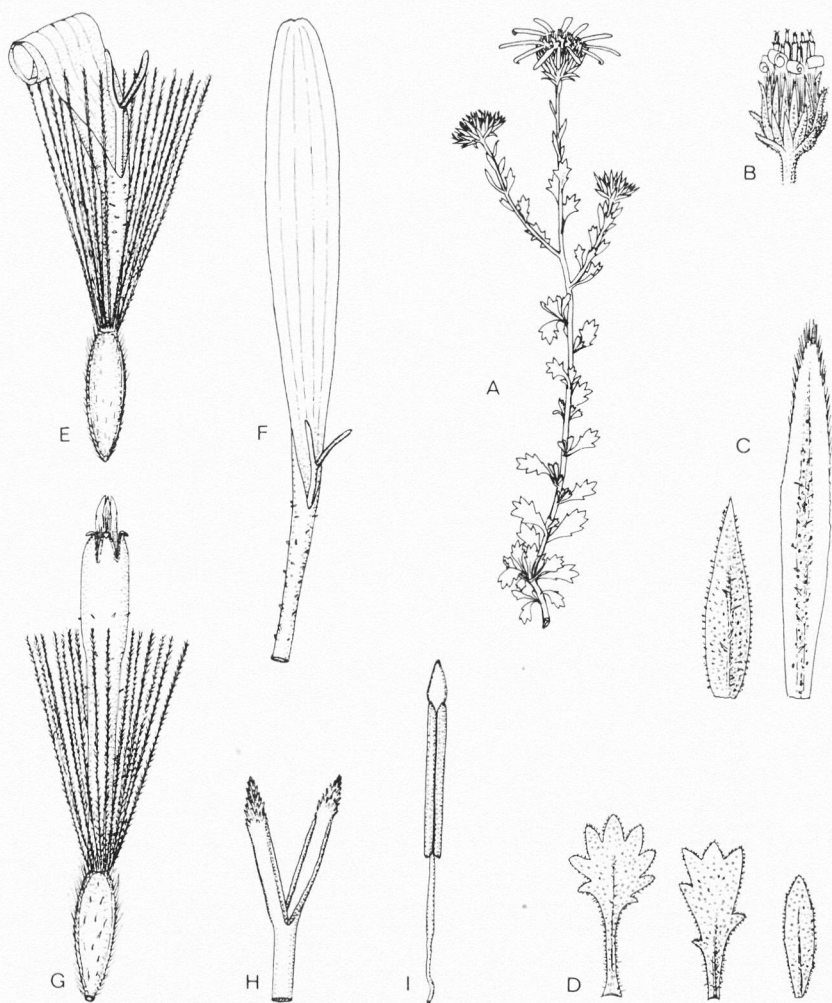
Fig. 1. *Felicia gunillae* B. NORD. — A: Portion of plant, ×¹/₂. — B: Capitulum, ×1. — C: Outer (left) and inner (right) involucral bracts, ×5. — D: Leaves, ×2. — E: Ray-floret, ×5. — F: Corolla of ray-floret, ×5. — G: Disc-floret, ×5. — H: Style branches (of disc-floret), ×10. — I: Anther, ×10. — Del. auct.

apice ciliatae. *Receptaculum* alveolatum epaleatum. *Flores radii* c. 10—15 lilacini. *Flores disci* c. 25—40, corolla tubulosa apice aliquantum ampliata quinquelobata. *Pappi setae* uniseriatae scabridae. *Achaenia* anguste elliptico-obovata complanata margine incrassata sericea.

An erect much-branched suffrutex, 1—1.5 m high. Older branches lignified, straight, nude; cortex grey, splitting longitudinally and peeling

off. Younger branches leafy and often with brachyblasts in the leaf-axils, yellowish green, faintly striate, c. 1—2 mm in diam., scabrid-echinate with short and spreading multicellular hairs and with numerous shortly stipitate glands. *Leaves* alternate, spreading, flat, spathulate—oblanceolate, c. 1(—2) cm long and 0.5(—1) cm wide, distinctly petioled with a linear petiole and a rounded—elliptic lamina, 5—7-lobed with ovate acute and apiculate lobes, yellowish green, densely glandular and echinate with short stiff and spreading hairs especially along the (at least basally distinct) midvein. Upper leaves cuneate—oblanceolate, few-toothed or entire, gradually diminishing to almost linear and bract-like below the flower-heads. *Capitula* terminal, solitary, erect. *Involucre* cup-shaped or almost hemispherical, 1—1.5 cm high and wide. *Involucral bracts* imbricated (in c. 3—4 'rows'), lanceolate, acute, glandular and sparsely setose with multicellular short hairs; outer ones 5—6 mm long and 1—1.5 mm wide; inner ones c. 1 cm long and 1—1.5 mm wide, acuminate, with membranous margins and ciliate tips. *Receptacle* alveolate, epaleate, slightly convex. *Ray-florets* c. 10—15; tube cylindrical, 4—5 mm long, puberulous; lamina narrowly elliptic-lorate, 10—13 mm long, c. 2 mm wide, purplish blue, 4-nerved. Style terete with flattened branches, much exserted. *Pappus bristles* uniseriate, 20—25, straight, erect, 6—8 mm long, scabrid, straw-coloured to almost white, somewhat glossy. *Achenes* narrowly elliptic-obovate, flattened, 3.5—4 mm long, c. 1—1.5 mm wide, light brownish, sparsely setose on the faces, with thickened sericeous margins. *Disc-florets* c. 25—40; corolla 8—9 mm long, yellow, tubular, slightly widening in the upper part; corolla lobes 5, triangular, 0.8—1 mm long, with oil vessels along the margins and recurved tips. Anthers 2—2.5 mm long with obtuse base; apical appendage narrowly ovate—lanceolate, c. 0.7 mm long, subacute. Style terete; style branches flattened, c. 2 mm long, with hairy acute sterile tips. *Pappus* and *achenes* as in ray-florets.

S.W. AFRICA. O m a r u r u D i s t r i c t : Brandberg, Königstein, W. slopes below the top, 2560 m, 31.V.1963, NORDENSTAM 2803 (LD, M).

Since the generic name happens to coincide with that of my daughter, I find it appropriate to form the specific epithet from my wife's Christian name.

The reasons for accepting the genus *Felicia* as distinct from *Aster* (in contrast to, e.g., PHILLIPS 1951) are discussed by MERXMÜLLER (1954).

Among the South West African Felicias the new species comes closest to *F. scabrida* (DC.) RANGE, from which it differs i.a. in leaf-shape, pubescence, and colour of vegetative parts and of disc-florets.
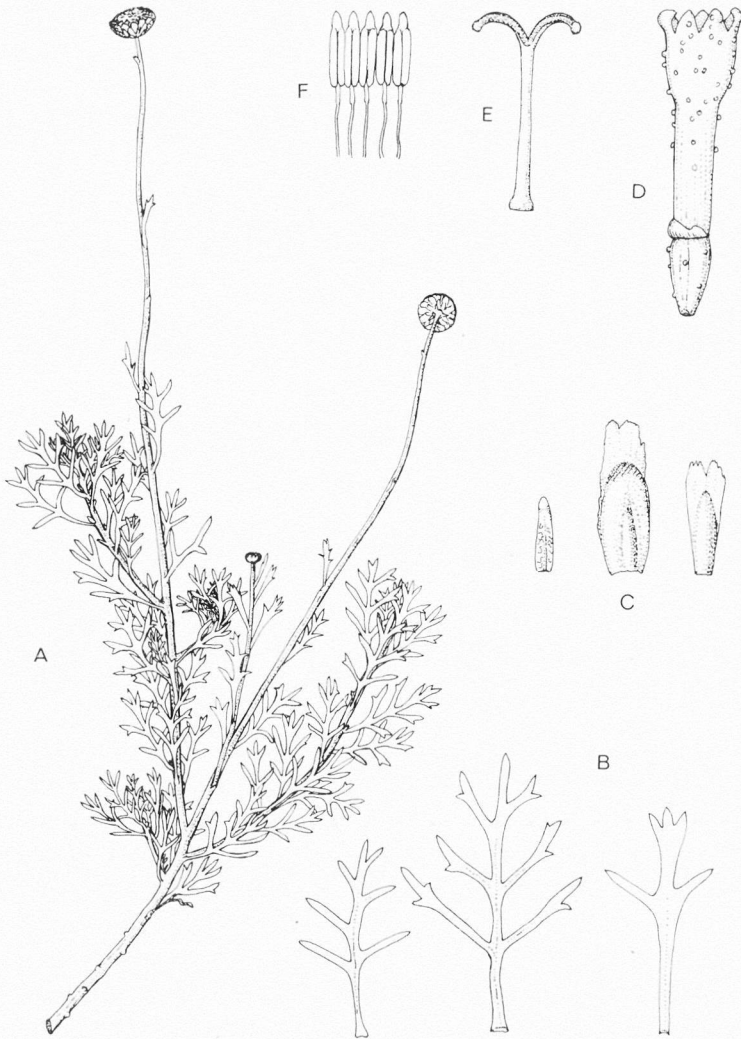
Fig. 2. *Pentzia tomentosa* B. Nord. — A: Portion of plant, ×½. — B: Leaves, ×1. — C: Involucral bracts (from left: outer, middle and inner ones), ×5. — D: Floret, ×5. — E: Style, ×10. — F: Anthers, ×10. — Del. auct.

Pentzia tomentosa B. Nord. sp. nov. (Fig. 2)

Holotype: Nordenstam 2821 (LD).

Suffrutex ramosus ad 1.5 m altus, ramuli annotini adpresse tomentosi dense foliati. *Folia* alterna erecto-patentia pinnatipartita adpresse cano-tomentosa et minute punctata, segmentis planis linearibus integris vel paucilobatis.

Capitula solitaria discoidea distincte pedunculata. *Involucri bracteae* imbricatae coriaceae apice membranaceae. *Receptaculum* convexum foveolatum. *Flores* numerosi, corollae tubulosae parce papillatae apice campanulatae quinquelobatae. *Pappus* auriculiformis brevis. *Achaenia* oblongo-obovata obscure costata glabra vel parce papillata.

A much-branched suffrutex 1—1.5 m high. Older branches nude and with knot-like remains of brachyblasts. Younger branches somewhat flexuous, closely leafy (but pedunculoid below the flower-heads), appressedly tomentose. *Leaves* alternate, often close together on brachyblasts in the leaf-axils, erecto-patent, appressedly canescent-tomentose, finely punctate with minute sessile glands, 2—4 cm long, pinnatipartite; segments erecto-patent, flat, linear, 0.5—2 cm long, entire or few-lobed or -toothed, faintly midveined, subacute—obtuse, minutely apiculate. Flowering branches pedunculoid with a few bract-like leaves; pedunculoid portions c. 0.5—1 dm long, c. 1 mm in diam. *Involucral bracts* spirally imbricated, coriaceous, membrane-tipped; outer ones lanceolate, c. 2 mm long, slightly keeled, greenish and ± pubescent in the middle, with straw-coloured margins and with a small membranous apical appendage; middle ones narrowly ovate-oblong, 3—4 mm long, glabrous, somewhat greenish in the middle, straw- or horn-coloured towards the margins and tips, with a distinct toothed or fringed membranous appendage; inner ones narrowly oblong-obovate, c. 3 mm long, glabrous, amply membrane-tipped and apically fringed. *Receptacle* convex, 4—5 mm in diam., nude of sparsely ciliate, finely pitted. *Florets* very numerous; corolla tubular below, narrowly campanulate in the upper portion, 2—3 mm long, with scattered papillae, yellow; lobes 5, distinctly cucullate. Style terete with thickened base; branches 0.8 mm long, truncate. Anthers c. 1 mm long; apical sterile appendage ovate with obtuse subcucullate tip. *Pappus* a single ear-shaped scale 0.2—0.5 mm long, white, entire or shallowly lobed to bluntly dentate. *Achenes* 1—1.3 mm long, oblong-obovate, slightly curved and few-angled, obscurely 4—7-ribbed, glabrous or with occasional papillae, whitish brown, mucilaginous when soaked.

S.W. AFRICA. Omaruru District: Brandberg, Königstein, sheltered stony places E. of the top. c. 2000 m, 31.V.1963, NORDENSTAM 2821 (LD, M).

According to HUTCHINSON's key (HUTCHINSON 1916 p. 242) the new species falls into sect. *Monocephalae* HUTCH., although it may have closer affinities to some species of sect. *Flabellifoliae* HUTCH. *Pentzia sphaerocephala* DC. is regarded by HUTCHINSON as a connecting link

between the two sections mentioned and in the key entered in both. *P. tomentosa* shows some resemblance to this species, which occurs in the Central and Eastern Cape Province. At any rate *P. tomentosa* is a very distinct species, easily recognized on its large pinnately divided leaves and the dense canescent tomentum covering branches and leaves.

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Intraspecific Variation in Clinopodium vulgare L. (Labiatae)

By *Roland von Bothmer*

Institute of Systematic Botany
University of Lund

ABSTRACT

The species *Clinopodium vulgare* L. is divided into three geographically vicarious subspecies, ssp. *vulgare*, ssp. *villosa* (DE NOÉ) BOTHM., and ssp. *orientale* BOTHM. They are morphologically characterized by differences especially in the size of calyx tube, calyx teeth, and leaves.

INTRODUCTION

In 1963 I began a cytological investigation upon Greek material of some species within *Labiatae*, among others *Clinopodium vulgare*. On the advice of Dr. H. RUNEMARK, Lund, a study was made of the morphological variation within *C. vulgare* on material from the whole distribution range of the species. About 550 collections constitute the basis for my subdivision of the species.

C. vulgare has a wide range. The species grows all over the Mediterranean area, and it extends northwards up to the middle part of Scandinavia and eastwards to Central Asia. It is also represented in North America.

The great morphological variation within *C. vulgare* has been observed before. In "Flora von Mitteleuropa" HEGI (1927) recognized 5 varieties.

K. H. RECHINGER (1961) investigated material from Macedonia, Thessaly, Euboea, and Cyprus. He found a calyx length of 10 to 11 mm. Calyx tube and lower calyx teeth were said to have approximately the same length. For Central European material RECHINGER gave a calyx length of 7 to 9 mm and the length of the lower calyx teeth was said to be about $^2/_3$ of the calyx tube (compare below).

As a result of my investigation 3 morphologically and geographically distinct subspecies are distinguished, one Eurasiatic and North American (ssp. *vulgare*), one East Mediterranean (ssp. *orientale* ssp. nov.) and one West Mediterranean [ssp. *villosa* (DE NOÉ) comb. nov.].

MORPHOLOGY

The habit of *C. vulgare* varies within wide limits. Specimens from Algeria, Morocco, and the south of Spain and Portugal, however, are considerably bigger and stouter than Central and North European and North American material.

The leaf shape in ssp. *villosa* (DE NOÉ) BOTHM. varies less than within the two other subspecies. The ratio length/breadth of leaves in ssp. *villosa* is 2.0 or more but only about 1.5 in Eurasiatic, North American, and East Mediterranean material. The leaf length of West Mediterranean material is 40 to 65 mm and of specimens from other areas less than 45 mm. All form series have a more or less serrate leaf margin.

Certain extraordinarily hairy types previously have been nomenclaturally distinguished, e.g. as var. *plumosa* OPIZ and var. *villosa* DE NOÉ, one even as a species, *C. plumosum* SIEB. However, there is normally great variation in pubescence in all regions but the degree of hairiness is of taxonomical importance only in the West Mediterranean area. The calyx is always thinly covered with small, 0.2—0.3 mm long, glandular hairs, the density of which is fairly constant. Mixed with these glandular hairs there are variably dense, 1.0—1.5 mm long, articulated hairs. In ssp. *villosa* calyx, leaves, and stem are richly covered with these woolly hairs (Fig. 1 A—C).

The flower shape does not vary much, while the size of the floral parts varies within wide limits. The two Mediterranean form series have somewhat bigger flowers than the Eurasiatic-North American one.

The zygomorphic calyx has five teeth, the lower two of which are curved and longer than the three straight upper ones. The length of calyx tube and teeth shows little variation and is suitable for taxonomical evaluations.

In ssp. *vulgare* the calyx length is 7—9.5 mm (cf. RECHINGER 1961), in the two Mediterranean subspecies 9.5—12 mm. The lower teeth are less than 4.0 mm long in ssp. *vulgare*, and in the Mediterranean subspecies 4.0—5.5 mm long. The length of the upper three calyx teeth in ssp. *villosa* and ssp. *orientale* varies between 2.5 and 4.0 mm, while on material of ssp. *vulgare* the length does not exceed 2.5 mm.

The length ratio of lower calyx teeth/upper calyx teeth on material from the middle and the north of Europe, Asia and North America is on the average 1.9 and in material from the Mediterranean area 1.4 (Fig. 1 E).

In plants from Greece cultivated in the Botanical Garden of Lund I found that the calyx tube and teeth became somewhat smaller than the corresponding parts on the mother plants. However, the length of the tube and teeth of the calyx in the cultivated material falls within the natural variation of the East Mediterranean type.

CYTOLOGY

The chromosome number of *C. vulgare* ssp. *orientale* was determined to 2n=20 on material from Euboea (bay 3 km WSW of Akr. Kafirevs) collected in 1958 by RUNEMARK and SNOGERUP (R 11709). Material was grown in the Lund Botanical Garden for the purpose of cytological investigations. After cooling for about 12 hours at a temperature of 2—4 centigrades, root-tips were fixed in the Svalöf modification of Navashin-Karpechenko, microtome-cut (14 μ) and stained in 1 % crystal-violet.

The length of the chromosomes is 1.5—2.0 μ. The centromere region is median to submedian (Fig. 1 D).

Previously 2n=20 has been determined for *C. vulgare*, apparently ssp. *vulgare*, by SCHEERER (1939) and by LÖVE (1954) and for *C. vulgare*, apparently ssp. *villosa*, by REESE (1953) and by LÖVE (1954) (cf. LÖVE 1961).

TAXONOMY

EARLIER TREATMENT

An extremely hairy type within *C. vulgare* from Dalmatia, was regarded by SIEBER (1822) as a separate species, *Clinopodium plumosum* SIEB. However, the hairiness varies within wide limits in *C. vulgare* and cannot be used for a division into species.

DE NOÉ (1855) described the very hairy material from Algeria and Morocco as a new species, *Clinopodium villosum* DE NOÉ. A somewhat less hairy form got the rank of variety (var. *villosa* DE NOÉ) of *C. vulgare*. MAIRE (1921) included DE NOÉ's species as a subspecies of *Calamintha Clinopodium*. In 1934 (in JAHANDIEZ & MAIRE 1934) he also made a new subspecies which he called *Satureja vulgaris* (L.) FRITSCH ssp. *eu-clinopodium*, a name not valid according to the nomenclature rules. Another subspecies of *C. vulgare*, ssp. *atlantica* BALL, was made by BALL in 1875 on material from North Africa. This is a low and small-leaved, not particularly hairy taxon with a creeping stem. It is
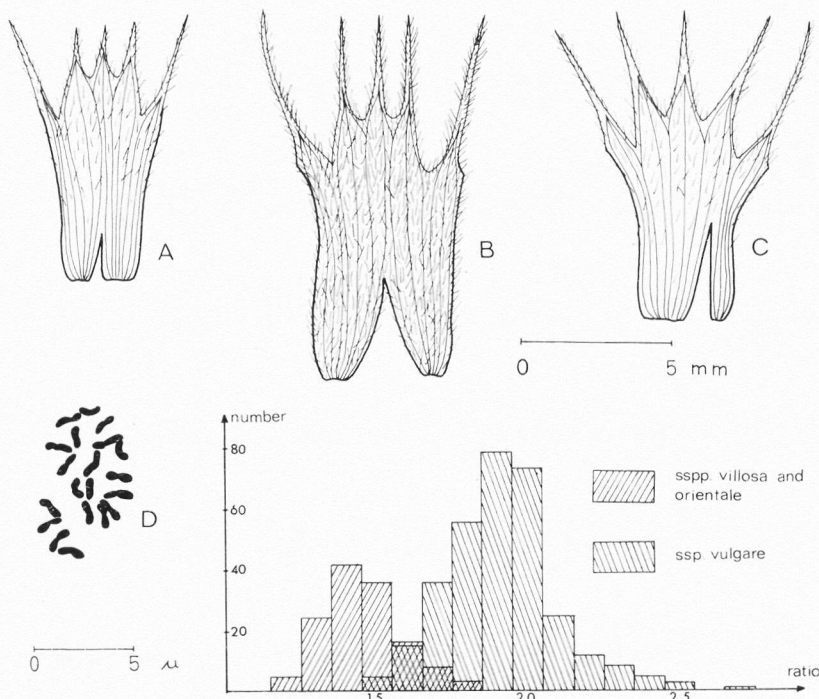
Fig. 1. — A—C: Calyx of *Clinopodium vulgare* L. — A: Ssp. *vulgare*. Sweden, Öster-götland. H. NILSSON 16.7.1940. — B: Ssp. *villosa* (DE NOÉ) BOTHM. Algeria. DUKERLEY no. 541. — C: Ssp. *orientale* BOTHM. Cyprus. SINTENIS no. 1052. — D: Chromosomes, 2n=20. — The histogram shows the ratio length of lower/upper calyx teeth.

distinct from all forms of *C. vulgare* and should be treated as a species of its own, which was done by MAIRE in 1934 [*C. atlantica* (BALL) MAIRE].

PRESENT TREATMENT

Clinopodium vulgare L. ssp. *vulgare*. 2n=apparently 20.

Calyx 7—9.5 mm long, lower calyx teeth up to 4.0 mm, upper ones up to 2.5 mm long. Ratio lower/upper calyx teeth about 2.0. Leaves up to 40 mm long and ratio leaf length/leaf breadth about 1.5.

Clinopodium vulgare L. ssp. *villosa* (DE NOÉ) comb. nov. 2n=apparently 20.

    Calamintha Clinopodium BENTH. ssp. *villosa* (DE NOÉ) MAIRE, 1921. — *Clinopodium villosum* DE NOÉ, 1855.

Calyx length 9.5—12 mm, lower calyx teeth 4.0—5.5 mm, upper ones 2.5—4.0 mm. The ratio lower/upper calyx teeth about 1.5. Very hairy. Leaf length 40—65 mm. Ratio leaf length/leaf breadth c. 2.0.

Though I have not seen DE NOÉ's type material there is no doubt about this taxon. I have seen a rich material from its area and the description is quite clear.

Clinopodium vulgare L. ssp. *orientale* ssp. nov. 2n=20.

Calyx 9.5—12 mm longus, dentibus inferioribus 4.0—5.5 mm longis, superioribus 2.5—4.0 mm longis. Ratio dentium inferiorum/superiorum c. 1.5. Folia ad 45 mm longa. Ratio longitudinis/latitudinis folii c. 1.5. In characteribus aliis ssp. *orientale* ssp. *vulgare* similis est.

Typus: Greece, Samos. The SW-part of Mt. Kerki 400—800 m.s.m. RUNEMARK & SNOGERUP 19642, collected in 1962, in herb. Lund.

DISTRIBUTION

Ssp. *vulgare* has a northern range and occurs in all Europe with the exception of the Mediterranean area. It extends to Central Asia along a zone south of the Black Sea and the Caspian Sea. It is also represented north of the Black Sea. The easternmost collections seen by me are from Afghanistan, Kashmir, and India. In North America ssp. *vulgare* is native in Canada to Newfoundland and in USA southwards to North Carolina and in the Rocky Mountains. Plants from the southernmost part of the American range are probably introduced from Europe (MACOUN 1883, GLEASON 1952, RYDBERG 1954, RICKETT 1966).

Ssp. *villosa* grows along the Mediterranean coast of North Western Africa, and in the south of Spain and Portugal.

Ssp. *orientale* has an East Mediterranean range and occurs in the whole of Greece, in Turkey south of the range of ssp. *vulgare*, and in Syria and Iran. The easternmost material which I have seen is from Afghanistan. Ssp. *orientale* is also native in South and Central Italy, on Sicily and Sardinia, and in southern France.

INTERMEDIATE TYPES

The ratio lower/upper calyx teeth in some forms is about 1.75 and consequently intermediate between ssp. *vulgare* on one hand and ssp. *villosa* and ssp. *orientale* on the other hand (Fig. 1 E). No intermediates between the two Mediterranean subspecies have been found owing to the fact that their ranges do not seem to meet.
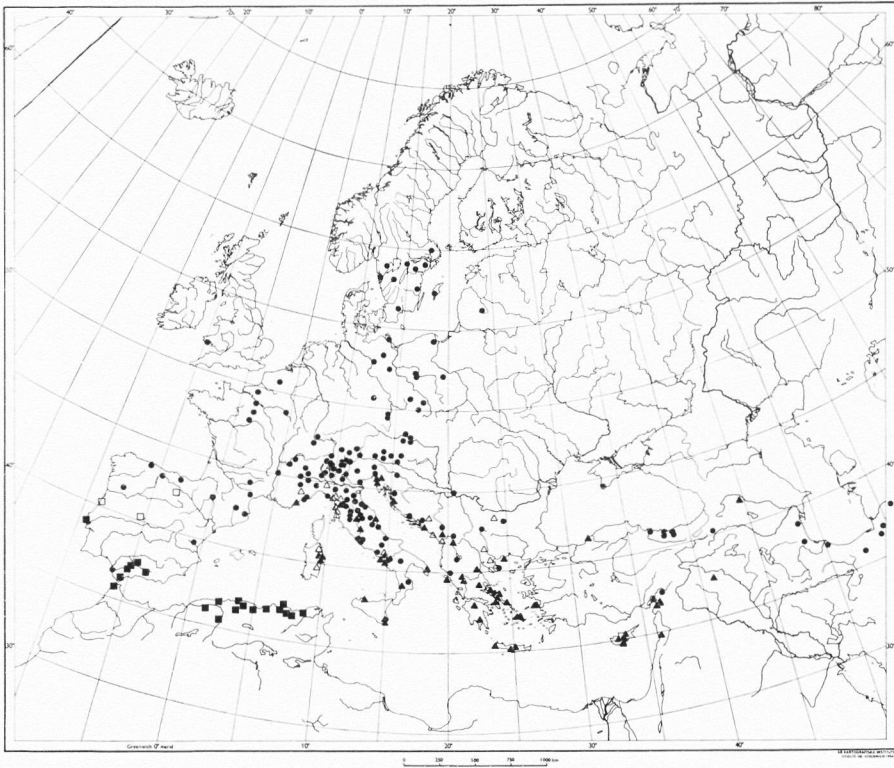
Fig. 2. Distribution map of investigated material of *Clinopodium vulgare* L.; ● ssp. *vulgare*; ▲ ssp. *orientale*; △ intermediates between ssp. *vulgare* and ssp. *orientale*; ■ ssp. *villosa*; □ intermediates between ssp. *vulgare* and ssp. *villosa*.

I have seen only three collections, from the middle of Spain, which are intermediate between ssp. *villosa* and ssp. *vulgare*. However, there is a large material of transitional types between ssp. *orientale* and ssp. *vulgare*. Especially in the coastal region of Dalmatia they are well represented. Intermediates are also common in western Italy, particularly in the neighbourhood of Toscana.

ACKNOWLEDGEMENTS

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Apomixis and Sexuality in Hierochloë australis and in Swedish H. odorata on Different Polyploid Levels

By *Gunnar Weimarck*

Institute of Systematic Botany
University of Lund

ABSTRACT

In taxa studied, the embryo sac has the normal eight-nucleate organization, but sometimes has four antipodals. Many embryo sacs degenerate. Collapsed older nucelli are frequent. Germinativeness is low. Male meiosis is often ± disturbed, in some samples badly so. Aneuploid plants have not been found in some 300 collections cultivated. — *H. australis*, diploid, is a facultative apomict with 0—5 megaspore mother cells and often some unreduced embryo sac initials. Meiosis may be normal, abnormal or quite suppressed. Most often the chalazal megaspore develops, in some cases one of the others also. Embryo sac mitoses with reduced and unreduced chromosome numbers have been observed. One case of twin embryos has been found. — Tetraploid *H. odorata* normally possesses only one megaspore mother cell. Unreduced initials are rare. Meiosis is most often regular. In certain cases, any of the megaspores can develop. Seed-setting is sexual. The rate of development of the embryo sac is slower than in other taxa. The variation in behaviour between samples of this taxon is greater than that between samples within each of other taxa studied. — In hexaploid and octoploid *H. odorata*, the number of megaspore mother cells rarely exceeds one. Most often none at all is found. Meiosis is rare, sometimes abnormal. Apomictic initials regularly occur, in the hexaploid, where only unreduced embryo sacs seem to develop, often in great number. Aposporous embryo sacs in anthers have been observed. In one case, in a hexaploid plant, sperm nuclei are present within an embryo sac.

INTRODUCTION

The embryology of certain types of *Hierochloë odorata* (L.) WAHLENB. from North America is treated by NORSTOG (1957, 1960, 1963). Tetraploid Connecticut plants (2n 28) investigated were according to him characterized by triad formation in female meiosis. The embryo sac was of the normal type but had most frequently four uninucleate antipodals. Pollen formation was normal.

In octoploid plants (2n 56) from Michigan, on the other hand, the

megaspore mother cell, if present, failed to divide or divided only once. One or two, rarely three apomictic embryo sacs developed either in the presence of a megaspore mother cell or instead of one. The embryo sac became eight-nucleate and had three antipodals, which later became multinucleate. Apomixis was stated to be obligate. The endosperm was developed by means of pseudogamy involving triple fusion.

The presence of twin embryo sacs resulted in a certain frequency of twin embryos. Irregularities in pollen formation gave rise to a high proportion of aborted grains.

In Scandinavia, tetraploid, hexaploid and octoploid *Hierochloë odorata* occur. A preliminary report has already been published (WEIMARCK 1963). *Hierochloë australis*, occurring in parts of Central and Eastern Europe, is known only as a diploid (VAARAMA in TISCHLER 1950 p. 209).

AIMS, METHODS AND GENERAL OBSERVATIONS

The aim of this work has been to investigate the embryo sac formation of some *Hierochloë* taxa of the northern hemisphere, viz., *H. australis* (SCHRAD.) ROEMER & SCHULTES, and tetraploid, hexaploid, and octoploid *H. odorata* (L.) WAHLENB., respectively. Collections cultivated in open air in Lund from different parts of the distribution areas have been studied. The plants cultivated originate (with the exception of A E K, which was obtained as caryopses) from rhizomes transplanted from the original locality into pots in the experimental garden. Instead of using more material from only one sample per taxon or polyploid level, two or three samples from each have been investigated. In order to yield as much information as possible, the samples have been chosen from widely separated localities (Fig. 1). Series, for the main part parallel to each other, were fixed in 1964 and 1965.

The chromosome numbers have been determined in root tip sections. Germination tests have been made after open pollination; the caryopses have been sown in a standard soil mixture.

Whole panicles or parts thereof were fixed in Müntzing's modification of Navashin-Karpechenko's fluid (MÜNTZING 1933 p. 131), with a few drops of a wetting agent (Agfa Agepon) added. After dehydration and embedding in paraffin, the spikelets were sectioned parallel to the flat side at 14 μ. The slides were pretreated for 8 hours in 3 % iron alum, stained for c. 15 hours in 0.5 % iron hematoxylin and for a few seconds in 0.5—0.25 % fast green in alcoholic solution.
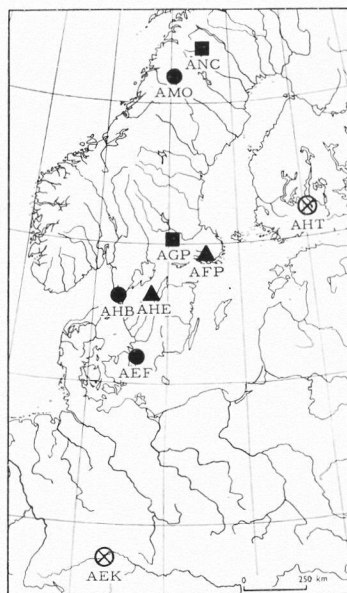
Fig. 1. Geographical distribution of localities furnishing investigation material.

⊗ *Hierochloë australis*
● Tetraploid *H. odorata*
▲ Hexaploid, *H. odorata*
■ Octoploid *H. odorata*

In *Hierochloë australis* (2n 14), c. 200 spikelets have been studied in plants from the locality A E K (Germany, Bayern, Weltenburg; leg. H. MERXMÜLLER), and c. 190 from the locality A H T (Finland, Tavastia australis, Hollola; leg. J. PURO).

In tetraploid *Hierochloë odorata* (2n 28), c. 370 spikelets have been studied in plants from the locality A E F (Sweden, Skåne, Kågeröd), c. 215 from the locality A H B (Sweden, Bohuslän, Stala), and c. 100 from the locality A M O (Sweden, Lycksele lappmark, Tärna).

In hexaploid *Hierochloë odorata* (2n 42), c. 180 spikelets have been studied in plants from the locality A F P (Sweden, Uppland, Uppsala Näs), and c. 160 from the locality A H E (Sweden, Västergötland, Kälvene).

In octoploid *Hierochloë odorata* (2n 56), c. 125 spikelets have been studied from the locality A G P (Sweden, Dalarna, Norrbärke), and c. 230 from the locality A N C (Sweden, Lule lappmark, Kvikkjokk).

Thus a total of c. 1770 well-stained and well-orientated spikelets have been used. Each spikelet contains two ♂ florets and one ♀ with a single ovule.

The ovule is anatropous and bitegmic. Male as well as female meiosis — if taking place — occurs when the spikelets are still

completely or partly enclosed within the sheath of the uppermost leaf
of the culm, the top of the panicle being c. 5—15 cm above the ground.
A variation in stage of development amounting to a few days occurs
between separate spikelets in a panicle and, as regards male meiosis,
between different florets in the same spikelet and even between anthers
in the same floret.

Hierochloë australis

Collection A E K

In the young nucellus most often some megaspore mother cells
(MMC) are found. In 106 cases investigated, 6 (6 %) had no MMC or
derivative thereof, 22 (21 %) had 1 (Fig. 2 A), 41 (39 %) had 2 (Fig.
2 B, C), 26 (25 %) had 3 (Fig. 2 D), and 11 (10 %) had 4 (Fig. 2 E).
In some cases, they were accompanied by unreduced embryo sac
initials (EI), such as in Fig. 2 C and E, in others apparently not. A
striking matter is the deep position of the reproductive cells, sexual or
apomictic, in the nucellar tissue.

In somewhat more advanced stages, one can observe different types
of development into a uninucleate embryo sac (ES) as follows:

1. The MMC divides apparently in a normal manner, forming a
tetrad either with or without competition with EI (Fig. 2 F and G).

2. The MMC divides irregularly with evidently unbalanced result
(Figs. 2 H, I, and 3 A). In the cases recorded, EI are present. The
chalazal tetrad cell or megaspore (MS) is not always the biggest one;
note in the illustrated case (Fig. 2 I) the close parallel between the
clearly more normal division in the micropylar dyad cell to the left and
the fact that the uninucleate ES in the central tetrad has developed
from one of the MS derived from the micropylar dyad cell.

3. The MMC fails to divide, persisting in prophase until it degenerates
at later stages (Fig. 3 B). In the case illustrated, the apomictic potency
seems to have activated not only cells in the vicinity of the more or less
degenerating MMC but also cells of the outer integument, which are
vacuolized and passing into prophase.

Fig. 2. *Hierochloë australis*, coll. A E K. — *A:* 1 MMC, prophase. — *B:* 2 MMC, pro-
phase. — *C:* 2 MMC, prophase; 1 EI. — *D:* 3 MMC, prophase. — *E:* 4 MMC, pro-
phase; 2 EI. — *F:* 1 MMC prophase; 1 telophase I. — *G:* 1 MMC, anaphase I; 1 dyad
(right); 2 tetrads; 2 EI (left). — *H:* 2 MMC, prophase; 1 MMC, disturbed anaphase
I; 1 tetrad (right); 6 EI (left and bottom). — *I:* 1 MMC, prophase; 1 ana- and
telophase II; 1 tetrad, second MS dominating.
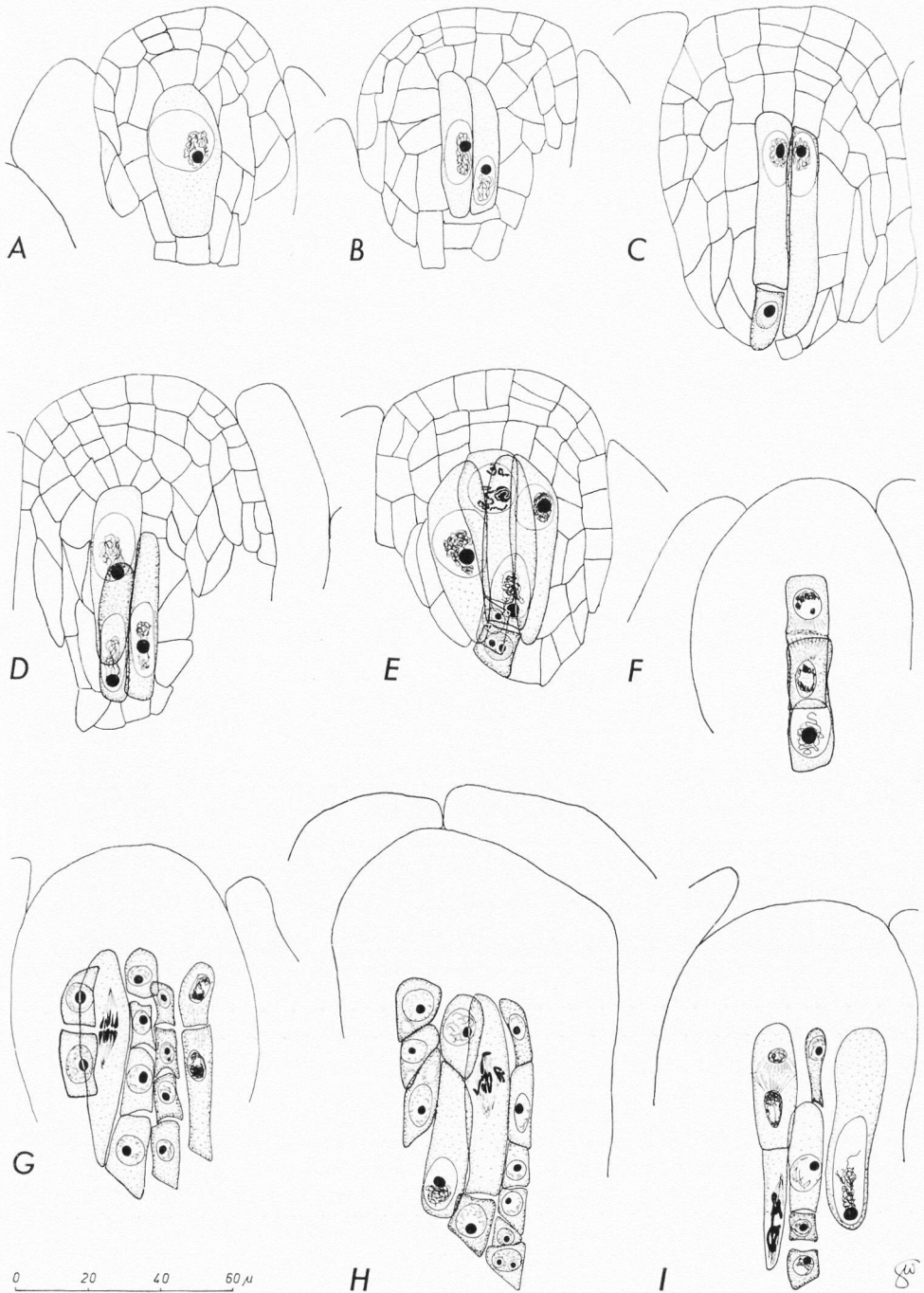
4. No MMC is observable but only EI (Fig. 3 C). A very early degeneration of an MMC cannot always be excluded.

In many cases, when two or more MMC are present, the one most proximal to the chalaza degenerates in a characteristic way, the chromosomes retaining their meiotic prophase structure but clustering around the nucleolus (Fig. 3 A, bottom right). In other cases, an EI. showing no meiotic tendency but sometimes seemingly degenerative. occupies a similar position at the base of the MMC (Figs. 2 C, E, H. bottom middle, 3 A, bottom left, and 3 B, bottom). The characteristic location of these EI indicates homology between them and the MMC mentioned. Other EI, however, are found in other positions (Figs. 2 G, 2 H. left, and 3 C). Apparently, EI can arise from the multicellulate archesporium as well as from somatic cells (which, according to STEBBINS 1950 p. 384, should be called diplospory and apospory, respectively. In this work, the apomixis terminology of STEBBINS l.c., where it is modified after GUSTAFSSON 1946, is adopted as being more convenient than those of e.g. FAGERLIND 1940, 1944, or BATTAGLIA 1963).

According to paragraphs 2, 3, and 4 above, the meiotic mechanism has failed beforehand; in the case described in paragraph 1, a competition between reduced and unreduced ES is conceivable. In one instance, it has been possible to count the chromosome numbers of divisions in two young ES in the same nucellus; one of the sacs, evidently reduced, has 7 chromosomes, the other, unreduced, c. 14. Neither of them would, however, have had any chance of maturing, since two other, more advanced ES also occupied the nucellus. — At later stages, it seems impossible to determine whether an ES is reduced or unreduced.

Binucleate, four-nucleate, eight-nucleate and mature ES are exemplified in Fig. 3 D, E, and F. A variation in number of antipodals is notable. Normally there are three, but also four may occur. Antipodals with more than one nucleus are relatively rare. The synergids degenerate at maturing, and at about the same time the stigmata become

Fig. 3. *Hierochloë australis.* — *A—F:* coll. A E K. — *G—H:* coll. A H T. — *A:* 2 MMC. prophase; 1 MMC, degenerating prophase (bottom right); 1 disturbed ana- and telophase II; 1 EI (bottom left). — *B:* 2 MMC. degenerating prophase; 2 EI; in outer integument, EI-looking cells. — *C:* 11 EI. — *D:* 2 binucleate ES; 2 four-nucleate ES. —*E:* 1 four-nucleate ES; 2 eight-nucleate ES. — *F:* 1 "eight-nucleate" ES with four antipodals; 1 mature ES. — *G:* 1 MMC, degenerating prophase; 2 pro- and anaphase II; 1 metaphase II and 2 chalazal MS; 1 tetrad. — *H:* 2 ES, each with one embryo, number of endosperm nuclei only suggested.

A, C, G
0   20   40   60 μ

B, D – F
0   50   100 μ

H
0   100   200   300 μ
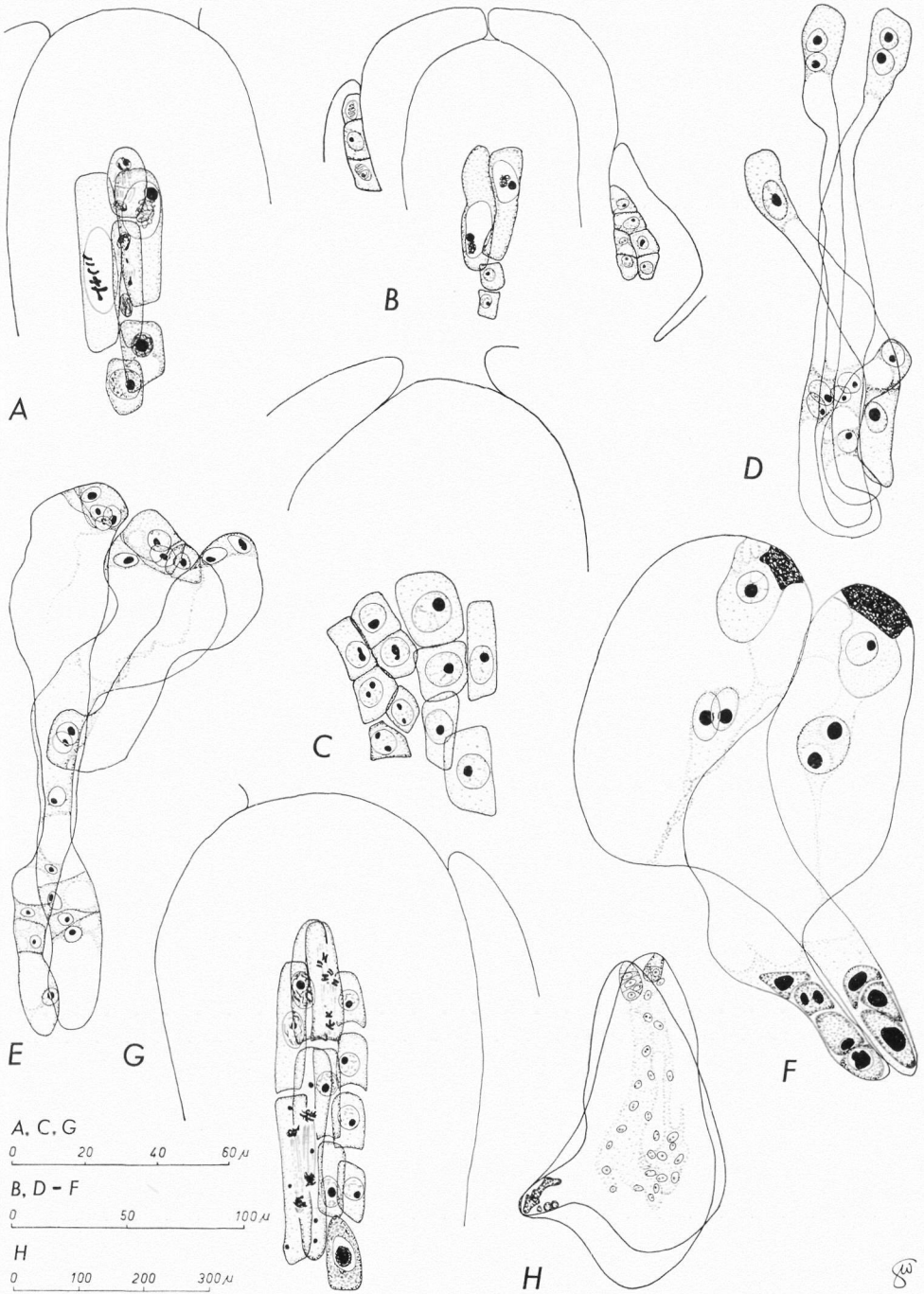
visible in the panicle. Anthesis occurs a few days later. The species is the earliest to flower in the spring, and the development from the beginning of meiosis in the pollen mother cells (PMC) to the first appearance of eight-nucleate ES is rapid (Table 1). Male meiosis is chosen as a starting-point because of the fact that in certain collections female meiosis is apparently delayed or so rare that it is unusable for this purpose. The fixations have been made every two—three days under uniform conditions, and some uncertainty (± a few days) must be conceded.

A fortnight after anthesis, almost the whole developmental series is still represented from uninucleate to mature ES, more or less degenerating, whereas other nucelli (or even the same ones) contain young embryos. In some other cases, the nucellar tissue is merely collapsed at stages corresponding to young embryos (cf. Table 2).

In the collection concerned, no case of twin embryos is recorded, a fact which may be ascribed to the comparatively small material from later developmental stages.

The bad germinativeness of the caryopses (Table 3) can only partly be due to the early abortion observed. A good deal of seemingly vital embryos may succumb later on. Possible factors involved might be lack of nutriment at later stages, demands for special treatment of the caryopses or low inherent vitality of certain embryos. The connexion between the extent of apomixis and the extent of fertility is not clear.

Collection A H T

As in A E K, a variation in number of MMC is observed. Of 93 young nucelli, 4 (4 %) contained no MMC or derivative thereof, 5 (5 %) had 1, 31 (33 %) had 2, 32 (34 %) had 3, 17 (18 %) had 4, and 4 (4 %) had 5 (Fig. 3 G). EI are present in some cases. The reproductive cells are as in A E K situated deep in the nucellus. — The same four developmental types have been found as in A E K.

One instance of twin embryos is noticed (Fig. 3 H). Nucelli with one

Fig. 4. Tetraploid *Hierochloë odorata*, coll. A E F. — *A:* MMC. — *B:* 1 MMC; 2 possible EI. — *C:* 1 MMC, degenerating metaphase; 2 possible EI. — *D:* telophase II, somewhat oblique micropylar spindle. — *E:* tetrad, chalazal MS grown to uninucleate ES. — *F:* tetrad, two chalazal MS grown to uninucleate ES. — *G:* binucleate ES. — *H:* four-nucleate ES. — *I:* eight-nucleate ES. — *J:* eight-nucleate ES, polar nuclei about to fuse. — *K:* mature ES. — *L:* 1 four-nucleate ES; 1 eight-nucleate ES.
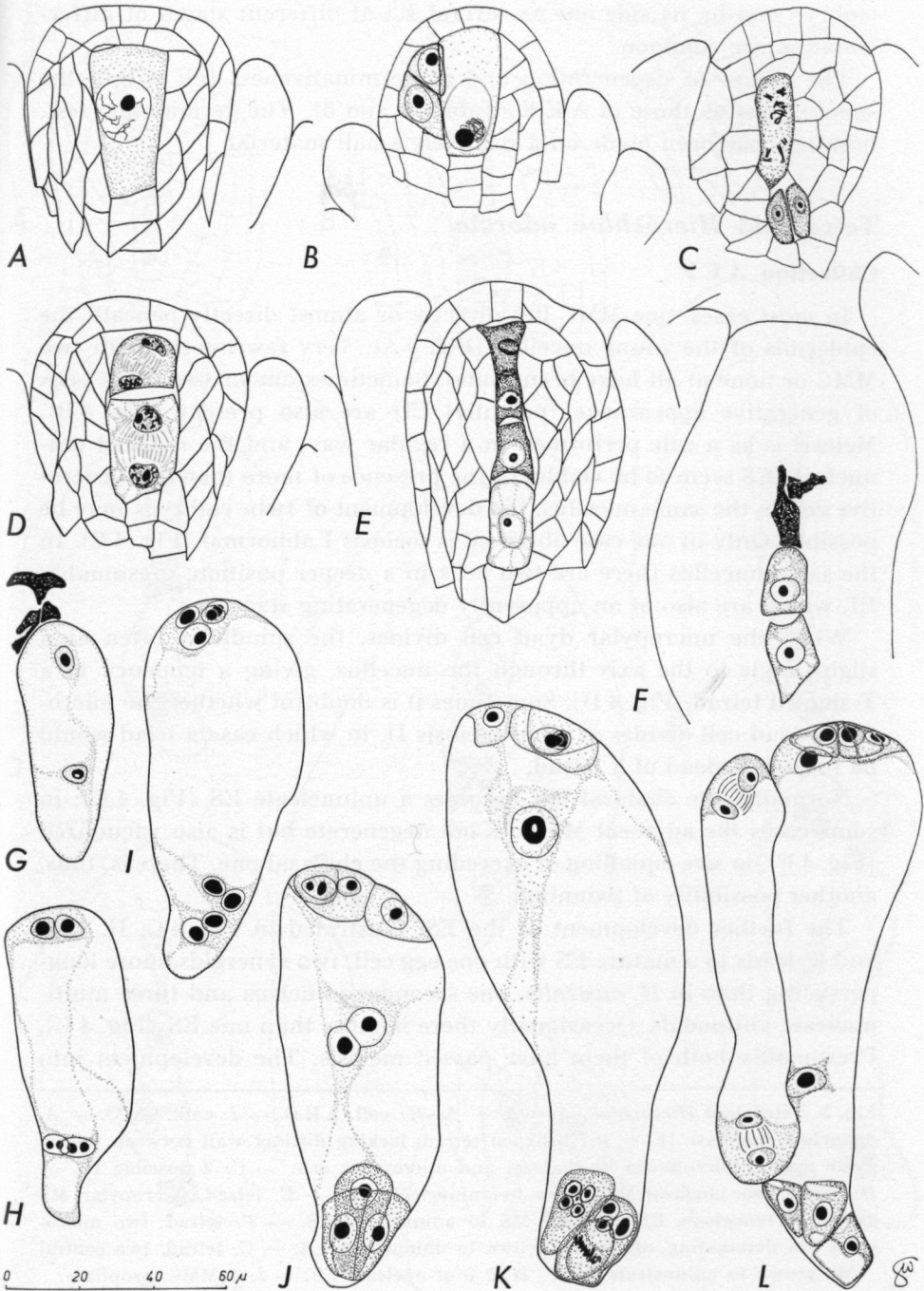
embryo and by its side one or several ES at different stages of differentiation are common.

The values of degeneration and of germinativeness fall within the same ranges as those of A E K (Tables 2 and 3). The germination test, however, has been made on a relatively small material.

Tetraploid *Hierochloë odorata*

Collection A E F

In most cases, one MMC lies directly or almost directly beneath the epidermis of the young nucellus (Fig. 4 A). Very few nucelli with two MMC or none at all have been found. Sometimes one or two other cells of generative appearance (potential EI) are also present (Fig. 4 B). Meiosis is as a rule performed in a regular way, and the reduced uninucleate ES seem to be viable. In the presence of more than one generative cell in the same nucellus, the development of twin embryos may be possible. Only in one case observed is meiosis I abnormal (Fig. 4 C). In the same nucellus there are two cells in a deeper position, presumably EI, which are also at an apparently degenerating stage.

When the micropylar dyad cell divides, the spindle is often at a slight angle to the axis through the nucellus, giving a tendency to a T-shaped tetrad (Fig. 4 D). Sometimes it is doubtful whether the micropylar dyad cell divides at all at meiosis II, in which case a triad would be formed instead of a tetrad.

Normally, the chalazal MS becomes a uninucleate ES (Fig. 4 E); in some cases the adjacent MS does not degenerate but is also vacuolized (Fig. 4 F), in size equalling or exceeding the chalazal one. There is, thus, another possibility of twinning.

The further development of the ES, illustrated in Fig. 4 G, H, I, J, and K, leads to a mature ES with one egg cell, two synergids, more long-persisting than in *H. australis*, one secondary nucleus and three multinucleate antipodals. Occasionally there is more than one ES (Fig. 4 L). Presumably both of them have passed meiosis. The development into

Fig. 5. Tetraploid *Hierochloë odorata*. — *A—H:* coll. A H B. — *I:* coll. A M O. — *A:* disturbed anaphase II. — *B:* T-shaped tetrad, lacking distinct wall between micropylar nuclei; micronuclei in chalazal and micropylar cell. — *C:* 2 possible EI. — *D:* tetrad, two chalazal MS grown to uninucleate ES. — *E:* tetrad, micropylar MS grown to binucleate ES, chalazal MS to uninucleate ES. — *F:* tetrad, two micropylar MS dominating, upper one grown to uninucleate ES. — *G:* tetrad, two central MS grown to uninucleate ES. — *H:* 2 four-nucleate ES. — *I:* 2 MMC, prophase.
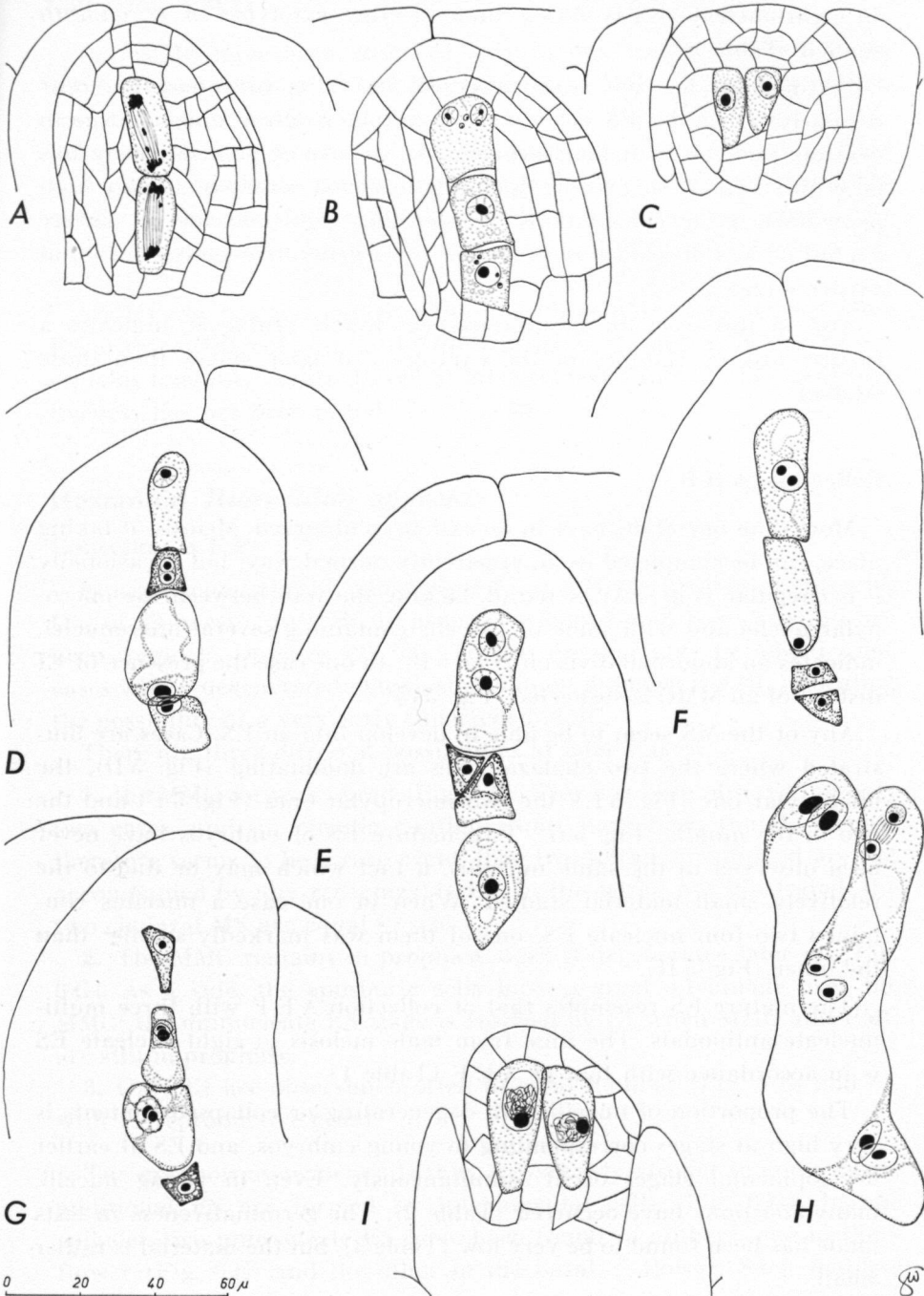
0   20   40   60 μ

an eight-nucleate ES is slower than in other cytotypes of *H. odorata* studied (Table 1).

Fertilization has not been observed, but it is presumed to occur regularly when the ES is of meiotic origin. Embryo and endosperm develop, and the antipodals degenerate. No case of polyembryony has been observed. At stages corresponding to young embryos, a fairly high percentage of nucelli contains degenerating eight-nucleate or mature ES but no less developed ones (Table 2). Degenerative signs are rare at earlier stages.

Also in this case the germinativeness found (Table 3) indicates a further loss of viability of the caryopses at later stages than those studied.

Collection A H B

More than one MMC have in no case been observed. Meiosis, if taking place, can be completed in an apparently normal way, but occasionally it is irregular (Fig. 5 A). A tetrad, lacking the wall between the micropylar nuclei and with some of its cells containing several micronuclei, indicates an abnormal division (Fig. 5 B). In one case the presence of EI instead of an MMC is suspected (Fig. 5 C).

Any of the MS seem to be able to develop into an ES. Cases are illustrated where the two chalazal ones are dominating (Fig. 5 D), the micropylar one (Fig. 5 E), the two micropylar ones (Fig. 5 F) and the two in the middle (Fig. 5 G). Two mature ES or embryos have never been observed in the same nucellus, a fact which may be due to the relatively small material studied. When in one case a nucellus contained two four-nucleate ES, one of them was markedly smaller than the other (Fig. 5 H).

The mature ES resembles that of collection A E F with three multinucleate antipodals. The time from male meiosis to eight-nucleate ES is in accordance with that of A E F (Table 1).

The proportion of nucelli with degenerating or collapsed contents is very high at stages corresponding to young embryos, and ES at earlier developmental stages occur simultaneously. Even in young nucelli, many abortions have occurred (Table 2). The germinativeness in tests made has been found to be very low (Table 3), but the material is rather small.

Collection A M O

Two MMC have been observed only in one nucellus (Fig. 5 I). In another case, cells similar to EI lie beneath an MMC in prophase. Often both the chalazal MS develop into uninucleate ES, whereas the micropylar ones always seem to degenerate. Later on, any of the uninucleate ES come to dominate, the frequency of both alternatives being roughly equal. In no case studied does more than one ES reach beyond the binucleate stage. The mature ES resembles that of the collections A E F and A H B.

A relatively low percentage of the nucelli contains only degenerative ES or traces thereof and, in the limited material studied, the proportion remains tolerably constant even at later stages (Table 2). The germinativeness has not been tested.

Hexaploid *Hierochloë odorata*

Collection A F P

In most young nucelli, aposporous EI or their derivatives are present. Out of 59 nucelli, an MMC in prophase stage (Fig. 6 A) or a tetrad has been found in 16 cases (27 %). To this number may be added some cases with a degenerated cytoplasm remnant amongst the EI, indicating the possibility of a very early superseded MMC.

There are three different possibilities at later stages:

1. the MMC forms a tetrad (Fig. 6 B). This has been observed in only two cases, and no meiotic configurations have been found; meiosis therefore seems to be a rare event. The two tetrads mentioned are not accompanied by any recognizable EI. In the tetrad not illustrated, the two chalazal MS are equal in size.

2. The MMC remains in prophase until it degenerates later on (Fig. 6 G). As a rule, the aposporic cells have a great advantage over the MMC; the uninucleate ES stage is reached by EI when MMC and PMC are still in prophase.

3. Only EI are observable, often in great number (Fig. 6 C_1 and C_2, with 11 reproductive cells).

The aposporous tendency is thus remarkably strong. In some cases, additional ES are formed by integumental cells (Fig. 6 D). In one spikelet, two uninucleate ES have been found in anthers, one in the ♀ flower (Fig. 6 E) and the other in the basal ♂ flower. Such features

certainly have only deleterious effects as regards fertility, but they must be the result of a strong tendency towards apospory. The ES in anthers seem to arise from the thecal wall. The author knows a few reported cases of conversion of male structures into female ones, but only so that pollen grains are differentiated to look like ES (in *Hyacinthus orientalis*, STOW 1930, 1933, and NAITHANI 1937, and in *Ornithogalum nutans*, GEITLER 1941). In the present case, however, an aposporous mechanism is active, in the anthers as in the nucellus.

No sure instances of a further development after meiosis are found. One or more of the EI can pass into an eight-nucleate ES (Fig. 6 F, G, H, and I). In contrast to the normal condition in *H. australis* and in tetraploid *H. odorata*, each nucleus often has more than one nucleolus, a fact which can be connected with the probable presence of a greater number of nucleolus organizers, in its turn due to the higher degree of polyploidy of the plant and the unreduced chromosome number of the ES. The rate of development into an eight-nucleate ES is very rapid (Table 1).

In Fig. 6 I, one nucleus is located next to the egg and another one next to the polar nuclei, the latter being markedly unequal in size as in Fig. 6 H and just about to fuse. It is probably a case of sperm nuclei before syngamy and triple fusion, respectively. The number of nucleoli, among other things, suggests that the ES is unreduced. If the embryo in this case were not to have an increased chromosome number, pseudogamy is taking place. Unfortunately, the interpretation must remain very vague.

The number of nuclei of the three antipodals is variable. Synergid degeneration takes place after anthesis. The endosperm undergoes a few divisions previous to the division of the egg (Fig. 6 J and K).

Even at late stages, members of the series from uninucleate to mature ES exist side by side in the nucelli. The percentage of nucelli

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Fig. 6. Hexaploid *Hierochloë odorata.* — *A—K:* coll. A F P. — *L:* coll. A H E. — *A:* MMC, prophase. — *B:* telophase II. — *C:* 6 EI; 4 unreduced uninucleate ES; 1 unreduced binucleate ES; the two parts, C_1 and C_2, represent different levels in the nucellus. — *D:* degenerated cytoplasm (MMC?); 7 EI; 1 aposporous uninucleate ES in integument. — *E:* aposporous uninucleate ES in anther; PMC, prophase, at a distance. — *F:* binucleate ES. — *G:* 1 MMC, degenerating prophase; 1 four-nucleate ES. — *H:* 1 binucleate ES; 1 eight-nucleate ES. — *I:* eight-nucleate ES with two possible sperm nuclei. — *J:* 1 eight-nucleate ES; 1 ES with undivided egg, just dividing central nucleus. — *K:* ES with undivided egg, eight-nucleate endosperm. — *L:* 1 MMC, abnormal metaphase; 2 EI.

A   B   C₁

D   E   C₂

G   F   H

J   K   I   L

A - G, I, L
0   20   40   60 μ

H, J, K
0   50   100   150 μ
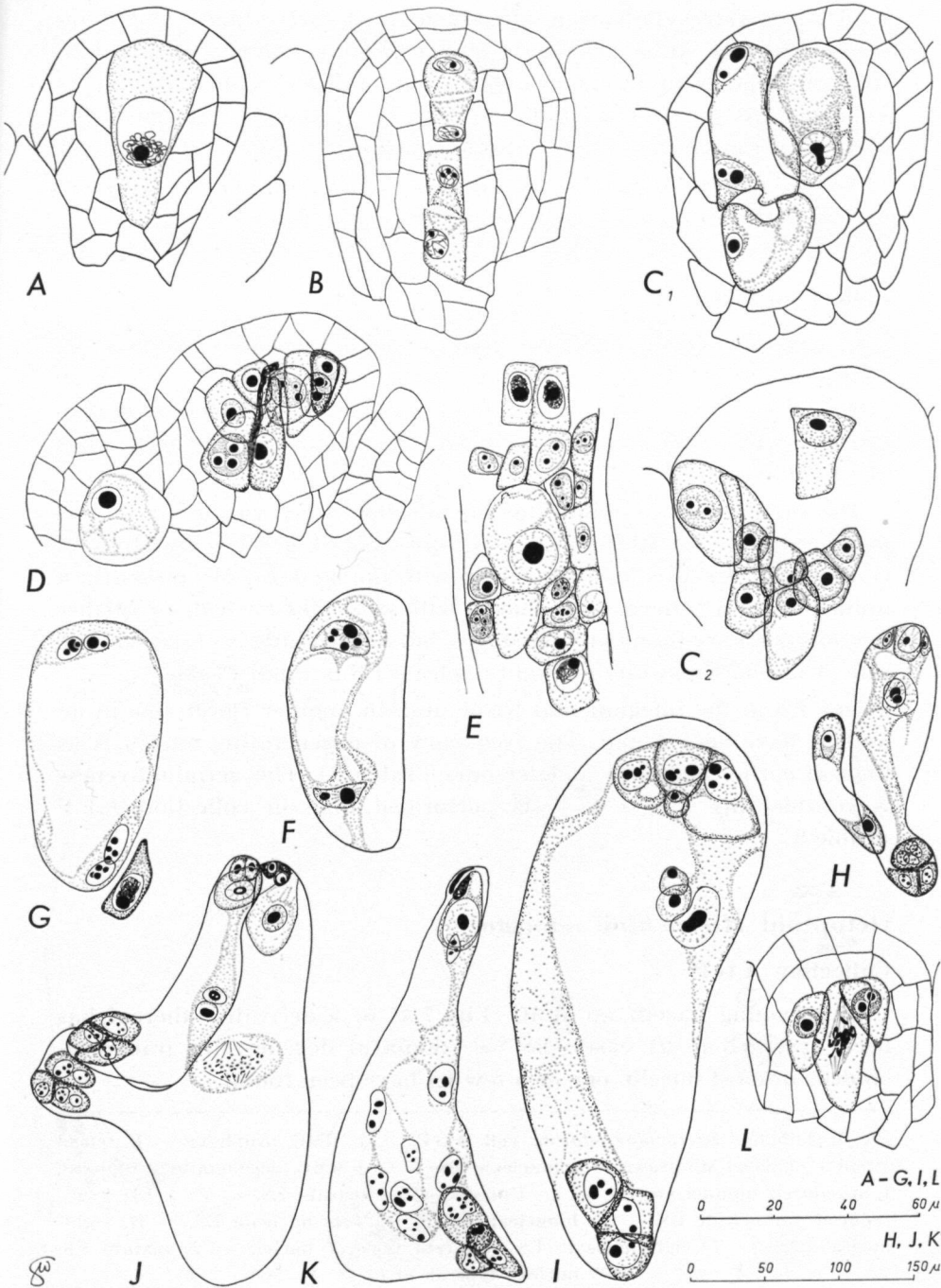
with degenerated contents is already high at early stages, and it in-
creases further at stages equivalent to young embryos (Table 2).
Another large group of embryos turns out to be less viable later on, as
indicated by the low germination figures (Table 3). However, the
material is too small to allow definite conclusions.

No case of twinning is recorded in the material, although two ES can
become eight-nucleate in the same nucellus (Fig. 6 J).

Collection A H E

In general, the conditions of young nucelli correspond to those of
collection A F P; 20 nucelli of 68 (29 %) have been found to contain an
MMC. In this case too, it is a minimum number, since an early degene-
ration of such cells cannot be excluded in some nucelli. The occurrence
of EI is the rule.

The same three possibilities as in collection A F P can occur. In one
instance only is an MMC in meiosis I observed (Fig. 6 L). The division
is abnormal. In three cases, a tetrad with the chalazal MS grown to a
uninucleate ES is developed. Nucelli with two eight-nucleate or further
developed ES are found at later stages, but no twinning is observed. The
rate of development into an eight-nucleate ES is rapid (Table 1).

One ES in the integumental tissue and, in another floret, one in an
anther, have been found. The frequency of degenerating nucelli is as
high at earlier stages as at later ones (Table 2). The germinativeness
is considerably higher in tests performed than in collection A F P
(Table 3).

Octoploid *Hierochloë odorata*

Collection A G P

In 56 young nucelli, an MMC (Fig. 7 A) or a derivative thereof has
been observed in 21 cases (38 %), doubtful degenerative traces ex-
cluded. In most nucelli, one or a few EI have been found.

Fig. 7. Octoploid *Hierochloë odorata*, coll. A G P. — *A:* MMC, prophase. — *B:* tetrad
(triad?), chalazal MS grown to uninucleate ES. — *C:* 1 MMC, degenerating prophase;
1 unreduced uninucleate ES. — *D:* Unreduced uninucleate ES. — *E:* 1 EI; 2 un-
reduced uninucleate ES. — *F:* binucleate ES. — *G:* four-nucleate ES. — *H:* eight-
nucleate ES. — *I:* eight-nucleate ES, different type of nuclei. — *J:* mature ES,
nucleus type as in *I.*

A
B
C
D
E
F
G
H
I
J

A–1

0   20   40   60μ

0   50   100   150μ
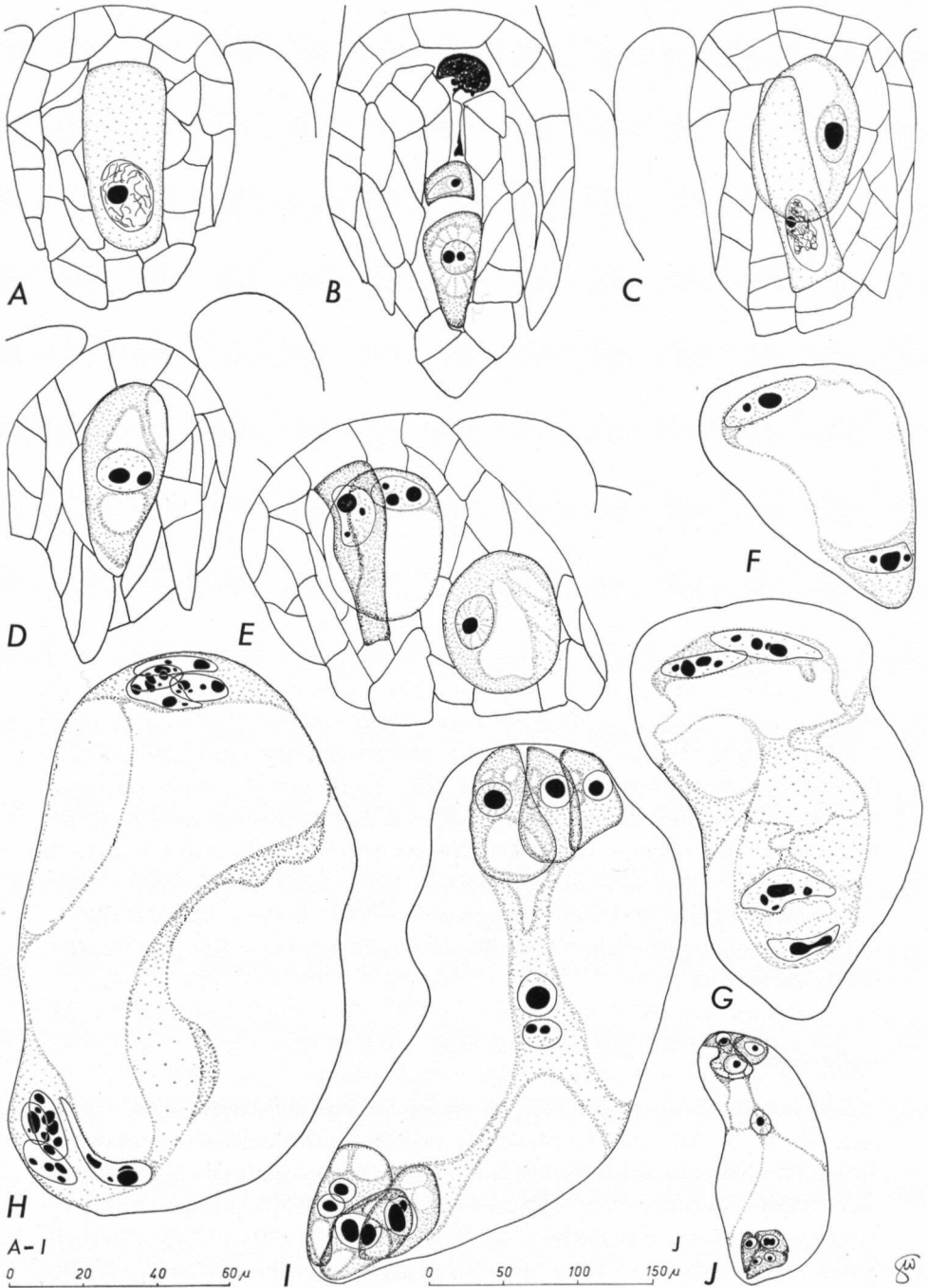
As in the hexaploid collection A F P, three possible courses can be followed at later stages:

1. The MMC undergoes meiosis. As regards this collection, it is still doubtful whether the result is a triad or a tetrad (cf., however, collection A N C) because of the rarity of this stage in the material studied (Fig. 7 B). According to evidence given by more developed ES, reduced ES can reach maturity. EI may be present or absent.

2. The MMC degenerates in the presence of one or several more viable EI without carrying through meiosis (Fig. 7 C).

3. Only EI or derivatives thereof are observable (Fig. 7 D and E). There never seem to be so many in each nucellus as in the hexaploid collections A F P and A H E.

The ES in Fig. 7 F, G, and H are all characterized by their flattened, disc-like nuclei with two or more nucleoli. In contrast to these ES, the ones in Fig. 7 I and J have only one nucleolus in each nucleus in the egg apparatus and as a rule also in the three antipodals. Some of the latter cells have, however, become multinucleate. A hypothetical explanation of the two types of nuclei is that ES which mainly have only one nucleolus per nucleus and more spherically formed nuclei have undergone meiosis.

The time from male meiosis to eight-nucleate ES is fairly short (Table 1).

The synergids degenerate shortly after anthesis, and the embryo develops. No signs of a fertilization are observed. In no case observed has more than one ES in a nucellus reached maturity. However, the material at this stage is small. On the whole, the number of ES in each nucellus relatively rarely exceeds one.

The percentages of nucelli collapsed or with degenerated ES at different stages appear in Table 2. In Table 3, a result from the germination test is presented.

Collection A N C

The results obtained are roughly in agreement with those from collection A G P. 65 (37 %) of 174 young nucelli in the material contain an MMC, to which number may be added some cases with possible degenerated MMC. Three of the 65 nucelli contain two MMC side by side.

The same three possibilities as in collection A G P can be observed. Some more instances of the meiotic process have been found, e.g. the
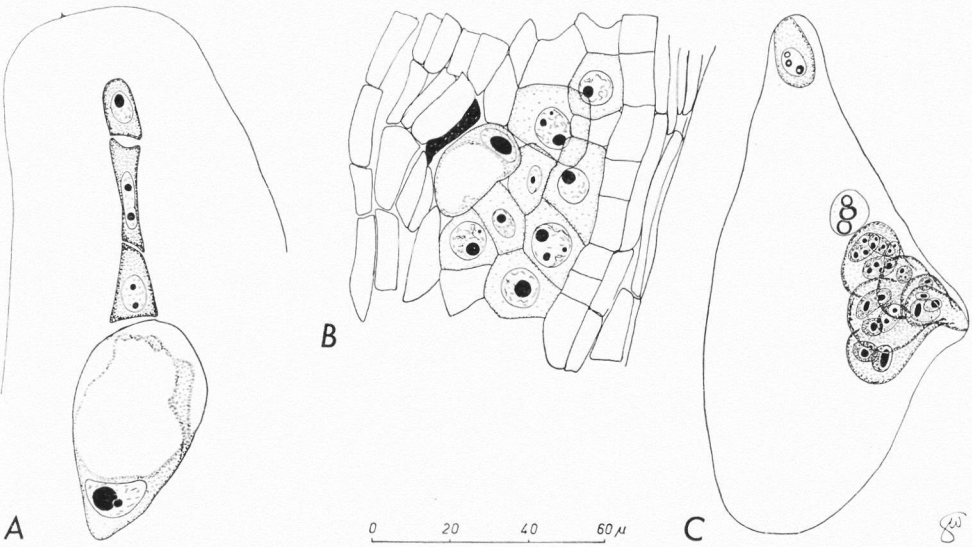
Fig. 8. Octoploid *Hierochloë odorata*, coll. A N C. — *A:* tetrad, chalazal MS grown to uninucleate ES. — *B:* Probably aposporous uninucleate ES in anther; PMC, early prophase, adjacent. — *C:* mature ES, six multinucleate antipodals.

dyad stage and some tetrads (Fig. 8 A). Meiosis is, however, also in this collection a rare event.

In one of the three nucelli with two MMC mentioned above, one of the MMC is in diakinesis. The number of chromosome configurations counted is c. 50, of which c. 45 look like univalents. It is in the present material impossible to know in what direction the further development would have run after the observed, possibly asynaptic meiosis, since the case is quite isolated.

The development of the ES seems to be in agreement with that of collection A G P and is performed in about the same time (Table 1). In one spikelet, a similar displacement of the apomictic potency as in the hexaploid collections A F P and A H E was observed, as a uninucleate ES could be stated to have occurred in an anther (Fig. 8 B).

In one case, an evidently degenerating mature ES contains more than three antipodals (Fig. 8 C). It is probably a secondary abnormality in conjunction with degeneration.

The proportion of nucelli with collapsed or degenerated contents at different stages is referred to in Table 2. The germination test in Table 3, although with a result similar to that of A G P, is too small to support definite conclusions.

SUMMARY AND DISCUSSION

1. EI are observed in all taxa dealt with.

They occur rarely in tetraploid *Hierochloë odorata*, not infrequently in *H. australis*, and regularly in hexaploid and octoploid *H. odorata*. In the latter two taxa the physiological tendency towards apospory is obviously strong, as indicated by the occurrence of ES in integuments and even in anthers. In the hexaploid, moreover, the EI occur in a rather high number per nucellus.

The aposporous ES in anthers are, as far as the author knows, as yet unparalleled.

2. More than one MMC occur regularly in *Hierochloë australis*, in other taxa studied only in isolated cases.

A multicellular archesporium has already been noted in several plant groups (see, e.g., SCHNARF 1929 pp. 73—96, and MAHESHWARI 1950 pp. 71, 73 for references). — The parallelism between the normal occurrence of a variable number of MMC in some samples and of EI in others indicates a physiological factor, acting on generative cells whether reduced or not.

3. Besides apospory, diplospory may be suspected in *Hierochloë australis* and in octoploid *H. odorata*.

In *H. australis*, the homology between MMC and certain EI is almost certain. — In octoploid *H. odorata*, a distinction between aposporous and possible diplosporous EI is uncertain, since one case in collection A N C may give an indication on the possibility of non-reductional division of the MMC. — In octoploid *H. odorata* from the USA, NORSTOG (1963 p. 819) has already described two alternative types of EI, which must be classified as diplosporous and aposporous, respectively.

4. The reproduction is in all collections badly disturbed (Tables 2 and 3), a fact partly connected with the presence of more than one MMC or EI, respectively, but also conspicious in the tetraploid samples, being almost normal in these respects.

In some cases, the great number of MMC or EI, respectively, must cause unfavourable nutritional and spatial conditions, leading to the collapse of the nucellar tissue. — In other cases, degeneration is evidently caused by a weak inherent viability of the MMC or EI at a young stage. — Seemingly normal MMC or EI appear to give rise to abnormal ES, e.g. cases with lacking egg apparatus, degenerating polar nuclei, and other aberrations. — Degeneration can also occur at the embryo stage in nucelli, up to then normal-looking. — Finally, the caryopses may require some particular conditions to germinate. For example NORSTOG (1957 pp. 315, 316), having found very low germination figures in octoploid *Hierochloë odorata* in the USA, obtained better germination after excising the embryos and transplanting them into WHITE's nutrient agar. However, REEDER & NORSTOG (1961 p. 84) found good germina-

Table 1. Number of days between first observation of meiosis in anthers and of eight-nucleate ES in fixations from 1964 and 1965 (collections A H T and A M O excluded, since different parts of the developmental series were fixed each year).

Collection		H. australis	H. odorata					
		diploid	tetraploid		hexaploid		octoploid	
		A E K	A E F	A H B	A F P	A H E	A G P	A N C
1964	Date	19.4.—29.4.	24.4.—8.5.	24.4.—13.5.	29.4.—5.5.	29.4.—8.5.	29.4.—11.5.	29.4.—11.5.
	Days	10	14	19	6	9	12	12
1965	Date	—	2.5.—21.5.	2.5.—21.5.	—	—	—	8.5.—21.5.
	Days	—	19	19	—	—	—	13

Table 2. Occurrence of degenerating nucellar contents at different stages of development.

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

Collection	A			B		
	a	b	c	a	b	c
H. australis						
A E K	64	3	5	28	7	25
A H T	30	0	0	55	19	35
Tetraploid H. odorata						
A E F	144	5	3	38	14	37
A H B	37	11	30	40	33	83
A M O	36	4	11	29	3	10
Hexaploid H. odorata						
A F P	84	36	43	34	22	64
A H E	66	27	41	27	11	41
Octoploid H. odorata						
A G P	53	13	25	15	8	53
A N C	35	18	51	23	12	52

Table 3. Results of germination tests after open pollination.

Collection	H. australis		H. odorata					
	diploid		tetraploid		hexaploid		octoploid	
	AEK	AHT	AEF	AHB	AFP	AHE	AGP	ANC
Number of sown caryopses	119	31	503	235	31	203	228	22
Number of obtained seedlings	3	0	183	14	1	54	20	2
Number of obtained seedlings in percents of sown caryopses	3	0	36	6	3	27	9	9

tion in the sexual tetraploid *H. odorata* which they studied, in contrast to the results obtained by the author on European material.

The seed-setting after open pollination is studied in *Poa pratensis* by NILS-SON (1933 p. 215; 1937 pp. 92—95) and by ÅKERBERG (1936 pp. 222—231, 241—245; 1942 pp. 28—35). The percentages found are variable but usually exceed 50 %. It must be remarked that the actual germination ability may be smaller than the ability to produce normal-looking caryopses. In any case it seems probable that the apomixis of *Poa pratensis* does not as a rule bring about such an upset of reproductive balance as is the case in the *Hierochloë* collections studied.

5. *Hierochloë australis* is to be regarded as a facultative apomict.

The author knows only six other genera in which diploid species have turned out to exhibit gametophytic apomixis in the sense of STEBBINS (1950 p. 384), viz., *Hieracium* (*H. umbellatum* f. *apomicta* 2n 18, GENTCHEFF 1941 pp. 114, 145), *Nardus* (*N. stricta* 2n 26, RYCHLEWSKI 1962), *Panicum* (*P. antidotale* 2n 18, SHAMA KUMARI 1960), *Pennisetum* (*P. ramosum* 2n 10, NARAYAN 1962; *P. hohenackeri* 2n 18, ib.), *Potentilla* (*P. argentea* 2n 14, MÜNTZING 1928 p. 281, 1931 pp. 167—170, HÅKANSSON 1946 pp. 26—34; *P. arguta* 2n 14, POPOFF 1935 p. 518; *P. aurea* 2n 14, SHIMOTOMAI 1936 p. 338), and *Ranunculus* (*R. cassubicifolius* 2n 16, HÄFLIGER 1943 pp. 349—364). *Nardus stricta*, however, has been supposed to be a secondarily diploidized tetraploid species (cf. RYCHLEWSKI 1962, p. 19), and the same may be true of *Panicum antidotale* and *Pennisetum hohenackeri*.

6. When the germinativeness of the caryopses approaches or equals zero, even the vegetative reproduction by creeping rhizomes in *Hierochloë odorata* may be classified as apomixis (cf. GUSTAFSSON 1946 pp. 50—55, STEBBINS 1950 p. 382).

On this assumption, the samples of tetraploid *H. odorata* can thus be regarded as facultative apomicts.

7. Aneuploid plants or clones have not been observed in a material, consisting of some 300 samples, mainly from Sweden, Norway and Finland.

In all taxa studied, disturbances in male meiosis have been observed in the form of bridges and fragments, laggards, restitution nuclei, &c. They seem to be less common in diploid and tetraploid samples (with the exception of A H B, in which male meiosis almost always has been found to break down totally), but occur quite regularly in hexaploid and octoploid ones. The development of the male gametophyte will be dealt with in a later paper. Also in female meiosis, some aberrations are met with.

Possibly, seedlings arising from the combination of aneuploid gametes are not viable. More likely the explanation may be that such seedlings are not produced. Indirectly, the absence of aneuploids in the material thus supports the opinion that apomixis, agamospermic or vegetative, is quite predominant

in the studied higher polyploids of *Hierochloë odorata*. As regards octoploid *H. odorata* from USA, NORSTOG (1963 p. 820) has considered apomixis to be obligate.

The cytological pattern found in *Hierochloë* is entirely different from that in e.g. *Poa alpina* (MÜNTZING 1933 pp. 132—136, 1940 pp. 116—120, 127—136, 139—145, 1954 pp. 461—468, 1966), *Poa pratensis* (MÜNTZING 1933 pp. 142—145; ÅKERBERG 1936 pp. 236—239, 1942 pp. 9—11), &c., where many aneuploid numbers are known.

8. In *Hierochloë australis* and tetraploid *H. odorata*, a certain variability is observed as to which of the MS develops into an ES.

The most striking instance is the sample A H B, in which any of the MS is able to develop, often more than one in the same tetrad. In sexual *Poa alpina*, a similar phenomenon is observed (HÅKANSSON 1943 pp. 28—30). In that case, however, the tetrad is not linear, leading HÅKANSSON to the conclusion that nutritional factors may be involved in the promotion of more than one MS. This explanation is not valid in *Hierochloë*. One is more inclined to postulate an unsteadiness of the regulation mechanism, parallelling the conditions discussed in paragraph 2. — For further references see e.g. SCHNARF (1929 pp. 108—115), and MAHESHWARI (1950 pp. 75—78).

9. In no instance has an embryo been observed to develop from any other cell than the egg.

NORSTOG (1963 p. 820; see also references) rejects the possibility that embryos might develop from synergids in his material from the USA. Likewise, no evidence suggests such a possibility in the studied European *Hierochloë*, as is observed e.g. in *Potentilla* (GENTCHEFF & GUSTAFSSON 1940 p. 115).

10. In those cases, where observations are available (in the samples A M O, A F P, A H E and A N C), the egg cell divides when the secondary nucleus has already passed some mitoses.

The same condition is reported by NORSTOG (1963 p. 819; see also references) to be the rule in the octoploid *Hierochloë odorata* from the USA which he studied. This behaviour is in contrast to that of e.g. apomictic *Poa alpina* (HÅKANSSON 1943 p. 39), the apomictic *Poa granitica* (SKALIŃSKA 1960 pp. 99, 101), the apomictic *Poa pratensis* (TINNEY 1940 p. 355; ÅKERBERG 1942 pp. 26—28, 1943) and the apomictic *Potentilla collina* (GENTCHEFF & GUSTAFSSON 1940 p. 116), where the embryo is large before the first division of the secondary nucleus. It agrees, however, with that of e.g. the facultatively apomictic *Hypericum perforatum* (NOACK 1939 pp. 597—598), the apomictic *Nardus stricta* (RYCHLEWSKI 1962 p. 13), sexual *Poa alpina* (HÅKANSSON 1943 p. 31), and the *Sanguisorba minor* complex, where facultative apomixis can occur (NORDBORG 1967).

11. The apomictic procedure obviously yields a certain gain of time (Table 1).

Out of necessity, the date of first observed male meiosis was chosen as the starting-point when estimating the rate of development, and it cannot be excluded that only the chronological correlation between male and female development is unequal in the samples studied. However, nothing speaks in favour of such an explanation of the different rates. Furthermore, it is true that the samples originate from different habitats and are grown under uniform and partly unnatural conditions. However, all but two of the *odorata* samples (of which only one, A N C, is listed in Table 1) are collected in climatically roughly intercomparable localities. Despite the lesser exactitude in defining the days of beginning male meiosis and of appearance of eight-nucleate ES in the samples, the difference in development rate between tetraploid *Hierochloë odorata* on one side and hexaploid and octoploid *H. odorata* on the other must be considered as a real one, hardly caused by chance. The tetraploid is earlier in the beginning, but the hexaploids and octoploids are very well compensated. This rapidity may be regarded as having a certain selective value, to some extent counterbalancing the evident disharmony of the reproductive system of the higher polyploids treated. *H. odorata* is pronouncedly early in the spring, flowering before the vegetative shoots are very much developed. All panicles are in anthesis within a few days, with the exception of the occasional reflowering in the autumn.

H. australis, occupying quite different habitats in nature, should not be directly compared with *H. odorata* in this connexion. It flowers still earlier in the spring.

12. The apomictic reproduction, by caryopses or vegetatively, evidently restricts the rate of genetic recombination and, at the same time, renders a strong heterozygosity possible.

The combination of perennial habit and a low degree of sexual reproduction in this case has given each taxon a rigid and in a sense conservative variation pattern. An analysis of these problems will be attempted in a later paper. — Some of the disturbances found, especially in male meiosis in certain samples, reveal structural heterozygosity.

13. Different samples on tetraploid level are dissimilar in behaviour, in other taxa they are relatively similar.

When trying to make such comparisons, one must, indeed, be aware of the restricted nature of the material. On the other hand, the time-consuming nature of embryological work does not make very extensive investigations justifiable. The difference in variation pattern distinguishing the obviously most sexually impressed samples from each other is, however, striking. The great polymorphism exhibited by certain apomicts, such as *Calamagrostis*, *Hieracium*, *Poa*, *Potentilla*, and *Rubus*, is obviously not met with among the apomictic *Hierochloë* material studied.

The present material does not permit an analysis of the possible variation between plants within one and the same sample. Most samples may, besides, be assumed as clones. Nor is it possible to make a comparison between differ-

ent panicles of the same plant at different age, such as has been performed by e.g. NYGREN (1949 pp. 288—289, 295) in *Calamagrostis*, or under different external conditions, as by GRAZI, UMAERUS & ÅKERBERG (1961 p. 503) in *Poa*.

Detailed study of other characters will surely add more to the knowledge of the variation pattern within each taxon. Nevertheless, the necessity of avoiding generalizations from an isolated investigation, however correct it may be in itself, has already been demonstrated.

ACKNOWLEDGEMENTS

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Brief Articles and Reports

Barbula rigidula (Hedw.) Mitt. in Denmark

In Bot. Notiser 1929 p. 150 HERMAN PERSSON published the first and until 1957, as far as known, the only finding in Denmark of *Barbula rigidula*, made in 1925 by O. GERTZ in the ruined castle of Lilleborg on the island of Bornholm.

In 1957 I collected the moss mentioned from calcareous walls close to the manor Krengerup in the western part of the island of Funen, where it grew in pure tufts. — Again, in 1965, I collected the moss as small pure tufts from calcareous stone accumulations close to the manor Ledreborg in the middle of the island of Zealand.

In both of the collections the specimens are a little slenderer than in the type material, but the gemmae are abundant and large and in a much better state of development than I have ever seen in material from Southern Europe.

At Krengerup the material was collected very close to stations for *Leptodontium gemmascens* (MITT.) BRAITHW., a moss mainly limited to Southern England, where *Barbula rigidula* also frequently occurs, while it seems rare in Denmark. — These facts might give rise to the question whether there is some particular connexion between the occurrences of the species in England and in Denmark and, in addition, whether it is a mere coincidence that the stations for *Barbula rigidula* in Funen and in Zealand both of them are great manors.

Samples are kept in the Botanical Museum in Copenhagen.

SVEND RUNGBY
Copenhagen

Mosses New to Crete

In 1966 I collected some bryophytes in Central and Western Crete. Of the species in question 10 are not mentioned with regard to Crete in the list of bryophytes in K. H. RECHINGER's Flora Aegaea nor, as far as I know, otherwise recorded from that island. They are:

Bryum caespiticium HEDW. — C. fr. Knossos, walls.

— — — var. *comense* (SCHPR.) HUSN. — Phaistós, walls.

Mniobryum albicans (WHLB.) LIMPR. — Knossos, clay soil near a brooklet.

Aloina ambigua (BR. EUR.) LIMPR. — C. fr. Roumeli and Souda, calcareous slopes.

Barbula revoluta BRID. — Knossos, walls.

Barbula sinuosa (WILS.) BRAITHW. — Defile of Xyloskala, 1100 m, rocks.

Grimmia trichophylla GREV. — C. fr. Defile of Xyloskala, rocks.

Ceratodon purpureus (HEDW.) BRID. — C. fr. Knossos, soil.

Saelania glaucescens (HEDW.) BROTH. — North of Paleochora; moist, calcareous slopes.

Isothecium filescens (BRID.) MÖNKEM. — Defile of Xyloskala, rocks.

Eurhynchium meridionale (SCHPR.) DE NOT. — Arkadi, calcareous slopes.

The samples are kept in the Botanical Museum in Copenhagen.

SVEND RUNGBY
Copenhagen

Återfynd av Aconitum napellus i Skåne

Aconitum napellus L. upptäcktes i Skåne av E. FRIES år 1828, vid Hasslemölla i Veberöds socken. Fyndet väckte visst uppseende i botaniska kretsar, då arten var känd som vildväxande närmast från Mellaneuropas bergstrakter. Den slutsats man drog härav var att växten spritt sig till Skånelokalen från någon närbelägen trädgård.

Växtplatsen är ett alkärr, som genomflytes av en ganska bred bäck. I gläntor, där solljuset når marken, är vegetationen mycket frodig. Den kan karaktäriseras som en högörtäng med bl.a. *Filipendula ulmaria*, *Melandrium rubrum*, *Platanthera chlorantha*, *Thalictrum flavum*, *T. aquilegiifolium*, *Dactylorchis incarnata*, alla växter med höga krav på riklig näringstillgång och stor markfuktighet. Det var i vegetation av denna typ som *A. napellus* förekom. Den sista iakttagelsen av *A. napellus* på nämnda lokal gjordes på 1950-talet. Området har noggrant genomsökts somrarna 1964 och 1965, under inventeringen av kärlväxtfloran i Veberöds socken, men utan resultat.

Av en tillfällighet påträffades emellertid sommaren 1966 en ny lokal. Omkring tio exemplar växer här på en skyddad plats inom samma bäcksystem, som det ursprungliga fyndet gjordes. Vegetationen är lik den från den förut kända lokalen.

Att döma av de funna plantornas utseende har *A. napellus* för närvarande svårt att hålla sig kvar här. Blomningen är inte särskilt riklig och flera plantor blommade ej. Fruktsättningen är dålig eller oftast helt felslagen. Stjälkarna är långa och slaka.

En viktig orsak till plantornas dåliga trivsel på platsen är en snabbt tilltagande överskuggning från uppväxande träd. En bidragande orsak kan eventuellt också vara, att arten här förekommer långt utanför sitt naturliga utbrednings-område.

Det kan diskuteras, hur *A. napellus* kommit till Skåne och huruvida den är spontan eller ej. Faktum kvarstår emellertid, att den inom samma bäcksystem lyckats hålla sig kvar i minst 150 år och att den förekommer på mer än en enstaka lokal.

SIGURD JÖNSSON

Meddelanden

FORSKNINGSBIDRAG

Ur Bokelundska naturvetenskapliga resestipendierna har utdelats: 1.350 kr till docent SVEN-OLOV STRANDHEDE för deltagande i ett sammanträde med Nordisk förening för taxonomisk botanik i Åbo i juli och en 4-dagars exkursion till Utsjoki — 550 kr till docent STIG FALK och 910 kr till fil. lic. LARS CHRISTENSSON för deltagande i den 8e nordiska kongressen för växtfysiologi i Bergen — 1.050 kr till fil. lic. FOLKE ANDERSSON för deltagande i ett symposium över »The measurement of environmental factors in terrestrial ecology» i Reading, England — och 630 kr till fil. lic. BERTIL NORDENSTAM för ett besök vid de Candolles herbarium i Genève.

Ur Nilsson-Ehlefonden har utdelats följande forskningsbidrag: 3.100 kr till fil. lic. SVEN ASKER för fortsatta cytogenetiska undersökningar inom apomiktiska *Potentilla*-arter — 1.000 kr till fil. lic. INGEMAR BJÖRKQVIST för att utreda och klargöra förhållandena mellan olika taxa inom släktet *Alisma* — 1.000 kr till fil. lic. KARIN BRUNSBERG för fortsatta meiosstudier inom *Lathyrus pratensis*-gruppen — 2.000 kr till fil. mag. LENNART ERJEFÄLT för framställning av dihaploida kloner av *Solanum tuberosum*, resistenta mot *Phytophthora infestans*, för studier av resistensgenernas nedärvning och resistensens natur på diploid nivå — 3.100 kr till fil. lic. GUNNAR ISING för cytologiska studier hos *Cyrtanthus* (*Amaryllidaceæ*) — 1.000 kr till docent dr HALINA JAWORSKA för undersökningar över DNA, RNA och syntes av äggviteämnen hos *Haplopappus gracilis* och *Secale cereale*. — 1.000 kr till fil. mag. BÖRJE LARSSON för morfologisk och genetisk analys av glesaxiga mutanter i korn — 3.100 kr till fil. lic. GÖRAN PERSSON för fortsatta studier av finstrukturen i muterade segment hos korn — 3.100 kr till fil. lic. JAN SJÖDIN för cytogenetisk analys av kromosomerna i *Vicia faba* L. med hjälp av inducerade strukturella omlagringar — 1.000 kr till fil. kand. KERSTI ZETTERSTRÖM för populationsstudier av olika sorter av ängsvingel — 600 kr till fil. kand. BENGT BENTZER för insamling av Östersjötyper och Atlanttyper av *Silene maritima*.

Ur Jubileums- och Tornblads-fonderna har av K. Fysiografiska Sällskapet i Lund utdelats följande belopp: 1.000 kr till Sektionen Blekinges Flora för inventering av Blekinges flora — 1.186 kr till fil. lic. TORE

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Ur anslaget avseende studier av Kullabergs natur har K. Fysiografiska Sällskapet slutligen utdelat följande belopp: 2.500 kr till docent Björn Berglund för studier av Kullabergs senglaciala vegetation och miljö — 300 kr till fil. lic. Karin Brunsberg för undersökningar av *Lathyrus sphaericus* — 600 kr till fil. mag. Nils Englesson för populationsstudier inom *Cerastium semidecandrum*-gruppen i Kullabergsområdet — 1.400 kr till fil. kand. Örjan Nilsson för materialinsamling för taxonomisk bearbetning bl.a. med tunnskiktskromatografering av arterna i släktet *Rosa* inom Kullabergsområdet – 1.400 kr till fil. mag. Torgny von Wachenfeldt för att fullfölja algologiska undersökningar samt undersöka, hur exponeringsförhållandena inverkar på algfloran, genomföra en algsociologisk undersökning och undersöka och uppmäta ståndortsfaktorerna hos en del alger, som växer ovan vattenytan.

Botanisk Litteratur
(Botanical Literature)

Flora of Southern Africa. – Vol. 26 (ed. R. A. DYER, L. E. CODD & H. B. RYCROFT), vii+307 pp., 42 figs., Pretoria 1963. Price R. 4.60 (overseas R. 5.75). — Vol. 1 (ed. L. E. CODD, B. DE WINTER & H. B. RYCROFT), ix+116 pp., 35 figs. 1966. Price R. 1.75 (overseas R. 2.20).

Almost the whole of Africa is today covered by flora projects in various stages of publication or preparation and of various scope and size. The steady progress and the cooperation between different teams or institutes to mutual benefit are constant sources of rejoicing.

A very urgent and one of the most ambitious projects is the new 'Flora Capensis', edited jointly by the Botanical Research Institute, Pretoria, and National Botanic Gardens, Kirstenbosch, under the name of 'Flora of Southern Africa'. More than 100 years have elapsed since the first volume of 'Flora Capensis' was published, and even the later volumes are largely outdated.

The territories covered by the flora are the Republic of South Africa, Basutoland, Swaziland, and South West Africa. It is a vast area with a wide range of climate, soils, and types of plant cover. The famous Cape floral kingdom occupies only a minor portion of the area. The number of species of flowering plants is likely to approach the imposing number of 20,000.

The flora gives a very complete treatment with full descriptions of families, genera and species, literature references, synonymy, citation of type specimens including their location (a few THUNBERG types are erroneously cited as located in UPSV instead of UPS; vol. 26 p. 23, 25), distribution and ecology, etc. Critical remarks and other comments are freely given. Quite obviously, precursory monographic studies are needed for most groups, and the rate of publication will be comparatively slow. The whole work is planned to comprise 33 volumes. Those volumes treating the largest families will have to appear in several parts.

Volume 26 was the first to appear. It deals with the families 147—156 of the Dalla Torre-Harms system, including, i.a., *Plumbaginaceae* (R. A. DYER), *Sapotaceae* (A. D. J. MEEUSE), *Ebenaceae* (B. DE WINTER), *Oleaceae* (I. C. VERDOORN), *Loganiaceae* (I. C. VERDOORN), *Gentianaceae* (W. MARAIS & I. C. VERDOORN), and *Apocynaceae* (L. E. CODD).

Volume 1 includes the *Gymnospermae* (various authors) and *Helobiae* (A. A. OBERMEYER). Mrs. OBERMEYER-MAUVE in many instances applies a fairly broad species concept. She drastically reduces the number of South

African species of *Triglochin* to two, but for good reasons, it seems. She also includes both *Aponogeton rehmannii* and *A. stuhlmannii* in *A. junceus*. It is a little surprising not to find *Vallisneria* included in the flora; according to MERXMÜLLER's 'Prodromus' the genus occurs in South West Africa. Some other discrepancies in the treatment of the *Helobiae* in the 'Prodromus' and 'Flora of Southern Africa' could be mentioned. E.g., the collection MERX- MÜLLER & GIESS no. 1889 is cited as *Potamogeton schweinfurthii* in the former but as *P. thunbergii* in the latter. Possibly the responsible authors have defined these two species differently.

The illustrations are useful complements to the text and of high quality. Only in some cases, e.g. some drawings by S. ROSS-CRAIG in vol. 1, one gets the impression that the printing has not done full justice to the artist's originals. It would be useful always to have the collections cited, from which the drawings were made; this is not consistently done. Even distribution maps are sometimes included, viz. in the case of *Encephalartos*.

South Africa is botanically unique, not least in phytogeographical and horticultural respects. It needs not be further emphasized, that the publication of 'Flora of Southern Africa' is an event of the utmost importance.

BERTIL NORDENSTAM

BACKER, C. A. (†) & BAKHUIZEN VAN DEN BRINK, R. C., Jr.: F l o r a o f J a v a. Vol. 2. — Groningen (P. Noordhoff) 1965. 72+641 pp. Price D.fl. 77.50; 155 s.

The modern English version of the late Dr. BACKER's life-work on the flora of Java approaches its completion. Volume one appeared in 1963, the second volume was published in 1965, and the third and last volume is expected to appear in 1967.

Volume two commences with a general part (72 pp.), consisting of a phyto- geographical account of Java, by C. G. G. J. VAN STEENIS. The text is accompained by numerous vegetation photographs and two coloured maps of vegetation and climate.

Java is an extremely densely populated island, and there is today very little natural vegetation left, mainly restriced to the mountains and a few other areas. Thus the features of the original plant cover have to be largely reconstructed. A notable fact in the phytogeography of Java is the low degree of endemism, mainly explained by the geologically recent volcanic origin of the island. The number of indigenous spermatophytes is 4598, of aliens and naturalized species 413, and of cultivated plants 1523, which is a very high percentage (23.4 %).

The special part (641 pp.) treats the families 111. *Salicaceae* to 190. *Lamia- ceae*, whereby the dicots are finished. There are descriptions of families and genera and keys to genera and species. The species descriptions are included in the keys, which become very elaborate and rather time-consuming to consult. Latinization of important key characters could have been employed to facilitate the identification work. Nomenclatural types are not cited, and with one ex ception there are no illustrations to the special part of the flora.

All weeds and numerous planted or cultivated species are treated, which fact renders the flora very useful far outside the borders of Malesia.

BERTIL NORDENSTAM

WILLIS, J. C.: A Dictionary of the Flowering Plants and Ferns. — 7th edition, revised, by H. K. AIRY SHAW. Cambridge University Press 1966. xxii+1214+liii pp. Price £5 net.

'A manual and dictionary of the flowering plants and ferns' by J. C. WILLIS first appeared in 1897. Several later editions were published, the sixth and last in 1931 (subsequently reprinted several times). During the three and a half decades that have passed since the last edition such an enormous amount of information has accumulated that it would seem too wishful to think of an up-to-date version. Nevertheless, the seventh edition is now a gratefully acknowledged fact, and the result of many years' indefatigable work by Mr. H. K. AIRY SHAW at Kew.

To keep the practicable one-volume size of the dictionary it was judged necessary to introduce certain limitations in the original scope of the work. Thus entries regarding botanical terms, common names and economic products have been omitted. The result is a purely taxonomical dictionary with a complete coverage of generic names (from 1753) and family names (from 1789) and many other names of suprageneric taxa, altogether something like 40,000 entries. Especially the family entries contain a mass of useful and interesting facts. Mr. AIRY SHAW is himself a specialist on the family concept and in his search for a more natural classification has proposed several new families (see Kew Bulletin 18: 249 ff., 1965). The synopses of the ENGLER-PRANTL and BENTHAM-HOOKER systems are retained from the older editions at the end of the book. It would have been useful to have all families recognized by AIRY SHAW included in the key to the families or to have at least an index to family names.

The somewhat confused gross taxonomy of the *Pteridophyta* required special care, and for this group Prof. R. E. HOLTTUM is responsible. His classification recognises, generally speaking, COPELAND's genera and PICHI SERMOLLI's families.

The new 'Willis' is an in valuable reference work for anyone who seeks quick information on genera and higher taxa.

BERTIL NORDENSTAM

DE WIT, H. C. D.: Alverdens Planter. — (Dansk redaktion T. W. BÖCHER, V. M. MIKKELSEN & O. HØST). Fröplanter. I. 340 sid. (187 färgbilder, 233 svartvitbilder, 48 teckningar). 1965. II. 382 sid. (175 färgbilder, 283 svartvitbilder, 29 teckningar). 1966. Hassings Forlag. Pris Dkr. 150: — per band.

Den danska utgåvan av det holländska praktverket »De Wereld der Planten» föreligger nu komplett beträffande fanerogamerna, som behandlas i två band. Ett tredje band omfattande kryptogamerna beräknas utkomma under 1967. Sammanlagt kommer verket att omfatta cirka 1000 sidor med omkring 1400 illustrationer, varav ungefär 500 utgöres av fotografier i fyrfärgstryck.

De båda hittills utkomna volymerna ger en översikt av angiospermerna, varvid uppställningen i huvudsak följer TAKTHAJAN för dikotyledonerna och HUTCHINSON för monokotyledonerna. Ett urval av släkten och arter av allmänt intresse behandlas i en lättläst men ändå saklig och innehållsrik text. Illustrationerna är slösande rikliga och av överdådig kvalitet. Urvalet av bilder har gjorts med största omsorg. Ibland avslöjas oanade skönhetsvärden hos triviala eller annorledes välbekanta arter, och ibland visas exotiska märkvärdigheter i extrema närbilder. Många arter är fotograferade i sina naturliga miljöer, och då rör det sig ofta om stora rariteter eller svårtillgängliga biotoper. Några exempel ur högen: *Aloë pillansii* och *Pachypodium namaquanum* från Oranjeflodens nedre lopp, *Senecio brassicae* och jättelobelior från de ostafrikanska bergen, *Azorella-* och *Puya*-arter från Andernas högfjäll.

Den danska redaktionen har omsorgsfullt omarbetat och anpassat texten till en dansk läsekrets. Sålunda har många uppgifter om arters förekomst i Danmark och på Grönland infogats. Ett utförligt avsnitt om gräs och halvgräs är helt nyskrivet (med illustrationer från 'Knaur's Pflanzenreich in Farben'), vilket avsevärt förhöjer verkets värde gentemot originalet.

Obetydliga tryckfel förekommer här och var, men rena sakfel är sällsynta. Man kan resa invändningar mot t.ex. utbredningsuppgiften för *Zygophyllum* (N.Am.!) och uppgiften att fotot på sid. 486 föreställer *Myosotis palustris* (foderhårigheten!) och några liknande relativa bagateller.

Tilltalande typografi och förnämligt konsttryckpapper bidrager också till att man ger sig på nåd och onåd inför detta praktverk.

BERTIL NORDENSTAM

HYLANDER, NILS: N o r d i s k k ä r l v ä x t f l o r a II. — Almqvist & Wiksell, Stockholm 1966. 456 sid. Pris häft. 58 kr., inb. 70 kr.

Andra delen av HYLANDERS flora kom äntligen i början av år 1966. Den hade då länge varit mycket efterlängtad. Man hoppas nu livligt, att det fortsatta arbetet skall gå fortare, ty annars är risken stor, att den nu levande generationen botanister blott får se en torso. Med denna andra del har ung. ¹/₃ av hela verket fullbordats.

Bearbetningen omfattar återstoden av monokotyledonerna och av dikotyledonerna familjerna från och med hängeväxter till och med *Polygonaceae*. Den andra delen är — bortsett från omkr. 50 sidor tillägg till del I — praktiskt taget lika stor som den första, men antalet arter, som behandlas, är betydligt mindre än i den första. Detta sammanhänger bl.a. med de långa resonerande partierna, som förf. tagit med beträffande kritiska eller på annat sätt svåra eller intressanta taxa. Dessa partier är man tacksam för, eftersom de innehåller viktiga upplysningar hämtade ur förf:s rika erfarenhet.

Diskussionerna är skrivna i en för förf. karakteristisk — man skulle (måhända) kunna säga underfundig — stil, med (talrika) parenteser, tankstreck och kommatecken, vilket visserligen gör betydelsen (synnerligen) klar, men denna text blir (onekligen — ej så obetydligt) trögläst.

Jämfört med förf:s tidigare utgivna »Förteckningar» är ändringarna i de vetenskapliga namnen även i denna del talrika. Detta beror på »litteratur-

botanisternas» verksamhet, genom vilken gamla växtnamn »grävs fram». Detta är i hög grad beklagligt och utan tvivel skadligt för systematikens goda namn och rykte. Namnändringarna observeras naturligtvis mest, då de träffar vanliga arter eller sådana som ofta återkommer i växtgeografisk och ekologisk litteratur. En sådan namnändring har t.ex. träffat det ur *Orchis* utbrutna släktet *Dactylorchis*, som nu måste heta *Dactylorhiza*.

Inom just detta släkte har en omfattande revidering genomförts, så att ett relativt fåtal arter nu upptagas: *D. sambucina, D. incarnata, D. majalis, D. purpurella, D. Traunsteineri* och *D. maculata. D. incarnata* har i gengäld begåvats med 6 varieteter, bland dem *cruenta*, vilket synes väl grundat.

Något liknande har skett inom *Polygonum aviculare*-gruppen, där den större delen av materialet samlats under *P. aviculare* som storart med 2 underarter och åtskilliga varieteter. Detta komplex är emellertid, trots de talrika, ± välgenomförda försöken att dela upp det på olika sätt, ännu ej så noggrant penetrerat, att den nu framlagda lösningen kan sägas vara slutgiltig.

Det är självklart, att uppdelningen av arter i taxa av lägre rang blir i hög grad beroende på en floraförf:s egna intressen. Så framstår här HYLANDERS stora dendrologiska kunskaper och intressen inom släktena *Betula* och *Alnus*, där enl. rec:s mening ett alltför stort antal former tagits med, vilket tynger framställningen.

Som vanligt, då det gäller förf:s verk, är även detta arbete nästan fritt från korrekturfel. De få fel, som rec. sett och som ej påpekats av andra rec., är så obetydliga, att de ej förtjänar nämnas.

HYLANDERS flora innehåller ofantligt mycket av förf:s egna iakttagelser och bedömningar. Han fördröjer inte, när en art eller ett komplex är otillräckligt undersökt, varigenom uppslag till vidgad forskning lämnas. Detta kommer visserligen med all sannolikhet att medföra, att åtskilligt vid avgränsningen av de olika taxa i framtiden kommer att ändras, men då har floran fyllt sin uppgift som stimulans.

Blott en liten anmärkning av språklig natur återstår. Förf. använder — liksom nästan alla svenska botanister — beteckningen »habituellt» i betydelsen »till habitus». Enligt de källor, som rec. har tillgång till, betyder emellertid »habituellt» något sedvanligt, inrotat.

<div align="right">HENNING WEIMARCK</div>

HANS STUBBE: G e n e t i k u n d Z y t o l o g i e v o n *A n t i r r h i n u m* L. s e c t. *A n t i r r h i n u m.* — Veb. Gustav Fischer Verlag, Jena 1966. 421 sid. 196 textfig. och 7 färgplanscher, 112 tab. Pris 82 DM (Ost).

Professor STUBBE är chef för Institut für Kulturpflanzenforschung i Gatersleben samt för Institut für Genetik vid universitetet i Halle. Vidare är han president för Deutsche Akademie der Landwirtschaftswissenschaften. Då denne författare nu presenterar ett sammanfattande arbete om genetik och cytologi inom lejongapssläktet, är det ett livsverk, som framlägges i en samlad och översiktlig form. STUBBES första arbeten om *Antirrhinum* publicerades redan år 1930, och sedan dess har mer än 40 arbeten om detta släkte utgått från hans hand.

Den nu föreliggande boken utgör inte blott en sammanfattning av STUBBES egna undersökningar utan är också en detaljerad redogörelse för hela den vetenskapliga litteraturen om *Antirrhinum*. Utan tvekan kommer boken att bli ett standardverk inte bara för växtförädlare, som sysslar med släktet, utan för mutationsforskare över huvud taget.

I första kapitlet presenteras *Antirrhinum* ur taxonomisk och växtgeografisk synpunkt. Den aktuella sektionen har sitt utbredningsområde i västra delarna av Europas mediterranområde, där 29 taxa urskiljes. Många av dessa, främst inom subsektionerna *Kickxiella* och *Streptosepalum*, har geografiskt mycket begränsade utbredningsområden.

I andra och tredje kapitlen redogöres för de genetiska undersökningarna inom släktet. Främst fäster man sig vid de ingående undersökningarna över kopplingsfaktorer, som kunnat utredas i de 8 kromosomparen tack vare en massiv insats från många *Antirrhinum*-genetiker. Dessa analyser har lett fram till stor kunskap om nedärvningsförhållandena för en mängd egenskaper, bland vilka blomfärgernas genetiska bakgrund kanske tilldragit sig det största intresset.

Kapitel IV ägnas åt mutabiliteten hos materialet. Den spontana mutationsfrekvensen har beräknats av flera forskare, bl.a. STUBBE. Redan år 1919 började man genom radioaktiva preparat framställa mutanter av *Antirrhinum majus*. Sedan dess har såväl bestrålning som kemikalier använts som mutagena ämnen. För dessa försök lämnar STUBBE detaljerade redogörelser med analyser av resultaten liksom också över egna och medarbetares ingående undersökningar över hur fysiologiska faktorer påverkar mutationsfrekvensen.

I kapitel V finner man analyser över de mutationer av de mest skiftande slag, som författaren till stor del själv framställt experimentellt. Speciell uppmärksamhet ägnas bl.a. vissa gener, vilka oftare än andra muterar i såväl generativ som somatisk vävnad. Ofta rör det sig om recessiva mutationer, som återgår till den normala, dominanta faktorstypen. Ett speciellt avsnitt ägnas också sådana mutationer, som uppvisar påtagliga variationer i sin manifestationsförmåga, och orsaken till denna variation diskuteras.

Ingående analys och diskussion av iakttagna heterosiseffekter i korsningar mellan olika muterade stammar presenteras. De morfologiska och utvecklingshistoriska undersökningarna hos en serie mutationer ägnas också ett separat avsnitt liksom kromosommutationer, främst trisomer och polyploider.

Sammanfattningsvis konstaterar författaren, att antalet verkligt nya mutationer minskade efter hand som mutationsförsöken pågick. Allt oftare hade samma mutation påträffats redan tidigare. Vidare konstaterar han, att alla iakttagna mutationer har modifikativt betingade motsvrigheter i materialet. — Ett faktum nog så väsentligt att ha i minne vid bedömning av förekommande naturlig variation även i andra material. Vidare visar författaren, att morfologiskt identiska mutationer kan uppkomma ur flera olika muterade faktorer. 19 fall av smalbladighet orsakad av mutationer betingades sålunda av icke mindre än 17 olika mutationstyper. Det förekommer således betydligt fler mutationer än muterade egenskaper.

Effekten av olika typer av trisomer diskuteras och illustreras liksom också haploidi och polyploidi. Ett särskilt avsnitt ägnar författaren åt icke kromosombunden nedärvning samt fysiologiska undersökningar av mutanter.

OPERA BOTANICA

is edited by the Lund Botanical Society in co-operation with the Institute of Systematic Botany, University of Lund. It consists of larger treatises issued at indefinite times. After vol. 12 the series is published in separate numbers, each with an individual price. The reduced prices for members of the Lund Botanical Society are indicated.

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