Drawings of Scandinavian Plants 69–74

Juncus L.

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69. **Juncus acutiflorus** EHRHARDT ex HOFFMANN 1791

Perennial, with a thick, creeping, sparsely branching rhizome with usually 0.5—1.5 cm long internodes. Stems 30—110 cm high, basally compressed, apically terete, with 2—3 basal sheaths, rarely one subbasal leaf and 2—4 cauline leaves. Leaves 5—50 cm long, unitubulose, thin-walled, perfectly and usually manifestly septate, auricles short, obtuse, firm. Inflorescence of (10—)50—80(—250) heads; heads (3—)5—8(—20)-flowered. Tepals 2—2.7 mm, inner ones longer, ovate to narrowly ovate, apiculate to cuspidate, their tips, especially those of the inner ones, usually reflexed, in their apical parts usually chestnut-coloured, basally green to light brown, with narrow scarious margins. Stamens 6, 1/2—2/3 as long as the tepals; anthers 0.8—1 mm, 1.5—2 times as long as the filaments. Style 0.5—1 mm, stigmata 1—1.5 mm. Capsule 2—3 mm, exceeding the tepals, trigono-ovoidal to narrowly pyramidal, tapering or rarely more abruptly contracted into a 0.5—1 mm long rostrum, usually light brown. Seeds c. 0.5 mm, ovoidal to ellipsoidal, with c. 25 longitudinal striae and weaker transverse ones. 2n=40.

J. acutiflorus is a plant of fens and moist meadows. It occurs mainly in C., W. and SW. Europe and NW. Africa, with scattered localities eastwards to Kurdistan. In Scandinavia, it is comparatively common only in southernmost Jylland, but has a few localities in Falster, middle and N. Jylland and southernmost Norway. All old reports from Sweden were based on mislabelled and misdetermined material.

70. **Juncus anceps** LAHARPE 1827

Perennial, with a creeping, sparsely branching rhizome of varying internode length. Stems 20—60 cm, usually rigid, with 0—2 basal sheaths and 3—5 cauline leaves. Leaves 5—25 cm long, unitubulose, perfectly septate, basally with a ± conspicuous dorsal furrow and sometimes with a ventral ridge, auricles firm, obtuse, 0.5—1.5 mm. Inflorescence usually consisting of 50—80 heads, lax or crowded, often divided into two discrete parts, primary branches ± erect, secondary ones erecto-patent; heads (2—)3—4(—8)-flowered. Tepals 2—2.7 mm, equal in length or almost so, ovate to oblong,

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with broad scarious margins apically, usually dark brown to chestnut-coloured, only in shade light brown to greenish, outer ones slightly boat-shaped, acutish, with a short mucro, inner ones broadly obtuse, the scarious apical part often cucullate at first. Stamens 6, about 2/3 as long as the tepals; anthers 0.7—1 mm, equalling or slightly longer than the filaments. Style 0.5—0.8 mm; stigmata 1—1.5 mm. Capsule 2.5—3.2 mm, slightly exceeding the tepals, ± broadly trigono-ovoidal, tapering or in inland forms almost blunt, with a usually 0.3—0.5 mm long mucro, usually dark brown to chestnut-coloured. Seeds c. 0.5 mm, narrowly ovoidal, reticulate due to c. 25 longitudinal and weaker transverse striae. 2n=40.

Danish forms with an extremely erect and crowded inflorescence and unusually dark flowers were described as *J. atricapillus* DREJ., and were treated, e.g. by HYLANDER (1953), as *J. anceps* var. *atricapillus* (DREJ.) BUCH. There are, however, many intermediates in different areas, and some Danish specimens are exactly like the southern forms of the species.

J. anceps is usually found on maritime sand, but also in open places in heaths and fens, and may even penetrate into denser vegetation in fens. It occurs in the coastal areas of W. and S. Europe and NW. Africa. In Scandinavia it is fairly common along the west coast of Jylland and in northern Jylland, and has also been recorded from one locality on northern Sjælland.

J. anceps also occurred in some fens in SW. Skåne, Sweden, but these localities have been destroyed and probably the species now occurs in only one of them. In these, as in other inland localities, it is no longer as morphologically characteristic as in the coastal localities. The variation is

Fig. 69. *Juncus acutiflorus* EHRH. ex HOFFM. — A: Habit, ×0.5. (The stem drawn is unusually short). — B: Tepals and stamens, ×8. — C: Flower with ripe capsule, ×8. — D: Seed, ×30. — E: Part of leaf transect, ×30. (Leaf unitubulose).

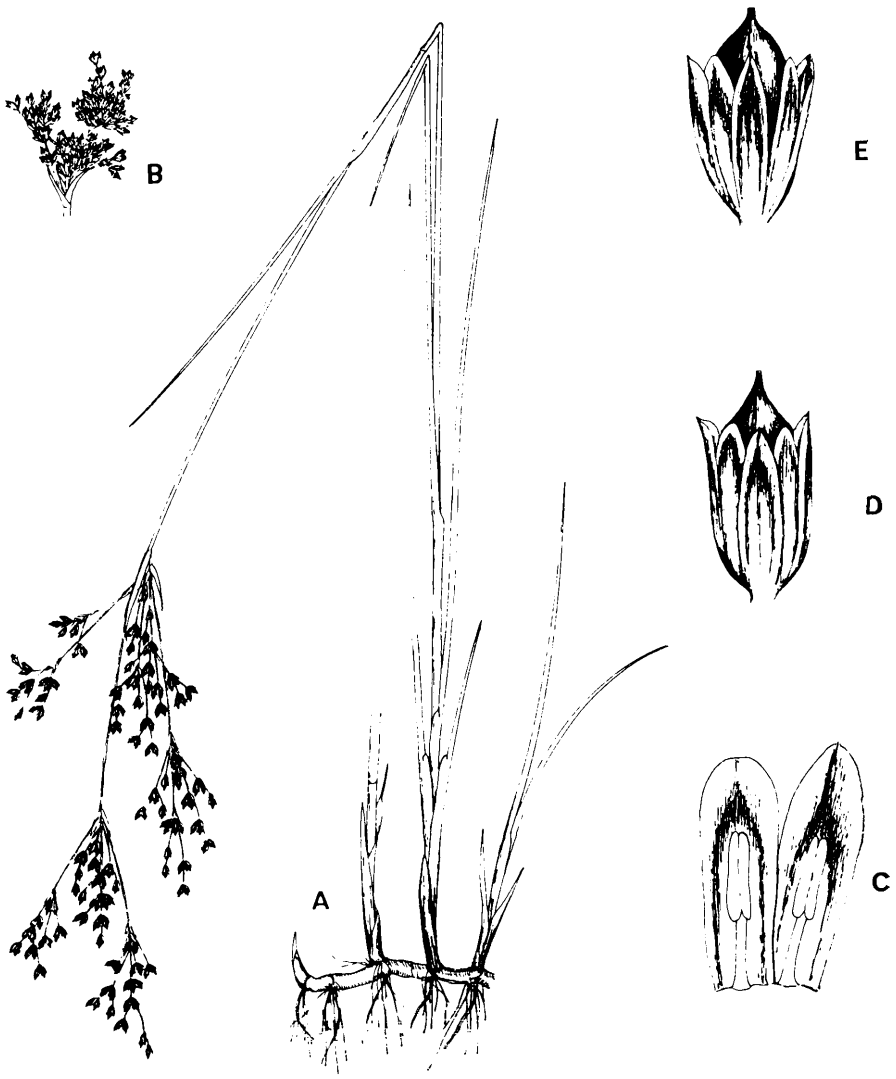

Fig. 70. *Juncus anceps* LAHARPE. — A: Habit, ×0.5. — B: Condensed inflorescence, ×0.5. — C: Tepals and stamens, ×12. — D and E: Flowers with ripe capsules, ×10. — E: inland form from S. Sweden.

in the direction of *J. alpinus* VILL., but there are no proofs as to its real cause. *J. anceps* has also been recorded as a casual in Finland.

Juncus alpinus VILLARS 1787

Perennial, with a creeping rhizome. Stems 5—60 cm, usually weak, with 0—1 (—2) basal sheaths and (2—)3(—5) cauline leaves. Leaves unitubulose, perfectly septate, basally usually with a ± conspicuous dorsal furrow, auricles obtuse, 0.5—1.5 mm. Inflorescence very variable in form and size. Tepals 2—3(—3.8) mm, equal or almost so, inner ones always broadly obtuse, outer ones obtuse or acut-

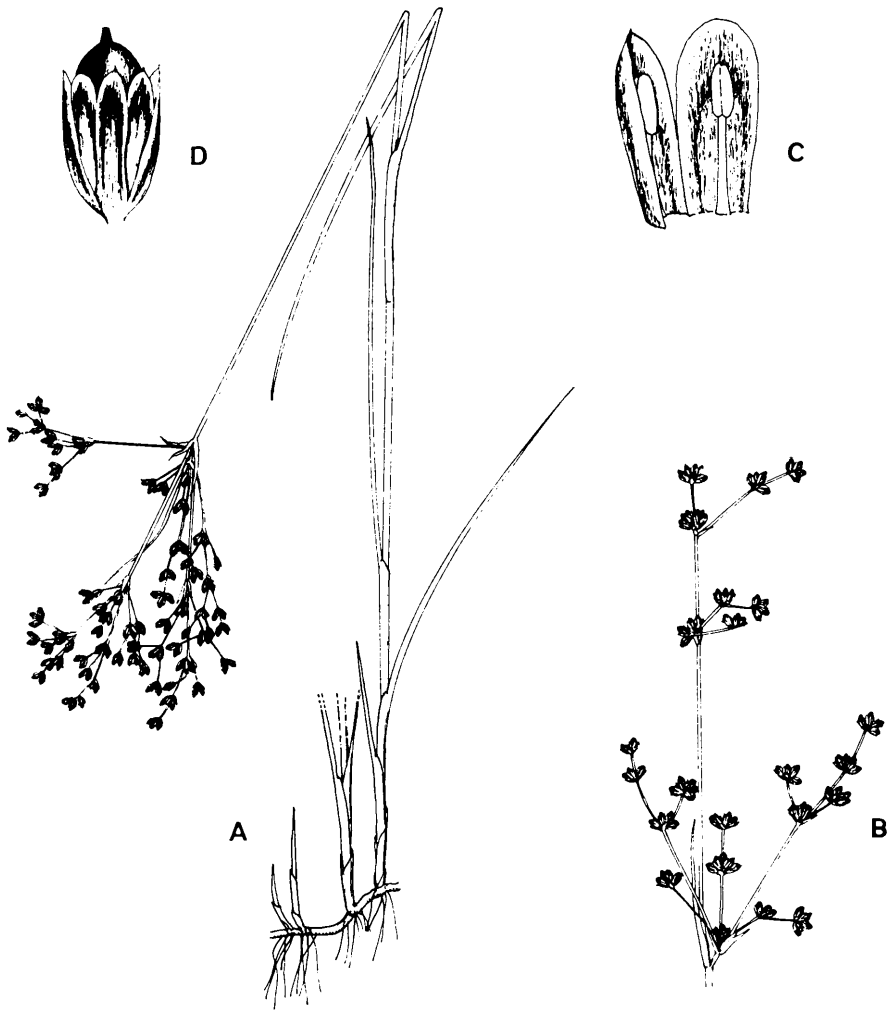

Fig. 71. *Juncus alpinus* VILL. ssp. *alpinus*. — A: Habit, ×0.5. — B: Inflorescence of form uncommon in Scandinavia, ×0.5. — C: Tepals and stamens, ×12. — D: Flower with ripe capsule, ×10.

ish and often mucronate. Stamens 6, 1/2—2/3 as long as the tepals; anthers 0.4—0.7 mm, 1/2—2/3 as long as the filaments. Style c. 0.5 mm, stigmata 1—1.5 mm. Capsule equal to or longer than the tepals, rather variable in form and colour, but always obtuse with a short mucro. Seeds 0.55—0.6 mm, ovoidal, sometimes slightly oblique, reticulate due to c. 30 longitudinal and many weaker transverse striae. 2n=40 in all forms checked by me.

J. alpinus has a wide circumpolar distribution and shows considerable geographical as well as local variation. I found it possible to accept 3 geographical subspecies among the Scandinavian material, the subarctic—subalpine ssp. *alpestris,* the N. European and N. American ssp. *nodulosus*

Fig. 72. *Juncus alpinus* VILL. ssp. *nodulosus* (WAHLENB.) LINDM. — A: Habit, ×0.5. — B and C: Details of inflorescences, ×1.5. — D: Tepals and stamens, ×12. — E: Flower with ripe capsule, ×10.

and the predominantly S. and middle European ssp. *alpinus*. Intermediates are common and often locally abundant, and they have often been described as separate taxa of different ranks. Thus certain specimens intermediate between ssp. *alpestris* and ssp. *nodulosus* have been treated as ssp. *Marshallii* (PUGSL.) L. & L. In the total area of the species further subspecies may possibly be accepted, and the Asiatic forms in particular need further study.

71. **Juncus alpinus** VILL. ssp. **alpinus**

(Syn. *J. fuscoater* SCHREBER in SCHWEIGGER & KÖRTE 1811)

Stems of varying height but usually 30—60 cm. Inflorescence rather wide with erecto-patent branches, heads usually 25—60, usually few-flowered in the Scandinavian forms, pedicellate flowers few or lacking. Flowers small, dark brown to chestnut-coloured. Tepals usually 2—

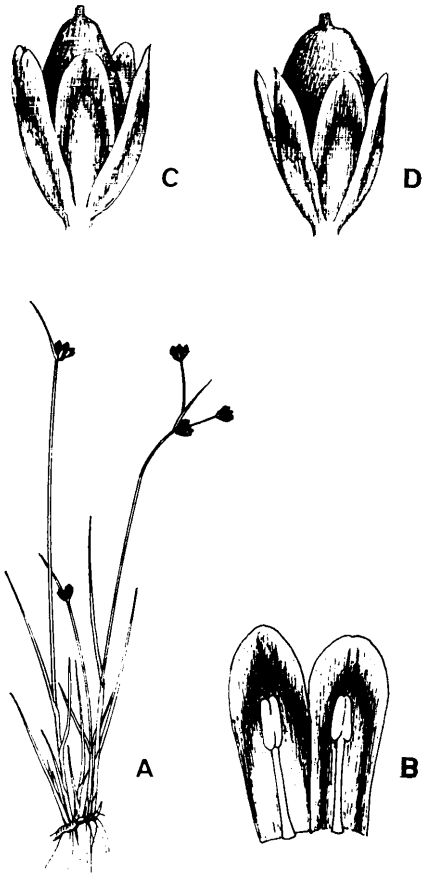

Fig. 73. *Juncus alpinus* VILL. ssp. *alpestris* (HARTM.) L. & L. — A: Habit, ×0.5. — B: Tepals and stamens, ×12. — C and D: Flowers with ripe capsules. ×10.

2.5 mm, all broadly obtuse, the outer ones often mucronate. Capsule broad, equal to or slightly longer than the tepals.

Ssp. *alpinus* occurs in the mountains of Caucasus, Anatolia, Balkan, Italy and Spain, and is fairly common in the Alps and in the lowlands northwards to W. Russia and middle Scandinavia. In Scandinavia it is known from Sjælland, S. Sweden up to Västergötland and Östergötland, the Baltic Islands and from scattered localities in Finland up to about 65°N. Intermediates to ssp. *nodulosus* are comparatively rare in Sweden and Denmark, probably because of the different ecological requirements of their representatives in this area. In Finland, on the other hand, such intermediates seem to be fairly common.

Ssp. *alpinus* grows in fens and on bare wet soil from sea level in the northern part of its range to 2500 m in the mountains. It is more strictly calciphilous in SW. Scandinavia than in other areas.

72. **Juncus alpinus** VILL. ssp. **nodulosus** (WAHLENBERG) LINDMAN 1918

(Syn. *J. alpinus* VILL. var. *rariflorus* (HARTMAN) HARTMAN 1858)

Length of stem variable, usually 20—40 cm. Inflorescence usually narrow, with rather long, erect primary branches and short secondary ones. Heads usually 5—25, few- to many-flowered, often 5—10-flowered, some pedicellate flowers usually present. Flowers usually greenish to light brown, rarely darker brown. Tepals usually 2.2—3 mm, outer ones acutish to obtuse, usually mucronate. Capsule usually considerably exceeding the tepals, almost cylindrical in form.

Ssp. *nodulosus* occurs outside Scandinavia in W. and N. Russia and in northern temperate N. America. Similar Asiatic plants need further study. In Denmark it is found only in the northern part, in Sweden, Norway and Finland throughout the area, though it is rare in the southern limestone areas and in the alpine and arctic regions.

In the northern part of its area, ssp. *nodulosus* occurs in very different types

Fig. 74. *Juncus articulatus* L. — A—E: Habit and inflorescences, ×0.5. — A: Form common on open shores. — B and D: Habit and inflorescence forms common in different habitats. — C: Sand ecotype. — E: Monstrosity caused by *Livia juncorum*. — F: Tepals and stamens, ×12. — G and H: Flowers with ripe capsules, ×10.


F
G
H
D
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of vegetation on wet soil. In the southern part, however, it is mainly found on open sand or gravel, such as on the shores of oligotrophic lakes.

73. **Juncus alpinus** VILL. ssp. **alpestris** (HARTMAN) LÖVE & LÖVE 1948

Lowgrown, usually 10—20 cm high, rhizome often shortnoded. Inflorescence of 1—7 heads, with short branches, heads usually 6—8-flowered, pedicellate flowers few or usually lacking. Flowers dark brown to chestnut-coloured. Tepals 2.0—3(—3.8) mm, all broadly obtuse, outer ones mucronate. Capsule slightly to considerably exceeding the tepals, usually slightly tapering in its middle part but abruptly contracted apically, rarely more acutish.

Ssp. *alpestris* has a circum-arctic distribution, but is also found in the subalpine belt of the Scandinavian mountains. Forms more or less transitional to ssp. *nodulosus* occur along river valleys down to the lowlands. Similar forms are also found in Scotland. The distribution of the subspecies in Scandinavia and in general calls for further study.

74. **Juncus articulatus** L. 1753

Perennial, caespitose or with a creeping rhizome of varying internode length, or rarely with subterranean stems rooting from the nodes. Stems 5—60 cm, or rarely floating and then up to 1 m, erect or in caespitose forms ascending, with 0—2 basal sheaths and 3—6 cauline leaves. Leaves unitubulose, perfectly septate, quite terete or somewhat laterally compressed. Inflorescence usually wide, with (1—)5—20(—80) heads; heads 5—15(—30)-flowered. Tepals 2.5—3.5 mm, equal or outer ones slightly longer, varying in colour from green with darker tips to dark brown, chestnut-coloured or reddish-brown, ovate or rarely lanceolate, outer ones boat-shaped, acute or rarely obtuse with a mucro, inner ones acute to obtuse, often mucronate. Stamens 6, 1/2—3/4 as long as the tepals; anthers 0.7—1 mm, equal to or slightly longer than the filaments. Style c. 0.5 mm, stigmata c. 1.5 mm. Capsule 2.5—3.5(—4) mm, usually exceeding the tepals, trigono-ovoidal or rarely ellipsoidal, acute or rarely obtuse, mucronate, straw-coloured or light brown to chestnut-coloured, often greenish when unripe. Seeds 0.5—0.6 mm, ovoidal, reticulate due to c. 25 longitudinal and many ± conspicuous transverse striae. $2n=80$.

J. articulatus is the most widespread species of subgenus *Septati*. It is probably indigenous to Europe, Asia, N. Africa and temperate N. America only. It is, however, also found in S. Africa, Australia and New Zealand, where it has probably been introduced by man. In Scandinavia it is very common in the southern lowlands up to about 61°N. with scattered localities up to 65°N. Along the Norwegian W. coast it is common up to c. 67°N. and occurs scattered up to 70°N. It grows in all sorts of ± wet environments and has formed many conspicuous ecotypes.

J. articulatus is extremely variable, but I find it impossible to sort out any regional races. The varieties described seem to rely on mere morphological appearences, often occurring together within the same natural breeding populations.

LITERATURE CITED

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Chromosome Studies in the Flora of Macaronesia

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ABSTRACT

BRAMWELL, D., HUMPHRIES, C. J., MURRAY, B. G. & OWENS, S. J. 1972. Chromosome studies in the flora of Macaronesia. — Bot. Notiser 125: 139—152.

Chromosome numbers have been determined for 51 species of flowering plants from Macaronesia. Of these, 32 species were hitherto unknown cytologically. The percentage of polyploidy in the Canarian flora has been calculated at 24.4 %. The system of classification of endemic species, introduced by FAVARGER & CONTANDRIOPOULOS (1961) is applied to the Canarian flora.

INTRODUCTION

Recent studies on the cytology of the Macaronesian flora (LARSEN 1960, 1962, 1963; BORGEN 1969, 1970; BRAMWELL et al. 1971) emphasize the low degree of polyploidy found in the endemic representatives.

The present contribution covers 51 species from the Canaries, Madeira and the Cape Verde Islands; of these 32 have not previously been studied cytologically. BORGEN (1969) reports 26.5 % polyploidy in the Canarian flora and with inclusion of our data this is further reduced to 24.4 %.

An attempt is made to apply to the Canarian flora the system of classification of endemic species (based on their level of polyploidy and that of their corresponding taxa) introduced by FAVARGER & CONTANDRIOPOULOS (1961). Most Canarian endemics are considered to be palaeoendemics or old schizoendemics and this supports the view expressed by BORGEN (1969), based on the level of polyploidy, that the Canarian endemic flora is an ancient one comprising a number of relict genera and species.

MATERIALS AND METHODS

Chromosome counts were made from material collected by D. BRAMWELL (from October 1968—August 1969) and C. J. HUMPHRIES and D. BRAMWELL (spring 1971) in the Canary Islands, and from spontaneous seed supplied by Dr. E. R. SVENTENIUS (Cape Verde Islands plants), the Jardin de Aclimatacion de Plantas de la Orotava and the Jardin Canario "Viera y Clavijo" (Tafira, Gran Canaria). Voucher specimens are preserved in the Herbarium of the University of Reading and Orotava Herbarium. Somatic counts were made from root-tips which were pretreated in a saturated solution of paradichlorobenzene for two hours, fixed in acetic alcohol (1 : 3), stained in basic fuchsin and squashed in acetic orcein. Meiosis was studied in pollen mother cells from material fixed in acetic alcohol and squashed in acetic orcein. The drawings were made with the aid of a Zeiss camera lucida.

RESULTS

Monocotyledonae

LILIACEAE

Scilla latifolia WILLD. — 2n=28 (Fig. 3 L).

Seed collection: Tenerife, Punta de Teno. 5-1969 D. BRAMWELL.

BORGEN (1970) reports the same somatic number in plants originating from Lanzarote. This is in contrast to GIMÉNEZ-MARTÍN (1959) who recorded 2n=40 from material of unspecified origin.

Urginea hesperia WEBB & BERTH. — 2n=28 (Fig. 4 A).

Seed collection: Tenerife, Punta de Teno. 3-1969 D. BRAMWELL.

This is the first report of the chromosome number of this endemic species. Somatic numbers of 2n=12, 20, 30, 40 and 60 are variously reported from the closely related widespread Mediterranean species *U. maritima* (L.) BAKER which is also found in the Canaries (2n=40, LARSEN 1969).

Dracaena draco L. — 2n=40 (Fig. 4 B).

Seed collection: Cape Verde Islands, Sant Antão. 3-1970 E. R. SVENTENIUS.

This count confirms the report by BORGEN (1970) from Canary Islands material of the same species. The Cape Verde Islands populations were previously cytologically uninvestigated.

Dicotyledonae

ASCLEPIADACEAE

Calotropis procera R. BR. — 2n=26 (Fig. 1 A).

Seed collection: Cape Verde Islands, Ihla da Sal. 3-1970 E. R. SVENTENIUS.

This species is a common subtropical weed and a chromosome count of 2n=22 has previously been reported by MIÈGE (1962). CHEVALIER (1935) refers the Sal populations of this species to var. *insularis* A. CHEV.

Ceropegia fusca BOLLE — 2n=22 (Fig. 1 C).

Seed collection: Tenerife, Montana Roja nr. Medano. 4-1971 BRAMWELL & HUMPHRIES.

BORGEN (1969) reports 2n=44 from plants of this species from Gran Canaria. Some morphological differences also exist between the populations from the two islands and it may be possible to recognize them as distinct subspecies when further investigations are completed.

Ceropegia hians SVENT. — 2n=22 (Fig. 1 B).

Seed collection: La Palma, coastal region below Fuencaliente. 6-1969 D. BRAMWELL.

This species, found only on the island of La Palma, was previously unknown cytologically.

BORAGINACEAE

Echium sventenii BRAMWELL[1] — n=8 (Fig. 4 D).

Bud collection: Gran Canaria Tafira Botanic Garden from specimens transplanted

[1] *Echium sventenii* BRAMWELL, sp. nov.
Ex affinitate *E. virescentis* DC. sed habitu altiore, ramosissimo; foliis linearibus vel lineari—lanceolatis, dense hirsutis, argenteis, margine revolutis, corolla brevi, dilute subrosea, subquadrilobata, lobis duobus dorsalibus conjunctis apice excepto, differt.
Holotypus: "Ex insula Tenerife, regione austro-occidentali in convalle dicta "Barranco Seco" prope oppidum Adexe versus 350 m. supra mare", 1.6. 1969, D. BRAMWELL 1718, in Herb. Univ. Radingensis (RNG) conservatus.

Fig. 1. Mitotic chromosomes of A: *Calotropis procera,* B: *Ceropegia hians,* C: *C. fusca,* D: *Messerschmidia fruticosa,* E: *Silene nocteolens,* F: *Centaurea canariensis* var. *subexpinnata,* G: *C. junoniana,* H: *C. duranii,* I: *Heywoodiella oligocephala,* J: *Senecio tussilaginis,* K: *Sonchus abbreviatus,* L: *S. bornmülleri,* M: *S. gummifer,* N: *Odontospermum stenophyllum,* O: *Convolvulus lopez-socasi.* — Scale 10 μ.

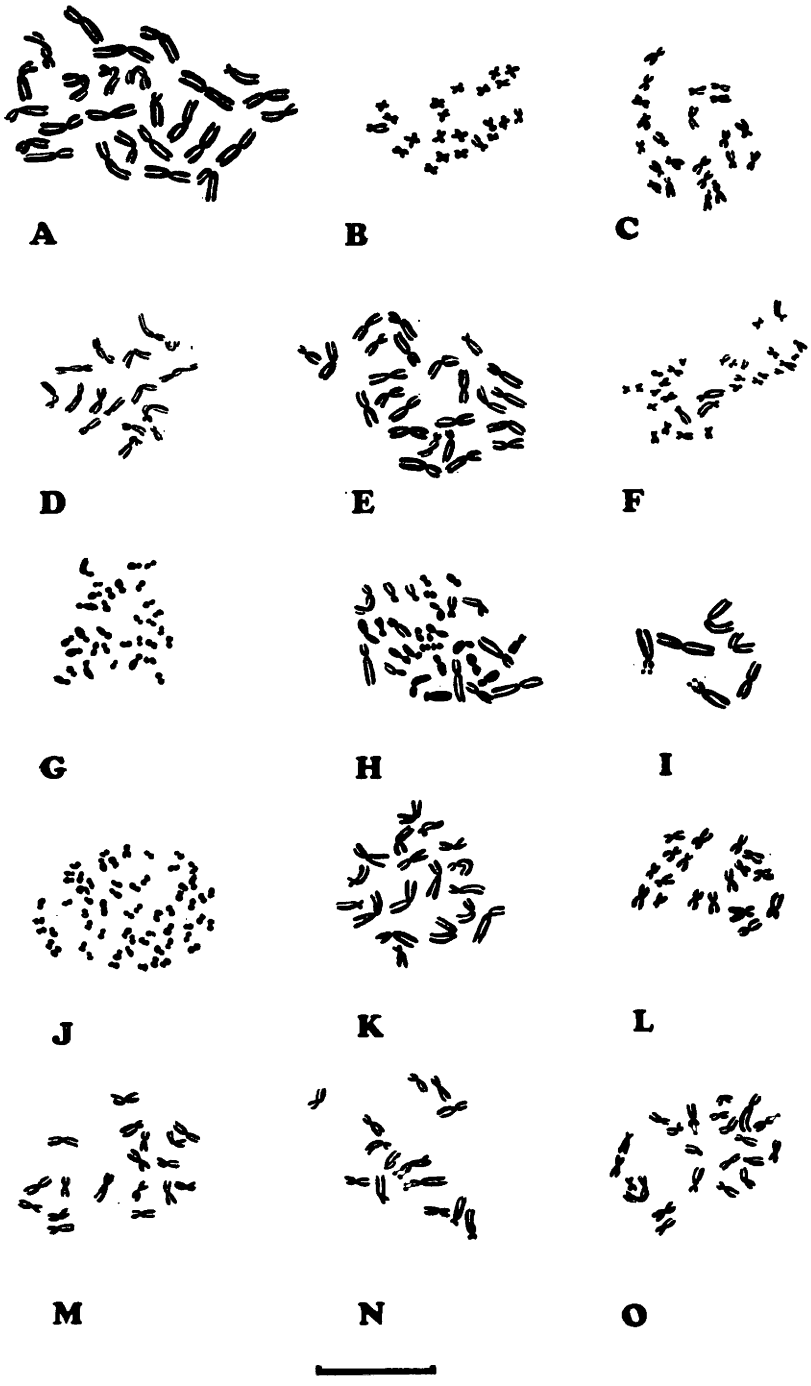

Fig. 1.

from Valle Seco de Adeje, Tenerife. 3-1971 BRAMWELL & HUMPHRIES.

This recently discovered endemic species is known from a single locality in the south of Tenerife and this is the first report of its chromosome number.

Echium triste SVENT. subsp. *nivariense* SVENT. — n=8 (Fig. 4 E).

Bud collection: Tenerife, Barranco de las Manchitas, Adeje. 4-1971 BRAMWELL & HUMPHRIES.

This rare endemic species occurs on Tenerife, Gomera and Gran Canaria. This count which is the first for the species refers to the biennial Tenerife subspecies.

Echium webbii COINCY — n=8 (Fig. 4 F).

Bud collection: La Palma, Los Tiles above San Andrés y Sauces. 4-1971 BRAMWELL & HUMPHRIES.

E. webbii is confined to the island of La Palma where it is locally frequent in pine and laurel forests. It had not previously been studied cytologically.

Messerschmidia fruticosa L. — 2n=16 (Fig. 1 D).

Spontaneous seed received from the Orotava Botanic Garden, originating from Tenerife, Teno.

This species is known from all the islands of the Canaries group. The present report refers to subsp. *fruticosa*. LARSEN (1960) reports 2n=16 from material of subsp. *angustifolia* from Tenerife.

CARYOPHYLLACEAE

Silene nocteolens WEBB — 2n=24 (Fig. 1 E).

Seed collection: Tenerife: La Fortaleza, Las Cañadas. 7-1969 D. BRAMWELL.

LARSEN (1960) records the same somatic chromosome number from this rare subalpine species.

COMPOSITAE

Centaurea canariensis WILLD. var. *subexpinnata* BURCHD. — 2n=30 (Fig. 1 F).

Seed collection: Tenerife, Punta de Teno. 6-1969 D. BRAMWELL.

The same number is reported by LARSEN (1960) from material collected at the nearby locality of Buenavista.

Centaurea duranii BURCHD. — 2n=32 (Fig. 1 H).

Spontaneous seed received from the Orotava Botanic Garden originating from Hierro, El Golfo.

This species is a very rare endemic of the island of Hierro where it is found only on coastal cliffs at El Golfo. The chromosome number has not been previously reported.

Centaurea junoniana SVENT. — 2n=32 (Fig. 1 G).

Seed collection: La Palma, Roque de Teneguia. 4-1971 BRAMWELL & HUMPHRIES.

This La Palma endemic is restricted to a single locality where it is extremely rare. The somatic chromosome number 2n=32 has been reported for several other species of section *Cheirolophus* (BRAMWELL et al. 1971). *C. junoniana* was previously uninvestigated cytologically.

Heywoodiella oligocephala SVENT. & BRAMWELL — 2n=6 (Fig. 1 I).

Root tips from living plants collected from the north coast of Tenerife. 4-1971 BRAMWELL & HUMPHRIES.

The genus *Heywoodiella* is a recently discovered endemic of the Canary Island of Tenerife (SVENTENIUS & BRAMWELL 1971) and its chromosome number is reported for the first time.

Senecio tussilaginis LESS. — 2n=60 (Fig. 1 J).

Seed collection: Tenerife, Cuesta de Bajamar. 4-1969 D. BRAMWELL.

This species is common on the north coast of Tenerife and it has also been re-

ported from Gran Canaria. The same chromosome number, 2n=60, was recorded by LARSEN (1960) and BORGEN (1969). It seems to be common throughout the Macaronesian section *Pericallis*.

Sonchus abbreviatus LINK — 2n=18 (Fig. 1 K).

Seed collection: Tenerife, El Bailadero de San Andres. 5-1969 D. BRAMWELL.

S. abbreviatus LINK was united by BOULOS (1967) with *S. congestus* WILLD. but it is probably best considered as a forest vicariant of that species as the morphological distinctions between the two (leaf-shape and inflorescence characters) are supported by phytochemical evidence (BRAMWELL & DAKSHINI 1971). The chromosome number has not been previously reported.

Sonchus bornmülleri PITARD — 2n=18 (Fig. 1 L).

Seed collected in the Tafira Botanic Garden, Gran Canaria, originating from La Palma.

A rare endemic species, *S. bornmülleri* is found only on coastal cliffs in the north of La Palma. This is the first report of its chromosome number.

Sonchus gummifer LINK — 2n=18 (Fig. 1 M).

Seed collection: Tenerife, Ladera de Guimar. 7-1969 D. BRAMWELL.

S. gummifer is confined to cliffs in the south of Tenerife where it is locally abundant. It has not been previously studied cytologically.

Odontospermum stenophyllum (LINK) SCH. BIP. — 2n=14 (Fig. 1 N).

Seed collection: Gran Canaria, Temisas. 3-1971 BRAMWELL & HUMPHRIES.

This report confirms a previous count of the chromosome number of this Gran Canarian endemic by BORGEN (1970).

CONVOLVULACEAE

Convolvulus lopez-socasi SVENT. — 2n=22 (Fig. 1 O).

Seed collection: Lanzarote, Famara. 4-1969 D. BRAMWELL.

SA'AD (1967) includes this species in *C. canariensis* L. It is, however, very distinct morphologically and in habitat (MENDOZER-HEUER 1971) and the somatic chromosome number, 2n=22, differs from that found by BORGEN (1969) for *C. canariensis* (2n=24).

CRUCIFERAE

Crambe arborea WEBB ex CHRIST — 2n=30 (Fig. 2 A).

Seed collection: Tenerife, Ladera de Guimar. 8-1969 D. BRAMWELL.

C. arborea is a very rare endemic species of section *Dendrocrambe* found only at Guimar on the south coast of Tenerife. BORGEN (1970) reports the same somatic number from material received from the Orotava Botanic Garden.

Parolinia ornata WEBB — 2n=22 (Fig. 2 C).

Seed collection: Gran Canaria, Barranco de Arguiniguin. 3-1969 D. BRAMWELL.

A rather confused report of the chromosome number of a *Parolinia* species is given by BORGEN (1969). From the locality given BORGEN's material was probably the Gomeran endemic *P. schizogynoides* SVENT. and our count therefore appears to be the first for *P. ornata*.

Parolinia intermedia SVENT. & BRAMWELL — 2n=22 (Fig. 2 B).

Seed collection: Tenerife, Punta de Teno. 4-1969 D. BRAMWELL.

This recently discovered species (BRAMWELL 1970) is endemic to Tenerife and its chromosome number is reported for the first time.

Parolinia schizogynoides SVENT. — 2n=22 (Fig. 2 D).

Seed collection: La Gomera, Barranco de Argaga. 6-1969 D. BRAMWELL.

P. schizogynoides is found only in the south-west of Gomera and this is the first authentic report of its chromosome number.

EUPHORBIACEAE

Euphorbia aphylla BROUSS. — 2n=20 (Fig. 2 E).

Seed collection: Tenerife, Punta de Teno. 7-1969 D. BRAMWELL.

E. aphylla is a halophytic species found on the north coasts of Tenerife, Gomera and Gran Canaria. The same somatic number was given by MICHAELIS (1964).

Euphorbia bourgeauana GAY — 2n=20 (Fig. 2 F).

Seed collection: Tenerife, Buenavista. 4-1969 D. BRAMWELL.

This endemic shrub of section *Pachycladae* is known from a few localities on Tenerife. Its chromosome number was previously unreported.

Euphorbia tuckeyana STEUDEL — 2n=20 (Fig. 2 G).

Seed collection: Cape Verde Islands, Sant Antão. 3-1970 E. R. SVENTENIUS.

This species is endemic to the Cape Verde Islands. It has the same chromosome number (2n=20) as the Canarian species of section *Pachycladae* reported above and by LINDER & LAMBERT (1965), PERRY (1943) and MICHAELIS (1964). The chromosome number of *E. tuckeyana* was previously unknown.

LABIATAE

Sideritis cabrerae CEB. & ORT. — 2n=44 (Fig. 2 H).

Seed collection: La Gomera, Barranco de Cabrito. Received from Orotava Botanical Garden.

Chromosome numbers for three out of the eighteen Canarian *Sideritis* species are now known. *S. gomerae* (2n=16, BRAMWELL et al. 1971) and *S. cabrerae* (2n=44) are both members of the Mediterranean section *Empedoclea* whereas *S. dendrochahorra* BOLLE var. *soluta* (WEBB) SVENT. (*Leucophae soluta* WEBB, *Sideritis soluta* (WEBB) CLOS) with 2n=36 (LARSEN 1960) is a member of section *Leucophae* which is endemic to Macaronesia.

The chromosome number of *S. cabrerae* was previously unreported.

LEGUMINOSAE

Anagyris latifolia BROUSS. — 2n=18 (Fig. 2 I).

Seed collection: Tenerife, below Guia de Isora. 6-1969 D. BRAMWELL.

LARSEN (1960) reports the same somatic number from Botanical Garden material of this species which is found only on the islands of Gran Canaria and Tenerife.

Dorycnium broussonetii (CHOISY) WEBB & BERTH. — 2n=14 (Fig. 2 J).

Seed collected in the Tafira Botanical Garden originating from Tenerife, Masca.

This rare species is endemic to Tenerife. Its chromosome number was previously unknown.

Dorycnium spectabile (CHOISY) WEBB & BERTH. — 2n=14 (Fig. 2 K).

Seed collection: Tenerife, Montañas de Teno. 5-1969 D. BRAMWELL.

Fig. 2. Mitotic chromosomes of A: *Crambe arborea,* B: *Parolinia intermedia,* C: *P. ornata,* D: *P. schizogynoides,* E: *Euphorbia aphylla,* F: *E. bourgeauana,* G: *E. tuckeyana,* H: *Sideritis cabrerae,* I: *Anagyris latifolia,* J: *Dorycnium broussonetii,* K: *D. spectabile,* L: *Lotus arenarius,* M: *L. hillebrandii,* N: *Vicia cirrhosa,* O: *Limonium braunii.* — Scale 10 µ.

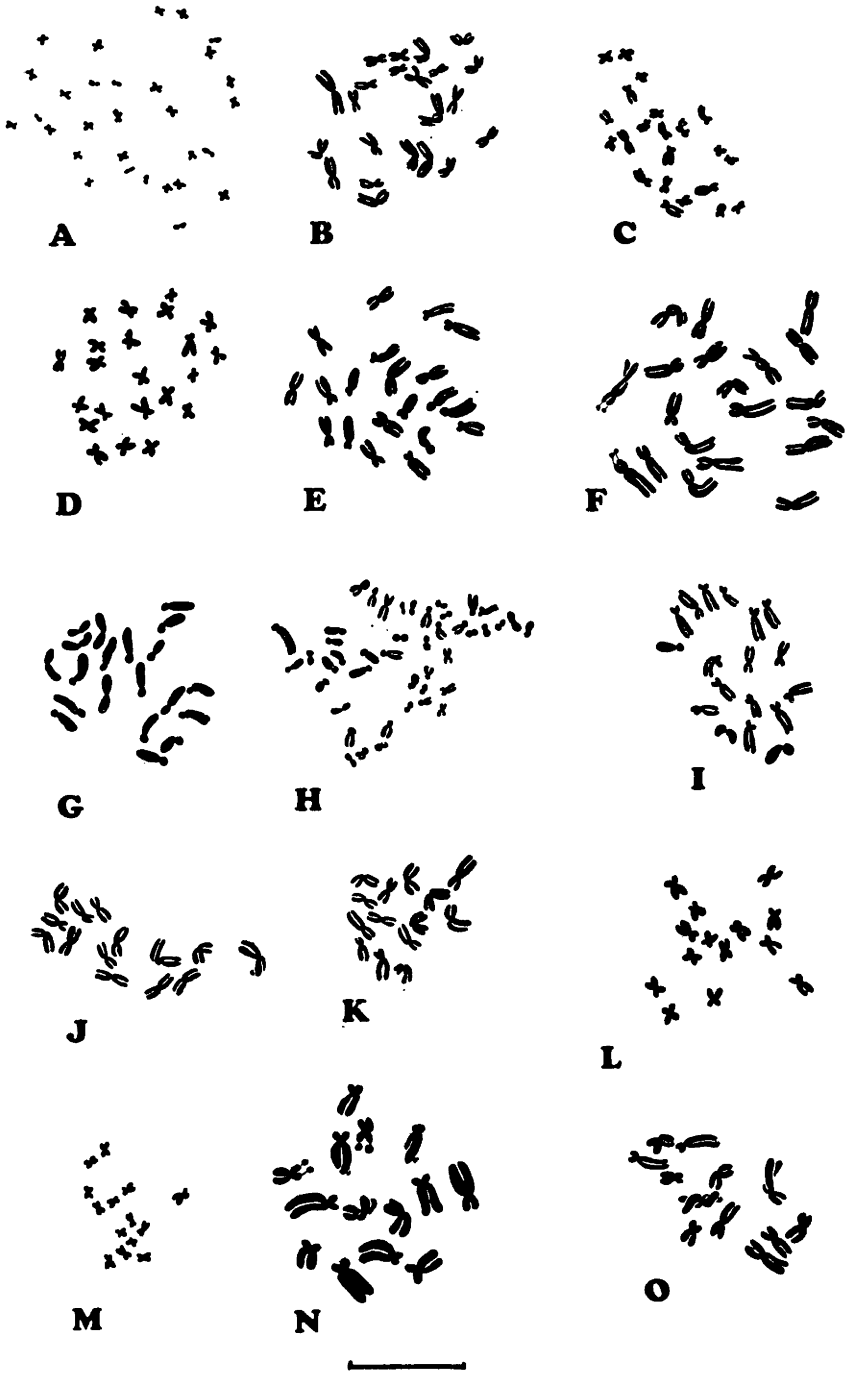

Fig. 2.

D. spectabile occurs sporadically on basalt cliffs in several areas of Tenerife. The species was previously uninvestigated cytologically.

Lotus arenarius BROT. — 2n=14 (Fig. 2 L).

Seed collection: Tenerife, Chio. 4-1971 BRAMWELL & HUMPHRIES.

L. arenarius is frequent in the south of Tenerife and the Canarian populations are somewhat different from those found in the south of the Iberian Peninsula in habit and leaf-shape. Further investigations may lead to the recognition of the Canarian plants as a distinct taxon. GRANT (1965) gives the same chromosome number from material of unspecified origin.

Lotus brunneri WEBB — 2n=14 (Fig. 4 I).

Seed collection: Cape Verde Islands, Sant Antão. 3-1970 E. R. SVENTENIUS.

This species, a member of the Macaronesian section *Pedrosia,* is endemic to the Cape Verde Islands and its chromosome number has not previously been reported.

Lotus hillebrandii CHRIST — 2n=14 (Fig. 2 M).

Seed collection: La Palma, Barranco de las Angustias. 4-1971 BRAMWELL & HUMPHRIES.

This widespread and variable endemic species of La Palma was previously uninvestigated cytologically.

Lotus holosericeus WEBB & BERTH. — n=7 (Fig. 4 H).

Bud collection: Gran Canaria, San Bartolomé de Tirajana. 3-1971 BRAMWELL & HUMPHRIES.

This species is found only in the montane regions of the south of Gran Canaria. Its chromosome number was previously unreported.

Lotus sessilifolius DC. — n=14 (Fig. 4 G).

Bud collection: Tenerife, Montana Roja near El Medano. 4-1971 BRAMWELL & HUMPHRIES.

BORGEN (1969) reports the diploid somatic number 2n=14 from Gran Canarian material. Our specimens from Tenerife are tetraploid but the two races are very similar morphologically.

Vicia cirrhosa CHR. SM. — 2n=14 (Fig. 2 N).

Spontaneous seed received from the Orotava Botanical Garden originating from La Gomera, Tagaluche.

LARSEN (1960) records the same chromosome number from this species which is confined to the Western Canaries.

PLUMBAGINACEAE

Limonium braunii (BOLLE) A. CHEV. — 2n=12 (Fig. 2 O).

Seed collection: Cape Verde Islands, Sant Antão. 3-1970 E. R. SVENTENIUS.

The chromosome number of this Cape Verde Islands endemic was previously unrecorded.

POLYGONACEAE

Rumex lunaria L. — 2n=36 (Fig. 3 A).

Seed collection: Gran Canaria, Santa Lucia de Tirajana. 3-1971 BRAMWELL & HUMPHRIES.

Rumex lunaria, a Macaronesian endemic, is widespread in the xerophytic zones of the Canary Islands. The same chromosome number is reported by LARSEN (1960, 1963) and BORGEN (1969).

Fig. 3. Mitotic chromosomes of A: *Rumex lunaria,* B: *Reseda crystallina,* C: *R. scoparia,* D: *Marcetella maderensis,* E: *Kickxia pendula,* F: *Campylanthus spathulatus,* G: *Drusa glandulosa,* H: *Melanoselinum bichoffii,* I: *M. hirtum,* J: *Todaroa aurea,* K: *Forskohlea procridifolia,* L: *Scilla latifolia.* — Scale 10 μ.

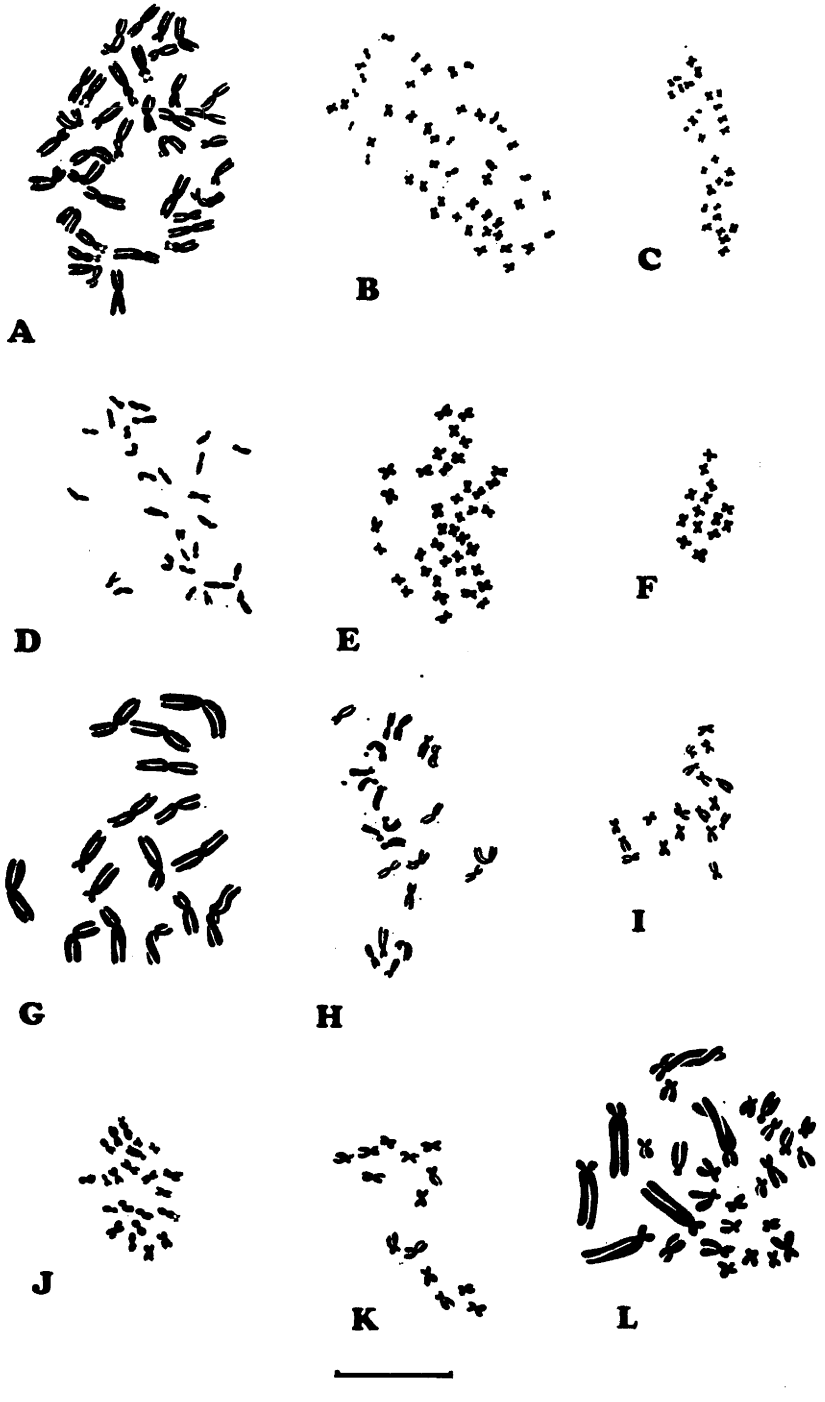

Fig. 3.

RESEDACEAE

Reseda crystallina WEBB & BERTH. — 2n=48 (Fig. 3 B).

Seed collection: Fuerteventura, Matas Blancas. 5-1969 D. BRAMWELL.

This species is found only on Lanzarote, Fuerteventura and Gran Canaria. EIGSTI (1936) records the same somatic chromosome number.

Reseda scoparia BROUSS. — 2n=30 (Fig. 3 C).

Seed collection: Tenerife, Adeje. 3-1971 BRAMWELL & HUMPHRIES.

This confirms the somatic chromosome number reported by LARSEN (1960).

ROSACEAE

Marcetella maderensis (BORNM.) SVENT. — 2n=28 (Fig. 3 D).

Seed received from the Jardin Canario, Tafira, Gran Canaria, from plants originating from Madeira.

This very rare species is endemic to Madeira and its chromosome number was previously unknown. The same somatic number was reported from the Canarian species *M. moquiniana* (WEBB & BERTH.) SVENT. by MICHAELIS (1964) and NORDBORG (1966).

SCROPHULARIACEAE

Kickxia pendula (KUNKEL) BRAMWELL[1] — 2n=40 (Fig. 3 E).

Seed collection: Gran Canaria, Termisas. 3-1971 BRAMWELL & HUMPHRIES.

This species which appears to be tetraploid is confined to a very small area of the south of Gran Canaria. It is closely related to *Kickxia spartioides* (BROUSS.) JANCHEN which is diploid.

Campylanthus spathulatus A. CHEV. — 2n=14 (Fig. 3 F).

Seed collection: Cape Verde Islands, Sant Antão. 3-1970 E. R. SVENTENIUS.

The same chromosome number is reported by LARSEN (1960) from Canarian material of *C. salsoloides* (L. fil.) ROTH. *C. spathulatus* is a Cape Verde Islands endemic and was not previously studied cytologically.

UMBELLIFERAE

Drusa glandulosa (POIRET) BORNM. — 2n=16 (Fig. 3 G).

Seed collection: Gran Canaria, Guayedra. 3-1971 BRAMWELL & HUMPHRIES.

The monotypic genus *Drusa* is endemic to the Macaronesian region and has, as its nearest relatives, *Bowlesia* (14 species) and *Homalocarpus* (6 species) in South America. MATHIAS & CONSTANCE (1965) report the same chromosome number from material of unspecified origin.

Melanoselinum bichoffii (SCHMIDT) A. CHEV. — 2n=22 (Fig. 3 H).

Seed collection: Cape Verde Islands, Sant Antão. 3-1970 E. R. SVENTENIUS.

LARSEN (1962) and BELL & CONSTANCE (1966) report 2n=20 and n=11 respectively for *M. decipiens* of Madeira. The chromosome number of *M. bichoffii,* a Cape Verde Islands species, was previously unreported.

Melanoselinum hirtum (SCHMIDT) A. CHEV. — 2n=18 (Fig. 3 I).

Seed collection: Cape Verde Islands, San Thiago. 3-1970 E. R. SVENTENIUS.

The somatic chromosome number in the Macaronesian genus *Melanoselinum* appears to be variable, 2n=18, 20 and 22 having been reported from the three species so far counted. *M. hirtum* was previously unknown cytologically.

[1] *Kickxia pendula* (KUNKEL) BRAMWELL, comb. nov.
Linaria pendula KUNKEL, Cuad. Bot. Canar. 9: 8 (1970).
Though originally described in the genus *Linaria* this species should be referred to *Kickxia* sect. *Valvatae* (WETTST.) JANCHEN (cf. LARSEN 1963).

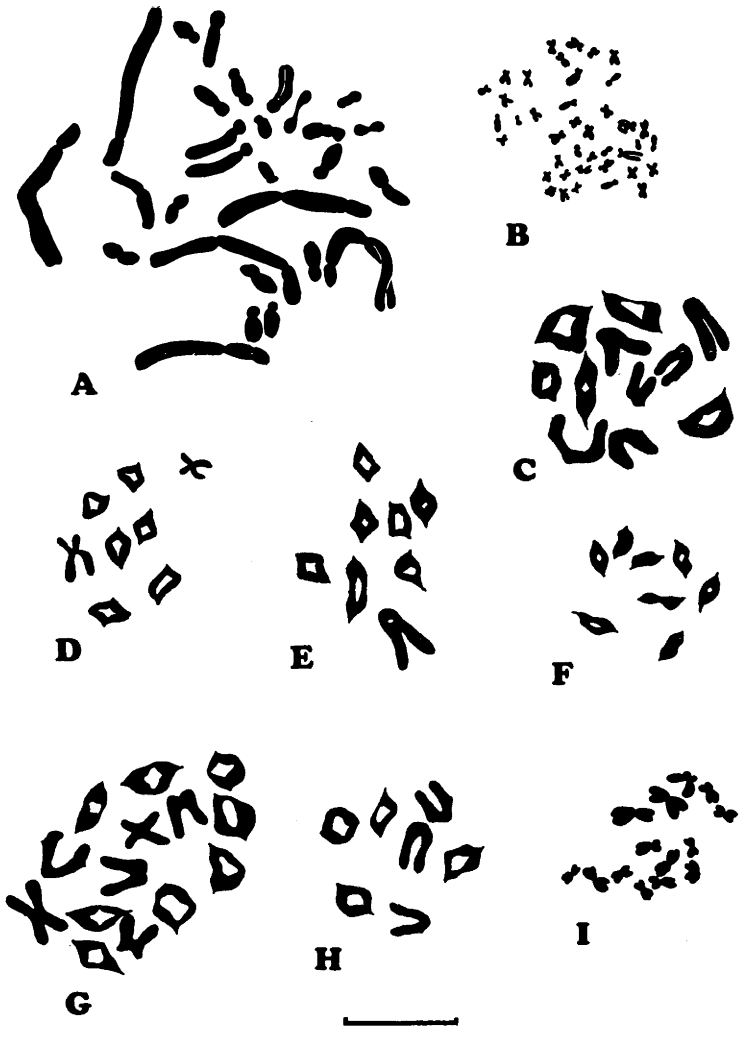

Fig. 4. Mitotic chromosomes (A, B, I) and first meiotic metaphase (C—H) of A: *Urginea hesperia,* B: *Dracaena draco,* C: *Seseli webbii,* D: *Echium sventenii,* E: *E. triste,* F: *E. webbii,* G: *Lotus sessilifolius,* H: *L. holosericeus,* I: *L. brunneri.* — Scale 10 μ.

Seseli webbii Coss. — n=11 (Fig. 4 C).

Bud collection: Gran Canaria, Guayedra. 3-1971 Bramwell & Humphries.

This Canarian endemic is known from coastal regions of Tenerife, Gran Canaria, Hierro and Gomera. Its cytology has not previously been investigated.

Todaroa aurea Parl. — 2n=22 (Fig. 3 J).

Seed collection: La Palma, Fuencaliente. 4-1971 Bramwell & Humphries.

In a recent paper (Bramwell et al. 1971) the authors reported the same somatic chromosome number from plants from Tenerife. The material investigated

in the present case was a dwarf, coastal ecotype from the south of La Palma.

URTICACEAE

Forskohlea procridifolia WEBB — 2n=14 (Fig. 3 K).

Seed collection: Cape Verde Islands, San Thiago. 3-1970 E. R. SVENTENIUS.

The chromosome number of this Cape Verde Islands endemic was previously unreported. LARSEN (1962) records 2n=22 from the Canarian species *F. angustifolia* RETZ.

POLYPLOIDY AND THE CLASSIFICATION OF ENDEMICS

FAVARGER & CONTANDRIOPOULOS (1961) have proposed a system of analysis of endemism based on the ploidy level of the endemic taxa and that of their nearest non-endemic relatives (corresponding taxa). Four classes of endemics are distinguished in this system: 1. palaeoendemics; 2. schizoendemics; 3. patroendemics and 4. apoendemics. With cytological data now available for 263 Canary Islands endemic species (BORGEN 1969, 1970, BRAMWELL et al. 1971 etc.) it is possible to begin to apply FAVARGER & CONTANDRIOPOULOS' system to the Canarian flora. In many cases this application is limited by the lack of cytological data for the Mediterranean and North African corresponding taxa. In view of this we have limited the discussion of each type of endemic to a few well documented examples.

1. Palaeoendemics

Palaeoendemics are species of mono- or oligotypic genera, or taxonomically isolated sections of genera with no non-endemic corresponding taxa. Cytologically palaeoendemics may be diploid or polyploid (palaeopolyploids, FAVARGER 1967).

Examples of both types can be readily found in the Canarian flora. The three species of the endemic genus *Parolinia* (Cruciferae) are all diploids (2n=22). *Drusa* (Umbelliferae), 2n=16, *Heywoodiella,* 2n=6, *Vieraea,* 2n=16 (Compositae) and *Gesnouinia* (Urticaceae), 2n=20, are all diploid monotypic genera and both species of the genus *Marcetella* (Rosaceae), 2n=28 are probably diploids. Ancient polyploids appear to occur in the Macaronesian endemic groups of *Isoplexis* (Scrophulariaceae), 2n=56, which is allied to the genus *Digitalis* (2n=16—168), and *Bystropogon* (Labiatae), 2n=42, a South American/Macaronesian disjunct genus, which according to BORGEN (1969) appears to be hexaploid.

2. Schizoendemics

The vast majority of endemic species in the Canarian flora appear to be schizoendemics, that is diploid or polyploid species whose corresponding taxa are at the same level of polyploidy as the endemic.

The species of endemic sections of large genera such as *Echium, Sonchus, Senecio* and *Limonium* are probably old schizoendemics which are the result of secondary evolution in relict groups (active epibiotics, BRAMWELL 1971). These endemics tend to be vicarious taxa, rarely occurring on more than a single island and in many cases restricted to one locality. Where there are non-endemic sections of these genera in the Mediterranean region they tend to exhibit a higher level of polyploidy, for example *Echium* in the Iberian Peninsula and North Africa.

The old schizoendemics are generally diploid and taxonomically isolated, and some, for example *Limonium* section *Nobiles,* have a different chromosome base number from the non-endemic sections.

MEUSEL (1952) has suggested that the Canarian taxa are relics of the ancestral forms of the Mediterranean representatives of these genera. From this viewpoint the Canarian taxa will be considered an-

cient diploids from which the continental taxa, with their higher level of polyploidy, have arisen.

The low level (25.7 %) of polyploidy in the Canarian endemic flora (BORGEN 1969) is consistent with MEUSEL's idea that the archipelago constitutes a refugium.

There also seems to be a second group of schizoendemic species: these are the species with close relatives in the Mediterranean region. Examples of these are found in Monocotyledons such as *Androcymbium psammophilum* (Liliaceae), endemic to Lanzarote and Fuerteventura, with the somatic chromosome number 2n=18, which has a corresponding species *A. gramineum,* 2n=18, in the Mediterranean region. *Pancratium canariensis* (Amaryllidaceae), 2n=22, is a widespread Canarian endemic reported from all the islands and it has a very similar corresponding species *P. maritimum* (2n=22) common in the Mediterranean region.

3. Patroendemics

Patroendemics are diploid species whose corresponding nonendemic taxa are polyploid. FAVARGER & CONTANDRIOPOULOS (1961) consider the endemic taxa to be older than the corresponding taxa in this case. An example in the Canarian flora is *Laurus azorica* (Lauraceae), 2n=36, now found only in Macaronesia but also known from Pliocene fossil deposits from Southern Europe. Its modern corresponding Mediterranean species is *Laurus nobilis,* 2n=48, which is probably a post-Tertiary derivative.

Adenocarpus viscosus, 2n=24, is endemic to Tenerife in the Canaries and its corresponding species is the Mediterranean *A. complicatus* (2n=52).

4. Apoendemics

These are polyploid endemics whose corresponding non-endemic taxa are diploid and there appear to be very few examples of this type of endemism in the Canaries. There are a few cryptic polyploids which might be considered as apoendemics such as *Silene vulgaris* which is usually diploid in Europe but which has a morphologically indistinguishable polyploid race on Gran Canaria and *Asphodelus fistulosus* which is tetraploid in Europe and octoploid in the Canaries.

CONCLUSIONS

The Canarian flora is rich in palaeoendemics and old schizoendemics and there are also a number of patroendemics present.

These all represent the ancient endemic elements of the flora. There are, however, comparatively few Canarian/Mediterranean modern schizoendemics and virtually no apoendemics so that the flora seems to be very poor in young or neoendemics.

As previously pointed out, this fact, coupled with the low degree of polyploidy, the predominance of woody lifeforms and the presence of representatives of many disjunctly distributed taxa in the Canarian endemic flora confirms that the islands are, indeed, a "refugium" for genera and species now extinct in the Mediterranean region and Northern Africa.

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Chromosome Morphology in Afghanian Bellevalias (Liliaceae)

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ABSTRACT

BENTZER, B., BOTHMER, R. VON & WENDELBO, P. 1972. Chromosome morphology in Afghanian Bellevalias. — Bot. Notiser 125: 153—156.

Chromosome morphology and a brief phytogeographical survey is given for *Bellevalia saviczii* WORON., *B. feinbrunae* FREITAG & WENDELBO, and *B. atroviolacea* REGEL.

INTRODUCTION

This study includes the three species of *Bellevalia* native to Afghanistan, and previously treated taxonomically by FREITAG and WENDELBO (1970). These species represent three of the four sections of the genus: *B. saviczii* WORON. (sect. *Conica* FEINBR.), *B. feinbrunae* FREITAG & WENDELBO (sect. *Bellevalia*), and *B. atroviolacea* REGEL (sect. *Muscarioides* FEINBR.).

The genus *Bellevalia* is mainly confined to the Mediterranean and adjacent areas to the east as far as Caucasus, NE. Iraq and W. Iran. The section *Muscarioides* with two or three species found in Uzbekistan, Tadjikistan and Afghanistan, is thus found at a considerable distance from the main centre of the genus.

The hexaploid *B. saviczii* found in NE. Iran, Afghanistan and adjacent areas of the USSR is the easternmost representative of the section *Conica*. It is practically never found outside wheat-fields and vineyards and there is reason to believe that it may be of fairly recent origin; probably having arisen in connection with cultivation.

B. feinbrunae is also the easternmost species in its section, and the gap between it and the nearest representative of sect. *Bellevalia,* in W. Iran, is considerable (about 1400 kms). There are, however, several examples from other genera of such disjunctions. It is native to Afghanistan and is found growing in natural vegetation (FREITAG & WENDELBO 1970).

This investigation concerns the determination of chromosome numbers and chromosome morphology. Karyotype similarities as well as differences between the species are briefly discussed.

MATERIAL AND METHODS

The investigation was carried out on material cultivated in the Botanical Garden, Gothenburg. Material from six populations

Table 1. Chromosome numbers in *Bellevalia,* mainly from Afghanistan. * The exact localities are given in FREITAG and WENDELBO (1970).

Species	Collection no.	Province	Number of individuals studied	2n
B. saviczii	W 7251	Farah *	2	24
	W 9101	Samangan *	2	24
	W 8102	Badghis *	3	24
	W 7768	Herat *	2	24
	W 7615	Zabul *	2	24
	Jörgensen 451	Logar	1	24
B. feinbrunae	W 7537	Kabul *	2	8
	W 7324	Farah	1	8
	Breckle A 394	Logar *	1	8
B. atroviolacea	Tashkent 1970, seed exchange		many seedlings	8
	Hedge & Wendelbo	Mazar-i-Sharif	1	8

of *B. saviczii,* three of *B. feinbrunae,* and two of *B. atroviolacea* (one of which from USSR) has been available.

The usual Feulgen squash method was used (cf. BOTHMER 1970). The root-tips were pre-treated in a mixture of 0.6 % colchicine and 2 mM 8-hydroxyquinoline for about 2 hours.

The idiograms for *B. feinbrunae* and *B. atroviolacea* are based on measurements of ten good metaphase plates of one individual from each species. From all other plants available at least one plate was drawn for comparison.

The karyological nomenclature suggested by LEVAN et al. (1965) is followed.

RESULTS

Chromosome numbers for the species studied are given in Table 1. The basic chromosome number in the genus is x=4. *Bellevalia atroviolacea* and *B. feinbrunae* were found to be diploid (2n=8) and *B. saviczii* hexaploid (2n=24).

The haploid karyotypes of the species studied (Fig. 1, 2) contains one *m* chromosome (no. 1), which also is the largest of the complement. The small *msm* chromosomes (nos. 2—3) are indistinguishable

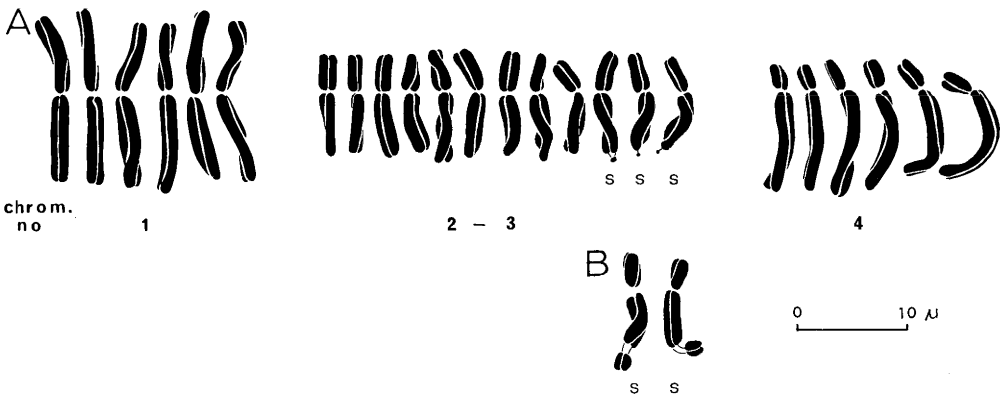

Fig. 1. Karyotype of *Bellevalia saviczii.* — A: Population no. W 7615. — B: Satellited chromosomes in population no. W 8102.

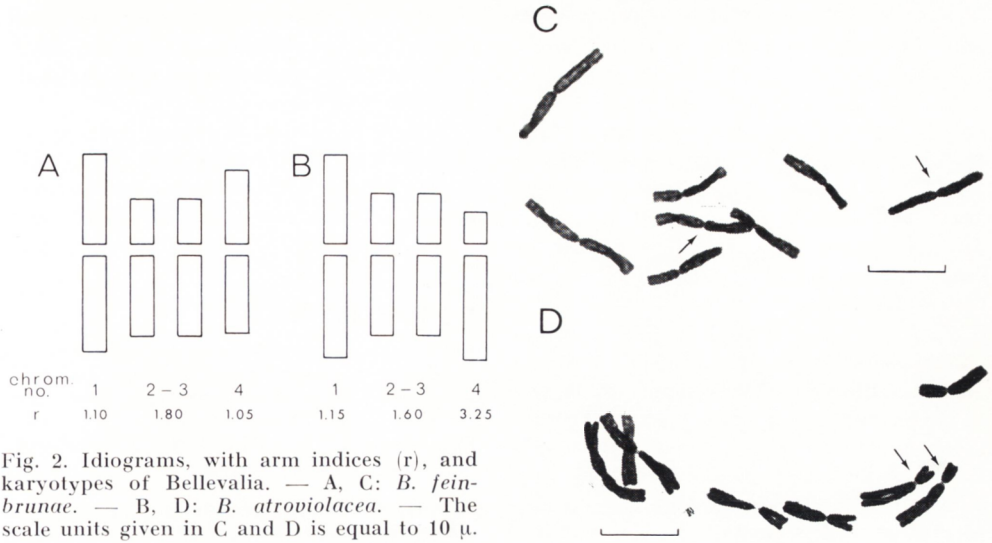

Fig. 2. Idiograms, with arm indices (r), and karyotypes of Bellevalia. — A, C: *B. feinbrunae*. — B, D: *B. atroviolacea*. — The scale units given in C and D is equal to 10 μ.

from each other by conventional cytological methods, and are here treated as a group (the r indices were calculated as mean values for the 2—3-chromosome group together).

Chromosomes no. 1—3 of the haploid karyotype show no apparent interspecific variation. Chromosome no. 4 is of about the same relative length in all species investigated but differs markedly in r index. In *B. atroviolacea* and *B. saviczii* it is subtelocentric ($r > 3.0$; Figs. 1, 2 B, D), but in *B. feinbrunae* it is metacentric (Fig. 2 A, C).

No satellites are present in the karyotypes of the diploid species. In *B. saviczii*, satellites have been observed on the *msm* chromosomes (nos. 2—3). They are variable in number as well as in size (Fig. 1).

DISCUSSION

In the genus *Bellevalia* di-, tetra-, hexa- and octoploids have previously been reported (see FEDOROV 1969 for references). Diploids are by far the most common. *B. longistyla* is the only species reported to be octoploid, with 2n=32 (ZAKHARIYEVA & MAKUSHENKO 1969). These authors also reported the chromosome numbers 2n=8 for *B. atroviolacea* and 2n=20 for *B. saviczii*. The former number is confirmed by the present investigation; the latter is, however, somewhat doubtful (Fig. 2 C, op. cit.).

It is evident from earlier studies that the chromosome complement in *Bellevalia* is more or less stable, having a "basic" karyotype represented in almost all species studied (see e.g. FEINBRUN 1938, LEVAN 1944, and GARBARI 1968). The extensive study by FEINBRUN (1938) indicates variation in the number and position of satellites and some minute variation in the relative lengths and arm indices of the chromosomes. The haploid karyotypes of the 16 species studied by FEINBRUN (1938) show one large metacentric chromosome (named chromosome P by FEINBRUN), one large subtelocentric (Q) and two smaller subtelocentric chromosomes (R and S). The latter are very much alike and difficult to distinguish from each other.

The "basic" karyotype is also visualized by LEVAN (1944) in *B. webbiana* (2x) and *B. romana* (2x), by GARBARI (1968) in *B. romana* (2x), *B. dubia* (2x) and

B. mauritanica (4x), and by ZAKHARIYEVA and MAKUSHENKO (1969) in *B. atroviolacea* (2x).

In this investigation *B. saviczii* (6x) and *B. atroviolacea* (2x) were both found to have the "basic" karyotype (Figs. 1, 2 B, D). It is thus of interest to note that karyologically *B. atroviolacea* does not differ from the typical pattern within the genus in spite of its extreme eastern distribution.

B. feinbrunae (2x) has the common chromosomes nos. 1—3 (Fig. 2 A, C) corresponding to chromosomes P, R and S in FEINBRUN's study (1938). Chromosome no. 4, however, deviates markedly in being metacentric (conferred to subtelocentric in the homologous chromosomes of other taxa). As the relative length of this aberrant chromosome in *B. feinbrunae* is similar to the corresponding one in *B. atroviolacea,* a simple pericentric inversion may have caused the deviation. None of its closest relatives, *B. cyanopoda* WENDELBO and *B. decolorans* BORNM., have been investigated karyologically. It is therefore unwise to draw any premature conclusions from the deviation from the "basic" karyotype shown by *B. feinbrunae.*

Satellites seem to occur irregularly and vary in number, size and position. They are found, for example, in *B. saviczii* (Fig. 1) and have also been found in Greek specimens of *B. dubia* and *B. trifoliata* (in press). In no case, however, have satellites been seen on the large, subtelocentric chromosome (no. 4) in the haploid karyotype.

Bellevalia satellites may possibly be regarded as "floating" within the populations, usually without value for distinguishing between non-homologous chromosomes.

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Cleome oligandra sp. nov. – a Two-staminate Species from Tanzania

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ABSTRACT

KERS, L. E. 1972. Cleome oligandra sp. nov. — a two-staminate species from Tanzania. — Bot. Notiser 125: 157—160.

Cleome oligandra is described from Tanzania. The androecium shows a unique condition because the flowers usually have only two stamens. Staminodes are lacking.

DIAGNOSIS. *Cleome oligandra* KERS, sp. nov. Species staminibus duobus a congeneris diversa est. — Herba parva suffruticosa 5—16 cm. Flores minuti cremei petalis circa 4 mm longis, bracteis unifoliolatis. Stamina 2 (rarius 3) inter se aequalia; staminodia nulla. Fructus nutans ellipticus brevisque 6—10 mm longus, apice in stylum 1 mm longum abiens, gynophoro 4—5 mm longo stipitato, stipite pedicellum longitudine aequante. — Habitat inter saxa rupesque.

DESCRIPTION. Small glabrous suffruticose *herb*, 5—16 cm high, richly branched from the woody base upwards. *Stems* thin, glabrous except near the racemes, striated—grooved, root crown up to 14 mm thick and woody. *Racemes* up to 6 cm in length. *Leaves* 3-foliolated, the lower ones glabrous, the upper ones sparsely glandular, petioles 2—27 mm long, glabrous to sparsely glandular. *Leaflets* elliptic to narrowly obovate, 2—14 mm long and 1—5 mm broad, of thin texture. *Floral bracts* unifoliolate, occasionally 2—3-foliolate at the very base of the racemes, lamina elliptic—obovate, 1—6 mm long, glandular-puberulous on both sides, petioles up to 2 mm long. *Pedicels* of flowers 2.5 mm long, elongating to 4—5 mm in fruit, horizontally spreading at anthesis, later becoming sharply reflexed at the very base, glandular-puberulous. *Sepals* 0.5 mm long, subequal, glabrous, obovate with an acute apex, long persisting in fruit. *Petals* subequal, glabrous, deciduous, cream-coloured, 3—4 mm long and 0.5 mm broad, narrowly lanceolate, the limb gradually tapering into a basal claw, the tip acute—minutely apiculate. *Stamens* 2, rarely (abnormally?) 3, equal and fertile, the one borne above and the other one borne below the base of the pistil, their filament bases united with the gynophore (in the pistillate flowers) and growing with this, hereby forming a minute androgynophore which is shorter than the persisting sepals; *filaments* up to about 4 mm in length, glabrous, delicate; *anthers* 1—1.5 mm long before anthesis. *Gynophore* 4—5 mm long in fruit, equalling the pedicel in length, glabrous, straight or slightly curved downwards, as it seems easily broken near the receptacle in the ripe fruits. *Fruits* elliptic, 6—10 mm long and 2—4 mm broad, bent downwards by the reflexed pedicel base; *valves* deciduous, longitudinally striated by many anastomosing veins, faintly glandular, papery; *replum* glabrous; *style* 1 mm long in fruit, straight, apically tapering; *stigma* truncate, hardly broader than the style. *Seeds* about 1.7 mm in diameter, comma-shaped in lateral view, flattened

from the sides, the radicula end extending beyond the blunt and swollen cotyledon end, the radicula end ± covered by a thin whitish—hyaline tissue, seed coat glabrous, shiningly brown, finely reticulated with longitudinal rows of minute pits.

TYPUS. A. BJÖRNSTAD 862, 20.IV. 1971, Tanzania, Iringa District, Ruaha National Park, on the top of the Kimiramatonge kopje (O holotype, UPS isotype).
ICON. Fig. nostra 1.

This is a distinct species not easily confused with any other one. It is characteristic due to the insignificant flowers which have normally two stamens only, the short hanging fruits, the comparatively long gynophore and the short style, the seeds (size, shape, surface pattern), the 3-foliolate leaves and the unifoliolate bracts.

At first sight, the plants may be taken for dwarfish specimens of *Cleome parvula* R. A. GRAHAM. The latter species is also found on kopjes in Tanzania (ELFFERS et al. 1964 p. 13). It differs from *C. oligandra* e.g. in the seeds, the number of stamens (5 in *C. parvula*) and the long narrow fruits which are not bent downwards by a reflexed pedicel. The morphological similarity between these two species is, however, apparent and it is highly probable that they are closely allied. Especially in the fruiting stage, the new species resembles *Cleome brachycarpa* DC. (habit, short fruits). *Cleome brachycarpa* is easily distinguished from *C. oligandra* in the spreading fruits, the very short gynophore (1 mm), the long style (3—4 mm) and the markedly broad stigma.

The available material is rather poor, especially as to flowering specimens. Two of the collections contain specimens with young inflorescences (BJÖRNSTAD 862, RICHARDS 21046). The third collection holds specimens in the fruiting stage on which leaves and flowers are lacking (THULIN & MHORO 701). A single flower with three stamens was found at the very base of a raceme (RICHARDS 21046). The odd stamen was borne very close to the upper normal stamen in that flower. Very likely the upper stamen primordium had been split into two buds and each had developed into a fertile stamen ("dédoublement"). Three stamens is certainly a rare abnormality in this species.

Cleome oligandra is known from a very restricted area, viz. the top of the Kimiramatonge kopje in S.E. Tanzania. There it has been collected three times. According to the information kindly given by Mr. M. THULIN, Uppsala, this kopje is fairly often visited by botanists because it is accessibly situated near the Station of the Ruaha National Park and also near a road. Other kopjes occur in the same area but these are situated far from each other and are not easy to reach. So, it is not known whether this species occurs on other kopjes in this part of Tanzania or not. The Kimiramatonge kopje reaches about 1100 m above sea-level and is situated on an undulating plain occupied by *Acacia—Commiphora—Combretum* woodland (M. THULIN, oral communication).

MATERIAL STUDIED

Tanzania: Iringa District, Ruaha National Park.

Fig. 1. *Cleome oligandra* KERS, sp. nov. — A: Top of raceme. — B: Petals. — C: Flower in lateral view. Staminate flower with a rudimentary pistil (black). — D: Stamens (before anthesis). — E: Sepals. — F: Floral bracts. — G: Stem leaf. — H: Floral diagram. — J: Seed. — K, M: Fruits. The left fruit with the valves detached to show the seeds. — L: Receptacle with portion of the gynophore to the left. L^1 seen in lateral view. L^2 seen from above. L^3 seen from below. Note the stamen scars. Petal scars pointed. — N: Aspect of plant. — A—G, N drawn from A. BJÖRNSTAD 862, J—M drawn from THULIN & MHORO 702.

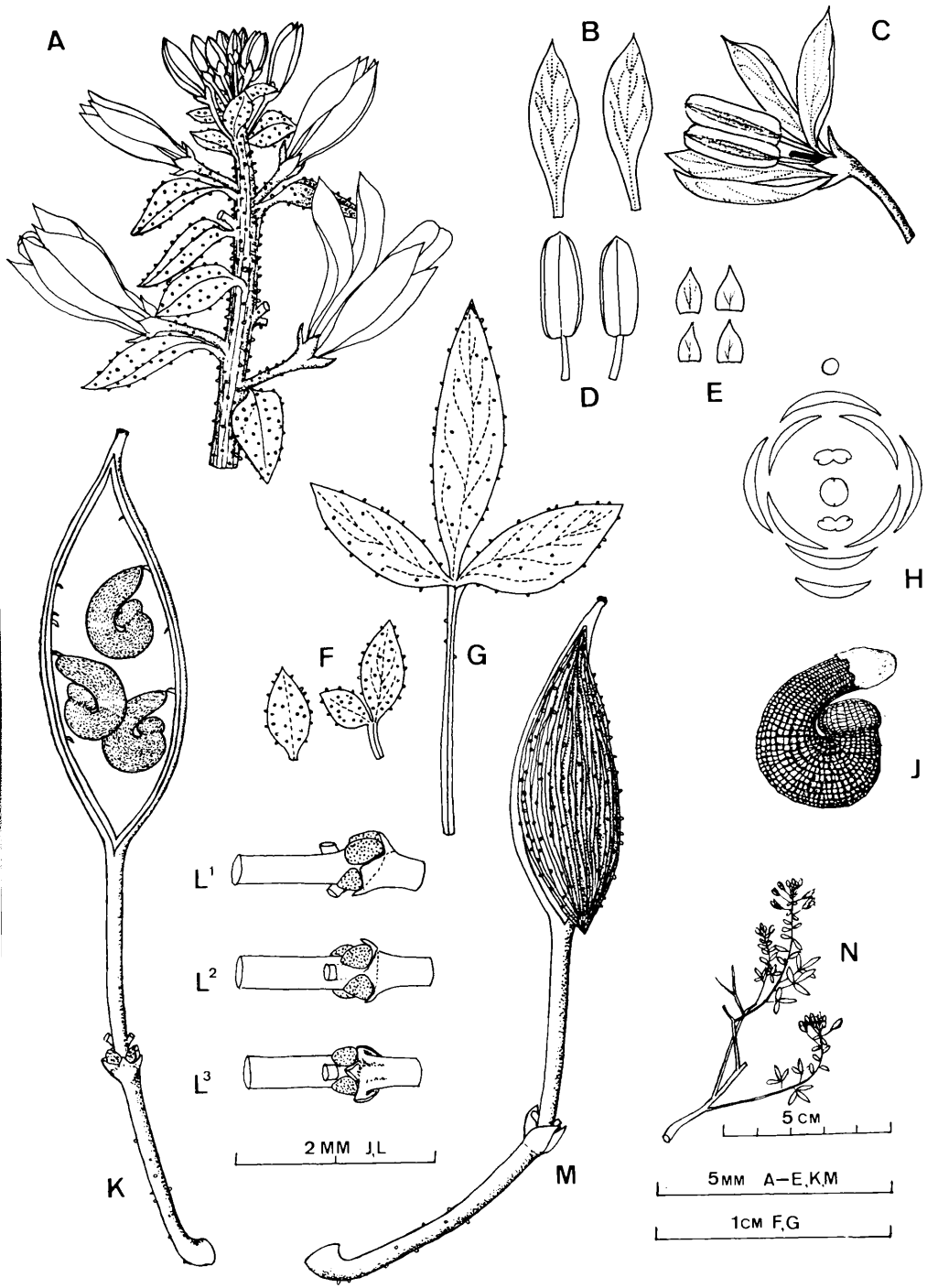

Fig. 1.

On the top of the Kimiramatonge kopje, on top of large boulders. A. BJÖRNSTAD 862, 20.IV. 1971 (O holotype, UPS isotype) — Kimiramatonge Hill. In crevices of large rocks on top of the mountain. Small prostrate plant with woody root. Flowers cream-coloured. H. M. RICHARDS 21046, 25.I. 1966 (K) — Kimiramatonge kopje. Growing exposed in dry crevices on large rocks. M. THULIN & B. MHORO 701, 11.VIII. 1970 (UPS).

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Embryological Studies in some Combretaceae

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ABSTRACT

VENKATESWARLU, J. & PRAKASA RAO, P. S. 1972. Embryological studies in some Combretaceae. — Bot. Notiser 125: 161—179.

The embryological studies now made on 18 species distributed over nine genera of Combretaceae disclose that the different members exhibit a somewhat uniform pattern of embryological development and constitute a natural assemblage of related taxa. The totality of embryological, floral anatomical, and morphological evidence support the removal of *Guiera* from EXELL's (1931) tribe, the Combreteae and the establishment of a monogeneric tribe, the Guieraeae. The retention of *Poivrea* as a distinct genus from *Combretum* is also indicated.

INTRODUCTION

The Combretaceae embraces 18 genera and 500 species (LAWRENCE 1951). They are trees, shrubs or climbers, confined predominantly to the tropics. The family is divided into two subfamilies, namely, the monogeneric Strephonematoideae and the Combretoideae. The latter has been further divided into four tribes, namely the Combreteae, Terminalieae, Calycopterideae and Laguncularieae (EXELL 1931). Very recently VENKATESWARLU and PRAKASA RAO (1971) on xylotomical basis suggested the separation of *Strephonema* into a distinct monogeneric family, the Strephonemataceae, a family to be considered allied to the Combretaceae. Therefore, Combretaceae, as comprehended by these authors, comprises the genera included by EXELL (1931) in the subfamily Combretoideae.

From a perusal of the literature it is obvious that several of the combretacean genera are still embryologically unexplored and the data formerly available for the few species studied are rather scanty and fragmentary (KARSTEN 1891; MAURITZON 1939; FAGERLIND 1941; NAGARAJ 1954 a—c, 1955; PRAKASA RAO 1963), except for *Poivrea coccinea* (VENKATESWARLU 1952 a). In *Combretum pincianum* and *C. paniculatum,* MAURITZON (1939) reported a 16-nucleate embryo-sac, but in all other species of this genus investigated it conforms to the Polygonum type. Thus there is a genuine need to extend embryological investigations to the other species of *Combretum* as well to the other genera of the family. To provide an embryological picture of the family was undertaken a comprehensive comparative study of as many members of the different tribes as possible and also as many species of *Combretum* as could be obtained. The present communication pertains to the structure and development of the anther and ovule, the male and female gametophytes, the endosperm and the embryo in 18 species of nine genera representing all tribes.

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Table 1. Survey of the material. + denotes the embryological aspects studied in each species.

Species studied (tribes according to EXELL 1931)	Collector	Origin	Structure and development of			
			Anther and male gametophyte	Ovule and female gametophyte	Endosperm	Embryo
COMBRETEAE						
Combretum ovalifolium ROXB.	Authors	Visakhapatnam, India	+	+	+	—
C. extensum ROXB.	Authors	Simhachalam, India	+	+	+	+
C. decandrum ROXB.	Dr. P. N. RAO	Anantagiri	+	+	+	+
C. grandiflorum G. DAN.	Dr. R. W. READ	Miami, Florida, U.S.A.	+	+	+	+
Quisqualis indica L.	Authors	Visakhapatnam, India	+	—	—	—
Guiera senegalensis LAM.	Director, Forest Research	Ibadan, Nigeria	+	+	+	+
TERMINALIEAE						
Terminalia catappa L.	Authors	Visakhapatnam, India	+	+	+	+
T. chebula RETZ.	Dr. L. L. NARAYANA	Visakhapatnam, India	+	+	+	+
T. bellerica ROXB.	Authors	Visakhapatnam, India	+	+	—	—
T. arjuna W. & A.	Dr. B. S. M. DUTT	Bapatla, India	+	+	—	—
T. muelleri ROTH	Prof. A. N. RAO	Singapore	+	+	+	+
T. paniculata ROTH	Shri R. S. RAO	Poona, India	+	+	+	+
Anogeissus latifolia WALL	Authors	Visakhapatnam, India	+	+	+	+
A. acuminata ROXB.	Authors	Ganjam, Orissa	+	+	+	+
Bucida buceros L.	Dr. R. W. READ	Miami, Florida, U.S.A.	+	+	+	+
Conocarpus erectus L.	Dr. R. W. READ	Miami, Florida, U.S.A.	+	—	—	—
CALYCOPTERIDEAE						
Calycopteris floribunda LAMK	Shri R. S. RAO	Poona, India	+	+	+	+
LAGUNCULARIEAE						
Lumnitzera racemosa WILLD.	Dr. P. V. B. MURTY	Koringa, India	+	+	+	+

MATERIALS AND METHODS

Table 1 gives a survey of the material and also of the embryological aspects studied in the respective species.

The flowers and fruits in all stages of development were fixed in formalin-acetic-alcohol and stored in 70 % alcohol-glycerine mixture for later handling. Most of the material offered difficulty in microtomy due to the presence of hairs on the different floral parts. It therefore became indispensable to dissect out anthers and ovules at different stages of development for embedding and sectioning. Sections 6 to 8 microns thick were cut for the study of microsporogenesis, megasporogenesis and embryo-sac development and 8 to 12 microns thick for endosperm and embryo development. Staining was done in DELAFIELD'S hematoxylin as well as safranin and fast green adopting the procedure outlined by JOHANSEN (1940). Since most of the developmental details are somewhat similar in the different members examined, a common account is presented drawing attention to the variation in any particular species. Where embryological features are uniform, they are represented by a single common diagram. Where variations are encountered, in respect of any one feature or taxon, they are individualised.

OBSERVATIONS

Microsporangium and Male Gametophyte

In all the members examined the stamens occur attached to the floral tube in

two whorls of 4 or 5 each. The transection of the four-lobed young anther shows the hypodermal archesporium at each corner which after periclinal divisions forms a parietal layer and an inner primary sporogenous layer (Fig. 1 A, B). A varying number of cell layers come to be differentiated below the epidermis as a consequence of periclinal divisions in the primary parietal cells (Fig. 1 D—J, T). The anther wall at the mother cell stage has one middle layer in *Guiera senegalensis* (Fig. 1 C), two in *Combretum ovalifolium, C. extensum, C. decandrum, Quisqualis indica* and *Lumnitzera racemosa* (Fig. 1 D, E) and three in *Terminalia catappa, T. arjuna, T. bellerica, T. paniculata, T. muelleri, Bucida buceros, Anogeissus latifolia, A. acuminata* and *Calycopteris floribunda* (Fig. 1 F, G, T). But yet in *Combretum grandiflorum* there are four to six middle layers (Fig. 1 H, I). In *Conocarpus erectus* the youngest anther available revealed the microspore tetrads surrounded by secretory tapetum, two middle layers, endothecium and an epidermis (Fig. 1 J). The anther tapetum is parietal in its origin and of the secretory type. It is usually one-layered throughout, but in *Quisqualis indica, Terminalia muelleri, Bucida buceros* and *Calycopteris floribunda* it becomes two-layered at some places (Fig. 1 E, G) due to a periclinal division of some of the tapetal cells. In *Combretum grandiflorum* it is multilayered (Fig. 1 H, I). The tapetal cells are at first uninucleate (Fig. 1 D, H), but become binucleate by the time spore mother cells enter into the meiotic prophase and correspond to the first type recognised by COOPER (1933). In *Combretum grandiflorum* and *Terminalia catappa* tri- and quadrinucleate conditions of the tapetal cells were encountered in a very few cases (Fig. 1 I), as was also the fusion of the tapetal nuclei leading to polyploid nuclei (Fig. 1 K—N). In an anther about to dehisce both the tapetum and the middle layers get crushed and distorted. The tapetal cells become consumed either at the uni- or binucleate stage of the pollen grains. The hypodermal layer develops fibrous thickenings except in the region of the stomium. Occasionally in *Terminalia arjuna, Anogeissus latifolia, A. acuminata* and *Lumnitzera racemosa* some of the cells of the connective and the cells adjacent to the middle layer also develop fibrous thickenings (Fig. 1 O, P). In *Terminalia arjuna* and *Lumnitzera racemosa* the endothecial cells become richly filled with darkly staining contents which may probably include tannins and phenolic substances (Fig. 1 P).

Concurrent with the aforesaid changes in the wall layers of the anther, the inner sporogenous cells undergo a few more mitotic divisions in all directions resulting in a mass of microsporocytes which secrete a thick mucilaginous wall, undergo meiosis and yield tetrahedral or isobilateral tetrads, the former arrangement being more frequent; cytokinesis is by furrowing. The mature pollen grains, which are spheroidal, triporate, ridged and furrowed with thick exine and delicate intine, are shed usually at the two-celled stage (Fig. 1 Q). In *Lumnitzera racemosa,* however, a few of the pollen grains showed six nuclei (Fig. 1 R). In such exceptional cases four nuclei were invariably larger than the rest and probably arose as a consequence of supernumerary divisions of the vegetative nucleus. The two smaller nuclei obviously resulted from the extra divisions of the generative nucleus.

Pollen sterility is very commonly observed in most of the taxa investigated. Apart from the sterility resulting from the pollen grains abortive when fully formed (Fig. 1 O), degenerations of the microspores at various other stages of development and to varying degrees, have been encountered in a few members. In *Quisqualis indica* and *Combretum grandiflorum,* a number of microsporocytes in some of the sporangia are seen to degenerate even before entering upon the

meiotic divisions (Fig. 1 E, H). In *Combretum extensum, Terminalia bellerica,* and *Calycopteris floribunda,* the entire sporogenous tissue in one or more lobes of an anther sometimes degenerates (Fig. 1 S). In such instances the degenerated contents remain as indistinct masses. Likewise, degeneration of one, two, three or even all the microspores in a tetrad, while still in the mother cell wall, has also been recorded in *Terminalia catappa* (Fig. 1 T).

Ovary and Megasporangium

In all the species studied the ovary is inferior and unilocular. It encloses 2 to 5 pendulous ovules; the number varies in different members. The ovular primordium develops towards the roof of the loculus and protrudes into the ovarian cavity as a blunt outgrowth being a homogeneous mass of parenchymatous cells delimited peripherally by a uniseriate epidermal layer (Fig. 1 U). During the further development, the ovular primordium increases in size and curves, whereafter the inner and outer integuments are differentiated. The ovule finally becomes anatropous, crassinucellar and two-integumented (Fig. 1 V, W). The integuments in general do not close the nucellus until after tetrad formation (Fig. 1 X). In fully grown ovules the two integuments which are free from each other overtop the nucellus completely constituting a narrow and roughly zigzag micropyle. In *Guiera senegalensis,* however, the micropyle is formed by the inner integument alone (Fig. 2 C). In a small percentage of ovules of *Terminalia catappa* and *Bucida buceros* the nucellus extends into the micropyle as a distinctive conical structure (Fig. 2 D). In the young ovules of *Combretum grandiflorum, C. extensum, C. ovalifolium, C. decandrum, Guiera senegalensis, Terminalia bellerica, Anogeissus latifolia, A. acuminata, Calycopteris floribunda* and *Lumnitzera racemosa* each of the two integuments is two-layered (Figs. 1 W, X, 2 G), while in *Terminalia catappa* and *Bucida buceros* the outer integument is

Fig. 1. A: *Combretum decandrum.* T.S., part of young anther showing archesporium. ×160. — B: *Anogeissus acuminata.* L.S., anther lobe displaying dividing archesporial cells. ×300. — C: *Guiera senegalensis.* T.S., portion of mature anther lobe showing epidermis, endothecium, single middle layer, the remnants of tapetal layer and the two-celled pollen grains. ×120. — D: *Combretum ovalifolium.* T.S., anther lobe with sporogenous cells. ×200. — E: *Quisqualis indica.* T.S., anther lobe with sporogenous cells and biseriate tapetal cells. ×200. — F: *Bucida buceros.* T.S., anther lobe with spore mother cells in division. ×280. — G: *Terminalia muelleri.* T.S., anther lobe with microspore tetrads, biseriate and binucleate tapetal cells. ×280. — H, I: *Combretum grandiflorum.* T.S., part of anther lobe showing functional and sterile spore mother cells, multiseriate tapetum, and bi-, tri-, and quadrinucleate tapetal cells. ×270. — J: *Conocarpus erectus.* T.S., anther lobe showing epidermis, endothecium, crushed middle layers, binucleate tapetal cells and microspore tetrads. ×340. — K—N: *Terminalia catappa.* Tapetal cells showing nuclear division and fusion. ×270. — O: *Anogeissus latifolia.* T.S., mature anther lobes with functional and sterile pollen grains and fibrous endothecium. ×270. — P: *Lumnitzera racemosa.* T.S., mature anther lobe. Note the darkly stained material in the endothecium. ×360. — Q: *Terminalia catappa.* T.S., part of old anther lobe showing mature pollen grains. ×360. — R: *Lumnitzera racemosa.* Mature pollen grain with 6 nuclei. ×270. — S: *Combretum extensum.* T.S., mature anther showing abortive sporogenous tissue in two anther lobes. ×200. — T: *Terminalia catappa.* T.S., portion of mature anther lobe showing the degenerated microspores in tetrads. ×270. — U: *Combretum ovalifolium.* L.S., ovule primordium. ×270. — V, W: *Combretum ovalifolium.* L.S., developing ovule showing integumentary primordia and megaspore mother cell. ×270. — X: *Combretum ovalifolium.* L.S., ovule at tetrad stage. ×120. — Y: *Combretum ovalifolium.* L.S., ovule showing funicular obturator at mature embryo-sac stage. ×120. — Z: *Lumnitzera racemosa.* L.S., part of mature ovule showing nucellar cap, developing embryo and endosperm. ×160. — END, endosperm; OB, obturator.

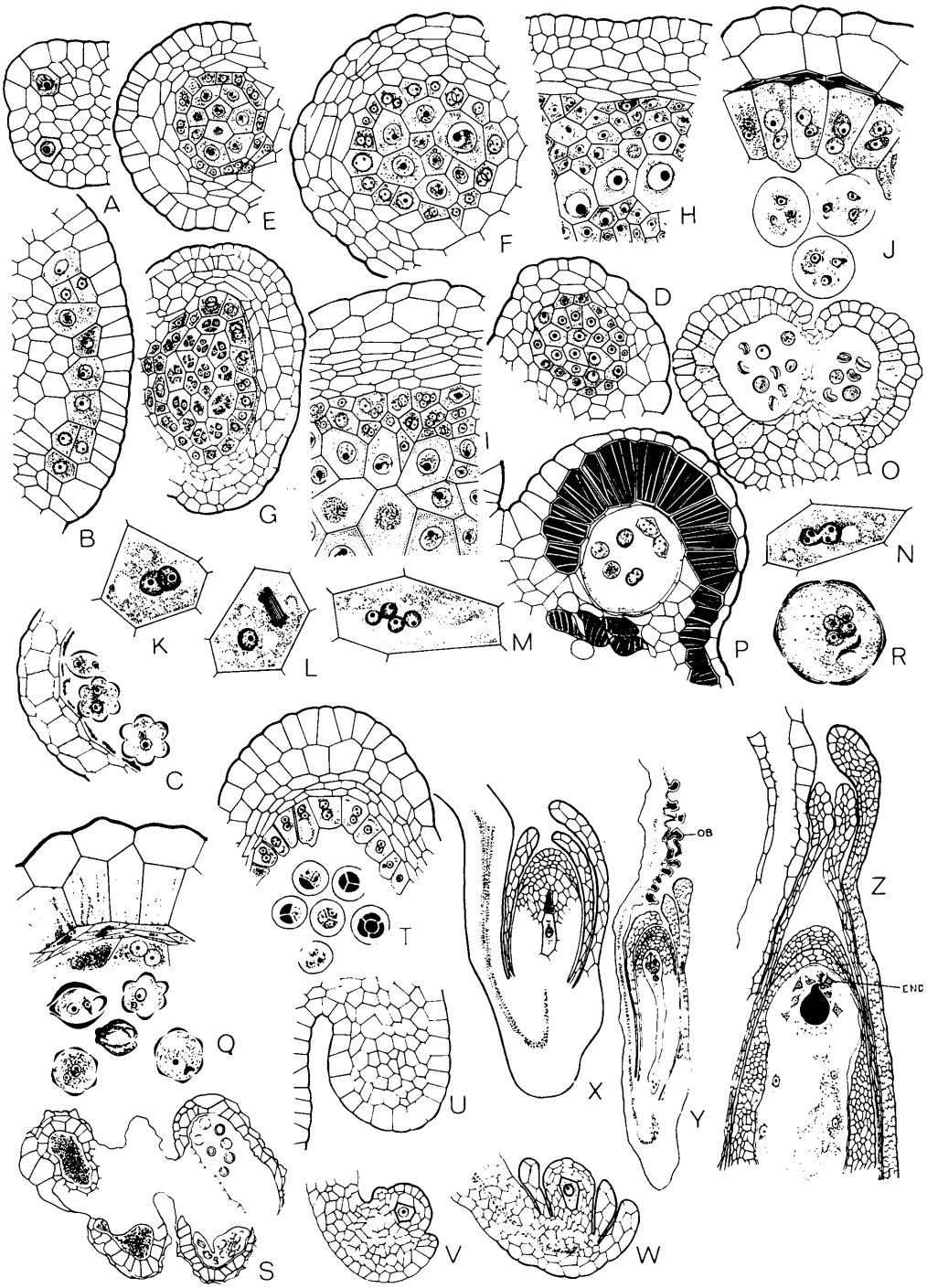

Fig. 1.

three-layered (Fig. 2 H). As the ovules mature the outer integument becomes three- to six-layered in the micropylar region (Figs. 1 Y, Z, 2 A—C). However, it remains two- to four-layered at the chalazal region. The inner integument always remains two-layered even in the mature ovules, except near the micropyle where it is three or four cells thick (Figs. 1 Y, Z, 2 A—C). In *Lumnitzera racemosa* the outer epidermal layer of the outer integument comprises prominently tangentially flattened cells which contain tannin (Fig. 2 E).

The nucellus is extensive in all species studied, excepting *Guiera senegalensis*. The few periclinal divisions that occur in the nucellar epidermis result in a nucellar cap. By the time the ovules mature, the nucellar cap is about three- to five-layered in *Combretum decandrum, C. extensum* and *C. ovalifolium, Anogeissus latifolia* and *A. acuminata*; four- to six-layered in *Combretum grandiflorum* and three- to six-layered in *Terminalia catappa, T. bellerico, T. muelleri, Calycopteris floribunda* and *Lumnitzera racemosa*. The different members investigated manifest a massive parietal tissue (Fig. 2 G, I—O), excepting *Guiera senegalensis,* in which in most ovules it is restricted to two to four layers only (Fig. 2 P—R) and in a few the parietal cell even remains undivided (Fig. 3 A). The extensive formation of parietal tissue keeps the megaspore mother cell deeply seated in the members (Fig. 2 G, I—N) with the sole exception of *Guiera* (Figs. 2 P, 3 A). During the course of the development of the embryo-sac there is a pronounced growth of the chalaza of the ovule similar to the one described for *Poivrea* (VENKATESWARLU 1952 a) and *Combretum paniculatum* and *C. pincianum* (MAURITZON 1939). In most of the species a greater number of cells of the parietal tissue get crushed by the enlarging embryo-sac which, when fully organised, almost abuts on the nucellar cap. Likewise, in the lower end of the ovule the embryo-sac penetrates the chalaza which by now has grown enormously to form the wall of the basal part of the ovule (Figs. 1 Y, 2 D—F). In *Guiera* the embryo-sac exhibits aggressive growth at the micropylar end and extends even into the micropyle absorbing its way through the parietal tissue and the nucellar cap (Fig. 2 C).

A well-developed hypostase which becomes more pronounced during post-fertilization stage is differentiated at the chalazal region of the ovule of *Lumnitzera racemosa* (Fig. 2 E). In *Combretum extensum* a group of nucellar cells extremely rich in plasma is encountered subjacent to the antipodal end of the

Fig. 2. A: *Calycopteris floribunda*. L.S., part of mature ovule with zygote, endosperm nuclei, synergids, degenerating mass, micropylar region of embryo sac, crushed parietal tissue, nucellar cap and two integuments. ×160. — B: *Combretum decandrum*. L.S., part of mature ovule. — C: *Guiera senegalensis*. L.S., part of mature ovule showing absence of parietal tissue and nucellar cap, micropyle formed by inner integument, persisting synergids, proembryo and nuclear endosperm. ×160. — D: *Terminalia catappa*. L.S., mature ovule showing the nucellar cap projecting into the micropyle. ×40. — E: *Lumnitzera racemosa*. L.S., mature ovule. Note hypostase and the epidermal cells of outer integument bearing colouring material. ×40. — F: *Combretum extensum*. L.S., mature ovule. Note hypostase. ×40. — G: *Combretum grandiflorum*. L.S., young ovule with single megaspore mother cell. ×160. — H: *Bucida buceros*. L.S., young ovule with single megaspore mother cell and thick outer integument. ×160. — I: *Combretum grandiflorum*. L.S., nucellus showing deep-seated megaspore mother cell. ×160. — J—O: L.S., nucellus showing tetrad of spores in different members. ×250. — P—R: *Guiera senegalensis*. L.S., young ovule showing nucellus of varying extent. ×400. — ANT, antipodals; DM, degenerating mass; E, egg; EMB, embryo; END, endosperm; ES, embryo-sac; HY, hypostase; II, inner integument; NC, nucellar cap; NU, nucellus; OB, obturator; OI, outer integument; PN, polar nuclei; PS, persisting synergids; S, synergid; VS, vascular strand; Z, zygote.

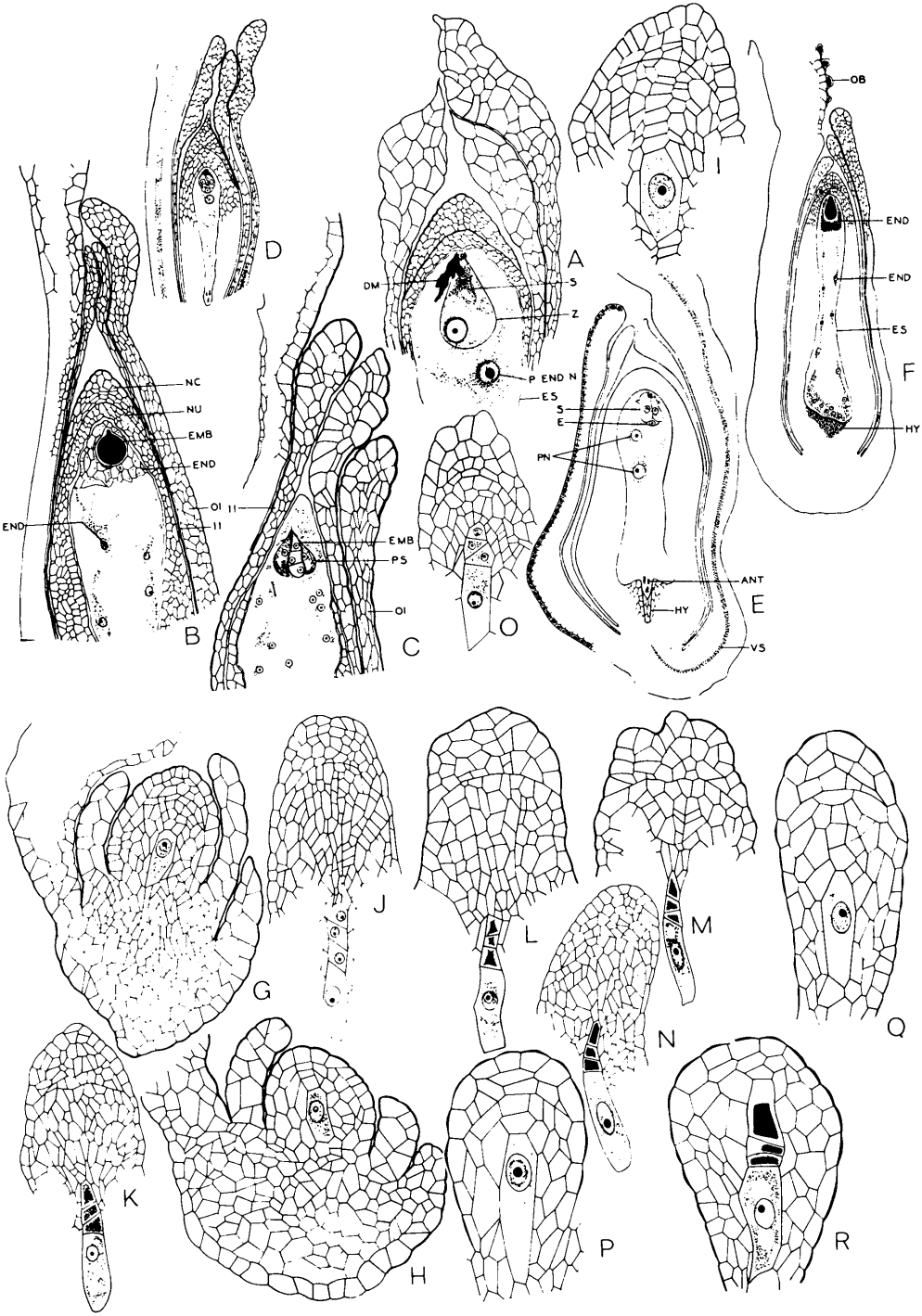
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Fig. 2.

embryo-sac (Fig. 2 F) this resembling the condition reported for Melastomaceae (SUBRAMANYAM 1942).

Megasporangium and Female Gametophyte

As the ovule begins to curve, prior to the appearance of the integumentary primordia, a single hypodermal archesporial cell differentiates from the cells of the nucellus (Fig. 3 B, C). However, in a few ovules of *Combretum grandiflorum, C. ovalifolium, Terminalia catappa, T. muelleri, Guiera senegalensis* and *Lumnitzera racemosa* two or more similar larger cells situated subepidermally may be seen grouped together simulating archesporial cells (Fig. 3 D), but in no case does more than one continue to develop. After some enlargement, the archesporial cell functions as the megaspore mother cell cutting off a primary parietal cell (Fig. 3 E). Occasionally, however, ovules with two megaspore mother cells have also been met with in *Terminalia bellerica, T. muelleri, Anogeissus latifolia, A. acuminata* and *Calycopteris floribunda* (Fig. 3 F). The deep-seated megaspore mother cell (Fig. 2 G, I) undergoes two meiotic divisions and forms a linear tetrad of megaspores (Figs. 2 J—O, 3 G—K) with an exception of a few ovules in *Terminalia catappa* showing a T-shaped tetrad (Fig. 3 L). Irrespective of the mode of arrangement of the four haploid megaspores, ultimately, three of them are crushed and the chalazal one alone functions to form the female gametophyte. The traces of the degenerating cells persist even up to the 8-nucleate stage of the embryo-sac in *Terminalia muelleri* (Fig. 3 M). The functional megaspore subsequently enlarges and through three successive divisions develops into a 2-, 4-, and 8-nucleated gametophyte (Fig. 3 N—P, M). The micropylar quartet organises earlier and the mature embryo-sac displays an egg apparatus, two polar nuclei and three antipodal cells (Fig. 3 Q—S, U). The mature embryo-sac is elongated and somewhat variable in form. It is broad at the micropylar end and tapers gradually towards the chalazal end in *Combretum extensum, C. grandiflorum, C. decandrum, Terminalia catappa, T. muelleri, T. bellerica, Bucida buceros, Anogeissus latifolia* and *A. acuminata* (Figs. 2 D, 3 Q); bulbous at the micropylar end and narrow towards the chalazal end in *Combretum ovalifolium* (Figs. 1 Y, 3 R); comparatively broad towards the chalazal end in *Lumnitzera racemosa* (Figs. 2 E, 3 S); and spindle-shaped in *Guiera senegalensis* and *Calycopteris floribunda* (Fig. 3 U). Thus in all the species studied here, the development of megagametophyte conforms to the monosporic *Polygonum* type (MAHESH-

Fig. 3. A: *Guiera senegalensis.* L.S., young ovule showing the division of megaspore mother cell. Note that the parietal cell has not undergone further division. ×400. — B: *Combretum ovalifolium.* L.S., ovule primordium showing single-celled hypodermal female archesporium. ×270. — C: *Bucida buceros.* L.S., young ovule showing the female archesporium. ×270. — D: *Terminalia muelleri.* L.S., ovule showing multiple archesporium. ×400. — E: *Combretum decandrum.* L.S., young ovule showing single megaspore mother cell and late emergence of integuments. ×200. — F: *Combretum grandiflorum.* L.S., ovule showing two deep-seated megaspore mother cells. ×270. — G—K: Linear tetrad of megaspores in different members. ×270. — L: *Terminalia catappa.* T-shaped tetrad of megaspores. ×270. — M—P: Development of embryo-sac in different members. ×80. — Q—S, U: Fully developed embryo-sac in different members. ×180. — T: *Lumnitzera racemosa.* Micropylar part of embryo-sac showing egg apparatus. ×270. — V: *Guiera senegalensis.* L.S., embryo-sac showing 6 antipodal cells and proembryo. ×180. — W: *Calycopteris floribunda.* Three embryo-sacs at different stages of development. ×180. — X: *Combretum grandiflorum.* Embryo-sac with developing embryos and aggregation of endosperm nuclei at both ends. ×160. — Y—H': Embryo development in different members. ×140. — ANT, antipodals; ♀ ARCHE, female archesporial cell.

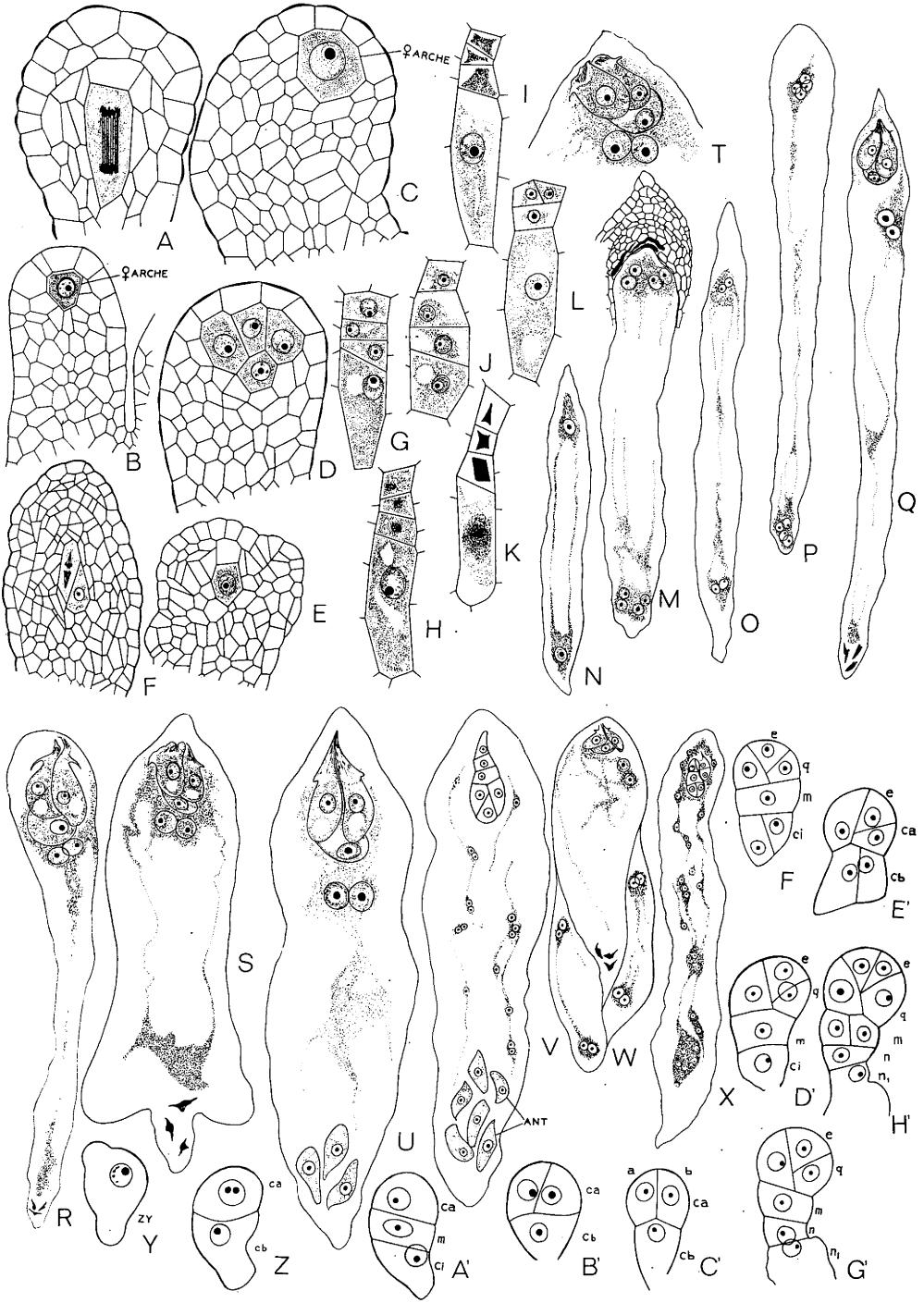
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Fig. 3.

WARI 1950). Each synergid develops hooks and a typical filiform apparatus and are usually ephemeral, but in *Guiera senegalensis* they persist up to the early stages of embryo formation. The egg cell is larger, flask-shaped, highly vacuolated and with the nucleus usually located in its lower part (Fig. 3 Q—U, W).

The three nuclei at the chalazal end of the embryo-sac go to organise the antipodal cells before the egg apparatus organises and disappear usually prior to triple fusion (Fig. 3 R—T, X). In *Guiera senegalensis,* however, the antipodal cells remain persisting healthy into early embryogeny and in certain ovules they even show a secondary increase in number up to a maximum of six (Fig. 3 V).

Usually, only one embryo-sac is formed in each ovule. Occasionally, however, the occurrence of three embryo-sacs within an ovule has been encountered in *Calycopteris floribunda* (Fig. 3 W). In such exceptional cases one embryo-sac showed the complete development of the egg apparatus, polar nuclei and the degenerating antipodal cells, while the others did not develop beyond the four-nucleate stage and ultimately degenerated.

Even when a single embryo-sac is present in an ovule several cases of degeneration of the embryo-sacs during the various stages of development were met with in *Combretum decandrum, C. extensum, Terminalia muelleri, Bucida buceros, Anogeissus latifolia, A. acuminata* and *Calycopteris floribunda.* In *Anogeissus* species and *Combretum extensum* all the megaspores of the tetrad degenerate in some ovules (Fig. 3 K), while in others degeneration sets in after the embryo-sac had reached the four-nucleate stage. About 60 % of the ovules examined contained degenerating embryo-sacs in *Calycopteris, Terminalia bellerica* and *Combretum extensum.* This abortion of megaspores and embryo-sacs recalls the parallel features in the development of the male gametophytes described earlier.

Fertilisation and Endosperm Formation

The style has a narrow canal lined by small richly protoplasmic cells which function as a transmitting tissue. Fertilisation is porogamous. At about the time of the organisation of the mature embryo-sac the long funicles in *Combretum ovalifolium, C. decandrum, C. extensum* and *C. grandiflorum* are lined with large papillate cells resulting in the formation of an obturator (Figs. 1 Y, 2 F). The formation of a funicular obturator has been observed earlier in *Combretum paniculatum, C. pincianum* (MAURITZON 1939), *Quisqualis indica* (FAGERLIND 1941) and *Poivrea coccinea* (VENKATESWARLU 1952 a).

The triploid primary endosperm nucleus is multiplied by a few divisions without the formation of septa long before the oospore divides for the first time. Thus the endosperm formed in the earlier stages is of the free nuclear type. The disposition of the endosperm nuclei is interesting in that there is a definite accumulation in the chalazal and micropylar regions of the megagametophyte, while at sides, the nuclei are not only relatively few but even spatially separated in the cytoplasmic lining of the megagametophyte (Fig. 3 X). This forms a characteristic feature in all the members under study. The cytoplasm at the antipodal region of the embryo-sac accumulates as a thick granular sheet in which a great number of endosperm nuclei is closely disposed. At the other end of the embryo-sac the nuclei stand apart from each other, and so there appears to be a dense aggregation of a larger number of nuclei at the chalazal end alone (Fig. 3 X). By about the time the developing embryo approaches the globular stage, wall formation sets in in the micropylar part of the free nuclear endosperm (Figs. 1 Z, 2 B). In the fully developed seed, the endosperm becomes consumed by the developing embryo.

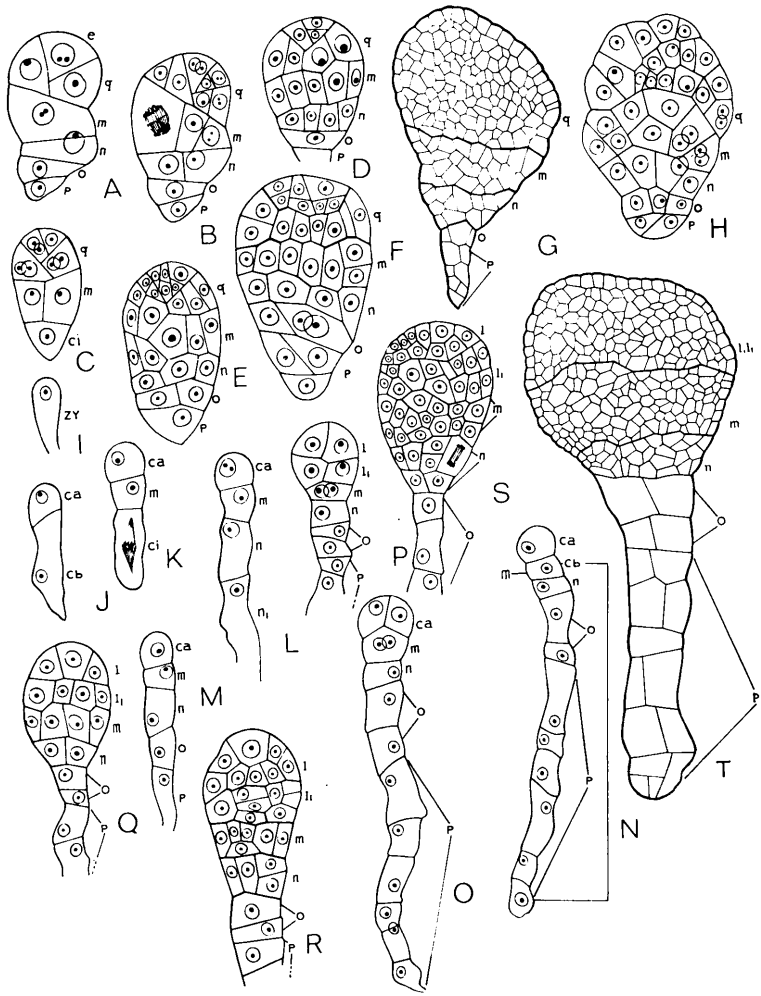

Fig. 4. A—H: Various stages in the embryo development in different members. ×140. — I—T: *Terminalia chebula.* Various stages of the embryo development. ×140.

Embryo Development

In all the members investigated here, the zygote divides only after the primary endosperm nucleus has divided a number of times (Fig. 3 Y). The first division of the zygote is transverse with the result that a two-celled pro-embryo comprising a terminal cell *ca* and a basal cell *cb* is organised (Fig. 3 Z). Generally, division in *ca* precedes that in *cb,* although very occasionally the reverse may be true in *Guiera senegalensis, Terminalia bellerica, Anogeissus latifolia, Combretum grandiflorum* and *Calycopteris floribunda* (Fig. 3 A'). *ca* divides by an oblique wall into two juxtaposed unequal cells, namely *a* and *b* (Fig. 3 B'). Occasionally in *Terminalia catappa, Bucida buceros, Combretum extensum, C. decandrum* and *Lumnitzera racemosa* this wall may be vertical

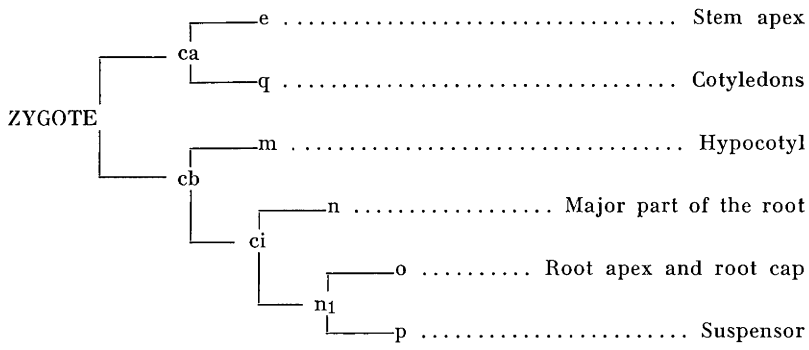

Fig. 5. Schematic representation of the embryogeny common to most of the Combretacean taxa in this study.

resulting in nearly equal cells (Fig. 3 C'). Next an oblique wall is laid down in the larger of the two resultant cells cutting off a triangular epiphyseal initial *e* distinguished from the rest by its shape and position (Fig. 3 D', E'). The three cells derived from *ca* constitute the portion designated *q* (Figs. 3 D'—G', 4 A). Concurrently with the above events in the terminal cell *ca,* the basal cell *cb* of the two-celled pro-embryo divides transversely forming two superposed cells *m* and *ci* (Fig. 3 G', H'). The divisions in *ci* may be also vertical or even oblique as in *Terminalia catappa* and *Bucida buceros* (Fig. 3 F'). A little later, the lower of the derivatives (n_1) of the cell *ci* undergoes a transverse division forming two more cells *o* and *p* (Fig. 4 A).

The course of events taking place subsequently in the different tiers of the pro-embryo is as follows:

As already described an epiphyseal initial *e* is differentiated early in the terminal tier. It usually divides longitudinally and the subepiphyseal cell by a vertical or oblique wall (Figs. 3 H', 4 B). Periclinal divisions take place in the daughter cells thus formed (Fig. 4 D). The derivatives of the epiphyseal initial form a group of cells which are quite distinct from the subepiphyseal cells and ultimately form the stem apex (Fig. 4 B—F). Subsequently the derivatives of the subepiphyseal cells also divide periclinally demarcating the epidermal initials (Fig. 4 F). Both anticlinal and periclinal divisions take place in the inner cells of the subepiphyseal region and the derivatives form the massive cotyledons of the mature embryo. The entire epiphyseal region, however, loses its identity during the advanced stages of embryo development (Fig. 4 G, H).

The middle cell *m* undergoes two longitudinal divisions at right angles to each other giving rise to four circumaxially arranged cells (Fig. 4 B). The first of these divisions may be completed much earlier than the formation of *n* and n_1 as in *Combretum grandiflorum, Calycopteris floribunda* and *Lumnitzera racemosa* (Figs. 3 H', 4 C). The differentiation of the dermatogen takes place following the periclinal divisions in the four cells of *m* a little later than the formation of the epidermal initials in the terminal tier (Fig. 4 E). The diverse histogenic layers in this tier are differentiated prior to the cotyledonary primordia making their appearance in the epiphyseal region.

The cell *ci,* as mentioned earlier, undergoes a transverse division forming two superposed daughter cells *n* and n_1 (Fig. 3 G'). The cell *n* soon divides by vertical and transverse walls and the dermatogen initials are differentiated following periclinal divisions (Fig. 4 B, D). The divi-

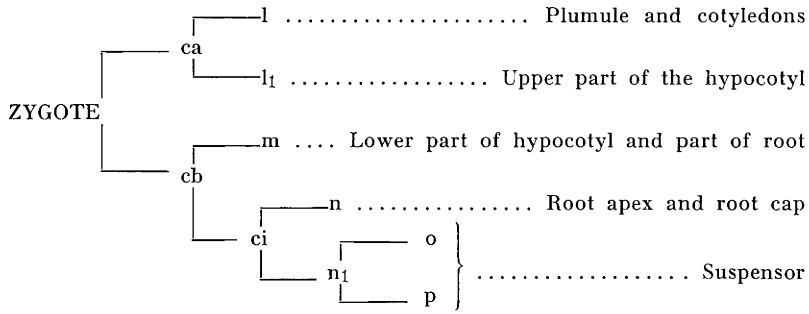

Fig. 6. Schematic representation of the embryogeny of *Terminalia chebula*.

sion in the tier *n* take place only subsequent to the formation of epidermal initials in the cells of the tier *m* (Fig. 4 D). The derivatives of the cell *n* contribute to the major part of the root. The cell n_1 divides transversely to form two superposed cells *o* and *p* (Fig. 4 A). The former divides longitudinally twice and then tangentially. The derivative cells that are cut off inwards form the root apex, while those cut off outwards form the root cap initials. Subsequent divisions in the initiating layer of the root cap result in a multi-layered root cap. The cell *p* divides transversely and obliquely a few times to form a several-celled suspensor in *Terminalia catappa, T. paniculata* and *Lumnitzera racemosa,* while in others it divides and forms a two-celled suspensor (Fig. 4 G—H).

From the foregoing details of embryogeny, it can be gathered that the embryo is formed from the derivatives of both the terminal (*ca*) and the basal (*cb*) cell of the two-celled pro-embryo. Thus the development of the embryo conforms to the Asterad type (JOHANSEN 1950). Further, since an epiphyseal cell is differentiated and the tier *n* is not involved in the formation of the suspensor, the embryogeny keys out to the Erodium Variation (JOHANSEN 1950). The schematic representation in Fig. 5 enumerates the derivatives of the diverse embryonic tiers.

All the members investigated here conform to the embryogeny described above. *Terminalia chebula* presents certain differences and therefore its embryo development is described separately below.

Embryo Development in Terminalia chebula

The first division in the zygote is transverse and takes place after a few free endosperm nuclei are formed as in other Combretaceae, and gives rise to a two-celled pro-embryo with the basal cell *cb* and terminal cell *ca* (Fig. 4 I, J). The cell *cb* divides transversely resulting in two superposed cells *m* and *ci* (Fig. 4 K). Further transverse division in *ci* produces the tiers *n* and n_1 (Fig. 4 K, L). The latter undergoes further divisions transversely resulting in a filamentous pro-embryo (Fig. 4 M—O).

The cell *ca* divides longitudinally into two juxtaposed cells about the time the cells *m, n, o* and *p* are differentiated (Fig. 4 O). The derivatives of *ca* form a quadrant consequent to the second longitudinal division at right angles to the first. Transverse division in the quadrant results in an octant comprising the tiers *l* and l_1 (Fig. 4 P). Following the segmentation in *ca,* a quadrant is organised in *m*. Periclinal division in tiers *l,* l_1 and *m* demarcates the dermatogen initials in each of them (Fig. 4 Q, R). Further divisions follow in the inner cells of each tier resulting in the differentiation of the periblem and plerome.

As a sequal to the aforesaid changes in *ca* and *m*, a quadrant is formed in the cell *n* (Fig. 4 Q—S). Further divisions occur in the tangential plane and the cells formed towards the inside give rise to the root apex while those laid down towards the periphery form the root cap.

The cell n_1 divides to form the superposed daughter cells *o* and *p* (Fig. 4 M). Both of these further divide to give rise to a suspensor, which is about eight cells long (Fig. 4 N, O) and remains two cells broad throughout its greater part and four cells broad at the basal region (Fig. 4 T).

From the details enumerated above it is clear that *ca* and *cb* are involved in the formation of the embryo proper. *Terminalia chebula* differs from the other combretacean taxa investigated in the absence of an epiphyseal cell, the derivative n_1 entering into the constitution of the suspensor and in the origin of the upper and lower parts of the hypocotyl. Therefore, though the embryogeny conforms to the Asterad type, it keys out to its Polygonum variation. The developmental details in respect of *Terminalia chebula* are schematically represented in Fig. 6.

Polyembryony

Normally a single embryo develops in the embryo-sac of the members studied here. However, in some taxa (*Combretum grandiflorum, C. decandrum, C. extensum, Terminalia catappa, Calycopteris floribunda, Guiera senegalensis* and *Lumnitzera racemosa*) two embryos were noticed in a few ovules (Fig. 3 X). In such cases the second embryo was disposed lateral to the zygotic embryo. This evidently suggests that the extra embryo originates from one of the synergids.

DISCUSSION AND CONCLUSIONS

It is evident from the preceding description that by and large there is a great uniformity in the embryological features, *Combretum grandiflorum, Guiera senegalensis* and *Lumnitzera racemosa* being most deviant.

The members exhibit two to three middle layers in the anther wall, except that *Combretum grandiflorum* shows a maximum of six middle layers and *Guiera senegalensis* only one. Thus all the members discussed here, with the exception of *Guiera,* conform to the basic type of anther-wall formation met with in the dicotyledonous plants and which in the opinion of DAVIS (1966) is a derived feature.

The glandular tapetum is parietal in origin as in *Poivrea coccinea* (VENKATESWARLU 1952 a). The tapetum remains one-seriate throughout, although a partly two-seriate condition was found in *Quisqualis indica, Terminalia muelleri, Bucida buceros* and *Calycopteris floribunda.* A feature of exceptional interest is the occurrence of a multi-layered tapetum in *Combretum grandiflorum.*

As has already been mentioned, there is a total collapse of the entire mass of the sporogenous cells in some of the lobes of the anthers in *Terminalia bellerica, Combretum extensum* and *Calycopteris floribunda,* while degeneration in *Combretum grandiflorum* is restricted to a few of the microsporocytes and in still others such as *Terminalia catappa* degeneration of microspores takes place at varying stages of development. Thus there seems to be a progressive degeneration of sporogenous cells in the family, leading to different degrees of sterility.

The functional significance, if any, of this consistent degeneration of some potential sporogenous cells is not obvious. KAUSIK (1939), MAHESHWARI (1934) and DNYANSAGAR (1947) suggested that the degeneration of sporogenous tissue may fulfil, at least in part, the function of the tapetum by furnishing nourishment to the developing sporogenous cells. The cells in the middle layers of the anther were also

considered as forming auxiliary nutritive tissue by COULTER and CHAMBERLAIN (1903) and SINGH (1936). It is not easy to understand how degenerated pollen mother cells can supply nourishment to the surviving pollen mother cells acting as an auxiliary nutritive tissue in addition to the tapetum. It seems especially improbable in *Combretum grandiflorum*, where the tapetum is several-layered; in the related species with single tapetal layers all the pollen mother cells could develop normally. Nor can the degeneration of all the mother cells in an anther lobe be explained on the basis of the 'auxiliary nutritive concept' visualised by KAUSIK (1929) and MAHESHWARI (1934). In the grasshopper *Melanoplus differentialis* and in many other insects the sperm mother cells are grouped into well-defined cysts within each of the testicular follicles. The cells within a cyst are well synchronised in DNA synthesis and stage of division indicating a uniform normality of cytoplasm. LIMA-DE-FARIA and NORDQUIST (1962) found that at the onset of meiosis and after DNA synthesis all the nuclei of the sperm mother cells in the same cyst broke down. One of the three cysts of each follicle behaved in this way. The degeneration of a few pollen mother cells in an anther lobe is similar to this situation. LIMA-DE-FARIA and NORDQUIST (1962) regarded the condition in *Melanoplus* as an adaptation by which a large amount of DNA is made available at a suitable time of development. JOHN and LEWIS (1965) have pointed out that such an interpretation is rather hazardous and suggested the condition to be somewhat similar to the degeneration of all but one of the growing embryos of gymnosperms where degenerated embryos may presumably be nutritive, the extra embryos making a contribution comparable to that of endosperm in angiosperms. The situation here may be the same as suggested by JOHN and LEWIS (1965) for the degeneration of some of the sperm cells in *Melanoplus*. Perhaps an alternative explanation can be sponsored for the condition in combretacean taxa. If a nutritional supply for a flower is not sufficient to enable all pollen mother cells to develop into mature pollen grains, then as a matter of biological economy some of the pollen mother cells may be supposed to be diverted from their reproductive function to a nutritional function thus making available the nutrients for the normal growth of the rest of the pollen mother cells. From the foregoing discussion it is quite likely that the causes for the degeneration of the pollen mother cells and the spores, therefore, may be more deep-seated and not so simple as described by KAUSIK (1939), MAHESHWARI (1934), DNYANSAGAR (1947) and COULTER and CHAMBERLAIN (1903).

All the taxa possess an inferior unilocular ovary. The number of ovules, which are pendulous and suspended by distinct funicles of varying lengths, is varied in the different taxa. The observations made now by us and those by others made earlier (MAURITZON 1939; FAGERLIND 1941; VENKATESWARLU 1952 a; NAGARAJ 1954 a—c, 1955) show that the anatropous configuration of the ovules, their bitegminous nature and the formation of zigzag micropyle seem to be common features in the combretacean taxa. One other feature of uniform occurrence in the family as observed now and earlier (MAURITZON 1939; FAGERLIND 1941; VENKATESWARLU 1952 a) is the formation of a multilayered nucellar cap and an extensive nucellar tissue. However, the occurrence of such crassinucellate ovules is not restricted to Combretaceae but also appears to be an established feature in Thymelaeaceae (VENKATESWARLU 1945, 1947), Melastomaceae (SUBRAMANYAM 1942), Punicaceae (MAURITZON 1939), Lythraceae (JOSHI & VENKATESWARLU 1935 a, b) and other families showing some relationship to Combretaceae.

Guiera senegalensis differs from other Combretaceae in the formation of a few-layered parietal tissue and nucellar cap.

Further in a restricted number of ovules the parietal cell does not even divide and such ovules, though crassinucellar, seem to approach a tenuinucellate condition. Thus in one and the same species a tendency towards a meagre development of the nucellar cap and parietal tissue is met with. It is therefore probable that *Guiera* represents a transitional stage in the evolution of the nucellar tissue and may be considered as a derived member among the combretacean stock foreshadowing the ultimate establishment of the tenuinucellate condition of the ovule such as met with in the Lecythidaceae. The latter possibility seems to receive some support from the highly condensed inflorescence of *Guiera,* which on exomorphic grounds must be regarded as a derived condition. In other members of the family the flowers are aggregated into spikes or racemes, a feature generally accepted as less evolved than the head. It may also be mentioned that the members of Lecythidaceae studied by MAURITZON (1939) and VENKATESWARLU (1952 b) show a tenuinucellate nature of the ovule such as foreshadowed by the above-mentioned exceptional ovules in *Guiera.*

A hypostase is present at the chalazal region in the ovules of *Lumnitzera racemosa,* a feature that has not been so far reported for the members of Combretaceae (MAURITZON 1939; FAGERLIND 1941; VENKATESWARLU 1952 a; PRAKASA RAO 1963). In *Combretum extensum* a region of cells with dense cytoplasm is encountered at the corresponding position in the chalazal end of the ovules. There are, however, no cells with thickened walls. If one were to concur with MAHESHWARI (1950) in that "the hypostase may not always consist of thick-walled cells" *Combretum extensum* may also be recognised as having a hypostase despite the morphological dissimilarities in the constituent cells.

Diverse opinions have been expressed about the function of the hypostase (HABERLANDT 1923; JOHANSEN 1928; JOSHI & VENKATESWARLU 1936; VENKATA RAO 1953). In the light of these conflicting views, it is rather difficult to assess the significance and importance of the hypostase in the restricted instances where it is met with. In this connection, the comparatively broader antipodal end of the embryo-sacs encountered in *Lumnitzera racemosa* in which a well-defined hypostase is manifested, may be of some interest. It is likely that in this species, the growth of the embryo-sac is rather vigorous at the antipodal end and that its sustained downward growth into the chalaza may crush it; this is arrested by the thick-walled cells of the hypostase. As a consequence, it would be natural for the lower part of the embryo-sac to enlarge in a different direction and thus to become comparatively broader at the antipodal end. Such a view was also expressed by VAN TIEGHEM (1901), who regarded the hypostase as forming a sort of barrier for the growing embryo-sac, thus preventing it from pushing its way into the base of the ovule.

The primary archesporium in the ovule is single-celled and hypodermal. This feature is uniformly met with in all the taxa examined now and earlier (VENKATESWARLU 1952 a). However, a few members like *Combretum ovalifolium, C. grandiflorum, Terminalia catappa, T. muelleri, Guiera senegalensis* and *Lumnitzera racemosa* display multiple archesporium in a small percentage of ovules. Such a condition was earlier reported by VENKATESWARLU (1952 a) in *Poivrea coccinea.* The presence of supernumerary embryo-sacs is recorded in a few ovules of *Calycopteris floribunda.* This may be ascribed to the functioning and further development of more than one archesporial cell or by apospory (MAHESHWARI 1950). In the former case the embryo-sacs would be almost of the same age while in the latter the embryo-sacs would be younger than the normally developed one. It has, however, been found in the present investigation that the ovules containing

plural embryo-sacs have been produced as a consequence of the functioning of more than one megaspore mother cell. The extra embryo-sacs eventually degenerate.

The occurrence of monosporic (VENKATESWARLU 1952 a; NAGARAJ 1955; PRAKASA RAO 1963) as well as tetrasporic (MAURITZON 1939) types of embryo-sacs have been reported in this family. However, only the Polygonum type of embryo-sac has been found to occur in the plants included in the present study. The development of 16-nucleate embryo-sacs in *Combretum paniculatum* and *C. pincianum* (MAURITZON 1939) is to be reckoned as being exceptional in the family and needs confirmation.

In all members excepting *Guiera* the synergids are ephemeral. In *Guiera* they degenerate only when the development of the embryo is well under way (Fig. 2 C). Such a persistance of the synergids has also been observed in *Poivrea* (VENKATESWARLU 1952 a).

The occurrence of three uninucleate antipodal cells is a usual feature of the family. They degenerate only after the organisation of the embryo-sac and the degenerated antipodals can be seen as deeply stained specks even after fertilisation (Fig. 3 Q—S, W). In *Guiera,* on the other hand, there is not only a secondary increase in their number, but they even persist up to a very late stage after fertilisation. This condition is to be treated as exceptional in the family and *Guiera* deviates from the rest of the members in this respect.

Although the endosperm is of the nuclear type, no detailed account of its development has been given except for *Poivrea coccinea* (VENKATESWARLU 1952 a). The present investigation indicates that the endosperm formation follows the conventional type. While describing the endosperm of *Lumnitzera* species, KARSTEN (1891) remarked the absence of cell formation. The present study clearly reveals the formation of endosperm cells at the micropylar region of the embryo-sac in *Lumnitzera racemosa,* so that KARSTEN's remark is not substantiated by our observation.

The detailed development of the embryo in the family has only recently been described by VENKATESWARLU (1952 a) in *Poivrea.* The embryo development in all the species studied here, with the sole exception of *Terminalia chebula,* agrees with that found in *Poivrea.* It keys out to the Erodium variation of the Asterad type, while in *Terminalia chebula* it is of the Polygonum variation of the Asterad type.

From the foregoing it can be seen that the combretacean taxa seem to display uniformity in the development of the anther, ovule, male and female gametophytes, endosperm and embryo development. However, *Guiera* differs from the rest of the Combretaceae in several features such as in having a single middle layer in the anther wall, the formation of the micropyle by the inner integument alone in mature ovules, the absence of funicular obturator, the sparse development of nucellus and nucellar cap, the shape of the embryo-sac, the persistance of the synergids and the antipodals and in the secondary increase of the antipodal cells. Likewise, in external morphology it deviates from the rest of the tribe Combreteae of EXELL (1931), as the flowers are aggregated into dense, capitulum-like masses while in the others they are grouped into racemes or spikes. Studies in floral anatomy (VENKATESWARLU & PRAKASA RAO 1970), have revealed that *Guiera* has a five-carpellate ovary, while the other representants have three or four carpels only. Thus from the point of view of comparative embryology, floral anatomy and exomorphic features *Guiera* seems to stand out from the rest of the Combretaceae in general and in particular from the tribe Combreteae and merits separation from the Combreteae into a separate monogeneric tribe, the Guieraeae. Among Combreteae *Poivrea,* on embryo-

logical and exomorphic features seems to be close to the genus *Combretum* except for the absence of a floral disc and possession of a three-carpellate ovary. In view of these points of difference the retention of *Poivrea* as a distinct genus is advocated as against DE CANDOLLE's (1828) suggestion to include it in the genus *Combretum*. It may be mentioned here that EXELL (1931) in his classification and regrouping of different genera within the family has made no mention of this genus.

Embryological and floral anatomical evidence support the distinctiveness of *Lumnitzera* and warrent placing it in a separate tribe, the Laguncularieae. *Lumnitzera* possesses a well-defined hypostase and the occasional occurrence of polyspermy — features hitherto unrecorded for Combretaceae. From an exomorphic point of view this genus stands apart from the rest in bearing bracteoles adnate with lower receptacle and 8-carpellate ovary (VENKATESWARLU & PRAKASA RAO 1970). This gains further support from EXELL's (1931) view; he commented that "the only criticism which might be made is that the Laguncularieae are obviously a much more distinct group than the other and should perhaps be placed in a different category".

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Structural Chromosome Polymorphism in Diploid Leopoldia weissii (Freyn) Freyn ex Heldr. (Liliaceae)

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ABSTRACT

BENTZER, B. 1972. Structural chromosome polymorphism in diploid Leopoldia weissii (Freyn) Freyn ex Heldr. (Liliaceae). — Bot. Notiser 125: 180—185.

A case of spread segmental chromosome aneuploidy in the diploid (2n=18) *Leopoldia weissii* (Liliaceae) is described. The additional segment is presumed to have originated by interchange, or by the breakage of a U-type chromatid bridge.

INTRODUCTION

Structural polymorphism in chromosome complements is a well-known and widely distributed phenomenon in many organisms (cf. DARLINGTON 1965, JOHN & LEWIS 1968). The origins of polymorphism are diverse, e.g. hybridization, inversions, interchanges, and duplications. A rarely studied phenomenon is the addition of a supernumerary chromosome segment to a particular chromosome of a complement. Such additional segments are described from zoological material (WHITE 1954, NUR 1961, COHEN & PINSKY 1966, and JOHN & HEWITT 1966), but it has not been possible to find contributions from botany. In most cases the segments involved are of a heterochromatic nature. In some instances it is a matter for discussion whether the inequality of a bivalent is due to a gain or a loss of genetic material in one of the chromosomes (JOHN & HEWITT 1966).

The standard chromosome complement in the genus *Leopoldia* PARL. is markedly bimodal (Figs. 1, 2 A) with n(4L+6M+8S) chromosomes (BENTZER 1969). The two pairs of long chromosomes are easily distinguishable from each other. One pair is telocentric (*t*) and the other is subtelocentric (*st*) (Table 1). The medium and short chromosomes are only identifiable as groups. The chromosome nomenclature follows LEVAN et al. (1964).

MATERIAL

Twelve specimens from two populations of the diploid (2n=18) *Leopoldia weissii* were studied. This species of Grape Hyacinth is restricted to the Aegean archipelago and adjacent areas. One population (no. 307) originates from the S. part of the island of Rhinia in the Kikladhes, Greece, while the other (no. 318) originates from the N. part of the same island. The plants have been grown for 3 years in the greenhouses of the Botanical Gardens of Lund.

METHODS

Mitotic chromosomes were studied in root-tip squashes. The fixative was Carnoy (3:1) and the squash technique used was the one described by ÖSTERGREN and HENEEN (1962) with minor modifications (BENTZER 1969).

Meiotic chromosomes were studied in Feulgen stained squashes of PMCs. The buds were fixed overnight in ethanol, propionic acid, and chloroform (6:1:3). They were then transferred to 70 % ethanol. The squash

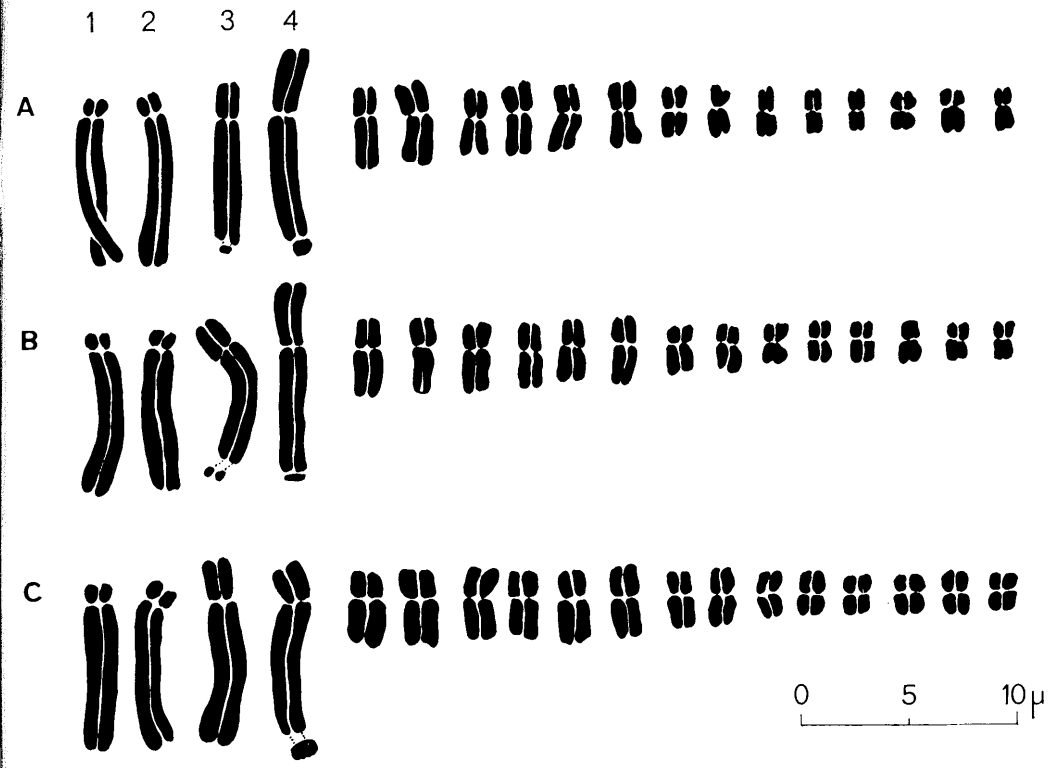

Fig. 1. Karyotypes from root tip mitoses in *Leopoldia weissii*. — A: Segmental aneuploid from population no. 307. — B: Segmental aneuploid from pop. no. 318. — C: Normal plant from pop. no. 318. The four long chromosomes are numbered.

technique for meiosis was similar to the one used for mitotic chromosomes.

Drawings were made with the aid of a Leitz binocular camera lucida and the photomicrographs were taken with a Nikon AFM camera on a Leitz Orthoplan microscope. The film was Scientia 39 C 56.

RESULTS

In population no. 307 the 4 individuals studied were all heterozygous for a supernumerary segment on the short arm of one long *st* chromosome (Figs. 1 A and 2 A, Table 1). A corresponding loss of genetic material was not found in any other chromosome.

In population no. 318, 2 of 8 individuals were heterozygous for a similar additional segment (Fig. 1 B). The remaining 6 specimens were all normal homozygotes (Fig. 1 C). The supernumerary segment was of almost the same size as the ordinary short arm of the *st* chromosomes. The long *st* chromosomes were structurally similar apart from the extra segment and the satellites. Satellites are unreliable chromosome markers in *Leopoldia* (BENTZER 1969), being variable in number, size and position even within populations.

Meiotic studies of the segmental aneuploid plants revealed normal pairing with 9 bivalents. Chromosomes nos. 3 and 4 formed a markedly unequal bivalent (Fig. 2 B). Some five hundred good diakinesis—

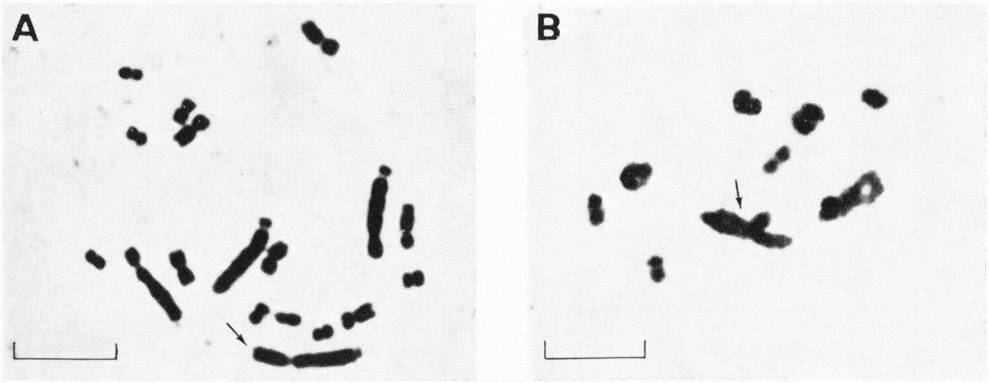

Fig. 2. A: Mitotic metaphase of segmental aneuploid from population no. 307. Arrow indicates abnormal chromosome. Scale unit equals 10 μ. — B: Diakinesis of segmental aneuploid from population no. 307. Arrow indicates unequal bivalent formed by the two *st* chromosomes. Scale unit equals 10 μ.

metaphase cells from 3 structurally heterozygous specimens were studied. Univalents were never observed. The 4 long chromosomes seemed to form weakly associated quadrivalents in a few early diplotene cells. These apparent associations were never maintained until metaphase I. Similar quadrivalents were rarely formed in normal homozygotes from population no. 318.

Anaphase I was studied in one heterozygous individual from population no. 318. A number of dicentric bridges occurred. Some of them were of chromatid origin, i.e., paracentric inversions and U-type exchanges, while others were of sub-chromatid origin (Fig. 3, Table 2).

The frequency of aberrant A I in the only individual investigated from population no. 307 was lower. Normal homozygotes from population no. 318 seemed to have few chromatid bridges while the sub-chromatid bridges were fairly frequent (Table 2). Diploid *L. weissii* from other populations have far fewer bridges in A I.

DISCUSSION

The origin of the segmental aneuploidy can not be stated with certainty. Outside the scope of what is reported in this paper some 200 population samples of *Leopoldia* species from the Aegean have been cytologically investigated. In none of these was there found a pair of homologous chromosomes similar to chromosome no. 4 in Fig. 1 A and B. The occurrence of segmental aneuploidy due to hybridization is therefore a scarcely tenable possibility. Two alternative explanations seem more plausible.

1. Unequal interchange and the subsequent elimination of the most deficient chromosome combination.

Interchange without elimination would presumably result in a certain amount of multivalent configurations. If, on the other hand, the interchange occurred long ago and the most deficient gametes have been eliminated, the interchanged segment would appear as a duplication, and multivalent configurations in meiosis would not be expected.

COHEN and PINSKY (1966) described a case of autosomal polymorphism in *Cavia porcellus* (Guinea Pig). Two homologous *st* chromosomes were present in three different combinations: 1. Both chromosomes normal. 2. One normal and one without the short arm. 3. One normal and one with the short arm duplicated. They

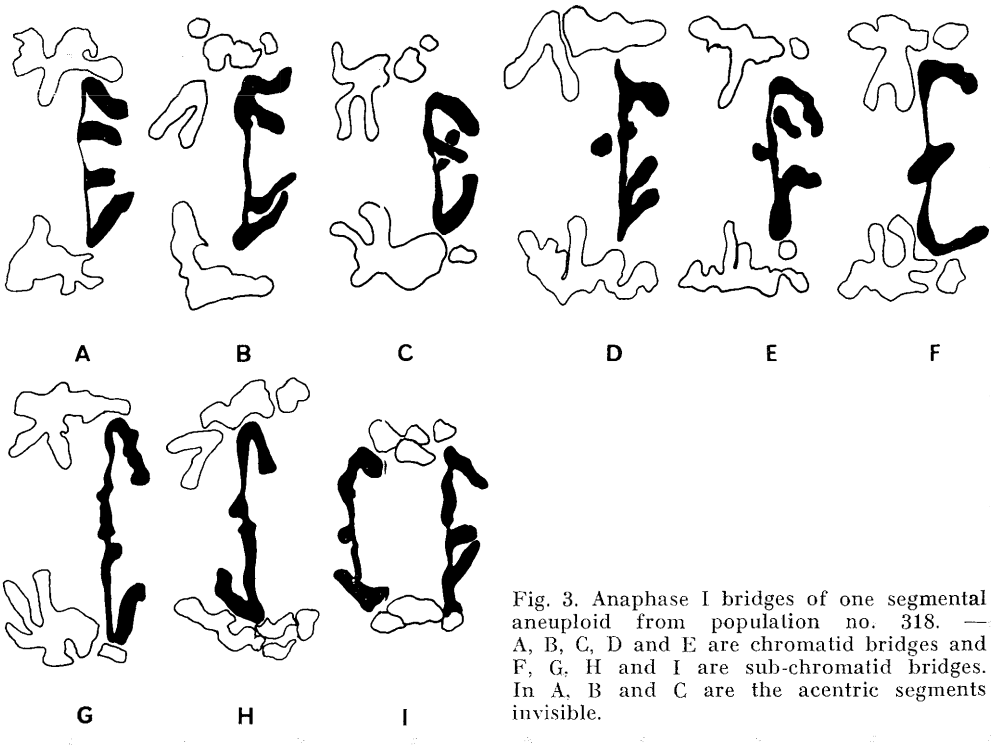

Fig. 3. Anaphase I bridges of one segmental aneuploid from population no. 318. — A, B, C, D and E are chromatid bridges and F, G, H and I are sub-chromatid bridges. In A, B and C are the acentric segments invisible.

concluded that the polymorphism was due to a translocation and that the observed chromosome combinations were the result of random mating. Other theoretical chromosome combinations may result in unbalanced genotypes and lethality.

YOSIDA et al. (1965) described a case of deletion of the entire short arm of one of the largest autosomes in *Rattus rattus* (Rat). They found the same polymorphism in two widely separated populations. In this case only normal homozygotes and deficient heterozygous individuals were found. The situation was in point of principle similar to the one described in this study.

2. The breakage of a U-type chromatid bridge in meiotic anaphase I.

Table 1. Arm index and relative length for the long chromosomes no. 1—4 (Fig. 1). Mean values ± sE. Each mean value is based on ten measurements. S, short arm. L, long arm. He, heterozygous for additional segment. Ho, normal. Chromosomes no. 3 and 4 are not kept separate in individual no. 318 Ho.

	Arm index			Relative length					
	Chromosome no.			Arm and Chromosome no.					
Pop. no.	1 & 2	3	4	1 & 2 S	1 & 2 L	3 L	4 L	3 S	4 S
307 He ...	8.7±0.2	3.7±0.1	1.9±0.0	2.5±0.1	21.7±0.2	17.8±0.3	18.8±0.3	4.9±0.1	10.0±0.2
318 He ...	8.4±0.2	3.6±0.1	2.0±0.0	2.6±0.1	21.0±0.2	18.7±0.3	19.2±0.3	5.3±0.1	9.5±0.1
318 Ho ...	8.0±0.2	4.0±0.1		2.7±0.1	21.2±0.2	20.9±0.2		5.2±0.1	

Table 2. Distribution of different aberrations in Anaphase I. He, heterozygous for additional segment. Ho, normal.

No.	Normal	Chromatid bridges	Sub-chromatid bridges	Laggards
307-1 He	80	2	—	1
318-7 He	177	16	26	1
318-3 Ho	24	—	—	1
318-4 Ho	151	3	14	—
318-5 Ho	73	1	7	—
Total:	505	22	47	3

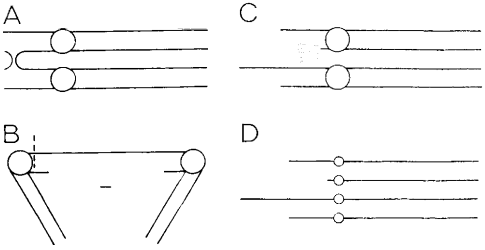

Fig. 4. A theoretical consequence of one breakage of a U-type chromatid bridge. — A: U-type chromatid reunion. — B: U-type dicentric bridge with fragment. The point of breakage is indicated by a dotted line. — C: Chromosomes before second meiotic division. — D: Chromosomes in gametes.

BRANDHAM (1970) made an investigation on the correlation between spontaneous chromatid and sub-chromatid aberrations in the Aloïneae. He concluded that the most plausible explanation of such aberrations was that they resulted from aberrant chiasmata. In one individual of *Gasteria* the frequency of sub-chromatid errors remained more or less constant for eight years, which suggests genetic control. BRANDHAM (op. cit.) further suggested that chromatid and sub-chromatid errors are basically the same thing, being the result of different reunions following four-strand sub-chromatid breakage.

If a bridge which originated from a very distal U-type chromatid exchange, was broken in a distal position in late anaphase I, the resulting karyotypes could be similar to those found in this study (Fig. 4).

It seems obvious that the frequency of chromatid and sub-chromatid errors are abnormally high, at least in population no. 318 from S. Rhinia. It is not only the heterozygous individuals that contain numerous errors but even normal homozygotes. If BRANDHAM's theory of genetically determined chiasmatic malfunction is correct then this polymorphism can be more easily explained and so can its geographical distribution.

WESTERMAN (1969) concluded that the polymorphism for supernumerary segments that is widespread in *Chorthippus parallelus* has been a feature of the species for 8—9000 generations and during that period of time has followed the migrating species from France to England and become stabilized in both countries. A similar segment in *Stethophyma* (SHAW 1970) has a much more limited extension in time and has evolved in only minor isolated populations (SHAW 1971).

The supernumerary segments in many animals are argued to be of adaptive significance since they tend to increase the over-all chiasma frequency (cf. HEWITT & JOHN 1967, WESTERMAN 1969, and SHAW 1971). Similarities between supernumerary segments and B-chromosomes have been discussed, since they both seem to have an effect on chiasma formation and both are mainly of a heterochromatic nature. In this study it has been possible to investigate neither heterochromatic content nor chiasmata frequencies.

With reference to literature one can sum up: — 1. Supernumerary segments are often of a heterochromatic nature. — 2. Heterochromatic units in the shape of supernumerary segments or B-chromosomes tend to increase the over-all chiasma frequencies of the genome. — 3. Malfunction of chiasmata is sometimes

genetically determined. — 4. Chromatid and sub-chromatid errors are correlated with chiasmata malfunction in some material.

In this case chromatid and sub-chromatid errors tend to be more frequent in populations with segmental aneuploid individuals than in others. The segmental aneuploidy may in other words be the result of a genetically determined chiasma malfunction with the subsequent formation of a dicentric chromatid bridge which was finally broken in a distal position.

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Typification of Species in the Lichen Family Thelotremataceae Described by Acharius

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ABSTRACT

HALE, M. E. Jr. 1972. Typification of species in the lichen family Thelotremataceae described by Acharius. — Bot. Notiser 125: 186—198.

ACHARIUS was the first lichenologist to describe species of Thelotremataceae, a unique lichen family with craterlike ascocarps. He published 15 taxa: *Thelotrema cavatum, Pyrenula clandestina, Urceolaria compuncta, Thelotrema discoideum, Pyrenula discolor, Thelotrema fumosum, T. henatomma, Lichen lepadinus, Thelotrema lepadinum* var. *bahianum* and var. *scutelliforme, T. obturatum, T. terebratum, Pyrenula trypanea, P. umbrata* and *Thelotrema urceolare*. Each of these taxa is typified and described and locations of type material designated.

INTRODUCTION

The lichen family Thelotremataceae is a crustose group of about 400 species found mainly in the tropics. Most are represented in herbaria by few specimens, oftentimes only the type, suggesting that either collectors have tended to overlook these rather inconspicuous lichens or there is a high degree of speciation in the family. The richest area in terms of number and diversity of species is southeast Asia, especially the dipterocarp forests of Malaya, Philippines, and Borneo. The West Indies (Lesser Antilles) and Colombia also have many species, while Africa, temperate South America, North America, Mexico, and Central America have by contrast a much smaller thelotreme flora.

LINNAEUS saw no specimens of the Thelotremataceae. The first species were described by ACHARIUS, who took considerable interest in the group, to the extent of publishing a separate paper on it (1812). He examined the AFZELIUS collections from Guinea and Sierra Leone, describing five species: *Thelotrema cavatum, T. discoideum, T. fumosum, T. obturatum,* and *Pyrenula trypanea*. A THUNBERG collection from the Cape of Good Hope was called *Thelotrema henatomma,* and a miscellaneous series from tropical America, mostly on *Cinchona,* yielded another five species: *Pyrenula clandestina, P. discolor, Thelotrema terebratum, Pyrenula umbrata,* and *Thelotrema urceolare,* and one variety, *T. lepadinum* var. *bahianum*. A specimen given the herbarium name *Urceolaria compuncta* by J. E. SMITH was published from Amboina (Indonesia) and the well-known *Thelotrema lepadinum* and its var. *scutelliforme* were based on European material. In total ACHARIUS published descriptions of 15 taxa, 13 species and two varieties, now recognized as members of the Thelotremataceae. Following him, incidentally, the most active workers were NYLANDER, who described about 100 species, and MÜLLER ARG. with 80 species.

The importance of the Acharian names as the effective starting date for the

Thelotremataceae makes revision and typification of the original material urgent. There has never previously been a comprehensive study of these specimens, although many in Helsinki show signs of sectioning and missing parts. A complete analysis of the species, of course, cannot be based on the material in Helsinki alone. While on the whole the largest specimens are there, one (*Urceolaria compuncta*) is represented only at BM and a few are not fertile. Better material is sometimes to be found in other herbaria, since ACHARIUS exchanged specimens with his contemporaries, RETZIUS and AGARDH (TÖRJE 1968) (LD), AFZELIUS and THUNBERG (UPS), and SWARTZ (S). In 1837 the University of Uppsala purchased a fairly large collection from A. J. AGRELIUS, a son-in-law of ACHARIUS. These lichens are now kept separately at UPS. ACHARIUS also sent some of the species published before 1807 to the Linnean Society (now at BM). Other duplicates have been found at C (herb. BUSE) and some were apparently acquired by BORRER (BM, formerly K), HAMPE, and KOERBER (L). It is possible to show that most of the specimens are in fact duplicates of the original Acharian material through similarity of bark characters and chemical reactions.

The typification of the Acharian species is still no easy or certain task. While he carefully listed habitat, substratum, and locality for each taxon in the publications, ACHARIUS did not label the specimens well. Many are also in poor physical condition, considerably abraded and badly preserved. Apothecia are often disintegrated; spores are sparsely developed and can sometimes barely be determined with polarized light. To make matters worse, the original descriptions are not very useful, microscopic details not being included, and few species are illustrated.

The Acharian herbarium was purchased by the University of Helsinki in 1834 (ELFVING 1918). NYLANDER was probably the first to make use of the material, taking out tiny study fragments before he went to Paris. These were eventually returned to Helsinki along with his main herbarium. He published very few observations on the types. VAINIO must also have had first hand knowledge of the Acharian material, especially when he revised his Brazilian collections (1890), but the only species noted in his publication was *Thelotrema terebratum*. He took out no kleptotypes. In revising the FÉE types, MÜLLER ARG. (1887 a and b) studied the Acharian isotypes at Uppsala and said that he borrowed the Helsinki material, although I found no annotations on the specimens at H. He may also have had access to duplicates at Berlin (herb. HAMPE) subsequently destroyed.

FÉE (1824, 1837) made detailed compilations of the lichens growing on *Cinchona* in tropical America, listing all of the Acharian thelotreme species from South America and one (*Pyrenula trypanea*) from Africa in addition to his own new species. As shown by the drawings and notes in the *Essai*, FÉE was quite familiar with ACHARIUS' species and may even have had some specimens checked by ACHARIUS (note for example "teste ACHARIO" for *Thelotrema bahianum* in FÉE 1824 p. 93 and *Pyrenula trypanea*, p. 72). It is even possible that some of FÉE's specimens were duplicates of Acharian material sent for inclusion in the *Essai*, although I have not been able to prove this yet.

MÜLLER ARG. (1887 a) arranged to borrow and revise the FÉE herbarium from Glaziou in Rio de Janeiro. These specimens were for the most part incorporated in the Geneva collection rather than being returned to the lender. KREMPELHUBER (M) somehow acquired a number of FÉE specimens which he labeled "Original zu FÉE, Essai . ." The Paris herbarium (PC) has a considerable collection of FÉE specimens. NYLANDER took a number of kleptotypes from it. There is also some FÉE material at Strasbourg (STR) and at Uppsala (UPS). I hope at a later date to revise the FÉE types and

the specimens identified by him with ACHARIUS' names.

There has been some unfortunate confusion concerning names used by FÉE and ACHARIUS. FÉE, for example, described a new species, *Thelotrema clandestinum,* while at the same time recognizing *Pyrenula clandestina* ACHARIUS. These are two separate entities; FÉE did not make a new combination. On the other hand, later authors often cite a *Thelotrema umbratum* "FÉE" but all that FÉE did here was to transfer ACHARIUS' *Pyrenula umbrata* to the genus *Thelotrema.*

REDINGER (1936) is the only modern lichenologist to revise a significant number of Thelotremataceae, specifically the important REGNELL collections from Brazil (S). I can find no indication, however, that he examined any of the Acharian types. For the most part he followed MÜLLER ARG.'s concepts of the species.

METHODS

During visits to Helsinki in 1970 and 1971 I was able to examine and section the specimens in the Acharian herbarium and make color tests with p-phenylenediamine. I was not prepared to take photographs, but duplicates from other herbaria from which loans could be made provided samples for photography and chromatographic tests at a later date in my own laboratory. Chemistry is an extremely valuable character in the family because of the constancy of the acids. It is not that the species lack good morphological differentiation; chemistry simply adds another character that can be easily and reliably determined. All specimens were chromatographed in two standard solvents (benzene-dioxane-acetic acid and hexane-ether-formic acid).

LIST OF SPECIES

Since the Acharian names take precedence over all other names in the family (except for homonymy), all of the species are "good". This does not by any means signify that the species are well known and understood. We lack sufficient material from Africa, for instance, to know how common they are or what the range of variation is. I am not prepared at this time to state for most the relationship to other species in the family, and for this reason the synonymy lists only basionyms and nomenclatorial synonyms for ACHARIUS' species. The type designation is quoted verbatim from the original publication. The species are listed in alphabetic order by species epithet.

Thelotrema cavatum ACHARIUS 1812 p. 92.

Ocellularia cavata (ACHARIUS) MÜLLER ARG. 1882 p. 499.

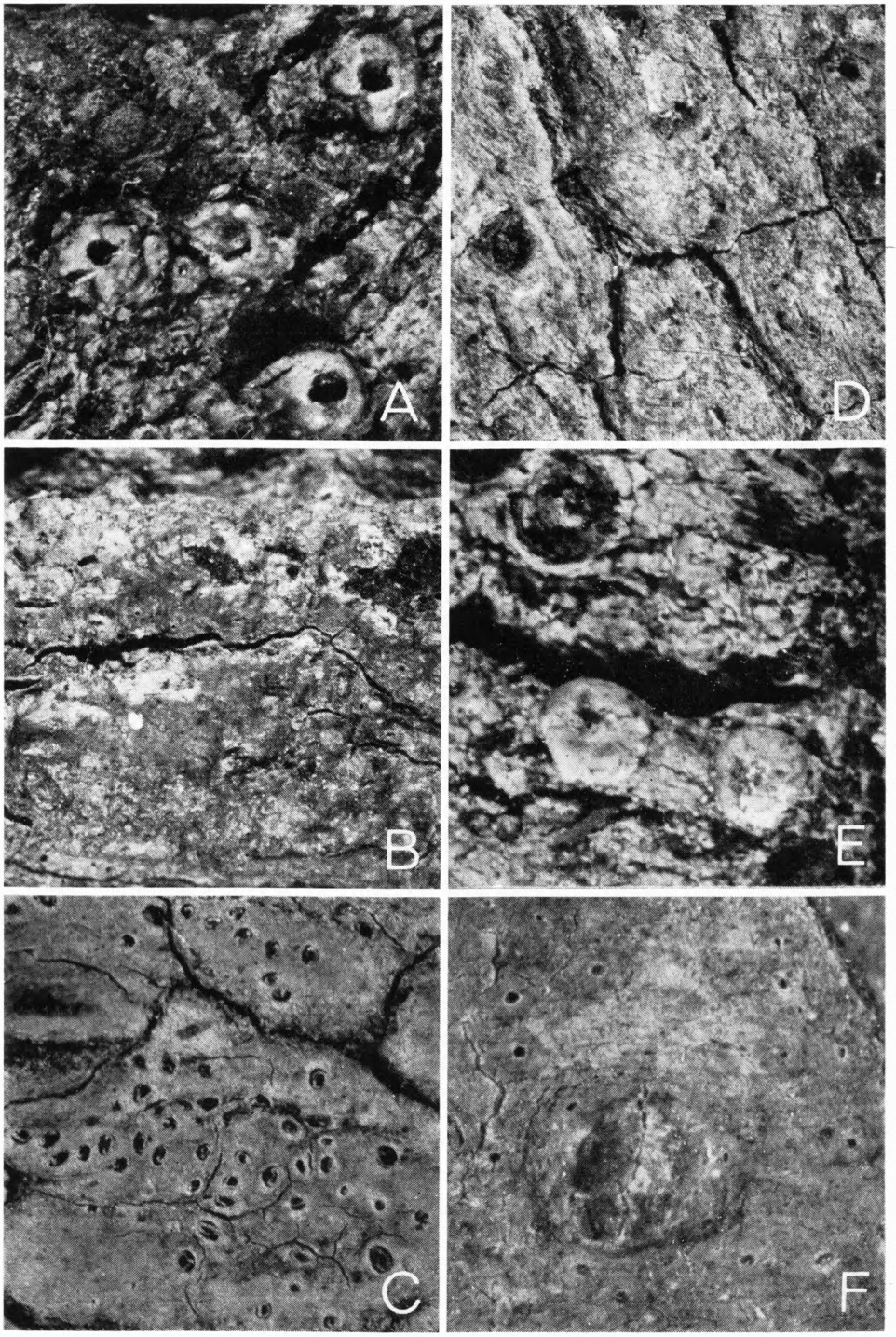
TYPE DESIGNATION: "Habitat in Africa ad Sierram Leonam supra corticem arborum."

SPECIMENS EXAMINED: H (lectotype, labeled "Guinea"); S (herb. SWARTZ labeled "e Guinea"); UPS (herb. THUNBERG labeled "e Guinea" and herb. AGRELIUS labeled "Africa: Guinea, ex herb. ACHARIANO"). All of these specimens probably came from the same piece of bark.

MORPHOLOGY (Figs. 1 A, 4 A): Thallus epiphloeodal, rough; ascocarps emergent, 0.7—0.9 mm in diameter; pore open, round to irregular, 0.2—0.4 mm wide; exciple apically carbonized; columella distinct, about 0.3 mm wide; spores colorless, 8/ascus, transversely septate, 8—10-loculate, 6—8×25—43 µ (MÜLLER ARG. 1887 a), 7—8×26—33 µ (SALISBURY, UPS AGRELIUS specimen), 6—8×30 µ (HALE, H specimen).

CHEMISTRY: P+ red, "A, B series" unknowns. These H_2SO_4+ spots fall between fumarprotocetraric and protocetraric acid and are best resolved in butanol-acetone-water on TLC plates. These un-

Fig. 1. Photographs of type specimens of Acharian Thelotremataceae. — A: *Thelotrema cavatum* (UPS). — B: *Pyrenula clandestina* (S). — C: *Urceolaria compuncta* (BM). — D: *Thelotrema discoideum* (S). — E: *Pyrenula discolor* (UPS). — F: *Thelotrema fumosum* (UPS). — All ×12.5.


A
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knowns are characteristic of *Ocellularia cinchonarum* (FÉE) MÜLLER ARG. Specimen in S tested.

The material on which *T. cavatum* was based is uniform and comparatively well developed. MÜLLER ARG. had examined the isotypes in UPS. NYLANDER identified the species in several collections and published drawings of the spores of the "archetypi ACHARIANI" (1863 a). The species is correctly figured by REDINGER (1936). It is apparently widespread in South America as well as in Africa.

Pyrenula clandestina ACHARIUS 1814 b p. 10, pl. 1, fig. 4.

Ocellularia clandestina (ACHARIUS) MÜLLER ARG. 1887 a p. 7.

TYPE DESIGNATION: "Habitat in America supra corticem *Cinchonae flavae*."

SPECIMENS EXAMINED: H (labeled "Amer. meridion., in *Cinchona flava*"); S (lectotype, labeled "*Pyrenula clandestina*, herb. SWARTZII"). These belong to the same piece of bark.

MORPHOLOGY (Fig. 1 B): Thallus thin and fragile; ascocarps rare, immersed, 0.1—0.2 mm in diameter; pore tiny, 0.05 mm wide; columella absent; spores colorless, 8/ascus, transversely 4—8-septate, longitudinally 2—3-septate, I—, 8—10×16—20 µ (HALE, S specimen).

CHEMISTRY: P+ faint orange, stictic and constictic acids. S specimen tested.

The specimen in Helsinki is small and apparently sterile. NYLANDER (1858) had studied it and concluded that "typus ACHARII suae *Pyr. clandestinae* visus nimis miser, quare hoc nomen ACHARII non interpretari possum". MÜLLER ARG. based his interpretation of the species on a FÉE specimen which had transversely septate spores. He therefore transferred it to *Ocellularia*. REDINGER (1936) followed in this error. The spore characters of the lectotype place the species in *Thelotrema*, but here it is preempted by *Thelotrema clandestinum* FÉE (1837 p. 90), an unrelated species. The next available name for *Pyrenula clandestina* appears to be *Thelotrema laevigans* NYLANDER. It is rather common at the base of trees in rain forests in the American tropics, Africa, and probably southeast Asia.

Urceolaria compuncta J. E. SMITH ex ACHARIUS 1803 p. 143.

Thelotrema compunctum (J. E. SMITH ex ACHARIUS) NYLANDER 1857 p. 118. — *Leptotrema compunctum* (J. E. SMITH ex ACHARIUS) MÜLLER ARG. 1888 p. 527.

TYPE DESIGNATION: "Habitat in arborum cortice Amboynae. D. CHR. SMITH."

SPECIMEN EXAMINED: BM (lectotype, labeled as in the type designation).

MORPHOLOGY (Fig. 1 C): Thallus rather thick, whitish; ascocarps numerous, immersed, 0.3—0.5 mm in diameter; pore open, 0.1—0.2 mm wide; exciple separating from the thalline margin; columella lacking; spores brown, 8/ascus, transversely 5—7-septate, longitudinally 1—2-septate, 9—11×23—26 µ (HALE, BM specimen).

CHEMISTRY: P+ orange, stictic and constictic acids. BM specimen tested.

The only specimen so labeled in the Acharian herbarium is a misidentified P negative *Leptotrema* from "Ind. Occid." NYLANDER (1863 a) had actually seen the BM specimen (then at Kew) and said that it was equal to *Thelotrema pertusarioides* NYLANDER, this being a nomen nudum. No other lichenologists have since examined the Amboina specimen.

Thelotrema discoideum ACHARIUS 1812 p. 94.

Ocellularia discoidea (ACHARIUS) MÜLLER ARG. 1887 a p. 8.

TYPE DESIGNATION: "Habitat in Africa prope Sierram Leonam ex corticem arboris *Dussa* ab incolis dictae."

SPECIMENS EXAMINED: H (lectotype, labeled "Guinea"); S (herb. SWARTZ labeled

"e Guinea"); UPS (herb. AGRELIUS labeled "e Guinea ex herb. ACHARIANO" and herb. THUNBERG labeled "e Guinea"). All seem to be parts of the same piece of bark.

MORPHOLOGY (Figs. 1 D, 4 B): Thallus thin and crumbling; ascocarps semiemergent, 0.4—0.8 mm in diameter; pore open, 0.15—0.30 mm wide; exciple apically carbonized; columella present, about 0.23 mm wide, 0.12 mm high; spores colorless, transversely septate, 4—5-loculate, 6×15—17 µ (MÜLLER ARG. 1887 a), 5—6×20—25 µ (HALE, H specimen); material in S and the herb. THUNBERG is sterile.

CHEMISTRY: P+ yellow, psoromic acid. S and UPS specimens tested.

The original collections, although uniform in appearance, are in very poor condition. The species is not easily characterized in this state.

Pyrenula discolor ACHARIUS 1814 b p. 9, pl. 1, fig. 2.

Ocellularia discolor (ACHARIUS) SPRENGEL 1827 p. 242. — *Ascidium cinchonarum* ssp. *discolor* (ACHARIUS) NYLANDER 1867 p. 319.

TYPE DESIGNATION: "Habitat in America ad corticem *Cinchonae flavae* (cortic. regiam vulgo dictam)."

SPECIMENS EXAMINED: H (lectotype, labeled "Amer. merid." with a fragment in herb. NYLANDER); C (labeled "ad corticem chinae regiae, herb. VAHL"); L (probable isotypes); UPS (two specimens, one (a mixture) labeled "America" and the other "ad corticem *Cinchonae*"). All the specimens are on similar *Cinchona* bark.

MORPHOLOGY (Fig. 1 E): Thallus distinct, epiphloeodal; ascocarps semiemergent to emergent, 0.7—1.0 mm in diameter; pore small, 0.1—0.15 mm wide; exciple apically carbonized; columella well developed, about 0.3 mm wide, 0.2 mm high; spores colorless, transversely septate, 12—14-loculate, 11—12×56—72 µ (NYLANDER, H specimen, 1867); 8—10×55—60 µ (HALE, H specimen).

CHEMISTRY: P+ red, protocetraric acid and an unknown; medulla pale yellow but no pigment proved. UPS specimen tested.

MÜLLER ARG. did not see this species. NYLANDER (1867) noted a mixture, saying "immixtum cum *Ascidio cinchonarum*". Material of this species does indeed consist of two different, externally similar plants, one with a distinct columella and a pale pigment in the ascocarps and one without a columella or pigment. Both contain protocetraric acid. Selection of a lectotype in this case is based chiefly on ACHARIUS' reference to "pallide flavicantes". All specimens listed above belong to this type. The noncolumellate type includes a specimen labeled "ad corticem *Cinchonae*" (apparently herb. FRIES) and part of the mixture with columellate material, both in UPS. The noncolumellate material can be identified with *Ocellularia verrucosa* (FÉE) MÜLLER ARG.

Thelotrema fumosum ACHARIUS 1812 p. 91.

Ocellularia fumosa (ACHARIUS) MÜLLER ARG. 1887 a p. 7.

TYPE DESIGNATION: "Habitat in Guinea ad corticem arborum circa Sierram Leonam."

SPECIMENS EXAMINED: H (lectotype, labeled "Guinea"); S (herb. SWARTZ labeled "e Guinea"); UPS (herb. AGRELIUS labeled "Guinea, ex herb. ACHARIANO").

MORPHOLOGY (Figs. 1 F, 4 C): Thallus distinct, epiphloeodal; ascocarps immersed to slightly emergent, 0.4—0.5 mm in diameter; pore tiny, 0.05—0.10 mm wide; columella present, weakly carbonized; spores colorless, transversely septate, 8-loculate, 8×27 µ (SALISBURY, UPS specimen), 6—8×25 µ (HALE, H specimen). The bark samples are identical.

CHEMISTRY: P+ red in part, variable, two unidentified substances present. S and UPS specimens tested.

The species is known only from the rather poorly developed type material.

No other specimens have been found with the same chemistry. MÜLLER ARG. (1887 a) saw material "ad specim. ACH."

Thelotrema henatomma ACHARIUS 1804 p. 109 (nomen novum).

Lichen pertusus "THUNBERG" 1800 p. 176 [=*Verrucaria pertusa* ACHARIUS 1798 p. 17]. — *Pyrenula henatomma* (ACHARIUS) ACHARIUS 1810 p. 316, pl. 5, fig. 4 a. — *Ocellularia henatomma* (ACHARIUS) MÜLLER ARG. 1887 a p. 6.

TYPE DESIGNATION: "Cap Bonae Spei, THUNBERG."

SPECIMENS EXAMINED: H (sterile); S (lectotype, labeled "*Pyrenula henatomma* ACHAR., herb. SWARTZII"); UPS (herb. THUNBERG, labeled "Cap Bonae Spei", only one ascocarp remaining).

MORPHOLOGY (Fig. 2 A): Thallus thick, warty; ascocarps large, emergent, 1.2—1.7 mm in diameter; pore small, depressed, 0.1—0.15 mm wide; exciple heavily carbonized; columella distinct; spores colorless, transversely septate, 9—10×23—26 µ (MÜLLER ARG., UPS specimen, 1887 a), 15—22×90—130 µ (HALE, S specimen).

CHEMISTRY: P−, hypoprotocetraric acid; a dark streak with triterpenes forms on the TLC plates. S specimen tested.

The original collection of this species had been identified by THUNBERG as *Lichen pertusus* (*Verrucaria pertusa*), a Swedish lichen. ACHARIUS recognized that it was misidentified (1804) and renamed it as a new species, *Thelotrema henatomma*. He did not give a description here, but his reference to the description of "*Lichen pertusus* THUNBERG" makes the species validly published. A full description was not published until 1810. The S specimen is large and well developed in contrast to the scraps in H and UPS. The species is common in South Africa.

Lichen lepadinus ACHARIUS 1798 p. 30.

Thelotrema lepadinum (ACHARIUS) ACHARIUS 1803 p. 132.

TYPE DESIGNATION: "Habitat ad corticem *Ulmi*."

SPECIMENS EXAMINED: H (lectotype); UPS (labeled "Omberg").

MORPHOLOGY (Fig. 2 B): Thallus distinct, thick, smooth to almost granular; ascocarps numerous, emergent, 1.0—1.6 mm in diameter; pore open, 0.5—0.8 mm wide; exciple separating from the thalline margin conspicuously; columella lacking; spores colorless, transversely 8—10-septate, longitudinally 2—5-septate, about 12×50 µ, I− (HALE, UPS specimen).

CHEMISTRY: P−, no substances detected on TLC plates. UPS specimen tested.

This is probably the commonest species in the family, known from most temperate areas in the world. The type material exhibits none of the yellowish pigment (K−) that is so evident in some specimens of this species.

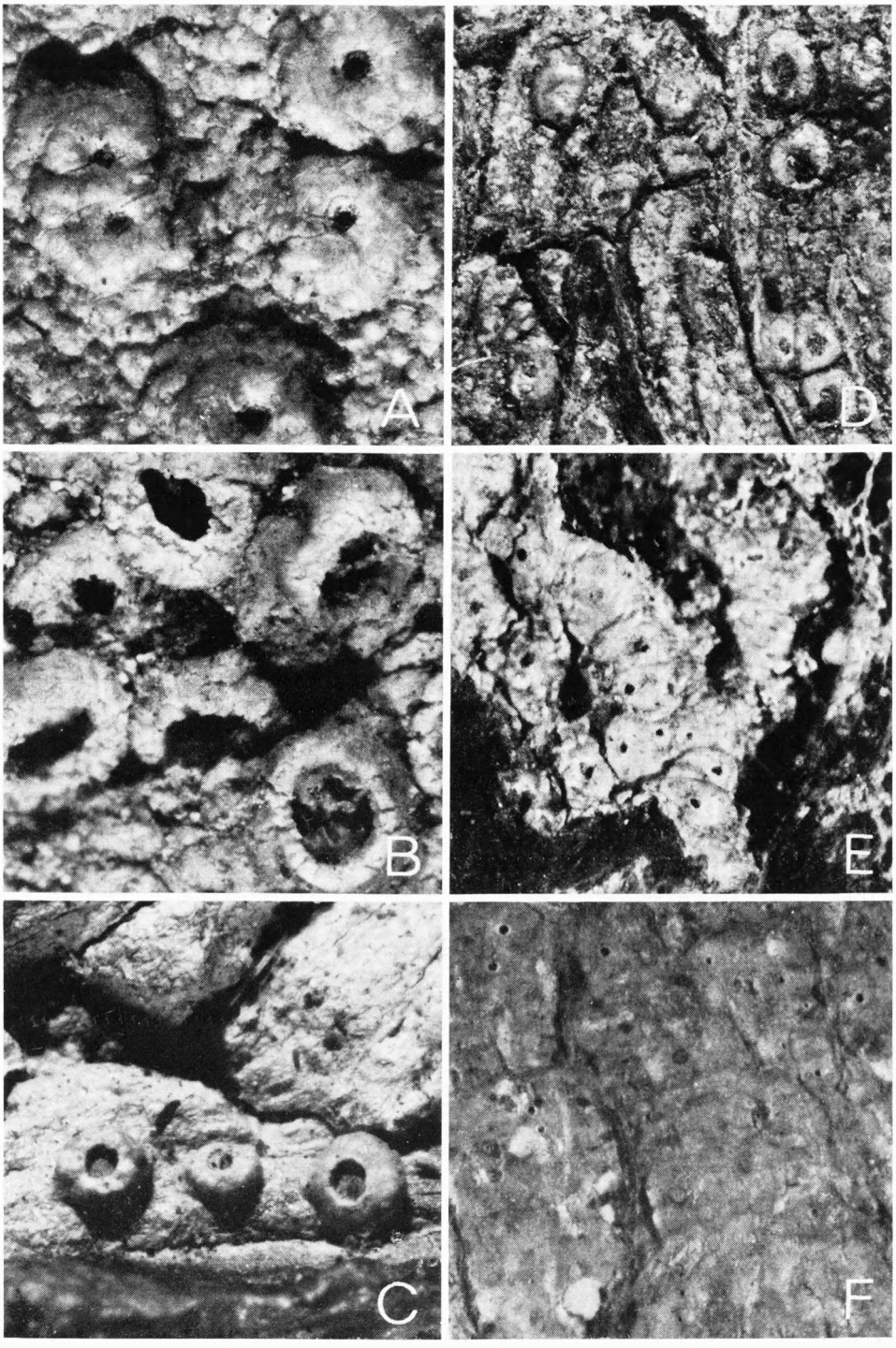
Thelotrema lepadinum var. **bahianum** ACHARIUS 1803 p. 132.

Thelotrema bahianum (ACHARIUS) ACHARIUS 1812 p. 87. — *Leptotrema bahianum* (ACHARIUS) MÜLLER ARG. 1887 a p. 12.

TYPE DESIGNATION: "In cortice arboris sub nomine Quina de Bahia e Brasilia advecta."

SPECIMENS EXAMINED: H (lectotype, labeled "Brasilia" with a fragment in herb. NYLANDER); L (labeled "*Thelotrema bahianum*, KOERBER Stammherbar").

Fig. 2. Photographs of type specimens of Acharian Thelotremataceae. — A: *Thelotrema henatomma* (S). — B: *Lichen lepadinus* (UPS). — C: *Thelotrema lepadinum* var. *bahianum* (C). — D: *Thelotrema obturatum* (BM). — E: *T. terebratum* (S). — F: *Pyrenula trypanea* (LD). — All ×12.5.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MORPHOLOGY (Fig. 2 C): Thallus thin, smooth; ascocarps emergent, 0.6—0.8 mm in diameter; pore open, 0.2—0.4 mm wide; columella lacking; spores brown, muriform, 2—3×5—6-loculate, 10×16—19 µ (HALE, H specimen).

CHEMISTRY: P+ red, protocetraric acid. L and H (herb. NYLANDER) specimens tested.

The type material is rather poor and represented at only two herbaria. NYLANDER (1863 a) had obviously seen the original since he illustrated spores from "archetypi herbarii ACHARIANI". This appears to be a widespread tropical species (cf. REDINGER 1936).

Thelotrema lepadinum var. **scutelliforme** ACHARIUS 1810 p. 313.

TYPE DESIGNATION: "Habitat ad saxa Angliae. TURNER."

SPECIMENS EXAMINED: H (lectotype, material on rocks); BM (on rock); UPS (mixed bark and rock specimens).

MORPHOLOGY: Essentially identical with the typical variety; thallus smoother with slightly smaller ascocarps; spores colorless, 1—2×8-loculate, 10×30 µ (HALE, bark specimen in UPS).

CHEMISTRY: P−, no chromatogram made.

This variety falls well within the range of variation of the typical form and appears to have no taxonomic significance.

Thelotrema obturatum ACHARIUS 1812 p. 92.

Ocellularia obturata (ACHARIUS) SPRENGEL 1827 p. 242.

TYPE DESIGNATION: "Habitat in Africa ad Sierram Leonam Guineae, supra corticem *Trichilae procerae* et aliarum arborum."

SPECIMENS EXAMINED: H (lectotype, labeled "Guinea" with a fragment in herb. NYLANDER); BM (one labeled "in *Trichil. procerae*" and two labeled "e Guinea from ACHARIUS"); LD (one labeled "e Guinea, digito ipsius ACHARII" and one labeled "e Guinea", both ex herb. AGARDH); UPS (one labeled "Guinea, herb. AGRELII and one "Guinea, herb. E. FRIES"). All collections appear to be from the same piece of bark.

MORPHOLOGY (Figs. 2 D, 4 D): Thallus thin and smooth; apothecia semi-emergent to emergent, 0.5—0.6 mm in diameter; pore irregular, 0.1—0.2 mm wide; exciple apically carbonized; columella present, well developed, 0.20 mm wide and 0.15 mm high; spores colorless, transversely septate, 8-loculate, 5—7× 28—34 µ (HALE, H specimen).

CHEMISTRY: P+ red, "A, B series" unknowns, the TLC profiles being exactly the same as in *Thelotrema cavatum*. S specimen tested.

This species is represented by a large number of uniform duplicates. MÜLLER ARG. had annotated the UPS specimens but did not publish any of the data since he considered it to be a synonym of *Thelotrema cavatum*. Chemistry confirms the identity of these two species although the total range of morphological variation is still unknown.

Thelotrema terebratum ACHARIUS 1812 p. 88.

Ocellularia terebrata (ACHARIUS) MÜLLER ARG. 1887 a p. 7.

TYPE DESIGNATION: "Habitat in America ad corticem *Cinchonae flavae*."

SPECIMENS EXAMINED: H (lectotype, labeled "America" with a fragment in herb. NYLANDER); S (labeled "in cortice *Cinch. flavae*, herb. SWARTZII"); UPS (labeled "America, ex. herb. ACHARIANO, herb. AGRELII"). All are part of the same bark collection.

MORPHOLOGY (Figs. 2 E, 4 E): Thallus thick, smooth; ascocarps immersed to semi-emergent, crowded, 0.4—0.5 mm in diameter; pore distinct, 0.1 mm wide; columella present, thin and weakly carbonized; spores colorless, transversely septate, 6—8-loculate, 7—8×20—30 µ

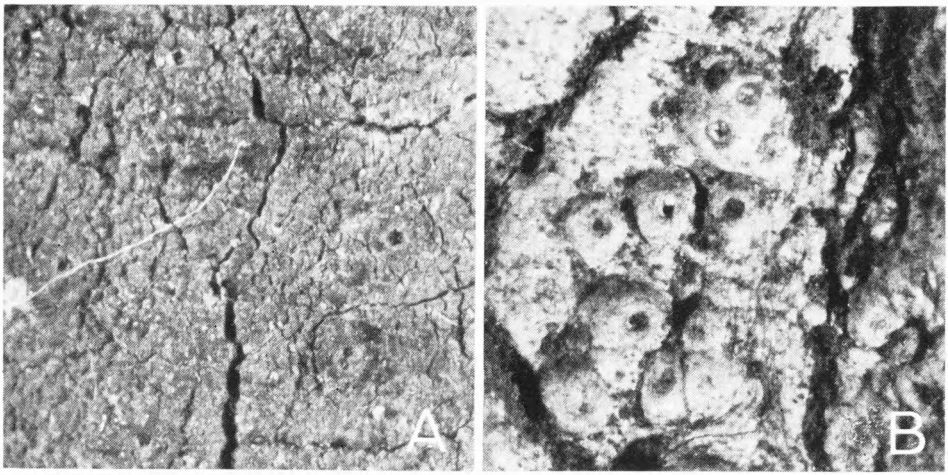

Fig. 3. Photographs of type specimens of Acharian Thelotremataceae. — A: *Pyrenula umbrata* (S). — B: *Thelotrema urceolare* (L). — All ×12.5.

(MÜLLER ARG., UPS specimen, 1887 a), 6—9×20—30 µ (SALISBURY, UPS specimen), 11×36 µ (NYLANDER, H specimen), 6—7×22—24 µ (HALE, H specimen), 5—7-loculate, 7—9×13—30 µ (VAINIO, H specimen (?), 1890).

CHEMISTRY: P+ yellow, psoromic and "neopsoromic" acids. H specimen (herb. NYLANDER) tested.

This seems to be a well characterized species, although we are still not sufficiently familiar with the range of variation. REDINGER (1936) identified and illustrated it, apparently correctly, among the REGNELL Brazilian collections.

Pyrenula trypanea ACHARIUS 1814 a p. 119.

Verrucaria trypanea (ACHARIUS) SPRENGEL 1827 p. 244. — *Ocellularia trypanea* (ACHARIUS) DODGE 1953 p. 344.

TYPE DESIGNATION: "Habitat in Guinea ad arborum corticem."

SPECIMENS EXAMINED: H (lectotype, labeled "Guinea" with fragment in herb. NYLANDER); LD (labeled "e Guinea dedit ACHARIUS" and a second specimen ex herb. AGARDH); S (labeled "e Guinea, herb. SWARTZII"); UPS (labeled "e Guinea ex herb. THUNBERG").

MORPHOLOGY (Figs. 2 F, 4 F): Thallus distinct, smooth; ascocarps flush, 0.3—0.4 mm in diameter; pore distinct, 0.05—0.1 mm wide; exciple weakly carbonized at the apex; columella present, weakly carbonized and thin; spores colorless, transversely septate, 6—7-loculate, 5—6×16—19 µ (HALE, H specimen).

CHEMISTRY: P+ yellow, psoromic and "neopsoromic" acids. S and UPS specimens tested.

This species was inexplicably overlooked by the 19th century lichenologists. MÜLLER ARG. (1887 a) seems to imply that it is a synonym of *Thelotrema* (*Ocellularia*) *fumosum* ACHARIUS without further elaboration, except for an annotation on the UPS specimen. DODGE (1953) did not see any type material but relied on the descriptions. In any event I believe this is a distinct species, unrelated to *O. fumosa*.

Pyrenula umbrata ACHARIUS 1814 b p. 9, pl. 1, fig. 3.

Thelotrema umbratum (ACHARIUS) FÉE 1837 p. 90. — *Verrucaria umbrata* (ACHARIUS) SPRENGEL 1827 p. 244. — *Leptotrema umbratum* (ACHARIUS) MÜLLER ARG. 1887 a p. 12.

TYPE DESIGNATION: "Habitat in America merid. ad corticem *Bonplandiae trifoliatae* WILLD. (*Cuspariae febrifugae* HUMB. et BONPL. vulgo cortic. *Angusturae* dictae.)"

SPECIMENS EXAMINED: H (apparently sterile); S (sterile, labeled "*Pyrenula umbrata* ACH. herb. SWARTZII"); UPS (lectotype, labeled "America merid. in cort. Angustur. Herb. AGREL. ex herb. ACHARIANO"). All specimens are from the same piece of bark.

MORPHOLOGY (Figs. 3 A, 4 G): Thallus warty, thick, shiny; ascocarps semi-emergent, 0.5—0.7 mm in diameter, barely visible among the warts; pore small, 0.10 mm wide; exciple apically carbonized; columella distinct, carbonized; spores colorless, transversely septate, 8-loculate, 6—7×18—26 µ (SALISBURY, UPS specimen; confirmed tentatively by HALE but spores poorly developed).

CHEMISTRY: P−, TLC negative or with faint triterpene spots. S specimen tested.

There are three specimens in UPS and one each in C and S labeled "*Pyrenula umbrata*", but only one collection, the matching bark samples in UPS and S appear to be part of the original Acharian material and agree in most essentials with ACHARIUS' drawing. Only the UPS specimen is fertile and although spores are poorly developed it is clearly an *Ocellularia*. MÜLLER ARG. did not see any authentic material and based his erroneous observations on a specimen determined by FÉE.

Thelotrema urceolare ACHARIUS 1812 p. 90.

Ocellularia urceolaris (ACHARIUS) SPRENGEL 1827 p. 242. — *Urceolaria thelotremoides* MASSALONGO 1852 p. 35. Based on *Thelotrema urceolare* ACHARIUS. — *Thelotrema distinctum* NYLANDER 1857 p. 118 (nomen); later (1859 p. 222) identified with *Thelotrema urceolare* ACHARIUS. — *Leptotrema urceolare* (ACHARIUS) MÜLLER ARG. 1887 a p. 12.

TYPE DESIGNATION: "Habitat in America supra corticem *Cinchonae rubrae*."

SPECIMENS EXAMINED: H (lectotype, labeled "America"); C (herb. BUSE labeled "Quinquina rouge"); UPS (labeled "America, herb. AGRELII ex herb. ACHARIANO"). All come from the same piece of bark.

MORPHOLOGY (Figs. 3 B, 4 H): Thallus distinct, smooth; ascocarps crowded, semi-emergent, 0.5—0.6 mm in diameter; pore conspicuous, 0.15—0.20 mm wide; exciple not carbonized, a columella lacking; spores brown, muriform, 11—14× 24—32 µ (NYLANDER 1859, MÜLLER ARG. 1887 a), 2×3—4-loculate, 12×24—29 µ (HALE, H specimen).

CHEMISTRY: P−, TLC negative with no spots. UPS specimen tested.

The specimen in H is fragmentary with only three ascocarps remaining. MÜLLER ARG. did not examine authentic material but cites NYLANDER for spore size, although one cannot be sure the reference to spore size in NYLANDER's publication (1859) is taken from ACHARIUS' type. The identity of the species is far from clear.

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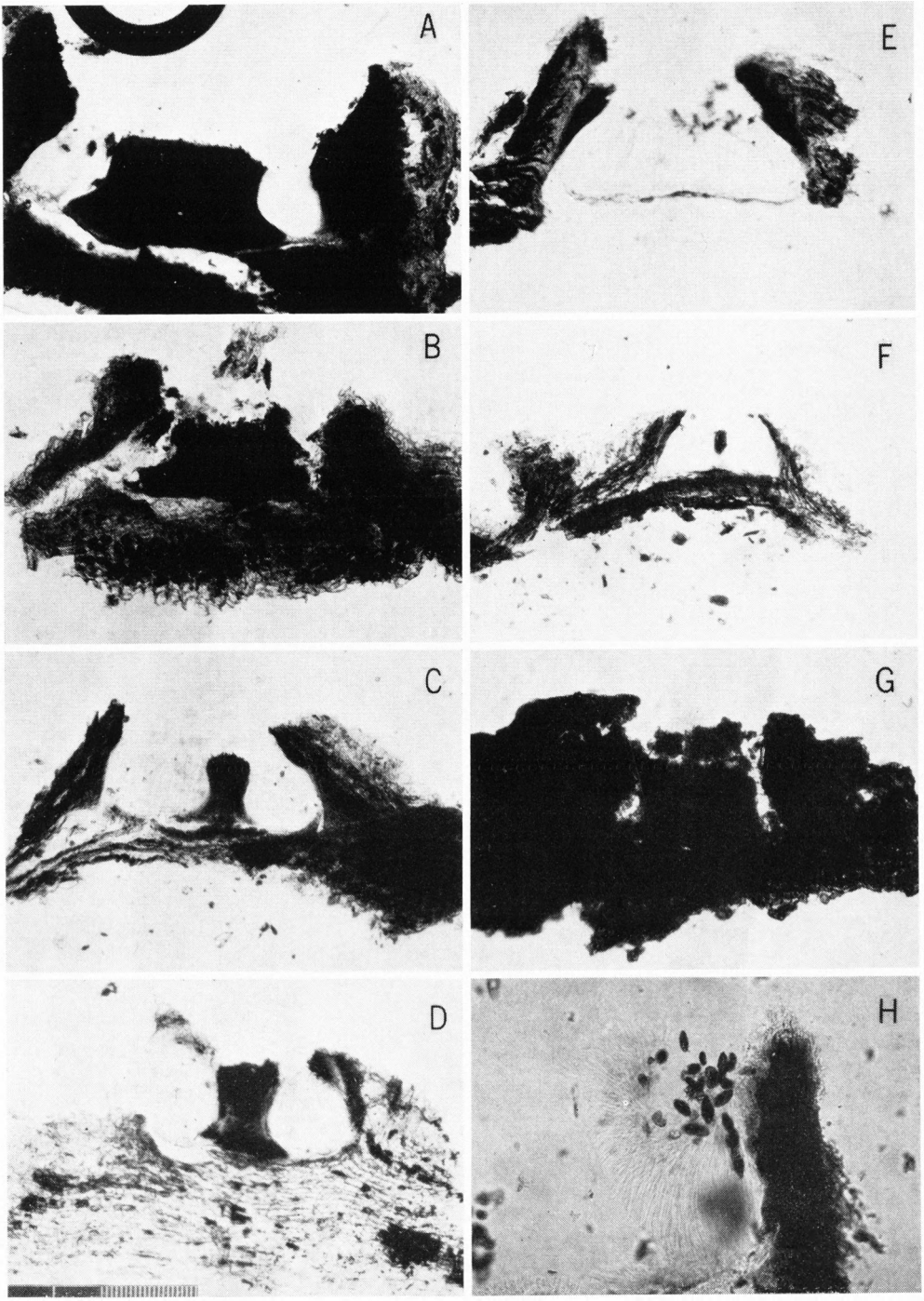
Fig. 4. Photographs of free-hand cross sections of some lectotypes in herb. ACHARIUS (H). — A: *Thelotrema cavatum*. — B: *T. discoideum*. — C: *T. fumosum*. — D: *T. obturatum*. — E: *T. terebratum*. — F: *Pyrenula trypanea*. — G: *P. umbrata*. — H: *Thelotrema urceolare*. — All are shown at the same magnification (scale at bottom in 0.1 and 0.01 mm divisions).


A
E
B
F
C
G
D
H

some of the old literature and checked the final manuscript. Part of the travel expenses for herbarium research were generously given by Mrs. WILLIAM J. MORDEN.

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Botanical Literature

MOORE, L. B. & EDGAR, E.: Flora of New Zealand. Volume II. Indigenous Tracheophyta. Monocotyledones except Gramineae. — Wellington 1970. 354 pp., 43 figures. Price $ 4.50.

The first volume of this flora appeared in 1961, with H. H. ALLAN as the main author. After his death it was completed by L. B. MOORE and M. B. ASHWIN, and later MOORE took up the work on its continuation together with E. EDGAR. It is now to be hoped that the entire work will be completed with the volume on grasses in the near future.

The descriptions are thorough, with notes on distribution and ecology. Practical keys for purposes of pure identification are given for all families and genera, and for most larger genera there are also synoptic keys to subgenera, sections or species groups. Many useful comments on nomenclature, unsolved taxonomic problems, untraced names etc. are also included. The figures mainly take the form of good analytical drawings, which give effective help in the identification of genera and species. There are morphological discussions on larger families, with, for example, for Orchidaceae an instructive drawing showing the meaning of the terms of floral morphology. A glossary of terms is also included.

This part has, as with the first volume, been limited to species regarded by the authors as being definitely indigenous. This is somewhat unsatisfactory as introduced species play an important role in the flora of New Zealand. There is also a tendency to regard as introduced several widespread species that were recorded from the area at an early date and might well be indigenous. The lists of introduced species thus have to be carefully studied for most genera if a full picture of the actual flora of the area is to be gained.

SVEN SNOGERUP

TRALAU, H. (editor): Index Holmensis. — Part I. Equisetales, Isoëtales, Lycopodiales, Psilotales, Filicales, Gymnospermae. 264 pp. Price SFr 100. — Part II. Monocotyledonae A—I. 224 pp. Price SFr 115. — The Scientific Publishers Ltd, Zürich. 1969 and 1972.

In systematic botany we are used to consulting Index Kewensis as an indispensible guide to the first description of plant species, without giving much thought to the possible difficulties of searching for them in a library with limited resources. There are also a few other standard works and abstract volumes that tremenduously facilitate botanists in finding the information desired.

With Index Holmensis, which is *a world index of plant distribution maps,* Sweden makes a contribution to service to botanical research. The importance of the index will be properly acknowledged when the work becomes better known — advertisement and information up till now have been far too diffident. With time the index will no doubt be found invaluable. It is to be sincerely hoped that facilities and funds will be provided for its completion and to ensure successive supplements to keep it up to date.

The work on Index Holmensis is directed from Naturhistoriska Riksmuseet, Stockholm, under the supervision and leadership of Dr. HANS TRALAU. It is based on a very rich, though by no means complete index of distribution maps compiled by Professor ERIC HULTÉN and used by him in his major works on phytogeography. This index has been complemented by means of a systematic examination of

botanical and other publications, a task carried out by a staff of several persons. Contributions to this work have also been made by representatives of various flora projects, especially by Professor VAN STEENIS at Leyden and Professor MEUSEL at Halle.

In Index Holmensis the genera are arranged in alphabetical order under the main groups given in the title, and the species are alphabetically arranged under each genus. Authors' names are omitted, which is perhaps wise, as these are often inaccurate and confusing.

The references appear under the scientific name used in the original publication. This is probably better than if the compilers had attempted to re-name or re-interpret the names of the species mapped, though it means that the reader will have to consult all possible synonyms. He will, for example, when looking up *Epipactis helleborine,* find numerous references under this name but also several under *E. latifolia* and *Helleborine latifolia.* It is necessary to know this before consulting Index Holmensis. An alternative would be to give cross references to important synonyms, a procedure that could possibly be considered in the preparation of coming volumes.

Maps of plant distributions are of very different types. Some are the result of the careful revision of a species over its whole range of distribution, some only a rough outline of its approximate distribution. Some again show only the records of a species in part of a single province of a country. No reference to the type of map is given in the index (it would be difficult to be fair in this respect), but the total area of the map (not of the distribution area within the map) is given. The title of the botanical publication is given in considerable detail, and the references are never obscured by the abbreviations used. — Maps of fossil plants and past distributions are included in the index and comprise a considerable part of the references in part I.

The second part differs from the first in having three columns on each page instead of two and in being in much smaller print, which makes this part more convenient to use. It could have been made even more compact by the more frequent use of "op. cit.".

In preparing vol. II Dr. TRALAU has also had more assistance than for vol. I, and he has been supported by an Editorial Board of specialists active in various parts of the world. Several of them have contributed substantially in completing the index. Inevitably, certain distribution maps have been overlooked, especially when published in inaccessible books or journals and in publications with mixed contents. These can, however, be included in later supplements. Dr. TRALAU is anxious to make further contacts with botanists willing to co-operate in the work on coming volumes of the index.

When going through the two volumes of Index Holmensis one is impressed by the great number of maps that exist for many species. Species such as *Cladium mariscus* and *Picea excelsa* are mapped in more than 50 different publications, and 44 more can be found for the synonym of the latter species, *Picea abies.* This may give a slight impression of what a gold-mine this work can prove to be to students of plant geography, ecology, vegetation history, etc. In the works cited, there is often additional information on the species concerned, as well as further references. Therefore, the index may also serve as an excellent gate-way to the literature on the species one wishes to study.

In sum, I wish to recommend Index Holmensis to any institute teaching and doing research in phytogeography, systematic botany including paleobotany, and ecology. It should take its place among other indispensible standard works. The index is not cheap, but considering the time gained by using it the costs are modest.

ROLF DAHLGREN

International Code of Botanical Nomenclature. Adopted by the Eleventh International Botanical Congress, Seattle, August 1969. — Regnum vegetabile 82. Utrecht 1972. 426 pp. Price (for members of I.A.P.T.) Sw. Kr. 61.80. Postgiro 43 35 39 - 4, Göteborg.

This new edition of the well-known Code of Nomenclature includes the decisions taken by the Nomenclature Section of the Seattle Congress in 1969. Compared to its predecessor "the Edinburgh Code", 1966, (reviewed in Bot. Notiser 120 (1967) p. 382) we find no major changes. An uncritical reader would get the impression that botanical nomenclature has reached a considerable degree of stability. This is true, however, only to a limited extent.

The Stockholm Congress in 1950 saw several important changes of the principles of plant nomenclature, e.g., the introduction of automatic tautonyms (without author's name) for infraspecific taxa including the nomenclatural type of the species. This "main type" must be called, e.g., *Salix alba* L. ssp. *alba* var. *alba* f. *alba*. The reform has been generally accepted by plant taxonomists with a few exceptions, e.g., the late author of the "Nordisk Kärlväxtflora" NILS HYLANDER.

In many other cases, however, the Nomenclature Section has been reluctant to major changes. At Stockholm a fairly large minority fought for retaining certain well-established species names which had proved to be invalid under the Code ("nomina specifica conservanda"). The same question (sometimes under the formula "nomina specifica rejicienda") was discussed again in Paris (1954), Montreal (1959) and Edinburgh (1964), but all proposals for conservation on species level were rejected. In Edinburgh a list was presented of some 70 specific names of "plants of economic importance", which were proposed for conservation. This question was postponed to the Seattle congress, but no action was taken there.

These examples concerning conservation of names may illustrate the restrictive attitude towards essential changes which has been prevailing among most nomenclaturists. Only 30 of the 226 proposals to the Nomenclature Section were accepted at Seattle, 120 were rejected, 55 were referred to the Editorial Committee and 18 were treated in other ways. The number of proposals has been decreasing considerably since the Stockholm Congress. It seems as if several botanists hesitate to challenge the conservative Establishment of Nomenclature even if their proposals are well-founded.

Some of the few amendments (all of them of minor importance) in the new Code are mentioned here. Further information on the problems under discussion can be obtained from "Synopsis of proposals on botanical nomenclature, Seattle 1969" (Regnum vegetabile vol. 60) and "Report on botanical nomenclature, Seattle 1969" (Regnum vegetabile 81). A brief survey of "Nomenclature at Seattle" was published by the Rapporteur-général Dr. F. A. STAFLEU in Taxon 19 (1970) p. 36. Dr. STAFLEU has also acted as editor of the present edition of the Code.

The principle of automatic tautonyms (cf. above, now called autonyms) was extended first to the generic (Paris 1954) and then to the familial level (Montreal 1959). A proposal by two American botanists (cf. Taxon 17 (1968) p. 645) showed in a well-documented way that, under certain circumstances, the extension of the tautonym principle can lead to the result that a taxon with a particular circumscription, position and rank can bear *two* correct names, which is contrary to one of the elementary principles of nomenclature. This proposal involving changes of arts. 19, 22 and 26 in order to provide against these deficiences in the Code was accepted without much discussion.

The Nomenclature Section also decided that the about 150 000 binomials ("espèces nouvelles") published by GANDOGER (Flora Europae, 27 volumes 1883—1891) shall be treated as not validly published. They have

been ignored by most taxonomists and were not quoted in Index Kewensis, but it is evident that they were effectively published. Dr. STAFLEU (Taxonomic Literature (1967) p. 163) argued that GANDOGER's "espèces nouvelles" are infraspecific "microspecies" and as such not validly published. As emphasized by the reviewer (Bot. Notiser 122 (1969) p. 148—150) this is contrary to G.'s own opinion in Flora Europae. G. definitely stated that his "espèces nouvelles" are the real specific units, whereas his "espèces linnéennes" are said to be collective species representing an oldfashioned (sensu G.) species concept.

It is puzzling to the reviewer that the blacklisting of GANDOGER's Flora Europae has taken place under art. 33 in the Code: "A combination is not validly published unless the author definitely indicates that the epithet or epithets concerned are to be used in that particular combination". Anyone who has read G.'s Préface (1883) must realize that G. did accept his "espèces nouvelles" as the real species and did not accept the "espèces linnéennes" otherwise than as aggregate species. The reviewer is fully convinced that it is necessary to exclude G.'s Flora Europae, but it is not honest to do that by means of attributing to him ideas that he did not express or terms that he did not use.

What is a microspecies? This term is not defined anywhere in the Code, nor in the "Annotated glossary of botanical nomenclature" (Regnum vegetabile 56, 1968). Using the same arguments as in the GANDOGER case ("it is impossible to have species within species") it would be possible to disqualify numerous "microspecies" in, e.g., *Alchemilla* and *Taraxacum* versus the "Linnaean" species *A. vulgaris* and *T. officinale*.

Appendix I "Names of hybrids" has been considerably remodelled, whereas the corresponding art. 40, which caused much disagreement at Seattle, has been changed only to a small extent. In other cases, e.g., nomenclature above the rank of family (art. 16), superfluous names (art. 63) and ambiguous names ("long-persistent sources of error", art. 69) the Nomenclature Section behaved like a Polish Diet: much discussion, few or no results. Most proposals were rejected or referred to special committees which are supposed to consider the controversies and report to the Leningrad Congress in 1975. A richer set of examples has been added to art. 63 and the classical (not well chosen) example *Rosa villosa* under art. 69 has been changed to *Cyclamen europaeum*.

When commenting upon the Edinburgh Code (cf. above) the reviewer questioned if the present shape of the Code is the most appropriate one. Is it necessary to have complete versions in English, French and German in the same volume? Undoubtedly, the English version would be sufficient. Part of the space gained by such a reform could be used for a more comprehensive set of examples under the articles and more references to the discussion (in Taxon and elsewhere) concerning nomenclatural rules and practice. It is a matter of fact that the Code, however indispensible it may be, is not easily accessible to many students, nor to several botanists lacking the necessary historical approach to the intricate pattern of botanical nomenclature.

OVE ALMBORN