Drawings of Scandinavian Plants 25-28

Rubus L. Subgen. Rubus

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Rubus laciniatus WILLD. 1809

Stem arching, hairy; *prickles* 5—8 mm long, falcate, base 4—7 mm long, rather narrow; *leaflets* 5, divided into pairs of laciniated segments, glabrous above, glabrescent or grey-tomentose below; *inflorescence* broad and leafy, prickles numerous, short, hooked, glands absent; *flowers* 2.5—3 cm across; *sepals* grey-tomentose with long, green tips, prickles often numerous; *petals* pink, irregularly incised at the apex, obovate when entire; *filaments* 4—5 mm long.

Normally, the stem is ridged, low-arched with a creeping tip, the hairs are sparse; no other blackberry found in Scandinavia has divided leaflets; the sepals are reflexed. *R. laciniatus* is cultivated for ornament and occurs sometimes outside gardens.

Rubus selmeri LINDEBERG 1884

(*Rubus nemoralis* PH. J. MÜLLER 1858 sensu HESLOP-HARRISON 1968 et WATSON 1958 non HUBER 1965 nec LID 1963.)

Stem arching, hairy; *prickles* 5—10 mm long, falcate or patent, base 3—7 mm long, rather strong; *leaves* 5-foliolate, sparsely hairy above,

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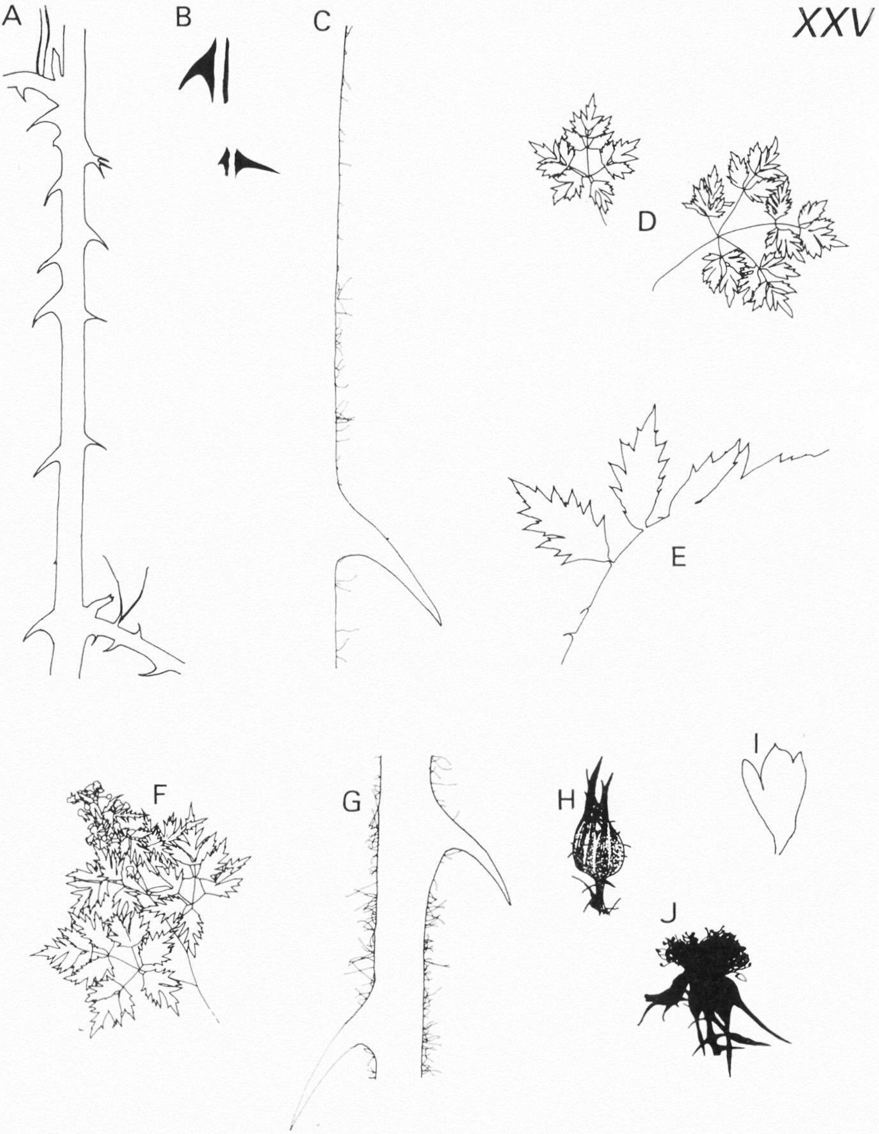
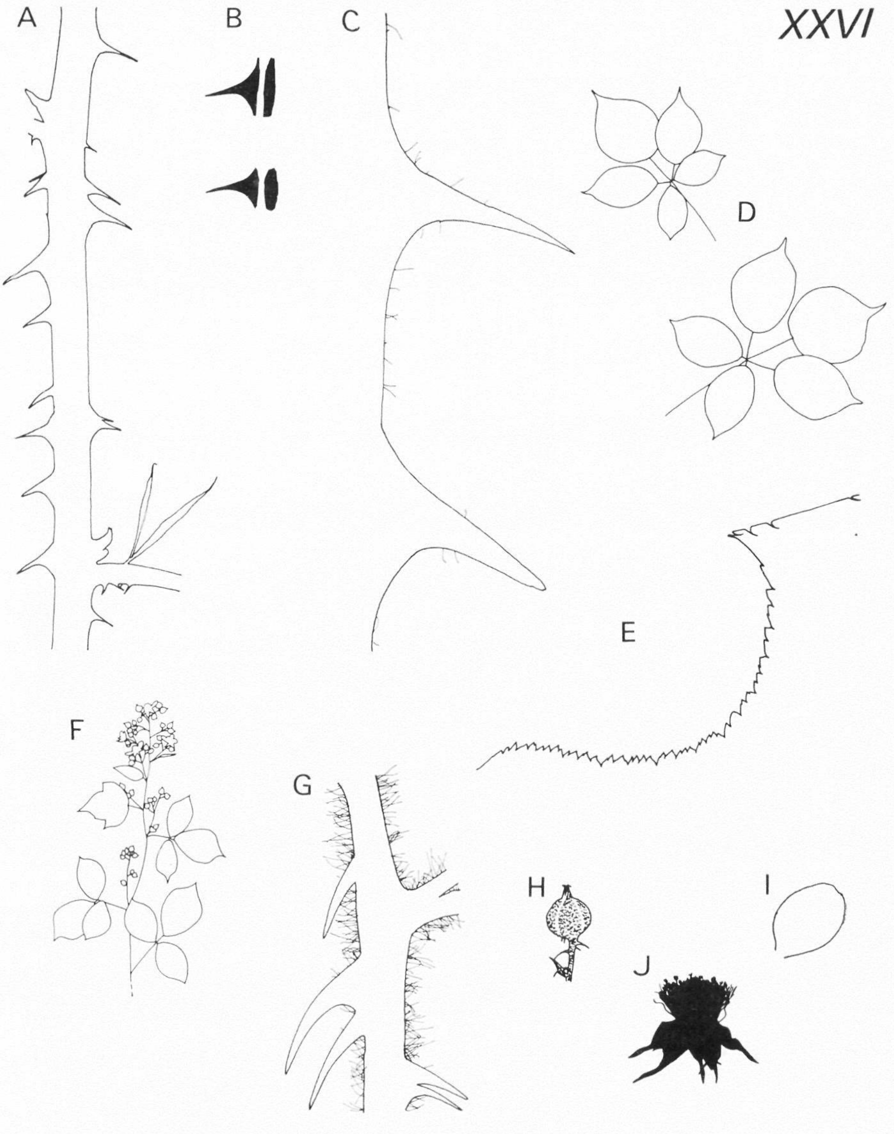
GENERAL LEGEND FOR THE PLATES

First-year growth (*primocane*): A. Stem with prickles. 1 : 1. — B. Prickles, drawn from the side and from above. 1 : 1. — C. Stem with prickles, glands, and hairs. 4 : 1. — D. Leaves (without serration and petiole diameter shown). 1 : 8. — E. Margin of a terminal leaflet with a petiolule. 1 : 2. — *Second-year growth* (*floricane*): F. Inflorescences (without prickles, serration of the leaves, and axis diameters shown). 1 : 8. — G. Rachis with prickles, glands, and hairs. 4 : 1. — H. Floral bud with prickles. 1 : 1. — I. Petal (without hairs). 1 : 1. — J. Flower (without petals, glands, and hairs). 1 : 1.

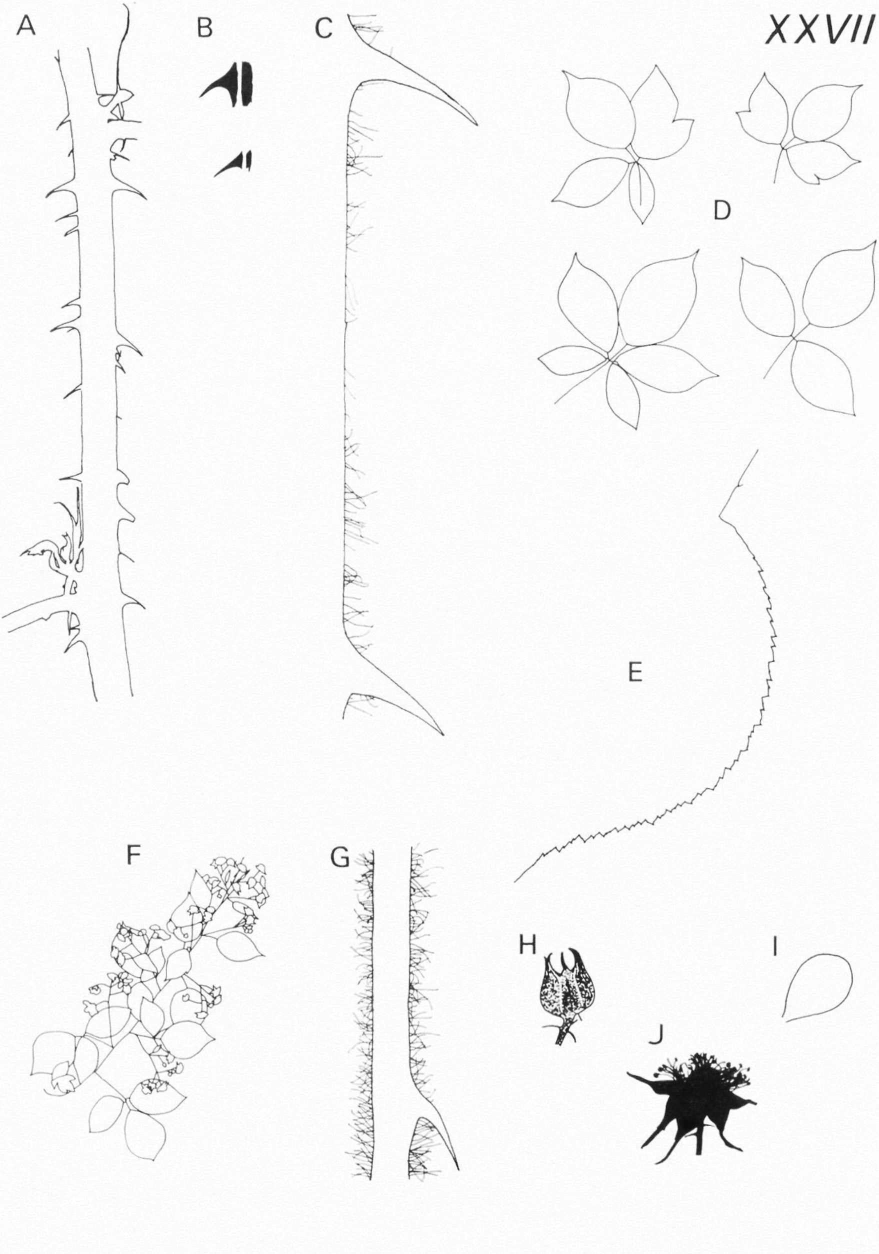


Pl. XXV. *Rubus laciniatus* WILLD. — Remarks: E shows the petiolule and margin of a terminal leaflet, divided into laciniated segments. — I. Entire petals also occur.



Pl. XXVI. *Rubus selmeri* LINDEBERG.

green—grey tomentose beneath; *terminal leaflet* broadly obovate, acuminate; *inflorescence* dense and leafy, prickles rather numerous, strong, falcate, glands few; *flowers* about 2.5 cm across; *sepals* grey-tomentose, sometimes with numerous prickles; *petals* white—pink, obovate with a narrow base; *filaments* 4—5 mm long.



Pl. XXVII. *Rubus sprengelii* Weihe. — Remarks: D: 3-foliolate leaves dominating. — E refers to a 3-foliolate leaf.

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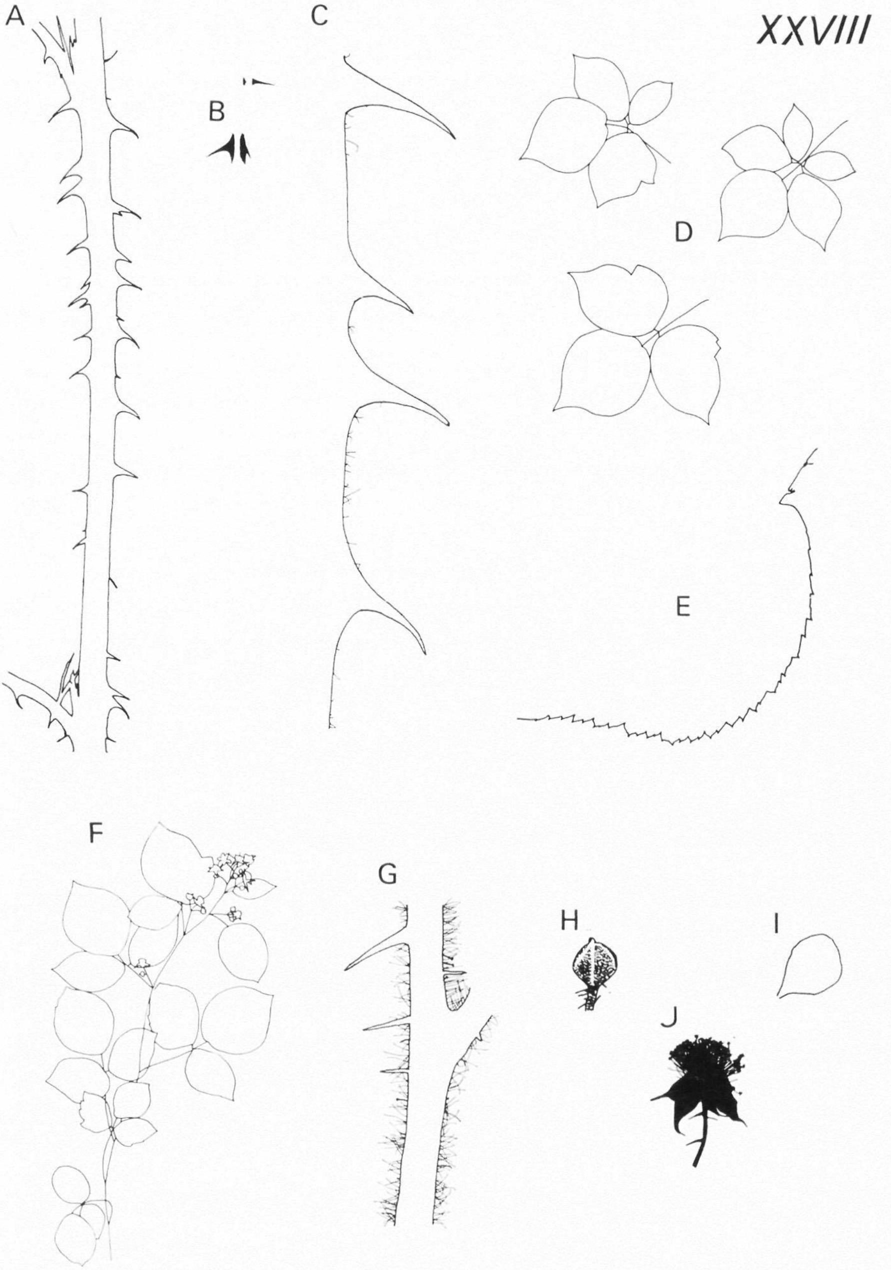

Pl. XXVIII. *Rubus axillaris* Lejeune. — Remark: E refers to a 4-foliolate leaf.

Normally, the stem is ridged, low-arched with a creeping tip, the hairs are sparse; the basal leaflets have about 3 mm long petiolules; the inflorescence is long and broad; the sepals are deflexed. *R. selmeri* grows on dry ground. The species is known from the counties of Hordaland and Rogaland in south-western most Norway.

Rubus sprengelii Weihe 1819

Stem arching—creeping, hairy; *prickles* 4—7 mm long, recurved, base 2—5 mm long; *leaves* 3 (—5)-foliolate, hairy beneath; *terminal leaflet* elliptic-obovate, acuminate; *inflorescence* broad, lax, branches and pedicels widely spreading, prickles hooked, glands few; *flowers* 2—2.5 cm across; *sepals* grey-tomentose, acuminate; *petals* bright rose-pink, obovate; *filaments* about 4 mm long.

Normally, the stem is more or less round, the hairs are sparse, the glands are absent; the prickles are relatively numerous and slightly bent; the leaves are bright green beneath; the sepals loosely clasp the fruit and lack prickles. *R. sprengelii* often grows in boggy areas associated with forests. In Sweden the species occurs on the coast in the environs of Marstrand near Göteborg, and in south-easternmost Skåne. In Denmark the species is rather rare on the islands; it also occurs along the eastern coast of Jylland.

Rubus axillaris Lejeune 1831

(*Rubus scanicus* F. Areschough 1881.)

Stem arching—creeping, hairy; *prickles* 3—6 mm long, retrorse, base 2—5 mm long; *leaves* 3—5-foliolate, glabrous above, sparsely hairy below; *terminal leaflet* orbiculate, subcordate; *inflorescence* pyramidal, leafy, prickles straight or slightly curved, glands few; *flowers* about 2 cm across; *sepals* grey-tomentose; *petals* light pink, orbicular; *filaments* about 2.5 mm long.

Normally, the stem is low-arched and somewhat ridged, the hairs are sparse, the glands are absent; the prickles are relatively numerous, straight or slightly curved; the leaves are yellowish green above; the sepals clasp the fruit loosely, the prickles are none or few, the glands are absent. *R. axillaris* is found in boggy forests and pasture-land. The species is known from several localities in north-western Skåne, and from Esrom on north-eastern Sjælland.

In the next paper, I shall deal with *R. scheutzii* Lindeb., *R. pyramidalis* Kaltenb., *R. insularis* F. Aresch., and *R. polyanthemus* Lindeb.

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Saxifragodes, a New Genus of Saxifragaceae from Tierra del Fuego

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ABSTRACT

Saxifragodes D. M. MOORE gen. nov. is described to accomodate the Fuegian species *S. albowiana* (F. KURTZ) D. M. MOORE. Hitherto, this species has been included in either *Saxifraga* L. or *Saxifragella* ENGLER, but it is here shown to differ from both in possessing 6 stamens and 2 staminodes, and from the latter in its habit and the presence of 5 petals. Pollen morphology as revealed by the scanning electron microscope supports the separation of the new genus. Synonymy, full description, distribution map and illustrations are provided.

Six species of *Saxifragaceae*, belonging to five genera, are known from Tierra del Fuego: *Escallonia serrata* SM., *Chrysosplenium macranthum* HOOK. F., *Tribeles australis* PHIL., *Saxifraga magellanica* POIR., *Saxifragella bicuspidata* (HOOK. F.) ENGLER and *S. albowiana* (F. KURTZ) ENGLER. The latter two species are closely related to *Saxifraga*, in which genus they were both first described.

Saxifraga bicuspidata HOOK. F. Fl. Antarct. 1(2): 281 (1847), was described from HOOKER's specimen collected on Isla Hermite, Islas Wollaston, Tierra del Fuego. This species did not fit happily into *Saxifraga* and was eventually placed in a new genus, *Saxifragella* ENGLER (in ENGLER and PRANTL, Natürl. Pflanzenfam. 3(2 a): 61 (1891), which was said to have its closest affinities with *Saxifraga* section *Dactyloides* TAUSCH. but differing by having 5 rather than 8 or 10 stamens, no corolla, and by the biscuspidate apices to the sepals and the elliptic-oblong leaves.

Saxifraga albowiana F. KURTZ ex ALBOFF, Revista Mus. La Plata 7(2): 370 (1896) was described from a specimen collected by ALBOFF in the mountains behind Ushuaia, Tierra del Fuego. The ample description is accompanied by a drawing showing the general habit and details of fruit and seed. The species is said to have affinities with *Saxifraga biscuspidata,* differing in its orbicular-spathulate, entire leaves, nonbicuspidate calyx-segments, 2—3 unequal lingulate petals and the long-papillose seed-testa. *S. albowiana* was subsequently included in *Saxifragella* by ENGLER in the monograph of *Saxifraga* in Das Pflanzenreich prepared by ENGLER and IRMSCHER. Subsequent to its collection and publication by ALBOFF (1896), this species has been recorded on four occasions (DUSÉN 1900; SKOTTSBERG 1905, 1906, 1916) without further discussion, although SKOTTSBERG (1906) noted that the leaves are often somewhat 3-lobed.

Whilst undertaking field studies in Tierra del Fuego between December 1967 and March 1968, I collected abundant material clearly referable to *Saxifragella albowiana* in the mountains behind Punta Segunda, which is situated on the north shore of the Canal Beagle in Argentinian Tierra del Fuego. On studying the specimens it became clear that they did not altogether correspond with the description given by ALBOFF; in particular, there was great discrepancy in the details of the corolla and androecium. A study of the type material showed that it was largely in a fruiting state, the few flowers being abnormally and incompletely developed, whilst my material was provided with buds and flowers but no fruits. Subsequent examination of the specimens collected by DUSÉN and SKOTTSBERG have confirmed the need to amend and amplify the description of this species, which has 5 petals, 6 stamens, and 2 staminodes.

This new information on floral characters reopens the question of the affinities of *Saxifragella albowiana*. It is clear that its separation from *Saxifraga* is still valid, because that genus always has twice as many fertile stamens as petals and no staminodes, but it is equally clear that it rests very unhappily in *Saxifragella* since the type species, *S. bicuspidata,* has 5 fertile stamens, no staminodes and no corolla. No other genus in the tribe *Saxifrageae* can accomodate *Saxifragella albowiana* and it is necessary, therefore, to describe a new genus, *Saxifragodes,* to do so.

Saxifragodes D. M. MOORE, gen. nov.

Typus. *Saxifragodes albowiana* (F. KURTZ) D. M. MOORE Syn.: *Saxifraga albowiana* F. KURTZ emend. D. M. MOORE).

Ex affinitate *Saxifraga* L. et *Saxifragella* ENGLER sed ab utroque structura florum differt. Sepala 5, petala 5, stamina antisepala 5, stamina antipetala 1, staminodia antipetala 2.

Hypanthium breve, in dimidio inferiore ovarii adnatum. Sepala 5, erecta.

Petala 5, elliptico-lanceolata vel oblanceolata. Stamina antisepala 5; stamina antipetala 1; staminodia antipetala 2, inaequalia. Ovarium semi-inferum, 2-loculare; carpella 2, in dimidio vel tertio inferiore connata, asymmetrice ovoideo-conica, stigmatibus capitellato-truncatis; ovula ∞, placentis in axi affixa. Capsula 2-rostrata, inter rostra 2-valvis. Semina parva, subreniformia; testa tuberculata. — Herba perennis, glabra, decumbens vel erecta. Folia alterna, petiolata, suborbiculata ad ovato- vel obovato-elliptica, integerrima ad 1-dentata vel 3-lobata, obtusa, saepe retusa, basi cuneati vel subtruncati. Flores solitarii, e foliorum summorum axillis ortae, cremei vel purpurei. Species 1, Fuegia et regionem proxime ad septentrio-occidentem freti Magellanici incola.

Having affinity with *Saxifraga* L. and *Saxifragella* ENGLER, from which it differs in floral structure. Sepals 5, petals 5, antisepalous stamens 5, antipetalous stamen 1, antipetalous staminodes 2.

Hypanthium short, basal half adnate to ovary. *Sepals* 5, erect. *Petals* 5, elliptic-lanceolate to oblanceolate. Antisepalous *stamens* 5; antipetalous stamen 1; staminodes 2, antipetalous, unequal. *Ovary* half-inferior, 2-locular; *carpels* 2, connate in basal half to third, asymmetrically ovoid-conical, with capitellate-truncate stigmas; ovules numerous, placentation axile. *Capsule* 2-beaked, 2-valved between beaks. *Seeds* small, subreniform, tuberculate. — Glabrous, perennial, decumbent to erect herb. *Leaves* alternate, petiolate, suborbicular to ovate- or obovate-elliptical, entire, or 1-dentate to 3-lobed, obtuse, often retuse, cuneate to subtruncate at base. *Flowers* solitary in axils of upper leaves, cream to purplish.

1 species inhabiting Tierra del Fuego and the region immediately to the north-west of the Straits of Magellan.

Saxifragodes albowiana (F. KURTZ) D. M. MOORE, comb. nov.

Saxifraga albowiana F. KURTZ ex ALBOFF, Revista Mus. La Plata 7(2): 370 (1896).

Saxifragella albowiana (F. KURTZ) ENGLER in ENGLER & IRMSCHER, Das Pflanzenreich 69(IV.117): 673 (1919).

Typus. Tierra del Fuego: Ushuaia; hauteurs de la rive droite du torrent "Ushuaia", région alpine, 29.II. 1896. ALBOFF 1133 (LP!).

Glabrous, perennial herb. *Stems* 1.5—10.0 cm, 0.3—0.5 mm in diameter, decumbent, rooted towards base and with decumbent to ascending or erect branches in axils of some leaves, green often purplish distally, yellow-brown towards base. *Leaves* alternate; lamina (1.2—) 2—5×(1—) 2—4 mm, suborbicular to ovate- or obovate-elliptical,

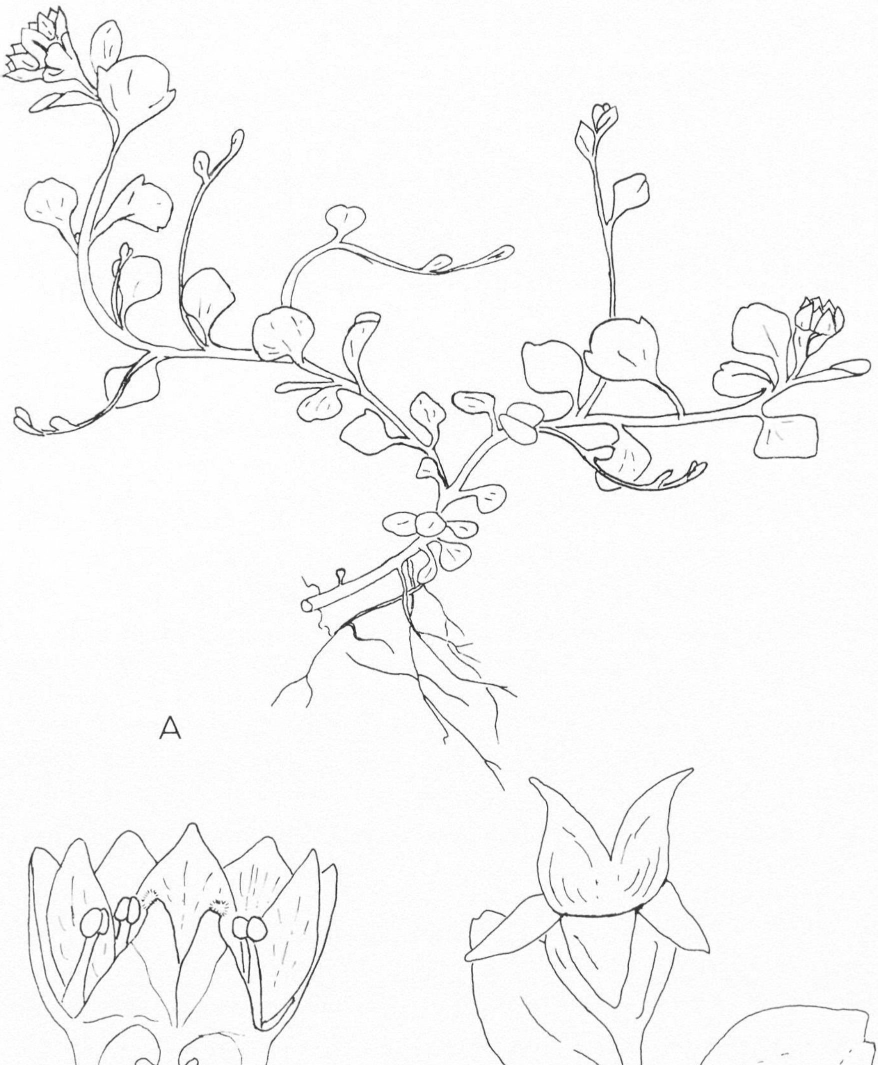


Fig. 1. *Saxifragodes albowiana* (F. Kurtz) D. M. Moore. — A: Habit. — B: Longitudinal section of flower. — C: Capsule. — Scale = 10 mm for A, 1.5 mm for B and C.

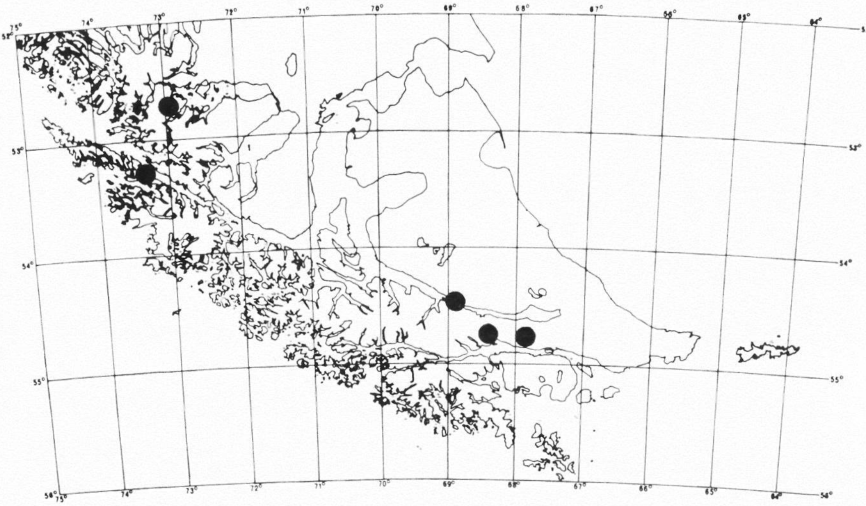
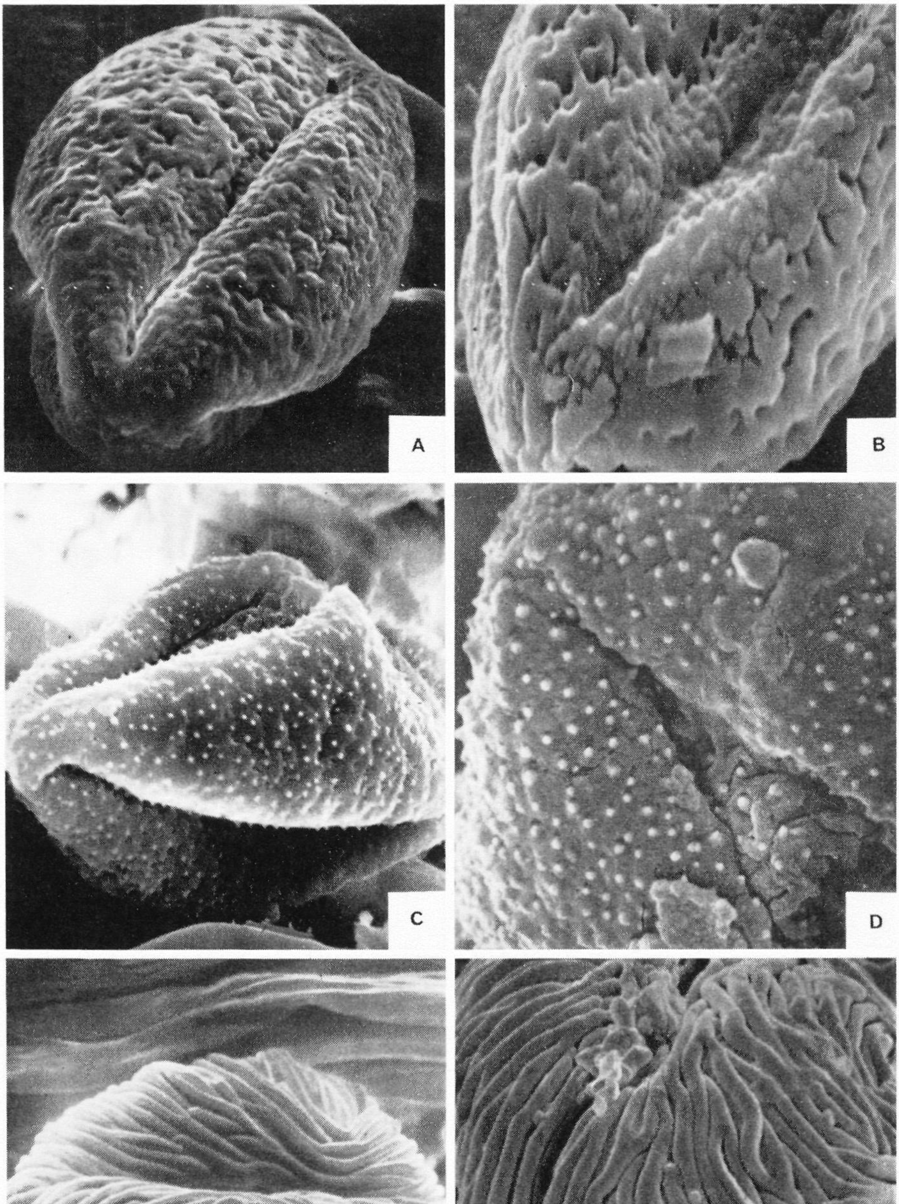


Fig. 2. Distribution of *Saxifragodes albowiana* (F. KURTZ) D. M. MOORE.

obtuse or rounded, often retuse, cuneate to rarely subtruncate at base, attenuate into winged petiole, entire or with single obtuse tooth or lobe on one or both sides, sometimes obtusely 3-lobed up to c. 1/3 length with central lobe c. 2—3 times as wide as laterals, somewhat fleshy, very rarely with occasional minute hairs near base; petiole 0.5—2.0 × c. 0.5—0.8 mm, sometimes almost absent. *Flowers* few, solitary in axils of upper leaves; peduncles up to 1.5 mm, slender, purplish. *Sepals* 5, free, erect, 0.8—2.1 × 0.8—1.7 mm, ovate to triangular-ovate, acute, rarely somewhat cucullate, green with small purple flecks near base. *Petals* 5, free, slightly shorter than to just exceeding sepals, elliptic-lanceolate to oblanceolate, subacute to obtuse, often retuse, cream with pinkish-purple flecks, sometimes purplish-suffused towards base. *Stamens* 6, free, equal, 5 inserted opposite and at base of sepals, the other antipetalous; anthers c. 0.3 × 0.7 mm, basifixed, introrse; 2 unequal antipetalous staminodes present, with filaments much slenderer than in stamens, one subequalling and the other much shorter than the stamens. *Carpels* 2, connate for basal 1/3—1/2, irregularly ovoid-conical, with simple terminal stigma. Ovary half-inferior, with axile placenta-

Fig. 3. Photographs of pollen grains taken with a JSM-2 Scanning Electron Microscope. — A—B: *Saxifragodes albowiana*. — C—D: *Saxifraga magellanica*. — E—F: *Saxifragella bicuspidata*. — A, C, and E × 2300; B, D, and F × 4400.


A
B
C
D
E
F

tion, green, purple on outer face. *Hypanthium* c. 0.8—1.5 mm, cupuliform, adnate to carpels up to c. 1/2 their length, green with purplish flecks and stripes. *Capsule* 3—4×2.5—3 mm, slightly shorter than to subequalling calyx, ovoid, compressed, deeply bifid; seeds numerous, 0.5—0.6 mm, subreniform, tuberculate, brown (Fig. 1).

Distribution. South and west Fuegia, southern West Patagonia (Fig. 2).

Other material examined. Tierra del Fuego: Ushuaia, in montibus, 330 m. 6.III. 1902, SKOTTSBERG 155 (S, UPS); Sierra Sorondo, behind Punta Segunda, 54° 47′ S., 67° 58′ W., c. 1000 m. 20.II. 1968, MOORE 1979 (LP, LTR, K); Río Azopardo, 600 m. 9.III. 1896, DUSÉN 651 (UPS); Isla Desolación, Puerto Angosto, 400—500 m. 1.IV. 1896, DUSÉN 691 (S, UPS). Chile: Magallanes, Seno Skyring, Estero de los Ventisqueros. 26.IV. 1908, SKOTTSBERG 280 (S, UPS).

It is possible that this species has been derived from *Saxifraga* by the gradual reduction of four of the antipetalous stamens. Two of the latter are completely absent while a further two are represented by staminodes of very different size, one being comparable in size to the stamens, the other very much reduced. The hypanthial disc may also be reduced since it appears much less conspicuous than is usual in *Saxifraga*. Although some leaves of *Saxifragodes albowiana* are sparsely and minutely hairy near their bases, the plant is otherwise glabrous, possible supporting ALBOFF's suggestion of affinity with *Saxifraga* section *Dactyloides* TAUSCH, which contains some glabrous species. However, the pollen morphology of *Saxifragodes* (Fig. 3 A, B), with its irregularly and shallowly to deeply pitted exine, is quite unlike the prominently tuberculate pollen of *Saxifraga magellanica* (section *Dactyloides*; Fig. 3 C, D), nor does it resemble closely the deeply furrowed pollen of *Saxifragella* (Fig. 3 E, F), although there may perhaps be some developmental affinity here.

ACKNOWLEDGEMENTS

I am grateful to the Royal Society of London for the award of a government grant-in-aid which enabled me to carry out the field work, and to the curators of the following herbaria for the loan of material in their care: Museo de La Plata; Naturhistoriska Riksmuseet, Stockholm; University Institute of Systematic Botany, Uppsala. Fig. 1 is based on a drawing prepared by Mrs. R. N. GOODALL of Estancia Harberton, Tierra del Fuego, with whom I enjoyed many days collecting. I am indebted to Professor D. A. WEBB for useful discussions about the new genus and to Professor V. H. HEYWOOD for kindly suggesting several improvements to the manuscript. — The scanning electron micrographs were prepared by Mr. S. K. IRTIZA-ALI.

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Garidella unguicularis Lam. (Ranunculaceae) – New for Europe

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ABSTRACT

Garidella unguicularis Lam. [*Nigella unguicularis* (Lam.) Spenner] is recorded from two localities on the island of Crete. Previously this species was only known from eastern Turkey, Syria, Lebanon, and Palestine. The differences between *G. unguicularis* and *G. nigellastrum* L., which also occurs on Crete, are briefly discussed.

The genus *Garidella* L. contains two species, *G. nigellastrum* L. and *G. unguicularis* Lam. Some authors (e.g., Davis 1965) include the genus in *Nigella* L. as subgenus *Garidella* (L.) Brand. In this case, the two species are named *N. nigellastrum* (L.) Willk. and *N. unguicularis* (Lam.) Spenner, respectively.

G. nigellastrum is widely distributed in the Mediterranean region and SW Asia, but always locally. It is known from Spain, S France, Crete, Rodhos, Cyprus, Turkey, Crimea, Caucasus, and N Iraq. *G. unguicularis* was previously recorded from eastern Turkey, Syria, Lebanon, and Palestine. It has recently been found in two localities on Crete.

Garidella differs from *Nigella* in the shape of the perianth and in the number and shape of the follicles. The sepals of *Garidella* are ovate-elliptic, scarcely petaloid, and shorter than the petals. The 2—3 united follicles are broadly oblong to elliptic, dehiscent on both sutures, and have very short (c. 1 mm), dehiscent styles. In *Nigella* the sepals are petaloi and longer than the petals, which are highly specialized, nectar-producing organs. The 2—14 (usually 5—8) partly united follicles are dehiscent only on the adaxial suture, and have long, indehiscent styles.

The two *Garidella* species differ in the shape of the petals. In *G. nigellastrum* they are about twice as long as the sepals (7—9 mm); the lower lip of the limb is cuneate-oblong, narrowed at the base, and deeply divided into two linear-oblong lobes (cf. Hiepko 1965). In *G. unguicularis* the petals are 3—5 times as long as the sepals (10—14 mm)

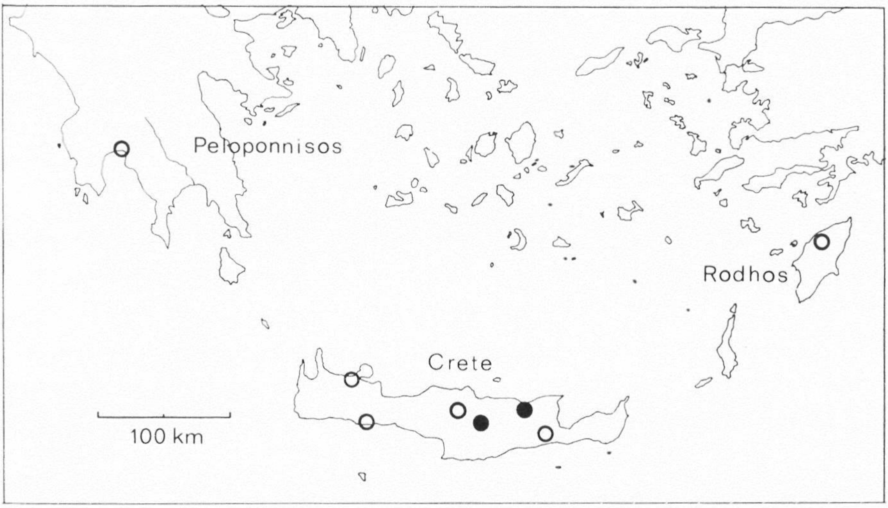

Fig. 1. Distribution of the two *Garidella* species in Greece, according to herbarium material and literature records. Open circles = *G. nigellastrum*. Solid circles = *G. unguicularis*.

and have long-exserted, narrow claws; the lower lip of the limb is about half as long as the claw, broadly ovate, cordate at the base, bifid, and incurved at right angles to the claw to form a peculiar "roof" over the follicles. An illustration of *G. unguicularis* clearly bringing out the features of the flower was published in ZOHARY (1966 plate 279). The anthers of *G. nigellastrum* are dark brown; in *G. unguicularis* they are yellowish. The sepals of *G. nigellastrum* are slightly longer and narrower than those of *G. unguicularis*. Apart from these differences the two species are very similar. The chromosome number is 2n=12 in both species (PEREIRA 1942 for *G. nigellastrum*; present count for *G. unguicularis*). Their karyotypes are very similar to *Nigella*, with five pairs of more or less metacentric chromosomes and one pair of almost telocentric chromosomes.

Fig. 1 shows the total distribution in Greece of the two *Garidella* species (cf. HALÁCSY 1901; RECHINGER 1943). The following material has been examined:

G. nigellastrum:

Crete: La Canée, les moissons. E. REVERCHON, 19.6. 1883 (W) — Distr. Hieraptera. Prope Malas. CHR. LEONIS no. 102, 16.5. 1900 (W) — Sfakia.

Olive plantation near the village. H. Runemark, S. Snogerup & al. no. 17002, 12.5. 1962 (LD).

Rodhos: Oros Prof. Elias near Salakos. C. Goulimi, 16.5. 1959 (Goulandris Botanical Museum, Kifissia, Athens).

G. unguicularis:

Crete: Katalagravi (S of Iraklion). Garigue, 500 m s.m. S. Snogerup, R. v. Bothmer & A. Strid no. 21704, 9.6 1964 (LD) — 2 km NE of Mallia (between Iraklion and Ay. Nikolaos), c. 30 m s.m. A. Strid, 19.6. 1966 (LD; only seeds collected, cultivated in Lund).

It appears from the several collections in various herbaria that *G. nigellastrum* is rather common on Cyprus. Otherwise both species are rare; the localities recorded in the literature are few and scattered.

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The Microclimate in a Beech and a Spruce Forest – a Comparative Study from Kongalund, Scania, Sweden

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ABSTRACT

A comparative climatic study of a 100-years old beech forest and a 55-years old planted spruce forest is reported. The stands are situated side by side with identical soil textural conditions. Results regarding light, temperature, relative humidity and wind velocity are given for three comparable days with clear weather, one from each of spring, summer and late autumn. Moreover, continuous measurements of soil temperature from two horizons are discussed. The greatest differences between the two stands were found in the spring before the time of leafing. Differences in radiation also caused differences in temperature and relative humidity. Thus in the beech forest there was a larger amount of incoming radiation rendering a higher soil temperature and, in the middle of the day, a lower relative humidity. During the summer the differences were small and insignificant with slightly higher soil temperatures in the beech forest. Light is discussed as a limiting factor for the ground vegetation in the spruce forest. Values of incoming radiation energy, estimated from a neighbouring meteorological station, are given. The temperature differences are discussed from an ecological point of view.

INTRODUCTION

The present paper is one part of an investigation with the purpose of elucidating the ecological-pedological changes occurring when spruce is planted on forest ground formerly covered with beech. It does in no way embrace a treatment of all climatic features. It aims mainly to illustrate certain similarities and differences in the climate near the ground which exist between beech and planted spruce forests. It is possible from periodical measurements to discuss some of the effects of the climate on ground and vegetation, without giving absolute values of continuous measurements throughout the whole year.

To some extent similar investigations are found, especially in Central European literature. Works of BURGER (1934 a, b) and COMBE (1957) may be emphasized. They have more or less directly compared beech and spruce from a forest climatic point of view. In the present paper light, temperature, relative humidity and wind are treated, while the precipitation will be dealt with in a future paper.

DESCRIPTION OF THE AREA

The investigation was carried out in Kongalund, a woodland situated south of the ridge of Söderåsen in the northwestern part of Scania, Sweden (55°59′N, 13°10′E). According to the bedrock map from the Institute of Geology, Lund, the bedrock consists of Cambrian shales and sandstones, which are overlaid by a thick layer of glacifluvial material and moraine with an even distribution of grainsizes. The climate is characterized by a yearly precipitation of 800 mm, a humidity of 270 mm (according to Tamm 1959) and an average temperature for the whole year of 6—7°C (Atlas över Sverige 1953).

Kongalund (Fig. 1) is mainly an old beech forest area but embraces several parts which have been planted with spruce during recent years. As appears from Fig. 1 two sampling areas have been worked with, one in the beech forest and one in the spruce forest, designated A and B respectively. They have been placed as close to each other as possible but yet sufficiently far apart that the reciprocal influence could be neglected. The sampling areas are situated on level ground with identical soil textural conditions.

The beech forest has an average age of 100 years with a tree density of 210 trees/ha. The spruce forest is 55 years old and contains 880 trees/ha. In both stands the tree height ranges from 25—30 m and the canopy cover is 80—90 %. The beech forest has a more or less closed field layer dominated by a *Stellaria nemorum* - *Lamium galeobdolon* community with *Anemone nemorosa* in the vernal aspect. In the spruce forest the field layer is absent except for a few individuals of *Oxalis acetosella* and some small plants of *Dryopteris spinulosa* and *Rubus idaeus*.

The climatic measurements were made between March 1967 and April 1968. They were performed partly as continuous measurements of the soil temperature and partly as day and night measurements of light, temperature, relative humidity and wind velocity during different seasons. These diurnal measurements were made on three comparable days in 1967 with clear weather: in the spring April 13—14, in the summer July 7—8 and in the late autumn November 8—9.

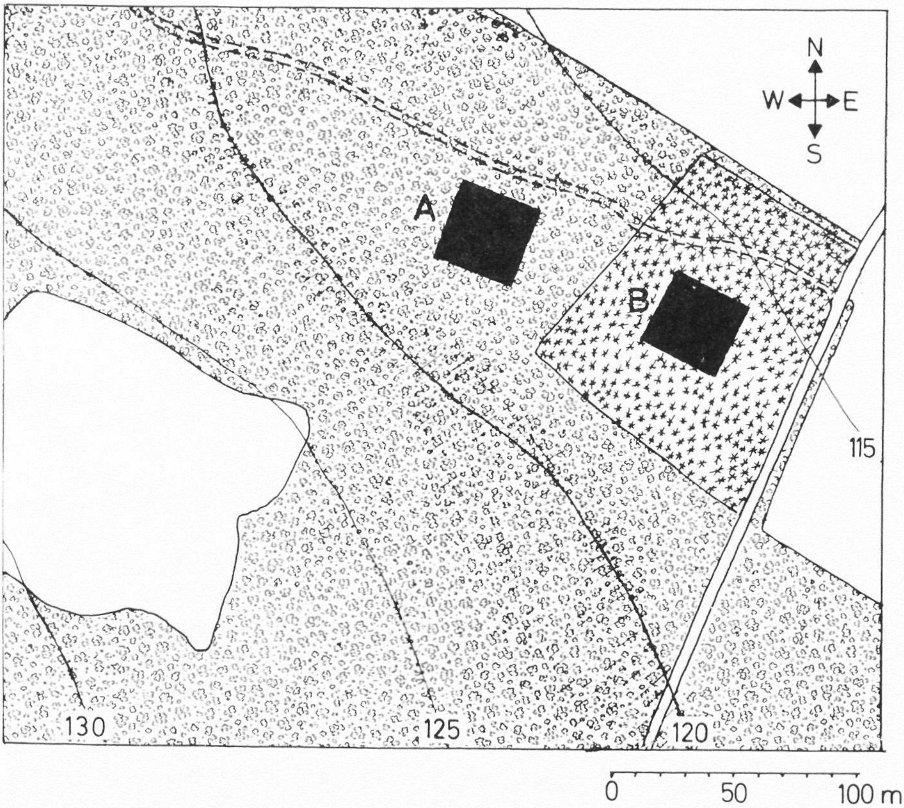

Fig. 1. Map of Kongalund, Scania, Sweden. Contourlines are indicated and height above sea level is given in metres. — A = measuring area in the beech forest. — B = measuring area in the spruce forest.

INSTRUMENTS, METHODS AND ERRORS

LIGHT was measured with an "Eel Lightmaster Photometer" which has a selenium cell and is directly read in lux (lumen/m^2). The effective range covers 300—700 mμ with a maximum sensitivity at 500—600 mμ. Incoming light was measured in a horizontal plane 50 cm above the ground at a fixed point. In this way incoming light through holes in the canopy may be included. During the summer day the light in an open field, north of the forests, was also measured in order to calculate the relative light intensities. As only one photometer was used all readings could not be done at exactly the same time but within a time interval of a few minutes. However, as the sky was cloudless this did not influence the comparison. The accuracy of the instrument is difficult to estimate, as the original calibration is gradually changing. According to TURNER (1958) it may amount to ±12 %. The values would therefore be better expressed as relative values (WALTER 1960 p. 355). However, using only relative values certain characteristic features might disappar and sometimes the values may be misleading (ANDERSSON 1964). In Fig. 2 the values measured directly in lux have been used. Due to the instability of the photometer these figures cannot be regarded as true values, but for an ecological comparison they are satisfying as they are measured with the same gauge.

In Table 1 the planimetric calculated light quantities/day (klux/day) are given, together with values in cal/cm^2/day which have been approximately transformed from lux/day, using values from TURNER (1958). For cloudy weather he states 1440 lux/hour=1 cal/cm^2/hour, for sunny weather 1260 lux/hour=1 cal/cm^2/hour. My measurements were made mostly in tree-shade and therefore the figure for cloudy weather was used.

This calculation and transformation must be regarded as rough, as TURNER's figures are valid for an open field and not a forest where the spectral composition of light is different (cf. p. 338). Radiation figures from Svalöv, ten km SW Kongalund, are also given in Table 1 (SMHI 1967). As can be seen the values from 7—8/7 in an open field in Kongalund and Svalöv differ only slightly. However, this does not ensure that the figures in cal/cm^2/day of the forests would be equally reliable. Including the instrumental error, the changes in light composition and the fact that the readings were made only once or twice an hour, it seems reasonable to estimate a total error of ±15 % of the transformed values.

TEMPERATURE. The three day and night temperature measurements were recorded by a Honeywell Brown Electronic recorder (driving force a 12 V battery converted to 120 V), fitted with wires and thermocouples of copper-constantan. The temperature was recorded directly in °C and 24 points were read within seven minutes. The recorder was placed in the middle between the two measuring points A and B and wires 30 m long were used.

The thermocouples were placed in a vertical profile at 100 cm, 25 cm, 10 cm and 5 cm above the ground and in the soil at ±0 cm (in the litter), —5 cm, —10 cm and —25 cm. The thermocouples in the soil were isolated with "RX-lim", a transparent cement. The thermocouples above the ground were protected from direct sunshine by a paper with black inside and bright outside surfaces (cf. PÅHLSSON 1966). The accuracy, including errors, in calibration and readings from the recorder paper, is estimated as ±0.2°C.

At the continuous recording of soil temperature throughout the year, thermographs fitted with distance wires (Lambrecht K.G. Göttingen, type 257) were used. Each thermograph had two sensitive bodies 15 cm long. One thermograph was placed inside each sampling area, with one sensitive body in the surface just below the litter and one at a depth of 25 cm.

The accuracy of this apparatus was ±0.3°C, providing calibration was made before and after measuring. The horizontal variation of temperature inside the whole sampling area at any one time was more than 0.3°C, at least in the surface layer. However in the calculated average values for whole days and weeks, as is the case in Figs. 4—5, this variation ought to be reduced.

Table 1

A. Planimetric calculated values in klux/day and approximately transformed values in cal/cm²/day (1967).

Period	Forest type	klux/day	cal/cm²/day		Ratio beech/spruce
13—14/4	Beech forest	239	166	(36%)	17.3/1
	Spruce forest	13.8	9.6	(2%)	
	In open field (Svalöv)	—	461	(100%)	—
7— 8/7	Beech forest	18.2	12.7	(3%)	0.8/1
	Spruce forest	22.6	15.7	(4%)	
	In open field (Kongalund)	—	461	(104%)	—
	In open field (Svalöv)	—	402	(100%)	—
8— 9/11	Beech forest	40.1	27.8	(25%)	7.3/1
	Spruce forest	5.5	3.8	(3%)	
	In open field (Svalöv)	—	111	(100%)	—
B. Calculated yearly energy input					
	Beech forest	cal/cm²/year			
	May—October	—	1890	(3%)	—
	November—February	—	1760	(30%)	—
	March—April	—	4510	(30%)	—
			Σ 8160		
	Spruce forest	—	Σ 2520	(3%)	3.2/1
	In open field (Svalöv)	—	Σ 84155	(100%)	—

The length of the sensitive body also ensured an integration of soil temperature.

WIND VELOCITY was measured with R. Fuess type anemometers, one of which was placed inside each sampling area at a height of 50 cm above the ground. This is a very sensitive instrument.

RELATIVELY HUMIDITY was measured with Lambrecht's hair hygrometers no. 194. These were placed at three levels: 0 cm (in the litter), 5 cm and 50 cm above the ground, with two meters at each level. They were protected against direct sunlight by aluminium sheets. All the hygrometers were calibrated before the measurements. The accuracy, estimated from the difference of the two meters at each level, was ±3 %. However the hygrometers never gave a 100 % deflection in total watersaturated air, but would stay at 95—98 %. Therefore a 95 % limit which can be regarded as 100 %, was drawn in the diagrams.

LIGHT — RESULTS AND CONCLUSIONS

During the three measuring days the light was read off once or twice an hour. As clear days were chosen for sampling, the sky was almost cloudless the whole time, except for July 8th, when there were some clouds. Apart from this the measured light intensities can be regarded as maximum values.

During the spring day (Fig. 2 A) high light intensities were obtained in the defoliated beech forest. In the middle of the day the light intensity could be up to forty times greater in the beech forest compared with the spruce forest. During the summer day (Fig. 2 B) the light conditions were similar in the two types of forests, or slightly higher in the spruce forest. During the late autumn day (Fig. 2 C) the light intensities were low but as the leaves had fallen the intensities were again greater in the beech forest. In the middle of the day the light intensity was ten times greater in the beech forest than in the spruce forest.

Out of the 24 hour period 14 hours were light during the spring day, 17 during the summer day and 9 during the late autumn day. In the planimetric calculation of light quantities/day (klux/day) the light proportion beech : spruce were 17 : 1 for the spring day, 0.8 : 1 for the summer day and 7.3 : 1 for the late autumn day. Expressed in energy units, cal/cm^2/day, the relative proportions would be the same (cf. Table 1). However, as mentioned earlier, this transformation is not absolutely correct, mostly owing to the changes in the spectral composition of light when passing through the canopy. Concerning the spectral composition several scientists have shown obvious differences between thinleaved deciduous forests and needle forests (KNUCHEL 1914, SEYBOLD 1936, EGLE 1939, COMBE 1957). ATKINS et al. (1937) found the same differences between a beech and an evergreen *Quercus ilex* forest. The difference is that in deciduous woods the transmission and reflection from leaves give rise to a dark red-green shade, rich in dark red and infrared rays. The blue and violet rays are absorbed to a great extent by the leaves. In spruce forests there is instead a blueshade, where the spectrum is almost the same as in full daylight, except for relatively more blue light during clear days. The ecological importance of these differences is not fully known. Taking the figures from Svalöv as 100 % and estimating the percentage of energy in the beech forest to 3 % during May—October, 30 % during November—April and in the spruce forest to 3 % during the whole year, it is possible to get an idea of the total radiation reaching the ground in the two ecosystems (Table 1 B). Incoming radiation to the ground of the beech forest is then three times greater than that of the spruce forest. It is worth

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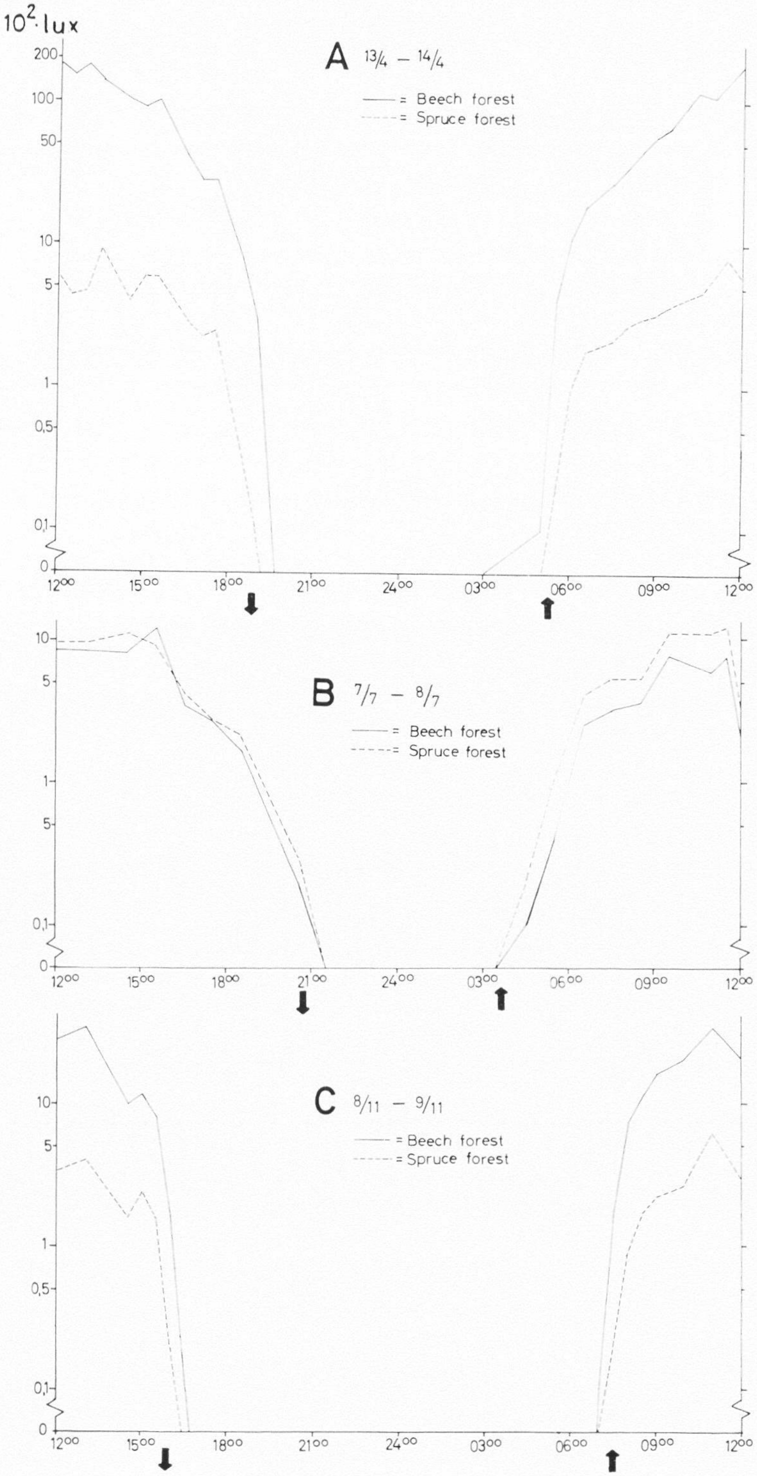
Fig. 2. Light conditions during the three measuring days. Lux are given on a logarithmic scale. Sunset and sunrise are indicated by arrows. — A: The spring day, April 13—14, 1967. — B: The summer day, July 7—8, 1967. — C: The late autumn day, November 8—9, 1967.


10²·lux
A 13/4 – 14/4
—— = Beech forest
- - - = Spruce forest
200
100
50
10
5
1
0,5
0,1
0
12⁰⁰
15⁰⁰
18⁰⁰
21⁰⁰
24⁰⁰
03⁰⁰
06⁰⁰
09⁰⁰
12⁰⁰
B 7/7 – 8/7
—— = Beech forest
- - - - = Spruce forest
10
5
1
5
0,1
0
12⁰⁰
15⁰⁰
18⁰⁰
21⁰⁰
24⁰⁰
03⁰⁰
06⁰⁰
09⁰⁰
12⁰⁰
C 8/11 – 9/11
—— = Beech forest
- - - = Spruce forest
10
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12⁰⁰
15⁰⁰
18⁰⁰
21⁰⁰
24⁰⁰
03⁰⁰
06⁰⁰
09⁰⁰
12⁰⁰

Table 2. Some calculated values on relative light intensities in percentage during July 7—8, 1967.

7/7—8/7	Beech forest	Spruce forest
12.00	2.9	3.1
14.00	2.9	4.0
16.00	3.4	2.7
18.00	2.1	2.8
20.00	4.6	7.0
22.00	—	—
24.00	—	—
02.00	—	—
04.00	3.1	6.2
06.00	2.8	4.5
08.00	4.0	6.0
10.00	4.3	5.8
12.00	2.6	4.1

noticing that more than half of this radiation of the beech forest comes during the spring period March—April before the leaves are bursting. However it is important to remember that the relative light intensities vary from hour to hour and from day to day, depending on diffuse or direct sunlight (ANDERSSON 1964). The yearly average values of relative light intensity given above, can be justified as the difference is great and similar fluctuations will occur in both stands.

During the summer day values of the relative light intensity, in percentage of the light in an open field have been calculated. This day may correspond to a day with high light intensities of the vegetation period June—July. At least during June there is a restricted growth of interalia *Stellaria nemorum* ssp. *glochidosperma, Lamium galeobdolon, Oxalis acetosella* and *Convallaria majalis* in the beech forest, while in the spruce forest a very restricted growth of scattered individuals of interalia *Oxalis acetosella, Rubus idaeus* and *Dryopteris spinulosa* can be seen, in spite of the relatively greater light intensities in the spruce forest (Table 2).

According to LUNDEGÅRD (1921) the compensation point of several shade plants is found at a relative light intensity of approximately 1 %. For positive assimilation the plants require more light. This condition seems to be fulfilled in both the beech and the spruce forest, but growth of the field layer occurs mainly in the former, in spite of more light in the spruce forest. A contributive reason for this could be that other site conditions, e.g. the water conditions and the degree of acidity demand more light for growth in the spruce forest. The volume percentage water in the upper horizons of the soil is thus almost double and the pH is half a unit higher in the beech forest compared with in the spruce forest. ELLENBERG (1939) has found that the minimum light for a particular species is higher on a more poor and acid soil than on a richer and more neutral one. This implies that "plants can manage with less light, the more favourable other growth conditions are" (WALTER 1960 p. 366, translated from German). The light spring period in the beech forest during April and the beginning of May might also be of importance to the summer plants, which are often able to start their growth at this time.

Judging from the summer day there seems to be no great difference between the beech and the planted spruce forest regarding the light conditions during the leafed period May—August. The light intensities in the spruce forest are surprisingly similar and very low on all three occasions and might be so during the whole year. In the beech forest light ought to be considerably higher during the period November—April and especially during the spring before the verdancy (cf. ANDERSSON 1964). The stronger radiation and energy input in the beech forest during this time makes the growth of spring species possible and causes an increased soil temperature (see p. 346). In the planted spruce forest the light must be considered as one of the most important limiting site factors for the ground vegetation. Probably it is the most important one, which has been stressed e.g. by SCHLÜTER (1966) and RHEINHEIMER (1959). The latter studied the immigration of plant species into planted spruce forests and found that plants will not immigrate to a great extent until there is a relative light intensity above 7 %. The spruce forest I have investigated is, in this respect, just on the limit to permit the growth of ground vegetation.

TEMPERATURE — RESULTS AND CONCLUSIONS

The daily variations during spring, summer and late autumn are given in Fig. 3 A—C. In these isoplete diagrams every second degree has been marked with isotherms (cf. PÅHLSSON 1966). During the spring day (Fig. 3 A) there was a quick warming of the air immediately above the soil surface in the beech forest, owing to the strong, direct incoming radiation. The warmth was soon transmitted to higher air layers. Maximum temperature of 12°C was reached in the afternoon. In the spruce forest the warming occurred more evenly, with a maximum temperature of about 10°C in the afternoon. Cooling at night

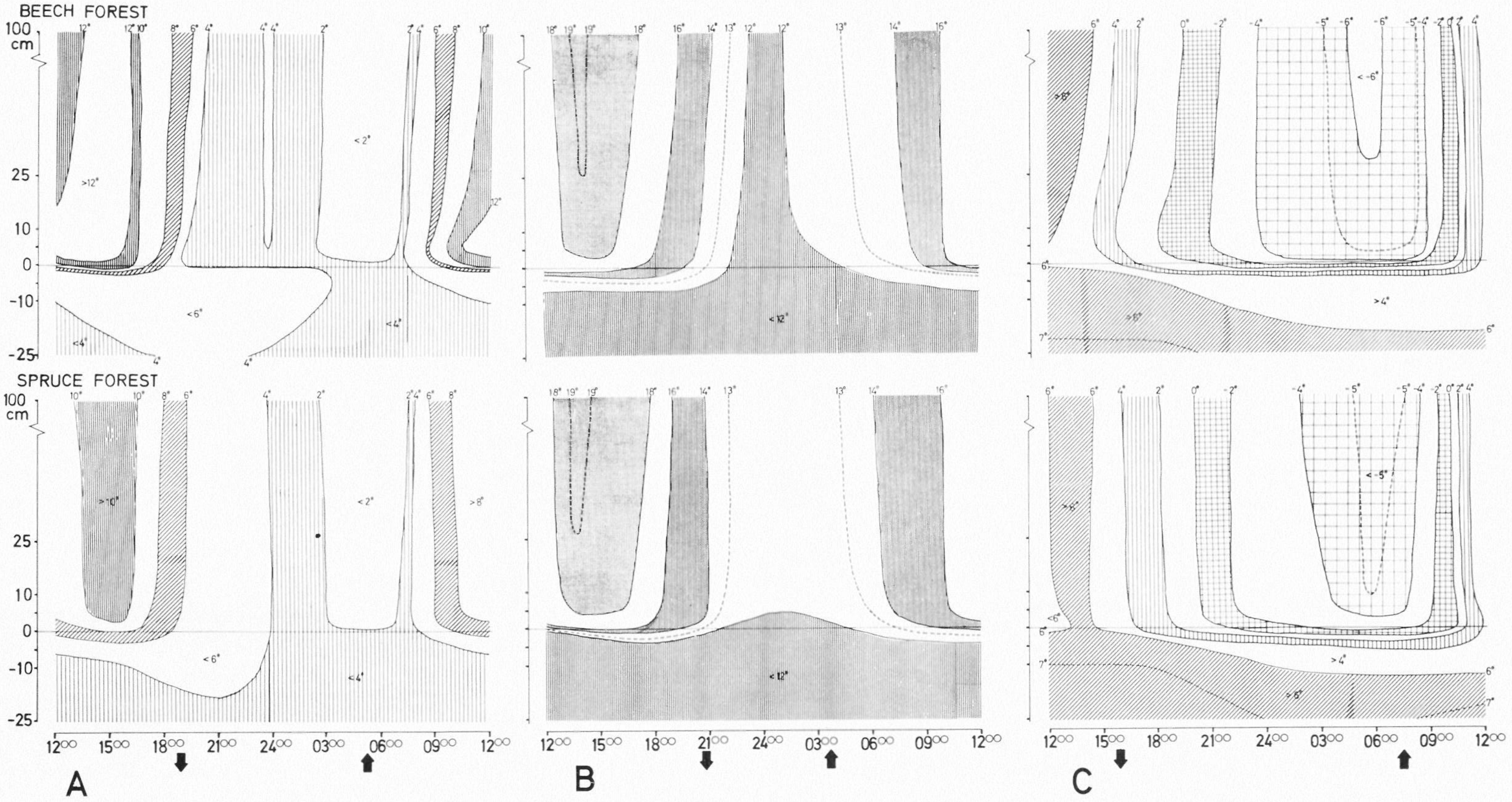

Fig. 3. Isoplete diagrams showing the daily variation of temperature in the beech and the spruce forests during the three measuring days. Sunset and sunrise are indicated by arrows. — A: The spring day, April 13—14, 1967. — B: The summer day, July 7—8, 1967. — C: The late autumn day, November 8—9, 1967.

occurred faster in the beech forest, due to a greater outgoing radiation, and the minimum temperature, which differed only slightly from that of the spruce forest, was reached just before sunrise nearest to the soil. It was half a degree cooler in the beech forest (0.8°C and 1.3°C respectively). In both the beech and spruce forest there were distinct litter layers, which owing to their loose structure and low heat-conductivities, must have acted as insulators. To some extent this may have levelled off the differences in radiation.

The soil temperatures fluctuated around 4°C but in the beech forest there was a relatively strong warming of the soil and the effect of this warming could be seen long into the night. The soil of the spruce forest was not warmed to the same degree and it cooled off faster. Contributing to the longer maintained warming effect in the beech forest soil was certainly the greater water content. In the upper soil horizons of the beech forest there were 40—45 vol.% water, while in the spruce forest there were only 25—30 vol.%. The higher incoming radiation in the beech forest made a warming of a greater volume of soil and water possible. The heat conductivity increases with increased water content (GEIGER 1961, WALTER 1960). The warmth was therefore transmitted quicker to greater depth in the beech forest soil and the result was a more retained warmth, which became evident at cooling.

During the summer day (Fig. 3 B) the temperature conditions in the beech and spruce forests were almost identical. A maximum temperature of 19°C was reached about two o'clock in the afternoon. The coldest air temperature was obtained immediately after midnight with 11.9°C in the beech and 12.2°C in the spruce forest. Cooling and warming occurred slowly and very uniformly in both the forests. The soil temperatures varied between 10°C and 13°C with the warmest parts nearest to the soil surface. The soil temperature at 25 cm depth in the beech forest was about 0.6—0.8°C higher than in the spruce forest; however this difference cannot be read off from these schematic diagrams.

The late autumn day (Fig. 3 C) happened to be the first real frost day during the autumn of 1967. This meant that the air temperature started to fall in the early afternoon. It fell more quickly in the beech forest, starting close to the soil surface, as the outgoing radiation was high in the defoliated forest. During the night the air temperatures dropped several degrees below zero. Minimum was reached at about six o'clock in the morning, with —6°C in the beech and —5°C in the spruce forest. However, these temperatures were not found nearest to the soil but at higher levels. This may be explained by a local cold fog

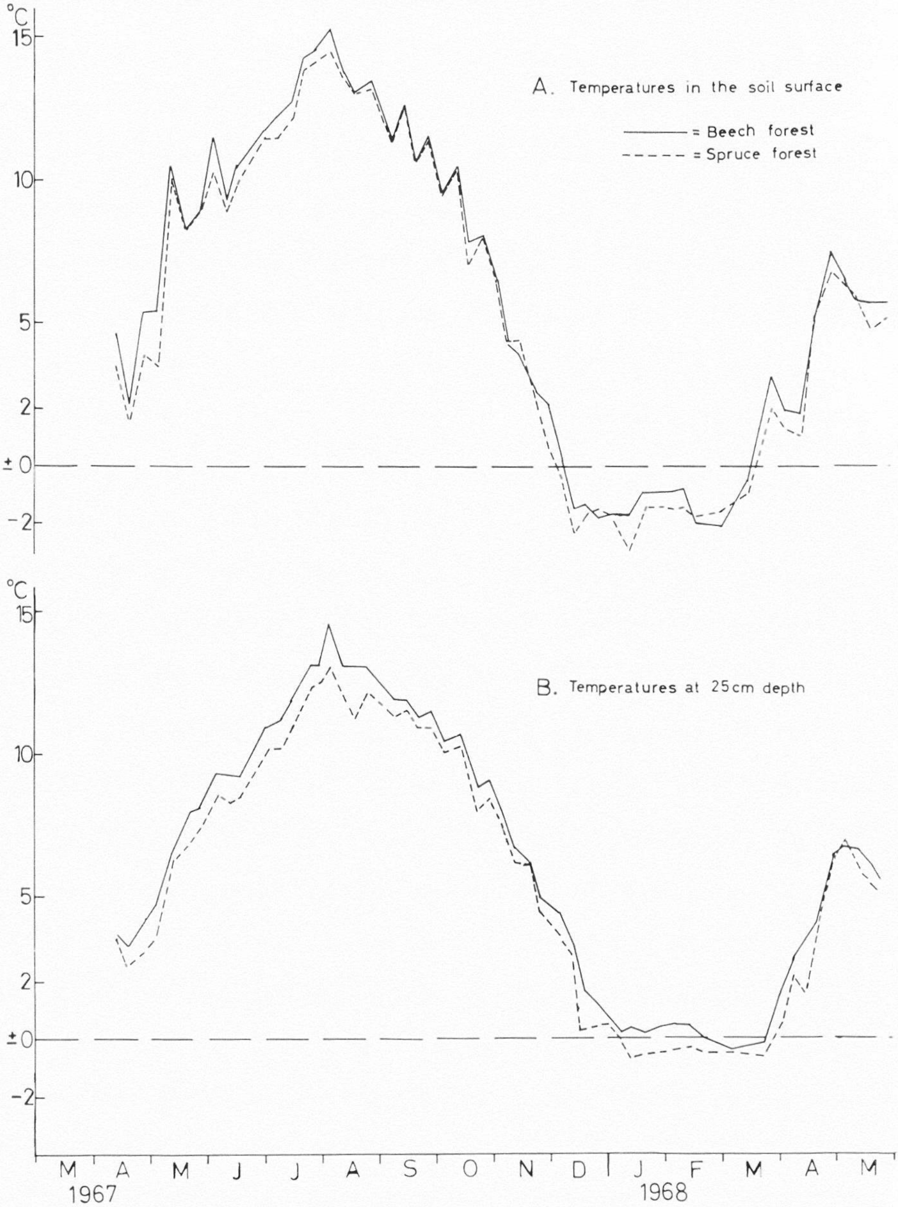

Fig. 4. The yearly variation of temperature in the soil, calculated as mean values per week. — A: The temperature in the soil surface just below the litter. — B: The soil temperature at 25 cm depth.

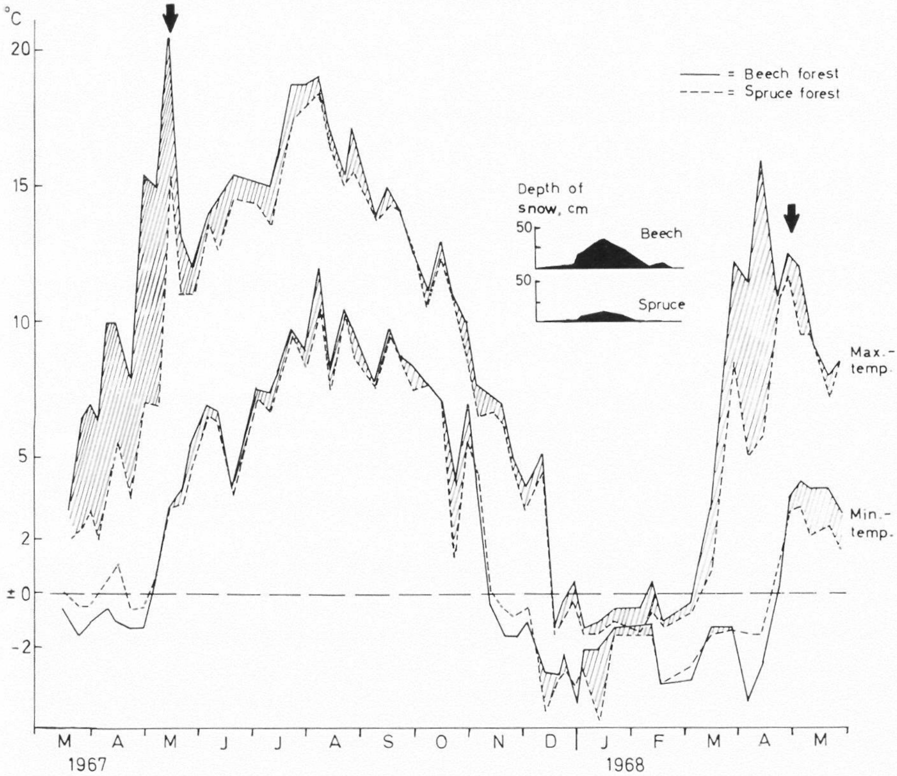

Fig. 5. The yearly variation of soil temperature. Maximum and minimum values every week from soil surface just below the litter. The beginning of verdancy in the beech forest is indicated by arrows and the higher temperature of the beech forest soil is marked with lines.

and the fact that warmth was released from the soil during the freezing period.

The soil temperatures were from the beginning 6—7°C, but during the night the upper 10—15 cm were cooled to such an extent that on the following day they were two degrees lower. The cooling was greater and occurred to a lower depth in the beech forest soil.

The yearly variation of temperature in the soil is illustrated in Figs. 4—5. In Fig 4 A and B the mean temperature/week has been calculated. This was done by reading off the temperature every second hour from the recorder paper, summing these figures for the whole week, then calculating an average week temperature. In Fig. 5 the minimum and maximum figures obtained during each week are shown. As can be seen from Fig. 4 A and B the mean temperatures show only small deviations. However, the temperature in the beech forest soil was constantly higher, especially at 25 cm depth. In the soil surface the beech forest temperature was higher particularly during the spring periods. Also in the surface there was a marked frost during the winter, whereas at 25 cm depth freezing occurred only during short intervals and more readily in the spruce forest soil.

The course of the minimum and maximum temperatures in the soil show obvious differences (Fig. 5). During the spring before leafing there were intense temperature variations in the beech forest soil. Sometimes the maximum temperature could be several degrees higher than in the spruce forest, while the minimum temperatures could be at least one degree lower than that of the spruce forest. After bursting of the beech leaves the temperature differences were insignificant but higher maximum temperatures could be seen in the beech forest. This was also confirmed during the measuring day of July 7—8 (cf. p. 343). During the late autumn after the fall of the leaves, the minimum temperature was again lower in the beech forest until a cover of snow prevented outgoing radiation from the soil. The maximum temperature was at the same time only slightly higher in the beech forest and was in no way comparable to the corresponding temperatures in the spring. This goes back to the radiation intensities.

During winter there was a relatively thick cover of snow in the beech forest with a maximum depth of 50 cm. In the spruce forest the cover of snow did not exceed 15 cm. Probably these insolation differences contributed to the fact that the temperature of the beech forest soil was highest. After the melting of snow the intense temperature variations in the beech forest occurred again.

CONCLUSION. The daily temperature variations differ mainly during the spring and late autumn days and are obviously intimately connected to the incoming and outgoing radiation factors. During the spring day the beech forest was more intensely warmed but on the other hand it was also cooled more intensely during the night. Due to a high accumulation of heat, in the soil, the warming effects were still stronger than in the spruce forest. During late autumn the outgoing radiation was of the greatest importance, which meant that the beech forest soil was cooled more intensely in spite of the higher incoming radiation during the day compared with the spruce forest. The soil temperatures in the two sites differed slightly throughout the year. Usually the beech forest soil was warmer, but except for the temperatures in the spring the differences were less than 1 °C and therefore within the error of the method.

The temperature is of great importance to most processes in the soil. To a certain degree it is a fact that higher temperatures imply higher biologic activity and growth and quicker mineralisation and decomposition. The higher temperature in the beech forest during the spring may contribute to the fast growth of the spring species, but it must also mean a greater activity of the microflora and the microfauna, which affects the turnover of organic matter. The lower temperature in the spruce forest must be considered as one of many contributing site factors, which cause the obvious trend in formation of mor that can be seen in planted spruce forests in Scania.

RELATIVE HUMIDITY — RESULTS AND CONCLUSIONS

The results of these measurements can be seen in Fig. 6 A—C. The course of relative humidity was to some extent a mirror image of that of the temperature. Low values of relative humidity prevailed when the temperature was high and vice versa. During the spring day therefore marked differences occurred between the forests. Very low relative humidity values (< 35 %) were obtained in the beech forest just above the soil surface in the afternoon. In the evening slowly maximum values (> 95 %) were reached. During the summer day the relative humidity, just as light and temperature, was very similar in the two sites. It was high, 60—100 %, during the whole day and changes occurred very slowly. The relative humidity for the late autumn day was even higher, with variations from 80 % to 100 %. Certain differences were noticeable. During the night thus the relative humidity was highest at the 50 cm level in the beech forest, but was found just above the soil in the spruce forest. This probably depended on supercooled mist, which occurred almost to the ground in the beech forest but which was lacking close to the ground in the spruce forest. In the latter there was instead a continuous dropping of precipitated mist from the canopy which caused high relative humidity in the soil surface. Later in the night the soil surface was frozen and then the relative humidity values decreased. This happened first and to a greater extent in the beech forest but the same tendency could be seen in the spruce forest. In the morning deposited rime thawed when the temperature rose, dropped

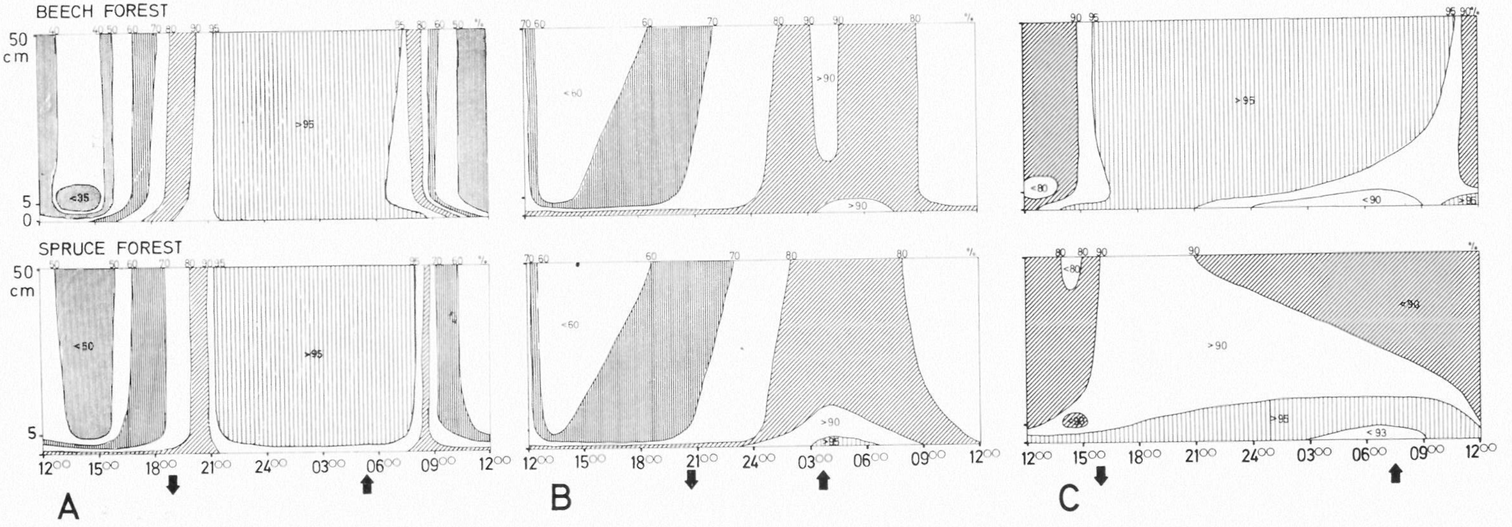

Fig. 6. The course of relative humidity during the three measuring days. Sunset and sunrise are indicated by arrows. — A: The spring day, April 13—14, 1967. — B: The summer day, July 7—8, 1967. — C: The late autumn day, November 8—9, 1967.

to the ground and caused high relative humidity values in the soil surface once again.

The humidity in the soil surface of the spruce forest was never below 80 %, though all three measuring days where chosen as days with clear weather. On the other hand in the soil surface of the beech forest the relative humidity was as low as 50 % during the spring day. Considered as an average during the whole year this implies that the soil surface in this planted spruce forest offers more humid conditions than does the beech. From the vegetation point of view this favours moist dependant shade plants, e.g. liverworts such as *Lophocolea heterophylla,* a species that is found in Kongalund and which is frequent in planted spruce forests in Scania.

Measurements of evaporation have not been performed but from the relative humidity it is possible to draw some conclusions as the evaporation ought to be inversely proportional to the relative humidity. BURGER (1934 a, b) found that the yearly evaporation in a beech forest was higher than in a spruce forest mainly because of the high evaporation in the defoliated beech forest during the spring. Certainly this also holds for Kongalund.

WIND VELOCITY

The wind velocities were very low during the three measuring days, with a maximum of 2 m/sec. The highest velocities were always obtained in the middle of the day, about noon. Due to the low wind velocities the stratification of temperature and relative humidity near the ground could be clearly illustrated (Fig. 7).

DISCUSSION

The measurements show obvious differences in the microclimate between the beech and the planted spruce forest. The climate in the beech forest was more variable with great differences between the leafed summer period and the other seasons. The climate in the spruce forest was more uniform throughout the year, which meant that the great variations valid for an open field were reduced (cf. MITSCHERLICH et al. 1965). The primary site factor causing differences between beech and spruce forests is probably incoming radiation which influences both the temperature and the relative humidity. All differences were greatest in the spring, while in the summer the conditions seemed

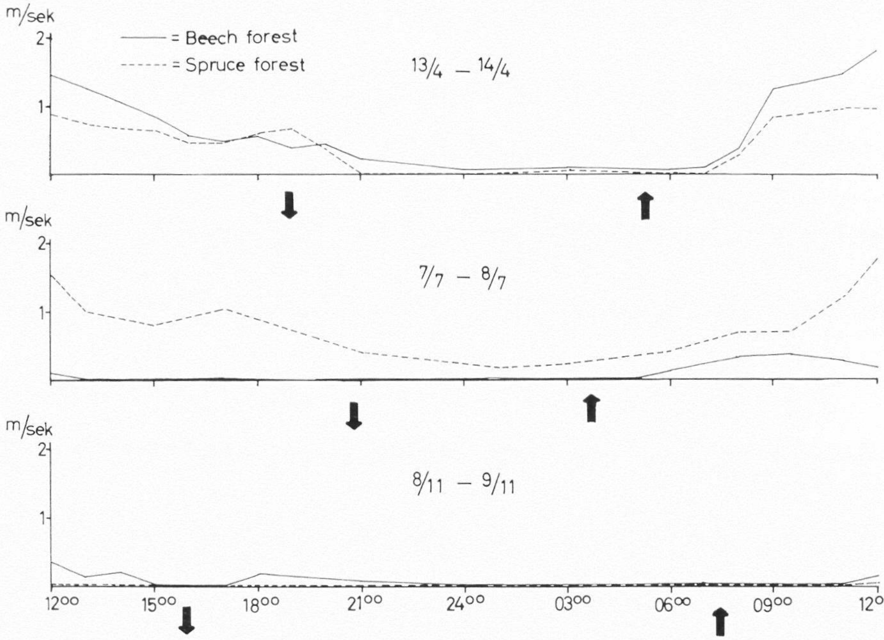

Fig. 7. The wind velocity during the three measuring days. Sunset and sunrise are indicated by arrows.

to be the same, although there were small differences in soil temperature. Also during late autumn when the beeches had dropped their leaves, the climatic differences were small owing to the low incoming radiation.

The light must be considered as the primary cause for the development of the spring flora in the beech forest and as a limiting site factor for the ground vegetation in the spruce forest. In the latter probably some other site conditions contribute to the poor development of the ground flora.

These results given are of course valid for this locality and cannot be directly applied to other forests. In addition to the general climatic features, both the cover of the canopy and the chemical and physical properties of the soil have an effect on the microclimate. Concerning planted spruce forests it might be stated that the microclimate in young, dense stands is still more unfavourable to the ground vegetation and to the microflora and microfauna of the soil, at least with regard to light and temperature conditions. In more open stands the microclimate ought to be more favourable, which is indicated mainly by a better development of the field layer. This has also been shown in several investigations on thinning plots, e.g. by OTT (1966) and MITSCHERLICH et al. (1965).

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Zygopleurage and Zygospermella (Sordariaceae s. lat., Pyrenomycetes)

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ABSTRACT

Zygopleurage, Zygospermella, and their known species are described and discussed, and all finds known to the author are compiled. *Zygopleurage faiyumensis* LUNDQ. and *Zygospermella striata* LUNDQ. are new species, whereas *Zygospermella setosa* (CAIN) CAIN has been found to be a synonym of the misinterpreted *Z. insignis* (MOUTON) CAIN.

INTRODUCTION

The present article is part of a larger treatise dealing with the taxonomy of the *Sordariaceae* s. lat. The living specimens studied have been collected by the author in Sweden, Corsica and Egypt, by Dr. R. SANTESSON in U.S.A., and by Dr. M. J. RICHARDSON in Scotland. Dried material for examination has also been gratefully received from BR, FH, NY, O, PAD. LMH means Lyallpur Mycological Herbarium (Lyallpur, West Pakistan). Some duplicates will be distributed to various herbaria.

ZYGOPLEURAGE BOEDIJN

Zygopleurage BOEDIJN, Persoonia 2: 316, 1962. — Type species and originally only species: *Sordaria zygospora* SPEG.

Fimicolous. *Perithecia* non-stromatic, obpyriform, ostiolate, with a pseudoparenchymatous, membranaceous to subcoriaceous peridium of 3 different layers with tangentially flattened cells in the medium layer. Paraphyses indistinct. *Asci* clavate, unitunicate, long-stipitate, rounded at the apex, without apical ring, or any thickened membranes, swelling at maturity, with longitudinal, cytoplasmic ribs visible after spore discharge. *Spores* at first hyaline, one-celled, fusiform, then strongly elongating, ± cylindrical, vermiform, straight, or spirally coiled around each other, arranged on about the same level, then normally 3-celled by a transverse septum laid down near both ends; end cells swelling, becoming dark brown, smooth, ± ellipsoidal, with a germ pore at the end; intercalary cell hyaline, with or without a small inflation in the middle, sometimes multiseptate and multinucleate, devoid of plasma, collapsing at maturity; gelatinous equipment present in the known species. Spores discharged in their pigmented stage.

The species of this characteristic genus have the strangest spores of all known coprophilous *Pyrenomycetes* and are equalled by few other *Ascomycetes*. I think this spore model must be explained as being advantageous for the fungus at its spore discharge. Such long spores with a heavy lump at each end swirling through the air have a large hitting surface or range, which augments the chances of striking a piece of vegetation. In reality the projectile is even larger, as all spores in an ascus are certainly ejected simultaneously, entangled in each other.

The origin of *Zygopleurage* should be sought close to *Lasiosphaeria*, where the vermiform, septate spore type still exists. At the transition to coprophily the presumed ancestor may be expected to have evolved pigmented spores, postponing their maturation and discharge to this stage. A reduction of the paraphyses and the apical apparatus of the asci followed too. What was left is the long type of immature spore only, and *Zygopleurage* has thus reached the same evolutionary level as the *Podospora decipiens* group. The occasional, multicellular nature of the connecting appendage is certainly a reminiscence of an ancestor with long, multiseptate spores. This opinion was also held by LEWIS (1911).

KEY TO THE KNOWN SPECIES

1. Spores strongly coiled in the ascus; end cells with c. 4 short, distal caudae; intercalary cell 130—185 μ long . . . . 3. *Z. zygospora*
1. Spore not coiled or coiled loosely in the ascus; end cells with short caudae all over; intercalary cell shorter
   2. End cells 35—46×20—28 μ; intercalary cell 75—95 μ long, inflated in the middle and covered all over with a gelatinous sheath . . . . 1. *Z. faiyumensis*
   2. End cells 21.5—32.5×14.5—19.5 μ; intercalary cell 43—80 μ long, without inflation (and sheath) . . . . 2. *Z. multicaudata*

1. **Zygopleurage faiyumensis** LUNDQ. sp. nov. (Figs. 1—4 A)

DERIVATION: Named after Faiyum, an Egyptian province and oasis.

Fimicola. *Perithecia* solitaria vel aggregata, semiimmersa vel fere superficialia, late obpyriformia, 1200—1500×860—960 μ, collo cylindraceo vel

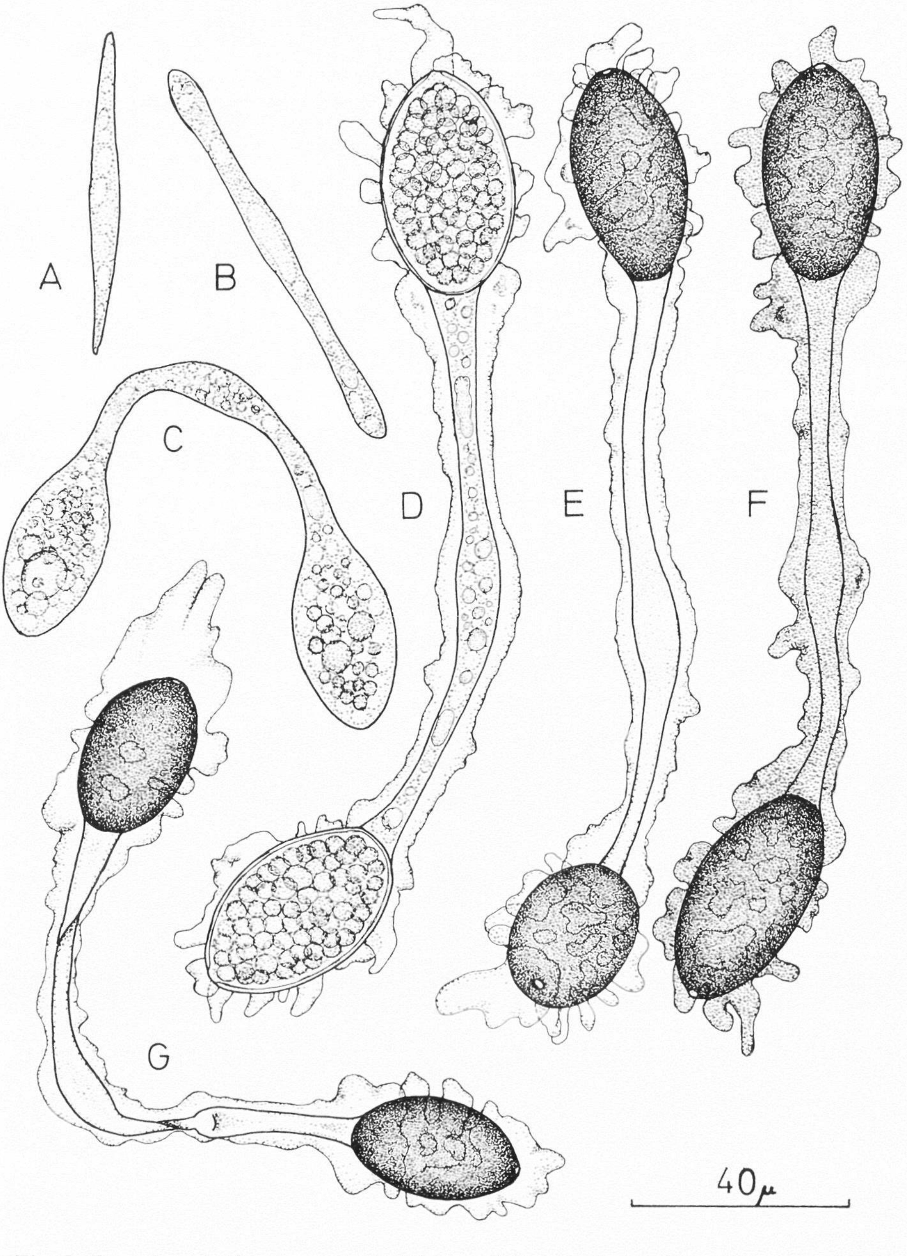

Fig. 1. *Zygopleurage faiyumensis,* holotype. All figures drawn from living specimens. — A—C: Young, hyaline spores in various stages of development. — D: Young, olivaceous spore with oil drops. — E—G: Mature spores; the strongly stippled figure shows the appearance of the gelatinous coating in Indian ink. — G: Spore with collapsed intercalary cell.

conico, 240—500×240 μ, pilis flexuosis, olivaceo-brunneis, c. 2.8 μ crassis obtecta. Peridium membranaceum vel subcoriaceum, subopacum, olivaceo-brunneum vel nigro-brunneum; cellulae externae peridii angulatae 4—9 μ diam., parietibus undulatis, modice incrassatis. *Asci* (4—6—) 8-spori, 350—420×60—70 μ, clavati, apice late rotundato. *Sporae* initio hyaline, fusiformes, unicellulares, deinde usque ad 200—240 μ, elongatae, 8-seriatae, partibus extremis transversaliter uniseptatis et tumescentibus; cellulae extremae demum nigro-brunneae, ellipsoideae, aequilaterales, 35—46 (—50)×20—28 μ, ad septa truncatae, extremo poro germinali instructa; cellula intercalaris ± recta, cylindracea, 75—95 μ longa, parte angustissima 4.5—6 μ lata, parte media inflata, 8—10 μ lata, strato gelatinoso cincta, maturitate sine plasmate, collabens. Caudae gelatinosae breves, magnitudine et forma irregulares cellulis extremis passim affixae; gelatina homogena, in aqua persistens, non vel vix tumescens, in atramento Indico nigrescens.

Perithecia scattered or in small groups, semi-immersed to almost superficial, broadly obpyriform, 1200—1500×860—960 μ, with a cylindrical or tapering neck, 240—500×240 μ, covered with simple, flexuous, olivaceous brown, septate, c. 2.8 μ thick hairs. Peridium 3-layered, pseudoparenchymatous, membranaceous, semitransparent to almost opaque, olivaceous brown to blackish brown, with irregularly shaped outer cells, 4—9 μ in diam., having slightly thickened, usually undulating walls; middle peridial layer composed of tangentially flattened cells, merging into a thin, inner layer of hyaline cells. Typical paraphyses not observed. *Asci* (4—6—) 8-spored, 350—420×60—70 μ (swelling up to 110 μ in width), clavate with a broadly rounded apex and a long stipe, unitunicate, J—, with longitudinal, cytoplasmic ribs visible after spore discharge; apical ring not observed; calotte thin; subapical chamber narrow. *Spores* at first hyaline, fusiform, one-celled, then vermiform, strongly elongating up to 200—240 μ, 8-seriate, not coiled, with monostichous oil drops, then swelling at both ends, becoming 3-celled by a transverse septum below and above each swelling, 2—4-seriate; end cells ranging through olivaceous to dark brown with a plasma containing large oil drops, ± ellipsoidal, equilateral, 35—46 (—50)×20—28 μ, a little truncate at the septum, with an apical and a basal germ pore respectively; intercalary cell more or less straight and cylindrical, 75—95 μ long, with an 8—10 μ wide inflation in the middle, 7—10 μ broad at the septa, 4.5—6 μ broad at the narrowest part between the septa and the inflation, hyaline, at maturity devoid of plasma and collapsing. Gelatinous caudae short, cylindrical or tapering, of irregular size and form sparsely attached to the end cells, sometimes drawn out at the spore ends to 40 (—60) μ; intercalary cell in its whole

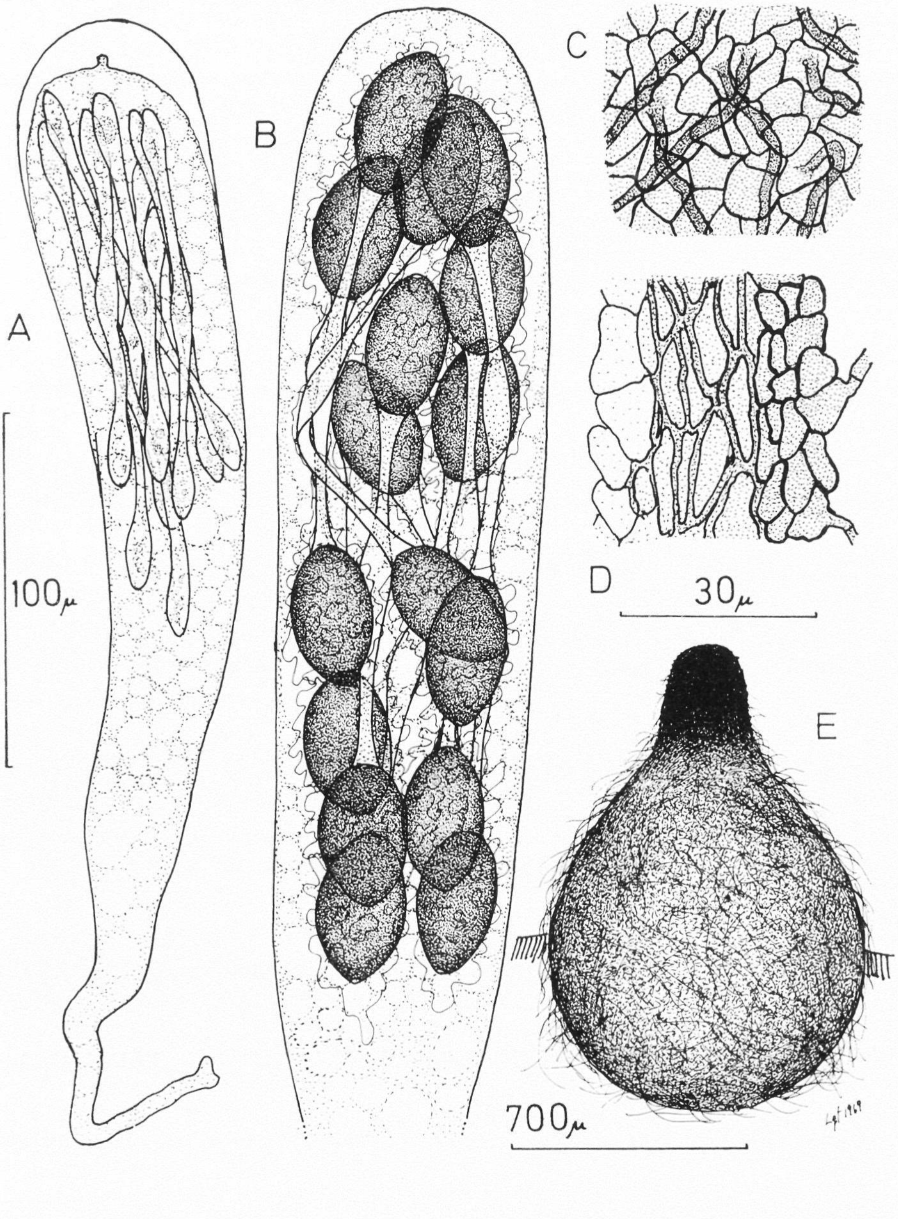

Fig. 2. *Zygopleurage faiyumensis*, holotype. All figures drawn from living specimens. — A: Young ascus and spores. — B: Ripe ascus and spores. — C: Peridium in horizontal view. — D: Peridium in median vertical section. — E: Perithecium.

length surrounded by a coating of mucus of irregular outline that increases in width at the septa and the adjoining parts of the end cells; all gelatinous equipment solid, homogenous, swelling little or not at all in water, blackening in Indian ink.

SPECIMENS EXAMINED: **Egypt:** Faiyum, 10 km NE of Lake Qarun at the dried-up marshes of Kom Aushim, on cow dung 1.III. 1968, LQT 5870-n, holotype (UPS); developed in moist chamber, Uppsala. Isotypes will be placed at IMI (slide), LMH, S, TRTC.

2. **Zygopleurage multicaudata** MIRZA

Zygopleurage muticaudata MIRZA in MIRZA & NASIR, Nova Hedwigia 16: 286, pl. 102, 1968. Holotype on cow dung from Lyallpur, West Pakistan (LMH 1081, not seen).

Perithecia 600—1200×480—865 µ, obpyriform, usually covered with flexuosus hairs. Peridium membranaceous, olivaceous, with angular, outer cells, 4.9—12 µ in diam. *Asci* 8-spored, 190—250×54—60 µ, clavate, broadly rounded at the apex. *Spores* at first cylindrical, one-celled, hyaline, in parallel fascicles, then loosely coiled; end cells brown, 21.5—32.5×14.5—19.5 µ, ± ellipsoidal, truncate at the septa and with a basal and an apical germ pore respectively, covered all over with short, scattered, gelatinous caudae; intercalary cell cylindrical, 43—80×6 µ, without median inflation and sheath.

The description is a modified version of the original one. As I have not examined of the species, the micro-morphology of its gelatinous equipment is not quite clear to me. There may thus be a sheath around the intercalary cell. This is rather difficult to discern without the help of India ink and the authors may have overlooked it. Although the variation in size and form in the *Zygopleurage* spores is considerable, I think the differences between *Z. multicaudata* and *Z. faiyumensis* are sufficient both as to number and quality to distinguish these fungi as separate species.

MIRZA and NASIR also reported the species from Lahore, and AHMED and ASAD (1968 p. 60, pl. III K) found it (under the name *Z. zygospora*) several times in the Karachi area. Unfortunately the reports are not detailed enough to inform about the number of finds and kind of substrate.

3. **Zygopleurage zygospora** (SPEG.) BOEDIJN (Figs. 4 B—E, 5).

Sordaria zygospora SPEG., Michelia 1: 227, 1878. Holotype on cow dung from Conegliano, Venezia, Italy, 5.IX. 1877, SPEGAZZINI (LPS 2981). — *Philo-*

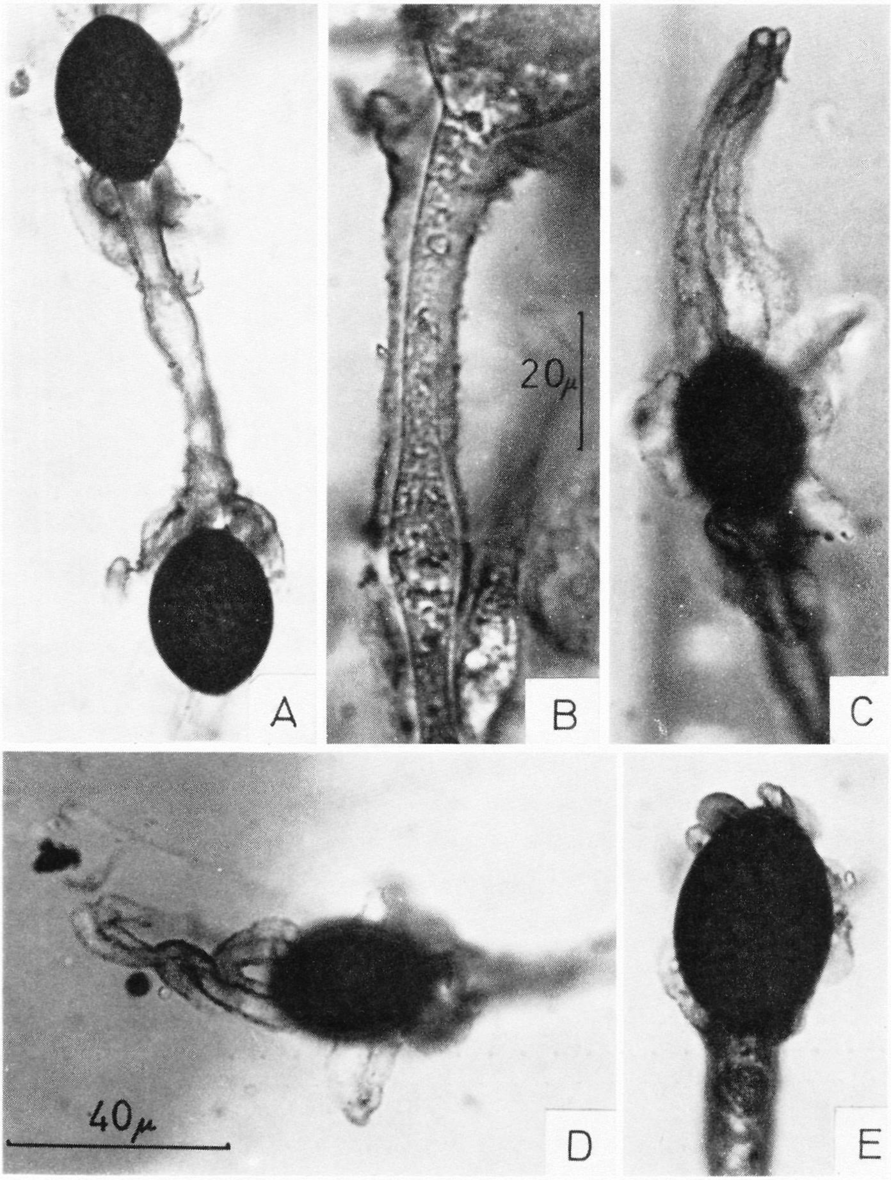

Fig. 3. *Zygopleurage faiyumensis,* holotype. — A—E: Spores in Indian ink; only A shows an entire spore; note the sheath around the intercalary cell and the median swelling in B. Magnifications: A, C, E = D.

copra zygospora (SPEG.) SACC., Syll. Fung. 1: 251, 1882. — *Podospora zygospora* (SPEG.) NIESSL, Hedwigia 22: 156, 1883. — *Pleurage zygospora* (SPEG.) O. K., Rev. Gen. Plant. 3(3): 505, 1898. — *Zygopleurage zygospora* (SPEG.) BOEDIJN, Persoonia 2: 316, 1962.

Perithecia obpyriform, 770—1200×480—815 μ, with a neck 190—620×135—240 μ. Peridium membranaceous, semitransparent, olivaceous brown. *Asci* 8-spored, 250—270×40—60 μ, swelling up to 90 μ in width. Young *spores* vermiform, elongated up to 200—230 μ, spirally coiled around each other; end cells dark brown, ellipsoidal, 29—38×15—23 μ; intercalary cell (100—) 130—185 (—200) ×5—6 μ, occasionally multiseptate and multinucleate, cylindrical, sometimes with an inconspicuous inflation in the middle; both end cells with 2—4 tapering, flattened, straight or curved, gelatinous caudae, 12—25 (—30) ×6—8×3.5—4 μ, attached to the germ pore; each cauda either with a longitudinal furrow or split in two filaments (of unequal width); intercalary cell with small caudae of irregular size and form attached near the septa and usually also with small patches or sheaths of mucus sparsely distributed all over; gelatinous equipment not swelling in water. Other characters as in *Z. faiyumensis*.

SPECIMENS EXAMINED: **Sweden:** Blekinge, Kristianopel, 7.VI. 1962, LQT 3364-h, EXS ined. (NY, slide, UPS). — Småland, Vimmerby, 3 km S of Storebro, 31.V. 1959, LQT 2307-b (BPI, IMI, L, M, S, TRTC, UPS). — Öland, Köping, between Borgholm and Köpingvik, 14.VII. 1960, LQT 2569-b (UPS). — Halland, Torpa, NE of Tångaberg, 4.VIII. 1961, LQT 3119-b (UPS); all on cow dung. — **France:** Corsica, Belgodere, Tour de Lozari (=6 km ENE of l'Ile Rousse), on the seashore, on cow dung, 21.V. 1965, LQT 4485-d (UPS). — Bonifacio, at the bridge over Ventilegne R. (=7 km NW of Bonifacio), on cow dung, 13.V. 1965, LQT 4425-u (UPS). — **Canada:** Ontario, Brant, Eatonia, on cow dung, 16.XI. 1929, CAIN (FH, slide 1754). — York, Maple, on cow dung, 1.X. 1938, CAIN 12309 (FH). — **U.S.A.:** Colorado, Boulder, W base of Mt. Steamboat in Front Range (= 3 km NW of Lyons near mouth of St. Vain Creek), alt. 1900 m, on cow dung, 30.IV. 1966, SANTESSON 18499-A (UPS, slide). — South Dakota, Aberdeen, on cow dung, IX. 1899, TOWNE, herb. GRIFFITHS (NY). — Redfield, on cow dung, 8.VII. 1899, CARTER, herb. GRIFFITHS (NY); GRIFFITHS 1901. — New Jersey, Fort Lee, on cow dung, 3.VIII. 1899, GRIFFITHS (NY, 2 slides); GRIFFITHS 1901. — S. loc., on guinea pig dung, IV. 1918, MCFARLANE, herb. FAULL 12055 (FH). — Massachusetts, Cambridge, on horse dung, X. 1897, FARLOW (?) as *Podospora vestita* (FH). — **Puerto Rico:** Mayaguez, on cow dung, s. dat., FINK (NY). — S. loc., on horse dung, 19.XII. 1901, THAXTER (FH 1116). — **Egypt:** Faiyum, in the dried-up salt marsh at Kom Aushim, c. 10 km NE of Lake Qarun, on cow dung, 1.III. 1968, LQT 5870-h (BUCU, C, PC, S, UC, UPS, W). — **Liberia:** S. loc., on horse dung (?), XII. 1896, THAXTER (FH 1096A, 1087A).

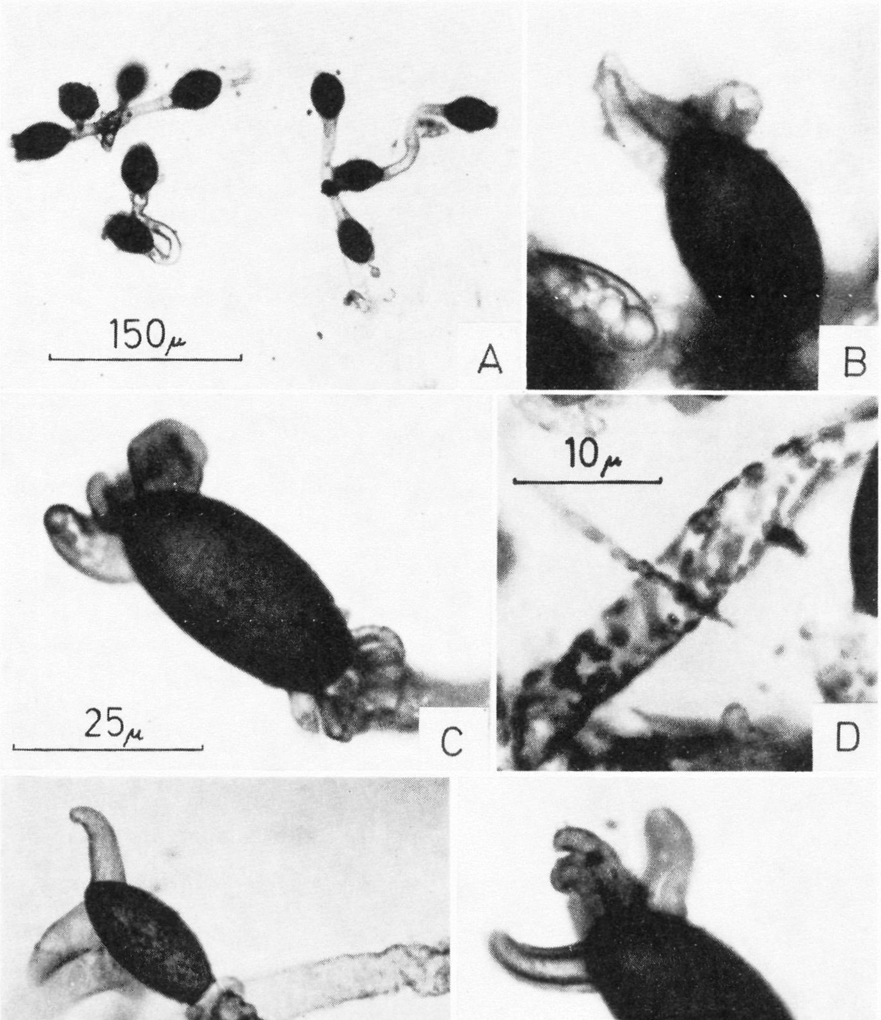

Fig. 4. A: *Zygopleurage faiyumensis*, holotype. — B: *Z. zygospora* LQT 5870-h. — E—F: Ditto, SANTESSON 18499-A.; — A—F: Spores in India ink; note the cross section of the cauda in B and the scattered, gelatinous covering on the intercalary cell in D; E shows an end cell with only two, distal caudae. Hagnifications: B, E, F = C.

UNVERIFIED RECORDS: **France:** on cow dung, MOREAU 1953; La Mycothèque 2, 1949; on dung of cow 3, and horse, BRETON 1966. — **Poland:** on cow dung, KOHLMAN-ADAMSKA 1965. — **Hungary:** on dung of hare and cow, TÓTH 1965. — **Bulgaria:** on dung of cow and sheep, FAKIROVA 1968, 1969. — **Canada:** on horse dung, GRIFFITHS 1901; substrate not mentioned, MAINS et al. 1939; esp. on dung of cow and horse, CAIN 1934. — **U.S.A.:** on dung of cow 7, horse 7, pig 2, goat, and sheep, GRIFFITHS 1901; substrate not mentioned, LEWIS 1911; on horse dung, MEYER 1941; on dung of cow and horse, STRATTON 1921; on horse dung, WILSON 1947. — **Algeria:** on human excrements, FAUREL & SCHOTTER 1965. — **Tchad:** on dung of donkey and camel, FAUREL & SCHOTTER 1966. — **Tanzania:** on dung of sheep and mule, SCHMIDT 1913. — **Indonesia:** on dung of rabbit, goat, and sheep, BOEDIJN 1962. — **West Pakistan:** substrate not mentioned 8 (?), AHMED & ASAD 1968.

CHOICE OF SUBSTRATE: (Figures without parentheses are the collections examined by the author; those within represent all records.) 18 (> 71): on dung of cow 14 (> 30), horse 3 (> 16), sheep (4), goat (2), pig (2), donkey (1), mule (1), camel (1), rabbit (1), hare (1), man (1), guinea pig 1; substrate not mentioned (c. 10).

ILLUSTRATIONS: SACCARDO 1879, fig. 618. GRIFFITHS 1901, pl. 1: 3; 9: 1—4; 15: 22; 18: 1, 9—13. TRAVERSO 1907, fig. 88: 8. LEWIS 1911, pl. 19. STRATTON 1921, pl. 10: 1—5. CAIN 1934, fig. 31. MOREAU 1953, figs. 51 a—e, 52 a—f. HESLOT 1958, pl. A 8, B 9, C 3; 24: 3—5. BOEDIJN 1962, figs. 8—10. KOHLMAN-ADAMSKA 1965, fig. 15 a—c. AHMED & ASAD 1968, pl. III. K. FAKIROVA 1968, fig. 23.

Little is known about the biology of *Z. zygospora*. According to my experience its development takes 3—4 weeks, which is normal for such a big species, but GRIFFITHS mentions 10 days (1901 p. 17). The fungus seems to belong mainly to warm-temperate and subtropical regions and prefer the dung of domesticated herbivores.

Z. zygospora varies considerably as to the size and form of the end cells of the spores, number of spores per ascus, and septation of the intercalary cell. These extremes are not all included in the description above. LEWIS, who in 1911 investigated its cytology and spore ontogeny, found similar anomalies. The genetics of the species was treated of by HESLOT (1958).

The American specimens have narrower spores than those from the Old World I have seen. (GRIFFITHS 1901: 24—40 × 13—19 μ; SANTESSON 18499-A: 30—41 × 15—19 μ). The Indonesian specimens examined by BOEDIJN have narrow spores too, and the ascus tip is said to have a thickened ring, although the latter feature cannot be seen on his drawings. In the Liberian specimens the spores are unusually long (up to 200 μ) with a multiseptate, intercalary cell. Very probably, however, all records refer to one and the same species.

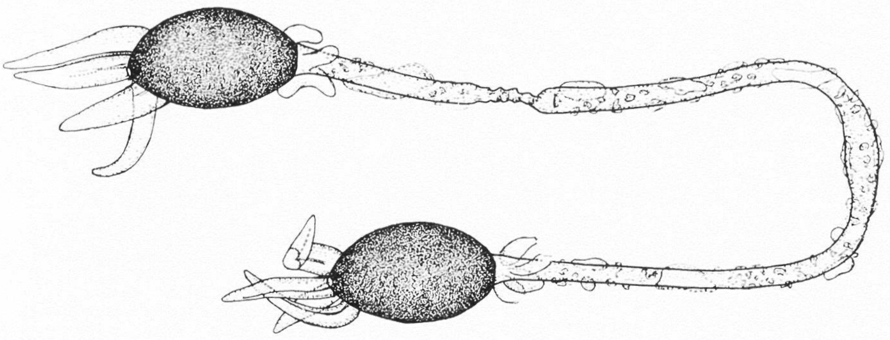

Fig. 5. *Zygopleurage zygospora,* LQT 2569-b. Mature spore. — Same magnification as in Fig. 1.

Spegazzini's description is somewhat misleading, as it states the asci to be "12-spored" (=6-spored), the end cells of the spores 40×20—25 μ, and the intercalary cell 70—100 μ long, which reminds one more of *Z. faiyumensis*. Saccardo's drawing, which was based on authentic specimens, gives a false picture, too. In the type specimens, however, the end cells measure 30—40×17—20 μ, having distinct, distal caudae. The intercalary cells, the length of which cannot be discerned, are strongly coiled, not only "subtortous". A perithecium measured 815× 625 μ (thus more than said by Spegazzini), and the asci are 8-spored.

ZYGOSPERMELLA Cain

Zygospermum Cain, Univ. Toronto Stud. Biol. Ser. 38: 73, 1934. — Type species: *Z. setosum* Cain, selected by Cain 1934; non *Zygospermum* Thwaites ex Baillon 1858 (*Euphorbiaceae*).

Zygospermella Cain, Mycologia 27: 227, 1935.

Fimicolous. *Perithecia* non-stromatic, ± obpyriform, ostiolate. Peridium pseudoparenchymatous, 3-layered, with an outer textura angularis, a middle layer of tangentially flattened cells, and an inconspicuous inner layer of hyaline, angular cells. Paraphyses longer than the asci and mixed with them, simple, filiform-ventricose, septate. *Asci* unitunicate, subclavate, long-stipitate, with a non-amyloid, hardly visible apical apparatus, at maturity swelling, rupturing below the tip which forms an adherent operculum, and provided with longitudinal, cytoplasmic ribs. *Spores* at first hyaline, one-celled, cylindrical, then equatorially constricted and transversely uniseptate at the constriction previous to the pigmentation; both cells finally dark brown, smooth, often separating, truncate at the septum and with a germ pore at the narrow end, gelatinous equipment present in the known species. Spores discharged at their pigmented stage.

Zygospermella is a very characteristic genus because of its two-celled, *Delitschia*-like spores. The genus is, I think, remotely related to *Bombardia* (FR.) ex KARST. s. lat. and *Lasiosphaeria* CES. & DE NOT., and its origin ought to be looked for in the *Lasiosphaeria* pool. The perithecial setae resemble those of *B. muskokensis* CAIN and some *Lasiosphaeria* species. The additional, transverse septa in the spores are exactly the kind found in several *Bombardiae* and *Zopfiella* WINT. as regards their position and late appearance in the spore ontogeny. The hollow, gelatinous caudae in *Z. insignis* have a counterpart in *Podospora appendiculata* (AWD ex NIESSL) NIESSL which species shows many connections with *Bombardia*. The basal cell in the *Zygospermella* spore is undoubtedly homologous with the pedicel of the spore in, for example, *Bombardia* and *Podospora*. It deserves being mentioned that an anomalous pigmentation of the pedicel is not uncommon in *Bombardia* spores.

Even though the origin of *Zygospermella* is indicated by a number of morphological features, the recent genus has evolved far beyond the limit of the *Bombardia* assemblage. The genus holds a position similar to *Podospora* regarding the reduction of the apical apparatus of the asci and the incapacity of the spores to germinate and be discharged in their hyaline state. *Zygospermella* and *Podospora* have probably separated early in their "*Lasiosphaeria*" period and then evolved in different directions. From the *Zygospermella* spore type I see a possible evolutionary bridge to *Arnium* NITSCHKE ex WINT. (=*Pleurosordaria* FERNIER). A more thorough analysis of the phylogenetic problems in the family is found in my above-mentioned, larger work.

KEY TO THE KNOWN SPECIES

1. Spores 38—48×11—14 μ; gelatinous caudae longitudinally fibrillate .... 1. *Z. striata*
1. Spores (46—) 50—68×11—17 μ; caudae hollow, not fibrillate .... 2. *Z. insignis*

1. **Zygospermella striata** LUNDQ. sp. nov. (Figs. 6—7, 8 B, D—E).

DERIVATION: Latin *striatus*, striped or striate, referring to the fibrillate nature of the gelatinous caudae of the spores.

Fimicola. *Perithecia* dispersa, immersa, obpyriformia, 625—670×335—

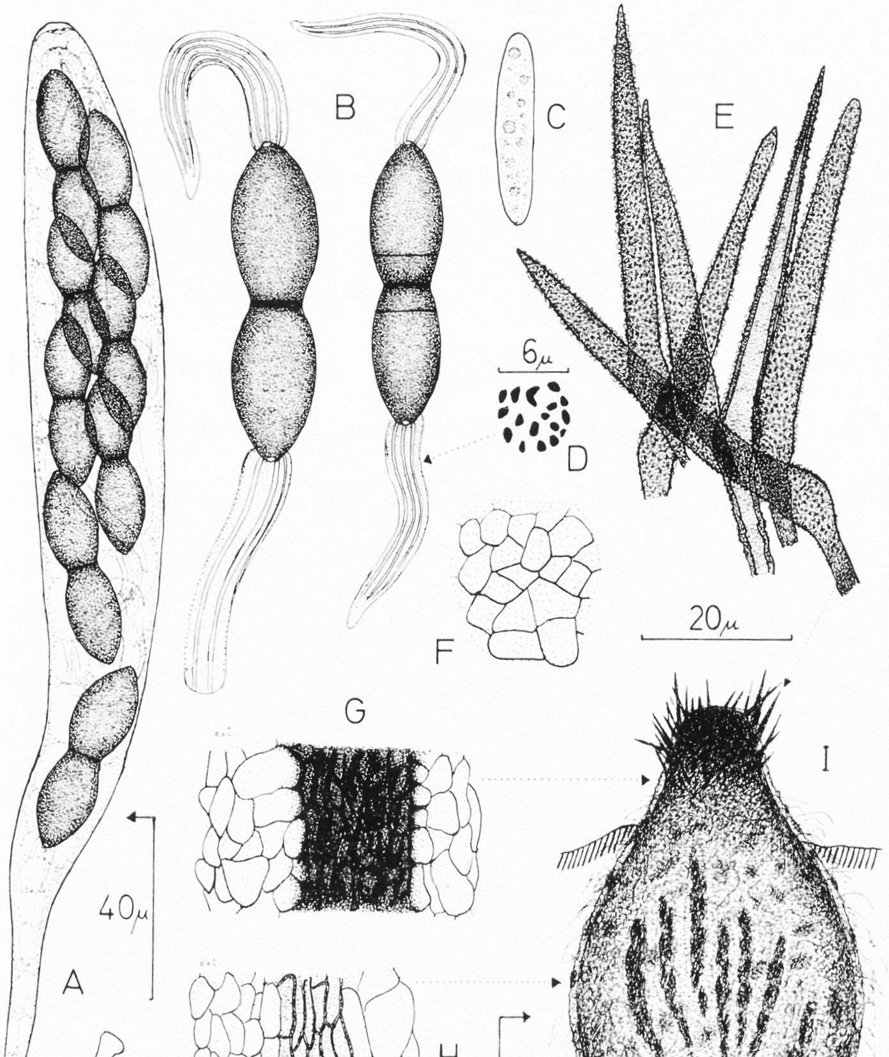

Fig. 6. *Zygospermella striata,* holotype. All figures drawn from specimens in water. — A: Mature ascus and spores. — B: Mature spores. — C: Young, hyaline spore. — D: Cross section of cauda. — E: Setae. — F: Peridium in horizontal view from middle part of the perithecium. — G—H: Vertical, median sections of peridium. — I: Perithecium.

400 μ, pilis flexuosis, ramosis, hyalinis, c. 2 μ crassis sparse obtecta; collum perithecii 145—240×135 μ, conicum, setis rectis vel modice curvatis, angustatis, acutis, unicellulatis vel raro 1—3-septatis, verrucosis, parietibus crassis, brunneis, profunde radicatis, 2—90×4.5—7.5 μ obtectum. Peridium 35—45 μ crassum, membranaceum, semipellucidum, ochraceo-olivaceum, in collo opaco, fusco, subcarbonaceo; cellulae externae peridii angulatae, hyalinae 5—10 μ diam., parietibus tenuibus. Paraphyses ascis longiores et mixtae, simplices, filiformi-ventricosae. *Asci* 8-spori, 290—370×25—32 μ, subclavati, longe stipitati, apicaliter rotundati et modice umbonati, apparato apicali indistincto instructi. *Sporae* biseriatae, initio hyaline, unicellulares, cylindraceae, deinde medio constrictae et transversaliter uniseptatae, saepe secedentes; ambae cellulae maturitate fusco-brunneae, ± ellipsoideae, ad septum truncatae, aequilaterales, 19—24×11—14 μ, extremo poro germinali instructae, plerumque transversaliter uniseptatae. Cauda gelatinosa c. 25×5—6 μ, ambobus extremis sporae affixa, angustata vel cylindracea, aliquot fibrillis composita, in aqua persistens, non tumescens, in atramento Indico nigrescens.

Perithecia scattered, immersed, obpyriform, 625—670×350—400 μ, with a conical neck, 145—240×135 μ, covered on the neck with straight or somewhat curved, usually tapering, pointed, one-celled or rarely 1—3-septate, thickwalled, mostly verrucose, brown setae, 20—90×4.5—7.5 μ, with a tapering or swollen, deeply rooted base, and provided also on the lower part with ± hyaline, flexuous, ramified, septate, c. 2 μ thick hairs. Peridium 35—45 μ thick, membranaceous, pseudoparenchymatous, semitransparent, yellowish to olivaceous except in the brown-black, opaque, subcarbonaceous neck, 3-layered; cells in the outer layer angular, thin-walled, 5—10 μ in diam., almost hyaline, forming scattered, low, reddish-brown, almost amorphous, flattened agglomerations or crusts; second layer composed of tangentially flattened cells, yellowish to olivaceous brown, becoming gradually darker and carbonized in the upper part of the perithecium. Paraphyses longer than the asci and mixed with them, simple, filiform-ventricose, septate. *Asci* 8-spored, 290—370×25—32 μ, with an almost cylindrical, sporidial part and a 100—120 μ long, tapering stipe, at maturity rupturing just below the rounded, slightly umbonate apex, which forms an adherent operculum; apical cushion well developed, but apical ring hardly viisble, non-amyloid, c. 2.8 μ in diam. *Spores* biseriate, at first hyaline, cylindrical, one-celled, then narrowly ellipsoidal, filled with numerous small oil drops, sometimes also with a few large drops, then a little equatorially constricted, finally transversely uniseptate at the constriction; both cells ranging from ochraceous, olivaceous to dark brown, of similar form and size, 19—25×11—14 μ, equilateral, ± ellipsoidal, smooth, truncate at the 6—7 μ wide septum, broadest in the

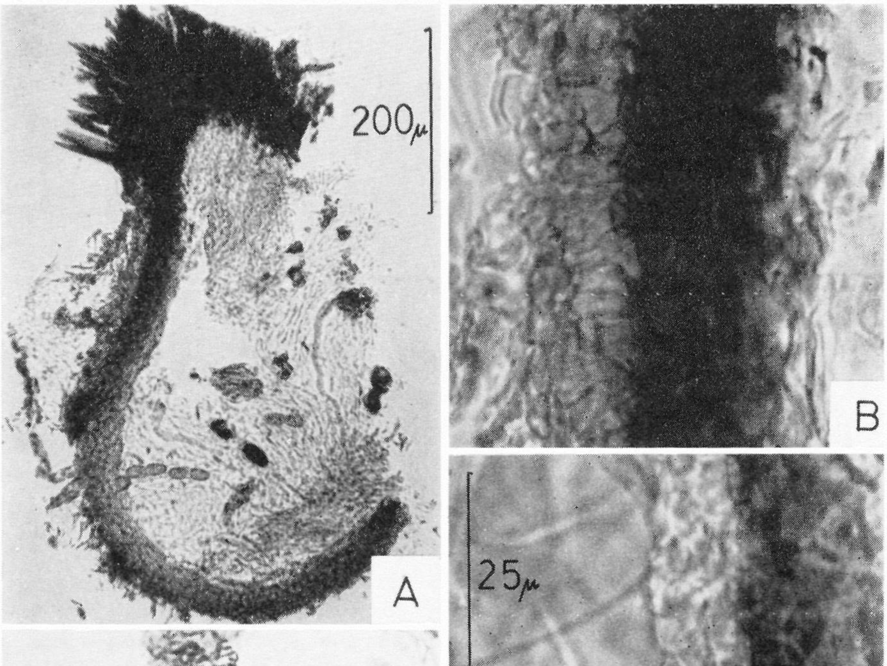

Fig. 7. *Zygospermella striata,* holotype. Material in water (A), lactophenol (B, D—E), Lactic blue (C). — A: Perithecium in median, vertical section (not intact). — B: Part of the peridium in the same section from upper part of the perithecium; note the dark, middle layer; exterior to the left. — C: Peridium in optical, vertical section; exterior to the left. — D: Setae from the perithecial neck; the crystals are dissolved. — E: Cauda in cross section showing the fibrils. — Magnification: B = C.

middle, at last often separating and frequently provided with a transverse septum c. 5 μ from the truncate end; whole spore 38—50 μ long with a germ pore and a gelatinous cauda at each end; both caudae of similar form, size and structure, tapering or cylindrical, 25×5—8 μ round in cross section, composed of a dozen or more longitudinally arranged fibrils, persistent, not swelling in water, blackening in Indian ink.

SPECIMENS EXAMINED: **Sweden:** Gotland, Hall par., at the church, on horse dung, 5.VI. 1959, LQT 2083-j, holotype (UPS); developed after one month in moist chamber, Uppsala. — **Canada:** Ontario, Muskoka, Fraserburg, on cow dung, 24. VIII. 1932, CAIN 5529 (FH slide 1781).

Z. striata is at first glance very similar to *Z. insignis*; the smaller perithecia, asci, and spores, and the fibrillate nature of the caudae being the distinguishing characters. The Canadian specimen deviates in being larger throughout with perithecia 1100×570 μ, spores 44—56×12—15 μ, and tapering caudae, 43—54×11 μ. It would have been referred to *Z. insignis,* had not the caudae been fibrillate. I am uncertain about the identity of this fungus, as long as I know it from this slide only.

2. **Zygospermella insignis** (MOUTON) CAIN. (Figs. 8 A, C, 9—10).

Delitschia insignis MOUTON, Bull. Soc. Roy. Bot. Belg. 36: 13, 1897. Holotype on cow dung from Gomzé near Liège, Belgium, s. dat., MOUTON (BR). — *Zygospermum insigne* (MOUTON) CAIN, Univ. Toronto Stud. Biol. Ser. 38: 76, 1943. — *Zygospermella insignis* (MOUTON) CAIN, Mycologia 27: 227, 1935.
Zygospermum setosum CAIN, Univ. Toronto Stud. Biol. Ser. 38: 74, 1934. Holotype on cow dung from Palmyra, Kent Co., Ontario, Canada, CAIN, TRTC 5310 (not examined). — *Zygospermella setosa* (CAIN) CAIN, Mycologia 27: 227, 1935.

Perithecia 700—1000×480—730 μ, with a conical to cylindrical neck, 145—385×135—200 μ. Setae amost always one-celled, sometimes scarce or lacking. *Asci* 360—400×30—48 μ, with a c. 150 μ long stipe and a 3.5 μ wide and 0.7—1 μ thick apical ring. *Spores* (46—) 50—68×11—17 μ, 5—9 μ wide at the septum. Caudae 25—50×6—10 μ, tapering, non-fibrillate, homogenous, but furnished with a narrow, longitudinal, central canal. Other characters same as those of *Z. striata.*

SPECIMENS EXAMINED: **Sweden:** Öland, Bredsätra, Kapelludden, near the beach, 15.VII. 1960, LQT 2593-j (UPS, slide). — Resmo, 4 km E of the church on the Great Alvar, 2.VI. 1968, SANTESSON 19615-m (M, UPS). — Västergötland, Hassle, NE of Hasslerör railway station, 13.VI. 1960, LQT 2444-h (IMI, UPS). — Södermanland, Aspö, on the N. shore of

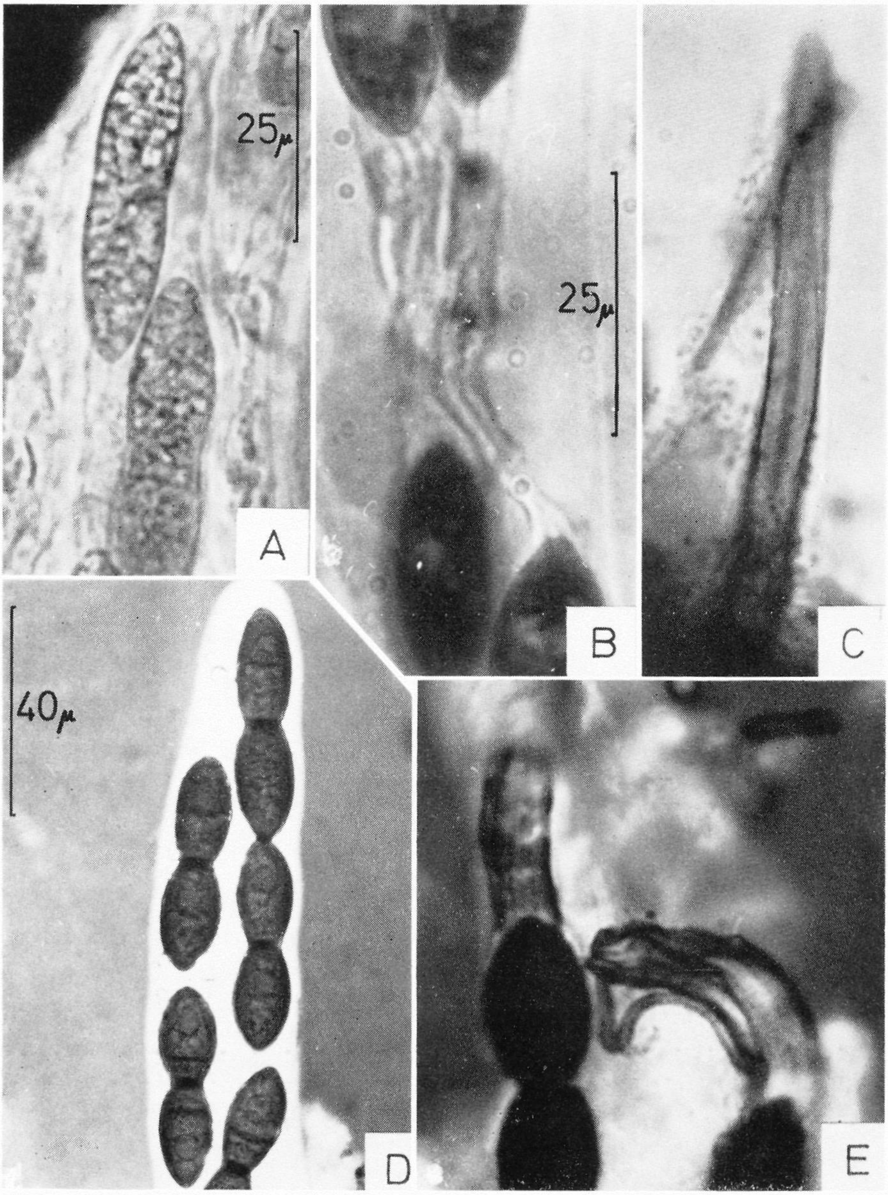

Fig. 8. A: *Zygospermella insignis*, LQT 2593-j. — C: Ditto: LQT 2022-m. — B, D—E: *Z. striata*, holotype. Material in Lactic blue (A—C), Indian ink (D—E). — A: Young, hyaline spores. — B: Caudae (spores in ascus). — A: Setae from the perithecial neck; note the narrow lumen. — D: Mature ascus and spores. — E: Caudae; one fibril has become somewhat detached. — Magnifications: C = B; E = A.

Aspö Isl., 30.V. 1959, LQT 2022-m (UPS). — Uppland, Husby-Långhundra, Steninge, 18.IX. 1960, LQT 2827-b (UPS). — Läby, Solsäter, 24.VIII. 1963, LQT 4074-d (UPS). — Vadbacka, 5.VIII. 1967, LQT 4656 (UPS); all on cow dung; the two latter collections will be distributed in LUNDELL & NANNFELDT's Fungi Exs. Suec. — **Norway:** Troms, Kvenangen, Olderfjord, Kjeldnes, on cow dung, ECKBLAD, herb. EGELAND 102 pp. (O, slides). — **Belgium:** the holotype (BR). — **Scotland:** Stirling, University of Stirling grounds, on cow dung, 5.X. 1968, RICHARDSON (UPS, slide). Dr. RICHARDSON has also communicated (in litt.) another Scottish find on sheep dung from Selmmuir Forest, Kirknewton near Edinburgh, 27.XI. 1965. — **England:** Essex, Epping Forest, on cow dung, [sic!] X. 1900, SALMON (PAD, herb. SACCARDO, (slide). MASSEE & SALMON 1901. — **Spain:** Asturias, Covadonga, 2 km W of the Parador, on goat dung [sic!], 1.V. 1959, LQT 1895-j (UPS slide); LUNDQVIST 1960. — **Canada:** Ontario, York, Nashville, on cow dung, 17.VIII. 1960, CAIN, TRTC 359 03 (UPS). — Lake Timagami, Bear Isl., on cow dung, 17.VI. 1933, CAIN 5533 (FH).

UNVERIFIED RECORDS: **England:** on horse dung, MASSEE & SALMON 1901. — **France:** on cow dung, BRETON 1965, 1966. — **Bulgaria:** on dung of cow and horse, FAKIROVA 1967. — **Canada:** on horse dung, BISBY et al. 1929; on dung of cow, horse, and rabbit, CAIN 1934. — **Indonesia:** on dung of sheep and rabbit, BOEDIJN 1962.

CHOICE OF SUBSTRATE: 14 (> 26): On dung of cow 13 (>17), horse (> 4), sheep (2), rabbit (> 2), goat 1.

ILLUSTRATIONS: MOUTON 1897, pl. A: 7[8?]. MASSEE & SALMON 1901, pl. 17: 20. CAIN 1934, fig. 53. BOEDIJN 1962, figs. 11—12. MÜLLER & VON ARX 1962, fig. 282. BRETON 1965, pl. 1.

Z. insignis seems to prefer the dung of domesticated herbivores and be distributed principally in temperate regions. BOEDIJN's Javanese records must be taken with some caution (see below).

The species has a detailed and fairly correct descriptions by CAIN, MÜLLER and VON ARX, and particularly by BRETON. They overlooked, however, that the setae are verrucose and deeply roted, nor did they clarify the microstructure of the gelatinous caudae. The longitudinal canal can be seen on a number of drawings, but is not recognized as such. BRETON was the first to notice the operculum formed at the ascus dehiscens, and concluded that *Z. insignis* thus has a functional, apical appartus. One may object that the spores must pass through the ring or the apex, leaving other parts of the ascus intact, before one can designate the apparatus as functional.

The setae are often short and few in the species, and sometimes lacking, as is often the case in many other coprophilous *Pyrenomycetes* with setose ascocarps. The deep roots of the setae are a property that should be emphasized and compared with the superficial origin of the

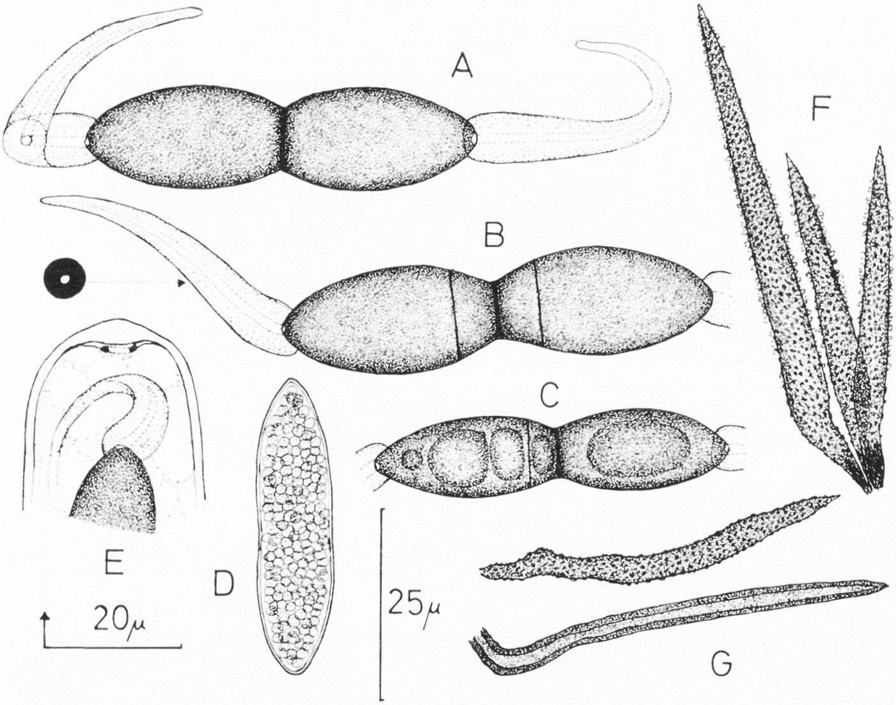

Fig. 9. *Zygospermella insignis*. A—B, D, F. LQT 2593-j. — C, E, G. RICHARDSON 5.X. 1968. All figures drawn from specimens in lactophenol. — A—C: Mature spores; note the cross section of the caudae. — D: Young, hyaline spore. — E: Ascus tip. — F—G: Setae from the perithecial neck.

rigid hairs in many *Podospora* species. MOUTON himself never observed the setae, and, besides, characterized incorrectly the peridium as coriaceous, which obviously misled CAIN to establish his *Zygospermum setosum*. CAIN referred to a Canadian find of "*Delitschia insignis*" by BISBY et al. (1929), but did probably not examine the material. The holotype of *Zygospermella insignis* in MOUTON's herbarium (BR) is in excellent condition and contains only fungi conspecific with *Zygospermella setosa*. This does not exclude, however, the possibility that there might exist an unnamed *Zygospermella* species with non-setose perithecia. It should be observed that BOEDIJN's specimens of *Zygospermella insignis* have glabrous ascocarps, and, what is most interesting, spores with a subapical and suprabasal germ pore. I have not investigated his material.

The origin of the reddish crusts on the peridium, found in both

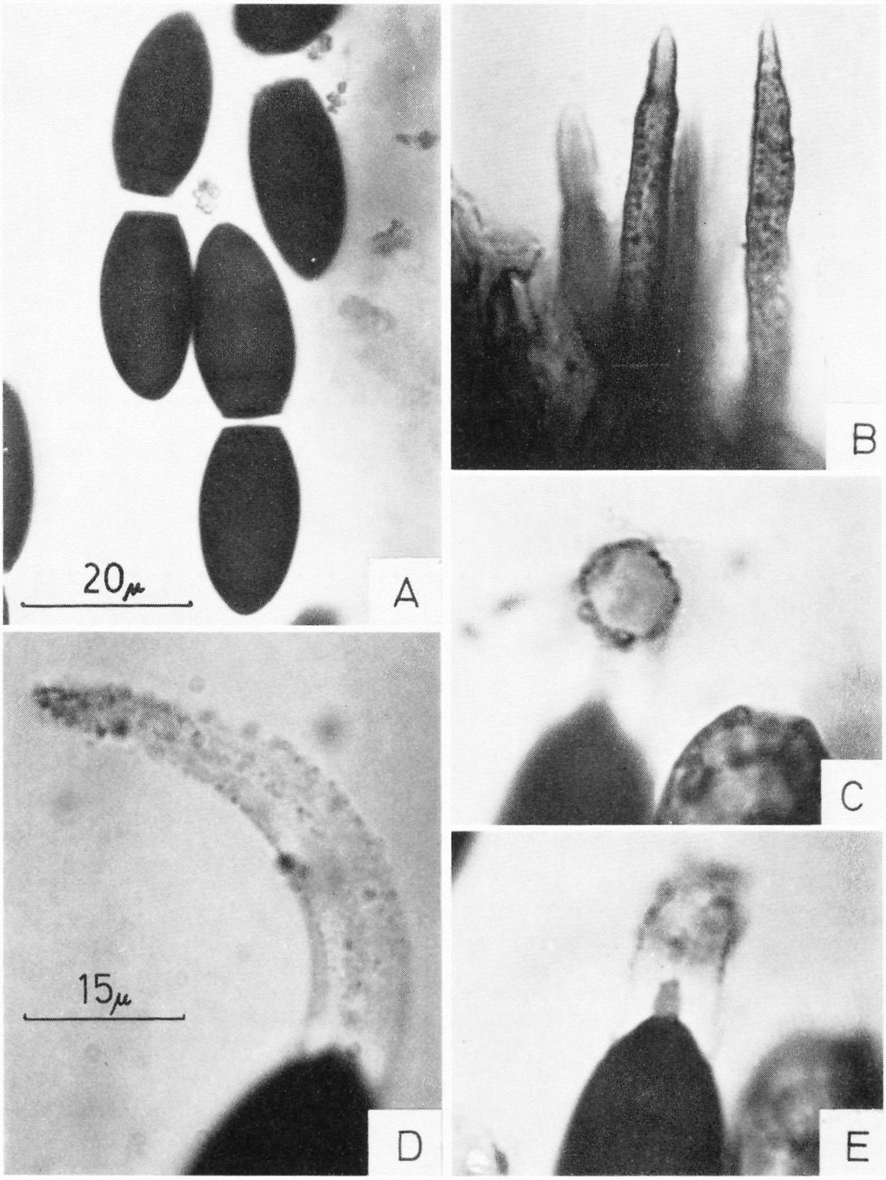

Fig. 10. A—B: *Zygospermella insignis,* holotype. — C—E: Ditto, Lqt 2022-m. Material in Lactic blue. — A: Mature spores. — B: Setae from the perithecial neck. — C: Cauda in cross section. — D: Caudae in lateral view; note the narrow, inner canal. In fig. E one can see that some stained cytoplasm has entered the canal from the germ pore. Magnifications: B—C, E = D.

Zygospermella species, may be disputed. I do not think they are fragments from the substrate as they are seldom met with in other species. Perhaps these structures are of a kind similar to those found on the perithecial necks in *Fimetariella* and some *Bombardiae*. The crusts are loosely attached and very amorphous, and it hard to say whether they are exudates from the perithecium or transformed cell agglomerations. MÜLLER and VON ARX (1962 p. 709) observed the phenomenon, calling the peridium "höckerig". Their drawing of a sectioned peridium shows protuberances with a distinct cell structure, but their figures are as a rule rather idealized.

The number of nuclei in the spores is two or more per cell in the 2-celled stage.

ACKNOWLEDGEMENTS

I am indebted to Dr. H. SMITH, Uppsala, and Mr. M. BRANDT, Uppsala, for correcting the Latin and the English respectively. Dr. R. SANTESSON, Uppsala, has kindly discussed some points in the manuscript.

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Siberian and Chinese Fresh Water Diatoms New to Science

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ABSTRACT AND ACKNOWLEDGEMENT

This paper contains brief diagnoses of six new species and two new varieties of fresh water diatoms collected by Mr. A. I. BARANOV (1) and P. J. USACHOW (6) in Siberia, and by Professor H. C. CHUNG (1) in China.

They have all been named in honor of the late Dr. ROBERT WILHELM KILBE (1882—1960), prominent expert on recent and fossil diatoms and research Associate of the Palaeobotanical Department, Swedish Museum of Natural History (now Naturhistoriska Riksmuseets Sektion för Paleobotanik), Stockholm, Sweden (SELLING 1962 a and b, ZHUZE & PROSHKINA-LAVRENKO 1966).

Dr. KOLBE and Professor S. M. WISLOUCH were my first teachers in diatomology, in 1913—17, when I was a student at St. Petersburg University. Dr. KOLBE invited me to his private laboratory, and the teaching and practice given by him for my studies of Ladoga and Onega diatoms gave a good foundation for my later researches in China (1917—62).

The slides containing these types belong to the Section for Palaeobotany, Swedish Museum of Natural History, Stockholm (S-PA).

I wish to express my thanks to Professor OLOF H. SELLING, D. Sc., for nomenclatural collaboration and for editorial help with this publication.

1. **Gomphonema Kolbei** SKVORTZOV sp. nov. — Fig. 1 A.

Valve clavate, gradually tapering from upper part to obtuse apex and base. Length 72 μ, breadth 10 μ. Axial area broad. Central area suborbicular, without isolated stigma. Costae distinctly compact and not lineate, radiate, 8 in 10 μ. Median line straight, without terminal fissures.

Valva clavata, parte anteriore dilatata, parte posteriore attenuata, apicibus rotundatis; lg. 72 μ, lt. 10 μ. Striae ad medium radiantes, ad polos convergentes, 8 in 10 μ. Area axillaris et centralis latae, lanceolatae. Puncta mediana nulliraphe lata marginatus.

Hab. in fl. Amour, Siberia. Leg. A. I. BARANOV a. 1951. Dedico hanc speciem in memoriam Dr R. KOLBE.

2. **Gyrosigma Kolbei** SKVORTZOV sp. nov. — Fig. 1 B, C.

Valve linear-lanceolate with attenuate and slightly sigmoid ends. Length 105—136 μ, breadth 12—17 μ. Transverse striae in median part distinctly parallel, 12 to 25 in 10 μ. Longitudinal striae very thin and indistinct.

Differs from *Gyrosigma acuminatum* (KÜTZ.) RABENH. in its striae.

Valva lineari-lanceolata, S-formis, apicibus attenuatis; lg. 105—136 μ, lt. 12—17 μ. Striae transversales in parte mediana parallelae, 12—25 in 10 μ. Striae longitudinales tenuissimae et inconspicuae.

Hab. in fl. Ienissei prope oppidum Krasnojarsk, Siberia. Leg. P. J. USACHOW.

3. **Gyrosigma Kolbei** SKVORTZOV var. *ienisseiensis* SKVORTZOV var. nov. — Fig. 1 D.

Differs from the main species in distinct longitudinal striae. Length 88 μ, breadth 14 μ. Transverse striae 15 in 10 μ, longitudinal striae 18 in 10 μ.

Minor quam planta typica; differt etiam striis longitudinalibus conspicuis, lg. 88 μ, lt. 14 μ. Striae transversales 15 in 10 μ, striae longitudinales 18 in 10 μ.

Hab. in fl. Ienissei prope oppidum Krasnojarsk, Siberia. Leg. P. J. USACHOW, 1925—1926.

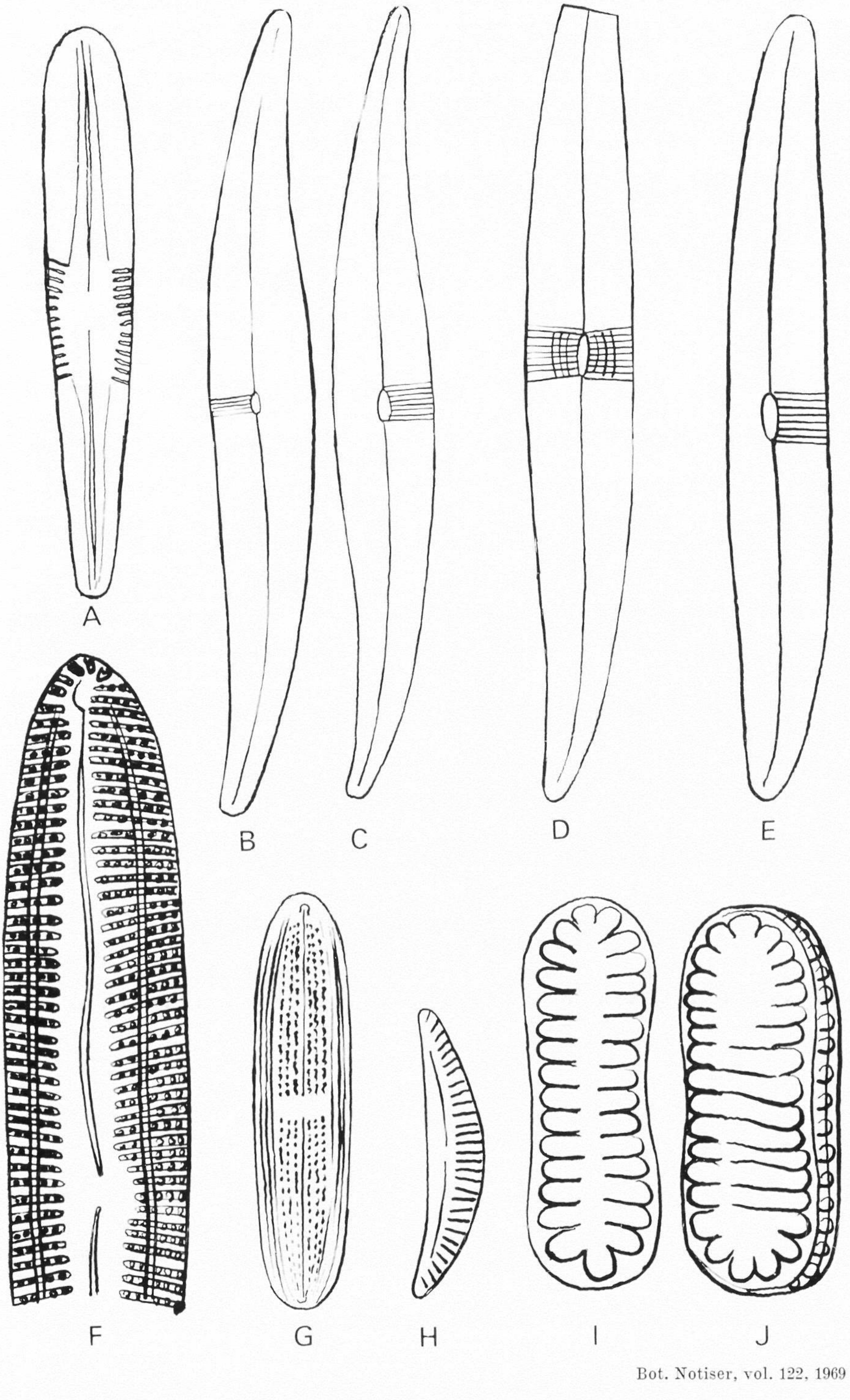
4. **Gyrosigma Kolbei** SKVORTZOV var. *obtusa* SKVORTZOV var. nov. — Fig. 1 E.

Differs from the main species in short obtuse ends. Length 96 μ, breadth 14 μ. Transverse striae 18 in 10 μ, longitudinal striae very thin and indistinct as in the main species.

Minor quam forma typica; differt etiam apicibus obtusioribus; lg. 96 μ, lt. 14 μ. Striae transversales 18 in 10 μ. Striae longitudinales tenuissimae et inconspicuae.

Hab. in fl. Ienissei prope oppidum Krasnojarsk, Siberia. Leg. P. J. USACHOW, 1925—1926.

Fig. 1. — A: *Gomphonema Kolbei* SKVORTZOV sp. nov. — B—E: *Gyrosigma Kolbei* SKVORTZOV sp. nov. — D: var. *ienisseiensis* SKVORTZOV var. nov. — E: var. *obtusa* SKVORTZOV var. nov. — F: *Pinnularia kolbeiana* SKVORTZOV & SELLING sp. nov. — G: *Anomoeoneis Kolbei* SKVORTZOV sp. nov. — H: *Amphora Kolbei* SKVORTZOV sp. nov. — I—J: *Cymatopleura Kolbei* SKVORTZOV sp. nov. — A—E × c. 1450, F × c. 1200, G—J × c. 1550. Drawings by the author.)


A
B
C
D
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5. **Anomoeoneis Kolbei** SKVORTZOV sp. nov. — Fig. 1 G.

Valve linear or elongate-elliptical with obtuse, rounded ends. Length 46 μ, breadth 12 μ. Transverse striae indistinct, longitudinal striae distinct, with undulations, 15 in 10 μ. Central area a broad transverse fascia.

Valva linearis vel elongato-elliptica, marginibus modice dilatatis, apicibus late rotundatis; lg. 46 μ, lt. 12 μ. Striae transversales indistinctae, lineae longitudinales undulatae, 15 in 10 μ.

Hab. in fl. Ienissei prope oppidum Krasnojarsk, Siberia. Leg. P. J. USACHOW, 1925—1926.

6. **Amphora Kolbei** SKVORTZOV sp. nov. — Fig. 1 H.

Valve semilunate with long attenuate ends. Length 30 μ, breadth 7.5 μ. Dorsal side arcuate with robust, not punctuate striae, 12 in 10 μ. Ventral side smooth.

Valva semilunata; lg. 30 μ, lt. 7.5 μ; dorsaliter arcuata, ventraliter recta, dorsaliter striata, striis in medio rectis, ad apicem convergentibus, 12 in 10 μ ventraliter sine striis.

Hab. in fl. Ienissei prope oppidum Krasnojarsk, Siberia. Leg. P. J. USACHOW, 1925—1926.

7. **Pinnularia kolbeiana** SKVORTZOV & SELLING sp. nov. — Fig. 1 F.
(Sect. *Majores* (CLEVE) SKVORTZOV.)

Valve linear lanceolate with attenuate ends. Length 102—171 μ, breadth 27—30 μ. Striae radiate in the middle and convergent at the ends, poroid or punctate, 6 in 10 μ; longitudinal bands narrow. Axial area linear-lanceolate. Central area slightly enlarged. Median line narrow and curved.

Valva linearis, apicibus plus minus attenuatis et rotundatis; lg. 102—171 μ, lt. 27—30 μ; striis in medio radiantibus 6 in 10 μ, apice modice convergentibus, poroidibus vel punctatis, punctis distinctis; lineis 2 longitudinalibus praeditis. Area axillaris lineari-lanceolata. Area centralis modice dilatata. Raphe robusta, curvata et non complexa.

Hab. in stagnis prope oppidum Amoy, prov. Fukien, China australis. Leg. H. H. CHUNG, a. 1924.

8. **Cymatopleura Kolbei** SKVORTZOV sp. nov. — Fig. 1 I, J.

Frustule narrow linear. Valve elongate-elliptic, slightly constricted in the middle part and more or less capitate, with broad, rounded ends. Length 39 μ, breadth 12 μ. Costae robust, 5 in 10 μ.

Frustulum anguste lineare. Valva elongato-elliptica, plana, apicibus capitatorotundatis. marginibus modice constrictis; lg. 39 μ, lt. 12 μ. Costae transversales, in area centrali percurrentes, 5 in 10 μ.

Hab. in fl. Ienissei, prope oppidum Krasnojarsk, Siberia. Leg. B. V. SKVORTZOV.

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Evolutionary Trends in the Breeding System of Nigella (Ranunculaceae)

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ABSTRACT

Self-pollination in *Nigella* L. appears to have evolved by the precise coordination of several independent developmental processes in the flower. Two species, namely the inbreeding *N. doerfleri* VIERH. and the outbreeding *N. degenii* VIERH., both endemic to the Aegean archipelago, have been studied in detail, and additional observations have been made on some other taxa.

In *N. doerfleri* the mature styles become curled and twisted around the dehiscing anthers ensuring self-pollination with a high degree of fidelity. The flowers of *N. degenii* are protandric and are usually pollinated by insects.

N. doerfleri is characterized by reduction in overall size, number and size of the flowers, etc., and by a more rapid development than *N. degenii*. It also has a more economic seed production, is morphologically more uniform, and occurs on small, arid islands, whereas *N. degenii* is restricted to large and more mesic islands. Essentially all *N. doerfleri* individuals are fertile, whereas a significant fraction of the *N. degenii* individuals are semi-sterile.

It is suggested that self-polliniation originally evolved in response to catastrophic selection due to exceptional drought. The present distribution of *N. degenii* is probably due to extinctions during the Würm glaciation and later. *N. doerfleri* is in many ways better adapted to arid habitats and has survived also on numerous small islands.

INTRODUCTION

Self-fertilization in the higher plants is generally regarded as a derived condition. Several authors have demonstrated the breakdown of self-incompatibility and outbreeding and its replacement by inbreeding in various groups (STEBBINS 1957, BAKER 1961, 1963, LLOYD 1965, MOORE & LEWIS 1965). Usually the outbreeding species or races have wide distributional areas and may have given rise to local inbreeding forms repeatedly in response to particular environmental stress.

The evolution of self-pollination is often accompanied by progressive reduction in overall size, number and size of flowers, etc., and by an

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earlier commencement of flowering. In a discussion on reproductive methods in speciation, BAKER (1959) pointed to the fact that differentiation is most likely to affect floral structure and colouration when an inbreeding population evolves from an outbreeding stock.

MATERIAL

Nigella is a Mediterranean genus of annual diploid plants with about 20 species belonging to the buttercup family (*Ranunculaceae*). The genus is characterized by pinnatisect leaves and large, solitary flowers with petaloid sepals and highly specialized, nectar-producing petals. The numerous stamens are initially erect and surround the immature follicles in young flowers. The development of the flower is characterized by progressive spreading of the stamens; the anthers are extrorse, and shed their pollen approximately when the stamens form a 45° angle to the floral axis. The partly united follicles are dehiscent only along the adaxial suture, and have long, indehiscent styles. These are erect in young flowers, but become excurved and finally curled as the floral development proceeds. They are receptive on the adaxial suture. After fertilization the styles straighten and finally form the characteristic beaks of the capsule.

The *Nigella arvensis* complex constitutes a widespread coenospecies of southern Europe, North Africa, and the Middle East. Taxonomically, it can be divided into several species and subspecies, most of which occur in the Aegean and surrounding areas. The two species included in the present study are *N. degenii* VIERH., a member of the *arvensis* coenospecies, and *N. doerfleri* VIERH., which is a distinct and taxonomically more isolated species. The former is restricted to the Kikladhian archipelago (between southern Greece and Turkey) and has differentiated to such a degree that almost every island population differs visibly from the others. Closely related species occur on the Greek mainland, on the East Aegean islands, and in Asia Minor. *N. doerfleri* occurs in the Kikladhes, but also on Crete and on the small island of Andikithera between Crete and Peloponnisos. Morphologically, it is much more uniform than *N. degenii*.

Three populations each of *degenii* and *doerfleri* have been studied with respect to morphology, development, pollen fertility, and seed production. All material has been cultivated under uniform conditions in the experimental garden at the Institute of Systematic Botany, Lund. The origins of the six populations are shown in Fig. 1, which also indicates the general distributions of the two species.

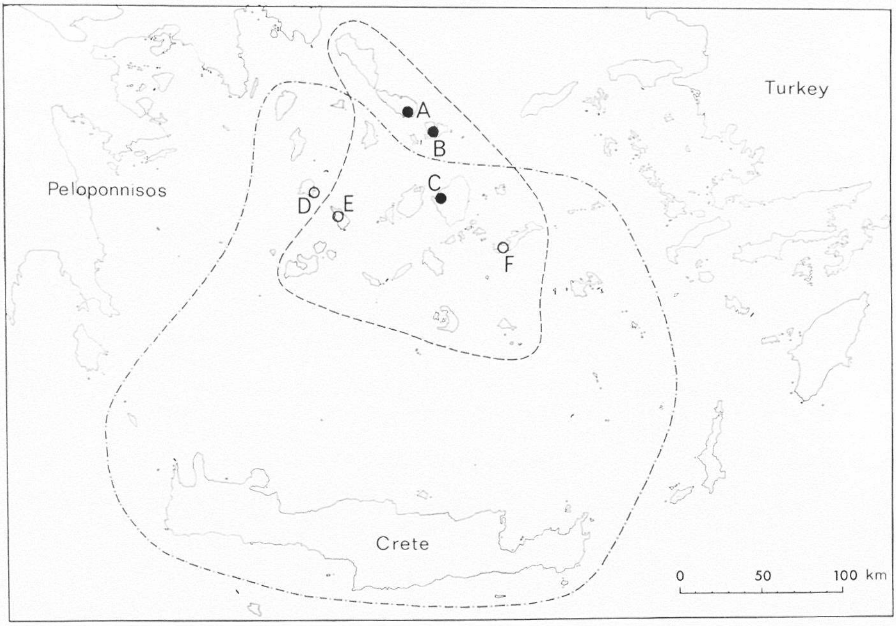


Fig. 1. Map of the South Aegean showing the total distributions of *Nigella degenii* (– – – –) and *N. doerfleri* (–·–·–·), as well as the origins of the six experimental populations. Solid circles = *N. degenii* (A=Tinos; B=Mikonos; C=Naxos). Open circles = *N. doerfleri* (D=Serifos, the small island of Vous; E=Sifnos; F=Amorgos).

POLLINATION MECHANISMS

Like the other taxa of the *arvensis* coenospecies, *Nigella degenii* is normally outbreeding. Observations indicate that bees are the chief pollinators; apparently they become attracted by the conspicuously coloured, nectar-producing petals. These have a complicated morphology, and their colour pattern varies from one island to another. Usually they have dark transverse bands and various combinations of red, blue, or violet fields. When moving around on the "plateau" formed by the sepals and petals, the bee incidentally collects pollen, which is brushed off onto its back from the dehiscing anthers.

The excurvation of the styles begins at about the same time as the first anthesis, but does not proceed as fast as the development of the stamens. Usually all the stamens will have spread horizontally before the styles reach their curled stage, which indicates that they are mature. Thus, the timing of the developmental processes in the flower prevents self-fertilization by keeping the male and female parts out of contact when mature. The pollen remains functional for several days after the stamens have reached the horizontal position, but by this time the mature styles are far above the stamens. Occasionally, however, the excurving styles reach the spreading stamens and become twisted around the anthers as the pollen is shed, which results in self-pollination. Obviously, there is no genetic incompatibility mechanism, since some populations of *N. degenii* have been artificially self-fertilized for several generations. These populations tend to suffer from some inbreeding degeneration, however, presumably due to the accumulation of recessive genes affecting vitality and fertility.

The situation is different in *N. doerfleri*. The entire plant is smaller, flowers earlier, produces a smaller amount of pollen, and develops seed faster. The flowers, and notably the petals, are smaller and less conspicuously coloured. Self-fertilization occurs regularly through precise co-ordination of the above-mentioned movements of the styles and stamens. The curling styles become twisted around the dehiscing anthers, and even when individual flowers are isolated in small bags in the experimental garden, seed setting occurs at a high and regular rate. Artificial outcrossing usually has no unfavourable consequences, however, and perfectly fertile, normal-appearing plants have been obtained in the F_1 and the F_2 generations after numerous crossings between different *doerfleri* populations. Semi-sterile F_1 plants appear in some combinations, probably as a result of small structural differences between the genomes.

DISTRIBUTION AND FLOWERING PERIOD

Although both species occur on the Kikladhian islands, there is a distinct difference in their distributions. With few exceptions, *Nigella degenii* is confined to large and more mesic islands, whereas *N. doerfleri* occurs also on small, low, and very arid islands. *N. degenii* flowers from the end of May to the end of July; it occurs mainly in uncultivated fields, along paths, and in other disturbed habitats. *N. doerfleri* flowers from mid-April to the end of May; it belongs to an element of spring-flowering annuals occupying the space between thorny, cushionlike shrubs forming the so-called garigue vegetation, which covers much of these islands. Before the hot and dry summer, these small annuals wither, leaving the soil naked.

The diagrams in Fig. 5 indicate the time from sowing to flowering

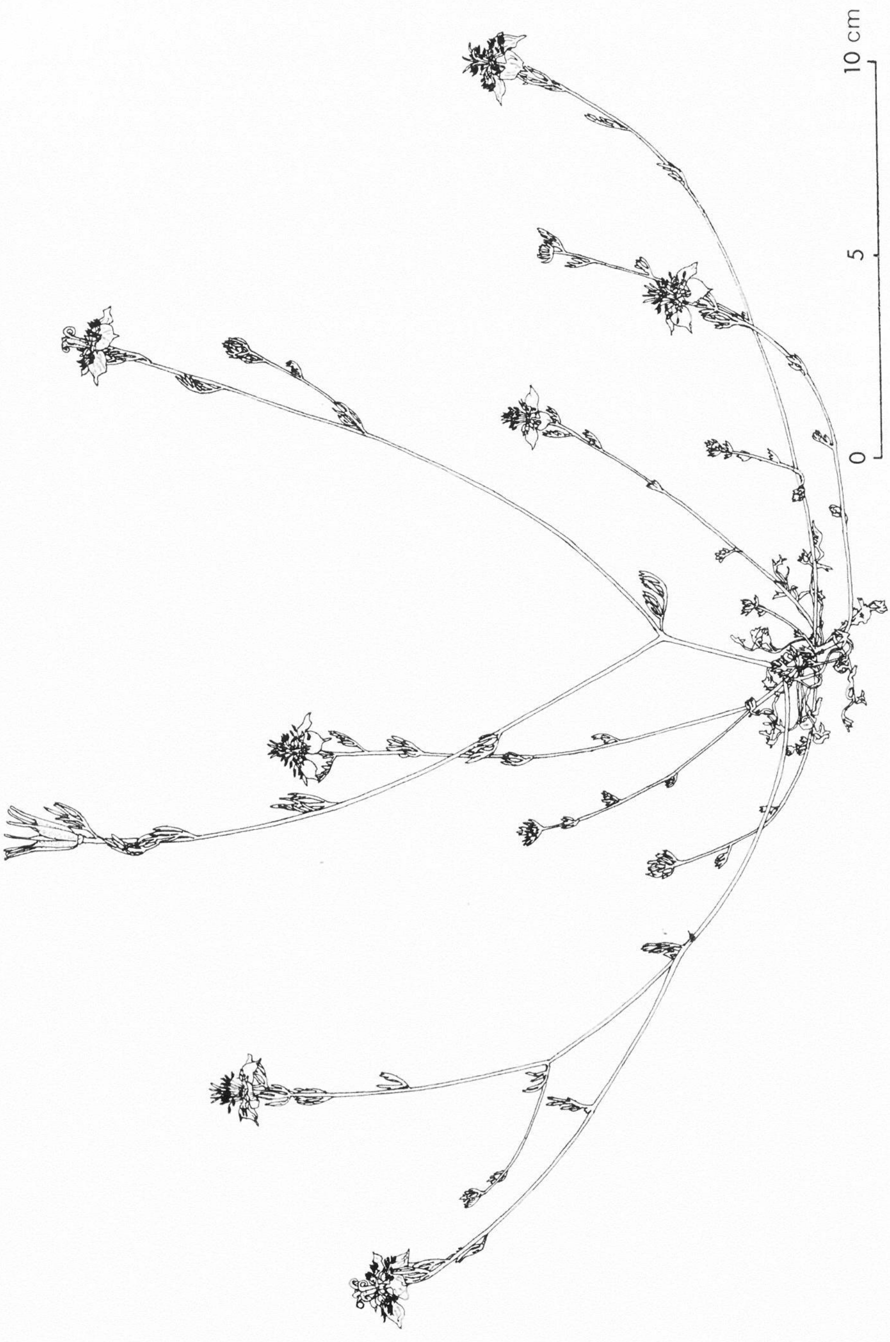


Fig. 2. *Nigella degenii* grown in the experimental garden in Lund. Seeds collected on the island of Mikonos (E in Fig. 1). Drawing by A. OREDSSON

Fig. 3. *Nigella doerfleri* grown in the experimental garden in Lund. Seeds collected on the small island of Vous near Serifos (D in Fig. 1). Drawing by A. Oredsson.

in three populations each of *N. degenii* and *N. doerfleri* cultivated in 1968 (sown 19 April). The letters A—F correspond to Fig. 1. *N. degenii* flowers later and shows a wider range of values, indicating greater genetic variability in this respect. The seeds of *N. degenii* mature 40—50 days after flowering; in *N. doerfleri* seed development takes only 20—30 days. The rapid development of *N. doerfleri* makes it particularly suited to inhabit arid places, since it escapes summer drought. It is probably significant that the only *degenii* race that occurs also on small islands (the Mikonos race, which has been found also on Delos, Rhinia, and some smaller islands in the Mikonos area) flowers on the average 10—20 days earlier than *degenii* races from the neighbouring islands of Naxos and Tinos (see Fig. 3).

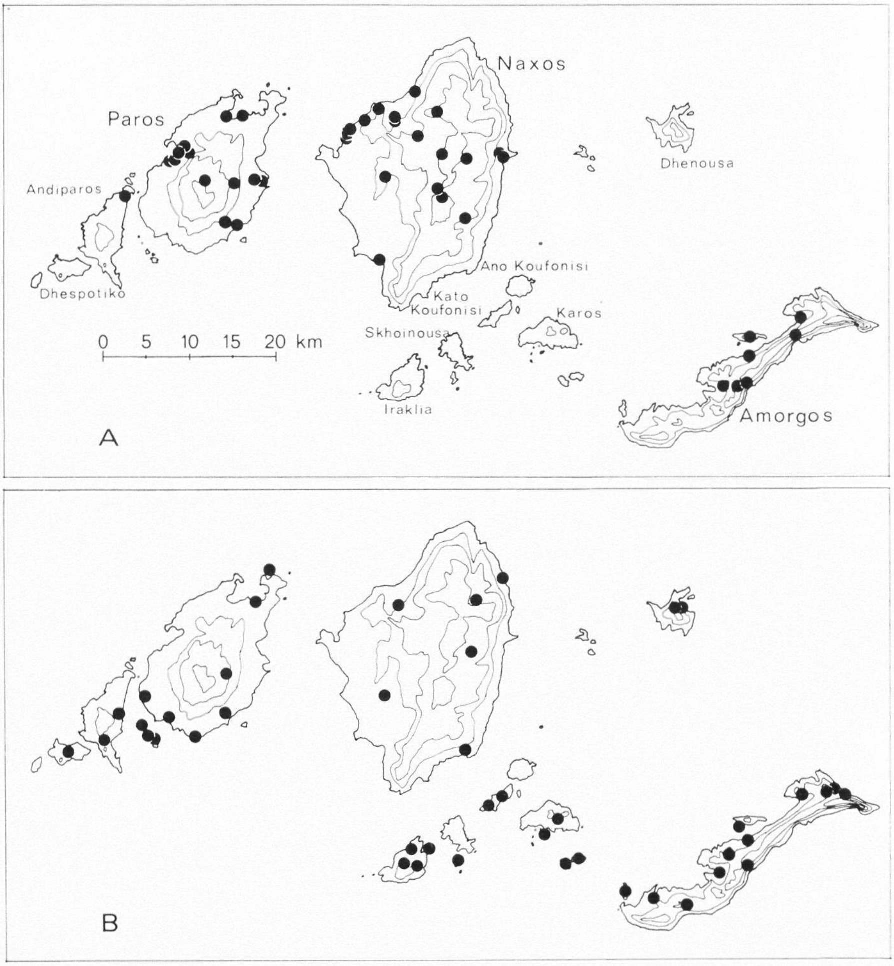


Fig. 4. Map of the central Kikladhes. — A: Collections and field records of *Nigella degenii*. — B: D:o of *N. doerfleri*. The former is restricted to the large islands, whereas the latter is more evenly distributed. Cf. discussion in the text.

FERTILITY

The three *degenii* and three *doerfleri* populations were compared with respect to fertility expressed as percentage of morphologically good pollen after staining with cotton blue. The diagrams in Fig. 6 show percentage frequencies in the six populations. *Nigella degenii* has a wider range of values, indicating a considerable load of fertility-

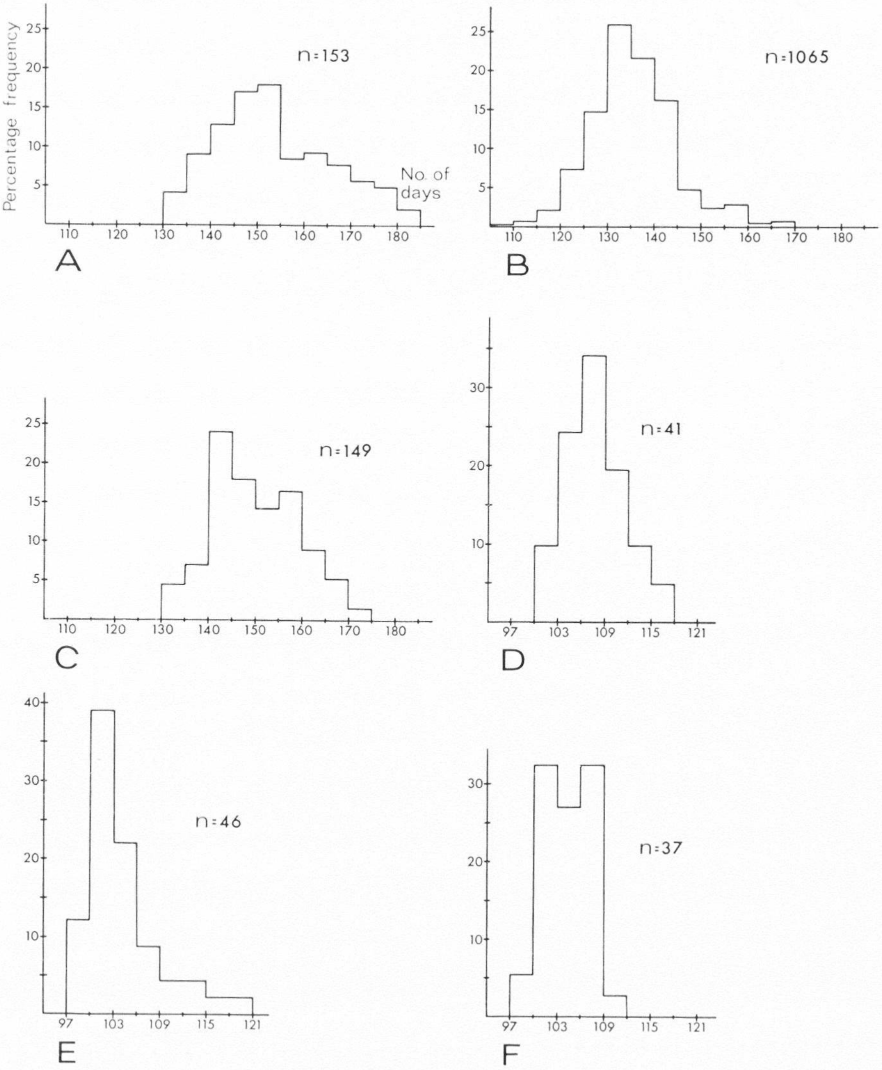


Fig. 5. Diagrams indicating the number of days from sowing to flowering in the six experimental populations. The letters A—F correspond to Fig. 1. — A—C: *N. degenii.* — D—F: *N. doerfleri.* — n=number of individuals.

reducing genes or structural hybridity or both in the populations. Seed setting decreases rapidly with diminishing percentages of stainable pollen, and individuals with pollen fertility values below c. 55 % can

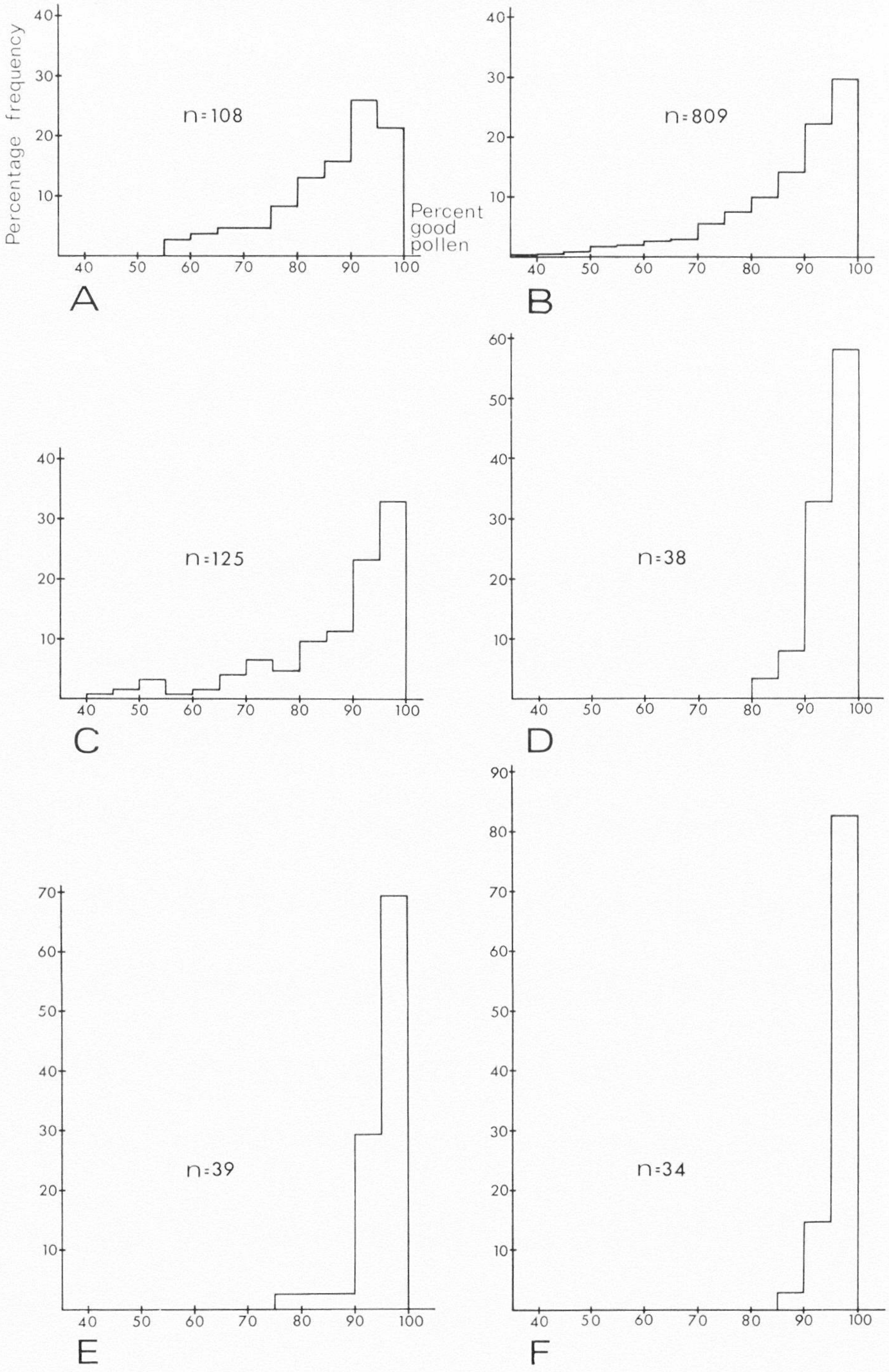

Percentage frequency
Percent good pollen
n=108
A
n=809
B
n=125
C
n=38
D
n=39
E
n=34
F
40
50
60
70
80
90
100

Table 1. Seed-production economy in the six experimental populations. All differences in number of flowers per gram dry weight between *Nigella degenii* and *doerfleri* are significant at the 0.1 % level.

Taxon	No. of flowers	Dry weight (g)	Flowers per g dry weight	N
N. degenii, Mikonos	16.0 ± 1.4	1.79 ± 0.29	10.8 ± 0.7	25
N. degenii, Tinos	10.5 ± 1.0	1.16 ± 0.14	9.8 ± 0.5	25
N. degenii, Naxos	10.2 ± 0.9	1.47 ± 0.20	8.3 ± 0.7	25
N. doerfleri, Amorgos	3.0 ± 0.2	0.18 ± 0.02	18.0 ± 0.8	25
N. doerfleri, Sifnos	2.9 ± 0.3	0.20 ± 0.02	15.3 ± 0.7	25
N. doerfleri, Vous	4.2 ± 0.3	0.24 ± 0.02	18.4 ± 0.9	25

be regarded as practically seed sterile. Pollen fertility values exceeding c. 90 % indicate full seed fertility.

In *N. doerfleri* almost all individuals have pollen fertility values between 90 and 100 %, which indicates that long-continued inbreeding has led to a high degree of homozygosity and elimination of unfavourable genotypes.

SEED PRODUCTION

One individual of *Nigella degenii* usually produces 10—20 flowers when grown in the experimental garden, whereas a *doerfleri* plant produces on the average only 2—5 flowers. A corresponding difference is found in nature. The number of ovules per flower is approximately the same in both species. The production of organic matter is considerably less in *N. doerfleri* (cf. Figs. 5 and 6). The "economy" of the seed production was estimated in the following way: 25 individuals were taken at random from each of the six experimental populations. After drying of the plants the number of flowers per gram dry weight was calculated. For a plant having limited supplies of water and nutriments, it is obviously essential to produce seed with as little waste of organic matter as possible. The results shown in Table 1 indicate that *N. doerfleri* produces a significantly larger number of flowers per gram dry weight than *N. degenii*. Provided that equal amounts of seeds per capsule are produced, *N. doerfleri* has a more economic seed production.

Observations indicate that the number of seeds in well-developed

Fig. 6. Diagrams indicating the percentage of morphologically good pollen (after staining with cotton blue) in the six experimental populations. The letters A—F correspond to Fig. 1. — A—C: *A. degenii.* — D—F: *A. doerfleri.* — n = number of individuals.

capsules of *N. degenii* and *N. doerfleri* is approximately the same. The size of the seeds are also quite similar. Two factors, however, contribute to a relative increase in the actual seed production of *N. doerfleri*. First, essentially all individuals are fertile, whereas a significant number of *degenii* individuals are semi-sterile. Second, the self-pollination mechanism of *doerfleri* operates with a high degree of fidelity ensuring that practically all flowers will be fertilized. The *degenii* flowers, which are dependent on insects for pollen transfer, fail to become pollinated to the same high degree. In nature empty, non-fertilized capsules are often observed.

It is hard to estimate the importance of these two factors, namely, difference in average fertility and difference in the pollination efficiency, but both will tend to increase the divergence in seed-production efficiency between the two species. It is reasonable to assume that the essential advantage of *doerfleri* is not in the economy of seed-production but in its safeguard.

INTERSPECIFIC CROSSES

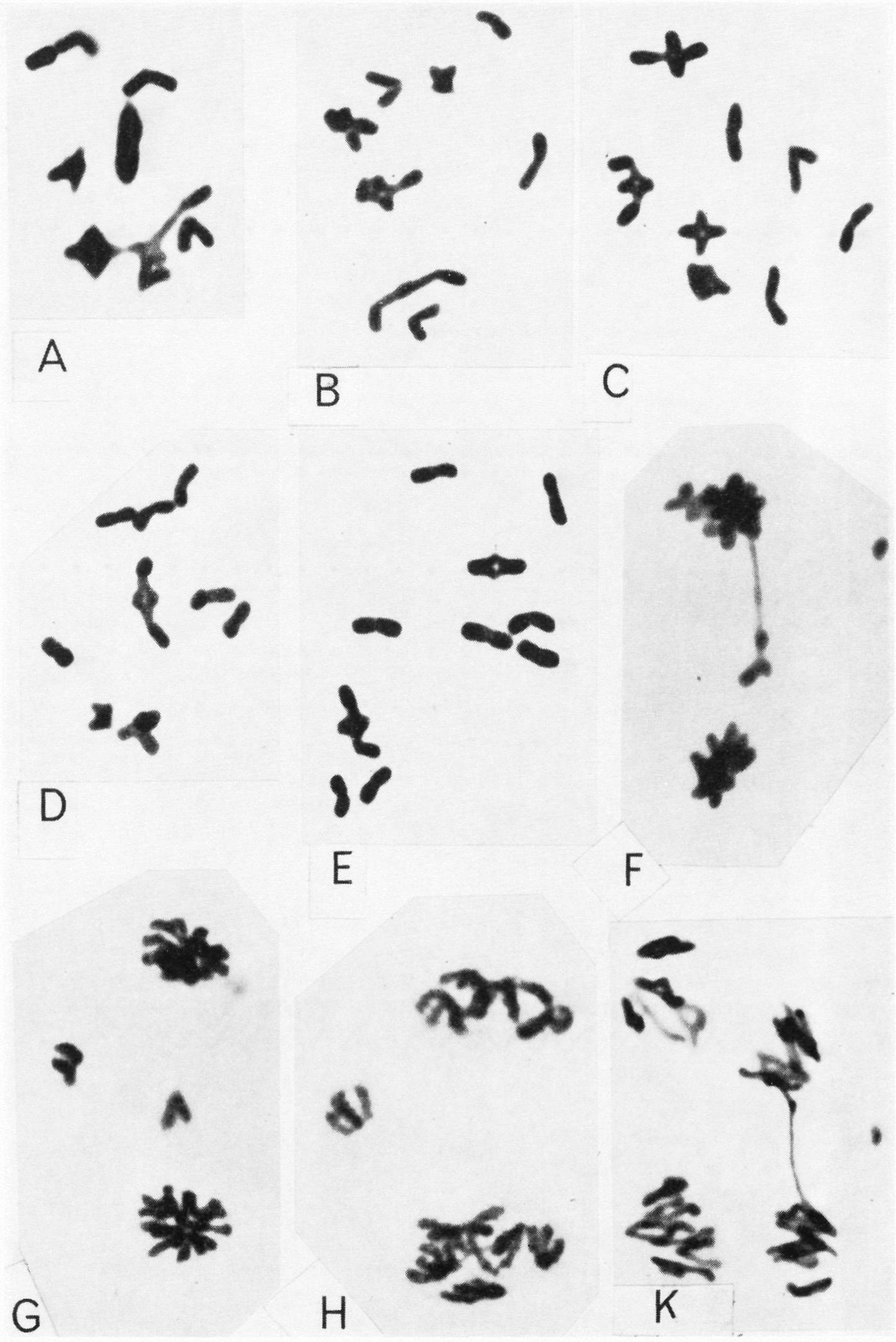
Most species of *Nigella* display very strong sterility barriers when attempts are made to hybridize them (REINDERS 1941). The members of the *arvensis* coenospecies are cross-compatible, however, and various F_1 hybrids have pollen fertility values ranging from about 30 % to almost 100 %.

N. degenii and *N. doerfleri* are very difficult to hybridize, and out of 62 attempts made over a period of several years, all but one failed to produce any offspring. The only successful combination was one with *degenii* from Mikonos as the pistillate parent and *doerfleri* from a small island close to Iraklia (see Fig. 4) as the staminate parent. This combination produced a single hybrid plant that was morphologically well-developed and intermediate between the parents but highly sterile, with only c. 5 % stainable pollen. No offspring were produced after self-fertilization of the hybrid, nor after attempted backcrossing to the parents. Thus, *doerfleri* should not be included in the *arvensis* coenospecies, according to the definition of CLAUSEN (1951).

All *Nigella* species are diploid with $2n=12$, and their karyotypes are very similar. Presumably the sterility barriers have mainly a genic or cryptic structural basis, and do not depend on major structural rearrangements. The results of an analysis of meiosis in the single *degenii*×*doerfleri* hybrid are shown in Table 2. The meiotic divisions

Table 2. A survey of meiosis in the *Nigella degenii* × *doerfleri* hybrid. The plant had about 5 % stainable pollen and did not produce any seed after self-pollination nor after attempted backcrossing.

	Metaphase I						Anaphase I			T I and Interphase I		A II and T II	
	6_{II}	$5_{II}+2_{I}$	$4_{II}+4_{I}$	$3_{II}+6_{I}$	$2_{II}+8_{I}$	$1_{II}+10_{I}$	Normal	With bridge + fragment	With laggards	Normal	With micronuclei	Normal	With bridge, laggards, or micronuclei
Slide no 1	16	34	37	8	4	1	2	4	9	19	26	1	3
Slide no 2	9	18	14	4	3	2	—	—	2	11	15	6	11
Slide no 3	10	16	10	6	3	—	1	1	4	11	11	1	5
Total	35	68	51	18	10	3	3	5	15	41	52	8	19


A
B
C
D
E
F
G
H
K

are severely disturbed, with a high frequency of univalents and laggards. Micronuclei are often formed in T I and T II. However, the frequency of apparently clean separations is distinctly higher than the percentage of well-developed pollen. Genic or microstructural factors with no mechanical influence on meiosis probably account for a considerable portion of the pollen sterility. This tendency is even more pronounced in hybrids within the *arvensis* coenospecies.

BREEDING SYSTEMS OF OTHER NIGELLA SPECIES IN THE AREA

Different species have established different levels of compromise between the two opposite evolutionary trends promoting self-fertilization and cross-fertilization. Out of fourteen species and subspecies from Greece and western Turkey kept in cultivation, only two appear to be almost exclusively self-fertilized, namely, *Nigella doerfleri* and a still undescribed species. The latter is known only from a few localities in western Crete and from the island of Kithera between Crete and Peloponnisos. The only population kept in cultivation originates from the south-western coast of Crete near the monastery of Ay. Christoskalatitis, where it grew in stable sand dunes about 50 m from the sea. Characteristically, the two selfers are smaller; they have smaller flowers and develop faster than the other species in the genus. They have floral structures or remnants of such structures, for example, nectar-producing petals that could only have an adaptive value in connection with insect pollination, and hence both species have most probably evolved from cross-fertilizing forms. The two selfers can be crossed with each other, but the hybrids are highly sterile. All attempts to produce hybrids between the undescribed, self-pollinating species from Crete and *N. degenii* or other members of the *arvensis* coenospecies have been unsuccessful.

Two other species, *N. damascena* L. and *N. fumariaefolia* KOTSCHY, appear to be self-fertilized to a moderate degree, but have not been studied in detail. All other taxa in the area are predominantly cross-fertilized.

Fig 7. Meiosis in the hybrid between *Nigella degenii* and *N. doerfleri*. — A: Metaphase I with two univalents and a multivalent configuration. — B—C: Metaphase I with $4_{II}+4_{I}$. — D: Metaphase I with $3_{II}+6_{I}$. — E: Metaphase I with $2_{II}+8_{I}$. — F: Anaphase I with bridge+fragment. — G: Late anaphase I with lagging chromosomes — H: Telophase I with a micronucleus. — K: Anaphase II with bridge+fragment persistent since anaphase I. — ×1200. — See also Table 2.

DISCUSSION

Changes in the breeding structure of populations, for instance, the evolution of self-fertilization, is often likely to be followed by rapid speciation. **Stebbins** (1957) believed the breakdown of outbreeding to take place gradually, and considered facultatively self-fertilizing forms as necessary intermediates. On the other hand, **Moore** and **Lewis** (1965) found that the evolution of self-fertilization in two local populations of *Clarkia xantiana* resulted from the early maturation of the stigma, which appeared to have a simple genetic basis. They postulated that "the initial event leading to self-pollination was the reduction of the population to extremely small size during a growth season truncated by water stress, and that the genotypes surviving the catastrophic selection were those produced by the earliest flowering individuals. In a very small population genes promoting self-fertilization would be at an advantage. Once established, the inbreeding race would become self-perpetuating." The term "catastrophic selection" was coined by **Lewis** (1962) to describe the sudden reduction of a population to a very small size owing to extraordinary environmental conditions, followed by its re-establishment from a small number of survivors presumably pre-adapted to the unusual conditions. Simultaneously, genetic drift in an allogamous population may result in rapid differentiation in non-adaptive characters owing to fixation or extinction of alleles when the population is at its minimum. One of the self-pollinating populations studied by **Moore** and **Lewis** was white-flowered and the other was pink-flowered, probably depending on the chance characteristics of its founder members.

Aridity may serve as a stimulus to plant evolution (cf. **Stebbins** 1952) not only because of the specialized morphological structures that may evolve to reduce loss of moisture but also on account of the population structures prevailing in arid or semi-arid areas. In such areas, populations are particularly likely to be broken up into partly isolated subunits, a pattern that was mathematically shown by **Wright** (1940) to be favourable for rapid evolution.

Newman (1967) found that the small, spring-flowering annual grass *Aira praecox*, which usually grows in sandy and arid places, was highly resistant to normal fluctuations in soil moisture during flower and seed development. In a year with exceptional drought, however, seed production was significantly reduced, and the original size of the population was only gradually restored during the following years. It is a common observation that the population size of desert annuals varies enormously from season to season (cf. CLAUSEN 1951), and similar fluctuations are likely to occur in less arid regions as well.

Germination and seedling establishment are usually the most critical phases for a population of annuals; but the length of the growing season, a character that is strongly inherited (LAMMERINK 1968), may also rapidly respond to selection pressure (THURSTON 1962, 1963). Drought at the time of flowering and seed development will put a high selective premium on earliness. It is a well-known fact that forms growing in arid regions usually develop faster than related forms growing under more mesic conditions. Self-fertilizing forms are likely to be more common in arid habitats, since they are better adaptad to survive occasional catastrophic selection due to exceptional drought.

The morphological reduction, rapid development, and arid habitat of *Nigella doerfleri* fit the general pattern of an inbreeder that has evolved in a normally outbreeding group. *N. doerfleri* is also characterized by an obvious overall reduction in morphological variability compared to its cross-fertilizing relative *N. degenii* (biometrical data to be published elsewhere). Evidence from other materials (KANNENBERG & ALLARD 1967) is somewhat contradictory and indicates that "any reduction in within-family variability is compensated by increases in the between-family component of genetic variation."

The present knowledge of the geological history of the Aegean area (since the Pliocene) has been summarized by CREUTZBURG (1963). The geology is only known along its major lines, and is sometimes contradictory to phytogeographical facts (RECHINGER 1950, SNOGERUP 1967). For instance, the distribution of several plant species, among them *N. doerfleri,* suggests a relatively late land connection between the south-eastern Kikladhes and eastern Crete (may be via a chain of islands close enough to permit occasional successful migration), but existing geological maps show deep sea in this area at least since early Pliocene, that is, 10—12 million years ago. The differentiation of *N. degenii* and *N. doerfleri* from a presumed common ancestor must have taken place before the breakdown of this supposed connection between the Kikladhes and Crete.

Sea regressions in the Aegean during the Pleistocene glaciations amounted to as much as c. 200 m during the Riss and c. 90 m during the Würm. The final formation of the present archipelago took place only after the breakdown of the land connections formed during these cool periods. Most floristic differences between the Kikladhian islands are probably due to extinctions during the Würm and later (Snogerup 1967, Runemark 1969). *N. degenii* has only survived on relatively large islands with a good water supply, whereas *N. doerfleri,* which is more drought resistant, has managed also on small and arid island.

The evolution of self-pollination required the perfection of a mechanism involving movements of styles and stamens during floral development. Independent developmental processes had to be precisely coordinated, and consequently the genetic basis of self-pollination may be complicated. No direct evidence was obtainable as the single *degenii*×*doerfleri* hybrid was highly sterile.

The establishment of self-fertilization followed by progressive changes in morphological and physiological features forms a long-continued evolutionary trend that has certainly been guided by natural selection. Catastrophic selection due to exceptional drought might have played an important role among the initial events leading to self-fertilization. Since this differentiation took place a very long time ago, and the selfers and crossers are now distinct species, any attempts to trace the processes originally involved must, however, be highly speculative.

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Chromosome Studies on South African Vascular Plants

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ABSTRACT

Somatic chromosome numbers of 55 taxa of vascular plants from South and South West Africa are reported. The majority of the species have not been investigated cytologically before, and the counts on *Colpias* (*Scrophulariaceae*), *Selago* (*Selaginaceae*), *Disparago, Mairea,* and *Phoenocoma* (*Compositae*) are first generic reports. Within the *Cineraria aspera* complex two cytotypes occur, and the first instance of polyploidy in *Gazania* is reported. The new combination *Steirodiscus speciosus* (PILL.) B. NORD. is made.

INTRODUCTION

The material used was cultivated in greenhouses in the Botanical Garden, Lund, from seeds or living plants collected by myself in Southern Africa in 1962—64. In addition some seeds were obtained from the National Botanic Gardens, Kirstenbosch, South Africa.

All counts were made on metaphase plates in sectioned root tips treated according to the paraffin method. The Svalöf modification of the Navashin-Karpechenko fixative was used, and crystal violet (in some cases with aniline) was used for staining.

Some metaphase plates are illustrated by camera lucida drawings in Fig. 1. Voucher specimens are preserved in the Natural History Museum, Stockholm (S).

RESULTS

Taxon	2n	Voucher	Origin
GRAMINEAE			
Eragrostis annulata RENDLE	20	N. 2459	S.W. Africa, Omaruru Distr.: Brandberg, 1963
E. rotifer RENDLE	40	N. 2476	S.W. Africa, Omaruru Distr.: Brandberg, 1963

Taxon	2n	Voucher	Origin
CYPERACEAE			
Cyperus marginatus Thunb.	32	N. 2479	S.W. Africa, Omaruru Distr.: Brandberg, 1963
LILIACEAE			
Albuca canadensis (L.) Leighton	18	N. 3941	National Botanic Gardens, Kirstenbosch, South Africa
Bulbine asphodeloides (L.) Roem. & Schult.	14	N. 3515	South Africa, Calvinia Div.: Northern Brandkop, 1963
	14	N. 3562	South Africa, Calvinia Div.: Langfontein, 1963
B. longifolia Schinz	14	N. 3073	South Africa, Clanwilliam Div.: Elandskloof, 1963
Dipidax triquetra (L. f.) Baker	20	N. 3942	National Botanic Gardens, Kirstenbosch, South Africa
Veltheimia capensis (L.) DC.	40	N. 3943	South Africa, sine loco
IRIDACEAE			
Gladiolus edulis Ker-Gawl.	30	N. 2366	S.W. Africa, Rehoboth Distr.: Farm Gamsberg, 1963
CARYOPHYLLACEAE			
Dianthus namaënsis Schinz	30	N. 2382	S.W. Africa, Rehoboth Distr.: Gamsberg, 1963
Silene burchellii Otth.	24	N. 1750	South Africa, L. Namaqualand Div.: Richtersveld, Hellskloof, 1962
CAPPARIDACEAE			
Cleome rubella Burch.	30	N. 2333	S.W. Africa, Rehoboth Distr.: 20 miles W. of Rehoboth, 1963
LEGUMINOSAE			
Crotalaria barnabassii Dinter ex Bak. f.	16	N. 2496	S.W. Africa, Omaruru Distr.: Brandberg, 1963
Rhynchosia memnonia DC.	22	N. 2474	S.W. Africa, Omaruru Distr.: Brandberg, 1963
GERANIACEAE			
Pelargonium rapaceum (L.) Jacq.	20	N. 3357	South Africa, Piketberg Div.: Versfeld Pass, 1963
P. tysonii Szysz.	20	N. 3467	South Africa, Clanwilliam Div.: Kouberg, 1963
CONVOLVULACEAE			
Ipomoea obscura (L.) Ker-Gawl.	30	N. 2678	S.W. Africa, Etosha Distr.: 8 miles N. of Namutoni, 1963
I. verbascoidea Choisy	30	N. 3647	S.W. Africa, Omaruru Distr.: Brandberg, 1964
Merremia multisecta Hall. f.	30	N. 3785	S.W. Africa, Outjo Distr.: 12 miles SE. of Torra Bay, 1964
BORAGINACEAE			
Heliotropium ovalifolium Forsk.	56	N. 3731	S.W. Africa, Outjo Distr.: Farm Rooiplaat, 1964
	56	N. 3766	S.W. Africa, Outjo Distr.: Unjabmund, 1964

Taxon	2n	Voucher	Origin
LABIATAE			
Plectranthus hereroensis ENGL.	30	N. 3656	S.W. Africa, Omaruru Distr.: Brandberg, 1964
SOLANACEAE			
Nicotiana glauca GRAHAM	24	N. 158	South Africa, Laingsburg Div.: Dwyka River, 1962
SCROPHULARIACEAE			
Colpias mollis E. MEY.	40	N. 1785	South Africa, L. Namaqualand Div.: Richtersveld, Granite Boss, 1962
SELAGINACEAE			
Selago albida CHOISY	14	N. 2810	S.W. Africa, Omaruru Distr.: Brandberg, 1963
LOBELIACEAE			
Lobelia coronopifolia L.	12	N. 47	South Africa, Somerset West Div.: Between Gordon's Bay and Steenbras River Mouth, 1962
COMPOSITAE			
Charieis heterophylla CASS.	10	N. 3949	National Botanic Gardens, Kirstenbosch, South Africa
Cineraria aspera THUNB.	20	N. 3539	South Africa, Calvinia Div.: Hantam Mts., 1963
	40	N. 3593	South Africa, Sutherland Div.: Swarweerberg, 1963
Cotula turbinata L.	16	N. 12	South Africa, Cape Town: Rondebosch, 1962
Disparago kraussi SCH. BIP.	18	N. 402	South Africa, Riversdale Div.: Still Bay, 1962
Eriocephalus africanus L.	36	N. 3944	National Botanic Gardens, Kirstenbosch, South Africa
E. racemosus L.	18	N. 3945	National Botanic Gardens, Kirstenbosch, South Africa
Felicia dregei DC.	18	N. 2993	South Africa, Calvinia Div.: Klip Koppies, 1963
F. filifolia (VENT.) BURTT DAVY	18	N. 3950	National Botanic Gardens, Kirstenbosch, South Africa, sub nom. "*Diplopappus filifolius*"
Gazania krebsiana LESS. ssp. *arctotoides* (LESS.) ROESSLER	20	N. 3954	National Botanic Gardens, Kirstenbosch, South Africa, sub nom. "*G. pinnata*"
Helichrysum odoratissimum (L.) SWEET	14	N. 3370	South Africa, Piketberg Div.: Levant Hill, 1963
H. vestitum (L.) SCHRANK	14	N. 3951	National Botanic Gardens, Kirstenbosch, South Africa
Kleinia crassulifolia DC.	20	N. 3399	South Africa, Piketberg Div.: Levant Hill, 1963
Mairea perezioides (LESS.) NEES	18	N. 3066	South Africa, Clanwilliam Div.: Elandskloof, 1963
Othonna euphorbioides HUTCH.	20	N. 1596	South Africa, L. Namaqualand Div.: Anenous Pass, 1962
O. filicaulis JACQ.	40	N. 471	South Africa, Malmesbury Div.: Mamre, 1962

Taxon	2n	Voucher	Origin
O. hallii B. NORD.	40	N. 939	South Africa, Vanrhynsdorp Div.: Holriver, 1962
O. lyrata DC.	20	N. 1000	South Africa, Clanwilliam Div.: 2 miles N. of Clanwilliam, 1962
O. incisa HARV.	60	N. 648	South Africa, L. Namaqualand Div.: Anenous Pass, 1962
	60	N. 1595	South Africa, L. Namaqualand Div.: Anenous Pass, 1962
O. macrophylla DC.	40	N. 573	South Africa, Clanwilliam Div.: Bulshoek, 1962
O. oleracea COMPTON	40	N. 500	South Africa, Ceres Div.: Karroo Poort, 1962
O. protecta DTR	20	N. 2842	South Africa, L. Namaqualand Div.: 18 miles S. of Violsdrift, 1963
O. retrorsa DC.	20	N. 1302	South Africa, L. Namaqualand Div.: 5 miles S. of Khamieskroon, 1962
Pentzia intermedia HUTCH.	16	N. 3946	National Botanic Gardens, Kirstenbosch, South Africa, sub nom. "*Matricaria grandiflora*"
P. suffruticosa (L.) HUTCH. ex MERXM.	16	N. 3947	National Botanic Gardens, Kirstenbosch, South Africa, sub nom. "*Matricaria suffruticosa*"
Phoenocoma prolifera (L.) D. DON	16	N. 3952	National Botanic Gardens, Kirstenbosch, South Africa
Steirodiscus speciosus (PILL.) B. NORD.	16	N. 3953	National Botanic Gardens, Kirstenbosch, South Africa, sub nom. "*Gamolepis speciosa*"
Ursinia anthemoides (L.) POIR. ssp. *anthemoides*	14	N. 3955	National Botanic Gardens, Kirstenbosch, South Africa, sub nom. "*U. speciosa*"
U. anthemoides ssp. *versicolor* (DC.) PRASSLER	16	N. 3956	National Botanic Gardens, Kirstenbosch, South Africa, sub nom. "*U. anethoides*"
U. cakilefolia DC.	16	N. 3948	National Botanic Gardens, Kirstenbosch, South Africa
Zinnia multiflora L.	24	DAHLGREN & STRID 4693	South Africa, Transvaal: Between Nelspruit and Barberton, 1965

DISCUSSION

GRAMINEAE

The counts in *Eragrostis* are first reports for the species concerned but in agreement with earlier authors' findings that x=10 is the basic number in the genus. Several diploids, tetraploids, hexaploids, and octoploids are known in the genus.

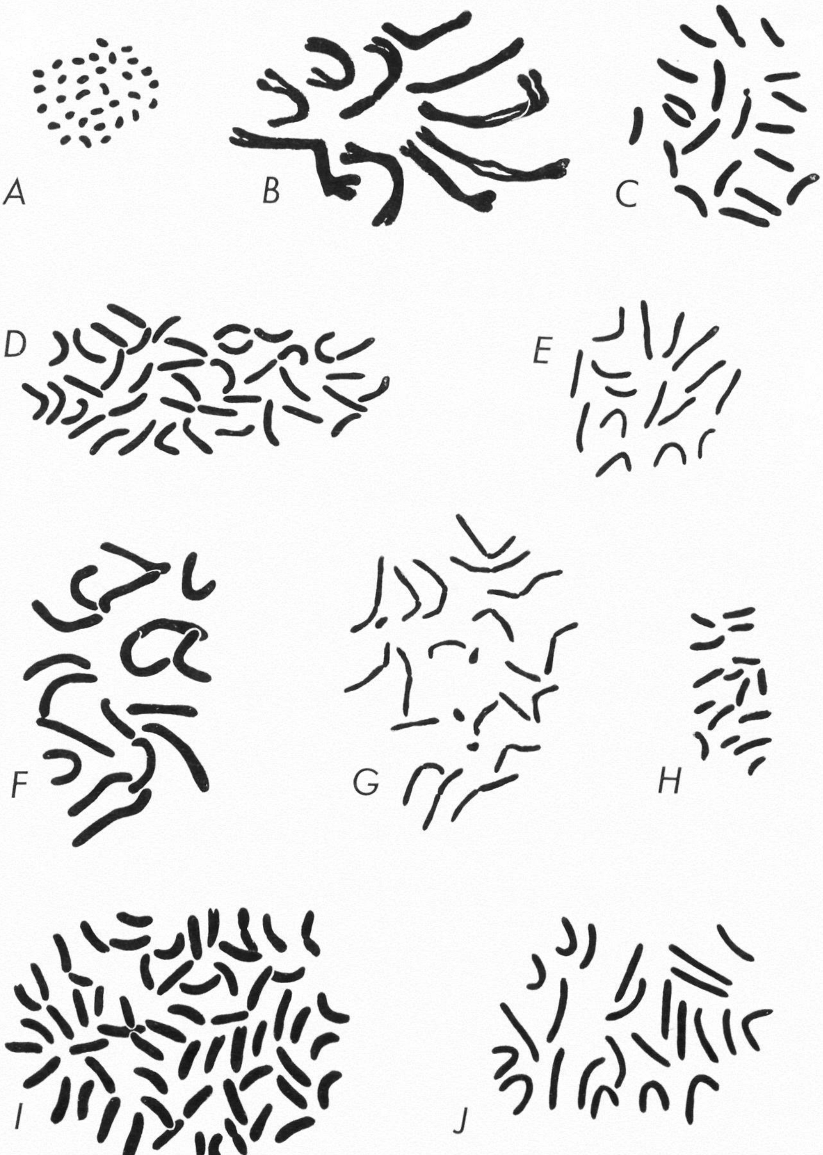

Fig. 1. Somatic metaphase plates of South African vascular plants. — A: *Cyperus marginatus* (2n=32). — B: *Charieis heterophylla* (2n=10). — C: *Cineraria aspera*, Nordenstam 3539 (2n=20). — D: *Cineraria aspera*, Nordenstam 3593 (2n=40). — E: *Disparago kraussii* (2n=16). — F: *Felicia dregei* (2n=18). — G: *Gazania krebsiana* ssp. *arctotoides* (2n=20+4 B). — H: *Steirodiscus speciosus* (2n=16). — I: *Othonna incisa*, Nordenstam 1595 (2n=60). — J: *Zinnia multiflora* (2n=24).

CYPERACEAE

Cyperus marginatus appears not to have been investigated cytologically before. The chromosome number found, viz. 2n=32, does not contradict the statement of DARLINGTON and WYLIE (1955) that the basic numbers in the genus are x=8 and 9. Some other species are known to have the same number, 2n=32.

LILIACEAE

My counts on *Albuca canadensis, Dipidax triquetra*, and *Veltheimia capensis* are all confirmations of earlier reports (DE WET 1957, DARLINGTON & WYLIE 1955). The number obtained in *Bulbine asphodeloides* (2n=14) also agrees with previous records (DARLINGTON & WYLIE 1955, FERNANDES & NEVES 1962), whereas *B. longifolia* appears not to have been cytologically studied before.

IRIDACEAE

Gladiolus edulis was found to have 2n=30 in agreement with the basic number, x=15, in the genus (DARLINGTON & WYLIE 1955).

CARYOPHYLLACEAE

2n=30 is the first report for *Dianthus namaënsis* and agrees with the observation that x=15 is a constant basic number in the genus.

My count on *Silene burchellii* (2n=24) confirms HEDBERG's report (1957) on East African material and RILEY and HOFF's count (1961) on South African material.

CAPPARIDACEAE

Although much cytological work remains to be done on the genus *Cleome*, great variation in chromosome number has already been found. The basic numbers vary from x=9, 10, and 11 up to at least 15. 2n=30 is the first report for *C. rubella*.

LEGUMINOSAE

The chromosome number (2n=16) in *Crotalaria barnabassii* is the first report for this species but agrees with earlier records of other species. Most species of *Rhynchosia* are characterized by 2n=22, and this number was recently published also for *R. memnonia* (FRAHM-LELIVELD 1969).

GERANIACEAE

The large and horticulturally important genus *Pelargonium* is surprisingly poorly known cytologically. Further knowledge of chromosome numbers is likely to contribute substantially to the understanding of the phylogeny and infrageneric classification of the genus. The basic numbers vary at least between 8 and 11 (cf. DARLINGTON & WYLIE 1955). The two species included in the present study belong to sect. *Hoarea,* which may prove to be largely characterized by x=10. *Pelargonium triste,* a well-known member of this section, has been reported to have 2n=60 (op. cit.).

CONVOLVULACEAE

The three species studied all had 2n=30. The count on *Ipomoea obscura* confirms a previous record (SHARMA & DATTA 1958), whereas the other counts are first reports. x=15 is known to be characteristic of *Ipomoea*, and in *Merremia* the basic number is either 14 or 15.

BORAGINACEAE

My two collections of *Heliotropium ovalifolium* from South West Africa both had 2n=56, a number remarkably different from that reported for Indian material of this species, viz. 2n=32 (PAL 1953, 1963). A closer taxonomic study of the material would be worth while *Heliotropium* is cytologically very diverse, with basic numbers ranging between 7 and 21.

LABIATAE

The *Plectranthus* species investigated is also known under the name *Neomuellera damarensis*. The generic limits in this group of *Labiatae* are obscure, and a future classification may have to draw on cytological data. In its usual circumscription *Plectranthus* comprises species with 2n=24, 28 and 30. The basic numbers are probably x=12, 14 and 15 rather than x=6 as postulated by DARLINGTON and WYLIE (1955) on the basis of the only count then available.

SOLANACEAE

Nicotiana glauca in South Africa is a common weed of South American origin. The species is already previously known to have 2n=24 (DARLINGTON & WYLIE 1955; LEWIS, STRIPLING & ROSS 1962).

SCROPHULARIACEAE

The monotypic genus *Colpias* has not been cytologically investigated before.

SELAGINACEAE

2n=14 for *Selago albida* is a first generic report. The same number has been recorded, however, for two species of the closely allied genus *Hebenstretia* (DARLINGTON & WYLIE 1955).

LOBELIACEAE

My count of 2n=12 in *Lobelia coronopifolia* is somewhat surprising, since the genus otherwise seems to have a very constant basic number of x=7.

COMPOSITAE

2n=10 in *Charieis heterophylla* confirms a previously published count (SOLBRIG et al. 1964).

My two collections of *Cineraria aspera* turned out to represent different levels of ploidy, viz. diploidy and tetraploidy. The two cytotypes differ in certain morphological characters, but their taxonomic status can only be decided in connection with a revision of the whole, rather variable species complex.

Cotula turbinata (syn. *Cenia turbinata*) has been reported previously to have 2n=18 (DARLINGTON & WYLIE 1955), but my specimen had without doubt 2n=16.

2n=16 in *Disparago kraussii* is the first report for this genus.

The counts in *Eriocephalus* are new species records but agree with my earlier findings of x=9 in the genus (NORDENSTAM 1967 b).

Felicia is a taxonomically intricate genus in urgent need of revision. Several basic numbers are known (x=6, 8, 9), but 2n=18 is a fairly common somatic number according to previous reports and my own unpublished counts on species not yet satisfactorily named.

Gazania has been reported earlier to have 2n=10 (cf. NORDENSTAM 1967 b), and the new count of 2n=20 in *G. krebsiana* is the first instance of polyploidy in the genus. ROESSLER (1959) gave this species a very wide circumscription, and no doubt the complex is worthy of a more detailed taxonomic analysis.

My two counts in *Helichrysum* are first species records but confirm earlier observations of x=7 as the basic number in the genus.

2n=20 in *Kleinia crassulifolia* agrees with a previous count (by J. G. BAKER, cited in ROWLEY 1965).

Mairea has not been cytologically investigated previously. The chromosome number, 2n=18, does not contradict the general opinion that the genus is a close ally of *Felicia,* from which it differs merely by the plumose pappus.

The new counts obtained in the genus *Othonna* (all except *O. protecta* are new) confirm my earlier assumption (NORDENSTAM 1967 a), that polyploidy has played a considerable evolutionary role in the genus, especially in the section of tuberous-rooted species. The tetraploid *O. filicaulis, hallii, macrophylla,* and *oleracea* belong here, and also the hexaploid red-flowered species, *O. incisa.* Within the *O. filicaulis* complex are now known diploids, tetraploids and hexaploids, and this group is in need of revision, like the whole, taxonomically very difficult genus.

My new counts in *Pentzia* add a new basic number, viz. x=8, to the previously recorded x=6 and 7 (NORDENSTAM 1967 b).

2n=16 in *Phoenocoma prolifera* is the first report for this monotypic genus, allied to the *Helichrysum - Gnaphalium* complex but obviously with a different basic number (cf. above under *Helichrysum*).

The genus *Steirodiscus* comprises some small annuals, some of which are usually found under the generic names *Gamolepis* and *Psilothonna.* As shown elsewhere (NORDENSTAM 1968), *Steirodiscus* is the correct generic name, however. A transfer of the species *Gamolepis speciosa* PILL. is necessary, resulting in the following new combination.

Steirodiscus speciosus (PILL.) B. NORD., comb. nov.

Basionym: *Gamolepis speciosa* PILLANS in Journ. Bot. 69, p. 50 (1931).

Synonym: *Psilothonna speciosa* (PILL.) PHILL. in Journ. S. Afr. Bot. 16, p. 17 (1950).

It is noteworthy that *Steirodiscus tagetes* (syn. *Gamolepis tagetes*) has been reported to have n=10 (MEHRA et al. 1965). *S. speciosus* is very closely allied but turned out to have 2n=16 in all six specimens studied.

2n=16 in *Ursinia cakilefolia* and 2n=14 in *U. anthemoides* ssp. *anthemoides* are confirmations of earlier counts (HAESLER 1967). The material studied of the latter species represents an unusually striking form with about two cm long and basally spotted ligules. *U. anthemoides* ssp. *versicolor* was found to have 2n=16. The two subspecies of *U. anthemoides* (cf. PRASSLER 1967) thus have different basic numbers. 2n = 16 seems to be the normal chromosome number in the genus, and the deviating number in ssp. *anthemoides* is most likely the result of a secondary reduction.

Zinnia multiflora, of South American origin, is a widespread weed in South Africa. The same chromosome number (2n = 24) has been reported previously (MEHRA et al. 1965).

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Embryology of Cereus jamacaru and Ferocactus wislizeni and Comments on the Systematic Position of the Cactaceae

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ABSTRACT

In the prefertilization stages of their embryology *Cereus jamacaru* and *Ferocactus wislizeni* closely resemble other cacti. Additional features of interest are the one- to three-layered endothecium and multicelled ovular archesporium in *C. jamacaru*. Both species show a nuclear endosperm with a chalazal accumulation of nuclei. The zygote divides transversely in *F. wislizeni* but by an oblique wall in *C. jamacaru*. In the latter, the derivatives of the basal cell proliferate to produce a massive suspensor which may bud off one or two additional embryos. There was, however, no sign of nucellar polyembryony in either species. Both the integuments take part in the formation of the seed coat but the cells of the outer layer of the outer integument become greatly enlarged, thick-walled and tanniniferous.

A reassessment is made of the affinities of the *Cactaceae* taking into consideration available data from all relevant disciplines. It is suggested that the *Cactaceae* are closest to families of the *Centrospermales,* especially the *Aizoaceae.*

INTRODUCTION

The *Cactaceae* is a large family of stem succulents, almost exclusive to dry tropical America, but introduced as exotics into several countries where some (like spp. of *Opuntia* and *Cereus*) became naturalised and constitute troublesome weeds. There are 50—150 genera and perhaps 2000 species (WILLIS & AIRY SHAW 1966). There has been considerable controversy regarding the systematic position of the family; affinities having been suggested with such diverse taxa as the *Centrospermales, Nymphaeaceae, Cucurbitaceae* and *Passifloraceae.*

So far, embryological data for the *Cactaceae* are available on *Mammillaria* (TIAGI 1956, 1957). *Opuntia* (ARCHIBALD 1939; CHOPRA 1957; MAHESHWARI & CHOPRA 1954, 1955; PHILBRICK 1963; TIAGI 1954), *Pereskia* (NEUMANN 1935; TIAGI 1967), *Rhipsalis* (MAURITZON 1934, *Astrophytum, Thelocactus* and *Toumeya* (ENGLEMAN 1960).

The junior author has earlier made a study of the embryology of members of the *Aizoaceae* (PRAKASH 1967 a, b, c) and the present investigation on the two cacti is an attempt to reevaluate the embryological similarities in these two groups of plants while providing additional data on the *Cactaceae* itself which, inspite of its largeness and taxonomic and horticultural interest, has not been sufficiently studied.

MATERIALS AND METHODS

Cereus jamacaru DC. was collected from plants cultivated in the Delhi University Botanical Garden and the Buddha Jayanti Park, New Delhi (India) in September 1963 and 1964 and fixed in F.A.A. (5 ml neutral formalin + 5 ml glacial acetic acid + 90 ml 70 per cent ethanol). *Ferocactus wislizeni* (ENG.) BR. & R. was collected by one of us (R.N.K.) near the Geochronology Laboratory and Santa Rita Experimental Station, Tuscon, Arizona (U.S.A.) in July, 1963. As the flowers and fruits of both the plants are very large, they were segmented into small pieces. Customary methods of infiltration and embedding were followed and the sections were cut at a thickness of 8—15 microns. They were stained either in safranin and fast green or iron haematoxylin and erythrosin. Propionocarmine squashes and dissected wholemounts were made to study the microsporogenesis and embryogeny respectively. Acetolysis method of ERDTMAN (1960) was followed to study the exine structure of pollen.

OBSERVATIONS

External Morphology

The plants of *Ferocactus wislizeni* are large columnar herbs bearing yellow or red flowers at the summit. In *Cereus jamacaru*, on the other hand, the plant body is profusely branched with a large number of creamy-white, night-blooming flowers borne along the ridges. In both, the perianth is not clearly distinguishable into calyx and corolla and a large number of stamens with long slender filaments are borne at its base. The ovary is inferior, unilocular and contains many parietal placentae each bearing numerous ovules. The style is thick and long

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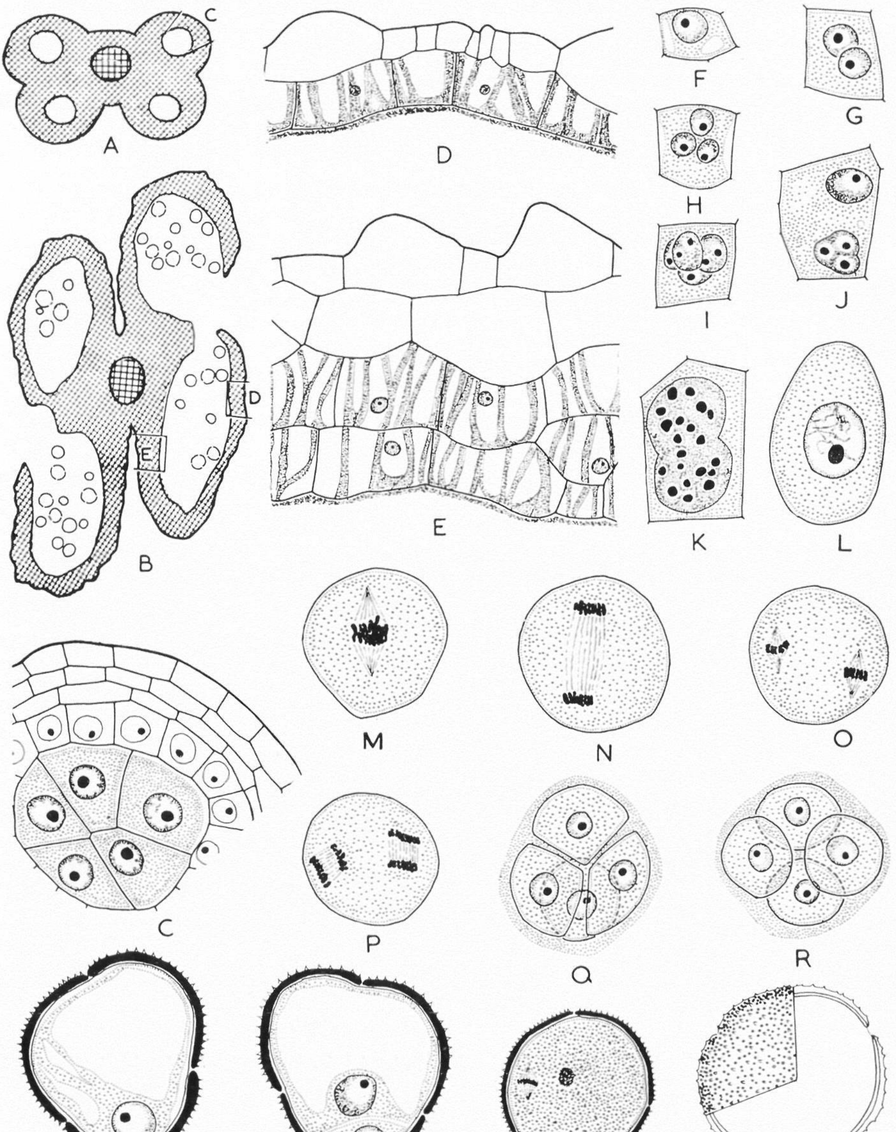
Fig. 1. *Cereus jamacaru,* microsporangium, microsporogenesis and male gametophyte. — A—B: Transections of young and dehiscing anthers (diagrammatic). — C: Enlargement of sector *C* marked in A to show microspore mother cells surrounded by



wall layers. — D—E: Portions of anther wall enlarged from B; the endothecium is 2- or 3-layered in the vicinity of connective (E) and 1-layered elsewhere (D). — F—K: Tapetal cells showing nuclear divisions and fusions. — L—R: Meiotic divisions in microspore mother cells leading to the formation of tetrahedral (Q) and decussate (R) tetrads. — S—T: One and 2-celled pollen grains. — U: Pollen grain; generative cell in metaphase. — V: Palynogram. — A ×108, B ×38, C, F—K, Q—T ×774, D, E, L—P, U, V ×368.

and ends in numerous stigmatic lobes. The fruit is a bright red berry containing a large number of black seeds borne on swollen, mucilaginous funiculi. Fruit set in the plants of *C. jamacaru* studied by us was very poor, presumably due to the lack of suitable pollinating agent.

Microsporangium, Microsporogenesis and Male Gametophyte

The anthers in both species are tetrasporangiate (Figs. 1 A, 2 A). The wall comprises of four cell layers, the epidermis, endothecium, middle layer and secretory tapetum (Figs. 1 C, 2 B). The tapetal cells become multinucleate and the nuclei, multinucleolate (Figs. 1 F—K, 2 C, D). The microspore mother cells undergo meiosis (Fig. 1 L—P) and form tetrahedral or decussate tetrads (Fig. 1 Q, R) as a result of simultaneous cytokinesis. The microspore enlarges and acquires a thick exine which is spiny in *C. jamacaru* (Fig. 1 S—V) but smooth in *F. wislizeni* (Fig. 2 E, F). A mitotic division in the microspore produces vegetative and generative cells and the latter divides forming two male gametes (Fig. 1 T, U). The pollen grains are shed at this stage and contain abundant starch. The wall of the dehiscing anther in *C. jamacaru* consists of an epidermis of tannin-filled cells with a thick cuticle, and a fibrous endothecium that becomes two- or three-layered in the vicinity of the connective (Fig. 1 B, D, E).

Megasporangium, Megasporogenesis and Female Gametophyte

The ovules arise as small protuberances on the placentae. They begin to curve at the time of differentiation of the inner integument (Fig. 3 A). As they bend (Fig. 3 B, C), the funiculus, which is frequently branched, elongates appreciably. The ovules containing an organized embryo sac are campylotropous, bitegminal and crassinucellar (Figs. 2 G, 3 D). The tip of the inner integument is swollen and a prominent air space is present at the chalazal end between the two integuments. The funicular epidermis facing the micropyle bears numerous richly cytoplasmic hairs comprising the transmitting tissue which is best developed at the time of fertilization but degenerates soon after. A part of the nucellar tissue persists in the seed as perisperm. Rarely *C. jamacaru* shows twin ovules which have a common funiculus and outer integument but separate vascular traces, inner integuments and micropyles (Fig. 3 E).

The archesporium is invariably one-celled in *F. wislizeni* (Fig. 2 H)

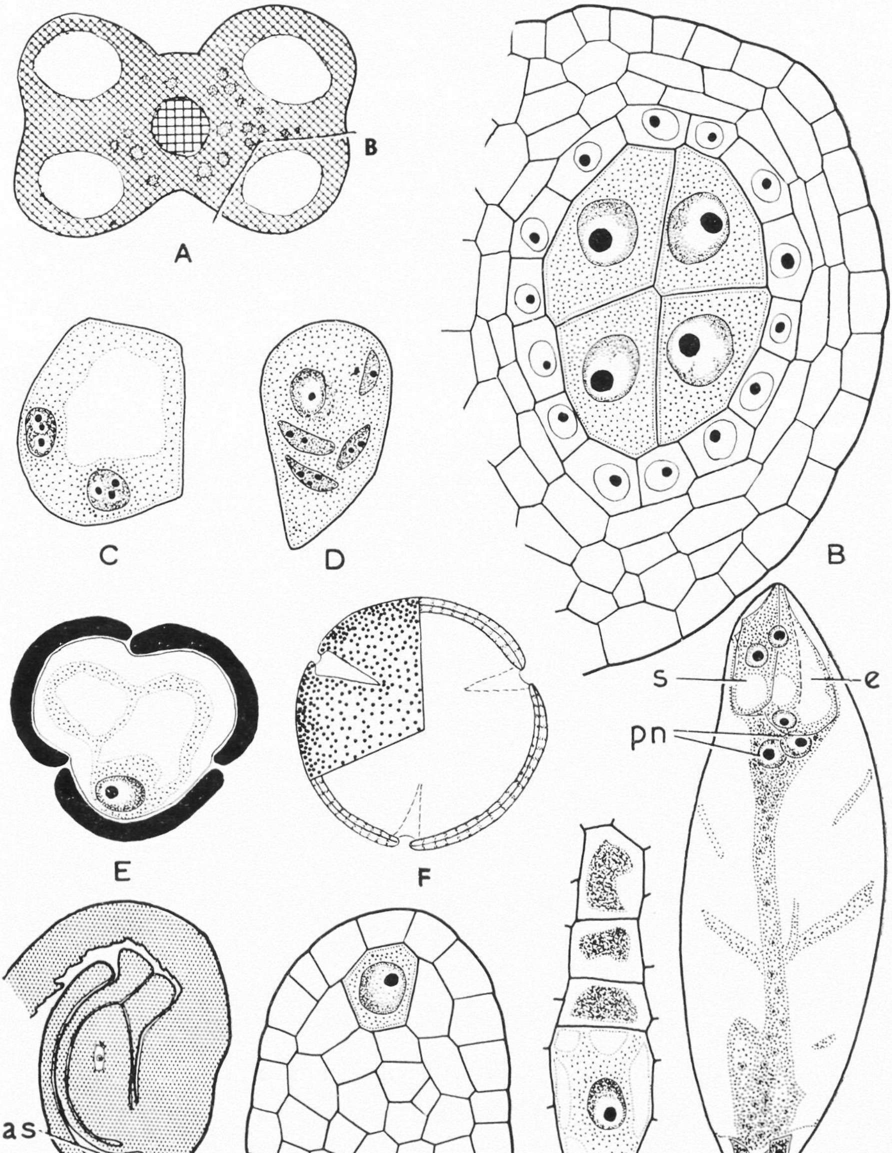


Fig. 2. *Ferocactus wislizeni*, male and female reproductive structures (*as*, air space; *e*, egg; *pn*, polar nuclei; *s*, synergid). — A: T.s. young anther (diagrammatic). — B: Portion *B* marked in A magnified to show sporogenous cells and wall layers. — C—D: Tapetal cells. — E: One-celled pollen grain. — F: Palynogram. — G: Longisections of ovule; note air space between outer and inner integuments at the chalazal end of the ovule. — H: L.s. nucellus showing archesporial cell. — I: Tetrad; micropylar megaspores have degenerated. — J: Organised embryo sac with degenerating antipodal cells. — A ×188, B—D, H, I ×979, E, F ×528, G ×98, J ×308.

but two- or three-celled in *C. jamacaru* (Fig. 3 F, G). The cell closest to the nucellar epidermis divides to form a sporogenous cell and the primary parietal cell. A massive nucellar cap is formed as a result of divisions in the nucellar epidermis and secondary parietal cells.

The sporogenous cell directly functions as the megaspore mother cell and undergoes meiosis forming a row of three or four megaspores (Figs. 3 H—K, 2 I). In either case the chalazal megaspore alone functions and through three successive mitoses forms an eight-nucleate embryo sac (Figs. 3 L, M, 2 J); the development conforming to the Polygonum type.

The synergids may sometime persist even after fertilization but the antipodal cells are ephemeral. The polar nuclei fuse before fertilization and form the secondary nucleus. Abundant starch is present in the embryo sacs of degenerating ovules of *C. jamacaru* but in the functional ovules also of *F. wislizeni*.

Endosperm

The primary endosperm nucleus lies immediately below the zygote (Figs. 3 N, 4 A) where it divides to form two nuclei (Fig. 4 B, C). Synchronous mitoses give rise to four (Fig. 4 D), eight and 16-nucleate stages (Fig. 4 E). After several nuclei are formed, a few of them lie around the base of the embryo whereas others migrate to the chalazal end of the embryo sac, become hypertrophied, and lie surrounded by an abundant mass of cytoplasm forming a caecum (Fig. 4 F). The hypertrophied nature of the nuclei and the breakdown of the surrounding nucellar cells suggests a haustorial function of the caecum. In the mature seed the endosperm is curved. Cell-formation occurs very late — at the dicotyledonous stage of the embryo — and results in a few sparsely cytoplasmic cells around the base of the radicle.

Embryogeny

The zygote in *F. wislizeni* is a pyriform structure with a prominent nucleus at the terminal end and a large vacuole at the basal end (Fig. 4 G). Although usually median, sometimes it is lateral in position and

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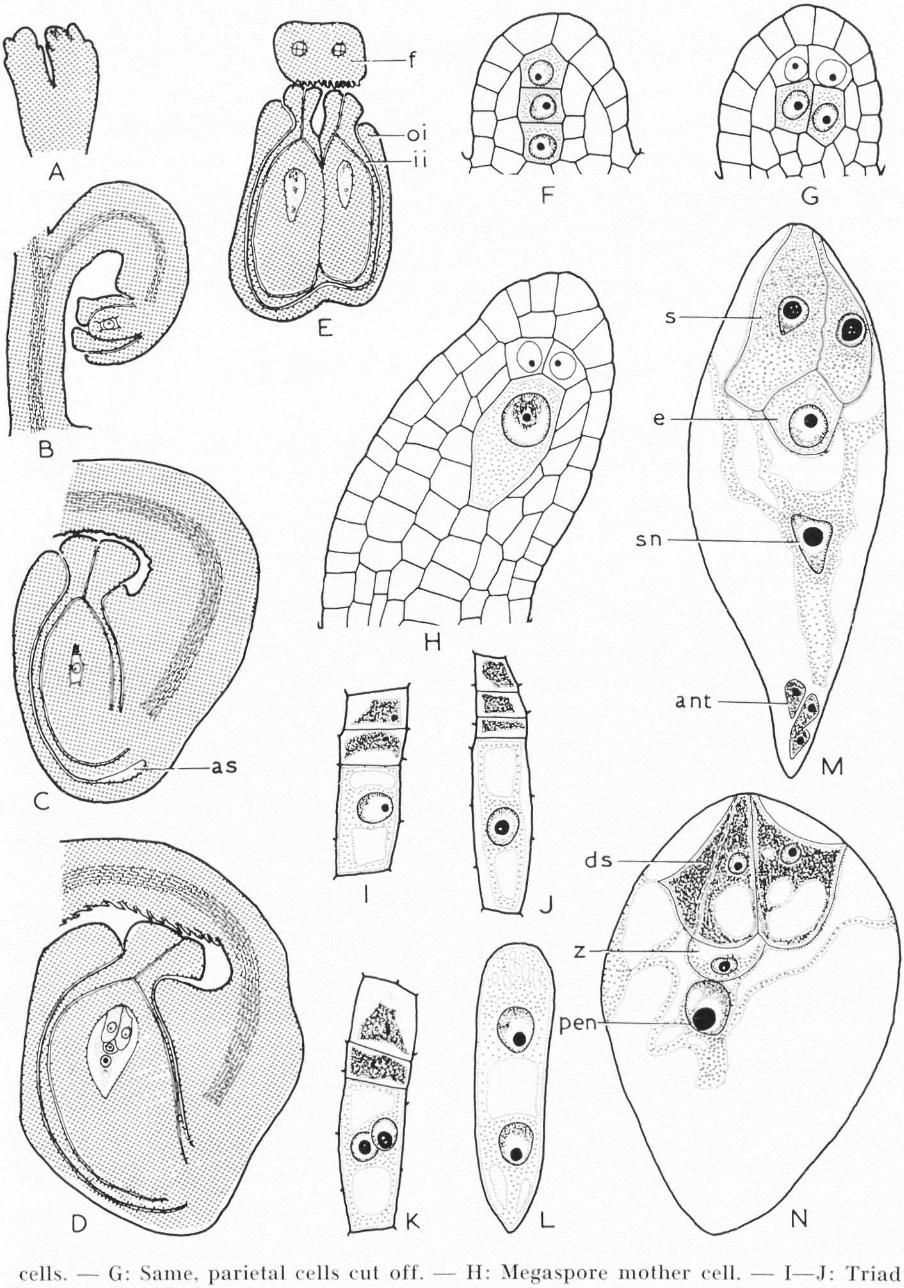
Fig. 3. *Cereus jamacaru,* megasporangium, megasporogenesis, female gametophyte and endosperm (*ant,* antipodal cells; *as,* air space; *ds,* degenerating synergid; *e,* egg; *f,* funiculus; *ii,* inner integument; *oi,* outer integument; *pen,* primary endosperm nucleus; *s,* synergid; *sn,* secondary nucleus; *z,* zygote). — A: Two ovular primordia. — B—D: Stages in curvature of ovules; note prominent air space between integuments near the chalaza in C, and funicular hairs in D. — E: Twin ovules with common outer integument. — F: L.s. nucellus showing a row of three archesporial



cells. — G: Same, parietal cells cut off. — H: Megaspore mother cell. — I—J: Triad and tetrad with functional megaspore. — K: Triad; nucleus of chalazal megaspore has divided. — L: Two-nucleate embryo sac. — M: Organized embryo sac. — N: Embryo sac soon after fertilization; antipodal cells have already degenerated and synergids are degenerating. — A—D ×108, E ×70, F—M ×683, N ×343.

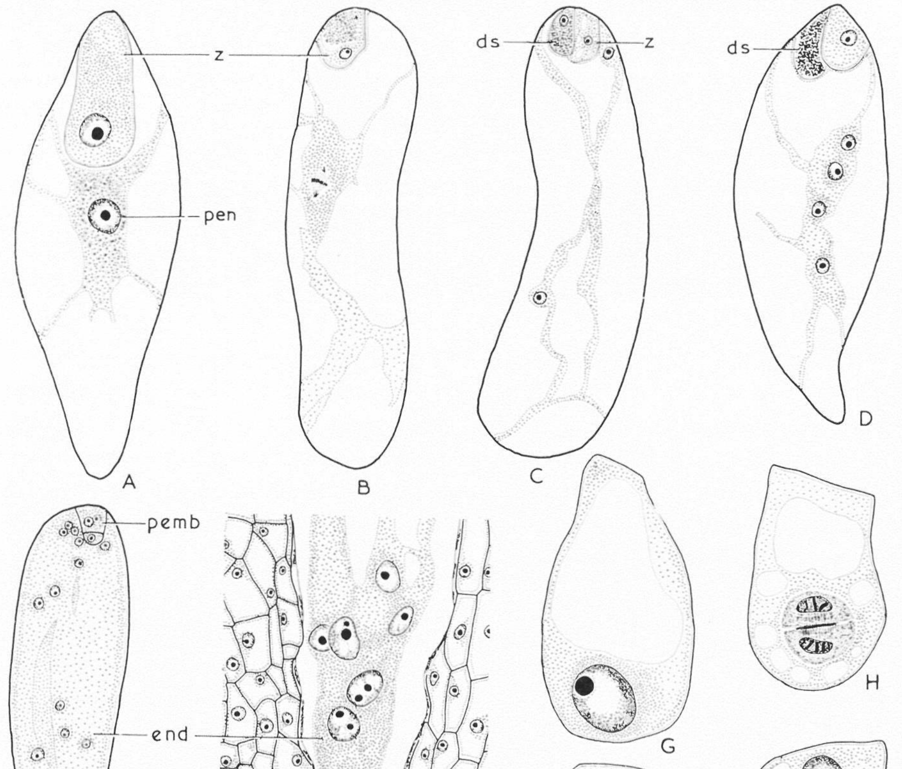
divides by a transverse wall into a terminal cell *ca* and a basal cell *cb* (Fig. 4 H, I). Transverse division occurs first in *cb* (Fig. 4 J) and then in *ca* (Fig. 4 K) to produce a linear tetrad (Fig. 4 L). Rarerly the cell *l′* divides by a vertical wall resulting in decussately arranged cells (Fig. 4 M). Subsequent divisions give rise to globular and heart-shaped embryos. The mature embryo is dicotyledonous and curved (Fig. 4 N, O).

In *C. jamacaru,* because of low fruit set and the consequent paucity of material of proper stages, early development of the embryo could not be followed closely. As is apparent from the subsequent stages, the zygote (Fig. 5 A) divides by an oblique wall. Next, a division occurs in the terminal cell and is either at right angles to the first one (Fig. 5 B) or transverse. The cells in the basal region of the proembryo undergo repeated divisions to produce a massive suspensor (Fig. 5 C, F, G). Preliminary divisions in the terminal cells of the proembryo are transverse (Fig. 5 C), vertical (Fig. 5 D) or oblique (Fig. 5 E) and eventually result in a globular embryo (Fig. 5 F—H, K). At this stage the suspensor is very massive and consists of large parenchymatous cells (Fig. 5 K). In two ovules one or two additional proembryos were seen budding off from the suspensor (Fig. 5 I, J) but their development could not be followed. The mature embryo is curved and has a massive radicle and two cotyledons (Fig. 5 L) containing a large quantity of oil and starch.

Seed coat

The seed coat is formed by both the integuments and in the initial stages both comprise two layers of cells each (Figs. 6 and 7 A, E) except around the micropyle, where the inner integument soon becomes several-layered. At the organised embryo sac stage of the ovule important differences can be noticed in the seed coat of the two species. In *C. jamacaru* (Fig. 6 B, F) the number of cell layers remains constant but tannin deposition occurs in the outer epidermis of the outer integument and the inner epidermis of the inner integument. In *F. wislizeni,* however, the entire outer integument becomes three- or four-layered and the inner three-layered but the tannin deposition does not take place

Fig. 4. *Ferocactus wislizeni,* endosperm and embryo (*ca, cb,* terminal and basal cells of bicelled proembryo; *ci,* lower daughter cell of tetrad; *ds,* degenerating synergid; *end,* endosperm; *l, l′,* daughter tiers of *ca*; *m,* intermediate cell of tetrad; *nu,* nucellus; *pemb,* proembryo; *pen,* primary endosperm nucleus; *rc,* root cap; *vs,* vascular supply; *z,* zygote). — A: Fertilized embryo sac containing zygote and primary endosperm nucleus. — B: Primary endosperm nucleus in metaphase. — C—E: Two-, four- and 16-nucleate endosperm. — F: L.s. portion of nucellus showing chalazal endosperm caecum; cytoplasm is dense and nuclei are hypertrophied; degenerating nucellar cells are seen around the caecum. — G: Zygote. — H: Division



of zygote. — I—K: Two and 3-celled proembryos. — L: Four-celled linear proembryo. — M: Same, *cb* has not yet divided but *l′* has undergone vertical division. — N: Young dicotyledonous embryo. — O: Embryo at maturity, the cotyledons are curved. — A, F ×336, B—E ×150, G—M ×690, N ×34, O ×17.

until after fertilization (Fig. 7 B, F). After fertilization, and until the formation of mature embryo (Figs. 6, 7 C, D, G, H) the amount of tannin increases and the cells of the outer layer of the outer integument become greatly enlarged and conspicuously sclerotic. The inner layer of the inner integument persists as a compressed but discernible layer whereas the other layers of the integument are very often completely obliterated.

DISCUSSION

Ovule

In *Cereus jamacaru* and *Ferocactus wislizeni* the ovules are borne on branched funiculi as has been recorded in many other cacti (BUXBAUM 1953; MAHESHWARI & CHOPRA 1955). The funicular transmitting tissue, along which the pollen tube grows towards the micropyle, is also present in *Mammillaria tenuis* (TIAGI 1957), *Opuntia dillenii* (TIAGI 1954; MAHESHWARI & CHOPRA 1955), and *Pereskia amapola* (NEUMANN 1935). Its maximum development at the time of fertilization suggests an active role in that process.

The ovules are described as circinotropous in *Opuntia aurantiaca* (ARCHIBALD 1939) and *O. dillenii* (TIAGI 1954; MAHESHWARI & CHOPRA 1955), and as hemicircinotropous in *Mammillaria tenuis* (TIAGI 1957). In both the species studied by us, the funiculus, although closely adpressing the micropyle, never encircles the mature ovule, and hence the term campylotropous seems more appropriate to describe them.

The presence of an air space between the outer and inner integuments at the chalazal end, which has been recorded in *Mamillaria, Opuntia* and *Pereskia,* has also been observed in the plants studied by us. It is produced by more rapid anticlinal divisions in the basal region of the outer integument which bulges out, resulting in a cavity. An air space is occasionally present in several centrospermalean plants also, but its functional significance, if any, is not known.

A nucellar cap, formed as a result of the activity of the cells of the nucellar epidermis and the parietal cells, is present in *Cereus* and *Ferocactus* as well as in *Rhipsalis* (MAURITZON 1934), *Pereskia* (NEUMANN 1935) and *Opuntia* (ARCHIBALD 1939; TIAGI 1954; MAHESHWARI & CHOPRA 1955). TIAGI (1957) distinguished two groups of cacti on the basis of the behaviour of nucellar epidermal cells in prefertilization stages. According to him, some taxa (*Opuntia, Rhipsalis*) always show only elongation of epidermal cells, others (*Pereskia, Mammillaria*)

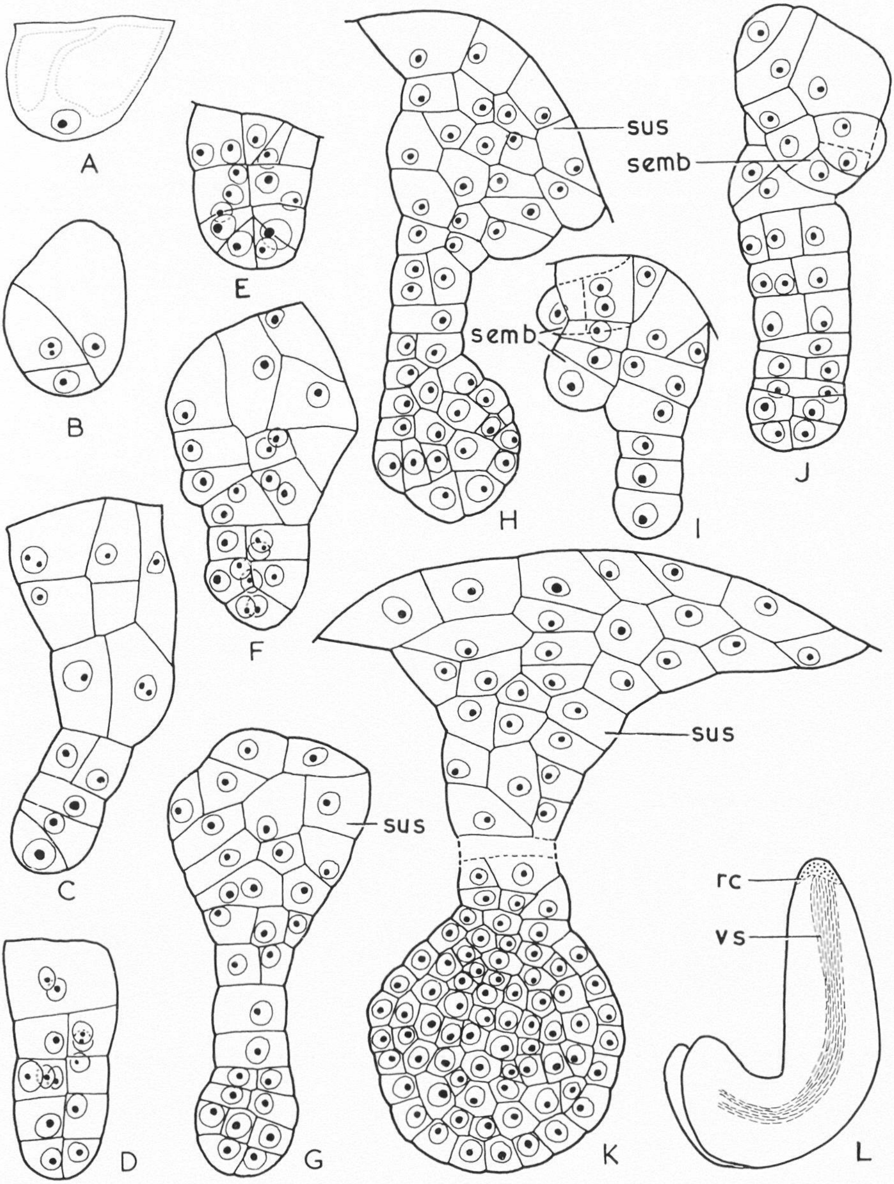


Fig. 5. *Cereus jamacaru,* embryogeny (*rc,* root cap; *semb,* suspensor embryo; *sus,* suspensor; *vs,* vascular supply). — A: Zygote. — B: Three-celled proembryo; separating walls are oblique. — C—H: Irregular divisions leading to formation of early globular embryo; cells of the suspensor undergo numerous divisions. — I—J: Proembryos showing suspensor budding. — K: Advanced globular embryo with massive suspensor. — L: Dicotyledonous embryo; cotyledons are curved. — A—K ×416, L ×22.

show their division but no stretching. However, *Cereus* and *Ferocactus* show both elongation and divisions of the nucellar epidermal and parietal cells before fertilization.

Starch in Embryo Sac

Tiagi (1954) observed that in *Opuntia dillenii* the healthy embryo sacs contain little starch whereas those showing signs of degeneration accumulate abundant starch. Likewise, in *Cereus jamacaru* starch is seen only in the degenerating embryo sacs. However, the healthy embryo sacs of *Ferocactus wislizeni* also contain it in large quantities. In the light of such occurrence, the correlation between degeneration and accumulation of starch needs further study.

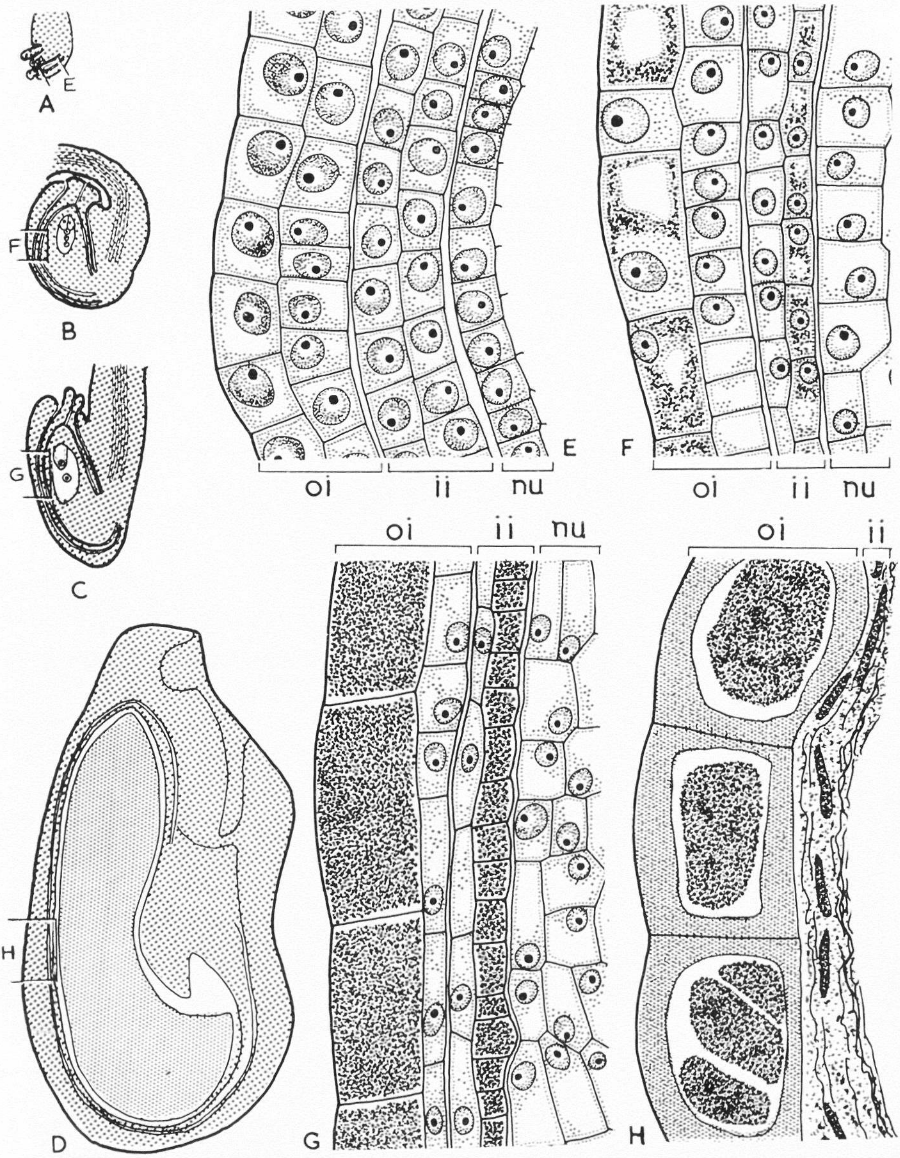
Polyembryony

Nucellar polyembryony is a common feature of the cacti and has been reported in several species of *Opuntia* (Schnarf 1931; Archibald 1939; Maheshwari & Chopra 1955; Philbrick 1963), *Mammillaria tenuis* and *Pereskia* (Tiagi 1956, 1957, 1967). The absence of data regarding zygotic embryos is mainly due to the predominance of adventive embryos which are supposed to suppress the development of the former. However, not all the cacti exhibit nucellar polyembryony, e.g. *Astrophytum myriostigma, Thelocactus bicolor, Toumeya papyracantha* (Engleman 1960), *Cereus jamacaru* and *Ferocactus wislizeni* (present work). Engleman believes that the presence or absence of adventive embryos may form an important taxonomic character of this family. But it would hardly constitute a useful criterion unless data are collected for a large number of plants. Unlike other cacti, *Cereus jamacaru* shows budding of the suspensor although these buds are not found to mature into suspensor embryos.

SYSTEMATIC POSITION

The *Cactaceae* constitute an odd group of angiosperms, not only because of their morphological peculiarities but also because taxonomically they form one of the most tossed about families of flowering plants. Amongst the families with which its affinities are suggested are the *Nymphaeaceae* (Arber 1910; Gundersen 1950; Mitra 1956), *Passifloraceae* (Engler & Diels 1936), *Cucurbitaceae* (Hutchinson 1959)

Fig. 6. *Cereus jamacaru*, seed coat (*ii*, inner integument; *nu*, nucellus; *oi*, outer integument). — A—D: L.s. ovules and seeds at different stages of development



(diagrammatic). — E: Enlarged view of portion *E* marked in A. Both integuments are 2-layered each. — F: Region *F* labelled in B magnified to show the beginning of deposition of tannin in outer layer of outer integument and inner layer of inner integument. — G: Magnified view of sector *G* marked in C; cells of outer layer of outer integument have stretched tangentially. — H: Portion *H* marked in D enlarged to bring out details of seed coat at dicotyledonous stage of embryo; outer layer of outer integument is prominent and comprises large tanniniferous cells while other layers are crushed; remnants of inner layer of inner integument are also discernible. — A—C ×46, D ×15, E—G ×860, H ×464.

and the families of the *Centrospermales* (WETTSTEIN 1935; ENGLER 1964), particularly the *Aizoaceae* (BUXBAUM 1961; MAHESHWARI 1963; TAKHTAJAN 1959). Evidence from cytology (DARLINGTON & WYLIE 1955) is inconclusive; the chromosome numbers being x=8, 9 for the *Aizoaceae,* x=11 for the *Cactaceae,* x=7—14 for the *Cucurbitaceae,* x=8, 10, 12, 14, 17 for the *Nymphaeaceae* and x=6, 9, 10 for the *Passifloraceae.* According to KURTZ (1962) "... pollen morphology only adds to the taxonomic chaos of the Cactaceae". A comparison of their morphological and embryological characters (for literature *see* AHUJA 1966; DAVIS 1966; LAWRENCE 1951; METCALFE & CHALK 1950; PRAKASH 1967 a, b, c; RAMJI & PADMANABHAN 1965; TIAGI 1967; present work) leads us to the following observations.

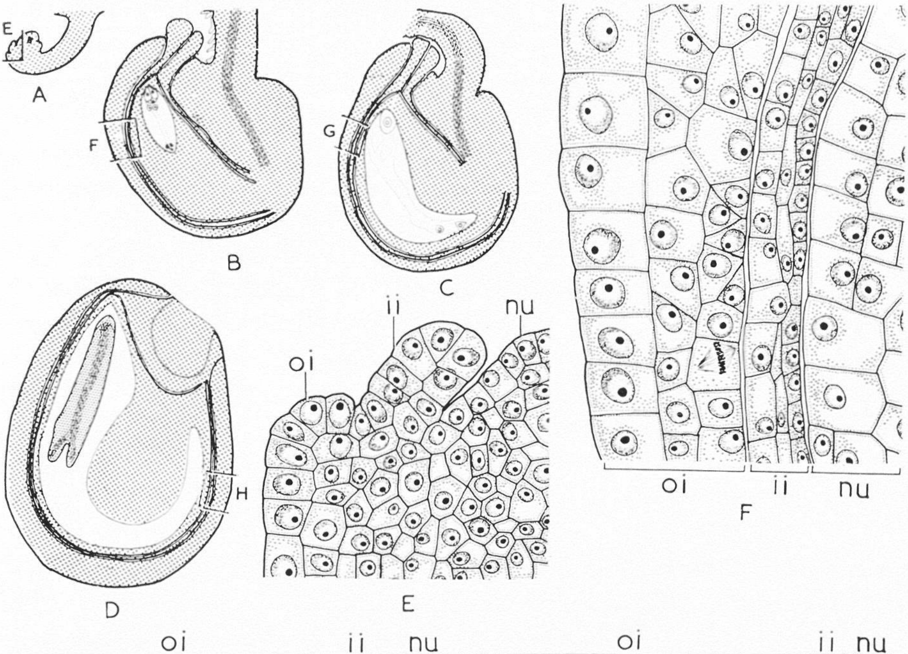
Despite a few resemblances with the Cactaceae especially in the presence of (1) parietal placentation, (2) secretory anther tapetum, (3) Polygonum type of embryo sac, and (4) Nuclear endosperm, the families Cucurbitaceae, Nymphaeaceae and Passifloraceae show an overwhelming number of contrasting characters.

For example, the Cucurbitaceae differ from the Cactaceae in the possession of (1) a climbing habit, (2) bicollateral vascular bundles in stem arranged in two rings, (3) indistinct subsidiary cells around the stomata, (4) dichlamydeous flowers, (5) five, often highly modified stamens, (6) 2-celled pollen grains, (7) anatropous ovules with integumentary vascular bundles, (8) nucellar beak, (9) chalazal endosperm haustoria, and (10) seed coat formed only by the outer integument. Moreover the cucurbits lack such characters of the cacti as the air space between the integuments, perisperm and nucellar polyembryony. Hence any close affinity between the two families is ruled out.

Similarly the *Nymphaeaceae* show the absence of (1) subsidiary cells in the stomata, (2) adventive embryony and (3) true vessels; and the presence of (1) aquatic or marshy habit, (2) peltate, long-petioled leaves, (3) multilocular ovary, (4) closed and scattered vascular bundles, (5) anatropous ovules, and (6) Nuclear or Cellular endosperm. All these characters make this family distinct from the Cactaceae.

Unlike the *Cactaceae,* the *Passifloraceae* exhibit (1) a climbing habit, (2) superior ovary, (3) 2-celled pollen grains, (4) ortho- or anatropous ovules, (5) micropyle formed by both integuments, (6) megaspore tetrad

Fig. 7. *Ferocactus wislizeni,* seed coat (*ii,* inner integument; *nu,* nucellus; *oi,* outer integument). — A—D: L.s. ovules and seeds at different stages of development (diagrammatic). — E: Enlarged view of portion *E* marked in A to show integuments at archesporial cell stage. — F: Portions of integuments enlarged at



organised embryo sac stage; outer and inner integuments are 3-layered each. — G: Area *G* labelled in C enlarged to show details of seed coat immediately after fertilization; tannin is deposited in cells of the outer layer of outer integument and inner epidermis of the inner. — H: Portion *H* marked in D magnified to bring out details of seed coat at dicotyledonous stage of embryo; cells of outer epidermis of outer integument have enlarged conspicuously and their walls are thickened but other layers are greatly compressed; whole of inner integument except the inner epidermis has been crushed. — A, B ×64, C ×50, D ×22, E—G ×638, H ×273.

of which the micropylar cell is functional, and (7) ruminate endosperm; but lack (1) well-defined subsidiary cells around the stoma, (2) air space between the integuments, and (3) perisperm. The structure and organisation of the seed coat is also different in both. Hence an alliance between the *Passifloraceae* and the *Cactaceae* seems far-fetched.

The *Aizoaceae* too differ from the *Cactaceae* in a few morphological characters like the presence of (1) well-developed leaves, (2) cyclic arrangement of floral parts, (3) pentamerous calyx, (4) multilocular ovary which forms a loculicidal capsule, and (5) the absence of petals. On the other hand, they share the following features: (1) bisexual flowers with numerous stamens, (2) an inferior ovary containing an indefinite number of ovules borne on parietal placentae, (3) secretory anther tapetum with multinucleate cells, (4) simultaneous cytokinesis in the pollen mother cells, (5) 3-celled pollen grains, (6) campylotropous, bitegminal and crassinucellar ovules, (7) micropyle formed by the collar-like tip of the inner integument, (8) an air space between the integuments at the chalazal end, (9) perisperm, (10) frequent occurrence of 'triads' of megaspores, (11) Polygonum type of embryo sac, (12) Nuclear endosperm with a chalazal caecum, and (13) seed coat formed by both the integuments of which only the outer layer of the outer and inner layer of the inner integuments are persistent. The cumulative evidence, therefore, suggests a close relationship of the two families *Aizoaceae* and *Cactaceae*. This is further confirmed by the presence of betacyanin pigment which is exclusive to the centrospermalean families and also occurs in the *Cactaceae* Reznik 1955; Mabry et al. 1963). Thus the inclusion of the *Cactaceae* in the order *Centrospermales* close to the *Aizoaceae* is most justified.

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Aktuella problemställningar II
(Current Problems II)

Synpunkter på algfloran i Öresund
(Some Aspects of the Algal Vegetation in the Öresund)

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ABSTRACT

In the Öresund (the Sound) between the Baltic and the North Sea (Kattegatt) there is a salinity gradient, due to the outflow of low salinity water from the Baltic.

The surface water in Kattegatt has a salinity of approximately 18—24 ‰. In the northern part of the Öresund the salinity varies from 8 to 26 ‰ (the mean value approximately 14 ‰) and in the southern part of the Öresund from 7 to 10 ‰ (the mean value 8 ‰). Near the bottom the salinity in the northern part varies between 20 and 34 ‰ (25—30 m) and in the southern between 8 and 10 ‰ (8—10 m). There is also a difference in salinity between the western and the eastern side of the Öresund. The reduction in salinity from the northern to the southern part of Öresund has a marked influence on the composition of the bentic algal vegetation. Thus within a distance of c. 100 km about 100 species disappear.

The decreasing salinity also influences the algal vegetation in other ways:

a. Reduction both in total size and cell size, e.g. *Delesseria sanguinea* and *Callithamnion hookeri.*

b. Reduction of life cycles. Several species loose their sexuality, som species even loose their ability to produce tetraspores. *Callithamnion corymbosum,* e.g., is completely sterile south of the line Helsingör—Helsingborg. Most of the *Rhodophyceae* in the Baltic have lost the sexual part of their life cycle.

Probably the meiosis in the tetrasporangium is disturbed and the border between specimens with normal and disturbed meiosis lies evidently somewhere in the southern part of the Öresund.

c. Change in the vertical distribution towards greater depth. *Trailliella intricata* and *Corallina officinalis,* e.g., appear below a depth of 18—20 m.

One can also distinguish between four distribution groups according to the lower salinity.

1. Species with definitely marked south border, no change in morphology, frutification or vertical distribution, e.g., *Ascophyllum nodosum.*

2. Species with relatively marked south border, decreasing abundance, no change in morphology, frutification and vertical distribution, e.g., *Fucus spiralis.*

3. Species with diffuse south border, gradually decreasing abundance and a fertility change in vertical distribution towards greater depth, e.g., *Dilsea edulis.*

4. Species with oscillating south border, decreasing abundance sterile, change in morphology and vertical distribution, e.g. *Callithamnion* sp. and *Antithamnion plumula.*

The Öresund is today a recipient of sewage from several industries and a population of approximately 1.5 million people.

The phosphorus content in the seawater has increased since of STEEMAN NIELSEN's investigation 1937 (Table 1). The result of this is that the productions of many species have increased, e.g., *Ectocarpus* and *Pylaiella* sp.

The hypothetical relations between the phosphorous content of sea water and the primary production is given in Fig. 1.

In the vicinity of Malmö, *Ulva lactuca, Blidingia minima, Scytosiphon lomentaria, Spermatochnus paradoxus* have completely disappeared in the last decades, probably due to some poisonous effect.

Preliminary investigations prove that the Cu-content in the water in this area is high, from 10—40 µg/l.

There are also strong indications of an accumulation in the discontinuity surface of organic particles emanating from the sewage tubes. This causes a reduction of the transmission in red light with 50 % and in blue light with 75 % and this will reduce the compensation depth. There is also some sedimentation of organic particles which successively will spoil the substratum. Hence the diaspores from algae cannot germinate on soft bottoms.

SALTHALTENS INVERKAN PÅ ALGFLORAN

Öresund är ett unikt område ur marinbiologisk synpunkt genom sitt läge mellan Östersjön och Kattegatt. Östersjön karakteriseras av en relativt homogen vattenmassa med låg salthalt, ca. 4—7 ‰. Förhållandena i Kattegatt är mera variabla, salthalten varierar mellan 18 och 24 ‰ i ytvattnet och mellan 30 och 34 ‰ i djupare lägen.

I Öresund, som ligger mellan dessa vattenmassor, uppstår en salthaltsgradient. Ytvattnet i norra Öresund har en salthalt, som varierar mellan 8 och 26 ‰, medan den i södra Öresund växlar mellan 7 och 10 ‰. Vid bottnen är motsvarande värden i norra Öresund 20—34 ‰ och vid Falsterborev 7—10 ‰.

Salthaltsgradienten är inte stabil, utan förskjuts ständigt i nord—sydlig riktning beroende på vind och strömförhållanden. Kraftiga ändringar i salthalten kan uppstå mycket hastigt, framförallt i det ytliga lagren. Förändringar på upp till 10 ⁰/₀₀ kan ske på mindre än ett dygn. Normalt är dock ändringarna inte så stora.

Salthalten visar även en säsongbetonad variation med lägre värden under mars—maj och högre värden under september—december, beroende på de förhärskande östliga—sydöstliga respektive nordvästliga—västliga vindarna under dessa tider.

En markant skillnad i salthalt kan iakttagas mellan den svenska och danska Öresundskusten. Denna betingas av Coriolis-kraften, som driver vatten med lägre specifik vikt mot den svenska kusten. Skillnaden i medelsalthalt mellan två närliggande lokaler på ömse sidor om Öresund, Ellekilde hage och Svinbådan, kan sålunda uppgå till ca 6 ⁰/₀₀ (HAGERMAN 1966).

Man finner även en mera långsiktig variation i salthalten. Om medelvärden beräknas för 3-årsperioder, finner man vid Svinbådan variationer på ca. 1 ⁰/₀₀ i ytvattnet och 4 ⁰/₀₀ på mer än 17 m djup. Vid Oskarsgrundet söder om Malmö är variationen vid ytan ca. 1 ⁰/₀₀ och vid bottnen 2 ⁰/₀₀. Vid Falsterborev är värdena naturligtvis lägre och ligger på ca. 0,75—1 ⁰/₀₀. Salthaltsmaxima har inträffat bl.a. 1950—52 och 1959—60.

Salthaltsförhållandena påverkar naturligtvis såväl fauna (NORDENBERG 1962) som flora. En organism kan överleva på en lokal endast om den kan anpassa sig till den dagliga variationen och överleva extremvärdena.

I norra Öresund finner man ca. 230 bentiska algarter, medan antalet vid Falsterbo uppgår till ca. 130, alltså ett bortfall av 100 arter på en sträcka av 100 km. Förutom att antalet arter reduceras sker även andra nedan omtalade förändringar av algfloran.

a. Ändrad morfologi. Algernas form ändras framför allt genom en minskning av såväl totalstorlek som cellstorlek. Som exempel kan nämnas *Delesseria sanguinea*: i norra Öresund, på 5—10 m djup, är arten i genomsnitt 10 cm lång, medan den under språngskiktet, d.v.s. på mer än 15 m djup, blir upp till 20 cm lång; söder om Malmö är längden endast ca. 2—3 cm. Ett annat exempel är *Callithamnion hookeri*, som vid Kullaberg blir 2—3 cm lång medan längden söder om Ven endast är några millimeter.

b. Ändrade fruktifikationsförhållanden. Hos många arter, främst rödalger, går den sexuella fasen i livscykeln förlorad i den nordligaste delen av Öresund eller i sydligaste delen av Kattegatt. Hos en del av dessa finner man även ett bortfall av tetrasporfasen; söder om linjen

Hornbeck—Domsten finns exempelvis endast helt sterila individer av *Callithamnion corymbosum.*

Flertalet rödalger saknar i Östersjön gamofytgeneration och förökar sig enbart med tetrasporer. Det är därför sannolikt att en störning av meiosen vid tetrasporbildningen har inträffat hos dessa arter.

Det är troligt att det i Öresund förekommer former, som i den norra delen av området har normal meios, medan de i södra delen av området saknar sådan. Frågan är då hur och vid vilken salthalt detta fenomen inträffar.

c. Ändrad vertikal utredning. Flera arter, som i Bohuslän är beståndsbildande i sublitoralzonens översta del, finner man i Öresund först i nedre delen av denna. Exempel på detta utgör *Trailliella intricata* och *Corallina officinalis.*

Sydgränserna för de olika arterna är naturligtvis ganska diffusa och svåra att kartlägga, då det sker en gradvis minskning i arternas frekvens samtidigt som det finns en tendens till ändrad vertikalutbredning mot djupare lokaler. Hos en del arter är sydgränserna förvånansvärt konstanta, medan de för flertalet alger naturligt fluktuerar mer eller mindre starkt under olika år. Man finner dock vissa gemensamma tendenser för algernas reaktion i sina marginalområden och kan urskilja fyra olika utbredningstyper:

1. Alger med markant sydgräns; ingen ändring i frekvens, morfologi, fruktifikationsförhållanden eller vertikal utbredning. Ett exempel på denna typ är *Ascophyllum nodosum,* som har sin sydgräns vid Mölle.

2. Alger med relativt markant sydgräns, minskad frekvens i marginalområdet, ingen ändring i morfologi, fruktifikationsförhållanden eller vertikalutbredning.

Exempel på denna grupp är bl.a. *Fucus spiralis*, som har sin sydgräns vid Kullaberg.

3. Alger med diffus och fluktuerande sydgräns; avtagande frekvens i marginalområdet, ingen ändring i morfologi, avtagande fertilitet, ändrad vertikalutbredning mot djupare lokaler. Som exempel kan väljas *Corallina officinalis* och *Dilsea edulis,* som har sin sydgräns vid linjen Hälsingborg—Helsingör.

4. Alger med diffus och fluktuerande sydgräns; minskad frekvens, ändrad morfologi (minskad storlek), sterilitet, ändrad vertikalutbredning (mot djupare lokaler). Som exempel kan nämnas *Callithamnion*-arter och *Antithamnion plumula* med sydgräns vid linjen Landskrona — Köpenhamn.

RECIPIENTFÖRHÅLLANDEN

Öresund är i dag recipient för drygt 1.5 miljoner människor och antalet väntas stiga till 2 miljoner inom en tioårsperiod.

Stora industriella avloppsutsläpp förekommer. I Landskrona släpper man t.ex. ut 650 ton $CaSO_4$ per dygn och liknande utsläpp sker även vid Hälsingborg. Vattendomstolen behandlar i dagarna en ansökan om ett värmekraftverk vid Barsebäck. Detta kommer fullt utbyggt att släppa ut 9000 m^3 kylvatten per minut med en temperatur, som överstiger recipientens med 8° C.

När man skall bedöma en eventuell påverkan av recipienten är det mycket viktigt att känna till de naturliga förhållandena i området så att man kan skilja på de förändringar i florans sammansättning, som betingas av salthaltsförhållanden och de som betingas av avloppsutsläppen.

Öresund har tidigare ansetts som ett relativt näringsfattigt vatten (STEMANN NIELSEN 1940). Som framgår av tabell nedan har P-PO_4-halten i vattnet stigit kraftigt sedan 1930-talet.

Höga fosfat- och nitratvärden är i och för sig inte farliga för en recipient av detta slag. Faran ligger i den sekundära förorening, som orsakas av en ökad algprodukiton. Genom denna bindes stora mängder fosfat till recipienten, då algerna i regel tar upp detta ämne för att täcka det aktuella behovet. Dessutom sker en i många fall avsevärd upplagring i dessa. Exempel på ökad produktion finner man bl.a. hos *Enteromorpha intestinalis*, som reagerar på »fosfatgödning» dels genom ökad storlekstillväxt, (1,5 m långa och 1—2 dm breda individer har iakttagits vid Malmö), dels genom tilltagande individrikedom. Det senare påverkar bl.a. balansen i de naturliga algsamhällena.

Tabell 1. Sammanställning över P-PO_4-halten (i µg/l) i vattnet under två tidsperioder med 34 års intervall.

(A summary of the P-PO_4-proportion (in µg/l) in the water during two periods with an interval of 34 years).

	1932—33	1967—68		1932—33	1967—68
Januari	0	28	Juli	0	3—8
Februari	5	67	Augusti	0	6
Mars	5	33	September	0	—
April	0	—	Oktober	5	—
Maj	0	—	November	0	—
Juni	0	68	December	10	22

Cladophora sp., *Ectocarpus* sp. och *Pylaiella* sp., har även iakttagits i massproduktion. Där dessa algmassor driver i land, kan bad omöjliggöras under längre eller kortare tid. Fytoplanktonproduktionen i Öresund (vid Helsingör) under mitten av 1930-talet, anges av STEEMANN NIELSEN (1944) till 120 g glykos/m^2. Undersökningar pågår för att bestämma den aktuella produktionen.

Genom att noga kartera utbredningen av litoralzonens alger visar det sig att bl.a. *Ulva lactuca, Blidingia minima* och *Scytosiphon lomentaria* saknas i Lommabukten, men förekommer både norr och söder om denna. *Spermathocnus paradoxus* har helt försvunnit från Öresund, men finns kvar i Kögebukt.

Ulva lactuca var mycket vanlig i Lommabukten under 1910- och 1920-talen. Arten bildade under denna tid mäktiga tångvallar längs stränderna (WEIBULL 1919). Detta tyder på någon form av giftverkan i vattnet. Preliminära undersökningar i Lommabukten visar att Cu-halten där varierar mellan 10 och 40 μg/l. Vid kontroll av det ingående vattnet vid avloppsreningsverket i Lund visade det sig att den sammanlagda Cu-mängden uppgick till ca. 4 kg/dygn (S. FLEICHER muntligt meddelande).

Odlingsförsök med *Ulva lactuca* visar att algen redan vid 5 μg Cu/l i näringslösningen får sin tillväxthastighet nedsatt med 50 % och att arten dör vid halter över 10 μg/l (KYLIN 1943). Man kan tänka sig att följande samband råder (se Fig. 1).

Vid utsläppspunkterna finner man höga fosfatvärden, men vissa arter har en produktion, som inte svarar mot dessa på grund av förekomst av gifter troligen i form av tunga metalljoner. När verkan av dessa avklingat ökar produktionen.

Genom avloppsutsläpp under språngskiktet kommer stora mängder organiska partiklar att fångas upp och inlagras i detta. De genomskinlighetsmätningar som gjorts, visar att transmissionen i horisontal led i språngskiktet minskar med ca. 75 % för blått ljus och 50 % för rött ljus jämfört med lagren över respektive under detta skikt. Detta måste innebära en kraftig reduktion av ljuset i vertikal led och även att kompensationsdjupet kommer att minska.

Genom att partiklarna senare sedimentera får sten och skalbottnar ett tunt täcke av sediment. Detta är särskilt märkbart på djup under 20 m där vattenomsättningen är långsammare; i Öresund ca. 30—45 dagar (ÖVK 1967). Förhållandet försvårar i hög grad återväxten av bentiska alger, då deras sporer inte kan gro på mjuka substrat.

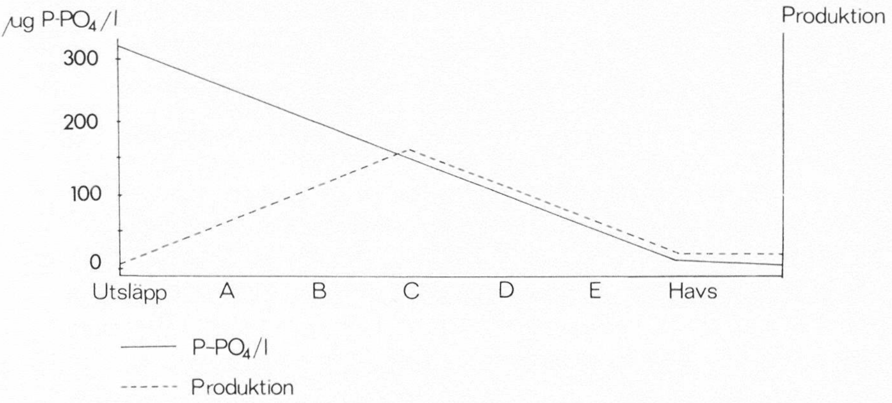

Fig. 1. Schmatisk framställning över det hypotetiska sambandet mellan fosfathalt (P-PO_4) i havsvatten och algproduktion i ett förorenat område. Avloppsutsläpp i origo. — A—E utgör godtyckligt valda provpunkter mellan utsläppspunkten (utsläpp) och opåverkat vatten (havs).

[The hypothetical relations between the phosphorus content of seawater and the primary production. Discharge in origo. — A—E is sampling points between the dischargeepoint ('utsläpp') and pure water ('havs')].

Organismer, som lever under suboptimala förhållanden, t.ex. vid gränsen för sitt utbredningsområde, är utsatta för ett betydligt hårdare miljötryck än inom sitt naturliga utbredningsområde. Små förändringar i miljön kan därför bli fatala, med svåröverskådliga konsekvenser som följd.

Öresundsområdet är i sig själv av mycket stort vetenskapligt värde genom att det utgör ett naturens eget experimentområde. Detta nödvändiggör en ytterst noggrann prövning och kontroll av utsläpp i alla former samt en kontinuerlig övervakning av de biologiska förloppen. Den senare sker lättast genom ett system av indikatororganismer. För detta krävs emellertid en intensiv forskning.

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Smärre meddelanden
(Brief Articles and Reports)

Viola pumila Chaix funnen i Skåne
(Viola pumila Chaix Discovered in Scania, South Sweden)

ABSTRACT. — *Viola pumila* CHAIX, not known from the Swedish mainland previously, is reported from a sea shore meadow in the parish of Eskilstorp, Scania, South Sweden. The species is also known from the Baltic Islands. Outside Scandinavia, the species is rather widespread in central and eastern Europe, not extending to northern Europe except for a few localities on the island of Ösel.

Viola pumila tillhör enligt HULTÉN (1950) en grupp osteuropeiska, kontinentala arter med anknytning till Skandinavien över Balticum. Den är ej sällsynt i centrala och östra Europa men förekommer endast lokalt i norra Europa, nämligen på Ösel och i Sverige, där den hittills varit känd från Öland och Gotland. Uppgifter i vissa floror, t.ex. HARTMAN (1870), att den skulle finnas i Rackeby vid Järlehus i Västergötland, avfärdas som varande oriktiga av SKÅRMAN i hans inventering av Kållandsö och angränsande områden (1927). Arten har ej återfunnits på den nämnda lokalen. Troligen har förväxling skett med *Viola stagnina* eller någon av dess hybrider.

I början av 1960-talet upptäckte jag på strandängarna i Eskilstorps socken ett fåtal blommande exemplar av *Viola pumila*. Under senare år har jag funnit ytterligare exemplar högre upp på stranden, inom ett område omfattande c:a 15×15 m. Biotopen utgöres av fuktig tuvmark, relativt hårdbetad, på vilken violen karakteristiskt växer högt uppe på tuvorna tillsammans med *Equisetum arvense, Briza media, Festuca ovina, F. rubra, Carex nigra, C. pilulifera, C. hostiana, C. panicea, Luzula campestris, Cerastium subtetrandrum, Ranunculus acris, Potentilla erecta, Myosotis discolor, Galium verum, Bellis perennis, Achillea millefolium* och *Taraxacum* sp. Tuvorna omges av *Agrostis stolonifera, Festuca rubra, Cardamine pratensis, Valeriana dioica* m.fl.

På Öland och Gotland är den för dvärgviolen vanligaste biotopen det gräsrika s.k. tuvalvaret med *Festuca ovina, Avena pratensis* och *Carex hostiana* samt på något fuktigare ställen *Sesleria caerulea* och *Molinia caerulea,* som karak-

Fig. 1. Utbredningen av *Viola pumila* CHAIX i Nordeuropa. Efter HULTÉN (1950) [The distribution of *Viola pumila* CHAIX in N. Europe. After HULTÉN (1950)].

tärsarter. Denna biotop är ganska lik den skånska. På Stora alvaret förekommer *Viola pumila* dessutom ibland på den torra busklavheden.

Viola pumila bildar sällan hybrider annat än med arter inom samma undersektion av släktet, subsect. *Rostratae* KUPFFER, till vilken även hör bl.a. *V. riviniana, V. reichenbachiana, V. canina* och *V. elatior*. Även dessa hybrider är emellertid sällsynta och i hög grad infertila (MURBECK 1943). Exemplaren i Eskilstorp har konstaterats vara fullt fertila. Kromosomtalet har bestämts till 2n=40, vilket är i enlighet med tidigare uppgifter för arten.

Till samma utbredningsgrupp som *Viola pumila* hör t.ex. *Gypsophila fastigiata* och *Carex tomentosa*. Speciellt den senares utbredning överensstämmer nästan exakt med dvärgviolens, då den förutom Öland och Gotland är funnen i SV Skåne (Limhamn, Vellinge, Hyllie). Det vore inte osannolikt att både den och *Viola pumila* skulle kunna finnas på fler lokaler i de fuktiga, kalkrika strandängsområdena mellan Malmö och Skanör.

Beläggexemplar av *Viola pumila* från Eskilstorp finns på Botaniska Museet, Lund. Dessutom finns ett par plantor i odling i Lunds Botaniska trädgård.

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KARIN PERSSON

Landskronatraktens adventiv- och ruderatflora. III (The Adventive and Ruderal Flora of Landskrona, South Sweden)

Anteckningar om Landskronatraktens flora VIII (Notes on the Flora of Landskrona VIII)

ABSTRACT. — In four separate sections (1—4) the adventive and ruderal flora of Landskrona, in the province of Scania, South Sweden, is discussed. The more interesting species are: *Cardaminopsis arenosa* (L.) HAYEK, *C. suecica* (FR.) HIIT., *Festuca arundinacea* SCHRAD. var. *aspera* (MUTEL) ASCHERS. & GRAEBN., *Corydalis solida* (L.) SW. s.lat., *Amelanchier alnifolia* NUTT., and *Inula britannica* L.

1. Växter från jordar gödslade med avfall från burfåglar (Plants from areas manured with offals from cagebirds)

Växterna i följande förteckning insamlades under eftersommaren och hösten 1966 på nyss röjda trädgårdskolonier inom S:t Olofs vång norr om lasarettet. Floran här överensstämde delvis med den på en liknande lokal vid Borstahusen (NILSSON 1964 a), ehuru åtskilliga nya arter tillkom. Nomenklaturen följer HYLANDER (1955), eller, för de växter, som ej finnes upptagna där, BLOM (1961). C. BLOM har bestämt mera kritiska och besvärliga arter.

Amaranthus chlorostachys WILLD., flera individ. — *Amaranthus lividus* (L.) THELL. var. *ascendens* (LOIS.) THELL., som föregående. — *Brassica juncea* (L.)

Czern., fåtalig. — *Bromus commutatus* Schrad., 3 individ. — *Anthemis altissima* L.; Spreng., 2 individ. — *Anthemis cotula* L., talrika individ. — *Cannabis sativa* L., 5 individ. — *Chenopodium album* L., storvuxen, senblommande form. — *Chenopodium opulifolium* Schrad., ca 10 individ. — *Chrysanthemum segetum* L., 1 individ. — *Digitaria sanguinalis* (L.) Scop., talrik. — *Echinochloa colona* (L.) Link, talrik. — *Echinochloa crus-galli* (L.) PB. var. *edulis* Hitchc. och var. *mitis* (Pursh) Peterm., båda talrika. — *Guizotia abyssinica* (L. fil) Cass. var. *sativa* (DC.) Oliver et Hiern, flera individ. — *Helianthus annuus* L., 3 individ. — *Hibiscus trionum* L., 1 individ. — *Linum usitatissimum* L., talrik. — *Lolium multiflorum* Lam. ssp. *italicum* Volk. med f. *submuticum* Mutel, talrika individ. — *Lolium multiflorum* Lam. ssp. *Gaudini* (Parl.) Sch. et K., flera individ. — *Malva neglecta* Wallr., 1 planta (utpräglat prostrat och mera mörkblommig än inhemska typer). — *Malva parviflora* L., 3 individ. — *Melilotus indicus* All., 1 individ. — *Melilotus officinalis* Lam.; Thuill., 2 individ. — *Panicum laevifolium* Hack., flera individ. — *Panicum miliaceum* L., flera individ. — *Papaver somniferum* L., några individ. — *Phalaris canariensis* L., talrik. — *Picris echioides* L., 1 individ. — *Plantago major* L. ssp. *intermedia* Lge var. *scopulorum* (Fr.) Hyl., talrik. — *Polygonum kitaibelianum* Sadl., 2 individ. — *Rapistrum rugosum* (L.) All. ssp. *orientale* (L.) R. et F., 1 individ. — *Rumex palustris* Sm., 3 individ. — *Setaria glauca* (L.) PB., flera individ. — *Setaria italica* (L.) PB. var. *breviseta* (Alef.) Hyl., talrik — *Setaria viridis* (L.) PB. var. *major* (Gaud.) Posp., flera individ. — *Sinapis alba* L. ssp. *eualba* Briq., flera individ. — *Sinapis arvensis* L. var. *schkuhriana* (Rchb.) Hagenb., 3 individ. — *Sisymbrium altissimum* L., 1 individ. — *Sporobulus* sp., flera mycket sent utvecklade individ, omöjliga att bestämma.

2. Gräsfröadventiver

(Adventive Plants From Grass Seeds)

Cardaminopsis arenosa (L.) Hayek och *C. suecica* (Fr) Hiit. har under senare år iakttagits på Weibullsholm och andra ställen i staden, såsom ogräs i gräsmattor besådda med frö av *Agrostis tenuis* Sibth. som odlats i Värmland.

Festuca arundinacea Schrad. var. *aspera* (Mutel) A. & G. Under beteckningen Backafall saluför firma W. Weibull, Landskrona, sedan några år tillbaka frö av en från ön Ven härstammande sydeuropeiska formserie av *F. arundinacea,* som nära överensstämmer med var. *aspera* (Mutel) A. & G. Gräset i fråga brukas framför allt på marker utsatta för stark förslitning men även som ett erosionsskyddande växttäckte på vägslänter och andra vägskärningar. Som ett insått, nyetablerat gräs förekommer därför denna typ av *F. arundinacea* på många håll i vårt land och så även i Landskrontrakten.

Fig. 1. Blomklasar av *Corydalis* från Weibullsholm. — A—B: *C. densiflora,* april 1968 (jämför Fig. 2 A, övre raden). — C—H: Övergångsformer från hybridpopulationer (jämför Fig. 2 A, de två nedre raderna). — I—M: Blomklasar med hela stödblad, *C. decipiens* - lika (jämför Fig. 2 B).

(Inflorescenses of *Corydalis* from Weibullsholm, Landskrona, the province of

Scania. — A—B: *C. densiflora*, April 1968 (cf. also Fig. 2 A, the upper row). — C—H: Intermediate forms from hybrid populations (cf. also Fig. 2 A, the two lower rows). — I—M: Inflorescences with entire bracts, similar to *C. decipiens* (cf. also Fig. 2 B).

Från nordisk *F. arundinacea* skiljer sig formserien främst genom en påfallande tidig utveckling (såväl vegetativ som floral), lösare byggda, till sist nästan mattbildande tuvor, lägre och spensligare, under vippan m.el.m. sträva strån, samt en ofta utpräglat kort och efter blomningen ibland nästan axlikt hopdragen vippa med påfallande korta vippgrenar. Hos den under namnet Backafall saluförda typen är emellertid den för typisk var. *aspera* karakteristiska strävheten under vippan mindre påtaglig och kan ofta saknas hos många plantor i en population (jfr Nilsson 1964 b), vari ges fylligare uppgifter om detta formkomplex).

Med detta har författaren velat fästa uppmärksamheten på en under senare år på många håll i vårt land insådd och spridd främmande typ av rörsvingel väl värd att särskiljas från indigena former av arten.

3. Corydalis solida (L.) Sw. s.lat. som förvildad i Landskrona

(Corydalis solida (L.) Sw. s.lat. in Landskrona, the Province of Skåne)

På Weibullsholm och andra ställen inom Landskronas gränser (t.ex. Karlslund, Strandgården) förekommer *Corydalis solida* förvildad, på Weibullsholm i oerhört vida och täta bestånd (jfr Nilsson 1963). Särskilt frapperar artens osedvanligt stora variation, en mångformighet, som träffar nära nog alla organ och egenskaper.

Vad populationerna på Weibullsholm beträffar kan mångformigheten direkt härledas från en på 1930-talet utförd plantering av tre ganska väl skilda typer, »arter», inköpta från den holländska firman van Tubergen, Haarlem, under beteckningarna *Corydalis solida, C. decipiens* och *C. densiflora.*

C. solida visade stor överensstämmelse med de typer man brukar förbinda med detta namn: medeltidig utveckling, ganska tät blomklase och relativt mörk blomfärg.

C. decipiens överensstämde i huvudsak med föregående i allt utom stödbladen, som var hela eller i klasens nedersta del djupare eller grundare oregelbundet tandade—grunt flikade.

C. densiflora avvek från ovan nämnda typer framför allt genom mera högvuxna örtstånd, tidigare utveckling och blomning samt längre och glesare blomklasar med djupare finflikiga stödblad och påfallande större och ljusare blommor.

De ursprungliga, i renbestånd tydligt skilda »arterna» har emellertid under årens lopp korsats fritt inbördes med den påföljden, att man numera sällan lyckas spåra plantor, som helt överensstämmer med ursprungsformerna *decipiens* och *densiflora.* I synnerhet förefaller former med de för *C. decipiens* karakteristiska hela stödbladen att ha blivit sällsynta i utpräglad form. Däremot är *C. densiflora* - lika typer vanligare.

Anmärkningsvärt är att vare sig Ryberg (1955 sid. 122) eller Boom (1950) — de enda tillgängliga arbeten, som omtalar *C. decipiens* — nämner något om de hela stödblad, som karakteriserar den under detta namn odlade »arten».

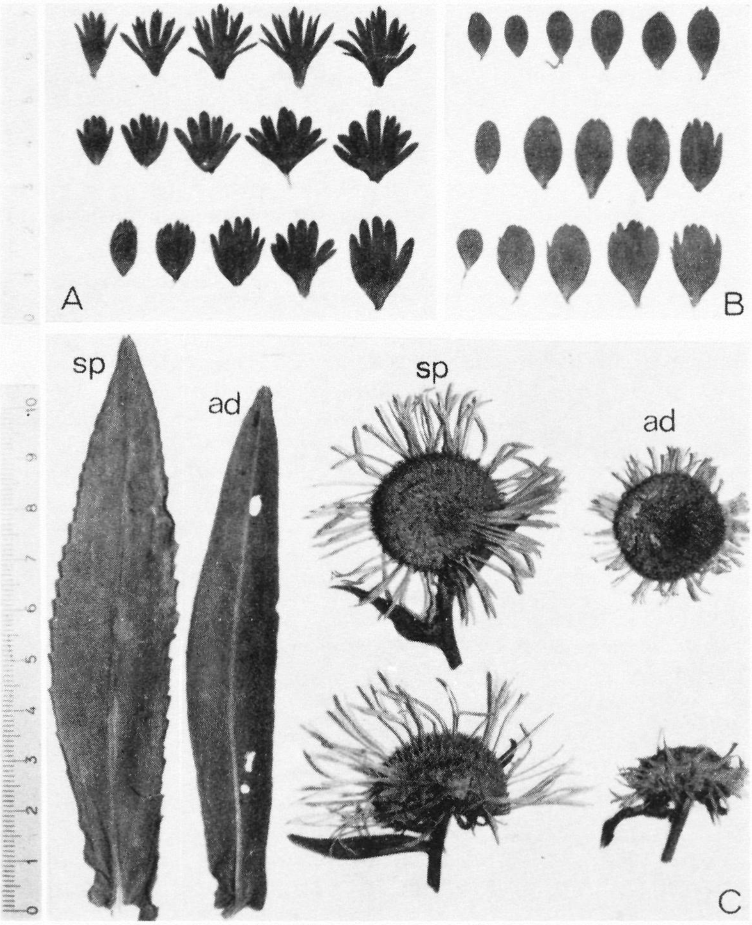

Fig. 2. A—B: Stödblad från 6 blomklasar av *Corydalis* från Weibullsholm, april 1968. — A: Övre raden *C. densiflora;* de två nedre raderna övergångsformer från hybridpopulationer. — B: *C. decipiens* - lika typer. — C: Blad och blomkorgar av *Inula britannica* L.; *sp,* spontan form från strandängarna söder om Klagshamn, Gässie, Skåne, 13 aug. 1966; *ad,* adventiv form från koloniträdgård i Landskrona, 20 aug. 1967.

(A—B: Bracts from 6 inflorescences of *Corydalis* from Weibullsholm, Landskrona, the province of Scania, April 1968. — A: The upper row *C. densiflora*; the two lower rows intermediate forms from hybrid populations. — B: Bracts similar to *C. decipiens.* — C: Leaves and inflorescences of *Inula britannica* L.; *sp,* a spontaneous form from the sea shores S. of Klagshamn, Gässie, the province of Scania, 13 August 1966; *ad,* en adventive form from an allotment garden in Landskrona, the province of Scania, 20 August 1967.)

Då en så markant egenskap knappast kan ha förbigåtts, förefaller det troligt, att en namnförväxling kan ha ägt rum hos den holländska firma, som levererade de nämnda *Corydalis*-formerna. Den »art», som salufördes under epitetet *decipiens*, är av allt att döma identisk med någon av de former med hela stödblad, som är kända och beskrivna som *C. solida* var. *integra* GODRON. Den under namnet *C. densiflora* erhållna typen överensstämmer däremot ganska väl med den hos HEGI (1958 sid. 59) givna diagnosen, särskilt beträffande de djupt mång- och smalflikiga stödbladen, vilka ofta är försedda med sekundärflikar.

Författaren har velat meddela dessa erfarenheter om en för mer än 30 år sedan företagen plantering av *Corydalis* ställd i relation till den mångformiga nutida population, som planteringen givit upphov till. Sannolikt kan liknande eller på annat sätt sammansatta populationer ha uppstått även på andra håll i vårt land. Under åren 1938—1948 importerades nämligen de nämnda »arterna» årligen från Holland och salufördes i Weibullsholms plantskolekataloger. Liknande mångformiga och svårtydda bestånd av *Corydalis* är för övrigt sedan länge kända från mellersta Sverige. LUNDMAN (1954 sid. 236) berättar t.ex. om sådana från Fredrikslund i Uppland och nämner därifrån även plantor med alldeles hela stödblad.

4. Diverse adventiver

(Some Adventive Plants)

Amelanchier alnifolia NUTT. I boken om Exercisfältet i Landskrona (NILSSON 1961 sid. 106) omtalas en meterhög, självspridd, förvildad *Amelanchier*-art, som jag inte lyckades identifiera, men som av andra botanister fördes till *A. spicata* (LAM.) C. KOCH. Vid en kritisk genomgång av det i Lunds Botaniska museum förvarade materialet av släktet fann emellertid Dr. F.-G. SCHROEDER, Göttingen, att ovan nämnda Landskrona-fynd i stället skall benämnas *A. alnifolia* NUTT., en art som tidigare inte lär ha blivit funnen förvildad i Europa (SCHROEDER in litt. 26/5 1966). På Exercisfältets nu röjda gränsvall mot norr förekom tillsammans med *Amelanchier*-busken ännu ett par sannolikt fågelspridda trädgårdsflyktingar nämligen *Sorbus decipiens* HEDL. (det. HEDLUND) och *Cotoneaster lucidus* SCHLECHT.

Inula britannica L. Som infört trädgårdsogräs har denna art nyligen rapporterats från Säby sn (NILSSON 1964 a). Ytterligare ett par lokaler för adventiv *I. britannica* har sedan dess upptäckts inom Landskrona stad, i båda fallen i trädgårdskolonier belägna inom de delar av Larvikområdet, som snart skall bebyggas. Samtliga dessa fynd tillhör en enhetlig, från inhemska former, som det förefaller, väl skild typ. Denna karakteriseras främst av en vid god utveckling rik förgrening, smala blad samt små korgar med påfallande korta strålblommor. Samma adventivtyp är känd från Råga Hörstad i Asmundtorp, där den under 1930-talet uppträdde som ogräs i en större odling av liljekonvaljer, till vilken utplanteringsmaterialet hade importerats från Tyskland (NILSSON 1952).

Vid granskning av *I. britannica* i Lunds Botaniska museum befanns följande bestämbara insamlingar helt eller nästan helt överensstämma med den från Landskronatrakten kända adventiva typen: Blekinge, Sölvesborg, på gräsmark i trädgård, sept. 1902, K. B. NORDSTRÖM. — Ytterligare en coll. utan närmare lokaluppgift föreligger från Sölvesborg, 17/8 1932, P. TUFVESSON. — Södermanland, Säfstaholms trädgård, 30/8 1879, C. KENTERMAN. — Västmanland, Västerås, hamnen, 24/7 1925, OSKAR OHLIN.

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ARVID NILSSON

Botanisk litteratur
(Botanical Literature)

Review of Palaeobotany and Palynology. An International Journal. Volume 1 published March 1967. Elsevier Publishing Company, Amsterdam. Present editor A. A. Manten, Utrecht. Subscription price US $ 15.00 per year, plus postage.

In 1967 a new scientific journal appeared, Review of Palaeobotany and Palynology.

The start of this journal was an excellent one. During the first year five different volumes were published. In these about 160 papers were presented, covering almost the entire field within which the two sciences of palaeobotany and palynology are meeting. These five volumes are special ones, each with its own title; 1. Palaeophytic and mesophytic palynology, 2. Cenophytic palynology, 3. Pollen and spore morphology, dispersal and classification, 4. Quaternary palynology and actuopalynology, and 5. Pre-quaternary palynology. The papers of these volumes were all contributions written in connection with the Second International Conference on Palynology in Utrecht 1966. The first issue of volume six published in 1968 is the first attempt of this journal to stand on its own feet.

In the first five volumes four issues were brought together into every volume. In the future the issues will be published separately. Eight issues are attempted to be published per year, that is two volumes. In 1968 the volumes 6 and 7 were published. Author and subject indexes of the first five volumes are found at the end of the fifth volume. Later volumes have their own indexes.

Authors are now invited to submit manuscripts. The manuscripts are considered by an "Editorial Board" before they become accepted for publication. Manuscripts can be sent to the Editor Office, Review of Palaeobotany and Palynology, P.O. Box 1345, Amsterdam C. Hints to authors planning to publish in this journal are given in the first issue of volume 6.

It is very welcome that this journal is open for research papers as long as their content remain within the scope of the journal. From the editor it is also said that there is no strict limitation for these papers concerning their length, subject and illustrative material. Thus it is possible to publish "long" monographic papers for which there are a few other journals open. However, it must be underlined, short papers will receive priority treatment.

In the journal there is an attempt to open each issue with an editorial in which general subjects will be discussed. Review articles will also be considered.

From the title of the journal it is evident that it tries to bridge over two scientific fields which seem to have very much in common. An important aim of the journal will be to widen the communication between the scientists in the various sub-disciplines of paleobotany and palynology and also to widen their mutual understanding. For this reason the contents of the journal will be kept rather wide. It is my whish and also my belief that the future of this journal will be as excellent as its start.

Örjan Nilsson

H. Mohr: Lehrbuch der Pflanzenphysiologie. — Springer-Verlag, Berlin-Heidelberg 1969. XVI, 408 S., 397 Abb. Gebunden DM 48,—.

Professor Hans Mohr, Biologisches Institut der Universität Freiburg, gibt mit dieser Arbeit eine Übersicht über das Gesamtgebiet der Pflanzenphysiologie. Laut der allgemeinen Einrichtung des Verfassers sind entwicklungsphysiologische Aspekte in den Vordergrund getreten. Ausgehend von „das Credo der Molekularbiologie“, die Ein Gen → ein Enzym-hypothese, werden Proteinsynthese, die Regulation der Wachstum durch Wirkstoffe, Differenzierung, Photomorphosen und die kritischen Faktoren der Blütenbildung eingehend diskutiert. Ein übersichtliches Kapitel ist der Bewegungsphysiologie gewidmet. Eine erstarrte reizphysiologische Terminologie ist hier wenn möglich durch eine „molekulare“ Begriffsbildung ersetzt.

Unter den allgemeinen metabolischen Aktivitäten ist die Photosynthese am ausführlichsten behandelt. Die modernen Struktur- und Funktionsdaten sind präsentiert. Eine Diskussion über den Quantenbedarf der Photosynthese scheint vielleicht im Zusammenhang mit den modernen Auffassungen ein wening veraltet und unnötig. Der Wasserzustand der Zelle ist sowohl in die klassische Terminologie als in moderne thermodynamische Begriffe geschildert.

Eine ernstliche Schwäche der Darstellung ist die unzureichende und zum Teil unklare Beschreibung von den Teilprozessen der Ionenaufnahme. Zum Beispiel wird aktive Ionenaufnahme ganz einfach wie eine Ionenanreichung entgegen einem Konzentrationsgefälle geschildert und die zusammengesetzte Natur des elektrochemischen Potentials ist ganz vernachlässigt.

Trotz der oben vorgebrachten Ausstellungen ist das Buch lesenswert und auch ungewöhnlich lesbar. Mit der bewussten Bestrebung auch komplizierte Zusammenhänge leicht verständlich zu machen ist es dem Verfasser gelungen, eine klare und leicht fassliche Darstellung zu leisten. Dazu trägt in hohem Grade die reichhaltige, einheitliche Illustrierung bei.

Sowohl Lehrer der elementaren Pflanzenphysiologie als Studenten mit grundlegenden Kentnisse in der Biologie und in der Biochemie können mit guten Ertrag das Buch studieren.

Sune Pettersson

BERGGREN, GRETA: Atlas of Seeds and small fruits of Northwest-European plant species with morphological descriptions. Part 2, Cyperaceae. — Edited and distributed by the Swedish Natural Science Research Council, Stockholm. Lund 1969. 68 pp. and 39 plates. Clothbound. Price including postage US $6:—, in Sweden Sw. kr. 30:—.

The Atlas of Seeds will present, by means of illustrations and descriptions, the seeds or small fruits of the entire phanerogamflora of Northwest-Europe (Sweden, Norway, Denmark, East Fennoscandia, and Iceland). It is planned to appear in four volumes. The present volume, Part 2, which is the first, comprises the family *Cyperaceae*. The remaining volumes are expected to be published within the course of a few years.

GRETA BERGGREN has obtained extensive experience in the analysis of seeds and other diaspores through her work at the Swedish Central Governmental Seed Testing Station. This atlas is excellent proof of her intensive studies and particular talent for the work. She has selected the material for her studies with the outmost care. Entirely ripe fruits have been taken from herbarium specimens. Several collections from different localities within the area of the species have been studied.

The illustrations in the book are of outstanding quality due to the skillful photographic labour of KARL-FREDRIK BERGGREN. However, the retouch has sometimes been a little too hard. The descriptions are quite accurate and give full information in a concise text. The organization of the descriptions makes it comfortable for the reader to compare the species and to find their particular characteristics.

The frontal cover of the book is given an attractive design. It is not much disturbed from the fact that one of the small figures has happened to be turned upside down.

The atlas is divided into two main parts, the descriptions and the illustrations. The illustration part comprises 39 wholepage plates with photos in black and white.

In the genus *Carex* both the perigynia and the nutlets are illustrated. The nutlets are shown in usually three different positions and in cross-section. The perigynia are also presented in different views. The illustrations are all reproduced in the same scale to facilitate the comparison of size relationship. The fruits are shown at about 12 times magnification. No scale is given in the figures but in plate 1 the natural size of the fruits is exhibited in a drawing. The different figures in the plates are numbered and the reader must consult a list to find the names of the illustrated species. Perhaps it might be possible in the future volumes to give the name of the species in direct connection with the illustration, which will spare the reader much search. The origin of the material used for the illustrations is marked out in the list of investigated collections.

The atlas comprises almost all species of *Cyperaceae* in northwestern Europe. Only a few rare *Carex* species are omitted, e.g. *C. pendula* and *C. strigosa*.

In the descriptive part (pp. 11—54) the different genera are introduced with a general account of the fruits. In *Carex* the greater sections are provided with similar accounts too. There is also an introducing key to the species of the genera and sections built on fruit characters. In *Carex* the keys are constructed chiefly on characters of the perigynia. Separate keys to the perigynia and the nutlets may be desirable in this genus Gecause of the fact that the perigynia often become destroyed, whereas the nutlets are more resistant and often found "fossilised" separate from the perigynia.

The nomenclature and taxonomy of the family follow Hylander 1955 and 1966. However, in the genus *Carex* some exceptions are found. Thus are, e.g., *C. hirta* and *C. lasiocarpa* removed from sect. *Paludosae* and placed in sect. *Hirtae,* probably due to the differences in the morphology of the perigynia. On the other hand, the sect. *Montanae* is left intact inspite of the very obvious differences between *C. montana* and the remaining species in nutlet characters. One sometimes misses a discussion of the many interesting results of this investigation. But this is outside the scope of the atlas.

The fruit descriptions are very detailed. In *Carex* the perigynia and the nutlets are given separate descriptions. Much consideration has been taken to the infraspecific variation, e.g., in size and shape. The shapes and colours of the fruits apply to charts at the end of the book. The descriptions terminate with the chromosome numbers.

The book is given a foreword by professor J. A. Nannfeldt, Uppsala.

This atlas gives exact identifications of the fruits in *Cyperaceae.* Such information is urgently needed in both pure and applied sciences. It has particular interest in agriculture and archaeology but also in pure taxonomy and for the knowledge of quaternary changes in our flora. One may speak of "seed analysis" in the same sense as "pollen analysis". The atlas will certainly be a reference in such work. The practical importance of the book can hardly be overestimated. It fills a gap felt for a long time.

Örjan Nilsson