Drawings of Scandinavian Plants 86–88

Chenopodium L.

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Sect. **Agathophyton** (MOQ.) HOOK. FIL.

Glabrous or somewhat farinaceous, perennial species. Flowers mostly 4—5-merous, with perianth lobes usually only united at base. Pistil with 2—3 long stigmas. Seeds exceeding the perianth, vertical except in some terminal flowers. Embryo annular to horseshoe-shaped.

Two species, *C. bonus-henricus* L., native to Europe and *C. californicum* S. WATS. to the U.S.A.

C. bonus-henricus has been widely cultivated in Europe and used as a vegetable before the introduction of spinach. The foliage and root have previously been used in the treatment of cutaneous and pulmonary diseases.

86. **Chenopodium bonus-henricus** L. 1753

Stout perennial, with a thick and woody root, usually 15—70 cm high, erect or ascending, often much-branched. The whole plant somewhat viscid and farinaceous. Stem angular. Leaves alternate, lower ones long-petiolate, triangular, hastate to subsagittate, up to 10 cm long, length about equal to breadth. Apex acuminate to acute, margins undulate, entire except for the prominent basal lobes. Upper leaves rhomboid, ovate or lanceolate. Inflorescence a terminal, elongated, rather dense, spikelike panicle, leafy and branched only in the lower parts. Terminal flowers in glomerules, 5-merous, perfect and lateral ones with 3- to 5-lobed perianth, pistillate or perfect with mostly 2—4 stamens. Perianth lobes united at base, rarely up to one half, lanceolate to ovate, not or scarcely keeled, membraneous in the outer parts, obtuse and usually fringed at the summit. Midvein indistinct. At maturity the perianth lobes only partly cover the seed. Pistil with 2—3 long, papillated stigmas. Seeds vertical, in some terminal flowers horizontal, ovoid, 1.5—2.0 mm in diameter, dark brown to black, with rounded margins, at maturity enclosed in the perianth. Pericarp thin and scarious. Testa lustrous, almost smooth. Radicula situated opposite the vestiges of the style, short and thick, apex attached to the seed. Embryo annular to horseshoe-shaped.

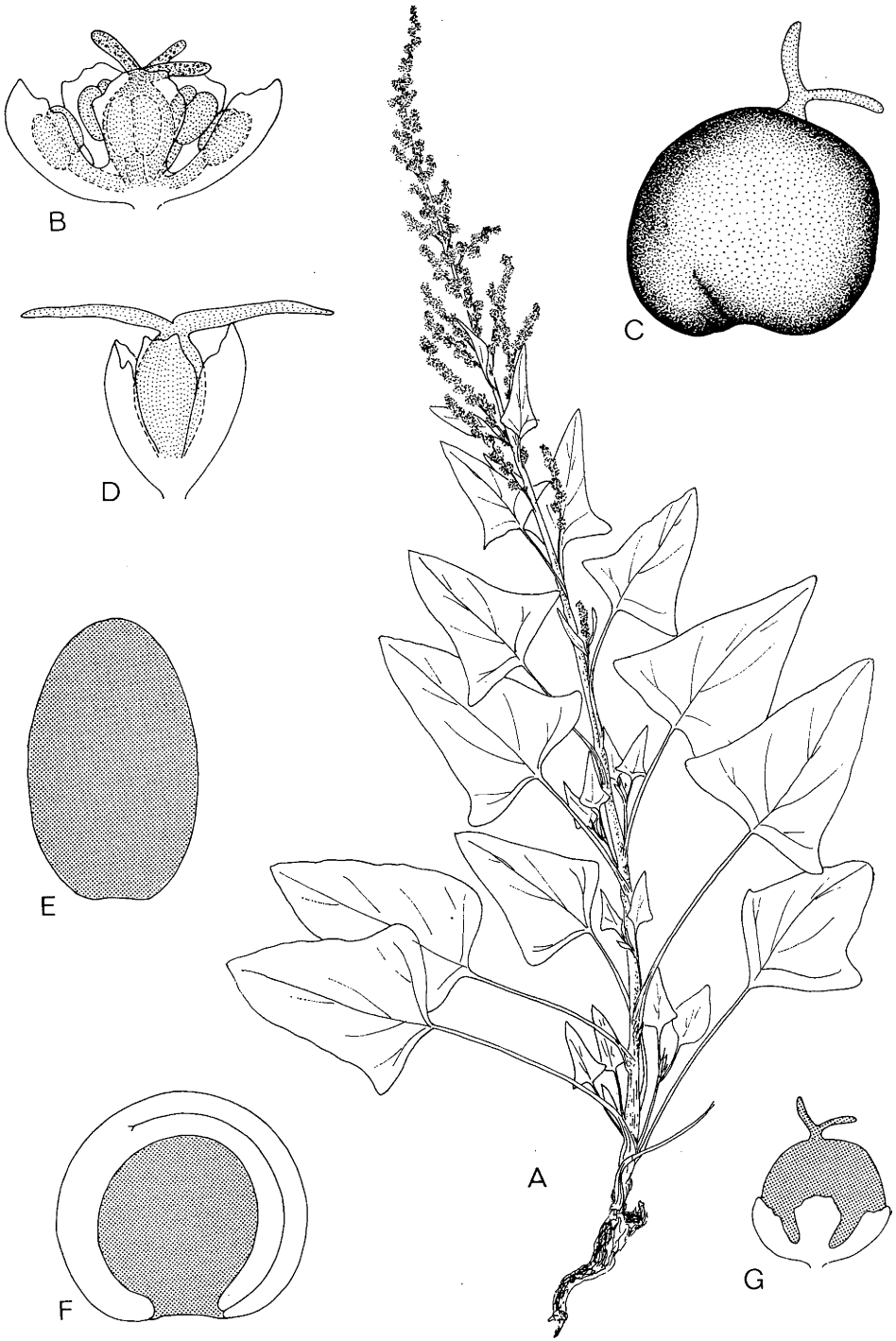
Flowering time: June to August.

Chromosome number: 2n=36.

Habitat and distribution: Introduced, often naturalized and well-established near buildings, especially in habitats rich in nitrogen, such as rich pastures, farmyards and road-sides.

C. bonus-henricus is distributed throughout most of Europe, except in the Iberian Peninsula, and in the European parts of U.S.S.R. Probably originating in the mountainous regions of Greece. In Scandinavia it is common in the southern parts, especially in Denmark and the Swedish provinces of Skåne to Småland and Öland and Gotland, northwards to

[1] ENGSTRAND is responsible for the drawings and GUSTAFSSON for the text.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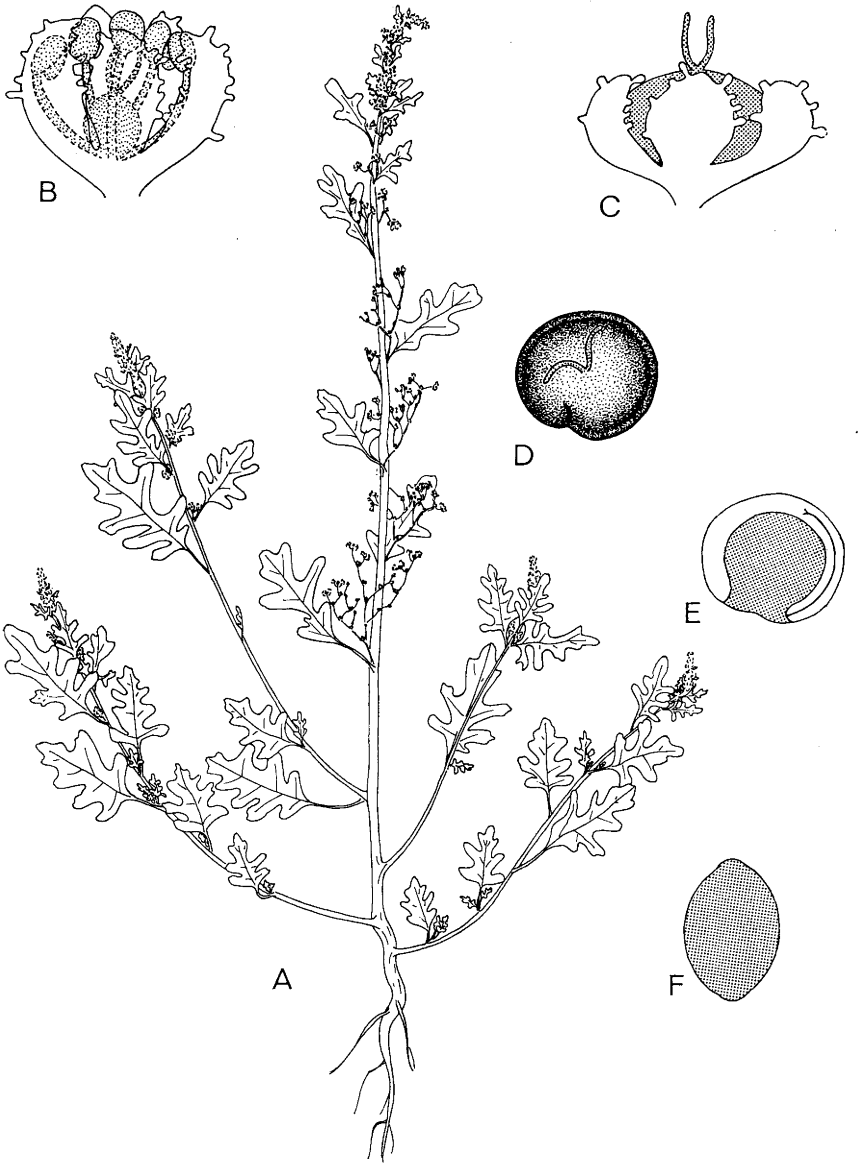

Fig. 87. *Chenopodium botrys* L. — A: Habit. — B: Hermaphrodite flower. — C: Fruit enclosed in the perianth. — D: Fruit with pericarp, showing the position of the radicula in relation to the vestiges of the style. — E: Section through a seed, showing the embryo. — F: Seed in transection. — A: ×0.5. — B—F: ×20.

Fig. 86. *Chenopodium bonus-henricus* L. — A: Habit. — B: Hermaphrodite flower. — C: Fruit with pericarp, showing the position of the radicula in relation to the vestiges of the style. — D: Pistillate flower. — E: Seed in transection. — F: Section through a seed, showing the embryo. — G: Fruit enclosed in the perianth. — A: ×0.5. — B—F: ×20. — G: ×10.

Gästrikland—Bohuslän. In Norway most records are from around Oslo and Bergen, and there are scattered localities in Finland.

Sect. **Botryoides** C. A. MEY.

Annual species, covered by amber-coloured, glandular hairs, rarely glabrous. Inflorescences composed of flowers in dichasia or monochasia, with 5-lobed perianth and lobes only united at base. Two stigmas. Seeds horizontal. Embryo horseshoe-shaped.

Sect. *Botryoides* comprises about seven species, distributed throughout most parts of the world. Owing to their aromatic smell and content of ethereal oils, they have been used in the treatment of asthma, migraine and gastric pains.

87. **Chenopodium botrys** L. 1753

Annual, up to 60 cm high, erect, branched, lower branches rather long and ascending. The whole plant somewhat viscid, covered with yellowish, sessile to shortly stalked, glandular hairs, which give rise to a sweet, aromatic smell. Stem round or somewhat angular. Foliage green to yellowish-green. Leaves alternate, the lower ones with a cuneate base, more or less petiolate, up to 7 cm long, but usually less, about 1.5 times as long as broad, in outline oblong to ovate, pinnatifid, with 4—6 lobes on each side, each lobe usually with a varying number of short, obtuse teeth. Veins often light and distinct. Upper leaves small, simpler, somewhat divided to entire. Inflorescences composed of small but distinct dichasial cymes, situated both in leaf-axils and terminally. The terminal inflorescence more or less leafy. Flowers perfect or pistillate, conspicuously glandular, perianth 5-lobed, lobes only united below, lanceolate to ovate, membraneous in the outer parts, rounded on the back, apex acute to acuminate. At maturity the perianth lobes exceed the seed. Stamens 3—5, not united at base. Pistil with two papillated stigmas. Seeds loosely enclosed in the perianth, mostly horizontal, ovoid, small, 0.5—1.0 mm in diameter, black, in transection with a groove, rounded or keeled by a narrow, elliptical ridge. Pericarp thin, whitish. Testa lustrous, more or less smooth. Radicula rather indistinct, short and thick, closely attached to the seed. Embryo horseshoe-shaped.

Flowering time: June to August.

Chromosome number: The chromosome number is not known for certain, both 2n=16 and 2n=18 having been reported (cf. LÖVE & LÖVE 1961 and FEDOROV 1969).

Habitat and distribution: In Scandinavia *C. botrys* occurs as a more or less occasional weed in habitats influenced by man. It is probably indigenous in the Mediterranean region, in the northern parts of Africa, and is also common in the southern and central parts of Asia, occurring eastwards to China. Introduced and more or less occasional in the central and northern parts of Europe and in North America. Most records from Scandinavia are old. In Denmark known from around Copenhagen (HANSEN & PEDERSEN 1968). In Sweden some records from the province of Skåne, scattered localities in most other provinces northwards to Dalarna. *C. botrys* is only known from two localities in Norway, Oslo and Kristiansand (JÖRGENSEN 1973).

Comments: Occasionally other aromatic species with yellowish glandular hairs occur in Scandinavia. *C. botrys* has been confused with *C. schraderianum* ROEM. & SCHULT., a closely related species belonging to the same subsection, *Botrys* (KOCH) AELLEN & ILJIN. They are best distinguished on the different features of the perianth. The perianth lobes of *C. botrys* are rounded on the back and have sessile to shortly stalked, glandular hairs, whereas the perianth lobes of *C. schraderianum* have prominent, dentate keels, and the glandular hairs are all sessile. It

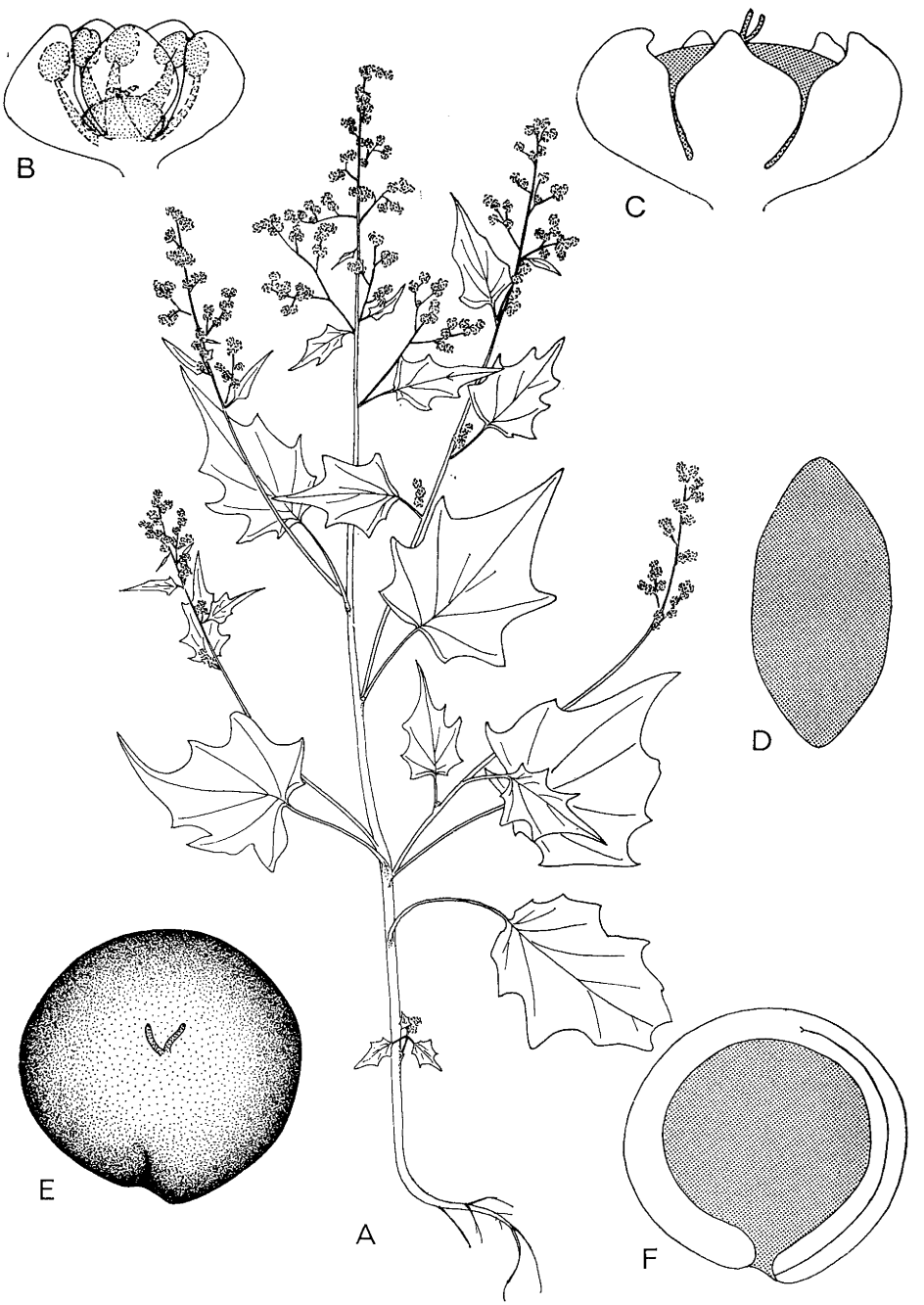

Fig. 88. *Chenopodium hybridum* L. — A: Habit. — B: Hermaphrodite flower. — C: Fruit enclosed in the perianth. — D: Seed in transection. — E: Fruit with pericarp, showing the position of the radicula in relation to the vestiges of the style. — F: Section through a seed, showing the embryo. — A: ×0.5. — B—F: ×20.

is known from a few localities in Denmark, Sweden and Norway.

In addition, two other glandular species have been recorded belonging to other sections. *C. multifidum* L. is distinguished from the other species by pinnatisect leaves and saccate, reticulate perianth (sect. *Roubieva* (MOQ.) VOLKENS). *C. ambrosioides* L. sensu lato is distinguished from *C. botrys* and *C. schraderianum* by having inflorescences composed of small, sessile clusters of flowers in the axils of leaves or bracts and not in dichasial cymes (sect. *Ambrina* BENTH. & HOOK.). For further information see AELLEN 1960.

Sect. **Chenopodium**

Annual, farinose, rarely glabrous species. Flowers normally 5-merous, perianth lobes united below or up to the middle, mostly keeled. Stigmas 2—3. Seeds mainly horizontal. Embryo annular.

Sect. *Chenopodium* comprises a large number of species distributed throughout most parts of the world. Many species have been used as vegetables, e.g. *C. album*, *C. murale* and *C. polyspermum*, or in the treatment of various kinds of diseases. According to ILJIN 1936, *C. album* has been used in the treatment of angina and gastric pains, *C. vulvaria* for rheumatism, colds and hysteria and *C. polyspermum* for headache.

88. **Chenopodium hybridum** L. 1753

Annual, 30—100 cm high, as young somewhat farinose, later glabrous, erect, simple or few-branched. Stem angular. Foliage green. Leaves alternate, thin, the lower ones usually long-petiolate, at base cordate to truncate, sometimes cuneate, up to 15 cm long, about 1.5 times as long as broad, in outline ovate to triangular ovate, sinuate, with 1—5 coarse acute teeth pointing forwards on each margin, apex acuminate to acute. Upper leaves rounded triangular to ovate, entire or with a few teeth on each margin. Inflorescences both axillary and terminally, lax, composed of flowers in dichasia or denser cymes, situated on rather long and divaricate branches. Flowers large, glabrous to somewhat farinose, perfect, with 5-lobed perianth. The lobes united below, ovate, obtuse, membraneous in the outer parts, mostly rather thick and dark-coloured in the middle and with a light, narrow midvein. Pistil with a short style, stigmas 2—3, papillate. Stamens 5, united at base. Seed horizontal, loosely enclosed and at maturity detached from the perianth, black, orbicular, large, 1.5—2.0 mm in diameter, depressed, in transection rounded or somewhat keeled. Pericarp closely attached to the seed, brownish, pitted. Testa pitted. Radicula rather insignificant, thick and short, closely attached to the seed. Embryo annular.

Flowering time: June to September.

Chromosome number: 2n=18.

Habitat and distribution: *C. hybridum* occurs in most waste places, such as farmyards, manure heaps, cultivated ground and road-sides.

Distributed in most parts of Europe, but rare in England and in the Mediterranean region, in North Africa and in Asia eastwards to China and Japan. In Scandinavia *C. hybridum* seems to have been more common in the past. In Denmark rather rare in the province of Jylland, more frequent in the other parts. In Sweden rather common in Skåne, on the islands of Öland and Gotland, and around Stockholm. Scattered localities northwards to Dalarna—Hälsingland. In Norway and Finland rare, most records from the southern parts.

Comments: In North America *C. hybridum* is replaced by a closely related, tetraploid species, *C. gigantospermum* AELLEN, which has occasionally been found introduced in Scandinavia. *C. hybridum* has distinctly pitted seeds and closely attached pericarp, while *C. gigantospermum* has almost smooth to indistinct, superficial pits and loosely attached pericarp. This taxon is probably only a geographical race of *C. hybridum*.

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A New Species of Aethionema from Skiros, Greece

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ABSTRACT

PHITOS, D. & SNOGERUP, S. 1973. A new species of Aethionema from Skiros, Greece. — Bot. Notiser 126: 142—145.

The species *Aethionema retsina* PHITOS & SNOGERUP is described. It is an obligate chasmophyte, endemic to the limestone cliffs of the islands of Skiros and Skiropoula. It is perennial, suffruticose, with fleshy leaves and a one-seeded silicula. The differences between it and *A. orbiculatum* (BOISS.) HAYEK are commented on. The chromosome number of the new species is 2n=24.

The genus *Aethionema* is represented in the Aegean by 3 or 4 previously known species. *A. saxatile* (L.) R. BR., under which we also include *A. graecum* BOISS. & SPR. and *A. creticum* BOISS. & HELDR., is fairly common throughout the area. It is distinguished from other species here discussed by its up to 8-seeded silicula, thin and moderately branched stem and small, predominantly obtuse leaves. *A. polygaloides* DC. was described from Chios, but there are also reports from Poros and Euboea. It is a short-stemmed, branched perennial, with alternate, narrow upper leaves and a 1-seeded, apically truncate silicula. *A. iberideum* (BOISS.) BOISS., which has been cited for Euboea, is characterized by a perennial, branched habit, numerous acute leaves, small flowers and a small, 4-seeded silicula. *A. orbiculatum* (BOISS.) HAYEK has been reported from the Athos Peninsula and the Taygetos Mts. It is a profusely branched perennial with opposite, obtuse leaves and a 1-seeded silicula which is basally cordate and apically obtuse to acute.

During our botanical investigation of the island of Skiros, we first discovered on the north-eastern limestone cliffs of Mt. Kochilas a new, very characteristic species of *Aethionema*. It has also since been found further south on Mt. Kochilas and on the small neighbouring island of Skiropoula. The actual cliffs and their vegetation were further commented on by GUSTAFSSON and SNOGERUP (1972).

Aethionema retsina PHITOS & SNOGERUP sp. nov. (Figs. 1, 2)

Typus: SNOGERUP & GUSTAFSSON 44328 (LD holotypus, PATRAS, W, G, K, BM).

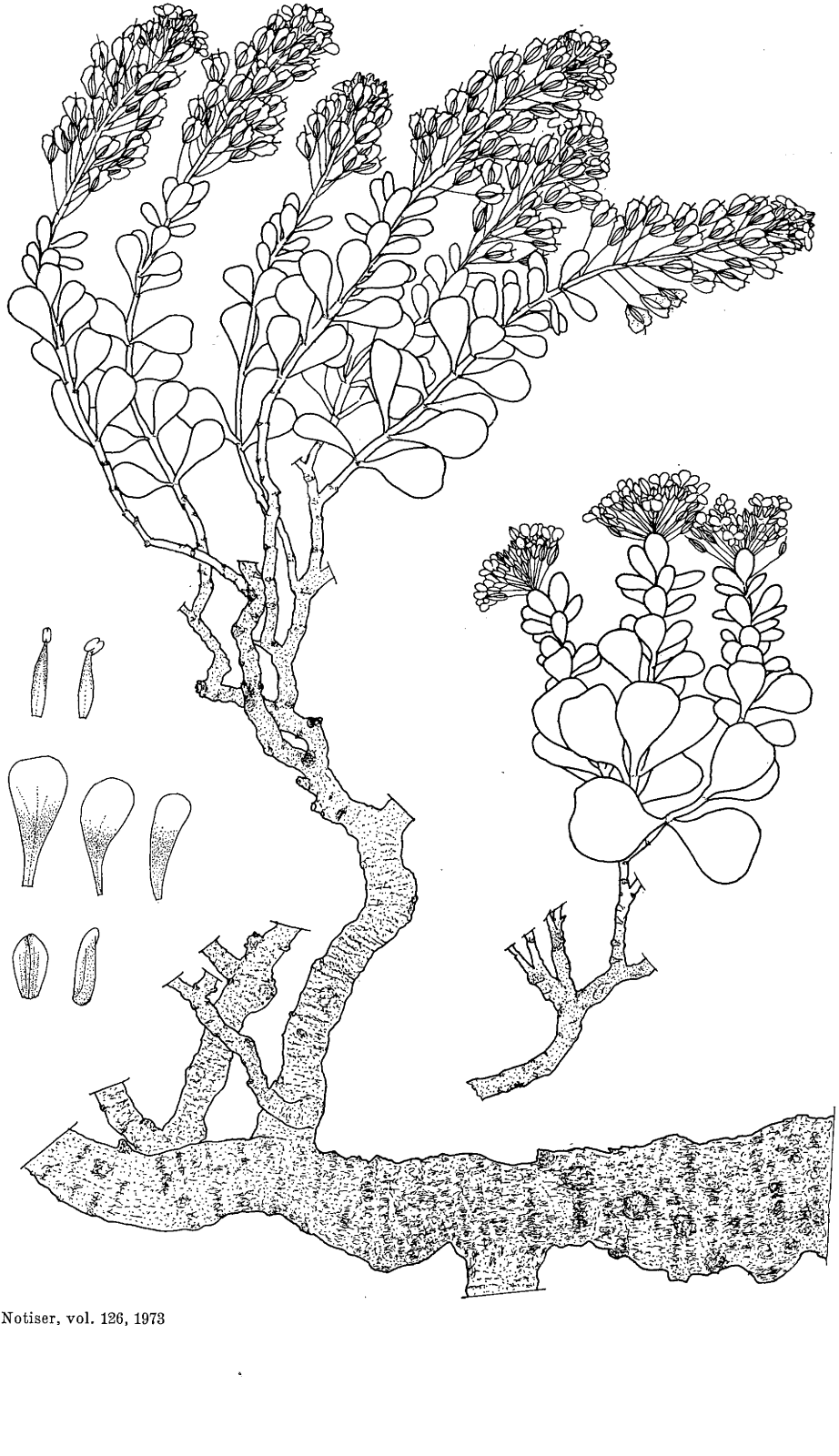
Planta perennis, suffruticosa, basi valde lignosa, caulibus floriferis pluribus, abbreviatis usque ad 10 cm longis, dense foliatis. Folia crassiuscula; inferiora subpetiolata, plerumque opposita, late spathulata, saepe retusa,

10—15 mm longa, 7—15 mm lata; superiora sessilia, obovata vel oblanceolata. Petala saepe inaequalia, superne albida, basi purpurea, unguis eorum majoribus 2.8—3.5 mm longis, lamina 2.2—2.5 mm longa et 2—2.5 mm lata. Siliculae obovatae, monospermae, 4—5 mm longae, 3.5—4 mm latae, stylo 1.0—1.3 mm longo, antice late alatae sensim undulatae, in dimidio superiore manifeste emarginatae.

Perennial, suffruticose, cushion-forming, up to 20 cm high and 40 cm wide, at least up to 15 years old. Stems branched from the base, up to 2 cm thick. Herbaceous flowering shoots formed in great numbers each year from the extremities of the woody twigs, 5—10 cm long, 1—2.5 mm thick, unbranched or with a few short, non-flowering basal branches, each carrying one or rarely two apical, simple inflorescences. *Leaves* all opposite or a few of the lowest ones sub-opposite, all quite entire, glaucous, somewhat crassulate, venation inconspicuous. Lower leaves 10—15 mm long, 7—15 mm broad, very broadly spathulate to obovate, obtuse to retuse. Upper leaves usually only 5—10 mm long, obovate to elliptic, obtuse. *Inflorescence* a simple, ebracteate, 25—50-flowered raceme, in early anthesis condensed, later elongating to a length of 25—40 mm. Pedicels erectopatent or in fruit rarely almost patent, slightly thickened apically, 4.5—5.5 mm long. *Sepals* 2.7—3.2 mm long, when young light yellowish-green in centre, the rest purplish, later ± entirely scarious. Outer sepals moderately saccate, boat-shaped, 1.2—1.5 mm broad, obovate, obtuse. Inner sepals flat, obovate, 1.5—1.7 mm broad, obtuse, slightly cucullate. *Petals* in most flowers to a varying extent unequal, in largest ones the claw 2.8—3.5 mm long, lamina 2.2—2.5 mm long and 2—2.5 mm broad, smaller ones often ± spathulate without a distinct claw. Petals white, when young usually with a purplish tinge, upper part of claw and basal part of lamina darker purplish. *Stamens* with 0.25—0.7 mm broad, flat, petaloid filaments. Filaments of the outer two stamens 2.0—2.3 mm long, those of the inner four stamens 2.7—3.2 mm long, basally white, apically purplish. Anthers 0.5—0.75 mm long and 0.4—0.5 mm broad, yellow. *Lateral nectaria* well developed, with up to 0.15 mm long, conical processes. Median nectaries lacking. *Pistil* at anthesis with an ovary 2—2.5 mm long, elliptic to obovate. Style 0.6—0.8 mm long, stigma capitate, c. 0.3 mm broad. *Fruit* a flat, angustisept silicula, septum early disappearing. Silicula 4—5 mm long, 3.5—4 mm broad, obovate to obcordate, apically notched, notch first narrow, then widening in ripe fruit. Alae basally 0.3—0.8 mm broad, apically 1.5—2.0 mm broad, apically widening greatly during later part of fruit ripening, in upper half emarginate and often slightly undulate. Style remaining and elongating to 1.0—1.3 mm. Midrib strong, sideribs few, irregular and inconspicuous. Normally only one seed developed per silicula. *Seed* lens-shaped, 2.1—2.2 mm long, 1.4—1.8 mm broad, and 0.6—0.7 mm thick, smooth, light brown. Radicle of embryo accumbent. *Chromosome number* 2n=24. Chromosomes all about equal in size, c. 1 μ long.

MATERIAL SEEN: Greece, Skiros: Limestone cliffs at Akr. Korakia and up to 1 km S of Akr. Korakia, 10—200 m, SNOGERUP & GUSTAFSSON 44328. Typus. (LD, Patras, W, G, K, BM). — 2.5—3 km N—NNW of the top of Mt. Kochilas, 100—200 m, cliffs of hard limestone, SNOGERUP & GUSTAFSSON 42665 (LD), SNOGERUP & v. BOTHMER 39066 (LD). — In declivibus boreali-orientalibus montis Kochilas, ca. 200 m. PHITOS 11846 (PATRAS). — The N side of Skiropoula, basal parts of cliffs facing the sea, hard limestone, 0—50 m. SNOGERUP & v. BOTHMER 39161 (LD), SNOGERUP & GUSTAFSSON 42543 (LD).

DISTRIBUTION AND HABITAT. *A. retsina* is only known from the cliffs of Mt. Kochilas facing E to NE and from the N precipices of the small island of Skiropoula only 7 km distant from Skiros. As the surrounding areas have now been rather well investigated it is probably a true local endemic. In all the three



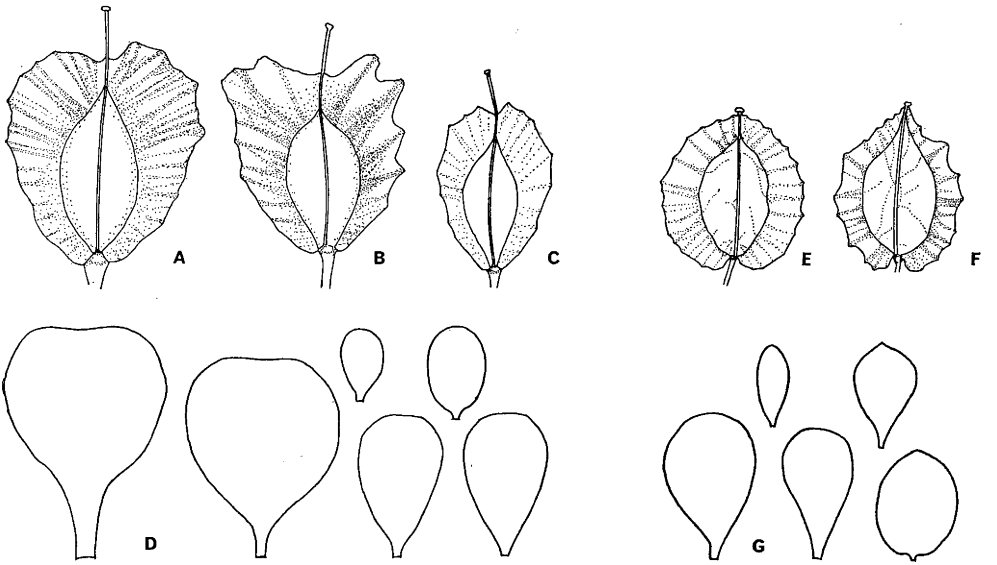


Fig. 2. A—D: *Aethionema retsina*, type collection. — A—B: Ripe siliculas, ×3. — C: Unripe silicula, ×3. — D: Leaves from different parts of the stem, ×1.5. — E—G: *Aethionema orbiculatum*, SINTENIS & BORNMÜLLER 886 (1891), Athos Peninsula. — E—F: Siliculas, ×3. — G: Leaves from different parts of the stem, ×1.5.

localities observed it occurs on the open surfaces of almost vertical limestone cliffs, growing in small crevices with very little or no soil. It has only been observed at altitudes of between 10 and 200 m above sea level, and not more than 0.5 km from the sea. Thus it belongs to the element of maritime limestone cliff plants which contains many taxonomically isolated and often locally endemic species in the Aegean.

TAXONOMIC RELATIONSHIP. *A. retsina* is no doubt most closely related to *A. orbiculatum* (BOISS.) HAYEK of the Athos Peninsula and the Taygetos Mountains, which is also a suffruticose perennial chasmophyte with opposite and slightly crassulate leaves and a one-seeded silicula. It is, however, distinguished from that species by its more erect, suffruticose habit as well as by the size and form of its leaves. *A. orbiculatum* has shorter, weaker, decumbent to pendular branches with smaller and narrower leaves. The siliculas of *A. orbiculatum* have a cordate base and an obtuse to acute apex and a very short stigma, and are thus very different from those of *A. retsina* (Fig. 2). The chasmophytic plants referred to *A. polygaloides* DC. also belong to the group with a one-seeded silicula, but are very different e.g. in leaf arrangement.

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Fig. 1. *Aethionema retsina*. Part of fruiting specimen of the type collection, Skiros, and flowering branch of SNOGERUP & GUSTAFSSON 42543, Skiropoula, ×0.9. Stamens, petals and sepals of the type collection, ×3.5. Drawing S. SNOGERUP.

Generic Delimitation of Bunium, Conopodium and Geocaryum (Umbelliferae)

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ABSTRACT

ENGSTRAND, L.: Generic delimitation of Bunium, Conopodium and Geocaryum (Umbelliferae). — Bot. Notiser 126: 146—154.

The genera *Bunium* L., *Conopodium* KOCH and *Geocaryum* COSSON are closely related and morphologically very similar. Formal definitions based on fruit characters are given for the genera. Based on these the combination *Conopodium glaberrimum* (DESF.) ENGSTR. is made, and *Hellenocarum* WOLFF is regarded as a distinct genus. The correct name of *Huetia* BOISS. (*Biasolettia* KOCH, *Freyera* REICHENB.) is found to be *Geocaryum* COSSON. A guide to the generic concepts of some previous authors is presented.

INTRODUCTION

The correct name of *Huetia* BOISS. has been found to be *Geocaryum* COSSON. In connection with a revision of the genus *Geocaryum* it has proved to be necessary to circumscribe the three genera *Geocaryum, Bunium* and *Conopodium*. These are all distinct genera but the morphological differences are small, which has resulted in a number of erroneous determinations especially where the areas of distribution overlap. New species have sometimes been referred to the wrong genera.

DRUDE (1898) placed *Geocaryum* (*Biasolettia*) in the tribe Scandicineae and *Bunium* and *Conopodium* in the tribe Ammineae. In a system of European Umbelliferae, CALESTANI (1905) suggested the tribe Bunieae including the latter group and *Diaphycarpus* (=*Bunium pachypodium*). This tribe was defined by "embryo monocotyleus".

CALESTANI's suggestion is considered to be the best, not only because the genera are pseudomonocotyledonous but also because of other similarities.

In connection with the circumscription of these genera their relations to some other genera and species must be considered. *Carum multiflorum* SIBTH. & SM. is pseudomonocotyledonous but the root is not tuberous. This species should be referred to a separate genus, *Hellenocarum* WOLFF. *Balansaea glaberrima* (DESF.) LANGE shows all the characteristics of *Conopodium* and should be transferred to this genus.

MATERIAL

European and NW African material from the following Herbaria has been used (abbreviations according to LANJOUW & STAFLEU 1964): BM, COI, E, FI, G, K, LD, LISU, LY, MA, P, S, UPS, W, WU. In addition, most form-series of *Geocaryum* have been studied in cultivation.

THE PROBLEM OF GENERIC CONCEPTS IN UMBELLIFERAE

The best existing systematic division of Umbelliferae is still DRUDE's (1898). As generic characteristics, different structures of the fruits are used almost entirely. However it has become evident that many genera, and also tribes, are highly artificial. In the last few years many efforts have been made to find better characteristics for delimitation of genera in the Umbelliferae. CERCEAU-LARRIVAL (1962) has demonstrated that structure and shape of pollen grains and cotyledons are valuable. GUYOT (1966) has classified the types of stomata and their relations in the family. Many authors have examined different chemical components in order to arrive at a better understanding of the relationships within the family (for a survey see HEYWOOD 1971).

All these facts have led to a much better understanding of the systematics of the family but in only a few cases can they be used as characteristics of genera.

The vegetative parts and the flowers of the umbelliferous plants are in general very uniform, at least in the subfamily Apioideae. Until now, cytological data have given little support to the problem. Within Apioideae c. 60 % of the species examined have 2n=22 (MOORE 1971). So far only the fruits show sufficient differentiation for generic delimitation and definition. The fruit characters must however be considered together with all other available data.

SIMILARITIES

There are three main reasons for grouping *Geocaryum, Bunium* and *Conopodium* together:

(1) Pseudomonocotyledonous embryo. In the generic description in Flora Europaea BALL states that *Bunium* has one cotyledon and *Conopodium* two; nothing is said about *Geocaryum*. However, the following taxa have been demonstrated to germinate with one cotyledon (cf. WEISSE 1930, HACCIUS 1952): *Bunium alpinum* ssp. *petraeum, B. alpinum* ssp. *montanum, B. bulbocastanum, B. pachypodium, Conopodium bunioides, C. capillifolium, C. bourgaei, C. majus, C. glaberrimum, Huetia cynapioides* ssp. *cynapioides, H. cynapioides* ssp. *macrocarpa* (nomenclature, where possible, according to Flora Europaea). In addition, the author has observed that all form-series of *Geocaryum* studied are pseudomonocotyledonous.

Dr CERCEAU, Laboratoire de Palynologie, Paris (personal communication) has confirmed that *Conopodium* is pseudomonocotyledonous.

Pseudomonocotyledonous taxa have also been found in the tribe Smyrnieae, e.g. *Scaligeria* and *Erigenia* (WEISSE, HACCIUS loc. cit.) but these differ in other respects such as shape of cotyledons and the fruits.

(2) Globose tuber. Usually the cotyledon is the only assimilating part of the plant during the first year. The plant survives the winter by means of a subterranean, globose tuber. In spring a leaf rosette is formed with part of the petioles underground. In *Geocaryum* the tuber has proved to live at least 11 years under greenhouse conditions.

(3) Other morphological similarities. The vegetative parts of plants in this group are very similar. It has not been possible to find any good character on which to distinguish them in the field or in herbarium material. All distinct differences are found in the fruits (see below).

The three genera are mainly montane. They have a similar pattern or differentiation, characterized by taxa with small areas of distribution. There are some exceptions, however, such as *Bunium bulbocastanum* and *Conopodium majus*. Extensive local and regional differentiation has made the taxonomy very confused.

Table 1. Some characters in *Bunium, Conopodium* and *Geocaryum.*

Character	*Bunium*	*Conopodium*	*Geocaryum*
Fruit	ovate—ellipsoid—oblong. [Exc. *B. ferulaceum, pachypodium*]	ovate—ellipsoid—lanceolate	narrow—linear oblong
Stylopodium	flat [Exc. *B. pachypodium*]	conical or flat	± flat, forming a "collar"
Angle between styles	180° [Exc. *B. pachypodium*]	0°—45° [Exc. *C. bunioides, thalictrifolia*]	0°—180°
Jugae	prominent, rounded, collenchyma stout	not prominent, rounded, collenchyma weak	prominent, sharp, collenchyma stout
Vittae/interval	1 or 3(4), conspicuous outside	1—4, conspicuous outside	0 or 1, not conspicuous outside
Endosperm	orthospermous	campylospermous	orto—campylospermous
Fruit surface	± smooth	± smooth	with small cones
Colour of fruit	brown—red-brown	brown—red-brown	brown-black—black
Bracts	present	(present or) lacking	lacking
Bractlets	present	sometimes lacking	present
Colour of leaf	green—blue-green	green	green
Chromosome number	20, 22	22	10, 18, 20, sometimes with B-chromosomes
Distribution	Mediterranean region, central Europe, SW Asia	Western Mediterranean region, W Europe	Central and eastern Mediterranean region

COMPARISON OF THE GENERA

A list of characters is given in Table 1. Most of them will be further discussed below.

SHAPE AND COLOUR OF FRUIT. The fruit of *Geocaryum* is linear-oblong, somewhat narrowed in the upper part; the ridges are sharp, and the colour blackish. In *Bunium* and *Conopodium* the ridges are rounded, the colour is brownish; more often the fruits are bi-coloured as the jugae are a lighter brown than the vittae (Fig. 1).

FRUIT SURFACE. The cuticula of the *Geocaryum* fruit is covered by minute cones which are visible as dots at a magnification of 10 diameters. The surface of *Bunium* and *Conopodium* fruits is almost smooth (Fig. 2).

STYLE AND STYLOPODIUM. The conical stylopodium of *Conopodium* is restricted to subgenus '*Eu-conopodium*' (cf. DRUDE 1898 p. 194). In ripe fruits the stylopodium tapers gradually into the styles which are more or less erect. In subgenus *Butinia* the stylopodium is almost flat and the two styles recurved to form an angle of 180°. However, the stylopodium still tapers into the styles. Most *Bunium* species also have styles which are recurved, but they seem to arise abruptly from the flat stylopodium. An exception is *B. pachypodium* where the stylopodium is rounded cylindric and the styles erect. In most forms of *Geocaryum* the central part of the stylopodium sinks during maturity and the peripheral part forms a "collar". The angle between the styles varies from 0° to 180° (Fig. 1).

ENDOSPERM. The endosperm of *Conopodium* is typically campylospermous, while that of *Bunium* is typically orthospermous. In *Geocaryum* the endosperm is usually concave, but never as deeply so as in *Conopodium* (Fig. 1).

VEGETATIVE PARTS. As already mentioned, differences in the vegetative parts of the plants are small and difficult to

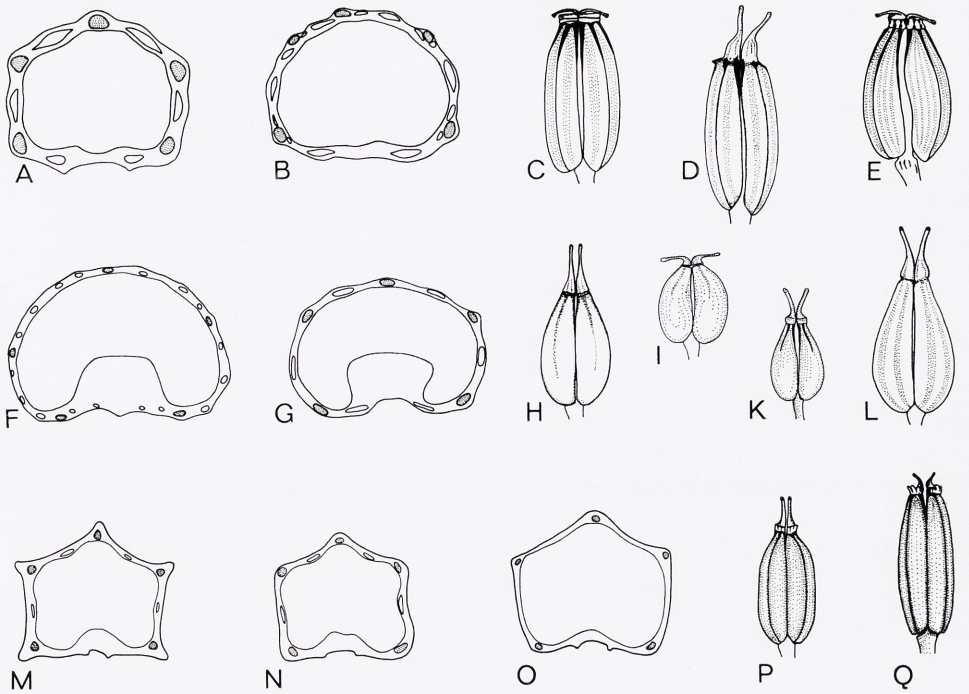

Fig. 1. Transverse sections (×20) and lateral views (×4) of mericarps and fruits. — A: *Bunium ferulaceum*. — B: *B. alpinum* ssp. *montanum*. — C: *B. ferulaceum*. — D: *B. pachypodium*. — E: *B. alpinum* ssp. *alpinum*. — F: *Conopodium bunioides*. — G: *C. glaberrimum*. — H: *C. majus*. — I: *C. bunioides*. — K: *C. bourgaei*. — L: *C. glaberrimum*. — M—Q: *Geocaryum species*.

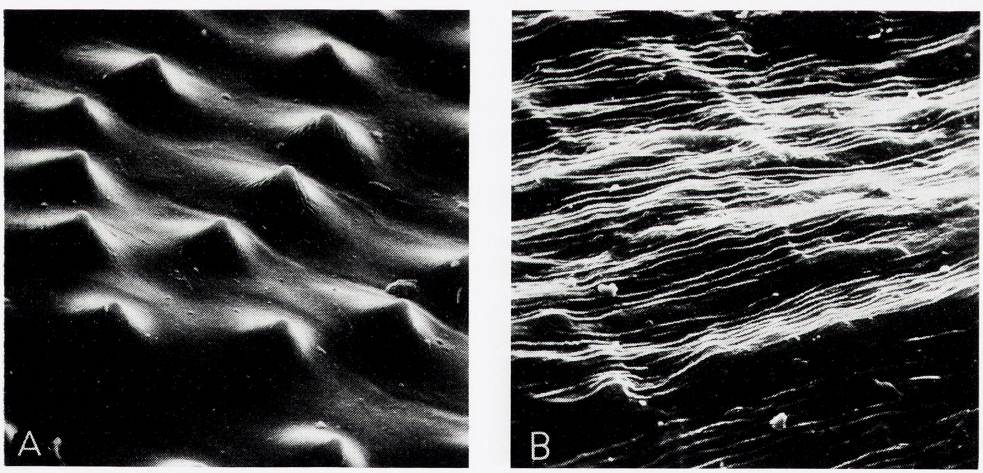

Fig. 2. View of fruit surface, ×650. — A: *Geocaryum*. — B: *Bunium*.

Table 2. Known chromosome numbers in *Conopodium, Bunium* and *Geocaryum.*

Taxon	2n	Reference or source of material
Conopodium capillifolium	22	GARDÉ & MALHEIROS-GARDÉ 1949
C. glaberrimum	22	Morocco, Berkane region, 850 m sm DAHLGREN et al.
Bunium bulbocastanum	22	SCHULZ-GAEBEL 1930
B. alpinum var. *nivale*	22	CAUWET 1967
B. alpinum ssp. *corydalifolium*	22	CONTANDRIOPOULOS 1962
B. alpinum ssp. *bulbocastanum*	22	CONTANDRIOPOULOS 1962
B. alpinum ssp. *montanum* ...	20	Yugoslavia, Cetinje, 950 m alt. ENGSTRAND
B. ferulaceum	20	Greece, Amorgos, M. GUSTAFSSON
Geocaryum	10, 18, 20	to be published in detail later

define. The leaves are 2—3-pinnate. The lobes are usually lanceolate to linear-filiform, gradually changing from the basal to the uppermost ones. Especially in *Conopodium* there are single species with broader leaf-lobes. In the area of distribution of *Geocaryum, Bunium* can be distinguished from it by having one or more bracts.

THE FLOWER. With some experience it is possible to distinguish living plants of *Bunium* from *Geocaryum* and *Conopodium* on the flowers only. The outer petal is only slightly larger than the others. The incisions between the petals are regular throughout which makes the flowers, as well as the whole inflorescence, look very regular and flat. In *Geocaryum* and *Conopodium* the outer petals of the umbel are clearly larger than the other, often also broader and overlapping the lateral ones. The umbels give an impression of umbrageousness.

CHROMOSOME NUMBER (see Table 2). As already mentioned c. 60 % of the species of Apioideae examined have the chromosome number 2n=22. The chromosomes are too small to encourage any detailed cytological studies. At the present time it seems pointless to draw any conclusions from the chromosome numbers in the group studied.

DISTRIBUTION

Geocaryum. Western and southern Turkey, The Aegean Islands, Crete, the Balkan Peninsula, central and southern Italy, Sicily.

Bunium. North-western Africa, south and central Europe, south-western and central Asia.

Bunium bulbocastanum has been cultivated for its edible tubers and consequently it is difficult to define the spontaneous area of distribution especially in central Europe.

Conopodium. North-western Africa, the Iberian Peninsula, Corsica, France, the British Isles, Norway, northern Italy.

Records from Greece should be referred to *Geocaryum.* There seems to be at least five collections from Sicily (Ficuzza), distributed in European Herbaria under the names of *Bulbocastanum capillifolium, Bunium capillifolium* or *Myrrhis capillifolia.* These specimens have been referred to *Conopodium* (cf. p. 151) by previous authors, but belong to *Geocaryum.*

Records of *Conopodium majus* from Sicily should probably be referred to a *Bunium* species which has been distributed by HUET DU PAVILLON as *Bulbocastanum denudatum* GUSS. var. *siculum* GUSS. It is very doubtful if *Conopodium* occurs in southern Italy. Not a single collection in the material studied belongs to this genus. PARLATORE (1889) lists several localities for *Conopodium denudatum* (=*C. majus*), but all material studied is definitely *Geocaryum* or *Bunium.*

Species from SW Asia, formerly referred to *Conopodium* (cf. DRUDE 1898), are now treated under several different genera (for details see Flora SSSR 16).

GENERIC CHARACTERS OF BUNIUM, CONOPODIUM AND GEOCARYUM

From what has been said above it is evident that vegetative characters are of little use for generic delimitation in this case. For a reliable determination the fruits must be studied. For formal definition the following key is suggested:

1 Fruit surface with small cones, ridges sharp ..... *Geocaryum*
Fruit surface without small cones, ridges rounded 2
2 Campylospermous ..... *Conopodium*
Orthospermous ..... *Bunium*

Geocaryum COSSON

The nomenclatural history of the genus *Geocaryum* is very confused. In 1827 GUSSONE described *Myrrhis capillifolia* from Sicily. This plant has been regarded as conspecific with certain Iberian material of *Conopodium* and has generally been treated as *Conopodium capillifolium* (GUSS.) BOISS. It has not been possible for the author to see GUSSONE's original material, but later GUSSONE collected more material from *locus classicus* (1831, in G) which is also named *Myrrhis capillifolia.* Besides this there are at least four other collections from the same locality. All this material belongs to the genus *Huetia* BOISS. (*Geocaryum*). When COSSON 1851 described *Geocaryum* with the single species *G. capillifolium* he cited *Myrrhis capillifolia* as the basionym. It is evident that *Geocaryum* should be typified with GUSSONE's material from Sicily. The oldest name for *Geocaryum* is *Biasolettia* KOCH (1836). This name had already been used for a genus in Hernandiaceae (PRESL 1835). This fact caused REICHENBACH (1837) to propose the name *Freyera.* Unfortunately *Freyera* must be regarded as an orthographic variant of *Freyeria* SCOPOLI (1777) in Oleaceae and is thus also illegitimate. *Huetia* BOISSIER was described in 1856 and was accepted for the whole genus by BALL (1968). However, *Geocaryum* is five years older than *Huetia* and should be used for the genus.

The species *Conopodium capillifolium* (GUSS.) BOISS. in the sense of BALL in Flora Europaea is also typified with the Sicilian material. The Iberian material is true *Conopodium* and must be given another name. The oldest synonym mentioned by BALL is *C. subcarneum* (BOISS. & REUT.) BOISS. However, even the Iberian material is complex and in need of revision.

Geocaryum as circumscribed here forms a distinct genus well separated from others. It is fairly homogeneous and there is no need for subdivision into subgenera or sections.

Bunium L.

Using the definition above *Bunium* can be readily separated from other genera. Material outside Europe and NW Africa has been studied only extensively by the author. However, it is clear that the Asiatic species will not contribute any further information about the generic circumscription. *Bunium* is more heterogeneous than *Geocaryum. B. pachypodium* differs in many respects from the general pattern (see Table 1). DRUDE (1898) has two sections based on the number of vittae per interval (Table 3). Further study may show that a subdivision of the genus is necessary.

BUNIUM VERSUS CARUM AND HELLENOCARUM

In the nineteenth century *Bunium* was most commonly defined as having three vittae between the ridges, and *Carum* as having one. According to this definition only the *Bunium alpinum* group would belong to *Bunium. B. bulbocastanum, B. ferulaceum* and *B. pachypodium* would have to be placed under *Carum* (Table 3).

BOISSIER (1872) did not use the number of vittae as an important character. Under *Carum* he made a section *Bunium* defined by "radix subglobosa".

Table 3. Treatments and definitions by some previous authors in the complex of *Bunium, Carum* and *Hellenocarum,* and the treatment in the present paper.

Author	Diagnostic characters	*Bunium* 1-vitt.	*Bunium* 3-vitt.	*multiflorum*
DE CANDOLLE 1830	*Carum* 1-vitt. *Bunium* 2—3-vitt.	*Carum*	*Bunium*	*Ligusticum*
KOCH 1843	*Carum* 1-vitt. *Bunium* 3-vitt.	*Carum*	*Bunium*	
BENTHAM & HOOKER 1862—1867	*Carum* 1-vitt. *Carum* sect. *Bunium* — Herbae rhizomate perenni tubiformi subterraneo, caulibus annuis.	*Carum* sect. *Bunium*	*Pimpinella* sect. *Bunioides*	
BOISSIER 1872	*Carum* sect. *Eucarum* — Radix fusiformis vel verticalis. *Carum* sect. *Bunium* — Radix subglobosa.	*Carum* sect. *Bunium*	*Carum* sect. *Bunium*	*Carum* sect. *Eucarum*
DRUDE 1898	*Carum* — Embryo dicotyledoneus. *Bunium* — Embryo pseudomonocotyledoneus.	*Bunium* sect. *Bulbocastanum*	*Bunium* sect. *Eubunium*	*Carum* sect. *Plurivittata*
CALESTANI 1905	*Carum* included in *Apium*. *Bunium* — Embryo monocotyleus.	*Bunium* sect. *Leucobunium*	*Bunium* sect. *Leucobunium*	*Ligusticum*
WOLFF 1927	*Bunium* — Embryo pseudomonocotyledoneus. *Carum* — Embryo dicot., umbellis involucro nullo vel oligophyllo. *Hellenocarum* — Umbellis involucratis.	*Bunium* sect. *Bulbocastanum*	*Bunium* sect. *Eubunium*	*Hellenocarum*
Present treatment	*Bunium* — Embryo pseudomonocot., radix (sub-) globosa. *Hellenocarum* — Embryo pseudomonocot., radix fusiformis. *Carum* — Embryo dicot., radix fusiformis vel verticalis.	*Bunium*	*Bunium*	*Hellenocarum*

DRUDE (1898) distinguished a genus *Bunium* with "embryo pseudomonocotyleus" versus *Carum* with "embryo dicotyledoneus". But he did not know that *Carum multiflorum* germinates with one cotyledon. This is very similar to the cotyledon of *Bunium* (personal observation). This was also unknown to WOLFF (1927) who described a new genus, *Hellenocarum,* with the type species *H. multiflorum* (SIBTH. & SM.) WOLFF. This genus is easily distinguished from *Carum* on "umbellis involucratis". Unfortunately, *Hellenocarum* was not accepted by later authors. The pseudomonocotyledonous embryo in addition to other characters mentioned in WOLFF's diagnosis make *Hellenocarum* a genus well separated from *Carum.* In fact it is very different in habit from e.g. *Carum carvi.* It is distinguished from "Bunieae" on the napiform root and the petioles of the basal leaves not being underground.

For the treatment by previous authors and the present treatment see Table 3.

Conopodium KOCH

DRUDE (1898) recognized two sections in *Conopodium,* which are based on the shape of the stylopodium (see p. 148).

BALANSAEA BOISSIER & REUTER INCLUDED IN CONOPODIUM KOCH

With the suggested definition it is evident that the monotypic, north-west African genus *Balansaea* must be included in *Conopodium.* The plant germinates with one cotyledon (HACCIUS 1952), the fruit surface is almost smooth and the endosperm is campylospermous. It is necessary to form a new combination:

Conopodium glaberrimum (DESF.) ENGSTR. comb. nov.

Scandix glaberrima DESFONTAINES 1798. Fl. Atl. vol. I: 260 (Tab. 74).

Chaerophyllum glaberrimum (DESF.) PERSOON 1805.

Bunium glaberrimum (DESF.) DE CANDOLLE 1830.

Heterotaenia glaberrima (DESF.) BOISSIER 1839.

Balansaea glaberrima (DESF.) LANGE 1865.

Balansaea glaberrima (DESF.) MAIRE 1924.

Balansaea Fontanesii BOISSIER & REUTER 1852 orig. superfl.

SELECTED GENERIC NAMES USED WITHIN THE GROUP

Balansaea BOISSIER & REUTER 1852. DRUDE (1898) included *Balansaea* in *Biasolettia* KOCH without any comments or combinations. It should be noted that DESFONTAINES (1798 p. 244) described a *Daucus glaberrimus,* which has sometimes been confused with *Balansaea glaberrima* (=*Conopodium glaberrimum*).

Biasolettia KOCH. See p. 151.

Bulbocastanum BAUHIN ex MILLER. The name was used by BAUHIN (1671) and cited by LINNAEUS (1753) under *Bunium. Bulbocastanum* MILLER (1754) contains species from several genera including *Bunium* and *Conopodium. Bulbocastanum* ADANSON (1763) and SCHUR (1866) refer to *Bunium* 1-vittatae. *Bulbocastanum* LAGASCA (1821) is *Conopodium.* DE CANDOLLE (1830) used the name as a section under *Carum* and DRUDE (1898) as a section under *Bunium,* both in the sense of *Bunium* 1-vittatae.

Bunium LINNAEUS (1753).

Butinia BOISSIER (1838). *Butinia* was originally described with one species, *B. bunioides* BOISS. (=*Conopodium bunioides* (BOISS.) CALESTANI). Later BOISSIER (BOISSIER & SPRUNER, BOISSIER & HELDREICH) included typical *Geocaryum* and *Scaligeria* species (BOISSIER 1844, 1849). DRUDE (1898) used the name for a section in *Conopodium.*

Carum L. BENTHAM & HOOKER (1862—1867) included many genera under *Carum* but made no formal new combinations. See further p. 151.

Conopodium KOCH (1824).

Diaphycarpus CALESTANI (1905) was described for the species *D. incrassatus* (BOISS.) CALESTANI (=*Bunium pachypodium* P. W. BALL). *Diaphycarpus* has not been accepted by later authors.

Freyera REICHENBACH. See p. 151.

Geocaryum COSSON. NYMAN (1854—1855) made the combination *G. pumilum.* He cited *Bunium pumilum* SIBTH. & SM. as a basionym (=*Huetia pumila* (SIBTH. & SM.) BOISS. & REUT.) but gave no reason for the combination. See further p. 151.

Heterotaenia BOISSIER (1839). Type species is *H. thalictrifolia* (BOISS.) BOISS. With some hesitation he also included *Scandix glaberrima* DESF. (see above). In 1851 COSSON described *H. arvensis* from Spain. All these species are now included in *Conopodium.*

Huetia BOISSIER. See p. 151.

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Révision Systématique du Genre Sonchus L. s.l.

IV. Sous-genre 1. Sonchus

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ABSTRACT

BOULOS, L. 1973. Révision systématique du genre Sonchus L. s.l. IV. Sous-genre 1. Sonchus. — Bot. Notiser 126: 155—196.

Twenty one species, four subspecies and one variety are discussed. For each taxon is given: nomenclature; vernacular names in different languages; uses where known; detailed description; general distribution; ecological and biological characters; chromosome numbers, where known; palynological particulars, if any. For each taxon relationships with other taxa are discussed as well as any characteristics calling for special emphasis. 19 distribution maps and 16 illustrations are included. The type of distribution ranges from cosmopolitan weeds to local endemics. Polyploids are known, in contrast to species of other subgenera. Chromosome numbers vary from 2n=14 to 54; x=7, 8, 9.

This monographic study will be followed by two more parts.

ABBRÉVIATIONS

Abbréviations des herbiers cités d'après l'Index Herbariorum I, ed. 5 (LANJOUW & STAFLEU 1964).

Bco	Barranco
Dj.	Djebel (Montagne)
E	est
ft	feet (pieds)
Mt., Mña	Mont, Montagne
N	nord
Riv.	Rivière, River
S	sud
W	ouest
!	échantillon examiné par l'auteur.

1. **Sonchus oleraceus** L.

LINNAEUS, Sp. Pl. (ed. 1) 794, 1753; non γ et δ; emend. GOUAN, Hort. Reg. Monsp. 407, 1762. — Lectotype: Savage Catalogue (1945) No 949-6, (LINN!), déterminé *S. oleraceus*.

Sonchus ciliatus LAM., Fl. Fr. 2: 87, 1778.

S. glaber GILIB., Fl. Lithuan. 1: 242, 1781.

S. laevis VILL., Hist. Pl. Dauph. 3: 158, 1789.

S. umbellifer THUNB., Prodr. Pl. Cap. 139, 1794.

S. asper HALL. ex GAERTN., MEY. & SCHERB., Fl. Wett. 3: 125, 1801; non *S. asper* (L.) HILL 1769.

S. lacerus WILLD., Sp. Pl. 3: 1513, 1803.

S. longifolius TREV., Ind. Sem. Hort. Vratisl. 6, 1818.

S. australis Hort. ex TREV., Ind. Sem. Hort. Vratisl. 6, 1818.

S. sundaicus BLUME, Bijdr. Fl. Ned. Ind. 888, 1825—1826.

S. roseus BESS. ex SPRENG., Syst. 3: 651, 1826.

S. parviflorus LEJ. ex REICHENB., 274, 1830—1832.

S. reversus E. MEY. ex DC., Prodr. 7: 186, 1838.

S. royleanus DC., PRODR. 7: 184, 1838.

S. zacinthoides DC., PRODR. 7: 184, 1838.

S. macrotus FENZL in Flora 27: 312, 1844; nom. nud.

S. schmidianus C. KOCH, App. Ind. Sem. Hort. Berol. 12, 1853.

S. schimperi A. BRAUN & BOUCHÉ, App. Ind. Sem. Hort. Berol. 1, 1857.

S. rivularis PHIL. in Linnaea 30: 194—195, 1859—1860.
S. tenerrimus SCHUR, Enum. Pl. Transs. 371, 1866; non *S. tenerrimus* L. 1753.
S. pallescens PANČ., Elench. Crna Gora 55, 1875.
S. gracilis PHIL. in Anal. Univ. Chil. 87: 325, 1894.
S. subbipinnatifidus (GUSS.) ZENARI in Nuov. Giorn. Bot. Ital. N.S. 31: 9, 1924.
S. runcinatus (FIORI) ZENARI in Nuov. Giorn. Bot. Ital. N.S. 31: 11, 1924; non *S. runcinatus* VENT. ex SCH. BIP. in WEBB & BERTH. 1849—1850.
S. fabrae SENNEN in Bol. Soc. Iber. 1929, 28: 114, 1930.
S. angustissimus H. LINDB., in Acta Soc. Sci. Fenn. n.s. B 1(2): 169, 1932; non *S. angustissimus* HOOK. FIL. 1864.
S. spinulifolius SENNEN & MAURICIO in Cat. Fl. Rif. Or. 72, 1933.

En outre, nous considérons toutes les formes, variétés et sous-espèces décrites sous le nom de *Sonchus oleraceus* L. commes synonymes (voir la discussion).

NOMS VERNACULAIRES: *En arabe*: Go'-odeid, Goo'-da', Galawein, Khousheir, Khoshkheish, Libbeyn (Egypte); Khas, Khas-Wez (Gaza); Libbayn (Palestine); Teffaf, Telfaf (Afrique du Nord); Morreir (Iraq, Yemen); Qarsana'a, Khas-el-Homar, Baqla-Yahoudiya (autres noms arabes) — *En français:* Laiteron maraîcher, Laiteron commun, Laiteron des jardins, Laiteron lisse, Palais de lièvre, Laitue de lièvre, Lait d'âne, Liarge — *En anglais:* Annual sow-thistle, Sow-thistle, Dindle, Hare's lettuce, Hares thistle, Hare's colewort, Milkweed, Milky tassel, Milk thistle, Saint Mary's-seed, Swinies — *En allemand:* Kohl-Gänsedistel, Daudistel, Dudistel, Fehedistel, Gansdistel, Hasendistel, Gemeine Saudistel, Hasen Kohl, Sanddistel, Wachtelweizen — *En alsacien:* Sau-gansedistel, Hasenkohl — *En flamand:* Maes-Melkdistel, Daw-Distel — *En hollandais:* Dauw-dissel, Doorn-dissel, Gansendijstel, Ganzedistel, Hasen-distel, Konijnblaren, Kooldistel, Lamsooren — *En italien:* Cicerbita domestica, Cicerbita liscia, Crespigno liscio, Sonco liscio — *En espagnol:* Serraja, Llensó, Lletsó — *En portugais:* Serralha, Serralha branca, Serralha macia — *En norvègien:* Haredylle — *En suèdois:* Mjölktistel — *En japonais:* No-geshi, Keshiazami — *Aux Indes:* Mahatra, Tilaliya, Dodak, Ratrinta — *En Indonesie:* Kauwahkau, Krèwè Kopèl — *En Ruanda et Burundi:* Rururira, Ikigembe Gembe.

USAGES. D'après BONNIER (1923), les feuilles sont consommées cuites ou en salade. La plante est recherchée par les vaches, les porcs, les lapins. Les propriétés médicales de cette plante sont analogues à celles de *Taraxacum densleonis*, c.-à-d. stomachiques, apéritives, diurétiques; le suc de la plante est employé contre les maladies des yeux.

BRITTON et BROWN (1898) constatent que la plante est utilisée comme salade au nord des États Unis et au Canada. En Égypte, Italie, Espagne, etc., elle est également consommée comme salade.

CHOPRA et al. (1956) écrivent «Gum formed by evaporation of the plant a powerful hydragogue cathartic. Infusion of root and leaves tonic, febrifuge».

Plante annuelle ou bisannuelle; herbacée, 10—140 cm de hauteur, généralement ramifiée, glabre, sauf les capitules qui sont quelquefois tomenteux à la base ou munis de poils glanduleux. *Racines* pivotantes, 10—35×0,5—1,5 cm, ligneuses vers le collet chez les bisannuelles. *Collet* simple ou ramifié, cylindrique. *Tige* tendre, cylindrique ou faiblement anguleuse, creuse. *Feuilles du collet* plus petites que les caulinaires, non auriculées, et possédant des pétioles étroitement ailés. *Feuilles caulinaires* 8—35×4—17 cm, très variables, donc entières, pinnatifides, pennipartite, pinnatiséquées, lyrées, etc.; amplexicaules à oreillettes acuminées; lobes entiers, dentés ou serrés-épineux. *Pédoncule* 0,5—7 cm, à une bractée, glabre ou muni de poils glanduleux. *Capitules* généralement nombreux, 10×6 mm, les ouvertes 20—30 mm diam. Nombre de fleurs par capitule 80—230. *Écailles de l'involucre* 27—35 par capitule; les externes 11—14, 2,5—7,5×1—2,5 mm, sommet obtus, glabre ou pourvu au niveau de la nervure médiane de poils glanduleux; les intermédiaires 8—11, étroitement triangulaires, 8—12×2—3 mm, nervure médiane souvent poilue glanduleuse; les internes 8—12, à sommet obtus, 9—12×1—2 mm. *Corolle* jaunâtre ou jaune-citron, ligules extérieures pourpres au-dessous, ± 12 mm. *Ligule* 6×1,5

mm. *Tube de la corolle* ± de la même longueur que la ligule. *Anthères* jaunâtres, brunâtres au sommet. *Akènes:* le rang extérieur jaune-verdâtre ou jaune-brunâtre, rugueux; les intérieures plus foncés, moins rugueux; tous oblancéolés, comprimés, non-ailés, 2,5—3,75×0,75—1 mm, à 2—4 côtes principales, irrégulièrement rugueuses. *Aigrette* deux fois plus longue que l'akène, ± persistante.

DISTRIBUTION. *Sonchus oleraceus* est une «mauvaise herbe» cosmopolite. Elle existe en Europe, Afrique, Asie et Australie. Elle est également bien distribuée dans le nouveau monde et y fut très probablement introduite, mélangée aux graines importées de l'Europe. Une fois introduite, elle s'est bien établie et demeure aujourd'hui une des mauvaises herbes la plus répandue dans les deux continents américains.

Nous citons ici quelques exemples pour illustrer l'extrême plasticité écologique et l'immense distribution géographique de cette espèce: Groenland, Siberie (Jenisei), Nepal (9000 pieds), Tibet, Corée, Taïwan, Nouvelle Zélande, Îles Atlantiques, Pacifiques et Antarctiques.

HUTCHINSON et DALZIEL (1931) n'ont pas mentionné *S. oleraceus* dans la flore de l'Afrique Tropicale Occidentale. BENTHAM et HOOKER (1924) ont douté de sa présence dans les pays tropicaux. Nous avons examiné des spécimens de l'Afrique Tropicale Occidentale déterminés *S. prenanthoides*, lesquels doivent être considérés comme *S. oleraceus*; et nous croyons donc, que l'absence de *S. oleraceus* est due aux déterminations inexactes. En outre, FRIES (1925) a cité *S. oleraceus* du Cameroun, d'Angola, de Kimbundo, du Kénya, d'Abyssinie, etc., ce que confirme la présence de cette espèce dans les pays tropicaux.

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus oleraceus* est une espèce très plastique du point de vue écologique. Dans les régions arides, où la pluie est très faible, il est chétif et sa période de végétation est courte. Son habitat normal est les jardins, les champs cultivés et, surtout, les régions humides et subhumides. Au milieu du Sahara, on ne le rencontre que dans les champs irrigués des oasis. Cette espèce n'a pas d'exigences du point de vue édaphique; on la rencontre sur tous les types de sols. Elle monte aussi à des altitudes très élevées.

Floraison et fructification ont lieu toute l'année, mais abondamment pendant le printemps et l'été.

CARACTÈRES CARYOLOGIQUES.[1] Le nombre chromosomique de *S. oleraceus* est 2n=32 d'après ISHIKAWA (1911, 1916), COOPER et MAHONY (1935), BARBER (1941), RUTLAND (1941), HEISER et WHITAKER (1948), PÓLYA (1949), RODRIGUES (1953), STEBBINS et al. (1953), JINNO (1956), MULLIGAN (1957), NISHIOKA (1958), HENIN (in BOULOS 1960); LARSEN (1960), TURNER et al. (1961), ROUX et BOULOS (1970).

MARCHAL (1920) donne le nombre 2n=16. STEBBINS et al. (1953) écrivent à propos de ce dernier nombre: «In view of definite errors made by MARCHAL in counting other species, this number must be considered doubtful».

STEBBINS et al. (1953) suggèrent que *S. oleraceus* est un amphidiploïde qui a reçu 18 chromosomes de *S. asper* et 14 chromosomes de *S. tenerrimus*.

BARBER (1941) considère *S. oleraceus* comme une espèce ayant deux formes qui se distinguent par leur nombre chromosomique, une forme diploïde: 2n=16 (d'après MARCHAL 1920) et une forme tétraploïde: 2n=32 (d'après ISHIKAWA 1916, etc.). Il ajoute que la forme tétraploïde parait avoir une distribution plus vaste.

En tenant compte des résultats obtenus par les differents auteurs, cités ci-dessus,

[1] Les travaux cités ci-dessous sont partiellement d'après LÖVE et LÖVE (1961), donc ne sont pas mentionés dans la bibliographie.

confirmant le nombre 2n=32, nous considérons, comme STEBBINS et al. (1953), le nombre 2n=16 comme non valable.

PARTICULARITÉES PALYNOLOGIQUES. Pollens tétracolporés et tricolporés en mélange; épaisseur de crète importante (5,2 μ).

DISCUSSION. *Sonchus oleraceus* est une espèce très polymorphe, en particulier en ce qui concerne les formes de ses feuilles. Cette variabilité foliaire est peut-être due, si nous acceptons la suggestion de STEBBINS et al. (1953), à sa constitution génétique (amphidiploïde). L'amplitude de la variabilité des feuilles chez *S. oleraceus* est illustrée par toutes les formes intermédiaires, c.-à-d. les lobes entiers et très étroits de *S. tenerrimus,* jusqu'aux feuilles presque complètes et avec les marges serrées épineuses de *S. asper*. Les formes des feuilles ne sont donc pas suffisantes à elles seules pour la détermination de cette espèce.

Dans le cas de *S. oleraceus* et des autres espèces, et surtout de celles du sous-genre *Sonchus*, les caractéristiques les plus importantes d'une espèce sont celles des corolles et des akènes. Si nous considérons, par example, *S. oleraceus, S. asper* et *S. tenerrimus*, on peut facilement les séparer par leurs corolles ou plutôt par le rapport entre la longueur de la ligule et la longueur du tube de la corolle, lequel est 1: 1 chez *S. oleraceus,* 2: 3 chez *S. asper* et 4: 3 chez *S. tenerrimus.* Ce rapport est utile quand les spécimens sont dépourvus d'akènes. Cette caractéristique a été presque toujours négligée par les auteurs des diverses flores; elle mérite d'être soulignée.

Plusieurs formes, variétés et sous-espèces de *S. oleraceus* ont été décrites, principalement d'après les variations morphologiques des parties végétatives. Dans cette espèce, où on peut reconnaître avec difficulté deux spécimens identiques, il est plus indiqué d'abandonner tous ces taxons infraspécifiques, surtout quand les données génétiques manquent. Nous considérons donc *S. oleraceus* comme une espèce multiforme ou polymorphe, avec une grande amplitude de variation morphologique due probablement à son origine hybride.

2. **Sonchus tenerrimus** L.

LINNAEUS, Sp. Pl. (ed. 1) 794, 1753. — Lectotype: Savage Catalogue (1945) No 949-9, (LINN!), déterminé *S. tenerrimus.*

Sonchus tener SALISB., Prodr. 179, 1796.

S. italicus SPRENG., Syst. 3: 651, 1826.

S. pectinatus DC., Prodr. 7: 186, 1838.

S. tenuifolius NUTT. in Trans. Am. Phil. Soc. N.S. 7: 438, 1841.

S. arborescens SALZM. ex BALL in J. Linn. Soc. 26: 549, 1878.

S. dianae LACAITA ex WILLK., Illustr. Fl. Hisp. 2: 16, t. 100, 1886—1892.

S. septensis GANDOGER in Bull. Soc. Bot. Fr. 44: 78, 1907.

S. perennis (LANGE) H. LINDB. in Acta Soc. Sci. Fenn. n.s. B, 1(2): 170, 1932.

Toutes les variétés et sous-espèces de *S. tenerrimus* L., nous les considerons comme synonymes.

NOMS VERNACULAIRES. *En arabe:* Zeizet el maza (Algérie). — *En français:* Laiteron délicat, Lanceron doux — *En anglais:* Clammy sow-thistle — *En italien:* Cicerbita, Cicerbita de'muri, Crespigno de'muri. — *En espagnol:* Cerraja, Llacó de paret, Llacó menut.

USAGES. D'après DEAKIN (1857), la plante est consommée comme salade dans certaines régions d'Italie.

Plante annuelle, bisannuelle ou vivace, 10—80 cm de hauteur, herbacée, partie basale ligneuse chez les bisannuelles et les vivaces; fortement ramifiée, sauf quelquefois chez les annuelles; capitules blancs tomenteux à leur base, rarement glabres, ou pourvus de poils glanduleux. *Racines* pivotantes, ramifiées. *Collet* ramifié, rarement simple, ligneux chez les plantes bisannuelles et vivaces. *Tige* tendre, sauf à la base, très ramifiée chez les plantes vivaces, non ou peu ramifiée chez les annuelles, cylindrique, quelquefois faiblement angulée, glabre, rarement poilue-glanduleuse vers le sommet. *Feuilles du*

collet c. 5×2 cm, glabres, lyrées, lobes peu nombreux, bases auriculées. *Feuilles caulinaires* 3—20×1,2—8 cm, glabres, les juvéniles blanches tomenteuses, pinnatiséquées; lobes de formes variables, donc triangulaires, ovales, elliptiques, hastées, linéaires, linéaires-lancéolées, etc., mais toujours resserrés vers la nervure médiane de la feuille; base auriculée; marges entières ou denticulées. *Pédoncule* 5—80× 1—2 mm, tomenteux au-dessous du capitule. *Capitules* généralement nombreux, ± cylindriques, 10×5 mm avant l'anthèse, 15×25—40 mm pendant l'anthèse; les fermés après l'anthèse 10×6 mm, coniques. Nombre de fleurs 80—120 par capitule. *Écailles de l'involucre* ± 30 par capitule; les externes 10, 1,5—4×1—1,5 mm, tomenteuse ou poilue glanduleuse, sommet obtus, marges entières; les intermédiaires 11, 10—12×1,5—2 mm, sommet obtus, cilié, moins tomenteuses ou poilues que les externes; les internes 9, 10—12× 1,5—2 mm, sommet obtus, cilié. *Corolle* jaune, devenant jaune-orangé après l'anthèse, 14—16 mm. *Ligule* 8—9×1,5—2,5 mm. *Tube de la corolle* 6—7 mm. *Anthères* 3,5—4,5×0,5 mm. *Akènes:* le rang extérieur jaune-verdâtre ou brun-verdâtre, les intérieurs brunâtres; tous étroitement oblancéolés, faiblement comprimés, non-ailés, 2,5—3,3×1,2 mm, à 1—3 côtes principales, tuberculés, rugueux. *Aigrette* 6—8 mm, ± persistante.

DISTRIBUTION. Îles d'Açores, Portugal, Espagne, Gibraltar, Îles Baléares, Îles Canaries, France, Corse, Monaco, Italie, Sicile, Sardaigne, Île de Malte, Grèce, Crète, Yougoslavie, Roumanie, Turquie, Chypre, Liban, Syrie, Palestine, Jordanie, Irak, Iran, Pakistan, U.R.S.S. (Arménie), Maroc, Algérie, Tunisie, Libye, Égypte, Éthiopie, Soudan, Île de Ste Hélène, République Sud-Africaine, Mexique (Île de Cedros), États-Unis (Californie), Australie (Sud) et Nouvelle Zélande.

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus tenerrimus* est une espèce croissant dans les régions tempérées humides, dans les champs négligés, sur les sables maritimes, les vieux murs et ruines. Quelquefois, dans les oasis, on le rencontre sur les palmiers sur lesquels la plante est protégée par l'ombre des couronnes. La plante a été rencontrée entre 0 et 700 m d'altitude, mais se rencontre généralement aux basses altitudes (sauf par example en Éthiopie). Floraison et fructification presque durant toute l'année.

CARACTÈRES CARYOLOGIQUES. Le nombre chromosomique de *Sonchus tenerrimus* est 2n=14 d'après STEBBINS et al. (1953), LARSEN (1956), ROUX et BOULOS (1972). Ce nombre est unique dans le genre *Sonchus* et est, à ce jour, le nombre le plus bas connu parmi les espèces étudiées.

LARSEN (1956) écrit: «The somatic chromosomes of the complement are of different length. The constrictions are median or sub median. No satellite chromosomes could be observed.»

PARTICULARITÉES PALYNOLOGIQUES. Nombre d'épines paraporales variable (6—9).

DISCUSSION. *Sonchus tenerrimus* est une espèce intéressante car elle existe sous des formes annuelles, bisannuelles et vivaces. Elle possède le nombre chromosomique 2n=14, le nombre le plus bas et, en même temps, unique parmi les espèces du genre *Sonchus*. Ces caractères nous permettent de penser que, très probablement cette espèce tire son origine par réduction du nombre chromosomique d'espèces possédant un nombre chromosomique plus élevé. Son existence sous plusieurs formes est probablement due à sa formation récente, c.-à-d. qu'il s'agit d'une espèce récente qui est en voie d'évolution. Nous croyons que les formes annuelles de cette espèce sont les plus anciennes, et que la tendance générale dans le genre *Sonchus* est vers les formes

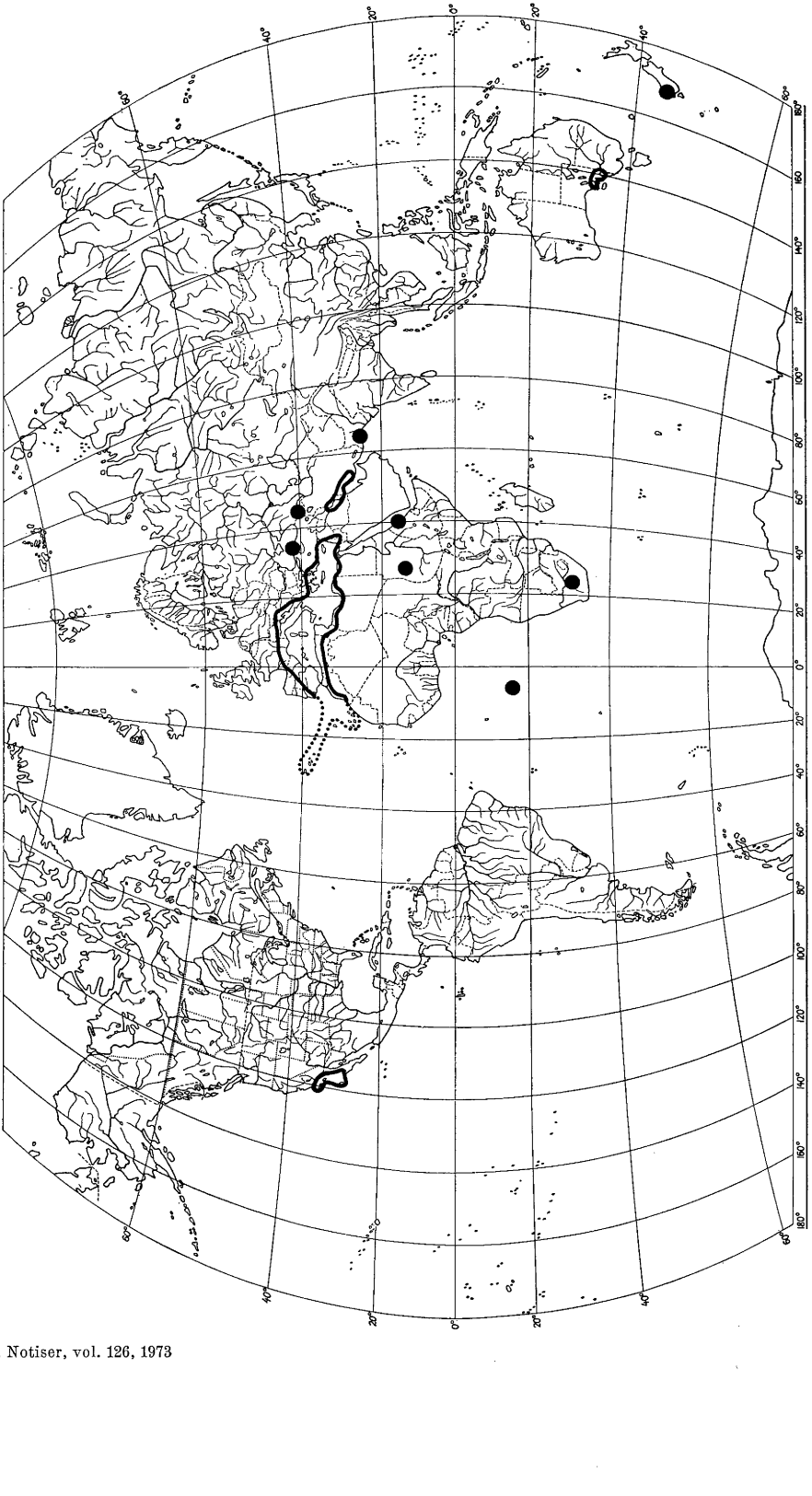

Fig. 1. *Sonchus tenerrimus*. Distribution.

vivaces. En outre, *Sonchus tenerrimus* est une espèce principalement représentée par des formes vivaces, et a conservé sa forme annuelle ancienne.

Ce mode d'évolution est illustré également par *S. asper*, espèce annuelle, ayant donné la sous-espèce bisannuelle *S. asper* ssp. *glaucescens*; les deux taxons possèdent le même nombre chromosomique, 2n=18.

Nous considerons toutes les formes vivaces, bisannuelles et annuelles de *S. tenerrimus* comme une espèce, un seul taxon. La «forme» bisannuelle de *S. asper* est considérée comme une sous-espèce en raison de difference dans la structure des chromosomes qui existent entre l'espèce et la sous-espèce, le nombre des chromosomes étant le même.

L'évolution à l'intérieur d'une troisième espèce polymorphe, *S. oleraceus*, va également vers la forme vivace. Nous avons observé des formes de *S. oleraceus* presque bisannuelles, ligneuse à leur base, et d'une durée de végétation dépassant une année.

Dans le genre *Sonchus*, les formes annuelles sont peu représentées, et nous pensons qu'elles sont en voie de disparition.

3. **Sonchus bourgeaui** Sch. Bip.

Schultz Bipontinus in Webb & Berth., Hist. Nat. Îles Canar. 3(2): 446—447, t. 136 B, 1849—1850. — Lectotype: E. Bourgeau, Plantae Canariensis, No 558. *Sonchus ciliatus*, Lam. variet. Fuerteventura — in lapide ignigeno Spiraculi olivae. Febr. 1846 (P!). Les spécimens de la même collection (exsicc. Bourgeau, Pl. Canar., No 558) sont distribués dans les herbiers de P! K! CGE!, etc., et sont donc considerés comme isolectotypes.

Sonchus tenerrimus L. var. *tuberculatus* Ball in Journ. Bot. 11: 372, 1873.

S. bourgeai Webb, Fl. Ins. Olim. Purpur. 246, 1892.

S. bourgeauxii Sch. Bip. in Pitard & Proust, Îles Canar. Fl. Archipel 258, 1908.

NOMS VERNACULAIRES. *En espagnol:* Serraja.

Plante annuelle, 20—70 cm de hauteur, herbacée, ramifiée; capitules généralement nombreux; pédoncules et capitules poilus-glanduleux; feuilles caulinaires légèrement pubescentes. *Racines* pivotantes, 10—20×0,5—0,8 cm. *Collet* simple, rarement ramifié, cylindrique, 4—8 mm diam. *Tige* ramifiée, rarement simple, cylindrique dans la partie supérieure, anguleuse et décurrente en bas. *Feuilles du collet* 5—8×2—4 cm, glabres, lyrées, pétioles étroitement ailés; lobes ± triangulaires, aigus, irrégulièrement dentés. *Feuilles caulinaires* 5—20×3—8 cm, glabres au-dessus, faiblement pubescentes au-dessous, décurrentes, pinnatiséquées, pourvues d'une grande oreillette chez les supérieures, devenant plus petite chez les basales; lobes ± triangulaires, aigus, dentés-piquants. *Pédoncule* 1—10 cm, poilu-glanduleux près du capitule, ± glabre au dessous. *Capitules* généralement nombreux, 10—13×8—10 mm avant l'anthèse, 30—40 mm diam. pendant l'anthèse, devenant coniques après la maturité. Nombre de fleurs 80—130 par capitule. *Écailles de l'involucre* ± 23 par capitule; les externes 8, 2—7×1—2 mm, poilues-glanduleuses, sommet obtus; les intermédiaires 7, 10—12×1,5—2,5 mm, sommet obtus; les internes 8, 10—12×1,5—2 mm. *Corolle* jaune-orangé, devenant orangé après l'anthèse, 14—20 mm. *Ligule* 9—13×2—3 mm. *Tube de la corolle* 5—7 mm. *Anthères* 3,5—4×0,5 mm. *Akènes* 2,5—3×1,25 mm, bruns, étroitement obovales, atténués vers la base, comprimés, très rugueux transversalement, pourvu de 3—4 côtes principales sur une face et une côte centrale sur l'autre. *Aigrette* ± 2 fois plus longue que l'akène, ± persistante.

DISTRIBUTION. Fuerteventura, Lanzarote, La Graciosa, Îles Canaries et Maroc.

Fuerteventura: Spiraculi olivae (La Oliva), Bourgeau 558 (lectotype P!, isolectotypes CGE! E! G! K!) — s. loc. Hartung s.n. (ZT!).

Lanzarote: Haria, 300 m, Burchard 296 (CAIM! G!) — Entre Arecife et Haria, Murray s.n. (K!) — Famara, Murray s.n. (MANCH!) — Montana Los Helechos, 520 m, Lid s.n. (O!) — s. loc., Lowe s.n. (K!).

Fig. 2. *Sonchus bourgeaui*. Lectotype, BOURGEAU 558 (P!).

La Graciosa: La Graciosa, KUNKEL 13218 (Herb. Canar.).

Maroc: Mogador (Essaouira), BOULOS s.n. (CAI! K! MPU!) — Îles de Mogador, BALL s.n. (K!); BANNERMAN s.n. (BM!); HOOKER s.n. (K!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. D'après PITARD (1918), *Sonchus bourgeaui* pousse dans les milieux arides, rocailleux et ensoleillés de la zone maritime inférieure. Dans L'île de Mogador, BALL (1873) l'a récolté sur les roches au voisinage de la mer. Nous avons également récolté des échantillons sur les sables maritimes d'Essaouira (Mogador). Floraison et fructification principalement d'avril à mai.

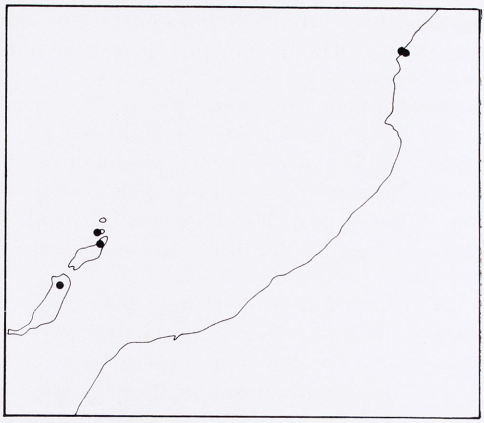

Fig. 3. *Sonchus bourgeaui*. Distribution.

CARACTÈRES CARYOLOGIQUES. Le nombre chromosomique de *Sonchus bourgeaui* est n=8; seule la méiose a été étudiée.

DISCUSSION. Nous considérons la variété *tuberculatus* BALL de *Sonchus tenerrimus* L. comme synonyme de *S. bourgeaui* SCH. BIP. La diagnose de BALL (1873) est la suivante: «*Sonchus tenerrimus* L. var. *tuberculatus* nov. A typo differt insigniter acheniis rugoso-tuberculatis, brevioribus et simulmajoribus, et insuper capitulis majoribus, ligulis aurantiacis, foliis minus profunde pinnatifidis, caulinis basi grosse auritis. — Hab. in rupibus arsis insulae Mogador. In copia magna speciminum (speciei summopere ludibundi) achenia nostris similia nunaquam observari». Le type de BALL ressemble à *Sonchus bourgeaui* à tous les points de vue; l'inflorescence, les capitules et les akènes sont typiquement ceux de *S. bourgeaui,* et les caractères donnés par BALL pour la variété *tuberculatus* de *S. tenerrimus* coïncident avec ceux de *S. bourgeaui.*

La présence de *S. bourgeaui* sur la côte occidentale du Maroc est très intéressante, car cette espèce était considérée comme endémique de l'archipel canarien. Le fait intéressant est la présence de cette espèce

dans le continent africain, dans la région littorale du Maroc occidental (Essaouira), à quelques centaines de kms. des îles orientales (Lanzarote et Fuerteventura) de l'archipel canarien, où elle est seulement connue.

Sonchus bourgeaui est la seule espèce connue du genre *Sonchus* ayant le nombre chromosomique de base x=8.

D'après les données énoncées ci-dessus, nous pensons que *S. bourgeaui* est l'espèce qui relie les deux sous-genres *Dendrosonchus* et *Sonchus*. En outre, croyons-nous qu'on peut la considérer comme une espèce descendant du sous-genre *Dendrosonchus* lequel a donné naissance au sous-genre *Sonchus*. Ce mode d'évolution a pu être réalisé à la suite d'une réduction du nombre de base des chromosomes de *Dendrosonchus* qui est x=9 (toutes les espèces de *Dendrosonchus* étudiées ont x=9, 2n=18) et qui est passé à x=8 donnant naissance, ainsi, à *S. bourgeaui*. Le passage direct d'espèces vivaces et ligneuse du sous-genre *Dendrosonchus* à des espèces annuelles et herbacées, peut paraître difficile à être réalisé par une simple réduction du nombre de chromosomes. Il nous semble que ces espèces ligneuses et vivaces de *Dendrosonchus* ont donné d'abord naissance à l'espèce herbacée, mais vivace avec un tubercule, telle que *S. tuberifer* SVENT. (2n=18), sans réduction du nombre chromosomique. Celle-ci, à son tour, a évolué par réduction du nombre chromosomique vers un étant d'espèce herbacée et annuelle avec une racine pivotante, *S. bourgeaui*.

Nous pensons, que *S. bourgeaui*, avec ses caractères nouveaux, et différents de ceux de l'ensemble des espèces endémiques de *Dendrosonchus* a réussi à émigrer jusqu'à la côte africaine occidentale. Dans cette région, deux directions d'évolution ont pris naissance; l'une par réduction des chromosomes donnant *S. tenerrimus* (x=7, 2n=14), l'autre par rétention du nombre de base originel, donnant des espèces avec x=9, 2n=18. Ces deux modes d'évolution ont engendré des caractères taxonomiques évolués, qui furent à la base de la formation du sous-genre *Sonchus*, lequel possède en particulier l'aptitude à occuper des aires géographiques très vastes.

Les espèces du sous-genre *Sonchus* possèdent des nombres de bases x=7, 8 et 9, parmi lesquelles on trouve aussi des espèces polyploïdes. Chez les deux autres sous-genres, par contre, *Dendrosonchus* et *Origosonchus*, le nombre de base est seulement x=9, et les espèces polyploïdes sont absentes, au moins chez les espèces étudiées. L'existence d'espèces polyploïdes parmi les espèces du sous-genre *Sonchus* nous montre clairement que ce dernier est d'une formation récente.

3 a. **Sonchus bourgeaui** SCH. BIP. var. **imbricatus** (SVENT.) BOULOS

BOULOS, Nytt Mag. Bot. 14: 7, 1967.

Sonchus imbricatus SVENT., Addit. Fl. Canar. 1: 75, t. 30, 1960. — Lectotype: *Sonchus imbricatus* SVENT. In parva insula «Roque del Este» dicta, versus 70 m. supra mare. In humosis inter rupes abruptas (locus classicus). Plus minusve abundanter. 16-IV-1954, SVENTENIUS s.n. (CAI!).

DISTRIBUTION. Roque del Este et Gran Canaria (La Islete), Îles Canaries; endémique.

Roque del Este: 70 m, SVENTENIUS s.n. (CAI!).

Gran Canaria: La Islete, SUNDING s.n. (O!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. La plante pousse dans les stations humides des rochers escarpés, exposés aux vents maritimes violents et humides. Elle se localise à basse altitude (100 m). Floraison et fructification mars —juin.

DISCUSSION. Cette variété est différente de l'espèce type par ses fleurs courtes (± 11 mm), la ligule (± 7 mm) plus longue que le tube de la corolle (± 4 mm), et non pas de la même longueur, comme l'a signalé SVENTENIUS (1960)

dans sa diagnose. Les écailles de l'involucre ne sont pas poilues-glanduleuses, comme dans l'espèce type.

Ces différences ne sont pas suffisantes pour considérer ce taxon comme une espèce, en particulier, dans les espèces du sous-genre *Sonchus*, où les différences entre les espèces sont généralement plus nettes.

4. **Sonchus asper** (L.) HILL

HILL, Herb. Brit. 1: 47, 1769.

Sonchus asper FUCHS, Hist. Stirp. 674, 1542 (nom. illegit.).

S. oleraceus L. γ et δ *asper* L., Sp. Pl. (ed. 1) 794, 1753. — Lectotype: Savage Catalogue (1945) No 949-8 (LINN!).

S. asper GARSAULT, Fig. Pl. Anim. Med. t. 565, 1764; et Descr. Pl. Anim. 332, 1767 (nom. illegit.).

S. asper BARTALINI, Cat. piante nasc. spont. int. Siena, 1776.

S. spinosus LAM., Fl. Fr. 2: 86, 1778.

S. asper ALL., Fl. Pedem., 1785.

S. carolinianus WALT., Fl. Carol. 192, 1788.

S. asper VILL., Hist. Pl. Dauph. 3: 158, 1789.

S. glaber THUNB , Prodr. Pl. Cap. 139, 1794.

S. fallax WALLR., Ann. Bot. 98, 1815.

S. longifolius TREV., Ind. Sem. Hort. Vratisl. 6, 1818.

S. umbellifer THUNB., Fl. Cap. 614, 1823.

S. spinulosus BIGEL., Fl. Bosn. (ed. 2) 292, 1824.

S. cuspidatus BLUME, Bijdr. Fl. Ned. Ind. 888, 1825—1826.

S. ferox WALL., Cat. No 3248, 1828—1832 (nom. nud.).

S. oleraceus WALL., Cat. No 3252 F, 1828—1832 (nom. nud.).

S. australis Hort. ex COLLA, Herb. Pedem. 3: 531, 1834.

S. eryngioides DC., Prodr. 7: 185, 1838.

S. umbellatus E. MEY. ex DC., Prodr. 7: 185, 1838.

S. infestus POEPP. ex DC., Prodr. 7: 185, 1838.

S. crocifolius HORT. ex SCH. BIP. in WEBB et BERTH., Hist. Nat. Il. Canar. 3(2): 449, 1849—1850.

S. borderi GANDOGER, Fl. Lyonn. 140, 1875.

S. sulphureus BOISS., Fl. Or. 3: 796, 1875.

S. aemulus MERINO in Brotéria, Sér. Bot. 14: 36, 1916.

S. viridis ZENARI in Nuov. Giorn. Bot. Ital. n.s. 31: 14, 1924.

S. decipiens ZENARI in Nuov. Giorn. Bot. Ital. n.s. 31: 15, 1924.

S. eryngiifolius SOSN. in SCHCHIAN in Not. Syst. Geogr. Inst. Bot. Tphilis (15): 71, 1949.

S. tibesticus QUÉZEL in Bull. Soc. Hist. Nat. Afr. Nord 50: 31, fig. 2 B, 1959.

En outre, nous considérons tous les taxons inférieurs à l'espèce, décrites sous *S. asper* (L.) HILL, comme synonymes.

NOMS VERNACULAIRES. *En arabe:* Galawein, Galawein-shouky (Égypte) — *En français:* Laiteron-épineux, Laiteron-piquant, Laiteron-rude — *En anglais:* Rough sow-thistle, Sharp-fingered sow-thistle, Sharp sow-thistle, Spiny sow-thistle — *En allemand:* Rauhe-Saudistel, Rauhe-Gänsedistel, Milchdistel, Harte-Gänsedistel, Dornige-Gänsdistel, Sögestike — *En flamand:* Rue-Melkdistel — *En hollandais:* Blauwedissel, Dauwdissel, Dauwdistel, Dauwkoolen, Malschdistelen, Melkdistel, Melkweid, Melkwiesel — *En italien:* Cicerbita selvatica, Cicerbita spinosa, Cicerbita crespina, Cicerbitone-salvatico, Cicerbitone, Sonco aspero — *En espagnol:* Serraja — *En portugais:* Serralha preta, Serralha áspera, Serralha espinhosa — *En norvègien:* Stivdylle — *En suèdois:* Svintistel — *En japonais:* Oninogeshi.

USAGES. D'après BONNIER (1923), les propriétés médicales de cette espèce sont analogues à celles de *Taraxacum densleonis* (voir les usages de *S. oleraceus*).

En outre, CHOPRA et al. (1956) écrivent: «In India the plant is pounded and applied to wounds or boils; it contains a bitter substance which is considered active in this respect.»

Les tiges de *S. asper* sont consommées comme salade dans certains pays.

Plante annuelle, très polymorphe, 10—120 cm de hauteur, généralement ramifiée et avec plusieurs capitules; glabre, ou quelquefois poilue-glanduleuse sur les parties supérieures. *Racines* pivotantes, ramifiées. *Collet* simple ou ramifié, cylindrique. *Tige* 2—10 mm diam., souvent anguleuse dans sa partie inférieure. *Feuilles du collet* 5—12×2—4 cm, moins séquées que les caulinaires. *Feuilles caulinaires* 5—25×3—8 cm, très variables, entières à pinnatiséquées, avec toutes les formes intermédiaires possibles, bases auriculées; lobes ± triangulaires, aigus, marges denticulées, piquantes. *Pédoncule*

0,5—5 cm, à une bractée. *Capitules* nombreux, 12×8 mm, plus larges après l'anthèse. Nombre des fleurs 80—300 par capitule. *Écailles de l'involucre* 35—45 (± 40) par capitule; les externes 13, 2—6× 1—2 mm, souvent poilues-glanduleuses; les intermédiaires 12, 10—13×0,8—1,2 mm; les internes 15, 8—11×0,8—1,25 mm. *Corolle* ± 10 mm, jaune-citron, devenant jaune-orangé après l'anthèse. *Ligule* 4×1 mm. *Tube de la corolle* ± 6 mm. *Anthères* 3×0,5 mm. *Akènes* variables: brunâtres à crème-jaunâtres, avec une série de couleurs intermédiaires, fortement comprimés, ± elliptiques, 2—3×1 mm, pourvus de 3 côtes caractéristiques sur chaque surface, marges largement ailées, souvent légèrement ciliées-recourbées vers la base, surtout chez les akènes extérieures. *Aigrette* ± caduque, ± 3 fois plus longue que l'akène.

DISTRIBUTION. La distribution de *S. asper* suit ± celle de *S. oleraceus*. D'après nos observations, *S. asper* croît mieux dans les régions tempérées que dans les régions chaudes, et dans les milieux humides que dans les milieux secs. En Égypte par exemple, *S. asper* est connu du delta du Nil, pas de la vallée sud du delta, région plus chaude et moins humide. En Europe, où les deux espèces existent, la limite de *S. asper* est plus nordique que celle de *S. oleraceus*.

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus asper* est une «mauvaise herbe» commune dans les champs cultivés, les jardins, sur les routes et dans les terrains négligés. Elle pousse principalement dans les milieux humides. Floraison et fructification presque durant l'année.

CARACTÈRES CARYOLOGIQUES.[1] Le nombre chromosomique de *S. asper* est 2n=18 d'après WULFF (1937), BARBER (1941), RUTLAND (1941), EISER et WHITAKER (1948), VAARAMA (in LÖVE & LÖVE 1948), STEBBINS et al. (1953), LÖVE & LÖVE (1956), MULLIGAN (1957), LÖVKVIST (in ERICSON 1958), NISHIOKA (1958), HENIN (in BOULOS 1960).

S. asper possède une paire de chromosomes avec des grands satellites attachés au bras court.

DISCUSSION. LINNAEUS (1753) a considéré *Sonchus asper* comme une variété de *S. oleraceus*. HILL (1769) l'a classé comme une espèce. Nous partageons l'avis de HILL d'avoir considéré *S. asper* comme une espèce, car les hybrides entre *S. asper* et *S. oleraceus* sont stériles (BARBER 1941), ce qui montre l'existence de barrières génétiques entre les deux taxons. (Voir aussi la discussion de *Sonchus oleraceus, S. tenerrimus, S. mauritanicus* et *S. asper* ssp. *glaucescens*.)

4 a. **Sonchus asper** (L.) HILL subsp. **glaucescens** (JORDAN) BALL

BALL in J. Linn. Soc. London (Bot.) 16: 548, 1878.

Sonchus nymanii TIN. & GUSS. in GUSS., Fl. Sic. Syn. 2: 860, 1844.

S. glaucescens JORD., Obs. Pl. Crit. 5: 75, 1847.

S. graecus REUT. ex WEISS in Verh. Zool.-Bot. Ges. Wien 19: 45, 1869.

S. giganteus SHUTTLEW. ex ROUY, Fl. Fr. 9: 203, 1905.

S. kralikii ROUY, Fl. Fr. 9: 203, 1905.

S. asper (L.) HILL subsp. *nymanii* (TIN. & GUSS.) HEGI, Illustr. Fl. Mittel-Europa 6(2): 1110, 1929.

DISTRIBUTION. Îles d'Açores, Madère, Portugal, Espagne, Îles Baléares, Îles Canaries, France, Corse, Italie, Sicile, Sardaigne, Grèce, Crète, Yougoslavie, Albanie, Suisse, Autriche, Grande Bretagne, Bulgarie, ?Roumanie, Turquie, Chypre, Liban, Syrie, Palestine, Jordanie, Iraq, Iran, Afghanistan, Maroc, Algérie, Tunisie, Libye, Égypte, Éthiopie, République Sud-Africaine, Australie, États-Unis (Hawaii) et Bolivie.

[1] Les travaux cités ci-dessous sont partiellement d'après LÖVE & LÖVE (1961), donc, ne sont pas mentionés dans la bibliographie.

Fig. 4. *Sonchus asper* subsp. *glaucescens*. SAMUELSON et SANDER 366 (S!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus asper* subsp. *glaucescens* pousse dans les champs cultivés, sur les bordures des canaux, près des champs et dans les terrains négligés. Floraison et fructification de février à octobre.

CARACTÈRES CARYOLOGIQUES. Le nombre chromosomique est 2n = 18. Parmi les 18 chromosomes de cette sous-espèce, deux paires de chromosomes possèdent des grandes satellites, tandis-que chez *S. asper* subsp. *asper*, une paire seulement possède des satellites.

PARTICULARITÉES PALYNOLOGIQUES. Nombre d'épines paraporales un peu variable (7 à 8).

DISCUSSION. La sous-espèce *glaucescens* de *Sonchus asper* est bisannuelle, morphologiquement assez difficile à distinguer de l'espèce type *S. asper* ssp. *asper* si l'échantillon est dépourvu de la racine ou du collet, parties importantes pour distinguer cette sous-espèce.

Les capitules sont généralement ombellés; les feuilles sont en rosette et plus rigides avec des marges plus piquantes que chez *S. asper* ssp. *asper*. Les akènes possèdent des marges ciliées et recourbées, caractère beaucoup moins répandu ou qui manque chez *S. asper* ssp. *asper*.

Nous avons observé que les caractères mentionnés ci-dessus ne sont pas très facile à distinguer, surtout quand on observe des échantillons intermédiaires. Nous pensons donc, que l'hybridation est possible entre *S. asper* et la sous-espèce *glaucescens* et que les barrières de stérilité ne sont pas complètes entre ces deux taxons; c'est ce qui nous a amné à considérer *Sonchus glaucescens* comme une sous-espèce de *S. asper*.

En outre, la différence structurelle entre les chromosomes de cette sous-espèce et celles de *S. asper* est très nette: *S. asper* ssp. *asper* ne possède qu'une paire de chromosomes pourvus de satellites, tandisque *S. asper* ssp. *glaucescens* en possède deux.

Les pollens de ces deux taxons sont également différents. Les dimensions des côtes et des épines sont indiquées ci-dessous d'après SAAD (1961).

Taxon	Épaisseur de la côte (μ)	Longueur des épines (μ)
S. asper ssp. *asper*	2,8	2,8
S. asper ssp. *glaucescens*	4,0	1,5

5. **Sonchus littoralis** (T. KIRK) ALLAN

ALLAN, Fl. N. Z. 1: 760, 1961.
Sonchus asper (L.) HILL var. *littoralis* KIRK, Trans. N. Z. Inst. 26: 265, 1894.

Fig. 5. *Sonchus littoralis*. MACMILLAN 65/1 (CHR!).

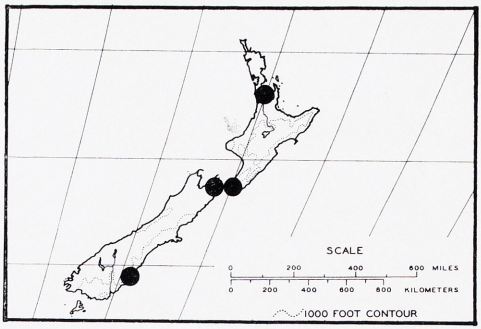

Fig. 6. *Sonchus littoralis*. Distribution.

Plante bisannuelle à vivace, 10—50 cm de hauteur; racines pivotantes, renflées vers le collet; feuilles glabres, principalement en rosette. *Racine* pivotante, 5—15 ×0,2—2 cm, renflée et ligneuse vers le collet. *Collet* court, ligneux, peu ou non ramifié, 1—1,5 cm diam. *Tige* herbacée, cylindrique, peu ramifiée. *Feuilles du collet* en rosette, 5—35×1,5—10 cm, subcoriaces, obovales, attenuées vers la base formant des petioles étroites, peu ou nonséquées, marges irrégulierement dentées. *Feuilles caulinaires* peu nombreuses, 3—15×1,5—5 cm, pinnatiséquées, marges dentées-spinellées, base amplexicaule. *Pédoncule* 5—50×1—2 mm, à une bractée. *Capitules* 1,5×2 cm. Nombre de fleurs ± 160 par capitule. *Écailles de l'involucre* ± 36; les externes 14, 3—8×2—3 mm; les intermédiaires 12, 10—12×3 mm; les internes 10, 10×1,5 mm, sommet obtus et cilié. *Corolle* jaune, ± 12 mm. *Ligule* 5×1,5 mm. *Tube de la corolle* ± 7 mm. *Anthères* ± 3 mm. *Akènes* 3,5—4×1,2—1,5 mm, brunâtres, ailés, fortement comprimés, elliptiques, pourvus de 2—3 côtes sur chaque surface. *Aigrette* ± 7 mm, caduque.

DISTRIBUTION. Nouvelle Zélande, endémique.

Nouvelle Zélande: Titahi Bay, ALLAN s.n. (CHR!); ZOTOV s.n. (CHR!); MASON s.n. (CHR!) — Seatoun, ALLAN s.n. (CHR!) — Tomahawk Bay, E end, OLIVER 9582 (WELT!) — Pencarrow, KIRK s.n. (WELT!) — Shag Point, Waihemo County, NE Otago, PETRIE s.n. (WELT!) — Wellington, PETRIE s.n. (CHR!) — Days Bay, Wellington, PETRIE s.n. (WELT!) — Port Nicholson, PETRIE s.n. (WELT!) — Ohau Bay, N of Cape Terawhiti, Cook Strait, ZOTOV s.n. (CHR!) — Anawhata, Auckland, MOORE s.n. (CHR!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus littoralis* croît dans les stations rocheuses maritimes et dans les prairies près de la mer. D'après ALLAN (1961), la floraison est d'août à avril et la fructification de septembre à juin.

DISCUSSION. *Sonchus littoralis* est une espèce bisannuelle avec une tendence d'être vivace. Les racines pivotantes et renflées vers le collet, et les feuilles glabres et subcoriaces en rosette sont très caracteristiques de cette espèce.

Fig. 7. *Sonchus mauritanicus*. REVERCHON 316 (P!).

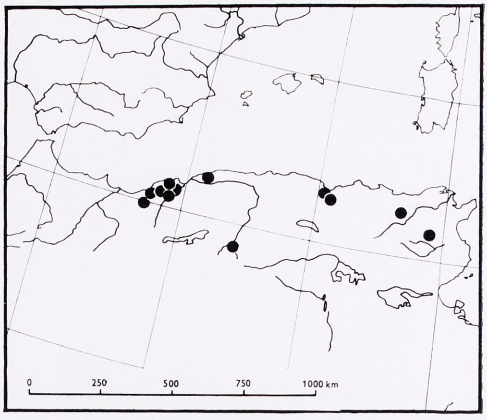

Fig. 8. *Sonchus mauritanicus*. Distribution.

6. **Sonchus mauritanicus** BOISS. & REUT.

BOISSIER & REUTER, Pugill. Pl. Nov. Afr. Bor. Hisp. Austr. 70, 1852. — Lectotype: In arvis argillosis à la tête du gr. lac salé près des Puits, entre Oran et Tlemcen. April 1849, leg. REUTER s.n. (G!).

Plante vivace, rhizomateuse, herbacée, 30—85 cm de hauteur, poilue-glanduleuse dans la partie supérieure, feuilles principalement basales. *Rhizome* solide, 4—15 mm diam., portant des racines fibreuses. *Collet* simple, rarement ramifié, cylindrique. *Tige* rarement ramifiée, cylindrique, poilue-glanduleuse vers le sommet, autrement glabre. *Feuilles du collet* 5—20×2—5 cm, auriculées, lancéolées, pennipartites à pinnatiséquées; marges irrégulièrement serrées-denticulées, blanches-mucronées et piquantes. *Feuilles caulinaires* 5—20×3—5 cm, principalement sur la partie basale de la tige, largement espacées, amplexicaule, pinnatiséquées, acuminées, auricules bien développées. *Pédoncule* 1—6,5 cm, unibracté. *Capitules* 12×10 mm. Nombre de fleurs par capitule 160—220. *Écailles de l'involucre* ± 27 par capitule; les externes 10, 3—8×1,5—2,5 mm, souvent avec poils glanduleux; les intermédiaires 7, 10—12×2—2,5 mm; les internes 10, 10—12×1—2 mm. *Corolle* jaunâtre, 13—16 mm. *Ligule* 5—6,5×1—2 mm. *Tube de la corolle* 8—10 mm. *Anthères* 3×0,5 mm. *Akènes* 2,25—2,75×0,6—0,8 mm, étroitement oblancéolés, comprimés, étroitement ailés, avec 3 côtes principales sur chaque face, pourvus de poils blanchâtres, solides et très fins. *Aigrette* ± 3 fois plus longue que l'akène, ± caduque.

DISTRIBUTION. Algérie, Tunisie et probablement au Maroc.

Algérie: Près Sidi-bel-Abbès, WARION s.n. (G!) — Tessala, près Sidi-bel-Abbès, WARION 145 (G! K! LD! LE! P!) — Mt. Babors, 1700 m, REVERCHON 316 (P!) — Kerrata, 800 m, REVERCHON s.n. (G! P!) — Environs Tlemcen, FAURE s.n. (LD!) — Tlemcen, FAURE s.n. (LD!) — Entre Oran et Tlemcen, REUTER s.n. (lectotype, G!) —

Valmy, près Oran, FAURE s.n. (LD! S!) — Bou-Kanéfis, Oran, WARION s.n. (P!) — Mazouna, Dahra, COSSON s.n. (G!) — Entre Laghouat et Tadjemout, c. 930 m, ALSTON et SIMPSON 84, 85 (BM!).

Tunisie: Oued Meliz, COSSON s.n. (P!) — Makhtar, Bou Ghazem, LETOURNEUX s.n. (K!).

?Maroc: s. loc. (in litt. ex BONNET et BARRATTE 1896).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus mauritanicus* pousse dans les lieux frais, sur le calcaire et dans les champs argileux, entre 800 et 1700 m d'altitude. Floraison et fructification mars à juin, principalement d'avril à mai.

DISCUSSION. *Sonchus mauritanicus* est une espèce vivace caractérisée par son rhizome, mais d'un aspect général ressemblant à *S. oleraceus* et *S. asper*, donc, facile à séparer de ces deux espèces qui possèdent des racines pivotantes. En outre, elle possède des akènes atténués à la base, donc facile à séparer des espèces qui possèdent des rhizomes, par exemple *S. maritimus* et *S. arvensis* qui ont des akènes presque ellipsoïdes.

SAAD (1961) écrit: «*Sonchus mauritanicus* and *S. oleraceus* were considered to be synonyms but their pollen studies show that they are completely different»; nous n'avons trouvé dans la littérature aucune référence considérant ces deux espèces comme synonymes.

7. **Sonchus macrocarpus** BOULOS & C. JEFFREY

BOULOS & JEFFREY in Taxon 18: 349, 1969. — Holotype: Egypt, between Kafr El Sheikh and Disuq, BOULOS s.n. (CAI!).

Sonchus gigas BOULOS in Bot. Not. 112: 365, 1959; nom. non rite publ.; non BOULOS ex HUMBERT 1963.

NOMS VERNACULAIRES: *En arabe:* Galawein (Égypte).

USAGES. La tige est consommée comme salade en Égypte.

Plante bisannuelle et probablement vivace, herbacée, 30—130 cm de hauteur. *Racines* pivotantes, 10—40×1,5 cm. *Collet* non ou peu ramifié, ± ligneux. *Tige* généralement ramifiée, 4—15 mm diam., angulée. *Feuilles du collet* 5—10×2—3 cm, pinnatiséquées, marges irrégulièrement denticulées. *Feuilles caulinaires* 10—50×7—20 cm, ± glabres, décurrentes, auriculées, pennipartites à pinnatiséquées; lobes 2—6×2 cm, triangulaires, souvent réfléchis, marges irrégulièrement denticulées. *Pédoncule* 20—30×1—2 mm, tomenteux au-dessous des capitules juvéniles, unibracté. *Capitules* nombreux, les juvéniles ± sphériques, plus tard ± cylindriques et de forme conique après l'anthèse, 15×12 mm, diam. pendant l'anthèse 25 mm. Nombre de fleurs 180—240 par capitule. *Écailles de l'involucre* ± 30 par capitule; les externes 10, 2—6×2 mm, blanches-tomenteuses à la base; les intermédiaires 9, 10—12×2—3 mm; les internes 11, 10—12×2 mm. *Corolle* ± 12,5 mm, jaune à jaune-orangé. *Ligule* 4—5×1—1,5 mm. *Tube de la corolle* ± 8 mm. *Akènes* 4—5,5×1,5—1,75 mm, oblong-elliptiques, brûnatres, faiblement lustrés, très légèrement rugueux, pourvus d'ailes marginales larges et de 3 côtes principales longitudinales et médianes, rapprochées les unes des autres. *Aigrette* ± 8 mm, caduque.

DISTRIBUTION. Égypte, endémique.

Égypte: Sherbin, MAIRE s.n. (CAI!) — El Zarqa, Sherbin, IMAM et al. s.n. (CAI!) — El Baramoun, IMAM et al. s.n. (CAI!) — Matariya, Dakahliya, BOULOS s.n. (CAI!) — El Tawila, N Mansoura, BOULOS s.n. (CAI!) — Between Kafr El-Sheikh and Disuq, on Faroun Drain, BOULOS s.n. (holotype, CAI!) — Masraf Abu-Aziza, at lake Manzala, MUSTAFA et SABET s.n. (CAI!) — El-Zeini, près de Sidi Salem, 4,5 km S lac Borullos, BOULOS s.n. (CAI!) — El-Mabkhar, Rosetta, IMAM et al. s.n. (CAI!) — Damanhour, MUSCHLER s.n. (K!) — Moharam bey, Alexandrie, LETOURNEUX s.n. (P!) — Belbeis, TÄCKHOLM s.n. (CAI!).

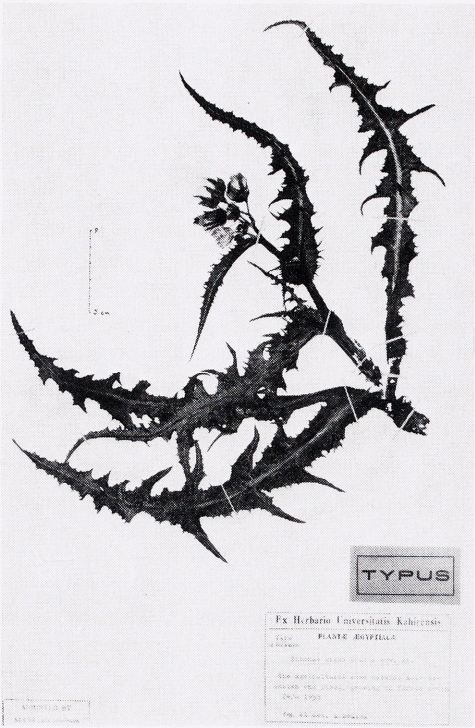

Fig. 9. *Sonchus macrocarpus*. Holotype, BOULOS s.n. (CAI!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. La plante se trouve dans les milieux humides, sur les canaux d'irrigations et de drainage, dans les champs de riz, etc. Floraison et fructification d'avril à octobre, principalement avril à juin.

CARACTÈRES CARYOLOGIQUES. *Sonchus macrocarpus* est une espèce tetraploïde, 2n=36 (HENIN in BOULOS 1959).

PARTICULARITÉES PALYNOLOGIQUES. Pollens tricolporés et tétracolporés en melange; les différences des tailles entre les deux types sont relativement peu accusées, respectivement: 42—44 μ et 44—48 μ.

DISCUSSION. *Sonchus macrocarpus* est une espèce tétraploïde (2n=36). C'est

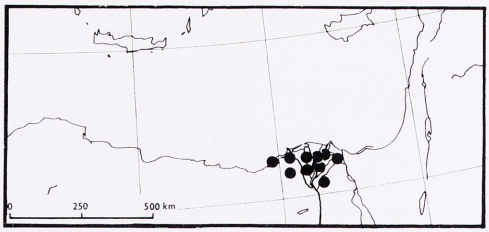

Fig. 10. *Sonchus macrocarpus*. Distribution.

donc une espèce récente. Elle est, très probablement, dérivée de *S. asper* (2n=18), qui est l'espèce la plus voisine du point de vue morphologique. *S. macrocarpus* est facile à séparer des espèces voisines et surtout de *S. asper*. Elle diffère de cette dernière espèce, principalement par ses akènes presque deux fois plus longs et deux fois plus larges, et par ses pollens plus grands et tétracolporés.

8. **Sonchus gigas** BOULOS ex HUMBERT

HUMBERT, Fl. Madag. 3: 887, 1963; quoad descr. lat. et typum, excl. descr. gall.; non BOULOS (1959) nom. non rite publ. — Holotype: Zambie, Muckle Neuk, 4200 ft, ROBINSON 904 (K!).

Plante bisannuelle ou vivace, hérbacée, ± glabre, 40—140 cm de hauteur. *Racine* pivotante, richement ramifiée, ligneuse dans la partie supérieure. *Collet* ligneux, généralement non ramifié. *Tige* herbacée, anguleuse, glabre. *Feuilles du collet* 8—20 ×1—5 cm, nonséquées à pinnatifides, marges irrégulièrement dentées. *Feuilles caulinaires* 5—30×1—8 cm, auriculées, pinnatifides à pennipartites; marges irregulièrement dentées, piquantes. *Pédoncule* 5—50×1—2 mm, pourvu d'une à deux bractées, souvent légèrement blanc-tomenteux ou poilu-glanduleux au-dessous des capitules. *Capitules* généralement nombreux, 10×8 mm. Nombre de fleurs ± 180 par capitule. *Écailles de l'involucre* ± 30; les externes 11, 4—9×2—3 mm, souvent poilues-glanduleuses; les intermédiaires 10, 10—12×2—3 mm; les

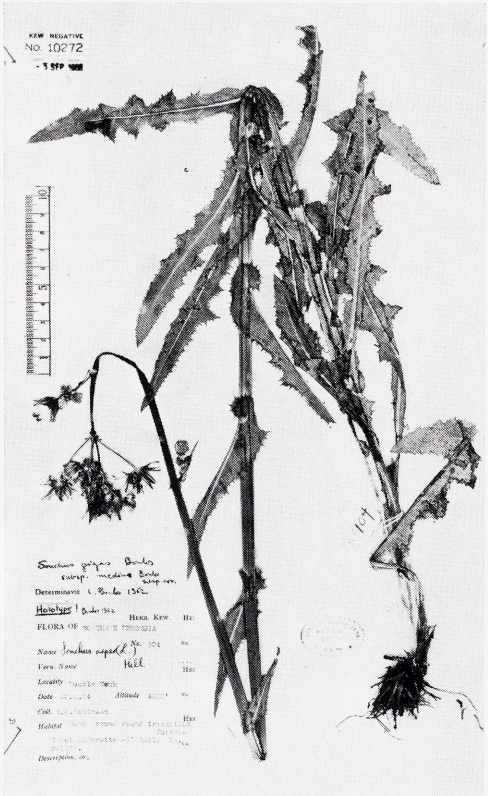

Fig. 11. *Sonchus gigas*. Holotype, ROBINSON 904 (K!).

internes 9, 10—13×1,5—2 mm. *Corolle* 9—12 mm, jaune. *Ligule* 4—5×1 mm. *Tube de la corolle* 5—7 mm. *Anthères* 2,25 mm. *Akènes* 2,75—3,75×1—1,25 mm, oblong-elliptiques, fortement comprimés, bruns ternes, largement ailés, à 3 côtes médianes. *Aigrette* ± 8 mm, très caduque.

DISTRIBUTION. Sénégal, Sudan, Zaïre, Angola, Zambie, Mozambique, Sud-Ouest Africain, République Sud-Africaine et Madagascar.

Sénégal: Kayar, BERHAUT 5040 (P!) — Tiaroy, près Dakar, BERHAUT 1046 (P!) — s. loc., TROCHAIN 4279 (P!).

Sudan. Jebel Marra: Tora Tonga, 8000 ft, WICKENS 1703 (K!) — Nyertete, 3700 ft, WICKENS 2165 (K!); 3000—5000 ft, MACINTOSH 85 (K!) — Nyuringya, c. 2000 m,

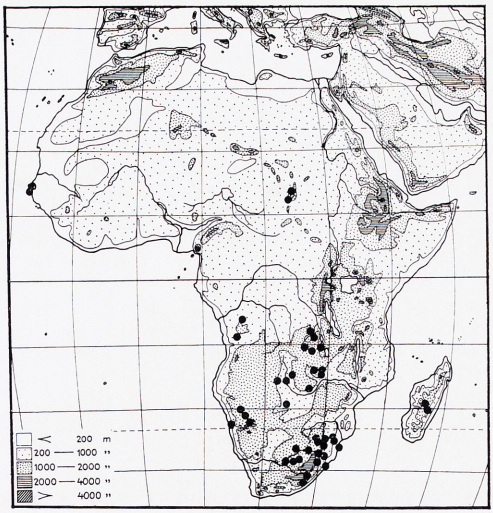

Fig. 12. *Sonchus gigas*. Distribution.

DANDY 147 (BM!) — Korana, DRAR 2318 (CAI!) — Yorna, DRAR 2179 (CAI!).

Zaïre: Likasi, c. 1400 m, ROBYNS 1712 (BR!) — Luiswishi, QUARRÉ 5247 (BR! CAI!) — Lukuni, QUARRÉ 5328 (BR! P!) — Keyberg, DETILLEUX 224 (BR!) — Riv. Luafi, Lufira, QUARRÉ 4627 (BR!) — NW Luafi, 1125 m, STREEL (BR!) — Elisabethville (Lumumbashi), SALÉSIENS 444 (BR!); HOCK s.n. (BR!).

Angola: Anizanga, GOSSWEILER s.n. (BM!) — Golungo, WELWITSCH 3640 (BM! COI!).

Zambie: Près Mumbwa, MACAULAY 384 (K!) — Lusaka, 4000 ft, BEST 100 (K!) — 12 miles S Lusaka, Mt. Makulu Research Station, ANGUS 1360 (K!) — Shangombo, 3400 ft, CODD 7459 (BM! COI! K!) — Muckle Neuk, 4200 ft, ROBINSON 904 (holotype, K!) — Mankoya, DRUMMOND et COOKSON (K!) — Senanga, Kaunga Mashi Riv., MUBITA B.4 (K!).

Mozambique: Inhaca Island, 23 miles E Lourenço Marques, MOGG 30105 (K!) — s. loc. LE TESTU 858 (P!); JUNOD 649 (LD!).

Sud-Ouest Africain: Mouth of Swakopmund Riv., GALPIN 7554 (K!); SEYDEL 641 (M!) — Swakopmund, SEYDEL 614 (M!) — Windhoek, MERXMÜLLER et GIESS 1050 (K!) — Omuramba Omatako, Okavango Distr., DE WINTER et MARAIS 4747 (PRE!) — Otjosongombe, Otjiwarongo, VOLK 1172 (M!) — Gross-Barmen, Okahandja, MERXMÜLLER et GIESS 1012 (M!).

République Sud-Africaine. Transvaal: Sekukuniland, 3000 ft, Lydenburg Distr., BARNARD 193 (PRE!) — Ermelo, LEENDERTZ 9839 (PRE!) — Warmbaths, LEENDERTZ 537 (PRE!) — Naboomspruit, GALPIN M 767 (PRE!) — Nelspruit, BREYER 17929 (PRE!) — Belfast, LEENDERTZ 9193 (PRE!) — Vryburg Distr., near Amersfoort, BURTT DAVY 4046 (PRE!) — Près Pretoria, MERXMÜLLER 26 (M!) — s. loc., WILMS 643 (K!) — État Libre d'Orange: Vals Riv., 4500 ft, Kroonstad Distr., PONT 645 (PRE!) — Bloemfontein, 4500 ft, POTTS 2658 (K!) — Natal: Dundee Townlands, Dundee Distr., SHIRLEY s.n. (NU!) — Mooi Riv., 4000 ft, WOOD 4023 (K!) — Foxhill, Pietermaritzburg Distr., HILLIARD 4043 (E! NU!) — Durban, R. E. FRIES et TH. FRIES 3102 (UPS!) — Province du Cap: Schanskop, Vaal Riv., ACOCKS 2524 (K! LD!) — Near Engcobo, 3000 ft, FLANAGAN 2814 (PRE!) — Amabele, 2601 ft, DE VRIES 80 (PRE!) — Dutoits Pan, Kimberley Distr., WILMAN s.n. (PRE!).

Madagascar: Antsirable, PIERRE 3378 (P!) — Plateau d'Ankara, PIERRE 1135 (P!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus gigas* pousse dans les milieux humides, sur les bordures des canaux, des rivières, etc., à une altitude de 200 à 2000 m, mais généralement à ± 1000 m. Floraison et fructification durant toute l'année, mais la période principale est d'août à janvier.

CARACTÈRES CARYOLOGIQUES. *Sonchus gigas* est une espèce polyploïde, 2n = 36 (MARCHANT 1970).

PARTICULARITÉES PALYNOLOGIQUES. Pollens tétracolporés et tricolporés en mélange; les tétracolporés étaient d'une taille plus grande (52—54 µ) que les tricolporés (36—41 µ).

DISCUSSION. *Sonchus gigas* est facile à distinguer de *S. macrocarpus* par ses feuilles plus courtes et moins séquées, ses capitules moins larges et ses akènes plus petits. Il diffère de *S. asper* par ses pollens tétracolporés en mélange avec des tricolporés (il n'y a que tricolporés chez *S. asper*). *S. gigas*, 2n = 36, est tetraploïde, tandis que *S. asper*, 2n = 18, est diploïde.

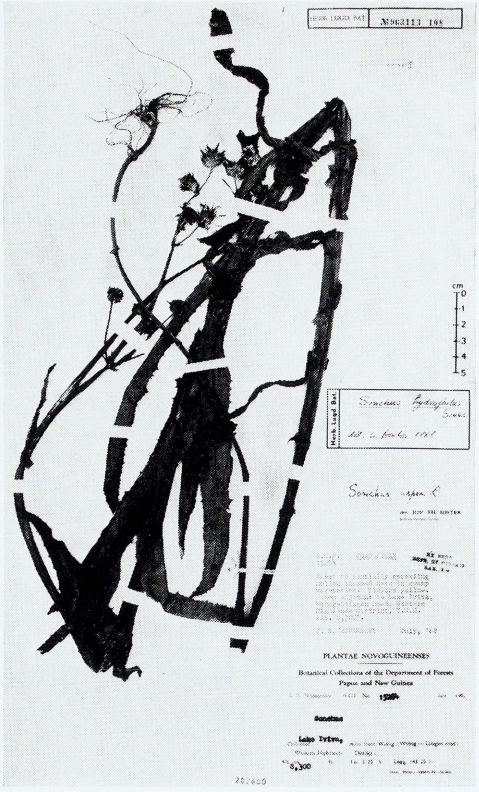

Fig. 13. *Sonchus hydrophilus*. WOMERSLEY 15284 (L!).

9. **Sonchus hydrophilus** BOULOS

BOULOS in EICHLER, Suppl. BLACK's Fl. S. Australia 331, 1965. — Holotype: South Australia, Fleurieu Peninsula, in watercourse c. 5 km N Victor Harbour, CLELAND s.n. (AD!).

Plante annuelle, bisannuelle et probablement vivace, herbacée, 50—120 cm de hauteur, peu ou non ramifiée à la base, poilue-glanduleuse dans la partie supérieure, autrement glabre. *Racines* généralement en groupes denses de la zone inférieure au collet; chez quelques specimens on peut distinguer une structure rhizomatique qui porte des racines fibreuses. *Collet* ligneux, non ramifié, 1 cm diam. *Tige* ± cylindrique, ligneuse à

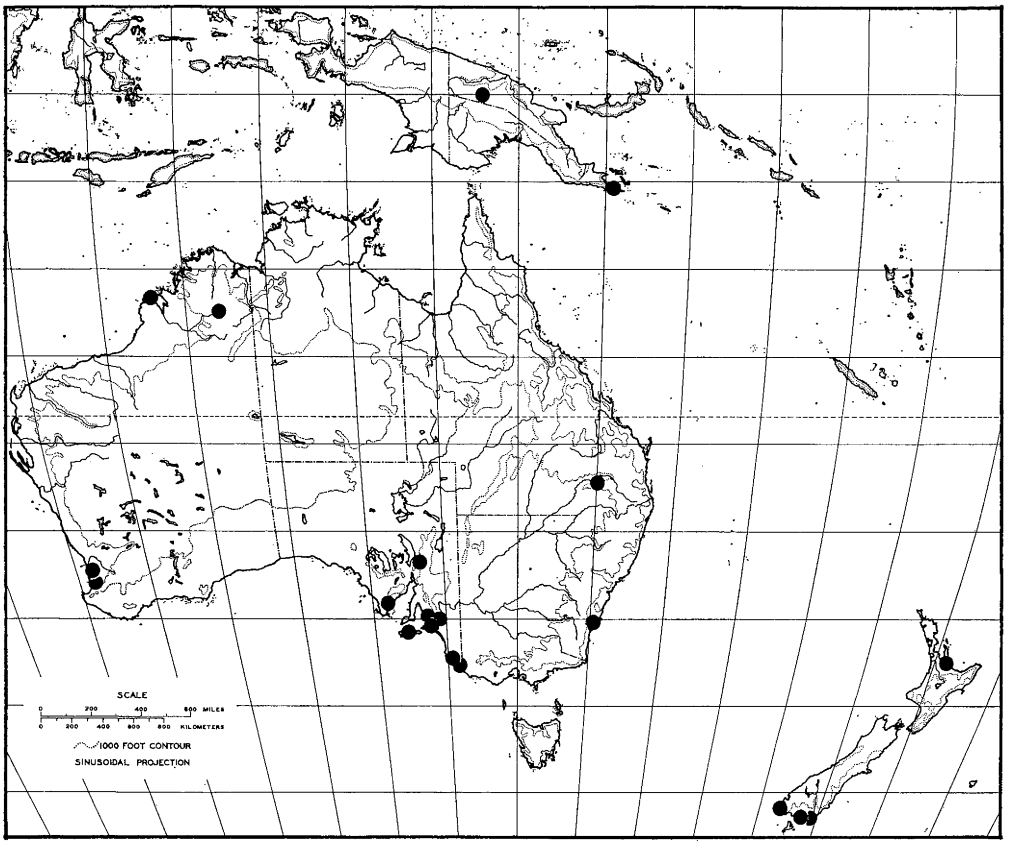

Fig. 14. *Sonchus hydrophilus*. Distribution.

la base. *Feuilles du collet* 5—30×1—3 cm, linéaires-oblancéolées, entières ou peu séquées, marges denticulées, piquantes. *Feuilles caulinaires* 12—40×2—7 cm, oblongues-triangulaires ou étroitement elliptiques, pinnatifides à pennipartites; auriculée, oreillettes arrondies; marges denticulées, piquantes; lobes ± triangulaires. *Pédoncule* 1—9×1—2 mm, poiluglanduleux, rarement glabre, à une bractée (rarement 3). *Capitules* 1,2×1 cm, plus larges pendant l'anthèse. Nombre de fleurs 100—200 par capitule. *Écailles de l'involucre* ± 28; les externes 10, 4—9×1,5—2,5 mm, poilues-glanduleuses, rarement glabres; les intermédiaires 11, 9—12×2—2,5 mm; les internes 7, 10—12×1,5—2,5 mm. *Corolle* jaune, ± 10,5 mm. *Ligule* 4×1,25 mm. *Tube de la corolle* 6,5 mm. *Anthères* 2,25 mm. *Akènes* 2,75—3,75×1,2—1,75 mm, brunâtres, rarement crème-jaunâtres, elliptiques à obovoïdes, fortement comprimés, à 3—5 côtes (généralement 3), marges et côtes ciliées vers les deux bouts. *Aigrette* ± 8 mm, ± caduque.

DISTRIBUTION. Nouvelle Guinée, Australie et Nouvelle Zélande.

Nouvelle Guinée: Wabag, c. 9500 ft, HOOGLAND et SCHODDLE 7073 (L!) — Lake Iviva, Wabag, c. 8300 ft, WOMERSLEY 15284 (L!) — Laiagam, c. 8500 ft, HOOGLAND et SCHODDLE 7581 (BM! L!) — Milne Bay Distr., Papua, 8500 ft, CRUTTWELL 1332 (K!).

Australie. Australie Occidental:

Darling Range, MORRISON s.n. (K!) — Swan Riv. DRUMMOND 75 (K!) — Riv. Cygnet, DE PREISS 116 (P!) — Halls Creek, CLELAND s.n. (AD!) — Australie Méridionale: Adelaide, University, CLELAND s.n. (AD!) — National Park Adelaide, CLELAND s.n. (AD!) — Hawker, BLACK s.n. (AD!) — Point McLeay, CLELAND s.n. (AD!) — Tumby Bay, SYMON s.n. (ADW!) — Narrung, CLELAND s.n. (AD!) — Murray, HILTON s.n. (ADW!) — Fleurieu Peninsula, c. 5 km N Victor Harbour, CLELAND s.n. (holotype, AD!) — Victor Harbour, CLELAND s.n. (AD!) — Goolwa Barrage, CLELAND s.n. (AD!); HILTON 19001 (ADW!) — Morialta, CLELAND s.n. (AD! K!) — Morialta Falls, HILTON s.n. (ADW!) — Waterfall Gully, CLELAND s.n. (AD!) — Rendelsham, CLELAND s.n. (AD!) — Rivoli Bay, CLELAND s.n. (AD! K!) — Walker's flat, CLELAND s.n. (AD!) — Cape Banks, CLELAND s.n. (AD!) — Robe Robe, CLELAND s.n. (AD!) — Nouvelle Galles du Sud (New South Wales): Gerringong, RODWAY s.n. (K!) — Tabourie Island, RODWAY 3056 b (P!) — Queensland: Darling Downs, JOHNSON 552 (K!) — Île Kangarou: Flinders Chase, CLELAND s.n. (AD!) — Stan's Sail, Boom Riv., CLELAND s.n. (AD! CAI!).

Nouvelle Zélande: Chalky Bay, LYALE s.n. (K!) — Waihi, Ohinemuri County, PETRIE s.n. (WELT!) — Bluff Hill, Southland, near Sea level, PETRIE s.n. (WELT!) — Curio Bay cliffs, Waikawa, PETRIE s.n. (WELT!) — s. loc., HOOKER 431 (K!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus hydrophilus* croît dans les stations très humides, sur les bordures des rivières, des canaux et des lacs, etc. Cette espèce monte jusqu'à 3000 m environ dans les pays tropicaux, par exemple Nouvelle Guinée. Floraison et fructification ont lieu toute l'année, mais principalement de janvier à mars et moins fréquement d'avril à juin.

PARTICULARITÉES PALYNOLOGIQUES. Présence de pollens tétracolporés en mélange avec des pollens tricolporés; la majorité sont tricolporés.

DISCUSSION. Il nous semble que *Sonchus hydrophilus* est une espèce polyploïde, très probablement autotétraploïde, ayant son origine de *S. asper* subsp. *glaucescens*.

Les caractères macromorphologiques voisins de ces deux taxons, l'abondance du dernier dans l'aire géographique occupée par le premier en Australie Méridionale, l'absence de *S. asper* subsp. *asper* dans la même aire, et le volume beaucoup plus large des grains de pollens de *S. hydrophilus* (45—49 µ) comparé à ceux de *S. asper* subsp. *glaucescens* (30—32 µ), nous a amné à vérifier cette hypothèse.

10. **Sonchus maritimus** L.

LINNAEUS, Syst. Nat. (ed. 10) 2: 1192, 1759; Sp. Pl. (ed. 2) 1116, 1763. — Lectotype: Savage Catalogue (1945), No 949-1 (LINN!), déterminé *S. maritimus*.

Sonchus angustifolius NECK., Delic. Gallo-Belg. 2: 326, 1768.

S. aquatilis POURR. in Mém. Acad. Toul. 3: 330, 1788.

S. balthicus FRIES ex LINK, Handb. 1: 784, 1829.

S. littoralis REICHENB., Fl. Germ. Excurs. 274, 1830—1832; non *S. littoralis* (T. KIRK) COCKAYNE 1907; non *S. littoralis* (T. KIRK) ALLAN 1961.

Sonchoseris maritima FOURR. in Ann. Soc. Linn. Lyon, n s. 17: 102, 1869.

Sonchus hieracioides WILLK. in WILLK. & LANGE, Prodr. Fl. Hisp. 2: 240, 1870.

Sonchidium maritimum POMEL, Nouv. Mat. Fl. Atl. 7, 1874.

Sonchus loscosii WILLK., Suppl. Prodr. Fl. Hisp. 115, 1893.

S. vulgaris ROUY, Fl. Fr. 4: 204, 1905; pro parte.

S. otaviensis DINTER in Fedd. Rep. 30: 90, 1932.

S. transcaspicus NEVSKI in Act. Inst. Bot. Acad. Sci. U.R.S.S., Ser. 1 (4): 293, 1937.

S. baburi M. POP. in Trudy Uzbekistansk. Gosud. Univ., N.S. 27, Biol. Vyp. 14: 106, 1941; nom illegit., descr. ross.

NOMS VERNACULAIRES. *En arabe:* Libbeyn, Lobbeina (Égypte); Agararam (Fezzan, Libye); Seif-el-ghorab (Algérie) — *En français:* Laiteron maritime — *En anglais:* Sea Sow-thistle. — *En allemand:* Seestrands-Gänsedistel — *En Italien:* Cicerbita marina — *En espagnol:* Cerrajón — *En portugais:* Serralha da praia.

USAGES. D'après CHOPRA et al. (1956), la plante est utilisée comme *Lactuca serriola*, où ils écrivent: «Decoction of seeds

used as demulcent. Plant cooling, sedative, diuretic, antispasmodic, hypnotic, expectorant, useful in the treatment of the coughs in phthisis, bronchitis, asthma and pertussis.»

Plante vivace, herbacée, 15—80 cm de hauteur, à rhizomes rampants, tige peu ou non ramifiée, au nombre faible des capitules, feuilles ± entières. *Rhizome* rampant, cylindrique, 3—8 mm diam., portant des racines fibreuses, fines. *Collet* non ramifié, cylindrique, 3—8 mm diam. *Tige* ramifiée dans la partie supérieure ou non ramifiée, cylindrique, 2—8 mm diam., glabre ou légèrement blanche-tomenteuse vers le sommet. *Feuilles du collet* glabres, subcoriaces, ± linéaires, entières, moins developpées que les caulinaires, base engainante, non auriculée. *Feuilles caulinaires* 5—28×0,4—4 cm, légèrement tomenteuses sur la face inférieure surtout chez les juvéniles; linéaires-lancéolées, ± oblongues à oblongues-oblancéolées, entières, rarement pinnatifides à pennipartites; base engainante et auriculée, oreillettes arrondies; nervure médiane proéminente. *Pédoncule* 0,5—7 cm, tomenteux vers le capitule. *Capitules* peu nombreux, 10—15×6—8 mm avant l'anthèse, 20—30 mm diam. pendant l'anthèse. Nombre de fleurs 80—150 par capitule. *Écailles de l'involucre* ± 27; les externes 10, 3—7×1—2 mm; les intermédiaires 8, 10—12×2—2,5 mm; les internes 9, 10—12×2 mm. *Corolle* jaune de citron, devenant orangé après l'anthèse, pourpre sur la face inférieure des fleurs externes des capitules, ± 18 mm. *Ligule* ± 12×2—2,5 mm. *Tube de la corolle* ± 6 mm. *Anthères* 3×0,4 mm. *Akènes* 2,25—3×1—1,6 mm, crème-jaunâtres à bruns clair, étroitement ellipsoïdes, plus atténués vers la base, légèrement ridés ou lisses, à marges épaisses et larges et une côte médiane sur chaque face. *Aigrette* ± 3 fois plus longue que l'akène, généralement caduque.

DISTRIBUTION. Portugal, Espagne, Îles Baléares, Îles Canaries, France, Corse, Italie, Sicile, Sardaigne, Yougoslavie, Albanie, Grèce, Crète, Turquie, Syrie, Palestine, Jordanie, Irak, Arabie Saoudite, Iran, Afghanistan, Pakistan, U.R.S.S., Maroc, Algérie, Tunisie, Libye, Égypte, République Sud-Africaine, Sud-Ouest Africain et Australie.

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus maritimus* croît dans des stations humides, sur les sables maritimes près de la mer, ainsi qu'au Sahara, dans les oasis, où l'eau est abondante, et dans les marécages, en mélange avec les plantes qui caractérisent ce milieu (*Juncus*, *Typha*, *Cyperus laevigatus*, etc.). Floraison et fructification presque toute l'année, mais principalement pendant le printemps et l'été.

CARACTÈRES CARYOLOGIQUES. n=9 (Boulos); 2n=18 (Boulos & Henin in Boulos 1960; Delay 1968).

DISCUSSION. *Sonchus maritimus* L., comme la majorité des espèces du sous-genre *Sonchus*, est une espèce polymorphe, surtout en ce qui concerne les formes des feuilles et le volume des capitules. Il nous semble que, les autres facteurs restant ± les mêmes, la variation des formes des feuilles est due aux différences des teneurs en sel du sol. Les sols à concentration saline élevée nourrissent des spécimens à feuilles étroites; au fur et à mesure que le pourcentage du sel diminue, les feuilles deviennent plus larges.

Nous avons aussi remarqué que cette espèce est également influencée par le degré d'intensité de la lumière; les individus mis en pots, à l'ombre, ont produit des parties végétatives plus développées et plus denses, et avaient une floraison plus tardive que les spécimens croissant dans des conditions normales de lumière.

S. maritimus est donc très sensible au milieu. Les akènes ne sont pas influencés par lui, et ont toujours les mêmes caractères.

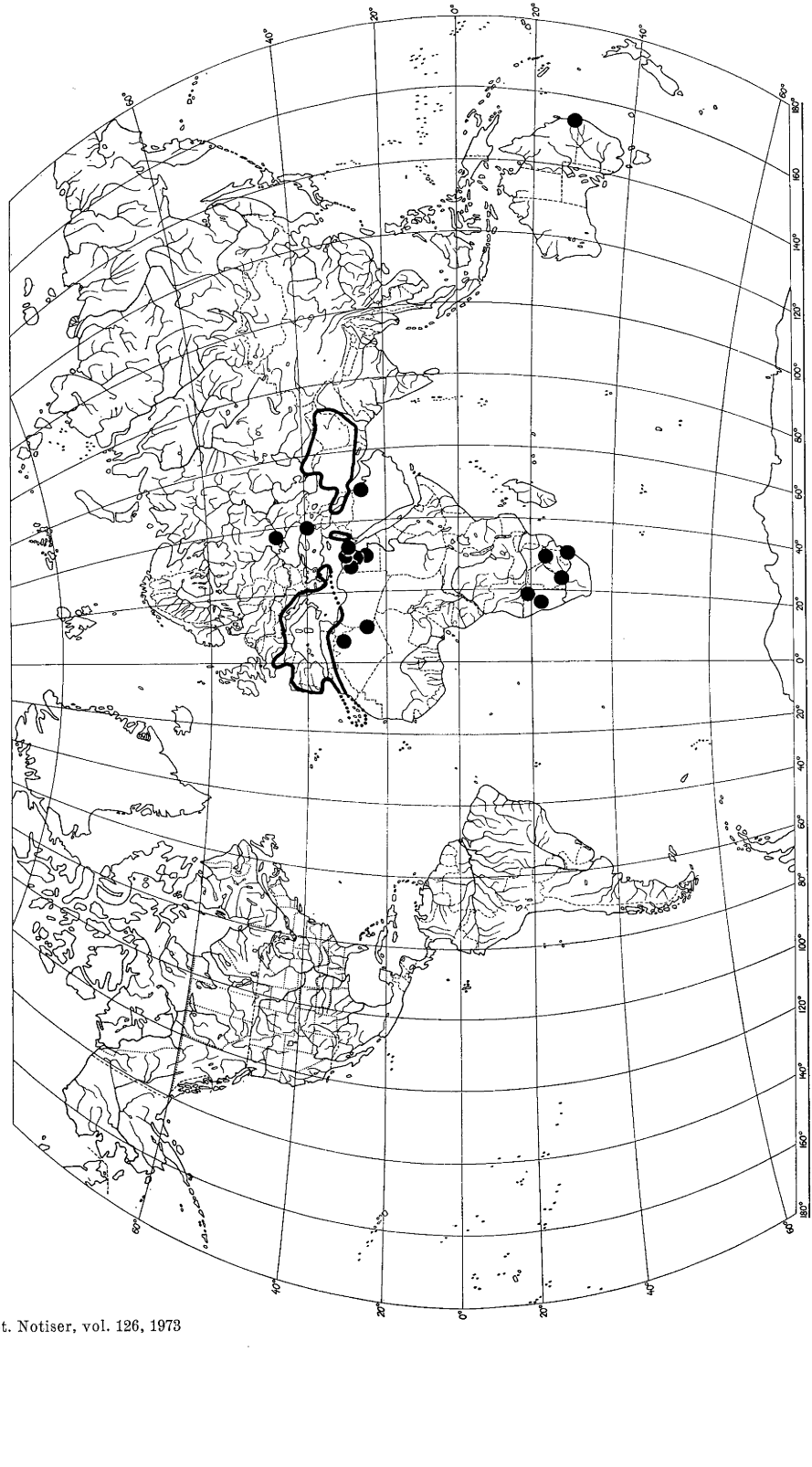

Fig. 15. *Sonchus maritimus*. Distribution.

11. **Sonchus palustris** L.

LINNAEUS, Sp. Pl. (ed. 1) 2: 793, 1753. — Lectotype: Savage Catalogue (1945), No 949-4 (LINN!).

Sonchus sexpedalis GILIB., Fl. Lithuan. 3: 241, 1781.

S. sagittatus MOENCH, Meth. Plant. Hort. Bot. 544, 1794.

S. paludosus GÜLDENTS. ex LEDEB., Fl. Ross. 2 (2): 836, 1845—1846.

S. maritimus ECHEAND. ex LOSC. & PARD., Ser. Inconf. (ed. 1) 64, 1863; non *S. maritimus* L. 1759.

Sonchoseris maritima FOURR. in Ann. Soc. Linn. Lyon, n.s. 17: 102, 1869.

Sonchidium palustre POMEL, Nouv. Mat. Fl. Atl. 6, 1874.

Sonchus inundatus M. POP. in Trudy Uzbekistansk. Gosud. Univ., N.S. 27, Biol. Vyp. 14: 105, 1941; nom illegit., descr. ross.

NOMS VERNACULAIRES: *En français:* Laiteron des marais, Laiteron aquatique — *En anglais:* Marsh sow-thistle, Tall marsh sow-thistle — *En allemand:* Sumpf-Gänsedistel, Sumpfsaudistel, Milchdistel, Saudistel — *En flamand:* Moeras Melkdistel — *En hollandais:* Melckweys, Melkriet — *En italien:* Crespigno di palude — *En suèdois:* Strandtistel.

USAGES. D'après BONNIER (1923), les propriétées médicales de cette espèce sont analogues à celles de *Taraxacum dens-leonis* et de *Sonchus oleraceus* (voir «Usages» sous *S. oleraceus*).

Plante vivace, herbacée, à rhizome rampant, 1—2,5 m de hauteur, capitules nombreux, densément poilus-glanduleux. *Rhizome* rampant, ± cylindrique, portant des racines fibreuses. *Collet* simple, ± cylindrique. *Tige* simple, cylindrique vers le sommet, angulée-ailée vers la base, à poils noirs glanduleux dans la partie supérieure. *Feuilles du collet* 5—13×1—4 cm, oblancéolées à oblongues-lancéolées, entières à pinnatifides. *Feuilles caulinaires* 10—35×3—20 cm, glabres, rarement légèrement poilues, sagittées, auriculées, décurrentes; les supérieures entières, oblongues-lancéolées, acuminées, engaînantes; les basales à ± 3 paires des lobes lancéolés, 2—8×1—3 cm, lobe terminal 5—22 cm; marges denticulées; nervure médiane 2—3 mm large à la base. *Pédoncule* 0,2—5 cm, à l'aisselle d'une bractée triangulaire. *Capitules* nombreux, densement poilus-glanduleux, poils bruns foncés à noirâtres. Nombre de fleurs ± 85 par capitule. *Écailles de l'involucre* ± 42; les externes 21, 2,5—9×1—1,5 mm, densément poilues-glanduleuses; les intermédiaires 11, 10—12×1,5 mm, à nervure médiane poilue-glanduleuse; les internes 10, 10—12×1,5 mm. *Corolle* jaunâtre, ± 12 mm. *Ligule* ± 6 mm. *Tube de la corolle* ± 6 mm. *Anthères* 3,5×0,4 mm. *Akènes* ± 3,75×1,2 mm, crème-jaunâtres, les externes quelquefois plus foncés; ± ellipsoïdes, légèrement atténués vers les deux bouts, légèrement comprimés, finement ridés transversalement, à une côte principale et ± 4 côtes moins importantes sur chaque face, marges épaisses. *Aigrette* ± 2 fois plus longue que l'akène, caduque.

DISTRIBUTION. France, Italie, Grande Bretagne, Suède, Danmark, Pologne, Belgique, Pays Bas, Allemagne, Autriche, Tchécoslovaquie, Hungarie, Roumanie, Bulgarie, Yougoslavie et U.R.S.S.

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus palustris* croît dans des stations très humides; les marais, fondrières, sur les bordures des étangs et des rivieres. Floraison et fructification de juillet à août.

CARACTÈRES CARYOLOGIQUES. 2n =18 (WULFF 1937, HENIN in BOULOS 1960).

DISCUSSION. *Sonchus palustris* possède un grand nombre des capitules. Les tiges florifères et les capitules sont poilus-glanduleux. Chaque capitule a un nombre élevé d'écailles (± 42); par contre, un nombre assez petit de fleurs (± 85). La forme sagittée des feuilles est caractéristique de cette espèce.

11 a. **Sonchus palustris** L. subsp. **sosnowskyi** (SCHCHIAN) BOULOS

BOULOS in Bot. Not. 125: 296, 1972.

Sonchus sosnowskyi SCHCHIAN in Not. Syst. Geogr. Inst. Bot. Tphilis 15: 72, 1949.

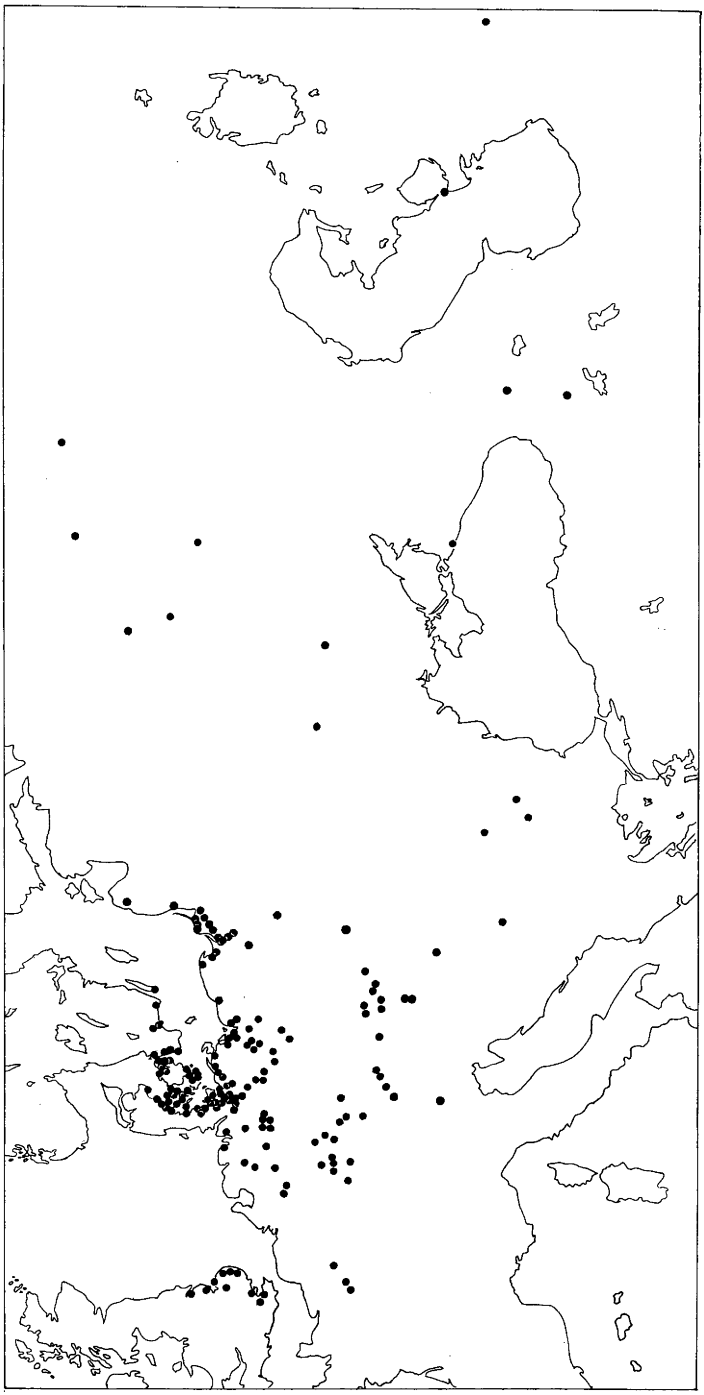

Fig. 16. *Sonchus palustris* subsp. *palustris*. Distribution.

DISTRIBUTION. U.R.S.S., endémique.

DISCUSSION. *Sonchus palustris* subsp. *sosnowskyi* est endémique dans la région du sud Caucase. Cette sous-espèce diffère principalement de *S. palustris* subsp. *palustris* par ses tiges et capitules glabres.

12. **Sonchus crassifolius** POURR.

POURRET ex WILLD. Sp. Pl. 3: 1509, 1803. — Type: Espagne, non vide.

Sonchus simplicissimus LAG. Gen. et Sp. Nov. 24, 1816.

NOMS VERNACULAIRES. *En espagnol:* Ensaladetas — *En allemand:* Dickblättrige Gänsedistel.

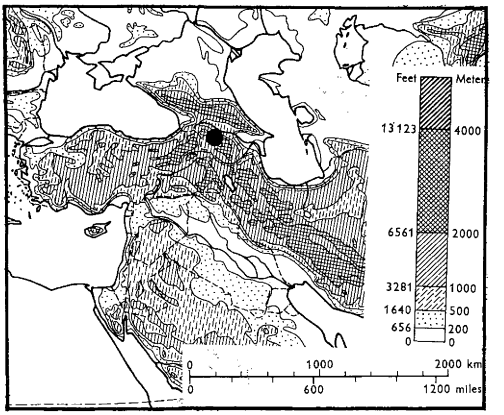

Fig. 17. *Sonchus palustris* subsp. *sosnowskyi*. Distribution.

Plante vivace, 10—40 cm de hauteur, glabre, non ramifiée, d'une forme pyramidale; feuilles coriaces, à marges très piquantes, capitules presque sessiles. *Rhizome* ligneux, cylindrique, ± 4 mm diam., portant des racines fibreuses fines. *Collet* simple, ligneux, ± cylindrique, ± 5 mm diam. *Tige* non ramifiée, glabre, cylindrique, 3—10 mm diam. *Feuilles du collet* plus longues que les caulinaires, 4—16×1—4 cm, spatulées, non sequées, à marges irrégulièrement dentées, pourvues d'épines très piquantes. *Feuilles caulinaires* 3—10×1—3 cm, auriculées, oblongues à oblongues-elliptiques, triangulaires vers le sommet, non sequées à pinnatifides, marges irrégulièrement dentées, à épines jaunâtres, mucronées et piquantes. *Pédoncule* 2—12 mm, à ± 3 bractées triangulaires. *Capitules* peu nombreux, denses, latéraux et terminaux, 15×10 mm. Nombre de fleurs ± 125 par capitule. *Écailles de l'involucre* ± 35, sommet obtus et cilié; les externes 12, 5—10×2,5 mm; les intermédiaires 10, 12—15×2,5—4 mm; les internes 13, 11—14×2,5 mm. *Corolle* jaune, 11—13,5 mm. *Ligule* 5,5—6 mm. *Tube de la corolle* 5,5—7,5 mm. *Anthères* 3×0,5 mm. *Akènes* 2—3×1—1,4 mm, comprimés, brunâtres, ± elliptiques à ± oblong, marges épaisses; à ± 3 côtes sur chaque face; transversalement rugueux. *Aigrette* ± 3,5 fois plus longue que l'akène, persistante.

DISTRIBUTION. Espagne, endémique.

Espagne: Urgell, prats del Catell del Remei, Los Coladors, 250 m, BEREST, BOLÓS et BRAUN-BLANQUET s.n. (BC!) — Urgell, Montsoà, FONT-QUER s.n. (BC!) — Aranjuez, REUTER s.n. (G!); GUINEA s.n. (RNG!); GRAELLS s.n. (CGE! MPU!) — Castella Nova, Aranjuez, versus Mar de Ontígola, BOLÓS s.n. (BC!) — Castella Nova, Aranjuez, 500 m, FONT-QUER 100 (BC! MA! ZT!) — Mar Chica, près Aranjuez, FONT-QUER s.n. (K! S! UPS!) — Ciempozuelos, près Aranjuez, HACKEL s.n. (W!); BOURGEAU 2231 (CGE! G! LD! P! W!); WINKLER 4725 (G!) — Entre Ontigola et Aranjuez, REUTER s.n. (G!) — La Tajodilla, Alhambra, 750 m, J. GONZÁLEZ s.n. (BC!) — Morata de Tajuña, près Madrid, 750 m, VICIOSO s.n. (BC!) — Laguna de Gallocanta, Teruel, c. 1050 m, SANDWITH 5410 (K!) — Albacete, 750 m, FONT-QUER s.n. (BC!); 800—1000 m, PORTA et RIGO 566 (FI! G! K! P!) — Entre Albacete et Balazote, PORTA et RIGO 312 (B! LD! P! W!) — El Mas-Blanco, Castelserás, LOSCOS 55 (FI! G! P! W!) — Rivas, REUTER s.n. (G!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus crassifolius* croît dans des stations humides à sols salés ou calcaires, sur les bords des rivières, dans les champs et les prés, à une altitude de 500—1000 m. Floraison et fructification de mai à août.

Fig. 18. *Sonchus crassifolius*. FONT QUER 100 (ZT!).

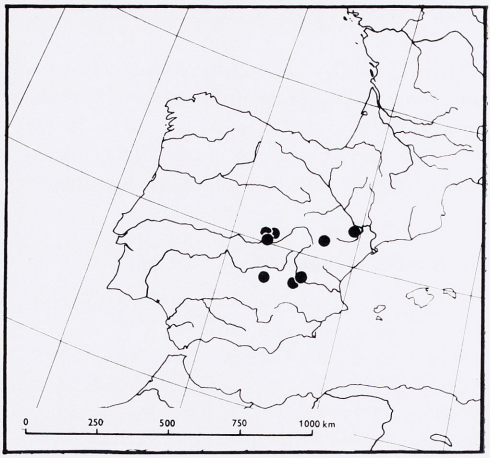

Fig. 19. *Sonchus crassifolius*. Distribution.

DISCUSSION. *Sonchus crassifolius* est la seule espèce parmi celles du genre *Sonchus* qui possède des tiges florifères courtes et denses. La plante est non ramifiée à feuilles coriaces et marges très piquantes. Elle présente aussi un port pyramidal très particulier.

13. **Sonchus arvensis** L.

LINNAEUS, Sp. Pl. (ed. 1) 2: 793, 1753. — Lectotype: Savage Catalogue (1945) No 949-5 (LINN!).

Hieracium arvense SCOPOLI, Fl. Carniol. (ed. 2) 2: 110, 1772.

Sonchus nitidus VILL., Prosp. Hist. Pl. 33, 1779.

S. hispidus GILIB., Fl. Lithuan. 3: 241, 1781.

S. hantoniensis SWEET, Hort. Brit. (ed. 2) 278, 1830.

S. intermedius KOCH, Syn. Fl. Germ. (ed. 1) 434, 1837.

S. exaltatus WALLR. in Linnaea 14: 659, 1840.

S. decorus CAST., Cat. Pl. Env. Marseille 91, 1845.

S. glandulosus SCHUR, Enum. Pl. Transs. 371, 1866.

S. laevissimus SCHUR, Enum. Pl. Transs. 371, 1866.

S. pratensis SCHUR, Enum. Pl. Transs. 968, 1866.

Sonchoseris decora FOURR. in Ann. Soc. Linn. Lyon, n.s. 17: 102, 1869.

S. arvensis FOURR. in Ann. Soc. Linn. Lyon, n.s. 17: 103, 1869.

Sonchus repens BUB., Fl. Pyren. 2: 110, 1897—1901.

S. vulgaris ROUY, Fl. Fr. 4: 204, 1905, pro parte.

S. humilis ORLOVA, Nov. Syst. Plant. Vascul. 1964: 344, 1964.

NOMS VERNACULAIRES. *En français:* Laiteron, Laiteron des champs — *En anglais:* Corn sow-thistle, Milk-thistle, Swine-thistle, Tree sow-thistle, Dindle, Gutweed — *En allemand:* Saudistel, Mag-Distel, Acker-Gänsedistel, Ackersaudistel, Feldgänsedistel, Gross-Habichkraut — *En suèdois:* Fet-tistel — *En flamand:* Akker-Melkdistel — *En hollandais:* Akker-melkdistel, Akker-melkwied, Dawdissel, Dawdistel, Dauwkoolen, Groote hawikskruid, Melkwiet, Melkriet, Milk-stammen, Molk-distel.

USAGES. D'après BONNIER (1923) «la racine, torréfiée, peut être employée comme celle de Chicorée, pour être ajoutée

au café, ou pour le remplacer. Les abeilles récoltent du nectar sur les fleurs. Les propriétées médicales sont analogues à celles de *Taraxacum dens-leonis*» (voir les usages de *Sonchus oleraceus*).

Plante vivace, 30—150 cm de hauteur, à rhizome rampant; glabre sauf les capitules qui sont poilus-glanduleux. *Rhizome* rampant, cylindrique, portant des racines fibreuses. *Collet* simple, cylindrique, 2—6 mm diam. *Tige* cylindrique, 3—10 mm diam., glabre et non ramifiée vers la base, ramifiée et poilue-glanduleuse vers le sommet. *Feuilles du collet* 5—15×2—4 cm, auriculées, entières, pinnatifides à pennipartites, lobes ± triangulaires, marges dentées. *Feuilles caulinaires* 5—30 ×2—10 cm, auriculées, pennipartites à pinnatiséquées, lobes ± triangulaires, marges dentées, piquantes. *Pédoncule* 20 —80×1,5 mm, poilu-glanduleux et plus épais vers le capitule. *Capitules* poilus-glanduleux, d'un nombre varié suivant la vigeur de la plante, 18×15 mm diam., 4 cm diam. lorsqu'ils sont ouverts. Nombre de fleurs 150—235 par capitule. *Écailles de l'involucre* 38—50, sommet obtus et cilié; dans un capitule à 47 écailles: les externes 22, 6—10×1,5 mm, densément poilues-glanduleuses; les intermédiaires 14, 12—15×2 mm, base et nervure médiane poilues-glanduleuses; les internes 11, 13—15×1—2 mm. *Corolle* jaune, devenant jaune-orangé après l'anthèse, 18—26 mm. *Ligule* 9—12×2 mm. *Tube de la corolle* 9—14 mm. *Anthères* 4×0,5 mm. *Akènes* d'une couleur brun foncé, moins fréquement brun, brun clair, orangé, jaune doré, etc., généralement le rang extérieur est d'une couleur plus claire que les intérieurs; comprimés, ± elliptiques, 2,5—3,5 ×1—1,5 mm, à 2 côtes principales sur chaque face; rugueux; marges épaisses; sommet à une partie circulaire où l'aigrette est attachée. *Aigrette* ± 4 fois plus longue que l'akène, persistante.

DISTRIBUTION. Espagne, France, Italie, Grande Bretagne, Irelande, Suède, Norvège, Finlande, Danmark, Faeröer, Pologne, Belgique, Luxembourg, Pays Bas, Allemagne, Autriche, Suisse, Tchécoslovaquie, Hungarie, Roumanie, Bulgarie, Yougoslavie, Albanie, ?Grèce, U.R.S.S., États-Unis et Canada.

Sonchus arvensis est une espèce commune du nord-ouest de l'Europe, moins commune en Europe Centrale et rare en Europe méridionale.

Les échantillons de l'Extrême Orient, déterminés *S. arvensis* L., doivent être considérés, soit comme appartenant à *S. brachyotus* DC. de Chine, Mongolie, Japon, etc. soit à *S. wightianus* DC. d'Afghanistan, Pakistan, Inde, Java, etc. (voir la distribution de *S. brachyotus* et *S. wightianus*).

Par ailleurs, les déterminations de *S. arvensis* de l'Afrique du Nord que nous avons pu vérifier, sont douteuses. Nous avons examiné certains specimens, par exemple de Tlemcen, FAURE s.n. (LD!), déterminé *S. arvensis* qui doit être considéré *S. mauritanicus* BOISS. & REUT.

En Amérique du Nord, *S. arvensis* a été introduit, très probablement de l'Europe; il y est complètement naturalisé et devenant l'une des «mauvaises herbes» des cultures surtout au nord et nord-est de ce continent.

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus arvensis* est une herbe très nusible aux cultures, à cause de ses rhizomes rampants, par lesquels la plante se multiplie rapidement. Elle se rencontre dans les stations humides, dans les cultures abandonnées et sur les sables maritimes. Floraison et fructification de juin à octobre et principalement de juillet à août.

CARACTÈRES CARYOLOGIQUES. 2n =54, cf. LÖVE & LÖVE (1961) et BOULOS (1961).

13 a. **Sonchus arvensis** L. subsp. **uliginosus** (M. BIEB.) BÉGUINOT

BÉGUINOT, Fl. Padovana 2(2): 591, 1911. — Type: ?LE, Turkestan.

Sonchus uliginosus M. BIEB., Fl. Taur.-Cauc. 2: 238, 1808.

S. glaber SCHULT., Obs. Bot. 162, 1809.

S. arvensis L. β *glabrescens* GUENTH., GRAB. & WIMM., Enum. stirp. phanerog. Siles. 127, 1824.

S. arvensis L. γ *laevipes* KOCH, Synops. Fl. Germ. et Helvet., ed. 2, 498, 1844.

S. arvensis var. *uliginosa* TRAUTV. in Bull. Soc. Nat. Mosc. 39 (2): 388, 1866.

S. arvensis L. β *laevipes* BOISS., Fl. Orient. 3: 798, 1875.

S. ketzkhovelii SCHCHIAN in Not. Syst. Geogr. Inst. Bot. Tphilis (15): 71, 1949.

S. arvensis L. f. *glabrescens* (GUENTH., GRAB. & WIMM.) KIRP., Fl. USSR 29: 251, 1964.

DISTRIBUTION. Espagne, France, Italie, Grande Bretagne, Suède, Norvège, Finlande, Danmark, Pologne, Allemagne, Autriche, Tchécoslovaquie, Hungarie, Roumanie, Bulgarie, Yougoslavie, Albanie, Grèce, Turquie, U.R.S.S., États-Unis et Canada.

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus arvensis* subsp. *uliginosus* croît dans les champs cultivés et les cultures abandonnées en stations mésophiles. Floraison et fructification principalement de juin à septembre.

CARACTÈRES CARYOLOGIQUES. 2n = 36, cf. LÖVE & LÖVE (1961) et SHUMOVICH & MONTGOMERY (1955).

DISCUSSION. *Sonchus arvensis* ssp. *uliginosus* est facile à distinguer de *S. arvensis* ssp. *arvensis* par ses capitules glabres (poilus-glanduleux chez *Sonchus arvensis* ssp. *arvensis*). Autres différences peu importantes existent entre les deux taxons et résident dans la vigueur de la plante, la taille des feuilles, etc.

Fig. 20. *Sonchus brachyotus*. ?MOELLENDORF s.n. (BR!).

14. **Sonchus brachyotus** DC.

DE CANDOLLE, Prodr. 7: 186, 1838. — Lectotype: Tucutiam, U.R.S.S., TURCZANINOV s.n. (G-DC!).

Sonchus chinensis FISCH., Hort. Gorenk. (ed. 2) 33, 1812; nom. nud.

S. maritimus TURCZ. in Bull. Soc. Nat. Mosc. 96, 1838; non *S. maritimus* L. 1759.

S. shzucinianus TURCZ. ex HERD. in Bull. Soc. Nat. Mosc. 43: 189, 1870.

S. fauriei LÉVEILLÉ & VANIOT in Feddes Rep. Nov. Sp. 7: 102, 1909.

S. taquetii LÉVEILLÉ in Feddes Rep. Nov. Sp. 8: 141, 1910.

S. cavaleriei LÉVEILLÉ in Feddes Rep. Nov. Sp. 8: 451, 1910.

S. arvensis L. subsp. *brachyotus* (DC.) KITAMURA in Mém. Coll. Sci. Univ. Kyoto, Ser. B, 23 (1): 148, 1956.

S. arvensis L. f. *brachyotus* (DC.) KIRP., Fl. USSR 29: 253, 1964.

NOMS VERNACULAIRES. *En japonais:* Hachijora, Hatijona, Hachijho-na, Hachijiôna.

Plante vivace, herbacée, 25—100 cm de hauteur, rhizomateuse, généralement non ramifiée, glabre à l'exception d'un tomentum blanc au-dessous des capitules, feuilles rarement peu séquées. *Rhizome* cylindrique, ± 4 mm diam., plein, portant des racines fibreuses, fines, 0,2—1,5 mm

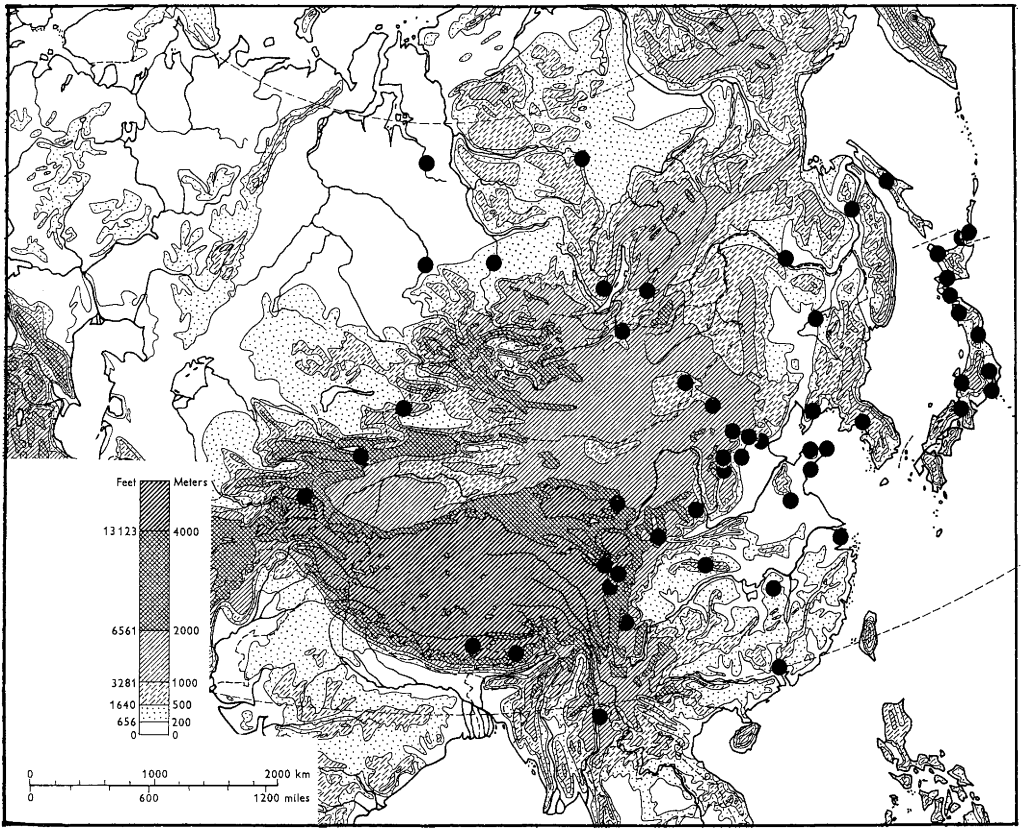

Fig. 21. *Sonchus brachyotus*. Distribution.

diam. *Collet* cylindrique, plein, non ramifié, ± 4 mm diam. *Tige* légèrement anguleuse par la décurrance des feuilles, 2—10 mm diam., rarement ramifiée. *Feuilles du collet* 5—12×1—2 cm, étroitement elliptiques, non séquées à pinnatifides, lobes triangulaires, marges denticulées, base engainante, auriculée. *Feuilles caulinaires* 5—22×1—5 cm, les basales décurrentes, ± elliptiques, étroitement elliptiques à étroitement obovales, non séquées, rarement pinnatifides à pennipartites; marges denticulées; base engainantes, auriculée. *Pédoncule* 0,3—7 (2,5) cm, blanc-tomenteux dans la partie supérieure, à ± 3 bractées triangulaires, 3×1 mm. *Capitules* d'un nombre varié suivant la vigueur de la plante, 1,5×1,2 cm, ± 4 cm diam. pendant l'anthèse. Nombre de fleurs 170—300 par capitule. *Écailles de l'involucre* 41—56; les externes 17—22, 4—9×1,5—3 mm; les intermédiaires 14—19, 13—15×2,5 mm; les internes 10—15, 12—15×2 mm. *Corolle* jaune, 16—24 mm. *Ligule* 7—11,5 mm. *Tube de la corolle* 9—12,5 mm. *Anthères* 3,5 mm. *Akènes* 2,2—4×±1 mm, comprimés, ± oblong à étroitement-elliptiques, crème-jaunâtres à brunâtres, à 1—3 côtes principales sur chaque face, légèrement ridés. *Aigrette* blanc brillant, ± 11 mm, persistante.

DISTRIBUTION. U.R.S.S., Mongolie, Chine, Asie Centrale, Tibet, Korée, Thaïlande et Japon.

U. R. S. S.: Sibérie orientale, MAINAN s.n. (P!) — Karakol, Turkestan, 5300—5400 ft, REGEL 268 (K!) — Région E lac Baïkal, STUKOW 172 (LE!) — Tucutiam, TURCZANINOW s.n. (lectotype, G-DC!) — Sakhalin Island, FAURIE 732 (Type de *Sonchus fauriei* LÉV., P!) — Blagowjeschtschensk (Blagověščensk), KARO s.n. (S!) — s. loc., STUKOW s.n. (LE!).

Mongolie: Tjaygan-Obo, ERIKSSON 916 (LD!) — Mongolie borealis, POTANIN s.n. (P!) — Hara Osso, ANDERSSON 434 a (UPS!) — Tang jeou fang K'ou louan, Mongolie centrale, LICENT 3396 (BM! P!) — Mongolie orientale, DAVID 2007 (P!) — Mongolie septentrionale, MOLLESON s.n. (G!) — s. loc., DAVID s.n. (P!).

Chine: Lac Hanka, Kirin, BOHNHOT 230 (P!) — Riv. Amur, Manchuria, KARO 1644 (BM! P!) — Manchuria austro-orientalis, MAXIMOWICZ s.n. (S!) — Manshuria chinensis, KARO 1644 (P!) — Peking, BRETSCHNEIDER s.n. (K!); COWDRY 139 (K!); SWINHOE 6532 (BM!); CHIEN 105 (W!); MSELLINDORF s.n. (W!) — La Trappe, E Peking, LICENT 3336 (BM! K!) — Po-hua-Shan, KING 596 (S!) — Eastern Tombe, Hopei (Hopeh), LICU 1203 (E!) — Hsiao-wu-tai Shan Mt., Hopei, WANG 61865 (E!) — Hopei, CHOW 42867 (E!) — Kalzau, Chihli (Tschili), COWDRY 1954 (K!) — Tientsin, Chihli, CLEMENTS 2032 (E!) — Yang-Kia-ping, 1000 ft, Chihli, SMITH 698 (BM! UPS!); SCHINDLER 25 a (BM!) — Près Choni, Kansu, 3100—3300 m, CHING 965 (E!) — Yao, près Lichen, Kansu, 1825—2500 m, CHING 276 (E!) — Kansu, POTANIN s.n. (P!) — Tsingtau, Shantung, SCHINDLER 207 a (K!) — Chantong Tch'eng chan tao (Miao tao) LICENT 6430 (BM! K! P!) — Che-foo, FAUVEL s.n. (P!); COWDRY 914, 929; DEBEAUX 69 (P!) — Tschifer, SCHOTTMULLER s.n. (P!) — Lingshankou, Choluhsien, 1550 m, HSIA 2420 (E!) — Yang Ts'ounn, LICENT 1496 (BM!) — San cheu li p'ou, LICENT 6188 (P!) — Tchenkéou-tin, Su-tchuen oriental, FARGES 204 (K! P!) — Yangtsoun, TCHELY 8195 (P!) — Ta-Wutai-schan, Schansi, SERRE 2423 (W!) — Chansi (Schansi, Shansi), LICENT 2233 (P!) — Kiangsi, READ 1256 (BM!) — Shanghai, DEBEAUX s.n. (P!) — Miao-Wang San Mt., HUGH s.n. (BM!) — Zeunteon Tenghosam, HUGH s.n. (BM!) — Sung Pan, 3000—3200 ft, SMITH 4085 (LD! UPS!); NEIGOLD s.n. (W!) — Pa-Shui-ko-shan, 2100 ft, SMITH 7462 (UPS!) — Yü-Tze, 8000 ft, SMITH 6869 (LD!) — Canton, DAHLSTRÖM 248 (S!) — Tche-Ly, Tchang Ting Fou, CHANET 607 (K!) — E Chine, s. loc., BALFOUR s.n. (K!); WILSON 3851 (BM! K!); SCHOTTMULLER s.n. (P!).

Asie Centrale: s. loc. CHAFFANJON 986 (P!); PELLIOT et VAILLANT 806 (P!).

Tibet: Pamir, APPLETON s.n. (K!) — Sanga Choling, 11,000—12,000 ft, KINGDON-WARD 12359 (BM! E!) — Gyangtse, WALTON 119 (BM! G! K!); 13,000 ft, LUDLOW (BM!); 13,190 ft, CUTTING et VERNEY 44 (K!); 4000—5100 m, MARAINI 213, 214 (FI!) — Lhasa, 13,000 ft, RICHARDSON 355 (BM!).

Korée: s. loc., FAURIE 428 (P!); FAURIE s.n. (P!).

Thaïlande: Doi Chiengdao, 1500—1800 m, KERR s.n. (BM!).

Japon: Hokkaido, Shiretoko, NARUHASHI 1135 (E!) — Île Kunashiri, FAURIE 5197 (P!) — Otaru, FAURIE 1379 (K! P!) — Sapporo, FAURIE 1322, 3142 (P!) — Hakodate, ALBRECHT 1973 (K!); MAXIMOWICZ s.n. (C! P!); FAURIE 907 (P!) — Yokohama, MAXIMOWICZ s.n. (BM! K! P! W!) — Yokosuka, SAVATIER 714 (P!) — Kanazawa, BISSET 1988 (BM!) — Kamakoura, SAVATIER 715 (P!) — Sagalien, FAURIE 732 (BM!) — Jeddaporo, FAURIE 1322 (P!) — Kitami, Yezo (Yeso, Jesso), FURUSE s.n. (S!); Yeso, FAURIE s.n. (P!) — Tokyo (Tokio), YATABE s.n. (UPS!) — Kuroishi, FAURIE 1203 (P!) — Miyagi, JISIBA s.n. (W!) — s. loc., FAURIE 2018 (P!); GREATREX s.n. (K!); PETERSEN s.n. (UPS!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus brachyotus* croît dans les champs cultivés, les cultures abandonnées, sur les lisières des forêts, etc. Floraison et fructification de mai à janvier et principalement d'août à septembre.

CARACTÈRES CARYOLOGIQUES. 2n =18, ROUX & BOULOS (1970).

DISCUSSION. *Sonchus brachyotus* est une espèce peu connue et qui était souvent prise pour *S. arvensis* de l'Europe occidentale, *S. arvensis* ssp. *uliginosus* de l'Europe orientale, ou *S. wightianus* de l'Inde, Java, etc. En outre, dans plusieurs ouvrages, on trouve *S. brachyotus* cité parmi les synonymes de *S. arvensis.*

Cependant, *S. brachyotus* est une espèce bien définie du point de vue morphologique, caryologique et géographique. C'est une plante non ramifiée, à feuilles non séquées (rarement peu ramifiée à feuilles peu séquées), à capitules glabres, pourvues d'un tomentum blanc à leur base

seulement. Il est aussi facile de distinguer *S. brachyotus* de *S. arvensis* ssp. *uliginosus*; la dernière sous-espèce a des feuilles séquées, des capitules moins grands, des écailles d'involucre moins larges et des akènes plus foncés et plus larges que chez *S. brachyotus*.

Le nombre chromosomique de *S. brachyotus*, 2n=18, est un caractère de valeur indiscutable pour distinguer les trois taxons, donc: *S. arvensis* ssp. *arvensis* 2n=54; *S. arvensis* ssp. *uliginosus* 2n =36 et *S. brachyotus* 2n=18.

D'autre part, le nombre 2n=18 de *S. brachyotus* montre que cette espèce est la plus primitive de ce groupe: *S. arvensis* étant hexaploïde et la sous-espèce *uliginosus* étant tétraploïde. Il est très probable qu'une multiplication des chromosomes a eu lieu dans le sens: *Sonchus brachyotus* → *S. arvensis* ssp. *uliginosus* → *S. arvensis* ssp. *arvensis*.

15. **Sonchus wightianus** DC.

DE CANDOLLE, Prodr. 7:187, 1838. — Lectotype: Peninsula Ind. orientalis, WIGHT 1505 (G-DC!); isolectotype (CGE!).

Sonchus orixensis ROXB., Hort. Beng. 60, 1814; nom. nud.

S. picris LÉVEILLÉ & VANIOT in Feddes Repert. Nov. Sp. 8: 451, 1910.

NOMS VERNACULAIRES. *En Inde:* Sahadevibari, Banpalang, Bhangra, Nallatapata (d'après CHOPRA et al. 1956) sous *S. arvensis*. Le dernière espèce n'existe pas en Inde, donc ces noms sont donnés pour *S. wightianus* et probablement pour la sous-espèce *wallichianus*. — *En Indonésie* (*Java*): Lempoeng.

USAGES. CHOPRA et al. (1956) écrivent pour *S. arvensis*, qui est, comme il a été dit plus haut, *S. wightianus* s.l. (voir le paragraphe au-dessus): «The plant is used as *Lactuca seriola* and *Sonchus maritimus*. Moreover, it contains a bitter principle, and its roots are given in jaundice» (voir *S. maritimus*, usages).

Plante vivace, 30—140 cm de hauteur, à racine pivotante, capitules densément poilus-glanduleux, feuilles séquées. *Racine* pivotante, ligneuse dans la partie supérieure, ramifiée; chez quelques specimens on peut distinguer une structure rhizomatique. *Collet* ligneux, non ou peu ramifié, 3—8 mm diam. *Tige* glabre, cylindrique, ramifiée, 3—10 mm diam. *Feuilles du collet* ± en rosette, 5—25× 2—6 cm, oblancéolées, entières à pennipartites; lobes ± triangulaires, triangulaires-déprimés ou ovales-déprimés, marges denticulées; base légèrement engaînante. *Feuilles caulinaires* assez denses sur la partie inférieure de la tige, espacées vers le sommet, 8—30×1—6 cm; les basales bien développées, longues, ± elliptiques, à bases engaînantes; auriculées, à oreillettes arrondies; pinnatifides à pennipartites; marges denticulées, assez piquantes; lobes des formes variées, donc ± triangulaires et légèrement réfléchis vers la base, triangulaires-déprimés, ovales-déprimés, oblong-triangulaires, etc. Feuilles supérieures courtes, lancéolées à étroitement triangulaires, généralement non séquées, auriculées à oreillettes aigues. *Pédoncule* 0,3—8,5 cm, à l'aisselle d'une bractée triangulaire, glabre dans la partie basale, densément poilu-glanduleux et souvent blanc-tomenteux vers le capitule, pourvu d'une bractée triangulaire dans la partie supérieure. *Capitules* normalement nombreux, 1,2—1,5×2,5—4 cm pendant l'anthèse, moins larges avant et après l'anthèse; densément poilus-glanduleux et souvent à un tomentum blanchâtre, dense. Nombre de fleurs 180—300 par capitule. *Écailles de l'involucre* ± 41; les externes ± 15, 5—11×1,5 mm, poilues-glanduleuses; les intermédiaires ± 11, 10—12 ×2,5 mm, nervure médiane poilue-glanduleuse; les internes ± 15, 12×2 mm. *Corolle* jaunâtre, 12—14 mm. *Ligule* 5—6 mm. *Tube de la corolle* 7—8 mm. *Anthères* 2,5 mm. *Akènes* 3,5—4,25×±1 mm, brunâtres, étroitement elliptiques, transversalement ridés, à une côte principale et ± 4 côtes moins importantes sur chaque face, marges épaisses. *Aigrette* ± 8 mm, ± persistante.

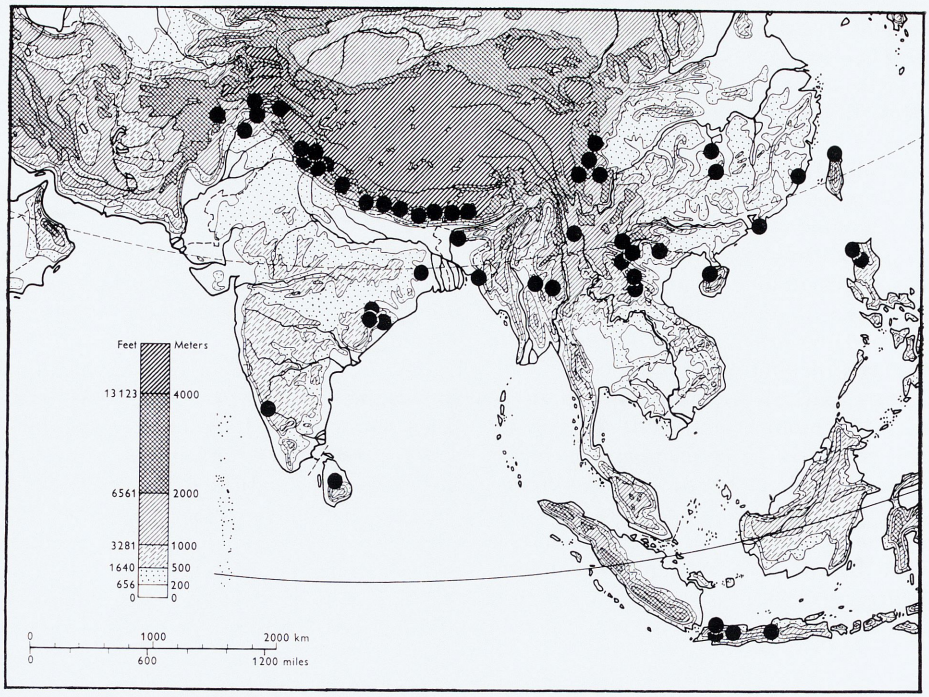

Fig. 23. *Sonchus wightianus* subsp. *wightianus*. Distribution.

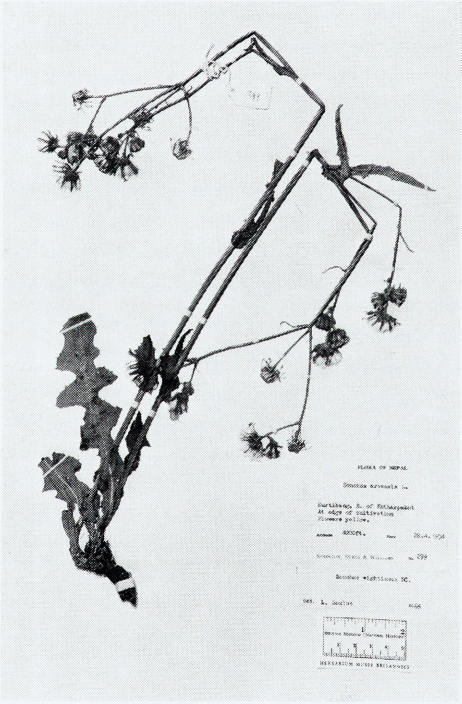

Fig. 22. *Sonchus wightianus* subsp. *wightianus*. STAINTON, SYKES et WILLIAMS 299 (BM!).

DISTRIBUTION. Afghanistan, Pakistan, Inde, Népal, Bhotan, Sikkim, Laos, Vietnam du Nord, Cry Lanka (Ceylan), Java, Philippines, Birmanie, Chine, Haïnan, Hong Kong et Formose (Taïwan).

Afghanistan: Kurrum valley, AITCHSON 303 (K!); GRIFFITH 872 (K!).

Pakistan. W Punjab: Rawalpindi, AITCHSON 202, 445 (K!); STEWART 7109 (K!) — Oghi-Battagram road, Hazara Distr., BURTT et ALI 736 (E!).

Inde. Cachmir: Srinagar, 5200 ft, CLARKE 29132 (BM! K!) — E. Punjab: Li, Bushahr, Simla, PARMANAND 710 (E!) — Kulu Lahauli, DRUMMOND 23058, 23144 (K!) — Sakeshar, DRUMMOND 14516 (K!) — Dhar, DRUMMOND s.n. (K!); DRUMMOND 25579 (K!) — Sutlez valley, 1000 ft, THOMSON s.n. (K!) — Himalaya: Bhinja, DUTHIE s.n. (K!); 4000—8000 ft, THOMSON s.n. (K!); GERARD s.n. (K!); 3000 ft, EDGEWORTH s.n. (K!);

DUTHIE 19746 (K!); RICHMOND 296 (K!) — Uttar Pradesh: Dehra Dun, New Forest, RAIZADA 6802 (E!); 2500 ft, GAMBLE 22610 (K!); 2200 ft, KANJILAL 797 (K!) — Simla, 4500—4700 ft, COLLETT 563 (K!) — Mobrikpoor, EDGEWORTH 212 (K!) — Tehri-Garhwal, 6000 ft, GAMBLE 26875 (K!) — Sub-Gangetic plain, 800 ft, THOMSON s.n. (K!) — Bihar et Orissa: Thuamul-Rampur, Kalahandi State, 2400 ft, MOONEY 1723 (K!) — Mile 57 on Rayagada-Koraput road, Orissa, 1600 ft, MOONEY 3329 (K!) — Near Gunpur, S Kalahandi, 2500 ft, MOONEY (K!) — Bengal: Sitapahar, COWAN 627 (E!) — S. Inde: Peninsula Indiae Orientalis, WIGHT 1505 (lectotype, G-DC! isolectotype CGE!); WIGHT 1680 (L!) — Cormon Ghat, 4000 ft, GAMBLE 11376 (K!) — Malabar, c. 2200 m, SLOOKEN 291 (L!) — Muthukulam, HENRY 626 (BLAT!) — Assam: Khasia, 5000—6000 ft, HOOKER FIL. et THOMSON s.n. (K!) — Chittagong, 5000 ft, HOOKER FIL. et THOMSON 551 (K!).

Népal: Jamal, Kathmandu, 4000—6000 ft, PANDE 48 (BM!) — Sarda Khola Valley, Dharkhani village, 3800 ft, POLUNIN, SYKES et WILLIAMS 1815 (E!) — Amrai, SE Bijauri, 2000 ft, POLUNIN, SYKES et WILLIAMS 3646 (BM!) — Mugu Karnali Valley, between Mangri and Daura, 8000 ft, POLUNIN, SYKES et WILLIAMS 5259 (BM! E! UPS!) — Baglung, 3000 ft, STAINTON, SYKES et WILLIAMS 74 (BM! E! UPS!) — Burtibang, E Kutharpekot, 4000 ft, STAINTON, SYKES et WILLIAMS 299 (BM! UPS!) — Near Bongakhani, 6000 ft, STAINTON, SYKES et WILLIAMS 2714 (BM! E! UPS!) — Gurjakhani, 8000 ft, STAINTON, SYKES et WILLIAMS 3661 (BM! E! UPS!) — Mayangdi Khola, 3000 ft, STAINTON, SYKES et WILLIAMS 4186 (BM! E! UPS!) — Arun Valley, Maghang Khola, E Num, 8000 ft, STAINTON 221 a (BM!).

Bhotan: Thimpu Chu, Namselling, 7200 ft, BOWES LYON 3054 a (BM!) — Rydak, Chukka Timpu, 4000 ft, COOPER 1257 (BM!).

Sikkim: Mongpu, 4000 ft, CAVE s.n. (E!) — Birick (Birik), 2000 ft, CAVE s.n. (E! G!) — Sembri, 2000 ft, CAVE s.n. (E!) — Rongbe (Rongbi), 5000 ft, CAVE s.n. (E!) — Sikkim, Regio temp. et trop., 1000—6000 ft, HOOKER s.n. (CGE! G! K! S!).

Laos: Muang Cha, c. 1100 m, KERR 20979 (BM! K!).

Vietnam du Nord: Tonkin occidental, BON 2166 a (P!) — Tonkin méridional, BON 3614, 2166 (P!) — Tonkin, PETELOT 353 (P!); BALANSA 3086 (P!); MOURET 159 (P!) — Cha pa, HAUTEFEUILLE 132 (P!) — Cha pa, Lào Kay, 1500 m, PÉTELOT s.n. (P!) — Bac Kan, EBERHARDT 4630 (P!).

Ceylan: Kislande, SIMPSON 8348 (BM!).

Java. W. Java: Sindanglaja, HOLSTVOOGD 53 (L!); VELETON s.n. (L!) — Pasir Karet, BACKER s.n. (L!) — Bandung, BACKER s.n. (L!) — Prov. Batavia, BAKHUIZEN VAN DEN BRINK 1278, 1279 (L!); Artja village, SCHIFFNER 2781 (L!) — Tjibodas, c. 1420 m, SCHIFFNER 2825 (L!); 600 m, HOCHREUTINER 2233 (L!) — Tjidadap, BAKHUIZEN VAN DEN BRINK 5599 (L!); c. 1000 m, WINCKEL 1161 (L!) — Buitenzorg, 250—275 m, HALLIERF 178 a, b (L!); BOERLAGE s.n. (L!); c. 240 m, BAKHUIZEN VAN DEN BRINK 1933 (L!); c. 250 m, BAKHUIZEN VAN DEN BRINK 7321 (L!); VAN OOSTSTROOM 12634, 12893, 14183 (L!) — Mt. Malabar, 2200 m, VAN SLOOTEN 291 (L!) — Sukabumi, BACKER 22157 (L!) — Kelapa Nugal, BACKER 5986 (L!) — Mt. Tjikoraj, BACKER 5412 (L!) — Java Central: Ketenger, 500 m, H. C. VAN DER GAAG 111 (L!).

Philippines. Luzon: Benguet, WILLIAMS 1437 (K!); MERRILL 1788 (BM! L! P!); Ifugao, Mt. Province, MENDOSA et BUWAYA 719 (L!) — Bontoc, VANOVERBERGH 2063 (P!).

Birmanie: Maymyo Distr., 3400 ft, KAN 14224 (E!).

Chine: P'ing T'ou Shan, T'ang Wan village, Yi Chang Distr., Hunan, TSANG 23565 (BM!) — Ichang, HENRY s.n. (K!) — Tchen-kéon-tin, Su-tchuen oriental, FARGES 348, 780 (P!) — Chengtu, CHIEN 5951 (E!); FANG 12319 (BM!) — Pao-hsing-hsien, CHU 2948 (E!) — Shap Man Taai Shan, TSANG 22597 (P!) — Amoy Hance, CHARY 1447 (K!) — NW Yunnan, 9—10,000 ft, FORREST 2365 (BM!) — Yun-nan, Mong-Tze, LEDUC s.n. (P!) — Yunnan, BODINIER et DUCLOUX s.n. (P!); DELAVAY 1928 b (P!); MAIRE s.n. (BM!) — W Chine, Kiao-kia, 400 m, MAIRE 972 (E!) — Yun-nan-sen, MAIRE 991, 1276 (E!) — Pin-fa, Yun-nan-sen Distr., CAVALERIE 3704 (E!) — Mt. Omi, W Chine, WILSON 4995 (BM! K!).

Haïnan: Tiu Lung Shan, Taam-chau Distr., TSANG et WAI-TAK 812 L.U. 16311 (K!).

Hong Kong: Victoria, LAMONT 400 (BM!) — Hong Kong, BODINIER 659 (P!).

Formose (Taïwan): Vicinity of Taihoku, TANAKA 5053 (L!) — Tamsuy, OLDHAM 283 (BM! K!) — Bunkiko, 1500 m, FAURIE 1422 (BM!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus wightianus* croît dans les stations assez humides, sur les bordures des champs de riz, des rivières et des canaux d'irrigation, dans les pelouses, etc., à une altitude de 200—

3200 m. Floraison et fructification ont lieu toute l'année.

CARACTÈRES CARYOLOGIQUES. n= 9, MITRA & DATTA 1967; erron. cité pour *S. brachyotus* DC.

PARTICULARITÉES PALYNOLOGIQUES. Pollens de taille importante (36—40 μ).

DISCUSSION. DE CANDOLLE (1838) a décrit *Sonchus wightianus* d'après les récoltes de WIGHT de l'Inde. Cette épithète était totalement négligée et était toujours considérée, dans les différents ouvrages, comme synonyme de *S. arvensis* L. Cependant, *S. wightianus* est une espèce très caractéristique, dont la morphologie et le port sont totalement différents de ceux de *S. arvensis*. Le premier possède des racines pivotantes, alors que *S. arvensis* est une espèce rhizomatique; l'akène est plus long, moins large et moins rugueux que chez *S. arvensis*.

15 a. **Sonchus wightianus** DC. subsp. **wallichianus** (DC.) BOULOS

BOULOS in Bot. Not. 125: 297, 1972.

Sonchus wallichianus DC., Prodr. 7: 185, 1838. — Lectotype: WALLICH et HAMILTON 361, Nepalia, déterminé *Sonchus longifolius* WALL. (G-DC!).

S. longifolius WALL., Cat. No 3251, 1828—1832; nom. nud.; non *S. longifolius* TREV. 1818.

S. cumbulus BUCH.-HAM. ex WALL., Cat. No 3251, 1828—1832; nom. nud.

S. lachnocephalus RECH. FIL., K. Dan. Vid. Selsk. Biol. Skrift. 8(2) Symb. Afghan. 2: 202, 1955.

DISTRIBUTION. Afghanistan, Pakistan, Inde, Népal, Bhotan, Assam et Chine.

Afghanistan: Kabul, 1800 m, HEDGE et WENDELBO 3074 (E!) — Prov. Kabul, Tang-i-Gharu, Mahi Parr, 1800 m, HEDGE et WENDELBO 4273 (E!) — Kurrum Valley, AITCHSON 35 (K!) — Mamakhel, 4000 ft, KOELZ 11588 (W!) — Nuristan, 1000 m, EDELBERG 131, 1165, 1573 (W!).

Pakistan. Provinces N.W.F.: Peshwar, DEANE s.n. (K!); Islamic College, SUHAIL 245 (K!) — Peshwar, 8 miles on Charsadda road by Kabul road, BURTT 597 (E!) — Dir, SALIM 94 (K!); 6500 ft, HARRISS 16297 (E!) — Swat: Near Saidu Sharif village, c. 3500 ft, RODIN 5435 (K!) — Khawazakhiela to Shangla, 1300 m, LAMOND 1699 (E!) — Between Oghi and Battal, W side of Kattai Gali, c. 4700 ft, BURTT 1455 (E!).

Inde. Punjab: AITCHSON 42 (K!); DRUMMOND 25578, 25729 (K!) — Bihar et Orissa: Singbhum, HAINES 468, 4823 (K!) — Nawadih, Surguja State, 3700 ft, MOONEY 1303 (K!) — Surguja State, Mainpat, 3300—3600 ft, MOONEY 798 (K!) — Kulta, E Bonai, 2000 ft, MOONEY 3805 (K!) — Gunpur, Kalahandi, 2400 ft, MOONEY 3499 (K!) — Karlapat, Kalahandi, 2000 ft, MOONEY 3464 (K!) — Chota Nagpur, Hazaribagh, Parasnah, 4000 ft, CLARKE 20217 B (BM!) — Bengal: Maradih, Manbhoon, 11,000 ft, WATT 9311 (E!).

Népal: Tamur Valley, Mewa Khola, 3500 ft, STAINTON 1277 (BM! E! UPS!) — Arum Valley, Maghang Khola, E Num, 8000 ft, STAINTON 2216 (BM! E!) — Shiar Khola, near Tumje, 8000 ft, GARDNER 819 (BM!) — Sarda Khola, Dharkhan, 3800 ft, POLUNIN, SYKES et WILLIAMS 1815 (BM!).

Bhotan: Tsalimape to Simo Sampa, 7500—7700 ft, GOULD 883 (K!) — Thimpu Chu, Namselling, 7200 ft, BOWES LYON 30546 (BM!).

Assam: Lohit Valley, Walong, 4000 ft, KINGDON-WARD 19192 (BM!) — Di Chu Gorge, 4500 ft, KINGDON-WARD 19364 (E!).

Chine: Province Yun-nan, DELAVAY 1928 a (P!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. Dans son aîre de répartition géographique, la sous-espèce *wallichianus* de *S. wightianus* croît mélangée avec la sous-espèce typique ayant presque les mêmes caractères écologiques, mais la floraison et fructification ont lieu principalement de février à août.

DISCUSSION. La sous-espèce *wallichianus* de *S. wightianus* diffère principalement de la sous-espèce typique par ses capitules blancs-tomenteux à la base et par l'absence presque totale de poils glanduleux.

Fig. 24. *Sonchus wightianus* subsp. *wallichianus*. STAINTON 2388 (BM!).

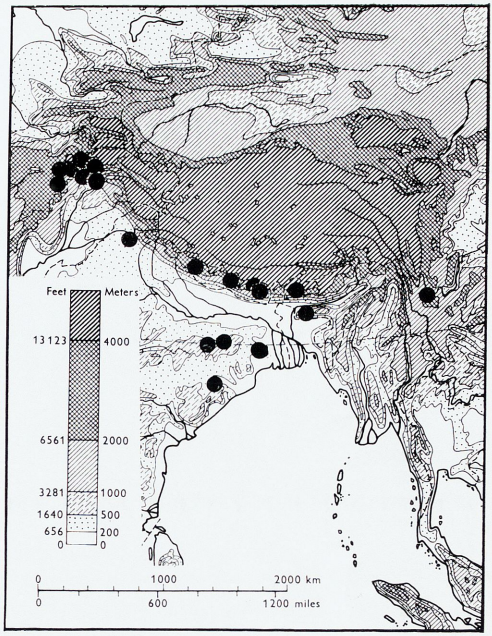

Fig. 25. *Sonchus wightianus* subsp. *wallichianus*. Distribution.

16. **Sonchus malaianus** MIQ.

MIQUELON, Fl. Ind. Bat. 2: 113, 1856. — Holotype: Java, Mt. Diëng, JUNGHUHN 344 (L!).

Sonchus javanicus JUNGH., Nat. et Geneesk. Arch. 2: 41, 1845; nom. illegit. (homonym); non *S. javanicus* SPRENG. 1826.

S. oreophilus MIQ., Fl. Ind. Bat. 2: 114, 1856.

S. maritimus L. var. *malaianus* (MIQ.) HOCHR. in Candollea 5: 338, 1931—1934.

Plante vivace, 60—180 cm de hauteur, ramifiée; glabre, sauf à la base des capitules; feuilles entières, subcoriaces. *Racines* pivotantes, richement ramifiées, ligneuses, 5—15 mm diam. *Collet* ligneux, 5—15 mm, généralement ramifié. *Tige* cylindrique, glabre, 3—15 mm diam., ligneuse à la base chez les individus âgés, portant les bases des feuilles tombées. *Feuilles caulinaires* 8—28×0,5—3,5 cm, entières, ± étroitement elliptiques à étroitement rectangulaires, subcoriaces, marges entières ou denticulées; sommet aigu ou légèrement obtus chez les feuilles basales, acuminé chez les supérieures; nervure médiane proéminente; base engainante, auriculée, à oreillettes ± triangulaires, aigues. *Pédoncule* 0,5—8 (3) cm, glabre ou quelquefois très légèrement poilu-glanduleux, tomenteux vers le capitule. *Capitules* généralement nombreux, 1,5×1 cm, plus larges pendant l'anthèse, blancs tomenteux à la base. Nombre de fleurs 100—150 par capitule. *Écailles de l'involucre* ± 35; les externes 11, 5—10×2—3,75 mm; les intermédiaires 12, 13—16×2—3 mm; les internes 12, 13—15×1,5—3 mm. *Corolle* jaune, 14—18,5 mm. *Ligule* 7—8,5 mm. *Tube de la corolle* 7—10 mm. *Anthères* 3,5 mm. *Akènes* 4—4,5×1,2 mm, comprimés, étroitement elliptiques, brunâtres, légèrement ridés transversalement, marges épaisses, à une côte

Fig. 26. *Sonchus malaianus*. ZOLLINGER 2198 (P!).

médiane principale et ± 4 côtes moins importantes sur chaque face. *Aigrette* ± 11 mm, ± persistante.

DISTRIBUTION. Îles de Sumatra et Java, Indonésie; endémique.

Sumatra: Atjeh, Gajo Lands, 1500 m, VAN STEENIS 9364 (K! L!).

Java. W Java: Priangan, Mt. Papandajan, 2050 m, ECOMA VERSTEGE s.n. (L!); c. 2041 m, VAN STEENIS 4248 (L!) — Java Central: S Pekalongan, Petung Kriana, BACKER 15788 (L!) — Mt. Diëng, JUNGHUHN 344 (holotype, L!) — E Java: Madium Prov., Ngebel, KOORDERS 29180 (L!) — Mt. Lawu, Gandong Dal (=Gandong Valley), 1300—1400 m, ELBERT 47 (L!); 2900—3200 m (top), ELBERT 46 (L!); 3250 m, VAN LEER (L!) — Mt. Welirang, 2700 m, BACKER 36963 (L!) — Mt. Tengger, WENT s.n. (L!) — Ngadisari, 2400 m, KOORDERS 37419, 37420 (L!) — Mt. Ardjuno, KOORDERS 38182 (L!);

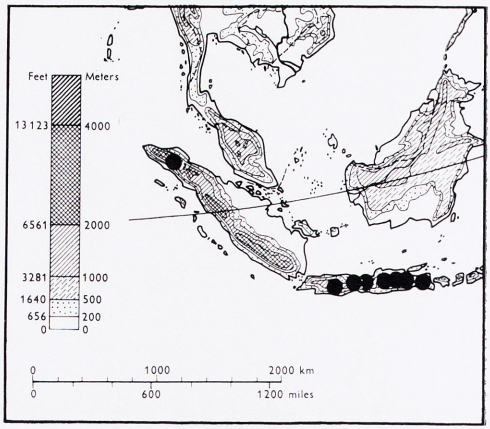

Fig. 27. *Sonchus malaianus*. Distribution.

4000—7000 ft, ZOLLINGER 2198 (P!) — Tosari, BACKER 36609 (L!); JESWIET s.n. (L!) — Mt. Widodaren, BACKER 3720 (L!) — Mt. Idjen, Gending Waluh, 1450 m, KOORDERS 43346 (L!) — Kawah Idjen, KOORDERS 43346, 43350 (L!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus malaianus* croît dans les forêts tropicales de Sumatra (rare) et de Java (assez commune), sur les bordures des chemins, à une altitude de 1100—3250 m. Floraison et fructification ont lieu presque toute l'année (rarement en avril et mai).

CARACTÈRES CARYOLOGIQUES. 2n =54, STEBBINS et al. (1953), sous *Sonchus javanicus* SPRENG.

PARTICULARITÉES PALYNOLOGIQUES. Pollens tri- et tetracolporés, en mélange. Lacunes polaires très floues, malgré le très petit nombre d'épines polaires (3 seulement chez certains tricolporés).

DISCUSSION. *Sonchus malaianus* est très probablement une espèce hexaploïde (2n=54) ayant le nombre de base x=9.

Elle est remarquable par ses feuilles entières et subcoriaces.

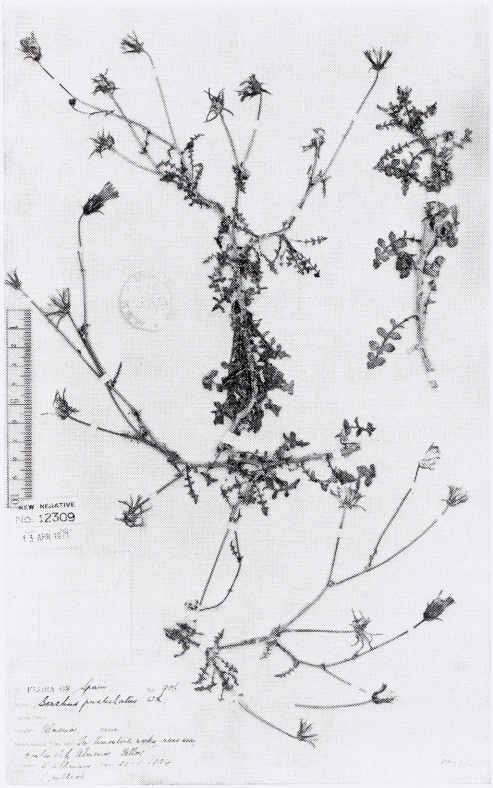

Fig. 28. *Sonchus pustulatus*. ELLMAN et HUBBARD 906 (K!).

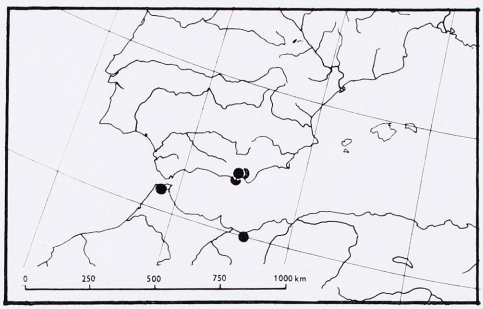

Fig. 29. *Sonchus pustulatus*. Distribution.

17. **Sonchus pustulatus** WILLK.

WILLKOMM in WILLK. & LANGE, Prodr. Fl. Hisp. 2: 242, 1865. — Paratype: Rochers abruptes à Nemours, ouest prov., Oran, BOURGEAU 84 (G!); isoparatypes (C! MPU! P! UPS! W!).

Plante vivace, ligneuse à la base, 15—30 cm de hauteur, feuilles en groupes à la base de l'inflorescence, pédoncule jusqu'à 10 cm. *Collet* simple ou ramifié, ± 5 mm diam., plein, ligneux. *Tige* ramifiée, cylindrique et herbacée dans la partie supérieure; angulée, ligneuse, à écorce crème-grisâtre vers la base. *Feuilles du collet* 4×1,5 cm, lyrées, non auriculées; lobes peu nombreux, ± triangulaires, marges entières, sommet pointu. *Feuilles caulinaires* 4—10×1,5—3,5 cm, tomenteuses à la base, autrement glabres, auriculées, pinnatiséquées; lobes d'une forme ovale caracteristique, rarement elliptiques, 0,5—1,8×0,2—1,5 cm, entières, sommet aigu. *Pédoncule* 3—10×0,2 cm, glabre, à une bractée triangulaire. *Capitules* peu nombreux, ± 3, souvent solitaires, 1,2×4 cm lorsqu'ils sont ouverts. Nombre de fleurs ± 100 par capitule. *Écailles de l'involucre* ± 24, sommet obtus et cilié; les externes ± 8, 4—8×2—3 mm; les intermédiaires ± 9, 12×3 mm; les internes ± 7, 14×2,5 mm. *Corolle* jaune, ± 21 mm. *Ligule* ± 14×2,5 mm. *Tube de la corolle* ± 7 mm. *Anthères* 4×0,5 mm. *Akènes* 3,5—5×1,5 mm, étroitement rectangulaires à elliptiques ou en forme de croissant; comprimés, faiblement rugueux, à marges épaisses et une côte médiane principale et ± 4 côtes moins importantes sur chaque face. *Aigrette* ± 8 mm; la majorité des soies ± 8 mm, caduques; les autres ± 2,5 mm, cotonneuses et persistantes.

DISTRIBUTION. Espagne, Maroc et Algérie.

Espagne. Almería: Almería, LANGE s.n. (C!); RIPLEY 73 (K!); DE COINCY s.n. (P!); 3 miles W Almería, ELLMAN et HUBBARD 906 (K!); Près Roqueta, environs d'Almería, BOURGEAU 1277 (G! K!) — Bco del Caballar, 20—50 m, PORTA et RIGO 138 (B! K! LD! P! W!); HUTER, PORTA et RIGO 1097 (CGE! G! P! UPS! W!); NILSON 532 (LD!).

Maroc: Dj. Afgal, 700 m, Bini Smih, FONT QUER 473 (BM! G! RAB!); FONT QUER 794 (S!) — Tanger, THRETHEY 213 (K!).

Algérie: Nemours, Prov. Oran, BOURGEAU 84 (paratype G!; isoparatypes C! MPU! P! W!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus pustulatus* croît dans les fentes des rochers calcaires maritimes à une altitude de 0—700 m. Floraison et fructification d'avril à juin.

CARACTÈRES CARYOLOGIQUES. 2n =18, STEBBINS et al. (1953).

DISCUSSION. *Sonchus pustulatus* forme avec les trois espèces suivantes: *S. fragilis*, *S. briquetianus* et *S. masguindalii* un groupe d'espèces affines, ayant des caractères morphologiques voisins et, en même temps, primitives par rapport aux autres espèces du sous-genre *Sonchus*.

L'aspect frutescent et la répartition géographique en Algérie, au Maroc et dans le Sud de l'Espagne, de ces quatre espèces, sont en faveur de considérer cette section (*Pustulati*) comme primitif, ayant son origine probablement dans le sous-genre *Dendrosonchus*.

18. **Sonchus fragilis** BALL

BALL in J. Bot. 11: 372, 1873. — Lectotype: Juxta Tetuan, BALL s.n. (P!).

Plante vivace, chétive, ± 10 cm de hauteur, peu ramifiée, ± glabre, capitules peu nombreux. *Racine* pivotante, ± cylindrique, ramifiée, ± 3 mm diam. *Collet* 3—6 mm diam., ligneux, plein, généralement ramifié. *Tige* courte, cylindrique, ligneuse, pleine, à écorce grisâtre. *Feuilles du collet* 3×1,2 cm, ± elliptiques, pinnatiséquées; lobes largement elliptiques, lobe terminal ± triangulaire, plus petit que les latéraux, marges entières, sommet pointu. *Feuilles caulinaires* 3—8 ×1—2 cm, auriculées, pinnatiséquées, lobes ± comme chez les feuilles du collet, mais lobe terminal quelquefois plus grand que les latéraux. *Pédoncule* 0,8—5,5 cm, à l'aisselle d'une bractée triangulaire. *Capitules* souvent solitaires, ± 10×8 mm, plus larges pendant l'anthèse. Nombre de fleurs ± 55 par capitule. *Écailles de l'involucre* ± 23; les externes 8, 3,5—8× 2—3 mm, triangulaires à étroitement ovales; les intermédiaires 8, 12×2 mm, étroitement elliptiques; les internes 7, 11 ×1,2—2,5 mm. *Corolle* jaune, 12—16 mm. *Ligule* 7—10 mm. *Tube de la corolle* 5—6 mm. *Anthères* ± 3,5 mm. *Akènes* 3,5—4,25×1 mm, comprimés, rugueux, étroitement elliptiques, souvent courbés, marges épaisses, à une côte médiane épaisse sur chaque face. *Aigrette* ± 6 mm, caduque.

DISTRIBUTION. Maroc (région Tetuan), endémique.

Maroc: Juxta Tetuan, BALL s.n. (lectotype P!) — Tetuan, BALL 676 (P!); PITARD 1013, 1015 (G! P!); PITARD 1014 (P!); WEBB et GOUDOT s.n. (C!) — Mt. Beni Hosmar, près Tetuan, BALL s.n. (K!); 700 m, FONT QUER 735 (BM! G!); MAS GUINDAL s.n. (CAI!); DAVIS 434 (K!) — Torsta, 3 km de Tetuan, WALL 794 (S!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus fragilis* croît dans les fissures des rochers calcaires de la région de Tetuan à une altitude de 700 m environ. Floraison et fructification d'avril à juillet.

PARTICULARITÉES PALYNOLOGIQUES. Brèches paraporales très ouvertes rappelant celles des *Launaea*.

DISCUSSION. *Sonchus fragilis* possède un nombre faible des fleurs (± 55) et des écailles d'involucre (± 23) par capitule (voir aussi la discussion de *S. pustulatus*).

19. **Sonchus briquetianus** GANDOGER

GANDOGER in Bull. Soc. Bot. France 55: 657, 1908. — Holotype: Ins. Congresso, 10—150 m, GANDOGER s.n. (G!).

Fig. 30. *Sonchus fragilis*. BALL s.n. (K!).

USAGES. D'après GANDOGER (1908), la plante est consommée par les habitants.

Plante vivace, 15—20 cm de hauteur, à feuilles coriaces, lobes foliaires imbriqués. *Collet* ligneux, plein, ± 4 mm diam., non ramifié. *Tige* cylindrique, creuse et poilue-glanduleuse vers le sommet; pleine et glabre vers la base. *Feuilles caulinaires* 2—9×0,8—2 cm, glabres coriaces, pinnatiséquées, lobes imbriqués, largement ovales, sommet pointu; base engainante, auriculées, oreillettes arrondies, 5—20 mm, nervure médiane proéminente, 2,5 mm à la base. *Pédoncule* 0,3—1,8 cm, glabre ou légèrement poilu-glanduleux. *Capitules* 1,2×0,8 cm. Nombre de fleurs ± 100 par capitule. *Écailles de l'involucre* ± 33; les externes 11, 3,5—7×2 mm; les intermédiaires 12, 11×2,5 mm; les internes 10, 10—12×1,5—2 mm. *Corolle* jaune-orangé, 11—15 mm. *Ligule* 5—7 mm. *Tube de la corolle* 6—8 mm. *Anthères* 3,5 mm. *Akènes*: D'après GANDOGER (1908), l'akène est rougeâtre, étroit, finement granulé. *Aigrette* ± 6 mm, ± caduque.

DISTRIBUTION. Île de Congresso, NE Maroc; endémique.

M a r o c: Ins. Congresso, archipel des îles Zafarinas (Chafarinas), 10—150 m, GANDOGER s.n. (holotype G!).

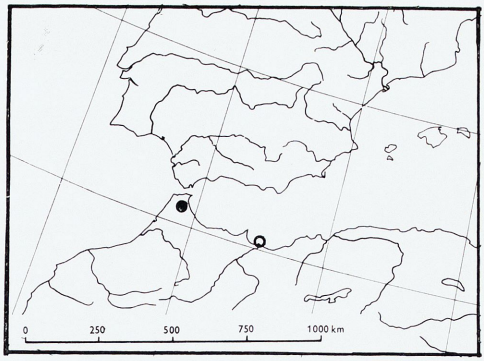

Fig. 31. *Sonchus briquetianus* (○), *S. fragilis* (●). Distribution.

DISCUSSION. *Sonchus briquetianus* est connu seulement de la collection du type (voir aussi la discussion sous *S. fragilis*).

20. **Sonchus masguindalii** PAU & FONT QUER

PAU & FONT QUER in FONT QUER, Iter Marocc. No 732, 1927. — Holotype: c. Marsa Quebira (Bocoya), 20 m, PAU et FONT QUER 732 (BM!); isotype (G!).

Plante vivace, 15—30 cm de hauteur, ramifiée, à tige ligneuse vers la base, feuilles à lobes largement elliptiques, capitules poilus-glanduleux. *Collet* ligneux, plein, ramifié ou simple. *Tige* ligneuse, pleine, à écorce crème-brunâtre, légèrement tomenteuse dans la partie basale, herbacée, creuse et lisse vers le sommet; feuilles tombant laissant des traces sur les vielles tiges basales. *Feuilles caulinaires* 3—8×1—2 cm, coriaces, bases engaînantes, tomenteuses; pinnatiséquées, lobes largement elliptiques, quelques lobes possèdent des parties basales ± rectangulaires, donnant une forme caractéristique à la plante, lobe terminal rénoforme, plus large que les latéraux. *Pédoncule* 2—8,5 cm, légèrement blanc-tomenteux vers le sommet, portant une bractée triangulaire, ± 3 mm. *Capitules* 2×4 cm lorsqu'ils sont ouverts. Nombre de fleurs ± 200 par capitule. *Écailles de l'involucre* ± 40; les externes 15, 3—10×1,5—3 mm, blanches

Fig. 32. *Sonchus masguindalii.* Isotype, PAU et FONT QUER 732 (G!).

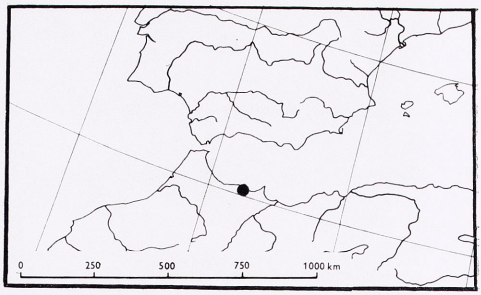

Fig. 33. *Sonchus masguindalii.* Distribution.

tomenteuses et pourvues de poils glanduleux denses; les intermédiaires 11, 11—13 ×2,5 mm, poilues-glanduleuses vers le sommet; les internes 14, 13×2 mm, glabres. *Corolle* jaune, 13—18 mm. *Ligule* 9—12 mm. *Tube de la corolle* 4—6 mm. *Anthères* 3,75 mm. *Akènes* 2,25—3,25× 0,6—0,8 mm, étroitement elliptiques, comprimés, brunâtres, marges épaisses, à une côte médiane épaisse et ± 4 côtes moins importantes sur chaque face; très faiblement rugueux ou lisses. *Aigrette* ± 7 mm, caduque, sommet pointu chez les deux types de soies.

DISTRIBUTION. Maroc, endémique.

Maroc: Près Marsa Quebira (Bocaya), 20 m, PAU et FONT QUER 732 (holotype BM!, isotype G!) — Maro-el-Borx, 200 m, PAU et FONT QUER 474 (BM! G! RAB! S!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus masguindalii* croît dans les fissures des rochers calcaires littoraux, à une altitude de 0—200 m. Floraison et fructification d'avril à mai.

DISCUSSION. L'aigrette chez *Sonchus masguindalii* possède un caractère particulier: le sommet chez les deux types des soies est pointu (voir aussi la discussion sous *S. pustulatus*).

21. **Sonchus tuberifer** SVENT.

SVENTENIUS in Boll. Inst. Nac. Invest. Agron. Madrid 18: 285, 1948. — Holotype: Île de Tenerife, archipel des îles canaries, Masca, entre Chierfe et Monte Guama, 1000 m, SVENTENIUS (in litt.); non vide.

Sonchus tuberifer SVENT. 1948, var. *latisecta* SVENT. in Boll. Inst. Nac. Invest. Agron. Madrid 18: 288, 1948.

Plante vivace, herbacée, 20—40 cm de hauteur, à racines tuberculeuses; tige non ramifiée, capitules peu nombreux, pédoncule à 3—8 bractées, la partie au-dessous du capitule renflée. *Racine:* d'après la diagnose de SVENTENIUS (1948): «Radice tuberculari, globoso-napiformi in juvenile statu, irregulariter sphaerica et ad vetustatem protuberanciis verrucosis munita valde lactifera corticeque nigra et rugosa.» *Collet* herbacé, ± 4 mm diam., non ramifié. *Tige* herbacée, cylindrique, creuse, tendre, 2—4 mm diam., non ramifiée, légèrement pubescente vers le sommet. *Feuilles du collet* 5—15×2—5 cm, ± glabres, pinnatiséquées; lobes ± triangulaires à étroitement rectangulaires, 1—5× 0,3—4 cm, marges entières ou irrégulière-

Fig. 34. *Sonchus tuberifer*. SVENTENIUS 194 (GB!).

ment dentées, sommet aigu; bases des feuilles engaînantes, auriculées, oreillettes ± triangulaires, aigues à acuminées. *Feuilles caulinaires* comme celles du collet, mais les basales bien développées, devenant plus courtes vers l'inflorescence, légèrement pubescentes. *Pédoncule* 8—40 ×0,5—1,5 mm, à 3—8 bractées, ± triangulaires; partie supérieure renflée et portant la majorité des bractées. *Capitules* 10×5 mm, plus larges pendant l'anthèse. Nombre de fleurs ± 40 par capitule. *Écailles de l'involucre* ± 20, sommet obtus et cilié; les externes 7, 2—5×1,5 mm; les intermédiaires 7, 10×2 mm; les internes 6, 11×1,5 mm. *Corolle* jaunâtre, 10—15 ×1,5 mm. *Ligule* 6,5—10,5×1,5 mm. *Tube de la corolle* 3,5—4,5 mm. *Anthères* 4 mm. *Akènes* 2,5×1 mm, ± étroitement obovale, rugueux, crème-jaunâtres à bruns clair, marges assez épaisses, à une côte épaisse médiane et 3 côtes moins importantes sur chaque face. *Aigrette* 4,5 mm, très caduque; le sommet est pointu chez les deux types des soies.

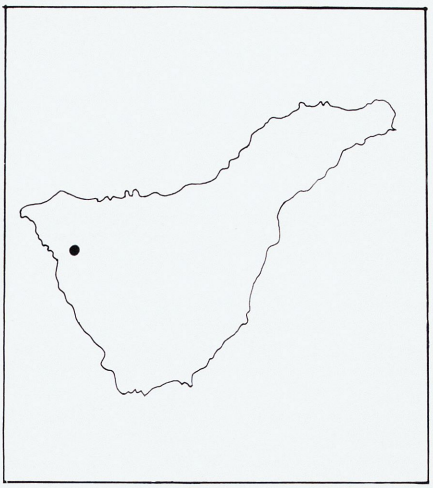

Fig. 35. *Sonchus tuberifer*. Distribution.

DISTRIBUTION. Tenerife (Masca), Îles Canaries; endémique.

Tenerife: Masca, 600 m, SVENTENIUS 96 (BC! GB! RAB!) — Roque Cantana, 600 m, SVENTENIUS 194 (BC! GB!) — El Guayo, 600 m, SVENTENIUS s.n. (CAI!) — El Chierfe, 500 m, SVENTENIUS s.n. (CAI!).

CARACTÈRES ÉCOLOGIQUES ET BIOLOGIQUES. *Sonchus tuberifer* croît dans les fissures des rochers, à une altitude de 500 à 1000 m. Floraison et fructification de janvier à mars.

CARACTÈRES CARYOLOGIQUES. 2n =18, ROUX & BOULOS (1972).

DISCUSSION. Comme chez *Sonchus masguindalii*, l'aigrette est composée des soies à sommet pointu. *Sonchus tuberifer* est caracterisé aussi par ses racines tuberculeuses et par le nombre assez élevé (3—8) des bractées sur un pédoncule renflé dans la partie supérieure.

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Pollen Development in the Eleocharis palustris Group (Cyperaceae)

I. Ultrastructure and Ontogeny

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ABSTRACT

DUNBAR, A. 1973. Pollen development in the Eleocharis palustris group (Cyperaceae). I. Ultrastructure and ontogeny. — Bot. Notiser 126: 197—254.

During the development of *Eleocharis* pollen three of the tetrad cells degenerate. The organelle population of the pollen mother cell, microspore and pollen has been investigated. Their distribution and possible functions have been linked to the degeneration of the abortive cells as well as to the ontogeny of the viable ones. Pollen mother cells are enveloped in callose layers before meiosis but no callose is deposited around each individual tetrad cell after meiosis, in marked distinction to the common mode of angiosperm pollen ontogeny. The primexine template is laid down around the entire outer surface of the tetrad beneath the callose wall. It does not form between microspores, presumably because the presence of callose is necessary for the development of the primexine template. Prior to the onset of probacula about the entire tetrad of microspores, the plasma membrane is strongly evaginated into the primexine template from the inside, simultaneous with an intrusion of callose into "gaps" in the template from the outside. Both the callose intrusions and plasma membrane evaginations are considered to influence exine pattern. After dissolution of the callose, a common wall of sculptured exine and of intine is evenly formed around the entire pollen, while between abortive cells, and between abortive and viable cells, only an inner wall of acetolyse-resistant globules is laid down.

LIST OF TERMS AND ABBREVIATIONS

Abaxial: opposite direction to adaxial

Adaxial: the part of the tapetum, pollen mother cell, tetrad or pollen grain facing towards the axis of the theca loculus

Cell plate vesicles: located in regions of cytokinesis; limited by a trilaminar membrane, inner leaflet denser than outer one

Inner wall: separates abortive cells from one another and from viable cell

Primexine template: fibrous layer beneath the callose into which probacula and protectum are laid down

Surface vesicles: located in contact with and on either side of the plasma membrane; limited by a trilaminar membrane similar to the plasma membrane

GA=glutaraldehyde; PA=periodic acid; T =thiocarbohydrazide; P=silver proteinate; PTA=phosphotungstic acid.

INTRODUCTION

A review of the literature regarding earlier opinions on the feature of the pollen morphology and development in *Eleocharis* is given by STRANDHEDE (1973).

The investigation concerning ultrastructure and ontogeny was undertaken to see whether any special cellular or extracellular phenomena arise during the life cycle of a *Cyperaceae* pollen, where, as far as is known, the tetrad generally gives rise to one viable pollen grain, while

three of the tetrad cells degenerate. In *Eleocharis*, in marked distinction to the common mode of angiosperm pollen ontogeny, no callose is deposited around the individual microspore after meiosis and hence the entire tetrad is surrounded by the pre-meiotically formed callose. This feature probably determines the future development of the outer and the inner walls of the pollen. In *Styphelia* (*Epacridaceae*) after normal meiosis in the pollen mother cell three nuclei migrate to one end of the cell and degenerate. Callose does not normally penetrate into the cell plate region and the absence of primary ektexine in this region has been related to the absence of callose (FORD 1971). While these findings offer some information on the role played by the callosic layer, there remains the question of how the initiation of this layer is controlled. Fine-structural studies have given some clues as to how the process may be established and the significance of these events will be discussed.

An attempt is made in the present study to follow general changes in cell organelles during pollen development, and to relate the findings to the critical periods in the life cycle of the pollen. Finally it touches on the development of the surrounding anther tissue and deals with the relationship of the pollen wall with tapetosomes (DUNBAR 1973) and Ubisch bodies. Cytokinesis will only be briefly mentioned as it is dealt with by STRANDHEDE (1973).

EVENTS AND STAGES DURING DEVELOPMENT OF THE ELEOCHARIS POLLEN

MATERIAL AND METHODS

For material see STRANDHEDE 1973.

METHODS FOR TRANSMISSION ELECTRON MICROSCOPY. Nearly mature anthers of *Eleocharis* were cut into segments immediately after immersion in the fixative, whereas young anthers were fixed intact. Most of the material was fixed in a stock solution of 0.1 M GA in 0.1 M cacodylate-HCl buffer at pH 7—7.2 adjusted to the calculated osmolality value (Table 1) by the addition of glucose of different molarities. The osmolality in milliosmols was calculated from tables in MASER et al. (1967), and further checked with a Fiske Osmometer. The osmolalities used were those which experience has shown to give proper preservation. In some of the young material the stock solution was diluted with distilled water. Stage 13 was fixed in 11 % GA in the same buffer. Stages 15 and 17 were fixed in 0.2 M GA in 0.1 M phosphate buffer (MILLONIG's in PEASE 1964) at pH 7.2. Half of the anthers from each flower bud were transferred without rinsing to osmium tetroxide in the same buffer followed by dehydration, the others were dehydrated direct. All the material was taken to an acetone series, without water rinsing, starting in 30 % acetone and proceeding to 95 % within 50 minutes; 5 changes followed of 100 % acetone within 1 hour. The anthers were infiltrated for several days with MOLLENHAUER's epon-araldite mixture no. 1 (MOLLENHAUER 1964). Sections were cut for examination with the light microscope of all material studied. Sections for examination by the electron microscope were cut with a DuPont diamond knife using an LKB Ultrotome. Some of all sectioned material was examined unstained. Some sections were treated with a methoxide solution to dissolve most of the embedding epon-araldite (PEASE 1964) and then placed in

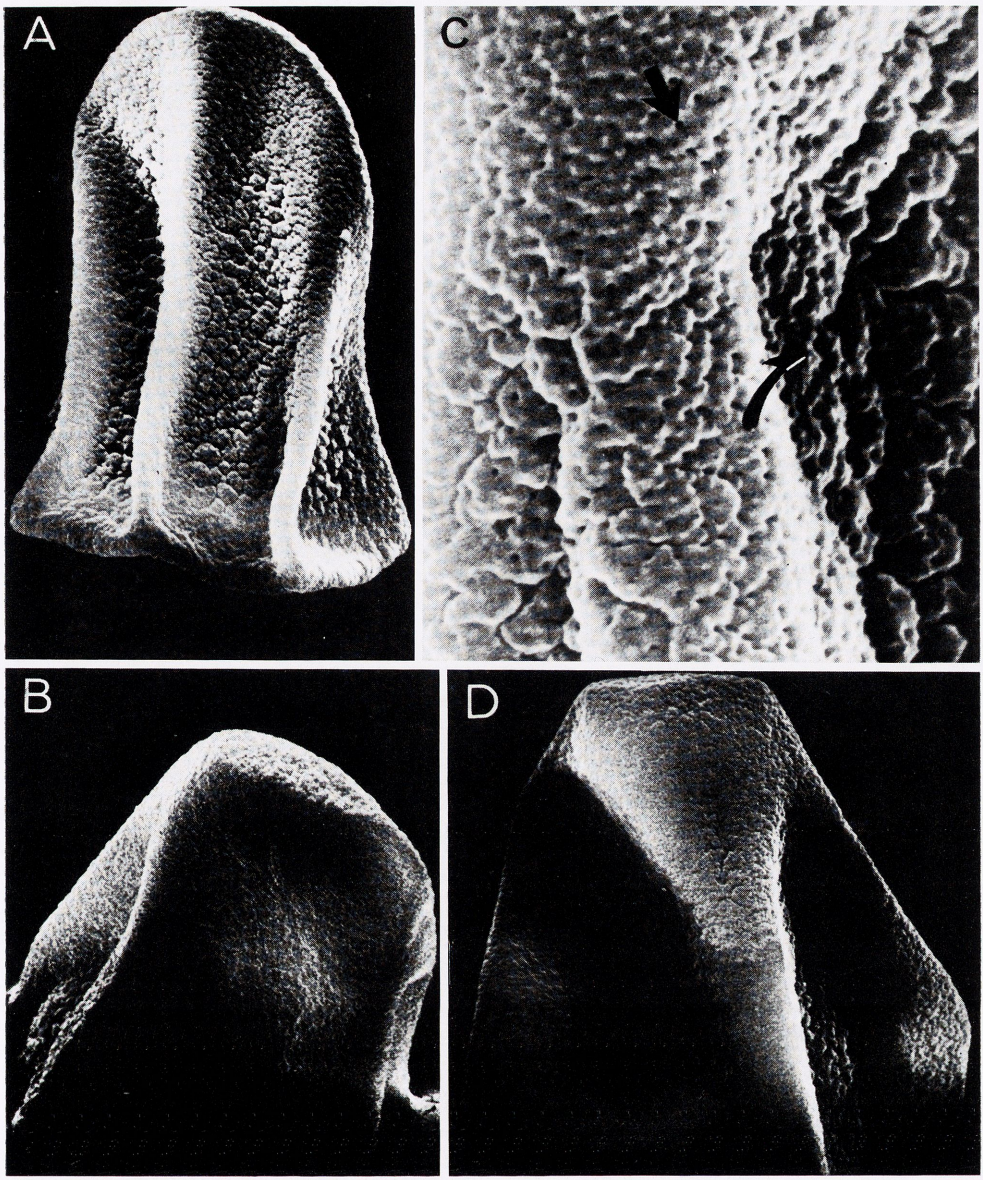


Fig. 1. Scanning electron micrographs of *Eleocharis* pollen grains collected at time of natural pollen shedding. — A: *E. palustris* ssp. *palustris*. Approx. ×2,000. — C: Higher magnification of same species as in A. Perforations in the tectum (arrow) and small pointed protrusions (bent arrow). Approx. ×26,000. — B: *E. mamillata* ssp. *mamillata*. Approx. ×2,000. — D: *E. uniglumis* ssp. *sterneri*. Approx. ×2,100.

Table 1. The osmolalities of fixation used in the different stages of development are shown. Where several osmolalities are indicated, the results proved to give about the same preservation quality.

Stages of development	Fixation osmolality						
	200	300	320	350	400	450	1,300
18	·	·	·	·	+	·	·
17	·	·	·	·	·	+	·
16	·	·	·	+	·	·	·
15	·	·	·	·	·	+	·
14	·	·	·	+	·	·	·
13	·	·	·	·	·	·	+
12	·	+	·	·	·	·	·
11	+	·	·	·	·	·	·
10	+	·	·	·	·	·	·
9	·	·	+	·	·	·	·
8	·	·	·	+	·	·	·
7	·	·	·	+	·	·	·
6	·	·	·	+	·	·	·
5	·	·	+	·	·	·	·
4	+	·	·	·	·	·	·
3	·	·	·	·	+	·	·
2	·	+	+	·	·	·	·
1	+	+	·	·	+	·	·

the acetolysis mixture (ERDTMAN 1960) at 100°C for 4 minutes to denaturate all organic material except sporopollenin from the exposed parts of the sections. After rinsing in water they were air-dried and a carbon film was evaporated at an angle of 15 degrees on the sections to shadow the sporopollenin. Some sections were PTA stained according to PEASE (1966). Where no staining information is included in the figure legend, the sections were stained with 1 % aqueous uranyl acetate for 5 minutes at room temperature and for an additional 5 minutes at 42°C followed by lead citrate (REYNOLDS 1963) for 10 minutes. In a modified treatment, sections were stained with uranyl acetate and REYNOLDS' lead citrate, as mentioned above, followed by 15 minutes' staining in KARNOVSKY's (1961) lead hydroxide, 10 % in water. GA fixation not followed by any osmium treatment was used for:

(1) unmounted sections stained with PA-T-P (THIERY 1967),
(2) unmounted sections treated for aldehyde blockade (PEARSE 1960) using 0.5 % ammonium oxalate in water to chelate metals followed by staining with T-P, and ammonium oxalate followed by phenylhydrazine (5 ml in 10 ml glacial acetic acid and 35 ml water) and stained with PA-T-P, and
(3) controls.

Micrographs were taken with a Zeiss EM-9S microscope on Gevaert 23 D 56 film.

METHODS FOR SCANNING ELECTRON MICROSCOPY. The surface of a metal holder was covered with a thin layer of Casco RX glue which was then allowed to partly dry. The air-dried (chemically untreated) pollen grains were dusted over the holder and adhered to the surface of the glue. The pollen grains were coated with a film about 20 nm thickness, of evaporated gold/palladium. During evaporation the holders were rotated on a helical path giving maximum variation of angle relative to the evaporating source. A Stereoscan Mk IIa (Cambridge Scientific Instrument Co.) at the Swedish Geological Survey was used for examination and for taking the micrographs.

RESULTS

To aid in the presentation of the results the period of development has been divided arbitrarily into 18 stages. These are not equally spaced in time. Stage 1 is at prophase of meiosis. Contrary to what is common in angiosperms, where a multi-layered tissue of pollen mother cells generally surrounds the longitudinal axis of the microsporangium (theca loculus), a single circle of pollen mother cells surrounds the axis in *Eleocharis*. At stages 1 and 2 the pollen mother cells are enveloped in callose. At stage 3, after meiosis, a cell plate has begun to form between the nuclei but is at this time incomplete towards the surface of the tetrad. In marked distinction to the common

Fig. 2. Scanning electron micrographs of *Eleocharis* pollen collected as in Fig. I. — A: *E. mamillata* ssp. *austriaca*. The pollen shows broad spaces in the invaginated areas of its wall (arrow). Perforations in the tectum (bent arrow). Approx. ×5,000. — B: Detail of A illustrating small pointed protrusions in the tectum (arrows). Approx. ×24,000. — C: *E. uniglumis* ssp. *uniglumis*. Approx. ×20,000. — D: Detail of C illustrating perforations (arrow) and small pointed protrusions in the tectum (double headed arrow). Approx. ×30,000.

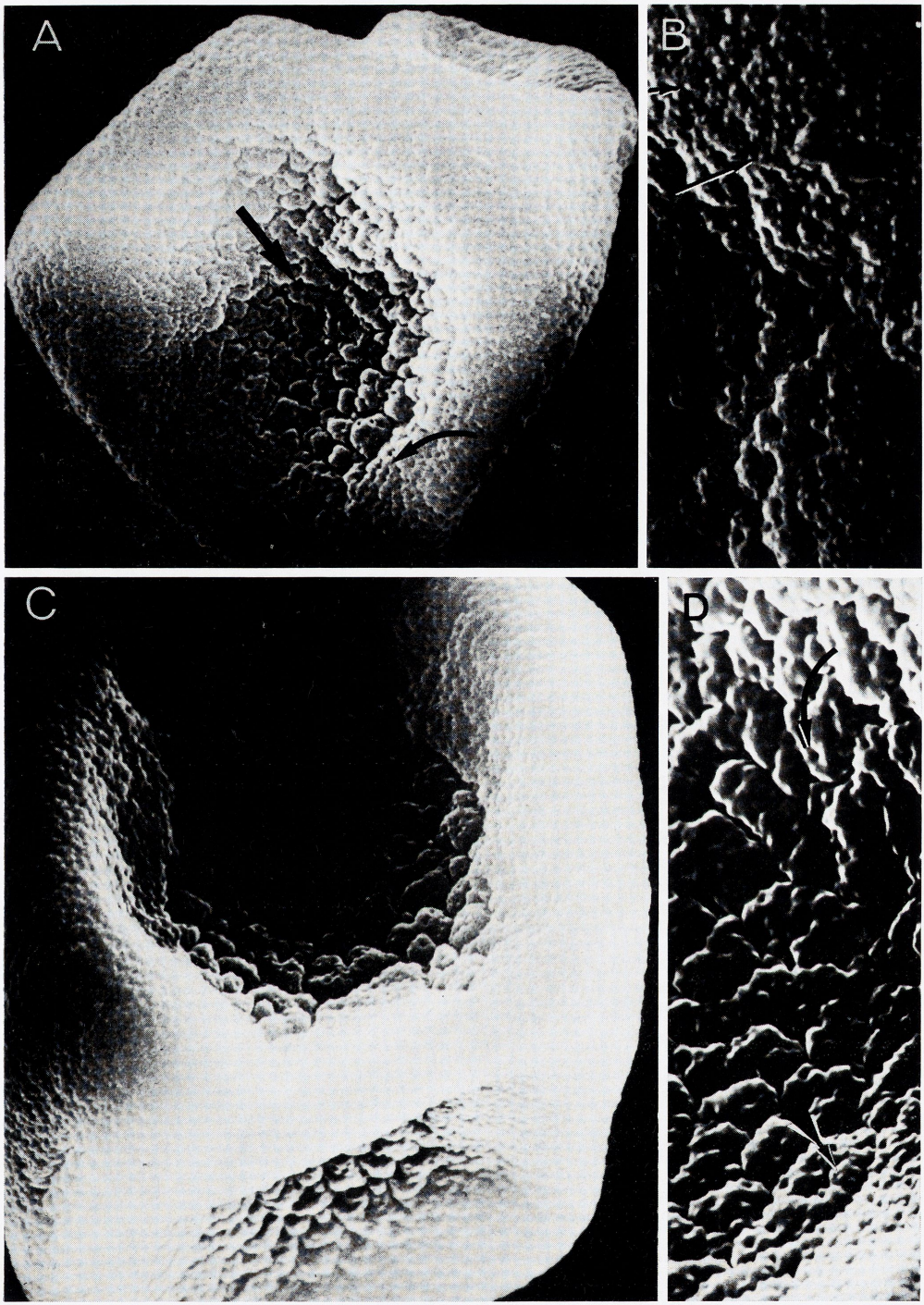


Fig. 2.

mode of angiosperm pollen ontogeny no callose is deposited around the individual microspore. The primexine template, next in turn to develop, is laid down around the entire outer surface of the tetrad beneath the callose layer, and does not form between the microspores. At stage 7 the cell plate is completed and has become continuous with the outside of the tetrad, i.e. the space where the primexine template has developed. At stage 8 the onset of the exine takes place and is laid down, as development proceeds, into the primexine template. Hence, at stage 10, after dissolution of the callose, a common, specifically sculptured exine is formed around the entire pollen grain, while between the abortive cells and between abortive and viable cells only a non-sculptured wall of acetolyse-resistant globules is formed.

Before stage 13 there is but little evidence of degeneration of the abortive cells. From stage 13 onwards degeneration becomes a fact, and during the following stages the aborting cells rapidly decrease in size to degenerate past recognition at stage 16. The residue is located in the adaxial part of the pollen and is embedded in the callose of the intine. The intine is the last layer of the pollen wall to be formed, and there seems to be a correlation in time between its final development and the sequence of degeneration of the abortive cells.

In *Eleocharis* as in certain advanced groups of plants such as *Poaceae*, *Asteraceae* and *Brassicaceae* the generative cell divides before the pollen grains are released from the anthers (SCHÜRHOFF 1926). In *Eleocharis,* at stage 17 two sperm cells have formed. The pollen wall has further developed and wall thickenings in the endothecial cells during stages 17 and 18 indicate that the anthers have reached maturity and soon will dehisce.

Stage 1. Prophase of Meiosis

At the earliest stage of development in the present study, tapetal cells line the inside of the anther wall, while the theca loculi are filled with pollen mother cells. In *E. uniglumis* a very thin layer (tapetum border) ca. 0.12 μ thick, separates the tapetal cells from the central part of the theca loculus (Fig. 9 A, B). Numerous dark stained bodies (tapetosomes) are located in the tapetal cells. They include a configuration composed of 50 Å thick lamellae separated by 20 Å thick spaces (Fig. 5 B). The lamellae are also distinct in material stained only by osmium tetroxide (Fig. 4 B) and in material treated with uranyl acetate followed by PTA. The lamellae become branched by the addition of further ones (Fig. 4 B). Small tapetosomes are located adjacent to larger ones. The small tapetosomes are sometimes entirely filled by lamellae, whereas the larger ones seem to lack lamellae with the exception of the region directed towards the small "lamellated" tapetosome. In such regions there seems to be a connection between the tapetosomes, as lamellae can be traced to extend from one tapetosome to another (Fig. 4 B). The tapetosomes are surrounded by ribosomes (Fig. 5 B) and segments of the rough endoplasmic reticulum are also present near the tapetosomes (Fig. 4 A). A callose layer is located between what seems to be the former pollen mother cell wall,

The marker is 0.2 μ unless otherwise indicated in the transmission electron micrographs. Fig. 3. *E. palustris* stage 1. Pollen mother cell at prophase of meiosis. — A: The large nucleus occupies a considerable portion of the cell. The chromosomes have begun to form bivalents. Chromatin substance (N). Dilations of the perinuclear cisterna with fibrous content (arrow heads); vesicular endoplasmic reticulum (arrow). Lipid droplets (O) are numerous. Approx. ×13,000. — B: Golgi body (arrow). Vesicles (bent arrow) in the midregion of the forming, proximal part of the Golgi body. Approx. ×50,000. The marker is 0.1 μ.

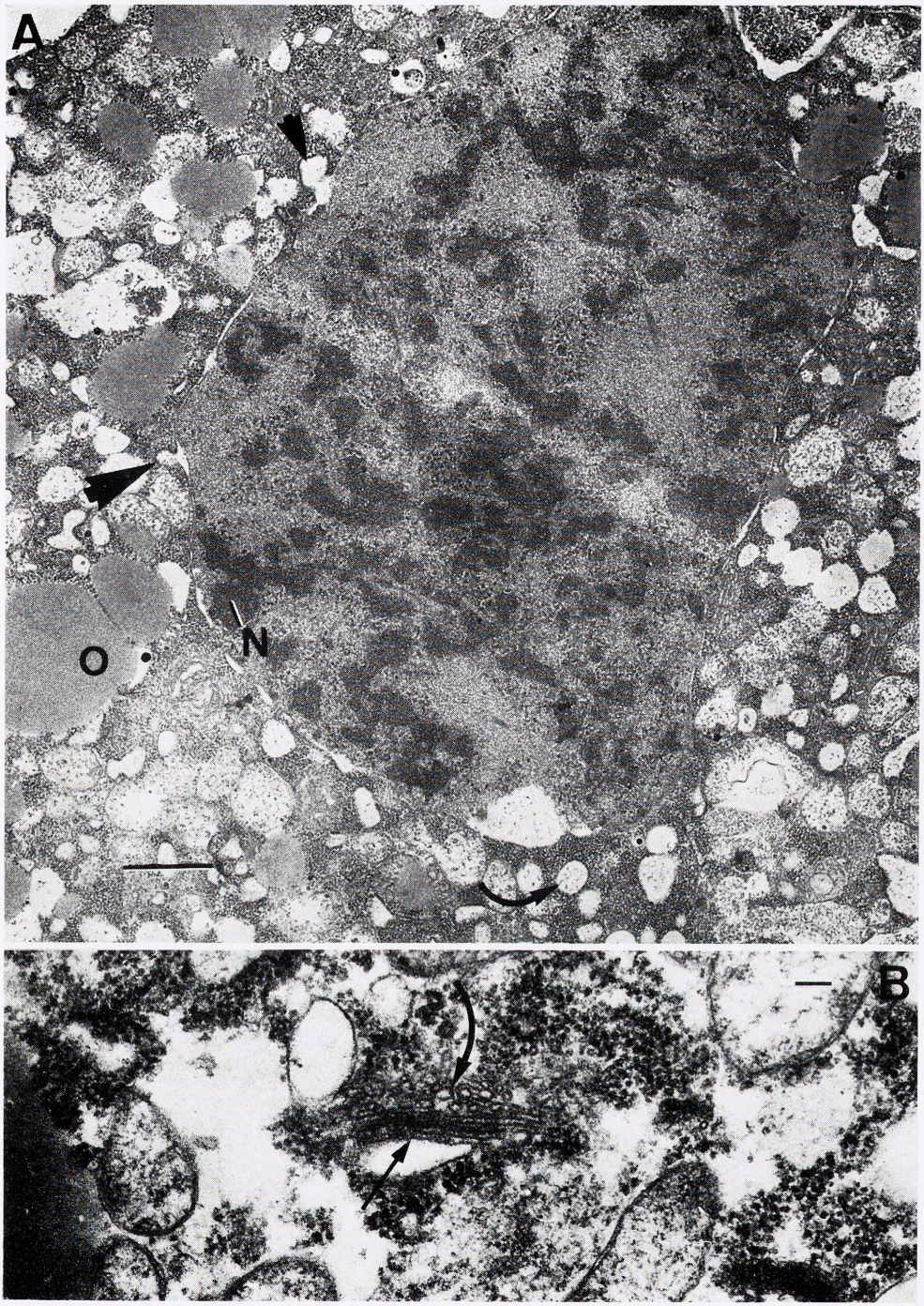


Fig. 3.

and the protoplast. In some material the callose layer is loosely composed. Fibrous substance occurs between this layer and the plasma membrane of the mother cells (Fig. 4 C). The plasma membrane is occasionally convoluted and at such points stacks of surface vesicles are in contact with the plasma membrane. Their limiting membrane, ca. 120 Å thick, is morphologically similar to the plasma membrane. The vesicles contain ribosome-like elements (Fig. 4 C).

A large nucleus fills a considerable part of the mother cell. Expansion of the outer nuclear membrane gives rise to blebs. A vesicular endoplasmic reticulum is obvious (Fig. 3 A). Thin bridges of moderately stained elements traverse the perinuclear cisterna. In addition intranuclear substance was found to extend beyond the nuclear envelope into the cytoplasm (Fig. 5 A). Golgi bodies are evenly dispersed in the cell. They consist of a few long, straight cisternae, the midregion of the proximal (forming) face being discontinuous. Vesicles are associated with this midregion (Fig. 3 B).

Further, the cytoplasm of the pollen mother cells includes large lipid droplets, occasionally in contact with vacuoles. The part of the globules which appears to protrude or dissolve into the vacuole shows a lower density than the rest (Fig. 5 A). Vacuoles with a dense inclusion are numerous. The number of ribosomes is rather large (Fig. 3 A, B).

Stage 2. Early Metaphase

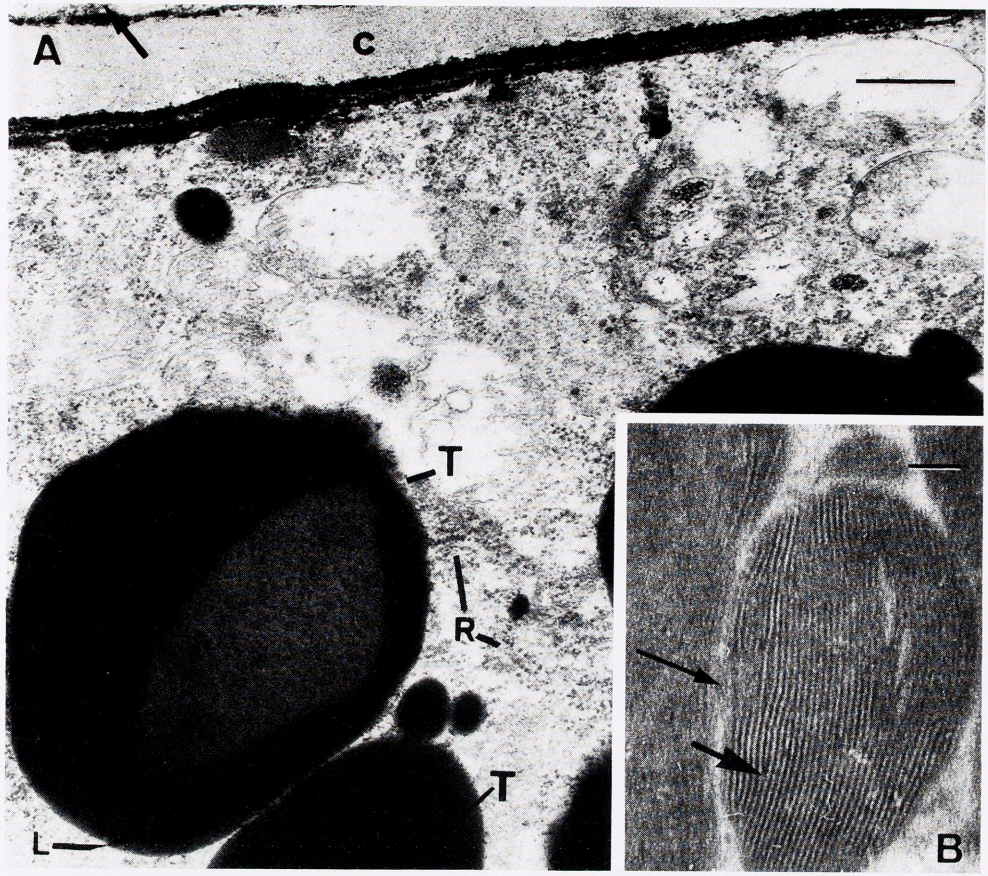
A tapetum border separates the tapetum from the central parts of the theca loculi as in stage 1.

In the pollen mother cells a large part of the volume is occupied by the nuclei, which are now devoid of an envelope. The nuclear region is surrounded by segments of rough endoplasmic reticulum. An impressive number of Golgi bodies are found near the nuclear zone. Their orientation could be interpreted as pairs of "twins", the numbers of a pair appearing more or less as mirror images of each other. The average number of cisternae in each individual dictyosome has increased from the preceding stage (Fig. 6). Vesicles containing a granular substance are located in connection with the Golgi bodies. Mitochondria and segments of rough endoplasmic reticulum are dispersed throughout the cell. Due to the presence of numerous ribosomes the cytoplasm appears rather dense (Fig. 6).

Stage 3. Early Tetrad Stage — a Primexine Template Appears — a Cell Plate Begins to Form

A thin layer of primexine template has formed around the entire tetrad adjacent to the inside of the callosic layer. The callosic envelope consists of two layers, a continuous inner one, poor in contrast, and an outer loosely granulated layer, slightly higher in contrast (Fig. 7). The four nuclei are located towards the adaxial part of the cytoplasm. They are situated in cross-wise planes, two opposing nuclei being the major axis of the somewhat pear-shaped tetrad, passing through the minor axis of the other two nuclei. Invaginations extend into the karyoplasm whereby small cytoplasmic pockets are formed (Fig. 7). Numerous microtubules and mitochondria are located in the zone

Fig. 4. *E. palustris* stage 1. — A: Tapetal cell with tapetosomes (T). A callosic wall (C) is adjacent to pollen mother cell (arrow). Segments of rough endoplasmic reticulum are evident near the tapetosomes (R). In one of the tapetosomes a lamella-configuration is discernible (L). Approx. ×26,000. The marker is 0 5 μ. — B: Small tapetosome between larger ones. Ramifying lamellae (arrow). A possible connection between tapetosomes (thin arrow). Material fixed in GA followed by osmium tetroxide, no section staining. Approx. ×70,000. The marker is 0.1 μ. — C: Part of a pollen mother cell enclosed in callose (C). Stacks of vesicles attached to the plasma membrane (arrow). Golgi body (G). Approx. ×21,000. The marker is 0.5 μ.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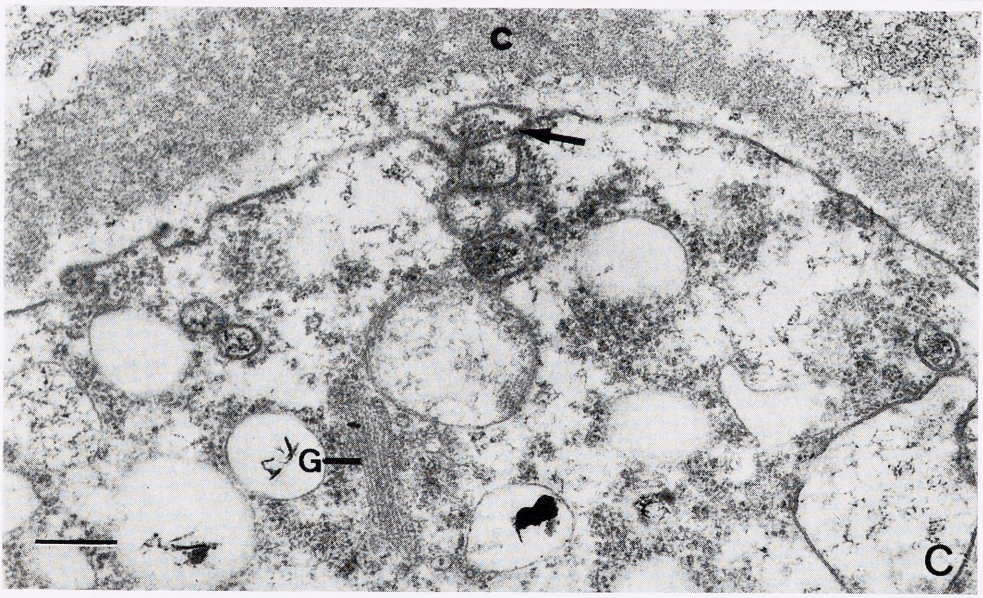
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between the nuclei. In this zone a cell plate has begun to form. Golgi bodies are numerous near the cell plate. In the abaxial part of the tetrad there are numerous mitochondria, rough endoplasmic reticulum, Golgi bodies and lipid droplets. The number of ribosomes decreases strikingly after meiosis.

Stage 4. Tetrad Stage

Small accumulations of a moderately dense material are observed at short distances beneath the primexine template and adjacent to, but not in direct contact with the plasma membrane (Fig. 9 C). Comparable accumulations occur in *E. uniglumis* at early tetrad stage (Fig. 9 B). Apart from the organelles observed during the preceding stage, the cytoplasm of *E. uniglumis* contains lysosome-like bodies with a very dense content. When located adjacent to the plasma membrane the bodies have a less compact content. Moderately dense bodies with an irregular shape and a dense periphery are associated with vacuoles with a fibrous content (Fig. 9 A, B). No Golgi bodies were noticed.

Stage 5. Continuation of Cytokinesis

The cell plate has advanced between the nuclei. Narrow contacts of membranes interrupt the forming cell plate (Fig. 10 A, C). An aggregate of the rough endoplasmic reticulum is situated near the cell plate (Fig. 10 C), and appears to be spheroidal seen in serial section. Vacuoles with a dense inclusion are mostly located in the abaxial part of tetrad (Fig. 10 B), relatively few are seen in the nuclear region. Golgi bodies are abundant, and so are lipid droplets.

Stage 6. The Primexine Template Grows Thicker

The primexine template first observed at stage 3 has developed into an intensely dense and extensive compact layer. This layer adheres to the inside of the callosic envelope and appears in both oblique (Fig. 9 D) and cross sections to be attached to it. Surface vesicles occur on both sides of, and in contact with, the plasma membrane. The region between the edges of the cell plate and the plasma membrane of the tetrad is filled with microtubules and vesicles. The vesicles are limited by a trilaminar membrane, the inner leaflet of which is denser than the outer one. They have a granular content; similar granules are conspicuous in the cytoplasm between the vesicles (Fig. 12 B).

At this post-meiotic stage the nuclei are markedly lobed. Microtubules extend between the nucleus and the cell plate. Occasionally they form a complex with ribosome-like particles. Thin, slender elements can be traced between adjacent microtubules (Fig. 12 A). Numerous mitochondria are located in the cell plate region between the nuclei; less frequently they occur at the abaxial part of the tetrad. Lipid droplets are found in both locations. Vacuoles are less abundant than in earlier stages. Relatively few Golgi bodies are observed at this period. Segments of rough endoplasmic reticulum are dispersed throughout the tetrad (Fig. 11). A concentric endoplasmic reticulum is present.

Stage 7. Late Tetrad Stage — Cell Plate Completed

The outer layer of the callosic envelope has by now become rather loose and is

Fig. 5. *E. palustris* stage 1. — A: Chromatin substance seems to protrude through the perinuclear envelope (arrow) into the cytoplasm (Ch). Nucleus (Nu), Golgi body (G). A possible interaction illustrated between lipid droplets (O) and vacuole (V). Approx. ×95,000. The marker is 0.1 μ. — B: Detail of tapetal cell. Tapetosome with lamella-configuration (arrow). A close contact between these lamellae and ribosomes is evident (arrow head). Approx. ×160,000. The marker is 0.1 μ.

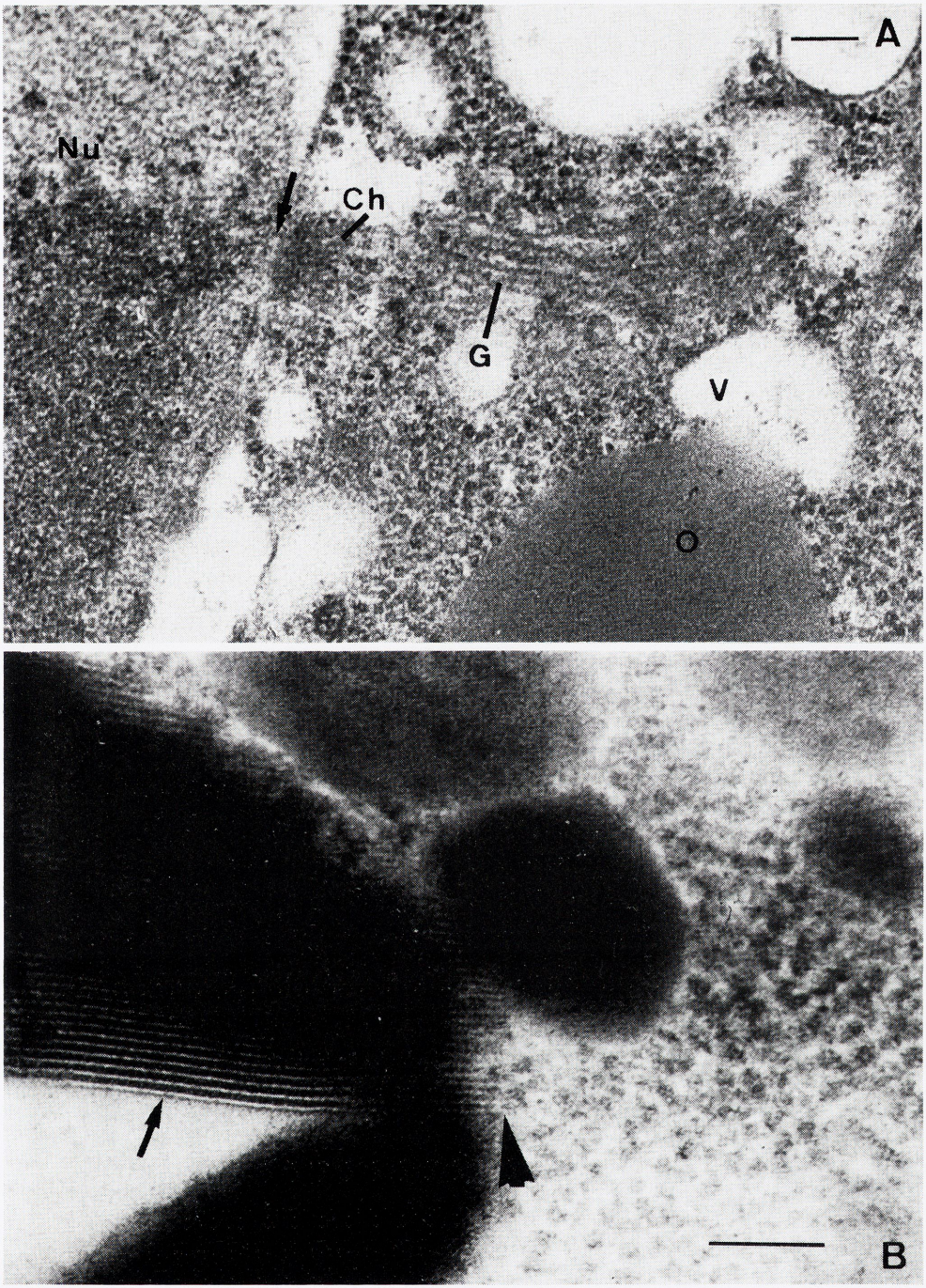


Fig. 5.

apparently dissolving, whereas the inner one is still intact. Inclusions of moderate to intense density are found within (Fig. 14 A) and also beneath, this layer. The primexine template has grown further and is now compact and fibrous. An impressive feature of this layer is the presence of "gaps" which open onto the callosic envelope (Fig. 13 B). They appear as round holes in oblique sections (Fig. 14 A). It is of interest that callose from the outside seems to protrude into these gaps (Fig. 15 B).

Bristle-coated vesicles are evident in the periphery of the cytoplasm. Sometimes they are attached to the plasma membrane by their bristles (Fig. 14 B). The cell plate has reached the surface of the cell and is from now on continuous with the space around the entire tetrad, where the primexine template has formed. Hence the microspores are separated by an inner wall.

During this period the plasma membrane is extensively evaginated; the evaginations extend into the primexine template (Fig. 14 A). Ribosome "crystals" are attached to the inside of the plasma membrane (Fig. 13 A) and they are also observed attached to the outer leaflet of the nucleus envelope. In the "crystals" the ribosomes are situated close together on parallel stacks of endoplasmic reticulum. Between some of the cisternae a trilaminar membrane occurs, consisting of a dense core sandwiched between less dense layers (Fig. 13 A).

As at stage 6 the nuclei are markedly lobed. In the karyoplasm of such lobes, bundles of microtubules are assembled (Fig. 15 A). The demarcation between them is indistinct. In the inner wall a fibrous material has formed (Fig. 15 A). Microtubules and cell plate vesicles are numerous in this region (Fig. 15 A). Only a small number of Golgi bodies are observed during this period, whereas segments of rough endoplasmic reticulum are numerous.

Stage 8. Initiation of the Exine

Between the primexine template and the plasma membrane a material of medium density is found. Evidently the onset of the exine has begun. At such points the plasma membrane is dilated and the leaflets of the membrane are indistinct (Fig. 15 C). Numerous Golgi bodies are located near the surface of the cytoplasm and they show evidence of considerable activity. Vesicles are located adjacent to the Golgi bodies. Bristle-coated vesicles are found adjacent to the plasma membrane (Fig. 15 C).

Stage 9. Formation of Probacula and Protectum

After the initiation of the exine a rapid development of its structures occur. In *E. uniglumis* probacula and protectum are formed. Large lumps of a homogeneous material, stained in the same way as the probacula, are located at the border of the protoplasts. Thin connections are resolved between them and the base of the bacula. In the cytoplasm droplets are associated with what appear to be vacuoles. They have an appearance similar to the droplets associated with the plasma membrane (Fig. 16 A).

Stage 10. Post Microspore Mitosis — Callose Dissolves

The callosic wall has by now almost dissolved. The primexine template is less compact as compared with previous stages. Its periphery is moderately dense and a protectum evidently begins to form. Globular spaces are obvious in this part of the young pollen wall (Fig. 17 A, C). Between the bases of the probacula short segments of a trilaminar membrane occur (Fig. 17 B). The plasma membrane is thrown into many folds and the peaks thereby formed are attached to the inside of the primexine template (Figs. 16 B, 17 A). From now on and during the two

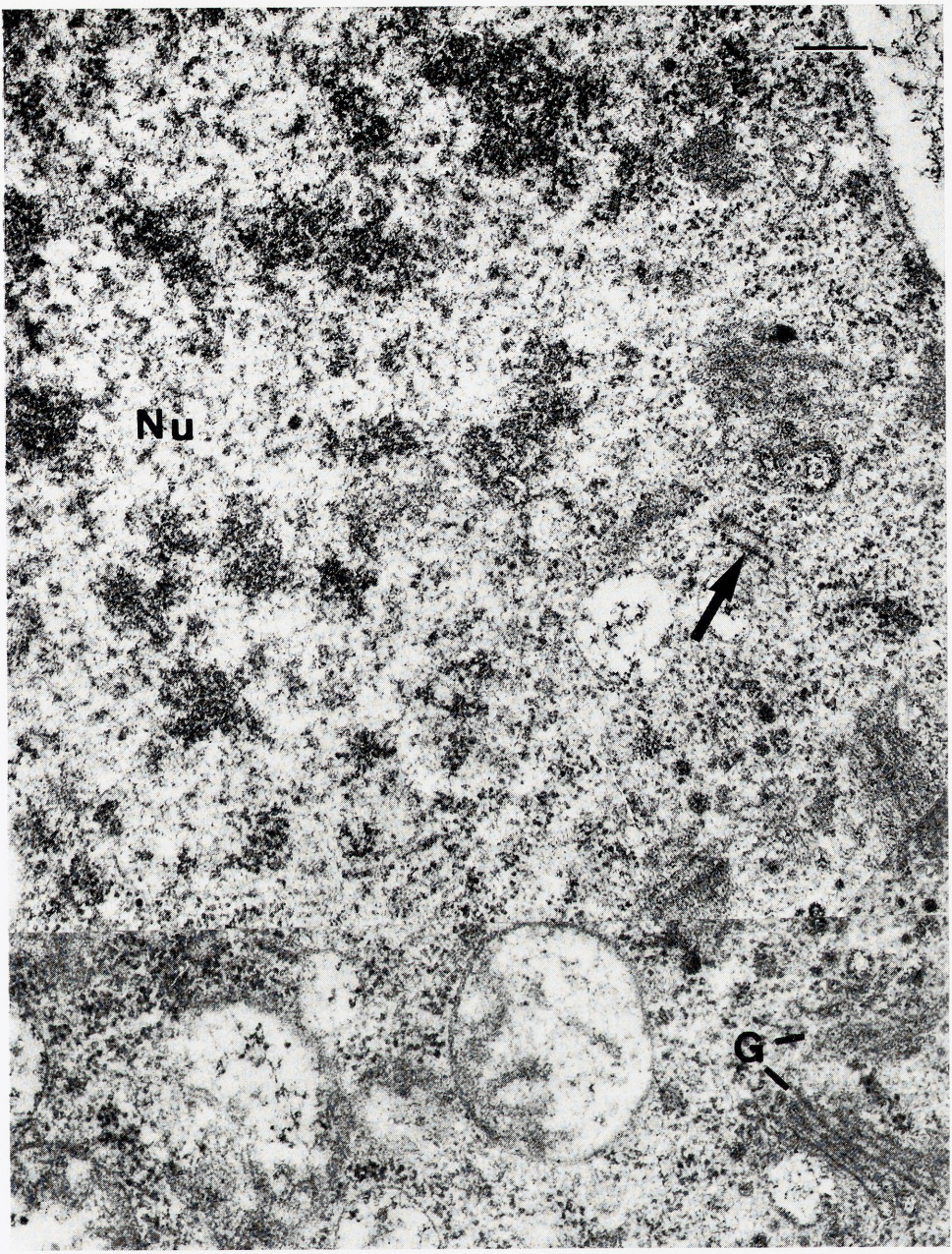


Fig. 6. *E. palustris* stage 2. Early metaphase. The nucleus (Nu) is devoid of an envelope. Segments of rough endoplasmic reticulum (arrow). An impressive number of Golgi bodies occur, some of which are evident close to each other (G). Approx. ×50,000.

following stages "droplets" are attached not only to the plasma membrane beneath the pollen wall but also to the plasma membrane of the inner wall (Figs. 16 C, 20 E). Similar droplets are attached to the entire plasma membrane of the tapetal cell, both on the side facing the pollen (Fig. 16 D) and on the side facing the endothecial cells. In addition a similar substance is observed in the cisternae of the rough endoplasmic reticulum (Fig. 16 D) in the tapetal cells.

After microspore mitosis a cell plate forms between the vegetative and the generative nuclei. Numerous microtubules are in contact with the cell plate (Fig. 17 D). Cell plate vesicles and microtubules are present in the regions where the cell plate formation is not yet complete between the generative cell and the inner wall separating the abortive cells from the viable ones. Segments of rough endoplasmic reticulum are abundant in the cell plate region and throughout the cytoplasm, and so are Golgi bodies, lipid droplets and vacuoles with a dense content (Figs. 17 D, 18 A, B). The number of ribosomes has increased strikingly. There is generally no marked difference between the organelles of the vegetative and the abortive cells.

Stage 11. Formation of Nexine, Sporopollenin Globules and Ubisch Bodies

A rapid development of the young pollen grains takes place after the dissolution of the callosic wall. The exine is about 0.35 μ thick (Fig. 8). The partly polymerised sporopollenin of the sexine appears to be very electron dense. While the interior of the sexine is made up of densely packed granules towards the surface of the tectum, the granules gradually become sparser and form a delicate lacework (Fig. 20 A). The bacula are generally thin (Fig. 19 A). The remaining primexine template is stretched in the arcades of bacula, and tends to accumulate in the region where by now the nexine is beginning to form (Fig. 20 B). Segments of plasma-membrane-like structures with some sporopollenin condensed onto them are seen close to, and occasionally at one end fused with, the plasma membrane of the pollen. They are directed almost parallel to the plasma membrane, whereas the lamellae near the nexine region are at an oblique angle to the pollen wall (Fig. 20 B).

At this time there are sporopollenin globules in the inner wall (Figs. 19 A, 21 A). They resist acetolysis to the same degree as does the partly polymerised sporopollenin of the exine (Fig. 23 C). Seen in serial section they are spheroidal.

Small densely stained accumulations are obvious in the perinuclear cisterna of all five nuclei (Fig. 20 C). Intranuclear vesicles are occasionally observed in the abortive nuclei (Fig. 20 D). Segments of endoplasmic reticulum are evident in close connection with Golgi bodies (Fig. 20 C). Lipid droplets are numerous, whereas the number of vacuoles is moderate. The cytoplasm appears to be less dense than at stage 10 due to a great drop in the number of ribosomes.

During this period of development tapetosomes are located in tapetal cells which are still intact. Young Ubisch bodies appear outside both radial and inwards surfaces of tapetal cells, within a fibrous layer, which is positive in the polysaccharide test (Fig. 22 C). These bodies consist of a moderately stained

Fig. 7. *E. palustris* stage 3, a rather young tetrad. A primexine template (arrow) has begun to develop inside the callose layer, outer callose (C_1), inner callose (C_2). A cell plate (P) is forming between the nuclei (Nu). Note folding of nuclear envelope (arrow head). Numerous mitochondria (M), microtubules in cross section (small arrow) and attached to nuclear envelope (bent arrow), lipid droplets (O), Golgi body (G) and myelin figures (star) are illustrated. Approx. ×20,000. The marker is 1 μ. — Insert: Dividing mitochondria. Same electron micrograph as Fig. 7.

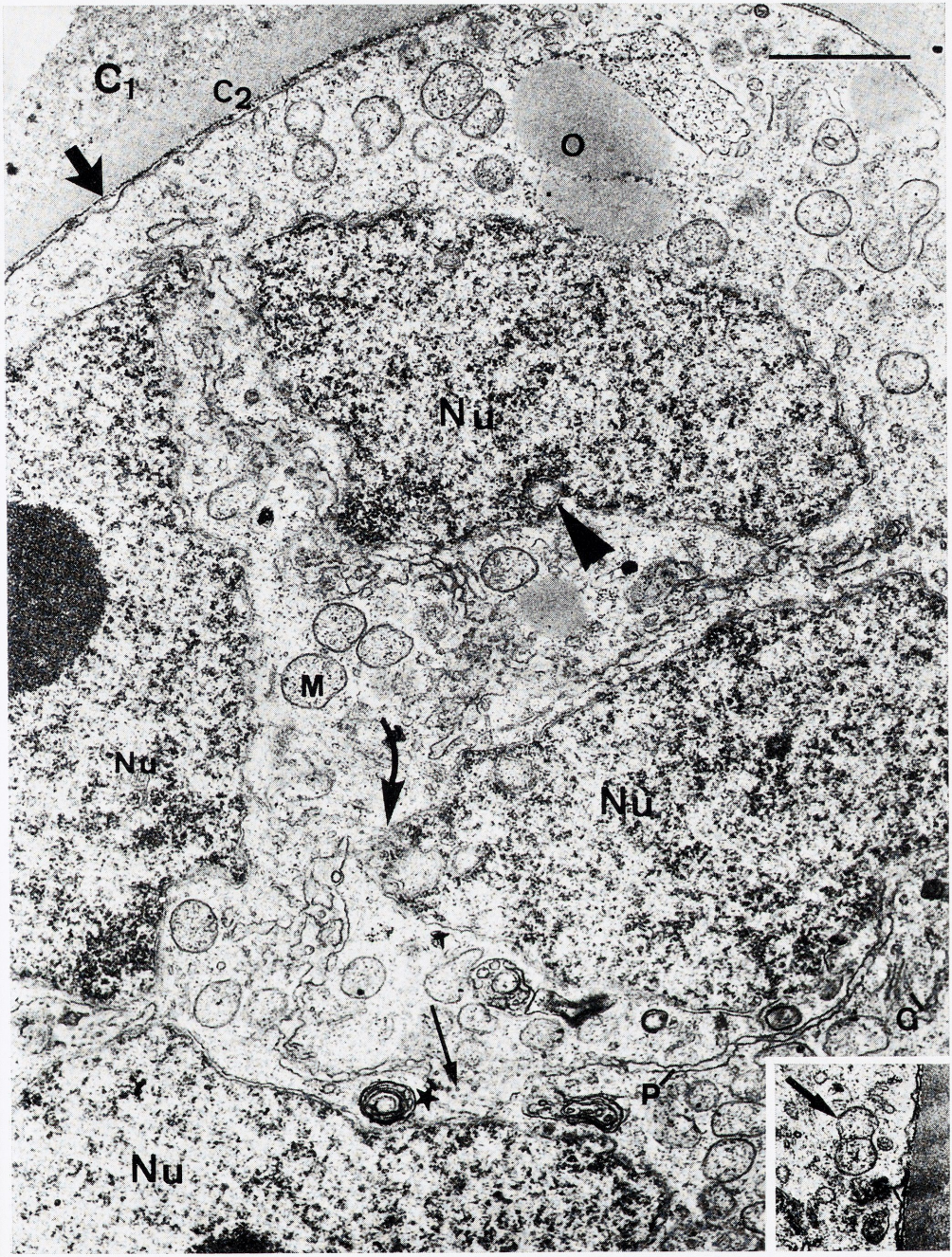


Fig. 7.

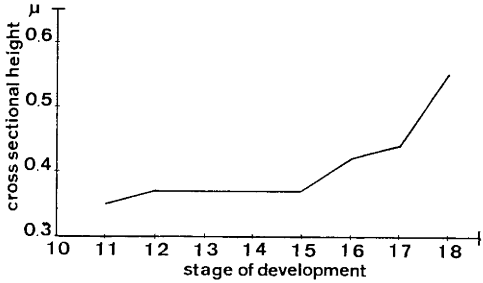


Fig. 8. Cross-sectional height of the *E. palustris* exine from the time when the exine becomes acetolyse resistant and until near anthesis. The exine obviously gains in height during the last 3 stages.

central zone onto which small amounts of sporopollenin have condensed.

In *E. mamillata* a surface membrane is observed covering larger parts of the tectum (Fig. 24 C), while in *E. palustris* it is observed only in spots. It consists of an outer electron dense and an inner electron transparent layer. Outside the plasma membrane of *E. mamillata* straight segments of a trilaminar membrane are located, and several such membranes lie on top of one another with only a narrow space between. Lamellae of the forming nexine fuse with these membranes (Fig. 24 C) in a similar way as in *E. palustris* (Fig. 20 B).

Stage 12. Degeneration Phenomena Begin to Appear

The exine is now slightly thicker than at the preceding stage, ca. 0.37 μ. The surface membrane which previously could be traced for only short distances, has extended and covers parts of the tectum. Hence the lace-like appearance of the sexine surface is less pronounced (Fig. 20 E). Surface vesicles are found on both sides of the plasma membrane. Vesicles are numerous in the inner wall (Fig. 21 A).

Dense accumulations are abundant in the perinuclear cisterna and on the outer membrane of all five nuclei and in the cisternae of the rough endoplasmic reticulum near the nuclei. In the cytoplasm of the three adaxial cells the number of organelles per unit of volume is smaller than in the abaxial ones, and this applies especially to the generative cell (Fig. 21 A), where among other organelles a large number of mitochondria are present. The number of ribosomes is still small.

The sporopollenin layer on Ubisch bodies has grown. A membrane structure, staining more intensely than does the sporopollenin, extends radially from the central area to the surface of the Ubisch body (Fig. 24 A). Where these structures occur the sporopollenin layer is lobed. As the membranous complex in lobes of the Ubisch body resembles feathers, the

Fig. 9. A, B. *E. uniglumis* ssp. *uniglumis* stage 4, early tetrad stage. — A: Abaxial parts of two tetrads enclosed in callosic layers (C). The tapetum (T) is separated from the mass of tetrads by a tapetum border (arrow). Note the structure outside the plasma membrane (bent arrow). Approx. ×8,400. The marker is 2 μ. — B: Higher magnification of same material as A. Callosic envelope (C). Upper left corner shows small part of tapetum. Note tapetum border (arrow). Accumulations of a moderately stained substance (double headed arrow) outside the plasma membrane and beneath a thin layer of primexine template. Lysosome-like bodies (L) include an extremely dense content, which is less compact when associated with the plasma membrane (bent arrow). Irregularly shaped bodies (P) associated with vacuoles (V) including fibrous substance are similar to the structures outside the plasma membrane (arrow head), cf. A. Approx. ×16,000. The marker is 1 μ. — C: *E. palustris* same stage of development as *E. uniglumis* in A, demonstrating similar accumulation of substance (arrow) between primexine template (bent arrow) and plasma membrane of tetrad (arrow head). Callosic envelope (C). Approx. ×60,000. — D: Oblique section of *E. palustris* stage 6. The primexine template (arrow) has become more extensive and is attached to the inside of the callose (C). Plasma membrane (bent arrow). Approx. ×64,000. The marker is 0.25 μ.

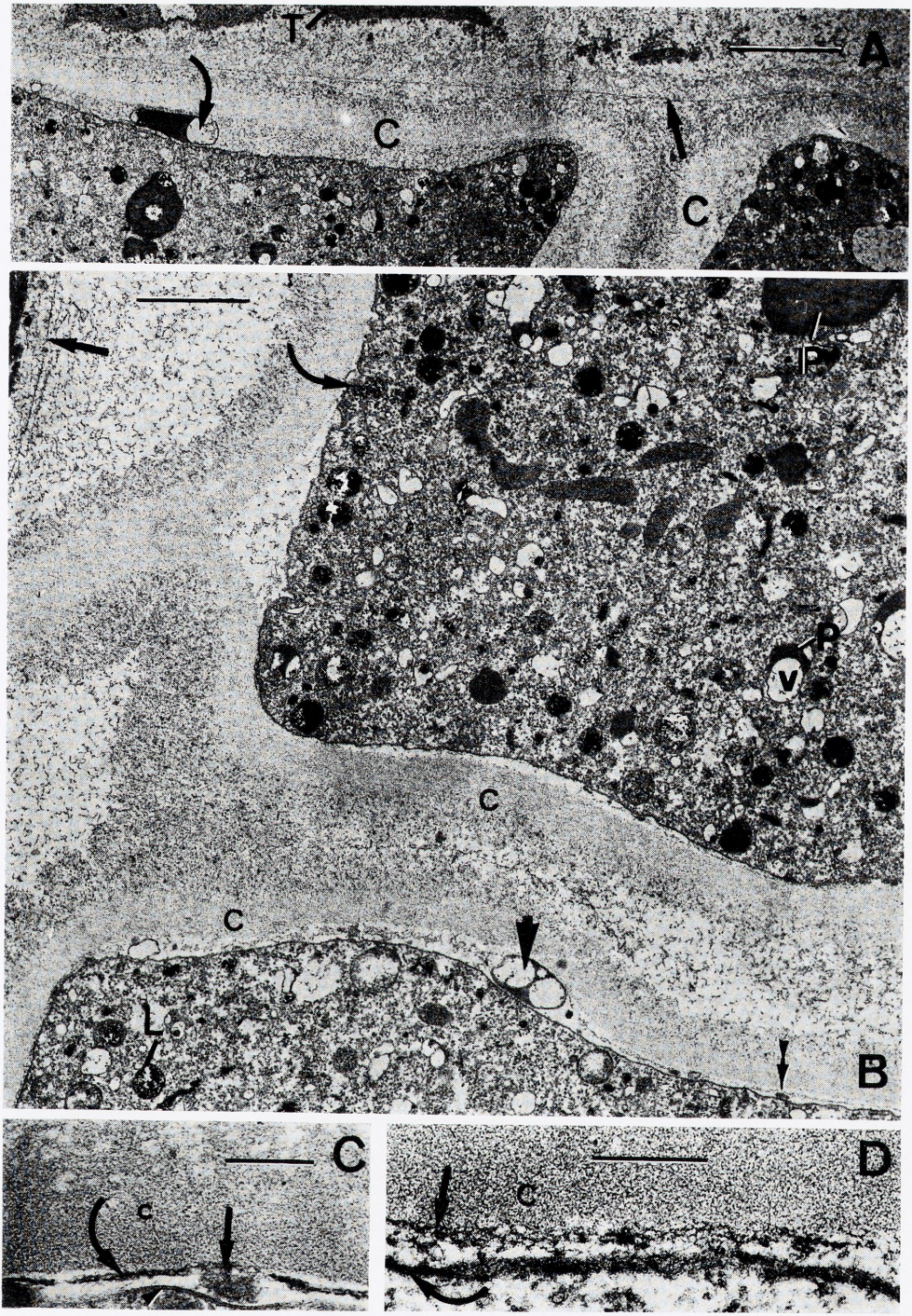


Fig. 9.

whole construction has a wing-like appearance (wing-structure). After acetolysis "lines" appear parallel to the surface of the Ubisch body (Fig. 23 A) and similar lines can be traced beneath the surface of the tectum (Fig. 23 B) evidently as a result of a chemical degradation of the sporopollenin. The wing-structure is not resistant to acetolysis (Fig. 23 A).

A test for free aldehydes gives a positive result in arcades of bacula, beneath the nexine and in vesicles in the peripheral cytoplasm, but not in the inner wall, however (Fig. 22 D). A test for aldehydes formed by oxidation of 1,2-glycols gives a positive result in the arcades of bacula, beneath the nexine, in vesicles and in part of Golgi body cisternae (Fig. 22 B). In the arcades of the bacula and in the inner wall a substance positive to the polysaccharide test is localized (Fig. 22 A). In controls treated only with PA or only with P almost no staining occurs. In controls fixed in GA without osmium treatment and section staining the exine and cytoplasm contrast only slightly with the background (epon-araldite) (Fig. 22 E).

Stage 13. Decrease of Abortive Microspores

As development proceeds the entire pollen grain grows and its wall becomes thicker by accretion of sporopollenin along with a possible expansion of the exine. The perforations and cavities of the tectum are reduced in size and the arcades between the bacula are diminished. The nexine consists by now of several stacked lamellae. The basal parts of the bacula grow laterally and seem to fuse with the nexine (Fig. 24 B). The tectum is covered by a surface membrane, although some pointed protrusions and cavities lack such cover. The surface membrane and the regions without a cover are both positive to the polysaccharide test (Fig. 24 D).

The sporopollenin layer on Ubisch bodies has increased in size and the wing-structure is by now more pronounced. Ubisch bodies are sometimes attached to the pollen surface by their wing-structure (Fig. 25 C). Each membrane of the wing-structure has an electron dense outer and an electron transparent inner layer. Apart from this membranous complex, a surface membrane covers most of the Ubisch body. As with the surface of the pollen, this cover is positive to the polysaccharide test, and so is the wing-structure (Figs. 22 C, 30 D). In addition a fibrous layer, positive to PA-T-P stain, connects Ubisch bodies which are no longer located outside the tapetum but are "free" in the theca loculus. A few tapetal cells have begun to rupture.

The three abortive cells have decreased in size and degeneration phenomena occur in their cytoplasm and in the inner wall. The inner wall has shrunk, except for regions where it connects with the outer wall. In the viable cytoplasm the number of ribosomes has again increased.

Stage 14. Senescence of the Tapetal Cells

The exine has the same thickness as at the preceding stage. The lamellae of the nexine tend to fuse, giving rise to a thicker, although by no means continuous nexine, as thin and thick lamellae

Fig. 10. *E. palustris* stage 5, somewhat later tetrad stage. — A: Callose envelopes (C) surround the tetrads. The cell plate (arrow) has advanced between the nuclei (Nu), but has not reached the periphery of the tetrad. Mitochondria are abundant between the cell plate and nuclei. Approx. ×14,000. The marker is 1 μ. — B: Abaxial part of tetrad. Numerous vacuoles (V) with dense content. Plasma membrane (arrow). Approx. ×17,000. The marker is 1 μ. — C: Detail of tetrad illustrating a rough endoplasmic reticulum configuration (R). The cell plate is interrupted by membrane-contacts (arrow). Approx. ×40,000. The marker is 0.5 μ.

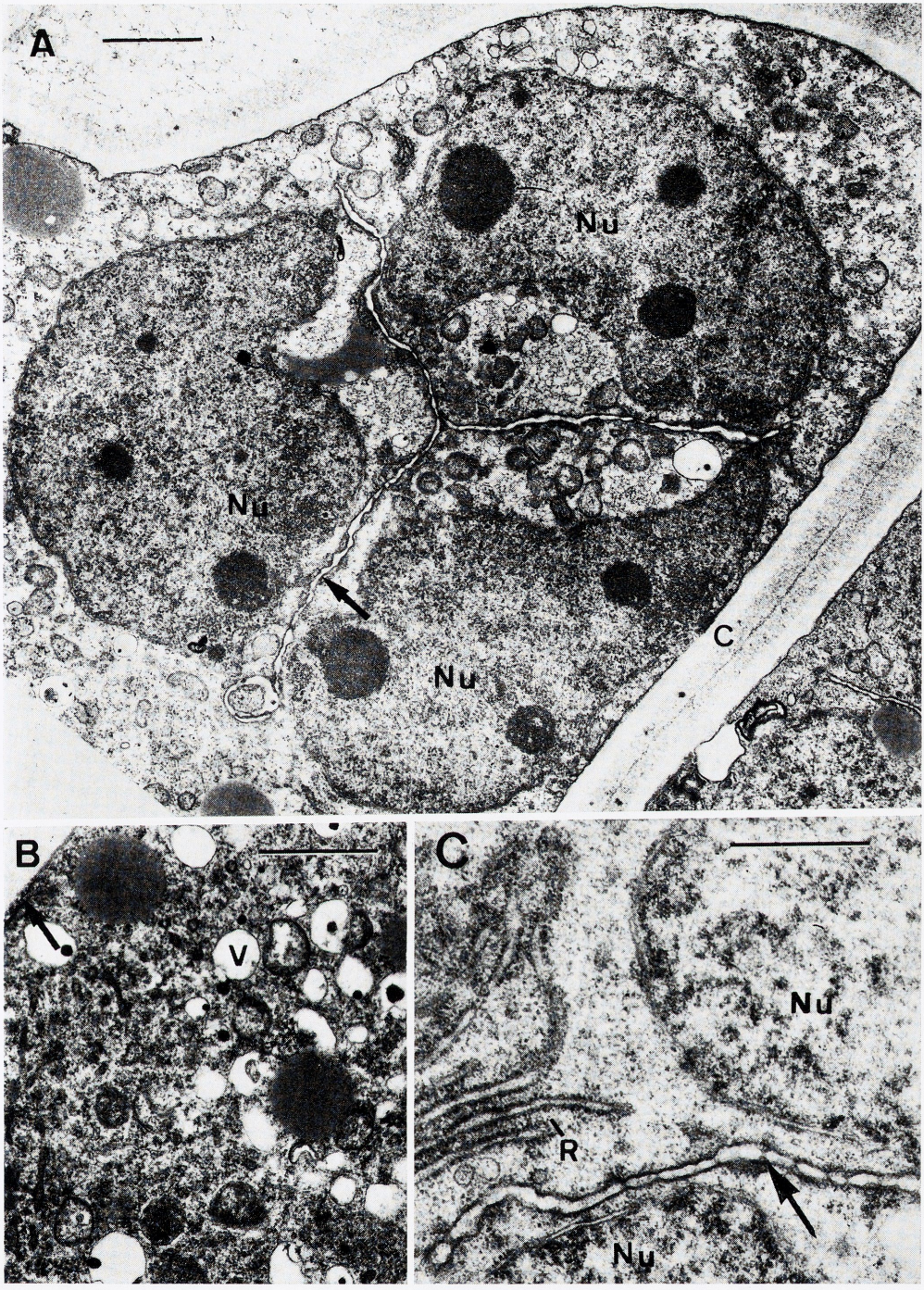


Fig. 10.

alternate (Fig. 25 C) and open spaces remain between them. A more general disintegration of the tapetum has begun.

In sections stained with uranyl acetate followed by PTA the wing-structure and surface membrane of the Ubisch bodies and pollen surface are heavily stained and so is the fibrous remainder of the primexine template (Fig. 25 C).

Stage 15. Formation of Intine

Vesicles limited by a trilaminar membrane and with a variable content are frequently observed beneath the nexine and are further evident between lamellae of the nexine, where they occasionally have an elongated, dumb-bell shape (Fig. 25 B). The plasma membrane withdraws from the exine and in the space thereby established the intine begins to form (Fig. 25 A). Golgi bodies with many vesicles are numerous near the plasma membrane and a considerable number of microtubules are located in the peripheral cytoplasm. Numerous mitochondria are present in the same region. The appearance of the aborting cells is as in the preceding stages.

Stage 16. Three Cells Have Degenerated

The exine is about 0.42 μ high. The three cells, which have now aborted, are located at the periphery of the adaxial part of *E. uniglumis* pollen. The organelles have degenerated past recognition (Figs. 26, 19 C). Their plasma membrane has disappeared and all that is left of the inner wall is the sporopollenin globules. Beneath a layer of moderate stainability an amorphous layer of low contrast consisting of callose as seen with fluorescence microscopy, separates the aborted cells from the viable part of the pollen, together with the sporopollenin globules (Fig. 19 C).

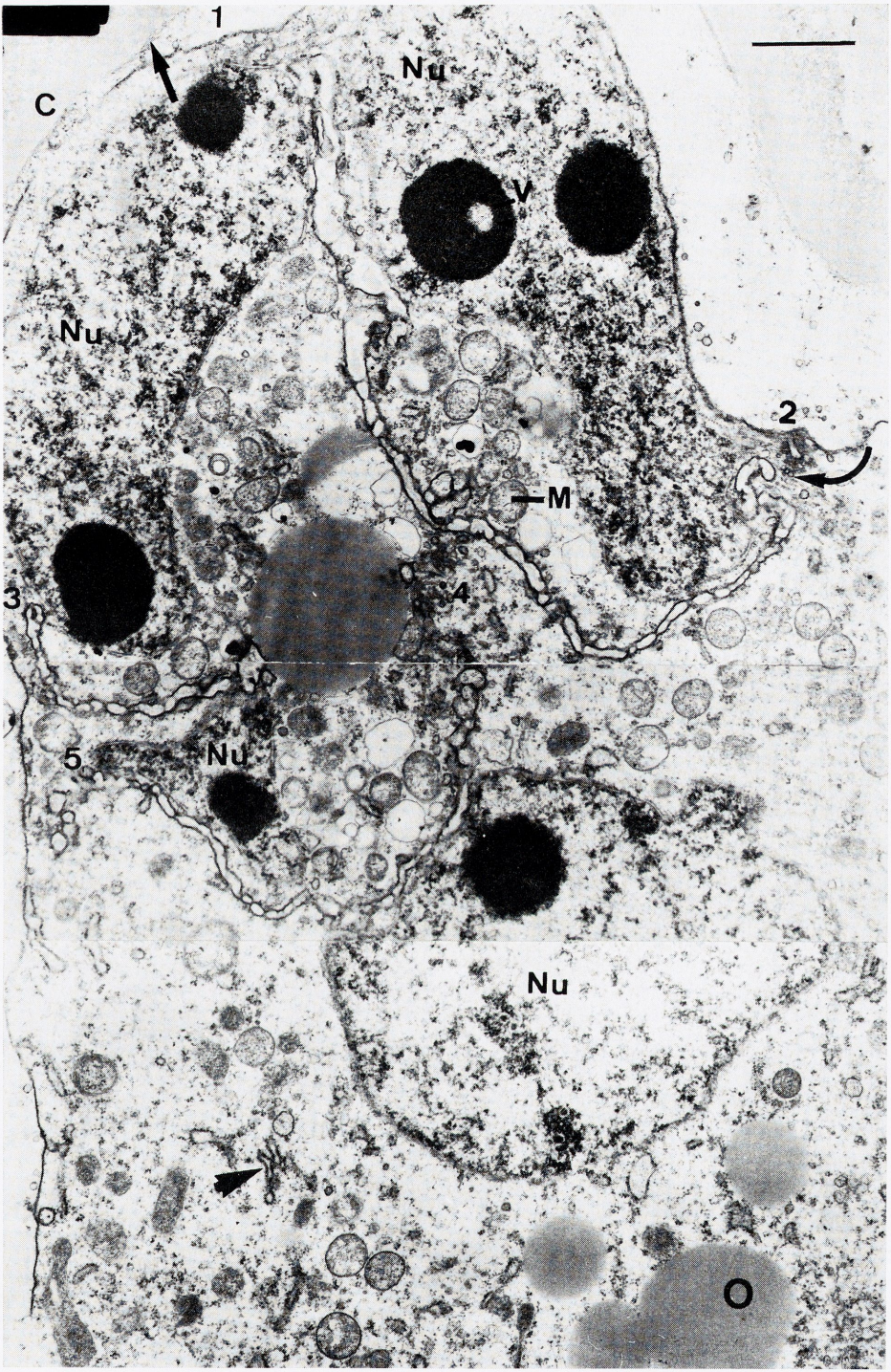
A granular substance is evenly dispersed in the theca locules. The tapetum is finally dissolved and tapetosomes are hence released into the theca loculus, where they are lined up around the pollen mass (Fig. 19 B).

Stage 17. Post Pollen Mitosis — Wall Thickenings Appear in the Endothecium

The exine is about 0.44 μ thick. The basal parts of the bacula have grown further (Fig. 27 A). Lamellae can be traced in the nexine, although they are more or less masked by the polymerised sporopollenin. By now a thick layer of intine has developed (Fig. 27 C). This layer is thicker in the abaxial parts of the pollen. Microvilli-like extensions of the cytoplasm occur in the intine in such regions. More towards the adaxial part of the pollen distinct thick parts of the intine extend into the cytoplasm. Membrane structures are located in such regions. The sporopollenin of the exine and Ubisch bodies stain less with heavy metals than in earlier stages, and the tapetosomes decrease in stainability too (Figs. 27 A, 29 A). The surface of the tectum is unchanged (Fig. 29 A, B) and so are the surface and wing-structure on Ubisch bodies.

No sporopollenin globules can be traced, although elongated structures of a more or less sporopollenin-like character occasionally occur in the intine. The intine consists of several layers with rather different staining properties. A densely stained layer seems to surround the entire

Fig. 11. *E. palustris* stage 6, tetrad stage. The three abaxial nuclei are almost completely enclosed by the cell plate, the fourth one is located closer to the bulk of cytoplasm. Callose envelope (C), primexine template (arrow), nucleus (Nu), lipid droplet (O), nucleolar vacuole (V), mitochondria (M), rough endoplasmic reticulum (arrow head). Five regions (1—5) are demonstrated where cytokinesis is portended by a microtubule-vesicle system (bent arrow). Approx. ×14,000. The marker is 1 μ.


1
C
Nu
V
Nu
2
M
3
4
5
Nu
Nu
O

protoplast. In this layer a substance of low contrast is embedded in some regions (Fig. 27 A) while it is lacking in others (Fig. 27 C). In sections stained by uranyl acetate and PTA, the intine of the nexine region is the most heavily stained part.

The intine often contains groups of membrane-bound vesicles. The vesicles contain a granular, fibrous substance. Another type of rather small vesicles occurs in groups adjacent to the outside of the plasma membrane (Fig. 27 C). The pollen cytokinesis is dealt with by STRANDHEDE (1973).

The sperm cells are surrounded by the rough endoplasmic reticulum. Between this reticulum and the sperm cells there is a narrow electron transparent space of cytoplasm, which is devoid of any organelles (Fig. 28 A). Numerous plastids have formed (Figs. 27 A, 28 A). Rough endoplasmic reticulum and microtubules are evident beneath the plasma membrane and occur also throughout the cytoplasm. Mitochondria are evenly dispersed. The pollen grains also contain a large number of Golgi bodies, which appear to be discontinuous (Fig. 27 B). Vesicles are found nearby. A modified type of vesicle is distinguished by its internal lining with a fibrous content which is separated slightly from the limiting membrane of the vesicle (Fig. 27 B). The vesicles seem to fuse. Lipid droplets are numerous (Fig. 27 A). The number of ribosomes has slightly decreased.

At this stage tapetosomes occur adjacent to the pollen surface and they have further penetrated into arcades of the bacula (Figs. 27 A, C, 29 A). Their multilayered configuration is obvious in both locations. Wall thickenings have developed in the endothecial cells.

Stage 18. Foldings in the Intine

In this, the last of the 18 stages into which the development has here been divided, the exine has reached a thickness of 0.55 μ. The pollen surface is still partly devoid of a membranous cover. The intine is deeply invaginated into a layer of low density which also belongs to the intine. From these invaginations fibres extend in a characteristically radial fashion (Fig. 30 A). Vesicles occur frequently in the intine. The appearance of the cytoplasm is as at the preceding stage.

The intine of *E. austriaca* is deeply invaginated (Fig. 30 C) in a similar way as the intine of *E. palustris*, mentioned above. The young pollen wall of *E. austriaca* (Fig. 30 B) has an appearance similar to that of the walls of *E. palustris* and *E. uniglumis* in ontogenetically comparable stages.

Observations with the scanning electron microscope of *Eleocharis* species show only small differences between the species as regards their fine structure. The surface of the pollen grains is covered with small pointed protrusions. The tectum is perforated between the protrusions (Figs. 1, 2). A difference in the distance between the protrusions is obvious in the taxa studied.

DISCUSSION

Nucleo-cytoplasmic Interaction

At prophase of meiosis intranuclear substance apparently protrudes through the perinuclear cisterna into the cytoplasm. This activity may be correlated with an increasing population of ribosomes as meiosis is approached. Further,

Fig. 12. *E. palustris* stage 6. — A: A microtubular complex is illustrated near the nucleus (Nu). Note the thin connection between microtubules (arrow). Ribosomes are lined along the microtubules (arrow head). Approx. ×85,000. — B: The distance left between the cell plate and surface of the tetrad; plasma membrane (bent arrow), is filled by microtubules and vesicles. The inner leaflet of the vesicle membrane appears more dense than the outer one (arrow). Note the density of the ground cytoplasm in this area. Microtubules (Mt) lateral to the nucleus. Approx. ×75,000.

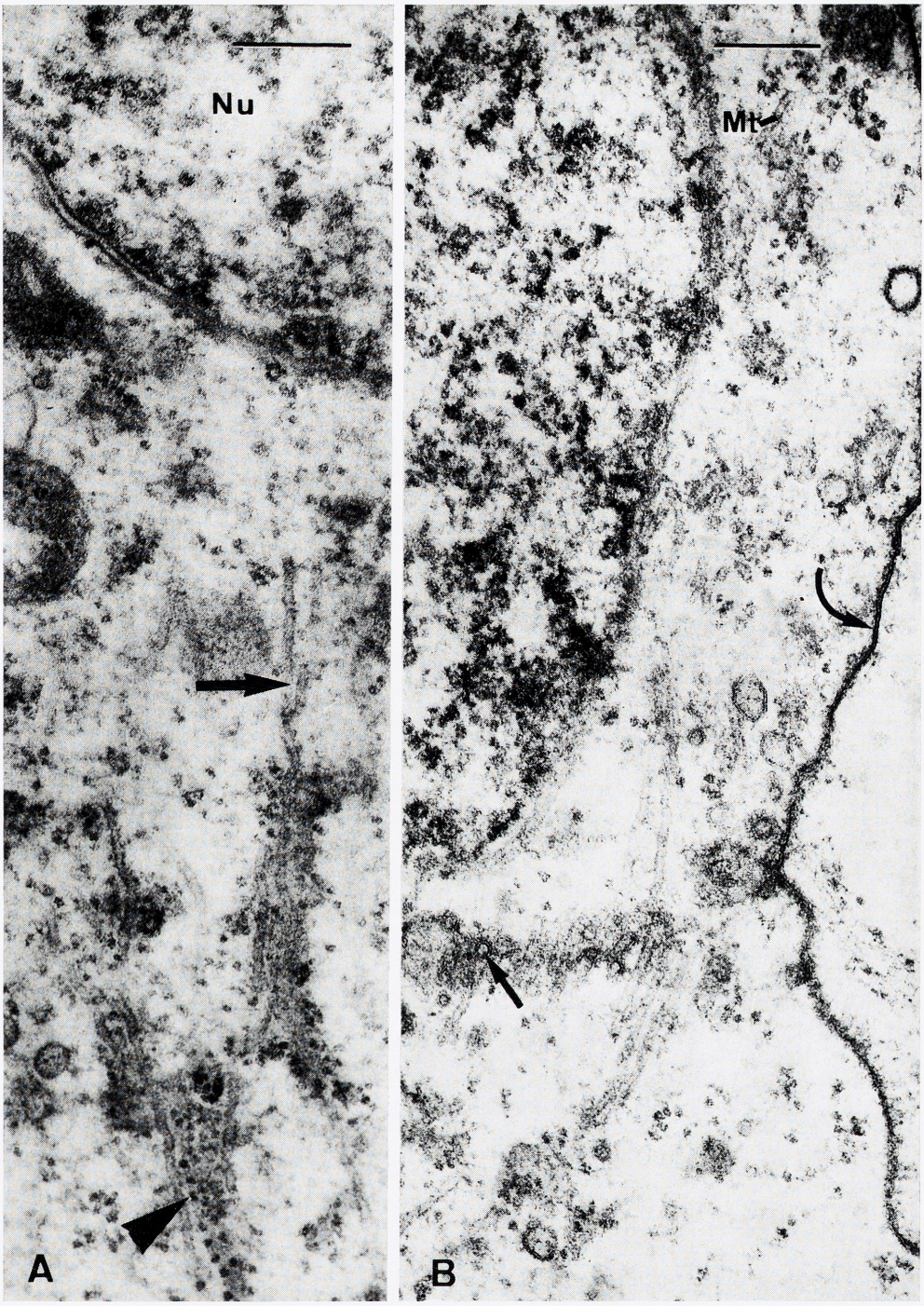


Fig. 12.

dilations of the perinuclear cisterna including fibrous substance may, although there is no direct evidence, become pinched off and contribute to the large amount of vesicular endoplasmic reticulum with a similar fibrous content, which at this stage fills the cell.

In post meiotic microspores of *Pinus banksiana* finger-like invaginations extended into the karyoplasm. They were formed by the nuclear envelope and contained cytoplasm. The invaginations swelled and became spherical. The nuclear envelope seemed to be concerned with active secretion on the part of the nucleus (DICKINSON and BELL 1970). In *Eleocharis* at stage 3, invaginations of the cytoplasm extend into the karyoplasm. Small cytoplasmic pockets are thereby formed in the nuclei. The event, which takes place soon after meiosis, probably reflects a change in the cytoplasm of the young tetrad influenced by the nucleus.

Small dense globules of what is thought to be lipoprotein commonly occur within the nuclear envelope and in the cisternae of the endoplasmic reticulum; they are demonstrated in root tip cells of *Elodea canadensis* (LEDBETTER & PORTER 1970 Pl. 1.1). A rather similar feature is evident in *Eleocharis* during stages 10—12. Dense material is located in the perinuclear cisterna and as "droplets" on the surface of all five nuclei, and in the cisternae of rough endoplasmic reticulum near the nuclei. Since these droplets resemble those on the plasma membrane of the outer and of the inner wall it is suggested that the nuclear envelope, the endoplasmic reticulum and plasma membrane are involved in a nucleo-endoplasmic-surface interaction. This activity may concern the approximately simultaneous exine formation (cf. p. 234).

At stage 10 dense droplets are attached to the surface of the entire tapetum and occur in the endoplasmic reticulum of tapetal cells as well. Since Ubisch bodies appear outside the tapetum at stage 11, it seems likely that the dense droplets portend the formation of Ubisch bodies. The Ubisch bodies appear only in the radial and adaxial regions of the tapetum while the droplets accumulate on its entire surface, a fact which in certain respects correlates with the formation of sporopollenin globules (cf. p. 236).

Ribosomes

The ribosome population diminishes drastically after stage 2 during the later part of meiosis, followed by an increase during stages 4—11. The change in ribosome population during meiosis supports the findings of MACKENZIE and HESLOP-HARRISON (1967), and DICKINSON and HESLOP-HARRISON (1970) in *Liliaceae* pollen. DICKINSON and HESLOP-HARRISON suggested that the appearance of the nucleoloids may be related to the meiotic nucleolar cycle and to the changes in the ribosome population of the meiocyte and its products. In *Eleocharis* a second drastic drop in the number of ribosomes occurs in stages 12—13 post microspore mitosis, and a third less drastic one in stages 17—18 post pollen mitosis. While the fact that a rapid growth in the size of the pollen grain is evident from stage 10 onwards and requires correction for change in volume, the pronounced decrease and increase of ribosomes is still a factor to be taken into account. It is

Fig. 13. Late tetrad stage of *E. palustris* stage 7. — A: A ribosome-"crystal" (R) is connected to the plasma membrane (Pl). Ribosomes are closely aligned on rough endoplasmic reticulum in stacks; a trilaminar membrane (arrow) occurs between some cisternae of the rough endoplasmic reticulum. Approx. ×55,000. — B: Note the "open spaces" in the periphery of the primexine template (arrow) evidently open onto the callosic envelope (C). Approx. ×17,000. The marker is 1 μ.

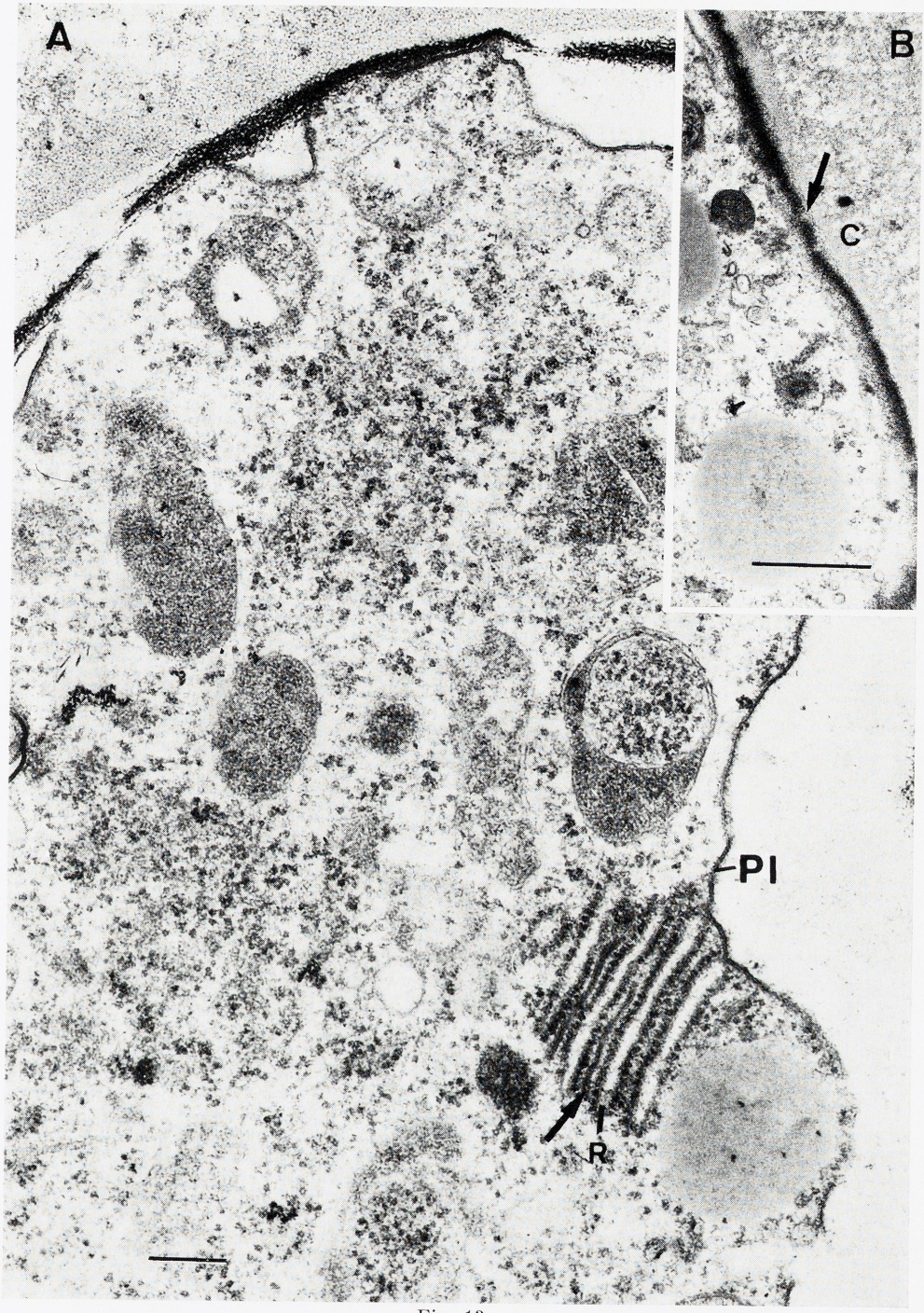


Fig. 13.

suggested that the event indicates periods of cytoplasmic reorganization due to meiosis as well as to microspore and pollen mitosis.

Lipid Droplets

Lipid droplets seem to be involved in different activities during the developmental sequence in *Eleocharis*. At prophase of meiosis and during meiosis an interaction between lipid droplets and vacuoles is obvious. In the stages following meiosis large lipid droplets are dispersed in the cytoplasm often close to the cell plate. After microspore mitosis lipid droplets are in contact with the generative cell wall. In the pollen of *Endymion non-scriptus* ANGOLD (1968) demonstrated an accumulation of lipid droplets in the vegetative cytoplasm lining the generative cell wall.

Mitochondria

During stages 1 and 2 mitochondria are generally evenly dispersed throughout the cell, whereas after meiosis their numbers rapidly increase in the zone of cytokinesis. This polarity is brought about by multiplication. The two daughter mitochondria eventually become located each in a different product of the mother cell. Hence the young microspores will be provided with an about equal number of mitochondria and the degeneration of three of the tetrad cells cannot be linked to a difference in the inherited number of these organelles.

A polarized distribution of the plastids in the megasporocytes of *Marsilea* at meiotic prophase suggests that when the cell divides only one of the spores will contain plastids, and it is assumed that the one meiotic product to be viable is the one with the pool of plastids and that the other three atrophy, there being in *Marsilea* a clear-cut cytoplasmic organization that determines spore survival (PETTITT 1970). Further, two kinds of megasporocytes, viable and non-viable, are represented in *Selaginella sulcata* (PETTITT 1971). The distinctive characteristic of the viable megasporocyte at prophase of meiosis, is the aggregation of mitochondria (or plastids) at the centre of the cell, and PETTITT has suggested that this arrangement may portend their distribution after meiosis, the success of megaspore development being attributable to the number of inherited mitochondria. In *Eleocharis*, in spite of careful examination, no marked polarity in the distribution of the mitochondria before meiosis has been found, and the success of one of the microspores may be attributable to the fact that its nucleus is adjacent to the larger bulk of cytoplasm and all its organelles, rather than isolated between the pollen wall and other cells.

After microspore mitosis there are numerous mitochondria in the generative cell. After pollen mitosis the number of mitochondria is large in the vegetative as well as in the sperm cells.

Golgi Bodies

At stage 1, Golgi bodies are arranged as long straight cisternae, the midregion of their proximal pole being discontinuous. In this midregion vesicles are evi-

Fig. 14. *E. palustris* stage 7. — A: Inclusions in the callosic layer (bent arrow) and low dense spaces in the primexine template (arrow), appearing as round holes in the semitangential section. The plasma membrane is extensively convoluted and the "peaks" thereby formed protrude into the primexine template (arrow head). Approx. ×70,000. — B: A bristle-coated vesicle (arrow) is evident close to the plasma membrane (bent arrow) and granular material occurs inside and between the vesicle and the plasma membrane. Callose (C). Approx. ×130,000. The marker is 0.1 μ.

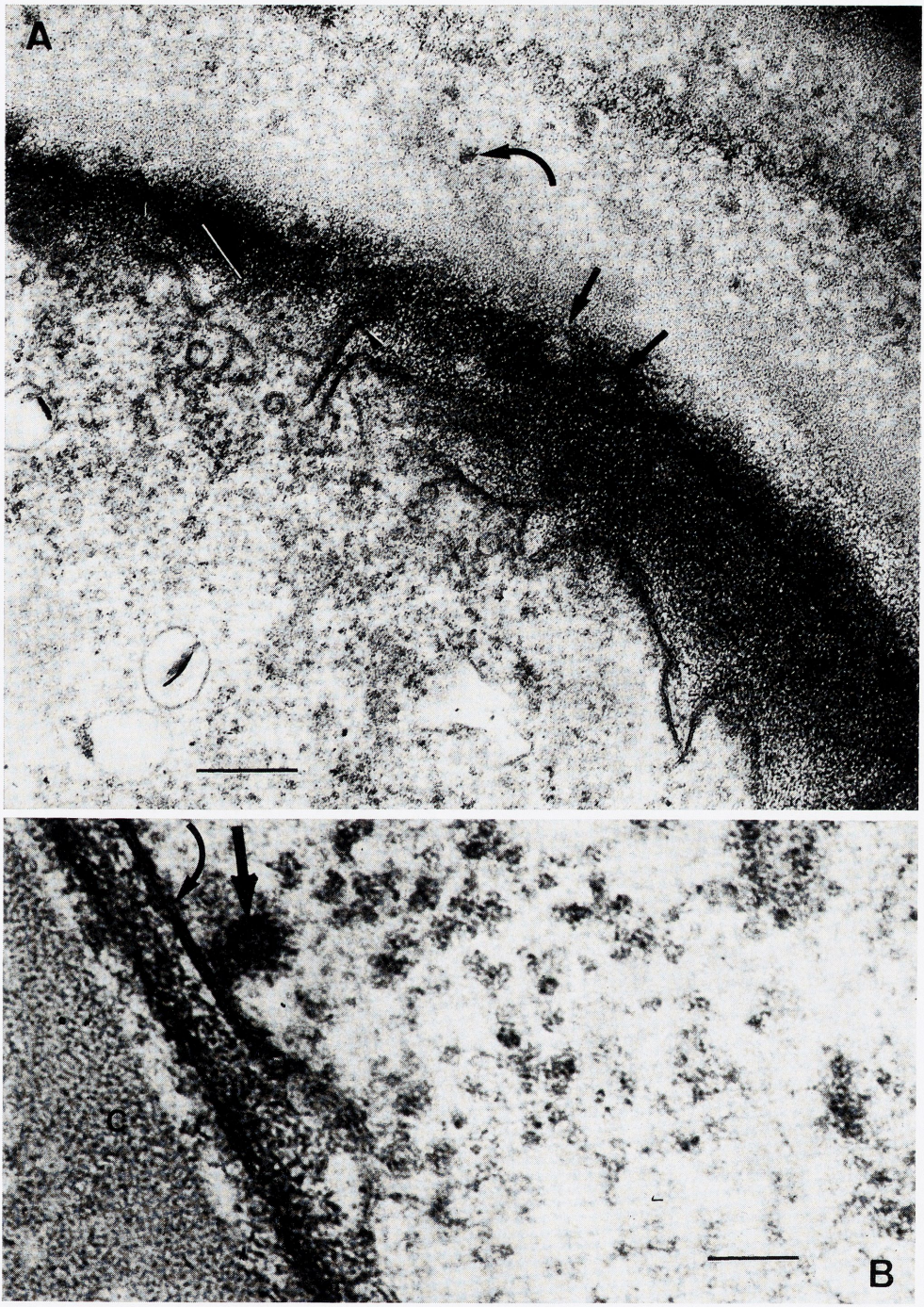


Fig. 14.

dent. The discontinuity of the midregion may indicate that multiplication of the Golgi body has begun. At stage 2 the multiplication seems to be a fact, and the Golgi bodies are arranged as members of a pair, appearing as mirror images of each other. Multiplication seems to occur in a way similar to that in microsporocytes of *Canna*, where the Golgi bodies grow by fusion of endoplasmic reticulum-elements until they attain a certain size, whereupon they fragment into "daughter" dictyosomes by vertical cleavage (SKVARLA 1971). A similar fission of Golgi bodies is reported to occur in the alga *Micrasterias* (KIERMAYER 1970).

At stages 6—7 in *Eleocharis* a temporary decrease in the number of Golgi bodies is obvious. A similar change in the number of Golgi bodies, although during meiotic divisions and hence earlier, is reported in the testicles of mice (SANDOZ 1972), in which modified Golgi bodies appear where dictyosomes have disappeared and only scattered saccules persist; as soon as the nuclear envelope has been reformed Golgi elements reaggregate. No further change in Golgi bodies occurs in *Eleocharis* until stage 17 when they become "fenestrated".

At stage 2, 8 and 15 an intense Golgi body activity is obvious near the cell surface, which more or less corresponds in time with the formation of the primexine template respectively exine and intine. A considerable activity of the organelle is further evident in the entire cytoplasm near maturity.

Microtubules

Microtubules are evident adjacent to the cell plate vesicles during the prophase of cytokinesis and during cytokinesis. They are stretched between the cell plate and the nuclei, sometimes being in connection with both. Occasionally they form a complex in which ribosome-like particles are situated between the microtubules. Fibrous elements connect the microtubules. MCINTOSCH and PORTER (1967), and TILNEY (1971) suggested that bridges which connect adjacent microtubules may provide the active force in diverse motile processes, the motion being carried out by the relative sliding of tubules past each other as in cilia. Since a movement of the nuclei is suggested in *Eleocharis* during this period (STRANDHEDE 1973), the microtubule-complex probably is involved in the transport. At stage 7 bundles of microtubules are assembled in lobed parts of the nucleus, forming a bulge probably caused by the microtubules. In freeze-etched yeast cells passing from anaerobiosis to aerobiosis a similar feature is illustrated in the nucleus after first cell division (MOOR 1967 Fig. 2 e).

At stage 15, when the intine begins to form, microtubules are numerous beneath the plasma membrane. HESLOP-HARRISON (1968) reported microtubules in *Lilium henryi* involved in the growth of intine. Where the microtubules approach the plasma membrane it loses its "unit membrane" aspect. This is in agreement with observations in *Eleocharis*. Near maturity microtubules are also located beneath the plasma membrane which is now intact.

Fig. 15. *E. palustris*. — A: Stage 7. A bundle of microtubules (arrow) is enclosed by nuclear substance. The micrograph is crossed by the cell plate which includes granular-fibrous substance (bent arrow). Microtubules in cross section (Mt) and longitudinal section (thin arrow), cell plate vesicles (V). The ground cytoplasm has a conspicuous density (arrow head). Approx. ×80,000. — B: Stage 7. Detail of primexine template with spaces opening onto the callosic envelope. Callose extends into these spaces (arrow). Plasma membrane of tetrad (Pl). Approx. ×90,000. — C: Stage 8. Two adjacent tetrads separated by callose (C). Outside the plasma membrane a finely-granular and moderately dense substance occurs (arrow) which may illustrate the initiation of probacula. Golgi bodies (G) show evidence of considerable activity. Coated vesicles (V) attached to the plasma membrane, cf. Fig. 14 B. Approx. ×40,000.

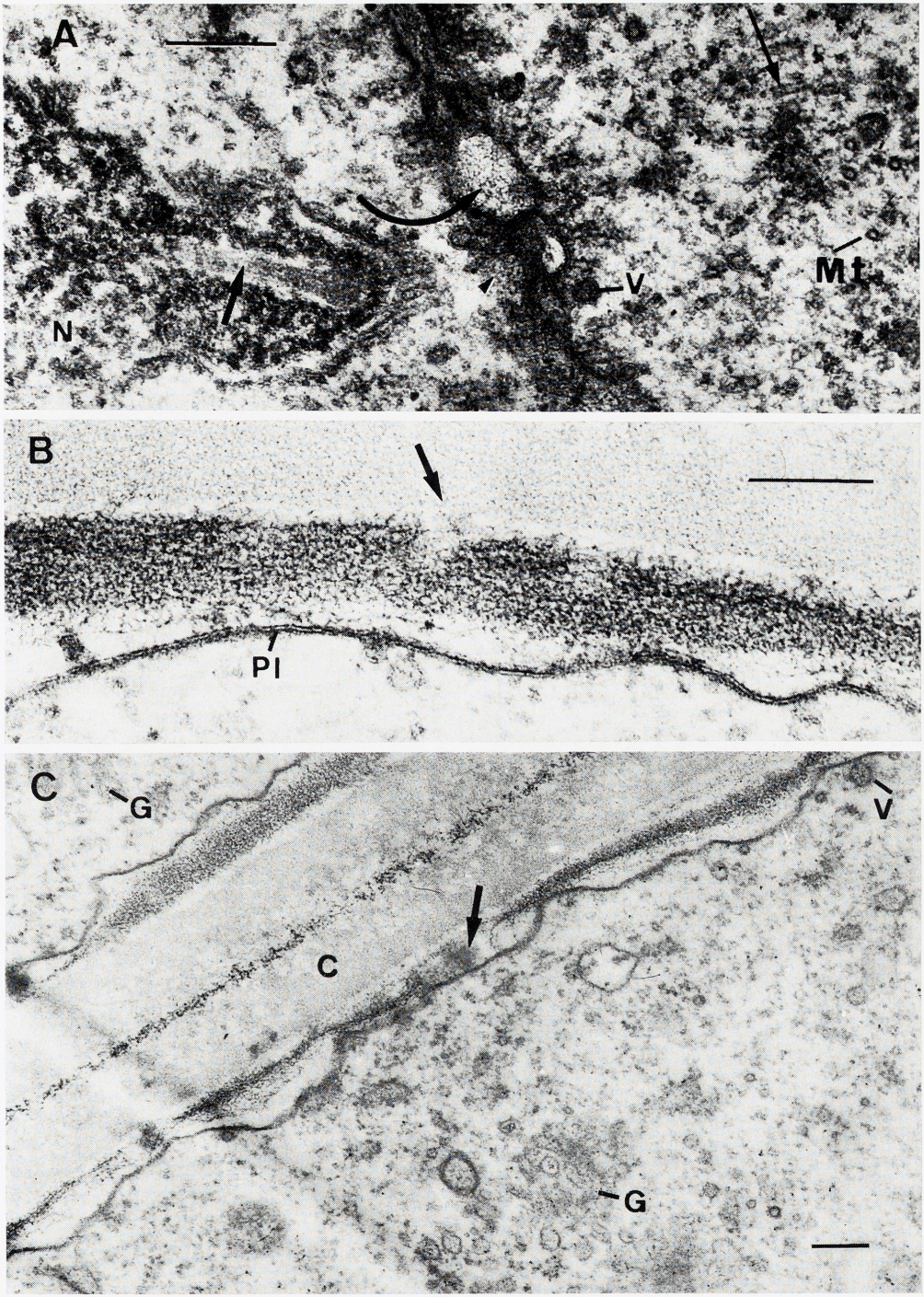


Fig. 15.

Cell Plate Formation

Post karyokinesis cell plates are formed between the nuclei (see STRANDHEDE 1973). CARNIEL (1972) reported that no plasmodesmata occur in *Eleocharis* during cytokinesis. In the present material the cell plate consists of segments interrupted by at first broad areas of cytoplasm which normally diminish gradually to form a continuous wall. Cytokinesis is portended by a microtubule-vesicle system in which the microtubules seem to be actively engaged in aligning vesicles into their proper place. It is well established that vesicles fuse, while forming the cell plate. In early studies of dividing cells PORTER and CAULFIELD (1960) reported aggregation of, and coalescence of vesicles which formed the new cell plate. WHALEY and MOLLENHAUER (1963) supported this observation and suggested that the vesicles derive from dictyosomes. They are, in *Eleocharis* as well as in dividing root tips of *Phaseolus* (HEPLER & NEWCOMB 1967), provided with bristles and the inner leaflet of their trilaminar membrane is more electron dense than the outer one. HEPLER and NEWCOMB suggested that the pattern of cell plate growth is regulated in some way by the adjacent cytoplasm. A "dense" material which grades off into the surrounding cytoplasm was observed by PORTER (1966) in a review of the microtubular-characteristics in the plane of plate formation. Concerning pollen BURGESS (1970) found that cell plate formation of the microspore of *Dactylorchis fuchsii* was preceded by the appearance of electron dense material between microtubules in the plane of the plate. A fine granular substance is conspicuous in the cytoplasm adjacent to cell plate vesicles in *Eleocharis*. While this substance may be involved in cell plate formation, it is likely that other factors cooperate in this process. Segments of rough endoplasmic reticulum and vesicular endoplasmic reticulum are numerous after meiosis as well as after mitosis near the forming cell plate. Since the endoplasmic reticulum is a highly differentiated membrane system in association with which phospholipids and proteins can be synthesized (WHALEY et al. 1971) it represents a source of membrane components. Hence the extensive rough endoplasmic reticulum is likely to contribute to the synthesis of the membranes of the cell plate together with the fusing cell plate vesicles.

Ribosome Crystals

DUCKETT (1972) demonstrated ribosome crystals in fertilized eggs of *Pteridium aquilinum*, and suggested that the formation of a unique form of rough endoplasmic reticulum indicates the activity of biochemical processes specific to this critical stage of the plant. MOTTET and HAMMAR (1972) noted ribosome crystals in many necrotizing cells from the posterior necrotic zone of developing chick limb and observed that the percentage of crystallized ribosomes appeared

Fig. 16. A: *E. uniglumis* ssp. *uniglumis* stage 9. The callose begins to dissolve. Probacula (B) and protectum (arrow) in the primexine template. Substance of medium density accumulates upon the plasma membrane (S). Similar material is illustrated in the cytoplasm (arrow head). Approx. ×32,000. The marker is 0.5 μ. — B, C, D: *E. palustris* stage 10, post microspore mitosis. — B: The cross-section of a probacula (arrow head) appears to have an electron transparent centre. Protectum (T), plasma membrane (Pl). Approx. ×85,000. — C: Same electron micrograph as B. Abaxial part of pollen grain. "Droplets" (D) attached to the plasma membrane (Pl). Approx. ×90,000. — D: Same electron micrograph as B, C. Droplets (bent arrow) attached to the plasma membrane of the tapetum (T). Similar staining substance (arrow) in cisternae of rough endoplasmic reticulum. Approx. ×88,000.

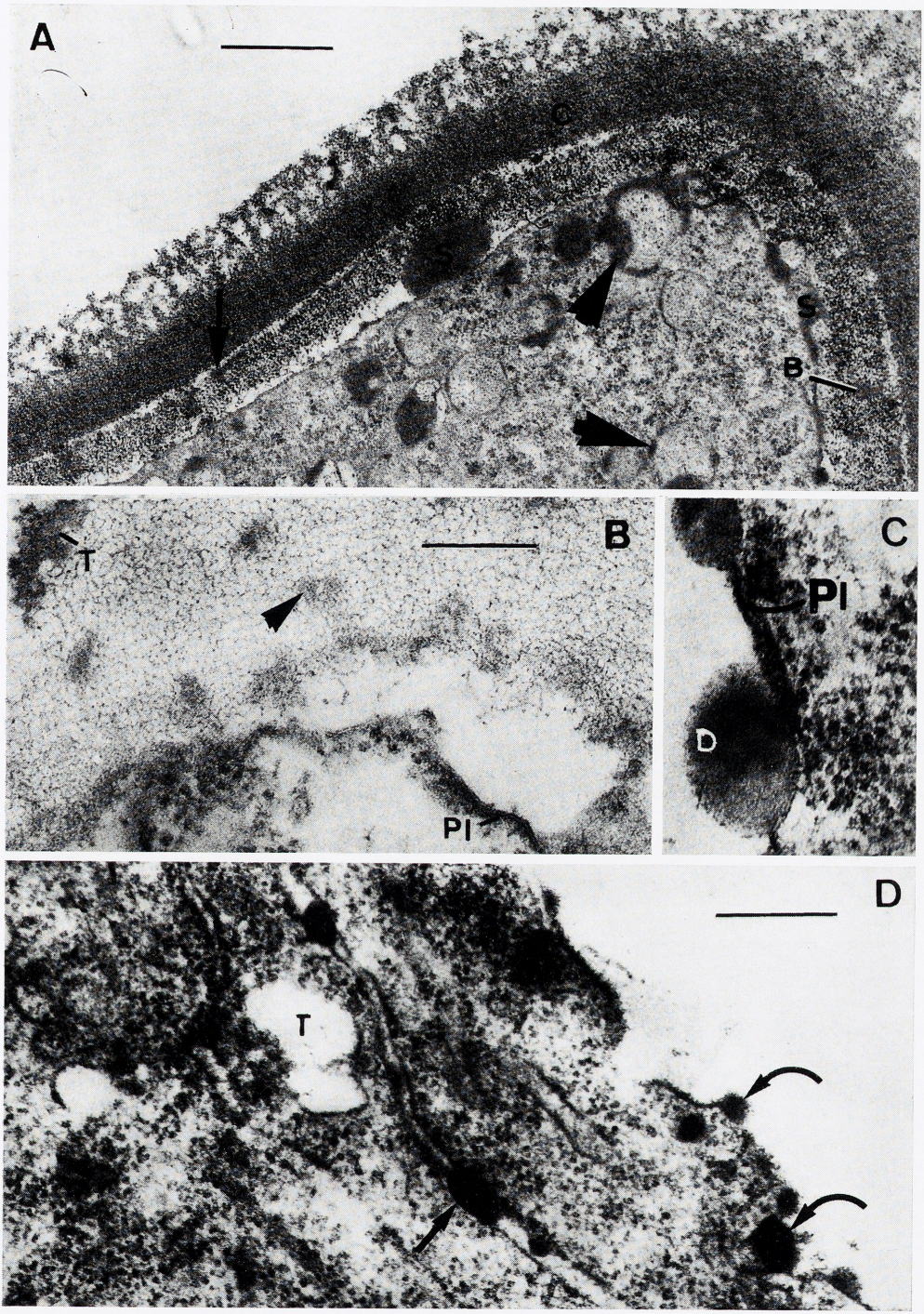


Fig. 16.

directly proportional to the degree of degeneration. Ribosome "crystals" are observed at one stage only during the ontogenesis of *Eleocharis* namely at a period, when there is no morphological difference between the four tetrad nuclei. As a hypothesis it is suggested that the ribosome "crystal" may reflect a gene-cytoplasmic interaction, which some stages later in development, would be one of the factors bringing about the degeneration of three of the four microspores. In *Selaginella* where, as mentioned above, viable and non-viable megasporocytes are present, a similar ribosome crystal has been observed (PETTITT, personal communication).

Degeneration Phenomena

Beside the ribosome "crystal", mentioned above, there are during ontogenesis different phenomena, which may be related to degeneration, although they may reflect a normal metabolism as well. Intranuclear vesicles may be related to degeneration, especially as they are observed in the abortive nuclei. In the inner wall small, heterogeneous vesicles are obvious from stage 12. At stage 13 they are numerous, especially near the connection of the inner wall with the outer one. Since the vesicles become irregularly shaped and differ from normal organelles, they are suggested to be involved in the degeneration of the abortive cells.

Tapetal Border

In *E. uniglumis* the tapetal cells are in a parietal position during stages 1—4, which seems to be due to a thin, one-layered tapetal border. This border is morphologically different from the ones described by BANERJEE (1967) as a tapetal membrane in various species of grasses, and from the extratapetal membrane observed by HESLOP-HARRISON (1969) in certain *Compositae*. Morphologically different is also a peritapetal wall reported by DICKINSON (1971) in *Pinus banksiana*. For a further report on tapetal membrane see GUPTA and NANDA (1972).

Callose

Ever since MANGIN (1890) identified the material of the special cell wall and named it callose, an extensive study on this subject has followed. ANGOLD (1967) showed evidence of "beaded" endoplasmic reticulum adjacent and connected to the surface of pollen mother cells in *Endymion non-scriptus* at metaphase of the first meiotic division, and he suggested that callose or its precursors are synthesized in, or near, the endoplasmic reticulum and passing along its cisternae to the developing callose wall. In *Eleocharis* at the prophase of meiosis dilations of the perinuclear cisterna give rise to blebs, which seem to become pinched off, and add to the vesicular endoplasmic reticulum occurring in the perinuclear cyto-

Fig. 17. *E. palustris* stage 10. — A, B, C: adaxial part of pollen grain. — A: "Open spaces" are illustrated in the protectum area (arrow) and cross section of probacula (bent arrow). The plasma membrane is strongly evaginated (Pl). The "peaks" thereby formed extend to the primexine template. Approx. ×16,000. The marker is 1 μ. — B: Segments of membranes (arrow). Note absence of droplets at the plasma membrane (bent arrow) at adaxial part of the pollen grain, see also Fig. 16 C. Probacula (B), protectum (T). Approx. ×80,000. — C: Detail of protectum and probacula illustrating open "spaces" in the protectum (arrow). Approx. ×120,000. The marker is 0.1 μ. — D: Cytokinesis of the generative cell. Numerous microtubules are attached to the cell plate and occasionally to the vegetative nucleus envelope (arrow head). Membrane-contacts interrupt the cell plate (arrow), see also Fig. 10 C for similar feature in cell plate of tetrad. Fibrous substance is shown in the cell plate (bent arrow). Segments and vesicular components of the rough endoplasmic reticulum are abundant (R). Vegetative nucleus (Nu), generative nucleus (GNu). Approx. ×45,000.

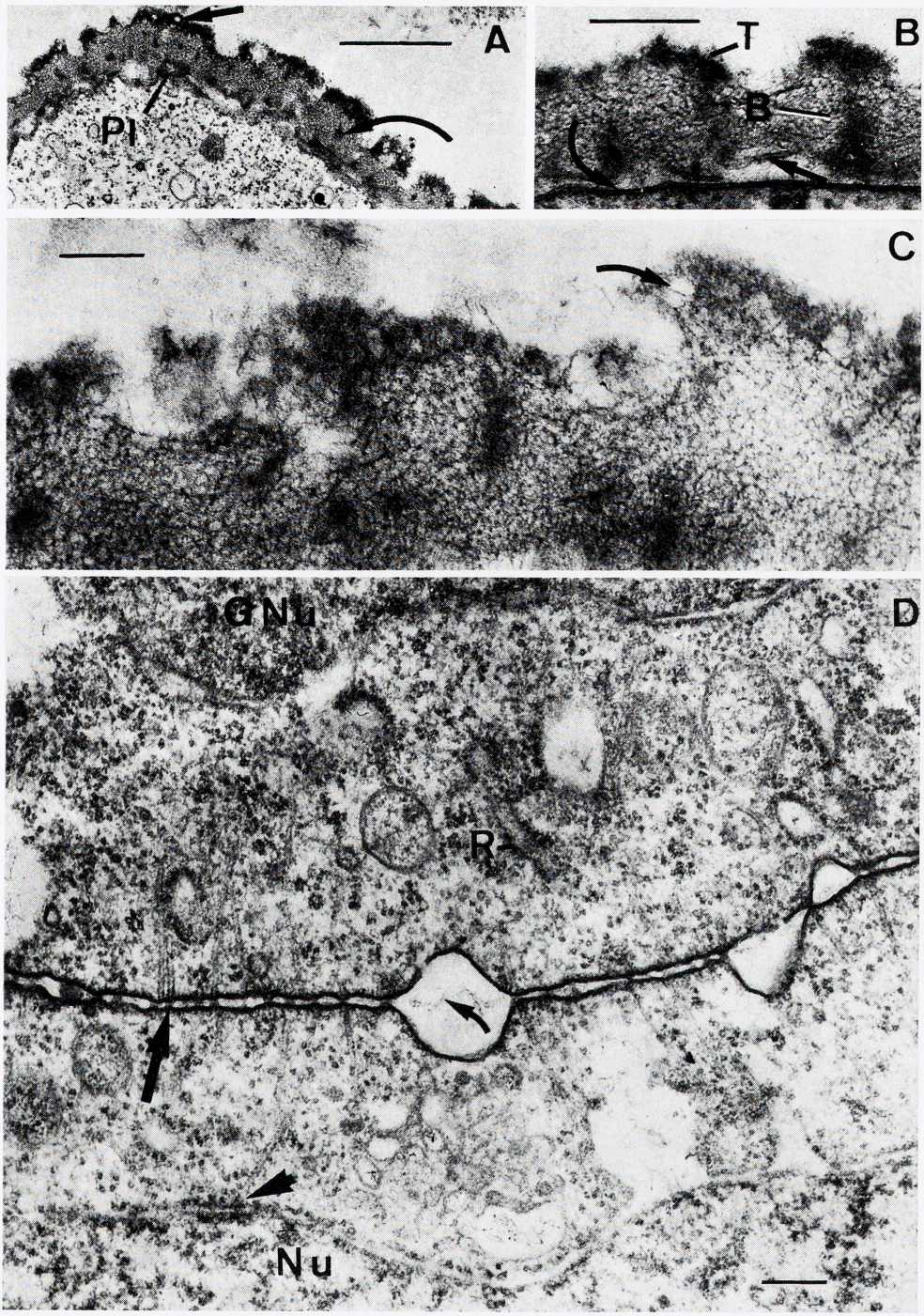


Fig. 17.

plasm as well as throughout the cell. Since the pollen mother cells are provided with a loose callose layer, the event could reflect a transport of substrate for the further synthesis of the callose wall. While callose forms around the pollen mother cells no callose is formed around each microspore post meiotic division. If the precursors of callose are initiated by the nuclear envelope, an inhibition of callose synthesis could easily be controlled by the microspore nucleus.

In *Eleocharis* the pattern for callose, or lack of callose formation seems to be of great significance, since the layer of the primexine template only forms in association with the callose envelope.

At stage 7 dense inclusions are located in the callosic envelope. They are similar to the rather dense inclusions observed in the callose of *Populus tremula* (ROWLEY & DUNBAR 1970), which probably were emphasized by the treatment with iron. HORVAT (1966) showed dense globular areas in the callose of *Tradescantia*, which he considered to be localizations of protein. The dense inclusions in *Eleocharis* appear at a period of great activity at the interface of the callose-primexine template. While their nature is unknown, it is tempting to assume that they represent enzymes with an influence on the formation of gaps in the primexine template into which callose obviously protrudes.

Exine. The Patterning of the Exine

Endoplasmic reticulum has been observed beneath the probacula by several authors. In *Silene pendula* HESLOP-HARRISON (1963) showed elements of endoplasmic reticulum, which approached the plasma membrane at intervals, and he suggested the arrangement to be the factor that determines the patterning of the primexine. This suggestion was supported by SKVARLA and LARSON (1966) in their study on *Zea mays* pollen, where a precise correlation between the endoplasmic reticulum and the bacula template was illustrated; they suggested an important role for the endoplasmic reticulum in the development of exine templates. A different feature was reported by VAZART (1970) who demonstrated mitochondria evenly dispersed beneath the plasma membrane, where they were closely arranged during probacula formation in *Linum*. On the other hand a lack of relationship between any special organelle and the pattern of exine has also been reported. FLYNN and VOLLMER (1972) found that in the tetrad stage of *Nuphar* electron dense granules and spines of sporopollenin constitute the forming pollen wall and, while the mature pollen has an aperture, no evidence of a furrow is observed in the early wall. The authors concluded that the generally accepted model for pollen wall development would have to be modified in order to explain development of *Nuphar* in view of the lack of a primexine template. The different interpretations of how the pattern of the pollen wall is first established are further reviewed by DICKINSON (1970).

While in *Eleocharis* many different components occur more frequently beneath the plasma membrane than elsewhere in the cytoplasm, there is no organelle whose arrangement obviously qualifies it as a factor responsible for

Fig. 18. *E. palustris* stage 10. Cytokinesis of the generative cell. — A: The activity is intense at the phragmosome near the inner wall (S); the adaxial microspore (A). The microtubule-vesicle system portends cytokinesis (arrow head). The inner wall is incomplete towards the cell surface (bent arrow). Abortive nucleus (Nu), generative cell (G), vegetative cell (V). Approx. ×48,000. The marker is 0.25 μ. — B: The generative cell has moved from its location in A. Connection between the generative cell wall and the wall of the abortive, adaxial microspore (arrow). Generative cell (G), vegetative cell (V), abortive microspore (A). Approx. ×35,000.

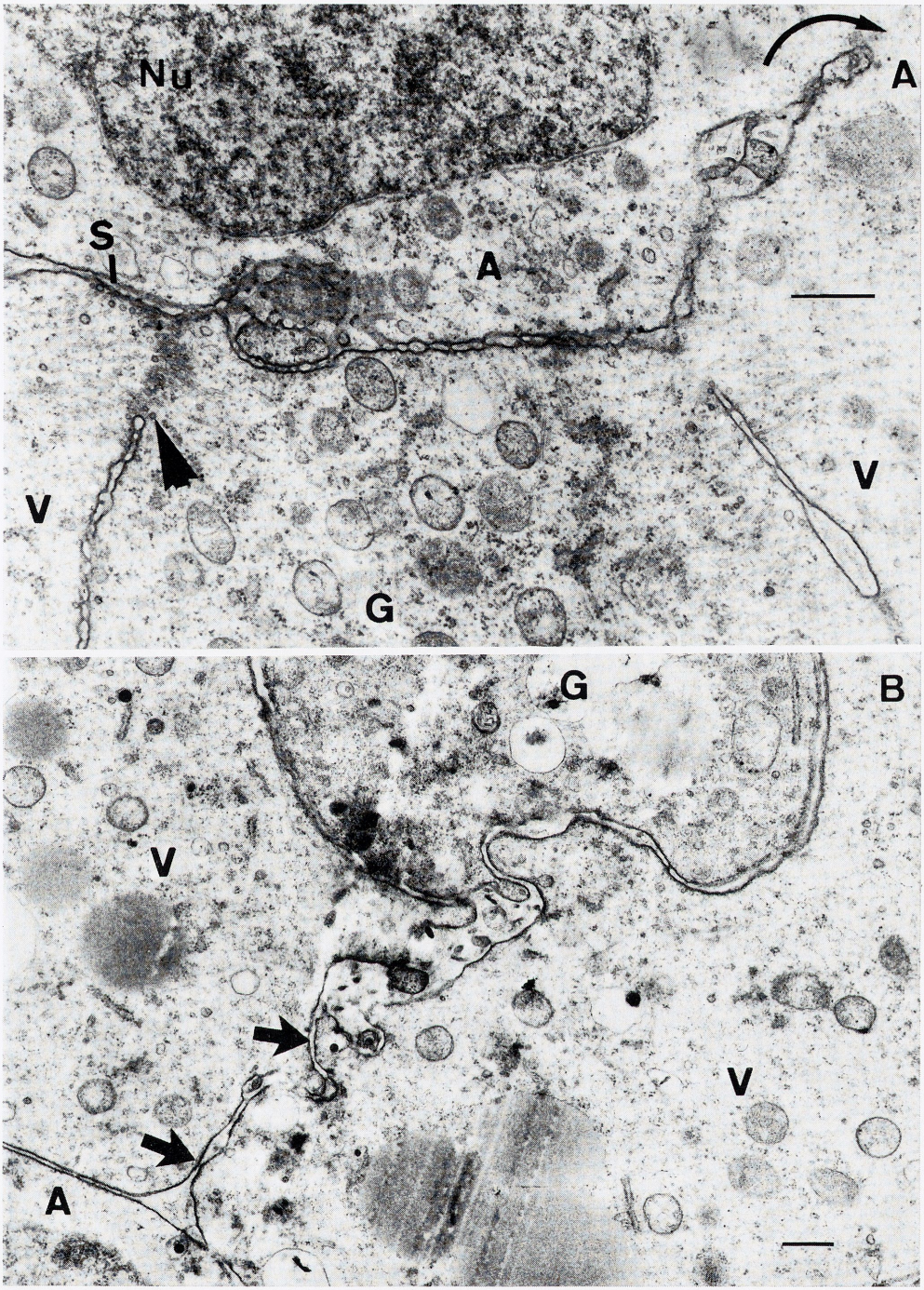


Fig. 18.

exine pattern. The pattern of the exine is a dynamic event, however which may never have been visualized in the material investigated. What has certainly been revealed, however, is the short period when the plasma membrane strongly evaginates into the primexine template simultaneously with an invasion of callose into this layer from the outside. This event takes place before exine initiation. WATERKEYN and BIENFAIT (1970) demonstrated a possible function of the callosic wall in *Ipomoea purpurea*, where a regular geometric pattern visible in phase contrast or in fluorescence microscopy constituted a template for the primexine template, which in turn influences the pattern of the exine. The role of the plasma membrane in determination of exine pattern is illustrated by DICKINSON (1968) in *Lilium longiflorum* pollen. In a later study of the same species DICKINSON (1970) showed that the pattern of the exine is established by outgrowths of the plasma membrane into a layer secreted between the protoplast and the callosic wall. The nature of general exine patterning is still unknown. In *Eleocharis* a pre-formed pattern for the sculptured part of the future wall is probably laid down in the primexine template by a combined influence from both callose layer and plasma membrane.

Exine. Sporopollenin Synthesis

It is well established that the common mode of exine formation includes an activity which requires substrates from more than one source. Chemical studies by BROOKS and SHAW (1968) have shown that sporopollenin is an oxidative copolymer of carotenoids and carotenoid esters, which are chemically bound together. In *Eleocharis*, material of increasing density is observed at the plasma membrane during successive stages of ontogeny. Since one of these stages is related in time to exine initiation the material probably contributes to the synthesis of this structure. Hence the monomers required for the synthesis may partly be a product of the microspores. Since Golgi bodies and associated vesicles are conspicuous in the peripheral cytoplasm at this period they are presumably involved in producing and forwarding some of the required substrate.

Further bristle-coated vesicles are frequently located beneath, or associated with the plasma membrane. In animal cells, coated vesicles are concerned in the selective accumulation and transport of protein (MAUNSBACH 1963). Surface invaginations characterized by a coat on their cytoplasmic side and coated vesicles probably deriving from the invagination were reported by BOWERS (1965); the author suggested their function to be uptake of protein from the extracellular environment. In plant cells they are characteristic of particular stages of development, for instance during slime production in root cells (NEWCOMB 1967). Their function has been suggested to be

Fig. 19. A: *E. palustris* stage 11. Adaxial parts of two adjacent pollen grains. The probacula and protectum have developed into sexine with a strongly increased stainability. A nexine begins to form (thin arrow). Sporopollenin globules are evident in the inner wall (arrows). The inner wall connects at C with the outer one, surrounding the entire pollen. Pores (arrow head) in the nuclear envelope. Nucleus (Nu). Approx. ×22,000. The marker is 0.5 μ. — B, C: *E. uniglumis* ssp. *uniglumis* stage 16, the same material as in Fig. 26. — B: Detail of Fig. 26. After the breakdown of the tapetal cells, tapetosomes (T) are released into the anther loculus where they surround the pollen mass along with Ubisch bodies. Wall of endothecial cell (arrow), pollen grain wall (double headed arrow). Approx. ×5,300. The marker is 2 μ. — C: Tangential section of pollen grain. Aborted cells (left corner) are separated from the rest of the pollen by sporopollenin globules (arrow). The fibrous material in the centre represents the forming intine (I), see also Fig. 25 A, B. Approx. ×11,000. The marker is 1 μ.

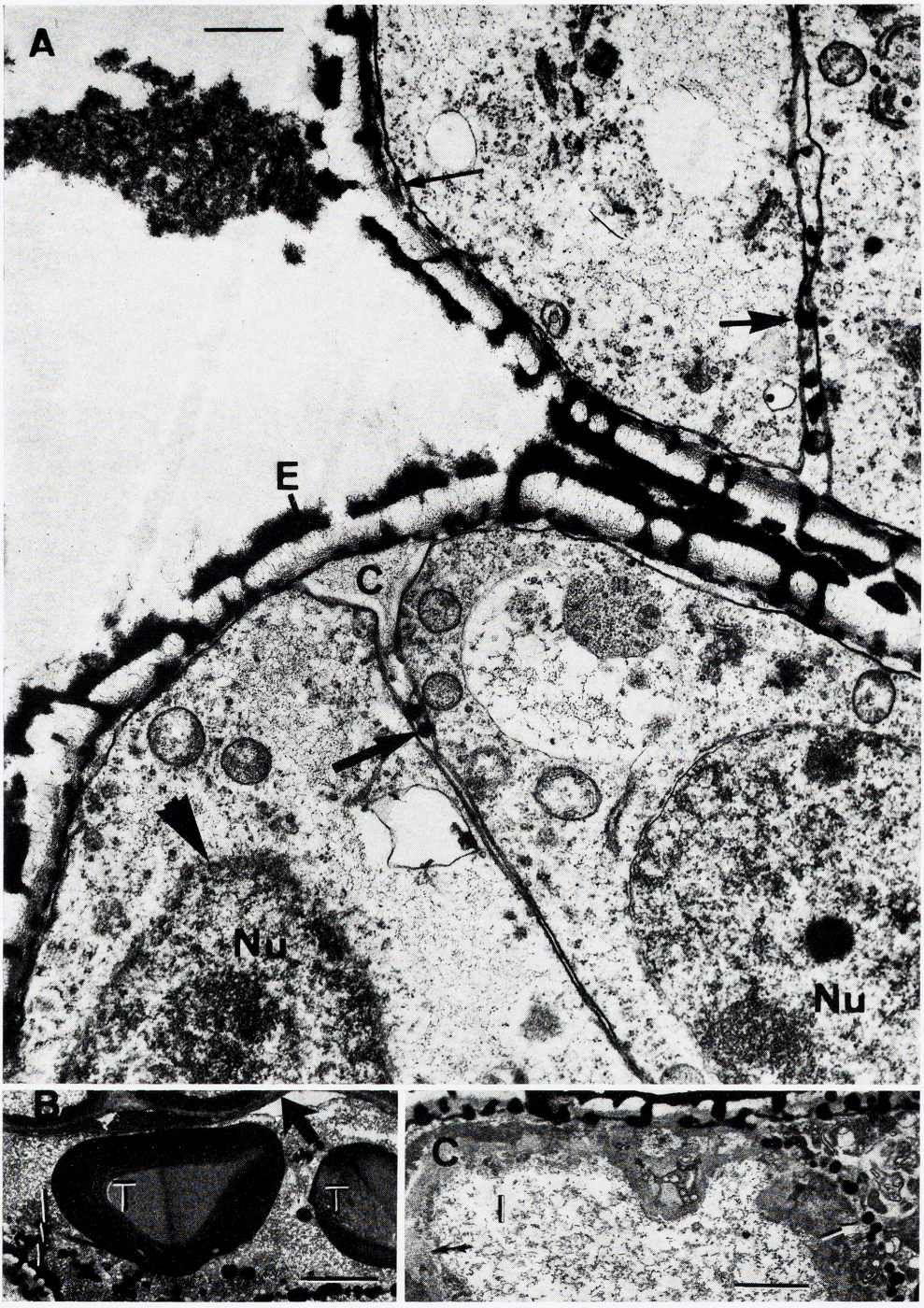


Fig. 19.

the transport of enzymes or structural proteins, required in wall synthesis, to specific sites at the cell surface (BONNET & NEWCOMB 1966). BENNETT (1969) interpreted coated vesicles as forming in pinocytosis, wherein the vesicle membrane is adorned with special components derived from localized specializations of the cell surface which serve functions in selective binding and vesiculation. In *Eleocharis* there is no evidence that coated vesicles take part in pinocytosis. It is likely that they are involved in the transport of enzymes to specific sites at the plasma membrane where the vesicle-content appears to be discharged from the vesicles.

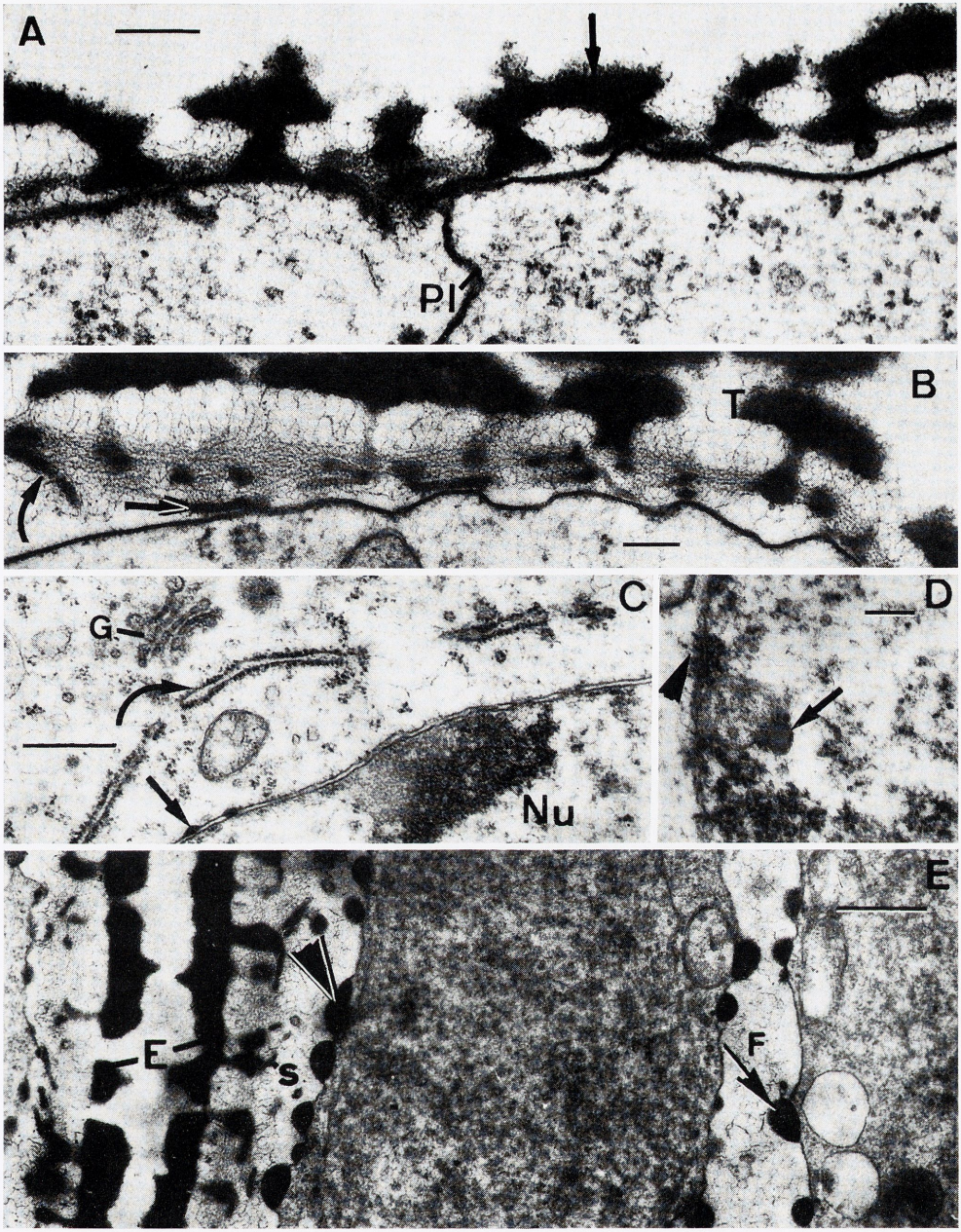
As the formation of probacula proceeds, the material located between the plasma membrane and the base of the probacula becomes as broad as the probacula. GODWIN et al. (1967) reported a material of increasing electron density located at the plasma membrane and continuous with the forming bacula of *Ipomoea purpurea*. In *Gerbera jamesonii* the probacula formed tenuous contacts with the plasma membrane, although no accumulation of material at this membrane was reported (SOUTHWORTH 1970).

In the protectum of *Eleocharis* round spaces of low electron density are obvious, and low dense areas are traced in the centre of probacula. Similar spaces are observed at a comparable stage of ontogeny in the protectum of *Betula verrucosa* (DUNBAR unpublished). Low dense, circular outlined spaces are demonstrated by ROWLEY (in press) in the young microspore wall of *Epilobium angustifolium* and *montanum* and a combination of observations made on transverse and tangential sections suggest them to have a cylindric or rod shape. ROWLEY points out that the extreme regularity of these holes provide additional evidence of the accumulation of sporopollenin around such rods. Further evidence to support this interpretation may be the demonstration by histochemical tests of mucopolysaccharide, glycocalyx, in the region of the rod-shaped units.

Further sources of monomers are known from experimental work with tracers on *Gerbera jamesonii* demonstrating that acetate and glucose can pass into callose-encased microspore walls (SOUTHWORTH 1969). Monomeric material may also derive from polysaccarides in the callosic wall or in the primexine template, both of which are degraded at the same time as the prosporopollenin is synthesized (SOUTHWORTH 1970).

While some material of increasing density in *Eleocharis* is located at the plasma membrane in relation with sexine initiation, an "excess" of such material is evident in the same location during nexine and non-sculptured inner wall formation (stage 11). Similar material occurs in the perinuclear cisterna and in segments of rough endoplasmic reticulum near the nuclei. The model for nexine formation is almost the same as for other angiosperm pollen, for instance *Hippuris vulgaris* (DUNBAR 1967 a). In *Eleocharis*, sporopollenin condenses on short lamellae with a low dense core. These lamellae are located outside the plasma membrane and are sometimes fused with the plasma membrane by a granular material. The

Fig. 20. *E. palustris* stage 11. — A: The sexine has a loosely granular surface (arrow) and becomes gradually more compact towards the interior. Plasma membrane (Pl) of inner wall is incomplete since a second plasma membrane is lacking, see also Fig. 21 A. Approx. ×57,000. — B: Lamellae of the forming nexine parallel to the plasma membrane (arrow) and connected to it. The lamellae are oriented obliquely, when located closer to the nexine region (bent arrow). Tectum (T). Approx. ×42,000. — C: Dense globules in, and at, the perinuclear cisterna (arrow) of the vegetative nucleus (Nu). Segments of rough endoplasmic reticulum (bent arrow) near the forming part of Golgi body (G). Approx. ×26,000. The marker is 0.5 μ. — D: A vesicle in an abortive nucleus (arrow). Short elements protrude from the nuclear envelope (arrow head). Approx. ×35,000. — E:



Section stained in REYNOLDS' lead citrate followed by KARNOVSKY's lead hydroxide. While the background cytoplasm is indistinct, the pollen wall (exine) and "droplets" are emphasized. Exine of two adjacent pollen grains (E), lamellae forming the nexine (S), inner wall (F) with droplets attached to its plasma membrane (arrow), droplets attached to the plasma membrane beneath the exine (arrow head). Approx. ×24,000. The marker is 0.5 μ.

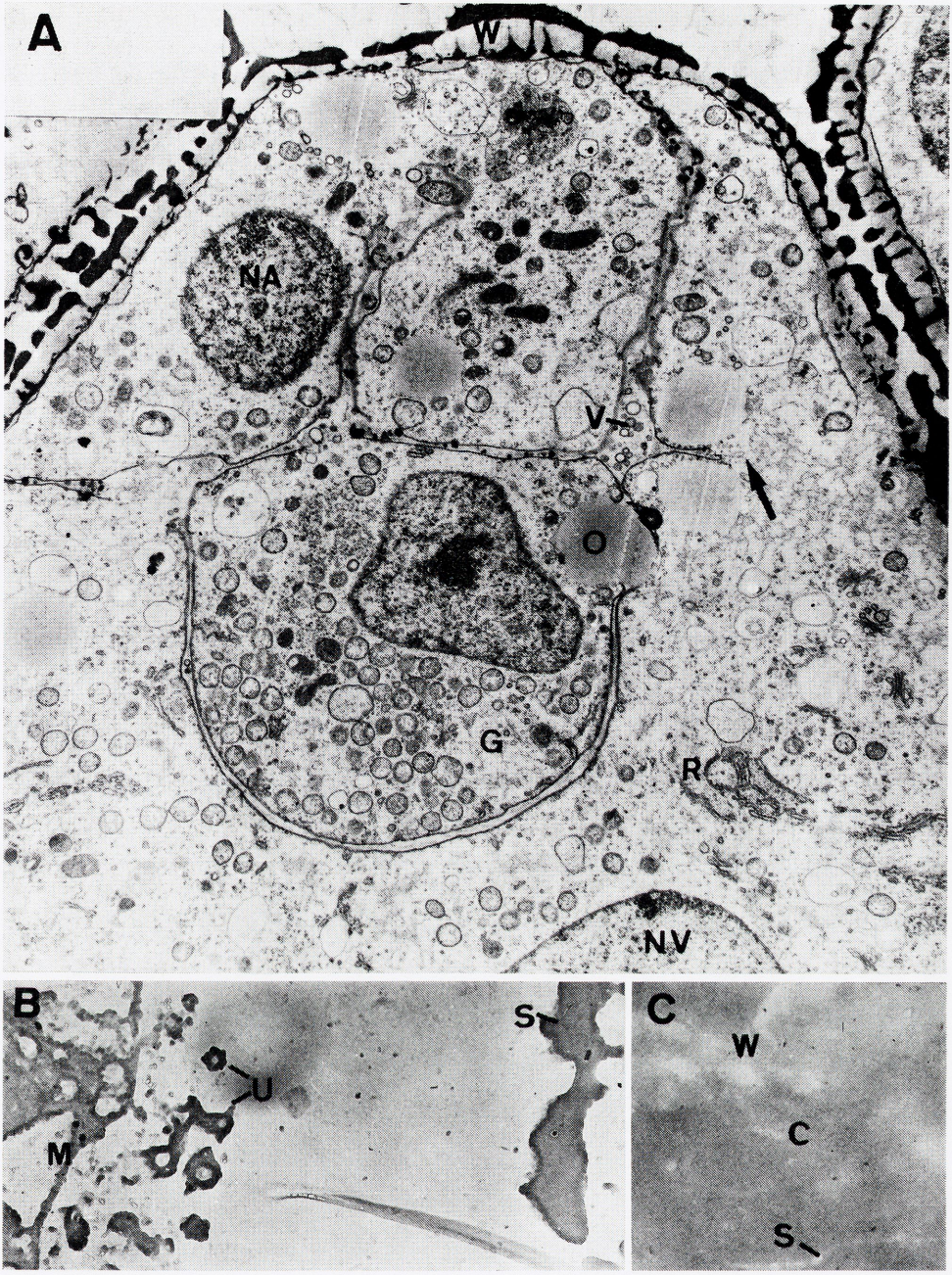
plasma membrane is indistinct in such areas. The lamellae are oriented parallel to the plasma membrane and become obliquely arranged when approaching the nexine region. As development proceeds they gradually form a nexine by way of addition of several lamellae on top of one another giving rise to short, thick nexine units. These units expand during pollen grain growth and, in addition, fuse laterally with the base of bacula. In favourable sections the primary low dense layer can be traced throughout maturity. Open spaces between nexine units remain in the entire nexine layer until maturity. For a review of published information on lamellae associated with exine formation see ROWLEY and DUNBAR (1967).

No kind of lamellae occur along with the formation of the inner wall. This wall consists of acetolyse-resistant globules. As trilaminar segments are lacking, the sporopollenin seems to condense directly onto the droplets which at this period are secreted onto the plasma membrane of the inner wall. This suggestion would explain some of the events concerning secondary wall formation. It does not explain why no sporopollenin is condensed on the droplets of the plasma membrane beneath the nexine however. Either the droplets are provided with different surface characteristics which promote, respectively resist, sporopollenin condensation, or the event is influenced by environmental factors. Some data on the environment are obtained in the present study. Sections of pollen grains have at this period, stage 12, been used for a series of reactions employing T-P and PA-T-P. In material treated by chelating agents such as ammonium oxalate, followed by a multidentate ligand such as T and then treated with P silver proteinate will be bound to free natural aldehydes, as cations should have been blocked or sequestered by the chelating agent (PEARSE 1960). The free aldehydes are localized between bacula, beneath the nexine and in vesicles or channels near the surface, which may open to the surface. However, no reaction occurs in the inner wall. The result obtained shows that in the region where free aldehydes are present no sporopollenin is condensed onto plasma membrane-bounded droplets. The most simple conclusion from this data would be that the aldehydes react with receptors on the surface of the droplets, thereby blocking a possible reaction with sporopollenin. It would be of interest to know if a similar reaction can be obtained around the tapetal cells since as mentioned above, droplets are situated on the entire tapetal surface, while Ubisch bodies are formed by condensation of sporopollenin only in radial and adaxial locations.

Intine

The inner layer of the pollen wall is, as stated by BOUVENG (1963) composed of different polysaccharides. In *Eleocharis* the plasma membrane has infoldings at stage 15. The space hence formed between the nexine and protoplast becomes filled by a fibrous, granular material of loose texture. Golgi bodies are at this time numerous in the peripheral cytoplasm. Vesicles with a fibrous content are associated to the Golgi bodies. These vesicles evidently approach the plasma membrane, where they discharge their content into the young layer of intine. In *Lilium henryi* material for the intine appears to be contributed by Golgi-derived coated vesicles (HESLOP-HARRISON

Fig. 21. *E. palustris* stage 12. — A: The three abortive microspores, one of them separated incompletely from the vegetative cell (arrow), the generative cell (G) with nucleus and large amount of mitochondria, part of vegetative nucleus (NV), one of the abortive nuclei (NA), vesicles in the inner wall (V), exine (W), segments of rough endoplasmic reticulum (R) and lipid droplet (O). Note sporopollenin globules in the inner wall (to the left side)



and between abortive and generative cells. Approx. ×10,000. — B: Acetolysed section with Ubisch bodies (U), tapetum with denaturated cytoplasm (M), sexine of pollen (S). For details see Fig. 22 A, B. Approx. ×2,100. — C: Control for PA stained material. Exine (W), cytoplasm (C), inner wall (S).

1968). The method of freeze-etching demonstrated vesicles which appear to fuse with, and pass through, the plasma membrane into the wall region in *Artemisia* pollen during intine formation (SOUTHWORTH & BRANTON 1971) and the authors suggested that this may represent two functions for the vesicles: the continued deposition of intine wall materials and discharge of wall-softening enzymes prior to pollen-tube formation. HORVAT (1969), in fact, localized enzyme activity in the intine of *Tradescantia paludosa* where the investigation showed a positive reaction for acid phosphatase. Further ROLAND (1971) noted that the intine of some *Ranunculaceae* reacted positively to tests for polysaccharides, and treatment with pectinase and EDTA revealed that the intine consisted of a mixture of pectic matrix and infrequent microfibrils. The isolated intine of *Viola tricolor* consisted of three layers, an outer one of pectin, a middle layer of cellulose and an inner layer of pectic material (FREYTAG 1968).

In *Eleocharis* at stage 12, as mentioned above, sections of pollen grains have been reacted with PA-T-P. In material treated with ammonium oxalate followed by phenylhydrazine not only cations but also free aldehydes will be blocked, and upon further treatment with PA-T-P aldehydes will hence be formed by oxidation of 1,2-glycols and some other hydroxy groups (BARKA & ANDERSON 1963). However fixation and embedding treatment would eliminate most of these other groups whereas most aldehydes formed by oxidation of 1,2-glycols are preserved (FLYNN 1969). The results obtained indicate that aldehydes formed by oxidation of 1,2-glycols are localized in part of the Golgi body cisternae, in associated vesicles and in vesicles or channels which may be in continuity with the plasma membrane. These data may show a pathway for the precursors of intine in *Eleocharis*. Since no positive reaction occurs further backward in the chain of synthesis (for instance the cisternae of endoplasmic reticulum) the precursors may be chemically altered by, or synthesized in, the Golgi body prior to transport to the cell surface. This hypothesis lends support to the results obtained on root-cap cells of wheat incubated with D-[1- or 6-^{3}H] glucose where labelled material is formed in the Golgi bodies, passes to associated vesicles, moves through the cytoplasm across the plasma membrane and is incorporated in the cell wall and slime layer (NORTHCOTE & PICKETT-HEAPS 1966).

The intine seems to develop rather slowly and a compact layer is formed only after the second pollen mitosis. The interface of the protoplast-intine has become more even than at stage 15; the plasma membrane is only slightly low folded. In the abaxial region, however

Fig. 22. *E. palustris* stage 12. GA fixed material, no osmium treatment. — A: Section stained with PA-T-P. Adaxial part of pollen with inner wall (S). Free aldehydes, cations and 1,2-glycols are localized in arcades of bacula (B) and in the inner wall. Approx. ×80,000. — B: Section treated with ammonium oxalate, phenylhydrazine and stained with PA-T-P. Exine (W). Aldehydes formed by oxidation of 1,2-glycols are localized between bacula (A), beneath the nexine (H), in part of the Golgi body cisternae (G), in vesicles (V) and in part of the tectum (arrows). Approx. ×54,000. — C: Tapetal cell (T), Ubisch body (U) in a layer positive to polysaccharide test (F); positive are the surface (arrow) and wingstructure (W) of Ubisch bodies, see also Fig. 30 D. Approx. ×60,000. — D: Adaxial part of pollen with inner wall (S); part of the generative cell (G) with generative wall (bent arrows). Section treated with ammonium oxalate, stained by T-P. Only free aldehydes are localized (since cations are removed) between bacula (arrow), beneath the nexine (arrow head), in vesicles or channels open to the surface (V) but not in the inner wall and generative wall. Approx. ×20,000. The marker is 1 μ. — E: Control without any staining. The electron density of the exine (W) and cytoplasm (C) is only slightly above that of the background (epon-araldite). Approx. ×33,000.

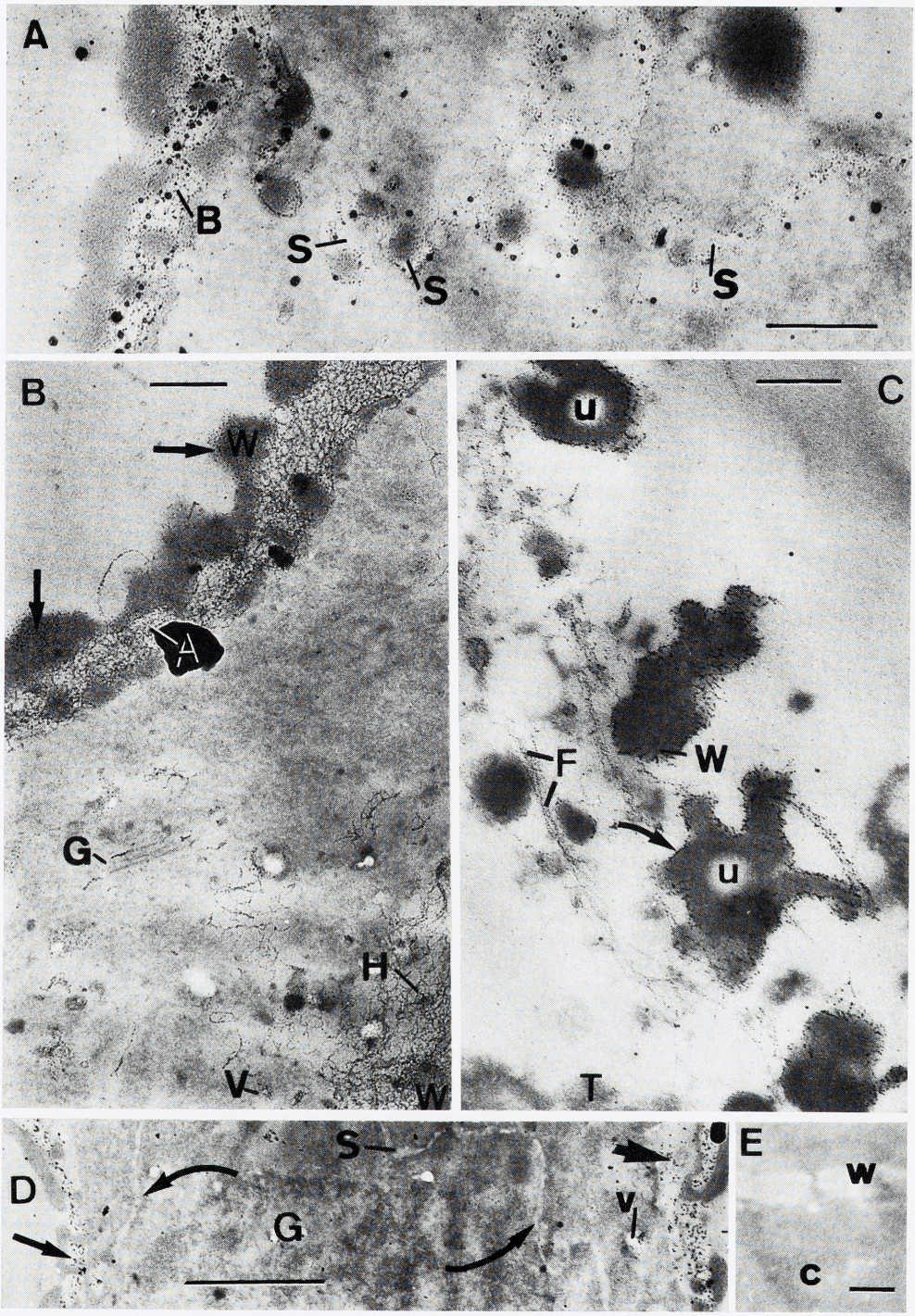


Fig. 22.

the feature of the protoplast-intine resembles the feature common for pollen provided with apertures. It is therefore suggested that this region is where the pollen tube will eventually grow. In the intine a rather electron transparent material is sandwiched in some regions within a more densely stained layer. The lightly stained material appears amorphous and presumably consists of callose, since callose was observed beneath the exine by fluorescence microscopy after aniline blue treatment. The intine of *Impatiens* near maturity contains callose, pectic materials solubilized by ammonium oxalate, hemicellulose and a small amount of cellulose (FLYNN 1969).

The slow development of the intine in *Eleocharis* may in some way be correlated to the degeneration of the abortive cells, since its final shape is not achieved before these cells are sequestered in the intine. At stage 18 the intine becomes undulated in both *E. palustris* and *E. austriaca*, which may indicate a general reorganization prior to the shedding of the pollen grains. A somewhat similar feature of the intine was shown in *Clivia miniata* (AFZELIUS 1955 Pl. 1).

Vesicles with an internal lining are a conspicuous feature in the cytoplasm of *Eleocharis*. Since they are observed only after pollen mitosis, they may become involved in pollen tube formation, or become an organelle of the pollen tube. Similar vesicles are observed as polysaccharide spheres in the pollen tube following discharge (JENSEN & FISCHER 1968), and in the cytoplasm of germinating pollen of *Impatiens pallida* (FLYNN 1969 Pl. 12).

Sporopollenin Globules

From the time when sporopollenin globules are formed and until they disappear, stages 11—16, they do not undergo any change. At stage 13 the inner wall has shrunk, except for the regions where it connects with the outer wall, and in the spots where sporopollenin globules seem to keep the plasma membranes of the inner wall apart. At stage 16 sporopollenin globules are distinct, while the plasma membrane of the inner wall seems to have denaturated. At stage 18 the sporopollenin globules have disappeared. There is a possibility that they fuse to form lumps of sporopollenin, which in fact occasionally are located in the intine.

Pollen Wall Growth

Sporopollenin is deposited on the units of the sexine during ontogenesis. At stage 18 the open spaces between elements of the tectum have decreased. The bacula have increased in width, especially at the base where, as mentioned above, they fuse with the nexine during stages 13—18. Consequently there is no strict limit between the two wall layers at maturity, since in addition the entire layer of exine has the same fine structure and stainability.

Eleocharis pollen grains increase in volume by some 100 % after liberation from the callose envelope and up to anthesis. The exine gains in height from 0.35—0.55 μ from the time when it becomes acetolyse-resistant and near maturity. In a work on *Endymion non-scriptus* ANGOLD (1967) reported a basic dimension in height for the exine which lasted through ontogenesis. Hence a difference in growth exists between the exine of the two species, and it would be of interest to know if the difference is common between the two families *Liliaceae* and *Cyperaceae*.

Surface Topography

In scanning electron micrographs of quite a number of *Eleocharis* species, see Material (STRANDHEDE 1973), perforations of the tectum and spaces between the tectum units are evident. The latter always occur at invaginating areas of the pollen. Since in sections it becomes

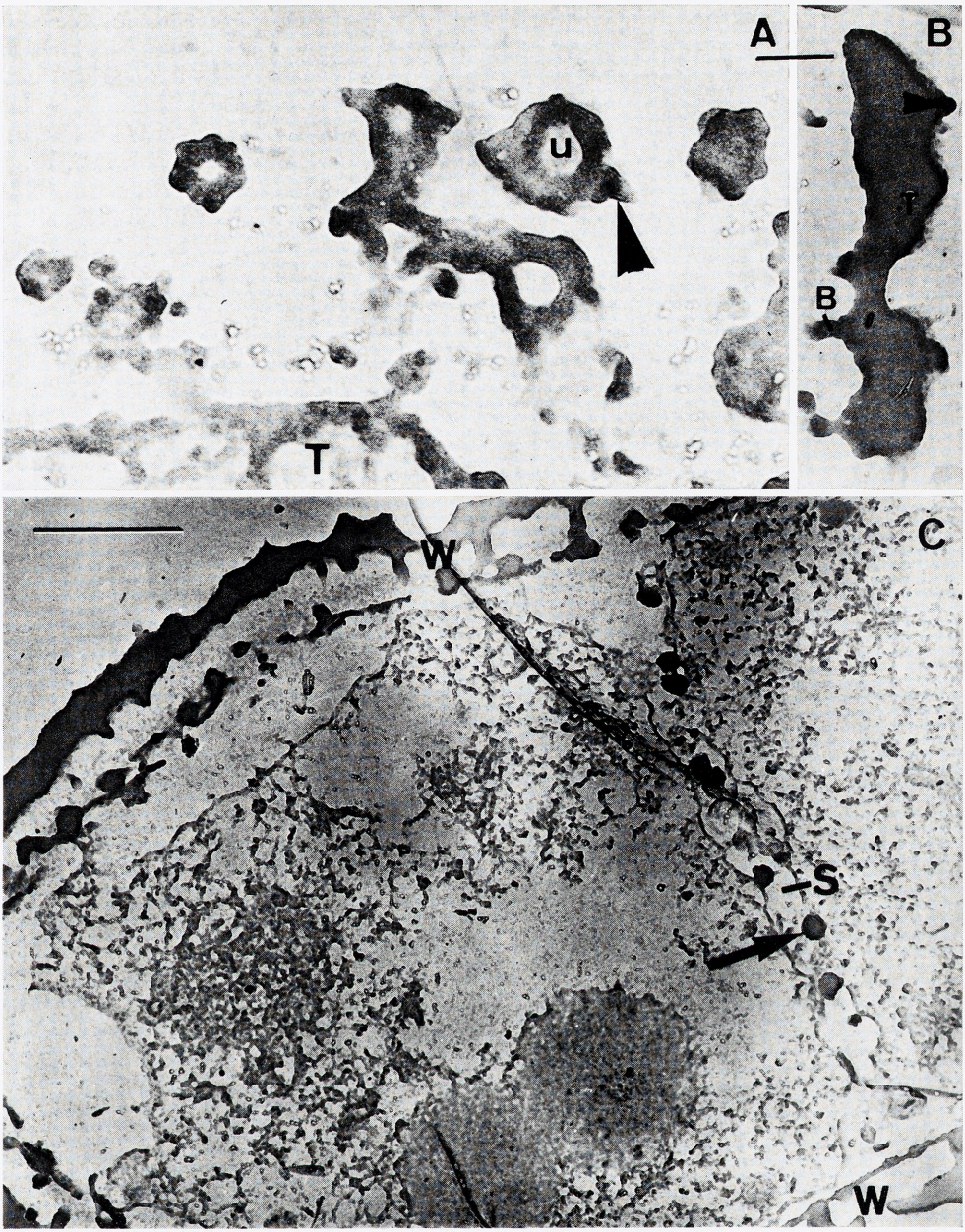


Fig. 23. *E. palustris* stage 12. — A, B belong to the same micrograph, see also Fig. 21 B. Acetolysed section with Ubisch body (U) outside tapetal cell (T). The outer part of the Ubisch bodies is acetolyse-resistant to about the same degree as the sporopollenin of the exine in B. There are "lines" beneath the surface of the Ubisch body and the tectum respectively (arrow heads) and also around the lumina of the Ubisch bodies. Tectum (T), bacula (B). Approx. ×53,000. — C: Sporopollenin globules (arrow) in the inner wall (S) are resistant to acetolysis to the same degree as the sporopollenin of the pollen wall (W). Approx. ×20,000. The marker is 1 μ.

obvious that *Eleocharis* pollen grains are devoid of a continuous nexine, the invaginations may reflect a flexibility due to the construction of its nexine.

Ubisch Bodies

The result of staining and acetolysis strongly indicates a significant similarity between Ubisch body and tectum in *Eleocharis*. The fact that Ubisch bodies react chemically in the same way as the exine and develop synchronously with it was pointed out as early as 1927 by UBISCH in pollen of *Oxalis* and *Lilium*, and was further supported by ROWLEY (1963) in experimental work in *Poa annua*. Evidence to support this statement was also gained by SKVARLA and LARSON (1966) and ECHLIN and GODWIN (1968). The latter described precursors of Ubisch bodies formed as spheroidal vesicles in the tapetal cells in *Helleborus foetidus*. While no such precursors are noticed in the tapetal cells of *Eleocharis,* the first appearance of Ubisch bodies outside the tapetum strongly resembles that in *Helleborus*. CARNIEL (1971 a) observed pro-Ubisch bodies only along the adaxial plasma membrane of the tapetum in *Eleocharis,* which may indicate that also the Ubisch bodies only occurred adaxially to the tapetum. In the present study, however, the first Ubisch bodies appear both at the radial and at the adaxial surfaces of the tapetum. A layer of polysaccharides keeps the Ubisch bodies in place. The elements of this layer are similar to the ones which at stage 13 connect Ubisch bodies to one another and sometimes to the pollen surface. Strands of material connected Ubisch bodies to the tapetum and to the microspore surface in *Poa annua* (ROWLEY 1963) and a review of information about different connections between Ubisch bodies and pollen walls was given in the study. These reports and the PA-T-P test performed in the present investigation leave little doubt that among different plants a connection does exist, firstly between the tapetum and the Ubisch body, and secondly between the Ubisch body and the pollen surface.

Only a small amount of sporopollenin is condensed onto these young Ubisch bodies. They rapidly develop to achieve their final shape and a membranous structure becomes evident in their sporopollenin-skin. The wing-structure and surface membrane of Ubisch bodies and the pollen surface are heavily stained by PTA. The specificity of the PTA staining appears to be strictly related to the physico-chemical conditions of the reaction, namely the pH in the acid range, which implies that the PTA staining is related to the presence of positively-charged groups which can react with the negatively-charged phosphoric groups present in the PTA; it has been suggested that some protein might be involved in the specific staining reaction, since a protease could remove the stainable mate-

Fig. 24. A, B, D: *E. palustris* stage 13. — A: Part of endothecial cell (E), tapetum which has begun to break down, Ubisch bodies outside the tapetum and pollen wall (W). Tapetosomes are located in the tapetal cells (arrow head). A membraneous structure is illustrated on the Ubisch bodies (arrow). Approx. ×24,000. The marker is 0.5 μ. — B: Part of the pollen wall covered by a surface membrane (short arrow), the basal parts of bacula have grown laterally and have fused with the lamellae of the nexine (arrow). Approx. ×24,000. The marker is 0.5 μ. — C: *E. mamillata* ssp. *mamillata* about same stage as *E. palustris* at stage 11. A surface membrane on part of tectum (bent arrow) the rest of the surface is loosely granular (stars), see also Fig. 20 A. A lamella of the forming nexine is in contact with trilaminar membranes (arrow head) on top of one another just outside the plasma membrane (arrow). Sexine (S). Approx. ×80,000. — D: PA-T-P stained material fixed in GA, no osmium treatment. Pointed protrusions of the tectum (arrow) are positive to the polysaccharide test, and so is the surface membrane (S). Approx. ×65,000.

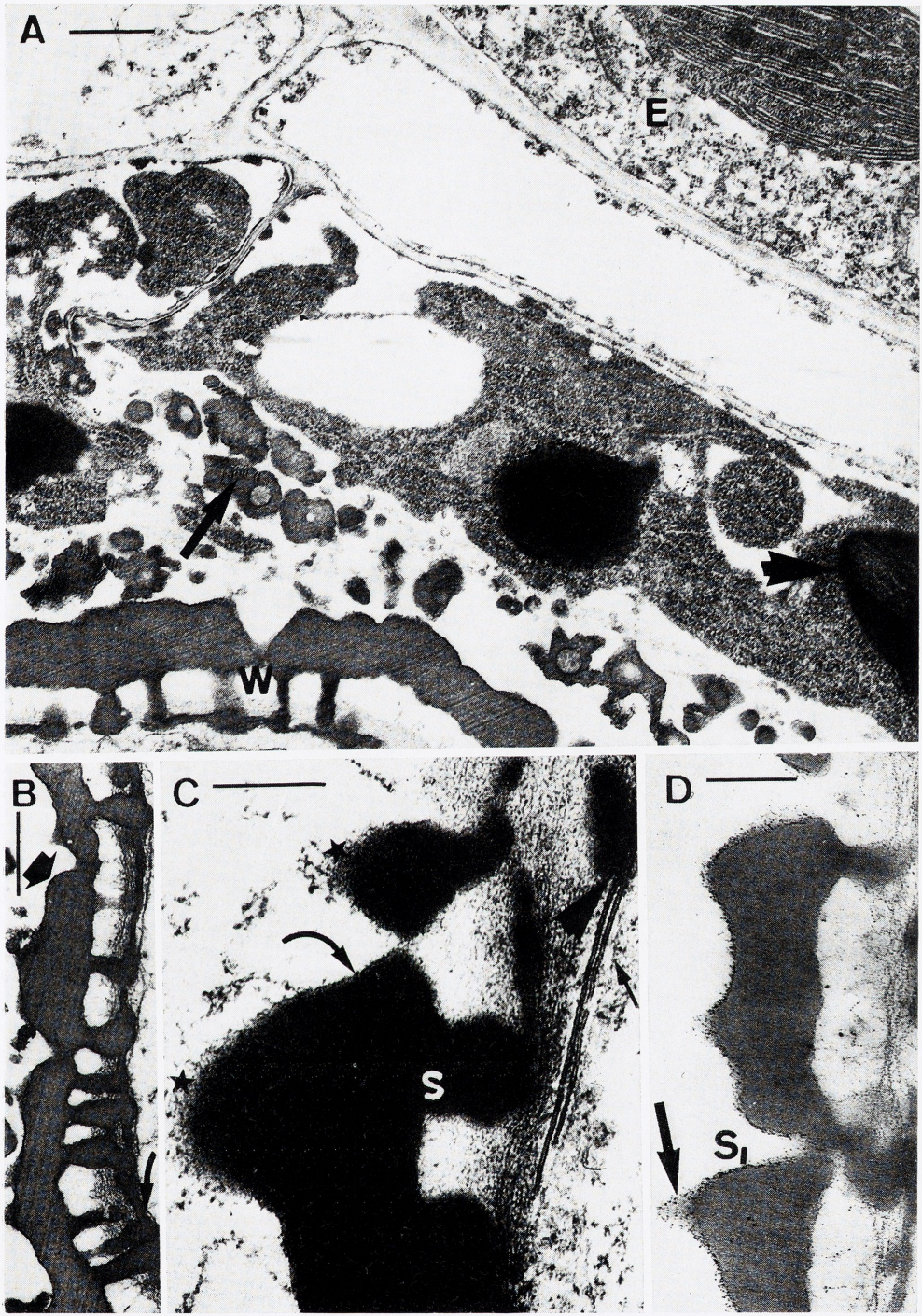


Fig. 24.

rial in selected regions of the plasma membrane of lactating mammary glands (BENEDETTI & BERTOLINI 1963). On the other hand, PEASE (1966) believed PTA to react specifically with polysaccharides.

SMOLA (1968, unpublished term paper) in a review of PTA staining, concluded that this staining possibly is neither strictly a protein nor a polysaccharide stain, but is a combination of the two which gives a more effective staining, since both molecules contain elements which lend themselves to PTA H-bonding. These data may help to partly explain the nature of the wing-structure and surface membrane in *Eleocharis*. While the wing-structure evidently has not been hitherto observed in Ubisch bodies of angiosperms a somewhat similar structure has been noticed on Ubisch bodies of *Selaginella* (PETTITT, personal communication).

Surface Membrane

At stage 11 a surface membrane appears on units of the tectum for short distances. In *Chamaenerion angustifolium* (DUNBAR 1968) a surface membrane appears at a comparable stage of development and has also been observed for short distances. The surface membrane in *Eleocharis* becomes rapidly spread out to cover most of the pollen surface towards maturity. However "open" areas remain throughout ontogenesis. Similar areas are obvious on the surface of Ubisch bodies, where a surface membrane has also developed during stage 12—18. Both regions are positive to a polysaccharide test. It is suggested that such regions constitute modified sites on the surface which facilitate the uptake of substrate and may in this respect be compared to a surface specialization (DUNBAR & ERDTMAN 1969, ROWLEY et al. 1970, DUNBAR 1970).

Tapetosomes

Large irregularly shaped lumps occur together with pollen in certain plants (CHAMBERS & GODWIN 1961). They are reported to contain lamellae (MEPHAM & LANE 1969, NABLI 1971, CARNIEL 1971). Since they develop in the tapetal cells they were named tapetosomes (DUNBAR 1973). From the results obtained in the present study it seems likely that the lamellae originate in some tapetosomes and spread to adjacent tapetosomes. After the breakdown of the tapetal cells tapetosomes are released into the theca loculi where they surround the pollen mass together with Ubisch bodies. Near anthesis some tapetosomes penetrate into the arcades of bacula while others connect to the surface of the tectum. As pointed out by CARNIEL (1971) they certainly are elastic, since in the present study they are able to "slide" through open spaces in the tectum. This characteristic seems to be common for different kinds of structures which contribute to the exine, for instance the wax in *Plumbago* (DUNBAR 1967 b). While several functions could be hypothesized for these structures, the fact that tapetosomes in *Eleocharis* fill a considerable part of the bacula region,

Fig. 25. *E. palustris*. — A, B stage 15. — A: The plasma membrane is partly "withdrawn" (Pl) from the pollen wall. In the space thereby formed the intine begins to develop (I). Polysomes are abundant in the periphery of the cytoplasm (arrow) and so are the Golgi bodies (G). Vesicles (V). Approx. ×24,000. The marker is 0.5 μ. — B: Higher magnification of a nearly tangential section of the same material as in A, illustrating unit membrane-bounded vesicles, some with dumb-bell shape (arrow). Intine (I), inner part of pollen wall (W). Approx. ×60,000. — C: Stage 14. Material stained by uranyl acetate followed by PTA. Ubisch bodies seem to be attached to the pollen surface by their wingstructure (arrow head). Ubisch body (U). Surface membrane of tectum (arrow) and remainders of primexine template (P) are heavily stained, while the exine (W) is more weakly stained. Approx. ×46,000. The marker is 0.5 μ.

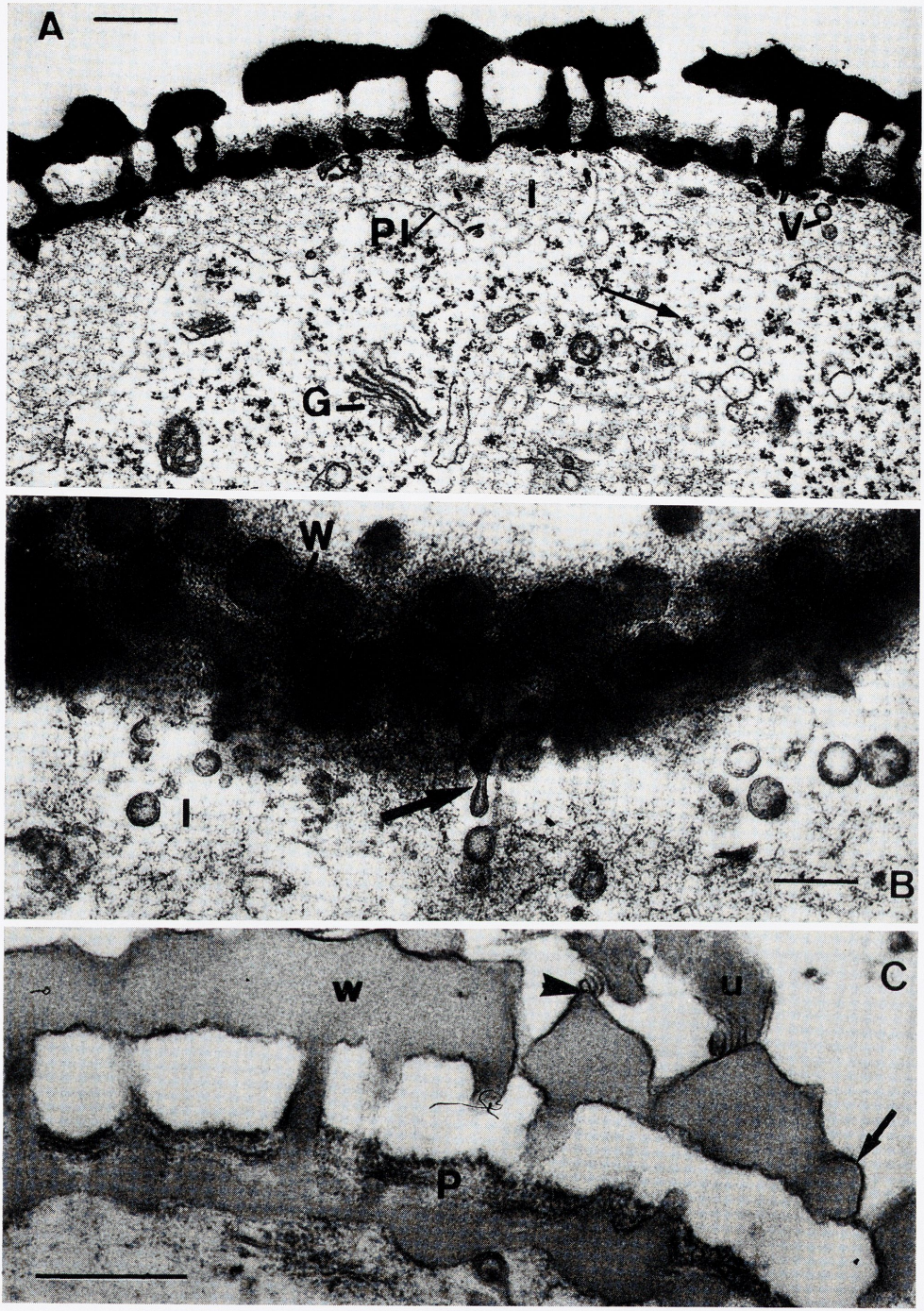


Fig. 25.

must be interpreted as evidence for the opinion (DUNBAR 1973) that the wall is thus given added resistance.

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Fig. 26. *E. uniglumis* ssp. *uniglumis* stage 16. The pollen grain is irregularly curved in some regions. To the right a part of a pollen grain with cross-sectioned bacula is visible (arrow). A granular, fibrous substance is evenly dispersed in the anther loculus. The aborted cells (A) are located in the adaxial part of the pollen grain. An inner wall of sporopollenin globules (bent arrow) separates this residue from the viable part of the pollen. Generative nucleus (G), generative cell wall (E), vegetative nucleus (V). Approx. ×8,000.

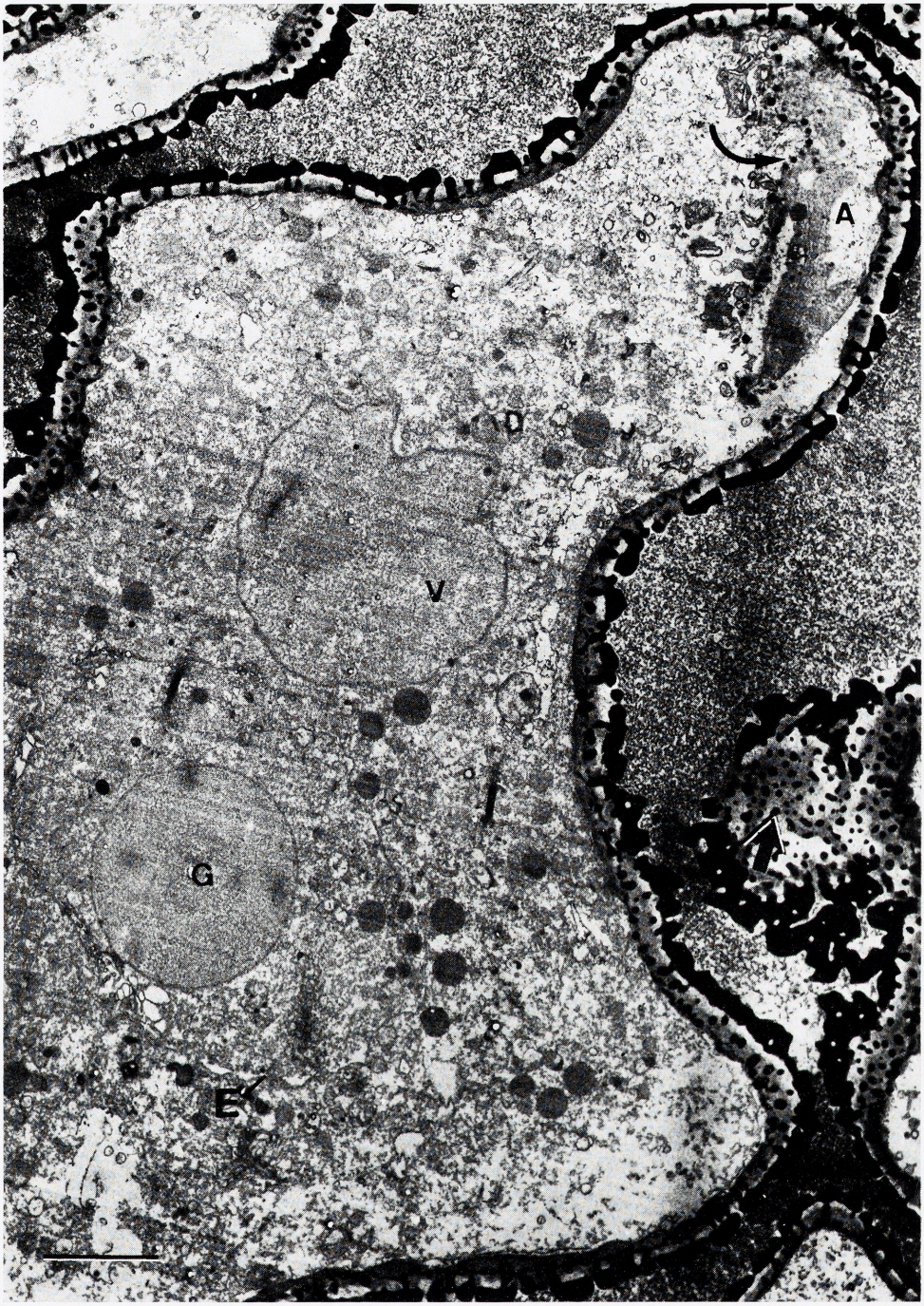

Fig. 26.

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Fig. 27. *E. palustris* stage 17, post pollen mitosis. — A: A substance of low contrast is embedded in the intine (I). Tapetosomes occur between the bacula (arrow) and outside the pollen grain (T). Plasma membrane (Pl), plastids (S), lipid droplets (O), pollen wall (W). Approx. ×17,000. The marker is 1 μ. — B: Within the vesicular membrane is a fibrous substance slightly separated from the limiting membrane (arrow). Golgi body with "fenestrated" appearance (G), lipid droplets (O), plasma membrane (Pl), intine (I). Approx. ×35,000. — C: A great number of small vesicles just outside the plasma membrane (V). Intine (I), tapetosome (T). Approx. ×36,000. The marker is 0.5 μ.

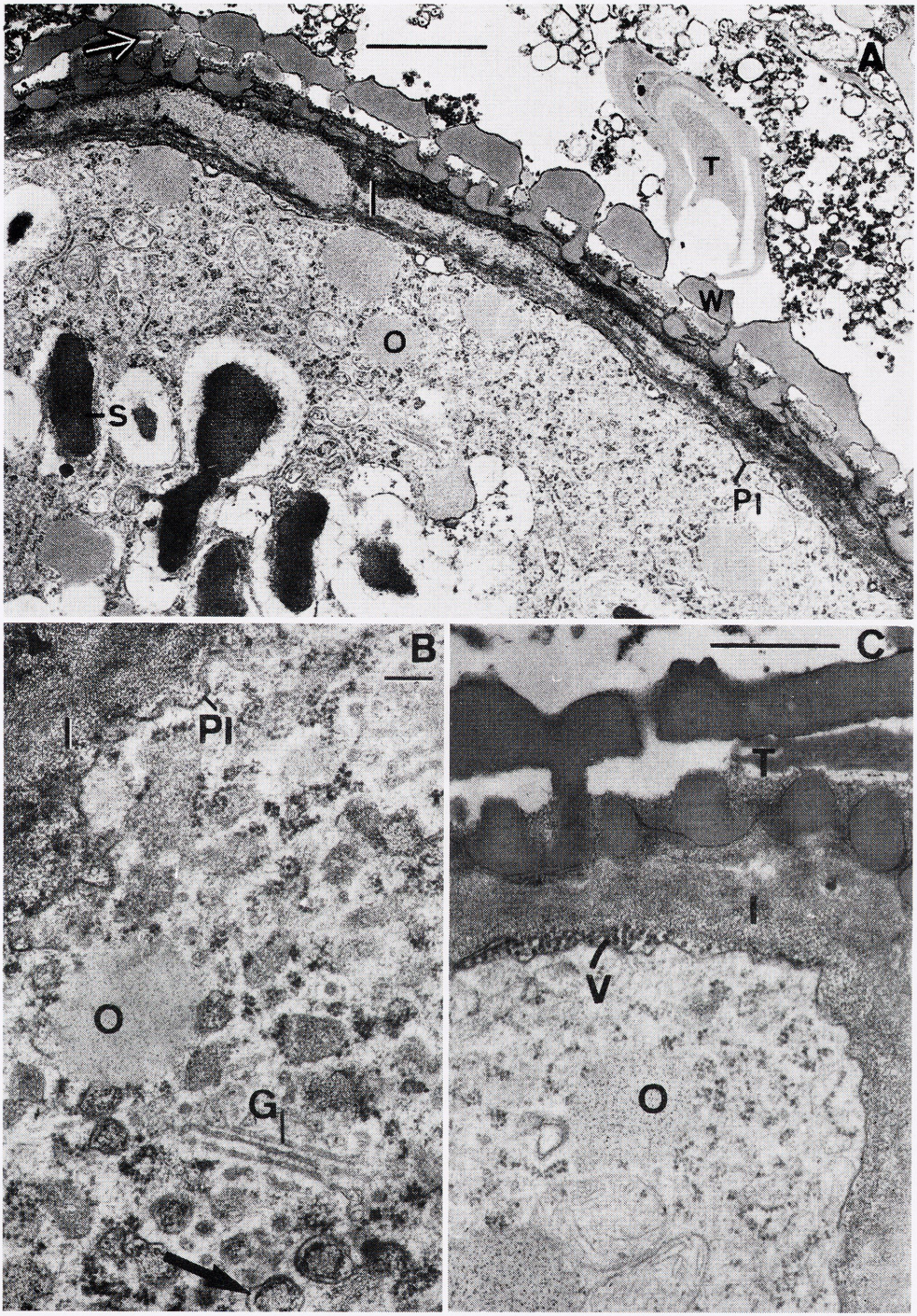

Fig. 27.

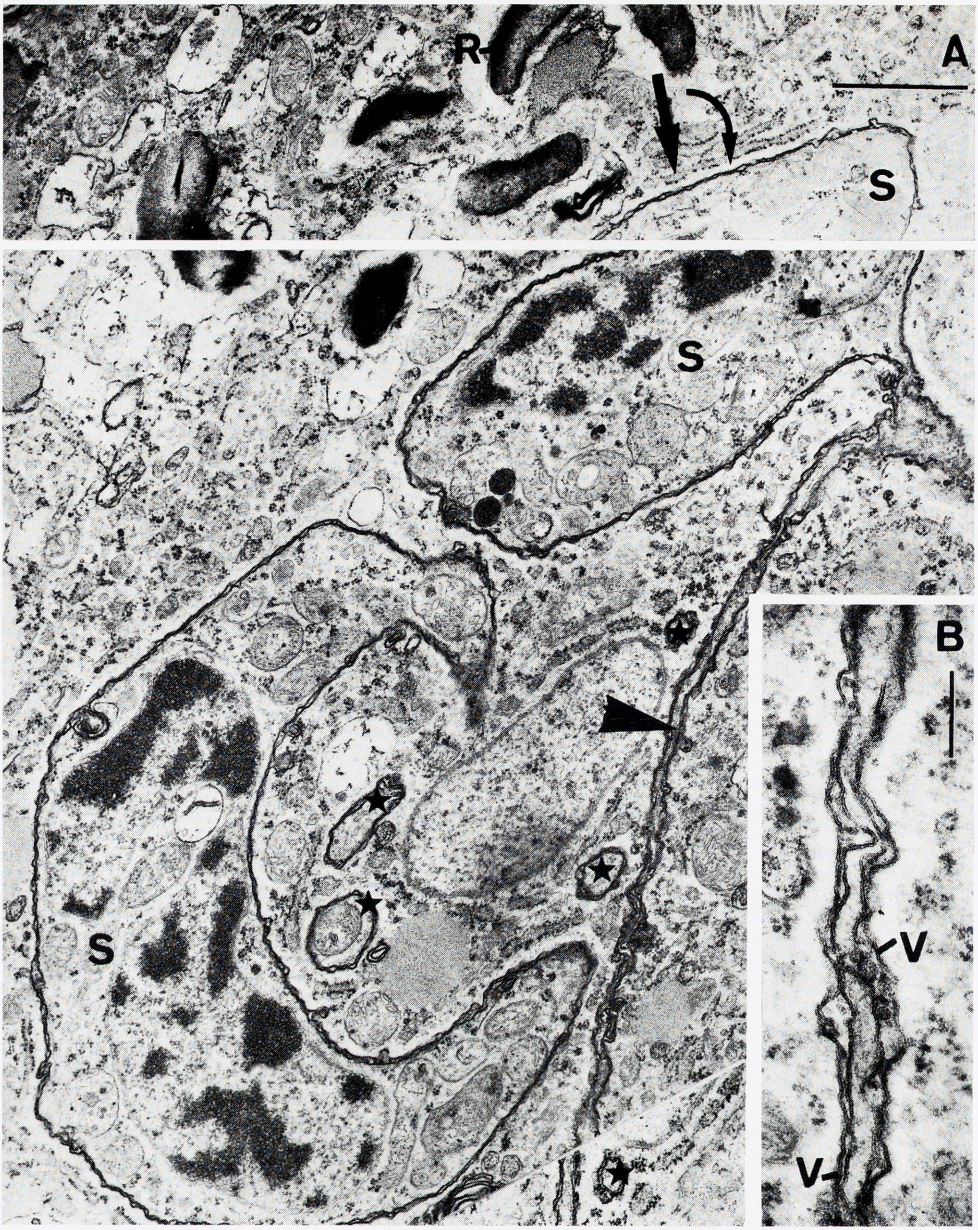

Fig. 28. *E. palustris* stage 17. — A: After pollen mitosis the sperm cells (S) are still connected by a string of plasma membranes (arrow head). The string is here seen near one of the sperm cells. A cross section of the string is also seen at the stars. A narrow, electron transparent space (bent arrow) is noted between the boundary of sperm cells and segments of rough endoplasmic reticulum (arrow). The sperm nuclei are lobed. Plastids (R). Approx. ×18,000. The marker is 1 μ. — B: A part of the string connecting the sperm cells immediately after pollen mitosis. The plasma membrane of the vegetative cell (V) is the outermost one; the innermost plasma membranes are those of the sperm cells. The inner space corresponds to the cell lumen of the former generative cell. Approx. ×60,000. All of the figure, except the insert, belongs to connected part of one EMG.

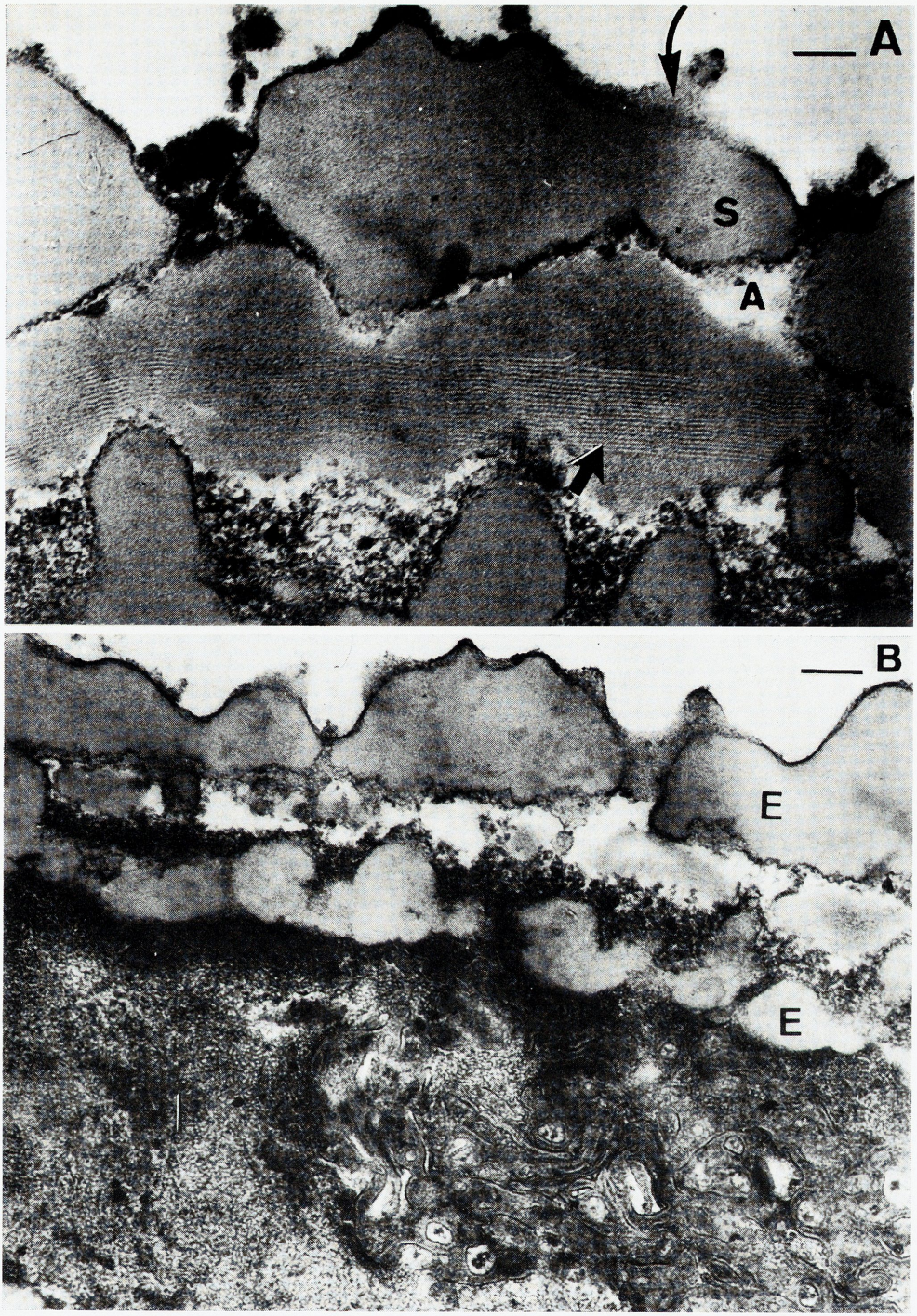

Fig. 29. *E. palustris* stage 17. Detail of pollen grain near maturity. — A: The exine stains less than in earlier stages, and so do the tapetosomes. Multilayered configuration of tapetosome (arrow), pointed protrusion lacking surface membrane (bent arrow). Tectum (S), arcades of bacula (A). Approx. ×90,000. The marker is 0.1 μ. — B: The adaxial part of the pollen grain with membrane profiles in the intine (I) interpreted as the remains of the aborted microspores. Exine (E). Approx. ×45,000.

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Fig. 30. A: *E. palustris* stage 18. A fibrous layer of the intine is strongly invaginated (arrow) into pockets of a low dense layer. Cytoplasm (C). Approx. ×22,000. The marker is 0.5 μ. — B: *E. mamillata* ssp. *austriaca*. Part of young pollen wall (T). Approx. ×24,000. The marker is 0.5 μ. — C: *E. mamillata* ssp. *austriaca* near maturity. Part of anther wall with epidermis (E), endothecium (D) and wall thickenings (W). Two pollen grains are seen with invaginated intine layer (bent arrow) (cf. A). Approx. ×8,000. The marker is 1 μ. — D: *E. palustris* stage 13. PA-T-P stained material fixed in GA, no osmium treatment. Note similarity between surface of Ubisch body (U) and that of pollen surface (P) with regard to the polysaccharide test. Approx. ×28,000. The marker is 0.5 μ.

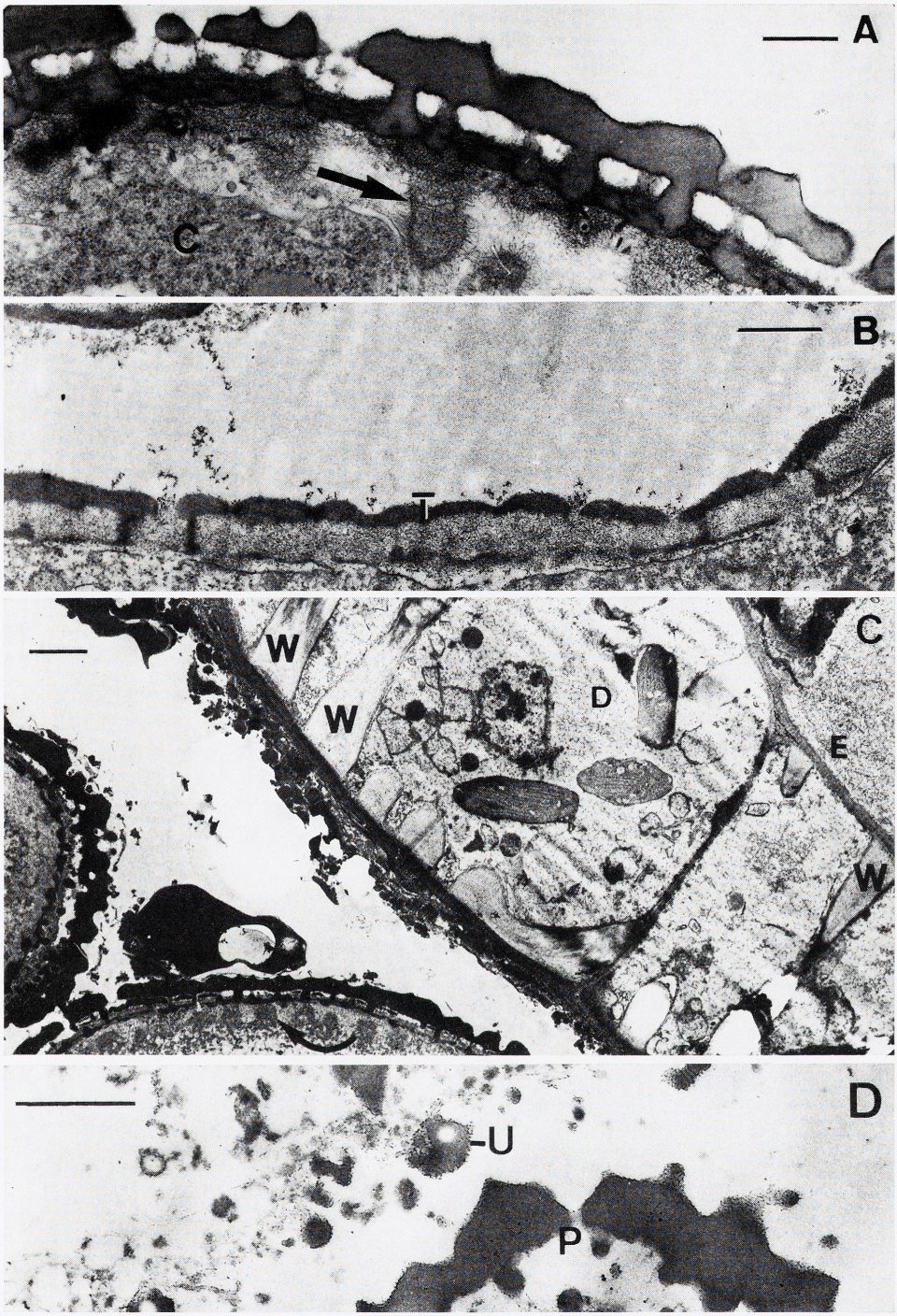

Fig. 30.

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Pollen Development in the Eleocharis palustris Group (Cyperaceae)

II. Cytokinesis and Microspore Degeneration

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ABSTRACT

STRANDHEDE, S.-O. 1973. Pollen development in the Eleocharis palustris group (Cyperaceae). II. Cytokinesis and microspore degeneration. — Bot. Notiser 126: 255—265.

Parts I and II constitute an electron microscopic analysis of pollen development in *Eleocharis*. In the genus three of the tetrad nuclei degenerate and only one remains viable. The results reported in Part II may be summarized as follows:

(1) The development of the walls separating the microspores is simultaneous and the walls complete or incomplete.

(2) The tetrad nuclei move adaxially during proceeding cytokinesis. Microtubules seem to play an active part in this movement.

(3) It is suggested that the break-down of the nuclear envelopes during microspore mitosis in combination with the scanty cytoplasm with only few organelles contribute to the diminished physiological activity causing degeneration of the three adaxial microspores.

(4) The aborted microspores form necrotic remains of cytoplasm enclosed by callose within the intine.

(5) The generative cell is formed in contact with the plasma membrane along the inner wall bounding the abortive microspores. It is successively released from contact with the microspore wall by centripetal growth of the proximal parts of the phragmoplast.

(6) The sperms are organized as cells connected for a period by a string of plasma membranes.

INTRODUCTION

This paper forms the second of two parts, the first being DUNBAR (1973). The figures illustrate Parts I and II jointly.

Mrs DUNBAR has focused her interest on the ultrastructure and ontogeny during the life cycle of *Eleocharis* pollen. The present author makes use of the ultrastructural data for an analysis of some old problems on the cytokinesis during the pollen development and the degeneration of three tetrad nuclei.

Pollen grains discharged as tetrads are known in a large number of quite unrelated plants such as in the families Ericaceae and Juncaceae and in several genera such as *Drosera*, *Epilobium*, *Typha*, and certain orchids such as *Listera*, *Epipactis*, *Orchis maculata*, etc. All four tetrad nuclei develop into functional pollen grains in the taxa mentioned. In the family Cyperaceae, however, three of the tetrad nuclei degenerate, and the tetrad gives rise to only one functional pollen grain. Similar pollen development

is known in *Styphelia* (Epacridaceae, Ericales) distributed mainly in Australia and New Zealand (cf. SMITH-WHITE 1948, 1955, 1959).

There is no real phylogenetic relation between Epacridaceae and Cyperaceae. The tetrad formation and the degeneration of three tetrad nuclei found in the two families have thus a diphyletic background. The Cyperaceae are regarded as being closely related to the Juncaceae and the families were grouped together in the order Juncales by HUTCHINSON (1959).

The pollen of Cyperaceae may be regarded as being the product of a further developmental reduction of the pollen type found in Juncaceae (SKOTTSBERG 1940, and others). The pollen grains of *Eleocharis* are thus tetrads where three tetrad nuclei have aborted, and one nucleus only remains viable. The mature pollen grains of this type were termed pseudomonads by SELLING (1947) and cryptotetrads by ERDTMAN (1952). The first term describes the product, the latter indicates the background of the product. The main features of the pollen morphology and pollen development found in *Eleocharis* are probably representative for the family, or at least for a large part of the family. (Very little information exists however about tropical groups of Cyperaceae.)

The pollen development in Cyperaceae early became a topic of controversy among cytologists. Among the classics in this subject may be mentioned ELFVING (1879), WILLE (1882, 1886), STRASBURGER (1884), and JUEL (1900). During the last two decades good surveys have been published by CRANWELL (1953), SHAH (1959) and CARNIEL (1962), who all also gave valuable information greatly extending our knowledge of the subject. Further information on the meiosis, pollen formation and chromosomes of *Eleocharis* was given by STRANDHEDE (1965 a, b, c, d). All this information deducted from investigations by compound microscopy has reached limits where the methods restrict further progress, leaving some questions open for speculation.

Since then, a transmission electron microscopic study on the subject has been published by CARNIEL (1972). His results will be taken into consideration when discussing the results of the present investigation.

To bring some of the old problems into focus they will be listed below together with short reviews of earlier opinions.

(1) The type of pollen development in Cyperaceae and the wall formation between the tetrad nuclei.

Concerning the microsporogenesis in angiosperms two main types of wall formation are commonly distinguished: the simultaneous type common in dicotyledons, and the succedaneous type common among monocotyledons and regarded as being an advanced type.

Pollen development in Cyperaceae is commonly regarded as being simultaneous as in Juncaceae (MALHEIROS, CASTRO & CÂMARA 1947). HÅKANSSON (1954) considered it to be a reduced form of the "successive type" relying upon his own observations in *Eleocharis* and JUEL's observations of an ephemeral cell plate in the dyad of *Carex acuta*. STRANDHEDE's (1965 b) observations of secondary reunion during first pollen mitosis of the chromosomes belonging to two different tetrad nuclei support the idea that cytokinesis takes place late and obviously after completed meiosis. According to PIECH (1924 b, 1928 a) the four tetrad nuclei remain as naked nuclei in a common cytoplasm which was also referred to by RUTISHAUSER (1969) and by ERDTMAN (1969).

(2) The background to the abortion or degeneration of three tetrad nuclei and the functional origin of the orientation of the abortive nuclei towards the proximal part of the pollen.

This central problem has been studied by several cytologists. PIECH (1924 a)

considered it to be a problem of the nutrition of the pollen from the adaxial tapetum. According to HEILBORN (1918) and HÅKANSSON (1954) the degeneration is a consequence of insufficient space in the adaxial part of the microsporangium. SHAH and PATEL & SHAH (1960) considered that plasmatic constrictions in the tetrad form the active physical background to the degeneration, and LEWIS & JOHN (1961) considered that there is a physiological gradient towards the centre of the cell, forcing the distribution and the degeneration of the three tetrad nuclei to take place.

(3) The fate of the abortive tetrad nuclei.

ELFVING and STRASBURGER considered the nuclei to be resorbed by the surrounding cytoplasm. According to WILLE (1886) they are associated with the fourth, viable nucleus. PIECH reported that they are excluded by the cytoplasm and then enclosed within membranaceous thickenings or callose accumulations. According to PFEIFFER (1942) they are incorporated into the pollen wall structures and SHAH observed them closely adpressed to the intine.

(4) The organization of the generative cell and the nature of the sperms.

STRASBURGER describes the generative cell as being connected with one of the side walls of the pollen grain and isolated by a hemispheric wall from the vegetative cell or tube cell. PIECH objected to this and illustrated by a series of drawings how the generative cell is organized by "free cell formation". This idea was also referred to by RUTISHAUSER and by GÓRSKA-BRYLASS (1970).

PIECH reported that the sperm nuclei of *Eleocharis palustris* only are enclosed in real sperm cells. The sperm cells of *E. uniglumis* were reported to be ephemeral with the nuclei soon being freed in the cytoplasm of the tube cell.

This question may however be only of historical interest as it is now generally accepted that the sperm nuclei are enclosed within cells (cf. SCHNARF 1941). Several of the other opinions referred to above could also be considered as being of mainly historical interest.

MATERIAL AND METHODS

A representative number of anthers have been studied from about 25 plants of the following taxa. The numbers in brackets refer to scanning electron micrographs of mature pollen grains collected by dusting them out of the open thecae.

E. palustris (L.) R. & S. ssp. *palustris* (Fig. 1 A, C).

E. uniglumis (LINK) SCHULT. ssp. *uniglumis* (Fig. 2 C, D)

E. uniglumis (LINK) SCHULT. ssp. *sterneri* STRANDH. (Fig. 1 D)

E. mamillata LINDB. FIL. ssp. *mamillata* (Fig. 1 B)

E. mamillata LINDB. FIL. ssp. *austriaca* (HAYEK) STRANDH. (Fig. 2 A, B).

Scanning electron micrographs of the North American taxa *E. smallii* BRITT. and *E. erythropoda* STEUD. have also been prepared and studied.

The plants investigated have been cultivated under uniform conditions as described by STRANDHEDE (1966 p. 9). The methods for the electron microscopic preparations are described by DUNBAR (1973).

The plants have previously been investigated under the compound microscope. Their pollen development was then found to be normal and the pollen viable.

The pollen grains form sectors in the cross-sectioned pollen loculus (microsporangium). The terms "adaxial" and "abaxial" as used in the following refer to this orientation. "Adaxial" thus means "directed towards the centre of the *loculus*" and "abaxial" means "away from the centre of the *loculus*".

OBSERVATIONS

Tetrad Stages and Microspores

Meiosis has previously been studied under the compound microscope by STRANDHEDE (1965 a, c). For details concerning the organelle population during pre-meiotic and meiotic stages, see DUNBAR (1973).

The tetrahedral and the isobilateral

forms are the most common positions of the tetrad nuclei. Less commonly the tetrad nuclei are arranged linearly immediately after meiosis (STRANDHEDE 1965 a, b, c). Their position is not fixed in the cytoplasm but can be more or less central or abaxial. More commonly the nuclei lie somewhat adaxially in the tetrad.

The first signs of the tetrad cytokinesis are accumulations of microtubules and vesicles where cell plates successively develop between the four nuclei. The vesicles unite into larger, sac-like structures interrupted and more or less separated for a time by broad or narrow plasmatic bridges. A fibrous material can be seen in the flat sacs forming the cell plates. The cell plates of the tetrad organize often markedly regular boundaries between the microspores (Fig. 10 A). They sometimes become deformed into a system of sacs, lacunae and whorls, and can be distinguished only with some difficulty (Fig. 7).

The cell plates remain as flat sacs in contact with each other for a comparatively long period. The sacs unite successively into intercellular spaces in the following text referred to as inner walls (see Discussion). These spaces sometimes enclose vesicles or lobes of cytoplasm in some parts. Large lipid bodies have been observed in zones of cytokinesis (Fig. 11). The inner walls are for a long time incomplete towards the periphery of the tetrad and the cytoplasms of the microspores thus remain in contact there (Fig. 11, 1—5).

The position of three tetrad nuclei is successively shifted adaxially and the fourth remains more central in the tetrad (Fig. 11). During this nucleus-shifting activity, microtubules (Fig. 12) and whorls of endoplasmatic reticulum (Fig. 10 C) are the most conspicuous organelles of the cytoplasm (cf. also DUNBAR).

Outside the lateral margins of the cell plates, vesicles and microtubules accumulate into phragmosomes. Microtubules are however not only concentrated in the phragmosomes and the cell plates, but also appear in the more peripheral parts lateral to the abaxial tetrad nucleus and parallel to the lateral plasma membrane of the tetrad (Fig. 12 B).

In some material where the nuclei have moved to the adaxial part, microtubules are less frequent, or absent, though the inner walls are still interrupted, leaving broad plasmatic connections between the microspores. In the parts where they are still incomplete, cytokinesis seems to have stopped as no microtubules are visible. Though Golgi stacks may occur close to these openings no signs of cytoplasmatic activity are noticeable. The inner walls are also often irregular forming lacunae with plasmatic protrusions or vesicles, or complexes of vesicles and membranes. These conditions may remain also after passed microspore mitosis (Fig. 21 A).

In other tetrads studied at the same stage of development cytokinesis is completed and the cell plates come into contact with the common plasma membrane surrounding the tetrad (Fig. 19 A). When this happens the intercellular spaces referred to as inner walls open into the extracellular space between the plasma membrane and the developing common pollen wall. The tetrad cell is thus divided into four microspores, the abaxial one large and the adaxial ones small with only little cytoplasm of their own.

The cytoplasm around the four tetrad nuclei is still loaded with mitochondria in the proximal microspores as well (cf. DUNBAR 1973). There are no obvious size differences between the four nuclei (Fig. 11).

Differentiation between the Microspores and Cytokinesis of the Generative Cell

Microspore mitosis, often called the first pollen mitosis, has been studied in detail by STRANDHEDE (1965 b, c). The abaxial nucleus is the only one to divide though the three adaxial nuclei pass into a stage similar to a mitotic prophase or

an early metaphase. Until then the nuclear envelopes of all the tetrad nuclei have been well organized, but as mitosis starts their envelopes become more or less disorganized.

Inclusions have been observed in the adaxial nuclei. Among these are lipid bodies and vesicles. Inclusions have also been observed in a few viable nuclei.

In contact with the inner walls multilayered membrane figures are sometimes developed. The membranes are similar to the plasma membranes. The lumens of the systems are usually electron transparent. In one of the proximal microspores studied, a multilayered membrane system includes nuclear substance. It is probably a lobe from the irregular nucleus in the immediate vicinity.

When the abaxial microspore divides during microspore mitosis, the nuclear spindle always takes up a longitudinal position in the tetrad. One of the telophase groups will thus move abaxially. The other one moves down to the vicinity of the inner wall bounding the adaxial microspores, where the generative cell develops.

A dense hemispherical phragmoplast of numerous microtubules is organized radially around the adaxial daughter nucleus and close to the inner wall bounding the adaxial microspores (Fig. 18 A). A hemispherical cell plate is formed in this phragmoplast. The cell plate is formed by vesicles which fuse to form sacs until a hemispherical intercellular space is formed (Fig. 21 A). Numerous microtubules are attached to the cell plate and occasionally also to the envelope of the vegetative nucleus (Fig. 17 D). The intercellular space is interrupted by narrow membrane contacts which successively disappear (Fig. 17 D). The intercellular space contains a sparse granular-fibrillar material forming a simple wall (Figs. 17 D, 21 A).

The cytoplasm near the active zone of the cytokinesis that forms the generative cell is heavily loaded with cisternae of various forms of the endoplasmatic reticulum, often in visible contact with the envelopes of the generative and the vegetative nuclei. Golgi bodies and vesicles are common, as are ribosomes and microtubules (Fig. 18 A). The cytokinesis of the generative cell is completed in the distal parts, while an annular phragmosome is developing in contact with the plasma membrane, towards the inner wall separating the viable abaxial part from the abortive adaxial microspores (Fig. 18 A). Abundant microtubules concentrate within this zone of contact.

The generative nucleus has an organized envelope and dense contents. The nuclear substance of the vegetative nucleus is less electron dense or diluted when compared with the generative nucleus (Fig. 21 A).

The synchronization between the development of the pollen wall and the cytokinesis of the generative cell is not absolute. Nor is the tetrad cytokinesis always complete at this stage after completion of the microspore mitosis. Figure 21 A illustrates a pollen grain displaying delayed or interrupted cytokinesis. The pollen wall has a rather well developed tectum. Tetrad cytokinesis is peripherally far from complete and the generative cell still has a broad zone of contact with the incomplete inner walls of the adaxial microspores. The cytokinesis of the generative cell is here complicated by the presence of a lipid body.

The generative cell is successively detached from the contact with the inner walls bounding the adaxial microspores by the action of the basal, annular phragmosome. The last point of contact is a narrow string or fold of plasma membranes, in pictures resembling an umbilical cord (Fig. 18 B). This "cord" is initially short but grows in length before contact with the inner walls ceases.

Degeneration of the Proximal Microspores

As mentioned, microspore cytokinesis is often complete (Fig. 19 A) but in several

pollen grains it remains incomplete to a varying extent even at stages after microspore mitosis (Fig. 21 A). Broad plasmatic connections may remain between the abortive microspores or between those and the viable part of the pollen grain. Cytokinesis has failed almost completely in one pollen grain studied, and appears only as fragmental extra-cellular spaces in the periphery of the pollen grain where cytokinesis should have taken place. Characteristic sporopollenin globules (cf. DUNBAR 1973) also occur here. They are normally formed in the intercellular spaces between the microspores. Sporopollenin globules are discussed in detail by DUNBAR.

The abortive microspores are successively depressed into the adaxial part of the pollen grain. Thus they become small with only little cytoplasm which still seems to be viable, but with a restricted number of organelles. Among the organelles are vacuoles often with rather complex, unidentifiable contents or sometimes with more or less recognizable remains of cytoplasmatic organelles. The vacuoles may be of varying appearance, often being somewhat irregular in form.

As mentioned, the adaxial microspores have been retarded in their development at a stage corresponding to late prophase or early metaphase in microspore mitosis. The nuclei have to a varying extent been deprived of their envelopes during the mitotic activity. After failure of microspore mitosis in the adaxial microspores, they soon become increasingly necrotic. Figure 26 illustrates this feature. The sporopollenin globules are easily recognized as a boundary to the viable part of the pollen grain. The protoplasts of the adaxial microspores have collapsed and are isolated in polysaccharide masses which will ultimately be enclosed in the intine.

A detail of the adaxial part of a pollen grain near maturity is shown in Figure 29 B. The intine encloses a complex of membranes and cytoplasmatic residues interpreted as the final remains of the abortive microspores. The remains lie deeply embedded in the intine, which is similar to the picture obtained by compound microscopy.

Organization of the Sperm Cells

The generative cell is ultimately freed from all contact with the inner walls bounding the abortive microspores. Then the generative cell moves into the cytoplasm of the vegetative cell in a position commonly abaxial to the vegetative nucleus. In Figure 26 the lobed nucleus is the vegetative one and the generative cell is noticeable distal to it. The boundary of the generative cell is a cell plate with vesicles and intercellular sacs rather than a real cell wall.

During pollen mitosis, often called the second pollen mitosis, the nucleus of the generative cell divides. Two daughter nuclei lie within the former generative cell which becomes dumb-bell-shaped. The middle part elongates successively until it looks like a thin string (Fig. 28 A). This string is built up of two plasma membranes (Fig. 28 B). The outermost one is the plasma membrane of the vegetative cell. The innermost one encloses the cytoplasm of the sperm cells. An intercellular space sometimes with vesicles is enclosed between the outermost and innermost plasma membrane.

The sperm cells are seen in Figure 28 A. They are bounded by two plasma membranes with an interlying narrow intercellular space or wall. The extension of one of the sperm cells is part of the connecting string mentioned. It has been sectioned and some cross sections are visible (asterisks).

When the string is ultimately broken the daughter cells, i.e. the sperm cells, are spindle-shaped, often somewhat bent or crescent-shaped. The shape of the nuclei is variable, often irregular.

DISCUSSION AND RESULTS

The discussion in this paper will be centred around the old questions listed in the introduction. For more detailed references to earlier investigations on the subject, see STRANDHEDE (1965 a, b, c). A detailed discussion on the ultrastructural features and the ontogeny is given by DUNBAR (1973).

Microspore Cytogenesis

The old question of whether the wall formation during the microspore development in *Eleocharis* is succedaneous or simultaneous should not present any difficulties using electron microscopy. The dyad stage has by no means been common in our preparations, but no sign of any cell plate has been observed during this stage. Even a very fragmental cell plate between first and second meiotic divisions should be discernible.

As far as the present author has been able to observe during this investigation and those in 1965, the microspore wall development of the *Eleocharis palustris* group is simultaneous. The same type occurs in Juncaceae. It can, however, hardly be disregarded that a certain variation occurs in Cyperaceae and also in *Eleocharis*, as JUEL (1900) as well as HÅKANSSON (1954) reported ephemeral cell plates at the dyad stage. These reports possibly indicate the existence of intermediate forms of cytokinesis during microsporogenesis.

When CARNIEL (1972) described cytokinesis at the tetrad stage of *Eleocharis palustris* he emphasized that it is complete, as in all other angiosperms, and that walls divide the tetrad into four microspore cells. According to the observations in the present study one cannot be so categorical. The schedule of the tetrad cytokinesis and of the segregation of the abortive microspores in the adaxial part of the tetrad varies between different tetrads. In some tetrads the nuclear spindles do not disappear after meiosis until the phragmoplasts of the cytokinesis have been formed. These phragmoplasts consist of microtubules as do the nuclear spindles, and they resemble accessory spindles under the compound microscope. In that way are formed the puzzling accessory spindles crossing in all directions as described by PIECH. They can thus be explained as being phragmoplasts of the tetrad cytokinesis as suggested by STRANDHEDE (1965 b p. 383).

In many tetrads cytokinesis is completed and four cells are formed (Fig. 19 A). The schedule of the cell plate development varies however from pollen grain to pollen grain and cytokinesis may be more or less complete at a certain stage of pollen development (cf. Figs. 19 A and 21). Retarded cytokinesis was indirectly demonstrated by HÅKANSSON (1954) and by STRANDHEDE (1965 b). STRANDHEDE showed that in a few cases the chromosomes from two microspore nuclei were included within one metaphase group during microspore mitosis giving rise to "secondarily unreduced" pollen grains with only two abortive microspores. This phenomenon is different from the formation of unreduced pollen by restitution where only one abortive and unreduced microspore is formed.

The intercellular spaces formed between the plasma membranes of the microspores during cytokinesis are extremely variable in width and have varying contents of substances and also of organelles. The boundaries between the microspores can hardly be regarded as well-defined walls. A thin, incomplete or almost ephemeral fibrillar structure resembling a middle lamella may occur (Fig. 19 A) and these intercellular substances may probably be regarded as primary components of walls (see further DUNBAR 1973). The term "inner wall" used in the present paper for these partitions is not ideal, but is the most neutral term I can find.

The inner walls are often perforated not only by holes similar to plasmodesmata

but also larger ones, leaving narrow to rather broad plasmatic connections between the microspores. In the material studied variations regarding this feature may occur in one and the same microsporangium and within one pollen grain. Whether or for how long these connections remain has not been studied to satisfaction but they obviously make possible the formation of the secondarily unreduced pollen grains mentioned above.

Degeneration of Three Microspores and the Fate of Their Residue

Many preparations have been studied in order to explain the abortive process in which the distal microspore only remains viable in the pollen grain. It is difficult to determine when and how the degenerative process begins. According to LEWIS & JOHN (1961) it is the position in the tetrad that decides which nucleus is to survive and the positions of the nuclei "over-ride" their cytotype. The same conclusion may be drawn from STRANDHEDE's (1965 b) observations on some strains with 15 chromosomes instead of the balanced chromosome number 2n=16. In these strains it was not always the cytologically most balanced tetrad nucleus with n=8 that survived. The chromosome number n=7 occurred with the same frequency as n=8 in the abaxial microspore.

When the tetrad nuclei and the developing inner walls are successively shifted towards the adaxial part of the former pollen mother cell during proceeding microspore cytokinesis, plasmatic connections still exist laterally in the tetrad out of the edges of the cell plates. Obviously, these marginal plasmatic connections make possible the transportation of the three tetrad nuclei with surrounding cytoplasm to their adaxial destination in the pollen grain. The microtubules found in the lateral parts of the cytoplasm outside the phragmoplasts and without direct contact with the cell plates (Fig. 12 B) seem to play an active part in these movements. The common deformation of the young cell plates is possibly caused by this plasmatic transport.

It may be discussed whether the orientation of the abortive microspores is in fact transportation or only the consequence of growth. It is obviously the result of a combination of an active transport of cytoplasm, cell plates and nuclei during the proceeding growth of the developing pollen grain.

By the characteristic orientation with three nuclei in the narrow adaxial part of the pollen grain and one nucleus in the broad abaxial end, the latter nucleus will be surrounded by the main part of the cytoplasm of the tetrad. The three adaxial nuclei are surrounded by only very little cytoplasm. A similar unequal distribution of cytoplasm during cytokinesis seems also to occur in *Rhynchospora japonica* MAKINO where, however, the abortive microspores are grouped in the abaxial end of the pollen grains (TANAKA 1941). Thus, the sector-shape of the pollen grains in *Eleocharis* is neither a reason in itself for the adaxial orientation nor for the ultimate degeneration of the adaxial microspores.

For a period there is little or no difference between viable and abortive protoplasts. No polarization has been observed in the organelle populations which are similar in the four microspores during this period (cf. DUNBAR 1973). In several organisms such polarization and other cytoplasmic properties seem to regulate the development of the gametes after meiosis (cf. SMITH-WHITE 1959).

Degeneration is common in meiotic products. In female animals the abortive three pole bodies are surrounded by only scanty cytoplasm. The viable tetrad cell develops into the egg and is surrounded by rich cytoplasm (cf. LINDAHL 1941 and GUSTAFSON 1946).

A corresponding situation is common in Fucales (Phaeophyta) where a restricted number of the oocytes develop

into viable eggs, while the abortive ones are surrounded by only scanty cytoplasms of their own.

In the macrosporogenesis of angiosperms also, three of the tetrad cells degenerate in favour of the fourth one which develops the embryo sac.

In *Eleocharis* the nuclei of the abortive microspores are obviously active until microspore mitosis. Mitosis also starts in the abortive microspores, but is interrupted. Some authors (JUEL 1900, TANAKA 1939, 1940, 1941, SHAH 1959, and others) have reported that this mitosis is fulfilled in other genera of Cyperaceae.

The fact that mitosis is not completed in *Eleocharis* is possibly due to the scanty cytoplasm of the adaxial microspores. After the break-down of the nuclear envelopes during microspore mitosis, the degeneration of the adaxial microspores accelerates markedly. The physiological activity seems to decrease abruptly which obviously leads to necrosis of their cytoplasm.

Efforts have been made to correlate this collapse with the occurrence of any particular structural details in the cytoplasm. One hypothesis tried has been that the scanty cytoplasm could be deprived of organelles by autophagocytotic vacuoles or lysosomes. It has however not been possible to correlate definitely the vacuoles observed with any autophagocytotic activity.

During the degeneration the cell structures successively decompose (Fig. 26) and ultimately become embedded in callose of the intine. In the remnants of the cytoplasm, whorls of disorganized membrane systems (Fig. 29 B) are long recognizable being mixed with callosic substances and cytoplasmic, probably dehydrated remnants. Similar pictures were published by CARNIEL (1972).

The basal background of the specific degeneration within Cyperaceae must be genetic and deeply laid down in heredity. Only the structural features related to this process are possible to observe, and its details are still unknown. The unequal distribution of the cytoplasm during cytokinesis is possibly one of the main reasons for this degeneration.

Formation of the Generative Cell and the Sperm Cells

As described above the cell plate of the generative cell forms a hemisphere with an annular contact towards the plasma membrane of the vegetative cell. Thus, the cell formation cannot be characterized as free (cf. PIECH). The generative cell is successively freed from the plasma membrane by the centripetal growth of the basal annular parts of the hemispheric cell plate. The last contact between the generative cell and the inner wall adjacent to the abortive microspores often resembles an umbilical cord (Fig. 18 B).

When the generative cell is freed it moves freely into the cytoplasm of the vegetative cell and can then be found in varying parts of that cell. This apparently free movement probably gave rise to the old idea of the free formation of this cell which was also referred to by GÓRSKA-BRYLASS. But in a picture published by that author a callosic protuberation of the generative cell is noticeable towards the inner wall. Free formation of the generative cell is reported by TANAKA (1941) in *Rhynchospora japonica*.

The narrow space between the plasma membranes of the generative and the vegetative cells contains a thin, electron lucent, fibrillar material similar to that observed in the inner walls around the abortive microspores. When CARNIEL (1972) discussed the boundary of the generative cell he referred to it as a wall. The content in the space between the plasma membranes seems to be continually changing. In Figure 26, the boundary is a complex of vesicles or sacs, a fact which renders the term "wall" unsuitable, at least at that stage.

The two sperm cells are formed by mitosis of the generative cell. Containing

the two sperm nuclei, this cell elongates until dumb-bell-shaped. The cytokinesis that follows is worthy of note. The generative cell is then further prolonged until two spindle-shaped parts are formed connected by a cord of plasma membranes (Fig. 28). The sperm cells are ultimately pinched off from their contact. CARNIEL made the same observation and considered this to be the background to the narrow spindle shape of the sperm cells. Sperm cells are organized in all species of *Eleocharis* studied.

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Chromosome Studies in Some Mediterranean Angiosperms

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ABSTRACT

KAMARI, G. & PAPATSOU, S. 1973. Chromosome studies in some Mediterranean angiosperms. — Bot. Notiser 126: 266—268.

The chromosome numbers of six species within the genera *Alkanna, Echium,* and *Trigonella* from Greece have been counted. Morphological observations and comparisons are also given for some of the species.

Recent botanical collections from the island of Nisyros (Dodekanisos), provided the opportunity for making cytological and morphological comparisons of some Mediterranean species. All specimens examined are from wild populations. Their geographical position is indicated in the appended table.

For the purpose of cytological study we have examined root-tips in all cases but *Trigonella corniculata* in which we studied meiosis in pollen mother cells. The material was pretreated in 2 mM 8-hydroxyquinoline and 0.2 % colchicine in the proportions of 2: 1 and was stained by the Feulgen method.

Our thanks are due to Prof. D. PHITOS for his continued help and encouragement.

1. **Alkanna hellenica** (BOISS.) RECH. FIL.
2. **Alkanna orientalis** (L.) BOISS.

The geographical distribution of the above taxa is well known. The first is found throughout Central Greece and Peloponnese and the second in the eastern Mediterranean. The morphological affinity of the two taxa is already known (RECHINGER 1965). However, one can detect at least subspecific differences between them. Comparative studies of *A. hellenica* from the locus classicus (Akrokorinthos) and *A. orientalis* from the island of Nisyros showed the following differences: The basal leaves of *A. hellenica* are oblanceolate, 14×2 cm, the bracts are ovate-lanceolate to ovate and the sepals are 4 mm wide at the fruiting stage. In *A. orientalis*, on the other hand, the basal leaves are widely oblanceolate, 11×3.5 cm, the bracts lanceolate to narrow lanceolate and the sepals 3 mm wide at the fruiting stage.

In *A. orientalis* the chromosome number previously known was 2n=22 (BRITTON 1951, STREY 1931). The source of this material is unknown. GRAU (1968) gave, for the first time, the chromosome number for *A. hellenica* as being 2n=28. He examined plants from Central Greece.

The present cytological work included plants of *A. hellenica* from locus classicus and parts of Central Greece and plants of *A. orientalis* from Nisyros. All plants examined were found to have the chromosome number 2n=28. The caryotype of both species did not show significant differences. In *A. orientalis* one pair of SAT chromosomes were present, whereas

Table 1. Chromosome numbers of some Mediterranean angiosperms. — PH.: D. PHITOS; PAP.: S. PAPATSOU.

Taxon	Locality	Collection	2n
BORAGINACEAE			
1. *Alkanna hellenica* (BOISS.) RECH. FIL.	Prov. Korinthia: ad Castrum Akrokorinthos, in petrosis.	PH. 11871	28
2. *Alkanna orientalis* (L.) BOISS.	Ins. Nisyros: ad locum Hagios Georgios dict., in incultis.	PAP. 69	28
3. *Alkanna tinctoria* (L.) TAUSCH	Ins. Nisyros: in arenosis maritimis.	PAP. 29	30
„ —	Prov. Attiki: in collibus Tourkovounia, in petrosis, ca 400 m.	PH. 11872	30
4. *Echium arenarium* GUSS.	Ins. Gyali: in arenosis maritimis.	PAP. 949	16
PAPILIONACEAE			
5. *Trigonella balansae* BOISS. & REUTER	Ins. Nisyros: prope pagum Mandrakion, in incultis.	PAP. 562	16
6. *Trigonella corniculata* (L.) L.	Ins. Kephallinia: prope vicum Assos.	PH. 10092	16

in *A. hellenica* two pairs were observed. Also, in prophase, the presence of two B-chromosomes was clearly evident in both species.

3. **Alkanna tinctoria** (L.) TAUSCH

Cytological data on this species are relatively limited (BAKSAY 1956: 2n=14, GRAU 1968: 2n=30 and DELAY 1970: 2n=30), although the geographical distribution (Asia Minor, Mediterranean, Hungary, Romania) is very wide.

The plants studied come from two not closely situated populations, that is from the island of Nisyros and the mainland of Greece (Attiki), and both gave 2n=30. Therefore, it seems that the chromosome number of this morphologically very variable species is constant, apart from the report by BAKSAY (2n=14).

4. **Echium arenarium** GUSS.

Cytological studies of some individuals of this species confirmed the already known chromosome number 2n=16 (see FEDOROV 1969). The plants examined

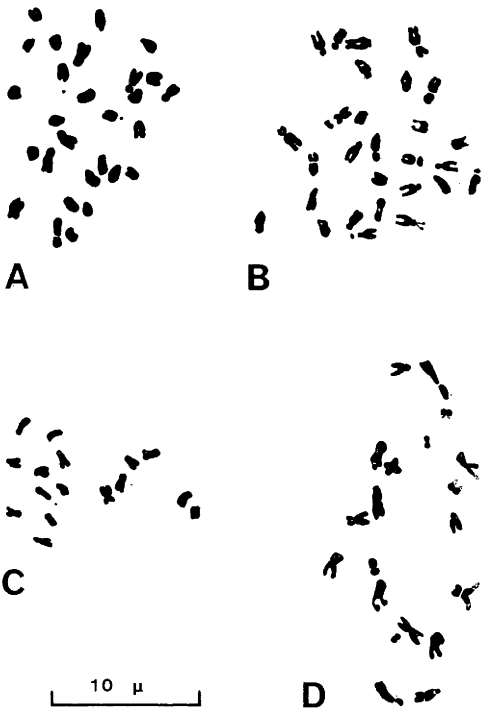

Fig. 1. Mitotic metaphase plates from root-tips. — A: *Alkanna orientalis* (2n=28). — B: *A. hellenica* (2n=28). — C: *Echium arenarium* (2n=16). — D: *Trigonella balansae* (2n=16).

come from the islet Gyali, which is ca. 3.5 km from the island of Nisyros.

5. **Trigonella balansae** BOISS. & REUTER in BOISS.

6. **Trigonella corniculata** (L.) L.

The affinity of the above two species is well known. In spite of this in typical representatives at least, morphological differences which can separate them into two distinct species do exist. In fact, one of the species is a characteristic taxon of the eastern and the other of the western Mediterranean.

Cytological studies confirmed the already known chromosome numbers 2n= 16 (see FEDOROV 1969) for both species. In addition to this four B-chromosomes have been observed in *T. balansae*. Our investigations were carried out on material collected in localities where typical plants of these species grow. Thus *T. corniculata* was examined on material from the island of Kephallinia (Ionian Sea) and *T. balansae* from the island of Nisyros (Aegean Sea).

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Botanical Literature

GALLØE, O. (†), Natural History of the Danish Lichens. Original Investigations Based upon New Principles. Part 10. Ed. M. SKYTTE CHRISTIANSEN. — Copenhagen 1972. 63+204+7 pp. 204 plates (50 in colour) comprising 1336 figures. Price D. Cr. 125: — (wrappers).

The present volume completes the magnificent work on the lichens of Denmark issued by Dr. O. GALLØE. From the preface of Vol. 1 (1927) we may cite some of his "new principles" which, in fact, have given his treatise a very unique position in lichenological literature.

Like LAMARCK he believed in the inheritance of qualities acquired by a single individual under the direct influence of external conditions. It is evident that such ideas will lead to a plastic species concept. Instead of defining the outlines of the lichen species in the traditional way, as we find in most floras and monographs, GALLØE selected one "typical" specimen (sometimes 2 or 3, in exceptional cases more) which he described in detail (in particular the microscopic anatomy) and figured in numerous drawings in colour or black-and-white. GALLØE was an excellent artist. Many of his illustrations are unrivalled and have often been reproduced in other lichenological textbooks.

At least in the earlier volumes GALLØE had a broad species concept somewhat similar (especially as regards the macrolichens) to the delimitation used by TH. M. FRIES (Lichenographia Scandinavica, 1871—1874).

In his later volumes he sometimes considered recent literature. He had no interest in nomenclature, typification, synonymy, variation (except for the differences discerned when more than one standard specimen was described), distribution, lichen chemistry, etc. Apart from the localities of the standard specimens there are no records of geographical distribution. In spite of these shortcomings the reviewer believes that GALLØE's Natural History will remain an indispensable lichenological work.

Volume 9 (*Cladonia*, 1954) was the last to be issued by GALLØE himself. When he died in 1965 he had completed the 50 colour plates of the final volume, 10, with their legends. He was working on the black-and-white figures but did not finish the corresponding legends. The publication of this volume was entrusted to M. SKYTTE CHRISTIANSEN who had aided GALLØE in many respects since the 1940's. Vol. 10 deals with the lichens known as Pyrenocarpeae, Coniocarpineae and Graphidineae. Cyclocarpineae, the main group in the classical ZAHLBRUCKNER system, is represented by the genus *Stereocaulon* only.

CHRISTIANSEN has paid much attention to the genus *Verrucaria*. GALLØE has reproduced several specimens collected by him and determined by him, often in cooperation with the late Czechoslovak lichenologist M. SERVIT. The latter was known for his "narrow" species often described on one single individual. GALLØE's figures are splendid as usual, and the descriptions are often detailed. There are no keys, however, as always in this work nor is there any discussion on the delimitation of the species. It is evident that we are still far from a stable taxonomy of this notoriously difficult genus.

At the end of this volume we find an index to all species (a total of 530) treated in the 10 volumes. As has been emphasized, GALLØE's species concept and nomenclature often differ widely from

current usage. A correlation of GALLØE's specific epithets to modern concepts would have been highly desirable. It is to be hoped that such a revision will be possible in the future.

Lichenologists owe many thanks to M. SKYTTE CHRISTIANSEN for his careful work for the publication of Vol. 10. Generous contributions from the Carlsberg Foundation have defrayed part of the high costs of the reproduction of the plates and the printing. Hence it is possible to sell this monumental work at a reasonable price. Copies of the complete series are available from Mrs. E. GALLØE, Bogmosen 15, 2890 Hareskovby, Denmark. Price D. Cr. 1000: —.

OVE ALMBORN

CAROLL W. DODGE: Some Lichens of Tropical Africa. V. Lecanoraceae to Physciaceae. — Beihefte zur Nova Hedwigia 38. Lehre 1971. 225 pp. No illustrations. Price DM 100: — (wrappers).

During the years 1953—1959 Dr. C. W. DODGE (Burlington, Vermont, U.S.A.) published a series entitled "Some lichens of Tropical Africa I—III. (Annals of the Missouri Botanical Garden 40—46). A continuation (Vol. IV) appeared in Nova Hedwigia 12 (1964). Cf. review in Bot. Notiser 118 (1965) p. 131. The present volume concludes this series.

The revision is founded on material received by the author from various sources, especially from the Herbaria in Kampala (Uganda), Nairobi (Kenya) and Salisbury (Rhodesia). It is to be regretted, however, that there is often no indication of where the specimens seen are preserved. Though the author always refers to type localities for the species treated he seldom cites any Herbaria. As several new taxa are described it would have been especially important to have information about the location of their types. Cf. Recommendation 37 B in the Code of Nomenclature.

As the reviewer pointed out in 1965 it is evident that the author has seen very few type specimens. He has identified his material with the aid of keys compiled from the literature. The keys often include only species described from Africa, whereas several species described from other parts of the world have been omitted though they occur in Africa. This is the case with *Xanthoria parietina*, for example, which is a fairly common species in parts of South Africa.

In many cases, subspecific taxa have been raised to specific level. Such a procedure demands an investigation of the type material.

Several of the many new combinations made are quite puzzling to the reviewer, e.g. "*Teloschistes capensis* var. *cinerascens*". As this "variety" (probably an environmental modification only) is said to be sorediate and to have eciliate apothecia it is definitely to be referred to *T. flavicans*.

ALMBORN, Lichenes Africani No. 69 issued as *Caloplaca subnitida* (MALME) ZAHLBR. has been identified by DODGE as *Gasparrinia platyna* (ZAHLBR.) DODGE. The reviewer has seen the types of both species. He can state with assurance that the latter is identical with *C. cinnabarina* (SW.) ZAHLBR. This species, one of the most conspicuous lichens in South Africa, is not mentioned in any way.

In many cases important literature references have been overlooked. One example only. "*Alectoria chalybeiformis* f. *terrestris*" described by STIZENBERGER from South Africa appears in the key, and another collection from Uganda is referred to the same taxon. The type material (in Herb. ZT) is a mixture of algae (KEISSLER in RABENHORST's Kryptogamenflora IX. 5: 1 (1960) p. 129). D. HAWKSWORTH has since confirmed this.

As previously the author has paid too little attention to formal detail. We often find an arbitrary alternation between masculine and female endings (e.g., in *Teloschistes*). *Triophthalmidium* (a typi-

cally neuter genus) has got a specific epithet with a female ending. Several lichens named after Miss A. M. BURNET have been called "*Burneti*" or "*Burnetae*" instead of "*burnetiae*".

The reviewer can in no way recommend this series. Its many errors and omissions are obvious. A critical worker in this field will have to check in detail all information taken from this source.

OVE ALMBORN

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