

# 20

## Polypodiaceae Bercht. & J.S. Presl

Genera 107–137



A widely distributed family that occurs throughout the world extending from the tropics to northern and southern latitudes. Thirty-one genera treated here have ellipsoidal, monolete spores with the exception of *Loxogramma*, which includes some species with trilete, globose spores. The blechnoid exospore usually forms the largest part of the sporoderm and is sometimes undulate, rugate, or verrucate, but is often plain. The perispore is usually thin, commonly beset with globules, and with a plain but sometimes tuberculate, verrucate, or granulate surface. In a few species of *Pyrrhosia* and *Polypodium* the perispore forms an irregularly winged envelope. The myrmecophytic species in *Solanopteris* have prominently echinate spores and some in *Lecanopteris* have a unique, stranded perispore.

## 107. *Platycerium* Desvaux

Figs. 107.1–107.9

### Genus

A pantropical group of 15 usually epiphytic species, monographed by Hennipman & Roos (1982).

### Range

Largely paleotropical in Africa and southeast Asia. In Central Africa, Madagascar, eastward to east India, Vietnam, and New Guinea, north to Yunnan, China, and the Philippines, and southward to eastern Australia; one species rare in the eastern Andes.

### Spores

Examined in 12 species.

**Size** 46–110  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  the length or shorter.

**Surface** Plain or slightly papillate to tubercu-

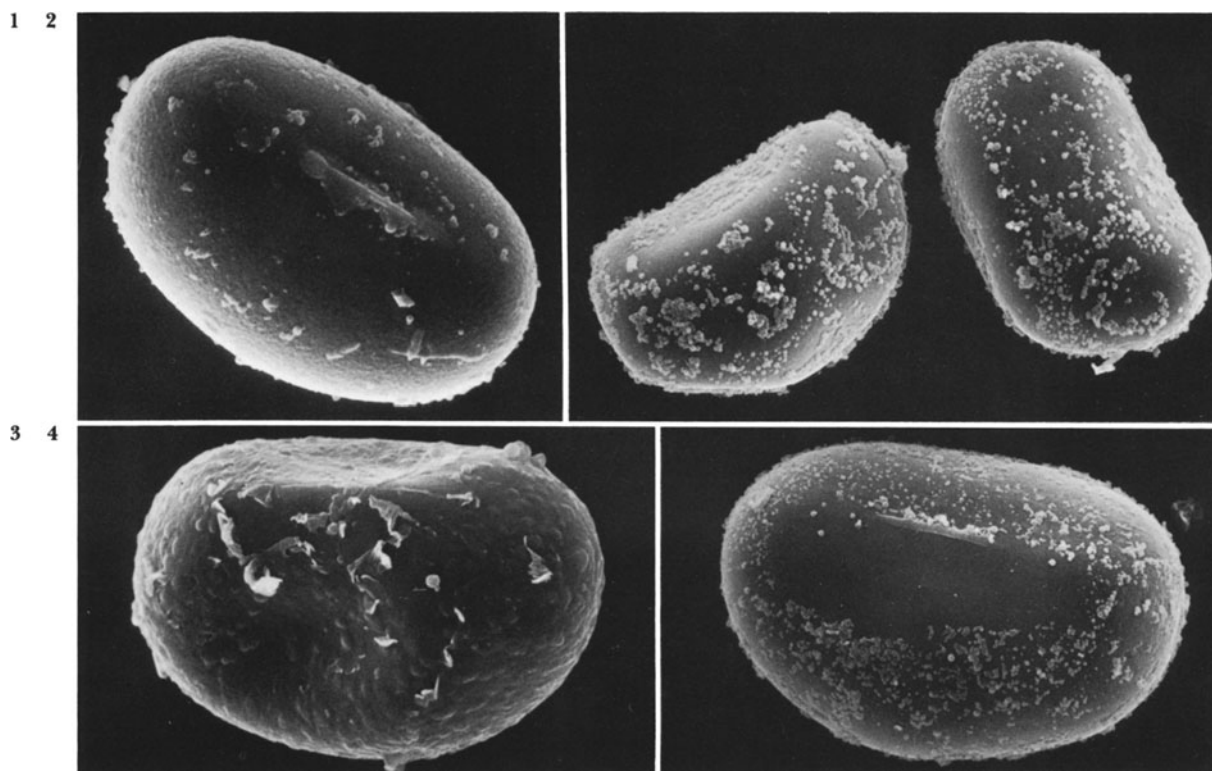
late, with globules sometimes dense, rarely with irregular, somewhat echinate elements.

**Structure** Exospore plain; perispore usually a single, thin layer with globules.

### Comments

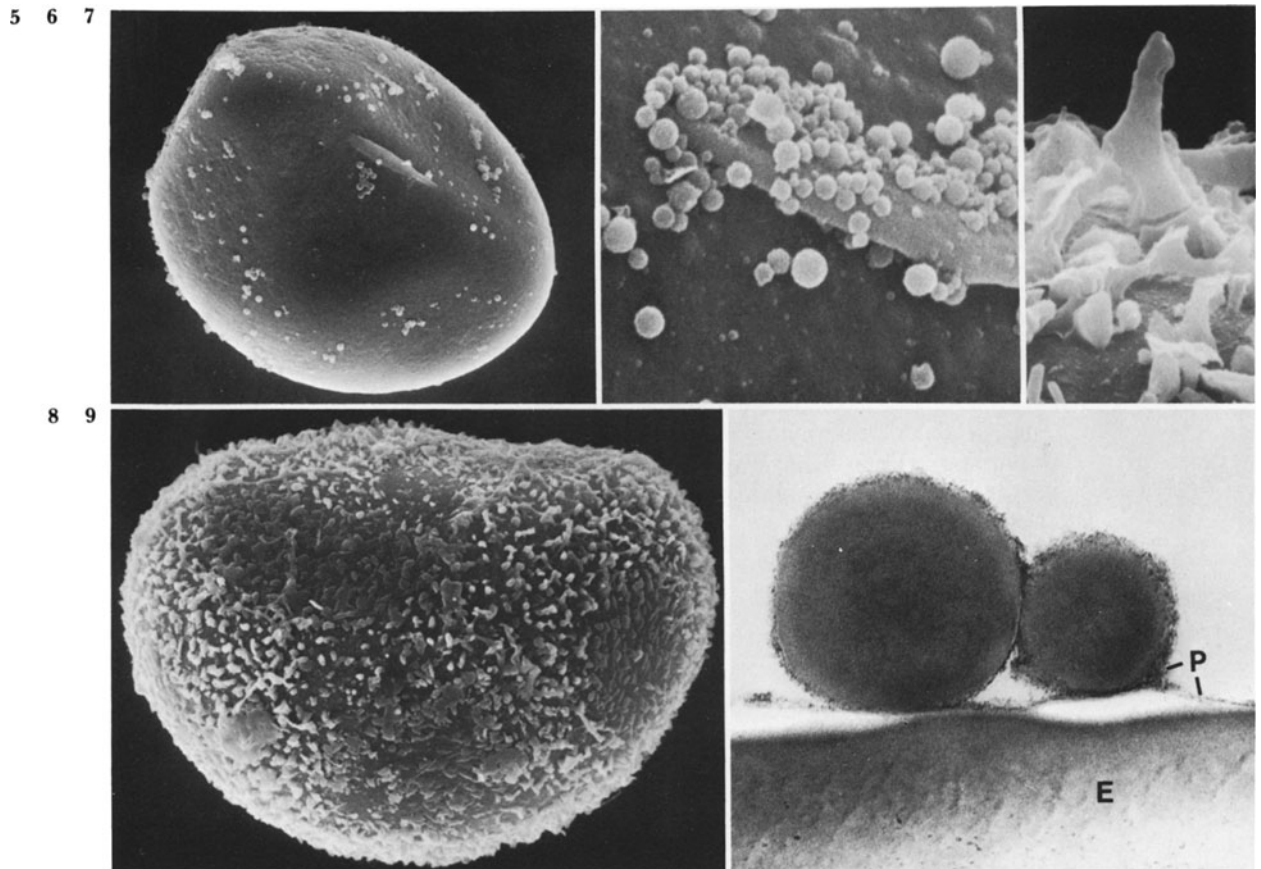
**Characteristics, Diversity** *Platycerium* spores have exceptionally short apertures (Figs. 1–6). The surface is essentially plain (Figs. 1, 3), or sometimes low papillate or tuberculate, usually with scattered globules. The spores of *P. ridleyi* are unusually elaborate with irregular, low echinae (Figs. 7, 8). The density of the globules may vary from slight, as in *P. elephantotis* (Fig. 5), to somewhat compact in *P. andinum* (Fig. 4).

The chromosome reports for three species are uniformly  $n = 37$ , but large size differences between the small spores of *P. bifurcatum* from Queensland (Fig. 2) and the large one of *P. ridleyi* from Borneo (Fig. 8) possibly reflect varied



Figs. 107.1–107.4. *Platycerium* spores,  $\times 1,000$ . 1, 2. *P. bifurcatum* (Cav.) C. Chr. 1. Slightly papillate surface, globules, short aperture, New South Wales, Australia, *Constable P7912*. 2. Abundant globules, Queensland, Australia, *Brass*

20158. 3. *P. stemaria* (Beauv.) Desv., slightly tuberculate surface, abraded thin perispore, Liberia, *Harley F16*. 4. *P. andinum* Bak., abundant globules, short aperture, Peru, *Schunke 2165*.



**Figs. 107.5–107.9.** *Platycerium* spores,  $\times 1,000$ , and wall section. 5. *P. elephantotis* Schweinf., very short aperture, Belgian Congo, *Pichi-Sermolli* 4511. 6. *P. wallichii* Hook., globules concentrated in apertural area, Hort. Leiden, 1981,  $\times 5,000$ . 7, 8. *P. ridleyi* Christ, Borneo, *Korthals* 177

(L). 7. Detail of elongate papilla,  $\times 5,000$ . 8. Large spore with irregular, somewhat echinate surface. 9. *P. allicorne* Desv., wall section, exospore (E) below thin perispore (P) and two captive globules, Cult. (TL),  $\times 60,000$ .

ploidy levels. However, there are only eight spores per sporangium in *P. ridleyi* and *P. coronarium*, compared to the usual 64 in the other species that may account for the size difference. **Relationships** Six monophyletic groups are recognized in the monograph on *Platycerium* based on shared characters. The spores are analyzed along with 32 other characters in a cladistic assessment of the genus. An indistinct perispore and 64 spores per sporangium were regarded as plesiomorphic states, in contrast to distinct flaky perispore and eight spores per sporangium, as the apomorphic states.

Relationships proposed in the monograph that differ from those in the review of *Platycer-*

*ium* by Joe (1964) are explained by Hennipman & Roos. There is general agreement in these and other works on the alliance of *Platycerium* with *Pyrrosia*, largely based on similarities of the stellate leaf trichomes, but this relationship is not evident in the spores.

### Literature

- Hennipman, E., and M.C. Roos. 1982. A monograph of the fern genus *Platycerium* (Polypodiaceae), 126 pp. North-Holland Publishing Co., Amsterdam.  
 Joe, B. 1964. A review of the species of *Platycerium* (Polypodiaceae). *Baileya* 12: 69–126.

## 108. *Pyrrosia* Mirbel

### Figs. 108.1–108.8

#### Genus

A paleotropical genus of about 50 largely epiphytic species, including *Drymoglossum* Presl and *Saxiglossum* Ching, monographed by Hovenkamp (1986).

#### Range

Especially diverse in Sumatra and Himalayas; central and eastern Africa eastward to India, Vietnam, the Philippines and New Guinea, northward to Japan; eastern Australia and New Zealand; on most South Pacific islands, extending eastward to Pitcairn and Henderson Islands.

#### Spores

Examined in 19 species.

**Size** 47–77  $\mu\text{m}$  (42–110  $\mu\text{m}$ , Hovenkamp).

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{1}{3}$  the length.

**Surface** Plain with globules, sometimes with parallel folds, often verrucate or colliculate, the verrucae sometimes prolonged in coarse echinae.

**Structure** Exospore two-layered, usually plain; perispore usually thin, sometimes enlarged, forming the surface contours, often with globules.

#### Comments

**Characteristics, Diversity** Most species of *Pyrrosia* are reported to have 64 spores, the normal number per sporangium, but in a few they are reduced to 32. An exceptional record of 128 spores per sporangium is reported for one species. Five spore types are recognized in *Pyrrosia* (Van Uffelen & Hennipman, 1985). The *P. princeps* type with plain to verrucate surface includes those of *P. costata* (Fig. 1). The *P. subfurfuracea* type has spheroidal elements in a thin, somewhat folded perispore, as in *P. mannii* (Fig. 2). The surface of the *P. christii* type, except for a plain area near the aperture, is covered with large globules, as in *P. lingua* (Fig. 3). In the *P. rupestris* type small verrucae may be combined with larger ones, as in *P. niphoboloides* (Fig. 4). These may be prolonged into coarse

echinate elements in *P. piloselloides* (Figs. 5, 7). The *P. nummulariifolia* type (Fig. 6) may have parallel folds that overlay the surface, as *P. angustata* (Fig. 8).

Van Uffelen & Hennipman consider *Pyrrosia* spores to be unique among the leptosporangiate ferns and exceptionally diverse, as compared with those of other genera in the Polypodiaceae. The diversity correlates in part with the 10 species groups recognized in the revision (Hovenkamp, 1986).

A SEM and LM review of spores in six species of *Pyrrosia* includes a key to the species based on the spores (Liew, 1976). The verrucate form is regarded as the basic one with trends toward the diminution in size and greater density of verrucae. Secondary changes were considered to account for an increase in size of the verrucae.

Mitui (1977) characterized spores of the Japanese *Pyrrosia lingua* and *P. linearifolia* (Hook.) Ching, by hyaline perispore and globules, and compared them with spores of several other genera of the Polypodiaceae. Additional work on *Pyrrosia* spores is included in the study of spores of Japanese ferns by Mitui. (1982)

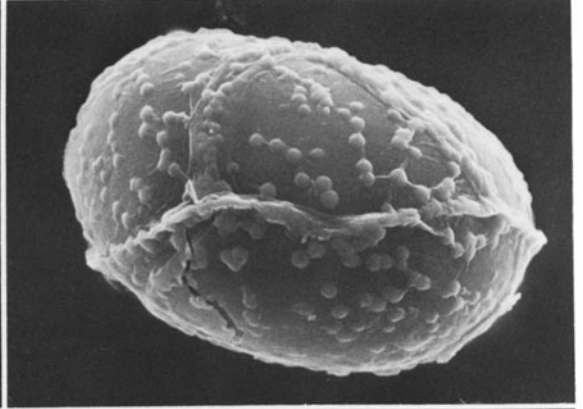
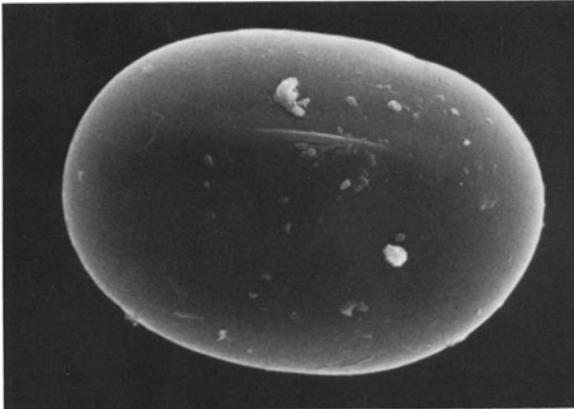
**Relationships** Similarities between the five spore types, recognized by Van Uffelen & Hennipman (1985) are evident in the tuberculate elements and spherical deposit, common to the *Nummulariifolia* and *Christii* types. The expansion of the perispore in folds may be slight in the *Subfurfuracea* group, or more prominent in the *Nummulariifolia* group. Spores with large perispore folds, also common to *Goniophlebium* and several species of *Polypodium* including *P. kunzeanum* C. Chr., and *P. sessilifolium* Desv., are probably convergent in the family.

The alliance of *Pyrrosia* and *Platyserium* by Hennipman & Roos (1982) is largely based on the stellate indumentum of the leaves. They describe *Platyserium* spores as usually having indistinct, or sometimes distinct and flaky perispore. *Platyserium* spores are usually plain, as the *Princeps* type in *Pyrrosia* spores, but often have abundant globules.

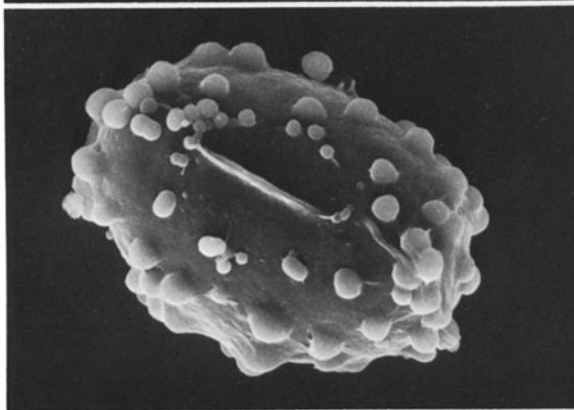
## Literature

- Hovenkamp, P. 1986. A monograph of the fern genus *Pyrrosia*. 280 pp. Leiden University Press, Leiden, Netherlands.
- Hennipman, E., & M.C. Roos, 1982. A monograph of the fern genus *Platyserium* (Polypodiaceae), 126 pp. North-Holland Publishing Company, Amsterdam.
- Liew, F.S. 1976. Scanning electron microscopical studies on the spores of pteridophytes. 1. The genus *Pyrrosia* Mirbel (Polypodiaceae) found in Taiwan. Q. J. Taiwan Mus. 29: 191–216.
- Mitui, K. 1977. Spore wall structure of some Japanese species in Polypodiaceae s.st. Bull. Nipp. Dent. Univ., Gen. Ed. 6: 119–124.
- Mitui, K. 1982. Spore morphology of Japanese ferns. 206 pp. K. Mitui, Dept. Biol. Nipp. Dent. Univ., Niigata (in Japanese).
- Van Uffelen, G.A., & E. Hennipman, 1985. The spores of *Pyrrosia* Mirbel (Polypodiaceae): A SEM study. Pollen Spores 27: 155–198.
- Figs. 108.1–108.8. *Pyrrosia* spores,  $\times 1,000$ .**—Princeps type: **1. *P. costata*** (Presl) Tagawa & Iwatsuki, the surface plain, Burma, *Kingdon-Ward 20455*.—Subfurfuracea type: **2. *P. mannii*** (Giesenh.) Ching, tuberculate with few folds, Nepal, *Hara et al. 630493*.—Christii type: **3. *P. lingua*** (Thunb.) Farw., tuberculate, Kwangtung, China, *Taam 328*.—Rupestris type: **4. *P. niphoboloides*** (Bak.) Price, tuberculate with gross verrucae, Madagascar, *Humbert 5813*. **5, 7. *P. piloselloides*** (L.) Price, Hainan Island, China, *Liang 64275*. **5.** Colliculate with coarse echinae. —Nummulariifolia type: **6. *P. nummulariifolia*** (Sw.) Ching, tuberculate with few folds, Sumatra, *Schiffner 912A*. **7.** Detail of colliculate elements and coarse echinae, as Fig. 5 above,  $\times 5,000$ . **8. *P. angustata*** (Sw.) Ching, prominent parallel folds, Malacca, *Cuming 372*.

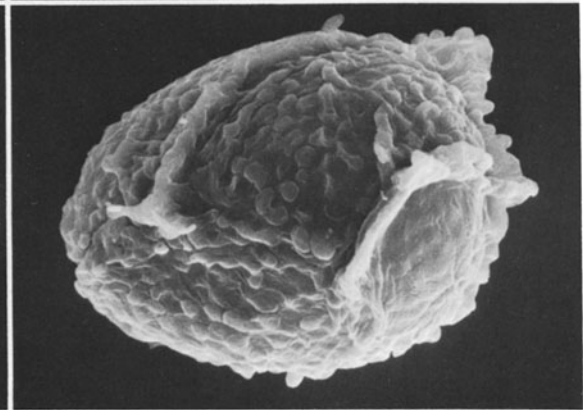
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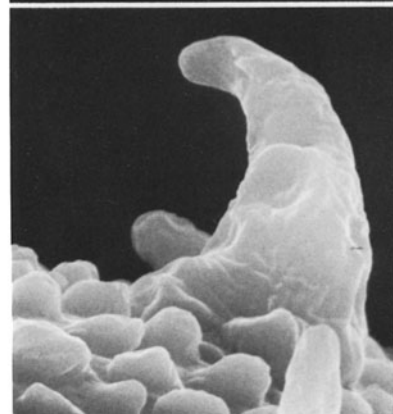
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## 109. *Aglaomorpha* Schott

**Figs. 109.1–109.13**

### Genus

Paleotropical epiphytes or plants of forest understory, with 15 species including *Pseudodrynaria* Ching, *Photinopteris* J. Sm., and *Thayeria* Copel., as revised by Roos (1985).

### Range

Largely Malesian, with one or few species reaching China, Taiwan, and Ryukyu Islands, east to New Guinea, in the south Pacific to the Solomon and Louisiades Islands.

### Spores

Examined in seven species.

**Size** 38–70  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{1}{2}$  the length.

**Surface** Plain or with low tubercles and globules, or coarsely tuberculate to verrucate, usually with blunt echinae.

### Comments

**Characteristics, Diversity, Relationships** The surface ranges from plain or low tuberculate to verrucate with varied accumulation of globules (Figs. 1–6), or frequently is somewhat echinate (Figs. 7–13). Those of *Aglaomorpha cornucopia* have a thin, irregular outer layer, often with denser echinae than shown here (Figs. 7–9).

Two main spore types are recognized in the work on *Aglaomorpha* and *Drynaria* (Roos, 1985). Both have contours formed by elaboration of the perispore. Those of *A. meyeniana* type are regarded as a special form without spines, but with a thick basal layer and smooth exospore. However, spores of this type, shown here, have some echinae but fewer than in the others (Figs. 10, 11). The second, quercifolia type, as in *A. coronans*, is plain or verrucate (Figs. 12, 13).

The treatment of *Aglaomorpha* by Roos includes *Photinopteris speciosa* and *Thayeria cornu-*

**Figs. 109.1–109.13. *Aglaomorpha* spores,  $\times 1,000$ .** 1, 2. *A. drynarioides* (Hook.) Roos. 1. Sparse globules, Papua, *Croft 689*. 2. Dense globules, Sumatra, *Schiffner 184*. 3. *A. splendens* (J. Sm.) Copel., sparse globules (rodlike structures are fungal hyphae), Philippines, *Copeland dist. 281*. 4–6. *A. speciosa* (Blume) Roos. (*Photinopteris*). 4, 5. Low tubercles, sparse globules, Borneo, *J. & M. Clemens 26005*. 6. Low verrucae on young spores, Singapore, *Holtum (53093 US, cult. Univ. Calif.)*. 7–9. *A. cornucopia* (Copel.) Roos, Philippines, *Copeland 17719 (Thayeria)*. 7. Echinate proximal face with globules. 8. Abraded perispore, lateral surface. 9. Abraded, thin perispore, plain exospore below,  $\times 5,000$ . 10, 11. *A. meyeniana* Schott, Philippines, *Topping 802*. 10. Abraded verrucate perispore, above plain exospore. 11. Detail of plain exospore below verrucate perispore,  $\times 5,000$ . 12, 13. *A. coronans* (Mett.) Copel., Hainan Island, China, *Gressett 845*. 12. Detail of verrucate elements and fine echinae,  $\times 5,000$ . 13. Abraded, irregularly verrucate perispore above plain exospore.

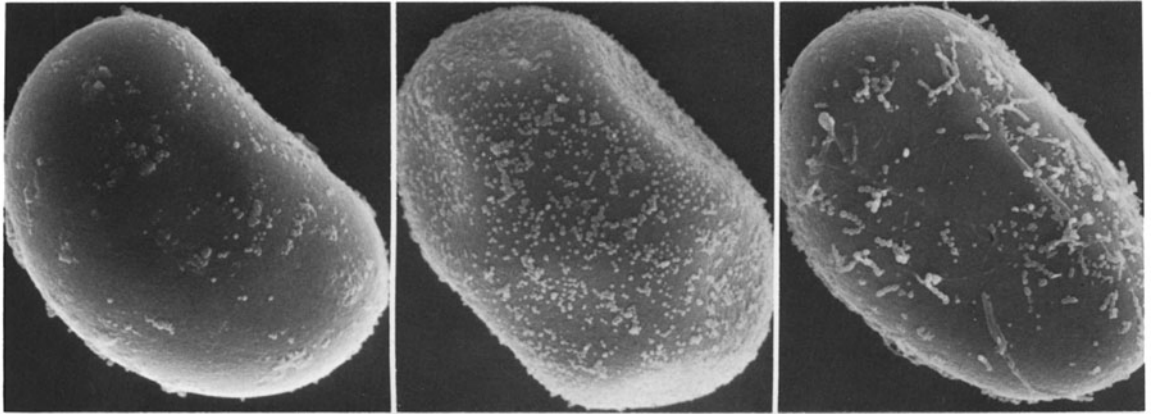
*copia*. Spores of these genera (Figs. 4–9) can be distinguished from the plain or verrucate ones examined in *Aglaomorpha*.

A specimen from the Upper Miocene of Sumatra, consisting of a basal fertile pinna, was recognized by Roos as the extant *Aglaomorpha heraclea* (Kze.) Copel. This was regarded as certain evidence for the existence of this species for as long as 10 million years. Fossil spores of the Polypodiaceae, included in a report of Neogene (Late Tertiary) palynomorphs from New Guinea (Playford, 1982), may support this record. The prominently tuberculate surfaces of the fossil spores were reported as similar to extant spores of *Aglaomorpha meyeniana*, *A. coronans*, *Drynaria delavayi*, or possibly others in *Microgramma* or *Polypodium* not currently reported from New Guinea.

### Literature

- Playford, G. 1982. Neogene palynomorphs from the Huon Peninsula, Papua New Guinea. *Palynology* 6: 29–54.
- Roos, M.C. 1985. Phylogenetic systematics of the Drynarioideae (Polypodiaceae), 300 pp. Leiden University Press, Leiden, Netherlands.

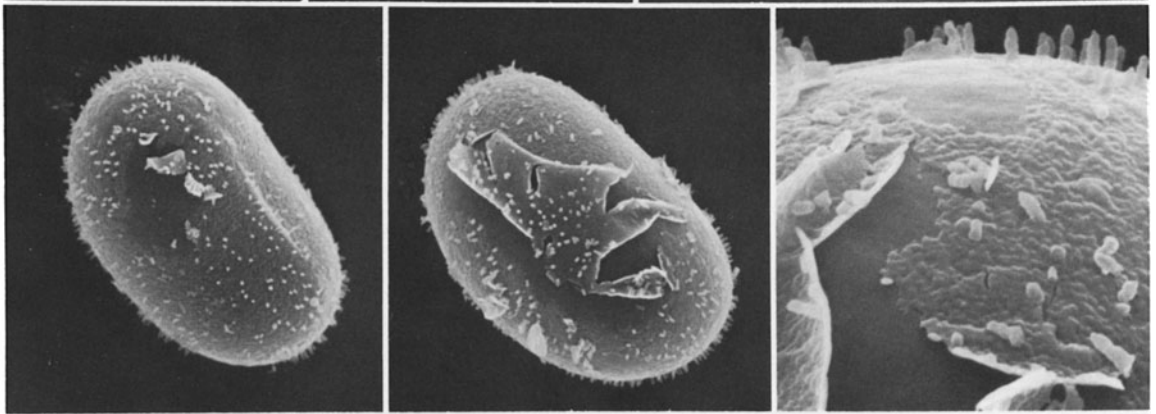
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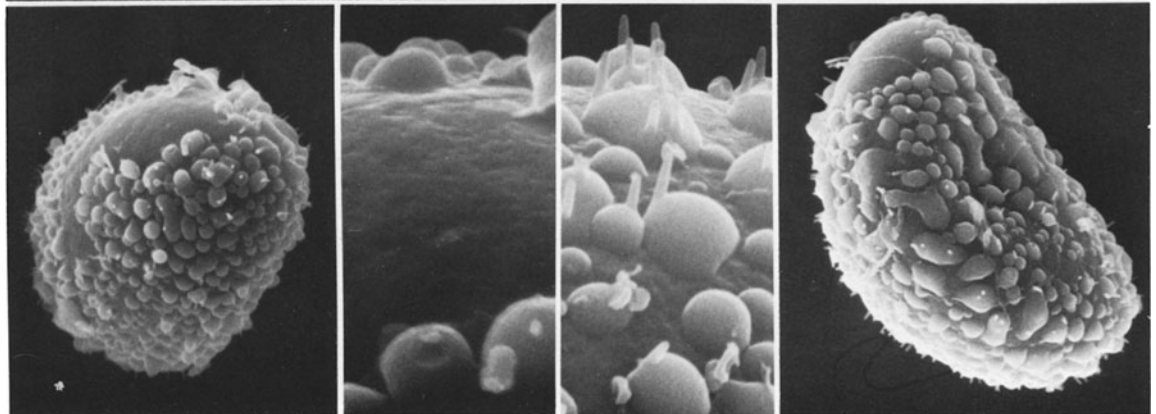
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## 110. *Drynaria* (Bory) J. Smith

### Figs. 110.1–110.13

#### Genus

A usually epiphytic genus of 16 species revised by Roos (1985).

#### Range

Widespread in the paleotropics: across central Africa and Madagascar, in eastern India eastward to New Guinea, north to China, south to Queensland, Australia, in the South Pacific islands east to Fiji and Samoa.

#### Spores

Examined in seven species.

**Size** 37–77  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{2}$  to  $\frac{2}{3}$  the length.

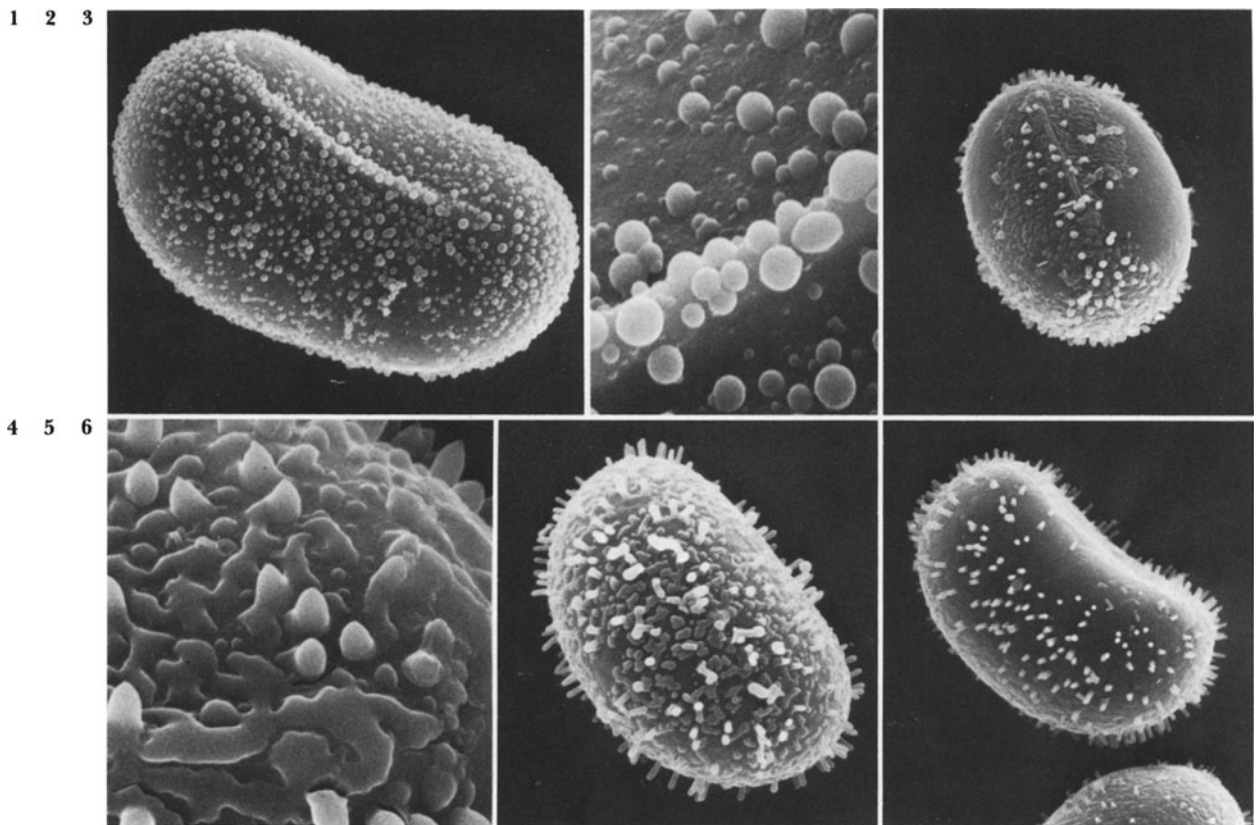
**Surface** Usually with tubercles prolonged

forming irregular echinae, sometimes with constrictions and blunt apex, or the surface plain with dense globules, or rarely verrucate.

**Structure** Exospore plain or verrucate; perispore of one layer forming tubercles and echinae, sometimes thin, following the exospore.

#### Comments

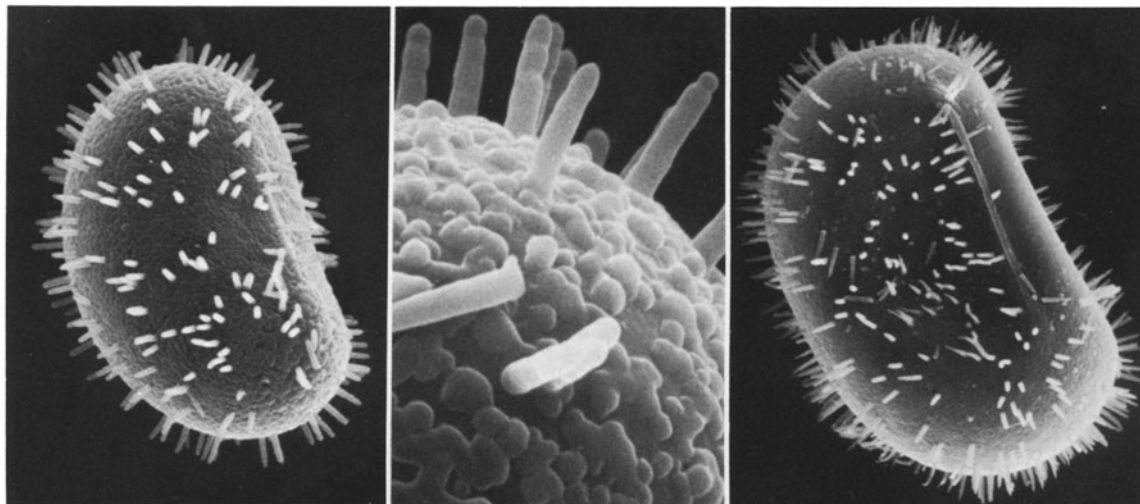
**Characteristics, Diversity** The surface is usually echinate in most species. The echinae project from the lower, irregular tuberculate elements, which are more or less prolonged in *Drynaria rigidula* (Figs. 3–5). They are constricted and blunt in *D. willdenovi* and *D. laurentii* (Figs. 6–8), and acuminate in *D. quercifolia* (Fig. 9). The exceptional verrucate structure in *D. delavayi* (Figs. 10, 11) is formed by the exospore,



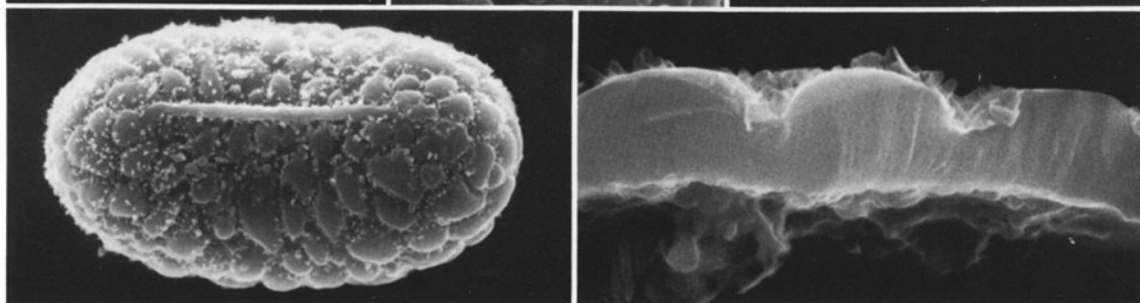
**Figs. 110.1–110.6.** *Drynaria* spores,  $\times 1,000$ . 1, 2. *D. fortunei* (Mett.) J. Sm., Kweichow, China, Steward *et al.* 881. 1. Proximal face with globules. 2. Surface detail, globules aggregated on part of aperture,  $\times 5,000$ . 3–5. *D. rigidula* (Sw.) Bedd. 3. Proximal face with short, blunt spines and

globules, Fiji, Smith 9393. 4, 5. Queensland, Australia, Clemens, in Oct. 1946. 4. Detail of irregular, somewhat prolonged tubercles,  $\times 5,000$ . 5. Dense tubercles and blunt echinae. 6. *D. willdenovi* (Bory) Moore, shallow tubercles and echinae, Mauritius, Ayres 946.

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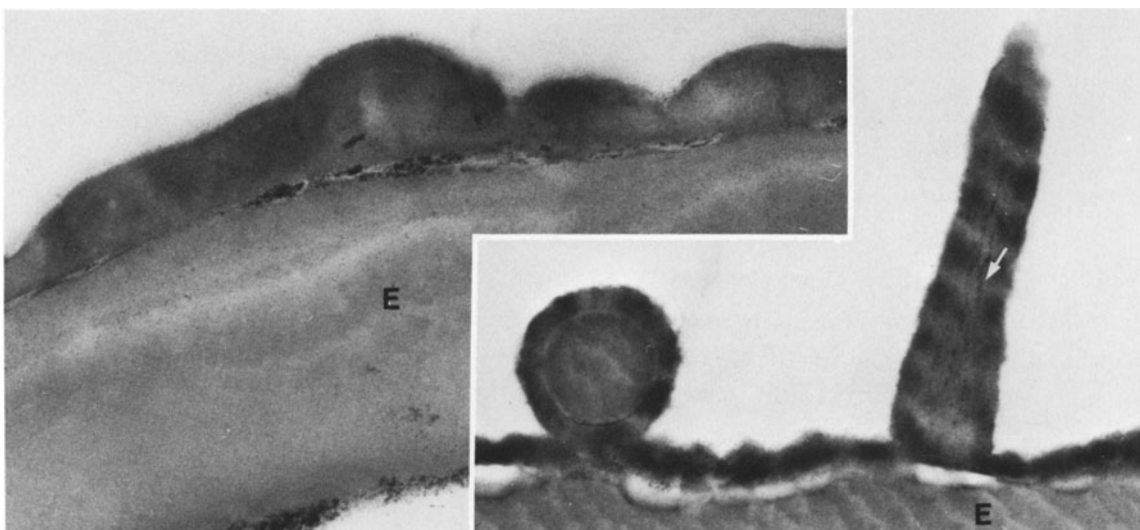
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**Figs. 110.7–110.11.** *Drynaria* spores,  $\times 1,000$ , and wall section. 7, 8. *D. laurentii* (Willd. & Durand) Hieron., Liberia, Linder 57. 7. Prominently echinate, short aperture. 8. Detail of constricted echinae with blunt apices,  $\times 5,000$ . 9. *D.*

*quercifolia* (L.) J. Smith, acuminate spines, Sarawak, J. & M. Clemens 20458. 10, 11. *D. delawayi* Christ, Yunnan, China, Schneider 2991. 10. Verrucate proximal face. 11. Fractured wall with verrucae formed by exospore,  $\times 5,000$ .

12 13



**Figs. 110.12–110.13.** Wall sections of *Drynaria quercifolia* spores, Sarawak, Clemens 20458. 12. Exospore (E) below, dark granules in lower part of perispore,  $\times 50,000$ . 13.

Exospore (E) below perispore, with globule and spine including central granulations (arrow),  $\times 32,000$ .

with a thin, slightly papillate perispore. Spores of *D. heraclea* and *D. fortunei* have copious globules and lack echinae (Figs. 1, 2). Deposits of thin, granulate material in the lower part of the perispore (Fig. 12) and dark granules in the

central part of the perispore spine (Fig. 13) are evident in thin sections of the wall.

Three distinct spore types, recognized by Roos (1985), including those of *Aglaomorpha*, are illustrated here. The most common are the

*Drynaria quercifolia* type (Fig. 9), with spines and globules; the *D. pleuridiodes* type, with verrucate exospore, as in *D. delavayi* (Figs. 10, 11), and the *Aglaomorpha meyeniana* type, unique to this species, with strongly verrucate perispore and thick basal exospore.

The spores, often abundant within root mats of *Drynaria*, may be carried there by ants living in the humus and matted roots at the base of the nest leaves. The elaboration of irregular tubercles and echinae in these spores possibly relates to myrmecophytic associations, as in

*Solanopteris* and other epiphytic genera of the Polypodiaceae.

**Relationships** Roos (1985) reviews four species groups in *Drynaria*, the close alliances with *Aglaomorpha*, and the possible sister group relations between the drynarioid and crypsinoid ferns.

### Literature

Roos, M.C. 1985. Phylogenetic systematics of the Drynarioideae (Polypodiaceae), 300 pp. Leiden University Press, Leiden, Netherlands.

## 111. *Belvisia* Mirbel

### Figs. 111.1–111.4

#### Genus

A paleotropical genus of epiphytes, including *Hymenolepis* Kaulf., with about 15 species.

#### Range

One species in tropical east Africa, Madagascar, and Mascarene Islands; the rest in Malesia eastward to New Guinea, northward to the Philippines and southern China, south to Queensland, Australia; in the Pacific extending to New Caledonia, Tahiti, and the Marquesas.

#### Spores

Examined in 4 species.

**Size** 63–86  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{1}{2}$  the length.

**Surface** Irregularly rugate.

#### Comments

**Characteristics** The large, prominently rugate spores are rougher than those of most genera

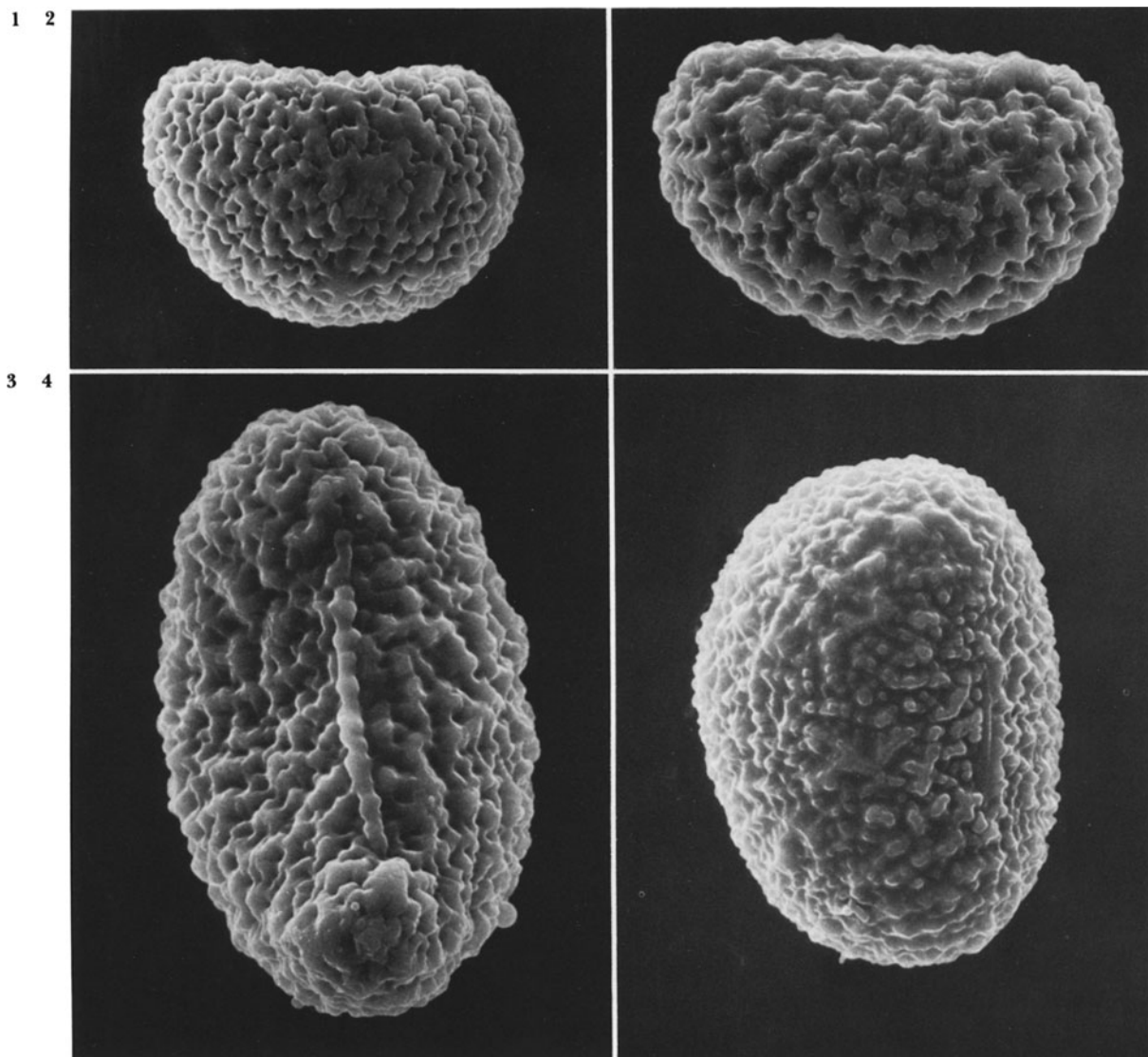
of the Polypodiaceae (Figs. 1–4). Wall sections of *Belvisia mucronata* spores examined by Van Uffelen (pers. comm.) are reported to have a prominent, undulate exospore below a thin, laminate perispore.

**Diversity** The exceptionally large spores of the Australian specimen of *Belvisia mucronata* (Fig. 3) and that of a Philippine collection of *B. platyrhynchos* (Fig. 4), compared with the small one from Java (Fig. 1), suggest that there are different ploidy levels among the species.

**Relationships** Christensen (1929) treated 11 species under the name *Hymenolepis* Kaulf., and regarded the group as being closely allied to *Lemmaphyllum*. The strongly rugate spores of both genera support this alliance.

### Literature

Christensen, C. 1929. Taxonomic fern studies. 1. Revision of the polypodioid genera with longitudinal coenosori (Cochliidiinae and "Drymoglossinae"), with a discussion of their phylogeny. Dansk. Bot. Ark. 6 (3): 3–93.



**Figs. 111.1-111.4.** *Belvisia* spores,  $\times 1,000$ . 1, 3. *B. mucronata* (Fée) Copel. 1. Irregularly rugate lateral face, Java, *Palmer & Bryant 89*. 2. *B. revoluta* (Bl.) Copel., coarsely rugate, Papua, *Brass 4477*. 3. Large, coarsely rugate,

Queensland, Australia, *White 10683*. 4. *B. platyrhynchos* (Kze.) Copel., partially discrete rugae, short aperture at right, Philippines, *Topping 1175*.

## 112. *Drymotaenium* Makino

Figs. 112.1–112.3

### Genus

An epiphytic genus of two species of China and Japan.

### Range

Southwestern China and southern Japan.

### Spores

Examined in two species.

**Size** 50–74  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{2}$  to  $\frac{3}{4}$  the length.

**Surface** Low rugate (Figs. 1–3).

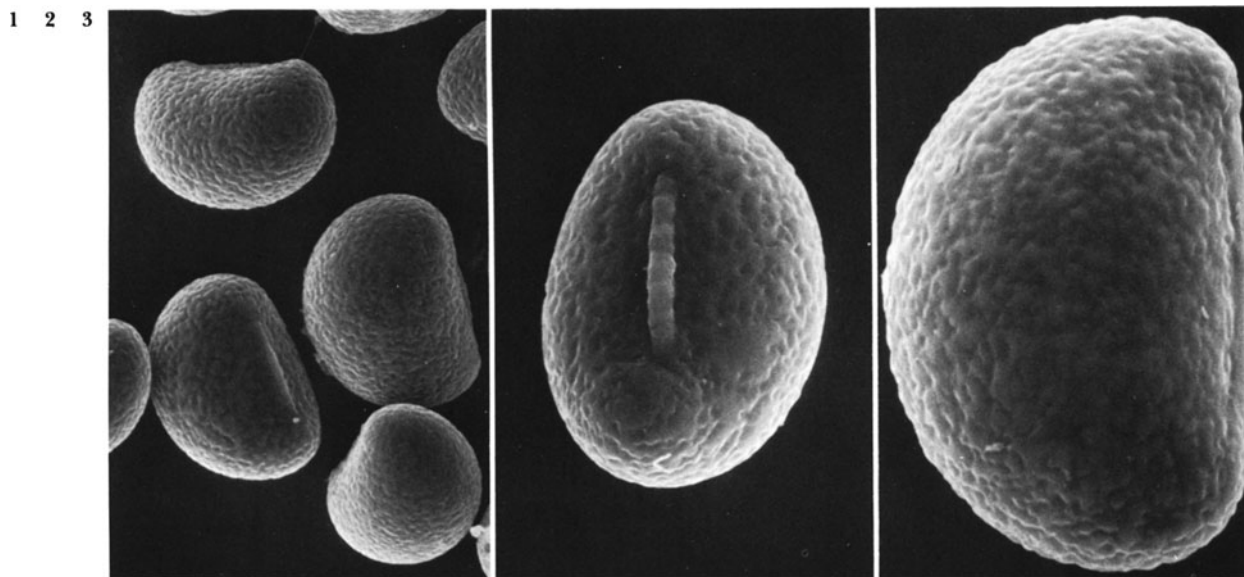
### Comments

**Characteristics, Diversity, Relationships** Chro-

mosome records are not reported for *Drymotaenium*, but the contrast between the large spore of *D. miyoshianum* from Kweichow and the small one of *D. nakaii* from Taiwan suggests there may be different ploidy levels within the genus (Figs. 2, 3). Christensen (1929) considered the genus to be one of the *Lepisorus* complex, related to *Lemmaphyllum*. The similar rugate spores in these genera support this alliance.

### Literature

Christensen, C. 1929. Taxonomic fern studies 1. Revision of the Polypodioid genera with longitudinal coenosori (Cochliidiinae and “Drymoglossineae”) with a discussion of their phylogeny. Dansk. Bot. Ark. 6: (3): 3–93.



Figs. 112.1–112.3. *Drymotaenium* spores,  $\times 1,000$ , except Fig. 1. 1, 2. *D. nakaii* Hayata, Taiwan, Suzuki, in 1929. 1. Spores with uniformly rugate surfaces,  $\times 500$ . 2. Proximal

face, short aperture. 3. *D. miyoshianum* Makino, large spore with long aperture at right, Kweichow, China, Tsang 5915.

## 113. *Lemmaphyllum* Presl

### Figs. 113.1–113.5

#### Genus

A paleotropical group of eight species.

#### Range

Himalayas eastward to New Guinea, northward to Japan, in the Pacific Islands on Fiji and Samoa.

#### Spores

Examined in four species.

**Size** 47–77  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{1}{2}$  the length.

**Surface** Irregularly rugate or tuberculate.

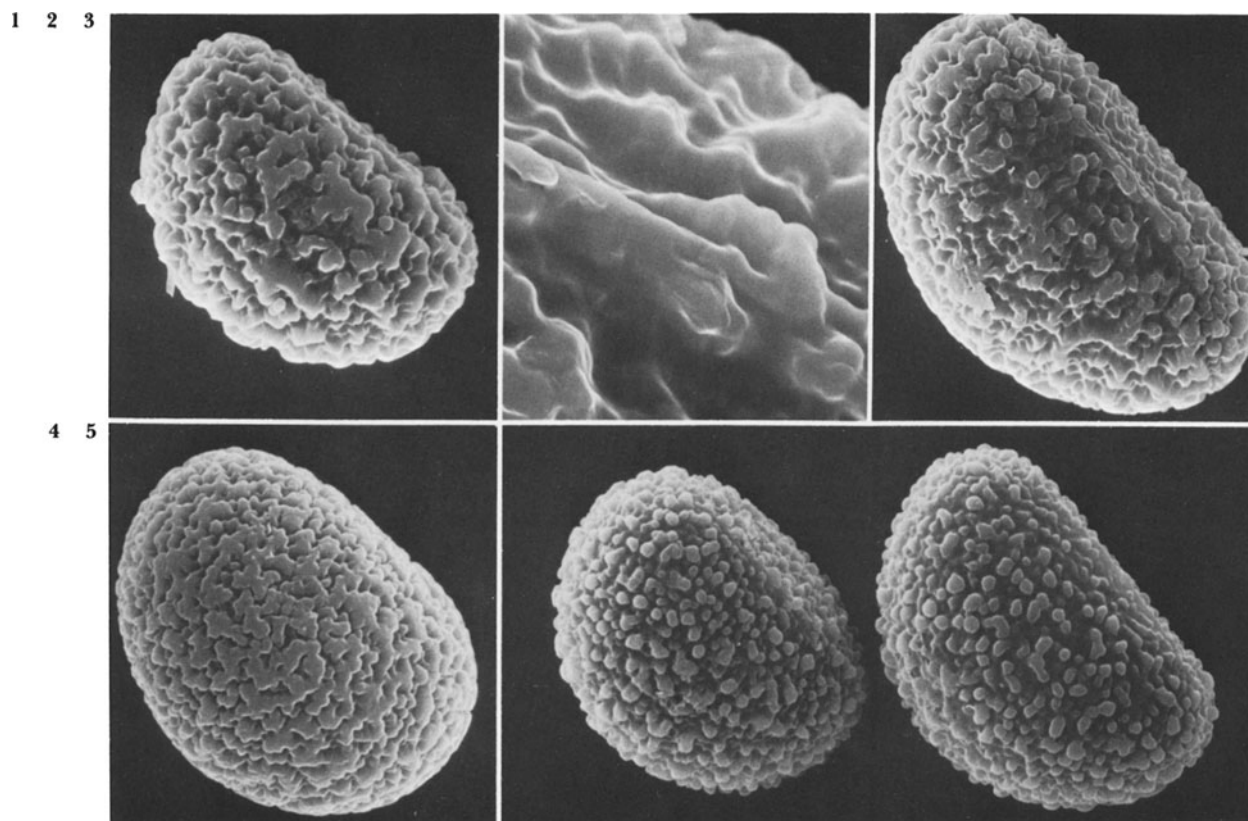
#### Comments

**Characteristics, Diversity, Relationships** *Lemmaphyllum* spores have prominent rugae (Figs.

1–4) or discrete tubercles, as in *L. accedens* (Fig. 5). The alliance of *Lemmaphyllum* with *Drymoetenium* and *Belvisia* (as *Hymenolepis*), proposed by Christensen (1929), indicated that these groups might represent separate offshoots of the *Lepisorus* complex. Ching supported the alliance of the three genera and enlarged *Lemmaphyllum* to include seven Chinese species (1933).

#### Literature

- Christensen, C. 1929. Taxonomic fern studies 1. Revision of the Polypodioid genera with longitudinal coenosori (Cochliidiinae and "Drymoglossinae"); with a discussion of their phylogeny. *Dansk. Bot. Ark.* 6 (3): 3–93.
- Ching, R.C. 1933. Studies of the Chinese ferns 9. *Bull. Fan Mem. Inst. Biol.* 4: 93–103.



**Figs. 113.1–113.5.** *Lemmaphyllum* spores,  $\times 1,000$ . 1. *L. drymoglossoides* (Bak.) Ching, irregularly rugate, Kwangsi, China, *Steward & Cheo* 339. 2, 3. *L. microphyllum* Presl, Hong Kong, *Hu* 9403. 2. Detail of rugae, aperture across lower part of figure,  $\times 5,000$ . 3. Irregularly rugate, aper-

ture near top. 4. *L. subrostratum* (C. Chr.) Ching, rugate lateral surface, Hainan, China, *Lau* 3144. 5. *L. accedens* (Bl.) Donk, tuberculate spores, New Guinea, *Croft & March* 915A.

## 114. *Lepisorus* (J. Smith) Ching Figs. 114.1–114.9

### Genus

A paleotropical, epiphytic group of about 25 species.

### Range

In India, Burma eastward to Malaya and Thailand, extending north to China, Japan, and the Philippines, and *Lepisorus thunbergianus* disjunct in Hawaii.

### Spores

Examined in 13 species.

**Size** 43–80  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{2}{3}$  the length.

**Surface** Rugate, the rugae often more or less fused, or coarsely tuberculate especially on the distal face.

**Structure** Exospore forming the main contours; perispore laminate (Fig. 8), or thicker and granulate (Fig. 9).

### Comments

**Characteristics, Diversity, Relationships** The diverse spore contours suggest that the genus may not be homogeneous. Spores with less prominent rugate surface (Figs. 1, 2, 7) are clearly distinct from those with coarse tubercles (Figs. 3–6). Observations of the surface details in

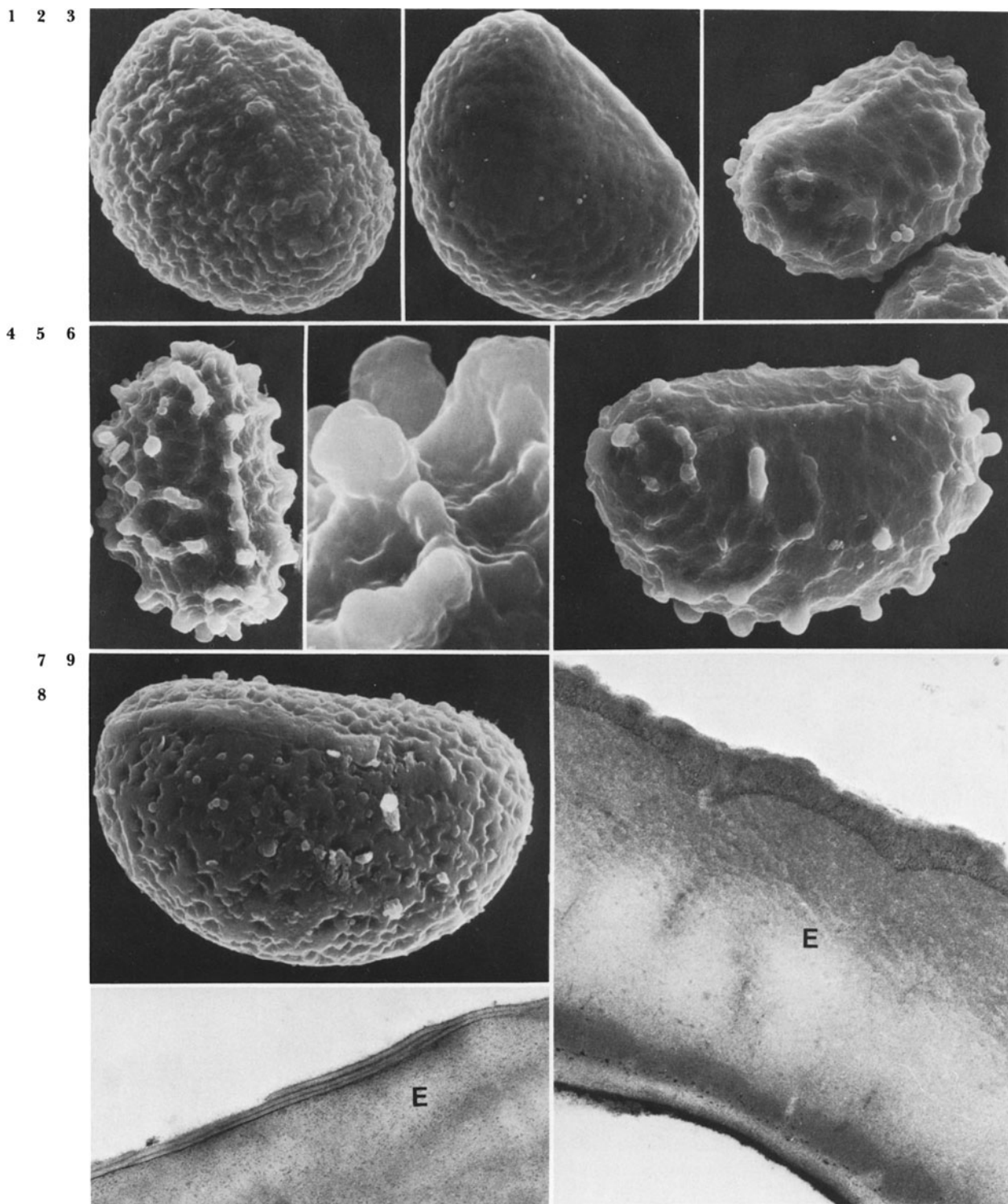
young spores of *Lepisorus thunbergianus* indicate that the contours may be formed by the perispore (Mitui, 1971). Correlations in the prominence and density of the surface elements and cytological levels of the Japanese species are also reported in the work of Mitui. Spores of collections at higher ploidy levels have coarser, more densely, rugate spores than those at lower chromosome levels.

The account of *Lepisorus longifolius*, the only species included in *Lepisorus*, in Holttum's *Malayan Ferns* (1955), includes observations on the abundance and ecological diversity of the plants. The species is recognized in *Paragramma* by Copeland (1947). The coalescent rugae forming the contours in these spores (Fig. 1) differ from the coarse tubercles in other species of *Lepisorus*, and may represent a distinct element in the genus.

The coarsely rugate spores are similar to those of *Lemmaphyllum* and *Belvisia*, and support the alliances in the tribe *Lepisorieae* based on other characters.

### Literature

- Copeland, E.B. 1947. See general literature.  
 Holttum, R.E. 1955. See general literature.  
 Mitui, K. 1971. Spore ornamentations of Japanese species of *Lepisorus*. *J. Jpn. Bot.* 46: 289–293.



**Figs. 114.1-114.9.** *Lepisorus* spores,  $\times 1,000$ , and wall sections. 1. *L. longifolius* (Bl.) Holtt., rugate proximal face, Malaya, Lee & Ul 48 (L). 2. *L. eilophyllus* (Diels) Ching, low rugae, Hupei, China, Henry 6859. 3. *L. ussuriensis* (Regel & Maack) Ching, more or less fused rugae, Japan, Ung 22225. 4, 5. *L. pseudo-ussuriensis*, Taiwan, Tagawa, Chuang & Kao 2430 (L). 4. Prolonged, fused rugae, or coarse tub-

ercules. 5. Detail of rugate surface,  $\times 5,000$ . 6. *L. onoei* (Fr. & Sav.) Ching, coarsely tuberculate, Japan, Furuse, in 1960. 7. *L. nudus* (Hook.) Ching, rugate, Szechuan, China, Fang 3769. 8. *L. ussuriensis*, section of outer exospore (E) below multilaminar perispore, Japan, Komeda 2597,  $\times 50,000$ . 9. *L. nudus*, wall section, exospore (E) below thick, compact perispore, as Fig. 3,  $\times 20,000$ .



## 115. *Christiopteris* Copeland

### Figs. 115.1–115.3

#### Genus

A paleotropical, epiphytic genus of two species, *Christiopteris tricuspis* of Asia, and the Philippine *C. sagitta* (Christ) Copel.

#### Range

Himalayas to Indochina, Malaya, and the Philippines.

#### Spores

Two species examined.

**Size** 43–53  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{1}{3}$  the length.

**Surface** Plain with globules, often dense.

#### Comments

**Characteristics, Diversity, Relationships** These as other ellipsoidal, monolete spores in the Polypodiaceae, have ends appearing blunt in proximal view (Figs. 1, 3). Nayar (1967) reports these spores have small green plastids and germinate irregularly, some before release from

the sporangium. He also indicates that fresh spores that were acetolysed, increased about a third in size.

These spores, with plain surface and abundant globules (Fig. 2), are distinguished from the tuberculate ones of the New Caledonian *Christiopteris varians* that Copeland (1947) included in the genus. The New Caledonian species has been transferred to *Microsorium* by Hennipman & Hetterscheid (1984) in an account of the history of *Christiopteris*. Copeland relates *Christiopteris* to *Crypsinus*, however the lack of echinae in *Christiopteris* does not support this alliance.

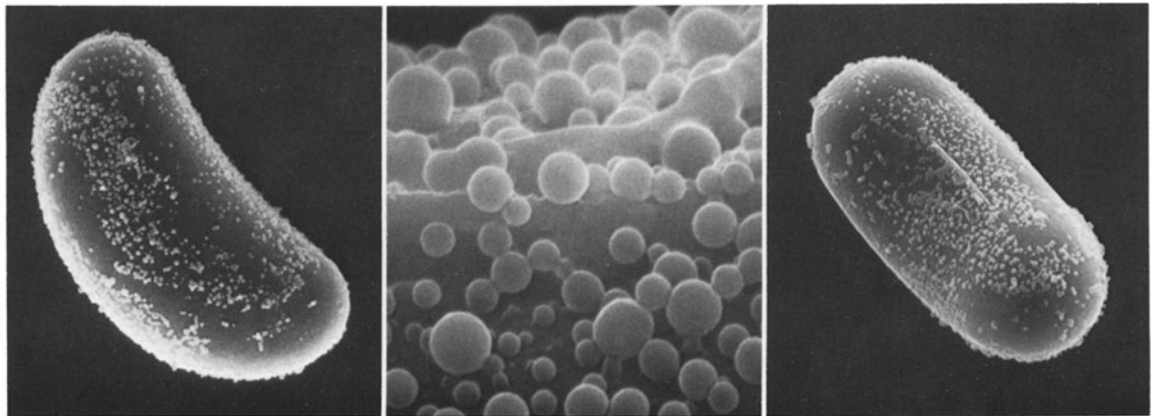
#### Literature

Copeland, E.B. 1947. See general literature.

Hennipman, E., & W.L.A. Hetterscheid. 1984. The emendation of the fern genus *Christiopteris*, including the transference of two taxa to the microsorioid Polypodiaceae. Bot. Jahrb. Syst. 105: 1–10.

Nayar, B.K. 1967. Morphology of the spores and prothallus of *Christiopteris tricuspis*. Am. Fern J. 57: 15–26.

1 2 3



**Figs. 115.1–115.3.** *Christiopteris* spores,  $\times 1,000$ . **1–3.** *C. tricuspis* (Hook.) Christ. **1, 2.** Laos, *Poilane 28570* (P). **1.** Dense globules on surface. **2.** Detail of globules, near ap-

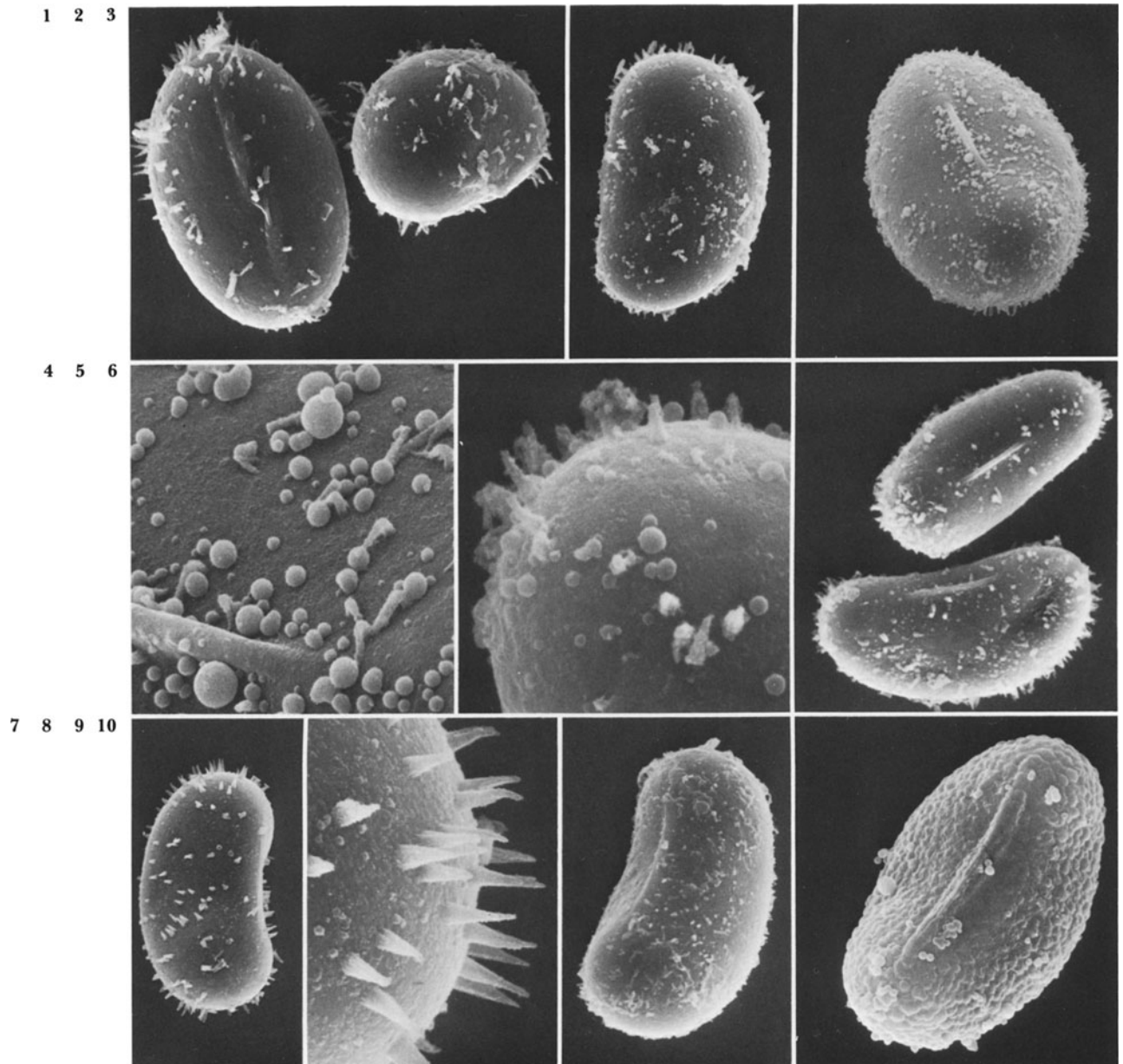
erture,  $\times 10,000$ . **3.** Proximal face with dense globules and short aperture, Indochina, *Eberhardt Herb. 1922* (P).

## 116. *Colysis* Presl

### Figs. 116.1–116.12

#### Genus

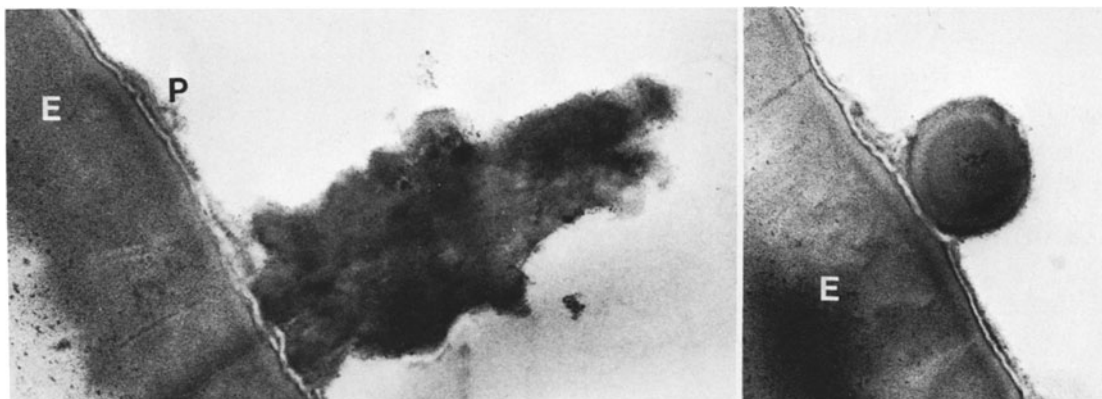
A paleotropical genus of 30 or fewer species, Copel., centering in the Himalayan-Indochina region, including *Dendroglossum* Pr. and *Paraleptochilis*



**Figs. 116.1–116.10.** *Colysis* spores,  $\times 1,000$ . 1. *C. flexiloba* (Christ) Ching, sparsely echinate, short aperture, Yunnan, China, *Tsai 60353*. 2. *C. henryi* (Bak.) Ching, echinae and globules on slightly papillate surface, Szechuan, China, *Fang 2383*. 3, 4. *C. macrophylla* (Bl.) Pr., Philippines, *Jacobs 755*. 3. Proximal face, short echinae and abundant globules. 4. Detail of globules near aperture,  $\times 5,000$ . 5, 6. *C. polysora* (Brause) Copel., Solomon Island, *Braithwaite 4335*. 5. De-

tail of granulate echinae and globules,  $\times 5,000$ . 6. Sparsely echinate proximal faces, short aperture. 7, 8. *C. pedunculata* (Hook. & Grev.) Ching, Malaya, *Molesworth-Allen 4132*. 7. Echinate lateral surface. 8. Detail of finely papillate surface and echinae,  $\times 5,000$ . 9. *C. acuminata* (Bak.) Holtt., sparsely echinate, proximal face, Sumatra, *Hotta 13307* (L). 10. *C. ampla* (Muell.) Copel., tuberculate, Queensland, Australia, *Smith 03371*.

11 12



**Figs. 116.11, 116.12.** *Colysis henryi* wall structure, Fang 2383. **11.** Exospore (E) below thin perispore (P) with ir-

regular spine,  $\times 50,000$ . **12.** Exospore (E) below perispore including a captive globule,  $\times 50,000$ .

### Range

In Africa eastward to Malesia, northward to the Philippines and Japan, and southward to Queensland, Australia.

### Spores

Examined in nine species.

**Size** 32–62  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{3}{4}$  the length.

**Surface** Short, irregular echinae and globules on plain, papillate, or sometimes tuberculate surface.

**Structure** Exospore plain with numerous canals; perispore thin, with spines formed of aggregated material.

### Comments

**Characteristics, Diversity, Relationships** The echinae, of an irregular, granulate material, vary in density and are often partly eroded (Figs. 1–3, 9, 11). The short aperture, as in *Colysis macrophylla* and *C. polysora* (Figs. 3, 6) is often covered with abundant globules that are attached to the perispore (Figs. 4, 12). The shape, long aperture, and tuberculate surface

of *C. ampla* spores (Fig. 10) differ from those of other species. Size differences, as in the spores of *C. flexiloba* (Fig. 1) and *C. pedunculata* (Fig. 7), suggest there may be different ploidy levels in the genus. Cytological study of six Japanese species clearly shows four diploids with  $2n = 72$ , and two triploids with  $2n = 108$  (Kurita, 1968).

Ching (1933) indicated a close relation of *Colysis* with *Leptochilus* and *Microsorium* in the treatment of these genera in southern China and the Himalayan area. Differences in the rhizome, leaves, and especially the scales were used to distinguish *Selliguea* from these genera. Hettterscheid & Hennipman (1984) recognize *Colysis* as one of the 19 groups within the Microsorioid complex and indicate that *Dendroglossa* Pr. and *Paraleptochilis* Copel. should be included in *Colysis*.

### Literature

- Ching, R.C. 1933. Studies of Chinese ferns 10. Bull. Fan Mem. Inst. Biol. 4: 293–362.  
 Hettterscheid, W.L.A., & E. Hennipman, 1984. Venation patterns, soral characteristics, and shape of the fronds of the microsorioid Polypodiaceae. Bot. Jahrb. Syst. 105:11–47.  
 Kurita, S. 1968. Cytotaxonomy of *Colysis*. Chiba Univ. Ann. Rep. Foreign Stud. Coll. 3: 47–51.

## 117. *Dictymia* J. Smith

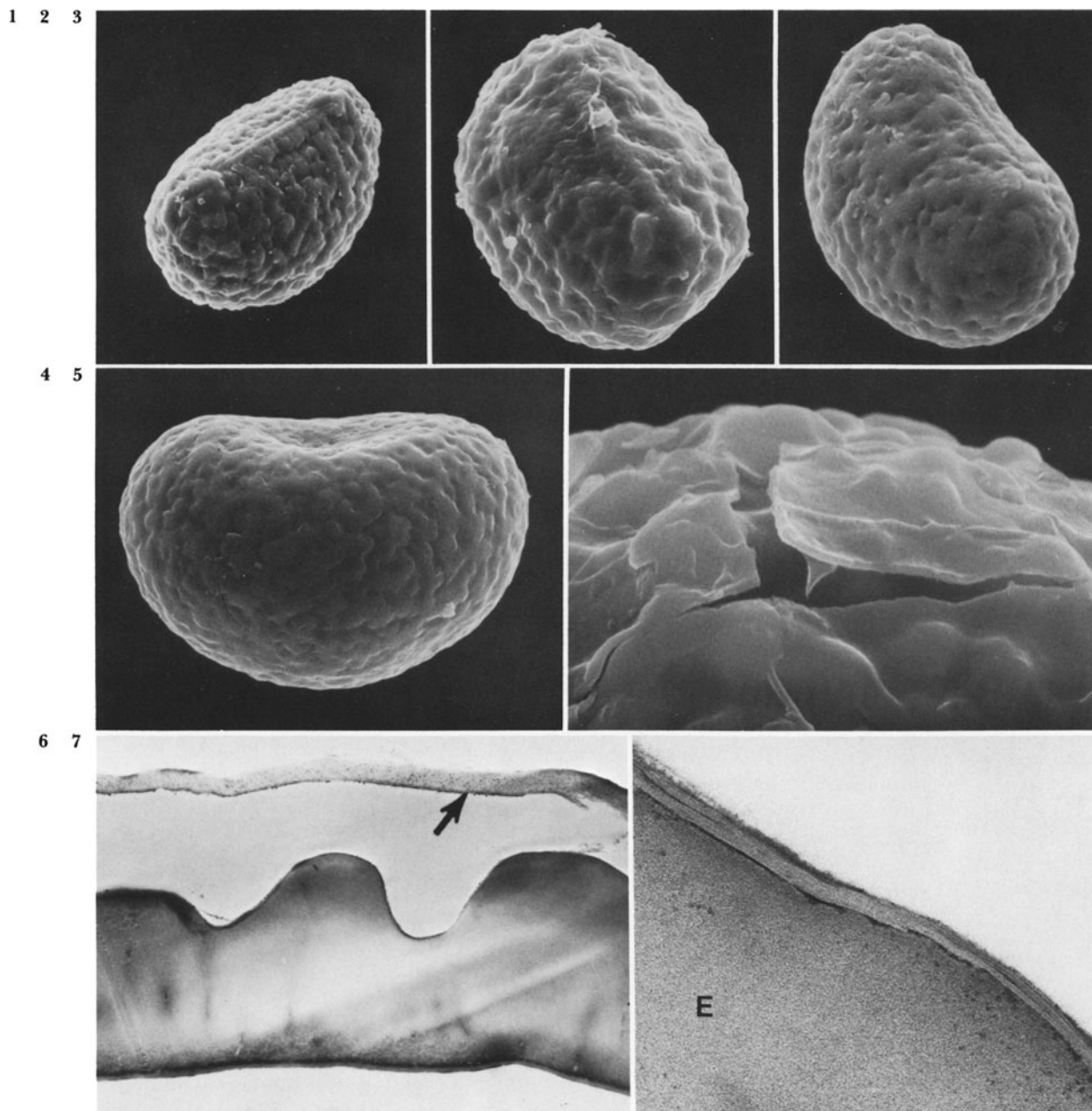
**Figs. 117.1–117.7**

### Genus

A paleotropical, epiphytic genus of three or four species.

### Range

Eastern Australia, New Caledonia, Fiji.



**Figs. 117.1–117.7.** *Dictymia* spores,  $\times 1,000$ , and wall sections. 1. *D. mckeeii* Tindale, discrete rugae, Fiji, *Smith 5865*. 2, 5. *D. mettenii* (Copel.) Copel. 2. Coarsely rugate proximal face, New Caledonia, *DePlanche 32 (K)*. **Figs. 3, 4, 6, 7.** *D. mckeeii* Tindale. 3. Low, coarsely rugate, aperture at right, New Caledonia, *Green 1173*. 4. Low rugate

lateral surface, Fiji, *Smith 9696*. 5. Abraded surface, the raised perispore conforms to exospore contours, *DePlanche 32 (K)*,  $\times 5,000$ . 6, 7. Sporoderm sections, *Smith 9696*. 6. Exospore section with thin, adherent perispore below raised, fibrous envelope (arrow),  $\times 6,000$ . 7. Detail of multilaminar perispore above exospore (E),  $\times 100,000$ .

**Spores**

Examined in three species.

**Size** 47–73  $\mu\text{m}$ .

**Shape** Ellipsoidal, the ends sometimes obtuse.

**Aperture** Monolete,  $\frac{1}{2}$  to  $\frac{3}{4}$  the length.

**Surface** Low, irregularly rugate.

**Structure** Exospore verrucate; perispore lamellate, covered by a thick, fibrous deposit, often detached (Figs. 6, 7).

**Comments**

**Characteristics, Diversity, Relationships** The low surface contours are derived from the exospore

(Figs. 1–4, 6). The thin perispore, abraded and partly raised, conforms to the lower contours (Fig. 5). Hennipman & Roos (1983) characterized this form as the *Lepisorus* type, representing one of the three main kinds of exospore in the Polypodiaceae. The spores suggest that *Diclymia* is allied with such other genera as *Lemmaphyllum*, *Drymotaenium*, and *Belvisia* in the Lepisoroid group, which represent one of the main lineages in the family.

**Literature**

Hennipman, E., & M.C. Roos. 1983. Phylogenetic systematics of the Polypodiaceae (Filicales). Verh. Naturwiss. Ver. Hamburg 26: 321–342.

## 118. *Lecanopteris* Reinwardt

### Figs. 118.1–118.20

**Genus**

A paleotropical genus of 20 or perhaps fewer species of epiphytic, ant-inhabited ferns.

**Range**

Sumatra eastward to New Guinea, north to the Philippines and Vietnam.

**Spores**

Examined in six species.

**Size** 35–75  $\mu\text{m}$ .

**Shape** Ellipsoidal to fusiform, free, or in tetrads, or clusters of 16 spores.

**Aperture** Monolete, usually short, about  $\frac{1}{2}$  the spore length or slightly longer, protruding to obscure.

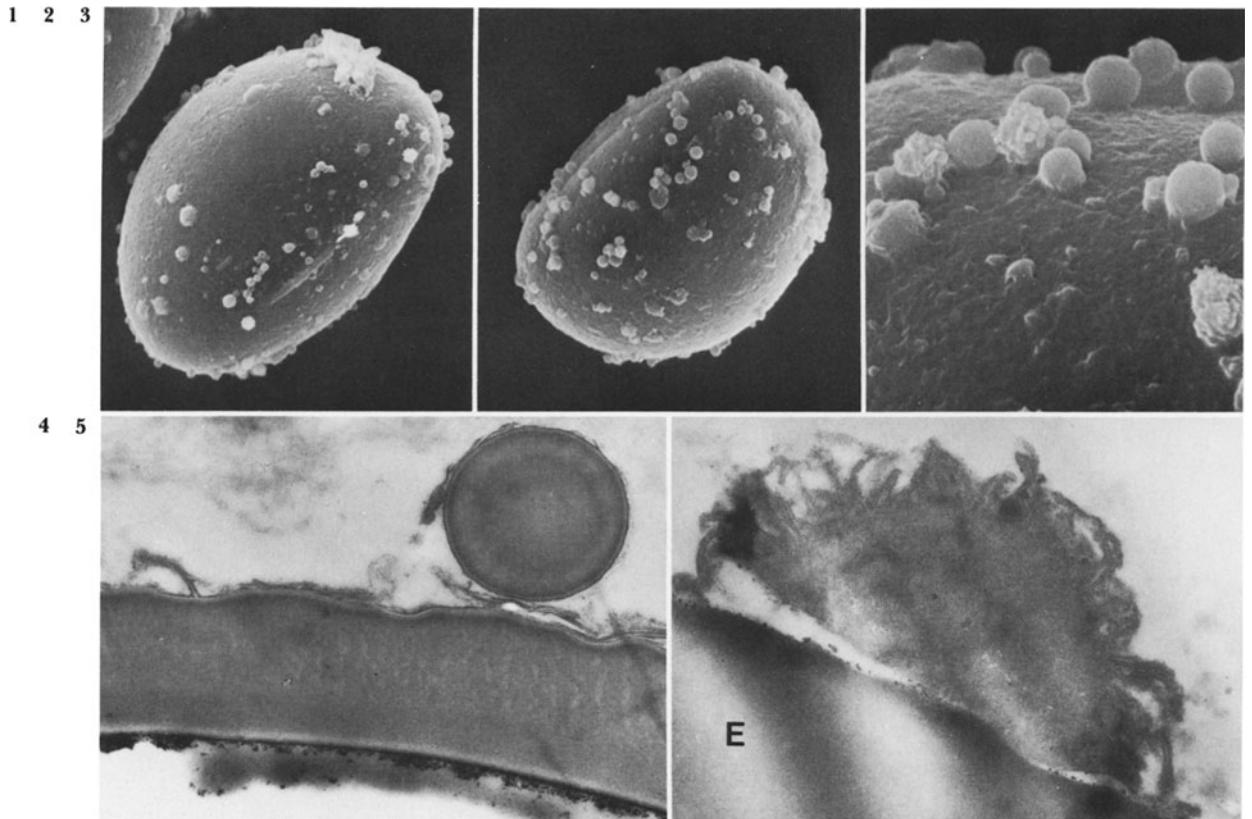
**Surface** Finely rugulate with globules, or sheaths, especially in the apertural area; or irregular sheaths, strands or cables enveloped by particulate material.

**Structure** Exospore plain; perispore thin, slightly rugulate, enveloping globules.

**Comments**

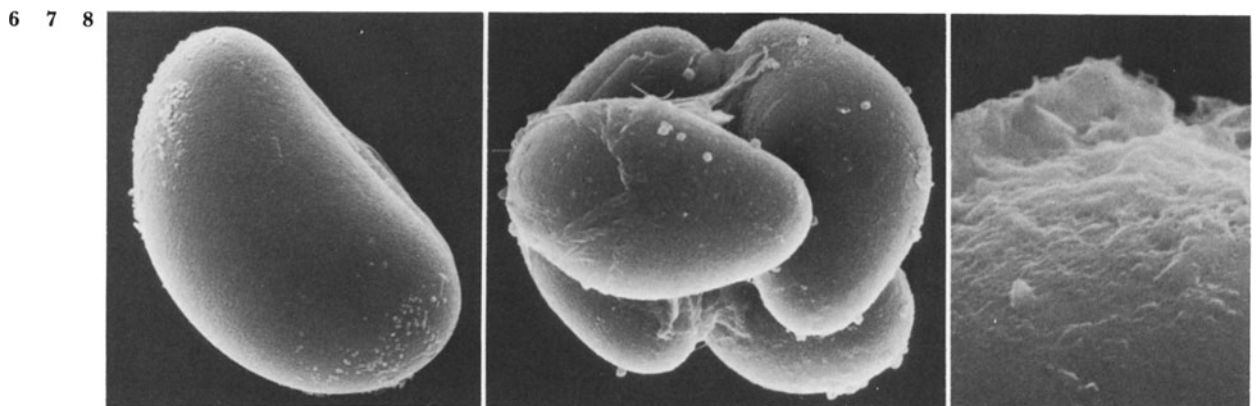
**Characteristics** The usually single, rugulate spores of *Lecanopteris sinuosa* are the simplest type in the genus, and characteristic of the generally ellipsoid type of Polypodiaceae spores (Figs. 1–4). These spores become attached to ants as shown by the spore on the head of *Iridomyrmex cordatus* within an enlarged stem (Tryon, 1985, plate 1, c, d). Field observations of this fern in Sarawak indicate that the ants harvest the contents of the sori overnight (Janzen, 1974). Another genus of ants, *Pheidolacanthinus*, inhabits the stems of species of *Lecanopteris* that have spores associated in tetrads. The copious lipids in the spores undoubtedly supply a source of nutrient for these insects, and the ants may be involved in spore dispersal of these epiphytic plants (Tryon, 1985, 1986).

Species with spores retained in tetrads, such as *Lecanopteris carmosa* and *L. lomarioides*, have fusiform spores enveloped by sheaths (Figs. 7–11). These and the strands and cables in *Lecanopteris* spores are specializations of the perispore. Spores of *L. mirabilis* are unusual as they



**Figs. 118.1–118.5.** *Lecanopteris sinuosa* (Hook.) Copel. spores,  $\times 1,000$ , and wall sections. 1. Ellipsoidal, short aperture below, Indonesia, *Kuswata & Soopadamo 147*. 2–5. New Guinea, *Van Royen 4644*. 2. Surface globules. 3. Slightly irregular surface with globules more or less at-

tached,  $\times 5,000$ . 4. Wall section, exospore below thin perispore enveloping the globule,  $\times 20,000$ . 5. Outer part of acetolysed spore, exospore (E) below mass with dissected surface,  $\times 40,000$ .



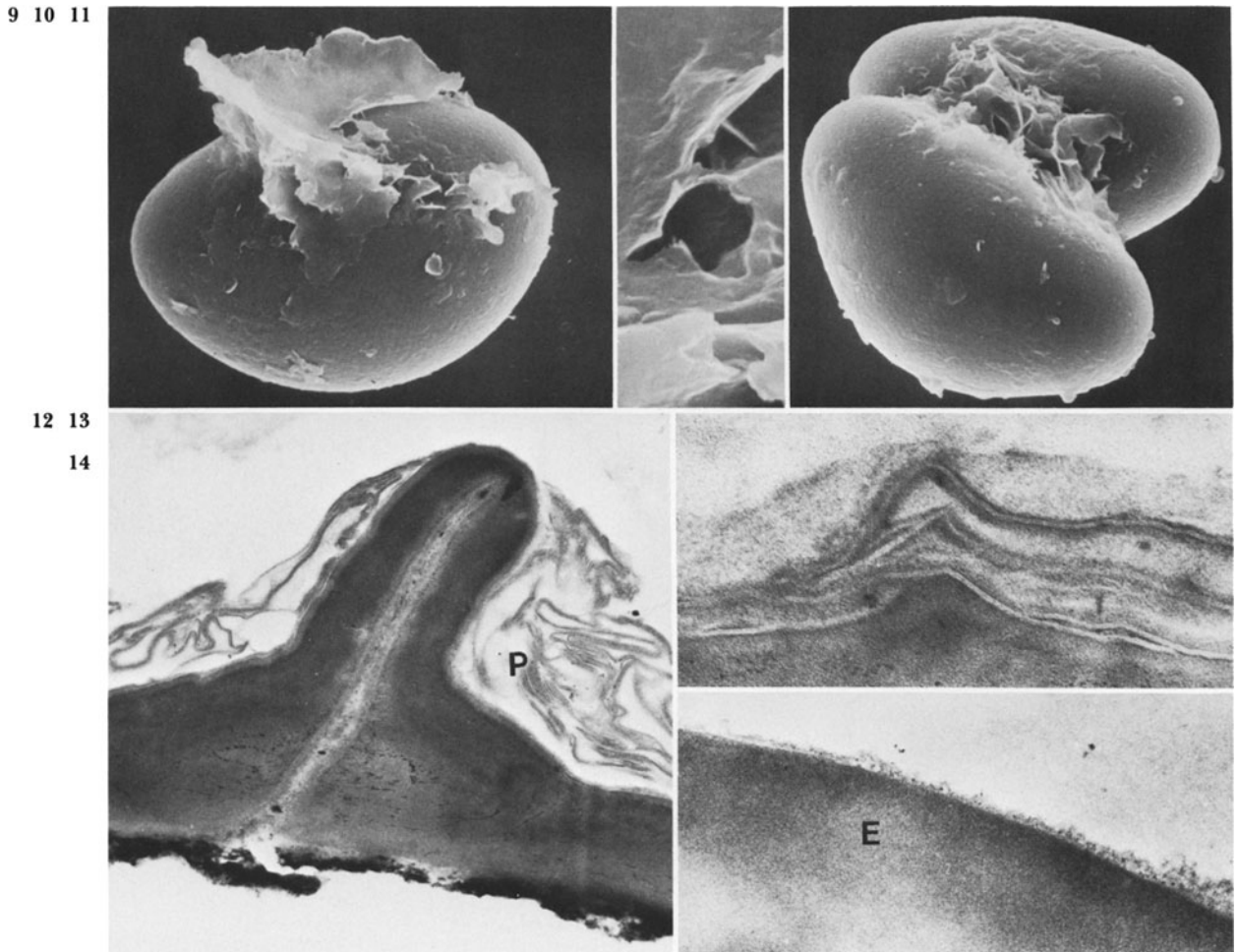
**Figs. 118.6–118.8.** *Lecanopteris* spores,  $\times 1,000$ . 6. *L. lomarioides* (Mett.) Copel., detached from tetrad, aperture above right, Malaya, *Molesworth-Allen 4629*. 7, 8. *L. carnosa*

(Reinw.) Bl., New Guinea, *Van Royen & Sleumer 6346*. 7. Spore tetrad, fused on apertural face. 8. Detail of finely rugulate surface, sheets above,  $\times 5,000$ .

are retained in clusters of 16 spores, enveloped by strands (Figs. 15–18). Spore clusters are found in the stems among roots, evidently transported there by the ants. The strands are prominent in partly opened sporangia (Figs. 15, 16). Sections of the strands show they are formed by the perispore.

The strands overlay a thick exospore, may ad-

here in cablelike forms, and are enveloped by particulate material (Fig. 20). These clearly differ from, but are reminiscent of, the viscine threads characteristic of *Epilobium* and some Ericaceae pollen, that are a glycocalyx specialization of the plasma membrane (Rowley and Dahl, 1983; Hesse, 1986).



**Figs. 118.9–118.14.** *Lecanopteris* spores,  $\times 1,000$ , and wall sections. **9, 10.** *L. carnosa*, Malaysia, *Burkill 740*. **9.** Irregular sheets above aperture. **10.** Surface detail of sheets,  $\times 5,000$ . **11.** *L. spinosa* Jermy & Walker, fusiform spores attached by sheets at aperture, Celebes, *Jermy 7609* (BM).

**12–14.** Wall sections. **12, 13.** *L. carnosa*, *Burkill 740*. **12.** Apertural area, exospore below laminate perispore (P),  $\times 15,000$ . **13.** Detail of perispore laminae below fibrous material,  $\times 65,000$ . **14.** *L. lomarioides* acetolized spore, exospore (E) below very thin perispore,  $\times 40,000$ .

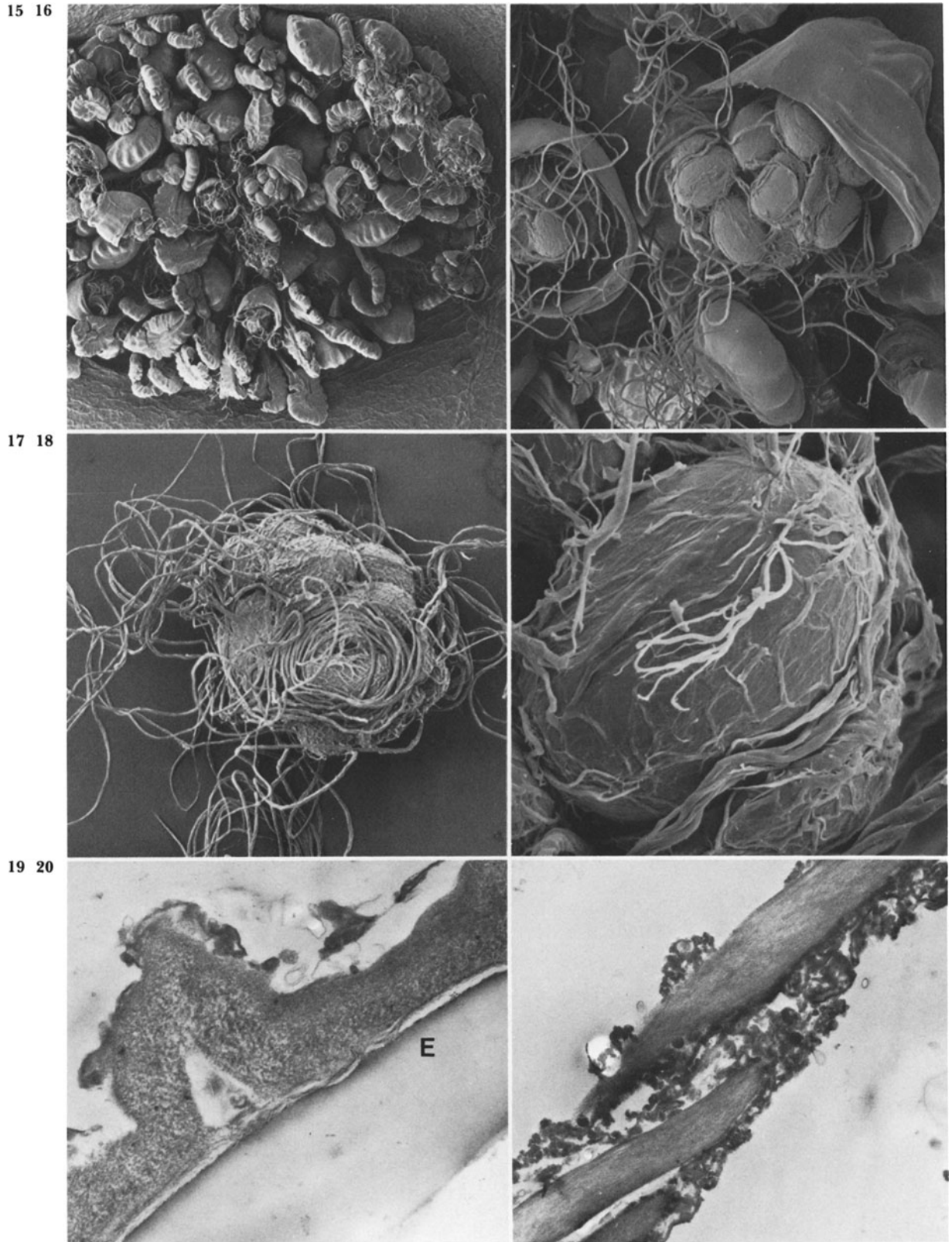
**Diversity** Spores of the collection of *Lecanopteris carnosa* from Malaysia are larger than those from New Guinea and may reflect differences in ploidy levels (Figs. 7, 9). Tetraploid reports of  $n = c 74$  are known for *L. mirabilis* and *L. deparioides* (Walker, 1986). The filamentous surface of the spores was regarded by Walker as a possible means of increasing the probability of intergametophytic selfing, ensuring lodging on substrate, and prolonging the period of spore dispersal.

**Relationships** Differences of the *Lecanopteris sinuosa* spores, with plain surface and unspecialized globular deposit, along with other characters such as the slender stems with coarse, bicolorous scales of these plants, support recognition of the species in a distinct group of *Myrmecopteris* (Hennipman & Verduyn, 1987). However, all of the species need to be assessed

before the genus can be delimited with confidence. Diversity within the genus has been reviewed by Jermy and Walker (1975), in an account of 10 species, including a new one from Indonesia. The spores of *Lecanopteris* will supply additional evidence pertinent to the systematic assessment. They are of special interest as examples of the unusually labile nature of the perispore and functional adaptations of spores.

## Literature

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- Hesse, M. 1986. Nature, form and function of pollen-connecting threads in angiosperms. In S. Blackmore & I.K. Ferguson (Eds.): *Pollen and spores: form and function*, pp. 109–118. Academic Press, London.



**Figs. 118.15–118.20.** *Lecanopteris mirabilis* (C. Chr.) Copel., New Guinea, *Wormersley 24942*. **15.** Portion of sorus with partly dehiscent sporangia,  $\times 35$ . **16.** Dehiscent sporangium with spore cluster exposed, and parts of other sporangia,  $\times 150$ . **17.** Spore cluster enmeshed by strands and cablelike filaments,  $\times 200$ . **18.** Strands on spore surface,

thicker cablelike strands below,  $\times 1,000$ . **19, 20.** Sections of sporoderm. **19.** Distal face, the exospore (E) below diffuse perispore with basal part of strands,  $\times 10,000$ . **20.** Longitudinal section of cable with compact strands enveloped by granulate material,  $\times 15,000$ .



Janzen, D.J. 1974. Epiphytic myrmecophytes in Sarawak: Mutualism through the feeding of plants by ants. *Biotropica* 6: 237–259.  
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 Rowley, J.R., and A.O. Dahl. 1983. Fine structure of viscin threads in *Epilobium angustifolium*. *J. Ultrastruct. Res.* 85: 112.

Tryon, A.F. 1985. Spores of myrmecophytic ferns. *Proc. R. Soc. Edinb.* 86B: 105–110.  
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 Walker, T.G. 1986. The ant-fern, *Lecanopteris mirabilis*. *Kew Bull.* 41: 533–545.

**119. *Leptochilus* Kaulfuss**  
**Figs. 119.1–119.6**

**Genus**

An Asiatic genus of about 12 species with strongly dimorphic leaves.

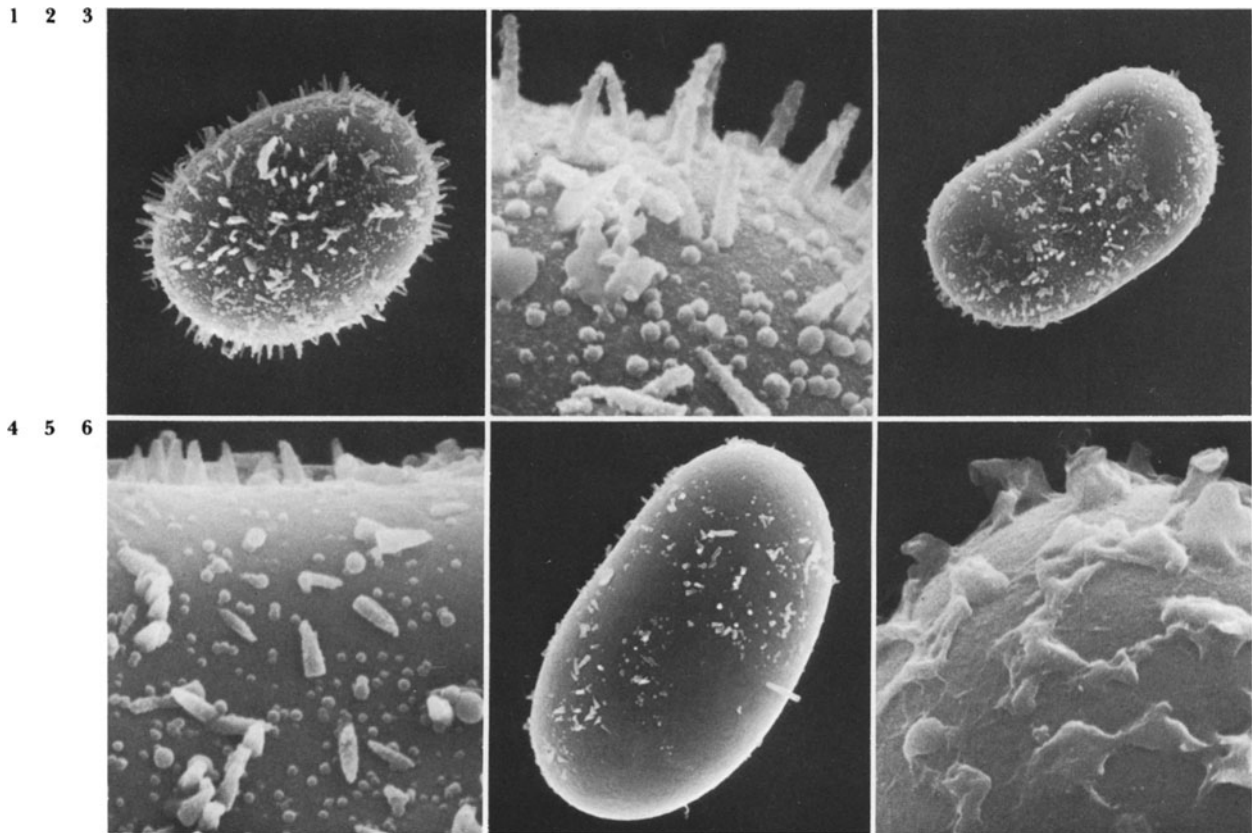
**Range**

Southern India, Ceylon, and the Himalayas,

southeast to Malaya and Java, northward to the Philippines, southern China, and Taiwan.

**Spores**

Examined in six species.



**Figs. 119.1–119.6. *Leptochilus* spores, ×1,000.** 1, 2. *L. decurrens* Bl., India, *Kostermans 26187* (US). 1. Echininate surface. 2. Surface detail of spines and globules, ×5,000. 3, 4. *L. minutulus* Fée. 3. Sparse spines. 4. Detail of detached spines and globules. 5. *L. axillaris* (Cav.) Kaulf., sparsely

echinate, distal face, Java, *Buysman 158* (US). 6. *L. accuminatus* White & Goy, surface detail of incompletely formed echinae, young spore, Queensland, Australia, *White 10652*, ×5,000.

**Size** 28–53  $\mu\text{m}$ .

**Shape** Ellipsoidal, the ends may be obtuse.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{2}{3}$  the length.

**Surface** Diffuse echinae and globules.

### Comments

**Characteristics, Diversity, Relationships** The spores are relatively plain with few to dense echinae and globules (Figs. 1–5). The echinae are often partially eroded (Fig. 4), and in the young spore of the Australian *Leptochilus acuminatus* are incompletely formed (Fig. 6). *Leptochilus axillaris* has been excluded from the genus by Hetterscheid & Hennipman (1984) although the sparsely echinate spores are generally similar to other species in the genus (Fig. 5).

Copeland (1928) regarded *Leptochilus* as a

small genus of two species based on *Leptochilus axillaris*. However, Ching (1933) included ten species and considered them to represent a closely related group, allied to *Colysis*. The echinate surface in spores of these genera supports this alliance. Hetterscheid & Hennipman also relate these genera, and with the exception of *L. axillaris*, place them among genera allied to *Microsorium*.

### Literature

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Copeland, E.B. 1928. *Leptochilus* and genera confused with it. Philip. J. Sci. 37: 333–416.

Hetterscheid, W.L.A., & E. Hennipman. 1984. Venation patterns, characteristics, and shape of the fronds of the microsoroid Polypodiaceae. Bot. Jahrb. Syst. 105: 11–47.

## 120. *Microsorium* Link

### Figs. 120.1–120.17

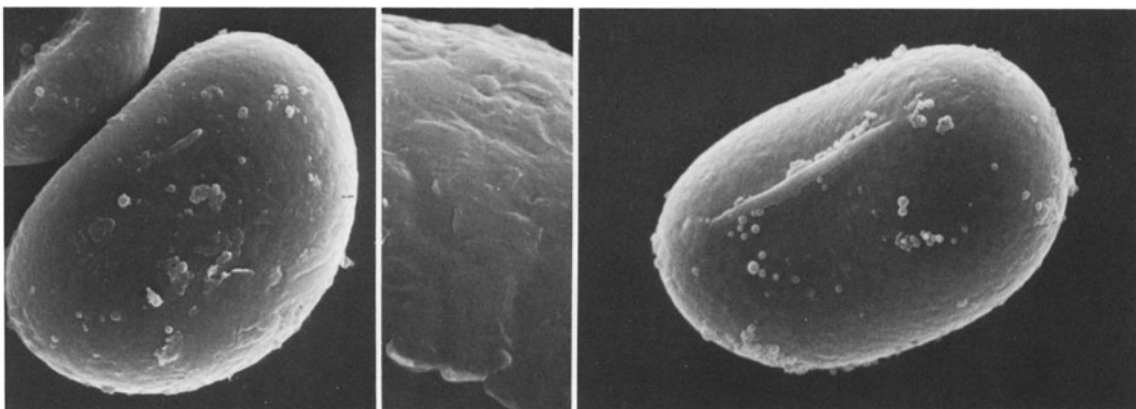
#### Genus

A paleotropical genus variously circumscribed in generic and floristic accounts. Forty species were recognized by Christensen (1938). Ching (1933) included about half of these in his treatment of Chinese and Himalayan species. Holttum included 10 in his work on Malayan ferns (1955).

#### Range

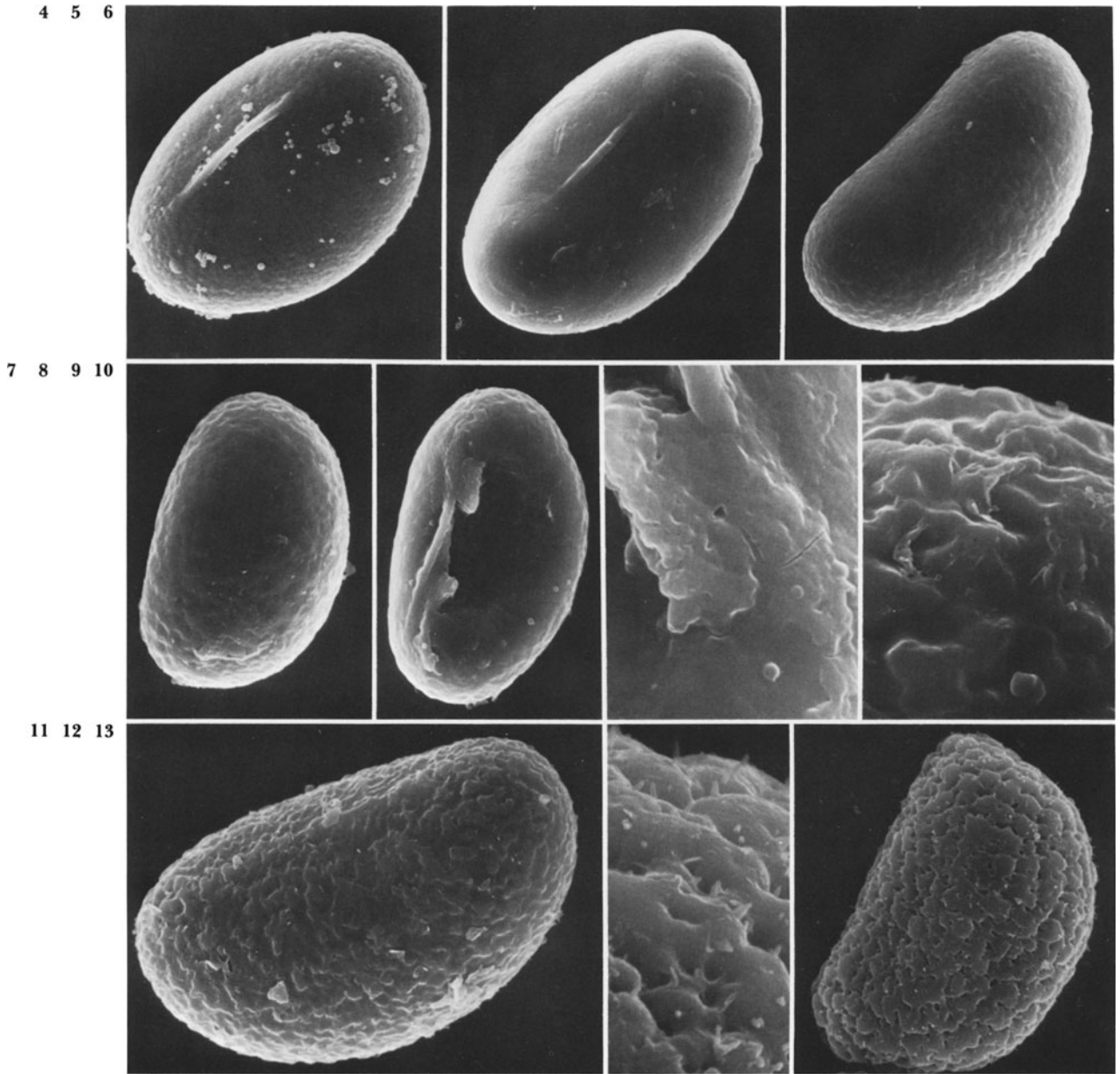
In west tropical Africa eastward to northern India and south China; in Malesia from Sumatra and Borneo eastward to the Philippines and New Guinea; in the Pacific in New Caledonia and Tahiti.

1 2 3



**Figs. 120.1–120.3.** *Microsorium* spores,  $\times 1,000$ . 1–3. *M. punctatum* (L.) Copel. 1, 2. Ceylon, *Beckett 648*. 1. Shallowly verrucate. 2. Detail of low verrucae,  $\times 5,000$ . 3.

Obtuse ends, low verrucae, Madagascar, *Croat 30124* (MBG).



**Figs. 120.4–120.13.** *Microsorium* spores,  $\times 1,000$ . 4. *M. varians* (Mett.) Hennip. & Hetter., low verrucae, New Caledonia, *McKee 14420* (P). 5. *M. sarawakense* (Bak.) Ching, plain to slightly verrucate, Borneo, *J. & M. Clemens 27349*. 6. *M. normale* (Don) Ching, shallow rugate contours, Yunnan, China, *Tsai 56433*. 7–9. *M. zippelii* (Bl.) Ching, Lombok, *Elbert 2454*. 7. Shallowly rugate distal face. 8.

Perispore fragmented near aperture. 9. Surface detail, foveolae below part of aperture,  $\times 5,000$ . 10, 11. *M. superficiale* (Bl.) Ching, Kuangtung, China, *Tsang 20242*. 10. Detail of rugate surface,  $\times 5,000$ . 11. Rugate proximal face. 12, 13. *M. membranaceum* (Don) Ching, Bhutan, *Ludlow et al. 17052*. 12. Detail of pitted, rugate surface,  $\times 5,000$ . 13. Lateral surface irregularly rugate.

### Spores

Examined in 17 species.

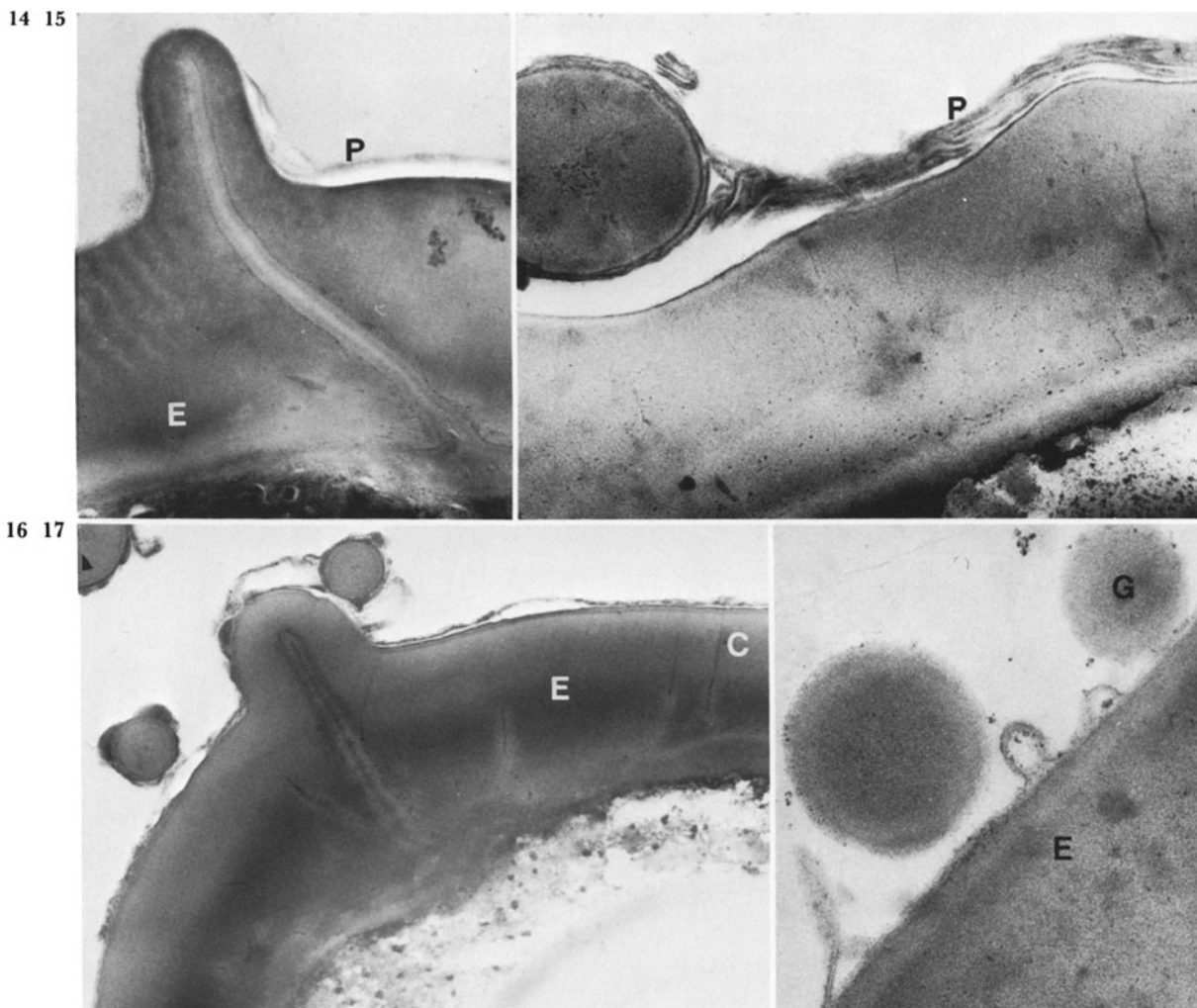
**Size** 40–70  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{2}{3}$  the length.

**Surface** Low tuberculate to nearly plain with globules, or irregularly rugate with papillae and depressed pits (foveolae).

**Structure** Exospore two layered, the outer plain or slightly undulate perispore usually thin, laminate (Figs. 14–17).



**Figs. 120.14–120.17.** Wall sections of *Microsorum* spores. 14. *M. punctatum* apertural area, exospore (E) below thin perispore (P), Siam, *Den Hoed* 56433,  $\times 18,000$ . 15. *M. normale*, exospore below multilaminar perispore (P) surrounding globule, as Fig. 6,  $\times 35,000$ . 16. *M. musifolium*

(Bl.) Copel., apertural area, thick exospore (E) including canals (C) thin perispore surrounding globules at surface, Papua, *Brass* 6602,  $\times 16,000$ . 17. *M. glossipes* (Bak.) Copel., exospore (E) below very thin perispore with globules, (G), Papua, *Brass* 23399,  $\times 50,000$ .

**Comments**

**Characteristics, Diversity** The surface is unusually diverse, but mostly low tuberculate to nearly plain as in *Microsorum punctatum*, *M. varians*, and *M. sarawakense* (Figs. 1–5). Shallowly rugate spores as in *M. normale* and *M. zippelii* (Figs. 6–9) are common to several species. Pits or foveolae such as those in *M. membranaceum* (Figs. 12, 13) are evident near the aperture of the abraded spore of the latter (Fig. 9). The smaller spores of this species (Fig. 7) possibly represent a lower ploidy level than the large one of *M. superficiale* (Fig. 11). The low surface contours formed by the exospore (Figs. 10, 15) are overlaid by the thin, laminate perispore that also envelop the globules (Figs. 15–17).

Hennipman & Roos (1983) recognize *Microsorum* spores as one of three main types in the Polypodiaceae, characterized by such exospore features as large canals only near the aperture, thickness of 1  $\mu\text{m}$ , microcanals, and lack of tangential banding. Hettterscheid & Hennipman’s studies of venation patterns in *Microsorum* and allied genera include 13 species groups in the genus and note the remarkably heterogeneous state of *Microsorum* (1984).

**Relationships** The problem of distinguishing *Phymatosorus* (as *Phymatodes*) from *Microsorum* is noted by Copeland: “Expecting to find somewhere a line between them, I have left this (*Microsorum*) as the last genus for final description, but am unable to separate them by any character. . .” (1947). Both Copeland (1947) and

Holttum (1955) regard *Microsorium* as a basic group from which other genera such as *Colysis*, *Leptochilus*, and *Drynaria* are derived.

### Literature

- Ching, R.C. 1933. Studies of Chinese ferns 10. Bull. Fan Mem. Inst. Biol. 4: 293–362.  
 Christensen, C. 1938. Filicinae. In F. Verdoorn (Ed.): Manual of pteridology, pp. 522–550. Martinus Nijhoff, The Hague.

- Copeland, E.B. 1947. Genera Filicum, 247 pp. Chronica Botanica, Waltham Massachusetts.  
 Hennipman, E., & M.C. Roos. 1983. Phylogenetic systematics of the Polypodiaceae (Filicales). Verh. Naturwiss. Ver. Hamburg 26: 321–342.  
 Hetterscheid, W.L.A., & E. Hennipman. 1984. Venation patterns, soral characteristics, and shape of the fronds of the microsorioid Polypodiaceae. Bot. Jahrb. Syst. 105: 11–47.  
 Holttum, R.E. 1955. See general literature.

## 121. *Neocheiropteris* Christensen

### Figs. 121.1–121.3

#### Genus

A paleotropical genus of about five species centering in western China.

#### Range

Northern India, China, and Burma, northward to Japan.

#### Spores

Examined in three species.

**Size** 43–55  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{2}$  to  $\frac{3}{4}$  the length.

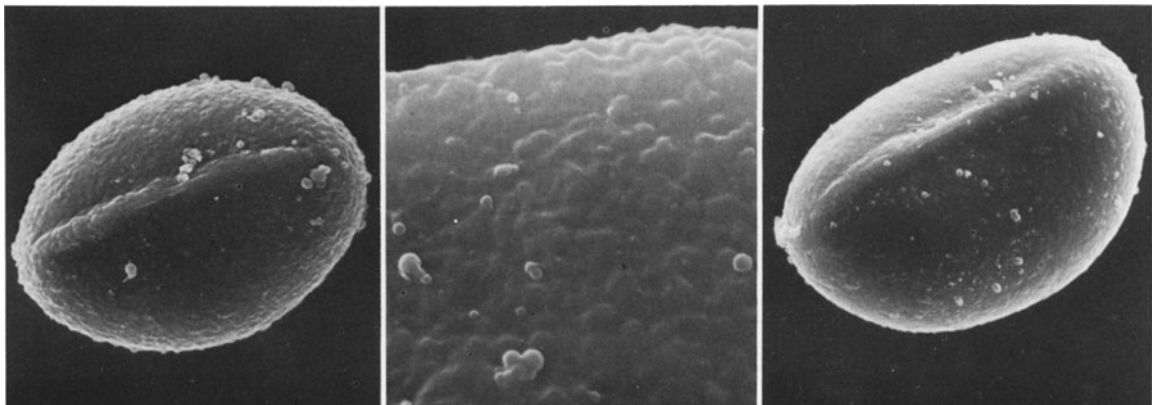
**Surface** Irregularly rugate or papillate.

#### Comments

**Characteristics, Diversity, Relationships** The two species figured here have low rugate to papillate spores (Figs. 1–3). The genus was formerly considered to be a connection between the Polypodiaceae and the Dipteridaceae. However, Bower (1913) showed that diverse leaf form in some species, especially the catadromic, helacoid leaves of *Neocheiropteris palmatopedata*, does not support the relationship. Ching's study of the five Chinese species (1933) includes an assessment of the unusual leaf diversity in species. He regarded the genus as intermediate to *Pleopeltis* and *Belvisia* (as *Hymenosorus*).

*Neocheiropteris* is allied with the microsorioid

1 2 3



**Figs. 121.1–121.3.** *Neocheiropteris* spores,  $\times 1,000$ . 1, 2. *N. ensata* (Thnbg.) Ching, Japan. 1. Low rugate surface, Ando 70312. 2. Detail of irregular papillae and small glob-

ules, Siebold, in 1829 (L),  $\times 5,000$ . 3. *N. palmatopedata* (Bak.) Christ, low papillae, Lou Pau, China, Maire, in 1910.

genera of the Polypodiaceae, based on studies of the venation patterns and stomata (Hettterscheid and Hennipman, 1984). The relatively low, rugate spores support this alliance.

## Literature

Bower, F.O. 1913. Studies in the phylogeny of the Filicales. 3. On *Metaxya* and certain other relatively

primitive ferns. *Ann. Bot.* 27: 443–477.

Ching, R.C. 1933. The studies of Chinese ferns 9. *Bull. Fan Mem. Inst. Biol.* 4: 103–113.

Hettterscheid, W.L.A., & E. Hennipman. 1984. Venation patterns, soral characteristics, and shape of the fronds of the microsorioid Polypodiaceae. *Bot. Jahrb. Syst.* 105: 11–47.

## 122. *Phymatosorus* Pichi-Sermolli Figs. 122.1–122.12

### Genus

A paleotropical, epiphytic genus of 12 species formerly under the name *Phymatodes* Presl. The concepts of Copeland, Ching, and Holttum are reviewed in an historical account of that genus that explains the need for the new name, *Phymatosorus* (Pichi-Sermolli, 1973).

### Range

Mainly tropical, from Africa eastward to the Himalayas, northward to Japan, southward to Australia and New Zealand; in the Pacific east to Samoa and Pitcairn Island.

### Spores

Examined in five species.

**Size** 37–68  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{3}{4}$  the length.

**Surface** Coarsely rugulate, or plain, with short echinae and globules.

**Structure** Exospore irregular forming the low, coarse contours; perispore thin forming the echinae, with globules.

### Comments

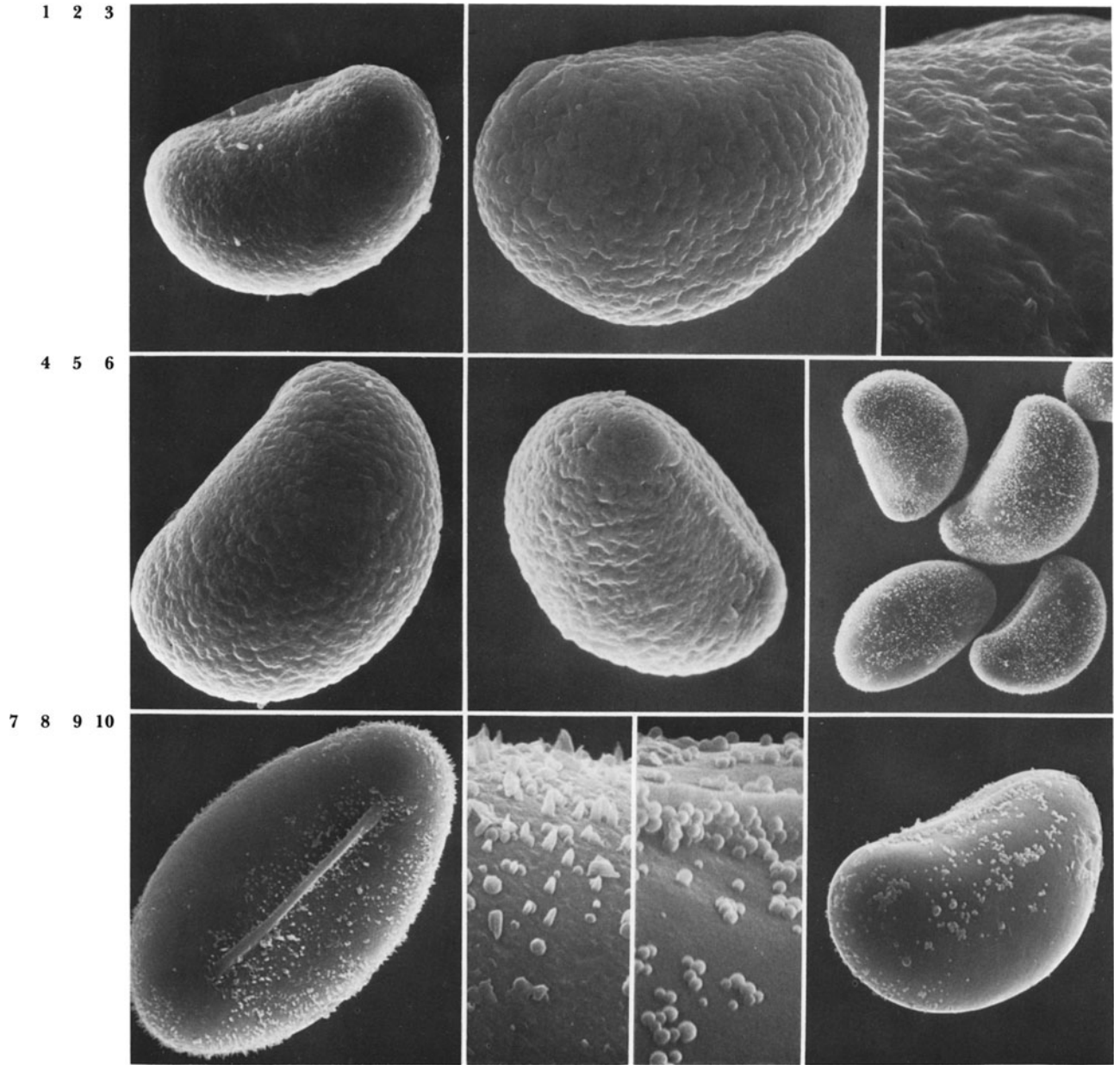
**Characteristics, Diversity** The diverse, plain to rugate surfaces of *Phymatosorus* spores, examined here, suggest that the group is not well defined. Spores of *Phymatosorus scolopendria* and *P. ensiformis* (Figs. 1–5, 11, 12) have an irregularly low, rugulate surface that is quite consis-

tant in collections of *P. scolopendria* over a wide geographic range of the species. The surface is covered with globules in *P. nigrescens* (Figs. 6–8) and *P. longissimus* (Fig. 9, 10) and numerous echinae in the former.

*Phymatosorus* spores are generally similar to those of *Microsorium*, and *P. nigrescens* is included in that genus by Hettterscheid & Hennipman (1984). In their remarks on the types of exospore in Polypodiaceae spores, Hennipman & Roos (1983) associate spores of *Phymatosorus* (as *Phymatodes*) with the *Lepisorus* type based on the presence of many small canals, a thickness of 2–4  $\mu\text{m}$ , with tangential banding, and absence of microcanals.

**Relationships** *Phymatosorus* is often associated with *Microsorium*, and the spores suggest that there may be close relations between certain species that are presently separated in these genera. Ching (1933) treated four species of China and the Sikkim Himalayan region in the “*Euphymatodes*” section within a broad context of *Phymatodes*. Copeland (1947) included *Phymatodes* in *Microsorium* with the remark that he was unable to separate it by any character or to assign a considerable number of species with any confidence to one genus or the other.

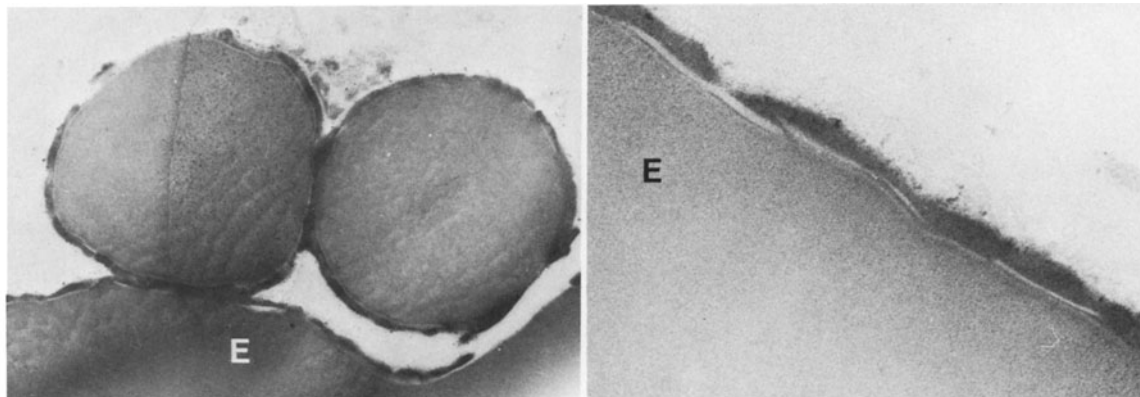
Species of *Lecanopteris* were included in *Phymatodes* by Holttum (1955). These ant-inhabited species were considered as a specialized development of *Phymatodes*. The spores support an alliance between *Phymatodes* and species treated in *Lecanopteris*, although the latter may be polyphyletic.



**Figs. 122.1–122.10.** *Phymatosorus* spores,  $\times 1,000$ , except 6,  $\times 500$ . 1–4. *P. scolopendria* (Burm. f.) Pic.-Ser. 1. Low rugulate, aperture above, Sumatra, *Korthals* s.n. 2. Large, rugate spore, Cameroons, *Tryon & Tryon* 6496. 3, 4. New Guinea, *Brass* 13738. 3. Detail of rugulate surface,  $\times 5,000$ . 4. Lateral surface. 5. *P. ensiformis* (Thunb.) Pic.-Ser., low, coarsely rugulate, South Africa, *Tryon & Tryon*

6380. 6–8. *P. nigrescens* (Bl.) Pic.-Ser. 6. Spores with dense globules, Ceylon, *Davidse* 8359,  $\times 500$ . 7, 8. India, *Kramer & Nair* 6153. 7. Finely echinate proximal face. 8. Surface detail of echinae, partly detached, and globules,  $\times 5,000$ . 9, 10. *P. longissimus* (Bl.) Pic.-Ser., Papua, *Brass* 27124. 9. Surface detail of globules near part of aperture,  $\times 5,000$ . 10. Plain surface with globules.

11 12



**Figs. 122.11, 122.12.** *Phymatosorus ensiformis* wall sections, South Africa, *Burchell 5536*. 11. Exospore (E) below peri-

spore that envelops the globules,  $\times 18,000$ . 12. Detail of perispore with scales above exospore (E),  $\times 60,000$ .

### Literature

Ching, R.C. 1933. Studies of Chinese ferns. 11. Contrib. Inst. Bot. Natl. Acad. Peiping 2: 31–100.  
 Copeland, E.B. 1947. See general literature.  
 Hennipman, E., & M.C. Roos. 1983. Phylogenetic systematics of the Polypodiaceae (Filicales). Verh. Naturwiss. Ver. Hamburg 26: 321–342.

Hettterscheid, W.L.A., & E. Hennipman. 1984. Venation patterns, soral characteristics, and shape of the fronds of the microsorioid Polypodiaceae. Bot. Jahrb. Syst. 105: 11–47.  
 Holtum, R.E. 1955. See general literature.  
 Pichi-Sermolli, R.G. 1973. Fragmenta Pteridologiae. 4. Webbia 28: 445–477.

## 123. *Campyloneurum* Presl

### Figs. 123.1–123.11

#### Genus

A neotropical, mostly epiphytic genus of 16 species.

#### Range

Southern Florida, the Bahamas, and northern Mexico, south to Catamarca, Argentina, Uruguay and Brazil; on Cocos and the Galápagos Islands.

#### Spores

Ten species examined.

**Size** 45–100  $\mu\text{m}$ .

**Shape** Ellipsoidal, more or less elongate.

**Aperture** Monolete,  $\frac{1}{3}$  to  $\frac{3}{4}$  the length.

**Surface** Shallowly to prominently verrucate, with irregular, often sparse globules (Fig. 4).

**Structure** Exospore seems to form the coarsely verrucate to plain contours; perispore thin, usually with globules.

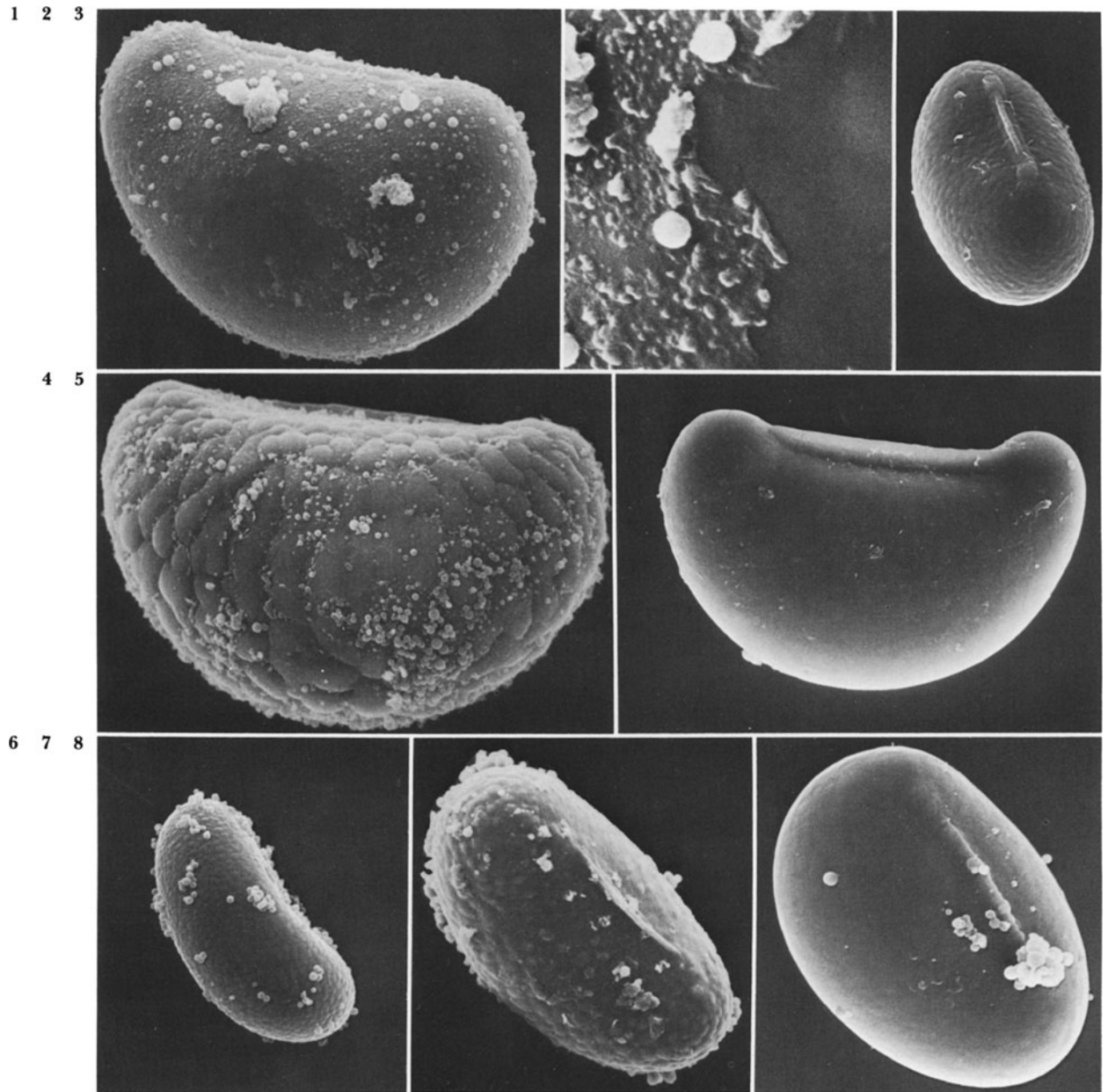
#### Comments

**Characteristics, Diversity** The shallow to prominently verrucate spores (Figs. 3, 11), with globules (Figs. 9, 10), common to all species, appear to be formed by the exospore although sections have not been examined. Spores are nearly plain with verrucae scarcely evident in *Campyloneurum falcoideum* and *C. anetioides* (Figs. 1, 5).

The generally large spores may reflect the prevalence of the tetraploid condition in *Campyloneurum* as the cytological reports are mostly tetraploid with  $n = 74$ . However, differences in spore size, as in *Campyloneurum costatum* and *C. angustifolium* var. *amphostenon* (Figs. 3, 4), suggest there are different ploidy levels. The small spores of *C. repens*, especially the very small one from Paraguay (Figs. 6, 7), suggest that diploid plants may exist in South America, in contrast to the tetraploid in Jamaica (Walker, 1985).

**Relationships** The usually verrucate surface and globules in *Campyloneurum* spores are common

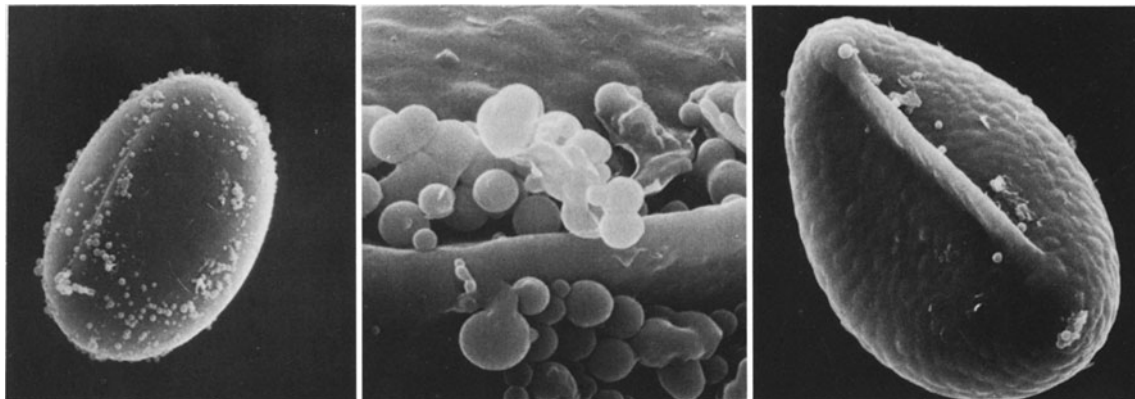




**Figs. 123.1–123.8.** *Campyloneurum* spores,  $\times 1,000$ . 1, 2. *C. falcoideum* (Hieron.) Lell., Panama, *McDaniel 10222*. 1. Thin, partly abraded perispore with globules. 2. Detail of abraded surface,  $\times 5,000$ . 3. *C. costatum* (Kze.) Presl, shallow verrucate elements, Jamaica, *Proctor 22107*. 4. *C. angustifolium* (Sw.) Fée var. *amphostenon* (Kl.) Farw., prominently verrucate, with globules, Colombia, *Smith &*

*Idrobo 1319*. 5. *C. anetioides* (Christ) R. & A. Tryon, lateral surface, aperture above, Costa Rica, *Skutch 2753*. 6, 7. *C. repens* (Aublet) Presl. 6. Elongate with globules on shallow verrucae, Paraguay, *Hassler 12241a*. 7. Large, rugate spore, Peru, *Mexia 8271*. 8. *C. fallax* Fée, plain, Brazil, *Smith 1780*.

9 10 11



**Figs. 123.9–123.11.** *Campyloneurum* spores,  $\times 1,000$ . 9. *C. chrysopodum* (Kl.) Fée, slender, low aperture, irregularly scattered globules, Colombia, Killip 7713. 10. *C. angustifolium* var. *solutum* (Kl.) Farw., dense globules on aperture,

Ecuador, Ollgaard & Balslav 8576,  $\times 5,000$ . 11. *C. phyllitidis* (L.) Presl, low, verrucate proximal face, Mexico, Moore 3058.

to several genera of the Polypodiaceae. They are especially similar to spores of *Niphidium* and some of species in *Polypodium*, and support other characters indicating relations with these genera. The cytological studies of Walker and the floristic work of Smith (1981) refer to the complex systematic problems and need of a modern revision of *Campyloneurum*.

## Literature

- Smith, A.R. 1981. Flora of Chiapas. 2. Pteridophytes, 370 pp. California Academy of Science, San Francisco.
- Walker, T.G. 1985. Cytotaxonomic studies of the ferns of Trinidad: The cytology and taxonomic implications. Bull. Br. Mus. Nat. Hist. 13: 149–249.

## 124. *Dicranoglossum* J. Smith Figs. 124.1–124.5

### Genus

An epiphytic American genus of perhaps three species.

### Range

Guatemala through Central America, Cuba, Hispaniola, St. Vincent, and Trinidad in the Caribbean; in South America southward to Bolivia, and to Paraná in southeastern Brazil.

### Spores

Examined in three species.

**Size** 50–74  $\mu\text{m}$ .

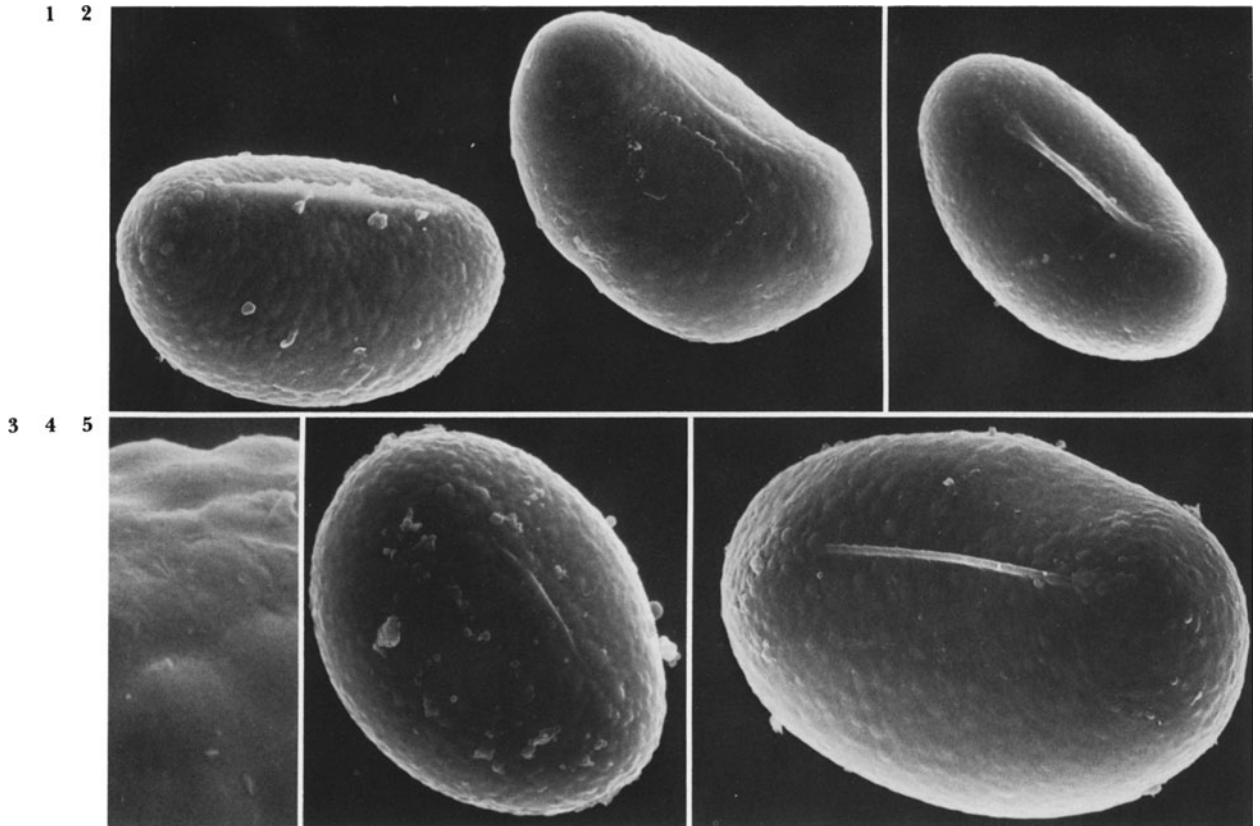
**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{1}{2}$  the length.

**Surface** Shallowly verrucate with few globules.

### Comments

**Characteristics, Diversity** The shallow verrucate contours are derived from the exospore, below a thin perispore (Figs. 1–3). The large spore of *Dicranoglossum furcatum* from Haiti (Fig. 5) contrasts with the smaller one from Venezuela (Fig. 4), and suggests there may be different ploidy levels among species. The small spores, as in *D. polypodioides*, may represent the diploid level, as Costa Rican specimens are reported with  $n = 36$ . The number is unusual, for most genera of the Polypodiaceae are based on  $n = 37$  (Wagner, 1980).



**Figs. 124.1–124.5.** Spores of *Dicranoglossum*,  $\times 1,000$ . 1. *D. polypodiioides* (Hook.) Lell., low verrucate contours, Peru, Schunke 5190. 2, 3. *D. desvauxii* (Kl.) Proct. 2. Shallowly verrucate to nearly plain surface, Peru, Hutchinson & Wright 8727. 3. Detail of shallow verrucae, Trinidad, Broadway 5497,  $\times 5,000$ . 4, 5. *D. furcatum* (L.) J. Sm. 4. Short aperture, sparse globules, Venezuela, Steyermark & Rabe 69310. 5. Large spore, Haiti, Ekman 4714.

A report of chlorophyll-bearing spores in *Dicranoglossum desvauxii* was questioned by Atkinson (1974), who suggests that the observations may have been based on chlorophyll in the initial gametophyte cell.

**Relationships** The genus is readily distinguished from other groups in the Polypodiaceae by the forked, sessile or subsessile leaves. It is regarded as possibly derived from *Pleopeltis* and also related to *Marginariopsis*, both of which have similar spores (Tryon & Tryon, 1982).

## Literature

- Atkinson, L.R. 1974. Gametophyte of *Dicranoglossum desvauxii*. *Phytomorph.* 24: 49–56.  
 Tryon, R.M., & A.F. Tryon. 1982. See general literature.  
 Wagner, F.S. 1980. New basic chromosome numbers for genera of neotropical ferns. *Am. J. Bot.* 67: 733–738.

## 125. *Microgramma* Presl

Figs. 125.1–125.8

### Genus

An American genus of about 13 species, one of them also in Africa, eastward to the Mascarene Islands.

### Range

Centering in the Andes and adjacent Amazon basin. In southern Florida, Tamaulipas, Mexico southward to Catamarca, and Buenos Aires, Argentina, and in Amazonia, Brazil; in Africa, Madagascar, and the Mascarene Islands.

### Spores

Examined in seven species.

**Size** 43–70  $\mu\text{m}$ .

**Shape** Ellipsoidal to somewhat ovate.

**Aperture** Monolete,  $\frac{1}{2}$  to  $\frac{2}{3}$  the length.

**Surface** Papillate, rugate or usually coarsely verrucate to irregularly tuberculate.

### Comments

**Characteristics, Diversity** The coarse surface elements (Figs. 1, 3) vary in size and density. The diffuse tuberculate ones in spores of *Microgramma reptans* (Fig. 4) contrast with the compact verrucate surface in spores of *M. tecta* (Fig.

3) and *M. vacciniifolia* (Fig. 5). Small papillae (Fig. 2) and globules (Figs. 4, 6) are often deposited on the prominent verrucae. Spores of the Jamaican collection of *M. lycopodioides* have exceptionally dense deposits that partly obscure the verrucae (Fig. 6). The coarsely rugate surface and exceptionally large spores of *M. megalophylla* (Fig. 7) may reflect a higher ploidy level of the collection.

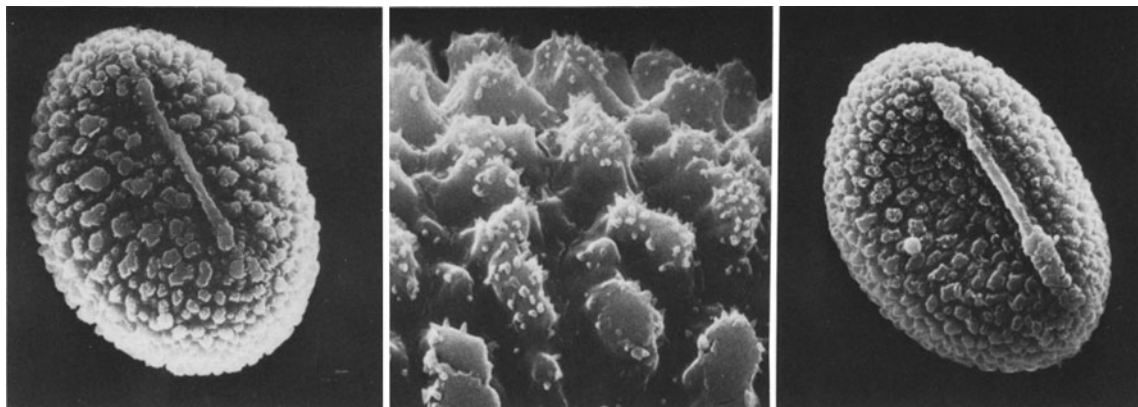
**Relationships** The verrucate spores support relations of *Microgramma* with *Pleopeltis* and *Campyloneurum* based on other features of the plants (Tryon & Tryon, 1982). There are also similarities with the verrucate spores in *Polypodium* that suggest possible connections with that genus. This alliance is also supported by report of a hybrid between *Microgramma lycopodioides* and *Polypodium pleisosorum* (Gómez, 1975).

### Literature

Gómez, L.D. 1975. Contribuciones a la pteridología Costarricense. 8. La hibridación en el trópico *Microgramma*, *Polypodium* y *P. aspidiolepis* Baker. *Brenesia* 6: 49–57.

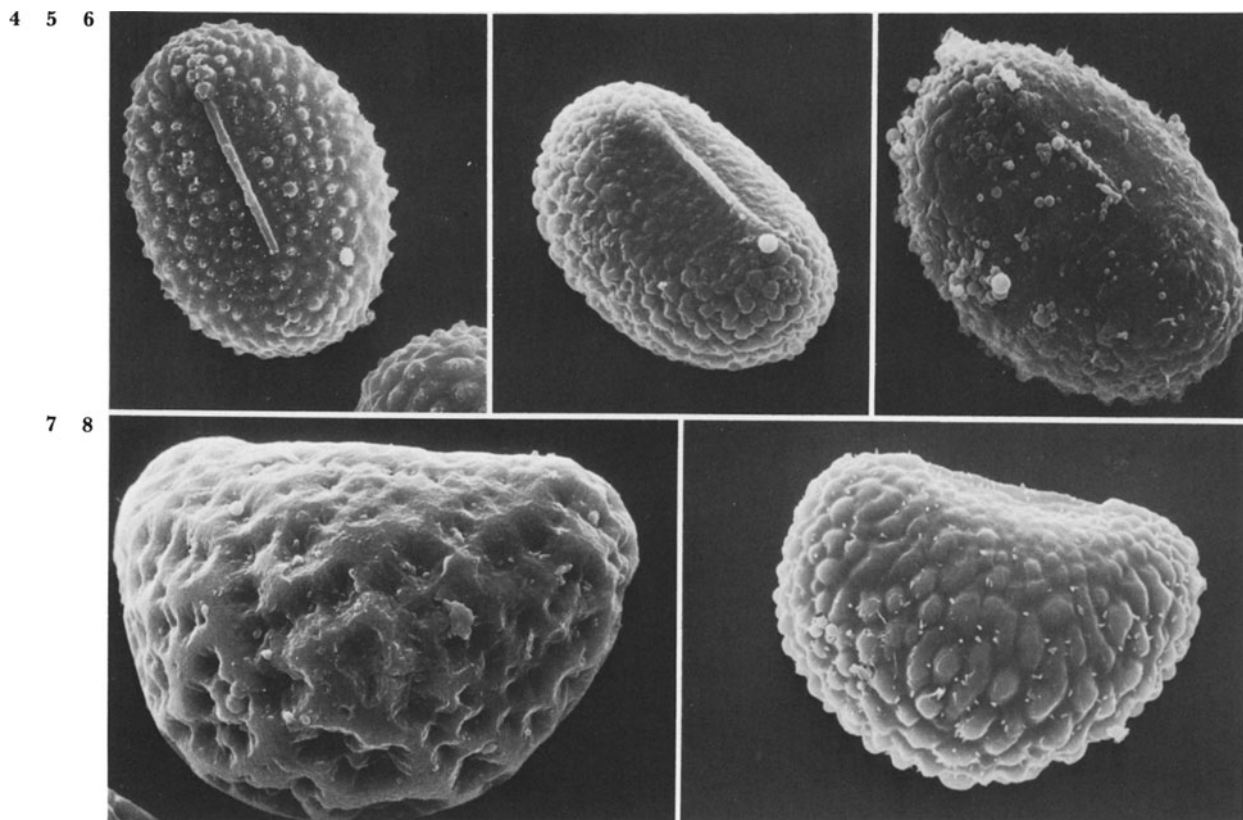
Tryon, R.M., & A.F. Tryon. 1982. See general literature.

1 2 3



Figs. 125.1–125.3. *Microgramma* spores,  $\times 1,000$ . 1, 2. *M. piloselloides* (L.) Copel., Ecuador, *Bell* 206. 1. Verrucate surface with papillae. 2. Surface detail of papillate verrucae,  $\times 5,000$ .

3. *M. tecta* (Kaulf.) Alston, proximal face with compact verrucae, Costa Rica, *Skutch* 2912.



**Figs. 125.4–125.8.** *Microgramma* spores,  $\times 1,000$ . 4. *M. reptans* (Cav.) A.R. Sm., papillate tubercles, Colombia, *Klug 1725*. 5. *M. vacciniifolia* (Langsd. & Fisch.) Copel., verrucate proximal face, Brazil, *Dusén 14159*. 6, 8. *M. lycopodioides* (L.) Copel. 6. Verrucate elements below globules

and residual tapetal material, Jamaica, *Orcott 3054*. 7. *M. megalophylla* (Desv.) Sota, rugate lateral surface, Brazil, *Krukoff 9031*. 8. Verrucate lateral surface, as 6, Mozambique, *Chase 4483*.

## 126. *Neurodium* Fée

### Figs. 126.1–126.3

#### Genus

A monotypic, mostly epiphytic species of the American tropics based on *Neurodium lanceolatum*.

#### Range

In the Florida Keys, the Bahamas, the Greater and most of the Lesser Antilles; in Central America from Guatemala south to British Honduras and Nicaragua.

#### Spores

Examined in two collections.

**Size** 48–55  $\mu\text{m}$ .

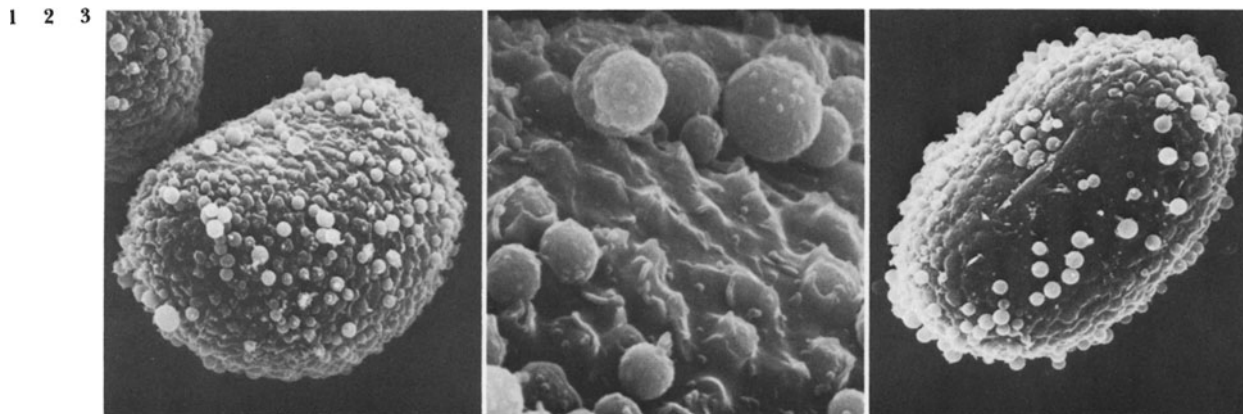
**Shape** Ellipsoidal.

**Aperture** Short, monolete,  $\frac{1}{4}$  to  $\frac{1}{2}$  the length.

**Surface** Low tubercles, with abundant globules.

#### Comments

**Characteristics, Diversity, Relationships** Dense globules partly obscure the low, tubercles forming the surface contours (Figs. 1–3). Additional, finer particulate surface deposit and globules appear to be perisporeal material (Fig. 2). The abraded spore wall of *Neurodium* figured in Tryon & Tryon (1982) illustrates the thin sur-



**Figs. 126.1–126.3.** *Neurodium lanceolatum* (L.) Fée, ×1,000. 1, 2. Jamaica, *Clute 288*. 1. Lateral surface with abundant globules. 2. Surface detail with particulate pro-

jections on the wall and globules, ×5,000. 3. Low tubercles with globules, short aperture, British Honduras, *Schipp S-780*.

face that overlays the thick exospore. The relationship of *Neurodium* to other genera of the Polypodiaceae is not clear, but the spores suggest possible connections with *Polypodium*.

### Literature

Tryon, R.M., & A.F. Tryon. 1982. See general literature.

## 127. *Niphidium* J. Smith

### Figs. 127.1–127.5

#### Genus

A largely Andean group of 10 or more species, revised by Lellinger (1972).

#### Range

Mainly in the Andes, Costa Rica, the Greater and Lesser Antilles, and disjunct in Bahia, Brazil, to Uruguay. *Niphidium crassifolium* most widely distributed from central Mexico southward in Central and South America to Jujuy, Argentina.

#### Spores

Examined in five species.

**Size** 42–80  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{2}$  to  $\frac{2}{3}$  the length.

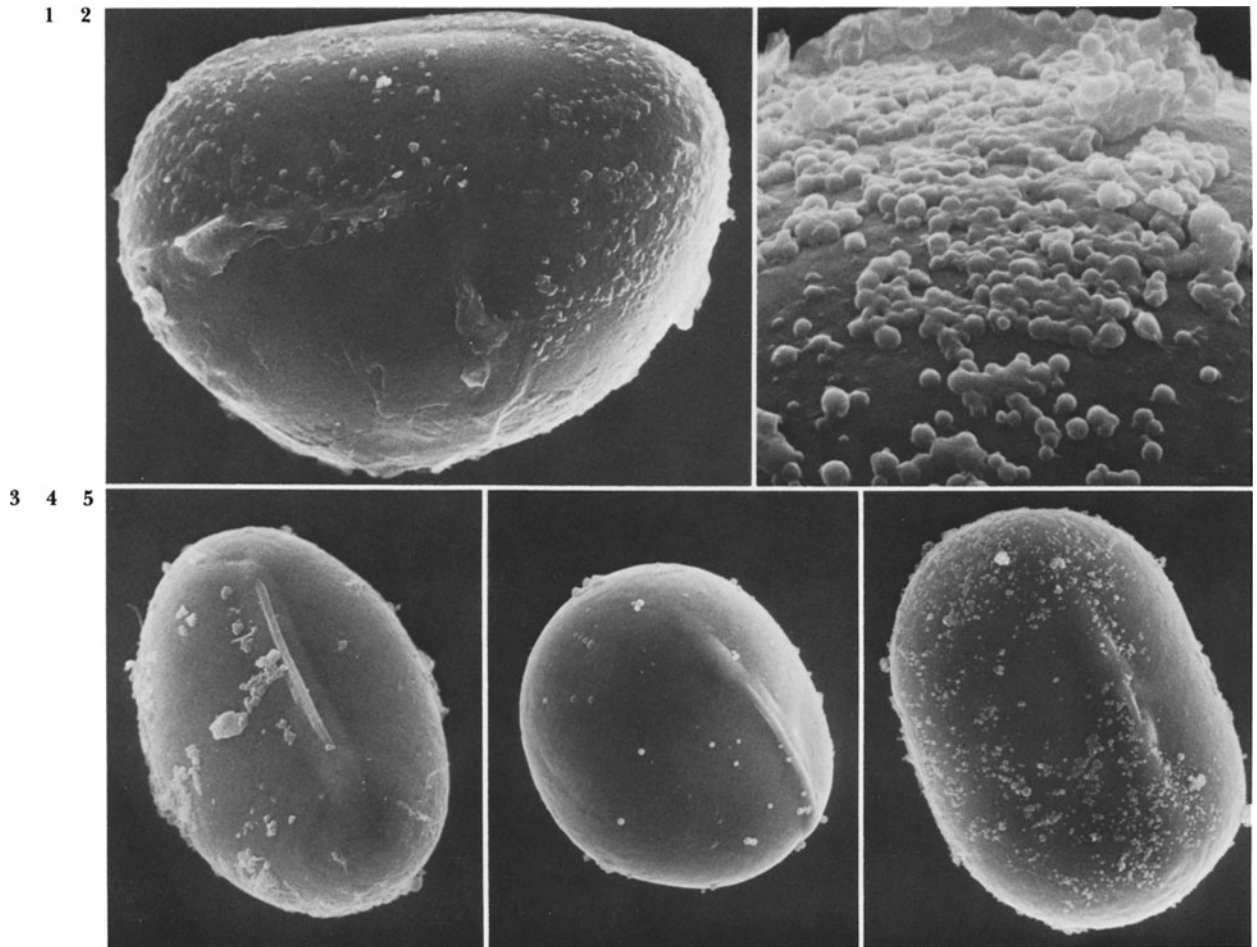
**Surface** Plain to slightly papillate, sometimes with dense globules.

#### Comments

**Characteristics, Diversity, Relationships** The globules vary in density and sometimes form coalescent masses, as in *Niphidium crassifolium* (Fig. 2). Variation in spore size between this (Fig. 1) and other species (Figs. 3–5) suggests that there may be different ploidy levels in the genus. Jamaican plants of *N. crassifolium*, reported as  $n = 74$ , evidently represent tetraploids. The smaller spores of the two South American species may represent plants at lower ploidy levels (Figs. 3–5). *Niphidium* has been allied to *Campyloneurum*, and the relatively plain spores in both genera support the alliance.

#### Literature

Lellinger, D.B. 1972. A revision of the fern genus *Niphidium*. *Am. Fern J.* 62: 101–120.



**Figs. 127.1–127.5.** *Niphidium* spores,  $\times 1,000$ . 1, 2. *N. crassifolium* (L.) Lell., Mexico, *Riba et al.* 313. 1. Thin irregular surface, with globules. 2. Surface detail of coalescent globules,  $\times 5,000$ . 3. *N. albopunctatissimum* Lell.,

nearly plain surface, short aperture, Bolivia, *Steinbach* 3401. 4. *N. mortonianum* Lell., plain with sparse globules, Colombia, *Schiefer* 567. 5. *N. longifolium* (Cav.) Mort. & Lell., proximal face, dense globules, Ecuador, *Rose et al.* 28816.

## 128. *Pleopeltis* Willdenow

### Figs. 128.1–128.6

#### Genus

A largely American, mostly epiphytic genus of about 10 species.

#### Range

In America from the southwestern United States and northern Mexico southward in Central and South America to Buenos Aires, Argentina, disjunct in Chile, in the Antilles, across northern South America, and in eastern Brazil; one species in Africa, Madagascar, the Mascarenes, and eastward to India.

#### Spores

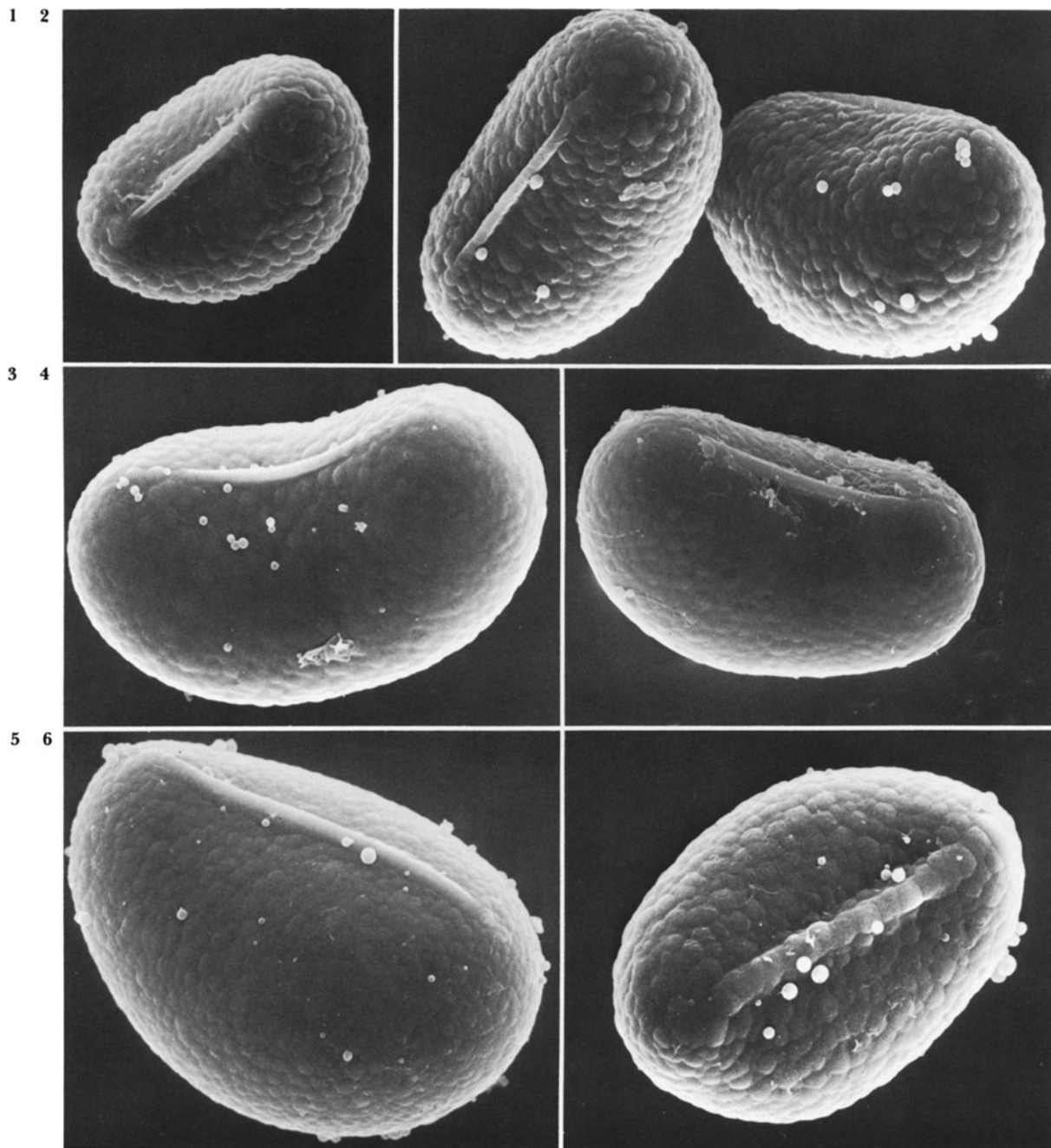
Examined in six species.

**Size** 48–78  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{2}{3}$  to  $\frac{3}{4}$  the length.

**Surface** Verrucate, usually low verrucae and sparse globules.



**Figs. 128.1–128.6.** *Pleopeltis* spores,  $\times 1,000$ . 1. *P. percussa* (Cav.) Hook. & Grev., verrucate proximal face, Colombia, *Plowman* 2322. 2. *P. polylepis* (Kze.) Fourn., sparse globules on low verrucae, Mexico, *Rose & Painter* 7877. 3. *P. revoluta* (Willd.) A.R. Sm., low verrucae, Honduras, *Williams*

11495. 4. *P. angusta* Willd. low verrucae, Mexico, *Fink* 72. 5, 6. *P. macrocarpa* (Willd.) Kaulf. 5. Large, verrucate spore, long aperture, Ethiopia, *Mooney* 6991. 6. Prominently verrucate, Peru, *Wurdack* 633.

### Comments

**Characteristics, Diversity, Relationships** The relatively large spores with long aperture, low verrucae, and sparse globules are consistent among these species (Figs. 1–6). Except for *Pleopeltis macrocarpa*, wide-ranging in America, also in Af-

rica, India, and Ceylon, the genus is primarily American. Specimens from the Old World have spores with low, verrucate contours and support treatment with the American plants (Figs. 5, 6). The American group of *Pleopeltis macrocarpa* was revised by Weatherby (1922) under the name *Polypodium lanceolatum*. *Pleopeltis* ap-



pears to be closely related to the scaly leaved species of American *Polypodium*; hybrids between them also support a close alliance.

According to the study of paraphyses in the Polypodiaceae, *Pleopeltis percussa* should be included in *Microgramma* (Baayen & Hennipman, 1987). Verrucate spores are characteristic of both *Pleopeltis* and *Microgramma*. However, since the latter group presently appears to represent a complex in need of systematic work, the species is retained in *Pleopeltis*.

## Literature

- Baayen, R.P., & E. Hennipman. 1987. The paraphyses of the Polypodiaceae (Filicales). *Biol. Pflanz.* 62: 251–316.  
 Weatherby, C.A. 1922. The group of *Polypodium lanceolatum* in North America. *Contrib. Gray Herb.* 65: 3–14.

## 129. *Polypodiopteris* Reed

**Figs. 129.1, 129.2**

### Genus

A paleotropical genus of three small, epiphytic species that Copeland (1947) recognized as *Polypodiopsis*. Reed (1948) determined that name was already used for a genus of the Taxaceae and used *Polypodiopteris* for Copeland's genus.

### Range

Borneo, Mt. Kinabalu.

### Spores

Examined in one species.

**Size** 75–80  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{2}{3}$  the length.

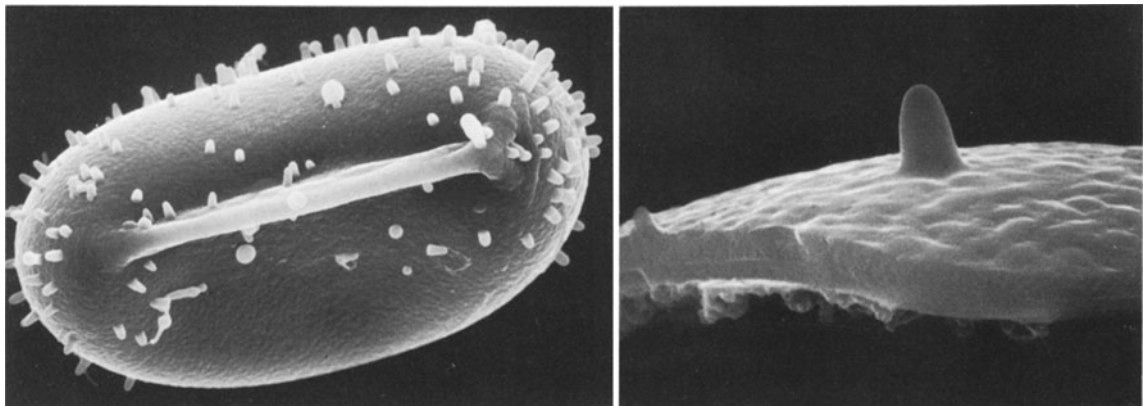
**Surface** Plain or very slightly irregular with sparse, coarse tubercles or blunt echinae.

**Structure** Exospore thin; perispore may be thicker than the exospore, forming the coarse tubercles (Fig. 2).

### Comments

**Characteristics, Diversity, Relationships** The thick outer layer that appears to be perispore in the fractured section (Fig. 2) is unusually developed, although TEM studies are needed to confirm the structure. The large size and sparsely tuberculate spores of *Polypodiopteris brachypoda* generally resemble those of *Selliguea*. However, a close relationship between these

1 2



**Figs. 129.1, 129.2.** *Polypodiopteris brachypoda* (Copel.) Reed spores, Mt. Kinabalu, Borneo, *J. & M. Clemens* 30/33.  
 1. Slightly irregular, proximal face with scattered,

blunt echinae, aperture at center,  $\times 1,000$ . 2. Fractured wall, the relatively thick outer wall with short tubercles, that seems to be perispore, is exceptionally large,  $\times 5,000$ .

genera is clearly untenable on the basis of gross differences in the leaves. Copeland (1947) initially compared the genus with *Goniophlebium* based on similarities of the rhizome and leaves, but this association was questioned by Christensen, who proposed an affinity with *Crypsinus* (now included in *Selliguea*). The alliance of *Polypodiopsis* with these genera is unclear.

According to Baayen & Hennipman in work on paraphyses (1987), *Polypodiopsis* is associated with *Pleopeltis* in the tribe Polypodieae, as a distinct element in this position. The large

spore size, and low, verrucate surface with coarse tubercles and globules also suggest possible relations with *Pleopeltis*.

### Literature

- Baayen, R.P., & E. Hennipman. 1987. The paraphyses of the Polypodiaceae (Filicales). *Biol. Pflanz.* 62: 251–316.
- Copeland, E.B. 1947. *Genera Filicum*. See general literature.
- Reed, C.F. 1948. Two new generic names of ferns. *Am. Fern J.* 38: 87.

## 130. *Marginariopsis* Christensen Figs. 130.1, 130.2

### Genus

A monotypic, American genus based on *Marginariopsis wiesbaurii*.

### Range

Costa Rica, Panama, and Ecuador.

### Spores

Examined in three collections.

**Size** 46–50  $\mu\text{m}$ .

**Shape** Ellipsoidal with blunt ends.

**Aperture** Monolete, about  $\frac{1}{2}$  the length.

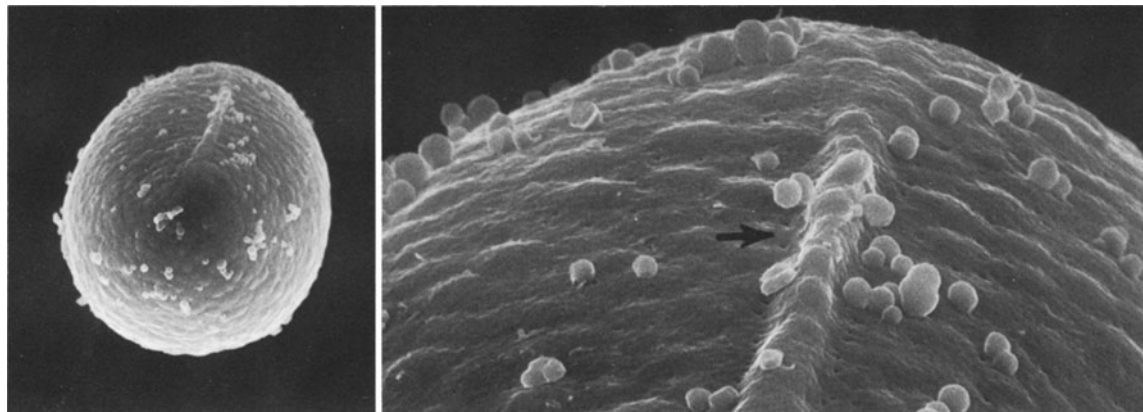
**Surface** Low tubercles, with sparsely scattered globules.

### Comments

**Characteristics** The low tuberculate surface is sparsely covered with globules, and small pits or foveolae are concentrated near the aperture (Figs. 1, 2). The spores are reported to be green with few chloroplasts when fresh, but become yellow 24–48 hours after collecting (Lloyd & Klekowski, 1970). Chandra (1978) also reports green spores, and observed that some spores germinate in the sporangium before being shed.

**Diversity** The range of the genus is probably more extensive than has been reported, for the plants are easily overlooked. They occur in large masses, as high epiphytes, in the low, tropical rain forest of Costa Rica.

1 2



**Figs. 130.1, 130.2.** *Marginariopsis wiesbaurii* (Sod.) C. Chr. spores, Costa Rica, *J.D. Smith 6941*. **1.** Low tubercles,

short aperture,  $\times 1,000$ . **2.** Surface detail with small pits especially near aperture (arrow), and globules,  $\times 5,000$ .

**Relationships** The low tubercles and globules are generally similar to those of *Pleopeltis*, *Campyloneurum*, and some *Polypodium* spores. The species is sometimes treated in *Pleopeltis* but can be distinguished by several unusual features figured in Tryon & Tryon (1982). The long receptacular system with vascular supply separated from that of other parts of the lamina, flattened rhizome, and chromosome number  $n = 35$ , as well as green spores, distinguish *Marginariopsis* from other genera in the Polypodiaceae.

## Literature

- Chandra, S. 1978. Studies on the morphology of the monotypic fern genus *Marginariopsis* (Polypodiaceae). *Brenesia* 14-15: 337-348.
- Lloyd, R.M., & E.J. Klekowski. 1970. Spore germination and viability in pteridophyta: Evolutionary significance of chlorophyllous spores. *Biotropica* 2: 129-137.
- Tryon, R.M., & A.F. Tryon. 1982. See general literature.

## 131. *Polypodium* Linnaeus

### Figs. 131.1-131.30

#### Genus

A genus of about 140 species, including *Pecluma* Price and *Thylacopteris* J. Sm., with about 100 in America.

#### Range

Largely centered in the American tropics from southern Mexico, southward in the Andes, to Peru, and in southeast Brazil. In the paleotropics centered in Asia, in South Africa, the Himalayas northeast to Japan, and in the Hawaiian Islands. The type of the genus, *Polypodium vulgare*, and closely related *P. virginianum*, form a widely distributed complex in temperate North America, Europe, and Asia.

#### Spores

Examined in 20 species.

**Size** 33-80  $\mu\text{m}$ .

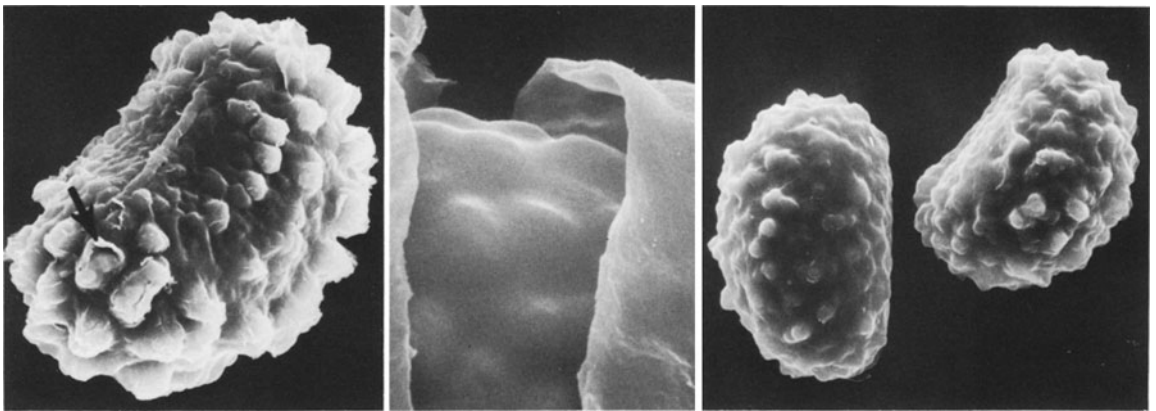
**Shape** Ellipsoidal or fusiform.

**Aperture** Monolete,  $\frac{1}{2}$  to  $\frac{3}{4}$  the length.

**Surface** Coarsely verrucate (Figs. 7, 18-23), sometimes low (Fig. 4), or tuberculate (Figs. 1, 3), or papillate (Fig. 9) with dense globules (Figs. 10-12), echinae (Figs. 15-17), or raised folds forming prominent wings (Fig. 6).

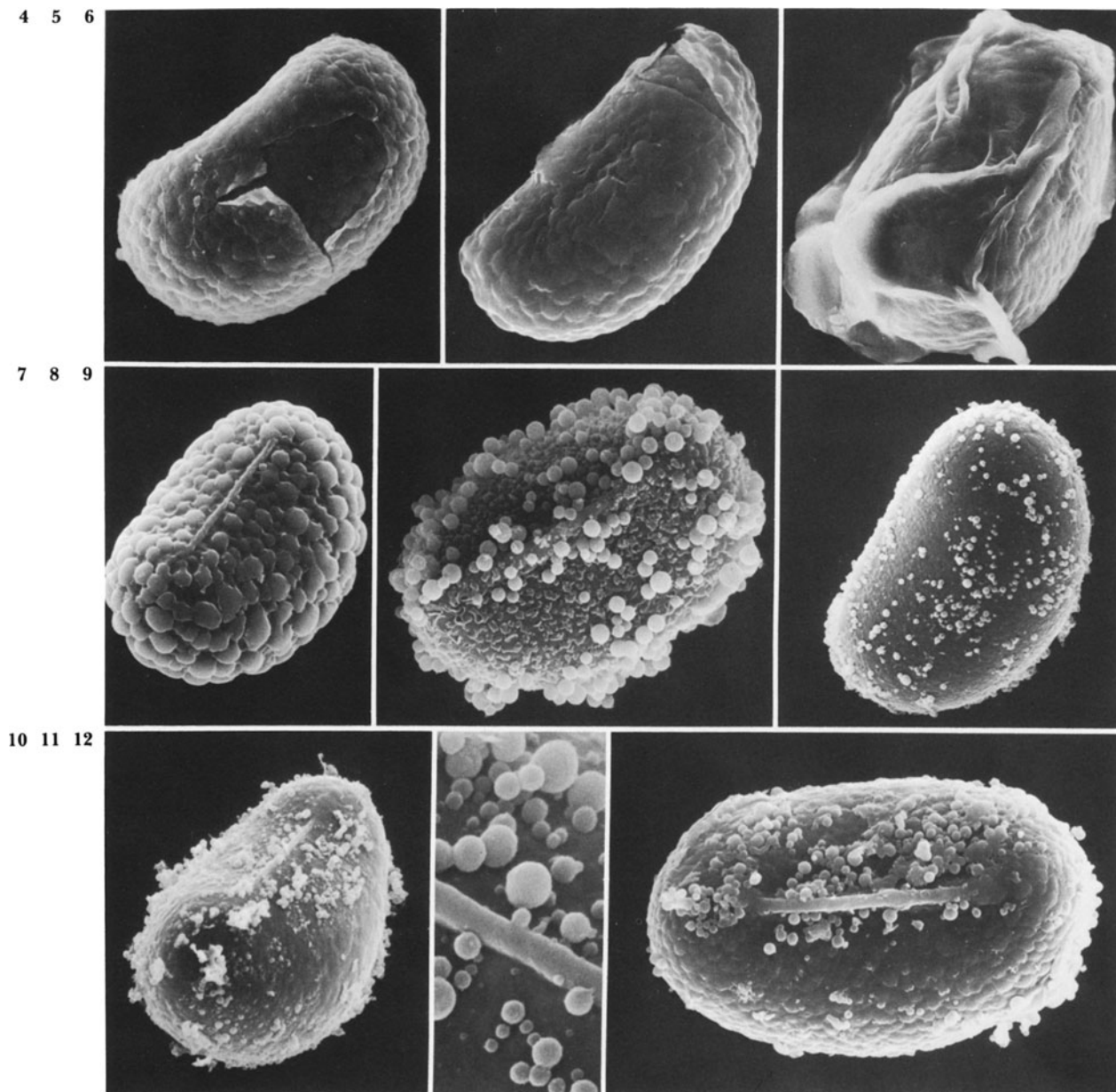
**Structure** Exospore two layered (Fig. 26), forming the surface contours (Figs. 2, 25, 27);

1 2 3



**Figs. 131.1-131.3.** *Polypodium* spores,  $\times 1,000$ . 1. *P. aureum* L., coarsely tuberculate proximal face, exospore exposed in abraded areas (arrow), Mexico, *Pringle* 2582. 2. *P. latipes* Langsd. & Fisch., low, verrucate exospore below

abraded perispore, Bolivia, *Mexia* 7797,  $\times 5,000$ . 3. *P. decumanum* Willd., coarsely tuberculate, Surinam, *Tryon & Kramer* 5604.



**Figs. 131.4–131.12.** *Polypodium* spores,  $\times 1,000$ . 4. *P. formosanum* Bak., low, verrucate exospore below abraded perispore, Formosa, *Faurie 8428*. 5. *P. amoenum* Mett., verrucate exospore below abraded perispore, Sikkim, India, *Hara et al.*, June 1960. 6. *P. sessilifolium* Desv., winged perispore folds, Ecuador, *Camp E4230*. 7. *P. curvens* Mett., verrucate, Ecuador, *Holdridge 1579*. 8. *P. minarum* Weath., dense globules on papillate perispore, Brazil, *Williams 5495*.

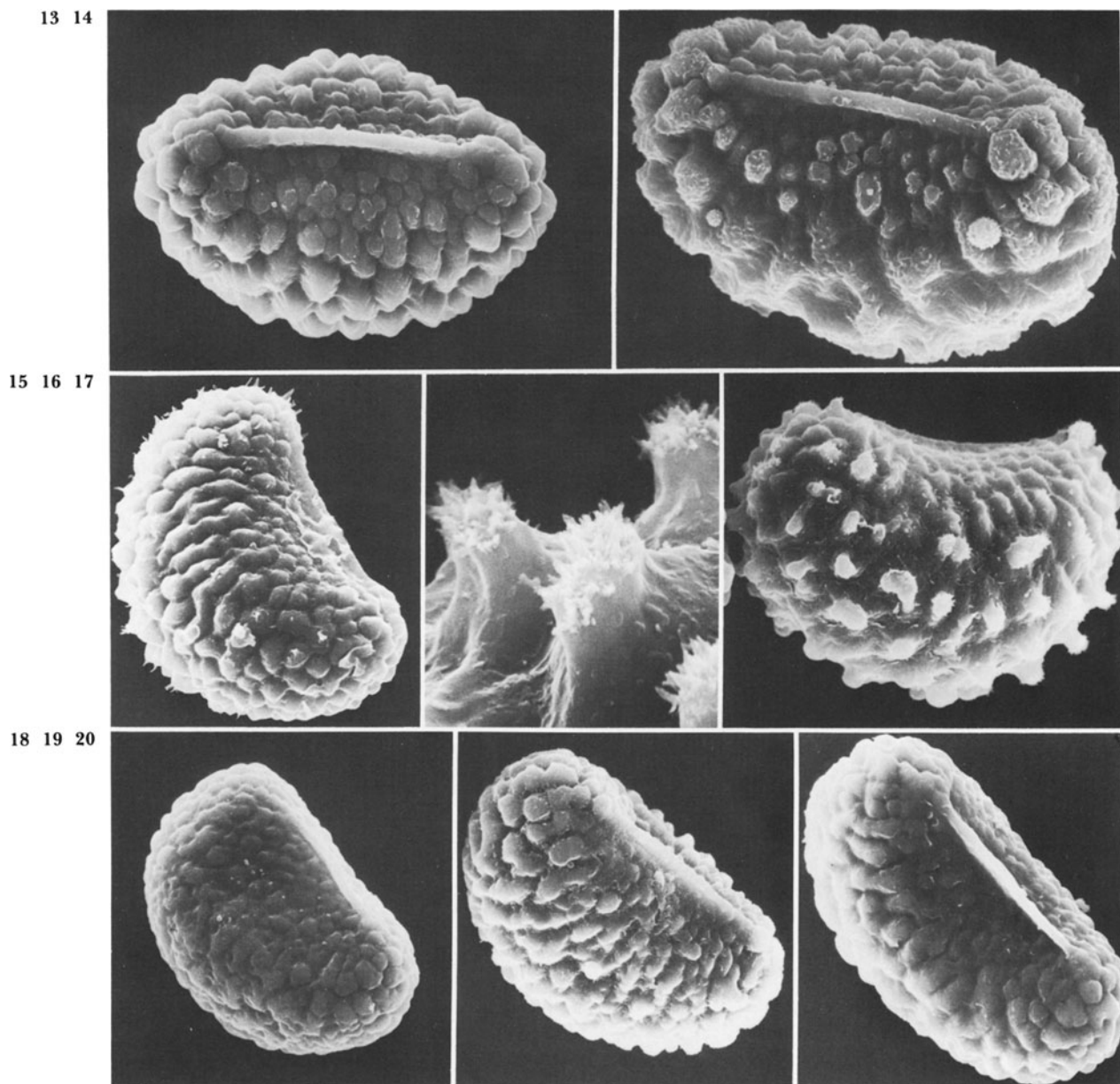
9. *P. polypodioides* (L.) Watt., globules on finely papillate surface, Peru, *Tryon & Tryon 5190*. 10, 11. *P. papillosum* Bl. 10. Dense globules at aperture, Philippines, *Elmer Dist. 1517* (L). 11. Detail of globules, part of aperture near center, Borneo, *Chew et al. 363*,  $\times 5,000$ . 12. *P. ecklonii* Kze., low, verrucate surface, abundant globules near aperture, South Africa, *Tryon & Tryon 64455*.

perispore usually thin, sometimes folded, or echinate (Figs. 27–30).

### Comments

**Characteristics, Diversity** The contours are mainly formed by low to prominent exospore verrucae or tuberculae. The thin perispore usu-

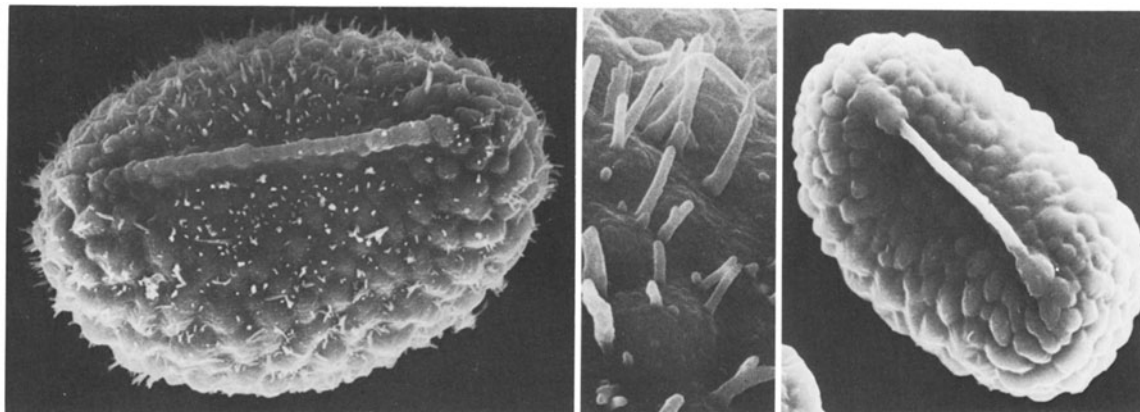
ally follows these but may be elaborated sometimes in prominent wings (Fig. 6). The echinate-tuberculate spores treated in the *Polypodium virginianum* complex (Figs. 16, 17) are sometimes recognized as characteristic of a distinct species *P. sibericum* Siplivinskij. Spores of the American *Lepidopteris* group have an elaborate



**Figs. 131.13–131.20.** Spores of the *Polypodium vulgare*-*P. virginianum* complex,  $\times 1,000$ . **13, 14.** *P. vulgare* L. **13.** Coarse tubercles, larger on distal face, Siberia, USSR, *Krylov* in 1901. **14.** Small tubercles near aperture, Sweden, *Samulson* 53. **15–17.** *P. virginianum* complex. **15.** Echininate tubercles, Amur, Manchuria, *Maak* 653. **16, 17.** Lake Bikal,

USSR., *Sokolov* 512. **16.** Detail of low, echinate tubercles,  $\times 5,000$ . **17.** Lateral aspect with discrete, echinate tubercles. **18, 19.** *P. virginianum* L. **18.** Verrucate lateral surface, Georgia, USA, *Brookout* 49. **19.** Coarsely verrucate, New Hampshire, USA, *Knowlton*, in 1902. **20.** *P. glycyrrhiza* D.C. Eaton, low verrucae, Oregon, USA, *Binns* s.n.

21 22 23



**Figs. 131.21–131.23.** *Polypodium vulgare*-*P. virginianum* complex,  $\times 1,000$ . **21, 22.** *P. amorphum* Suksd., Washington, USA, Suksdorf 2336. **21.** Prominent, slender echinae

on verrucate surface. **22.** Detail of echinae,  $\times 5,000$ . **23.** *P. fauriei* Christ, proximal face, smaller verrucae near aperture, Japan, Tagawa 8500.

perispore with abundant globules on the prominently papillate surface (Fig. 8, 24). The tufted echinate elements on the tubercles consist of coalescent stranded material (Figs. 27, 28). The long echinae of *P. amorphum* spores are more compact (Figs. 21, 22, 30).

**Relationships** Four main spore types are included in the SEM study of wall structure of Japanese Polypodiaceae (Mitui, 1977). These are based on perispore and exospore structure, and characterized by the genera *Crypsinus*, *Pyrrosia*, *Microsorium*, and *Polypodium*. The last group, described in the study as “*Polypodium* type; thick exine (over 3  $\mu\text{m}$ ) forms ornamentation and perispore is a hyaline membrane in many cases. *Loxogramma*, *Lemmaphyllum*, *Lepisorus* and *Polypodium* have spores of this type.”

Lloyd (1981) recognized three types of exospore and five major types of perispore, in a review of spores of *Polypodium* and some allied genera. Hennipman & Roos (1983) include three main types of spores in the Polypodiaceae, based on canalization, banding, and thickness of the exospore that correspond to the *Lepisorus*, *Microsorium*, and *Polypodium vulgare* types. The latter is characterized by exospore with canals only near the aperture, 1.5–2.0  $\mu\text{m}$  in thickness, and absence of both tangential bandings and microcanals. Possible connections with *Pyrrosia* are also shown in characters designated by Van Uffelen & Hennipman (1985) as the *P. principis* type with thin perispore over a nearly plain to prominently verrucate exospore, and the *P. nummulariifolia* type with perispore forming prominently raised hyaline wings.

The group of *Polypodium pectinatum* has been

recognized as *Pecluma* (Price, 1983). However, the genus is not clearly distinguished by characters such as the rhizome branching, lamina division, and paraphyses that were reported to differ from *Polypodium*. The prominently verrucate spores (Fig. 7) support treatment of the group in *Polypodium*.

*Polypodium papillosum* has been recognized in a monotypic genus *Thylacopteris* J. Sm. It is considered here in *Polypodium* on the basis of the copious globules and verrucate surface (Figs. 10, 11) although these features are clearly less prominent than in the characteristic verrucate spores of *Polypodium*.

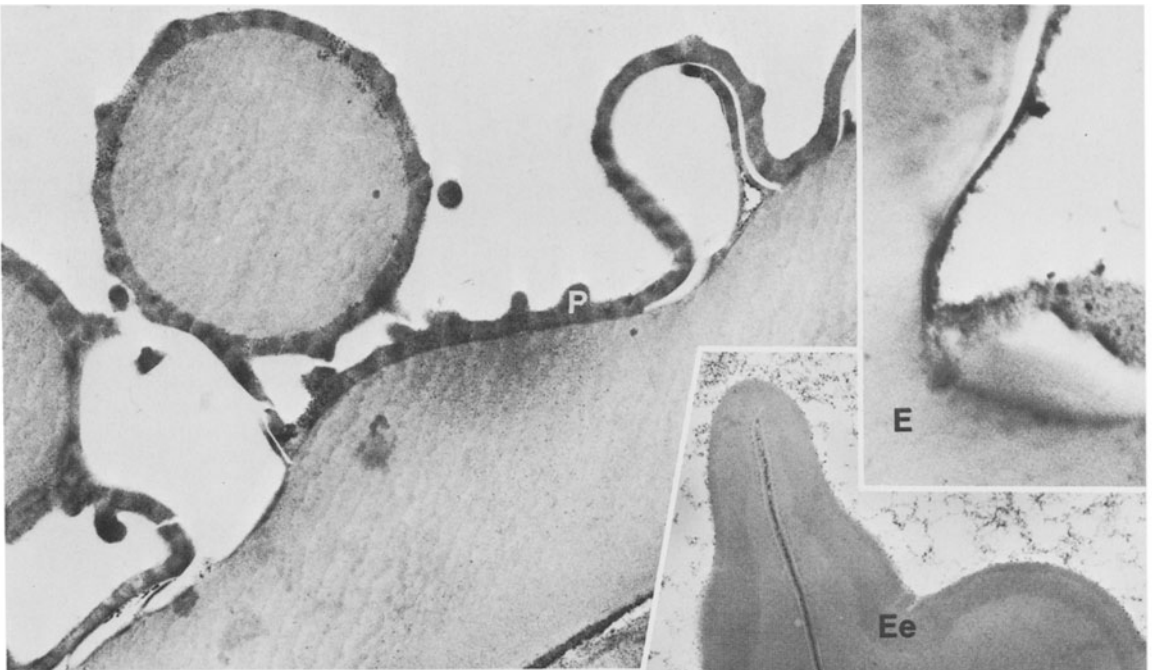
The origin and significance of spore diversity in the genus, evident in those studies as well as that shown here, will be pertinent to the systematic assessment needed for this large, conspicuous group.

## Literature

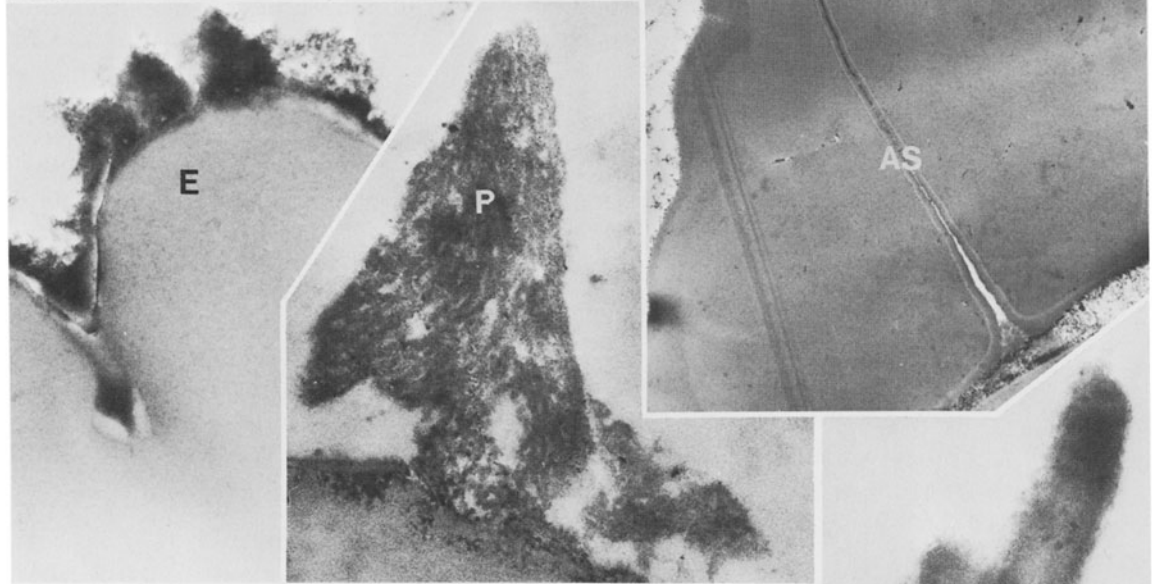
- Hennipman, E., & M.C. Roos. 1983. Phylogenetic systematics of the Polypodiaceae (Filicales). Verh. Naturwiss. Ver. Hamburg 26: 321–342.
- Lloyd, R. 1981. The perispore in *Polypodium* and related genera (Polypodiaceae). Can. J. Bot. 59: 175–189.
- Mitui, K. 1977. Spore wall structure of some Japanese species in Polypodiaceae s.st. Bull. Nippon Dent. Univ. Gen. Ed. 6: 119–124.
- Price, M.G. 1983. *Pecluma*, a new tropical American fern genus. Am. Fern J. 73: 109–116.
- Van Uffelen, G.A., & E. Hennipman. 1985. The spores of *Pyrrosia* Mirbel (Polypodiaceae): A SEM study. Pollen Spores 27: 155–198.

**Figs. 131.24–131.30.** Wall sections of *Polypodium* spores. **24.** *P. minarum*, perispore (P) with captive globules and small projections above exospore, as Fig. 8,  $\times 25,000$ . **25, 26.** *P. vulgare*, France, *Lugardon 817*. **25.** Perispore, oblique section at right, exospore (E) below,  $\times 25,000$ . **26.** Apertural area of young spore, apertural slit (As), lined with thin, inner exospore, outer exospore (Ee) forming contours,  $\times 15,000$ . **27, 28.** *P. virginianum*, *Maak 653*. **27.** Echinae above apical part of verrucate exospore (E),  $\times 15,000$ . **28.** Detail of stranded perispore echinae (P),  $\times 40,000$ . **29, 30.** *P. amorphum*, as Figs. 21, 22. **29.** Perispore (P) with spine and a captive globule slightly detached from exospore (E),  $\times 30,000$ . **30.** Detail of perispore (P) spine, above exospore (E),  $\times 50,000$ .

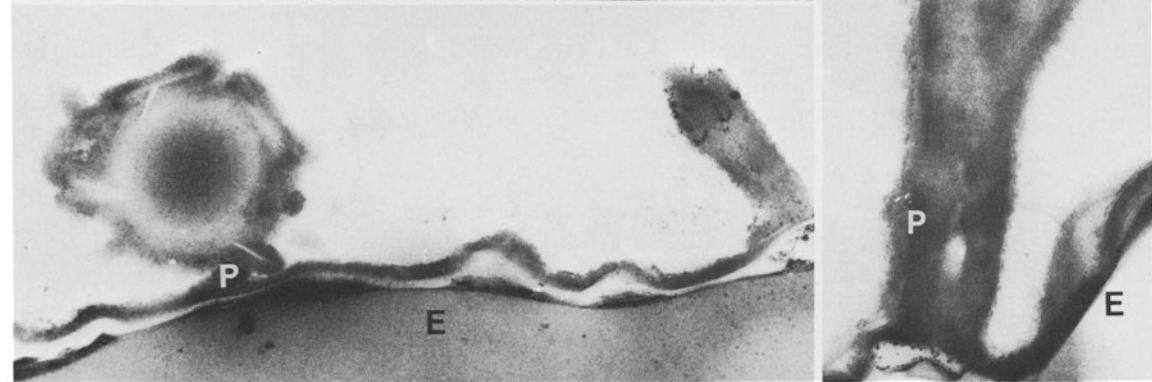
24 25



27 28 26



29 30





## 132. *Goniophlebium* (Blume) Presl

Figs. 132.1–132.9

### Genus

A paleotropical, mostly epiphytic group of about 20 species. The proposal to use the name *Schellolepis* J. Sm. for these Asiatic species (Pichi Sermolli, 1973) has recently been shown to be incorrect (Zijlstra et al., 1987). The Asiatic species *Polypodium cuspidatum* Bl. was among the species included by Presl in raising Blume's *Goniophlebium* to a genus. This has been designated as the type in treatments of Old World species of the group in the work of Copeland and others, so *Goniophlebium* is correctly applied to the paleotropical species noted below.

### Range

India, Malesia east to New Guinea, northward to the Philippines and China, southward to Australia; in the Pacific islands reaching New Caledonia, Fiji, and Samoa.

### Spores

Examined in nine species.

**Size** 32–52  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete, the aperture obscured by winged folds.

**Surface** Prominent, parallel, undulate folds above a usually verrucate exospore.

**Structure** Exospore usually with low verrucae; perispore of fibrous textured material forming the folds.

### Comments

**Characteristics, Diversity** The nearly parallel, undulate wings, formed by thickened perispore above a low verrucate exospore, are consistent in the genus (Figs. 1–7).

**Relationships** The winged form of perispore is similar to that in *Pyrrosia* and also spores of *Polypodium latipes*, and other *Polypodium* species reported by Lloyd (1981). The spores support similarities between *Polypodium* and *Goniophlebium* in other characters and suggest possible

**Figs. 132.1–132.9.** *Goniophlebium* spores,  $\times 1,000$ , except 1,  $\times 500$ , and wall sections. 1, 2. *G. percussum* (Cav.) Wag. & Greth., New Guinea, *Brass* 14032. 1. Spores with parallel, undulate wings,  $\times 500$ . 2. Parallel wings, distal face. 3. *G. percussum*, branched wings, New Guinea, *Brass* 7672. 4. *G. argutum* (Hook.) Bedd., undulate folds above verrucate exospore, Kweichow, China, *Tsiang* 5911. 5. *G. subauriculatum* (Bl.) Presl, young spores, vague verrucae under wings, Philippines, *Bartsch* 501. 6. *G. persicifolium* (Desv.) Bedd., partially fused wings, Malaya, *Molesworth-Al-len* 3484. 7. *G. verrucosum* (Hook.) J. Sm., slight verrucae below wings, Borneo, *Kostermans* 5840 (L.). 8, 9. *G. argutum*, wall sections, as Fig. 4. 8. Perispore wing of fibrous material, separated from exospore (E),  $\times 9,000$ . 9. Slightly undulate exospore (E) below perispore thinner between wings,  $\times 8,000$ .

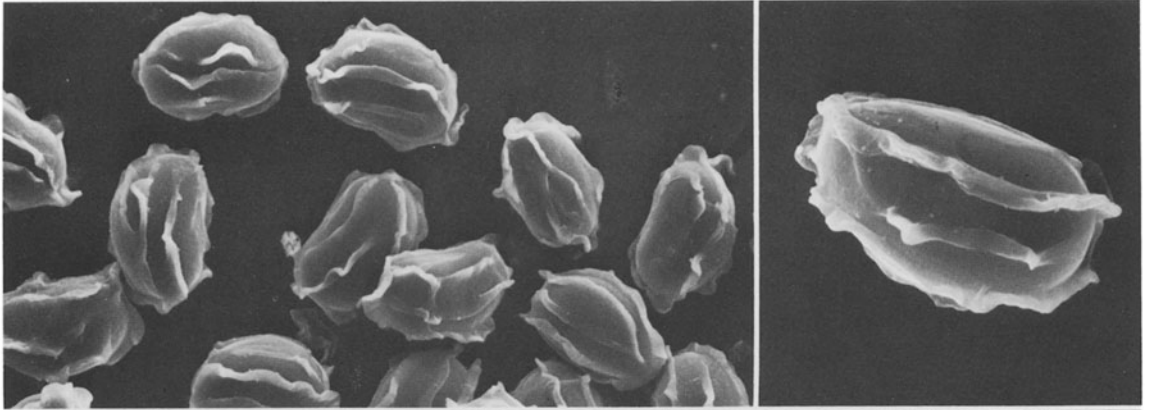
connections between the genera. Spores of *Pyrrosia* species, in the *P. nummulariifolia* group, shown in the spore study of Van Uffelen & Hennipman (1985), have strongly projecting wings. However, they are distinguished from most spores of *Goniophlebium* by the plain exospore or the verrucate surface formed by perispore.

Spores from the Neogene (Late Tertiary) of New Guinea with prominent parallel wings are similar to these. They have been recognized as *Stenochlaenidites papuanus* (Cookson) Khan (Playford, 1982). The size and surface of the fossil material clearly correspond to spores of *Goniophlebium* species, several of which presently occur in New Guinea.

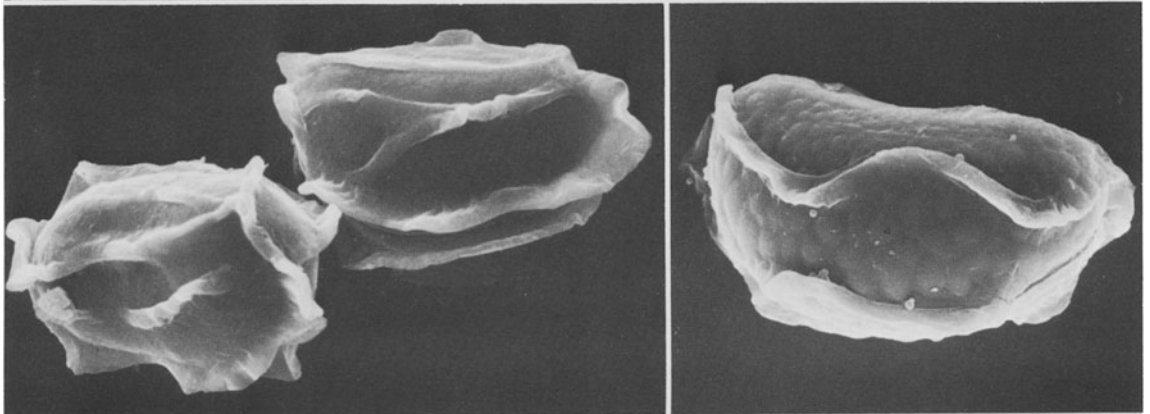
### Literature

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- Playford, G. 1982. Neogene palynomorphs from Huon peninsula, Papua, New Guinea. *Palynology* 6: 29–54.
- Van Uffelen, G.A., & E. Hennipman. 1985. The spores of *Pyrrosia* Mirbel (Polypodiaceae): A SEM study. *Pollen Spores* 27: 155–198.
- Zijlstra, G., R. Tryon, & G. Rödl-Linder. 1987. Correct application of *Goniophlebium* (Polypodiaceae). *Taxon* 36: 759.

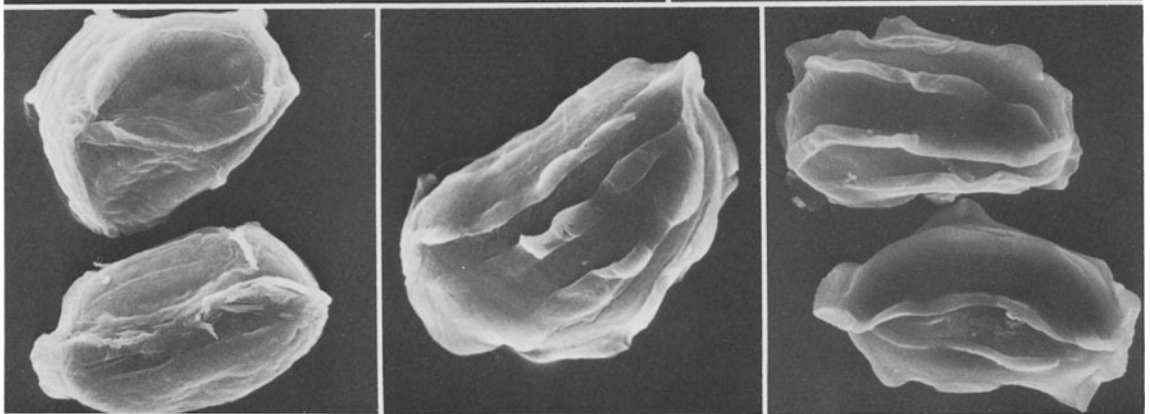
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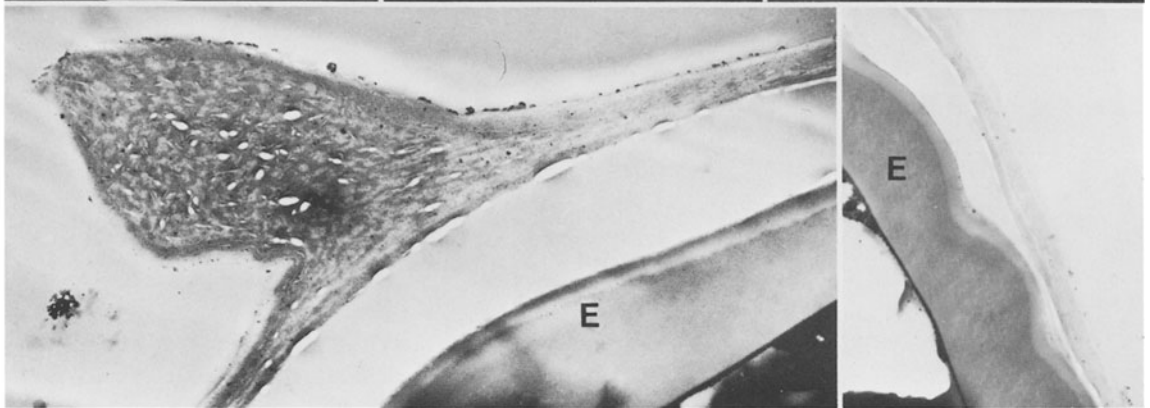
3 4



5 6 7



8 9



### 133. *Solanopteris* Copeland Figs. 133.1–133.7

#### Genus

An epiphytic genus of tropical America, with three or four species.

#### Range

Costa Rica, south to Cuzco and Madre de Dios, Peru.

#### Spores

Seven collections examined of two species.

**Size** 50–60  $\mu\text{m}$ .

**Shape** Ellipsoidal.

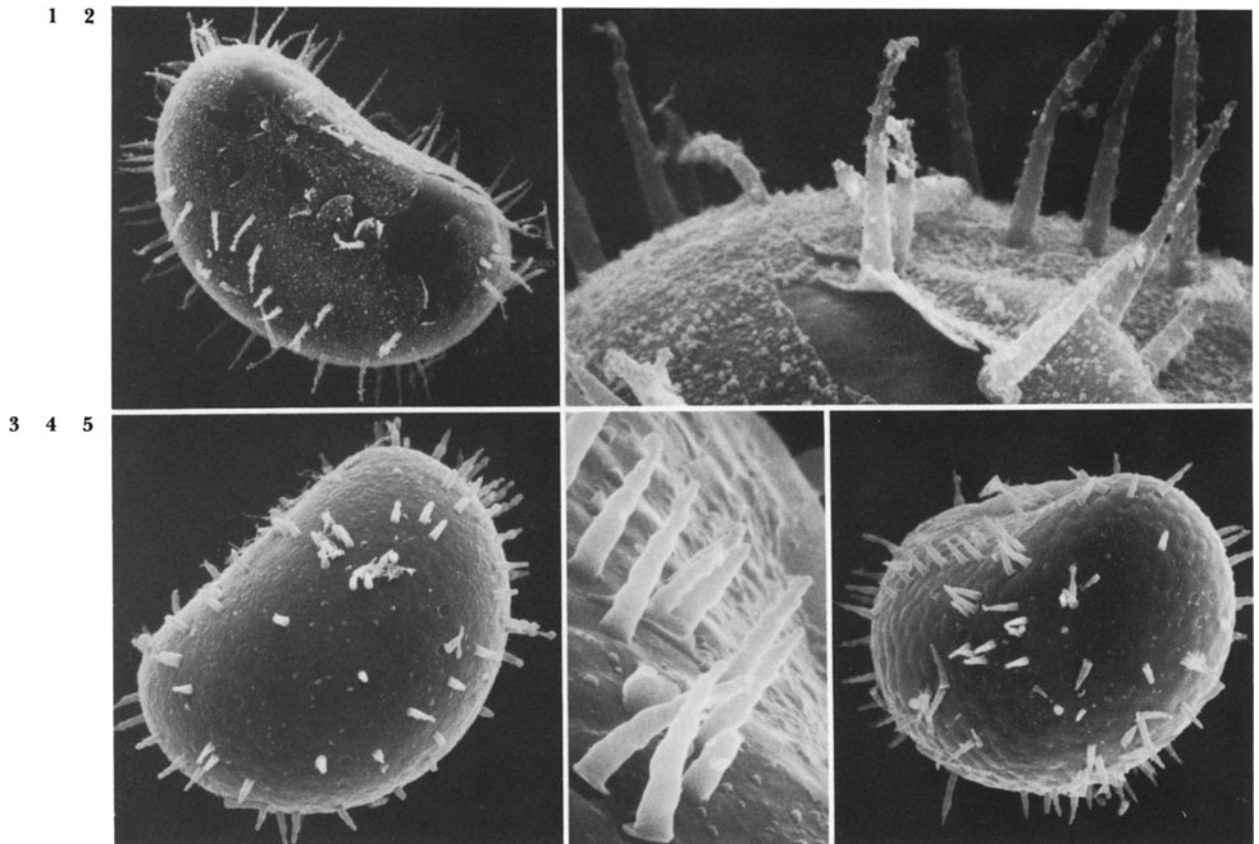
**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{1}{3}$  the length.

**Surface** Low tuberculate to papillate, with prominent echinae.

**Structure** Plain exospore readily separating from the thin perispore that forms the surface and echinae.

#### Comments

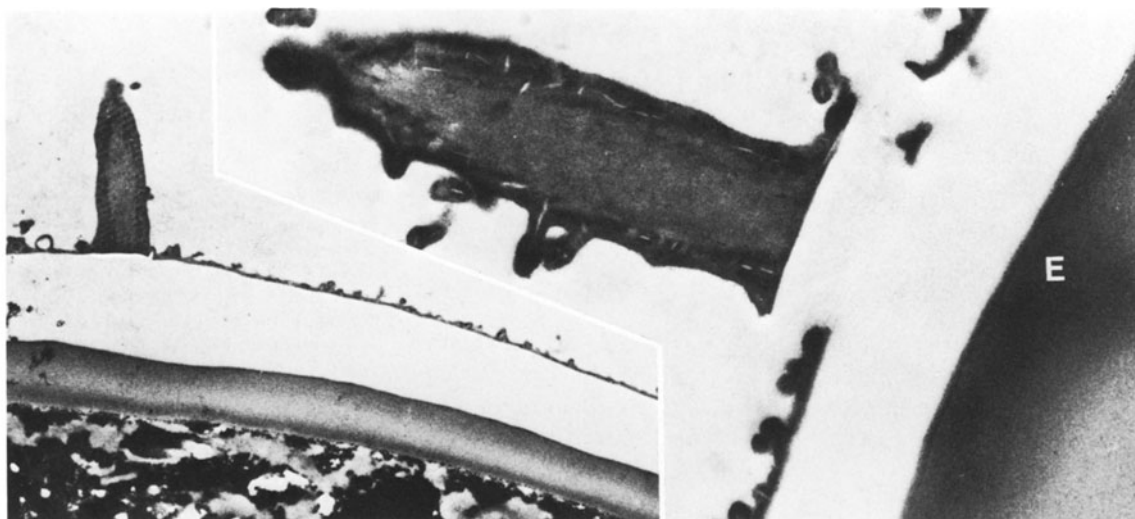
**Characteristics, Diversity, Relationships** The echinae have a central striated zone and are covered by an irregular, thin surface similar to that of the continuous perispore layer (Figs. 1, 2, 6, 7). Spores of *Solanopteris brunei* from Costa Rica and Panama have somewhat shorter, beaded echinae (Figs. 3–5). Rauh (1973) reports that spores of *S. bismarckii* have short spines. Although these are from Peruvian collections, they more closely resemble spores of Central



**Figs. 133.1–133.5.** *Solanopteris* spores,  $\times 1,000$ , and wall sections. 1, 2. *S. bifrons* (Hook.) Copel., Ecuador, *Del Tredici*, Feb. 1983. 1. Short aperture, long, acute spines. 2. Abraded surface of thin perispore forming irregular papillate spines, undulate exospore below,  $\times 5,000$ . 3–5. *S. bru-*

*nei* (Christ) Wagner. 3. Lateral surface with short, beaded spines, Panama, *Correa* 2013. 4, 5. Costa Rica, *Gómez* 3437. 4. Detail of beaded spines,  $\times 5,000$ . 5. Shallowly tuberculate surface below beaded spines.

6 7



**Figs. 133.6, 133.7.** *Solanopteris bifrons* wall sections, as Figs. 1, 2. 6. Slightly undulate exospore, below raised perispore with spine,  $\times 7,500$ . 7. Detail of longitudinal section of

perispore spine with diffuse, striate central area, above exospore (E),  $\times 25,000$ .

American plants than those of the Ecuadorian *S. bifrons*.

*Solanopteris* is a genus of myrmecophytic plants, often with tuberous stems that may be inhabited by ants, largely of the genus *Azteca*. Field studies on plants of Costa Rica report these and other insects inhabit the potatolike tubers (Gómez, 1974).

Transport of *Solanopteris* spores by ants needs to be confirmed by field observation. However, the long echinate elements in these spores may well be adaptations relating to insect dispersal, or other factors as in some species of *Lecanopteris* (Tryon, 1985, 1986).

## Literature

- Gómez, L.D. 1974. Biology of the potato fern, *Solanopteris brunei*. *Brenesia* 4: 37–61.
- Rauh, W. 1973. *Solanopteris bismarckii* Rauh. *Abhan Akd. Wiss. Lit. Mainz. Math-Natur. Kl.*: 223–256. (*Trop. Subtrop. Pflanzenwelt.* 5: 5–38).
- Tryon, A.F. 1985. Spores of myrmecophytic ferns. *Proc. R. Soc. Edinb.* 86B: 105–110.
- Tryon, A.F. 1986. Stasis, diversity and function in spores based on an electron microscope survey of the Pteridophyta. In S. Blackmore & I. Ferguson (Eds): *Pollen and spores: form and function*, pp. 233–249. *Linn. Soc. Symp. Ser.* 12, 233–249.

## 134. *Arthromeris* (Moore) J. Smith

### Figs. 134.1–134.11

#### Genus

A paleotropical genus of nine or fewer species, treated by R.C. Ching (1933).

#### Range

In the Sikkim Himalayas and southwestern China, one species reaching Taiwan, perhaps one in New Guinea, and another in the Philippines.

#### Spores

Examined in four species.

**Size** 40–50  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{1}{4}$  to  $\frac{1}{3}$  the length.

**Surface** Tuberculate or verrucate, usually with dense echinae.

**Structure** Exospore plain; perispore of one layer forming verrucae and echinae, sometimes cavate.

#### Comments

**Characteristics, Diversity, Relationships** The surface varies from low tuberculate in *Arthromeris lehmannii* (Figs. 4, 5) to coarsely verrucate in *A. himalayensis* (Figs. 8, 9), and is usually echinate. The echinae may be prolonged or beaded, as in *A. tenuicauda* (Figs. 1, 2), or sparse

**Figs. 134.1–134.11.** *Arthromeris* spores,  $\times 1,000$ , and wall sections. **1–3.** *A. tenuicauda* (Hook.) Ching, Yunnan, China, *Tsai 54920*. **1.** Densely echinate young spore. **2.** Detail of irregular, beaded echinae,  $\times 5,000$ . **3.** Old spore with sparse, eroded echinae. **4, 5.** *A. lehmannii* (Mett.) Ching, Yunnan, China, *Tsai 58472*. **4.** Dense echinae on irregular verrucae. **5.** Detail of verrucate surface with echinae,  $\times 5,000$ . **6, 7.** *A. wallichiana* (Spreng) Ching, E. Nepal, *Hara et al. 6302025*. **6.** Verrucate contours. **7.** Detail of verrucae with prolonged echinae,  $\times 5,000$ . **8, 9.** *A. himalayensis* (Hook.) Ching, E. Nepal, *Hara et al. 6302019*. **8.** Short echinae on coarse tubercles. **9.** Detail of echinate tubercles,  $\times 5,000$ . **10, 11.** Wall sections. **10.** *A. lehmannii*, exospore (E) below perispore tubercle, Yunnan, *Ching 21434*,  $\times 16,000$ . **11.** *A. wallichiana*, exospore below cavate perispore, as in Figs. 6, 7,  $\times 20,000$ .

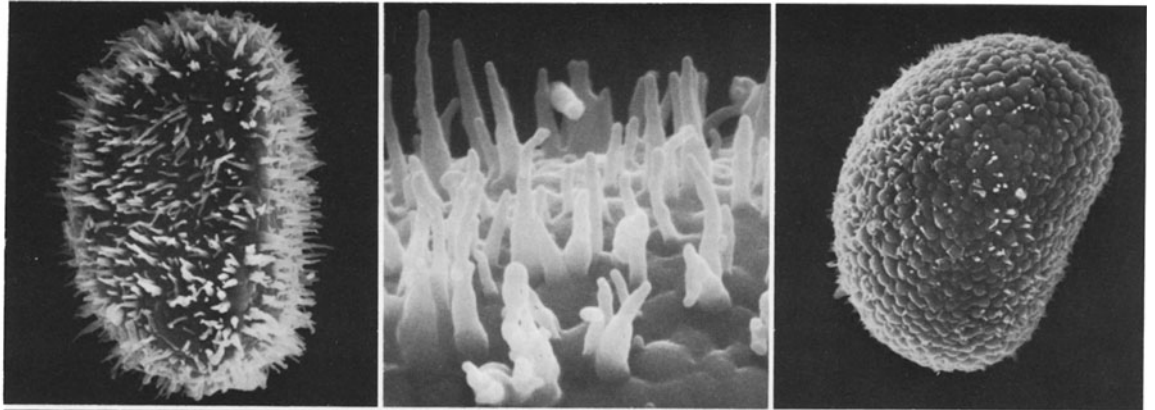
and eroded in older spores (Figs. 3, 7). Size differences between *A. tenuicauda* and the smaller spores of *A. lehmannii* or *A. wallichiana* (Figs. 4–6) suggest there are different ploidy levels.

Ching transferred several species from *Polypodium* to *Arthromeris* in studies of the genus in China, and regarded this as more closely related to *Drynaria* than to *Polypodium*. *Arthromeris himalayensis* is one of the most distinctive species, and the unusual, coarsely verrucate spores (Figs. 8, 9) support this assessment.

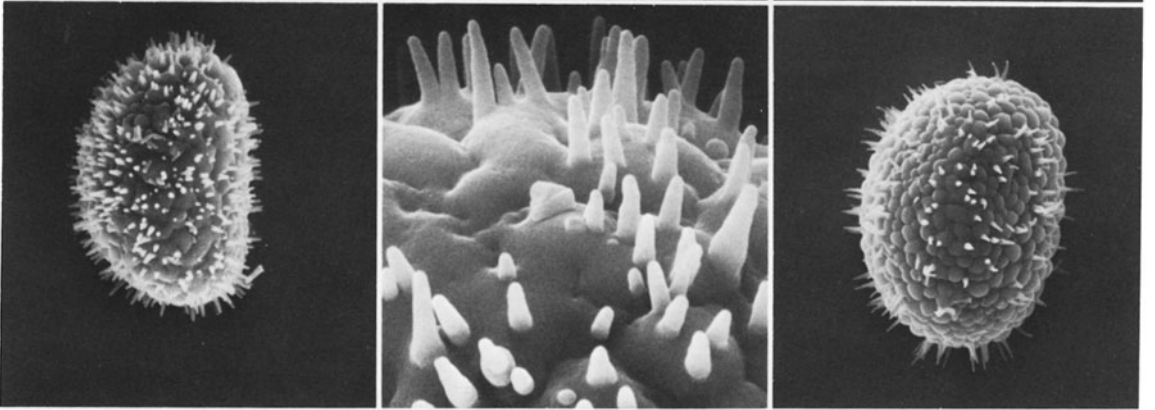
#### Literature

Ching, R.C. 1933. The studies of Chinese ferns 11. *Contrib. Inst. Bot. Natl. Acad. Peiping* 2: 31–100.

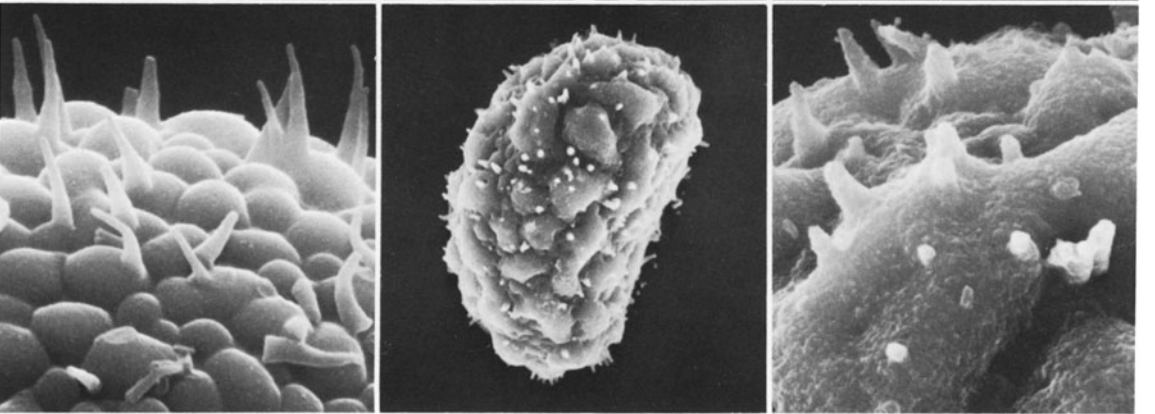
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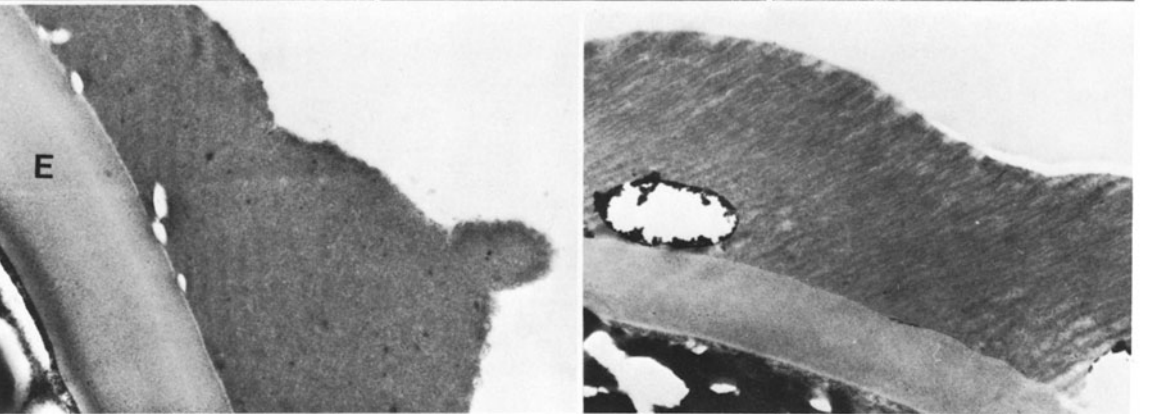
4 5 6



7 8 9



10 11



E

## 135. *Selliguea* Bory

### Figs. 135.1–135.11

#### Genus

A small paleotropical genus that includes species formerly treated in *Crypsinus* Presl and in *Polypodium* L.

#### Range

Centered in southeast Asia and Malesia; in India northward to Indochina and the Philippines, eastward to New Guinea; in the Pacific extending to Fiji, Samoa, and the Marquesas.

#### Spores

Examined in 11 species.

**Size** 38–80  $\mu\text{m}$ .

**Shape** Ellipsoidal, the ends often obtuse.

**Aperture** Monolete,  $\frac{1}{3}$  to  $\frac{3}{4}$  the length.

**Surface** More or less verrucate with prominent, often blunt (Figs. 7–9) or attenuate echinae (Figs. 5, 6).

**Structure** Exospore plain; perispore of one layer, forming the papillae and prominent echinae (Figs. 10, 11).

#### Comments

**Characteristics, Diversity** Sparse to dense echinate elements that project from a usually low, verrucate surface are formed by the perispore (Figs. 1–3, 8, 10). The study of spores of Japanese species in *Crypsinus*, including *C. hastatus* (Thunb.) Copel., *C. veitchii* (Bak.) Copel. and *C. yakushimensis*, also shows that the spines are formed by the thin, outer perispore (Mitui, 1977). Prolongation of the papillae in *Selliguea* spores may relate to insect associations, as it does in other epiphytic genera such as *Lecanopteris* and *Solanopteris*. Specimens of *Selliguea*, especially the sori, often show depredation by insects. Ants that occur in the stems invade small chambers formed by a cylinder of scales surrounding the stem (Tryon, 1985). Field observations on the association of these plants and insects and study of variation of the papillate spores are needed to establish the extent and effect of myrmecophytic relations.

**Figs. 135.1–135.11.** *Selliguea* spores,  $\times 1,000$ , and wall sections. **1.** *S. pedunculata* Presl, sparsely echinate, Assam, India, Lyell s.n. (donor). **2.** *S. (Polypodium) crassisorum* C. Chr., densely echinate distal face, New Guinea, Brass 4201. **3.** *S. (Crypsinus) quasidivariata* (Hayata) Copel., low verrucae with sparse, blunt echinae, Formosa, Kramer et al. 7785. **4.** *S. feeioides* Copel., detail of slightly prolonged papillae, and likely globules, Marquesas, Gillett 2146. **5.** *S. (Crypsinus) yakushimensis* (Makino) Tagawa, irregularly echinate, Japan, Iwatsuki 3340. **6.** *S. feei* Bory, detail of echinae, Java, Smith, in 1899,  $\times 5,000$ . **7, 8.** *S. (Polypodium) bellisquamatum* C. Chr., New Guinea, Van Royen 5928. **7.** Detail of papillae,  $\times 5,000$ . **8.** Various prolonged papillae on verrucate surface. **9.** *S. (Polypodium) ferreum* (Brause) Copel.; (*Oleandropis ferrera* (Brause) Copel.), coarse echinae with capitate apices, New Guinea, Eyma 4406. **10, 11.** *S. (Polypodium) bellisquamatum* wall sections, as Figs. 7, 8. **10.** Low, verrucate perispore with papillae above plain exospore,  $\times 15,000$ . **11.** Detail of perispore with scales adjacent to exospore (E),  $\times 50,000$ .

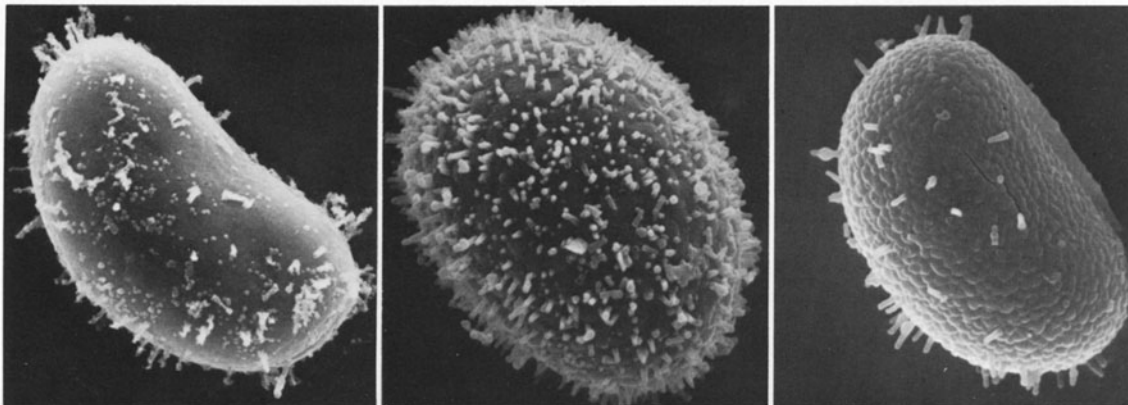
**Relationships** Copeland (1947), in a lengthy review of *Crypsinus*, noted the need for examination of the boundaries of *Crypsinus* and *Selliguea*. On the basis of the venation *Selliguea* was considered to be derived from *Crypsinus*. Similarities in the form and development of the spore surface in *Crypsinus* support its inclusion within *Selliguea*.

Spores recognized as *Polypodioidites* from the Late Tertiary of New Guinea have similar coarsely verrucate surfaces that may relate to recent species of *Selliguea* from the same island (Playford, 1982). Absence of echinae in the fossil spores may be due to erosion in preparation of the specimens.

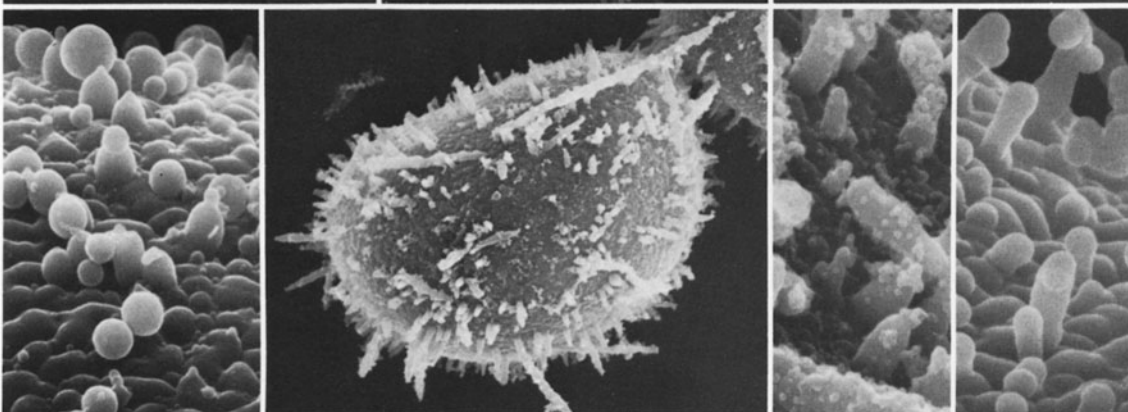
#### Literature

- Copeland, E.B. 1947. See general literature.  
 Mitui, K. 1977. Spore wall structure of some Japanese species in Polypodiaceae s.st. Bull. Nippon Dent. Univ., Gen. Ed. 6: 119–124.  
 Playford, G. 1982. Neogene palynomorphs from the Huon Peninsula, Papua, New Guinea. Palynology 6: 29–54.  
 Tryon, A.F. 1985. Spores of myrmecophytic ferns. Proc. R. Soc. Edinb. 86B: 105–110.

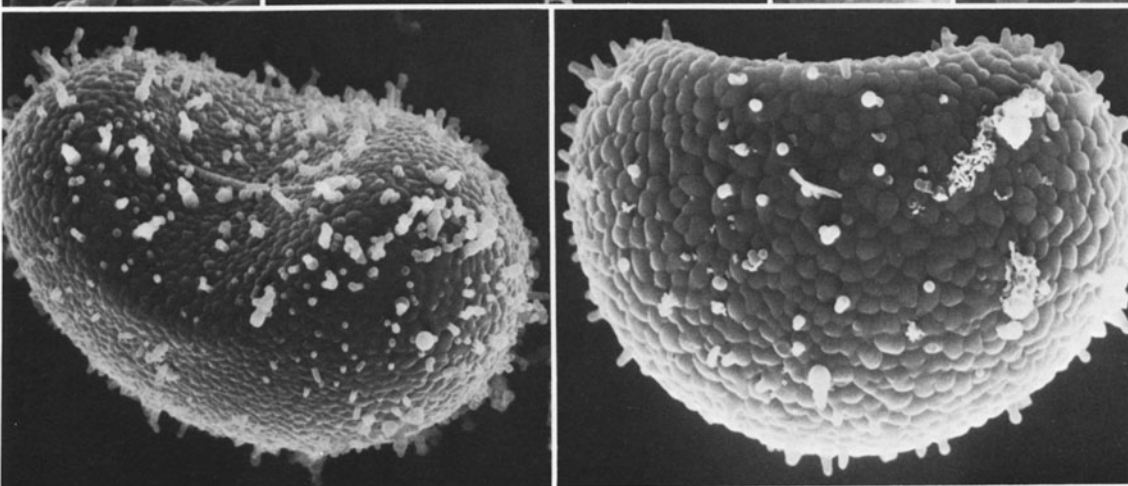
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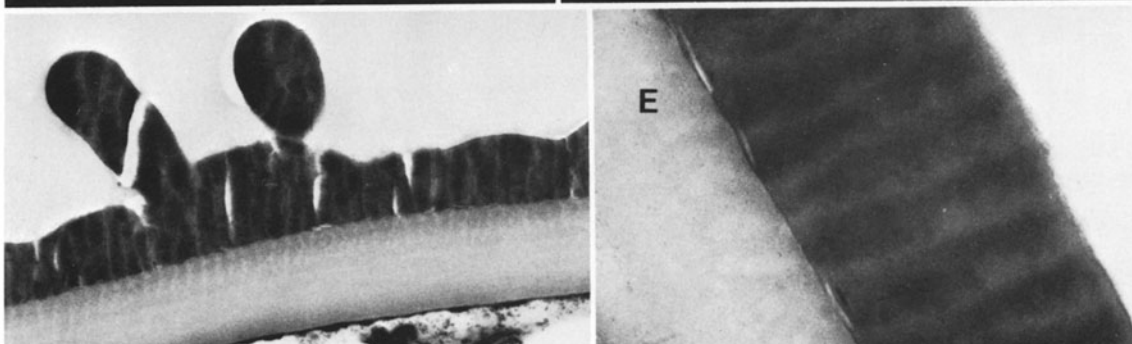
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8 9



10 11





## 136. *Anarthropteris* Copeland

**Figs. 136.1–136.4**

### Genus

A monotypic genus based on *Anarthropteris lanceolata* (Hook. f.) L. B. Moore.

### Range

New Zealand.

### Spores

Examined in two collections.

**Size** 55–70  $\mu\text{m}$ .

**Shape** Ellipsoidal.

**Aperture** Monolete,  $\frac{2}{3}$  the length.

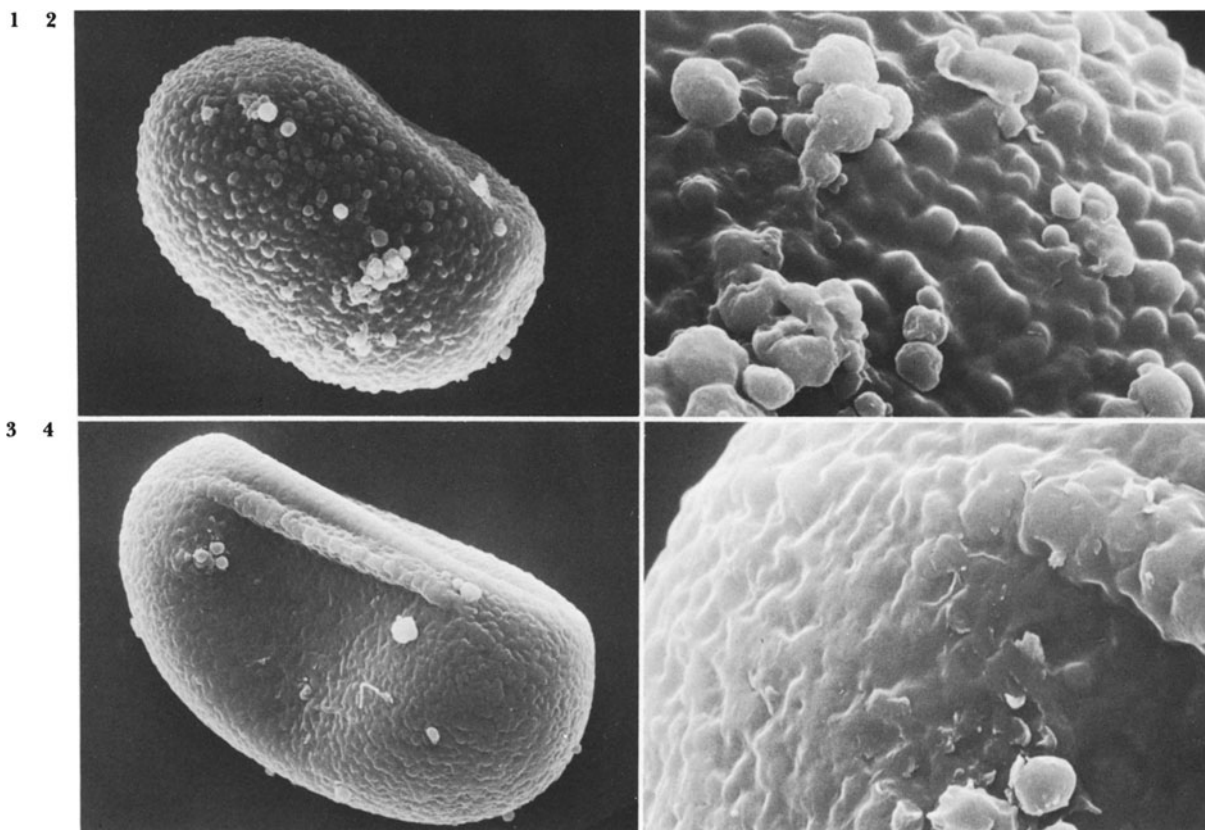
**Surface** Papillate to somewhat rugate with scattered, irregular globules.

### Comments

**Characteristics, Diversity, Relationships** The prominently papillate (Figs. 1, 2) or low rugate

(Figs. 3, 4) surface is formed by a thin outer layer bearing globules. This surface is generally similar to that of *Loxogramme* spores, although the aperture is consistently linear. The shape and surface are common to spores of several genera of Polypodiaceae.

*Anarthropteris* is placed in the Polypodiaceae by Copeland. It is treated along with *Loxogramme* in the Loxogrammaceae, by Pichi-Sermolli (1975), and among the genera of the Grammitidaceae according to Brownsey et al. (1985). It is not clear from present evidence which of these associations of *Anarthropteris* best reflects its natural alliances. The usually simple type of perispore suggests basic connections among the Polypodiaceae, Loxogrammaceae, and Grammitidaceae. The relatively simple spores in many genera of these families clearly contrast with the elaborated forms of perispore



**Figs. 136.1–136.4.** *Anarthropteris lanceolata* (Hook. f.) L. B. Moore, New Zealand,  $\times 1,000$ . 1, 2. Parris & Keen, in 1966. 1. Papillate distal face. 2. Detail of papillae and

scattered globules,  $\times 5,000$ . 3, 4. Prince, in 1898. 3. Rugate surface, broad aperture. 4. Detail of shallow rugae,  $\times 5,000$ .

in the Dryopteridaceae, Thelypteridaceae, and Blechnaceae.

### Literature

Brownsey, P.J., D.R. Given, & J.D. Lovis. 1985. A revised classification of New Zealand Pterido-

phytes with a synonymic checklist of the species. *N. Z. J. Bot.* 23: 431–489.  
Pichi-Sermolli, R.E.G. 1975. *Fragmenta Pteridologie*. 5. *Webbia* 29: 1–16.

## 137. *Loxogramme* (Blume) Presl Figs. 137.1–137.9

### Genus

A mostly paleopantropical genus of about 35 species, ranging into temperate areas, with one species in America.

### Range

In America from southern Mexico to Panama; in tropical Africa and Madagascar, extending to India, northward to China and Japan, and eastward to New Guinea; in the Pacific to Tahiti.

### Spores

Examined in eight species.

**Size** 50–90  $\mu\text{m}$ .

**Shape** Globose or ellipsoidal.

**Aperture** Trilete sometimes with unequal arms,  $\frac{1}{8}$  to  $\frac{3}{4}$  the radius, or monolete,  $\frac{1}{4}$  to  $\frac{2}{3}$  the length.

**Surface** Papillate to somewhat rugate or tuberculate with globules on and below the surface.

**Structure** Exospore forms the surface contours; perispore usually thin, laminate, some parts thickened (Figs. 8, 9).

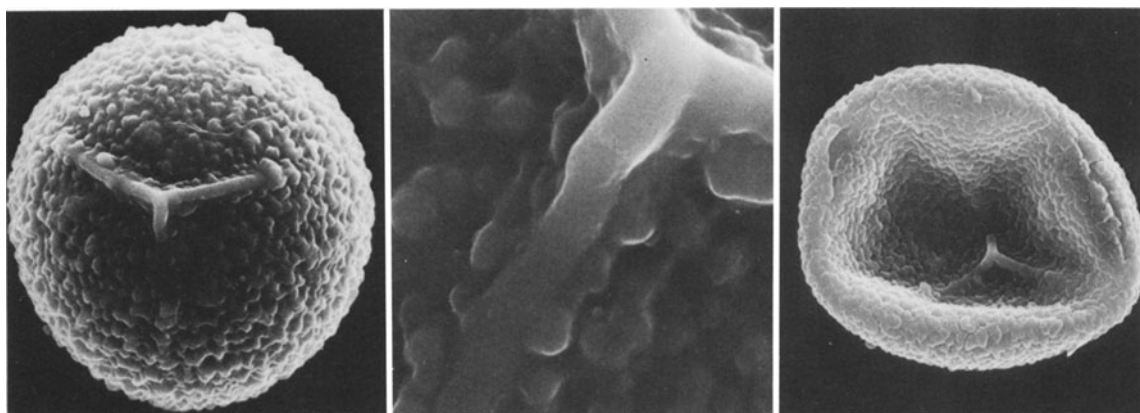
### Comments

#### *Characteristics, Diversity, Relationships*

*Loxogramme* spores have diverse forms of aperture varying from triradiate to linear. The length and angle of the aperture arms may also vary sometimes in the same species or within spores of the same sporangium. (Figs. 1–3).

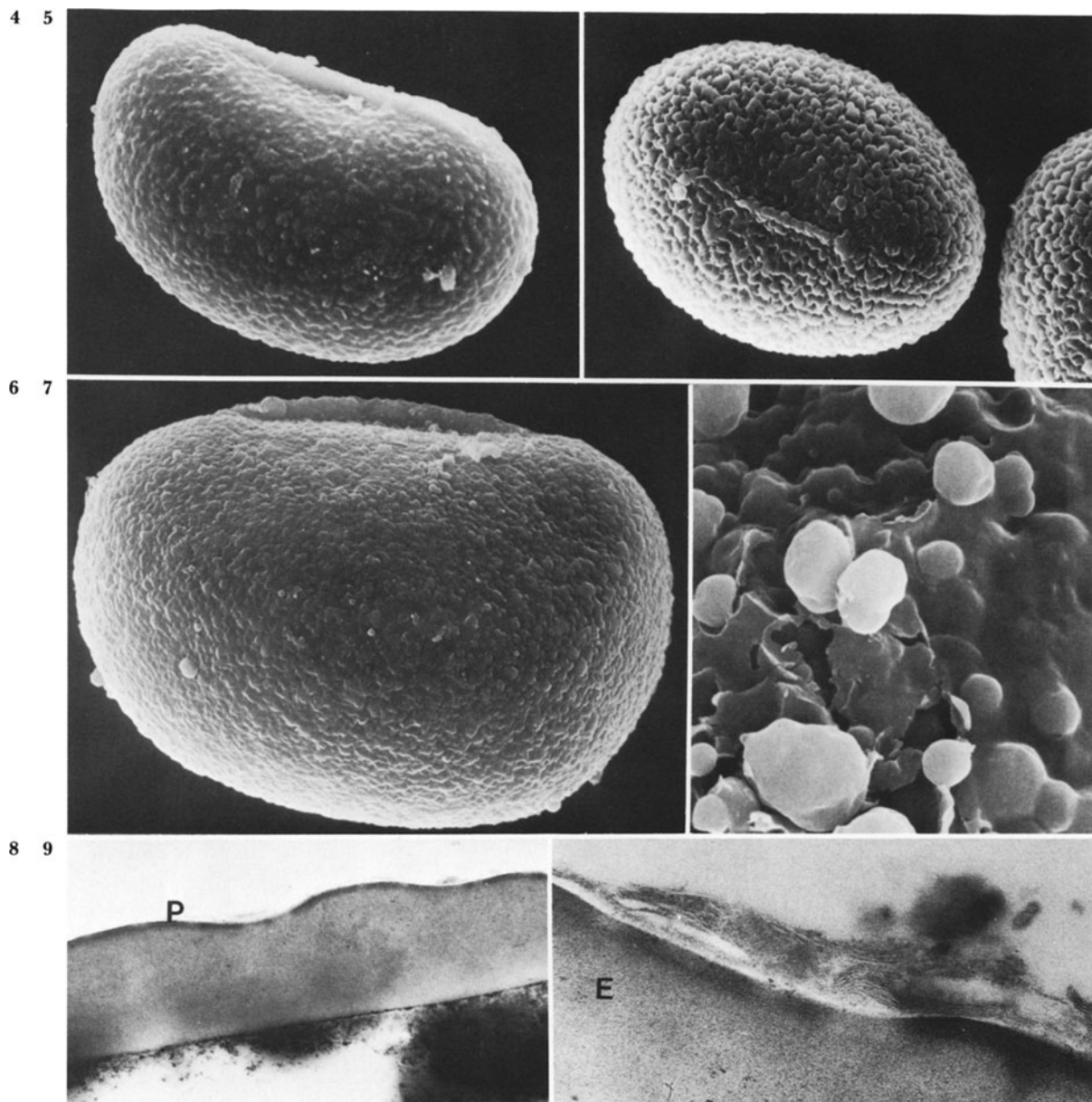
Spores of some Asiatic species are about one fourth as large as the spore of *Loxogramme mexicana* from Veracruz and may reflect different ploidy levels in the species, although gametophyte development within unopened spores

1 2 3



**Figs. 137.1–137.3.** *Loxogramme* spores,  $\times 1,000$ . 1, 2. *L. chinensis* Ching, Yunnan, China, *Tsai* 62620. 1. Globose, trilete, one of the aperture arms depressed below surface. 2. Detail of depressed short arm,  $\times 5,000$ . 3. *L. subcostata*

(Hook.) C. Chr. depressed proximal face with irregular aperture in incompletely filled spore, Thailand, *Tagawa et al.* T5574.



**Figs. 137.4–137.9.** *Loxogramme* spores,  $\times 1,000$ , and wall sections. 4. *L. porcata* Price, linear aperture, low papillate, India, Hara et al. 2162. 5. *L. saziran* Tagawa ex Price, coarsely papillate, monolete, Japan, Furuse, in 1960. 6. *L. mexicana* (Fée) C. Chr., large papillate spore, Veracruz, Mexico, Copeland, Mex. Ferns 156. 7. *L. subselliguea* (Bak.)

Alston, globules on and within perispore, New Guinea, Womersley NGF 8941,  $\times 5,000$ . 8, 9. *L. chinensis*, wall sections, as Figs. 1, 2. 8. Discrete, thin perispore (P) above undulate exospore,  $\times 20,000$ . 9. Varied thickness of laminate perispore above exospore (E),  $\times 65,000$ .

may account for the exceptionally large spore size. The globules are usually on but may be enveloped by the perispore (Fig. 7). The coarsely rugate spores (Figs. 4–6) resemble those of some species in *Colysis*, *Lepisorus*, and *Microsorium*.

Trilete to monolete forms of aperture were observed in three species of *Loxogramme* from Assam (Nayar, 1963). A shorter arm length was correlated with an increase in the angle of arm divergence to  $180^\circ$ . The type of aperture was

examined in spores of 20 species of *Loxogramme* (Chang, 1963). These were trilete in 11 species and monolete in nine. The trilete spores were assessed as primitive, similar to or probably derived from the type in *Grammitis*. Chang considered *Loxogramme* to be more closely related to the Grammitideaceae than to the Polypodiaceae based on palynological evidence.

On the basis of revisionary studies of *Loxogramme*, the genus is regarded by M.G. Price (pers. comm.) to be more closely allied with

others in the Polypodiaceae. He also regards the linear form of aperture, characteristic of spores of the Polypodiaceae, as representing a less derived spore type, and the trilete one a specialized form in *Loxogramme*.

The triradiate aperture, rugate to verrucate surface, and thin perispore of *Loxogramme* spores do not support recognition of a distinct family.

## Literature

- Chang, Y.L. 1963. Studies in the spore morphology of *Loxogramme* Presl. Acta Bot. Sinica 11: 26–37.  
Nayar, B.K. 1963. Spore morphology of *Loxogramme*. Grana Palynol. 4: 388–391.