

POLLEN MORPHOLOGY AND EVOLUTION OF THE GENUS *HARPULLIA*
(SAPINDACEAE – HARPULLIEAE)*

J. MULLER †

Rijksherbarium, Leiden, The Netherlands

CONTENTS

Summary	161
1. Introduction	162
2. Materials and methods	162
3. General morphology	162
4. Systematic descriptions	167
5. Pollen types	175
6. Pollen morphology and taxonomy	177
7. Evolution: a. Introduction – b. Functional pollen morphology – c. Character analysis – d. Phylogenetic values – e. Phylogeny	178
8. Conclusions	191
Acknowledgements	193
References	193
Explanation of plates I–XIX	194

SUMMARY

The pollen morphology of 20 out of 26 species at present recognised in *Harpullia* is described. Laminations in the endexine and the presence of a mixed endexine-ectexine layer are demonstrated with TEM sections. Four pollen types, one of which can be subdivided into 8 subtypes, are distinguished and related to each other. The functional morphology and phylogeny of these types is compared with macromorphologic, ecologic and geographic evidence and expressed in a cladogram. The genus probably originated in East Gondwanaland and secondarily invaded South-east Asia. Its position within Harpullieae is briefly discussed.

* The textual part of the present paper was completed before the sudden death of Dr. J. Muller on 5 October 1983. His student, Marianne Pacqué, who is preparing a Ph.D. thesis supported by the Netherlands Organization for the Advancement of Pure Research (Z.W.O.), took it upon her to prepare the manuscript for publication. She made a small number of corrections in the text in the conviction that the author would have done the same if he had the opportunity to go over the manuscript again. The illustrative part of the paper was far from ready and M. Pacqué made the LM photographs of plates XVI–XIX, gave the directions for the composition of the photo plates, supervised the making of the drawings from the rough draughts left by the author, and prepared the captions of all illustrations in complete agreement with the text.

1. INTRODUCTION

The present study deals with the pollen morphology of the genus *Harpullia*, and is based on the taxonomic revision by Leenhouts & Vente (1982). Of the 26 species of *Harpullia* recognised by these authors, 20 were available for pollen studies, the others were represented by specimens lacking sufficiently well developed male buds. The genus proved to possess four distinct pollen types and it is unfortunate that no pollen was available of the relatively primitive species *H. giganteacapsula* and *H. spec. nov.*

The first part of this paper is descriptive and contributes to a taxonomy in which species are grouped according to their overall similarity as was done by Leenhouts & Vente (l.c.).

The second part is interpretative and attempts to trace the evolutionary history, first of the pollen characters and next to integrate this evidence with the phylogenetic analysis of the genus by Leenhouts (1985) and with evidence from ecology, distribution and geologic history of the area occupied at present. This finally leads to a discussion of the development of the genus.

2. MATERIALS AND METHODS

Only herbarium material was available for examination. As far as possible male flowers were sampled since; as is usual in Sapindaceae, the reduced anthers of female or possibly hermaphroditic flowers yield poorly developed pollen.

For light (LM) and scanning electron microscopy (SEM) mature buds were first treated with wetting agent and anthers subsequently acetolysed according to standard procedures. For SEM acetolysed pollen grains were sputtercoated with gold and sectioned with a freezing microtome. Observation was with a Cambridge or a Jeol-35 instrument. Measurements were taken with LM. For transmission electron microscopy (TEM) anthers were rehydrated and fixed in 0.1% glutar aldehyde and 1% OsO₄, prestained with uranylacetate, embedded in Epon 3/7 and poststained with Reynold's lead citrate, or acetolysed material was embedded omitting the rehydration.

3. GENERAL MORPHOLOGY

The size of *Harpullia* pollen generally varies between 23 μm (*H. rhyticarpa*) and 29 μm (*H. cauliflora*), but the pollen of *H. austro-caledonica* clearly falls outside this range because of its large size (44 μm).

Shape varies between spherical-suboblate (P/E = 0.92 in *H. rhachiptera*) and prolate (P/E = 1.38 in *H. austro-caledonica*).

The apertures are basically tricolporate, but in some species a small percentage of tetracolporate grains occur. The development of the colpate ectoapertures is very variable. In some species the colpi may be long and well developed and clearly harmo-

megathically functional (plates I: 6; IV: 1; VI: 1), while in others they are more or less reduced and non-functional (plates X: 5; XII: 3) or even absent and in the latter conditions the grains may be termed cryptoporate, the endoapertures being hidden from view, at least with SEM (plate XIII: 1, 3). The length of the ectoapertures is expressed as $P/\text{length colpi}$ and this ratio may vary between 1.14 (long colpi in *H. arborea*) and 12.0 (short colpi in *H. crustacea*). Endoapertures are invariably present and generally equatorially elongated. The colpi are closed by apertural membranes consisting of endexine and reduced ectexinous elements (plates IV: 2; VI: 4). The colpus membrane is strongly reduced above the endoapertures (plate II: 3). The exine consists of an inner nexine, a layer of columellae and an outer tectum, but in those species for which TEM observations are available, a distinct separation in the nexine was mostly visible, indicating the presence of a more or less well developed sole with the same density for the electron beam as columellae and tectum and together constituting the ectexine and thus distinguishable from the inner endexine (plates II: 3, 4; V: 4). In *H. longipetala* the sole appeared much reduced. The endexine thickens near the apertures (plates II: 1, 4; III: 1; V: 3) and may show a lamellar-imbricated structure (plate IX: 2, 3). However, in some species the clear staining contrast shows that interbedding of ectexine and endexine occurs. In *H. crustacea*, but to a lesser degree also in other species, the endexine shows an imbricated structure in the apertural thickenings, which changes away from the apertural regions into a laminated structure (plate IX: 1). The endexine layer is here interbedded with material which has the same density of and is partly continuous with the sole (plates IX: 3; XIVa: 1, 2). Both endexinous and ectexinous material are in the form of lamellae, thus forming a mixed lamellated layer. It must be emphasised here that the endexinal laminae are ± 40 nm thick and do not show a central white line. Therefore they do not represent unit-membranes, but larger structures which, however, may have developed ontogenetically from single or fused unit-membranes. In general the endexinal laminae are closer together on the inner side than on the outer (plates IX: 2; XIVa: 1).

In the *H. arborea* pollen type (plate II: 1–3) the endexine appears to be more homogeneous than in the *H. cupanioides* type (plates IX: 1–3; XIVa: 1) and it is possible that in the latter a younger stage has been preserved by a neotenic process than in the *H. arborea* type, in which all traces of an original lamination may have been obliterated by a more massive sporopollenin deposition.

Laminated structures in the exine have been described in several angiosperm families. In Annonaceae (Le Thomas, 1980) and Dipterocarpaceae (Maury et al., 1975) they are attributed to the ectexine and the phenomenon of interbedding between ectexine and endexine does not occur, the endexine being considered absent.

In Annonaceae there is interbedding with the intine, while in Dipterocarpaceae the laminae are extensions of the columellar structures and often still show a central white line and little or no intine interbedding.

The situation in the *H. cupanioides* type, as exemplified by *H. crustacea*, thus appears to be different in that the columella bases are continuous with the interbedded material, thus forming a mixed layer (plate XIVa: 2). A similar case has been re-

ported by Skvarla & Larson (1965) for some Compositae. The mixed layer in *Passiflora*, described by Larson (1966), is not comparable because of the absence of laminae.

Guédès (1982) has recently discussed the homology of the different laminated layers in angiosperm exines. His presupposition, however, is the non-existence, except at maturity in some cases, of the basic stain-differentiated twofold subdivision of the exine originally described by Faegri (1956) and Larson et al. (1962) and since recognised in many angiosperm exines and also clearly present in *Harpullia*. In contrast, Guédès considers as basic the difference between periclinal (tangential) deposition of sporopollenin in the inner layer and the primexine-based radial deposition in the ectexine.

It would seem that the interbedding observed in *Harpullia* indeed can be traced back to a difference between the ectexine and the endexine in the way sporopollenin is deposited, but it is clear that the processes are not spatially, nor in time, clearly separated. Moreover, the staining contrast is clear as well as the continuity of interbedded ectexine material with the bases of the columellae and the sole.

Perhaps the processes described in *Lilium* by Dickinson (1976) offer a clue to this situation. He found evidence in an early ontogenetic stage for the formation of endexine plaques in a fibrillar matrix, which become adpressed against the sole (foot layer) of the ectexine. If in this fibrillar matrix ectexinous sporopollenin is condensing in a different, more diffuse way, it could keep the endexine plaques separated. In this connection it is significant that in the innermost part of the endexine the amount of ectexinous material is least, indicating, assuming centripetal formation of the endexine, two different processes which change in relative significance during ontogeny. A similar situation was also observed in *Bebbia juncea* (Compositae) by Skvarla & Larson (1965). Detailed ontogenetic studies will be necessary for further clarification in *Harpullia*.

The terminological problem needs to be solved, however, on the basis of evidence available now. While at the apertural margins the thickenings are clearly mainly endexinous in nature, a mixed zone is present over the remaining part of the exine, which, as emphasised by Larson (1966), cannot properly be designated as either ectexine or endexine.

Guédès (1982) is convinced of the strict homology of all inner periclinal laminated exine strata from ferns, gymnosperms and angiosperms, which he designates as endexinous, regardless of chemical composition as indicated by stain differentiation. This extreme point of view, which disregards the difference in endexine laminations between gymnosperms and angiosperms, first demonstrated by Doyle et al. (1975), is not followed here. Instead it is recommended that homologies can best be detected by recognition of homologous processes, rather than finished structures. Thus the stain stratification which appears most clearly in mature exines, as admitted by Guédès (l.c.), can remain incorporated in the endexine-ectexine definitions. Also, the possibility of laminated soles as in Annonaceae and Dipterocarpaceae remains.

In cases where only LM observation without staining of sections is possible, sole + endexine will here be designated as nexine, the term being derived from 'nescio' (= I do not know) rather than from 'non-sculptured' as originally proposed by Erdtman (1948).

A second terminological problem connected with the endexine is concerned with the nature of the apertural thickenings. If colpi are present the endexine starts thickening already some distance away from the colpus margin, further increasing in thickness under the median zone of the colpus, reaching maximal thickness around the endoapertures (plate II: 1–4). The endexinal thickenings thus form the bulk of the colpus membranes and they appear in LM surface view as darker areas surrounding the colpus borders, due to the fact that total exine thickness is here larger than on either side. Thus these areas can easily be mistaken for true costae colpi in the sense of Iversen & Troels-Smith (1950), which are ridges of thickened endexine underlying the margins of the colpi only and not forming part of the apertural membrane. The thickenings around the endoapertures do fall within the definition of costae endopori, however. Especially serial TEM sections clarify this situation, which comes close to case 11 (*Gyrostemon*, *Paeonia*) described by Roland (1968, pl. B, p. 515), and which is undoubtedly prevalent in many colpiate angiosperm pollen types.

It is clear now that colpiate and porate thickenings form a single structural unit, the shape of which in *Harpullia* is closely correlated with the different development of colpi and pores. It thus is considered inadvisable to make a terminological separation. Since the function of these apertural thickenings appears to be protective, shielding the intine from contact with the atmosphere and strengthening the apertural region structurally and also because of their shape, the term 'apertural shield' or 'scutum' (from the Latin '*scutum*' = elongated shield) is proposed. The tricolporate grains with this structure could then be called scutate and one can talk of a shielded or scutate aperture system. No confusion appears to be possible with the term 'scutulium', introduced by Potonié (1956) for equatorial exine thickenings in trilete spores.

Functionally, two aspects are notable. Firstly, it is a structure which prevents the separation of endexine and tectum at the colpus borders as happens in fastigiate tricolporate grains (Reitsma, 1966) or in grains with an endexinal fold (Lobreau-Callen & Lugardon, 1973). Secondly, the resulting rather thick colpus membrane diminishes the harmomegathic infolding potential of the colpus, while the costate edge around the endoaperture prevents the collapse during shrinkage of the central part of the aperture system. It thus appears to be a specialised condition, compared to the primitive situation in which the colpus is closed with a thin flexible membrane as is the case in many monosulcate pollen types.

The shielded tricolporate aperture thus can be considered pre-adapted to loss of harmomegathic functioning of the colpi and their subsequent reduction towards the cryptoporate condition found in some species of *Harpullia*.

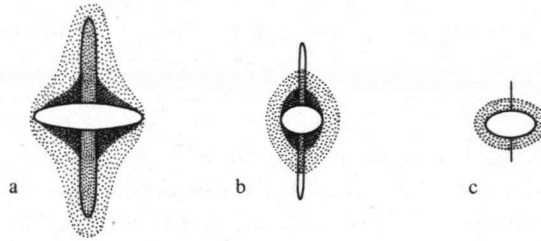


Fig. 1. — a: Apertural shield fully developed, relatively thick and extending over a broad marginal zone outside the ectoapertures, with more or less distinct costae bordering the endoapertures on the polar sides. — b: Apertural shield moderately developed, relatively thin and extending over a narrow marginal zone outside the ectoapertures, the costae partly surrounding the endoapertures. — c: Apertural shield reduced and mainly developed as pronounced costae surrounding the endoapertures.

The nature and development of the apertural thickenings of the endexine have been characterised in figure 1. It will be noted that these categories correlate with and form an intrinsic part of the reduction of the ectoapertures, leading from the tricolporate to the cryptoporate condition.

As will be clear from the foregoing discussion of the endexine and from the TEM graphs, the sole is generally not well developed in *Harpullia* and is much reduced especially in *H. longipetala*. Columellae are always present, but may vary in size. In striate-rugulate grains they do not occur in a pattern except that they are of course not present underneath the tectal perforations, but in reticulate grains the muri are mostly simplicolumellate; however, when they are especially broad, they may be multicolumellate as in *H. rhachiptera*.

The tectum forms the most variable part of the exine and consists basically of a perforate layer (plate III: 2) with either a ridged or an echinulate suprategal sculpture. In the striate-rugulate pollen types the perforations remain small and are aligned between the ridges (plates I: 2–4, IV: 2). In the echinulate-perforate type the perforations are more irregularly dispersed, although occasionally alignments may be present (plate VI: 2, 6). In the echinulate-reticulate type the perforations have enlarged to lumina separated by rather thick and more or less broad muri. The echinae are fairly short and conical. In *H. rhachiptera* these muri do not carry echinae but a fairly irregular striation.

Sculpture distribution is generally uniform, except in *H. arborea* where in some collections a coarser sculpture is present on the poles (plate I: 3) and in *H. austrocaledonica* where a finer sculpture may be present bordering the colpi (plate IV: 2).

The intine could be studied only in *H. arborea* and *H. cupanioides* and showed evidence of comprising three or four distinct layers. Slight differences between the two species in structure and staining are probably due to different preservation and maturity of these rehydrated herbarium samples. This complexity is comparable to that found in Magnoliaceae by Pragłowski (1974), the main difference being that in *Harpullia* intine differentiation is related to the apertures, while in the former family this appears not to be the case.

Although it is at present not yet possible to homologise the intine layers described for various angiosperm taxa, the numbering introduced by Praglowski (l.c.) is provisionally adopted here for ease of reference.

The intine-1 layer which is situated outermost is only well developed underneath the endoaperture and consists of a rather homogeneous electron transparent (*H. cupanioides*, plate IX: 2) or more opaque (*H. arborea*, plate II: 3) matrix, which at its outer border mixes with endexinous granular material.

The intine-2 is structured and consists in *H. cupanioides* of an electron transparent matrix with tubular-alveolar cytoplasmic tracts which appear as opaque inclusions in section (plate IX: 2, 3). This structure is less obvious in *H. arborea* (plate II: 2).

The intine-3 is electron transparent in *H. cupanioides* (plate IX: 3) and relatively more opaque in *H. arborea* (plate II: 3). It is diminishing in thickness in polar and mesocolpial direction away from the apertures (plate II: 1-3).

Only in *H. arborea* there is an indication for a fourth intine layer, restricted to the endospertural region (plate II: 3).

4. SYSTEMATIC DESCRIPTIONS

The numbers and sequence refer to Leenhouts & Vente (1982).

Harpullia Roxb. subg. **Otonychium** Bl.

1. *Harpullia pendula* Planch. ex F.v.Muell.

Material studied: Australia: *Beckler s.n.*; *Williams s.n.*

Pollen grains subprolate, P/E 1.26, tricolporate. Size P 27 μm , E 21 μm . Ectoapertures 21 μm long, P/l.c. 1.28, 2 μm wide, tapering with rounded ends. Endoapertures $5 \times 2 \mu\text{m}$ with polar costae. Exine uniformly 1.5 μm thick, nexine 0.5 μm thick. Apertural shield extending alongside ectoapertures, thickened on the polar side of the endoapertures. Columellae 0.5 μm long, < 0.5 μm in diameter, indistinct, tectum 0.5 μm thick, finely perforate-striate. Perforations < 0.5 μm in diameter, ridges predominantly meridionally oriented, anastomosing, < 0.5 μm wide.

2. *Harpullia arborea* (Blanco) Radlk. — Plates I: 1-6; II: 1-4; III: 1-3.

Material studied: Ceylon: *Jayasuriya s.n.* Thailand: *Larsen 9272*. Indochina: *Vidal 1078*. Sumatra: *Meijer 5049*. Borneo: *SAN 34023*. Philippines: *Cuming 1269*. Moluccas: *Buwalda 4579*; *Atje 338*. New Guinea: *Ledermann 6760*. Solomons: *BSIP 14577*. Tonga: *Yuncker 15624*.

Pollen grains spherical to prolate, P/E 1.07 (1.20) 1.34, tricolporate, rarely tetra-colporate. Size P 22 (25.4) 31 μm , E 19 (21.2) 23 μm . Ectoapertures 22 μm long, P/l.c. 1.05 (1.14) 1.24, 1-2 μm wide with pointed ends, colpus membrane covered with irregular ridge fragments. Endoapertures $4.5 \times 2.6 \mu\text{m}$ or absent. Exine general-

ly of uniform thickness, 1.5 μm , occasionally up to 2 μm thick on poles (*Meijer 5049*), nexine 0.5 μm thick, on TEM graphs separable into thin endexine, which is thickened underneath colpus membranes, and a sole which has a very irregular upper surface and connects the basally broadened columellae (plate II: 4). Apertural shield variably developed, mostly indistinct, and polar thickenings of endoapertures weakly developed. The columellae are 0.5 μm long, < 0.5 μm in diameter, indistinct. The tectum consists of a basal perforate stratum (plate III: 2), which is 0.3–0.5 μm thick and superposed ridges, which are 0.5–1 μm high, subparallel anastomosing and meridionally oriented. The perforations are < 0.5 μm in diameter. The striate pattern is rather uniform (plate I: 1), but may change into a slightly coarser, more reticulate pattern on the poles (plate I: 3).

Comments: In view of the considerable macromorphological variability of this species described by Leenhouts & Vente (1982), special care was taken to sample a representative number of specimens over the whole range of its occurrence. Although some variability was found in the uniformity of the striate tectum (finely reticulate on poles in *Ledermann 6760* and *BSIP 14577*) and in the presence of a polarly thickened tectum (*Meijer 5049*) this is minor compared to macromorphology and in general the pollen of *H. arborea* is identical with that of *H. pendula*.

Harpullia Roxb. subg. **Harpullia**

3. Harpullia austro-caledonica Baillon — Plates IV: 1–5; V: 1–4; XVI: 9–12.

Material studied: New Caledonia: *McKee 19469, 21634, 24002, 26770*.

Pollen grains subprolate to prolate, P/E 1.23 (1.38) 1.50, tricolporate. Size P 37 (43.8) 50 μm , E 28 (29.9) 33 μm . Ectoapertures 35 μm long, P/l.c. 1.13 (1.25) 1.36, 3–4 μm wide, tapering with pointed ends, colpus membranes covered with irregular verrucate-rugulate elements. Endoapertures 9.5 \times 4.5 μm . Exine of uniform thickness (2 μm) or thicker on poles (up to 3 μm in *McKee 26770*), sole 1–1.5 μm thick. Apertural shield well developed, polar endexinal thickenings rather distinct (plate V: 3). Columellae 0.5–1.5 μm long, < 0.5 μm in diameter, rather indistinct, tectum 0.5–1 μm thick, perforate-rugulate. Rugulate pattern irregularly oriented, sometimes only present on mesocolpia (*McKee 21634*), or fully developed over the whole tectum and submeridionally arranged (*McKee 26770*). Perforations < 0.5 μm in diameter, rugulate ridges 0.5 μm in width.

Comments: The pronounced variability in the flowers of this species is not matched by pollen morphological variability. The differences found in exine structure may be connected with developmental stages.

5. Harpullia longipetala Leenh. — Plate X: 3–4; XVI: 13–16.

Material studied: New Guinea: *Carr 11498; NGF 19671, 30337*.

Pollen grains spherical, P/E 0.95 (0.98) 1.01, tricolporate. Size P 25 (28.1) 32 μm , E 26 (28.7) 32 μm . Ectoapertures variably developed, 11–14 μm long, P/l.c. 1.9 (2.3) 2.6, narrow, non functional. Endoapertures 7 \times 4.9 μm . Exine uniformly 2 μm

thick, nexine 0.5 μm thick, on TEM graphs almost completely formed by a faintly lamellar endexine. Sole fragmentary. Apertural shield reduced to thickenings on the polar sides of the endoapertures. Columellae 1 μm long, 0.5 μm in diameter, rather distinct. Tectum regularly finely reticulate, lumina 0.5–1.5 μm in diameter, irregularly shaped, muri 0.5–1 μm thick, 0.5–1 μm wide, irregularly broadened, simpli- or duplicolumellate. Supratectal spines up to 1 μm high, rather distinct, rather numerous, irregularly shaped.

6. *Harpullia frutescens* F.M. Bailey — Plates VI: 1, 2; VIIa: 1, 2; VIIb: 1, 2; XVI: 17–20.

Material studied: Australia: *Hutchins s.n.*; *cult. Melbourne 71665*; *Queensl. Herb. 72381*; *Rudder 3640*.

Pollen grains spherical-subprolate, P/E 1.06 (1.15) 1.23, tricolporate. Size P 24 (28.4) 32 μm , E 23 (24.6) 26 μm . Ectoapertures 24 μm long, P/l.c. 1.1 (1.2) 1.3 μm , 2–3 μm wide, tapering, colpus membrane densely covered with minute rugulae and irregular spinules. Endoapertures 6.5 \times 2 μm , sometimes constricted in the middle. Exine uniformly 1.5 μm thick, nexine 0.5 μm thick. Sole very irregularly developed (plate VIIb: 1); endexine mixed with laminar elements of sole. Apertural shield indistinct, broadly tapering in polar direction, but distinctly thickened on polar sides of endoapertures. Columellae 0.5 μm long, < 0.5 μm in diameter, indistinct, tectum 0.5 μm thick, perforate. Lumina < 0.5 μm in diameter, rather widely spaced, occasionally linearly arranged. Supratectal spines conspicuous, 1–2 μm long, variably spaced.

Comments: The pollen of this species is characterised by its scattered fine perforations and long colpi. The spine density is rather variable; in *Melbourne 71665* spines are widely spaced.

7. *Harpullia alata* F.v. Muell. — Plate VI: 3–6; XVII: 1–4.

Material studied: Australia: *Johnson, Pickard & Baxel 1313*; *Melbourne 71391*; *NSW 136084, 136086*.

Pollen grains spherical-subprolate, P/E 1.05 (1.11) 1.16, tricolporate. Size P 26 (28.4) 33 μm , E 23 (25.6) 28 μm . Ectoapertures 23.5 μm long, P/l.c. 1.1 (1.2) 1.3, 1–2 μm wide, tapering, apertural membrane densely covered with minute irregularly shaped spinules and verrucae. Endoapertures 6.5 \times 2 μm . Exine uniformly 1.5 μm thick, nexine 0.5 μm thick. Apertural shield distinct but rather narrowly bordering the ectoapertures, gradually tapering, polar thickenings bordering the endoapertures rather small. Columellae 0.5 μm long, < 0.5 μm in diameter, indistinct, tectum uniformly 0.5 μm thick, perforate. Lumina < 0.5 μm in diameter, variable in shape and size, variably spaced, occasionally linearly arranged (plate VI: 6). Supratectal spines conspicuous, 1–2 μm long, densely spaced.

8. *Harpullia rhyticarpa* C.T. White & Francis. — Plate XVII: 5–8.

Material studied: Australia: *White 52/214*; *Winkel 14791*.

Pollen grains spherical, P/E 1.05 (1.08) 1.11, tricolporate. Size P 22 (22.5) 23 μm , E 20 (20.5) 31 μm . Ectoapertures 19 μm long, P/l.c. 1.1 (1.2) 1.3, 2 μm wide, paral-

lateral sides with rounded tips. Endoapertures $6 \times 3 \mu\text{m}$. Exine $1-1.5 \mu\text{m}$ thick, nexine $0.5 \mu\text{m}$ thick. Apertural shield moderately developed, endoapertural polar thickenings rather distinct. Columellae $0.5 \mu\text{m}$ long, $< 0.5 \mu\text{m}$ in diameter, very indistinct, tectum $0.5 \mu\text{m}$ thick, with scattered perforations, lumina $< 0.5 \mu\text{m}$ in diameter, muri $0.5-1 \mu\text{m}$ wide, locally broadened. Supratectal spines $0.5 \mu\text{m}$ long, densely spaced.

9. *Harpullia rhachiptera* Radlk. — Plate XV: 1–4; XVII: 9–12.

Material studied: New Guinea: *LAE 51779*.

Pollen grains spherical-suboblate, P/E 0.92, tricolporate or cryptoporate. Size P 23 (24) $25 \mu\text{m}$, E 26 (26.2) $27 \mu\text{m}$. Ectoapertures very indistinct or absent, $0-12 \mu\text{m}$ long, narrow, P/l.c. 2.3. Endoapertures $6 \times 2 \mu\text{m}$. Exine $2.5 \mu\text{m}$ thick, nexine $1 \mu\text{m}$ thick. Apertural shield reduced to indistinct endoapertural costae. Columellae $0.5 \mu\text{m}$ long, $< 0.5 \mu\text{m}$ in diameter, distinct. Tectum reticulate with up to $2 \mu\text{m}$ broad multicolumellate muri and irregularly shaped, $1-2 \mu\text{m}$ wide lumina. Surface sculpture of muri varying between densely, finely striate with the ridges fairly short, often in subparallel arrangement (plate XV: 1, 2) and irregularly oriented or with an irregular verucate-rugulate sculpture (plate XV: 3, 4).

Comments: The combination of a fairly coarse reticulum with striate muri and absence of supratectal spines is unique for this species. The rather large variability in tectum development suggests disturbances in the final ontogenetic phase and points to possible hybrid origin.

10. *Harpullia hillii* F.v.Muell. — Plate VIII: 1, 2; XVII: 13–16.

Material studied: Australia: *Gittins 1134; NSW 22442; Queensl. Herb. 71177; Smith 4408*.

Pollen grains spherical-subprolate, P/E 1 (1.09) 1.13, tricolporate, occasionally dicolporate. Size P 26 (27) $28 \mu\text{m}$, E 24.4 (24.8) $25.2 \mu\text{m}$. Ectoapertures $21-25 \mu\text{m}$ long, P/l.c. 1.1 (1.2) 1.3, $2 \mu\text{m}$ wide, tapering. Endoapertures $4.4 : 2.3 \mu\text{m}$, occasionally equatorial bridge present. Exine uniformly $1.5-2 \mu\text{m}$ thick, nexine $0.5 \mu\text{m}$ thick. Apertural shield reduced or absent in polar direction, polar endoapertural costae variably developed. Columellae $0.5-1 \mu\text{m}$ long, $< 0.5 \mu\text{m}$ in diameter, distinct tectum uniformly $0.5-1 \mu\text{m}$ thick, perforate-reticulate. Lumina $1-3 \mu\text{m}$ in diameter, rather uniform in size and shape. Muri $0.5-1 \mu\text{m}$ wide, irregularly broadened, sometimes interrupted in the larger lumina, occasionally multicolumellate. Supratectal spines small, $1 \mu\text{m}$ long, variably spaced.

Comments: Although macromorphologically uniform*, this is pollen morphologically a variable species, both within and between individual specimens. Variant A found in *Gittins 1134* and *Queensl. Herb. 71177* differs from the *H. frutescens* subtype in its reticulate tectum, more spherical shape and slightly shorter colpi with less distinct costae and more distinct columellae. Variant B, only found in *Smith*

* Macromorphologically too, *H. hillii* is not at all uniform but is rather one of the most variable species. — PWL.

4408, is unique in its combination of its spherical-subprolate shape, long colpi and rather coarsely reticulate tectum.

NSW 22442, cultivated in Sydney, is very variable in number of apertures (tri- and dicolporate), development of endoapertures, which are occasionally absent, and in the often irregularly developed reticulate tectum which may be locally reduced to a clavate structure. It appears probable that there have been disturbances in the development of the pollen grains.

11. *Harpullia cupanioides* Roxb. — Plates VIII: 6; IX: 1–3; XVII: 17–20.

Material studied: Laos: *Kerr 20862*. Hainan: *Hou 70717*. Borneo: *SAN 28985*. Timor: *Spanoghe s.n.* New Guinea: *NGF 7600*; *Pleyte 824*.

Pollen grains spherical, P/E 0.91 (0.99) 1.10, tricolporate, occasionally tetracolporate (20% in *Kerr 20862*). Size P 22 (24) 26 μm , E 23 (24.6) 28 μm . Ectoapertures variable in length, 10–20 μm long, P/l.c. 1.2 (1.6) 2.2, 1 μm wide, tapering, membrane covered with minute, irregularly shaped spinules and verrucae. Endoapertures $4.7 \times 2.7 \mu\text{m}$. Exine uniformly 1.5–3 μm thick, nexine 0.75 μm thick. Sole very irregularly developed, sometimes discontinuous (plate IX: 1). Mixed laminated ectexine-endexine layer well developed (plate IX: 2). Apertural shield reduced to polar endoapertural costae, endexine distinctly imbricated (plate IX: 3). Columellae 1 μm long, distinct, < 0.5 μm in diameter, tectum 0.75 μm thick, reticulate. Lumina 1–2 μm in diameter, rather uniform. Muri 0.5–1.5 μm in width. Supratectal spines small to medium sized, rather numerous.

Comments: This widespread and macromorphologically fairly uniform* species shows only minor pollen morphological variability, mainly in degree of coarseness of the reticulum and in relative length of the colpi. In three samples P/l.c. varied between 1.5–2.2, in two others between 1.2–1.3.

12. *Harpullia vaga* Merr. & Perry — Plates X: 5, 6; XVIII: 1–4.

Material studied: Solomon Islands: *BSIP 9716, 15803*.

Pollen grains suboblate-spherical, P/E 0.88 (0.98) 1.10, tricolporate. Size P 26 (27.7) 29 μm , E 29 (29.1) 30 μm . Ectoapertures 4–14 μm long, P/l.c. 2.1 (4.1) 6.5, rather indistinct, variably developed or non-functional, membrane covered with minute, irregular verrucae. Endoapertures $6.4 \times 3.9 \mu\text{m}$. Exine uniformly 2.5–3 μm thick, nexine 0.5–1 μm thick. Apertural shield reduced to polar endoapertural costae. Columellae 0.5–1 μm long, distinct, 0.5 μm in diameter, tectum 1 μm thick, reticulate. Lumina 1–2 μm , occasionally up to 3 μm in diameter, more or less elongated and irregularly shaped. Muri 1 μm wide, irregularly broadened, simplicolumellate. Supratectal spines small, not numerous.

Comments: The pollen of this species is characterised by its thick exine and irregularly broadened muri enclosing more or less elongated lumina. It is variable in shape and development of colpi.

* Macromorphologically, *H. cupanioides* is rather variable. — PWL.

13. *Harpullia crustacea* Radlk. — Plates XIII: 1–4; XIVa: 1, 2; XIVb: 1, 2; XVIII: 5–8.

Material studied: New Guinea: *Brass 21643; NGF 11839, 28767.*

Pollen grains spherical, P/E 0.94 (0.95) 0.96, tricolporate or cryptoporate. Size P 23 (24.4) 26 μm , E 23 (25.7) 27 μm . Ectoapertures 0 (5.7) 7 μm long, P/l.c. 3 (12) 25, 1–2 μm wide, narrow, non-functional. Endoapertures 5.5 \times 2.7 μm . Exine uniformly 2.5–3 μm thick, nexine 0.5–1 μm thick. Sole reduced to scattered granular masses which are connected to laminae mixed with the well developed endexine (plate XIVa: 1, 2). Apertural shield reduced to endoapertural costae (plate XIVb: 1). Columellae 0.5–1 μm long, 0.5 μm in diameter, distinct, tectum 1–1.5 μm thick, reticulate. Lumina 2–4 μm in diameter, variable and irregularly shaped, sometimes isolated verrucae are present in the lumina (plate XIII: 2). Muri 1 μm broad, sometimes interrupted. Supratectal spines small and indistinct, rather scattered.

Comments: This species is characterised by the high proportion of cryptoporate grains without colpi and the coarsely reticulate structure of the tectum. The different collections appear to vary especially in the proportion of cryptoporate grains which is especially high in *NGF 28767*.

14. *Harpullia camptoneura* Radlk. — Plate XVIII: 9–12.

Material studied: New Guinea: *Brass 32077.*

Pollen grains spherical, P/E 0.98, tricolporate, occasionally tetracolporate. Size P 25 (27.8) 30 μm , E 25 (28.2) 30 μm . Ectoapertures 0 (11.5) 17 μm long, P/l.c. 2.4, 1.5 μm wide, tapering. Endoapertures 6.4 \times 3.4 μm . Exine uniformly 3 μm thick, nexine 2 μm thick. Apertural shield reduced to indistinct polar endoapertural costae. Columellae 1 μm long, 0.5 μm in diameter, fairly distinct, tectum 1 μm thick, reticulate. Lumina 2–3 μm in diameter, irregularly shaped. Muri 1 μm wide. Supratectal spines small and inconspicuous.

17. *Harpullia carrii* Leenh. — Plate XVIII: 13–16.

Material studied: New Guinea: *Carr 12466.*

Pollen grains spherical, P/E 0.98, tricolporate. Size P 33 (34.4) 36 μm , E 33 (35) 37 μm . Ectoapertures 11 (19.2) 26 μm long, P/l.c. 1.8, 2 μm wide, tapering, membrane covered with minute, irregularly shaped verrucae. Endoapertures 7.3 \times 6.5 μm . Exine uniformly 2 μm thick, nexine 1 μm thick. Apertural shield absent. Columellae 0.5 μm long, 0.5 μm in diameter, few in number, tectum 0.5 μm thick, reticulate. Lumina 1.5 μm in diameter, fairly regularly shaped. Muri 0.5 μm wide. Supratectal spines < 1 μm long, inconspicuous.

19. *Harpullia solomonensis* M. Vente — Plates VIII: 5; XVIII: 17–20.

Material studied: Solomon Islands: *Waterhouse 645-B.*

Pollen grains spherical, P/E 0.93, tricolporate. Size P 25 (26.8) 29 μm , E 27 (28.6) 30 μm . Ectoapertures 13 (18.2) 22 μm long, P/l.c. 1.5, 2 μm wide, membrane covered with minute, irregularly shaped verrucae. Endoapertures 6.3 \times 4 μm . Exine uniformly 1.5 μm thick, nexine 0.5 μm thick. Apertural shield absent. Columellae 0.5

μm long, $< 0.5 \mu\text{m}$ in diameter, distinct, tectum $0.5 \mu\text{m}$ thick, reticulate. Lumina $0.5\text{--}1 \mu\text{m}$ in diameter, rather regularly shaped. Muri $0.5\text{--}1 \mu\text{m}$ wide. Supratectal spines very small.

20. *Harpullia ramiflora* Radlk. — Plates VIII: 3, 4; XI: 1–3.

The material studied shows considerable variation in pollen morphology and can be subdivided into three groups: A, B and C, which will be described separately below.

A. Aru Islands: *Beccari 2823*. New Guinea: *Aet 299*; *LAE 51886*; *Reksodihardjo 22*; *Versteeg 1134* — Plates XI: 1–3; XIX: 1–4.

Pollen grains spherical, P/E 0.96 (1.04) 1.10, tricolporate. Size P 25 (26.9) 29 μm , E 25 (27.1) 30 μm . Ectoapertures 13 (14.9) 17 μm long, P/l.c. 1.5 (1.85) 2.2, $0.5\text{--}1 \mu\text{m}$ wide, indistinct. Endoapertures $6.4 \times 3.4 \mu\text{m}$. Exine uniformly $2.5\text{--}3 \mu\text{m}$ thick, nexine $0.5\text{--}1 \mu\text{m}$ thick, mainly consisting of finely laminated-imbricated endexine, sole very much reduced and mainly consisting of discontinuous verrucate elements, $< 0.5 \mu\text{m}$ in diameter (TEM). Apertural shield reduced to rather distinct polar endoapertural costae, $1.5 \mu\text{m}$ thick, in which the endexine has a faintly imbricated structure (plate IX: 1–2). Columellae $1 \mu\text{m}$ long, $< 0.5 \mu\text{m}$ in diameter, rather distinct, tectum $1 \mu\text{m}$ thick, reticulate. Lumina $1\text{--}2 \mu\text{m}$ in diameter. Muri $1 \mu\text{m}$ wide. Supratectal spines rather numerous, small, $0.5 \mu\text{m}$ long.

B. New Guinea: *NGF 43625*.

Pollen grains spherical, P/E 0.95, tricolporate. Size P 28 (29.6) 33 μm , E 30 (31.2) 33 μm . Ectoapertures 13 (18.6) 22 μm long, P/l.c. 1.6, $2 \mu\text{m}$ wide, tips rounded. Endoapertures $7 \times 3 \mu\text{m}$. Exine uniformly $2 \mu\text{m}$ thick, nexine $0.5 \mu\text{m}$ thick. Apertural shield reduced to polar endoapertural costae. Columellae $1 \mu\text{m}$ long, $0.5 \mu\text{m}$ in diameter, tectum $0.5 \mu\text{m}$ thick, reticulate. Lumina $1 \mu\text{m}$ in diameter. Muri $0.5\text{--}1 \mu\text{m}$ wide. Supratectal spines numerous and small, up to $1 \mu\text{m}$ long.

C. New Guinea: *Hoogland 4950* — Plate VIII: 3, 4.

Pollen grains spherical-suboblate, P/E 0.92, tricolporate. Size P 28 (28.2) 29 μm , E 29 (30.4) 31 μm . Ectoapertures 22 (22.7) 23 μm long, P/l.c. 1.3, $1 \mu\text{m}$ wide, membranes smooth, tips pointed. Endoapertures $7 \times 3.5 \mu\text{m}$. Exine uniformly $2 \mu\text{m}$ thick, nexine $0.5 \mu\text{m}$ thick. Apertural shield reduced to indistinct endoapertural costae. Columellae $1 \mu\text{m}$ long, $< 0.5 \mu\text{m}$ in diameter, tectum reticulate. Lumina $2\text{--}3 \mu\text{m}$ in diameter, irregular in shape and variable in size (plate VIII: 4). Muri $0.5 \mu\text{m}$ in width. Supratectal spines very scarce, up to $0.5 \mu\text{m}$ long, indistinct.

Comments: The marked pollen morphological variability in this species is matched by macromorphological variability which suggests, according to Leenhouts & Vente (1982) a mosaic of geographical and ecological races, with a possibility that the delimitation against the related species *H. solomonensis*, *H. myrmecophila*, *H. cauliflora*, *H. petiolaris* and *H. largifolia* is not sharply defined. On pollen morphological evidence *H. ramiflora* appears especially close to *H. solomonensis* and *H. largifolia* only.

21. *Harpullia myrmecophila* Merr. & Perry — Plates XII: 3, 4; XIX: 5–8.

Material studied: New Guinea: *Brass 13285*.

Pollen grains spherical, P/E 0.95, tricolporate-cryptoporate. Size P 28 (29) 31 μm , E 30 (30.6) 32 μm . Ectoapertures 0 (9.3) 17 μm long, P/l.c. 3.2, 0.5–1 μm wide, indistinct, non-functional (plate XII: 3). Endoapertures 6.5 \times 4 μm . Exine uniformly 2 μm thick, nexine 0.5 μm thick. Apertural shield reduced to polar endoapertural costae. Columellae 1 μm long, 0.5 μm in diameter, tectum 0.5 μm thick, reticulate. Lumina 2–3 μm in diameter, variable in size and shape. Muri 1 μm wide. Supratectal spines small, up to 1 μm long, densely spaced.

Comments: This collection shows striking variability in the development of the ectoapertures which may be totally absent in some grains, thus being truly cryptoporate.

22. *Harpullia cauliflora* K. Schum. & Lauterb. — Plates XII: 1, 2; XIX: 9–12.

Material studied: Cult. Hort. Bogor., Java: *III-I-12a*.

Pollen grains spherical, P/E 0.99, tricolporate-cryptoporate. Size P 28 (29) 30 μm . Ectoapertures 0 (8.1) 11 μm long, P/l.c. 3.6, 0.5 μm wide, very indistinct, non-functional. Endoapertures 6.4 \times 4 μm . Exine uniformly 3 μm thick, nexine 1 μm thick. Apertural shield reduced to polar endoapertural costae. Columellae 1 μm long, 0.5 μm in diameter, tectum 1 μm thick, reticulate. Lumina 1–2 μm in diameter, irregularly shaped. Muri 1–2 μm wide, locally broadened, simpli-, occasionally dupli-columellate. Supratectal spines rather short, up to 0.5 μm long, inconspicuous.

Comments: Also in this species some grains are cryptoporate. A further characteristic are the locally widened muri.

23. *Harpullia petiolaris* Radlk. — Plates XII: 5, 6; XIX: 13–16.

Material studied: Moluccas: *Kostermans 631* (subsp. *moluccana*). New Guinea: *Docters van Leeuwen 9139*; *NGF 13258* (subsp. *petiolaris*).

Pollen grains spherical, P/E 0.96 (0.96) 0.97, tricolporate-cryptoporate. Size P 24 (25.9) 28 μm , E 25 (26.3) 28 μm . Ectoapertures 2 (5.1) 8 μm long, P/l.c. 2.9 (7.1) 13, 0.5–1 μm wide, indistinct, non-functional. Endoapertures 5.3 \times 3.6 μm . Exine uniformly 2.5–3 μm thick, nexine 0.5–1 μm thick. Apertural shield reduced to indistinct polar endoapertural costae. Columellae 1–2 μm long, 0.5 μm in diameter, conspicuous, tectum 0.75–1 μm thick, reticulate. Lumina 2–5 μm in diameter, irregularly shaped. Muri 0.5–1 μm wide. Supratectal spines up to 0.5 μm long, fairly densely spaced.

Comments: The ectoapertures are variably developed both within and between collections, but there is no distinct correlation in this respect with the subspecific taxa recognised for this species by Leenhouts & Vente (1982).

24. *Harpullia largifolia* Radlk. — Plates X: 1, 2; XIX: 17–20.

Material studied: Solomon Islands: *BSIP 6712*, *13220*.

Pollen grains spherical, P/E 0.99 (0.99) 1, tricolporate. Size P 24 (26.3) 29 μm , E

24 (26.5) 29 μm . Ectoapertures 12 (16) 20 μm long, P/l.c. 1.5 (1.7) 1.9, 0.5–1 μm wide, indistinct, non-functional. Endoapertures $6.4 \times 2.9 \mu\text{m}$. Exine uniformly 3 μm thick, nexine 0.5–1 μm thick. Apertural shield reduced to polar endoapertural costae. Columellae 1.5–2 μm long, 0.5 μm in diameter, tectum 1 μm thick, reticulate. Lumina 1–2 μm in diameter. Muri 1 μm wide. Supratectal spines up to 1 μm long, fairly densely spaced.

5. POLLEN TYPES

In *Harpullia* the following four pollen types can be distinguished, one of which can be subdivided into eight subtypes.

- I. **Harpullia arborea type** (Plates I: 1–6; II: 1–4; III: 1–3): *H. arborea*, *H. pendula*.
Subprolate, P/E 1.20–1.26. Medium size, P 25.4 \times 26.9 μm , E 21.2–21.4 μm . Ectocolpi functional, long, P/l.c. 1.14–1.28, 2 μm wide. Endopores 4.5–5 \times 2–2.5 μm . Apertural shield well developed. Columellae indistinct, < 0.5 μm in diameter, 0.5 μm long. Tectum 0.5 μm , finely striate-perforate, perforations < 0.5 μm in diameter.
- II. **Harpullia austro-caledonica type** (Plates IV: 1–5; V: 1–4): *H. austro-caledonica*.
Subprolate-prolate, P/E 1.23–1.50. Large, P 36.8–50.4 μm , E 27.8–33 μm . Ectocolpi functional, long, P/l.c. 1.13–1.36, 3 μm wide. Endopores 8–12 \times 2–7 μm . Apertural shield well developed. Columellae rather indistinct, < 0.5 μm in diameter, 0.5 μm long on mesocolpia, up to 1.5 μm long on poles. Tectum 0.5 μm on mesocolpia, up to 1 μm on poles, finely perforate-rugulate, often with the strongest development of the rugulae on the mesocolpia. Perforations < 0.5 μm in diameter.
- III. **Harpullia cupanioides type**.
Suboblate-subprolate, P/E 0.92–1.15. Tricolporate-cryptoporate. Tectum perforate-reticulate with supratectal spines.
This type can be subdivided on the basis of degree of development of the colpi, shape and coarseness of reticulation. While the extremes are clearly distinct, they are linked by transitions. The main boundary is between subtypes with functional and those with non-functional colpi. In the first group the subtypes are rather distinct and cannot all be arranged in a series, but in the second group there is a clear trend towards reduction of colpi and increase in coarseness of reticulation, culminating in the cryptoporate *H. crustacea*.
- IIIa. **Harpullia frutescens subtype** (Plates VI: 1–6; VIIa: 1, 2; VIIb: 1, 2): *H. frutescens*, *H. alata*, *H. rhyticarpa*.
Spherical-subprolate, P/E 1.08–1.15. Medium size, P 23.3–28.4 μm , E 21.2–25.6 μm . Ectocolpi functional, long, P/l.c. 1.2, 2–3 μm wide. Endopores 6–7 \times

2–3 μm . Apertural shield well developed. Columellae indistinct, < 0.5 μm in diameter, 0.5 μm long. Tectum thin, with scattered, sometimes linearly arranged perforations 0.5 μm in diameter. Supraterectal spines conspicuous, rather densely spaced.

IIIb. *Harpullia hillii* subtype (Plate VIII: 1, 2): *H. hillii*.

Spherical, P/E 1–1.1. Medium size, P 26–28 μm , E 24–25 μm . Ectocolpi functional, long, P/l.c. 1.1–1.3, 2 μm wide. Endopores 5 \times 2 μm . Apertural shield moderately developed, mainly as polar endoapertural costae. Columellae thin but distinct, < 0.5 μm in diameter, 0.5–1 μm long. Tectum rather thin, uniformly finely reticulate, lumina 1–3 μm . Supraterectal spines small, medium to rather densely spaced.

IIIc. *Harpullia ramiflora* subtype (Plate VIII: 3, 4): *H. ramiflora* C.

Spherical-suboblate, P/E 0.92. Rather large, P 28 μm , E 30.4 μm . Ectocolpi functional, long, P/l.c. 1.3, 1 μm wide. Endopores 6–8 \times 3–4 μm . Apertural shield reduced. Columellae distinct, 1 μm in diameter. Muri simplicolumellate, 0.5 μm wide, 1 μm long. Lumina 2–3 μm . Supraterectal spines very small, widely spaced.

III d. *Harpullia cupanioides* subtype (Plates VIII: 5, 6; IX: 1–3): *H. cupanioides*, *H. solomonensis*.

Spherical-suboblate, P/E 0.93–0.99. Medium size, P 24–27 μm , E 25–29 μm . Ectocolpi functional, rather long, P/l.c. 1.5–1.6, 1–2 μm wide. Endopores 5–6 \times 3–4 μm . Apertural shield reduced to polar endoapertural costae. Columellae distinct, < 0.5 μm in diameter, 0.5–1 μm long. Tectum thin, uniformly finely reticulate, lumina 1–1.5 μm . Supraterectal spines rather distinct, rather densely spaced.

IIIe. *Harpullia carrii* subtype (Plates X: 1, 2; XI: 1–3): *H. carrii*, *H. largifolia*, *H. ramiflora* A + B.

Spherical, P/E 0.95–1.04. Rather large, P 26–34 μm , E 27–35 μm . Ectocolpi non-functional, variably developed, P/l.c. 1.6–1.8, 1–2 μm wide. Endopores 6–7 \times 3–7 μm . Apertural shield reduced to polar endoapertural costae. Columellae distinct, 0.5 μm in diameter, 0.5–1.5 μm long. Tectum 0.5–1 μm thick, uniformly finely reticulate, lumina 1–2 μm . Supraterectal spines rather distinct, densely spaced.

III f. *Harpullia longipetala* subtype (Plate X: 3, 4): *H. camptoneura*, *H. longipetala*.

Spherical, P/E 0.98. Medium large, P 27–28 μm , E 28–29 μm . Ectocolpi non-functional, P/l.c. 2.4–2.6, 1.5 μm wide. Endopores 6–7 \times 3–5 μm . Apertural shield reduced to polar endoapertural costae. Columellae distinct, 0.5 μm in diameter, 1 μm long, muri simpli- or duplicolumellate. Tectum 2–3 μm thick, uniformly finely to medium coarsely reticulate, lumina 0.5–3 μm . Supraterectal spines small, rather densely spaced.

IIIg. *Harpullia vaga* subtype (Plates X: 5, 6; XII: 1–4): *H. cauliflora*, *H. myrmecophila*, *H. vaga*.

Spherical, P/E 0.95–0.99. Medium large, P 28–29 μm , E 29–31 μm . Ectocolpi indistinct, non-functional, P/l.c. 3.2–4.1, 0.5–1 μm wide. Endopores 6–7 \times 4 μm . Apertural shield reduced to polar endoapertural costae. Columellae distinct, 0.5 μm in diameter, 1–1.5 μm long, muri simpli-, occasionally duplicolumellate. Tectum 0.5–1 μm thick, uniformly reticulate, lumina often irregularly shaped, 1–3 μm . Supratectal spines rather short, densely spaced.

IIIh. *Harpullia crustacea* subtype (Plates XII: 5, 6; XIII: 1–4; XIVa: 1, 2; XIVb: 1, 2): *H. crustacea*, *H. petiolaris*.

Spherical, P/E 0.95–0.96. Medium large, P 24–26 μm , E 26 μm . Ectocolpi absent or very indistinct, variably developed and non-functional. P/l.c. 7.1–12, 0.5–2 μm wide. Endopores 5–6 \times 3–4 μm . Apertural shield reduced to polar endoapertural costae. Columellae 0.5 μm in diameter, 0.5–2 μm long. Tectum 1–3 μm thick, uniformly reticulate, muri simplicolumellate. Lumina variably shaped, 2–5 μm . Supratectal spines rather small, medium densely spaced.

IV. *Harpullia rhachiptera* type (Plate XV: 1, 2): *H. rhachiptera*.

Spherical-suboblate, P/E 0.92. Medium large, P 23–25 μm , E 26–27 μm . Ectocolpi absent or very indistinct, non-functional. P/l.c. 2.3. Endopores 6 \times 2 μm , polar costae indistinct. Apertural shield reduced to indistinct polar endoapertural costae. Columellae < 0.5 μm in diameter, 0.5 μm long. Tectum 1 μm thick, uniformly reticulate with broad multicolumellate muri, lumina 1–2 μm . Surface of muri striate-rugulate.

6. POLLEN MORPHOLOGY AND TAXONOMY

The tribe Harpullieae is, in the original circumscription of Radlkofer (1933–34), characterised by a not fully developed leaf tip, curved cotyledons and a dehiscent fruit. There is no pollen morphological character which unites the tribe, in which 7 main pollen types are present distributed as follows:

1. *Delavaya* type: small, spherical, tricolporate, perforate-rugulate, only found in *Delavaya*.
2. *Harpullia austro-caledonica* type: large, subprolate, tricolporate, rugulate, only found in *H. austro-caledonica*.
3. *Harpullia arborea* type: small, subprolate, tricolporate, striate, occurring in *Harpullia* subg. *Otonychium*, *Conchopetalum*, *Majidea*, *Arfeuillea*, *Ungnadia* and, in a slightly modified form, in Aceraceae and Hippocastanaceae.
4. *Harpullia cupanioides* type: small, spherical tricolporate/cryptoporate, reticulate-echinate, occurring in *Harpullia* subg. *Harpullia* p.p.
5. *Harpullia rhachiptera* type: small, spherical, cryptoporate, reticulate-striate, only found in *H. rhachiptera*.

6. *Xanthoceras* type: large, subprolate, tricolporate, densely finely perforate with large scattered conical spines, only occurring in *Xanthoceras*.
7. *Magonia* type: large rugulate tetrads, only found in *Magonia*.

It will be clear that especially the taxonomic distribution of the *Harpullia arborea* pollen type can hardly contribute to an improved classification. Only the genera *Delavaya*, *Xanthoceras* and *Magonia* appear to be well characterised pollen morphologically.

It is also evident that within the genus *Harpullia* itself, pollen morphological characters can make only a limited contribution to its taxonomic subdivision. While the separation into two subgenera does find support because the *H. arborea* pollen type is restricted to subg. *Otonychium*, the very characteristic *H. austro-caledonica** and *H. rhachiptera* pollen types are not correlated with distinct taxonomic groups within subg. *Harpullia* and also the subtypes of the *H. cupanioides* type have little taxonomic significance. Moreover, the pollen morphology of several rare species of subg. *Harpullia*, notably *H. giganteacapsula* and *H. spec. nov.*, is not known yet and it is conceivable that the pollen morphological spectrum of *Harpullia* presented here is incomplete.

The relations between pollen morphology and the phylogenetic interpretation by Leenhouts (1985) will be discussed in the next chapter.

7. EVOLUTION

a. Introduction

The interpretation of the evolutionary history of the genus *Harpullia* and its position in the tribe Harpullieae which follows is based on a combination of the macromorphological evidence summarised by Leenhouts (1985), the pollen morphological and the geographical evidence, integrated by a cladistic methodology comparable to the groundplan-divergence method developed by Wagner (1980). This method is better adapted to the peculiarities of botany than the methodology of Hennig (1966) which appears to have originated mainly out of difficulties encountered in the taxonomy of Diptera and which has subsequently found wide acceptance in zoology.

The analysis will start with a functional interpretation of pollen morphology in *Harpullia*, which is considered a prerequisite for the subsequent character analysis. This will lead to the recognition of homologies, the establishment of transformation series and their polarity under due recognition of the probability of parallel development. It will next be possible to estimate phylogenetic values which are comparable to those recognised by Leenhouts (l.c.) on macromorphology. Integration of morphological data with ecology and distribution will then be attempted in a cladistic framework on the principle of recognising related groups on shared derived character

* Finally, in my paper 'An attempt towards a natural system of *Harpullia* (Sapindaceae)' a separate section *Harpulliastrum* has been accepted for *H. austro-caledonica*. – PWL.

states and vicariance patterns in distribution. Thus a hypothesis on the evolutionary history of the genus in relation to the tribe Harpullieae can be formulated.

b. Functional pollen morphology

The main factors determining the evolution of pollen grains appear to relate to efficient transport and germination and survival from anthesis to germination. Airborne transport generally leads to relatively small, smooth surfaced grains, but transport by animal vectors can lead to a large number of exine modifications. Unfortunately, no observations on pollination ecology in *Harpullia* exist, although it appears most likely that ubiquitous small insects like trigonid bees could be responsible. However, the cauliflorous species evidently may be pollinated quite differently.

Germination may be preceded by a recognition phase in which compatibility is determined by exchange of exine held substances and stigmatic fluids, but again nothing is known about these processes in *Harpullia*. The fact that in some species the pollen grains are cryptoporate suggests that interchange via the apertures is not significant, but the possibility that the infratectal cavities contain recognition substances remains.

The presence of pollen kitt which improves clustering and attachment to vectors could be demonstrated in *Harpullia crustacea* where it enters the lumina in the ectexine (plate XIVb: 1, 2) and a comparative study of the pollen kitt development in the different exine types could be rewarding. Survival is mainly related to protection of the protoplast and intine against desiccation during the cycle of dehydration and rehydration in which considerable stress develops (Payne, 1981).

To a large extent these different factors interact and the pollen morphology at any stage in evolution represents a compromise between the selective pressures acting on the pool of genetic variability. Thus pollen characters cannot be taken as functionally independent in the way that leaf-, wood- and flower characters are, and in the following discussion the pollen type will form the basic unit for comparison.

The types recognised in chapter 6 can, from a functional point of view, be divided into three groups.

The first, including the *H. arborea* and *H. austro-caledonica* types, is characterised by tricolporate apertures with well developed long colpate ectoapertures and distinct endoapertures and a thickened apertural shield, which restricts the infolding of the colpi during harmomegathic movements (plate I: 6). The ectexine is relatively thin and in the *H. arborea* type striate perforate, the ridges being predominantly oriented meridionally. It thus appears that the main harmomegathic flexibility is located in the mesocolpia, where overall exine thickness is least, and that especially the endoapertural region represents the more rigid areas. While in this type the meridional folding direction of the mesocolpia is strengthened by the orientation of the ridges, in the *H. austro-caledonica* type it is multidirectional because of the rugulate sculpture. This type differs also from the preceding one in the presence of a minor differentiation of sculpture towards apertures and poles and in the pronounced thinning of the nexine in the extra-apertural areas.

The second group consists of the *H. frutescens*, *H. hillii* and *H. ramiflora* C subtypes of the *H. cupanioides* type. Here the tricolporate aperture system with well developed apertural shield is essentially the same as in the preceding group, but the tectum is perforate-reticulate with suprategal spines, which is the main difference with the preceding group. While in the rather uniform *H. frutescens* subtype the perforations appear comparable to those of the *H. arborea* type, the absence of ridges causes the extra-apertural exine to be flexible in all directions. The spines may promote clustering during transport and thus reflect a different pollination. In the *H. hillii* and *H. ramiflora* C subtype the tectum has become reticulate with long colpi, which in the latter have become very narrow, and it is of interest that this reticulum is quite uniform without differentiation towards the poles or apertures, resulting in evenly distributed harmomegathic stresses and probably a higher rigidity than in the *H. frutescens* subtype. It is of interest here that the change towards a reticulate tectum has not been accompanied by any reduction in the length of the colpi, although in *H. ramiflora* C they have become very narrow and probably already non-functional. This suggests genetic independence between these two characters. In contrast, in the following group a reticulate tectum is accompanied by a reduction in length of the colpi.

In the third group, consisting of the *H. cupanioides*, *H. carrii*, *H. longipetala*, *H. vaga* and *H. crustacea* subtypes of the *H. cupanioides* type and of the *H. rhachiptera* type, the ectoapertures are reduced, the shape is spherical-suboblate and the extra-apertural exine becomes relatively thick with well developed columellae and a more or less coarse reticulum. Clearly, the ectoapertures have lost completely their original function as separate harmomegathic organs, a function which is already impeded by the apertural shield in the first group. The harmomegathic stresses are equally distributed over the whole grain, which is accentuated by the spherical shape compared to the more subprolate shape of the preceding group, and the fairly heavy columellae and well developed thick muri are clearly adapted to absorb these stresses. Especially the *H. crustacea* subtype and the *H. rhachiptera* type thus exhibit clearly a peristatic stress pattern (Muller, 1979).

The germinative function is probably concentrated in the endoaperture, which remains surrounded by costate thickenings, but which is not visible from the exterior. It would appear that these costae protect the differentiated intine localised in the endoapertural cavity and may prevent premature rupture of the exine during hydration.

While in those subtypes belonging to the *H. cupanioides* type the spines are always present, in the *H. rhachiptera* type only a striate-rugulate sculpture is present. It is not known whether this latter condition is related to any difference in pollination or just represents a genetic abnormality due to hybridisation.

It will be clear from the foregoing that the three groups recognised above represent different stages of transference of harmomegathic functioning from a meridionally oriented stress pattern in a subprolate-tricolporate grain with already partly immobilised apertures, via reduction of ectoapertures towards cryptoporate spherical to brevix grains characterised by a peristatic stress pattern. Comparable changes

have taken place in other families (Muller, l.c.). The development of spines represents a new element in the evolution of *Harpullia* pollen, but also this has many parallels in other families and probably has identical functional significance.

c. Character analysis

This analysis will first establish homologies, then proceed to the recognition of transformation series and finally attempt to determine their polarity.

In the various pollen types described in the preceding chapters the homology of certain basic structures of the exine appears well established. The apertures, the subdivision of the exine in endexine, footlayer, columellae and tectum no doubt are homologous and any changes which must have taken place in evolution can be seen as transformation series. There is only one character where homology is in doubt and this is the suprategal sculpture. While the tectal perforations found in the *H. arborea* type, *H. austro-caledonica* type and *H. frutescens* subtype are clearly comparable and homologous with the lumina of the reticulum found in the other subtypes of the *H. cupanioides* type and in the *H. rhachiptera* type, for the suprategal elements this is not obvious. The ridges of the *H. arborea* and *H. austro-caledonica* types are of course homologous, but those found on the broad muri of the *H. rhachiptera* type look different, since they are not separated by grooves with tectal perforations and are situated in one plane, in contrast to the three-dimensional anastomosing in the former types.

This is probably caused by the fact that there is no single genetic factor responsible for 'striation', but that it is a result of the interaction of a great many factors determining dimensions, orientation both in the horizontal and vertical direction, degree of anastomosing, etc. In *H. rhachiptera* the genetic expression of the striate pattern appears to be weak compared to the complex structures which have evolved in the other types and one is tempted to call it rudimentary.

A bigger problem is involved in the comparison of the striate pattern with the echinate one found in the *H. cupanioides* type and more specifically the question whether the spines are homologous with the ridges and may have developed from them, or represent independently evolved structures. A close study of SEM graphs only revealed slight evidence of transitional structures in the shape of somewhat elongated spine bases. Ontogenetical studies will be necessary to settle this.

On the other hand the occasional presence of distinct alignments of the tectal perforations in the *H. frutescens* type suggests that the spines themselves may also conform to a linear arrangement and thus could be equivalent to shortened ridges.

The transformation series (evolutionary trends) which can be recognised in *Harpullia* pollen characters are the following:

- a. Shape: subprolate – spherical – suboblate.
- b. Apertures: long colpi – short colpi – absence of colpi.
- c. Tectum: perforate – reticulate.

The suprategal sculptural elements can be divided into striate and echinate, but as discussed above on presently available evidence, they cannot be derived from each

other and it seems most probable at present that they have diverged independently from a perforate tectum without any suprategal elements. This is supported by the fact that a perforate tectum is present both in the striate-rugulate group and in some subtypes of the echinate groups, as well as in many other Sapindaceous pollen types.

Before attempting to determine the polarity of these series it must be pointed out that they are not independent and that there is a close correlation between a subprolate shape, long colpi and either a striate-rugulate or a perforate-echinate sculpture, while the spherical-suboblate shape is correlated with reduced or absent colpi and a reticulate sculpture, and that these represent different structural solutions to harmomegathy. In detail it was also clear that colpus reduction and increase in coarseness of reticulum is less closely correlated and may indicate genetic independence of the underlying factors.

The polarity of the separate series based on in-group and out-group comparison is for shape and apertures from subprolate with long colpi to spherical-suboblate with reduced colpi and for tectum structure from perforate to coarsely reticulate. For the suprategal elements the most likely development has been from smooth to striate and from smooth to echinate, thus recognising that both striate and echinate may be considered as derived. To assume a development from striate via a despecialised condition into a new direction towards the echinate condition appears decidedly less parsimonious.

Within the striate condition it could further be investigated whether the striate sculpture with parallel orientation or the striate-rugulate pattern with random orientation can be recognised as a transformation series and here the random orientation may have preceded the parallel one, because it is functionally less specialised.

What counts, however, in natural selection is the viability of the entire organism, i.e. the pollen grain resulting from the combined action of its individual characters, part of which may be linked and which actually may represent a compromise solution for conflicting demands. Even small genetic differences in survival during transport and in germination efficiency will be directly acted upon and lead to differential reproduction. Thus it may be more logical to consider the pollen type itself and not the separate component characters as the evolutionary unit and it will next be attempted to arrange at a higher level the types in transformation series.

For the echinate series there is a distinct arrangement of subtypes from the *H. frutescens* subtype to the *H. crustacea* subtype and the same trend towards reduction of colpi and a peristatic stress pattern is known from other families, indicating that the former is primitive, the latter advanced. Since spines are very rarely developed in pollen of Sapindaceae, it can be considered an advanced condition and the *H. frutescens* subtype can be derived in its turn from a subprolate tricolporate perforate pollen type which is probably basic in Sapindaceae (Muller & Leenhouts, 1976) and which is preserved in Harpullieae in the genus *Delavaya*.

The striate-rugulate type, in contrast, is actually widespread both in Harpullieae where it is found in *Arfeuillea*, *Majidea*, *Harpullia*, *Conchopetalum*, *Sinoradlkofera*, and *Ungnadia* and in Sapindaceae in general (cf. Muller & Leenhouts, l.c.), as well

as in many other families such as Anacardiaceae, Burseraceae, Leguminosae, and Rosaceae. However, parallel evolution from the same basic tricolporate-perforate pollen type is a more parsimonious assumption than disregarding the overwhelming macromorphological evidence against close taxonomic relations.

As already discussed the *H. rhachiptera* type cannot easily be derived from a single ancestral type because it combines features from both the striate and reticulate groups, although the latter predominate. It probably represents a genetic anomaly caused by hybridisation and backcrossing.

Thus, while pollen morphological evidence can indicate monophyly for the species characterised by the *H. cupanioides* type on one hand and the species with the *H. arborea* and the *H. austro-caledonica* types on the other, there is no evidence indicating monophyly for the genus as a whole, except for the rather tenuous evidence provided by the possible hybrid nature of *H. rhachiptera*.

Finally, it could be argued that the *H. cupanioides* type involves a more complex reorganisation from the postulated common prototype than the *H. arborea* and *H. austro-caledonica* types and therefore has a lesser probability to evolve and thus a lesser chance to occur in outgroups. In fact, the only comparable type known is found in *Commiphora* (Burseraceae), undoubtedly due to parallel development.

d. Phylogenetic values

Leenhouts (1985) has calculated the degree of macromorphological advancement for the different species of *Harpullia* and this can be supplemented by the pollen morphological evidence according to table 1, which summarises the evidence discussed in the preceding paragraphs:

Table 1

0 ancestral	1 derived
colpi long	colpi reduced
subprolate	spherical-suboblate
rugulate perforate	striate perforate
perforate	reticulate

In table 2 on the next page the values obtained are listed together with the values based on macromorphology, while the species are arranged according to the total values obtained.

It will be clear that there is a distinct positive correlation between the macromorphological and pollen morphological values and it is thus possible to utilise the total values in the final interpretation of the evolutionary history of the genus. However,

Table 2

	Pollen	Macromorphology	Total
<i>H. austro-caledonica</i>	0	1–2	1–2
<i>H. pendula</i>	1	½–3	1½–4
<i>H. arborea</i>	1	1–5	2–6
<i>H. alata</i>	1	3	4
<i>H. frutescens</i>	1	3	4
<i>H. hillii</i>	2	2–5	4–7
<i>H. cupanioides</i>	2	2½–4	4½–6
<i>H. longipetala</i>	2	3–3½	5–5½
<i>H. rhyticarpa</i>	1	4–6	5–7
<i>H. solomonensis</i>	1	5	6
<i>H. vaga</i>	3	3½	6½
<i>H. camptoneura</i>	3	4	7
<i>H. crustacea</i>	3	4	7
<i>H. ramiflora</i>	2–3	5	7–8
<i>H. carrii</i>	3	4–5	7–8
<i>H. largifolia</i>	3	5	8
<i>H. cauliflora</i>	3	5	8
<i>H. myrmecophila</i>	3	5	8
<i>H. petiolaris</i>	3	5	8
<i>H. rhachiptera</i>	3	5	8

there is generally no clear correlation between individual macromorphological and pollen characters with the exception of the characters separating the two subgenera. However, a correlation exists, within the species united in the *H. cupanioides* type with two character series, winged vs. non-winged rachis and terminal/axillary vs. rami/cauliflorous inflorescences, both of which were not used by Leenhouts (1985) because the polarity could not be sufficiently well established.* The distribution of these character states is shown in table 3.

These data suggest that, at least within the group of species considered, a winged rachis may be primitive and rami/cauliflory advanced. However, in Leenhouts' phylogenetic interpretation the species listed fall into two separate series, suggesting that there has been parallel evolution in pollen morphology, therefore the evidence can only suggest that the pollen morphologically advanced rami/cauliflorous species represent a grade, not a clade.

* Finally, these two characters have also been included in the macromorphological phylogenetic system. In accordance with palynology, rami- and cauliflory has been accepted as derived; more hesitatingly and contrary to palynology a winged petiole and leaf rachis is also accepted as the derived state (see Leenhouts 1985: chapter 5A). – PWL.

Table 3

		phylogenetic value	winged rachis	rami/cauliflory
primitive	<i>H. frutescens</i>	1	+	
	<i>H. rhyticarpa</i>	1	+	
	<i>H. alata</i>	1	+	
	<i>H. solomonensis</i>	1		×
	<i>H. hillii</i>	2		
	<i>H. cupanioides</i>	2		
	<i>H. longipetala</i>	2		×
	<i>H. carrii</i>	3		
	<i>H. largifolia</i>	3		×
	<i>H. ramiflora</i>	2-3		×
	<i>H. camptoneura</i>	3		
	<i>H. cauliflora</i>	3		×
	<i>H. vaga</i>	3		
	<i>H. myrmecophila</i>	3		×
advanced	<i>H. petiolaris</i>	3		×
	<i>H. crustacea</i>	3		

e. Phylogeny

In the following paragraphs the pollen morphologic evidence will be further integrated with the macromorphological, ecological and distributional evidence to come to a synthesis of the evolutionary history of *Harpullia*. The relevant data have been assembled in a cladistic scheme in figure 2, which will be discussed in detail next.

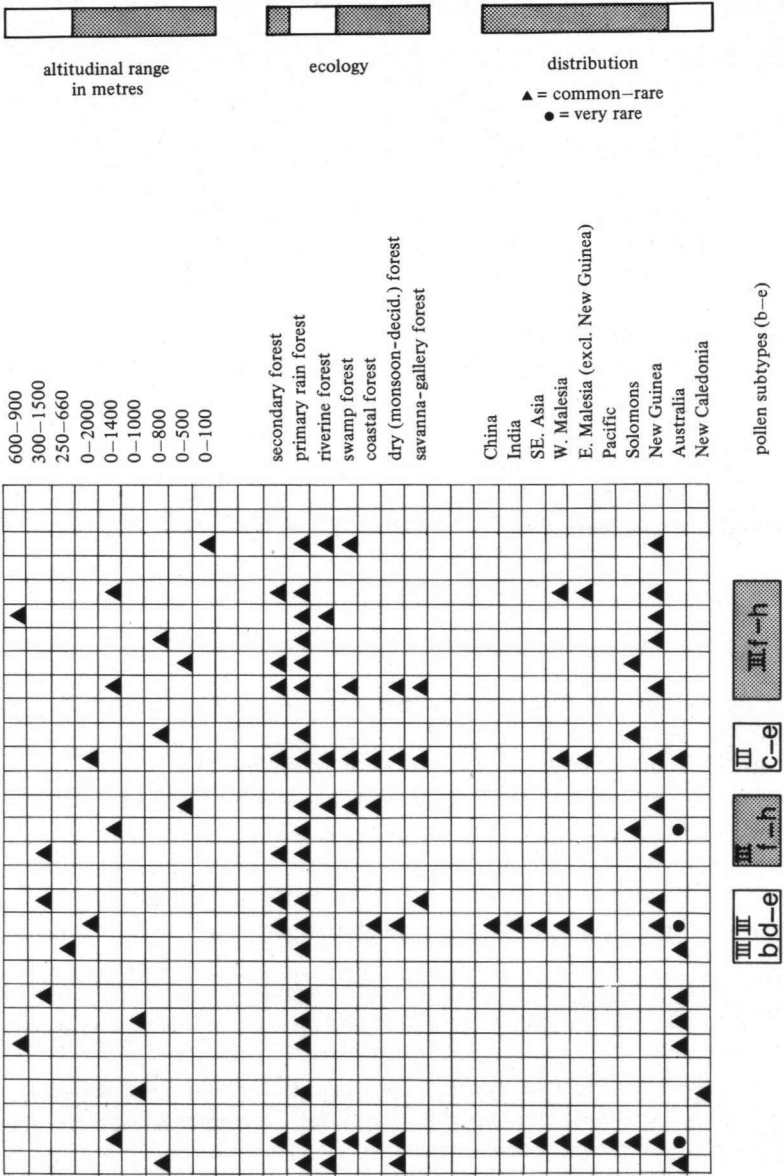
First of all it must be emphasised that this analysis is only valid when *Harpullia* forms a monophyletic group, held together by one or more advanced character states. In the original circumscription of Radlkofer (1933-34) *Harpullia* is keyed out against the other genera by a combination of characters, none of which is unique to the genus.

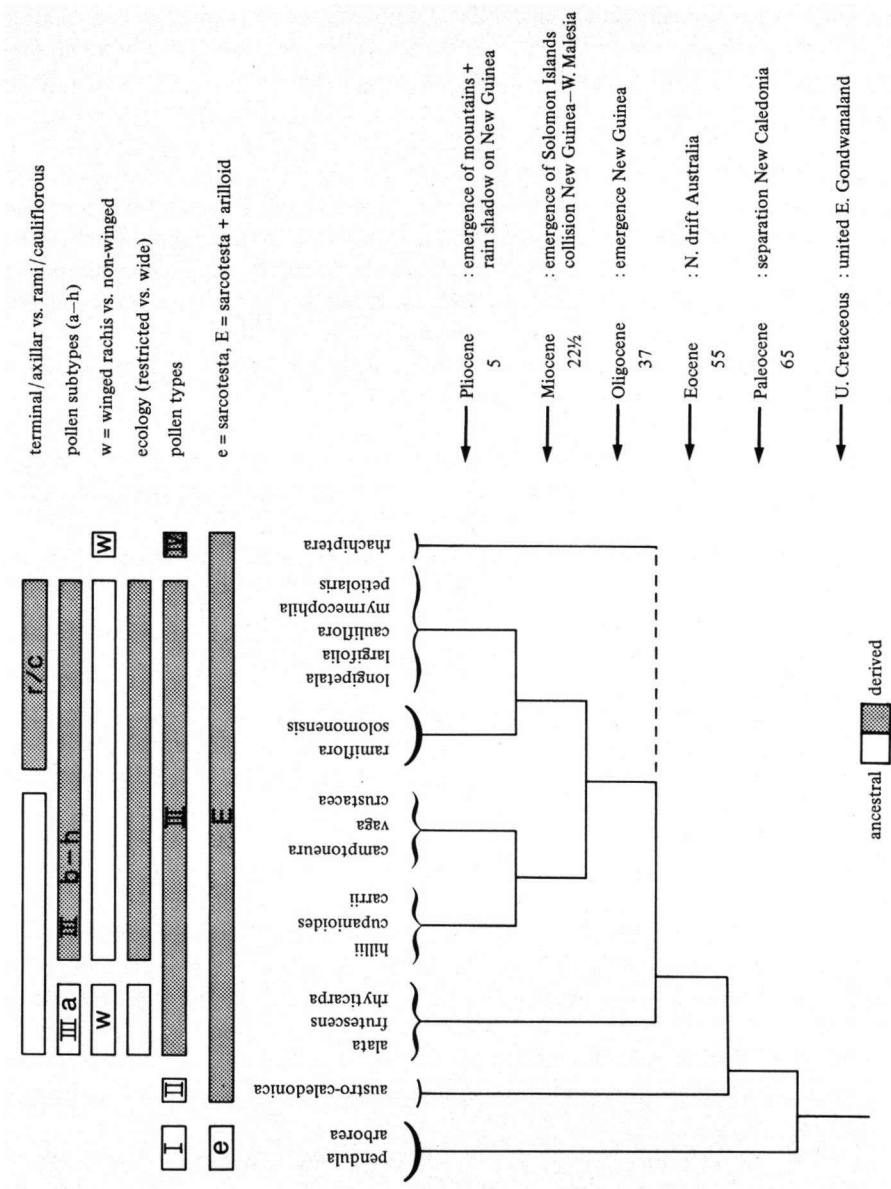
According to Leenhouts (pers. comm.) the relatively large, usually short-stipitate, 2-3-lobed dehiscent fruits with erect to spreading inflated lobes are characteristic for the genus.*

Within *Harpullia* the main macromorphological character, on which the separation in two subgenera is based, is concerned with the development of sarcotesta and ariloid and here the presence of both is taken by Leenhouts (1985) as derived. The interpretation of the other macromorphological characters on which the distinction of species is based cannot at present be utilised for a cladistic interpretation, with the possible exception of rami/cauliflory and winged rachis.

* In combination with arillate, glabrous seeds to distinguish it from *Majidea*. - PWL.

Figure 2





The pollen evidence is utilised at the level of types and subtypes which, as discussed before, give a better overall indication of relative degree of advancement than the separate but functionally linked characters. Ecology is added as an equivalent character because a compilation of the ecological data on the field labels of *Harpullia*, presented in figure 2, shows that the genus occurs in a wide range of altitude and climate, some species showing a wide tolerance, others being much more restricted.

Primary rain forest appears to be the original habitat and it is significant that the Australian species may occur at fairly high altitudes, suggesting an original adaptation to a subtropical-tropical/montane rather than to a tropical lowland climate. The widespread species have nearly always been recorded also from secondary forest. Occurrence in riverine and swamp forest is also quite frequent, but coastal forest and especially climatically dry forests have been colonised by only a few species, suggesting that this may be a secondary adaptation and is thus derived.

The altitudinal range is indicated separately and is mostly very wide, although restricted montane as well as lowland species occur.

The distribution of the species is also indicated and it is not surprising that widely ranging species such as *H. arborea*, *H. cupanioides* and *H. ramiflora* have a wide ecological tolerance, while restricted species such as the Australian species and some of the New Guinean endemics are very narrowly confined ecologically.

The recent species of *Harpullia* appear to be concentrated in two principal areas, Northeast Australia and New Guinea. In order to understand the significance of the distribution patterns, it is necessary to summarise first the relevant geological events which, together with dispersal, have caused them. For this the synthesis by Raven & Axelrod (1974) is followed.

Basic is the recognition of a united East Gondwanaland in the Upper Cretaceous including Australia, New Caledonia and possibly a small southern part of New Guinea. In the Paleocene New Caledonia separated from Australia, carrying and preserving in a highly equable climate relict taxa derived from the eastern Australian Upper Cretaceous flora.

During the Eocene Australia gradually moved northwards, entering tropical latitudes. New Guinea was largely submerged during this period, but in the Late Oligocene moderate uplift started, resulting in full lowland emergence in the Miocene.

At the same time the north moving Australian–New Guinean plate collided with the West Malesian area, resulting in the first interchange between Southeast Asian and Australian floral elements. Also in the Miocene the Solomon Islands started to emerge, consisting of rocks formed in inner island arcs behind a frontal arc system to the northeast: they were probably populated over water barriers, mainly by way of New Guinea.

The last event of significance for the history of *Harpullia* was the emergence of the high central mountain chain of New Guinea in the Pliocene, which led to the development of a dry climate in the rainshadow in the southeast and of an accompanying drier vegetation type here.

It thus appears probable that New Caledonia has received its single endemic species at a time when it was still connected with Australia, a clear example of vicari-

ance, and no long-distance dispersal needs to be involved here. New Guinea, because of its younger age and geologically different environment (Van Steenis, 1979) no doubt represents a secondary centre of speciation.

On the other hand, colonisation of the Solomon Islands probably has involved short-distance overseas dispersal, followed by local endemism. But it is especially in the case of the widely distributed species that dispersal must have been more significant than vicariance. In this connection it is of interest that only one species, *H. arborea*, has reached both the West Pacific and Southeast Asia. The first dispersal direction may be older than the second one which cannot be older than Miocene, but high dispersal capacity must have been a prerequisite.

A similar interplay of vicariance and dispersal has been postulated for Aceraceae on the base of an extensive fossil record by Wolfe (1981).

Harpullia cupanioides, *H. ramiflora* and *H. petiolaris* also did manage to reach West Malasia, but their recent distribution patterns are significantly different from that of *H. arborea*, probably indicating random influences in their dispersal.

The combined information can now be utilised in the construction of the cladogram in the lower left hand corner of figure 2.

The main division is on the presence of a sarcotesta as primitive (plesiomorphous) or a sarcotesta + arilloid as advanced (apomorphous), leading to the taxonomic separation in two subgenera.

The next dichotomy is based on pollen type II (primitive) against III + IV (advanced). This represents the separation between the ancestral line of *H. austro-caledonica* and the group of species characterised by perforate-reticulate pollen.

Next a separation in a group with IIIa pollen, a narrowly restricted ecology and a winged rachis and a group without a winged rachis, IIIb-h pollen and a highly variable ecology appears possible, the character states in the first group with a lesser or greater probability being primitive, in the second group being advanced. At this level the anomalous *H. rhachiptera* is tentatively connected, its pollen probably being more derived than IIIa.

The following dichotomy is based on rami/cauliflory, interpreted as advanced against axillary inflorescences, although parallel development cannot be excluded. In both groups a basal species complex can be recognised (*H. hillii/cupanioides* and *H. ramiflora* respectively).

The final separations in each sister group are both based on a supposedly parallel evolution in pollen morphology.

The validity of the resulting cladogram can next be tested against the taxonomy, the degree of morphological advancement of the taxa, their distribution and the succession of geological events.

The basic taxonomic separation in two subgenera, *Otonychium* and *Harpullia*, is of course equally reflected in the cladogram. The separation between *H. austro-caledonica* and the other species of subg. *Harpullia* appears more strongly emphasised in the cladogram than in the taxonomy. The recognition of *H. alata*, *H. frutescens* and *H. rhyticarpa* as a related group is also expressed both in taxonomy and in the cladogram, but the taxonomic affinity with the *H. ramiflora*-complex rather than with the

H. hillii-complex cannot be decided on the basis of the cladogram which rather indicates that the *H. alata*-complex is the sister group of the ancestors of both the latter groups. The cladistic separation of a ramiflorous versus of an axillary group has the consequence that *H. longipetala* is removed from the *H. hillii*-complex to the *H. ramiflora*-complex. The position of *H. rhachiptera* finally appears more uncertain on the cladogram than in the taxonomy.

Furthermore it is of interest to compare the degree of morphological advancement of each cladistic group, in the expectation that those groups that branch off at high (young) levels should be more advanced than those which have resulted from more ancient dichotomies. To a certain extent this is a logical consequence of the method of construction of the cladogram, but the phylogenetic values are also based on interpretation of characters, mainly macromorphological, which have not been utilised.

In general the expected relation appears to be present. *H. pendula*, *H. arborea* and *H. austro-caledonica* have clearly retained less advanced character states than their sister group, while at a higher level again *H. alata*, *H. frutescens* and *H. rhyticarpa* have remained at a lower degree of advancement than the species to the right of them on the cladogram. Even within the *H. hillii/camptoneura*- and the *H. ramiflora/longipetala*-groups this tendency appears to be present. This may be seen as a general support for the cladogram. However, in the comparison between *H. arborea* + *H. pendula* and *H. austro-caledonica* an anomaly is indicated by the very low phylogenetic value of the latter, meaning probably that the true relation of this species has not yet been correctly interpreted.

The distribution pattern as a result of both adaptive radiation and geological events should also be reflected in the cladogram and it is here because of the time element involved that the most stringently independent check on its validity can be obtained.

In general, the oldest fragments of the present day distributional area of *Harpullia*, viz. Northeast Australia and New Caledonia, are occupied by the more archaic groups and this is especially true of New Caledonia, where the primitive *H. austro-caledonica* has been preserved, presumably with little morphologic change since pre-Eocene time. Also, the fairly primitive *H. alata*-group occurs in an area which probably was occupied by the ancestral stock of *Harpullia* subg. *Harpullia* at least since Paleocene time and which has been stable geomorphologically, if not climatologically. For the younger species groups a shift in concentration of adaptive radiation to the younger emergent area of New Guinea is very obvious and since this probably reflects adaptation to new climatic conditions and colonisation of a young landscape with soils very different from Australia, and with certainly a very restricted niche saturation because the West Malesian flora would hardly have entered yet, the increase in species differentiation reflected by the higher (= younger) part of the cladogram checks very well. Only the distribution pattern of the widespread species found in both subgenera cannot be predicted from this cladistic analysis and reflects a random element of chance dispersal.

The place of *Harpullia* in the tribe Harpullieae is less clear and no cladogram can be presented yet.

Of the types listed earlier, the *H. austro-caledonica* and especially the *Delavaya* type appear to be closest to the basic tricolporate-perforate pollen type of Sapindaceae. However, in an evaluation of the macromorphological evidence Leenhouts (unpublished) does not regard these two genera as especially primitive nor as closely related.* Moreover, they are widely separated geographically. On the other hand the close relations between the Chinese genera *Delavaya* and *Xanthoceras* are intriguing because they indicate the independent development of an echinate pollen type and are thus reminiscent of the *H. austro-caledonica*–*H. cupanioides* type pair in *Harpullia*.

The occurrence of the striate *H. arborea* pollen type in so many genera of Harpulleae is, as already argued previously, most probably due to parallel evolution. The *Magonia* type finally is undoubtedly derived, but completely isolated.

Four principal areas have been significant in the development of Harpulleae, of which Africa – Madagascar, East Australia – New Caledonia and South America formed part of Gondwanaland. As discussed earlier, the presence of *Harpullia* in Southeast Asia is most probably due to secondary immigration from Australia and New Guinea in the Miocene. The other Asian genera may have immigrated via Africa or India at an earlier time and a secondary diversification can have led to the origin of Aceraceae and Hippocastanaceae. Since the oldest known macrofossils of Aceraceae date from the Paleocene (Wolfe, 1981), the original invasion of ancestral Harpulleae in Asia must date back to an even earlier period and an Upper Cretaceous origin for the tribe itself is likely, which is in agreement with the postulated pre-Eocene origin for the genus *Harpullia*. But it is evident that too many connecting links have become extinct, resulting in the present disjunct distribution of the genera, to allow a more detailed interpretation.

8. CONCLUSIONS

The origin of *Harpullia* was probably in the Upper Cretaceous/Paleocene of East Gondwanaland which still consisted of Antarctica, Australia, New Caledonia and New Zealand. The genus may have originally adapted to subtropical rainforest, in view of the latitudinal situation of the area, and this preference is probably still expressed in the present-day Australian species *H. alata*, *H. frutescens* and *H. rhyticarpa*. The first separation of the two subgenera probably took place in this area. In subg. *Otonychium*, *H. pendula* appears to be the more primitive species, still adapted to Australian conditions, while *H. arborea* developed a wider tolerance and managed to colonise via New Guinea a very wide area. It is significant that the latter species is rare in Queensland.

H. austro-caledonica probably represents a very early branching off in subg. *Harpullia*, became subsequently isolated in New Caledonia in the Paleocene and has not changed markedly from the original primitive condition due to the climatically stable, but geologically peculiar local environment.

* In a provisional study on the phylogeny of Harpulleae it appeared that *Harpullia* is the most primitive genus; *Delavaya* is macromorphologically distinctly more derived; *Xanthoceras* may be closely allied to *Delavaya* but is distinctly more primitive. – PWL.

The *H. alata*–*H. frutescens*–*H. rhyticarpa*-group remained adapted to subtropical rainforest, but developed a new pollen type and a winged rachis. Significantly, they did not participate in the colonisation of New Guinea. Also the related but more advanced *H. hillii* remained restricted to Australia, but it was probably from its ancestors that the successful *H. cupanioides* emerged, analogous to the postulated origin of *H. arborea* from *H. pendula* stock. Again *H. cupanioides* occurs only very rarely along the north coast of Australia, emphasising its ecologic adaptation to soil and climatic conditions different from the original Australian cradle of the genus. From *H. cupanioides* various segregates can be derived, mostly higher evolved and adapted to specific ecologic conditions. *H. carrii* entered the savanna-gallery forest in Southeast New Guinea and is therefore likely to be one of the youngest species; *H. camptoneura* is a montane New Guinean species, *H. vaga* entered the Solomon Islands, and *H. crustacea* entered the swamp and coastal forests of New Guinea.

The sister group of this *H. cupanioides*-complex can probably be derived from *H. ramiflora*, which may have the widest ecological tolerance of all species of *Harpullia* still occurring in Australia, although its distribution is not as extensive as that of *H. cupanioides*, not having reached Borneo, Java, Sumatra, and the Southeast Asian mainland. It may have reached the Solomons but then developed probably in two species: *H. solomonensis* and *H. longifolia*, both therefore young species. In this complex there is also an altitudinal segregate; in New Guinea *H. myrmecophila*, while *H. petiolaris*, which is most advanced pollen morphologically, shows a curious disjunction between Borneo and the Moluccas–New Guinea probably due to Pleistocene extinction in the intermediate area. *H. longipetala* has invaded the dry area of Southeast New Guinea, as did *H. carrii*.

It is obvious that in both groups parallel evolution took place both as regards ecologic adaptation to the newly emerging New Guinean environment, in pollen morphology and possibly also in rami/cauliflory, casting some doubt on the monophyly of the different subgroups. However, it is quite likely that the two groups together form a monophyletic complex with the *H. alata*-group as its sister complex.

Harpullia rhachiptera, finally, is ecologically rather restricted to lowland tropical swamp and riverine environments and shows no clear relation to any of the other complexes. It probably branched off the ancestral complex at an early stage, presumably in the transition zone between North Australia and an emergent New Guinea and may reflect, because of its curious combination of characters, an origin from hybridising populations which were intermediate between the *H. alata*- and the *H. cupanioides*-complex, thus being a comparatively ancient relict rather than a young segregate. The evolution of its peculiar pollen type may be due to an initially unbalanced genetic combination of characters.

This synthesis indicated that, with younger age, the narrative becomes much more detailed, and it is to be hoped that fossil evidence may in future provide a further test for its reliability. At a higher taxonomic level the story for the Harpullieae is less clear, due no doubt to developments at a much earlier period, and much further taxonomic and morphologic study is needed.

ACKNOWLEDGEMENTS

The author is much indebted to Mr. W. Star for skillful TEM work, to Mr. B. Kieft for photographic reproduction and to Dr. P.W. Leenhouts for critical discussions and co-operation.

M. Pacqué, who prepared the manuscript for publication, is indebted to Dr. W. Punt (Utrecht) for suggesting some corrections and to Dr. P.W. Leenhouts for providing a few footnotes marked PWL. Mr. J. Wessendorp arranged some photo plates and drew figure 1; Mr. M. Groeneveld constructed figure 2.

REFERENCES

- DICKINSON, H.G. 1976. Common factors in exine deposition. In: I.K. Ferguson & J. Muller (eds.), *The evolutionary significance of the exine*. Linn. Soc. Symp. Ser. 1: 67–89.
- DOYLE, J.A., M. VAN CAMPO & B. LUGARDON. 1975. Observations on exine structure of Eucommiidites and Lower Cretaceous angiosperm pollen. *Pollen et Spores* 17: 429–486.
- ERDTMAN, G. 1948. Did dicotyledonous plants exist in early Jurassic times? *Geol. Fören. Stockh. Förh.* 70: 265–275.
- FAEGRI, K. 1956. Recent trends in palynology. *Bot. Rev.* 22: 639–664.
- GUÉDÈS, M. 1982. Exine stratification, ectexine structure and angiosperm evolution. *Grana* 21: 161–170.
- HENNIG, W. 1966. *Phylogenetic systematics*. Univ. Illinois Press.
- IVERSEN, J. & J. TROELS-SMITH. 1950. Pollenmorfologiske definitioner og typer. *Danm. Geol. Undersog.* IV, 3: 1–52.
- LARSON, D.A. 1966. On the significance of the detailed structure of *Passiflora caerulea* exines. *Bot. Gaz.* 127: 40–48.
- , J. SKVARLA & C.W. LEWIS. 1962. An electron-microscopic study of exine stratification and fine structure. *Pollen et Spores* 4: 233–246.
- LEENHOUTS, P.W. 1984. An attempt towards a natural system of *Harpullia* (Sapindaceae). *Blumea* 31: 219–234.
- & M. VENTE. 1983. A taxonomic revision of *Harpullia* (Sapindaceae). *Blumea* 28: 1–51.
- LE THOMAS, A. 1980. Ultrastructural characters of the pollen grains of African Annonaceae and their significance for the phylogeny of primitive Angiosperms (first part). *Pollen et Spores* 22: 267–342.
- LOBREAU-CALLEN, D. & B. LUGARDON. 1973. L'aperture a repli du pollen des Celastraceae. *Naturalia Monspel. Ser. Bot.* 23/24: 205–210.
- MAURY, G., J. MULLER & B. LUGARDON. 1975. Notes on the morphology and fine structure of the exine of some pollen types in Dipterocarpaceae. *Rev. Palaeobot. Palynol.* 19: 241–289.
- MULLER, J. 1979. Form and function in angiosperm pollen. *Ann. Missouri Bot. Gard.* 66: 593–632.
- & P.W. LEENHOUTS. 1976. A general survey of pollen types in Sapindaceae in relation to taxonomy. In: I.K. Ferguson & J. Muller (eds.), *The evolutionary significance of the exine*. Linn. Soc. Symp. Ser. 1: 407–445.
- PAYNE, W.W. 1981. Structure and function in angiosperm pollen wall evolution. *Rev. Palaeobot. Palynol.* 35: 39–59.
- POTONIÉ, R. 1956. Synopsis der Gattungen der Sporae dispersae. I. Sporites. *Beih. Geol. Jahrbuch.*
- PRAGLOWSKI, J. 1974. Magnoliaceae Juss. *World Pollen Spore Flora* 3: 1–44. Almquist & Wiksell, Stockholm.
- RADLKOFER, L. 1933–34. Sapindaceae. In: A. Engler, *Das Pflanzenreich IV*. Engelmann, Leipzig.
- RAVEN, P.H. & D.I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* 61: 539–673.

- REITSMA, I. 1966. Pollen morphology of some European Rosaceae. *Acta Bot. Neerl.* 15: 290–307.
- ROLAND, F. 1968. Etude de l'ultrastructure des apertures. II. Pollens a sillons. *Pollen et Spores* 10: 479–519.
- SKVARLA, J. & D.A. LARSON. 1965. Interbedded exine components in some Compositae. *Southwestern Naturalist* 10: 65–68.
- STEENIS, C.G.G.J. VAN. 1979. Plant geography of East Malesia. *Bot. J. Linn. Soc.* 79: 97–178.
- WAGNER, W.H. 1980. Origin and philosophy of the groundplan-divergence method of cladistics. *Syst. Bot.* 5: 173–193.
- WOLFE, J.A. 1981. Vicariance biogeography of angiosperms in relation to paleobotanical data. In: G. Nelson & D.E. Rosen (eds.), *Vicariance biogeography*: 411–445. New York.

EXPLANATION OF PLATES I–XIX

Plate I. *Harpullia arborea* (1–4 *Ledermann 6760*, 5–6 *A. Gibot 34023*). – 1: Polar and equatorial view, rather uniform striate pattern; $\times 2,050$. – 2: Detail of colpus, membrane with reduced ectexinous elements; $\times 9,000$. – 3: Polar view, slightly coarser, more reticulate pattern on the pole; $\times 3,900$. – 4: Detail of figure 3, small perforations between the ridges; $\times 15,500$. – 5: Expanded grain, colpi long and well developed; $\times 3,100$. – 6: Shrunken grain with meridionally infolded mesocolpia; $\times 3,100$. – All SEM.

Plate II. *Harpullia arborea* (*Vidal 1078*). – 1: Section of colpate area near the pole. Endexine (en) rather homogeneous, three intine layers (i_1, i_2, i_3) present, i_3 very thin; $\times 21,000$. – 2: Section of colpate area near the equator. Three intine layers (i_1, i_2, i_3) present, i_3 thick; $\times 16,500$. – 3: Section of endoapertural area. Four intine layers (i_1, i_2, i_3, i_4), i_1 mixing with endexinous granular material underneath endoaperture, i_4 exclusively present underneath endoaperture, only in *H. arborea*; $\times 21,000$. – 4: Section of intercolpate area. Sole (s) with very irregular upper surface, connecting the basally broadened columellae; $\times 21,000$. – All TEM.

Plate III. *Harpullia arborea* (*Vidal 1078*). – 1: Meridional section, endexine (en) thickens towards the margins of the endoapertures; $\times 9,200$. – 2: Section of tectum at high level, meridionally oriented anastomosing ridges with basal, perforate stratum; $\times 15,000$. – 3: Section of tectum at lower level; $\times 11,500$. – All TEM.

Plate IV. *Harpullia austro-caledonica* (1–3 *McKee 21634*, 4–5 *McKee 26770*). – 1: Equatorial view, colpi long and well developed; $\times 2,600$. – 2: Detail of colpus, membrane with reduced ectexinous elements. Finer sculpturing borders the colpus; $\times 5,000$. – 3: Rugulate pattern not present towards the poles; $\times 5,000$. – 4: Equatorial view, mesocolpium; $\times 2,600$. – 5: Detail of mesocolpium, rugulate pattern irregularly oriented; $\times 6,900$. – All SEM.

Plate V. *Harpullia austro-caledonica* (McKee 26770). — 1: Section of colpate area, endexinous (en) apertural shield well developed; $\times 8,500$. — 2: Nearly equatorial section; $\times 2,700$. — 3: Detail of figure 2, section of endoaperture with distinct endexine (en) thickening at the marginal part; $\times 25,000$. — 4: Section of intercolpate area, well developed sole (s) and thin endexine (en); $\times 63,500$. — All TEM.

Plate VI. 1–2. *Harpullia frutescens* (Hutchins s.n.). — 1: Equatorial view, colpi long and well developed, reticulate tectum with conspicuous supracteal spines; $\times 2,300$. — 2: Detail of colpus, membrane covered with minute rugulae and irregular spines; $\times 7,800$. — 3–6. *Harpullia alata* (Melbourne 71391). — 3: Equatorial view, colpi long and well developed, reticulate tectum with conspicuous supracteal spines; $\times 2,500$. — 4: Detail of colpus, membrane densely covered with minute irregularly shaped spines and verrucae; $\times 7,800$. — 5: Equatorial view, mesocolpium; $\times 2,400$. — 6: Detail of mesocolpial tectum with lumina variable in shape and size and conspicuous supracteal spines; $\times 7,800$. — All SEM.

Plate VIIa. *Harpullia frutescens* (Hutchins s.n.). — 1: Equatorial section of shrunken acetolysed grain with infolding mesocolpia; $\times 4,800$. — 2: Slightly oblique equatorial section of expanded acetolysed grain; $\times 4,800$. — All TEM.

Plate VIIb. *Harpullia frutescens* (1 Rudder 3640, 2 Hutchins s.n.). — 1: Section of intercolpate exine of unacetolysed grain. Sole (s) very irregularly developed, mixed laminated endexine-ectexine layer (m), endexinal laminae (arrowheads) closer together at the inner side, ectexinal laminae (arrows) partly continuous with sole; $\times 25,000$. — 2: Section of intercolpate exine of acetolysed grain. Sole (s) irregularly developed, mixed laminated endexine-ectexine layer (m) thin; $\times 33,500$. — All TEM.

Plate VIII. 1–2. *Harpullia hillii* (Gittins 1134). — 1: Equatorial view of reticulate variant A; $\times 3,100$. — 2: Detail of mesocolpium, irregularly reticulate tectum with small supracteal spines; $\times 4,800$. — 3–4. *Harpullia ramiflora* (Hoogland 4950). — 3: Polar view, colpi very long and narrow with smooth membranes; $\times 2,700$. — 4: Detail of reticulate tectum with scarce, indistinct supracteal spines; $\times 3,900$. — 5. *Harpullia solomonensis* (Waterhouse 645-B). Polar view, colpi long and narrow, with verrucate membranes, tectum with very small supracteal spines; $\times 2,700$. — 6. *Harpullia cupanioides* (SAN 28985). Detail of colpus, tectum reticulate with small supracteal spines; $\times 5,800$. — All SEM.

Plate IX. *Harpullia cupanioides* (SAN 28985). — 1: Section of intercolpate area of unacetolysed grain. Sole (s) very irregularly developed, mixed laminated endexine-ectexine layer (m); $\times 17,500$. — 2: Detail of mixed laminated endexine-ectexine layer (m), endexinal laminae (arrowheads) closer together at the inner side, ectexinous

material (arrows) partly continuous with sole(s); $\times 36,500$. — 3: Section of endoapertural area of unacetolysed grain. Mixed laminated endexine-ectexine layer (m) lamellar-imbricated towards endoaperture, three intine layers (i_1, i_2, i_3) present, i_2 with tubular-alveolar cytoplasmic tracts, i_3 electron transparent; $\times 25,000$. — All TEM.

Plate X. 1–2. *Harpullia largifolia* (BSIP 13220). — 1: Oblique polar view, colpi indistinct (arrowheads); $\times 2,700$. — 2: Detail of mesocolpium; tectum reticulate with suprategal spines; $\times 7,800$. — 3–4. *Harpullia longipetala* (Carr 11498). — 3: Equatorial view, colpi narrow; $\times 2,350$. — 4: Detail of colpus and endoaperture, tectum finely reticulate with suprategal spines; $\times 7,800$. — 5–6. *Harpullia vaga* (BSIP 9716). — 5: Equatorial view, colpi rather indistinct, $\times 3,100$. — 6: Detail of colpus, tectum irregularly reticulate with small suprategal spines; $\times 7,800$. — All SEM.

Plate XI. *Harpullia ramiflora* (Versteeg 1134). — 1: Tangential section of acetolysed grain; $\times 3,400$. — 2: Detail of figure 1, polar endoapertural costae (enc) rather distinct; $\times 9,200$. — 3: Intercolpate section of unacetolysed grain. Endexine (en) finely laminated-imbricated; $\times 3,100$. — All TEM.

Plate XII. 1–2. *Harpullia cauliflora* (Hort. Bog. III-I-12a). — 1: Equatorial view, colpi very indistinct (arrowheads); $\times 2,350$. — 2: Detail of mesocolpium, tectum reticulate with rather short suprategal spines, muri wide, locally broadened, $\times 7,800$. — 3–4. *Harpullia myrmecophila* (Brass 13285). — 3: Oblique equatorial view, colpi indistinct; $\times 2,700$. — 4: Detail of colpus, tectum irregularly reticulate with small suprategal spines; $\times 5,000$. — 5–6. *Harpullia petiolaris* (NGF 13258). — 5: Oblique equatorial view, colpi indistinct (arrowheads); $\times 2,700$. — 6: Detail of mesocolpium, tectum irregularly reticulate with suprategal spines; $\times 7,800$. — All SEM.

Plate XIII. *Harpullia crustacea* (NGF 11839). — 1: Cryptoporate grain, colpi absent; $\times 2,800$. — 2: Detail of coarsely reticulate tectum with indistinct suprategal spines, verrucae present in lumina; $\times 7,800$. — 3: Inner side of sectioned acetolysed grain with endoaperture; $\times 3,500$. — 4: Cross-section of exine; $\times 15,500$. — All SEM.

Plate XIVa. *Harpullia crustacea* (NGF 11839). — 1: Section of exine of unacetolysed grain. Sole (s) reduced to scattered granular masses, mixed laminated endexine-ectexine layer (m), endexine laminae (arrowheads) closer together at the inner side, ectexinal laminae (arrows) partly continuous with sole; $\times 73,000$. — 2: Detail of mixed laminated endexine-ectexine layer (m), bases of columella (c) continuous with interbedded ectexinous material (arrows); $\times 87,000$. — All TEM.

Plate XIVb. *Harpullia crustacea* (NGF 11839). — 1: Section of endoapertural area of unacetolysed grain with endoapertural costae (enc), pollenkitt present in the lumina;

× 12,500. — 2: Section of intercolpate area of unacetolysed grain with pollen kitt in- and outside the lumina; × 25,000. — All TEM.

Plate XV. *Harpullia rhachiptera* (LAE 51779). — 1: Cryptoporate grain, colpi absent, reticulum fairly coarse with striate muri; × 2,700. — 2: Detail of figure 1, ridges of muri in subparallel arrangement, fairly short, no supracteal spines; × 20,000. — 3: Cryptoporate grain, colpi absent, sculpture irregularly verrucate-rugulate; × 2,700. — 4: Detail of figure 3, supracteal spines present; × 13,500. — All SEM.

Plate XVI. From left to right: polar view, upper focus; polar view, optical section; equatorial view, colpus; equatorial view, endoaperture. — 1–4. *Harpullia pendula* (Williams s.n.): 1 & 2: same grain; 3 & 4: same grain. — 5–8. *Harpullia arborea* (Cuming 1269): 7 & 8: same grain. — 9–12. *Harpullia austro-caledonica* (McKee 24002): 9 & 10: same grain; 11 & 12: same grain. — 13–16. *Harpullia longipetala* (NGF 30337): 15 & 16: same grain. — 17–20. *Harpullia frutescens* (Hutchins s.n.). 17 & 18: same grain; 19 & 20: same grain. — All LM; × 1,000.

Plate XVII. From left to right: polar view, upper focus; polar view, optical section; equatorial view, colpus; equatorial view, endoaperture. — 1–4. *Harpullia alata* (Melbourne 71391): 3 & 4: same grain. — 5–8. *Harpullia rhyticarpa* (Winkel 14791): 5 & 6: same grain; 7 & 8: same grain. — 9–12. *Harpullia rhachiptera* (LAE 51779): 9 & 10: same grain; 11 & 12: same grain. — 13–16. *Harpullia hillii* (Queensl. Herb. 71177): 13 & 14: same grain; 15 & 16: same grain. — 17–20. *Harpullia cupanioides* (Pleyte 824): 17 & 18: same grain; 19 & 20: same grain. — All LM; × 1,000.

Plate XVIII. From left to right: polar view, upper focus; polar view, optical section; equatorial view, colpus; equatorial view, endoaperture. — 1–4. *Harpullia vaga* (BSIP 9716): 1 & 2: same grain; 3 & 4: same grain. — 5–8. *Harpullia crustacea* (NGF 11839): 5 & 6: same grain; 7 & 8: same grain. — 9–12. *Harpullia camptoneura* (Brass 32077): 9 & 10: same grain; 11 & 12: same grain. — 13–16. *Harpullia carrii* (Carr 12466): 13 & 14: same grain; 15 & 16: same grain. — 17–20. *Harpullia solomonensis* (Waterhouse 645-B): 17 & 18: same grain; 19 & 20: same grain. — All LM; × 1,000.

Plate XIX. From left to right: polar view, upper focus; polar view, optical section; equatorial view, colpus, equatorial view, endoaperture. — 1–4. *Harpullia ramiflora* (Aet 299): 1 & 2: same grain; 3 & 4: same grain. — 5–6. *Harpullia myrmecophila* (Brass 13285): 7 & 8: same grain. — 9–10. *Harpullia cauliflora* (cult. Hort. Bogor. Java III-I-12a): 9 & 10: same grain; 11 & 12: same grain. — 13–16. *Harpullia petiolaris* (Kostermans 631: subsp. *moluccana*): 13 & 14: same grain; 15 & 16: same grain. — 17–20. *Harpullia largifolia* (BSIP 6712): 17 & 18: same grain; 19 & 20: same grain. — All LM; × 1,000.

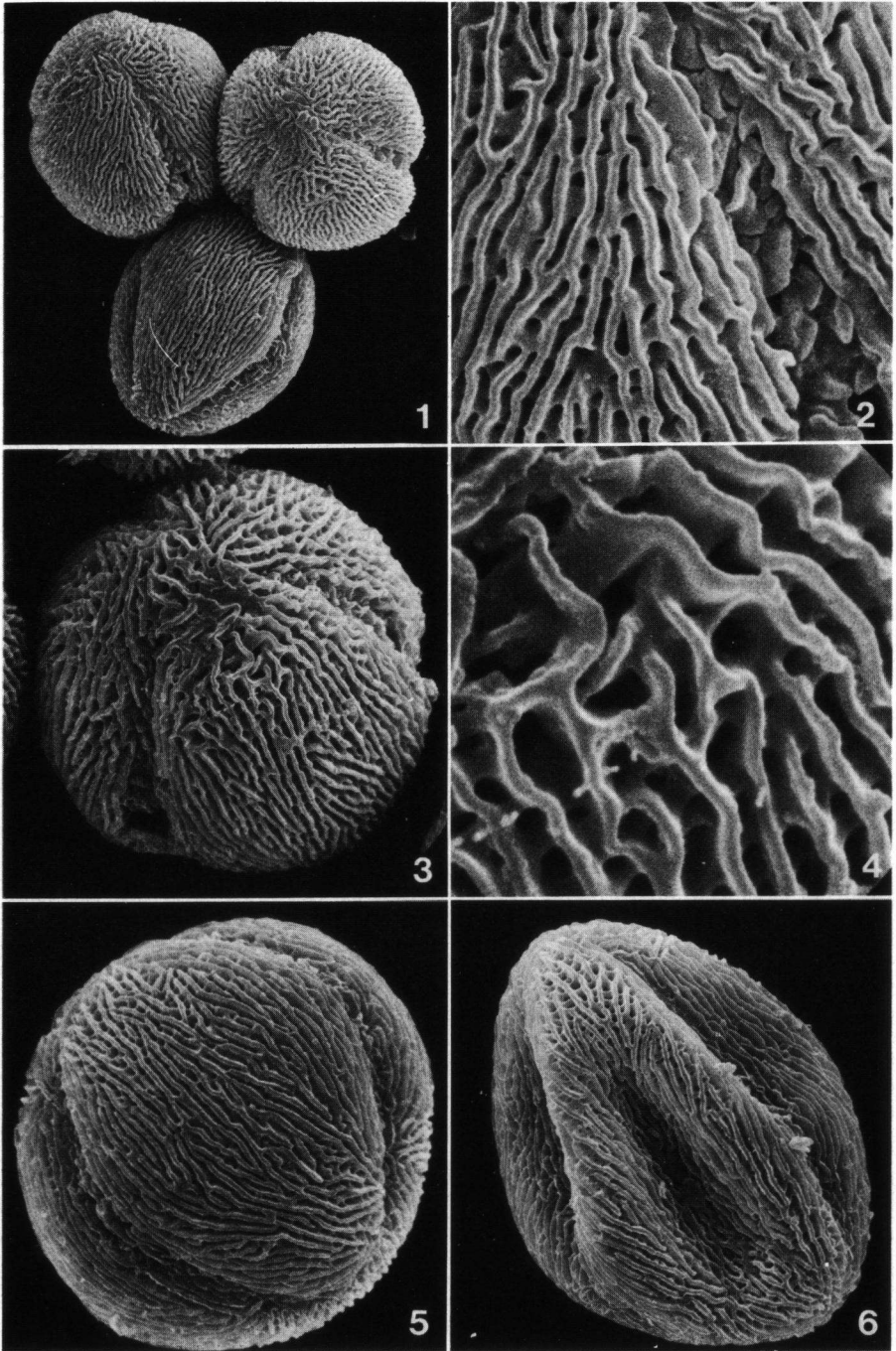


PLATE I

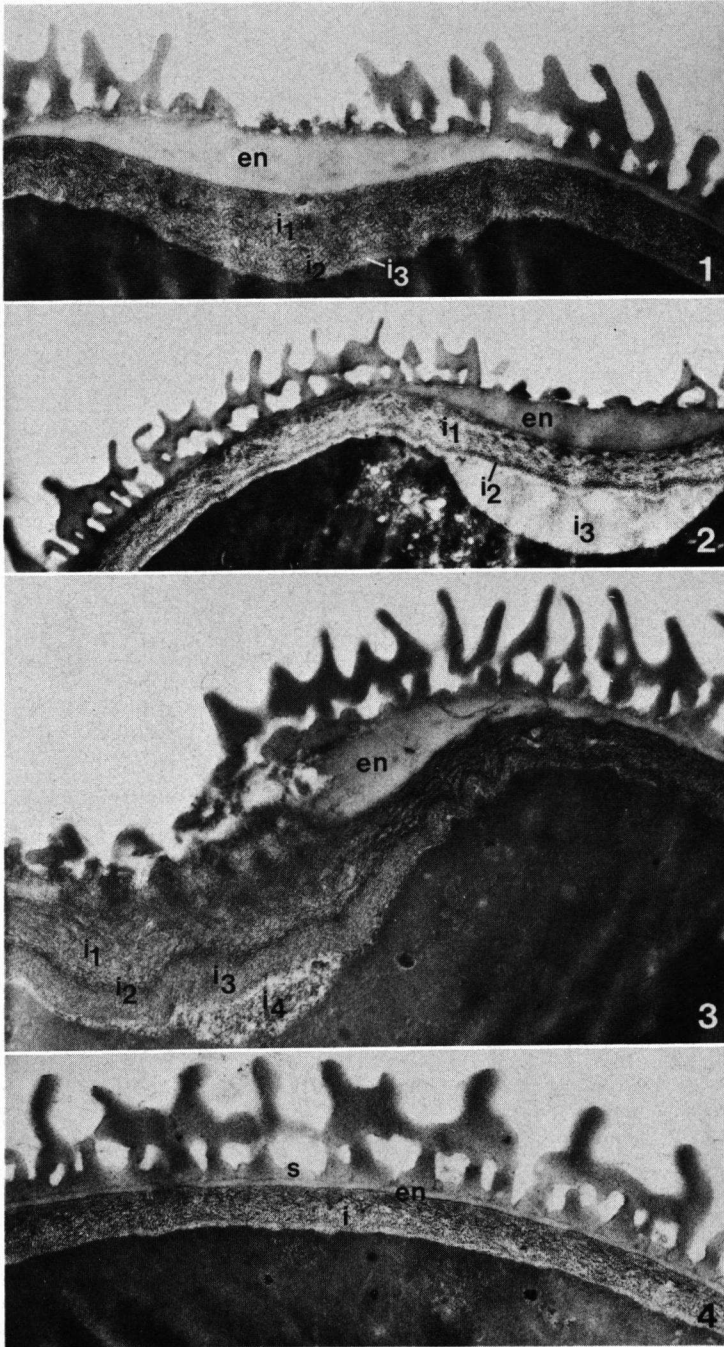


PLATE II

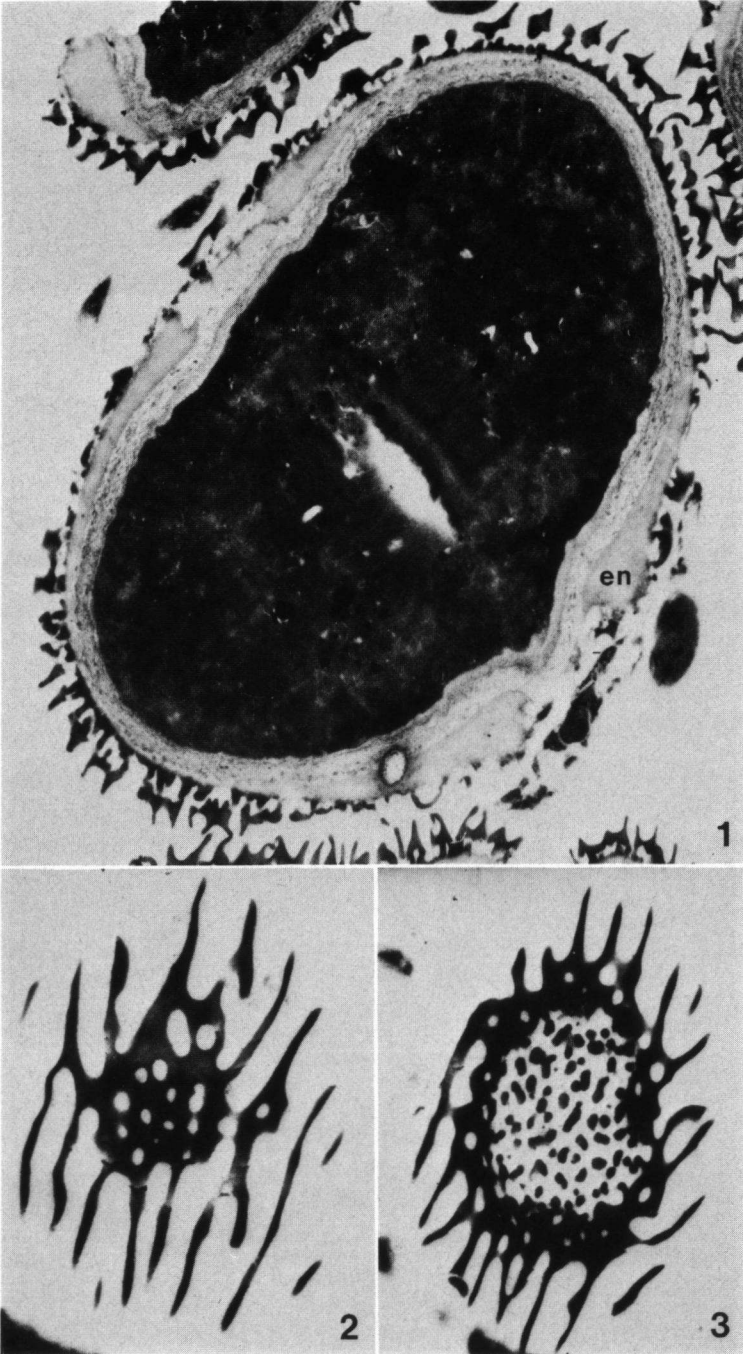


PLATE III

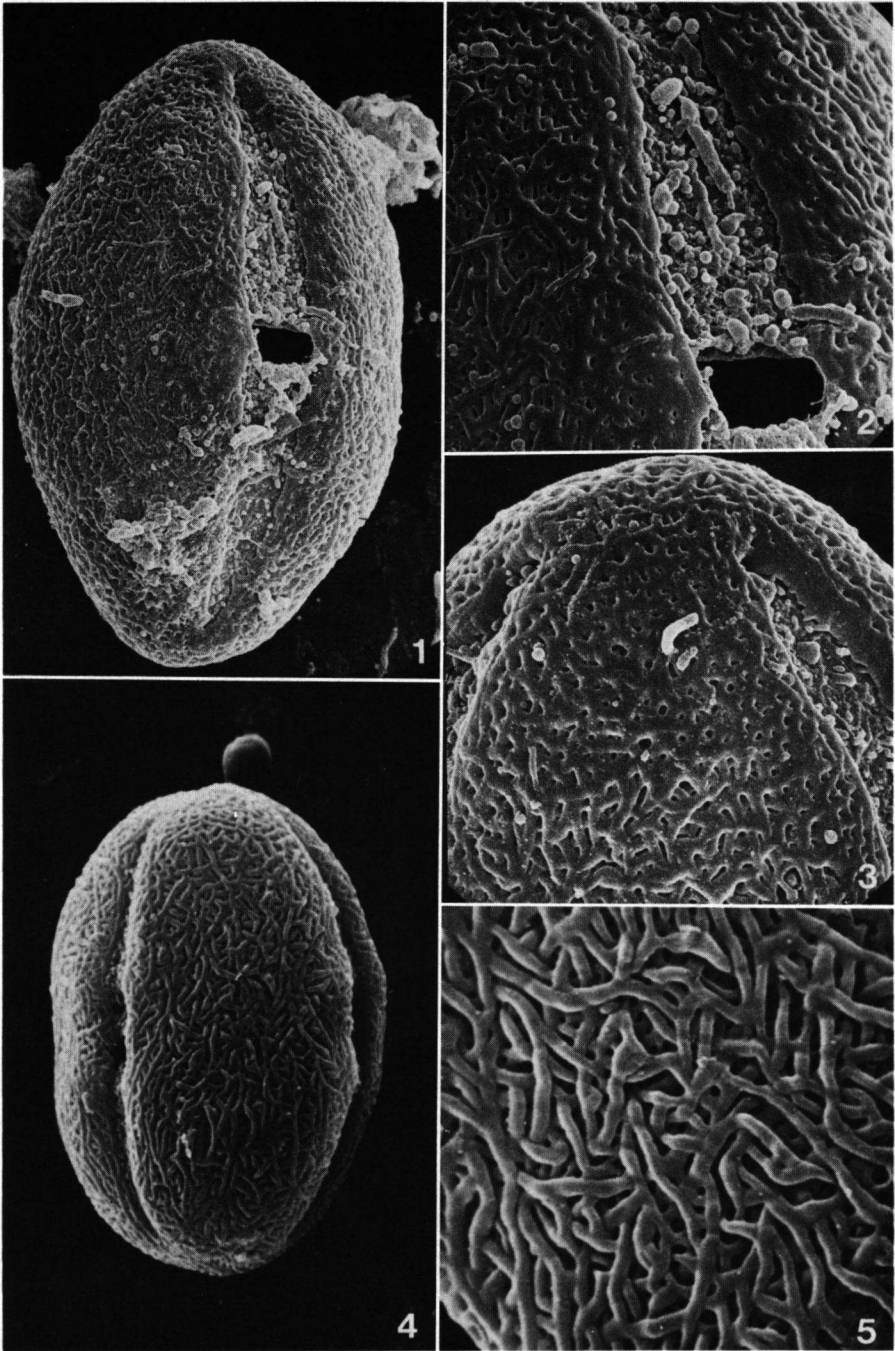


PLATE IV

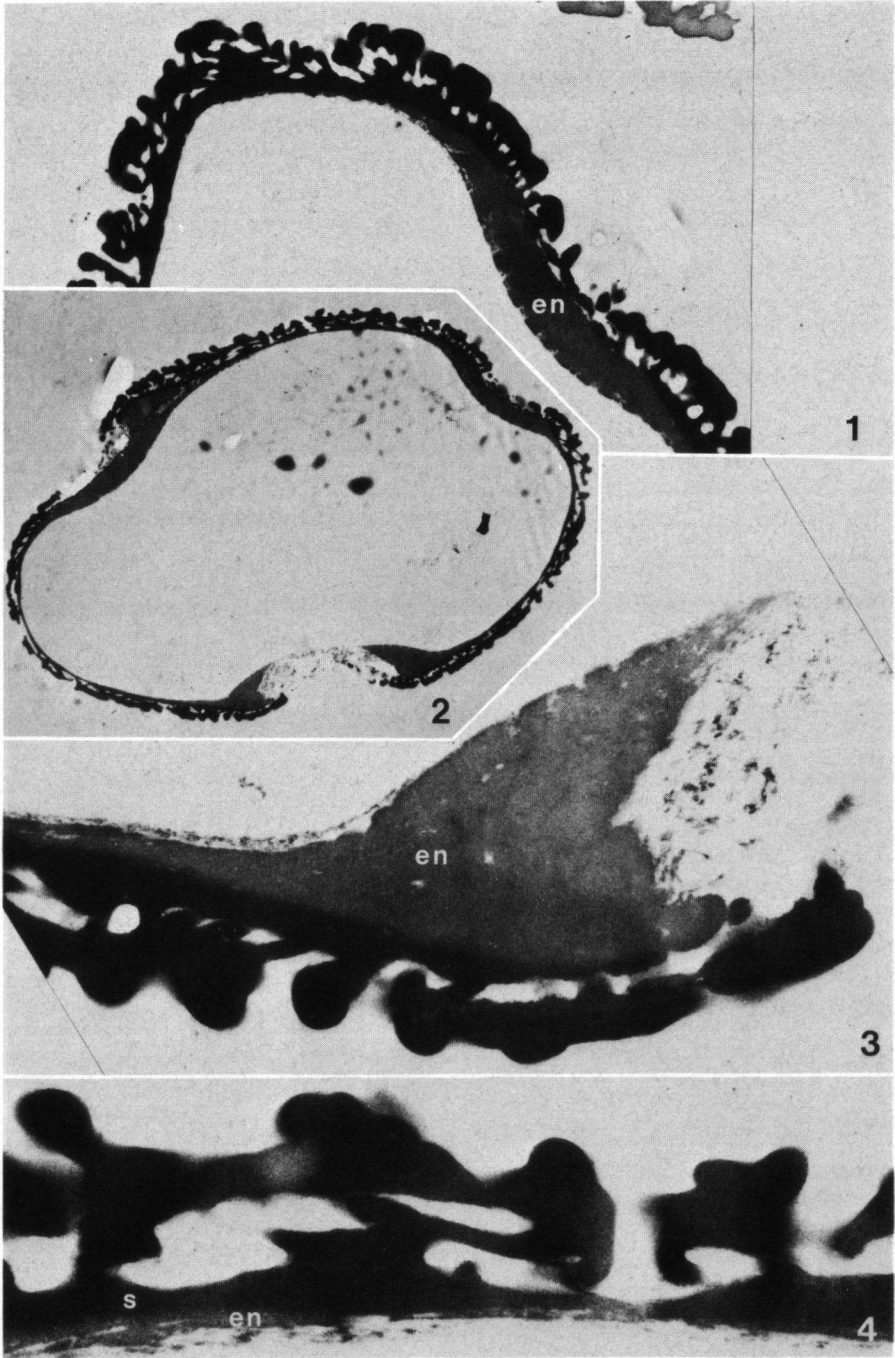


PLATE V

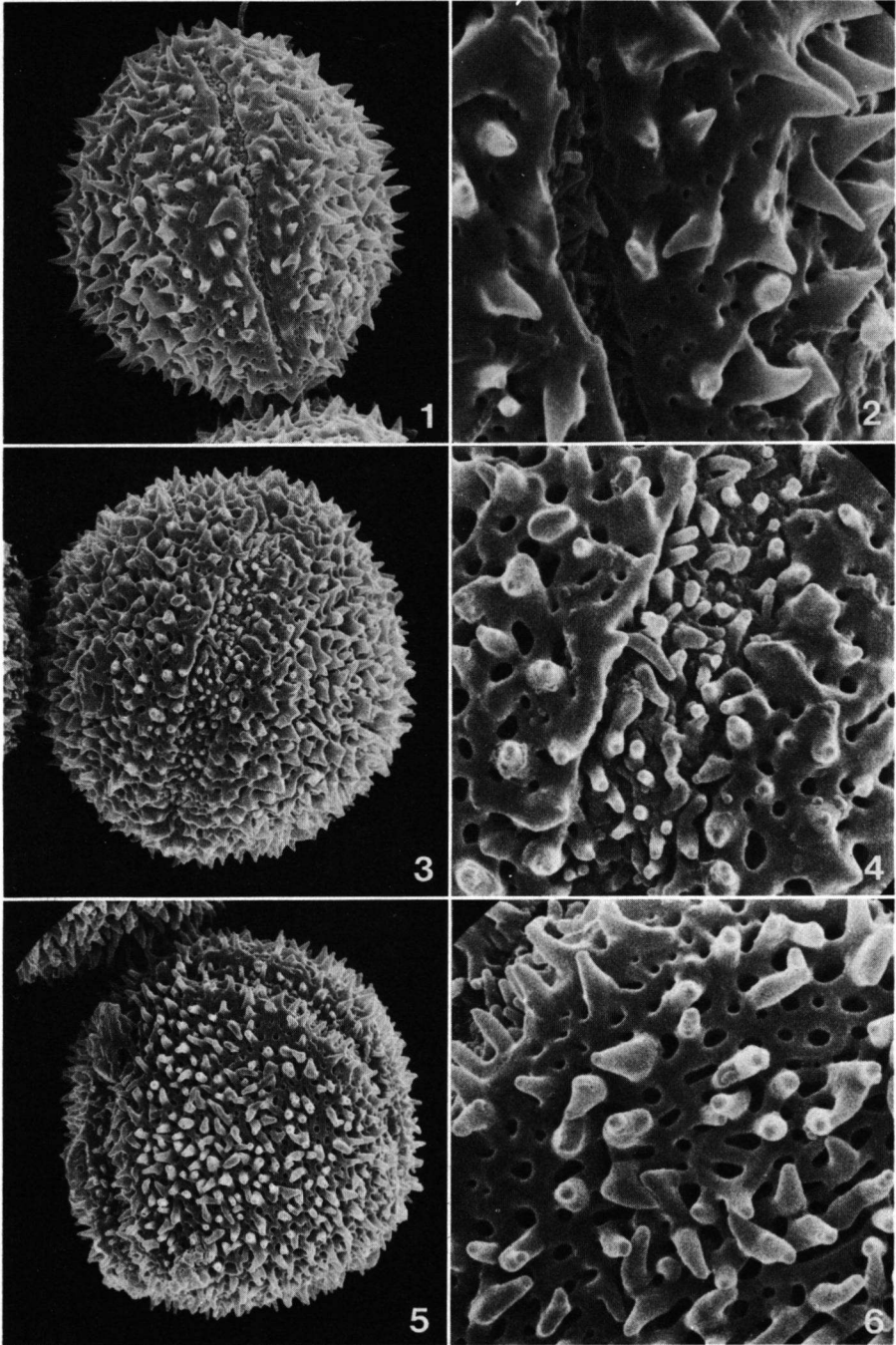


PLATE VI

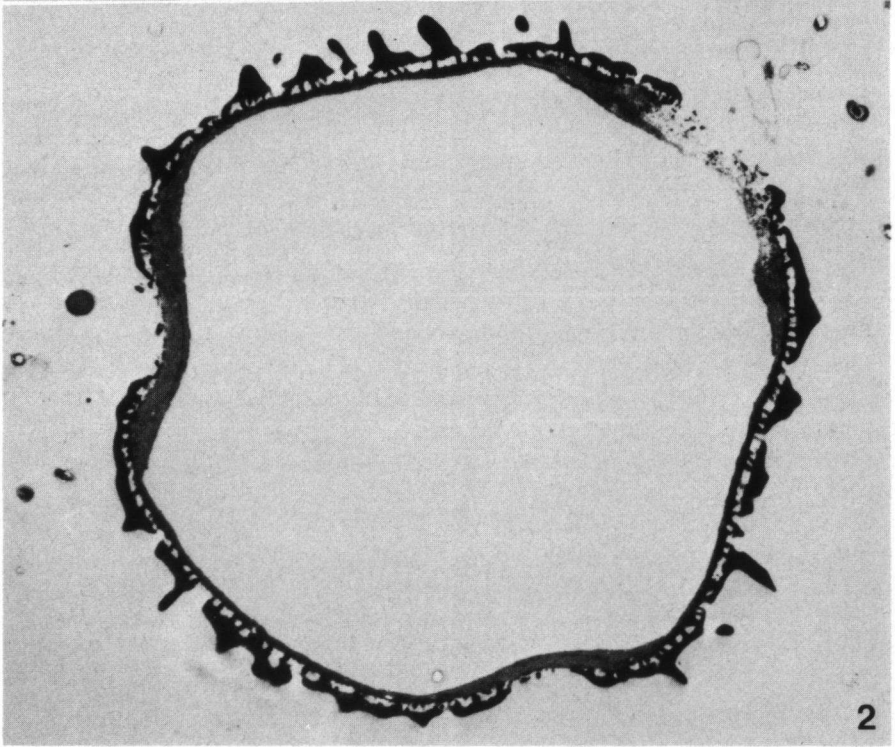
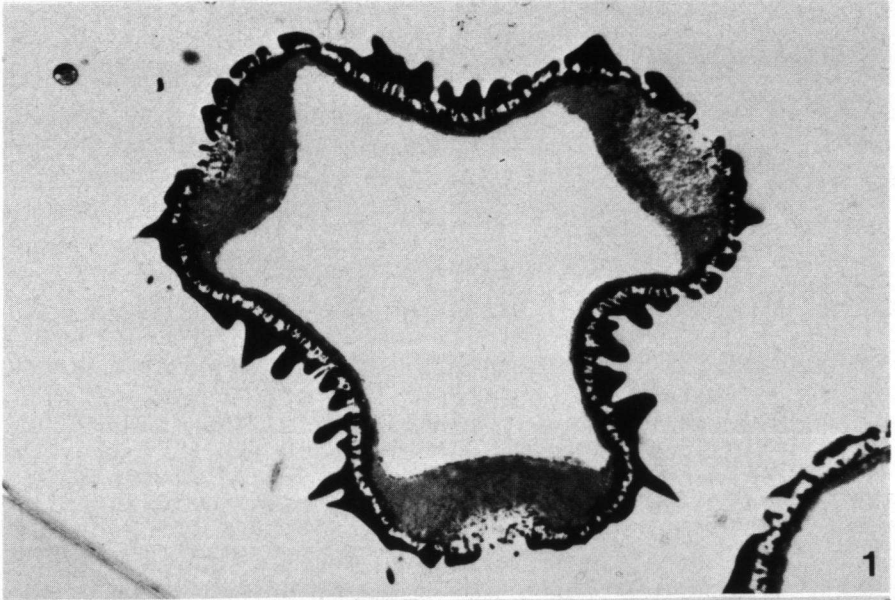


PLATE VIIa

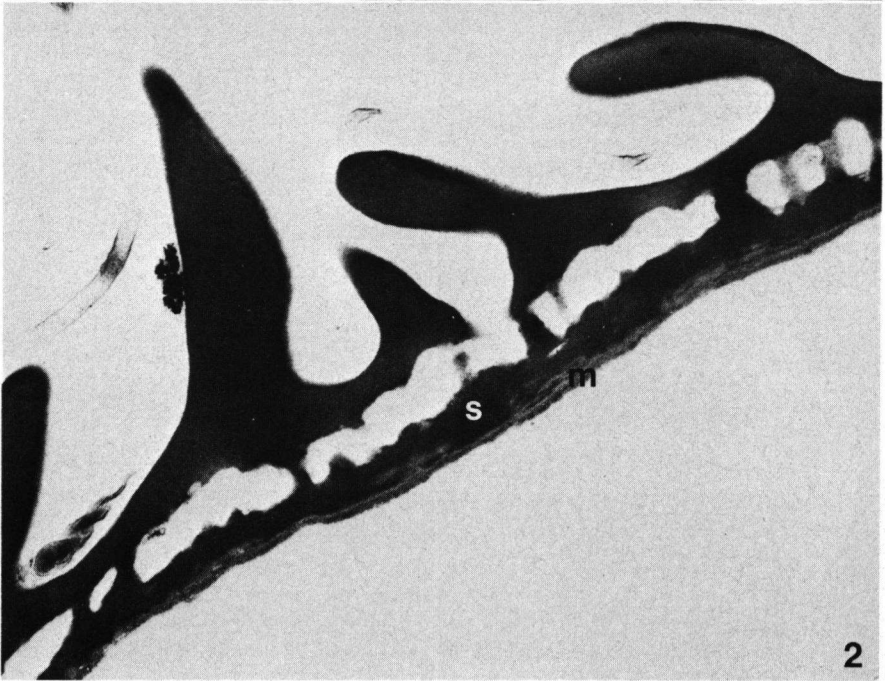
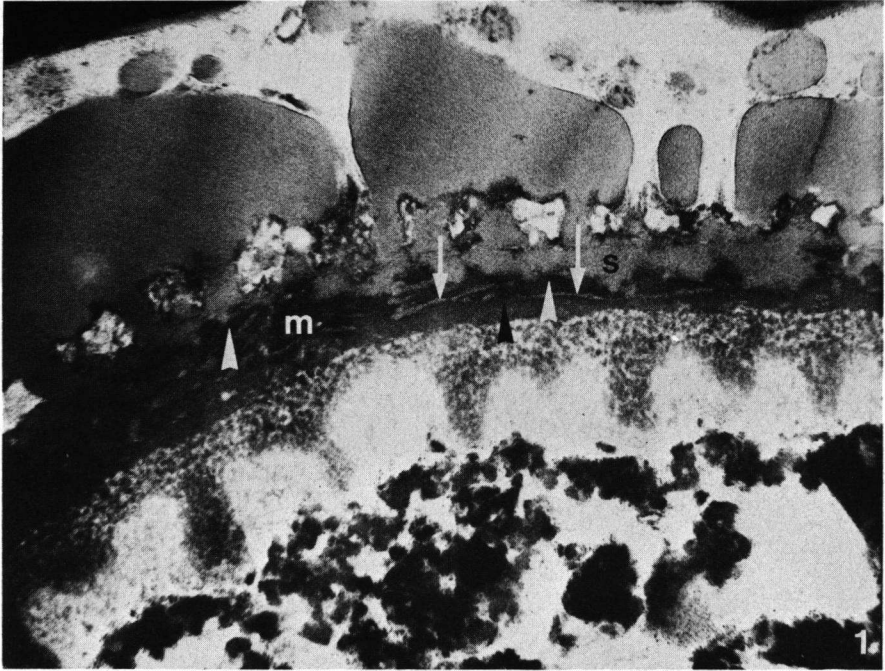


PLATE VIIb

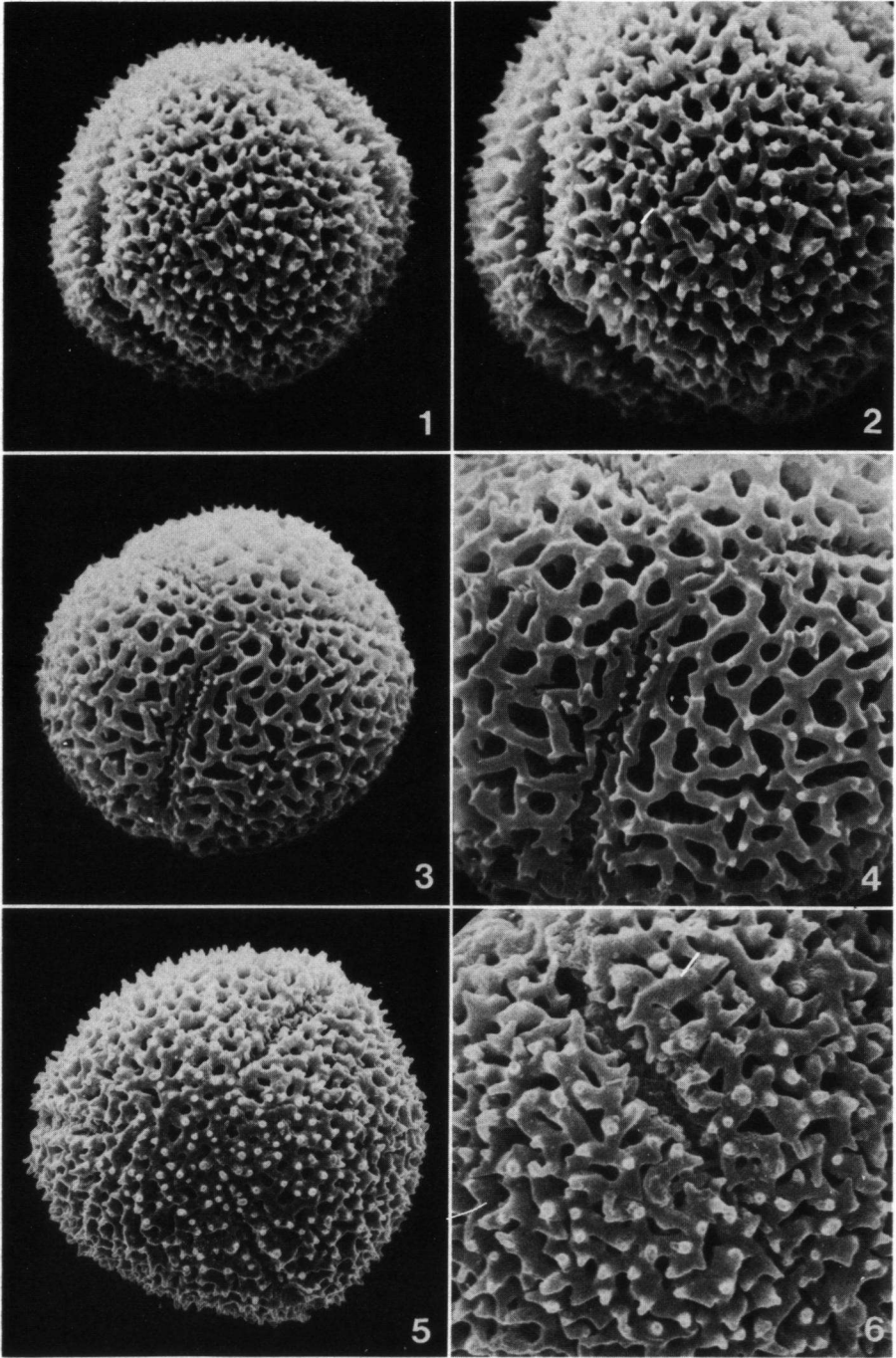


PLATE VIII

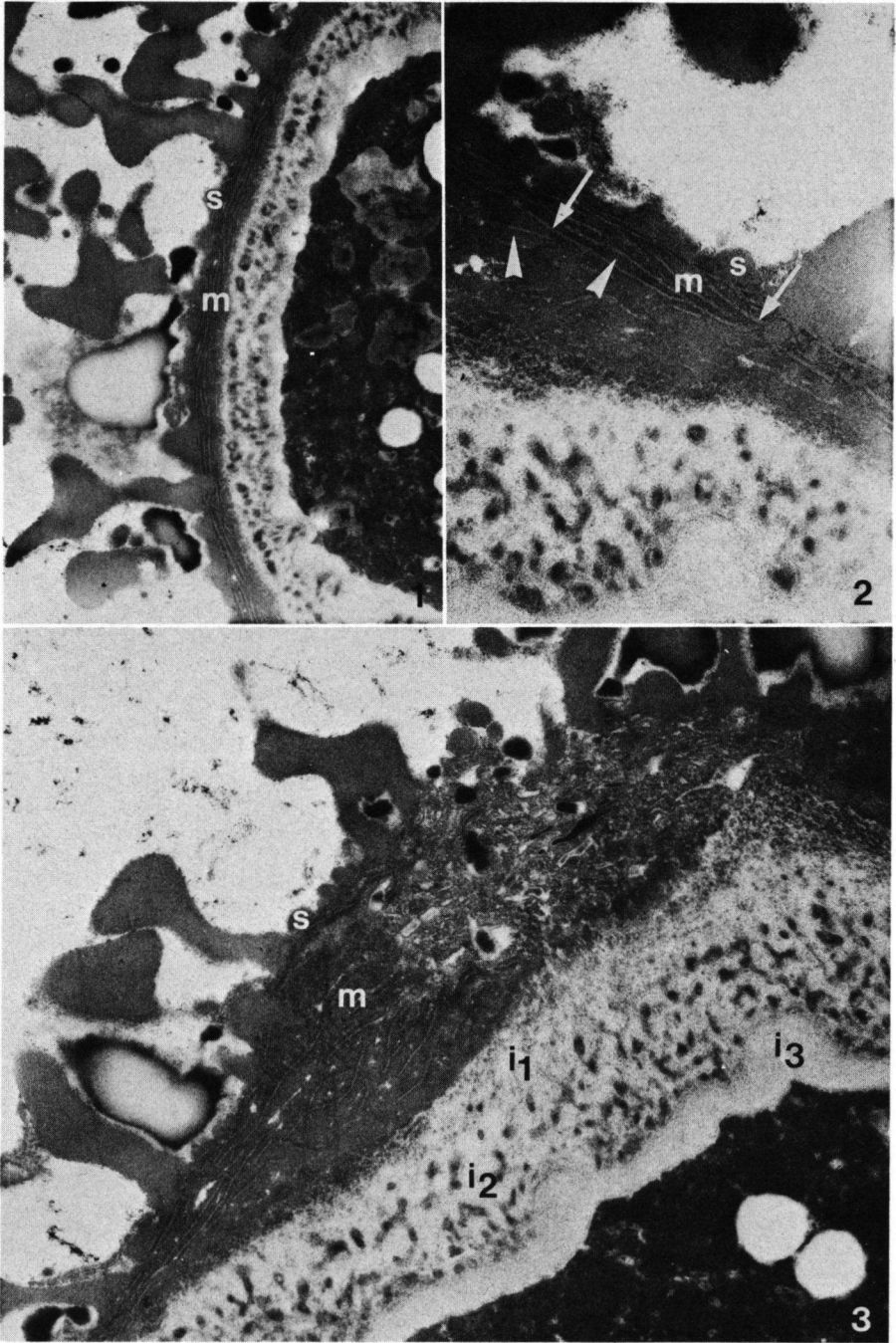


PLATE IX

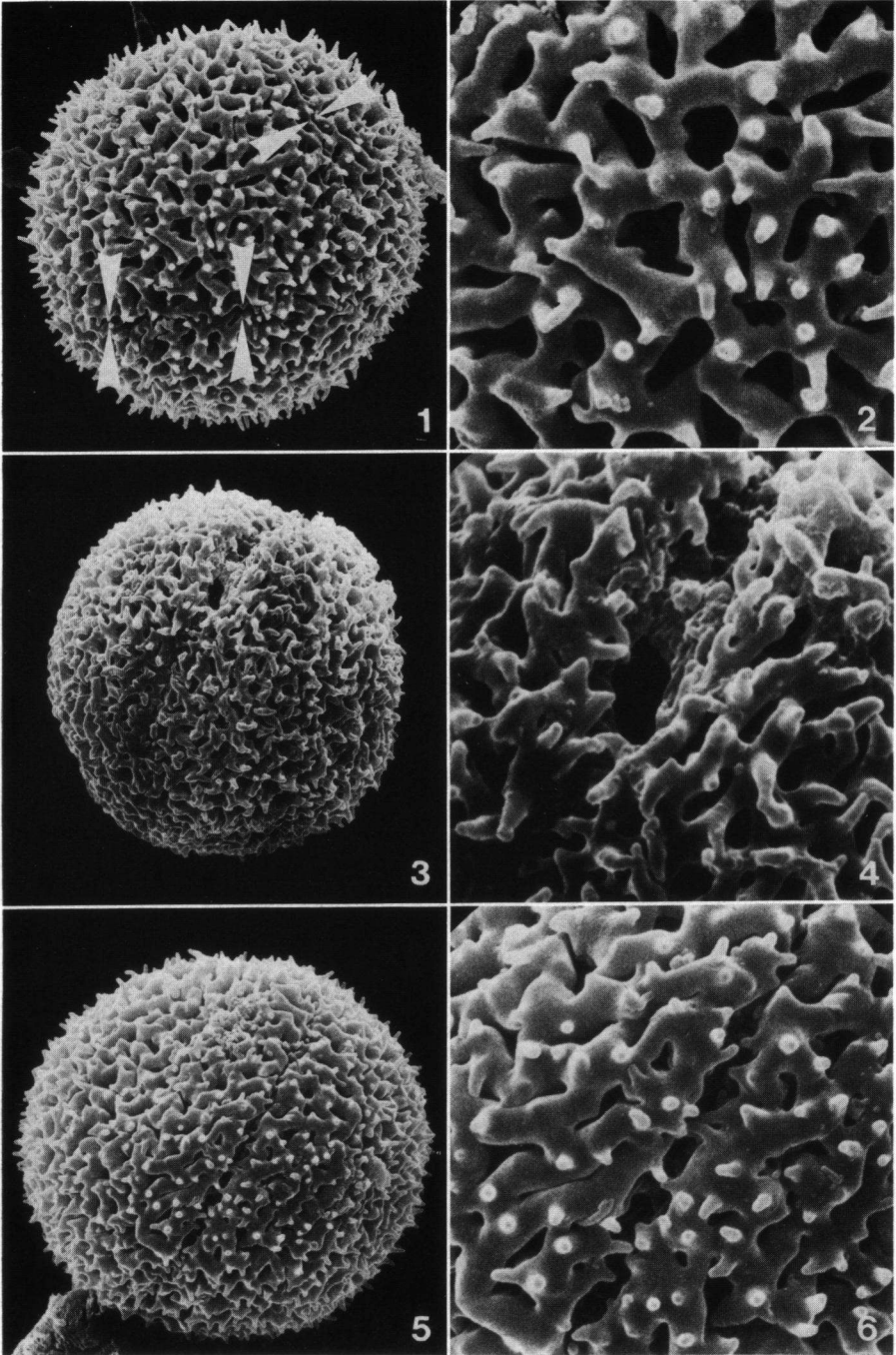


PLATE X

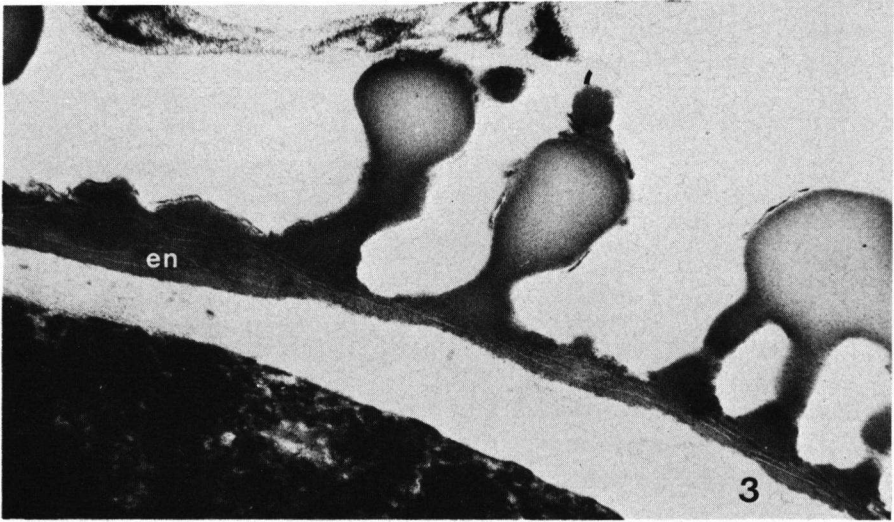
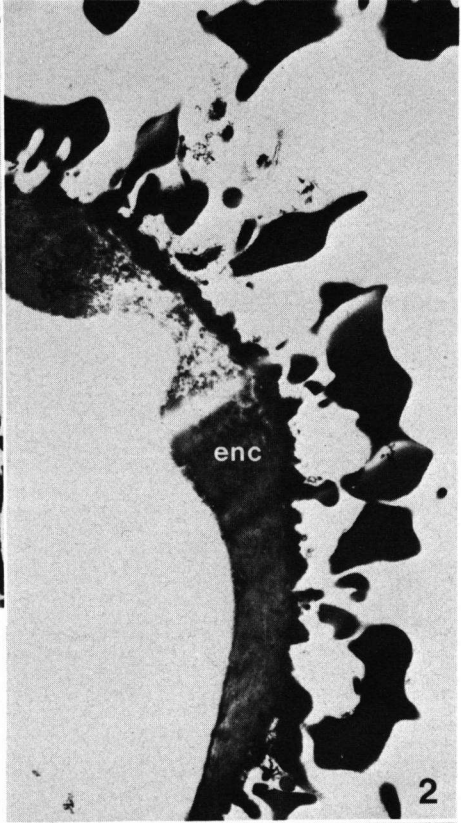
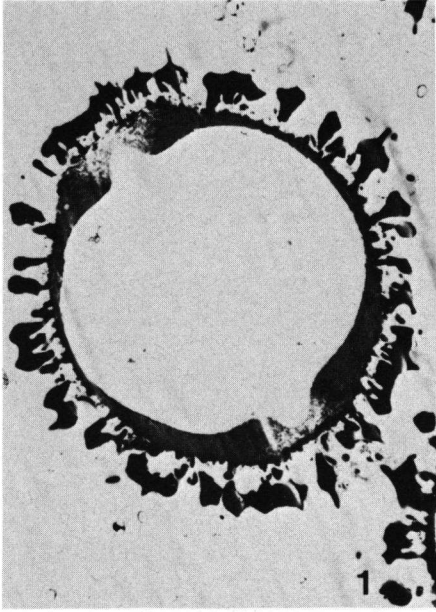


PLATE XI

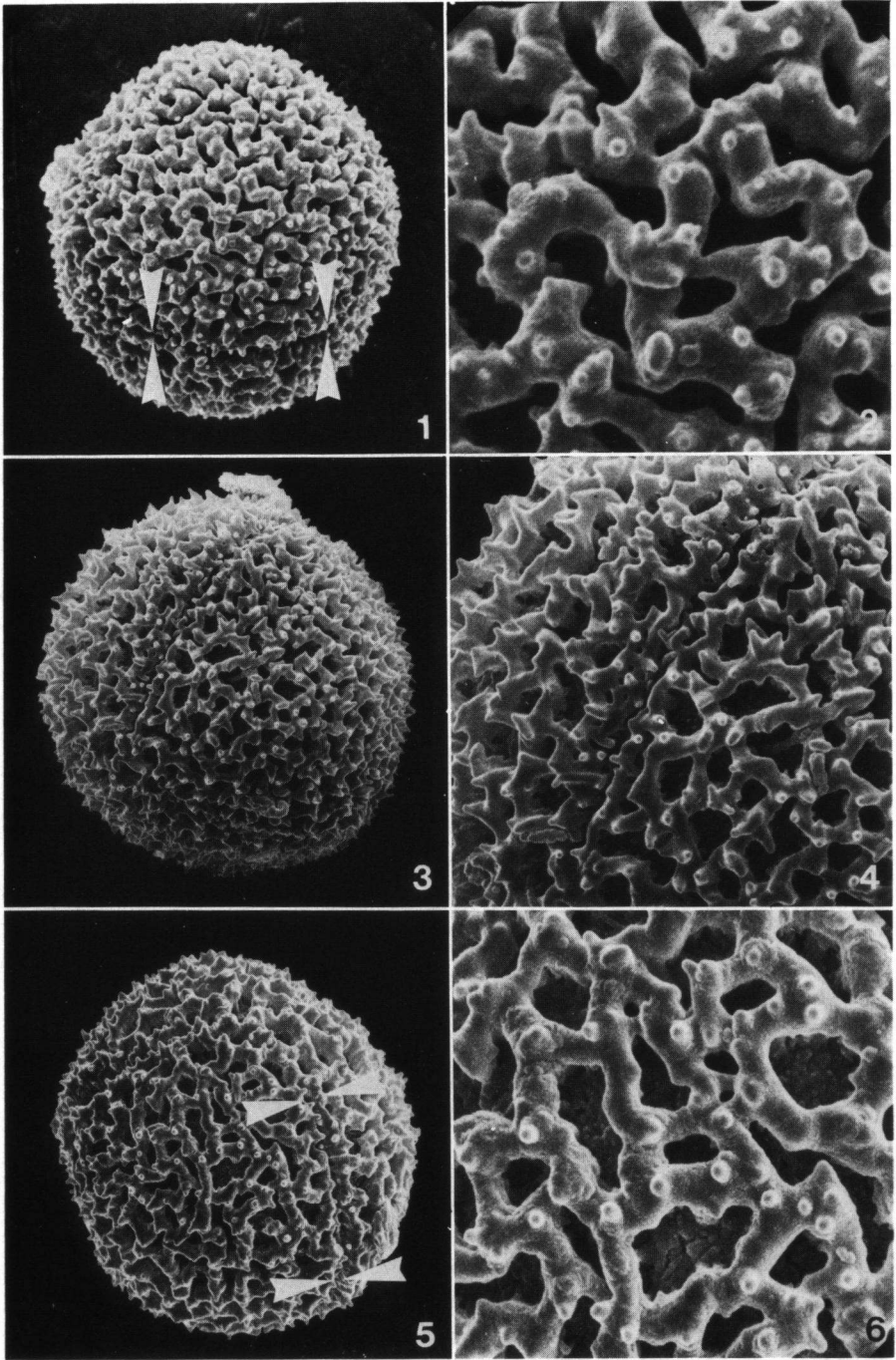


PLATE XII

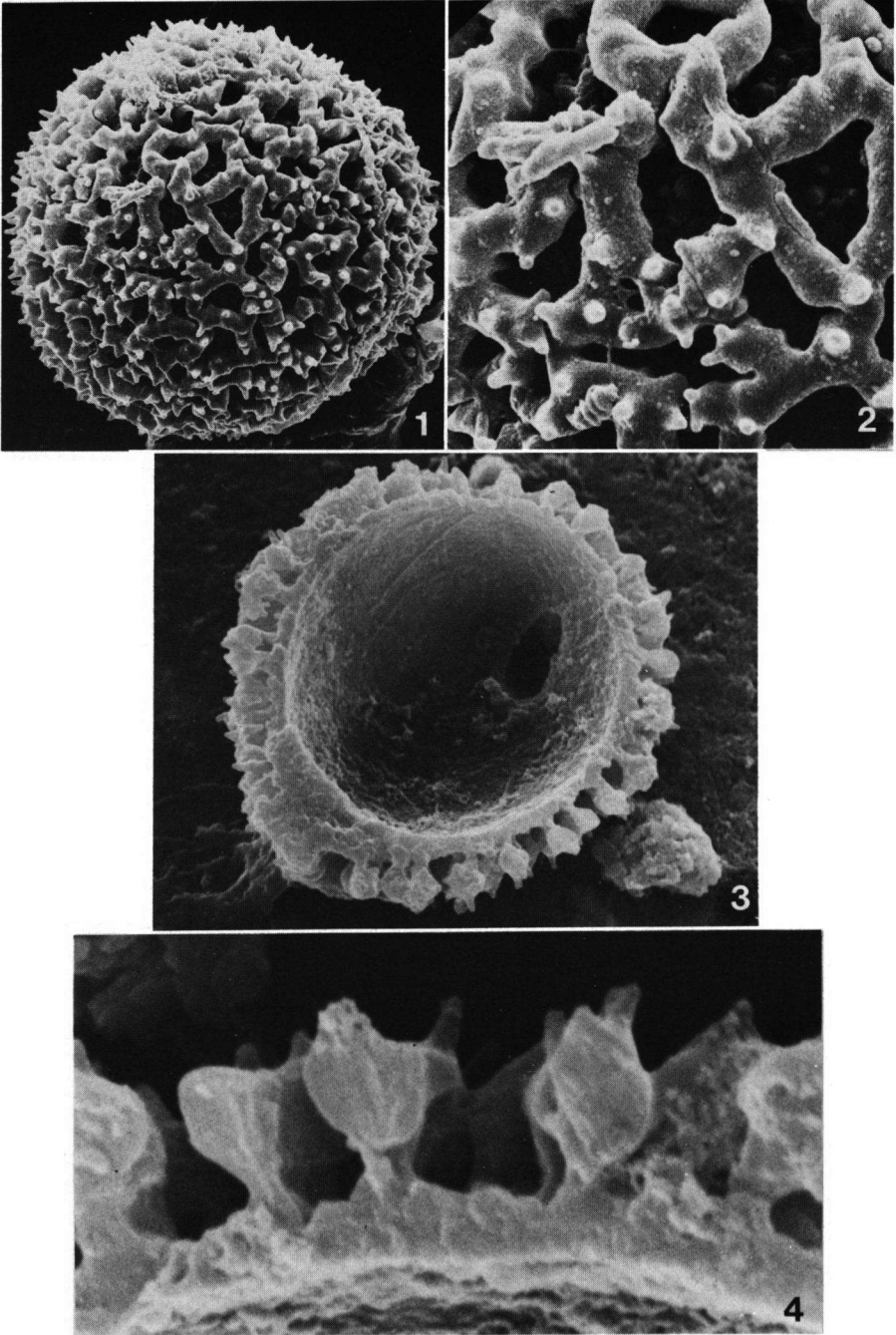


PLATE XIII

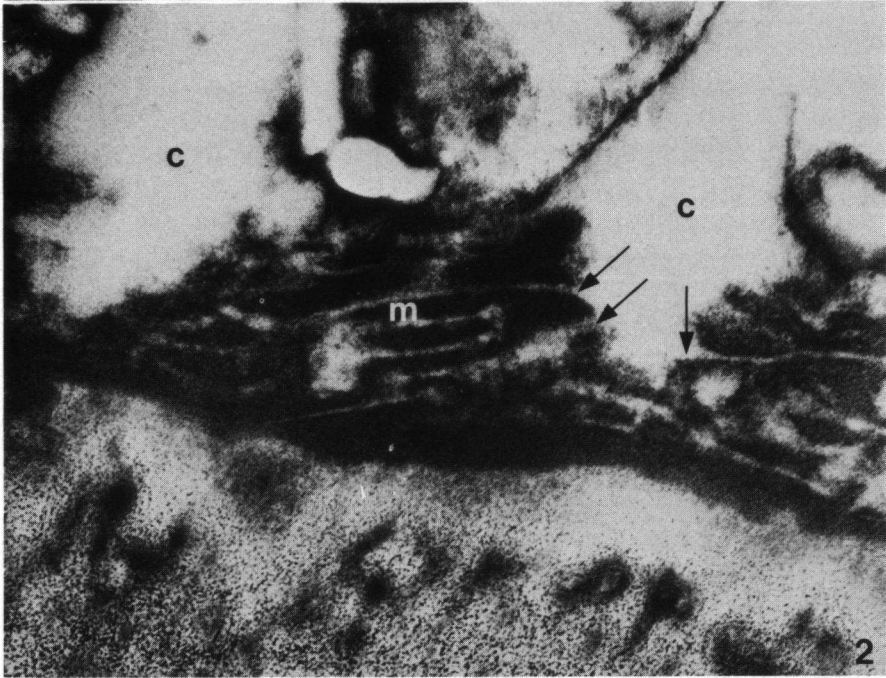
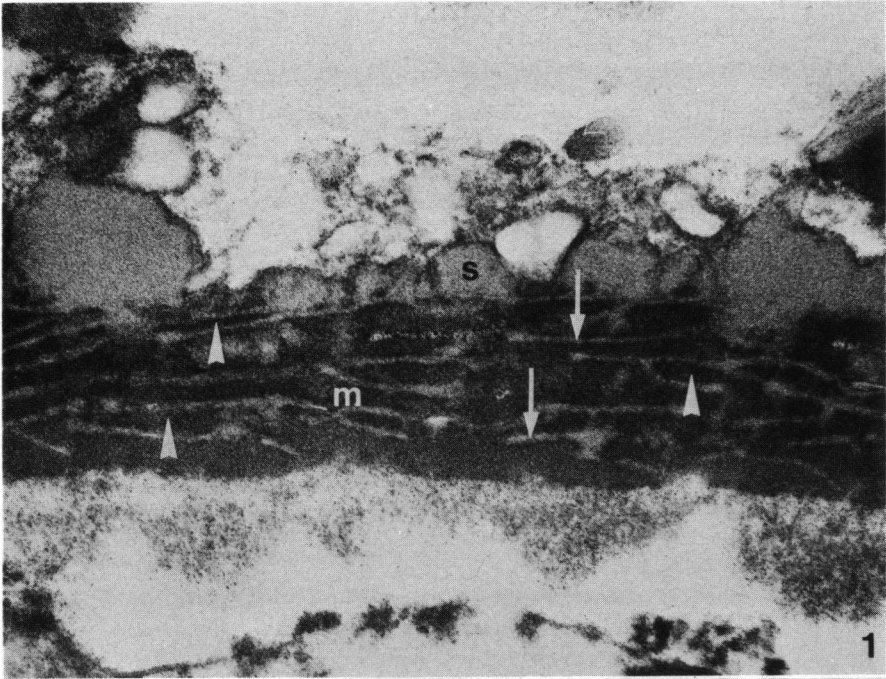


PLATE XIVa

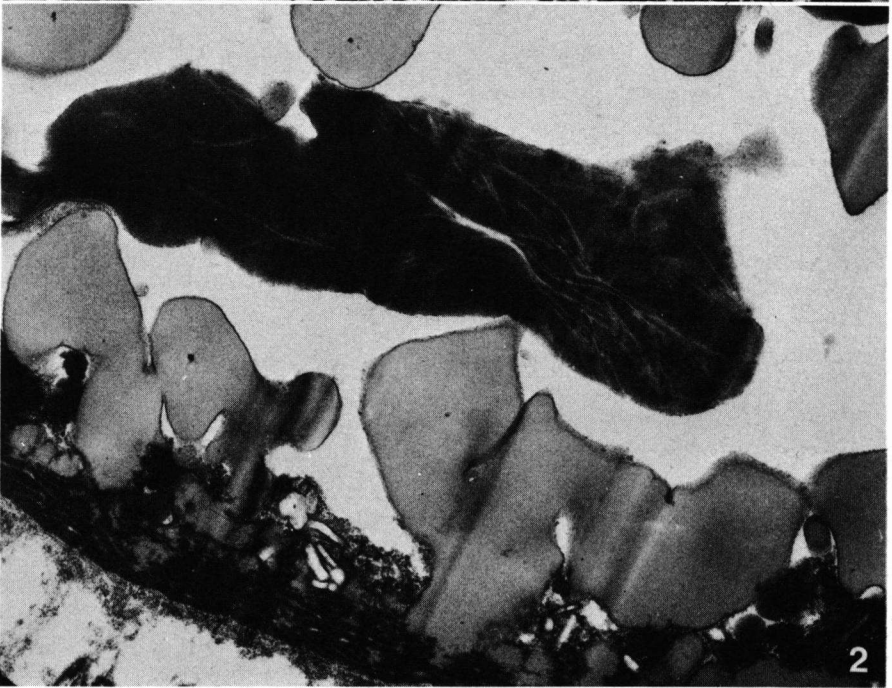
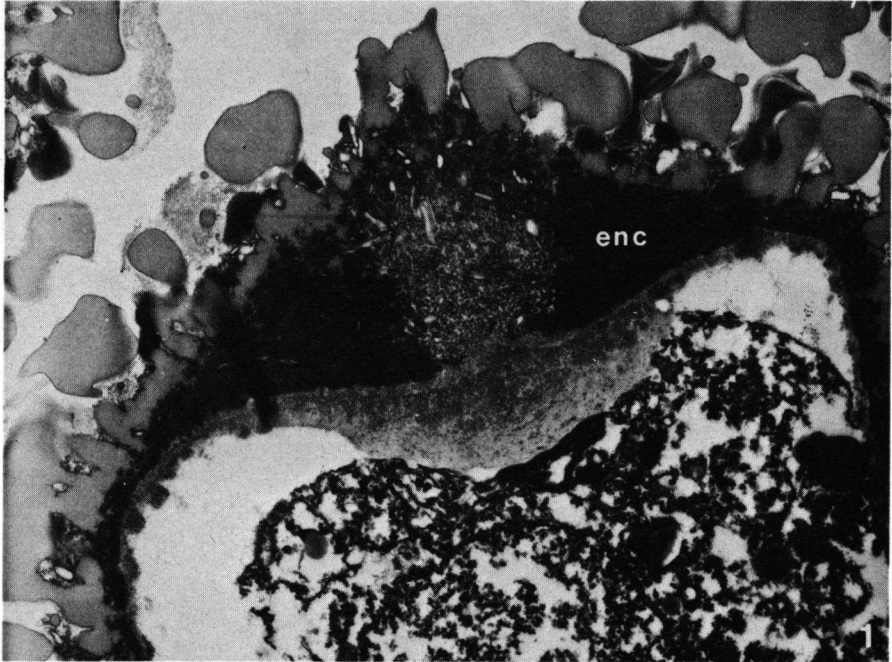


PLATE XIVb

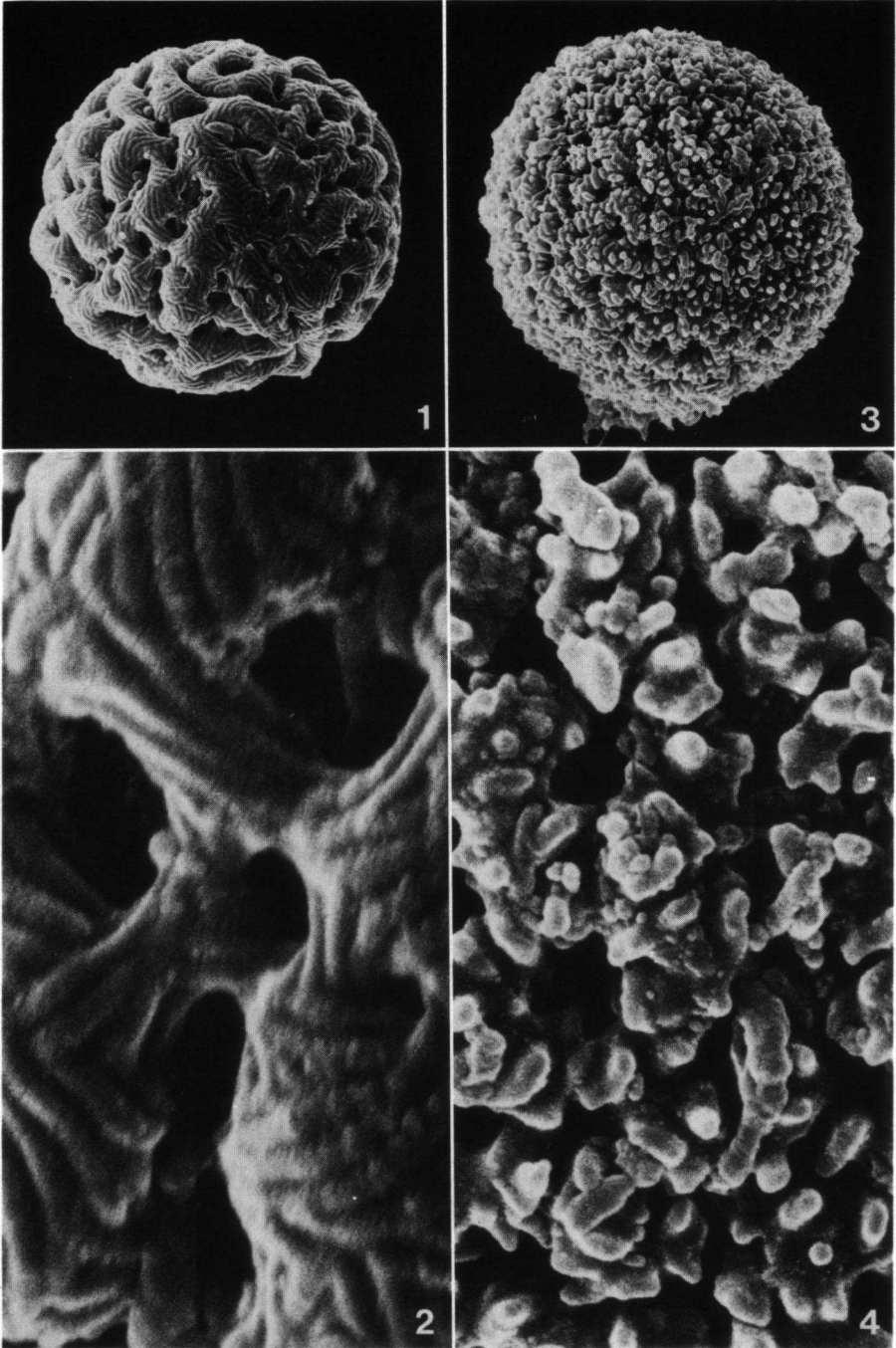


PLATE XV

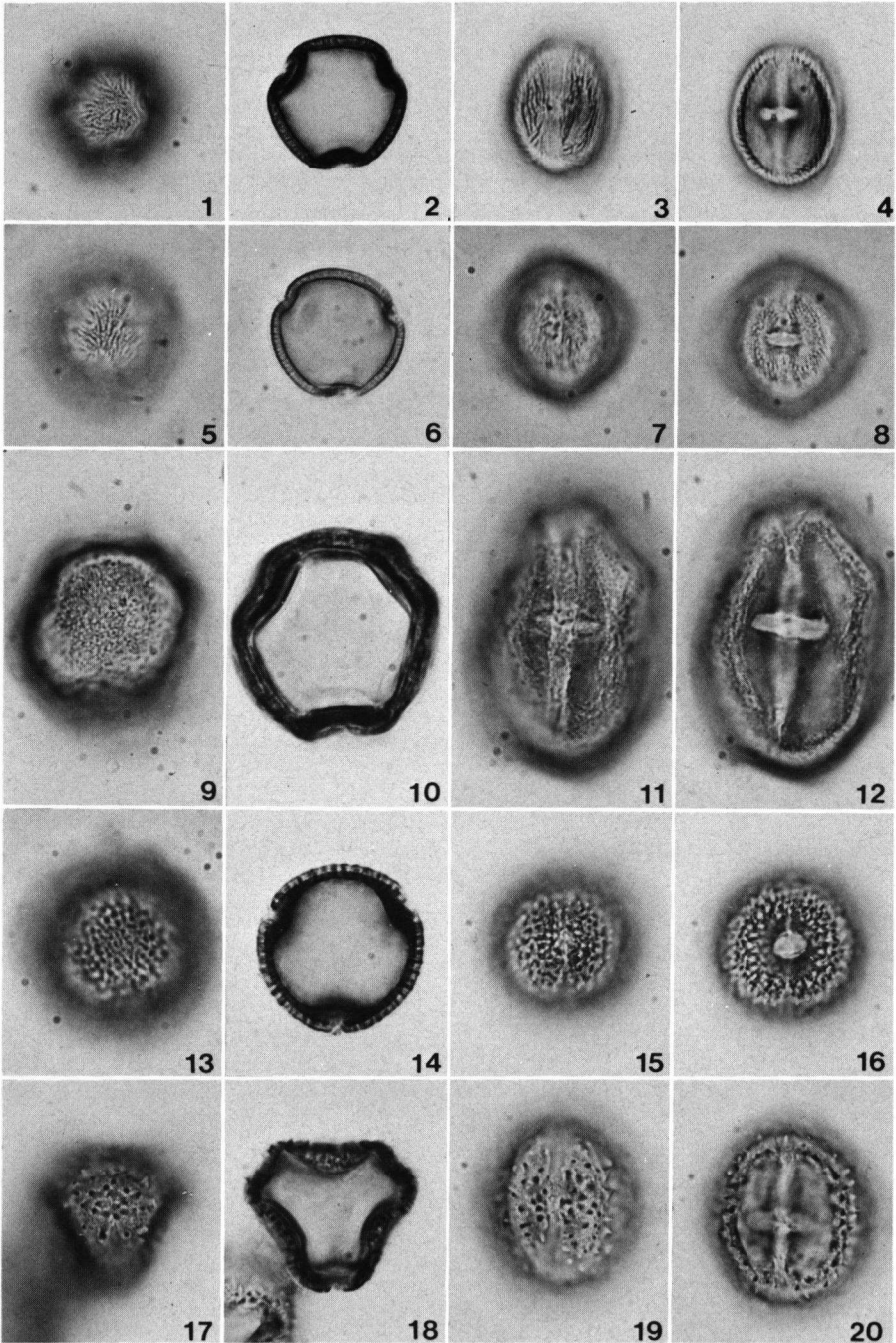


PLATE XVI

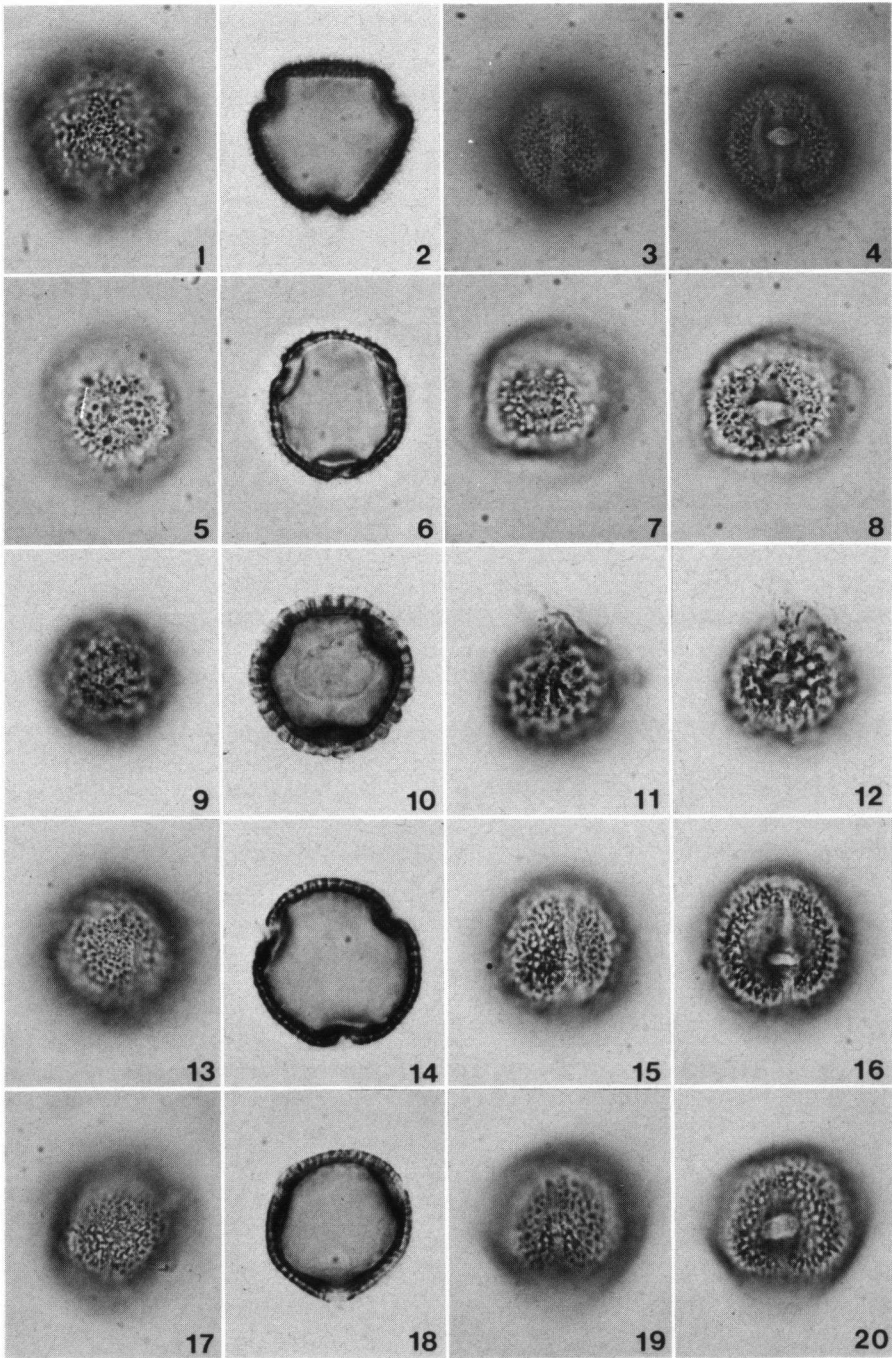


PLATE XVII

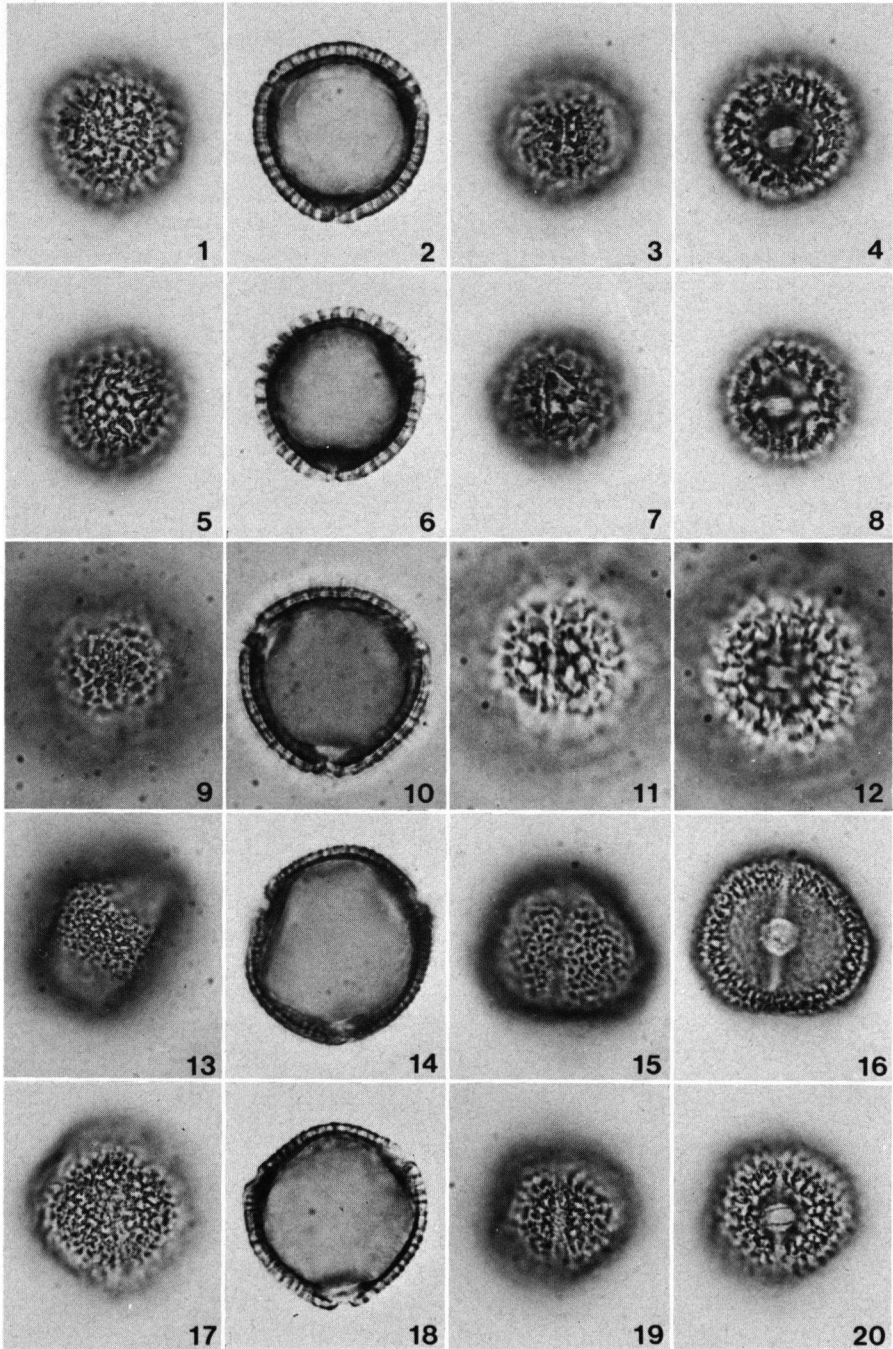


PLATE XVIII

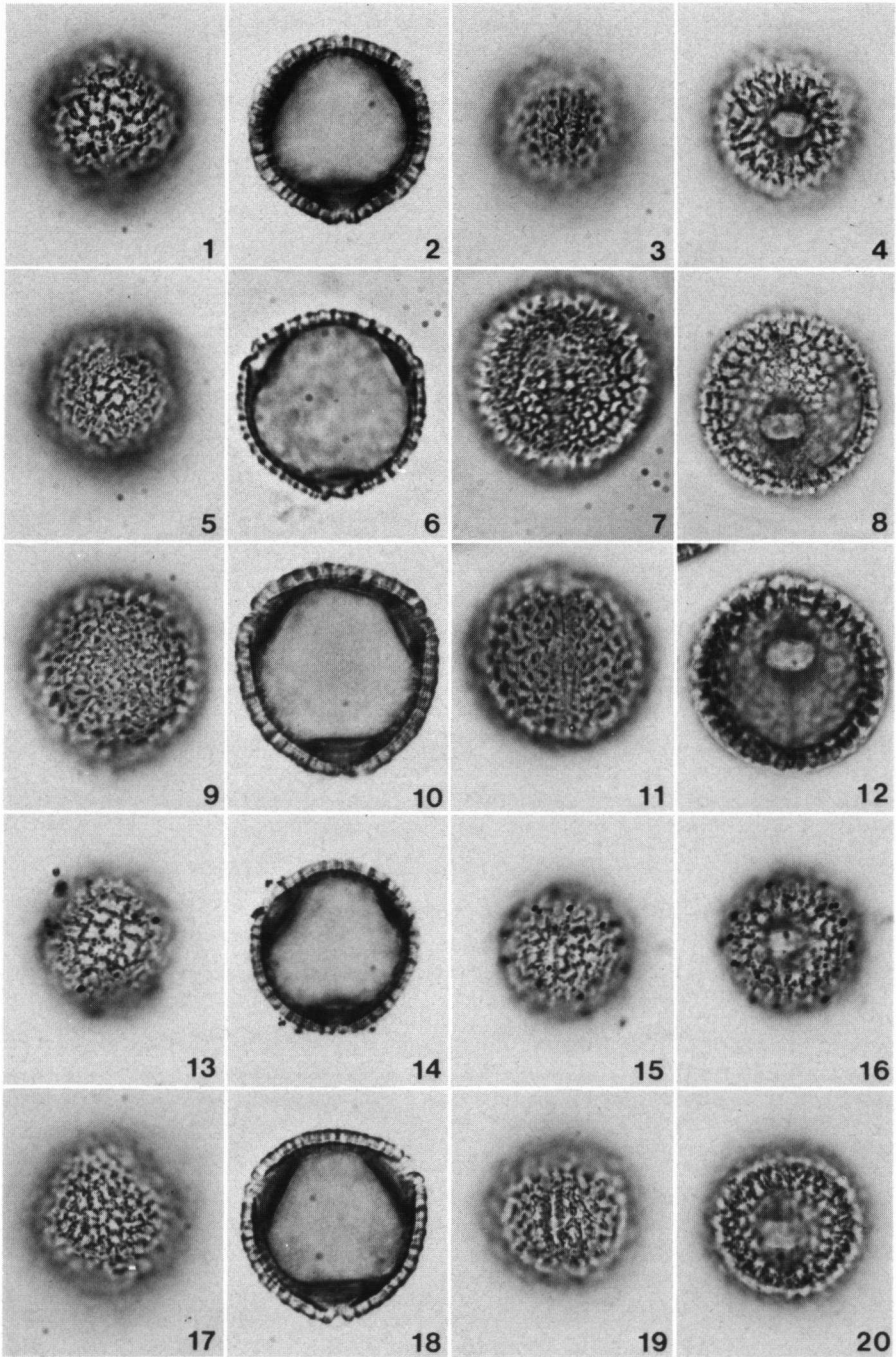


PLATE XIX