

## NOTE ON THE POLLEN MORPHOLOGY OF CRYPTERONIACEAE s.l.

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### SUMMARY

The pollen morphology of the genera *Crypteronia*, *Dactylocladus*, *Axinandra*, *Alzatea* and *Rhynchoalix* is compared in view of a proposal to unite these genera in *Crypteroniaceae*. Three pollen types are recognized, differing in aperture and shape symmetry, but showing distinct similarities in exine and aperture structure. It is argued that the heterocolpate type found in *Dactylocladus*, *Axinandra*, and *Rhynchoalix* and the bisyn-colporate type characterizing *Crypteronia*, may both have been derived from a less-specialized tricolpate ancestral type which has been retained in *Alzatea*. The wider affinities of *Crypteroniaceae* are discussed and thought to be with *Lythraceae* and *Melastomataceae*, although a more remote relationship with *Cunoniaceae* is also possible.

### INTRODUCTION

The revision of the *Crypteroniaceae*, precursory to "Flora Malesiana", by Van Beusekom-Osinga & Van Beusekom (1975) has resulted in a new delimitation of the family by Van Beusekom (1975), now including *Crypteronia*, *Dactylocladus*, *Axinandra*, *Alzatea*, and *Rhynchoalix*. The pollen morphology of these genera was studied in order to supplement the macromorphological and anatomical (Van Vliet, 1975; Van Vliet & Baas, 1975) data. This note is restricted to a presentation of the pollen morphological results only, and for a full discussion of the taxonomical problems involved reference is made to the papers cited.

The pollen of the genus *Crypteronia* has been studied previously by Erdtman (1946, 1952), who was much handicapped by its small size; that of *Alzatea* was described by Lourteig (1965). The pollen of the remaining genera has not been described before.

*Dactylocladus*, *Rhynchoalix*, and *Alzatea* are monotypic genera, *Crypteronia* contains four species which were all available for pollen morphological examination. Of *Axinandra*, however, only one of its three species could be studied. Unless indicated otherwise, all material originates from the Rijksherbarium (L).

Ripe anthers, taken from closed buds, produced best results. Acetolysis was applied for two minutes according to standard procedure, and the pollen grains were mounted in glycerine-jelly for light microscopical (LM) examination. For scanning electron microscopy (SEM) the acetolysed grains were coated under vacuum with carbon, followed by gold. Sections were cut with a freezing microtome according to a technique, described in detail elsewhere (Muller, 1973). For transmission electron microscopy (TEM) the acetolysed grains were fixed in 2% OsO<sub>4</sub> (cacodylate buffer), pre-stained in 5% uranylacetate and embedded in Epon 3/7.

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#### GENERAL MORPHOLOGY

Three pollen types can be recognized in *Crypteroniaceae*: the tricolporate *Alzatea*-type, the heterocolpate *Dactylocladus*-type (*Dactylocladus*, *Axinandra*, and *Rhynchocalyx*) in which three colporate apertures alternate with three pseudocolpi, and the bisyncolporate *Crypteronia*-type. While the orientation of the apertures in the first two types is clearly meridional, that in the *Crypteronia*-type was not self-evident. Erdtman (1952) assumed a meridionally oriented, encircling colpate aperture to be present, with two minute endoapertures situated at the short ends of the grain on the equator. The observations reported here, which were greatly assisted by the higher resolution of the stereoscan images, essentially confirm this interpretation. Moreover, in some samples heteropolar grains occur in which the distal pole would be situated on the more convex side, according to observations made during tetrad development in other bicolporate pollen types by Huynh (1968). However, the two equatorially oriented grooves, mentioned by Erdtman, have proven to be pseudocolpoid depressions, and these are not invariably present.

The colporate apertures are in all pollen types more or less strongly invaginated and closed by a membrane which is rather distinctly outlined against the border of the thicker mesocolpia. At the equator these apertures may be bridged and the underlying endoapertures, representing interior, thinned endexine areas, may be more or less distinctly developed. The pseudocolpi are rather similar in general construction but are not bridged, nor do they possess endoapertures. The pseudocolpoid depressions found in some species of *Crypteronia* are only defined by a sculptural differentiation and probably have no thinned exine.

In the description of the bilaterally flattened *Crypteronia* pollen grains the following terms and measurements are used. The long equatorial axis, connecting the centres of the endoapertures, is called  $E_1$ ; the short equatorial axis at right angles to  $E_1$  is called  $E_2$ . The shape is further defined by the outline in lateral view when facing the mesocolpium, the outline in median view when facing the endoaperture, and the outline in polar view.  $P$  is the polar axis. The respective shape ratio's are  $P/E_1$ ,  $P/E_2$  and  $E_1/E_2$ .

The following discussion of the subdivision of the exine is mainly based on observations made with the TEM. The small size of the pollen grains made it virtually impossible, with the exception of the somewhat larger *Rhynchocalyx* grains, to observe the details with the LM, and also the SEM could only suggest that a subdivision was present. Unfortunately, the *Alzatea* sample was not suitable for TEM studies and the fine structure of this pollen type remains unknown.

The subdivision of the exine in the *Dactylocladus*- and *Crypteronia*-type proved to be basically similar. The main subdivision appears to be between an inner, less electron-dense layer, equivalent to the endexine *s. str.*, and an outer, more electron-dense layer, the ektexine, which in its turn can be subdivided into a footlayer, a layer of columellae, and an outer tectum. The thickness of these layers varies between mesocolpia and apertural areas.

The endexine appears to be thickest near the endoapertures, decreasing in thickness towards the mesocolpia, but it is occasionally also relatively thick under the pseudocolpi. The endexine generally shows a finely granular structure.

The inner boundary of the footlayer is smooth and distinct, but the outer one is rather

irregular and can only be arbitrarily delimited from the often broadened basal parts of the columellae. The footlayer is generally thickest on the mesocolpia. Near the colpi it appears to be reduced and changed from a homogeneous structure into a granular (*Dactylocladus*) or into a lamellar structure (*Rhynchocalyx*, *Crypteronia*). It is not quite clear in these genera whether the footlayer is also reduced under the pseudocolpi. In *Axinandra* the footlayer appears reduced or absent both under colpi and pseudocolpi.

The columellate layer in *Axinandra* is formed by rather widely and regularly spaced short columellae only, but in *Dactylocladus*, *Rhynchocalyx*, and *Crypteronia* the columellae are variable in shape and size, and are interspersed with and transitional to small granules. These granules are best developed in *Dactylocladus* and *Rhynchocalyx*, where they are concentrated in the outer zone, partially fusing with the lower tectum surface. In *Crypteronia* only weak evidence for the presence of granules could be found. Both columellae and granules are reduced or absent on the colpus membranes. On the pseudocolpi they are reduced but probably present over the entire membrane.

The tectum is generally homogeneous with a more or less irregular inner and outer surface. In *Axinandra* and *Dactylocladus* it has a rather smooth surface, but in *Crypteronia* and *Rhynchocalyx* it is more irregular with perforations centred in the depressions. In *Rhynchocalyx* the tectum dissolves into separate granules near the apertures. This is less noticeable in *Crypteronia*, where the tectum is absent on the colpus membrane and dissolved into separate verrucae on the pseudocolpoid areas.

In *Axinandra* the tectum is probably still present as a very thin membrane on the colpi and clearly present on the pseudocolpi.

In *Dactylocladus* and *Rhynchocalyx* the tectum appears to be more or less continuous, although much thicker on the mesocolpia and probably absent in the centre of the colpi.

Detailed studies, preferably of fresh material, are necessary to verify these preliminary observations on the fine structure of the wall. Until then, an evaluation of the differences found between the genera is not advisable.

#### SYSTEMATIC DESCRIPTION

##### subfamily CRYPTERONIOIDEAE

##### CRYPTERONIA BL.

##### section *Crypteronia*

##### *Crypteronia paniculata* Bl.

Pl. I: 1—5; Pl. II: 1—4; Pl. VI: 1—4.

##### var. *paniculata*

Material studied. BANGLADESH. Chittagong: *King's Coll. 235*. — JAVA: *Koorders 4355; Schiffner 2285*.

##### var. *affinis*

Material studied. BURMA. Mergui: *Griffith & Helfer 2512/1*.

Pollen grains spindle shaped, bisyncolporate, equatorial outline elliptic,  $E_1/E_2$  1.52, lateral outline apiculate-elliptic,  $P/E_1$  0.71, median outline rounded quadrangular with concave sides,  $P/E_2$  1.09. The concave sides are caused by the invaginated colporate aperture and pseudocolpoid depressions. Size: P 8 (8.2) 8.4  $\mu\text{m}$ ,  $E_1$  11 (11.4) 12  $\mu\text{m}$ ,  $E_2$  7 (7.5) 8  $\mu\text{m}$ . Colporate aperture rather deeply invaginated,  $\pm 0.5$   $\mu\text{m}$  wide at bottom, closed by a smooth membrane (Pl. II, 2) which is sharply outlined against the irregularly verrucate and raised border of the mesocolpium. Equatorial bridges present (Pl. II, 3),

endoapertures indistinct. Mesocolpia with elliptic pseudocolpoid depressions. The exine is, on TEM evidence, subdivisible into outer tectum, layer of columellae, and footlayer, which are all electron-dense, and an endexine *s. str.* which is less electron-dense. The tectum is  $0.2 \mu\text{m}$  thick, massive, except for occasional perforations. The outer surface is irregularly pitted on borders of mesocolpia, pits  $0.01$ — $0.2 \mu\text{m}$  in diameter. Between these border areas and the pseudocolpoid depressions the tectum surface is almost smooth. The pseudocolpoid depressions are again rather densely pitted or subverrucate (Pl. II, 1). The inner surface of the tectum is fairly flat but dissolves into separate granules on the pseudocolpoid depressions (Pl. VI, 1). The tectum is absent on the colpi (Pl. VI, 1).

The columellae are  $0.1 \mu\text{m}$  long,  $0.05 \mu\text{m}$  in diameter and are most distinct in the intercolpate areas, while they are reduced in the pseudocolpate areas. There is some evidence that separate granules are also present in this layer. The columellae are absent on the colpi.

The footlayer is  $0.1$ — $0.2 \mu\text{m}$  thick in the intercolpate and pseudocolpate areas, away from the equatorial zone. It is reduced in the colpate areas and lamellated at the endoapertures (Pl. VI, 2).

The endexine *s. str.* is probably present as a  $0.1 \mu\text{m}$  thick granular layer in the endoapertural areas, but is  $<0.1 \mu\text{m}$  thick in the remainder.

**C o m m e n t s.** *C. paniculata* is characterized by the almost square median outline and the rather distinct pseudocolpoid depressions.

#### section *Basispermia* Niedenzu

#### *Crypteronia cumingii* (Planch.) Planch. *ex* Endl.

Pl. I: 6—10; Pl. II: 5—8; Pl. III: 1 & 2.

Material studied. PHILIPPINES: *Mendoza 18241*.

Pollen grains bilaterally flattened, bisyncolporate, equatorial outline elliptic,  $E_1/E_2$  1.64, lateral outline apiculate-elliptic, occasionally heteropolar with one side more convex than the other,  $P/E_1$  0.70, median outline rounded quadrangular,  $P/E_2$  1.14. Size: P 8 (8.5)  $9 \mu\text{m}$ ,  $E_1$  12 (12.1)  $13 \mu\text{m}$ ,  $E_2$  7 (7.4)  $8 \mu\text{m}$ . Colporate aperture fairly shallowly invaginated, narrow,  $0.2 \mu\text{m}$  wide (Pl. II, 7), closed by a smooth membrane (Pl. II, 8), equatorially bridged. Endoapertures distinct, elliptic in outline,  $4 \mu\text{m}$  wide in equatorial direction,  $2 \mu\text{m}$  in polar direction (Pl. I, 9). Mesocolpia flat or invaginated, but without clearly differentiated pseudocolpoid areas. Exine structureless,  $0.5 \mu\text{m}$  thick, slightly thinner at the centre of the colporate aperture, slightly thicker at the borders of the mesocolpia, surface smooth to slightly and irregularly verrucate-pitted.

**C o m m e n t s.** The LM sections (Pl. II, 7 & 8) show a homogeneous structure of the exine; the narrow ektoaperture which is V-shaped in cross section, and the lack of any distinct pseudocolpoid structure are visible. Upon shrinkage the major part of the mesocolpium is invaginated as a whole.

#### *Crypteronia griffithii* C. B. Clarke

Pl. III: 3 & 4.

Material studied. MALAY PEN. MALACCA: *Griffith s.n.*

Pollen grains bilaterally flattened, bisyncolporate, equatorial outline elliptic,  $E_1/E_2$  1.80, lateral outline apiculate-elliptic,  $P/E_1$  0.65, median outline rounded quadrangular,  $P/E_2$  1.17. Size: P 7 (7.9)  $8 \mu\text{m}$ ,  $E_1$  11 (12.2)  $13 \mu\text{m}$ ,  $E_2$  6 (6.8)  $7 \mu\text{m}$ . Colporate aperture equatorially bridged, endoapertures indistinct. Mesocolpia with fairly large, elliptic, pseudocolpoid

depressions. Exine  $0.5 \mu\text{m}$  thick, surface smooth to slightly verrucate along the borders of the ektoapertures, but densely and distinctly verrucate-areolate on the pseudocolpoid depressions, verrucae  $0.2\text{--}0.3 \mu\text{m}$  in diameter.

**C o m m e n t s.** The wide pseudocolpoid depressions with a distinct verrucate surface sculpture appear to be the most characteristic feature of the pollen of this species. On Pl. III, 3, narrow threads are seen, connecting three grains approximately at the centres of their endoapertures, possibly indicating a tetrad position in which these apertures were connected two by two in a square configuration.

### **Crypteronia macrophylla** Beus.-Osinga

Pl. III: 5—8.

Material studied. BORNEO. S a r a w a k: *Ashton S19607 & S19621; Ilias Paie S24282; Sibat ak Luang S22356.* — K a l i m a n t a n: *Endert 4040; Amdjah & Nieuwenhuis 301.*

Pollen grains bilaterally flattened, bisyncolporate, equatorial outline elliptic,  $E_1/E_2$  1.69, lateral outline apiculate-elliptic,  $P/E_1$  0.71, median outline rounded quadrangular,  $P/E_2$  1.18. Size: P 8 (9.0)  $10 \mu\text{m}$ ,  $E_1$  11 (12.9)  $14 \mu\text{m}$ ,  $E_2$  6 (7.6)  $8 \mu\text{m}$ . Colporate apertures narrow, invaginated and equatorially bridged. Endoapertures indistinct. Mesocolpia without any structurally differentiated pseudocolpoid area, but often invaginated. Exine  $0.5 \mu\text{m}$  thick, surface entirely, rather densely verrucate. Verrucae  $0.2\text{--}0.3 \mu\text{m}$  in diameter,  $0.1\text{--}0.2 \mu\text{m}$  high.

**C o m m e n t s.** The densely verrucate sculpture, which is beyond the resolving power of the light microscope, is the most typical feature of the pollen of this newly described species.

### DACTYLOCLADUS OLIV.

#### **Dactylocladus stenostachys** Oliv.

Pl. I: 11—14; Pl. IV: 1—3; Pl. VIII: 1—4.

Material studied. BORNEO. B r u n e i: *Ashton Brun. 280.*

Pollen grains spherical-subprolate,  $P/E$  1.04, equatorial outline rounded hexangular, heterocolpate with three colporate apertures alternating with three pseudocolpi. Size: P 12 (13.2)  $15 \mu\text{m}$ , E 12 (12.7)  $14 \mu\text{m}$ . Colporate ektoapertures are medium long ( $PI$  0.4), slightly invaginated, equatorially bridged and passing very gradually into the surrounding mesocolpia; their outer surface is smooth or irregularly verrucate. The equatorial bridges are rather irregular and not very pronounced (Pl. IV, 2), the exine is thinner here and the underlying endoapertures are irregular and ill defined. The pseudocolpi are rather similar in size and general appearance to the colporate apertures, except that they are not equatorially bridged and have a more distinct verrucate sculpture in their centre (Pl. IV, 1). On the section shown on Pl. IV, 3, the rather deeply invaginated pseudocolpus is visible in the upper part, the central part of the folded area being partly covered with densely spaced verrucae  $0.2\text{--}0.4 \mu\text{m}$  in diameter.

The exine is, on TEM evidence, subdivisible into outer tectum, layer of columellae, and footlayer, all relatively electron-dense, and an inner endexine *s. str.* which is less electron-dense.

The tectum is up to  $0.25 \mu\text{m}$  thick on the mesocolpia, decreasing to  $0.1 \mu\text{m}$  near the colpi, and forms a nearly continuous layer. Its outer surface is smooth or slightly uneven near the colpi, due to undulations of the whole layer. The inner surface of the tectum is smooth or slightly irregular and it appears to be much reduced and possibly locally absent over the ektoapertures and pseudocolpi.

The columellae are 0.10—0.15  $\mu\text{m}$  long, 0.10—0.05  $\mu\text{m}$  in diameter, irregularly shaped, best developed and widely spaced on poles and mesocolpia; elsewhere they have an irregular granular appearance. Interspersed with the columellae, separate granules 0.025—0.05  $\mu\text{m}$  in diameter are present, mostly attached to the inner tectum surface, or gradually merging with it as is visible on the oblique section (Pl. VIII, 3). Both columellae and granules are very much reduced near the apertures, but probably do not disappear completely.

The footlayer is up to 0.3  $\mu\text{m}$  thick on the intercolpate areas and gradually decreases in thickness to 0.02  $\mu\text{m}$  near the apertures, where it consists of isolated granules and sometimes faintly shows a lamellate structure (Pl. VIII, 1).

The endexine *s. str.* is 0.1  $\mu\text{m}$  thick and homogeneous on mesocolpia and increases in thickness to 0.25  $\mu\text{m}$  near the endoapertures where it shows a granular structure. Under the pseudocolpi it is 0.2  $\mu\text{m}$  thick and appears to be homogeneous.

#### AXINANDRA THWAITES

##### *Axinandra beccariana* Baill.

Pl. I: 15—17; Pl. IV: 4 & 5; Pl. VI: 5.

Material studied. BORNBO. S a r a w a k: *Brain ak Tudo S15909*.

Pollen grains spherical-subprolate, P/E 1.04, equatorial outline rounded hexangular, heterocolpate with three colporate apertures alternating with three pseudocolpi. Size: P 13 (14.6) 15  $\mu\text{m}$ , E 13 (14.1) 15  $\mu\text{m}$ . Colporate apertures are long (Pl 0.25), invaginated and equatorially bridged (Pl. IV, 5). They pass gradually into the mesocolpia, are fairly wide at the equator, while their tips are pointed and indistinctly outlined. Their surface is smooth to finely verrucate, the scattered verrucae being  $\pm 0.2 \mu\text{m}$  in diameter. The equatorial bridges may show a protruding aperture membrane (Pl. IV, 4). The endoapertures, underlying the equatorial bridges, are irregularly shaped, 2—3  $\mu\text{m}$  in diameter with an indistinct outline. The pseudocolpi are elliptical in outline and do not reach as far towards the poles as the colporate apertures (Pl. IV, 5). They are more or less invaginated, depending on the state of shrinkage of the grain and their surface is densely verrucate. The verrucae are  $\pm 0.2 \mu\text{m}$  in diameter.

TEM evidence indicates subdivision of the exine into a relatively electron-dense outer tectum, layer of columellae, and footlayer, and an inner endexine *s. str.* which is less electron-dense.

The tectum is 0.3  $\mu\text{m}$  thick on the mesocolpia, decreasing in thickness to 0.1  $\mu\text{m}$  near the edge of the apertures. It is probably still present as a very thin layer both on the membranes closing the colpi as well as the pseudocolpi. The outer surface is smooth, with isolated small verrucae 0.1  $\mu\text{m}$  in diameter on mesocolpia, but on the membranes of the pseudocolpi these verrucae are more prominent and densely spaced.

The columellae are 0.05—0.10  $\mu\text{m}$  long, 0.01—0.20  $\mu\text{m}$  in diameter, show a concave profile and are regularly spaced. They disappear near the colpi but appear still indistinctly present on the pseudocolpi.

The footlayer is 0.3  $\mu\text{m}$  thick on mesocolpia, decreasing in thickness towards the edge of the apertures, and is probably absent on colpi and pseudocolpi. The upper surface is smooth to slightly irregular, the inner boundary smooth.

The endexine *s. str.* has a homogeneous appearance, is 0.05  $\mu\text{m}$  thick on the mesocolpia, 0.3  $\mu\text{m}$  thick on the colpi, and 0.2  $\mu\text{m}$  under the pseudocolpi.

C o m m e n t s. The grain shown on Pl. IV, 5 appears to be partly covered with

extraneous acetolysis-resistant globulate material which may have been derived from the tapetum and could represent clustered Ubisch bodies, secondarily attached to the exine surface during maturation.

### subfamily ALZATEOIDĒAE

#### ALZATEA RUIZ & PAV.

##### *Alzatea verticillata* Ruiz & Pav.

Pl. I: 18—20; Pl. IV: 6—9.

Material studied. PERU. *Ule* 6750.

Pollen grains spherical-subprolate, P/E 1.05, equatorial outline rounded, triangular, tricolporate, rarely bicolporate. Size: P 17 (17.9) 19  $\mu\text{m}$ , E 15 (16.9) 19  $\mu\text{m}$ . Ektoapertures distinct, invaginated and equatorially bridged (PI 0.30), closed by a flat, slightly and irregularly verrucate membrane, and with pointed tips (Pl. IV, 6). Their sides are rather distinctly outlined by the raised, irregularly verrucate borders of the mesocolpia (Pl. IV, 7). The equatorial bridge is shown in close-up on Pl. IV, 9: in its centre the apertural membrane protrudes slightly. The endoapertures, underlying the equatorial bridges are developed as irregular-circular thinned areas on the inner side of the exine, with a fairly distinct outline, 3—5  $\mu\text{m}$  in diameter. (Pl. I, 20). Exine homogeneous or very indistinctly differentiated into endexine and ectexine (LM!), 1  $\mu\text{m}$  thick, its surface smooth to irregularly pitted or, especially in the centre of the mesocolpia (Pl. IV, 6 & 7), irregularly verrucate-areolate. The pits are funnelshaped,  $\pm$  0.1—0.4  $\mu\text{m}$  in diameter and very shallow. The verrucae are often ill-defined and could be considered as irregular elevations separating the pits; only in the centre of the mesocolpia they are more distinct, densely spaced, with a diameter up to 0.4  $\mu\text{m}$ , while the pits are here less prominent.

**C o m m e n t s.** Lourteig (1965) describes the exine of *Alzatea* pollen as finely reticulate, but on the SEM photomicrographs shown here, no trace of such a sculpture type is seen. The presence of a slight differentiation in sculpture in the centre of the mesocolpia, as well as the fact that the equatorial outline of the grain also sometimes shows slight invagination here, is interesting in suggesting the incipient development of a pseudocolpoid structure.

#### RHYNCHOCALYX OLIV.

##### *Rhynchocalyx lawsonioides* Oliv.

Pl. V: 1—11; Pl. VII: 1—3.

Material studied. S. AFRICA. *Natal*: *Strey* 6539.

Pollen grains spherical-subprolate, P/E 1.08, equatorial outline rounded hexangular, heterocolpate with three colporate apertures alternating with three pseudocolpi. Size: P 19 (19.6) 20  $\mu\text{m}$ , E 17 (18.1) 19  $\mu\text{m}$ . Colporate ektoapertures long (PI 0.20), invaginated, without or with indistinct equatorial bridges. As shown on Pl. V, 7 & 8, the aperture membrane has a rather densely and finely verrucate surface and as such is rather distinctly outlined against the mesocolpia. The tips of the ektoapertures are narrow and rather distinctly outlined. The endoapertures are ellipsoidal areas in which endexine appears absent (Pl. V, 2, 9); they measure 3  $\mu\text{m}$  in equatorial direction and 1.5  $\mu\text{m}$  in polar direction. They may also be developed as two circular areas separated by an equatorial bridge (Pl. V, 10). The pseudocolpi are similar in size and general appearance to the colporate apertures and can only be differentiated by their lack of endoapertures.

LM and SEM already suggest a threefold subdivision of the exine, but TEM clearly shows the presence of an electron-dense outer layer, differentiated into a tectum, a layer of columellae, and a footlayer, and an inner endexine *s. str.* which is less electron-dense. The latter layer is not clearly visible on the fuchsin stained LM micrographs of sections shown on Pl. V, 4 & 5.

The tectum is 0.3  $\mu\text{m}$  thick, with a shallowly pitted verrucate outer surface. The individual verrucae are 0.1–0.5  $\mu\text{m}$  in diameter, the pits are < 0.2  $\mu\text{m}$  deep. The inner boundary of the tectum is rather irregular. The tectum is absent in the centre of the colpi, but appears to dissolve into separate granules, 0.1–0.05  $\mu\text{m}$  in diameter, on the membranes of the pseudocolpi (Pl. VII, 3).

The columellae are 0.3  $\mu\text{m}$  long, 0.05–0.1  $\mu\text{m}$  in diameter. A layer of granules 0.05  $\mu\text{m}$  in diameter appears to be present in the outer zone of the columellate layer, partly attached to the inner side of the tectum. Over the apertural areas the columellae are much reduced or absent altogether, although a few granules may still be present, suggesting continuity.

The footlayer is up to 0.3  $\mu\text{m}$  thick and homogeneous on the mesocolpia, but reduced to 0.1  $\mu\text{m}$  or less over the colpate areas where it appears to be composed of electron-dense lamellae of < 0.05  $\mu\text{m}$  thickness (Pl. VII, 1). The footlayer is probably also reduced at the pseudocolpi.

The endexine *s. str.* is clearly visible on Pl. VII, 2 as a granular deposit 0.8  $\mu\text{m}$  thick underneath the colpate apertures, gradually thinning in the direction of the mesocolpia, in the centre of which it may be absent. It is probably absent underneath the pseudocolpi.

#### DISCUSSION

From the preceding descriptions it will be clear, that the pollen grains of the five genera are comparable in: small size, long ektoapertures which may be equatorially bridged and generally are provided with small endoapertures, thin exine with a similar structural differentiation and a smooth or finely verrucate to pitted surface. The principal differences are in the symmetry of the apertures, and in the shape and development of pseudocolpi or pseudocolpoid areas on the centres of the mesocolpia. The main problem is, whether pollen morphology can provide arguments pro or contra Van Beusekom's inclusion of all five genera in *Crypteroniaceae*. At first sight, of course, a major gap appears to exist between *Crypteronia* on one hand and the remainder of the genera on the other. Since no transitions could be observed between the bisyncolporate bilateral *Crypteronia*-type and the heterocolporate triradiate *Dactylocladus*-type, it appears difficult to derive these two pollen types directly from each other. However, it is possible to derive both types from a common, tricolporate ancestral type, which is close to the *Alzatea*-type and this is schematically shown in fig. 1.

The symmetry of the tricolporate type is defined by one equatorial and three polar planes of symmetry. Change *A*, towards the heterocolpate type involves no change in symmetry, but merely the addition of three, meridionally oriented pseudocolpi.

Guers (1970) has established that, within the genus *Rotala* (*Lythraceae*), species occur which are characterized respectively by three colpate apertures, by three colpate apertures with three indistinct pseudocolpi, and by three colpate apertures with three distinct pseudocolpi, while in *Rotala mexicana* differing degrees of heterocolpateness where found by Coz Campos (1964). Moreover, in *Alzatea* faint traces of incipient pseudocolpi are visible, approaching the condition of some *Rotala* species with indistinct pseudocolpi. All this would indicate that change *A* as depicted in the scheme is not inconceivable.

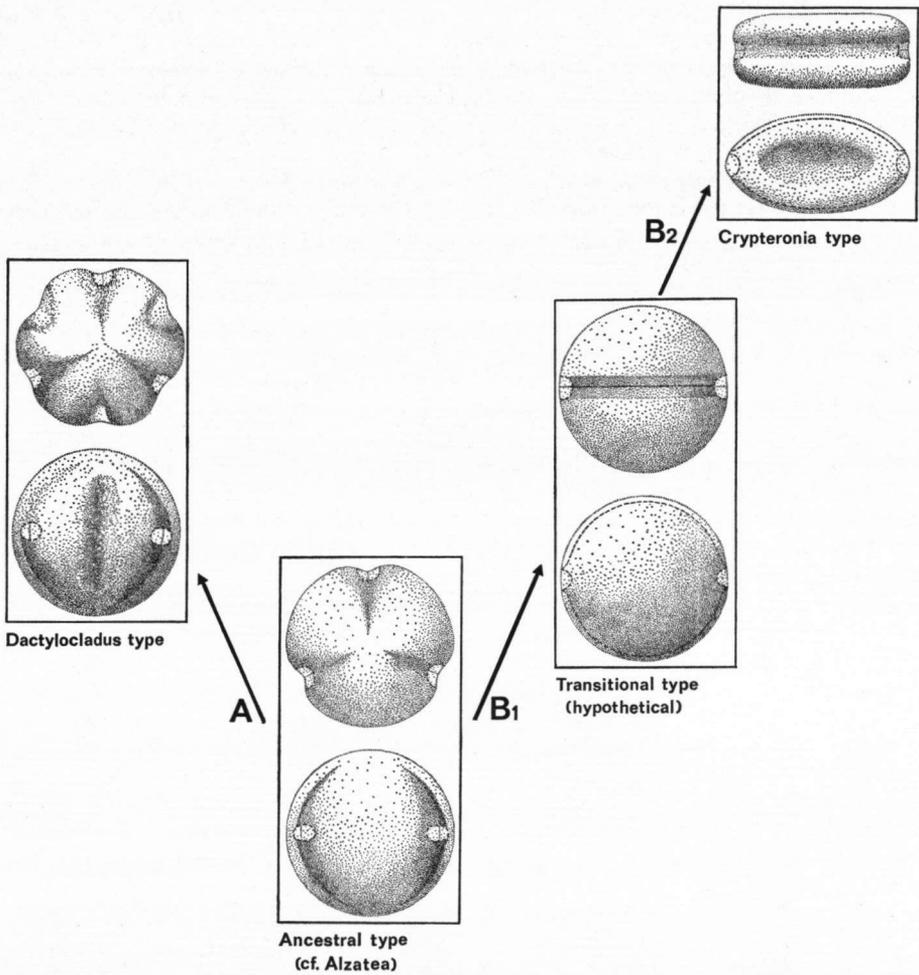


Fig. 1. Relations between pollen types in *Crypteroniaceae* (polar view uppermost, equatorial view lowermost).

Change *B1* towards a spherical, bisyncolporate grain involves a decrease in aperture symmetry from three to two polar planes of symmetry and a fusion of the two apertures at the poles. Similar transitions are known from *Phyllonoma integerrima* (*Saxifragaceae*; cf. Erdtman, 1952, fig. 231) and *Crossosoma californicum* (*Crossosomataceae*; cf. Erdtman, 1952, p. 133). In *Alzatea* bicolporate grains occur very rarely. In all these cases both tricolporate and bicolporate grains are present. Such a reduction in number of apertures therefore appears to be a not uncommon phenomenon. Huynh (1968) has shown that this may be caused by a change in orientation of the two couples of sister-microspores in the post-meiotic tetrad with respect to each other and this is not considered a fundamental change. The transitions to syncolporate grains are also regularly observed in some of these cases.

The final step (*B*<sub>2</sub>), towards the *Crypteronia* pollen type, involves firstly the development of bilateral shape symmetry by means of flattening parallel to the apertural symmetry plane and, secondly, a relative shortening of the polar axis. It will be obvious that the change from tricolporate to bicolporate has preceded, or occurred simultaneously with, the change in shape. The fact that in the taxa listed above, such an apertural change may occur without a change in shape, suggests that the former is primary, however. Thirdly, pseudocolpoid depressions in equatorial orientation may develop. Here the question arises, in how far these are comparable to the pseudocolpi found in the *Dactylocladus*-type. As is clear from the descriptions, the construction of both appears similar, only the orientation is equatorial in *Crypteronia*, meridional in *Dactylocladus*. Functionally they are no doubt comparable, both acting as additional harmomegathic structures and as such they represent specializations in comparison with the postulated simple ancestral tricolporate type. It will also be obvious that a meridionally oriented pseudocolpus is difficult to visualize in *Crypteronia* pollen and their equatorial orientation is structurally only to be expected. In the sense that in both cases they have originated from the centre of the mesocolpia, they may be considered homologous, and their appearance in otherwise diverging lineages, as shown in fig. 1, suggests independent, parallel development.

It thus appears that the differences in symmetry between the three pollen types may not be fundamental and can be explained as a case of diverging evolution. This, added to the obvious similarities in exine and aperture structure, supports the inclusion of the five genera in *Crypteroniaceae*.

The wider affinities of *Crypteroniaceae* remain to be discussed, as far as they are expressed in the pollen morphology. The relatively unspecialized *Alzatea*-type is widespread in many dicotyledonous families. It occurs in *Lythraceae*, in which *Alzatea* was placed by Lourteig (1965), in the genera *Adenaria*, *Pemphis*, *Pehria*, *Pleurophora*, *Physocalymna*, *Woodfordia*, and in some species of *Rotala*. It is also known from several other families of the Myrtalean alliance (*Punicaceae*, *Lecythidaceae*, *Rhizophoraceae*, *Combretaceae*).

The more specialized *Dactylocladus*-type is less widespread in *Lythraceae* and occurs only in *Lythrum*, *Peplis*, and in some species of *Ammania*, *Nesaea*, and *Rotala*. It is, however, also the dominant pollen type in *Melastomataceae*, *Combretaceae*, *Penaeaceae*, and *Oliniaceae*. These families appear to be closely related on macromorphological grounds.

The *Crypteronia*-type, as befits a fairly specialized pollen type, is more difficult to relate to other families. Erdtman (1952) has stated that *Crypteronia* pollen is similar to that found in *Corynocarpaceae*, *Cunoniaceae* (*Belangera*, *Geissois*), *Eucryphiaceae*, and *Saxifragaceae* (*Bauera*). In *Bauera* and *Geissois* the bicolporate grains are normal variants of tricolporate subprolate grains and no relations are indicated. The characteristic bilaterally flattened shape of the *Crypteronia*-type does, however, occur in the other taxa mentioned by Erdtman and, as I was recently informed by Dr. M. Hideux, also in *Platylophus*, *Anodopetalum*, *Ceratopetalum*, and *Schizomeria* (*Cunoniaceae*). In the latter genera a marked structural modification of the mesocolpium is also found, which is, perhaps, comparable to the pseudocolpoid depressions found in *Crypteronia* pollen. On the other hand, the finely reticulate wall found in the pollen grains of *Cunoniaceae* and *Eucryphiaceae* militates against a very close relationship.

Erdtman's (1952) and Takhtajan's (1959) suggestions of a relationship between *Crypteronia* and *Cunoniales* thus cannot be ruled out, although it may only be a remote one. In future, detailed comparisons of the fine structure of exine and aperture may yield decisive evidence.

In this connection, the interesting geographical distribution of the family, as conceived by Van Beusekom and of its pollen types should also be mentioned. *Alzatea* only

occurs in the Amazonian region of Peru, S. America, and may be an ancient relic. The *Dactylocladus* pollen type occurs in *Rhynchocalyx*, a local endemic of South Africa, and in the Asiatic genera *Axinandra* and *Dactylocladus*. Finally, the advanced *Crypteronia* pollen type is restricted to SE. Asia and suggests a young endemic development.

#### CONCLUSIONS

The present day lack of pollen morphological transitions between the pollen types within *Crypteroniaceae s.l.* would at first sight tempt one to dismiss any likelihood of a close taxonomic relationship. However, the fact that the three pollen types recognized can be arranged in an evolutionary scheme, as well as the pronounced similarities in aperture and exine fine structure, support Van Beusekom's delimitation of the family. His recognition of two subfamilies is not expressed in pollen morphology, the *Dactylocladus* pollen type occurring in both.

At the same time it must be stressed that pollen morphology provides no unique character separating *Crypteroniaceae s.l.* from other related families. Similar, if not identical, pollen types occur in *Punicaceae*, *Lythraceae*, *Melastomataceae*, *Combretaceae*, *Oliniaceae*, and *Penaeaceae* and this is supporting macromorphological and anatomical evidence. A more remote relationship to *Cunoniaceae* suggested by the *Crypteronia* pollen type is also indicated by macromorphology but not by anatomy. A relationship to *Sonneratiaceae* is improbable since their pollen grains are entirely different (Muller, 1969).

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Plate I. — Fig. 1—5. *Crypteronia paniculata*. 1. King's Coll. 235, polar view, U.F.; 2 & 3. Schiffner 2285, polar view, same grain, U.F. and L.F.; 4. Griffith & Helfer 2512/1, lateral view, U.F.; 5. Schiffner 2285, median view, L.F. — Fig. 6—10. *Crypteronia cumingii*, Mendoza 18241; 6. Polar view, U.F.; 7. Lateral view, L.F.; 8. Lateral section; 9. Median view, U.F.; 10. Median section, Ph. C. — Fig. 11—14. *Dactylocladus stenostachys*, Ashton Brun. 280; 11 & 12. Polar view, same grain, U.F. and L.F.; 13. Equat. section, Ph. C.; 14. Equat. view, U.F. — Fig. 15—17. *Axinandra beccariana*, S 15909; 15. Polar view, U.F.; 16. Polar view, L.F.; 17. Equat. view, U.F. — Fig. 18—20. *Alzatea verticillata*, Ule 6750; 18 & 19. Polar view, same grain, U.F. and L.F.; 20. Equat. view, U.F. — All x 2000, O.I.

Plate II. — Fig. 1—4. *Crypteronia paniculata*. 1. King's Coll. 235, lateral view, x 2500; 2—4. Griffith & Helfer 2512/1; 2. Polar view, x 5000; 3. Polar and apertural view, x 5000; 4. Polar view, x 5000. — Fig. 5—8. *Crypteronia cumingii*, Mendoza 18241; 5. Lateral view, x 5000; 6. Polar view, x 5000; 7. Median section and oblique polar view, x 5000; 8. Median section at apertural end and oblique polar view, x 5000. — All: SEM.

Plate III. — Fig. 1 & 2. *Crypteronia cumingii*, Mendoza 18241; 1. Median section, x 5000; 2. Median section, x 5000. — Fig. 3 & 4. *Crypteronia griffithii*, Griffith s.n.; 3. Lateral view, x 5000; 4. Lateral view, x 5000. — Fig. 5—8. *Crypteronia macrophylla*, Endert 4040; 5. Lateral view, x 5000; 6. Lateral view, x 5000; 7. Polar view, x 5000; 8. Oblique polar view, x 5000. — All: SEM.

Plate IV. — Fig. 1—3. *Dactylocladus stenostachys*, Ashton Brun. 280; 1. Polar and equat. view, x 2500; 2. Equat. view, x 2500; 3. Equat. section, x 3500. — Fig. 4 & 5. *Axinandra beccariana*, S 15909; 4. Polar view, x 2500; 5. Equat. view, x 2500. — Fig. 6—9. *Alzatea verticillata*, Ule 6750; 6. Polar view, x 2500; 7. Oblique polar view, x 2500; 8. Equat. view, x 2500; 9. Aperture, x 3500. All: SEM.

Plate V. — Fig. 1—11. *Rhynchocalyx lawsonioides*, Strey 6539; 1. Polar view; 2. Equat. view of endoaperture; 3. Equat. view of pseudocolpus; 4. Equat. section; 5. Meridional section; 6. Inner view of endoaperture; 7. Equat. view of colporate aperture at left and pseudocolpus at right, x 2500; 8. Equat. view centred on colporate aperture, x 2500; 9 & 10. Interior view of endoaperture, x 2500; 11. Interior polar view, x 10.000. — 1—6: LM, x 2000, O.I.; 7—11: SEM.

Plate VI. — Fig. 1—4. *Crypteronia paniculata*, King's Coll. 235; 1. Oblique section, at top right corner through endoapertural region, at bottom through ektoaperture on pole (c) and at left through pseudocolpoid area (pc), x 10.000; 2. Detail of fig. 1 showing granular-lamellar structure of endexine, x 25.000; 3. Meridional section approximately through centre of pseudocolpoid areas, polar sections of ektoaperture at bottom right and top left, x 10.000; 4. Oblique section through pseudocolpoid area at bottom, x 10.000. — Fig. 5. *Axinandra beccariana*, S 15909, equat. section through pseudocolpus at bottom and colporate aperture at left, x 10.000. — 1—5: TEM.

Plate VII. — Fig. 1—3. *Rhynchocalyx lawsonioides*, Strey 6539; 1. Oblique section through endoapertural region, x 20.000; 2. Equat. section through endoapertural region at top, pseudocolpus at right, x 10.000; 3. Equat. section, colporate apertures (c) alternating with pseudocolpi (pc), x 10.000. — All: TEM.

Plate VIII. — Fig. 1—4. *Dactylocladus stenostachys*, Ashton Brun. 280; 1. Oblique section through intercolpate area, x 20.000, detail of fig. 2; 2. Oblique section, colporate aperture (c) and pseudocolpus (pc), x 10.000; 3. Tangential section through intercolpate exine, tectum in centre, footlayer at periphery, x 20.000; 4. Equat. section, colporate apertures (c) alternating with pseudo-colpi (pc), x 10.000. — All: TEM.

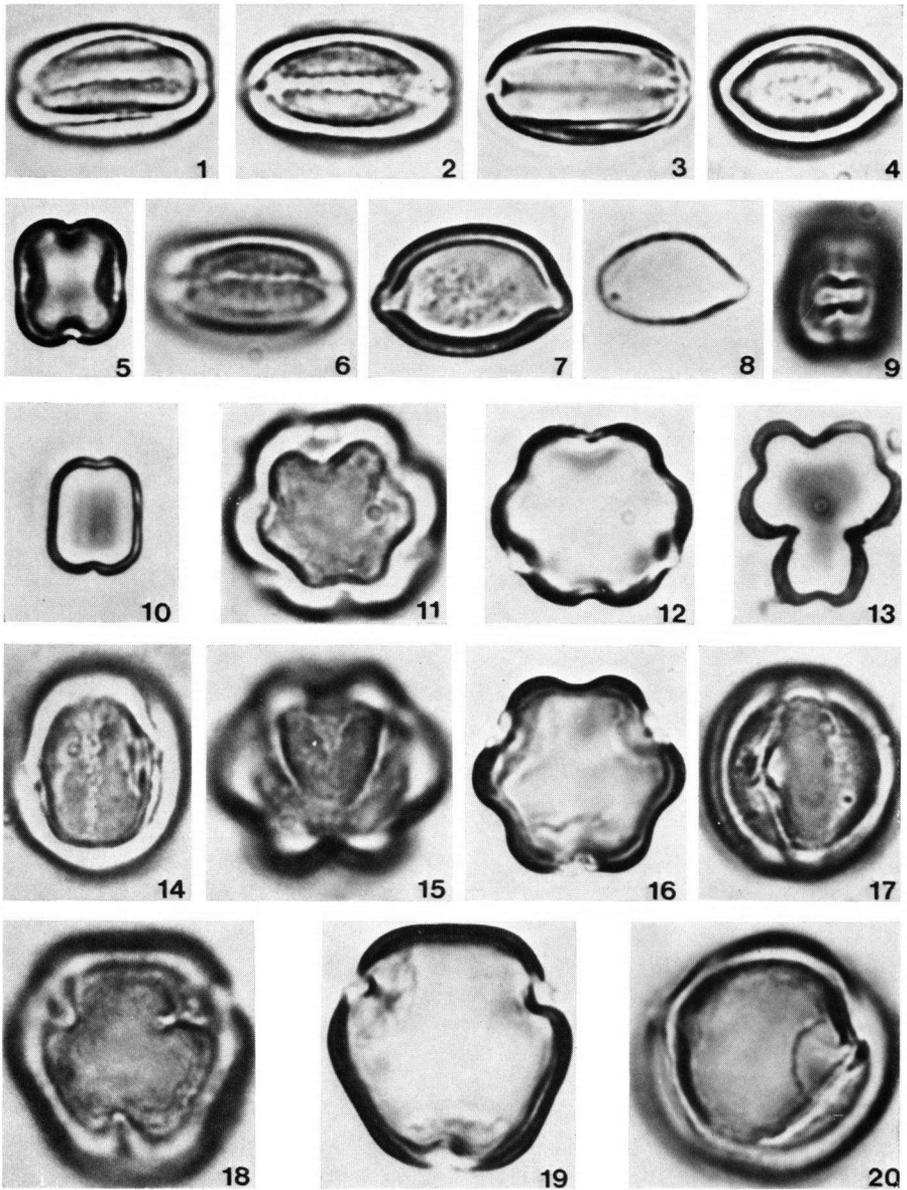


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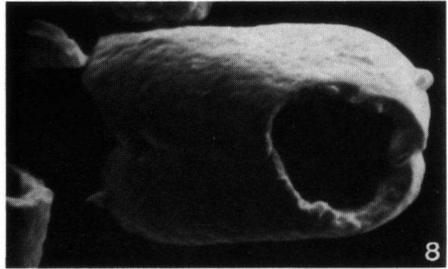
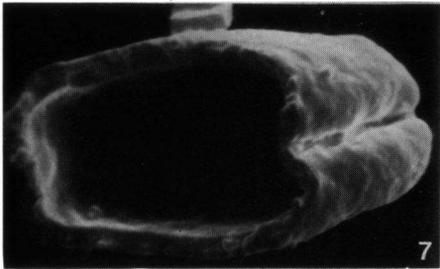
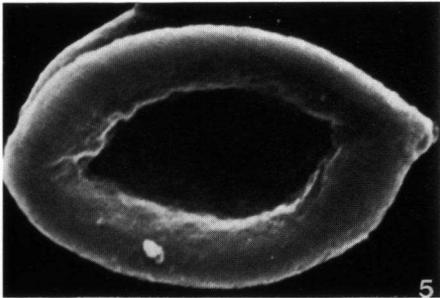
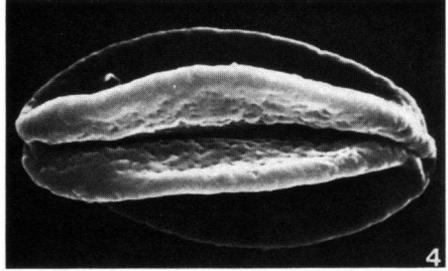
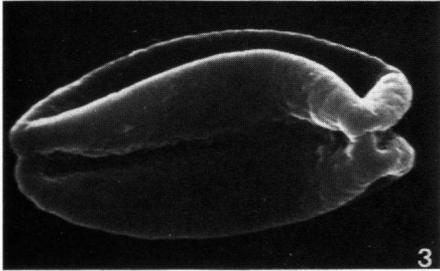
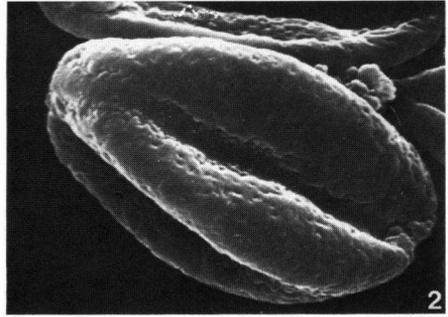
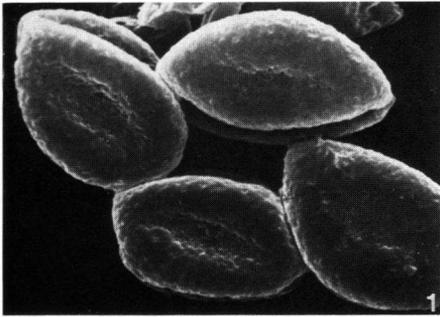


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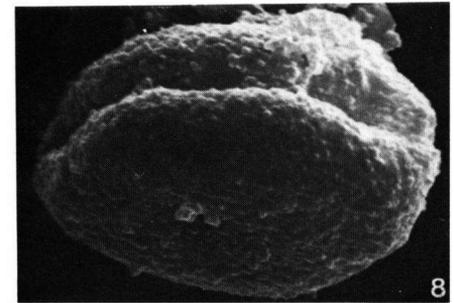
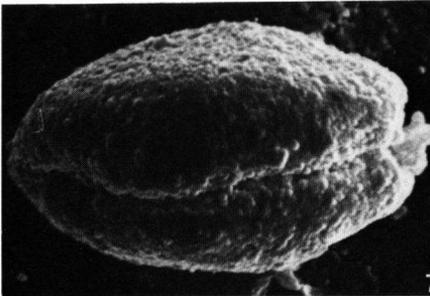
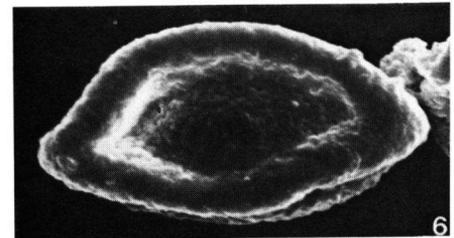
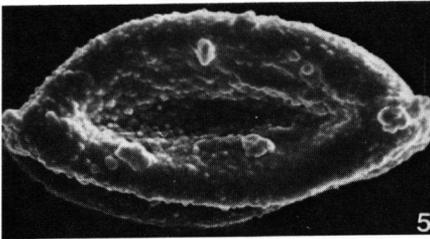
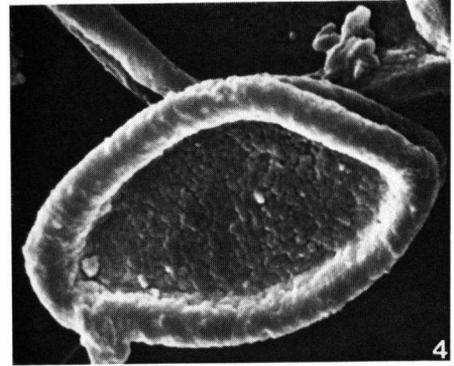
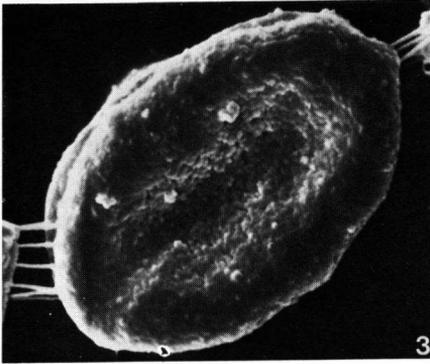
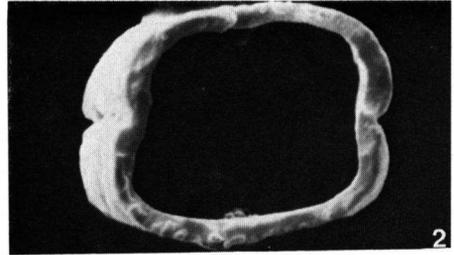
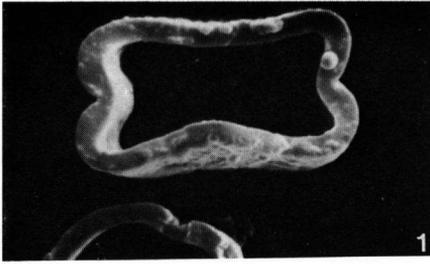


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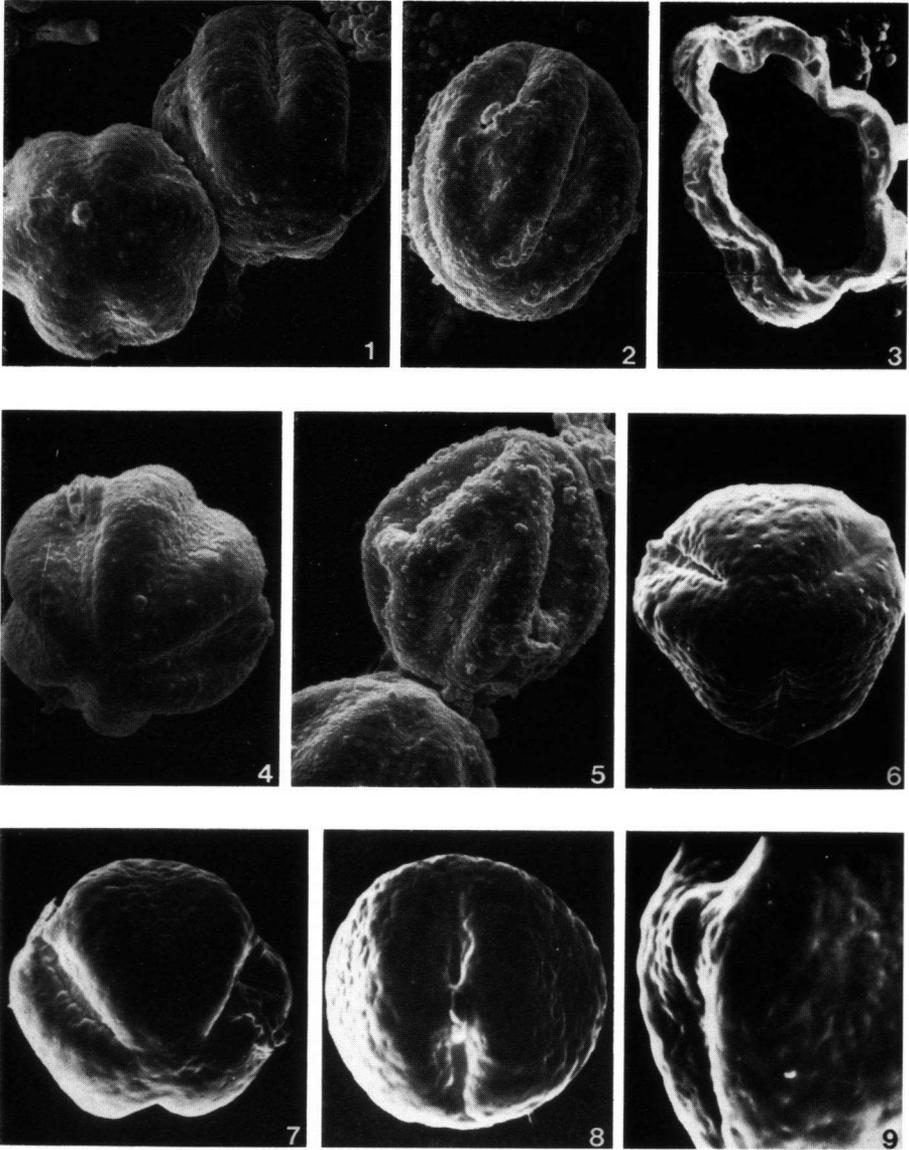


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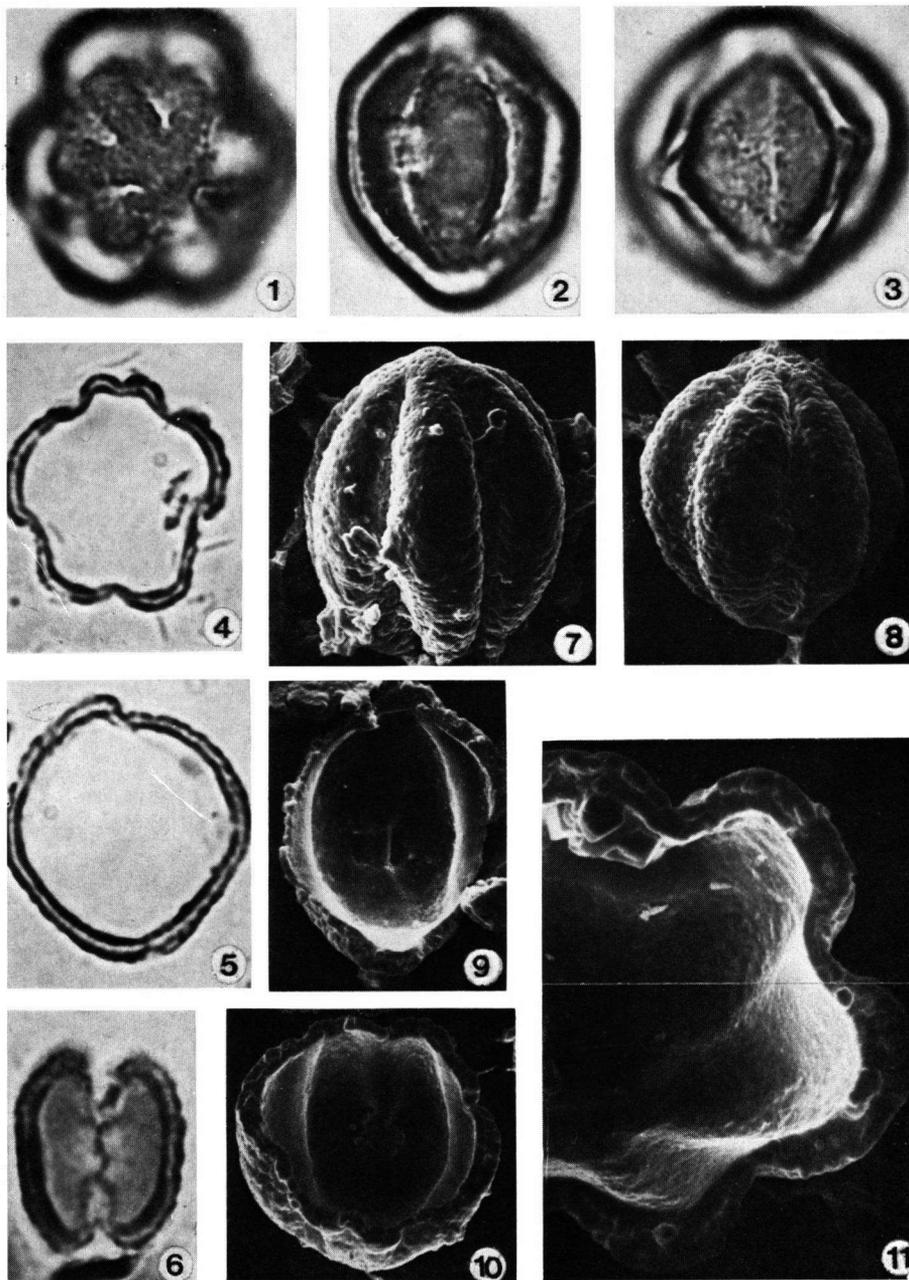


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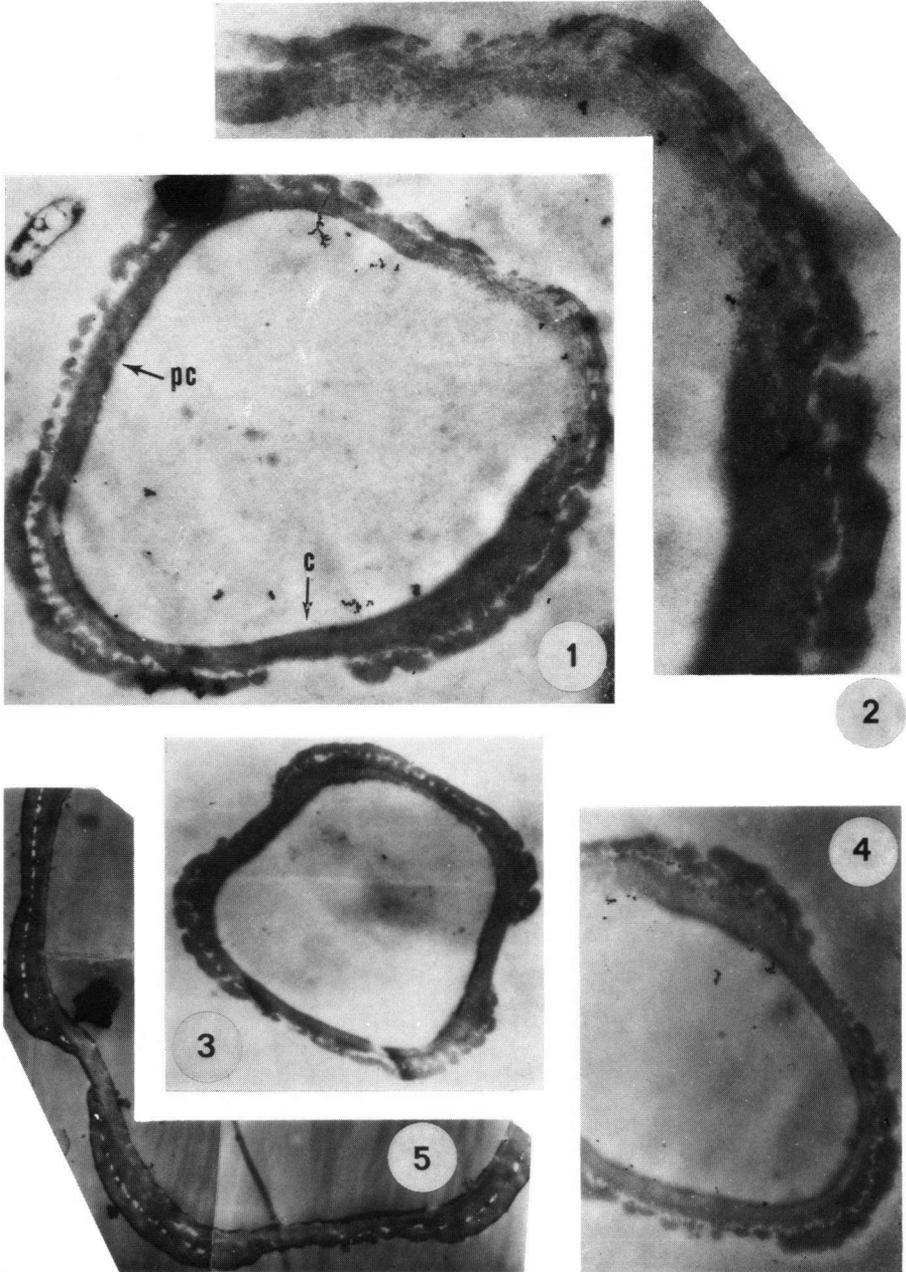


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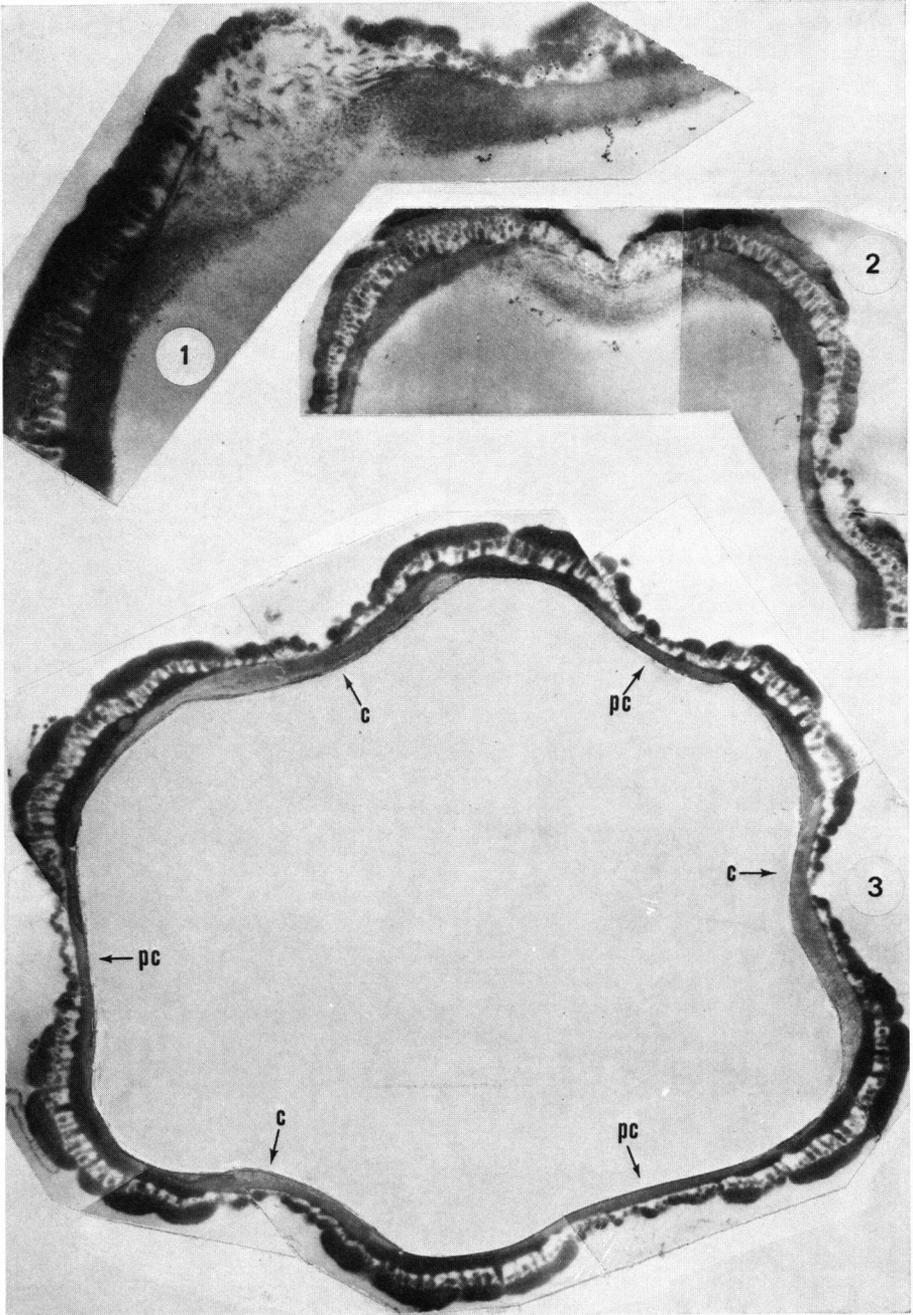


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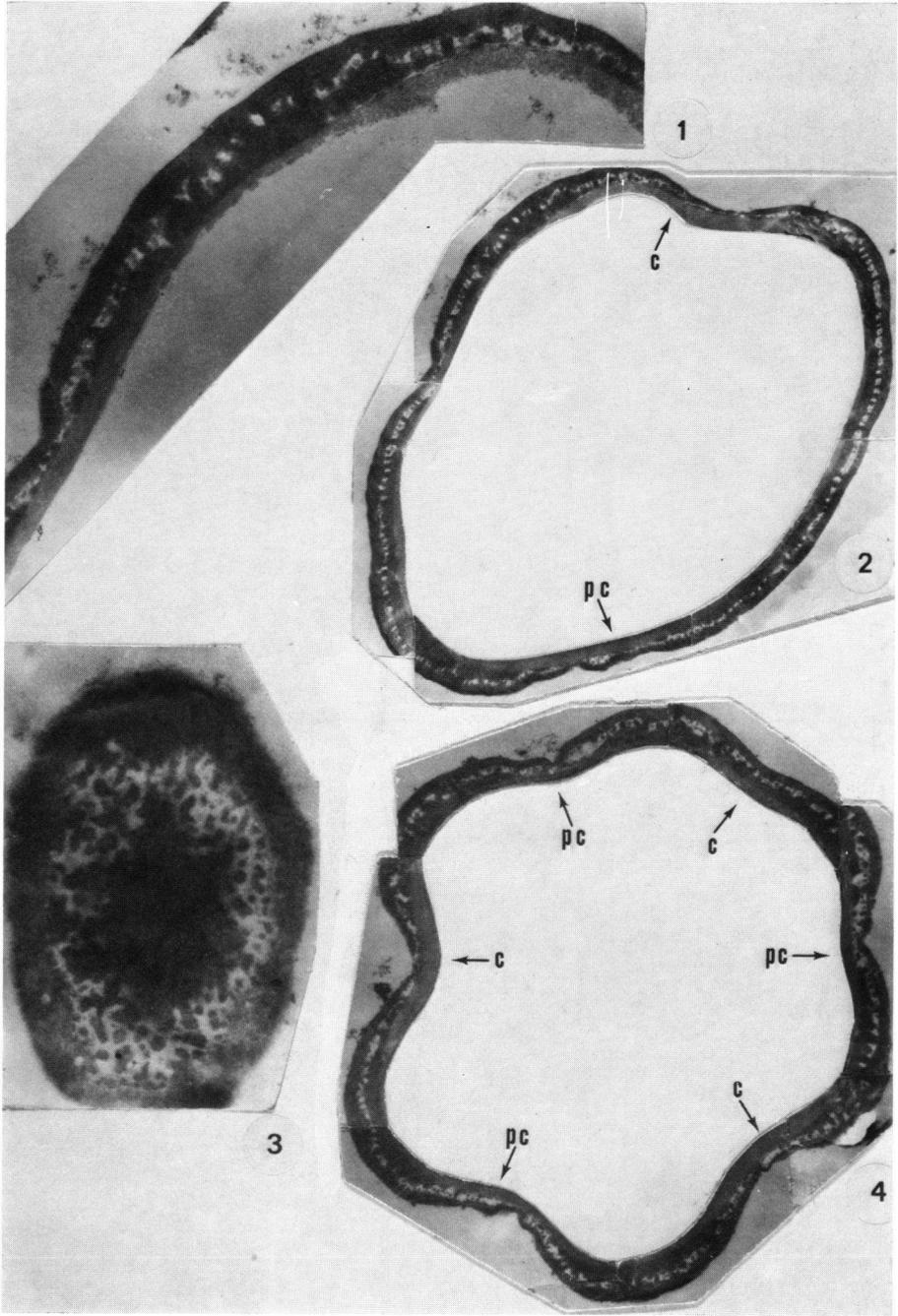


Plate VIII