

**POLLEN MORPHOLOGY OF THE GENUS *CROSSONEPHELIS*
(SAPINDACEAE)¹**

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SUMMARY

The pollen morphology of all 7 species of the genus *Crossonephelis* was studied and found to be rather uniform, supporting Leenhouts' circumscription of the genus. Minor inter- and intraspecific differences are present. Within *Lepisantheae* a close resemblance exists with the pollen of some species of *Placodiscus*, while the pollen of *Lepisanthes* is less similar and specialized in a different direction.

I. INTRODUCTION

This note is a further contribution to the pollen morphology of *Sapindaceae* and deals with *Crossonephelis*, a genus revised by Leenhouts in this volume. All seven species recognized by him could be investigated and proved to have the same pollen type, with only minor interspecific differences. It is thus possible to present one general morphologic description for the genus, followed by a discussion of these differences and their taxonomic significance. Some remarks on relationships with other genera, as far as indicated by the still incomplete pollen evidence, are added.

The fine sculptural details of the rather small grains of *Crossonephelis*, which are at the limit of resolution of the light microscope (LM) could be studied in detail with the scanning electron microscope (SEM). This study has therefore relied heavily on observations with the latter instrument (Cambridge A II, Geological Institute, Leiden). Wall and endoaperture structure could be observed by means of freeze microtome sections, following a technique described in detail elsewhere (Muller, 1973). Otherwise, methods of investigation were the same as used in previous studies on the genera *Lepisanthes* and *Dimocarpus* (Muller, 1970, 1971).

The author is much indebted to Mr. W. Star (Rijksherbarium) for sectioning and Mr. H. Kammeraat (Geological Institute) for producing the scanning electron micrographs.

¹ This paper was already in the hands of the editor when Fouilloy's description of a new species, *C' adamii* (*Adansonia* II, 12, 1973, p. 551) came to our notice. It proved, unfortunately, impossible to obtain a pollen sample of this species in time to include a description.

II. GENERAL MORPHOLOGY

The pollen grains in *Crossonephelis* are single, isopolar, and mostly tricolporate, although di- and tetracolporate grains occur in a low percentage in some species. A dicolporate grain is shown on Pl. V, 21, while tetracolporate grains are visible on Pl. III, 1, and Pl. V, 3. The latter grain is, exceptionally, syncolpate.

Average size varies between 17 and 26 μm . Shape, as defined by the ratio between length polar axis and equatorial axis (P/E) is mostly spherical, P/E varying between 0.93 and 1.10. A spherical outline is shown on Pl. V, 11, while a subprolate grain such as occurs rather frequently in some species, notably *C. africanus*, is pictured on Pl. V, 4. The equatorial outline is mostly circular (Pl. IV, 5; Pl. V, 2), occasionally rounded triangular with the apertures situated at the angles (Pl. IV, 2; Pl. V, 19–20).

Observations of wall structure with LM and SEM show the presence of an inner homogeneous layer and an outer structured layer (Pl. II, 4; Pl. V, 7–8, 12). Since both layers stain with basic fuchsin, it would appear doubtful whether an endexine s. str. is present. Pending transmission electron studies, the inner layer is here referred to as endexine in a topographical sense. This endexine is generally fairly thin (0.5 μm) and even in thickness, as is visible on Pl. II, 3–4 and Pl. V, 12, although occasionally it may be slightly thicker on the centres of the mesocolpia and on the apertural membranes (Pl. III, 4; Pl. V, 8). The outer structural layer will be referred to as ektexine and is generally developed as an inner layer of, mostly inconspicuous, columellae and an outer striate or reticulate-striate layer which may be the equivalent of the tectum.

The columellate layer is most distinct in *C. palawanicus* (Pl. II, 4; Pl. V, 7–8), but in the other species it is either very thin, or hardly distinguishable from the overlying striate sculptural elements. In general the columellae are short (<0.5 μm high), thin, circular in cross section, and arranged in a striate, substriate, or striate-reticulate pattern, in conformity with the overlying sculptural pattern of the tectate layer. In some species the columellae are slightly longer in the central areas of the mesocolpia (Pl. V, 8).

The tectate layer consists of a system of two- (Pl. I, 2) or threedimensionally (Pl. I, 6) anastomosing ridges. The orientation of the ridges may be subparallel (Pl. I, 1) or irregular (Pl. I, 4), dense (Pl. IV, 6) or rather loose (Pl. I, 6). The width of the ridges varies between 0.3–0.4 μm . Their dominant orientation, which is most clearly visible on the densely striate grains, is meridional (Pl. I, 1; Pl. II, 6). On the poles the patterns of two mesocolpia often join, overriding the pattern of the third one (Pl. II, 5; Pl. III, 6). The loose, irregularly striate patterns, especially when they are three-dimensional, create under the LM the impression of a reticulate pattern (Pl. V, 5, 18), but SEM micrographs show that this is caused by two differently oriented superimposed systems of subparallel ridges (Pl. I, 6). The lowermost level of the striate pattern conforms to the columellate pattern and probably originates by fusion of the tips of the columellae. On Pl. V, 8 and 18, it appears that at this level very thin membranes are locally present on which, at a later stage, the striate superstructure is deposited. The exact mode of formation would have to be studied in detail ontogenetically with transmission electron microscopical methods. In cases where the columellae are not visible, it is assumed that the ridges are directly fused with the endexine surface. This also seems to be the case close to the apertures (Pl. V, 8). In some species the upper ridges may degenerate into an irregular rugulate pattern which may, on occasion, even bridge the ektoaperture (Pl. III, 6). It appears likely that this represents a last stage of sporopollenin deposition, in which strict morphogenetic control has been partly lost.

The ektoapertures are colpate, meridionally oriented, long to medium long, E/C

(= equatorial diameter/length ektoaperture) varying between 1.09 and 1.34 and more or less invaginated, without costae (Pl. V, 12). They are closed by a membrane, the surface of which is covered with a finely verrucate sculpture (Pl. I, 3—4; Pl. II, 3; Pl. III, 2). While the bulk of the membrane, as can be seen on Pl. V, 12, appears to be formed by the endexine, the verrucae may be ektexinous in nature. This is suggested by the fact that, as can be observed on Pl. III, 2, occasionally the apertural verrucae are partly continuous with adjoining striate ridges of the mesocolpium. Also, the transition with the striate sculpture of the mesocolpia may be rather sharply defined (Pl. III, 2) or indistinct (Pl. II, 3).

The endoapertures are equatorial circular-oval or rather irregularly shaped holes or thinned areas in the apertural membranes, rarely exceeding the width of the ektoapertures (Pl. II, 1; Pl. V, 14, 17). Occasionally, an equatorial bridge is present, as shown on Pl. IV, 4 in the left hand aperture. The endoapertures are in general rather small (2—3 μm in diameter), variably developed, even in a single grain (Pl. IV, 4), and appear rather insignificant.

The foregoing general description covers all species of the genus. The minor inter-specific differences which exist will be discussed in the following systematic account in which also detailed measurements are presented. Intraspecific variability will be described for *C. palawanicus*.

III. SYSTEMATIC DESCRIPTIONS

CROSSONEPHELIS BAILL.

Crossonephelis africanus (Radlk.) Leenh.

Pl. I: 1—3; Pl. V: 1—4.

Material studied. Africa, Rhodesia: *Chase 4419*. — Tanzania: *Lewis 236*. — Uganda: *Sangster S 20*, *Scheffler 343*. — Nigeria: *Lobe Babute Cam. 5236*.

P/E 0.99 (1.10) 1.14, equatorial outline circular, number of apertures 2 (4%), 3 (94%), 4 (2%). Size P 18 (19.3) 22 μm , E 16 (17.7) 20 μm . Ektoapertures 14 (15.6) 18 μm long, E/C 1.14. Endoapertures 2.5 (3.0) 4.3 μm . Total wall thickness uniform, 0.9 μm . Columellae indistinct, <0.5 μm high. Tectum densely finely striate, ridges subparallel, predominantly meridionally oriented, frequently anastomosing, but mostly in one plane. Surface of ridges smooth or slightly rugulate, occasionally a thicker ridge or verrucae on top.

C o m m e n t. The pollen of this species is characterized by its spherical-subprolate shape (Pl. I, 1; Pl. V, 4), densely striate sculpture (Pl. I, 2), long colpi (Pl. I, 3; Pl. V, 1), indistinct columellae (Pl. V, 4), and variable number of apertures (Pl. V, 3). The aperture membrane appears to bear only a few scattered verrucae (Pl. I, 3). It shows great resemblance with the pollen of *C. unijugatus*.

Crossonephelis palawanicus (Radlk.) Leenh.

Pl. I: 4—6; Pl. II: 1—6; Pl. V: 5—11.

Material studied. Group A. Philippines, Mindanao: BS 49205. — Papua: Brass 7980. Group B. Sumatra: Lambach 1336; v/d Zwaan 114. T 3. P 513.

Group A. P/E 1.02 (1.03) 1.04, equatorial outline circular, number of apertures 3 (100%). Size P 25.8 (25.9) 26.0 μm , E 24.7 (25.0) 25.3 μm . Ektoapertures 18.8 (20.1) 21.3 μm , E/C 1.24. Endoapertures 4.6 (5.4) 6.1 μm . Total wall thickness uniform, 1.5

μm . Columellae distinct, $0.3 \mu\text{m}$ in diameter, $0.5 \mu\text{m}$ high, arranged in a reticulate pattern. Tectum striate-reticulate, ridges $0.3 \mu\text{m}$ wide, subparallel or in an irregular criss cross pattern, strongly anastomosing and intertwining in three dimensions. Lumina $0.3\text{--}0.5 \mu\text{m}$ in diameter.

Group B. P/E 0.96 (0.98) 0.99, equatorial outline circular, number of apertures 3 (100%). Size P 18.3 (18.8) 19.2 μm , E 18.5 (19.2) 19.9 μm . Ektoapertures 14.2 (14.7) 15.2 μm . E/C 1.31. Endoapertures 2.7 (3.4) 4.1 μm . Total wall thickness uniform, 1.1 μm . Columellae present, but indistinct, arranged in a striate pattern. Tectum striate, ridges rather coarse, $0.4 \mu\text{m}$ wide, infrequently anastomosing, rather densely packed in parallel rows at different levels, showing a variable orientation, sometimes in a curvi-linear pattern, mostly subparallel to the margins of the ektoapertures.

C o m m e n t. The two groups of samples clearly differ in size and in sculptural pattern of the tectum.

Group A has the largest grains of all the species investigated and, possibly as a consequence, also the most distinct columellae, which are reticulately arranged (Pl. V, 5). On Plate I, 6 a few columellae are visible in surface view, bordering a lumen in the lower right hand corner. On the sections of Pl. V, 7—8 the columellae are clearly visible and form a layer which shows a sharp transition with the overlying tectate layer. The rather loosely reticulate-striate sculpture of the tectum, with conspicuous lumina, is also highly typical for this group (Pl. I, 4). Occasionally a closed tectum is locally developed as can be seen on Pl. I, 6 at the right hand side. Some variability in sculpture is apparent also, as shown by comparing Pl. I, 4 and Pl. I, 5. The relatively short ektoapertures are visible on Pl. I, 4 and Pl. V, 5.

Group B, in contrast, has much smaller grains, with a coarse striate sculpture (Pl. II, 5—6; Pl. V, 9).

It is of interest that Leenhouts has noticed also differences in macromorphology between material from Borneo and Sumatra on one hand and the Philippines and New Guinea on the other. When more good flowering material becomes available this could lead to a taxonomic subdivision of *C. palawanicus*.

Crossonephelis penangensis (Ridl.) Leenh.

Pl. III: 1—4; Pl. V: 12.

Material studied. Malay Pen.: KEP 4212.

P/E 1.01, equatorial outline circular, number of apertures 3 (99%), 4 (1%). Size P 18.8 μm , E 18.0 μm . Ektoapertures 15.9 μm long, E/C 1.13. Endoapertures 3.1 μm . Total wall thickness uniform, 1.0 μm . Columellae present, but indistinct. Tectum reticulate-striate, ridges predominantly in a meridional pattern, anastomosing, moderately intertwining, medium dense, leaving irregularly shaped lumina between them.

C o m m e n t. On Pl. III, 1 an irregular tetracolorate grain is shown in polar view, while the uppermost apertural region is enlarged on Pl. III, 2. Here the endoaperture is visible as a small irregular hole in the apertural membrane which does not extend beyond the margins of the colpi. The rather sparse verrucation of the membrane and the partial attachment of individual verrucae to the striate ridges are also shown here. The same SEM micrograph shows the presence of two levels of ridges and the reticulate appearance

caused by the irregular orientation of the rather widely spaced ridges. On Pl. III, 3 the ridges are submeridionally oriented at the right hand side, but at the left the orientation is different. Columellae, although visible on the LM micrograph of Pl. V, 12, are invisible on the equatorial section of the SEM micrograph of Pl. III, 4. Only a slightly narrowed basal part of the ridges is suggested here (Pl. V, 12). The slightly thickened and shallowly verrucate, invaginated aperture membrane is visible on Pl. III, 3 and Pl. V, 12.

The pollen of this species comes closest to that of *C. philippinensis*, from which it only differs in the slightly longer ektoapertures and the more spherical shape.

***Crossonephelis pervillei* Baill.**

Pl. III: 5—6; Pl. V: 13—15.

Material studied. Madagascar: *Capuron SF 18413, Humbert 18833, 24241, RN 4325.*

P/E 0.98 (1.01) 1.05, equatorial outline subangular, number of apertures 3 (99%), 4 (1%). Size P 18 (20.2) 23 μm , E 19 (20.1) 22 μm . Ektoapertures 15 (16.0) 18 μm long, E/C 1.25. Endoapertures 2.6 (3.4) 4.8 μm . Total wall thickness on mesocolpia 1.2 μm , thinner towards apertures and poles. Columellae present but indistinct, arranged in a reticulate pattern. Tectum densely reticulate-rugate or striate. Ridges irregularly submeridionally oriented, subparallel, strongly anastomosing and frequently intertwining. Ridges occasionally fused without intervening grooves. The uppermost level is formed by widely scattered, irregular, rugulate-verrucate ridge elements which occasionally bridge the ektoapertures.

C o m m e n t. The pollen of this species appears to be uniquely characterized by its subangular equatorial outline with thickened wall on the centres of the mesocolpia and its very dense and irregular striate-rugulate sculpture. The apertures are narrowly invaginated on Pl. III, 5 and almost covered with rugulate sculpture on Pl. III, 6. In this grain the ridges are converging from two mesocolpia over the pole, overriding the third system. The main, underlying striate pattern is rather dense and visible on Pl. III, 6 and Pl. V, 13—15.

***Crossonephelis philippinensis* (Radlk.) Leenh.**

Pl. IV: 1; Pl. V: 18.

Material studied. Philippines, Luzon: *FB 25719.*

P/E 0.93, equatorial outline circular, number of apertures 3 (100%). Size P. 18.6 μm , E 20.0 μm . Ektoapertures 14. 9 μm long, E/C 1.34. Endoapertures rather distinct, 4.1 μm . Total wall thickness uniform, 1.0 μm . Columellae present but indistinct, arranged in a reticulate pattern. Tectum reticulate-striate, ridges rather irregularly meridionally oriented, densely or rather widely spaced.

C o m m e n t. This sample appears to be characterized by short colpi, spherical-sub-oblata shape, and often more reticulate than striate sculptural pattern. The apparent shortness of the ektoapertures may, however, be due to the indistinct outline, as shown on Pl. IV, 1 where a gradual transition between the striate sculpture of the mesocolpium and the densely rugulate-verrucate sculpture of the apertural membrane is visible.

Crossonephelis thorelii (Pierre) Leenh.

Pl. IV: 2—4; Pl. V: 16—17.

Material studied. S. Vietnam: *Pierre 4089*.

P/E 1.07, equatorial outline circular to slightly subangular, number of apertures 3 (100%). Size P 21.3 μm , E 19.9 μm . Ektoapertures 18.2 μm long, E/C 1.09. Endoapertures irregularly developed, 3.2 μm . Total wall thickness uniform, 1.0 μm . Columellae present, 0.2 μm high, arranged in a reticulate pattern. Tectum striate-reticulate, ridges in a very irregular pattern, leaving lumina of 0.2 μm in diameter. A few larger rugulae overriding the striate pattern.

C o m m e n t. Although the type specimen bore only a few male buds, the pollen extracted appeared nevertheless fully developed. It is characterized by its long ektoapertures and often more reticulate than striate sculpture. This pattern is most clearly shown on Pl. IV, 2, while on Pl. IV, 3 a more rugulate pattern is dominant. The aperture membranes in both cases are locally bridged by rugulate extensions from the mesocolpial sculpture. The subangular outline is shown on Pl. IV, 2. The meridionally sectioned grain on Pl. IV, 4 shows a side view of the invaginated ektoapertures with the two corresponding endoapertures. The one at left has a closed membrane and is thus clearly an equatorial bridge only, while the one at right appears irregularly torn open. This section shows at right also rather distinctly the division of the wall in an endexine, layer of columellae, and a rather dense tectum which consists of a single level of striate ridges.

The pollen of this species is close to that of *C. penangensis*, from which it differs only in the slightly more striate-reticulate sculpture. It differs from *C. palawanicus* form A in size and relative length of ektoapertures and from B in sculptural pattern. This confirms Leenhouts' opinion that these two species are distinguishable.

Crossonephelis unijugatus (Pellegrin) Leenh.

Pl. IV: 5—6; Pl. V: 19—21.

Material studied. Africa, Gabon: *Le Testu s.n.*

P/E 0.97, equatorial outline circular-subtriangular, number of apertures 2 (18%), 3 (82%). Size P 17.0 μm , E 17.4 μm . Ektoapertures 14.4 μm long, E/C 1.14. Endoapertures 3.6 μm . Total wall thickness uniform, 0.8 μm . Columellae present, but indistinct, <0.5 μm high, arranged in a striate-reticulate pattern. Tectum densely striate, ridges subparallel, mainly meridionally oriented, frequently anastomosing, probably mostly two-dimensional, with a smooth or slightly irregular surface.

C o m m e n t. This species is characterized by its densely striate sculpture, long ektoapertures, indistinct columellae, and high percentage of dicolporate grains (Pl. V, 21). The grain on Pl. IV, 5 shows that the ektoapertures are rather indistinctly outlined. Pl. IV, 6 shows narrowly invaginated ektoapertures, while the mesocolpium on the right is also somewhat invaginated. The ridges are very dense on this grain and mainly meridionally oriented, although some oblique bundles occur near the aperture.

The pollen of this species shows great resemblance with that of *C. africanus*. It was already described from a different specimen by Merville (1965), under the name *Melano-*

discus unijugatus, as having a reticulate sculpture with angular lumina, distinct columellae, indistinct annuli and costae due to endexinal thickening. Her photomicrograph (l.c. Pl. IV, 5) shows what could be termed a reticulate-striate pattern of ridges, but the other details mentioned in the description are not visible. Without further detailed investigation the significance of the discrepancies between the two descriptions is not clear.

IV. POLLEN MORPHOLOGY AND TAXONOMY

The species known to Radlkofer (1932), which are here united in *Crossonephelis*, were placed by him in six separate genera, assigned to three different tribes. The main question which has therefore to be answered is, whether Leenhouts' circumscription of the genus, which was in part already anticipated by Capuron (1969), is supported by pollen morphology. It will at once be obvious that the large degree of uniformity of the pollen grains can be taken as a powerful reinforcement of the present conception of *Crossonephelis*.

At the same time, however, this uniformity allows only rather vague suggestions as to the affinities and distinctness of the species within the genus. It appears that the two species of the mainland of Africa, *C. africanus* and *C. unijugatus*, have nearly identical pollen characterized by a variable number of apertures, long ektoapertures, and densely striate sculpture. *C. africanus* has slightly more subprolate grains. *C. pervillei* from Madagascar is somewhat isolated because of its subangular equatorial outline with higher columellae in the centres of the mesocolpia and rugulate-striate sculpture. The East Asian species *C. penangensis* and *C. philippinensis* are again very similar and characterized by a striate-reticulate sculpture. *C. palawanicus* A is similar to this group, while *C. palawanicus* B differs in the coarsely striate sculptural pattern. *C. thorelii*, finally, appears closest to *C. palawanicus*. The differences in pollen morphology between these two species, although minute, are probably real and may be taken as an additional argument for keeping them separate, as was done by Leenhouts on macromorphological grounds.

The existence of two geographically separated groups in *C. palawanicus*, which appears to parallel macromorphological evidence, as well as the differences between the African and Asian species in general, suggest that, as found earlier in *Lepisanthes* and *Dimocarpus* (Muller, 1970, 1971), geographical isolation may lead to differences in pollen morphology.

A second problem is, whether *Crossonephelis* is at home in *Lepisantheae* and what could be its closest relatives within this tribe. Of the twelve genera included by Radlkofer (1932) only *Lepisanthes*, *Chytranthus*, *Pancovia*, and *Crossonephelis* have been studied pollen morphologically (Merville, 1965; Muller, 1970, 1971).

Crossonephelis pollen differs from that of *Lepisanthes* in its smaller size, striate sculpture, and inconspicuous endoapertures. *Lepisanthes* pollen, in contrast, shows great variability, is generally larger, mostly reticulate-perforate, has a variable length of the ektoapertures, and may have conspicuous costate endoapertures. Especially the derived coarsely reticulate pollen types in *Lepisanthes* are very different from *Crossonephelis* pollen. Radlkofer's idea that *C. palawanicus* might be related to *Lepisanthes* thus finds no support in pollen morphology.

Leenhouts considers *Lepisanthes* and *Chonopetalum* to be the nearest allies of *Crossonephelis*. As stated above, it is difficult to find any close resemblance with *Lepisanthes* pollen. In aperture construction *Crossonephelis* comes closest to the *Lepisanthes tetraphylla* type and the finely reticulate sculpture of the latter could conceivably have given rise, by means of a re-arrangement of the columellae, to a striate type. It is, however, significant that within *Lepisanthes* this did not happen.

Much depends also on whether in *Lepisantheae* a striate sculpture is derived or not. In

Dimocarpus, which belongs to the tribe *Nephelieae*, both reticulate and striate patterns are known and the latter is considered to be derived (Muller, 1971).

The pollen of *Chonopetalum* has, unfortunately, not yet been described, but a comparison with *Placodiscus*, the pollen of which has been described by Merville (1965), is of interest, since *Crossonephelis* pollen appears to be very similar to that of *Placodiscus angustifolius* and *P. letestui*, which are both characterized by a finely striate sculpture. The other species of *Placodiscus* are stated by Merville to possess reticulate pollen grains. *Crossonephelis* pollen would thus fall under Merville's '*Lychmodiscus*-type', except for the fact that the '*replis*' or endexinal fold is absent in *Crossonephelis*. However, whether this '*replis*' is really present in *Placodiscus* is difficult to judge from the photomicrographs presented by Merville.

It would appear significant that in Radlkofer's key *Placodiscus* is close to *Crossonephelis* and that Leenhouts considers both genera to be derived at about the same level. The close similarity between their pollen grains could thus support the idea of a closer taxonomic relationship between them, rather than with *Lepisanthes*.

The pollen of *Crossonephelis* is less similar to that of *Chytranthus* and of *Pancovia*, as described by Merville, which is characterized by much shorter ektoapertures, although their rugulate sculptural pattern approaches that of certain species of *Crossonephelis*.

In conclusion, the available evidence suggests closer relationship to *Placodiscus* than to *Lepisanthes*, but a more definite statement will only be possible after a detailed study of the entire tribe *Lepisantheae*. Nevertheless, it can be stated already that *Crossonephelis* certainly appears at home in this tribe.

REFERENCES

- CAPURON, R. 1969. Révision des Sapindacées de Madagascar et des Comores. Mém. Mus. Nat. Hist. Nat. n.s. B 19: 83—84.
- LEENHOUTS, P. W. 1973. A revision of *Crossonephelis* (Sapindaceae). *Blumea* 21: 91—103.
- MERVILLE, M. 1965. Le pollen des Sapindacées d'Afrique occidentale. *Pollen et Spores* 7: 465—489.
- MULLER, J. 1970. Pollen morphology of the genus *Lepisanthes* (Sapindaceae) in relation to its taxonomy. *Blumea* 18: 507—561.
- , 1971. Pollen morphological notes on the genus *Dimocarpus* (Sapindaceae). *Blumea* 19: 133—145.
- , 1973. The pollen morphology of *Barringtonia calyptrocalyx* K. Sch. (Lecythidaceae). *Grana* 13, in print.
- RADLKOEFER, L. 1932. Sapindaceae. *Das Pflanzenreich*, Heft 98.

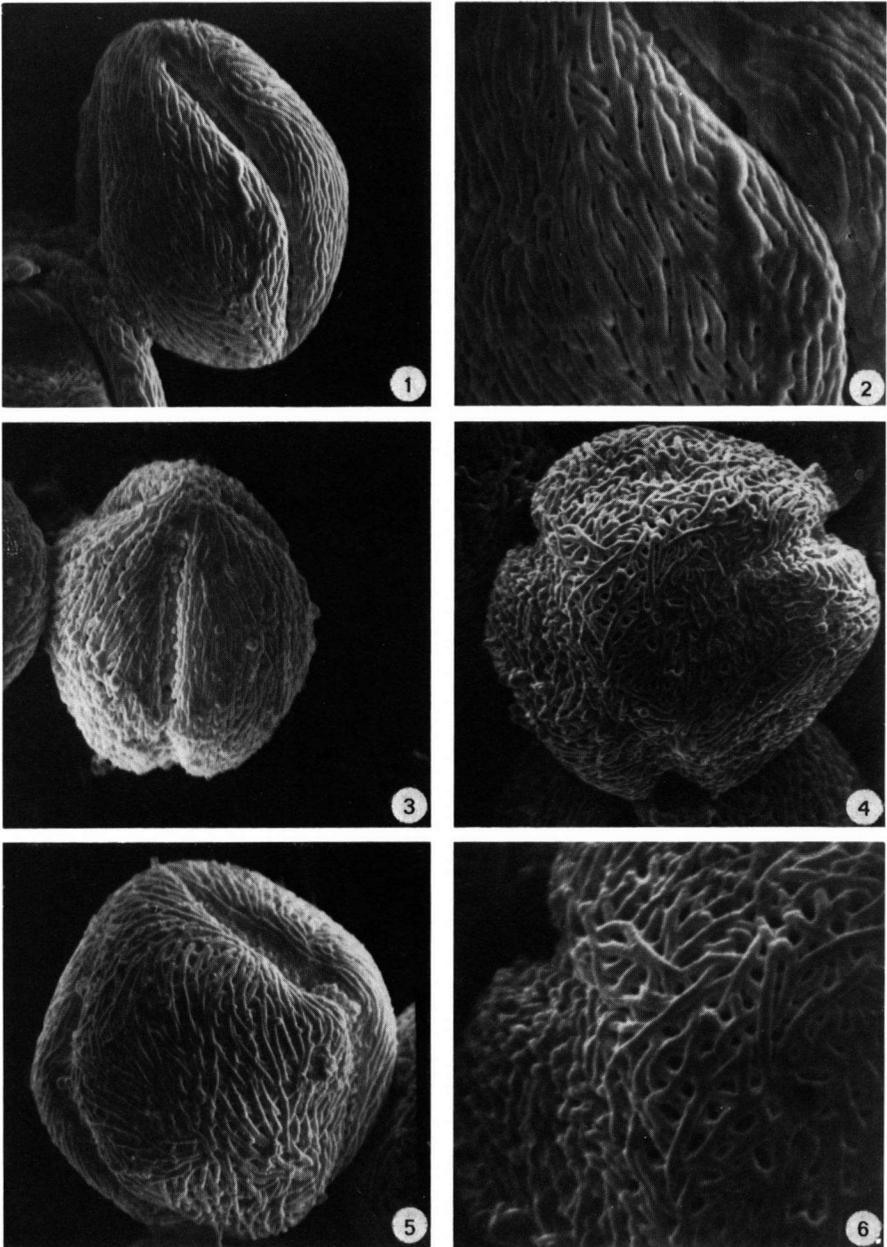


Plate I. SEM micrographs. Fig. 1, 2650 x, Fig. 2 (detail of Fig. 1), 5000 x, Fig. 3, 2650 x: *Crossonephelis africanus* (Chase 4419). — Fig. 4, 2900 x, Fig. 5, 2900 x, Fig. 6 (detail of Fig. 4), 5200 x: *C. palawanicus* A (4, 6: Brass 7980; 5: BS 49205).

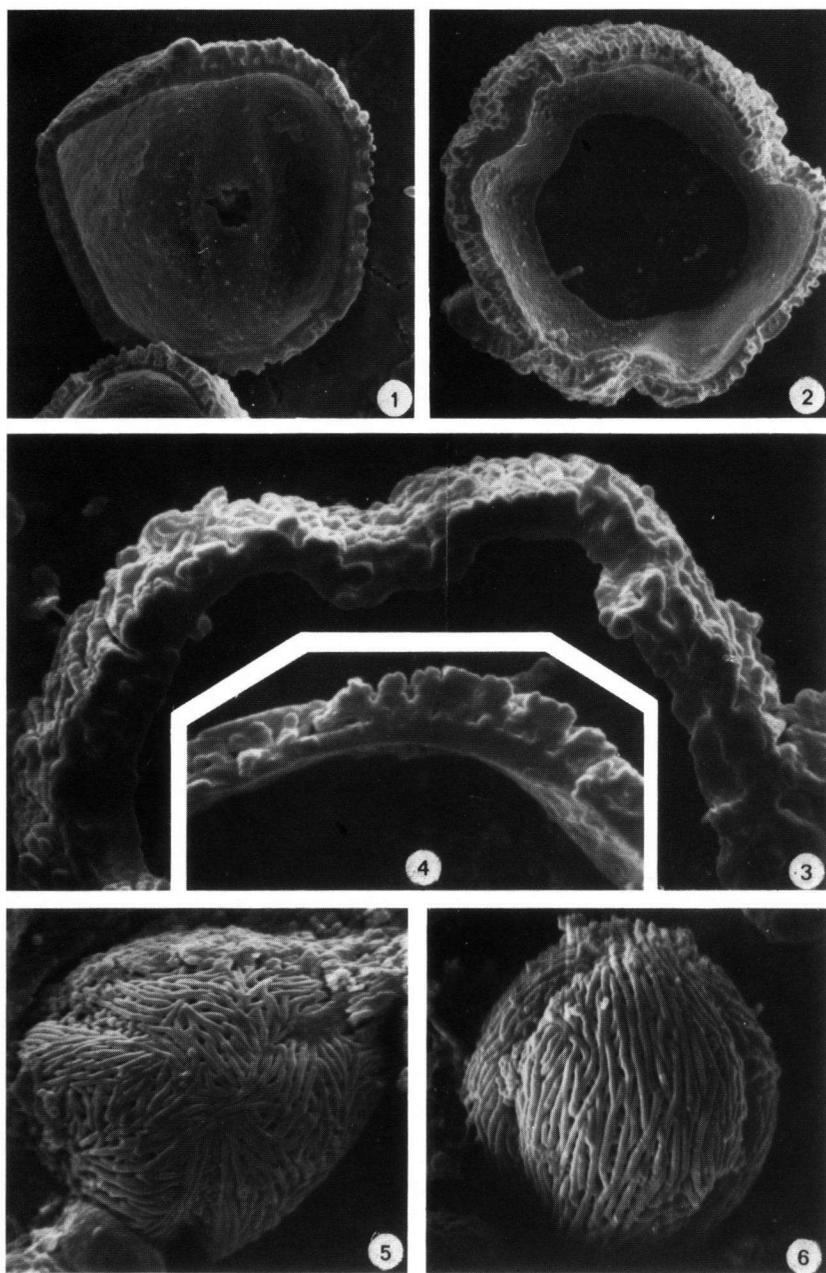


Plate II. SEM micrographs. Fig. 1, 3000 x, Fig. 2, 2650 x, Fig. 3, 5400 x, Fig. 4, 5700 x: *Grossonephelis palawanicus* A (Brass 7980). — Fig. 5, 2650 x, Fig. 6, 2650 x: *C. palawanicus* B (5: Lambach 1336; 6: v.d. Zwaan 114. T.3. P 513).

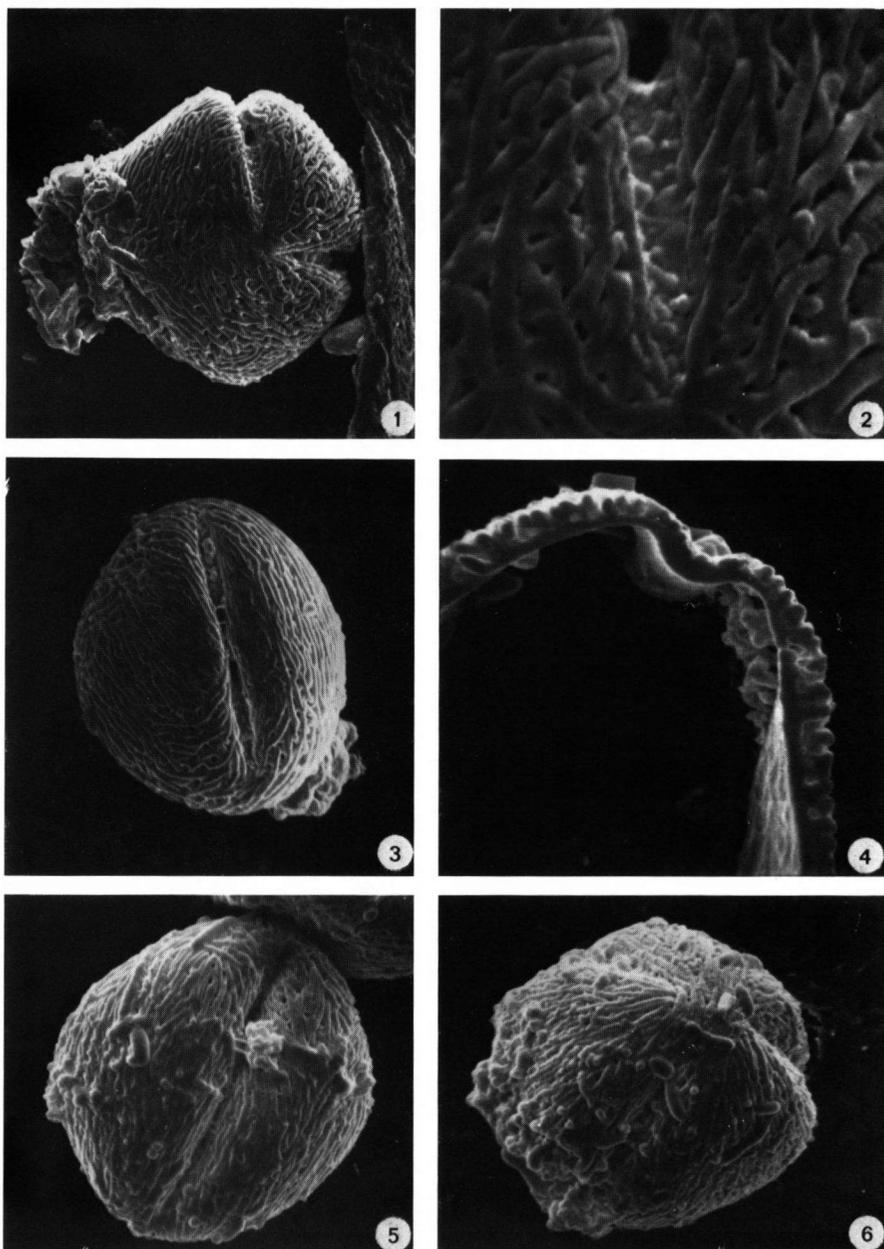


Plate III. SEM micrographs. Fig. 1, 2650 x, Fig. 2, 11.000 x, Fig. 3, 2650 x, Fig. 4, 6500 x: *Crossonephelis penangensis* (Kep. 4212). — Fig. 5, 3000 x, Fig. 6, 3000 x: *C. pervillei* (Capuron SF 18413).

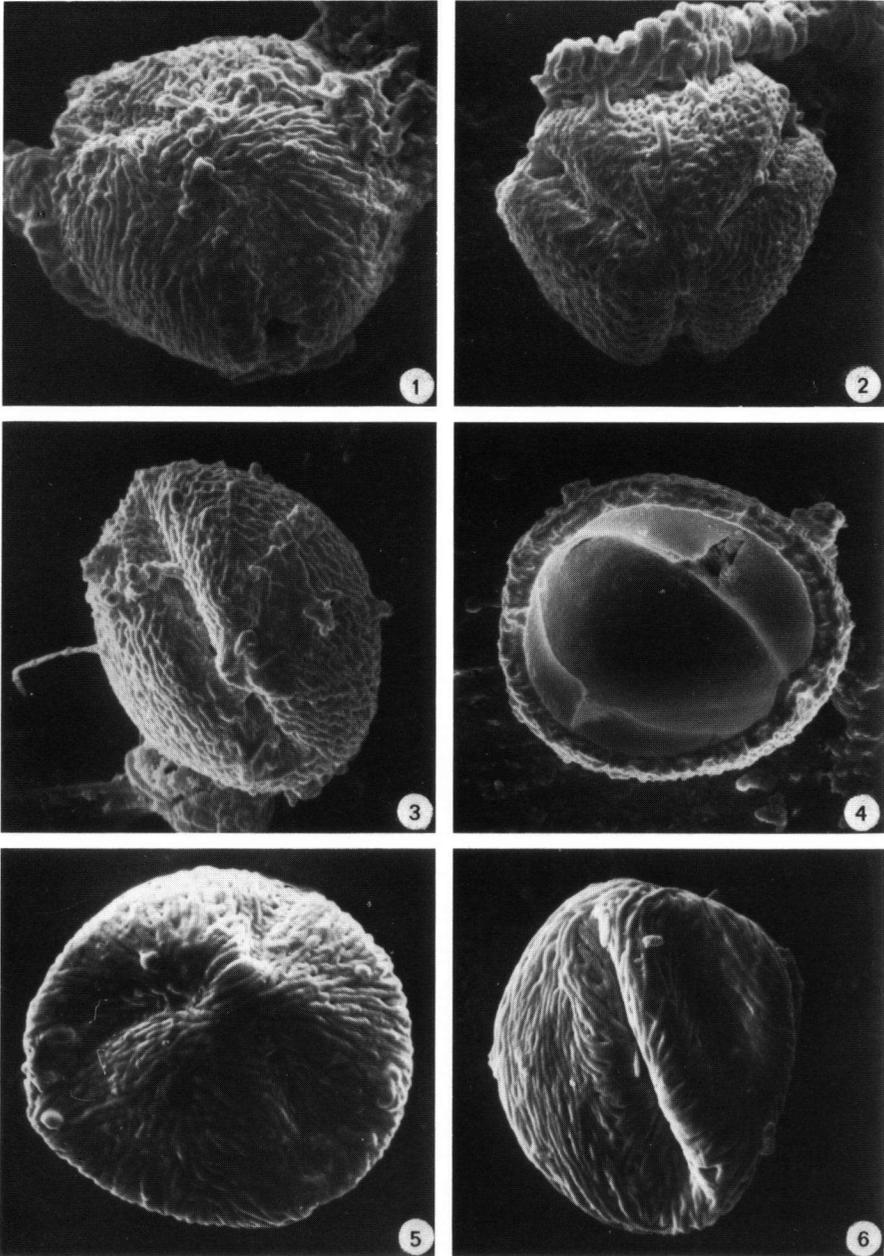


Plate IV. SEM micrographs. Fig. 1, 2800 x: *Crossonephelis philippinensis* (FB 25719). — Fig. 2, 2650 x, Fig. 3, 2650 x: *C. thorelii* (Pierre 4089). — Fig. 5, 2650 x, Fig. 6, 2650 x: *C. unijugatus* (Le Testu s.n.).

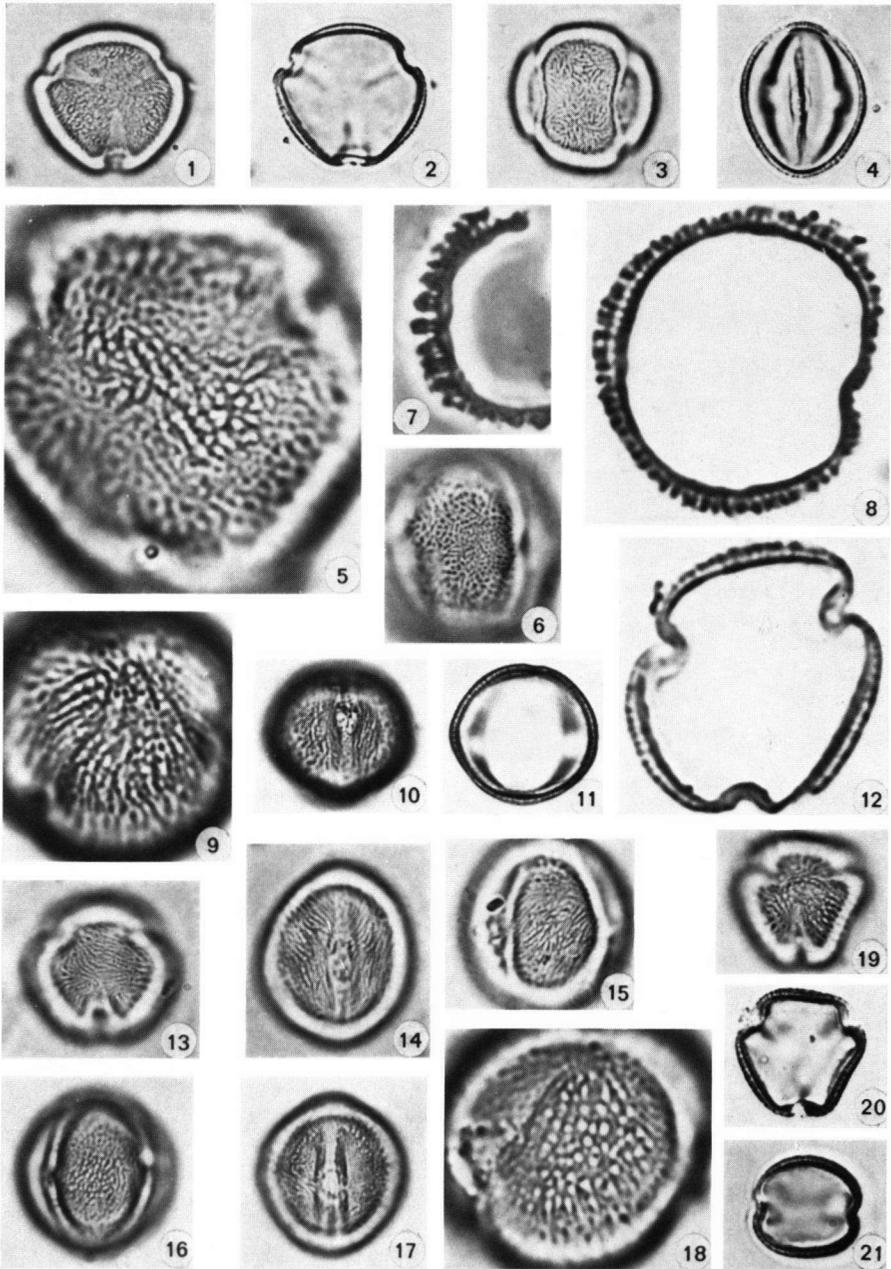


Plate V. Photomicrographs. Fig. 1—4: *Crossonephelis africanus* (Scheffler 343). — Fig. 5—8: *C. palawanicus* A (Brass 7980). — Fig. 9—11: *C. palawanicus* B (v.d. Zwaan 114. T. 3. P 513). — Fig. 12: *C. penangensis* (Kep. 4212). — Fig. 13—15: *C. pervillei* (Humbert 24241). — Fig. 16, 17: *C. thorellii* (Pierre 4089). — Fig. 18: *C. philippinensis* (FB 25719). — Fig. 19—21: *C. unijugatus* (Le Testu s.n.). 1000 x, OL: 1—4, 6, 10—11, 13—17, 19—21; 2000 x, OL: 5, 8, 9, 12, 18; 2000 x, OL, Ph.C: 7.

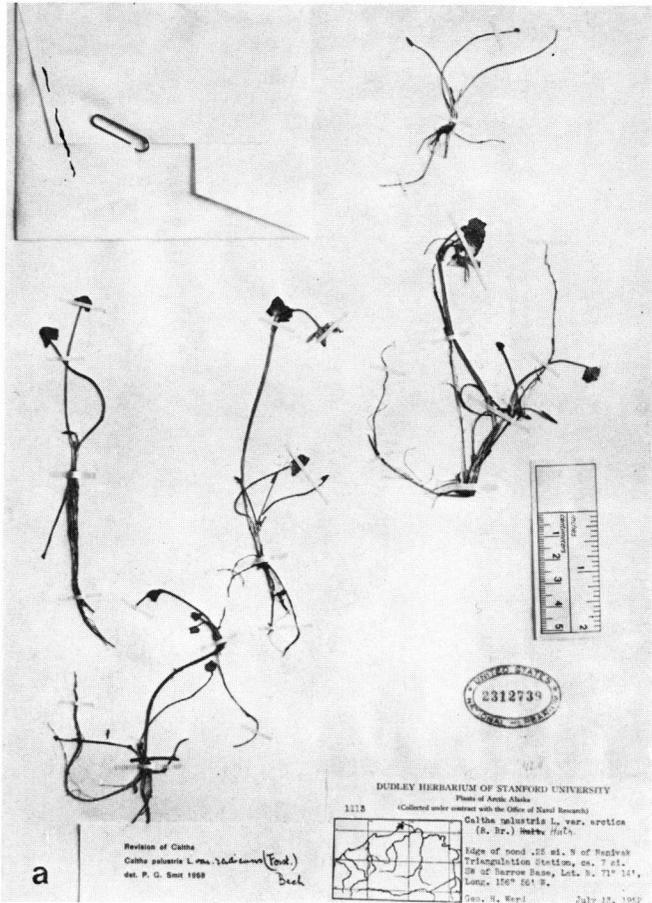


Fig. 3. Herbarium specimens of *C. palustris* var. *radicans* from the vicinity of Point Barrow, Alaska. a. Very small, creeping plants from 71° 14' N. Lat. b. Plants intermediate between 3a and 3c from 70° 40' N. Lat. c. Larger, more erect plants from 69° 50' N. Lat. (turn over please).

