

CNESMOCARPON (GEN. NOV.), JAGERA, AND TRIGONACHRAS (SAPINDACEAE–CUPANIEAE): PHYLOGENY AND SYSTEMATICS

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SUMMARY

Cladistic analyses of pollen-morphological, leaf-anatomical and macromorphological data of *Jagera*, *Trigonachras*, and several new species lead to the conclusion that a new genus, *Cnesmocarpon*, has to be described (see the Taxonomic Part on p. 195).

Two pollen types are described, one including *Cnesmocarpon*, the other including *Jagera* and *Trigonachras*. The morphologies of these pollen types suggest different harmomegathic systems: non-apertural and apertural folding respectively. The ornamentation of *Cnesmocarpon* pollen resembles that of several other Cupanieae genera. The scabrate ornamentation of *Jagera* and *Trigonachras* pollen, often provided with hair-like appendages, is unique in that tribe.

Leaf-anatomically *Jagera* is characterised by the presence of glands with a multicellular head and by the absence of papillae. *Cnesmocarpon* is characterised by the presence of papillae (one species has glands with a unicellular head). *Trigonachras* is characterised by the absence of both papillae and glands.

Macromorphologically *Jagera* and *Cnesmocarpon* share the irritating hairs on the fruit. *Jagera* and *Trigonachras* share the character of lower surface of leaflets with 'naked glands'.

The phylogenetic analysis of the complete data set shows *Jagera* and *Trigonachras* as more closely related to each other than to *Cnesmocarpon*.

INTRODUCTION

Jagera Blume is one of the small genera belonging to the large tribe Cupanieae of the Sapindaceae. Until recently it included three species, *J. dasyantha*, *J. javanica* and *J. pseudorhus*, which occur in Australia and E Malesia. They have irritating hairs on their fruits, which is a unique feature in the Sapindaceae. Several undescribed species from New Guinea were discovered during the final stage of the family revision for Flora Malesiana, and provisionally designated to *Jagera* on account of irritating hairs on their fruits.

A pollen-morphological survey of *Jagera* (Van der Ham, 1990: 139, fig. 14) revealed two distinct ornamentation types: rugulate/psilate (*J. dasyantha*) and scabrate (*J. javanica*, *J. pseudorhus*). The new species appeared to have the former type. The scabrate type, which at first was considered to be restricted in the Cupanieae to *Jagera*, was found also in *Trigonachras* Radlk. This is another small genus in the Cupanieae, comprising eight species that are all distributed in Malesia (Leenhouts, 1988). The pollen morphology suggests a very close relationship between *Jagera* and *Trigonachras*. However, none of the *Trigonachras* species has irritating hairs on its fruits.

A cladistic analysis of *Jagera* (including the undescribed species) and *Trigonachras*, using pollen morphology, leaf anatomy and macromorphology, suggested that the taxa with nonscabrate pollen (*J. dasyantha* and three new species) and those with scabrate pollen (*J. javanica*, *J. pseudorhus*, *Trigonachras*) represent separate monophyletic groups. Consequently the nonscabrate species were recognised as a new genus: *Cnesmocarpon* Adema.

The first part of this paper presents the results of the pollen-morphological, leaf-anatomical and macromorphological studies. Subsequently, the cladistic analyses, and the phylogenetic and taxonomic conclusions will be presented. The last part provides the formal descriptions of *Cnesmocarpon* and the new species.

MATERIAL AND METHODS

Pollen morphology

The following herbarium specimens were sampled for the pollen-morphological study. They are all kept in the Rijksherbarium at Leiden (L).

Cnesmocarpon dasyantha (Radlk.) Adema: Papua New Guinea, Hartley 10765, NGF 21918, Schodde 3030; Australia, L.S. Smith 2048. — *C. dentata* Adema: Papua New Guinea, Jacobs 9524, Pullen 7462. — *C. discoloroides* Adema: Papua New Guinea, NGF 26913. — *C. montana* Adema: Papua New Guinea, Carr 13519. — *Jagera javanica* (Blume) Blume ex Kalkman subsp. *australiana* Leenhouts: Australia, Gray 1455, 4083, Irvine 516. — *J. javanica* subsp. *javanica*: Moluccas (Halmahera), Idjan & Mochtar 391; Papua New Guinea, Brass 3587, NGF 31693. — *J. pseudorhus* (A. Rich.) Radlk.: Australia, Dietrich 2512; Papua New Guinea, Brass 7943, Pullen 7235. — *Trigonachras acuta* (Hiem) Radlk.: Borneo, SAN 24349. — *T. celebensis* Leenhouts: Celebes, NIFS Cel./II-400. — *T. cultrata* (Turcz.) Radlk.: Philippines, Cuming 1304. — *T. cuspidata* Radlk.: Philippines: BS 20467. — *T. papuensis* Leenhouts: Papua New Guinea, Brass 28919.

Acetolysed pollen of all collections was studied with LM and SEM. Brass 7943 (*J. pseudorhus*) was studied with TEM by Jan Muller (unpublished). Acetolysis was carried out according to Erdtman (1960); see Van der Ham (1990) for further handling of the material. Preparation for TEM included fixing with 2% OsO₄ (1 hour), prestaining with 5% uranylacetate (1 day), inbedding in 3/7 Epon, and poststaining with 0.5% uranylacetate (30 minutes) and Reynolds' lead citrate (10 minutes). The observations and photography were carried out with a Leitz Dialux 20 microscope (NPL Fluotar 100/1.32 oel ICT), a Jeol JSM 35, a Jeol JSM 5300, and a Philips EM 300.

Leaf anatomy

Herbarium material was used for the leaf anatomical study. This material is kept in the Rijksherbarium at Leiden (L). Usually only one sample per species was studied, with the exception of *Cnesmocarpon dasyantha* (3 samples), *Euphorianthus euneu-*

rus (2 samples), *Jagera javanica* subsp. *javanica* (5 samples) and *Jagera pseudorhus* (4 samples).

Transverse sections and cuticular macerations of leaflet laminae were prepared using standard anatomical techniques (Adema, 1991: 13; Van Welzen, 1989: 19, 20).

Leaflet surfaces were studied with a Jeol JSM 5300 scanning electron microscope, after sputter-coating with gold (Polaron SEM coating unit E5100).

The following species and specimens were studied:

Cnesmocarpon dasyantha (Radlk.) Adema: Papua New Guinea, *Forbes 1*, *Leder-mann 10365*; Australia, *Clemens s.n.* — *C. dentata* Adema: Papua New Guinea, *Pullen 7462*. — *C. discoloroides* Adema: Papua New Guinea, *NGF 26792*. — *C. montana* Adema: Papua New Guinea, *Carr 13519*. — *Diploglottis australis* (G. Don) Radlk.: Papua New Guinea, *Carr 16052*. — *Euphorianthus euneurus* (Miq.) Leenhouts: Moluccas, *de Vogel 3356*; Papua New Guinea, *Womersley 6*. — *Jagera javanica* (Blume) Blume ex Kalkman subsp. *australiana* Leenhouts: Australia, *B. Gray 1455*. — *J. javanica* subsp. *javanica*: Moluccas, *Boerlage 66*, *Idjan & Mochtar 391*, *van Balgooy 4566*; Irian Jaya, *Aet & Idjan 704*; Papua New Guinea, *Brass 3587*. — *J. pseudorhus* (A. Rich.) Radlk.: Papua New Guinea, *Pullen 7235*, *UPNG s.n.*; Australia, *Dietrich 203*, *L.S. Smith 12416*. — *Sarcopteryx brachyphylla* Radlk.: Papua New Guinea, *Pullen 7969*. — *S. caudata* Welzen: Papua New Guinea, *Hoogland & Pullen 5437*. — *S. coriacea* Radlk.: Irian Jaya, *van Royen & Sleumer 8084*. — *S. squamosa* (Roxb.) Radlk.: Papua New Guinea, *NGF 42169*. — *Toechima erythrocarpum* (F. Muell.) Radlk. subsp. *papuanum* Leenhouts: Irian Jaya, *Kostermans & Soengeng 271*. — *Trigonachras acuta* (Hiern) Radlk.: Sabah, *SAN 40845*. — *T. celebensis* Leenhouts: Celebes, *Prawiroatmodjo & Soewoko 1747*. — *T. cultrata* (Turcz.) Radlk.: Philippines, *PNH 37151*. — *T. cuspidata* Radlk. Philippines, *BS 20467*. — *T. papuensis* Leenhouts: Papua New Guinea, *LAE 68754*.

Macromorphology

Of *Cnesmocarpon* all existing material (21 specimens) was studied. For *Jagera* and *Trigonachras* the manuscripts for Flora Malesiana, and a paper by Leenhouts (1988: 204–213) were used. In addition 29 specimens of *Jagera* and 23 specimens of *Trigonachras* were studied to check the presence of naked glands on the lower surface of the leaflets, and the indumentum of the fruits.

Phylogeny

HENNIG86 1.5 (Farris, 1988) with the option *ie*, all characters unordered (*ccode -*), was used for the cladistic analyses. 'Farris-weighting' was used several times to reduce the number of cladograms.

The program HENNIG86 needs an a priori designated outgroup. As such *Cupaniopsis*, *Diploglottis* and *Euphorianthus* were tried alone or in pairs. All trial runs gave essentially the same results. For the present paper *Euphorianthus* was selected. The cladograms generated with this genus as outgroup tend to be slightly shorter, and

have higher scores for the consistency (CI) and redundancy (RI) indices than those generated with *Cupaniopsis* or *Diploglottis* as outgroups. Furthermore, *Euphorianthus* is monotypic and, hence, selection of a species and questions about the monophyly of the outgroup are of no account.

All characters were entered in the datamatrix for the cladistic analyses using multi-state coding (see also Van Welzen, 1989: 55, 56). For each character complex (pollen morphology, leaf anatomy, macromorphology) a selection was made of those characters that showed differences and/or a promising distribution pattern.

All three genera studied, viz. *Cnesmocarpon*, *Jagera*, and *Trigonachras* are probably monophyletic. They all have unique characters or unique combinations of characters that in the cladograms show up as synapomorphies.

RESULTS AND DISCUSSION

Pollen morphology

Cnesmocarpon – Table 1; Plates 1, 2, 9

Pollen grains isopolar to slightly heteropolar (see apocolpium), generally 3-aperturate. $P = 10\text{--}17\ \mu\text{m}$, $E = 20\text{--}29\ \mu\text{m}$, $P/E = 0.45\text{--}0.65$. Equatorial outline obtusely triangular, with concave to convex sides, meridional outline obtusely rhombic to elliptic, sometimes more or less rectangular.

Aperture system syncolporate or parasyncolporate. Apocolpia up to $5\ \mu\text{m}$ ($A/E = 0\text{--}0.25$), often differently sized and shaped in a single grain, causing a slightly heteropolar condition (a few samples contain only syn-/parasyncolporate grains), usually isolated from the mesocolpia, sometimes \pm connected with 1, 2 or 3 mesocolpia (Plate 1: 5).

Colpi usually very narrow; several species show connections between adjacent mesocolpia (Plates 1: 1, 4, 5; 2: 3–5). Colpus membranes covered with scabrae.

Endoapertures lalongate, elliptic to irregular rectangular pori, $3\text{--}5\ \mu\text{m}$ wide; polar margins thicker than the lateral ones, no fastigium.

Exine thickness $0.7\text{--}1.0\text{--}(1.4)\ \mu\text{m}$, usually constant in the greater part of a mesocolpium; in *C. discoloroides* the central part is relatively thick (up to $1.4\ \mu\text{m}$).

Nexine thickness $0.4\text{--}0.6\ \mu\text{m}$ in the central part of a mesocolpium. The nexine thickens near the colpi. The faint relief and discontinuities sometimes observed (LM and SEM) between the central part of a mesocolpium and its margins (Plates 1: 2; 9: 1, 2) might represent the transition zone of ectexine and endexine (see also *Jagera*).

Columellate layer $0.1\text{--}0.2\ \mu\text{m}$ thick, usually indistinct with LM; in *C. dentata* more or less distinct, and in *C. discoloroides* distinct in the centres of the mesocolpia. Individual columellae small, and indistinct with LM.

Tectum $0.2\text{--}0.3\ \mu\text{m}$ thick, constant throughout a mesocolpium. Perforations always present.

Ornamentation psilate or indistinctly to shallowly rugulate, usually less prominent and with smaller perforations along the colpi.

Jagera – Table 1; Plates 3–5, 9, 10

Pollen grains isopolar to slightly heteropolar (as to apocolpium size and shape), generally 3-aperturate. $P = 15\text{--}25\ \mu\text{m}$, $E = 24\text{--}37\ \mu\text{m}$, $P/E = 0.50\text{--}0.78$. Equatorial outline obtusely triangular, with convex sides; apertures sometimes slightly protruding, meridional outline obtusely rhombic to elliptic.

Aperture system syncolporate or parasyncolporate. Apocolpia up to $11\ \mu\text{m}$ ($A/E = 0\text{--}0.36$), usually isolated from the mesocolpia; rarely indistinctly connected with 1 or 2 mesocolpia.

Colpus width depends much on the harmomegathic state of the grain (Plate 3: 1; see also the paragraph about Harmomegathy, below). Uninvaginated colpi $0\text{--}2\ \mu\text{m}$ wide. Colpus membranes smooth to \pm densely covered with scabrae.

Endoapertures lalongate, elliptic to irregular rectangular pori, often meridionally constricted, $3\text{--}4\ \mu\text{m}$ wide. Their shape depends much on the harmomegathic state of the grain (see also Van der Ham & Van Heuven, 1989). Polar margins thicker than the lateral ones (Plate 3: 4), no fastigium.

Exine thickness $1.1\text{--}1.8\ \mu\text{m}$, constant in the greater part of a mesocolpium.

Nexine thickness $0.4\text{--}0.6\ \mu\text{m}$ in the central part of a mesocolpium. The nexine thickens near the colpi, providing an up to $3\ \mu\text{m}$ thick layer underlying the margins of the adjacent mesocolpia. Colpus membranes relatively thin. TEM (Plate 10: 6) showed them to consist mainly of endexine. Towards the centre of a mesocolpium the endexine thins rather sharply to become very thin or perhaps nonexistent in the central part. The transition zone often shows discontinuities.

Cummellate layer $0.2\text{--}0.4\ \mu\text{m}$ thick, distinct with LM. Thickness constant or decreasing slightly towards the colpi. Individual columellae large, and \pm distinct with LM.

Tectum thickness $0.5\text{--}0.7\ \mu\text{m}$, constant throughout a mesocolpium. Perforations always present; pollen of *J. javanica* subsp. *australiana* shows large lumina in the centres of the mesocolpia.

Ornamentation perforate or reticulate, with low isodiametric scabrae that are often provided with slender, up to $1\ \mu\text{m}$ long tapering appendages (Plates 3: 2; 5: 5, 6). Usually these hair-like structures adhere to the tectum, often descending in the perforations/lumina. Ornamentation different towards the colpi, the margins of the mesocolpia showing distinctly smaller perforations/lumina. Size of the scabrae does diminish towards the colpi.

Anomalous apertures and ornamentation in Jagera pseudorhus

Several deviating aperture systems and ornamentation patterns occur in *Pullen 7235 (J. pseudorhus)*. About a quarter of the grains in this sample is anomalous. Apart from regular and irregular 2-syncolporate grains, forms with 2 more or less circular ectoapertures were found. Among these, a form showing a small elliptic ectoaperture with 2 pori at one side (Plate 5: 1) and a larger, slightly angular one with 3 or 4 pori at the other (Plate 5: 2) was encountered several times. The pori are distinct with LM, but with SEM their position is often difficult to determine. One grain with a single looping ectoaperture ('tennis ball pattern') was found (Plate 5: 3). The position of the poles in all these anomalous forms is unknown.

Table 1. Values/states of a number of pollen characters in *Cnesmocarpon*, *Jagera*, and *Trigonachras*.

Notes:

- 1) as to apocolpium size (A): - = apocolpia not or slightly different; ± = one apocolpium 1 to 3 µm larger; + = one apocolpium more than 3 µm larger.
- 2) in the unfolded state.
- 3) between mesocolpia (MM), or between apocolpium and mesocolpium/mesocolpia (AM): - = absent; [] = rarely; { } = sometimes; () = often.
- 4) shape of the sides: cv = concave, s = ± straight, cx = convex.
- 5) psi = psilate; rug = indistinctly to shallowly rugulate; ret = reticulate; per = perforate; sca = scabrate; (+) = at least part of the scabrae provided with a slender tapering appendage.

	P (µm)	E (µm)	P/E	A (µm)
<i>Cnesmocarpon</i>				
<i>dasyantha</i>	12.6	23.7	53	0-5
<i>dentata</i>	14.6	24.7	59	0-4
<i>discoloroides</i>	12.0	23.8	50	0 (1)
<i>montana</i>	13.2	25.0	54	0 (1)
<i>Jagera</i>				
<i>javanica australiana</i>	18.9	32.4	58	2-9
<i>javanica javanica</i>	19.8	32.1	62	0-11
<i>pseudorhus</i>	17.7	26.9	65	0-9
<i>Trigonachras</i>				
<i>acuta</i>	22.5	37.7	60	0-4
<i>celebensis</i>	20.2	37.1	54	0-6
<i>cultrata</i>	19.4	32.1	61	0
<i>cuspidata</i>	18.4	32.9	56	4-9
<i>papuensis</i>	16.7	27.4	61	0-4
	heteropolarity ¹	colpi ²	colpus bridges ³	
<i>Cnesmocarpon</i>				
<i>dasyantha</i>	-, ±, +	narrow	{MM + AM}	
<i>dentata</i>	-, ±	± wide	-	
<i>discoloroides</i>	-	narrow	(MM)	
<i>montana</i>	-	narrow	[MM]	
<i>Jagera</i>				
<i>javanica australiana</i>	±, +	wide	-	
<i>javanica javanica</i>	-, ±	wide	{AM}	
<i>pseudorhus</i>	-, ±	wide	-	
<i>Trigonachras</i>				
<i>acuta</i>	-	± wide	(AM)	
<i>celebensis</i>	±	wide	-	
<i>cultrata</i>	-	wide	(AM)	
<i>cuspidata</i>	±	wide	[MM]	
<i>papuensis</i>	±	± wide	(AM)	

(Table 1 continued)

	exine (μm)	columellate layer (μm)	equatorial outline ⁴
<i>Cnesmocarpon</i>			
<i>dasyantha</i>	0.7(-1)	0.1	cv(-s)
<i>dentata</i>	± 1	0.1	s-cv
<i>discoloroides</i>	1.4	0.2	cv
<i>montana</i>	± 1	0.1	cv-cx
<i>Jagera</i>			
<i>javanica australiana</i>	1.4-1.8	0.3-0.4	cx
<i>javanica javanica</i>	1.1-1.8	0.2-0.4	cx
<i>pseudorhus</i>	1.8	0.4	cx
<i>Trigonachras</i>			
<i>acuta</i>	1.2	0.2	s-cx
<i>celebensis</i>	1.2	0.2	s-cx
<i>cultrata</i>	1.2	0.2	cx
<i>cuspidata</i>	± 1	0.2	cx
<i>papuensis</i>	1.2	0.4	cx
	ornamentation ⁵	pollen type	
<i>Cnesmocarpon</i>			
<i>dasyantha</i>	psi, rug	1	
<i>dentata</i>	rug	1	
<i>discoloroides</i>	rug	1	
<i>montana</i>	rug	1	
<i>Jagera</i>			
<i>javanica australiana</i>	ret/sca (+)	2	
<i>javanica javanica</i>	per/sca (+)	2	
<i>pseudorhus</i>	per/sca (+)	2	
<i>Trigonachras</i>			
<i>acuta</i>	per/sca	2	
<i>celebensis</i>	per/sca (+)	2	
<i>cultrata</i>	per/sca (+?)	2	
<i>cuspidata</i>	per/sca	2	
<i>papuensis</i>	per/sca (+)	2	

Furness (1985) described pollen with sinuous or winding apertures of 9 families (both dicots and monocots) as spiriaperturate. The spiriaperturate condition was not found morphologically uniform. It was considered to represent a derived aperture type evolved in several unrelated groups, probably as a result of an ontogenetic accident that had been retained due to germination advantages. The anomalous circular and looping apertures in *J. pseudorhus* might result from similar ontogenetic deviations. Both, circular and spiral apertures were found in a single sample also in *Mimusulus guttatus* and *M. luteus* of the Scrophulariaceae (Furness, 1985, 1988).

Many grains show a coarsely verrucate surface and thick mesocolpium margins. The verrucae are often fused, mutually as well as with the margins, to form a pattern of anastomosing bulging ridges (Plate 4: 5). With LM the verrucae and ridges appeared to represent thickened, solid tectum parts only; the underlying columellate layer and nexine are quite normal. In contrast with the unthickened tectum parts the verrucae and ridges are imperforate. They do, however, display the typical scabrae that occur on normal tectum. On ridges these scabrae are arranged in short series that are perpendicular to the sides of the ridges. Heavily verrucate and ridged grains are connected with the regular form through a complete series of intermediates (Plate 4: 1–5). Similar patterns of perpendicular series of scabrae on tectum elements occur also in, for example, *Buxus* of the Buxaceae, where they are considered as a derived feature (Köhler & Brückner, 1989).

Generally, grains with deviating ornamentation have the usual 3-syncolporate aperture system. Sometimes, a ridge bridges a colpus (Plate 4: 5). Rarely, a grain with anomalous ornamentation has a deviating aperture system as well (Plate 4: 6).

Trigonachras – Table 1; Plates 6–8, 10

Pollen grains isopolar to slightly heteropolar (as to apocolpium size and shape), generally 3-aperturate. $P = 15\text{--}24\ \mu\text{m}$, $E = 26\text{--}41\ \mu\text{m}$, $P/E = 0.45\text{--}0.73$. Equatorial outline obtusely triangular, with straight to convex sides, meridional outline obtusely rhombic to elliptic.

Aperture system syncolporate or parasyncolporate. Apocolpia up to $9\ \mu\text{m}$ ($A/E = 0\text{--}0.33$). *Trigonachras papuensis* shows small apocolpia that are nearly always connected with 1, 2 or 3 mesocolpia, which results in a more or less colporate condition (Plates 7: 5; 8: 1, 3); connections with 1 mesocolpium occur often in *T. acuta* (Plate 6: 1).

Colpus width $1\text{--}2\ \mu\text{m}$ in the uninvaginated state. Colpus membranes smooth to densely covered with scabrae (in *T. acuta* within a single sample).

Endoapertures much the same as in *Jagera* pollen, $3\text{--}7\ \mu\text{m}$ wide.

Exine thickness $1\text{--}1.2\ \mu\text{m}$, constant in the greater part of a mesocolpium.

Nexine thickness $0.4\text{--}0.7\ \mu\text{m}$ in the central part of a mesocolpium. Nexine thickening near and under the colpi as in *Jagera* pollen.

Columellate layer $0.2\text{--}0.4\ \mu\text{m}$ thick, usually distinct with LM. Individual columellae $0.2\text{--}0.4\ \mu\text{m}$ in diameter, usually indistinct with LM.

Tectum thickness $0.2\text{--}0.4\ \mu\text{m}$, constant throughout a mesocolpium. Perforations always present.

Ornamentation perforate, more or less scabrate, several species with the same kind of hair-like appendages that occur in *Jagera* pollen (Plates 6: 8; 8: 1–5). Ornamentation of the mesocolpium margins and centres usually not different; only *T. papuensis* shows considerable difference in perforation size, the centres of the mesocolpia being often more or less reticulate (see for example Plate 8: 2).

Immature pollen in Trigonachras papuensis

Due to the inclusion of unripe flower buds many immature and submature grains could be observed in *Brass 28919* (*T. papuensis*). With LM such grains are small ($E = 12\text{--}19\ \mu\text{m}$), and have an irregular dented translucent exine. With SEM they differ from mature grains, apart from being smaller, in their very low, hardly perceptible scabrae and the much smaller perforations (Plate 7: 6); at first sight the exine is psilate/perforate.

It seems that the scabrae including the appendages develop late in ontogeny. Occasionally, large, thick-walled, apparently mature grains in several *Jagera* and *Trigonachras* samples show low scabrae or no scabrae at all. This may be due to several factors:

1. the pertinent grains are not really mature;
2. the grains are mature, but by slightly different timing (heterochrony) the scabrae did not develop or incompletely so (paedomorphosis; see Van der Ham, 1990);
3. the grains stem from staminodes, which in Sapindaceae often yield less developed pollen (Van der Ham, 1990).

It is hard to decide between these possibilities in individual samples. The degree of apo-/mesocolpium coherence does not differ between immature and mature grains of *Brass 28919*. Apparently, connections and separations between apocolpia and mesocolpia are established in an early stage.

Harmomegathy

Harmomegathy is envisaged here as the complex of integrated mechanisms in which a number of elements operating together contribute to the accommodation of volume changes of a pollen grain during dehydration after anther dehiscence and rehydration after capture on a receptive stigma (Blackmore & Barnes, 1986). True harmomegathy is performed only by living pollen grains. However, much of the shape variation due to harmomegathy in living grains can be deduced from acetolysed grains. It is assumed here that relatively flexible, thin areas of the acetolysed exine function in living pollen also, and that the range of folding in a sample reflects an important portion of the harmomegathic possibilities (Van der Ham & Van Heuven, 1989; Van der Ham, 1990).

Blackmore & Barnes (1986) distinguished three distinct elements in the harmomegathy of pollen grains: folding of the pollen wall (flexibility), contraction and stretching of the wall (elasticity), and compression of internal wall cavities. Van der Ham (1990) introduced another element: invagination of apertural intine. The latter two elements, both peristatic (see also Muller, 1979), do not occur in pollen of *Cnesmocarpon*, *Jagera* and *Trigonachras*; the most important one is folding, to which contraction and stretching may contribute.

Muller & Leenhouts (1976) mentioned that the slit-like ectoapertures in (para)syncolporate Sapindaceae pollen appear to have lost their harmomegathic function. In addition to this type Van der Ham & Van Heuven (1989) and Van der Ham (1990) described a second harmomegathic type in (para)syncolporate Sapindaceae pollen in

which relatively wide colpi represent distinct harmomegathic structures. Both types occur in the genera studied here, but it is not easy to determine the prevalent type in each species.

The first type shows non-apertural folding, the mesocolpia being the most flexible parts of the pollen wall. Colpi are narrow, apocolpia are absent or small, and the sides of the equatorial outline are usually concave (Plate 1: 3). This type occurs in *Cnesmocarpon dasyantha*, *C. discoloroides* and *C. montana*. In *C. discoloroides* the colpi are nearly always bridged (Plate 2: 3–5), which surely hampers their folding. Occasionally, also the other species show bridged colpi, between mesocolpia mutually as well as between apocolpia and mesocolpia. Pollen of *C. discoloroides* resembles that of Myrtaceae, which also has rigid apertures and folding mesocolpia (see Blackmore & Barnes, 1986, figs. 13, 14; Knox, 1984, fig. 5.8D).

The second type shows apertural folding, the colpi being the preferred sites of invagination. Colpi are wide and never bridged, apocolpia are usually present and often large, and the sides of the equatorial outline are usually convex (Plate 3: 1). This type occurs in *Cnesmocarpon dentata* (?), *Jagera javanica*, *J. pseudorhus*, *Trigonachras acuta* (?), *T. celebensis*, *T. cultrata* and *T. cuspidata*. Pollen of *T. papuensis* seems to have an 'intermediate' mechanism with apo-/mesocolpium coherence, wide colpi and flexible mesocolpia (Plate 7: 5).

Table 2. Diagnoses of the two pollen types in *Cnesmocarpon*, *Jagera*, and *Trigonachras*.

	type 1	type 2
ornamentation	shallowly to indistinctly rugulate, psilate	perforate, reticulate
scabrae	absent	present
∅ perforations/lumina	< 0.1 μm	0.1–2.5 μm
average grain size (E)	≤ 25 μm	≥ 26 μm
apocolpium	absent or small (up to 5 μm)	usually present (up to 11 μm)
colpi	usually narrow	wide
sides in equatorial view	usually concave or straight	usually convex
exine thickness	usually ≤ 1.0 μm	≥ 1.0 μm
thickness columellate layer	≤ 0.2 μm	≥ 0.2 μm
harmomegathy	usually by nonapertural folding	usually by apertural folding
taxa	<i>Cnesmocarpon</i>	<i>Jagera</i> , <i>Trigonachras</i>

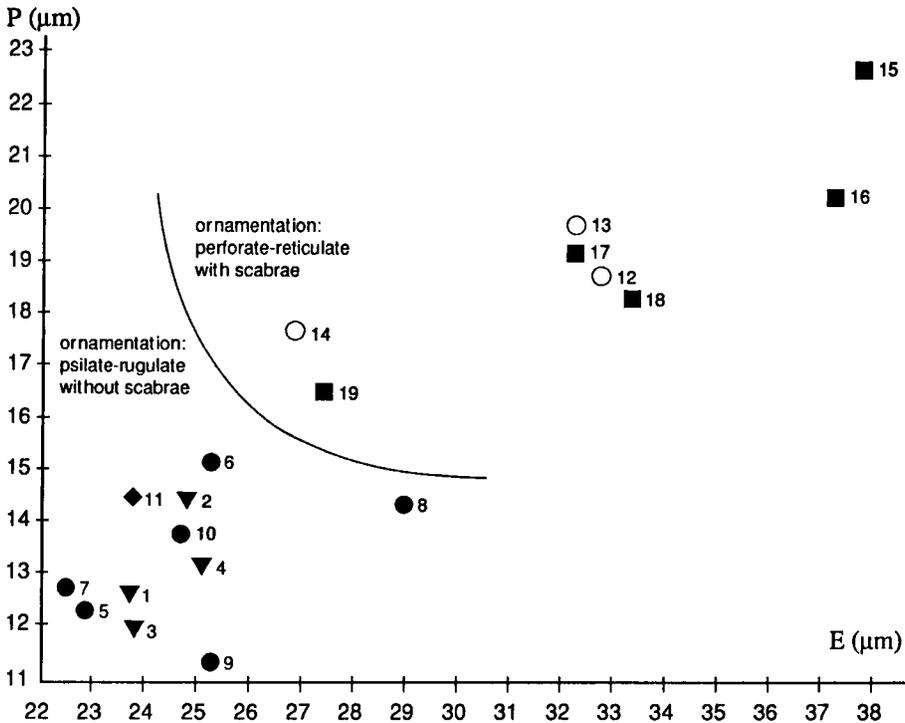


Fig. 1. Graphical representation of average grain size in *Cnesmocarpon* (▼), *Diploglottis* (●), *Euphorianthus* (◆), *Jagera* (○), and *Trigonachras* (■). 1 = *C. dasyantha*, 2 = *C. dentata*, 3 = *C. discoloroides*, 4 = *C. montana*, 5 = *D. australis*, 6 = *D. bracteata*, 7 = *D. campbelli*, 8 = *D. macrantha*, 9 = *D. obovata*, 10 = *D. smithii*, 11 = *E. euneurus*, 12 = *J. javanica* subsp. *australiana*, 13 = *J. javanica* subsp. *javanica*, 14 = *J. pseudorhus*, 15 = *T. acuta*, 16 = *T. celebensis*, 17 = *T. cultrata*, 18 = *T. cuspidata*, 19 = *T. papuensis*. Small pollen has psilate to rugulate ornamentation without scabrae, large pollen has perforate to reticulate ornamentation with scabrae.

Pollen types

On the basis of exine ornamentation two pollen types can be readily distinguished (Table 2).

Scabrate pollen is always larger than nonscabrate pollen (Fig. 1). The taxa belonging to type 2 form a coherent group by the occurrence of scabrae, but much and continuous variation exists with respect to the size of the perforations/lumina (compare Plate 3: 3, 5). On one hand there is perforate pollen (Plate 6: 7; perforations 0.1–1 µm), with little variation in perforation size in a single grain (*T. acuta*, *T. celebensis*, *T. cultrata*, *T. cuspidata*, *J. javanica* subsp. *javanica* p.p.), on the other reticulate pollen (Plate 3: 3; lumina 1–2.5 µm), with considerably larger lumina in the centres of the mesocolpia (*J. javanica* subsp. *javanica* p.p., *T. papuensis*, *J. pseudorhus*, *J. javanica* subsp. *australiana*). Variation in columella size corroborates this range: the larger the perforations/lumina, the larger (height and width) the columellae. There is no correspondence with the size and shape of the scabrae.

The distribution areas of *Jagera* and *Trigonachras* form a single large area from the Malay Peninsula and the Philippines to E. Australia. The more perforate form of *Jagera* and *Trigonachras* pollen (*T. acuta*, *T. celebensis*, *T. cultrata*, *T. cuspidata*, *J. javanica* subsp. *javanica* p.p.) is found in the northwestern part, and the more reticulate form (*J. javanica* subsp. *javanica* p.p., *T. papuensis*, *J. pseudorhus*, *J. javanica* subsp. *australiana*) in the southeastern part. Both forms overlap in New Guinea (*J. javanica* subsp. *javanica*, *T. papuensis*).

Comparisons with pollen of other Cupanieae

The shallowly to indistinctly rugulate and the psilate ornamentation found in *Cnesmocarpon* (pollen type 1) are not rare in the Cupanieae. They are closely related forms that often occur together, and are connected by intermediates (*Cupania*, *Cupaniopsis*, *Diploglottis*, *Euphorianthus*, *Guioa*), just as in *Cnesmocarpon*. Among the genera allegedly related to *Jagera* and *Trigonachras* (Muller & Leenhouts, 1976), *Diploglottis* and *Euphorianthus* have pollen that is much alike that of *Cnesmocarpon dentata*. Pollen of these genera is also small-sized (mostly < 25 µm; see Fig. 1), psilate or indistinctly to prominently rugulate, and has rather wide colpi. Pollen of the other *Cnesmocarpon* species seems more derived, having narrow, often bridged colpi (see for example *C. discoloroides*, Plate 2).

Scabrate ornamentation is rare in the Cupanieae, being known only in *Jagera* and *Trigonachras* (pollen type 2). A remarkable trait of the scabrate ornamentation in these genera is formed by the slender tapering appendages of the scabrae. It is not a general feature; actually, most scabrae are devoid of appendages. However, they were found in nearly all samples. Only in *T. acuta* and *T. cuspidata* they are completely wanting. *Jagera pseudorhus* and *T. papuensis* possess the largest and most distinct appendages (Plate 8). On the whole they look very much the same in both genera. Other scabrate Sapindaceae pollen does not show such structures: the scabrae may be higher and echinate (see for example *Cubilia* pollen in Van der Ham, 1990), but they never have a long tapering end that adheres to the exine.

Leaf anatomy

The leaf-anatomical characters of all taxa studied are summarised in Table 3. Leaf-anatomical descriptions of the genera *Cnesmocarpon*, *Jagera* and *Trigonachras* have been given below.

Cnesmocarpon

In surface view — *Non-glandular unicellular hairs* with thick sclerified walls adaxially absent or present on the midrib only, abaxially rare to abundant. *Glandular hairs* usually absent, in *C. dentata* both surfaces with few glandular hairs consisting of 1–3 stalk cells and 1 large glandular top cell. *Papillae* abundant, elongate and usually connected by cuticular rims; in *C. dentata* only around the stomata, shorter and mostly without cuticular connections. *Cuticle* smooth or rarely striate, not granular. *Unspecialised epidermal cells* polygonal, with straight, or in *C. dentata* and sometimes in

C. dasyantha undulate anticlinal walls; around hairs and stomata in a radiating pattern; above midrib and veins square to rectangular, in rows parallel to the veins, showing the venation pattern. *Stomata* predominantly cyclocytic, abundant on abaxial surface (in *C. dasyantha* in one of the samples rare), absent on adaxial surface.

In transverse section – *Lamina* dorsiventral. *Unspecialised epidermal cells* square or above midrib and along margin \pm erect. *Hypodermis* only present above midrib and rarely above major veins. *Mesophyll*: palisade tissue usually composed of 1 layer of long, erect cells, in *C. montana* a second layer of much shorter palisade cells present; spongy tissue compact or loose. *Midrib* raised abaxially, slightly sunken adaxially; ground tissue of parenchymatous cells; vascular system collateral, with an almost flat adaxial strand and an abaxial arch, surrounded by a sclerenchyma sheath. *Veins*: minor ones embedded in mesophyll, larger ones usually transcurrent. *Margin* with (*C. dentata*) or without marginal vein and normal mesophyll. *Crystals* rhomboidal, present in ground tissue around midrib and veins, in *C. discoloroides* also in pith. *Secretory idioblasts* usually abundantly present, small to large, round to more or less erect rectangular in palisade tissue, occurring in palisade and spongy tissue, often also in ground tissue of midrib; with unidentified contents.

Jagera

In surface view – *Non-glandular unicellular hairs* with thick, or more rarely thin, sclerified walls, very variable in length, adaxially abundant on midrib, abaxially rather rare to abundant. *Glandular hairs* adaxially rare, abaxially abundant, consisting of 1 or 2 stalk cells and a glandular head consisting of several cells. *Papillae* absent. *Cuticle* striate, not granular, if anticlinal walls undulate then cuticle thinner in the loops of the undulations. *Unspecialised epidermal cells* polygonal, with straight to undulate anticlinal walls; around hairs and stomata in a radiating pattern; above midrib and veins square to rectangular, in rows parallel to the veins showing the venation pattern. *Stomata* predominantly cyclocytic, abundant on abaxial surface, on adaxial surface absent or scarce along the midrib.

In transverse section – *Lamina* dorsiventral. *Unspecialised epidermal cells* square, very large. *Hypodermis* only present above midrib and veins. *Mesophyll*: palisade tissue usually composed of 1 layer of (rather) long erect cells; spongy tissue rather loose. *Midrib* raised abaxially and adaxially; ground tissue of parenchymatous cells; vascular system collateral, with an arched adaxial strand and an abaxial arch, surrounded by a sclerenchyma sheath. *Veins*: minor ones embedded in mesophyll, some of the larger ones transcurrent. *Margin* usually with a marginal vein and normal mesophyll. *Crystals* rhomboidal, few to many in ground tissue around midrib and veins, often also present in pith. *Secretory idioblasts* rare to abundant in palisade and spongy tissue, often also in ground tissue around midrib; with unidentified contents.

Trigonachras

In surface view – *Non-glandular unicellular hairs* absent or rare in *T. acuta* and *T. celebensis*, when rare, then with thick sclerified walls. *Glandular hairs* absent. *Papillae* absent. *Cuticle* smooth to striate, if anticlinal walls undulate then cuticle usually

Table 3. Leaf-anatomical characters.

Legend: - = absent; + = present; (+) = few, or weakly developed; ± = present in some of the samples.

Columns:

1. Species name
2. Number of samples
3. Type of glandular hairs on adaxial surface; C = 1(-3) stalk cells and a large glandular head consisting of several cells; G = 1-3 stalk cells and 1 large glandular top cell; P = several to many stalk cells and 1 (or 2) small glandular top cell(s)
4. Type of glandular hairs on abaxial surface. For legend see 3
5. Papillae on abaxial surface; A = with cuticular connections; B = cuticular connections absent or rare; BS = like B, papillae only around stomata
6. Adaxial cuticle striate
7. Abaxial cuticle striate

Columns:

8. Anticlinal walls of adaxial epidermis cells undulate
9. Anticlinal walls of abaxial epidermis cells undulate
10. Stomata in adaxial epidermis
11. Mean lamina thickness in cross section
12. Additional vascular strands in pith of midrib
13. Crystals in ground tissue around veins
14. Crystals in pith of midrib
15. Crystals in abaxial subepidermal mesophyll tissue
16. Secretory idioblasts in palisade tissue
17. Secretory idioblasts in spongy tissue
18. Secretory idioblasts in ground tissue of midrib
19. Veins transcurrent; T = most veins transcurrent; LT = only larger veins transcurrent

1	2	3	4	5	6	7	8	9	10	11	12
<i>Cnesmocarpon</i>											
<i>dasyantha</i>	3	-	-	A	±	±	±	-	-	177	-
<i>dentata</i>	1	(G)	(G)	BS	-	-	+	+	-	155	-
<i>discoloroides</i>	1	-	-	A	+	(+)	-	-	-	168	-
<i>montana</i>	1	-	-	A	-	-	-	-	-	228	-
<i>Diploglottis</i>											
<i>australis</i>	1	P	P	-	+	-	-	-	(+)	80	+
<i>Euphorianthus</i>											
<i>euneurus</i>	2	P	P	B	+	+	-	-	(+)	156	+
<i>Jagera</i>											
<i>javanica australiana</i>	1	C	C	-	+	+	(+)	-	(+)	176	-
<i>javanica javanica</i>	5	C	C	-	+	+	(+)	-	(+)	146	-
<i>pseudorhus</i>	4	C	C	-	+	+	+	(+)	-	143	-
<i>Sarcopteryx</i>											
<i>brachyphylla</i>	1	-	G	-	-	-	+	+	-	139	-
<i>caudata</i>	1	-	G	-	-	-	-	+	-	189	-
<i>coriaceae</i>	1	-	G	-	-	-	(+)	(+)	-	184	-
<i>squamosa</i>	1	-	G	-	-	-	-	(+)	(+)	195	-
<i>Toechima</i>											
<i>erythrocarpum papuanum</i>	1	(G)	(G)	-	+	-	-	-	+	128	-
<i>Trigonachras</i>											
<i>acuta</i>	1	-	-	-	+	+	+	(+)	-	123	-
<i>celebensis</i>	1	-	-	-	-	(+)	-	-	-	199	-
<i>cultrata</i>	1	-	-	-	-	-	+	(+)	-	143	-
<i>cuspidata</i>	1	-	-	-	+	+	-	-	(+)	188	-
<i>papuensis</i>	1	-	-	-	+	(+)	+	-	-	170	-

(Table 3 continued)

1	13	14	15	16	17	18	19
<i>Cnesmocarpon</i>							
<i>dasyantha</i>	+	-	-	+	+	+	-
<i>dentata</i>	(+)	-	-	+	+	+	T
<i>discoloroides</i>	+	(+)	-	+	+	+	T
<i>montana</i>	(+)	-	-	+	+	+	T
<i>Diploglottis</i>							
<i>australis</i>	(+)	-	-	(+)	+	+	LT
<i>Euphorianthus</i>							
<i>euneurus</i>	(+)	-	-	-	(+)	-	LT
<i>Jagera</i>							
<i>javanica australiana</i>	+	+	-	(+)	(+)	-	(LT)
<i>javanica javanica</i>	(+)	(+)	-	+	(+)	(+)	(LT)
<i>pseudorhus</i>	+	+	-	+	+	+	(LT)
<i>Sarcopteryx</i>							
<i>brachyphylla</i>	+	-	-	+	+	+	-
<i>caudata</i>	+	-	-	+	+	+	LT
<i>coriacea</i>	-	-	-	+	+	(+)	-
<i>squamosa</i>	+	-	+	+	+	+	-
<i>Toechima</i>							
<i>erythrocarpum papuanum</i>	+	-	-	(+)	(+)	-	-
<i>Trigonachras</i>							
<i>acuta</i>	(+)	-	-	(+)	+	+	LT
<i>celebensis</i>	(+)	-	-	(+)	+	+	LT
<i>cultrata</i>	+	+	-	(+)	+	+	LT
<i>cuspidata</i>	+	-	-	(+)	+	+	LT
<i>papuensis</i>	(+)	-	-	(+)	+	+	LT

thinner in the loops of the undulations. *Unspecialised epidermal cells* polygonal, with straight to undulate anticlinal walls, around hairs (if present) and stomata in a radiating pattern, above midrib and veins square to rectangular, in rows parallel to the veins, showing the venation pattern. *Stomata* predominantly cyclocytic, adaxially absent to rarely present along the midrib; giant stomata abaxially rarely present.

In transverse section – *Lamina* dorsiventral. *Unspecialised epidermal cells* square. *Hypodermis* only present above midrib and veins. *Mesophyll*: palisade tissue composed of 1 or 2 layers of long erect cells; spongy tissue rather loose. *Midrib* raised abaxially and adaxially; ground tissue of parenchymatous cells; vascular system collateral, with an arched, rarely almost flat adaxial strand and an abaxial arch, surrounded by a sclerenchyma sheath. *Veins*: minor ones embedded in mesophyll, often the larger ones transcurrent. *Margin* with marginal vein and normal mesophyll. *Crystals* rhomboidal, few in ground tissue around midrib and veins, in *T. cultrata* also in pith. *Secretory idioblasts* ± abundant in ground tissue of midrib and in spongy tissue, rare in palisade tissue, with unidentified contents.

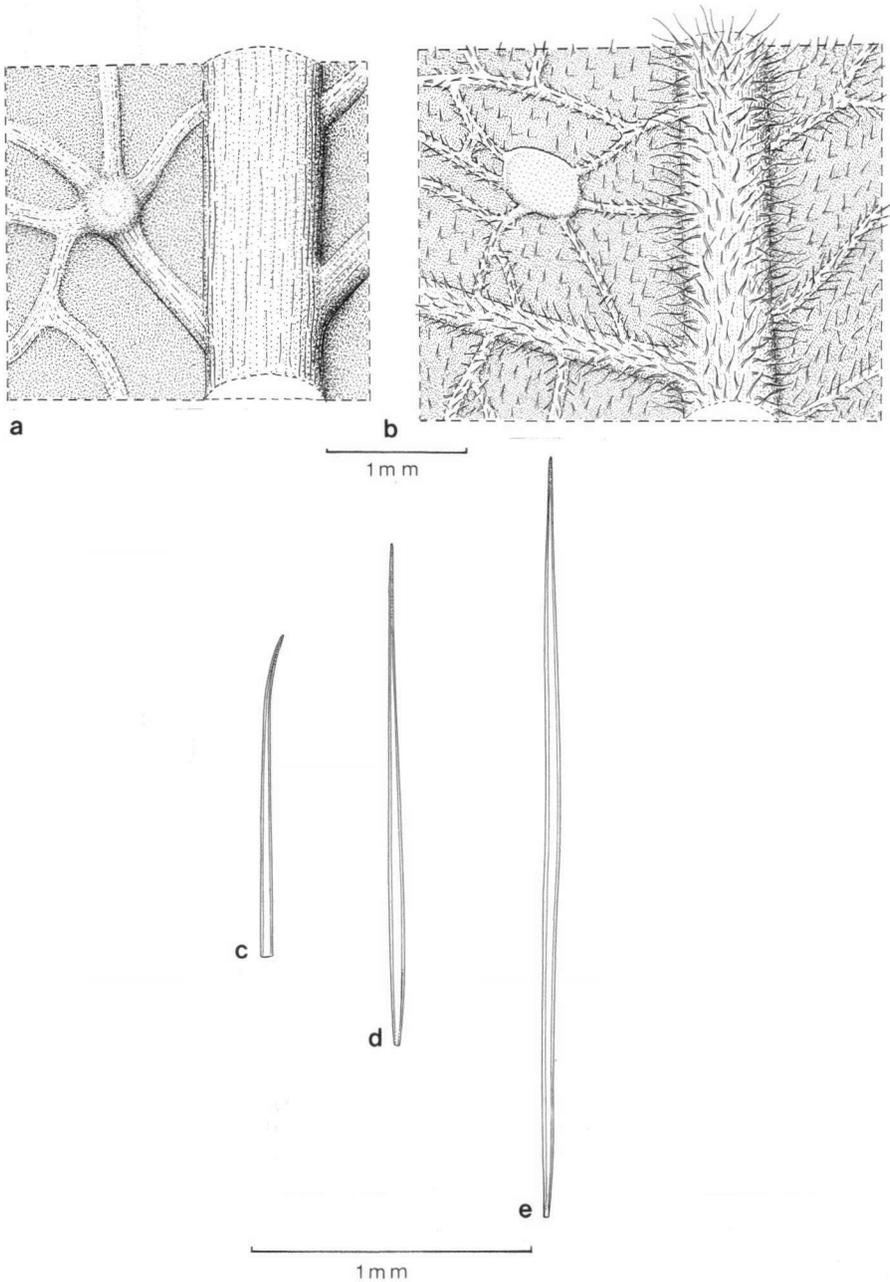


Fig. 2a, b. Naked glands on lower surface of leaflets. a. *Trigonachras celebensis* Leenhouts; b. *Jagera javanica* Blume ex Kalkman subsp. *javanica*. — Fig. 2c–e. Irritating hairs from fruits. c. *Cnesmocarpon dentata* Adema; d. *Cnesmocarpon dasyantha* (Radlk.) Adema; e. *Jagera javanica* Blume ex Kalkman subsp. *javanica* (a: Prawiroatmodjo & Soewoko 1747; b, e: Brass 2587; c: Pullen 7462; d: Clemens s.n.).

Macromorphology

The genera *Cnesmocarpon*, *Jagera* and *Trigonachras*, and the outgroup *Euphorianthus* are briefly described below.

Note – Naked glands are \pm circular, glandular spots not covered by hairs or any other substance (see also Leenhouts, 1978b).

Cnesmocarpon

Small to medium-sized trees. Leaves spirally arranged, 1–8-jugate. Leaflets: margin entire or (*C. dentata*) remotely dentate; surface above glabrous or hairy at least on the midrib, below strigose or puberulous, without naked glands. Petals with not-crested scales or auricles, exceptionally without scales or auricles (*C. dentata*). Fruits winged, exocarp velutinous and with irritating hairs, these in *C. dasyantha*, *C. discoloroides* and *C. montana* fusiform, 1.0–2.6 mm long (Fig. 2d), in *C. dentata* awl-shaped, c. 1 mm long (Fig. 2c). Seeds with a small hilar sarcotesta.

Euphorianthus

Small to rather large trees. Leaves spirally arranged, 4–9-jugate. Leaflets: margin entire; surface above and below hairy on the midrib, below without naked glands. Petals with not-crested scales. Fruits not winged, exocarp short-velutinous. Seeds with a small hilar sarcotesta.

Jagera

Usually pachycaulous trees or shrubs. Leaves verticillate, rarely opposite or spirally arranged, (4–)15–40-jugate. Leaflets: margin serrate to dentate, exceptionally entire; surface above hairy at least on the midrib, below glabrous to puberulous, with round naked glands (Fig. 2b). Fruits not winged, exocarp velutinous and with irritating hairs, these fusiform, 1.1–3.1 mm long (Fig. 2e). Seeds with a small hilar sarcotesta.

Trigonachras

Small to medium-sized trees. Leaves spirally arranged, 1–9-jugate. Leaflets: margin entire; surface above and below glabrous, exceptionally with few short hairs, below with naked glands (Fig. 2a). Petals with not-crested scales. Fruits not winged, exocarp at least in young fruits short-velutinous, often soon glabrous. Seeds without sarcotesta or ariloid.

Phylogeny

For the cladistics analyses the datamatrix of Table 4 was used. The data for the three character sets, as well as the complete dataset, were analysed separately.

The analysis with pollen-morphological characters only (Table 4, columns 1–6) resulted in the cladogram of Figure 3. This cladogram shows a close relationship between *Jagera* and *Trigonachras* as can be expected from the paragraphs on pollen morphology.

Table 4. Characters and datamatrix.

- | | |
|--|--|
| <p>A. Pollen morphological characters</p> <ol style="list-style-type: none"> 1. Equatorial diameter <ol style="list-style-type: none"> a. average $\leq 25 \mu\text{m}$ b. average $\geq 26 \mu\text{m}$ 2. Colpi <ol style="list-style-type: none"> a. narrow b. rather wide c. wide 3. Colpus bridges <ol style="list-style-type: none"> a. absent b. rare or sometimes between mesocolpia c. often between mesocolpia d. sometimes between mesocolpia and apocolpia e. often between mesocolpia and apocolpia 4. Ornamentation <ol style="list-style-type: none"> a. psilate to shallowly rugulate b. reticulate c. perforate 5. Scabrae <ol style="list-style-type: none"> a. absent b. present c. present with an appendage 6. Sides of equatorial outline <ol style="list-style-type: none"> a. concave (rarely up to straight) b. concave to convex c. straight to convex d. convex <p>B. Leaf anatomical characters</p> <ol style="list-style-type: none"> 7. Glandular hairs <ol style="list-style-type: none"> a. absent b. 1 or 2 stalk cells and a glandular head of several cells c. 1 or 2 stalk cells and a large glandular head of 1 (or 2) cells d. several stalk cells and a small glandular head 8. Papillae on abaxial epidermis <ol style="list-style-type: none"> a. absent b. present on most cells c. present around stomata only 9. Cuticular connections between papillae <ol style="list-style-type: none"> a. absent b. present 10. Adaxial cuticle <ol style="list-style-type: none"> a. striate b. not striate 11. Anticlinal walls of adaxial epidermal cells <ol style="list-style-type: none"> a. undulate b. straight or slightly undulate 12. Abaxial cuticle <ol style="list-style-type: none"> a. striate b. not or slightly striate c. striate only around stomata | <ol style="list-style-type: none"> 13. Anticlinal walls of abaxial epidermal walls <ol style="list-style-type: none"> a. undulate b. straight 14. Veins <ol style="list-style-type: none"> a. embedded in mesophyll b. transcurrent c. only larger veins transcurrent 15. Vascular strands in pith of midrib <ol style="list-style-type: none"> a. present b. absent <p>C. Macromorphological characters</p> <ol style="list-style-type: none"> 16. Leaves <ol style="list-style-type: none"> a. (4-)15-40-jugate b. 1-9-jugate 17. Leaflets <ol style="list-style-type: none"> a. finely serrate to dentate or crenate b. remotely dentate c. entire 18. Upper side of leaflets <ol style="list-style-type: none"> a. glabrous b. hairy at least on the midrib 19. Lower side of leaflets <ol style="list-style-type: none"> a. glabrous b. puberulous, especially on midrib c. strigose d. sericeous 20. Lower side of leaflets <ol style="list-style-type: none"> a. without naked glands b. with naked glands 21. Petalar appendages <ol style="list-style-type: none"> a. 1 or 2 scales b. scales or auricles c. auricles 22. Petalar scales or auricles <ol style="list-style-type: none"> a. not crested b. crested 23. Disc <ol style="list-style-type: none"> a. complete b. interrupted 24. Fruit <ol style="list-style-type: none"> a. not winged b. winged 25. Exocarp of fruit <ol style="list-style-type: none"> a. without irritating hairs b. with awl-shaped (irritating) hairs c. with fusiform irritating hairs 26. Seeds <ol style="list-style-type: none"> a. thinly to thickly lenticular b. ellipsoid to obovoid 27. Seeds <ol style="list-style-type: none"> a. without ariloid or sarcotesta b. with an ariloid c. with a short sarcotesta around the hilum |
|--|--|

(Table 4 continued)

	A					B					C																		
	1	2	3	4	5	6	7	8	9	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2
<i>Euphorianthus euneurus</i>	1	2	2	1	1	2	4	2	1	1	2	1	2	3	1	2	3	2	2	1	1	1	1	1	1	1	1	2	3
<i>Cnesmocarpon dasyantha</i>	1	1	2	1	1	1	1	2	2	2	2	2	2	1	2	2	3	1	3	1	3	1	1	2	2	2	2	3	
<i>dentata</i>	1	2	1	1	1	3	3	3	1	2	1	2	1	2	2	2	2	2	2	1	2	1	2	2	3	2	3	2	3
<i>discoloroides</i>	1	1	3	1	1	1	1	2	2	1	2	2	2	2	2	2	3	2	2	1	3	1	1	2	2	2	3	2	3
<i>montana</i>	1	1	2	1	1	2	1	2	2	2	2	2	2	2	2	2	3	1	3	1	3	1	1	2	2	2	2	3	
<i>Jagera javanica australiana</i>	2	3	1	2	3	4	2	1	1	1	2	1	2	3	2	1	1	2	2	2	1	2	1	1	2	2	3		
<i>javanica javanica</i>	2	3	4	3	3	4	2	1	1	1	2	1	2	3	2	1	1	2	2	2	1	1	1	2	2	3			
<i>pseudorhus</i>	2	3	1	3	3	4	2	1	1	1	1	1	2	3	2	1	1	2	2	1	1	1	1	2	2	3			
<i>Trigonachras acuta</i>	2	2	5	3	2	3	1	1	1	1	1	1	2	3	2	2	3	1	1	2	1	1	1	1	1	2	1		
<i>celebensis</i>	2	3	1	3	3	3	1	1	1	2	2	3	2	3	2	2	3	1	1	2	1	1	1	1	1	2	1		
<i>cultrata</i>	2	3	2	3	3	4	1	1	1	2	1	2	2	3	2	2	3	1	1	2	1	1	1	1	1	2	1		
<i>cuspidata</i>	2	3	1	3	2	4	1	1	1	1	2	1	2	3	2	2	3	1	1	1	1	1	1	1	1	2	1		
<i>papuensis</i>	2	2	5	3	3	4	1	1	1	1	1	2	2	3	2	2	3	1	1	2	1	1	1	1	1	2	1		
<i>Cupaniopsis macropetala</i>	2	3	1	1	1	3	3	1	1	1	1	2	2	1	2	2	2	2	2	1	1	1	1	1	1	2	2		
<i>Diploglottis australis</i>	1	3	1	1	1	2	4	1	1	1	2	2	2	3	1	2	3	2	4	1	1	1	2	1	1	1	2		

The analysis with leaf-anatomical characters only (Table 4, columns 7–15) resulted in seven cladograms. This set of cladograms offers three different solutions: 1) *Cnesmocarpon* and *Trigonachras* are more closely related to each other than each is to *Jagera* (Fig. 4); 2) *Cnesmocarpon* is closely related to *Trigonachras celebensis* and *T. cultrata*, while *Jagera* is closely related to *Trigonachras acuta*, *T. cuspidata* and *T. papuensis*; 3) *Trigonachras acuta*, *T. cuspidata* and *T. papuensis* are sister species of all other taxa, *Cnesmocarpon* is closely related to *Trigonachras celebensis* and *T. cultrata*.

The analysis with macromorphological characters only (Table 4, columns 16–27) resulted in the cladogram of Figure 5. This cladogram gives *Cnesmocarpon* and *Jagera* as closely related groups, and *Trigonachras* as a sistergroup of these two.

The analysis with the complete dataset resulted in the cladogram of Figure 6. This cladogram gives *Jagera* and *Trigonachras* as closely related groups, and *Cnesmocarpon* as the sistergroup of this pair. The branch leading to *Jagera* and *Trigonachras* is strongly supported by pollen-morphological characters, together with one leaf-anatomical character (absence of papillae on lower leaflet surface) and one macromorphological character (naked glands on lower leaflet surface); *Jagera* is furthermore supported by one leaf-anatomical and one macromorphological character, while *Trigonachras* is supported by macromorphology only. The branch leading to *Cnesmocarpon* is supported by leaf-anatomical characters and one macromorphological character.

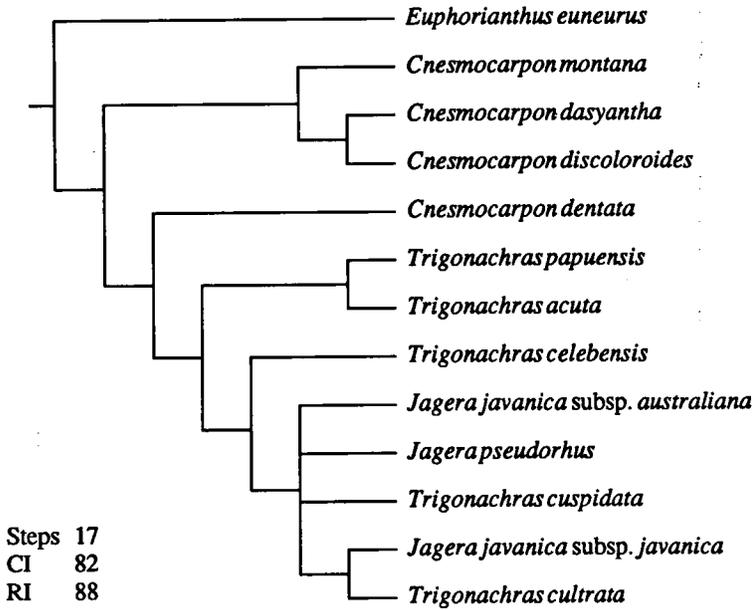


Fig. 3. Cladogram of *Cnesmocarpon*, *Jagera*, and *Trigonachras* for pollen-morphological characters only; outgroup *Euphorianthus*.

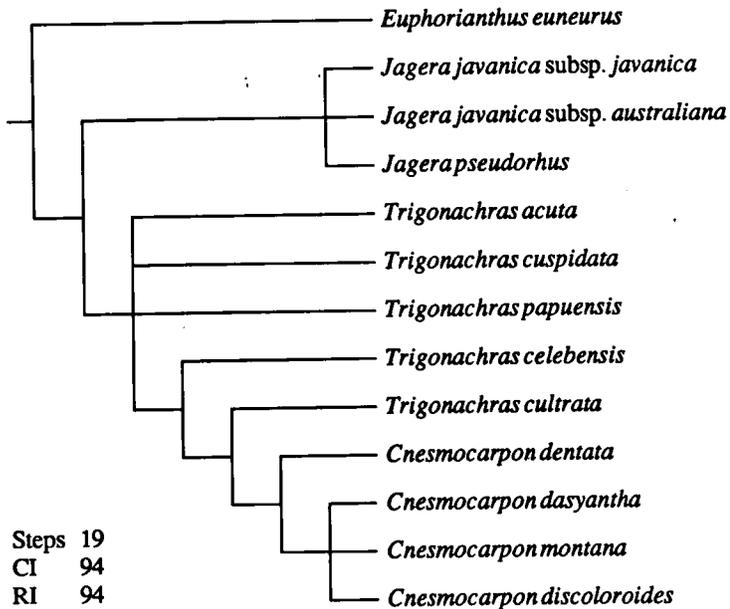


Fig. 4. Cladogram of *Cnesmocarpon*, *Jagera*, and *Trigonachras* for leaf-anatomical characters only; outgroup *Euphorianthus*.

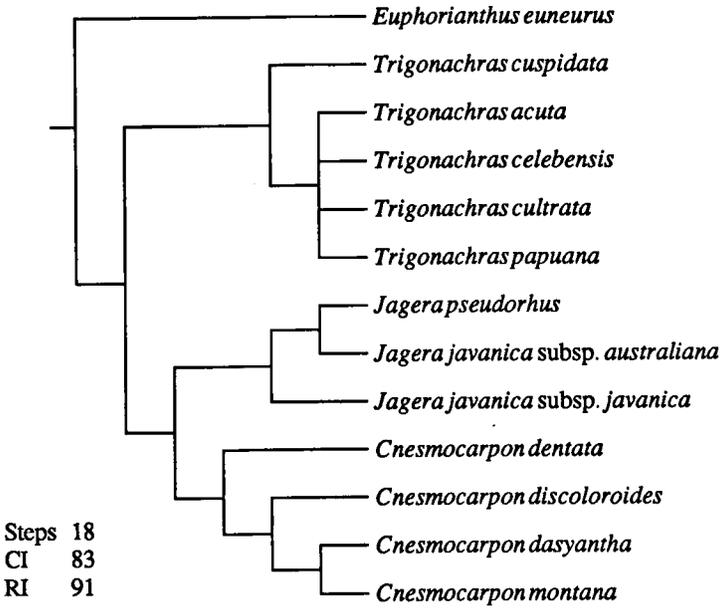


Fig. 5. Cladogram of *Cnesmocarpon*, *Jagera*, and *Trigonachras* for macromorphological characters only; outgroup *Euphorianthus*.

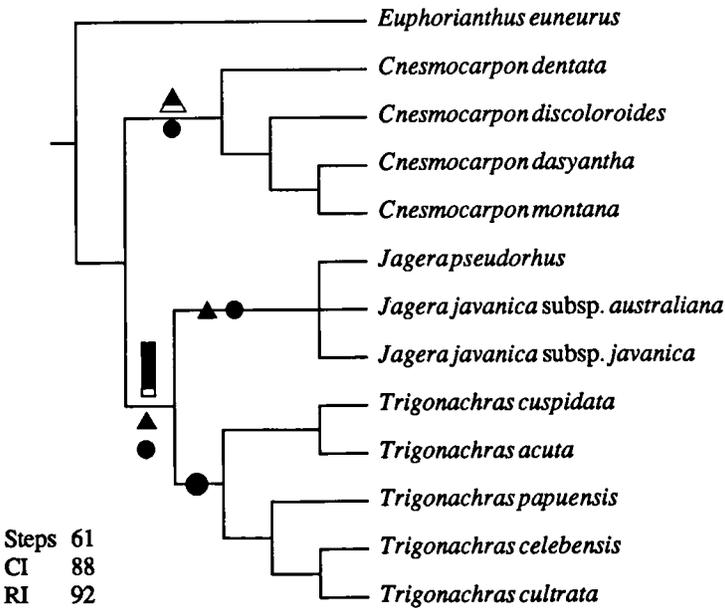


Fig. 6. Cladogram of *Cnesmocarpon*, *Jagera*, and *Trigonachras* for the complete dataset; outgroup *Euphorianthus*. ■ = pollen-morphological, ▲ = leaf-anatomical, and ● = macromorphological characters.

Discussion

Cladograms for the different parts of the character set (pollen morphology, leaf anatomy, macromorphology) are presented to show how easily different researchers working independently can reach conflicting solutions concerning the relationship between the taxa studied.

To solve these conflicts the complete dataset was analysed, which resulted in one cladogram (Fig. 6). This cladogram shows a close relationship between *Jagera* and *Trigonachras*; *Cnesmocarpon* is a more distant relative of this pair. In studying the result more closely, the cladogram proved to be robust. Changes in the data matrix, by either deleting characters (character states) that, after analysis, were shown to be autapomorphous, or adding more synapomorphies for *Jagera*, did not change the architecture of the cladogram. Replacing *Euphorianthus* as outgroup by either *Cupaniopsis* or *Diploglottis* did not result in different cladograms. It is concluded here that the cladogram of Figure 6 probably represents the best solution for the relationship between *Cnesmocarpon*, *Jagera*, and *Trigonachras*.

According to Muller & Leenhouts (1976), *Euphorianthus*, *Sarcopteryx*, and *Trigonachras* are closely related and best to be placed near *Toechima* and *Synima*. *Jagera* also belongs to this group and may be slightly more derived. *Diploglottis* is in their view highly specialised, to be placed in the vicinity of the *Euphorianthus-Sarcopteryx-Trigonachras*-group.

Leenhouts (1978a, 1988) concluded that *Euphorianthus* and *Diploglottis* are closely related yet separate genera.

The results of the present study largely confirms these views: *Euphorianthus* and *Diploglottis* are closely related; *Jagera* clearly belongs to a group that includes *Euphorianthus* and *Trigonachras* also.

CONCLUSIONS

The results of the cladistic analyses as given in Figure 6 lead to the following conclusions:

- 1) *Cnesmocarpon*, *Jagera*, and *Trigonachras* are separate and probably monophyletic groups.
- 2) All groups studied are of more or less the same taxonomical level and status. They may be either subgenera in a larger genus, or separate genera. Seen in the light of the historical developments in the taxonomy of this group (Radlkofer, 1879; see also Leenhouts, 1988) we have chosen for the latter solution: all groups are genera.
- 3) As a consequence of point 2, a new genus to accommodate the taxa included in *Cnesmocarpon* has to be described. This is done formally in the taxonomic part of this article.
- 4) *Diploglottis* and *Euphorianthus* are indeed closely related; however, contrary to the views of Muller & Leenhouts (1976) *Diploglottis* is probably not as highly specialised as they thought.

TAXONOMIC PART

CNESMOCARPON Adema, *gen. nov.*

Arbusculae vel arbores statura mediocri. Rami petioli rachidesque lenticellis obsitis. Folia spiratim disposita paripinnata sine pseudo-stipulis. Inflorescentiae axillares raro ramiflorae. Flores unisexuales regulares pentameri. Sepala libera imbricata non petaloidea parum inaequalia appresse pubescentia. Petala unguiculata duabus squamis vel auriculis raro inappendiculata. Discus completus vel interruptus glaber. Stamina 8, filamentis pubescentibus, antheris glabris vel sparse pubescentibus. Ovarium 3-loculare, stylo apicali lineis stigmaticis 3. Fructus 3-ocularis basi 3-alatus extus velutinus necnon pilis prurientibus dense obsitus. Semina obovoidea sarcotesta parva carunculoidea. — Typus: *Guioa dasyantha* Radlk. [= *Cnesmocarpon dasyantha* (Radlk.) Adema].

Small or medium-sized trees. Twigs, petioles and rachises lenticellate. Indumentum consisting of solitary simple hairs. *Twigs* terete, striate to grooved. *Leaves* spirally arranged, paripinnate, 1–8-jugate, without pseudo-stipules, neither petiole nor rachis winged. *Leaflets* alternate to opposite, asymmetric, below with papillae, base cuneate to rounded, apex obtuse or acuminate, rarely cuspidate, margin entire or remotely dentate, midrib not or slightly prominent above, domatia absent or pocket-like; petiole 3–16 mm, pulvinate. *Inflorescences* axillary or rarely ramiflorous, with or without branches. *Bracts* and *bracteoles* subulate to triangular or ovate, outside and inside appressed-hairy. *Flowers* unisexual, regular. *Sepals* 5, free, imbricate, not petaloid, slightly unequal, outside and inside appressed-hairy. *Petals* 5, spatulate, shorter to longer than the sepals, clawed, with 2 scales or auricles (in *C. dentata* sometimes absent). Disc complete or interrupted, glabrous. *Stamens* 8; filaments patently hairy; anthers glabrous or thinly hairy. Ovary 3-celled, outside hairy; style apical with 3 stigmatic lines. *Fruit* 3-celled, basally 3-winged, outside velutinous and densely covered with irritating hairs, inside tomentose to appressed-hairy. *Seeds* obovoid, testa shiny black; sarcotesta small carunculoid; cotyledons unequal, parallel or obliquely superposed.

Distribution – Four species in Australia and in Malesia: Papua New Guinea.

Habitat – Primary forest, lowland to montane; altitude up to 2000 m.

KEY TO THE SPECIES

- 1a. Leaflets entire, lower side whitish or glaucous 2
- b. Leaflets remotely dentate, lower side green 2. *C. dentata*
- 2a. Indumentum strigose. Upper side of leaflets totally glabrous 3
- b. Indumentum puberulous to tomentose. Upper side of leaflets usually with a densely hairy midrib 3. *C. discoloroides*
- 3a. Leaves (3–)4–5-jugate. Leaflets 6–18.5 × 2.5–5.5 cm, nerves 6–12 per side, 7–20(–28) mm apart. – Up to 1000 m altitude 1. *C. dasyantha*
- b. Leaves 2–3(–4)-jugate. Leaflets 8.5–19 × 3.5–8 cm, nerves 5–10 per side, 9–30 mm apart. – Altitude between 1600 and 2000 m 4. *C. montana*



Fig. 7. *Cnesmocarpon dasyantha* (Radlk.) Adema. a. Habit; b. lower surface of leaflet (NGF 21918).

1. *Cnesmocarpon dasyantha* (Radlk.) Adema, *comb. nov.* – Fig. 7

Guioa dasyantha Radlk., Bot. Jahrb. 56 (1920) 277; in Engler, Pflanzenr. 98 (1933) 1159; Welzen, Leiden Bot. Series 12 (1989) 304. — *Jagera dasyantha* (Radlk.) Reynolds, Austrobaileya 3 (1991) 500. — Type: *Ledermann 10365*, Papua New Guinea, Sepik Area, 1912–'13 (holo, ?; iso L). *Jagera discolor* L. S. Smith ex Reynolds, Austrobaileya 1 (1981) 407, f. 28A; Fl. Australia 25 (1985) 67. — Type: *L. S. Smith 4977*, Australia, Queensland, Clump Mountain, 1951 (holo BRI; iso L).

Trees 5–28 m high, d. b. h. 15–30(–92.5) cm. *Twigs* striate to grooved, 2–5 mm in diameter, (thinly) strigose, soon glabrous. *Leaves* (3–)4–5-jugate; petiole 15–95 mm, strongly pulvinate; rachis 25–190 mm; both semiterete, striate, strigose to glabrous. *Leaflets* alternate or opposite, elliptic to ovate, 6–18.5 × 2.5–5.5 cm, index 1.9–3.4, thickly chartaceous, above glabrous, below glabrous to thinly strigose, whitish when dry, base cuneate to rounded, apex acuminate, exceptionally cuspidate, margin entire, midrib not prominent above, nerves 6–12 per side, 7–20(–28) mm apart, angle to midrib 40–60°, domatia absent or small pocket-like; petiolule 3–16 mm, semiterete, grooved above, strigose to glabrous. *Inflorescences* axillary, 6–10 cm, with 1 to many branches, in fruit 5.5–15 cm. *Bracts* and *bracteoles* subulate to triangular or ovate, 0.2–2.5 × 0.1–1.0 mm. *Pedicels* 3.7 mm, articulated at 1/2, strigose. Buds ± globular, 1.9–2.5 × 2.2–2.5 mm. *Sepals* (broadly) ovate to triangular, 1.7–3.7 × 1.6–2.5 mm. *Petals* 2.1–2.4 × 1.2–1.7 mm, claw 0.5–0.9 mm, outside appressed-hairy at the claw, ciliate, inside appressed-hairy except apex, auricles woolly. Disc complete. Filaments of *staminodes* 1.5–2.1 mm; anthers 0.6 mm, glabrous. Style 1.2–1.4 mm, thinly hairy, stigma 0.2 mm. *Fruits* about globular, thickly winged, triquetral in cross section, 15 × 16 mm, wall at base very thick, thinning upwards, inside tomentose (but appressed-hairy by the seeds). *Seeds* 9 × 5 mm; cotyledons obliquely superposed.

Distribution – Australia: N Queensland, between Mt Lewis and Mt Fox; Malasia: Papua New Guinea (Sepik, West New Britain, Central and Western Prov.). Specimens studied: *Forbes 1*, *Hartley 10765*, *NGF 7362*, *21918*, *Schodde 2954*, *3030*.

Habitat – Primary forest. Altitude 400–1000 m. Fl.: March, Sept.; fr.: March.

Field notes – Bark smooth, light grey to red brown, inner bark pink to orange or red brown. Wood pale creamy pink to reddish. Leaflets mid or dark green above, greyish green or glaucous below. Inflorescence pale green. Flowers white or cream.

2. *Cnesmocarpon dentata* Adema, *spec. nov.* – Fig. 8

Arbor 6–26 m alta. Folia 1–3-jugata; foliolis ellipticis dentatis. Discus interruptus. Capsulae plusminusve globosae, basaliter trialatae, pericarpio circa 6 mm crasso succulento, exocarpio velutinoso necnon pilis prurientibus dense obsito. — Typus: *Jacobs 9524*, Papua New Guinea, N side of Mt Bosavi, 1973 (holo L; iso BISH, BO).

Trees 6–26 m high. *Twigs* striate, 2–5 mm in diameter, short tomentose, glabrescent. *Leaves* 1–3-jugate; petiole 15–50 mm and ± pulvinate, semiterete; rachis (0–) 15–120 mm and about terete; both striate, short tomentose. *Leaflets* opposite to alternate, ± elliptic, 4.5–17.5 × 2.5–8 cm, index 1.8–2.8, chartaceous, above and below almost glabrous, lower side green, midrib densely, nerves thinly puberulous, margin dentate, midrib slightly prominent above, nerves 7–12 per side, mostly end-

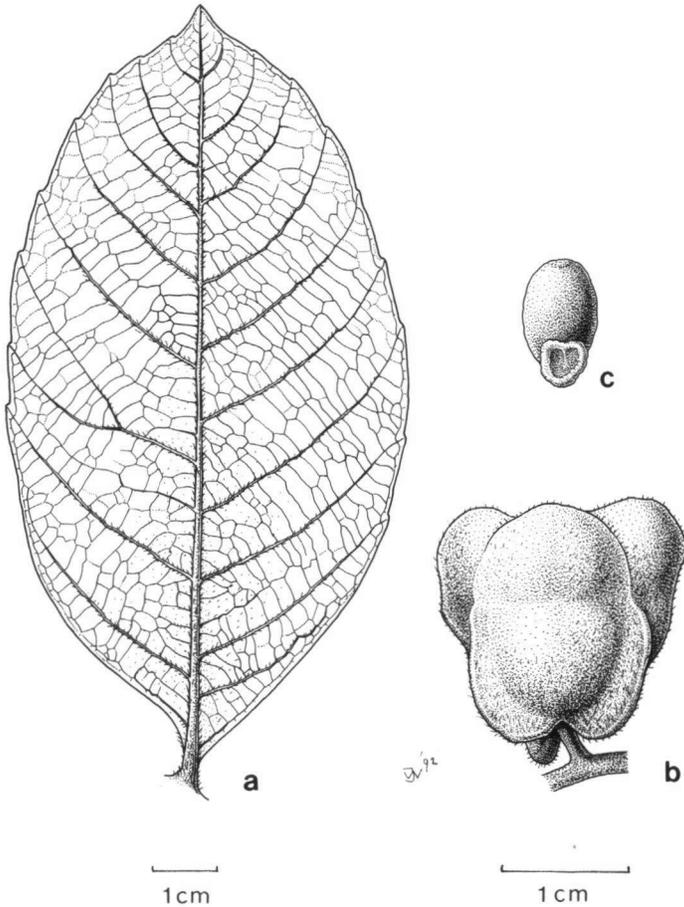


Fig. 8. *Cnesmocarpon dentata* Adema. a. Lower surface of leaflet; b. fruit (Jacobs 9524).

ing in a tooth, 5–20 mm apart, angle to midrib 45–75°; petiolule 3–8 mm, semiterete, grooved, short tomentose. *Inflorescences* axillary, 3–8 cm, with or without branches, in fruit 5–13.5 cm. *Bracts* and *bracteoles* triangular, 0.3–1.9 × 0.2–1.2 mm. *Pedicels* c. 3 mm, short tomentose. *Sepals* triangular to deltoid, 1.7–2.5 × 1.0–1.8 mm. *Petals* 1.2–3.0 × 0.6–1.9 mm, claw 0.4–0.6 mm, outside appressed-hairy up to halfway, ciliate, inside appressed-hairy in lower half, appendages absent, or either 2 scales or auricles, woolly. Disc interrupted. Filaments of *staminodes* 1.9–2.2 mm; anthers 0.6 mm, glabrous or thinly hairy. Style 2–3 mm, glabrous or thinly hairy, stigma 0.5–0.9 mm. *Fruits* about globular, basally 3-winged, 22 × 20 mm, wall c. 6 mm thick, succulent, inside ± appressed hairy. *Seeds* 11 × 5 mm; cotyledons parallel.

Distribution — Malesia: Papua New Guinea (Western and Southern Highlands Prov.). Specimens studied: Jacobs 9524, Pullen 7462.

Habitat – Primary forest. Altitude 10–700 m. Volcanic soil. Fl. and fr.: Oct.

Field notes – Bark moderately smooth, patchy light and dark grey and brown, blaze thin, red brown. Corolla white. Fruits glossy bright red to orange, succulent, very sour. Seed black with yellow aril.

3. *Cnesmocarpon discoloroides* Adema, *spec. nov.* – Fig. 9a–c

Arbor 5–16 m alta; ramulis tomentellis glabrescentibus. Folia (2–)4–5(–8)-jugata; foliolis ellipticis ad ovatis raro obovatis integris, supra glabris ad sparsissime puberulis, costa puberulior, infra fere glabris ad sparse puberulis, costa nervis lateralibusque puberulioribus. Capsulae ubi juvenes alatae, exocarpio velutinoso necnon pilis prurientibus obsito. — Typus: LAE 58053, Papua New Guinea, Morobe Prov., bottom of Mt Shugol, above Gurakor, 1973 (holo L; iso A, BISH, L).

Trees 5–16 m high, d.b.h. 5–25 cm. Twigs striate to grooved, 2–5(–10) mm in diameter, shortly tomentose, glabrescent. Leaves (2–)4–5(–8)-jugate; petiole 30–110 mm, strongly pulvinate, semiterete, upwards terete; rachis (25–)95–305 mm, about terete; both striate, shortly tomentose, glabrescent. Leaflets alternate to opposite, elliptic to ovate, rarely obovate, 6–22 × 2.5–8.5 cm, index 1.7–3.2(–4.2), thickly chartaceous, above glabrous to thinly puberulous, midrib more densely so, below almost glabrous to thinly puberulous, midrib and nerves more densely so, ± whitish when dry, base cuneate to rounded, apex short- or long-acuminate, margin entire, exceptionally undulate, midrib not prominent above, nerves 8–16 per side, 5–20 mm apart, angle to midrib 45–65°, domatia inconspicuous, pocket-like; petiole 2–15 mm, semiterete, grooved above, shortly tomentose, glabrescent. Inflorescences axillary or ramiflorous, c. 1 cm, branched or not, in fruit 3–17 cm. Bracts and bracteoles subulate to deltoid, 0.2–1.2 × 0.1–1.1 mm. Pedicels 1.5 mm, articulated at 1/4, shortly tomentose. Buds about globular, 1.7 × 1.9 mm. Flowers only known from buds or from below the young fruits. Sepals ± elliptic, inner ones apically with scarious rims, 1.7–3.1 × 1.5–2.2 mm, ciliate. Petals 3.0 × 1.2 mm, claw 1.2 mm, outside appressed-hairy at the claw, ciliate at the base of the plate, inside appressed-hairy except apex, auricles woolly. Disc complete. Filaments of staminodes 2.2–2.5 mm; anthers 0.5–0.6 mm, glabrous. Style 1.0–1.9 mm, glabrous, stigma 0.4–0.7 mm. Young fruits winged, triquetral in cross section, inside tomentose.

Distribution – Malesia: Papua New Guinea (West New Britain, Morobe and Milne Bay Prov.). Specimens studied: LAE 58053, 67902, 68680, 70906, NGF 17886, 25007, 26792, 26913, 49947.

Habitat – Montane or hill forest. Altitude 0–1300 m. Stoney ground. Fl.: May, Oct.; fr.: Jan.–May, Oct.–Dec.

Field notes – Bark (greenish) grey to brown or black, slightly cracked, inner surface straw to dark (reddish) brown, underbark red or greenish, inner bark red or orange. Wood white to orange brown. Leaflets mid or dark green above, pale green, greyish or glaucous below. Flowerbuds yellow green. Flowers white. Fruits red.

4. *Cnesmocarpon montana* Adema, *spec. nov.* – Fig. 9d

Arbor 8–10 m alta; ramulis strigosis. Folia 2–3(–4)-jugata; foliolis ellipticis ad ovatis integris, infra densissime strigosis. Capsulae ubi juvenes alatae, exocarpio velutinoso necnon pilis prurientibus dense obsito. — Typus: Carr 14154, Papua New Guinea, Alola, 1936 (holo L; iso BM, G, SING).

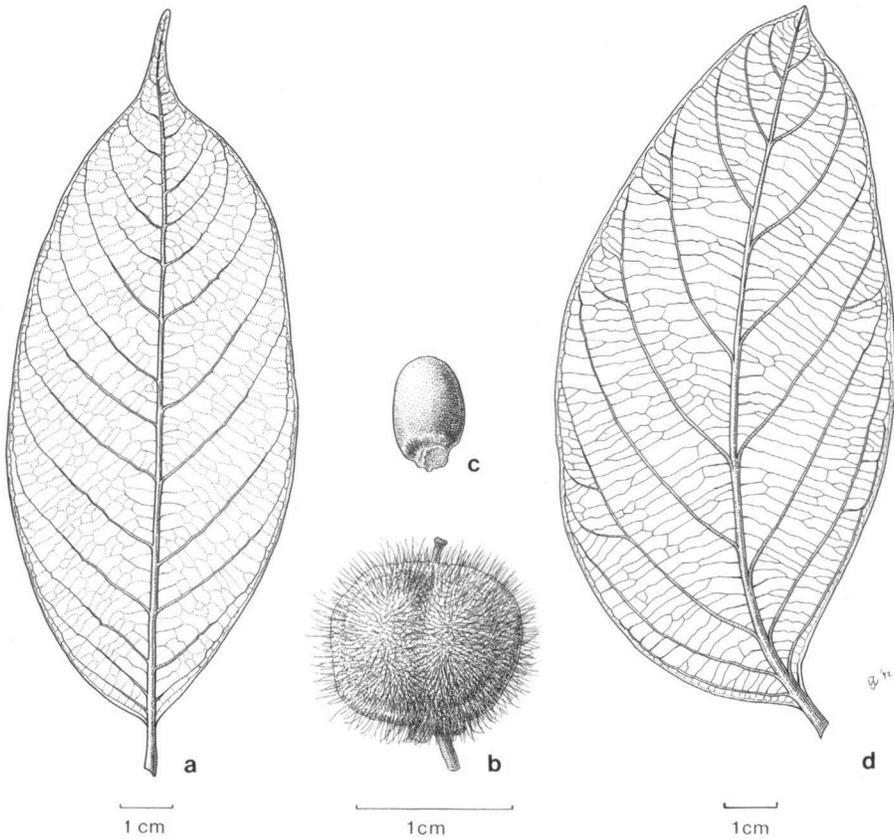


Fig. 9. *Cnesmocarpon discoloroides* Adema. a. Lower surface of leaflet; b. fruit; c. seed. — *C. montana* Adema. d. Lower surface of leaflet (a–c: LAE 58053; d: Carr 13384).

Trees 8–10 m high. Twigs grooved, 2–3 mm in diameter, strigose. Leaves 2–3(–4)-jugate; petiole 45–70 mm, strongly pulvinate, semiterete, rarely upwards terete; rachis 45–120 mm, semiterete, rarely terete; both striate, (thinly) strigose. Leaflets alternate to opposite, elliptic to ovate, 8.5–19 × 3.5–8 cm, index 1.8–3, coriaceous, above glabrous, below rather densely strigose, whitish when dry, base cuneate to rounded, apex shortly and obtusely acuminate, margin entire, midrib not prominent above, nerves 5–10 per side, 9–30 mm apart, angle to midrib 40–45°, domatia absent; petiolule 5–10 mm, semiterete, grooved above, strigose. Inflorescences axillary, 16–19 cm, with (long) branches, in fruit 7 cm. Bracts and bracteoles ± triangular, 0.4 × 0.4 mm. Buds flattened globular, 2 × 2.0–2.5 mm. Pedicels 4 mm, articulated halfway, strigose. Young fruits 3-winged, inside tomentose.

Distribution – Malesia: Papua New Guinea (Central Prov.). Specimens studied: Carr 13384, 13519, 14154, 14604.

Habitat – Forest. Altitude 1600–2000 m. Fl.: Sept.–Nov.; fr.: Jan..

Field notes – Buds brownish. Flowers green or white. Fruits reddish.

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EXPLANATION OF THE PLATES

Plate 1 — *Cnesmocarpon*, pollen, SEM.

- 1, 2: *C. dasyantha* (Hartley 10765) – 1: polar views, with connections between adjacent mesocolpia, × 1800; 2: oblique section, × 2900.
- 3: *C. dasyantha* (Schodde 3030): polar view, × 2450.
- 4: *C. montana*: polar views, left one with connection between adjacent mesocolpia, × 2250.
- 5, 6: *C. dasyantha* (NGF 21918): polar views, in 5 with connections between adjacent mesocolpia and between apocolpium and mesocolpia, × 2850.

Plate 2 — *Cnesmocarpon*, pollen, SEM.

- 1: *C. dentata* (Jacobs 9524): polar view, × 2350.
- 2: *C. dentata* (Pullen 7462): polar view, × 2250.
- 3–6: *C. discoloroides* – 3: polar and oblique view, × 1700; 4: polar view, showing distinct connections between adjacent mesocolpia, × 2300; 5: oblique view, with distinct mesocolpium connections, × 2500; 6: section through aperture lobe parallel to polar axis, × 4700.

Plate 3 — *Jagera*, pollen, SEM.

- 1–3: *J. javanica* subsp. *australiana* (Gray 4083) – 1: polar views, left one with unfolded colpi, right one with invaginated colpi, × 1200; 2: detail of 1, showing scabrae with slender appendage, × 4500; 3: polar view, × 1900.
- 4: *J. javanica* subsp. *australiana* (Gray 1455): oblique section, × 2150.
- 5, 6: *J. javanica* subsp. *javanica* (Brass 3587) – 5: polar view, × 2100; 6: oblique section, × 2650.

Plate 4 — *Jagera*, pollen, SEM.

- 1–6: *J. pseudorhus* (Pullen 7235) – 1: usual aperture system and ornamentation, × 1900; 2–5: usual aperture system and slightly to strongly deviating ornamentation, in 5 with a bridged colpus, × 2300 (2), × 2150 (3), × 2400 (4), × 2550 (5); 6: deviating aperture system and ornamentation, × 2000.

Plate 5 — *Jagera*, pollen, SEM.

- 1–3: *J. pseudorhus* (Pullen 7235): several deviating aperture systems, × 2000 (1), × 1700 (2), × 1900 (3).
- 4–6: *J. pseudorhus* (Dietrich 2512) – 4: polar view, × 2050; 5: detail showing scabrae with slender appendage, × 6500; 6: section showing exine stratification and scabrae with appendage, × 8600.

Plate 6 — *Trigonachras*, pollen, SEM.

- 1–3: *T. acuta* – 1: polar and oblique view, left one with heavily scabrate colpus membranes, right one with distinct colpi, × 1350; 2: detail showing low scabrae without appendage and densely scabrate cover of colpus membranes in polar area, × 6500; 3: cross section exine, × 6500.
- 4, 5: *T. cultrata* – 4: polar view, showing invaginated colpi and connection between adjacent mesocolpia, × 1700; 5: cross section exine, × 6500.
- 6–8: *T. celebensis* – 6: cross section exine, × 6500; 7: polar view, with invaginated colpi (compare with Plate 10: 7); 8: detail of 7, showing scabrae with slender appendage, × 7000.

Plate 7 — *Trigonachras*, pollen, SEM.

- 1–4: *T. cuspidata* – 1: polar view, with invaginated colpi, × 2550; 2: detail of 1, showing scabrae without appendage, × 7000; 3: polar view, with partly invaginated colpi, × 2800; 4: polar view, with unfolded colpi, × 2200.
- 5, 6: *T. papuensis* – 5: polar view, showing well-developed scabrae, invaginated colpi, and apocolpium connected with 3 mesocolpia, × 2000; 6: immature grain with very low scabrae, × 2850.

Plate 8 — *Trigonachras*, pollen, SEM.

- 1–6: *T. papuensis* – 1: polar area with apocolpium connected with 3 mesocolpia, and scabrae with slender appendage, × 5500; 2: polar area showing syncolpate aperture system, × 5500; 3: polar area with apocolpium partly connected with 3 mesocolpia, × 6500; 4: detail of 3, showing scabrae with appendage, × 9750; 5: detail of ornamentation, with scabrae + appendage, × 7600; 6: cross section exine, colpus to the left, mesocolpium to the right, × 6000.

Plate 9 — *Cnesmocarpon, Jagera*, pollen, LM (× 1000; 1–3, 6, 7, 11 with 'interference contrast').

- 1–6: *C. dasyantha* (Hartley 10765) – 1, 2, 4: polar views, upper focus (2 slightly lower than 1) and middle focus; 3: polar view, upper focus, showing connections between mesocolpia; 5, 6: equatorial views, middle focus and endoaperture.
- 7–11: *C. discoloroides* – 7, 8: polar views, upper focus (showing connections between mesocolpia) and middle focus; 9–11: equatorial views, middle focus, colpus and endoaperture.
- 12–18: *J. javanica* subsp. *australiana* (Gray 1455) – 12, 13: polar views, upper and middle focus; 14: equatorial view endoaperture; 15–18: equatorial view mesocolpium (16 slightly lower than 15) and middle focus (17: endoaperture level; 18: apocolpium level).

Plate 10 — *Jagera, Trigonachras*, pollen, LM (× 1000), TEM (6: × 4700).

- 1–5: *J. javanica* subsp. *javanica* (Brass 3587) – 1, 2: polar views, upper and middle focus; 3, 4: equatorial views, mesocolpium and middle focus; 5: equatorial view endoaperture.
- 6: *J. pseudorhus* (Brass 7943): oblique section through colpus and adjacent mesocolpium parts, showing discontinuities (arrows) between endexine (en) and ectexine (ec); several scabrae show a slender appendage (a).
- 7–12: *T. celebensis* – 7, 8: polar views, upper and middle focus; 9, 10: equatorial views, colpus and endoaperture; 11, 12: equatorial views, mesocolpium and middle focus (12 with intine remains).
- 13, 14: *T. acuta*: polar views, upper and middle focus.

Plate 11 — *Euphorianthus, Jagera, Cnesmocarpon*, leaf-anatomy, 1, 2: LM (1: × 40; 2: × 50); 3–6: SEM (bar = 10 µm).

- 1, 3, 4: *E. euneurus* (Womersley 6) – 1: cross section midrib leaflet; 3: glandular hair on lower surface leaflet; 4: papillae on lower surface of leaflet.
- 2, 5: *J. javanica* subsp. *javanica* (Brass 2587) – 2: cross section midrib leaflet; 5: glandular hair on lower surface of leaflet.
- 6: *C. dentata* (Pullen 7462): glandular hair on lower surface of leaflet.

Plate 12 — *Cnesmocarpon*, leaf-anatomy, 1, 2: SEM (bar = 10 µm); 3, 4: LM (3: × 250; 4: × 100).

- 1, 3: *C. dasyantha* (Clemens s.n.): papillae on lower surface leaflet.
- 2, 4: *C. dentata* (Pullen 7462): papillae on lower surface of leaflet.

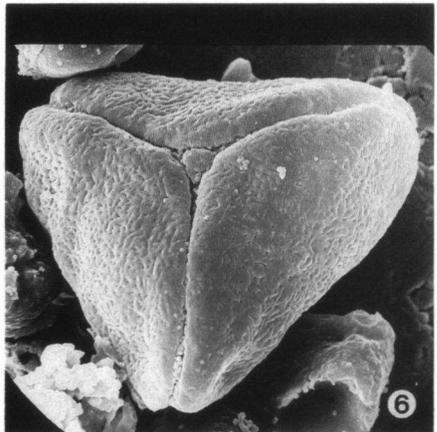
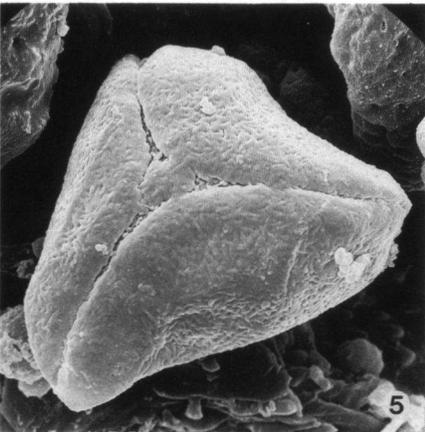
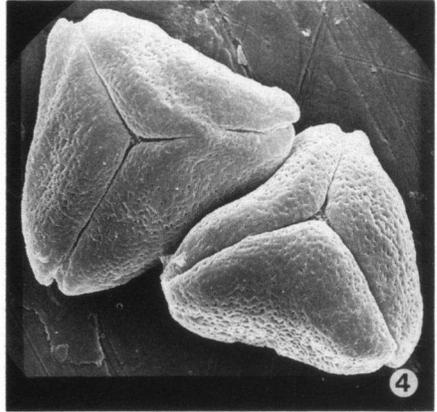
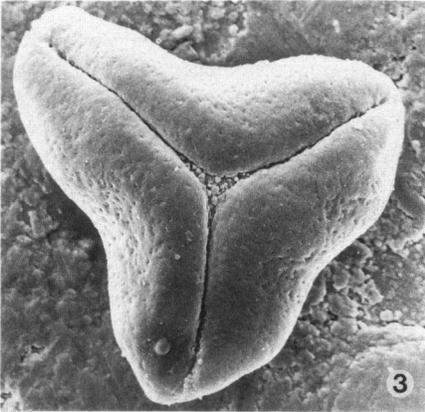
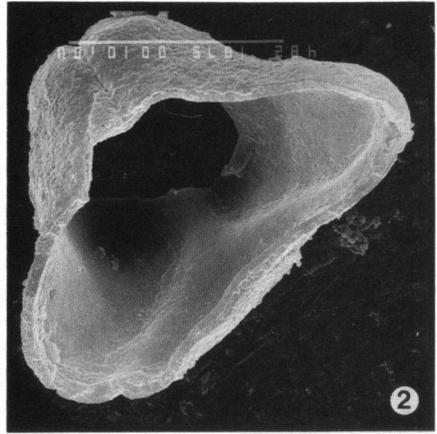
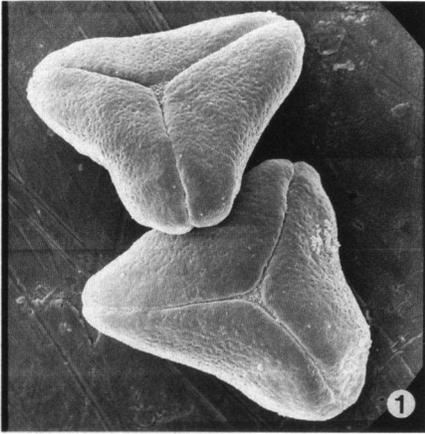


Plate 1 — *Cnesmocarpon*, pollen, SEM.

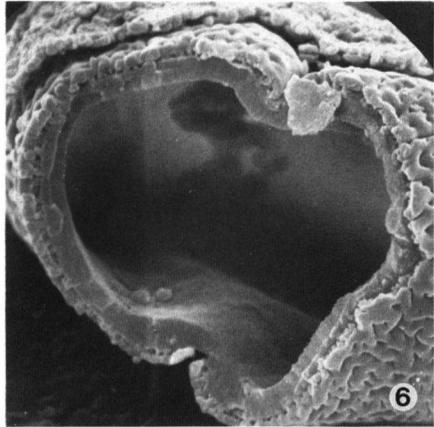
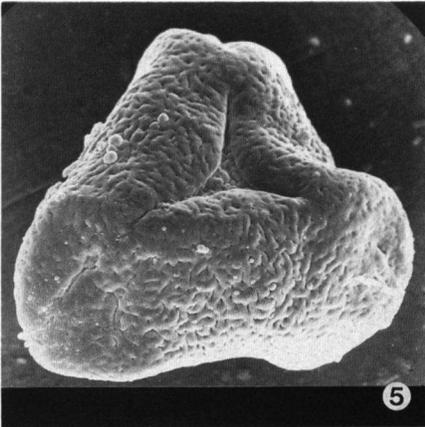
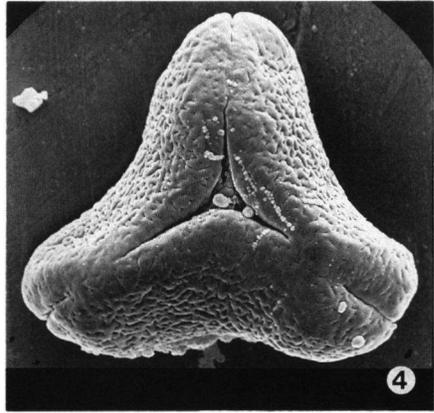
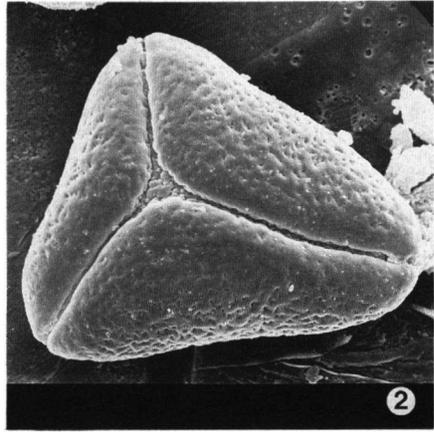
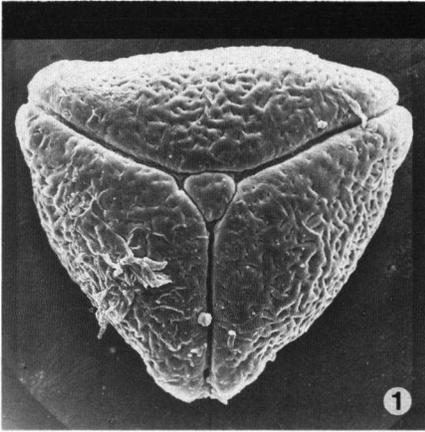


Plate 2 — *Cnesmocarpon*, pollen, SEM.

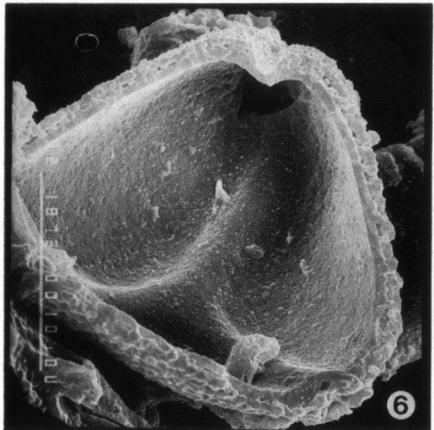
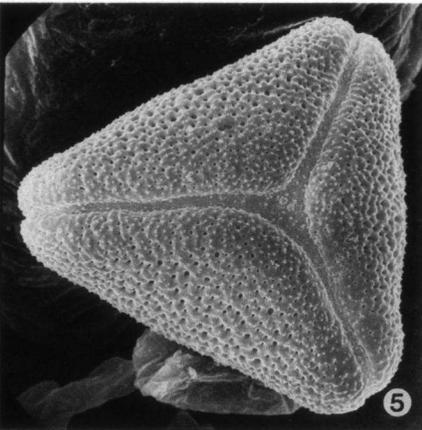
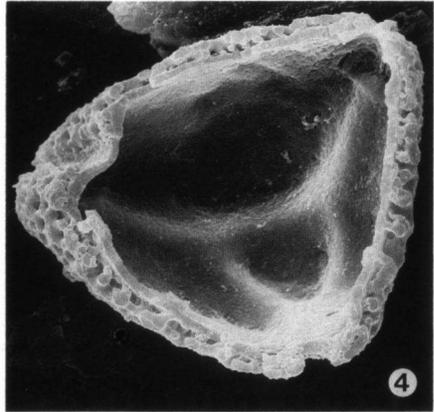
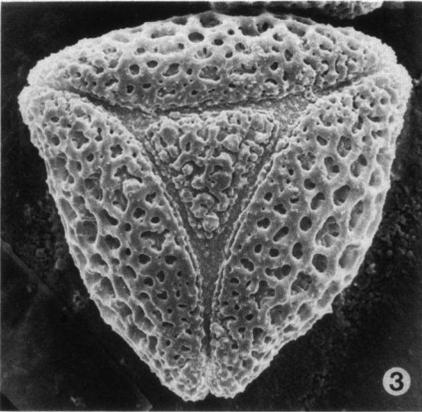
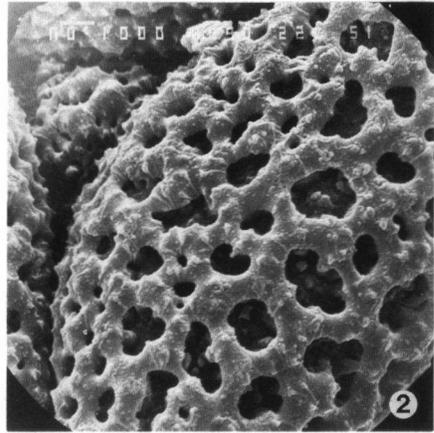
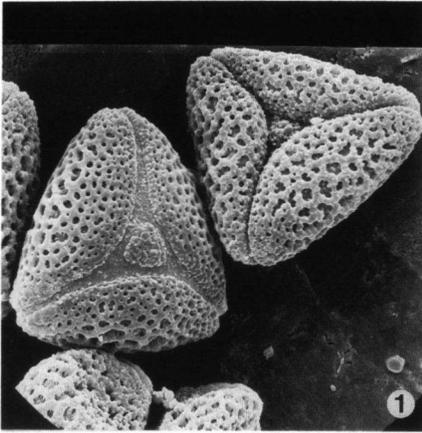


Plate 3 — *Jagera*, pollen, SEM.

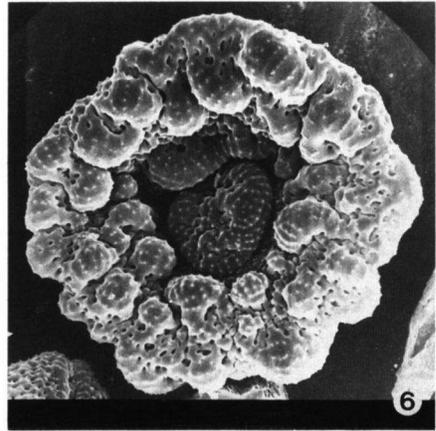
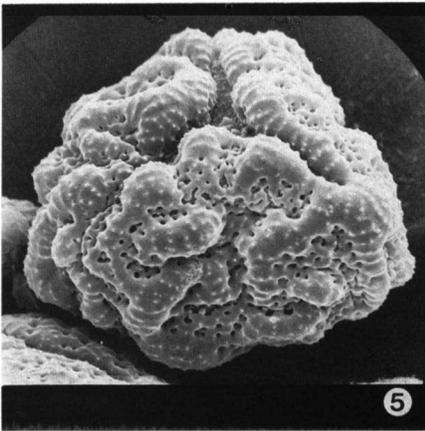
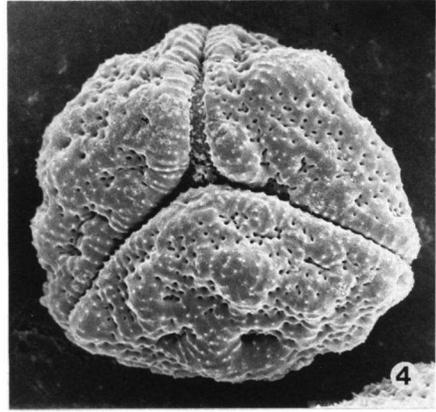
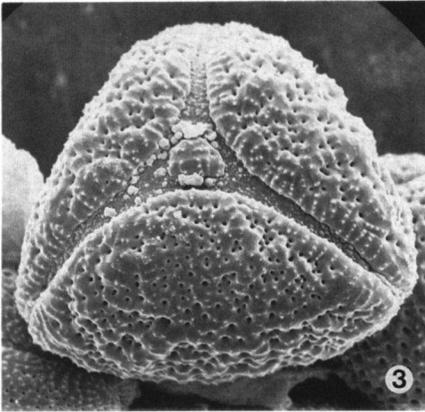
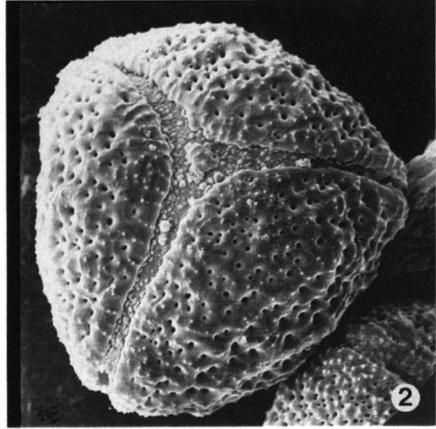
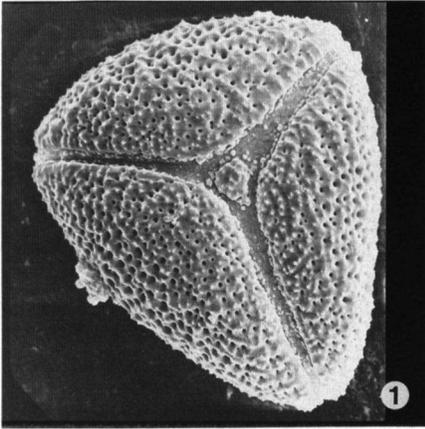


Plate 4 — *Jagera*, pollen, SEM.

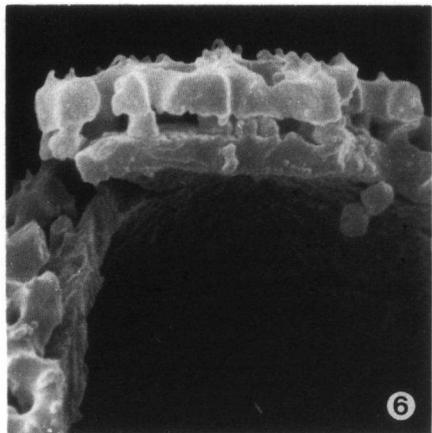
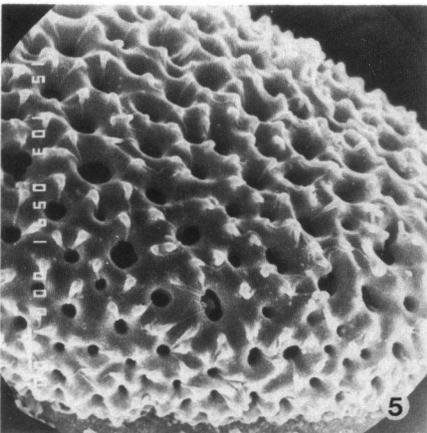
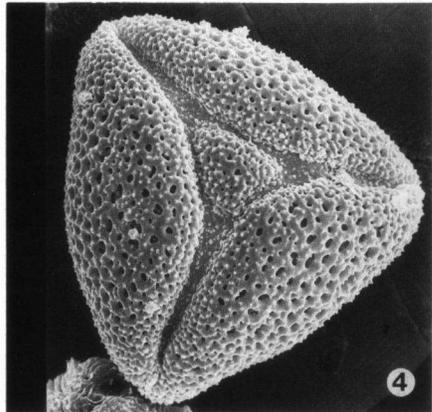
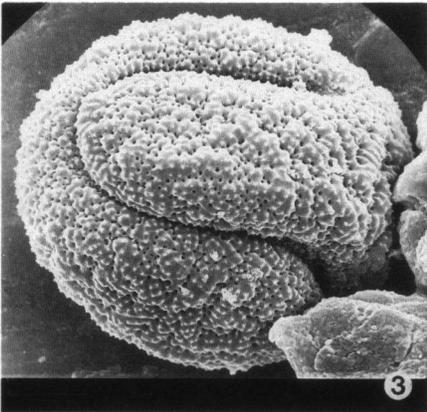
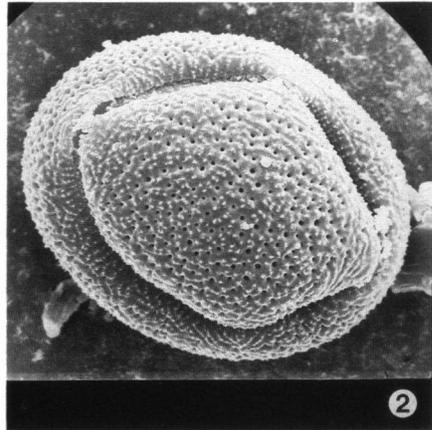
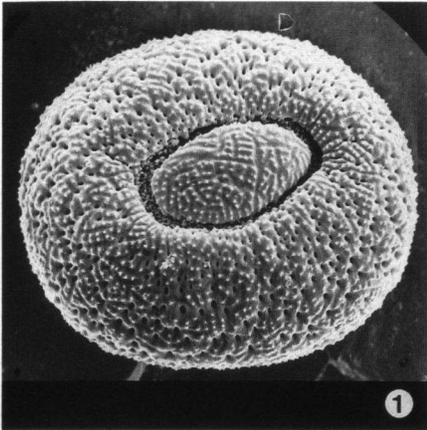


Plate 5 — *Jagera*, pollen, SEM.

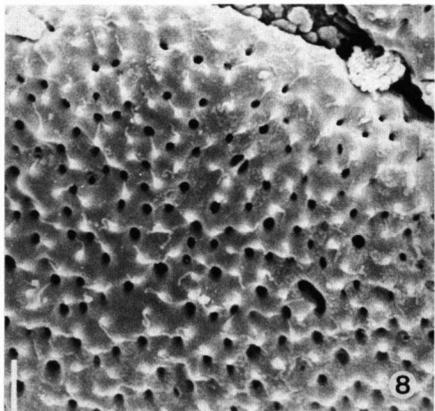
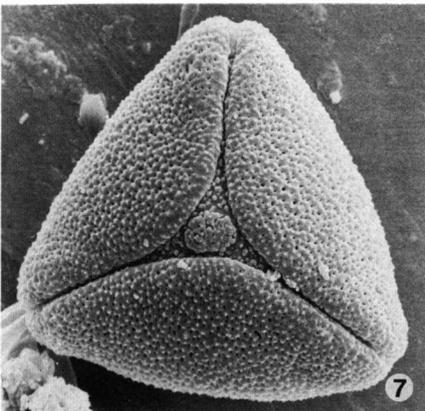
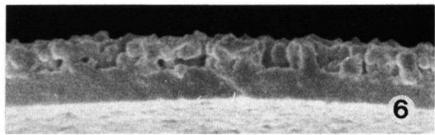
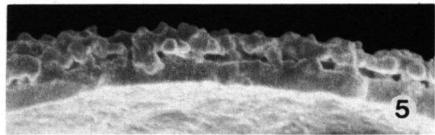
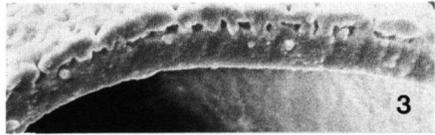
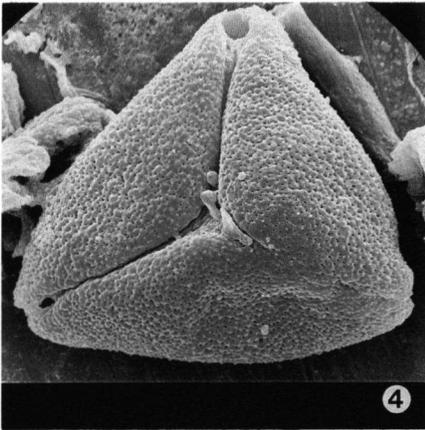
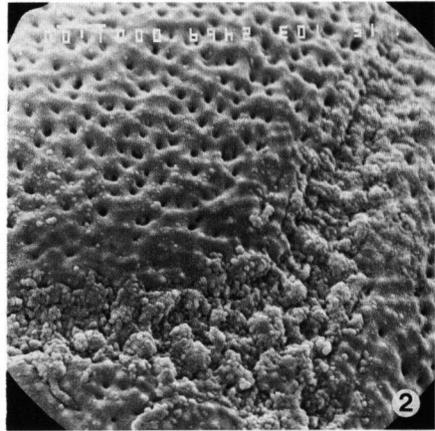
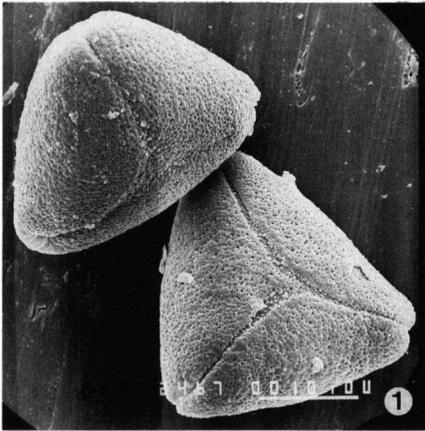


Plate 6 — *Trigonachras*, pollen, SEM.

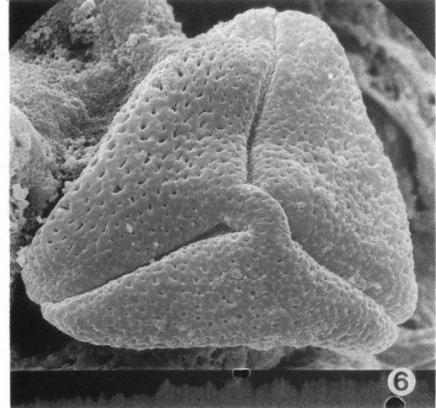
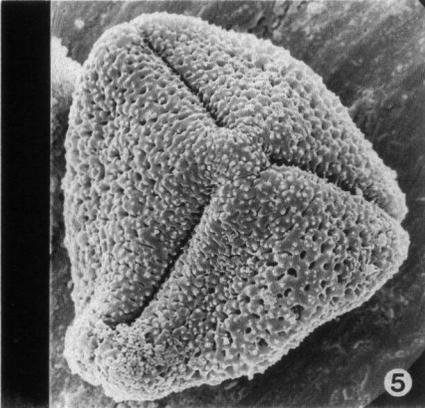
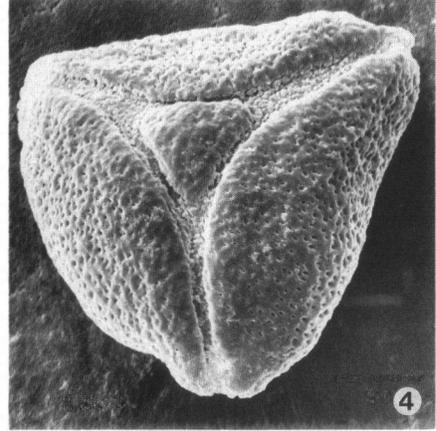
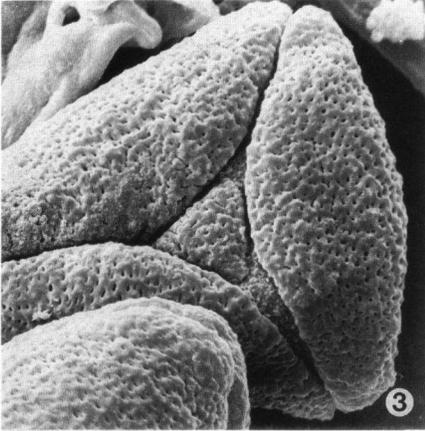
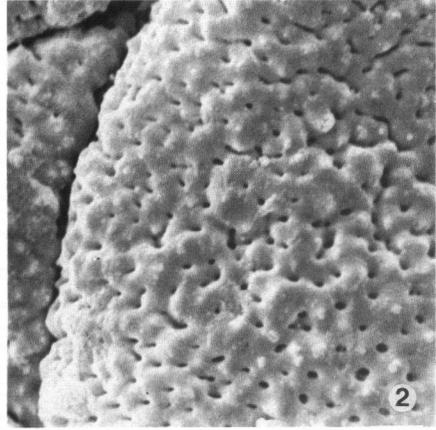
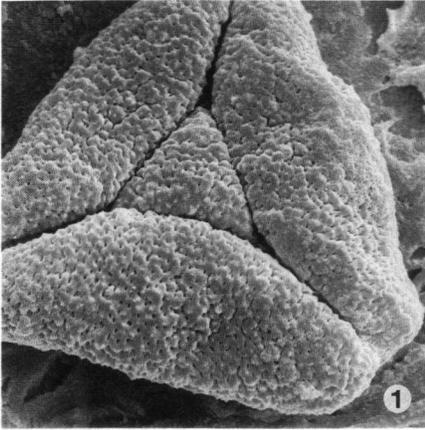


Plate 7 — *Trigonachras*, pollen, SEM.

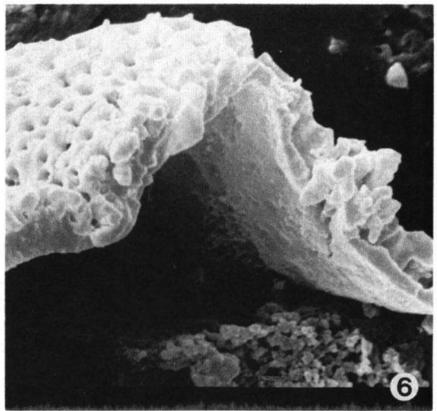
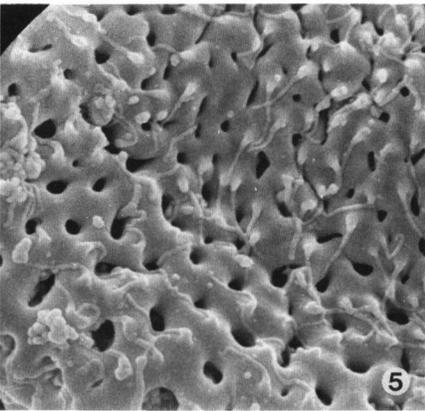
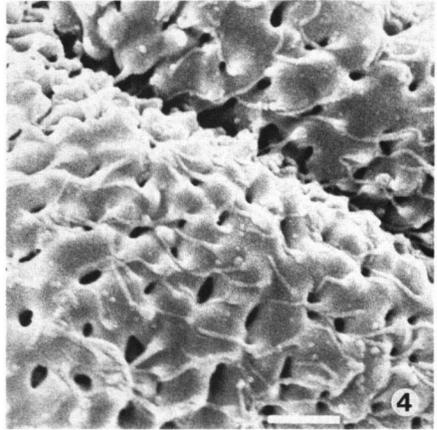
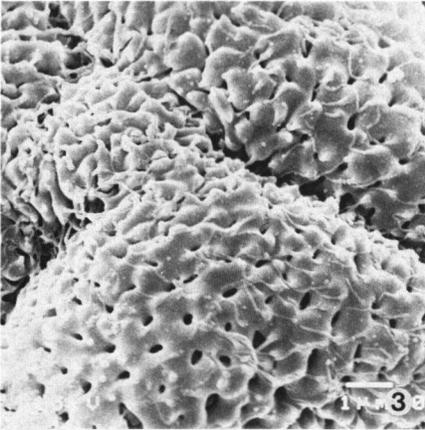
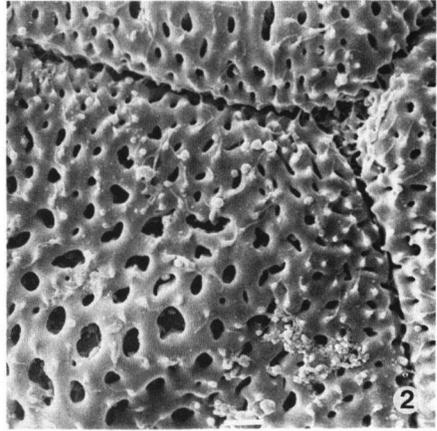
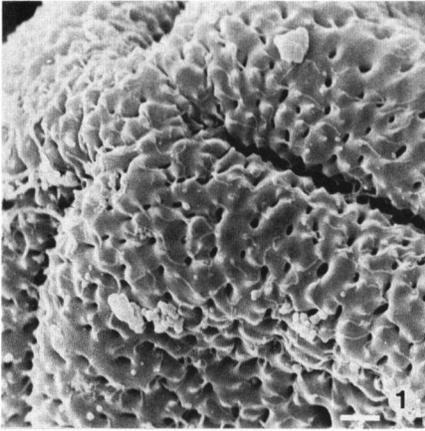


Plate 8 — *Trigonachras*, pollen, SEM.

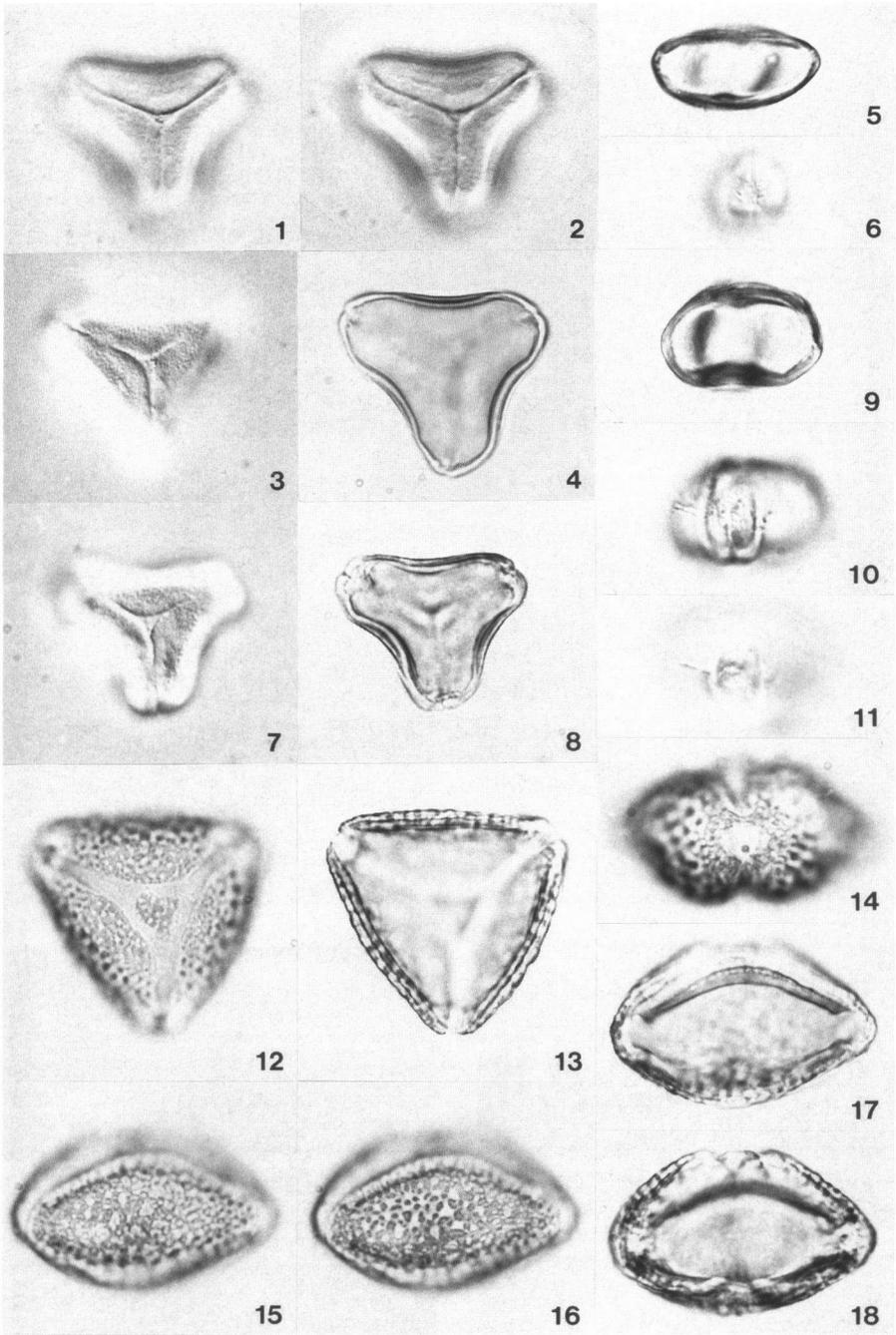


Plate 9 — *Cnesmocarpon, Jagera*, pollen, SEM.

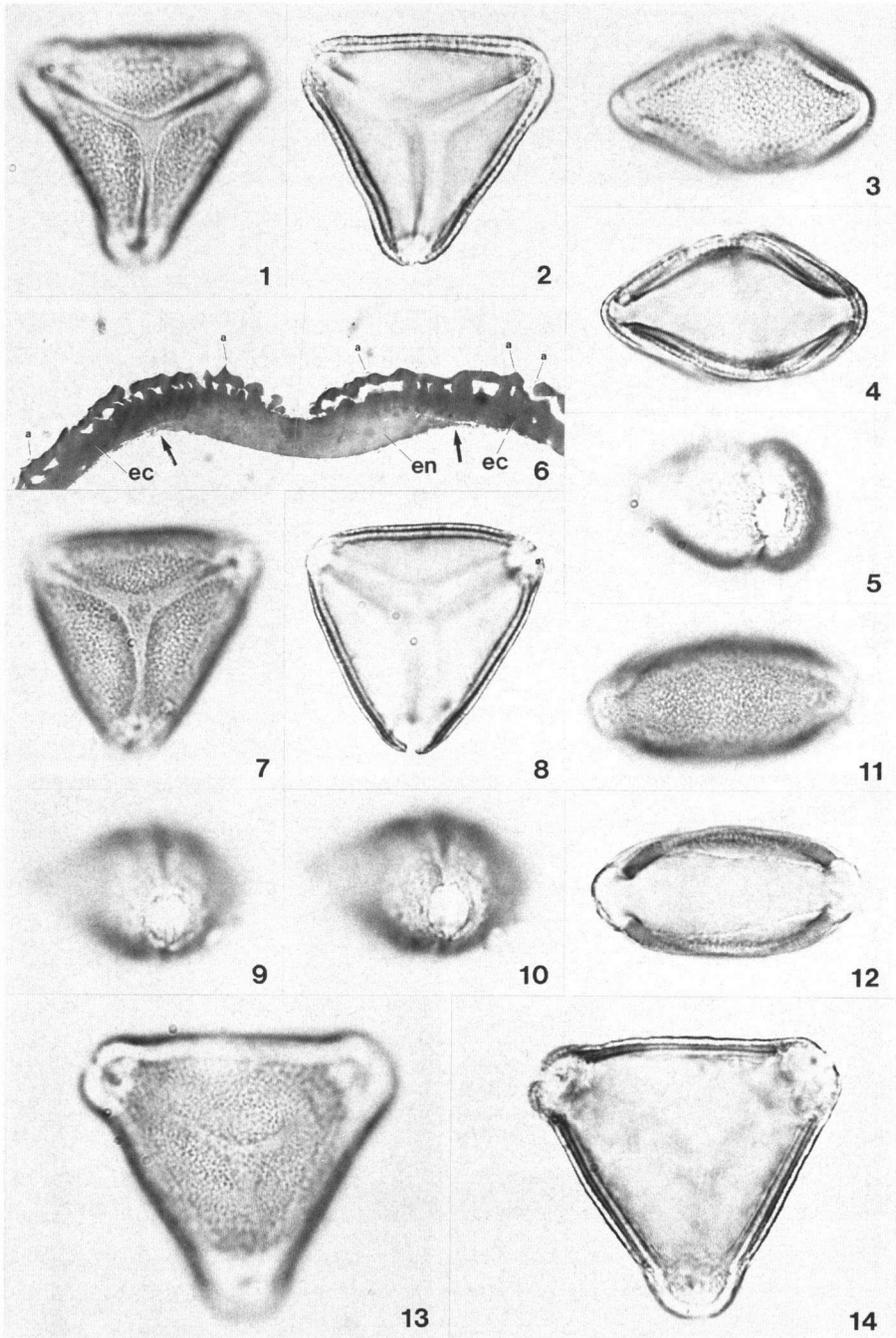


Plate 10 — *Jagera, Trigonachras*, pollen, SEM.

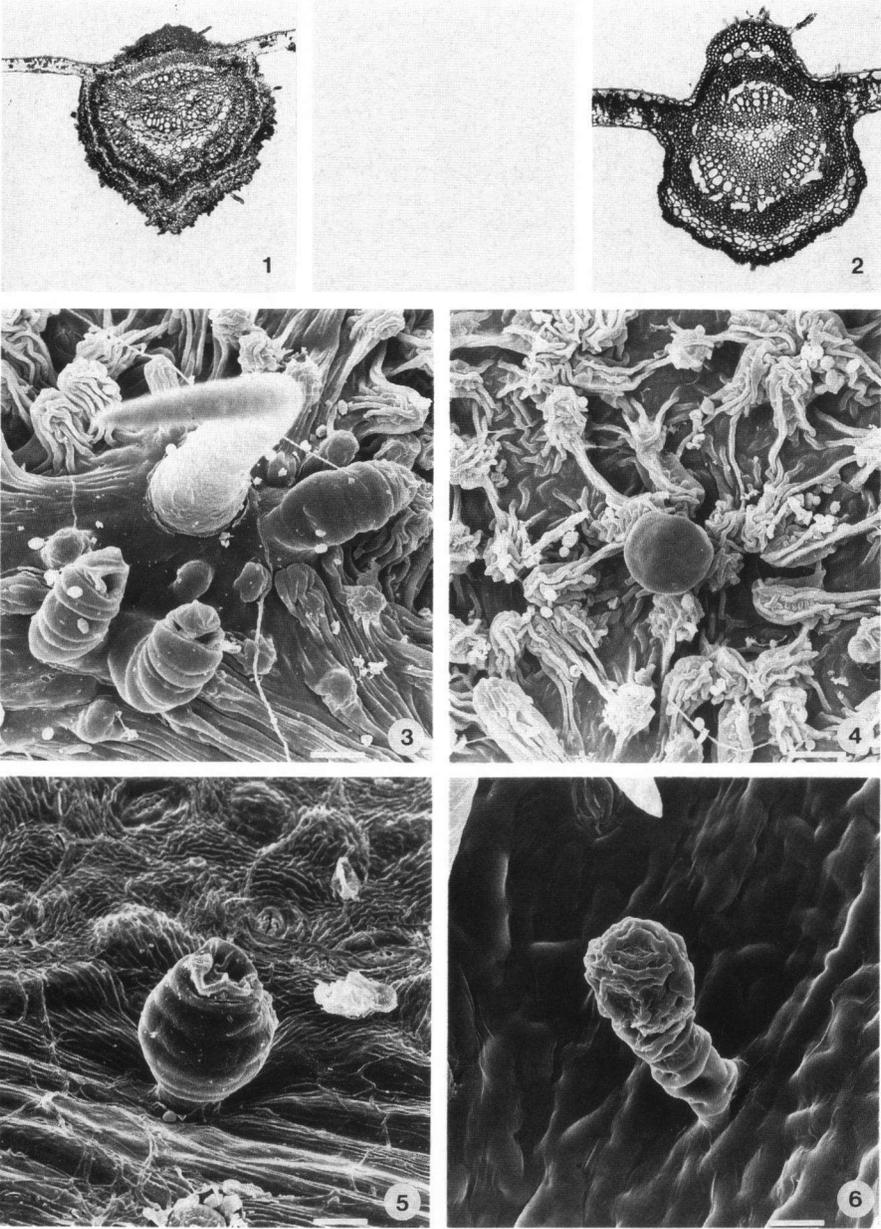


Plate 11 — *Euphorianthus*, *Jagera*, *Cnesmocarpon*, leaf-anatomy; 1, 2: LM; 3–6: SEM.

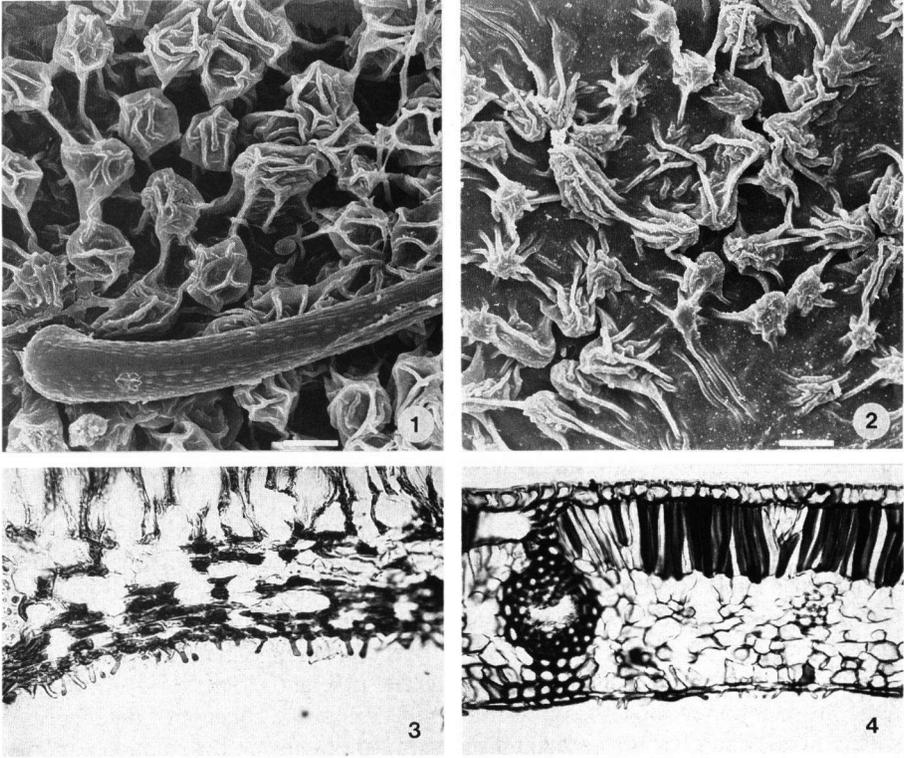


Plate 12 — *Cnesmocarpon*, leaf-anatomy; 1, 2: SEM; 3, 4: LM.