

MUTISIEAE (ASTERACEAE) POLLEN ULTRASTRUCTURE ATLAS

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Abstract: The tribe Mutisieae (excluding Barnadesieae) traditionally comprises 84 genera and approximately 900 species in three subtribes: Gochnatiinae, Mutisiinae, and Nassauviinae. We examined whole and fractured pollen grains of 51 genera from these subtribes by scanning electron microscopy (SEM) and light microscopy (LM). Additionally, we also examined 11 genera (*Adenocaulon*, *Berardia*, *Brachylaeana*, *Cratystylis*, *Dipterocome*, *Eriachaenium*, *Gymnarrhena*, *Hesperomannia*, *Hoplophyllum*, *Tarchonanthus*, and *Warionia*) whose tribal positions have been controversial. We present detailed tables of pollen characters for each taxon and 13 plates of SEM photos of representative taxa. We also provide limited discussion of pollen variation in the subtribes Gochnatiinae, Mutisiinae, and Nassauviinae and the tribal and subfamilial placement of the 11 problematic genera.

Key words: Asteraceae, exine, Gochnatiinae, Mutisieae, Mutisiinae, Nassauviinae, pollen.

The tribe Mutisieae, one of the basal lineages in the Asteraceae (Bremer, 1987, 1994; Jansen and Kim, 1996), is extremely diverse in morphology and biogeography. Classification of the tribe largely began with the system of Bentham (1873), who recognized five subtribes: Barnadesiinae, Onoseriinae, Gochnatiinae, Gerberiinae, and Nassauviinae. Bremer and Jansen (1992) elevated the Barnadesiinae to subfamilial rank as the Barnadesioideae based on both morphological and DNA data. This subfamily is defined by a number of morphological synapomorphies, including the presence of axillary spines and peculiar “barnadesioid” hairs on corollas, achenes and pappus, and a distinctive pollen morphology (Gamerro, 1985; Urtubey, 1997; Urtubey and Telleria, 1998; Zhao et al., 2000). The other three subtribes have been maintained within the heterogeneous tribe Mutisieae until recently when Panero and Funk (2002) elevated several groups to subfamilial and tribal status.

The tribe Mutisieae (excluding Barnadesieae) comprises 84 genera and approxi-

mately 900 species. Most genera of the tribe are from the New World, mainly from Central and South America, while 11 genera are distributed in Africa and Madagascar, and 12 genera in Asia. The tribe has many genera that are monotypic or that have relatively few species occurring in restricted areas that are sometimes completely isolated from their closest relatives. The tribe has very few weedy species and only a few species are cultivated.

Pollen of the Mutisieae has been included in several broad floristic and palynologic studies (Wodehouse, 1929a, b; Carlquist, 1957; Stix, 1960; Askerova, 1970; Heusser, 1971; Skvarla et al., 1966, 1977; Dimon, 1971; Parra and Marticorena, 1972; Crisci, 1974; Markgraf and D’Antonio, 1978; Wigenroth and Heusser, 1983; Moreira et al., 1981; Nair and Lawrence, 1985; Hansen, 1991a, b; Jones et al., 1995; Perveen, 1999; Rull, 2003; Lin et al., 2005), as well in treatments of individual genera. This atlas utilizes SEM (scanning electron microscopy) and LM (light microscopy) to present pollen wall patterns that will be

TABLE 1. Taxon sampling for pollen comparisons. Herbarium acronyms follow Holmgren et al. (1990).

Taxon	Locality	Collector	Herbarium
Mutisieae			
Gochnatiinae			
<i>Achyrothalamus marginatus</i> O. Hoffm	Tanganyika	Tanner 1199	UC
<i>Actinoseris corymbosa</i> (Less.) Cabrera	Argentina	Tressens et al. 3840	GH
<i>Ainsliaea acerifolia</i> Sch.Bip.	Korea	Lee & Lee 657	US
<i>Aphyllocladus</i> sp.	Argentina	Simpson 1-21-86-4	TEX
<i>Chimantaea eriocephala</i> Mag., Steyerm. & Wurdack	Venezuela	Huber 12052	K
<i>C. humilis</i> Mag., Steyerm. & Wurdack	Venezuela	Pruski & Huber 3643	MO
<i>Cnicothamnus lorentzii</i> Griseb.	Bolivia	Smith et al. 13512	GH
<i>Dicoma carbonaria</i> Humbert	Madagascar	Schatz et al. 1772	GH
<i>Erythrocephalum zambesianum</i> Oliver & Hiern.	Malawi	Pawek 5068B	UC
<i>Gladiopappus vernonioides</i> Humb.	Madagascar	Humbert 20526	K
<i>Gochnatia argentina</i> Cabrera	Argentina	Venturi 1553	US
<i>G. curviflora</i> (Griseb.) O. Hoffm.	Bolivia	Smith et al. 13510	US
<i>Hochstetteria schimperi</i> DC.	Saudi Arabia	Collenette 1525	K
<i>Nouelia insignis</i> Franch.	China	Rock 24253	GH
<i>Oldenburgia papionum</i> DC.	South Africa	H. Bolus 402	GH
<i>Onoseris brasiliensis</i> Carb.	Brazil	Hatschbach 34719	UC
<i>Pasaccardoa grantii</i> (Benth. ex Oliver) Kuntze	Zambia	Pope et al. 2153	MO
<i>Pertya glabrescens</i> Sch.Bip.	Japan	Tateishi & Sato 9774	GH
<i>Plazia daphnoides</i> Wedd.	Argentina	Cabrera 22463	K
<i>Pleiotaxis dewevrei</i> O. Hoffm.	Burundensis	Lewalle 1696	UC
<i>Quelchia bracteata</i> Mag., Steyerm. & Wurdack	Bolivia	Huber & Lolella 8678	K
<i>Stenopadus crassifolius</i> Blake	Venezuela	Maguire et al. 30115	GH
<i>Stiffia chrysantha</i> Mikan	Jamaica	Howard et al. 20536	GH
<i>Stomatochaeta condensata</i> (Baker) Mag. & Wurdack	Venezuela	Steyermark 112497	K
<i>Wunderlichia crulsiana</i> Taub.	Brazil	Prance & Silva 58282	NY
Mutisiinae			
<i>Achnopogon virgatus</i> Mag., Steyerm. & Wurdack	Venezuela	Steyermark & Wurdack 681	NY
<i>Chaetanthera elegans</i> Phil.	Chile	Gardner & Knees 4590	UC
<i>C. flabellata</i> D. Don	Chile	Zilner 10658	MO
<i>Chaptalia nutans</i> (L.) Polak.	Mexico	Patterson 7327	TEX
<i>Duidaea marabuacensis</i> Steyerm.	Venezuela	Steyermark et al. 126003	COL
<i>Eurydochus cortesii</i> S. Diaz	Colombia	Barbosa & Madrinan 8396	COL
<i>Gerbera lanuginosa</i> Benth.	India	Koelz 20040	UC
<i>G. linnaei</i> Cass.	India	Werdermann et al. 749	GH
<i>Glossarion rhodanthum</i> Mag. & Wurdack	Venezuela	Boom 5819	K
<i>Guaiacaia glabratus</i> Mag.	Brazil	Maguire 60475	NY
<i>Hyaloseris cinerea</i> Griseb.	Argentina	Bacon 1535	TEX
<i>Leibnitzia seemannii</i> (Sch.Bip.) G. L. Nesom	Mexico	Nesom 4946	TEX
<i>Mutisia acerosa</i> Poepp. ex Less.	Chile	Skog 1091	UC
<i>M. acuminata</i> Ruiz & Pavón	Bolivia	Spooner & Fernandez 6610	TEX

TABLE 1. Continued.

Taxon	Locality	Collector	Herbarium
<i>M. spinosa</i> Ruiz & Pavón	Argentina	King & Heinz 9371	GH
<i>Neblinea promontorium</i> Mag. & Wurdack	Venezuela	Maguire et al. 42296	UC
<i>Pachylaena atriplicifolia</i> D. Don	Argentina	Kiesling 7452	MO
<i>Piloselloides hirsuta</i> (Forssk.) C. Jeffrey	Madagascar	Croat 29410	MO
<i>Trichocline reptans</i> (Wedd.) Rob.	Argentina	Bacon 1510	TEX
Nassauviinae			
<i>Acourtia runcinata</i> D. Don	Mexico	Patterson 6583	TEX
<i>Holocheilus brasiliensis</i> (L.) Cabrera	Caxias Do Sul	Gelain 4771	US
<i>Jungia paniculata</i> (DC.) A. Gray	Peru	Dillon et al. 3180	TEX
<i>Leucheria achillaeifolia</i> Hook. & Arn.	Argentina	Pisano 4177	GR
<i>Lophopappus foliosus</i> Rusby.	Bolivia	Beck 16836	US
<i>Nassauvia axillaris</i> (Lag.) D. Don	Argentina	King & Heinz 9385	US
<i>N. lagascae</i> (D. Don) Hauman	Argentina	Wall 12-22-46	GH
<i>Pamphalea heterophylla</i> Less.	Caxias Do Sul	Wasum 4730	US
<i>Perezia multiflora</i> Less.	Bolivia	Luteyn & Dorr 13812	TEX
<i>Pleocarpus revolutus</i> D. Don	Chile	Norrbom 92ch6	S
<i>Polyachyrus glabratus</i> Phil.	Chile	Hellwig 1671	FH-LS
<i>Proustia cuneifolia</i> D. Don	Bolivia	Torrico & Peca	US
<i>Triptilion spinosum</i> Ruiz & Pavón	Chile	Walker 230	GH
<i>Trixis californica</i> Kellogg	United States	Butterwick & Strong 901	TEX
Tribal Placement Uncertain			
<i>Adenocaulon bicolor</i> Hook.	United States	Heckard 5970	UC
<i>Berardia subacaulis</i> Vill.	France, Italy	Gottingen 6-11-1994	FH-LS
<i>Brachylaena nereifolia</i> R. Br.	Australia	Wilson 8488	KEW
<i>Cratystylis subspinescens</i> S. Moore	South Africa	Goldblatt 12696	NY
<i>Dipterocome pusilla</i> Fisch. & Mey.	Iraq	Rawi 30211	KEW
<i>Eriachaenium</i> sp.	Argentina	Goodall 975	NY
<i>Gymnarrhena micrantha</i> Desf.	Kuwait	Boulos & Cope 17694	KEW
<i>Hesperomannia arborescens</i> A. Gray	Hawaiian Islands	Takeuchi 2206	GH
<i>H. lydgatei</i> C. N. Forbes	Hawaiian Islands	Stauffer & Dehler 5912	UC
<i>Hoplophyllum spinosum</i> DC.	South Africa	Acocks 13216	KEW
<i>Tarchonanthus camphoratus</i> L.	South Africa	Drewe 639	US
<i>Warionia saharae</i> Benth. & Coss.	Morocco	Davis 48679	NY

helpful in: 1) providing a framework for understanding evolutionary history of early branches of the Asteraceae, 2) resolving the relationships among subtribes, and 3) determining the taxonomic placement of some problematic genera.

MATERIALS AND METHODS

Pollen grains of 62 genera (68 species) were examined, 23 genera (25 species) from

Gochnatiinae, 15 genera (19 species) from the Mutisiinae, 13 genera (14 species) from Nassauviinae, and 11 genera (12 species) whose tribal positions are uncertain (Table 1). Pollen was removed from herbarium sheets and acetolyzed according to the method of Erdtman (1960). Preparation for LM and SEM was as described in our previous investigation (Zhao et al., 2000). All measurements are based upon an average of five pollen grains.

TABLE 2. Gochnatiinae.

Taxon	Size (μm)	Shape ¹	Colpus (μm)	Endocolpus (μm)
<i>Achyrothalamus marginatus</i>	37.8 \times 37.8	Sph	25.0 \times 0.8	6.0 \times 9.0
<i>Actinoseris corymbosa</i>	37.6 \times 30.6	SSph	29.5 \times 6.0	6.0 \times 8.0
<i>Ainsliaea acerifolia</i>	33.2 \times 32.0	SSph	24.0 \times 3.0	9.0 \times 13.0
<i>Aphyllocladus</i> sp.	41.6 \times 30.6	Ssph	30.0 \times 3.5	5.0 \times 11.5
<i>Chimantaea eriocephala</i>	48.5 \times 36.0	Pro	39.0 \times 3.0	3.5 \times 12.0
<i>C. humilis</i>	50.5 \times 37.8	Pro	38.0 \times 3.0	3.0 \times 11.0
<i>Cnicothamnus lorentzii</i>	40.0 \times 37.8	SSph	30.0 \times 7.0	4.0 \times 15.0
<i>Dicoma carbonaria</i>	40.5 \times 40.5	Sph	30.0 \times 7.5	2.8 \times 11.8
<i>Erythrocephalum zambesianum</i>	39.0 \times 39.0	Sph	21.5 \times 2.0	2.5 \times 10.0
<i>Gladiopappus vernonioides</i>	40.5 \times 39.5	Sph	28.0 \times 5.0	7.0 \times 14.0
<i>Gochnatia argentina</i>	28.0 \times 27.0	SSph	21.0 \times 4.0	4.0 \times 9.0
<i>G. curviflora</i>	44.6 \times 37.6	SSph	33.0 \times 4.0	4.5 \times 10.0
<i>Hochstetteria schimperi</i>	37.5 \times 31.8	SSph	22.6 \times 3.2	5.3 \times 9.2
<i>Novelia insignis</i>	55.4 \times 45.4	SSph	41.8 \times 4.9	5.5 \times 10.6
<i>Oldenburgia papionum</i>	50.0 \times 50.0	Sph	35.0 \times 8.0	9.5 \times 15.0
<i>Onoseris brasiliensis</i>	43.2 \times 39.0	SSph	36.0 \times 5.0	6.5 \times 10.0
<i>Pasaccardoa grantii</i>	32.3 \times 32.3	Sph	18.5 \times 5.0	6.2 \times 11.2
<i>Pertya glabrescens</i>	36.4 \times 33.8	SSph	23.5 \times 3.0	3.0 \times 7.0
<i>Plazia daphnoides</i>	54.8 \times 45.5	SSph	38.5 \times 7.7	7.8 \times 18.2
<i>Pleiotaxis dewevrei</i>	40.0 \times 40.0	SSph	23.0 \times 3.0	5.0 \times 8.5
<i>Quelchia bracteata</i>	42.0 \times 35.3	SSph	26.0 \times 8.0	8.0 \times 10.0
<i>Stenopadus crassifolus</i>	45.0 \times 33.6	Pro	35.0 \times 3.0	3.0 \times 9.0
<i>Stiffitia chrysantha</i>	60.0 \times 48.5	SSph	45.0 \times 5.0	4.0 \times 10.0
<i>Stomatochaeta condensata</i>	48.6 \times 35.7	Pro	42.8 \times 4.6	6.9 \times 13.8
<i>Wunderlichia crulsiana</i>	53.7 \times 52.0	SSph	40.0 \times 5.0	6.0 \times 14.0

1 - Sph = spheroidal; SSph = subspheroidal; Pro = prolate

2 - Spinate = spine height $> 1 \mu\text{m}$; spinose = spine height $< 1 \mu\text{m}$

3 - thickness measured at equator

4 - 1L, single layer of columellae (usually distally branched as in Figs. 12i, k and in Marticorena and Parra, (1975); P = D, proximal (basal) columellae layer equal in height to distal (upper) columellae layer; P>D, proximal (basal) columellae greater in height than distal (upper) columellae layer(s); P<D, distal (upper) columellae layer(s) greater in height than proximal (basal) columellae layer; ML, possibly more than one columellae layer above proximal (basal) columellae; +, observation confirmed; ?, observation not confirmed but problematic; -----, data not available; *, data supplemented from reference citations to extend morphological parameters. In rows where there are more than one symbol, for example: ? ?; + + ?; or other combinations, the height of the proximal and distal columellae vary according to where on the exine the observation was taken. Fig. 1f, of *Ainsliaea acerifolia*, is an example of a fracture made at a colpal margin. In equatorial regions of *A. acerifolia* the proximal and distal columellae are either equal or slightly variable in heights (Telleria and Katinas 2005). Under spine areas the distal columellae will appear longer than under the exine surface away from spine areas (see Stix 1960 and Roque and Silvestre-Capelato, 2001 for excellent illustrations of how these difference in height can be explained).

RESULTS AND DISCUSSION

Tables 2–5 summarize various features of the pollen of the 62 genera examined and

constitute an extension of those typical palynological features (size, shape, exine thickness, etc.) used in other studies of the Mutisieae. They are supplemented by SEMs

TABLE 2. Continued.

Surface ²	Spine (μm) H × W	Exine (μm) ³	Nexine (μm)	1L	Columellae ⁴			ML	Figure Citations
					P=D	P>D	P<D		
Spinate	3.5 × 6.0	5.0	1.2			+		+	1a,b
Spinate	1.0 × 4.0	4.0	1.0			+			1c,d
Spinate	1.0 × 4.0	3.5	0.5		*	?	?		1e,f
Spinate	1.0 × 4.0	5.5	1.5			+		?	1g,h
Spinose	0.4 × 1.5	4.0	1.0		?	?			1i,j
Spinose	0.7 × 1.5	5.2	1.6		-----				1k,L
Spinate	1.0 × 2.2	4.5	1.5			+		?	2a-c
Spinate	2.2 × 5.0	5.2	1.2			+			2d-f
Spinate	3.0 × 5.0	8.0	3.0			*	?	?	2g,h
Spinate	2.5 × 5.0	7.2	2.0			+		?	2i-k
Spinose	0.3 × 0.7	2.5	0.8		+	?			2L,3a
Spinate	1.0 × 2.5	5.5	1.2			+		?	3b
Spinate	2.2 × 4.2	--	--			+		+	3c
Spinose	0.5 × 1.8	5.3	1.3		+		?	?	3d,e
Spinate	1.5 × 3.5	7.5	2.0			+		+	3f-h
Spinose	0.6 × 1.5	7.8	2.8			+		?	3i,j
Spinate	1.3 × 3.0	4.8	1.5			+		+	3k,L
Spinose	0.7 × 2.0	3.0	0.6		+				4a,b
Spinose	0.6 × 1.3	5.5	1.5		?	+		+	4c,d
Spinose	0.7 × 2.0	--	--		+				4e,f
Spinate	1.2 × 4.0	4.6	1.0		?	+		+	4g,h
Spinose	.35 × 0.7	2.5	0.6		+	+			4i,j
Spinose	0.4 × 1.5	6.4	0.8		+	+	?	+	4k,L
Spinose	0.2 × 0.5	--	--			+			5a
Spinate	2.5 × 3.5	5.0	1.0			+			5b-d

of fractured surfaces through the pollen wall. Figures 1–11 illustrate SEM photos of representative species from the subtribes Gochnatiinae, Mutisiinae, and Nassauviinae of the Mutisieae. Whole pollen grains are depicted in SEM, primarily in equatorial (apertural or side) view and general shape parameters were determined from this orientation with light microscopy. However, depending upon conditions under which the measurements were taken (e.g., dry or rehydrated pollen removed from herbarium sheets, acetolyzed pollen, pollen in the vacuum of the SEM, etc.), overall shape may vary with results from other studies. Polar and partial polar views are indicated in Figures 1e (*Ainsliaea*), 1L (*Chimantaea*), 2b (*Cnicothamnus*), 2L (*Gochnatia*), 3g (*Oldenburgia*), 4e (*Pleiotaxis*), 5c (*Wunderlichia*), and 7e (*Mutisia*). With fractured

grains an attempt was made to standardize the area of SEM photography in order to describe with consistency the heights of the proximal and distal columellae. This was essentially at the midpoint on the equatorial surface. When fractured walls are examined in different areas such as near aperture regions, heights become greatly skewed (see as examples Figs. 1f of *Ainsliaea acerifolia* with an explanation in table legend and Fig. 2g of *Gochnatia* in Roque and Silvestre-Capelato, 2001).

Lastly, on Figs. 11–13 and in Table 5 we present pollen SEMs and data, as well as brief discussions of some taxa of uncertain tribal position (Table 1).

With the possible exception of the Vernonieae, pollen of Mutisieae has been the most intensively investigated of all Compositae tribes. Given that this paper is an

TABLE 3. Mutisiinae. See footnotes at bottom of Table 2.

Taxon	Size (μm)	Shape ¹	Colpus (μm)	Endocolpus (μm)
<i>Achnopogon virgatus</i>	46.2 × 40.5	SSph	27.0 × 6.5	6.2 × 9.5
<i>Chaetanthera elegans</i>	54.2 × 34.3	Pro	45.0 × 3.4	3.5 × 7.5
<i>C. flabellata</i>	51.0 × 35.7	Pro	40.2 × 3.6	3.8 × 8.5
<i>Chaptalia nutans</i>	33.2 × 25.0	SSph	24.0 × 2.6	3.1 × 6.8
<i>Duidaea marabuacensis</i>	57.2 × 53.5	SSph	42.0 × 13.0	7.6 × 13.4
<i>Eurydochus cortesii</i>	63.2 × 52.6	SSph	45.5 × 6.1	3.0 × 11.0
<i>Gerbera lanuginosa</i>	46.2 × 37.7	SSph	35.5 × 3.0	4.2 × 8.5
<i>G. linnaei</i>	48.1 × 40.5	SSph	36.3 × 2.8	7.2 × 11.8
<i>Glossarion rhodanthum</i>	54.7 × 52.6	SSph	45.2 × 7.9	6.6 × 13.6
<i>Guaiacacia glabratus</i>	57.3 × 49.1	SSph	42.7 × 9.2	7.3 × 15.3
<i>Hyaloseris cinerea</i>	45.5 × 40.9	SSph	35.5 × 2.8	3.8 × 8.8
<i>Leibnitzia seemannii</i>	30.2 × 25.3	SSph	23.6 × 3.6	3.7 × 7.2
<i>Mutisia acerosa</i>	52.7 × 52.7	SSph	40.9 × 7.8	6.8 × 14.5
<i>M. acuminata</i>	58.3 × 45.8	SSph	47.6 × 5.4	6.9 × 13.2
<i>M. spinosa</i>	48.3 × 38.2	SSph	39.2 × 5.8	7.5 × 13.5
<i>Neblinaea promontorium</i>	46.9 × 41.5	SSph	38.0 × 7.0	4.5 × 13.0
<i>Pachylaena atriplicifolia</i>	43.3 × 37.3	SSph	29.5 × 4.0	6.6 × 13.3
<i>Piloselloides hirsuta</i>	32.4 × 28.2	SSph	25.3 × 5.2	5.5 × 11.6
<i>Tricholine reptans</i>	42.5 × 29.4	Pro	32.5 × 2.8	5.6 × 10.2

atlas of Mutisieae pollen we do not discuss in the details the pollen morphology in detail. However, in concert with Tables 2–4 we provide below overall summaries of some of the more outstanding morphological characteristics of each subtribe.

GOCHNATIINAE. In addition to references provided earlier, pollen of the Mutisieae has been examined by Barroso and Maquire, 1973; Marticorena and Parra, 1974; Moreira et al., 1981; Robinson, 1991; Chissoe et al., 1994; Ortiz and Coutinho, 2001; Roque and Silvestre-Capelato, 2001; Sancho et al., 2005; Rodriguez et al., 2004; and Telleria and Katinas, 2005. Spines, while not prominently developed in any of the three subtribes of Mutisieae, are best expressed in the Gochnatiinae. Most taxa are considered as barely spinate (ca. 1 μm in height and most favorably viewed by light microscopy) loosely following the terminology of Erdtman (1952). The largest spines occur on pollen of *Achyrothalamus* (Figs. 1a, 1b; Ortiz and Coutinho, 2001), *Erythrocephalum* (Figs. 2g, 2h), *Hochstetteria* (Fig. 3c) and *Wunderlichia* (Figs. 5b, 5c; Wodehouse,

1929a). Spines in these taxa also have comparatively wide bases where they unite with their respective exine surfaces.

Columellae structure, as viewed in fractured sections by SEM, always shows at least two levels (layers) with each separated by a horizontal, often not clearly defined, internal tectum layer (Skvarla and Turner, 1966; Skvarla et al., 1977). Multilevel columellae are characteristic of all three Mutisieae subtribes, and to our knowledge, all pollen studies in the tribe, without exception, support this observation. As indicated in Table 2, in most taxa the proximal columellae are greater in height than the distal columellae immediately beneath the exine surface. The exceptions appear to be in *Gochnatia argentina*, *Nouelia*, *Pertya*, *Pleiotaxis*, *Stenopadus* and *Stiffitia* where proximal and distal columellae are approximately equal. However, as indicated in Table 2 (as well as in Tables 3 and 4) it is difficult to calculate these parameters precisely. These parameters are even more difficult to calculate when the distal columellae appear to greatly ramify such as in *Old-*

TABLE 3. Continued.

Surface ²	Spine (μm) H \times W	Exine (μm) ³	Nexine (μm)	1L	P=D	Columellae ⁴		ML	Figure Citations
						P>D	P<D		
Spinose	0.9 \times 2.2	8.0	1.2			+		?	5e,f
Spinose	0.5 \times 1.4	11	1.2			+			5g,h
Spinose	0.3 \times 0.8	8.5	1.5			+			5i,j
Spinose	0.3 \times 0.7	4.2	0.5		?	+			5k,L
Spinose	0.8 \times 1.9	7.5	1.2			+		+	6a,b
Spinose	1.4 \times 3.1	6.5	1.4			+	?	+	6c,d
Spinose	0.3 \times 0.8	5.3	0.8		?	+			6e,f
Spinose	0.3 \times 0.5	7.1	1.5			+			6g,h
Spinose	1.4 \times 2.5	8.3	2.1		+				6i,j
Spinose	0.3 \times 1.2	5.8	1.2				+	?	6k,L
Spinose	0.4 \times 0.9	5.0	1.2			-			7a,b
Spinose	0.35 \times 0.7	3.5	0.6			+			7c,d
Spinose	0.6 \times 1.8	5.5	0.9			+			7e,f
Spinose	0.7 \times 2.2	8.1	1.2						7g
Spinose	0.6 \times 2.0	7.7	1.4			+	?		7h
Spinose	0.7 \times 2.5	--	--			+			7i
Spinose	0.6 \times 1.4	6.2	1.5			+			7j
Spinose	0.4 \times 0.9	5.5	1.5						7k
Spinose	0.4 \times 0.9	5.6	1.4			+		+	7L,8a

enburgia (Fig. 3h) and other taxa designated with "ML."

A columellae character not taken into consideration in this atlas format, and one possibly of significance in a more detailed SEM study, is the thickness of the columellae. Frequently, the proximal and distal columellae appear to be equal in thickness or often, the proximal columellae are thicker (wider) than the distal columellae. Sometimes, proximal columellae thickness appears to be highly exaggerated (i.e., extremely thickened) as illustrated by *Nouelia* (Fig. 3e), perhaps of importance beyond the scope of this report.

Yet another characteristic of potential importance in a more in depth study is that of exine surface texture. In general, in the Gochnatiinae the exine surface of at least some pollen grains appears to be more perforated (see for example *Achyrothalamus*, Fig. 1a and *Erythrocephalum*, Figs. 2d, 2f) than in Mutisiinae and Nassuviinae.

MUTISIINAE. This subtribe has been studied by Erdtman, 1952; Southworth,

1966, 1983; Telleria and Katinas, 2004; and Telleria and Forcone, 2002, as well as by workers cited earlier. Pollen size is greatest in Mutisiinae, although only slightly more so than in the Gochnatiinae. With the exceptions of *Eurydochus* (Figs. 6c, 6d) and *Glossarion* (Figs. 6i, 6j) the surface is spinose (spines less than 1 μm in height). Height of the proximal columellae is greatest in this subtribe and reaches considerable length in genera such as *Chaetanthera* (Figs. 5h, 5j), *Gerbera* (Figs. 6h), *Hyaloseris* (Fig. 7b), and *Mutisia* (Fig. 7f). Columellae thickness (width) is comparatively less variable than in Gochnatiinae with the proximal columellae always thicker than the distal columellae. The most recent study of the Mutisiinae clearly indicated that infrageneric pollen morphology was uniform and that species within genera were usually similar to each other (Lin et al., 2005).

NASSAUVIINAE. Pollen of this subtribe was studied extensively by Wodehouse, 1929b; Hernandez, 1966; Crisci, 1971a, 1971b, 1974, 1976; Crisci and Marticorena,

TABLE 4. Nassuviinae. See footnotes at bottom of Table 2.

Taxon	Size (μm)	Shape ¹	Colpus (μm)	Endocolpus (μm)
<i>Acourtia runcinata</i>	35.5 × 32.6	SSph	32.5 × 2.8	3.4 × 6.2
<i>Holochelus brasiliensis</i>	28.2 × 24.3	SSph	22.2 × 2.5	3.9 × 6.8
<i>Jungia paniculata</i>	24.1 × 20.2	Sph	19.2 × 2.2	2.5 × 4.8
<i>Leucheria achillaeifolia</i>	23.0 × 20.0	SSph	18.3 × 2.5	3.3 × 5.2
<i>Lophopappus foliosus</i>	31.2 × 28.3	SSph	28.7 × 2.1	3.7 × 8.2
<i>Nassauvia axillaris</i>	20.8 × 20.2	Sph	16.8 × 1.8	1.7 × 3.2
<i>N. lagascae</i>	18.6 × 18.6	Sph	13.6 × 2.0	2.2 × 4.6
<i>Pamphalea heterophylla</i>	18.4 × 18.3	Sph	16.3 × 2.5	2.8 × 5.4
<i>Perezia multiflora</i>	24.7 × 24.4	Sph	19.2 × 4.8	4.5 × 9.2
<i>Pleocarpus revolutus</i>	32.7 × 27.8	SSph	27.2 × 1.8	3.3 × 6.1
<i>Polyachyrus glabratus</i>	28.9 × 28.9	Sph	24.7 × 3.2	2.6 × 4.6
<i>Proustia cuneifolia</i>	31.8 × 30.8	Sph	25.5 × 2.2	3.3 × 7.1
<i>Triptilion spinosum</i>	17.0 × 19.2	SSph	16.7 × 2.3	1.7 × 4.8
<i>Trixis californica</i>	35.5 × 21.0	Pro	28.5 × 1.5	2.5 × 7.2

1978; Fagundez, 2003; Cabrera and Dieringer, 2003; and Telleria et al., 2003 (also see earlier cited references). Of the three subtribes, pollen size is clearly the smallest in Nassauviinae (Wodehouse, 1929b). Furthermore, all pollen is spinose. These characters of small size and spinose surface were key in leading Wodehouse (1929b) to distinguish this subtribe from the Gochnatiinae and Mutisiinae. In Nassauviinae there tend to be more columellae with proximal and distal segments equal than in the Gochnatiinae and Mutisiinae, although, like these two subtribes the most dominant feature is that the height of proximal columellae is greater than the distal columellae. Crisci (1974) indicated several possible variations in heights of proximal and distal columellae and Cabrera and Dieringer (2003) clearly showed in various species of *Acourtia* differences in the heights of the proximal and distal columellae and established types on this basis. Telleria et al. (2003) indicated that exine types, also based on differences in heights of proximal and distal columellae, overlap in the Gochnatiinae and Mutisiinae. In contrast, Nassauviinae has distinct types not noted in these other subtribes. While not quantitatively measured, the overall height of

columellae in this subtribe appears to be shorter than in Gochnatiinae and Mutisiinae. Further, thickness of the proximal and distal columellae is often approximately equal. The internal tectum layer in the Nassauviinae is considerably better developed than in either of the other subtribes, often distinctly demarcating proximal and distal columellae.

TAXA OF UNCERTAIN TRIBAL PLACEMENT

Adenocaulon. This genus has been positioned in four different tribes: Heliantheae (Bentham, 1873), Inuleae (Hoffmann, 1890), Senecioneae (Cronquist, 1955) and Mutisieae (Ornduff et al., 1967; Grau, 1980; Bittmann, 1990; Kim et al., 1998). Some features, particularly the rather deeply lobed, sometimes bilabiate corolla and the calcarate anthers, contradict a position within any of the asteroid tribes, and the testa epidermis (Grau, 1980) is consistent with a relationship to the Mutisieae. Hansen (1991a) did not include *Adenocaulon* in the Mutisieae because it had several features that are unknown in the group. These include: 5 or 4-lobed florets with rigid, short

TABLE 4. Continued.

Surface ²	Spine (μm) H × W	Exine (μm) ³	Nexine (μm)	1L	P=D	Columellae ⁴			ML	Figure Citations [•]
						P>D	P<D			
Spinose	0.5 × 0.7	3.9	1.1		+					8b–d
Spinose	0.3 × 0.9	3.7	0.9		?	?				8e–g
Spinose	0.3 × 0.5	2.5	0.4			+				8h–j
Spinose	0.5 × 0.7	2.4	0.4			+				8k,L,9a
Spinose	0.3 × 0.5	6.1	0.9		?	+				9b–d
Spinose	0.3 × 0.5	3.6	0.5			+				9e–g
Spinose	0.3 × 0.5	2.7	0.6		+					9h,i
Spinose	0.4 × 0.8	2.0	0.3		+					9j–L
Spinose	0.3 × 0.4	3.2	0.4		+					10a–c
Spinose	0.4 × 0.8	4.8	0.8			+				10d–f
Spinose	0.2 × 0.4	2.9	0.7		?	+				10g–i
Spinose	0.2 × 0.3	4.5	0.7		+		?			10j–L
Spinose	0.2 × 0.3	2.6	0.4	-----						11a–c
Spinose	0.3 × 0.5	2.8	0.7			+				11d–f

petals; very widened styles; club-shaped achenes; anthers with minute tails; petals and styles indistinctly hairy; and an involucre of very few bracts. Kim et al. (1998) placed *Adenocaulon* in the Nassauviinae based on sequences of the chloroplast gene *ndhF*. All of the pollen characters described for this genus (Stix, 1960; Liens, 1969; Heusser, 1971; Skvarla et al., 1977) are consistent with its placement in the Nassauviinae (Figs. 11g, 11h; Tables 4–5).

Berardia. Following Bentham (1873) and Hoffman (1890), Grau (1980) also favored a position of *Berardia* within the Mutisieae. Hansen (1991a) excluded the genus from the Mutisieae in his review of the tribe. Karis et al. (1992) placed *Berardia* near the genus *Carlina* in the Cardueae. Bremer (1994) also accepted *Berardia* in the Cardueae, but did not assign it to any particular subtribe. More recently a supertree of the Asteraceae clearly positioned *Berardia* with the Cardueae (Funk et al., 2005). Our pollen data is insufficient (Table 5; Figs. 11i, 11j) but the large spines and coarsely granulate exine surface do not favor a position within Mutisieae.

Brachylaena and *Tarchonanthus*. Pollen morphology has been examined by several workers including Erdtman (1952), Liens

(1969), Skvarla et al. (1977) and Cilliers (1991) and is described in Table 5 and Figs. 11k, 13b, 13c. The uniform and equal lengths of the proximal and distal columellae resemble Nassauviinae of the Mutisieae. A cpDNA restriction site analysis indicated that these two genera form the distinct tribe Tarchonantheae at or near the base of the subfamily Cichorioideae (Keeley and Jansen, 1991). This tribe, along with the Cardueae and Dicomeae, is now placed in the subfamily Carduoideae (Panero and Funk, 2002; Funk et al., 2005).

Cratystylis. This genus was unassigned to a tribe in the subfamily Cichorioideae by Bremer (1994). A phylogenetic analysis based on morphological and phytochemical data also concluded that the genus represents an isolated lineage within the Cichorioideae (Anderberg et al., 1992). The unique pollen morphology (Anderberg et al., 1992; Table 5; Figs. 11L, 12a), characterized by the single but complex columellae layer (Fig. 12a) removes it from a position in the Mutisieae and more closely places it in a tribe such as Inuleae. However, a recent molecular phylogeny based on three cpDNA markers provided strong support for the placement of *Cratystylis* in

TABLE 5. Taxa with uncertain tribal placement. See footnotes at bottom of Table 2.

Taxon	Size (μm)	Shape ¹	Colpus (μm)	Endocolpus (μm)
<i>Adenocaulon bicolor</i>	26.5 × 25.5	Sph	21.0 × 2.5	3.9 × 7.3
<i>Berardia subacaulis</i>	45.5 × 45.5	Sph	28.2 × 5.2	8.5 × 11.3
<i>Brachylaena neriifolia</i>	27.3 × 25.2	SSph	18.0 × 3.1	2.0 × 6.2
<i>Cratystylis subspinescens</i>	36.7 × 36.7	Sph	23.3 × 5.2	6.3 × 10.2
<i>Dipterocome pusilla</i>	25.0 × 25.0	Sph	18.2 × 4.1	4.0 × 9.3
<i>Eriachaenium</i> sp.	35.5 × 24.4	Pro	25.8 × 2.1	4.5 × 6.4
<i>Gymnarrhena micrantha</i>	32.5 × 32.5	Sph	21.8 × 3.8	4.1 × 9.0
<i>Hesperomannia arborescens</i>	42.0 × 42.0	Sph	30.0 × 2.5	2.5 × 7.0
<i>H. lydgatei</i>	44.0 × 44.0	Sph	34.0 × 2.8	3.0 × 8.0
<i>Hoplophyllum spinosum</i>	40.5 × 43.8	Sph	25.4 × 6.2	7.3 × 13.8
<i>Tarchonanthus camphoratus</i>	28.6 × 26.5	SSph	22.5 × 2.7	3.5 × 7.2
<i>Warionia saharae</i>	60.0 × 60.0	Sph	33.0 × 5.0	5.0 × 9.0

the tribe Plucheeae of the subfamily Aster-
oideae (Bayer and Cross, 2003).

Dipterocome. This is a monotypic genus
that Bremer (1987) placed in the Mutisieae
(following work of Praglowski and Graf-
strom, 1980). Pollen morphology (Table 5),
especially prominent spines and question-
able second level of columellae (Fig. 12c),
suggests that *Diptercome* is not related to
any examined members of the Mutisieae.

Eriachaenium. This Patagonian genus
was originally positioned in the primarily
African tribe Calenduleae. However, no
characters were provided supporting its re-
lationships to this tribe, although the very
short style branches may have contributed
to this placement. *Eriachaenium* was trans-
ferred to the Inuleae-Adenocauliinae by Ca-
brera (1961). No explanation was given for
this placement, although certain features
such as caudate anthers and wooly pubes-
cence of the leaves and flowers give the ge-
nus a superficial resemblance to the Inuleae.
In contrast, Merxmuller et al. (1977) ex-
cluded it from the Inuleae. Hansen (1991a)
noted that *Eriachaenium* has the mutisoid
epidermal pattern of the corollas and sug-
gested that it may belong to the subtribe
Nassauviinae. Our SEM (Figs. 12d, 12e; Ta-
ble 5) suggests possible placement in the
Mutisiinae.

Gymnarrhena. This genus has been

classified in the Inuleae because of the sim-
ilarity of its habit to that of *Geigeria* of the
same tribe (Bentham, 1873). Bremer (1994)
classified the genus in the subfamily Cicho-
rioideae but did not assign it to any tribe.
Panero and Funk (2002) placed *Gymnar-
rhena* in a monotypic tribe and subfamily
that is sister to a large clade including Ci-
chorioideae, Corymboideae, and Astero-
ideae. *Gymnarrhena* pollen, as noted else-
where (Skvarla et al., 1977), is difficult to
place but it does not suggest Mutisieae. The
multilevel columellae (Table 5; Fig. 12g) are
found in the Mutisieae but also elsewhere
(for example, Anthemideae and Cardueae)
and the distinctly spinate surface (Fig. 12f)
is rare, if at all present in Mutisieae.

Hesperomannia. This genus is endemic
to the Hawaiian Islands, and was placed in
the Gochnatiinae by Cabrera (1977). Mar-
ticorena and Parra (1975) suggested that
the pollen morphology (along with *Moqui-
nia*) indicated that it was isolated within the
Mutisieae. Our SEMs (Figs. 12h–k) of pol-
len of *H. arborescens* and *H. lydgatei*, par-
ticularly, fractured sections (Figs. 12i, 12k),
strongly support a position within the Ver-
nonieae. This conclusion is based on a sin-
gle columellae layer that is distally highly
branched. Recent DNA studies (Kim et al.,
1998) positioned the genus within Vernoni-
aeae and indicated that it was closely allied

TABLE 5. Continued.

Surface ²	Spine (μm) H × W	Exine (μm) ³	Nexine (μm)	1L	P=D	Columellae ⁴			ML	Figure Citations
						P>D	P<D			
Spinose	0.8 × 1.0	3.2	0.8			+				11g,h
Spinate	3.8 × 8.5	--	--			*				11i,j
Spinose	0.5 × 0.5	--	--							11k
Spinate	4.5 × 4.5	2.0	0.5	?,*						11L,12a
Spinate	2.2 × 3.6	3.9	1.1			?				12b,c
Spinose	0.4 × 0.6	4.7	0.9			+				12d,e
Spinate	2.2 × 3.5	3.6	1.2			+				12f,g
Spinate	2.8 × 1.5	4.0	1.0	+						12h,i
Spinate	2.5 × 1.2	4.5	1.0	+						12j,k
Spinate	2.5 × 1.2	4.5	1.0	+						12L,13a
Spinose	0.5 × 0.7	1.3	0.4	?	+					13b,c
Spinate	3.0 × 3.0	8.0	1.8				+			13d-f

to African members of *Vernonia*, subsection *Strobocalyx*.

Hoplophyllum. This South African genus is usually classified in the Vernonieae. Bolick (1978) noted that the genus is morphologically aberrant within the Vernonieae. Bremer (1994) positioned it in the subfamily Cichorioideae but left it unassigned as to a tribe. A chloroplast DNA phylogeny based on *ndhF* gene sequences placed *Hoplophyllum* sister to *Eremothamnus* in the tribe Arctoteae (Karis et al., 2001). The entirely spinate pollen surface (Fig. 12L; Robinson, 1994) and single layer of columellae (Fig. 13a; Table 5) most definitely removes it from Mutisieae, Vernonieae, or Cichorioideae.

Warionia. The genus is an herb endemic to the Sahara of Africa. It has coarsely lobed leaves and large discoid capitula. *Warionia* was placed in the Mutisieae by Cabrera (1977), although affinities with the Cardueae have been suggested. Hansen (1991a) excluded *Warionia* from the Mutisieae. In the cladogram of Karis et al. (1992), the genus appeared as an independent branch between the Cardueae and the vernonioid complex. Like the latter, *Warionia* has vernonioid styles, but it is not readily assigned to any of the tribes in the Vernonioid complex, and it cannot be ac-

commodated in the Cardueae (Dittrich, 1977). Bremer (1994) did not assign a tribal position to *Warionia*. Molecular phylogenies placed *Warionia* sister to *Gundelia* in the tribe Gundelieae, and this tribe is sister to the Cichorieae (Panero and Funk, 2002; Funk et al., 2005). Dimon (1971, Plate V, Figs. 3–5) depicted pollen of *Warionia* as having proximal columellae considerably greater in height than distal columellae in agreement with our SEM fractured image (Fig. 13 f) and data (Table 5). Further, the highly perforate exine surface (Figs. 12, d, 12e) resembles some Gochnatinae.

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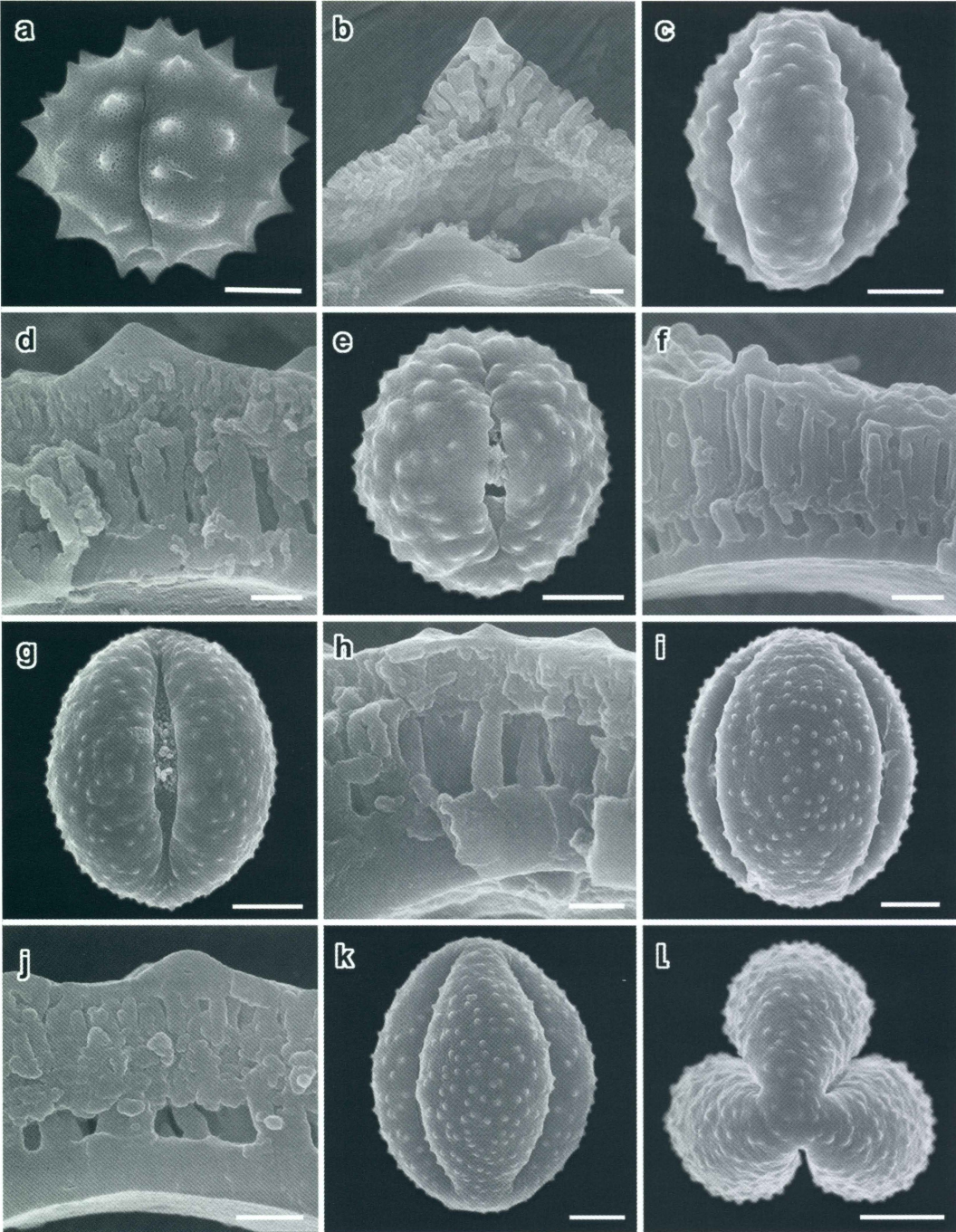


FIG. 1. a–l. SEMs of Gochnatiinae pollen. Scale bars for whole pollen grains = 10μm; for fractured pollen grains scale bars = 1μm. **a, b.** *Achyrothalmus marginatus*; **c, d.** *Actinoseris corymbosa*; **e, f.** *Ainsliaea acerifolia*; **g, h.** *Aphyllocladus* sp.; **i, j.** *Chimantaea eriocephala*; **k, l.** *C. humilis*.

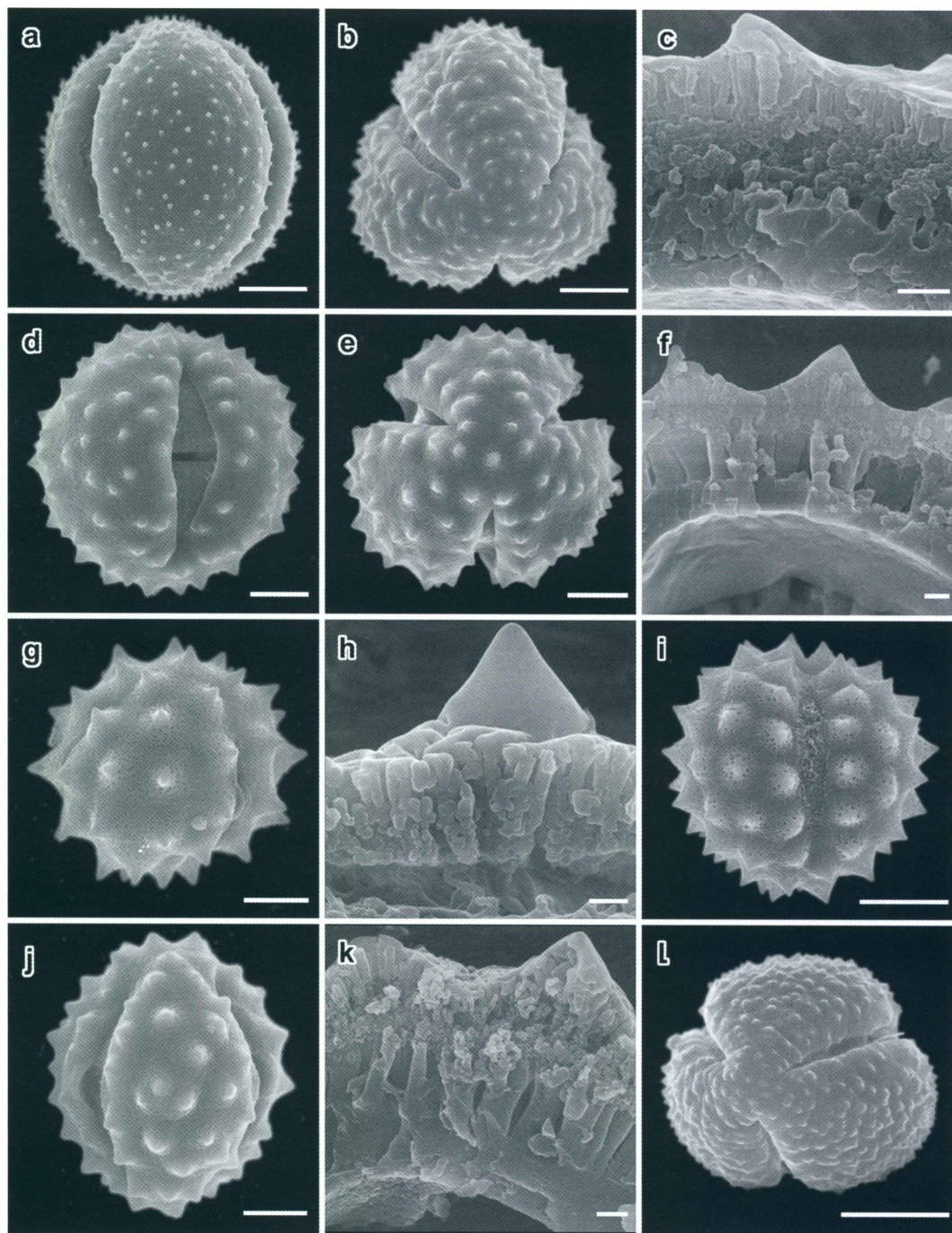


FIG. 2. a–L. SEMs of Gochnatiinae pollen. Scale bars for whole pollen grains = 10 μ m; for fractured pollen grains scale bars = 1 μ m. a–c. *Cnicothamnus lorentzii*; d–f. *Dicoma carbonaria*; g, h. *Erythrocephalum zambesianum*; i–k. *Gladiopappus vernonioides*; L. *Gochnatia argentina*.

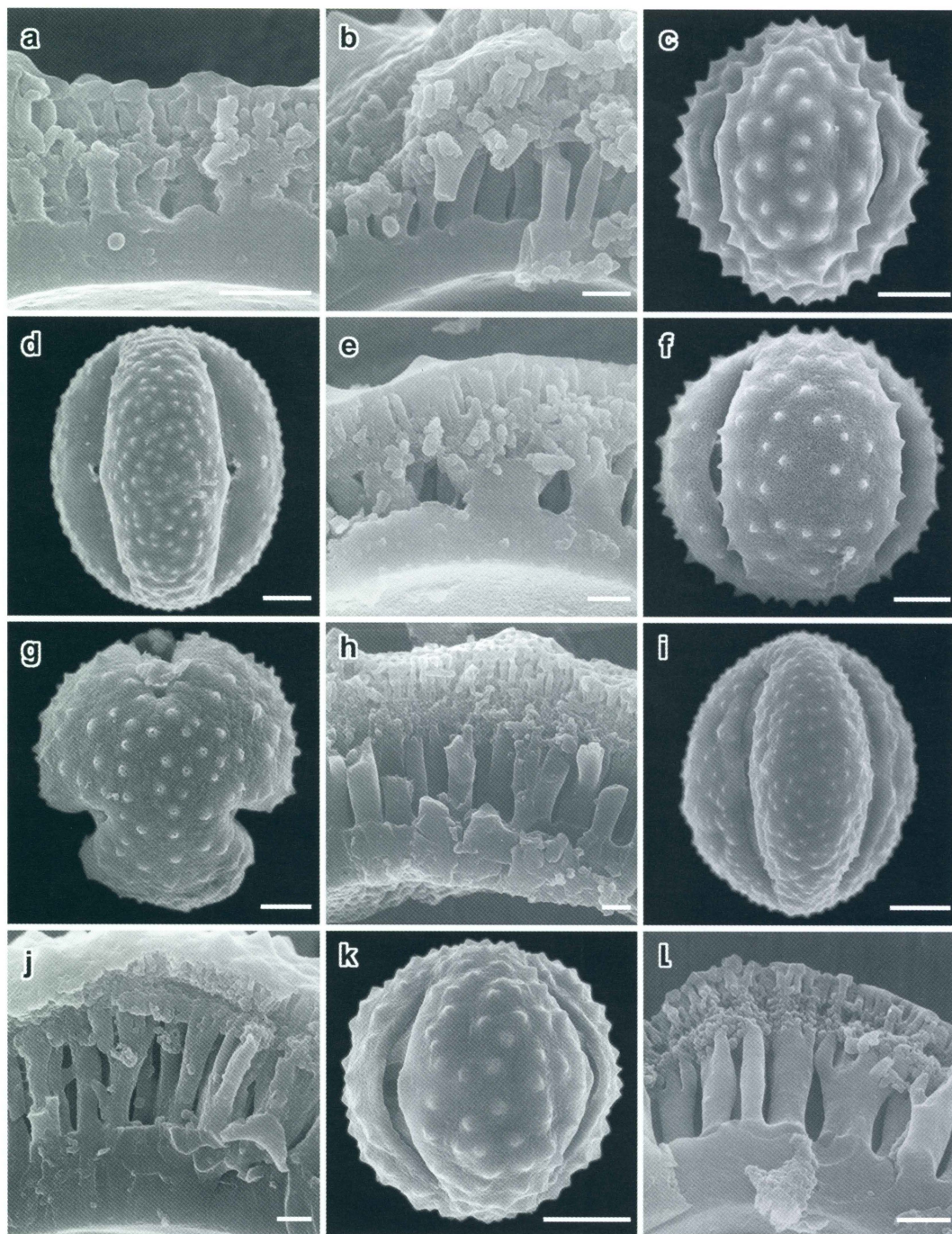


FIG. 3. a–L. SEMs of Gochnatiinae pollen. Scale bars for whole pollen grains = 10 μ m; for fractured pollen grains scale bars = 1 μ m. **a.** *Gochnatia argentina*; **b.** *G. curviflora*; **c.** *Hochstetteria schimperi*; **d, e.** *Nouelia insignis*; **f–h.** *Oldenburgia papionum*; **i, j.** *Onoseris brasiliensis*; **k, L.** *Pasacardoa grantii*.

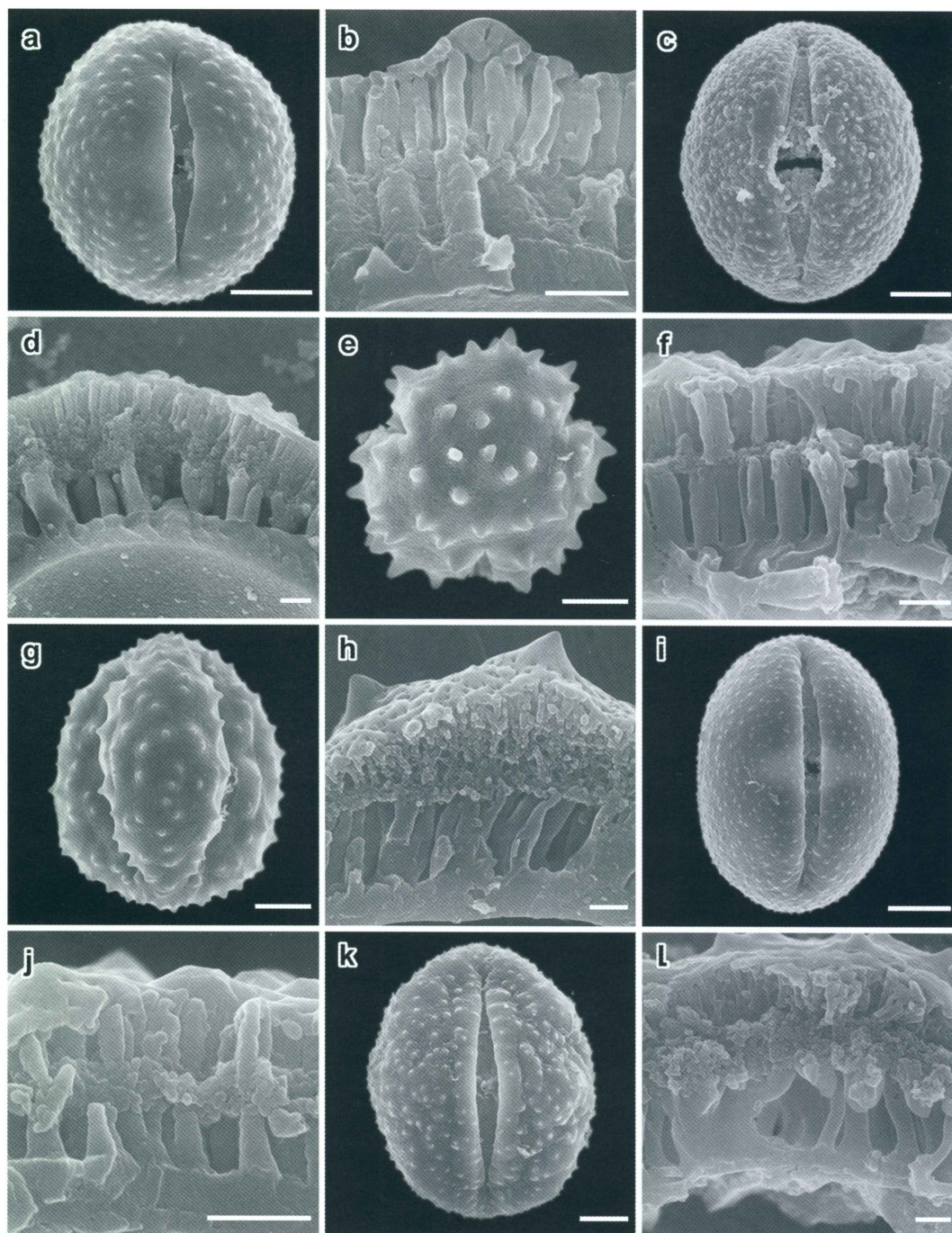


FIG. 4. a–L. SEMs of Gochnatiinae pollen. Scale bars for whole pollen grains = 10 μ m; for fractured pollen grains scale bars = 1 μ m. a, b. *Pertya glabrescens*; c, d. *Plazia daphnoides*; e, f. *Pleiotaxis dewevrei*; g, h. *Quelchia bracteata*; i, j. *Stenopadus crassifolius*; k, L. *Stiffitia chrysantha*.

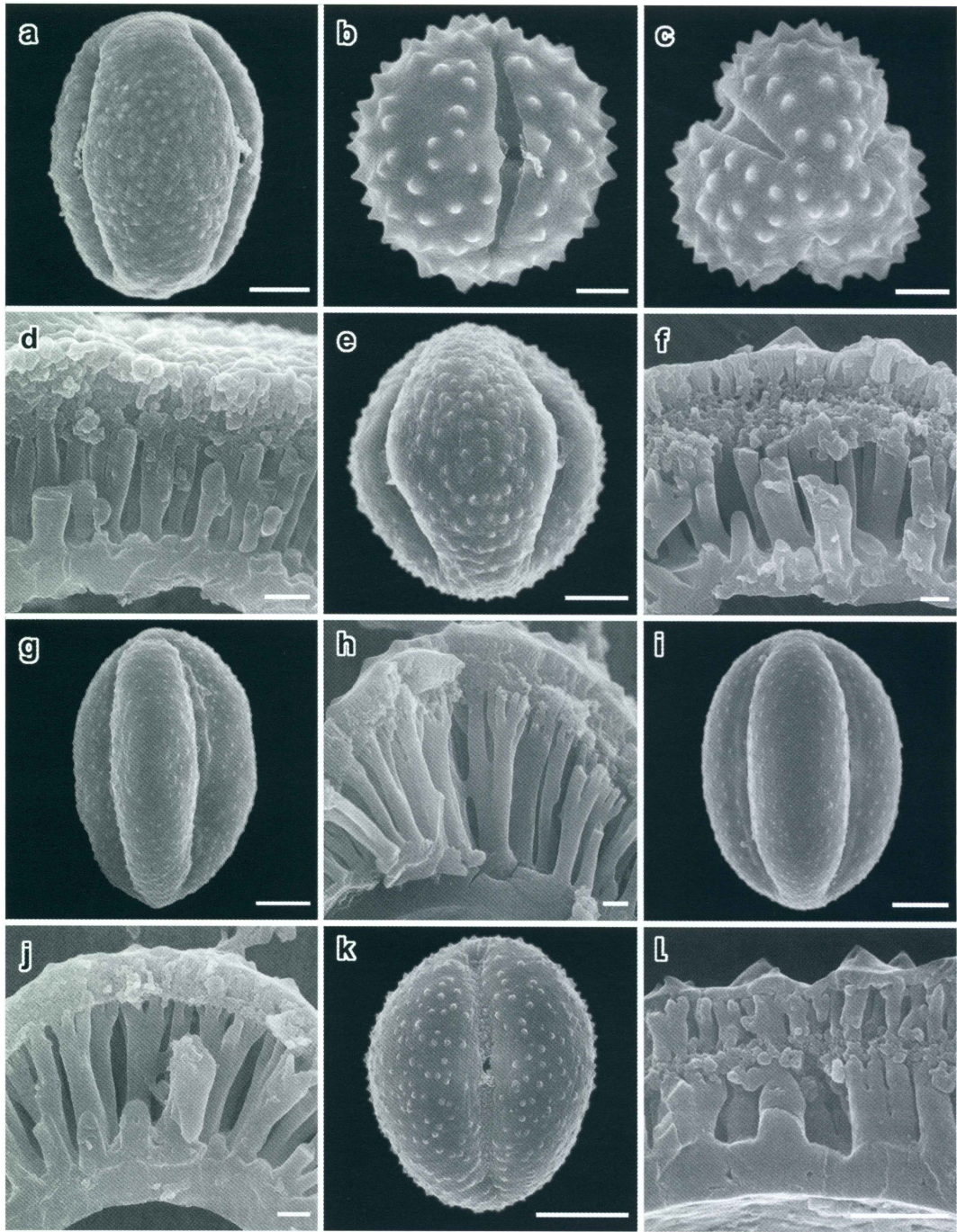


FIG. 5. a–d. SEMs of Gochnatiinae pollen. e–L. SEMs of Mutisiinae pollen. Scale bars for whole pollen grains = 10 μ m; for fractured pollen grains scale bars = 1 μ m. a. *Stomatochaeta condensata*; b–d. *Wunderlichia crulsiana*; e, f. *Achnopogon virgatus*; g, h. *Chaetanthera elegans*; i, j. *C. flabellata*; k, L. *Chaptalia nutans*.

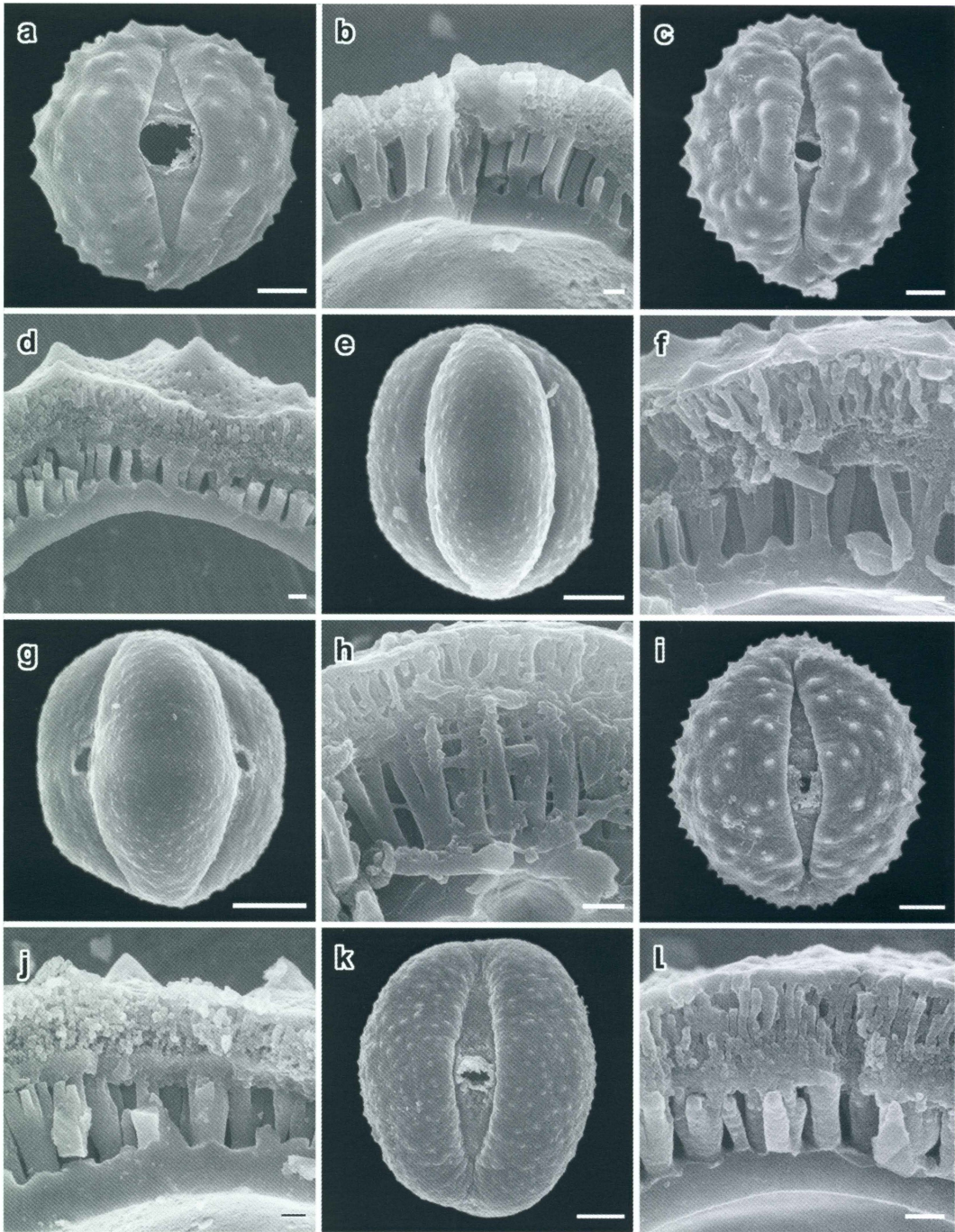


FIG. 6. a–l. SEMs of Mutisieae pollen. Scale bars for whole pollen grains = 10 μ m; for fractured pollen grains scale bars = 1 μ m. a, b. *Duidaea marabuacensis*; c, d. *Eurydochus cortesii*; e, f. *Gerbera lanuginosa*; g, h. *G. linnaei*; i, j. *Glossarion rhodanthum*; k, l. *Guaiacaia glabratus*.

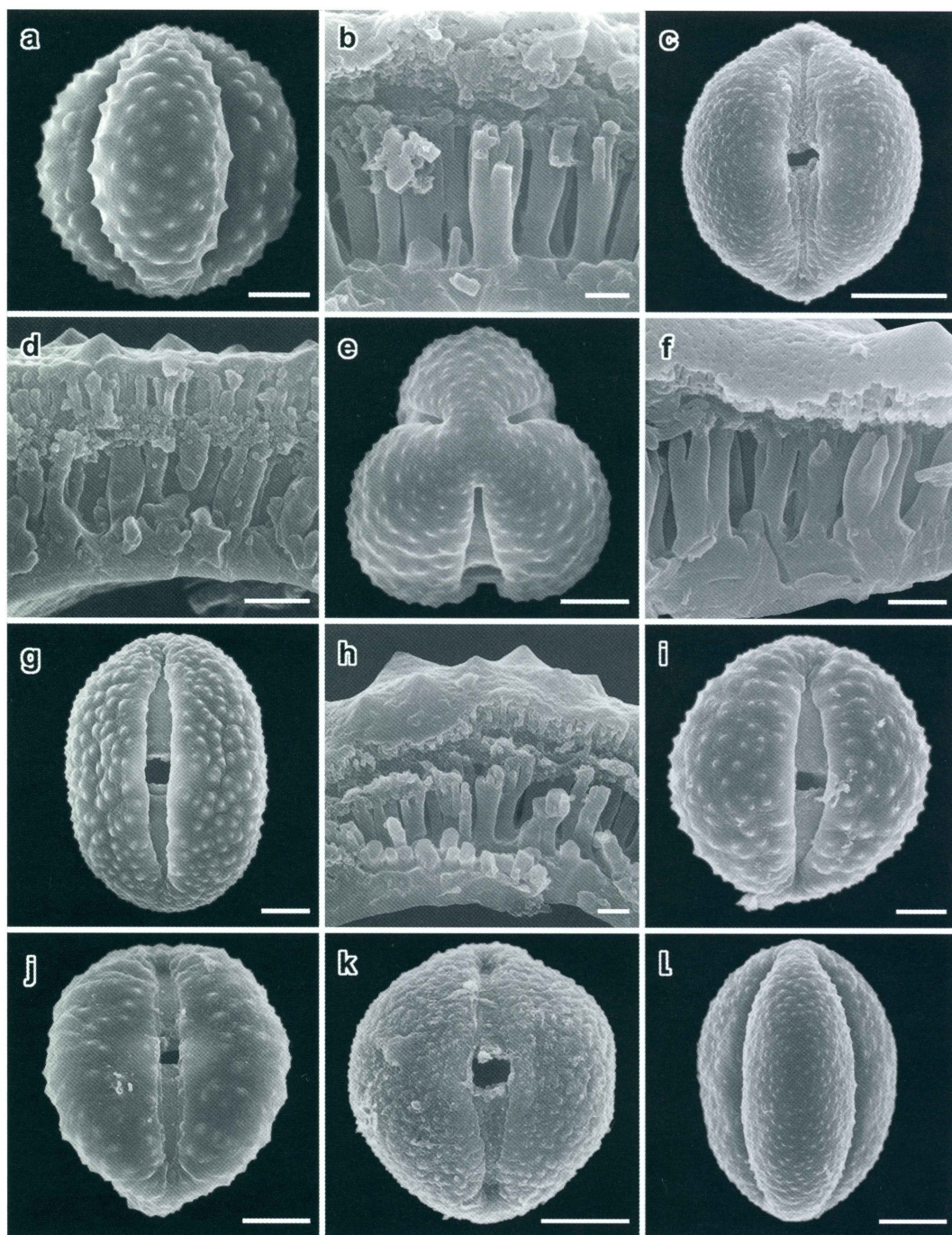


FIG. 7. a–L. SEMs of Mutisiinae pollen. Scale bars for whole pollen grains = 10 μ m; for fractured pollen grains scale bars = 1 μ m. **a, b.** *Hyaloseris cinerea*; **c, d.** *Leibnitzia seemannii*; **e, f.** *Mutisia acerosa*; **g.** *M. acuminata*; **h.** *M. spinosa*; **i.** *Neblinaea promontorium*; **j.** *Pachylaena atriplicifolia*; **k.** *Piloselloides hirsuta*; **L.** *Tricholine reptans*.

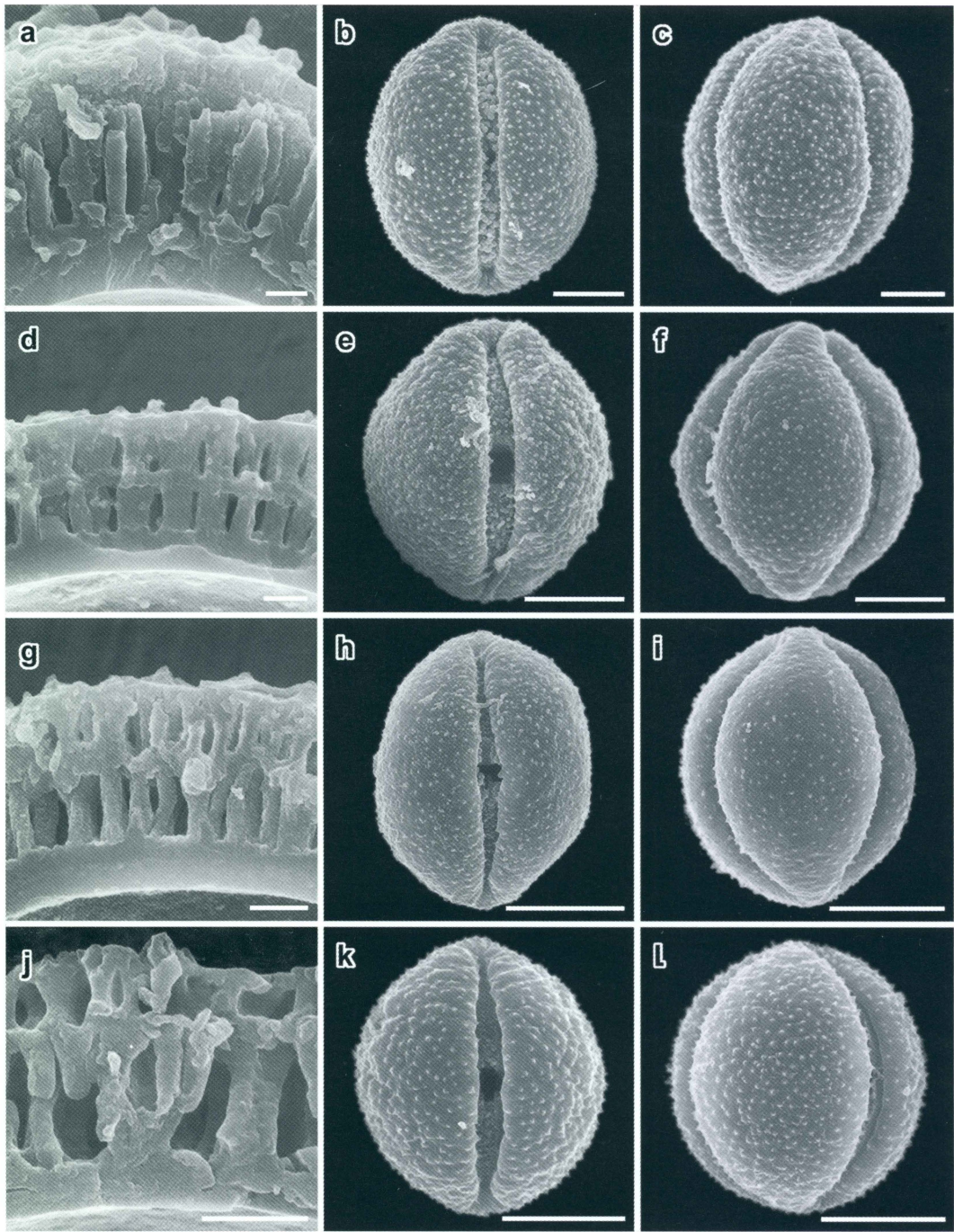


FIG. 8. a. SEM of Mutisieae pollen. b–l. SEMs of Nassauviinae pollen. Scale bars for whole pollen grains = 10μm; for fractured pollen grains scale bars = 1μm. a. *Tricholine reptans*; b–d. *Acourtia runcinata*; e–g. *Holocheilus brasiliensis*; h–j. *Jungia paniculata*; k, l. *Leucheria achillaeifolia*.

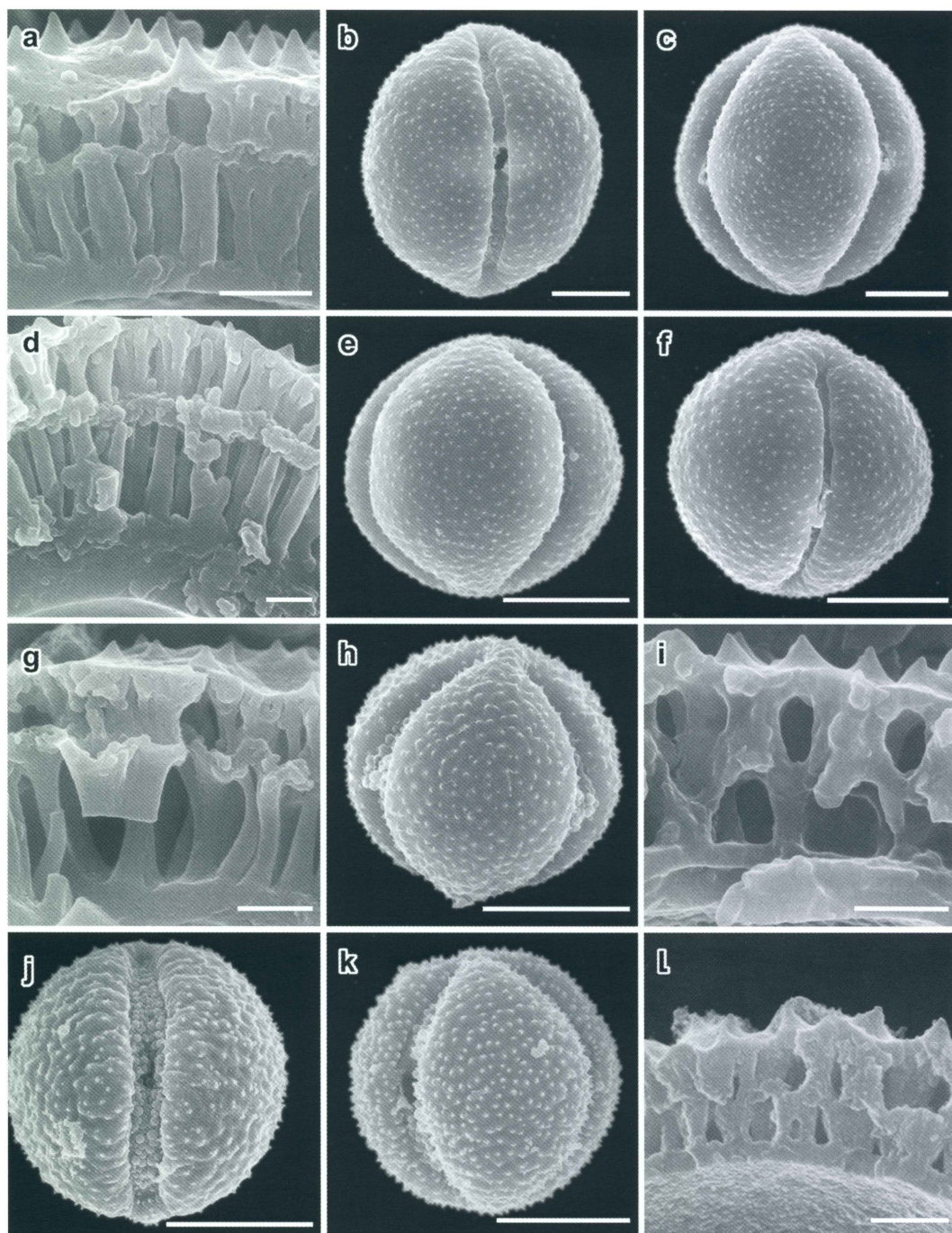


FIG. 9. a–l. SEMs of Nassauviinae pollen. Scale bars for whole pollen grains = 10 μ m; for fractured pollen grains scale bars = 1 μ m. **a.** *Leucheria achillaeifolia*; **b–d.** *Lophopappus foliosus*; **e–g.** *Nassauvia axillaris*; **h, i.** *N. lagascae*; **j–l.** *Pamphalea heterophylla*.

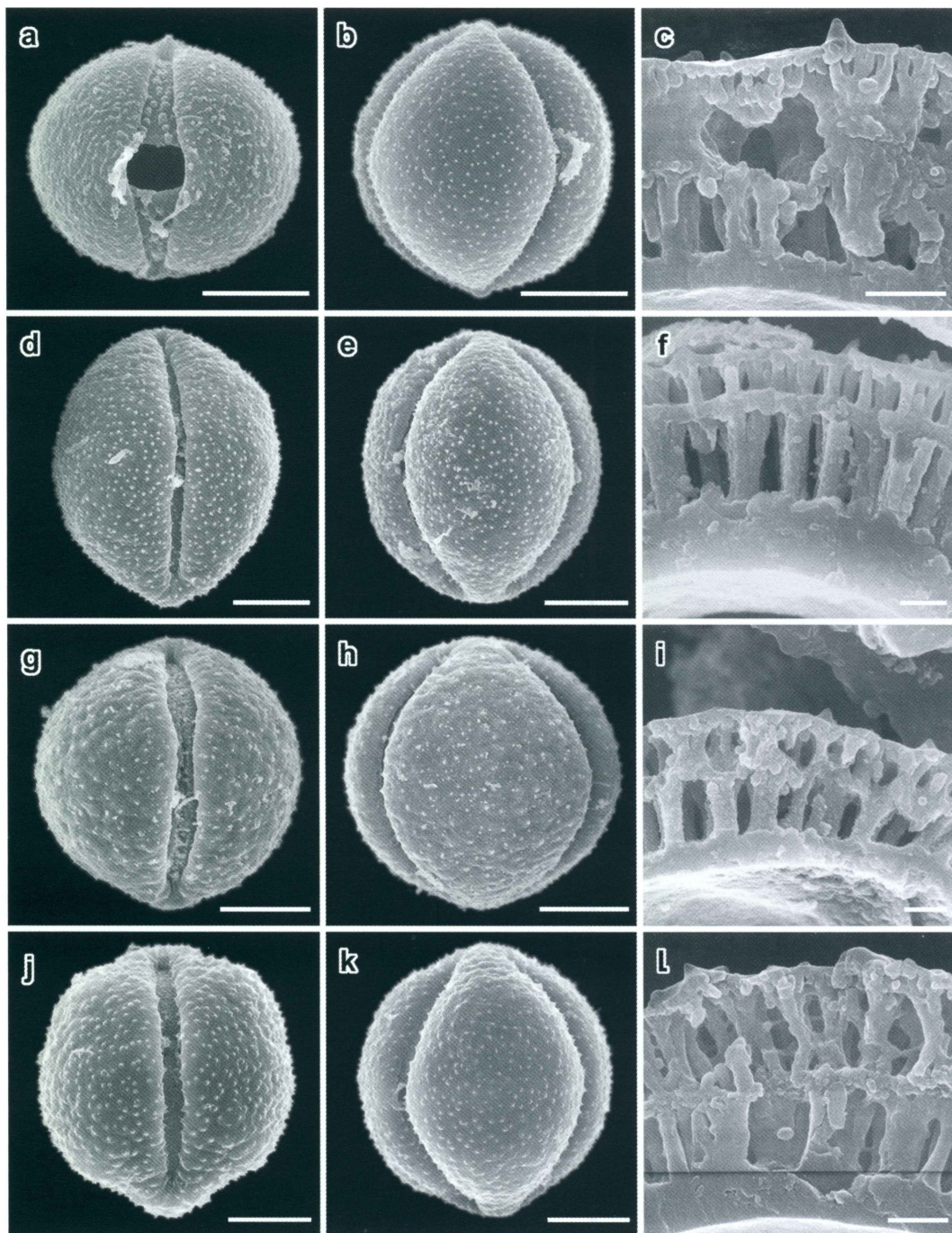


FIG. 10. a–L. SEMs of Nassauviinae pollen. Scale bars for whole pollen grains = 10 μm; for fractured pollen grains scale bars = 1 μm. a–c. *Perezia multiflora*; d–f. *Pleocarpus revolutus*; g–i. *Polyachyrus glabratus*; j–L. *Proustia cuneifolia*.

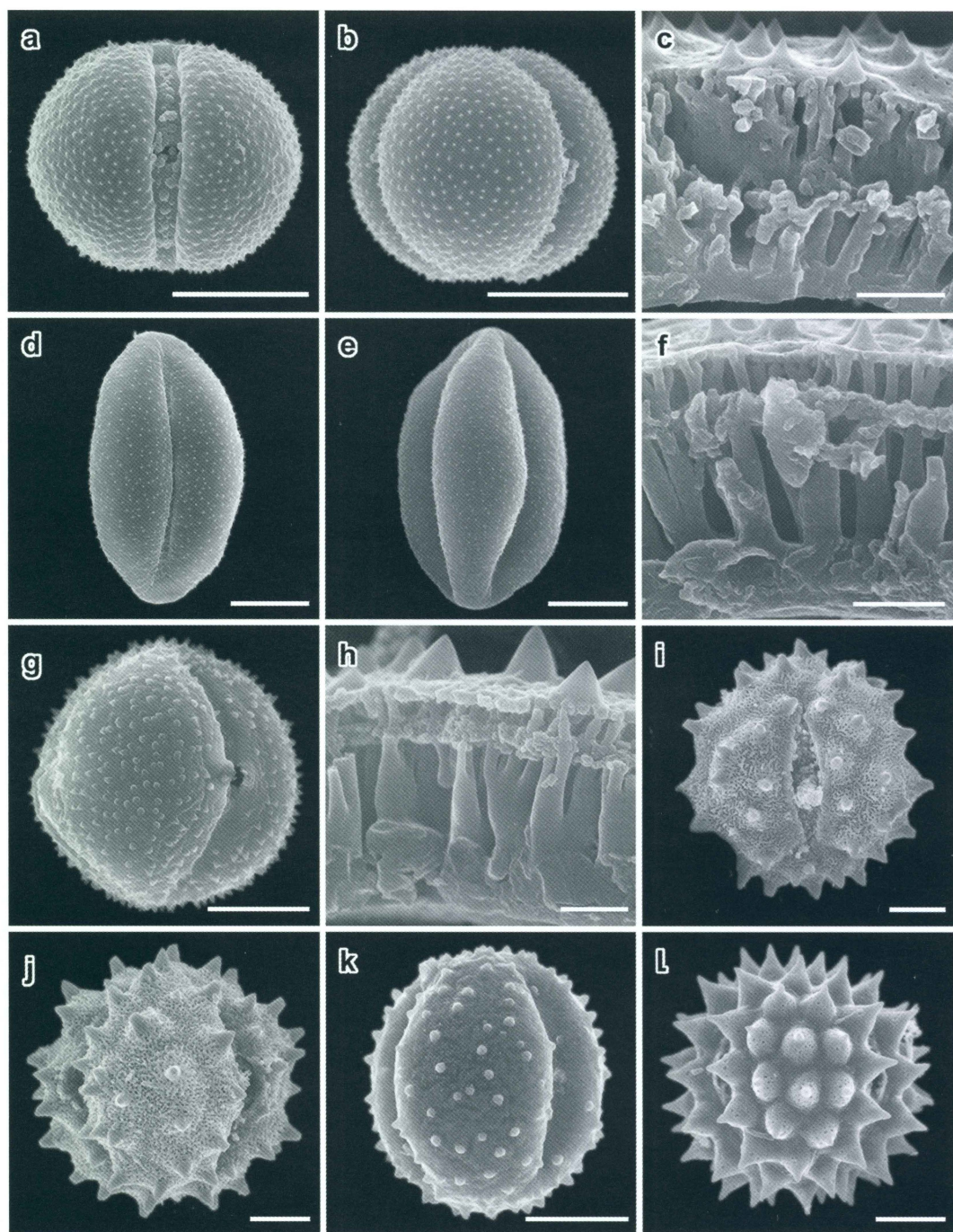


FIG. 11. a–e. SEMs of Nassauviinae pollen. f–L. SEMs of pollen with uncertain tribal positions. Scale bars for whole pollen grains = 10 μm; for fractured pollen grains scale bars = 1 μm. a–c. *Triptilion spinosum*; d–f. *Trixis californica*; g, h. *Adenocaulon bicolor*; i, j. *Berardia subacaulis*; k. *Brachylaena nereifolia*; L. *Cratystylis subspinescens*.

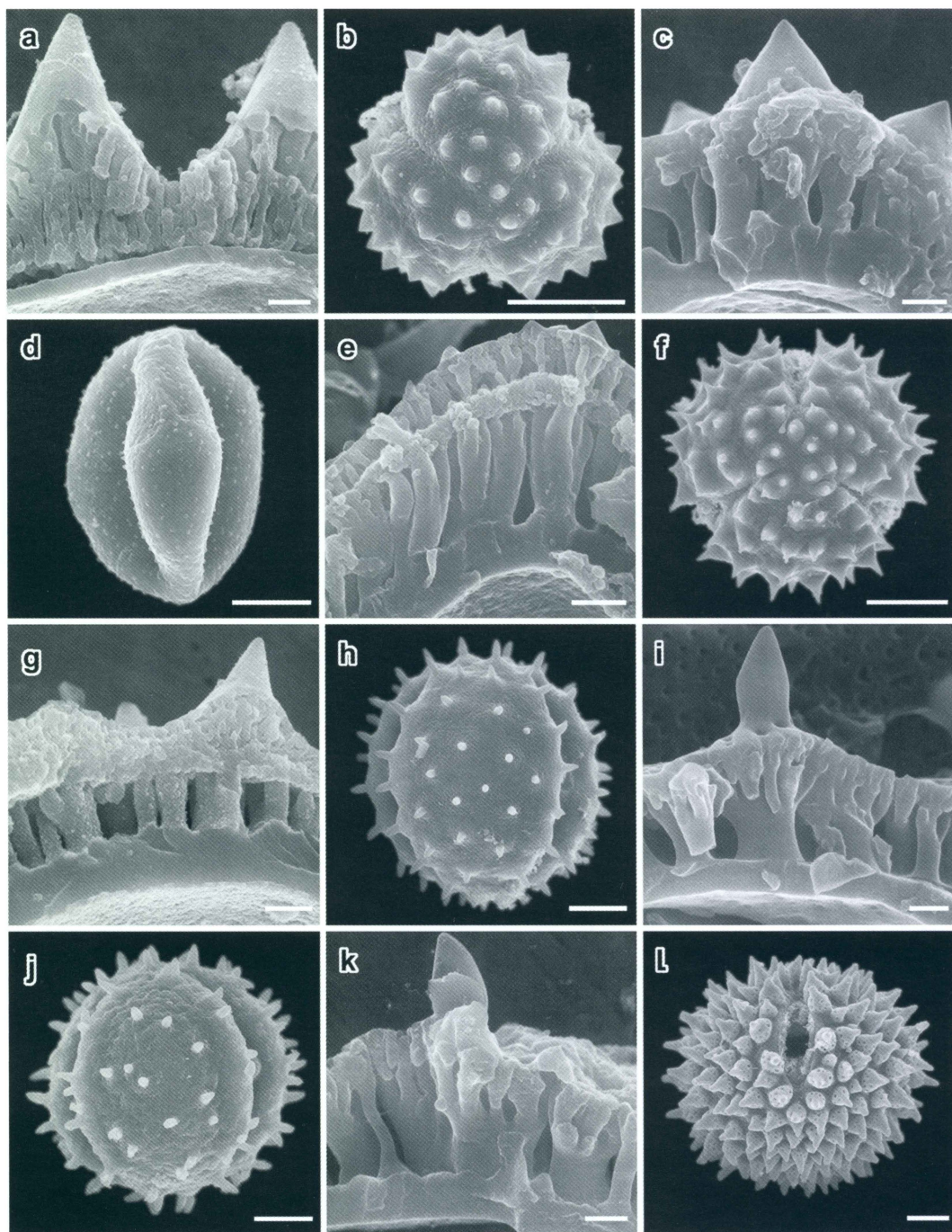


FIG. 12. a–L. SEMs of pollen with uncertain tribal placement. Scale bars for whole pollen grains = 10 μ m; for fractured pollen grains scale bars = 1 μ m. **a.** *Cratystylis subspinescens*; **b, c.** *Dipterocome pusilla*; **d, e.** *Eriachaenium* sp.; **f, g.** *Gymnarrhena micrantha*; **h, i.** *Hesperomannia arborescens*; **j, k.** *H. lydgatei*; **L.** *Hoplophyllum spinosum*.

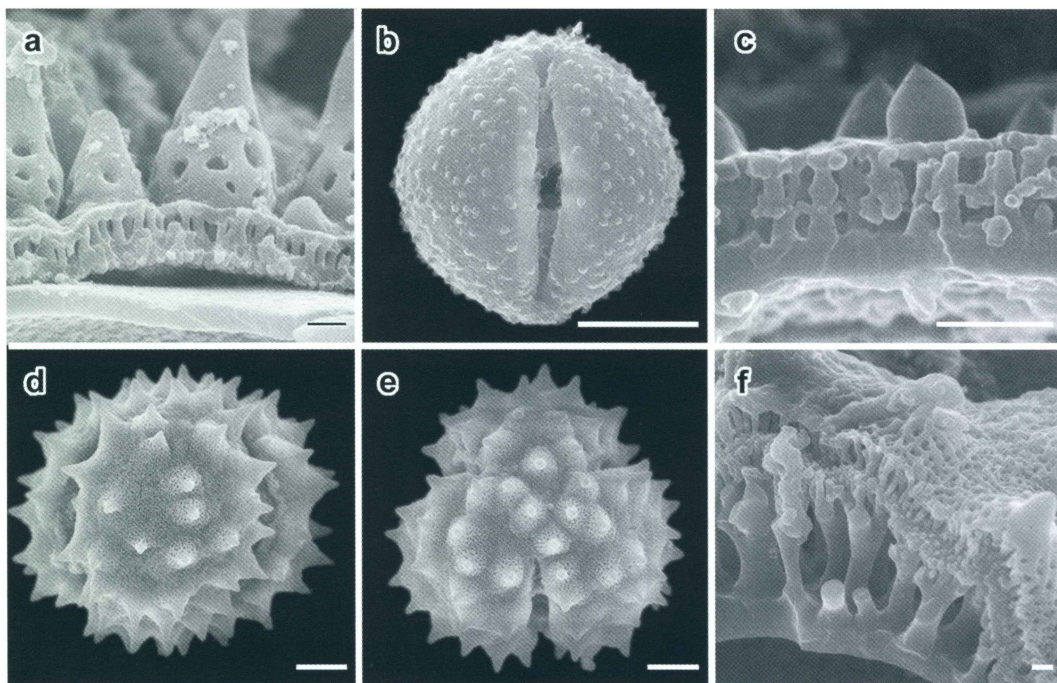


FIG. 13. a–f. SEMs of pollen with uncertain tribal positions. Scale bars for whole pollen grains = 10 µm; for fractured pollen grains scale bars = 1 µm. **a.** *Hoplophyllum spinosum*; **b, c.** *Tarchonanthus camphoratus*; **d–f.** *Warionia saharae*.

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