

The unusual occurrence of tricolpate pollen within Mutisieae (Asteraceae)

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The monotypic genus *Hecastocleis* and species of *Ainsliaea* DC. (Asteraceae, Mutisieae) have tricolpate pollen, which is unusual in Asteraceae. The pollen morphology of *H. shockleyi* and species of *Ainsliaea* were studied with light microscope and scanning electron microscope. Pollen of *H. shockleyi* and some species of *Ainsliaea* have tricolpate aperture but differ in size and exine features. The pollen of *Ainsliaea* is bigger than that of *Hecastocleis*, and has more conspicuous microspines, a *Mutisia*- or an *Ainsliaea*-exine type, and is slightly thickened at the poles. The pollen of *H. shockleyi* is scabrate-microechinate with small puncta, and has the *Mutisia*-exine type, which is regularly thickened over the complete grain. The occurrence of tricolpate pollen supports previous studies that *Hecastocleis* and *Ainsliaea* stand apart from other genera of Mutisieae, but the occurrence of *Mutisia*-exine type does not suggest complete independence of the tribe.

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During palynological studies of the tribe Mutisieae (Asteraceae) (Tellería et al. 2003, Katinas et al.: In prep.), the tricolpate pollen grains of the genera *Hecastocleis* and some species of *Ainsliaea*, versus the tricolporate pollen of other genera in the tribe, attracted our attention. In the family Asteraceae the pollen is generally tricolporate (Erdtman 1966) whereas tricolpate pollen is found in some families related to Asteraceae such as Lobeliaceae (=Campanulaceae), Menyanthaceae, and Pentaphragmataceae (Lammers 1992).

The genus *Hecastocleis* (Asteraceae) with only one species, *H. shockleyi* A. Gray, is endemic to the western United States: California and Nevada (Hickman 1993). *Hecastocleis* has a distinctive and peculiar morphology when compared with other genera of Mutisieae, with its single-flowered capitula aggregated into compound heads, and each aggregation of one to five heads is surrounded by spiny, ovate bracts. *Ainsliaea* DC. is a genus with about 50 herbaceous species distributed in southeast Asia (Freire 2002). *Ainsliaea* forms part, together with three other genera, of the *Ainsliaea* group (Bremer 1994) mainly characterized by ligulate corollas.

The taxonomic position of *Hecastocleis*, the *Ainsliaea* group, and other genera of Mutisieae, is currently under discussion. In the most recent molecular phylogenetic studies (Panero & Funk 2002) *Hecastocleis* and the *Ainsliaea* group appear as independent clades separated from the rest of Mutisieae. This position on the cladogram combined with their peculiar morphology led us to question if the lack of endoapertures, along with the whole pollen

morphology, supported the recent molecular and morphological observations.

The second question that arose was: whether there are other genera of Mutisieae with tricolpate pollen. Reports on tricolpate pollen in Asteraceae are limited, and often incorrect. For instance, pollen of *Ambrosia* and *Xanthium* (Asteraceae, Heliantheae) are described as tricolpate (Faegri & Iversen 1989), but other studies (e.g., Wodehouse 1935, Payne & Skvarla 1970, Tellería 1995) reveal that they are tricolporate. Ferreira & Janick (1996) indicated that the pollen of *Artemisia annua* (Asteraceae, Anthemidae) is tricolpate, although the figure in their work shows a tricolporate pollen grain. Within the tribe Mutisieae, Wodehouse (1929) in his study with light microscopy, presented a table of the distribution of various palynological characters among different genera of the tribe. Wodehouse referred to the endoapertures as “transverse furrows”, and included a column in his table for the presence or absence of endoapertures. He did not explain the symbols in this column but it can be assumed that his “0”=no endoaperture in at least some species.

According to the table of Wodehouse (1929), species of *Ainsliaea*, *Chuquiraga*, *Hecastocleis*, *Lycoseris*, *Moquinia*, *Schlechtendalia*, and *Trichocline* have tricolpate pollen. Marticorena & Parra (1975) mentioned tricolpate pollen for *Ainsliaea angustifolia*, *A. apiculata*, *A. aptera*, *A. fragrans*, *A. hypoleuca*, *A. macroclinioides*, *A. pteropoda*, *A. triflora*, and *A. yunnanensis*, but without a detailed pollen description of these species. Hansen’s (1991) palynological study by SEM of the Mutisieae focused on exine surface features and

Table I. *Re-analysis of the species considered by Wodehouse (1929) that lack endoapertures (as “transverse furrows”) in the literature and this study.*

Species cited by Wodehouse (1929)	Current name	Additional literature	Endoapertures	Observations
<i>Ainsliaea pteropoda</i> DC.	<i>Ainsliaea latifolia</i> (D. Don) Sch. Bip.	Marticorena & Parra 1975	Absent	Endoapertures are present or absent in the different species of <i>Ainsliaea</i> . See text.
<i>Chuquiraga acicularis</i> D. Don	<i>Chuquiraga ulicina</i> (Hook. & Arn.) Hook & Arn. subsp. <i>acicularis</i> (D. Don) Ezcurra	Urtubey & Tellería 1998	Endoapertures are lalongate with acute equatorial ends	
<i>C. avellanadae</i> Lorentz	<i>Chuquiraga avellanadae</i> Lorentz	Urtubey & Tellería 1998	Endoapertures are lalongate with acute equatorial ends	
<i>C. ferox</i> (Wedd.) Britton	<i>Dasyphyllum ferox</i> (Wedd.) Cabrera	Urtubey & Tellería 1998	Endoapertures have acute equatorial ends	
<i>C. floribunda</i> (Gardner) Baker	<i>Dasyphyllum floribundum</i> (Gardner) Cabrera	Urtubey & Tellería 1998	Endoapertures have acute equatorial ends	
<i>C. hystrix</i> D. Don	<i>Chuquiraga erinacea</i> D. Don subsp. <i>hystrix</i> (D. Don) Ezcurra	Urtubey & Tellería 1998	Endoapertures are lalongate with acute equatorial ends	
<i>C. inermis</i> (Rusby)	<i>Dasyphyllum inerme</i> (Rusby) Cabrera	Urtubey & Tellería 1998	Endoapertures have acute equatorial ends	The name <i>Chuquiraga inermis</i> was never published. Wodehouse probably referred to <i>Barnadesia inermis</i> Rusby
<i>C. leptacantha</i> (Gardner) Blake	<i>Dasyphyllum leptacanthum</i> (Gardner) Cabrera	Urtubey & Tellería 1998	Endoapertures inconspicuous	
<i>C. sprengeliana</i> (Gardner) Blake	<i>Dasyphyllum sprengelianum</i> (Gardner) Cabrera	Urtubey & Tellería 1998	Endoapertures have acute equatorial ends	
<i>C. vagans</i> (Gardner) Blake	<i>Dasyphyllum vagans</i> (Gardner) Cabrera	Urtubey & Tellería 1998	Endoapertures have acute equatorial ends	
<i>C. varians</i> (Gardner) Rusby	<i>Dasyphyllum brasiliensis</i> (Spreng.) Cabrera var. <i>varians</i> (Gardner) Cabrera	Urtubey & Tellería 1998	Endoapertures have acute equatorial ends	
<i>Hecastocleis shockleyi</i> A. Gray	<i>Hecastocleis shockleyi</i> A. Gray	Studied in this work	Absent	
<i>Lycoseris boliviana</i> Britton	<i>Lycoseris boliviana</i> Britton	Egeröd & Ståhl 1991	Described as tricolpate and fossaperturate, but see text	
<i>L. oblongifolia</i> Rusby	<i>Lycoseris triplinervia</i> Less.	Egeröd & Ståhl 1991; Also studied in this work.	Described as tricolpate and fossaperturate, but see text	
<i>L. squarrosa</i> Benth.	<i>Lycoseris crocata</i> (Benth.) Blake	Egeröd & Ståhl 1991; Also studied in this work.	Described as tricolpate and fossaperturate, but see text	
<i>Moquinia boliviana</i> Rusby	<i>Gochmatia rusbyana</i> Cabrera	Sancho 2000	Present	
<i>M. gardneri</i> Baker	<i>Gochmatia gardneri</i> (Baker) Cabrera	Sancho 2000	Present	
<i>M. macrocephala</i> Rusby	<i>incertae sedis</i> , not belonging to Mutisieae		Not known	Only the type specimen is known from this species. <i>Moquinia macrocephala</i> Rusby was transferred to <i>Gochmatia</i> as <i>G. macrocephala</i> by Cabrera (1950), and then excluded from <i>Gochmatia</i> and from the tribe Mutisieae by the same author (Cabrera 1971).

Table I. (Continued).

Species cited by Wodehouse (1929)	Current name	Additional literature	Endoapertures	Observations
<i>M. polymorpha</i> (Less.) DC.	<i>Gochmatia polymorpha</i> (Less.) Cabrera	Marticorena & Parra 1975, Roque & Silvestre-Capelato 2001, Telleria & Katinas 2004	Present	
<i>M. racemosa</i> (Spreng.) DC.	<i>M. racemosa</i> (Spreng.) DC.	Marticorena & Parra 1975, Gamero 1990, Robinson 1994	Present	
<i>M. velutina</i> Bong.	<i>Gochmatia velutina</i> (Bong.) Cabrera	Marticorena & Parra 1975, Sancho 2000	Present	
<i>Schlechtendalia luzulaefolia</i> Less.	<i>Schlechtendalia luzulaefolia</i> Less.	Urtubey & Telleria 1998	with acute equatorial ends	
<i>Trichoclina araneosa</i> Baker	<i>Chaptalia araneosa</i> Casaretto		Probably present	Only the type specimen is known from this species. <i>Trichoclina araneosa</i> was transferred to <i>Chaptalia</i> by Zardini (1975). Both, <i>Chaptalia</i> and <i>Trichoclina</i> are tricolporate (Zardini 1975, Parra & Marticorena 1972, Telleria & Katinas 2004).

did not refer to aperture types. Egeröd & Ståhl (1991) described the pollen of *Lycoseris* as tricolpate and fossaperturate.

Therefore an investigation of the extent of the tricolpate pollen type in the tribe Mutisieae seemed worthwhile. The objectives of this paper are to: (1) examine genera of Mutisieae suggested by other authors to have tricolpate pollen; (2) describe and illustrate the pollen of *Hecastocleis* and *Ainsliaea*; and (3) relate the pollen morphology to the taxonomic position of *Hecastocleis* and *Ainsliaea*.

MATERIAL AND METHODS

This study is based both on the literature (see Table I) and examination of specimens (Specimens Investigated list). Acronyms of herbaria are cited according to Holmgren et al. (1990).

Pollen was acetolyzed and chlorinated according to standard procedures (Erdtman 1960). For light microscopy (LM), slides were prepared by mounting the pollen in glycerol jelly and sealed with paraffin. Measurements of the polar axis (P) and equatorial (E) diameter of pollen grains are based on 25 grains, and measurements of exine thickness are based on 15 grains. The P/E ratio was calculated for the specimens analyzed. For scanning electron microscopy (SEM), acetolyzed pollen grains were suspended in 90 % ethanol and mounted on stubs. The samples were sputter-coated with gold palladium and examined in a JEOL JSM T-100 SEM. Due to the paucity of *Ainsliaea* pollen, only pollen of *Hecastocleis* was photographed with SEM. The terminology in general follows Punt et al. (1994) and the types of exine were taken from Stix (1960) and Telleria et al. (2003).

RESULTS

A re-analysis of Wodehouse's table together with our own observations (Table I) show that: (1) the species of *Chuquiraga*, *Dasyphyllum*, *Gochmatia*, *Moquinia*, *Schlechtendalia*, and *Trichocline/Chaptalia* are clearly tricolporate; (2) the genus *Hecastocleis* has tricolpate pollen; (3) the genus *Ainsliaea* has species with tricolpate pollen and species with tricolporate pollen, and (4) the genus *Lycoseris* is clearly tricolporate (Fig. 1A).

The pollen morphology of *Ainsliaea* and *Hecastocleis* is described below.

Pollen of *Hecastocleis shockleyi* (Fig. 1B–F)

Pollen spheroidal in equatorial view, $P \times E = (38-46 \times 42-46) \mu\text{m}$; circular in polar view. Tricolpate, colpi long and broad, with scabrate apertural membrane. Exine tectate, scabrate, 6–7 μm thick in the complete grain, ectosexine with compact aspect, endosexine with stout and ramified columellae (*Mutisia*-type). Ratio ectosexine/endosexine: ca. 1:1. Nexine ca. 1.5 μm . SEM-tectum microechinate with very small puncta.

Pollen of *Ainsliaea* (Fig. 1G–J)

Pollen spheroidal to prolate, elliptic in equatorial view; circular in polar view. Tricolpate or tricolporate with endoaperture lalongate with acute ends, colpi long with psilate or slightly microgranulate membrane. Exine always

microechinate, equally thickened in complete grain or slightly thickened at the poles, two types of exine with imperforate tectum were recognized: – with ectosexine equally thicker than endosexine, both layers little differentiated, with compact aspect or slightly columellate (*Ainsliaea*-type) or, -ectosexine as thin as, or thicker than endosexine, ectosexine slightly columellate or with compact aspect, endosexine with stout and ramified columellae, both layers separated by an internal tectum (*Mutisia*-type).

Of the seven species of *Ainsliaea* examined, four had tricolpate pollen and three, tricolporate pollen. Only tricolpate pollen is described.

A. lancangensis – Pollen spheroidal, $P \times E = (56-64 \times 48-54) \mu\text{m}$. Tricolpate, colpi long, with apertural membrane slightly microgranulate. Exine *Mutisia*-type slightly thickened at the poles, 6–10 μm thick. Ratio ectosexine/endosexine: 2:1. Nexine: ca. 2 μm .

A. latifolia – Pollen spheroidal, $P \times E = \text{ca. } (48-54 \times 38-42) \mu\text{m}$. Tricolpate, colpi long. Exine *Ainsliaea*-type, ca. 5–6.5 μm thick. Ratio ectosexine/endosexine: 1:1. Nexine: ca. 1.5 μm . Note: due the paucity of pollen it was possible to measure only two grains.

A. okinawensis (Fig. 1G–J) – Pollen spheroidal, elliptic in equatorial view, $P \times E = (47-54 \times 42-46) \mu\text{m}$. Tricolpate, colpi long. Exine *Ainsliaea*-type, 5–6 μm thick at the equator, 8 μm thick at the poles. Ratio ectosexine/endosexine: 1:1. Nexine: ca. 1.5 μm .

A. pertyoides – Pollen prolate, $P \times E = (67-73 \times 32-54) \mu\text{m}$. Tricolpate, colpi long, with psilate membrane; endoaperture type I. Exine *Mutisia*-type, 6–8 μm equally thick in complete grain. Ratio ectosexine/endosexine: 1.5:1. Nexine: ca. 1 μm .

DISCUSSION

The discussion focuses on a palynological comparison between *Hecastocleis* and *Ainsliaea* highlighting resemblances and differences. The palynological findings are discussed in relation to the taxonomic position of both genera.

Palynological comparison between *Hecastocleis* and *Ainsliaea*

The results of this study develop the observations of Wodehouse (1929) that the pollen of *Ainsliaea* and *Hecastocleis* share the tricolpate aperture type, but pollen from the two genera show differences in size, exine sculpture and exine thickness. Wodehouse (1929) established that the pollen grains of *Hecastocleis* are rather dissimilar to any in the tribe except those of *Ainsliaea*. He described the pollen of *Hecastocleis* as flattened and deeply lobed, with broad, smooth furrows contrasting sharply with the granular texture of the exine, as in *Ainsliaea*. The differences established by Wodehouse between both genera were the almost total lack of spines and the greater thickening of the

exine in *Hecastocleis*. He emphasized that there is only a remote connection between these taxa.

The genus *Ainsliaea* combines certain pollen features: tricolpate versus tricolporate grains, and the *Mutisia*-type exine as well as the *Ainsliaea*-type exine. Four of the seven species analyzed here, i.e. *A. lancangensis*, *A. latifolia*, *A. okinawensis*, and *A. pertyoides* are tricolpate and augment the list of Marticorena & Parra (1975) of tricolpate species in the genus. From these species, *Ainsliaea lancangensis* and *A. pertyoides* share the *Mutisia*-type exine with *Hecastocleis* whereas the other two species have the *Ainsliaea*-type.

The pollen of *Ainsliaea* is generally bigger than that of *Hecastocleis* (the polar axis of *Ainsliaea* ranges between 48 and 73 μm , and in *Hecastocleis* 38–46 μm), the microspines are conspicuous, and the exine is generally slightly thickened at the poles, while in *Hecastocleis* the exine is similar in thickness in polar and mesocolpial regions.

The tricolpate pollen of *Hecastocleis* and *Ainsliaea*, add to the apertural diversity found in Mutisieae (Tellería & Katinas 2004, Katinas et al. in prep.). The tricolporate aperture is morphologically and physiologically more complex (Blackmore & Barnes 1986), and regarded as more specialized in comparison with the tricolpate condition (Thanikaimoni 1986).

Taxonomic significance of *Hecastocleis* and *Ainsliaea* pollen morphology

The tribe Mutisieae, with approximately 74 genera and 850 species, is considered the most important tribe for understanding the systematics and evolution of the Asteraceae because it represents a basal lineage in the family. Cabrera (1977) considered the Mutisieae comprised four subtribes: Barnadesiinae, Gochnatiinae, Mutisiinae, and Nassauviinae. Later, Barnadesiinae was raised to the rank of subfamily when Jansen & Palmer (1987) found that a large chloroplast DNA inversion, present in Asteraceae, is absent in this subtribe. Finally, Robinson (1991) and then Bremer (1994) abolished the limits between Mutisiinae and Gochnatiinae, and thus within Mutisieae only two subtribes were recognised: Mutisiinae and Nassauviinae. According to this classification *Hecastocleis* and *Ainsliaea* are placed in the subtribe Mutisiinae.

Since Cabrera's work, a number of authors redefined the limits of the tribe by excluding genera. The most drastic taxonomic change in the Mutisieae was that of Panero & Funk (2002) who divided the tribe into smaller segregates on the basis of a molecular-based cladogram. They proposed the new subfamilies Gochnatioideae (six genera), Hecastocleioideae (with its only genus and species *Hecastocleis shockleyi*), and Pertyoideae (five genera, one of them *Ainsliaea*), and the tribe Dicomeae (seven genera) included in the subfamily Carduoideae. The rest of Mutisieae constituting two branches near the base of the tree.

The unique occurrence of tricolpate pollen in *Hecastocleis* and *Ainsliaea* provides additional evidence supporting the monophyly of these taxa from other genera of Mutisieae as suggested by Panero & Funk (2002). However, the presence of the *Mutisia*-type exine in *Hecastocleis*, and in some species of *Ainsliaea*, indicates a link with the Mutisieae and

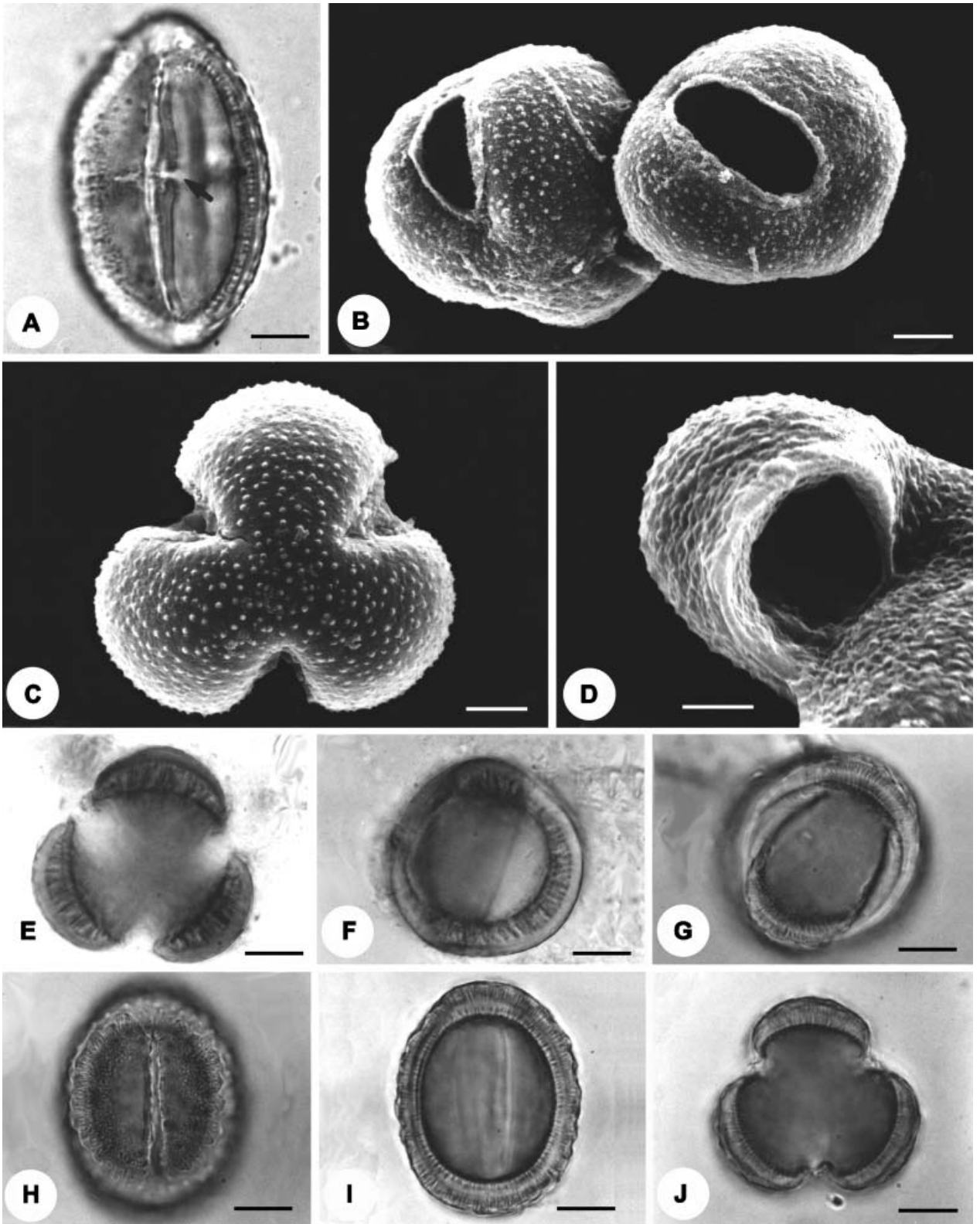


Fig. 1. A. *Lycoseris crocata*, equatorial view, endoaperture distinguishable (arrow). LM, optical section. B–F. *Hecastocleis shockleyi*. SEM & LM: (B) Slightly oblique equatorial view. Note the apertures. SEM; (C) Polar view. SEM; (D) Collapsed grain, lateral view of colpus. Note the absence of endoaperture. SEM; (E) Polar view. LM, optical section; (F) Equatorial view. Note the *Mutisia* exine-type. LM, optical section. G–J. *Ainsliaea okinawensis*. LM: (G) Oblique equatorial view, mesocolpium in high focus; (H) Equatorial view, colpus in high focus; (I) Equatorial view, optical section. Note the *Ainsliaea* exine-type; (J) Polar view, optical section. Scale bar: 12.5 μm (A, E–J); 10 μm (B, C); 5 μm (D).

does not suggest a complete independence of these genera from the tribe.

Although this work draws attention to the occurrence of tricolpate pollen in Asteraceae and answers our initial questions, it also raises important questions such as: Are there genera in other tribes of Asteraceae with tricolpate pollen? Are the tricolpate pollen grains a primitive or an evolved condition in the family? Additional studies of pollen morphology in other tribes focusing on their apertures are needed to understand more fully the underlying explanations of this exciting topic.

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SPECIMENS INVESTIGATED

Pollen grains were removed from the following specimens:

Hecastocleis shockleyi A. Gray

USA: California, Inyo Co., Eureka valley to Fish Lake valley, Alexander & Kellogg 5301 (US); Death Valley region, Leadfield. Gilman 1144 (US); Nevada State, Esmeralda Co., 5 miles of Basalt, on Mt. Montgomery - Tonopah highway, Mineral-Esmeralda Co. line. Train 3973 (LP).

Ainsliaea acerifolia Schultz var. *subapoda* Nakai. Japan: Honshu, Pref. Migayi. Boufford 19871 (CM).

A. apiculata Sch. Bip. Japan: Kyushu, Pref. Kagoshima, Mt. Kaimon. Saito 1846 (US).

A. lancangensis Y. Y. Qian. China: Prov. Yunnan, Lancang. Qian 3343 (SMAO).

A. latifolia (D. Don) Sch. Bip. var. *latifolia*. China: Prov. Yunnan. Handel & Mazzetti 8501 (W).

A. pertyoides Franchet var. *pertyoides*. China: Prov. Yunnan. Delavay s/n^o (UC).

A. okinawensis Hayata. Japan: Ryukyu Is., Pref. Okinawa. Murata 17066 (AAU).

A. spanocephala Y. C. Tseng. Thailand: Loei. Nuijomdha & Vidal 438 (C); Smithland 077323 (BKF).

Lycoseris crocata (Benth.) Blake. Colombia: Dept. Atlántico, cerca de Usiacurí. Araque Molina & Barkley 19At063 (LP).

L. trinervis (D. Don) S. F. Blake. Peru: Dpto. Chanchamayo. Diers 1249 (LP).

L. triplinervia Less. Venezuela: s.loc.. Vogl 680 (LP).

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