

A search for pollen morphological synapomorphies to classify rogue genera in Compositae (Asteraceae)

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Received 16 November 2006; received in revised form 8 March 2007; accepted 27 March 2007

Available online 1 April 2007

Abstract

Focusing on Compositae, this paper highlights and exemplifies the range of questions to which pollen morphology may contribute in the investigation of problematic taxa. Using a literature survey and new palynological data from LM and SEM studies, the pollen of a number of “rogue genera” was described and compared with that of potential related taxa in Compositae. Rogue genera are defined as taxa that have traditionally been difficult to classify, usually having highly divergent macro-morphological characters compared to the rest of Compositae. They include genera of known tribe but unknown position within that tribe and genera or small tribes of uncertain position in Compositae, as well as taxa that have recently been placed using molecular data but whose morphology continues to intrigue synantherologists.

In the majority of cases, palynology was found to provide new sets of characters which could be compared to the robust hypothesis of relationships shown in the recent DNA-based supertree. Pollen variously provided support and diagnostic characters for some groups (e.g. *Hesperomannia*, *Hoplophyllum*, *Eremothamnus*, Tarchonantheae, Corymbieae and Gymnarrheneae), suggested some possible affinities for taxa currently excluded from phylogenetic studies using DNA (such as *Moquinia*, *Catananche*, *Pacourina* and *Platycarpha*), or to some degree contradicted existing phylogenies (e.g. *Gundelia* and *Warionia*), suggesting areas for future research.
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Keywords: classification; molecular data; morphological data; palynology; problem genera; systematics

1. Introduction

The past thirty years have been a time of considerable change and progress in the systematics of Compositae. Throughout that time, it has been recognised that there are a number of problematic (“rogue”) taxa which have been difficult to classify to tribe, primarily because of their

anomalous morphological features (Carlquist, 1976; Wagenitz, 1976; Bremer, 1994; Jansen and Kim, 1996). These often continue to be the “thorn in the side” of Compositae systematists even as the major questions of phylogenetics and evolution begin to be answered. Rogue taxa (usually genera) are defined as taxa that have proven difficult to place within a higher-level classification, through formal phylogenetic analysis or classification, and using either morphological or molecular data. Often, they are ecologically specialised — apomictic, aquatic,

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parasitic, xerophytic or woody — and this has resulted in morphological or even molecular-level adaptations that take them outside the realm of the characters most commonly used in classification of the family.

In 1975, at a major conference in Reading, U.K. on *The Biology and Chemistry of the Compositae* (Heywood et al., 1977), Compositae was formally recognised as a natural family with well-defined limits and a diagnostic floral structure. However, the taxonomic arrangement within the family, comprising 13 tribes, remained little different from that of Bentham (1873), a century before. Over the next 20 years, with the rise of phylogenetic systematics (Hennig, 1966), a large number of morphological cladistic analyses were conducted, and molecular sequence data also began to be applied to systematic questions. This growing body of data was collated by Bremer (1987, 1994, 1996) and presented at a second International Compositae Conference at Kew, in 1995. Compositae was by this time classified into some 17 tribes in four subfamilies. However, it was recognised that several genera (such as *Brachylaena*, *Eremothamnus*, *Gundelia*, *Moquinia* and *Tarchonanthus*) were not members of the major tribes in which they had been placed, and were highlighted as clear examples of what we now call rogue genera.

The vast influx of molecular phylogenetic analyses over the decade following the Kew conference has been integrated by Funk et al. (2005) into a Compositae “meta-supertree”. During this decade, the work of Baldwin et al. (2002) in Heliantheae and Panero and Funk (2002) in Mutisieae led to the recognition of many more tribes — a

total of 34, plus two tribal-level clades — in ten subfamilies. No doubt there will be a few more changes before the classification stabilizes. Some of the new tribes are small, comprising genera that had previously been considered as rogues; and many have not been placed within any of the three traditional subfamilies. Several genera (e.g. *Athroisma*, *Corymbium*, *Cratystylis*, *Gymnarrhena* and *Hecastocleis*) were found to constitute the sister-groups of major evolutionary radiations in Compositae, while yet others remained unplaced at tribal level (e.g. *Catamixis*, *Gladiopappus*). Thus over the past thirty years, while there has been a move towards a more settled phylogeny of Compositae and delimitation of tribes, some problematic taxa have been placed and others thrown out of their traditional positions, leaving a pool of rogue genera that is as large as ever.

1.1. Rogue genera in Compositae

The genera studied here are summarised in Table 1 and can be divided into two categories. Firstly, there are those of known tribe, but whose position within that tribe is in some way unclear. These include *Hesperomannia* A.Gray, a genus of three or four species of small, apomictic trees from Hawaii, traditionally placed in Mutisieae (Cabrera, 1977) but recently transferred to Vernonieae on the basis of molecular sequence data (Kim et al., 1998). In Vernonieae it lies in an uncertain position within a wholly Old World or African clade. In macro-morphology, the sweeping hairs of the styles characteristic of the Vernonieae have been reduced to papillae in

Table 1
Summary of genera investigated

Genus	Number of species	Distribution	Best present estimate of systematic position	Reference
<i>Catananche</i> L.	5	Mediterranean	Unplaced in Cichorieae	Blackmore (1976)
<i>Corymbium</i> L.	c. 9	South Africa	Corymbieae, tribe of uncertain position	Funk et al. (2005)
<i>Eremothamnus</i> O.Hoffm.	1	Namibia	Sister to <i>Hoplophyllum</i> , unplaced in Arctotideae	Karis et al. (2001)
<i>Fitchia</i> Hook. & Arn.	7	Polynesia	Unplaced in Heliantheae	Ryding and Bremer (1992)
<i>Gundelia</i> L.	1	Mediterranean–Middle East	Possible sister group to <i>Warionia</i> , unplaced in Cichorioideae (close to Cichorieae)	(Karis et al., 2001; Panero and Funk, 2002)
<i>Gymnarrhena</i> Desf.	5–6	Middle East	Gymnarrheneae, tribe of uncertain position	Funk et al. (2005)
<i>Hecastocleis</i> A.Gray	1	Nevada, U.S.A.	Hecastocleiae, tribe of uncertain position	Funk et al. (2005)
<i>Hesperomannia</i> A.Gray	3–4	Hawaii, U.S.A.	Unplaced in Vernonieae	Kim et al. (1998)
<i>Hoplophyllum</i> DC.	2	South Africa	Sister to <i>Eremothamnus</i> , unplaced in Arctotideae	Karis et al. (2001)
<i>Moquinia</i> DC.	2	Eastern Brazil	Unplaced in Cichorioideae (Vernonieae–Liabeae)	Funk, pers. comm.
<i>Pacourina</i> Aubl.	1	Tropical America	Unplaced in Vernonieae	Jones (1977)
<i>Platycarpha</i> Less.	3	South Africa	Unplaced in Cichorioideae	Wortley et al. (submitted for publication)
<i>Tarchonanthus</i> L.	2	Africa and Middle East	Tarchonanthae, tribe of uncertain position within Cichorioideae	(Keeley and Jansen, 1991; Kim et al., 2002)
<i>Warionia</i> Benth. & Coss.	1	North-western Sahara	Possible sister group to <i>Gundelia</i> , unplaced in Cichorioideae (close to Cichorieae)	Panero and Funk (2002)

Hesperomannia. Micro-morphological features may also have been structurally simplified, so that they no longer bear much resemblance to most Vernoniaeae. These characters, including pollen, which have been studied by Marticorena and Parra (1975), Hansen (1991a,b) and (Zhao et al., 2006), require further study to provide evidence to support, refute, or refine this placement.

Moquinia DC., was once thought a member of Mutisieae (Candolle, 1838; Cabrera, 1977) and originally interpreted to include many species of *Gochnatia* Kunth. More recently the genus has been placed with *Pseudostiffia* H. Rob. (Vernoniaeae), on the basis of its uniquely thickened upper style shaft and short scabrim form sweeping hairs (Gamerro, 1990). Gamerro (1990) combined *Moquinia* and *Pseudostiffia* into a single genus, while Robinson (1994) maintained them as separate genera in tribe Moquinieae. *Moquinia* and *Pseudostiffia* have not been included in any published molecular studies, but unpublished DNA sequences (Funk and Chan, submitted for publication) place the tribe close to the base of the Vernoniaeae–Liabeae clade but still of uncertain position. Pollen characters formed part of the evidence for separating tribe Moquinieae, but there remains a need for further study of the species' unusual palynology, previously investigated by Wodehouse (1929), Skvarla and Turner (1966), Marticorena and Parra (1975), Skvarla et al. (1977), Gamerro (1990), Hansen (1991a,b) and Telleria and Katinas (2005).

Catananche L. has long been regarded as a highly anomalous and “primitive” member of Cichorieae, perhaps providing a link between the lophate pollen of that tribe and the non-lophate pollen in some of its sister-groups (Wodehouse, 1928). The genus was not included in the recent supertree. Lophate pollen is now considered to have evolved at least four times in Cichorieae (Blackmore, 1986), and also elsewhere in Cichorioideae and Barnadesioideae, making the position of *Catananche* even less clear, particularly since the internal structure of the pollen grains is very different to other Cichorioideae. *Catananche* pollen has been widely studied (Mohl, 1835; Fischer, 1890; Wodehouse, 1928, 1935; Askerova, 1970; Dimon, 1971a,b; Askerova, 1973; Tomb, 1975; Blackmore, 1976; Lack et al., 1980; Blackmore and Dickinson, 1981; Blackmore, 1981, 1982a,b, 1984; Blackmore and Claugher, 1984; Diez, 1987; Barnes and Blackmore, 1987, 1988; Blackmore and Barnes, 1988; Blackmore, 1992) but would benefit from a re-examination in the light of new hypotheses of relationships and pollen data for related taxa.

The monotypic genus *Eremothamnus* O. Hoffm. has previously held positions in Senecioneae (subtribe Liabinae), Arctotideae and Eremothamneae, and has had

little palynological study (Leins, 1970). A series of structural characters including elongate style branches with long and uniquely bifid or trifid sweeping hairs have been invoked to relate the genus to *Hoplophyllum* DC., previously placed in Vernoniaeae (Karis, 1992; Robinson, 1992a). Recent molecular sequence-based studies also suggest that *Eremothamnus* is sister to *Hoplophyllum* (Karis et al., 2001) and that, together, the two genera are most likely related to Arctotideae (Bergqvist et al., 1995). *Hoplophyllum* has itself been proposed as a possible basal branch of the Arctotideae, but has not been included on the supertree. Its pollen has previously been studied by Bolick (1978a,b), Bremer (1987), Robinson (1992a, 1994, 1996) and Zhao et al. (2006).

Another monotypic genus, *Pacourina* Aubl., generally treated as a somewhat isolated and difficult to classify member of the Vernoniaeae (Jones, 1977) has also been omitted from published molecular study. Previous studies of its palynology (Wodehouse, 1928, 1934; Cabrera, 1944; Erdtman, 1952; Bolick, 1978a, 1981; Blackmore, 1986; Robinson, 1992a,b, 1996, 1999a,b) have been inconclusive as to the position of *Pacourina* within Vernoniaeae. There is a need for further study of this genus and its putative relatives, which all share triporate pollen: New World *Acilepidopsis*, *Mesanthophora*, *Telmatophila* and various Old World genera including *Cyanthillum*, *Cabobanthus*, and *Phyllocephalum*. Study is needed to show whether these genera might form a small clade within Vernoniaeae, characterised by pororate pollen.

Fitchia Hook. & Arn. is an unusual woody genus from the Pacific Islands of Polynesia, with complex floral anatomy (Carlquist, 1957). It was previously placed in Cichorieae (e.g. Bentham, 1873) because of its homogamous heads with liguliform corollas, but the position was questioned due to its lack of latex. A position in Mutisieae was suggested by Stebbins (1953). More recently the genus has been placed in Heliantheae or separated into tribe Coreopsidae (Turner and Powell, 1977). Carlquist's (1957) classic study showed that Coreopsidinae could be characterised by strongly obcompressed achenes combined with radial style branches and style traces, and suggested a close relationship of *Fitchia* to *Oparanthus* Sherff, also of the Pacific (Shannon and Wagner, 1997). Morphological cladistic analysis also suggested a placement in Coreopsidae (Ryding and Bremer, 1992), but due to its anomalous morphology and lack of molecular data, the placement of *Fitchia* remains intriguing. Its pollen morphology has been studied using SEM and TEM but remains inconclusive (Carlquist, 1957; Carlquist and Grant, 1963; Skvarla et al., 1977; Bolick, 1984).

Platycarpha Less. has been treated as a member of Mutisieae (Stix, 1960), Arctotideae (Norlindh, 1977), and possibly Cardueae (Robinson and Brettell, 1973). The three species are acaulescent with capitula crowded onto large, sessile, secondary heads. In addition, the anthers are tailed, the florets are purple, and the style branches short and oblong. Based on molecular data (Funk and Chan, submitted for publication) the genus lies on a long branch within Cichorioideae, perhaps close to the basal branches of Arctotideae or Vernonieae, but none of these placements have strong support. *Platycarpha* was not included in the recent supertree, and its pollen has not been investigated since 1960 (Stix, 1960), but is presently being studied in the context of its exclusion from Arctotideae (Wortley et al., submitted for publication).

Gundelia L. also has unusual inflorescences for Compositae, involving tertiary heads. Previously it was placed in Cardueae and then subtribe Gundeliinae of Arctotideae (Norlindh, 1977). Molecular sequence-based analyses have suggested it is more likely a near relative of Cichorieae (Karis et al., 2001; Panero and Funk, 2002) and linked it with *Warionia* Benth. & Coss. (Panero and Funk, 2002; Funk et al., 2005). *Warionia* has been linked to Cardueae and Mutisieae, as well as Cichorieae (Cabrera, 1977; Dittrich, 1977). However, recent work in Cichorieae by Gemeinholzer (pers. comm.) using a much large sampling of the tribe found little support for the sister-group relationship of *Warionia* and *Gundelia*. The two genera may form separate branches at the base of Cichorieae, and their position remains uncertain. The pollen of *Gundelia* has previously been studied only by Stix (1960) and Robinson (1994); that of *Warionia* was studied more intensively, by Dimon (1971a,b), Marticorena and Parra (1975), Dittrich (1977), Qaid (1990), Hansen (1991a,b), Petit et al. (1996) and Zhao et al. (2006).

A second group of rogue genera, outside the major tribes of Compositae, have been grouped into small tribes or elevated as monotypic tribes, and these tribes themselves are of uncertain position in Compositae. They have mostly been elevated in status due to an exceptional degree of divergence and are therefore likely to be particularly interesting and intractable. One such tribe is Tarchonantheae, comprising two genera of dioecious shrubs and trees: *Brachylaena* R.Br., (15 species) and *Tarchonanthus* L. (two species; studied here) which have a highly derived flower type. These two genera were previously considered a subtribe of Inuleae (Bentham, 1873) or Mutisieae. Based on pollen types it was suggested that they may be an early-branching group of Anthemidae (Skvarla et al., 1977).

Molecular sequence analyses confirmed the affinity of the two genera, that they belong in subfamily Cichorioideae (Keeley and Jansen, 1991) and are one of the groups most closely related to the Cardueae (Kim et al., 2002; Funk et al., 2005), so a re-examination of palynological data (previously generated by Erdtman, 1952; Wittenbach, 1970; Leins, 1971; Cilliers, 1991; Hansen, 1991a; Zhao et al., 2006) is needed to see if it is congruent with this placement.

Gymnarrhena Desf. and *Hecastocleis* A.Gray are also the only members of their respective tribes (and subfamilies). They are both highly localised in distribution and very unusual in gross morphology. *Gymnarrhena* was once placed in Inuleae (Bentham, 1873; Hoffmann, 1890) and *Hecastocleis* was considered a member of Mutisieae. *Hecastocleis*, from around Death Valley, Nevada, is placed in molecular phylogenies of Compositae between branches that are largely South American and African in distribution. A better understanding of its pollen may help resolve this biogeographic puzzle. *Gymnarrhena*, from the Middle East, is amphycarpic (having two different types of heads), with one cleistogamous underground type of head and one above ground secondary type containing male and female florets. Both these genera occupy important positions on the main trunk of the supertree which are fundamental to our understanding of Compositae evolution (Funk et al., 2005). *Gymnarrhena* pollen was previously studied by Wittenbach (1970), Dimon (1971a,b), Leins (1973), Skvarla et al. (1977) and Zhao et al. (2006); that of *Hecastocleis* by Wodehouse (1929), Hansen (1991a,b) and Telleria and Katinas (2004, 2005).

Finally *Corymbium* L., a South African genus of about nine species has an unusual morphology, including secondary heads and long, thin, longitudinally-veined leaves, but has undergone little palynological study (Mohl, 1835; Bolick, 1978a,b; Bremer, 1987). It was previously considered to be a slightly anomalous member of Vernonieae (Jones, 1977), but is now placed in its own tribe, Corymbieae, which is thought to be sister to the entire Asteroideae, giving it a crucial position in understanding the evolution of Compositae as a whole.

From this brief overview it can be seen that rogue genera conform to a variety of patterns in terms of historical study and current situation. Although they are found throughout Compositae, there is a concentration of such taxa outside the Asteroideae, in the more basally-branching tribes, particularly Mutisieae or ex-Mutisieae (Zhao et al., 2006). This may be because these tribes and genera are older than those within Asteroideae and have had a longer period over which to evolve or because they have experienced more extinction in intermediate types;

both possibilities leading to exceptionally divergent morphological characters and making relationships harder to infer.

1.2. The role of palynology

During the course of reviewing palynological characters across c. 400 genera in the Compositae supertree (Blackmore et al., submitted for publication), it became apparent that pollen characters form useful patterns in the context of recent molecular hypotheses of relationship, and could be used to support these relationships, or provide diagnostic characters for groups at a variety of levels. We therefore set out to investigate whether palynological characters could also provide new insights into the relationships of previously enigmatic taxa — rogue genera — regardless of whether they had been included in molecular analyses. Palynology provides a whole new set of characters (we defined 52) compared to conventional macro-morphological study. Moreover, while ecological specialisation may lead to morphological divergence at the large scale, it is conceivable that many pollen characters may be exempt from such influences. We are sceptical of using only morphological characters to analyse and determine relationships per se, due to their susceptibility to homoplasy, lack of independence, and difficulty in conceptualisation (Scotland et al., 2003). However, in the context of a robust hypothesis of relationships, such as that provided by the molecular supertree (Funk et al., 2005), morphological characters can provide useful support and confirmation, in terms of synapomorphies for groups and diagnostic characters. They can also

indicate potential relationships which would be worthy of investigation with other types of data, particularly for taxa which are not at present included in the tree. Finally, palynological characters might be found to be completely incongruent with the molecular phylogeny and therefore indicate groups for which the phylogeny needs to be reassessed or investigated further.

2. Materials and methods

From a survey of the literature on Compositae systematics, and our experience, we identified a set of fourteen rogue genera to investigate. We surveyed the extensive literature to document the pollen morphology of these genera and their putative relatives among the members of the Compositae. For those taxa where sufficient data were not available, pollen was extracted from herbarium specimens at the collections of E, K and US (see Table 2). Pollen was prepared by acetolysis as described by Erdtman (1960) and viewed with light (LM) and scanning electron microscopy (SEM). Pollen mounted in glycerine jelly was examined in transmitted light using Leitz Wetzlar and Zeiss Axioscop microscopes. Pollen for SEM examination was pulse sputter coated with a gold or gold/palladium (60/40) target and examined with JEOL 880, Leica Stereoscan 440, Hitachi S800 and Zeiss Supra 55VP scanning electron microscopes.

The pollen of each selected genus was then described and compared with that of potential related taxa in Compositae, as documented in Blackmore et al. (submitted for publication). Conventional pollen morphological terminology is used, as described in Blackmore et al. (submitted for publication).

Table 2
List of voucher specimens from which material was taken for SEM study

Species	Collection	Locality and date	Herbarium	Figure
<i>Catananche caerulea</i> L.	Lipert 25532	Morocco, s.d.	US	I,7–8
<i>Catananche caerulea</i> L.	No voucher	Cult., Chelsea Physic Garden, s.d.	–	I,3–4
<i>Corymbium africanum</i> L.	Hanekom 2547	Kaap, South Africa, 25 Dec 1978	US	I,11–12
<i>Eremothamnus marlothianus</i> O.Hoffm.	Durham 25	South Africa, 16 Oct 1925	K	I,11–12
<i>Eremothamnus marlothianus</i> O.Hoffm.	Dinter 6408	South Africa, 28 May 1929	K	I,13–14
<i>Fitchia tahitensis</i> Nadeaud	Florence 3881	Mount Marau, Tahiti, 29 Sep 1982	US	I,19–20
<i>Gundelia tournefortii</i> L.	Altas 18685	Unknown	K	II,7–8
<i>Gymnarrhena micrantha</i> Desf.	Mandavilla 157	Dharan, Saudi Arabia, 2 Apr 1964	US	II,9–10
<i>Hecastocleis shockleyi</i> A.Gray.	Alexander & Kellogg 5301	California, USA, 4 Jun 1947	US	I,1
<i>Hesperomannia arborescens</i> A.Gray	Takeuchi 2206	Hawaiian Islands, s.d.	GH	I,2
<i>Hesperomannia lydgatei</i> C.N.Forbes	Stauffer & Dehler 5912	Hawaiian Islands, s.d.	UC	I,9–10
<i>Hoplophyllum spinosum</i> DC.	Koekemeer 2045	South Africa, 25 Oct 2000	US	I,3–4
<i>Moquinia racemosa</i> DC.	Hatschbach & Nicolack 53407	Bahia, Brazil, s.d.	K	I,5–6
<i>Pacourina edulis</i> Aubl.	Sandeman 4857	South Chaho, Paraguay, s.d.	K	I,15–16
<i>Platycarpha carlinoides</i> Oliver & Hiern.	Bergland 3549	Vorberge de Anausberge, Namibia, 1963	US	II,3–4
<i>Tarchonanthus camphoratus</i> L.	Barbex 760	Eritrea, 4 Mar 1892	US	II,1–2
<i>Warionia saharae</i> Benth. & Coss.	Forthher s.n.	Morocco, 13 Apr 1986	US	I,19–20

3. Results and discussion

New palynological data were obtained for fourteen rogue genera in Compositae (Table 2). These are described below, along with a discussion of the implications of palynological characters for the systematics of rogue genera.

3.1. Genera of unknown position within tribe

The pollen of *Hesperomannia* (Plate I, Figs. 1,2) is c. 45 μm in diameter, oblate-spheroidal in equatorial view, circular in polar view and tricolporate. The ectoapertures are separate and narrow with acute ends, the endoapertures lalongate; a mesoaperture is sometimes visible. The grains are echinate and non-lophate, the spines few, sparsely and unevenly distributed, conical–cylindrical, 2.5–3.5 μm long, the spines forming a right-angle with the surface of the grain. The tectum is microperforate. The infratectum consists of a single layer of very thick, distally-branching columellae, which are slightly aggregated beneath the spines; the grains are ecaveate and the endexine is thicker than the foot layer.

This type of pollen grain is unlike any other in Compositae, particularly in its cylindrical, isolated spines. However, as noted by Zhao et al. (2006), it is profoundly unlike the typical prolate, psilate grains of Mutisieae (Zhao et al., 2006), and shares a number of palynological characters with African Vernoniae (Robinson, 1999b), among them an uneven distribution of spines and aggregation of columellae beneath them. In the context of the great variability of pollen types within the African Vernoniae (Robinson, 1999b), ranging from echinate

and non-lophate in *Polydora* Fenzl to nearly psilate and lophate in *Cabobanthus* H. Rob., the pollen of *Hesperomannia* could more plausibly fit into this tribe than into Mutisieae, where it was previously placed (Cabrera, 1977). This would support the results of molecular phylogenetic analysis (Kim et al., 1998). The apomictic nature of *Hesperomannia* may have provided a relaxation of the selective constraints on some features of pollen morphology which, in a tribe with extraordinarily plastic pollen morphological characters, resulted in the distinctive grains seen in Plate I, Figs. 1,2.

The pollen of *Moquinia* (Plate I, Figs. 3,4), is c. 30 μm in diameter, spheroidal in equatorial view, sub-triangular in polar view, and tricolporate. The ectoapertures are often syncolpate and of medium width with obtuse ends (where separate), the endoapertures lalongate; a mesoaperture is sometimes visible. The grains are echinate and non-lophate, the spines unevenly distributed, conical-pointed, 4–5 μm long, solid, sometimes with swollen bases or linked by a raised tectum. The tectum is microperforate and microreticulate. The infratectum comprises two distinct layers, a spongy outer layer and an inner supporting layer of thick, distally-branched columellae, forming channels beneath the spines; the grains are ecaveate and the endexine is thicker than the foot layer.

As noted by Skvarla et al. (1977), this combination of characters is very unusual for Mutisieae, in which it has been placed (Cabrera, 1977) and, like that of *Hesperomannia*, more suggestive of a relationship to Vernoniae. However, it differs from the most similar, echinate pollen of Vernoniae in the comparatively random arrangement of columellae in relation to the spines, rather than columellae

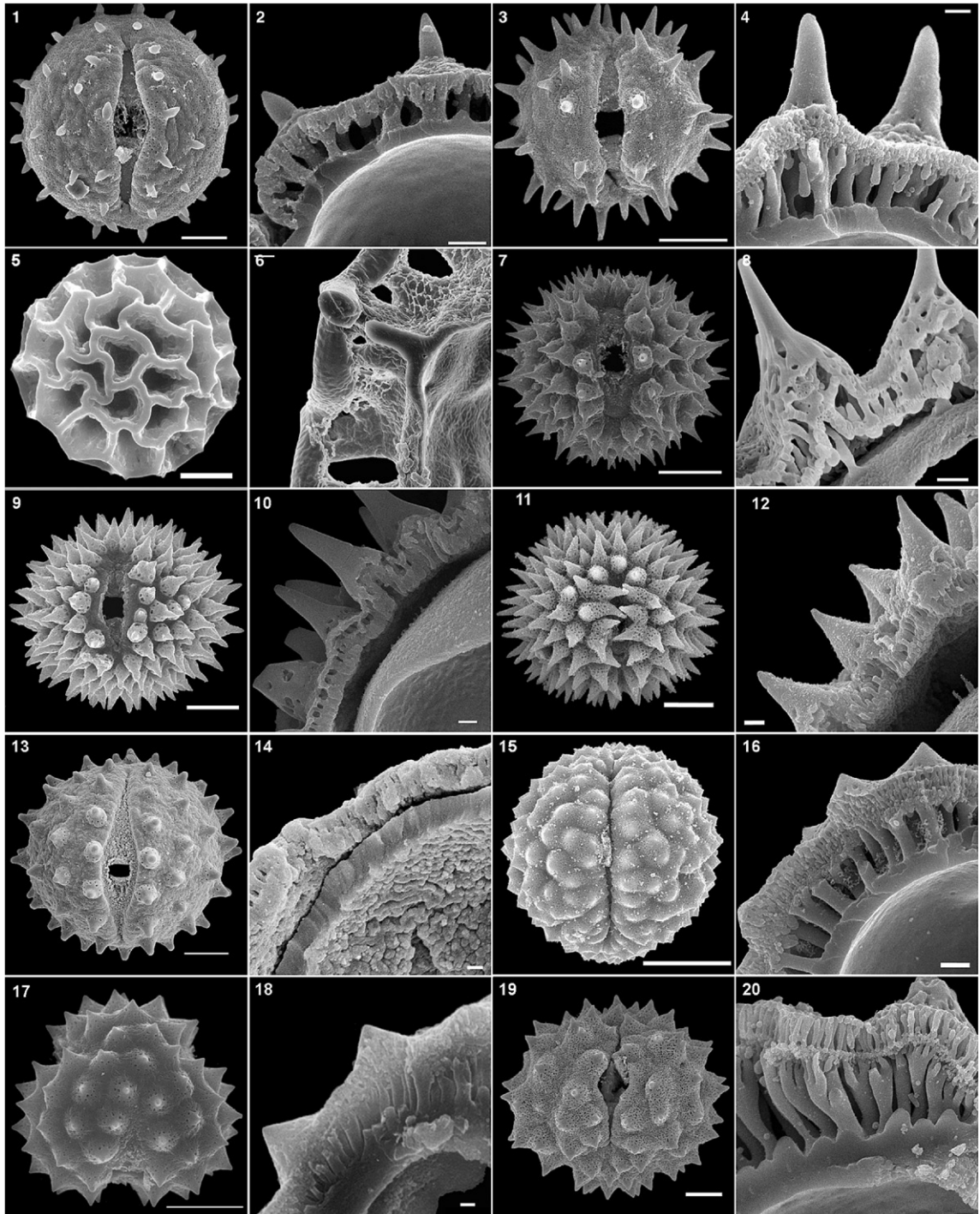
Plate I. SEMs of pollen of Compositae rogue genera. Scale bars: whole grains 10 μm , sections 1 μm .

1. *Hesperomannia lydgatei* Forbes, apertural view.
2. *Hesperomannia arborescens* A. Gray, section through exine.
3. *Moquinia racemosa* DC., apertural view.
4. *M. racemosa* DC., section through exine.
5. *Pacourina edulis* Aubl., apertural view.
6. *P. edulis*, exine structure.
7. *Catananche caerulea* L., apertural view.
8. *C. caerulea*, section through exine.
9. *Hoplophyllum spinosum* DC., apertural view.
10. *H. spinosum*, section through exine.
11. *Eremothammus marlothianus*, apertural view.
12. *E. marlothianus*, section through exine.
13. *Fitchia tahitensis* Nadeaud., apertural view.
14. *F. tahitensis*, section through exine.
15. *Platycarpha carlinoides* Oliver & Hiern., apertural view.
16. *P. carlinoides*, section through exine.
17. *Gundelia tournefortii* L., apertural view.
18. *G. tournefortii*, section through exine.
19. *Warionia saharae* Benth. & Coss., apertural view.
20. *W. saharae* Benth. & Coss., section through exine.

being centred under each spine. These observations highlight the need for better molecular sequence data to test the potential affinities of *Moquinia*, and suggest Vernoniaeae as a starting point for such an analysis.

Unplaced within Vernoniaeae, *Pacourina* pollen (Plate I, Figs. 5,6) is c. 45 μm in diameter, spheroidal

in equatorial view, circular in polar view, and triplicate. The endoapertures are circular. The grains are psilate (lack spines) and lophate, the lacunae irregular, 4–12 μm in diameter. The tectum is imperforate. The infratectum comprises a single solid layer. The grains are ecaevate, the endexine thicker than the foot layer.



The lack of a perforated tectum is very characteristic of many Vernoniae, especially the tripororate genera. *Pacourina* pollen is thus very similar to that of *Cabobanthus* H. Rob., *Centauroopsis* Boj. ex DC., *Cyanthillium* Blume and some species of *Polydora*. These taxa are part of a well-defined, intermittently pororate clade within Old World Vernoniae, and pollen characters strongly suggest that *Pacourina*, despite being restricted to Tropical America, is also a member of this clade, along with the South American tripororate genera *Acilepidopsis* H. Rob., *Mesanthophora* H. Rob. (Robinson, 1992b), and *Telmatophila* Mart. ex Baker.

Catananche pollen (Plate I, Figs. 7,8), unplaced in Cichorieae, is c. 35 μm in diameter, spheroidal in equatorial view, sub-triangular in polar view, and tricolporate. The ectoapertures are separate and of medium width with obtuse ends, the endoapertures circular. The grains are echinate and non-lophate, the spines many, dense, unevenly distributed, conical-pointed, 5–6 μm long, with distinctly swollen bases and internal cavities, the tectum slightly raised between some spines. The tectum is microperforate and microreticulate. The infratectum comprises a single layer of short, unbranched columellae and a partial cavea spanned by thin, un-branched columellae, swollen at the base and passing into the hollow spines; there are prominent internal foramina (Skvarla et al., 1977). The endexine is thicker than the foot layer.

This set of characteristics is very unlike the pollen of any other Cichorieae, in particular in the absence of lophae and presence of internal foramina. The closest overall match to the pollen of *Catananche* is found in another rogue genus, *Hoplophyllum* (Plate I, Figs. 9,10), which has very similar ornamentation: the pollen of *Hoplophyllum* is c. 42 μm in diameter, spheroidal in equatorial view, circular or sub-triangular in polar view, and tri- or tetra-colporate. The ectoapertures are separate and of medium width with obtuse ends, the endoapertures lalongate. The grains are echinate and non-lophate, the spines many, dense, unevenly-distributed, conical-pointed, 5–8 μm long, with bases slightly swollen and internal cavities. The tectum is microperforate. The infratectum comprises two indistinct layers, the outer layer columellate, the inner supporting layer spongy. The grains are caveate, the endexine thicker than the foot layer.

In *Hoplophyllum* the cavea is not spanned by columellae, but their scarcity in *Catananche* and the presence of occasional unattached columellae extending into the cavea of *Hoplophyllum* suggests it could be easy to switch between these two states, which are part of a broad continuum between fully caveate and fully

columellate. A partial cavea spanned by thin, unbranched columellae passing into the hollow spines is also approached in the pollen of *Munnozia lyrata* (A.Gray) H. Rob. & Brettell (Liabeae; Robinson and Marticorena, 1986). Both genera are considered to be relatively basal branches of the cichorioid tribes (Cichorieae and Arctotideae), suggesting their pollen might provide an insight into the ancestral pollen characters of the sub-family.

Recent morphological and molecular sequence-based studies have suggested that *Hoplophyllum* is the sister-group of *Eremothamnus* (Karis et al., 2001; Funk et al., 2004). The pollen of *Eremothamnus* (Leins, 1970; Plate I, Figs. 11,12) is c. 48 μm in diameter, oblate-spheroidal in equatorial view, sub-triangular in polar view, and tri- or tetra-colporate. The ectoapertures are separate and of narrow-medium thickness with obtuse ends, the endoapertures lalongate. The grains are echinate, the spines many, dense, conical with a long tapering point, up to 8 μm long, the bases slightly swollen. The tectum is microperforate. The infratectum comprises two indistinct layers, the outer layer columellate, the inner supporting layer spongy — which might indicate the presence of internal foramina. The grains are caveate, with a few narrow columellae rising from the foot layer (Fig. 12) as in *Catananche*. The endexine is thicker than the foot layer. Thus the grains of *Eremothamnus* are strikingly similar to those of both *Catananche* and *Hoplophyllum*. The results of the pollen analysis for these three genera suggest either that the three are very closely-related, or, if they are members of different tribes (*Catananche* of Cichorieae and *Eremothamnus* and *Hoplophyllum* of Arctotideae), that they share the plesiomorphic pollen condition for the Cichorioideae as a whole. Molecular data have now suggested a placement for *Eremothamnus* and *Hoplophyllum* within or close to Arctotideae (Funk et al., 2004). Molecular data are urgently needed for *Catananche* in order to assess its position relative to these and other taxa in Cichorioideae, and thus to determine the primitive pollen type for this particularly interesting and morphologically plastic subfamily. Pollen characters may be able to provide a morphological link between these three genera that are so different in gross morphology and distribution.

Fitchia pollen (Plate I, Figs. 13,14) is c. 48 μm in diameter, spheroidal in equatorial view, circular in polar view, and tricolporate. The ectoapertures are very long, separate or syncolpate and of medium width with acute ends; the endoapertures are circular. The grains are echinate, non-lophate, the spines spaced well apart, conical with rounded or pointed tips, 3–5 μm long, forming an obtuse angle with the surface of the grain. The tectum is microperforate. The infratectum comprises a

single layer of short, straight, unbranched columellae, evenly-distributed across the grain, with abundant internal foramina (Skvarla et al., 1977). The grains are fully caveate, the cavea shallow and the endexine thicker than the foot layer.

Fitchia's blunt, rounded spines are unlike anything in Heliantheae or Coreopsideae, where the genus is now placed (Ryding and Bremer, 1992; Shannon and Wagner, 1997), or indeed anywhere in Asteroideae, yet the single-layered exine with a full cavea strongly suggests affinity to Asteroideae. Syncolpate grains are rare and homoplastic in Compositae. To date, the pollen morphological characters of *Fitchia* have proven as inconclusive as all other characters in determining the relationships and evolution of the genus and we continue to rely on the molecular data for its placement.

The pollen of South African *Platycarpha* (Plate I, Figs. 15,16; see also Wortley et al., submitted for publication) is c. 25 μm in diameter, prolate-spheroidal and tricolporate. The ectoapertures are long and narrow with acute ends, the endoapertures alongate. The grains are echinate and non-lophate, the spines sparse, rounded-triangular, 1 μm long, forming an obtuse angle with the surface of the grain. The tectum is microperforate. The infratectum comprises two distinct layers, an outer layer of very small overlapping columellae or spongy and an inner supporting layer of long straight columellae, sometimes distally-branching, evenly-distributed across the grain. The grains are ecaveate and the endexine is thicker than the foot layer.

These pollen characters suggest nothing to link *Platycarpha* to any genera of Cichorioideae, the subfamily of which it is thought to be a member. In particular, like *Moquinia*, it lacks the aggregation of columellae underneath spines which is thought to be characteristic of this group (Blackmore et al., submitted for publication). In fact the closest match to the pollen of *Platycarpha* is found in the Madagascan *Gladiopappus* Humbert (Mutisieae). The pollen of *Gladiopappus* has very similar robust, inner columellae and finer outer columellae extending into triangular spines. These data suggest that the pollen of the two Old World genera *Platycarpha* and *Gladiopappus*, neither of which was included on the recent supertree, may indicate a relationship to other elements placed in the Mutisieae which should be further investigated through phylogenetic analysis.

The pollen of *Gundelia* (Plate I, Figs. 17,18) is c. 48 μm in diameter, spheroidal in equatorial view, circular in polar view, and tricolporate. The ectoapertures are separate and of medium width with acute ends, the endoapertures are alongate and a mesoaperture is

present. The grains are echinate and non-lophate, the spines evenly-distributed, conical-pointed, 4 μm long, with swollen bases. The tectum is microperforate. The infratectum comprises up to four indistinct layers, including columellate outer and inner layers and a spongy internal tectum; the inner columellae are thick, branched, and aggregated beneath the spines, where they hang without meeting the foot layer. The grains are partially caveate and no endexine layer was seen under SEM.

The pollen of its putative sister-group *Warionia* (Plate I, Figs. 19,20) is very different at the ultrastructural level. It is c. 58 μm in diameter, spheroidal in equatorial view, circular or sub-triangular in polar view, and tricolporate. The ectoapertures are separate with acute ends, the endoapertures alongate. The grains are echinate and non-lophate, the spines unevenly-distributed, conical-pointed or rounded, 5 μm long, with bases slightly swollen and internal cavities, linked by raised areas of tectum. The tectum is microperforate. The infratectum comprises three distinct layers, an outer layer of fine, straight columellae, a well-defined, spongy internal tectum and an inner supporting layer of large, smoothly undulating columellae, distally-branching and slightly swollen at the base. The grains are ecaveate and the endexine is thinner than the foot layer.

The linking of these two genera into the tribe Gundelieae is still controversial and the pollen data are strongly incongruent with this, suggesting instead that the two genera may lie on separate branches within the Cichorioideae, where highly plastic pollen characters are the norm. Contrary to the conclusions of Karis et al. (2001), their non-lophate pollen suggests neither is a member of Cichorieae, although the pollen of *Gundelia* does bear some superficial similarity to the one other non-lophate Cichorieae genus, *Catananche* (Plate I, Figs. 7,8).

3.2. Unplaced tribes

The pollen of Tarchonantheae, represented by *Tarchonanthus* (Plate II, Figs. 1,2) is c. 25–28 μm in diameter, prolate-spheroidal in equatorial view, circular-triangular in polar view, and tri- or tetra-colporate. The ectoapertures are separate with acute or obtuse ends, the endoapertures alongate or circular. The grains are non-lophate and scabrate with rounded or conical micro-ornamentation. The tectum is microperforate or imperforate. The infratectum comprises one or two distinct layers of unbranched, evenly-distributed, solid columellae, separated by a spongy internal tectum (not shown). The grains are ecaveate with an endexine thicker than or the same thickness as the foot layer (Wittenbach, 1970; Leins, 1971; Cilliers, 1991; Hansen, 1991a; Zhao et al., 2006).

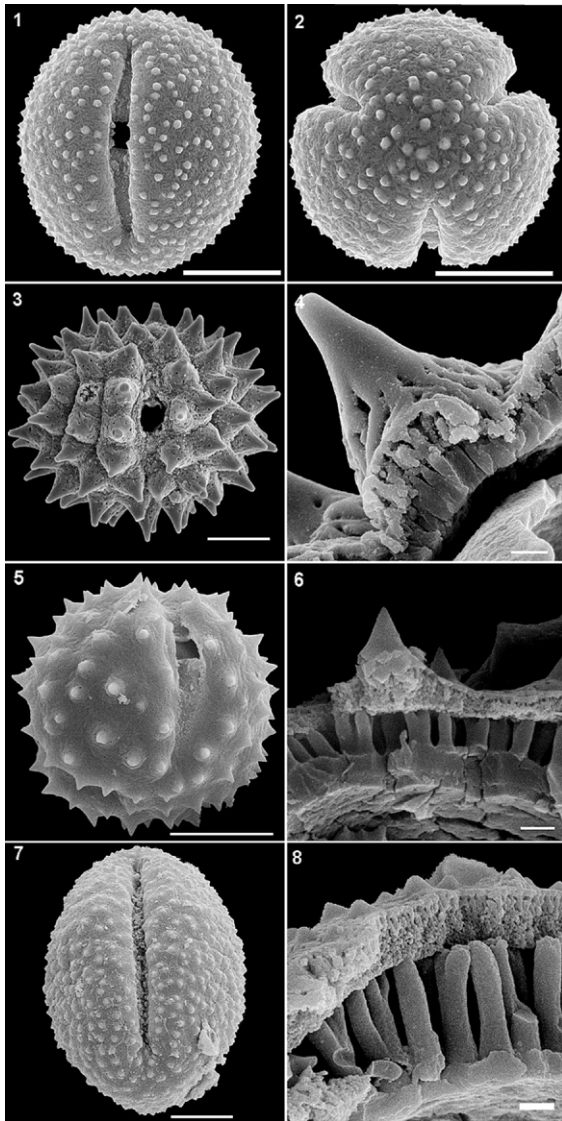


Plate II. SEMs of pollen of Compositae rogue genera. Scale bars: whole grains 10 μm , sections 1 μm .

1. *Tarchonanthus camphoratus* L., apertural view.
2. *T. camphoratus*, polar view.
3. *Corymbium africanum* L., apertural view.
4. *C. africanum*, section through exine.
5. *Gymnarrhena micrantha* Desf., apertural view.
6. *G. micrantha*, section through exine.
7. *Hecastocleis shockleyi* A.Gray., apertural view.
8. *H. shockleyi*, section through exine.

Zhao et al. (2006) noted that the approximately equal thickness of the two columellate layers seen in Tarchonantheae is reminiscent of *Nassauvia* in the Mutisieae. The scabrate, slightly prolate nature of these grains and their evenly-distributed columellae is certainly incongruent with a placement in Cichorioideae and sug-

gests Tarchonantheae is more likely found on an earlier branch of Compositae, as suggested by recent analyses which place it close to the base of Cardueae (Funk et al., 2005).

The pollen of *Corymbium* (Plate II, Figs. 3,4) is c. 43 μm in diameter, oblate-spheroidal in equatorial view, sub-triangular in polar view, and tricolporate. The ectoapertures are separate with obtuse ends, the endoapertures lalongate. The grains are echinate and non-lophate, the spines evenly-distributed, conical-pointed, 4–5 μm long, forming an obtuse angle with the surface, with internal cavities. The tectum is reticulate and microperforate. The infratectum comprises two distinct and separate layers, both layers columellate, without an internal tectum. The columellae are unbranched and evenly-distributed. The grains are caveate, the cavea shallow, and the endexine is thicker than the foot layer. Thus despite its past placement in Vernonieae (Jones, 1977), the pollen characters of *Corymbium* show a high degree of congruence with its newly-proposed position as sister to Asteroideae. These include the cavea, reticulate surface and spine shape.

Gymnarrhena, the sole member of tribe Gymnarrheneae has pollen (Plate II, Figs. 5,6) that is c. 25 μm in diameter, spheroidal in equatorial view, circular in polar view, and tricolporate. The ectoapertures are separate with acute ends, the endoapertures lalongate. The grains are echinate and non-lophate, the spines unevenly-distributed, conical-pointed, 1–2 μm long, with bases slightly swollen and internal cavities. The tectum is microperforate. The infratectum comprises two distinct layers which are not clearly attached to one another; the outer layer is columellate or spongy, the inner supporting layer made up of thick, unbranched, solid columellae, evenly-distributed around the grain. The grains are ecaveate and the endexine is thinner than the foot layer.

Despite the sparse spines and lack of a cavea, the ultrastructure of these grains, with unattached layers of evenly-distributed columellae, does not fit into the Cichorioideae (Anderberg et al., 2005) and is suggestive of the characteristics of Corymbieae, the sister group of Asteroideae. This is not as incongruent with the molecular phylogeny as it might seem, since *Gymnarrhena*, the Cichorioideae, and *Corymbium* lie on successive branches of the tree.

Conversely, the pollen of *Hecastocleis* raises more questions than it solves (Plate II, Figs. 7,8). It is c. 25 μm in diameter, prolate-spheroidal in equatorial view, circular or triangular in polar view, and tricolpate. The ectoapertures are separate and broad. The grains are psilate at the 1 μm level (having spines reduced to minute bumps) and non-lophate, granulose. The tectum is microperforate.

The infratectum comprises two very distinct layers, an outer, spongy layer and unattached inner supporting layer of robust, straight, evenly-distributed columellae. The grains are ecaevate and the endexine is thicker than the foot layer.

This exine ultrastructure is also very similar to that of *Gymnarrhena* and the caveate *Corymbium*. However the prolate shape and psilate, granulose surface are clearly similar to more basally-branching taxa such as Mutisieae. Its colpate grains are extremely rare in the Compositae and remain enigmatic at this time.

4. Conclusions

In two of the case studies outlined above (*Fitchia* and *Hecastocleis*), pollen characters proved to be of questionable value in the placement of the genera, with the taxa displaying a mixture of characters of different groups as well as some that are unique. However, in the majority of case studies pollen morphological characters were at least interesting and sometimes highly informative. For a number of taxa (including *Hesperomannia*, *Hoplophylum* and *Eremothamnus*, Tarchonantheae, Corymbieae and Gymnarrheneae), pollen morphological characters were found to provide support, in the form of synapomorphies, and diagnostic characters, for the relationships proposed through the use of molecular sequence data, or to support one molecular-based hypothesis over another. For others (including *Moquinia*, *Catananche*, *Pacourina* and *Platycarpha*), pollen characters suggested potential relationships for taxa that had not yet been included in the supertree based on molecular sequence data, and thereby help to target future research. In a final example, *Gundelia* and *Warionia*, pollen characters were incongruent with the relationships suggested by molecular data. These instances can also provide useful insights into character evolution, such as the potential for the shared pollen characters of *Eremothamnus*, *Hoplophylum* and *Catananche* to provide insights into the plesiomorphic condition underlying the variety of pollen characters seen in subfamily Cichorioideae. In addition the affinities suggested by palynological data raise interesting biogeographic questions, such as the relationship between the New World *Pacourina* and its most similar relatives in Vernonieae, all from the Old World.

Pollen morphology in Compositae, particularly outside Asteroideae, is highly variable and can provide a large number of characters for study. These characters may be useful in placing rogue genera for which traditional morphological studies have been inconclusive, due to their distinctness and large number of autapomorphies. As with all morphological data, pollen characters

are highly homoplastic and subject to convergence through repeated, parallel evolutionary events, so they should not be used to build a systematic scheme in isolation. However, in the context of a robust hypothesis of phylogeny derived from an independent data source (such as the molecular sequence-based supertree), they can provide support and diagnosis for groupings on the tree, suggest possible affinities for taxa not yet included in the tree, or contradict the relationships seen and suggest areas for future research.

Acknowledgements

The authors would like to thank the staff of the molecular and microscope laboratories at the Royal Botanic Garden Edinburgh for their help, including Frieda Christie and Ruth Hollings; Marjorie Knowles and Carol Kelloff at the Smithsonian's National Museum of Natural History, Washington DC; Gregory Strout and William Chissoe of the Noble Electron Microscopy Lab, University of Oklahoma, Norman, Oklahoma; and Zaiming Zhao and Robert Jansen for provision of images. We also thank the herbaria at E, K and US, from which pollen was taken from specimens for analysis. We would also like to thank Editor-in-Chief Henk Visscher and two anonymous reviewers for their very useful comments on the manuscript. These data were first presented as a contributed paper at the third meeting of the International Compositae Alliance, Barcelona, July 2006.

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