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Pollen of the Asteraceae from the Paleocene-Eocene of South Africa

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Two species of dispersed pollen (*Tubuliforidites antipodica* and *T. viteauensis*) that have affinity with the Asteraceae were recovered from Paleocene-Eocene sediments of South Africa. This is the earliest unequivocal record of the Asteraceae. The two species were examined with light, scanning, and transmission electron microscopy. The pollen wall structure of both taxa are of the Anthemoid type, a pollen wall structural type considered to be primitive among asteraceous pollen. The wall structure type is indicative of many taxa of the Mutisieae. The appearance of this pollen type in the Paleocene-Eocene of South Africa supports a early Tertiary, west Gondwana origin of the Asteraceae, and the evolutionary basal position of the Mutisieae.

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The Asteraceae are comprised of about 1,500 genera and 23,000 species arranged in 3 subfamilies and 17 tribes. The Asteraceae have a cosmopolitan distribution, and may be one of the most conspicuous plant families in the world. The size and distribution of the family intuitively suggest a long evolutionary history.

The Asteraceae are separated into three subfamilies, the Barnadesioideae, the Cichorioideae and the Asteroideae (after Bremer 1994). The numerous palynological studies on extant asteraceous pollen provide a substantial data base (e.g Thanikaimoni 1977) for comparison with fossil dispersed pollen. Many taxa in the Asteraceae have distinctive pollen characteristics that can be easily recognized in dispersed fossil pollen record using light, scanning and transmission electron microscopy. Paleopalynologists traditionally separated the pollen into two groups based on the gross morphology of the pollen grain, the liguliflorae-type characterized by echinolophate pollen, which is generally found in the Cichorieae, and the tubuliflorae-type, which is found in many other tribes (Muller 1981). Skvarla & Turner (1966) and Skvarla et al. (1977) using gross morphology of extant pollen recognized three pollen types, i.e., psilate (this type can not be easily recognized as Asteaceae in the dispersed pollen record), echinate, and lophate pollen. Based on pollen wall ultrastructure, Skvarla & Turner (1966) and Skvarla et al. (1977) further refined these pollen types and recognized five major pollen wall types, the Helianthoid, the Senecioid, the Arctotoid, the Anthemoid type and pollen types without designated patterns. These pollen types are variously distributed among the Cichorioideae and the Asteroideae. Pollen of the Barnadesioideae is similar to the echinolophate pollen of the liguliflorae-type, but lacks the spines. Comparison of the pollen types of extant taxa in the Asteraceae with dispersed pollen may provide insight into the time and place of origin of the Asteraceae.

Dispersed pollen recovered from the Oligocene and younger sediments is assignable to the Asteraceae based on features examined with the light and scanning electron microscopy (Muller 1981, and references therein; Barreda 1993). There are reports of Eocene Asteraceae pollen from Egypt (Kedves 1971) and Afghanistan (Lang & Meon-Vilian 1976), which may be the oldest record of pollen of the Asteraceae, however, these reports are unconfirmed by detailed morphological investigation. There are other reports of pre-Oligocene dispersed asteraceous pollen (Turner 1977, Kemp & Harris 1975, 1977), however, Muller (1981) rejects these as being unreliable. Dettmann & Jarzen (1988) report the occurrence of the genus *Tubulifloridites* from the Upper Cretaceous of Australia and Antarctica, however, these taxa, although morphologically assignable to this form genus, lack the characteristics that permit their unequivocal association with the Asteraceae.

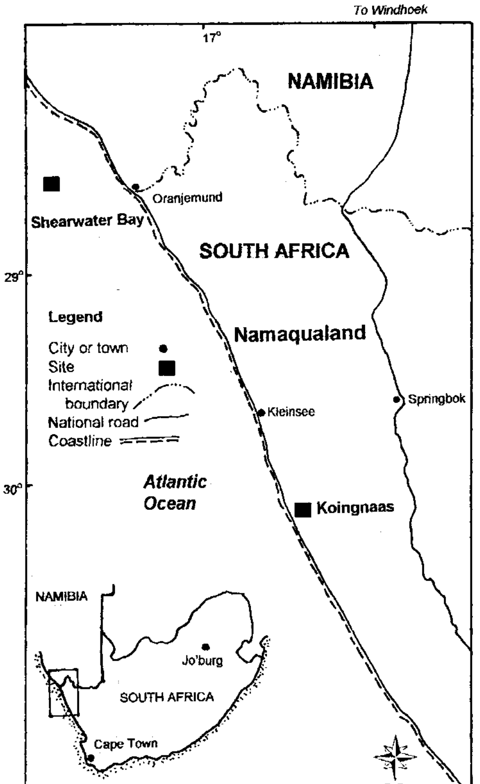
The first megafossil evidence for the Asteraceae may be an Eocene leaf, *Hieracites salyorum* from Aix-en-Provence, France (Saporta 1862), and Collinson et al. (1993) compared a fruit recovered from the Eocene of Europe with the Asteraceae, however, other than superficial appearance, there are no other features to suggest affinity with the Asteraceae. The Oligocene-Miocene taxon *Viguiera cronquistii* from Montana (Becker 1969) was thought to be the first unequivocal megafossil of the Asteraceae, however, Crepet & Stuessy (1978) presented evidence to suggest that this fossil may represent a plant organ from a variety of other families. Despite the precociousness of the extant Asteraceae the megafossil record is meager, and provides little insight into the time and origin of the family. The dispersed pollen record of the Asteraceae suggests that the family was widespread by the Upper Oligocene and subsequently diversified.

This paper reports the occurrence of two asteraceous dispersed pollen types, *Tubulifloridites antipodica* Cookson 1947 ex Potonie 1960 and *T. viteauensis* Barreda 1993 from the Upper Paleocene – Eocene of South Africa. This constitutes the earliest unequivocal occurrence of asteraceous pollen in the fossil record. We amend the descriptions of these taxa to include pollen wall ultrastructure and discuss the importance of these taxa to the evolution of the Asteraceae.

MATERIALS AND METHODS

Samples were collected from two localities, one offshore locality and one onshore locality. Samples were collected offshore on the research vessel Shearwater Bay, approximately 50 km due west of Orangemund and Alexander Bay (Text-Figure 1). They were initially used for a micropalaeontological study (McMillan & Dale, unpublished data) and those which appeared to contain sufficient organic debris were submitted to the Bernard Price Institute (BPI) for palynological analysis. The onshore samples were taken from a paleochannel at Koingnaas (Text-Figure 1). The site consisted of a quarry as described by de Villiers & Cadman (1997). The two sample suites are referred to in this paper as Shearwater Bay meaning those of Eocene age derived from the continental shelf, and Koingnaas meaning the onshore paleochannel sediments of Paleocene-Eocene age. The maceration of the samples follow Faegri & Iversen (1992), Gray (1965), and Doher (1980).

One portion of the residue was used to prepare slides for light microscopy and scanning electron microscopy (SEM) at BPI. Another portion was sent to Providence College for further SEM and transmission electron microscopy (TEM). For light microscope slides, residues where dehydrated in an alcohol series and mounted with D.P.X. (BHD Chemicals, UK), the coverslips were sealed with nail polish and were examined using a Zeiss microscope. For SEM the Koingnaas material was mounted on SEM stubs with DAG-580 and coated with gold-palladium and viewed with an Amray-1000 scanning electron microscope in the University of the Witwatersrand Electron Microscopy Unit.



Text-Figure 1. Locality Plan.

To isolate individual pollen grains from the pollen residues for SEM and TEM, the pollen residues were first dehydrated in an alcohol series (10%, 50%, 95%, 100%, acetone, xylene) followed by acetone and ultimately brought into xylene. The residue was then mixed with a polystyrene based mounting medium ProTexx and smeared on a microscope slide and allowed to polymerize without a cover slip. The slides were then scanned, and individual pollen grains were cut out of the hardened polystyrene and placed on a 0.05 μm pore Millipore filter that was on several sheets of filter paper. Xylene was then dripped over the polystyrene square containing the pollen grain until all of the polystyrene was removed. The pollen grain was then transferred to an SEM stub that had been previously prepared by melting a thin coating of the high vacuum wax Apiezon W-100 on the stub (Wachtel 1980), on which a numbered grid was inscribed. The pollen grain was placed within a grid square. This was repeated until the 16 grid squares each contained a single pollen grain. The SEM stub was coated with gold-palladium and the pollen was viewed on an Amray-1000. After photographing the pollen viewed with the SEM, the individual pollen grains were then transferred to a small agar block, dehydrated in an alcohol series, embedded in Spurr's low viscosity resin, sectioned on a MT-2b ultra-microtome and viewed, without staining, on a Philips EM-300.

A total of 24 specimens of *Tubulifloridites vitauensis* and 19 specimens of *T. antipodica* were photographed and studied with light microscopy. Approximated 16–26 specimens of each species were viewed with the SEM and six specimens of each species were examined with the TEM.

RESULTS

Samples recovered from the Shearwater Bay locality on western continental shelf of South Africa were dated as Eocene (54–38 Mya).This is based on the occurrence of the foraminifera, *Globigerinatheka index*, *Turborotalia centralis* and *Eponides lisbonensis* (McMillan & Dale, unpublished data). The palynological analysis, based on known age ranges of *Clavatricolporites*, *Oacolpopollenites* and *Porosipollis* supports this age determination. The Shearwater Bay pollen assemblage is dominated by pollen of dicotyledonous angiosperms (de Villiers & Cadman 1997, de Villiers 1998). The most abundant palynomorphs are of *Rhoipites*, a genus accommodating reticulate tricolporate grains of generalized morphology. This pollen type accounted for about 50% of the assemblage. Other common palynomorphs include *Nyssapollenites* (7% of the assemblage), *Retitriletes* (5% of the assemblage), and low percentages of *Cyathidites*, *Laevigatosporites*, *Proteacidites*, *Arecipites*, *Liliacidites*, *Podocarpidites* and *Cupaniedites*. Pollen exhibiting features of the Asteraceae were present in all of the Shearwater Bay samples and comprise 14–27% of the total palynomorph content depending on the sample.

Another suite of samples derived from Koingnaas locality, which are sediments that infill a paleochannel adjacent to the coast were subject to routine palynological analysis, and were found to contain similar asteraceous pollen in only 1/3 of the samples, and comprise 2% of the total palynomorph content. The samples from Koingnaas are considered older than the Shearwater Bay samples and are dated as Paleocene-Eocene based on the age range of various palynomorphs in the assemblage (de Villiers, in preparation).

Systematic Palynology

Tubulifloridites antipodica Cookson 1947 ex Potonie 1960

Description. – The pollen of this species recovered from the Paleocene-Eocene of South Africa is tricolporate, spherical to subprolate (Figs. 1, 4) with a circular to lobate amb (Fig. 1), and oval outline in equatorial view (Fig. 4). The pollen averages about 21 µm in polar diameter and about 20 µm in equatorial diameter. The colpi are long, extending 3/4 or slightly more of the polar diameter (Figs. 1, 4). The pores are circular to slightly lalongate (Fig. 3). The sculpturing is echinate with supratectal spines that are evenly distributed, about 1 – 2.5 µm high and averaging 4 µm from the tip of each spine to the tip of the neighboring spine. The spines taper to a fine point (Figs. 2, 5). The tectum is microperforate (Figs. 2, 5) except at the tips of the spines where it is imperforate. The pollen wall is comprised of an ektexine and endexine. The ektexine is comprised of a thick tectum that is made up of thick interconnected rods that grade into a homogeneous layer just above the columellae (Figs. 6, 7). The columellae are thick, stout structures that rest on a relatively thin homogeneous footlayer (Figs. 6, 7). The footlayer rest on a thick, slightly more dense, endexine (Figs. 6, 7).

Comments. – The specimens found in this study show similarity to specimens recovered from the Oligocene of Argentina (Guerstein 1990, Barreda 1993), from the Upper Cretaceous and Tertiary of Australia (Martin 1973, Stover & Partridge 1973, Dettman & Jarzen 1988), and the Late Tertiary of Africa (Partridge 1978). This taxon ranges from the Upper Cretaceous to the Pliocene, becoming abundant in a wide geographical area in the Miocene.

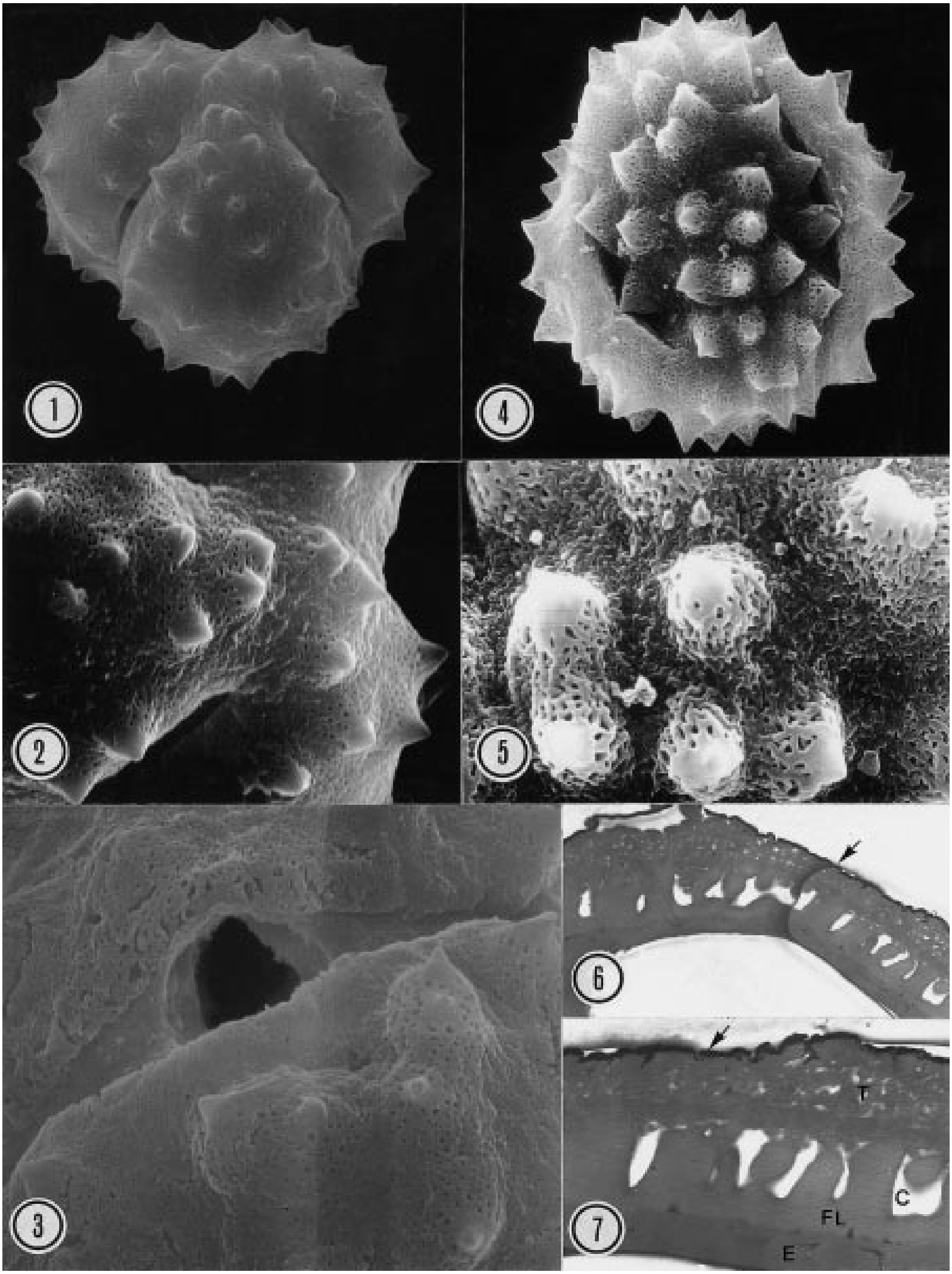
Tubulifloridites viteauensis Barreda 1993

Description. – The pollen of this species recovered from the Eocene of South Africa are isopolar, tricolporate, echinate, subprolate to spheroidal (Figs. 8 – 10). Amb is subcircular to slightly trilobate (Fig. 10) and is oval in equatorial view (Figs. 8, 9). The colpi are long extending well into the polar region (Figs. 8 – 10). The pores are circular and relatively large. The spines, unlike those found in *T. antipodica*, are more widely spaced (Figs. 8 – 10), averaging 5.5 µm from the tip of each spine to the tip of the neighboring spines. The spines average less than 1 um high and are rounded at their apexes (Figs. 8 – 10). The pollen wall is comprised of an ektexine and endexine. The ektexine is comprised of a thick tectum that is made up of interconnected rods that grade into a thick homogeneous layer above the columellae (Figs. 11, 12). The homogenous layer above the columellae appear to be comprised of very thick compressed rod-like elements (Figs. 11, 12). Although there are occasional inter-elemental spaces in this wall layer (Fig. 11), the lack of spaces may be due to compression during fossilization. More numerous spaces may have been evident between these rod-like elements in living material. The columellae are thick, stout structures that rest on a relatively thin homogeneous footlayer (Fig. 11). The footlayer rest on a thin, slightly more dense, endexine (Fig. 11).

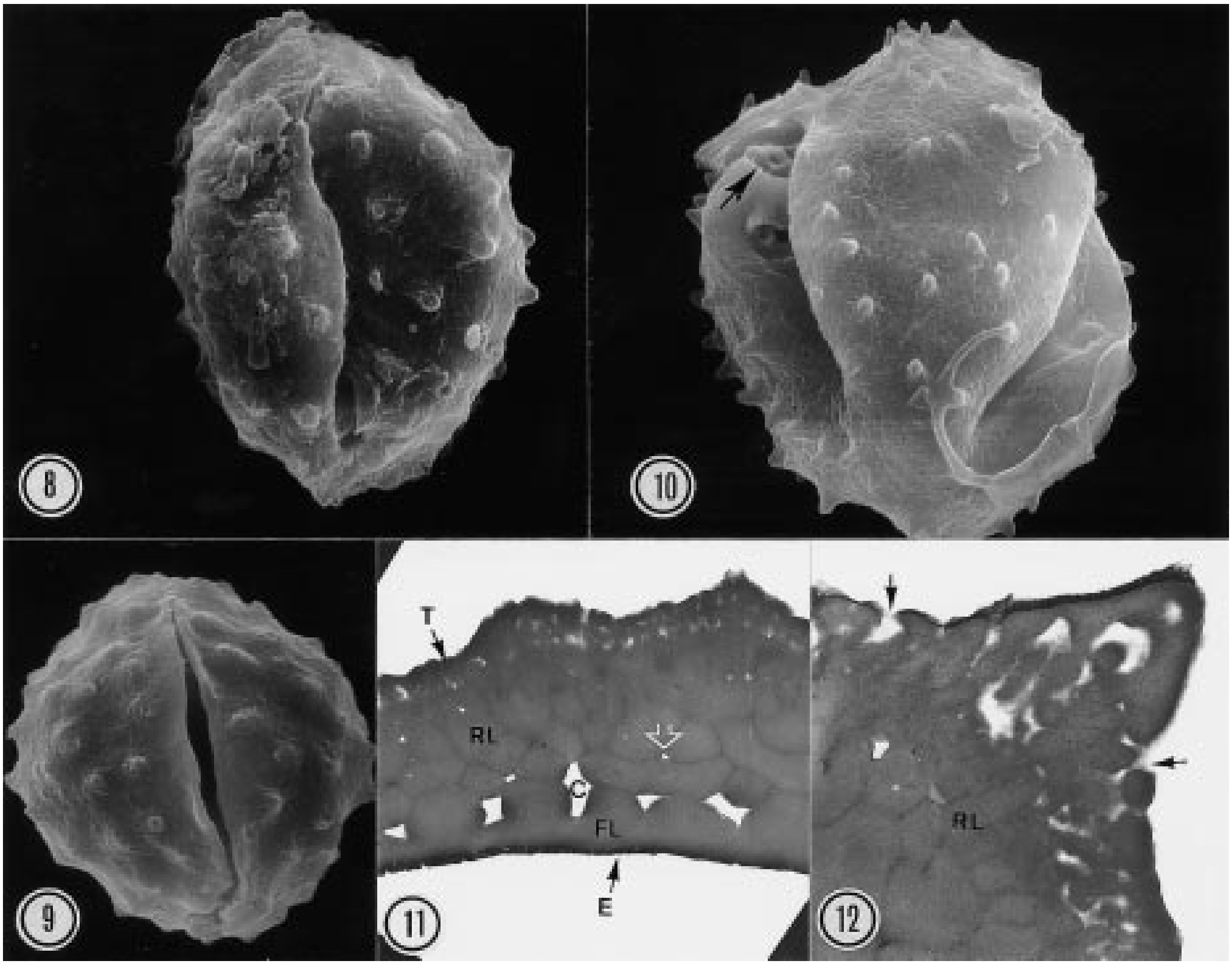
Comments. – Barreda (1993) compared the Argentinian specimens of *T. antipodica* with those of *T. vitauensis*. The latter species was found to be larger with smaller spines. The South African species show the same variances. Barreda (1993) also compared *T. vitauensis* with *Tubulifloridites* sp. of Partridge (1978), and concluded that the two forms might be the same species. The South African specimens also resemble those from Angola.

DISCUSSION

The pollen recovered from the Paleocene-Eocene of South Africa shows affinity with Asteraceae based on exine morphology. Extant pollen of this family is generally divided into three types, these are, a) psilate, b) echinate and c) lophate, the lophate pollen type being further divided into the echinolophate type and the psilolophate type (Skvarla & Turner 1966, Skvarla et al. 1977). The psilate pollen of the Asteraceae has surficial characters that can easily be confused with pollen from other families, which make recognition of the dispersed fossil pollen with this morphology difficult to assign to the Asteraceae. Echinate and lophate pollen, however, are characteristic of the Asteraceae and pollen of these morphologies can be easily recognized in the dispersed pollen record. Pollen wall ultrastructural data have been examined for a number of taxa in the Asteraceae. Skvarla et al. (1977) have distinguished five basic groups of wall ultrastructural patterns, the Helianthoid pattern, the Senecioid pattern, the Arctotoid pattern, the Anthemoid pattern and taxa without designated patterns. When the surficial characters of the exine are coupled with pollen wall ultrastructural data, pollen can often be associated with taxonomic groups below the family level. Pollen recovered from the Paleocene-Eocene of South Africa have characteristics indicative of the Anthemoid pollen wall pattern (Skvarla & Turner 1966, Skvarla et al. 1977). The Anthemoid pollen type is generally characterized by echinate, non-caveate exines, that have a wall structure composed of thick basal columellae (Figs. 6, 7, 11) which support shorter levels of columellae or rods alternating with internal tecta. This latter layer is described in this paper as a tectal layer comprised of thick interconnected rods (Figs. 6, 7, 11, 12) that are not necessarily vertically oriented. One of the differences between the fossil pollen and extant taxa with this pollen type is that the layer of columellae supported by the thick basal columellae are more vertically oriented and more regularly shaped in the extant taxa, than the interconnected rods observed in this layer in the fossil pollen (Compare 6, 7, 11 with the Figs. 27 and 28 in Skvarla & Turner (1966), and Plate 21, Figures A – D in Skvarla et al. (1977)). The layer of interconnected rods is more comparable to a similar layer



Figs. 1–7. Tubulifloridites antipodica. (1) SEM showing circular amb, echinate sculpturing and the extension of the colpi well into the polar region, ×2,500. (2) SEM of the same grain as in Fig. 1 showing the perforate tectum and the psilate, tapered, distal ends of the spines, ×5,000. (3) SEM of a grain showing the colporate condition and the slightly lalongate ora, ×5,200. (4) SEM of a grain showing the oval outline in equatorial view, perforate exine and long colpi, ×2,000. (5) SEM of the same grain as in Fig. 4 showing similar exine and spine morphology to that observed in the specimen in Figs. 1–2, ×5,000. (6) TEM of the pollen wall of the grain in



Figs. 8–12. Tubulifloridites viteauensis. (8) SEM showing the long colpi which extend well into the polar region and the widely spaced blunt spines, ×1,800. (9) SEM showing the echinate sculpturing, the long colpus and oval outline in equatorial view, ×1,800. (10) SEM showing the long colpi, and widely spaced spines, note the columellate structures where the wall has been fractured (*arrow*), ×1,800. (11) TEM showing the outer portion of the tectum (*T*) comprised of interconnected rods which is underlain by a thick homogeneous layer that appears to be comprised of robust rod-like structures (*RL*) note the occasional spaces among the rod-like (*RL*) structures that rest on the short, stout columellae (*C*). The columellae are underlain by a relatively thin footlayer (*FL*) and a thin more dense endexine (*E*), ×17,000. (12) TEM showing the wall structure of the tectum and associated spine. The outer portion of the tectum is comprised of interconnected rods that grade into what appear to be large, thick robust rod-like (*RL*) structures just above the columellae layer. Note that the spine is comprised of a similar structure to the outer tectum with occasional tectal perforations (*arrows*), ×24,000.

found in the Anthemoid-like pollen of the Valerianaceae, Apiaceae, and Dipsicaceae (Skvarla et al. 1977), families that have at one time or another been considered related to the Asteraceae (Bremer 1994). The wall structure of the two dispersed pollen types from South Africa unequivocally establishes their affinity with the Asteracaeae, and in particular their affinity with asteraceous taxa that possess echinate, non-caveate, Anthemoid-type pollen (mostly the Anthemideae and the Mutisieae). Skvarla et al. (1977), based on their studies of extant asteraceous pollen, determined that the Anthemoid pollen wall is the primitive type. Although this pollen wall type is named for the tribe Anthemideae of the Asteroideae, it is more commonly found in the Mutisieae of the Cichorioideae, a tribe that Bremer (1994) consideres to be basal within the Cichorioideae and the Asteraceae in general.

Determining the time and place of origin of the Asteraceae based on the fossil record has been problematic. Some investigators place the origin of the Asteraceae in the Oligocene (Raven & Axelrod 1974, Muller 1981). Turner

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Figs. 4 & 5 showing the tectum, which is comprised of interconnected thick rods that grade into a homogeneous layer just above the columellae, the columellae lye on a relatively thin footlayer, which is above the thick slightly more dense endexine, the arrow indicates the gold-palladium coating for SEM, ×6,800. (7) TEM of the same grain (figured in 4–6), showing the nature of the tectal layer (*T*), the thick, stout columellae (*C*), the thin footlayer (*FL*) and more dense endexine (*E*), arrow indicates the gold-palladium coating for SEM, X 16,000.

(1977), and Kemp & Harris (1975, 1977), however, opted for an Upper Cretaceous origin for the family, accepting many of the reports of pre-Oligocene asteraceous pollen at face value. Turner (1977) considered the Upper Cretaceous origin important to explaining the cosmopolitan distribution of asteraceous taxa as a vicariance event (in part). Bremer (1993, 1994) in a review of these reports considers a lower Tertiary origin and does not consider the current distribution of the Asteraceae related to continental movements. There are a number of *bona fide* Oligocene reports of pollen of the Asteraceae and by the Miocene asteraceous pollen has a cosmopolitan distribution. There are a number of pre-Oligocene reports of asteraceous pollen which are usually based on the similarities of the exine morphology to the morphology of extant asteraceous pollen, or by the assignment of dispersed pollen to a form genus that is suggestive of a Asteraceae affinity, e.g. *Tubuliforidites lilliei* (Couper) Farabee & Canright (1986). Whether or not these pre-Eocene reports of Asteraceae pollen are valid, awaits further study of their pollen wall structure, however, the fact that all of the earliest reports of asteraceous pollen are restricted to Gondwanaland, suggest a southern hemisphere origin of the family. Bremer (1994) also suggests a southern hemisphere origin for the family, and specifically places the origin in South America. Based on the fossil record, however, an Australian (Bremer & Gustafsson 1997) or African origin (this study) is more likely with subsequent dispersal to southern South America, given that the earliest occurrence of Asteraceae pollen in South America is in the Oligocene (Barreda 1993). This is possible especially given the close proximity of the tip of South America with Antarctica, and Antarctica with Australia maintaining a dispersal corridor well into the Eocene. It is also likely that a South African origin could lead to dispersal to any of these more southern continents that form a dispersal corridor from South America to Australia. It is imprudent at this time to suggest that this early South African occurrence of primitive asteraceous pollen represents the origin of the Asteraceae, especially given the number of unconfirmed or inadequately studied dispersed pollen grains exhibiting asteraceous features from as early as the Upper Cretaceous. It is significant, however, that the origin of this large cosmopolitan family does appear to be in Gondwanaland (Australia: Bremer & Gustafsson 1997 or South Africa: this study), or possibly South America (Bremer 1994) and it appears that the Asteraceae has a longer evolutionary history than previously suspected.

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