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Coprolites in a Middle Triassic cycad pollen cone: evidence for insect pollination in early cycads?

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ABSTRACT

Question: What evidence is there for cycad–insect interactions in the fossil record?

Organism: The pollen cone *Delemaya spinulosa* Klavins, Taylor, Krings et Taylor.

Locality: Fremouw Formation (Middle Triassic), Fremouw Peak, Central Transantarctic Mountains, Antarctica.

Methods: We document the presence of pollen-laden coprolites in pollen sacs of a Middle Triassic cycad.

Conclusions: These coprolites are comparable with fecal pellets of modern arthropods and we suggest that they were produced by beetles. This provides the oldest unequivocal evidence for a cycad–insect interaction and may represent a precursory stage in the establishment of a more complex cycad–pollinator relationship.

Keywords: coprolites, Cycadales, insects, pollinivory, Triassic.

INTRODUCTION

Flowering plants have evolved a variety of pollination syndromes since their diversification during the Cretaceous (ca. 130 million years before present), with wind, water and animals – such as insects, bats and birds – acting as pollinating agents (Proctor *et al.*, 1996). Gymnosperms, on the other hand, have historically been hypothesized to be exclusively wind-pollinated; however, it has now been established that at least two orders (Cycadales and Gnetales) also contain insect-pollinated species (Bino *et al.*, 1984; Norstog *et al.*, 1986; Kato and Inoue, 1994). In extant cycads, insect pollination appears to be widespread and in many cases involves specialist pollinators (e.g. Norstog and Nicholls, 1997); some have even speculated that most cycads are insect-pollinated (Vorster, 1995; Jones, 2002). Beetles (Coleoptera) are the primary pollinators identified to date (see Hall *et al.*, 2004, and references therein), although thrips (Thysanoptera) also act

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as pollinators in several species of *Macrozamia* Miquel (Mound and Terry, 2001; Terry, 2001). While the evolutionary origins of cycads continue to be debated (e.g. Rydin *et al.*, 2002; Soltis *et al.*, 2002; Axsmith *et al.*, 2003), there is an increasing body of fossil evidence which demonstrates that they were already well-established and diverse by the beginning of the Mesozoic (Mamay, 1969; Zhu and Du, 1981; Gao and Thomas, 1989). Moreover, the fossil record for some insect orders involved in cycad pollination today extends into the Permian (Crowson, 1981; Vishniakova, 1981; Ponomarenko, 1995); recent phylogenies of cycad pollinators have positioned these taxa as relatively basal (Farrell, 1998; Grimaldi *et al.*, 2004; Hall *et al.*, 2004). It is thus possible that insect interactions with cycads also may have originated in the late Palaeozoic or early Mesozoic. Based on the geographic distribution and evolutionary history of modern cycads and their pollinators, this relationship is believed to represent one of the oldest plant–pollinator interactions (Labandeira, 2000; Brenner *et al.*, 2003). However, there is currently no information in the fossil record as to the time of origin, evolutionary history and diversity of interactions between cycads and insects that ultimately resulted in the establishment of the complex cycad–pollinator relationships that are known in extant cycads.

Here we describe coprolites that occur in pollen sacs of the cycad pollen cone *Delemaya spinulosa* Klavins, Taylor, Krings et Taylor from the Middle Triassic of Antarctica (Klavins *et al.*, 2003). The coprolites are composed solely of relatively unaltered pollen from *D. spinulosa*. These trace fossils are significant in that they represent the oldest unequivocal evidence for the existence of a cycad–arthropod pollinivorous interaction.

MATERIALS AND METHODS

In situ pollen grains and coprolites were identified within pollen sacs of *Delemaya spinulosa*, an anatomically preserved cycad pollen cone that was discovered in permineralized peat from Fremouw Peak in the Queen Alexandra Range of the central Transantarctic Mountains [84°17′41″S, 164°21′48″E, 2385 m altitude, Buckley Island Quadrangle (Barrett and Elliott, 1973)]. The upper Fremouw Formation of Fremouw Peak is early Middle Triassic (Anisian) in age, based on palynostratigraphic analysis and vertebrate fossils (Elliott *et al.*, 1970; Farabee *et al.*, 1990).

Silicified peat was sectioned into slabs using lapidary saws; individual slabs (10424 L_{top} and 10424 M) were serially etched and peeled using standard techniques for silicified material (Galtier and Phillips, 1999). Peels were mounted on standard microscope slides, which are housed in the Paleobotany Division of the Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, under accession numbers 22,300–22,308 and 26,026–26,058.

For scanning electron microscopy (SEM), wax wells were built directly around pollen sacs on the surface of the silicified peat slabs. *In situ* material containing pollen grains and coprolites was macerated using 49% (concentrated) hydrofluoric acid. The macerate was transferred into microcentrifuge tubes and rinsed with several changes of water. Pollen grains and coprolites were also isolated from acetate peels by excising selected pollen sacs, which were then placed into microcentrifuge tubes. The acetate was dissolved in several changes of acetone, leaving an organic residue. With both methods, after fresh acetone was pipetted into the tubes, disaggregated pollen and coprolites were transferred to a microscope slide and picked up by double-sided adhesive tape mounted on an aluminium stub. Stubs were sputter-coated with palladium-gold and viewed with a JEOL JSM-6100 at 6 kV.

RESULTS

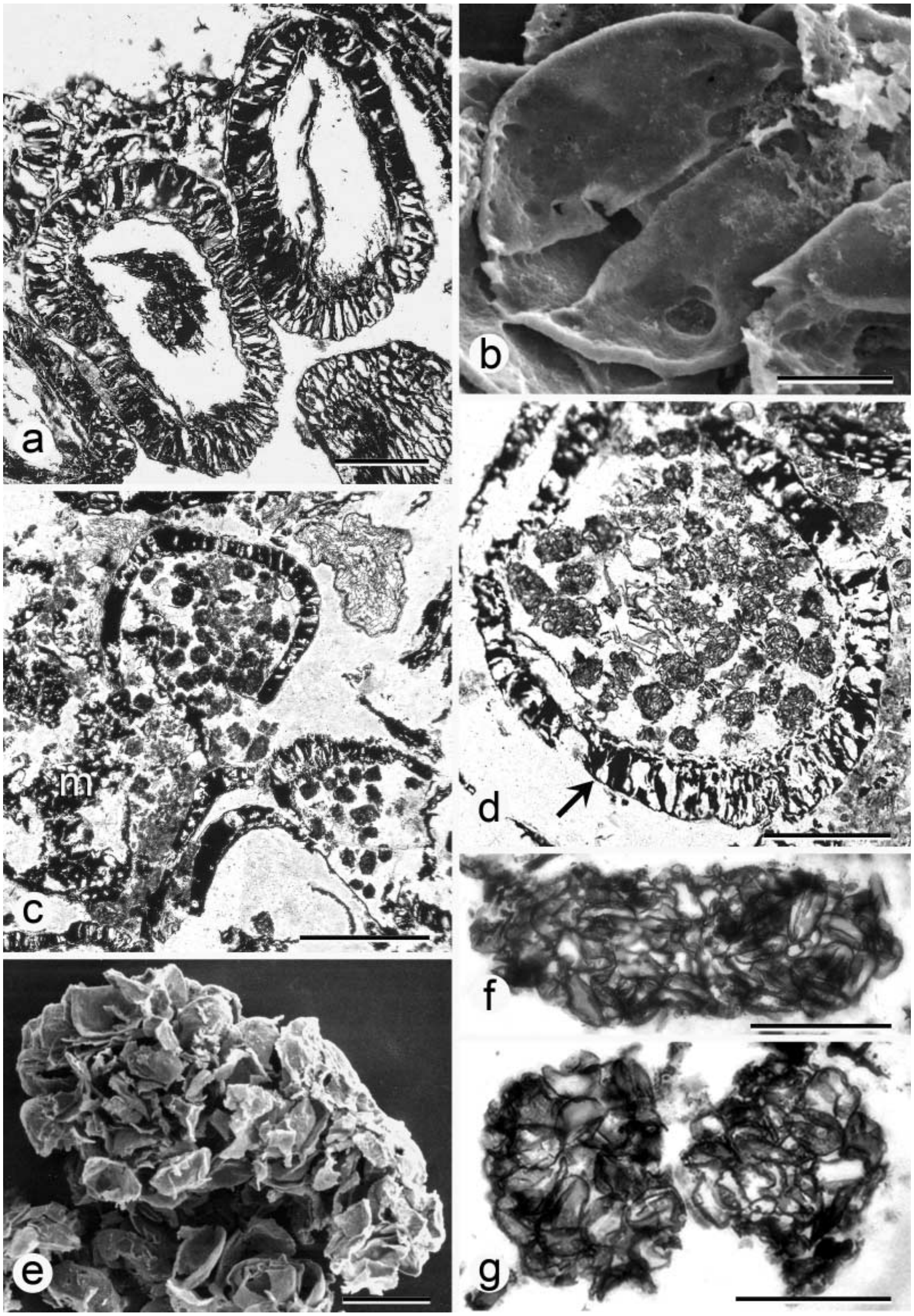
Pollen sacs of *Delemaya spinulosa* are small (up to 1 mm long and 500 μm wide) and roughly obovoid in shape. Each sac has a multilayered wall, with a single epidermal layer of elongate, thick-walled cells (Fig. 1a). *In situ* pollen of *D. spinulosa* frequently appears flattened (Fig. 1b). In general, however, pollen grains are broadly ovoid (ellipsoidal), with a single longitudinal furrow (monocolpate), bilaterally symmetrical and small, with an average length of 20 μm, width of 13 μm (W/L = 0.670), and measuring up to 10 μm in height from distal to proximal surface. The pollen thus falls into the small size range (< 24 μm) of Dehgan and Dehgan (1988). The surface of the pollen grains is smooth (psilate) and the colpus is slit-like, with flared ends (Fig. 1b).

Isolated, disaggregated microsporophylls occur close to the cone (Fig. 1c). The pollen sacs are dehisced and their wall organization is similar to that observed in pollen sacs of *D. spinulosa* (Fig. 1d). Numerous tiny coprolites occur within most of these pollen sacs. When present, coprolites completely fill the interior of the pollen sac (Fig. 1d); no pollen grains occur in the interior. All of the coprolites are comprised entirely of monocolpate pollen grains (Fig. 1e), identical to those that occur in the attached pollen sacs of *D. spinulosa*. Individual coprolites are elongate in longitudinal section, terete in cross-section, and measure up to 120 μm in length and 60 μm in diameter (Figs. 1f, 1g). Pollen grains in the coprolites appear to be relatively intact (Fig. 1e).

DISCUSSION

The occurrence of insect pollination (entomophily) in extant cycads has been documented with certainty by detailed field and experimental studies only within the last 20 years, although the interaction was first reported nearly a century ago (Rattray, 1913). Research on cycad–insect interactions has now established that several cycads are dependent on specific and faithful pollinators (Norstog *et al.*, 1986; Tang, 1987a; Norstog and Fawcett, 1989; Ornduff, 1991; Chadwick, 1993; Donaldson, 1997; Terry, 2001; Wilson, 2002; Hall *et al.*, 2004). This has important implications for conservation. For example, *Microcycas calocoma* (Miquel) A. de Candolle from Cuba is critically endangered, possibly due to the extinction of its obligate pollinator, and as a result continuation of the species is dependent on artificial pollination by humans (Whitelock, 2002).

To date, all pollinivorous arthropods identified as being associated with modern cycads are insects (e.g. Norstog and Nicholls, 1997), and include beetles in the superfamilies Cucujoidea (Families Boganiidae and Erotylidae) and Curculionoidea (Families Anthribidae, Belidae, Brentidae and Curculionidae) (Schneider *et al.*, 2002; Leschen, 2003). The fossil record for both cycads and beetles extends into the Permian (Ponomarenko, 1995; Zhu and Du, 1981), which, in addition to the modern geographic distribution of these organisms, has been cited as evidence to support the hypothesis that the relationship between cycads and pollinating insects is likely to have evolved in the Mesozoic, possibly prior to the Jurassic (Farrell, 1998; Labandeira, 1998, 2000; Hall *et al.*, 2004). The occurrence of pollen-laden coprolites in pollen sacs of *D. spinulosa* represents the first documentation of insect pollinivory in a fossil cycad. This offers a rare opportunity to explore the early history of insect–cycad interactions, and perhaps eventually reconstruct precursory stages in the establishment of a complex plant–pollinator relationship. Although they offer only indirect information on the animal that produced the coprolites, these ichnofossils are highly significant because they provide direct evidence for a specific feeding behaviour.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With respect to the taxonomic affinities of the animal that produced the coprolites, research on extant arthropod fecal pellets has established that morphological characters of coprolites can be used to distinguish among the various groups (Weiss and Boyd, 1950; Labandeira *et al.*, 1997; Kellogg and Taylor, 2004). Based on their size and shape, the coprolites appear to be most similar to the fecal pellets of insects, rather than mites, myriapods or other arthropod groups [compare Figs. 1e, 1f with figures 4, 5 in Chadwick (1993)]. Insects that have been documented in association with extant cycads include members of the Coleoptera (beetles), Collembola (springtails), Hemiptera (true bugs), Hymenoptera (bees and wasps), Lepidoptera (moths and butterflies) and Thysanoptera (thrips) (Tang, 1987a; Ornduff, 1991; Mound and Terry, 2001; Hall *et al.*, 2004). Adults of the Lepidoptera, Hemiptera and Thysanoptera, and nymphal stages of Hemiptera and Thysanoptera, are not candidates for consideration, since these animals are fluid feeders and do not produce preservable fecal pellets. Although Collembola have been observed in pollen cones, there is no evidence at this time that they are specialist feeders (Ornduff, 1991; Hopkin, 1997). Lepidopteran larvae are known to feed on cycad foliage and the microsporophylls of pollen cones, although no pollination behaviour is suggested for these taxa (Tang, 1990; Clark and Clark, 1991; Terry, 2001). Among the Hymenoptera, the sole taxon reported in association with cycads is *Trigona* Jurine (Apidae) (Ornduff, 1991); however, the fossil record of these bees extends only into the Late Cretaceous (Michener and Grimaldi, 1988). Specialized feeders on cycad pollen that also consume the pollen grains whole are found only in the Coleoptera. Thus it is likely that the coprolites were produced by a beetle; however, it remains possible that they were produced by a representative of an extinct insect order.

The insect responsible for producing the coprolites in *Delemaya* was diminutive, as the coprolites themselves are small (120×60 μm), and the animal apparently entered into pollen sacs with maximum dimensions up to 1 mm. The means by which the pollinivorous insect entered the pollen sacs cannot be determined based on the material at hand; however, in modern cycads, many pollinivorous insects enter the pollen sacs after maturation of the pollen and pollen sac dehiscence (Norstog and Nicholls, 1997). Modern cycads are known to have many beetle associates, including members of the Cucujoidea, Tenebrionoidea (darkling beetles) and Curculionoidea (weevils) (Norstog *et al.*, 1986; Endrödy-Younga, 1991; Ornduff, 1991). While some of these are simply destructive pollinivores, others act as pollinators, some of which have established complex life histories with specific cycad taxa (e.g. *Rhopalotria mollis* (Sharp) with *Zamia furfuracea* Aiton, *Pharaxonotha zamiae* Blake with *Z. integrifolia* Aiton) (Norstog and Fawcett, 1989; Fawcett *et al.*, 1995). The body fossil record of weevils and darkling beetles extends into the Jurassic and that of the cucujoid beetles into the Cretaceous (Arnoldi, 1977; Gratshev and Zherikhin, 2003; Kirejtshuk, 2003). Additionally, the morphology of the coprolites in these pollen sacs is similar to that documented for modern pollinivorous beetles (Pant and Singh, 1990; Chadwick, 1993). It is possible, therefore, that the coprolites occurring in the pollen sacs of *D. spinulosa* were produced by a member of one of these beetle groups. At present, not enough is known about the biology of extinct insects to suggest specific feeding

Fig. 1. (a) *Delemaya spinulosa* pollen sacs in transverse section, 10424 $\mathrm{M}_{\mathrm{bot}}$ 7α, #26045; bar = 100 μm. (b) SEM of *D. spinulosa* pollen grain; bar = 5 μm. (c) Isolated microsporophyll (m) with pollen sacs filled with coprolites, 10424 $\mathrm{L}_{\mathrm{top}}$ 13α, #22302; bar = 150 μm. (d) Detail of pollen sac filled with coprolites; note similarity of wall (arrow) to walls in (a), 10424 $\mathrm{L}_{\mathrm{top}}$ 7α, #26057; bar = 200 μm. (e) SEM of macerated coprolite; bar = 20 μm. (f) Coprolite in longitudinal section, 10424 $\mathrm{L}_{\mathrm{top}}$ 7α, #26057; bar = 50 μm. (g) Coprolites in transverse section, 10424 $\mathrm{L}_{\mathrm{top}}$ 6α, #26055; bar = 50 μm.

behaviours; however, it has been hypothesized that the morphology of Triassic obrieniid beetles is convergent with that of weevils, and that their frequent co-occurrence with cycadophyte remains in the fossil record suggests a potential relationship (Zherikhin and Gratshev, 1993; Gratshev and Zherikhin, 2003).

Although the interaction that we are documenting here is not as complex as the brood-site pollination of certain cycad–beetle associations (e.g. Fawcett *et al.*, 1995), nonetheless these modern strategies evolved from more basic biological associations (e.g. pollinivory). Sporivory has been documented in the Early Devonian [ca. 400 million years before present (e.g. Edwards *et al.*, 1995; Habgood *et al.*, 2005)] and pollinivory by the Late Carboniferous [ca. 310 million years before present (e.g. Baxendale, 1979)]. By the Middle Triassic (>75 million years later), biological structures such as mouthparts had diversified for a variety of spore and pollen predation patterns (piercing, rasping, whole grain consumption, etc.) (Labandeira, 2000, 2002). The question remains as to whether the pollinivory we document here represents opportunistic detritivory or a more specialized feeding behaviour. If this were a case of opportunistic detritivory, one would expect that the pollen sacs would show evidence of herbivory and/or that the coprolites would include other plant tissues (e.g. recognizable components of the pollen sac wall or parenchymatous tissues of the microsporophyll). Although the pollen sacs are dehisced (Fig. 1c, d), there is no indication of damage. The coprolites are notable in that they consist solely of cycad pollen. Together, these data suggest specialized pollinivory.

Some of the complexities of cycad–insect interactions today [e.g. cone thermogenesis and the production of volatiles that attract pollinators (Tang, 1987b; Terry *et al.*, 2004)] may not be accessible in the fossil record; however, there is the potential for preservation of key structural features in cycad cones, as well as evidence left by their insect associates. Although the original specimen is not a complete cone, it is apparent that *Delemaya spinulosa* had a morphology strikingly similar to that seen in pollen cones of extant cycads (Klavins *et al.*, 2003). The cone is compact, with pollen-bearing units (microsporophylls) helically arranged around a central axis. Each microsporophyll has an expanded, upturned face with spiny projections that interlace with surrounding microsporophylls. Pollen sacs are borne on the lower surface in pendant clusters approximately halfway along the microsporophyll. Although *D. spinulosa* was not found in organic connection with the vegetative parts of its source plant, it is very likely that it was produced within a crown of leaves at the stem apex, as has been documented in the Triassic cycad *Leptocycas gracilis* Delevoryas et Hope (Delevoryas and Hope, 1971), as well as in all extant cycads. Also significant is the fact that pollen of *D. spinulosa* is small and falls within the size range reported for the pollen of extant cycads (Dehgan and Dehgan, 1988). Moreover, the pollen corresponds structurally to that of modern cycads. These features stand in stark contrast with those seen in pollen cones and pollen of gymnosperms known to be wind-pollinated. For example, in conifers, clusters of tiny pollen cones occur at the tips of branches and bear pollen sacs that extend radially along most of the length of the microsporophyll. When mature, the pollen cones elongate slightly and become increasingly dry. As a result, even the slightest air currents cause the release of pollen grains. Additionally, the pollen grains of many wind-pollinated gymnosperm taxa are saccate, which may facilitate transport by wind. Conversely, the suite of characters displayed by the cone and pollen of *D. spinulosa* (e.g. overall appearance, small size, few pollen sacs per microsporophyll, relatively low amount of pollen produced) does not explicitly support the existence of wind pollination (anemophily) in this Middle Triassic cycad.

In both angiosperm and pollinating insect lineages, two major radiation events took place in the Cretaceous and Palaeocene. This has raised the question of whether angiosperms predate pollinating insects or vice versa. Over the past 30 years, evidence has increasingly supported the hypothesis that pollination interactions between early angiosperms and their insect pollinators did not arise *de novo*, but rather were a modification of a syndrome already present within insect groups associated with gymnosperms, possibly the cycadeoids (Bennettitales) and/or cycads (Crepet, 1979). To date, although arthropod damage has been documented, no evidence has been found for pollinivory in bennettitalean reproductive structures (Crepet, 1972; Stockey and Rothwell, 2003). Thus, the occurrence of cycad pollen coprolites within pollen sacs of *Delemaya spinulosa* is the first direct evidence of insect–cycad pollinivory in the fossil record. This may represent one of the initial stages in the establishment of more complex interactions, such as a specialized pollinator–plant relationship.

Fossil plants, especially those preserved in a way in which it is possible to examine cell and tissue types, can provide clues not only regarding affinities to other plant organs and lineages but also about life-history biology. Integration of information from disparate subdisciplines of palaeontology is rapidly moving forward and promises an expanded view of plant–animal interactions at various levels of inquiry. Ancient ecosystems constitute complex associations that are difficult to characterize accurately, since many of the components remain unknown. However, as the pollen coprolites of *Delemaya* underscore, details of the life histories of organisms in fossil ecosystems can be approached and, when placed within the context of evolutionary patterns, offer an expanded view of evolution in both plant and animal groups during the Mesozoic.

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