Probable oribatid mite (Acari: Oribatida) tunnels and faecal pellets in silicified conifer wood from the Upper Cretaceous (Cenomanian–Turonian) portion of the Winton Formation, central-western Queensland, Australia

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Tunnels and faecal pellets likely made by oribatid mites have been found in silicified conifer wood from the Upper Cretaceous (Cenomanian– Turonian) portion of the Winton Formation, central-western Queensland, Australia. Although this is the first identified and described record of oribatid mites in the Mesozoic of Australia, other published, but unassigned material may also be referable to Oribatida. Current understanding of the climatic significance of mite distribution is limited, but the presence of oribatids and absence of xylophagus insects in the upper portion of the Winton Formation are consistent with indications that the environment in which this unit was deposited was relatively warm and wet for its palaeolatitude. Such traces may provide useful and durable proxy evidence of palaeoclimate, but more detailed investigation of modern taxa and their relationship to climate is still needed.

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OUR UNDERSTANDING of the evolution and biogeography of terrestrial fossil arthropods is constrained by their sporadic representation in a Lagerstätte-driven record and the limited examination of available specimens (Labandeira & Eble 2000). Ichnofossils provide a potentially invaluable source of ecological information on the evolutionary history of these groups, and indeed Scott *et al.* (1992) suggested that much of our knowledge of the evolution of feeding habits in terrestrial fossil arthropods must be inferred from damage to plants.

The record of wood-boring arthropods, a common plant–arthropod interaction, is usually preserved in silicified woods (Feng *et al.* 2010), which are durable and somewhat plentiful, occurring sporadically throughout the fossil record. However, the important role that borers play in the breakdown of wood, both directly and by providing improved conditions for colonizing bacteria and fungi (Kellogg & Taylor 2004), may decrease the likelihood of their preservation (Scott *et al.* 1992). Although oribatid mite borings and coprolites are common on Gondwanan landmasses back to the Palaeozoic (Slater *et al.* 2012, 2014), published accounts of oribatid mites in the Australian fossil record are rare, with only one occurrence from the Eocene (O'Dowd *et al.* 1991) and one from the Pliocene–Pleistocene (Womersley 1957) having been described. Faecal pellets and boring structures with characters that appear consistent with oribatid mites have been noted from Australian Mesozoic material previously, but lack either detailed examination or confident assignment to the group (see Tidwell & Rozefelds 1991, Tidwell & Clifford 1995, Tosolini & Pole 2010, Tidwell *et al.* 2013, McLoughlin *et al.* in press). Herein we describe three Australian Mesozoic ichnofossils from a woodboring arthropod, and attempt to identify a likely maker from the morphology of these traces.

Geology

The specimens (QM F44338 and QM F44332) were collected from a locality in the vicinity of Lovelle Downs Station and Elderslie Station, 38 km WNW of Winton and 8 km east of the Diamantina River, and originate from the Winton Formation of the Rolling Downs Group. The Winton Formation crops out throughout western Queensland, northwestern New South Wales and northeastern South Australia (Fig. 1; Gray *et al.* 2002). The Winton Formation comprises

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Fig. 1. Map of Australia showing the location from which QM F44338 and QM F44332 were collected (QM L311). Grey indicates exposures of the Winton Formation in Queensland. State abbreviations: NT, Northern Territory; QLD, Queensland; NSW, New South Wales; ACT, Australian Capital Territory; VIC, Victoria; TAS, Tasmania; SA, South Australia; WA, Western Australia.

repeated facies interpreted as deposits of freshwater fluvial-lacustrine environments on an extensive coastal plain as the epicontinental Eromanga Sea withdrew (Exon & Senior 1976, Tucker *et al.* 2013).

Silicified wood is commonly exposed on the soil surface in areas where the Winton Formation crops out, but blocks are rarely found in situ. Such occurrences are considered to represent lag from previously eroded portions of the formation since the Winton Formation is the youngest Cretaceous stratum of the Eromanga Basin (Gray et al. 2002), and additionally because of the indurated nature of the wood compared with the surrounding sediment, even where that sediment has been strongly lithified (pers. obs.). The uppermost exposed portions of the Winton Formation at QML311, the Queensland Museum locality at which this wood was found, have had their maximum age constrained to close to the Cenomanian-Turonian boundary through the use of U-Pb isotope dating of detrital zircons by laser ablation (Tucker et al. 2013). At that time, centralwestern Queensland would have been at approximately 50°S (Li & Powell 2001).

Palaeoenvironment of locality

The palaeoenvironmental setting of the Winton Formation has been the subject of recent investigation. The climate is considered to have been warm-summer mesothermal, with seasonal but high rainfall (Fletcher *et al.* in press). In addition to seasonality inferred from multivariate leaf analysis (Fletcher *et al.* in press), variability of the climate based on silicified wood growth indices, including the material used herein (QM F44338 and QM F44332), is under investigation. Sedimentological evidence suggests periodic flooding (Romilio *et al.* 2013, Tucker *et al.* 2013), although the wood described herein does not show structures indicative of waterlogging.

Description of gallery and faecal pellets

Three bored tunnels through wood that was subsequently silicified were discovered. Each of the wood specimens

containing borings represents a new species of conifer wood. Candidate conifer families currently known from the Winton Formation based on leaf, cone and pollen assemblages include Cupressaceae, Araucariaceae, Podocarpaceae and Cheirolepidiaceae (Peters & Christophel 1978, McLoughlin *et al.* 1995, 2010, Pole 2000, Dettmann *et al.* 2009, 2012). The total length of the tunnels is greater than the prepared thin-sections. The tunnels appear to change direction at each end of the visible portion and continue into the wood at an angle to the thin-sections. Consequently, the total length can not be ascertained, as it is not captured in these sections. The portion of the tunnel that is visible in the prepared section of QM F44338 is 5 mm long and 0.7 mm in diameter (Fig. 2).

This tunnel is filled with structures that are predominantly ovoid with rounded ends (Fig. 3). In terms of their size and shape, they correspond to the fossilized faecal pellets of arthropods. There are no pellets that could be described as sub- or weakly hexagonal in cross-section. The pellets are 140–(183)–224 μ m wide, and 207–(267)–375 μ m long. The surface and cut sections suggest that the material comprising the pellets was heterogeneous and fibrous, but no recognizable



Fig. 2. Preserved tunnel and faecal pellets of a suspected oribatid mite, QM F44338. The tunnel length is 5 mm, and the diameter is 0.7 mm. Scale bar = 500μ m.



Fig. 3. Preserved faecal pellets of a suspected oribatid mite, QM F44338. Scale bar = $100 \,\mu$ m.

plant or fungal structures could be identified within them.

The second and third tunnels (QM F44332) are less well preserved, but consistent in general features with QM F44338, unless otherwise noted. The portion of the second tunnel in the prepared section is 9 mm long and 2 mm in diameter (Fig. 4). This tunnel is also filled with fossilized faecal pellets. Few of the faecal pellets in QM F44332 can be measured precisely, owing to crowding and apparent degradation. Overall, the pellets are larger than those preserved in QM F44338, approximately 350 μ m wide and 500 μ m long. The third tunnel, also preserved in QM F44332, is only partially captured in the thin-section but is consistent in size and texture with the second, and thus may be contiguous.

Comparisons

We follow the procedure of Labandeira et al. (1997) in comparing these structures with known arthropod faecal pellet/tunnel specimens using five characteristics: coprolite size, shape, surface texture, contents and surrounding tissue. Compared with the traces and body size of known wood-boring arthropods, the size of the pellets in the tunnels, a proxy for body size, and the relatively broad tunnel diameter are suggestive of either a large size class of oribatid mite or a sub-adult endopterygote coleopteran larva. The recorded faecal pellets and tunnels of even the smallest xylophagous insects are larger than those of OM F44338 (Labandeira et al. 1997, Kellogg & Taylor 2004), suggesting that referral to that group is unwarranted. The ovoid shape, fine but rough surface texture, and non-recognizable plant material comprising the pellets are characteristics consistent with oribatid mites (Labandeira et al. 1997, Kellogg & Taylor 2004, Feng et al. 2010). The pellets are the wrong shape and too smooth in texture to suggest production by a collembolan (Lesnikowska 1990, Kellogg & Taylor 2004). Although there is much variation in the size, shape, packing and composition of the faeces of the endopterygote larvae of coleopterans (Solomon 1977), some do produce faecal pellets that are rounded or ovate in cross-section (Francis & Harland 2006). However, endopterygote larvae produce extruded cylinders with ends that usually exhibit brittle fracture or similar breakages (Labandeira et al. 1997), rather than the smooth, rounded termini evident in QM F44338 and OM F44332. There is also no evidence of the pellets having a hexagonal shape, an identifying character of termite faeces (Genise 1995). The position of the bored wood within the conifers is likely trunk for QM F44338 and stump for QM F44332 based on the gross architecture of the samples. As there is no evidence of a response to the tissue damage, the trees may have been dead when the tunnels were made. Many wood-boring arthropods feed on dead wood, so this is not useful for diagnosis. Finally, the packing of the faecal pellets in the tunnel behind the feeding areas is consistent with that of oribatid mites, as they ingest all or almost all of



Fig. 4. Preserved tunnel and faecal pellets of a suspected oribatid mite, parallel to the growth ring, in QM F44332. The tunnel length is 9 mm, and the diameter is 2 mm. Scale bar = $500 \,\mu$ m.

ALCHERINGA

the wood but digest only a small amount of it and pack the tunnel behind them (Kellogg & Taylor 2004, Feng *et al.* 2010). On the basis of these observations, we propose that the probable producers of the borings and faeces in QM F44338 and QM F44332 were oribatid mites.

Palaeoenvironmental significance

Although Kellogg & Taylor (2004) suggested that our understanding of oribatid mites in palaeoecosystems is limited by our knowledge of modern mites, some broad generalizations have been ventured. It has been noted that insects form a more important component of xylophagous communities in dry environments, whereas oribatid mites dominate in swampy environments (Labandeira et al. 1997, Kellogg & Taylor 2004). This is supported by the successful colonization by modern mites of habitats with 4-6 months of inundation per year (Franklin et al. 2007), and by studies that show a reduction in oribatid richness and abundance if soil moisture is lowered (e.g., Lindberg et al. 2002). However, oribatid mites can occur anywhere there is sufficient moisture, and may occur in moist microhabitats, even in arid environments (Cepeda-Pizarro et al. 1996, Fernandez et al. 1997). They also appear to have a broad range of tolerances to temperature and are abundant in the high Arctic (Coulson et al. 1996, Webb et al. 1998), in temperate forest systems (Feng et al. 2010) and throughout the tropics (Labandeira et al. 1997, Franklin et al. 2007).

In spite of their broad distribution, oribatids have been investigated as climate and environmental indicators (Gergócs et al. 2009, Riva-Caballero 2011), and specifically as indicators of climate change (Gergócs et al. 2012). Current studies focus on changes in species richness or total abundance, and thus are difficult to utilize when investigating ichnofossils. An analysis of the distribution of attributes that are more likely to be detectable in the fossil record, such as size classes by environment or climate, may allow these mites and their ichnofossils to be used as an informative palaeoclimatic proxy, but currently this is untested. The discovery of oribatid mite traces in conifer wood from the Winton Formation but not yet xylophagus insect species, if their relative proportions are taken to indicate a humid climate as per Labandeira et al. (1997) and Kellogg & Taylor (2004), is consistent with current climatic indicators that point to the palaeoenvironment being relatively warm and humid, and with high rainfall for its palaeolatitude (Fletcher et al. in press). However, it should be noted that the sample of arthropods known from the Winton Formation is small, and further examination of the characteristics of modern oribatid mites, and the correlation of their occurrence and distribution with climate, is needed to confirm potential trends.

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