The record of Australian Jurassic plant–arthropod interactions[☆]

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ABSTRACT

A survey of Australian Jurassic plant fossil assemblages reveals examples of foliar and wood damage generated by terrestrial arthropods attributed to leaf-margin feeding, surface feeding, lamina hole feeding, galling, piercing-and-sucking, leaf-mining, boring and oviposition. These types of damage are spread across a wide range of fern and gymnosperm taxa, but are particularly well represented on derived gymnosperm clades, such as Pentoxylales and Bennettitales. Several Australian Jurassic plants show morphological adaptations in the form of minute marginal and apical spines on leaves and bracts, and scales on rachises that likely represent physical defences against arthropod herbivory. Only two entomofaunal assemblages are presently known from the Australian Jurassic but these reveal a moderate range of taxa, particularly among the Orthoptera, Coleoptera, Hemiptera and Odonata, all of which are candidates for the dominant feeding traits evidenced by the fossil leaf and axis damage. The survey reveals that plant–arthropod interactions in the Jurassic at middle to high southern latitudes of southeastern Gondwana incorporated a similar diversity of feeding strategies to those represented in coeval communities from other provinces. Further, the range of arthropod damage types is similar between Late Triassic and Jurassic assemblages from Gondwana despite substantial differences in the major plant taxa, implying that terrestrial invertebrate herbivores were able to successfully transfer to alternative plant hosts during the floristic turnovers at the Triassic–Jurassic transition.

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1. Introduction

Several major tectonic and climatic events, including the breakup of Pangaea and extended greenhouse conditions, shaped the structure of terrestrial environments and the evolution of life on land during the Jurassic (Hallam, 1969; Rees et al., 2004). The Triassic–Jurassic transition was marked by a mass-extinction event that affected both marine and terrestrial biotas (Raup and Sepkoski, 1982; van de Schootbrugge et al., 2009), although the magnitude and global expression of this event have been questioned (Lucas, 1994; Tanner et al., 2004), and the event appears to have had little impact on entomofaunas (Labandeira and Sepkoski, 1993; Rasnitsyn and Quicke, 2002; Grimaldi and Engel, 2005). In Gondwana, this event is evidenced by the demise of the *Dicroidium* flora, which had dominated the terrestrial landscape for most of the Triassic, and by significant turnovers in synapsid and diapsid vertebrate clades (Anderson et al., 1999; Bandyopadhyay, 1999). The Early Jurassic is generally interpreted to have experienced relatively warm climates (Steinthorsdottir and Vajda, 2015). Towards the end of this interval, an early Toarcian anoxic event or multiphased Pliensbachian–Toarcian crisis saw further significant extinctions and environmental perturbations in the oceanic realm (Wignall et al.,

2005; Caruthers et al., 2013). However, the impact of this event on terrestrial biotas is poorly understood (Zakharov et al., 2006). Coarse-scale studies of macro- and palynofloras from the Australian region suggest no major extinction, but rather reveal significant changes in the relative abundance of major plant groups around the end of the Early Jurassic (Helby et al., 1987; Hill et al., 1999; Turner et al., 2009). Although these two major events appear to have fundamentally reorganized southern floras, the extent of their effect on the associated terrestrial invertebrate faunas is less clear.

The remainder of the Jurassic and transition into the Cretaceous is not marked by any further first-order mass-extinction events. Traditionally, this interval was considered to have been characterized by high temperatures globally (Frakes et al., 1992), linked to elevated atmospheric CO₂ concentrations (Bernier and Kothavala, 2001). Recently, this scenario of a long equable greenhouse climate in the mid-Mesozoic has been challenged using isotopic data that suggest that the interval was punctuated by periodic short-term cooling events (Dera et al., 2011; Jenkyns et al., 2011). Furthermore, pronounced eustatic sea-level fluctuations throughout the Jurassic indirectly suggest episodic polar or extensive montane ice accumulation (Price, 1999). Nevertheless, the majority of the Jurassic appears to have been characterized by warm and equable conditions, allowing plants and their dependent fauna to colonize even polar latitudes (Pole, 1999; Rees et al., 2004; Vajda and Wigforss-Lange, 2009). These relatively warm, high-latitude, terrestrial environments experiencing strong annual changes

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in photoperiod have no modern analogues (Creber and Chaloner, 1985) and are of interest in terms of forecasting the biotic response to future global warming (Meehl et al., 2007).

The Jurassic also witnessed the start of Pangaeian breakup—linked initially to Central Atlantic Magmatic Province (CAMP) volcanism and later to the Karoo–Ferrar and Chon–Aike volcanism in Gondwana (Storey, 1995; Pankhurst et al., 1998). These eruptive phases potentially generated environmental changes that drove first- and second-order mass-extinction events (Pálffy and Smith, 2000; Whiteside et al., 2007; van de Schootbrugge et al., 2009), and the ensuing continental breakup had significant consequences for terrestrial biogeography (Molnar, 1991; Damborenea et al., 2013). Jurassic Earth also experienced at least two major asteroid impacts on land that generated craters in excess of 40 km in diameter. These include the Puchezh–Katunki impact structure in Russia, dated to 167 ± 3 Ma (Bajocian–Bathonian: Pálffy, 2004), and the Morokweng crater in South Africa, dated to 145.0 ± 0.8 Ma (end-Oxfordian: Hart et al., 1997). Although it is unlikely that either of these impacts was large enough to generate global extinction events, they were probably of sufficient size to greatly alter the local landscape and decimate regional ecosystems.

The Gondwanan Jurassic floras reflect the peak manifestation of plant communities dominated by araucariacean, podocarp and cheirolepid conifers, advanced pteridosperms (Corystospermales, Caytoniales) and non-angiosperm ‘anthophytes’ (Bennettitales and Pentoxylales) prior to the explosive diversification of flowering plants in the Cretaceous (Anderson et al., 1999; Friis et al., 2011). This was also a time of transition in the terrestrial arthropod fauna, witnessing the radiation of several orders (particularly the Coleoptera, Hemiptera and Diptera), the appearance of Lepidoptera and, towards the end of the period, the rise of key behavioural traits including the earliest likely blood feeders and parasites, the earliest probable specialist pollinators (Mecoptera with elongate mouthparts), and the expansion of coleopteran boring and seed-feeding guilds, possibly at the expense of oribatid mites (Grimaldi and Engel, 2005; Labandeira, 2006; Ren et al., 2009). Nevertheless, the temporal development of these feeding syndromes and their representation across host-plant groups remain poorly resolved owing to a stratigraphically and geographically patchy fossil record of arthropod–plant interactions (Labandeira, 2013).

In a recent review of plant tissue consumption patterns by terrestrial invertebrates through the Phanerozoic, Labandeira (2013) noted a marked deficiency in published records of plant–animal interactions from a 30-million-year interval of the Early Jurassic. His survey of the fossil record also revealed that the Middle and Late Jurassic yielded more extensive and diverse examples of phytophagy by arthropods than the Early Jurassic and noted that essentially all the major tissue-feeding strategies adopted by modern arthropods were already in place by that time (well before the appearance of flowering plants). However, it is noteworthy that the great majority of phytophagy records of this age are from the Laurasian sector of Pangaea, and the record of Gondwanan terrestrial arthropod macrofossils is similarly sparse. Although a few isolated records of specialized phytophagy categories have been reported from the Southern Hemisphere (e.g. Rozefelds, 1988; Genise and Hazeldine, 1995; García Massini et al., 2012), only a single systematic survey of plant–arthropod interactions has been carried out on a Gondwanan Jurassic flora—that of Edirisooriya and Dharmagunawardhane (2013) from an unnamed and poorly dated sedimentary succession in Sri Lanka. However, many of the damage types on plants illustrated in that study may be diagenetic features or the result of attrition during collection.

Although Australian Jurassic plant fossils are widespread and abundant, evidence of plant–animal interactions is sparse thus far. Only a few isolated examples of leaf mining, leaf-margin feeding and stem boring have been documented in past reports (Rozefelds, 1988; Tidwell and Clifford, 1995; Beattie and Avery, 2012; Tidwell et al., 2013). Beattie and Avery (2012) undertook the only attempt to resolve broader patterns of trophic interactions within an Australian Jurassic continental

fossil assemblage based on a lake and lake-margin ecosystem preserved in an outlier of the Surat Basin at Talbragar, New South Wales. They inferred diverse energy pathways and multiple trophic levels based on fossil evidence of herbivory, analogies with modern relatives, co-preservation of fossils, vertebrate gut contents, the disarticulation state of fossils and other aspects of taphonomy. Arthropod fossils are much less abundant than leaves and, to date, are only known from two Jurassic deposits in Australia: the Lower Jurassic Cattamarra Coal Measures of Western Australia (Mintaja locality) and the Upper Jurassic Talbragar Fossil Fish Bed of New South Wales (Talbragar locality).

One of the authors (SMcL) undertook a survey of plant fossils in several major palaeontological collections in order to assess the diversity of plant–animal interactions in Australia (representing the middle- to high-latitude southeastern fringe of Pangaea) during the Jurassic. The other authors surveyed the diversity and evaluated the likely feeding traits of the insects preserved in the two known Australian Jurassic entomofaunas. The aim of this study is to present baseline data on the categories of arthropod interactions with plants in the Australian Jurassic and the range of plant groups involved in these associations, which will provide a basis for quantitative analyses of individual biotas and improved reconstructions of Mesozoic trophic webs in the future.

2. Material and methods

We undertook a survey of past literature and personally examined several institutional collections containing major Australian Jurassic terrestrial fossil assemblages to identify plants with convincing evidence of damage attributable to arthropods. We have also undertaken intensive sampling of Jurassic plant and arthropod fossils over the past two decades from sites such as Talbragar, Durikoi, Inverleigh and Mintaja (Fig. 1A–C). As arthropod damage expressed in plant fossils can be difficult to differentiate from abiotic trauma, we used the criteria outlined by Labandeira (2006, and the references therein) to identify arthropod-generated damage and also to distinguish herbivory from saprotrophy. Most importantly, herbivory damage is typically expressed by stereotypical feeding patterns consistent with modern analogues, the development of reaction tissue around the wound, development of necrotic flaps or veinal stringers around damaged tissue, and distinctive and consistent phytotissue–herbivore linkages that are incompatible with other forms of biological or physical trauma, such as that caused by fungi (Parbery, 1996; Taylor and Osborn, 1996) or abiotic processes (Wilson, 1984; Michels et al., 1995; Wright and Vincent, 1996; Rácskó et al., 2010). We sought to assign examples of plant damage to the principal functional feeding groups outlined by Labandeira et al. (2007a): viz., external foliage feeding (here subdivided into the categories of leaf-margin feeding, apical feeding, surface feeding and hole feeding), piercing-and-sucking, boring, leaf mining, galling, seed feeding, palynophagy, nectarivory and oviposition. We also examined plant fossils for evidence of vegetative physical defences against herbivory, and insect fossils for evidence of mimesis. Collections examined and fossils illustrated include those held in the Queensland Museum, Brisbane (QMF); the Geological Survey of Queensland (GSQ) and University of Queensland’s Department of Earth Sciences (UQF) collections—both held at the Queensland Museum, Brisbane; the Western Australian Museum, Perth (WAM); Museum Victoria, Melbourne (MVP); the Geological Survey of New South Wales, Sydney (MMF); the Australian Museum, Sydney (AMF), the Natural History Museum, London (NHMV); Lund University Geology Department, Lund (LO); and the Swedish Museum of Natural History, Stockholm (NRMS).

Since there is little data available regarding the sampling strategies employed to assemble the material examined in this study (some of these museum collections date back over a century), all the fossil suites likely suffer from strong collection biases that favour well-preserved or rare plant remains. Consequently, no attempt has been made to quantify the intensity of arthropod damage within individual assemblages. However, we sought to identify the diversity of damage types within

Fig. 1. Palaeogeography of Australia for three intervals of the Jurassic, showing the key fossil localities mentioned in the text; A) Early Jurassic; B) Middle Jurassic; C) Late Jurassic. Major sedimentary basins are indicated in C. Base maps adapted from Veevers (2000) and Geoscience Australia (2002).

assemblages and analyse how that diversity is represented through time based on our survey of available collections. Further systematic sampling will be required for quantitative analyses of palaeoherbivory in individual assemblages.

Plant fossils were photographed with a Canon EOS 40D digital camera under strong unilateral light from various angles to obtain optimum expression of surface relief for features that are commonly subtle and difficult to illustrate. In some cases, a polarizing filter was employed to enhance the image contrast.

3. Geological setting

Pangaea began to rift apart during the Early Jurassic, with new sea-floor initially developing in the North Atlantic and Wedell Sea regions (Leitchenkov and Masolov, 1997; Schettino and Turco, 2009). Throughout the remainder of the Jurassic and Cretaceous, Gondwana (that component of Pangaea south of the Tethys Sea) progressively fragmented, giving rise to the modern continental configuration. Australia was positioned in the middle- to high-latitude parts of southeastern Gondwana during the Jurassic and retained terrestrial connections with most of the other southern landmasses throughout the period (Grant-Mackie et al., 2000; McLoughlin, 2001).

Reconstructions based on palaeomagnetic data indicate that Australia lay at latitudes of 30–60°S in the Early Jurassic, with the continent then rotated roughly 70° clockwise with respect to its current orientation, such that Western Australia lay in the lowest latitudes. Slow rotation of Gondwana brought Australia to 35–65°S by the end of the Middle Jurassic (~165 Ma), and to 45–80°S by the end of the Jurassic (Veevers et al., 1991; Klootwijk, 1996; Veevers, 2000). Fossil assemblages from each of these broad time slices were investigated in this study (Fig. 1A–C).

Australia experienced a broadly quiescent tectonic phase during the Jurassic, although there was subsidence in several broad epicratonic basins in the east, incipient rifting along the continent's western margin, and localized volcanism, especially in Tasmania (Bradshaw and Yeung, 1990; Veevers, 2000, 2005). Orogenic processes were confined to the Panthalassan margin of Zealandia, which was then connected to Australia's eastern margin (Adams et al., 2007). One outcome of the intermediate volcanism associated with distant convergent-margin tectonism to the east, and of intermediate to mafic mantle-plume related volcanism in Tasmania, was the distribution of thin but extensive pyroclastic and epiclastic sedimentary deposits across eastern Australian epicratonic basins (Exon, 1976; Wells and O'Brien, 1994; Fielding, 1996). Some of this volcanogenic material contributed to the exceptional permineralization of a broad range of buried plant organs (Tidwell, 1987, 1992; Tidwell and Jones, 1987; Tidwell and Rozefelds, 1990; White, 1991; Tidwell and Pigg, 1993; Tidwell and Clifford, 1995), and this mode of preservation provides the only evidence of the activities of wood-boring arthropods in the Australian Jurassic.

Turner et al. (2009) recently summarized sedimentary basin development and the evolution of floras and faunas through the Jurassic of Australia. In general, the broad eastern Australian epicratonic basins contain several hundred metres of non-marine sedimentary strata. Western Australian basins contain a mix of continental and marine strata, with the marine units hosting dinoflagellate and invertebrate fossil suites enabling correlation to the international chronostratigraphic scale (Arkell and Playford, 1954; Helby et al., 1987; Hall, 1989; Riding et al., 2010; Mantle and Riding, 2012); these suites are critical due the relatively few radiometric dates available to calibrate the Australian Jurassic sedimentary succession. Within Australia, stratigraphic correlations are primarily achieved on the basis of spore-pollen assemblages (Helby et al., 1987; Mantle et al., 2010). Palynological and macrofossil data indicate a broadly pan-Australian flora for the Jurassic, with some minor west to east (at that time north to south) provincialism and diachroneity in the first appearances of taxa, particularly in the Early Jurassic (Gould, 1975; Helby et al., 1987; Turner et al., 2009).

Grant-Mackie et al. (2000) reviewed the fossil biotas, biogeography and climate of the Australasian Jurassic and concluded that conditions were generally warm but not arid, and that ice caps were lacking even from the highest latitude regions. The palaeogeographic evolution of the Australian Jurassic has also been outlined in a series of time slices by Bradshaw and Yeung (1990, 1992) and Geoscience Australia (2002). Consistently humid conditions were experienced in some areas of the continent based on the accumulation of thick coal deposits in several basins throughout the Jurassic (Goscombe and Coxhead, 1995; Sappal and Suwarna, 1997). These coal-rich successions and a series of exceptionally preserved intermontane silicified deposits provide the dominant sources of plant fossils for this study.

4. Results: arthropod–plant interactions

4.1. Leaf-margin feeding

4.1.1. Descriptions and remarks

Leaf-margin feeding is the most common form of arthropod damage in Australian Jurassic assemblages and is identified on at least six genera of gymnosperms with varying degrees of confidence. Two fern genera also possibly show damage of this type.

Early Jurassic plant assemblages reveal margin feeding on both pteridosperms and ferns. *Sagenopteris nilssoniana* (Brongniart) (Caytoniales) leaves from the Marburg Subgroup (Pliensbachian) at Durikai (Fig. 1A) show sparse, simple-scalloped damage to the proximal or central margins of pinnules. The excision illustrated (Fig. 2A) is 4 mm long, 1 mm deep and is flanked by a weakly developed reaction rim; similar-shaped scallops on the margins of other examples of this leaf type from the same locality (e.g., NHMV21338) reach twice these dimensions.

Phlebopteris sp. (Matoniaceae) fronds from the same deposit at Durikai show zones of feeding damage up to 8 mm long on the basiscopic margins of the distal parts of pinnules. Contraction of the lamina through development of reaction tissue has caused basiscopic arching of the tips of several consecutive pinnules (Fig. 2B). Locally, complete removal of pinnule tips is evident (Fig. 3H).

Middle Jurassic plant assemblages, though represented extensively in institutional collections, show surprisingly few examples of leaf-margin feeding, and some well-studied assemblages appear to be devoid of arthropod damage (e.g. McLoughlin and Drinnan, 1995). *Cladophlebis* (?Osmundaceae) fronds from the Walloon Coal Measures at Bexhill, Clarence-Moreton Basin, show possible removal of whole pinnules, in some cases leaving only a stub of the midvein (Fig. 2C), but the lack of clear reaction tissues associated with the damage makes attribution to arthropod feeding equivocal.

Pachydermophyllum sp. (?Corystospermaceae) leaves from the Injune Creek Group at Eumamurrin in the Eromanga Basin show rare, deep, U-shaped notches in pinnule margins, extending almost to the midvein (Fig. 2E). Some examples of this species may have also experienced pinnule apex removal. A second putative corystosperm species from this deposit (*Pachypteris* sp.) shows simple scalloped damage on the basiscopic side of pinnule apices (Fig. 2D), similar to damage described for *Rintoulia* species below. A third possible corystosperm, referable to either *Pachypteris crassa* (Halle) Townrow or *Komlopteris* sp., has simple scalloped damage at various positions along the margins of pinnae/pinnules (Fig. 2F).

Some specimens of *Otozamites* sp. (Bennettitales) from Eumamurrin show complete removal of leaflets in what are otherwise well-preserved leaves (Fig. 2H). Whether this damage is from physical (abiological) trauma or from herbivory is unclear.

Late Jurassic plant assemblages show leaf-margin feeding on a greater range of plants. *Podozamites* (Araucariaceae) leaves from the Talbragar Fossil Fish Bed (latest Oxfordian–Callovian) show similar damage to that described on *Sagenopteris* above; viz. simple isolated marginal scallops about mid-leaf that extend through several longitudinal veins almost to the centre of the leaf. Such scallops are flanked by a

well-defined reaction rim up to 1 mm wide. In one case, scalloped damage extending from opposite margins of the leaf appears to have led to the loss of the entire leaf apex (Fig. 2G).

Taeniopteris spatulata McClelland (Pentoxylales) leaves from the same deposit show probably the most abundantly represented damage of any Australian Jurassic plant taxon. Numerous examples show damage in the form of: (1) simple shallow scallops ~5 mm long and 1–2 mm deep, similar to those described above for *Podozamites* and *Sagenopteris* (Fig. 2I, J); (2) distortion, flexure or complete removal of the leaf tip by apical attack (Fig. 2K); and (3) elongate (up to 35 mm long) but mostly shallow (rarely up to 3 mm deep) zones of leaf margin removal causing wrinkling, splitting and flexure of the remaining lamina (Fig. 2L, M). Narrow (<0.2 mm) reaction rims are evident on all these damage types. Damage tends to be focused in the middle to distal parts of these leaves. Beattie and Avery (2012) attributed the damage on *Taeniopteris* leaves at Talbragar to orthopterans. Care must be taken in evaluating arthropod damage to *T. spatulata* leaves because this taxon is known to express natural variation in margin form, ranging from entire to deeply notched or lobed in regular or irregular fashion (Drinnan and Chambers, 1985; Howe and Cantrill, 2001; McLoughlin et al., 2002).

Rintoulia sp. (?Corystospermaceae) leaves from the Talbragar Fossil Fish Bed show simple scallops locally excavated in the tips of pinnules, or more commonly, slightly offset from the apex on the basiscopic or acroscopic side of the pinnule's apical margin (Figs. 2N, 3A, B). Reaction rims, similar to those on *T. spatulata*, are ~0.2 mm wide.

Komlopteris sp. (?Corystospermaceae) leaves from the same deposit bear shallow scallops along pinnule margins that commonly generate distortion in the pinnule's growth (Fig. 3C, E, F). In some cases, apex removal during early development has left a distal notch on truncated pinnules (Fig. 3D).

One specimen of *Ptilophyllum cutchense* Morris (Bennettitales) from the Yarragadee Formation (Upper Jurassic), northern Perth Basin, shows at least two gently scalloped truncations of pinnule apices (Fig. 3G; see also McLoughlin and Pott, 2009, fig. 11C). These damaged zones are flanked by 0.3 mm wide, darkened reaction rims.

Pachypteris sp. or *Lepidopteris* sp. (?Corystospermaceae/?Peltaspermaceae) fronds from the Battle Camp Formation (latest Jurassic or earliest Cretaceous), Laura Basin, show selective scalloped removal of pinnule apices and the distal margins of pinnules (Fig. 3I). Narrow (<0.2 mm), darkened reaction rims typically flank these damaged areas. *Pachypteris crassa* leaves from this same deposit also show scalloped excision of pinnule apices.

4.2. Surface feeding between veins

4.2.1. Remarks

There is scant evidence for surface feeding amongst the collective Jurassic floras of Australia. Two specimens of *Otozamites feistmanteli* Zigno from the Pliensbachian Marburg Subgroup at Durikai show linear traces parallel to the secondary venation, spanning at least two interveinal areas (~0.2 mm wide) and extending from the proximal quarter of the pinnule to the leaflet's distal margin (Fig. 3J, L). These features may represent surface feeding traces similar to damage type 75 of Labandeira et al. (2007a) and are also similar to examples of slot feeding illustrated by the same authors, although the evidence is equivocal in the absence of other clear examples. A few neighbouring pinnules on the same specimen have raised areas in the same orientation but their attribution to arthropod damage is not certain.

4.3. Hole feeding

4.3.1. Description

Cladophlebis australis (Morris) Seward fronds from the Middle Jurassic Walloon Coal Measures at Bexhill, Clarence-Moreton Basin, show sparse indications of hole feeding within lanceolate pinnules. This damage is in the form of 0.5 mm wide holes in the pinnule laminae that are circular

Fig. 2. Examples of leaf-margin feeding from various Australian Jurassic fossil assemblages; A) scalloped feeding on a pinna margin of *S. nilssoniana* (Brongniart) (arrowed), Durikai, Marburg Subgroup, AMF57722; B) distal margin feeding and twisted pinnule apices on *Phlebopteris* sp. (arrowed), Durikai, Marburg Subgroup, GSQF135001; C) possible whole pinnule removal, *Cladophlebis australis* (arrowed), Bexhill, Walloon Coal Measures, AMF49491; D) scalloped feeding on basiscopic margin of *Pachypteris* sp. pinna (arrowed), Eumamurrin, Injune Creek Group, GSQF13552; E) scalloped feeding (arrowed) on pinna of *Pachydermophyllum* sp., Eumamurrin, Injune Creek Group, GSQF13550; F) broadly scalloped margin feeding on *Komlopteris* sp. pinnules (arrowed), Eumamurrin, Injune Creek Group, GSQF13560; G) scalloped feeding on *Podozamites jurassica* (White) leaves (arrowed), Talbragar Fossil Fish Bed, AMF58402; H) possible whole pinnule removal (arrowed), *Otozamites* sp., Eumamurrin, Injune Creek Group, GSQF13537; I) scalloped feeding on distal margin of *Taeniopteris spatulata* leaf (arrowed), Talbragar Fossil Fish Bed, AMF72404; J) scalloped feeding on distal margin of *T. spatulata* leaf (arrowed), Talbragar Fossil Fish Bed, NRM S087611; K) apex feeding and growth distortion on *T. spatulata* leaf (arrowed), Talbragar Fossil Fish Bed, AMF59994; L) continuous margin feeding on *T. spatulata* leaf (arrowed), Talbragar Fossil Fish Bed, MVP182593; M) continuous margin feeding and growth distortion on *T. spatulata* leaf (arrowed), Talbragar Fossil Fish Bed, AMF62039; N) scalloped feeding on *Rintoulia* sp. pinnae (arrowed); Talbragar; MMF3141. All scale bars = 10 mm except for I (= 5 mm).

or oblong, following the course of the interveinal tissues for lengths up to 2.5 mm (Fig. 3K).

4.3.2. Remarks

Little reaction tissue is evident in the *C. australis* impressions, but the consistent interveinal positions, rounded termini and the general lack of lamina splitting in the fronds suggest that these features are not from mechanical (e.g. wind or percussive) damage. Although numerous other broad-leafed ferns and gymnosperms are represented in the Australian Jurassic, none shows unequivocal evidence for hole feeding. In broad terms, the damage on the Bexhill fern pinnules is similar to the slot feeding or intercostal hole-feeding represented by damage type 78 of Labandeira et al. (2007a), although the latter is recorded on dicot angiosperm leaves and results in substantially greater amounts of tissue loss.

4.4. Galls

4.4.1. Descriptions

An isolated, linear, univeined leaflet from the Upper Jurassic Talbragar Fossil Fish Bed (outlier of the Surat Basin), 135 mm long and 1.6 mm wide, with a rounded apex and weak transverse striae flanking the midrib, bears a solitary gall or oviposition scar 8 mm from the base (Fig. 4A). The feature is obovate, 11.4 mm long and 4 mm wide, with the widest point at three-quarters of the object's length. Apart from weak curvilinear striations and arching of the leaf tissue around the margins, this object has no clear structural characters (Fig. 4B). Several other examples of this damage type are represented in specimens within private collections (R. Beattie pers. obs.). A specimen of *Elatocladus* sp. from the Middle Jurassic Injune Creek Group, Eromanga Basin, bears an elliptical (2 × 2.5 mm) enlargement near the tip of a linear leaf attached to a short-shoot (Fig. 4C).

4.4.2. Remarks

The isolated needle-like leaf from Talbragar is attributable to *Rissikia* (= *Elatocladus*) *talbragarensis* White, 1981, a probable podocarp or cupressacean conifer. This linear leaf also resembles a detached isoetalean sporophyll but the lack of any indication of microspore or megaspore impressions on the expanded section of the leaf or in the surrounding fine tuffaceous sediment and the absence of a flared base on the leaf suggest that it is more likely to be coniferous. Moreover, the leaf bears weak transverse striae across the narrow lamina—a feature typical of *R. talbragarensis*. This species is known to have much longer (though usually less than 60 mm long) leaflets than otherwise similar *Elatocladus* or *Rissikia* species from the Australian Mesozoic (Nagalingum et al., 2005). The specimen from Eumamurrin belongs to a species of *Elatocladus* with markedly shorter, but otherwise similar, leaves.

Galls can be induced on plants as a host response to a wide range of parasitic organisms (Mani, 1992; Shorthouse et al., 2005). Some galls, especially those generated by viruses and bacteria, may persist over the life of the plant, whereas others may detach or be shed with the foliage on a seasonal basis. Mesozoic *Rissikia*/*Elatocladus* species typically shed either individual leaves or whole short-shoot complexes seasonally, similar to extant *Metasequoia glyptostroboides* Miki ex Hu and W.C. Cheng and *Taxodium distichum* (L.) Richard (Nagalingum et al., 2005). Hence, it is likely that the gall on the Jurassic *Rissikia*/*Elatocladus* leaves was formed as a component of the infecting organism's seasonal life cycle. A range of galls on modern deciduous plants (e.g. oak galls: Stone et al., 2002; poplar galls: Harper, 1959) have a strongly seasonal developmental cycle.

Almost all modern plant groups, including needle-leafed conifers, host galls. The larvae of the gall midges *Itonida pinirigidae* Packard and *Thecodiplosis japonensis* Uchida & Inouye (Diptera: Cecidomyiidae) form galls on the needles of various *Pinus* species. Various Cecidomyiidae [e.g. *Taxodiomyia cupressiananassa* (Osten Sacken)] also produce galls on the terminal branch buds (Chen and Appleby, 1984) and on individual leaves (e.g. *Itonida taxodii* Felt) of extant *Taxodium* species (Felt,

1940) that are superficially similar to those on Mesozoic *Rissikia* and *Elatocladus* species. However, the modern galls tend to be much more elaborate or more numerous on individual leaves (Felt, 1940; Knor et al., 2013) than the examples on Australian *Rissikia*/*Elatocladus* specimens. The earliest body fossil attributed to Cecidomyiidae is Cretaceous in age, although there are several extinct ancestral Sciaroidea recorded from Triassic strata (Blagoderov and Grimaldi, 2004). Although there is no evidence that the Australian Jurassic traces are attributable to gall midges, these fossils show that ecological strategies analogous to modern cecidomorph traits were already developed by the Jurassic.

An alternative interpretation of these aberrant fossil structures is that they represent arthropod oviposition scars. Extant European pine sawflies can produce similar oviposition scars on linear needle-leafed conifers, but usually several scars are developed per leaf (Ghent, 1959). Two species of Xyelidae (sawflies) are known from the Late Triassic (Carnian) of eastern Australia—*Archexyela crosbyi* Riek, 1955, and *Archexyela ipswichensis* Engel, 2005—together representing the oldest records of the family. Hence, oviposition by representatives of this family cannot be excluded on stratigraphic grounds.

4.5. Piercing-and-sucking

4.5.1. Descriptions

Ginkgoaleans are extremely rare in the Australian Jurassic, being apparently restricted to the Hettangian–Sinemurian Razorback beds in east central Queensland. Most of the few ginkgoalean leaves known from this unit bear numerous small indentations and scars situated over the lamina veins (Fig. 4H). Their irregular distribution suggests piercing-and-sucking damage but the depressions may alternatively represent very small oviposition scars. Several conifer and bennettitalean species show similar minute circular indentations or pustules that may represent sites of piercing-and-sucking attack. A single unidentified *Otozamites* species from the Marburg Subgroup (Pliensbachian) at Durikai has a scar 0.25 mm in diameter situated over veins in the distal part of the pinnule (Fig. 4E). Another *Otozamites* species from the same deposit shows a similar minute scar in the centre of a pinnule (Fig. 4D). A smaller-leafed *Ptilophyllum* species from the Bajocian–Bathonian Walloon Coal Measures at Rosewood, Clarence–Moreton Basin, has similar circular scars of 0.2 mm diameter, positioned over veins in the mid-region of several pinnules (Fig. 4I). Several leafy short-shoots of *Rissikia* (= *Elatocladus*) *talbragarensis* from the Bajocian–Bathonian Walloon Coal Measures at Bexhill, southern Clarence–Moreton Basin, bear 0.4 mm diameter circular scars positioned on the midveins of linear leaves and on the slender axis of the foliar-bearing short-shoot (Fig. 4F, M). Specimens attributed to *Araucarites gracilis* Arber from Bexhill (Walkom, 1919) and *Agathis* (= *Podozamites*) *talbragarensis* White, 1981 from the Talbragar Fossil Fish Bed (latest Oxfordian–Tithonian) bear circular indentations over veins in the mid-lamina region of multi-veined leaves (Fig. 4G, J). In the former species, these indentations are associated with deformation and deflection of neighbouring secondary veins. Ferns, e.g., the osmundacean *C. australis*, also show sparse evidence of piercement damage in the form of minute pustules situated on secondary veins immediately adjacent to the midrib (Fig. 4K, L).

4.5.2. Remarks

Many plants develop an array of secondary compounds to defend against herbivores and pathogens (Bennett and Wallsgrrove, 1994), but piercing-and-sucking insects can avoid many chemical defences (e.g. those stored in specialized cells and tissues, such as oil glands and mucilage canals) by tapping directly into the phloem tissues of the vascular system. All examples of piercing-and-sucking damage illustrated here are equivocal, since similar features can be caused by small galls, oviposition scars, mechanical injury or diagenetic processes. However, the consistent position of the damage features over the veins and

Fig. 3. Examples of margin, hole and surface foliar feeding from various Australian Jurassic fossil assemblages: A) scalloped feeding (arrowed) on *Rintoulia* sp. pinna margins, Talbragar Fossil Fish Bed, NRM S087618b; B) scalloped margin and apex feeding on *Rintoulia* sp. pinnae, Talbragar Fossil Fish Bed, MMF17857; C, E, F) scalloped margin feeding and pinnule distortion on *Komlopteris* sp., Talbragar Fossil Fish Bed, AMF106464; D) apex feeding on *Komlopteris* sp. pinna (arrowed), Talbragar Fossil Fish Bed, AMF138074; G) apical feeding (arrowed) on leaflets of *Ptilophyllum cutchense* Morris, Mingenev, Yarragadee Formation, AMF58756; H) pinna apex feeding (arrowed) on *Phlebopteris* sp., Durikai, Marburg Subgroup, AMF358; I) pinnule apex and margin feeding (arrowed) on ?*Lepidopteris* or *Pachypteris*, sp., Clack Island, Battle Camp Formation, QMF15346; J) possible interveinal surface feeding (arrowed) in *Otozamites feistmanteli* Zigno pinna; Durikai, Marburg Subgroup, NHMV21351; K) small hole feeding (arrowed) on *Cladophlebis australis* (Morris) Seward, Bexhill, Walloon Coal Measures, AMF49491; L) possible interveinal surface feeding (arrowed) in *O. feistmanteli* Zigno pinnae; Durikai, Marburg Subgroup, NRM S081406. All scale bars = 10 mm.

in middle to distal regions of leaves, leaflets and short-shoot axes lends some support to their origin as piercement scars.

The putative piercing-and-sucking damage seen in the Australian Jurassic was identified mainly on podocarp and araucariacean conifers and Bennettitales. Several aphids and scale insects attack the leathery leaves and ultimate stems of modern members of the Araucariaceae and Podocarpaceae in this fashion (Ridley et al., 2000; Austin et al., 2004; Miller and Davidson, 2005) in addition to cycads (Howard et al., 1999; Heu et al., 2003), which are morphologically similar to Bennettitales.

Aphids (e.g. *Triassoaphis cubitus* Evans) are known from fossils as old as the Late Triassic (Carnian) in eastern Australia (Evans, 1956) and are potential candidates to have caused such leaf damage. Similarly, scale insects are also inferred to have originated in the Triassic (Koteja, 2001), although their fossil record is generally poor (Grimaldi and Engel, 2005). The oldest fossil scale-insect shields from Australasia are of Cretaceous age (Tosolini and Pole, 2010), though this group is inferred to have had a much longer history in the region (Harris et al., 2007).

Several hemipteran taxa in the two major Australian Jurassic insect assemblages (Mintaja and Talbragar faunas) have mouthparts adapted to piercing-and-sucking. These are the 'Fulguridiidae' (inferred to be either ancestral to, or an extinct sister group of, modern planthoppers, the Fulgoroidea) in the Mintaja insect locality, and the Protopsyllidiidae (variably considered ancestral to the plant lice (Psylloidea) or an extinct sister-group to the Sternorrhyncha) in the Talbragar assemblage. Protopsyllidiidae are numerous at Talbragar but of low diversity. However, all 'homopteran' (Auchenorrhyncha and Sternorrhyncha) hemipterans have mouthparts adapted to the piercing-and-sucking feeding habit and feed on plant metabolite fluids, and virtually all major lineages of this order were likely present in the Jurassic (Shcherbakov and Popov, 2002; Grimaldi and Engel, 2005).

4.6. Leaf-mining

4.6.1. Description

Several well-defined leaf mines are developed on pteridosperm leaves from the Battle Camp Formation of latest Jurassic to earliest Cretaceous age on Clack Island in the Laura Basin, northeastern Australia. On impressions, these mines are paler than the surrounding leaf lamina and lack evidence of frass (Fig. 5A–D). They initiate in the middle or distal regions of pinnae and expand gradually from 0.1 to 1.5 mm in width. They generally lie 0.5–1 mm inside the edge of the lamina and follow the course of the pinna margins, only rarely crossing the pinna midvein, then flank the opposite margin of the pinna. Each trace is restricted to a single pinna and, in most cases, no more than one mine is present within any pinna. Entrance points for the mines are cryptic, but exit points are, in some cases, expressed by an elliptical scar, generally in the proximal region of the pinna.

4.6.2. Remarks

These traces were described and illustrated by Rozefelds (1988). We concur with most of the details noted in that original study but we interpret slight differences in the course of some traces. The principal mined leaf illustrated by Rozefelds (1988) is similar to *Pachypteris* species in general leaflet form but is unusual for that genus and related forms, such as *Archangelskya*, in that pinnae commonly have their widest point around mid-pinna length, rather than at the base, and because *zwischenfiedern* ('rachis leaflets') are present between the major pinnae. The latter are represented in some members of *Pachypteris* (Harris, 1964), but they are more common in members of the Peltaspermales, such as *Lepidopteris* (Anderson and Anderson, 1989; Kustatscher and van Konijnenburg-van Cittert, 2013) and *Autunia* (Barthel et al., 2010). Further, the leaf in question is preserved on the same slab as a circular organ 13 mm in diameter with radiating segments that strongly resembles a *Peltaspermum* peltate cupule (Fig. 5D). Another leaf referable to *P. crassa* is present in the same assemblage but appears to lack leaf mines. We find no evidence of *Pachypteris*

(= *Pachydermophyllum*) *austropapillosa* (Douglas) McLoughlin and Nagalingum in this assemblage. Pinna fragments likely to have been attributed to that species by Rozefelds (1988) are probably smaller examples of *P. crassa* or *Archangelskya furcata* (Halle) Herbst.

Rozefelds (1988) considered members of the Nepticuloidea, a relatively basal clade of Lepidoptera, to be most likely responsible for the leaf mines, and we find no evidence to dispute that interpretation. Evidence of broadly similar mining is preserved on fossil angiosperm leaves, but the examples on the Australian pteridosperm do not precisely correspond to any of the damage types illustrated by Labandeira et al. (2007a), especially in their lack of frass and their serpentine form that generally follows the dissected pinna margins.

Lepidopterans are considered to have undergone extensive radiation in the mid-Cretaceous, accompanying the expansion and diversification of angiosperms, since all but the most primitive groups in this order have mouthparts and feeding strategies intimately associated with pollen and nectar feeding (Pellmyr, 1992; Grimaldi, 1999). However, the order originated in the Early Jurassic and some extant lepidopteran clades may have been established by the Late Jurassic, prior to the emergence of flowering plants (Labandeira et al., 1994; Labandeira, 1998), including groups with the larval leaf-mining trait that had diverged from probable folivore and detritivore precursors (Grimaldi and Engel, 2005). Hence, lepidopterans probably diversified initially in association with an array of Mesozoic pteridosperms, later transferring to angiosperms as the dominant hosts.

4.7. Seed predation

4.7.1. Remarks

Seeds and bract-seed complexes, particularly of pentoxylaleans and araucarian conifers, are moderately to well represented in Australian Jurassic plant assemblages. None has yet revealed any evidence of seed predation.

4.8. Boring

4.8.1. Remarks

Permineralized wood belonging to a broad range of gymnosperms and ferns is widely distributed in eastern Australian Jurassic strata, but only a small selection of this wood has been investigated systematically thus far (Tidwell, 1987, 1992; Tidwell and Jones, 1987; Tidwell and Rozefelds, 1990; White, 1991; Tidwell and Pigg, 1993; Tidwell and Clifford, 1995; Tidwell et al., 2013). Of these studies, Tidwell and Clifford (1995) noted loosely packed elliptical coprolites, 50–150 µm in diameter, within 300 µm diameter galleries in the stipules and inner cortex of a petiole of the osmundaceous fern *Millerocaulis juandahensis* Tidwell and Clifford from the Birkhead Formation at Cattle Downs Station northwest of Wandoan (Surat Basin). Based on their size and morphology, these coprolites likely derive from oribatid mites, but the larvae of various insects or even detritivorous collembolans feeding on dead plant tissues are also potential candidates for the source of the faecal pellets.

White (1991, pp. 98, 99) illustrated transverse sections of *Osmundacaulis jonesii* Tidwell axes from Lower Jurassic deposits at Lune River, with scattered granular-textured pellets located in cavities within the decomposed inner cortex of petiole bases and in cavities between the petiole bases. White (1991) attributed these structures to spores or pollen, but their granular texture, large size (up to five times the diameter of typical xylem tracheids) and barrel-like shape suggest that they are invertebrate (possibly mite) coprolites.

Recently, Tidwell et al. (2013) illustrated masses of spherical, ellipsoidal, and reniform coprolites within isolated or clustered chambers excavated in parenchymatous material between the secondary xylem wedges of the polystelic gymnosperm *Donponoxylon* (probably Pentoxylales). Tidwell et al. (2013) recognized three size ranges of coprolites (20 × 30 µm, 40 × 60 µm and 58 × 116 µm), and suggested that

Fig. 4. Examples of galls and piercing-and-sucking damage (arrowed) from various Australian Jurassic plant fossil assemblages: A, B) gall on proximal part of leaf of *Rissikia talbragarensis* White, Talbragar Fossil Fish Bed. AMF138073; C) gall near tip of *Elatocladus* sp. leaf, Eumamurrin, Injune Creek Group, GSQF13514; D) possible piercing-and-sucking damage on *Otozamites feistmanteli* Zigno, Durikai, Marburg Subgroup. NRM S088646; E) possible piercing-and-sucking damage on *Otozamites* sp., Durikai, Marburg Subgroup, QMF55918; F) possible piercing-and-sucking damage on *Elatocladus* sp. leaf, Bexhill, Walloon Coal Measures, AMF25243; G) possible piercing-and-sucking damage on *Podozamites* leaves, Talbragar Fossil Fish Bed, NRM S087604; H) possible piercing-and-sucking or oviposition damage on portion of a ginkgoalean leaf, Mt Morgan, Razorback beds, V21509a; I) possible piercing-and-sucking damage on *Ptilophyllum* sp. pinnae, Rosewood, Walloon Coal Measures. AMF68434; J) possible piercing-and-sucking damage on *Podozamites* sp. leaves, Bexhill. AMF25236; K and L) *Cladophlebis australis* (Morris) Seward pinnules with piercement scars on secondary veins adjacent to the midrib, Caledonia Colliery, Rosewood, Walloon Coal Measures, AMF78337; M) possible piercing-and-sucking damage on *Elatocladus* sp. short-shoot axis, Bexhill, Walloon Coal Measures AMF66597. All scale bars = 10 mm except for F (= 5 mm).

these were produced by at least three different animals (inferred by the authors to most likely be mites, collembolans and/or millipedes). However, similar coprolites in Late Triassic wood from Svalbard (Strullu-Derrien et al., 2012) have an equivalent range of sizes within individual excavations—this variation likely reflecting developmental stages of a single species of feeding organism. The *Donponoxylon* specimens show no obvious reaction response to the boring, but the parenchymatous host tissue is not well preserved, and it is unclear whether the chambers are the product of strict xylophagy or saproxylophagy.

Both the Mintaja and Talbragar entomofaunas in Australia have high numbers of xylo- or xylomycetophagous coleopterans (possibly Elateridae and probably Ommatidae at Mintaja, and possibly Elateridae and probably Cupedidae and Ommatidae at Talbragar). Such coleopteran groups potentially contributed to the limited boring damage evident in Australian Jurassic fern and gymnosperm axes.

4.9. Palynophagy

4.9.1. Remarks

No evidence of palynophagy has yet been seen in the very limited record of microsporangiate macrofossils from the Australian Jurassic. The only study of Jurassic mesofossil assemblages in Australia obtained via bulk maceration of sediments yielded only a single ambiguous ellipsoidal body that may represent either a degraded lycophyte megaspore or a densely granulate arthropod coprolite (McLoughlin et al., 2014, fig. 10C, D). If this specimen is a coprolite, it lacks any evidence of recognizable spore or pollen fragments that might indicate true palynophagy (cf. Scott and Taylor, 1983; Klavins et al., 2005; Slater et al., 2012). However, Oberprieler and Oberprieler (2012) suggested that the nemomychid weevil *Talbragarus averyi* fed on pollen within the cones of the dominant araucariacean plant in the Talbragar assemblage [*Podozamites jurassica* (White)], based on the observation that adults and larvae of extant Nemomychidae have a consistent feeding association with this plant family in the modern Australian flora.

4.10. Oviposition

4.10.1. Description

Distinctive spindle-shaped oviposition scars occur consistently in the apical parts of *O. feistmanteli* pinnules from the Marburg Subgroup (Pliensbachian) at Durikai (outlier of the Surat Basin; Fig. 5F–I) and in equivalent positions on pinnules of both *Otozamites bengalensis* Oldham and Morris and *Otozamites linearis* Halle from the Yarragadee Formation (Upper Jurassic), Perth Basin (Fig. 5E). The scars are arranged singly in some cases, most commonly in pairs, or less frequently in subparallel groups of up to four. The scars are typically 0.75 mm wide and 1.8–2.5 mm long, although a few are as small as 0.5×1 mm. They either abut the apical margin of the pinnule or are set back from the apical margin by up to 2.5 mm. On impressions, each scar is typically represented by a depressed rim surrounding a slightly raised centre. The scars are orientated parallel to the venation and are otherwise featureless.

4.10.2. Remarks

Though separated by a ~25 myr stratigraphic gap, the Marburg Subgroup and Yarragadee Formation traces are confidently attributed to the same behavioral trait and were likely produced by the same clade of insects, based on their strong similarity in shape and distribution on the host pinnules. Their spindle-like shape, simple morphology and regular arrangement suggest that these traces probably represent the oviposition scars of odonatans and imply that a lineage of this group maintained a consistent oviposition association with short-pinnuled bennettitaleans through a large part of the Jurassic in Australia. Numerous fossil traces with similar basic morphology and assorted regular arrangements recorded on a range of host plants have been attributed to this insect group from the Pennsylvanian to Cenozoic (e.g. van Konijnenburg-van Cittert and Schmeißner, 1999; Béthoux et al., 2004;

Vasilenko, 2008; Sarzetti et al., 2009; Wappler, 2010; Petrulėvičius et al., 2011; Moisan et al., 2012), and similar scars are produced by modern members of this order (Matushkina, 2007).

Of particular similarity to the Australian forms are scars on *Pterophyllum* sp. leaves illustrated by Popa and Zaharia (2011) from the Hettangian–Sinemurian of Romania. The Romanian forms, attributed to the ichnospecies *Paleoovoidus rectus* (Vasilenko) Sarzetti et al., 2009, are similarly elliptical or spindle-shaped scars, 2–3 mm long, 1–1.5 mm wide, and arranged in groups of 2–3 parallel marks. However, the Romanian forms differ in that the scars are distributed in two rows on each side of the rachis. One set of scars is positioned in the proximal half of the leaflet and the other is located at about mid-length of the leaflets. Apart from the Australian and Romanian forms, eggs and oviposition damage on bennettitaleans are evident on the leaves of *Nilssoniopteris haidingeri* (Stur ex Krasser) Pott, Krings et Kerp and *Nilssoniopteris angustior* (Stur Ex Krasser) Pott, Krings et Kerp from the Carnian of Austria (Pott et al., 2007). These records suggest that bennettitalean foliage was a common host for odonate oviposition in the Mesozoic. Various modern lepidopterans [e.g. *Eumaeus* spp., *Lasippa tiga* (Moore), *Athyma asura* Moore and *Zerenopsis lepida* Walker] also utilize the middle to apical regions of morphologically similar cycad (*Cycas* and *Zamia* species) leaflets as sites for egg laying (Stamp, 1980; Culbert, 1994; Contreras-Medina et al., 2003; Robbins, 2004), but the eggs are attached by secretions and usually do not damage the pinnules. Damage to the leaflets in these modern examples is normally caused by early-instar larvae eating trenches into the surface and later instars devouring the leaflets from the edges, hence, they do not generate the distinctive spindle-shaped scars typical of the Jurassic fossils.

4.11. Nectarivory

4.11.1. Remarks

Both Bennettitales and Cheirolepidiaceae have been considered possible candidates for entomophily prior to the rise of angiosperms, via the production of pollen or exudates as rewards for arthropod visitors (Labandeira et al., 2007b; Ren et al., 2009). Both plant groups are widely represented in Australian mid-Mesozoic assemblages, although it remains equivocal whether either group produced nectar-like rewards. We find no palaeobotanical evidence of nectarivory, and unfortunately, it is difficult to tell if any of the insects preserved in the Mintaja or Talbragar entomofaunas fed on nectar. The Mintaja fossils lack visible mouthparts, although based on the feeding preferences of their modern relatives, the dipteran *Austrothyphus moryi* Martin, 2008b and the as-yet undescribed mecopteran and neuropteran are possible candidates for nectarivory. No lepidopterans or other definitive nectar-feeders are known from Talbragar, although a single mecopteran wing is known, and some extant members of this group are reported to be nectarivorous.

4.12. Other biological damage

4.12.1. Remarks

Leaf impressions of assorted taxa from various Australian Jurassic deposits show areas of poor preservation or irregularly disrupted venation, commonly in consistent distributions (e.g. along pinnule margins). It is possible that some of these areas of deteriorated lamina represent zones of fungal degradation, but this is difficult to differentiate from diagenetic staining and alteration in weathered leaf impression assemblages. Other evidence for fungal damage is less equivocal. White (1991, pp. 75–77) illustrated several examples of Early Jurassic wood from Lune River, Tasmania, with extensive damage attributable to pocket rot. Similar pocket rot is widely represented in the fossil record back to at least the Middle Permian (Stubblefield and Taylor, 1986; Weaver et al., 1997). Modern damage of this type (white pocket rot) is generally produced by members of the Agaricomycetes (Basidiomycota: Boyce, 1961; Blanchette, 1984).

Tidwell (1987, pls II.3, IV.2, Fig. 1) noted that a portion of the pith and one of the medullary traces in a specimen of *O. jonesii* from the Early Jurassic of Lune River had disintegrated, due possibly to fungal activity. Some anomalous meristomatic activity was associated with this disintegration.

Fine fungal hyphae are evident on the external surface of the acid-macerated cuticle of *Allocladus helgei* Jansson (Araucariaceae) leaves from the Lower Jurassic Marburg Subgroup at Inverleigh (Jansson et al., 2008b, Fig. 7F). These filaments are concentrated around stomata and may be either epiphyllous or invasive pathogenic fungi.

4.13. Plant defences

4.13.1. Remarks

Plants employ a range of physical and chemical defences against herbivory (Levin, 1973; Edwards and Wratten, 1985; Jeffree, 1986; Bennett and Wallsgrave, 1994; Fernandes, 1994; Müller, 2006). Some biochemical products, such as resin, do not necessarily prohibit initial damage to the plant but serve to plug wounds and inhibit further infection and damage. Plant chemical defences are difficult to detect in the fossil record. However, in some cases, their presence can be inferred by the development of specialized cells and tissues, such as resin and mucilage canals and glandular trichomes. No such specialized tissues have been detected on Australian Jurassic plants thus far. Resinite is a minor component of Australian Jurassic coals (Salehy, 1986; Sappal and Suwarna, 1997), but no major amber deposits of this age have yet been detected on the continent or elsewhere in Gondwana.

Several Australian Jurassic plants do possess morphological characters that may represent adaptations for physical defence against arthropod herbivory. These include the presence of microspinose margins on the leaves of *A. helgei* (Early Jurassic: Durikai; Fig. 6A–C; see also Jansson et al., 2008b, figs. 6, 7) and *Allocladus milneanus* (Tenison-Woods) Townrow (Late Jurassic: ?Talbragar; Townrow, 1967). Such minute spines (375 µm long) are unlikely to have had value as a defence against megaherbivores but may have functioned to inhibit or disrupt systematic leaf-margin feeding by arthropods. Jurassic araucariacean ovuliferous cone scales (*Araucarites* spp.) and polleniferous bracts (e.g. of *Masculostrobus* sp.; Fig. 6E) also possess spines (Gould, 1980). The spines on ovuliferous scales may reach in excess of 1 cm long (Fig. 6D). A densely arrayed armour of these spines consisting of the numerous, tightly packed scales and bracts forming the cones may have provided an effective defence of the ovules and pollen sacs against a range of larger arthropod and even some vertebrate herbivores.

Other Jurassic plants, especially ferns, possessed hairs or scales along their rachises (Figs. 2C, 6G) that may have provided defence of the principal vascular supply particularly against piercing-and-sucking attack. Extreme defences of this type, in the form of dense and robust bristles, were recently illustrated by Pott et al. (2012a) on Jurassic bennettitalean leaves from China.

Amongst Australian Jurassic Bennettitales, *Pterophyllum* sp. from the Walloon Coal Measures at Tannymorel bears a solitary, short spine at the apex of each leaflet, which may have provided defence against apical feeding (Fig. 6F). Such apical spines in modern plants may also function as drip tips to shed water from the leaf surface in moist climates (Dean and Smith, 1978), but the absence of similar high-humidity adaptations in other plants of the assemblage suggests that these structures functioned primarily for defence. *Cycadolepis* bracts, forming the outer part of the bennettitalean inflorescence (Harris, 1969), are also endowed with dense, long spines along their margins

(Fig. 6H). These structures may have been particularly beneficial during early development of the ‘flowers’ for defending against herbivory of both the microsporangiate and ovulate reproductive structures that were positioned in the inner whorls of the inflorescence.

5. Insect responses

A broad array of insect taxa has been recovered from the two Australian Jurassic entomofaunas (Mintaja and Talbragar). Collation of these published and unpublished records reveals a diverse array of inferred feeding strategies (Appendix 1) that might account for the range of damage types here identified on the leaf and wood fossils. Unfortunately, mouthpart details are unavailable for many of the taxa, so feeding preferences have been inferred from those of extant relatives or from limited coprolite, gut-content and mouthpart evidence from related fossil taxa in other parts of the world. Ongoing work at Mintaja and Talbragar is likely to significantly expand the diversity of insects in these assemblages and broaden the potential range of candidates directly interacting with plants.

Some of the insects in the Mintaja assemblage (Sinemurian–Toarcian: Perth Basin) show distinct patterning that may represent a camouflage response. This wing patterning is best seen in two blattodean species of the Liberi-blattinidae (*Kurablattina mintajaensis* Martin, 2010a and *Elisamoides cantabillingensis* Martin, 2010a), and in the wings of the largest species of ‘fulgoridiid’ (Fig. 7). The ‘fulgoridiid’ was almost certainly phytophagous, using its elongate mouthparts to pierce-and-suck plant fluids; its large size would have made it a target for vertebrate and insect predators. The two liberi-blattinids from Mintaja were smaller than the ‘fulgoridiids’, but their wing patterning also suggests some adaptation for camouflage. Wing patterning is a common trait amongst the liberi-blattinids and it has been suggested that these blattodeans were non-cryptic day fliers of some skill, a direct contrast to the cryptic, nocturnal, poor fliers typical of most blattodeans (Vršanský, 2002). Amongst the Mintaja insects, the largest likely aerial predator would have been the neuropteran (Appendix 1), and it is possible that there were other aerial insect or vertebrate predators feeding on these insects; consequently, adaptations for camouflage on plant hosts may have been the focus of strong positive selection. No wing patterning has yet been reported in the Talbragar insect assemblage.

6. Discussion

6.1. Patterns of Australian Jurassic arthropod herbivory

This study begins to fill the global gap noted by Labandeira and Currano (2013) of a dearth of studies on Jurassic plant–arthropod interactions. The general patterns observed here are similar to those expressed in other Jurassic assemblages across the world (see Labandeira, 2013, Fig. 1) and provide evidence of a broad range of arthropod–plant interactions involving numerous plant groups in middle to high southern latitudes.

Although the record of Australian Jurassic terrestrial arthropods is essentially confined to two assemblages, numerous insect families are represented in the entomofaunas (Martin, 2008a; Beattie and Avery, 2012), together with a single spider (Selden and Beattie, 2013), and these are associated with some non-arthropod, non-marine invertebrates (Beattie and Avery, 2012). The relatively diverse Australian Jurassic entomofauna and vascular flora are consistent with previous interpretations of warm, equable climates throughout the mid-Mesozoic (Rees et al., 2000, 2004), permitting rich biotas to thrive even at high latitudes.

Fig. 5. Leaf mining and oviposition features on leaves from various Australian Jurassic fossil assemblages: A–D) leaf mining in ?*Lepidopteris* or *Pachypteris* sp., Clack Island, Battle Camp Formation, QMF15346 (arrow in D indicates *Peltaspermum*-like organ); E) oviposition scars near pinnule apices (arrowed), *Otozamites linearis* Halle, Mingenev, Yarragadee Formation, AMF58731; F–I) oviposition scars near pinnule apices (arrowed), *Otozamites feistmanteli* Zigno, Durikai, Marburg Subgroup, (F, AMF66657; G, H, NRM S081421; I, MVP2025. All scale bars = 10 mm.

Fig. 6. Physical defensive structures in various Australian Jurassic plants: A–C) microspinose margins on leaves of *Allocladus helgei* Jansson; Inverleigh, Marburg Subgroup (A, B, scanning electron micrographs; C, fluorescent light micrograph). L09936t-B, L09936t-A, L09938t; D) prominent apical spine on dispersed araucariacean cone scale, Eumamurrin, Injune Creek Group GSQF13541; E. *Masculostrobis* sp., microsporangiate cone with spinose bract tips, Tannymorel, Walloon Coal Measures, AMF78330; F) *Pterophyllum* sp. with apical spines on leaflets, Tannymorel, Walloon Coal Measures, AMF78329; G) scale scars on rachis of *Sphenopteris* sp. frond, Talbragar Fossil Fish Bed, AMF38833; H) *Cycadolepis* bract with spinose margins, Durikai, Marburg Subgroup, QMF56037. Scale bars = 10 mm for A, D–H, 1 mm for B, 100 μ m for C.

At least seven feeding strategies and an example of oviposition are recognized from the damage to plant remains. Leaf-margin feeding is by far the most common damage type. Amongst the known Australian Jurassic insect groups, members of the Orthoptera and some Coleoptera are the primary candidates to have caused such damage. A few taxa within the Grylloblattidae, Coleoptera and Orthoptera were potentially specialist spore-pollen feeders (Appendix 1). A broad range of taxa were potentially generalist herbivores or adopted saprophagous habits (including members of the Plecoptera, Coleoptera and Blattodea: Appendix 1).

Records of plant damage from hemipterans are notably sparse from the Jurassic world-wide (Labandeira, 2006), especially given that this group is well represented in entomofaunas of this period. The new records of putative piercing-and-sucking attack from the Australian Jurassic begin to illuminate the cryptic record of this feeding behaviour through the mid-Mesozoic. Taxa and individuals specialized for feeding on plant fluids (piercing and sucking) are well represented in

the Australian Jurassic insect assemblages, particularly among the Hemiptera and Diptera (Appendix 1).

An additional large contingent of taxa in the Australian Jurassic entomofaunas represents probable specialist predators in either the juvenile or adult stages of their life cycle. These taxa presumably only interacted indirectly with plants. However, some (e.g. Odonata) may have employed plants as hosts for their eggs (Appendix 1).

Essentially all plant groups represented in the Australian Jurassic, except lycophytes and sphenophytes, show clear evidence of arthropod interactions (Fig. 8). Mesozoic pteridosperms and non-angiosperm ‘anthophytes’ were particularly subject to herbivory and oviposition and this pattern appears to have persisted globally into the Early Cretaceous until the rise of the angiosperms (e.g. Labandeira, 2006; Pott et al., 2012a,b). These gymnosperms include clades that are considered close Mesozoic relatives of flowering plants (Corynospermales, Caytoniales, Pentoxylales and Bennettitales). Their interactions with arthropods

Fig. 7. Selected insects from the Jurassic of Australia. A–C) Insect wings from the Mintaja fossil locality (Mintaja 1 outcrop), Lower Jurassic (Sinemurian–Toarcian) Cattamarra Coal Measures, Western Australia, showing varied patterning that may represent camouflage responses: A) undesciption 'fulgoridiid' (Hemiptera, Fulgoroidea, ?'Fulgoridiidae'), photomicrograph of fore wing part, WAM 08.72; B) undesciption 'fulgoridiid' (Hemiptera, Fulgoroidea, ?'Fulgoridiidae'), photomicrograph of fore wing counterpart, WAM 08.46; C) *Elisamoides cantabillingensis* Martin, 2010a (Blattodea, Libellulidae), photomicrograph of tegmen part, showing basal macula, WAM 08.116. D–F) Herbivorous insects from the Talbragar locality, Talbragar Fossil Fish Bed (latest Oxfordian–Callovian): D) Orthoptera, Abolilinae, female, AMF110537; E) Hemiptera, Procercopidae, AMF110076; F) Hemiptera, Protosyllididae (AMF138078). Scale bars = 1 mm except for D (= 10 mm).

might represent precursor traits to the range of insect feeding-strategies that diversified with the rise of broad-leaved angiosperms in the mid-Cretaceous. The Jurassic assemblages represent a manifestation of Labandeira's (2006) 'Arthropod Herbivore Expansion 3', which developed prior to the explosive diversification of insects and angiosperms in the mid-Cretaceous. There is no evidence of social insects in the Australian Jurassic, either in the form of body fossils or distinct traces, such as termite galleries.

Neither the plant nor arthropod fossil records are yet sufficiently complete to track the co-evolutionary patterns for individual genera or families through time. No extinctions of major plant groups are evident during the Jurassic of southeastern Gondwana. Although certain groups (e.g. Caytoniales and pinnate Dipteridaceae) disappear or markedly decline at the end of the Early Jurassic in Australia (Hill et al., 1999), they persist into younger deposits elsewhere in the world (Vakhrameev, 1991).

This study provides a foundation for understanding the diversity of plant–arthropod interactions in the middle- to high-latitude regions of Gondwana during the mid-Mesozoic. It serves as a springboard for quantitative evaluation of herbivory traits within individual floras and in discrete time intervals. The results also provide primary data that can be used to evaluate levels of herbivory in immediately older (Triassic) and younger (Cretaceous) biotas. Trace evidence on the plants also offers insights into the guilds of plant herbivores represented in the Australian Jurassic entomofauna in the absence of a rich insect fossil record.

6.2. Stratigraphic distribution of plant damage types

Even though there was a dramatic turnover in plant genera at the Triassic–Jurassic transition, it is conceivable that terrestrial arthropod herbivores experienced little overall change in feeding strategies if they were able to transfer to alternative, related and morphologically similar host plants. To date, only broad-scale evaluation of Mesozoic entomofaunas and plant–arthropod interactions have been undertaken (Labandeira, 2006). These do not show a marked turnover in feeding traits at the Triassic–Jurassic transition. However, the evidence to date is sparse for the Early Jurassic and, apart from the reasonably well-studied Molteno Formation biota in South Africa (Scott et al., 2004), examples of Triassic–Jurassic plant–animal interactions are strongly biased towards Northern Hemisphere records.

Triassic plant–insect interactions have not yet been fully surveyed from Australia, although individual cases of arthropod damage have been identified (Rozefelds and Sobbe, 1987; McLoughlin, 2011). Although numerous genera of gymnosperms are unique to either the Late Triassic or Jurassic assemblages of southern Gondwana, many families span this interval. A comparison of data from the Late Triassic Molteno Formation biota and the collective Australian Jurassic biotas reveals similar diversities of plant–arthropod interactions (Table 1), though particular feeding traits are not always consistently represented between these floras in particular plant families.

No clear patterns are evident in the stratigraphic distribution of arthropod damage types through the Australian Jurassic, other than those floras represented by the most abundant plant specimens reveal the greatest range of damage categories (Fig. 8). We contend that, on the available evidence, any apparent spikes in the diversity of arthropod interactions in the Pliensbachian, Bathonian–Callovian and Kimmeridgian of Australia (Fig. 8) are simply the result of sampling biases. Leaf-margin feeding and putative piercing-and-sucking damage are distributed throughout all three epochs of the Jurassic. Other damage types have patchy stratigraphic distributions and, in some cases, are confined to fossils of rare and exceptional preservation (e.g. borings and coprolites within permineralized wood). Many of the assemblages yielding no evidence of arthropod damage (Fig. 8) are represented by small numbers of specimens, and we contend that more thorough sampling would likely identify a diverse array of

Fig. 8. Distribution of arthropod damage-types amongst Australian Jurassic floras and plant groups. The stratigraphic positions of the two Australian Jurassic insect assemblages are marked by insect symbols. Solid bars represent range of uncertainty for the ages of some assemblages. Assemblages indicated by text, arrows and range bars in grey did not yield any obvious evidence of arthropod damage. Solid black squares indicate confident records; question marks indicate equivocal occurrences. Abbreviations: Fm = Formation; Sst = Sandstone; Cyst = Claystone; CM = Coal Measures; Gp = Group; Sgp = Subgroup (Gradstein et al., 2004; Ogg et al., 2008).

interactions in these biotas, thereby providing a more complete picture of herbivory through the Jurassic. Thorough and systematic sampling from beds that can be characterized within a sedimentological context, from which taphonomic biases can be evaluated, is required in order to confidently quantify the patterns of plant damage through time.

7. Conclusions and recommendations

Further studies of Jurassic permineralized wood and peat are warranted as this material provides the best opportunities for identifying arthropod borings and damage by other biotic groups (e.g. true fungi and Peronosporomycetes; Slater et al., 2013). Moreover, permineralized driftwood of this age preserved in marine environments may yield important evidence for the global development of xylem-boring teredid and pholidid bivalves, which arose in the Jurassic (Savrdá, 1991; Vahldiek and Schweigert, 2007). The oldest such *Teredolites* traces in the Australian region are known from Hauterivian–Barremian strata of Western Australia (McLoughlin et al., 1995; McLoughlin, 1996). Several marine Jurassic units in Western Australian basins host fossil wood (McLoughlin and Pott, 2009), and these deposits offer potential for elucidating the early evolutionary development of wood-boring molluscs.

Early Jurassic floras are not well documented in Australia, and several significant gaps are also evident in the remainder of the Jurassic palaeobotanical record (Turner et al., 2009). Systematic analyses of floras from these time intervals would greatly clarify the development of the Australian vegetation and increase the opportunities to document the pattern of plant–animal interactions through time.

Coal-bearing successions are well represented in the late Early and Middle Jurassic of Australia and offer opportunities for the extraction of organically preserved mesofossils (e.g. coprolites, plant cuticles and scale-insect shields) that may help elucidate the development and diversity of key feeding traits (especially palynophagy and piercing-and-sucking behaviour). A reconnaissance study of mesofossils from the Marburg Subgroup revealed diverse, well-preserved cuticles, megaspores and annelid egg cases (Jansson et al., 2008a,b; McLoughlin et al., 2014), but firm evidence for plant–insect interactions was lacking.

The Late Jurassic of Australia incorporates an important Lagerstätte—the biota of the Talbragar Fossil Fish Bed. A preliminary ecosystem reconstruction has been compiled for this biota (Beattie and Avery, 2012), but this site continues to yield a wealth of new plant, vertebrate and invertebrate fossils that will doubtless offer greater insights into Late Jurassic ecosystem structure and the autecology of individual taxa; as such its study deserves high priority.

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Table 1

Comparison of plant–arthropod feeding interactions between the Molteno Formation (Carnian), Karoo Basin, South Africa (Scott et al., 2004) and the collective Jurassic floras of Australia (this study) sorted according to plant groups and broad feeding category. Abbreviations: – = no interactions identified; X = plant group not present.

Plant group	Molteno Formation (Carnian), Karoo Basin, South Africa	Combined Jurassic records, Australia
Bryophyta	–	–
Lycophyta	–	–
Sphenophyta	–	–
Filicales	Non-defined damage	Leaf-margin feeding; Hole feeding; Axis/petiole boring X
Cycadales	Apical feeding; Mining	
Pinales (conifers)	Leaf-margin feeding; Apical feeding; Mining	X
	Araucariaceae	Leaf-margin feeding; Piercing-and-sucking? Galling; Piercing-and-sucking?
	Podocarpaceae	–
	Cheileropidiaceae	–
Ginkgoales	Leaf-margin feeding; Apical feeding; Mining	Piercing-and-sucking or oviposition?
Pteridosperms	Leaf-margin feeding	Leaf-margin feeding; Apical feeding; Mining
	Corystospermales (Umkomasiates)	Leaf-margin feeding; Apical feeding
	Other pteridosperms (Hamshawviales etc.)	X
	Caytoniales	Leaf-margin feeding
'Anthophytes'	Pentoxylales	Leaf-margin feeding; Boring
	Bennettitales	Leaf-margin feeding?; Apical feeding; Leaf-surface feeding?; Piercing-and-sucking?; Oviposition
	Gnetales	X
	Leaf-margin feeding (<i>Yabeiella</i>); Hole feeding (<i>Yabeiella</i>)	

Appendix 1. Table of the main insect taxa recorded from the Australian Jurassic and their inferred feeding preferences

Locality; unit; age	Order and suborder; taxon and reference	Probable feeding strategy	Basis for interpretation
Talbragar, NSW; Talbragar Fossil Fish Bed; Late Jurassic	Odonata: Anisoptera: <i>Austroprotolindenia jurassica</i> (Beattie and Nel, 2012)	Adults aerial predators; naiads aquatic predators. Potential oviposition on plant foliage and slender stems	Biology of extant Anisoptera
	Plecoptera	Adults phytophagous or saprophagous; nymphs saprophagous in cool, well-oxygenated water	Biology of extant Plecoptera
	Orthoptera: Ensifera: Elcanidae?	Adults and nymphs phytophagous	Biology of most extant Ensifera
	Orthoptera: Ensifera: Prophalangopsidae: Aboilinae?	Adults and nymphs palynophagous or phytophagous	Gut contents of fossils: <i>Aboilus</i> sp. (Krassilov et al., 1997)
	Hemiptera: Sternorrhyncha: Protopsyllidiidae (Beattie and Avery, 2012)	Adults and nymphs sap-suckers on young foliage and twigs	Mouthparts of Talbragar fossils (S.M. pers. obs.) and biology of extant Psyllidae and Aphididae
	Hemiptera: Auchenorrhyncha: Palaeontinidae	Adults and nymphs sap-suckers on plant vascular tissue	Biology of extant cicadoids (Cicadidae, Tettigarctidae)
	Hemiptera: Auchenorrhyncha: Cicadelloidea: Proceropidae: (e.g. <i>Griphologus</i> <i>lowei</i> : Etheridge and Olliff, 1890; Handlirsch, 1906)	Adults and nymphs sap-suckers on foliage and young stems	Biology of extant cicadeloids (leaf hoppers)
	Hemiptera: Heteroptera: Corixidae	Adults and nymphs aquatic predators (at water-sediment interface)	Biology of extant Corixidae
	Hemiptera: Heteroptera: Notonectidae	Adults and nymphs aquatic predators (at water surface)	Biology of extant Notonectidae
	Hemiptera: Heteroptera: Gelastocoridae?	Adults and nymphs terrestrial predators (on shoreline)	Biology of extant Gelastocoridae
	Raphidioptera	Adults and larvae predators in low vegetation	Biology of extant Raphidioptera (not present in Australia)
	Coleoptera: Archostemata: Cupedidae	Larvae borers in decayed, fungus-infected wood	Biology of extant Cupedidae
	Coleoptera: Archostemata: Ommatidae	Larvae and ?adults: probably specialist xylomycetophage borers in decayed wood	Biology of extant Ommatidae. Adult life history poorly known but probably similar to larvae
	Coleoptera: Adephaga: Trachypachidae?	Adults and larvae predators in leaf litter	Biology of extant Trachypachidae (not present in Australia)
	Coleoptera: Polyphaga: Hydrophilidae?	Adults saprophagous and phytophagous; larvae aquatic predators	Biology of extant Hydrophilidae
	Coleoptera: Polyphaga: Staphylinidae: <i>Juroglypholoma talbragarensis</i> , <i>Protachinus minor</i> (Cai et al., 2013)	Adults and larvae predators in leaf litter	Biology of extant Staphylinidae
	Coleoptera: Polyphaga: Nemonychidae: <i>Talbragarus averyi</i> (Oberprieler and Oberprieler, 2012)	Adults and larvae palynophagous (probably on Araucariaceae)	Biology of extant Australian Nemonychidae
	Coleoptera: Polyphaga: Elateridae	Adults probably phytophagous; larvae probably saprophagous in the leaf litter and soil	Biology of extant Australian Elateridae (family also in- cludes rare taxa with predatory or phytophagous larvae)
	Mecoptera: Bittacidae?	Adults ambush predators in foliage; larvae scavengers in leaf litter	Biology of extant Bittacidae
	Mecoptera: Panorpidae?	Adults and larvae scavengers (decomposing insects and plants)	Biology of extant Panorpidae (not present in Australia)
	Diptera: Nematocera: Culicimorpha	Adults ephemeral; larvae aquatic filter-feeders or predators	Biology of extant Chaoboridae and Chironomidae
	Diptera: Brachycera: Archisargidae (Oberprieler and Yeates, 2012)	Adults nectarivorous; larvae saprophagous	Biology of extant Stratiomyidae
	Hymenoptera: Apocrita: Praeaulacidae: <i>Gulgonga beattiei</i> , <i>Apocrita</i> sp. (Oberprieler et al., 2013)	Larvae parasitoids of wood-boring beetle larvae	Biology of extant Aulacidae
Mintaja insect locality, WA;	Blattodea: Caloblattinidae: <i>Rhipidoblattina boya</i> Martin, 2010a, plus two indeterminate species	Adults and nymphs: probably saprophagous generalists	Biology of extant Blattaria
	Blattodea: Liberiblattinidae: <i>Kurablattina mintajaensis</i> Martin, 2010a, <i>Elisamoides cantabillingsensis</i> Martin, 2010a	Adults and nymphs: probably saprophagous generalists	Biology of extant Blattaria; many liberiblattinids show wing coloration patterns suggesting crypsis (Vršanský, 2004)
	Blattodea: Blattulidae: <i>Blattula willmotti</i> Martin, 2010a	Adults and nymphs: probably saprophagous generalists	Biology of extant Blattaria
	Blattodea: Indeterminate taxa	Adults and nymphs: probably saprophagous generalists	Biology of extant Blattaria
	Grylloblattidae: Geinitziidae	Adults and nymphs: probably polyphagous (including predation, scavenging and palynophagy)	Biology of extant Grylloblattidae
	Grylloblattidae: ?Blattogryllidae	Adults and nymphs: probably polyphagous (including predation, scavenging and palynophagy)	Biology of extant Grylloblattidae; a related fossil taxon (<i>Plesioblattogryllus</i>) considered predatory based on mouthparts (Huang et al., 2008)
	Orthoptera: ?Prophalangopsidae	Adults and nymphs: mostly phytophagous (including palynophagy and probable phyllophagy)	Biology of Prophalangopsidae
	Hemiptera: Fulgoridiidae	Adults and nymphs: sap feeders, probably on gymnosperms with thick bark	Atrophied clypeus and extremely elongate rostra seen in other fossil 'Fulgoridiidae' (Szwedo, 2007), and the biology of extant Fulgoroidea; some Mintaja fulgoridiids with coloration patterns on their wings that may relate to crypsis

Appendix 1 (continued)

Locality; unit; age	Order and suborder; taxon and reference	Probable feeding strategy	Basis for interpretation
Mintaja insect locality, WA;	Coleoptera: Ommatidae: <i>Zygadenia westraliensis</i> (Riek, 1968), <i>Zygadenia</i> sp., <i>Tetraphalerus</i> sp. (see Martin, 2010b)	Larvae and ?adults: probably specialist xylomycetophage borers in decayed wood	Biology of Ommatidae. Adult life history poorly known but probably similar to that of larvae
	Coleoptera: Elateridae: <i>Lithomerus wunda</i> Martin, 2010b	Adults probably phytophagous; larvae probably saprophagous in the leaf litter and soil	Biology of extant Australian Elateridae (family also includes rare taxa with predatory or phytophagous larvae)
	Coleoptera: Schizocoleidae and other morphotaxa	Adults and larvae: uncertain	Fossils are of unknown familial affinities, or known only from isolated body parts (particularly elytra)
	Diptera: Protorhynchidae: <i>Austrorhynchus moryi</i> Martin, 2008b	Adults: polyphagous fluid feeders (mostly xylem and phloem); larvae: saprophagous on rotting wood and other plant materials	Biology of inferred extant relatives (Anisopodidae)
	Neuroptera: ?Osmyliidae	Adults: probably predatory (possibly opportunistic polyphages); larvae: obligatory predators	Biology of extant Osmyliidae
	Mecoptera Family uncertain	Adults and larvae: uncertain	Biology of extant Mecoptera is variable; order includes scavengers, phytophages, predators and saprophages; Mintaja fossils lacking evidence for feeding preferences

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