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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, in press). 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 in photoperiod have no modern analogues (Creber and Chaloner,

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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, Durikai, 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; Racsó 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 assemblages and analyse how that diversity is represented through time

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