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Species abundance, richness and body size evolution of kangaroos (Marsupialia: Macropodiformes) throughout the Oligo-Miocene of Australia

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ABSTRACT

The Riversleigh World Heritage Area, northwestern Queensland, Australia, contains numerous Oligo-Miocene and Pleistocene fossil bearing deposits. Species of the suborder Macropodiformes (kangaroos and allies) described from Oligo-Miocene sediments at Riversleigh include representatives of all three macropodiform families: Macropodidae, Hypsiprymnodontidae and Balbaridae, a family of extinct fanged kangaroos. Despite extensive taxonomic study, few studies have focused on the ecology of balbarids that are present in Late Oligocene to Late Miocene faunal assemblages. Recently, several macropodiform species from Riversleigh have been described or revised that significantly alter previous interpretations of species richness and abundance at Riversleigh. In this study, Riversleigh macropodiform species richness and relative abundance is explored against a framework of recently revised taxonomic interpretations and biostratigraphy. With the exception of the Early Miocene, our results suggest that balbarids were less abundant than macropodids at Riversleigh. Balbarid species richness declined by the Early Miocene while macropodid species diversity declined from the Early Miocene to Middle Miocene and again in the Late Miocene. We also estimate body mass for macropodiform taxa throughout the Oligo-Miocene. A statistically significant increase in body mass is evident for most taxa through time. A number of ancestral macropodid genera suffer extinction in the Middle Miocene and are replaced by larger sthenurine macropodids around the time of the Miocene Climatic Optimum. Trends in faunal turnover (extinction and replacement of several macropodiform species) in the Middle Miocene are consistent with trends for other mammalian groups both from Riversleigh and globally.

1. Introduction

The suborder Macropodiformes includes two extant families, Hypsiprymnodontidae (musky rat-kangaroos) and Macropodidae (rat-kangaroos, kangaroos and wallabies) and the extinct family Balbaridae ('fanged' kangaroos with hypertrophied canines). Currently 21 macropodiform species are listed as vulnerable or endangered on the IUCN Red List of Threatened Species with 19 listed as occurring solely in 'forest'-type habitats (IUCN, 2017). In particular, those species that occur in rainforest or closed forest environments face threats from habitat reduction and climate change (Newell, 1999; Kanowski, 2001). An understanding of how macropodiform ancestors responded to climate change and other environmental perturbations is required in order to anticipate the potential response of today's kangaroos to climate change in the future and to understand the potential impact local extinctions may have on ecosystems. One area that provides an opportunity to study macropodiform ancestors in closed and open forest environments, and during a time of significant climatic change and without the influence of anthropogenic activity, is the Riversleigh World Heritage Area (WHA) of northern Australia. Hundreds of mid to late Cenozoic vertebrate-bearing fossil deposits have been recorded from the region, many of which contain fossil remains of all three macropodiform families (Archer et al., 1991; Archer, 1979; Cooke, 1992, 1997c, 1997b; Wroe et al., 1998; Cooke, 1999; Kear et al., 2001; Kear et al., 2007; Bates et al., 2014; Black et al., 2014; Travouillon et al., 2014; Cooke et al., 2015; Travouillon et al., 2015; Butler et al., 2016; Travouillon et al., 2016).

Balbarids are known from Oligo-Miocene assemblages thought to be associated with rainforest and open forest environments (Travouillon et

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al., 2009) and are hypothesised to have become extinct during a period of significant climatic change in the Middle Miocene (Cooke, 1997a). Balbarid specimens have been reported from the Namba Formation, South Australia (Flannery and Rich, 1986), the Etadunna Formation, South Australia (Woodburne et al., 1994) and the Camfield Fossil Beds of the Northern Territory (Schwartz and Megirian, 2004; Black et al., 2014) but are most abundant in deposits of the Riversleigh WHA (e.g., Cooke, 1992; Cooke, 1997c; Kear et al., 2007; Black et al., 2014). Oligo-Miocene deposits from which macropodiform specimens have been identified at Riversleigh have previously been separated into three Systems (A, B and C), and more recently into five Faunal Zones (A, B, C, D and E), dating to the Late Oligocene (FZA), Early Miocene (FZB), Middle Miocene (FZC), Late Miocene (FZD) and Early Pleistocene (FZE) with no macropodiform material recorded from the Pliocene (Archer et al., 1989; Archer et al., 1997; Davis and Archer, 1997; Travouillon et al., 2006; Travouillon et al., 2011). Faunal Zones B and C have been further subdivided into 'intervals' including B1, B2, B3, and C1, C2 and C3 (Arena et al., 2015).

A study of Riversleigh macropodiform biostratigraphy and species diversity by Cooke (1997a) indicated that balbarids were the most diverse family (highest species richness) within the suborder during the Late Oligocene and Early Miocene. During the Middle Miocene, macropodids were most diverse, with only a single species of balbarid present (Cooke, 1997a). That species was later formally described as *Balbaroo nalima* (Black et al., 2014). Cooke (1997a) suggested that the apparent decrease in balbarid diversity through the Late Oligocene to Middle Miocene may correlate with significant climate change, from humid to dry conditions, during the Middle Miocene as proposed by McGowran and Li (1994). Cooke (1997a) recognised ten species of macropodid, two hypsiprymnodontids and twenty morphospecies of balbarid, the majority of which were undescribed at the time of his study (see also Cooke, 1996). Since Cooke (1997a), several new fossil kangaroo specimens have been recovered from Riversleigh and many new taxa have been described (e.g., Kear et al., 2007; Bates et al., 2014; Travouillon et al., 2014; Cooke et al., 2015; Travouillon et al., 2015; Butler et al., 2016). Furthermore, several of the earlier described taxa have been taxonomically revised. For example, *Nowidgee matrix* is now considered to be a junior synonym of *Bulungamaya delicata* (Travouillon et al., 2014). In light of such recent taxonomic work, our understanding of macropodiform species diversity at Riversleigh requires revision.

The apparent decline in balbarid diversity in the Middle Miocene proposed by Cooke (1997a) may have coincided with the Middle Miocene Optimum, a period of global climatic change that is also associated with significant faunal turnovers across the planet (e.g. Janis et al., 2000; Barnosky, 2001; Janis et al., 2004; Kay and Madden, 1997; Flynn et al., 2003; Fortelius et al., 2006; van Dam, 2006; Badgley et al., 2008; Bobe, 2006). Given the additional specimens and revised taxonomic work for Oligo-Miocene macropodiforms, a revised analysis of species richness of macropodiforms is required in order to determine whether changes in macropodiforms also coincide with global changes in climate. In conjunction with an understanding of changes in species richness, analyses of relative species abundance can also provide additional insight into Oligo-Miocene macropodiform ecology by determining whether macropodids, hypsiprymnodontids or balbarids are the most common macropodiform family (with respect to number of specimens) throughout the Oligo-Miocene.

In addition to a revised analysis of species diversity, further study of balbarid ecology is required in order to properly understand whether factors such as body size evolution, differences in diet, competition and/or response to climatic change contributed to balbarid extinction and to allow us to understand what factors may have played a role in the local extinction of an entire macropodiform family. The majority of studies of balbarids have focused extensively on taxonomy, with few addressing aspects of palaeoecology. Animal ecology is strongly influenced by body mass which correlates with such factors as growth rate, food requirements and life expectancy (Kozlowski and Weiner, 1997). Prediction of body mass has proved useful for understanding the biology of extinct Australian animals and for placing them within broader ecological contexts (e.g., Wroe et al., 1999; Myers, 2001; Wroe et al., 2003; Travouillon et al., 2009). Several studies have also linked climate change with changes in body mass (e.g., Legendre, 1986; Yom-Tov and Nix, 1986; Alroy, 1998; Guthrie, 2003; Hunt and Roy, 2006; Price and Piper, 2009). Published estimates of balbarid body mass are based on a single study focused more broadly on the palaeoenvironment of the Riversleigh WHA throughout the Oligo-Miocene (Travouillon et al., 2009). Further study of trends in balbarid body mass through time, relative to other macropodiform groups, and placed in context with trends in macropodiform species richness and abundance, is important in order to gain a better understanding of macropodiform ecology.

In this study, we aim to: 1) analyse species diversity (as represented here by richness and the results of rarefaction data) and abundance of macropodiform families from Riversleigh using recently collected specimens and revised taxonomic data; and 2) to estimate body mass for several lineages of macropodiforms through the Oligo-Miocene. It is hypothesised, following Cooke (1997a) that: 1) species richness and relative abundance of balbarids was highest in the Late Oligocene and decreased progressively throughout the Oligo-Miocene until their extinction by the beginning of the Late Miocene; and 2) an increase in relative species richness or relative abundance of macropodids occurred during the Middle Miocene at Riversleigh. With regards to body mass, we hypothesise that changes in the estimated body mass of macropodiforms from Riversleigh throughout the Oligo-Miocene followed Cope's rule (i.e., that animal lineages evolve towards larger body sizes over time; Stanley, 1973; Alroy, 1998; Hunt and Roy, 2006).

2. Methods and materials

2.1. Materials

Specimens used in this study were collected from the Riversleigh WHA and are housed in the Queensland Museum fossil collection (prefix QM F), Brisbane, Australia, and the University of New South Wales (UNSW), Sydney, Australia. 1073 specimens (listed in Supplementary Data File 1) were used in this analysis and consist of all macropodiform specimens that have been taxonomically identified to a genus or species level from Oligo-Miocene fossil sites at Riversleigh. Taxonomic identifications were taken from the literature (Archer, 1979; Cooke, 1992, 1997c, b; Wroe et al., 1998; Cooke, 1999; Kear et al., 2001; Kear et al., 2007; Bates et al., 2014; Black et al., 2014; Travouillon et al., 2014; Cooke et al., 2015; Travouillon et al., 2015; Butler et al., 2016; Travouillon et al., 2016) or were assigned to existing taxa in our current study (Supplementary Data File 1). Macropodiform-bearing assemblages from Riversleigh examined in this study are listed in Supplementary Data File 2, Table S1.

2.2. Temporal framework and biostratigraphy

Radiometric dates (Woodhead et al., 2016) and a revised biochronological framework for fossil sites from Riversleigh (Arena et al., 2015) were used to provide a geochronological context for this study in which Faunal Zones B, Early Miocene, and C, Middle Miocene, were further separated into intervals B1, B2, B3, C1, C2 and C3. Radiometric dates are available only for sites in this study from Faunal Zone interval B3 (18.24 to 16.55 Ma) and AL90 Site which is interpreted as 14.82 ± 0.27 Ma (Woodhead et al., 2016). AL90 Site is interpreted as either Faunal Zone interval C2 or C3 by Arena et al. (2015). Dates for Faunal Zone A (Late Oligocene) of 28.1–23.03 Ma and Faunal Zone D (Late Miocene) of 10–12 Ma are based on estimates from biocorrelation (Woodhead et al., 2016). Several Faunal Zone intervals in this study (e.g. B1, B2, C2 and C3) are represented by a single site and therefore are likely to span significantly shorter time periods than intervals such