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Extending dental mesowear analyses to Australian marsupials, with applications to six Plio-Pleistocene kangaroos from southeast Queensland

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ABSTRACT

Mesowear analysis is a form of dental wear analysis used to infer the diets of herbivorous mammal species. It makes use of percentage indices of blunt, round and sharp cusp shape and high occlusal relief to classify the diet of species into one of three categories: browser, grazer or mixed feeder. Previously, this form of analysis has been limited to placental mammals, restricting the use of such analyses in Australia where the dominant herbivorous mammalian fauna consist of marsupials. In order to address this limitation, mesowear variables of extant marsupials were examined to determine whether their diets can accurately be predicted using mesowear analyses. Discriminant Function Analysis of mesowear variables and analysis of variance (ANOVA) of univariate mesowear scores for marsupial species demonstrate that mesowear analysis can be used to classify marsupial diets. A dataset of 24 typical marsupial species considered to be representative of the three dietary categories with respect to mesowear was generated and significantly increased cross-validated classification levels from 74.4% to 100% for the second molar. Mesowear analysis for marsupial species is most effective for the second molar with high predictive power also being evident for the first and third molars. When mesowear analysis was applied to six Plio-Pleistocene macropods (Marsupialia: Macropodidae) from the Darling Downs region, southeast Queensland, all species were classified as mixed feeders with the exception of *Protemnodon roechus* which was classified as a grazer. This study demonstrates the effectiveness of mesowear analysis as a dietary proxy for herbivorous marsupial species.

1. Introduction

Dental wear analyses can be used to reconstruct the diets of extinct mammals in order to infer their palaeobiology and the environments in which they lived. This allows for the palaeoecological context in which those species evolved to be established. Tooth wear can result from a number of processes but is primarily driven by attrition and abrasion (Lucas, 2004). Attrition, referred to as tooth-on-tooth contact, results from the occlusion of tooth surfaces against each other, most often from the high bite forces associated with chewing cellulose-rich plant material consistent with browsing diets (Fraser and Theodor, 2010). Abrasion, or food-on-tooth wear, is the loss of tooth tissue as a result of contact with a 'tougher' object than the tooth, resulting in wear of cusp tips (Butler, 1972). In herbivores such wear is often the result of the silica content of grasses or ingestion of dirt or grit associated with low-lying plants (Massey et al., 2007; Jardine et al., 2012). As such, abrasion-dominated diets are often associated with grazing, while attrition-dominated diets are primarily associated with browsing. Because of this dichotomy, the relative contribution of attrition and abrasion to tooth wear can be used to infer diet.

Dental wear can be examined on a microscopic level using microwear analysis. This method quantifies the ratio of pits and scratches on teeth, which informs on the relative contribution of abrasion to dental wear (King et al., 1999). Because seasonal or short-term changes in diet over an animal's lifetime can affect microwear patterns (Grine, 1986; Gogarten and Grine, 2013), such analyses are only capable of providing information on the nature of the last several meals of an animal's life. Conversely, dietary proxies based on morphology such as index of hypsodonty—crown height relative to occlusal width—portray a phylogenetic signal indicating dietary adaptions over deep evolutionary time (Semprebon and Rivals, 2010). The very short and deep evolutionary timescales represented by such proxies indicate the need for a form of analysis spanning intermediate ecological timescales. One such method of dental wear analysis is mesowear.

The macroscopic contributions of abrasion and attrition, or gross dental wear, are the basis on which mesowear analysis is employed. The traditional mesowear method was developed by Fortelius and Solounias (2000), who scored cusp shape and occlusal relief of the upper second molars of a number of ungulates and used these variables to classifying species as browsers, grazers and mixed feeders. Because

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mesowear analysis is capable of recording wear which occurs over the last few months or years of an animal's life (Rivals et al., 2007a), it can be used to determine diets on ecological timescales. Since its inception, the mesowear method has been refined and amended by: (1) expansion of the method to other upper and lower molars; (2) development of a univariate mesowear score; (3) in some cases the inclusion of a fourth, or frugivore, category in addition to the browser, grazer and mixed feeder dietary categories and (4) the inclusion of additional categories within the occlusal relief and cusp shape variables (e.g. Kaiser and Solounias, 2003; Rivals et al., 2008; Louys et al., 2011; Winkler and Kaiser, 2011; Taylor et al., 2013). Independent support for mesowear analysis has come from comparisons of mesowear variables with hypsodonty, microwear and stable isotopes (Rivals et al., 2007b, 2008; White et al., 2009; Louys et al., 2012). Mesowear analysis is also considered to be a taxon-free form of analysis (Blondel et al., 2010).

Mesowear has been applied to a number of extant and fossil groups including bovids, giraffes, equids and notoungulates (e.g., Kaiser and Solounias, 2003; Clauss et al., 2007; Croft and Weinstein, 2008; Gentry and Kaiser, 2009). Despite the use of mesowear for these groups, this form of analysis has to date been entirely restricted to placental mammals. This severely limits the use of mesowear analyses in areas such as Australia. There, the predominant herbivorous mammals are marsupials which have different evolutionary origins to placental mammals, having diverged from a common ancestor approximately 168–178 Ma ago (dos Reis et al., 2012). Ungulates, which are commonly used in mesowear studies, have only recently been introduced to Australia and are thus not present in the fossil record. Although comparisons of masticatory motor patterns of koalas, *Phascolarctos cinereus*, appear similar to those of placental herbivores (Crompton et al., 2010), a number of kangaroo species exhibit molar progression—the forward movement of molars and premolars during the life of an animal (McArthur and Sanson, 1988) which could affect the way in which teeth wear along the molar row. Variation in dental wear along the tooth row is also evident in some marsupials. A gradient of increasing wear towards anterior teeth has been noted in the swamp wallaby, *Wallabia bicolor* (Sanson, 1980) and koalas, *P. cinereus* (Lanyon and Sanson, 1986). Such variation may result in differences in mesowear score along the tooth row.

This study aims to test the applicability of the mesowear method, as developed for placental mammals, for use with herbivorous marsupials by classifying and analysing extant marsupial species using mesowear variables. The method will be applied to a number of fossil kangaroo species from the Darling Downs region in Queensland, in order to inform on the palaeobiology of the fossil species and to aid in palaeoenvironmental reconstructions for these sites. The diets of a number of fossil kangaroo species from the Darling Downs region, southeast Queensland, have been the subject of varying dietary interpretations. Bartholomai (1973) for example suggested that *Protemnodon* spp. were primarily grazers, while others have classified the majority of species of this genus as browsers (Johnson and Prideaux, 2004). Few studies to date have made use of dental wear analyses to make inferences about the diets of these species. In this study, the following hypotheses will be tested: (1) that the results of mesowear analyses will reflect the diets of marsupial species with a high degree of significance as in placental mammals; (2) that the second and third molars will have the highest discriminating power for marsupials as is the case for placental mammals; and (3) that the results of mesowear analysis for marsupial species from the Darling Downs region will reflect previous interpretations of diet for these species.

2. Methods

2.1. Extant species

A total of 981 specimens (listed in Supplementary information) from 43 extant marsupial species were examined from the Queensland Museum, the Western Australia Museum, Museum Victoria and the Australian Museum. This dataset represents all species for which sufficient sizes of upper molars with sufficient taxonomic data were available. Species selected encompassed all strictly herbivorous marsupial families including kangaroos (Macropodidae), koalas (Phascolarctidae), wombats (Vombatidae) and ringtail possums (Pseudocheiridae). Mesowear variables were collected from 20 to 30 specimens per species wherever possible (the numbers of specimens per species are listed in Table 1). When this was not achievable a minimum of 10 specimens per species were used. Geographic information for each specimen was recorded where available, in order to ensure that species from a broad range of both habitat types and localities were sampled. The species sampled encompass a wide range of habitat types including rainforest, woodland and grassland, from multiple localities around Australia (Supplementary information).

Each species was classified as a grazer, browser or mixed feeder with 'known' diet based on published dietary information for each species (Van Dyck and Strahan, 2008; Menkhorst and Knight, 2010). Where these sources showed discrepancy or ambiguity with regard to the diet of a species, additional sources were consulted, and the more frequently recorded dietary classification was used. Where possible, grazers were defined as consuming more than 90% graze, such as grasses, while browsers were classified as consuming more than 90% browse, such as leaves and shrubbery. Percentage graze and browse were not available in all cases, and in such instances diets could only be determined on the basis of classifications of diets provided based on other methods such as behavioural studies (e.g., Kaufmann, 1974) or where diets were justified in the publication on the basis of previous knowledge/studies (e.g., Lentle et al., 2003). Mixed feeders refer to species with diets which make use of any other combination of browse and graze. Diets for each extant species and respective dietary authorities are listed in Table 1. The number of mixed feeders in the marsupial dataset is higher than that of grazers, and as such reflects the higher numbers of mixed feeders among marsupials in general based on dietary information listed in literature (e.g. Van Dyck and Strahan, 2008; Menkhorst and Knight, 2010).

2.2. Mesowear

For each specimen, the sharpest buccal cusp of all four upper left molars was scored as sharp, round or blunt and occlusal relief was scored as high or low (Fig. 1). In order to account for potential effects of age on mesowear signals in marsupials, specimens were used only if all four upper molars were present and in occlusion, and where specimens were not in very early or late stages of wear. While left molars were preferred in order to ensure consistency of data, where the upper left molars were unavailable or had broken cusps the upper right molars of the same tooth position were used. Lower molars were not included in this study.

More recent studies have made use of an extended mesowear method, which subdivides occlusal relief and cusp shape into additional categories (Winkler and Kaiser, 2011; Taylor et al., 2013). However in order to ensure direct comparisons with Fortelius and Solounias (2000) the two categories of high and low occlusal reliefs are maintained. In borderline cases where occlusal relief could not be simply scored as high or low, occlusal relief height was divided by the entire tooth length. Where this value was greater than 0.3, cusps were classified as high occlusal relief. Cusp shape is also defined similarly to that of Fortelius and Solounias (2000) in that a sharp cusp has little, or no, rounded area between the mesial and distal facets, a round cusp has a distinctly rounded tip without planar facet wear, and a blunt cusp lacks all distinct facets (Fig. 1).

The percentage of sharp, round and blunt cusp shapes and high occlusal relief for each species was calculated, and a mesowear score calculated. Previous mesowear scoring conventions vary in the values assigned to combinations of occlusal relief and cusp shape. While