Hammer-toothed ‘marsupial skinks’ from the Australian Cenozoic

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Extinct species of *Malleodectes* gen. nov. from Middle to Late Miocene deposits of the Riversleigh World Heritage Area, northwestern Queensland, Australia are enigmatic, highly specialized, probably snail-eating marsupials. Dentally, they closely resemble a bizarre group of living heterodont, wet forest scincid lizards from Australia (*Cyclodomorphus*) that may well have outcompeted them as snail-eaters when the closed forests of central Australia began to decline. Although there are scincids known from the same Miocene deposits at Riversleigh, these are relatively plesiomorphic, generalized feeders. This appears to be the most striking example known of dental convergence and possible competition between a mammal and a lizard, which in the long run worked out better for the lizards.

Keywords: Riversleigh; Miocene; metatherians; scincids; molluscivory; convergent evolution

1. INTRODUCTION

The Cenozoic biota from the Riversleigh World Heritage area in northwestern Queensland, Australia spans the Late Oligocene to Holocene [1,2]. Today, this area is semi-arid with a seasonal climate that alternates between dry winters and wet summers. As currently understood (e.g. [3]), the Early to Middle Miocene deposits accumulated in freshwater pools and caves that occurred within species-rich, climatically temperate, lowland closed-forest palaeoenvironments. With the onset of the Middle to Late Miocene transition [4] and a decline in the rainfall and opening of forests, Riversleigh’s faunas began to transform including the loss of many groups that today survive only in the rainforests of eastern Australia and/or New Guinea [5]. The mammals we describe here as species of *Malleodectes* were small, relatively rare Middle to Late Miocene marsupials that appear to have occupied a very specialized feeding/behavioural niche in Riversleigh’s forests—snail-eating. They appear to have been subsequently replaced in this niche by an equally specialized and dentally strikingly similar group of heterodont scincid lizards that now thrives in Australia’s wet forests—the snail-eating species of *Cyclodomorphus*.

Higher systematic nomenclature follows Archer & Kirsch [6]. Dental homology follows Flower [7] and Lockett [8]. Specimen numbers are those of the Queensland Museum and South Australian Museum. Details of the type localities are held by the Queensland Museum and Queensland Parks and Wildlife Service.

2. SYSTEMATIC PALAEONTOLOGY

Infraclass. Metatheria.

Order and Family. *Incertae sedis.*

Genus. *Malleodectes* new.

Generic diagnosis. P³ massive; crown ovate in occlusal profile and dome-shaped in lateral profile with no cingula; crown height exceeded by a minimum dimension of basal width; basal width approaches basal length; either three or four roots; tiny posterobuccal cuspule; robust anterior and posterior roots continue arc of crown along their outer edges; much larger anterior root recurves producing distinctive oval-shaped lateral profile for entire tooth; upper molars (based on *M. mirabilis*) reduced and decline in size posteriad. M¹ has at least two roots; M² appears to have at least one shallow root; M³ and M⁴ absent; dental formula I²/₂ C¹/₂ P¹⁻³/₂ M^{1,2-2}/₂.

Etymology. *Malleo* is Latin for hammer; *dectes* is Greek for biter; alludes to the interpreted occlusal action of hypertrophied P³.

Type species. *Malleodectes mirabilis* new (figure 1a–c).

Holotype. Partial left maxilla with partial C¹ alveolus, fragment of two-rooted P¹, complete P²⁻³ and alveoli for M¹⁻² (QM F50847).

Type locality, local fauna, geology and age. RRR Site in the Riversleigh World Heritage Area, northwestern Queensland contains terrestrial carbonates that appear to represent a vadose cave deposit. They are phosphate-rich and have crystalline lithotextures that are distinct from adjacent tufaceous lithologies [9]. Although no other taxa have been recovered from RRR Site, other cave deposits in the same area have produced bats that appear to be late-Middle Miocene in age.

Diagnosis. P³ of *M. mirabilis* differs from that tooth in *M. moenia* in its near semicircular lateral profile being smaller and lower-crowned with relatively smaller principal cusp and posterobuccal cuspule.

Etymology. *Mirabilis* is Latin for extraordinary, unusual or strange.

Description. Specimen is bounded dorsally by nasomaxillary suture, terminated anteriorly by part of premaxillary–maxillary suture, posterior margin of incisive foramen and part of a smaller foramen lingual to

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Figure 1. *Malleodectes mirabilis* n. gen. n. sp., Holotype QM F50847, from the Middle Miocene RRR Site at Riversleigh, NW Queensland. (a)(i),(ii) Stereophotos of palatal view of left maxillary fragment retaining P^{2-3} and alveoli for C^1 , P^1 , M^1 and M^2 . (b) Lateral view. (c) Mesial view.

canine alveolus, lingually by intermaxillary suture and posteriorly by anterolateral edge of maxillary vacuity and posterior extremity of maxilla. Palate appears to have been narrow.

Laterally compressed canine alveolus extends postero-dorsally to point dorsal to the anterior root of P^2 .

As indicated by alveoli, anterior end of small, two-rooted P^1 -abutted posterior flank of C^1 .

P^2 robust, larger than P^1 , lacks cingula, two-rooted and leans against P^3 . Posteriorly positioned conical principal cusp has weak anterior and posterior crests and exhibits single small apical wear facette. Tiny posterior cuspsule overlaps the anterior edge of crown of P^3 . Robust posterior root abuts anterior root of P^3 .

P^3 massive compared with P^2 , almost circular in occlusal view (part of buccal margin missing) and dome-shaped in lateral view. The centrally positioned principal cusp has a single apical subhorizontal wear facette. Tiny cuspsule occurs posterobuccal to the principal cusp. Two robust roots evident (figure 1b) of which anterior is longer than posterior. Both roots extend the curvature of the crown along their outer edges.

Closely spaced, relatively small alveoli suggest M^1 was two- or three-rooted, much smaller than P^3 , compressed anteroposteriorly and positioned very close to the posterior margin of P^3 . It is possible that M^1 helped to buttress the P^3 crown. A shallow interdental fossa appears to be present between the lingual alveoli for M^1 and M^2 .

A single alveolus for M^2 appears shallow and relatively small when compared with the albeit small alveoli for M^1 . It is probable that M^2 was reduced and possibly vestigial. A posterior edentulous maxillary ridge appears to extend from this alveolus to the posterior margin of the maxilla.

Malleodectes moenia new (figure 2a,b).

Holotype. Isolated right P^3 (QM F30464) from the Late Miocene Encore Site, Riversleigh World Heritage Area, northwestern Queensland.

Type locality, geology, fauna and age. Encore Site, which occurs in the Riversleigh World Heritage Area,

Figure 2. *Malleodectes moenia* n. gen. n. sp., Holotype QM F30464, from the Late Miocene Encore Site at Riversleigh, NW Queensland. (a) Occlusal view. (b) Buccal view. The lingual (fourth) root is not visible in this view.

northwestern Queensland. Fossiliferous deposits at this site are associated with flowstones that suggest it was a cave deposit. The Encore Local Fauna (e.g. [10]) has been interpreted to be early-Late Miocene in age.

Diagnosis. Differs from *M. mirabilis* in P^3 being larger and higher-crowned with a more pronounced principal cusp, distinct posterobuccal cuspsule and P^3 with four roots—two large roots (posterior and anterior) and two small roots (lingual and buccal).

Etymology. *Moenia* is Latin for fortifications with reference to the robust morphology of the four-rooted P^3 .

Description. Apart from diagnostic differences, P^3 is similar to that of *M. mirabilis*. Principal cusp displays slight apical wear. In occlusal view, crescent-shaped major roots support segments of crown margin (figure 2b) with larger anterior root occupying about 50 per cent and smaller posterior root occupying about 30 per cent of crown circumference. Smaller additional lingual and buccal roots have equivalent-sized circular sections. Underside of crown has slight concave curvature with pronounced alveolar ridge.

Remarks. Although the holotype of *M. moenia* was previously referred to the dasyurid *Ganbulanyi djadjinguli* [11], the maxilla of *M. mirabilis* demonstrates that the holotype of *G. djadjinguli*, a large, well-formed, isolated anterior upper molar from Encore Site, could not have belonged to the same species as the Holotype of *M. moenia*. Further, the overall similarity in highly apomorphic features exhibited by the P^3 of *M. moenia* and *M. mirabilis* justifies placing both species in the same genus.

3. DISCUSSION

The material described here representing species of *Malleodectes* is clearly mammalian rather than lacertilian because the teeth have large, well-developed roots that sit within the well-formed alveoli. The presence of a maxillary vacuity in combination with three premolars tentatively supports the interpretation of the species of *Malleodectes* as metatherian. Otherwise, the features displayed by these species are, among metatherians, either plesiomorphic, derived but homoplasious in a diverse range of other groups (e.g. hypertrophied P^3 and reduced molars), or autapomorphic. This genus therefore cannot yet be conclusively excluded from or included within any particular group of metatherians. However, given that no other metatherian taxa known from Australia appear to represent any group other than Marsupialia, it is highly probable that the species of *Malleodectes* are specialized marsupials.

The four-rooted P^3 of *Malleodectes moenia* is unique among marsupials. The unusual number of roots is evidently an indication of the exceptional need this crown had for foundational support.

Hypertrophy of P^3 is commonly associated in marsupials with atrophy or loss of posterior molars [12,13]. These apomorphic attributes (though dissimilar in detail) co-occur in Australian marsupial lions (thylacoleonids; e.g. species of *Thylacoleo*), burramyids (e.g. species of *Burramys*) and some phalangeroids (e.g. species of *Strigocuscus* as well as some ameridelphians (e.g. polydolopoids such as species of *Epidolops*). However, the extent of posterior molar reduction apparent in *Malleodectes* is only matched or exceeded by much larger, highly specialized carnivorous Plio-Pleistocene thylacoleonids (e.g. *Thylacoleo crassidentatus* and *T. carnifex*; *ibid*). In these taxa, occlusal function in the post-canine dentition shifted forward from the molar row to the P^3 as the posterior molars became vestigial or even lost.

The massive, hammer-like, blade-less P^3 of species of *Malleodectes*, despite being the focus of the cheektooth dentition, could not pierce or cut food—unlike the P^3 of

thylacoleonids. It may instead have been used like a ball-peen hammer to smash hard objects.

Wroe [11] suggested the P^3 of *M. moenia* (which he interpreted to be referable to *Ganbulanyi djadjinguli*) may have been used to crush bones. While this is possible, there are no other ossivorous adaptations evident in the dentition of *M. mirabilis* such as a strongly braced canine, low-crowned, powerfully-braced anterior premolars or robust molars for further processing the fragments of the kind seen in other mammalian ossivores such as hyaenids or, among marsupials, species of *Sarcophilus*. Hence, we conclude it is more likely that the hard objects being crushed by the P^3 of species of *Malleodectes* were gastropod shells as discussed below.

There is a single, small wear facette on the apical tip of P^3 in both species of *Malleodectes*. While this could indicate a horizontal shearing component in mastication, it is more likely to be the result of concussing hard objects such as shells. The stress-distributing, dome-like structure of the crown and multiple-roots below suggest that this tooth was capable of exerting and sustaining enormous pressure during mastication.

In contrast, the apparently relatively small M^1 and reduced M^2 suggest these teeth, like the molars of Plio-Pleistocene thylacoleonids, might have been vestigial in terms of masticatory function. In those thylacoleonids in which only M^1 remains of the original four marsupial molars (e.g. *Thylacoleo carnifex*) that molar functions as a thegotic tool to help hone the blade of P^3 [13]. The lack of blades on P^3 in the species of *Malleodectes* suggests that the vestigial molars in these species probably retained a diminished role in segmenting food items following the crushing activity of the premolars. Masticating shell pieces would, however, rapidly reduce the ability of the other teeth in the dentition to cut anything soft. Hence, if they were eating snails, tissues exposed by the crushing P^3 would probably have been swallowed without further processing by the dentition.

Dental adaptations for crushing are known to occur in a number of mammals. Of these, members of the Mid-Cenozoic placental insectivoran genus *Apternodus* exhibit a suite of specializations in the anterior dentition [14] resembling aspects of the specialized cheektooth dentition in *Malleodectes*. However, none exhibits the striking pattern of dental merism dominated by a single 'hammer-tooth' as in *Malleodectes*. Furthermore, the proportions of the broad-based, low, dome-like crown, and the number and arrangement of the roots are unique to the 'hammer-tooth' of *Malleodectes*.

While no other mammals have a dentition similar to that seen in the species of *Malleodectes*, its specialized teeth are similar to the hypertrophied, molariform teeth occurring in various heterodont, durophagous lizards. Enlarged, rounded posterior teeth occur in some scincids, varanids, anguids, iguanids and teiids [15].

Among these, the proportions, size and positioning of cheekteeth in *Malleodectes* exhibit a striking resemblance to the dentition of the pink-tongued skink, *Cyclodomorphus gerrardii* (figure 3a). This medium-sized (40 cm) lizard, which inhabits rainforests and wet sclerophyll forests on the Australian east coast, has a single hypertrophied ball-peen hammer-like tooth in the dentition that does not directly occlude with the similar tooth in the dentary. These powerful, well-buttressed teeth are used

Figure 3. *Cyclodomorphus gerrardii* SAM R47699, palatal view of the skull (a) to reveal striking convergence in form between the posterior teeth of this snail-eating lizard, including the hammer-tooth that is the largest in the tooth row, and the teeth of *Malleodectes mirabilis* (b). The reduction in the size of teeth posterior to the hammer-tooth, disposition of palatal vacuities and palatal bones are also very similar.

to crush the shells of snails. This skink also eats slugs, insects, spiders and fruits [16].

Like the species of *Malleodectes*, these skinks have only small, increasingly-reduced 'molars' posterior to the hammer tooth, a palatal vacuity bordering the posterior portion of the maxilla, and a strongly reinforced palate adjacent to the hammer tooth. Given that the only molluscs that have ever been found in the Cenozoic rocks of Riversleigh are freshwater/terrestrial gastropods, which are also abundant in most of the sites, it is likely that these rather than pelecypods were the shelled-molluscs eaten by species of *Malleodectes*.

The striking similarity in the dentition of these Riversleigh mammals and the dentition of *Cyclodomorphus* skinks represent an extraordinary example of convergence between a lizard and a mammal. The degree of similarity also signals the probability that if they were sympatric they would almost certainly have competed.

So far, the only lizards known from the Miocene of Riversleigh do not include hammer-toothed taxa [17–19]. Because hammer-toothed, snail-eating marsupials no longer exist in Australian wet forests but species of *Cyclodomorphus* do, the former must have been replaced in this specialized terrestrial niche sometime within or subsequent to the Late Miocene. This was an increasingly difficult and testing time for forest groups because of the gradual collapse of the biodiverse late-Middle Miocene forests that characterized at least the Riversleigh region of northern Australia. Given these stresses, the ancestors of hammer-toothed lizards may have been advantaged in the increasingly unpredictable environments that characterized the Late Miocene to Pleistocene because of their more resilient, wider metabolic scope.

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