A Peculiar Faunivorous Metatherian from the Early Eocene of Australia

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A peculiar faunivorous metatherian from the early Eocene of Australia

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I describe *Archaeonothos henkgodthelpi* gen. et. sp. nov., a small (estimated body mass ~40–80 g) tribosphenic metatherian from the early Eocene Tingamarra Fauna of southeastern Queensland, Australia. This taxon, known only from a single isolated upper molar (M2 or M3) is characterised by a very distinctive combination of dental features that, collectively, probably represent faunivorous adaptations. These include: a straight, elevated centrocrista; a metacone considerably taller than the paracone; a wide stylar shelf (~50% of the total labiolingual width of the tooth); reduced stylar cusps; a long postmetacrista; a small and anteroposteriorly narrow protocone; an unbasined trigon; and the absence of conules. Some of these features are seen in dasyuromorphians, but detailed comparisons reveal key differences between *A. henkgodthelpi* and all known members of this clade. *A. henkgodthelpi* also predates recent molecular estimates for the divergence of crown-group Dasyuromorphia. Similar dental features are seen in a number of other metatherians, including the South American sparassodonts, *Wirunodon chanku* from the ?middle–late Eocene Santa Rosa local fauna of Peru, and *Kasserinotherium tunisiense* from the early Eocene Chambi fauna of Tunisia, although whether *A. henkgodthelpi* is closely related to any of these taxa is unclear based on available evidence. I therefore refer *A. henkgodthelpi* to Metatheria *incertae sedis*. Potential relatives of *A. henkgodthelpi* are unknown from any other Australian fossil deposit.

Key words: Mammalia, Metatheria, Marsupialia, Sparassodonta, Eocene, Tingamarra Fauna, Australia.

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Introduction

With a handful of exceptions (e.g., Archer et al. 1988; Beck et al. 2008a), all fossil Australian metatherians known from the late Oligocene onwards can be confidently referred to one of the four Australian marsupial (i.e., crown-group metatherian) orders still extant today, namely Dasyuromorphia (predominantly faunivorous forms such as quolls, marsupial "mice", the numbat, and the extinct thylacine), Diprotodontia ("possums", kangaroos, wombats, and the koala), Notoryctemorphia (marsupial moles), and Peramelemorphia (bandicoots and bilbies). The only known Australian metatherians older than the late Oligocene are from the early Eocene Tingamarra Local Fauna in southeastern Queensland (Godthelp et al. 1992). In direct contrast to younger Australian deposits, none of the fossil metatherians described to date from Tingamarra can be referred to a modern marsupial order (Archer et al. 1993; Godthelp et al. 1999; Beck et al. 2008b; Sigé et al. 2009; Beck 2012). The Tingamarran metatherians are

therefore of critical importance for understanding the early evolutionary history of the clade in Australia, and the timing of diversification of modern Australian marsupials. However, they are represented by highly fragmentary specimens, mainly isolated teeth, and much of this material remains to be described.

Here, I describe a new metatherian from Tingamarra, *Archaeonothos henkgodthelpi*, that also does not appear to be a member of any known Australian marsupial order. Given that this taxon is currently represented by extremely limited material (a single upper molar), and pending a formal phylogenetic analysis that includes a suitably diverse sample of potential relatives, I simply discuss its derived similarities to other metatherians, and refer it to Metatheria incertae sedis.

Institutional abbreviations.—EY, Service de la Carte collections, Office National des Mines, Tunis, Tunisia; LACM, collection of the Natural History Museum of Los Angeles County, Los Angeles, USA; MHNC, Museo de Historia Natural Alcide d'Orbigny, Cochabamba, Bolivia; QM F, Queensland

Museum Fossil Collection, Brisbane, Australia; YPFB Pal, Yacimientos Petrolíferos Fiscales Bolivianos, Colección de Paleontología, Santa Cruz, Bolivia.

Other abbreviations.—L, maximum anteroposterior length; M, upper molar; StA–E, stylar cusps A–E; W, maximum labiolingual width.

Material and methods

As with all other mammalian fossils collected to date from the early Eocene Tingamarra Local Fauna (Godthelp et al. 1992, 1999; Archer et al. 1993; Hand et al. 1994; Beck et al. 2008b; Sigé et al. 2009; Beck 2012), the holotype and only known specimen of *Archaeonothos henkgodthelpi* gen. et sp. nov. (QM F53825) was recovered by repeated screen-washing of illite-smectite clay samples and subsequent microscope-assisted sorting of the concentrate. Following Luckett (1993), the plesiomorphic upper molar formula for Metatheria is assumed to be M1–4, although it has been proposed that the "M1" of metatherians is in fact a retained deciduous premolar (Averianov et al. 2010; O'Leary et al. 2013). Maximum anteroposterior length (L) of a molar is here measured parallel to a line running through the apices of the paracone and metacone, while maximum labiolingual width (W) is measured perpendicular to this (see Muizon 1998: 137, A4, A5).

Body mass estimates were calculated for *Archaeonothos henkgodthelpi* and other metatherian taxa discussed in the text (Table 1) using regression equations for upper molar dimensions from two different datasets: the "pooled Didelphidae and Dasyuridae" dataset of Gordon (2003: fig. 7), and the "all species" dataset (based on Australian marsupials only) of Myers (2001: table 2). The most accurate (as indicated by R^2 values) measurement available was used for each locus: for the Gordon (2003: fig. 7) dataset, this was L for M1, M2, and M3; for the Myers (2001: table 2) dataset, this was maximum occlusal area for M1, and L for M2 and M3. Estimates based on Myers (2001: table 2) include the appropriate smearing estimate. If the precise dental locus represented was uncertain, body mass estimates were calculated for each of the different possible loci.

Systematic palaeontology

Mammalia Linnaeus, 1758

Infraclass Metatheria Huxley, 1880

Order and family incertae sedis

Genus *Archaeonothos* nov.

Type species: *Archaeonothos henkgodthelpi* sp. nov., monotypic; see below.

Etymology: From Ancient Greek *arkhaios*, ancient and *nothos*, illegitimate; in reference to the uncertain affinities of this fossil taxon.

Diagnosis.—As for type species.

Archaeonothos henkgodthelpi sp. nov.

Fig. 1.

Etymology: In honour of my colleague, friend, and mentor Henk Godthelp, who has led research at Tingamarra for over 20 years. The genus name can be rendered into colloquial English as "the old bastard", which is an affectionate nickname for Henk.

Holotype: QM F53825, a slightly worn M2 or M3 (Fig. 1).

Type locality: Tingamarra Local Fauna, Boat Mountain area, Murgon, southeastern Queensland, Australia 26°S 152°E.

Type horizon: Potassium/argon dating of authigenic clays give a minimal age of 54.6 +0.05 MY BP for this site (Godthelp et al. 1992), i.e., earliest Eocene, a date congruent with geological and biocorrelative evidence (Beck et al. 2008b: text S1; Sigé et al. 2009).

Diagnosis.—Small (estimated body mass of ~40–80 g; Table 1), tribosphenic metatherian characterised by the following features: centrocrista straight and elevated above the level of the trigon; metacone much larger than paracone; protocone small and anteroposteriorly narrow; conules indistinct or absent; trigon unbasined; stylar shelf broad (~50% of the total labiolingual width of the tooth); StB tallest cusp, other stylar cusps weakly developed; preparacrista anteriorly convex and terminating at StB; small but distinct StA present; very narrow but continuous cingulum along the anterior margin of tooth, formed by preprotocrista and anterolabial cingulum; postmetacrista longer than preparacrista. Differs from many metatherians with straight centrocristae (e.g., *Kokopellia juddi* Cifelli, 1993, peradectids, alphadontids, "pediomyids", microbiotherians, *Caluromysiops irrupta* Sanborn, 1951) in that the apex of the centrocrista is elevated far above the trigon rather than level with it, the metacone is much taller than (rather than subequal in height to) the paracone, and the protocone is small and anteroposteriorly narrow, without a distinct trigon basin. Differs from most didelphimorphians and most dasyuromorphians in that the centrocrista is straight rather than V-shaped, the stylar shelf is wide (~50% of the total labiolingual width of the tooth), StD is very small, and the protocone is small and anteroposteriorly narrow, without a distinct trigon basin. Differs from dentally derived thylacinids, such as *Wabulacinus ridei* Muirhead, 1997 and species of *Thylacinus*, in its much smaller size (estimated body mass of 40–80 g versus >5 kg), wider stylar shelf, shorter and less oblique postmetacrista (resulting in the tooth as a whole being proportionally not as elongate anteroposteriorly), and a StD that is positioned labially (rather than posterolabially) relative to the metacone. Differs from the possible sparassodont *Mayulestes ferox* Muizon, 1998 in its smaller size, more reduced stylar cusps (particularly StD), shallower ectoflexus, less well-developed conules, smaller protocone, and more oblique postmetacrista. Differs from the sparassodont *Allqokirus australis* Marshall and Muizon, 1998 in its smaller size, shorter and less oblique postmetacrista, less closely approximated paracone and metacone, less well-developed conules, and a metacone that does not overhang the posterior margin of the tooth. Differs from most other sparassodonts in its much smaller size (estimated body mass of 40–80 g versus >800 g), less
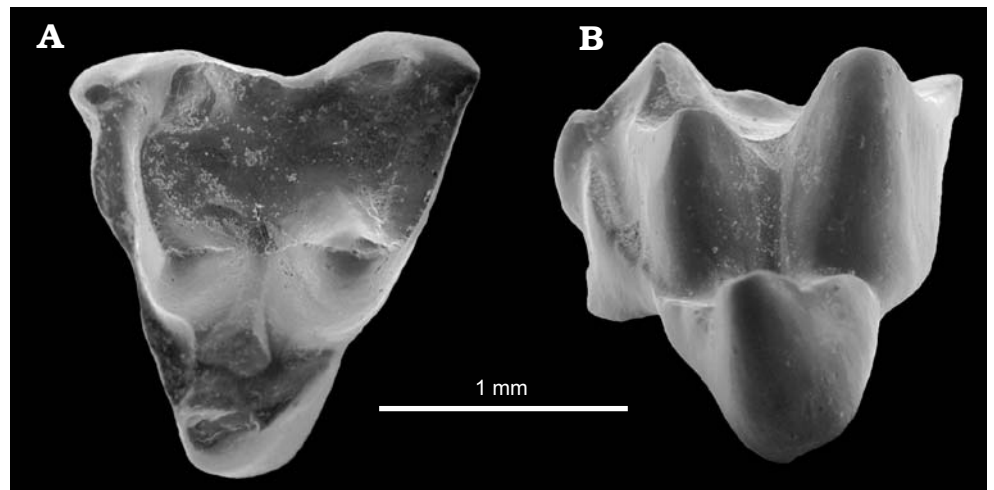
Fig. 1. Holotype and only known specimen of the metatherian mammal *Archaeonothos henkgodthelpi* gen. et sp. nov. (QM F53825; M2 or M3) from the early Eocene Tingamarra Fauna, southeastern Queensland, Australia; in occlusal (**A**) and lingual (**B**) views. Both SEM micrographs.

closely approximated paracone and metacone, less oblique postmetacrista, broader stylar shelf, and larger protocone. Differs from *Wirunodon chanku* Goin and Candela, 2004 in its more closely approximated paracone and metacone, more compressed protocone, metacone being proportionately larger than paracone, preparacrista terminating at StB (instead of StA), larger StB, wider stylar shelf, larger size (estimated body mass approximately twice as large), and the presence of a (very small) StC. Differs from *Kasserinotherium tunisiense* Crochet, 1986 in its more anteroposteriorly compressed protocone, wider stylar shelf, much greater size difference in paracone and metacone, and larger StB.

Description.—QM F53825 is a small (Table 1), lightly worn tribosphenic upper molar (either an M2 or M3) with promi-

nent crests and sharp cusps (Fig. 1). Three distinct roots are present: an intact lingual root below the protocone, and broken roots at the anterolabial and posterolabial corners. In occlusal view (Fig. 1A), the tooth is close to triangular in outline, with a moderately well-developed ectoflexus. When oriented such that the apices of the paracone and metacone are anteroposteriorly aligned, the metastylar lobe projects slightly further labially than does the parastylar lobe.

A low, but distinct, StA is present at the anterolabial corner of the tooth, sitting at the anterior end of the anterolabial cingulum. Immediately lingual to StA, there is a shallow notch ("metastylar indent" sensu Cramb and Hocknull 2010) in the anterolabial cingulum, which would have housed the posterolabial (metastylar) corner of the preced-

Table 1. Body mass estimates for *Archaeonothos henkgodthelpi* gen. et sp. nov. and other metatherian taxa discussed in the text, calculated using regression equations from the "pooled Didelphidae and Dasyuridae" dataset of Gordon (2003: fig. 7) and the "all species" dataset (which is based on Australian marsupials only) of Myers (2001: table 2). Measurements were taken from the indicated references. The holotype and only known specimen of *Chulpasia jimthorselli* (QM F50411, an M1 or 2) is damaged (see Sigé et al. 2009), and hence measurements for this specimen represent minimum values; as a result, body mass estimates for *C. jimthorselli* are probably underestimates. Abbreviations: L, maximum anteroposterior length; M1A, body mass estimate based on regression equation of M1 maximum occlusal area (calculated as L × W); M1L, body mass estimate based on regression equation of M1 maximum anteroposterior length; M2L, body mass estimate based on regression equation of M2 maximum anteroposterior length; M3L, body mass estimate based on regression equation of M3 maximum anteroposterior length; W, maximum labiolingual width.

Taxon	Specimen	Locus	L [mm]	W [mm]	Estimated body mass [g]		References
					Gordon (2003)	Myers (2001)	
Archaeonothos henkgodthelpi gen. et sp. nov.	QM F53825	M2 or 3	1.88	1.73	43.6 (M2L)	54.3 (M2L)	this study
					48.7 (M3L)	76.0 (M3L)	
Mayulestes ferox	MHNC 1249	M2	3.09	3.91	212.1 (M2L)	355.5 (M2L)	Muizon (1998)
		M3	2.89	4.29	181.3 (M3L)	317.7 (M3L)	
Allqokirus australis	YPFB Pal 6104	?M3	3.2	3.4	247.7 (M3L)	445.9 (M3L)	Marshall and Muizon (1988)
Kasserinotherium tunisiense	EY 10	M3	1.6	1.75	29.7 (M3L)	44.4 (M3L)	Crochet (1986)
	EY 12	M1 or 2	1.42	1.55	19.2 (M1L)	29.7 (M1A)	
					17.9 (M2L)	18.8 (M2L)	
Wirunodon chanku	LACM 140621	?M3	1.27	1.12	14.7 (M3L)	20.6 (M3L)	Goin and Candela (2004)
Djarthia murgonensis	QM F31458	M2	1.8	–	38.0 (M2L)	46.1 (M2L)	Godthelp et al. (1999)
		M3	1.67	–	33.9 (M3L)	51.2 (M3L)	
Thylacotinga bartholomaii	QM F16835	M2	5.53	–	1351.3 (M2L)	3212.3 (M2L)	Sigé et al. (2009)
Chulpasia jimthorselli	QM F50411	M1 or 2	2.48	2.58	120.7 (M1L)	237.9 (M1A)	Sigé et al. (2009)
					105.3 (M2L)	154.8 (M2L)	

ing molar in the intact tooth row. StB is the tallest stylar cusp, only slightly shorter than the paracone, and also the largest in terms of occlusal area. StB represents the labial terminus of the preparacrista. A weak, vertically-directed "keel" is present at the base of the anterior flank of StB, and is separated from StA by a very small, but distinct, notch. StC is extremely small and labiolingually compressed; it is identifiable only as a very slight rise on the labial margin of the tooth, immediately anterior to the deepest point of the ectoflexus and in line with midpoint of the centrocrista, merging anteriorly with the base of StB. StD is the second tallest stylar cusp, approximately 40% the height of StB. StD is located slightly more posteriorly than the apex of the metacone, and is labiolingually compressed. A slight rise at the posterolabial corner of the tooth, at the terminus of the postmetacrista, may represent StE.

The stylar shelf is broad, comprising about 50% of the total labiolingual width of the tooth, and hence the paracone and metacone are located quite centrally on the tooth crown. The metacone is much taller than the paracone, and is also larger in occlusal area, with its base extending further lingually towards the protocone. The labial face of the metacone shows slight labial buttressing such that the cusp is distinctly conical, whereas the labial face of the paracone is flatter. A very short, weak crest extends lingually from the base of the lingual margin of the paracone, and another extends lingually from the base of the anterolingual margin of the metacone; these indistinct crests may represent vestiges of the postparaconule crista and the premetaconule crista, respectively, although a distinct paraconule is absent and the metaconule is barely identifiable. The preparacrista is slightly convex anteriorly, but extends in an overall labial direction from the paracone to the large StB. The centrocrista is essentially straight, and the bases of the paracone and metacone are somewhat approximated. In labial view (Fig. 1B), the centrocrista appears elevated far above the level of the trigon. The postmetacrista is at an angle of ~65 degrees relative to an axis passing through the apices of the paracone and metacone. The trigon is not distinctly basined.

The protocone is small in terms of both height and occlusal area, and its posterior flank slopes more shallowly than its anterior flank. The apex of the protocone is located slightly more posteriorly than that of the paracone. In lingual view, the protocone apex appears distinctly anteriorly directed. A paraconule does not appear to be present anywhere along the preprotocrista. The preprotocrista does not terminate at the base of the paracone, but forms an extremely narrow cingulum along the anterior flank of the latter, which is continuous with the anterolabial cingulum labially. A remnant of the metaconule may be present as a slight bulge in the postprotocrista, as it descends from the apex of the protocone. The postprotocrista terminates at the base of the lingual flank of the metacone. The base of the metacone extends slightly further posteriorly than the terminus of the postprotocrista, and hence the posterior margin of the trigon appears slightly "pinched in" relative to the stylar region.

Discussion and conclusions

Two eutherians have been described from Tingamarra (Godthelp et al. 1992; Hand et al. 1994), namely the bat *Australonycteris clarkae* and the probable condylarth *Tingamarra porterorum*. However, *Archaeonothos henkgodthelpi* gen. et sp. nov. can be confidently identified as metatherian based on the following combination of (not always apomorphic) features characteristic of Metatheria, or subclades within Metatheria: metacone much larger than paracone; stylar shelf broad; presence of distinct stylar cusps including StD; absence of a postcingulum; postprotocrista does not extend past the base of the metacone (Luo et al. 2011). The presence of a straight centrocrista is probably plesiomorphic for Metatheria, as in, for example, the North American *Kokopellia*, "pediomyids", alphadontids, and peradectids (Johanson 1996; Cifelli and Muizon 1997; Case et al. 2005; Davis 2007; Williamson et al. 2012). However, in these forms the apex of the centrocrista descends to the level of the trigon, and the paracone and metacone are similar in height (features also seen in some crown-marsupials, such as microbiotherians and the extant didelphid *Caluromysiops*; see Wroe et al. 2000: character 10; Voss and Jansa 2003, 2009). By contrast, in *Archaeonothos henkgodthelpi* the apex of the centrocrista is elevated far above the trigon, and the metacone is much taller than the paracone; I interpret this as a derived condition, probably functionally connected with faunivory. Similarly, it seems more likely that the small protocone and weakly developed stylar cusps of *A. henkgodthelpi* are secondarily derived, faunivorous adaptations, rather than plesiomorphic retentions.

Within Metatheria, *Archaeonothos henkgodthelpi* has the following apomorphic features seen to various degrees in faunivorously-adapted forms: small, anteroposteriorly compressed protocone; metacone much larger than paracone; metacone and paracone slightly approximated basally; postmetacrista longer than preparacrista; conules very reduced; centrocrista straight and elevated above the level of the trigon; and stylar shelf wide, but with reduced stylar cusps. Amongst known Australian marsupials, only some dasyurids and thylacinids (both members of Dasyuromorphia) show similar dental specialisations. However, dasyurids and most thylacinids appear less derived than *A. henkgodthelpi* in, for example, their more V-shaped centrocristae and better-developed protocones and conules. A straight centrocrista occurs only in the modern thylacinid *Thylacinus cynocephalus* and the Oligo-Miocene fossil forms *T. macknessi*, *T. potens*, and *Wabulacinus ridei* (Wroe and Musser 2001: character 10), all of which are much larger than *A. henkgodthelpi* (estimated body mass >5kg; Wroe et al. 2004, Travouillon et al. 2009). Dasyurids are also characterised by a relatively anteriorly-placed StD (further anterior than the metacone, close to the ectoflexus) that is distinctly larger than StB, particularly in smaller (<100g) forms, such as species of *Sminthopsis*, *Antechinus* and *Planigale* (Archer 1976; Wroe 1997); this is unlike the very small, labiolingually compressed StD directly labial to the metacone seen in *A. henkgodthelpi*. Further, in

most dasyuromorphians StA is not identifiable as an obviously distinct cusp (particularly on M2–4), whereas this cusp is low, but cusp-like and clearly distinct from StB in *A. henkgodthelpi*.

Molecular divergence dates suggest that the modern dasyurid families Dasyuridae, Thylacinidae and Myrmecobiidae probably diverged from each other less than 40 million years ago (Krajewski et al. 2000; Beck 2008; Meredith et al. 2009, 2011). If these molecular dates were accurate or overestimated the true divergence times, members of these families could not have been present at Tingamarra during the early Eocene, thus excluding *A. henkgodthelpi* from crown-Dasyuromorphia. However, it is clear that rates of molecular evolution within mammals are more variable than previously appreciated (Kitazoe et al. 2007; Steiper and Seiffert 2012; Dornburg et al. 2012), and hence molecular estimates of divergence times should not be viewed uncritically. Even if *A. henkgodthelpi* is not a member of crown-group Dasyuromorphia, it is possible that it belongs to the dasyuromorphian stem. If so, however, its faunivorous dental specialisations must have evolved independently prior to the similar apomorphies seen in some dasyurids and thylacinids.

Most other faunivorously-specialised metatherians, such as sparassocynid and didelphin didelphimorphians (Reig and Simpson 1972; Voss and Jansa 2003, 2009; Forasiepi et al. 2009), differ from *Archaeonothos henkgodthelpi* in exhibiting a V-shaped, rather than straight, centrocrista. The centrocrista is straight in the Cretaceous Laurasian deltatheroidans, but the latter differ markedly from *A. henkgodthelpi* in having a paracone that is taller than the metacone (probably a boreosphenidan plesiomorphy; Rougier et al. 2004; Davis et al. 2008). Members of the Cenozoic South American clade Sparassodonta typically possess a straight, elevated centrocrista (or the centrocrista is no longer identifiable as a distinct structure, owing to fusion of the bases of the paracone and metacone), a metacone that is considerably taller than the paracone, and a small protocone (Marshall 1978; Forasiepi 2009). Dentally plesiomorphic sparassodonts that retain identifiable stylar cusps also resemble *A. henkgodthelpi* (but differ from dasyuromorphians) in that StD is usually reduced, but not shifted anteriorly or posteriorly relative to the metacone (Marshall and Muizon 1988; Muizon 1998). *A. henkgodthelpi* appears more derived than the dentally most plesiomorphic known sparassodont, the early or middle Palaeocene *Mayulestes ferox* (if the latter is indeed a member of Sparassodonta; see Rougier et al. 2004: Forasiepi 2009) in its smaller protocone, more reduced stylar cusps, and absence of distinct conules (Muizon 1998). *Allqokirus australis*—which, like *Mayulestes*, is from the early or middle Palaeocene Tiupampa fauna (Marshall and Muizon 1988)—resembles *Archaeonothos henkgodthelpi* in terms of its broad stylar region and overall morphology of the stylar cusps (particularly the very small, labiolingually-compressed, crest-like StD), but differs from the latter in terms of its better-developed conules, more closely approximated paracone and metacone, and longer postmetacrista

(Marshall and Muizon 1988; Muizon 1998). Other sparassodonts exhibit more specialised dental morphologies, usually with narrower stylar shelves, more closely approximated paracones and metacones, smaller protocones, and more elongate postmetacristae (Marshall 1978; Forasiepi 2009). If *Archaeonothos henkgodthelpi* were a sparassodont, it would represent the first member of this clade known outside of South America, and, with an estimated body mass of ~40–80 g, by far the smallest known. By comparison, *Mayulestes ferox* probably weighed ~180–360 g (Table 1; see also Argot 2004), while *Allqokirus australis* probably weighed ~250-450 g (Table 1; see also Prevosti et al. 2013: electronic supplementary material), and all other known sparassodonts are estimated as weighing >800 g (Wroe et al. 2004; Prevosti et al. 2013: electronic supplementary material).

Finally, *Archaeonothos henkgodthelpi* also shows derived similarities to two other probable metatherians: *Kasserinotherium tunisiense* from the early Eocene Chambi fauna of Tunisia (Crochet 1986), and *Wirunodon chanku* from the ?middle–late Eocene, or possibly early Oligocene, Santa Rosa Fauna of Peru (Goin and Candela 2004). Goin and Candela (2004: 43) noted that these two taxa share the following features that are also present in *A. henkgodthelpi*: "very small size, straight centrocrista, conules absent, reduced protocone and trigon fossa, reduced and labiolingually compressed stylar cusps, wide stylar shelf, and well-developed postmetacrista". *A. henkgodthelpi* has an estimated body mass about twice as large as that of *W. chanku*, but is only slightly larger than *K. tunisiense* (Table 1). However, *A. henkgodthelpi* differs from both of these taxa in its smaller, more anteroposteriorly compressed protocone, a much greater height differential between the paracone and metacone, larger StB, smaller StD, and a preparacrista that ends at StB rather than StA. In addition, *K. tunisiense* resembles peradectids, but is unlike *A. henkgodthelpi*, in that the paracone is subequal in height to, as opposed to much smaller than, the metacone. An unpublished phylogenetic analysis by Maga (2008) placed *Kasserinotherium* as sister-taxon to the peradectid *Junggaroperadectes* from the early Oligocene of China (Ni et al. 2007).

Archaeonothos henkgodthelpi is a rare component of the Tingamarran mammal fauna: no other upper molars resembling the distinctive morphology of the holotype have been found to date, and I have been unable to identify lower molars that might be plausibly referred to this taxon. Instead, the fauna is dominated by small-bodied, dilambdodont, presumably faunivorous-omnivorous forms such as *Djarthia murgonensis*, and larger, bunodont, presumably omnivorous-frugivorous forms such as *Thylacotinga bartholomaii* and *Chulpasia mattaueri* (Table 1). Nevertheless, this peculiar taxon adds significantly to the known morphological and ecological diversity of the Tingamarran metatherians. The small size of *A. henkgodthelpi* would appear to preclude a predominantly vertebrate-based diet; instead, its small protocone and stylar cusps, as well as its relatively elongate postmetacrista may reflect a specialisation towards softer-bodied invertebrates

compared to the likely diet of *D. murgonensis* (Strait 1993; Beck 2009), although possibly also with a vertebrate component. However, confirmation of this hypothesis will require quantitative functional analysis of dental morphology and, ideally, the discovery of additional specimens, particularly lower molars. Regardless of its true affinities, *A. henkgodthelpi* further emphasises the fact that the Australian mammal fauna during the early Eocene was radically different from that characteristic of the late Oligocene onwards, and included taxa that lack obvious relatives in younger deposits.

Acknowledgements

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