EARLIEST MODERN BANDICOOT AND BILBY (MARSUPIALIA, PERAMELIDAE, AND THYLACOMYIDAE) FROM THE MIOCENE OF THE RIVERSLEIGH WORLD HERITAGE AREA, NORTHWESTERN QUEENSLAND, AUSTRALIA

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ABSTRACT—Recent molecular phylogenies of peramelemorphians suggest that thylacomyids (bilbies) and peramelids (modern bandicoots) diversified sometime in the late Oligocene or early Miocene. Until now, however, the earliest fossil evidence of thylacomyids and peramelids was from the Australian Pliocene. Here we describe the oldest peramelid and thylacomyid from the middle Miocene of the Riversleigh World Heritage Area, northwestern Queensland. The peramelid, *Crash bandicoot*, gen. et sp. nov., is represented by a single maxilla containing M1–3 that exhibits peramelid synapomorphies, including development of a metacoonular hypocone, an incomplete centrocrista, and well-developed anterior cingulum. The thylacomyid, *Liyamayi dayi*, gen. et sp. nov., is represented by M2 and m1, which show thylacomyid synapomorphies including a conical entoconid, a conical stylar cusp B (StB) and StD, and reduced distance between the metastyle and StD. The results of our phylogenetic analysis indicate that both species are part of crown-group Peramelemorphia.

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

Peramelemorphians (bandicoots and bilbies) are small- to medium-sized omnivorous, terrestrial marsupials present in diverse modern habitats from rainforest to deserts in Australia, New Guinea, and surrounding islands. Modern bilbies are represented by two (one extant but vulnerable and one recently extinct) desert-adapted (but not -restricted) species, whereas modern bandicoots are far more speciose and ecologically diverse. They are characterized by having syndactylous hind limbs (a derived feature shared with diprotodontians) and polyprotodonty (a plesiomorphic condition shared with dasyuromorphians, notoryctemorphians, and extant amelobatids). On morphological grounds, all bandicoots have traditionally been regarded to be members of the Peramelidae; however, Archer and Kirsch (1977) argued that the bilbies (species of *Peroryctes*, *Echymipera*, *Rhynchomeles*, *Microperoryctes*), and Peramelinae (species of *Isoodon*, *Perameles*), Westerman et al. (2012) estimate divergence times from relaxed-clock Bayesian methods and suggest that crown-group bandicoots originated in the late Oligocene or early Miocene, much earlier than currently suggested by the fossil record. The earliest known fossil peramelids are *Perameles bowensis* from the Bow Local Fauna (LF; see Fig. 1), Big Sink LF, and Chinchilla LF (Muirhead et al., 1997; Mackness et al., 2000) and *Perameles allinghamensis* from the Bluff Downs LF (Archer and Wade, 1976) are Pliocene in age and as such at least 15 million years younger than the estimated antiquity for crown-group bandicoots (Westerman et al., 2012). The earliest thylacomyid, *Ischnodon australis* from the Palankarinna LF (Fig. 1), South Australia (Stirton, 1955), is also Pliocene in age.

Here we describe two new peramelemorphians from the middle Miocene of the Riversleigh World Heritage Area that appear to represent the earliest known representatives of the Peramelidae and Thylacomyidae.

MATERIALS AND METHODS

Collecting and Processing

Specimens described here were collected from the Riversleigh World Heritage Area, northwestern Queensland, by Archer et al. between 1983 and 2011, and are registered in the fossil collection of the Queensland Museum (QM F), Brisbane, Australia. All specimens were obtained by acid-processing freshwater limestones recovered in the field.

Anatomical Nomenclature

Dental terminology follows Turnbull et al. (2003) and Luckett (1993) for the homology of molariform teeth. Peramelemorphan systematics follows Muirhead (1994, 2000), Muirhead and Filan...
(1995), Groves (2005), and Travouillon et al. (2010). Higher-level marsupial systematics follows Aplin and Archer (1987).

Body Mass Estimates

Tooth lengths and widths were measured for each specimen (Table 1). These were then used to estimate individual body mass using Myers’ (2001) regression equations, which correlate dental variables with marsupial body mass. We used the highest possible ranked equation from the ‘all species excluding dasyuromorphians’ data set from Myers (2001:table 3) as follows: equation ‘3UMA’ (3rd upper molar area) for QM F56245; equation ‘2UMA’ (2nd upper molar area) and equation ‘1LMA’ (1st lower molar area) for QM F56250.

Phylogenetic Analysis

We used the data matrix by Travouillon et al. (2013) and Gurovich et al. (2013), revised from Travouillon et al.’s (2010) matrix, to assess the phylogenetic relationships within Peramelemorpha of the two species described here. The matrix comprises 42 taxa and 156 qualitative morphological characters, of which 33 are cranial and 123 dental (see Supplementary Data 1 and 2). Several characters from Travouillon et al.’s (2010) matrix were deleted (to be replaced by more comprehensive characters) and some modified (see Supplementary Data 1). Because they represent putative morphclines, 71 characters were ordered in all analyses (see Supplementary Data 1). The matrix was completely rescored to avoid repeating mistakes that may have been present in earlier iterations of this matrix. The following fossil bandicoots were added to the analysis: cf. Peroryctes tefordi, cf. P. sp., Perameles sobbei, P. bowensis, P. allinghamensis, Ischodon australis, Yarala burchfieldi, Y. kida, Galadi speciosus, G. gran-dis, G. amplus, G. adversus, and Bulungu palara. These species were omitted from previous studies because they contained too much missing data and some of them weren’t yet described. Microperoryctes ornata was removed from the matrix because specimens used to score this taxon previously have subsequently been reassigned by Australian Museum staff to Microperoryctes longicauda (Sandy Ingleby, pers. comm.). In addition to the fossil dasyuromorphians Barinya wangala and Mutupurinus archibaldii and the early Eocene stem australidelphan Djarthia murgonensis, five extant outgroup species from the family Dasyuridae were added: Dasyurus hallucatus, Dasyuroides byrnei, Phascogale tapoatafa, Antechinus stuartii, and Sminthopsis macroura.

Parsimony Analysis

A parsimony analysis was performed using PAUP* 4.0b10 (Swofford, 2002) using a two-stage search strategy following Worthy et al. (2006) and Beck et al. (2008). An initial search comprising 1000 heuristic replicates, saving 10 trees per replicate, was followed by a second heuristic search within the saved trees. Multiple most parsimonious trees produced were summarized using strict consensus. Bootstrap values for each node were calculated using 1000 bootstrap replicates of 10 random addition sequence replicates. Decay indices were also calculated using TreeRot.v3 (Sorenson and Franzosa, 2007).

A second analysis was performed repeating the same steps but with a ‘molecular scaffold’ as a ‘backbone’ constraint. For the backbone, relationships among extant peramelemorphians were constrained to reflect the molecular phylogeny of Westerman et al. (2012). Only taxa analyzed by Westerman et al. (2012) were included in the molecular scaffold, and only those clades that received ≥70% partitioned maximum likelihood bootstrap support and ≥0.95 partitioned Bayesian posterior probability in the analyses of Westerman et al. (2012:table 2) were enforced as monophyletic. The five extant dasyurid outgroup taxa were also included in the molecular scaffold, with their relationships constrained to match those recovered by Krajewski et al. (2007:fig. 5) and Westerman et al. (2008:fig. 2). The molecular scaffold topology is included in Supplementary Data 3.

SYSTEMATIC PALEONTOLOGY

Order PERAMELEMORPHIA (Kirsch, 1968)

Aplin and Archer, 1987

Family PERAMELIDAE (Gray, 1825) (sensu Groves, 2005)

| Taxa                  | Specimen | Locality         | M1 L  | M1 W  | M2 L  | M2 W  | M3 L  | M3 W  |
|-----------------------|----------|------------------|-------|-------|-------|-------|-------|-------|
| Crash bandicoot       | QM F56245| AL90 Site        | 3.97  | 2.84  | 3.81  | 3.36  | 3.4   | 4.00  | 1076.24 |
| Liyamayi dayi         | QM F56246| Rick’s Sausage Site | 3.46  | 3.63  | 3.22  | 3.1   | 966.5 |
|                       | QM F56247| Rick’s Sausage Site | 3.34  | 1.89  | 2.26  |       | 674.18 |
|                       |          |                  | L     | AW    | PW    |       |       |
| Liyamayi dayi         | QM F56250| Rick’s Sausage Site | 3.34  | 1.89  | 2.26  |       | 879.45 |

Abbreviations: AW, maximum width of trigonid; L, maximum anteroposterior length; M, upper molar; m, lower molar; PW, maximum width of talonid; W, maximum lingual-buccal width.
**CRASH BANDICOOT**, gen. et sp. nov.

(Fig. 2)

**Type Species**—*Crash bandicoot* by monotypy.

**Generic and Specific Diagnosis**—*Crash* species differ from all other bandicoots in the following combination of features: posterior cingulum present on M1 but not M2 or 3; centrocrista incomplete on M1–3; small bridge connects parastylar shelf to metastylar shelf on M1 or 2 but not on M3; metaconular hypocone large and distinct on M1–3; anterior cingulum complete on M1–3; StB conical on M2 and 3; StD conical on M3; StD1 present on M2; StC present on M3; preparacrista connects to StA on M2 and 3; StC present as a distinct cusp on M2 only; and stylar crest connects metastyle to StD on M1 and 2 only.

**Etymology**—Named after Crash Bandicoot, the popular video game character created by Andy Gavin and Jason Rubin, with a related inference that this was the start of a new radiation of more modern bandicoots that ‘crashed’ through to dominate younger, drier ecosystems of Australia. The genus is here assigned masculine gender.

**Holotype**—QM F56245, right maxilla containing M1–3 and the alveoli for M4 (Fig. 2).

**Type Locality and Age**—Alan’s Ledge 1990 Site (AL90), Riversleigh World Heritage Area, northwestern Queensland, Australia. AL90 Site is interpreted to be part of Riversleigh’s Faunal Zone C and as such middle Miocene in age (Archer et al., 1997; Arena, 2004; Travouillon et al., 2006, 2011).

**Description**

The M1 is longer than wide (Fig. 2). Stylar cusp A (StA) is a low cusp on the anterobuccal corner of the tooth. A crest runs from the tip of StA posteriorly and ends at the anterior flank of StC. StC (Fig. 2B) is on the parastylar region of M1, directly posterior to StA. StB, if present, is indistinguishable from StC. The preparacrista is curved and connects StC to the paracone anterolingually. The postparacrista runs from the paracone anterobuccally, almost parallel to the preparacrista, and ends at the base of the posterolingual flank of StC. It does not form a centrocrista with the premetacrista. Instead, a small bridge connects the parastylar region to the metastylar region at the ectoloph and probably represents a remnant of the centrocrista, a condition also seen in *Peroryctes broadbenti* (see Aplin et al., 2010). The metacone is situated posterolingual to the paracone. The metacone is the tallest cusp on the crown, followed in decreasing order by StD, paracone, StC, metastyle, StA, protocone, and metaconular hypocone. The premetacrista, which is longer than the postparacrista, runs from the metacone.

![Figure 2. Crash bandicoot, gen. et sp. nov., right maxilla with M1–3 (QM F56245). A, occlusal view; B, lingual view. Abbreviations: ac, anterior cingulum; ect, ectoloph; mcl, metaconular hypocone; me, metacone; mst, metastyle; M1–M3, upper molar 1 to upper molar 3; pa, paracone; pc, posterior cingulum; pmc, premetacrista; pome, postmetacrista; popc, postparacrista; ppc, preparacrista; pr, protocone; St A, St B, St C, St D1, St D, St E, Stylar cusps A, B, C, D1, D, and E. Scale bar equals 3 mm.](image-url)
antlerolingually and ends at the base of the anterolingual flank of StD. The postmetacrista, the longest crest on the crown, connects the metacone to metastyle posterobuccally. A stylar crest connects the metacone to metastyle to the tip of StD anteriorly (Fig. 2B). StE, if present, is not distinguishable from this stylar crest. StD is a large round cusp directly buccal to the metacone. StD1 is absent. The protocone is posterolingual to the paracanone. The preprotocrista runs from the protocone anterobuccally and ends at the lingual flank of StA, forming a complete anterior cingulum. The postprotocrista is almost straight and connects the protocone to the metacanular hypocone posteriorly. This crest then continues posterobuccally to end below the postmetacrista, past the midpoint between the metacone and metastyle, forming a posterior cingulum. The metacanular hypocone is large and is level with the protocone lingually.

The morphology of M2 is similar to that of M1 except as follows (see Fig. 2A and B). The crown is much wider, elongating the preparacrista, postparacrista, premetacrista, postmetacrista, and preprotocrista. StA is taller, on the parastylar shelf, and connects to the paracone via the preparacrista. StC is absent. Instead, StB is a large conical cusp, located posterior to StA. StB remains taller and bigger than StA. A short crest runs from the tip of StB anterolingually to the base of StD. A small crest is also present on the posterior side of StB and may represent a remnant of StC. StE is present as a small cusp on the stylistic crest midway between the metastyle and StD. StD1 is a miniscule cusp and directly anterior to StD. A short crest connects StD1 anterolingually to the bridge connecting the parastylar and metastylar regions. The anterior cingulum is a larger shelf that is widest just lingual to StA. The metacanular hypocone is smaller than in M1 but more cusp-like on the lingual margin of the tooth. The postprotocrista ends at base of the posterior flank of the metacone; hence, the posterior cingulum is incomplete.

The morphology of M3 is similar to that of M2 except as follows (Fig. 2). The crown is wider than long, with the protocone and paracone positioned more lingually. StA is taller, almost level with StD. The preparacrista is straighter and longer. StB is smaller, but StC is present as a small cusp directly posterior to StB. The parastylar and metastylar regions are not connected by a bridge because the ectoloph is breached. StE is absent and no stylar crest connects the metacone to the metaconid hypocone. StD1 is smaller. The metacanular hypocone is smaller.

Measurements of Crash bandicoot are presented in Table 1.

Family THYLACOMYIDAE (Bensley, 1903); sensu Archer and Kirsch (1977)

LIYAMAYI DAYI (sensu Archer and Kirsch 1977) (Fig. 3)

Type Species — LIYAMAYI DAYI (sensu Archer and Kirsch 1977) (Fig. 3)

Type Locality and Age — Crash bandicoot is from the Waanyi word in the Riversleigh District of northwestern Queensland meaning round and ‘mayi’ meaning tooth (Breen, 1985), in reference to the rounded shape of the teeth and cusps. The genus is here given masculine gender.

Specific Etymology — The species name honors geologist and palaeontologist Dr. Robert Day, who generously supported this research.

RESULTS

The unconstrained parsimony analysis of our 156 craniomental character matrix recovered 21 most parsimonious trees of 835 steps. The strict consensus is illustrated in Figure 4A, with bootstrap values above branches and decay indices below branches. Crash bandicoot is recovered within crown-group Peramelemorpha, unresolved within a clade containing species of Isodon and Perameles, with weak support (bootstrap <50%; decay index +1; Fig. 4A). LIYAMAYI DAYI is also recovered within the crown-group Peramelemorpha, sister to a clade containing...
thylacomyids (*Macrotris + Ischnodon*), *Chaeropus* and *Perameles + Crash + Isoodon* (bootstrap <50%; decay index +2; Fig. 4A).

The constrained parsimony analysis, enforcing a molecular scaffold as a ‘backbone’ constraint, recovered 478 most parsimonious trees of 864 steps. The strict consensus is illustrated in Figure 4B, with bootstrap values above branches. Again, *Crash bandicoot* is recovered within the crown-group Peramelemorpha, and unresolved within the same clade as in the unconstrained analysis. However, the rest of the crown group is fairly unresolved and fails to identify the relationship between *Liya-mayi dayi* and other peramelemorphians.

**DISCUSSION**

Until now, the oldest fossil members of the family Peramelidae were the Pliocene *Perameles bowensis* from Big Sink and Bow LFs, New South Wales (Muirhead et al., 1997), and Chin-chilla LF, Queensland (Mackness et al., 2000), and *Perameles allinghamensis* from Bluff Downs LF, Queensland (Archer and Wade, 1976). The most recent molecular phylogeny of peramelomorphians (Westerman et al., 2012) suggests that peramelids diversified in the middle Miocene, and estimated that the split between the three peramelid subfamilies Peramelinae (species of *Isoodon* and *Perameles*), Peroryctinae (species of *Peroryctes*), and Echymiperinae (species of *Echymipera*, *Rhyncholemes* and *Microperoryctes*) occurred at ~13.8 million years ago. *Crash bandicoot* (Fig. 2), from AL90 Site in the Riversleigh World Heritage Area, is here recognized as the oldest member of this family, and our phylogenetic analysis and shared synapomorphies (see below) suggests that it belonged to the subfamily Peramelinae. AL90 Site is estimated to be middle Miocene in age (Archer et al., 1997; Travouillon et al., 2006, 2011) and radiometric dating for this site (work in preparation) is congruent with this assessment (Woodhead et al., 2011). This species pushes back the first
FIGURE 4. Phylogenetic relationships of Crash bandicoot and Liyamayi dayi, gen. et sp. nov., based on our 156 character craniodental matrix. Fossil and recently extinct taxa are indicated by †. Crash bandicoot and Liyamayi dayi are highlighted in bold. Crown-group Peramelemorphia is bracketed. A, strict consensus of 21 most parsimonious trees (tree length = 835; consistency index excluding uninformative characters = 0.30; retention index = 0.66) from unconstrained parsimony analysis of the matrix. Numbers above branches represent bootstrap values (1000 replicates). B, strict consensus of 478 most parsimonious trees (tree length = 864; consistency index excluding uninformative characters = 0.293; retention index = 0.639) that result when the matrix is analyzed using maximum parsimony and enforcing a ‘backbone’ molecular scaffold based on Westerman et al. (2012).

occurrence of the family in the fossil record at least 5 to 10 million years earlier than previously thought. AL90 Site is considered to represent a rainforest community (Travouillon et al., 2009; Black et al., 2012) based on the high proportion of arboreal folivores within the assemblage, including five species of pseudocherid possums, two species of phalangerid possums, one small species of koala, and the arboreal diprotodontid Nimbadon lavarackorum. The presence of C. bandicoot, the earliest peramelid, in AL90 Site suggests that peramelids evolved in rainforest before subsequently diversifying into other types of environments.

Crash bandicoot (Fig. 2) shares a number of synapomorphies with peramelines. For example, the position and development of the metaconule on M2 and 3 is similar to that of Perameles gunnii and P. bougainvillei; the centrocrista is incomplete in all molars and StD and StB are conical and not connected by any stylar crests; the preparacrista connects to Sta on M2 and 3; and StE is absent on M3. Crash bandicoot also retains a number of plesiomorphies shared with species of the extinct genus Galadi. These include the presence of a stylar crest connecting StD to the metastyle on M1 and 2 and the absence of a posterior cingulum on M2 and 3. Travouillon et al. (2010, 2013) identified a number of synapomorphies (e.g., well-developed lingual shelf and larger major cusp on P3; large metaconule; incomplete centrocrista on M3; and paraconid-metacnonid distance is reduced on posterior molars) shared between species of Galadi and crown-group peramelemorphians (and C. bandicoot), suggesting a close relationship between the two clades. It is possible that C. bandicoot shared a common ancestor with species of Galadi.

Thylacomyids are distinct from all other peramelemorphians in possessing the following combination of molar synapomorphies: metaconule absent; posterior cingulum absent; conical StB and StD; lingual displacement of the metacone (although less extreme in M. leucura than M. lagotis) such that it comes to function as a topographic ‘hypocone’; shortened distance between metastyle and StD; preparacrista connects paracone to base of StB; conical entoconid; markedly reduced paraconid; and presence of a cusp in the hypoflexid region. Ischnodon australis shares all lower molar synapomorphies with species of Macrotis, although the paraconid is less reduced than in Macrotis lagotis, but closer in size to Macrotis leucura (no upper dentition has yet been recovered for I. australis). Liyamayi dayi shares some of those synapomorphies with species of Macrotis and Ischnodon australis:
shortened distance between metastyle and StD; posterior cingulum absent; conical StB and StD (but stylar crests are still present on both stylar cusps); preparacrista connects paracone to base of StB (but also connects to StA); conical entoconid; and presence of cusp in hypoflexid region. However, some of these features are also present in peramelids, such as species of *Isoodon* (shortened distance between metastyle and StD; conical StB and StD; conical entoconid; presence of cusp in hypoflexid region) and *Chaeropus ecaudatus* (shortened distance between metastyle and StD; conical StB and StD; conical entoconid). These features probably represent homoplasies related to similarities in diet (i.e., omnivory). The shortened distance between the metastyle and StD is seemingly more significant because it is only present in species of *Macrotis*, *Isoodon*, and *Chaeropus*. This distance is long in species of *Perameles*, all New Guinea genera, and all other fossil peramelmorphians. However, *Liyamayi dayi* lacks key synapomorphies linking it to species of *Isoodon* (presence of posterior cingulum; well-developed metaconular hypocone) or *C. ecaudatus* (absence of anterior cingulum; well-developed metaconular hypocone), therefore supporting its placement within thylacomyids. *Liyamayi dayi* exhibits many plesiomorphic features (e.g., presence of metaconeul; stylar crest connecting StD to metastyle; connection of preparacrista to StA; incomplete anterior cingulum) features that might be expected to be present in a Miocene perameliphilous. The earliest fossil notoryctid, *Naraboryctes philcreaseri* (Archer et al., 2011), retains a number of dental plesiomorphies, such as the presence of a paracone, StB, StC, and StD on the upper molars. However, the paracone in *N. philcreaseri* is highly reduced, and absent in all other notoryctids (species of *Notoryctes*). In late Cenozoic thylacomyids, the metaconeul is absent, but it might be expected that a more pleiomorphic thylacomyid would retain a small metaconeul as *L. dayi* does. Interestingly, both notoryctids and thylacomyids have modern desert-adapted species (*Notoryctes* and *Macrotis*, respectively) that evolved in rainforest.

The age of the Riversleigh deposit that has produced *L. dayi* is not clear. Rick’s Sausage Site is an isolated deposit that occurs on the southern Gag Plateau, west of AL90 Site (Faunal Zone C, middle Miocene) and Encore Site (Faunal Zone D, early late Miocene). The fauna is as yet poorly understood but the assemblage includes the bandicoot *Bulungu palara* and the pseudocheirid *Pildra* sp. 1, which are found in Faunal Zones A–C, a pseudoneurodrilid species, found in Faunal Zones A–D, and *Wambaroo hilurus*, a Miocene macropodid only found in Faunal Zone C (Archer et al., 2006; Travouillon et al., 2011). The presence of the latter (also found in AL90 Site) suggests a middle Miocene age for Rick’s Sausage Site.

The earliest thylacomyid, *Ischnodon australis* (Stirton, 1955) from the Palankarina LF, South Australia, is Pliocene in age. However, Westerman et al. (2012) estimated a late Oligocene molecular divergence date of ~25.8 million years for the split between thylacomyids and peramelids. The presence of a thylacomyid in the Miocene of Riversleigh would not be inconsistent with this estimate. This is around 10 million years before the occurrence of *L. dayi* in the Riversleigh deposits. The absence of thylacomyids in earlier Faunal Zones of Riversleigh suggests that either thylacomyids first evolved elsewhere on the continent before colonizing the Riversleigh rainforest, or that earlier Riversleigh thylacomyids had not evolved their dental synapomorphies and were dentally indistinguishable from other peramelmorphians until the middle Miocene.

**CONCLUSIONS**

The oldest peramelid and thylacomyid are described from middle Miocene deposits in the Riversleigh World Heritage Area. Although both retain a number of plesiomorphies, they display a number of apomorphies linking them to crown-group peramelmorphians. The presence of the two new species presented in this paper is congruent with the most recent peramelmorphian molecular divergence times and suggest that peramelids and thylacomyids diversified in middle Miocene rainforests.

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