THREE NEW MIOCENE SPECIES OF MUSKY RAT-KANGAROOS (HYPSIPRYMNODONTIDAE, MACROPODOIDEA): DESCRIPTION, PHYLOGENETICS, AND PALEEOECOLOGY

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ABSTRACT—Three new species of the macropodoid genus Hypsiprymnodon are described from early to middle Miocene fossil deposits in the Riversleigh World Heritage Area, northwestern Queensland. A phylogenetic analysis of macropodoid relationships that includes these new taxa is presented. Monophyly of Macropodinae + Sthenurinae is recovered, as is a clade comprising macropodines, sthenurines, bulungamyines, and potoroids to the exclusion of hypsiprymnodontids and balbarids. Monophyly of Balbaridae is also supported, but hypsiprymnodontids are unresolved at the base of Macropodoidea, rather than forming a clade; this is probably because the new Hypsiprymnodon species described here are currently known from relatively incomplete material (isolated maxillae and dentaries). On the assumption that these extinct forms were ecologically similar to the living species H. moschatus (as suggested by close similarities in dental morphology), their presence in Riversleigh Faunal Zones B and C corroborates previous interpretations of a wet rainforest environment in northwestern Queensland during the early to middle Miocene of Australia.

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

INTRODUCTION

Kangaroos and wallabies (superfamily Macropodoidea) are among the most iconic of Australian marsupials. The musky rat-kangaroo Hypsiprymnodon moschatus is considered by many researchers to be the most primitive extant macropodoid (e.g., Pearson, 1950; Woods, 1960; Ride, 1961, 1971, 1993; Johnson and Strahan, 1982; Szalay, 1994; Burk et al., 1998; Cooke, 2006). It exhibits several plesiomorphic features that have been lost in all other extant macropodoids such as a simple (non-sacculated) stomach and retention of the hallux (Johnson and Strahan, 1982). It is also unique among extant macropodoids in that it does not hop, but instead uses a quadrupedal bound. As a result, it lacks several derived features of the pes and tarsus that are presumed to be adaptations for bipedal hopping (Szalay, 1994). Hypsiprymnodon moschatus occurs only in tropical rainforests in northeastern Queensland and is principally frugivorous but is also opportunistically omnivorous. It is known to consume the fruits of 40 species of plants as well as fungi and small animals (Dennis, 2002). Along with the cassowaries, it has been shown to be one of the most important seed dispersers of rainforest plant species in Australia (Dennis, 2003).

Hypsiprymnodon currently contains two species: the extant H. moschatus, first described by Ramsay in 1876, and the extinct H. bartholomaii described by Flannery and Archer in 1987. The latter is known from a fragmentary fossil cranium and two isolated molars (M3 and M3) from the middle Miocene (Riversleigh Faunal Zone C) Gag Site in the Riversleigh World Heritage Area, northwestern Queensland. To date, the only other fossils that have been identified as Hypsiprymnodon-like are an anterior fragment of an isolated m1 (FM 4575) from the early Pliocene Hamilton Local Fauna of western Victoria (Turnbull and Lendelius, 1970), and two isolated lower molars (NMV P172991 and NMV P157583) from the late Oligocene Namba Formation (Flannery and Rich, 1986).

As a result of their possession of many unique plesiomorphic macropodoid features, controversy exists about their phylogenetic position within Macropodoidea (Flannery and Archer, 1987; Cooke, 1992, 1997a; Burk et al., 1998; Burk and Springer, 2000; Kear and Cooke, 2001). Flannery and Archer (1987) proposed, on morphological grounds, that species of Hypsiprymnodon were members of the family Potoroiidae. Subsequently, most other authors have suggested that Hypsiprymnodon is the sister taxon to all other extant macropodoids (e.g., Potoroiidae + Macropodidae; Ride, 1993; Cooke, 1997a; Burk et al., 1998; Burk and Springer, 2000; Kear and Cooke, 2001; Meredith et al., 2009). It has also regularly been argued that Hypsiprymnodon is key to understanding the relationship of macropodoids to other members of Phalangerida (which also includes the various families of ‘possums’) because of its retention of many plesiomorphic character states typical of ‘possums’ that have been lost in other extant macropodoids Flannery, 1987, 1989; (Flannery and Archer, 1987; Burk et al., 1998; Wroe et al., 1998; Burk and Springer, 2000; Dennis, 2002, 2003; Lloyd et al., 2002).

In a review of macropodoid systematics, Kear and Cooke (2001) identified four macropodoid families: Balbaridae (which is known only from fossils and was argued by Kear and Cooke [2001] to represent the sister group of all other macropodoids), Potoroiidae, Macropodidae, and Hypsiprymnodontidae. According to Kear and Cooke (2001), Hypsiprymnodontidae comprises the extinct subfamily Propoleopinae (giant rat-kangaroos of the genera Ekaladeta, Jackmahoneya, and Propoleopus) and the extant subfamily Hypsiprymnodontinae, which is represented by a single genus Hypsiprymnodon.

Here, we describe three new fossil species of Hypsiprymnodon based on dental remains recovered from early to middle Miocene (Riversleigh Faunal Zones B–C) freshwater limestone deposits in the Riversleigh World Heritage Area, northwestern Queensland. We provide a phylogenetic analysis of Macropodoidea that includes these three new Hypsiprymnodon species using morphological characters and discuss the ecological implications of their presence at Riversleigh during the early to middle Miocene.
MATERIALS AND METHODS

Materials
Specimens used in this study were collected from various fossil sites within the Riversleigh World Heritage Area, northwestern Queensland (18°59′–19°08′S, 138°34′–138°43′E). Specimens are from the Queensland Museum fossil collection, Brisbane, Australia (prefix QM F).

Terminology
Dental terminology follows Luckett (1993) for molar and deciduous premolar homology and Flower (1868) for adult premolar homology. Cusp nomenclature follows Archer (1984). Systematic nomenclature follows Aplin and Archer (1987) for higher-level marsupial relationships and Kear and Cooke (2001) for Macropodoidea (note that Wilson and Reeder, 2005, and Meredith et al., 2009, refer to Macropodoidea as ‘Macropodiformes’). Riversleigh ‘Faunal Zone’ nomenclature is based on Arena (2004) and Travouillon et al. (2006). ‘Precingulum’ is used in this study to refer to the anterior cingulum extending buccally from the preprotocrista, following the usage of Szalay (1969) and Cooke (1997a). Ride (1993) called this structure the ‘anterolingual cingulum.’ The terms, ‘transcristae’ and ‘transcristids’ have been adopted from Ride (1993) to refer to the vertical, enamel ridges on the lateral walls of the upper and lower premolar crowns. We utilize Cooke’s (1997b:fig. 6F) understanding of cusp homologies for the m1 of Hypsiprymnodon, in which the anterobuccal cusp is identified as a protostylid, with the protocristid more lingually located.

Phylogenetic Analyses
We assessed the phylogenetic relationships of Hypsiprymnodon species to other macropodoids using the matrix published by Kear and Pledge (2007). The original matrix comprises 108 qualitative morphological characters that involve cranial, dental, and postcranial features (see Supplementary Data). We deleted character 33 (hypolophid formation) because we were unable to consistently score this character. We rescored characters 17, 20, and 24 for Trichosurus vulpecula, Ekaltadeta ima, and Hypsiprymnodon moschatus. We also scored and added to the matrix the three fossil Hypsiprymnodon species described in this paper, as well as the following additional fossil hypsiprymnodontids: Hypsiprymnodon bartholomaii (scored from holotype QM F13051), Propleopus oscillans (scored from Woods, 1960), and Jackmahoneya toxoniensis (scored from Ride, 1993).

A parsimony analysis was performed using a two-stage search strategy with PAUP* 4.0b10 (Swofford, 2002) 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 version 3 (Sorenson and Franzosa, 2007).

SYSTEMATIC PALEONTOLOGY
Family HYPSIPRYMNODONTIDAE Collett, 1887
Subfamily HYPSIPRYMNODONTINAE Collett, 1887
Genus HYPSIPRYMNODON Ramsay, 1876
HYPSIPRYMNODON PHILCREASERI, sp. nov. (Figs. 1, 2)
FIGURE 2. Hypsiprymnodon philcreaseri, sp. nov. (holotype QM F24148), left (A–C) and right (D–F) dentaries. A, occlusal stereopair; B, buccal view; C, lingual view; D, occlusal stereopair; E, buccal view; F, lingual view. Scale bar equals 10 mm.
M1–4; QM F24154, right maxilla with P3, M1, 2; QM F24155, right maxilla with P3, M1, 2; QM F24157, right maxilla with P3, M1, 2; QM F24158, left maxilla with P3, M1–4; QM F24159, right maxilla with P3, M1, 2; QM F24160, right maxilla with P3, M1; QM F24161, left maxilla with P3, M1–4; QM F24162, left maxilla with P3, M1, 2; QM F24165, right maxilla with P3; QM F24171, left maxilla with P3, M1–3; QM F56273, right maxilla with P3, M1–4; QM F56275, left maxilla with P3; QM F23463, left dentary with p3, m1–4; QM F24166, right dentary with p3, m1–3; QM F24167, right dentary with p3, m1; QM F24168, right dentary with p3, m1; QM F24169, right dentary with p3, m1–4; QM F24170, left dentary with p3, m2.

Age—The holotype and referred material are all from sites recognized as representing Riversleigh Faunal Zone B, which is currently interpreted as early Miocene in age (Archer et al., 1997; Travouillon et al., 2006, 2011).

Etymology—The species name honors Phil Creaser, instigator for the World Heritage listing for the Riversleigh fossil deposits, founder of the CREATE palaeoscience fund in the University of New South Wales (UNSW) Foundation, and for his dedication, enthusiasm, and continued support for Australian palaeontology.

Diagnosis—Hypsiprymnodon philcreaseri can be distinguished from H. bartholomaii because the P3 of H. bartholomaii is anterobuccally flexed out of alignment with the long axis of the molar row, whereas the P3 of H. philcreaseri is aligned with the molar row. H. philcreaseri can be distinguished from H. dennisi and H. karenblackae in lacking the following features on M1: lingual precingulum, parastyle, stellate cusps C and D, and a protostyle.

Description

Maxilla and Upper Dentition—Left maxilla preserves entire cheek tooth row (P3, M1–4). Anterior portion of jugal process preserved, starting above M1 on the maxilla. Jugal process is thin, gracile, and relatively smaller in size compared with specimens of H. moschatus and H. bartholomaii. In occlusal view, the molar row is buccally convex. The occlusal margin of P3 is aligned with the buccal cusps of the molar row. The height of the crown of P3 is greater than that of any of the molars. Molar gradient decreases in size anteroposteriorly. Molar teeth are low-crowned and bunolophodont.

P3 is a plagiaulacoid tooth with a longitudinal median occlusal ridge intersected by eight transcristae arising from lingual and buccal faces. Eight cusps are positioned ventrally along the median ridge where the cristae intersect, forming a serrated cutting edge. The lingual side of the crown is damaged, preventing an unambiguous description of lingual transcristae. In buccal view, the transcristae are posteroventrally inclined. P3 meets the anterior margin of M1 anterior to the paracone. The crown is widest at the seventh transcrista. Two roots are present on the buccal side of the tooth and one on the lingual side. The P3 is tall and slender in comparison with the P3 of Hypsiprymnodon dennisi. The P3 does not overhang the M1. The posterior margin of P3 is ventrally inclined.

In occlusal view, M1 is rectangular in outline, with the surface of the crown slightly lingually oriented. The buccal surfaces of the crown are more steeply inclined than are the lingual surfaces. The trigon basin slopes ventrolingually from the apex of the paracone down to the protocone and is rectangular in shape. The paracone and metacone are taller and acutely pointed compared with the shorter, more bulbous protocone and metacone. The postparacrista and premetacrista are well defined, more so than the postprotocrista and premetaconulocrista. Enamel on the protocone and metacone has been breached by wear. A single large root supports the lingual side of the tooth and two roots are present on the buccal side. The protoloph and metaoph are transversely oriented. The protoloph runs lingually from the apex of the paracone but does not reach the apex of the protocone. The preparacrista and preprotocrista enclose the anterior margin of the trigon basin, which is not elevated above the level of the basin floor. A gap is present in the centrocrista between the postparacrista and premetacrista. The posterior margin of the talon basin is enclosed by the postmetacrista and postmetaconulocrista, which form a continuous crest. This continuous posterior margin sits level with the talon basin, whereas it is elevated above the basin floor in H. karenblackae.

M2 is similar to M1 in shape and morphology but differs as follows: in occlusal view the protocone is larger; the occlusal surface faces directly ventrally, rather than slightly lingually as in M1; the protoloph runs from the apex of the paracone to the lingual margin of the preprotocrista; a thin crista runs longitudinally on the lingual side from the protoloph to the metaloph, although this crista is in fact an artifact of wear of the specimen; the cusps of the trigon and talon are of equal width; the talon basin is larger than the trigon basin. In lingual and buccal views, the crown of M2 is shorter than that of M1.

In occlusal view, M3 is similar in overall shape and morphology to M1 and M2 but differs in the following: M3 is smaller in overall size; the talon basin is reduced and of equal size and width to the trigon basin; the paracone and protocone are equal in height, as are the metacone and metaconule; the gap in the centrocrista is not as wide; the protocone is wider and more bulbous than the metaconule.

M4 differs in size and morphology from the anterior molars. It is considerably smaller in size and triangular in occlusal outline, with the lingual and buccal sides posteriorly converging. Protocone and paracone are of equal height, although the protocone is wider and more massive than the paracone. The trigon basin is reduced to a small fossa positioned between the paracone and protocone. In occlusal view, the tooth is out of alignment with the anterior molars and slightly buccally positioned. The talon is greatly reduced. The metacone is so reduced and obscured that it has become incorporated into a posterior extension of the postparacrista, which forms the nearly straight crest bounding the buccal margin of the tooth.

Dentary and Lower Dentition—The right dentary preserves i1, a single-rooted tooth (possibly i2) immediately posterior to i1, p3, and a complete molar row. The lingual side of the horizontal ramus is damaged. Three holes, possibly puncture wounds from a predator/scavenger, are present below the molar row: the first occurs anteroventrally to m1, the second ventral to m1, and the third ventral to m3 along the horizontal ramus. The entire ascending ramus is missing except for the anterior portion of the coronoid crest. A single mental foramen is present on the buccal side of the dentary posterior to i1. The left dentary contains p3, m1–3, and an alveolus for a tooth (?i2) directly posterior to i1. The base of i1 is preserved slightly anterior to this alveolus. The mase- teric foramen, masseteric canal, and coronoid crest are preserved, but the coronoid process, mandibular condyle, and angular process are missing. In posteroconcavolingual view, the mandibular foramen can be seen below the coronoid process. The angular process is broken off.

The complete right i1 curves dorsoventrally and is shaped like a cavalry saber. An alveolus for a single-rooted tooth (possibly i2) occurs immediately posterior to the base of i1.

The p3 is a plagiaulacoid tooth with eight cuspsids on its me- dian occlusal ridge. Lingual and buccal transcristae are associ- ated with the first seven cuspsids. The eighth cusp is the largest and lacks transcristae. All other cuspids are of equal size. The width of the tooth increases posteriorly until the seventh cusp, which marks the broadest part of the tooth, posterior to which it decreases in width. The right dentary is damaged on the lingual side below the eighth cuspid. In lateral view, the occlusal margin of p3 is higher than that of the molars. Two roots are present on the buccal side of p3 and one on the lingual side.
In occlusal view, the molar row is relatively straight, and $p_3$ is aligned with the lingual cusps of the molar row. The molar row is slightly anterolingually angled. The $m_2$ and $m_3$ are larger than $m_1$ and $m_4$. The height of the crown of $p_3$ is greater than that of any of the molars. The molars are low crowned and bunolophodont.

The $m_1$ is rectangular in occlusal outline. The occlusal surface of the crown slopes ventrobuclcally from the apices of the lingual cusps to meet the corresponding buccal cusps, which are much lower. A protostylid is present buccal to the larger protoconid. The entoconid is taller than the hypoconid. The enamel of the hypoconid on the right $m_1$ has been breached by wear. The talonid is considerably wider than the trigonid. The talonid basin declines in height posteriorly from the hypoconulid to the posterior margin of the crown. The posterior margin of the talonid basin is enclosed by the posthypocristid and postentocristid, which form a continuous crest. This continuous posterior margin is level with the talonid basin. Both the protolophid and the hypolophid are ventrobuclcally inclined. The protolophid slopes transversely from the apex of the protoconid to the apex of the protostylid.

The $m_2$ is similar to $m_1$ in occlusal outline but differs as follows: the protostylid is absent; the tooth as a whole is larger in occlusal area; the trigonid is wider; the protolophid and hypolophid are of equal length; the protolophid is well defined; the protoconid and hypoconid are considerably larger; the apices of the metaconid and entoconid are more acutely pointed than those of the more bulbous protoconid and hypoconid; the apices of the protoconid and hypoconid are taller and of equal height to those of the metaconid and entoconid; the trigonid basin is enlarged and inclines anteroventrally from the protolophid to the anterior margin of the crown.

The $m_3$ is similar in size, shape, and morphology to $m_2$. In occlusal view, $m_3$ differs from $m_2$ as follows: the metacristid and entocristid are better defined; the crown is taller.

The left $m_4$ is missing, but alveoli are present for two roots. The right $m_4$ differs in size and slightly in shape from $m_2$–$3$ as follows: in occlusal view it is smaller; the trigonid is wider than the talonid; the entoconid and hypoconid are closer together; the talonid basin and hypolophid are greatly reduced in size; the protoconid and hypoconid are larger than the metaconid and entoconid. Measurements of the upper and lower dentition are listed in Tables 1 and 2.

HYPSIPRYMNODON DENNISI, sp. nov.  
(Figs. 3, 4)

**Holotype**—QM F20840, left maxilla with $P_3$, $M_1$–4.

**Paratype**—QM F24621, left dentary with $p_3$, $m_1$–4.

**Type Locality**—Cleft of Ages 4 Site, Gag Plateau. Riversleigh World Heritage Area, northwestern Queensland.

**Referred Material**—Cleft of Ages 4 Site: QM F56270, RP3; QM F56271, LP3; QM F29659, left dentary with $m_2$–4; QM F29730, left dentary with $p_3$, $m_1$, 2; QM F29736, right dentary with $m_1$–4; QM F31349, left dentary with $p_3$.

**Distribution**—All material comes from Cleft of Ages 4 Site, Riversleigh World Heritage Area, northwestern Queensland.

**Age**—Cleft of Ages 4 Site is considered to represent Riversleigh Faunal Zone C, which is interpreted as middle Miocene in age (Archer et al., 1997; Travouillon et al., 2006, 2011).

**Etymology**—The species name honors Dr. Andrew Dennis for his research contributions, which are providing critical understanding about the biology of the threatened living musky rat-kangaroo, *Hypsiprymnodon moschatus*.

**Diagnosis**—*Hypsiprymnodon dennisi* can be distinguished from all other species in: wider and more robust jugal process; possessing a protostyle and stylar cusp C on $M_1$; upper and lower $P_3$ relatively longer and with nine transcrietiae and cuspsids on unburn specimens; occlusal surface of $P_3$ overhangs the anterior occlusal margin of $M_1$ in a ventroposterior direction.

**Description**

**Maxilla and Upper Dentition**—The left maxilla preserves the entire adult cheek tooth row ($P_3$, $M_1$–4). The anterior portion of the jugal process begins above $M_1$ on the maxilla. The jugal process is wider and more robust than in *H. philcreaseri* and *H. bartholomaii*. The molar row is slightly buccally convex. $P_3$ is flexed anterobuccally out of alignment with the long axis of the tooth row. The height of the crown of $P_3$ is greater than that of any of the molars. Molar gradient decreases in size posteriorly. Molars are low crowned and bunolophodont.

The $P_3$ is a plagiaulacoid tooth that has a median occlusal ridge intersected by nine transcrietiae arising from lingual and buccal flanks of the crown. $P_3$ is long and robust compared with those of other species of *Hypsiprymnodon*. Nine cusps are positioned along the median ridge where the cristae intersect forming a
TABLE 1. Measurements (in mm) of the upper dentition of type and referred material.

| Species                  | Specimen number | Side     | Site                        | P3   | M1          | M2          | M3          | M4          |
|--------------------------|-----------------|----------|-----------------------------|------|-------------|-------------|-------------|-------------|
| Hypsiprymnodon philcreasi | QM F31609       | Right    | Boid Site East              | 2.5  | 2.5         | 2.3         |             |             |
| Hypsiprymnodon philcreasi | QM F24148       | Right    | Camel Sputum Site           | 4.7  | 3.4         | 2.8         | 2.5         | 2.3         | 2.4         | 2.3         | 1.9         | 1.9         | 1.3         |
| Hypsiprymnodon philcreasi | QM F24150       | Right    | Camel Sputum Site           | 4.5  | 3.4         | 2.7         | 2.6         | 2.3         | 2.6         | 2.6         | 2.2         | 2.7         | 2.3         | 2         |
| Hypsiprymnodon philcreasi | QM F24151       | Left     | Camel Sputum Site           | 5    | 3.7         | 3           | 2           | 2.8         | 2.6         | 2.7         | 2.7         | 2.6         |             |             |
| Hypsiprymnodon philcreasi | QM F39983       | Right    | Creaser’s Ramparts Site     | 2.8  | 2.7         | 2.5         | 2.8         | 2.6         | 2.6         |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F56276       | Left     | Judith’s Horizontalis Site  | 2.9  | 2.7         | 2.6         |             |             |             |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F23464       | Right    | Mike’s Menagerie Site       | 5.1  | 3.4         | 2.7         | 2.4         | 2.4         | 2.5         | 2.4         | 2.2         |             |             |             |
| Hypsiprymnodon philcreasi | QM F24149       | Left     | Upper Site                  | 5    | 3.5         | 2.8         | 2.5         | 2.5         | 2.8         | 2.6         | 2.4         | 2.7         | 2.4         | 2.3         | 2.1         | 1.6         |
| Hypsiprymnodon philcreasi | QM F24153       | Right    | Upper Site                  | 5.1  | 3.4         | 2.9         | 2.8         | 2.7         | 2.7         | 2.8         | 2.5         | 2.7         | 2.7         | 2.1         | 2.4         | 2.3         | 1.6         |
| Hypsiprymnodon philcreasi | QM F24154       | Right    | Upper Site                  | 5    | 3.3         | 2.9         | 2.6         | 2.6         | 3           | 2.7         | 2.6         |             |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F24155       | Right    | Upper Site                  | 5.1  | 3.6         | 2.9         | 2.8         | 2.7         | 2.8         | 2.3         | 3           |             |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F24157       | Right    | Upper Site                  | 5.5  | 3.5         | 2.8         | 2.7         | 2.7         | 2.8         | 2.8         | 2.7         |             |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F24158       | Left     | Upper Site                  | 5.1  | 3.3         | 2.8         | 2.7         | 2.8         | 2.6         | 2.7         | 2.5         | 2.8         | 2.7         | 2.3         | 2.7         | 2.4         | 1.6         |
| Hypsiprymnodon philcreasi | QM F24159       | Right    | Upper Site                  | 4.8  | 3.4         | 2.8         | 3           | 2.7         | 2.8         | 3.1         | 2.5         |             |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F24160       | Right    | Upper Site                  | 4.6  | 3.5         | 2.9         | 2.8         | 2.8         | 2.6         |             |             |             |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F24161       | Left     | Upper Site                  | 5.1  | 3.6         | 2.9         | 2.6         | 2.6         | 2.5         | 2.8         | 2.6         | 2.6         | 2.5         | 2.1         | 2.4         | 2.3         | 1.7         |
| Hypsiprymnodon philcreasi | QM F24162       | Left     | Upper Site                  | 5    | 3.6         | 2.8         | 2.3         | 2.3         | 3           | 2.5         | 1.9         |             |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F24165       | Right    | Upper Site                  | 4.9  | 3.7         |             |             |             |             |             |             |             |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F24171       | Left     | Upper Site                  | 4.4  | 3.4         | 2.7         | 2.3         | 2.3         | 3           | 2.5         | 2.4         | 2.9         | 2.3         | 2.2         |             |             |             |
| Hypsiprymnodon philcreasi | QM F56273       | Right    | Upper Site                  | 4.5  | 3.3         | 2.7         | 2.6         | 2.4         | 2.6         | 2.7         | 2.5         | 2.6         | 2.5         | 2.1         | 2.3         | 2.1         | 1.5         |
| Hypsiprymnodon philcreasi | QM F56275       | Left     | Upper Site                  | 5    | 3.4         |             |             |             |             |             |             |             |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F20840       | Left     | Cleft of Ages Site          | 5.2  | 3.6         | 2.8         | 3           | 2.6         | 2.8         | 2.4         | 2.6         | 2.7         | 2.7         | 2.2         | 2.5         | 2.4         | 1.8         |
| Hypsiprymnodon philcreasi | QM F56270       | Right    | Cleft of Ages Site          | 5.1  | 3.5         |             |             |             |             |             |             |             |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F56271       | Left     | Cleft of Ages Site          | 5.1  | 3.8         |             |             |             |             |             |             |             |             |             |             |             |             |
| Hypsiprymnodon philcreasi | QM F24152       | Left     | Camel Sputum Site           | 4.8  | 3.6         | 2.9         | 2.9         | 2.5         | 2.8         | 2.6         | 2.3         | 2.9         | 2.4         | 2           |             |             |             |

**Abbreviations:** AW, maximum width of trigonid; L, maximum anteroposterior length; M, molar; P, premolar; PW, maximum width of talonid; W, maximum lingual-buccal width.
| Species            | Specimen number | Side     | Site          | p3 L | p3 W | m1 L | m1 AW | m1 PW | m2 L | m2 AW | m2 PW | m3 L | m3 AW | m3 PW | m4 L | m4 AW | m4 PW |
|--------------------|-----------------|----------|---------------|------|------|------|-------|-------|------|-------|-------|------|-------|-------|------|-------|-------|
| Hypsiprymnodon     | QM F24148       | Left     | Camel Sputum Site | 4.3  | 3.3  | 2.5  | 2.2   | 2.3   | 2.8  | 2.4   | 2.3   | 2.8  | 2.4   | 2.3   | 2.1  |       |       |
| philcreaseri       | QM F24148       | Right    | Camel Sputum Site | 4.3  | 3.2  | 2.6  | 2.3   | 2.3   | 3    | 2.4   | 2.3   | 2.8  | 2.3   | 2.1   | 2.7  | 2.1   | 1.9   |
| philcreaseri       | QM F24173       | Left     | Camel Sputum Site | 4.2  | 3.8  | 3    | 2.3   | 2.4   | 3.3  | 2.4   | 2.3   |      |       |       |      |       |       |
| philcreaseri       | QM F24174       | Right    | Camel Sputum Site | 4.8  | 3.9  | 2.8  | 2.4   | 2.3   | 2.4  | 2.4   | 3    | 2.4  | 2.2   | 2.9   | 2.3  | 2.1   |       |
| philcreaseri       | QM F24175       | Left     | Mike’s Menagerie Site | 4.5  | 3.3  | 2.7  | 2.1   | 2.2   | 2.9  | 2.4   | 2.4   | 2.9  | 2.4   | 2.2   | 2.8  | 2.3   | 2     |
| philcreaseri       | QM F56272       | Right    | Mike’s Menagerie Site | 3.9  | 3    | 2.8  | 2.2   | 2.2   | 2.5  | 2.6   | 2.2   | 2.2  | 2.1   | 1.9   | 1.9  |       |       |
| philcreaseri       | QM F23463       | Left     | Upper Site     | 4.7  | 3.5  | 2.8  | 2.1   | 2.3   | 2.9  | 2.3   | 2.4   | 2.8  | 2.3   | 2.2   | 2.7  | 2     | 1.8   |
| philcreaseri       | QM F24166       | Right    | Upper Site     | 4.6  | 3.5  | 2.9  | 2.3   | 2.4   | 3    | 2.7   | 2.5   | 3    | 2.5   | 2.3   |      |       |       |
| philcreaseri       | QM F24167       | Right    | Upper Site     | 4.5  | 3.5  | 2.9  | 2.3   | 2.4   |      |       |       |      |       |       |      |       |       |
| philcreaseri       | QM F24168       | Right    | Upper Site     | 4.3  | 3.7  | 3    | 2.1   | 2.2   |      |       |       |      |       |       |      |       |       |
| philcreaseri       | QM F24169       | Right    | Upper Site     | 4.4  | 3.4  | 2.7  | 2.1   | 2.3   | 2.9  | 2.5   | 2.4   | 2.8  | 2.4   | 2.3   | 2.7  | 2.1   | 1.9   |
| philcreaseri       | QM F24170       | Left     | Upper Site     | 4.6  | 3.4  |      |       |       | 2.8  | 2.5   | 2.3   |      |       |       |      |       |       |
| philcreaseri       | QM F24621       | Left     | Cleft of Ages Site | 5.2  | 3.8  | 3    | 2.3   | 2.4   | 3    | 2.5   | 2.6   | 3    | 2.5   | 2.6   | 2.9  | 2.1   | 1.9   |
| philcreaseri       | QM F29659       | Left     | Cleft of Ages Site | 3.1  | 2.4  | 2.3   | 3.1  | 2.4   | 3.1  | 2.4   | 2.6   | 2.2  | 2     |       |      |       |       |
| philcreaseri       | QM F29730       | Left     | Cleft of Ages Site | 5.1  | 3.8  | 3.3   | 2.5   | 2.5   | 3.1  | 2.7   | 2.6   |      |       |       |      |       |       |
| philcreaseri       | QM F29736       | Right    | Cleft of Ages Site | 3    | 2.3  | 2.3   | 3    | 2.4   | 2.4   | 3    | 2.3   | 2.3   | 2.9  | 2.2   | 2     |      |       |       |
| philcreaseri       | QM F31349       | Left     | Cleft of Ages Site | 5.4  | 3.8  |      |       |       |      |       |       |      |       |       |      |       |       |

**Abbreviations:** AW, maximum width of trigonid; L, maximum anteroposterior length; m, molar; p, premolar; PW, maximum width of talonid; W, maximum lingual-buccal width.
serrated cutting edge. The eighth and ninth cusps are closely positioned and from certain angles, these two cusps appear as though they have merged into one long cusp. On the lingual side, the tooth is slightly damaged making the sixth, seventh, and eighth transcristids hard to differentiate. In buccal view, the transcristids are posterovertrally inclined. P3 meets the anterior margin of M1 anterior to the paracone of the latter tooth. The anterior root, exposed in part of the preserved maxilla, is posteriorly dorsal to the crown and longer than the crown height of P3. A total of three roots are present on P3. In buccal view, two of these are evident but in lingual view the roots are difficult to discern. In buccal view, the posterior occlusal margin of P3 slightly overhangs the anterior occlusal surface of M1 ventroposteriorly.

In occlusal view, M1 is roughly rectangular in shape. The buccal surfaces of the crown are more steeply inclined than the lingual surfaces. The paracone and metacone are taller than the protocone and metaconule. The paracone and metacone are of similar height, as are the protocone and metaconule. A protoconulecrista is present on the anterolingual margin, anterior to the protocone. The enamel of the protostyle, protocone, and metacone apices has been breached by wear. A prominent stylar cusp C is present on the buccal side of the interloph valley posterior to the paracone. A small cristae, separate from and buccal to the postparacrista, runs from the apex of the stylar cusp to the apex of the paracone. The metaloph is longer and better defined than the protoloph. The anterior width of the tooth is greater than the posterior width. The protoloph runs from the apex of the paracone to the apex of the protocone. The trigon and talon basins are rectangular in shape. The trigon basin is anteriorly enclosed by the preprotocrista and pretalocrista, which connect to form a continuous anterior margin. This margin is not elevated above the basin floor. The basin slopes from the apex of the protocone lingually, down to the level of the protostyle. The talon basin is larger than the trigon basin. The talon basin inclines posteriory so that the posterior margin is the lowest point of the tooth. The postmetaconulocrista and postmetacrista decline in height posteriorly from the apices of the metaconule and metacone, joining on the slope of the talon basin. Small crenulations can be seen between the premetacrista and postmetacrista. The premetacrista is well defined in comparison with the relatively worn premetaconulecrista.

The M2 is similar to M1 in shape and morphology but differs as follows: in occlusal view the protostyle is reduced; stylar cusp C is reduced to a small hiatus on the centrocrista; the trigon basin dorsally inclines anteriorly instead of lingually; crenulations are present in the trigon and talon basins; the protocone is larger and more bulbous; the protoloph runs from the apex of the paracone to the apex of the protocone; the preparacrista is slightly anteriorly angled, but less so than on M1.

In occlusal view, M3 is similar to the anterior molars in overall morphology. It differs from more anterior molars as follows: the paracone, metacone, protocone, and metaconule are of similar height; the protocone and metaconule are broader than the paracone and metacone; the slope of the trigon basin faces the buccal side because the protocone is positioned more anteriorly than in M1 or M2, filling the gap of the slope on the lingual side; the talon basin, which is more conspicuously crenulated than on M1 or M2 probably due to heavier wear on the latter two teeth, is reduced in size; the occlusal surface of the crown is ventrobuccally oriented.

The M4 differs in size, morphology, and slightly in shape from the anterior molars as follows: it is considerably smaller than the anterior molars; in occlusal view it is triangular, with lingual and buccal sides converging posteriorly; the trigon is wider than the talon; the talon basin is reduced to a small fossa; the occlusal surface of the crown is ventrobuccally oriented, more so than in M3; the protocone and paracone are of equal height; the metacone and metaconule are considerably reduced and closer together than the protocone and paracone; the trigon basin occurs on the buccal side of the occlusal surface; the metaloph is greatly reduced; the posterior margin is slightly elevated, being almost level with the metacone and metaconule; small stylar cusps C and D are present on the buccal side of the tooth near the centrocrista.

**Dentary and Lower Dentition**—Paratype QM F24621 is a left dentary referred to *H. dennisi* because it occludes perfectly with the maxilla described above, and both specimens were retrieved from the same site. It retains p3 and m1–4, all heavily worn. The part of the dentary anterior to p3, the angular process, and the mandibular condyle are missing. The anterior portion of the coronoid crest is present but only to the level of the cheek teeth. A small foramen is present on the ventral surface of the dentary below the masseteric fossa.

The plagiaulacoid p3 has a median occlusal ridge intersected by eight transcristids arising from lingual and buccal faces. Eight cusps occur ventrally along the median ridge where the cristids
intersect, forming a serrated cutting edge. The crown is widest at the seventh transcristid. The buccal side of the tooth is damaged, making it hard to differentiate all of the transcristids. In lateral view, the transcristids are posteroventrally inclined. The sixth, seventh, and eighth cuspids are heavily worn. The p3 is buccally flexed, with the posterior end meeting the anterior margin of m1, towards the far lingual side of the tooth. The p3 is aligned with the lingual cusps of the molar row. The molar row is angled anterobuccally with respect to the long axis of the horizontal ramus. The molar teeth are low crowned and bunolophodont.

The m1 is roughly rectangular in occlusal outline. The lingual surfaces of the crown are more steeply inclined than the buccal surfaces. A crevice created by wear runs anteroposteriorly dividing the tooth in half. A protostylid is present buccal to the protoconid. The protolophid and hypolophid are obscured because of wear, but the protolophid is clearly shorter than the hypolophid. The protolophid runs from the apex of the protoconid to the apex of the protostylid; the hypolophid runs from the apex of the entoconid to the apex of the hypoconid. The talonid is wider than the trigonid. The trigonid is considerably longer than in other species of Hypsiprymnodon. The trigonid and talonid basins are hard to recognize. The enamel of the apices of the protoconid and entoconid has been breached by wear. The protoconid is the tallest cusp, followed by protostylid, entoconid, and hypoconid.

The m2 has a similar occlusal structure compared with m1 but differs as follows: a protostylid is not present; there is no longitudinal crevice dividing the tooth in half; the trigonid basin is well defined and larger than the talonid basin; the hypolophid and protolophid are of equal length; the protolophid runs from the apex of the protolophid to the apex of the metaconid; the hypolophid runs from the apex of the hypoconid to the apex of the entoconid; the protoconid and hypoconid are taller than the metaconid and entoconid; the protoconid is the widest cusp on the crown; the metaconid and entoconid are bulbous in shape and larger in size.

The m3 is similar in shape and morphology to m2 but differs as follows: the protolophid is angled slightly more anteroposteriorly than the transverse hypolophid; the trigonid basin inclines lingually from the metaconid.

The m4 differs from m2 and m3 as follows: it is smaller in size; the talonid is smaller and more compact than the trigonid; the talonid slopes posteriorly down the side of the crown sitting lower than the trigonid; the protolophid, interloph valley, and hypolophid are poorly defined; the protoconid and metaconid are considerably larger than the hypoconid and entoconid, which can only just be distinguished. Measurements of the upper and lower dentition are listed in Tables 1 and 2.

**HYPSIPRYMNODON KARENBLACKAE**, sp. nov.

(Fig. 5)

**Holotype**—QM F24152, left maxilla preserving entire cheek tooth row (P3, M1–3).

**Type Locality and Age**—Camel Sputum Site, Riversleigh World Heritage Property, northwestern Queensland. Camel Sputum Site is considered to represent Riversleigh Faunal Zone B, which is interpreted as early Miocene in age (Archer et al., 1997; Travouillon et al., 2006, 2011).

**Etymology**—In honor of Dr. Karen Black from the University of New South Wales, for her significant contribution to Australian paleontology, particularly Riversleigh, and her inspirational success as a female scientific researcher.

**Diagnosis**—Hypsiprymnodon karenblackae can be distinguished from all other species of Hypsiprymnodon in possessing a lingual precingulum, parastyle, and stylar cusp D on M1. It can be distinguished from *H. moschatus* by possessing eight rather than seven transcristae and cusps on unworn P3, and from *H. moschatus* and *H. bartholomaii* in its upper third premolar being considerably less anterobuccally flexed out of alignment with respect to the molar row.

**Description**

**Maxilla and Upper Dentition**—The left maxilla, which preserves P3, M1–3, also retains a small portion of the anterior part of the jugal process. This process originates dorsal to M1 and is robust in structure. In dorsal view, the anterior orifice of the infraorbital foramen is visible, opening anterodorsal to P3. The maxillary foramen is dorsal to M1. Molars decrease in size posteriorly. The occlusal margin of P3 meets the anterior margin of M1 anterior to the parastyle. The molar row is slightly buccally convex. The crown height of P3 is greater than that of any of the molars. In occlusal view, the longitudinal axis of P3 is flexed slightly buccally out of alignment with the molar row. Molar teeth are low crowned and bunolophodont.
P3 is a plagiaulacoid tooth with a longitudinal median occlusal ridge intersected by eight transcristae arising from lingual and buccal faces. Eight cusps are positioned ventrally along the median ridge where the cristae intersect, forming a serrated cutting edge. The crown is widest at the sixth transcrista. In lateral view, the transcristae are posteroventrally inclined. The crowns of P3 and M1 are in contact ventrally. The crown of P3 sits low on the maxilla so that no roots are exposed, unlike other species of Hypsiprymnodon in which roots are partially visible in buccal view. The P3 is tall and slender in comparison with the P3 of H. dennisi. The P3 does not overhang the M1. The posterior margin of P3 is ventrally inclined.

In occlusal view, M1 is rectangular in shape. In lingual view, a horseshoe-shaped precingulum extends dorsoventrally, bordering the protocone on the lingual side of the crown. The precingulum starts half way up the crown, then runs ventrally from the anterior part of the protocone (posterior to the preprotocrista), along the top of the protocone, then dorsally half way down the lingual side of the crown on the posterolingual side of the protocone (anterior to the postprotocrista), then finally it curves slightly anteriorly. A parastyle is present anterior to the paracone. The parastyle and paracone are connected by the precingulum. The trigon basin slopes ventrolingually from the apex of the paracone down to the protocone. The paracone and metacone are taller than protocone and metaconule, which are more bulbous in shape. The protoloph runs transversely from the apex of the paracone to the apex of the protocone. A buccal kink is present on the buccal side of the centrocrista at the interloph valley. Crenulations are present along the metacrista sloping anteriorly into the interloph valley. A small stylar crest D is present anterior to the preprotocrista, connecting with the buccal kink along the centrocrista. The metallocip is better defined than the protoloph. A single root is exposed on the lingual side; two roots are exposed on the buccal side. The posterior margin of the talon basin is enclosed by the postmetacrista and postmetaconulecrista, which merge into each other. This continuous posterior margin is elevated above the level of the talon basin floor.

The morphology, size, and shape of M2 are similar to that of M1. It differs from M1 as follows: the precingulum is reduced; the buccal kink in the centrocrista and stylar crest D are more prominent; the parastyle is reduced to a fossa; the talon basin is larger than the trigon basin; the paracone is taller than the other cusps; the metacone, protocone, and metaconule are of equal height; crenulations are present in all basins and in the interloph valley. The M3 is similar to the anterior molars in size, shape, and morphology except as follows: the paracone, protocone, metacone, and metaconule are of equal height; the paracone and metacone are more bulbous; the precingulum is further reduced in occlusal and lingual views; the trigon basin is larger than talon basin; the buccal kink is reduced; stylar crest D is absent; crenulations are present in all basins and the interloph valley. Measurements of the upper and lower dentition are listed in Tables 1 and 2.

RESULTS

Analysis of the morphological matrix resulted in 6960 most parsimonious trees (tree length = 276; consistency index excluding uninformative characters = 0.4361; retention index = 0.7483). The strict consensus tree of these is given in Figure 6, with bootstrap and Bremer support values indicated.

Relationships within Macropodidae are highly unresolved in the strict consensus. However, two major clades are recognized: a clade comprising macropodines, sthenurines, bulungamynes, and potoroids (bootstrap = 61%) and another comprising balbarid clades. The relationship between potoroids and bulungamynes is unresolved, with monophyly of Potoroidae not recovered. A Macropodinae + Sthenurinae clade is recovered (which receives moderate support; bootstrap = 68%, Bremer = +3). Balbarid clades is also recovered as monophyletic, but support for this clade is weak (bootstrap <50%). The species of Hypsiprymnodon and the propleopines (Jackmahoneya, Ekaladeta, and Proleopues) form an unresolved polytomy at the base of Macropodoidea, together with the macropodine + sthenurine + bulungamyne + potoroid and balbarid clades.

DISCUSSION

Morphological variation among specimens of the extant Hypsiprymnodon moschatus is low (Fig. 7). All 13 extant specimens available from the Queensland Museum were examined and the only noticeable difference between specimens was due to wear (e.g., the number of transcristae on P3 varied from seven to five, with fewer visible transcristae on specimens having more molar wear; however, all unworn specimens exhibit seven transcristae). No stylar cusp C or D or lingual precingulum were present on any of the specimens examined. However, slight sexual dimorphism is reflected in body mass differences in the living species (Johnson and Strahan, 1982; Dennis, 2002): males are approximately 20 g heavier than females, although the magnitude of this difference may change during and after the mating season (Dennis, 2002). In our opinion, the limited degree of dental variation and sexual dimorphism observed in H. moschatus justifies recognition of the Riversleigh taxa H. philcreaseri, H. dennisi, and H. karenblackae as three distinct species, in addition to H. bartholomai, also from Riversleigh and the extant H. moschatus (Fig. 7).

The phylogenetic analyses of Cooke (1997a) found strong support for the monophyly of Hypsiprymnodontidae and Balbaridae, with both clades receiving 100% bootstrap support. By contrast, monophyly of both Balbaridae and Hypsiprymnodontidae was only weakly supported (bootstrap <50%) in the analysis of recovered by Kear and Pledge (2007). In our analysis, neither Balbaridae nor Hypsiprymnodontidae were recovered as monophyletic, which is almost certainly the result of the addition of more fossil taxa (notably the three new Hypsiprymnodon species). Addition of fossil taxa can reduce support values by (1) exhibiting combinations of character states that are intermediate between clades that previously appeared clearly distinct; (2) increasing the total amount of homoplasy; and (3) by increasing the proportion of missing data (Horovitz, 1999). In the future, these issues could be at least partially alleviated by increasing the number of dental characters (given that most fossil taxa are described based on dental material only), increasing the number of modern species scored, and discovering more complete fossil material to reduce the amount of missing data and potentially result in a greater resolution of relationships within Macropodoidea. Although monophyly of Hypsiprymnodon was not recovered in our analysis, we consider that the very close morphological similarity (i.e., plagiaulacoid premolars, bunolophodont molars, and small size) of H. moschatus, H. bartholomai, and the three new species described here warrants referral of all five species to the same genus (Fig. 7).

This study does, however, support the recognition of Hypsiprymnodontidae as representing a family distinct from Macropodidae and Potoroidae, and is in agreement with the findings of Langer (1979, 1980a, 1980b), Cooke (1997a), Burke et al. (1998), and Meredith et al. (2009). Langer (1979, 1980a, 1980b) found the simple forestomach in Hypsiprymnodon (presumably a pleiomorphic retention) to be more similar to ‘possums’ than to the complex sacciform forestomach (presumably a derived specialization) of potoroids and macropodids. Our results are congruent with the molecular phylogenies presented by Burke et al. (1998) and Meredith et al. (2009), which also separated Hypsiprymnodontidae from a Macropodidae + Potoroidae clade.

Tertiary carbonate deposits at Riversleigh occur adjacent to, within, and upon Proterozoic siliclastic, chert deposits, and Cambrian marine limestone that form the northeastern edge of the
Barkly Tableland in northwestern Queensland (Archer et al., 2006). Depositional history of these deposits involves a complex sequence of fluvial and karst processes (Archer et al., 1989, 1994, 1997; Arena, 2005). Faunas from these deposits are considered to range in age from the late Oligocene to Holocene (Archer et al., 1989, 1994, 1997; Travouillon et al., 2006, 2011). These deposits are grouped into faunal zones (previously ‘systems’; Archer et al., 1989) that define the different sequential combinations of rock/faunal assemblages interpreted to span the late Oligocene to late Miocene sediments of Riversleigh (Travouillon et al., 2006, 2011). Within Riversleigh deposits, specimens of Hypsiprymnodon are distributed in sites occurring in Faunal Zone B and Faunal Zone C.

Specimens of _Hypsiprymnodon philcreaseri_ and _Hypsiprymnodon karenblackae_ have been collected from sites within Faunal Zone B (interpreted as early Miocene in age; Archer et al., 1989, 1994, 1997, 2006; Travouillon et al., 2006, 2011), stratigraphically rendering them the oldest known _Hypsiprymnodon_ species. The single known specimen of _Hypsiprymnodon karenblackae_ was collected from Camel Sputum Site. Specimens of _Hypsiprymnodon philcreaseri_ have also been collected from this site, suggesting that _Hypsiprymnodon philcreaseri_ and _Hypsiprymnodon karenblackae_ species were sympatric during the early Miocene. Hypsiprymnodon philcreaseri is the most abundant Hypsiprymnodon species known from Riversleigh, of seven sites, all occurring within Faunal Zone B. Specimens of _Hypsiprymnodon bartholomaii_ and _Hypsiprymnodon dennisi_ have been collected only from sites within Faunal Zone
Today the only surviving member of the hypsiprymnodontid lineage, Hypsiprymnodon moschatus, exists in refuge rainforest habitats of northeastern Queensland (Johnson and Strahan, 1982). H. moschatus is predominantly frugivorous (Dennis, 2002) and the only living member of Macropodoidea to possess short and wide plagiaulacoid third premolars with simple bunolophodont molars. H. moschatus is also the only known kangaroo to scatterhoard fruit and seeds (Dennis, 2003). The fossil record indicates the presence of Hypsiprymnodon species in Queensland during the early to middle Miocene and Victoria during the early Pliocene in rainforest habitats (Turnbull and Lundelius, 1970; Archer et al., 1989, 1997; Travouillon et al., 2009). Considering how the minor differences in the dental morphology between the Miocene species of Hypsiprymnodon and the extant species H. moschatus, it seems likely that they had very similar diets (i.e., predominantly frugivorous) and ecologies. Hence, the presence of Hypsiprymnodon in fossil deposits may be an indication of a rainforest habitat.

CONCLUSION

Three new species of musky rat-kangaroos are described from the Riversleigh World Heritage Area, Queensland, Australia. Our phylogenetic analysis does not resolve the relationship of these species within Hypsiprymnodontidae. However, we suggest that more morphological characters (particularly from the dentition) and more complete specimens are required to fully resolve their relationships. Two species co-occur in Riversleigh Faunal Zone B (early Miocene), Hypsiprymnodon philcreaseri and H. karenblackae, whereas two species are present in Faunal Zone C (middle Miocene), H. bartholomaii and H. dennisi, both of which are thought to represent rainforest habitats (Travouillon et al., 2009). This is consistent with the only other fossil record of Hypsiprymnodon from the Pliocene rainforests of Hamilton (Victoria) and the modern taxon, currently restricted to rainforest habitats of northeastern Queensland. Hypsiprymnodon may be a potential marker species for rainforest habitats.

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