Chapter 18

Dasyurids, Perameloids, Phalangeroids, and Vombatoids from the Early Pliocene Hamilton Fauna, Victoria, Australia

WILLIAM D. TURNBULL,1 ERNEST L. LUNDELIUS, JR.,2 AND MICHAEL ARCHER3

ABSTRACT

New material of dasyurids, peramelids, phalangerids, pseudocheirids, burramyids, ektopodontids, and vombatids from the early Pliocene Hamilton fauna of Victoria, Australia, includes a new perameloid species and the first record of vombatids in the Hamilton fauna. The earlier interpretation of the assemblage as representing a rain forest fauna is confirmed.

INTRODUCTION

The discovery of a fossil potoroine tooth at the Grange Burn, Hamilton, Victoria, by Gill (1952, 1957) and further studies by Stirton (1957) and Ride (1964) stimulated additional field work that yielded a number of taxa, now termed the Hamilton fauna (Turnbull and Lundelius, 1970). Subsequent work by Turnbull and Lundelius and later by Rich, produced more material that was the basis for the following publications: Archer (1982); Rich (1986); Flannery et al. (1987); Turnbull et al. (1987a, 1987b, 1987c); Flannery et al. (1992); and Ride (1993). This paper reviews the material assigned to the dasyurids, perameloids, and phalangeroids and describes specimens not dealt with in earlier publications. Included are descriptions and assessments of new specimens that add understanding to taxa previously reported.

LOCALITY AND AGE

All of the fossil material was recovered from an unnamed lithic unit, considered to represent a fossil soil (Gill, 1957), exposed along the Grange Burn, 7 km west of Hamilton, Victoria at 37°43′58″ ± 03″ S, 141°57′14″ E (sheet 7222, Coleraine 1:100,000, edition 1, series R652). The outcrop, about 100 m long, is downstream from a waterfall that flows over the overlying basalt on the Grange Burn. The fossil soil is overlain by a basalt flow dated at 4.35 ± 0.1 Ma (Turnbull et al., 1965). The age was recalculated as 4.46 ± 0.1 Ma by I. McDougall (personal commun., 1980, using decay constants recommended by Steiger and Jager, 1978). This sequence overlies the Grange Burn Formation, earliest Pliocene, Kalimnan Age (Ludbrook, 1967).

MATERIALS AND METHODS

All measurements were taken with a graduated reticle or with micrometer calipers graduated to 0.01 mm. Abbreviations are:

- NMV: Victorian Museum, Melbourne
- FM and PM: Field Museum of Natural History, Chicago
- TMM: Texas Memorial Museum, University of Texas, Austin.

Dental nomenclature used here is that of Thomas (1887), for example, for Antechinus dI1–4, di1–3, I1–4, i1–3, dC1, dC1, C1, c1, dP3, dp3, P1–3, p1–3, M1–4, m1–4, unless

1 Curator Emeritus, Department of Geology, Field Museum of Natural History, Chicago, Illinois, 60605.
2 Professor Emeritus, Department of Geological Sciences and Vertebrate Paleontology Laboratory, Texas Memorial Museum, University of Texas at Austin, Austin, Texas, 78712.
Fig. 18.1. Diagram of the perameloid upper molar cusp terminology used in this paper for tooth features, particularly those of the stylar shelf. Occlusal and ventrolabial views are based on scaled camera lucida renditions of NMV P 178073, cf. *Peroryctes tedfordi*. Abbreviations of features of the stylar shelf are: B, *stylocone*; C, D, and E are cusps bearing those letters; C₁, D₁, and E₁ are subsidiary cuspules to cusps C, D, and E; Mest = *metastyle*; Past = *parastyle*; Mele = *metaconule*; Pale = *paraconule*; ME = *metacone*; PA = *paracone*; PR = *protocone*.

otherwise noted. Terminology for cusps of the stylar shelf of peramelomorphian upper molars is shown in figure 18.1.

**SYSTEMATICS**

**MARSUPIALIA**

**AUSTRALDELPHIA**

**DASYUROMORPHA**

**FAMILY DASYURIDAE**

**Genus Antechinus**

Antechinus sp. Archer, 1982

**MATERIAL:** One isolated left M1 (NMV P 160482), one isolated right m4 NMV P 160483.

**DISCUSSION:** These were described and one was figured by Archer who stated (1982: 425) “… The Hamilton *Antechinus* appears to be related to a particular modern species, the Mt. Wilhelm *Antechinus*.” To date no further specimens of the genus have been recognized with certainty from the Hamilton fauna. Subsequently Dawson, Muirhead, and Wroe (1999: 271) compared four teeth of *Antechinus* sp. from Wellington, Big Sink with *A. stuartii*, *A. flavipes*, *Murexia longicaudata*, *Phascogale calura*, and with *A. leo* and *A. puteus* (Van Dyck, 1980, 1982) and “with unnamed species of *Antechinus* from the Hamilton Local Fauna, and from Floraville in Queensland (Archer, 1982).” They stated that the Hamilton material differs from the Big Sink *Antechinus* in that the M1 lacks the distinctive narrow stylar cusp D and full posterior cingulum. They agreed with Archer (1982) that the Hamilton *Antechinus* is close to *A. naso* from New Guinea and they considered it unlikely that the Big Sink and Hamilton species represent the same unnamed taxon.

**INDETERMINATE DASYUROID MATERIAL:** PM 50919, a P3 (or P2), similar in size and proportions to *Phascogale calura* (FM 36052). It may be an *Antechinus*, but its central main cusp is not as tall as that of *A. stuartii* (FM 35337). It is 1.48 mm long and 0.84 mm wide.

NMV P 54070, a partial trigonid of an m3 or m4 that is dasyurid-like in that it has a notch between the parastylid and the anterior cingulid.

NMV P 54110, a *Dasyurus*-like last upper premolar, possibly *Antechinus*.

NMV P 54194, a poorly preserved edentulous mandibular ramus with part of the ascending ramus and the base of the angular process. The anterior edge of the ascending ramus rises at a steeper angle than is usual in bandicoots (more like that of dasyurids). The posterior alveoli for m1–3 are not expanded laterally as in bandicoots.

NMV P 177974, a lower canine (fig. 18.2A–C) that appears to be too robust to be from a bandicoot. It is intermediate in size between *Dasyurus geoffroyi* and *D. hallucatus*. It is probably a dasyurid; however, the large upper canines of *Yarala burchfieldi* suggest the possibility that this tooth may be-
Fig. 18.2. Scanning electron microscope photos. NMV P 177974, dasyurid or perameloid (see text) lower canine, (A) left lateral, (B) dorsal, and (C) medial views. NMV P 177975, left upper incisor of *Dasyurus*, (D) anterodorsal, (E) medial, (F) a view halfway between those of E and G, and (G) posterodorsal views.
long to one of the new species of perameloid described here that have other Yarala-like features.

NMV P 177975, a left I2 (fig. 18.2D–G), cf. Dasyurus sp. The root and crown of the tooth are thin, about equal in thickness, and the crown is only slightly expanded anteroposteriorly beyond the root. The anterior surface of the crown is smoothly rounded except for a weak central elevation near the tip. The posterior face of the crown has an undulating ridge extending from tip to base.

NMV P 177976, an upper canine or anterior premolar of a dasyurid or phalangerid (fig. 18.3A–C).

NMV P 177997, a part of a heavily worn left upper molar consisting of the area from the paracone to the stylocone and parastyle. An anterior cingulum extends from just lingual to the parastyle, half way to the paracone. There is a low cingular bulge on the labial side of the stylocone. The tooth is about the size of an upper molar of Dasyurus hallucatus. Neither that species nor D. geoffroyi have the labial cingular bulge.

NMV P 177998, a fragment of a left lower molar with a protoconid and the base of the paracone. There is no carnassial notch or wear facet on the paralophid. It is either a dasyurid or a peramelid.

NMV P 177999, a left I4 that is smaller and relatively thicker than that of D. geoffroyi (FM 34718) and is most like that of Dasyuroides byrnei (FM 104786).

NMV P 180041, a tall trigonid comparable to NMV P 180041.

NMV P 210913, a tall trigonid comparable to NMV P 180041.

NMV P 210915, a ?right I1 with similarities to that of Dasyurus viverrinus (FM 34727), and to the left I3 of a peramelid.

**DISCUSSION:** The new dasyurid material is too fragmentary to identify below the family level. It is clear that in addition to Antechinus sp. there is more than one other taxon represented. The scarcity of dasyurid material in the Hamilton assemblage is puzzling. However, Muirhead and Filan (1995: 133) point out that in the Riversleigh deposits bandicoots far outnumber small dasyurids, with whom they appear to have been in direct insectivorous–carnivorous competition. Over all, Riversleigh bandicoots include both insectivorous–carnivorous and insectivorous–omnivorous forms, with the former being by far the most abundant. They consider the living bandicoots to be restricted primarily to insectivorous–omnivorous species and that, “It appears that since the Miocene Australian bandicoots may have had the number of potential niches available to them restricted, which consequentially channelled bandicoots into a more omnivorous and less carnivorous lifestyle. In contrast dasyurids have become more diverse, occupying and today totally filling both insectivorous and carnivorous niches. It is possible that dasyurids have subsequently taken the role that was at least partially exploited by bandicoots.”

The Early Pliocene Hamilton faunal record, with its few dasyurids in contrast to multiple specimens of the two cf. Peroryctes taxa (see below) supports that view, and accounts in part for the otherwise puzzling great abundance of dasyurids in Pleistocene cave deposits. In the post-Hamilton Late Pliocene to Middle Pleistocene, dasyurids outcompeted bandicoots for more carnivorous niches. It is probable that the late Cenozoic rise in dasyurid diversity was either a cause or a consequence of the decline in thylacinid as well as in peramelid diversity (Wroe, 1999).

**SYNDACTYLI**

**PERAMELOMORPHA**

**SUPERFAMILY PERAMELOIDEA**

**FAMILY PERORYCTIDAE**

Five partial teeth, PM 4446, 4499, 4600, 4748, and NMV P 26406 (PM 4445) were
the only perameloids recognized in 1970. New material shows there are two size groups in the fauna, one consistent in size with the five specimens listed above and one significantly larger (figs. 18.4–18.8).

Genus *Peroryctes*

*Cf. Peroryctes tedfordi*, new species


*Etymology:* Named for R.H. Tedford, long-time contributor to Australian vertebrate paleontology and the honoree of this volume.

*Material:* Holotype, a left horizontal ramus with m1–3 NMV P 157329 (fig. 18.5J–N).

*Referred Specimens:* Lower teeth: NMV P 180042, tentatively referred right p2 or p3 (fig. 18.3G–I); premolar NMV P 180043; NMV P 210911, right m1 (fig. 18.6D, E); NMV P 157136, a deeply worn right m2 or m3 (fig. 18.6F); NMV P 158727, left m2 or m3; NMV P 180038, left m2 or m3; NMV P 210912, right m2 or m3 (fig. 18.6A–C); NMV P 210975, right m2 or m3 (fig. 18.6G); NMV P 157138, talonid of a right lower molar; NMV P 158084, talonid of a left m2 or m3; NMV P 158721, talonid of a right lower molar; NMV P 158728, edentulous left ramus (fig. 18.3O, P). Upper teeth: NMV P 158739, P1 or P2 (fig. 18.3D–F); NMV P 157140, premolar fragment; NMV P 157131, right M1 (fig. 18.7B); NMV P 178073, complete right M1 (fig. 18.1); NMV P 158720, complete left M1 or M2; NMV P 54144, right M2 or M3 (fig. 18.7C–F); NMV P 157133, left M3 (fig. 18.7G). Tentatively referred: NMV P 178000, proximal end of humerus (fig. 18.7H–K).

*Diagnosis:* The cheek teeth of *Peroryctes tedfordi* are smaller than those of most other perameloids with the exception of *Yarala burchfieldi* and the lower molars (figs. 18.4, 18.5) referred to *Perameles bowensis* by Muirhead et al. (1997). The entoconids of the lower molars are large, elongate, and laterally compressed above their rounded, nearly circular bases. Initial wear on these cuspids begins on their anterolabial sides (fig. 18.6E, G), and extends to the entire labial side (fig. 18.6B, C, then 6F, 7A). The lateral compression toward the apices distinguishes this taxon from all known perameloids. Some species of *Peroryctes* show thinning of the entoconids at the apices as a result of wear. The assignment of this species to *Peroryctes* is provisional but is our best estimate; better material will be needed to settle its generic allocation.

Distinguishing features of the M1–3, in addition to their small size, are the much smaller size of the metaconules (fig. 18.7B, D, F, G) in comparison with the protocones. The posterior metaconule crest is limited and does not curve around the base of the metacone or become a cingulum. Some specimens of *Peroryctes raffrayanus*, *P. broadbenti*, *Microperorytes papuensis*, and *M. murina* have small metaconules but not as small as in the Hamilton species. The characteristic peramelid/peroryctid pattern of a breached ectoloph between stylar cusps C and D is present, but the breach is narrower than in living peramelemorphans.

*Description:* The description of the lower dentition is based primarily on the holotype (fig. 18.3J–N), with notes on referred specimens that show variations. The dentition is smaller than that of any other known peramelemorph except *Yarala burchfieldi* and possibly the lower molars referred to *Perameles bowensis* by Muirhead et al. (1997; tables 18.1, 18.2; figs. 18.4, 18.5). As in almost all perameloids, the lower molars except m4 have talonids that are markedly wider than trigonids because of the large hypoconids that project farther labially than do the protoconids. The protoconids and hypoconids are joined at their bases by a cingulid that does not extend onto the labial side of those cusps. This cingulum is small in m, progressively larger in m2 and m3. In *Perameles bougainville* it forms more of a shelf confined to the sulcus obliquid. The Hamilton *cf. Peroryctes* more closely resembles *Isoodon obesulus* in this regard.

The trigonid of the m1 is extensively worn anteriorly. Making allowances for wear, the m1 is similar to that of *P. bougainville* in the following ways: (1) The paraconid is located low on the anterior end of the tooth. (2) The metaconid appears to have been only slightly
Fig. 18.3. Scanning electron microscope photos. NMV P 177976, an upper canine or anterior pre-molar of a dasyurid or phalangerid shown in (A) anterior, (B) ?medial, and (C) posterior views. NMV
smaller than the protoconid. (3) The paracristid is oriented at a right angle to the long axis of the tooth and there is no cingulum on the anterolabial base of the tooth. (4) The entoconid is nearly as large as the hypoconid; it is elongated and becomes increasingly laterally compressed towards its apex. (5) It is separated from the hypoconulid by a shallow groove.

In the m2, wear has reduced the paracristid and metaconid below the level of the protoconid. The entire area of the trigonid basin has had the enamel removed. There appears to have been a parastylid poorly separated from the paraconid. There is a weak cingulid on the anteroexternal edge of the tooth that extends from the parastylid to the base of the paracristid and then rises and disappears on the base of the protoconid. Much of the cingulid has been removed by wear on this specimen.

The m2 and m3 are very similar, the latter being the less worn. The sulcus obliquid (hy poloexid) is larger in m3 than in m1 or m2 and the cingular shelf between the hypoconid and protoconid is correspondingly larger. The paracristids and metacristids of the trigonids form an angle of about 45° at the protoconid.

In the holotype, the size order of the cusps of the trigonid is protoconid > metaconid > paraconid in m1 and m3 and protoconid = metaconid > paraconid in m2. There is a small but distinct anterior cingulid cuspule (parastylid) on the anterolingual corner of the m1. In the holotype, the trigonid/ talonid width ratios are 0.837 in the m1, 0.828 in m2, and 0.932 in m3. The hypoconid and entoconid are decidedly higher and more massive than the hypoconulid, which is ridgelike, extending diagonally from the posterior end of the base of the entoconid into the talonid basin.

The entoconid has an oval to nearly circular base but becomes compressed laterally toward its crest. NMV P 157136 (fig. 18.6F), which is heavily worn, shows the circular base, whereas NMV P 210975, a right m2 or m3 (fig. 18.6G), and 210912 (fig. 18.6A–C) show earlier wear stages. NMV P 210911 (fig. 18.6D, E) shows an intermediate stage of wear cutting across the full length of the labial side of the cusp.

The upper P1 or P2, NMV P 157139, is most like that of Microperoryctes longicauda dorsalis (FMNH 128356) of the comparative specimens we have examined. NMV P 157140 is either a single-rooted partial premolar or a mitten-shaped incisor. Both are tentatively referred to cf. P. tedfordi. The description of the upper molars is based on NMV P 157131, a right M1 (fig. 18.7B), with exceptions noted for other teeth. The outline drawing (fig. 18.1) is based on NMV P 178073, which differs slightly from NMV P 157131 in its postparacrista and premetacrista. The protocone and paracone are close to the anterior edge of the tooth. The latter cusp is smoothly fused with the stylar cusps B and C. The protocone has a crescent-shaped wear facet whose labial ends are crests that extend to the paraconule and metaconule. The metaconule is the more developed of the two. The postparacrista is weak, but extends to the rear of the base of cusp C. The premetacrista is prominent and extends to the anterior base of stylar cusp D, to its accessory cuspule (D1). The cleft in the ectoloph is deep and narrow, and is set off by the large relief difference between the anterior and posterior parts of the worn paracone, metacone, and ectoloph. There is an elongate stylar cusp E that is nearly as large as cusp D, which connects to the metastyle. The parastyle is a prominent, protruding ectoloph feature. NMV P 178073 (fig. 18.1) is similar to NMV P 157131 (fig. 18.7B), but the postprotocrista and premetacrista are

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P 157139, a right lower premolar (?p3) tentatively referred to cf. Peroryctes tedfordi, shown in (D) lingual, (E) occlusal, and (F) labial views. NMV P 180042, a left upper premolar, ?P2 or P3, of cf. Peroryctes tedfordi, shown in (G) lingual, (H) occlusal, and (I) labial views. NMV P 157329, holotype of cf. Peroryctes tedfordi, partial left ramus with m1–3 shown in (J) postero-dorsal, (K) anterodorsal, (L) lingual, (M) labial, and (N) occlusal views. NMV P 158728, an edentulous left ramus referred to cf. Peroryctes tedfordi shown in (O) labial and (P) dorsal views.
Fig. 18.4. Bivariate graphs of maximum length versus talonid width (A), and maximum length versus trigonid width (B) of lower molars, showing clear size differences between the two cf. Peroryctes species in the Hamilton Fauna. Data from *Yarala burchfieldi*, *Perameles bowensis*, and other peramelemorphians are included for comparison. The plots of *Perameles bougainville* in B are given to indicate the extent of the range that might be expected in the Hamilton sample.
Fig. 18.5. Bivariate graph, trigonid length versus trigonid width of lower molars. Size differences between the two cf. _Peroryctes_ species are evident. Data for _Yarala burchfieldi_, _Perameles bowensis_, and other peramelemorphians are included for comparison.

DISCUSSION: There is no close size comparison between cf. _Peroryctes tedfordi_ and the similar-age _Perameles allinghamensis_ Archer and Wade (1976). The Hamilton M1s measure 2.14 and 2.15 mm in length versus...
Fig. 18.6. Scanning electron microscope photos of cf. Peroryctes tedfordi. NMV P 210912, an m2 or m3 in three views [(A) lingual, (B) occlusal, (C) antero-dorso-labial], showing the characteristic large procingulid, elongate, laterally compressed entoconid (arrows), and wide talonid. NMV P 210911, an m1 lacking much of the talonid, is shown in (D) lingual and (E) occlusal views. The arrow points to
6.0 mm for the *P. allinghamensis* holotype. Cf. *Peroryctes tedfordi* is a perameloid that is in some regards intermediate morphologically and possibly phylogenetically between the yaraloid *Yarala burchfieldi* (Muirhead and Filan, 1995) with its strong centrocrista, and modern perameloids, which lack that feature and instead have both postparacrista and premetacrista extending well onto the stylar shelf. Cf. *P. tedfordi* is much closer to modern perameloids than to *Y. burchfieldi* because it lacks a centrocrista and retains only a few remnants of features of the postparacrista and premetacrista that must have accompanied the final stages of that transition. These are (1) a postparacrista that is weak in its buccal part and does not extend as far onto the stylar shelf as do those of modern perameloids (fig. 18.7D, G), and (2) a premetacrista that varies from being strong throughout (fig. 18.7B) to weak labially (fig. 18.7D).

Comparison with *Perameles bowensis* is difficult for we believe that the holotype, AMF 98809 designated as RM3 (Muirhead et al., 1997: 165, fig. 1B), and one of the paratypes, RM2 AMF 98810 (fig. 1A) are not from the same taxon! The holotype is similar to cf. *Peroryctes tedfordi* in its small size, and to a lesser degree in the expanded and posteriorly extended metastylar area. They both have the lingual moiety smaller mesio-distally than in the paratype, although reduction of that dimension in cf. *Peroryctes tedfordi* is not as extreme, as is seen in the holotype of *Perameles bowensis*. *Perameles bowensis* has a more reduced parastylar region than does cf. *Peroryctes tedfordi*.

The mentioned paratype of *Perameles bowensis* appears to belong to a separate taxon. Its overall proportions are decidedly different from those of the holotype, being more rectangular (less triangular) in occlusal outline. Contributing to this difference is the much greater mesio-distal dimension of the entire lingual side of the tooth, and this difference is further accentuated by the lesser development of metastylar area.

A comparison of the lower molars of cf. *Peroryctes tedfordi* and *Perameles bowensis* shows similarities in small size and the greater difference in width of talonids versus trigonids in the anterior molars. They differ in entoconid development; the former has that cuspid laterally pinched distally (apically), although its base can be round or oval. Cf. *Peroryctes tedfordi* has a well developed parastylid. This is in marked contrast to the absence of that stylid in the two illustrated *Perameles bowensis* paratypes, AMF98812 and AMF98813.

Muirhead and Filan (1995: 131) considered *Y. burchfieldi* to be a peramelemorphian in spite of its strong centrocrista, because it shows a combination of six apomorphic features inclusive to that group and exclusive to all other polyprotodonts. Although we see this as a valid general assessment, we would note some disagreement with Muirhead and Filan (1995) about the structural interpretation and description of features that distinguish *Y. burchfieldi* from other peramelemorphians. For example, they characterize the preparacrista on M1 as being posteriorly oriented, as in all bandicoots. We disagree with their use of the term preparacrista. That crest is one that extends from paracone to stylocone (= B) and on to the parastyle (via the post parastylocrista). It does not include the crest extending posteriorly from the stylocone (= B) to cusp C. In bandicoot M1s, paracone and stylocone are close, and the fusion of the those cusps and associated crests into a continuous crest that extends buccally, then posteriorly, accounts for the confusion. Contributing to potential error in interpretation is the absence of a blade from stylar cusp B to the parastyle of M1 (although it is present in M2–3). In Trinity therians (Turnbull, 1971: 161) the crista from the paracone always goes first to the stylocone, then turns anteriorly to the parastyle. However, in some

the elongate, laterally compressed entoconid. NMV P 157136, a right m2 or m3 shown in (F) occlusal view, with the compressed part of the entoconid worn to the round base (arrow). NMV P 210975, a right m2 or m3 at an early wear stage (G) showing the almost vertical wear facet of the entoconid (arrow).
Fig. 18.7. Scanning electron microscope photos of cf. Peroryctes tedfordi. NMV P 157138, the talonid of a worn right lower molar shown in occlusal view (A). NMV P 157131, right M1 shown in occlusal view (B). NMV P 54144, a lightly worn upper M2 or M3 shown in (C) labial, (D) occlusal,
peradectids and pediomyids, this condition is variable (Archer, 1976a) with the prepara-
crista sometimes bypassing stylar cusp B to
link directly with the parastyle. Muirhead
and Filan (1995: figs. 1.1, 1.2; 2.1, 2.2) show
the preparactrista continuing anteriorly from
stylar cusp B to the parastyle of M3 and M4,
the more common marsupial pattern.

Muirhead and Filan (1995) also see no
trace of a metaconule in Y. burchfieldi. We
see one, albeit small, in their figures 1.1, 1.2,
2.1. Paraconules and metaconules are Y-
shaped features that develop at the buccal
ends of the pre- and postprotocristae. These
include a low crest on the mesial side leading
to the base of the paracrista and metacone and
a low crest on the outer side, which often
curves around the outer (buccal) bases of
those cusps to approach the level of the cin-
gulid or crown-root junction. Muirhead and
Filan (1995: 132) state that stylar cusp E is
not present in Y. burchfieldi but do note that
on M1 and M2 there is a crest ‘‘. . . that runs
from stylar cusp D to the metastylar tip. This
crest may represent final stage in the phylo-
genetic loss of stylar cusp E.’’ We think sty-
lar cusp E can be detected in their figure 2.1
(on both M1 and M2) where the ectoloph
crest between D and the metastylar corner of
the tooth can be seen to rise in the usual po-
sition of stylar cusp E.

Inasmuch as cf. Peroryctes tedfordi has an
entoconid that is laterally compressed (not
conical) and its preentocristid is anteriorly
(not anterobuccally) directed, and there is no
continuous preentocristid onto the metaconid
(i.e., there is a valley between the cusps), it
does not display the apomorphic state de-
scribed by Muirhead and Filan (1995: 132,
point 4) for Y. burchfieldi. Neither does it
conform neatly to their hypothetical plesiom-
orphic condition, for while it has an oval to
circular base, it is nevertheless elongated,
with its cusp being high and increasingly lat-
erally compressed toward its tip. Perhaps
there is more than one apomorphic form.
Phylogenetically, P. tedfordi could be seen
as a descendant of Y. burchfieldi en route to
the morphological state of peramelids.

Cf. Peroryctes sp. Large Form

MATERIAL: NMV P 158722, left m1 (fig.
18.8I–K); NMV P 54147 and 54182, left and
right m2 or m3; NMV P 158724, moderately
worn left m2 or m3 (fig. 18.8E–H); NMV P
158725, worn right m4 or m3 (fig. 18.8A–
D); NMV P 158726, trigonid of right m2 or
m3; NMV P 178002, lingual side of a right
horizontal ramus; NMV P 54039, right M1
(fig. 18.9A–E); NMV P 158719, partial tri-
gon of M2 or M3; NMV P 180040, partial
M2 or M3.

DESCRIPTIONS: The description of NMV P
158722, a complete m1, will suffice for m2
and m3 except that they have a full anterior
cingulid that extends labially from the par-
astylid to the base of the protoconid. The m1
lacks an anterior cingulid, or may have a
very weak one. NMV P 158722 is almost
twice the size of NMV P 157329, and is
about the size of the m1 of Perameles bou-
gainville from the Holocene deposits of the
Nullarbor Plain (tables 18.2, 18.3). The tri-
gonid and talonid are subequal in length. The
protoconid is the largest cusp followed by the
metaconid and paraconid. The talonid is wider
than the trigonid because of the extreme
labial extent of the hypoconid. Before wear,
the entoconid was probably almost as tall as
the metaconid. It is oval at its base, but is
compressed laterally near its apex with a
sharp anterior edge. Even in deeply worn
teeth such as NMV P 158725, the elongate
form of the entoconid is evident. A remnant
of the preentocristid can be seen to join the
postmetacristid in the intervening valley.
There is a small parastylid that is lower than
the paraconid. The hypoconulid is located
immediately posterior to the entoconid, but
is not connected to the postcristid. NMV P
158724 (fig. 18.8E–H) shows moderate wear
that has exposed the dentine of each cristid.
There is a full anterior cingulid that extends

(E) anterior, and (F) lingual views. NMV P 157133, a worn left M3 or M2 shown in occlusal view
(G); NMV P 178000, proximal end of a humerus tentatively referred to the species. It is shown in (H)
top, (I) anterior, (J) anterolateral, and (K) lateral views.
Fig. 18.8. Scanning electron microscope photos of cf. *Peroryctes* sp., Large Form. NMV P 158725, a worn right m3 or m2 shown in (A) lingual, (B) anterior, (C) occlusal, and (D) labial views. NMV P 158724, a left m2 or m3 shown in (E) labial, (F) occlusal, (G) lingual, and (H) posterior views. NMV P 158722, a left m1 shown in (I) labial, (J) occlusal, and (K) lingual views.

**TABLE 18.1**

Measurements of Lower Dentitions of Cf. *Peroryctes tedfordi*

<table>
<thead>
<tr>
<th>Specimen no.</th>
<th>Tooth position</th>
<th>Maximum length</th>
<th>Trigonid length</th>
<th>Trigonid width</th>
<th>Talonid length</th>
<th>Talonid width</th>
</tr>
</thead>
<tbody>
<tr>
<td>NMV P 210911</td>
<td>m1</td>
<td>—</td>
<td>1.12</td>
<td>—</td>
<td>—</td>
<td>1.22</td>
</tr>
<tr>
<td>NMV P 157329</td>
<td>m1</td>
<td>2.09</td>
<td>1.02</td>
<td>1.08</td>
<td>—</td>
<td>1.29</td>
</tr>
<tr>
<td>NMV P 157329</td>
<td>m2</td>
<td>2.10</td>
<td>1.33</td>
<td>1.20</td>
<td>—</td>
<td>1.45</td>
</tr>
<tr>
<td>NMV P 157329</td>
<td>m3</td>
<td>2.22</td>
<td>1.39</td>
<td>1.24</td>
<td>—</td>
<td>1.33</td>
</tr>
<tr>
<td>NMV P 157136</td>
<td>m2 or m3</td>
<td>2.31</td>
<td>1.26</td>
<td>1.22</td>
<td>0.71</td>
<td>1.33</td>
</tr>
<tr>
<td>NMV P 158727</td>
<td>m2 or m3</td>
<td>2.08</td>
<td>1.39</td>
<td>1.18</td>
<td>0.66</td>
<td>1.33</td>
</tr>
<tr>
<td>NMV P 180038</td>
<td>m2 or m3</td>
<td>2.27</td>
<td>1.02</td>
<td>1.23</td>
<td>0.90</td>
<td>1.43</td>
</tr>
<tr>
<td>NMV P 210912</td>
<td>m2 or m3</td>
<td>2.48</td>
<td>1.12</td>
<td>1.16</td>
<td>0.86</td>
<td>1.53</td>
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<tr>
<td>NMV P 210975</td>
<td>m2 or m3</td>
<td>2.59</td>
<td>1.33</td>
<td>1.20</td>
<td>0.78</td>
<td>1.37</td>
</tr>
<tr>
<td>NMV P 157138</td>
<td>m2 or m3</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1.37</td>
</tr>
<tr>
<td>NMV P 158721</td>
<td>m2 or m3</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1.37</td>
</tr>
<tr>
<td>NMV P 210914</td>
<td>m2 or m3</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>1.39</td>
</tr>
</tbody>
</table>
labially from the parastylid to the base of the protoconid. NMV P 158725 (fig. 18.8A–D) is worn down to the base of both trigonid and talonid basins with protoconid, metaconid, and entoconid reduced to about half of the original height. In spite of this wear, the elongate form of the entoconid is evident, and a remnant of the preentocristid can be seen to join the postmetacristid.

NMV P 178002 is the lingual side of a right horizontal ramus fragment that can be only tentatively assigned to cf. **Peroryctes**, large form. The lingual side and lingual alveolar border are the only preserved natural edges. The fragment measures 7.3 mm long by 3.7 mm deep. There are 5+ alveoli, presumably for p3, m1, and m2. The posterior alveolus of the m2 is just a small portion of its anterior side.

Only one complete and two partial upper molars have been recognized. NMV P 54039, a complete right M1 (fig. 18.9A–E) of maximum length 3.56 mm and maximum width 2.25 mm, falls outside the range of size of the upper teeth of cf. **Peroryctes tedfordi** (table 18.4) but overlaps **Peroryctes longicauda**, **Microperoryctes longicauda dorsalis**, and **Echimypera kalabu** (table 18.5). The large protocone is located on the anterolingual corner of the tooth. It has cristae leading to the paraconule and metaconule, the latter being the more developed of the two (fig. 18.9B, C, E) although it is small and the ridge to the base of the metacone is
Fig. 18.9. Scanning electron microscope photos. NMV P 54039, right M1 of cf. *Peroryctes* sp., Large Form, shown in (A) labial, (B) posterior, (C) occlusal, (D) anterior, and (E) lingual views. Note that in C and E, the postparacrista and premetacrista almost meet in the cleft between stylar cusps C.
weak. Protocone and paracone are located on the anterior edge of the tooth. The paracone is smaller than the protocone or metacone and is located on the labial half of the tooth. The stylar shelf is narrow anteriorly, widens posteriorly, and there is a tight, shallow ectoflexus cleft between stylar cusps C and D. A crista joins the paracone to the laterally compressed stylar cusp B to form a continuous cleft that extends back to the usual position of cusp C. The M1 of *P. bougainville* is similar but the paracone and cusp B are less compressed and retain their identities. Wear has breached the enamel of cusps C and D and the metastyle. There is a weak cleft labially behind cusp D, which suggests that there may have been a small stylar cusp E fused with the metastyle.

The metacone has a prominent postmetacrista that extends straight to the metastyle. This is similar to but more extreme than in *P. bougainville*. A low premetacrista connects the metacone to a cuspule (D₁) at the base of stylar cusp D. Stylar cusp D is round in cross section and stands slightly lower than the metacone and is joined by a low ridge to a small stylar cusp E. There is a large anteriorly projecting parastyle on the anteroexternal corner of the tooth, lower than the apex of the paracone. It is similar to, but more compressed laterally than in *P. bougainville*. The metastyle is low and shelf-like. All the crests are worn into the dentine.

The postparacrista and the premetacrista weaken as they approach the stylar shelf, where they nearly meet at the labial side of the cleft between cusps C and D. This feature approaches the usual dasyurid-like condition of molars of *Yarala burchfieldi* (Muirhead and Filan, 1995), where those crests meet well lingual on the stylar shelf. It has cristae leading to the paraconule and metaconule, the latter cusp being more developed (fig. 18.9A, C–E).

In the NMV P 158719 partial trigon, the parastyle is more completely fused with cusp B than in NMV P 54039. The anterior cingulum is represented by an oval cuspule located on the lingual side of the parastyle. There is no crista extending from the mid-point of the preparacrista to the anterior edge of stylar cusp C as there is in *P. bougainville*. The postparacrista extends to the rear side of stylar cusp C. The NMV P 180040 molar fragment includes the metacone, metastyle, and stylar cusp D. The last is a low, conical cusp with a strong crest from its tip that connects to the metacone.

**DISCUSSION:** This large species from the Hamilton fauna differs from *cf. Peroryctes tedfordi* primarily in size, but there is insufficient material currently available to describe another species. The peramelemorphians from the Hamilton fauna are unusual because the two species are similar morphologically except for size. In most of Australia, the living sympatric species of peramelids are quite different both in morphology and size. Possibly, at least for bandicoots, niche partitioning was achieved first by size differentiation, followed by morphologic change.

**DIPROTODONTA**

**FAMILY PHALANGERIDAE**

Genus *Strigocuscus*

*Strigocuscus notialis* Flannery et al., 1987


*Phalanger or Trichosurus* or an unnamed related genus, Turnbull and Lundelius, 1970.

**HOLOTYPE:** NMV P 54133 (casts PM 53913 and PM 51495), a partial dentary (right horizontal ramus) with i₁, p₃, m₁–₃.

**REFERRED MATERIAL:** In addition to the type, 23 isolated teeth were available for the earlier studies (appendix). Eleven previously unreported teeth are PM 17525, partial p₃; PM 50764, three quarters of an upper molar; PM 60711, worn p₃; PM 60720, tentatively referred M₁ or M₂; NMV P 160157, right lower incisor; NMV P 162773, right p₃; NMV P 177965, very worn right lower in-
TABLE 18.3

<table>
<thead>
<tr>
<th>Specimen no.</th>
<th>Tooth position</th>
<th>Maximum length</th>
<th>Trigonid length</th>
<th>Trigonid width</th>
<th>Talonid length</th>
<th>Talonid width</th>
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<tr>
<td>NMV P 158722</td>
<td>ml</td>
<td>3.12</td>
<td>1.73</td>
<td>1.55</td>
<td>1.25</td>
<td>1.76</td>
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<tr>
<td>NMV P 54147</td>
<td>m2 or m3</td>
<td>3.31</td>
<td>1.55</td>
<td>1.70</td>
<td>1.10</td>
<td>2.10</td>
</tr>
<tr>
<td>NMV P 54182</td>
<td>m2 or m3</td>
<td>—</td>
<td>—</td>
<td>1.73</td>
<td>—</td>
<td>—</td>
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<tr>
<td>NMV P 158724</td>
<td>m2 or m3</td>
<td>3.48</td>
<td>1.62</td>
<td>1.68</td>
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<td>3.38</td>
<td>—</td>
<td>1.65</td>
<td>1.47</td>
<td>1.95</td>
</tr>
<tr>
<td>NMV P 158726</td>
<td>m2 or m3</td>
<td>—</td>
<td>1.47</td>
<td>1.70</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

DISCUSSION: The P3 of S. notialis, PM 60711, has the four central cuspules of its apical ridge deeply worn to expose the pulp cavity (fig. 18.10). It is puzzling that the expansions of the exposed pulp do not correspond well with either the ridge cuspsules or the side ridglets as might be expected. Further, the wear facet is essentially a flat truncation of the ridge and its cuspsules, not an undulating one that might be expected from the presence of the strong cuspsules. This wear strongly suggests propalinal, orthal movements if indeed wear caused the flat truncation. This wear pattern is not present in the other worn upper or lower premolars. Addition to the specific diagnosis: cuspsules and their ridgelets are relatively more massive and more evenly sized in both upper and lower teeth in this species than they are in the teeth of Trichosurus hamiltonensis.

Genus Trichosurus

Trichosurus hamiltonensis Flannery et al., 1987

Holotype: NMV P 54138 (PM 39762), right maxilla with P3, M1–4.

Referenced Material: In addition to the holotype, 62 specimens were reported in earlier studies (appendix). Five previously unreported specimens are upper molar ectoloph PM 50975, left M2 anterior loph PM 60741, and tentatively PM 50958 (anterior part of an ectoloph), PM 60713 (protoloph and cingulum), and PM 60729 (?partial hypoloph or protolophid). These increase the sample but add little to knowledge of the species.

Incertae sedis: Near Phalanger or Tricho- surus Turnbull and Lundelius 1970

Material: PM 4721–24 and 4726.

Referenced Material: Nine new indeterminate specimens, most of them considered to be near T. hamiltonensis or Strigocuscus notialis, are as follows: PM 4556, part of an unworn crest; PM 4558, posterior half of a p3 rather like Wyulda squamicaudata (FM 110919) in that the posterior end of its crest is more attenuated than in T. hamiltonensis or S. notialis, but the cuspsides of the ridge are more widely spaced than in any of the others; PM 4559, the posterior end of a premolar blade; PM 4581, left I1 (possibly a pseudocheirid); PM 4740, large worn cusp, maybe a hypocone; PM 4741, large worn bulbous cusp; PM 60756, tooth fragment; and NMV P 177948, left I2 that compares best with Dactylopsila trivirgata (FM 8363).
TABLE 18.5
Measurements of Upper Dentitions of Perameloids

<table>
<thead>
<tr>
<th>Taxon and specimen no.</th>
<th>Tooth position</th>
<th>Maximum length</th>
<th>Maximum width</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peroryctes broadbenti</td>
<td>M1 5.28</td>
<td>3.36</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M2 4.60</td>
<td>3.62</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M3 5.21</td>
<td>4.34</td>
<td></td>
</tr>
<tr>
<td>Peroryctes longicauda</td>
<td>TMM M3519</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>M1 3.94</td>
<td>2.14</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M2 5.00</td>
<td>2.96</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M3 3.44</td>
<td>2.36</td>
<td></td>
</tr>
<tr>
<td>Microperoryctes longicauda dorsalis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>FM 128356</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>M1 3.11</td>
<td>2.04</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M2 3.27</td>
<td>2.72</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M3 3.09</td>
<td>2.76</td>
<td></td>
</tr>
<tr>
<td>Echimyces kalabu</td>
<td>FM 56367</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>M1 3.91</td>
<td>3.05</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M2 3.56</td>
<td>3.58</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M3 4.52</td>
<td>4.44</td>
<td></td>
</tr>
<tr>
<td>FM 56390</td>
<td>M1 3.60</td>
<td>2.86</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M2 3.38</td>
<td>3.12</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M3 3.92</td>
<td>3.88</td>
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<tr>
<td>FM 56388 juv.</td>
<td>M1 3.94</td>
<td>3.04</td>
<td></td>
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<tr>
<td>Echimyces sp.</td>
<td>FM 121679</td>
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</tr>
<tr>
<td></td>
<td>M1 3.54</td>
<td>2.58</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M2 3.34</td>
<td>3.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>M3 3.66</td>
<td>3.24</td>
<td></td>
</tr>
</tbody>
</table>

FAMILY BURRAMYIDAE

Genus *Burramys*

*Burramys triradiatus* Turnbull et al., 1987a

*Burramys* sp. Turnbull and Lundelius, 1970.


**HOLOTYPE:** NMV P 158628, a nearly complete left lower jaw with five teeth and alveoli for the others.

**REFERRED MATERIAL:** In addition to the holotype, 62 specimens were reported in earlier studies, 59 of which are listed in the appendix. The following new specimens are now available: TMM 41265–151, anterior third of P3 with seven ridges preserved; TMM 41265–152, anterior part of P3 or p3 with seven cusps and ridges preserved; TMM 41265–153, posterior part of P3 or p3 with six cusps and ridges preserved; TMM 41265–154, posterior third of P3 or p3 with five cusps and ridges preserved; TMM 41265–159.1–159.16, molar fragments; TMM 41265–163, anterior quarter of p3 with four cusps and ridges preserved; TMM 41265–171, anterior quarter of P3 or p3 with edge and five ridges preserved; TMM 41265–174, I1; TMM 41265–189.1–189.34, fragments of P3 or p3; PM 4716, m1 fragment that consists of the high anterior portion that contacts and “continues” the crest of the premolar blade; PM 16827, unworn complete left P4;

![Fig. 18.10](image_url)  
Scaled, camera lucida drawings of PM 60711, a worn right P3 of *Strigocuscus notialis* shown in labial (A), occlusal (B), and lingual (C) views. The wear pattern is atypical and unexpected: the cusps of the serrated blade are truncated to a planar surface without undulations. The pulp cavity is extensively exposed with no sign of any secondary dentine. The configuration of the pulp does not conform neatly to the presence of the cusps or lingual and labial ridges associated with them.
PM 60750, posterior two-thirds of a left p3; NMV P 210935, unworn complete right p3; NMV P 210983, lower incisor in two pieces (A, B); NMV P 210984, part of the root and base of crowns of right lower incisor.

Discussion: The new material does not add appreciably to our knowledge of the morphology of the taxon. However, some of the new material does show aspects of wear that were not reported earlier. TMM 41265–152 shows wear on one side of the three posterior ridges. No striae can be seen on these surfaces. TMM 41265–154 shows wear on one side of the last posterior “cusp”. This is a flat surface with traces of vertically oriented striae. PM 16830 is a more heavily worn tooth with a wear facet that unites the bases of the facets of the last four lateral ridges into one irregularly shaped planar surface with fine vertical striae. This differs from the horizontally oriented stria noted by Krause (1982) on the plagiaulacoid teeth of the multituberculate *Ptilodus*. This specimen also appears to have lost chips from the apices of three cusps. TMM 41265–151 shows heavy wear on the apices of the first three cusps.

Ride et al. (1997) described wear conditions for the sectorial premolars of *Propleopus oscillans* wherein wear is shown to begin at the tips of the lateral ridges (their figs. 5A, B and 13A). With further wear, the ridge facets grow wider and fuse, obliterating the ridges. Our worn *B. triradiatus* specimens, PM 16830 and TMM 41265–152–154, differ from *P. oscillans* in that wear on them is initially confined to the sides of the ridges, and only reaches to the tips at the crest as the facet becomes more deeply worn. These apparent differences in the orientation of the striae on the wear surfaces of the plagiaulacoid premolars of *Burraramys* and *Ptilodus* raise interesting questions about possible differences in masticatory movements and function in these two taxa.

Ride and Davis (1997) concluded that the present distribution of *B. parvus* in the high mountain heath (Calaby et al., 1971; Dixon, 1971; Dimple and Calaby, 1972; Gullan and Norris, 1984) indicated a very narrow environmental tolerance. However the Pleistocene distribution of *B. parvus* was wider than is presently the case (Ride, 1960; Wakefield, 1960a, 1960b, 1967, 1972; Hope, 1982; Broom and Mansergh, 1989; Ride et al., 1989). An analysis of Pleistocene occurrences by Broom and Mansergh (1989) indicates that those localities lay at elevations between the permanent snow line and tree line during the Pleistocene glacial stages. Several authors (Flood, 1980; Hope, 1982; Caughley, 1986) have suggested that the occurrence of *Burraramys parvus* in a fossil fauna might indicate periglacial conditions. Clearly this is not the case for either *B. triradiatus* or the Riversleigh *Burraramys* species, since they are associated with species whose close living relatives are temperate and tropical rain forest species (Turnbull and Lundelius, 1970; Flannery et al., 1992). Hence it appears that not only were the tolerance limits of the various pre-Pleistocene species of *Burraramys* quite different from those of *Burraramys parvus*, but that the modern species and its Pleistocene ancestors had adapted to the harshest of environments. Probably their ability to store fat and to hibernate is a key factor in their survival (Broom and Mansergh, 1989). What triggered this shift is unclear.

**Family Pseudechiridae**

**Genus Pseudokoala**

*Pseudokoala erlita* Turnbull and Lundelius 1970

*Pseudokoala erlita* Turnbull et al., 1987b.

**HoloType**: NMV P 26399 and 26400 (M3 and M4) shown to be adjacent teeth from the same mouth by the concordance of their interdental wear facets.

**Referred Specimens**: In addition to the type, 29 specimens were reported in previous studies (appendix). Three newly identified specimens (PM 4580, premolar or molar fragment, PM 60744, left lower molar labial fragment, and NMV P 177977, anterolingual corner of a left p3) do not add to our knowledge of the species.

**Genus Petauroides**

*Petauroides stirtoni* (near *P. volans minor*)


*Petauroides stirtoni* Archer, 1984 (generic reassignment).

*Pseudocheirus stirtoni* Turnbull et al., 1987b.
HOLOTYPE: NMV P 26401–04, left m1–4.

REFERRED MATERIAL: In addition to the type and previously reported specimens (appendix) there are the following new specimens: PM 4455, right m1; PM 4752, right talonid of m1, m2, or m3; PM 50984, left I1; TMM 41265–155, posterior half of right upper molar; TMM 41265–156, anterior two-thirds of a right? M4; TMM 41265–157, anterior three-fourths of a right upper molar; TMM 41265–160, anterior half of left upper molar; TMM 41265–161, anterior three-fourths of a right m2 or m3; TMM 41265–162, complete left? M3; TMM 41265–164, right upper molar lacking protocone; TMM 41265–165, three-fourths of left upper molar; TMM 41265–169, posterior two-thirds of a right upper molar; TMM 41265–170, anterior half right m1; TMM 41265–176, left talonid; TMM 41265–181, most of left m1; TMM 41265–184, anterior half right m1; TMM 41265–188, three-fourths left m1; NMV P 210917, right m2 or m3; NMV P 210918 and 210919, left and right M1. Cf. Petauroides stirtoni: TMM 41265–168, right lower incisor; TMM 41265–178,? P1; TMM 41265–185, anterolabial third of upper molar; TMM 41265–186 posterior two-thirds left molar; TMM 41265–187 labial right upper molar half; NMV P 166247A, complete left m1; NMV P 210921, complete right M2; NMV P 210978, complete left m1.

DISCUSSION: In the original description of Pseudocheirus stirtoni, its Petauroides-like attributes were noted. Its dental morphology is intermediate between Pseudocheirus and Petauroides (Turnbull and Lundelius 1970: 40). Because of this and because the most striking feature of Schoinobates [Petauroides], the gliding membrane, cannot be demonstrated, it was conservatively assigned to Pseudocheirus. The strongest argument for assignment to Petauroides is the change in tooth proportions from p3 to m4 (P/4–M/3 in previous terminology) as can be seen in graph E of Turnbull and Lundelius (1970).

The Hamilton species fits the Petauroides pattern more closely than that of any of the subgenera of Pseudocheirus (Petropseudes, Pseudocheirops, Pseudocheirus, or Hemibelideus) although several species of P. (Pseudocheirus) also have a somewhat similar pattern of tooth proportions. However Petauroides stirtoni and Petauroides volans are similar to Pseudocheirops archeri in having strong entostylids and multiple small cristids (crenulations) on the lower molars, as well as most of the other features described for P. archeri (Archer, 1984: fig. 186 caption).

Archer (1984: 712, 714) reinterpreted the 1970 data, was convinced that P. stirtoni was a glider, and transferred it from Pseudocheirus to Petauroides. Bassarova and Archer (1999: 25–26, in Archer et al., 1999) continued that allocation, and went further to include Pseudocheirus marshalli in Petauroides. We retain the reassignment of P. stirtoni to Petauroides and find it closest to P. volans minor.

Genus Pseudocheirus

Pseudocheirus marshalli Turnbull and Lundelius, 1970

Pseudocheirus marshalli Turnbull et al., 1987b.

Petauroides marshalli Bassarova and Archer, 1999; reassignment from Pseudocheirus.

HOLOTYPE: NMV P 26405, left M1 (casts PM 4481 and 4490).

REFERRED MATERIAL: In addition to the type and the specimens listed in previous studies (appendix), eight new specimens are tentatively assigned to this taxon: NMV P 210920, 210922, 210979, three M1; NMV P 210918 and 210919, left and right M1. Cf. Petauroides stirtoni: TMM 41265–168, right lower incisor; TMM 41265–178,? P1; TMM 41265–185, anterolabial third of upper molar; TMM 41265–186 posterior two-thirds left molar; TMM 41265–187 labial right upper molar half; NMV P 166247A, complete left m1; NMV P 210921, complete right M2; NMV P 210978, complete left m1.

Indet. Pseudocheirids (near Petauroides stirtoni or Pseudocheirus marshalli)


Pseudocheirus sp. Indet. Turnbull et al., 1987b; of 41 specimens initially included only NMV P 26415 and PM 4472 were specified (appendix).

REFERRED MATERIAL: New materials include PM 50922 and 50923, unerupted I3s.

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4 G.M. McKay (1982) and later, C.P. Groves (1993: 58) have shown Petauroides, not Schoinobates, to be the proper name for the great glider, the latter having been used for a placental glider.
of a pseudocheirid, or possibly a petaurid. Both teeth are strongly convex buccally and gently concave lingually with a weak longitudinal buttress near the tip; cross-sectional shape near the base is asymmetrical with the anterior side thicker than the posterior. Other materials are PM 60723, left upper molar protocone; TMM 41265–166, anterior part of the ectoloph of an upper molar; NMV P 54052, most of the ventrolateral half of a lower incisor (possibly a large petaurid); NMV P 177965, worn right i1; NMV P 210929, three-fourths of a left? M3; NMV P 210930, posterior part of a right m2 or m3; NMV P 210932, anterior half of a right m2 or m3; NMV P 210933, tooth fragment (possibly a phalangerid); NMV P 210957, buccal part of a left lower molar, notable for its lateral wear facets; NMV P 210958, labial side of m2, m3, or m4; NMV P 210984, most of root and base of i1 crown; NMV P 210997, anterior third of right lower molar; NMV P 210998, anterolingual third of a left? M1.

**DISCUSSION:** Bassarova and Archer (1999) followed Archer (1984) in assigning *Pseudocheirus stirtoni* to *Petauroides* and included *Pseudocheirus marshalli* in that genus. We do not see many *Petauroides* features in *P. marshalli* and question that reassignment.

Dawson et al. (1999) assigned a Wellington Caves Big Sink specimen to *Pseudocheirus stirtoni*. Bassarova and Archer (1999: 26) concluded that there are “no pre-Pleistocene records for *Pseudocheirus, Pseudocheirulus* or *Hemibelideus.*” With *P. marshalli* remaining within the genus *Pseudocheirus*, rather than being transferred to *Petauroides*, that argument fails.

Woodburne et al. (1987) considered the Miocene *Paljara kitaenias* to possess the most plesiomorphic dental morphology of any known fossil or living pseudocheirid. *Petauroides stirtoni* and to a lesser extent *Pseudocheirus marshalli* show some of the features they listed as indicative of a plesiomorphic condition: (1) large paraconid present on m2 in both species; (2) cristid obliqua connects to the metaconid on m1 (as a probable intermediate stage, in both species it connects to the metastylid, which in turn is connected to the metaconid); (3) entoconid not connected to the metastylid by a continuous crest in m2–4 and teeth do not overlap one another *en echelon* (again both are intermediate in that, although they do not have a continuous crest, they do overlap *en echelon*); (4) postprotocristid and cristid obliqua meet as a continuous crest in m2–4 in both of the Hamilton species.

Thus both *Petauroides stirtoni* and *Pseudocheirus marshalli* are seen to be less derived than most Plio-Pleistocene and Recent pseudocheirids, but not as plesiomorphic as the older Oligocene and Miocene species.

Miscellaneous tooth and bone fragments, possibly pseudocheirid, are listed in the appendix.

**FAMILY PETAURIDAE**

Genus *Petaurus*

*Petaurus* sp. (near *P. norfolkensis* and *P. australis*) Turnbull et al., 1987a.

**REFERRED MATERIAL:** In addition to material previously reported (appendix) only two new specimens are tentatively referred: NMV P 166247C, a right lower incisor, near *P. breviceps* in both size and its fully rounded cross-sectional form; NMV P 179555, posterior half of upper molar (previously no upper tooth had been recognized in the Hamilton Fauna).

**DISCUSSION:** In 1970, no petaurids were identified in the Hamilton collections, but nine teeth recognized in Turnbull et al. (1987). These were considered to represent two species, one near *P. norfolkensis* (referred to as cf. *P. norfolkensis* in figs. 2, 5), the other near *P. australis* (referred to as cf. *P. australis*, fig. 3A). It should be noted that although the two-species interpretation is the most probable, there could be as many as three, or as few as one highly variable species. None of the fossil specimens plotted within the ranges of the small samples of the living species then available, which suggests that they differ from any living form.

**FAMILY EKTOPODONTIDAE**

Genus *Darcius*

*Darcius duggani* Rich 1986

**MATERIAL:** This genus and species is based on its holotype, NMV P 54185, and paratype
NMV P 54184 (probably part of holotype), and five isolated teeth (appendix), all well described and illustrated by Rich (1986).

**REferred MATERIAL:** The following new material is now available: NMV P 54013, cf. *D. duggani*, molar fragment; NMV P 54034, nearly complete upper molar; NMV P 54151, molar fragment; NMV P 54164, molar fragment (may go with 54151); NMV P 158451, tooth fragment; NMV P 167854, tentatively referred worn left lower incisor; PM 39852 three-fourths of molar (T.H.R. #1979-o); PM 60725, molar fragment; PM 4582, indeterminate worn tooth fragment, possibly *D. duggani*.

**DESCRIPTION:** The heavily worn lower incisor, NMV P 167854, has a gently curved, concave up form when viewed from the side. It is narrow, and has enamel covering the ventrolateral side of the crown, but only a thin band on the anteromedial side. Much of the crown appears to have been worn away, so that dorsally wear has extended beyond any enamel, onto the tapered root. The preserved portion measures 2.68 cm long, by 3.0 mm maximum width, by 5.5 mm maximum depth.

**FAMILY VOMBATIDAE**

Genus and species indet.

One specimen, NMV P 178072, is tentatively assigned. It is only a fragment of the side of one lobe of a wombat molar. Its curvature is similar to that of an upper molar. The preserved portion is 2.65 cm long by a nearly uniform width of 0.5 cm.

**DISCUSSION OF THE HAMILTON FAUNA IN THE LIGHT OF NEW MATERIAL**

The Hamilton dasyurid remains are not sufficiently well represented to enable their phylogenetic or palaeobiogeographic significance to be determined with confidence. Wroe (1999) has made the point that taxa such as *Ankotarinja tirarensis* Archer, 1976, previously regarded to indicate at least a late Oligocene age for the family, lack unambiguous dasyurid synapomorphies. Consequently, the oldest known undoubted dasyurid is the early to middle Miocene *Barinya wanga*, representing a monotypic subfamily. Because of the abundance of small carnivorous marsupials known from the late Oligocene to late Miocene of Riversleigh, mostly archaic Miocene peramelemorphians and thylacinids, and the corresponding rarity of dasyurids in these assemblages, Wroe (1999) and Muirhead and Filan (1995) concluded that the radiation of modern subfamilial groups in this family may have been a relatively recent event, possibly no earlier than the late Miocene. Whether the rise in diversity of dasyurids opportunistically followed or in some way caused the corresponding declines in yaraloids and thylacinids is not clear. Occurrence of *Antechinus* species in the early Pliocene Hamilton Local Fauna may well represent the earliest appearance of species of this otherwise diverse modern genus. That this Hamilton taxon should show at least some superficial affinities with contemporary New Guinean taxa is perhaps not surprising if the latter are descendants of a late Miocene to early Pliocene invasion of New Guinea by Australian taxa, a late Cainozoic event for which there is some biomolecular evidence (Aplin et al., 1993).

Systematic allocation of relatively plesiomorphic peramelemorphians is difficult because of increasing controversy about the phylogenetic relationships of bandicoots to other groups of marsupials. Although traditionally regarded to be most closely related to dasyuromorphians (e.g., Bensley, 1903), disquiet about this view has been expressed by some morphologists (e.g., Archer, 1976b) and more recently by some molecular systematists such as Kirsch et al. (1997) who regard peramelemorphians to be possibly outside of all other Australian marsupials.

Muirhead (2000) distinguishes *Yarala burchfieldi* as the first-named member of a distinct family (Yaralidae) and superfamily (Yaraloidea) of peramelemorphians, most species of which have yet to be described from the Oligo-Miocene deposits of Riversleigh and central Australia. Yaraloids are distinguished from all other peramelemorphians by a combination of mostly plesiomorphic features such as the continuous centrocrista of the upper molars, vestigial to absent metaconules and relatively labial position in which the cristid obliquis intersect.
the trigonid, as well as several cranial features including a distinctive alisphenoid/parietal suture on the sidewall of the braincase. Although *Y. burchfieldi* is clearly more plesiomorphic than other named peramelemorphians, all of which are united by synapomorphies absent in this taxon, the monophyly of forms currently anticipated to be yaraloids has yet to be demonstrated.

Muirhead and Filan (1995) argued that relatively plesiomorphic living peramelemorphians such as peroryctids had a preentocristid blade with a carnassial notch between it and the distinct postmetacristid. In modern peramelids, this blade and the notch are reduced or lost. Although this feature clearly varies in other groups of marsupials, as summarized by Muirhead and Filan (1995), it is the reason we have chosen here to tentatively refer the Hamilton taxon to *Peroryctes* rather than another genus of peramelids.

The Hamilton taxa are clearly more derived than yaraloids mainly because of their breached centrocrista, a diagnostic synapomorphy for perameloids. It also appears to have what may be an autapomorphic form of the entoconid insofar as this cusp, although round at the base, becomes transversely compressed towards its tip. However, because it also has some arguably plesiomorphic peramelomorphian features (see Muirhead, 2000) such as a relatively buccal position of the anterior end of the cristid obliqua, preentocristid blade with a notch between it and the postmetacrista, and postparacrista with relatively limited buccal development compared with that seen in most perameloids, it is possible that this taxon represents a plesiomorphic group of perameloids structurally annec tant between the latter and yaraloids. Given the total absence to date of perameloids from pre-Pliocene deposits and total dominance of the same deposits by yaraloids, annec tant taxa should eventually turn up somewhere in the late Miocene. Cf. *Peroryctes tedfordi*, and possibly its larger but morphologically similar Hamilton congenor, may represent late survivors of such a group.

The new materials of most of the other taxa add little. Wear conditions of the premolar blades of *Strigocuscus notialis* and *Burramys triradiatus* add information that relates to masticatory function in both species. The presence of *Burramys triradiatus* in a rain forest assemblage raises the question as to when and where some species of this genus made the shift to the alpine conditions under which the modern species lives.

**CONCLUSIONS**

The preservation and distribution of the fossils in the Grange Burn deposit have been discussed only superficially. A very large proportion of the fossils is only enamel caps of teeth. Bone is uncommon and tends to occur in patches. This may reflect the chemical environment of the sediment, which is a fossil soil (Gill, 1957). It is likely that the soil-forming processes dissolved much of the bone. The enamel, being less porous and more heavily mineralized, seems to have been more resistant. Many of the teeth show no wear and could be interpreted as either unerupted or newly erupted teeth with unformed roots. Although the enamel shows no pitting or other solution features, the bone generally shows some evidence of dissolution, having usually lost the dense outer surface. These features are consistent with burial in an active soil.

Although no detailed records are available, it is clear that the fossils were not distributed evenly through the deposit but occurred in local concentrations. In a few concentrations, bone is better preserved than in others, suggesting differences in the chemical environment in these locations. The implications of this are not clear but do indicate that more, and perhaps better, material may be recovered with further excavation.

The new material confirms our previous interpretation of the paleoecology of the locality. As pointed out in earlier studies (Turnbull and Lundelius, 1970; Archer, 1984; Flannery et al., 1992), the closest living relatives of the taxa represented are found today in rain forests.

The Hamilton fauna is now known to contain at least 28 taxa of marsupials. There is at least one representative of each of the families Burramyidae, Petauridae, Ektopodontidae, and Vombatidae. The Dasyuridae and Peramelidae each have two or more species. The Phalangeridae and Diprotodontidae each have two genera and species, the Pseudo-
chiridae three genera and species, the Macropondae 13 genera (3 Potoroinae, 8 Macropondinae, 2 Stenuraninae). In 1970, we reported a single microchiropteran tooth, but here note that it may be modern because its preservation differs from that of most of the other specimens. Despite considerable additional collecting since the last faunal report, no rodent material has been recovered. Possibly rodents had not yet colonized this area of Australia at the time of deposition of the Hamilton unit.

Other unreported vertebrate remains include pavement teeth of fish, and frog and lizard bones and teeth. In addition to possible insect egg cases, there are a few beetle elytra, a few small gastropods and other invertebrates, and many plant fragments. The diversity of the Hamilton fauna and flora, with its precise date, makes it one of the more significant fossil faunas in Australia.

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**APPENDIX**

**HOLOTYPES AND REFERRED MATERIAL**

*Strigocuscus notialis* Flannery, Turnbull, Rich, and Lundelius, 1987: Holotype: NMV P 54133 (PM 51495, PM 53913), right horizontal ramus with i1, p3, m1–3. PM 4457, 4555, 4571, 4728, 4735, NMV P 26407 (PM 4554), 54005 (PM 51492), 54038 (PM 53910), 54064, 54197 (PM 51493), 158403, 158435 (PM 60763), 54064, 54077, 54083 (PM 53911), 54197 (PM 51493), 158430, 158435 (PM 60763), 173401–04 (PM 51497, 51494, 53912), 177949–50, 177984, 178076, 178078.
Trichosurus hamiltonensis Flannery, Turnbull, Rich, and Lundelius, 1987: Holotype: NMV P 54047 (PM 51505), right maxilla with P3, M1±4. PM 4571, 4726, 4728, 16836, 50962, NMV P 54047 (PM 51505), 54065 (PM 51500), 54079 (PM 51501), 54080, 54089 (PM 51502), 54098 (PM 51506), 54103, 54125±26, 54132 (PM 51409, 53914), 54158 (PM 60762), 54166 (PM 51507), 54170 (PM 51499), 173405 (PM 51508), 173406, 173407 (PM 51498), 177946, 177952, 180066–67 (PM 51503).


Petaurus sp. (near P. norfolkensis, P. australis): PM 17519, 17536, 50766, 50921, NMV P 180026–30 (cast PM 53915–19).