A review of macropodoid (Marsupialia) systematics with the inclusion of a new family

B.P. KEAR & B.N. COOKE


A review of higher level macropodoid systematics is presented. The origins and monophyly of Macropodoidea are reviewed, as are hypotheses on inter/intra-relationships of each of the major families and subfamilies. Revised taxonomic arrangement includes an additional family, Balbaridae (Cooke & Kear, 1999), which incorporates the existing Balbarinae Flannery, Archer & Plane, 1983 and the new subfamily Nambarinae n. subfam. Genera included within Balbaridae and Bulungamayinae are amended.

B.P. Kear (kear.ben@sa.gov.au), South Australian Museum, North Terrace, Adelaide, South Australia, 5000; B.N. Cooke, School of Natural Resource Sciences, Queensland University of Technology, GPO Box 2434, Brisbane, Queensland, 4001. Received 3 June 2000

Keywords: Marsupialia, Macropodoidea, systematics, new taxa, phylogeny.

The recent discovery and assessment of near complete fossil material representing members of the Oligocene-Miocene macropodoid subfamilies Balbarinae (sensu Flannery 1989) and Bulungamayinae has prompted a review of macropodoid systematics and a reevaluation of many Oligocene-Miocene macropodoid taxa. Balbarinae was first erected by Flannery et al. (1983) for a group of extinct medium-sized macropodoids of late Oligocene to late-middle Miocene age. Bulungamayinae, also described by Flannery et al. (1983), comprises a group of small to large extinct macropodoids from the late Oligocene to early-late Miocene.

Archer (1984) and Flannery (1989) concluded that balbarines were the ancestor or sister-group of macropodids and bulungamayines the derived sister-group of potoroids. This was in the context of a two family subdivision of Macropodoidea: Potoroidae (subfamilies Palaeopotoroinae, Hypsipyrrnomodontinae, Potoroinae, Bulungamayinae) and Macropodidae (subfamilies Balbarinae, Sthenurinae, Macropodinae). However, more recent reviews of Cooke (1997a) and Cooke & Kear (1999), propose a revision with balbarines representing the plesiomorphic sister-group of all other macropodoids and bulungamayines the sister-group of macropodids (suggested by Case 1984; Woodburne 1984; Cooke 1997d, 1997e, 1999; Kear et al. this volume). This prompts a four family division of Macropodoidea into Balbaridae (subfamilies Nambarinae n. subfam. and Balbarinae), Hypsipyrrnomontidae (subfamilies Hypsipyrrnomontinae and Propleopinae sensu Ride 1993), Potoroidae (subfamily Potoroinae only, sensu Cooke 1997a; Cooke & Kear 1999; Kear et al. this volume) and Macropodidae (subfamilies Bulungamayinae, Sthenurinae and Macropodinae, sensu Cooke 1997a; Cooke & Kear 1999; Kear et al. this volume).

This paper presents a revised hierarchy of the subfamilies Balbarinae and Bulungamayinae within a systematic review of all macropodoid subdivisions to subgenus level. Published assessments from molecular, chromosomal and morphological character systems are included and lists of potential morphological synapomorphies given for major taxa. Preliminary diagnoses of Balbaridae and Nambarinae are also provided.


A REVISED CLASSIFICATION OF MACROPODOIDEA

Systematic methodology

The classification presented here (Table 1) has been constructed to reflect the current understanding of macropodoid phylogenetics and includes all genera described to date. Hierarchical
Suborder PHALANGERIDA Aplin & Archer, 1987
Superfamily TARSIPEDOIDEA (Gervis & Verreaux, 1842)
Superfamily PETAUROIDEA (Gill, 1872)
Superfamily BURRAMYOIDEA (Broom, 1898)
Superfamily PHALANGEROIDEA (Thomas, 1888)
Superfamily MACROPODOIDEA (Gray, 1821)
Family Balbaridae (Flannery, Archer & Plane, 1983)
Subfamily indet.
  Galanarla Flannery, Archer & Plane, 1983
Subfamily Nambarinae n. subfam.
  Nambaroo Flannery & Rich, 1986
  Wururoo Cooke, 1997
  Gunawamaya Cooke, 1992
Subfamily Balbarinae Flannery, Archer & Plane, 1983
  Balbaroo Flannery, Archer & Plane, 1983
Family Hypsiprymnodontidae (Collett, 1887)
Subfamily Propleopinae Archer & Flannery, 1985
  Ekaltadeta Archer & Flannery, 1985
  Jackmahoneya Ride, 1993
  Propleopus Longman, 1924
Subfamily Hypsiprymnodontinae Collett, 1887
  Hypsiprymnodon Ramsay, 1876
Family Potoroidae (Gray, 1821)
Subfamily Potoroinae (Gray, 1821)
Tribe indet.
  Kyeema Case, in press (cited, Woodburne et al., 1993)
Tribe Potoroini Trouessart, 1898
  Potorous (Kerr, 1792)
  Tribe Bettongini Flannery & Archer, 1987
  Bettongia (Desmarest, 1822)
  Borungaboodie Prideaux, 1999
  Caloprymnus (Gould, 1843)
  Milliyowi Flannery, Rich, Turnbull & Lundelius, 1992
  Aepyprymnus (Gray, 1837)

Table 1. Hierarchical classification of macropodoids modified according to Cooke (1997a, 1997c), and Cooke & Kear (1999). ‘Possum’ superfamilies Phalangeroidea, Burramyoidae, Petauroidea and Tarsipedoidea are included to provide perspective on macropodoid origins and higher level taxonomic relationships. Superscripts Sm = sedis mutabilis; In = incertae sedis.

arrangement follows the methods of Aplin & Archer (1987) in which no single character system determines position unless where (i) fossil taxa are established on limited material or (ii) there is no contradiction made by analyses of other character systems. Where contradicting phylogenetic interpretations occur, the best supported hypothesis is used.

Sister-group relationships are presented in a ‘ranked’ format, again following Aplin & Archer (1987). Poorly understood phylogenetic relationships of taxonomic units are expressed as sedis mutabilis (for unresolved polytomies with changeable position) or incertae sedis (for taxa of doubtful positioning within the hierarchy or questionable monophyly).

Revised positioning of balbarine and bulungamayine taxa and designation of Balbaridae and Nambarinae is derived via cladistic analyses (Cooke 1997a, 1997b; Kear 1998; Kear et al. this volume). Reconstruction of superfamilies follows Aplin & Archer (1987), family to subgenus level arrangements are modified from Flannery (1989) according to review consensus. Areas of controversy are discussed in the text.
1. $P^1$ lost\(^{1,2,4}\)
2. $P^2$ large and finely ridged\(^{1,2,4}\)
3. $P^3$ with ridgelets extending up the entire height of the crown, (lost in some derived taxa)\(^{1,2,4}\)
4. $dP^3$ with distinct hypocone\(^{1,4}\)
5. Masseteric canal opens into dental canal of mandible\(^{1,2,4}\)
6. Postglenoid process hollow, downward pointing projection of squamosal (postglenoid process may be absent in some plesiomorphic macropodoids, e.g. species of *Potorous* and *Hypsiprymnodon*)\(^4\)
7. Stepped calcaneum-cuboid face\(^{1,3,2,4,5}\)
8. Astragalus-tibia articulation saddle-shaped with prominent troclear crests\(^{4,5}\)
9. Astragalus-calcaneum articulation modified to restrict movement, being medially pinched, divided or fused\(^{2,4}\)
10. Mesocuneiform not in contact with navicular\(^5\)
11. Tibia and fibula in contact along \(\frac{1}{3}-\frac{2}{3}\) of their distal length (secondarily lost in members of the genus *Dendrolagus*)\(^{1,2,4}\)

**Table 2. Potential morphological synapomorphies uniting Macropodoidea (after Archer 1984; Flannery 1982\(^{4}\), 1984\(^{4}\), 1987\(^{4}\); Kear et al., this volume\(^5\)).**

**SYSTEMATIC PALAEONTOLOGY**

**Superfamily MACROPOODOIDEA Grey, 1821**

**Family BALBARIDAE (Flannery, Archer & Plane, 1983)**

**Familial diagnosis.** Molars lophodont and brachydont with hypolophid formed by lingually displaced component of posthypocrystid linked to a buccal crest from the entoconid; hypocingulid present on lower molars; $M_1$ protolophid markedly compressed with 'forelink' absent; $I_1$ with lingual and dorsal enamel ridgelets; $P_3$ with posterobuccal cusp (may not be present in all taxa). Frontal sinus of skull markedly inflated; postorbital portion of skull laterally constricted; hypertrophied mastoid processes; absence of auditory bulla formed by an inflated tympanic wing of the alisphenoid.

**Subfamily NAMBARINAE n. subfam.**

**Subfamilial diagnosis.** Posterior positioning of the digastric eminence; $I_1$ occlusal surface lying below the molar occlusal plane.

**SYSTEMATIC REVIEW OF SUPERFAMILY MACROPOODOIDEA**

**Macropodoid monophyly and origins**

Macropodoid monophyly is supported by molecular/chromosomal evidence and morphological synapomorphies. Molecular and chromosomal data include amino-acid sequences (Air et al. 1971), enzyme serum compatibility (Kirsch 1977), chromosomal number and morphology (Sharman 1961; Rofe 1978) and mitochondrial DNA (Kirsch et al. 1997; Burk et al. 1998). Morphological evidence has been reviewed by several authors (e.g. Archer 1984; Flannery 1982, 1984, 1987). Potential morphological synapomorphies for Macropodoidea are listed in Table 2.

Suggested macropodoid sister-taxa include: a tribosphenic form such as microbiotheres (Ride 1971, 1993); wynyardiids (Rich & Archer 1979); phalangeriforms including phalangerids (Kirsch 1977; Archer 1984; Flannery 1987; Aplin & Archer 1987; Flannery 1987; Springer & Woodburne 1989; Szalay 1994) and burramyids (Broom 1896; Wroe et al. 1998).

Ride (1971) proposed a tribosphenic origin for Macropodoidea on the basis of premolar/molar cusp homology between plesiomorphic macropodoids, particularly *Dorcopoides fossilis*, and tribosphenic mammals. Ride (1993) reiterated this conclusion, citing as further evidence the molar morphology of propleopines and hypsiprymnodontines. However, this arrangement implies convergence between both macropodoids and diprotodontian marsupials (in diprotodonty) and between macropodoids and peramelemorphians (in syndactyly).

Archer & Bartholomai (1978) and Bartholomai (1978) suggested that wynyardiids and macropodoids may share a common ancestor, a conclusion also reached by Rich & Archer (1979) based on their assessment of the Miocene wynyardiid *Namilamadeta sniderii*. This taxon possesses many kangaroo-like features including: $P^1$ bearing strong buccal groove; $P^3$ long and sectorial; enlarged masseteric process on maxilla; and most significantly, styal cusps situated at the ends of the transverse lophs (considered present in plesiomorphic macropodoids such as hypsiprymnodontines, propleopines and balbarines [Archer 1984] although Cooke [1997c] regards the paracone and metacone as the terminal buccal cusps with styal cusps reduced or absent). Basicranial (Aplin 1987), cranial and postcranial morphology of wynyardiids, however, particularly incorporation of the squamosal into the tympanic wing of the ventral ear canal (Archer 1984) and pes form (Munson 1992), more closely resembles that of vombatids, suggesting that the apparent dental synapomorphies may be convergent.
The most commonly accepted hypothesis for macropodoid origins involves Phalangeriformes (Szalay, 1982), of which phalangerids are thought to be the closest to stem-macropodoids. The nature of this relationship, however, (phalangerids as a plesiomorphic ancestor or sister-taxon) is the subject of much debate. Archer (1984) summarised the morphological evidence, suggesting phalangerids are not likely macropodoid ancestors because of their reduced P2 and retention of P1. Flannery (1987) reinforced this hypothesis, placing macropodoids as the plesiomorphic sister-group to all other phalangeriforms (forming Phalangerida). This conclusion is also supported by basicranial (Aplin & Archer 1987; Flannery 1987; Springer & Woodburne 1989), postcranial (Szalay 1994), serological (Kirsch 1977) and DNA hybridisation (Springer & Kirsch 1991) data. More recently, Kirsch et al. (1997) revised this relationship, removing kangaroos from Phalangeriformes and placing them in a separate sister-group, suborder Macropodiformes.

Questions regarding the monophyly of Phalangerida (Murray et al. 1987; Springer et al. 1990; Luckett 1994) have also prompted reconsideration of a burramyid-macropodid relationship (Wroe et al. 1998) first proposed by Broom (1896). Broom regarded the genus *Burramys* as an intermediate between macropodoids and possums, a conclusion abandoned following assessment by Ride (1956). Inclusion of previously undescribed basicranial characters by Wroe et al. (1998), however, reasserts placement of *Burramys* as the immediate outgroup to Macropodoidea.

**Relationships within Macropodoidea**

High-level taxonomy within the Macropodoidea (Fig. 1) is contentious, traditionally involving division into two families (Pearson 1946, 1950a, 1950b; Archer & Bartholomai 1978; Archer 1984; Aplin & Archer 1987; Flannery 1989), Macropodidae and Potoroidae. Others, such as Marshall et al. (1990), Szalay (1994), Kirsch et al.
1. Molars lophodont and brachyodont with hypolophid formed by lingually displaced component of posthypocristid linked to a buccal crest from the entoconid.
2. Hypocingulid present on lower molars.
3. M₃ protolophid markedly compressed and with "forelink" absent.
4. I₁ with lingual enamel and dorsal enamel ridgelets.
5. P₃ with posteroconid cusp (may not be present in all taxa).
7. Postorbital lateral constriction of skull.
8. Hypertrophy of the mastoid processes.
9. Lack of auditory bulla formed by an inflated tympanic wing of the alisphenoid.


Flannery et al. (1983) established the similarity of balbarids (their Balbarinae) to plesiomorphic macropodids. This was expanded by Archer (1984) who proposed a sister-taxon relationship to macropodines. Flannery (1989) suggested Balbaridae may be paraphyletic with the derived species of Balbaroo being directly ancestral to both macropodines and sthenurines (Table 4).

1. Loss of protostylid.
2. Cristid obliqua contacts protoconid.
3. Neomorphic posterior cingulum present.
4. Loss of posthypocristid.
5. Presence of a posterior mental foramen on mandible.

Table 4. Potential synapomorphies uniting the derived balbarine taxon Balbaroo with plesiomorphic macropodids (after Flannery 1989; Cooke 1992).

Revision by Cooke (1997a, 1997c) and Cooke & Kear (1999), however, suggested balbarines are the plesiomorphic sister-group to all other macropodoids, constituting Balbaridae. The possibility of monophyly with Propleopinae was also indicated by Wroe et al. (1998) and Cooke & Kear (1999) on the basis of basicranial synapomorphies shared with the plesiomorphic propleopine Ekaltadeta ima (Table 5).

Flannery (1989) proposed division of Balbarinae into two clades: a plesiomorphic Nambaroo and more derived Balbaroo clade. These are distinguished primarily by presence or absence of the protostylid on M₃ and were awarded subfamilial status by Cooke (1997b).

Subfamily Nambarinae

Nambarines are known from the late Oligocene to late-early Miocene and include the genera Nambaroo Flannery & Rich, 1986, Wururoo Cooke, 1997c and Ganawamaya Cooke, 1997c. Monophyly of the Nambaroo clade can be established with the apomorphies listed in Table 6.

Cooke (1997b) determined relationships within Nambarinae, placing the genus Nambaroo as plesiomorphic (due to retention of a well developed M₃ protostylid) relative to Wururoo and Ganawamaya. Wururoo is considered more derived (Cooke 1997c) due to its reduction of the M₃ protostylid, partial formation of a neomorphic anterior cingulid and partly enclosed trigonid basin. Ganawamaya may represent an intermediate taxon between Nambaroo and Balbaroo as it lacks an M₃ protostylid but retains the plesiomorphic gracile P₃, reduced molar size, absence of separate paraconid on lower molars and shortened posterior cingulum present in species of Nambaroo.
Subfamily Balbarinae

Balbarines are currently known from deposits of late Oligocene to late-middle Miocene age. Flannery (1989) included only the genus Balbaroo Flannery, Archer & Plane, 1983, indicating its monophyly with apomorphies listed in Table 7 (Flannery 1989 cited absence of an M1 protostylid as the only potential synapomorphy for the Balbaroo clade). Cooke (1997e) also included Galanarla tesselata (placed in Macropodinae by Flannery 1989) on the basis of its well developed posterior cingulid linked to postentocristid of the lower molars. The worn condition of the specimen’s dentition, however, renders the relationship of Galanarla to other balbarine taxa difficult to discern.

Family Hypsiprymnodontidae

Hypsiprymnodontidae includes the extinct Propleopinae and extant Hypsiprymnodontinae, which incorporates the most plesiomorphic extant kangaroo species Hypsiprymnodon moschatus. Hypsiprymnodontids have been considered plesiomorphic members of the Potoroidae (e.g.

---

### Table 7. Potential synapomorphies uniting Balbarinae

<table>
<thead>
<tr>
<th>Number</th>
<th>Character State</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>P3 plagiaulacoid</td>
</tr>
<tr>
<td>2.</td>
<td>Premolars buccally flexed</td>
</tr>
<tr>
<td>3.</td>
<td>dP3 and M1 with principal crest formed from parametacristid</td>
</tr>
<tr>
<td>4.</td>
<td>M1 with cusp-like protostylid and reduced protoconid</td>
</tr>
<tr>
<td>5.</td>
<td>P3 retained and withdrawn from occlusion when P3 erupts</td>
</tr>
<tr>
<td>6.</td>
<td>Masseteric canal deeply invading ramus and confluent with inferior dental canal</td>
</tr>
<tr>
<td>7.</td>
<td>Mandible robust and ventrally arched, with greatest depth below M1/M2</td>
</tr>
<tr>
<td>8.</td>
<td>Calcaneum-cuboid facet lacks medial and plantar extensions (represents autopomorphy in Hypsiprymnodon; unknown in propleopines)</td>
</tr>
</tbody>
</table>

### Table 8. Potential synapomorphies uniting Propleopinae (after Ride 1993; Szalay 1994; Cooke 1997b).

<table>
<thead>
<tr>
<th>Number</th>
<th>Character State</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Anterior cristid emanating from both the protostylid and metaconid on M3</td>
</tr>
<tr>
<td>2.</td>
<td>I1 with enamel restricted to ventral margin only</td>
</tr>
<tr>
<td>3.</td>
<td>I1 develops elongate horizontal wear facet</td>
</tr>
<tr>
<td>4.</td>
<td>P3 large, tall and strongly ridged</td>
</tr>
<tr>
<td>5.</td>
<td>Protoconid, metaconid and protostylid are all incorporated into M3 protolophid</td>
</tr>
<tr>
<td>6.</td>
<td>Basally broad and conical upper molars</td>
</tr>
</tbody>
</table>

---

Subfamily Propleopinae


Archer & Flannery (1985) considered Propleopinae monophyletic (Table 9), with Ekaltadeta being plesiomorphic relative to Jackmahoneya and Propleopus. Plesiomorphy of Ekaltadeta was discussed by Wroe (1996, 1997) who suggested it represented the stem-group of two morphotypes within Propleopinae: E. ima/P. chillagoensis, exhibiting emphasis on vertical premolar/molar shear; and E. jamie mulvaneyi/ Jackmahoneya toxoniensis/P. oscillans/P. wellingtonensis, which accentuate horizontal shear in the dentition. This arrangement makes Propleopus polyphyletic and Ekaltadeta paraphyletic.

Relative apomorphy within the genus Propleopus is controversial and bears on intergeneric relationships. Wroe (1996, 1997) placed P. chillagoensis as plesiomorphic relative to P. oscillans and P. wellingtonensis. Archer & Flannery (1985) and Archer et al. (1978), however,
interpreted *P. chillagoensis* as the derived sister-taxon of *P. wellingtonensis*. This conclusion was supported by Ride (1993) who also suggested *Jackmahoneya toxoniensis* may be intermediate between *E. ima* and *P. oscillans*.

Sister-group relationships of Propleopinae are controversial. Comparable morphology (De Vis 1888; Tate 1948; Woods 1960) and potential dental and mandibular apomorphies (Table 8) uniting propleopines and hypsiprymnodontines have been identified (Ride 1993; Szalay 1994; Cooke 1997b). Pledge (1981) tentatively attributed an isolated humerus to the propleopine *Propleopus oscillans* on the basis of size and overall similarity to *Hypsiprymnodon moschatus*. Ride et al. (1997) reiterated propleopine affinity for the element, citing reduced deltoid and supinator crests and a straightened humeral shaft as plesiomorphic character states for Macropodoidea. However, no synapomorphies uniting hypsiprymnodontines and propleopines were established by either analysis. Wroe et al. (1998) proposed monophyly of propleopines with balbarids (Table 5) on the basis of basi-cranial synapomorphies. This was supported by Cooke (1997b) who suggested that many of the features shared by propleopines and hypsiprymnodontines may be symplesiomorphic.

**Subfamily Hypsiprymnodontinae**

Hypsiprymnodontinae includes the most plesiomorphic extant macropodoid *Hypsiprymnodon moschatus* and the middle Miocene taxon *H. bartholomaii* (Flannery & Archer 1987b). Additional isolated hypsiprymnodontine teeth have been described from the Oligo-Miocene Namba Formation of South Australia (Flannery & Rich 1986) and the early Pliocene Hamilton Fauna of Victoria (Flannery et al. 1992).

Synapomorphies uniting Hypsiprymnodontinae (Table 10) are questionable and may represent symplesiomorphic or convergent states (Flannery et al. 1984; Flannery & Archer 1987b; Flannery 1989).

Within Hypsiprymnodontinae, *H. bartholomaii* is regarded as plesiomorphic relative to *H. moschatus*, possessing features such as a phalangerid-like constriction in the alisphenoid hypotympanic sinus roof (Flannery & Archer 1987b).

**Family Potoroidae**

Potoroids constitute the second major radiation of extant macropodoids. Subfamilial divisions and inclusions vary with author: Bensley (1903) included Potoroinae (*Potorous* and *Caloprymnus*) and Bettonginae (*Hypsiprymnodon, Bettongia* and *Aepyprymnus*); Pearson (1946, 1950a, 1950b), Hypsiprymnodontinae and Potoroinae; Flannery (1989) included Potoroinae, Hypsiprymnodontinae, and the extinct Propleopinae, Bulungamayinae and Palaeopotoroinae; Cooke (1997a), Cooke & Kear (1999) and Kear et al. (this volume) included Potoroinae only. Alternatively, Szalay (1994), Kirsch et al. (1997) and Burk et al. (1998) advocate reduction of Potoroidae to subfamily level (within Macropodidae), with Potoroinae, Bulungamayinae and Palaeopotoroinae retained as tribes.

Potoroid monophyly (to include members of Potoroinae only) has been proposed using molecular (Kirsch 1977; Baverstock et al. 1989), mitochondrial DNA/ribosomal RNA (Burk et al. 1998) and morphological (Flannery 1982, 1989; Flannery et al. 1984) data, although polyphyly has been suggested (Bensley 1903). Potential morphological synapomorphies are listed in Table 11.

**Subfamily Potoroinae**

Potoroinae are confidently known from the early Pliocene to Recent though their origins are
1. Masseteric canal confluent with inferior dental canal and extends anteriorly to below P₃.
2. Frontal and squamosal bones in contact, separating the parietal from the alisphenoid.
3. Bunolophodont upper and lower molar dentition.
4. I with enamel restricted to ventrolateral surface with only ventral enamel flange present.
5. F lost.
6. Overlap of masseteric and mandibular foramen.
7. Mesially positioned foramen ovale incompletely floored by a narrow ventral process of the alisphenoid.
8. Endocranial exposure of anterior periotic face sharply angled relative to posterior periotic face.
9. Crista petrosa and anterior subarcate sulcus of periote well developed.
10. Transverse process of periote spine-like.
11. Tensor tympanic fossa well developed.
12. Extreme forward position of the attachment of the urinary bladder with the ureters entering the bladder at the anterior end of the median vaginal cul-de-sac.
13. Long posterior vaginal sinus and urethra and short urogenital sinus.
14. Os uteri well inside anterior vaginal expansion.

Table 12. Potential synapomorphies uniting Potoroinae (after Pearson 1946, 1950a, b; Case 1984; Flannery 1989; Cooke 1997b). Character states listed may also be considered potential synapomorphies for Potoroidae.

1. I crown short (not assessable in some poorly known fossil taxa).
2. Upper molars with well developed buccal crests (not assessable in some poorly known fossil taxa).
3. I lacks a dorsal enamel flange.
4. P₃ with many fine vertical ridgelets.
5. Buccal crests of lower molars less well developed than lingual counterparts.
6. Dentary stout with convex ventral margin.
7. Postglenoid process present (not assessable in some poorly known fossil taxa).
8. Only small portion of the periote (its anteroventral end) is visible on ventral surface of basicranium (not assessable in some poorly known fossil taxa).
9. Digital pads of pes are fused into a single unit (not assessable in fossil taxa).

Table 13. Potential synapomorphies uniting Bettongini (after Flannery & Archer 1987a; Prideaux 1999).

and Prideaux (1999) divided Bettongini into two clades, Bettongia and Aepyprymynus/Caloprymnus. Bettongia was considered plesiomorphic, with Aepyprymynus and Caloprymnus being more derived. Synapomorphies uniting Aepyprymynus and Caloprymnus include relatively high-crowned molars with well developed posthypocristid and postmetaconule cristae (extending across the entire posterior face of the hypolophid and metaloph respectively), premaxilla extremely foreshortened, shortened P³-C¹ diastema, and I³ occlusional crest offset from those of I¹ and I² (Flannery 1989). Prideaux (1999) supported all but the last of these synapomorphies noting that an offset I³ occlusional crest also occurs in some species of Bettongia.

The fossil taxa Bettongia moyesi Flannery & Archer, 1987a, Wakiewakie lawsoni Woodburne, 1984 and Gumardee pascuali Flannery, Archer & Plane, 1983 were placed within Bettongini by Flannery (1989) on the basis of their elongate premolars and apparent bunolophodont molars. Cooke (1997a) and Cooke & Kear (1999), however, suggested Bettongia moyesi and Wakiewakie lawsoni may be basal to Bulungamayinae. Gumardee pascuali is tentatively interpreted as a bulungamayine, because of its possible lophodonty (Flannery pers. comm.; Cooke 1997e). Bulungamayine affinity has also been proposed for Purtia mosaicus Case, 1984 from the Miocene Etadunna Formation of Lake Ngapakaldi, South Australia which, though bunolophodont, shares many dental apomorphies with bulungamayines, particularly its P morphology (Flannery 1989; Cooke & Kear 1999).

Flannery et al. (1992) described Milliyowi bungandij from the early Pliocene Hamilton Fauna.
of Victoria placing it within Bettongini as sedis mutabilis. This was revised by Prideaux (1999) who allied Milliyowi bungandij with Aepyprymnus on the basis of its high crowned, sublophodont molars and antero-posterorly elongate trigonids. Prideaux (1999) also described the giant bettong Boringaboodie hatcheri from Pleistocene deposits of Tight Entrance Cave, southwestern Western Australia, placing it as the plesiomorphic sister-taxon to Caloprymnus, Milliyowi and Aepyprymnus.

Woodburne et al. (1993) recorded the enigmatic potoroine Kyemma mahoneyi from late Oligocene deposits of the Etadunna Formation, Lake Palankarinna, South Australia. This taxon is described as being more derived than the probable bulungamayine (see below) Palaeopotorous priscus Flannery & Rich 1986, in possessing an M3 with more lingually situated protoconid and well-developed protostylid, but plesiomorphic to Partia mosaicus Case, 1984 (also a putative bulungamayine), Wakiwakie lawsoni and the propleopine Ekaltaueta ima in its smaller size, absence of lophid between paraconid and metaconid and presence of remnant crest between protoconid and paralophid in the trigonid of M2. A full description of the taxon has not yet been published and it is included here as incertae sedis.

Family Macropodidae

Macropodidae is arguably the most morphologically and behaviourally diverse macropodid family. Bensley (1903) and Raven & Gregory (1946) proposed an origin of Macropodoidea from within Potoroidea although Kirsch (1977) and Richardson & McDermid (1978) favoured a sister-taxon relationship. Flannery & Rich (1986) and Flannery (1989) alternatively indicated balbarids (their Balbarinae) as the ancestral group to Macropodidae with potoroids forming a separate sister-group radiation.

Archer (1984) and Flannery (1989) divided Macropodidae into subfamilies Macropodinae, Sthenurinae and Balbarinae. Assessment of more complete dental/cranial (Cooke 1997a, 1997c, 2000; Wroe et al. 1998) and postcranial (Kear 1998; Cooke & Kear 1999) balbarine fossil material, however, suggests Macropodidae may be paraphyletic and include bulungamayines rather than balbarines as its basal group.

Macropodid monophyly is supported by serological (Kirsch 1977; Baverstock et al. 1989), mitochondrial DNA (Burk et al. 1998) and morphological (Flannery 1982, 1989; Murray 1995; Table 14) data.

1. Well developed lophs on molars and posthypocristid lingually shifted (developed to varying degrees in different taxa)1,2,4
2. Loss of M3 protostylid2
3. Molar size increases posteriorly with M4 not markedly smaller than M3 and with low molar gradient2
4. P4 elongate and coarsely ridged2,4
5. Separation of masseteric and inferior dental canals by bony lamina2
6. Reduction in length of masseteric canal2
7. Coalescence of mandibular and masseteric foramina2
8. Parietal and alisphenoid contact each other1
9. Plantar fascia insert over nearly whole length of well-developed calcaneal rugose-plantar surface2,3
10. Well developed plantar crest on metatarsals IV2,3
11. Reduced ventromedial process on metatarsals V2,3

Table 14. Potential synapomorphies uniting Macropodidae (after Flannery 19821, 1989; Murray 19953; Cooke 1997b4). Murray (1995) includes a side-by-side arrangement of mesocuneiform and entocuneiform facets on navicular as an additional potential synapomorphy, however, the mesocuneiform does not contact the navicular in macropodoids (Bishop 1997; Kear et al. this volume) therefore this feature is omitted here.

Subfamily Bulungamayinae

Bulungamayines are currently known from the late Oligocene to early-late Miocene. Flannery et al. (1983, 1984) designated Bulungamayinae as the derived monophyletic (characters states diagnosing Bulungamayinae are listed in Table 15) sister-group to potoroines on the basis of dental synapomorphies (Table 16).


1. P1 elongate and crescentic with many fine transverse cristae and bulbous bases1,2,3
2. Small I3 (possibly small canine) present just posterior to dorsal margin of I1, alveolus3
3. I, enamel area extensive and confined to buccal surface of tooth3
4. I1, with both dorsal and ventral enamel flanges present3
5. Digastric process of dentary expanded such that ventral margin is convex below molar row1,2,3
6. Buccally expanded masseteric canal, confluent over its length with inferior dental canal both penetrating deeply within dentary below molar row1,2,3

Table 15. Potential synapomorphies uniting Bulungamayinae (after Flannery, Archer & Plane 1982, 1984; Cooke 1997d). Cooke (1997d) uses more complete material to designate apomorphies 2 and 4 which Flannery et al. (1983, 1984) cite as not present (2) and lacking dorsal flange (convergent feature present only in Bulungamaya delicata, 4) respectively.
1. Dentin greatly thickened, obscures dorsal enamel crest of crown giving tooth an oval cross-section
2. P3 elongate with many fine ridgelets and straight occlusional edge
3. Opening of masseteric canal buccally expanded
4. Dentary strongly convex below tooth row


1. II with only minor anteroposterior orientation of protoconid-metaconid crest
2. Protostylid lacks any anterior crest

Table 17. Potential synapomorphies uniting Bulungamayinae and plesiomorphic macropodids (species of Hadronomas and Dorcopsoides, after Cooke 1997c; Cooke 1999).

1. I, with horizontal orientation
2. Anterior cingulids long in lower molars
3. Molars low-crowned and bilophodont
4. M1 protolophids not laterally compressed
5. M1 lacking posterior cingulids
6. Premolars elongate with at least incipient development of lingual cingula on upper premolars
7. dP3, with metaconid reduced or absent
8. Alisphenoid-parietal contact on lateral wall of cranium
1. Upper incisors form a narrow V-shaped group in ventral view.
2. P with high, posteriorly elongate crown which lacks lateral grooves.
3. 11 with short crown and sharply produced dorsal margin.
4. P3 with high lingual crest extending full length of tooth and connected to labial or main crest by transverse laminae.
5. P3 with deep posterior buccal crest.
6. P3 with extreme development of the raised lingual cingulum.
7. Anteriorly shifted premetacristid occurring on anterior cingulum.
8. Permanent premolars erupt late in ontogeny, usually after eruption of M4.
9. Mandibular symphysis strongly sutured or ankylosed with boss formed at union.
10. Horizontal rami deep and thick with depth at symphysis not appreciably shallower than beneath cheek teeth.
11. Skull brachycephalic with deep, broad rostra.
12. Squamosal with deep zygomatic process.
13. Masseteric process of zygoma very robust.
14. Palatal vacuities large and palatine bars narrow.
15. External auditory meatus very long, ventrally keeled and strongly sutured to squamosal.
16. Manus with digits I and V greatly reduced, elongate metacarpals and long curved ungulae.
17. Lower ankle joint divided into anterior and posterior sections.
18. Pes with digits II, III and V reduced to vestiges.
19. Distal end of metatarsal IV and digit IV phalanges transversely broad.
20. Proximal digit IV phalanx with lateral scars on midshaft for sesamoid ligaments.

Table 19. Potential synapomorphies uniting the crown group sthenurines Sthenurus, Simosthenurus and Procoptodon (after Flannery 1989; Wells & Tedford 1995; Murray 1995).

Table 20. Potential synapomorphies uniting Lagostrophus, Troposodon and the sthenurine clade (after Flannery 1983, 1989; Wells & Tedford 1995). Wells & Tedford (1995) also include I, with enamel completely encircling crown as an apomorphy for this group, however, the feature is not present in Lagostrophus.

Intergeneric relationships within Sthenurinae are controversial. Flannery (1983) created two clades: a derived Sthenurus/Simosthenurus/Procoptodon; and a plesiomorphic Lagostrophus/Troposodon group. This was revised by Flannery (1989), who placed Troposodon with crown-group sthenurines and erected the tribes: Lagostrophini (containing Lagostrophus) and Sthenurini (containing crown-group sthenurines and Troposodon).

Hadronomas puckridgi was regarded by Woodburne (1967) as having affinity to either Protemnodon or sthenurines. This arrangement was followed by Campbell (1973), Archer (1981) and Murray (1989, 1990, 1995), the latter citing extensive cranio-dental and postcranial synapomorphies (Table 21) supporting placement with sthenurines. Bartholomai (1978) and Flannery (1989) both proposed placement with macropodines as 'tribe indet.'.

1989; Wells & Tedford 1995; Murray 1995) although relationships of more basal taxa are unclear. Flannery (1983, 1989) and Wells & Tedford (1995) cite dental character states (Table 20) uniting the genera Lagostrophus and Troposodon with the crown sthenurine clade. Murray (1995), however, questioned inclusion of Lagostrophus and Troposodon listing potential synapomorphies for an alternative Hadronomas-sthenurine clade (Table 21).
1. Laterally expanded supraorbital crest of frontals
2. P1 reduced and P1 enlarged
3. Posterior mental foramen well-developed
4. Straight molar lophs with definite shearing crests
5. Elevated pterygoid fossa of dentary
6. Deep jugal expansion forming ectopterygoid process
7. Ectotympanic thick, wide and keeled ventrally
8. Equal termination of anterior ends of astragalar trochlear crests
9. Reduced lateral tuberosity of astragalus
10. Lateral astragalar trochlear crest aligned with medial margin of dorsolateral calcaneal facet
11. Astragalar head medially deflected
12. Transversely narrow sustentaculum tali on calcaneum
13. Dorsolateral facet of calcaneum mesially elongate
14. Dorsomedial and ventromedian calcaneal facets divided by lateral groove
15. Cuboid body transversely compressed and with shallowly stepped calcaneum-cuboid facet
16. Elongate dorsolateral facet of cuboid
17. Dorsomedial and ventromedian facets of cuboid separated by groove
18. Lobate salient present on metatarsal IV facet of cuboid
19. Entocuneiform facet reduced to sulcus on internal side of navicular
20. Metatarsal IV curved in lateral view, with concave profile and assymmetrical section
21. Distomedian keel of metatarsal IV reduced
22. Angled metatarsal IV facets on metatarsal V
23. Proximal phalange IV articular facets dorsoventrally compressed
24. Reduced intra-articular fossa on proximal phalange IV
25. Broad, shallow cruciate fossa on proximal phalange IV
26. Distinct crossed sesamoid and oblique ligament scars on proximal phalange IV
27. Enlarged collateral prominences on medial phalange IV
28. Distal phalange IV broad, blunt and planoconvex in section
29. High, narrow coracovertebral process of scapula
30. Iliopubic arch elongate and with broad, flat section
31. Tibial crest elongate and gradually proximally expanding
32. Distal articular surface of tibia rotated
33. Caudal vertebrae transversely broad


Tedford (1966) included *Simosthenurus* (describing the brachycephalic forms *S. occidentalis*, *S. ores*, *S. pales*, *S. antiquus*, *S. orientalis* with *S. cegsai* Pledge, 1992, 1999, *brachyselenis* Prideaux & Wells, 1997 and *S. euryskaphus* Prideaux & Wells, 1997 subsequently included) as a subgeneric division within *Sthenurus* (describing the dolichocephalic forms *S. andersoni*, *S. notabilis*, *S. tindalei*, *S. atlas* with *S. gilli* Merilees, 1965, *S. brownii* Merilees 1967, *S. maddocki* Wells & Murray, 1979 and *S. stirlingi* Wells & Tedford, 1995 also included) and suggested its direct ancestry to *Procoptodon*. Pledge (1980) raised *Simosthenurus* to generic level, a conclusion followed by others such as Wells & Tedford (1995) who united *Simosthenurus* and *Procoptodon* as sister taxa to the exclusion of *Sthenurus* (Table 22). Flannery (1989), however, considered *Simosthenurus* the polyphyletic ancestor of *Sthenurus* and *Procoptodon*, also incorporating plesiomorphic taxa related to *Troposodon*. The questionable validity of *Simosthenurus* as both a generic and subgeneric division was raised by Prideaux & Wells (1997) who proposed inclusion of all taxa within *Sthenurus*.

Kear et al. (this volume), in describing postcranial elements of the derived buluangamine genus *Wanburoo*, suggested it is the sister-taxon to *H. puckridgi* and all other sthenurines. The relationship of *Lagostrophus* and *Troposodon* to this clade is unclear and requires more inclusive phylogenetic assessment.

**Subfamily Macropodinae**

Macropodinae is the most speciose and arguably most successful of all kangaroo subfamilies, including the major radiation of
1. Tip lies within arcade formed by upper incisors
2. Occlusal edge broad, forming elongate blade
3. Mandibular condyle oval
4. Mandibular symphysis weakly ankylosed
5. Navicular facet on astragalus head broad and flat
6. Sustentaculum tali on calcaneum with rounded or flattened ventral surface
7. Calcaneum-astragalus articular facet hourglass-shaped, being strongly medially constricted (may become completely divided in derived taxa)
8. Plantar surface of calcaneum anteroposteriorly elongate, laterally extensive and associated with a distinct transverse plantar sulcus
9. Enlarged medial plantar tuberosity of cuboid
10. Navicular with broad astragalus facet
11. Narrow cuboid facet on metatarsal
12. Coracoid process on scapula reduced
13. Coronoid fossa larger than radial fossa on humerus
14. Ectepicondyle of humerus reduced
15. Capitalutum of humerus goblet-shaped
16. Distal extremity of humerus deep and narrow
17. Condylar surface of tibia oriented in a horizontal plane
18. Tibial diaphysis straight in anterior-posterior view
19. Thoracic vertebral body narrow and ventrally keeled, may be elongate in lower thoracics
20. Ligamentum flavium sulcus on vertebrae lost or reduced
21. Rib apophyses short and elliptical

Table 23. Potential synapomorphies uniting the Macropodinae (after Flannery 1989; Murray 1995).

Grazing kangaroos. The macropodine fossil record extends from late Miocene to Recent.

Macropodine monophyly is supported by serological (Kirsch 1977; Baverstock et al. 1989), allozyme, cytological and immunological (Richardson & McDermid 1978) and morphological (Flannery 1989; Szalay 1994) evidence (Table 23).

Flannery (1989) divided Macropodinae into three tribes (followed in this phylogeny): Macropodini, including Thylogale, Setonix, Baringa, Lagorchestes, Onychogalea, Petrogale, Kurrabi, Wallabia and Macropus; Dendrolagini, containing the tree kangaroos Bohra and Dendrolagus; and tribe indet. containing the plesiomorphic forms Dorcopsoides, Dorcopsulus, Dorcopsis, Watutia, Proteemonodon, Congrus and Prionotemnus, all of uncertain affinity (the genera Watutia and Congrus were not described at the time of Flannery’s 1989 analysis but are included here as sedis mutabilis).

Within Macropodini, Macropus is considered derived, and monophyletic on the basis of molecular (Kirsch 1977), electrophoretic, immunological and karyological (Richardson & McDermid 1978) and morphological (Flannery 1989) evidence. DNA hybridisation studies of Kirsch et al. (1997), however, suggest paraphyly. Dawson & Flannery (1985) subdivided Macropus into the subgenera M. (Macropus), M. (Osphranter) and M. (Notamacropus). Monophyly for each is supported by Baverstock et al. (1989), Flannery (1989) and Kirsch et al. (1997) though the morphological synapomorphies uniting members of M. (Notamacropus) are weak (Dawson & Flannery 1985). Species of M. (Notamacropus) have been regarded as plesiomorphic relative to those of M. (Macropus) and M. (Osphranter) (Dawson & Flannery 1985). Serological data, however, suggests that species of M. (Macropus) may be sister taxa to those of M. (Osphranter) and M. (Notamacropus) (Baverstock et al. 1989; Sharman 1989).

Wallabia is placed as sister-taxon to Macropus by both the molecular analyses of Kirsch (1977), Richardson & McDermid (1978) and Baverstock et al. (1989) and the morphological studies of Flannery (1982, 1984, 1989). DNA hybridisation work carried out by Kirsch et al. (1997), however, include Wallabia as the plesiomorphic sister-taxon to M. (Osphranter), implying that Macropus may be paraphyletic.

Molecular (Sharman 1961; Kirsch 1977; Richardson & McDermid 1978), immunological (Baverstock et al. 1989; Baverstock et al. 1990) and DNA hybridization (Kirsch et al. 1995) assessments of Petrogale and Thylogale suggest a monophyletic sister-taxon relationship. The morphological data of Flannery (1989), however, indicated that Petrogale may be a sister-taxon to Macropus, Onychogalea and Lagorchestes though these features may be convergent (Sanson 1978; Flannery 1989). Serological assessments of Baverstock et al. (1989), Baverstock et al. (1990) and Kirsch et al. (1995) suggested an alternative relationship with Dendrolagus.

Sharman (1989) and Kirsch et al. (1995) placed Setonix as the derived sister-taxon of Thylogale though Baverstock et al. (1989) and Baverstock et al. (1990) support a relationship with Wallabia and Macropus.

The fossil taxa Kurrabi Flannery & Archer, 1984 and Baringa Flannery & Hann, 1984 were placed within Macropodini by Flannery (1989). Flannery & Archer (1984) suggest Kurrabi may be related to species of Proteemonodon, Wallabia and Macropus. Flannery & Hann (1984) demonstrated similarity of Baringa to Lagorchestes and Onychogalea. Exact relationships of these taxa, however, remain
1. Cuboid articulation of calcaneum wide and not distinctly stepped\(^1,3\)
2. Calcaneum flattened and broad\(^1,3\)
3. Astragalar head near horizontally oriented\(^1,2,3\)
4. Median trochlear ridge of astragalar-tibial articulation tall\(^1\)
5. Tibia epiphyseal length-width ratio high\(^1,3\)
6. Fibular crest on tibia weak and rotated towards tibial crest\(^1,3\)
7. Latissimus muscle insertion placed low on humeral shaft, lateral to apex of pectoral crest\(^1\)
8. "Rotator Cuff" ligament formed from combined tendons of supraspinous, infraspinous and teres minor present on humeral head\(^1\)
9. Hind foot with fused pads\(^1\)

**Table 24.** Potential synapomorphies uniting tribe Dendrolagini (after Flannery & Szalay 1982\(^1\); Szalay 1994\(^2\); Flannery et al. 1996\(^3\)).

unclear.

Tribe Dendrolagini is considered monophyletic by Flannery & Szalay (1982), Flannery (1989) and Szalay (1994) on the basis of potential synapo-morphies in the postcranial skeleton (Table 24).

Groves (1982) divided the extant tree-kangaroos into two distinct clades: *Dendrolagus insitus*, *D. lumholtzi* and *D. bennettianus*; and *D. ursinus*, *D. matschiei*, *D. dorianus* with *D. spadix*, *D. goodfellowi*, *D. scottae* and *D. mbaiso* added by Flannery et al. (1996). Flannery & Szalay (1982) designated a third plesiomorphic clade containing the fossil taxon *Bohra paulae*.

Baverstock et al. (1990) and Kirsch et al. (1995) suggested that *Dendrolagus* forms a monophyletic assemblage with *Petrogale* and *Thylogale*. This contrasts with the morphological data of Tate (1948) and Flannery (1989), which indicates monophyly with *Dorcopsis* and *Dorcopsulus*.

*Dorcopsis*, *Dorcopsulus* and *Dorcopsoides* represent the most plesiomorphic macropodine taxa. Tate (1948) and Flannery (1989) placed *Dorcopsis* and *Dorcopsulus* with *Dendrolagus* as a basal plesiomorphic group within Macropodinae. Burk et al. (1998), however, suggested *Dorcopsis* and *Dorcopsulus* form the sister-group to all other macropodines. *Dorcopsoides* was placed with potoroinae by Woodburne (1967), on the basis of a deeply penetrating and confluent masseteric/dental canal and general dental morphology. Bartholomai (1978) proposed macropodine affinity for *Dorcopsoides* and suggested synonymy with *Wallabia*. Flannery (1989) and Cooke (1999), however, reaffirmed the validity of the generic term *Dorcopsoides*, with Cooke (1999) suggesting it may be derived relative to *Hadronomas puckridgi* (*H. puckridgi* being treated as a plesiomorphic macropodid of uncertain affinity by Cooke 1999).

Flannery et al. (1989) described the monotypic genus *Wattutia* (type species *Wattutia novaeguineae*) from the Pliocene Otibanda formation of Papua New Guinea. They suggested placement as a plesiomorphic macropodine and cite phenetic similarity to species of *Protemnodon*, *H. puckridgi* and undescribed macropodine remains (now assigned to the bulungamayine genus *Wanburoo* by Cooke 1999) from Tertiary deposits of Riversleigh, northwestern Queensland. Despite this, no synapomorphies were provided to unite *Wattutia* with any of these taxa and it is therefore regarded as *sedis mutabilis*.

Placement of the enigmatic fossil taxon *Protemnodon* is highly controversial. Menzies & Ballard (1994) described a partial skeleton of *Protemnodon tumbuna* from the Pleistocene of Papua New Guinea. They noted some similarity to plesiomorphic macropodines such as *Dorcopsis* and particularly *Dendrolagus*, however, no synapomorphies were identified. Dental similarities with *Wallabia* (Stirton 1963; Flannery 1984) and *H. puckridgi* (Woodburne 1967; Bartholomai 1973) have also been established.

Dawson & Flannery (1985) showed the genus *Prionotemnus* to be distinct from the *Macropus* clade, although all constituent species except *Prionotemnus palankarinnicus* were reassigned to *M. (Notamacropus)*. *Prionotemnus palankarinnicus* was placed as a plesiomorphic macropodine of uncertain affinity.

McNamara (1994) described the monospecific fossil genus *Congruus congruus* (Pleistocene, Naracoorte region, S. Aust.) and suggested affinity with *Prionotemnus*. The limited type material (a single skull), however, precludes any definitive placement of this taxon.

**ACKNOWLEDGEMENTS**

Many thanks to M. Archer and T. Flannery for reading earlier drafts of this paper and to staff and students at the University of New South Wales for providing much needed critical discussion. Thanks to S. Ingleby and the Australian Museum, H. Godthelp and the University of New South Wales for provision of specimens. Support for this research was provided by: the Australian Research Grant Scheme (grants to M. Archer); National Estate Grants Scheme (grants to A. Bartholomai and M. Archer); Commonwealth Department of Environment, Sports and Territories;
Queensland National Parks and Wildlife Service; Commonwealth World Heritage Unit; University of New South Wales; Queensland Museum; Australian Museum; IBM Australia Pty Ltd; ICI Australia Pty Ltd; Australian Geographical Society; Earthwatch Australia; Wang Australia Pty Ltd; Century Zinc Pty Ltd; Mount Isa Mines Pty Ltd; Surrey Beatty & Sons Pty Ltd; Riversleigh Society Inc.; Royal Zoological Society of New South Wales; Linnean Society of New South Wales; and private supporters.

REFERENCES


Abstracts, 27.


FLANNERY, T.F., 1983. Revision in the macropodid subfamily Sthenurinae (Marsupialia: Macropodidae) and the relationships of the species of Troposodon and Lagostrophus. Australian Mammalogy 6, 15-28.


Surrey Beatty & Sons, Sydney.


SPRINGER, M.S. & WOODBURNE, M.O., 1989. The distribution of some basicranial characters within the Marsupialia and a phylogeny of the Phalangeriformes. Journal of vertebrate Paleontology 9, 210-221.


