

A PRE-NEOGENE PHALANGERID POSSUM FROM SOUTH AUSTRALIA

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ABSTRACT--Phalangeridae is one of the most widely dispersed families of possums (Marsupialia, Diprotodontia) in the Australasian region, extending from Tasmania in the southeast to Sulawesi of the Greater Sunda Islands of Indonesia in the northwest. Yet this one family of possums has generated the most morphological and biochemical phylogenetic uncertainties of any family within Order Diprotodontia. The various phylogenetic relationships for the family have led to different biogeographic models in regard to the site of origin and directions of dispersal for taxa within the family. The recovery of a maxilla from faunal zone B of the late Oligocene Etadunna Formation at Lake Palankarina, South Australia (ca. 25 mya), results in the oldest known phalangerid to date, some ten million years older than the numerous Middle Miocene fossil phalangerids described from Riversleigh, Queensland. Whereas the Riversleigh phalangerids are similar enough to modern taxa to have originally been included in modern genera, the Etadunna specimen has morphologies that are very plesiomorphic for the family. These include a bladed P3 with a central main cusp that has denticles posteriorly, but no ridges; P3 aligned with tooth row; M1 with parastyle shear aligned with blade of P3; and M2 and M3 more square in occlusal outline. Autapomorphic character states include an infraorbital canal anterior to the second premolar, lack of an intraorbital groove, and the opening of the lacrimal canal inside the orbit. With substantial molecular time-of-divergence data now available, plus the addition of this new pre-Neogene phalangerid from South Australia, a new biogeographic model for site of origin and dispersal can be offered where phalangerids originate in Australia, diversify and give rise to the cuscus subfamilies, which disperse to New Guinea and then to Indonesia.

INTRODUCTION

The Australian possum family Phalangeridae, which includes cuscuses and brush-tailed possums, is the most widely distributed Australasian marsupial family with approximately two-dozen recognized extinct and extant species that range over most of Australia (including Tasmania), New Guinea, and northwestward to the Celebes Islands (Flannery, 1994; Hamilton and Springer, 1999; Osborne and Christidis, 2002; Springer et al., 1990; Fig. 1). This one family has generated the most phylogenetic and taxonomic uncertainties of any family within Order Diprotodontia, whether those phylogenies are based on morphological data or on biochemical data (e.g., Flannery et al., 1987; George, 1987; Groves, 1987a; Norris, 1994; Springer et al., 1990; Kirsch and Wolman, 2001; Ruedas and Morales, 2005). The various phylogenetic relationships for the family have led to different biogeographic models in regard to the site of origin (Australia or Sulawesi in the Celebes) and directions of dispersal (Australia to the Celebes or from the Celebes to Australia), for taxa within the family (e.g., Flannery et al., 1987 or Ruedas and Morales, 2005).

Late Oligocene deposits in South Australia from the Etadunna and Wipajiri formations in the Lake Eyre Basin, and from the Namba Formation in the Frome Basin, have produced a wide range and the earliest records of most of the extinct and extant possum families (Fig. 2). Burramyidae, Ektopodontidae, Miralinidae, Pilkipildridae, and Pseudocheiridae have all been recovered from deposits of the Etadunna Formation, yet there had been no positive sign that Phalangeridae was present at all (see the series of papers in Archer, 1987, or those cited in Woodburne et al., 1993). The absence of phalangerids in the late Oligocene had been confusing considering that the earlier molecular studies (e.g., Springer et al., 1990; Springer, 1997), which produced divergence time data from molecular sequences, indicated that the phalangerid lineage should be present by the Eocene.

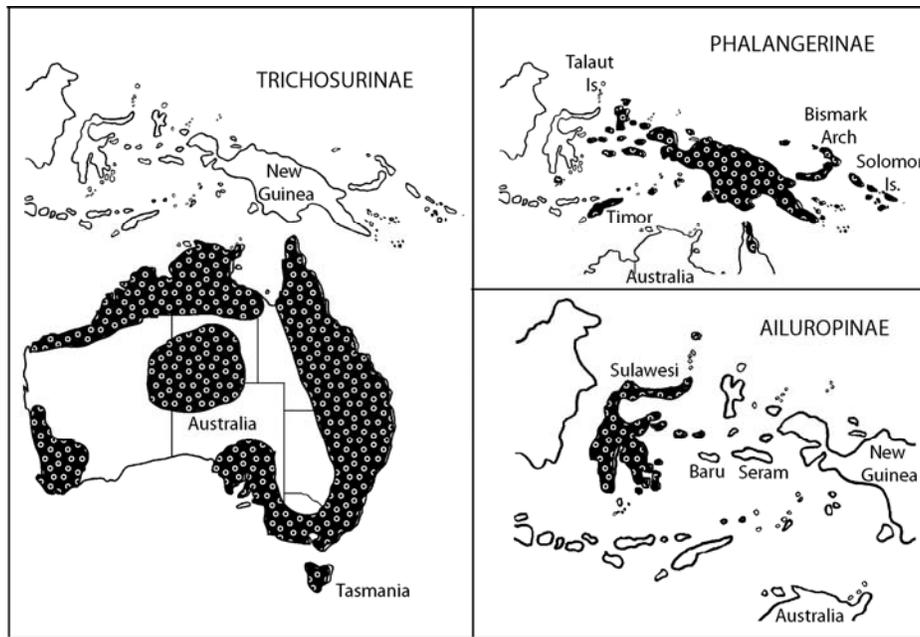


Figure 1. Distribution of Phalangeridae subfamilies proposed by Ruedas and Morales (2005). Distributions based on Flannery (1994).

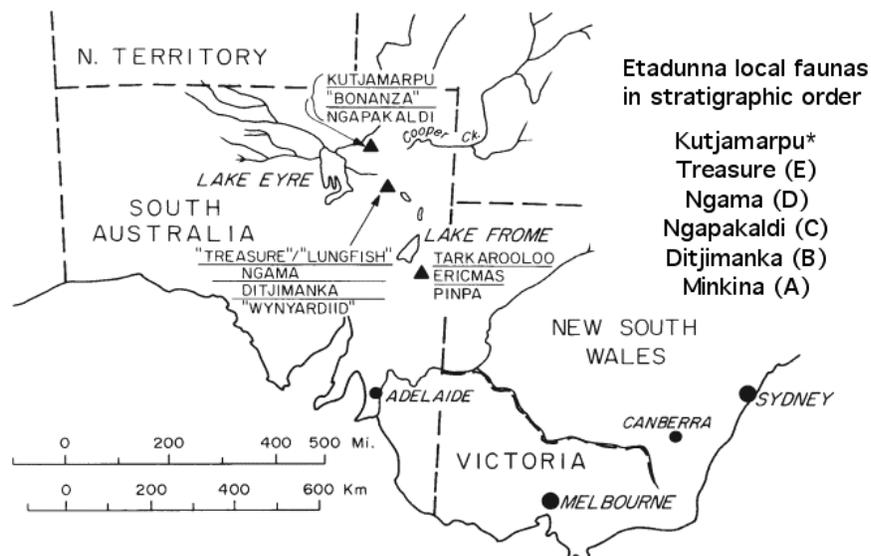


Figure 2. Locality map for outcrops of the Etadunna Formation and the contemporaneous Namba Formation (black triangles), which have produced late Oligocene-aged marsupial fossils (Etadunna Formation outcrops indicated by arrows pointing to triangles). *Eocuscus sarastamppi* was recovered from informal faunal zone B, representing the Ditjimanka local fauna, at Lake Palankarinna (middle triangle). The inset list indicates the local faunas from the Etadunna Formation in stratigraphic order and the informal faunal zone with which they are associated. The Kutjamarpu local fauna has an asterisk, as it is from the Wipajiri Formation, which unconformably overlies the Etadunna Fm. and would represent an additional faunal level ("F") younger than those of the Etadunna Formation (after Woodburne et al., 1993).

Here we report on the first record of a phalangerid from the Etadunna Formation and, thus far, the oldest record of a phalangerid from Australia. This record is based on a maxilla with P3-M3 found by one of us (JP) in a buff-colored clay layer in a deposit representing informal faunal zone B of the Etadunna Formation at Lake Palankarinna and the Ditjimanka local fauna (Woodburne et al., 1993).

Dental morphology clearly places the specimen within Phalangeridae (semilophate occlusal pattern of the upper molars, molar shape, premolar number), whereas cranial features and other dental features indicate that this late Oligocene species is the sister-taxon to all other phalangerids. The late Oligocene presence of phalangerids in central South Australia, the diversity of trichosurine phalangerids from the middle Miocene deposits of northern Queensland (Crosby, 2007), plus data from a recent nuclear gene molecular study by Meredith et al. (2008), all indicate a change from the prevailing biogeographical model of Flannery et al. (1987) to a newer model where Australia is the site of origin for the family followed by subsequent dispersal to the Celebes.

Definitions and Institutional Abbreviations--Dental nomenclature follows Lockett (1993), where premolars (P-upper and p-lower) are numbered 1-3 and molar designation is M1-4 (upper molars) and m1-4 (lower molars). Molar occlusal surface terminology for diprotodontian marsupials follows that of Woodburne et al. (1987) and is illustrated in Figure 3. Anatomical directions are **L** (left) and **R** (right); measurements are in millimeters. **SAM**, South Australia Museum, Adelaide, South Australia; **QM**, Queensland Museum, Brisbane, Queensland.

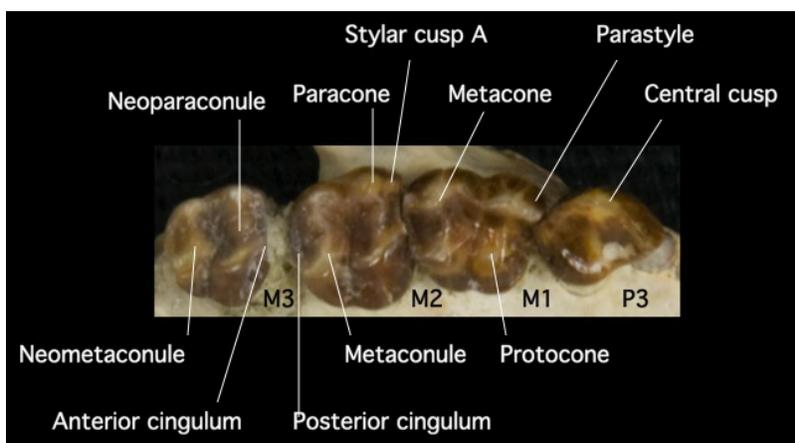


Figure 3. Diagram of the holotype of *Eocuscus sarastamppi*, SAM P44324, illustrating the dental terminology and locations used herein. Additional terminology; preparacrista and postparacrista are the crests anterior and posterior to the paracone; premetacrista and postmetacrista are the crests anterior and posterior to the metacone; preprotocrista and postprotocrista are the crests anterior and posterior to the protocone; premetaconular crista and postmetaconular crista are the crests anterior and posterior to the metaconule; and the centrocrista is composed of the postparacrista anteriorly and the premetacrista posteriorly.

SYSTEMATIC PALEONTOLOGY

Cohort AUSTRALIDELPHIA Szalay 1982
 Order DIPROTODONTIA Owen, 1866
 Family PHALANGERIDAE Thomas, 1888
EOCUSCUS gen. nov.

Etymology--*Eo-*, Greek for dawn, representing the earliest known member of the family of cuscuses and brush-tail possums; *-cuscus*, aboriginal word in reference to a phalangerid possum.

Type species-- *Eocuscus sarastamppi* sp. nov.

Diagnosis-- As for the holotype and the only known species.

Eocuscus sarastamppi sp. nov.

(Figs. 4 and 5; Table1)

Etymology--In honor of Dr. Sara K. Stamp, former provost at Saint Mary's College of California, under whose auspices the project resulting in the collection of the holotype received funding.

Locality and Age-- Holotype recovered from lacustrine to fluvial deposits of the Etadunna Formation, Lake Palankarina, Lake Eyre Basin of South Australia; specifically from the SAM Quarry, bottom of the white clay unit above the sandy unit at the base of the quarry wall, faunal zone B, Ditjimanka local fauna of late Oligocene age (ca. 25 mya, Woodburne et al., 1993).

Holotype-- SAM P44324, right maxilla with P3-M3.

Diagnosis-- *Eocuscus sarastamppi* gen. et sp. nov. is distinguished from other phalangerid possums, both extant and extinct, by the following eleven unique autapomorphic (A) or plesiomorphic (P) character states (where character state polarities have been determined by the distribution of character states within phalangerid possums and within other possum families): 1) P3 bladed with a central main cusp having denticles present on posterior crest, but without vertical ridges on buccal and lingual faces (P); 2) P3 aligned with tooth row and not set obliquely to it (P); 3) M1 with parastyle shear aligned with blade of P3 (P); 4) M2 and M3 more square (i.e., wider per length) in occlusal outline (P); 5) infraorbital canal anterior to second premolar (A); 6) lack of intraorbital groove on maxillary shelf forming floor on inside of orbit (A); 7) sphenopalatine foramen does not lie within intraorbital groove (groove not present) and opens medially into nasal cavity near posterior end of maxilla (A); 8) lacrimal foramen inside orbit relatively close to floor of orbit (A); 9) lacrimal foramen formed equally by maxilla, anteroventrally, and by lacrimal, posterodorsally (A); 10) nasolacrimal canal runs horizontally in nasal cavity from lacrimal foramen to at least maxillary-premaxillary suture (A); P1 not separated from P3 by diastema (P).

Description-- SAM P44324, the holotype, is a right maxilla, which retains the maxilla-premaxilla suture anteriorly. The preorbital wing is broken just below the level of the orbital process of the lacrimal, and it retains some of the maxillary-palatine suture posteriorly. Much of the palatal process of the maxillary is still present, indicating that the palatal fenestra extended anteriorly to the level of the interloph valley of M2. The anterior extent of the palatine along the lateral margin of the right palatal fenestra is to the level of the anterior loph of M3. The floor of the orbit is very broad and long anteroposteriorly creating an extensive flat aspect to it. There is no intraorbital groove medial to the alveolar bone of the maxilla leading to the orbital entrance to the infraorbital canal (Fig. 4). The sphenopalatine foramen opens medially into the posterior nasal cavity through the sidewall of the maxilla at the posterior end of the maxilla near the triple junction of the maxilla, palatine, and the frontal. The opening of the nasolacrimal canal, the lacrimal foramen, is inside the orbit and the sutures for the lacrimal bone are visible. The anteroventral half of the circular lacrimal foramen is formed from the maxilla, and the maxillary-lacrimal sutures can be traced indicating that there is an equal contribution to the lacrimal foramen by the lacrimal bone, as it would form the posterodorsal border of the foramen. The lacrimal foramen is low on the orbit margin, as the dorsal margin of the jugal and the maxilla process of the zygomatic arch do not rise very far above the floor of the orbit. There are only 4.0 mm of vertical distance from the floor of the orbit at the opening of the infraorbital canal to the level of the lacrimal foramen. This is only half the vertical distance between those same anatomical features in extant phalangerids. A broad groove on the internal surface of the maxilla within the anterior nasal cavity begins at the lacrimal foramen and extends anteriorly to the maxillary-premaxillary suture where the specimen ends. This internal groove indicates the path of the nasolacrimal canal within the nasal cavity. The canal is nearly horizontal along its entire length, and only slightly higher at the lacrimal foramen than at the anterior end of the maxilla. This near horizontal orientation of the nasolacrimal canal differs from the condition for extant taxa and presumably extinct taxa such as the mid-Miocene *Oniroscus* from Riversleigh, where the lacrimal foramen is much higher than the palate resulting in a substantial vertical drop in the nasolacrimal canal before it becomes horizontal. The anterior portion of the jugal, which is only ~5 mm in length, remains attached to the base of the maxillary process of the zygomatic arch.

Dentally, P3 and M1 through M3 are present. Alveoli for the C and P1 are present anterior to P3, as is the alveolus for a tri-rooted M4 (Fig. 5).

P1--There are two circular alveoli anterior to P3, with the anterior of the two having the greater diameter. There is no diastema between the posterior alveolus and P3, but there is a diastema between the canine alveolus and the anterior of the two premolar alveoli (see below for a discussion on the determination that these two alveoli represent those for a P1).

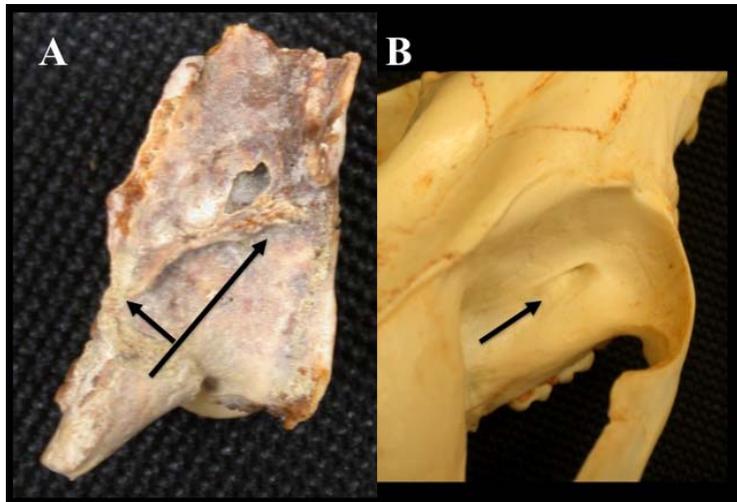


Figure 4. Comparison of the anterior orbital region of the holotype of *Eocuscus sarastamppi* (SAM P44324; left in dorsal view) and the extant species of Brushtail Possum, *Trichosurus vulpecula* (right). As shown here for *Trichosurus* and all extant phalangerids, plus all Neogene phalangerids, the sphenopalatine foramen lies in a groove, which leads to the orbital opening of the infraorbital canal as indicated by the arrow. *Eocuscus* lacks the groove leading to the infraorbital canal (indicated by the long arrow) and the sphenopalatine foramen (indicated by the short arrow) opens to the posterior nasal cavity further posteriorly at the triple junction of the maxillary, palatine and frontal bones.

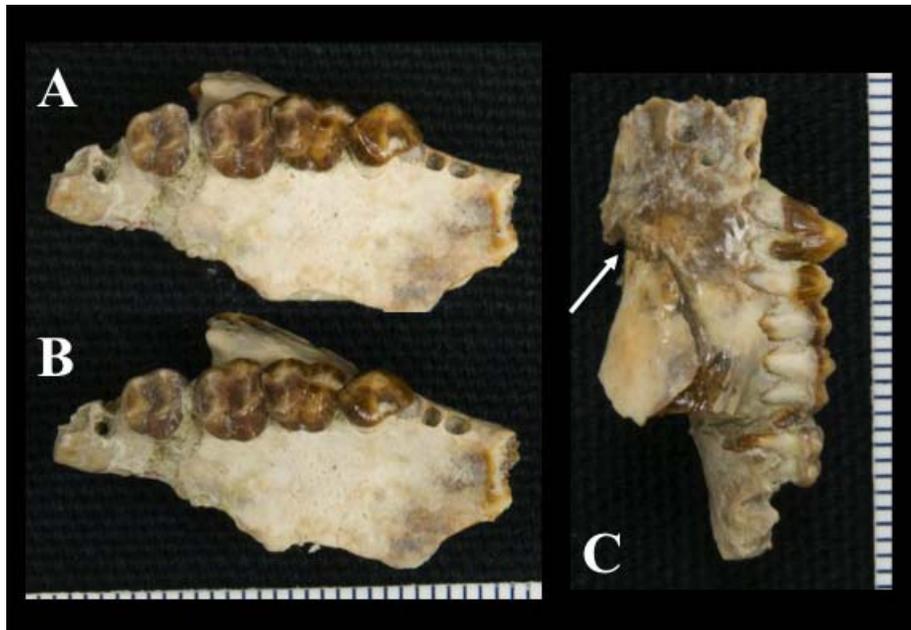


Figure 5. Holotype of *Eocuscus sarastamppi*, SAM P44324, a right maxilla with P3-M3 present, plus the alveoli for double-rooted P1 and M4. A) Occlusal view, note the extended parastyle and lack of anterior cingulum on M1; B) Occlusal view, to complete a stereopair of the dentition; and C) Labial view, note the continuous shearing surface from P3 onto the parastyle of M1, also note the opening of the lacrimal foramen which is inside the border of the orbit, the maxilla contributes to the anteroventral half of the foramen, while the lacrimal bone contributes to the posterodorsal half of the foramen. The scale is marked in millimeters.

P3--The third premolar is aligned with the arch of the upper molar arcade. The blade of P3 has its shearing angle continued on the anteroposterior bladed paracone. P3 has a single central cusp with a crest descending to the crown, both anteriorly and posteriorly, and the cusp extends well past the occlusal

level of M1 creating a dagger-like shape in lateral view. There are three small cuspules or denticles posterior to the central cusp along the steeply inclined posterior crest. There are no vertical ridges associated with the cuspules. The anterior crest curves lingually and creates a concave space on the anterolingual face of the tooth, whereas the anterobuccal face is convex. The tooth is widest in occlusal aspect below the central cusp. It then narrows posteriorly in a slightly shorter distance than the anterior half of the tooth. A posterolingual ridge descends from the posterior crest at a point where the posterior crest contacts the parastyle of M1. This ridge continues along the crown margin trending in an anterolingual direction, creating a lingual cingulum that extends anteriorly for two-thirds the crown length.

M1--This tooth is rectangular in occlusal outline. There is an extreme height differential between the buccal cusps and the lingual cusps, which is independent of wear. The paracone and metacone are tall and are at the labial margin of the tooth. Their respective labial faces are rounded with a slight ectoflexus between them. In contrast, the lingual faces of the paracone and metacone are vertical and flattened, and with their associated cristae, present a bladed appearance, anteroposteriorly. The preparacrista is oriented anteriorly and continues the shearing effect of the P3 in a carnassial notch-like morphology. The preparacrista has two cuspules along the crest, one halfway along and the second almost at its anterior terminus. The centrocrista between the paracone and metacone is linear and anteroposteriorly oriented. The centrocrista acts as a bladed crest on the posterior face of the paracone and the anterior face of the metacone as two cusps adjacent to each other. There is a larger cuspule on the premetacrista portion of the centrocrista. The postmetacrista has a kink near the apex of the lingually oriented metacone, and then bends at a right angle resulting in a longer posterior segment; it is thus parallel to, but offset lingually from, the centrocrista and preparacrista. At the corner of the metastyle is a small stylar cusp in the E position. The protocone is a low, conical cusp with a low transverse ridge that extends from near the apex of the protocone to the base of the paracone. The ridge then extends partially up the lingual face of the paracone forming the typical semilophate morphology seen in the phalangerids and other diprotodontians. There is no preprotocrista nor is there an anterior cingulum. These latter characters are the result of the bladed paracone and its continuation of the shearing surface of P3. The metaconule is fully hypertrophied to make the fourth cusp in the posterolingual position equal in size to the protocone and like that cusp, it is low and conical. A more robust ridge than present in the paraloph connects the metacone to the metaconule, which begins at the kink in the postmetacrista and continues transversely to the metaconule. At the midpoint of the ridge is a distinct swelling indicating the position of the neometaconule. The postmetaconular crista continues around the posterior margin of the tooth to form a posterior cingulum.

M2--The second molar is distinctly wider than M1, both anteriorly and posteriorly, but shorter because it lacks the anteriorly expanded parastyle. As with M1, there is a distinct stylar cusp present along the buccal margin. The stylar cusp on M2 is anterior to the paracone in the position of a stylar cusp A, whereas on M1 the stylar cusp is in the E position. There is a cuspule on a crest extending anteriorly from the metacone, which is separate from the centrocrista. If this is a stylar cusp and not a neomorphic cuspule, then the cuspule would be a stylar cusp C. The anteriorly directed parastyle is less well developed on M2 than on M1. The paracone has a conical buccal face, but the lingual face is flat and vertical as on M1. The centrocrista is not linear, as the postparacrista is oriented posterolingually, while the premetacrista is oriented posterobuccally. The metacone, like the paracone, is a more conical cusp than on M1. The postmetacrista descends from the metacone apex and about halfway down the posterior face it begins to bend lingually, eventually becoming continuous with the postmetaconular crista to form a laterally wide posterior cingulum. The protocone is pyramidal in shape because of the formation of the paraloph. Without the influence of an extended parastyle, the pre- and postprotocristae form a more acutely angled structure around the protocone; the preprotocrista extends buccally to the parastyle forming an anterior cingulum. The paraloph is kinked anteriorly just lingual to the apex of the paracone and then extends transversely as a raised ridge to intersect the preprotocrista just anterior to the protocone. In the middle of the paraloph is a neomorphic cusp, the neoparaconule. The metaconule is smaller than the protocone which corresponds to a smaller metacone than paracone. The premetaconular crista is short and anterobuccally directed, and it meets with the postprotocrista at the lingual margin of the interloph valley. The post metaconular crista helps form the posterior cingulum. The metaloph is slightly V-shaped

anteriorly, beginning at the apex of the metacone and terminating at the metaconule. The metaloph is a robust structure with sloping anterior and posterior faces. A small cuspule is present near the midline representing a neometaconule.

M3--The third molar is both shorter and narrower than M1 or M2 (Table 1). The paracone is the largest buccal cusp and is pyramidal in shape with a flattened buccal face and a pointed lingual face. The preparacrista is short, anteriorly directed, and it terminates in a cuspule in the styler cusp A position. The postparacrista is longer, posteriorly directed, and it runs buccally to the premetacrista, which is shorter and terminates on the flank of the postparacrista forming a high wall on the labial side of the interloph valley. The paraloph is segmented with a short crest from the apex of the paracone that is truncated at a narrow anteroposteriorly oriented groove just labial to the neoparaconule. The latter has a short, lingually directed crest that terminates on the flank of the preprotocrista, just anterior to the apex of the protocone. The metacone is pyramidal in shape, like the paracone, with the buccal face flattened and the lingual face pointed. The postmetacrista is initially posteriorly directed, but bends at a right angle lingually to form, with the postmetaconular crista, the posterior cingulum. The protocone is very broad and is the largest cusp of the tooth, with the pre- and postprotocristae forming a very obtuse angle that is nearly linear in shape. The preprotocrista is thicker as it descends from the apex of the protocone anteriorly and then thins as it bends labially at a right angle to form the anterior cingulum. The postprotocrista is truncated and ends at the lingual opening of the interloph valley. The metaconule is conical in shape and lacks a premetaconular crista. The postmetaconular crista is labially directed and forms part of the posterior cingulum. The metaloph is much narrower mediolaterally than the paraloph, reflecting the abrupt decrease in tooth size from the M3 to M4. The metaloph is a narrow transverse ridge with low sloping anterior and posterior faces. A neometaconule occurs midway along the metaloph.

M4--The morphology of this tooth is presented only by the root pattern of the alveoli posterior to the M3. The breadth across the two anterior roots indicates that the anterior half of the tooth was no wider than the posterior half of M3, while the posterior half of the M4 probably ended in a round point as there is only a single circular root to support the posterior crown of the tooth.

Table 1. Measurements of the dentition of the Oligocene phalangerid, *Eocuscus sarastamppi* gen. et sp. nov., from the Etadunna Formation, South Australia (mm).

Tooth	Length	Ant. Width	Post. Width
P3	4.34	2.28	3.36
M1	4.74	4.15	4.14
M2	4.19	4.49	4.24
M3	4.00	3.49	3.08

Discussion

Premolars anterior to P3--There are two circular alveoli anterior to P3 with the anterior of the two having the greater diameter (Fig. 5). There is no diastema between the posterior alveolus and P3, but there is a diastema between the canine alveolus and the anterior of the two premolar alveoli. These two alveoli raise the question of whether the two alveoli represent a double-rooted P1 or P2, or the combination of a single-rooted P1 and a single-rooted P2. In *Onirotociscus reidi* (type specimen, QMF42702; Crosby, 2007) there is also an anterior set of paired alveoli, although they are separated anteromedially from P3 by a diastema. Also anteromedially to P3, but located at its base, is a small alveolus for a single rooted premolar. Thus, the single rooted tooth immediately anteromedial to P3 would be a regressive, single-rooted P2, and the two alveoli anterior to P3 would represent a double-rooted P1 separated from the P3 by a diastema. In extant phalangerids, the P1 has become single-rooted and separated from both the P3 and the C by a diastema. The P1 can be either caniniform or a regressive peg. In some phalangerid specimens a nubbin premolar is present just anterior to P3 (representing a regressive P2), where the P1 is present in the middle of the diastema between P3 and the canine. The condition in *Eocuscus* of having no diastema between P1 and P3 is a plesiomorphic state relative to all other known extinct and extant phalangerids.

Comparison to Middle Miocene phalangerids--*Eocuscus sarastamppi* differs from phalangerids from the middle Miocene, Riversleigh local faunas from northwest Queensland by a number of autapomorphies or plesiomorphies absent in the Riversleigh taxa. *Onirotocuscus reidi* (Crosby, 2007) resembles extant phalangerids to the point that *O. reidi* was originally assigned to the extant genus *Stigocuscus* (Flannery and Archer, 1987).

Eocuscus differs from *Onirotocuscus* by the following features, where the plesiomorphic states and autapomorphic states for *Eocuscus* are designated (P) and (A), respectively: lacrimal foramen inside orbit and not on face (A); lacrimal foramen shared between maxilla and lacrimal rather than entirely within lacrimal (A); sphenopalatine foramen not in a groove leading to infraorbital foramen (A); no diastema between P1 and P3 (P); P3 aligned with arch of upper molar arcade (P); blade of P3 has shearing angle continued onto anteroposterior bladed paracone (P), whereas P3 of *Onirotocuscus* is set at a distinctly oblique angle to molar row.

The P3 of *Eocuscus* has a single central cusp with a crest descending to the crown both anteriorly and posteriorly (P). In *Onirotocuscus*, the P3 has its major cusp located anteriorly followed by four cuspules or denticles set posteriorly creating a more horizontally oriented blade rather than the dagger-like shape of *Eocuscus*. There is an extreme height differential between the buccal cusps and the lingual cusps which is independent of wear on the M1 of *Eocuscus* (A). The paracone and metacone are tall and bladed anteroposteriorly (A). Conversely the protocone and the metaconule are conical cusps with little to no cresting associated with them outside of the loph structures (P). There is no anterior cingulum on the M1 of *Eocuscus* (P), where an anterior cingulum is present in *Onirotocuscus*.

Eocuscus retains distinct stylar cusps on the first two molars. On M1 the stylar cusp is posterior to the metacone in the E position, while on the M2 the stylar cusp is anterior to the paracone in the A position (P). *Onirotocuscus* does not appear to have any stylar cusps, which is typical of modern phalangerid taxa.

The molar morphology present in extant phalangerid taxa and the morphology of the upper molars of *Onirotocuscus* are clearly semilophate in overall form with a distinct crest extending from the apex of each buccal cusp to the base of the opposing lingual cusp. The upper molars of *Eocuscus* exhibit no continuous cresting between the buccal cusps and the lingual cusps. Instead, there are prominent intermediate neomorphic conules (neoparaconule and neometaconule, respectively) between both the anterior major cusps and between the posterior major cusps. Thus, the upper molars of *Eocuscus* are more plesiomorphic in their molar loph morphology than in *Onirotocuscus* or any modern phalangerid.

Eocuscus differs in its morphology, both in autapomorphic and plesiomorphic character states, from *Trichosurus dicksoni* from the middle Miocene Riversleigh local faunas and *T. hamiltonensis* from the Hamilton local fauna of Hamilton, Victoria, both of which were described by Flannery and Archer (1987). The comparisons will be based solely on the dentition, as these are the only corresponding parts between these taxa.

Again for *Eocuscus*, the P3 is aligned with the arch of the upper molar arcade. The blade of P3 has its shearing angle continued on the anteroposterior bladed paracone (P). The P3 of *T. hamiltonensis* is set at a distinctly oblique angle to the molar row based on the oblique orientation of p3. Additionally, the P3 of *Eocuscus* has a single central cusp with a crest descending to the crown both anteriorly and posteriorly (P). In both *Trichosurus dicksoni* and *T. hamiltonensis*, the P3 has its major cusp anteriorly followed by a series of cuspules set posteriorly creating a more horizontally oriented blade rather than the dagger-like shape of *Eocuscus* (P). Again, the P3 morphology of the *Trichosurus* species is based on and correlated to the morphology of the p3.

For M1, there is an extreme height differential between the buccal cusps and the lingual cusps, which is independent of wear in *Eocuscus* (P). The paracone and metacone are tall and bladed anteroposteriorly (P). Conversely, the protocone and metaconule are conical with little to no cresting (P). There is a very low parastyle along the lingual face, and extending to the base, of the paracone (P). There is no anterior cingulum (P). These latter characters are the result of the bladed paracone and its continuation of the shearing of the P3. All of the above features are different from the conditions seen in *T. dicksoni* or *T. hamiltonensis*, where the development of the paraloph and the metaloph is more substantial and thus the upper molar has the more typical and more derived condition of a semilophate

appearance as in modern phalangerids. Additionally, the preparacrista in *Trichosurus dicksoni* or *T. hamiltonensis* drops from the cusp apex to the crown base over a very short distance compared to the anteriorly bladed preparacrista in *Eocuscus*.

On both M1 and M2 of *Eocuscus*, there are distinct styler cusps present along the buccal margins. The M1 has a styler cusp posterior to the metacone in the styler cusp E position, while the M2 has a styler cusp that is anterior to the paracone in the styler cusp A position. Neither *Trichosurus dicksoni* nor *T. hamiltonensis* appear to have styler cusps on M1 or M2, which is typical of the upper molar morphology in modern phalangerids.

Upper molars of *Trichosurus dicksoni* and *T. hamiltonensis* strongly resemble those of extant phalangerids in their semilophate (paraloph and metaloph) morphology. There is also a distinct crest extending from the apex of each buccal cusp to the base of the opposing lingual cusp, which is absent in *Eocuscus*. Rather, in the latter there are intermediate conules (neoparaconule and neometaconule, respectively) between the anterior and posterior major cusps, which are not incorporated into the lophs. These features indicate that the upper molar pattern of *Eocuscus* is more plesiomorphic in its morphology than in either *Trichosurus dicksoni* or *T. hamiltonensis*, or in any modern phalangerid. Thus, the extant phalangerid taxa differ from *Eocuscus* in nearly all of the same cranial and dental character states as do the extinct phalangerid taxa. Based on this, *Eocuscus sarastamppi* from the late Oligocene of South Australia represents an archaic sister taxon to all extant phalangerid species as well as all fossil Neogene species (Fig. 6).

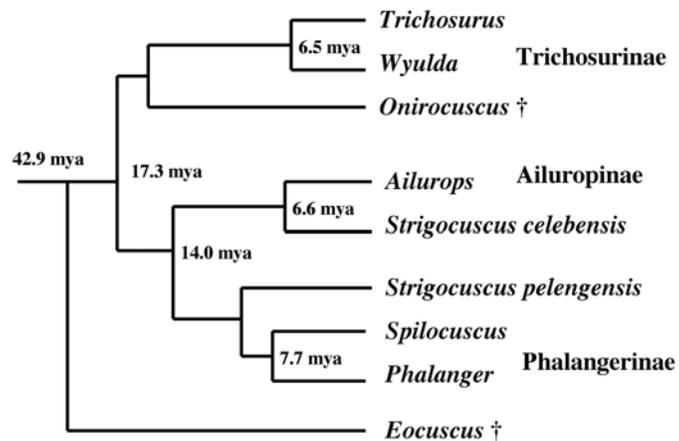


Figure 6. Generic level phylogeny of Phalangeridae based on the molecular studies of Meredith et al. (2009) Ruedas and Morales (2005) and Kirsch & Wolman, (2001) with the inclusion of fossil genera *Onirocuscus* (Crosby, 2007) and *Eocuscus* (this study) Note that *Eocuscus* is the sister taxon to all of the other phalangerid taxa and is not a member of the three known subfamilies. All numbers are divergence data in million of years from Meredith et al. (2008).

PHYLOGENY AND BIOGEOGRAPHY

Phylogeny

Since phalangerids were first described, their taxonomy has been in a constant state of flux (Pallas, 1766; Tate, 1945; Colgan et al., 1993; Flannery 1994, 1995a, 1995b; Flannery and Calaby, 1987; Flannery et al., 1987; George, 1987; Groves, 1987a, 1987b, 1993; Norris and Musser, 2001; Ruedas and Morales, 2005; Fig. 7). Ruedas and Morales (2005) divided Phalangeridae into the three subfamilies (Phalangerinae, Trichosurinae, Ailuropinae) based on analyses of mitochondrial DNA. Phalangerinae (*Phalanger* and *Spilocuscus*) and Ailuropinae (*Ailurops* and *Stringocuscus*) are sister groups to each other and comprise the sister group to Trichosurinae (*Trichosurus* and *Wyulda*) (Fig. 8B). These evolutionary relationships are also supported by the DNA hybridization (Kirsch and Wolman, 2001), the BRCA1 gene sequences (Raterman et al., 2006), and the five-gene nuclear concatenation analysis of Meredith et al.

(2009). However, *Strigoscus* and *Wyulda* were not included in the analyses of Raterman et al. (2006) or Kirsch and Wolman (2001).

Prior to the aforementioned molecular studies, most workers viewed *Ailurops* (Ailuropini) as basal to a Trichosurini (*Strigoscus*, *Trichosurus*, and *Wyulda*) + Phalangerini (*Phalanger* and *Spilocus*) clade, i.e., Phalangerinae (George, 1987; Flannery et al., 1987; Norris, 1994; Fig. 8A). These results were based on putative shared derived cranial and dental features even though Phalangeridae is considered morphologically conservative with few cranial and dental synapomorphies (Flannery et al., 1987). In fact, Flannery et al. (1987) suggested that only some species of *Trichosurus* are moderately divergent from what they considered the “basic phalangerid ground-plan.” Many of the features used in their phylogenetic analysis are minute and may with further scrutiny turn out to be variable for a given genus/species.

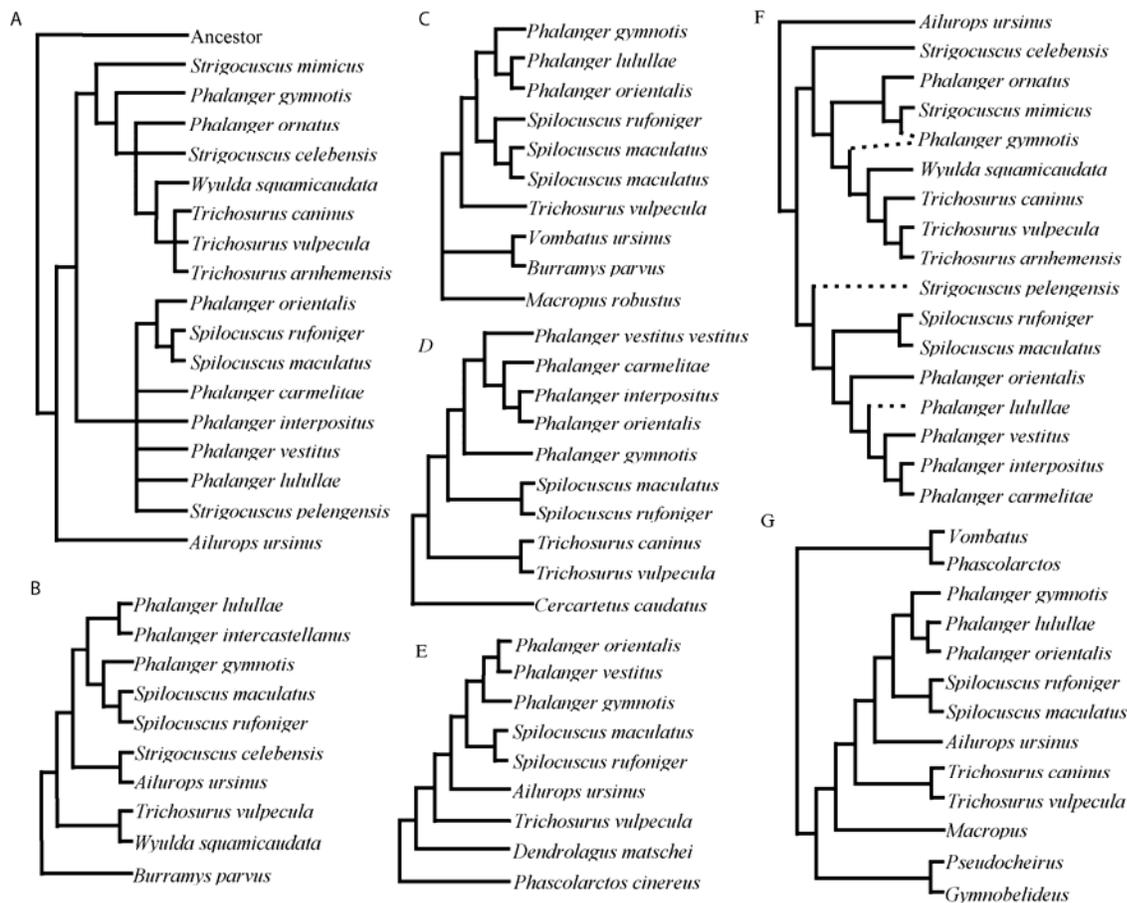


Figure 7. Previously obtained phylogenies for Phalangeridae. **A**, Morphological consensus tree of 94 most parsimonious trees of Flannery et al. (1987), data set reanalyzed by Ruedas and Morales (2005); **B**, Partial 12S rRNA ML tree (Ruedas and Morales, 2005); **C**, Partial 12S rRNA ML tree (Hamilton and Springer, 1999); **D**, DNA-DNA hybridization tree (Springer et al., 1990); **E**, DNA-DNA hybridization tree (Kirsch and Wolman, 2001); **F**, Proposed morphological phylogeny of Flannery et al. (1987); **G**, ML tree of the nuclear gene BRCA1 of Raterman et al. (2006). Dashed lines indicate uncertain relationships.

Biogeography

Ailurops is found on Sulawesi and the nearby islands of Togian, Peleng, Muna, Buton, and Lirong, while *Strigoscus* is found only on Peleng and Taliabu just east of Sulawesi. The range of *Spilocus* includes northern Australia, New Guinea, Baro, Ceram, and Selayar, whereas the range of

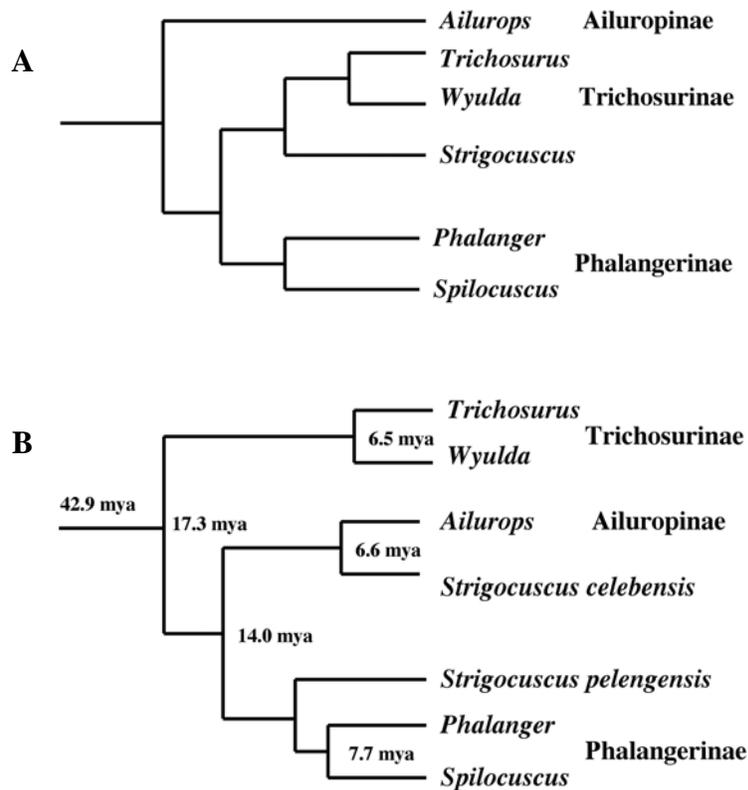


Figure 8. Generic and subfamilial relationships within Phalangeridae. **A**, Phylogeny based on morphological data of Flannery et al. (1987). **B**, Phylogeny based on molecular data of Meredith et al. (2009), Raterman et al. (2006), Ruedas and Morales (2005), and Kirsch and Wolman (2001). All numbers are divergence data in million of years (from Meredith et al., 2008).

Phalanger extends from northern Australia to New Guinea. *Wyulda* is restricted to northern Australia while *Trichosurus* is found throughout Australia and Tasmania (Flannery, 1994; Kirsch and Wolman, 2001) (Fig. 1).

Reconstructing the biogeographical history of the Phalangeridae is complicated by the very intricate and poorly understood geological history of Southeast Asia (Hall, 1998). As a result, the interpretation of the biogeographic history of phalangerids that we provide can only be considered tentative. The molecular phylogenies presented in this paper are considered more reflective of the true evolutionary relationships of Phalangeridae than previous morphological analyses, as the molecular phylogenies show high levels of congruence between them versus what has been seen in the morphologically based phylogenies.

The favored morphological phylogeny of Flannery et al. (1987) suggests that the most primitive members of Ailuropinae and Phalangerinae (*Ailurops* and *Strigocuscus*, respectively) are found on islands west of New Guinea (Fig. 1). According to Flannery et al. (1987) the ancestors of Ailuropine were widespread throughout Australasia. Subsequently, the ancestor of *Ailurops* became isolated on Sulawesi shortly after its emergence in the middle Miocene. Trichosurins then replaced ailuopins over the rest of Australasia, except for Sulawesi. At about the same time, the ancestor of *Strigocuscus* arrived in the Sulawesi region. However, none of the described forms from the early Tertiary of Australasia are allied to the supposed basal Ailuropini, but instead are placed in Trichosurini (*sensu* Flannery et al., 1987). As a result, Flannery et al. (1987) suggested that *Ailurops*, and possibly *Strigocuscus*, reached Sulawesi soon after it emerged from the ocean possibly by waif dispersal. *Trichosurus* diversified in Australia and by the late Miocene or early Pliocene *Phalanger* and *Spilocuscus* diversified in the newly formed northern

parts of New Guinea. In summary Flannery et al.'s (1987) phylogeny requires multiple invasions of the Sulawesi region to account for the distribution of plesiomorphic taxa in Sulawesi and their disappearance from Australia.

The congruent molecular phylogenies, which support a basal split between trichosurines and other phalangerids and a sister group relationship between *Ailurops* and *Strigocuscus celebensis*, favor a different and less complex biogeographical hypothesis. Accordingly, the current biogeographical distribution and evolutionary relationships of Phalangeridae can be explained by two dispersal/vicariant events. The first vicariant/dispersal event accounts for the basal split between Trichosurinae and the Phalangerinae + Ailuropinae clade, and the second dispersal/vicariant event accounts for the split between the Ailuropinae and Phalangerinae (Kirsch and Wolman, 2001; Ruedas and Morales, 2005; Raterman et al., 2006; Meredith et al., 2009).

Molecular divergence dates from DNA hybridization (Kirsch et al., 1997; Kirsch and Wolman, 2001), mitochondrial DNA studies (Springer, 1997; Ruedas and Morales, 2005), and nuclear DNA studies (Meredith et al., 2008) suggest that Trichosurinae and Phalangerinae + Ailuropinae diverged from one another 17.3-27.3 mya (Fig. 8B). This is concordant with the geological reconstructions proposed by Flannery (1995a, b) and Hall (1998). Flannery suggested that New Guinea and Australia were continuous with one another 37-24 mya, but by 20-25 mya New Guinea consisted of several isolated islands separate and distinct from the Australian mainland. Hall, on the other hand, suggested that New Guinea and Sulawesi were submerged until 20-25 mya. Either way, the isolation/emergence of these islands possibly facilitated this basal phalangerid split.

The molecular divergence between Phalangerinae and Ailuropinae has been estimated to have occurred 16-23.3 mya (Kirsch and Wolman, 2001; Ruedas and Morales, 2005). The movement of crustal fragments in Southeast Asia can possibly explain the divergence of the Phalangerinae from the Ailuropinae. The Philippine or Molucca Sea plate had been carrying the Bird's Head microcontinent westward for the past 50 million years (Hall, 1996, 1998). The Buton-Tukang Besi block separated from the Bird's Head microcontinent 17-15 mya, accreting onto the Sulawesi Southeastern Peninsula approximately 11 mya (Hall, 2002), and possibly transporting an Ailuropinae ancestor. It is also a possibility that the ancestral Ailuropinae dispersed westward, island to island, eventually ending up in the Sulawesi region. Furthermore, the radiation of *Phalanger* and *Spilocuscus* can be explained by the rising of the New Guinean highlands approximately 15 mya (George, 1987; Archer et al., 1989). The presence of *Phalanger* and *Spilocuscus* in Cape York (mainland Australia) are only recent arrivals from their northerly distribution during one of the more recent lowerings of sea level separating mainland Australia from New Guinea and its adjacent islands (Kirsch and Wolman, 2001).

Fossil Phalangerids

Establishing a robust hypothesis of evolutionary relationships among Phalangeridae has important ramifications for naming and interpreting the fossil record of this family. Currently, the fossil phalangerid record of Australasia is depauperate and very poorly known. Previous to this study the earliest record of possible phalangerids consisted of undescribed species from the early Miocene Geilston Bay Fauna in Tasmania (Tedford et al., 1975). Neogene fossils from the mainland of Australia are only known from Riversleigh in northwestern Queensland. The Riversleigh specimens were assigned to the living genera *Trichosurus*, *Wyulda*, and *Strigocuscus* (Flannery and Archer, 1987). Recently, Crosby (2007) reassigned the Riversleigh specimens of *Strigocuscus* to the new genus *Onirocuscus*. Crosby (2007) also suggested that *Trichosurus dicksoni* may require a new generic assignment. Rich et al. (1982) mentioned the presence of phalangerids from the late Oligocene Pinpa, Ericmas, and Tarkarooloo local faunas of east central South Australia. (Frome Basin, Namba Formation; Fig. 2) However, Archer et al. (1987) identified the material from the Pinpa local fauna as pilkipildrids. Furthermore, much of the remaining material from the other localities is scrappy and fragmentary and may as well be referable to the pilkipildrids and/or miralinids (Flannery et al., 1987). Phalangerid fossils are more common in late Tertiary and Holocene deposits. There are early Pliocene forms of living genera from the Hamilton local fauna of Victoria (Turnbull and Lundelius, 1970), the Chinchilla local fauna from the Chinchilla Sands of

southeastern Queensland (Archer and Hand, 1984), and the Bow local fauna of eastern New South Wales (Archer and Hand, 1984).

With Crosby's (2007) reassignment of *Strigocuscus* to *Onirotocuscus*, the suggestion that *Strigocuscus*, and even perhaps *Ailurops* (Ailuropinae), once had a much larger geographic distribution over much of northern Australia, New Guinea, and the surrounding islands connecting Sulawesi begins to fall away. It is also possible that this misidentification is simply the result of the unstable nomenclature associated with the ground cuscus, *Phalanger gymnotis* (see George, 1987; Flannery et al., 1987; Hamilton and Springer, 1999, for a more detailed account of its nomenclatural history). Flannery et al. (1987) considered *P. gymnotis* a species of *Strigocuscus*, placing it within the Trichosurini. With this classification Flannery and Archer (1987) and Flannery et al. (1987) described two fossil phalangerids as *Strigocuscus*: *S. reidi* and *S. notialis* from the Miocene deposits of Riversleigh and the early Pliocene Hamilton local fauna of western Victoria, respectively, both of which are now placed in *Onirotocuscus*, a trichosurine genus. In the description of both of these fossil forms it was suggested by the authors (Flannery et al., 1987) that the specimens were closely allied to *P. gymnotis* and possibly even ancestral. However, there is now overwhelming evidence suggesting that *P. gymnotis* is more closely related to species of *Phalanger* than to species of *Strigocuscus* (George, 1987; Norris, 1994; Springer et al., 1990; Hamilton and Springer, 1999; Kirsch and Wolman, 2001; Ruedas and Morales, 2005; Raterman et al., 2006; Meredith et al., 2009). Meredith et al. (2009) also demonstrated that *Strigocuscus* is diphyletic in that *Strigocuscus celebensis*, as indicated above, is closely related to *Ailurops*, as both are ailuropines, while *Strigocuscus pelengensis* from the Moluccan islands, east of the Celebes islands, groups with high levels of support with *Phalanger* and *Spilocuscus*, and is thus a phalangerine phalangerid (Fig. 8B). Consequently, ailuropine phalangerids would represent the furthest dispersal of the family from Australia by the most derived species within the family contrary to the interpretations based on the morphological studies (e.g., Flannery et al., 1987).

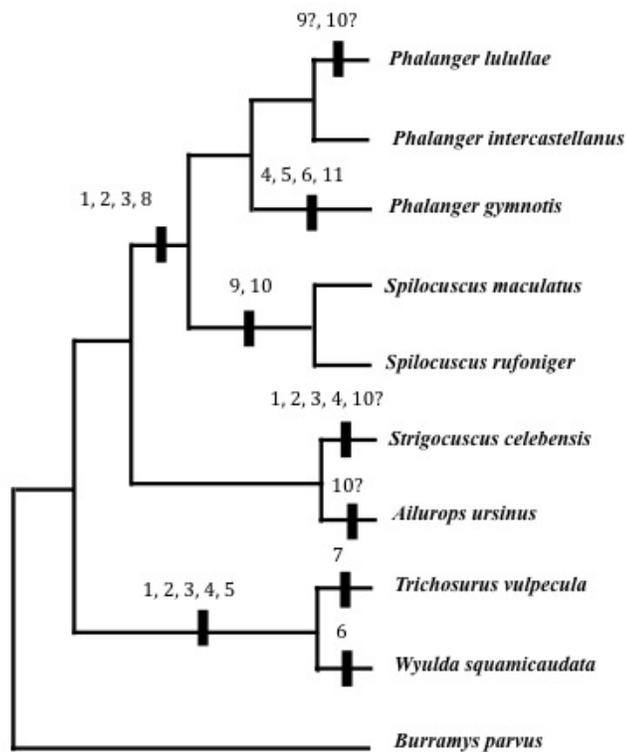


Figure 9. The phylogenetic tree of Flannery et al. (1987) illustrating the twelve characters applicable to those characters present in *Eocuscus sarastamppi*. *Phalanger intercastellanus* has not been coded for any of these characters, but is assumed to have the same states as *Phalanger lulullae*, which it may or may not. Numbers refer to characters listed in Table 2; Character 12 from Table 2 is absent in all the taxa represented in the above phylogeny. ?= character state unknown.

The new referral of the Riversleigh and Hamilton specimens of *Strigoscus* to *Oniroscus*, which is not related to extant species of *Strigoscus*, also explains the lack of Phalangerinae fossils in Australia, given that they are the most speciose phalangerids in the rainforest habitats of New Guinea and the surrounding islands (Springer et al., 1990; Hamilton and Springer, 1999). However, it is commonly thought that the presence of Phalangerinae on mainland Australia is relatively recent and that their presence may represent re-entry dispersal. Furthermore, the unusual sympatry of *Trichosurus* with *Strigoscus* at the Riversleigh and Hamilton localities can be explained away by Crosby's (2007) reinterpretation as being two trichosurines, *Oniroscus* and *Trichosurus* (Fig. 6).

Eoscus, the new fossil phalangerid described herein, in addition to the above line of reasoning concerning the absence of *Strigoscus* in the Australian fossil record, has important ramifications for the possible origin of Phalangeridae. *Eoscus* extends the fossil range of Phalangeridae back to the late Oligocene and represents the oldest identifiable phalangerid anywhere in Australia. Due to the limited number of phylogenetically informative characters preserved in the new fossil specimen, and that the character states preserved represent either plesiomorphic or autapomorphic states peculiar to *Eoscus*, it is not possible to place *Eoscus* into one of the three extant phalangerid subfamilies of Ruedas and Morales (2005) (Fig. 6). The only two morphological studies that have looked at more than a couple of phalangerid species are those of Flannery et al. (1987) and Norris (1994). Only the Flannery et al. (1987) study is applicable to the character states present in *Eoscus* (Table 2). Of these characters, only the lack of an I³-C¹ diastema can be considered a definitive synapomorphy of the Phalangerinae + Ailuropinae clade (Fig. 9) and this illustrates the incompatibility between molecular and morphological data for phalangerids.

Table 2. Of the 35 morphological characters used by Flannery et al. (1987), only these twelve are applicable to elucidating the placement of *Eoscus sarastamppi*. The (F + no.) after each character state are those from Flannery et al. (1987).

Derived Morphological Character State
1. I ³ reduced in size (F5)
2. Molar lophids relatively well-developed (F6)
3. P ² single rooted (F10)
4. P ³ is at oblique angle to the molar row (F15)
5. P ³ has at least four cuspules (F16)
6. P ³ very large (F18)
7. P ³ as high posteriorly as anteriorly (F20)
8. I ³ -C ¹ diastema lost (F27)
9. Molars complexly crenulated (F28)
10. M ¹ has metacone (F32)
11. I ³ is extremely small (F34)
12. Very large protoconule and neometaconule are present (F35)

CONCLUSIONS

A specimen of a phalangerid possum recovered from late Oligocene deposits of the Etadunna Formation, Lake Eyre Basin, South Australia, represents the oldest species of this family currently known. The numerous autapomorphic features and the retention of many plesiomorphic features places this new taxon, *Eoscus sarastamppi*, as the sister taxon to all other known phalangerids.

The presence of *Eoscus* in the late Oligocene of South Australia, and species of the Trichosurinae (*Oniroscus* and *Trichosurus*) from the Middle Miocene of Queensland, strongly suggest that the origin for the Phalangeridae resides in Australia and that the Trichosurinae is the first subfamilial branch within the phalangerid family tree. This interpretation implies that the phalangerid taxa of New Guinea and the Celebes are more derived and that they have established themselves through dispersal and vicariant events from a common ancestor after the radiation of the Trichosurinae on the mainland of

Australia. This biogeographic interpretation is supported by several recent molecular studies which indicate that the extant Trichosurinae (*Trichosurus* and *Wyulda*) is the sister taxon to the more derived Phalangerinae (*Phalanger* and *Spilocuscus*) + Ailuropinae (*Stigocuscus* and *Ailurops*) clades.

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