



Strigocuscus reidi AND *Trichosurus dicksoni*, TWO NEW FOSSIL PHALANGERIDS (MARSUPIALIA: PHALANGERIDAE) FROM THE MIOCENE OF NORTHWESTERN QUEENSLAND

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Two new phalangerids (Tribe Trichosurini) from Miocene sediments on Riversleigh Station, northwestern Queensland, are described. *Strigocuscus reidi* n. sp. is closely related to although more plesiomorphic than the living *Strigocuscus gymnotis*. *Trichosurus dicksoni* n. sp. shares a number of synapomorphies with living species of *Trichosurus* but is more plesiomorphic than any living form.

The presence of these species at Riversleigh indicates that the trichosurin radiation dates to at least the Miocene and that plesiomorphic phalangerids such as the living *Ailurops ursinus* diverged from other forms before Middle Miocene times.

Key Words: *Strigocuscus reidi*; *Trichosurus dicksoni*; Phalangeridae; Marsupialia; Miocene; Australia; Systematics.

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INTRODUCTION

TERTIARY phalangerids have been reported from the early Miocene Geilston Bay Local Fauna (Tedford *et al.* 1975), several central Australian Middle Miocene local faunas (e.g., Rich *et al.* 1982), the early Pliocene Hamilton Local Fauna (Turnbull and Lundelius 1970) and the early to Middle Pliocene Chinchilla and Bow Local Faunas (e.g., Archer and Hand 1984). Some of these occurrences, such as the taxa reported by Rich *et al.* (1982) from the Pinpa Local Fauna, have now been determined to represent pilkipildrids (a new family of phalangeriform marsupials) (Archer *et al.* 1987) and further notice of the Hamilton taxa is given in this Volume (Flannery *et al.* 1987). The remainder have yet to be described.

Only a single fossil species of phalangerid has previously been named. *Phalangista sicca* Owen, 1877 is based on an anterior portion of a dentary containing a broken I_1 , a P_3 and M_2 . The specimen, which is evidently now lost (Mahoney and Ride 1975) was said by Owen to come from an unspecified (Australian) cave deposit. Owen (1877) gives no description of the specimen and the buccal view illustrated (plate 5, fig. 12) is not sufficient to enable taxonomic assessment below the level of family. We therefore suggest that *Phalangista sicca* Owen, 1877 be considered a *nomen dubium* and that the name be allowed to lapse.

The systematics of the living phalangerids have until recently been poorly-understood. Flannery *et al.* (1987) is a revision of the living

forms in which eighteen species and five genera are divided between three tribes and two subfamilies. This taxonomy is followed here. Additional characterisation of the living species is given by George (1986).

Here we describe two new trichosurin species from Miocene deposits on Riversleigh Station, northwestern Queensland. One is closely related to the living *Strigocuscus gymnotis* and the other is the sister taxon to the previously known species of *Trichosurus*. This latter species is phenetically similar to the living *Strigocuscus celebensis*.

Interpretation of tooth number follows Archer (1978). QM F is a prefix for Queensland Museum fossil specimens.

SYSTEMATICS

Family Phalangeridae Thomas, 1888
Subfamily Phalangerinae Thomas, 1888
Tribe Trichosurini (Flynn, 1911)
Genus *Strigocuscus* Gray, 1861

Strigocuscus reidi n. sp.
(Fig. 1, Table 1)

Holotype. QM F13078, a partial skull with parts of the left and right premaxillae (edentulous), frontals, nasals, parietals, periotics, squamosals and a right maxilla fragment containing P^3 , M^{2-3} and a partial M^5 from Last Minute Site.

Paratypes. QM F13060, left M^3 , Gag Site; QM F13076, right dentary with, P_3 , M_{2-3} , Last Minute Site; QM F13075, left dentary with M_{3-5} , Last Minute Site; QM F13073, left M_2 , Gag Site; QM F13070, right M_2 , Gag Site.

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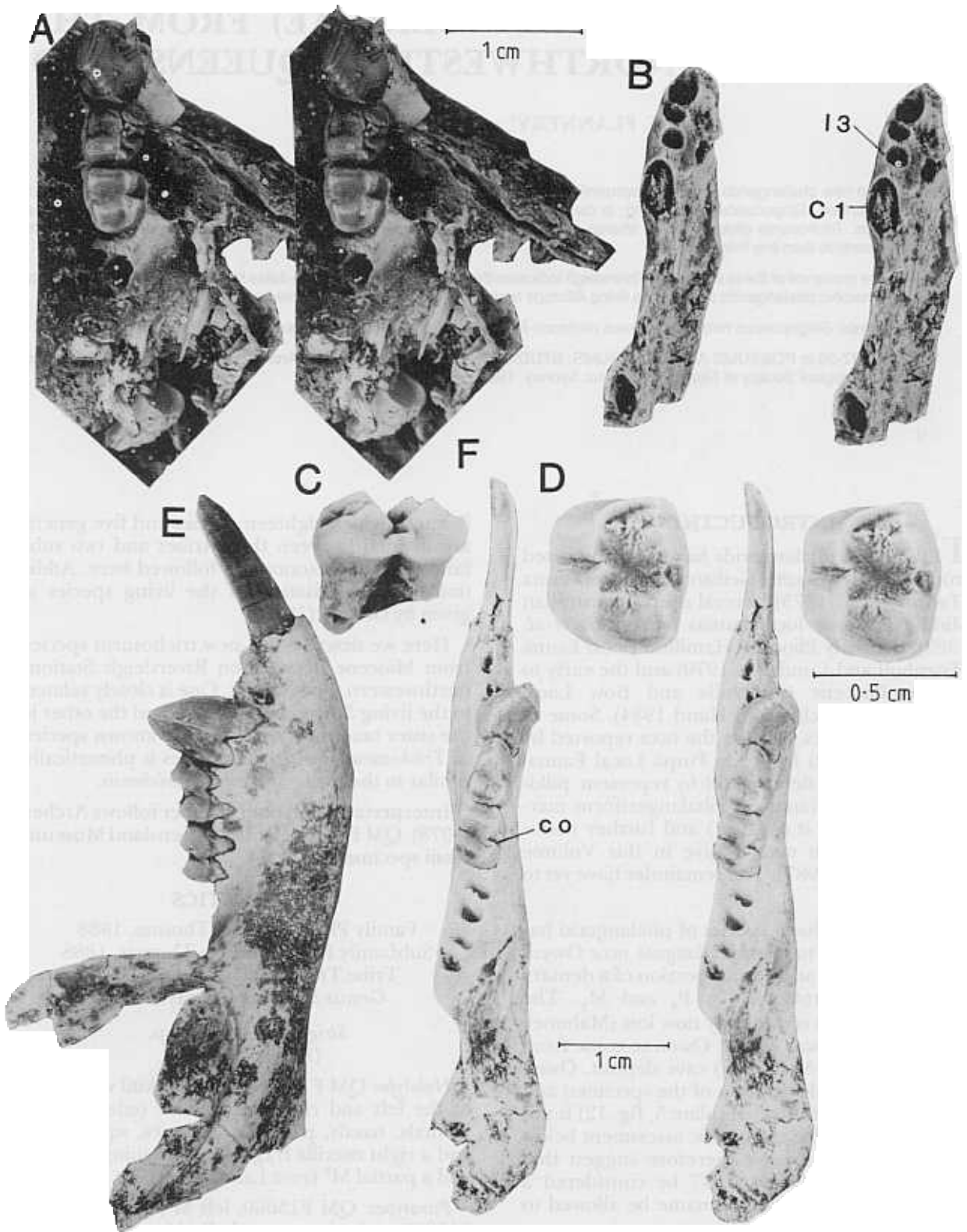


Fig. 1. A, stereopair of the occlusal view of the right P³, M²⁻³ and partial M⁵ of the holotype (QM F13078) of *S. reidi*. B, stereopair of the occlusal view of the right premaxilla of the holotype of *S. reidi*. C, buccal view and D, stereopair of occlusal view of a left M³ (QM F13060) referred to *S. reidi*. E, buccal view, and F, stereopair of occlusal view of a right dentary (QM F13076) with P₃, M_{2,3}, referred to *S. reidi*. Abbreviations: co, cristid obliqua; I³, alveolus for I³; C¹, alveolus for C¹.

Table 1. Dental measurements (in mm) for *Strigocuscus reidi*.

Specimen Number	Tooth	Length	Anterior Width	Posterior Width	Maximum Width
QM F13078 (Holotype)	P ³	6.2	—	—	5.0
	M ²	5.0	4.6	4.3	—
	M ³	5.0	4.9	4.5	—
QM F13060	M ³	5.4	4.7	4.8	—
QM F13076	P ₃	6.9	—	—	5.0
	M ₂	6.2	3.5	4.2	—
	M ₃	5.7	4.5	4.6	—
QM F13073	M ₂	6.2	3.3	4.5	—
QM F13070	M ₂	6.0	3.0	3.7	—
QM F13075	M ₃	5.9	4.5	4.6	—
	M ₄	5.7	—	4.4	—
	M ₅	5.1	4.2	3.6	—

Diagnosis. *Strigocuscus reidi* differs from all other members of the genus in possessing double-rooted lower premolars(?) anterior to P₃. In addition, it differs from all species except *S. gymnotis* in exhibiting extreme hypertrophy of P₃. It possess a short C¹-I³ diastema (not seen in *S. gymnotis*), has a preprotocrista that contacts the parastyle (not seen in *S. gymnotis* or *S. mimicus*), lacks the "accessory preprotocrista" seen on M² of *S. celebensis* and is larger than all species except *S. gymnotis*.

Etymology. This species is named in honour of Neil H. Reid, the Manager of Corporate and Scientific Programmes for IBM Australia Ltd, who has through IBM Australia Ltd, provided much-needed assistance for the Riversleigh Project.

Age and stratigraphy. The type locality, the Last Minute Site, occurs within isolated and unnamed Tertiary limestones on Riversleigh Station, northwestern Queensland. It is possible that these sediments are a lateral equivalent or previously unrecognized upper unit of the Carl Creek Limestone. Understanding of the stratigraphy and age of these sediments is presently being developed (Archer *et al.* in prep.). Because of overlap with marsupial taxa known from the Kutjamarpu Local Fauna, the age of these newly discovered Riversleigh deposits (Archer and Hand 1984) is tentatively concluded to be Middle Miocene.

Description. The skull of the holotype is badly crushed and broken. However, it retains portions of a number of bones.

The fragments of the premaxillae are very similar in morphology to those of *Strigocuscus gymnotis*. The premaxillae of *S. reidi*, however, are slightly more elongate and there is a small diastema (L = 1.2 mm) between the alveoli for I³ and C¹. The nasals are represented only by fragments of the anterior ends. They differ from those of *S. gymnotis* in being broader and in narrowing more rapidly from the point where

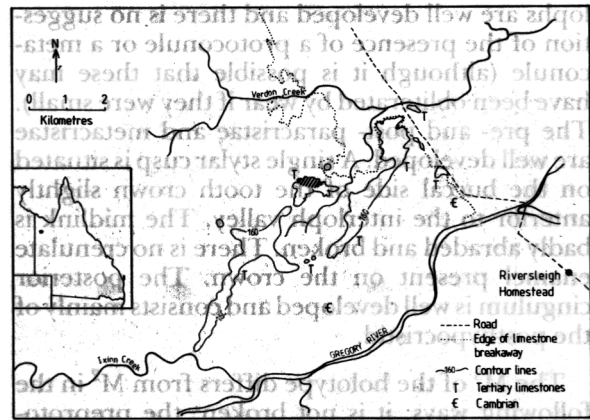


Fig. 2. Location of type localities of *Strigocuscus reidi* and *Trichosurus dicksoni*. The obliquely hatched area between Verdon Creek and the Gregory River contains Gag Site, Phalanger Site, Henk's Hollow and Last Minute Site. Detailed mapping of this region is underway.

they lose contact with the premaxilla to their anterior tip. Only the dorsal-most portion of the frontals are preserved. They show the presence of two well developed supraorbital ridges placed dorsal and posterior to the orbits. On the parietals, these ridges fuse to form a well developed sagittal crest. A fragment of the posterodorsal portion of the squamosal is preserved, and it shows that this element was highly pneumatised, as in other phalangerines.

The periotic is very similar in morphology to that of *S. gymnotis*. Its ventral edge was apparently visible in a gap between the basioccipital and alisphenoid as in *S. gymnotis*.

Judging from the alveoli of the holotype, I¹ was larger than I³ and I³ slightly smaller than I² (Fig. 1b). The alveolus for the canine is situated about 1.2 mm posterior to the I³ alveolus and, judging from its size, the canine was larger than I¹. A badly broken alveolus for P¹ is situated approximately 4.2 mm posterior to the C¹ alveolus and 8.5 mm anterior to the P³. Because of breakage, it is not possible to determine if a P² was present.

The P³ of the holotype is set at a sharply oblique angle to the molar row with its long axis oriented anterobuccally (Fig. 1a). Its crown stands well above those of the molars. A deep depression, beginning posterior to the anterior-most cuspule and ending near the posterior edge of the tooth, is present on the buccal side. No such depression exists on the lingual side. Four cuspules are present along the apex of the tooth. A slight swelling suggests a posterolingual cusp. The anterior face of the tooth slightly overhangs the root.

The M² of the holotype is moderately worn, the enamel of the protocone and hypocone being breached by wear. The preprotocrista extends anterobuccally and contacts the parastyle. The

lophs are well developed and there is no suggestion of the presence of a protoconule or a metaconule (although it is possible that these may have been obliterated by wear if they were small). The pre- and post-paracristae and metacristae are well developed. A single stylar cusp is situated on the buccal side of the tooth crown slightly anterior to the interloph valley. The midlink is badly abraded and broken. There is no crenulate enamel present on the crown. The posterior cingulum is well developed and consists mainly of the posthypocristid.

The M^3 of the holotype differs from M^2 in the following ways: it is not broken; the preprotocrista is better developed; the single stylar cusp is reduced; and the midlink is interrupted at its lowest point by a fissure. It is not determinable whether this last feature was present in M^2 because of breakage.

An unworn M^3 (QM F13060, Fig. 1c-d) preserves details of the molar morphology not visible on the holotype. The crown differs from that of *S. gymnotis* in being less crenulate, in having the preprotocrista ascend in a more gentle arc towards the parastyle and in having a small cingulum present at the buccal end of the interloph valley. The protoloph is poorly developed relative to the hypoloph. A small, ill-defined cuspule which may be a protoconule is present in the middle of the protoloph. No such structure is present on the hypoloph, although a slight fissure interrupts the hypoloph at its lowest point.

Only a posterior fragment of M^5 remains. It is apparent that the hypoloph is narrower than the protoloph, that the protoloph is poorly formed and that the remaining enamel is non-crenulate.

A nearly complete right dentary (QM F13076) and a posterior portion of a left dentary of an older animal (QM F13075) are known. The dentary appears to increase greatly in robustness with age. QM F13076 has a relatively slender dentary and its molars exhibit only light wear while the dentary of QM F13075 is very robust and its molars are well worn. The ascending ramus rises at an angle of between 80-90 degrees from the plane of the molar row. The condyle is transversely elongate as in other phalangerids. Overall the dentary is very similar to that of *S. gymnotis*.

The I_1 is narrow and lanceolate and indistinguishable in morphology from that of *S. gymnotis*. A single small alveolus is present posterior to I_1 . This may possibly represent an I_2 . Immediately posterior to this and anterior to P_3 are two pairs of alveoli for two double-rooted teeth. These teeth are here designated P_1 and P_2 but they might alternatively be a canine and/or incisors.

The crown of the P_3 stands high above the molar row (Fig. 1e). Its occlusal edge is gently arcuate and ornamented by six cuspules. The tooth is tallest at the point of the second anterior-most cuspule. Only the anteriormost cuspule has long ridges descending buccally, lingually and anteriorly towards the crown base. The buccal and anterior ridges actually reach the base of the crown but the lingual ridge terminates about half way to the crown base. A well-developed wear facet is present on the posterobuccal portion of the tooth.

The trigonid of M_2 consists of a principal cusp which is the protoconid and a smaller, lingually positioned metaconid. A groove suggests the presence of a small protostylid on QM F13070 but the other M_2 's, possibly because of more extensive wear, do not clearly show this feature. A well-developed ridge descends anteriorly from the protoconid. A very slight anterior cingulum may be developed buccally and lingually at the anterior end of the paracristid. The cristid obliqua is well developed and bears a slight buccal kink near its posterior end. The hypolophid is low but well defined and the posterior cingulum is well developed.

The M_3 is broader than M_2 and the protolophid and hypolophid are subequal in width. The four conids are also subequal in height. The cristid obliqua bears a marked buccal kink and the paracristid exhibits a fissure anterior to its junction with the protoconid.

A single worn and broken M_4 (QM F13075) is known. It is similar in morphology to M_3 .

The only M_5 known (QM F13075) is extremely worn. It differs from M_4 in being smaller and in having a hypolophid that is markedly narrower than the protolophid.

Discussion. *Strigocuscus reidi* and *S. gymnotis* are clearly closely related. Phenetically they are very similar and are highly unusual among phalangerids in exhibiting extreme hypertrophy of P_3 , a feature otherwise seen only in *Trichosurus squamicaudata*. However, *S. reidi* is not thought to be related to *Trichosurus squamicaudata* because it lacks all of the synapomorphic features of the species of *Trichosurus*. Further, the I^3-C^1 diastema is relatively shorter than in species of *Trichosurus*. Diastema reduction is a derived condition seen among trichosurins only in *S. gymnotis* and *S. mimicus*. Flannery *et al.* (1987) note that *S. gymnotis* is probably a trichosurin convergent on phalangerins. This hypothesis receives some support from the morphology of *S. reidi* because this Miocene taxon lacks some of the possible synapomorphic features shared between *S. gymnotis* and phalangerins, such as absence of a C^1-I^3 diastema, presence of a contact between the preprotocrista and parastyle and lack of noticeably

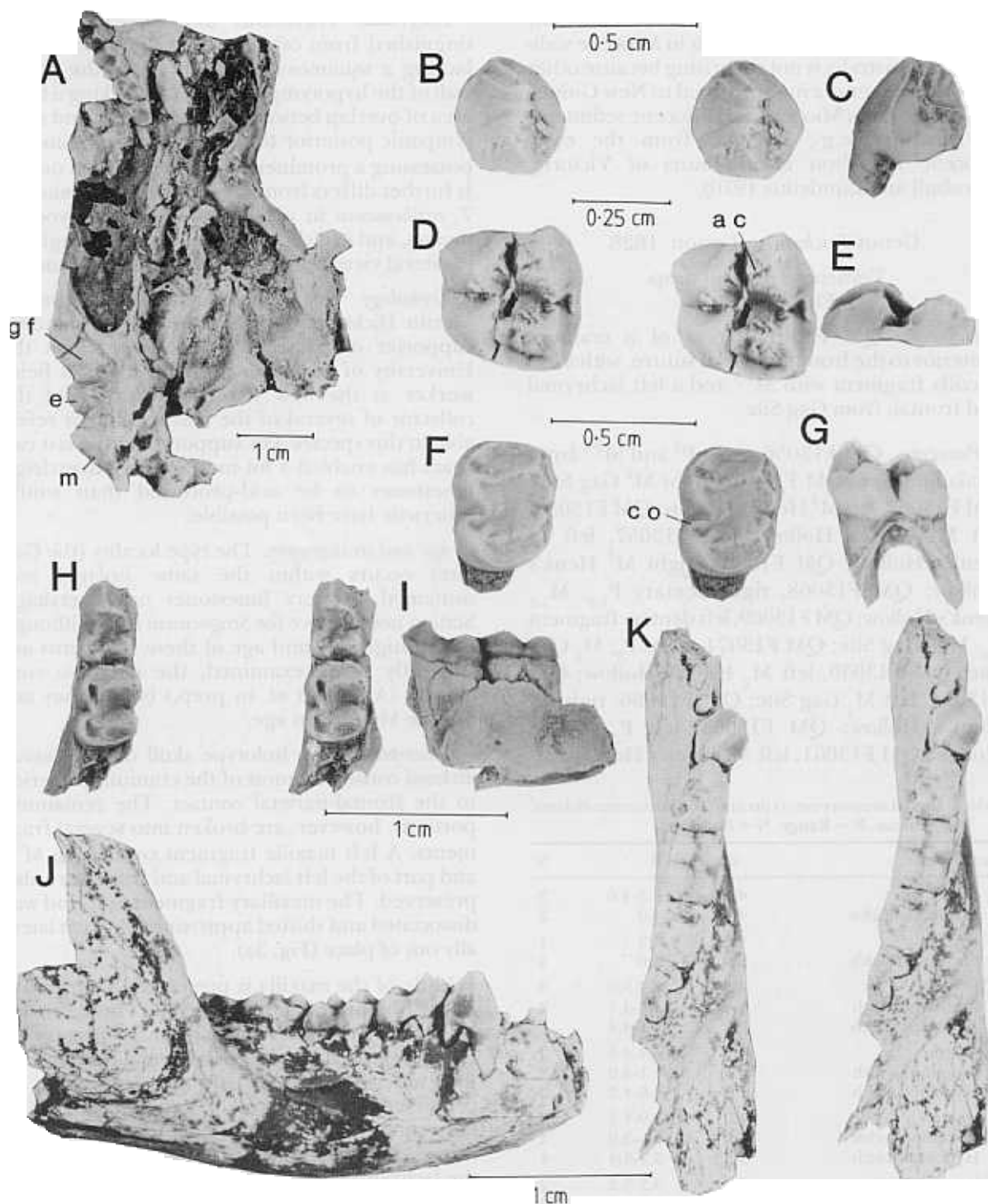


Fig. 3. A, occlusal view of the holotype skull of *Trichosurus dicksoni* (QM F13077). B, stereopair of occlusal view and C, buccal view of P_3 (QM F13057) referred to *T. dicksoni*. D, stereopair of occlusal view and E, buccal view of M_2 (QM F13058) referred to *T. dicksoni*. F, stereopair of occlusal view and G, buccal view of M_4 (QM F13061) referred to *T. dicksoni*. H, stereopair of occlusal view and I, buccal view of $M_{2,3}$ (QM F13071) referred to *T. dicksoni*. J, buccal view and K, stereopair of occlusal view of dentary (QM F13068) with P_3 , $M_{2,3}$ referred to *T. dicksoni*. Abbreviations: ac = accessory preprotocrista of M_2 , co = cristid obliqua, e = ectotympenic, gf = glenoid fossa, m = mastoid.

crenulate molar enamel. It also possesses an apparent synapomorphic feature shared with *S. gymnotis* (P3 hypertrophy). This suggests that if *S. gymnotis* is a phalangerin, phalangerins must have arisen after the divergence of *S. reidi*

and *S. gymnotis*. This in turn would imply that phalangerins convergently lost P3 hypertrophy. Such additional homoplasy makes the hypothesis that *S. gymnotis* and *S. reidi* are phalangerins seem less parsimonious and more untenable.

The presence of a suitable structural ancestor for the New Guinean *S. gymnotis* in Miocene sediments in Australia is not surprising because other mammalian genera now confined to New Guinea are known from Miocene and Pliocene sediments in Australia (e.g., *Dorcopsis* from the early Pliocene Hamilton Local Fauna of Victoria; Turnbull and Lundelius 1970).

Genus *Trichosurus* Lesson, 1828

Trichosurus dicksoni n. sp.
(Fig. 3, Table 2)

Holotype. QM F13077, most of a cranium posterior to the frontal-parietal suture, with a left maxilla fragment with M²⁻⁵ and a left lachrymal and frontal, from Gag Site.

Paratypes. QM F13056, right P³ and M²⁻⁴ from Phalanger Site; QM F13072, right M¹ Gag Site; QM F13062, left M⁴ Henk's Hollow; QM F13058, left M² Henk's Hollow; QM F13057, left P³ Henk's Hollow; QM F13064, right M⁴ Henk's Hollow; QM F13068, right dentary P₁₋₃, M₂₋₅ Henk's Hollow; QM F13069, left dentary fragment P₃, M₂₋₃ Gag Site; QM F13071, right P₃, M₂ Gag Site; QM F13059, left M₂ Henk's Hollow; QM F13074, left M₂ Gag Site; QM F13066, right P₃ Henk's Hollow; QM F13065, left P₃ Henk's Hollow; QM F13061, left M₃ Henk's Hollow.

Table 2. Dental measurements (in mm) for *Trichosurus dicksoni*.
x = mean, R = Range, N = Number.

Measurement	x	R	N
P ³ length	4.6	4.5-4.6	2
Maximum width	4.0	4.0	2
	4.2	4.2	
	3.0	3.0	
	4.8	4.7-5.0	
	4.4	4.3-4.5	2
	4.2	4.1-4.4	3
	4.5	4.4-4.5	2
	4.5	4.1-4.9	2
	3.9	3.6-4.2	2
	4.0	3.9-4.1	4
	3.8	3.5-3.9	4
	3.3	3.1-3.4	4
	3.3	3.2-3.3	2
	3.1	3.0-3.1	2
	2.4	2.4	2
	3.9	3.3-4.2	5
	3.1	2.7-3.5	4
	4.9	4.0-5.5	5
	2.8	2.7-2.9	5
	3.4	3.2-3.6	5
	4.5	4.3-4.8	3
	3.6	3.5-3.7	3
	3.5	3.3-3.7	3
	4.3	4.3	
	3.5	3.5	
	3.2	3.2	
	3.7	3.7	

Diagnosis. *Trichosurus dicksoni* can be distinguished from other species of *Trichosurus* in lacking a squamosal contribution to the lateral wall of the hypotympanic sinus, in lacking a large area of overlap between the squamosal and ectotympanic posterior to the glenoid fossa, and by possessing a prominent accessory ridgelet on M². It further differs from *T. vulpecula*, *T. caninus* and *T. arnhemensis* in possessing more brachyodont molars, and in lacking P³'s that are "rectangular" in lateral view (see Flannery *et al.* this Volume).

Etymology. The specific name is in honour of Martin Dickson who has been a long-standing supporter of palaeontological research at the University of New South Wales, a fellow field-worker at the new Riversleigh sites and the collector of several of the best specimens referable to this species. His support over the last two years has enabled a lot more of the Riversleigh limestones to be acid-processed than would otherwise have been possible.

Age and stratigraphy. The type locality (the Gag Site) occurs within the same isolated and unnamed Tertiary limestones on Riversleigh Station noted above for *Strigocuscus reidi*. Although the stratigraphy and age of these sediments are presently being examined, the tentative conclusion (Archer *et al.* in prep.) is that they are Middle Miocene in age.

Description. The holotype skull of *Trichosurus dicksoni* consists of most of the cranium posterior to the frontal-parietal contact. The remaining portions, however, are broken into several fragments. A left maxilla fragment containing M²⁻⁵ and part of the left lachrymal and frontal are also preserved. The maxillary fragment as found was dissociated and shifted approximately 2 cm laterally out of place (Fig. 3a).

Little of the maxilla is preserved. The ventral rim of the orbit is not preserved. There was no masseteric process. A left lachrymal is preserved. It possesses a single large lachrymal foramen. If the anterior portion of the lachrymal as preserved is not broken, the facial portion of the lachrymal was very short. That this is so is reinforced by the fact that parts of what is apparently the lachrymal-maxillary suture are preserved on the anterior edge of the lachrymal.

Only the internal surfaces of the parietals can be seen but, judging from the cross section of their posterior edge, there was no large sagittal crest. Broken fragments of the zygomatic arch suggest that this structure was more robust than in *S. celebensis*. Broken sections through the squamosal show that it is highly pneumatized in the region of the basicranium, as in other phalangerines. The mastoid is restricted to a small ventral area of the rear face of the cranium, also as in other phalangerines. The glenoid cavity is similar in construction to that of *S. celebensis*

(Fig. 3a). However, medial to the glenoid cavity the basicranium is inflated by the presence of a large hypotympanic sinus such as occurs otherwise only in species of *Trichosurus*. This affects the outline of the cranium externally because the lamina of bone lateral to the hypotympanic sinus is more vertically oriented relative to the cheek-tooth row in these forms than in other phalangerines. Unlike the condition seen in the other species of *Trichosurus*, however, in *T. dicksoni* this bony wall is composed of the alisphenoid rather than the squamosal.

The mastoid is relatively broad and not as rounded laterally as in *S. celebensis*. The periotic is similar in morphology to that of *S. celebensis*. The alisphenoid terminates at the base of the paroccipital process. The ventral edge of the periotic is exposed in a broad gap between the alisphenoid and basioccipital.

Dentition. An isolated P^3 (QM F13057) and a P^3 associated with M^{2-4} (QM F13056) are referred to *T. dicksoni* on the basis of size and morphology. The P^3 is a bulbous tooth and is subovate in basal outline (Fig. 3b, c). The occlusal crest is ornamented with four cuspsules that descend in height posteriorly. All have buccal and lingual ridgelets that descend towards the crown base. However, only those of the anterior-most cusp reach the crown base. An anterior ridgelet also descends from the anteriormost cusp which defines the anterior edge of the tooth. The buccal and lingual ridgelets of the more posterior cuspsules shorten posteriorly. The longest reaches only a third of the way to the crown base. The anterobuccal ridgelet unites with a buccal basal cingulum which extends posteriorly from where the ridgelet connects with the crown base. There is a less well-defined basal cingulum and small crenulations in the posterolingual corner of the tooth which suggest the incipient presence of a posterobuccal cusp.

A referred, isolated M^1 (QM F13072) consists of a high anterobuccal and a lower posterobuccal cusp (which are connected by a crista) and a lower lingual cusp. A slight ridge descends buccally from the anterobuccal cusp. This tooth is similar in morphology (although it has a lower lingual cusp) to that of *T. squamicaudata*.

The M^2 is known from three specimens (QM F13077, F13056 and F13058). The protoloph and hypoloph are subequal in width. The protoloph is poorly developed. A linguallly-oriented crest descends from the paracone for about one quarter of the width of the tooth. It then bifurcates and shortly thereafter terminates. A more anteriorly placed ridge, running from a point midway between the paracone and parastyle to the lingual edge of the anterior cingulum, is also present. This structure is otherwise well developed only in *S. celebensis* and is here called the accessory preprotocrista. The preprotocrista

is poorly developed but contacts the parastyle. The parastyle is small though distinct. The pre- and postpara- and metacrists are well defined. A single stylar cusp is present buccal to the interloph valley. The hypoloph is well developed. The midlink, though worn, was apparently well defined. The posterior cingulum is worn, but also appears to have been well developed.

The M^3 differs from M^2 in the following ways. The parastyle is further reduced and the accessory preprotocrista is absent. The protoloph is much better developed, forming a well-defined ridge running between the protocone and paracone. The stylar cusp buccal to the interloph valley is less well developed.

The M^4 is distinctly more heavily worn than M^3 on the holotype and differs from it in that the hypoloph is narrower than the protoloph and the stylar cusp buccal to the interloph valley is absent.

The M^5 is less worn than M^4 , and differs from M^4 in that the hypoloph is further reduced relative to the protoloph and in that the hypoloph is very poorly developed.

A single near complete dentary (QM F13068) appears to represent *T. dicksoni*. It is very similar in morphology to that of *S. celebensis* (Fig. 3j, k). The I_1 is broken off in the alveolus and only the root remains. The root is laterally compressed. Three tiny, single-rooted teeth were present (the posteriormost two of which are well preserved) between I_1 and P_3 .

The P_3 (e.g., QM F13068) is similar in basal outline to P^3 . Its occlusal crest is also ornamented by four cuspsules. The anteriormost cuspsule has buccal and lingual ridgelets that descend to the crown base. Very slight basal buccal and lingual cingula are preserved.

The M_2 is represented by an unworn isolated tooth (QM F13058) and by several worn specimens (e.g., QM F13068) in dentary fragments. The trigonid of M_2 consists of a primary conid (the protoconid) and a posterolingually placed and lower metaconid which is connected to the protoconid by a crest. A groove on the posterior face of the trigonid buccal to the protoconid suggests the presence of a protostylid. The cristid obliqua is well developed. A slight buccal kink is present in the cristid obliqua near its junction with the hypoconid. The hypoconid is low but well developed and is uninterrupted by any fissures. The posterior cingulum is well developed.

There are two worn M_3 's (QM F13063 and QM F13069) and an unworn isolated M_3 (QM F13061). The protolophid and hypolophid are well developed and continuous, being uninterrupted by fissures (Fig. 3f, g). The paracristid is located on the buccal margin of the tooth and is interrupted near its junction with the protoconid

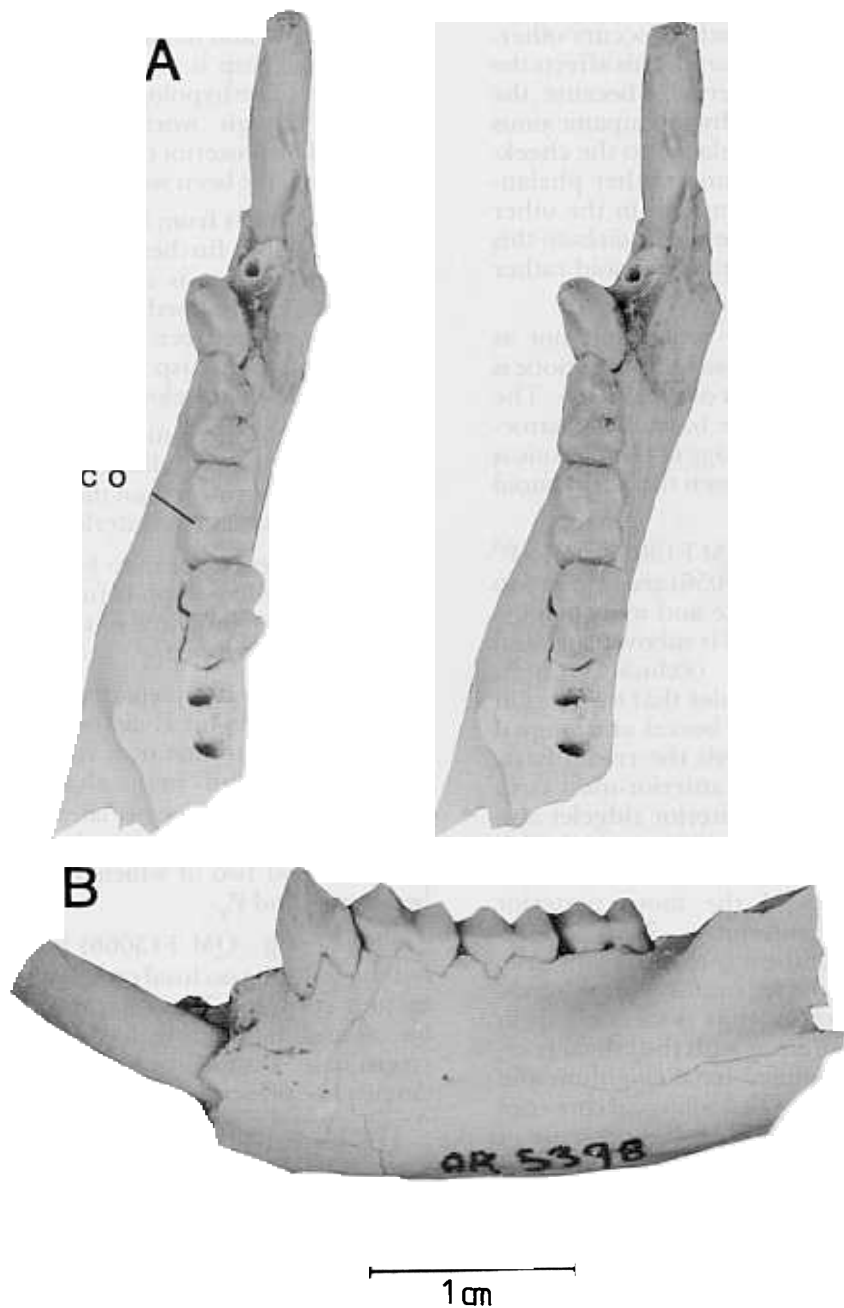


Fig. 4. A, stereopair of occlusal view and B, buccal view of a dentary (QM F13067) with P_3 and $M_{2,4}$, of *Trichosurus* sp. Abbreviations: co = cristid obliqua.

by a fissure. The cristid obliqua is well developed and possesses a distinct kink near its posterior end. The cristid obliqua is uninterrupted by a fissure in the interloph valley as in the other species of *Trichosurus*. An accessory ridge runs from the apex of the hypoconid anterolingually towards the interloph valley. The posterior cingulum is well developed. The M_4 and M_5 are known from very worn specimens only (QM F13068). Little of their crown morphology is preserved.

Discussion. *Trichosurus dicksoni* is placed within the genus *Trichosurus* for the following reasons. It possesses a lachrymal that is retracted from the face and a squamosal that forms the ventral edge of the postglenoid process; synapomorphic features for the Trichosurini (Flannery *et al.* 1987). Further, it possesses a posteriorly displaced metaconid, a lengthened protoconid-metaconid crest on M^2 , an enlarged hypotympanic sinus (with a concomitantly more vertically oriented lamina of bone medial to the

Table 3. Dental measurements (in mm) for *Trichosurus* sp.

Specimen Number	Tooth	Length	Anterior Width	Posterior Width	Maximum Width
	P ₃	3.9	—	—	2.4
	M ₂	5.0	2.6	3.0	—
	M ₃	4.1	3.4	3.2	—
	M ₄	4.1	3.1	3.0	—

glenoid fossa), an elongate ventral edge of the periotic exposed in a broad groove on the basi-cranium, and cristids obliqua on M₃₋₅ and midlinks on M³⁻⁵ that are not interrupted by a fissure in the interloph valley. These features are unique to, and presumably synapomorphies for, the species of *Trichosurus* (see Flannery *et al.* 1987). *Trichosurus dicksoni*, however, lacks some derived features present in all other members of the genus *Trichosurus*. These include presence of a squamosal contribution to the lateral wall of the hypotympanic sinus, a broad area of overlap between the ectotympanic and the squamosal posterior to the glenoid fossa, and extreme elongation of the ventral edge of the periotic. This suggests that *T. dicksoni* is more plesiomorphic than the other species of the genus and that it is their sister taxon.

Strigocuscus celebensis and *T. dicksoni* are unusual in possessing a well-developed accessory preprotocrista anterior to the protoloph on M². This feature is present, although less well developed, in other species of *Trichosurus* (e.g., *T. squamicaudata*). A well-developed accessory preprotocrista in this position may be plesiomorphic for trichosurins and may have been lost in other lineages.

A peculiar feature of the dentition of *T. dicksoni* is that the posterior molars are more heavily worn than the anterior ones. This is particularly marked on the referred dentary (QM F13068), where M⁵ is worn to the roots but M² is little worn. It seems unlikely that both known cheektooth rows (which represent different individuals) of *T. dicksoni* would be afflicted by a pathological condition if this is the sole cause of this unusual wear. This feature has not been observed in the dentition of any living phalangerid nor in other extinct forms. Its significance remains unclear.

Trichosurus sp.
(Fig. 4, Table 3)

A left dentary (QM F13067) from Henk's Hollow may represent an extreme variant of *Trichosurus dicksoni* or a second, closely related species. It is assigned here to the genus *Trichosurus* because it possesses an M₂, with an elongate protoconid-metaconid crest with a posteriorly displaced metaconid. It differs from *T. dicksoni* in that the P₃ is much narrower and less bulbous, although some isolated P₃'s (e.g., QM F13066 and QM F13069) referred to *T.*

dicksoni seem to be intermediate in morphology between this specimen and that of the nearly complete dentary of *T. dicksoni*, and in that the molars are slightly smaller and narrower than those of *T. dicksoni*. Additional material is necessary before the status of this potentially distinctive taxon can be clarified.

DISCUSSION

The Riversleigh phalangerids reveal much about the timing of the phalangerid radiation. It is clear from the Riversleigh fossil record that the endemic Australian genus *Trichosurus* must have differentiated by Middle to Late-Middle Miocene times because of the presence of *T. dicksoni* at Riversleigh. We can also hypothesise that the ancestors of the more plesiomorphic *Strigocuscus celebensis* must have differentiated and probably reached the Celebes or nearby islands prior to Middle Miocene time because a more advanced species only, *T. dicksoni*, is known from Australia by Riversleigh times. The presence of a form which is closely related to and a suitable structural ancestor for *S. gymnotis* at Riversleigh indicates that this lineage of *Strigocuscus* extends back at least as far as the Miocene.

Peculiarly, phalangerins, which today almost completely dominate the phalangerid assemblages of New Guinea, are apparently absent from the Miocene deposits of Riversleigh. It is difficult to imagine that this is due to habitat differences because the Riversleigh faunas appear to represent a rainforest habitat (Archer *et al.* in prep.) and phalangerins are abundant in all rainforest types in New Guinea. Perhaps phalangerins had not evolved by the time the Riversleigh deposits were accumulating or perhaps their ancestors were then restricted to the islands to the north of Miocene Australia. It is clear that several lineages of trichosurins and, by implication at least, ailuropines, had differentiated by the Miocene. The isolation of the ancestors of plesiomorphic phalangerids such as the living *Ailurops ursinus* and *Strigocuscus celebensis* on the Celebes probably occurred prior to Riversleigh times. In fact, for at least the former species, we suspect that this isolation took place long before Riversleigh time.

CONCLUSIONS

At least two previously undescribed trichosurin phalangerids are present in Miocene deposits from Riversleigh Station, northwestern Queensland. The larger species, *Strigocuscus reidi* is closely related to and possibly ancestral to *S. gymnotis*. Its morphology adds supporting evidence to the hypothesis that *S. gymnotis* is a trichosurin.

The smaller Riversleigh species, *Trichosurus dicksoni*, is the most plesiomorphic known member of the genus *Trichosurus*. Its presence in the

Riversleigh local faunas indicates that this lineage was also differentiated by Miocene times.

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