

This article was downloaded by:[MARTY, Daniel]

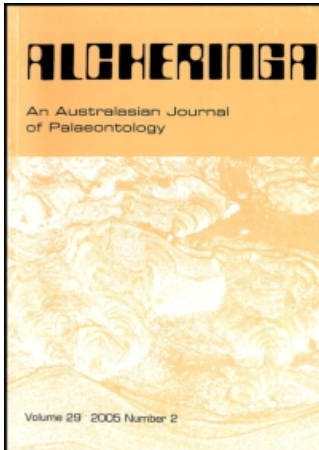
On: 2 August 2007

Access Details: Sample Issue Voucher: Alcheringa: An Australasian Journal of Palaeontology [subscription number 781076595]

Publisher: Taylor & Francis

Informa Ltd Registered in England and Wales Registered Number: 1072954

Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Alcheringa: An Australasian Journal of Palaeontology

Publication details, including instructions for authors and subscription information:

<http://www.informaworld.com/smpp/title~content=t770322720>

Rediagnosis of the fossil species assigned to *Strigocuscus* (Marsupialia, Phalangeridae), with description of a new genus and three new species

Online Publication Date: 01 March 2007

To cite this Article: Crosby, Kirsten (2007) 'Rediagnosis of the fossil species assigned to *Strigocuscus* (Marsupialia, Phalangeridae), with description of a new genus and three new species', *Alcheringa: An Australasian Journal of Palaeontology*, 31:1, 33 - 58

To link to this article: DOI: 10.1080/03115510601123619

URL: <http://dx.doi.org/10.1080/03115510601123619>

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: <http://www.informaworld.com/terms-and-conditions-of-access.pdf>

This article maybe used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

© Taylor and Francis 2007

Rediagnosis of the fossil species assigned to *Strigocuscus* (Marsupialia, Phalangeridae), with description of a new genus and three new species

KIRSTEN CROSBY

CROSBY, K., March 2007. Rediagnosis of the fossil species assigned to *Strigocuscus* (Marsupialia, Phalangeridae), with description of a new genus and three new species. *Alcheringa* 31, 33-58. ISSN 0311-5518.

The skull of the Miocene phalangerid *Strigocuscus reidi* is described for the first time. Anatomy of the new skull and the periotic of the holotype leads to a rediagnosis of the species and its placement in a new genus, *Onirocuscus*. Three new species are described from Riversleigh, Queensland, ranging from early to middle Miocene: *O. silvacultrix*, *O. notialis*, and *O. rupina*. *Strigocuscus notialis*, a Pliocene species from Victoria is also transferred to the new genus based on phenetic similarity of its dentition to that of other species assigned to the genus.

Kirsten Crosby [k.crosby@three.com.au], School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW, 2052, Australia; received 4.2.2005, revised 1.7.2005.

Key words: Phalangeridae, *Strigocuscus*, periotic, Riversleigh, Miocene.

TAXONOMY WITHIN the extant Phalangeridae has long been controversial. Tate (1945) included all cuscus species in the genus *Phalanger* Storr, 1780. Tate divided the genus into three subgroups: the *P. orientalis* (Pallas, 1766) Group, the *P. maculatus* Geoffrey Saint-Hillaire, 1803 Group and the *P. ursinus* (Temminck, 1824) Group. His *P. orientalis* group was further divided by Menzies & Pernetta (1986) into four subgroups: 1. *P. permixtio* Menzies & Pernetta, 1986 and *P. orientalis* Pallas, 1766; 2. *P. vestitus* Milne-Edwards, 1877, *P. carmelitae* Thomas, 1898a and *P. sericeus* Thomas, 1907; 3. *P. gymnotis* (Peters & Doria, 1875), *P. ornatus* (Gray, 1860), *P. rothschildi* Thomas, 1898b and *P. lullulae* Thomas, 1896; and 4. *P. celebensis* Gray, 1858. A large number of other species have been proposed over the last two centuries that are currently considered

synonyms, and recently a smaller number have been raised to species level (see Flannery 1994 for more information regarding currently accepted species).

Molecular evidence suggested that *Phalanger* Storr, 1780 was paraphyletic with *Trichosurus* Lesson, 1828 and *Wyulda* Alexander, 1919, with some species being more closely related to the trichosurines than to other cuscuses (Baverstock 1984). Flannery *et al.* (1987a) studied phalangerid morphology and phylogeny. Their results suggested that the bear cuscus, *Ailurops ursinus*, was the most plesiomorphic phalangerid known, and they placed it in a monotypic genus *Ailurops* Wagler, 1830. Groups three and four (minus *P. lullulae*) recognized by Menzies & Pernetta (1986) were placed in the genus *Strigocuscus* Gray, 1861. Flannery *et al.* (1987a) placed this genus as the sister group to the trichosurines, *Trichosurus* and *Wyulda*. In that paper, Tate's *P. maculatus* group was also raised to generic level (*Spilocuscus* Gray, 1861) and was proposed as the sister group to the

remaining *Phalanger*. George (1987) also recognized these genera, but included only *Strigocuscus celebensis* in *Spilocuscus*. Molecular studies (Springer *et al.* 1990, Hamilton & Springer 1999) later showed that *P. gymnotis* belonged in *Phalanger*. A study of periotic morphology (Norris 1994) agreed with this placement, showing that *P. gymnotis* had a typically phalangerin periotic. Norris' (1994) study showed overall agreement with the division of the Phalangeridae proposed by Flannery *et al.* (1987a), separating the periotic morphology of phalangerids into three groups: ailuropin, trichosurin and phalangerin. Other recent molecular studies have suggested the removal of *Strigocuscus celebensis* from the Trichosurini, suggesting a closer relationship with *Ailurops* (Kirsch & Wolman 2001, Ruedas & Morales 2005).

Two species of fossil cuscus have been described: a Miocene species from Riversleigh, northwest Queensland, and a Pliocene species from Hamilton, Victoria. The Riversleigh species was named *Strigocuscus reidi* Flannery & Archer, 1987, assigned by the authors to this genus based on its resemblance to what was then *S. gymnotis*. The Hamilton species, *S. notialis* Flannery *et al.* 1987b, was referred to this genus based on its resemblance to *S. reidi*. The movement of *P. gymnotis* from *Strigocuscus* to *Phalanger* brought the taxonomic position of the fossil species into debate. Crosby *et al.* (2004) reported three undescribed Riversleigh phalangerid genera, including the genus described herein.

The presence of a preserved periotic of *Strigocuscus reidi* allows a comparison with those of *S. celebensis* and *P. gymnotis*. Crosby & Norris (2003) showed that the periotic of *S. celebensis* was very similar to those of *Trichosurus* and *Wyulda*. Crosby (2002) described a new phalangerid periotic morphotype, restricted to fossil species. This included the periotic of *S. reidi*, which is quite different from those of both

S. celebensis and *P. gymnotis*, with which it shows dental similarities. These differences meant that a new genus needed to be erected for *S. reidi*, and its phylogenetic position determined.

An almost complete skull has now been recovered from Riversleigh World Heritage Fossil Property in north-west Queensland, allowing a complete description of the cranial and dental anatomy of this species. Studies of phalangerid periotics (Norris 1994, Crosby & Norris 2003) now enable the phylogenetic placement of this species based on the morphology of the periotic. Fossil species previously assigned to *Strigocuscus* are here placed in a new genus. Other Miocene cuscus species from Riversleigh are also described and referred to the new genus.

Materials and methods

Systematic nomenclature follows Aplin & Archer (1987) and Flannery *et al.* (1987a). Premolar numbering follows Flower (1867), and homology of the premolar/molar boundary and molar numbering follows Luckett (1993). Fossils have been assigned Queensland Museum fossil numbers (QMF). The dating of Riversleigh sites has been by biocorrelation with magnetostratigraphically dated sites in South Australia with similar faunas or species, as well as by 'stage of evolution' of species within the sites (Tedford 1967, Archer *et al.* 1989, 1997). System B sites at Riversleigh are considered to be early Miocene in age and System C middle Miocene (Archer *et al.* 1997). The position of measurements of the skull and dentition can be found in Fig. 1 and Table 1.

Systematic palaeontology

Order DIPROTODONTIA Owen, 1866
 Family PHALANGERIDAE Thomas, 1888

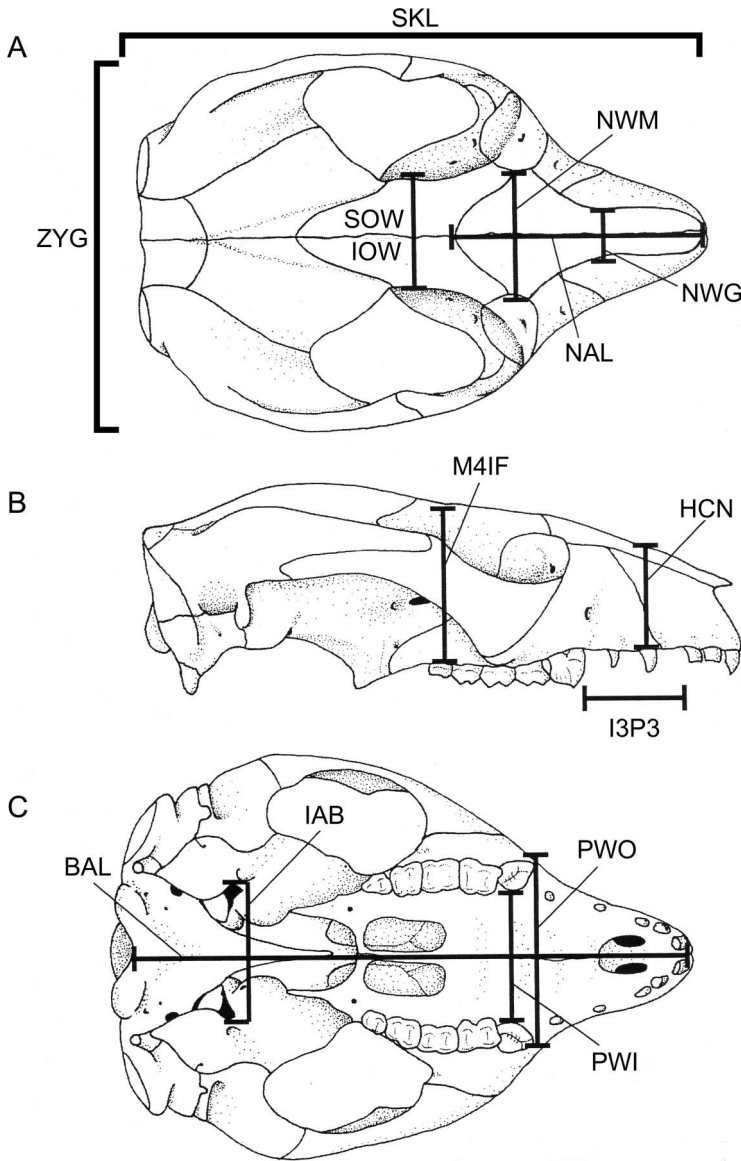


Fig. 1. Measurements of the skull: A, dorsal; B, lateral; C, ventral.

Subfamily PHALANGERINAE Thomas, 1888

Tribe TRICHOSURINI (Flynn, 1911)

Onirocuscus gen. nov.

Distribution and age. Species in this genus first appear in the early Miocene of River-

sleigh (System B of Riversleigh: Camel Sputum Site, Waynes Wok Site, Creasers Ramparts Site, Dirks Towers Site) and continue through the middle Miocene (System C of Riversleigh: Last Minute Site, Gag Site and Kangaroo Jaw Site, as well as Keiths Chocky Block Site, of uncertain age but probably System B or C). A Pliocene

ABBREVIATION	MEASUREMENT
DENT	Total length of dentary including incisor
DHT	Maximum height of dentary at coronoid process
MLR	Total length of molar row
P3L	Total length of P ₃ in line with axis of the tooth
P3W	Maximum width of P ₃ perpendicular to axis of tooth
P3H	Maximum height of tooth from base of crown to apex
M × L	Length of molar parallel to axis of tooth
M × A	Anterior width of molar perpendicular to axis of the tooth (i.e. along the line of the loph/lophid)
M × P	Posterior width of molar perpendicular to axis of the tooth (i.e. along the line of the loph/lophid)

Table 1. Measurements used for dentition.

species is known from the Hamilton Local Fauna in western Victoria.

Diagnosis. Species of this genus can be distinguished from all other phalangerids by the extreme size of the third premolar (both in length and height), the large molars, and the ridged promontorium/pars cochlearis of the periotic. *Onirocuscus* can be distinguished from all phalangerids except the extinct Phalangerid genus 2 and Phalangerid genus 3 from Riversleigh by the distinct sulcus on the periotic that runs anterior to the internal auditory meatus and drops vertically beside the aqueductus cochleae.

Etymology. ‘Oniros’ from the Greek meaning ‘dream’, for the Dreamtime, hence ‘Dreamtime Cuscus.’

Type species. *Onirocuscus reidi* (Flannery & Archer, 1987)

Holotype. A partial skull containing parts of edentulous premaxillae, frontals, nasals, parietals, periotics, and squamosals. A right maxillary fragment is present containing P³-M³. The specimen, from Last Minute site at

Riversleigh, was described by Flannery and Archer (1987) in their description of the species *Strigocuscus reidi*.

Onirocuscus reidi (Flannery & Archer, 1987) emend. (Figs 2A-D, 3A-D)

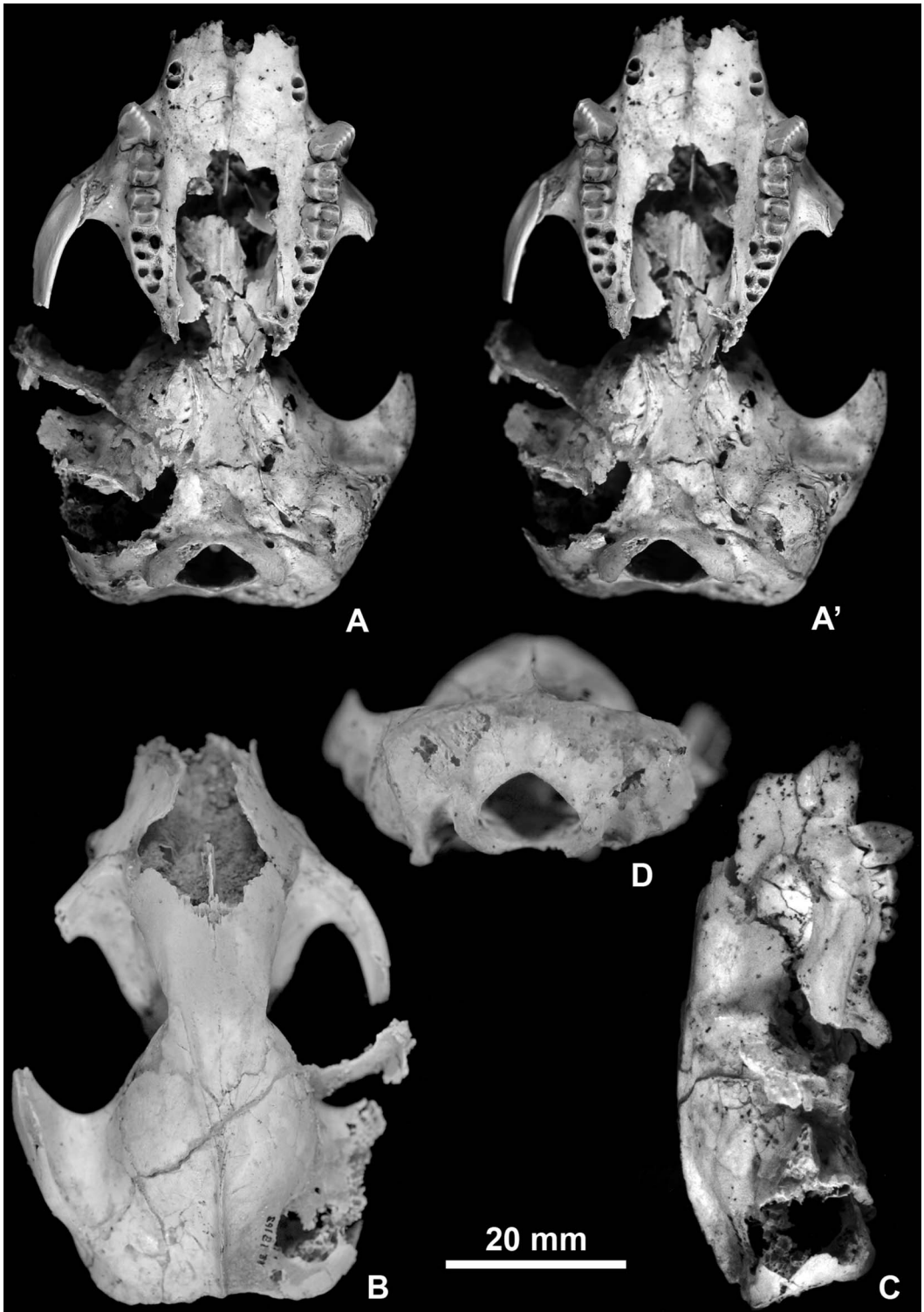
Topotype. An almost complete skull, QMF42702, missing nasals, premaxillae, part of right zygoma, right mastoid process. Dentition present includes left and right P³-M². Alveoli present on both sides for C¹, P¹⁻² and M³⁻⁴ (Fig. 2).

Locality and age. Jims Carousel Site, Riversleigh World Heritage fossil property, north-western Queensland. This site is in an area where most sites are interpreted as System C or middle Miocene.

Emended diagnosis. Extremely large phalangerid with rounded mastoid, small paroccipital processes, and hypotrophied postglenoid process, which, together with unexpanded bullae, give the basicranium a flattened appearance. Large and robust P₃, inflated parietals, and the base of the orbit being visible from the central surface distinguish this species from other phalangerids. It is distinguished from other

Fig. 2. Skull of *Onirocuscus reidi* (Flannery & Archer, 1987) emend., QMF42702. **A**, **A'**, ventral stereoview; **B**, dorsal view; **C**, lateral view; **D**, posterior view.

Downloaded By: [MARTY, Daniel] At: 14:48 2 August 2007



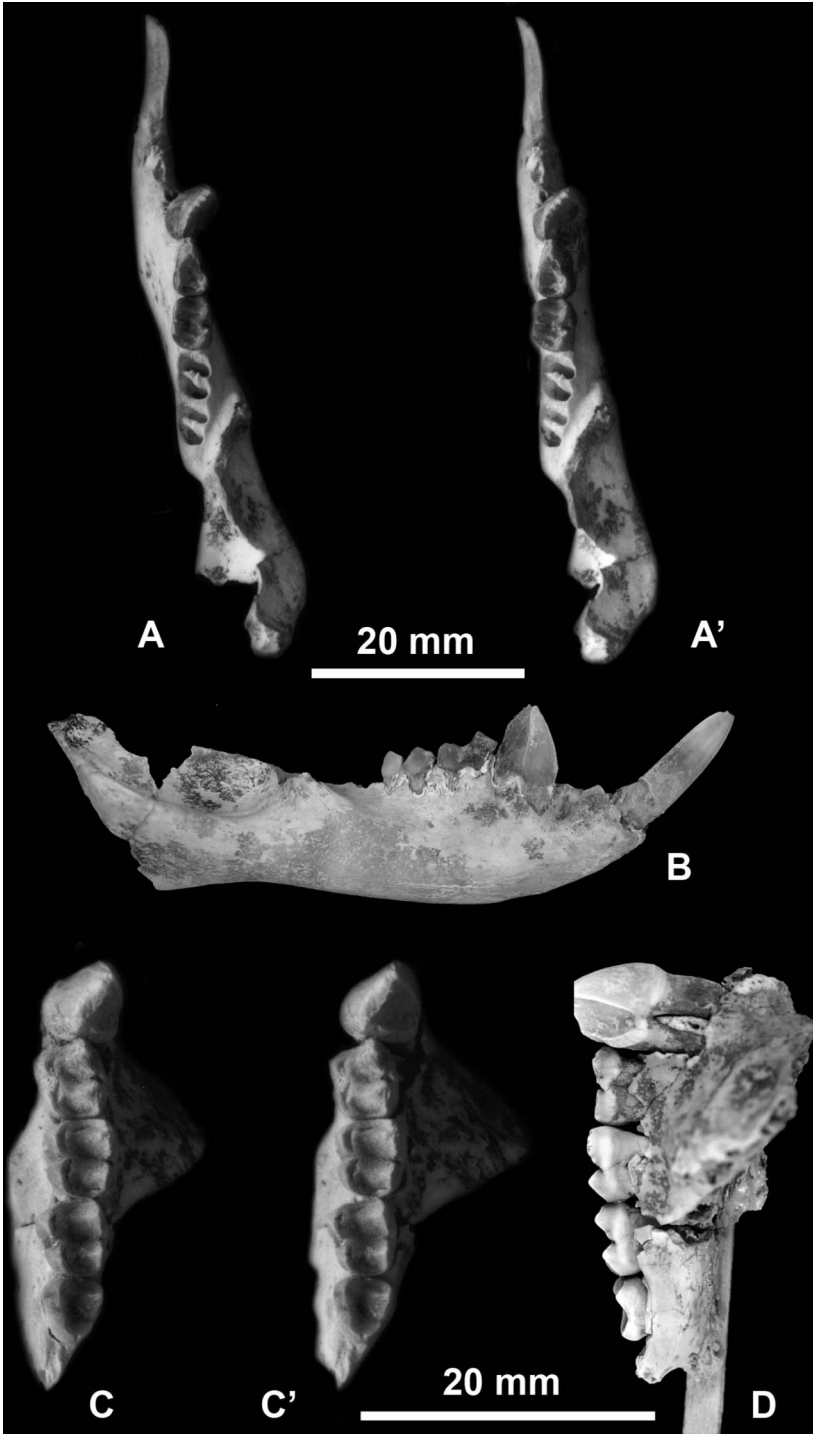


Fig. 3. Dentition of *Onirocuscus reidi* (Flannery & Archer 1987) emend. A, A', stereoview of dentary, QMF13076; B, buccal view of dentary, QMF13076; C, C', stereoview of maxilla, QMF24084; D, buccal view of maxilla, QMF24084.

trichosurins by its very large P², straight molar row and no maxillary process on the zygoma.

Description of the skull, QMF42702

Measurements of the skull are provided in Table 2. There is no flexion of the skull, the palatine region and the basicranium being at the same plane. The frontals are inflated lateral to their contact with the nasals. The skull is constricted about three-fifths of the way along the orbital region. At this point on the dorsal surface, the two postorbital crests are formed, which then run posteriorly before merging to become the sagittal crest. This occurs a third of the distance along the dorsal surface of the neurocranium, between the frontal/parietal suture and the nuchal crest. The sagittal crest is low. The back of the skull is curved, unlike that seen in *Wyulda*, which has a square posterodorsal surface. The occiput is subvertical, slanting anteroventrally at an angle of approximately 10°. The lateral edges are rounded due to the lack of inflation of the mastoid. There is no mastoid process. The paroccipital processes barely reach below the level of the exoccipital condyles. The external auditory meati are oval and slant anteroventrally at an angle similar to that of the occiput. The glenoid fossa is broad and flat, with a poorly developed postglenoid

process. The zygomatic arches are quite fine and are narrow dorso-ventrally. There appear to be no high dorsal wings as are seen in *Trichosurus*.

Premaxillae. Missing

Maxillae. Both maxillae preserve the P³-M². A double rooted alveolus is present for the P¹ and is situated 3.05 mm behind the alveolus for the canine and 4.22 mm anterior to the P³. A small alveolus for the P² is present at the base of the P³. The maxillopalatal ridges run between the P³s and P²s and are gently curved anteriorly. The curvature is similar to that seen in *Trichosurus* and less than in *Spilocuscus*. A foramen is situated medial to the P², with a small sulcus running anteriorly. The maxillary process of the zygomatic arch is a rounded eminence, not ending in a point. The rim of the orbit is visible from the ventral surface. There is no suture with the frontal, the lacrimal and palatine interdigitating between. The rostrum pinches in anterior to the P³, at the point where the infraorbital foramen exits. This is also seen in *Trichosurus*, but not in *Phalanger gymnotis*, where the rostrum continues at the same level, leading the rostrum to appear broader. Dental measurements for specimens of *Onirocuscus reidi* are provided in Tables 3 and 4.

QMF	SPECIES	SKL	ZYGA	ZYGP	ZYGL	SOW	ORB	OCH
42702	<i>O. reidi</i>	78.39	47.16	52.885	48.42	13.165	23.855	20.345
QMF	SPECIES	POH	OCL	EAR	SAG	OBR	NAL	NWM
42702	<i>O. reidi</i>	21.555	39.555		19.86	24.56		
QMF	SPECIES	NWG	PWO	PWI	IAB	POC	BAL	I3P3
42702	<i>O. reidi</i>		26.435	17.85	14.715	21.64		
QMF	SPECIES	P2P3	C1P2	HCN	M4IF	CAN	IOF	
42702	<i>O. reidi</i>	4.38	4.1	14.91	22.885	16.715	18.41	

Table 2. Measurements of the skull of *Onirocuscus reidi*.

NUMBER	SITE	DENT	DHT	MLR	P3L	P3W	P3H	M1L	M1A	M1P
QMF13076	LM	68.05	.	.	6.9	5	.	6.2	3.5	4.2
NUMBER	SITE	M2L	M2A	M2P	M3L	M3A	M3P	M4L	M4A	M4P
QMF13076	LM	5.7	4.5	4.6

Table 3. Tooth measurements for *Onirocuscus reidi* (lowers).

NUMBER	SITE	MLR	P3L	P3W	P3H	M1L	M1A	M1P		
QMF18163	JC	.	5.91	5.54	.	5.01	4.36	4.37		
QMF13078	LM	.	6.09	5.44	.	5.1	4.63	4.52		
QMF24084	LM	.	6.03	5.09	.	5.03	4.09	4.14		
NUMBER	SITE	M2L	M2A	M2P	M3L	M3A	M3P	M4L	M4A	M4P
QMF18163	JC	4.87	4.72	4.19
QMF13078	LM
QMF24084	LM	5	4.68	4.11	4.91	4.48	3.69	4.23	3.9	2.94

Table 4. Tooth measurements for *Onirocuscus reidi* (uppers).

Palatine. The palatine contacts the lacrimal. The suture with the lachrymal is approximately 4 mm long.

Lacrimal. The lacrimal is gently rounded where it moves from the orbit to the rostrum. The lacrimal foramen is small and round, and appears to sit on the orbital margin. The orbital margin is not strongly defined at this point. The lacrimal extends slightly to the anterior of the orbital margin. The lacrimal is only a small contribution to the mesial wall of the orbit. The suture with the frontal is vertical.

Frontals. The frontals are rounded and mildly flared posterior to where they meet the nasals. This flaring is more than is seen in *Trichosurus* but not as extreme as in species of *Spilocuscus*. The orbital crests are weak, originating at the point of the interorbital constriction of the skull. The frontals make up the majority of the mesial wall of the orbit. The interorbital area is broad and flat, not furrowed as it is in some

Trichosurus. This may be due to the lack of strong interorbital ridges.

Nasals. Although these bones are missing, the positions of the edges of the maxillae and frontals suggest that the nasals were broad above the lachrymal. The posterior junction of the nasals points strongly to the posterior. This is the case in most phalangerids; however, in another Riversleigh species, *Illungalya aletes*, the nasals are flat across their suture with the frontals. The nasals are highly constricted above the level of the P². In all other phalangerids, the nasals are broader posteriorly than anteriorly; it is assumed that this also applies to *O. reidi*.

Jugal. The jugals have a furrow where they meet the rostrum. The curve of the jugal from the rostrum to the arch is slightly squared. The lateral edges of the jugals appear to be parallel (in many phalangerids these are slightly convergent anteriorly, although this may vary within a species). A ridge follows the midline of the lateral face

of the arch (this ridge follows the top of the zygoma in *Caudipilosus vellicodens*).

Parietals. The parietals appear to be pointed anteriorly. Only the left parietal shows this, the anterior of the right parietal having been damaged. The most anterior point at which the left and right parietals are in contact is anterior to the rise of the sagittal crest, within the boundaries of the interorbital basin. The parietals appear to have overgrown the interparietals at the rear of the skull. The parietals are broad at this point, not being restricted by any dorsal growth of the squamosals.

Squamosal. The squamosal does not reach far mesially and is restricted by the parietals or interparietals from nearing the sagittal crest. The anteriormost point is the same as that reached by the posterior orbital rim. The squamosal is broad in the valley between the neurocranium and the zygomatic arch. The external auditory meatus is not as large as is seen in modern *Trichosurus*. The external auditory meatus is sloped and is oval in shape. The glenoid region is unusual. The glenoid fossa is shallow (i.e. the postglenoid process does not rise far above the glenoid fossa). The squamosal meets the ectotympanic on the edge of the postglenoid process. The neurocranium is domed when observed from the occiput. This is not an obvious feature of *Trichosurus* but is found in phalangerins (*P. gymnotis*). This feature could be exaggerated in *Trichosurus* by the inflation of the squamosal on the dorsal surface. In *Trichosurus*, the squamosal foramen is at the most dorsal point of the posterior squamosal, whereas in this specimen and other phalangerids, the lambdoidal crest is dorsal to the foramen. The parietal/squamosal suture curves down anteriorly.

Occipitals. The foramen magnum is directed dorsally. There are large troughs above the foramen magnum, where the neck

muscles would have attached. The centre of the top surface of the foramen magnum is higher than the rest of the dorsal surface, becoming almost triangular.

Alisphenoid. The alisphenoid extends anteriorly as far as the interorbital constriction of the skull. The dorsal edge of the alisphenoid is horizontal, whereas the anterior edge is nearly vertical. The slope from the squamosal to the alisphenoid tympanic bulla is gentle. The suture between these bones is closer to the glenoid fossa than the tympanic bulla. The tympanic bulla is not expanded. The alisphenoid does not extend far posteriorly, reaching only the anterior base of the paroccipital process.

Basicranium. The basicranium appears very flat. This is due to the lack of expansion of the alisphenoid tympanic wing, the low postglenoid process, the rounded mastoid that is lacking a ridge, and the short paroccipital processes. The basioccipital does not have a strong centre line. There is a sharp vertical ridge between the alisphenoid and the basioccipital, on the edge of the alisphenoid tympanic wing. The entocarotid foramen (Archer 1976) is well defined, as it is in other species, however, the foramen of the transverse canal is extremely poorly defined, as are the foramina anterior to it. This is very unusual in phalangerids.

Mastoid. The ventral mastoid area is broad and rounded, and does not form a ridge or process. In many other phalangerids the occiput is flat, with the junction between it and the ear area quite marked. In *O. reidi*, however, the roundedness of the mastoid leaves this junction quite obscure, the mastoid curving gently between the occipital face and the outer ear region.

Periotic. The right periotic shows all the features typically found in phalangerid periotics from Riversleigh. The promontorium is

long, the internal auditory meatus is large, and the sulcus for the inferior petrosal sinus cuts across the promontorium below the internal auditory meatus. There is no expansion of lamella dorsal to the subarcuate fossa. The semicircular canal that forms the rim of the subarcuate fossa is raised above the level of the aqueductus cochleae. The pars cochlearis is furrowed, and there is no projection of the rostral tympanic process, which lies against the pars cochlearis instead. The periotic is damaged, missing the crista petrosa and the area that is exposed in the mid-cranial fossa. The left periotic is *in situ*. The periotic of this specimen has several differences from that of the holotype. The periotic of the holotype has a much shorter promontorium and has a distinct sulcus running across the pars cochleae.

C¹. The alveolus for the canine is thin vertically and extends back into the maxilla.

P¹. The alveolus for the P¹ is large and double-rooted.

P². The alveolus for this tooth is at the base of the P³. The right alveolus is larger and better developed than the left.

P³. This is a very large tooth with four to five cuspules. The crest is mostly horizontal, only dipping at the posterior of the tooth. There are five cuspules, four sitting along the top of the crest. Three ridges run down from the anterior cuspule: one anterior, one buccal, and one lingual. The latter very closely abuts the anterior ridge near the dorsal crest, before curving lingually near

the crown base. There is a posterolingual bulge at the base of the crown, with a faint cingulum. The posterobuccal cingulum is very well defined, with the basin between it and the buccal ridge from the first cuspule also being well defined.

M¹. The molars of this species are large and robust. The paracone is displaced lingually from the buccal edge of the crown. The paracone is the tallest cusp, followed by the metacone. A distinct parastyle is anterior to this cusp. There is no fissure present between these cusps. The anterior cingulum is well defined, as is the posterior cingulum. The lophs run directly between the buccal and lingual cusps, except in the case of the RM¹, where the protoloph is split in the middle, with the lingual portion sitting more anteriorly than the buccal section. Styler Cusps B and D are present. The tooth is near square, with the posterolingual corner curved.

M². The anterior half of this tooth is much wider than the posterior half. The paracone is displaced slightly lingually compared to the metacone and is taller. The lophs and cingulae are well defined. There are no styler cusps.

Fig. 3 shows previously described specimens of *O. reidi*. Dental measurements of the previously described *O. notialis* are listed in Table 5.

Description of the periotic of the holotype, QMF13077

Cerebellar face. The dorsal margin of the subarcuate fossa is damaged, but the

NUMBER	SITE	DENT	DHT	MLR	P3L	P3W	P3H	M1L	M1A	M1P
NMV54133	Ham	.	.	.	5.2	4	.	5.5	3.8	4
NUMBER	SITE	M2L	M2A	M2P	M3L	M3A	M3P	M4L	M4A	M4P
NMV54133	Ham	5.3	4.2	4.1	5.3	4	3.9	.	.	.

Table 5. Tooth measurements for *Onirocuscus notialis* (lowers).

entrance to the subarcuate fossa seems quite large. The margin crista petrosa is broken, but there seems to be limited expansion. There is a fissure between the crista petrosa and the area of the petrosal that is exposed in the middle cranial fossa. The opening of the internal auditory meatus is short rostro-dorsally, but quite long laterally. The opening for the facial nerve is small. There is no pronounced ridge between the crus commune and the prefacial commissure. The opening of the aqueductus cochleae is very well defined, forming a vertical, V-shaped fissure. The aqueductus vestibuli is also very well defined, forming a relatively large, horizontal foramen in the caudal margin of the subarcuate fossa. This is similar in morphology to that of *P. gymnotis*, but in that species the aqueductus vestibuli is recessive into the crus commune. The promontorium has a very unusual morphology: a ledge is present anterior to the internal auditory meatus, which covers a well-defined sulcus. This is similar in morphology to *Spilocuscus maculatus*. The promontorium emerges beneath this. This sulcus drops vertically beside the aqueductus cochleae. This also seems to be the case in *Phalanger gymnotis*. In *P. gymnotis*, this is the sulcus for the inferior petrosal sinus.

Tympanic face. The rostral tympanic process is large and rounded, and there is little or no ectotympanic process. The promontorium is of medium length, shorter than in *Trichosurus*, but longer than *Phalanger*. The progression of the pars cochlearis onto the promontorium is interrupted by a sulcus as it is in *Ailurops*, causing the promontorium to appear discontinuous with the remainder of the pars cochlearis. In *Ailurops*, this is the sulcus for the inferior petrosal sinus. However, as mentioned above, there is another well-defined sulcus on the cerebellar face that may be for the inferior petrosal sinus. It is possible that the

inferior petrosal sinus diverges into two sinuses on the lambdoidal face. The epitympanic recess is quite small. There are three folds in the wall of the tegmen tympani, the middle one being the probable entrance to the prootic canal. The recessus mesotympanicus is curved.

Squamosal face. There is a gap between the middle cranial exposure and the lateral wall of the epitympanic recess. This is seen in *P. gymnotis* (AR11397) but not in the specimen discussed by Norris (1994). The hiatus Fallopi (hF) is rostral to this area. The exposure of the petrosal in the middle cranial fossa (MCF) is limited, much like in *Ailurops*. The area that contains the trigeminal fossa is large and crossed by the sulcus of the greater petrosal nerve.

Remarks. The skull of *Onirotuscus reidi* shows typical trichosurin characters. Its smooth molar enamel differentiates it from species of *Phalanger*, including *P. gymnotis*. The skull is considerably larger than other phalangerid skulls retrieved from Riversleigh.

***Onirotuscus silvicultrix* sp. nov.** (Fig. 4A-D, Table 6)

Holotype. QMF24743, a right dentary with I_1 , P_3 and M_{1-4} . *Paratype.* QMF41197, a left partial dentary with M_{2-5} (Waynes Wok Site).

Type locality and age. Camel Sputum Site, Riversleigh World Heritage Property, Lawn Hill National Park, northwestern Queensland. On the basis of stratigraphy and contained faunas, Camel Sputum Site deposits are interpreted to be early Miocene in age (Archer *et al.* 1989, 1995, 1997, Creaser 1997).

Etymology. From the Latin 'silvicultrix' meaning 'to live in the woods', in reference to the supposed rainforest habitat of this species.

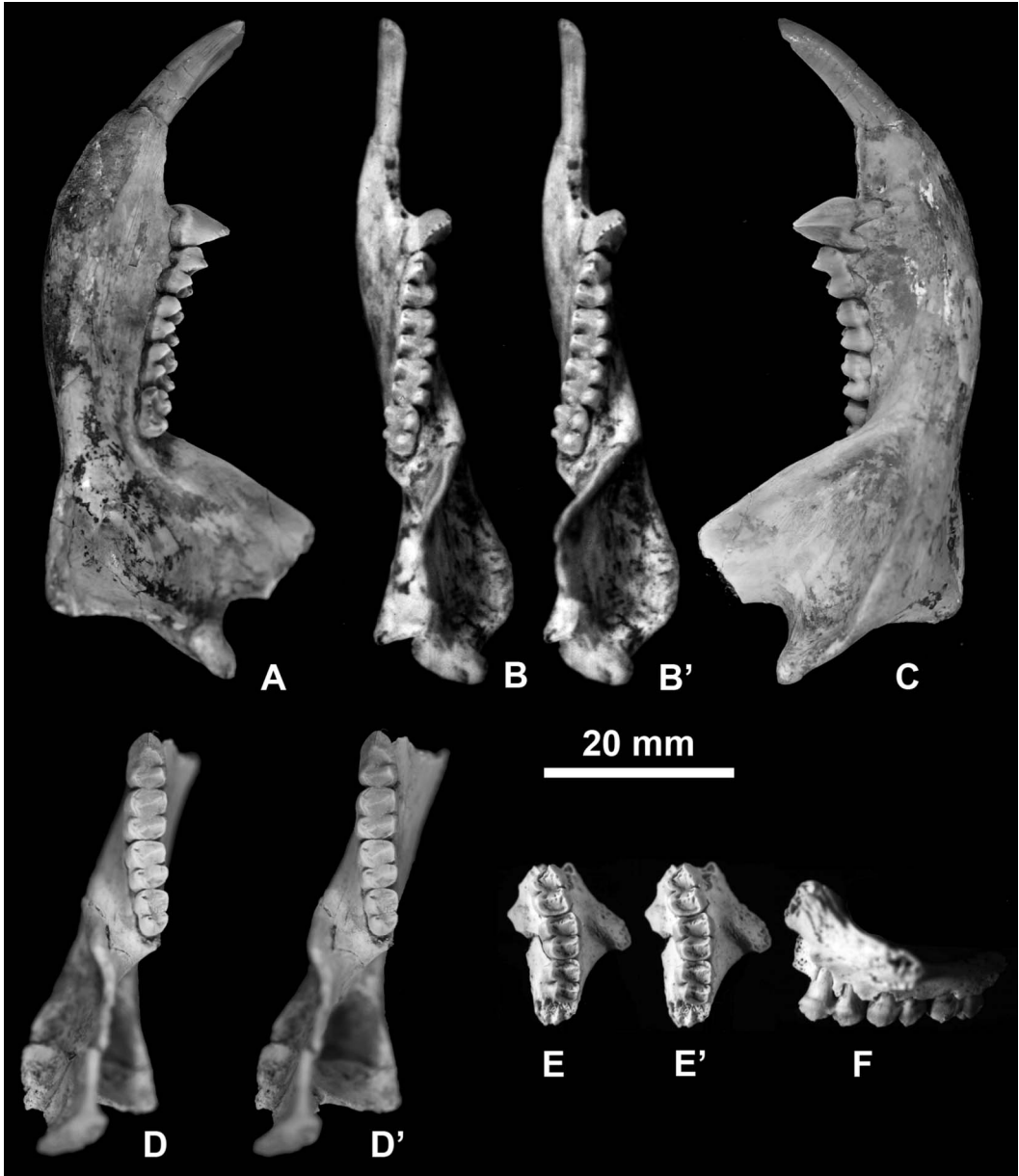


Fig. 4. A-D: Dentition of *Onirocus silvacultrix* sp. nov. A, lingual view of dentary, QMF23743; B, B', stereoview of right dentary, QMF23743; C, buccal view of dentary, QMF23743; D, D', stereoview of left dentary, QMF41197; E, F cf. *Onirocus silvacultrix* sp. nov. E, E', stereoview of left maxilla, QMF30420; F, buccal view of maxilla, QMF30420.

Diagnosis. *Onirocus* species having a P_3 that is rotated at a high angle (55°) from the axis of the molar row.

Description

The dentary is complete, except for the top of the coronoid process (Fig. 4A-D). It is

NUMBER	SITE	DENT	DHT	MLR	P3L	P3W	P3H	M1L	M1A	M1P
QMF24743	CS	62.45	12.29	18.81	5	3.87	5.97	4.88	3.2	3.81
QMF41197	WW	5.1	2.95	3.71
QMF13101	BSE	4.89	2.77	3.42
NUMBER	SITE	M2L	M2A	M2P	M3L	M3A	M3P	M4L	M4A	M4P
QMF24743	CS	4.5	3.97	4.04	4.24	3.8	3.66	4.3	3.34	3.09
QMF41197	WW	4.84	3.98	4.09	4.58	3.79	3.66	4.22	3.31	2.83
QMF13101	BSE

Table 6. Tooth measurements for *Onirocuscus silvacultrix* (lowers).

very deep below M_1 , but quite shallow below M_4 , making the ventral surface of the dentary markedly curved. I_1 and P_3 - M_4 are present. Three alveoli are present between I_1 and P_3 . The first (I_2) and third (P_2) are single-rooted. The P_{17} is possibly double-rooted. The I_1 is narrow and lanceolate. The mental foramen is directly anterior to the anterior root of the P_3 .

P_3 . This tooth is very large (Table 6), its crown being almost twice as high as that of the M_1 . In species of *Trichosurus* and many species of *Phalanger*, the crown of the P_3 is at the level of the crown of the M_1 . The base of the crown is set quite low compared to that of the M_1 . Four cuspules are present along the top of the crest, which then runs convexly down to the base of the crown. Faint serrations can be seen posterior to the cuspules. The anterior cuspule is the highest. This cuspule has buccal and lingual ridgelets that descend to the crown base. There is a short ridgelet posterior to the anteriormost ridgelet that descends halfway down the lingual face of the tooth. There are very small ridgelets connected to other cuspules. The axis of the tooth is deflected buccally at an angle of 55° to that of the molar row. The anterior root is very large.

M_1 . The anterior of the M_1 is quite wide (Table 6). There is no anterior cingulum. The interlophid valley is deep. The primary cusp of the trigonid is the protoconid. A

small metaconid is lingual to this, separated by a slight groove. The twinned protoconid/metaconid is much taller than the entoconid and hypoconid, and significantly taller than cusps on the other molars. A faint notch on the preprotocristid suggests the presence of a protostylid. The cristid obliqua is well developed. The hypolophid is uninterrupted by fissures. The posterior cingulum is well developed. The enamel of this and other molars is smooth.

M_2 . The metaconid is the tallest cusp on the M_2 , followed by the entoconid (Table 6). The protolophid and hypolophid are well developed and uninterrupted. The protolophid curves posterobuccally. The interlophid valley is deep. The preprotocristid has a faint groove near the protoconid, suggesting the presence of a protostylid. The cristid obliqua has a slight kink. The anterior and posterior cingulids are well developed.

M_3 . The M_3 is very similar to the M_2 , but the kink in the cristid obliqua is more obvious, and the fissure in the preprotocristid is larger. The M_4 is the smallest molar. It is very similar to the M_2 and M_3 , except that the kink in the cristid obliqua and the fissure in the preprotocristid are more pronounced. Some enamel is missing from the posterolingual portion of the tooth.

Remarks. *Onirocuscus silvacultrix* is phenetically similar to *O. notialis* from Hamilton,

Victoria. General proportions of the dentary and the molars are almost identical in the two species. The major difference is the morphology of the P_3 . *Onirocuscus silvicultrix* has a much taller P_3 , which is deflected at a much greater angle from the axis of the molar row (55° as opposed to 30° in *O. notialis*). *Onirocuscus silvicultrix* further differs from *O. notialis* in having buccal ridgelet that descends directly to the crown base (instead of curving posteriorly), a short lingual ridgelet attached to the first cuspule on the P_3 , and having the mental foramen in front of the anterior root of the P_3 . *Onirocuscus silvicultrix* is much smaller than *O. reidi*. However, the P_3 morphology of *Onirocuscus reidi* is more similar to that of *Onirocuscus silvicultrix* than is *O. notialis*. The P_3 of *Onirocuscus reidi* is deflected at an angle of 45° to the molar row.

***Onirocuscus inversus* sp. nov.** (Fig. 5, Table 7)

Holotype. QMF24037 right dentary, fragment with I_1 , and P_3 to M_4 . *Material*. QMF24080, left dentary with P_3 to M_3 , Camel Sputum Site; QMF31312, RM_1 , Wang Site.

Type locality and age. Camel Sputum Site, Riversleigh World Heritage Fossil Property, northwestern Queensland; the deposits are interpreted to be of early Miocene age. Riversleigh's Wang Site is thought to be of middle Miocene age.

Etymology. 'Inversus', for the concave posterior edge of the P_3 .

Diagnosis. *Onirocuscus* species with an anterior cingulum on the M_1 that sits up against the P_3 and the posterior surface of the P_3 being concave rather than convex.

Description

The dentary is robust (Fig. 5A-F). The molar row is slightly concave lingually. There is very little gradient in the size of

the molars. QMF24037 has seven alveoli between I_1 and P_3 , the posterior three being double-rooted. QMF24080 has five alveoli, the posterior two being double-rooted. The mental foramen is directly anterior to the anterior root of the P_3 . QMF24037 is broken posterior to the M_3 , and the I_1 has been broken off. QMF24080 has a damaged I_1 and a fracture below M_{2-3} , and the ascending ramus and articular condyle are missing.

P_3 . The crown of P_3 stands higher than that of the M_1 , but these teeth are otherwise similar in length (Table 7). The anterior root of P_3 is very large. The axis of the tooth is deflected buccally at an angle of 40° to that of the molar row. The four to five cuspules are at approximately the same height, with the second and third being slightly taller than are the others. The anteriormost cuspule has buccal and lingual ridgelets that descend to the crown base. These are not particularly distinct. Posterior to the last cusp, the crest drops almost vertically, before sloping gently toward the M_1 . There is a distinct basal lingual cingulum. This ledge may sit above a small second premolar (the alveolus for which is at the base of the P_3).

M_1 . The anterior of this tooth is narrower than the P_3 . A crest runs buccally from the preprotocristid (portion of anterior cingulum?). There is a well-defined fissure along the preprotocristid. The trigonid is significantly taller than the talonid. The main cusp on the trigonid is the protoconid, with a faint metaconid lingual to this. The cristid obliqua and postprotocristid are continuous. There is no faint ridgelet descending from the protoconid to the interlophid valley. The hypolophid runs directly across from the hypoconid to the entoconid. The posterior cingulid is well developed.

M_2 . The protolophid and hypolophid of the M_2 are continuous, uninterrupted by any fissures. The protolophid curves anteriorly to its junction with the protoconid.



Fig. 5. A-E: Dentition of *Onirocuscus inversus* sp. nov. A, A', stereoview of left dentary, QMF24037; B, B', stereoview of right dentary, QMF24080; C, lingual view of left dentary, QMF24037; D, buccal view of right dentary, QMF24080; E, lingual view of right dentary, QMF24080; F, F', cf. *Onirocuscus inversus* sp. nov. stereoview of maxilla, QMF30701.

NUMBER	SITE	DENT	DHT	MLR	P3L	P3W	P3H	M1L	M1A	M1P
QMF24080	CS	.	11.75	18.48	4.9	3.67	5.51	4.9	2.7	3.54
QMF24037	CS	.	12.16	.	4.99	3.54	4.95	4.94	2.45	3.46
NUMBER	SITE	M2L	M2A	M2P	M3L	M3A	M3P	M4L	M4A	M4P
QMF24080	CS	4.64	3.8	3.96	4.37	3.96	3.85	3.97	2.96	2.53
QMF24037	CS	4.65	3.51	3.7	4.57	3.64	3.67	.	.	.

Table 7. Tooth measurements for *Onirocuscus inversus* (lowers).

There is a small ridgelet between the hypolophid and cristid obliqua, running down to the interloph valley. The interloph valley and anterior and posterior valleys are all quite shallow. There is a faint groove on the preprotocristid, suggesting the presence of a protostylid. The cristid obliqua is kinked. The anterior and posterior cingulids are well defined.

M_3 . The M_3 is similar to the M_2 (Table 7). The M_4 is present only on QMF24080. The crown is damaged, but the overall shape and size are clear. It is slightly smaller than the M_3 .

***Onirocuscus rupina* sp. nov.** (Fig. 6, Table 8)

Holotype. QMF30478, a partial right dentary with M_{2-3} . *Paratypes*. QMF31491, RP_3 ; QMF31492, RM_2 ; QMF31493, LP_3 ; QMF31495, RM_4 (broken); QMF31496, LM_3 ; QMF40213, $LM_{2/3}$.

Type locality and age. All specimens are from Keiths Chocky Block Site (KCB) at the Riversleigh World Heritage Fossil Property, north-western Queensland. KCB is a fissure fill deposit that appears to span the early and middle Miocene (Morrell 2002). Macropodoids from this site include species only known from early Miocene sites and species known only from middle Miocene sites at Riversleigh (B. Cooke pers. comm., in Morrell 2002).

Etymology. ‘Rupina’, from the Latin for cleft in a rock, in reference to the supposed

fissure fill nature of the type locality (Morrell 2002).

Diagnosis. *Onirocuscus rupina* differs from *O. reidi* in having a much smaller P_3 , from *O. silvicultrix* and *O. notialis* in having a fissure in the hypolophid of the M_1 , and from *O. notialis* in having a much larger P_3 .

Description

P_3 . This is a large tooth with six cusplules along the crest (Fig. 6, Tables 8 and 9). The anterior cusplule is the tallest. From this cusplule, two distinct ridgelets descend to the crown base: one anteriorly and one buccally. The buccal ridgelet curves posteriorly at its base. A faint ridgelet can be seen on the lingual side of the anterior ridgelet that also descends to the crown base. A ridge descends from below the fifth cusplule along a posterobuccal bulge. A lingual cingulid is present.

M_1 . The crests of M_1 run buccally and lingually from the parastyle (possibly a remnant of an anterior cingulum). On the buccal side, this creates a small fissure. The preprotocristid has a notch half way along its length. The protoconid and metaconid are fused. Two ridgelets descend from this fused conid to the interlophid valley. The cristid obliqua meets the postprotocristid at a slight notch. The hypolophid has a fissure at its mid-point. The posterior cingulum is well defined.

M_2 . The protolophid and hypolophid of the M_2 are well developed. The hypolophid has a small fissure at its mid-point. The

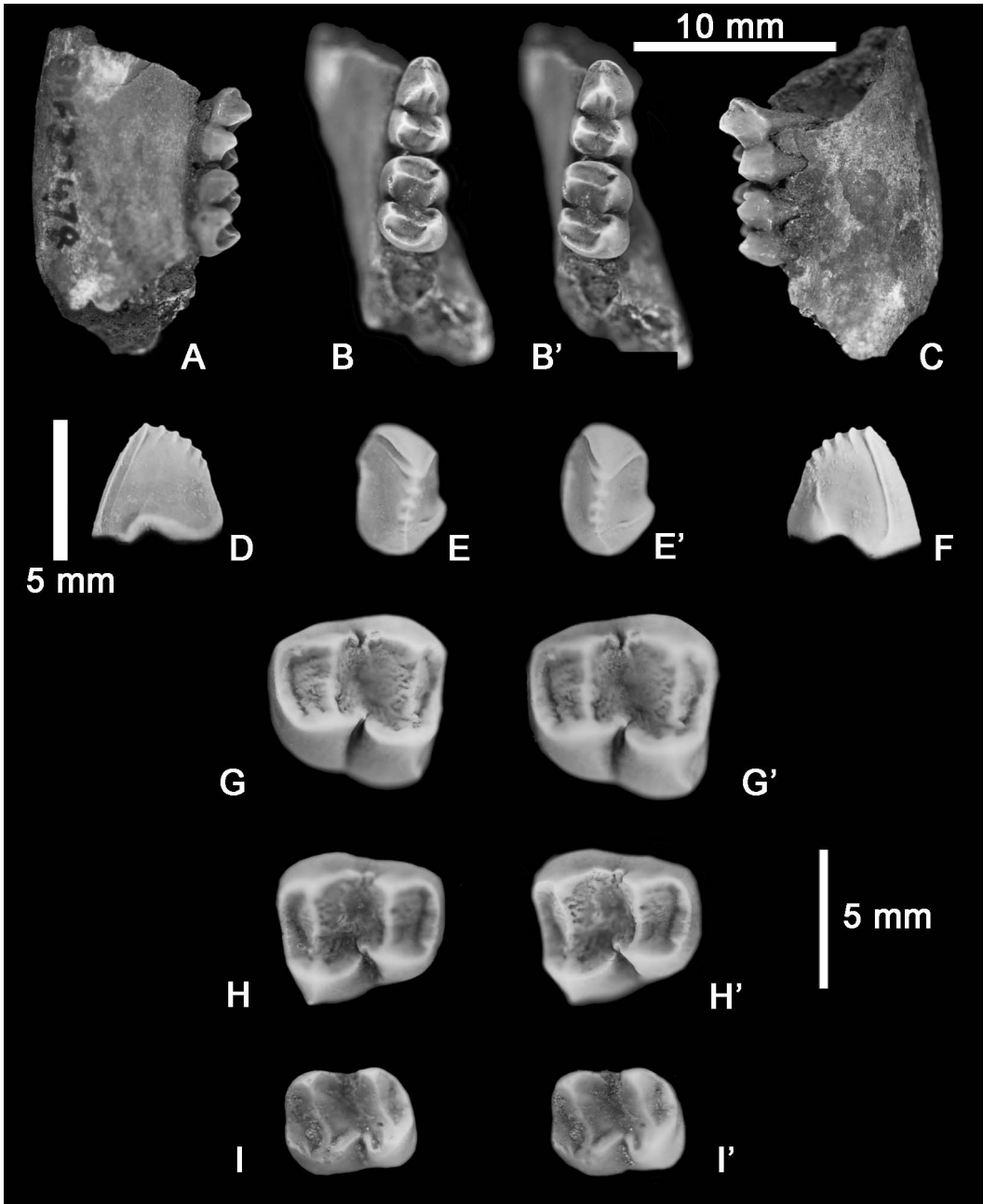


Fig. 6. Dentition of *Onirocuscus rupina* sp. nov. A, lingual view of right dentary, QMF30478; B, B', stereoview of dentary, QMF30478; C, buccal view of dentary, QMF30478; D, lingual view of right P₃, QMF31491; E, E', stereoview of P₃, QMF31491; F, buccal view of P₃, QMF31491; G, G', stereoview of right M², QMF31492; H, H', stereoview of left M², QMF40213; I, I', stereoview of left M_{2/3}, QMF40213.

NUMBER	SITE	MLR	P3L	P3W	P3H	M1L	M1A	M1P		
QMF30478	KCB					5.18	3.12	3.77		
	KCB		5.67	4.15	6.29					
NUMBER	SITE	M2L	M2A	M2P	M3L	M3A	M3P	M4L	M4A	M4P
QMF30478	KCB	4.94	4.03	4.08						

Table 8. Tooth measurements for *Oniroscuscupus rupina* (lowers).

NUMBER	SITE	MLR	P3L	P3W	P3H	M1L	M1A	M1P		
31492	KCB		
NUMBER	SITE	M2L	M2A	M2P	M3L	M3A	M3P	M4L	M4A	M4P
31492	KCB	4.76	4.71	4.06

Table 9. Tooth measurements for *Oniroscuscupus rupina* (uppers).

interlophid valley is deep. The preprotocris- tid has a groove anterior to the protoconid, suggesting the presence of a protostylid. The cristid obliqua has a slight kink. The anterior and posterior cingulids are well developed.

M_4 . The metaconid of the M_4 is much taller than the other cusps. The entoconid on this tooth is very small. A well-defined notch on the preprotocris- tid suggests the presence of a protoconule. The kink in the cristid obliqua is distinct. The proto- lophid curves posteriorly to meet the proto- conid. The hypolophid is very short, making the posterior basin very small. The anterior and posterior cingulids are well defined.

M^2 . The cusps are of a similar height, with the paracone being the tallest. The protocone bulges anterobuccally, with a ridge curving anteriorly from the protocone and descending to the crown base. The protoloph and meta- loph run straight between their respective cusps. The anterior and posterior cingulae are well defined. The anterior basin is smaller than the posterior. There is a small fissure between

the postparacrista and the premetacrista. The enamel is faintly crenulated.

M^3 . This tooth is almost identical to the M^2 but smaller. There is a small cusp on the premetacrista (possibly a styler cusp?).

Unassigned specimens

Two maxillae fragments are unassigned to species and are described separately: QMF30701, left maxilla with M^{1-4} and alveoli for C^1 and P^{2-3} (Creasers Ramparts Site), and QMF30420, left maxillary frag- ment holding M^{1-3} (Dirks Towers Site). The morphology of the molars of QMF30701 (CR) and QMF30420 (DT) is slightly different (see below and Table 10). Since neither specimen has the premolar pre- served, precise assignation is difficult; how- ever, it is suggested that QMF30420 (Fig. 4E, F) is most likely to be *Oniroscuscupus silvacultrix*, whereas the less defined fea- tures, broader fissures between cusps and more robust look of QMF30701 could suggest that this specimen belongs to *O. inversus*. The deposits at Creasers Ram- parts and Dirks Towers are thought to be of

NUMBER	SITE	MLR	P3L	P3W	P3H	M1L	M1A	M1P		
QMF30701	CR	17.62	.	.	.	4.67	4.22	4.17		
QMF30420	DT	4.71	3.83	3.83		
NUMBER	SITE	M2L	M2A	M2P	M3L	M3A	M3P	M4L	M4A	M4P
QMF30701	CR	4.5	4.42	4.25	4.3	4.22	3.71	3.94	3.57	2.76
QMF30420	DT	4.46	4.11	3.76	4.19	3.81	3.28	.	.	.

Table 10. Tooth measurements for *Onirotococcus silvacultrix/inversus* (uppers).

a similar age (early Miocene) to the Camel Sputum deposit (Archer *et al.* 1989, 1994, 1995, 1997, Creaser 1997).

QMF30420: Dirks Towers specimen
(Fig. 4E, F)

The maxilla is broken anterior to the M¹, with just the posterior root of the P³ preserved, and posterior to the M³ (Fig. 4E, F). The maxillary contribution to the zygomatic arch is present. There is no obvious maxillary process of the zygomatic arch.

M¹. This is a square, high-crowned tooth. The paracone is the tallest cusp, followed by the metacone. The protocone and metaconule are of a similar height, with the latter being the slightly taller. The parastyle is separated from the paracone by a slight notch. There is a deep (but not broad) fissure between the paracone and metacone, with no buccal basin. The protoloph is divided, with the main part running towards the parastyle, with a smaller ridge attached to the paracone. The lingual side meets the preprotocrista rather than the protocone. The anterior cingulum appears to pass under the parastyle, instead of running through it. The metaloph runs between the metacone and the metaconule. The posterior cingulum is rounded, forming a large posterior basin. The enamel is faintly crenulated.

M². This is of similar size to the M¹ but has a broader anterior half. Again, the

paracone is the tallest cusp, followed by the metacone. The protocone and metaconule are the same height. The lophs run directly between the major cusps. The postparacrista and premetacrista curve in where they meet each other, interrupting the ectoloph. A fissure separates the postprotocrista and premetaconulecrista. The anterior cingulum runs continuously between the protocone and paracone. The posterior cingulum is rounded and the basin quite large. The M³ is smaller but follows a similar morphology. The main differences are the small size of the metacone and the smaller posterior basin.

QMF30701: Creasers Ramparts specimen
(Fig. 5F)

M¹. This molar is a square, very worn tooth (Fig. 5F). The protocone and metaconule show the strongest wear. The cusps seem to be low-crowned, but this may be due to wear. The tallest cusp of the M¹ is the paracone, followed by the metacone. The paracone is set in from the buccal face. The parastyle is indistinct. There is a large fissure between the paracone and metacone. A ridge curves buccally from the postparacrista to form a basin at this fissure. The protoloph runs directly between the paracone and protocone. The metaloph runs directly between the metacone and metaconule. There are no crenulations in the tooth enamel. M²⁻³ follow the same pattern. The M⁴ is a small triangular tooth. There is a faint protoloph but no metaloph.

Comparison of periotic morphology in phalangerids

Norris (1994) described three phalangerid periotic morphotypes, which demarcated the genera into three groups as suggested by Flannery *et al.* (1987a): ailuropin, phalangerin, and trichosurin. Crosby & Norris (2003) described the periotic morphology of *Strigocuscus celebensis* and *Wyulda squamicaudata* in detail, confirming the inclusion of the former in the Trichosurini. Periotics of trichosurins are characterized by an elongate promontorium, a small internal auditory meatus, and an expanded crista petrosa, among other features. Phalangerins are characterized by a short promontorium, large internal auditory meatus, and an unexpanded crista petrosa (Crosby & Norris 2003). The main differences between the three genera of trichosurins are the depth (or robustness) of the promontorium and the morphology of the sulcus for the inferior petrosal sinus as it runs across the face of the promontorium, below the internal auditory meatus.

Periotics from three new genera of phalangerid have been recovered from Riversleigh. These are the newly described *Onirocuscus* and the undescribed phalangerid genera 1 and 2. Phalangerid genus 1 appears to include the species currently diagnosed as *Trichosurus dicksoni* and one other species, also from middle Miocene sites. Phalangerid genus 2 contains two species from early Miocene deposits at Riversleigh. Features of the periotic shared by trichosurins and Riversleigh genera are: a large subarcuate fossa, a reduction of the sulcus running across the cerebellar surface of the promontorium, some expansion of the crista petrosa, presence of a notch in the subarcuate fossa where it meets the crista petrosa, and a medium-width promontorium. Features of the periotic found only in Riversleigh genera are a ridged promontorium, a large epitympanic recess, and a

sulcus for the inferior petrosal sinus that is notched, undercutting the surface.

Dental characters of species of *Onirocuscus*

Onirocuscus is the most diverse fossil genus of phalangerids, containing five species. A phylogeny is proposed here (Fig. 7) based on information from Flannery *et al.* (1987a,b) and Crosby & Norris (2003). Five characters of the P3 were found that may elucidate the relationships within this genus:

1. Position of crown base of P3. In *Trichosurus vulpecula*, the crown base of the P3 is level with the crown base of the first molar. In species of *Onirocuscus*, the crown base of the P3 is much lower than that of the molar.
2. Prominent posterobuccal bulge of the P3. In *Trichosurus vulpecula*, there is a faint posterobuccal bulge in the P3. This is also the case in *Onirocuscus reidi*, *O. silvacultrix*, and *O. rupina*. The bulge is prominent in *O. inversus* and *O. notialis*.
3. Position and direction of foramen. In *Trichosurus vulpecula*, the mental foramen of the dentary is below the level of the P₃ roots and runs downwards. *Onirocuscus inversus* and *O. notialis* also show this morphology. In *O. reidi*, *O. silvacultrix*, and *O. rupina*, the mental foramen is positioned beside the P₃ root and runs behind it.
4. Size of the P3. *Trichosurus vulpecula* has a P3 that is similar in size to the first molar. The P3 is larger in *Onirocuscus inversus* and *O. notialis*, much larger in *O. silvacultrix*, and extremely large in *O. reidi*.
5. Great angle of deflection of the P3 from the molar row. The P3 of *Trichosurus vulpecula* has a low angle of deflection from the molar row (*c.*25°). In *Onirocuscus inversus*, *O. rupina* and *O. notialis*, the P3s have an angle of deflection of about

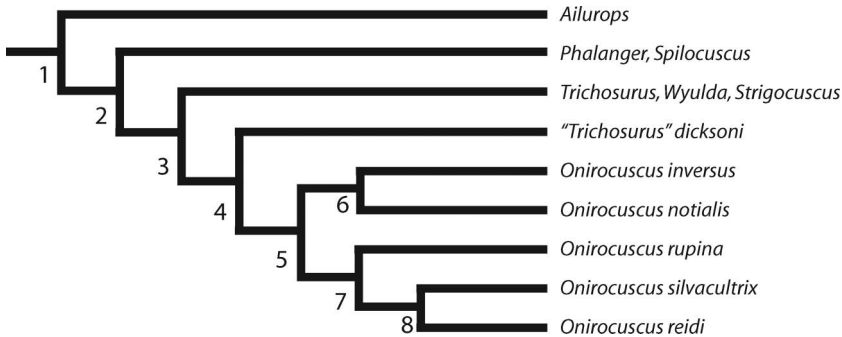


Fig. 7. Proposed phylogeny of the Phalangeridae, focussing on *Onirotococcus*. **1**, Family Phalangeridae: kite-shaped pars cochlearis of the periotic (Crosby 2002), long (uncovered) facial nerve canal (Norris 1994); **2**, Subfamily Phalangerinae: dorsal restriction of the squamosal, groove between mastoid and ectotympanic, crest of P₃ as high posteriorly as anteriorly (Flannery *et al.* 1987a); **3**, Tribe Trichosurini: the rim of the orbit is visible when viewed ventrally, weak lambdoidal crests on the skull, and inflated parietals (Flannery *et al.* 1987a), a small internal auditory meatus (Crosby 2002); **4**, sulcus for the inferior petrosal sinus of the periotic is notched, undercutting the surface (Crosby 2002); **5**, Genus *Onirotococcus*: P₃ crown base lower than molar crown bases, large size of P₃, angle of deflection of the P₃ from the axis of the molar row over 30°; **6**, *O. inversus* + *O. notialis*: more prominent posterobuccal bulge on the P₃; **7**, *O. rupina* + *O. silvicultrix* + *O. reidi*: further increase in the size of the P₃; **8**, *O. silvicultrix* + *O. reidi*: presence of the mental foramen beside and running behind the root of the P₃, increase in the angle of deflection of the P₃ to greater than 40°.

30-35°. In *O. reidi*, this angle is approximately 40-45°, whereas *O. silvicultrix* has an angle of 50-55°.

Discussion

Five 'cuscus' species have been placed in the new genus *Onirotococcus*, four (*O. reidi*, *O. silvicultrix*, *O. inversus*, and *O. rupina*) from the late Oligocene and early to middle Miocene deposits at Riversleigh, and one (*O. notialis* Flannery *et al.* 1987b) from Pliocene sediments at Hamilton, Victoria. *Onirotococcus* has the longest time span of any fossil phalangerid genus. Its temporal range is surpassed only by *Wyulda*, which first appears in the early Miocene and is still present today. *Onirotococcus silvicultrix* and *O. inversus* may both first appear in the late Oligocene (depending on the identity of specimens from Creasers Ramparts Site and Dirks Towers Site, both possibly late Oligocene deposits). *Onirotococcus silvicultrix* has not been found in any System C (middle Miocene) deposits, unlike *O. inversus*, which

is also known from the System C Wang Site. The age of Keiths Chocky Block Site, at which *Onirotococcus rupina* is found, is uncertain. Macropodoids from this site include species known only from System B sites and species known only from System C sites (Cooke 1997). It has been suggested that KCB is a fissure fill deposit (M. Archer, pers. comm.), and the evidence from the macropodoid fauna could suggest two episodes of deposition. Thus, *Onirotococcus rupina* may be present in one or other of these Systems, or possibly both.

Onirotococcus reidi is the only species of the genus for which cranial material is known. The flatness of the topography of the basicranium is distinctive, as are the hypertrophied P₃s. Although this species also shows a reduced mastoid, it has long paroccipital processes, a small P₃ and crenulate molars. Trichosurin features of the skull of *Onirotococcus reidi* include the rim of the orbit being visible when viewed ventrally, and the presence of weak lambdoidal crests and inflated parietals at the rear of the skull.

The morphology of the skull is, however, similar in some ways to that of species of *Spilocuscus* and *Phalanger gymnotis*. Similar features include the inflated frontals and large P₃. *Oniroscus reidi* may have been filling a niche in the Miocene at Riversleigh that is similar to that inhabited by these modern taxa. Despite these similarities, *O. reidi* can easily be distinguished from *P. gymnotis*, with which it was thought to be closely related, in the following features: *O. reidi* lacks a distinct mastoid process on the zygoma; the zygomatic arches appear to be more curved, compared with the straight-edged zygomatic arches of *P. gymnotis*; the P³ of *O. reidi* is much larger and more robust than that of *P. gymnotis*; the paroccipital processes are smaller and the mastoid rounded in *O. reidi*; and the molars of *O. reidi* are not crenulated, unlike those of *P. gymnotis*.

The skull shows trichosurin affinities, i.e. there is no special relationship with *Phalanger gymnotis*. There is little in the skull to link it with the morphology of *Strigocuscus celebensis*, with which it was previously placed. The cranium of *S. celebensis* is markedly domed, whereas in *Oniroscus reidi*, the skull is relatively flat in lateral view. The canine of *O. reidi* appears to be very large and abuts the third incisor (in QMF13078—this area is missing in QMF42702). The canine is smaller in *S. celebensis* and is separated from the incisors by a small diastema. The third premolar of *O. reidi* is much larger than that seen in *S. celebensis*. There is a small P² at the base of the P³ in *O. reidi*. This is missing in *S. celebensis*. The alisphenoid tympanic wing of *O. reidi* is flattened, and the paroccipital process is very short. These features are in direct contrast to those of *S. celebensis*.

All the features discussed above suggest that *Oniroscus reidi* is quite different from taxa with which it was previously associated. Rather, similarities lie with other taxa from Riversleigh, which are still to be

described. The third premolar of species of *Oniroscus*, '*Trichosurus dicksoni*', and other undescribed species is significantly larger than that seen in modern species of *Trichosurus*, *Strigocuscus*, and *Wyulda*.

Species of *Oniroscus* can be separated based on the morphology of the P₃. Phalangerids tend to maintain a conservative dental morphology, with only the P₃ showing any major variation. The genus *Oniroscus* is defined by the following dental characters: P₃ crown base low; large size of P₃; and increased angle of the P₃ to over 30° from the molar axis. A more prominent posterobuccal bulge on the P₃ defines a clade containing *Oniroscus inversus* and *O. notialis*. The clade containing the species *Oniroscus rupina*, *O. silvicultrix*, and *O. reidi* is defined by a further increase in the size of the P₃. The clade *Oniroscus silvicultrix* and *O. reidi* is defined by the presence of the mental foramen beside and running behind the root of the P₃ and an increase in the deflection of the P₃ to an angle over 40°. Apomorphies of individual taxa are as follows: *O. inversus*—concave slope of the crest of the P₃; *O. silvicultrix*—deflection of the P₃ to an angle of 55° from the molar axis; and *O. reidi*—a further increase in overall size, especially of the P₃.

Myers (2001) studied body weights of extinct marsupials. He developed formulae to determine body weights of fossil taxa based on a range of variables, including total jaw length and length of molars. Body weights for species of *Oniroscus* were calculated using these formulae (see Table 11). *Oniroscus reidi* had a calculated weight of between 2554 g and 4417 g (mostly <3300 g). This is similar to the size of the ground cuscus *Phalanger gymnotis* and is thus medium in size for phalangerids, while on the larger size it is closer in weight to *Spilocuscus maculatus*, the spotted cuscus. Large cuscuses (e.g. *Spilocuscus rufoniger*) weigh up to 6000 g, while very

SPECIES	NUMBER	VARIABLE	WEIGHT	AVERAGE
<i>O. reidi</i>	QMF13076	TJL	2554	
	QMF24084	4UML	2184	
	QMF18163	2UML	4417	
	QMF13078	1UMW	3300	3114
<i>O. notialis</i>	NMV54133	3LML*	2718	2718
<i>O. silvacultrix</i>	QMF24743	TJL	1903	
	QMF41197	4LMW	4299	
	QMF13101	1LML**	3443	3215
<i>O. inversus</i>	QMF24080	4LMW	3641	
	QMF24037	3LML*	1761	
<i>O. rupina</i>	QMF30478	2LML**	2520	
	QMF31492	2UML	4093	
?	QMF30701	UMORL*	2050	
?	QMF30420	3UMW	1633	

Table 11. Species weights. Weights are calculated using 'Dip' equations from Myers (2001) unless indicated: *All—dasy; ** All. TJL (total jaw length) is the most reliable measurement, but this was generally not available.

large cuscuses (e.g. *Ailurops ursinus*) weigh up to 10 000 g. Small phalangerids weigh around 1000 g. *Onirocuscus notialis* had a calculated weight of 2718 g, also medium in size. *Onirocuscus silvacultrix* had a estimated weight of 3215 g, while the calculated weight of *O. inversus* was 2701 g. Calculations of weight for these two species based on upper dentition, however, showed a smaller size, with the weight estimate being 1842 g. Body-weight calculations for *Onirocuscus rupina* showed a range between 2520 g and 4093 g. *Onirocuscus* appears to be a genus of medium to large cuscuses, larger than other species in the fossil record.

Many studies have been performed on habitat separation in extant mammal species. Emmons (1980) studied a squirrel community in Gabon where nine species were found in sympatry. Species richness was attributed to the mosaic nature of the forest, which provides specialized habitats, and locomotor habit. Large numbers of plant species fruiting asynchronously allow continuous production of fruit throughout the year. This may also have held true for the Miocene Riversleigh environments. Similarly, Leite *et al.* (1996) suggested that

marsupials in Brazil segregated according to vertical space first, and then by diet and weight. Phalangerids in New Guinea appear to separate niches based on weight and altitude: when cuscuses are in sympatry, they tend to differ in size and habits (Dickman, in MacDonald 1995, pp. 854-855). The larger species is often herbivorous and lives in the canopy, whereas the smaller species are more frugivorous and insectivorous, and live in the understorey. Two of the newly described fossil species are found within the same fossil sites. *Onirocuscus inversus* has more robust molars and a third premolar that has a more curved apex descending posteriorly in a concave shape. *Onirocuscus silvacultrix* has more delicate molars and a finer, pointed third premolar. These differences suggest some difference in diet, possibly in the type of fruit or nut being eaten. These species are found at the same sites as *Wyulda asherjoeli* (Crosby *et al.* 2001) and another undescribed species, the latter two being smaller than the species of *Onirocuscus*. *Onirocuscus reidi* is the largest phalangerid described from Riversleigh, occurring in sympatry with '*Trichosurus*' *dicksoni* and another undescribed species.

The description of three new species of fossil phalangerid greatly increases our knowledge of the diversity of phalangerids in the Miocene. Previously, only two phalangerid species had been described from Riversleigh, and none from central Australian deposits. Crosby *et al.* (2004) summarized current knowledge of possum diversity in the Australasian fossil record. Pseudocheirids currently have the most species known at Riversleigh (both described and undescribed). This is similar to modern possum diversity, with most species known from this family. Crosby *et al.* (2004) mentioned the presence of two more undescribed genera of phalangerid that have been identified from Riversleigh. Phalangerid diversity at Riversleigh is much higher than previously thought.

Acknowledgements

Many thanks to everyone involved with the Riversleigh project, especially my supervisor Michael Archer, Dr Sue Hand, Henk Godthelp and Anna Gillespie, as well as other students in the lab, including Troy Myers, Ben Kear, Mina Bassarova, and Karen Black. Vital support for this research has been provided by (among others): the Australian Research Grant scheme (grants to M. Archer); the University of New South Wales; the National Estate Grants Scheme (Queensland); the Riversleigh Society Inc.; the Queensland National Parks and Wildlife Service; Century Zinc Pty Ltd; Pasminco Pty Ltd; Earthwatch Australia; ANSETT Australia; ICI Australia Pty Ltd; the Australian Geographic Society; the Queensland Museum; the Australian Museum; the Royal Zoological Society of New South Wales; the Linnean Society of New South Wales; Mount Isa Mines and private supporters. Thanks to Dr Christopher Norris of the American Museum of Natural History for all his help with periotic morphology.

References

- ALEXANDER, W.B., 1919. A new species of marsupial of the subfamily Phalangerinae. *Journal of the Royal Society of Western Australia* 4, 31-36.
- APLIN, K.P. & ARCHER, M., 1987. Recent advances in marsupial systematics with a new syncretic classification. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed. Surrey Beatty & Sons & the Royal Zoological Society of New South Wales, Chipping Norton, NSW, xv-lxxii.
- ARCHER, M., 1976. The basicranial region of marsupial carnivores (Marsupialia), interrelationships of carnivorous marsupials, and affinities of the insectivorous peramelids. *Zoological Journal of the Linnean Society* 59, 217-322.
- ARCHER, M., GODTHELP, H., HAND, S.J. & MEGIRIAN, D., 1989. Fossil mammals of Riversleigh, north-western Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Journal of Zoology* 25, 29-65.
- ARCHER, M., HAND, S.J. & GODTHELP, H., 1994. *Riversleigh: the Story of Animals in Ancient Rainforests of Inland Australia*, Reed Books, Sydney, 264 pp.
- ARCHER, M., HAND, S.J. & GODTHELP, H., 1995. Tertiary environmental and biotic change in Australia. In *Paleoclimate and Evolution, with Emphasis on Human Origins*, E. VRBA, G.H. DENTON, T.C. PARTRIDGE & L.H. BURCKLE, eds, Yale University Press, New Haven, CT, 77-90.
- ARCHER, M., HAND, S.J., GODTHELP, H. & CREASER, P., 1997. Correlation of the Cainozoic sediments of the Riversleigh World Heritage fossil property, Queensland, Australia. In *Actes du Congres Biochrom'97*, J.-P. AGUILAR, S. LEGENDRE & J. MICHAUX, eds., Ecole Pratique des Hautes Etudes Institut de Montpellier, Montpellier, France, 131-152.
- BAVERSTOCK, P.R., 1984. The molecular relationships of Australasian possums and gliders. In *Possums and Gliders*, A.P. SMITH & I.D. HUME, eds, Australian Mammal Society, Sydney, 1-8.
- COOKE, B.N., 1997. Biostratigraphic implications of fossil kangaroos at Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum* 41, 295-302.
- CREASER, P., 1997. Oligocene-Miocene sediments of Riversleigh: the potential significance of topography. *Memoirs of the Queensland Museum* 41, 303-314.
- CROSBY, K. 2002. *Studies in the diversity and evolution of phalangeroid possums (Marsupalia; Phalangerida; Phalangeroidea)*, PhD dissertation, University of New South Wales.
- CROSBY, K., BASSAROVA, M., ARCHER, M. & CARBERY, K., 2004. Fossil possums in Australasia: discovery, diversity and evolution. In *The Biology of Australian Possums and Gliders*, R.L. GOLDINGAY & S.M. JACKSON, eds, Surrey Beatty & Sons, Chipping Norton, Australia, 161-176.

- CROSBY, K., NAGY, M. & ARCHER, M., 2001. *Wyulda asherjoeli*, a new phalangerid (Diprotodontia: Marsupialia) from the early Miocene of Riversleigh, northwestern Queensland. *Memoirs of the Association of Australasian Palaeontologists* 25, 77-82.
- CROSBY, K. & NORRIS, C.A., 2003. Periotic morphology in the trichosurin possums *Strigocuscus celebensis* and *Wyulda squamicaudata* (Diprotodontia, Phalangeridae) and a revised diagnosis of the tribe Trichosurini. *American Museum Novitates* 3414, 14 pp.
- EMMONS, L.H., 1980. Ecology and resource partitioning among nine species of African rain forest squirrels. *Ecological Monographs* 50, 31-54.
- FLANNERY, T. & ARCHER, M., 1987. *Strigocuscus reidi* and *Trichosurus dicksoni*, two new phalangerids (Marsupialia: Phalangeridae) from the Miocene of northwestern Queensland. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons & the Royal Zoological Society of New South Wales, Chipping Norton, Australia, 527-536.
- FLANNERY, T.F., 1994. *Possums of the world: a monograph of the Phalangeroidea*, Geo Productions Pty Ltd, Sydney, 240 pp.
- FLANNERY, T.F., ARCHER, M. & MAYNES, G., 1987a. The phylogenetic relationships of living phalangerids (Phalangeroidea: Marsupialia) with a suggested new taxonomy. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons & the Royal Zoological Society of New South Wales, Sydney, 477-506.
- FLANNERY, T.F., TURNBULL, W.D., RICH, T.H.V. & LUNDELIUS, E.L., 1987b. The phalangerids (Marsupialia: Phalangeridae) of the early Pliocene Hamilton Local Fauna, southwestern Victoria. In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons & the Royal Zoological Society of New South Wales, Chipping Norton, Australia, 537-546.
- FLOWER, W.H., 1867. On the development and succession of teeth in the Marsupialia. *Philosophical Transactions of the Royal Society of London* 157, 631-641.
- FLYNN, T.T., 1911. Notes on marsupial anatomy. 1. The condition of the median vaginal septum in the Trichosuridae. *Papers and Proceedings of the Royal Society of Tasmania* 1911, 120-123.
- GEOFFROY SAINT-HILAIRE, E. & CUVIER, G.F., 1803. Catalogue des mammifères du Musée National d'Histoire Naturelle (Ouvre inachevé), Paris, 1802. In *Bibliotheca Historico-Naturalis*, Verzeichniss der Bucher uber Naturgeschichte von Wilhelm Engelmann (1846), Leipzig, 374 pp.
- GEORGE, G.G., 1987. Characterisation of the living species of cuscus (Marsupialia: Phalangeridae). In *Possums and Opossums: Studies in Evolution*, M. ARCHER, ed., Surrey Beatty & Sons & the Royal Zoological Society of New South Wales, Chipping Norton, Australia, 507-526.
- GRAY, J.E., 1858. Observations on the genus *Cuscus*, with the description of a new species. *Proceedings of the Zoological Society of London* 1858, 100-105.
- GRAY, J.E., 1860. Description of a new species of cuscus (*C. ornatus*) from the island of Batchian with a list of Mammalia collected on that island by Mr A. R. Wallace. *Proceedings of the Zoological Society of London* 1860, 1-5.
- GRAY, J.E., 1862 (1861). Additional observations on the genus *Cuscus*. *Proceedings of the Zoological Society of London* 12, 314-321.
- HAMILTON, A.T. & SPRINGER, M.S., 1999. DNA sequence evidence for placement of the ground cuscus, *Phalanger gymnotis*, in the tribe Phalangerini (Marsupialia: Phalangeridae). *Journal of Mammalian Evolution* 6, 1-17.
- KIRSCH, J.A.W. & WOLMAN, M.A., 2001. Molecular relationships of the bear cuscus, *Ailurops ursinus* (Marsupialia: Phalangeridae). *Australian Mammalogy* 23, 23-30.
- LEITE, Y.L.R., COSTA, L.P. & STALLINGS, J.R., 1996. Diet and vertical space use of three species of sympatric opossums in a Brazilian Atlantic forest reserve. *Journal of Tropical Ecology* 12, 435-440.
- LESSON, R.P., 1828. Manuel de Mammalogie. In *Dictionnaire classique d'histoire naturelle*, vol. 13, J.V. AUDOUIN & J.B.G.M.B. d. SAINT-VINCENT, eds, Paris, 333 pp.
- LUCKETT, W.P., 1993. An ontogenetic assessment of dental homologies in therian mammals. In *Mammal Phylogeny: Mesozoic Differentiation, Multituberculates, Monotremes, Early Therians and Marsupials*, F.S. SZALAY, M.J. NOVACEK & M.C. MCKENNA, eds, Springer, New York, 182-204.
- MACDONALD, D. (ed.), 1995. *The Encyclopedia of Mammals*, Andromeda, Oxford, 895 pp.
- MENZIES, J.I. & PERNETTA, J.C., 1986. A taxonomic revision of of cuscuses allied to *Phalanger orientalis* (Marsupialia: Phalangeridae). *Journal of Zoology, London, Series B* 1, 551-618.
- MILNE-EDWARDS, A., 1877. Notes sur quelques mammifères nouveaux provenant de la Nouvelle-Guinée. *Comptes rendus de l'Académie des sciences. Paris* 85, 1079.
- MORRELL, A., 2002. The geology and palaeontology of Keith's Chocky Block Site, Riversleigh World Heritage Fossil Property, northwestern Queensland. Honours Thesis. Sydney: University of New South Wales.
- MYERS, T.J., 2001. Prediction of marsupial body mass. *Australian Journal of Zoology* 49, 1-20.
- NORRIS, C.A., 1994. The periotic bones of possums and cuscuses: cuscus polyphyly and the division of the marsupial family Phalangeridae. *Zoological Journal of the Linnean Society* 111, 73-98.
- OWEN, R., 1866. *On the Anatomy of Vertebrates*, Longmans, Green, London.

- PALLAS, P.S., 1766. *Miscellanea Zoologica, Quibus Novae Imprimis Atque Obscurae Animalium Species Describuntur Et Observationibus Iconibusque Illustrantur*, van Cleef, The Hague, 224 pp.
- PETERS, W.C.H. & DORIA, G., 1875. Diagnosi di alcunenuove specie di marsupiali appartenenti alla fauna papuana. *Annali del Museo Civico di Storia Naturale di Giacomo Doria* 7, 541-544.
- RUEDAS, L.A. & MORALES, J.C., 2005. Evolutionary relationships among genera of Phalangeridae (Metatheria: Diprotodontia) inferred from mitochondrial DNA. *Journal of Mammalogy* 86, 353-365.
- SPRINGER, M.S., KIRSCH, J.A.W., APLIN, K. & FLANERNY, T., 1990. DNA hybridization, cladistics, and the phylogeny of phalangerid marsupials. *Journal of Molecular Evolution* 30, 298-311.
- STORR, G.C.C., 1780. *Prodromus methodi mammalium et avium*. Tubingen, 43 pp.
- TATE, G.H.H., 1945. Results of the Archbold Expeditions. No. 52 The marsupial genus *Phalanger*. *American Museum Novitates* 1283, 1-41.
- TEDFORD, R.H., 1967. Fossil mammals from the Carl Creek Limestone, northwestern Queensland. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia* 92, 217-236.
- TEMMINCK, C.J., 1824-1827. *Monographie de mammalogie ou dexcription de quelques genres de mammiferes, dont les espèces ont été observées dans les différents musées de l'Europe*.1, Dafour et d'Ocagne, Paris.
- THOMAS, O., 1888. *Catalogue of the Marsupialia Monotremata in the Collection of the British Museum (Natural History)*, British Museum (Natural History), London, 401 pp.
- THOMAS, O., 1896. On mammals collected by Mr Albert Meek on Woodlark Island, and on Kiriwina in the Trobriand group. *Novitates Zoologicae (British Museum, Natural History, London)* 3, 526-529.
- THOMAS, O., 1898a. Descriptions of two new cuscuses (*Phalanger*) obtained by Dr. Loria in British New Guinea. *Estratto dagli annali del Museo Civico di Storia Naturale di Giacomo Doria* (2a) 19, 5-8.
- THOMAS, O., 1898b. Descriptions of two new cuscuses (*Phalanger*). *Novitates Zoologicae (British Museum, Natural History, London)* 5, 433-434.
- THOMAS, O., 1907. On three new mammals from British New Guinea. *Annals and Magazine of Natural History, Including Zoology, Botany and Geology, Series 7*, 20, 74.
- WAGLER, J., 1830. *Natürliches System der Amphibien, mit vornagehender Classification der Säugethiere und Vögel. Ein Beitrag zur Vergleichenden Zoologie*, München, Stuttgart, 354 pp.