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Australian Oligo-Miocene Mystacinids (Microchiroptera): upper dentition, new taxa and divergence of New Zealand species

Microchiroptera Mystacinidae oligo-miocènes d'Australie : dentition supérieure, nouveaux taxons, et divergence de l'espèce de Nouvelle-Zélande

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Abstract

The upper dentition of two Australian early Miocene mystacinids, *Icarops paradox* and *I. aenae*, from Riversleigh, Queensland, are described for the first time. Also recognised is a late Oligocene mystacinid from Lake Palankarinna, South Australia. The new fossils help refine understanding about the evolutionary history of mystacinids in Australia, including their temporal and geographical range, possible dietary and roosting habits, and likely separation time of New Zealand mystacinids.
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Résumé

Les dentitions supérieures de deux mystacinidés du Miocène inférieur d'Australie, *Icarops paradox* et *I. aenae*, de Riversleigh dans le Queensland, sont décrites pour la première fois. Un mystacinidé a également été identifié dans l'Oligocène supérieur du lac Palankarinna, South Australia. Ces nouveaux fossiles apportent une contribution à l'histoire évolutive des mystacinidés en Australie, en particulier leur répartition géographique au cours du temps, leur régime alimentaire, leurs habitats, et la période probable de leur séparation des mystacinidés de Nouvelle-Zélande.
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Keywords: Chiroptera; Mystacinidae; Oligo-Miocene; Australia; New Zealand; Gondwana

Mots clés : Chiroptera ; Mystacinidae ; Oligo-Miocène ; Australie ; Nouvelle-Zélande ; Gondwana

1. Introduction

Over the past two decades, Oligo-Miocene and Pliocene freshwater limestones in the Riversleigh World Heritage Property in northwestern Queensland, Australia have produced a rich vertebrate fauna including more than 50 new bat species (Hand, 1999). Six microchiropteran families are represented:

the Hipposideridae, Megadermatidae, Molossidae, Vespertilionidae, Mystacinidae and, in Pliocene sediments, Emballonuridae. These include at least 20 species of eight hipposiderid genera (*Hipposideros*, *Brachipposideros*, *Rhinonycteris*, *Riversleigha*, *Xenorhinos*, *Archerops*, *Brevipalatus*, *Miophyllorhina*), eight megadermatids representing two genera (*Macroderma*, *Megaderma*), five molossids of at least two genera (*Petramops*, *Mormopterus*) and two species of *Taphozous* (References in Hand, 1999; Hand and Kirsch, 2003; Hand and Archer, 2005). Vespertilionids include a species of *Leu-*

conoe from the early Miocene (Menu et al., 2002) and four Pliocene species probably representing the modern Australian genera *Chalinolobus* and *Scotorepens* (Archer et al., 1994).

Two mystacinids have previously been described from Riversleigh's Miocene sediments (*Icarops aenae* and *I. paradox*) and a third species from the middle Miocene Bullock Creek deposit in Australia's Northern Territory (*I. breviceps*; Hand et al., 1998, 2001). These fossils provided the first pre-Pleistocene record for the Mystacinidae, which is otherwise known only from two Quaternary New Zealand species (Lloyd, 2001).

The Australian mystacinids were described on the basis of dentaries and, additionally in the case of *Icarops breviceps* and *I. paradox*, the lower dentitions (Hand et al., 1998, 2001). On the basis of that material, the Australian Tertiary mystacinids were interpreted to be generally more plesiomorphic than their New Zealand Quaternary relatives, and Australia implicated as the immediate source of New Zealand's mystacinids.

New mystacinid material now recovered from several Riversleigh sites includes the upper dentition of at least two mystacinid species and enables revision of the diagnosis of the genus *Icarops*, as well as the species *I. paradox* and *I. aenae*. It has also prompted reassessment of the identity of a single bat tooth from the Ditjimanka Local Fauna of northeastern South Australia, interpreted previously to be a possible rhinolophid (Archer, 1978).

Taxonomy and dental terminology follows Miller (1907); Hand et al. (1998). Stratigraphic nomenclature for the Riversleigh region follows Archer et al. (1989, 1994) and Creaser (1997). The prefix QMF refers to specimens held in the fossil collections of the Queensland Museum, Brisbane.

2. Systematics

Order CHIROPTERA Blumenbach, 1779.
Suborder MICROCHIROPTERA Dobson, 1875.
Superfamily NOCTILIONOIDEA Van Valen, 1979.
Family MYSTACINIDAE Dobson, 1875.

Genus *Icarops* Hand, Murray, Megirian, Archer and Godthelp, 1998.

Type species: *I. breviceps* Hand, Murray, Megirian, Archer and Godthelp, 1998.

Revised diagnosis: Species of *Icarops* differ from *Mystacina* species in the following features: P^4 length approximately two-thirds M^1 length; M^{1-2} conspicuously wider than P^4, with large posterolingually directed heel and lacking paraconule; M^3 premetacrista unreduced, equal in length to postparacrista; I_1 width and length approximately equal (i.e. not especially wide); P_3 smaller than P_4 (i.e. not subequal in length and width), lacking an extensive posterior heel, with only incipient posterolingual cingular cusp; P_4 less than half M_1 length with two roots oriented longitudinally or only slightly

obliquely with respect to the tooth row; all cusps of lower molars including entoconids taller and more distinct, with M_{1-2} talonid wider than trigonid.

Other species: *I. aenae* Hand et al., 1998; *Icarops paradox* Hand et al., 1998.

Remarks: The anterior premolars of *Icarops* and *Mystacina* species have been generally interpreted (e.g. Miller, 1907) to be P2 (rather than P3). Primitively, bats retain in each maxilla and mandible a canine, three premolars and three molars, but in the majority of microchiropterans at least one premolar is lost from each quadrant. Where two premolars are retained, the anterior one is usually regarded to be to be P2 in rhinolophoids, emballonuroids, vespertilionids, molossids and mystacinids, but P3 in other noctilionoids and in natoloids. If mystacinids are truly noctilionoids (see Section 3 below), then it is likely that embryological studies will establish the anterior premolar to be P3. The diagnosis of *Icarops* is revised thus (above) and that nomenclature used hereafter.

Icarops paradox Hand et al., 1998.
Figs. 1 and 2.

Holotype: QMF20808, partial mandible preserving fragments of left and right dentaries with alveoli for L I_1, C_1 and P_3 and R C_1, $P_{3,4}$ and M_1.

Type locality: Neville's Garden Site, D Site Plateau, Riversleigh World Heritage Property, Lawn Hill National Park, northwestern Queensland (Archer et al., 1989, 1994).

Other material: QMF31561, a partial, fused mandible with left dentary preserving C_1 and M_{1-3} and alveoli for I_1 and $P_{3,4}$, and right dentary with I_1, $P_{3,4}$ and M_{1-3}; from Judith's Horizontalis Site, D Site Plateau, Riversleigh (Hand et al., 1998).

New, referred material: QMF30582, a left maxilla fragment containing P^4-M^3 (Figs. 1(1) and 2) from Judith's Horizontalis Site, Riversleigh World Heritage Property; QMF30583, a left skull fragment preserving P^4 and alveoli for C^1, P^3 and M^1 (Fig. 1(2)) from Wayne's Wok Site, Hal's Hill, D Site Plateau, Riversleigh World Heritage Property; QMF30581, a left maxilla fragment with M^{2-3} (Fig. 1(3)) from Neville's Garden Site, D Site Plateau, Riversleigh World Heritage Property; QMF30590, a left M^1 (Fig. 1(4)) from Neville's Garden Site, D Site Plateau, Riversleigh World Heritage Property Lawn Hill National Park, northwestern Queensland.

Revised diagnosis: Smaller than *I. breviceps* and *I. aenae*, and with P_3 larger and P_4 more transversely oriented than in *I. aenae* (Hand et al., 1998). Additionally, it differs from *I. breviceps* in M_3 being less reduced (with trigonid and talonid of subequal width), and from *I. aenae* in its more transversely developed M^1 with longer and narrower heel with basin, and broader paracingulum.

Locality, age and depositional environment: Neville's Garden Site is a freshwater limestone deposit interpreted to be part of Riversleigh's System B deposits and as such early Miocene in age (Archer et al., 1989, 1994; Creaser, 1997). Numerous aquatic vertebrates such as lungfish, turtles, croco-
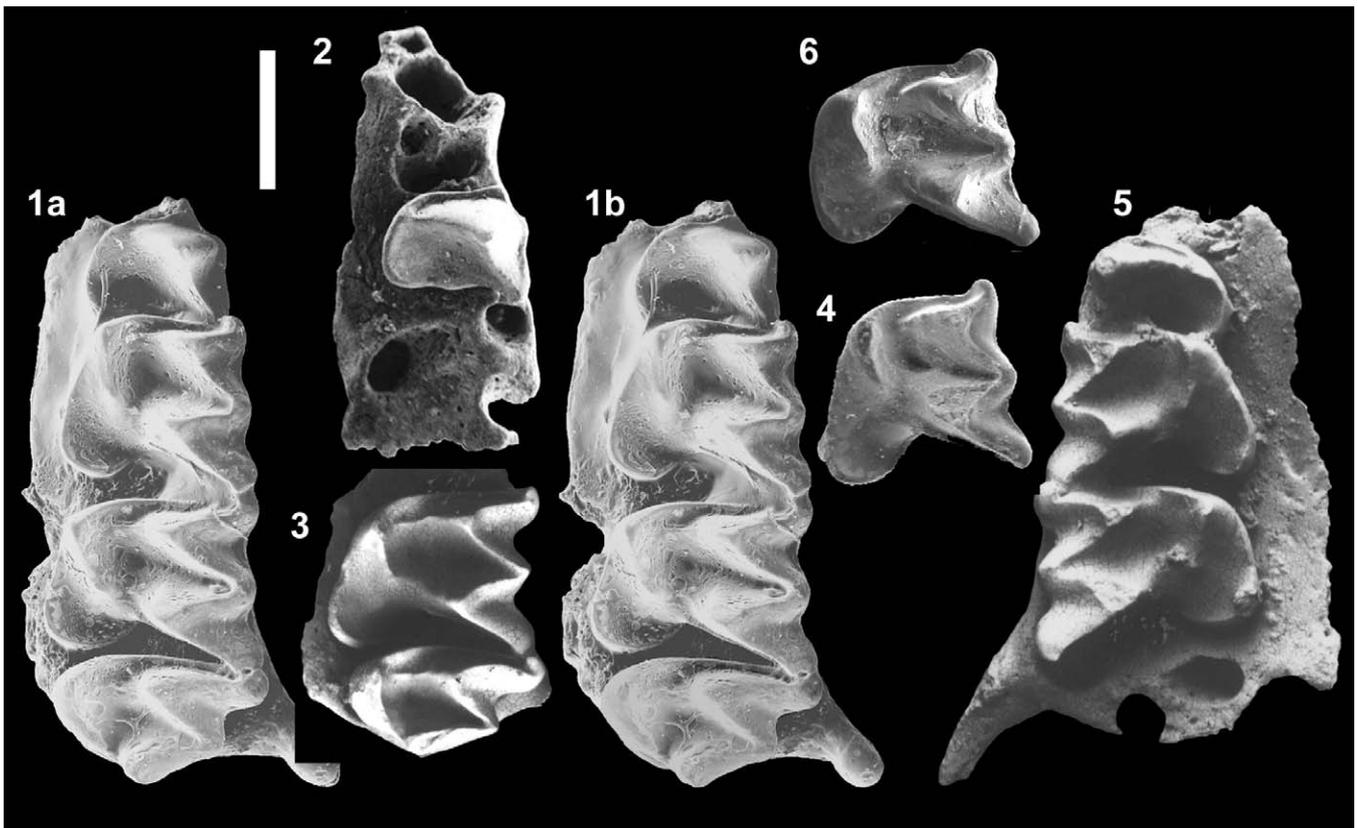
Fig. 1. *I. paradox*, Riversleigh World Heritage Property, northwestern Queensland, Australia. **1a**, **b**. QMF30582, P^4-M^3, Judith's Horizontal Site, stereopair. **2**. QMF30583, P^4, Wayne's Wok Site. **3**. QMF30581, M$^{2–3}$, Neville's Garden Site. **4**. QMF30590, M^1, Neville's Garden Site. *Icarops* sp. cf. *I. paradox*, Riversleigh World Heritage Property. **5**. QMF30580, P^4-M^2, Neville's Garden Site. Mystacinid indet., Tedford Locality, Lake Palankarinna, northeastern South Australia. **6**. QMF9033, M^1. Scale bar = 1 mm.

diles and platypus suggest that the main part of the Neville's Garden deposit accumulated in water, while delicate cave straws, travertine rim pool ridges on a rock surface and two small stalagmites found buried in situ indicate that a cave was developed at one edge of this pool. Other bats recovered from the deposit include six hipposiderids (Hand, 1997), at least one megadermatid, and at least one other mystacinid (see below).

Wayne's Wok Site occurs on the western edge of freshwater limestones comprising Hal's Hill, on the D Site Plateau, Riversleigh World Heritage Property. It is interpreted as part of Riversleigh's System B limestone deposits and hence early Miocene in age. The diversity of vertebrates represented in the deposit (including lungfish, teleost fish and chelid turtles), together with the fact that it contains complete skulls of marsupials but only fragmentary bat material, suggests that these fossils probably accumulated in a pool or lake rather than a cave (Hand et al., 1998).

The depositional environment of Judith's Horizontalis Site is less well understood but, on the basis of its stratigraphic and topographic position, and its contained marsupial fauna, it is also interpreted to be early Miocene in age (Creaser, 1997). Like Neville's Garden Site, Judith's Horizontalis Site contains a diverse vertebrate fauna including frogs, lizards, birds, many marsupials, and a megadermatid bat (Hand et al., 2001). The fragmentary nature of some of the smaller fossils

recovered from this site may indicate that they represent prey remains, possibly of the large megadermatid bat represented in the deposit.

Description: QMF30583 preserves a left skull fragment consisting of a fused premaxilla and maxilla, broken anteriorly and posteriorly but containing LP^4 and alveoli for C^1, P^3 and M^1, and at least one incisor. Anteriorly, the fragment is broken such that it is clear that the premaxilla was fused to the maxilla but not if the palatal branches were complete. Neither is it possible to determine the number of incisors retained. A small foramen occurs immediately anterior to the alveolus for the canine (Fig. 1(2)), but this may represent a nutrient foramen since it occurs well dorsal to what would have been the base of the upper canine. If it is an incisor alveolus it is likely to have been for the second incisor since further anteriorly are remnants of the alveolus for the first incisor.

QMF30582 preserves the ventral margin of the orbit which extends to a point level with the M^1 metacone (Fig. 2). Its anterolateral rim was evidently low and rounded, rather than raised and sharp, and the lateroventral fossa very wide. The infraorbital foramen opens anteriorly immediately dorsal to M^1. The canal is narrow and relatively small but the foramen extends anteroventrally onto the face as a deep fossa.

QMF30583 and QMF30582 preserve alveoli for the anterior premolar which was relatively large and had three roots.
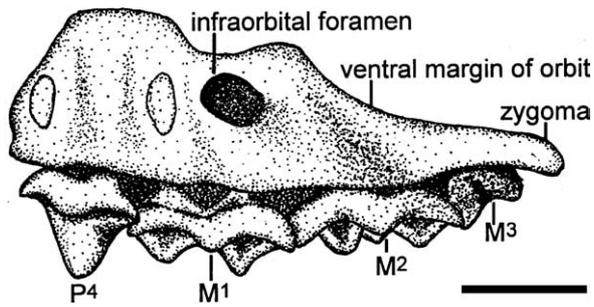
Fig. 2. *I. paradox*. QMF30582, P^4-M^3, Judith's Horizontal Site. Scale bar = 1 mm.

One root occurs at the buccal margin of the tooth row, lingual to the anterobuccal root of P^4; the second root occurs lingual to the first, approximately level with, or buccal to, the small anterolingual root. The anterior premolar would have been narrower and shorter than P^4. P^4 is wider than long, and subrectangular in occlusal view, the anterior margin not much shorter than the posterior margin, a small anterobuccal cingular cusp giving the tooth a squared appearance. In this view, the main cusp (paracone) occurs slightly anterobuccal to the centre of the crown; there is little posterolingual lobe development. The paracone is tall, with relatively straight crests running posterobuccally and anterolingually to the small protocone. The crown is surrounded by a narrow cingulum which is interrupted anterolingually by the protocone and buccally by a small cingular cuspule, and which is indistinct posteriorly.

QMF30582 and QMF30581 preserve P^4-M^3 and M$^{2–3}$, respectively. M^1 is just wider than long and conspicuously wider and longer than P^4. The metacone is larger and taller than the paracone, which is just taller than the protocone. The protocone is directed anterolingually; its apex occurs posterolingually to the paracone apex. The ectoloph is W-shaped with the centrocrista reaching the buccal margin of the tooth. The preparacrista is shorter than the postparacrista and premetacrista which are shorter than the postmetacrista. The preparacrista meets the short, anteriorly directed parastyle at approximately right angles. A buccal cingulum occurs between the smoothly rounded buccal flanks of the parastyle, mesostyle and metastyle. The pre- and postparacrista meet at an angle of approximately 70° which is slightly greater than that formed between pre- and postmetacristae (60°) and postparacrista and premetacrista (55°). The posteriorly opening protofossa is longer than broad and is relatively deep. A paraloph is clearly developed. It extends lingually from the base of the paracone towards but does not reach the protocone tip. There is no swelling (paraconule) where it terminates. An almost indistinct metaloph extends lingually from the base of the metocone to the postprotocrista closing the protofossa. The preprotocrista continues buccally as the paracingulum to the base of the parastyle. The posterobuccally directed postprotocrista terminates well short of the metacone base, terminating in a small metaconule. A very narrow, indistinct posterior cingulum extends from a point posterior to the metacone base to the metastyle. The posterior cingulum is not continuous with the narrow cingulum enclosing the well developed heel.

This lingual cingulum extends from a point posterior to the metacone base to the base of the protocone; it is very slightly swollen at its most posterolingual point. The heel is long, relatively wide, directed posterolingually, and has a pronounced basin. It lacks a hypocone and there is no lingual notch separating it from the protocone base. The tooth has three roots; the protocone root is very long, broad and obliquely angled, the metacone root large and posteriorly directed, and the paracone root straighter and smaller.

M^2 is described in so far as it differs from M^1. M^2 is wider than long and conspicuously wider than P^4 and M^1. The metacone is just taller than the paracone, which is significantly taller than the protocone. The broad, deep protofossa is defined by the paraloph, metaloph and adjacent bases of the paracone, metacone and protocone. A well developed paraloph extends posterolingually from the base of the paracone but does not reach the tip of the protocone. A much less distinct metaloph extends lingually from the base of the metacone to meet (QMF30581) or nearly meet (QMF30582) the posterobuccally directed postprotocrista at the metaconule, thereby closing the protofossa. The preparacrista, postparacrista, premetacrista and postmetacrista are of increasing length. The preparacrista meets the parastyle at an angle of less than 90°. The buccal flanks of the parastyle, mesostyle and metastyle are smoothly rounded. A mesostylar shelf extends from the parastyle to metastyle; poorly developed buccal cingulae occur between the buccal flanks of the parastyle, mesostyle and metastyle. The pre- and postparacristae, pre- and postmetacristae and postparacrista and premetacrista meet at angles of approximately 48–50°. The very narrow posterior cingulum is better developed than in M^1. The heel is long, relatively narrow, directed posterolingually, and also has a pronounced basin.

M^3 is wider than long and similar in width to M^2 (i.e. wider than P^4 and M^1). It retains a metacone, which was shorter than the paracone and subequal in height with the protocone. The preparacrista is longer than the subequal postparacrista and premetacrista. The protofossa is broad and deep and is defined by the paraloph, postprotocrista and adjacent bases of the paracone, metacone and protocone. The lingually directed paraloph is well developed but does not reach the tip of the protocone. The posterobuccally directed postprotocrista meets the base of the metacone without room for a metaloph, closing the protofossa. The paracingulum is nearly as wide as in M^2. The parastyle is conspicuously larger, cuspidate and anterolingually directed. There is no lingual, buccal or posterior cingulum. The posterior root is lingually displaced such that it occurs beneath the metacone, level with the M^2 metacone and M^3 paracone, at approximately the crown's mid-width.

Measurements of all new mystacinid specimens are given in Table 1.

Comparisons: The specimens referred here to *I. paradox* share a combination of features found only in bats of the family Mystacinidae. These features include: premaxilla fused to maxilla; infraorbital canal short with a very large external foramen low on the face and dorsal to M^1; retention of two

Table 1

Measurements (mm) of the dentition of Australian Oligo-Miocene mystacinid species: L, maximum length (in toothrow); w, maximum width; LT, trigonid length; Lt, talonid length; wT, trigonid width; wt, talonid width

Dimensions (mm) de la dentition des espÈces de Mystacinidae oligo-miocÈnes d'Australie : L, longueur maximale (rangÈe dentaire) ; w, largeur maximale ; LT, longueur du trigonide ; Lt, longueur du talonide ; wT, largeur du trigonide ; wt, largeur du talonide

Upper dentition													
QMF		30583	30582	30581	30580	30590	30575	30586	30587	30576	30588	30589	9033
P^4-M^3			4.5										
P^4-M^2			3.6		3.5								
M^{1-3}			3.6										
M^{2-3}			2.3	2.3									
P^4	L	1.1	0.9		0.8								
	w	1.2	1.1		1.1								
M^1	L		1.3		1.3	1.5	1.9	2.0					1.5
	w		1.5		1.6	1.6	1.9	2.1					1.7
M^2	L		1.3	1.4	1.5				1.8	2.0	1.9	2.0	
	w		1.7	1.8	1.8				2.2	2.3	2.3	2.2	
M^3	L		1.0	1.0									
	w		1.7	1.6									
Lower dentition													
QMF		30584	24509	30585									
M_{2-3}		3.4		3.4									
M_1	L		1.9										
	LT		1.1										
	Lt		0.8										
	wT		1.4										
	wt		1.5										
M_2	L	1.8		1.8									
	LT	1.0		1.0									
	Lt	0.8		0.8									
	wT	1.3		1.3									
	wt	1.4		1.4									
M_3	L	1.7		1.7									
	LT	0.9		0.9									
	Lt	0.8		0.8									
	wT	1.0		1.0									
	wt	0.9		0.9									

upper premolars, the anterior premolar large and with three roots, the posterior premolar non-molariform with small protocone, small buccal cingular cusp and continuous cingulum; M^{1-2} with low protocone, some heel development, lacking hypocone, with small metaconule, large mesostyle, central crests of ectoloph not parallel, paracingulum extending preprotocrista, and long protocone root; M^2 wider than M^1; M^3 large, with metacone, paraloph, and weak metaconule; parastyles increasing in size and more lingually directed from M^1 to M^3.

I. paradox differs from species of *Mystacina* as follows: the ventral margin of the orbit extends anteriorly to the M^1 metacone rather than to the M^2 mesostyle; the upper dentition is more crowded anteriorly, with P^3 and P^4 being relatively smaller teeth than in *M. tuberculata* or *M. robusta*; the C^1 alveolus is rounded rather than laterally flattened; P^4 is wider than long, of smaller dimensions than M^{1-3}, and has an only poorly developed anterolingual cusp; M^{1-2} are more transversely developed (wider than long, rather than square), with much larger heels; M^{1-2} lack paraconules; M^{1-2} with long metalophs that close the protofossa; and M^3 relatively longer in the tooth row. In *I. paradox* P^4 is wider than long

with no anterior expansion of the crown such that the paracone forms its anterior face; in *M. robusta* P^4 is more or less square with little anterior expansion of the crown, and in *M. tuberculata* P^4 is longer than wide with conspicuous anterior expansion of the crown such that the paracone occurs in the centre of the crown.

Remarks: QMF30590 is similar in size and overall morphology to M^1 in QMF30581. It is referred here to *I. paradox* although it appears to be slightly more gracile than M^1 in QMF30581, with a narrower, slimmer heel and longer postmetacrista.

Icarops sp. cf. *I. paradox*.
Fig. 1.
Material: QMF30580, a right maxilla fragment preserving P^4-M^2 and alveoli for P^3 and M^3.

Locality: Neville's Garden Site, D Site Plateau, Riversleigh World Heritage Property, Lawn Hill National Park, northwestern Queensland (Archer et al., 1989, 1994; Hand, 1997).

Age and depositional environment: As above.

Description: QMF30580 preserves P^4-M^2 and alveoli for an anterior premolar and M^3. It is described in so far as it: 1, differs from specimens confidently referred to *I. paradox* (above); and 2, contains additional information about a species of *Icarops*. The anterior margin of P^4 is shorter than the posterior margin, due to rounding of the anterobuccal and anterolingual margins of the crown, resulting in an oval rather than rectangular occlusal outline. There is little posterolingual lobe development, a very narrow anterior margin and no anterobuccal extension. The paracone is tall but more bulbous than in QMF30583, but with a relatively straight crest running posterobuccally and a curved crest running anterolingually to the low protocone. The M^1 protocone is directed anterolingually such that its apex occurs directly lingually to the paracone apex or slightly anterior to it. The posteriorly opening protofossa is broad but not especially deep and is defined by the adjacent bases of the paracone, metacone and protocone. There is no paraloph or metaloph. The preprotocrista terminates directly anterior to the base of the paracone, such that there is no paracingulum. There is a very narrow metacingulum extending from a point posterior to the metacone base to the metastyle. The heel is narrower and more lingually directed than in QMF30582 but not QMF30590. In M^2, as in M^1, the preprotocrista terminates directly anterior to the base of the paracone and does not continue buccally to form a paracingulum. The protofossa is broad but again not especially deep and is defined by the adjacent bases of the paracone, metacone and protocone, there being no paraloph or metaloph. The postprotocrista terminates well short of the metacone base, terminating in a small metaconule and only a very narrow metacingulum extends from a point posterior to the metacone base to the metastyle. The heel is narrower and appears to be more lingually directed and less distally extended (with respect to the position of the metacone) than in QMF30582 or QMF30581.

Features not preserved in other *Icarops* specimens are as follows. The palate's posterior border has a posterolateral indentation (incisura) that extends anteriorly to the level of the lingual root for M^3. A shallow palatal foramen is developed at a point level with the posterior face of M^1. The anterior root of the zygoma extends from a point lateral to the M^2 metacone to a point lateral to the midpoint of the posterior alveoli for M^3, at an angle of approximately 20° to the buccal margin of the tooth row. The postpalatal foramen is not preserved. In cross-section, the zygoma is small and round, rather than laterally flattened.

Comparisons: QMF30580 is slightly smaller than *I. paradox*, and unlike specimens of both *I. paradox* and *I. aenae* (see below), M$^{1-2}$ lack a paraloph, metaloph and paracingulum. P^4 also lacks the conspicuous anterobuccal cingular cusp seen in *I. paradox* (e.g. QMF30582 from Judith's Horizontal Site and QMF30583 from Wayne's Wok).

Remarks: Features distinguishing QMF30580 from *I. paradox* (and *I. aenae*, see below), including lack of M$^{1-2}$ paraloph, metaloph and paracingulum, do not appear to vary intraspecifically in Quaternary mystacinids (*M. tuberculata*

and *M. robusta*), and it is likely that *I. paradox* and QMF30580 represent different species; particularly striking in this context is the absence of the M$^{1-2}$ paracingulum in QMF30580. However, because QMF30590, an M^1 from Neville's Garden Site (Fig. 1(4)), lacks a paraloph and metaloph but has a broad paracingulum, it would appear that at least some of these features may vary intraspecifically in *Icarops* species. Until additional *Icarops* specimens are known, the taxonomic position of QMF30580 remains unclear.

Mystacinid indet.
Fig. 1(6).
Material: QMF9033, a left M^1.

Locality, age and depositional environment: Tedford Locality, Ditjimanka Local Fauna, Lake Palankarinna, Etadunna Station, northeastern South Australia (Archer, 1978; Woodburne, 1986). Sediments from this South Australian locality are interpreted to be late Oligocene in age (Woodburne et al., 1994; see Section 3).

Tedford Locality, on the western side of Lake Palankarinna, is a lacustrine deposit containing the Ditjimanka Local Fauna (Woodburne, 1986) which includes a platypus, archaic dasyurids, koalas, a bandicoot, zygomaturine, ilariid, and phalangerid, pilkipildrid and pseudocheirid possums (Rich et al., 1991).

Description: QMF9033 is described in so far as it differs from, or resembles, the M^1 of species of *Icarops* and *Mystacina*. It is just wider than long. A buccal cingulum occurs between the smoothly rounded buccal flanks of the parastyle, mesostyle and metastyle. The pre- and postparacrista meet at an angle of approximately 80° which is slightly greater than that formed between pre- and postmetacristae, and postparacrista and premetacrista (both 65°). The mesostylar area, where the two latter crests meet, is more rounded that in *I. paradox*, and the parastyle is better developed and anteriorly projecting. The posteriorly opening protofossa is longer than broad and is relatively deep. There is no sign of a paraloph nor paraconule. There is no metaloph but there is a conspicuous metaconule. The paracingulum is broad. A narrow but distinct posterior cingulum extends from the metastyle to a point posterior to the metacone base. A cingulum encloses the well developed heel; it is slightly swollen at its most posterolingual point. The heel is long, relatively wide and directed posterolingually. It lacks a hypocone and there is no lingual notch separating it from the protocone base. The tooth had three roots but only the metacone root is undamaged; the protocone root was very long and broad.

Comparisons: Archer (1978) compared QMF9033 with representatives of all modern microchiropteran groups and fossil taxa then known. He found that the tooth differed in particular characters from all bats examined, including rhinolophids and *Mystacina tuberculata*. Although he tentatively referred to it as a possible rhinolophid, it differs from species of *Rhinolophus* in its deep, posteriorly open protofossa; narrow anterior margin and broader posterior margin; less even ectoloph; long metastyle; and conspicuous metaconule.

The tooth resembles more closely the M^1 of species of *Icarops*, mystacinids with well developed heels, whose upper dentitions are described for the first time above. QMF9033 appears to exhibit a combination of features found only in bats of the family Mystacinidae, including $M^{1–2}$ with low protocone, some heel development, lacking hypocone, with small metaconule, large mesostyle, central crests of ectoloph not parallel, paracingulum typically extending preprotocrista and long protocone root. QMF9033 appears to be intermediate in size between the M^1 of *I. paradox* and *I. aenae*. It differs from that tooth in *I. paradox*, *I. aenae* and *I.* sp. cf. *I. aenae* (see below), and resembles M^1 in QMF30580, in lacking a paraloph and metaloph. It differs from the latter in its broad paracingulum and slightly wider heel. QMF9033 is smaller and more transversely developed than M^1 in *Mystacina* species and has a much better developed heel and longer metastyle.

Remarks: QMF9033 is referred here to the family Mystacinidae. Within the Mystacinidae, it appears to more closely resemble species of *Icarops* than those of *Mystacina* and probably represents a new species of *Icarops*.

Icarops aenae Hand et al., 1998.
Fig. 3.

Holotype: QMF30567, edentulous mandible preserving a fragment of the left dentary with alveoli for I_1 C_1 $P_{3,4}$ $M_{1–3}$ and right dentary fragment with alveoli for I_1 C_1 $P_{3,4}$.

Type locality: Wayne's Wok Site, Riversleigh World Heritage Property, Lawn Hill National Park, northwestern Queensland (Archer et al., 1989, 1994).

New material: QMF30584, left dentary containing M_2 and M_3 (Fig. 3(1)); QMF24509, right M_1 (Fig. 3(2)); QMF30575, left M^1 (Fig. 3(3)); all from the type locality.

Revised diagnosis: Larger than *I. paradox*, with P_3 smaller and P_4 more longitudinally oriented and M_3 more reduced (with talonid narrower than trigonid). Similar in size and $M_{1–2}$ morphology to *I. breviceps* but with P_4 roots more crowded and transversely oriented. Additionally, it differs from *I. paradox* in its square rather than transversely developed M^1 with much shorter and broader heel without basin, narrower paracingulum, lack of metaloph, and much shorter paraloph that runs anterolingually rather than lingually.

Locality, age and depositional environment: Wayne's Wok Site, Hal's Hill, D Site Plateau, Riversleigh World Heritage Property (see above).

Description: The dentary QMF30584 is broken anteriorly through the anterior root of M_2 and posterodorsally such that the mandibular foramen and part of the ascending ramus and masseteric fossa are preserved but not the condyle or angular process. The mandibular foramen is large, its dorsal margin level with the toothrow, and dentary depth is greater beneath M_2 than beneath M_3.

M_2 has two roots and five cusps. The paracone is damaged, the hypoconulid is a small cingular cusp, and the tips of all other cusps show considerable wear. Although the cusps are individualised, they are relatively low and inclined rather than tall and upright. The trigonid is narrower and slightly longer than the talonid. The protoconid and hypoconid are the dominant cusps in height and volume, but they are not massive. The protoconid is taller than the hypoconid which is taller than the metaconid which is taller than the entoconid (and probably the paraconid). All are much taller than the hypoconulid. The protoconid shows more wear than other cusps. The cristid obliqua, in occlusal view, is uncurved and contacts the trigonid at a point directly below the junction of the components of the metacristid. In lateral view there is no inflexion along the cristid obliqua close to the trigonid. The hypocristid extends from the hypoconid directly to the entoconid, almost perpendicular to the axis of the toothrow, isolating the small hypoconulid and thereby exhibiting the myotodont condition. The greatly bowed inflexion in the hypocristid, best seen in posterior view, occurs approximately midway between the hypoconid and entoconid. A preentocristid, straight and gently dipping, links the entoconid to the trigonid at the base of the metaconid (making an angle with the metaconid of just less than 90°). The angle between the para- and metacristids is relatively broad, at approximately 45°. The cristid obliqua and paracristid were probably almost parallel to each other. There is a uniform, nonsinuous, continuous anterior, buccal and posterior cingulum, terminated at its posterolingual end well short of the hypoconulid providing a notch for the anterior cingulum of M_3.

M_3 is described in so far as it differs from M_2. It is a narrower, shorter tooth. The trigonid is wider and just shorter than the talonid. The protoconid is the tallest and most massive cusp, the paracristid is longer than the metacristid, the protoconid contribution to the paracristid being particularly long. All cusps are present, including the hypoconulid.

QMF24509, an isolated right M_1 (Fig. 3(2)), is described in so far as it differs from M_2. The M_1 talonid is wider and longer than in M_2. The trigonid and talonid are narrower and slightly longer, the protoconid is shorter (and more worn) but the hypoconid is of similar size, and the metaconid and protoconid contributions of the metacristid are more unequal and meet at a less acute angle. The angle made between the paracristid and metacristid is wider, approximately 60°.

QMF30575, a left M^1 (Fig. 3(3)), is described in so far as it differs from that tooth in *I. paradox*. QMF30575 is just wider than long. Only a feint buccal cingulum occurs between the smoothly rounded buccal flanks of the parastyle, mesostyle and metastyle. The pre- and postparacrista meet at a slightly narrower angle of approximately 60° which is slightly greater than that formed between pre- and postmetacristae (55°) and postparacrista and premetacrista (50°). There is no metaloph and the paracingulum is relatively narrow. A narrow but distinct posterior cingulum extends from the metastyle to a point posterior to the metacone base. The heel is relatively wide, not especially posteriorly extended, and directed posterolingually.

Comparisons: The dentary QMF30584 is the same size and has the same alveolar pattern as QMF30567 (the holotype of *I. aenae*), the masseteric foramen and dentary depth being also similar. The lower molars of *I. aenae* closely resemble those of *I. breviceps* in size and morphology, dif-
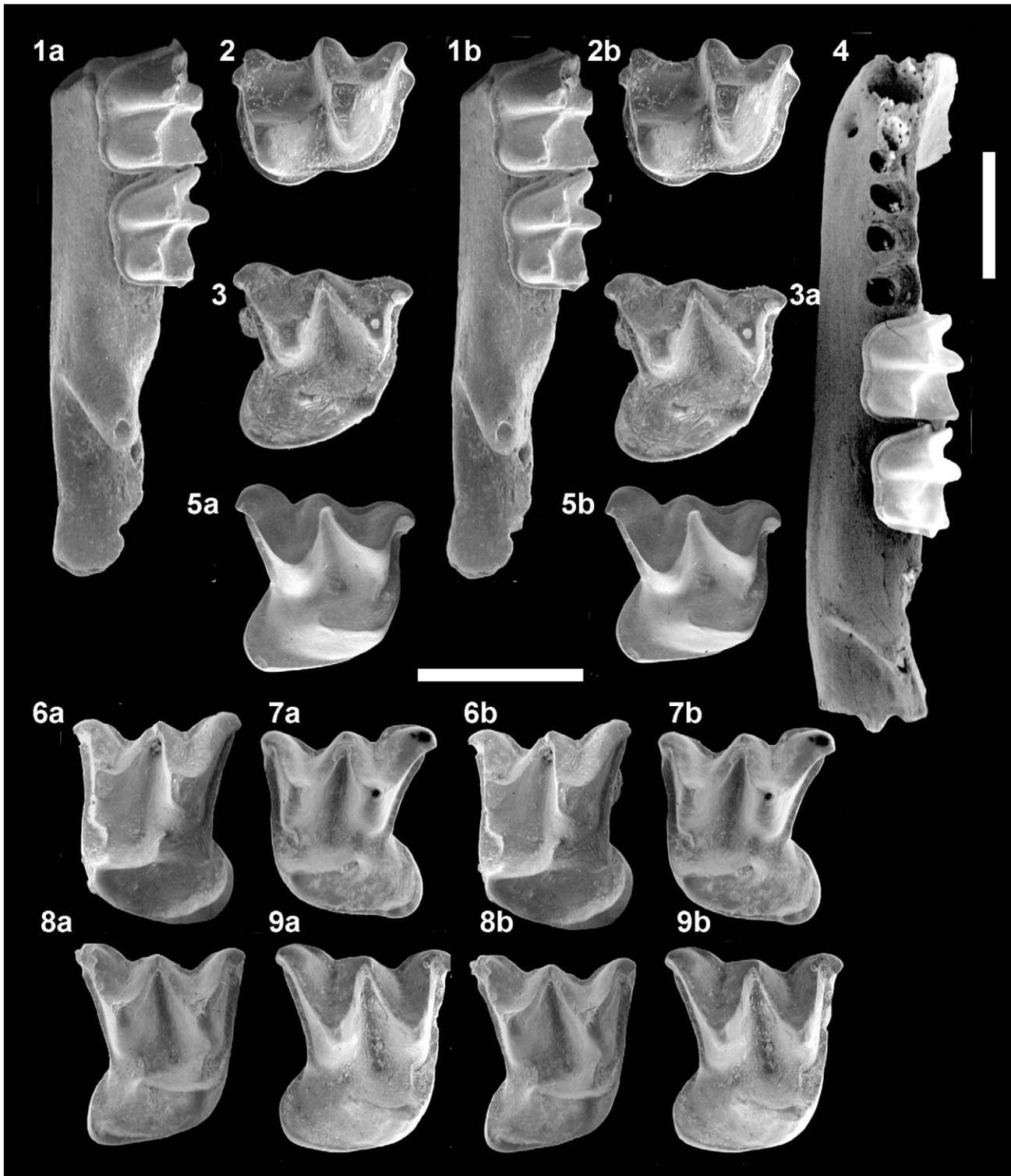
Fig. 3. *I. aenae*, Wayne's Wok Site, Riversleigh World Heritage Property, northwestern Queensland. **1a**, **b**. QMF30584, M_{2-3}, stereopair. **2a**, **b**. QMF24509, M_1, stereopair. **3a**, **b**. QMF30575, M^1, stereopair. *Icarops* sp. cf. *I. aenae*, Outasite, Riversleigh World Heritage Property, northwestern Queensland. **4**. QMF30585, M_{2-3}. **5a**, **b**. QMF30586, M^1, stereopair. *Icarops* indet., Riversleigh World Heritage Property, northwestern Queensland. **6a**, **b**. QMF30587, M^2, stereopair. **7a**, **b**. QMF30576, M^2, stereopair. **8a**, **b**. QMF30588, M^2, stereopair. **9a**, **b**. QMF30589, M^2, stereopair. Scale bars = 1 mm.

fering more from those of *I. paradox* in being much larger and more myotodont. The M_{1-3} of *I. aenae* are also very similar to those teeth in New Zealand's Quaternary *M. tuberculata* and *M. robusta*. They are smaller than those of *M. robusta* and the M_2 trigonid not as wide, but are slightly larger than (or within the size range of) those teeth in *M. tuberculata*.

Because QMF30575 is a very square tooth it appears to be more similar to M^1 in *Mystacina* species than in *I. paradox*. However, it differs from M^1 in *Mystacina* spp. in being slightly more transversely developed due to its larger, posterolingually directed heel, and in its narrower paracingulum. In *Mystacina* species, an anteriorly directed paraloph on M^1 extends to a conspicuous paraconule swelling on the preprotocrista. In QMF30575, a weak, short paraloph extends to the anterior margin of the protofossa but there is no paraconule. QMF30575 is smaller than that tooth in *M. robusta* and within the size range of *M. tuberculata*. Like *M. robusta*, it lacks a metaloph on M^1. QMF30575 differs from M^1 in *I. paradox* in its larger size, square rather than transversely developed shape, its much shorter and broader heel, much narrower paracingulum, lack of metaloph, and much shorter paraloph that runs anterolingually rather than lingually. A basin is developed in the large heel of M^{1-2} in *I. paradox* which is lacking in QMF30575. As in *I. paradox* and *Mystacina* species, QMF30575 has a long protocone root, and the metacone root is larger than the paracone root.

Icarops sp. cf. *I. aenae*.
Fig. 3.

Material: QMF30585, left dentary containing M_2 and M_3 with alveoli for C_1, P_3, P_4 and M_1 (Fig. 3(4)); QMF30586, left M^1 (Fig. 3(5)).

Locality: Outasite, Godthelp's Hill, D Site Plateau, Riversleigh World Heritage Property, Lawn Hill National Park, northwestern Queensland (Archer et al., 1989, 1994).

Age and depositional environment: Outasite, on the northwest facing slope of Godthelp's Hill, is interpreted as the lower part of Riversleigh's System B limestone deposits (Creaser, 1997) and as such early Miocene in age. Few taxa have been described yet from this deposit, but they include the swiftlet *Collocalia buday* (Boles, 2001), the possum *Burramys brutyi* (Brammall and Archer, 1997), kangaroo *Balbaroo fangaroo* (Cooke, 2000), as well as skinks (*Sphenomorphus* spp.) and leptodactylid frogs. The presence of a swiftlet but absence of abundant, well-preserved hipposiderid remains (found in most Riversleigh cave deposits) suggests the proximity of Outasite to cliffs or caves but not necessarily its deposition within a cave (see also Boles, 2001).

Description: The dentary QMF30585 (Fig. 3(4)) is described in so far as it differs from QMF30567 and QMF30584 from Wayne's Wok Site (see above, and Hand et al., 1998). QMF30585 is broken posteriorly such that the condyle and angular process are not preserved. It is of same size and alveolar pattern as QMF30567 and QMF30584, the mental and anterior foramina are positioned similarly, and dentary depth decreases posteriorly similarly. The overall morphology and size of M_{2-3} are also similar to those teeth in QMF30584.

QMF30586, an M^1 (Fig. 3(5)), is described in so far as it differs from QMF30575 from Wayne's Wok Site. It is relatively wider than QMF30575, with better developed and nar-

rower heel with deeper heel basin. The paracingulum is much wider than in QMF30575, and because QMF30586 is a higher crowned tooth, the protofossa appears to be deeper. The parastyle, mesostyle and metastyle are better developed, post- and preectoflexus notches deeper, and the buccal cingulum more pronounced. A short paraloph is clearly developed, as in QMF30575, but does not reach the preprotocrista. As in QMF30575, there is a conspicuous metaconule but no metaloph.

Comparisons: QMF30585 confirms the differences between *I. aenae* and *I. breviceps* noted by Hand et al. (1998): *I. aenae* has a shallower dentary (especially anteriorly), a smaller P_3 alveolus, less bossing in the anterior part of the jaw, and less well developed ventral mandibular shelf. The mandibular foramen is not quite as large as in *I. breviceps*, the shelf for attachment of mandibular muscles not as distinct, and the ascending ramus possibly not as vertical. The M_{2-3} are very similar to those of *I. breviceps* but in lateral view the buccal cingulum is curved or dipping in the talonid rather than straight. Compared with *I. paradox*, QMF30585 is larger, more robust and the anterior teeth less crowded (as indicated by alveolar pattern). In occlusal view, the dentary is much thicker (especially anteriorly) and the ventral mandibular shelf better developed. The teeth are larger, cusps more vertical, M_1 trigonid less open, hypocristid (in posterior view) taller (more myotodont), and alveolus for C_1 conspicuously larger than P_3. Compared with *Mystacina* species, the mental foramen in QMF30585 is located more anterodorsally; in *M. tuberculata* and *M. robusta* it is ventral to the anterior root of P_4 and at more than two-thirds dentary depth. The teeth are smaller than in *M. robusta*, the M_2 trigonid not as wide, and the anterior dentition (including P_4) occupies less than half the tooth row length. The teeth are slightly larger than *M. tuberculata* (or within that size range), and the anterior alveoli (C_1 and P_3) are less flattened and less procumbent.

Compared with M^1 in *I. aenae*, QMF30586 is larger, has a longer heel, broader paracingulum, narrower cingulum surrounding the heel, greater basin development in the heel, deeper pre- and postectoflexus notches, and better developed parastyle, mesostyle and metastyle. QMF30586 differs from M^1 in *I. paradox* in its larger size, square rather than transversely developed shape, its much shorter and broader heel, shorter paraloph and less well developed heel basin. It differs from M^1 in *Mystacina* species in being more transversely developed due to its longer, broader, posterolingually directed heel, and lacking a paraconule. QMF30586 is smaller than that tooth in *M. robusta* but may fall within the size range of *M. tuberculata*.

Remarks: Although QMF30585 and QMF30586 are most similar overall to material of *I. aenae* from the type locality Wayne's Wok, and may ultimately be referred to that species, differences in size and morphology (especially in M^1) suggest the material could represent a different taxon. Until more data on intraspecific variation in *Icarops* species is available, the specimens from Outasite are described and figured separately from those of the type locality.

Icarops species undetermined.
Fig. 3.

Material: QMF30587, M^2 (Fig. 3(6)) from Neville's Garden Site, D Site Plateau, Riversleigh World Heritage Property; QMF30576, left M^2 (Fig. 3(7)) from Upper Site, Godthelp Hill, D Site Plateau, Riversleigh World Heritage Property; QMF30588, M^2 (Fig. 3(8)) from Upper Site; QMF30589, M^2 (Fig. 3(9)) from P Site, Godthelp Hill, D Site Plateau, Riversleigh World Heritage Property.

Locality, age and depositional environment: Upper and P Sites, Godthelp Hill, D Site Plateau, Riversleigh World Heritage Property; Neville's Garden Site, D Site Plateau, Riversleigh World Heritage Property. On the basis of stratigraphy and faunal assemblages, the Upper, Neville's Garden and P Site deposits have been interpreted to be part of Riversleigh's System B limestone deposits (Archer et al., 1989, 1994; Creaser, 1997) and therefore early Miocene in age (approximately 20 million years old). The vertebrate fauna from Upper Site, one of the most diverse and best preserved at Riversleigh, includes more than 60 monotreme, marsupial and bat species, in addition to lungfish, teleost fish, hylid and leptodactylid frogs, chelids, lizards, snakes, and birds. The depositional environment is interpreted to have been a rainforest pool or lake (Archer et al., 1988, 1994). Far less is known about the fauna or likely depositional environment of P Site, also on Godthelp Hill, from which only a species of *Yalkaparidon* has been recorded (Archer et al., 1988). Details about the Neville's Garden deposit are given above.

Description: These four upper molars are similar to each other in size and overall morphology. They differ from QMF30575 (*I. aenae*) and QMF30586 (cf. *I. aenae*) in features typically distinguishing M^2 from M^1 in bats, and are described in so far as they differ from those teeth. They are broader (especially anteriorly) so that the teeth are conspicuously wider than long. They have a slightly more posteriorly directed heel, a broader ectoloph, taller mesostyle, more lingually directed parastyle, and slightly deeper pre- and postectoflexus notches. The metacone is taller than the paracone (although the difference in height between the two cusps is not as great as in QMF30575 and QMF30586). The apex of the protocone is more posteriorly located than in QMF30575 and QMF30586. The pre- and postparacrista and pre- and postmetacristae meet at angles of approximately 50°, slightly greater than that formed between the postparacrista and premetacrista (45°). The preparacrista is only just shorter than the subequal postparacrista and premetacrista and longer postmetacrista. The buccal cingulum is more distinct. The distinctive paraloph extends lingually, rather than anterolingually, from the base of the paracone towards the protocone, petering out approximately halfway. In QMF30588 and QMF30587 the metaloph is distinct and closes the protofossa; it is indistinct in QMF30576. The lingual cingulum enclosing the well developed heel is very broad posterolingually. The paracone and metacone root are more similar in size, the protocone root being again very long and broad. QMF30589, an M^2 from P Site, differs from the other three molars in its slightly longer heel. It has a distinct metaloph.

Comparisons: These isolated molars are probably referable to *I. aenae* and/or *I.* sp. cf. *I. aenae* and are compared to those taxa in the description above. They differ from M^2 in *I. paradox* in their larger size, less transversely developed shape, shorter and broader heel, and less well developed heel basin. They differ from M^2 in *Mystacina* species in being more transversely developed due to their longer, broader, posterolingually directed heel, and in lacking a paraconule. Most appear to have a metaloph. They are smaller than that tooth in *M. robusta* but probably larger than in most *M. tuberculata*.

Remarks: Uncertainty about the amount of variation expected in a Tertiary mystacinid species makes the allocation of these isolated M^{2}s to species premature. It is likely, however, that they are referable to *I. aenae* and/or *I.* sp. cf. *I. aenae*.

3. Discussion

3.1. Diversity, age and geographic range

Several species of the family Mystacinidae are now known from Australian Oligo-Miocene fossil deposits. At least two taxa appear to be represented in Riversleigh sediments (*I. aenae* and *I. paradox*), another from Bullock Creek in the Northern Territory (*I. breviceps*) and one from Lake Palankarinna, northeastern South Australia (mystacinid indet.). The family is otherwise known only from New Zealand where two widespread species of *Mystacina* (*M. robusta* and *M. tuberculata*) are known from Quaternary sediments. Only *M. tuberculata* now survives, and with the vespertilionid *Chalinolobus tuberculata*, are New Zealand's only native mammals.

Australian Tertiary mystacinids range in age from late Oligocene (ca. 26 my; Woodburne et al., 1994) to middle Miocene (ca. 12 my; Murray and Megirian, 1992; Archer et al., 1997). The oldest is the isolated mystacinid molar from Lake Palankarinna, which is the first, and so far only bat fossil recovered from Tertiary sediments in South Australia. Although interpreted to be middle Miocene in age when first described, the vertebrate fauna recovered from Tedford Locality (Ditjimanka Local Fauna; Archer, 1978; Woodburne, 1986; Rich et al., 1991) is now interpreted to be late Oligocene in age on the basis of magnetostratigraphy, illite dating and biocorrelation of foraminifera (Woodburne et al., 1994). At Riversleigh, mystacinids are so far recorded from early Miocene deposits, but not late Oligocene, middle Miocene, Pliocene or Quaternary sediments. At least two mystacinid taxa co-occur in some early Miocene Riversleigh deposits (e.g. Neville's Garden and Wayne's Wok Sites). These are interpreted to be around 20 million years old based on biocorrelation with South Australian and Northern Territory mammal-bearing deposits (Archer et al., 1997). Australia's youngest mystacinid, at an estimated 12 million years old (Murray and Megirian, 1992; Archer et al., 1997), is *I. breviceps* from a middle Miocene deposit at Bullock Creek in the Northern Territory (Hand et al., 1998). It is known from a dentary and

two lower teeth, and is the only bat fossil recovered so far from that deposit.

Recognition of South Australia's Ditjimanka bat molar as a mystacinid extends both the geographic and temporal distribution of Australian Tertiary mystacinids, while recovery of additional *Icarops* specimens from Riversleigh indicates that in the early Miocene at least two Australian mystacinids were probably sympatric. In the recent past, *M. robusta* and *M. tuberculata* were broadly sympatric throughout New Zealand's indigenous Gondwanan forests (Worthy et al., 1996).

3.2. Roosting preferences

New Zealand's surviving mystacinid, *M. tuberculata*, is restricted to extensive (> 1000 ha) areas of undamaged old-growth forest containing many large trees suitable for colonial roosts (> 1 m girth and > 25 m high), numerous epiphytes and deep leaf-litter (Lloyd, 2001). Colonial roost trees include species of *Nothofagus*, *Agathis*, *Metrosideros*, *Vitex*, *Podocarpus*, *Weinmannia* and *Dacrydium* (Lloyd, 2001). Australian fossil pollen records indicate that in the late Oligocene Lake Palankarinna in the Lake Eyre basin of South Australia enjoyed humid, equable climatic conditions supporting rainforests dominated by *Nothofagus* (*Brassopora* type) species, at least along water courses and lakes (Martin, 1994). The region became warmer and much drier in the Neogene and Quaternary and is now a desert. Pollen and macrofossil data are lacking for early Miocene Riversleigh deposits, but the vegetation has been interpreted to be cool temperate rainforest (Archer et al., 1995), while Murray and Megirian (1992) suggest seasonally dry conditions for the Bullock Creek deposit in the later middle Miocene. By the late Miocene, mystacinids seem to have disappeared from much of Australia (Hand et al., 1998, 2001), perhaps as a result of cooling temperatures and reduced rainfall which began in the mid to late Miocene. This climatic change resulted in gradual replacement of wet forests by dry forests, woodlands and eventually grasslands over much of the continent. Wet forests retreated to the coastal margins of Australia and it is possible that mystacinids survived there during the later Cainozoic.

Although *M. tuberculata* roosts only in trees today, both *Mystacina* species used granite sea caves on small off-shore islands before their local extinction there, and Quaternary fossils of both species have been found in abundance in limestone caves in New Zealand (e.g. Worthy and Holdaway, 1994; Worthy et al., 1996; Lloyd, 2001). The Riversleigh and Bullock Creek mystacinids have all been recovered from freshwater limestone deposits, but not necessarily caves. The conspicuous absence of mystacinid remains from recognised cave deposits at Riversleigh (e.g. Bitesantennary Site, Microsite, etc.; Archer et al., 1989, 1994), together with their fragmentary nature and relative scarcity in the Riversleigh deposits overall, suggests that their remains accumulated in freshwater lakes or pools along with more than 200 early Miocene species of fish, frogs, reptiles, birds, marsupials and monotremes (Archer et al., 1994). At Bullock Creek, the depo-

sitional setting appears to have been fluvio-lacustrine, perhaps a water hole or small lake in which the remains of fish, crocodiles, other reptiles, birds and diverse marsupials accumulated (Murray and Megirian, 1992). The mystacinids probably foraged over these waters (Hand et al., 1998). South Australia's Ditjimanka mystacinid was recovered from clays that accumulated in a large freshwater lake. There is no geological or faunistic evidence for caves in the area at the time of deposition. Several arboreal marsupials (three families of possums and a koala) are preserved with the mystacinid.

On balance, the evidence suggests that Australian Oligo-Miocene mystacinids were probably preferentially tree-dwelling bats like their Recent relatives, but it is not yet known whether or not they used their anterior teeth to routinely excavate roosting cavities in rotten wood inside hollow trees like their living relatives (Dwyer, 1962). No upper incisors (worn or otherwise) have been found for *Icarops* species. The lower incisor and canine are known only for *I. paradox*: the incisor is not particularly wide and, although the canine is relatively large, it is less procumbent than in *Mystacina* spp. and the notch in the posterior cingulum for P$_3$ is not nearly as deep, suggesting less imbrication and perhaps buttressing in the anterior lower teeth.

3.3. Dietary habits

Were Australian Oligo-Miocene mystacinids omnivores like their Quaternary New Zealand relatives? The omnivorous diet of *M. tuberculata* is broader than that of any bat recorded and includes flying and terrestrial invertebrates as well as nectar, flowers and fruit (Daniel, 1979; Lloyd, 2001), while the extinct *Mystacina robusta* also reportedly ate carrion (Daniel, 1990, but see Lloyd, 2001). It has been suggested that the breadth of the mystacinid diet (and their semi-terrestrial foraging habits) resulted from isolated evolution in New Zealand in the absence of other terrestrial mammals. It would appear from the dentition of some Australian Oligo-Miocene mystacinids (see below) that at least the *capacity* for omnivory was present before isolation of the lineage in New Zealand.

In *Mystacina* species, the dilambdodont molars are typical of insect-eating bats (there are no obvious specialisations for carnivory) but the anterior teeth indicate adaptations for both frugivory and nectarivory as defined by Freeman (1988, 1995) in her quantitative studies of craniodental features of bats. Like other microchiropteran frugivores, *Mystacina* species have a greater allocation of tooth area at the anterior end of the tooth row (individually large teeth accounting for half the upper tooth row length) than in more animalivorous (insectivorous and carnivorous) species. They also have a reduced number of lower incisors, a fused mandibular symphysis and large canines-features Freeman (1995) has argued act together to support a quickly moving, extensible tongue in nectar-feeding bats. (A fused mandibular symphysis also occurs in molossids that eat prey with a tough exocuticle and in *Mystacina* species may help them to process heavily sclerotinised arthropods such as wetas and beetles.)

All *Icarops* species share with *Mystacina* species dilambdodont molars, a fused mandibular symphysis, reduced (single pair) of lower incisors, retention of a three-rooted P^3 and large M^3. But the dentition of the Australian Miocene *I. aenae* most closely resembles that of *Mystacina* species: upper and lower molars are very similar in relative size and morphology and the anterior lower tooth row (the upper tooth row is unknown) is relatively long as in *Mystacina* species. Further, postcranial remains referable to *I. aenae* (including a humerus) are almost indistinguishable from those of *M. tuberculata*, suggesting that its flight characteristics and quadrupedal locomotion capabilities may not have been very different either (Hand et al., submitted for publication).

In contrast, the anterior tooth row of *I. paradox* is relatively short, the premolars small, and the upper molars are much more transversely developed with conspicuously large heels and elongated metastyles. Together, these features suggest that this smaller species may have been better equipped to deal with insect prey rather than fruit and nectar, and indicate dietary as well as taxic diversity among Australian Oligo-Miocene mystacinids. As yet, no postcranial remains of *I. paradox* have been identified.

In Australia today there are no omnivorous bats among its 90 species. Most are insect-eaters, but 13 pteropodids (flying-foxes, fruit-bats and blossom-bats) are fruit-, flower- and/or nectar-feeders. Pteropodids do not appear in the Australian fossil record until the late Pleistocene (Hand, 1999) and it is possible that mystacinids may have at least partly filled the chiropteran frugivore and nectarivore niches during the Tertiary.

3.4. Separation of Australian and New Zealand lineages

Molecular analyses (Pierson et al., 1986; Kirsch et al., 1998; Kennedy et al., 1999; Van Den Bussche et al., 1999) and recent analyses of mostly morphological data (Simmons and Geisler, 2002) place the family Mystacinidae somewhere within Noctilionoidea. This superfamily is otherwise known from 158 extant insectivorous, carnivorous, omnivorous, frugivorous, nectarivorous and sanguivorous species in central and South America. The molecular studies estimate likely times of separation of mystacinids from other noctilionoids ranging from 35 to 68 million years ago. On the basis of modern and fossil distributions, Hand et al. (1998, 2001) suggest that mystacinids, as noctilionoids, were part of a Gondwanan bat fauna that became isolated because of the vicariant event that separated Australia from Antarctica/South America ca. 35 million years ago. From Australia they dispersed to New Zealand. NZ had separated ca. 82 million years ago (Wiessel and Hayes, 1977), long before the oldest known earliest Eocene bats.

The close similarity in dentition (and postcranials) between Australia's *I. aenae* and New Zealand's *Mystacina* species suggests that the most likely time of separation of the lineages, via a trans-Tasman dispersal event, was the early Miocene, ca. 20 million years ago. By that time, New Zealand had re-emerged from the Oligocene marine transgression that had reduced it to a series of small low-lying islands collectively representing only ca. 18% of the modern landmass (Cooper and Millener, 1993). This inundation resulted in the extinction of many Gondwanan plants and terrestrial animals (McGowran et al., 2000). By the early Miocene, New Zealand had reached its present latitude and its climate and flora were as diverse as any other time in its history, opening up many new ecological niches (Mildenhall in McGowran et al., 2000). New Caledonia and other islands of the Tasman Rise were emergent and these may have facilitated dispersal, as has been suggested for ratities (Sibley and Ahlquist, 1981; Cooper and Cooper, 1995).

New Zealand's only other endemic modern mammal, the vespertilionid *Chalinolobus tuberculatus*, may also have used such a route, though somewhat later. This species is closely related to others of the endemic Australian radiation of *Chalinolobus* species, and in particular *C. gouldii* from Australia and Norfolk Island, and *C. neocaledonicus* from New Caledonia (Tidemann, 1986). The modern Australian and New Zealand *Chalinolobus* species are only specifically distinct, unlike the mystacinid taxa, and suggest a more recent dispersal. There are few vespertilionids represented in the early Miocene at Riversleigh (Menu et al., 2002) but at least two "Chalinolobus" species occur in the Pliocene (Archer et al., 1994; Hand et al., 1999).

Historical records of Australian flying-foxes storm-blown to New Zealand (Daniel, 1975) suggest it is possible that other bat groups possibly also reached New Zealand throughout the Cainozoic. Severe cooling in the later Miocene in New Zealand (Mildenhall in McGowran et al., 2000) may have wiped out strictly tropical to subtropical bats occurring in the region in the Oligo-Miocene (e.g. hipposiderids and megadermatids), but others might be expected to have survived there. For example, molossids and emballonurids are cosmopolitan groups, good long-distance fliers and, although most are tropical to subtropical species, some occur at higher latitudes. Recent discoveries of fossil mammals in the New Zealand Tertiary record (Worthy et al., 2002) should eventually shed more light on the history of colonisation of NZ by bats.

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