

# New Miocene *Icarops* material (Microchiroptera: Mystacinidae) from Australia, with a revised diagnosis of the genus

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New fossil material referable to *Icarops paradox* Hand *et al.*, 1998 is described from the early Miocene Judith's Horizontalis Site in the Riversleigh World Heritage Property of northwestern Queensland. Fused dentaries contain the partial lower dentition of *I. paradox*. The diagnosis of the genus *Icarops* is revised. The new material confirms the identity of *Icarops* species as mystacinids and enables re-examination of interrelationships between extinct and extant members of this Gondwanan bat family.

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THE FIRST pre-Pleistocene record for the Mystacinidae and first record of this bat family from outside New Zealand were reported by Hand *et al.* (1998) from Miocene sediments in Australia. Three species of the new mystacinid genus *Icarops* were described: *Icarops breviceps* from the middle Miocene Bullock Creek deposit of the Northern Territory; *I. aenae* from the early Miocene Wayne's Wok deposit, D Site Plateau, Riversleigh, northwestern Queensland; and *I. paradox* from the early Miocene Neville's Garden Site, D Site Plateau, Riversleigh. The Australian mystacinids were described mainly on the basis of dentaries; only *I. breviceps* was represented also by teeth: an  $M_2$  and  $M_3$  preserved in the holotype.

Additional mystacinid material has since been collected from another early Miocene deposit on Riversleigh's D Site Plateau, Judith's Horizontalis Site. This material includes a mandible with fused dentaries containing the partial lower dentition for a small species of *Icarops*. Based on comparisons of size and alveolar patterns, the new material is referable to *I. paradox*. *Icarops paradox* is one of 44 species of fossil microchiropterans recorded from Riversleigh's Oligo-Miocene and Pliocene limestone deposits (Archer *et al.* 1994, Hand 1999).

In this paper, the new *Icarops* material is described and the diagnosis of the genus revised. Taxonomy and dental terminology follows Miller (1907) and Hand *et al.* (1998). Stratigraphic nomenclature for the Riversleigh region follows Archer *et al.* (1994) and Creaser (1997). The prefix

QMF refers to specimens held in the fossil collections of the Queensland Museum, Brisbane.

## SYSTEMATIC PALAEOLOGY

Order CHIROPTERA Blumenbach, 1779  
Suborder MICROCHIROPTERA Dobson, 1875  
Superfamily NOCTILIONOIDEA Van Valen, 1979  
Family MYSTACINIDAE (Gray, 1843)

*Icarops* Hand *et al.*, 1998

*Type species. Icarops breviceps* Hand, Murray, Megirian, Archer & Godthelp, 1998

*Revised diagnosis.* Species of *Icarops* differ from *Mystacina* species in the following combination of features:  $I_1$  width and length approximately equal (i.e. not especially wide);  $P_4$  less than half  $M_1$  length, with two roots oriented longitudinally or only slightly obliquely with respect to the tooththrow; all cusps of lower molars including entoconids taller and more distinct, with  $M_{1-2}$  talonid wider than trigonid.

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

*Icarops paradox* (Fig. 1A-D)

*Holotype.* QMF20808, partial mandible preserving fragments of left and right dentaries with alveoli for  $L I_1$ ,  $C_1$  and  $P$ , and  $R C_1$ ,  $P_4$  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.* 1994).

*New material.* QMF31561, a partial, fused mandible with left dentary preserving  $C_1$  and  $M_{1,3}$  and alveoli for  $I_1$  and  $P_{2,4}$ , and right dentary with broken  $P_4$ ,  $M_{1,3}$  and associated  $RI_1$ .

*Locality, age and lithology.* Judith's Horizontalis Site, D Site Plateau, Riversleigh (see Creaser 1997), a freshwater limestone deposit interpreted as early Miocene, based on stratigraphy and contained local fauna (Archer *et al.* 1994; Creaser 1997).

*Associated fauna.* Other vertebrates recovered so far from the Judith's Horizontalis Site include: frogs, lizards, turtles, passerine birds, bandicoots, a marsupial mole, yalkaparidontid, burramyid possum, balbarid kangaroo, carnivorous kangaroo, and a megadermatid bat (A. Gillespie, pers. comm.).

*Revised diagnosis.* Smaller than *I. breviceps* and *I. aenae*, and with  $P_2$  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).

*Description.* The left and right dentaries of QMF31561 are completely fused, with no sign of the symphysis, and meet at an angle of approximately 45°. The mandible's anterior margin, in lateral profile, is receding ventrally, rounded and without a chin process. A ventral mandibular shelf extends posteriorly to the alveolus for the anterior root of  $P_4$ . A small but deep invagination in the shelf's posteroventral face marks the attachment point for the digastric muscle/s (in the holotype of *I. paradox*, QMF20808, the site for attachment of the digastric muscles was not clear). The dentary decreases in depth only slightly from  $P_2$  to below the posterior root of  $M_3$ . The ascending ramus, condyle and angular process are not preserved.

Unlike other *Icarops* specimens (including the holotype of *I. paradox*), there is no mental foramen beneath  $P_2$  nor further posteriorly. There is, however, a small, dorsally directed foramen below and between the alveoli for  $C_1$  and  $I_1$ . This foramen appears to be homologous with that found in this region in other *Icarops* specimens. The incisor alveolar region is well preserved and contained a single pair of incisors. The canine alveolus is large and oval. The single alveolus for  $P_4$  is smaller than the canine alveolus. As in the holotype, there is

evidence of crowding of teeth with overlapping of the alveoli. Most of the crown of  $P_4$  is broken off but it has two roots oriented slightly obliquely with respect to the toothrow; the anterior alveolus is significantly smaller than the posterior one and displaced towards the buccal margin of the toothrow. The anterior alveolus for  $M_1$  is also slightly buccally displaced.

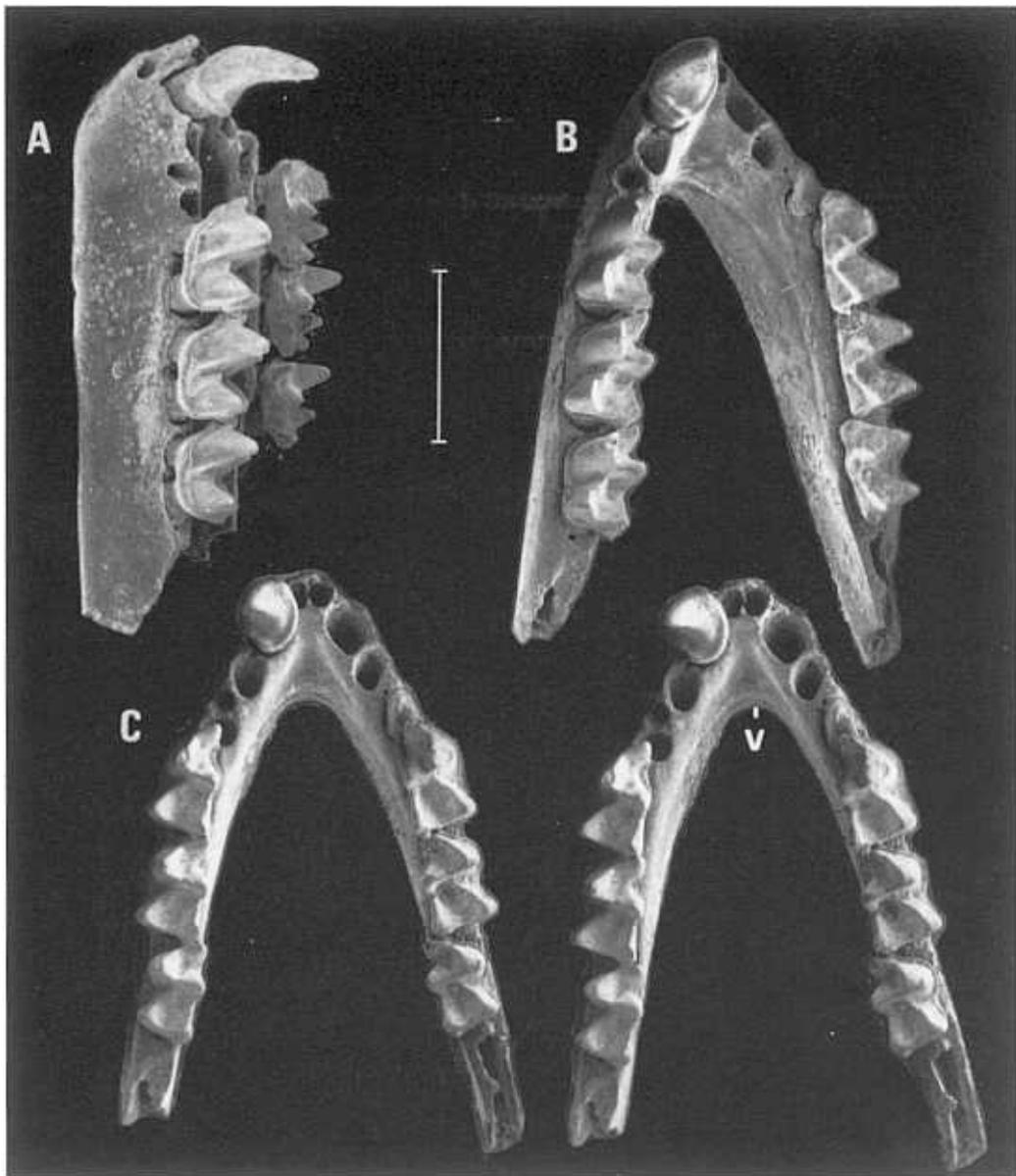
The lower dental formula is  $I_1, C_1, P_{2,4}, M_{1,2,3}$ . The alveoli for the canines (but not the incisors; *contra* Hand *et al.* 1998) are ventrally displaced with respect to the toothrow. The margins of the canine alveoli are smooth and complete. The posterior alveolus of  $P_4$  is compressed by the anteriorly inclined alveolus for the anterior root of  $M_1$ . The posterior alveolus for  $M_1$  is larger than the anterior one.

$RI_1$  was found within the jaw but was removed during preparation of the mandible. It is relatively large, and deeply and evenly trifid. The crown is not markedly extended backwards; its width and length are approximately equal.

$C_1$  is simple in form; its posterior base has a small, rounded median cusp, marked by a small notch for the anterior edge of  $P_2$ . The basal cingulum is almost complete except at its most anterolingual point; its anterolingual edge has a distinct convexity just above the level of the incisors; here the cingulum is broken and connected to a short crest on the lower part of the crown.

Most of the crown of  $RP_4$  is missing; the roots remain. Judging from its alveoli and remaining crown,  $P_4$  was longer than  $P_2$  and less than half the length of  $M_1$ . Its two roots are oriented slightly obliquely with respect to the toothrow; the anterior alveolus is smaller than the posterior one and is close to the buccal margin of the dentary.

$M_1$  has two roots and five distinct cusps, the hypoconulid being a small cingular cusp. Although individualised, the cusps appear relatively low and inclined rather than tall and upright. The trigonid is conspicuously narrower, but approximately the same length as the talonid. The protoconid and hypoconid are the dominant cusps in height and volume, but they are not massive. The protoconid is only just taller than the hypoconid which is taller than the metaconid; the entoconid and paraconid are subequal in height; all are much taller than the hypoconulid. The protoconid shows conspicuously more wear than the other cusps. The paracristid is just longer than the metacristid; the protoconid contributions to the paracristid and metacristid are longer than the paraconid and metaconid contributions; the metaconid and protoconid contributions of the metacristid are more equal and meet at a more acute angle. The cristid obliqua, in occlusal view, is



*Fig. 1. Icarops paradox* Hand, Murray, Megirian, Archer & Godthelp, 1998. QMF31561, from the early Miocene Judith's Horizontalis Site, Riversleigh World Heritage Property, Lawn Hill National Park, northwestern Queensland. A, lateral view; B, oblique occlusal view; C, stereopair, occlusal view. Scale bar indicates 2 mm. v = ventral mandibular shelf.

uncurved and contacts the trigonid at a point directly below the junction of the components of the metaclistid. In lateral view there is an 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 (Menu & Sigé 1971). The greatly bowed inflexion in the hypocristid occurs approximately midway

between the hypoconid and entoconid. A pre-entocristid, straight and steeply dipping, links the entoconid to the trigonid at the base of the metaconid (making an angle with the metaconid of just less than  $90^{\circ}$ ). The angle between the para- and metaclistids is relatively broad, at approximately  $75^{\circ}$ . The cristid obliqua and paracristid are almost parallel to each other. There is a uniform, non-sinuuous, continuous anterior, buccal and posterior cingulum, terminated at its

posterolingual end well short of the hypoconulid providing a notch for the anterior cingulum of  $M_2$ . A relatively strong but short lingual cingulum occurs at the base of the trigonid.

$M_2$  is described insofar as it differs from  $M_1$ .  $M_2$  is narrower and shorter in length but taller than  $M_1$ . The trigonid and talonid are wider but slightly shorter, the protoconid is taller (and not as worn) but the hypoconid is of similar size, and the metaconid and protoconid contributions of the metacristid are more equal and meet at a more acute angle. The angle made between the paracristid and metacristid is approximately  $60^\circ$ . The short lingual cingulum at the base of the trigonid is weaker in  $M_2$  (and  $M_3$ ).

$M_3$  is described insofar as it differs from  $M_{1,2}$ . It is a slightly narrower, shorter tooth. The trigonid is similar in width to the talonid, and the talonid is longer than the trigonid. 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.

**Measurements.** Maximum dentary depth (below alveolus for  $P_2$ ) 1.30 mm,  $C_1$ - $M_3$  length 5.65 mm,  $M_{1,3}$  length 3.83 mm.

## COMPARISONS

**Comparisons with other mystacinids.** *Icarops paradox* differs from the Australian Miocene *I. breviceps* and *I. aenae* in being smaller, with  $M_3$  less reduced (with trigonid and talonid of subequal width) than in at least *I. breviceps*;  $P_2$  larger and  $P_4$  more transversely oriented than in *I. aenae*. As in other *Icarops* species, the area of attachment for digastric muscle(s) appears to be well developed in this specimen of *I. paradox* (see Hand *et al.* 1998). Unlike the holotype QMF20808 (and all other extinct and extant bats examined), QMF31561 has no mental foramen; the condition is interpreted to be an aberrant condition in this individual.

*Icarops paradox* and New Zealand's Quaternary *Mystacina* species (i.e., *M. tuberculata* and the recently extinct *M. robusta*) share the following dental and mandibular features: a fused dentary symphysis; a single trifold lower incisor;  $C_1$  with posterior heel and posterobasal cusp; and myotodont lower molars. *Icarops paradox* differs from *Mystacina* species in the following features:  $I_1$  width and length approximately equal (i.e. not especially wide); far less massive canine with shorter heel, less developed posterobasal cusp and better developed buccal cingulum;  $P_4$  less than half  $M_1$  length with its two roots oriented slightly obliquely to the tooththrow; all cusps of lower

molars, including entoconids, taller and more distinct,  $M_{1,2}$  talonid wider than trigonid.

**Comparisons with molossids.** *Icarops* species share with many molossids (Hand *et al.* 1998): a deep and robust dentary with mental foramen occurring beneath  $P_2$ ; a single pair of lower incisors; two anterior premolars overlapping so that their roots are oblique in the tooththrow; general appearance of  $M_1$  and  $M_2$ , notably myotodonty, talonid wider than trigonid, tall hypoconid, paraconid development similar to metaconid (i.e. without strong reduction; except in the molossid *Cheiromeles torquatus*), cristid obliqua complete (Sigé 1985, p. 170-1). Additional dental features now found to be similar to molossids include  $C_1$  being simple in form without a long heel, and  $P_4$  being smaller than  $M_1$ .

Dental features of *Icarops paradox* now known to differ from molossids include: a trifold rather than bifid single incisor;  $C_1$  with posterobasal cusp;  $P_2$  less reduced than in most molossids (although in molossids it is double-rooted even when very reduced e.g. molossines, cheiromeles etc.); no sinuous buccal cingulum in  $M_{1,3}$ , talonid not much wider than trigonid, without pronounced buccal bulging of the protoconid and hypoconid; less hypsodont. Also unlike *Icarops* species, many molossids (e.g. *Cheiromeles*) have nyctalodont or submyotodont lower molars, and in *Cheiromeles* and many molossines  $M_3$  is more reduced.

**Comparisons with noctilionoids.** *Icarops* species share with South America's noctilionids a deep and robust dentary with tall ascending ramus (as in *I. breviceps*) and fused dentary symphysis, a single pair of lower incisors, two anterior premolars, and myotodont lower molars (Hand *et al.* 1998). However, noctilionids differ strikingly from *Icarops* (and *Mystacina*) species in having  $M_2$  with extremely wide talonid, wall-like pre-entocristid and cristid obliqua extending to the lingual margin of the crown, more obliquely oriented  $P_4$ , and small, lingually displaced  $P_3$ . The new *Icarops paradox* material additionally differs in its  $C_1$  with posterobasal cusp, and the single lower incisor being trifold rather than bifid.

The speciose bat family Phyllostomidae exhibits an enormous range of dental morphologies which reflects a great variety of diets (including blood, nectar, fruit, flesh and insects) making phyllostomids much more difficult to characterise than other bat groups. However, *Icarops* species appear to differ from phyllostomids (and mormoopids) in the following combination of features: reduction of the lower incisors to one pair, fusion of dentary symphysis,

relatively large  $P_2$  with small  $P_4$ , and myotodont lower molars. *Icarops* species share with many phyllostomids and mormoopids trifold rather than bifid lower incisors.

*Comparisons with vespertilionids.* Vespertilionids lack a fused dentary symphysis, retain two or more pairs of lower incisors, and tend to have lower molars with talonid wider than trigonid. Most groups are dominated by taxa with nyctalodont lower molars but some (e.g. *Myotis*, *Plecotus*, *Scoteanax*, *Chalinolobus*) have myotodont molars like *Icarops* species. Similarities with the new *Icarops paradox* material include: trifold lower incisors;  $P_2$  and  $P_4$  relatively small and with  $P_2$  singly rooted. No vespertilionids have reduced the lower incisors to one pair, nor have a fused dentary or an extended heel on  $C_1$ .

*Comparisons with nataloids s. l.* Natalids, thyropterids, furipterids and myzopodids are grouped together here in the superfamily Nataloidea following Simmons (1998). Also grouped here are the kerivoulines (species of *Kerivoula* and *Phoniscus*) which are generally included in either the Natalidae or Vespertilionidae. All taxa lack a fused dentary symphysis, retain two or more pairs of lower incisors, and tend to have lower molars with talonid wider than trigonid. The lower canine is generally exceptionally slender with a subterete shaft. Most have nyctalodont lower molars but kerivoulines have myotodont molars like *Icarops* species. Similarities to the new *Icarops paradox* material include: the presence of trifold incisors (although they retain three pairs);  $P_2$  and  $P_4$  being relatively small; and  $P_2$  singly rooted.

*Comparisons with rhinolophoids.* *Icarops* species differ from rhinolophoids in their fused dentary symphysis, single pair of lower incisors and in their talonid morphology. Three pairs of lower incisors are retained by nycteridids and two by megadermatids and hipposiderids; these are commonly trifold. In rhinolophoids  $P_2$  is small,  $P_3$  is retained by rhinolophids and some archaic hipposiderids, the talonid of the lower molars tends to be rather low, narrow and short and displays the nyctalodont pattern.

*Comparisons with emballonuroids.* Three pairs of lower incisors are retained by *Emballonura* and New World emballonuroid taxa, and two pairs by *Taphozous* and *Saccolaimus*; these are typically trifold and the outer incisor is sometimes separated from the canine by a small gap. The molars are usually but not always nyctalodont, and the paraconid is reduced and conspicuously

lower than the metaconid. The talonid of  $M_3$  may be greatly or little reduced.

*Comparisons with extinct bat families (archaeonycteridids, palaeochiropterygids and hassianycteridids).* The most archaic of early and middle Eocene bats are referred to a number of extinct families and lack most of the derived features that distinguish bats of modern families (see Russell & Sigé 1970, Russell *et al.* 1973, Smith & Storch 1981, Habersetzer & Storch 1987, Simmons & Geisler 1998). *Icarops* species differ from these early bats as follows. In archaeonycteridids, palaeochiropterygids and hassianycteridids (including species of *Archaeonycteris*, *Ageina*, *Australonycteris*, *Icaronycteris*, *Palaeochiropteryx*, *Cecilionycteris*, *Matthesia*, *Stehlinia* and *Hassianycteris*), unlike species of *Icarops*, the dentary symphysis is not fused, at least two pairs of lower incisors are present,  $P_3$  is retained, the trigonid cusps of the lower molars are typically much taller than the talonid cusps, the talonid is unreduced and hypoconulid more buccally situated, and all cusps are more individualised. The lower molars of most of these archaic bats exhibit the nyctalodont pattern (or pre-nyctalodont pattern with the hypoconulid more buccally situated) but some palaeochiropterygids (e.g. in the genera *Palaeochiropteryx* and *Stehlinia*; see Sigé 1997 on the reassignment of *Stehlinia* to this family) exhibit the myotodont pattern. In *Icarops* species the toothrow is relatively much shorter (foreshortened) than in archaic bats.

## DISCUSSION

Comparisons of the lower dentition of *Icarops paradox* with those of other microchiropterans confirm its identity as a member of the family Mystacinidae. *Icarops paradox* and New Zealand's Quaternary *Mystacina tuberculata* and *M. robusta* share a unique combination of dental and dentary features including a fused dentary symphysis; presence of a single trifold incisor;  $C_1$  with posterior heel and posterobasal cusps; and myotodont lower molars.

The new material also enables further examination of the relationships within this Australasian bat family. Hand *et al.* (1998) suggested, on the basis of the fossil material then known, that *Icarops* species were probably plesiomorphic with respect to Quaternary mystacinids, i.e. *M. tuberculata* and *M. robusta*. Study of more of the lower dentition supports this hypothesis. *Icarops paradox* differs from *Mystacina* species in:  $I_1$  width and length being approximately equal;  $C_1$  far less massive with shorter heel, less developed posterobasal cusps

and better developed buccal cingulum;  $P_4$  less than half  $M_1$  length with its two roots oriented slightly obliquely to the toothrow; all cusps of lower molars, including entoconids, taller and more distinct,  $M_{1-2}$  talonid wider than trigonid. All of these dental features appear to be less specialised than in New Zealand's *Mystacina* species, although some (e.g. loss of two pairs of lower incisors, fused dentary symphysis) are more derived than found in other microchiropteran families including, for example, rhinolophoids, emballonuroids, vespertilionids, archaeonycterids, palaeochiropterygids and hassiaonycterids.

The relationships of mystacinids to other families of bats are less clear. *Mystacina tuberculata*, a semi-terrestrial microchiropteran endemic to New Zealand, is the sole surviving member of the Mystacinidae. The oldest record of the family in New Zealand is 18,000 years bp (*Mystacina* spp.) from Hermit's Cave, near Charleston, South Island, NZ (Worthy & Holdaway 1994). *Mystacina* was interpreted by Pierson *et al.* (1986), on the basis of immunological distance, to be a member of the South American superfamily Noctilionoidea, evidently dispersing from South America to New Zealand some 35 million years ago. Subsequently, Simmons (1996) found, using a 'total evidence' approach in which morphological, reproductive, behavioural, DNA and other data are included in a single data set, that mystacinids are probably basal to a large group of bats including the cosmopolitan Vespertilionidae, Molossidae and South American Nataloidea, implying that ancestral mystacinids diverged from other bats at least 55 million years ago. DNA-DNA hybridisation studies by Kirsch *et al.* (1998) confirmed the affinity of *Mystacina* with noctilionoids as suggested by earlier serological studies (*contra* Simmons 1996) but suggested separation from its South American relatives occurred between 54 and 66 million years ago. DNA sequencing studies (Kennedy *et al.* 1999) also indicate a mystacinid-noctilionoid relationship, but differ from other molecular results in placement of *Mystacina* within the superfamily closer to phyllostomids and mormoopids; they calculate the time of divergence of *Mystacina* from other bat taxa to be anywhere from 45 to 68 million years ago.

Hershkovitz (1972) and Pierson (1986) have argued for a Southern Hemisphere origin for the world's extant bat radiation on the basis of distributions of endemic bat families. Sigé (1991) proposed that modern bat groups evolved from isolated immigrant archaic groups in the Southern Hemisphere in the early Eocene. The oldest bat in the Southern Hemisphere is a 55-million-year-old

archaeonycterid from Australia (Hand *et al.* 1994), to which the much younger and more derived mystacinids bear little resemblance. The oldest fossil bats in South America are a late Oligocene Brazilian molossid and middle Miocene Colombian taxa, including the phyllostomids *Notonycteris magdalenensis* and *Tonatia* sp., a glossophagine, phyllostomine and *Noctilio albiventris* (Czaplewski 1997).

Isolated teeth of mystacinids (yet to be described) have now been recovered from late Oligocene deposits at Riversleigh (and possibly South Australia) confirming that the family Mystacinidae was represented in Australia at least 25 million years ago. It survived here until at least 12 million years ago, occurring in middle Miocene deposits at Bullock Creek, Northern Territory, but had disappeared from at least the Riversleigh area by 3-5 million years ago as evidenced by their absence from the early Pliocene Rackham's Roost deposit (Archer *et al.* 1994). The decline and, ultimately, extinction of this lineage in Australia may reflect the intense drying of Australia since the late Miocene which resulted in the replacement of wet forests by open woodlands and grasslands over much of the continent. The sole surviving member of the mystacinid lineage is now restricted to New Zealand's endemic Gondwanan-type forests dominated by *Nothofagus*, *Podocarpus*, *Dacrydium* and kauri trees (Daniel & Williams 1984).

Hand *et al.* (1998) have argued that the presence of plesiomorphic mystacinids in the Australian Tertiary record (the only pre-Pleistocene record for mystacinids) most parsimoniously suggests that Australia was the immediate source of New Zealand's Quaternary mystacinids. New Zealand separated from the rest of Gondwana 80-90 million years ago (Fleming 1979), long before the world's first bats had evolved. Australia, Antarctica and South America were connected as the last fragments of Gondwana until about 35 million years ago (Veevers 1991), throughout the period when most modern bat lineages first appeared in the fossil record (Sigé 1991, Simmons 1996, 1998). The southern supercontinent possibly shared a number of bat families, but precisely when and where the curious mystacinids originated is yet to be discovered.

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