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 M₂ and M₃ 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.

**SYSTEMATICAL PALAEONTOLOGY**

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: I₁ width and length approximately equal (i.e. not especially wide); P₄ less than half M₁ length, with two roots oriented longitudinally or only slightly obliquely with respect to the toothrow; all cusps of lower molars including entoconids taller and more distinct, with M₁₂ 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 I₁, C, and P, and R C₁, P₇₈ and M₁.

New material. QMF31561, a partial, fused mandible with left dentary preserving C1 and M1, and alveoli for I1 and P2, and right dentary with broken P4, M1, and associated R1.

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, 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 P2 larger and P4 more transversely oriented than in I. aenae (Hand et al. 1998). Additionally, it differs from I. breviceps in M1 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 P4. 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 P2 to below the posterior root of M3. 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 P2 nor further posteriorly. There is, however, a small, dorsally directed foramen below and between the alveoli for C1 and I1. 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 P4 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 the alveoli 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 M1 is also slightly buccally displaced.

The lower dental formula is I1', C1', P2,4', M1,2,3. 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 P4 is compressed by the anteriorly inclined alveolus for the anterior root of M1. The posterior alveolus for M1 is larger than the anterior one.

R1 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.

C1 is simple in form; its posterior base has a small, rounded median cusp, marked by a small notch for the anterior edge of P2. 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 RP3 is missing; the roots remain. Judging from its alveoli and remaining crown, P4 was longer than P2 and less than half the length of M3. 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.

M3 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 paraenamel is just longer than the metaenamel; the protoenamel contributions to the paraenamel and metacristid are longer than the paraenamel and metaenamel contributions; the metaenamel and protoenamel contributions of the metacristid are more equal and meet at a more acute angle. 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 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°). The angle between the para- and metacristids is relatively broad, at approximately 75°. The cristid obliqua and paracristid are almost parallel to each other. There is a uniform, non-sinuous, continuous anterior, buccal and posterior cingulum, terminated at its
posterolingual end well short of the hypoconulid providing a notch for the anterior cingulum of M₁. A relatively strong but short lingual cingulum occurs at the base of the trigonid.

M₂ is described insofar as it differs from M₁. M₂ is narrower and shorter in length but taller than M₁. 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°. The short lingual cingulum at the base of the trigonid is weaker in M₂ and M₃.

M₃ is described insofar as it differs from M₁ and M₂. 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 P₄) 1.30 mm, C₁-M₃ length 5.65 mm, M₁-3 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 M₁ less reduced (with trigonid and talonid of subequal width) than in at least I. breviceps; P₂ larger and P₄ more transversely oriented than in I. aenae. As in other Icarops species, the area of attachment for the digastic 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 pair of lower incisors; two anterior premolars, and myotodont lower molars. Icarops paradox differs from Mystacina species in the following features: I₁ 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; P₂ less than half M₁ length with its two roots oriented slightly obliquely to the toothrow; all cusps of lower molars, including entoconids, taller and more distinct, M₄ 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 P₂; a single pair of lower incisors; two anterior premolars overlapping so that their roots are oblique in the toothrow; general appearance of M₁ and M₂, notably myotodonty, talonid wider than trigonid, tall hypoconid, paracristid 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 C₁ being simple in form without a long heel, and P₄ being smaller than M₁.

Dental features of Icarops paradox now known to differ from molossids include: a trifid rather than bifid single incisor; C₁ with posterobasal cusp; P₂ 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 M₁, 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 nycitodont or submyotodont lower molars, and in Cheiromeles and many molossines M₃ 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 M₁ with extremely wide talonid, wall-like pre-enctocristid and cristid obliqua extending to the lingual margin of the crown, more obliquely oriented P₄ and small, lingually displaced P₅. The new Icarops paradox material additionally differs in its C₁ with posterobasal cusp, and the single lower incisor being trifid 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 bifid rather than trifid 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. *Mystis*, *Plecotus*, *Scoteanax*, *Chalinolobus*) have myotodont molars like *Icarops* species. Similarities with the new *Icarops paradox* material include: trifid 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 \( C_2 \).

**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 trifid 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 trifid. 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 trifid 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, palaeochiropteridids 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, palaeochiropteridids and hassianycteridids (including species of *Arachaeonycteris*, *Ageina*, *Australononycteris*, *Icaronycteris*, *Palaeochiropteryx*, *Cecilonycteris*, *Matthesia*, *Stehlinia* and *Hassianycteris*), unlike species of *Icarops*, the dentary symphysis is not fused, at least two pairs of lower incisors are present, \( P_2 \) 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 palaeochiropteridids (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 trifid incisor; \( C_2 \) 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: \( I \), width and length being approximately equal; \( C_1 \) far less massive with shorter heel, less developed posterobasal cusps
and better developed buccal cingulum; P, less than half M, length with its two roots oriented slightly obliquely to the toothrow; all cusps of lower molars, including entoconids, taller and more distinct, M, 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, palaeochopterygids and hassianycterids.

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-noctilionid 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 archaeoonycterid 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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