Mystacinid Bats (Microchiroptera) from the Australian Tertiary

S. J. Hand; P. Murray; D. Megirian; M. Archer; H. Godthelp


Stable URL:
http://links.jstor.org/sici?sici=0022-3360%28199805%2972%3A3%538%3AMB%28FTA%3E2.0.CO%3B2-5

*Journal of Paleontology* is currently published by Paleontological Society.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR’s Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR’s Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/paleo.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.
MYSTACINID BATS (MICROCHIROPTERA) FROM THE AUSTRALIAN TERTIARY

S. J. HAND,1 P. MURRAY,2 D. MEGIRIAN,3 M. ARCHER,3 and H. GODTHELP1

1School of Biological Science, University of New South Wales, Sydney, New South Wales 2052, Australia,
2Northern Territory Museum of Arts and Sciences, GPO Box 2109, Alice Springs, Northern Territory 0871, Australia,
3Northern Territory Museum of Arts and Sciences, PO Box 4646, Darwin, Northern Territory 0801, Australia

ABSTRACT.—A new genus and three new species of the microchiropteran family Mystacinidae are described from Miocene freshwater limestones in northern Australia. The type species, Icarops breviceps new genus and species, is from the middle Miocene Bullock Creek deposit, Northern Territory; I. aenae new species and I. paradoxus new species are from the slightly older (early Miocene) Wayne’s Wok and Neville’s Garden Sites at Riversleigh, northwestern Queensland. Fossil mystacinids are rare in each deposit and represented so far only by lower teeth and dentary fragments. They are characterized by a suite of apomorphies shared only with Quaternary mystacinids endemic to New Zealand. The family Mystacinidae has no pre-Pleistocene record and its relationships to other groups of bats remain unclear. Possible sister-groups include South American noctilionoids and the cosmopolitan molossoids and/or vespertilionoids. The presence of plesiomorphic mystacinids in the Australian Tertiary suggests an Australian origin for the family.

INTRODUCTION

The first pre-Pleistocene record for New Zealand’s only endemic mammal family, the Mystacinidae, has been found in Australia. Previously, the family was known only from the living Mystacina tuberculata and the larger, recently extinct M. robusta, as well as subfossil and late Pleistocene remains of these species. All records were from New Zealand, the oldest being 17–18,000 year old remains from Hermit’s Cave, near Charleston, West Coast, South Island (Worthy and Holdaway, 1994). Three species of this bat family have now been identified from early to middle Miocene limestone deposits at Bullock Creek in the Northern Territory and Riversleigh, Queensland. The Australian fossil mystacinids are represented so far only by isolated teeth and dentary fragments but these exhibit a combination of apomorphies shared only with M. tuberculata and M. robusta. The Australian fossil taxa were previously regarded by Hand et al. (1995) as molossoids.

The vespertilionid Chalinolobus tuberculatus, New Zealand’s only other endemic mammal, has been demonstrated to be most closely related to Australian species of that genus (Dwyer, 1962), but the origins and relationships of mystacinids have remained obscure. Taxonomists have placed the family in three of the four microchiropteran superfamilies (Miller, 1907, p. 239–40). The issue appeared resolved when Pierson et al. (1986) used albumen immunology to suggest that Mystacina tuberculata is a basal member of the South American superfamily Noctilionoidea (=Phylllostomoidae), with dispersal to New Zealand from South America interpreted to have occurred more than 35 million years ago. Recent phylogenetic analyses, based on morphological, anatomical, physiological, and molecular data, suggest mystacinids are basal members of either the superfamly Molossoidae (i.e., molossoids plus tomopteniids) or Noctilionoidea, or the plesiomorphic sister-group of all other vespertilionoids sensu lato (Simmons, in press).

In this paper, Australian fossil mystacinids are described and their paleogeographic significance discussed. Taxonomy and dental terminology follows Legendre (1985) and Hand (1990). Stratigraphic nomenclature for the Riversleigh region follows Archer et al. (1989, 1994). The prefix P refers to specimens held in the fossil collections of the Northern Territory Museums and Art Galleries, Darwin; QM F refers to specimens held in the fossil collections of the Queensland Museum, Brisbane.

SYSTEMATIC PALEONTOLOGY

Order CHIROPTERA Blumenbach, 1779
Suborder MICROCHIROPTERA Dobson, 1875
Superfamily incertae sedis
Family MYSTACINIDAE (Gray, 1843)

Type species.—Mystacina tuberculata Gray, 1843
Familial assignment.—The bats described here share with mystacinids (Mystacina species) the unique condition in which two lower incisors are lost but P3 is large, though single-rooted, and M3 is only moderately reduced. Other shared apomorphies include the robust dentary with fused dentary symphysis, ventral mandibular shelf, tall ascending ramus and deep maseteric fossa, myotodont lower molars, and M3 trigonid not much wider than talonid.

ICAROPS new genus

Type species.—Icarops breviceps new species
Diagnosis.—Species of this genus differ from other mystacinids (i.e., species of Mystacina) in having less procumbent lower incisors, canines and anterior premolars, a more anterodorsally-situated mental foramen (mid-dentary depth beneath P2), and a shorter, more robust dentary relative to tooth size. Additionally, Icarops species differ from M. robusta in their smaller size.
Etymology.—From Icaros, the mythological Greek who flew

FIGURE 1—1–3. Icarops breviceps n. gen. and sp., Blast Site, Bullock Creek, Northern Territory, Australia. 1,2, P895-14a, holotype, ×7.5; 1, 1', buccal stereo pair; 2, 2', occlusal stereo pair; 3, P895-14b, holotype, ×17; 3, 3', M3, oblique-occlusal stereo pair. 4, 5. Icarops paradox n. gen. and sp., QMF20808, holotype, Neville’s Garden Site, Riversleigh, Queensland, ×10; 4, 4', buccal stereo pair; 5, 5', occlusal stereo pair. 6, 7. Icarops aenae n. gen. et sp., QMF30567, holotype, Wayne’s Wok Site, Riversleigh, Queensland, Australia, ×10; 6, 6', buccal stereo pair; 7, 7', occlusal stereo pair. Scale bars indicate 2 mm.
towards the sun, in reference to the ancient mystic and that flew eastwards from Australia to New Zealand.

*Reflected species.*—*Icarops aenae* n. sp.; *Icarops paradox* n. sp.

*Age and distribution.*—Early to middle Miocene of northern Australia.

**Icarops breviceps** new species

Figsures 1.1–1.3, 2.2

*Diagnosis.*—Deeper dentary than in *I. aenae* and with *P*₂ roots more transversely oriented. Larger than *I. paradox* and with anterior teeth less crowded. Broader ventral mandibular shelf than both *I. aenae* and *I. paradox*.

*Description.*—Left and right dentaries of the holotype P895-14a are completely fused, with no sign of the original position of the symphysis. They meet at an angle of approximately 20°. The mandible’s anterior margin, in lateral profile, is smoothly rounded without a chin process. A ventral mandibular shelf extends posteriorly to a point level with the alveolus for the posterior root of *P*₂. A small but deep invagination in its posteroventral face marks the attachment point for the digastric muscle(s). The dentary decreases markedly in depth from *P*₂ to below the posterior root of *M*₃. The small, dorsally directed mental foramen occurs at approximately mid-dentary depth below the alveoli for *P*₂. Anterodorsally, a small, paired foramen occurs immediately adjacent to the position of the fused symphysis. The anterior margin of the ascending ramus is tall and rises almost vertically with respect to the horizontal ramus. A minimum height for the ascending ramus (the tip of the coronoid process is missing) is approximately three times the maximum height of *M*₃ or twice its length. The condyle and angular process are missing. It has a deep masseteric fossa and the horizontal ramus is thickest (greater than any molar width) posterior to *M*₃. The large mandibular foramen is preserved, its dorsal margin level with the toothrow.

The lower dental formula appears to be *I*₁ *C*₁ *P*₂, *M*₁,₂,₃. Only *M*₂ and *M*₃ are known, represented by P895-14b and in P895-14a respectively.

The alveoli for the incisors and canines are ventrally displaced with respect to the toothrow. While it is possible that this is an artefact of damage, the margins of the canine alveoli are smooth and complete. The dentary is damaged between the canines but a single pair of incisors appears to have been present. A single alveolus for *P*₂ is present. It is relatively large, not much smaller than the alveolus for the canine. There is no evidence for two coalescent roots. *P*₄ has two roots oriented more or less longitudinally with respect to the toothrow, although there is some crowding of the alveoli such that the posterior edge of the *P*₂ alveolus is slightly flattened. The anterior alveolus for the *P*₂ root is smaller than the posterior one and is close to the buccal margin of the dentary. The posterior alveolus is compressed by the anteriorly inclined/directed alveolus for the anterior root of *M*₁. The posterior alveolus for *M*₁ is larger than the anterior one. The *M*₃ (P895-14b) has two roots and five distinct cusps, the hypoconulid being a small circular cusp. The trigonid is only slightly narrower and shorter than the talonid. The protoconid and hypoconid are the dominant cusps in height and volume. The protoconid is tall and massive but broken. The metaconid is just taller than the paraconid and more massive; the entoconid and metaconid are probably subequal in height but the entoconid tip is also broken and the metaconid slightly damaged. All cusps show signs of wear but to various degrees. The hypoconid is very large, taller than the metaconid, paraconid and probably entoconid. It is much taller than the hypoconulid.

All cusps are connected by crests, except for the hypoconulid which is isolated. Because the protoconid is broken, it is difficult to assess the relative lengths of the paraenarid and metaenarid or their paraconid, protoconid and metaconid contributions. The cristid obliqua, in occlusal view, is uncurved and contacts the
trigonid at a point directly below the junction of the components of the metacistid. In lateral view there is an inflexion along the cristid obliqua midway between the hypoconid and trigonid. The hypocristid extends from the hypoconid directly to the entoconid, almost perpendicular to the axis of the tooththrow, isolating the small hypoconulid and thereby exhibiting the myotodont condition. The inflexion in the hypocristid occurs closer to the hypoconid than the entoconid, reflecting the almost vertical rise from the talonid basin of the hypoconid before lingually recurving only slightly. A pre-entocristid, straight and gently declining, links the entoconid to the trigonid at the base of the metaconid. The angle between the para- and metacristids is relatively acute, as might be expected in an M₃, these crests being relatively transverse with respect to the tooththrow. The cristid obliqua and paracristid are almost parallel to each other. There is a well-developed, uniform, noniusinuous and continuous anterior, buccal and posterior cingulum, terminated anterolingually by notch for the hypoconulid of M₃ and, at its posterolingual end, well short of the hypoconulid thus providing a notch for the anterior cingulum of M₃.

M₃, represented in P895-14a, is described in so far as it differs from M₂. It is a narrower, more rectangular tooth, being conspicuously longer than wide. It is shorter than M₁. The trigonid is conspicuously wider than the talonid, and the talonid longer than the trigonid. The protoconid is the tallest and most massive cusp, the paraconid is longer than the metaconid, the protoconid contribution to the paracristid being particularly long. The anterior fossa in the talonid basin is not as deep and there is less inflexion in the cristid obliqua. Although M₃ is reduced, remnants of all cusps are present, including the hypoconulid.

Etymology.—breviceps, Greek, short-headed.

Holotype.—P895-14a, partial mandible preserving a fragment of left dentary with alveoli for I₁ and C₁, and right dentary containing M₁ and alveoli for C₁, P₃, and M₃. P895-14b, right M₂ almost certainly from P895-14a.

Type locality and age.—Blas Site, Bullock Creek, Camfield Beds, Northern Territory, Australia (Murray and Megirian, 1992). Blas Site is topographically low in the fossiliferous freshwater limestone sequence at Bullock Creek but its stratigraphic relationship to other fossiliferous units is not known. The Camfield Beds are considered to be middle Miocene (approximately 12 million years old) on the basis of stage-of-evolution biochronology of marsupial taxa (Murray and Megirian, 1992).

Associated fauna and palaeoenvironment.—The Bullock Creek Local Fauna contains teleosts, lungfish, hyliid and myobatrachid frogs, pythons, madtsoiids, elapid snakes, meiolanids, chelids, crocodylids, dromornithids, casuariids, anatids, dasyurids, thylacinids, peramelemorphians, thylacoleonids, di-protocondontids, palorchestids, phalangerids, pseudocheirids, potoro- ids, and macropodids (Murray and Megirian, 1992). The geology and biology of the Bullock Creek assemblage indicate a fluvo-lacustrine environment with permanent or at least seasonally-abundant water. The fauna reflects a waterhole assemblage around which larger predators would be expected to congregate. Blas Site may represent point bar accumulations or low energy fluvo-lacustrine deposits in which minimal transport and dissociation has occurred (Murray and Megirian, 1992).

ICAROPS AENAE new species
Figures 1.6, 1.7, 2.1

Diagnosis.—Shallow dentary, and less crowded anterior dentition than in I. breviceps, and larger and with P₃ less transversely oriented than I. paradox (see below).

Description.—The species is represented only by the holotype QMF30567, an edentulous mandible preserving a fragment of left dentary with alveoli for I₁, C₁, P₃, M₂, and right dentary with alveoli for I₁, C₁, P₃, M₃. A ventral mandibular shelf extends posteriorly to a point directly beneath the alveolus for P₂. The area for attachment of the diastiga muscle(s) is smaller than in I. breviceps. The dentary decreases in depth from below P₂ to beneath the anterior root for M₃, and is thickest (greater than any molar width) posterior to M₃. The small, antero-vdorsally directed mental foramen occurs below the alveolus for P₂ close to C₁. A small, paired foramen occurs immediately adjacent to the fused symphysis close to the alveolar border, just dorsal to the level of the mental foramen. The mandibular foramen is not preserved, nor is the ascending ramus, condyle or angular process.

The lower dental formula appears to be I₁, C₁, P₃, M₂, M₃. The teeth are unknown.

The area between the canines is damaged and the alveolar pattern difficult to interpret. By analogy with I. breviceps, a single pair of incisors appears to have been present. The alveolus for C₁ is large and round but broken anteroventrally and it is not possible to determine whether or not the alveoli for the incisors and canines were ventrally displaced like those in I. breviceps. The single alveolus for P₂ is conspicuously smaller than that for the canine and similar in size to the alveolus for the posterior root of P₃. Unlike I. breviceps, a relatively thick wall of bone separates the alveoli of C₁ and P₃. The P₂ alveolus is oval in shape with smooth sides and there is no evidence for two coalescent roots. P₃ has two roots oriented longitudinally in the tooththrow, the anterior alveolus being smaller than the posterior one. Alveoli for M₁, M₂ are similar to those of I. breviceps with M₃ larger than M₁ larger than M₂, the latter not being particularly reduced.

Etymology.—aenae, Greek, old, ancient.

Holotype.—QMF30567, edentulous mandible preserving a fragment of the left dentary with alveoli for I₁, C₁, P₃, M₂, and right dentary fragment with alveoli for I₁, C₁, P₃.

Type locality and age.—Wayne’s Wok Site occurs on the western edge of freshwater limestone comprising Hal’s Hill, on the D Site Plateau, Riversleigh World Heritage Property, Lawn Hill National Park, Queensland, Australia (Archer et al., 1989, 1994). On the basis of Riversleigh stratigraphy and faunal assemblages, the Wayne’s Wok deposit has been interpreted to be part of Riversleigh’s System B limestone deposits (Archer et al., 1989, 1994; Creaser, 1997) and as such early Miocene in age (approximately 20 million years old).

Associated fauna and palaeoenvironment.—The associated fauna from Wayne’s Wok includes lungfish, teleost fish, frogs, chelids, scincids, agamids, pythoids, crocodiles, birds, pilkipilrids, acrobatids, petaurids, pseudocheirids, bururai- myids, ektomodontids, phalangerids, macropodids, potoroids, wynyardiids, diptroodontids, palorchestids, yalkaparidontids, dasyurids, thylacinids, perameloids, notoryctids, megadermatids and hipposiderids. The diversity of vertebrates represented in the Wayne’s Wok deposit, together with the fact 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. Archer et al. (1989, 1994) give reasons for regarding early Miocene assemblages at Riversleigh as representing rainforest communities.

ICAROPS PARADOX new species
Figures 1.4, 1.5, 2.3

Diagnosis.—Smaller than I. breviceps and I. aenae, and with P₃ larger and P₂ more transversely oriented than I. aenae. Unlike other Icarops species, I. paradox lacks the area of attachment for diastiga muscle(s).
Description.—This species is known only by the holotype QMF20808 a partial mandible preserving fragments left and right dentaries with alveoli for L₁, C₁, and P₂ and R C₁, P₂₄, and M₁. A ventral mandibular shelf extends posteriorly only to the alveolus for the anterior root of P₁. The site for attachment of the digastic muscles is not clear in this specimen. The small, dorsally directed mental foramen occurs below the alveolus for P₁. The area between the canines is damaged anterodorsally. Foramina posteroventral to the midline and just dorsal to the level of the mental foramen are probably homologous with the foramina found in other Icarops species, other foramina in this area evidently being for the incisors. Given the similarity in morphology and available space in this region of the mandible a single pair of incisors was probably present. The canine alveolus is large and oval. The single alveolus for P₁ is larger than in I. aenae but much smaller than the canine alveolus. There is evidence of crowding of teeth with overlapping of the alveoli. P₁ 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.

Etymology.—paradox, in reference to its curious mixture of primitive and derived features.

Holotype.—QMF20808, partial mandible preserving fragments of left and right dentaries with alveoli for L₁, C₁, and P₂ and R C₁, P₂₄, and M₁.

Type locality and age.—Neville’s Garden Site occurs on the northern edge of the D Site Plateau, Riversleigh World Heritage Property, Lawn Hill National Park, Queensland, Australia (Archer et al., 1989, 1994). On the basis of stratigraphy and faunal assemblages, the Neville’s Garden deposit has been interpreted (Archer et al., 1989, 1994) to be part of Riversleigh’s System B, and as such early Miocene in age. It is topographically higher, and therefore possibly slightly younger than the Wayne’s Wok deposit (Creezer 1997). The palaeoenvironment of the deposit has been discussed by Archer et al. (1994) and Hand (1997), but is interpreted to represent a deep pool, associated with a limestone cave, surrounded by forest. The associated fauna includes numerous aquatic vertebrates, diverse amphibians, reptiles, birds, marsupials, and at least seven bat species.

Measurements of the types of Icarops breviceps, I. aenae and I. paradox are given in Table 1.

COMPARISONS

Comparison of the three new species.—Based on size and morphology, three species appear to be represented by the Australian specimens. Icarops breviceps from Bullock Creek and I. aenae from Wayne’s Wok are similar in size but very different in morphology, with I. breviceps having a deeper dentary but slightly shorter toothrow than I. aenae. Both species are about 20 percent larger than I. paradox from Neville’s Garden. In I. aenae there is little crowding of alveoli of the anterior dentition (C₁–M₁), the alveoli for P₂₄, for example, being oriented longitudinally in the toothrow (Fig. 2). In I. paradox, crowding of the anterior alveoli is conspicuous with the anterior root of P₁ (and M₁) buccally displaced with respect to the toothrow and the alveoli tend to be transversely flattened rather than rounded as in I. aenae. This condition appears to be intermediate in I. breviceps, although P₂₄ was evidently very large in both I. breviceps and I. paradox. The I. paradox specimen does not appear to represent a juvenile animal; for example, there are no alveoli for the deciduous dentition. However, the ventral mandibular shelf border is not as well developed as in other Icarops specimens and a digastic scar is not evident; this condition occurs in juvenile Cheirotherium torquatus which later develop extensive ventral mandibular shelves.

Comparisons with other mystacinaids.—Species of Icarops share with Mystacina species a unique combination of features whereby two lower incisors are lost but P₁ is large, though single-rooted, and M₁ is only moderately reduced. Other shared apomorphies include the robust dentary with fused dentary symphysis, ventral mandibular shelf, tall ascending ramus and deep masseteric fossa, myotodont lower molars, and M₁ trigonid not much wider than talonid.

Conspicuous differences between Icarops and Mystacina species include Mystacina’s more procumbent lower incisors, canines and anterior premolars, and more posteroventrally-located mental foramen (beneath P₁). These are apomorphies clearly separating the New Zealand species from the Australian fossil taxa (for discussion regarding position of the mental foramen in bats see Sigé, 1985, p. 169–72). Synapomorphies of Icarops species not shared by Mystacina species are more difficult to discern but might include a deeper, shorter dentary relative to tooth size. Icarops breviceps and I. aenae are approximately equal in size to New Zealand’s living M. tuberculosis; the extinct M. robusta is some 20 percent larger.

Comparisons with molossids, vespertilionoids (s.l.), and noctilionids.—Features exhibited by Icarops species also found in some molossids include: a deep and robust dentary with tall ascending ramus; a single pair of lower incisors; two anterior premolars often obliquely or transversely oriented in the toothrow; and myotodont lower molars. However, features characterising molossids but not represented in Icarops species include: P₁ with two roots; M₁₄ with relatively short trigonid (i.e., not antero-posteriorly compressed) and sinusuous buccal cingulum; and M₁ with talonid much wider than trigonid; massive protoconid and hypoconid (resulting in pronounced buccal bulging); and tall hypoconid (Sigé, 1985, p. 170–171).

Of molossids, Icarops species are perhaps most similar to southeastern Asia’s monotypic Cheirotherium torquatus, with its massive dentary, fused symphysis, broad ventral mandibular shelf with a deep pocket in posteroventral face for attachment...
of the digastic muscles, tall ascending ramus and deep masticatory fossa, single pair of lower incisors and relatively long trigonids. This similarity was the basis for the suggestion by Hand et al. (1995) that the *Icarops* material represented molossoids. It is now clear, however, that *Icarops* species are: smaller and more gracile with a less extensive ventral mandibular shelf, less reduced but single-rooted P3 and less transversely oriented P4; and have myotodont (rather than submyotodont) lower molars, buccal cingula less sinuous and without a break between trigonid and talonid portions, M3 with narrower talonid and unreduced paracodon, and less reduced M4 (with complete posterior cingulum, hypoconulid and entoconid).

Various subsets of features found in *Icarops* species are represented in some molossine bats (sensu Legendre, 1984). Most similarities are shared with species of *Molossops* (e.g., *M. temminckii*), *Neoplatymops*, *Cynomops* (e.g., *C. brachymeles*), and *Myopterus* (e.g., *M. albatis*). These features include a deep dentary with tall ascending ramus, tendency to lose I1, and in some cases a fused dentary symphysis. However, in general, these same features are accompanied by a striking reduction in the size of P3 and M4, and transverse orientation of P4, features not seen in *Icarops* species.

*Icarops* species compare with Australia’s nine living molossid species and two fossil taxa as follows. *Petramops creaseri*, from the middle Miocene of Riversleigh (Hand, 1990), differs from *Icarops* spp. in its unfused dentary symphysis, two pairs of lower incisors, nictalodont molars with anteroposteriorly compressed trigonids, and two-rooted lower premolars both obliquely oriented in the toothrow. Living species of *Micronus* and Miocene *Hydromops* lack the fused symphysis, broad ventral mandibular shelf, have at least two pairs of lower incisors, and P4 with roots transversely oriented. Living species of *Tadarida* and *Chaeorhipida* differ in their long, shallow, unfused dentaries with low ascending rami, nictalodont lower molars, and transversely to slightly obliquely oriented lower premolars.

Other vesperilionoids (s.l.), including vesperilionids, natalids, furiferids, thyropterids, myzopodids, and the extinct philisids, 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 nictalodont lower molars (generally interpreted to be the pleiomeromorphic condition in bats; e.g., Sigé, 1985, p. 181) but philisids, some natalids (i.e., *Kerivoula* and *Phoniscus* spp.), and vesperilionids (e.g., *Myotis*, *Plecotus*, *Sconeecha*, *Chalinolobus*) have myotodont molars like *Icarops* species. Few, if any, species in this very large bat group exhibit the short, robust dentary and crowded anterior toothrow seen in *Icarops* species.

*Icarops* species share with South America’s noctilionids (i.e., species of *Noctilio*) a deep and robust dentary with tall ascending ramus and fused dentary symphysis, a single pair of lower incisors, two anterior premolars, and myotodont lower molars. However, noctilionids differ strikingly from *Icarops* (and *Mystacina*) species in having M4 with extremely wide talonid, wall-like pre-entocristid and cristid obliqua meeting the metaconid, obliquely oriented P4, and small, single-rooted, lingually-displaced P4. In *Noctilio* species, cheek pouches are formed from posterolateral extensions of the buccinator muscle, the resulting sacculation lying over the buccal side of the mandible and occupying the posterior one-third of the horizontal ramus (Murray and Strickler, 1975). In *N. leporinus*, these pouches serve as temporary storage reservoirs for fish plucked from the water by the bat’s long talons. In *Icarops breviceps*, the subalveolar crest is strong (but not nearly as well-developed as in *Noctilio* species) and there is a boss not far behind the mental foramen that corresponds to the fibrous origins of the lower part of the buccinator in *N. leporinus*. However, without a maxilla of *I. breviceps* to examine it is impossible to gauge the extent and development of the buccinator, as an indicator of the presence of cheek pouches, and the possible fishing habits of this species.

**DISCUSSION**

The three new mystacinids described here are the first bats identified from among numerous vertebrates recovered from Bullock Creek (Murray and Megirian, 1992), and two of more than 35 Tertiary bats described from Riversleigh (Archer et al., 1994). This brings to six the number of Australian fossil localities that have now produced bats of Tertiary age. The oldest of these is an early Eocene archaeoonycterid from lacustrine sediments near Murgon, southeastern Queensland (Hand et al., 1994), and the youngest an early-middle Pliocene megadermatid from limestone breccias at Wellington Caves, New South Wales (Hand et al., 1988). Hipposiderids and megadermatids dominate the Riversleigh freshwater limestone deposits, and hence represent more than half of Australia’s Tertiary bats, with emballonurids, molossids, vesperilionids, and a possible rhinolophid comprising the rest of Australia’s Tertiary bats. Australian Pliocene bats are generally closely related to, or represent early populations of, extant Australian bats (e.g., *Taphozous* spp., *Macrotis* gigas). Oligo-Miocene bats include ancestors or close relatives of extant Australian taxa (e.g., *Macroderma* and *Brachyopsidos* spp.), relatives of extinct and extant non-Australian taxa (e.g., *Xenorhinus* and *Riversleighia* spp.), and taxa representing archaic cosmopterigian groups with no living descendants (e.g., *Petramops* and *Hydromops* spp.). The Australian Miocene mystacinids described here provide the only Tertiary record of a very distinctive southern bat lineage of which a single, threatened species survives in New Zealand.

Based on the degree of crowding of the anterior dentition, *Icarops aenae* from Wayne’s Wok is interpreted here to be the most plesiomorphic of *Icarops* species and (if it is adult) *I. paradox* from Neville’s Garden probably the most derived. The Wayne’s Wok and Neville’s Garden assemblages are approximate contemporaries, both being early Miocene in age, and older than the middle Miocene Bullock Creek assemblages (Archer et al., 1989; Murray and Megirian, 1992; Creaser, 1997). *Icarops breviceps* and *I. paradox* could represent separate branches of the *Icarops* lineage, both possibly derived from *I. aenae* or a closely related species. There is nothing known about *Icarops aenae* that would preclude it from ancestry of Quaternary species of *Mystacina*.

If species of *Icarops* and *Mystacina* are sister-groups, then the common ancestor of Australian and New Zealand mystacinids must be at least early Miocene in age. The plesiomorphic nature of the Australian fossils suggests that Australia was the source of New Zealand’s mystacinids. New Zealand separated from the rest of Gondwana approximately 80 million years ago, carrying with it terrestrial vertebrates such as leioptelmatid frogs, tuataras, ratite birds, and possibly monotremes. Some 25–37 million years ago, in the Oligocene, much of New Zealand was submerged (Fleming, 1979) and any Gondwanan mammals it might have retained were evidently lost. In the early Miocene vulcanism and other tectonic activity recommenced and New Zealand began to rise. Since the mid-Tertiary the geographic relationship of Australia and New Zealand has changed little, a distance of 1600 km still separating the two landmasses. Isolated, wind-assisted dispersals by bats from Australia to New Zealand have been recorded during historic times (Daniel and Williams, 1984). There are no records of dispersals in the opposite, westerly direction, against the prevailing winds. It is likely that the first intrepid mystacinids arrived on the islands of New Zealand, from Australia, sometime after the late Oligocene.
The ultimate origin of the family Mystacinidae is less clear. Pierson et al.'s (1986) albumen data, which closely links mystacinids to noctilionoids, argue for a South American origin for the family. Recent phylogenetic analyses by Simmons (in press) using a "total evidence" approach, in which morphological, reproductive, behavioral, DNA, and other data are included in a single data set, suggest that mystacinids could represent the pleiomorphic sister-group of all other vespertilionoids sensu lato (i.e., vespertilionids, nataloids, molossoids, etc.). Based on the latter phylogeny, optimisation of biogeographic data (Simmons, 1995), we find that the radiation of the Yangochiroptera (Vesper-tilionoidea + Noctilionoidea; Koopman, 1985) took place in the New rather than Old World, possibly in the Neotropics. 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. Archaic bats are now known to have occurred in the Southern Hemisphere as well as the North by the early Eocene, and modern bat clades overlapped widely with more primitive bats, in both time and space (Sigé, 1991; Beard et al., 1992; Ducrocq et al., 1993). There is yet no pre-Oligocene record of bats in South America, the oldest bat in the Southern Hemi-sphere being an archaeoemydid from Australia (Hand et al., 1994).

At least two apomorphies (a single-rooted P1 and narrow talonid) exclude species of Icarops and Mystacina from ancestry of molossids, noctilionoids and vespertilionoids (s.l.). Further assessment of phylogenetic relationships between Icarops species and other members of the Yangochiroptera awaits discovery of additional fossil material. It is noteworthy, however, that several distinct characteristics of mystacinids occur in various combinations in certain (closely related) yangochiropteran groups. For example, loss of two pairs of lower incisors (I1 and I2) occurs in mystacinids, noctilionids, and some molossid lineages (i.e., the African Mops (some species) and Myopterus and Neotropical Molossus and Molossops as well as Asian Chei-meleis), as does fusion of the dentary symphysis (although not in Mops). A deep dentary, tall coronoid process, and short tooth-row, with concomitant reduction in M1 and transverse orientation of premolars, has also been derived independently within the Molossidae (e.g., in Molossus, Molossops, Cheiromeles, Mormopterus, Micronomus). To what extent these features in Icarops represent apomorphies shared with other yangochiropterans or autapomorphies related perhaps to diet is unclear. Freeman (1984, 1988) found in microchiropterans a strong correlation between diet (prey hardness) and dentary depth and shortness, height of coronoid process and width of face, with, for example, molossines and Cheiromeles torquatus found to be well-adapted for beetle-eating, and Noctilio leporinus for eating fish.

Similar characteristics in Mystacina seem to have at least facilitated their peculiar terrestrial and dietary habits detailed by Daniel (1979, 1990) and Daniel and Williams (1984). Species of Mystacina have very short wings and sturdy hindlimbs and spend up to 30 percent of their time on the ground or on tree trunks or branches. Mystacinids feed on ground and flying arthropods, nectar, fruit and pollen, as well as mutton bird flesh, nestlings, and adult birds as large as Yellow-crowned Parakeets (Daniel, 1990). They roost in tree hollows and limestone caves but will also burrow into rotten, fallen logs to make their roosts and will enter seabird burrows to forage. The surviving species, Mystacina tuberculata, occurs on New Zealand's North Island and nearby offshore islands where it survives in indigenous native forests dominated by Podocarpus, Dacrydium, and kauri trees. Threats to its survival include feral cats, rats, honey bees, and possums. Mystacina tuberculata has been identified as the sole pollinator of the endemic, parasitic rhizome the Wood Rose Daecylanthus taylorii, the only bat-pollinated plant to produce its flowers at ground level (Eckroyd, 1993).

It is not clear which if any of the terrestrial habits of Mysta-cina species were shared by Australian Icarops species. How-ever, the short, robust jaw, tall ascending ramus, fused dentary symphysis, and broad ventral mandibular shelf suggest that the Miocene species were capable of consuming very hard prey. These features are most conspicuous in the Australian species Icarops breviceps, which appears to have been most similar in morphology and size to M. tuberculata, and perhaps as catholic in its diet. The paleoenvironmental setting for the early Miocene of Riversleigh includes limestone caves fringing lakes and pools in temperate, closed-canopy forest (Archer et al., 1994). At Bullock Creek, the middle Miocene habitat is interpreted to be a meandering river on a wide floodplain with oxbow lake and streambank communities predominating and local fringing woodland or tree savannah (Murray and Megirian, 1992). Paleoenvironmental elements in common between the sites include water and limestone, suggesting that Miocene mystacinids may have roosted in limestone caves and foraged for insects, or perhaps even fish, over water.

ACKNOWLEDGMENTS

Field work at Camfield (Bullock Creek Local Fauna) is partially supported by a Northern Territory Heritage Grant. Work at Riversleigh has been supported by the Australian Research Council, the Department of the Environment, Sport and Territories, National Estate Programme Grants (Queensland), Queensland National Parks and Wildlife Service, the Australian Geographic Society, the Linnean Society of New South Wales, ICI, the Queensland Museum and the University of New South Wales. The following people kindly provided access to comparative specimens in their institutions: A. Tennyson and T. Worthy (Museum of New Zealand, Te Papa Tongarewa), T. Flannery and L. Gibson (Australian Museum), D. Kitchener (Western Australian Museum), J.E. Hill and P. Jenkins (British Museum [Natural History]), S. Van Dyck (Queensland Museum), C. Kemper (South Australian Museum), K. Koopman, N. Simmons, and W. Fuchs (American Museum of Natural History). J. Muirhead and R. Murphy, University of New South Wales, produced the SEM photographs. We thank K. Koopman and an anonymous referee for constructively criticizing a draft of this paper.

REFERENCES


----. AND G. R. WILLIAMS. 1984. A survey of the distribution, sea-


ACCEPTED 25 October 1997