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MYSTACINID BATS (MICROCHIROPTERA) FROM THE AUSTRALIAN TERTIARY

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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. paradox* 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 molossids.

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 (=Phyllostomoidea), 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 superfamily Molossoidea (i.e., molossids plus tomopeatinids) 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 P_2 is large, though single-rooted, and M_3 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 M_2 trigonid not much wider than talonid.

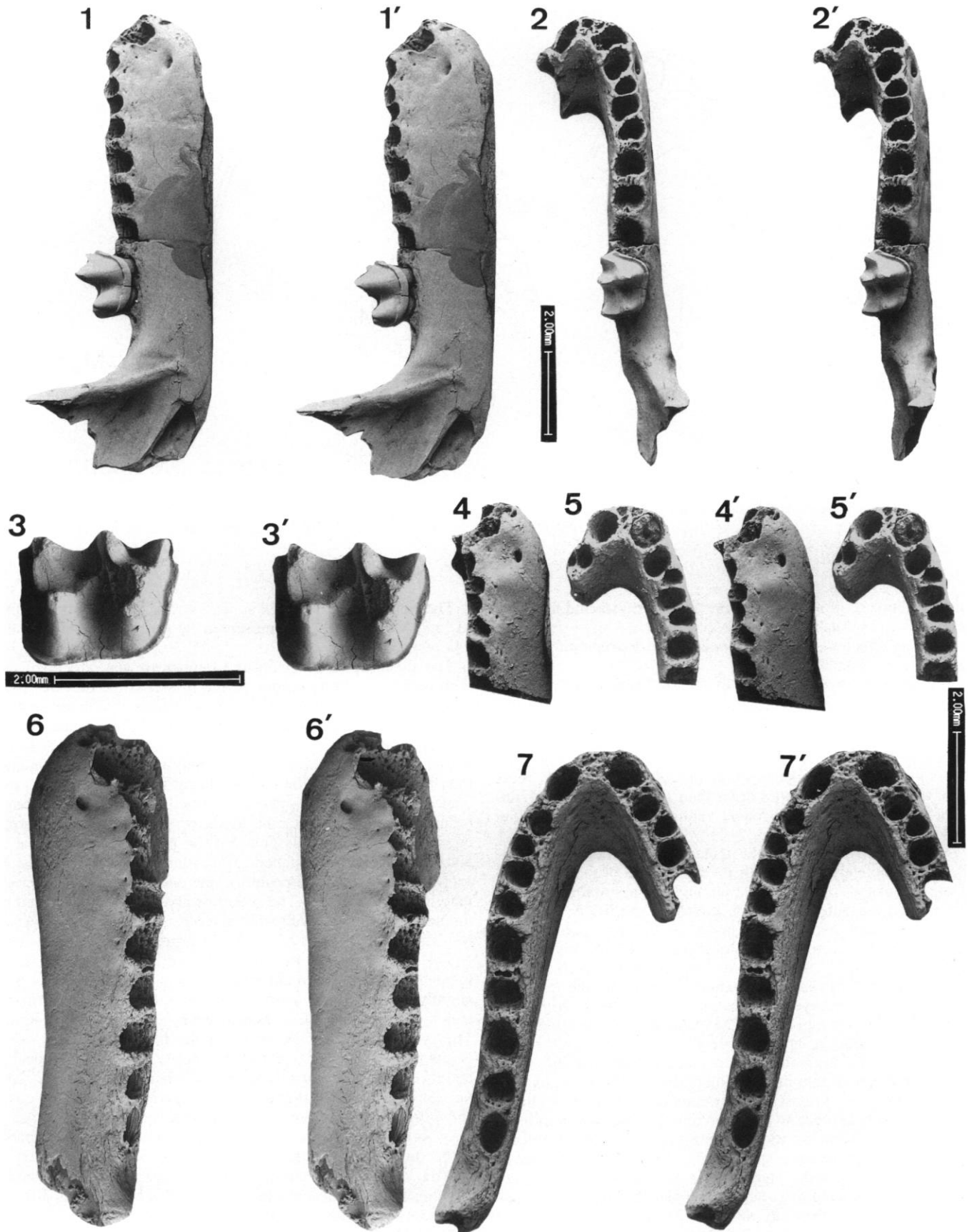
ICAROPS new genus

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 P_2), 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, $\times 7.5$; 1, 1', buccal stereo pair; 2, 2', occlusal stereo pair; 3, P895-14b, holotype, $\times 17$; 3, 3', M_3 , oblique-occlusal stereo pair. 4, 5, *Icarops paradox* n. gen. and sp., QMF20808, holotype, Neville's Garden Site, Riversleigh, Queensland, $\times 10$; 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, $\times 10$; 6, 6', buccal stereo pair; 7, 7', occlusal stereo pair. Scale bars indicate 2 mm.



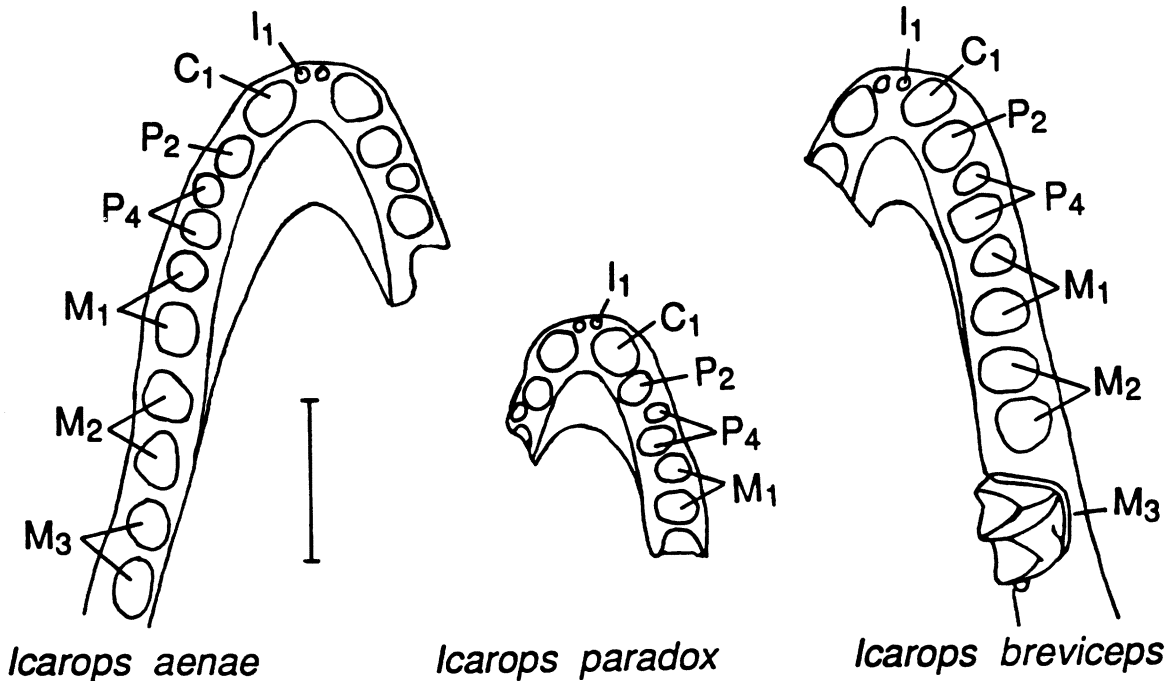


FIGURE 2—Dentary alveoli patterns in species of *Icarops*. *Icarops aenae* n. gen. and sp., QMF30567, holotype, Wayne's Wok Site, Riversleigh, $\times 10$. *Icarops paradox* n. gen. and sp., QMF20808, holotype, Neville's Garden Site, Riversleigh, $\times 10$. *Icarops breviceps* n. gen. and sp., P895-14a, holotype (part), Blast Site, Bullock Creek, Northern Territory, $\times 10$.

towards the sun, in reference to the ancient mystacinid that flew eastwards from Australia to New Zealand.

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

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

ICAROPS BREVICEPS new species

Figures 1.1–1.3, 2.2

Diagnosis.—Deeper dentary than in *I. aenae* and with P_4 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_4 . 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 tooththrow.

The lower dental formula appears to be $I_1 C_1 P_{2,4} M_{1,2,3}$. 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 tooththrow. 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 tooththrow, 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_4 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_2 (P895-14b) has two roots and five distinct cusps, the hypoconulid being a small cingular 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 paracristid and metacristid 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 metacristid. 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 toothrow, 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 M_2 , these crests being relatively transverse with respect to the toothrow. The cristid obliqua and paracristid are almost parallel to each other. There is a well developed, uniform, nonsinuous and continuous anterior, buccal and posterior cingulum, terminated anterolingually by notch for the hypoconulid of M_1 and, at its posterolingual end, well short of the hypoconulid thus providing a notch for the anterior cingulum of M_3 .

M_3 , represented in P895-14a, is described in so far as it differs from M_2 . It is a narrower, more rectangular tooth, being conspicuously longer than wide. It is shorter than M_2 . 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 paracristid is longer than the metacristid, 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 M_3 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 I_1 and C_1 , and right dentary containing M_3 and alveoli for C_1 , $P_{2,4}$, and $M_{1,2}$. P895-14b, right M_2 almost certainly from P895-14a.

Type locality and age.—Blast Site, Bullock Creek, Camfield Beds, Northern Territory, Australia (Murray and Megirian, 1992). Blast 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, hylid and myobatrachid frogs, pythons, madtsoiids, elapids, varanids, meiolaniids, chelids, crocodylids, dromornithids, casuariids, anatids, dasyurids, thylacinids, peramelemorphians, thylacoleonids, diprotodontids, palorchestids, phalangerids, pseudocheirids, potoroids, and macropodids (Murray and Megirian, 1992). The geology and biology of the Bullock Creek assemblage indicate a fluvio-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. Blast Site may represent point bar accumulations or low energy fluvio-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.—Shallower dentary, and less crowded anterior dentition than in *I. breviceps*, and larger and with P_4 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 I_1 , C_1 , $P_{2,4}$, M_{1-3} and right dentary with alveoli for I_1 , C_1 , $P_{2,4}$. A ventral mandibular shelf extends posteriorly to a point directly beneath the alveolus for P_2 . The area for attachment of the digastric muscle(s) is smaller than in *I. breviceps*. The dentary decreases in depth from below P_2 to beneath the anterior root for M_3 , and is thickest (greater than any molar width) posterior to M_3 . The small, anterodorsally directed mental foramen occurs below the alveoli for P_2 close to C_1 . 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 $I_1 C_1 P_{2,4} M_{1,2,3}$. 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 C_1 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 P_2 is conspicuously smaller than that for the canine and similar in size to the alveolus for the posterior root of P_4 . Unlike *I. breviceps*, a relatively thick wall of bone separates the alveoli of C_1 and P_4 . The P_2 alveolus is oval in shape with smooth sides and there is no evidence for two coalescent roots. P_4 has two roots oriented longitudinally in the toothrow, the anterior alveolus being smaller than the posterior one. Alveoli for M_{1-3} are similar to those of *I. breviceps* with M_1 larger than M_2 larger than M_3 , 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 I_1 , C_1 , $P_{2,4}$, M_{1-3} and right dentary fragment with alveoli for I_1 , C_1 , $P_{2,4}$.

Type locality and age.—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, 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, pythonids, typhlopids, crocodylids, birds, pilkipildrids, acrobatids, petaurids, pseudocheirids, burramyids, ektopodontids, phalangerids, macropodids, potoroids, wynyardiids, diprotodontids, palorchestids, yalkaparodontids, 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 P_2 larger and P_4 more transversely oriented than *I. aenae*. Unlike other *Icarops* species, *I. paradox* lacks the area of attachment for digastric muscle(s).

Description.—This species is known only by the holotype QMF20808 a partial mandible preserving fragments left and right dentaries with alveoli for L I₁, C₁ and P₂ and R C₁, P_{2,4} and M₁. A ventral mandibular shelf extends posteriorly only to the alveolus for the anterior root of P₄. The site for attachment of the digastric muscles is not clear in this specimen. The small, dorsally directed mental foramen occurs below the alveolus for P₂. 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 P₂ 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. P₄ 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 L I₁, C₁ and P₂ and R C₁, P_{2,4} 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 (Creaser 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 tooththrow 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 P₄, 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 P₂ (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 P₂ 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 digastric scar is not evident; this condition occurs

TABLE 1—Measurements (mm) of type specimens of *Icarops* n. gen. from northern Australia: holotype (P895-14) of *I. breviceps* n. sp. from the middle Miocene Bullock Creek Local Fauna, Camfield Beds, Northern Territory; holotype (QMF30567) of *I. aenae* n. sp. from the early Miocene Wayne's Wok Site, Riversleigh, Queensland; holotype (QMF20808) of *I. paradox* n. sp. from the early Miocene Neville's Garden Site, Riversleigh, Queensland. Abbreviations: L, length; TL, trigonid length; tl, talonid length; Tw, trigonid width; tw, talonid width.

	<i>Icarops breviceps</i> P895-14b P895-14a	<i>I. aenae</i> QMF30567	<i>I. paradox</i> QMF20808
Max. dentary depth	3.17	2.32	1.89
Min. dentary depth	2.04	1.77	—
Symphysis to M3 post. alveolus	7.95	7.78	—
Symphysis to M1 post. alveolus	4.43	4.31	3.26
Symphysis to P4 post. alveolus	3.04	2.78	2.25
Symphysis to P2 post alveolus	1.97	1.77	1.58
M ₂ L	1.89		
TL	0.97		
tl	0.91		
Tw	1.33		
tw	1.36		
M ₁ L	1.71		
TL	0.91		
tl	0.79		
Tw	1.21		
tw	1.00		

in juvenile *Cheiromeles torquatus* which later develop extensive ventral mandibular shelves.

Comparisons with other mystacinids.—Species of *Icarops* share with *Mystacina* species a unique combination of features whereby two lower incisors are lost but P₂ 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 masseteric fossa, myotodont lower molars, and M₂ 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 P₄). 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. tuberculata*; 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: P₂ with two roots; M₁₋₃ with relatively short trigonid (i.e., not anteroposteriorly compressed) and sinuous buccal cingulum; and M_{1,2} 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 *Cheiromeles torquatus*, with its massive dentary, fused symphysis, broad ventral mandibular shelf with a deep pocket in posteroventral face for attachment

of the digastric muscles, tall ascending ramus and deep masseteric 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 molossids. 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 P_2 and less transversely oriented P_4 ; and have myotodont (rather than submyotodont) lower molars, buccal cingula less sinuous and without a break between trigonid and talonid portions, M_2 with narrower talonid and unreduced paraconid, and less reduced M_3 (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. albatrus*). These features include a deep dentary with tall ascending ramus, tendency to lose I_2 , and in some cases a fused dentary symphysis. However, in general, these same features are accompanied by a striking reduction in the size of P_2 and M_3 , and transverse orientation of P_4 , 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, nyctalodont molars with anteroposteriorly compressed trigonids, and two-rooted lower premolars both obliquely oriented in the toothrow. Living species of *Micronomus* and Miocene *Hydromops* lack the fused symphysis, broad ventral mandibular shelf, have at least two pairs of lower incisors, and P_4 with roots transversely oriented. Living species of *Tadarida* and *Chaerephon* differ in their long, shallow, unfused dentaries with low ascending rami, nyctalodont lower molars, and transversely to slightly obliquely oriented lower premolars.

Other vespertilionoids (s.l.), including vespertilionids, natalids, furipterids, 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 nyctalodont lower molars (generally interpreted to be the plesiomorphic condition in bats; e.g., Sigé, 1985, p. 181) but philisids, some natalids (i.e., *Kerivoula* and *Phoniscus* spp.), and vespertilionids (e.g., *Myotis*, *Plecotus*, *Scoteanax*, *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 M_2 with extremely wide talonid, wall-like pre-entocristid and cristid obliqua meeting the metaconid, obliquely oriented P_4 , and small, single-rooted, lingually-displaced P_2 . In *Noctilio* species, cheek pouches are formed from posterolateral extensions of the buccinator muscle, the resulting sacculations 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 recovered 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 archaeonycterid 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, vespertilionids, 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., *Macroderma gigas*). Oligo-Miocene bats include ancestors or close relatives of extant Australian taxa (e.g., *Macroderma* and *Brachipposideros* spp.), relatives of extinct and extant non-Australian taxa (e.g., *Xenorhinos* and *Riversleigha* spp.), and taxa representing archaic cosmopolitan 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 leopelmatid 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 plesiomorphic sister-group of all other vespertilionoids sensu lato (i.e., vespertilionids, nataloids, molossoids, etc.). Based on the latter phylogeny, optimisation of biogeographic data (Simmons, 1996) suggests that the radiation of the Yangochiroptera (Vespertilionoidea + 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 Hemisphere being an archaeonycterid from Australia (Hand et al., 1994).

At least two apomorphies (a single-rooted P_2 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 distinctive characteristics of mystacinids occur in various combinations in certain (?closely related) yangochiropteran groups. For example, loss of two pairs of lower incisors (I_2 and I_3) occurs in mystacinids, noctilionids, and some molossid lineages (i.e., the African *Mops* (some species) and *Myotis* and Neotropical *Molossus* and *Molossops* as well as Asian *Cheiromeles*), 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 M_3 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, *M. 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 *Dactylanthus 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 *Mystacina* species were shared by Australian *Icarops* species. However, 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.

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REFERENCES

- ARCHER, M., H. GODTHELP, S. J. HAND, AND D. MEGIRIAN. 1989. Fossil mammals of Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zoologist*, 25:35–69.
- , S. J. HAND, AND H. GODTHELP. 1994. Riversleigh. The Story of Animals in Ancient Rainforests of Inland Australia. 2nd edition. Reed Books, Sydney, 264 p.
- BEARD, K. C., B. SOGÉ, AND L. KRISHTALKA. 1992. A primitive vespertilionoid bat from the early Eocene of central Wyoming. *Comptes Rendus de l'Académie des Sciences, Paris*, 314, II:735–741.
- CREASER, P. 1997. Oligocene–Miocene sediments of Riversleigh: the potential significance of topography. *Memoirs of the Queensland Museum*, 41:303–314.
- DANIEL, M. J. 1979. The New Zealand short-tailed bat, *Mystacina tuberculata*, a review of present knowledge. *New Zealand Journal of Zoology*, 6:357–370.
- . 1990. Lesser short-tailed bat, p. 123–130. In C. M. King (ed.), *The Handbook of New Zealand Mammals*. Oxford University Press, Auckland.
- , AND G. R. WILLIAMS. 1984. A survey of the distribution, sea-

- sonal activity and roost sites of New Zealand bats. *New Zealand Journal of Ecology*, 7:9–25.
- DUCROCQ, S., J.-J. JAEGER, AND B. SIGÉ. 1993. Un mégachiroptère dans l'Eocène supérieur de Thaïlande. Incidence dans la discussion phylogénique du groupe. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 1993 (9):561–575.
- DWYER, P. D. 1962. Studies of the two New Zealand bats. *Zoology Publications from Victoria University of Wellington*, 28:1–28.
- ECKROYD, C. 1993. In search of the wood rose. *Forest and Bird*, Feb. 93:24–28.
- FLEMING, C. A. 1979. *The Geological History of New Zealand and its Life*. Auckland University Press, Auckland, 141 p.
- FREEMAN, P. W. 1984. Functional analysis of large animalivorous bats (Microchiroptera). *Biological Journal of the Linnean Society*, 21:387–408.
- . 1988. Frugivorous and animalivorous bats (Microchiroptera): dental and cranial adaptations. *Biological Journal of the Linnean Society*, 33:249–272.
- HAND, S. J. 1990. First Tertiary molossid (Microchiroptera: Molossidae) from Australia: its phylogenetic and biogeographic implications. *Memoirs of the Queensland Museum*, 28:175–192.
- , L. DAWSON, AND M. AUGÉE. 1988. *Macroderma koppa*, a new Pliocene species of false vampire bat (Microchiroptera: Megadermatidae) from Wellington Caves, New South Wales. *Records of the Australian Museum*, 40:343–351.
- , P. MURRAY, AND D. MEGIRIAN. 1995. A new genus and three new species of molossid bats from the Miocene of Northern Australia. *Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics 95*, Canberra, Abstracts:12.
- , M. NOVACEK, H. GODTHELP, AND M. ARCHER. 1994. First Eocene bat from Australia. *Journal of Vertebrate Paleontology*, 14:375–381.
- HERSHKOVITZ, P. 1972. The recent mammals of the neotropical region: a zoogeographic and ecological review, p. 311–432. *In* A. Keast, F. C. Erk and B. Glass (eds.), *Evolution, Mammals and Southern Continents*. State University New York Press, Albany.
- KOOPMAN, K. F. 1985. A synopsis of the families of bats, Pt. VII. *Bat Research News*, 25:25–29.
- LEGENDRE, S. 1984. Étude odontologique des représentants actuels du groupe *Tadarida* (Chiroptera, Molossidae). Implications phylogéniques, systématiques et zoogeographiques. *Revue suisse de Zoologie*, 91:399–442.
- . 1985. Molossidés (Mammalia, Chiroptera) cénozoïques de l'Ancien et du Nouveau Monde; statut systématique; intégration phylogénique des données. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 170:205–227.
- MILLER, G. S. 1907. The families and genera of bats. *Bulletin of the United States National Museum*, 57:1–282.
- MURRAY, P. F., AND D. MEGIRIAN. 1992. Continuity and contrast in middle and late Miocene vertebrate communities from the Northern Territory. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences*, 9:195–217.
- , AND T. STRICKLER. 1975. Notes on the structure and function of cheek pouches within the Chiroptera. *Journal of Mammalogy*, 56:673–676.
- PIERSON, E. D. 1986. Molecular systematics of the Microchiroptera: higher taxon relationships and biogeography. Unpubl. Ph.D. dissertation, University of California, Berkeley, California, 262 p.
- , V. M. SARICH, J. M. LOWENSTEIN, M. J. DANIEL, AND W. E. RAINEY. 1986. A molecular link between the bats of New Zealand and South America. *Nature*, 6083:60–63.
- SIGÉ, B. 1968. Les chiroptères du Miocene inférieur de Bouzigues. I. Étude systématique. *Palaeovertebrata*, 1:65–133.
- . 1985. Les chiroptères oligocènes du Fayum, Egypte. *Geologica et Palaeontologica*, 19:161–189.
- . 1991. Rhinolophoidea et Vespertilionoidea (Chiroptera) du Chambi (Eocène inférieur de Tunisie). Aspects biostratigraphique, biogéographique and paléoécologique de l'origine des chiroptères modernes. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 182:355–376.
- SIMMONS, N. B. 1996. Bat diversification and palaeobiogeography: implications of a new higher-level phylogeny. *Journal of Vertebrate Paleontology*, 16 (3) Abstracts:66A.
- . In press. A reappraisal of interfamilial relationships of bats. *In* T. Kunz and P. Racey (eds.), *Proceedings of the 10th International Bat Research Conference*. Smithsonian Institution, Washington.
- WORTHY, T. H., AND R. N. HOLDAWAY. 1994. Scraps from an owl's table—predator activity as a significant taphonomic process newly recognised from New Zealand Quaternary deposits. *Alcheringa*, 18:229–245.

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