

# A NEW HIPPOSIDERID GENUS (MICROCHIROPTERA) FROM AN EARLY MIOCENE BAT COMMUNITY IN AUSTRALIA

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**Abstract:** A new genus and species of hipposiderid bat is described from an early Miocene cave deposit (Bitesantennary Site) in the Riversleigh World Heritage fossil property, northern Australia. Eight hipposiderid genera are now recorded from Riversleigh's Miocene sediments: *Hipposideros*, *Brachhipposideros*, *Rhinonycteris*, *Riversleigha*, *Xenorhinos*, *Miophyllorhina*, *Archerops* and *Brevipalatus* gen. nov. The new taxon appears to be most closely related to Australian endemic *Rhinonycteris* and *Brachhipposideros* species, but its autapomorphically very short palate distinguishes it from

other members of this relatively plesiomorphic group. It is one of eight hipposiderid species recovered from the Bitesantennary Site deposit, and one of 11 recorded from Riversleigh's early Miocene sediments. Compared with modern bat faunas, the early Miocene Riversleigh bat community differs strikingly in its high hipposiderid diversity but may differ less in its overall trophic structure.

**Key words:** Miocene, Australia, Riversleigh, *Brevipalatus*, hipposiderids, bat community.

THE Tertiary freshwater limestone deposits of the Riversleigh World Heritage property, in Lawn Hill National Park, north-western Queensland, Australia, have produced a diverse array of fossil bats with more than 40 species identified from cave, fissure fill and lacustrine sediments spanning the period from 25 to 4 Ma (Archer *et al.* 1994; Hand 1999). Fossil bats are much rarer in other Australian fossil deposits, with fewer than ten Tertiary species described from the rest of the continent, the oldest of which is the 55-myr-old *Australonycteris clarkae* (Hand *et al.*, 1994).

The Riversleigh fossil bat faunas are dominated, in both diversity and abundance, by hipposiderids, or Old World leaf-nosed bats, with a minimum of 22 species represented, most by dozens of individuals and many by cranial material. Hipposiderids thus comprise more than half of Australia's Tertiary bats, with megadermatids, emballonurids, molossids, vespertilionids and mystacinids making up the rest (Hand 1999).

The family Hipposideridae contains some 60 living species referred to the genus *Hipposideros*, and eight other genera of one to two species each. These generally have short, broad (low aspect) wings and are slow, weaving fliers that forage for insects by hovering and gleaning, hawking from observation perches, or by aerial pursuit, always near or within vegetation. All have a complex

noseleaf, large ears and emit their echolocation calls through the nose rather than mouth. Seven extant hipposiderid species occur in the tropical areas of northern Australia: five species of *Hipposideros* and two of *Rhinonycteris* (Duncan *et al.* 1999). The two species of *Rhinonycteris* and *H. stenotis* are Australian endemics while the other species occur also in New Guinea and/or south-eastern Asia.

The modern geographical range of the predominantly cave-dwelling family Hipposideridae is restricted to the Old World tropics and subtropics, but Tertiary fossils indicate that its range was once much wider and included a large part of western Europe. There, the bat-rich Tertiary cave and fissure-fill deposits indicate that from the middle Eocene to the Miocene, hipposiderids were the most diverse and numerous of cave-dwelling bats, with five species occurring together in some deposits (Remy *et al.* 1987). The oldest hipposiderids date from early Tertiary (middle Eocene) European deposits (e.g. Revilliod 1917, 1920). Middle Tertiary hipposiderids are known from Africa, Asia and Australia (Sigé *et al.* 1982, 1994; Mein and Ginsburg 1997).

The Bitesantennary Site deposit, one of nearly 200 fossil sites identified in the Riversleigh World Heritage fossil property, contains the remains of thousands of

well-preserved hipposiderid skulls and limb bones that suggest fossilization at or near the point of accumulation. The deposit is interpreted to be an early Miocene cave-fill (Archer *et al.* 1989, 1994; Megirian 1992; Creaser 1997). Vertebrate taxa recovered from the deposit include the hipposiderid bats *Rhinonycteris tedfordi* Hand, 1997a, *?Brachipposideros watsoni* Hand, 1997a, *Xenorhinos halli* Hand, 1998a, *Riversleigha williamsi* Hand, 1998b and the megadermatid *Macroderma* sp. cf. *M. godthelpi* (Hand 1985), as well as rarer frogs, lizards, a boid, a stork, a swift, perameloids, a dasyurid and a bulungamayine kangaroo (Archer *et al.* 1994; Cooke 1997; Wroe 1999).

In this paper, a new genus and species of hipposiderid is described from Riversleigh's Bitesantennary Site. Terminology for skull and dental morphology and orientation is given in Sigé *et al.* (1982) and Hand (1993, 1997a).

## SYSTEMATIC PALAEOLOGY

Suborder MICROCHIROPTERA Dobson, 1875  
 Family HIPPOSIDERIDAE Miller, 1907  
 Tribe RHINONYCTERINI Gray, 1866  
 Subtribe RHINONYCTERINA Gray, 1866  
 (*sensu* Hand and Kirsch 2003)

Genus BREVIPALATUS gen. nov.

*Derivation of name.* Latin, *brevis*, short, and *palatum*, palate.

*Type species.* *Brevipalatus mcculloughi* gen. et sp. nov.

*Diagnosis.* As for the type species until others are recognized.

*Age and distribution.* Early Miocene, northern Australia.

*Brevipalatus mcculloughi* sp. nov.

Text-figure 1

*Derivation of name.* The species is named after Ron McCullough, Mayor of Mount Isa, north-western Queensland, in recognition of his unflagging logistical and financial support of fossil research in the Riversleigh World Heritage property and for his support for the development of the Riversleigh Interpretive Centre in Mount Isa, Queensland.

*Holotype.* Queensland Museum fossil specimen QMF22821, a skull preserving LM<sup>1-3</sup> and RP<sup>4</sup>-M<sup>3</sup> from the Bitesantennary Site (see type locality below).

*Paratypes.* QMF22836, a partial skull with LM<sup>2</sup> and RM<sup>1-3</sup>; QMF22879, a partial skull with RP<sup>4</sup>-M<sup>3</sup>; QMF22825, a partial skull with LP<sup>4</sup>-M<sup>3</sup> and RP<sup>4</sup>-M<sup>3</sup>; QMF22822, a skull with

RC<sup>1</sup>-M<sup>3</sup> and periotics *in situ*; QMF22832, a partial skull with LP<sup>2</sup>-M<sup>3</sup> and RC<sup>1</sup>-M<sup>3</sup>; QMF30578, a maxilla with worn RC<sup>1</sup>-M<sup>3</sup>; QMF22876, an edentulous skull; QMF41306, a skull with LM<sup>2</sup>. All from the type locality.

*Referred material.* QMF22823, a partial skull with LP<sup>4</sup>-M<sup>2</sup> and RP<sup>4</sup>-M<sup>2</sup>; QMF22849, a rostrum with LM<sup>1-3</sup>; QMF22851, a maxillary fragment with LP<sup>4</sup>-M<sup>3</sup>; QMF22852, a partial skull with LC<sup>1</sup> and M<sup>2</sup>; QMF22863, a partial skull with RP<sup>4</sup>-M<sup>3</sup>; QMF22864, a partial skull with LP<sup>4</sup>-M<sup>3</sup> and RM<sup>2-3</sup>; QMF22868, an edentulous skull; QMF22872, a partial, edentulous skull; QMF22889, a rostrum with RP<sup>2</sup>-M<sup>3</sup> and LM<sup>2</sup>; QMF22895, a rostrum with RM<sup>1-3</sup>; QMF22897, a rostrum with LM<sup>1-3</sup> and RM<sup>2-3</sup>; QMF22901, a palate with LP<sup>4</sup> and RP<sup>4</sup>-M<sup>2</sup>; QMF22905, a rostrum with RP<sup>4</sup>-M<sup>3</sup>. All from the type locality.

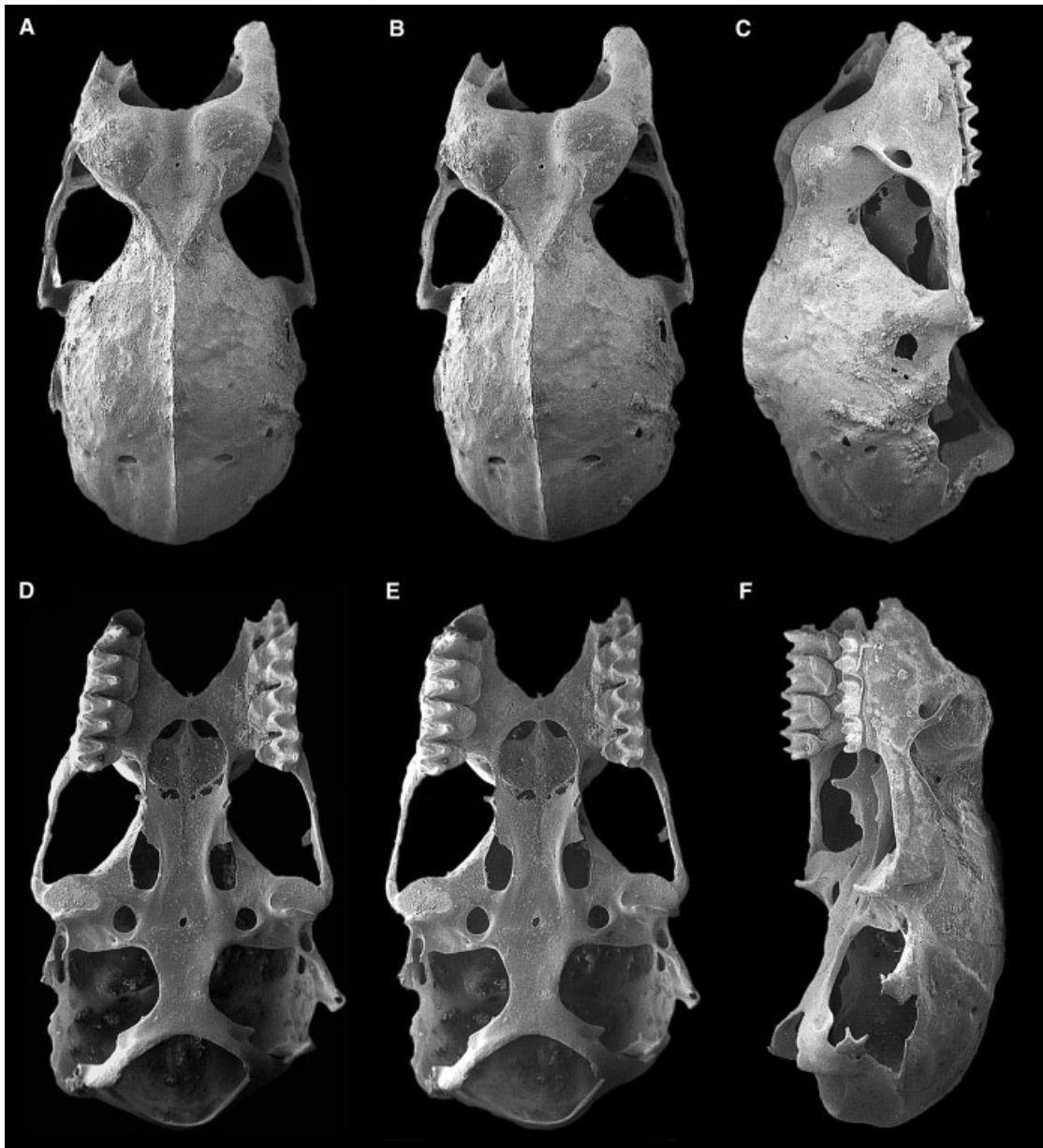
*Type locality.* Bitesantennary Site, on the D Site Plateau, Riversleigh World Heritage property, Lawn Hill National Park, north-western Queensland, Australia. On the basis of stratigraphy and contained local faunas, the deposit is interpreted to be part of Riversleigh's System B deposits and, as such, early Miocene in age (Archer *et al.* 1994; Creaser 1997); see Discussion for interpretation of palaeohabitat and summary of other taxa recovered from this site.

*Diagnosis.* *Brevipalatus mcculloughi* differs from species of *Archerops*, *Asellia*, *Aselliscus*, *Brachipposideros*, *Cloeotis*, *Coelops*, *Hipposideros*, *Palaeophyllophora*, *Paracoelops*, *Pseudorhinolophus*, *Rhinonycteris*, *Riversleigha*, *Syndesmotis*, *Triaenops* and *Vaylatsia* in having a very short hard palate that in length is equivalent to, or less than, M<sup>1</sup> length. It differs from *Miophyllorhina riversleighensis*, an early Miocene hipposiderid known only from dental remains, in retaining P<sup>2</sup>.

*Brevipalatus mcculloughi* differs from *Xenorhinos halli* in its narrower rostrum, narrow interorbital region, and less voluminous and more completely divided nasal cavities.

*Description.* The skull is small but relatively broad, with a marked interorbital constriction. Rostral length is more than half braincase length, rostral width is approximately two-thirds or more zygomatic width, and interorbital width is less than half rostral width. Rostral height is more than half braincase height. The braincase is inflated, longer than wide, and broadest across the mastoids (at the level of the post-tympanic processes). Maximum zygomatic width is approximately equal to mastoid width.

Rostral width and length are approximately equal (Table 1), with lateral borders only slightly converging anteriorly. The anterior emargination of the nasals describes a broad and very deep arc between the maxillae. Rostral inflations are well defined, the supraorbital crests defining a triangular frontal depression. Anterior and posterior inflations appear confluent; an unpaired nasal foramen occurs in the trough separating left and right inflations. There is a deep frontal depression bound laterally by well-developed supraorbital crests; the latter extend from within the rostral inflations to meet the sagittal crest at a point well posterior to minimum interorbital width and in



**TEXT-FIG. 1.** *Brevipalatus mcculloughi* sp. nov., Bitesantennary Site, Riversleigh, north-western Queensland, Australia. Holotype, QMF22821, a skull with LM<sup>1-3</sup> and RP<sup>4</sup>-M<sup>3</sup>. A-B, dorsal view, stereopair. C, lateral view. D-E, ventral view, stereopair. F, oblique-occlusal view. All  $\times 4$ .

some specimens (e.g. QMF22832) level with the glenoid process. The zygomatic arch extends onto the face as a thin, slightly curved antorbital bar that often has a wing at its midpoint. The large, oval to circular infraorbital foramen is dorsal to M<sup>2-3</sup>.

In the lateral wall of the face, at the anterodorsal edge of the circumorbital rim and above the anterior attachment point of the antorbital bar, a large circular foramen opens. The latero-ventral fossa is deep and broad. At the most anteroventral point of the orbit is the postpalatal foramen.

The toothrows are only slightly convergent anteriorly. A deep, broad V-shaped indentation marks the palate's junction with the

premaxillae. The palate is very short: it extends from a point level with the posterior face of M<sup>1</sup> to approximately the M<sup>2</sup> metacone (in the holotype QMF22821, and in QMF22836, 22879); or from the midpoint of M<sup>1</sup> to the midpoint of M<sup>2</sup> in other specimens. Hard palate length is thus less than M<sup>1</sup> length (Tables 1-2). Maximum width of the palate occurs at M<sup>2-3</sup>. Palatal foramina are scattered and poorly developed.

The nasals are divided by a median septum that is bordered ventrally by the dorsal palate and dorsally by the nasals (anteriorly) and cribriform plate (posteriorly). Lateral development of the mesethmoid plates results in separation of the ventral respiratory

**TABLE 1.** Measurements (mm) of the holotype and paratypes of *Brevipalatus mcculloughi* sp. nov. from the early Miocene Bitesan-tennary Site, Riversleigh, north-western Queensland. Numbers in parentheses indicate estimates.

QMF	Holotype 22821	Paratype 22822	Paratype 22823	Paratype 22825	Paratype 22832	Paratype 22836	Paratype 22879	Paratype 30578	Paratype 41306
Greatest skull length	17.9	(16.2)	—	—	(16.2)	—	—	—	(16.0)
Rostrum length	6.5	(5.3)	—	(6.4)	5.8	5.6	(6.3)	—	(5.0)
Braincase length	11.4	10.9	—	—	(10.4)	—	—	—	11.0
Rostral width	7.0	6.2	6.5	6.4	6.3	7.0	7.0	—	6.4
Minimum interorbital width	3.0	2.5	2.7	2.5	2.8	2.7	3.4	—	2.7
Zygomatic width	9.4	9.4	9.0	9.2	(8.6)	9.4	(10.2)	—	9.4
Rostral height	5.7	4.9	4.5	4.9	4.6	4.8	5.5	—	5.0
Braincase height (max.)	8.2	(7.0)	—	—	—	—	—	—	7.9
Palate length	0.8	1.1	1.0	0.9	1.1	0.8	0.8	—	1.0
Palate width (base of M <sup>2</sup> )	3.5	3.3	2.9	3.0	2.9	3.3	(4.0)	—	—
Interperiotic distance	1.5	1.4	—	—	—	—	—	—	1.4
C <sup>1</sup> -M <sup>3</sup>	—	—	—	—	6.2	—	—	5.7	—
P <sup>4</sup> -M <sup>3</sup>	4.6	4.5	—	4.5	4.8	—	4.8	4.1	—
M <sup>1</sup> -M <sup>3</sup>	3.8	—	—	3.7	3.8	4.0	3.9	3.3	—
P <sup>4</sup> length	1.0	1.1	1.1	1.0	1.1	—	1.1	0.9	—
P <sup>4</sup> width	1.4	1.3	1.1	1.4	1.4	—	1.4	1.1	—
M <sup>1</sup> length	1.6	1.3	1.4	1.5	1.5	1.6	1.6	1.3	—
M <sup>1</sup> width	1.5	(1.6)	1.3	1.6	1.5	1.7	1.6	1.4	—
M <sup>2</sup> length	1.3	1.4	1.3	1.3	1.5	1.6	1.5	1.4	1.3
M <sup>2</sup> width	1.5	(1.5)	1.4	1.6	1.6	1.6	1.6	1.5	1.5
M <sup>3</sup> length	1.0	1.0	—	1.1	1.1	1.2	1.1	0.9	—
M <sup>3</sup> width	1.4	1.4	—	1.4	1.5	1.5	1.5	—	—

**TABLE 2.** Measurements (mm) of additional specimens referred to *Brevipalatus mcculloughi* sp. nov. Numbers in parentheses indicate estimates.

QMF	22849	22851	22852	22889	22895	22897	22905
Rostrum width	—	—	6.5	6.1	6.2	6.4	6.6
Minimum interorbital width	2.5	—	2.4	—	2.8	—	2.7
Zygomatic width	—	—	9.0	—	—	—	—
Palate length	0.9	0.9	0.9	0.9	1.0	1.0	0.8
Palate width (base of M <sup>2</sup> )	—	(3.0)	—	2.8	—	3.0	—
P <sup>4</sup> -M <sup>3</sup>	—	4.5	—	4.4	—	—	4.6
M <sup>1</sup> -M <sup>3</sup>	3.7	3.6	—	3.5	3.6	3.6	3.6
P <sup>4</sup> length	—	1.0	—	1.0	—	—	1.1
P <sup>4</sup> width	—	1.3	—	1.2	—	—	1.4
M <sup>1</sup> length	1.6	1.4	—	1.4	1.4	1.4	1.4
M <sup>1</sup> width	1.4	1.6	—	1.5	1.6	1.4	1.6
M <sup>2</sup> length	1.4	1.4	1.5	1.3	1.4	1.3	1.4
M <sup>2</sup> width	1.5	1.6	1.6	1.6	1.6	1.5	1.7
M <sup>3</sup> length	1.0	0.9	—	0.9	0.9	1.0	1.0
M <sup>3</sup> width	1.4	1.5	—	1.5	1.5	1.4	1.5

passages from dorsal and lateral olfactory chambers. The median septum is only slightly swollen throughout its length; it carries a duct that exits beyond the posterior extent of the vomer. The vomer does not extend posteriorly beyond the palate.

Between the orbital fossae, the braincase narrows markedly. The point at which the two supraorbital crests unite (i.e. where

the sagittal crest originates) is well posterior to the point of narrowest constriction. The palatines and pterygoids are normally developed. The sphenoidal bridge is broad anteriorly, slightly constricted posteriorly. In ventral view, the sphenorbital fissure, which is long and oval, is exposed posteriorly and is separated from the relatively small optic foramen by a narrow

bony splint. Pterygoid processes occur approximately midway along the sphenorbital bridge. These processes have a long secondary flange directed posteroventrally.

Immediately anterolateral to the sphenorbital fissure is a relatively large foramen that drains the anterior transverse sinus. Posterodorsal to the postpalatal foramen is the small sphenopalatine that leads into the posteroventral part of the nasal cavity. Posterodorsally and medially, several small foramina open into a long, curved, shallow groove that leads posterodorsally from the postpalatal foramen to the optic foramen. Dorsally and medially again is a deeper, shorter, anteroposteriorly directed sinus into which a number of foramina also open at the level of, or just posterior to, the cribriform plate of the ethmoid. These foramina vary in number, form and position. The mesopterygoid roof is grooved but is very short and, in ventral view, dips steeply anteriorly. The hard palate is so short that the dorsal nasal cavities anterior to the mesopterygoid roof are visible in ventral view.

The zygoma (e.g. in QMF22832, 41306) has a very tall projection that occupies approximately half its length. The ventral margin of the zygomatic arch is only slightly arched and lies dorsal to the tooth row. Posteriorly, the dorsal margin rises nearly vertically to form the projection, which rises to the level of the dorsal edge of the lacrimal foramen. Its maximum height occurs dorsal to the glenoid surface. Its apex is rounded, converging slightly towards the skull, and its posterior margin is convex and vertical to backward-sloping. A masseteric scar occurs on the anterolateral ventral surface of the arch. The zygomatic arches gradually diverge posteriorly slightly.

The braincase is oval in shape in dorsal view. It is widest at the level of the post-tympanic processes, narrowest in the interorbital area, and highest dorsal and posterior to the postglenoid processes. The lambdoidal crest is weakly developed. The relatively low sagittal crest extends from the supraorbital ridges to the parietal region. Approximately two-thirds along the length of the braincase, within the parietals, is the posterior transverse sinus, along which several small orifices open extracranially.

The glenoid surface is anterodorsally posteroventrally inclined, only slightly concave and approximately circular. The postglenoid process is low, its anterior face slightly anteriorly recurved. The postglenoid foramen is elongate and opens immediately posteriorly to the postglenoid process. Posteromedial to the glenoid surface, the foramen ovale opens in the alisphenoid. It is slightly elongate and, in area, it is less than one-quarter that of the glenoid fossa.

Posterior to the glenoid region and immediately anterior to the mastoid region, the post-tympanic process of the squamosal is developed with a vertical process that forms a long, slim, ventromedially directed point. The posterolateral wall of the skull between this process and the paroccipital process shows a distinct, rounded indentation for the mastoid of the petiotic.

The basisphenoid is hexagonal though elongate in large specimens. The anterior margin of the basicranial area is relatively wide, the sphenoidal bridge being only moderately constricted posterior to the second pterygoid flange. Faint, anteriorly convergent ridges extend from the sphenoidal bridge and define the shallow basisphenoid fossa. The lateral edges of the basisphenoid–basioccipital complex are biconcave curves. There is no lateral extension of the basisphenoid into the cavity for the

petiotic. Minimum basioccipital width is narrow relative to cavity width. The petrosals (e.g. QMF22822) are moderately enlarged (in width approximately twice the shortest distance between them).

The most posterior point of the skull is the junction of the interparietal and supraoccipitals, which is marked by a poorly developed lambdoidal ridge. The latter parallels the dorsal edge of the foramen magnum, terminating anteriorly in the region dorsal to the paroccipital process. A supramastoid foramen opens on the occipital surface dorsal to the ventral condyloid fossa. In ventral view, the posterior skull contour of the supraoccipital at the level of the lambdoidal ridge is rounded. The dorsal edge of the posteroventrally directed foramen magnum is rounded and unthickened. The foramen magnum is oval, being slightly wider than deep. Between the occipital condyle and paroccipital process is a deep condyloid fossa. The paroccipital process is well developed with a bifurcated tip. The condyle projects most strongly ventrally at the posterior extremity, its thickened lip partially concealing the condyloid foramen in the anterolateral face.

The upper dental formula of *Brevipalatus mcculloughi* is  $I^{21} C^1 P^{2,4} M^{1-3}$ . The premaxillae and upper incisors are unknown.  $C^1$  (e.g. in QMF22832, 30578, 22822) is a relatively narrow tooth (conspicuously less than the width of  $M^1$ ) with a distinct posterior accessory cusp. Its lingual and posterobuccal cingulum is uniformly low and shallow. It is taller but still shallow anterobuccally (but not developed into an anterior cusp) and appears to have been continuous buccally.  $P^2$  is a very small, low-crowned and extruded from the toothrow so that  $C^1$  and  $P^4$  are in contact.  $P^4$  is wider than long, and narrower and shorter than  $M^1$ ; it has a pronounced anterolingual cusp but only poorly developed anterobuccal cusp. The cingulum is virtually continuous except in the extreme posterobuccal corner at the end of the posterobuccally directed crest from the main cusp.  $M^1$  has four roots and  $M^2$  has three. In  $M^1$  and  $M^2$  the protofossa is open. The  $M^1$  postprotocrista makes a dihedral angle to form a crest that reaches the posterolingual cingulum. The  $M^2$  postprotocrista is directed posterobuccally and almost closes the protofossa; there is no clear dihedral angle in this crest. The  $M^1$  heel is posterolingually directed and is much better developed than in  $M^2$ . If present, the  $M^2$  heel is short and posteriorly (not posterolingually) directed.  $M^3$  is reduced in length and width, but has a distinct postmetacrista; the premetacrista is half to three-quarters paracrista length.

Dentaries of this species have not been positively identified from among the hundreds recovered from the Bitesantennary deposit. Several hipposiderid taxa of similar size (identified on the basis of cranial material) are represented in the same deposit. All dentaries examined have a low ascending ramus.

Measurements of the holotype and paratypes, and referred specimens, of *Brevipalatus mcculloughi* are given in Tables 1 and 2, respectively. With a skull length of 16–18 mm, *B. mcculloughi* was probably similar in size to the living Australasian hipposiderids *Hipposideros cervinus* and *H. galeritus*. Forearm length appears to have been 45–50 mm, with at least two other taxa possibly also represented by complete but dissociated radii in this size range in the Bitesantennary deposit.

*Comparisons.* *Brevipalatus mcculloughi* shares with all hipposiderids a number of characteristic cranial and dental

features, including: premaxilla not fused to maxilla; rostrum and braincase separated by a marked interorbital constriction; rostrum conspicuously inflated; supraorbital crests present; elongated braincase; petrosals enlarged such that the diameter of the cavities for the periotics is twice to six times the minimum distance between them; retention of, at most, two upper premolars, with  $P^2$ , if present, greatly reduced and displaced buccally;  $M^3$  at least moderately reduced, usually in length if not width.

Additionally, *Brevipalatus mcculloughi* exhibits a number of features commonly (but not always) found in hipposiderids, including:  $C^1$  with posterior accessory cusp; an elongated infraorbital foramen with slim antorbital bar; well-developed supraorbital crests defining a depression between nasal inflations and merging with a sagittal crest; a tall projection on the zygoma; the sphenorbital fissure separated from the optic foramen by a splint of bone; sphenorbital bridge moderately constricted posteriorly.

However, in its possession of an extremely short, hard palate (which is equal to or less than  $M^1$  length) the new species from Riversleigh differs strikingly from all other hipposiderids for which the palate is known. This includes extant and extinct species of *Archerops*, *Asellia*, *Aselliscus*, *Brachipposideros*, *Cloeotis*, *Coelops*, *Hipposideros*, *Palaeophyllophora*, *Paracoelops*, *Pseudorhinolophus*, *Rhinonycteris*, *Riversleigha*, *Syndesmotis*, *Triaenops* and *Vaylatsia* (> 80 species). The length of the hard palate does vary between hipposiderid genera (e.g. it is relatively longer in *Asellia* and *Pseudorhinolophus* than in *Cloeotis* and *Antrops*) and within the paraphyletic genus *Hipposideros* (e.g. relatively longer in the 'ater group' than in the 'cyclops group'; see Hand and Kirsch 1998), but in all cases it significantly exceeds that found in *B. mcculloughi*.

Among hipposiderids, only *Xenorhinos halli* Hand, 1998a has a palate length similar to that of the new Riversleigh species. Recovered from the same Bitesantennary Site deposit, *X. halli* has a palate length equivalent to 1–1.5 upper molar lengths. However, it differs strikingly from *Brevipalatus mcculloughi* (and all other hipposiderids) in its very broad rostrum (mean 9.5 mm), exceptionally broad interorbital region (mean 4.45 mm), and more voluminous and less completely divided nasal cavities. Its much larger size (mean 23.75 mm) and markedly constricted sphenorbital bridge additionally clearly distinguish *X. halli* from the new Bitesantennary species.

The only other bats with comparably short palates are species of the family Nycteridae, once referred to the same superfamily Rhinolophoidea but now interpreted on the basis of molecular evidence (Hulva and Horacek 2002; Teeling *et al.* 2002) to be only distantly related to that group. All nycteridids (some 20 species living in Africa and Asia) have extremely short hard palates. However, nycteridids (or slit-faced bats) differ from *Brevipalatus mcculloughi* in possessing a large, concave frontal

shield that dominates the facial part of skull and departs markedly from the inflated rostrum characterizing hipposiderids.

*Remarks.* It is possible that more than one species of *Brevipalatus* is represented in the Bitesantennary sample. At least three specimens (QMF22821, 22836, 22879) have a shorter palate (posterior face of  $M^1$  to  $M^2$  midline), lack nasal and postpalatal spines, have more pronounced rostral inflations and deeper frontal depression, more pronounced and shorter supraorbital crests (e.g. compare QMF22821 and 22832), and have a slightly wider  $P^4$  than the majority of specimens. They also appear to be larger (e.g. rostral width) than other specimens (Tables 1–2). Large and small specimens show the same (variable) degree of tooth wear suggesting size is not (purely) age-related. However, one specimen of *Brevipalatus* (QMF22905) displays a mixture of features from both morphotypes (e.g. postpalatal spine, but short palate and wide  $P^4$ ), suggesting a single species is represented. The differences observed in the sample are thus interpreted to represent intraspecific variation.

## PHYLOGENETIC RELATIONSHIPS

The phylogenetic relationships of bats in the family Hipposideridae have been examined most recently by Bogdanowicz and Owen (1998) and Hand and Kirsch (1998). Neither cladistic study was able fully to resolve the interrelationships between genera and species groups but each found that: (1) the family is probably monophyletic; (2) the speciose and widespread genus *Hipposideros* is probably paraphyletic; and (3) the composition of previously proposed divisions within *Hipposideros* needs re-examination. The analysis by Hand and Kirsch (1998) included fossil as well as modern taxa. Employing 59 cranial, dental and skeletal discrete characters and 37 taxa, it identified a basal group of largely endemic, autapomorphically specialized African, Australian and Eurasian taxa (including species of *Brachipposideros*, *Rhinonycteris*, *Cloeotis*, *Coelops* and possibly *Xenorhinos*, *Riversleigha* and *Triaenops*) which appears to lie outside the large and relatively more derived crown group (consisting of species of *Hipposideros*, *Asellia*, *Pseudorhinolophus* and *Palaeophyllophora*).

*Brevipalatus mcculloughi* lacks apparent apomorphies of crown group hipposiderids (e.g.  $C^1$  accessory cusp low or absent, infraorbital foramen elongate, mesopterygoid roof without groove,  $P^4$  small, ascending ramus tall and, in various subgroups, enlarged petrosals, loss of  $P^2$  and further reduction of  $M^3$ ; Hand and Kirsch 1998). Australian Tertiary representatives of this crown group include Riversleigh's Miocene *Hipposideros bernardsigei*

Hand, 1997c (with its greatly enlarged petrosals) and the Pliocene *H. winsburyorum* Hand and Godthelp, 1999 (lacking P<sup>2</sup> and with M<sup>3</sup> reduced in both width and length).

*Brevipalatus mcculloughi* appears instead to be part of a basal hipposiderid group to which most of Riversleigh's bats belong. Within this group, it shares most features with *Brachipposideros*–*Rhinonycteris* species, lacking the apomorphies exhibited by the *Coelops*–*Cloeotis*–*Archerops* clade (narrow rostrum, tall anterior accessory on C<sup>1</sup>), *Aselliscus* (incompletely separated optic foramen and sphenorbital fissure), *Xenorhinos halli* (broad interorbital region, constricted basisphenoid), or *Riversleigha williamsi* (long interorbital region, enlarged teeth, well-developed sagittal and lambdoidal crests) (Hand 1997a, b, 1998a, b; Hand and Kirsch 1998, 2003).

Legendre (1982), Sigé *et al.* (1982) and Hand and Kirsch (1998) give reasons for interpreting *Brachipposideros* and *Rhinonycteris* as sister groups. Among hipposiderids, a unique combination of dental characters is shared by species of *Brachipposideros* and *Rhinonycteris* (Sigé *et al.* 1982): small size; C<sup>1</sup> with posterior secondary cusp; P<sup>2</sup> between C<sup>1</sup> and P<sup>4</sup> near or on the buccal margin of the tooth row; P<sup>4</sup> slender with respect to other teeth; M<sup>1</sup> with four roots (loss in some), M<sup>2</sup> with three roots (advanced forms have four); heel of M<sup>1</sup> separated from the protocone by a notch (loss secondary) and forming a posteriorly directed lobe; M<sup>2</sup> heel relatively weakly developed and, primitively, the postprotocrista has a prominent anterior portion and only an incipiently developed posterior part. Cranial features characterizing species of *Brachipposideros* and *Rhinonycteris* are given by (Hand 1993, 1997a). Synapomorphies for *Rhinonycteris* species appear to include an anteriorly vaulted braincase and low but conspicuously inflated rostrum, a round infraorbital foramen bordered by a curved anteorbital bar, a postpalatal spine, a narrow, scalloped mesopterygoid fossa, a poorly (posteriorly) constricted sphenorbital bridge with long (anteroposteriorly) pterygoid wings, and M<sup>2</sup> with four (rather than three) roots and postprotocrista with dihedral angle (Hand 1997a). *Brevipalatus mcculloughi* shares some of these apparent apomorphies (e.g. a round infraorbital foramen and postpalatal spine) but lacks others (e.g. an anteriorly vaulted braincase and elongated M<sup>2</sup> with fourth root) and cannot be placed comfortably in either existing genus.

Further, in its peculiar palate development (and probably its echolocation production and transmission; see below), *Brevipalatus mcculloughi* appears to be autapomorphically derived with respect to both *Brachipposideros* and *Rhinonycteris* species and is here regarded to represent a separate but closely related lineage. Here it is placed with *Brachipposideros* and *Rhinonycteris* species in the subtribe *Rhinonycterina*. Plesiomorphic *Brachipposideros*-like hipposiderids were widespread throughout the Old World tropics in the early to middle Tertiary. Hand

and Kirsch (1998) have suggested that because many evidently plesiomorphic hipposiderid taxa (e.g. species of *Aselliscus*, *Rhinonycteris*, *Brachipposideros*, *Riversleigha*, *Xenorhinos*) occur in the Australian region, the early radiation of the family could have occurred there. By the middle Eocene relatively derived hipposiderids (e.g. species of *Pseudorhinolophus* and *Palaeophyllophora*) were present in European fossil deposits.

## DISCUSSION

### *Riversleigh hipposiderid diversity and palaeohabitat*

Riversleigh's Tertiary freshwater limestone sediments, which span (with gaps) the period from 25 to 4 Ma, have produced the remains of at least 22 hipposiderid species in eight genera: *Archerops*, *Brachipposideros*, *Brevipalatus*, *Hipposideros*, *Miophyllorhina*, *Rhinonycteris*, *Riversleigha* and *Xenorhinos* (Sigé *et al.* 1982; Hand 1993, 1997a–c, 1998a, b; Hand and Kirsch 2003). The latter six genera are as yet known only from Australia. *Brachipposideros* and *Hipposideros* have much broader distributions: *Brachipposideros* is represented by some ten species in Oligo-Miocene sediments of western Europe, Asia and northern Africa (Sigé 1968; Ziegler 1993; Sigé *et al.* 1994; Mein and Ginsburg 1997), and *Hipposideros* by at least 55 modern species throughout the Old World tropics and subtropics.

At least six species of the *Brachipposideros*–*Rhinonycteris* group are represented in Riversleigh's Oligo-Miocene sediments and five in Pliocene sediments, including the oldest representatives of the extant *R. aurantius*. *Hipposideros* is represented by two species, and *Archerops*, *Brevipalatus*, *Miophyllorhina*, *Riversleigha* and *Xenorhinos* so far by single species. A possible species of the European genus *Vaylatsia* and at least two new hipposiderid genera appear to be also present in Riversleigh's Oligo-Miocene sediments.

Eight hipposiderid species, representing five genera, have been recovered from the Bitesantennary Site deposit: ?*Brachipposideros watsoni* Hand, 1997a, two *Brachipposideros* species (*B. sp. cf. B. ?nooraleebus* and *B. sp.*), *Brevipalatus mcculloughi*, *Rhinonycteris tedfordi* Hand, 1997a, *Riversleigha williamsi* Hand, 1998b, *Xenorhinos halli* Hand, 1998a and a new species of *Rhinonycteris* (Hand and Godthelp submitted). The nature of the Bitesantennary deposit suggests that the eight hipposiderids (and a megadermatid) were syntopic species sharing a cave roost. The deposit covers an area of approximately 150 m<sup>2</sup> and is cut into an older, relatively unfossiliferous Tertiary limestone that forms the eroded walls of the cave and part of the fallen roof. Contact between the cave fill and the older wall has been identified at several points around its perimeter. A travertine floor, including a large stalagmite, forms the base of the 0.75-m-deep deposit.

The cave-fill sampled is uniformly fossiliferous (and bat-rich) with no indication of a hiatus in deposition. Other vertebrate taxa in the Bitesantennary deposit, including the dasyurid *Barinya wangala* Wroe, 1999 and kangaroo *Ganguroo bilamina* Cooke, 1997 co-occur with *Rhinonycteris tedfordi* in other early Miocene Riversleigh sites such as Upper Site (Archer *et al.* 1994), while *Brachiposideros nooraleebus* (to which one of the Bitesantennary taxa may be referable) occurs in Microsite, another Riversleigh deposit interpreted to be early Miocene in age (Sigé *et al.* 1982).

In Europe from the middle Eocene to the Miocene, hipposiderids were the most diverse and numerous of cave-dwelling bats, with commonly five species occurring together in some deposits (Remy *et al.* 1987). Five to six hipposiderid species coexist today in rainforested limestone areas of south-eastern Asia and New Guinea (e.g. Payne *et al.* 1985; Heller and Helversen 1989; Flannery 1995). These fossil and modern faunas also include many other bat species (e.g. the closely related rhinolophids, as well as emballonurids, nycteridids and pteropodids) that are not represented in Riversleigh's Oligo-Miocene deposits. For example, in the modern rainforests of western Malaysia, 12 syntopic species of hipposiderids and rhinolophids occur (Heller and Helversen 1989; Francis 1990). It is not until the Pliocene that Riversleigh's cave bat faunas gain a 'modern' appearance with hipposiderids comprising fewer than half the taxa, and emballonurids and vespertilionids (but still no rhinolophids) making up the rest (Archer *et al.* 1994; Hand 1999).

By analogy with modern bat communities, the diversity and abundance of hipposiderids in the Bitesantennary deposit suggest that the cave microhabitat was warm and humid. Living hipposiderids do not hibernate and depend on precise and stable roost microclimates for their survival (Kunz 1982). In Australia, availability of suitable roost sites appears to be the limiting factor in restricting their distribution today to the tropics (Strahan 1995; Churchill 1998). The closest living relative of the Miocene *Brevipalatus*, *Brachiposideros* and *Rhinonycteris* species is northern Australia's *R. aurantius* (Sigé *et al.* 1982; Hand and Kirsch 1998), an endangered hipposiderid that is dependent, particularly during the dry season, on caves and mines with hot and humid roost sites (28–30°C and 96–100 per cent humidity; Churchill 1998).

The broader Riversleigh palaeoenvironment is interpreted to have been cooler lowland rainforest (Archer *et al.* 1995). In the early Miocene, Australia lay approximately 8 degrees to the south of its present position such that the latitude of the Riversleigh area was probably around 27°S (Veevers 1984, fig. 24) and in the subtropics rather than tropics. The suite of early Miocene Riversleigh frogs suggests, based on the ecological requirements of closely related living species, that the climate was

relatively cool and wet, without seasonal aridity or temperatures exceeding 20–25°C for long periods (M. Tyler, pers. comm. 1997, in Archer *et al.* 1997). Drying since the beginning of the late Miocene has resulted in the replacement of rainforests by open forest and savannah woodlands over much of northern Australia and a marked drop in faunal diversity (McGowran *et al.* 2000).

#### *Ecomorphology and resource partitioning*

The eight Bitesantennary hipposiderids range in size from large (e.g. *Riversleigha*, forearm length 70 mm) to tiny (e.g. *Brachiposideros* sp., estimated forearm 25 mm), with a number of species appearing to overlap in skull length/forearm length (e.g. *Brevipalatus mcculloughi*, ?*Brachiposideros watsoni* and *Rhinonycteris tedfordi*, forearms 45–50 mm). The large *Riversleigha williamsi*, with its very robust, crested skull, was probably capable of eating relatively durophagous prey, such as armoured beetles (Hand 1998b), as well as the more typical hipposiderid diet of moths, other beetles, flies, termites, cicadas, hemipterans and cockroaches (Fenton 1984; Findley 1993). The species of *Brachiposideros*, *Brevipalatus*, *Rhinonycteris* and *Xenorhinos* exhibit a more gracile dentition that is probably plesiomorphic for hipposiderids (Hand 1998a). Dental differences distinguishing taxa within this latter group include size, P<sup>4</sup> width, M<sup>2</sup> length and heel development, and degree of M<sup>3</sup> reduction.

Heller and Helversen (1989) examined resource partitioning in a community of 12 species of hipposiderids and rhinolophids hunting in the same place in the rainforest of western Malaysia. Hipposiderid and rhinolophid bats emit their echolocation calls through their noses and have a characteristic call pattern (a constant frequency with terminal FM downsweep) that is specialized for short-range hunting of fluttering insects in relatively cluttered environments, i.e. in and around vegetation. These bats use Doppler shift to calculate their speed relative to objects around them and to detect and identify prey. Call frequencies are distinctly different between species, and there is an inverse relationship between body size and frequency, with small species typically using very high-frequency calls (short wavelengths being needed to detect very small prey) and large species using lower frequencies (in that study the range for the six hipposiderids was 58–200 kHz with forearm lengths of 35–91 mm).

Heller and Helversen (1989) also found, however, that the distribution of call frequencies was far more even than could be expected from the body sizes alone, with avoidance of call frequencies that were very similar. They suggested that this was a consequence of resource partitioning possibly with respect to prey size, but also perhaps for recognition of conspecifics, with slight



differences in call frequency being detected between sexes and individuals. Riversleigh's *Brevipalatus mcculloughi* is very similar in size and dental morphology to species of *Brachipposideros* and *Rhinycteris* in the Bitesantennary deposit, but its short palate and short dorsal nasal cavity are strikingly different. In Old World nasal-emitting bats, such as rhinolophids and hipposiderids, there is a fixed relationship between the length of the nasal cavity and the frequency of the standing wave of the second harmonic, the part of the emission typically emphasized by hipposiderids in their constant frequency calls (Pedersen 2000). In *Brevipalatus mcculloughi*, the palate and nasal cavities are shorter than in any other hipposiderid, which suggests that *Brevipalatus* used an echolocation call of shorter wavelength and therefore higher frequency than might otherwise be expected in a hipposiderid of similar size. In this way, its distinctive palatal morphology could be indicative of further spatial resource partitioning in a hipposiderid-rich bat community.

In nycteridids, which appear to have convergently developed an extremely short bony palate, greater relative soft palate involvement in acoustic processing produces additional harmonics, with greater intensity in low harmonics and shortening of the pulse length (I. Horacek, pers. comm. 2003). These bats specialize in sallying from perches to glean sedentary prey rather than aerial hawking. However, nycteridid rostral design (with a large, concave frontal shield dominating the facial part of the skull) is quite different from that of hipposiderids and to what extent extrapolation of form/function interpretations can be made between the two apparently distantly related families remains unclear.

Echolocation-call design in bats has been found to be compatible with wing morphology (e.g. Aldridge and Rautenbach 1987), and flight morphology and echolocation-call design are good predictors of habitat use, including within Australia (e.g. McKenzie and Rolfe 1986; Crome and Richards 1988). Aldridge and Rautenbach (1987) found significant correlations between echolocation calls that are resistant to clutter (such as the CF/FM calls used by hipposiderid bats) and morphological traits that improve manoeuvrability (low wing loading and aspect ratio, i.e. short, broad wings). Direct measures of aspect ratio and wing loading are not available for the Bitesantennary hipposiderids because, although their postcranial remains are abundant in the Riversleigh deposits, they are not typically associated with individual skulls. In lieu of this, body size data, information retrieved from near-complete skulls and phylogenetic relationships have been used to estimate habitat use for Riversleigh bats. For example, Hand (1997c) speculated that the Miocene *Hipposideros bernardsigei* from Riversleigh's Neville's Garden Site may have been a foliage gleaner on the basis of its small size, markedly enlarged cochleae (indicative of

highly specialized clutter-foraging) and close phylogenetic relationship to foliage gleaners in the New Guinea-centred *H. muscinus* group. In the case of *Brevipalatus mcculloughi*, its gracile dentition, broad and inflated rostrum, only moderately expanded cochleae and close phylogenetic relationship to *Rhinycteris aurantius* suggests that, like *R. aurantius* (see Churchill 1998), it may have been an aerial insectivore that predominantly ate moths.

#### *Trophic roles and community structure*

In most modern bat communities, small aerial insectivores form a core within which many species resemble one another closely in diet, foraging mode, echolocation-call characteristics and morphology, with other taxa occupying more divergent trophic categories (see Findley 1993, chapter 4 for a review). Core species are typically morphologically invariable (intraspecifically) and taxonomically similar, and divergent species more variable in morphology, diet and taxonomy (Findley and Black 1983). In regions of high bat diversity (i.e. the tropics and/or rainforests), the number of species within the core group is greatest, but the number of more divergent taxa also increases. Within the Bitesantennary community there appears to be a core of five or six *Brachipposideros*, *Rhinycteris* and *Brevipalatus* species that are very similar to each other in size, dental morphology and taxonomy, which were probably predominantly aerial insectivores like the living *R. aurantius*. More divergent are the larger *Riversleigha williamsi* and *Xenorhinos halli*, which, although similar to each other in skull length, are very different in skull morphology, dentition and, Hand (1998a, b) has argued, echolocation call and feeding behaviour. *Riversleigha* probably included more beetles in its diet than the core aerial insectivore group; the likely diet of *Xenorhinos* remains unclear. Most divergent, trophically and taxonomically, is the megadermatid *Macroderma* sp. cf. *M. godt-helpi*. Although it is only slightly larger than *Riversleigha* (forearm 80 mm), its dentition indicates that, like other megadermatids, it was a facultative carnivore (Hand 1985).

Other members of this early Miocene bat community probably included the molossid *Mormopterus (Hydromops) riversleighensis*, the mystacinids *Icarops aenae* and *I. paradox*, and the vespertilionid *Leuconoe* sp. (Hand *et al.* 1997, 1998; Menu *et al.* 2002). These taxa have been described from early Miocene Riversleigh sites interpreted to be lacustrine, fissure-fill or mixed cave deposits that are located within a 2-km radius of Bitesantennary Site and Microsite (i.e. Upper, Wayne's Wok, Neville's Garden and RV Sites, respectively; Archer *et al.* 1994). They represent additional, divergent ecomorphologies not otherwise represented in the Bitesantennary community: living species of *Mormopterus* are fast-flying, open-air aerial insectivores that

forage in clearings and above the canopy; *Leuconoe* species are insectivores/piscivores that hunt over water; and mystacinids are omnivores that feed on the wing, in tree branches and on the ground on nectar, flowers, fruit, and flying and terrestrial invertebrates. It is possible that all three genera were tree-dwelling bats: New Zealand's mystacinids and all living Australian molossids roost in trees, while *Leuconoe* species roost in both trees and caves.

Three additional hipposiderids have been recorded from early Miocene Riversleigh sites identified as mixed lacustrine and cave deposits, which occur within the same 2-km radius of Bitesantennary Site (Archer *et al.* 1994; Creaser 1997): *Miophyllorhina riversleighensis*, a small species (estimated forearm 30–40 mm) from RV Site (Hand 1997b); *Hipposideros bernardsigei*, a small species (est. forearm 44–50 mm) from Neville's Garden Site (Hand 1997c); and *?Xenorhinos* sp., a medium-sized species (est. forearm 50–55 mm) identified but not yet described from CS, RSO and Upper Sites (Hand 1998a). The absence of these three hipposiderids from the Bitesantennary deposit may reflect differences in roost site preference and/or cave microhabitat, rather than a significant difference in the time of accumulation of deposition, as Hand (1997c) has argued previously in the case of *H. bernardsigei*. All three taxa lie outside the Rhinonycterini tribe (and probably within the more derived hipposiderid crown group; Hand and Kirsch 1998), and are taxonomically and morphologically more divergent than the core group of *Brachhipposideros*, *Brevipalatus* and *Rhinonycteris* species.

Today, hipposiderid diversity is greatest in the tropics and rainforests, as is overall bat diversity. However, in its exceptionally high hipposiderid diversity (11 of 16 bat species recorded so far), Riversleigh's early Miocene bat community differs strikingly from modern northern Australian bat communities, where a maximum of four hipposiderids out of 35 bat species occurs in the Wet Tropics of north-eastern Australia (H. Spencer, pers. comm. 2003; G. Richards, pers. comm. 2003), and three of 19 species in the Riversleigh area (A. White, pers. comm. 2003). This high Miocene hipposiderid diversity does not appear to be an artefact of sampling. There is nothing to indicate that more than one period of deposition is represented at the Bitesantennary site (see above), nor to indicate a bias against forest-dwelling taxa, with over 200 species of fish, frogs, reptiles, birds, marsupials and monotremes recovered from Riversleigh's early Miocene lacustrine, cave and fissure-fill deposits (Archer *et al.* 1994). In northern Australia today (and in the Pliocene, Archer *et al.* 1994), more than half the bat species are vespertilionids, with various species feeding within cluttered vegetation, in open areas, in forest gaps, above water or above the canopy. In the Australian Miocene, except for the single *Leuconoe* species from Riversleigh's RV Site (interpreted to be a water-surface forager), no

vespertilionids are known and no rhinolophids. At that time and in that place, hipposiderids may have occupied more of these niches, or alternatively the habitat may have supported more hawking and gleaning specialists, such as hipposiderids, than it does today.

In its broader trophic structure, Riversleigh's early Miocene bat community may differ less from modern northern Australian bat faunas. Wilson (1973) defined seven trophic categories to which he allocated bats in order to estimate and compare trophic diversity or structure in and between modern bat communities. The trophic modes he defined were: carnivore, sanguinivore, piscivore, foliage gleaner, aerial insectivore, frugivore and nectarivore. Wilson's method continues to provide broad estimates of trophic activity in bat communities (e.g. Findley 1993), although the precise categories are sometimes modified to enable meaningful comparisons between data sets (e.g. Simmons and Voss 1998). In modern northern Australian faunas and Riversleigh's early Miocene bat community, six of Wilson's seven categories are represented (with only the sanguinivore niche unrepresented). In modern southern Australian faunas, the carnivore niche is also unfilled, and in Tasmanian faunas only the aerial insectivore and foliage gleaner categories are represented. Note that mystacinids are interpreted here to have at least partially occupied the frugivore and nectarivore categories in Oligo-Miocene Australian bat communities (also Hand *et al.* in press). Today, *Mystacina tuberculata* occupies these niches in New Zealand (see, e.g. Lloyd 2001), while diverse members of its superfamily, Noctilionoidea, do so in South America. In Australia today, the pteropodids (flying-foxes, fruit-bats and blossom-bats) fill that niche, with between two species (Riversleigh area) and six (Wet Tropics) occurring syntopically in northern Australia. Pteropodids are absent from the Australian Tertiary, the earliest records being late Pleistocene remains from late Quaternary archaeological deposits [e.g. White (Schrire) 1967; Archer and Brayshaw 1978; Aplin 1985, as cited in Attenbrow 1987].

The relative importance (proportion vs. presence or absence) of trophic categories or activities within a bat community is a more informative measure used to compare bat faunas from different geographical areas or regions (e.g. Simmons and Voss 1998), and potentially different times. For example, Wilson (1973) found that although aerial insectivory was the most important trophic mode for bats in all six zoogeographical regions identified, the relative importance in each region varied, from a high of 84 per cent of trophic activity in the Palearctic, to 48.4 per cent in the Australian Region and a low of 43.6 per cent in the Neotropics. Furthermore, Wilson found that foliage gleaning today is lower in the Australian Region (9.3%) than anywhere else. To what extent this trophic activity may have been different in the Australian Miocene is yet to be determined. The potential

of this comparative method to compare trophic structure between extinct and extant bat communities depends on the depositional periods and geographical areas being compared, adequate sampling of those faunas, and careful allocation to likely trophic mode for each species. For Riversleigh's early Miocene bat community, such data are potentially recoverable following further sampling of fossil sites and continuing ecomorphological studies.

## CONCLUSIONS

The high diversity of hipposiderids in Riversleigh's Miocene deposits appears to result from a combination of factors, including: (1) high hipposiderid diversity in the early and middle Tertiary Old World tropics and temperate regions; (2) the absence of closely related rhinolophids and low diversity of vespertilionids in northern Australia at that time; (3) the cave-dwelling habits of hipposiderids; (4) the high propensity for cave formation in Riversleigh's Tertiary limestones; (5) a local palaeoenvironment of cool, wet rainforest; and (6) few geographical or climatic barriers to hipposiderid dispersal in the palaeotropics of the early and middle Tertiary. Furthermore, the exceptional preservation of cranial material for most Riversleigh hipposiderids has facilitated description of taxa that may not have been recognized in other Old World Tertiary deposits on the basis of dental material alone. Combined, these factors have resulted in Australian Miocene hipposiderid faunas that are as speciose as any modern or fossil hipposiderid fauna, and generically more diverse.

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## REFERENCES

- ALDRIDGE, H. D. J. N. and RAUTENBACH, I. L. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. *Journal of Animal Ecology*, **56**, 763–778.

- ARCHER, M. and BRAYSHAW, H. 1978. Recent local faunas from excavations at Herveys Range, Kennedy, Jourama, and Mount Roundback, north-eastern Queensland. *Memoirs of the Queensland Museum*, **18**, 7.
- GODTHELP, H., HAND, S. J. and MEGIRIAN, D. 1989. Fossil mammals of Riversleigh, northwestern Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zoologist*, **25**, 29–65.
- HAND, S. J. and GODTHELP, H. 1994. *Riversleigh: the story of animals in the ancient rainforests of inland Australia*. Second edition. Reed Books, Sydney, 264 pp.
- — — 1995. Tertiary environmental and biotic change in Australia. 77–90. In VRBA, E. S., DENTON, G. H., PARTRIDGE, T. C. and BURCKLE, L. H. (eds). *Paleoclimate and evolution, with emphasis on human origins*. Yale University Press, New Haven, 547 pp.
- — — and CREASER, P. 1997. Correlation of the Cainozoic sediments of the Riversleigh World Heritage Fossil Property, Queensland, Australia. 131–152. In AGUILAR, J.-P., LEGENDRE, S. and MICHAUX, J. (eds). *Actes du Congrès Biochrome'97*. Mémoires et Travaux de l'EPHE, Institut de Montpellier, **21**, 818 pp.
- ATTENBROW, V. 1987. The Upper Mangrove Creek catchment. A study of quantitative changes in the archaeological record. Unpublished PhD thesis, University of Sydney, vol. 1, 422 pp. (text); vol. 2, 254 pp. (figs).
- BOGDANOWICZ, W. and OWEN, R. D. 1998. In the Minotaur's labyrinth: a phylogeny for the Hipposideridae. 27–42. In KUNZ, T. and RACEY, P. (eds). *Bats, biology and conservation*. Smithsonian Institution, Washington, 365 pp.
- CHURCHILL, S. 1998. *Australian bats*. Reed New Holland, Chatswood, 230 pp.
- COOKE, B. N. 1997. New Miocene bulungamayine kangaroos (Marsupialia: Potoroidae) from Riversleigh, northwestern Queensland. *Memoirs of the Queensland Museum*, **41**, 281–294.
- CREASER, P. 1997. Oligocene–Miocene sediments of Riversleigh: the potential significance of topography. *Memoirs of the Queensland Museum*, **41**, 303–314.
- CROME, F. H. J. and RICHARDS, G. C. 1988. Bats and gaps: microchiropteran community structure in a Queensland rainforest. *Ecology*, **69**, 1960–1969.
- DOBSON, G. E. 1875. Conspectus of the suborders, families and genera of Chiroptera arranged according to their natural affinities. *Annals and Magazine of Natural History*, **4**, 16, 345–357.
- DUNCAN, A., BAKER, G. B. and MONTGOMERY, N. (eds) 1999. *The action plan for Australian bats*. Natural Heritage Trust, Canberra, 104 pp.
- FENTON, M. B. 1984. Echolocation: implications for ecology and the evolution of bats. *Quarterly Review of Biology*, **59**, 33–53.
- FINDLEY, J. S. 1993. *Bats. A community perspective*. Cambridge University Press, Cambridge, 167 pp.
- and BLACK, H. 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. *Ecology*, **64**, 625–630.
- FLANNERY, T. F. 1995. *Mammals of New Guinea*. Revised edition. Reed Books, Chatswood, 568 pp.

- FRANCIS, C. M. 1990. Trophic structure of bat communities in the understorey of lowland dipterocarp rainforest in Malaysia. *Journal of Tropical Ecology*, **6**, 421–431.
- GRAY, J. E. 1866. A revision of the genera of Rhinolophidae, or horseshoe bats. *Proceedings of the Zoological Society, London*, **1866**, 81–83.
- HAND, S. J. 1985. New Miocene megadermatids (Megadermatidae, Chiroptera) from Australia, with comments on megadermatid phylogenetics. *Australian Mammalogy*, **8**, 5–43.
- 1993. First skull of a species of *Hipposideros* (*Brachhiposideros*) (Microchiroptera: Hipposideridae), from Australian Miocene sediments. *Memoirs of the Queensland Museum*, **31**, 179–192.
- 1997a. New Miocene leaf-nosed bats (Microchiroptera: Hipposideridae) from Riversleigh, Queensland. *Memoirs of the Queensland Museum*, **41**, 335–349.
- 1997b. *Miophyllorhina riversleighensis* n. gen. et sp., a new Miocene leaf-nosed bat (Microchiroptera: Hipposideridae) from Riversleigh, Queensland. *Memoirs of the Queensland Museum*, **41**, 351–354.
- 1997c. *Hipposideros bernardsigei*, a new hipposiderid (Microchiroptera) from the Miocene of Australia and a reconsideration of the monophyly of related species groups. *Münchner Geowissenschaftliche Abhandlungen A*, **34**, 73–92.
- 1998a. *Xenorhinos*, a new genus of Old World leaf-nosed bats (Microchiroptera: Hipposideridae) from the Australian Miocene. *Journal of Vertebrate Paleontology*, **18**, 430–439.
- 1998b. *Riversleigha williamsi* gen. et sp. nov., a large Miocene hipposiderid (Microchiroptera) from Riversleigh, Queensland. *Alcheringa*, **22**, 259–276.
- 1999. Australian fossil bat diversity and evolution. *Australian Mammalogy*, **21**, 34–45.
- ARCHER, M. and GODTHELP, H. 1997. First record of *Hydromops* (Microchiroptera: Molossidae) from Australia: its biocorrelative significance. 153–162. In AGUILAR, J.-P., LEGENDRE, S. and MICHAUX, J. (eds). *Actes du Congrès BiochroM'97*. Mémoires et Travaux de l'EPHE, Institut de Montpellier, **21**, 818 pp.
- — — in press. Australian Oligo-Miocene mystacinids (Microchiroptera): upper dentition, new taxa and divergence of New Zealand species. *Geobios*.
- and GODTHELP, H. 1999. First Australian Pliocene species of *Hipposideros* (Microchiroptera: Hipposideridae). *Records of the Western Australian Museum, Supplement*, **57**, 299–306.
- and KIRSCH, J. A. W. 1998. A southern origin for the Hipposideridae (Microchiroptera)? Evidence from the Australian fossil record. 72–90. In KUNZ, T. and RACEY, P. (eds). *Bats: biology and conservation*. Smithsonian Institution, Washington, 365 pp.
- — — 2003. *Archerops*, a new annectant hipposiderid genus (Mammalia: Microchiroptera) from the Australian Miocene. *Journal of Paleontology*, **77**, 943–955.
- MURRAY, P. F., MEGIRIAN, D., ARCHER, M. and GODTHELP, H. 1998. Mystacinid bats (Microchiroptera) from the Australian Tertiary. *Journal of Paleontology*, **72**, 538–545.
- NOVACEK, M., GODTHELP, H. and ARCHER, M. 1994. First Eocene bat from Australia. *Journal of Vertebrate Paleontology*, **14**, 375–381.
- HELLER, K. G. and HELVERSEN, O. V. 1989. Resource partitioning of sonar frequency bands in rhinolophid bats. *Oecologia*, **80**, 178–186.
- HULVA, P. and HORACEK, I. 2002. *Craseonycteris thonglongyai* (Chiroptera: Craseonycteridae) is a rhinolophoid: molecular evidence from cytochrome *b*. *Acta Chiropterologica*, **4**, 107–120.
- KUNZ, T. 1982. Roosting ecology. 1–56. In KUNZ, T. (ed.). *Ecology of bats*. Plenum Press, New York, 425 pp.
- LEGENDRE, S. 1982. Hipposideridae (Mammalia: Chiroptera) from the Mediterranean Middle and Late Neogene and evolution of the genera *Hipposideros* and *Asellia*. *Journal of Vertebrate Paleontology*, **2**, 386–399.
- LLOYD, B. 2001. Advances in New Zealand mammalogy 1990–2000: short-tailed bats. *Journal of the Royal Society of New Zealand*, **31**, 59–81.
- MCGOWRAN, B., ARCHER, M., BOCK, P., DARRAGH, T. A., GODTHELP, H., HAGEMAN, S., HAND, S. J., HILL, R., LI, Q., MAXWELL, P. A., MCNAMARA, K. J., MACPHAIL, M., MILDENHALL, D., PARTRIDGE, A. D., RICHARDSON, J., SHAFIK, S., TRUSWELL, E. M. and WARNE, M. 2000. Australasian palaeobiogeography: the Palaeogene and Neogene record. *Memoirs of the Association of Australasian Palaeontologists*, **23**, 405–470.
- MCKENZIE, N. L. and ROLFE, J. K. 1986. Structure of bat guilds in the Kimberley mangroves, Australia. *Journal of Animal Ecology*, **55**, 401–420.
- MEGIRIAN, D. 1992. Interpretation of the Miocene Carl Creek Limestone, northwestern Queensland. *Beagle*, **9**, 219–248.
- MEIN, P. and GINSBURG, L. 1997. Les mammifères du gisement miocène inférieur de Li Mae Long, Thaïlande: systématique, biostratigraphie et paléoenvironnement. *Geodiversitas*, **19**, 783–844.
- MENU, H., HAND, S. J. and SIGÉ, B. 2002. Oldest Australian vespertilionid (Microchiroptera) from the Miocene of Riversleigh. *Alcheringa*, **26**, 319–331.
- MILLER, G. S. 1907. The families and genera of bats. *United States National Museum, Bulletin*, **57**, 1–282.
- PAYNE, J., FRANCIS, C. M. and PHILLIPPS, K. 1985. A field guide to the mammals of Borneo. The Sabah Society with World Wildlife Fund Malaysia, Kuala Lumpur, 332 pp.
- PEDERSEN, S. C. 2000. Skull growth and the acoustical axis of the head in bats. 174–213. In ADAMS, R. A. and PEDERSEN, S. C. (eds). *Ontogeny, functional ecology and evolution of bats*. Cambridge University Press, Cambridge, 398 pp.
- REMY, J. A., CROCHET, J.-Y., SIGÉ, B., SUDRE, J., DE BONIS, L., VIANEY-LIAUD, M., GODINOT, M., HARTENBERGER, J.-L., LANG-BADRE, B. and COMTE, B. 1987. Biochronologie des phosphorites de Quercy: mise à jour des listes fauniques et nouveaux gisements de mammifères fossiles. *Münchner Geowissenschaftliche Abhandlungen A*, **10**, 169–188.
- REVILLIOD, P. 1917. Contribution à l'étude des chiroptères des terrains tertiaires, première partie. *Mémoires de la Société Paléontologique Suisse*, **43**, 1–58.

- 1920. Contribution à l'étude des chiroptères des terrains tertiaires, deuxième partie. *Mémoires de la Société Paléontologique Suisse*, **44**, 63–129.
- SIGÉ, B. 1968. Les chiroptères du Miocène inférieur de Bouzigues. I. Étude systématique. *Palaeovertebrata*, **1**, 65–133.
- HAND, S. J. and ARCHER, M. 1982. An Australian Miocene *Brachipposideros* (Mammalia, Chiroptera) related to Miocene representatives from France. *Palaeovertebrata*, **12**, 149–171.
- THOMAS, H., SEN, S., GHEERBRANDT, E., ROGER, J. and AL-SULAIMANI, Z. 1994. Les chiroptères de Taqah (Oligocène inférieur, Sultanat d'Oman). Premier inventaire systématique. *Münchner Geowissenschaftliche Abhandlungen A*, **26**, 35–48.
- SIMMONS, N. B. and VOSS, R. S. 1998. The mammals of Paracou, French Guiana: a neotropical lowland rainforest fauna. Part 1. Bats. *Bulletin of the American Museum of Natural History*, **237**, 219 pp.
- STRAHAN, R. (ed.). 1995. *The mammals of Australia*. Australian Museum and Reed Books, Sydney, 756 pp.
- TEELING, E. C., MADSEN, O., VAN DEN BUSSCHE, R. A., DE JONG, W. W., STANHOPE, M. J. and SPRINGER, M. S. 2002. Microbat paraphyly and the convergent evolution of a key innovation in Old World rhinolophid microbats. *Proceedings of the National Academy of Sciences*, **99**, 1431–1436.
- VEEVERS, J. J. 1984. *Phanerozoic Earth history of Australia*. Oxford University Press, Oxford, 418 pp.
- WHITE (SCHRIRE), C. 1967. Plateau and plain; prehistoric investigations in Arnhem Land, Northern Territory. Unpublished PhD thesis, Australian National University, Canberra, vol. 1, viii+510 pp.; vol. 2, viii+figs (unpaginated).
- WILSON, D. E. 1973. Bat faunas: a trophic comparison. *Systematic Zoology*, **22**, 14–29.
- WROE, S. 1999. The geologically oldest dasyurid, from the Miocene of Riversleigh, north-west Queensland. *Palaeontology*, **42**, 501–527.
- ZIEGLER, R. 1993. Die Chiroptera (Mammalia) aus dem Untermiozän von Wintershof-West bei Eichstätt (Bayern). *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie*, **33**, 119–154.