XENORHINOS, A NEW GENUS OF OLD WORLD LEAF-NOSED BATS (MICROCHIROPTERA: HIPPOSIDERIDAE) FROM THE AUSTRALIAN MIOCENE

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ABSTRACT—A new genus and species of hipposiderid is described from the Bitesantennary Site, Riversleigh, northwestern Queensland, Australia. *Xenorhinos halli*, gen. et sp. nov., differs from all other hipposiderids in, among other features, its broad rostrum and interorbital region, exceptionally short palate, constricted sphenoidal bridge, and pronounced rotation of the rostrum. Its precise phylogenetic relationships remain obscure, but it appears to be part of an early hipposiderid radiation that includes species of *Coelops, Cloeotis, Triaenops*, and *Rhinonycteris*, and that is widely distributed throughout the Old World tropics. From analogy with living hipposiderids, the peculiar rostral and palatal morphology of *X. halli* is probably correlated with ultrasound production and emission, and, less certainly, with size and structure of the noseleaf.

INTRODUCTION

Acetic acid-processing of Tertiary freshwater limestones from the Riversleigh World Heritage property, Lawn Hill National Park, northwestern Queensland, Australia, has produced a number of new late Oligocene of early Pliocene microchiropteran species (Archer et al., 1994). These bats include hipposiderids, megadermatids, molossids, vespertilionids, and emballonurids (Sigé et al., 1982; Hand, 1985, 1990, 1995, 1996, 1997a, b, in press). Hipposiderids are by far the most abundant and diverse chiropteran group represented.

Living hipposiderids, commonly known as Old World leafnosed bats, are mostly cave-dwelling. They are referred to 65 extant species (Koopman, 1994); the most speciose genus, *Hipposideros*, contains 53 species, with eight other genera (*Rhinonycteris*, *Coelops*, *Paracoelops*, *Triaenops*, *Cloeotis*, *Anthops*, *Asellia*, and *Aselliscus*) containing one to two species each. The family has an Old World tropical to subtropical modern distribution, and apparently similar fossil distribution. Tertiary hipposiderids are known from mainly karstic sediments, with the oldest representatives being from the middle Eocene of Europe, early Oligocene of Arabia, late Oligocene of Australia, early Miocene of Africa, and Pleistocene of Asia. Riversleigh's fossil hipposiderids are referable to the genera and subgenera *Rhinonycteris*, *Riversleigha*, *Hipposideros*, and *Brachipposideros* (Sigé et al., 1982; Hand, 1997a, b).

The new hipposiderid described here is represented by many hundreds of well-preserved skulls, dozens of which have been prepared. It is so far known only from Bitesantennary Site, a deposit interpreted to be of early Miocene age (Archer et al., 1994). This site was the first of the many deposits at Riversleigh to be interpreted as representing an ancient cave-fill (Hand et al., 1989). It contains at least eight other hipposiderid species, a megadermatid bat, many snails, and rarer marsupials, birds, reptiles, and frogs.

The new species differs strikingly from all other hipposiderids in, among other features, its broad rostrum and interorbital region, its exceptionally short palate, pronounced rostral rotation, and narrow sphenoidal bridge that completely exposes the optic foramen and sphenoidal fissure. Its many autapomorphies and probable phylogenetic relationships support its referral to a new genus.

Skull terminology follows Hand (1993, and Fig. 1); dental terminology follows Sigé et al. (1982). The prefix **QM F** refers to specimens held in the fossil collections of the Queensland

Museum, Brisbane. Stratigraphic nomenclature for the Riversleigh region follows Archer et al. (1994).

SYSTEMATIC PALEONTOLOGY

Suborder MICROCHIROPTERA Dobson, 1875 Superfamily RHINOLOPHOIDEA Bell, 1836 (Weber, 1928) Family HIPPOSIDERIDAE Miller, 1907

XENORHINOS, gen. nov.

Type and Only Species—*Xenorhinos halli*, gen. et sp. nov. (Figs. 1–2).

Age and Distribution—Early Miocene of northern Australia.

Diagnosis—The genus diagnosis is the same as that for the type species until additional species are known.

Etymology—The name refers to the strange and unique structure of the rostrum and palate.

XENORHINOS HALLI, sp. nov. Figures 1–2

Holotype—QM F22918, skull with left C1, P4–M3 and right P4–M3.

Paratypes—QM F22919, right dentary with m1–m3; QM F22920, left maxillary fragment with C1–M3; QM F22921, right maxillary fragment with C1–M3; QM F22922, left dentary with c1, p4–m3; QM F22923, left dentary with c1–m3; QM F22924, skull with left and right periotics in situ.

Diagnosis—Differing from all other hipposiderids in its broad rostrum and interorbital region, exceptionally short palate, constricted sphenoidal bridge, and pronounced rostral rotation.

Locality, Stratigraphic Position, and Age—The Bitesantennary Site occurs on the northeastern edge of the D Site Plateau, in the Riversleigh World Heritage property, Lawn Hill National Park, northwestern Queensland (Hand et al., 1989; Archer et al., 1994). The 150 square metre deposit is cut into an older, relatively non-fossiliferous limestone that may be contiguous with limestones underlying or containing three adjacent Oligo–Miocene fossil deposits: VIP, Burnt Offering, and Neville's Garden sites. On the basis of stratigraphy and contained local faunas, the latter have been interpreted to be part of Riversleigh's System B deposits and, as such, early Miocene in age (Archer et al. 1994; Hand, 1997a, b).

Etymology-The species is named for Dr. Leslie S. Hall of

the University of Queensland, Brisbane, in recognition of his pioneering work on all aspects of Australian chiropteran biology.

Associated Fauna and Taphonomy—The Bitesantennary deposit contains thousands of bat skulls, limb bones, and snails. Almost all are complete, suggesting fossilisation occurred at or very near the point of accumulation. The boundary or contact between the fossiliferous fill and remnants of the older, nonfossiliferous cave wall has been identified at several points around the perimeter of the deposit. For these reasons, the deposit is interpreted to be a cave-fill (Hand et al., 1989). The many snails of the deposit and what seem to be extensive algallike mats suggest that, for some period during its history, the depositional area was open to light and under water.

Xenorhinos halli is preserved in the deposit with at least eight other hipposiderids (Hand, 1997b) and a megadermatid. Less well represented in the Bitesantennary deposit are frogs, lizards, a boid, a stork, a swift, peramelids, a dasyurid, and a bulungamayine macropodid.

DESCRIPTION

Xenorhinos halli is known from many well-preserved skulls and dentaries. The description of the skull is based primarily on the holotype (QM F22918), but other referred specimens (list available through the author and/or Queensland Museum) provide additional material. As in the skull of *Brachipposideros* nooraleebus (Hand, 1993) from Riversleigh, it has not been possible to determine the precise limits of each bone of Xenorhinos halli due to fusion of elements during development (a common feature of microchiropteran bats). However, as a guide for interpreting the approximate boundaries between bones, several juvenile rhinolophoids were examined (i.e., specimens of *Hipposideros diadema*, *Rhinolophus megaphyllus*, and *Macroderma gigas*).

Skull

General Outline and Proportions—The skull is relatively long and broad, with little interorbital constriction. Rostral length is more than two-thirds braincase length, maximum rostral width is almost as great as mastoid width, and interorbital width is more than half rostral (and mastoid) width; rostral height is subequal to braincase height. The braincase is moderately inflated, as long as wide, and broadest across the mastoids (at the level of the posttympanic processes); maximum zygomatic width is subequal to mastoid width. In lateral view, rostral rotation (Pedersen, 1993, 1995) or flexure of the head on the basicranial axis (as defined by Freeman, 1984) is pronounced, i.e., greater than -25° .

Rostrum—The rostrum is slightly longer than wide; its lateral borders converge anteriorly. The anterior emargination of the nasals, which is marked by a broad median spine, describes a broad arc between the maxillae. Rostral inflations are poorly defined; an unpaired nasal foramen (for the noseleaf nerve) occurs in the shallow trough separating the inflations. A more pronounced depression, pierced by one or two foramina, occurs laterally at the junction of the ?nasal and maxilla (above the level of M1). Supraorbital ridges are poorly developed; they meet the sagittal crest relatively posteriorly (i.e., at a point almost level with the posterior roots of the zygoma). The zygomatic arch extends onto the face as an antorbital bar, which is roughly uniform in width but has a conspicuous 'wing' developed anterodorsally. The elongated infraorbital foramen occurs above M2-3; it is low on the face—level with the root of the anteroventrally directed alveolus of C1.

In the lateral wall of the face, at the anterodorsal edge of the circumorbital rim and under the anterior attachment point of the antorbital bar, a large dorsoventrally elongated foramen opens (?lacrimal foramen; Pedersen (1995) has found that the lacrimal bone does not develop in at least some living hipposiderids). A smaller, circular foramen opens posteroventrally to this. Medially, at the most anteroventral point of the orbit, is the postpalatal foramen.

Palate—The tooth rows are convergent anteriorly. The deep, V- to U-shaped indentation that marks the junction of the palate with the premaxillae extends posteriorly to the level of the metacone of M1. The midline of the palate extends posteriorly level with the posterior face of M2, resulting in a strikingly short palate, equal in length to 1-1.5 molar lengths. Two posterolateral indentations extend anteriorly to at least the level of the paracone of M3. Maximum width of the palate occurs at M3, and palatal foramina are well developed adjacent to the paracone of M3. Paired, anteroposteriorly elongated foramina occur adjacent to the anterior face of M1, close to the border between the premaxillae and palate.

Nasals-The inflated nasal cavities are incompletely divided by a median septum. The septum is fused with the anterior onethird of the dorsal palate, such that the left and right nasal passages are incompletely separated. Further, there is little lateral development of the mesethmoid plates so that the choanae or ventral respiratory passages are not separated by bone from the dorsal, olfactory chambers. Limited lateral development of the plates occurs well posterior to the posterior limit of the hard palate. These plates extend anteroventrally only for a short distance (to a point that is still posterior to the level of the hard palate), but extend dorsally to reach the roof of the nasal cavity and anterodorsally branch to almost fill the nasal cavity. In anterior view, an ethmoidal lattice partially divides each nasal cavity into an anterolateral maxillary chamber and a narrower median passage. In this view, a large, paired hook-like swelling, developed in the ethmoid lattice and protruding into the median passageway of each nasal cavity, is conspicuous. Posterodorsally, the median septum meets the anteriorly inclined cribriform plate. Ventrally, it extends further posteriorly and probably fuses with the vomer, which protrudes very conspicuously beyond the palate. The median septum is only slightly swollen throughout it length, suggesting that, as in other rhinolophoids, the vomeronasal organ was poorly developed. The septum carries a large duct that exits posteriorly at the posterior limit of the ?vomer. The cribriform plate is sparsely perforated dorsally but not perforated at all ventrally.

Interorbital and Pterygoid Region-Between the orbital fossae, the braincase narrows only moderately. The point at which the two supraorbital crests unite (i.e., where the sagittal crest originates) is clearly posterior to the point of narrowest constriction. The palatines and pterygoids are evidently extremely reduced such that the roof and side walls of the most posterior part of the nasal passage are poorly formed and the sphenoidal bridge is narrow, almost splint-like. In ventral view, the sphenorbital fissure, which is large and circular, is almost completely exposed. What are probably pterygoid processes occur at a point anterior to the cribriform plate, well anterior to the junction of the supraorbital ridges. These processes have a secondary flange directed posteroventrally. A narrow bony bridge separates the sphenorbital fissure from the large, almost semicircular optic foramen. A splint of bone separates the paired optic foramina. Anterodorsally, in most specimens, are closely paired fenestrae that lead into the nasal cavity. Immediately anterolateral to the sphenorbital fissure are two foramina that drain the anterior transverse sinus. In the lateral wall of the interorbital region, at the level of the pterygoid processes, is a large circular foramen (?sphenopalatine) that leads into the posteroventral part of the nasal cavity; anterior to this, the postpalatal foramen opens.

Zygomatic Arch—The zygoma has a tall projection that occupies approximately half its length. The ventral margin of the



zygomatic arch is only slightly arched and is dorsal to the tooth row. The dorsal margin rises nearly vertically to form the tall projection that rises to the level of the dorsal edge of the ?lacrimal foramen. Its maximum height is dorsal to the glenoid surface. Its apex is rounded, converging slightly towards the skull, and its posterior margin convex and vertical to backwardsloping. A masseteric scar occurs on the anterolateral ventral surface of the arch. In dorsal view, the junction between the zygomatic arch and antorbital bar is not greatly marked by a change in direction, the antorbital bars not diverging posteriorly much more than the zygomatic arches proper. The latter diverge only slightly posteriorly.

Cranial Vault—The braincase is rather square in shape. It is widest at the level of the posttympanic processes, narrowest in the interorbital area, and highest dorsal and posterior to the postglenoid processes. A sagittal crest is present but low, extending anteriorly to the supraorbital ridges and posteriorly to the lambdoidal crest; it is tallest in the parietal region. There is moderate development of the lambdoidal crests, which rise posteriorly to form a peak with the posterior extremity of the sagittal crest. Approximately two-thirds along the length of the braincase, within the parietals, is the posterior transverse sinus. It tracks laterally, then anterolaterally, before opening extracranially in the posterior part of the postglenoid foramen. Along the sinus several small foramina open to the exterior.

Glenoid—The glenoid surface is anterodorsally-posteroventrally inclined, only slightly concave, and wider than long. The postglenoid process is equal in height to almost half the length of the glenoid surface; its anterior face is 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.

Temporal Region-The posttympanic process of the squamosal is developed with a vertical process that forms a slim, posteromedially directed point. In lateral view, the posteroventral part of the lateral face of the periotic is exposed. In the otic region, the squamosal swells slightly laterally and circumscribes and indentation that would have accomodated the tympanic ring. The squamosal laterally and ?anterolaterally, the alisphenoid anteriorly, and the basisphenoid medially, contribute to the anterior edge of the cavity occupied by the periotic. At the anterolateral corner of the tympanic cavity, the pyriform fenestra forms a broad gap separating the posterior face of the glenoid from the anterolateral wall of the periotic. The posterolateral wall of the skull is deeply notched along an extent anterior to the post-tympanic process of the squamosal and posterior to the paroccipital process. This notch is filled by the mastoid of the periotic.

Basicranium—The diamond-shaped basisphenoid is slightly concave in its central region. Faint, anteriorly convergent ridges define the basisphenoid fossa (and probably mark the boundary between the alisphenoid and basisphenoid posteriorly). The anterior margin of the basicranial area is constricted. Where and how the presphenoid joins the vomer is not clear, but the junction is probably dorsal to the duct that runs through the septum (vomer). The periotic is bordered posteromedially by the basioccipital. Anteromedially, the periotic abuts the basisphenoid; there is no lateral extension of the basisphenoid nor medial extension of the petrosal.

Occipital—The most posterior point of the skull is posterior to the junction of the interparietal and supraoccipitals. In lateral view, the supraoccipital is not very convex posteriorly, but the exoccipitals nonetheless overhang the posteroventrally directed foramen magnum. The dorsal edge of the foramen magnum is rounded and not thickened. Lambdoidal crests form a distinct ridge marking the most dorsal junction of the interparietal and supraoccipitals. This parallels the dorsal edge of the foramen magnum, terminating anteriorly in the region dorsal and lateral to the paroccipital process. A supramastoid foramen opens on the occipital surface dorsal to the ventral condyloid fossa.

In ventral view, the contour of the supraoccipital at the level of the lambdoidal ridge is rounded. The foramen magnum is round, being approximately as deep as wide. Between the occipital condyle and paroccipital process is a deep condyloid fossa. The paroccipital process is well developed and forms the most lateral part of the occipital bone. The tip of the process articulates with the mastoid. The condyle projects most strongly ventrally at the posterior extremity, its thickened lip partially concealing the condyloid foramen in the anterolateral face.

Ear Region—The ectotympanics and auditory ossicles are missing. The anterior part of the middle ear cavity is unossified as a pyriform fenestra, a restricted opening between the periotic and the squamosal, and the most posterolateral part of the alisphenoid. There is moderate development of an epitympanic recess and ectotympanic groove. Posteriorly, the large jugular foramen and the more medial, narrow basicochlear fissure coalesce. In the periotic, the cochlear labyrinth is only just visible through the bone of the promontorium. Three turns of the labyrinth can be seen in section. The mastoid wall is relatively thick but through it can be seen the three semicircular canals. The petrosal is slightly enlarged, its width being 2.5 to 3 times the minimum basioccipital width.

Dentition

The dental formula of *Xenorhinos halli* is I ?1/2 C1/1 P2/2 M3/3.

Upper Dentition—The premaxillae and upper incisors are unknown. C1 is tall, slender, and anteroposteriorly short, with a tall posterior accessory cusp and well-developed buccal cingulum. P2 is positioned in the tooth row such that C1 and P4 are not in contact. P4 is approximately as long as wide, and conspicuously smaller (although taller) than M1. On P4, the anterior and lingual cingulum are sometimes continuous with a pronounced anterolingual cusp. In other specimens, the welldeveloped anterolingual cusp terminates the anterior cingulum, so that the lingual cingulum arises on the cusp as a crest linking the apex of the cusp to the main cusp (?paracone). On M1 and M2, the protofossa is open, and the postprotocrista makes an obtuse angle to form a crest that reaches the lingual cingulum.

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FIGURE 1. Xenorhinos halli, sp. nov., Bitesantennary Site, Riversleigh, northwestern Queensland. Holotype, QM F22918, skull with right left P4-M3 and left C1, P4-M3; lateral, dorsal and ventral views. Paratype, QM F22919, right jaw with m1-3; lateral view (reversed). Drawings by Jeanette Muirhead. Bar indicates 5 mm. Abbreviations: AB anteorbital bar, ABW anteorbital bar wing, AP angular process, BO basioccipital, BS basisphenoid, C1 upper canine, CF condyloid foramen, CFO condyloid fossa, CON condyle, COR coronoid, FM foramen magnum, FNL foramen for noseleaf nerve, FO foramen ovale, FOR foramen, G glenoid, IF infraorbital foramen, LR lambdoidal ridge, LVF lateroventral fossa, M1 first upper molar, M3 third upper molar, MF mental foramen, MFO mandibular fossa, NS nasal spine, OC occipital condyle, OF optic foramen, P2A alveolus for second upper premolar, P4 fourth upper premolar, PGF postglenoid foramen, PTP post-tympanic process, PLF palatal foramina, PTP post-tympanic process, SS sphenorbital bridge, SC sagittal crest, SF spenorbital fissure, SMF supramastoid foramen, SO supraoccipital, SR supraorbital ridge, VO vomer, ZP zygomatic projection.



FIGURE 2. Xenorhinos halli, sp. nov., Bitesantennary Site, Riversleigh, northwestern Queensland. Paratypes. A. QM F22920, occlusal view. B, QM F22921, occlusal view. C-D', QM F22922: C, lateral view; D-D', occlusal view, stereopair. Bar indicates 1 mm.

On M1 and M2, a notch is present in the lingual margin of the tooth at the level of the posterior face of the protofossa, i.e., basal to the lingual edge of the base of the metacone. The M1 heel is lingually directed and is better developed than on M2. Nonetheless, M2 has a well-developed heel, which is postero-lingually developed and narrow. M3 is little reduced in length or width, with the premetacrista being half to three-quarters of the length of the paracrista.

Dentary and Lower Dentition—The dentary symphysis is vertically oriented, with a conspicuously developed chin. A large mental foramen opens beneath the anterior edge of p2. The coronoid is subequal in height to the tip of c1, and hence is only about one molar crown height above the apices of m3. The condyle is low, equal in height to the hypoconids of m1–3. The angular process is broad and splayed laterally. There are alveoli for two pairs of lower incisors. The canine is relatively tall and straight, being approximately twice the height of p4. The p2 is of similar length to p4 but half its height. Lower molar length decreases from m1 to m3, as does relative length of the trigonid. The m3 is little reduced and retains an entoconid and hypoconulid. On m1–3, the protoconid is the tallest cusp, followed by the metaconid, entoconid, paraconid, hypoconid, and hypoconulid.

Measurements of the holotype and referred specimens of *Xenorhinos halli* are given in Table 1. A study of intraspecific morphological variation, including possible sexual dimorphism, in the large sample of *X. halli* from the Bitesantennary Site is in progress.

PHYLOGENETIC RELATIONSHIPS

The phylogenetic interrelationships of genera and species groups in the family Hipposideridae have recently been examined by Hand and Kirsch (in press) and Bogdanowicz and Owen (in press). In their PAUP 3.1.1 (Swofford, 1993) and Hennig-86 (Farris, 1988) analyses, Hand and Kirsch (in press) included 30 extant hipposiderid species and seven fossil taxa, which they scored for 59 discrete characters (36 cranial, 20 dental, and three skeletal). In Bogdanowicz and Owen's analvsis, 45 metrical and 30 discrete-state characters in 57 extant hipposiderid species (but no fossil taxa) were examined. Although the results of these two studies differed significantly from each other in many respects (e.g., in interpreted relationships among Hipposideros species), they agreed in a number of points, including that the family Hipposideridae is probably monophyletic, that the genus Hipposideros is probably paraphyletic, and that the composition of previously proposed divisions within Hipposideros needs reexamination. Both studies suggested associations of geographically widely separated taxa, including species of Coelops and Cloeotis, and Triaenops and Rhinonycteris (see below).

Xenorhinos halli was included in the phylogenetic study by Hand and Kirsch. The analysis could not unambiguously resolve the relationships of *X. halli*, with two alternative, equally parsimonious hypotheses proposed (Fig. 3). In the first hypothesis of relationship (Fig. 3A), *X. halli* appears to be a basal member of a clade that includes species of *Anthops, Asellia*, *Hipposideros, Palaeophyllophora*, and *Pseudorhinolophus*, and is not especially closely related to other Australian fossil hipposiderids, including species of *Brachipposideros, Rhinonycteris*, and *Riversleigha*. In the second hypothesis (Fig. 3B–C), *X. halli* appears to be most closely related to other extinct and/ or endemic Australian taxa, as well as to African species of *Triaenops* and, more distantly, *Cloeotis* and *Coelops*. In both hypotheses, *X. halli* lies outside (i.e., is basal to) the large *Hipposideros* crown group.

Hill (1982) suggested that *Rhinonycteris aurantius* of northern Australia, *Triaenops* species of southwestern Asia and AfTABLE 1. Skull, dentary and tooth measurements (mm) of the holotype and paratypes of *Xenorhinos halli*, sp. nov., from the Miocene Bitesantennary Site, Riversleigh, northwestern Queensland. **Abbreviations: max.**, maximum; **min.**, minimum; I, length; **w**, width; T, trigonid; t, talonid; *, measured perpendicular to hard palate; #, measured perpendicular to basicranium. Numbers in parentheses indicate estimates.

	Holo- type		Para- type	Para- type	Para- type
QM F	22918		22924	22920	22921
Greatest skull length (dorsal)	23.9		23.6		
Rostral length	9.5		9.2		
Braincase length	13.1		13.4		
Rostral width (max.)	9.4		9.6		
Min. interorbital width	4.3		4.6		
Zygomatic width			(12.9)		
Restral height*	7 1		(12.1)		
Braincase beight (max.)#	8.2				
Palate length	1.5		1.8		
Max palatal width (base of M3)	4.8				
Interperiotic distance	1.6		1.5		
	L	R			
C1-M3		8.05		7.70	6.73
P4-M3	5.8	(5.9)		4.89	5.08
M1-M3	4.7	4.7		3.93	4.00
C1 1	2.19		2.06	1.73	1.61
W	1.44		1.49	1.26	1.34
P4 1	1.25	1.32	1.29	1.22	1.31
W	1.30	1.34	1.40	1.54	1.20
MII I	1.98	1.69	1.75	1.50	1.50
M2 1	1.07	1.02	1.05	1.00	1.50
	1.79	1.72	1 79	1.70	1.50
M3 1	1.27	1.28	,	1.07	1.17
W	1.69	1.75		1.60	1.60
	Para-	Para-	Para-		
OME	22010	22022	22022		
QMF	22919	22922	22925		
Max. dentary length	12.7	1 (7	12.9		
Dentary depth below m2	1.8	1.07	1.62		
al m ²	4.3	8.00	4.9 8.24		
$p_{1}^{-m_{3}}$		5.92	6.23		
$p_{-m3} = m_{-m3} = 1$	4 99	4 87	5.17		
		1.31	1.08		
W		1.27	1.17		
p2 1			1.12		
W			0.92		
p4 l		1.16	1.16		
W		1.02	0.92		
m1 l	1.72	1.71	1.85		
		1.00	0.94		
WI		0.72	1.02		
11		0.72	1.10		
m2 l	1.67	1.61	1.10		
	1.07	0.96	0.89		
wT		1 31	1.22		
lt lt		0.67	0.83		
wt		· · · · · ·	10 C C C C C C C C C C C C C C C C C C C		
		1.31	1.16		
m3 1	1.6	1.31 1.62	1.16 1.71		
m3 1 1T	1.6	1.31 1.62 0.92	1.16 1.71 0.87		
m3 l lT wT	1.6	1.31 1.62 0.92 1.23	1.16 1.71 0.87 1.04		
m3 l IT wT lt	1.6	1.31 1.62 0.92 1.23 0.72	1.16 1.71 0.87 1.04 0.80		

rica, and *Cloeotis percivali* of southern and eastern Africa form a group characterised principally by a number of common features of the noseleaf. Gray (1866) earlier recognised the uniqueness of the noseleaf of *Rhinonycteris*, separating the genus from other hipposiderids and rhinolophids as the sole member of a



FIGURE 3. Phylogenetic hypotheses of hipposiderid relationships presented by Hand and Kirsch (in press) resulting from analyses conducted on 40 living and extinct taxa and 59 dental, cranial and skeletal characters: **A**, strict consensus of 4 PAUP trees, all unordered characters (CI = 0.25; 87.5% resolution); **B**, strict consensus of 8 PAUP trees, some ordered characters (CI = 0.23; 82.5% resolution); **C**, Hennig86 Nelson consensus, unordered characters.

distinct group, the Rhinonycterina. Gray's definition of the last group, as pointed out by Hill (1982), would also include species of the more recently described genera *Triaenops* and *Cloeotis*. Hill (1982:174–175) interpreted *Triaenops* as being possibly closer to *Rhinonycteris* than to *Cloeotis*, sharing a similar structure of the interorbital region, the architecture of the jugal prominence of the zygoma, and curously thickened premaxillae. Koopman (1994) included the three genera in his subtribe Rhinonycterina.

Xenorhinos halli may belong to this group (Fig. 3B-C). Features shared by species of Triaenops, Rhinonycteris, and Xenorhinos include the accessory cusp on C1, little reduction of M3, presence of P2, and apomorphies such as markedly expanded zygoma, and thickened and crested premaxillae. Further, Xenorhinos halli may be more closely related to Triaenops persicus than to the living Australian R. aurantius (e.g., Fig. 3B). Apparent apomorphies shared by species of Xenorhinos and Triaenops, but not Rhinonycteris, include a broad, flattened rostrum nearly as deep as the braincase, very broad anterior nares with a short but distinct median spine on the posterior border, and enlarged petrosals that in diameter are more than twice as wide as the basioccipital-characters noted by Hill (1982) to be unique to Triaenops. Features shared by species of Xenorhinos and Cloeotis include marked constriction of the basisphenoid, as well as the accessory cusp on C1, little reduction of M3, and retention of P2. On the other hand, apparent apomorphies shared by X. halli and species of Anthops, Asellia, Hipposideros, Palaeophyllophora, and Pseudorhinolophus but not other Australian fossil taxa (Fig. 3A), include an elongate and medially positioned infraorbital foramen, a mesopterygoid roof that lacks a groove, and small P4. In this hypothesis (Fig. 3A), the subtribe Rhinonycterina is interpreted to be paraphyletic and shared features (see above) are interpreted as symplesiomorphies.

The precise relationships of the Australian Miocene Xenorhinos halli to other living and fossil hipposiderids are not clear. However, X. halli evidently lies outside the large, relatively derived Hipposideros crown group, and within or close to a group of old endemic African, Australian, and Asian taxa, including extant species of Triaenops, Rhinonycteris, Cloeotis, and Coelops. The latter appear to be early but autapomorphically specialized offshoots of the Old World hipposiderid radiation.

DISCUSSION

At least some of the most strikingly distinctive characteristics of *Xenorhinos halli*, such as its broad, deep rostrum, voluminous nasal cavities, broad interorbital region, extremely short palate, splint-like sphenoidal bridge, and conspicuous angle in the basicranial axis, are probably specializations correlated with echolocation. Pedersen (1993, 1995) found that head posture and skull form in bats is constrained by the demands of vocalization during echolocation, with profound differences in skull morphology between oral- and nasal-emitting bats occurring early in embryonic development. Nasal emission radically affects those structures immediately adjacent to the vocal tract, with strong selective forces acting on the form and function of the pharynx and larynx during echolocation (Pedersen, 1995).

Rotation of the rostrum is one of the most conspicuous correlates of nasal emission (Freeman, 1984; Pedersen, 1993). In nasal-emitting bats (hipposiderids, rhinolophids, phyllostomids, mormoopids, nycterids, megadermatids, and possibly rhinopomatids), the rostrum is rotated ventrally to align the nasopharynx with the direction of flight, the foramen magnum is moved ventrally, and the inner ear is rotated posteriorly to compensate for the general rotation of the skull ventrally about the cranio-cervical axis (Pedersen, 1993). Like other hipposiderids and rhinolophids, X. halli exhibits pronounced rostral rotation, the angle between the planes of the hard palate and basicranial axis being greater than 25° and hence as large or larger than that observed in other bats (Freeman, 1984; Pedersen, 1993: table 2).

The nasal cavities of rhinolophoid bats are radically modified into 'resonators' that amplify the echolocation call (Suthers et al., 1988). The rostrum morphology of X. halli appears to have been similarly modified. This fossil species has particularly voluminous nasal cavities, with incomplete separation between the nasal chambers and little bony separation of the buccal and nasal cavities. The ethmoturbinals are unlike those of all other hipposiderids examined. A comparative study of the nasal cavities of hipposiderids, including their structure/function relationships as a potentially rich source of phylogenetic information, is in progress. Rostral fontanels, found by Pedersen (1995) between the nasal, maxillary, and frontal bones in Old World nasal-emitters, are also large and extensive in X. halli. Unlike other hipposiderids, X. halii has a broad, but flattened, interorbital region. Nevertheless, the olfactory lobe was probably not large since the cribiform plate is only sparsely perforated and only so dorsally (Bhatnagar and Kallen, 1974), and the vomeronasal organ, as in other rhinolophoids (Cooper and Bhatnagar, 1976), was probably not well developed.

The palate is extremely short in *X. halli* (less than 1.5 molar lengths) as is the ventral (but not dorsal) interorbital region, with the pterygoid processes located less than a molar length posterior to the level of M3 and occurring in the rostral portion of the skull. The nasopharynx was thus also presumably very short, probably radically affecting the echolocation call of this bat. This morphology is unique among bats, and quite unlike that found in its possible relatives—species of *Rhinonycteris*, *Triaenops*, and *Cloeotis*. Marked constriction of the sphenorbital bridge occurs in *Cloeotis percivali*, but the rostrum is not large nor the palate exceptionally short.

The broad, deep rostrum of X. halli cannot be directly correlated with size or complexity of the noseleaf. For example, although living members of the Rhinonycterina (the hipposiderid subtribe to which X. halli is probably referable) may be identified and clustered on the basis of their distinctive noseleaves (Hill, 1982) and less clearly on features of the premaxilla, zygoma, basicranium, and dentition (Hand and Kirsch, in press), rostral morphology in this group varies widely, from the very small, poorly inflated rostrum of *Cloeotis percivali* to the large, inflated rostrum of Rhinonycteris aurantius and Triaenops persicus. The relative size of the noseleaf also varies among living rhinonycterinae: in Rhinonycteris, the noseleaf is relatively large and completely covers the muzzle; in Cloeotis, it is relatively small, and in Triaenops it is narrow, in neither case covering the muzzle (Hill, 1982). There are also conspicuous interspecific differences in noseleaf and rostral morphology: Triaenops furculus of Madagascar and islands of the western Indian Ocean has a much less complex noseleaf but more inflated rostrum than T. persicus of Madagascar, Afica, Iran, Oman, and Aden (Hill, 1982). In this hipposiderid subtribe, at least, it appears that size and shape of the rostrum are not directly correlated with-nor an accurate predictor of-size and complexity of the noseleaf. The morphology of the noseleaf has been used extensively in systematic studies of extant hipposiderids, particularly in alpha taxonomy (e.g., Gray, 1866; Peters, 1871; Tate, 1941a, b; Hill, 1963, 1982; Flannery and Colgan, 1993; Hill et al., 1986; Kitchener et al. 1992), but structural and functional relationships of the noseleaf are not well understood. Pye (1988) suggested that it possibly serves to beam ultrasonic calls and thus to contribute to the directionality of the signal. The complex flaps and folds may also serve to shield the ears from outbound, nasally-emitted signals and so increase overall sensitivity to returning echoes (Hill and Smith, 1984).

The dentition of X. halli appears to be relatively unspecialized. It is similar to that found in species of *Rhinonycteris*, *Triaenops*, *Brachipposideros*, *Riversleigha*, and to a lesser extent *Cloeotis*. These bats exhibit a broad range of skull shapes and morphology but preserve a dentition that is probably plesiomorphic among hipposiderids. Hipposiderids typically feed on moths and beetles caught in the wing or tail membrane while foraging low over ground and bushes. The unusual structure of the rostrum of X. halli, however, suggests that this species may have had a unique feeding behavior.

At least 12 hipposiderid species are known from the Oligo-Miocene freshwater limestone deposits at Riversleigh, northwestern Queensland (Archer et al., 1994). Xenorhinos halli is preserved at the early Miocene Bitesantennary Site along with frogs, lizards, birds, marsupials, a megadermatid bat, and at least eight other hipposiderids, representing at least four genera, Xenorhinos, Riversleigha, Rhinonycteris, and ?Brachipposideros (Hand, 1997b, in press). The Bitesantennary hipposiderids, which appear to have coexisted, range in size from an estimated 20 to 60 mm in forearm length (skull lengths 12-24 mm) and show a wide range of skull shapes. They appear to be less diverse in dental and postcranial morphology. The immediate depositional environment of the Bitesantennary Site is interpreted to have been a cave developed in Tertiary limestone surrounded by lowland rainforest (Archer et al. 1994, and see above). The closest modern analogy to this environment is found in rainforested limestone regions of southeastern Asia and possibly New Guinea, where as many as six hipposiderid species occur sympatrically (Payne et al., 1985; Flannery, 1990). In many early to middle Tertiary sites in Europe, up to five hipposiderid taxa, representing three genera, are found together (Remy et al., 1987). Xenorhinos halli has possible close relatives in other Riversleigh Oligo-Miocene deposits (?X. sp. from RSO, CS, and Upper Sites on Godthelp Hill), but there appears to be none among the five or six hipposiderid species represented in Riversleigh's Pliocene Rackham's Roost Site deposit.

The diverse Riversleigh hipposiderid assemblage is indicative of an earlier radiation. A minimum Eocene age for the early radiation of the family Hipposideridae is provided by the age of relatively derived fossil taxa from Europe (e.g., species of *Pseudorhinolophus* and *Palaeophyllophora*). However, Hand and Kirsch (in press) have suggested that because many evidently plesiomorphic hipposiderid taxa (e.g., species of *Aselliscus*, *Rhinonycteris*, *Brachipposideros*, etc.; Fig. 3) occur in the Australian region, the early radiation of the family could have occurred there. Certainly bats were present in the region at that time, as the early Eocene archaeonycteridid *Australonycteris clarkae* from Murgon, southeastern Queensland, demonstrates (Hand et al., 1994).

The closest relatives of *Xenorhinos* appear to be spread throughout the Old World tropics (e.g., *Cloeotis* from Africa, *Coelops* from Asia, and *Rhinonycteris* from Australia), and as widely as the Palearctic and Ethiopian regions (e.g., *Brachipposideros* and *Triaenops*). There is evidence of endemic radiation of hipposiderids in areas such as Europe and northern Australia during the Paleogene and Neogene respectively (Sigé et al., 1994; Hand and Kirsch, in press), but less evidence of profound or long-lasting barriers to dispersal for hipposiderids throughout the Tertiary. The wide distribution of hipposiderids in the Old World, coupled with their relatively good fossil record, makes these bats potentially very useful biocorrelators of intercontinental Tertiary sediments (Sigé et al., 1982; Hand 1997b).

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LITERATURE CITED

- Archer, M., S. J. Hand, and H. Godthelp. 1994. Riversleigh: The Story of Animals in the Ancient Rainforests of Inland Australia. Reed Books, Sydney, 256 pp.
- Bhatnagar, K. P., and F. C. Kallen. 1974. Morphology of the nasal cavities and associated structures in Artibeus jamaicensis and Myotis lucifugus. American Journal of Anatomy 139:167–190.
- Bogdanowicz, W., and R. D. Owen. In press. In the Minotaur's labyrinth: a phylogeny for the Hipposideridae; in T. Kunz and P. Racey (eds.), Proceedings of the 10th International Bat Research Conference, Boston. Smithsonian Institution, Washington.
- Cooper, J. G., and K. P. Bhatnagar. 1976. Comparative anatomy of the vomeronasal complex in bats. Journal of Anatomy 122:571–601.
- Farris, J. S. 1988. Hennig86, Version 1.5. Computer Program and Documentation. Port Jefferson Station, New York.
- Flannery, T. F. 1990. Mammals of New Guinea. Robert Brown and Associates, Carina, Queensland, 439 pp.
- and D. J. Colgan. 1993. A new species and two new subspecies of *Hipposideros* (Chiroptera) from western Papua New Guinea. Records of the Australian Museum 45:43–57.
- Freeman, P. 1984. Functional analysis of large animalivorous bats (Microchiroptera). Biological Journal of the Linnean Society 21:387– 408.
- 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.
- 1990. Australia's first Tertiary molossid (Microchiroptera: Molossidae): its phylogenetic and biogeographic implications. Memoirs of the Queensland Museum 28:175–192.
- 1993. First skull of a species of *Hipposideros* (*Brachipposideros*) (Microchiroptera: Hipposideridae), from Australian Miocene sediments. Memoirs of the Queensland Museum 31:179–192.

- 1997a. *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.
- 1997b. New Miocene leaf-nosed bats (Microchiroptera: Hipposideridae) from Riversleigh, Queensland. Memoirs of the Queensland Museum 41:335–349.
- In press. Riversleigha williamsi, a new Miocene hipposiderid from Riversleigh, Queensland, Alcheringa.
- and J. A. W. Kirsch. In press. A southern orgin for the Hipposideridae (Microchiroptera)? Evidence from the Australian fossil record; *in* T. Kunz and P. Racey (eds.), Proceedings of the 10th International Bat Research Conference, Boston. Smithsonian Institution, Washington.
- —, M. Archer, and H. Godthelp. 1989. A fossil bat-rich, Oligo-Miocene cave-fill from Riversleigh Station, northwestern Queensland. Conference on Australasian Vertebrate Evolution, Palaeontology and Systematics, Sydney, March 1989, Abstracts:7.
- M. Novacek, H. Godthelp, and M. Archer. 1994. First Eocene bat from Australia. Journal of Vertebrate Paleontology 14:375–381.

- Hill, J. E. 1963. A revision of the genus *Hipposideros*. Bulletin of the British Museum (Natural History), Zoology 11:1–129.
 - —— 1982. A review of the leaf-nosed bats *Rhinonycteris*, *Cloeotis* and *Triaenops* (Chiroptera: Hipposideridae). Bonner zoologische Beiträge 33:165–86.
 - ----- and J. D. Smith 1984. Bats: A Natural History. Rigby, Adelaide, 243 pp.
- —, A. Zubaid, and G. W. H. Davison. 1986. The taxonomy of leafnosed bats of the *Hipposideros bicolor* group (Chiroptera: Hipposideridae) from southeastern Asia. Mammalia 50:535–540.
- Kitchener, D. J., R. A. How, N. K. Cooper, and A. Suyanto. 1992. *Hipposideros diadema* (Chiroptera Hipposideridae) in the Lesser Sunda Islands, Indonesia: taxonomy and geographic morphological variation. Records of the Western Australian Museum 16:1–60.
- Koopman, K. F. 1994. Chiroptera: systematics. handbook of zoology, VIII, 60, Mammalia:1–217.
- Payne, J., C. M. Francis, and K. Phillips. 1985. A Field Guide to the Mammals of Borneo. The Sabah Society with World Wildlife Fund Malaysia, Kuala Lumpur, 332 pp.
- Pedersen, S. C. 1993. Cephalometric correlates of echolocation in the Chiroptera. Journal of Morphology 218:85–98.
- Peters, W. 1871. Über die Gattungen und Arten der Hufeisennasen. Rhinolophi. Monatsberichte K. preuss. Akad. Wiss. 301–332.
- Pye, J. 1988. Noseleaves and bat pulses; pp. 791–796 in P. Nachtigall and P. Moore (ed.), Animal Sonar: Processes and Performance. Proceedings NATO Advanced Study Institute on Animal Sonar Systems. Plenum Press, New York.

- Remy, J. A., J.-Y. Crochet, B. Sigé, J. Sudre, L. de Bonis, M. Vianey-Liaud, M. Godinot, J.-L. Hartenberger, B. Lange-Badre, and B. Comte. 1987. Biochronologie des phosphorites du Quercy: mise à jour des listes fauniques et nouveaux gisements de mammifères fossiles. Münchner Geowissenschaftliche Abhandlungen, A, 10: 169–188.
- Sigé, B., S. J. Hand, and M. Archer. 1982 An Australian Miocene Brachipposideros (Mammalia, Chiroptera) related to Miocene representatives from France. Palaeovertebrata 12:149–171.
- —, H. Thomas, S. Sen, E. Gheerbrandt, J. Roger, and Z. Al-Sulaimani. 1994. Les chiroptères de Taquah (Oligocène inférieur, Sultanat d'Oman). Premier inventaire systématique. Münchner Geowissenschlaftliche Abhandlungen A 26:35–48.
- Suthers, R. A., Hartley, D. J., and Wenstrup, J. J., 1988. The acoustic role of tracheal chambers and nasal cavities in the production of sonar pulses by the horseshoe bat, *Rhinolophus hildebrandti*. Journal of Comparative Physiology A 162:799–813.
- Swofford, D. L. 1993. PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1. Computer Program Distributed by the Illinois Natural History Survey, Champaign, Illinois.
- Tate, G. H. H. 1941a. A review of the genus *Hipposideros* with special reference to Indo-Australian species. Bulletin of the American Museum of Natural History 78:353–393.
- 1941b. Results of the Archbold Expeditions. No. 36. Remarks on some Old World leaf-nosed bats. American Museum Novitates 1140:1–11.
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