Riversleigha williamsi gen. et sp. nov., a large Miocene hipposiderid (Microchiroptera) from Riversleigh, Queensland

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BATS ARE among the most common vertebrate fossils in Tertiary freshwater limestone deposits in the Riversleigh World Heritage Fossil Site, Lawn Hill National Park, northwestern Queensland (Archer et al. 1994). Of the 200-plus fossil-bearing localities (local faunas) now recognised from Riversleigh only a handful are devoid of bat fossils. In most Riversleigh sites, bat remains are numerous but often fragmentary. In other Riversleigh deposits they are extremely well preserved, with most taxa being represented by hundreds of near-complete skulls, dentaries, and complete but dissociated postcranials. Such sites appear to represent limestone cave deposits in which fossilisation occurred rapidly and in situ (Hand et al. 1989; Megirian 1992, Archer et al. 1994).

Riversleigh’s Bitesantennary Site cave deposit is situated on the northeastern edge of the Site D Plateau (Archer et al. 1989, 1994). It contains at least 10 bat species: nine hipposiderids and a megadermatid. At least two of the hipposiderids belong to the Brachipposideros-Rhinonicteris clade (Hand 1997b), and a third represents the new genus Xenorhinos (Hand 1998). Other hipposiderids previously described from Riversleigh’s Miocene deposits include Brachipposideros nooraleebus from Microsite (Sigé et al. 1982), Hipposideros bernardsigei from Neville’s Garden Site (Hand 1997a), and Miophyllorhina riversleighensis from RV Site (Hand 1997c).

In this paper, a new genus and species of hipposiderid bats is described from skull material collected from Bitesantennary Site. A phylogenetic analysis involving the new species and most hipposiderid genera and species groups has been previously conducted by Hand and Kirsch (in press). Here, the possible phylogenetic position of the new Riversleigh bat and its palaeogeographic implications are briefly discussed, as well as the ecological significance of some aspects of its morphology. Skull terminology follows (Hand 1993, 1994); dental terminology follows Sigé et al. (1982). The prefix QMF refers to specimens held in the fossil collections of the Queensland Museum, Brisbane.
Stratigraphic nomenclature for the Riversleigh region follows Archer et al. (1989, 1994).

Systematic palaeontology

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

Riversleigha gen. nov.

Type species. Riversleigha williamsi gen. et sp. nov.

Age and distribution. Early Miocene of northern Australia.

Diagnosis. Rostrum longer than broad, supraorbital crests distinct and meeting tall sagittal crest in interorbital region, zygoma with very tall projection, sphenorbitabral bridge broad, petrosal not greatly enlarged (in width less than four times interperiotic width), C1 with well-developed secondary cusp, P2 in tooth row, little reduced M3/3, and coronoid process of the dentary relatively tall (in height approximately twice the height of M1).

Etymology. The name is derived from the Riversleigh World Heritage Fossil Site, Lawn Hill National Park, northwestern Queensland.

Riversleigha williamsi sp. nov. (Figs 1-3)

Holotype. QM F24100, skull containing left and right C1 P2,4 M1-3, lacking premaxillae and periotics.

Paratypes. QM F24101, right dentary containing C, P2,4 M1,3; QM F24102, right maxilla with C1 P2,4 M1,3; QM F24103, left dentary containing I1, C1, P2,4 M1,3; QM F24104, skull containing left P2 M1,2; QM F24105, left dentary with C, P2,4 M1,3

Diagnosis. As for genus by monotypy.

Locality, stratigraphic position and age. Bitesantennary Site covers an area of approximately 150 square metres on the northeastern edge of the D Site Plateau (Hand et al. 1989; Archer et al. 1989, 1994). It is etched into an older, relatively non-fossiliferous limestone that appears to be contiguous with Site D limestones (Creaser 1998) containing the Riversleigh Local Fauna (Tedford 1967) and interpreted to be late Oligocene in age (Archer et al. 1989, 1994). On the basis of stratigraphy and contained local fauna (Archer et al. 1989, 1994; Hand 1997a, b), the Bitesantennary Site deposit is interpreted to be early Miocene in age.

Associated fauna and taphonomy. The Bitesantennary deposit is interpreted to be a cave-fill (Hand et al. 1989, Hand 1997b). It contains thousands of near-complete bat skulls and limb bones, and fossilisation appears to have occurred rapidly and in situ. The boundary or contact between the fossiliferous fill and remnants of the older, non-fossiliferous cave wall has been identified at several points around the perimeter of the deposit. Riversleigha williamsi is preserved in the deposit with at least eight other hipposiderids (Hand 1997b) and a megadermatid. Many snails, frogs, lizards, a boid, stork, swift (Collocalia sp., W. Boles pers. comm.), peramelids, a dasyurid, and a bulungamayine macropodid (Gangaroo bilamina, Cooke 1997) are also preserved in the Bitesantennary deposit.

Etymology. The species is named after Stephan Williams of the University of New South Wales in appreciation of his invaluable help in collecting, processing and sorting the many tonnes of Bitesantennary Site bat-bearing limestone.

Description

Skull

General outline and proportions. The skull is relatively long and narrow with pronounced interorbital constriction. The rostrum is very long, in length at least two-thirds that of the braincase.
Its greatest width, at the level of the most anterior point of the orbit, is more than two-thirds the mastoid width, and more than twice the minimum interorbital width. The interorbital region is long, representing approximately one-quarter skull length. The rostrum is deep, in height not much lower than the braincase (without its tall sagittal crest). The braincase is not greatly inflated and is almost as wide as long. It is broadest across the mastoids. Maximum zygomatic width exceeds mastoid width.

Rostrum. The rostrum is longer than wide. Its lateral borders converge anteriorly only slightly. The nasals form well-developed rostral inflations. A trough or frontal depression is formed between the distinct supraorbital ridges (viz. QM F24105). The latter join the sagittal crest in the mid-interorbital region. The sagittal crest is tall, its greatest height occurs just anterior to the posterior roots of the zygoma. There is an unpaired nasal foramen at the anterior edge of the frontal depression. The antorbital bar is straight and of equal thickness throughout. The elongated infraorbital foramen occurs above M1-2. In the lateral wall of the face, at the front of the orbital fossa, a large foramen (?lacrimal) opens under the anterior attachment point of the arch at the edge of the circumorbital rim. It is separated from the infraorbital foramen by a thin wall of bone. The lateroventral fossa is deep and very broad (almost equal to minimum interorbital width). The postpalatal foramen and sphenopalatine appear to be twinned. Posterodorsally and medially is a single foramen (?ethmoid/diploic) that leads into the posteroven tral part of the nasal cavity. Posterodorsally again, level with the infraorbital foramen, is a large foramen (?cranio-orbital).

Palate. The palate is relatively long. Its midline, which exhibits twinning of the median spine, extends posteriorly to approximately level with the paracone of M3. The palate’s anterior edge forms a deep, stepped V-shaped indentation, which extends posteriorly to the level of the paracone of M1. The palate’s posterior border has two posterolateral indentations that extend anteriorly to at least the level of the paracone of M3. The palate is flat with shallow palatal foramina developed, mid-palate, at a point level with P4, and well developed foramina occur adjacent to the M3 paracone. The toothrows are slightly convergent anteriorly.

Nasals. The inflated 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 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.

Interorbital and pterygoid region. Immediately to the rear of the face and between the orbital fossae, the braincase narrows. The point at which the two supraorbital ridges unite (i.e. where the sagittal crest originates) is close to the point of narrowest constriction and well posterior to the posterior face of M3. A bony bar separates the optic foramen from the sphenorbital fissure. Anteriorly the sphenorbital fissure is narrow and completely concealed by the broad sphenoidal bridge. Posteriorly it is partially exposed by the slightly constricted sphenorbital bridge. Immediately lateral to the most anterolateral margin of the sphenorbital fissure is the anterior transverse diploic foramen. Small pterygoid processes occur and almost immediately posterior to these are a second pair of laterally-directed flanges. A groove running the length of the mesopterygoid roof is absent or only incipiently developed.

Zygomatic arch. The zygoma has a very tall projection that extends over almost its entire length. The ventral margin of the zygomatic arch is arched and is dorsal to the tooth row. In dorsal view, the junction between the zygomatic arch and antorbital bar is not marked by a change in direction. The zygomatic arches diverge gently posteriorly. The tip of the zygomatic projection
Fig. 1. *Riversleigh williamsi* n. gen. et sp., Bitesantennary Site, Riversleigh, northwestern Queensland. QM F24100, holotype, skull containing left and right C¹ P₃ M¹²: A, dorsal view; B, lateral view; D-D', ventral view, stereopair. QM F24101, paratype, right dentary containing C₁ P₂₃ M₁: C, lateral view. Bar indicates 5 mm.
converges towards the side wall of the braincase.

Cranial vault. The braincase is relatively round. It is little inflated, widest at the level of the post-tympanic processes, narrowest in the interorbital area and highest dorsal and posterior to the postglenoid processes. A tall sagittal crest extends anteriorly to the supraorbital ridges and posteriorly to the lambdaoidal crest which is also well-developed. The posterior transverse sinus occurs approximately two-thirds along the length of the braincase. Foramina opening extracranially are conspicuous along its course to the posterior part of the postglenoid foramen.

Glenoid. The glenoid fossa is subcircular and only slightly concave. The postglenoid process is not particularly tall being less than half the length of the glenoid fossa; its anterior face is anteriorly recurved; its posterolateral margin has a posterolaterally directed flange. The large postglenoid foramen is elongate and opens on the gently sloping posterior face of the glenoid. It opens immediately posteriorly to the postglenoid process. The postglenoid fossa is directed forwards rather than ventrally. Medial to the posterior part of the glenoid fossa, the foramen ovale opens in the alisphenoid. (No second posterodorsal or lateral foramen opens into the pyriform fenestra.)

Temporal region. 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 slim posteromedially 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 periotic.

Basicranium. The basisphenoid is hexagonal and shallowly concave in its central region. Faint, anteriorly convergent ridges extend from the sphenoidal bridge and define the basisphenoid fossa. The anterior margin of the basicranial area is relatively wide, the sphenoidal bridge being only slightly constricted posterior to the second pterygoid flange. Posteriorly, the basioccipital is also relatively wide, its minimum width about one-third that of the cavity for the periotic. The lateral edges of the basisphenoid-basioccipital complex are bi-concave lateral curves. There is no lateral extension of the basisphenoid.

Occipital. The most posterior region of the skull coincides with the junction of the interparietal and supraoccipitals. In lateral view, the supraoccipital is not very convex posteriorly but the exoccipitals and well developed lambdaoidal crests clearly overhang the posteroventrally directed foramen magnum. The posterior edge of the foramen magnum is squared but not thickened. The lambdaoidal crests are well developed and parallel the posterior edge of the foramen magnum, terminating anterodorsally to the paroccipital process; a thin strip of occipital extending the lambdaoidal crest over the mastoid as far as the contact with post-tympanic process. The ventral condyloid fossa is well developed. In ventral view, the posterior skull contour of the supraoccipital at the level of the lambdaoidal ridge is square. The foramen magnum is oval in shape and wider than tall. Between the occipital condyle and paroccipital process is a relatively narrow condyloid fossa. The paroccipital process is well developed; the lambdaoidal crest extends further laterally. The condyle projects most strongly ventrally at the posterior extremity, its not greatly thickened lip only partially conceals the condyloid foramen in the anterolateral face.

Upper dentition. The premaxillae and incisors are unknown, although all large (i.e. appropriately sized) isolated premaxillae from the Bitesantennary Site deposit are crested and contain alveoli for two incisors. C1 is tall and long, with a relatively tall (almost half the height of the main cusp) but poorly separated, slightly lingually displaced posterior accessory cusp. It has a thick lingual vertical crest, vertical anterobuccal groove, and complete cingulum which is mostly of uniform depth but thickened at the anterobuccal
corner and with faint buccal cingulum (development of the anterobuccal cingulum may be variable). P2 is small but still mostly within the toothrow and thus separating C1 and P4. P4 is slightly wider than long, with a continuous buccal, lingual and posterolingual cingulum, an anterolingual cingular cusp and widened anterobuccal cingulum with small cingular cusp.

M1-3 have narrow buccal cingula and small parastyles. M1-2 have four roots and are wider than long. They have posteriorly directed heels, the metacone slightly larger than paracone, postprotocrista with dihedral angle not reaching metacone base so that the protofossa is open. The posterolingual crest on the protocone is better developed in M1 than M2 as is the heel. Both have narrow anterior and posterolingual cingula, with the latter being thickened posterolingually around the heel. The posterior cingulum ends at the base of the metacone and does not join either the postprotocrista or the cingulum of the heel. In M1-2 the subequal preparacrista and premetacrista are slightly shorter than the subequal postparacrista and postmetacrista; the preprotocrista is continuous with the anterior cingulum.

M3 is only moderately reduced in width and length, and a metacone is present. The premetacrista is more than half the length of the subequal pre- and postparacristae; the preprotocrista is continuous with the anterior cingulum. M3 has a straight posterior edge, no pos-
terior cingulum, and rounded rather than acute lingual margin (i.e. protocone base).

**Dentary and lower dentition.** The dentary is straight and is deeper anteriorly (e.g. beneath P$_2$) than posteriorly. Beneath M$_3$, it is slightly more than one molar height in depth. The symphys

is vertically orientated, there is some chin development and a large mental foramen occurs beneath the posterior margin of C$_3$. The ascending ramus (coronoid process) is approximately twice the height of M$_1$, or approximately 1.5 times the length of M$_2$; its anterior edge is only slightly recurved. The angular process is well developed.

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Fig. 3. *Riversleigha williamsi* n. gen. et sp., Bitesantennary Site, Riversleigh, northwestern Queensland. QM F24103, paratype, left dentary containing I$_1$, C$_1$, P$_2$-$4$, M$_{1,3}$; A, buccal view; B-B', occlusal view, stereopair. Bar indicates 1 mm.
and strongly splayed posterolaterally. It is very broad, as is the articular condyle. The ventral margin of the dentary is straight, rising just posterior to M3. The masseteric fossa is deep and area of muscle attachment very broad.

In the dentary are alveoli for two lower incisors. I3 is unknown. I1 is trilobed but not greatly imbricated, the anterior lobe larger than the others. C3 is subcircular in occlusal outline, relatively tall, being more than 1.5 times the height of P4, with a lingual crest and stronger posterobuccal crest, continuous cingulum thinner buccally than lingually, with tiny anterolingual cingular cusp and conspicuous posterolingual cingular cusp. P3 is relatively large, being greater than or equal in length to P4 and more than half its height, and is laterally flattened with separate lingual and buccal cingula, one root. P4 has a subrectangular outline in occlusal view, and is relatively short and narrow. It has one main cusp at the centre of the crown, with a poorly developed metaconid and strong buccal cingulum.

M1,3 are nyctalodont, with relatively straight pre-entocristids, tall entoconids, protoconids much taller than hypoconids, no elaboration of buccal cingula and no lingual cingula. The M1 cingulum thickens slightly between the trigonid and talonid. M1,2 have wide talonids, with the M2 talonid slightly narrower than that of M1, and trigonid wider than in M1. M1 is only slightly reduced, with a narrow but long talonid, entoconid more buccal but hypoconid in approximately the same position, and hypoconulid not reduced. In M1,2 the relative heights of the cusps in decreasing order are protoconid, metaconid, entoconid, paraconid and subequal hypoconid and hypoconulid. In M3 the order is metaconid, protoconid, paraconid, entoconid and subequal hypoconid and hypoconulid.

Measurements. Measurements of the holotype and paratypes of Riversleigha williamsi are given in Table 1.

Comparisons

Riversleigha williamsi gen et sp. nov. shares many similarities in skull and dental morphology with other endemic Australian hipposiderids, including northern Australia’s living Rhinonicteris aurantius and the Riversleigh Miocene taxa Brachipposideros nooraleebus, ?B. watsoni and R. tedfordi (Sigé et al. 1982; Hand 1997b). Similarities include the broad rostrum, subparallel tooth rows, very tall zygomatic projection, pronounced accessory cusp on C1 and little reduced upper and lower M3s. Several of these features are also shared with the Riversleigh Miocene Xenorhinus halli gen. et sp. nov. (Hand 1998). However, Riversleigha differs from species of Rhinonicteris and Brachipposideros in its longer, more constricted interorbital region, deeper rostrum, less inflated braincase, incipient groove developed in the mesopterygoid roof, its robust dentary and taller C1, and coronoid process. Additionally, it differs from Rhinonicteris species in its anteriorly extended sagittal crest, and from species of Brachipposideros in the strong development of its sagittal and lambdoidal crests. It differs from the peculiar Xenorhinus halli in, among other features, its much longer palate, less ventrally rotated rostrum, narrow interorbital constriction and strong development of its sagittal and lambdoidal crests. It differs from Miophyllorhina riversleighensis of Riversleigh’s early Miocene RV Site in, among other features, its retention of P2.

It appears to share less similarities with Australia’s other five living hipposiderid species, all of which belong to the genus Hipposideros. Within this speciose and morphologically diverse genus (containing at least 55 species), a number of species groups are recognised (e.g. Hill 1963; Koopman 1994), although some of these may not be monophyletic (Hand & Kirsch in press, Bogdanowicz & Owen in press). Living Australian hipposiderids belong to the three major divisions traditionally recognised (e.g. Koopman 1994): Hipposideros ater and H. cervinus to Division 1 (>32 species), H. semoni and H. stenotis to Division 2 (8 species), and H. diadema to Division 3 (>15 species). Division 1 and 3 taxa are widely distributed throughout the Old World tropics, while Division 2 taxa are restricted to the
<table>
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<tr>
<th>Measurement</th>
<th>Holotype QM F24100</th>
<th>Paratype QM F24103</th>
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Table 1. Skull, dentary and tooth measurements of the holotype and paratypes of *Riversleigha williamsi* n. gen. et sp. from the Miocene Bitesanternary Site, Riversleigh, northwestern Queensland. Abbreviations: max. = mamimum; l = length; w = width; T = trigonid; t = talonid. Numbers in parentheses indicate estimates.

Australia's *Hipposideros ater* and *H. cervinus* and other species of Hill's Division I are generally small species characterised by a narrow, usually short rostrum and conspicuously broader, inflated braincase, anteriorly convergent toothrows, marked constriction of the posterior sphenorbital bridge, a diamond-shaped basisphenoid, gracile dentary, and usually reduced M3s. *Riversleigha williamsi* shares with these taxa similar proportions of P4 (short and narrow), an elongate infraorbital foramen and V-shaped anterior palate, but differs from them in its much broader and longer rostrum (except perhaps in the *calcarius* subgroup), longer and more constricted interorbital region, smaller and narrower braincase, well-developed sagittal and lambdoidal crests, more distinct supraorbital ridges, much taller zygomatic projection, subparallel toothrows, poorly developed groove in mesopterygoid roof, hexagonal basicranial region, robust dentary, (typically) better developed secondary cusp on C′, and less reduced M3s.

The living East African species *H. megalotis* is also generally referred to Hill's (1963) Division 1, although some authors refer it to the subgenus *Syndesmotis* along with North African and European Neogene species (e.g. Legendre 1982). *Syndesmotis megalotis* differs from *Riversleigha williamsi* in many of the features noted above for Division I taxa, but additionally in its U-shaped junction between premaxillae and maxillae, round sphenoidal fissure, very narrow basicranial, greatly enlarged petrosals, absence of P2, more reduced M3 and relatively much shorter C1.

Australia's *Hipposideros semoni* and *H. stenotis* and other Division 2 species are generally characterised by a long, broad, very inflated rostrum, constricted and usually short interorbital region, inflated braincase, subparallel toothrows, marked posterior constriction of the sphenorbital bridge, extremely enlarged petrosals and narrow basioccipital. *Riversleigha williamsi* shares with these species subparallel toothrows and little reduced M3s, but differs most conspicuously in its narrower skull, much less expanded petrosals, less inflated rostrum and braincase, elongated infraorbital foramen, tall zygomatic projection, V-shaped anterior palate, posteriorly broad sphenorbital bridge, poorly developed groove in mesopterygoid roof, separate optic foramen and sphenorbital fissure (i.e. not confluent), only moderately enlarged petrosals, broader basioccipital region, secondary cusp on C′, narrower P4 with lingual cingulum and cusp, and its robust dentary.

*Hipposideros diadema* from Australia and other Division 3 species (*pratti*, *armiger*, *speoris*, *diadema* and *commersoni* groups) are generally large species characterised by a long, broad, poorly inflated rostrum, moderately constricted and long interorbital region, poorly inflated braincase, subparallel toothrows, tall zygomatic projection, poor posterior constriction of the sphenorbital bridge, only moderately expanded petrosals and hexagonal basioccipital. It is with Division 3 taxa that *Riversleigha* perhaps shares most similarities, particularly with species of the *diadema* group. Similarities include the relative proportions and height of the rostrum and braincase, overall skull shape, broad V-shaped anterior palate (although this is U-shaped in some *diadema* group taxa), tall sagittal crest extending posteriorly to well developed lambdoidal crests and anteriorly into the interorbital region, elongate infraorbital foramen, subparallel toothrows, long palate, and moderate expansion of the petrosals. Features shared additionally with other Division 3 taxa include: with the *commersoni* group, a very similarly constricted posterior sphenorbital bridge; and with the *speoris* group a similarly extruded P2, similar P4 and distinct supraorbital crests.

*Riversleigha williamsi* differs from Division 3 taxa in its relatively long, narrower skull with wider zygomata and taller projections, large accessory cusp on C1 and little reduction of M3s. Additionally, *Riversleigha williamsi* differs: from species of the *diadema* group in its much taller and longer zygomatic projection, more constricted posterior sphenorbital bridge, less extruded P2 and narrow P4; from species of the *pratti*, *armiger* and *commersoni* groups in its V-shaped
anterior palate; from the *pratti* and *speoris* groups in its taller, more complete sagittal crest, hexagonal basisphenoid and less expanded petrosals; from the *armiger* group in its longer, more constricted interorbital region, taller rostrum, greater zygomatic width, elongate infraorbital foramen, slightly more constricted posterior sphenorbital bridge, lack of basisphenoid attachment to periotics, and shorter coronoid process; from the *speoris* group in its broader foreanum and more robust dentary; and from the *commersoni* group in its less developed sagittal and lambdoidal crests, elongate infraorbital foramen, inflated frontal region, more gracile dentary, lower coronoid process, smaller upper and lower canines, and larger, less extruded P2.

Hugueney (1965) noted that fossil species of *Pseudorhinolophus* appear to have a similar basic morphology to that of some large Recent species of *Hipposideros* (e.g. *H. armiger*, *H. diadema* and *H. commersoni*). Because of similarities in teeth, skull and postcranial anatomy, Sigé (1968) regarded *Pseudorhinolophus* to be a fossil subgenus of *Hipposideros*. At least seven species of *Pseudorhinolophus* are reported from middle Eocene to middle Miocene sediments of Europe (Sigé 1995) and possibly the early Oligocene of northern Africa (Sigé et al. 1994). *Riversleigha williamsi* shares with *Pseudorhinolophus* species many of the features noted above for Division 3 taxa, including large size and similar basic proportions, large rostrum, distinct supraorbital ridges, V-shaped anterior palate, tall zygomatic projection, distinct lambdoidal crests, and sagittal crest continuous from anterior to posterior extremity of the skull. *Riversleigha williamsi* shares several similarities, particularly in dentition, with species of *Palaeophyllophora*, extinct taxa known only from late Eocene to late Oligocene karstic sediments of Quercy, France (Remy et al. 1987). *Palaeophyllophora* species are ancient but autapomorphically highly specialised hipposiderids which exhibit conspicuous elongation of the M1-2 postmetacristae and lateral compression of the M3 trigonid as well as M1-3 with low, short talonids and hypoconulids medially situated, reduced M3s, P3 wider than long and C1 lacking accessory cusp. In skull morphology, *Riversleigha williamsi* differs from species of *Palaeophyllophora* in, among other features, its V-shaped anterior palate, distinct supraorbital ridges, narrower zygomatic width, much taller zygomatic projection, hexagonal basisphenoid and less expanded petrosals.

The genus *Asellia* is known from two living species distributed in northern Africa and southwestern Asia and fossil taxa from the Neogene of Africa and Europe (Legendre 1982). Similarities shared by *R. williamsi* and *Asellia* species include the tall sagittal crest in the interorbital area, well-developed lambdoidal crests, relatively tall coronoid process and broad sphenorbital bridge. It differs from species of *Asellia* in its relatively much longer skull, longer and narrower interorbital area, longer rostrum, taller braincase and lower rostrum, taller sagittal crest, much taller zygomatic projection, lower coronoid process, different shaped accessory cusp on C1, presence of P2, much less reduced M3, larger P2, and less enlarged petrosals.

*Riversleigha williamsi* shares fewer similarities, particularly in dentition, with species of *Palaeophyllophora*, extinct taxa known only from late Eocene to late Oligocene karstic sediments of Quercy, France (Remy et al. 1987). *Palaeophyllophora* species are ancient but autapomorphically highly specialised hipposiderids which exhibit conspicuous elongation of the M1-2 postmetacristae and lateral compression of the M3 trigonid as well as M1-3 with low, short talonids and hypoconulids medially situated, reduced M3s, P3 wider than long and C1 lacking accessory cusp. In skull morphology, *Riversleigha williamsi* differs from species of *Palaeophyllophora* in, among other features, its V-shaped anterior palate, distinct supraorbital ridges, narrower zygomatic width, much taller zygomatic projection, hexagonal basisphenoid and less expanded petrosals.

Three other hipposiderid genera, represented by living species, are also autapomorphically highly specialised. The genus *Coelops* contains two species distributed throughout southeast Asia and west to northeastern India; the evidently closely related *Paracoelops* is known only from the type specimen collected in Vietnam; and the monotypic *Cloeotis* occurs in southeastern Africa. Species of *Coelops*, *Paracoelops* and *Cloeotis* differ strikingly from *R. williamsi* in having a much smaller rostrum with less inflated na-
sals, an inflated braincase, short, unconstricted interorbital region, poorly developed sagittal and lambdoidal ridges, small zygomatic projection, conspicuously enlarged foramen magnum and foramen ovale, C\textsuperscript{1} with anterior accessory cusp, \textit{C}, much shorter, and very gracile dentary with low coronoid process. Similarities include little reduced M3s and posterior cusp of C\textsuperscript{1}. Additionally, species of \textit{Coelops} and \textit{Paracoelops} differ from \textit{R. williamsi} in having \textit{C}\textsubscript{2} separated from \textit{C}\textsubscript{1} by a conspicuous gap, and \textit{\textit{P}^2-M^3} more rhinolophid-like than hipposiderid-like; \textit{Cloeotis percivali} differs from \textit{R. williamsi} in its markedly constricted posterior sphenorbital bridge and divergent ridges running from the base of the pterygoids to the petrosals.

Sigé (1990) erected the genus \textit{Vaylatsia} in the Hipposideridae for fossil taxa with dental morphology very close to that of Neogene (and extant) \textit{Rhinolophus} species but with the distal end of the humerus exhibiting morphology characteristic of hipposiderids. Little is yet known about the cranial morphology of species of \textit{Vaylatsia} but preliminary examination of a crushed, partial skull of \textit{Vaylatsia cf. prisca} from the early Oligocene Quercy deposit of Mas de Got indicates that \textit{Riversleigha williamsi} differs strikingly from \textit{Vaylatsia} in, among other features, its long, constricted interorbital region, less inflated rostrum, shorter braincase, well-developed sagittal and lambdoidal crests, \textit{V}-shaped anterior palate, posterior cusp on \textit{C}\textsuperscript{1}, and robust dentary with taller \textit{C}\textsuperscript{3} and somewhat taller coronoid process.

\textit{Riversleigha williamsi} shares more similarities with species of \textit{Anthops}, \textit{Triaenops} and \textit{Aselliscus}. The rare, monotypic, living \textit{Anthops ornatus} of the Solomon Islands is one of two genera (the other being \textit{Rhinonicteris}) endemic to the Australian region. \textit{Triaenops} is known from two living species in Africa, Madagascar and southwestern Asia. The genus \textit{Aselliscus} has a disjunct distribution, with \textit{A. stoliczkanus} being confined to southeastern Asia and \textit{Aselliscus tricuspidatus} to the Moluccas and islands east to the New Hebrides. \textit{Riversleigha williamsi} shares with these species little reduced M3s as well as the following: with species of \textit{Triaenops} and \textit{Aselliscus}, a broad sphenobrachial bridge and \textit{P}^2 in the toothrow; with species of \textit{Anthops} and \textit{Triaenops}, tall upper and lower canines; with \textit{Anthops ornatus}, very marked interorbital constriction and relatively tall coronoid process; and with species of \textit{Triaenops}, a very tall zygomatic projection. \textit{Riversleigha williamsi} differs most conspicuously from these species in its very long interorbital region, less inflated and shorter braincase, and less expanded petrosals. Additionally, it differs: from species of \textit{Anthops} and \textit{Aselliscus}, in its relatively much larger rostrum, much taller zygomatic process, well-developed sagittal and lambdoidal crests, and robust dentary; from species of \textit{Triaenops} and \textit{Aselliscus}, in its longer, narrower skull, much more constricted interorbital region and taller coronoid process; from \textit{Triaenops} species, in its smaller rostrum and absence of the infra-condyloid dentary foramen unique to \textit{Triaenops} species; from \textit{Anthops ornatus} in its broad posterior sphenobrachial bridge; and from \textit{Aselliscus} species in its much less inflated rostrum, posterior cusp on \textit{C}\textsuperscript{1} and much taller \textit{C}\textsuperscript{3}.

\textit{Riversleigha williamsi} gen et sp. nov. is a relatively large hipposiderid. Based on skull length, it is larger than Division 1 \textit{Hipposideros} taxa and most Division 2 species, falling within the size range of Division 3 taxa (Hill 1963, table 2) as well as species of \textit{Pseudorhinolophus} and \textit{Palaeophyllophora} (Reviilliod 1917, 1922; Sigé 1968, 1978), and \textit{Xenorhinos} (Hand 1998). It is probably comparable in size to living species such as \textit{Hipposideros cyclops}, \textit{H. turpis} and \textit{H. larvatus} but smaller than, among others, \textit{H. diadema}, \textit{H. lankadiva}, \textit{H. inexpectatus} and \textit{H. commersoni} (Hill 1963, table 2; Kitchener et al. 1992, table 1a; Kitchener & Maryanto 1993). A detailed study of intraspecific morphological variation in the large sample of \textit{R. williamsi} from Riversleigh's Bitesentenary Site is underway.

### Phylogenetic relationships

On balance, the phenetic comparisons above suggest apparent affinities of \textit{Riversleigha
to other Australian endemic and fossil hipposiderids (species of *Rhinonicteris*, *Brachipposideros* and possibly *Xenorhinos*) as well as some groups of *Hipposideros* species (e.g. Division 3 species). However, phylogenetic analysis does not clearly resolve the relationships of this new hipposiderid. Hand & Kirsch (in press) included *R. williamsi* in a phylogenetic analysis of the interrelationships of genera and species groups in the family Hipposideridae. Included in their PAUP 3.1.1 (Swofford 1993) and Hennig86 (Farris 1988) analyses were 30 extant hipposiderid species and seven fossil taxa which they scored for 59 discrete characters (36 cranial, 20 dental, and 3 skeletal). Results of these analyses indicate that the family Hipposideridae is probably monophyletic, that the genus *Hipposideros* is probably paraphyletic, and that the composition of some previously-proposed divisions within *Hipposideros* may need re-examination. These same general conclusions were also reached by Bogdanowicz and Owen (in press) in their recent phylogenetic analysis of the family Hipposideridae in which they examined 45 metrical and 30 discrete-state characters in 57 extant hipposiderid species (but no fossil taxa).

The study by Hand & Kirsch (in press) could not unambiguously resolve the relationships of several endemic Australian taxa, including *Riversleigha williamsi*, finding that craniodental data alone were insufficient to resolve the phylogenetic history of the family Hipposideridae. A number of equally parsimonious hypotheses of the interrelationships of hipposiderid taxa were proposed and these are summarised here in Fig. 4. In the first hypothesis of relationship (Fig. 4A), *R. williamsi* appears to be a basal member of a clade comprised of species of *Anthops*, *Asellia*, *Hipposideros*, *Palaeophyllophora*, *Pseudorhinolophus* and *Xenorhinos*, and not especially closely related to other Australian fossil hipposiderids including species of *Brachipposideros* and *Rhinonicteris*. Apparent, unequivocal apomorphies shared by *R. williamsi* and species of *Anthops*, *Asellia*, *Hipposideros*, *Xenorhinos*, *Palaeophyllophora* and *Pseudorhinolophus*, but not most other Australian fossil taxa, include an elongate and medially positioned infraorbital foramen, mesopterygoid roof with groove, a small P4 and relatively tall ascending ramus.

In the second hypotheses (Fig. 4B-C, based on PAUP and Hennig86 analyses respectively), *R. williamsi* appears to be most closely related to other extinct and/or endemic Australian taxa, as well as African species of *Triaenops* and, more distantly, *Cloeotis* and *Coelops*. Bogdanowicz & Owen (in press) also suggested close relationships between *Cloeotis* and *Cloeotis*, and *Triaenops* and *Rhinonicteris*. Hill (1982) grouped species of *Rhinonicteris*, *Triaenops* and *Cloeotis* on the basis of external as well as craniodental features, interpreting *Triaenops* as being possibly closer to *Rhinonicteris* than to *Cloeotis*. Koopman (1994) included the three genera in his subtribe Rhinonycterina. Apparent apomorphies shared by Australian endemic hipposiderid genera and species of *Triaenops* include thickened, crested premaxillae, a posteriorly placed (dorsal to M3) infraorbital foramen, and mesopterygoid roof without, or with incipient, groove.

**Discussion**

Hipposiderids, or Old World leaf-nosed bats, dominate Riversleigh’s Oligo-Miocene bat faunas in both abundance and diversity, representing 22 of 40 bat species identified, with megadermatids, molossids, vespertilionoids and emballonurids comprising the rest (Archer et al. 1994). Almost all living hipposiderids are cave-dwellers and most extinct taxa have been recovered from cave or karstic deposits. In some Riversleigh deposits (e.g. Upper and Bitesantennary Sites), as many as eight hipposiderid species (representing four genera) appear to be syntopic. This exceeds the number known from modern faunas (5-6 species in parts of southeastern Asia and New Guinea; e.g. Payne et al. 1985; Flannery 1990) and European Tertiary assemblages (commonly 5 species, Remy et al. 1987). However, these same fossil and modern bat faunas also include many species of the fam-
family Rhinolophidae, the closely related sister-group of the Hipposideridae. Today, in unspoilt rainforest areas such as in western Malaysia, it is not uncommon to find 12 syntopic species of hipposiderids and rhinolophids (Heller & Helversen 1989; Francis 1990). No rhinolophids (nor pteropodids; the other two bat families represented in the modern Australian fauna) have been found at Riversleigh, or elsewhere in the Australian Tertiary record. Only two living (non-endemic) Rhinolophus species occur in Australia, a relatively depauperate and possibly recent fauna compared with those of southeastern Asia and New Guinea. In Australian tropical palaeofaunas, such as those of Riversleigh, hipposiderids perhaps filled the rhinolophid niche.

Riversleigha is one of six genera of hipposiderids now recorded from Riversleigh, and one of four (with Rhinonicteris, Xenorhinos and Miophyllorhina) known only from Australia (Hand 1997a, b, c, 1998). Species of Brachipposideros and Hipposideros have broader distributions: the former in Oligocene-Miocene sediments of western Europe and northern Africa (Sigé et al. 1994), and the latter represented by at least 55 modern species throughout the Old World tropics. Hipposideros bernardsi is of Riverseigh’s early Miocene Neville’s Garden Site is the first Tertiary species to be referred to H. (Hipposideros) (Hand 1997a). Skulls have been described for all hipposiderid genera represented at Riversleigh with the exception of Miophyllorhina, although additional, generically-distinct, but less well-represented hipposiderid taxa have yet to be described. Hipposiderid taxa occurring in European and African Tertiary deposits but not known from Australia include Palaeophylylophora, Vaylatsia, Asellia and the Hipposideros subgenera Pseudorhinolophus and Syndesmotis.

Phylogenetic analyses by Hand & Kirsch (in press) have produced two equally parsimonious interpretations of the interrelationships of most hipposiderid genera and species groups (Fig. 4), and the exact phylogenetic position of R. williamsi remains unclear. It appears to represent a relatively plesiomorphic lineage of hipposiderids, occurring towards the base in all phylogenetic trees. Nevertheless, the two equally parsimonious phylogenetic interpretations (Fig. 4) have quite different biogeographic implications. As a member of a monophyletic group dominated by Australian taxa (as suggested by Fig. 4A), its origins probably lie in the Australian region, if not northern Australia itself, possibly being derived from a Brachipposideros-like ancestor. Hand & Kirsch (in press) have argued that the primary radiation of the family Hipposideridae could have occurred in the Australian Region, since many of the most plesiomorphic hipposiderid taxa occur there. If, on the other hand, it is not especially closely related to other Australian taxa (as suggested in Fig. 4B-C) and instead is a basal member of a clade of more derived hipposiderid taxa dominated by non-Australian taxa (species of Hipposideros, Asellia, Palaeophylylophora and Pseudorhinolophus), then its origins may lie further afield.

Riversleigha williamsi seems to share a number of cranial features in common with relatively large hipposiderid species, probably convergently. The tall sagittal crest, well-developed lambdoidal crests and relatively large teeth are features that characterise diverse groups of hipposiderids whose members are generally large, such as Hill’s (1963) H. diadema group and Tertiary species of Pseudorhinolophus. These features are not found in all large hipposiderids; for example, Xenorhinos hallii (with its otherwise similar skull but not dental dimensions; Hand 1998,

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Fig. 4. Summary of 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. Symbols: † Tertiary species, * taxon includes Tertiary representatives.
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Table 1) and *Triaenops* species show little development of these features. They are developed to the extreme in Africa’s *Hipposideros commersoni*, at 150 g the world’s largest insectivorous bat, which specialises in eating large, heavily armoured beetles but also feeds on termites and other insects (Kingdon 1974; Vaughan 1977). Well-developed cranial crests provide large areas for muscle attachment (e.g. the temporalis) and large teeth ( occlusal surface area relative to skull length) provide broad crushing surfaces. Such features have generally been correlated in mammals with the type and volume of prey consumed (e.g. Lucas & Luke 1984; Freeman 1988); orientation of the temporal muscle and the height of the condyle above the toothrow has been correlated with bite force (Emerson & Radinsky 1980). The sagittal crest is tall in *R. williamsi*, the temporalis evidently vertically-oriented, and the condyle is relatively tall. However, Freeman (1984, 1988) has found that several of the features usually correlated with prey capture and consumption in mammals are, in bats, also correlated with the degree of rostral rotation of the skull and ultimately by the type of echolocation used (i.e. nasal- or oral-emission; see also Pedersen 1993, 1995). It appears that prey detection may be affecting the cranial morphology of microchiropterans as much as or more than prey consumption.

Kingdon (1974) has suggested that the tall projections of the zygoma in *Triaenops persicus* may be for broad attachment of the muscles supporting this species’ large rostrum and complex nose-leaf. The same zygomatic projections also occur in most endemic Australian hipposiderids, that is, in species of *Rhinonycteris*, *Brachipposideros*, *Xenorhinos* and *Riversleighia*. Hill (1982) cited this feature as part of the evidence supporting a close evolutionary relationship between species of *Triaenops* and *R. aurantius*. Zygomatic projections do occur in other evidently unrelated taxa, including, again, large hipposiderids such as *H. commersoni*, *H. larvatus* and species of *Pseudorhinolophus*. It is unclear whether or not in *R. williamsi* this feature represents an apomorphy shared with members of the subtribe Rhinonycterina or an autapomorphy related perhaps to its diet or nose-leaf construction. The very tall projection is probably not plesiomorphic for hipposiderids since it is not especially common, nor does it occur in potential sister-groups (i.e. rhinolophids, megadermatids or nectaruids).

All living hipposiderids appear to be insectivorous, dietary generalists whose size determines maximum but not minimum prey size (Fenton 1984; Findley 1993). They are slow manoeuvrable fliers with short, broad wings, which forage by hovering and gleaning, hawking from observation perches, or by aerial pursuit (Findley 1993), evidently always near and within vegetation (Heller & Helversen 1989). Among hipposiderids, there is an inverse relationship between body size and call frequency, with larger species that catch larger prey able to use lower frequency (longer wavelength) calls (Novick 1977; Heller & Helversen 1989; Hall 1989). This is also generally reflected in the relative size of the petrosal: the greater petrosal expansion, the higher the frequency of the call (Novick 1977). Not surprisingly, most large hipposiderids (e.g. Division 3 taxa of the genus *Hipposideros*) have relatively unexpanded petrosals, as does *R. williamsi*, although other groups (e.g. species of *Anthops*, *Palaeophyllophora* and Division 2 *Hipposideros* taxa) include relatively large species with greatly enlarged petrosals. Large species also appear to have higher aspect ratio wings and be faster, more direct fliers (e.g. *Hipposideros diadema* of the rainforests and woodlands of northern Australia, New Guinea and southeastern Asia; Hall 1989).

Among Riversleigh hipposiderids, *R. williamsi* is one of the largest species (based on skull length), has the largest teeth (occlusal surface area), and exhibits the most pronounced development of the sagittal and lambdoidal crests. Only Riversleigh’s megadermatid species are bigger bats, these showing the conspicuous dental adaptations for facultative carnivory that characterise that family (Hand 1996). By analogy with modern hipposiderid species, *R. williamsi* probably used a lower frequency call and had higher
aspect ratio wings than other hipposiderids in the Riversleigh forests of the early Miocene, and perhaps like Australia's largest living hipposiderid *H. diadema*, it preyed upon large, heavily armoured beetles, as well as moths, weevils, ants and parasitic wasps that commonly comprise the diet of all living hipposiderids.

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REFERENCES


