First Australian Pliocene species of *Hipposideros* (Microchiroptera: Hipposideridae)

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Abstract – A new Australian Pliocene hipposiderid is described on the basis of maxillary fragments representing at least four individuals recovered from Rackham's Roost Site, Riversleigh World Heritage property, Lawn Hill National Park, northwestern Queensland. *Hipposideros winsburyorum* sp. nov. is distinguished from all other *Hipposideros* species (and all other hipposiderids) by its very large, round infraorbital foramen. Dentally, it shares most similarities with members of the diverse and widespread *Hipposideros bicolor* group of Hill (1963) as well as *Hipposideros megalotis* of East Africa and the extinct *H. (Syndesmotis) vetus* lineage from the middle Miocene of Morocco and Pliocene of France.

INTRODUCTION

Tertiary deposits in the Riversleigh World Heritage property, Lawn Hill National Park, northwestern Queensland are particularly rich in the remains of members of the bat family Hipposideridae (Sigé *et al.* 1982; Hand 1993, 1997a, 1997b, 1997c, 1998a, 1998b). This Old World family contains 65 living species, referred to the genus *Hipposideros* (53 species) and eight other genera (of one or two species each): *Rhinonicteris, Coelops, Paracoelops, Triaenops, Cloeotis, Anthops, Asellia,* and *Aselliscus* (Koopman 1994). Within *Hipposideros*, a number of species groups is generally recognized (e.g., Gray 1866; Peters 1871; Tate 1941; Hill 1963). Recent authors (e.g., Koopman 1994) generally accept Hill's (1963) seven species groups or subgroups (i.e., the *H. megalotis, bicolor, cyclops, speoris, pratti, armiger,* and *diadema* subgroups), with some also recognizing the subgenus *Syndesmotis* for *H. megalotis* (e.g. Legendre 1982). Hill (1963) further grouped *Hipposideros* species into three primary divisions (i.e., the *bicolor, cyclops* and *diadema* groups) interpreted to represent three distinct evolutionary trends within the genus.

Recent Australian hipposiderids include five species of *Hipposideros* (representing the *bicolor, cyclops* and *diadema* groups) and the endemic *Rhinonicteris aurantius*, all of which inhabit warm humid caves in tropical to subtropical latitudes. In the Australian (i.e. Riversleigh) Tertiary record several hipposiderid genera or subgenera are represented: *Brachipposideros, Hipposideros, Rhinonicteris, Miophyllorhina, Xenorhinos* and *Riversleigha* in Oligo-Miocene deposits (Sigé *et al.* 1982; Hand 1997a, 1997b, 1997c, 1998a, 1998b), and *Brachipposideros* and *Rhinonicteris* in Riversleigh's only Pliocene deposit, Rackham's Roost Site (Archer *et al.* 1994). A number of other distinctive Oligo-Miocene hipposiderid taxa awaits description.

In this paper, the first species of *Hipposideros* from the Australian Pliocene is described, based on maxillary fragments from Rackham's Roost Site. Skull terminology follows Hill (1963) and Hand (1997a). Dental terminology follows Sigé *et al.* (1982). The prefix QM F refers to specimens held in the fossil collections of the Queensland Museum, Brisbane.

SYSTEMATIC PALAEONTOLOGY

Authorities for all scientific names not specifically referenced in this paper can be found in Koopman (1994).

Suborder Microchiroptera Dobson, 1875

Superfamily Rhinolophoidea Weber, 1928

Family Hipposideridae Miller, 1907

Hipposideros Gray, 1831

Hipposideros winsburyorum sp. nov.
Figure 1; Table 1

Material Examined

Holotype
    QM F30571, a right maxilla fragment with P⁴-M² and alveoli for C¹ and M³.

Paratypes
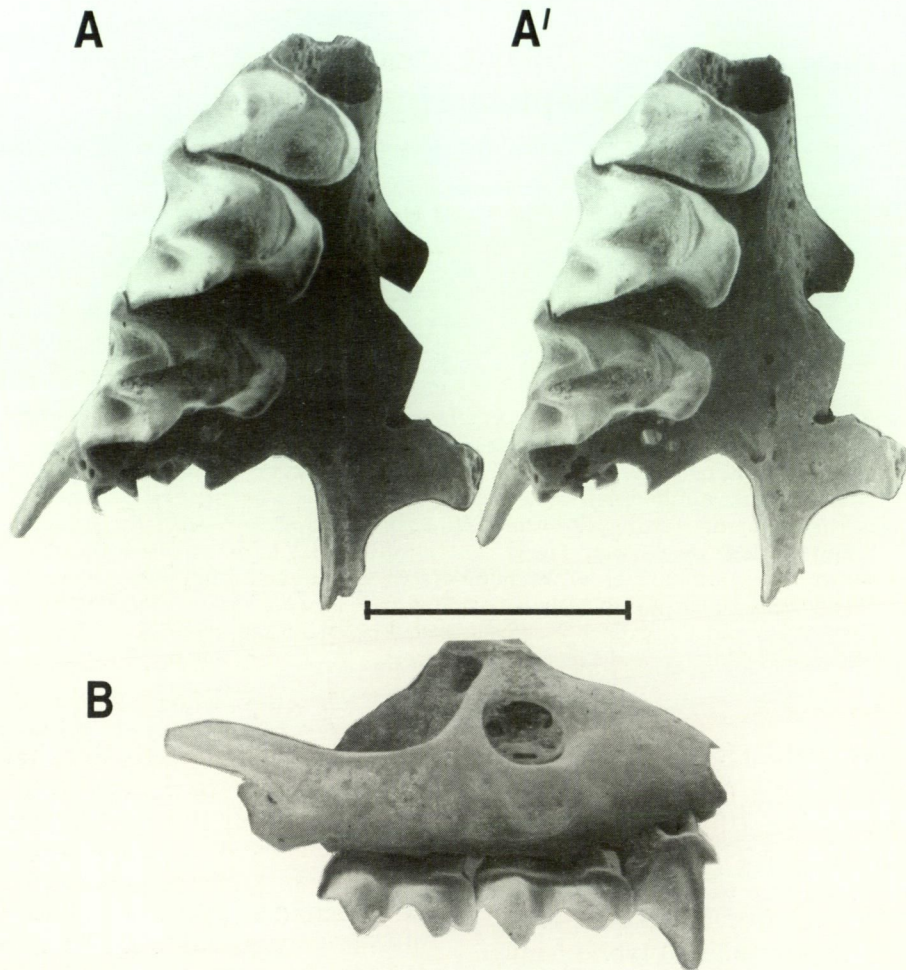   QM F30572, a right maxilla fragment with P⁴-M²

Figure 1 *Hipposideros winsburyorum* sp. nov., from the Pliocene Rackham's Roost Site, Riversleigh World Heritage property, Lawn Hill National Park, northwestern Queensland. QM F30571, holotype, right maxilla containing P^4, M^{1-2}. A-A', oblique-occlusal view, stereopair; B, lateral view. Scale = 2 mm.

and alveoli for C^1 and M^3; QM F30573, a left maxilla fragment with M^1 and alveoli for P^4 and M^{2-3}; QM F30574, a right maxilla fragment with P^4-M^1 and alveolus for C^1 and M^2; QM F30575, a left maxilla fragment with P^4-M^1; QM F30576, a right maxilla fragment with P^4-M^2.

Type Locality, Age and Associated Fauna

The type locality, Rackham's Roost Site (Godthelp 1987, 1997; Archer *et al.* 1989, 1994; Hand 1995, 1996), occurs at 19°02.09'S., 138°41.60'E. (Global Positioning Satellite device) in the Riversleigh World Heritage property, Lawn Hill National Park, northwestern Queensland. It appears to represent the indurated floor of a long, narrow cave developed in Cambrian Thorntonia Limestone. The sediment is a breccia of tiny, mostly fragmented, bones and teeth set in a fine-grained, pink-coloured (presumably iron-stained) limestone. The deposit covers an area of approximately 200 m², with a maximum depth of 0.5 to 1.0 m.

The deposit is interpreted to be Pliocene in age

because it contains a macropodid similar to *Protemnodon snewini* Bartholomai, 1978 from the early Pliocene Bluff Downs Local Fauna of northeastern Queensland (Archer and Wade 1976) and abundant plesiomorphic murids, including *Zyzomys rackhami* Godthelp, 1997, several species of *Pseudomys* and a number of new genera. The Rackham's Roost deposit also contains the remains of crustaceans, fish, frogs, lizards, small crocodiles, snakes, birds, dasyurids, peramelids, a pseudocheirid, an extinct potoroid, two emballonurids (*Taphozous* spp.), at least four other hipposiderids, four vespertilionids, the small megadermatid *Megaderma richardsi* and the large, living Ghost Bat *Macroderma gigas* (Hand 1995, 1996; Boles 1998). The very finely broken remains of the small vertebrates and depressed fractures and impressions in the bones characteristic of Recent *Macroderma gigas* canines suggest that the deposit largely represents the remains of prey accumulated by an early population of that species. Boids, the emballonurids, hipposiderids and vespertilionids probably cohabited the megadermatid roost; the

Table 1 Measurements (in mm) of types of *Hipposideros winsburyorum* sp. nov. from the Pliocene Rackham's Roost Site, Riversleigh, northwestern Queensland. l = maximum length; w = width; – = tooth absent.

		Holotype	Paratypes				
	QM F	30571	30572	30573	30574	30575	30576
P^4	l	0.91	0.86	–	0.80	0.81	0.82
	w	1.25	1.28	–	1.20	1.20	1.10
M^1	l	1.36	1.34	1.39	1.30	1.22	1.28
	w	1.34	1.30	1.38	1.35	1.29	1.37
M^2	l	1.25	1.21	–	–	1.18	–
	w	1.39	1.39	–	–	1.34	–

macropodid remains were recovered from what was possibly an entrance to the cave.

Diagnosis

This *Hipposideros* species differs from all others in the following combination of features: exceptionally large, round infraorbital foramen, low on the face and dorsal to P^4-M^1; anteriorly convergent toothrows; anterior margin of palate U-shaped; loss of P^2; P^4 wider than long, with shallow lingual cingulum and poorly developed anterolingual cingular cusp; M^1 with small, posterolingually developed heel and posteriorly opening protofossa; M^2 with little heel development; M^3 reduced in length and width. Assignment of the new species to the genus *Hipposideros* is discussed in Remarks (below).

Etymology

The species is named for Keith and Janet Winsbury, long-term supporters of the Riversleigh fossil research.

Description

The new taxon is known from six maxillary fragments: the holotype QM F30571 and the five paratypes listed above. The material represents at least four individuals. All specimens preserve the infraorbital foramen and all clearly lack an alveolus for P^2. The lower dentition is not yet known. Several dentary fragments of appropriate size, and possibly dental morphology, have been recovered from among hundreds of Rackham's Roost hipposiderid specimens, but they are not sufficiently complete to confidently assign to *Hipposideros winsburyorum* (see also Remarks below).

The infarorbital foramen is extremely large and round, with a minimum diameter of 0.5 mm. It is situated low on the face and dorsal to P^4-M^1. It is enclosed by a narrow bar of bone (the antorbital bar) that is straight, almost perpendicular to the zygoma and of equal thickness throughout (i.e. it lacks a wing). A foramen (?lacrimal) opens directly above the anterior attachment point of the antorbital bar at the edge of the circumorbital rim. The lateroventral fossa, a deep and very broad fossa in the ventral part of the anterior recess of the orbital fossa, exposes the maxillary covering the roots of the posterior cheek teeth; in this region, the maxillary is perforated by many foramina. In lateral view, the ventral margin of the orbit extends to a point level with the posterior face of M^1, its anterolateral rim being low and rounded (rather than raised and sharp).

The midline of the palate is preserved posteriorly but not anteriorly; it appears, however, to have been quite short. The posterior extension of the midline of the palate is level with the posterior face of M^2; it does not extend posteriorly beyond the toothrow. The palation (Hill 1963) appears to have been shallow but round with no postpalatal spine. The posterolateral indentation (incisura) extends anteriorly to at least the level of the posterior face of M^2. The palate's anterior border, for the junction with the premaxillae, extends posteriorly at least to the level of the metacone of M^1, has a rounded lateral margin and was evidently a broad U-shape. Assuming that the anterolateral margins of the sphenorbital bridge were subparallel (as in most hipposiderids), the toothrows would have converged anteriorly.

The alveolus for C^1 is broken anteriorly in QM F30571 but is complete in QM F30572 and QM F30574. These alveoli indicate that it was not a particularly long tooth, with a relatively rounded rather than flattened root. P^2 is completely lacking, there being no sign of an alveolus for this tooth either within or extruded (lingually or buccally) from the toothrow. P^3 is also absent, as in all hipposiderids. P^4 is wider than long, and only just narrower than M^1 and M^2. The lingual cingulum is shallow but distinct and virtually complete. The anterobuccal cingular cusp is poorly developed and the anterolingual cingular cusp lacking.

M^{1-3} all have three roots. In M^{1-2} the heels are poorly developed such that the teeth are conspicuously shorter lingually than buccally (i.e., they are not squared). M^1 has a small but distinct posterolingually-directed heel, while M^2 virtually lacks a heel. In these teeth the postprotocrista approaches but does not meet the base of the metacone so that the protofossa is open posteriorly, noticeably more so in M^1 than in M^2. There is no crest issuing from the end point of the postprotocrista in either M^1 or M^2. The lingual and posterior cingula are continuous in M^{1-2} and the posterolingual cingulum surrounding the heel only slightly thickened. The three alveoli for M^3 indicate it was reduced in both length and width. The

paracone root alveolus occurs on the buccal margin of the toothrow, but that for the metacone is lingually displaced such that it occurs on the posterior border of the maxilla. The alveolus for the metacone root is damaged posteriorly but M^3 appears to have been between one-half and two-thirds the length of M^1 or M^2. The alveolus for the protocone root (also damaged) occurs level with the protofossa of M^{1-2}, indicating that M^3 was also signficantly narrower than the other cheekteeth.

Remarks

In lacking P^2, the Rackham's Roost hipposiderid differs from extinct species of *Palaeophyllophora*, *Pseudorhinolophus*, *Brachipposideros* and *Vaylatsia*, and extant species of *Coelops*, *Paracoelops*, *Triaenops*, *Rhinonicteris*, *Anthops* and *Aselliscus*. (*Paracoelops megalotis*, known only from the type specimen, was not examined in this study; its description suggests it is very similar to species of *Coelops*.) In this feature *H. winsburyorum* resembles living and extinct species of *Asellia*, *Cloeotis* and *Miophyllorhina* as well as some species of *Hipposideros*, i.e. *H. megalotis*, *H. sabanus* of the *bicolor* group, *H. stenotis* of the *cyclops* group and the extinct *H.* (*Syndesmotis*) *vetus* lineage of the Miocene of North Africa and Pliocene of southern France (Lavocat 1961; Sigé 1976; Legendre 1982).

The new hipposiderid further shares with species of *Asellia* and some species of *Hipposideros* a significantly reduced M^3. In *A. tridens*, *H. megalotis* and *H. vetus*, M^3 is significantly reduced such that the premetacrista is lost and the tooth is much shorter (just more than one-half the length of M^1 or M^2) and much narrower than P^4-M^2. In *H. sabanus* and the French Miocene *Asellia mariaetheresae* Mein, 1958, M^3 is slightly less reduced, in this way perhaps more closely resembling *H. winsburyorum*. The Rackham's Roost hipposiderid differs from Riversleigh's Miocene *Miophyllorhina riversleighensis* Hand, 1997c (the only other Riversleigh hipposiderid lacking P^2) in its broad P^4 with indistinct anterolingual cingular cusp, and poorly developed heel on M^2.

Of hipposiderids lacking P^2 and with a reduced M^3, only *H. megalotis* and *H. vetus* further share with *H. winsburyorum* a P^4 that is wider than long and lacks an anterolingual cingular cusp.

Hipposideros winsburyorum resembles many species of the *bicolor* group, as well as *H. megalotis* and *H. vetus*, in its small molar heels, posteriorly open protofossae and gracile nature of M^{1-2}. These teeth differ markedly from the squared M^{1-2} typically found in species of *Brachipposideros*, *Rhinonicteris*, *Triaenops*, *Xenorhinos*, *Riversleigha*, *Asellia*, *Aselliscus* and many (but not all) *diadema* group taxa. *Coelops* species differ from *H. winsburyorum* in their M^{1-2} with pronounced heels and very tall posterolingual cingular cusps.

Further, in *Coelops* species the postprotocrista continues posterobuccally as a metacingulum thereby closing the protofossa in M^{1-3}; in species of *Cloeotis* the protofossa is also closed in M^{1-3}, but here the postprotocrista meets the base of the metacone (as it does also in species of the *cyclops* group and *Palaeophyllophora*).

The anterior convergence of the toothrows observed in *H. winsburyorum* is similar to that seen in *H. megalotis* and members of the *bicolor* group as well as species of *Coelops* and *Cloeotis*. In *Cloeotis* species the palate extends posteriorly only to the posterior face of M^2, as in *H. winsburyorum*; in *Coelops*, *H. megalotis* and in most *H. bicolor* species it extends further posteriorly. In species of *Asellia*, *Aselliscus*, *Triaenops*, *Anthops*, *Brachipposideros*, *Rhinonicteris* and the *H. cyclops* and *diadema* groups the toothrows are subparallel reflecting the typically broad rostrum in these groups. The anterior margin of the palate is U-shaped in species of *Asellia*, *Coelops*, *H. megalotis* and some members of the *cyclops* and *diadema* groups, as it is in *H. winsburyorum*, but is more typically V-shaped in species of the *bicolor* group and other hipposiderid genera.

C^1 morphology distinguishes various hipposiderid groups. *Hipposideros megalotis*, *H. vetus*, and species of *Rhinonicteris*, *Triaenops*, *Coelops*, *Cloeotis*, *Anthops*, *Brachipposideros*, *Xenorhinos* and *Riversleigha* possess a well-developed secondary posterior cusp on C^1. Species of *Aselliscus*, *Palaeophyllophora* and members of the *cyclops* group lack this cusp. In *Pseudorhinolophus*, *Asellia* and the *H. diadema* group, the cusp, if present, is generally less well developed. In the *bicolor* group, a tall posterior cusp is variably present and/or developed. The morphology of the C^1 of *H. winsburyorum* is not yet known. Most isolated hipposiderid C^1s from the Rackham's Roost deposit have a discrete posterior secondary cusp but some completely lack the secondary cusp. In hipposiderids, the relative length of the C^1 alveolus does not necessarily reflect secondary cusp development (e.g. *Coelops* and *Cloeotis* spp.).

No dentary fragments have been referred to *H. winsburyorum*. The ascending ramus is taxonomically important in hipposiderids but is missing in all specimens of appropriate size and dental morphology (e.g., P_2 and M_3 reduced) to potentially represent this species. This part of the dentary is diagnostic for *H. megalotis* and *H. vetus* (i.e. low coronoid process and long and outwardly deflected angular process; Legendre 1982) and appears to be characteristic for some species groups of *Hipposideros* (e.g., tall coronoid process in species of the *diadema* and *cyclops* groups). Its height and shape are also diagnostic for species of the *Brachipposideros-Rhinonicteris* lineage (i.e. low coronoid process and broad angular process; Sigé et al. 1982; Legendre 1982).

Hipposideros winsburyorum is unique among hipposiderids in its exceptionally large, rounded infraorbital foramen. At least four individuals, all of similar morphology, are represented in the Rackham's Roost sample, indicating that this is not an aberration. The foramen is unlike the typically elongate infraorbital foramen characterizing most hipposiderids, including *H. megalotis* and members of the *bicolor* group (notwithstanding the fact that the foramen was described by Hill (1963) as somewhat rounded in *H. megalotis*, *H. pygmaeus*, *H. curtus* and *H. beatus* among others). The foramen is also relatively much larger and rounder than in the *speoris*, *pratti*, *armiger* and *diadema* groups. *Hipposideros commersoni* of the *diadema* group is a notable exception but otherwise differs strikingly from *H. winsburyorum* in its very large size, P^4-M^2 morphology, and in the position of the infraorbital foramen (high on the face and dorsal to M^{2-3} rather than very low and dorsal to P^4-M^1 in *H. winsburyorum*). The foramen is perhaps more similar to the foramen characterizing many members of the *cyclops* group, which otherwise differ from *H. winsburyorum* in, among other features, their distinctive molar morphology and subparallel toothrows, as discussed above.

Based on comparisons of tooth size (e.g., Hill 1963, table 2), *Hipposideros winsburyorum* would be similar in size to *Hipposideros ater* and *H. megalotis* both of which are small hipposiderids with forearm lengths of 34–38 mm and 33–43 mm respectively (e.g., Koopman 1994). Other *bicolor* species of similar size include *H. cineraceus* (32–37 mm), *H. pygmaeus* (36–40 mm), *H. sabanus* (37–48 mm), *H. pomona* (37–44 mm), and *H. hallophyllus* (35–39 mm).

DISCUSSION

On the basis of its dental formula and dental and palate morphology, the Rackham's Roost hipposiderid appears to be most similar to East Africa's *Hipposideros megalotis*, the Tertiary *H. vetus* lineage from North Africa and France, and members of the *H. bicolor* group, 33 species of which are distributed widely from Africa to northern Australia and Vanuatu. The relationship of *megalotis* to other *Hipposideros* species is far from clear. Hill (1963) interpreted *megalotis* to be an early but specialized offshoot of the *Hipposideros* lineage and the sole living member of the *megalotis* group, a combined *megalotis-bicolor* group comprising his Division 1 of *Hipposideros*. Legendre (1982) interpreted *megalotis* to be a derived offshoot of the *Brachipposideros* radiation, resurrecting the subgenus *Syndesmotis* for *megalotis* and the Miocene *H. vetus* from North Africa and the Pliocene *H.* sp. cf. *H. vetus* from southern France (Lavocat 1961; Sigé 1976; Legendre 1982). Hand and Kirsch (1998), in

their phylogenetic analysis of fossil and living hipposiderids, found no clear division between the *bicolor* and *megalotis* groups; in some analyses *megalotis* appeared to be among the most plesiomorphic of *Hipposideros* taxa (figure 1b) while in others it nested among *bicolor* taxa (figures 1a and 2b). Additionally, they found no special relationship between *H. megalotis* and the Australian *Brachipposideros-Rhinonicteris* lineage. Bogdanowicz and Owen (1998) also failed to resolve the relationships of *megalotis* in their phylogenetic analysis of 57 living hipposiderid taxa, although in some trees (e.g. figure 3) *megalotis* clustered with *H. sabanus* (among other *bicolor* taxa). In no case, however, did it group with *Rhinonicteris aurantius*.

Hill (1963: 15) described the *megalotis-bicolor* group as a wide variety of loosely-allied species, few of them widespread, and many apparently representing independent lineages. He interpreted them to be the most primitive group in the genus and the group from which the other more specialized sections had been derived. Members of this group are generally small, with broad, usually rounded, ears, typically a simple noseleaf, an elongate skull with moderately inflated braincase, a narrow rostrum and an unspecialized auditory region. Hand and Kirsch (1998) concluded that the genus *Hipposideros* is probably paraphyletic (see also Hugueney 1965; Sigé 1968; Legendre 1982; Bogdanowicz and Owen 1998) with species of *Asellia*, *Palaeophyllophora* and *Pseudorhinolophus* nesting within it (these three commonly being associated with *cyclops* taxa). They agreed, however, that Hill's (1963) Division 1 taxa (the *megalotis-bicolor* group) was probably the most plesiomorphic within *Hipposideros*.

The new Pliocene hipposiderid from Rackham's Roost appears to be a member of the *megalotis-bicolor* group. However, although *H. winsburyorum* is perhaps closer in overall dental morphology to *H. megalotis* and *H. vetus* than *bicolor* taxa such as *H. sabanus*, the lack of complete dentaries and/or associated upper canines precludes a more precise placement of this Riversleigh hipposiderid within the *megalotis-bicolor* group at this stage. Further complicating placement is the fact that this species exhibits a complex mix of plesiomorphic and apomorphic features. For example, the small heel size of M^{1-2} is probably a plesiomorphic feature, while the lack of a prominent anterolingual cingular cusp on the broad P^4 is possibly derived among hipposiderids (see Hand 1997a; Hand and Kirsch 1998). The loss of P^2 is a derived feature for hipposiderids, evidently independently acquired in a number of separate lineages (e.g., in species of *Asellia* and *Cloeotis*) including perhaps the *winsburyorum*, *megalotis* and *sabanus* lineages. The reduced M^3 is probably derived among

hipposiderids (e.g., in *Hipposideros* species) but is possibly plesiomorphic in some subgroups (for example, species of the *H. cyclops* group; see Hand 1997a). The short palate with U-shaped anterior margin and convergent toothrows are probably also derived features among hipposiderids but plesiomorphic among Division 1 taxa. The very large infraorbital foramen appears to be an autapomorphy of this species, although the round shape could be plesiomorphic (being found in rhinolophid and megadermatid sister-groups).

The unique combination of features exhibited by *H. winsburyorum* precludes it from direct ancestry of any living Australasian members of the *bicolor* group (or indeed any hipposiderid living in the Australian Region) including *H. ater*, a common cave-dwelling species in the Riversleigh region today. It is likely that skull material will be required to more precisely determine the relationships of *H. winsburyorum*. Hand and Kirsch (1998) found in their phylogenetic analyses of 37 hipposiderid taxa that although dental features (20 characters) alone were insufficient to resolve relationships among hipposiderid genera and species groups, a combination of cranial and dental features (56 characters) provided greater resolution. Ongoing taxonomic revisions of Indonesian *Hipposideros* by Kitchener and co-authors (e.g., Kitchener *et al.* 1992; Kitchener and Maryanto 1993; Kitchener and Maharadatunkamsi 1995; Kitchener *et al.* 1996) have highlighted the taxonomic problems still to be resolved in this genus.

Hipposideros winsburyorum is the second species of *Hipposideros* described from the Australian Tertiary and one of few recorded from the Tertiary worldwide. *Hipposideros bernardsigei* was described from Riversleigh's early Miocene Neville's Garden Site on the basis of near-complete skull material and is the first and only known fossil member of the *cyclops* group (Hand 1997a). *Hipposideros felix* has been described on the basis of an upper third molar and lower first molar from early Miocene deposits at Li Mae Long, Thailand (Mein and Ginsburg 1997). From East African Miocene deposits, Butler (1969, 1984) recorded three unnamed hipposiderids, one of which was reported to be very similar to the European *Pseudorhinolophus bouziguensis*. The living *H. commersoni* and *Triaenops persicus*, and a smaller, now locally extinct, unidentified hipposiderid, have been reported from the Pliocene of Madagascar (Sabatier and Legendre 1985). North Africa's *H. (Syndesmotis) vetus* and France's *H. (S.) sp. cf. H. vetus* (Lavocat 1961; Sigé 1976; Legendre 1982) are the only other records of *Hipposideros* from the Tertiary.

Compared with the early Eocene appearance of European species of *Pseudorhinolophus* and *Palaeophyllophora*, *Hipposideros* species appear relatively recently in the world hipposiderid record. However, this is possibly an artefact of the Tertiary fossil bat record. Hand and Kirsch (1998) found Eocene *Pseudorhinolophus* and *Palaeophyllophora* to be relatively derived hipposiderids nesting within *Hipposideros*. Basal to this *Hipposideros*-dominated clade was a group containing widely distributed species of *Brachipposideros*, *Rhinonicteris*, *Coelops*, *Cloeotis* and *Triaenops* among others. If the phylogenetic interpretation by Hand and Kirsch is correct, then representatives of almost all hipposiderid lineages, including the *bicolor* group, might be expected to be found in the early Tertiary record, with their earliest members possibly in the Asian or Australasian region. Sigé (1977) and Sigé and Legendre (1983) have suggested that the origin of the family was outside Europe, probably in the Southern Hemisphere (Sigé 1991). Unfortunately, the Asian fossil bat record is poor and there is a profound gap in the Australian fossil mammal record from the earliest Eocene to late Oligocene. Nevertheless, the appearance of a member of the highly specialized *H. cyclops* group in the Australian early Miocene (Hand 1997a) indicates that species of *Hipposideros* had already radiated by that time.

Hipposideros almost certainly had its primary radiation in Asia or Australasia. The *bicolor* and *diadema* groups are interpreted to be predominantly Indo-Australian-centred (e.g. Hill 1963), while most members of the *cyclops* group are endemics of Australo-Papua (although the roots of the latter specialized group possibly lie in Africa: Hill 1963; Flannery and Colgan 1993; Hand 1997a; Hand and Kirsch 1998). The genus appears to have radiated rapidly and widely with many closely related species pairs living in Asia and Africa (Hill 1963). There appear to have been few barriers to dispersal for hipposiderids in the middle and later Tertiary as indicated by the wide distribution of species of *Brachipposideros* and related taxa (Sigé *et al.* 1982, 1994; Hand 1997b, 1998a, 1998b). The long history and wide distribution of the *H. megalotis* lineage, from contemporary East Africa to middle Miocene North Africa and Pliocene Europe (and perhaps even Australia), is further evidence of this dispersal capacity.

By Riversleigh standards, *Hipposideros winsburyorum*, known from only six maxillary fragments from a single deposit, is poorly represented. Most hipposiderids recovered from Riversleigh's Oligo-Miocene deposits are represented by several if not dozens of specimens, typically skulls. The remains of these older, better-represented hipposiderids are interpreted to have gradually accumulated within or adjacent to the limestone caves in which they roosted. *Hipposideros*

winsburyorum, however, appears to have suffered the same fate as most Rackham's Roost vertebrates: to become the finely comminuted prey of the Ghost Bat *Macroderma gigas*.

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