Cranial shape variation and phylogenetic relationships of extinct and extant Old World leaf-nosed bats

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Old World leaf-nosed bats (Hipposideridae and Rhinonycteridae) currently have an Old World tropical to subtropical distribution, with a fossil record extending back to the middle Eocene of Europe. The Riversleigh World Heritage fossil site in northwestern Queensland constitutes a particularly rich archive of faunal diversity for Old World leaf-nosed bats, having yielded more than 20 species. In this paper we used 2D geometric morphometrics to quantify cranial shape in hipposiderids and rhinonycterids, with the aim of referring unallocated fossil species, particularly from Riversleigh, to each family within a phylogenetic framework, and using a quantitative approach to reconstruct cranial shape for key clades in these Old World radiations. Our sample comprised 23 extant species and eight extinct species of hipposiderids and rhinonycterids, in which 31 landmarks were placed in lateral and ventral views, and five measurements were taken in dorsal view. The phylogeny used as the

framework for this study was based on an analysis of 64 discrete morphological characters from the dentition, cranium and postcranium scored for 42 extant and fossil hipposiderids and rhinonycterids and five outgroup taxa (rhinolophids and megadermatids). The phylogenetic analysis was conducted using maximum parsimony, with relationships among selected extant taxa constrained to match the results of recent comprehensive molecular studies. Our phylogenetic results suggest that the Riversleigh leaf-nosed bats probably do not represent an endemic Australian radiation, with fossil species spread throughout the tree and several with sister-group relationships with non-Australian taxa. Discriminant analyses conducted separately on each data set resulted in cross-validated classification success ranging from 61.9% for ventral landmarks to 71.4% for lateral landmarks. Classification of the original grouped cases resulted in success of 81% for each data set. Of the eight fossil taxa included as unknowns in the discriminant analyses, six were found to be assigned to the same group as recovered by the phylogenetic analysis. From our results, we assign the Riversleigh Miocene species *Archerops annectens*, *Brachipposideros watsoni*, *Brevipalatus mcculloughi*, *Rhinonicteris tedfordi* and *Xenorhinos halli* to Rhinonycteridae, and *Riversleigha williamsi* and *Hipposideros bernardsigei* to Hipposideridae. Our results support *Pseudorhinolophus bouziguensis*, from the early Miocene of Bouzigues in southern France, as belonging to Hipposideridae, and probably *Hipposideros*. The reconstructed ancestor of hipposiderids was distinguished from the reconstructed ancestor of rhinonycterids by showing a shorter rostrum, and less distinction between the rostrum and braincase.

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OLD WORLD leaf-nosed bats (65 extant spp.) have a tropical to subtropical distribution at present, and a fossil record extending back to at least the early middle Eocene of Europe (Remy *et al.* 1987, Eiting & Gunnell 2009, Maitre 2014). They generally have short, broad wings with a low aspect (Norberg & Rayner 1987) and are slow, weaving fliers that forage for insects near or within vegetation by hovering and gleaning, hawking from observation perches, or by aerial pursuit (Findley 1993, Heller & Helversen 1989), although flight in some species is swift and acrobatic (Bullen & McKenzie 2002). All have a complex noseleaf, medium to large ears and emit their echolocation calls through the nares rather than the mouth. Their skulls have variably expanded nasal chambers and petrosals that are associated with energy transmission and reception (Hartley & Suthers 1988, Heller & Helversen 1989). These bats are predominantly cave-dwellers and their fossil remains are relatively well represented in Paleogene and Neogene cave and karst deposits (Eiting & Gunnell 2009).

Until recently, all Old World leaf-nosed bats were referred to the family Hipposideridae Miller, 1907, and within that to a variable/changing number of tribes, based largely on

external and cranial morphology (e.g., Gray 1866, Tate 1941, Hill 1963, 1982, Koopman 1994, McKenna & Bell 1997, Bogdanowicz & Owen 1998, Hand & Kirsch 1998, 2003, Simmons 2005, Benda & Vallo 2009). On the basis of multi-gene molecular data, Foley *et al.* (2015) recently raised the hipposiderid subtribe Rhinonycterina Gray, 1866 to family status, assigning to it the four extant genera *Rhinonicteris* Gray, 1847 (Australia), *Cloeotis* Thomas, 1901 (Africa), *Triaenops* Dobson, 1871 (Africa, Madagascar) and *Paratriaenops* Benda & Vallo, 2009 (Madagascar), as well as the fossil taxa *Brachipposideros* Sigé, 1968 and *Brevipalatus* Hand & Archer, 2005. *Brachipposideros* species are known from lower Miocene to Pliocene sediments in Europe, Oman, Australia and Thailand (Sigé 1968, Sigé *et al.* 1982, 1994, Legendre 1982, Ziegler 1993, Mein & Ginsburg 1997, Hand 2006, 2012); the monotypic *Brevipalatus* is recorded only from the early Miocene of Australia (Hand & Archer 2005).

Fossil deposits in the Riversleigh World Heritage Area, located in Boodjamulla (Lawn Hill) National Park (northwestern Queensland, Australia), occur mostly in limestone karst and include tufa, cave, fissure-fill and lake deposits (Archer *et al*. 1989). They range in age from late Oligocene (ca 25 Ma) to modern (Woodhead *et al.* 2016), and they sample palaeohabitats ranging from open forests in the late Oligocene and late Miocene, closed forests in the early and middle Miocene, and tropical savannah grass- and woodlands in the Quaternary (Archer *et al.* 1994, Travouillon *et al*. 2009). A particularly rich archive of faunal diversity for bats is present in the Riversleigh deposits: of the around 350 mammal species represented there are 44 species of bats, and at least half of these are Old World leaf-nosed bats (Long *et al.* 2002, Archer *et al*., 2006, Hand 2006), including, among others, species of *Rhinonicteris*, *Brachipposideros*, *Brevipalatus*, and *Hipposideros*.

When the fossil leaf-nosed bats included in this study were described (1968–2005), all were assigned to Hipposideridae. Phylogenetic analyses of craniodental features facilitated

their placement in various subfamilial groups and tribes, including the Rhinonycterina (e.g., Hand & Kirsch 2003), although several species were assigned only tentatively to these narrower groups (e.g., Hand 1998a, b). Recognition of family status for Rhinonycteridae (Foley *et al.* 2015), description of new extant and extinct leaf-nosed bat genera and species (e.g., Benda & Vallo 2009), and a revised understanding of relationships within Hipposideridae and Rhinonycteridae based on molecular data (e.g., Murray *et al.* 2012) compels a fresh consideration of the taxonomy of Riversleigh's fossil leaf-nosed bats.

In this study, we used 2D geometric morphometrics to quantify skull shape in Old World leaf-nosed bats; to allocate fossil taxa to either Hipposideridae or the recently recognized Rhinonycteridae; and to assess the utility of morphometric characters for describing and reconstructing patterns of shape variation in these groups. Geometric morphometric techniques, based on the analysis of landmark configurations (Bookstein 1991, Dryden & Mardia 1998, Adams *et al.* 2013), have been employed to quantify shape and size in a wide range of studies on mammals (e.g., Goswami 2006, Cardini *et al.* 2009, Drake & Klingenberg 2010, Wilson *et al.* 2011, Wilson 2013). Within the Chiroptera, several studies have investigated patterns of shape evolution, particularly in relation to ecomorphological diversity in phyllostomids (Nogueira *et al.* 2009, Monteiro & Nogueira 2010, 2011), the potential utility of geometric morphometric variables in taxonomy when combined with genetic markers and other character data sets (e.g., Evin *et al.* 2008, Sztencel-Jablonka *et al.* 2009), and evolutionary changes in shape covariance patterns (Santana & Lofgren 2013, López-Aguirre *et al.* 2015).

By focusing on the identification and quantification of cranial shape characteristics using geometric morphometric methods, we aim to identify features that may guide assigning fossil bats to Rhinonycteridae or Hipposideridae. At present, this task remains a challenge for fossils because the diagnostic features described for Rhinonycteridae *sensu* Foley *et al.* 2015

are either not observable in the fossil taxa, or else they have not yet been identified. Foley *et al.* (2015) described five features of the noseleaf, and a 128bp retrotransposon insertion in the THY gene fragment that can be used to distinguish Hipposideridae and Rhinonycteridae, but unique and diagnostic craniodental features were not identified.

Materials and Methods

Study sample

Our morphometric sample comprised adult skulls of 21 extant and eight extinct Old World leaf-nosed bats (seven from the Miocene of Riversleigh and *Pseudorhinolophus bouziguensis* from the Miocene of Europe) and two outgroup taxa (one rhinolophid and one megadermatid), as follows (see also Appendix A).

Hipposideridae: *Anthops ornatus, Asellia tridens, Aselliscus tricuspidatus, Coelops frithi, Hipposideros armiger, H. ater, H. bicolor, H. caffer, H. cervinus, H. commersoni, H. diadema, H. galeritus, H. jonesi, H. megalotis, H. pomona, H. semoni, H. speoris, H. stenotis.* Rhinonycteridae: *Cloeotis percivali, Paratriaenops furculus, Rhinonicteris aurantius, Triaenops persicus.* Fossil taxa: *Archerops annectens, Brachipposideros watsoni, Brevipalatus mcculloughi, H. bernardsigei, Pseudorhinolophus bouziguensis, R. tedfordi, Riversleigha williamsi, Xenorhinos halli.* Outgroups: *Rhinolophus megaphyllus* (Rhinolophidae, horseshoe bats), *Macroderma gigas* (Megadermatidae, false vampire bats).

Data collection

Specimens were photographed in dorsal, lateral and ventral views using Canon EOS 20D (at NHM London) and Nikon SLR F50 and DSLR D5100 (at University of New South Wales) cameras fitted with a macro lens, mounted on a tripod. To prevent error in data collection associated with pitch and roll of the specimen, each specimen was fixed in a standardized

position such that the specimen was parallel to the photographic plane: this was achieved using clay and non-invasive support (rigid foam structures).

Morphometric data were collected from raw image files using TPS Dig 2.0 (Rohlf 2010). For each specimen, a total of 31 two-dimensional (2D) landmarks were placed in lateral (N=16) and ventral (N=15) views and five measurements were collected in dorsal view (see Fig. 1). The dorsal measurements were derived from nine landmarks (see Fig. 1). The lateral and ventral landmarks partly followed those selected by Santana & Lofgren (2013) in their study of rhinolophids (Table 1). Most landmarks were type II landmarks, defined by Bookstein (1991) as curvatures and tips. Type II landmarks were chosen because, unlike many terrestrial mammals, bats typically have few open sutures in the cranium as adults, hindering the selection of type I landmarks. Tertiary analyses require complete matrices without missing data, therefore a subset of landmarks were chosen that could be recorded on all specimens. As such, several landmarks commonly captured for extant species were not included in this study, particularly those placed on the anterior margin of the canine, and the premaxilla, since those regions are commonly broken in fossil crania. Dorsal measurements (see Fig. 1) follow standard metric characters (Kitchener *et al.* 1996) (see Table 1).

Dorsal measurements were log transformed prior to further analyses. The lateral landmark and ventral landmark data sets were each aligned using Procrustes superimposition, which removes non-shape differences due to rotation, translation and scale (Dryden & Mardia 1998). Centroid size (CS), the square root of the squared distance between each landmark and the centroid of the landmark configuration and summed across all landmarks (Bookstein 1991), was extracted and saved for each landmark configuration.

In addition to the morphometric data sets, a fourth data set that built upon the morphological character-taxon matrix of Hand & Kirsch (2003) was used to assess the likely phylogenetic relationships of the fossil taxa to extant Old World leaf-nosed bats. This matrix

consisted of cranial, dental and postcranial morphological characters, coded in discrete states. Characters for fossil taxa described since 2003 (*Brevipalatus mccullough*i; Hand & Archer 2005) were added to the matrix, together with those from extant rhinolophid species analysed by Foley *et al.* (2015). Dental terminology follows Sigé *et al.* (1982).

Phylogenetic analysis of character data matrix

The augmented matrix from Hand & Kirsch (2003) consisted of 64 characters scored for 47 taxa (Supplementary File S2), including outgroups *Rhinolophus megaphyllus*, *R. euryale* and *R. hipposideros* and *Megaderma spasma* and *Macroderma gigas* (Supplementary File S3). The fossil species *Brachipposideros nooraleebus* was included in the phylogenetic analysis but its cranial remains were too fragmentary to include in the geometric morphometric analyses. Using this matrix, we constrained the phylogenetic analysis using a backbone scaffold based on the molecular results of Foley *et al*. (2015; Fig. 2). Analyses were carried out using maximum parsimony with all characters unordered, as implemented in PAUP4.01b10 (Swofford 2003); the tree search was heuristic, comprising 1000 random addition replicates. Bootstrap values were calculated only for the purpose of providing a preliminary indication of support for the groupings generated in the analysis. Bootstrap values should not be interpreted in the usual way because relationships among some extant taxa were specified a priori by the molecular scaffold.

Data analysis of lateral and ventral landmark

To examine the relationship between shape and size for the lateral and ventral landmark data sets, a multivariate regression of Procrustes-superimposed landmarks on log centroid size was performed. A permutation test was performed using 10000 rounds to test the null hypothesis

of independence between shape and size. Regressions were performed using MorphoJ (Klingenberg 2011).

Each data set was entered into a separate Principal Components Analysis (PCA) to extract axes of maximum shape variance in the sample. The broken stick model (Jackson 1993) was used to determine the number of Principal Components (PCs) that captured significant proportions of the variance for each data set. To further aid visualization of shape patterns, landmark data were mapped onto the tree derived from the phylogenetic analysis above, which included fossil and modern representatives of all major clades and was constrained by the molecular scaffold of Foley *et al.* (2015). Lateral landmark data were mapped onto the phylogeny using squared-change parsimony (Maddison 1991), enabling ancestral shape at internal nodes to be reconstructed. This was implemented in MorphoJ (Klingenberg 2011), using a rooted phylogeny. Lateral landmarks were chosen because they provided a visual of whole cranial shape in outline.

Classification of fossil taxa

Discriminant Analysis (DA) was used to classify fossil taxa. DA was performed on each data set separately (lateral landmarks, ventral landmarks, dorsal measurements). For the lateral landmark and ventral landmark data sets, significant PCs, according to the broken stick test result, were used as input to the DA. For the dorsal measurements, log-transformed values were used for the DA. In all cases, the data sets were pruned to remove the two outgroup taxa (*Rhinolophus megaphyllus* and *Macroderma gigas*), this was because all fossil taxa were hypothesized to belong to either Hipposideridae or Rhinonycteridae, based on results from the phylogenetic analysis, and hence the learning sample for DA comprised only extant members belonging to those two groups. A leave-one-out cross-validation was also performed or each data set, in addition to a DA in which all specimens in the analysis were

classified with functions created using all specimens. The cross-validation analysis removes one specimen from the analysis sequentially and uses the remaining cases to classify that specimen, and repeats this for all specimens.

Results

Phylogenetic analysis of character matrix

The Phylogenetic analysis, which was constrained by using a backbone scaffold based on the molecular results of Foley *et al*. (2015), identified a total of 63 characters that were parsimony informative. Constrained parsimony analysis found nine most parsimonious trees (tree length 419 steps, CI 0.222, RI 0.561; Fig. 2). Rhinonycteridae and Hipposideridae were both monophyletic. Relationships among hipposiderids were better resolved than among rhinonycterids. The fossil taxa were divided between the two families: three of our eight extinct species grouped with extant hipposiderids and five with extant rhinonycterids.

Within Hipposideridae, *Pseudorhinolophus bouziguensis* clustered with *Hipposideros* species including *H. cyclops, H. larvatus, H. armiger* and *H. semoni*, and within the same group *Hipposideros bernardsigei* formed the sister-taxon to a *H. muscinus–H. wollastoni* clade. *Riversleigha williamsi* grouped with species of *Coelops* and *Aselliscus*, and outside the field of most species of *Hipposideros* (except *H. megalotis*, which is sometimes referred to the monotypic subgenus *H. (syndesmois)*; e.g., Legendre 1982).

Within Rhinonycteridae, *Archerops annectens* was the sister-taxon to the extant *Cloeotis percivali*, and *Brevipalatus mccullough*i formed the sister-group to that clade; *Xenorhinos halli* was the sister-taxon of extant *Triaenops persicus* and together they formed a clade with *Rhinonicteris tedfordi*. The relationship between these two clades and to *Brachipposideros watsoni* was unresolved. *Brachipposideros nooraleebus*, extant *Rhinonicteris aurantia* and

extant *Paratriaenops furculus* formed successively more distant sister-groups within Rhinonycteridae (Fig. 2).

Morphometric analysis

Results for multivariate regression of Procrustes superimposed landmarks and log centroid size revealed that allometry explained a small component of variation in the data sets. For both the lateral landmark (1.33% variance, P =0.88) and ventral landmark (6.07%, P=0.15) data sets, the relationship between shape and size was not significant.

PCA of five dorsal measurements resulted in a single axis (PC1) capturing 94.06% of the variance in the sample (Fig. 3). This axis mainly separated fossil taxa and *R. megaphyllus* from extant taxa; most notably *Rhinolophus megaphyllus* and *Brevipalatas mccullоughi* occupied the most negative region of PC1. PC1 was associated with positive loading for all measurements; therefore, movement along PC1 from negative to positive scores reflected an increase in size for each of the five measurements.

PCA of lateral landmarks resulted in three PCs that captured significant proportions of shape variance (PC1 = 46.98%, PC2 = 16.23%, PC3 = 9.90%). A clear separation between rhinonycterids and hipposiderids was not evident along the main axes (PC1–PC2; Fig. 4A) of shape variation. There was some separation along PC1 (46.98%) between outgroup taxa, whose position occupied the positive region of the axis, and rhinonycterid species, located more towards the negative end of PC1. PC1 captured differences in shape of the rostrum, such that outgroup taxa and others with positive PC1 scores possessed a dorso-ventrally expanded (taller) rostrum, longer sphenorbital region (landmarks #2–4), maximum braincase height further anterior and/or taller anterior sagittal crest, and less dorsally inflated cranium (landmarks #8–10; Fig. 1). Species with positive scores along PC2 (16.23%) displayed a shorter rostrum and proportionately more elongate yet shallower cranium and/or lower

sagittal crest compared with those species with negative PC2 scores (mainly fossil taxa and rhinonycterids; Fig. 4B). There was some separation between hipposiderids, having negative scores, and rhinonycterids, having positive scores (except *Cloeotis percivali*), along PC3 (9.90%). Positive scores on PC3 were associated with increased rostrum height, deeper frontal depression, shallower braincase and more vertically orientated occiput.

The broken stick model identified PC1–PC5 as significant components for the PCA of ventral landmarks and, together, these three axes accounted for 74.69% of shape variance in the sample. Along PC1 (32.40%), three taxa had larger positive scores than other species: these were *Macrodermas gigas*, *Pseudorhinolophus bouziguensis* and *Hipposideros bernardsigei*. Positive scores along PC1 were associated with lengthening of the rostrum (palate and tooth row), longer sphenorbital region (landmarks #2–3), slightly widened glenoid fossa, and a more vertically directed foramen magnum (Fig. 5). PC2 (17.97%) mainly separated *Coelops frithi*, located at the most extreme negative end of the axis, from other taxa. In contrast, *H. stenotis*, *H. armiger* and *H. commersoni* were located at the most positive end of PC2. Taxa at the positive end of PC2 had a longer sphenorbital region, more posteriorly positioned and widened glenoid fossa, shortened (anteroposteriorly) occipital region, and less medially and anteriorly expanded petrosals (Fig. 5B). Hipposiderids occupied mainly the negative portion PC3 (10.00%) compared with fossil taxa. *Hipposideros megalotis* had the most negative PC3 score, whereas *Brevipalatus mccullоughi* had the most positive PC3 score. Taxa with positive PC3 scores had a widened rostrum, shortened palate and widened glenoid fossa.

Classification of fossil taxa

Discriminant analyses conducted separately on each data set resulted in cross-validated classification success ranging from 61.9% for ventral landmarks to 71.4% for lateral

landmarks. Classification of the original grouped cases resulted in success of 81% for each data set (Table 2). Taxa that were misclassified varied between the data sets (Supplementary File S1) with only *Coelops frithi* featuring as misclassified in more than one data set (both lateral and ventral landmarks). All rhinonycterids were correctly classified using dorsal measurements, whereas for the lateral landmark data set *Rhinonicteris aurantia* was misclassified, and for the ventral landmarks *Cloeotis percivali* was misclassified. Posterior probabilities for classification were slightly higher for dorsal measurements ($p = 0.64–1.0$) than for the other two data sets ($p = 0.60–0.99$, lateral landmarks; $p = 0.61–0.98$, ventral landmarks) (Supplementary File S1).

Overall, there was good agreement between the hypothesized grouping of the fossil taxa and the group assignment recovered in this study, when taking the consensus result across the three data sets (Table 3). Of the eight fossil taxa, six consensus group assignments were in agreement with the hypothesized group for that taxon. *Archerops annectens* was classified as a rhinonycterid by both dorsal measurements and ventral landmarks, whereas it has been hypothesized previously to belong to the Hipposideridae (Hand & Kirsch 2003). Moreover, *Riversleigha williamsi* was identified as a rhinonycterid based on discriminant analysis of dorsal measurements and lateral landmarks, conflicting with its assignment to Hipposideridae in our phylogenetic analysis based on discrete cranial, dental and postcranial characters (Fig. 2).

Five of the eight fossil taxa were classified as belonging to the same group by all data sets (Table 3). The taxa with conflicting results among data sets were *A. annectens*, *Hipposideros bernardsigei* and *R. williamsi*. In the case of *A. annectens*, which was classified as a rhinonycterid based on discriminant analysis of dorsal measurements and ventral landmarks, its classification as a hipposiderid using the lateral landmarks is likely reflected in that taxon being closely located to several hipposiderids in PC1–PC2 morphospace, including *H.*

cervinus, *H. jonesi* and *H. speoris*. Like these taxa, and unlike most rhinonycterids, *A. annectens* is characterized by a very narrow and low rostrum. In the case of *H. bernardsigei*, contra the results from the other two data sets for this taxon, dorsal measurements classify it as a rhinonycterid, sharing with definitive rhinonycterids a broad and tall rostrum; however, this morphology is also found in some hipposiderids, such as *H. semoni* and *Aselliscus*.

Hand & Kirsch (1998) were unable to confidently place *Riversleigha* in their phylogenetic analysis of leaf-nosed bats. In our GMM analysis, *R. williamsi* was identified as a rhinonycterid based on dorsal measurements and lateral landmarks. This conflicts with its placement in the Hipposideridae by our phylogenetic analysis, which places it as a close relative of *H. cervinus*, *H. jonesi* and *H. speoris* that have a narrow, low rostrum (Fig. 2) and the ventral landmark data set. In the latter, *R. williamsi* is located away from extant rhinonycterids and in close proximity to several extant hipposiderids, including *H. diadema*, *H. armiger* and *H. commersoni* in PC1–PC2 morphospace and *H. commersoni*, in PC1–PC3 morphospace. With these hipposiderid taxa, it shares a lengthened palate, lengthened sphenorbital region, and widened glenoid fossa.

Of note, dorsal measurements classify nearly all fossil taxa (seven out of eight) as rhinonycterid, although this assignment is not clearly reflected in the PC1–PC2 plot for the dorsal measurements, which reveals a considerable amount of overlap in morphospace between hipposiderids and rhinonycterids, and most fossil taxa (except *Xenorhinos halli*) are located separate from the extant grouping.

Ancestral cranial shape reconstructions for major nodes in our phylogeny showed marked shape changes occurring across the tree. For lateral landmarks, from *H. bernardsigei* to the base of the hipposiderid radiation (Node a) differences in cranial shape include less distinction between the rostrum and braincase, reflecting the absence of a frontal depression, lower anterior braincase, and a shorter sphenorbital region (Fig. 6). From *Rhinonicteris*

tedfordi to the base of the rhinonycterid radiation (Node b) differences in skull shape include a longer rostrum and shorter braincase, with a lower peak or crest in the braincase anteriorly (Fig. 6). Shape differences between the reconstructed ancestor shape of hipposiderids (Node a) and the reconstructed ancestor shape of rhinonycterids (Node b) reflect a shorter rostrum and less distinction between the rostrum and braincase (Fig. 6), as discussed below. For ventral landmarks, shape changes occurring from *H. bernardsigei* to the base of hipposiderids (Node a), mainly reflected a narrowing and shortening of the maxilla with a slight anterior displacement of the pterygoid (Fig. 7). The ancestral reconstruction for ventral shape at Node b reflected a slight extension of the maxilla, and an anterior shift of the posteromedial flange of the basioccipital. The reconstructed ancestral shapes for hipposiderids and rhinonycterids were highly similar, and differences were limited to a slight extension of the maxilla for the ancestor shape of rhinonycterids (Node b) (Fig. 7).

Discussion

Geometric morphometric and phylogenetic analyses undertaken in this study have facilitated assignment of several extinct species of Old World leaf-nosed bats, previously all referred to family Hipposideridae *sensu* Miller, 1907, or to either Hipposideridae or Rhinonycteridae *sensu* Foley *et al.* (2015). When the rhinonycterid family-group was formally elevated to family level by Foley *et al.* (2015), only two fossil genera (*Brachipposideros* and *Brevipalatus*) were included in Rhinonycteridae. Allocating all candidate fossil genera to either of these families (and confirming the affiliations of *Brachipposideros* and *Brevipalatus*) is made difficult owing to a lack of information about diagnostic genetic and external morphological features in fossils, and limited diagnostic craniodental characters. Shape analysis provides the most robust approach currently available to allocate candidate fossil genera to these two families. On the basis of our morphometric and phylogenetic

results, we taxonomically assign the Riversleigh Miocene species *Archerops annectens*, *Brachipposideros watsoni*, *Brevipalatus mcculloughi*, *Rhinonicteris tedfordi* and *Xenorhinos halli* to Rhinonycteridae, and *Riversleigha williamsi* and *Hipposideros bernardsigei* to Hipposideridae. The results support the allocation of *Pseudorhinolophus bouziguensis*, from the early Miocene of Bouzigues in southern France, to Hipposideridae, and probably *Hipposideros*, as originally described by Sigé (1968).

For all geometric morphometric data sets, extant hipposiderid and rhinonycterid cranial shapes overlapped significantly in morphospace, as did fossil cranial forms. This result lends support to the difficulty in identifying diagnostic craniodental features for Rhinonycteridae, as encountered by Foley *et al.* 2015. Overlap was slightly greater for ventral landmarks, where shape variation among rhinonycterids was completely encompassed within the morphospace occupied by hipposiderids for the main axes of shape variance (Fig. 5A). The more speciose hipposiderids showed greater variability in cranial shape than rhinonycterids, as captured by lateral and ventral landmarks. Similarly, variation in dorsal measurements was much greater among hipposiderids, but following allocation of fossil species to Rhinonycteridae based on the classification results of the DA (Table 3), this difference was less marked.

One of the most conspicuous features of the Hipposideridae, Rhinonycteridae and Rhinolophidae is the inflated nasal chambers of the rostrum, and there are considerable differences in size among the different species that mirror the remarkable diversity of form in the noseleaf (Hill 1963, 1982, Csorba et al. 2003). There have been many studies that have described how wing morphology and echolocation call design relate to flight space, prey capture strategy, diet and community structure in bats (e.g., Norberg & Rayner 1987, Kingston *et al.* 2000, Bullen & McKenzie 2001, Denzinger *et al.* 2004). However, we still have a relatively poor understanding of the function of the nasal chambers, the influence of

various parts of the vocal tract and noseleaf on echolocation signals generated by the glottis and the ecological factors that might influence the shape and size of the echolocation apparatus and characteristics of the signals themselves (Armstrong 2002, Jones & Barlow 2004, Armstrong & Coles 2007, Armstrong & Kerry 2011). One of the most fundamental relationships between skull size and echolocation call frequency is known—Hartley & Suthers (1988) discounted a role for Helmholtz resonance in the nasal chambers but also established that the wavelength of the second harmonic of tonal components was one quarter the length of the vocal tract (including soft tissue between the glottis and the nares; see also Pedersen 2000). This opens the possibility for estimating echolocation call frequency in fossil taxa from palatal lengths and, together with information on skull size and shape, could help with reconstructions of flight space ecology, diet and community structure of extinct bat assemblages (Hand 1998b, Hand & Kirsch 2003, Hand & Archer 2005).

Most hipposiderids and rhinolophids forage within forest habitats and their echolocation calls are 'clutter-resistant' in two ways—the tonal component allows the fluttering wings of insects to be detected in close proximity to vegetation 'clutter' and the longer calls (Rhinolophidae) are resistant to the effects of emission-echo overlap (Fenton *et al.* 1995, Denzinger *et al.* 2004). Some of the rhinonycterids, however, have been observed foraging in more open habitats, such as hummock grasslands, and have the capability for swift and acrobatic flight (e.g., *Rhinonicteris*; Churchill *et al.* 1988, Armstrong 2001, Bullen & McKenzie 2002). Given the general ecology of bats in these three families, *Hipposideros bernardsigei* has previously been inferred to be typical of small hipposiderids that are specialized for foraging within and around clutter, given its small body size, markedly enlarged petrosals (a feature of highly specialized clutter-foraging bats) and close phylogenetic relationship to other ecologically similar species in the New Guinea-centred *H. muscinus* group (Hand 1997). This is consistent with our results, which show *H. bernardsigei*

grouped in all three data sets with *Aselliscus*, *H. stenotis* and *H. semoni* (Fig. 2). A previous study suggested that *Brevipalatus mccullоughi* was an aerial insectivore specializing on moths, on the basis of its gracile dentition, enlarged rostrum, moderately expanded petrosals and close relationship to the extant *Rhinonicteris aurantia* (Hand & Archer 2005). In the current study, by contrast, we find that *Brevipalatus mccullоughi* grouped with a very broad suite of species, which differed among the three data sets, and did not reflect a clear grouping according to similarity in feeding habit. In this case, the very short palate and relatively large nasal inflations might simply indicate that it is one of the smaller species that emits relatively high frequency echolocation calls, which does not always reflect phylogenetic relationships. *Riversleigha williamsi* may have been a hard food specialist, perhaps including large, armoured beetles in its diet, as suggested by its long palate, well-developed cranial crests and large crushing teeth (Hand 1998a). Consistent with this suggestion, we find in dorsal, lateral and ventral data sets that *R. williamsi* grouped closely with extant large, hard food specialists that emit lower frequency echolocation calls and who hunt their prey from perches via a sit-and-wait strategy (e.g., *Hipposideros armiger*, *H. commersoni*, *H. diadema* and *Macroderma gigas*; Vaughan 1977, Thabah 2005, Churchill 2008).

The elevation of Rhinonycteridae to a distinct family by Foley *et al.* (2015) follows long recognition of the morphological distinctiveness of this group (e.g., Gray 1866, Tate 1941, Sigé 1968, Hill 1963, 1982, Koopman, 1994, McKenna & Bell 1997, Bohdanowicz & Owen 1998, Hand & Kirsch 1998, 2003, Simmons 2005, Benda & Vallo 2009). Their peculiar noseleaf structure, tall postorbital zygomatic processes and genetic differences distinguish the nine living rhinonycterid species from the other 56 Old World leaf-nosed bats (Hill 1982, Hand & Kirsch 2003, Foley *et al.* 2015). However, these nine species have different skull morphology and retain a dentition that appears to be essentially plesiomorphic, featuring an unreduced M3/m3, the presence of P2, a tall posterior accessory cusp on C1, relatively small

c1 and relatively large p2 (Hand 1998 a). Rostrum and noseleaf morphology varies considerably among rhinonycterids, and Hand (1998 b) noted that size and shape of the rostrum did not appear to be directly correlated with noseleaf size and complexity, although further quantitative work to systematically evaluate this relationship is needed. Our analyses of lateral landmarks are able to detect some of the distinguishing features among rhinonycterids, particularly rostral height, which is reflected in the main axes of shape variance in the sample (Fig. 4). Along PC1, Africa's *Cloeotis percivali* is separate from other taxa, reflecting the very low rostrum in that species, in contrast to the Australian *Rhinonicteris aurantia*, which has a tall, broad rostrum clearly distinct from a uniquely anterior-crested braincase, and is located at the extreme positive end of PC1 occupation for rhinonycterid, beyond *Paratriaenops furculus* and *Triaenops persicus*, both displaying intermediate rostral height. Variation in rostrum height in the Hipposideridae ranges from low in species of *Coelops* to tall in species of *Aselliscus* and the *Hipposideros semoni* group. Investigations by the authors on the functional and evolutionary significance of the observed morphological differences among Old World leaf-nosed bat taxa are underway.

By mapping lateral landmark data onto our phylogeny (Fig. 2) we reconstructed ancestral shape at the base of families Hipposideridae (Node a) and Rhinonycteridae (Node b). Attributes of the ancestral skull form for Rhinonycteridae (Fig. 6 C) include a relatively long rostrum and tooth row (with anterior premolar P2 present), conspicuous posterior nasal inflation, a clear distinction between rostrum and braincase with a frontal depression, steep increase in braincase height and anteriorly tall sagittal crest, and, with respect to hipposiderids, a more ventrally directed foramen magnum. To these features, we would add a tall postorbital zygomatic process; this is present in most rhinonycterids we have examined, including extinct taxa known from this region of the zygoma, but is typically broken in fossil skulls and not included as a landmark in our study (Fig. 1). Attributes of the ancestral cranial

form for Hipposideridae (Fig. 6–7), with respect to rhinonycterids, include a shorter rostrum and tooth row (P2 reduced or absent), equally inflated anterior and posterior nasal inflations, and a gradual increase in cranial height from rostrum to braincase, with deeper interorbital region.

The fossil species included in this study are well-dated members of their respective families. Most were recovered from radiometrically (U–Pb) dated Riversleigh cave deposits (Woodhead *et al.* 2016): *Brachipposideros watsoni, Brevipalatus mcculloughi, Rhinonicteris tedfordi, Riversleigha williamsi* and *Xenorhinos halli* from Bitesantennary Site (17.11 +/- 0.24 Ma), *Hipposideros bernardsigei* from Neville's Garden Site (17.85 +/- 0.06 Ma, 18.24 +/- 0.27 Ma), and *Archerops annectens* from AL90 Site (14.64 +/- 0.46 Ma, 14.82 +/- 0.27 Ma). *Pseudorhinolophus bouziguensis* occurs in early Miocene (latest Aquitanian) sediments near Bouzigues in Hérault, southern France (Sigé 1968), correlated in the European Neogene land mammal chronostratigraphic scale as MN2 (ca 19 Ma; Aguilar *et al.* 1997). A minimum age for the early radiation of Old World leaf-nosed bats is provided by the early middle Eocene age (ca 45 Ma) of relatively derived fossil taxa from southwestern Europe (e.g., species of *Pseudorhinolophus*; Revilliod 1922, Maitre 2014). The oldest representatives of the Rhinonycteridae are late Oligocene *Brachipposideros* species from France, Oman and Riversleigh, at around 25 Ma (Sigé 1968, Sigé *et al*. 1994, Long *et al.* 2002). Analyses of molecular data estimate the time of divergence of Old World leaf-nosed bats from rhinolophids to be ca 39–42 Ma (Lavery *et al.* 2014, Foley *et al.* 2015), and that for the split of rhinonycterids and hipposiderids at ca 34–39 Ma (Lavery *et al.* 2014, Foley *et al.* 2015). The base of the modern rhinonycterid radiation has been estimated to be ca 19 Ma by Foley *et al.* (2015) but our results indicate it is older, given the proposed phylogenetic position of *Brachipposideros* species nested within the modern rhinonycterid clade (Fig. 2) and their appearance on three continents by 25 Ma.

Our phylogeny suggests that the Riversleigh leaf-nosed bats probably do not represent an endemic Australian radiation, with fossil species spread throughout the tree and several with sister-group relationships with non-Australian taxa (*Xenorhinos–Triaenops*, *Archerops–Cloeotis*, *Riversleigha–Aselliscus–Coelops*, *Hipposideros bernardsigei–muscinus–wollastoni*) (Fig. 2). The relationships of other Riversleigh taxa (e.g., species of *Brachipposideros* and *Rhinonicteris*) to each other and to others are unresolved or appear to be paraphyletic. Foley *et al.* (2015) suggested an African origin for Rhinonycteridae and Hipposideridae, and the fossil record suggests that both families were widespread throughout the Old World tropics and paratropics in the Paleogene and Neogene (40–15 Ma). The disjunct distribution of modern rhinonycterids, including their absence from most of Asia and from New Guinea, could be the result of differential extinctions, particularly given that they are recorded from the Miocene of Thailand (Mein & Ginsberg 1997), but improved resolution of the phylogenetic relationships of extinct and extant members is required to determine this.

Conclusions

Geometric morphometric and phylogenetic analyses carried out in this study have facilitated assignment of several extinct species of Old World leaf-nosed bats, previously all referred to family Hipposideridae *sensu* Miller, 1907, to either Hipposideridae or Rhinonycteridae *sensu* Foley *et al.* (2015). Our results indicate that taxonomic and functional information can be extracted from the quantification of cranial shape in Old World leaf-nosed bats. Furthermore, insights into the magnitude and mode of variation in cranial shape in extinct species have implications for trophic niche partitioning in palaeotropical bat communities. Particularly, we note convergences in shape between hard-food specialists among extant species and Riversleigh taxon *Riversleigha williamsi* and similarly *Hipposideros bernardsigei* was found to share cranial shape features with extant species that are known to be specialized in

foraging within and around vegetation clutter. Future geometric morphometric analyses of crania and partial crania of undescribed Riversleigh leaf-nosed species to retrieve both taxonomic and ecomorphological data (e.g., diet, acoustics, habitat use) is underway. The abundance and diversity of the bats that are available for quantitative analysis from the Riversleigh deposits is expected to yield further insights into the macroevolutionary dynamics underpinning the radiation of Old World leaf-nosed bats.

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Supplemental Material

Supplementary File S1: Detailed classification results from the Discriminant Analyses conducted on the following data sets: dorsal measurements, lateral landmarks, ventral landmarks.

Supplementary File S2: Data matrix for PAUP analysis. Available to download from Figshare as a nexus file. DOI: 10.6084/m9.figshare.3190114

Supplementary File S3: Characters and states used in the phylogenetic analysis of rhinolophoid taxa. Available to download from Figshare as a nexus file. DOI: 10.6084/m9.figshare.3190117

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APPENDIX A. List of specimens used in this study.

Institutional abbreviations: AM, Australian Museum, Sydney; AMNH, American Museum of Natural History, New York; AR, Vertebrate Palaeontology Collection, University of New South Wales, Sydney; BM(NH), Natural History Museum, London; QM, Queensland Museum, Brisbane; SMF, Naturmuseum Senckenberg, Frankfurt; UM, Université Montpellier, Montpellier; USNM, National Museum Natural History, Smithsonian Institution, Washington D. C.; WAM, Western Australian Museum, Perth.

Hipposideridae: *Anthops ornatus* AM M5831, AM M6351; *Asellia tridens* AR21820; *Aselliscus tricuspidatus* AR21823; *Coelops frithi* BM(NH) 20.11.1.23, USNM 308425, AMNH107508; *Hipposideros armiger* AR21821, WAM M21164; *H. ater* AR17662, WAM M15920; *H. bicolor* AM M9231; *H. caffer* AM M9950; *H. cervinus* QM J15117; *H. commersoni* AR21822, WAM M32679; *H. diadema* AR5194, WAM M32581; *H. galeritus* WAM M25961; *H. jonesi* BM(NH) 66.6244, BM(NH) 63.1605; *H. megalotis* SMF47960, AMNH M219738; *H. pomona* BM(NH) 2003.298, BM(NH) 1997.387; *H. semoni* AM M10207, WAM M18055; *H. speoris* WAM M23642, AMNH M208842; *H. stenotis* AM M9852, WAM M19319. Rhinonycteridae: *Cloeotis percivali* SMF47483, AMNH168160; *Paratriaenops furculus* BM(NH) 95.1.6.8, BM(NH) 95.1.6.17; *Rhinonicteris aurantia* AR2050; *Triaenops persicus* AR21824. Megadermatidae: *Megaderma spasma* AR21825; *Macroderma gigas* AR20505, AR5193. Rhinolophidae: *Rhinolophus megaphyllus* AR1655, AM M12549; *R. euryale* AR21828; *R. hipposideros* AMNH 245359. Fossil taxa: *Archerops annectens* QM F31570; *Brachipposideros watsoni* QM F22915; *Brevipalatus mcculloughi* QM F22821; *H. bernardsigei* QM F23859; *Pseudorhinolophus bouziguensis* AR21819, UM CB172; *Rhinonicteris tedfordi* QM F22910; *Riversleigha williamsi* QM F24100; *Xenorhinos halli* QM F22918.

APPENDIX B

Molecular scaffold topology used as a ‘backbone’ constraint in the phylogenetic analysis (based on Foley *et al.* 2015) in parenthetical format:

((Megaderma_spasma,Macroderma_gigas),((Rhinolophus_hipposideros,Rhinolophus_euryale),((Asellia_tridens,(Hipposideros_commersoni,(Hipposideros_galeritus,Hipposideros_jonesi,(Hipposideros_armiger,Hipposideros_larvatus),(Hipposideros_pomona,Hipposideros_caffer)),(Aselliscus_tricuspidatus,Coelops_frithii))),(Paratriaenops_furculus,(Rhinonicteris_aurantia,(Cloeotis_percivali,Triaenops_persicus))))));

Figure captions

Fig. 1. Illustration of geometric morphometric landmarks collected in this study, showing (**A**) dorsal view, (**B**) lateral view and (**C**) ventral view. Descriptions of dorsal measurements, lateral and ventral landmarks are provided in Table 1. Landmarks shown on a fossil Old World leaf-nosed bat (*Brachipposideros* sp.) cranium from the middle Miocene AL90 Site, Riversleigh World Heritage Area, northwestern Queensland.

Fig. 2. Phylogenetic relationships based on analysis of the morphological characters described in Supplementary File S2 and S3. 50% majority rule consensus of nine most parsimonious trees (length = 419 steps, CI 0.222, RI 0.561). Bootstrap values >50% are indicated at nodes using dashed lines. Branches that are not present in a strict consensus are coloured light grey. Nodes labelled (a) and (b) were selected for ancestral shape reconstruction, shown in Fig. 6. The molecular scaffold used for the analysis is provided in Appendix B. Fossil taxa are denoted with a dagger.

Fig. 3. Plot of Principal Components (PC) describing the main axes of shape variance in dorsal measurements, showing PC1 vs PC2. Taxa are coloured according to phylogenetic group, and fossils are (a) *Archerops annectens*, (b) *Xenorhinos halli*, (c) *Brevipalatus mcculloughi*, (d) *Pseudorhinolophus bouziguensis*, (e) *Brachipposideros watsoni*, (f) *Rhinonicteris tedfordi*, (g) *Hipposideros bernardsigei* and (h) *Riversleigha williamsi*. Photographs of *A. annectens* and *X. halli* (dashed boxes), illustrate shape variation captured by PC1.

Fig. 4. Plot of Principal Components (PC) describing the main axes of shape variance in lateral landmarks, showing (**A**) PC1 vs PC2 and (**B**) PC1 vs PC3. Taxa are coloured

according to phylogenetic group, and fossils are (a) *Archerops annectens*, (b) *Xenorhinos halli*, (c) *Brevipalatus mcculloughi*, (d) *Pseudorhinolophus bouziguensis*, (e) *Brachipposideros watsoni*, (f) *Rhinonicteris tedfordi*, (g) *Hipposideros bernardsigei* and (h) *Riversleigha williamsi*. Shape models illustrate the main aspects of shape variance associated with each axis, moving from negative scores (black solid line) to positive scores (grey dashed line).

Fig. 5. Plot of Principal Components (PC) describing the main axes of shape variance in ventral landmarks, showing (**A**) PC1 vs PC2 and (**B**) PC1 vs PC3. Taxa are coloured according to phylogenetic group, and fossils are (a) *Archerops annectens*, (b) *Xenorhinos halli*, (c) *Brevipalatus mcculloughi*, (d) *Pseudorhinolophus bouziguensis*, (e) *Brachipposideros watsoni*, (f) *Rhinonicteris tedfordi*, (g) *Hipposideros bernardsigei* and (h) *Riversleigha williamsi*. Shape models illustrate the main aspects of shape variance associated with each axis, moving from negative scores (black solid line) to positive scores (grey dashed line).

Fig. 6. Illustrations of shape reconstructions using squared-change parsimony methods to map lateral landmark data onto a pruned version of the phylogeny presented in Fig. 2. The positions of Node a and Node b are shown in Fig. 2, and shape differences are illustrated from *Hipposideros bernardsigei* (solid line) to Node a (dashed line) and from *Rhinonicteris tedfordi* (solid line) to Node b (dashed line). Hipposideridae–Rhinolophidae shows shape differences between the reconstructed ancestor shape (solid line) of hipposiderids (Node a) and the reconstructed ancestor shape (dashed line) of rhinonycterids (Node b).

Fig. 7. Illustrations of shape reconstructions using squared-change parsimony methods to map ventral landmark data onto a pruned version of the phylogeny presented in Fig. 2. The positions of Node a and Node b are shown in Fig. 2, and shape differences are illustrated from *Hipposideros bernardsigei* (solid line) to Node a (dashed line) and from *Rhinonicteris tedfordi* (solid line) to Node b (dashed line). Hipposideridae–Rhinolophidae shows shape differences between the reconstructed ancestor shape (solid line) of hipposiderids (Node a) and the reconstructed ancestor shape (dashed line) of rhinonycterids (Node b).

Table 1. Landmarks and measurements collected in this study.

Dorsal landmark	Measurement description
1–2	Rostral length from anterior margin of nasal to minimum interorbital width
2–3	Braincase length from minimum interorbital width to dorsal posterior-most point of cranium
4–5	Maximum rostrum width, across lacrimals
6–7	Minimum interorbital width
8–9	Maximum braincase width, across mastoids
Lateral landmark	Description
1	Anterior root of P4
2	Posterior margin of M3
3	Anterior margin of the glenoid fossa
4	Tip of the posterior glenoid process
5	Dorsal point of the external auditory meatus
6	Ventral edge of the occipital condyle
7	Most ventral point of the supraoccipital
8	Most posterior point of the cranium, at the junction of sagittal and lambdoidal crests
9	Most dorsal point of the parietal venous sinus
10	Equidistant between points 9 and 11, following the cranial contour
11	Perpendicular to point #5, following the cranial contour
12	Perpendicular to point #3, following the cranial contour
13–15	Equidistant between points #12 and #16, following the cranial contour
16	Anterior margin of the nasal
Ventral landmark	
1	Most anterobuccal point of the P4
2	Most posterobuccal point of the M3
3	Most anterolateral point of the glenoid fossa
4	Most anteromedial point of the glenoid fossa

5	Most anterior point of the pyriform fenestra
6	Narrowest point of the basioccipital
7	Posteromedial flange of the basioccipital
8	Lateral edge of the foramen magnum
9	Posterior edge of the foramen magnum
10	Anterior edge of the foramen magnum
11	Most anterior point of the basisphenoid
12	Tip of the posterior pterygoid process
13	Tip of the anterior pterygoid process
14	Most posterior point of the suture between palatines
15	Anterior margin of the maxilla

Table 2. Summary of classification results from discriminant analyses (DA) conducted separately on (A) dorsal measurements, (B) lateral landmarks and (C) ventral landmarks captured on bat crania. Overall, original grouped cases correctly classified were 81% for dorsal measurements (66.7% cross-validated), 81% for lateral landmarks (71.4% cross-validated), and 81% for ventral landmarks (61.9% cross-validated). Log transformed measurements or principal components capturing significant proportions of sample variance were used as input for the DA.

	Group	**Predicted group membership**		
(A) Dorsal				
		Rhinonycteridae	Hipposideridae	Total
Original	Rhinonycteridae	4 (100%)	0 (0%)	4 (100%)
	Hipposideridae	4 (23.5%)	13 (76.5%)	17 (100%)
	Ungrouped (fossil)	7 (87.5%)	1 (12.5%)	8 (100%)
Cross-validated	Rhinonycteridae	2 (50%)	2 (50%)	4 (100%)
	Hipposideridae	5 (29.4%)	12 (70.6%)	17 (100%)
(B) Lateral				
		Rhinonycteridae	Hipposideridae	Total
Original	Rhinonycteridae	3 (75%)	1 (25%)	4 (100%)
	Hipposideridae	3 (17.6%)	14 (82.4%)	17 (100%)
	Ungrouped (fossil)	5 (62.5%)	3 (37.5%)	8 (100%)
Cross-validated	Rhinonycteridae	2 (50%)	2 (50%)	4 (100%)
	Hipposideridae	4 (23.5%)	13 (76.5%)	17 (100%)
(C) Ventral				

		Rhinonycteridae	Hipposideridae	Total
Original	Rhinonycteridae	3 (75%)	1 (25%)	4 (100%)
	Hipposideridae	3 (17.6%)	14 (82.4%)	17 (100%)
	Ungrouped (fossil)	5 (62.5%)	3 (37.5%)	8 (100%)
Cross-validated	Rhinonycteridae	2 (50%)	2 (50%)	4 (100%)
	Hipposideridae	6 (35.3%)	11 (64.7%)	17 (100%)

Table 3. Results for classification of fossil taxa using Discriminant Analysis (DA), conducted separately for (A) Dorsal measurements, (B) Lateral landmarks and (C) Ventral landmarks captured on bat crania. Fossils were assigned as unknown, and the classified as either belonging to Rhin=Rhinonycteridae or Hipp=Hipposideridae. Consensus of classification results across all three data sets is provided for comparison with group affiliation hypotheses based on Fig. 2. Cases of agreement between the consensus predicted group and hypothesized group are shaded.

Taxon	Grouping result			Consensus	Hypothesis
	(A) Dorsal	(B) Lateral	(C) Ventral		
Archerops annectens	Rhin	Hipp	Rhin	Rhin	Hipp
Brevipalatus mcculloughi	Rhin	Rhin	Rhin	Rhin	Rhin
Brachipposideros watsoni	Rhin	Rhin	Rhin	Rhin	Rhin
Hipposideros bernardsigei	Rhin	Hipp	Hipp	Hipp	Hipp
Pseudorhinolophus bouziguensis	Hipp	Hipp	Hipp	Hipp	Hipp
Rhinonicteris tedfordi	Rhin	Rhin	Rhin	Rhin	Rhin
Riversleigha williamsi	Rhin	Rhin	Hipp	Rhin	Hipp
Xenorhinos halli	Rhin	Rhin	Rhin	Rhin	Rhin