ARCHEROPS, A NEW ANNECTENT HIPPOSIDERID GENUS (MAMMALIA: MICROCHIROPTERA) FROM THE AUSTRALIAN MIocene

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ABSTRACT—A new genus and species of hipposiderid bat is described from an early to middle Miocene cave deposit (AL90) Site, estimated to be between 15 and 20 million years old) at Riversleigh, northwestern Queensland, Australia. Archerops anneceticus new genus and species is interpreted to be most closely related to species of the Asian genera Coelops and Paracoelops and southeastern Africa’s Cloeotis perivialis, none of which has a fossil record. The new Australian fossil bat: 1) shares a number of aomorphoses with species of Coelops, Paracoelops, and Cloeotis; 2) lacks striking autapomorphies characterizing each of the three extant genera; 3) exhibits few autapomorphies of its own; and 4) forms a structural intermediate between pleiometorphic Tertiary hipposiderids (e.g., Bra- chioposidbo species) and the aberrant Coelops, Paracoelops, and Cloeotis species.

INTRODUCTION

Living hipposiderids, or Old World leaf-nosed bats, have an Old World tropical to subtropical modern distribution and are referred to 65 species (Koopman, 1994). The most speciose genus, Hipposideros, contains 53 species, with eight other genera (Rhinonycteris, Coelops, Paracoelops, Triaenops, Cloeotis, Antechinus, Asellia, and Aselliscus) containing one to two species each. Old World leaf-nosed bats are sometimes regarded as a subfamily of the Rhinolophidae; either the Hipposiderinidae Lydekker, in Huwer and Lydekker, 1891 (e.g., Koopman; 1994); or Rhinonycterinae Gray, 1866 (e.g., McKenna and Bell, 1997). Here, we follow Miller (1907) in recognizing them as a separate but closely related family.

Most hipposiderids are cave-dwelling bats and the family is well represented in Tertiary karstic sediments, the oldest representatives being from the middle Eocene of Europe, early Oligocene of Arabia, late Oligocene of Australia, early Miocene of Asia, and early Miocene of Europe. Tertiary taxa include species of the modern genera Hipposideros, Rhinonycteris, Triaenops, and Asellia and the Tertiary genera sensu Hand (1997b) Pseudorhinolophus, Palaeophyllophorina, Vayalata, Brachiposideros, Xenorchis, Riversliguh, and Miophylodonh. Six genera (Hipposideros, Rhinonycteris, Brachiposideros, Xenorchis, Riverselegh, and Miophylodonh) have been recorded from the bat-rich late Oligocene-middle Miocene and Pliocene sequences of freshwater and karstic limestones at Riversleigh in northwestern Queensland, which range in age from 25 to 4 million years old (Archer et al., 1994; Sigé et al., 1982; Hand, 1997a, 1997b, 1997c, 1998a, 1998b).

In the most recent systematic summary of hipposiderids, McKenna and Bell (1998) recognized two tribes: Coelops (for species of Coelops and Paracoelops) and Rhinonycterina containing the two subtribes Hipposiderina (Hipposideros, Antechinus, Aselliscus, Asellia) and Rhinonycterina (Rhinonycteris, Brachipossideros, Cloeotis, Triaenops). Cladistic analyses of living and fossil hipposiderids by Hand and Kirsch (1998) suggested that close relatives of the Rhinonycterina/Cloeotis-Triaenops group include not only species of Brachiposideros but probably Xenorchis and Riverselegh. However, Hand and Kirsch (1998), also Bogdanowicz and Owen (1998) in their phylogenetic analysis of living hipposiderids, suggested a closer relationship between species of Coelops and Cloeotis than is indicated by current taxonomic arrangements. The latter two studies also indicated that Hipposideros is a paraphyletic group, as suggested previously by paleontologists Hugueny (1965), Sigé (1968), and Legendre (1982). In their phylogenetic supertree of bats, Jones et al. (2002) reiterated that most higher-level relationships within the Hipposideridae remain unresolved but supported recognition of the tribe Coelopsini for species of Coelops and Paracoelops.

The new Miocene hipposiderid from northwestern Queensland, Australia, described here as a close relative of Cloeotis and Coelops species, appears to form a structural link between relatively pleiometorphic hipposiderids (e.g., Brachiposideros species) and the highly specialized African Cloeotis and Asian Coelops and Paracoelops lineages, neither of which has a fossil record. In this sense, it represents an annectent form that links two otherwise morphologically very distinct groups of hipposiderids.

In this paper, skull terminology follows Hand (1993, 1998); dental terminology follows Sigé et al. (1982). Stratigraphic nomenclature for the Riversleigh region follows Archer et al. (1994) and Creaser (1997). Repositories of specimens are indicated by prefixes as follows: QME; fossil collections of the Queensland Museum, Brisbane; AMNH, American Museum of Natural History, New York; AR, temporarily held in collections at the University of New South Wales, Sydney.

SYSTEMATIC PALEONTOLOGY

Suborder MICROCHIROPTERA Dobson, 1875
Family HIPPOSIDERIDAE Miller, 1907
ARCHEROPS new genus

Type and only species.—Archerops anneceticus new species

Diagnosis.—Species of this genus differ from species of Hipposideros, Rhinonycteris, Brachiposideros, Triaenops, Aselliscus, Asellia, Xenorchis, Riverselegh, Pseudorhinolophus, Vayalata, Sydnesemantis, and Palaeophyllophorina in having a narrow and low rostrum with postero-lateral quadrants most conspicuously inflated.

They differ from species of Coelops (i.e., frishi and robinsoni) in their less developed supraorbital crests and frontal plate, less anteriorly extended maxilla (= less retracted nasals, see Comparisons below), tall zygomatic process, smaller foramen ovalis, narrow antorbital bar, shorter antero-lateral cingular cup on C1, wider C1–P4, and squarer molars.

They lack the peculiar basioccipital morphology of Cloeotis perivialis (including the very constricted sphenoorbital bridge and pronounced ridge extending from pterygoid to petrosal) and have a longer rostrum, better defined supraorbital ridges and frontal depression, taller zygomatic process, and shorter antero-lateral cingular cup on C1.

Etymology.—For Professor Michael Archer, Director of the
Australian Museum, in recognition of his leadership of the Riversleigh fossil project for the past 25 years and for his unaltering support of fossil bat research.

Occurrence.—Early to middle Miocene of northern Australia (approximately 15 to 20 million years old). Known only from the type locality for *Archeros annectens*.

**Archeros annectens** new species

**Figure 1**

**Diagnosis.**—As for the genus until additional species are known.

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

The rostrum is longer than wide; its lateral borders slightly converge anteriorly. The anterior emargination of the nasals describes a broad and very deep arc between the maxillae and is marked by a broad median spine. Rostral inflations are low but relatively well defined, most conspicuously posterolaterally. A depression (best seen in lateral view or profile) defines anterior and posterior inflations; an unpaired nasal foramen occurs in the shallow trough separating left and right inflations. There is a deep frontal depression bound laterally by well-developed supraorbital crests; the latter extend from within the postero lateral rostral inflations to meet the low sagittal crest at a point level with the pterygoid processes. The supraorbital crests are better developed in some specimens (e.g., QMF31572) than in others (QMF31570), and in the former more clearly define a triangular frontal depression that is perforated by many tiny foramina. A very slight depression, pierced by one or two foramina, occurs laterally at what is probably the junction of the nasal and maxilla (above the level of M1). The zygomatic arch extends onto the face as a very thin (in QM31571 thread-like) antorbital bar. The elongated infraorbital foramen is dorsal to M2.

In the lateral wall of the face, at the anterodorsal edge of the circumorbital rim and above the anterior attachment point of the antorbital bar, a large circular foramen opens (?lacrimal foramen, but see Pedersen, 1995). The lateralventral fossa (Hans, 1993, 1997a) is deep and broad (forming a large pocket or recess inside the maxillary root of the zygoma in the terminology of Tate, 1941 and Hill, 1972). At the most anteroventral point of the orbit is the postpalatal foramen.

The toothrows are slightly convergent anteriorly. The deep, broad V-shaped indentation that marks the palate's junction with the premaxillae extends posteriorly to the level of the M2 metacone. The palatal midline and posterolateral indentations extend posteriorly to approximately level with the M3 protocone. Maximum width of the palate occurs at M3. Palatal foramina are scattered and poorly developed.

The nasals are divided by a median septum that is bordered ventrally by the dorsal palate and dorsally by the nasals (antero- orry) 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.

Between the orbital fossae, the braincase narrows markedly. The point at which the two supraorbital crests unite (i.e., where the sagittal crest originates) is posterior to the point of narrowest constriction. The palatines and pterygoids are normally developed. The sphenoidal bridge is broad anteriorly, constricted posteriorly. In ventral view, the sphenoidal fissure, which is long and oval, is exposed posteriorly and is separated from the relatively small optic foramen by a narrow bony splint. Pterygoid processes occur at a point approximately midway along the sphenoidal bridge. These processes have a secondary flange directed posteroventrally.

Immediately anterolateral to the sphenoidal fissure is a relatively large foramen that drains the anterior transverse sinus. Postero-dorsal to the postpalatal foramen is the small sphenopalatine that leads into the posteroventral part of the nasal cavity. Posterodorsally and medially, several small foramina open into a long, curved, shallow groove that leads posterodorsally from the postpalatal foramen to the optic foramen. Dorsally and medially again is a deeper, shorter, anteroposteriorly directed sinus into which a number of foramina also open at the level of, or just posterior to, the cribriform plate of the ethmoid. These foramina vary in number, form and position. There is a slight groove in the mesopterygoid roof.

The jugal has a very tall projection that occupies approximately half its length. The ventral margin of the zygomatic arch is only slightly arched and lies dorsal to the toothrow. Posteriorly, the dorsal margin rises nearly vertically to form the projection which rises to the level of the dorsal edge of the? lacrimal foramen. Its maximum height occurs dorsal to the glenoid surface. Its apex is rounded, converging slightly towards the skull, and its posterior margin convex and vertical to backward-sloping. A mastoideal scar occurs on the anterolateral vertical surface of the arch. The zygomatic arches diverge posteriorly at first then flatten to become less divergent posteriorly.

The braincase is oval in shape in dorsal view. It is widest at the level of the post-tympanic processes, narrowest in the interorbital area, and highest dorsal and posterior to the postglenoid processes. There is little development of the lambdoidal crest but in some specimens (QMF31572) it is slightly better developed than in others (QMF31571). A low sagittal crest extends from the supraorbital ridges to the parietal region. Approximately two-thirds along the length of the braincase, within the parietals, is the posterior transverse sinus, along which several small orifices open extracranially.

The glabeloid surface is anterodorsally-posteroventrally inclined, only slightly concave and approximately as long as wide. The postglenoid process is low, its anterior face slightly anteriorly recurved. The postglenoid foramen is elongate and opens immediately posteriorly to the postglenoid process. Posteromedial to the glenoid surface, the foramen ovalis opens in the alisphenoid. In area, it may be as much as one-third that of the glenoid fossa (e.g., QMF31572).

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

The basisphenoid is hexagonal. The anterior margin of the basi- cranial area is relatively wide, the sphenoidal bridge being only moderately constricted posterior to the second pterygoid flange. Faint, anteriorly convergent ridges extend from the sphenoidal bridge and define the shallow basisphenoid fossa. The lateral edges of the basisphenoid-basioccipital complex are biconcave curves. There is no lateral extension of the basisphenoid into the cavity for the petrosal. Minimum basioccipital width is narrow relative to cavity width, suggesting the petrosals would have been moderately enlarged (in width two to three times the shortest distance between them).
Figure 1—Archerops annectens n. sp., AL90 Site, Riversleigh, northwestern Queensland. Holotype, QM F31570, skull with left C1–M3 and right C1–M2. 1, dorsal view; 2–3, ventral view, stereopair; 4, lateral view; 5–6, dentition, oblique-occlusal view, stereopair.
The most posterior point of the skull is the junction of the interparietal and supraoccipitals which is marked by a poorly developed lambdoidal ridge. The latter parallels the dorsal edge of the foramen magnum, terminating anteriorly in the region dorsal to the paroccipital process. A supramastoid foramen opens on the occipital surface dorsal to the ventral condyloid fossa. In ventral view, the posterior skull contour of the supraoccipital at the level of the lambdoidal ridge is rounded. The dorsal edge of the posteroventrally directed foramen magnum is rounded and unthickened. The foramen magnum is oval, being slightly wider than deep. Between the occipital condyle and paroccipital process is a deep condyloid fossa. The paroccipital process is well developed with a bifurcated tip. The condyle projects most strongly ventrally at the posterior extremity, its thickened lip partially concealing the condyloid foramen in the anterolateral face.

The upper dental formula of *Archerops annectens* is I1 C1 P2 M3. The premaxillae and upper incisors are unknown. C1 is tall, slender and relatively short in the toothrow, with a tall posterior accessory cusp and incomplete buccal cingulum. The lingual cingulum is deep anteriorly and the anterior cingulum forms a low but distinct cingular cusp. P2 is very small, low-crowned and extruded from the toothrow so that C1 and P4 are in contact. P4 is wider than long, almost as wide as M1, and has a pronounced anterolinguall cusp. The cingulum is virtually continuous except in the extreme posteroauricular corner at the end of the posteroauricularly directed crest from the main cusp. In M1 and M2 the protofossa is open and the protostyristis makes dihedral angle to form a crest that reaches the lingual cingulum. The M1 heel is postero lingually directed and is much better developed than in M2. Nonetheless M2 has a well-developed, postero lingually developed heel. M3 is little reduced in length or width, with a distinct postmetacrista; the premetacrista is half to three-quarters paracrista length.

Dentaries of this species have not been positively identified from among the hundreds recovered from the AL90 deposit. Several hipposiderid taxa of similar size (identified on the basis of cranial material) are represented in the AL90 deposit but none have yet been found with a dentition occluding exactly with that of any of the four skulls referred to *A. annectens*.

Measurements of the holotype and referred specimens of *Archerops annectens* are given in Table 1.

**Eymology.**—From the Latin *annect* meaning to link, in reference to its interpreted intermediate position between pleistomorph hipposiderids (such as *Brachhipiphitoides* species) and the specialised *Coelops*, *Paracoelops*, and *Cloeotis* species.

**Types.**—Holotype, QM F31570, skull with left C1–M3 and right C1–M2. Paratypes, QM F31571, skull with right M2–3; QM F31572, skull with left P4 and right P4 and M2–3; QM F31573, skull with left M2 and right M2–3.

**Occurrence.**—AL90 Site occurs in the southern section of the Gag Plateau, in the Riversleigh World Heritage property, Lawn Hill National Park, northwestern Queensland, Australia (Archer et al., 1994; Creaser, 1997). Arena and Black (1997) described the AL90 deposit as an early to middle Miocene primary cave system with later secondary cave formation and infill, characterised by contrasts in geology and associated fossil faunas. On the basis of contained local faunas and stratigraphy, the AL90 assemblage containing *A. annectens* is interpreted to be early to middle Miocene in age or approximately 15 to 20 million years old (Archer et al., 1994; Black, 1997; Arena and Black, 1997).

**Associated fauna and taphonomy.**—The AL90 deposit probably represents a pit-fall trap that accumulated a large number of associated and sometimes articulated skeletons of the sheep-sized diptodontid *Nimbudon lavarackorum* Hand et al., 1993, a thylacine, and a balarine kangaroo. Other vertebrates in the deposit include other balarine and bulangumayine kangaroos, bandicoots, a ringtail possum, snakes, a dromornithid bird, and six other hipposiderid referable to the *Brachhipiphitoides-Rhabaneciotis* group and an undescribed genus.

**Comparisons.**

*Archerops annectens* differs from most hipposiderids in its narrow and very low rostrum. Among hipposiderids, only species of *Coelops*, *Paracoelops*, and *Cloeotis* share this striking characteristic. *Hippopoides* (*Synedmomys* *)* *megaleutus* and species of the *Hippopidoides bicoelar group* (sensu Hall, 1963) have a narrow rostrum, but it is not as low as in species of *Coelops*, *Paracoelops*, *Cloeotis*, and *Archerops*. *Archerops* additionally differs from *H. megaleutus*, which perhaps most closely approaches the latter group in rostral shape, in, among other features, its well defined supralingual crest, flattened frontals, narrow antorbital bar, more constricted interorbital region, tall zygomatic process, retention of P2, large M3, anteriorly extended maxilla, and broad V-shaped anterior margin of palate.

**Comparisons with Coelops and Paracoelops spp.**—Species of *Coelops* and *Paracoelops* are distinguished from other hipposiderids by the following combination of features (see Fig. 2A–2C): low rostrum; forward extension of the canine-bearing portion of the maxilla; upper canines pro-odont with anterolinguall cusp and well-developed posterior cusp; basicanal foramina greatly enlarged; mandibular symphysis U-shaped; lower incisors separated from canines by a distinct gap; first metacarpal greatly lengthened; ears without strengthening ribs of cartilage; a deep notch in the anterior noseleaf, which is expanded to the sides; lateral leaflets large and expanded forwards; no external tail but interfemoral membrane fully developed (e.g., Koopman, 1984). Two *Coelops* species are currently recognized: *C. frithii* Blyth, 1848, of eastern Asia from Bengal to Taiwan and Bali (forearm 25–47 mm), and the smaller (forearm 33–37 mm) *C. trotternisi* Hornb., 1908, of Thailand, peninsular Malaysia and Borneo (Koopman, 1994).

*Paracoelops* is known only from the badly damaged type specimen of *P. megaleutus* Dorst, 1947, collected in Vietnam in 1945 and held in the Museum National d’Histoire Naturelle, Paris; it was not examined in this study. Craniodontically, it apparently differs little from *Coelops* species but has a more inflated rostrum and better developed upper incisors (Dorst, 1947). It also has larger ears and an unemarginated uroptagium (Dorst, 1947; Koopman, 1994).

Koopman (1994) placed species of *Coelops* and *Paracoelops* in a separate hipposiderid tribe, the *Coelopini*, McKenna and Bell (1997) subsequently recommended the name Coelopini for...
the same tribe. Previously, Tate (1941) had referred Coelops species to the subfamily Coelopinae on the basis of characters of the tail, pinna, noseleaf, metacarpals, and four cranial features. Two of the latter features (i.e., greatly extended canine-bearing portion of the maxilla, U-shaped symphysis portion of combined mandibles) are autapomorphies shared by no other living hipposiderid taxa, while two (C with anterior and posterior accessory cusps, much fenestrated basicanium) are shared with Clooetis percuti.

Apart from a very low rostrum, Archerops annectens (Fig. 2.7–2.9) shares a number of striking features with species of Coelops. Among these is the apparent forward extension of the canine-bearing portion of the maxilla. Although this is less marked in A. annectens than in species of Coelops, it is much greater than in any other hipposiderid. This feature, however, needs clarification. Using a broad range of fossa and extant hipposiderids for comparison, it is evident that it is not the canine-bearing portion of the maxilla that is greatly extended forwards in species of Coelops, Archerops, and evidently Paracoelops, but rather posterior retraction of the nasals. In Coelops species, C1–P4 length is not unusually long relative to toothrow length (less than half C1–M3 length), and neither measure is long relative to skull length (C1–3 length approximately one-third skull length). The canine-bearing portion of the maxilla (i.e., C1 length in the toothrow) in Coelops species is in fact shorter than in most hipposiderids, although C1 is more pro-odont than in other hipposiderids. However, C1–P4 are remarkably narrow, as is the maxilla (due to the very broad and deep emargination of the palate), both factors contributing to the “extended” appearance of the anterior part of the maxilla. Further, in Coelops species and in A. annectens, the nasal inflations are not only low relative to braincase height but are also short relative to both rostral length and skull length compared with other hipposiderids.

Craniodentially, Coelops robinsoni is distinguished from the type species C. frithi by the following features (Miller, 1928; Tate, 1941; Hill, 1972): rostral elevations larger, separated by a more prominent sulcus, in profile more distinct convexity; posterior part of the upper surface of the rostrum more nearly horizontal and only slightly inclined anteriorly; a small foramen but no definite pocket or recess within the maxillary root of the zygoma, the upper edge of which is more sharply curved anteriorly to terminate on the rostrum above the posterior (rather than anterior) face of M2; upper toothrows nearly parallel rather than anteriorly convergent; P4 relatively wider; lower molars with low, upwardly curving rather than horizontal buccal cingula. Archerops annectens shares with C. frithi a broad recess within the maxillary root of the zygoma (or broad lateral ventral fossa; Hand, 1993) (Fig. 2), but has a prominent sulcus between the rostral inflations as in C. robinsoni. The slightly anteriorly convergent toothrows of A. annectens represent a condition intermediate between those observed in the two Coelops species.

Compared with the C1 of Coelops species, C1 in Archerops annectens does not project as far forward but is proportionately longer in the toothrow. The C1 anterior cingulum, which forms the anterior secondary cusp of C1 in Coelops (and Clooetis) species, does not extend as far down the shaft (less than halfway) in A. annectens. In these ways, the C1 of Archerops annectens is more typically hipposiderid-like (i.e., plesiomorphic) than in Coelops spp.

The cheekteeth of A. annectens are, however, quite different from those of Coelops species. In Archerops annectens P4–M3 are very similar to those of other hipposiderids, perhaps closest to the dentition found in members of the Brachhippoidea group. In Coelops species, the cheekteeth are basically triangular in shape rather than square or rectangular; P4 is very long and narrow (unlike all other hipposiderids), and M1–2 have taller cusps and narrow, almost pointed, posteroconically directed heels with very tall posteroconical cusps. In M1–3 the postprotoconid is continuous with the posterior cingulum to form a metaconid (as in Rhinolophidae). In Coelops spp., P2 is extruded from the toothrow but still separates C1 and P4; in A. annectens, P2 is completely extruded such that C1 and P4 are in contact. The M1 of Coelops species has a more complete ectoloph with the postmetacrista just shorter than the premetacrista.

Archerops further differs from Coelops species in its tall zygomastic process, smaller foramen ovale, and very narrow antorbital bar. The anterior margin of the palate (where the premaxillae abut) is a deep U-shape in Coelops species whereas in A. annectens it is slightly more V-shaped; this difference in shape is mostly due to lateral reduction of the palate adjacent to P4 in Coelops spp. The posterior margin of the palate is rectangular in Coelops spp., round in A. annectens; the infratrobiatal foramen is round in Coelops spp., oval in A. annectens; the optic foramen is in Coelops frithi, large in A. annectens; the sphenorbitals bridge is of similar width but more constricted posteriorly in A. annectens. In species of Coelops and Archerops, the petrosals appear to have been similarly (moderately) inflated, the cavity for the periotic being either the same width (with same bone thickness) or slightly smaller anteriorly (as in A. annectens).

Like Coelops species, Archerops has well developed supraorbital crests and postero-lateral rostral inflations, but the frontal plate is not as well developed.

Comparisons with Clooetis percuti.—The type and only species of Clooetis Thomas, 1901 is a small bat (forearm 30–39 mm) confined to southeastern Africa from Kenya to Transvaal. Distiguishing features of C. percuti (Fig. 2.4–2.6) include: rostrum unusually short with inflations poorly developed, C1 with anterior and posterior accessory cusps, P2 sometimes lost, zygoma not especially expanded, much fenestrated basicanium, posterior noseleaf with three tall pointed projections, ears unusually short (Koopman, 1994).

The dentition of Archerops annectens is generally more similar to that of Clooetis percuti than Coelops and Paracoelops species. As in A. annectens, in C. percuti P2 is reduced and almost completely extruded (sometimes absent) from the toothrow, P4 is wider than long with an anteroconid, anterior cingulum 1–2 lack posteroconid cusp, and M3 is large with the premetacrista half to three-quarters arciatcrista length but the postmetacrista more reduced than in Coelops spp. In C. percuti, the M1–2 heels are short and the postprotocrista reaches the base of the metaconid, closing the protoconid; in A. annectens the M1–2 heels are better developed and the protoconid open posteriorly with dihedral crest reaching the posteroconid cingulum.

The C1 of Clooetis percuti is more similar to that of Coelops species than to A. annectens; the tooth is shorter in the toothrow, the cingulum is unthickened anteroconidally and extends further down the shaft, forming a distinct anterior cingulum cusp. Both features are less pronounced than in Coelops species.

As well as a very low rostrum and generally similar dentition, Archerops annectens shares with species of Clooetis a tall zygomastic process, postero-laterally inflated rostrum, and reduced antorbital bar. In Clooetis the antorbital bar is lost completely; in some specimens of A. annectens (e.g., QMF35175) it is reduced to a thread-like condition. In A. annectens the zygomatic process is much taller than in C. percuti. Archerops annectens lacks the peculiar basi-branchial morphology seen in Clooetis percuti (including the extreme constriction of the sphenorbitals bridge and hyperdevelopment of a ridge running from pterygoid to petrosal) and has better defined supraorbital crests and frontal depression. In Archerops annectens, the rostrum is flatter and relatively much longer than in C. percuti (in which it is less than half braincase length) and hence much more like other hipposiderids, including
Figure 2—Lateral, dorsal and ventral views of: 1–3, Coelops frithi bernsteini (AMNH 107508); 4–6, Cloucaitis percivalii australis (AMNH 168160); 7–9, Archerops annecetus n. sp. (QMF31570); 10–12, Rhinonycteris aurantius (AR 15400). Scale bar indicates 5 mm.
species of Coelops (rostrum length more than half braincase length).

No dentaries have been referred to A. annuens. A U-shaped mandibular symphysis is diagnostic for species of Coelops and Paracoelops (Koopman, 1994), and a gap between the lower out-
cr incisor and canine, and a very long p2 and p4 are found in at least Coelops species. No dentaries exhibiting these features have been found in the A1.90 deposit. Many dentaries recovered are
very small and shallow with a low ascending ramus as seen in
species of both Coelops and Cloeotis but these features are also
characteristic of species of Synadoxmor and the Branchipside-
eros-Rhynochyterid lineage among others (Legendre, 1982). No
unique features appear to distinguish the dentary of Cloeotis per-
rcivali from other hipposiderids.

In summary, Archeros annuens shares a number of cranio-
dental features in common with species of both Coelops and
Cloeotis. Overall, it shares perhaps more similarities with Coelops
species than Cloeotis perrcivali, but it lacks a number of striking
features that distinguish species of Coelops (and evidently
Paracoelops) from all other hipposiderids.

PHYSIOGENETIC ANALYSIS

The phylogenetic interrelationships of genera and species
groups in the family Hipposideridae have been examined by Hand
and Kirsch (1998) and Bogdanowicz and Owen (1998). In their
PAUP 3.1.1 (Swoford, 1993) and Henning-Bg (Farris, 1988) anal-
yses, Hand and Kirsch (1998) included 30 extant hipposiderid
species and seven fossil taxa which they scored for 59 discrete
dimensions (26 cranial, 20 dental, and 3 skeletal). In Bogdanowicz
and Owen's analysis, 45 metrical and 30 discrete-state characters
in 57 extant hipposiderid species were examined. The results of
these 2 studies differed significantly from each other in many
respects (e.g., in interpreted relationships between Hipposiderid
species), but they agreed in a number of points, including that the
family Hipposideridae is probably monophyletic, that the genus
Hipposideros is probably paraphyletic, and that the composition
of previously-proposed divisions within Hipposideros needs re-
examination. Both studies suggested associations of geographi-
cally widely separated taxa, including species of Coelops and
Cloeotis.

In the study by Hand and Kirsch (1998), Coelops frithi and
Cloeotis perrcivali were paired in seven out of eight analyses, and
were often associated with Trinaceus pterus and a group of
Riversleigh fossil taxa including species of Branchipsideis and
Rhynochyteris. In the study by Bogdanowicz and Owen (1998),
Coelops and Cloeotis were again paired but in that case the clade
appeared distally in trees (a terminal pair among mostly Hipposi-
deros species) rather than towards the base of trees as in most

When Archeros annuens is included in PAUP analyses
(PAUP 4.0, v. 10) of characters modified from Hand and Kirsch
(1998, Appendix 1, Table 2, Characters 1-59), relationships of
hipposiderid taxa are identical to those previously found by those
authors, but Archeros annuens forms part of an unresolved
multictomy with species of Coelops, Cloeotis, Trieneopis, and
Australian species Branchipsideos and Rhynochyteris, as well
as with species of Riversleigh and Xenorhinos in some cases
(some characters ordered). However, characters used by Hand
and Kirsch (1998) did not include cranialid autapomorphies for
Coelops and Cloeotis. When five such characters (e.g., degree of
nasal retraction, relative length of rostrum, width of lateral ventral
fossa) are added to the data matrix (Table 2, Characters 60-64),
as well as the second species of Coelops (C. robustissim), the mul-
ticity is fully resolved (Fig. 3): species of Coelops form a
cladc, with Cloeotis perrcivali their immediate sister-group, and
Archeros annuens the sister-group once removed.

The sister-group to the Coelops-Cloeotis-Archeros clade varies
dependng on whether character transformations are ordered:
when transformations are unordered the sister-group is
formed by species of Rhynochyteris and Branchipsideis (Fig.
3); when some transformations are ordered (Characters 11, 17,
18, 19, 22, 28, 34, 37, 43, 51) the sister-group consists of species
of Rhynochyteris, Branchipsideos, Riversleigha, Trieneopis, and
Xenorhinos (see also Hand and Kirsch, 1998). Further, the latter
group occurs as the sister-group of the Coelops-Cloeotis-
Archeros when the enigmatic Riversleigh Miocene hipposiderid ?Brac-
chipsideos watsoni Hand, 1997b, is included in analyses, regard-
less of whether transformations are ordered (Fig. 3.2). Al-
though relationships between species of Coelops, Cloeotis, and
Archeros were resolved in all analyses, ordering transformations
significantly reduced resolution of other hipposiderid relation-
ships, specifically among Hipposideros species. When transfor-
mations were unordered, four or eight shortest trees were found
(depending on inclusion of ?B. watsonii; Fig. 3.1, 3.2), compared
to 202 shortest trees ordered transformations (irrespective of the
inclusion of ?B. watsonii). Because the distribution of syn-
apomorphies in the Coelops-Cloeotis-Archeros clade did not sig-
ificantly differ when transformation series were ordered, only
the best resolved trees (unordered transformations) are shown
in Figure 3. Bootstrap percentages of 50 percent or more, based
on 100 replicates with standard defaults, are also shown.

We were able to perform a branch-and-bound analysis (other-
wise using the defaults in PAUP 4.0, v. 10) on 20 of the included
hipposiderid taxa, indicated in boldface in Table 2. Given the
consistent placement of Aselliscus tricuspidatus as sister to the
remaining hipposiderid in all our computations, we assume the
root about these 20 to lie between the two major non-Asel-
listiscus clades shown in 3.2. Twenty-five equally most-parsoni-
omous trees resulted from the branch-and-bound analysis, the strict
consensus of which resolved only a trinity consisting of Archer-
os annuens, Cloeotis perrcivali, and Coelops frithi; and a sec-
ond trinity consisting of these three together with Branchipside-
eros noordveelbus and Rhynochyteris aurantiss. This group of
two then constituted one clade among 16 in an otherwise unre-
solved bush.

Unequivocal craniodental synapomorphies of the Arche-
ros-Coelops-Cloeotis clade include a narrow, low rostrum and
V-shaped anterior palate, tall C1 posterior accessory cusp, pre-
nounced nasal retraction, and conspicuous posterostral rostral
inflations (5, 6, 11, 40r, 60, 64, where r indicates reversal; see
Fig. 3). Synapomorphies of the Cloeotis-Coelops clade recognized
by these analyses vary, and in all analyses, at least one synapomor-
phy is unequivocal (C1 with tall anterolingual cingular cusp). Other
craniodental synapomorphies potentially include an anteriorly-po-
ositioned, round infraorbital foramen, a rounded anterovelmental
rim of the orbital floor, enlarged foramen ovale, a reduced latero-
velentral fossa, and M1 with closed protossofa (17r, 18r, 20r, 37, 49,
62; see Fig. 3). Other unique (soft tissue) synapomorphies for this
cladc appear to include a reduced pinna.

Because information about its basicranial morphology is not
available, the damaged skull of Paracoelops davisii was not in-
cluded in the PAUP analyses. However, from its description, and
from comparisons by other workers (e.g., Koopman, 1994), it is
likely that it would cluster tightly with Coelops species, sharing
with them greatly enlarged foramen ovale and C1 with tall an-
terolingual cingular cusp.

DISCUSSION

Hill (1982) suggested that the living Rhynochyteris auranti-
iss of northern Australia, Trieneopis species of southwestern Asia
and Africa, and Cloeotis perrcivali of southern and eastern Africa form
groups characterised principally by a number of common features.
of the nodule, and considered them ancient but specialised offshoots of the hipposiderid radiation. Koopman (1994) recognized the subtribe Rhinonycterina for these taxa (Table 3). Sigé et al. (1982) and Hand (1997b) found a close relationship between Rhinonycteris and extinct Bradicippospositides species, and McKenna and Bell (1997; Table 3) added Bradicippospositides species to the subtribe Rhinonycterina. Hand and Kirsch (1998) suggested that the Australian Miocene taxa Xerorhinus halli and Riversleigh williamsoni could also belong to this group.

McKenna and Bell (1997) referred species of Coelops and Paracaelops to a separate tribe Coelopini (supported by Jones et al., 2002; Table 3). However, Hand and Kirsch (1998) suggested that Coelops fitchi might also be a member of the Rhinonycterina, recognising a special relationship between Coelops and Cloweitis species (see also Bogdanowicz and Owen, 1998).

Results presented here (Fig. 3; Table 3) suggest a close phylogenetic relationship between species currently referred (e.g., McKenna and Bell, 1998) to different tribes: the Coelopini and Rhinonycterina. The new Riversleigh bat Archersanctides appears to embody a structural link, or annectent form, between the aberrant Coelops, Paracaelops, and Cloweitis lineages and more plesiomorphic hipposiderid species such as Brachicippuspositides species. Brachicippuspositides species are now known from Tertiary sediments (ranging in age from 25 to 4 million years old) of Europe, Arabian Peninsula, Australia and Asia (Sigé, 1968; Sigé et al., 1982, 1994; Legendre, 1982; Ziegler, 1993; Hand, 1997b; Mein and Ginsburg, 1997) and their living relatives appear to be distributed from Africa (Trinacops, Cloweitis) to Asia (Coelops and Paracaelops) and Australia (Rhinonycteris). These bats exhibit a broad range of skull shapes and morphology but preserve a dentition that is evidently plesiomorphic among hipposiderids (Hand, 1998b). As a group they appear to be more derived than Asellus species but basal to a Hipposideros-dominated clade that also includes species of Asellus, Anloaps, Pseudorhinolophus, and Palaeoplagyptodon (Hand and Kirsch, 1998; Fig. 3).

The phylogeny presented here and the preceding ones of Hand and Kirsch (1998) indicate that species of Coelops and Paracaelops might be better referred to a subtribe of the tribe Rhinonycterini (Table 3), containing: the Rhinonycterina (for species of Rhinonycteris, Bradicippospositides, and possibly Trinacops, Xerorhinus, and Riversleigh); and the Coelopini (for Coelops, Paracaelops, Cloweitis, and Archersanctides). Other hipposiderid species may form the tribe Hipposiderini, although further taxonomic revision within the family is needed to help interpret the interrelationships of other hipposiderid taxa, particularly Hipposideros and Asellus species.

Biogeographically, it would appear that plesiomorphic, Brachicippuspositides-like hipposiderids were widespread throughout the
Old World tropics in the early to middle Tertiary (40 to 15 million years ago). Among their ranks was at least one branch whose members are characterized by very narrow and low rostra and which in Africa is represented by *Clautis percivali*, in Asia by *Coelops* and *Paracoelops*, and in Australia by the Miocene *Archergops annecetus*. In Australia the lineage has not survived nor does there appear to be any obvious descendants in the Tertiary record (Miocene and Pliocene Riversleigh deposits spanning the period from around 15 to 4 million years ago). Its line does not seem to occur in the slightly older early Miocene Bitesantennary Site cave deposit (estimated to be approximately 20 million years old) which has produced the skulls of at least eight hipposiderid species (Hand, 1997b, 1998a, 1998b), although its absence could reflect microhabitat differences between sites. *Archergops annecetus* could be close to the ancestral stock that gave rise to modern coelopins but a number of autapomorphies...
TABLE 2—Classifications of Old World leaf-nosed bats proposed by Koopman (1994), McKenna and Bell (1997), and Hand and Kirsch (this paper); + extinct taxon; * paraphyletic taxon; unallocated genera are incertae sedis within Hipposideridae.

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<td>Tribe Hipposiderini</td>
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preclude Archerops annucens from a patristic relationship with either Africa’s Cloeotis percivali (e.g., a flatter rostrum in Archerops) or Asia’s Coelops and Paracoelops lineage (e.g., in Archerops a reduced antorbital bar, constricted sphenoidal bridge, extruded P2). The modern distribution of Paracoelops megalolit (Vietnam and Coelops species eastern Asia extending as far as Bali, Borneo, and the Philippines, but not the Lesser Sunda Islands) suggests radiation of this branch of the Coelopina may be tied to the Sunda Shelf (see Heaney, 1986). The apparent absence of relatives of the monotypic Cloeotis percivali from Tertiary deposits in Europe and northern Africa suggests early isolation of that lineage in what is now sub-Saharan Africa.

If Coelops, Paracoelops, Cloeotis, and Archerops species form a natural clade, as presented here, then the evolution of development of some of the most characteristic features of coelopins might be traced. For example, the small, low rostrum with retracted nasals and postero-laterally inflated ethmoids which so clearly distinguishes coelopins appears to represent a modification of the large, inflated rostrum seen in related and generally more pleiomorphic hipposiderids such as Asellus, Rhinonycteris, Brachipyridos, and Trianeops (and many species of Hipposideros). Cloeotis percivali has retained the distinct juvenile crest premaxillae (found in Brachipyridos, Rhinonycteris and Trianeops, unknown in Archerops), very large M3 (as in Brachipyridos, Rhinonycteris, Trianeops, and Archerops) and peculiar noseleaf structure shared by species of Rhinonycteris and Trianeops (i.e., noseleaf with anterior strip-like process extending anteriorly from the internarial region, posterior noseleaf with a number of deep pockets and cells). This noseleaf morphology has been extensively modified in species of Coelops and Paracoelops (i.e., horseshoe of noseleaf divided into two parts by a notch which extends back to the nasal septum), and the premaxillae crest and well-developed tail of sister taxa are lost. In Cloeotis percivali the pinna is very reduced and in species of Coelops and Paracoelops the pinna’s cartilage ribbing lost. C1 is shortened but is distinctly pro-odont (projects forward) in Coelops, Paracoelops, and Cloeotis species. Freeman (1992) discussed the advantages for a small, flying, insectivorous bat to have long, slender and “edged” (blade-like rather than conical) canines in order to generate a swift slicing penetration into insect prey. She described a posterior secondary cusp on C1 as enhancing the shearing mechanism of the upper and lower teeth by functioning as an additional serration and by increasing the bladed condition of the tooth. An additional anterior accessory cusp, as found in Coelops, Paracoelops, and Cloeotis species, would presumably increase this advantage. In Coelops and Paracoelops species, the dentition has been further modified by the narrowing of C1–P4 and reduction of heels on M1–2 (while retaining a very large M3).

The extensive modification of the rostrum and dentition in coelopins suggest possibly concomitant specialisations in ecolocation and feeding mode. Hipposiderids are typically generalist insectivores (Fenton, 1984; Findley, 1993) which feed on moths, beetles, flies, termites, cicadas, hemipterans, and cockroaches. They are slow maneuverable flyers with short, broad wings, which forage by hovering and gleaning, hawking from observation perches, or by aerial pursuit, near and within vegetation (Findley, 1993; Heller and Helversen, 1989). Insects are often caught in the wing or tail membrane while foraging low over ground and bushes. In Zambia at least, Cloeotis percivali is an aerial insectivore feeding almost exclusively on adult moths (Whitaker and Black, 1976), irrespective of seasonal or short term changes in their abundance (Black, 1979), and has very high frequency ecolocation call of >200 kHz, among the highest recorded for a bat (Fenton and Bell, 1981). Findley and Black (1983) categorized Cloeotis as a moth specialist with relatively narrow wings, short ears and a short noseleaf, traits fitting it for rapid aerial pursuit. Its habitat in southeastern Africa appears to be woodland savannah (D. Jacobs, personal commun.) where it roosts in large numbers in caves, but also in porcupine holes and disused mine adits (Kingdon, 1974).

Nothing is known about the biology, ecolocation call, or feeding habits of Paracoelops megalolit, and little about that of the Coelops species. Coelops frithi is a closed forest species, which in Szechwan and Taiwan typically roosts in caves and bunkers (Jones et al., 1969; Nowak and Paradiso, 1983), and in Java in hollow trees or caves, usually in groups of 16 or less (Lekagul and McNeely, 1977). A recording of the ecolocalization call of a hand-held C. frithi suggests that it may have a very high
frequency call of over 200 kHz (C. Francis, personal commun.). Because of striking similarities between Coelops and Cloeon species in size, wing proportions, rostral morphology, ear shape, skewer-like C1 morphology, relative petrosal size, and possibly echolocation call, as well as a close phylogenetic relationship, it is tempting to predict that Coelops species, like C. periculatus, might also have a dietary preference for, and ability to catch, moths in flight. A possible counter to that argument are equally striking differences between the two groups in noiselike morphology, a number of basicranial features, habitat preference, and lack of a tail in Coelops (and Paracloeon) species.

Archerops annectens is known from four well-preserved skulls recovered from Riversleigh’s early-middle Miocene AL90 Site. The AL90 Site deposit is interpreted to have accumulated in a cave developed in Tertiary limestone and surrounded by forest (Archer et al., 1994; Arens and Black, 1997). The nature, extent, and history of this forest is still being debated (Archer et al., 1994, 1995; Megirian, 1992; Boles, 1997), but Hand (1997a) suggested that the closest modern analogy to the early to middle Miocene of Riversleigh (approximately 15 to 20 million years ago) may be found in rainforested limestone regions of southeastern Asia and possibly New Guinea, where as many as six hipposiderid species occur sympatrically. The AL90 cave appears to have had a restricted entrance (or been water-filled), and acted as a selective pitfall trap from which large mammals (e.g., the sheep-sized Ninabulon sawarackorum and some kangaroos), fewer smaller species (e.g., a primitive carnivorous thylacine), and, rarely, small creatures (bandicoots and possums) were unable to escape. Archerops annectens and six other hipposiderids (representing at least three genera) appear to have roosted in the cave.

Archerops annectens provides a fossil record for some of the world’s most distinctive hipposiderid taxa and represents another basal group of hipposiderids for the Australian Region. Hand and Kirsch (1998) suggested that because many evidently pleisiomorphic hipposiderid taxa (e.g., species of Axeliusus, Rhinonycteris, Brachhiposideros, Riversligha, Xenorhinus; Fig. 3) occur in the Australian Region, the early radiation of the family could have occurred there. A minimum Eocene age for the early radiation of the Hipposideridae is provided by the late Eocene age of already relatively derived fossil taxa from Europe (e.g., species of Pseudorhinolophus and Palaeocynopterus). Archai batha were present in the Australian Region in the earliest Eocene (Hand et al., 1994), and the diverse Oligo-Miocene Riversleigh hipposiderid assemblage is indicative of earlier radiation. Other very distinctive Riversleigh hipposiderid genera currently being described underscore the rich and complex history of hipposiderids in the Australian Region.

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REFERENCES


DIXON, G. E. 1875. Conspectus of the suborders, families and genera of Chiroptera arranged according to their natural affinities. Annals and Magazine, Natural History Series 4, 16:345–357.


GRAY, J. E. 1838. A revision of the genera of Bats (Vespertilionidae), and the descriptions of some new genera and species. Magazine of Zoology and Botany, 2:483–505.


Character 13: Posterior extent of palate midline: 0 = posterior or equal to level of posterior lateral palatal incisura, 1 = anterior to posterior lateral incisura.

Character 14: Frontal depression: 0 = deep or conspicuous, 1 = absent or shallow.

Character 15: Supraorbital ridges: 0 = present, 1 = absent.

Character 16: Supraorbital crest development: 0 = pour, 1 = strong.

Character 17: Position of infraorbital foramen dorsal to: 0 = dorsal to M1, 1 = dorsal to M2, 2 = dorsal to M3.

Character 18: Shape of infraorbital foramen: 0 = round, 1 = subrounded, 2 = elongate.

Character 19: Lacrimal foramen size: 0 = small, 1 = enlarged.

Character 20: Anterior rim of orbital floor: 0 = rounded, 1 = raised and sharp.

Character 21: Zygomatic width compared with maximum braincase width: 0 = less than or equal to, 1 = greater than.

Character 22: Height of zygomatic process: 0 = low, 1 = moderate height, 2 = very tall.

Character 23: Sagittal crest: 0 = low, 1 = tall.

Character 24: Sagittal crest: 0 = incomplete, 1 = complete.

Character 25: Sphenorbital bridge: 0 = constricted (width posterior to pterygoid processes), 1 = wide (lateral margins posterior to the pterygoid processes are parallel), 2 = greatly constricted (width posterior to pterygoid processes half anterior width), 3 = very greatly constricted (width posterior to pterygoid processes less than half anterior width), 4 = no constriction.

Character 26: Sphenorbital fissure: 0 = fissure and optic foramen small, paired, 1 = fissure elongated.

Character 27: Posterior extent of sphenorbital fissure: 0 = level with glenoid fossa, 1 = anterior to glenoid fossa.

Character 28: Optic foramen: 0 = completely separated from sphenorbital fissure by bar of bone, 1 = incompletely separated, 2 = confluent with sphenorbital fissure.

Character 29: Mesopterygoid roof: 0 = without groove, 1 = with groove opening into basi-sphenoid depression, 2 = with deep, broad groove terminating in excavation anterior to basisphenoid (no depression).

Character 30: Protraction of vomer posterior to palate: 0 = in conspicuous, 1 = conspicuous.

Character 31: Position of hamular processes: 0 = middle third of sphenoidal bridge, 1 = posterior third, 2 = middle to posterior third, 3 = anterior third.

Character 32: Glenoid fossa shape: 0 = round, 1 = wide (conspicuously wider than long).

Character 33: Basi-sphenoid depression: 0 = present, 1 = absent.

Character 34: Basi-sphenoid shape: 0 = long and broad, 1 = diamond, 2 = extremely short.

Character 35: Petro-oral expansion: 0 = width of cavity for periotic ×6 interperiotic distance (basiscapitular width), 1 = ×1–3, 2 = ×4, 3 = ×5, 4 = ×8.

Character 36: Foramen ovale position level with: 0 = anterior to mid glenoid fossa, 1 = mid to posterior glenoid fossa.

Character 37: Foramen ovale size: 0 = less than half glenoid area, 1 = half to two thirds glenoid, 2 = more than two thirds glenoid area.

Character 38: Accessory foramina to foramen ovale (?Subovale): 0 = absent, 1 = present.

Character 39: Paroccipital processes: 0 = slender, 1 = broad, laterally expanded.

Character 40: C1 posterior accessory cusp: 0 = very low or absent, 1 = tall.

Character 41: C1 anterior accessory cusp: 0 = low or absent, 1 = greater height than or equal to half main cusp height.

Character 42: P1 reduction: 0 = reduced but present, 1 = absent.

Character 43: P1 extinction: 0 = in toothrow, 1 = extended from toothrow (but still partially separating C1 and P1), 2 = greatly extended.

Character 44: P1 size with respect to M1: 0 = approximately equal, 1 = conspicuously smaller.

Character 45: P4: 0 = width approx. equal to length, 1 = wider than long, 2 = longer than wide.

Character 46: P4 anterior margin: 0 = narrow, 1 = wide.

Character 47: P4 antero-lateral cingular cusp: 0 = present, 1 = absent.

Character 48: P4–M2 posterior cingula: 0 = narrow, 1 = thick.

Character 49: M1 morphology: 0 = protofossa open with or without dihedral crest, 1 = protofossa closed without dihedral crest, 2 = protofossa closed with weak dihedral crest, 3 = protofossa closed with strong dihedral crest, 4 = protofossa closed by joining posterior cingulum rather than base of metacone.

Character 50: M1 w-pattern: 0 = little reduced (premetacrista half to three-quarters preparacrista length), 1 = reduced (premetacrista one-third or more preparacrista length), 2 = very reduced (premetacrista less than one-third preparacrista length), 3 = complete (premetacrista more than three-quarters preparacrista length).

Character 51: M1 size: 0 = little reduced, 1 = reduced in length and/or width, 2 = extremely reduced (compare with P4).

Character 52: Ascending ramus height: 0 = short (less than twice M1 height), 1 = tall (more than twice M1 height).

Character 53: Lower incisor size: 0 = less than 1, 1 = subequal, 1 = conspicuous larger than 1.

Character 54: L1: 0 = trilobed, 1 = bilobed.

Character 55: P4 reduction: 0 = reduced, 1 = very reduced (much less than half P4 height).

Character 56: P4: 0 = absent, 1 = present.

Character 57: M3 talonid width: 0 = complete, 1 = narrow.

Character 58: Elongation of M3? postmetacristae: 0 = absent, 1 = conspicuous.

Character 59: Lateral compression of M4, trigonid: 0 = absent, 1 = conspicuous.

Character 60: Relative length of rostral inflation: 0 = greater than half rostrum length, 1 = less than or equal to half rostral length (rostral length = from canine alveolus to minimum interorbital width).

Character 61: Anterior bar: 0 = little or no reduction, 1 = conspicuously reduced, 2 = absent.

Character 62: Latero-oral fossa: 0 = present, 1 = reduced or absent.

Character 63: Relative length of rostrum: 0 = half braincase length or greater, 1 = less than half braincase length.

Character 64: Rostral inflation: 0 = postero-lateral quadrant not especially inflated, 1 = postero-lateral quadrant most conspicuously inflated.