

FIRST SKULL OF A SPECIES OF *HIPPOSIDEROS* (*BRACHIPPOSIDEROS*)  
(MICROCHIROPTERA: HIPPOSIDERIDAE), FROM AUSTRALIAN MIOCENE  
SEDIMENTS

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Hand, S.J. 1993 06 30: First skull of a species of *Hipposideros* (*Brachipposideros*) (Microchiroptera: Hipposideridae), from Australian Miocene sediments. *Memoirs of the Queensland Museum* 33(1): 179-192. Brisbane. ISSN 0079-8835.

Cranial material of a species of *Hipposideros* (*Brachipposideros*) is figured and described for the first time. The skull of the Australian Tertiary leaf-nosed bat *Brachipposideros nooraleebus* Sigé, Hand & Archer, 1982 is described on the basis of new material recovered from the type locality on Riversleigh Station, northwestern Queensland. As part of this study, morphological differences between three hipposiderids, *Hipposideros* (*Brachipposideros*) *nooraleebus*, *Rhinonicteris aurantius* and *Hipposideros* (*Hipposideros*) *speoris*, are reported. *Hipposideros* (*B.*) *nooraleebus* appears to be more similar to *R. aurantius* than to its congener *H. speoris*. □ Tertiary, fossil, bat, skull, Hipposideridae, Riversleigh, Microsite.

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In 1982, the Tertiary leaf-nosed bat *Hipposideros* (*Brachipposideros*) *nooraleebus* was described from collections made between 1976 and 1981 from the Microsite locality on Riversleigh Station, northwestern Queensland (Sigé, Hand & Archer, 1982). The Microsite deposit, which contains the Nooraleeba Local Fauna (Sigé et al., 1982), is one of more than 150 Oligo-Miocene fossil-bearing, freshwater limestone deposits on Riversleigh Station (Archer et al., 1989, 1991).

*Hipposideros* (*Brachipposideros*) *nooraleebus* was the first Australian Tertiary bat to be named and the first species of the subgenus *H.* (*Brachipposideros*) recorded from outside of France. In France, the subgenus is known from six other species also of Oligo-Miocene age (Sigé, 1968; Legendre, 1982; Sigé et al., 1982). The Australian bat was found to most closely resemble the French Burdigalian (early middle Miocene) species *H.* (*B.*) *agulari* (Sigé et al., 1982). The appearance of closely related taxa in Australian and European sediments is enabling intercontinental biocorrelation of Australian Tertiary mammal-bearing deposits. Sigé et al. (1982) regarded *Brachipposideros nooraleebus* to be a possible ancestor of northern Australia's living endemic Orange Horseshoe Bat *Rhinonicteris aurantius*.

In 1982, *B. nooraleebus* was described, like the French *Brachipposideros* species, mainly on the basis of its teeth. By 1982, thousands of well-preserved dentaries and partial maxillae had been collected from Microsite. Subsequently, the deposit yielded partial skulls referable to this spe-

cies. In this paper, cranial material of *H.* (*Brachipposideros*) is described for the first time and compared with the skulls of *R. aurantius* and the type species *Hipposideros speoris speoris* of India and Sri Lanka.

Dental nomenclature follows Sigé et al. (1982). Skull terminology is modified from Sigé (1966), Barghoorn (1977) and Novacek (1986, 1991). The prefix QMF refers to the fossil collections of the Queensland Museum, Brisbane. Repositories of comparative Recent specimens are indicated by prefixes as follows: M, Australian Museum, Sydney; CM, CSIRO Division of Wildlife and Ecology, Canberra; AR, temporarily held in collections at the University of New South Wales. Stratigraphic nomenclature for the Riversleigh region follows Archer et al. (1989, 1991).

## SYSTEMATICS

### *Hipposideros* (*Brachipposideros*) *nooraleebus* Sigé, Hand & Archer, 1982 (Figs 1-4, Table 1)

#### REFERRED SPECIMENS

QMF19034, a rostrum preserving the palate, left  $M^1$ - $M^3$  and alveoli for  $P^4$  and anterior roots for left zygomatic arch (Figs 1A, 2A, 3); QMF19035, a braincase preserving the skull roof and basicranium with petriotic bones in situ (Figs 1B, 2B, 3); QMF19036, a right maxillary fragment with  $C^1$ - $M^3$ ; QMF19037, a left maxillary fragment with  $P^4$ ,  $M^1$ ,  $M^3$  and anterior zygomatic arch; QMF19038, a rostrum (edentulous) with



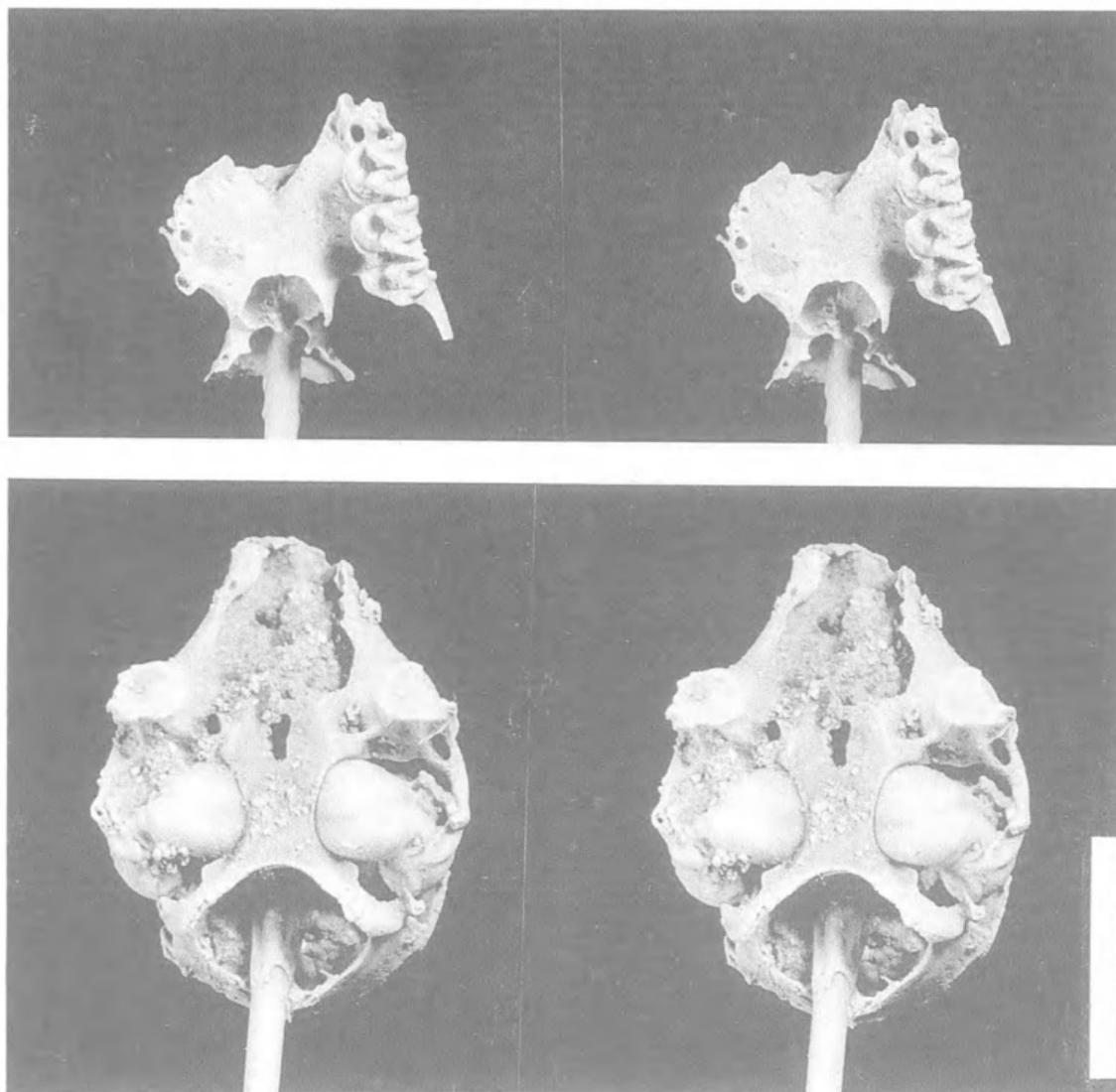


FIG. 1. *Hipposideros (Brachipposideros) nooraleebus*, Microsite, Riversleigh Station, northwestern Queensland: A, QMF19034, ventral view, stereopair; B, QMF19035, ventral view, stereopair. Bar indicates 5mm.

incomplete specimens. The most complete of these are QMF19034, a rostrum preserving the nasals, palate, anterior root for the left zygomatic arch, left  $M^{1-3}$  and alveoli for  $P^4$ , and QMF19035, a braincase preserving the skull roof, basicranial and ear regions, with periotics in place. Matrix obscures part of the right ear region but has been left in place for structural support. The description is based primarily on these two specimens but other referred specimens (see list above) provide additional information. There is no evidence of crushing of cranial material but some breakage has occurred. Some details of the medial skull region are lacking.

It has not been possible to determine the precise limits of each bone in the skull. In microchiro-

pteran bats, sutures between bones of the skull fuse completely early in development, and no juvenile specimens of *Brachipposideros nooraleebus* have yet been recovered. However, as a guide for interpreting approximate bone boundaries in the fossil hipposiderid, several juvenile rhinolophoids were examined in this study, i.e. specimens of *Hipposideros diadema* (M20478), *Rhinolophus megaphyllus* (AR17575) and *Macroderma gigas* (M11762, M27675).

*General outline and proportions.* The skull is small, slender and strongly constricted in the interorbital region. The rostrum is relatively broad and long. The rostral length is approximately half the length of the braincase and its greatest width, at the level of the most anterior point of the orbit

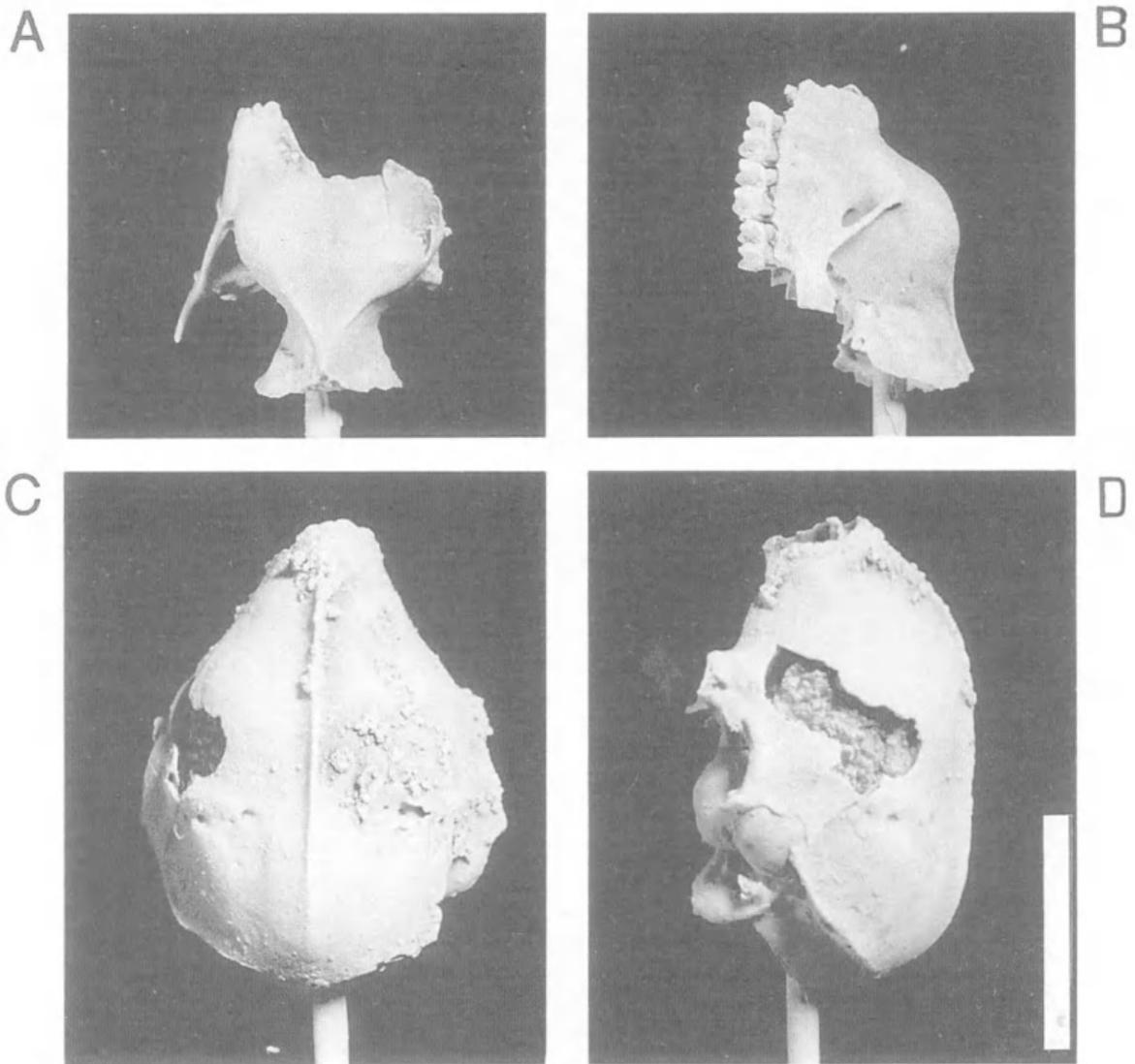


FIG. 2. *Hipposideros* (*Brachipposideros*) *nooraleebus*, Microsite, Riversleigh Station: A-B, QMF19034, dorsal and lateral views; C-D, QMF19035, dorsal and lateral views. Bar indicates 5mm.

(the lacrimal foramen), approximately two-thirds the mastoid width and more than twice the interorbital width. In height, the rostrum is lower than the braincase. The braincase is broadest across the mastoids (at the level of the post-tympanic processes). The maximum zygomatic width is not known.

**Rostrum.** The rostrum is square in outline, being approximately as long as wide and with sub-parallel lateral borders. It is deeply notched anteriorly, this indentation describing a broad arc between the maxillae. Conspicuous rostral inflations are separated by a broad, shallow trough delimited by well-developed supraorbital ridges. These are better defined posteriorly than anteriorly

where they are attenuated by the nasal inflations. In the trough, at a point approximately midway between the anterior margin of the nasals and the junction of the supraorbital ridges, is a small, unpaired foramen. The rostral inflations are most conspicuous in lateral view, such that in profile the face is not gently inclined but rises almost vertically from the level of the palate to the maximum height of the rostrum.

The zygomatic arch extends onto the face as a very thin arch that joins the lateral wall of the maxilla. Under this arch (i.e. enclosed by a narrow bar of bone) opens the anteroposteriorly elongated infraorbital foramen. Hidden in lateral view by the arch, two orifices open in the lateral

wall of the face at the front of the orbital fossa. The first, the lacrimal foramen, opens under the anterior attachment point of the arch at the edge of the circumorbital rim, and is separated from the infraorbital foramen by only a thin wall of bone. Posteriorly, at the ventral part of the anterior recess of the orbital fossa, is the second orifice: a broad, deep fossa that exposes the maxillary bone covering the roots of the posterior cheekteeth. Medial to this, at the most anteroventral point of the orbit, is a post-palatal foramen which leads through into the palate. More posterodorsal and medially, in the lateral wall of the interorbital constriction, two small foramina open into a long, curved, shallow groove that leads posterodorsally from the post-palatal foramen to the optic foramen. Dorsal and medial again in the interorbital region 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 appear to vary in number, form and position (and from one side of the skull to the other) perhaps varying epigenetically.

*Palate.* The palate is short. The toothrows are not convergent anteriorly. At the palate's anterior edge is a deep, V-shaped indentation, which extends posteriorly to the level of the posterior face of  $M^1$ , for the junction with the premaxillae. The palate's posterior border has two deep posterolateral indentations that extend anteriorly to at least the level of the anterior face of  $M^3$ . Each closely skirts  $M^3$  and forms a recess beside the palatine. The posterior extension of the midline of the palate is level with the anterior face of  $M^1$ ; a medial palatal spine is variably developed. The maximum width of the palate is at the level of  $M^2$ . The palate is almost flat though slightly concave longitudinally. The most constant and well developed palatal foramina are medial to the anterior face of  $M^1$ . Other foramina appear to be variable but a fossa medial to  $M^{2-3}$  is usually perforated by a number of foramina and on the midline, medial to the posterior face of  $M^1$ , an unpaired foramen occurs in some specimens.

*Premaxillae.* The ankylosed premaxillae comprise a small, loose element that bears a single pair of incisors. The best preserved specimens are QMF19044 (Fig. 4) and QMF19045 but the incisors have been lost from both. The premaxillae gently flare anteriorly. The incisor alveoli occur at the anterior edge in a medial position. Posteriorly, two thin premaxillary processes probably do not fully enclose large anterior palatal foramina. The premaxillae are very thick with, at their line

of contact, a distinct crest on the dorsal surface. The dorsal surface is convex in both horizontal and longitudinal axes. In anterior view, the convexity is rather gentle. In lateral view, it is more acute and is accentuated by the distinct posteriorly directed crest. This reaches its maximum height about one-third the distance from the premaxillae's anterior edge. The incisors would have been directed ventrally. The ventral surface of the premaxillae is generally gently concave longitudinally but posteriorly it is domed.

*Nasals.* The inflated nasal cavities are bilaterally symmetric, being divided by a median septum. The dorsal border of the septum parallels the palate rather than the contour of the face. Posteriorly, the septum fuses with the anteriorly inclined cribriform plate. The posterior face of the plate is deeply concave and perforated by many foramina of varying sizes. The endocranial space is arched over the inclined cribriform plate. Posteriorly, curved lateroventral extensions of the median septum (subethmoidal shelves) partially separate each nasal cavity into a ventromedial respiratory section and more extensive dorsal and lateral olfactory sections. The latter are further subdivided, by a thin ethmoidal lattice, into anterior and posterior chambers. The ethmoturbinal mass appears to have been very simple but is not well enough preserved to be confidently described. Above the cribriform plate, the nasal cavity expands into a broad chamber roofed by the frontals.

*Interorbital and pterygoid region.* Immediately to the rear of the face and between the orbital fossae, the braincase narrows. The point at which the two supraorbital crests unite (i.e. where the sagittal crest originates) is clearly posterior to the point of narrowest constriction. The pterygoid wing, sloping ventrally and laterally, forms the posteromedial wall of the orbital fossa. The side wall of the skull is pinched in between the cranium and the palatine and pterygoid wings, and hence the optic foramen and sphenorbital fissure open ventrally from the braincase. The sphenorbital fissure was evidently long and wide, a very narrow bony bridge separating it from the large, almost semicircular optic foramen. Immediately lateral to the most anterolateral margin of the sphenorbital fissure is a small, round foramen. Anterior to the optic foramen is the cribriform plate of the ethmoid. Small pterygoid processes occur at a point laterally in line with the junction of the supraorbital ridges and posterior to  $M^3$  at a distance approximately equal to the length of  $M^1$ . If hamular processes were present they are now

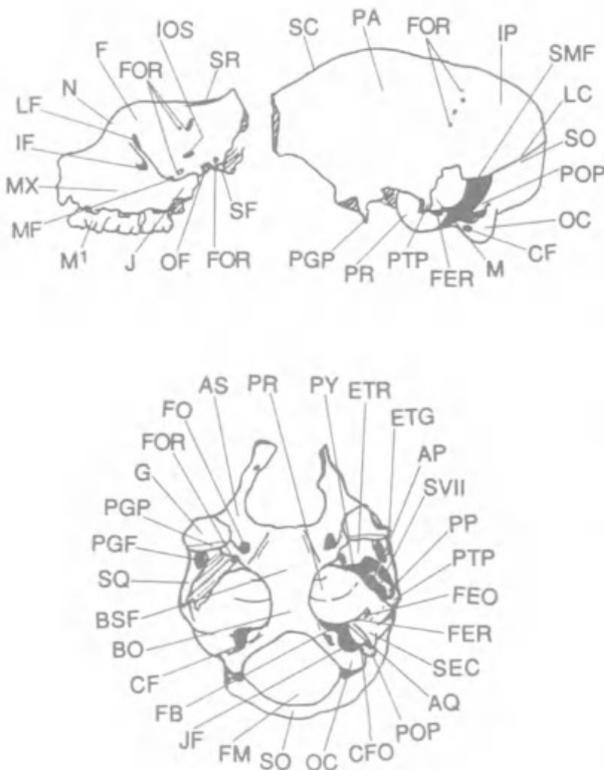


FIG. 3. *Hipposideros (Brachipposideros) nooraleebus*, Microsite, Riversleigh Station. Top, QMF19034 and QMF19035, lateral views. Bottom, QMF19035, ventral view. AP anterior process; AQ aqueductus cochleae; AS alisphenoid; BO basioccipital; BSF basisphenoid fossa; CF condyloid foramen; CFO condyloid fossa; DC dorsal crest; ETG epitympanic groove; ETR epitympanic recess; F frontal; FB basicochlear fissure; FEO oval window; FER round window; FM foramen magnum; FO foramen ovale; FOR foramen; G glenoid; IA incisor alveolus; IF infraorbital foramen; IOS interorbital sinus; IP interparietal; J jugal; JF jugular foramen; LC lambdoidal crest; LF lacrimal foramen; M mastoid; M<sup>1</sup> first molar; MF maxillary fossa; MX maxilla; N nasal; OC occipital condyle; OF optic foramen; P periotic; PA parietal; PGP postglenoid foramen; PGP postglenoid process; PL palatine; PM premaxilla; PMP premaxillary process; POP paroccipital process; PP posterior process; PR promontorium; PS presphenoid; PT pterygoid; PTP post-tympanic process; PY pyriform fenestra; SC sagittal crest; SEC semicircular canals; SF sphenorbital fissure; SMF supramastoid foramen; SO supraoccipital; SQ squamosal; SR supraorbital ridge; SVII sulcus for facial nerve (VII). Bar indicates 5mm.

missing. The posterior edge of the pterygoid wing curves ventrally and posteriorly and slightly medially before forming a second, laterally-directed flange.

**Zygomatic arch.** The ventral margin of the zygomatic arch is slightly arched and lies dorsal to

the tooth row. Anteriorly, the dorsal margin sinks in the jugal region then, posteriorly, rises at an angle of approximately 45 degrees to the ventral surface to form the very tall squamosal projection. The latter rises to at least the level of the dorsal edge of the infraorbital foramen. Its maximum height occurs dorsal to the glenoid surface. A masseteric scar occurs on the anterolateral ventral surface of the arch. In dorsal view, the junction between the zygomatic arch and its anterior extension onto the face is marked by a change in direction of the arch from posterolateral (anteriorly) to posterior, the anterior extensions diverging far more than the zygomatic arches proper. The latter appear to have been almost parallel for much of their length.

**Cranial vault.** The braincase is widest at the level of the post-tympanic processes, narrowest in the interorbital area and highest dorsal to the postglenoid processes. There is little development of the lambdoidal crests and no nuchal crest so that the braincase is rounded at its posterior extremity in lateral and dorsal views. The sagittal crest is variably developed (perhaps reflecting sexual dimorphism). Where it occurs, the sagittal crest is low and extends anteriorly to the supraorbital ridges and posteriorly to the interparietal at a point dorsal to the paroccipital processes. Approximately two-thirds along the length of the braincase, within the parietals, are bilaterally depressed areas that mark a conspicuous venous sinus. Its trajectory is easily traced in a lateral then anterolateral direction before it opens to the exterior in the posterior part of the postglenoid foramen. Along the sinus several small orifices open to the exterior.

**Glenoid.** The glenoid surface is only slightly concave and is subcircular, being almost as long as wide. It ends medial to the zygomatic process of the squamosal. The postglenoid process is weak. In height it is less than one quarter the length of the glenoid surface; its anterior face is not noticeably anteriorly recurved. The large postglenoid foramen opens vertically on the steeply sloping posterior face of the glenoid, giving the opening an elliptical shape. It opens immediately posterior to the postglenoid process. Medial to the glenoid surface, the foramen ovale opens in the alisphenoid on the side of a bony prominence or ridge. The latter separates the ventrally opening foramen ovale from a second, more posterodorsal and lateral foramen that opens posterolaterally (i.e. into the pyriform fenestra).

**Temporal region.** Posterior to the glenoid region and immediately anterior to the mastoid



FIG. 4. *Hipposideros (Brachyhipposideros) nooraleebus*. Microsite, Riversleigh Station. QMF19044, left ventral view; right lateral view. Bar indicates 1mm.

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

**Basicranium.** The medial sphenoid series (basisphenoid and presphenoid) is broadly fused with the palatine, pterygoid, alisphenoid and basioccipital. The basisphenoid appears relatively flat in its central region or perhaps only slightly concave. Faint, anteriorly convergent ridges define the basisphenoid fossa (and mark the boundary between the pterygoid and basisphenoid anteriorly and probably the alisphenoid and basisphenoid posteriorly). The petiotics are not enlarged, their width being about twice the shortest distance between the two. Thus the lateral edges of the basisphenoid-basioccipital complex are relatively straight with only shallow biconcave lateral curves. The anterior margin of the basicranial area is not preserved. The petiotic is bordered medially and posteriorly by the

basioccipital. Anteromedially, the basisphenoid abuts the petiotic; there is no lateral extension of the basisphenoid or medial extension of the petrosal.

**Occipital.** The most posterior region of the skull coincides with the junction of the interparietal and supraoccipitals. In lateral view, the supraoccipital is not very convex posteriorly but the exoccipitals nonetheless overhang the posteroventrally directed foramen magnum. The posterior edge of the foramen magnum is straight and not thickened. There is little development of the lambdoidal crests but a distinct ridge marks the junction of the interparietal and supraoccipitals. It parallels the posterior edge of the foramen magnum, terminating anteriorly in the region dorsal and lateral to the paroccipital process, i.e. immediately to the rear of the mastoid region. A supramastoid foramen opens on the occipital surface dorsal to the ventral condyloid fossa. There are no parietal crests and no posteriorly directed point on the skull: the nuchal line continues smoothly over the top of the skull.

In ventral view, the posterior skull contour of the supraoccipital at the level of the lambdoidal ridge is rounded. The foramen magnum is oval in shape and wider than high. Between the occipital condyle and paroccipital process is a deep condyloid fossa. The paroccipital process is well developed and forms the lateral-most part of the occipital bone. The tip is not preserved but the process appears to have articulated with the mastoid. The condyle projects most strongly ventrally at the posterior extremity, its thickened lip partially concealing the condyloid foramen in the anterolateral face.

**Ear region.** The ectotympanics and auditory ossicles are missing. The petiotic is only weakly articulated with the surrounding basicranial elements and exhibits the condition described by Novacek (1991) as 'phanerocochlear' found in most adult microchiropterans. In this species, attachment of the petiotic appears to be solely via connective tissue although the petiotic closely abuts the basicranial elements medially via the basisphenoid-occipital complex and laterally via the post-tympanic process of the squamosal and the paroccipital process. The anterior part of the middle ear cavity is unossified as a pyriform fenestra which is a restricted opening between the petiotic and the squamosal and most posterolateral part of the alisphenoid. There is little development of an epitympanic recess or ectotympanic groove, the bone here being no thicker than the squamosal that bounds it. Posteriorly, the large

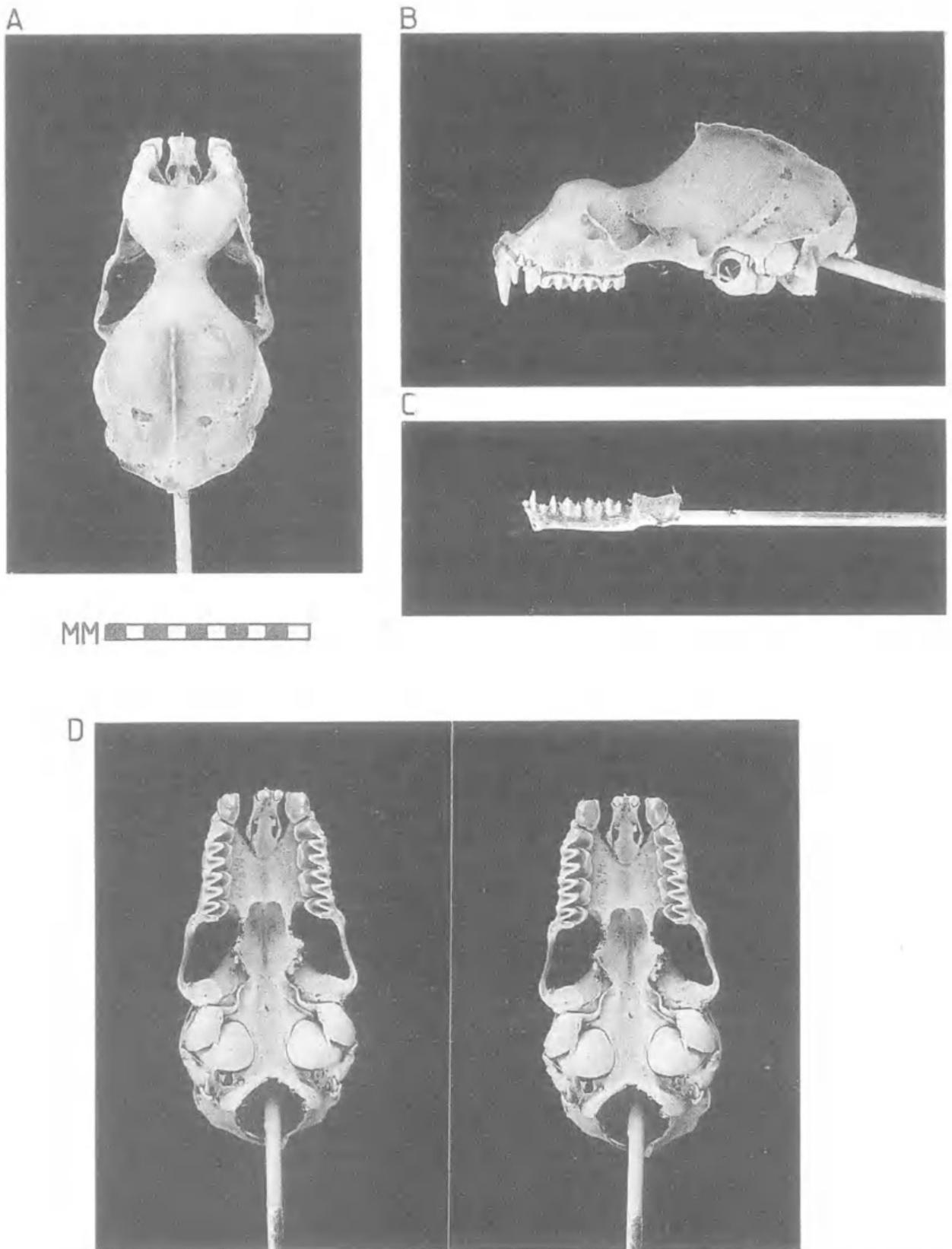


FIG. 5. *Rhinonictes aurantius*, AR15400, Klondyke Queen Mine, Marble Bar, Western Australia. A, skull dorsal view; B, skull lateral view; C, jaw lateral view; D, skull ventral view, stereopair. Scale in mm.

jugular foramen and the more medial, very narrow basicochlear fissure are coalescent.

In ventral view, the cochlear labyrinth is visible through the thin bone of the promontorium so that the petrosal has a snail-like appearance. Three turns of the labyrinth can be detected through the bone and this is confirmed by examination of sectioned periotics.

In the lateral face of the periotic the following structures are visible. Most posteriorly, above the ventral plane of the basioccipital and facing the jugular foramen, is the aqueductus cochleae. Lateral and ventral to this, at the posterolateral corner of the periotic and distinct in ventral view, is the round window, a large, flattened oval orifice. More anteriorly and dorsally, the oval window is slightly more elongate. A very slight transverse groove, barely imprinted on the promontorium medial to the round and oval windows, marks the passage of the stapedial artery, a branch of the internal carotid. Lateral to the round and oval windows, and at the base of the promontorium, is a deep, elongate, curved depression or canal which dips from front to rear. This is the canal for the facial nerve (VII). The canal terminates posteriorly a little anterior to the round window in the region of the stapedial fossa and continues anteriorly beyond the oval window via an orifice (the *apertura tympanica canalis facialis*).

The lateral margin of the canal is a vertical, curved face. Anteriorly, a small process (the anterior process of the petrosal; Henson, 1970) protrudes anteromedially into the pyriform fenestra. It does not articulate with the squamosal. Near its base is a small foramen (possibly for the superior ramus of the stapedial artery). Behind this process the lateral edge of the periotic curves back and dorsal and is appressed closely to the squamosal. Immediately medial to the post-tympanic process, the lateral edge terminates in a prominent process (posterior process of the petrosal; Henson, 1970) that overhangs the stapedial fossa.

The mastoid occupies a lateral, posterior and dorsal position in the periotic. The mastoid wall only thinly covers the three semicircular canals.

*Incisors.* The dentition of *B. nooraleebus* has been described previously by Sigé et al. (1982), except for the incisors which are now known as follows. There is one pair of upper incisors,  $I_1^1$ , and two pairs of lower incisors,  $I_{1,2}$ . The upper incisors are bilobed with the outer lobe slightly wider but shorter than the inner lobe. The lower incisors are tricuspidate and  $I_1$  is smaller than  $I_2$ .

## COMPARISONS

### *RHINONICTERIS AURANTIUS*

The skull of *B. nooraleebus* is smaller than that of *R. aurantius* (Gray, 1847) (AR17573, M8416, AR15400; Fig. 5) being approximately three quarters its size. Its shape is generally similar but differs as follows. The rostrum is lower in *R. aurantius* and has less prominent inflations. The trough separating the rostral inflations is deeper and narrower, poorly delimited by supraorbital ridges and is perforated by tiny foramina. The bar of bone that extends the zygomatic arch anteriorly onto the face, and encloses the infraorbital foramen, is directed dorsally (i.e. vertically) then anterodorsally so that it appears much more convex.

The postpalatal foramen is much smaller in *R. aurantius* and is surrounded by many small foramina. Dorsal and medial to this, there is one foramen (rather than two) opening into a groove. In general, unlike *B. nooraleebus*, the skull of *Rhinonicterus* is perforated by many tiny foramina, particularly in the interorbital and pterygoid regions. The palates are similar. The premaxillae are strikingly similar except that in *R. aurantius* the anterior premaxillary processes completely enclose the anterior palatal foramina. The premaxillae of both taxa exhibit a very distinctive dorsal crest as well as a dorsal convexity that results in the incisors being directed ventrally rather than anteriorly.

The sagittal crest is quite different. In *R. aurantius* it is tall and originates abruptly (with an anteriorly curved point) at the highest point of the skull (i.e. dorsal to the postglenoid process) and does not extend as far posteriorly. The vertical projection of the zygomatic arch is possibly taller and extends further anteriorly, involving the jugal and hence most of the zygomatic length. The lambdoidal crests are better developed (especially laterally) giving the posterior margin of the braincase a squared rather than rounded appearance. The postglenoid process is better developed (being more curved) and the pterygoid region less constricted. Ridges defining the basisphenoid fossa are weak and almost parallel (rather than convergent). The postglenoid foramen is elliptical and proportionately smaller. The dorsal margin of the foramen magnum is indented.

The ear region is very similar in the two taxa. The general orientation and attachment of the periotic to surrounding basicranial elements is similar and periotic morphology very similar. In the periotic the bony wing developed lateral to the

anterior and posterior processes is not as well developed.

As described by Sigé et al. (1982),  $C^1$  of *R. aurantius* has a better developed secondary cusp and less developed cingulum, and there is more expansion of the heel on  $M^2$ . The dentaries are similar. In both taxa the horizontal ramus is short and slender with a chin process, the coronoid process is very low (the tip only exceeding the molar heights by a molar crown height or less) and the masseteric fossa has a very expanded, almost horizontal border which extends posteriorly into a wide, rounded angular process that is buccally markedly extended.

#### *HIPPOSIDEROS (HIPPOSIDEROS) SPEORIS*

The skull of *H. speoris* (Schneider, 1800) (M3468; Fig. 6) is described in so far as it differs from both *B. nooraleebus* and *R. aurantius* except where specifically stated. It is similar in size to *R. aurantius* and approximately one-third larger than *B. nooraleebus*. The rostrum is proportionately narrower, the braincase wider and the rostral inflations, and trough separating them, less conspicuous. The posterior trough is also shallower. The supraorbital ridges are much better defined laterally (being less attenuated by inflations). The facial portion of the skull slopes posterodorsally more gradually. The bar of bone anteriorly extending the zygomatic arch onto the face is directed anterodorsally and is straight (or even concave) rather than convex. The infraorbital foramen occurs above  $M^1$  rather than  $M^2$  and is lower on the face. The lacrimal foramen is larger (than in *R. aurantius* at least) and the ventral fossa much broader and alveolar foramina more conspicuous than in *B. nooraleebus* and *R. aurantius*. More of the lateral face is visible (i.e. the bar of bone hides less) and a third foramen, occurring dorsal and posterior to the lacrimal, is visible on the lateral wall of the rostrum.

There appear to be two foramina posterior to the palate (the more lateral one perhaps being homologous to the postpalatal foramen observed in *B. nooraleebus*). Unlike *B. nooraleebus* but like *R. aurantius*, the skull is perforated by many tiny foramina especially in the interorbital region, where, for example, many open into the interorbital sinus. Note that although the sinus is present in the three taxa examined it has a different form in each. The sphenoidal fissure is relatively shorter perhaps because the skull proportions differ. Compared to *R. aurantius*, the braincase of *H. speoris* is relatively longer and the interorbital region shorter.

The palate differs in that the tooththrows are anteriorly convergent, the posterolateral indentations extend to the posterior faces of  $M^2$  and the posteromedial palate is marked by an indentation rather than a spine. There are many tiny palatal foramina but most pronounced are a pair of foramina medial to the anterior faces of  $M^2$  and the anterior limits of the lateral indentations (i.e. medial to the posterior faces of  $M^2$ ). In the premaxillae, the processes only partially enclose the anterior palatal foramina (these processes appear to diverge posteriorly), there is no dorsal crest, little lateral convexity and the incisors are directed anteriorly. The supraorbital ridges unite at the level of the narrowest constriction in the interorbital region rather than posterior to it.

The pterygoids are more constricted and there is no second flange on the pterygoid wing. The squamosal projection of the zygoma is much less well developed. In *H. speoris* it rises from approximately halfway along the zygomatic arch to quickly reach its maximum height (level with the dorsal margin of the ectotympanic ring). In *R. aurantius* it arises further anteriorly, so that its development involves almost the entire length of the zygomatic arch, to more gradually reach at least twice this height. (Note that there may be some variation in the height and shape of this projection in *R. aurantius*: cf. AR15400 and AR17573.) In both, however, the maximum height of the projection is reached at a point above the glenoid surface. In *R. aurantius* the projection leans dorsomedially towards the braincase; it is vertical in *H. speoris*.

The braincase narrows immediately anterior to the post-tympanic process rather than anterior to the postglenoid process. Like *B. nooraleebus* but unlike *R. aurantius*, there is little development of the lambdoidal crests so that the posterior margin of the skull appears rounded. The sagittal crest is similar to *B. nooraleebus* but the latter extends further posteriorly. The postglenoid process is better developed than in *B. nooraleebus* and *R. aurantius*. The articulating surface is wider; it is oval rather than subcircular. The postglenoid foramen is small and circular rather than large and oval. Dorsally and posteriorly are a number of tiny foramina which vary in number, size and position from one side of the skull to the other.

Medial to the glenoid surface are a number of foramina, the largest and most medial presumably being the foramen ovale. The sphenoid complex is concave rather than flat and the lateral margins of the basisphenoid-occipital more concave than in *B. nooraleebus* and much more so

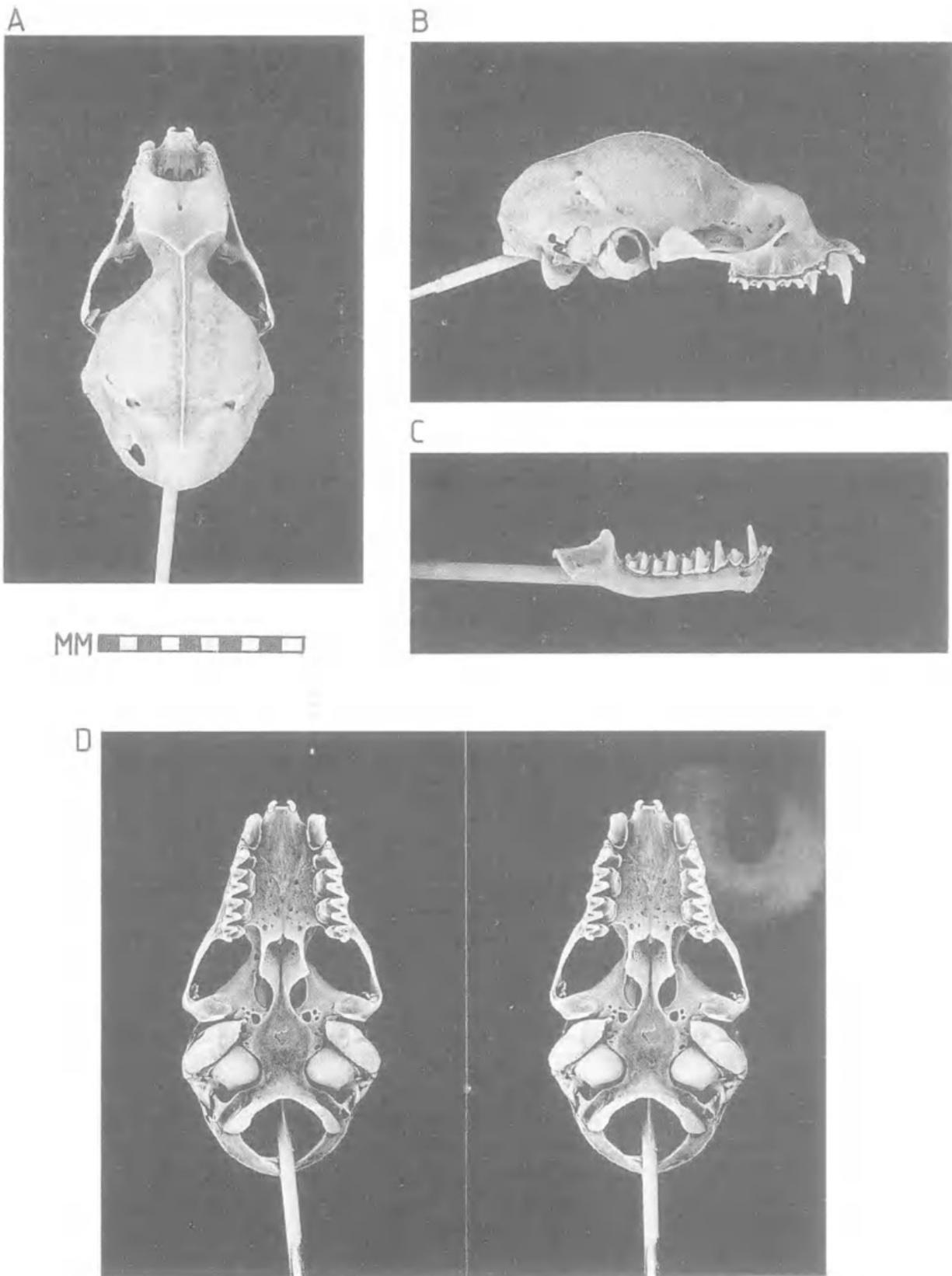


FIG. 6. *Hipposideros speoris speoris*, M3468, Kalutara, Sri Lanka. A, skull dorsal view; B, skull lateral view; C, jaw lateral view; D, skull ventral view, stereopair. Scale in mm.

than in *R. aurantius*. There is a lateral extension of the basisphenoid over the anteromedial corner of the periotic and foramina occur at the most lateral point of the extension. As in *B. nooraleebus*, the dorsal margin of the foramen magnum is straight. The foramen magnum is oval, being conspicuously wider than long. The junction of the interparietal and supraoccipitals terminates laterally at the paroccipital process (rather than dorsolateral to it). Differentiation of the jugular foramen and basicochlear fissure is less conspicuous (i.e. their coalescence is more gradual) due to the different shape of the occipital (i.e. its lack of an extra wing). The paroccipital process articulates with the mastoid and squamosal. The notch between the paroccipital process and post-tympanic process is shallower (i.e. is filled in more posterodorsally by the squamosal and the supramastoid foramen is round rather than triangular in lateral view).

Attachment of the periotic to surrounding basicranial elements differs. The periotic abuts the basisphenoid anteromedially rather than medially and the basisphenoid extends onto the anterior promontorium. The basicochlear fissure is located medially and posteromedially and is much larger and more coalescent with the jugular foramen. The anterolateral face of the periotic is flattened. The anterior process of the periotic probably abuts the squamosal which contributes to the better-developed epitympanic recess. The pyriform fenestra appears to be narrower.

In *H. speoris*,  $I^1$  has a reduced outer lobe,  $C^1$  has a less developed secondary cusp and cingulum,  $P^2$  is slightly less buccally extruded from the tooth row than in *B. nooraleebus*,  $M^2$  heel less expanded, and  $M^3$  more reduced such that it is narrower and shorter and the premetacrista is shorter. The coronoid process of the dentary is not as low and the angular process is narrower and extends more posterobuccally than buccally. The lower incisors protrude anteriorly,  $C_1$  is relatively tall,  $P_2$  small and  $M_3$  more reduced (shorter and narrower but with a hypoconulid).

## DISCUSSION

The Old World tropical to subtropical bat family Hipposideridae contains sixty-plus living species referred to the genus *Hipposideros* (approximately 50 species) and eight other genera (of one to two species each) including *Rhinonictis*, *Coelops*, *Triaenops*, *Cloeotis*, *Asellia* and *Aselliscus* (Hill & Smith, 1984). Tertiary-aged hipposiderids, which have been recovered

from mainly karstic sediments in Europe, Africa and Australia, are referred to the genera *Palaeophyllophora*, *Asellia* and the subgenera *Hipposideros* (*Pseudorhinolophus*) Schlosser, 1887 (late Eocene-middle Miocene taxa), *Hipposideros* (*Brachhipposideros*) Sigé, 1968 (late Oligocene-middle Miocene taxa) and *Hipposideros* (*Syndesmotis*) Peters, 1871 (middle Miocene-Recent taxa). *Hipposideros* (*Hipposideros*) has generally been reserved (e.g. by Sigé, 1968) for Recent hipposiderid species.

Riversleigh's *Brachhipposideros nooraleebus* is known from thousands of specimens and dominates the vertebrate fauna of Microsite. All other vertebrate taxa in the deposit are known from at most a few specimens each. Microsite is the only Riversleigh fossil deposit dominated by a single bat species. Because of this, it has been possible to refer incomplete hipposiderid cranial material collected from Microsite to the single taxon *Brachhipposideros nooraleebus*. Most of Riversleigh's other 150-plus Oligo-Miocene fossil vertebrate deposits contain between three and ten microchiropteran taxa (see Archer et al., 1991). French fossil faunas containing *Brachhipposideros* species also commonly contain more than one hipposiderid taxon and no skull material referable to a species of *Brachhipposideros* has previously been described.

In the present study, the skull of *H. (B.) nooraleebus* has been compared with the skulls of a modern representative of the genus *Hipposideros*, the type species *Hipposideros speoris* of India and Sri Lanka; and a probable Recent descendant of the Australian *Brachhipposideros* lineage, *Rhinonictis aurantius* (Sigé et al., 1982).

Many striking differences distinguish *H. (B.) nooraleebus* from its congener *H. (H.) speoris*. In particular, differences were observed in: overall skull proportions; rostral morphology, including the size and position of the infraorbital and lacrimal foramina and maxillary fossa; morphology of the palate, premaxilla and zygomatic arch; attachment of the periotic to the surrounding basicranial elements; squamosal articulation with the paroccipital process; and, in the dentition, the reduced  $M_3$ s,  $I^1$  with reduced outer lobe,  $M^2$  with less expanded heel, tall  $C_1$  and small  $P_2$ . Similarities between the two skulls include the form of the sagittal crest and general shape of the braincase.

On the other hand, the skull of *H. (B.) nooraleebus* appears to be very similar in overall form to that of *R. aurantius*. Similarities include the general proportions of the skull, the broad rostrum,

subparallel tooth rows, morphology of the palate and zygomatic arch, the crested premaxillae, general basicranial morphology, very similar periotic and otic morphology, the pronounced accessory cusp on C<sup>1</sup> and little reduced upper and lower M3s. Obvious differences occur in the shape of the braincase and form of the sagittal crest.

In his study of the phyletic relationships of fossil hipposiderids, Legendre (1982) recognised that *Hipposideros* probably represents a paraphyletic group (see also Sigé, 1968) and that current taxonomy does not accurately reflect understanding about the evolutionary relationships of its supraspecific groups. Species of *Brachiposideros* have been recognised to have special affinities with small Recent species of *Hipposideros* (e.g. *H. caffer*), *Syndesmotis* and *Rhinonycteris* (Sigé, 1968; Legendre, 1982; Sigé et al., 1982). Those of *Pseudorhinolophus* appear to have affinities with species of *Asellia* and some large Recent *Hipposideros* species (e.g. *H. armiger*, *H. diadema* and *H. commersoni*) (Hugueney, 1965; Sigé, 1968; Legendre, 1982).

To refine understanding about the relationships of *Brachiposideros nooraleebus* to *Rhinonycteris aurantius* and other hipposiderids, further comparisons of skull and postcranial morphology of many additional hipposiderid groups are required. Pending this much larger study, comparisons made here support Sigé et al.'s (1982) hypothesis that the Australian taxa *B. nooraleebus* and *R. aurantius* are closely related.

#### ACKNOWLEDGEMENTS

Work at Riversleigh has been supported by the Australian Research Council, the Department of the Arts, Sport, the Environment, Tourism and Territories, National Estate Programme Grants (Queensland), the Australian Geographic Society, ICI, the Queensland Museum and the University of New South Wales. The photos were taken by Ross Arnett of the University of New South Wales. Study of the Riversleigh bat material would not have been possible without the generosity, support and advice of Michael Archer, Henk Godthelp and all in the Vertebrate Palaeontology Unit of the University of New South Wales's School of Biological Science. Harry Parnaby, Linda Gibson and Tim Flannery of the Australian Museum and Greg Richards from CSIRO Division of Wildlife and Ecology Research, Canberra kindly provided access to comparative specimens in their institutions.

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