

**AN AUSTRALIAN MIOCENE *BRACHIPPOSIDEROS*
(MAMMALIA, CHIROPTERA) RELATED TO MIOCENE
REPRESENTATIVES FROM FRANCE**

by

Bernard SIGÉ*, Suzanne HAND** and Michael ARCHER**

SUMMARY

	page
Abstract, Résumé	150
Introduction	150
Systematics	151
Holotype	151
Etymology	151
Paratypes	151
Type locality and lithology	151
Stratigraphic position and age	151
Palaeoenvironment	152
Diagnosis	152
Description	152
Comparison between <i>Hipposideros</i> (<i>Brachipposideros</i>) <i>nooraleebus</i> and related forms	161
Phylogenetic position and interpretative history of the radiation of species referable to <i>Brachipposideros</i>	167
Palaeogeographic significance of the Riversleigh bat	170
Acknowledgements	171
Literature	171
Caption of the plates	172

*Laboratoire de Paléontologie, U.S.T.L., Place Eugène Bataillon, Montpellier, France (L.A. 327 du C.N.R.S.).

**School of Zoology, University of New South Wales, P.O. Box 1, Kensington, New South Wales, Australia 2033.

RÉSUMÉ

Un nouveau chiroptère hipposidéridé d'âge miocène moyen est décrit d'un sédiment calcaire de Riversleigh Station (N-W Queensland, Australie). *Hipposideros (Brachipposideros) nooralebus* n. sp. représente la première découverte mondiale de ce sous-genre réalisée hors de France.

Le paléoenvironnement local de ce chiroptère paraît avoir été un bassin tropical ensoleillé, calme, richement approvisionné en limon, peuplé par des tortues, crocodiles et poissons. Il est possible que les restes de chiroptères aient été drainés jusqu'au bassin depuis une caverne voisine.

La forme dont le chiroptère de Riversleigh se rapproche le plus étroitement est l'espèce du Burdigalien de France *H. (B.) aguillari* (Miocène inférieur-moyen). Il est possible, d'autre part, que *H. (B.) nooralebus* soit relié au stock initial australien dont se différencie la forme monotypique endémique *Rhinonycteris aurantius*.

La distribution disjointe des espèces de *H. (Brachipposideros)* suggère que des représentants de ce sous-genre restent à découvrir au moins dans la zone tropicale sud-asiatique.

ABSTRACT

A new middle Miocene hipposiderid bat is described from a limestone deposit on Riversleigh Station in north-western Queensland. *Hipposideros (Brachipposideros) nooralebus* n. sp. is the first record of this subgenus from anywhere in the world outside of France.

The palaeoecological setting of the fossil bats appears to have been a relatively quiet, sunny lime-enriched tropical pool that contained tortoises, crocodiles and fish. It is possible that the bats were washed into the pool from an adjacent cave.

The Riversleigh bat most closely resembles the French Burdigalian (early middle Miocene) bat *H. (B.) aguillari*. It is also possible that it may have been closely related to the original Australian hipposiderid stock that ultimately gave rise to the endemic monotypic *Rhinonycteris aurantius*.

The disjunct distribution of species of *H. (Brachipposideros)* suggests that representatives of this subgenus will be found in at least tropical southern Asia.

INTRODUCTION

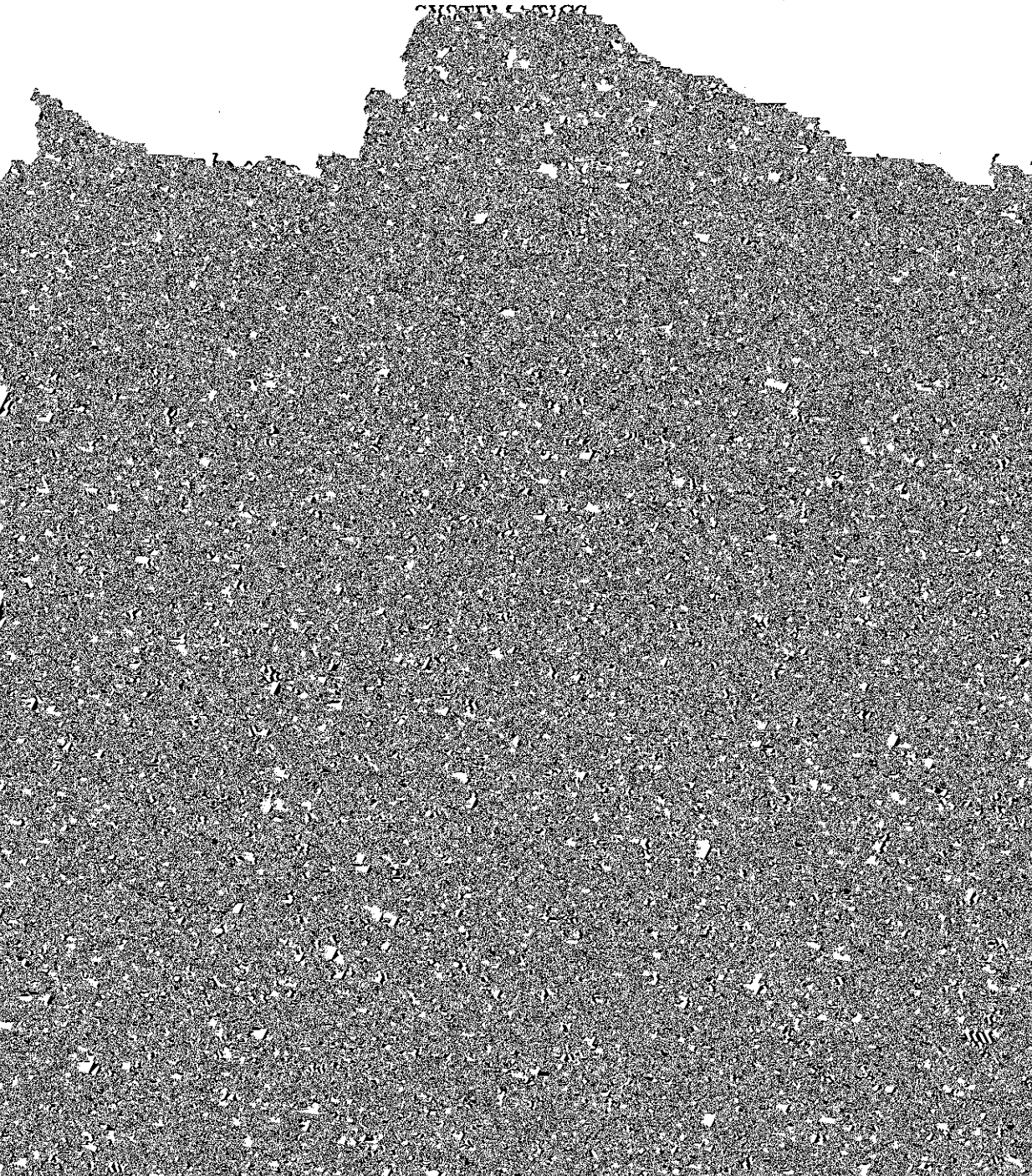
The history of bat evolution in Australia, a group that comprises 25 % of the modern terrestrial mammal species of that continent, has, until recently, been almost entirely unknown. Only two Tertiary bats were known (Turnbull and Lundelius 1970 ; Archer 1978) and these were too poorly preserved to enable even familial determination. Accordingly, the basis for hypotheses about the origins of these animals in Australia has been speculation.

The absolute age of many of the Australian Tertiary mammal faunas, particularly those from what is today arid inland Australia and northern Australia, is unknown. Correlation with better dated coastal Tertiary faunas, based on the interpreted stage of evolution, has been the basis for dating such assemblages as the Riversleigh, Kutjamarpu and Bullock Creek local faunas.

Recent discovery of masses of microchiropteran remains from a Tertiary limestone in northwestern Queensland has enabled important new insights into both the history of Australian bat evolution and the approximate age of a least one otherwise undated assemblage based on intercontinental correlations with European Tertiary deposits.

In this paper we present a description of one of these Queensland fossil bats. Because its affinities clearly lie with a particular group of Neogene European hipposiderids, the phylogenetic and zoogeographic implications of this surprising find are of considerable interest.

The Australian stratigraphic nomenclature used follows that summarized in Archer and Bartholomai (1978) and Archer (1981). The European stratigraphic nomenclature is that used by Aguilar (1982). Cusp, crest and tooth number terminology for bats is modified from that used by Sigé (1968) and is set out in Fig. 1.



preserved with the bats. For similar reasons, which we can also confirm, Tedford (1966) has concluded that the immediately adjacent Carl Creek Limestone is middle Miocene in age. *If* the two limestones are contemporaneous (although isolated), they must represent different facies. However, at present, there is no reason for assuming contemporaneity. To date, the species recovered from the two limestones are different, although this may be due to a facies difference and/or to sampling error.

Palaeoenvironment : Interpretation of the palaeoenvironment of the local fauna which includes the bats is speculative. At present, because the fauna also contains small fish, crocodiles, tortoises and what appear to be algal encrustations, we conclude that the immediate environment was a relatively quiet, sunny, lime-enriched pool. Because of the kinds of terrestrial mammals present (represented by almost unabraded remains), we further presume that immediately adjacent to this pool there were trees with an understorey containing little grass but probably abundant shrubs. Additionally, the hundreds of hipposiderid bats represented suggest that in the area adjacent to the pool there was either a limestone overhang, or a cave developed in the Thornton Limestone. The broken and disassociated (but not abraded) condition of the bat bones suggests either that they were washed into the pool from an adjacent accumulation in a cave, or, perhaps less likely, that the bones of bats falling directly into the pool were broken by other animals or subsequent mild turbation of the muddy bottom.

Diagnosis : This species of *Hipposideros* (*Brachhipposideros*) differs from all others in the following combination of features : 1, a slender, tall vertically oriented lower canine with a rectilinear crest ; 2, the buccal position of P2/ outside the toothrow and the approximation of C1/ and P4/ ; 3, the heel of M1/ and M2/ which is developed at the posterolingual angle of the tooth, separated from the protocone by a notch, and posteriorly directed ; 4, the presence of a well-developed posterior portion of the postprotocrista ; and, 5, the presence of four roots on M1/ but only three on M2/.

Description :

Dentary :

The dentary increases in depth from below the anterior root of M/1 to C/1. The large mental foramen (= chin foramen) occurs beneath P/2. A second smaller foramen occurs immediately adjacent to the symphysis and midway between the alveolar border and the base of the dentary. The symphysis is vertically oriented. Its ventral edge is developed as a discrete chin process. The tip of the ascending ramus is subequal in height to the tip of C/1 and thus only about one molar crown's height above the apices of the M/3. The large anteroposteriorly elongate masseteric fossa is well-developed and extends ventrally on the ramus down to a level approximately equivalent to the base of the crowns. The angular process is well-developed and extends buccally for twice the distance of the width of the articular condyle. The articular condyle is transverse, about four times as wide as long, and just wider than any molar. The mandibular foramen is about as large as the mental foramen and faces posteriorly.

Lower dentition (the lower dental formula is I/1,2, C/1, P/2,4, M/1,2,3).

The incisors are unknown.

The unworn C/1 is a powerful vertically oriented tooth. There is one principal cusp and a minute posterolingual cingular cuspule. The posterior face of the main cusp is flattened from base to tip. The anterior face is anterobuccally convex and reflexed posteriorly from base to tip. Posteriorly, there is a low transversely oriented shelf extending from the buccal to the lingual side of the tooth (which underrides the anterior edge of P/2). The posterolingual cuspule protrudes lingually to the anterior overlapping edge of P/2. The posterior transverse flank of C/1 has an indentation for the anterior root of P/2 and is thereby posteriorly concave. Viewed from the posterior side, the crown of C/1 extends further ventrally on the buccal than on the lingual side and thus appears to slope dorsolingually. A very poorly-developed (sometimes absent) cingular ridge extends from the buccal side of the posterior cingular shelf to the anterior edge of the crown. There is no lingual cingulum. The C/1 crown height is approximately twice the height of P/2.

The unworn P/2 has a large single root and one large cusp. This cusp is posterior to the midpoint of the crown and is connected by steep crests to the anterior and posterior edges of the crown. The anterior crest is about twice the length of the posterior crest. Both crests are gently concave occlusally. The anterior end of the anterior crest terminates in a very poorly-defined cingular cuspule. The posterior end of the posterior crest also terminates in a very small cingular cuspule. The portion of crown lingual to these crests is distinctly smaller than the portion buccal to these crests. The crests and the long axis of the tooth are oriented anterolingually with respect to the molar tooth row. There is a poorly-developed posterobuccal cingular swelling. The anterior end of the tooth overlaps C/1 and the posterior end overlaps the anterobuccal flank of P/4. The crown height of P/2 is less than that of any other cheektooth and about half the height of C/1. As in the case of C/1, the buccal side of the crown is taller than the lingual side.

The unworn P/4 has two roots, the posterior being slightly wider than the anterior root. In general form, P/4 is very like the C/1 and unlike P/2. There is one very large median cusp, tiny anterolingual cingular cusp and an even smaller posterolingual cingular cusp (in the topographic position of a hypoconulid). The nearly vertical anterior face of the crown is anteriorly convex and bears a vertical ridge connecting the protoconid to the anterolingual cuspule. The posterior face of the protoconid is transversely flattened and gently concave posteriorly. The lingual edge of this flattened area forms a vertical crest that connects the protoconid to the posterolingual cingular cuspule. The buccal margin of this flattened area is a prominent vertical ridge extending from the tip of the protoconid to the posterobuccal cingular edge of the crown. A prominent cingulum extends all around the buccal half of the crown. There is a small anterolingual cingular shelf. There is no posterolingual cingulum. The posterobuccal corner of the crown is posteroventrally extended, distorting the crown outline into a somewhat triangular form. The posterobuccal corner itself is smoothly rounded. The portion of the crown buccal to the protoconid tip is much larger than the portion lingual to the protoconid. The buccal height of the crown is

much greater than the lingual height. The anterolingual cuspule rests against the posterolingual edge of P/2. The posterolingual cuspule is impressed into the anterior cingulum of M/1, much as in the manner of the hypoconulids on M/1-2. The P/4 height exceeds that of all crowns except C/1.

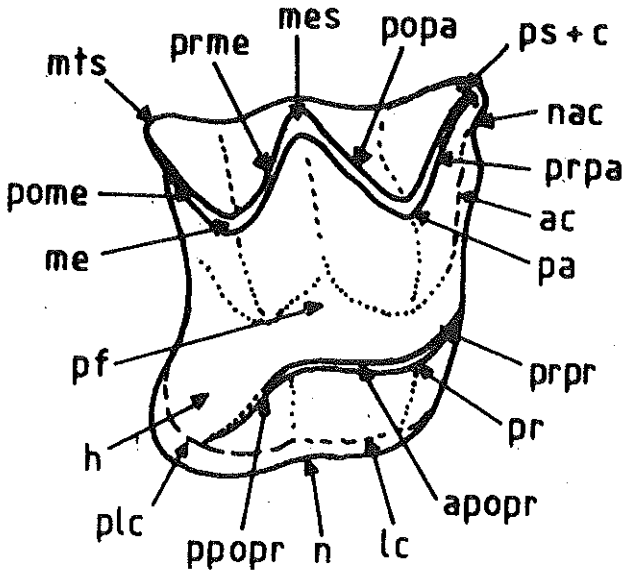
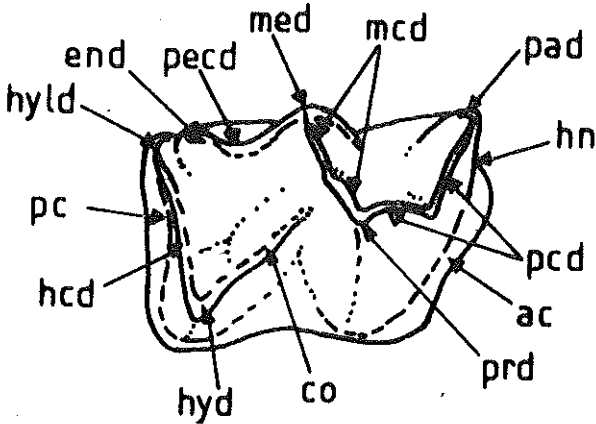


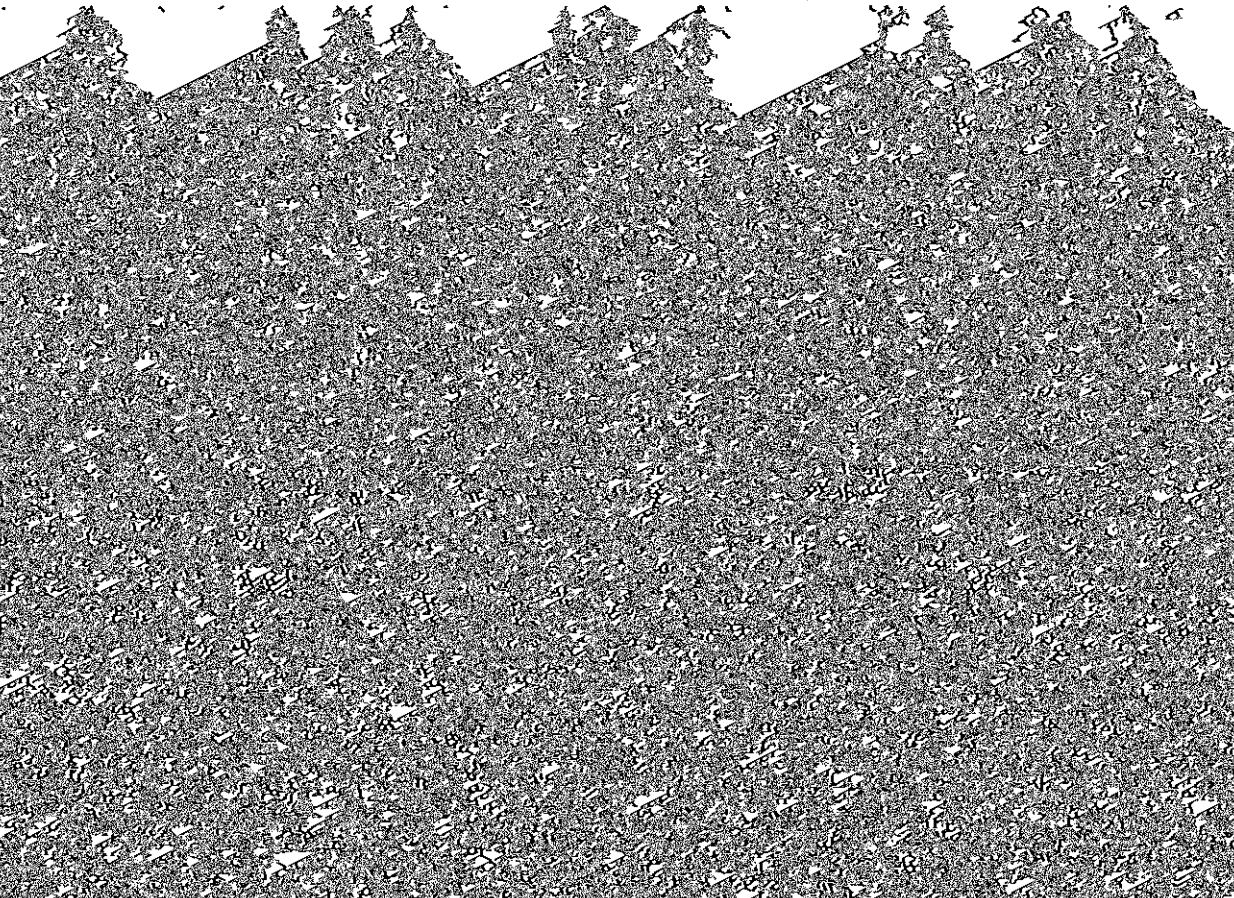
Fig. 1. TOOTH TERMINOLOGY

Abbreviations : apopr, anterior portion of the postprotocrista ; ac, anterior cingulum ; co, cristid obliqua ; end, entoconid ; pf, protofossa ; h, heel ; hcd, hypocristid ; hn, hypoconulid notch ; hyd, hypoconid ; hyld, hypoconulid ; lc, lingual cingulum ; mcd, metacristid ; me, metacone ; med, metaconid ; mes, mesostyle ; mts, metastyle ; n, lingual notch ; nac, notch in the anterior cingulum for hypoconulid ; pa, paracone ; pad, paraconid ; pc, posterior cingulum ; pcd, protocristid ; pecd, preentocristid ; plc, posterolingual cingulum ; pome, postmetacrista ; popa, postparacrista ; ppopr, posterior portion of postprotocrista ; pr, protocone ; prd, protoconid ; prme, premetacrista ; prpa, preparacrista ; prpr, preprotocrista ; ps + c, parastyle and parastylar crest.



The unworn M/1 has two roots and six distinct cusps. In height, the protoconid exceeds the metaconid which exceeds the entoconid which exceeds the subequal paraconid and hypoconid. The hypoconulid is a small cingular cusp. The trigonid is just

narrower than the talonid. All cusps are interconnected by crests. The paracristid is just longer than the metacristid. Its protoconid contribution exceeds that of its paracristid contribution. The protoconid contribution to the metacristid is markedly longer than the contribution from the metaconid. There are no distinct vertical carnassial notches. On unworn specimens, the uncurved cristid obliqua contacts the trigonid at a point (or just lingual to the point) directly below the junction of the components of the metacristid. There is an inflexion along the cristid obliqua at a point closer to the trigonid than the hypoconid. The hypocristid extends from the hypoconid directly to the hypoconulid. It also has an inflexion but one closer to the hypoconid than the hypoconulid. There is a well-developed crest (preentocristid) linking the metaconid to the entoconid. The metaconid component of this crest is just longer than the entoconid component. The point of junction of these components (which is the point of inflexion in this crest) is directly lingual to the point of inflexion in the cristid obliqua. The paracristid is oriented anterolingually. The metacristid, although close to being transverse to the long axis of the molar row, is oriented slightly posterolingually. The cristid obliqua parallels the paracristid. The hypocristid parallels the metacristid. The pre-entocristid is basically anteroposteriorly oriented although some specimens show a slight lingual concavity. There is a well-developed continuous anterior, buccal and posterior cingulum terminated near its anterolingual end by a notch for the posterior cingular cusp of P/4 and near its posterolingual end by a notch for the anterior cingulum of M/2. The cingulum at the base of the protoconid is taller than that at the base of the hypoconid. There is no lingual cingular development, except immediately



more acute posteriorly. The posterolingual corner of the crown becomes less lingually protrusive from M/1 to M/3. The height and width of the buccal cingulum conspicuously decreases from M/1 to M/3. The distance from the paraconid to the metaconid is subequal to that from the metaconid to the entoconid in M/1-2, but markedly shorter than this distance in M/3.

The upper dentition (the upper dental formula is I?/, C1/, P2,4/, M1,2,3/).

The upper incisors are unknown.

The unworn single-rooted C1/ is very large and bicuspid. The anterior cusp is over twice the height of any other tooth. The posterior cusp is approximately half the height of the main cusp. The two cusps are connected by a crest formed by a very short gently sloping segment from the posterior cusp and a very long vertical crest from the main cusp. The anterior face of the main cusp is flattened and has in its middle a shallow, narrow vertical groove extending from the anterior cingulum to just short of the tip of the crown. The anterolingual vertical corner of the main cusp would form an acute angle in sagittal section. The anterobuccal vertical corner of the

mentary cingulum is developed at points all around the crown as a series of tiny cuspules or crests. The crown is widest buccal to the posterobuccal crest and slopes gently up towards the buccal margin of the tooth. Lingual to the median crests and the main cusp, the crown is narrower and slopes more steeply towards the lingual edge of the crown.

The unworn P4/ is three-rooted, the largest root being that for the lingual cingular cusp and the smallest that for the main cusp. The main cusp root is immediately posterolingual to the small root for P2/. There are two principal cusps, the very large main cusp and the very much smaller cingular cusp. There are additionally a small anterior cingular cuspule, a large posterobuccal end to the postparacrista, and a low but distinct cingular «heel». The main cusp is taller than the posterior cusp of C1/ and any molar cusp, but markedly shorter than the main cusp of C1/. It is connected to the posterobuccal corner of the crown by a well-developed arcuate postparacrista. The well-defined anterior flank of the main cusp is very gently convex anteriorly. A fine vertical crest near its base connects the tiny anterior cingular cusp to the basal part of the flank of the main cusp. The lingual edge of the anterior flank becomes a comparably small crest near the lingual base of the main cusp and connects the main cusp to the small cingular cusp. The small buccal face of the main cusp, extending between the anterobuccal corner of the tooth and the postparacrista, is very gently concave buccally. The posterolingual flank of the main cusp is the largest vertical surface of the tooth and extends from the anterolingual corner of the crown to the postparacrista. It is, overall, gently concave posterolingually. Except for the posterobuccal corner, the entire crown is surrounded by a basal cingulum. Anteriorly, it is analagous to the preprotocrista of M1/ in that it emanates from the cingular cusp and, posteriorly, it is analagous to the postprotocrista of M1/. However, unlike the latter crest in M1/, this cingular «postprotocrista» connects directly to the cingular analogue of the heel. The cingular «heel» is serially analagous to the true heel of M1/, and like that structure forms a prominent posterolingual basal shelf on the crown. In lingual view, it also forms a distinct cingular cuspule posterior to the lingual cusp in much the same way that the true heel does posterior to the protocone of M1/. The height of the cingulum is greatest above the lingual cusp. Buccally and posteriorly from this point, the height decreases. The height of the buccal cingulum is relatively uniform along its length and shorter than the height of the lingual cingulum.

The little worn M1/ exhibits seven principal cusps and a low cingular heel. The metacone is taller than the paracone which is taller than the protocone which is taller than the mesostyle, which is just taller than the subequal parastyle, metastyle and protocone which are taller than the hypocone. There is no paraconule or metaconule. The posterolingual cingular cusp is much shorter than any other cusp. With slight wear, the preparacrista contacts the parastyle. Although the completely unworn condition is unknown, little worn specimens suggest that the parastyle is just distinct. The postparacrista and premetacrista contact at the mesostyle, and the postmetacrista contacts the metastyle. The parastyle, in just worn specimens, is a short anterolingually oriented crest developed at right angle to the preparacrista. Its anterobuccal flank is smoothly rounded. The mesostyle is not cuspidate and, buccally, is smoothly

rounded. Similarly, the metastyle is only the end of the postmetacrista, and has a smoothly rounded posterobuccal flank. The angle formed between the pre- and postparacristae is about 70° . The comparable angle formed between the pre- and postmetacristae is less, being about 60° . All crests connecting to paracone and metacone are occlusally concave. The subequal postparacrista and postmetacrista are just longer than the subequal preparacrista and premetacrista. The preprotocrista is continuous with the anterior cingulum and thus connects to the parastyle. This whole shelf shortens (anteroposteriorly) at a point half way along its width. There is also a notch near the parastyle that represents the position of the addressed posterobuccal corner of P4/. The postprotocrista extends posteriorly to a point about halfway between the protocone and metacone, and then sharply turns posterolingually descending steeply to the posterolingual cingulum forming the heel of the crown. The preprotocrista and anterior part of the postprotocrista form a buccal angle of about 90° . The short anterior and longer posterior parts of the postprotocrista form a lingual angle of about 170° . The heel, or posterolingual basal cingulum, extends anteriorly to a point just basal to the tip of the protocone, and posterobuccally to a point just short of the metastyle. The heel is longest (anteroposteriorly) and widest around the posterolingual base of the crown. In occlusal view, there is no slope change (*i.e.* no notch) in the lingual portion of this basal cingulum, but there is a distinct notch in the posterior portion at a point directly basal to the lingual edge of the base of the metacone. The adjacent bases of the paracone, metacone and protocone conscribe a small confined profossa. The posterior margin of this central basin is the lowest. The crown bears four roots, subequal paracone and metacone roots, a larger lingual medial protocone root, and a very small posterolingually oriented root below the heel.

The M2/ is comparable to M1/ except as follows. The paracone and metacone are subequal in height. There is almost no shortening (anteroposteriorly) of the anterior cingulum at the base of the paracone. The posterolingual heel is poorly developed, being little more than a basal cingulum. There is a slight enlargement at the point of inflexion between the anterior and posterior portions of the postprotocrista. This could be described as a miniscule metaconule. The posterior and anterior parts of the postprotocrista are subequal in length. The lingual basal cingulum is little more than half the length of the same structure on M1/. There is no root below the posterolingual heel.

The M3/ resembles M2/ except as follows. The metacone is shorter than the paracone and subequal in height to the parastyle. There is no heel or posterolingual cingular development at all. The postmetacrista is reduced to a steeply ascending swelling on the posterobuccal flank of the metacone. There is no metastyle. The premetacrista is posteriorly concave. The preparacrista and postparacrista are subequal in length and markedly longer than the premetacrista. The metaconule of M2/ is here represented by a comparable cuspule on the postprotocrista but one occurring immediately adjacent to the base of the metacone. It is connected by the postprotocrista directly to the base of the metacone, there being no posterolingual component to the postprotocrista.

Meristic gradients along the upper molar row (Table 1).

The protocone and metacone decrease in height from M1/ to M3/. The paracone of M2/ is slightly taller than the paracone of M1/ which is slightly taller than the paracone of M3/. The parastyle of M3/ is taller than that of M2/ which is taller than that of M1/. The anterolingual parastylar crest of M1/ is longer than that of M2/ which is longer than that of M3/. From the buccal view, the parastyle is most anteriorly inclined on M1/, less so on M2/ and nearly vertical on M3/. The metastyle height of M1/ is greater than that of M2/ ; it is missing on M3/. The preparacrista of M1/ is just shorter than the preparacrista of M2/ which is just shorter than the preparacrista of M3/. The subequal postparacristae of M1/ and M3/ are just shorter than that crest on M2/. The premetacrista of M2/ is just longer than that of M1/ which is just longer than that of M3/. The postmetacristae of M1/ and M2/ are subequal in length ; this crest is absent on M3/. In occlusal view, the anterior margin of M1/ is sinuous (s-

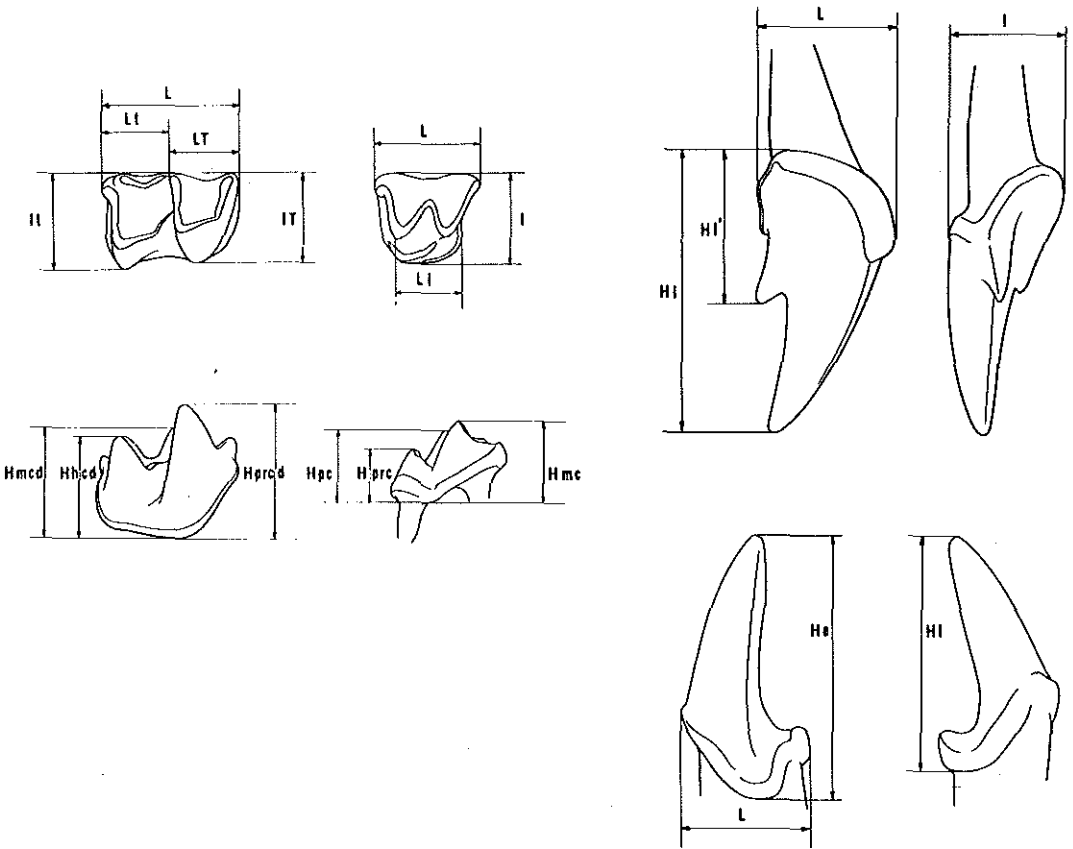


Fig. 2. — Mensuration of the various types of teeth. L, length ; Li, internal length ; l, width ; H, height ; He, external height ; Hi, internal height ; Hi', internal height of second cusp ; LT, length of trigonid ; Lt, length of talonid ; IT, width of trigonid ; lt, width of talonid ; HPrC, protocone height ; HMc, metacone height ; HPC, paracone height ; HPrCd, protoconid height ; HMcd, metaconid height ; HHcd, hypoconid height ; (from Sigé 1968).

Lower teeth				Upper teeth			
	N	Observed range	Mean		N	Observed range	Mean
C/1 L	10	0.82 - 1.02	0.96	C1/ L	10	1.38 - 1.54	1.43
l	10	0.84 - 1.06	0.98	l	10	1.08 - 1.26	1.2
He	10	1.76 - 2.44	2.12	Hi	10	2.36 - 2.96	2.67
Hi	10	1.5 - 1.94	1.8	Hi'	10	1.02 - 1.58	1.32
P/2 L	10	0.9 - 1.06	0.98	P2/ L	4	0.4 - 0.42	0.41
l	10	0.66 - 0.8	0.73	l	4	0.34 - 0.36	0.36
He	10	0.78 - 1.0	0.93	He	4	0.32 - 0.36	0.35
P/4 L	10	0.86 - 0.98	0.94	P4/ L	10	0.92 - 1.1	1.01
l	10	0.68 - 0.88	0.79	l	10	1.18 - 1.38	1.25
He	10	1.26 - 1.54	1.41	Hi	10	1.72 - 2.02	1.83
				*HMes	10	1.36 - 1.72	1.55
M/1 L	10	1.36 - 1.5	1.42	M1/ L	10	1.36 - 1.48	1.43
LT	10	0.76 - 0.9	0.8	l	10	1.34 - 1.62	1.51
IT	10	0.8 - 0.96	0.86	Li	10	1.12 - 1.36	1.21
Lt	10	0.58 - 0.66	0.62	HMc	10	1.16 - 1.44	1.34
lt	10	0.88 - 1.02	0.94				
HPred	10	1.3 - 1.5	1.35	HPrc	10	0.98 - 1.2	1.09
HMcd	10	1.04 - 1.26	1.18	i $\frac{Li \times 100}{L}$	10	75.7 - 94.4	86.4
HHcd	10	0.88 - 1.08	0.99				
M/2 L	10	1.34 - 1.44	1.39	M2/ L	10	1.32 - 1.44	1.38
LT	10	0.7 - 0.82	0.75	l	10	1.44 - 1.7	1.55
IT	10	0.86 - 0.94	0.92	Li	10	0.88 - 1.08	0.95
Lt	10	0.58 - 0.68	0.64	HMc	10	0.8 - 1.4	1.11
lt	10	0.92 - 1.06	1.0				
HPred	10	1.12 - 1.48	1.35	HPrc	10	0.76 - 1.0	0.88
HMcd	10	1.04 - 1.36	1.24	i $\frac{Li \times 100}{L}$	10	62.5 - 79.4	68.5
HHcd	10	0.86 - 1.06	0.99				
M/3 L	10	1.32 - 1.42	1.35	M3/ L	10	1.0 - 1.2	1.09
LT	10	0.68 - 0.78	0.72	l	10	1.4 - 1.56	1.47
IT	10	0.86 - 0.96	0.91				
Lt	10	0.6 - 0.68	0.63	HPc	10	0.84 - 1.04	0.93
lt	10	0.84 - 1.04	0.92	HPrc	10	0.52 - 0.72	0.61
HPred	10	1.16 - 1.28	1.21				
HMcd	10	1.16 - 1.38	1.23				
HHcd	10	0.74 - 0.94	0.83				

*HMes refers to height of mesostyle.

TABLE 1

Measurements of upper and lower teeth of *H. (Brachipposideros) nooraleebus* n. sp. In mm.

shaped), of M2/ sublinear, and of M3/ gently convex. The metaconule of M2/ is most distinct, on M1/ it is just less so, and on M3/ considerably less distinct. The heel of M1/ is much larger than that of M2/ ; it is missing on M3/. In occlusal view, the posterior margin of M1/ is markedly concave, of M2/ gently concave, and of M3/ gently convex. The posterior part of the postprotocrista is much longer on M1/ than it is on M2/ ; this part of the postprotocrista is missing on M3/. From a lingual point of view, the protocone of M1/ is steeply inclined anteroventrally, just less so in M2/, but nearly vertical in M3/. Also from a lingual point of view, the metacone of M1/ slopes anteriorly, vertically in M2/, and posteriorly in M3/.

COMPARISON BETWEEN *HIPPOSIDEROS* (*BRACHIPPOSIDEROS*) *NOORALEEBUS* AND RELATED FORMS

The Riversleigh bat and some species of early and middle Miocene bats of Europe clearly belong to the same subgenus *Brachipposideros*. Species of this subgenus are distinguished (Sigé 1968) by the following combination of features : 1. small size ; 2. shape of the ascending ramus of the dentary which has a low coronoid process ; 3. vestigial P2/ located between the C1/ and P4/ near or on the buccal margin of the tooth row ; 4. C1/ with a pronounced posterior cusp ; 5. P4/ which is slender relative to the other cheekteeth ; 6. M1/ which is four-rooted (secondary loss of the fourth root occurs in some species) ; 7. M2/ which is three-rooted (some advanced forms have four) ; 8. the heel of M1/ is separated from the protocone by a slight lingual notch (which may be secondarily lost in later forms) and forms a posteriorly directed lobe ; 9. the heel of M2/ is relatively weakly-developed ; 10. primitively, the postprotocrista consists of a prominent anterior portion and an only incipiently developed posterior portion (secondary loss or further development occurs in later species) ; and 12. the lower canine is small.

Many French fossil faunas, notably peri-mediterranean one, have bats referable to *Brachipposideros* (Fig. 7) :

1. Chattian (late Oligocene), St-Victor-la-Coste (Gard, France), an unnamed taxon similar to *H. (Brachipposideros) branssatensis* (hereafter called, illustrated in Figs 3 to 6, and shown in Fig. 8, as « Form X ») ;
2. Lower Aquitanian (early Miocene), La Colombière (Hérault, France), *H. (B.)* sp. cf. *H. (B.) branssatensis* and Coderet (Allier, France), *H. (Brachipposideros) branssatensis* (Hugueney, 1965) ;
3. Upper Aquitanian (early Miocene), Bouzigues (Hérault, France), *H. (B.)* sp. cf. *H. (B.) collongensis* and *H. (B.) dechaseauxi* Sigé, 1968 ;
4. Lower Burdigalian (early Miocene), Serre de Vergès (Pyrénées Orientales, France), *H. (B.)* sp. cf. *H. (B.) collongensis* and *H. (B.) aguilari* ;
5. Upper Burdigalian (early middle Miocene), Vieux Collonges (Rhône, France), *H. (B.) collongensis* (Depéret, 1892), and Port-la-Nouvelle (Aude, France), *H. (B.) aguilari* Legendre, 1982, and *H. (B.) dechaseauxi* ;

6. Serravalien (middle Miocene), Cases de Pène (Pyrénées-Orientales, France), *H. (B.) collongensis*, and La Grive St-Alban (Isère, France), *H. (B.) collongensis*.

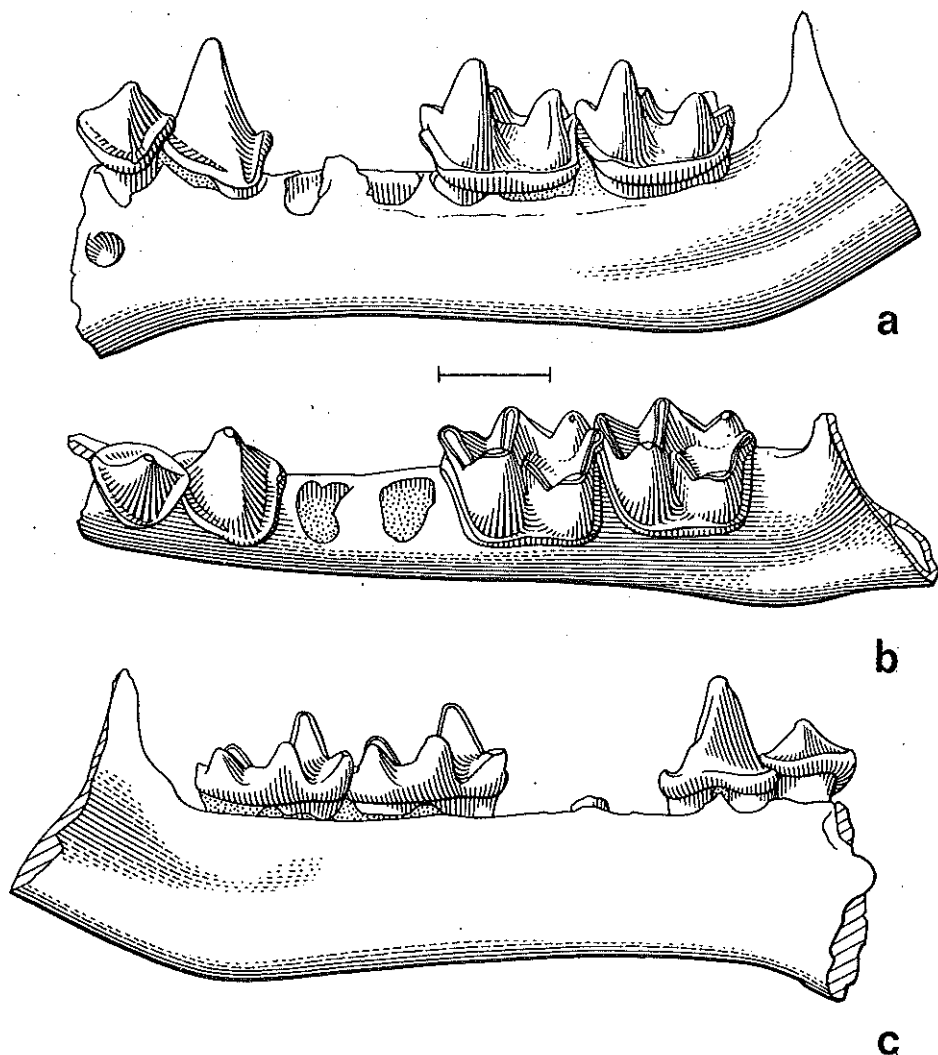


Fig. 3. — *Hipposideros (Brachipposideros)* «Form. X», (close to *H. (B.) branssatensis*), from St-Victor-la-Coste (Gard, France). SVC 4571-B; left jaw with P/2 - P/4, M/2 - M/3. a. labial view; b. occlusal view; c. lingual view. $\times 15$. The scale indicates 1 mm.

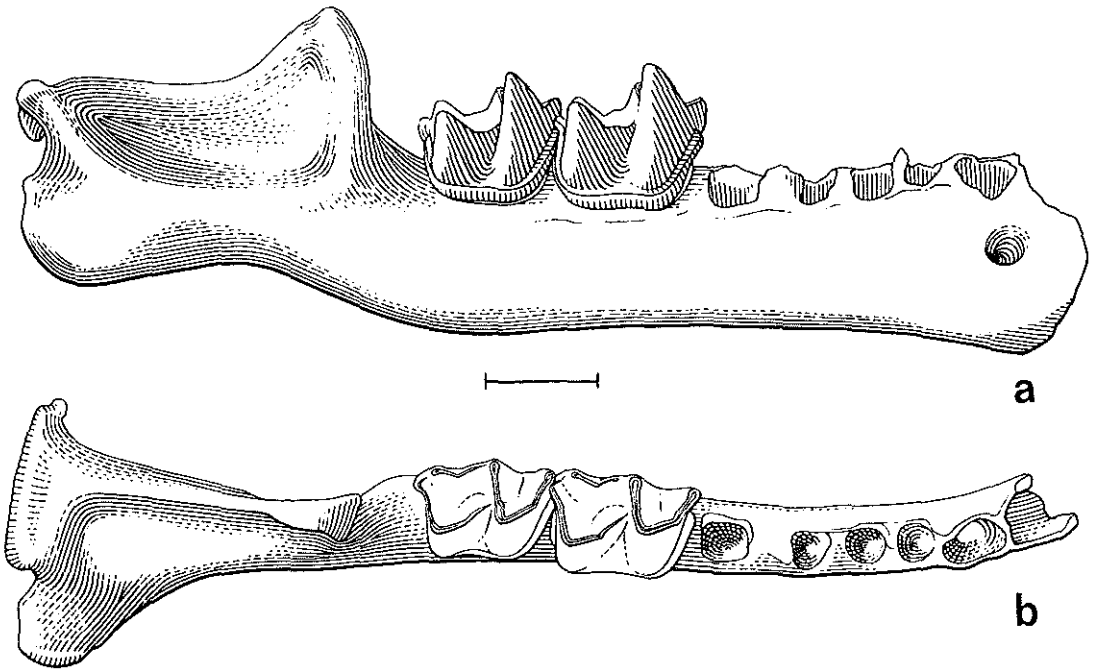


Fig. 4. — *Hipposideros* (*Brachipposideros*) «Form X», (close to *H. (B.) branssatensis*), from St-Victor-la-Coste (Gard, France). SVC 4631-A ; right jaw with ascending ramus preserved and M/2 - M/3. a. labial view ; b. occlusal view $\times 15$.

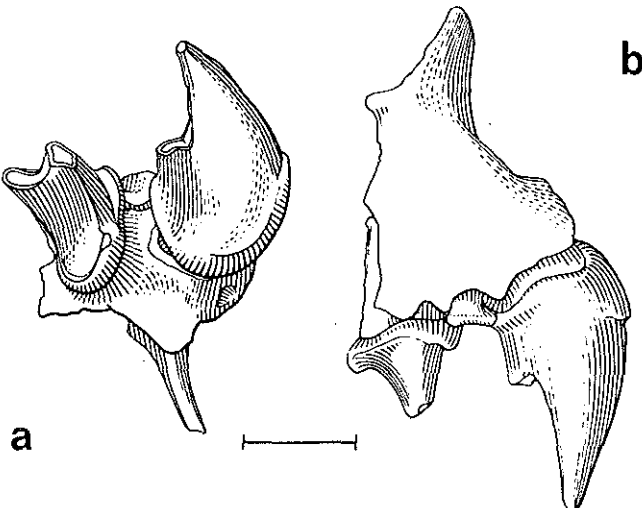
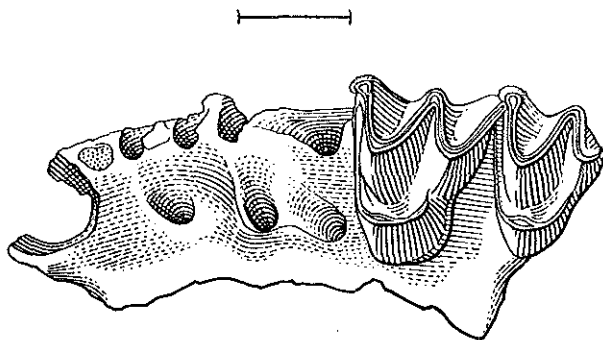


Fig. 5. — *Hipposideros* (*Brachipposideros*) «Form X», (close to *H. (B.) branssatensis*), from St-Victor-la-Coste (Gard, France). SVC 4886-B, fragment of right maxillary with C, P2/, P4/. a. occlusal view ; b. labial view. $\times 15$.

Fig. 6. — *Hipposideros* (*Brachipposideros*) «Form X», (close to *H. (B.) branssatensis*), from St-Victor-la-Coste (Gard, France). SVC 4881-B, fragment of left maxillary with M2/-M3/. Occlusal view. $\times 15$.
Drawings of Figs 3 to 6 by Ariane Böyer.



The biostratigraphic sequence used here is that provided by Aguilar (1982) for the western European Neogene.

A recent phylogenetic study (Legendre 1982) suggests that the oldest and evidently ancestral species from the Oligo-Miocene transition gave rise to three distinct lineages

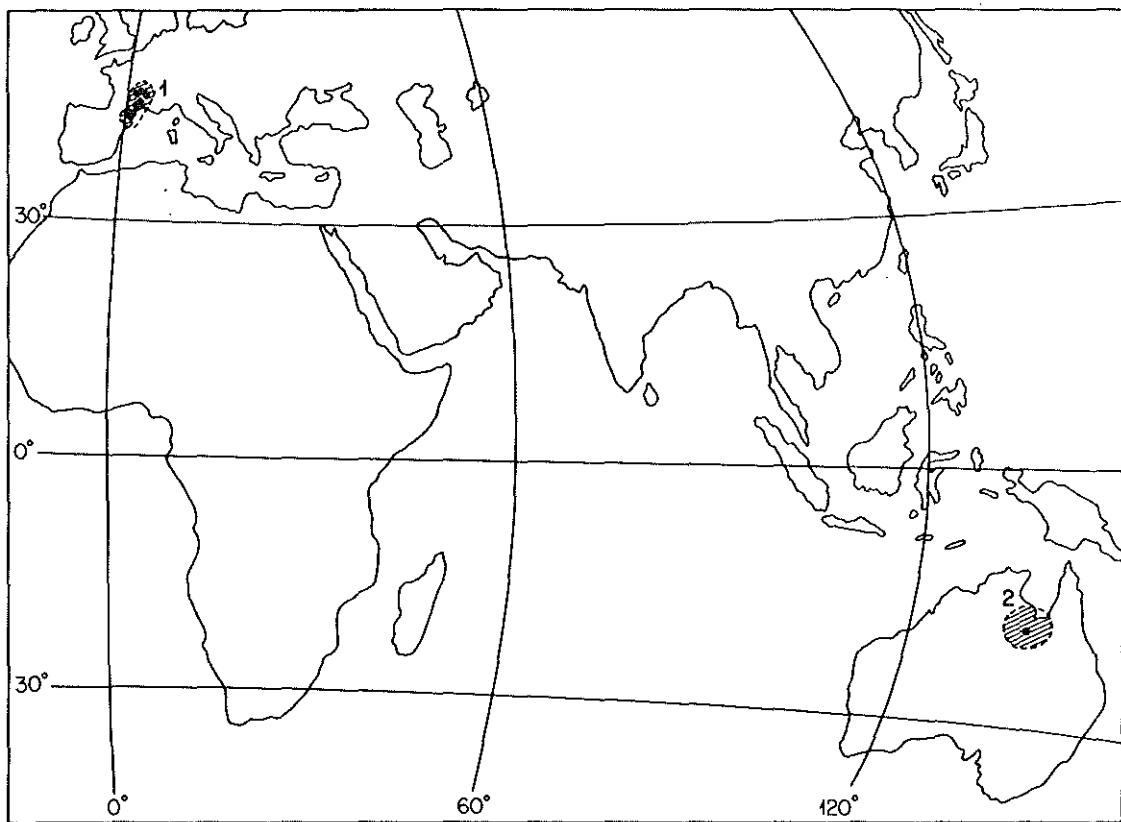


Fig. 7. — Geographic distribution of Miocene forms of *Hipposideros* (*Brachipposideros*). 1. European zone ; 2. Australian zone.

known from the early to middle Miocene : *collongensis* ; *dechaseauxi* (which is also the largest) ; and *aguilari* from Serre de Vergès and Port-la-Nouvelle.

The characteristic dentary morphology of species referable to this subgenus occurs in the Australian Riversleigh bat. The horizontal ramus is relatively short and slender and shows, in occlusal view, a sinuosity which is not pronounced. Further, all known forms bear a chin process. This feature is constant in at least one large sample (e.g. *H. (B.)* «Form X» from St-Victor). In all forms, the chin foramen occurs on the side of the dentary at a point below P/2 or a point below a position between C/1 and P/2. The height of this foramen on the dentary varies. Another smaller foramen, present in all forms, occurs ventral to the alveolus for I/1.

In all forms, the coronoid process is very low, its tip only exceeding the molar heights by a molar crown height or less. The lateral profile of the ascending ramus varies within populations such that the anterior crest can be more or less sinuous, and the posterior crest more or less angular. In all forms the masseteric fossa has a very expanded, almost horizontal lower border which extends posteriorly into a wide, rounded angular process that extends buccally further than it does in the majority of other microchiropterans.

The dental formula is the same in all forms referable to *Brachipposideros*. Variation in relative proportions and morphology of different teeth serve to diagnose individual species or groups of species (Table 2).

Among the lower teeth, the C/1 shows most variation between species. In the Australian form, the lower canine is taller and more slender than in most European forms, its posterior buccal edge being acute and more vertically oriented than in the latter forms. The P/4 commonly shows intraspecific differences in the shape of the ventral buccal edge. For example, it may be bent in occlusal outline, evenly rounded, or subrectilinear and ascending.

Among upper teeth, P2/, P4/, M1/ and M2/ exhibit most interspecific differences. In all forms the morphology of the P2/ is similar, but in the oldest known forms (*H. (B.)* «Form X», *branssatensis*, and cf. *B. branssatensis*) this tooth is larger with respect to the other cheekteeth. Moreover, in these oldest forms, P2/ is situated on the buccal edge of the alveolar row. These two features contribute to differences in the degree of separation of C1/ and P4/. In all later European forms (*B. collongensis*, *B. dechaseauxi*, *B. aguilari* lineages) and in the Australian species, P2/ is more buccally situated, protruding outside of the tooth row, and thereby allowing close approximation (sometimes contact) of the C1/ and P4/.

The shape of P4/ is also similar in all forms, but more slender relative to the other cheekteeth in the older forms [*H. (B.)* «Form X», *branssatensis* and cf. *B. branssatensis*].

Species and species groups are most easily distinguished on the basis of the relative size and morphology of M1-2/. In occlusal view, the general shape of these teeth is subquadrate, but the later European forms (*collongensis*, *dechaseauxi* and *aguilari*) have a slightly less deeply indented ectoloph than the older forms («Form X», *branssatensis* and cf. *branssatensis*). In these, as in the Australian form, M1/ and (particularly) M2/, are generally proportionally wider than those teeth in the later forms.

Variation in the development of the heel of M1-2/ is also apparent. In *B. branssatensis* from Coderet and *B.* «Form X» from St-Victor-la-Coste, the heel makes a rather distinct posteriorly directed lobe that is sometimes separated from the protocone by a slight notch. The heel is relatively well-developed on M1/ and weak or very weak on M2/. In the *B. collongensis* and *B. dechaseauxi* lineages, the heel makes a lobe that is less distinct from the protocone. This heel is widest at the mid-width of the tooth, thereby giving the impression that the lobe is buccally directed. In the Australian form, the heel is developed posterolingually and directed backwards and the lingual notch is more pronounced. The forms *B.* sp. cf. *B. branssatensis* from La Colombière and *B. aguillari* from Port-la-Nouvelle also show this tendency (particularly on M1/) and retain a slight lingual notch.

The M1/ (commonly) and M2/ (sometimes) have four roots. The fourth root (below the heel) is either barely functional (*i.e.* with a small alveolus) or non-functional and sometimes confluent with the protocone root.

In *B. branssatensis* from Coderet, a heel root occurs on both M1/ and M2/. This is also generally the case (variable on M2/) in *B. collongensis* and *B. dechaseauxi*. In *B.* «Form X» from St-Victor and in the Australian form, the fourth root occurs only on M1/. *Brachiposideros aguillari* from Port-la-Nouvelle is distinguished by the lack of the fourth root on both M1/ and M2/.

Species group differences are also apparent in the development of the postprotocrista of the upper molars. In some forms, this crest is simple and reaches only to the base of the metacone. In the forms from La Colombière, *aguillari* from Port-la-Nouvelle and *nooraleebus*, a distinct posterior part of the postprotocrista is always developed and links the anterior part of the postprotocrista to the cingulum of the heel. This postprotocrista forms a dihedral crest on the posterior side of the protocone. A dihedron is present but rare and slight in samples from St-Victor-la-Coste and Coderet. In other forms, lacking the posterior part of the postprotocrista, the posterior flank of the protocone is simply rounded.

	<i>B. branssatensis</i> and cf.			<i>B. collongensis</i> and cf.		<i>B. dechaseauxi</i>	<i>B. aguillari</i>	<i>B. nooraleebus</i>	
	SVC	COD	COL	BZS	VXC	BZS	PON	PON	RIV
P4/-M3/	-	-	-	4.20	4.5-4.7	5.64	-	-	4.58
M1/ L	1.46	1.4	1.61	1.38	-	1.67	1.8	1.4	1.43
1	1.48	1.55	1.6	1.45	-	1.82	1.96	1.47	1.51
P4-M/3	4.9	4.35	-	4.87	4.9-5.3	6.04	-	-	4.81
M/1 L	1.42	1.35	-	1.43	-	1.81	1.83	1.28	1.42
1	0.92	0.8	-	0.84	-	1.01	1.17	0.75	0.94

TABLE 2

Relative sizes of the European and Australian Miocene *Brachiposideros*.

Localities are abbreviated as in Fig. 9. SVC and COL, mean values obtained from small samples (2 to 6 specimens); RIV, 10 specimens; COD, from Huguenev 1965; BZS, from Sigé 1968; VXC, from Mein 1958; PON, from Legendre 1982. In mm.

The Riversleigh bat also exhibits a striking resemblance to Australia's only endemic hipposiderid, *Rhinonycteris aurantius*. The latter may be distinguished from *H. (B.) nooraleebus* by, among others, the following features : larger size ; further expansion of the heel on M2/ ; a more pronounced accessory cusp and a much deeper lingual cingulum on C1/.

PHYLOGENETIC POSITION AND INTERPRETATIVE HISTORY OF THE RADIATION OF SPECIES REFERABLE TO *BRACHIPPOSIDEROS*

Based on a parsimonious interpretation of the particular share-derived character-states so far used to diagnose species (Sigé 1968), a tentative phylogenetic hypothesis involving forms referable to *Brachipposideros* is given in Fig. 8. A more detailed phylogenetic analysis is in progress as part of a broader study of the complete skeleton of *H. (B.) nooraleebus*. The same forms, placed in these hypothetical lineages, are arranged stratophenetically in Fig. 9.

The oldest known representative of *Brachipposideros* is a European form from the Oligo-Miocene transitional sediments of the St-Victor-la-Coste karstic fillings. The rich upper Eocene and Oligocene fissure fillings of the Quercy phosphorites have been the object of intense investigations for several years, and the reviews of de Bonis *et al.* (1973) and Crochet *et al.* (1981) reveal no representative of *Brachipposideros* in these faunas. This absence is despite the fact that hipposiderids represent the main group (in number of individuals and number of species) in the Quercy bat faunas. The family is here represented *nec varietur* by species of two main morphological types : the genera *Palaeophyllophora* and *Hipposideros (Pseudorhinolophus)*. The oldest representatives of these bats exhibit an advanced character-state in the reduction of M3/3, in particular the ectoloph of M3/ which is reduced to only one V. This feature excludes them from being ancestral to species of *Brachipposideros*.

Therefore, species of *Brachipposideros* appear rather suddenly in the early Miocene faunas of Europe without any evident autochthonous ancestors. This leads up to propose an immigration into Europe in the late Oligocene. This probably came from an Asiatic or African palaeotropical area of the old world, and from a more generalized but as yet unrecognized ancestral hipposiderid.

From the lower Miocene to the middle upper Miocene, a period of about twelve million years, different localities show the persistence and radiation of this group in western Europe. From Burdigalian times on, three European localities (Bouzigues, Serre de Vergès and Port-la-Nouvelle) show the simultaneous occurrence of two species of *Brachipposideros* (Fig. 9). The subgenus vanished from Europe during the late Miocene or the Pliocene.

Even though non-European palaeontological date are poor, it is likely that the geographic area of species of *Brachipposideros* extended much further than western Europe. Clearly, at least one significant extension occurred to bring *Brachipposideros* to the Australasian region. Here, if the endemic Australian hipposiderid *Rhinonycteris aurantius* is a descendant of an ancestral species of *Brachipposideros*, a *Brachipposideros* lineage persisted into modern times.

In Europe, representatives of *Brachiposideros* are always fossilized in karstic sediments, with the exception of Coderet. This suggests the troglophilism of the Miocene species of *Brachiposideros*, a hypothetical characteristic consistent with the general troglophilism of living species of *Hipposideros*.

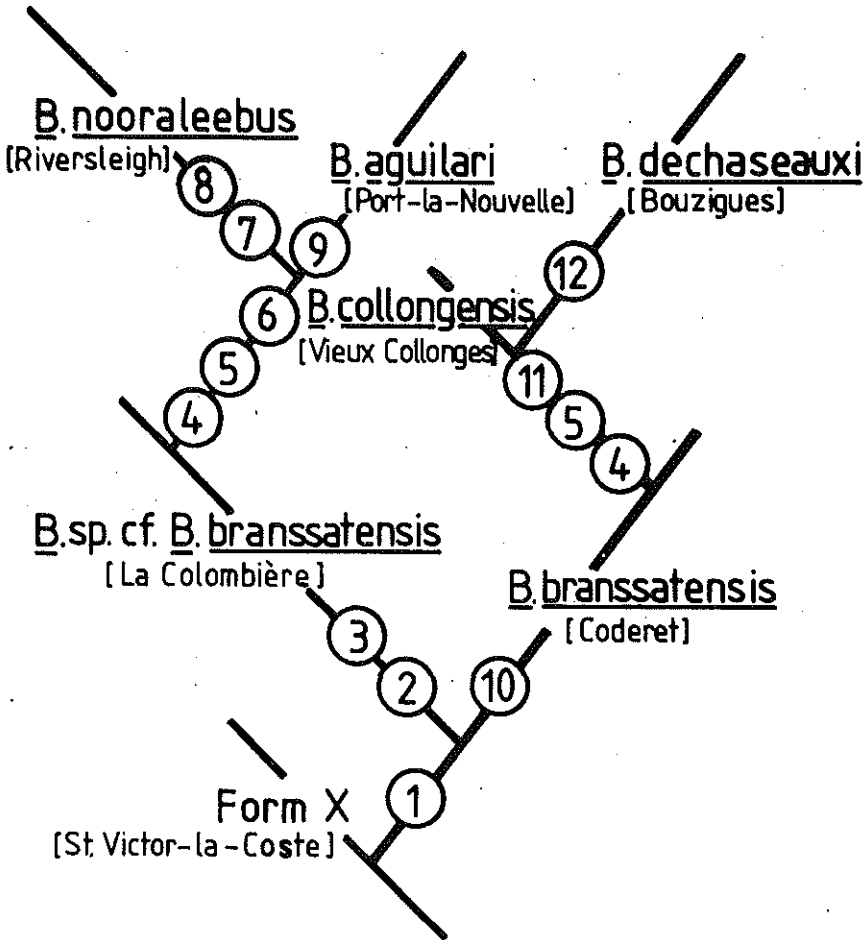


Fig. 8. — Tentative phylogeny of the Miocene European and Australian forms of *Hipposideros* (*Brachiposideros*). This hypothesis is based on a parsimonious interpretation of the following share-derived character-states (which are indicated as circled numbers in the figure) :

1. heel of M2/ more expanded ; 2. heel of M1/ and M2/ separated from the protocone by a slight lingual notch ; 3. heel of M1/ and M2/ developed posterolingually and directed posteriorly ; 4. P2/ further reduced, restricted to the buccal edge of the tooth row and, consequently, the C1/ and P4/ are approximated (and sometimes even contact) ; 5. P4/ relatively larger ; 6. a posterior part of the post-protocrista forms a pronounced dihedral crest on the posterior side of the protocone ; 7. heel of M1/ and M2/ separated from the protocone by a pronounced lingual notch ; 8. a taller, vertically-oriented lower canine ; 9. three-rooted M1/ ; 10. four rooted M2/ ; 11. heel of M1/ and M2/ posterobuccally extended ; 12. larger size.

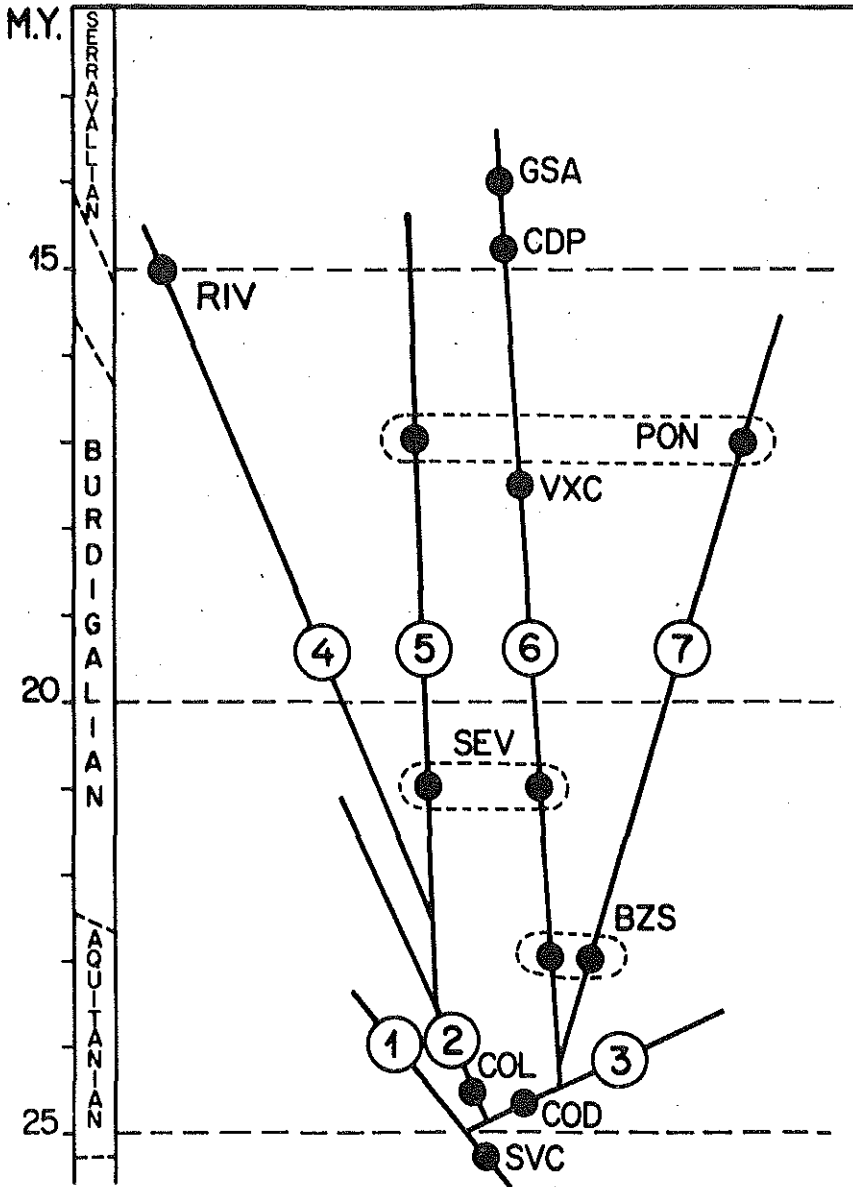


Fig. 9. — Tentative stratophenetic phylogeny of forms referable to *Hipposideros* (*Brachipposideros*). The correlations used for Europe are from Aguilar (1982). The circled numbers indicate the following forms :

1. *Brachipposideros* « Form X » ; 2. *B. sp. cf. B. branssatensis* ; 3. *B. branssatensis* ; 4. *B. nooraleebus* n. sp. ; 5. *B. aguilari* ; 6. *B. collongensis* ; 7. *B. dechaseauxi*. The letters indicate populations from : SVC, St-Victor-la-Coste ; COL, La Colombière ; COD, Coderet ; BZS, Bouzigues ; SEV, Serre de Vergès ; VXC, Vieux-Collonges ; PON, Port-la-Nouvelle ; RIV, Riversleigh ; CDP, Cases de Pène ; GSA, La Grive St-Alban.

PALAEOGEOGRAPHIC SIGNIFICANCE OF THE RIVERSLEIGH BAT

Although native Australian placental mammals (rodents, bats and the Dingo) comprise fifty per cent of the Australian non-marine mammal species, they evidently did not have a long evolutive history on this continent (Archer 1981). It is generally accepted that bats were the first placental pioneers (Archer 1978). According to Simpson (1965), bats probably arrived in successive waves from continental Asia through the East Indian Archipelago to Australia.

The palaeontological history of placental settlement of Australia is not well-documented. Until 1978, the oldest Australian bats (of an undetermined family) were represented by isolated lower teeth of early Pliocene age from Victoria (Turnbull and Lundelius 1970). The discovery of a microchiropteran tooth from the middle Miocene Etadunna Formation, South Australia (Archer 1978) is presently the oldest known record of bats from Australia. Its affinities are presently under study by one of us (S.H.) who has tentatively concluded that it is probably a rhinolophoid.

The middle Miocene, Australian species of *Brachiposideros* from Riversleigh Station, Queensland, differs from the Etadunna bat in that it is represented by abundant and well-preserved material. Because of this, its affinities to Miocene forms known from western Europe have been able to be determined. The dental structure of this Riversleigh bat is more advanced than that of Aquitanian forms in Europe and as advanced as that of Burdigalian species of this continent. The close similarity to European Burdigalian forms leads us to suggest that the Riversleigh *Brachiposideros nooraleebus* had only recently arrived in Australia. Its structure does not suggest a long period of evolution in isolation. Therefore, the immigration into Australia might have occurred in the interval roughly between 20 and 15 million years ago.

Curiously, if we consider available data on flying aptitudes of bats (see literature in Brosset 1966), living hipposiderids are not considered to be able to perform long non-stop flights over water. The arrival of these bats into Australia, possibly as early middle Miocene times, must then have depended on relatively contiguous areas of land from Europe to Australia. In fact, the longest water gap presently separating these areas is about 150 kilometres. Close land connections have existed since early to middle Miocene times. Invasion prior to this time is progressively less probable.

From what is also known of the palaeoclimatology of western Europe, the appearance of species of *Brachiposideros* in the French fossil record coincides with a period of steadily increasing temperature (Aguilar *et al.*, *in sched.*). Similarly, the disappearance of these forms could correlate with the climatic deterioration across Europe during the Pliocene (*o.c.*). This suggests that perhaps climatic requirements for these ancient hipposiderids were as restrictive as they are today for most hipposiderids. For example, Australia's *Rhinonycteris aurantius* is found only in the most humid parts of its northern Australian distribution and is well known to quickly expire when physically removed from this type of environment.

ACKNOWLEDGEMENTS

Many people and institutions have helped in the gathering of the Nooraleeba fossils. Mr Henk Godthelp was the keen-eyed finder of the first bones of the Nooraleeba site at Riversleigh. With the backing of Dr Ray E. Lemley, the Queensland Museum and Australian Research Grants Committee award to Archer, many tons of Nooraleeba limestone have been collected and processed. During 1975, 1977 and 1981, collections were made by Mr H. Godthelp, Mr D. Joff, Mr R. Kahout, Mr T. Flannery (U.N.S.W.), Dr R. Lemley, Ms. G. Clayton, Prof. R. Pascual, Ms S. Hand and Dr M. Archer. Sorting of the masses of concentrate has been variously carried out by Ms G. Clayton (U.N.S.W., the principal preparator of Riversleigh fossils provided by the A.R.G.C. Grant to Archer), Mr R. Kahout (Queensland Museum), Ms J. Taylor (U.N.S.W.), Ms S. Churchill (U.N.S.W.), Mr H. Godthelp and Ms S. Hand.

Permission to collect on Riversleigh over the last few years was kindly granted by Mr and Mrs T. Naughton, and Mr and Mrs J. Nelson and the present owners. The late Ms Ivy Stinken kindly spent several evenings with Archer communicating the vocabulary of the otherwise vanished Aboriginal peoples of the Riversleigh area. Modern bats important for comparisons with the fossil forms have been provided by Mr L. Hall (Univ. of Queensland), Ms S. Churchill, Ms L. Gibson (Australian Museum), and Dr J. Calaby (C.S.I.R.O.). The scanning electron microscope photographs were taken by Dr M. Dickson (U.N.S.W.). The figures were finally drafted by Ms A. Boyer and Ms J. Taylor. The manuscript was typed by Ms P. Lawry.

LITERATURE

- AGUILAR J.-J., 1982. — Biozonation du Miocene d'Europe occidentale à l'aide des Rongeurs et corrélations avec l'échelle stratigraphique marine. *C.R. Acad. Sci.*, Paris, 294 : 49-54.
- AGUILAR J.-J., BESSEDIK M., CAPPETTA H., MICHAUX J., et SUC J.-P. (*in shed*). — Le climat du Néogène dans le Sud-Est de la France (Provence, Languedoc, Roussillon) d'après l'analyse des faunes (Rongeurs, Sélaciens) et des flores polliniques.
- ARCHER M., 1978. — Australia's oldest bat, a possible rhinolophid. *Proc. R. Soc. Qd.*, 89 : 23, 1 pl.
- ARCHER M., 1981. — A review of the origins and radiations of Australian mammals. Pp. 1437-1488 in *Ecological Biogeography of Australia*. A. Keast edit. Junk, The Hague.
- ARCHER M. and BARTHOLOMAI A. 1978. — *Tertiary mammals of Australia: a synoptic review*. *Alcheringa*

- SIMPSON G.G., 1965. — The Geography of Evolution. *Chilton Book Co.*, Philadelphia.
- TEDFORD R.H., 1966. — Fossil remains from the Tertiary Carl Creek Limestone, northwestern Queensland. *Palaeo. Papers, Bur. Min. Res. Bull.*, 92 : 217-217.
- TURNBULL W.D. and LUNDELIUS E.L., 1970. — The Hamilton fauna, a late Pliocene mammalian fauna from the Grange Burn, Victoria, Australia. *Fieldiana : Geol.*, 19 : 1-163.

CAPTION OF THE PLATES

PLATE 1

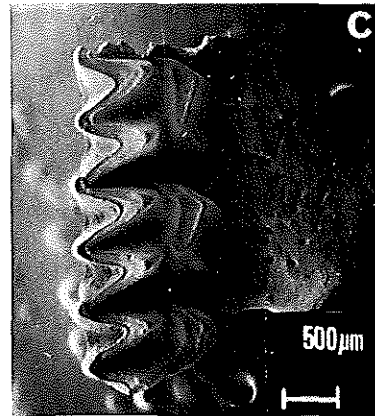
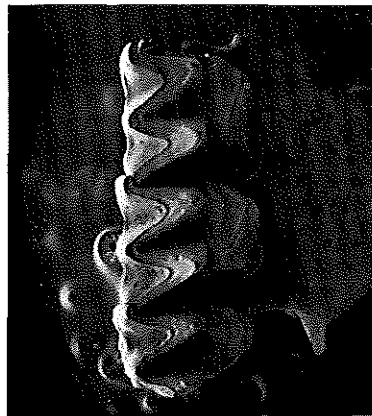
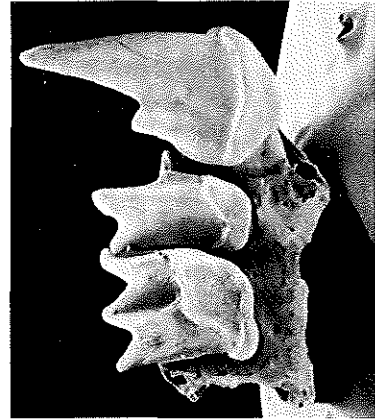
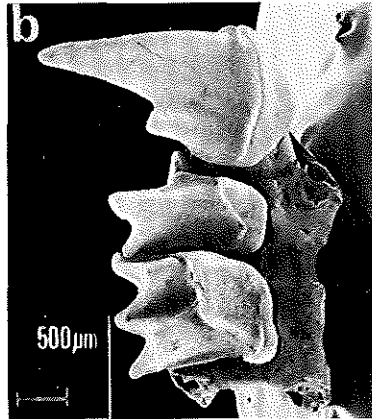
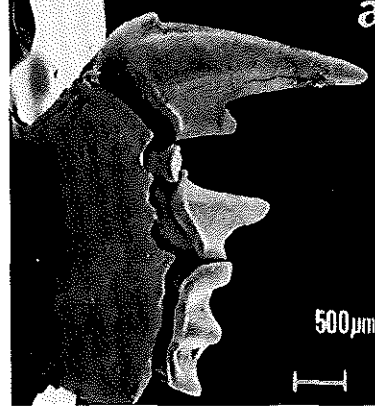
Hipposideros (Brachipposideros) nooraleebus n. sp., Riversleigh Station (northwestern Queensland, Australia).

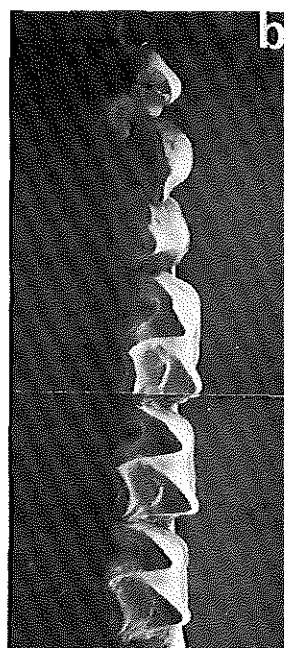
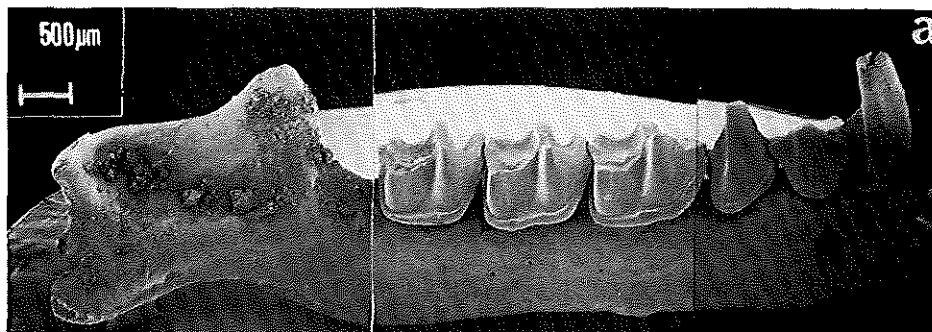
- a. QM F10656, holotype, right maxillary fragment with C1/, P2/, P4/, M1/, buccal view ;
- b. QM F10656, holotype, lingual view ;
- c. QM F10657, paratype, right maxillary fragment with M1-3/, occlusal view.

PLATE 2

Hipposideros (Brachipposideros) nooraleebus n. sp., Riversleigh Station (northwestern Queensland, Australia).

- QM F10658, paratype, right dentary with C/1, P/2, P/4, M/1, M/2, M/3.
- a. buccal view ;
 - b. occlusal view.





PALAEOVERTEBRATA

ERRATA

VOLUME 12, Fascicule 5

Contribution of Bernard Sigé, Suzanne Hand*, and Michael Archer
"An Australian Miocene *Brachipposideros* (Mammalia, Chiroptera) related
to Miocene representatives from France".

- p. 151, § Paratypes, line 3 : QM F 10657
- p. 154, l. 1 : against
- p. 155, last line : M/1-3
- p. 158, l. 22 : is the lowest
- p. 161, l. 17 : peri-mediterranean ones
 l. 26 : *collongensis*
- p. 167, l. 22 : leads us
 l. 32 : data
- p. 170, l. 20 : that continent
 l. 27 : as early as
 l. 34 : increasing
- p. 171, l. 8 : add : Ms. C. Hann
 l. 43 : 372-385
- p. 172, l. 3 : 217-237.

* Present address : School of Biological Sciences, Macquarie University,
North Ryde, New South Wales, Australia 2113