NEW MIOCENE AND PLIOCENE MEGADERMATIDS (MAMMALIA, MICROCHIROPTERA) FROM AUSTRALIA, WITH COMMENTS ON BROADER ASPECTS OF MEGADERMATID EVOLUTION

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ABSTRACT - *Macroderma malugara* nov. sp., a new false vampire from the middle Miocene Gotham City Site of Riversleigh Station in northwestern Queensland, is described and three others discussed. Seven megadermatids are now known from the Australian fossil record. Morphological changes in the Australian *Macroderma* lineage are traced from the Oligo-Miocene to the present. In some Riversleigh deposits, there is evidence for sympatry of very differently-sized megadermatids. Riversleigh megadermatids provide an opportunity to trace an apparent trend to shorten the face in the *Macroderma* lineage from the Oligo-Miocene to the present and to further document a tendency to gigantism in independent megadermatid lineages.

KEY-WORDS : CHIROPTERA, NEW SPECIES, EVOLUTION, MIOCENE, PLIOCENE, AUSTRALIA

RÉSUMÉ - *Macroderma malugara* nov. sp., un nouveau faux vampire du Miocène moyen de Gotham City, Riversleigh Station, Queensland NW, est décrit, et trois autres formes sont discutées. Sept mégadermatidés fossiles sont maintenant connus d'Australie. Les modifications morphologiques dans la lignée australienne de *Macroderma* sont retracées depuis l'Oligo-Miocène jusqu'à l'Actuel. Dans certains dépôts de Riversleigh, la sympatrie de mégadermatidés de différentes tailles est évidente. Les mégadermatidés de Riversleigh montrent une apparente tendance au raccourcissement du museau dans la lignée des *Macroderma* de l'Oligo-Miocène à l'Actuel et, de plus une tendance au gigantisme dans des lignées de Mégadermatidés indépendantes.

MOTS-CLÉS : CHIROPTÈRES, NOUVELLE ESPÈCE, ÉVOLUTION, MIOCÈNE, PLIOCÈNE, AUSTRALIE.

INTRODUCTION

More than 33 new microchiropterans have been identified from Oligo-Miocene and Pliocene freshwater limestone deposits of northwestern Queensland's Riversleigh Station (Archer *et al.* 1989, 1991). Many of these species, including *Hipposideros (Brachipposideros) nooraleebus* SIGÉ, HAND & ARCHER, 1982, are represented by partial skulls, complete dentaries and most postcranial elements. Others are currently known from less complete but nonetheless distinctive remains (e.g. *Petramops creaseri* HAND, 1990) that significantly contribute to the picture of high bat species diversity emerging from study of the Riversleigh fossil mammal faunas (Archer *et al.* 1989, 1991).

Riversleigh Tertiary deposits are particularly rich in the remains of members of the Old World rhino-lophoid families, the Hipposideridae (minimum 12 species) and Megadermatidae (minimum 7 species). Riversleigh fossil hipposiderids (Sigé *et al.* 1982 ; Hand *et al.* 1989 a,b, 1990 ; Hand 1993) are the subject of an extensive study in progress. Two Riversleigh megadermatids (*Macroderma godthelpi* and the Dwornamor Variant) have been previously described (Hand 1985).

In this paper, a new Tertiary megadermatid is described and three others discussed. Morphological changes in the Australian *Macroderma* lineage are traced from the Oligo-Miocene to the present and comments are made on broader aspects of megadermatid evolution.

Dental terminology follows Hand (1985). The prefix QM F____ indicates the fossil collections of the Queensland Museum, Brisbane.

SYSTEMATICS

Order CHIROPTERA Blumenbach, 1779
Suborder MICROCHIROPTERA Dobson, 1875
Superfamily RHINOLOPHOIDEA Weber, 1928
Family MEGADERMATIDAE Allen, 1864

Genus *Macroderma* MILLER, 1907

Macroderma malugara nov. sp.

Holotype (Pl. 48) - Queensland Museum F23611, right maxillary fragment containing P⁴, M¹ and alveolus for P².

Etymology - The species name comes from the local Aboriginal word (Wanyi language) *malugara* meaning a good killer. It alludes to the apparent carnivorous habits of this large megadermatid; the fossil fauna with which *Macroderma malugara* is preserved appears to mainly represent the accumulated remains of its prey.

Paratypes (Pl. 48) - QM F23612, right C₁ ; QM F23613, right P₄; QM F23614, left M₂ ; and QM F23615, right M₂.

Referred material - QM F23616, a large periotic from the Henk's Hollow Local Fauna is tentatively referred to this taxon. By comparison with living and fossil species, this periotic represents a much larger megadermatid than the Henk's Hollow megadermatid described below as megadermatid indet. or the Oligo-Miocene *Macroderma godthelpi* HAND, 1985.It is comparable in size to, but morphologically different from, that of the living *Macroderma gigas* (DOBSON, 1880).

Type locality, age and lithology - The type locality, Gotham City Site (Hand 1990), occurs within the Tertiary sequence of limestones outcropping on Riversleigh Station, northwestern Queensland (Archer *et al.* 1989, 1991). It is situated near the northeastern edge of Ray's Amphitheatre (Archer *et al.* 1989, 1991) at approximately 19.00.88 N, 138.39.07 E (Global Positioning Satellite Device, co-ordinates for Ringtail Site located aproximately 30 metres southwest of Gotham).It is stratigraphically near the top of the System C sequence as defined by Archer *et al.* (1989, 1991). This is interpreted to be stratigraphically higher than Site D (System A containing the Riversleigh Local Fauna ; Archer *et al.* 1991), Microsite (containing the Nooraleeba Local Fauna ; Sigé, Hand & Archer 1982 ; Hand 1993) and Gag Site (near the base of System C, containing the Dwornamor Local Fauna ; Archer & Flannery 1984 ; Hand 1985 ; Archer *et al.* 1991), close to the level of Two Trees Site (containing the Two Trees Local Fauna ; Flannery & Archer 1987) and below the Henk's Hollow Site (Flannery & Archer 1987 ;Archer *et al.* 1989, 1991).
The sediment is a horizontally-bedded, fine-grained argillaceous limestone representing an as yet unnamed formation. It is cur-

rently understood to outcrop over an area of approximately 16 square metres. Vertebrate fossils are concentrated in a 15 centimetre-thick band within the limestone. The fossils are mostly small, fragmentary bones and teeth but include occasional larger, often worn bone fragments.
On the basis of its stratigraphic position and mammal fauna (Hand 1990), the Gotham City deposit is interpreted to be middle Miocene in age and slightly younger than the South Australian Kutjamarpu Local Fauna (Woodburne *et al.* 1985) but older than the Riversleigh Jaw Junction and Northern Territory late Miocene Alcoota Local Faunas (Woodburne *et al.* 1985 ; Archer *et al.* 1989, 1991).

Associated fauna and taphonomy - The nature of the Gotham City deposit and fauna has been discussed previously (Hand 1990). Preserved in the deposit are the remains of small teleost fish, tiny lungfish, frogs, lizards, small freshwater crocodiles and turtles, a passerine bird, dasyurids, peramelids, petaurids, pseudocheirids, acrobatids, a phalangerid, a diminutive phascolarctid, a potoroid, four hipposiderids and the molossid *Petramops creaseri* (HAND, 1990). Some of the mammal species are shared with contemporaneous Riversleigh deposits, but others are unique to Gotham City and, judging by the size and fragmentation of the material, probably represent the remains of prey brought from adjacent habitats by *Macroderma malugara*. Larger, worn bone fragments representing large turtles, a balungamayine potoroid, a zygomaturine and a possible *Wakaleo* species may have been washed into the limestone roost during changes in the level of the water table. Boids and some of the hipposiderids probably co-habited the megadermatid roost as they commonly do today.

Diagnosis - This fossil species differs from Recent populations of Australia's only living megadermatid, *Macroderma gigas*, in its retention of P², its double infraorbital foramina, its less well-developed heels on P⁴ and M¹ and parastyle on P⁴, its M¹ with strongly-developed anterior cingulum and heel with lingual cingular cusp, its less posteriorly-recurved anterior cutting crests on P⁴, its more reduced and buccally-situated M₂ metaconid, its broader and more robust M₂ cingulum, its very poorly-developed and less posteriorly-situated M₂ hypoconulid, its less anteroposteriorly-compressed M₂ talonid, its less lingually-open M₂ talonid with better-developed pre-entocristid and its tall but much less posterolingually-extended C₁ that lacks an anterolingual cingular cusp. It differs from the Pliocene Wellington Caves species, *Macroderma koppa* (Hand *et al.* 1988), in its retention of P², its smaller size, its less well-developed heels on P⁴ and M¹ and parastyle on

PLATE 48

Macroderma malugara nov. sp. from Gotham City Site, Riversleigh Station, northwestern Queensland. Holotype, QM F23611, a right maxillary fragment with P⁴, M¹ and alveolus for P². **A**, buccal view ; **B-B'**, stereopairs, occlusal-oblique view ; **D-D'**, stereopairs, occusal view. Paratypes : QM F23612-23615. QM F23612, a right C₁ : **C-C'**, stereopairs, occlusal view ; **E**, lingual view. QM F23613, a right P₄ : **F**, buccal view ; **G**, lingual view ; **H-H'**, stereopairs, occlusal view. QM F23614, a left M₂ : **I-I'**, stereopairs, occlusal view ; **J**, buccal view. QM F23615, a right M₂ : **K**, buccal view ; **L**, lingual view; **M-M'**, stereopairs, occlusal view. Scale = 1mm. *Fragment de maxillaire droit avec , P⁴, M¹ et l'alvéole de P². A, vue buccale ; B-B', vues occlusales obliques en stéréo. D-D', vues stéréo de la surface occlusale. Paratypes : C₁ droite. C-C', vues stéréo de la surface occlusale. E, vue linguale. P₄ droite, vue buccale. G, vue linguale. H-H', vue stéréo de la surface occlusale M₂ droite, K, vue buccale. L, vue linguale. M-M', vue stéréo de la surface occlusale.*
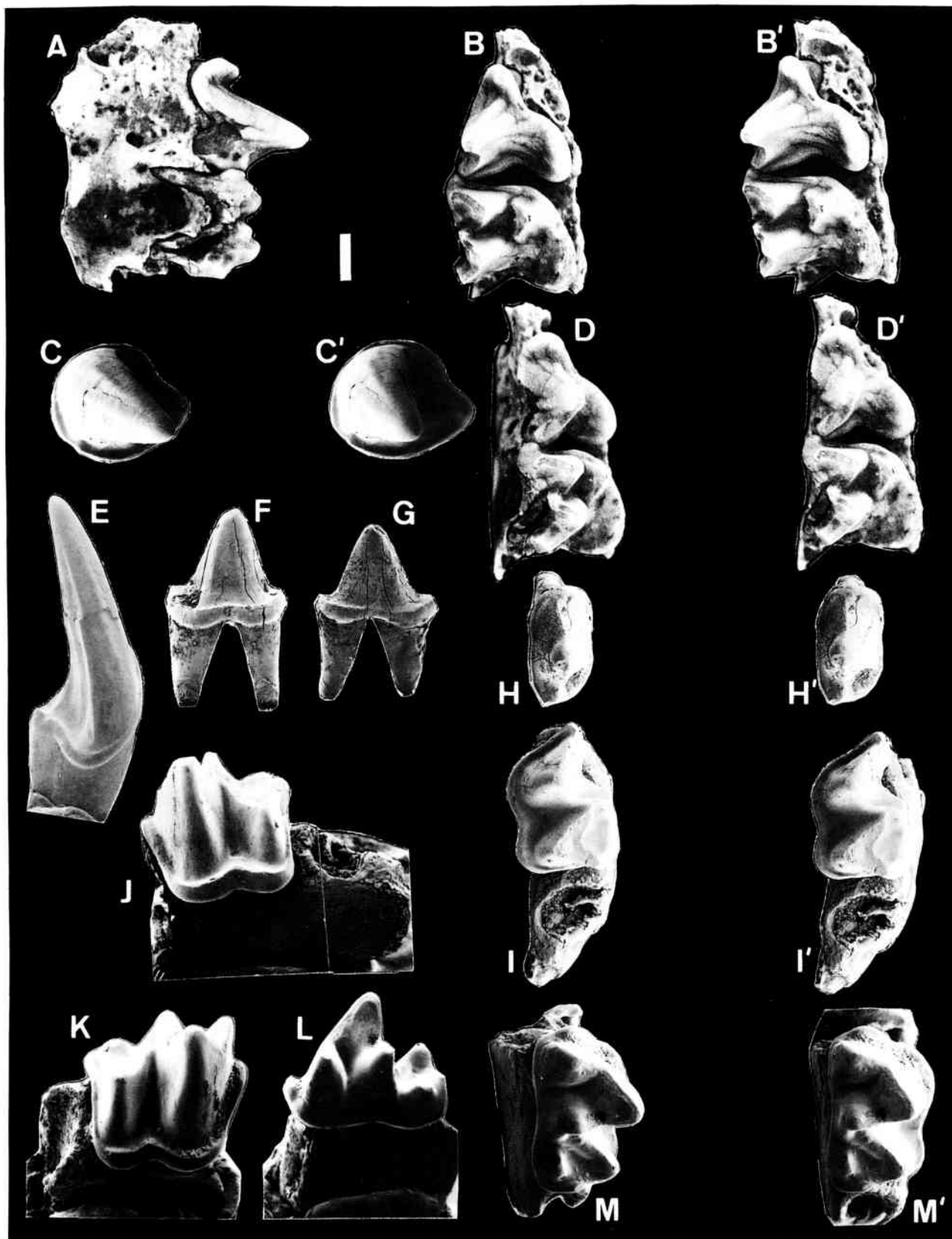
P⁴, its M¹ heel with distinct lingual cingular cusp, its less posteriorly-recurved anterior cutting crest on P⁴, its much less well-developed P⁴ posterior cingulum and lingual cingular cusp, its P⁴ with postero-lingual groove or depression only weakly developed, its broader M₂ anterior cingulum, its very poorly developed and less posteriorly-situated M₂ hypoconulid, its better-developed pre-entocristid, its more reduced and buccally-situated M₂ metaconid and its much less posterolingually-extended C₁ that lacks an anterolingual cingular cusp. It differs from the Riversleigh middle Miocene species, *Macroderma godthelpi* (HAND, 1985), in its much larger size, its taller crowned teeth, its smaller and more lingually-situated P², its better-developed heel on P⁴ and lingual cingular cusp on M¹, its more robust and broad anterior cingulum on M₂, its more anteroposteriorly-compressed talonid and its complete cingulum on C₁.

Description - The only maxillary fragment is the holotype QM F23611 which preserves part of the cheek region. Two infraorbital foramina are exhibited. The anterior foramen is large and opens onto the cheek with a fossa developed above the anterior end of P⁴. A second, much smaller and more posterior fossa is developed in a position above the posterior root of P⁴. This appears to lead to a second foramen that penetrates the maxilla, possibly for a lateral branch of the trigeminal or facial nerve. The anterior fossa is directed anteriorly ; the smaller fossa appears to lead more anteroventrally. The upper dentition is known from the holotype, QM F23611. The P² is represented by a single alveolus. It appears to have been a very small, single-rooted

tooth that occurred on the lingual side of the tooth row immediately anterolingual to the anterior cingular cusp of P⁴.

The P⁴ is represented by a complete tooth in QM F23611. This tooth is remarkably similar in morphology to its counterpart in *Macroderma gigas* but in contrast has an almost complete anterobuccal and lingual cingulum. (The tooth is fractured such that the posterobuccal cingulum is not preserved.) The posterior cingulum merges smoothly with the extended heel rather than meeting its buccal edge at an angle. This apparently reflects the more lingual (rather than posterior) direction of heel development in *M. malugara*. The heel, although large, is less well-developed than in *M. gigas*. A lingual cingular cusp is only very faintly developed and there is little parastylar development. The anterior cutting crest of the paracone is less posteriorly-recurved.

The M¹ is known from the nearly-complete RM¹ of the holotype QM F23611. It is very similar in morphology to that tooth in *M. gigas* (HAND, 1985, fig. 16) but differs in its shorter, broader and generally less well-developed heel and its very pronounced lingual cusp.

The lower dentition is known from four teeth : a lower canine, a right P₄ and two specimens of M₂ in dentary fragments. The lower canine is represented by an isolated, right C₁, QM F23612. It is similar to C₁ in *M. gigas* but the posteriorly-extended heel is less well-developed so that its basal crown area is smaller than that in *M. gigas*. The basal cingulum is complete and well-defined. Unlike *M. gigas*, there

TABLE 1 - Measurements (mm) of the holotype (QM F23611) and paratypes (QM F23612-23615) of *Macroderma malugara* nov. sp. from the Miocene Gotham City Site, Riversleigh Station, northwestern Queensland. *Mensurations (mm) de l'holotype et des paratypes de* Macroderma malugara *nov. sp. du Miocène de Gotham City, Riversleigh Station, Queensland NW.*

	Holotype	Paratypes			
	QM F23611	QM F23612	QM F23613	QM F23614	QM F23615
P⁴ buccal length	3.35				
P⁴ lingual length	3.20				
P⁴ width	3.15				
M¹ width	4.14				
C₁ length		2.99			
C₁ width		2.77			
C₁ height (He)		7.18			
C₁ height (Hi)		6.50			
P₄ length			2.72		
P₄ anterior cingulum to protoconid length			1.23		
P₄ width			1.55		
M₂ length (in situ)				3.44	3.60
M₂ trigonid length				1.99	2.17
M₂ talonid length				1.46	1.42
M₂ trigonid width				2.27	2.61
M₂ talonid width				2.21	2.45

is no development of an anterolingual cingular cusp adjacent to where the outer lower incisor would abut.

The P_4 is represented by a complete, isolated tooth, QM F23613. This tooth is laterally compressed as in *M. gigas*, but is relatively smaller. Lower molars are known from a left and right M_2 (QM F23614 and QM F23615 respectively). The morphology of M_2 in *M. malugara* differs from that of *M. gigas* in its more reduced and buccally-situated metaconid and its less anteroposteriorly-compressed talonid. The hypoconulid is less well-developed and less posteriorly-situated. The talonid is less open lingually, its pre-entocristid extending further anteriorly and being better-developed. The cingulum is broader and more robust, particularly anteriorly. Fragments of dentaries associated with these teeth confirm that they are M_2's but provide little additional information. Measurements of the holotype and paratypes of *Macroderma malugara* nov. sp. are given in Table 1.

Macroderma gigas (DOBSON, 1880)
Fig. 1

Referred material - QM F23560, a partial skull with P^4, M^1, M^2 and M^3 and single infraorbital foramen ; QM F23561, a dentary containing P_4, M_{1-3} and alveoli for I_{1-2} and P_2 ; QM F23562, maxillary fragment with P^4, M^1 and M^2 and two infraorbital foramina; QM F23563, maxillary fragment with P^4-M^3 ; QM F23578, distal end of humerus ; QM F23579, proximal end of ulnar ; QM F23580, partially erupted M_2 ; QM F23590, periotic.

Locality, lithology and age - Rackham's Roost Site (Godthelp 1988 ; Archer *et al.* 1989, 1991) occurs at 19.02.09 N, 138.41.60 E (Global Positioning Satellite Device) on Riversleigh Station, northwestern Queensland. It appears to represent the indurated floor of a long, narrow cave developed in Cambrian Thorntonia Limestone. At one end, the cave evidently opened onto a vertical cliff flanking what is now the Gregory River. More than 50 metres away in the opposite direction, another larger, lower opening appears to have been developed. The sediment is a breccia of tiny, mostly fragmented bones and teeth set in a fine-grained, pink-coloured (presumably iron-stained) limestone. The deposit covers an area of approximately 200 square metres, with a maximum depth of 0.5 to 1.0 metre. On the basis of its mammal fauna, the Rackham's Roost deposit is interpreted to be early to middle Pliocene in age. It contains abundant plesiomorphic murids (at least 12 species) and a macropodid similar to *Protemnodon snewini* BARTHOLOMAI, 1978 from the early Pliocene Bluff Downs Local Fauna of northeastern Queensland (Archer & Wade 1976).

Associated fauna and taphonomy - This species occurs in the Rackham's Roost deposit with fragmentary remains of crustaceans, frogs, lizards, small crocodiles, birds, dasyurids, peramelids, a pseudocheirid, an extinct macropodid and potoroid, at least 12 murids, an emballonurid, four hipposiderids, four vespertilionids and a second, tiny megadermatid (Archer *et al.* 1991; Hand 1987, 1995). The very finely broken remains of the small vertebrates and depressed fractures and impressions in the bones characteristic of Recent *Macroderma gigas* canines suggest that the deposit represents the remains of prey accumulated by this species. Boids, the emballonurid, hipposiderids and vespertilionids probably co-habited the megadermatid roost.

Comments - Specimens of *Macroderma gigas* so far recovered from the Rackham's Roost deposit (e.g. QM F23560-23562) are relatively small (Table 2), being much closer in size to small representatives from Recent *M. gigas* populations such as Pine Creek, Camooweal, the Kimberley Range, the Pilbara and Groote Eylandt (Hand & York 1990) than to large individuals from, for example, existing Cape York and Rockhampton populations. They appear to be much smaller than large individuals of *M. gigas* collected as subfossils from the McDonnell and Flinders Ranges and fossils from Pleistocene deposits in southwestern Western Australia (Hand & York 1990).

Small size in the Rackham's Roost *Macroderma* population is perhaps most evident in skull and dentary characters such as palate length and den-
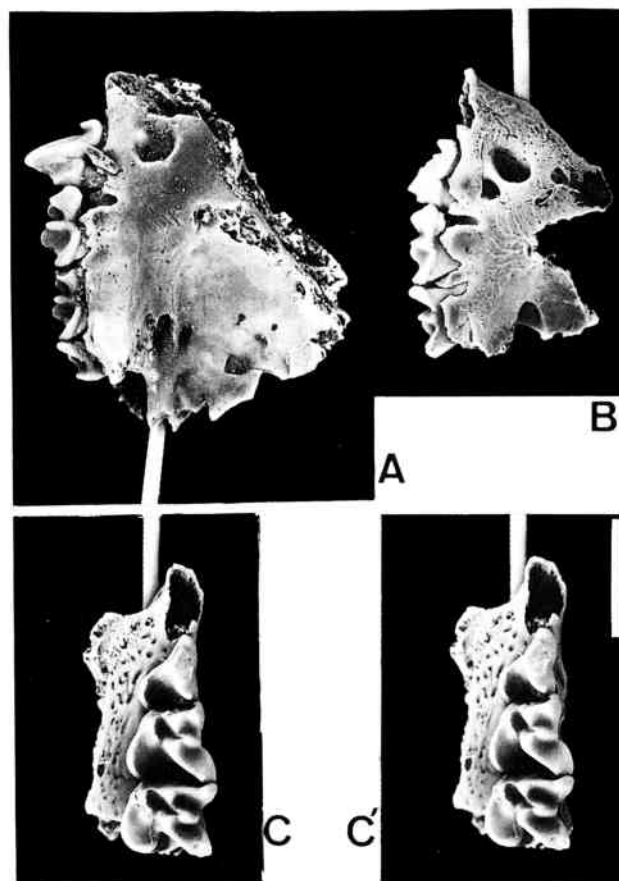

FIGURE 1 - Specimens of *Macroderma gigas* recovered from Rackham's Roost Site, Riversleigh Station. **A**, QM F23560, a partial skull with P^4, M^1, M^2 and M^3 and single infraorbital foramen: lateral view. QM F23562, maxillary fragment with P^4, M^1 and M^2 and two infraorbital foramina : **B**, lateral view ; **C-C'**, stereopairs, occlusal view. Scale = 5 mm. *A, crâne incomplet avec P^4, M^1, M^2 et M^3 et un foramen infraorbitaire unique : vue latérale. QM, fragment de maxillaire avec P^4, M^1 et M^2 et 2 foramens infraorbitaires. B, vue latérale. C-C', vues stéréo de la surface occlusale.*

tary length and depth (compare Table 2 and Hand & York 1990, table 2), but too few individuals have been collected to determine whether they are significantly smaller in these features than Quaternary specimens. Preliminary study suggests that measurable characters that are most variable in Quaternary specimens of *M. gigas* (e.g. lower tooth widths and lengths) are less variable in the Rackham's Roost population. At least one character that appears to be fixed in Quaternary populations of *M. gigas*, however, seems to be variable in the Rackham's Roost population. While in most Rackham's Roost specimens (n=5), as in Quaternary *M. gigas*, a single infraorbital foramen on the facial side of the maxilla is exhibited (Fig. 1A), in a sixth Rackham's Roost specimen (QM F23562, which otherwise appears to be morphologically identical ; Fig. 1B-C') there are two infraorbital foramina. In this specimen, the fossa for the second foramen is much larger than that described above for the Miocene *Macroderma malugara* nov. sp. or that in the Miocene *M. godthelpi* (Hand 1985), being closer in size to that of the Pliocene Wellington Caves *M. koppa* (HAND *et al.* 1988). In position, the posterior fossa is much closer to the large anterior fossa than it is in *M. godthelpi, M. malugara* or *M. koppa*. Variation in the number of infraorbital foramina exhibited by Rackham's Roost megadermatids is attributed here to intraspecific variation in *M. gigas*. This feature is, however, invariant in all other known *M. gigas* populations. It is therefore possible that the Rackham's Roost maxilla which exhibits two infraorbital foramina may represent a parent species for *M. gigas*, perhaps closely related to *M. koppa* and/or *M. malugara*. However, its size and all other aspects of its morphology suggest that this maxilla represents either an aberrant specimen of *M. gigas* or morphological variation in an early population of *M. gigas* (see Discussion).

Macroderma sp.
Fig. 2A-A'

A right M^2, QM F23617, appears to represent a small species of *Macroderma* from the middle Miocene Henk's Hollow Local Fauna (Flannery and Archer 1987 ; Archer *et al.* 1989, 1991). Although less than two thirds the size of the middle Miocene *M. godthelpi* (HAND, 1985) from the Nooraleeba and Dwornamor Local Faunas (Archer *et al.* 1989), it is very similar in overall morphology to this species, differing noticeably, apart from size, only in the shortness of its anterior cingulum and perhaps a slight indentation in occlusal crown outline at the base of the protocone. It differs strikingly from *M. gigas* and *M. koppa* HAND, DAWSON & AUGEE, 1988 in among other features its small size.

	QM F23560	QM F23562
Palatal length	8.80	
P^4-M^3	10.75	
M^1-M^3	8.01	
P^4 buccal length	3.00	3.05
M^1 buccal length	3.36	3.52
M^2 buccal length	3.27	3.57
M^3 buccal length	1.81	
P^4 lingual length	3.21	3.47
M^1 lingual length	3.59	3.85
M^2 lingual length	3.33	3.73
P^4 width	2.51	2.60
M^1 width	3.43	3.94
M^2 width	3.54	4.17
M^3 width	3.38	

	QM F23561
Condylo-canine length	25.00
Dentary depth below M_2 protoconid	3.45
C_1-M_3	15.65
P_4-M_3	11.63
M_1-M_3	9.25
P_4 length	2.53
P_4 anterior cingulum to protoconid	1.43
M_1 length (in situ)	3.31
M_2 length (in situ)	3.27
M_3 length (in situ)	3.00
M_1 trigonid length	2.09
M_1 talonid length	1.12
M_2 trigonid length	2.10
M_2 talonid length	1.19
M_3 trigonid length	1.93
M_3 talonid length	1.03
P_4 width	1.62
M_1 trigonid width	2.02
M_1 talonid width	1.96
M_2 trigonid width	2.26
M_2 talonid width	2.02
M_3 trigonid width	2.18
M_3 talonid width	1.72

TABLE 2 - Measurements (mm) of upper and lower teeth of Rackham's Roost specimens of *Macroderma gigas*. (See Hand & York 1990 for explanation of measures.) *Mensurations (mm) des dents supérieures et inférieures des spécimens de* Macroderma gigas.

Megadermatid indet.
Fig. 2B-D

A left M_1 QM F23618, from the middle Miocene Henk's Hollow Local Fauna, appears to represent a very small megadermatid whose affinities probably lie outside the Australian *Macroderma* lineage. This lower molar is similar in size to the upper molar from Henk's Hollow referred to above as *Macroderma* sp. However, a number of features appear to prohibit inclusion of this taxon in
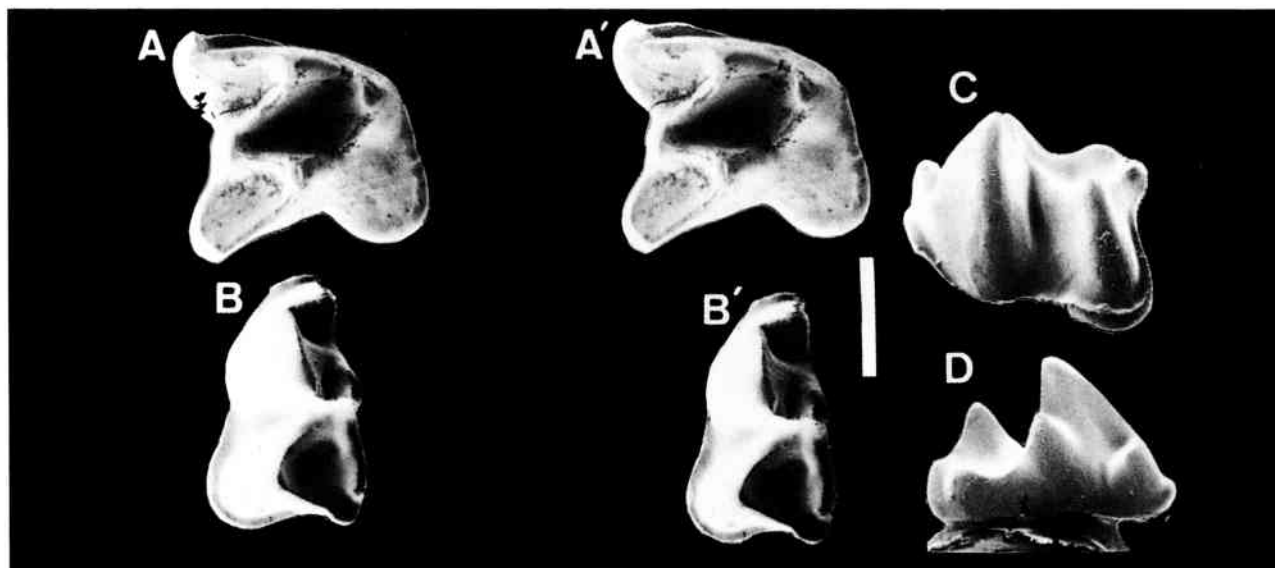
FIGURE 2 - *Macroderma* sp. from Henk's Hollow Site, Riversleigh Station, QM F23617, a right M² : **A-A'**, stereopairs, occlusal view. Megadermatid indet. from Henk's Hollow, QM F23618, b left M₁ : **B-B'**, stereopairs, occlusal view ; **C**, buccal view ; **D**, lingual view. Scale = 1 mm. *M² droite : A-A', vues stéréo de la surface occlusale. M₁ gauche : B-B, vues stéréo de la surface occlusale. C, vue buccale. D, vue linguale.*

Macroderma. Features of the M₁ shared with other megadermatids include : nyctalodonty (as defined by Menu & Sigé 1971) ; laterally-compressed trigonid and anteroposteriorly-compressed talonid ; reduced paraconid, the paracristid being much longer than the metacristid ; and twinned entoconid and hypoconulid. Features that appear to exclude it from the Australian genus *Macroderma* include its gracile cingulum and the unique development of its pre-entocristid which lingually walls the talonid basin in a manner not unlike that in the living African megadermatid *Lavia frons* (see Hand 1985, fig. 18). Features that distinguish the Henk's Hollow M₁ from its counterpart in *L. frons* include its markedly compressed trigonid and talonid.

DISCUSSION

PHYLOGENETIC RELATIONSHIPS

Seven megadermatids are now known from the Riversleigh Tertiary deposits (Table 3). The oldest are the Oligo-Miocene *Macroderma godthelpi* from the Nooraleeba and Dwornamor Local Faunas and the Dwornamor Variant from the Dwornamor Local Fauna (Hand 1985 ; Archer *et al*. 1989, 1991). Representatives of the *Macroderma* lineage now appear to also include (apart from the living Ghost Bat *M. gigas*) the later middle Miocene Gotham *M.*

malugara nov. sp. and Henk's Hollow *Macroderma* sp., and the Pliocene Wellington Caves *M. koppa*. The genus *Megaderma* GEOFFROY, 1810 is represented in Australia for the first time by a tiny new species from the Pliocene Rackham's Roost deposit (Hand 1995). Another new megadermatid whose dental morphology appears to place it outside both the *Macroderma* and *Megaderma* lineages, is represented by an isolated M₁ from the later middle Miocene Henk's Hollow Local Fauna.

A phylogenetic hypothesis based on shared-derived character states involving all adequately-represented fossil and living megadermatids was given by Hand (1985 ; and see Hand *et al*. 1988). In that hypothesis, species of *Macroderma* were interpreted to be the most derived megadermatids and *Lavia frons* the most plesiomorphous of living megadermatids. The French fossil *Necromantis adichaster* was considered to be the most plesiomorphous member of the Megadermatidae. *Macroderma* species formed a clade with *Lyroderma* species, *Megaderma* species formed its sister-group, and *Cardioderma cor* was the sister-group of a *Megaderma-Lyroderma-Macroderma* clade.

Sigé (1976) also regarded the dentition of *Lavia frons* to be "peu évoluée" with respect to other living megadermatids and excluded it from a group in which he placed *Macroderma gigas, Megaderma spasma, M. lyra* and *Cardioderma cor* megaderma-

tids he described as having "denture morphologiquement évoluée".

Griffiths *et al.* (1992), however, reached contradictory conclusions on the basis of a cladistic analysis of hyoid morphology in living megadermatids. In that analysis, *Macroderma gigas* is interpreted to be the most plesiomorphous and *Lavia frons* the most apomorphous of living megadermatids. The phylogenetic positions of species of *Cardioderma* and *Megaderma* (including *Lyroderma*) are, as pointed out by Griffiths *et al.*, not very different in the models of Hand and Griffiths *et al.* In both, species of *Megaderma* are considered relatively derived and *Cardioderma cor* intermediate in the cladogram.

If Griffiths *et al.*'s interpretation is correct, then the polarity of dental characters used by, among others, Sigé (1976) and Hand (1985) is in doubt. However, for the dental characters to concord with Griffith *et al.*'s cladogram, an unacceptable amount of homoplasy would be required. For example, if transverse compression of the M_1 trigonid is considered to be the result of homoplasy rather than a synapomorphy for most megadermatids then it must be hypothesised that its absence in *Lavia frons* represents a reversal event, or that it has been independently acquired in megadermatids several times. This would be true also for a number of other characters that are diagnostic for most megadermatids except *Lavia frons* (e.g. reduction in the pre-entocristid to open the talonid basin in M_{1-3}) and are not found in the potential sister-groups nycterids, rhinolophids, emballonurids or rhinopomatids. This is by no means impossible but it is less parsimonious.

On the basis of fossil material and characters available for study, the majority of Australian Tertiary megadermatids appear referable to a clade (Fig. 3) which also includes *Macroderma gigas*, and are referred here to that genus. A combination of features appears to define this clade : a massively-rooted, posteriorly-recurved C^1 with tall, slender, dominant main cusp and large posterior accessory cusp well-separated from the paracone but occurring within the cingular rim and a well-developed anterolingual cingular cusp ; enlarged heels on P^4-M^2 ; only moderately elongate postmetacristae on M^{1-2} ; lower molars with laterally-compressed trigonid, anteroposteriorly-compressed talonid, reduced paraconid with the paracristid longer than the metacristid (although both crests are relatively transversely oriented), twinned entoconid and hypoconulid, reduced pre-entocristid such that the talonid is open lingually, reduced metaconid contribution to the cristid obliqua, and robust, continuous anterior, buccal and posterior cingula.

It is noteworthy that species of *Macroderma* tend to be large in absolute size and apparent synapomorphies for the clade include an exaggeration of fea-

	Oligo-Miocene				Pliocene		Quat
	Microsite, Riv.	Gag Site, Riv.	Gotham City Site, Riv.	Henk's Hollow Site, Riv.	Big Sink, Wellington C.	Rackham's Roost Site, Riv.	Australia, many sites
Macroderma gigas						x	x
Macroderma koppa					x		
Megaderma richardsi						x	
Megadermatid indet.				x			
Macroderma sp.				x			
Macroderma malugara			x				
Dwornamor Variant		x					
Macroderma godthelpi	x	x					

TABLE 3 - Distribution of megadermatids in Australian fossil deposits. Abbreviations : Riv., Riversleigh Station, Queensland ; Wellington C., Wellington Caves, New South Wales ; Quat, Pleistocene and Recent. Sites are shown (left to right) in probable stratigraphic sequence (i.e decreasing age) following Archer *et al.* (1991). *Répartition des mégadermatidés dans les sédiments fossiles d'Australie. Les gisements sont rangés de la gauche vers la droite dans l'ordre stratigraphique probable.*

tures exhibited to varying degrees in other megadermatids (e.g. very enlarged heels on P^4-M^2, a very tall, prominent paracone on C^1, and robust cingula on the lower molars). It is possible that such characters may be the result of allometry rather than phylogeny, but they are not all present to the same degree in large non-Australian taxa such as the Miocene European and North African *Megaderma gaillardi* (TROUESSART, 1898) and *M. brailloni* SIGÉ, 1968.

Within the Australian radiation, *Macroderma malugara* shares a number of apparent synapomorphies with the Pliocene species *M. koppa* and Pliocene to Recent *M. gigas* that are not shared with the older Dwornamor *M. godthelpi* (Fig. 3). These include large size, taller-crowned teeth, well-developed P^4 heel and more anteroposteriorly-compressed talonid. There is nothing known about *M. godthelpi* that would exclude it from the ancestry of *M. malugara*.

The evolutionary relationships of the poorly-known middle Miocene *Macroderma* sp. and megaderma-

tid indet. from Henk's Hollow Site are unclear. However, with species of *Megaderma, Lyroderma* and *Macroderma,* megadermatid indet. shares a markedly laterally-compressed trigonid while lacking the extreme degree of anteroposterior compression of the talonid exhibited by species of *Lyroderma* and *Macroderma.* In the development of its pre-entocristid, it more closely resembles the primitive African megadermatid *Lavia frons* (but it is possible that the derived condition of this character may have been autapomorphically lost in the Henk's Hollow animal). Although this megadermatid appears to lie outside the *Macroderma* lineage, neither can it be positively referred to the lineage represented in Australia by the middle Miocene Dwornamor Variant.

MORPHOLOGICAL TRENDS IN TERTIARY MEGADERMATIDS

In the Australian megadermatid radiation, three distinctly differently-sized species are now known from both the Oligo-Miocene and the Pliocene. Represented in the Australian Oligo-Miocene are the small Henk's Hollow *Macroderma* sp., the inter-

mediate Dwornamor *M. godthelpi* and the large Gotham *M. malguara.* Known from the Pliocene are a tiny megadermatid (Hand 1987 ; 1995), the larger Rackham's Roost *Macroderma gigas* and the very large *M. koppa* from Wellington Caves, New South Wales.

Sigé (1976) has suggested that in megadermatids a trend to gigantism may have occurred in a number of separate lineages (e.g. the middle Tertiary
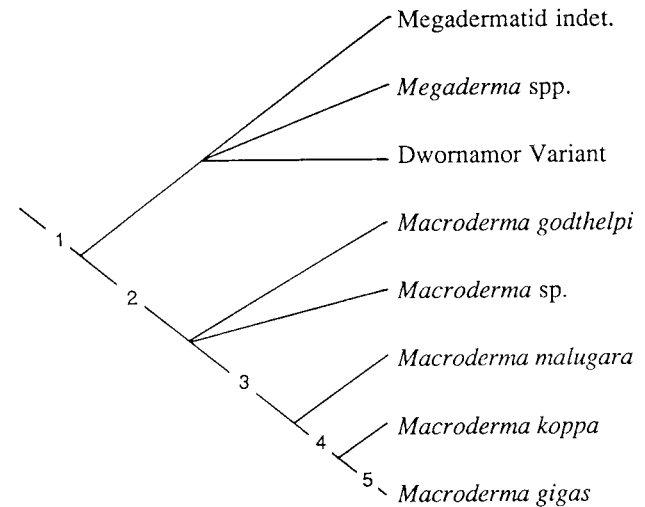
*Hypothèses phylogéniques sur les relations de mégadermatidés fossiles de Riversleigh avec les autres mégadermatidés à partir des caractères dérivés partagés ; les hipposidéridés (*Hipposideros ater*) sont pris comme extra-groupe (voir aussi Sigé 1976 ; Hand 1985 ; Hand et al. 1988 ; Hand 1995). Apomorphies possibles : 1, longueur de M₁ plus courte ou égale à celle de M₂ ; trigonide de M₁ comprimé latéralement, paraconide réduit avec paracristide beaucoup plus long que métacristide ; pré-entocristide de M₁₋₃ court (interrompu) si bien que le bassin du talonide est ouvert lingualement ; talonide comprimé antéro-postérieurement ; C¹ avec un tubercule accessoire postérieur haut, généralement en forme de lame ; M¹⁻² à paracone réduit, métacone massif, mésostyle déplacé lingualement et post-metacrista allongée. 2, C¹ avec un tubercule accessoire postérieur conique relativement court, bien séparé du paracone mais inclus dans la bordure cingulaire et avec un tubercule cingulaire antéro-lingual bien développé ; P⁴ et M¹⁻² avec un talon allongé ; P⁴ haute avec tubercule principal en position buccale ; M¹⁻² avec large bordure buccale et mésostyle nettement déplacé lingualement mais post metacristae modérément allongées ; compression antéro-postérieure du talonide de M₁₋₃ plus poussée ; paracristide plus long que métacristide mais les deux crêtes orientées relativement transversalement, contribution réduite du métaconide à la crista obliqua ; cingulum antérieur, buccal et postérieur robustes et continus. 3, dents de grande taille, à couronne haute ; P² plus petite et située lingualement ; talon de P⁴ plus large ; C₁ avec cingulum complet ; compression antéro-postérieure supplémentaire des talonides de M₁₋₃ ; cingulum antérieur robuste et large. 4, P² disparue ; talons de P⁴ et M¹ encore plus développés ; P⁴ avec parastyle et crête antérieure coupante plus recourbée postérieurement ; C₁ nettement étirée postéro-lingualement et avec un tubercule cingulaire antéro-lingual ; M₁₋₂ plus grande, avec un hypoconulide situé plus postérieurement et le préentocristide encore plus réduit. 5, foramen infra-orbitaire unique (populations quaternaires) ; bouclier frontal bien développé ; C¹ avec une flexure de compression antéro-postérieure prononcée ; P⁴ plus courte et à couronne plus haute ; talonides de M₁₋₃ encore plus comprimés antéro-postérieurement. Les relations phylogéniques du Mégadermatidé indet. de Riversleigh, du variant de Dwornamor et de* Macroderma *sp. restent incertaines.*

FIGURE 3 - Hypothesis of phylogenetic relationships of Riversleigh fossil megadermatids to other megadermatids based on shared-derived dental character states using hipposiderids (e.g. *Hipposideros ater*) as an outgroup (see also Sigé 1976 ; Hand 1985 ; Hand et al. 1988 ; Hand 1995). Potential apomorphies include : **1**, M₁ shorter than or equal in length to M₂, M₁ trigonid laterally compressed, paraconid reduced with paracristid much longer than metacristid, M₁₋₃ pre-entocristid short (disrupted) so that talonid basin drains lingually, talonid anteroposteriorly compressed, C¹ with tall, usually blade-like posterior accessory cusp, M¹⁻² with reduced paracone and massive metacone, lingually displaced mesostyle and elongated postmetacrista ; **2**, C¹ with relatively short, conical posterior accessory cusp well-separated from the paracone but occurring within the cingular rim and with well-developed anterolingual cingular cusp, P⁴ and M¹⁻²with elongated heel, tall P⁴ with buccally situated main cusp, M¹⁻² with broad buccal shelf and markedly lingually displaced mesostyle but only moderately elongate postmetacristae, further anteroposterior compression of M₁₋₃ talonid, paracristid longer than metacristid but both crests relatively transversely oriented, reduced metaconid contribution to the cristid obliqua, robust, continuous anterior, buccal and posterior cingula ; **3**, large size, tall crowned teeth, P² smaller and lingually situated, P⁴ heel larger, C₁ with complete cingulum, M₁₋₃ further anteroposterior compression of talonid, robust and broad anterior cingulum ; **4**, P² lost, P⁴ and M¹ heels further expanded, P⁴ with parastyle and more posteriorly-recurved anterior cutting crest, C₁ markedly posterolingually-extended and with anterolingual cingular cusp, M₁₋₂ larger and more posteriorly-situated hypoconulid and pre-entocristid further reduced ; **5**, single infraorbital foramen (Quaternary populations), frontal shield well developed, C¹ with pronounced anteroposterior compressional flexure, P⁴ shorter and higher crowned, M₁₋₃ talonids further compressed anteroposteriorly. The phylogenetic relationships of Riversleigh's Megadermatid indet., Dwornamor Variant and *Macroderma* sp. remain unclear

Megaderma gaillardi and *Megaderma lugdunensis* (DEPERET, 1892) species groups). If the phylogenetic hypothesis based on the character analysis of Hand (1985) reflects actual phylogeny, then large size has also been acquired independently in Australian megadermatids. At least some Australian taxa increased in size (e.g. *Macroderma koppa*) while others such as the tiny Rackham's Roost megadermatid became very small.

In the later middle Miocene Henk's Hollow and the Pliocene Rackham's Roost deposits, there is evidence for sympatry of very differently-sized megadermatids (i.e. greater than 30% difference). A comparable difference in size in contemporaneous fossil megadermatids is seen in the middle Miocene Beni Mellal Local Fauna of Morocco with the large *Megaderma gaillardi* and very small *M. jaegeri* (SIGÉ, 1976). Presumably, this difference in size of sympatric carnivorous megadermatids relates to competition for resources. While there is little obvious increase in carnassialization in very large forms, an evident increase in the crushing component of the dentition may reflect an important shift in diet. In the Riversleigh Dwornamor Local Fauna, two similarly-sized sympatric megadermatids (*M. godthelpi* and the Dwornamor Variant) are referable to two separate lineages. Living non-Australian megadermatids that exist sympatrically over part of their range are either significantly different in size (e.g. the Asian *Megaderma spasma* and *Lyroderma lyra* ; av. 25g vs 50g, Lekagul & Mc Neely 1977) or represent two distinct lineages (e.g. the African *Lavia frons* and *Cardioderma cor* ; Hand 1985 ; also Griffiths *et al.* 1992). The latter in each of these species pairs consumes significantly more vertebrate prey than the other (Brosset 1962; Wickler & Uhrig 1969 ; Kingdon 1974 ; Vaughan 1976 ; Advani 1981 ; Advani & Makwana 1981).

Another general trend in megadermatid lineages, evident also in the Australian *Macroderma* lineage, involves marked shortening of the face and tooth row. Brachycephaly of this kind is even evident in the oldest known megadermatid, the French early Tertiary short-faced *Necromantis adichaster* REVILLIOD, 1922. Megadermatids are distinguished from other bats by the following combination of cranial and dental characters associated with a shortening of the face : almost complete loss of the premaxillaries ; loss of the upper incisors ; reduction of the lower incisors ; anteroposterior compression of M_1 such that it is shorter than or equal in length to M_2 ; anteroposterior compression of the talonids of M_{1-3} ; marked reduction of M_3 ; reduction in the number of premolars to a maximum of two in the upper and lower tooth rows (*N. adichaster* retains a tiny P_3) ; and posterior extension of the palate lingual to M^3 presumably for compensatory support (see below).

Although carnivorous bats have been described (e.g. Freeman 1984) as having longer faces than their insectivorous relatives, megadermatids are in fact shorter-faced than most other rhinolophoids, the shorter face in this case perhaps being correlated with a more powerful bite by bringing the canines closer to the fulcrum of the jaw. In megadermatids, the mandibular condyle is relatively low and the coronoid process high, a condition typical in carnivores whereby the temporalis (the primary prey-seizing muscle) is developed at the expense of the masseter (Maynard Smith & Savage 1959). This allows less transverse activity but greater vertical movement and slicing ability (Freeman 1984). The direction of pull of the temporalis in megadermatids has been found to be much more vertical than in other rhinolophoids (Freeman 1984, fig. 7), thus presumably providing a more powerful bite force (see also Emerson & Radinsky 1980). However, as Freeman (1984) points out, a more vertically-oriented temporalis also tends to be negatively correlated with the tilting of the head on the basicranial axis. The latter appears to be controlled at least in part by the functional requirements of echolocation such that orally emitting echolocators have positively tilted heads with respect to the basicranial axis while nasal emitters (e.g. megadermatids and other rhinolophoids) have negatively tilted heads (Freeman 1984, fig. 6).

In the *Macroderma* lineage, the trend to shorten the face and thereby apparently increase the power of the canines, can be traced from the Oligo-Miocene *M. godthelpi* to the middle Miocene *M. malugara*, the early Pliocene *M. koppa* and Pliocene and Quaternary specimens of M. gigas. *Macroderma godthelpi* has a relatively elongate face (P^2 being large and in the tooth row), a plesiomorphic double infraorbital foramen, an unmodified frontal nose-shield and a discrete and well-separated posterolingual accessory cusp on C^1. The later middle Miocene *M. malugara* retains the double infraorbital foramen but has reduced the P^2 to a rudimentary tooth that lies lingual to the tooth row. The early Pliocene *M. koppa* has lost the P^2 but retains the double infraorbital foramen and isolated cusp on C^1 and exhibits little modification of the frontal nose-shield. Quaternary specimens of *M. gigas* are more short-faced exhibiting a lack of P^2, reduction of P^4 from a more sectorial to a higher crowned stabbing tooth, a C^1 with less discrete accessory cusp and pronounced anteroposterior compressional flexure (that is most obvious in the lingual cingulum) and a modified nose-shield. These animals exhibit a single infraorbital foramen, but at least some Pliocene specimens of *M. gigas* retain two infraorbital foramina.

Of *Macroderma* species, specimens of the Pliocene *M. koppa* and Pliocene to Recent *M. gigas* are best

preserved. At some point in the evolutionary history of these two species, a shortening in the anterior part of the face appears to have resulted in a relative decrease (from *koppa* to *gigas*) in the size of incisors, canines and premolars, possibly a modification of the frontal nose-shield and a fusion of the plesiomorphic double infraorbital foramen into the autapomorphic single foramen of Quaternary *M. gigas* (there being little concomitent measurable difference in the molar region between the two species). Speciation events associated with changes of shape linked with size are often described in terms of heterochrony and allometry. A change in the rate of growth and development of a feature due to a minor genetic change may have a large impact upon the adult phenotype. Such a change in gene regulation may have occurred during the phylogenetic history of the lineage spawning *M. koppa* to produce the shorter-faced *M. gigas*.

Useful gene combinations may be preserved in a species to adapt local populations in minor ways to fluctuating environments. That at least the premolar region has remained 'plastic' in *M. gigas* is suggested by the fact that these characters are among those that appear to distinguish geographic populations of Quaternary *M. gigas* (Hand & York 1990) ; premolar characters are the only ones found in *M. gigas* to be highly correlated with each other and to covary relatively independently of other groups of characters (Hand & York 1990). It is also in this region that Pliocene representatives of *M. gigas* differ from Quaternary specimens by way of variation in the number of infraorbital foramina.

The short face and expansion of the frontal nose-shield in megadermatids may also correlate with the very large nose-leaf. Following Freeman's (1984) argument, the head would need to be less negatively tilted on the basicranial axis for the nose-leaf to be directed forward. The large eyes, large nose-leaf, large erect ears and powerful canines could thus be trained simultaneously on their prey, a procedure that typifies the hunting behaviour of living megadermatids who inspect their surroundings from a perch before ambushing and killing their prey usually with one swift bite to the back of the head (Kulzer *et al.* 1984).

PALAEOECOLOGY

Both the Gotham City and Rackham's Roost deposits are interpreted to largely represent the remains of prey accumulated by, respectively, *Macroderma malugara* nov. sp. and *M. gigas*, megadermatids of approximately equal size. However, in terms of vertebrate diversity, the far more extensive Rackham's Roost deposit appears depauperate with respect to the Gotham City deposit. For example, among marsupial families represented in the Gotham City deposit, but missing from Rackham's Roost, are acrobatids, burramyids, petauroids, small phalangerids, peroryctids and a new family of tiny perameloids (all small enough to be megadermatid prey). Although some marsupial families are known from Rackham's Roost (e.g. dasyurids, peramelids, potoroids, etc.) most are represented by one or two specimens each. Dominating the assemblage is a single mammal family, the Muridae, represented by at least 12 species, many of which are represented by hundreds of specimens each (Archer *et al.* 1991).

Arboreal mammals make up a large proportion of the prey collected by *Macroderma malugara* most of which are missing from the Rackham's Roost assemblage collected by *M. gigas*. The observed shift in prey assemblages between the sites might be due to a change in prey availability in the immediate area, probably as the result of a gradual drying in climate in northern Australia at the end of the Tertiary. The middle Miocene Gotham City Local Fauna appears to have been culled from a rainforest environment, the Pliocene Rackham's Roost Local Fauna from a dry sclerophyll or woodland, probably not unlike the Riversleigh area today (Archer *et al.* 1991). Douglas (1967), Toop (1985) and Schulz (1986) have studied the prey of modern *M. gigas* which inhabits a wide range of environments in northern Australia, from semi-arid to rainforest habitats. In the forested coastal environment around Rockhampton, central Queensland, the prey chosen by *M. gigas* was found by Toop (1985) to be predominantly arboreal. Rodent remains were collected, but only in roosts adjacent to cleared and ploughed agricultural land where the hunting of ground-dwelling animals was possible. In semi-arid and desert areas of northern Australia, the most common mammalian remains in the feeding roosts of *M. gigas* have been found to be, like in the Rackham's Roost deposit, rodents, dasyurids and small bats (Douglas 1967 ; Schulz 1986).

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