FIRST RECORD OF THE GENUS *MEGADERMA* Geoffroy (MICROCHIROPTERA : MEGADERMATIDAE) FROM AUSTRALIA

by

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ABSTRACT

A new Tertiary megadermatid is described from Rackham's Roost Site, a Pliocene limestone cave deposit on Riversleigh Station, northwestern Queensland, Australia. It appears to represent the first Australian record of *Megaderma* GEOFFROY, 1810, a genus otherwise known from Tertiary African and European taxa and the living Asian species *M. spasma* (LINNAEUS, 1758) and *M. (Lyroderma) lyra* PETERS, 1872. *Megaderma richardsi* n. sp. is one of the smallest megadermatids known. It exhibits a mixture of plesiomorphic and autapomorphic features, the latter appearing to exclude it from being ancestral to any living megadermatid. The new species is one of eight megadermatids identified from the Australian fossil record, most of which are referable to *Macroderma* MILLER, 1906.

RESUME

Un nouveau mégadermatidé tertiaire est décrit de la localité Rackham's Roost, un gisement cavernicole pliocène de Riversleigh Station, Nord-Ouest Queensland, Australie. Il représente la première decouverte australienne du *Megaderma* GEOFFROY, 1810, un genre connu jusqu'ici par des espèces tertiaires africaines et européennes et par les espèces récentes asiatiques *M. spasma* (LINNAEUS, 1758) et *M. (Lyroderma) lyra* PETERS, 1872. *Megaderma richardsi* n. sp. est un des plus petits mégadermatidés connus. Il montre un mélange de plésiomorphies et d'autapomorphies, ces dernières l'excluant de toute ascendance à l'égard des mégadermatidés récents. L'espèce nouvelle est l'un des huit mégadermatidés dénombrés dans le régistre fossil australien, dont la plupart sont référables de *Macroderma* MILLER, 1906.

INTRODUCTION

The bat family Megadermatidae is an Old World tropical group with five extant species. These are commonly (e.g. Honacki *et al.* 1982, Hill & Smith 1984) referred to four genera. Three genera, *Lavia* GRAY, 1938, *Cardioderma* PETERS, 1873 and *Macroderma* MILLER, 1906, are considered to be monotypic. *Megaderma* GEOFFROY, 1810 then contains two species, *Megaderma spasma* and *M. (Lyroderma) lyra*. *Lavia frons* and *Cardioderma cor* are African species, *Megaderma lyra* and *M. spasma* are Asian and *Macroderma gigas* Australian.

Megadermatids are insectivorous (e.g. *L. frons*) or facultatively carnivorous and are generally characterised by a dentition adapted for meat-eating. The family is well represented in the fossil record, being known from at least 19 fossil taxa from early Tertiary to Quaternary sediments in Europe, Africa and Australia (e.g. Sigé 1976; Hand 1985, table 8; Sevilla 1990; Ziegler 1993). The majority of Tertiary megadermatids are referred to the genus *Megaderma*, a notable exception being the oldest known megadermatid, *Necromantis adichaster* WEITHOFER, 1887 from late Eocene French sediments (Remy *et al.* 1987).

In 1976, Sigé examined the evolutionary history of megadermatids and recommended recognition of only three megadermatid genera, *Necromantis*, *Lavia* and *Megaderma*, the latter containing *Cardioderma* and *Macroderma* as subgenera. He

argued that, without rarely preserved cranial material, fossil megadermatids could not be confidently assigned to the more restricted species groups commonly used for living taxa. Subsequently, however, after examination of new Australian fossil megadermatid material, Hand (1985) suggested that the generic name *Macroderma* be retained for an Australian clade which now includes at least three Tertiary species (*M. godthelpi* HAND, 1985, *M. koppa* HAND *et al.*, 1988 and *M. malugara* HAND, submitted) as well as Australia's only living megadermatid *M. gigas* (DOBSON, 1880). She also suggested that the name *Lyroderma* might be resurrected for *M. lyra* and the middle Miocene *M. gaillardi* (TROUESSART, 1898).

Although most Australian Tertiary megadermatids appear referable to *Macroderma*, Miocene deposits on Riversleigh Station, northwestern Queensland, have also produced enigmatic taxa such as the Dwornamor Variant (Hand 1985) and the Henk's Hollow megadermatid indet. (Hand submitted) that lack apparent synapomorphies for this clade. These taxa are represented by isolated teeth and cannot be confidently assigned to any other species group. A tiny, new megadermatid from Riversleigh's Pliocene Rackham's Roost Site (Hand 1987, Archer *et al.* 1989, 1991) is possibly allied to these Miocene forms but is better represented, by a maxillary fragment and several isolated teeth, and is tentatively described here as the first representative of the genus *Megaderma* from Australia.

Dental terminology follows Hand (1985). The prefix QM F_____ indicates that the source of specimens is the Queensland Museum fossil collection.

SYSTEMATICS

Order **CHIROPTERA** BLUMENBACH, 1779
Suborder **MICROCHIROPTERA** DOBSON, 1875
Superfamily **RHINOLOPHOIDEA** GRAY, 1825
Family **MEGADERMATIDAE** ALLEN, 1864

Genus *MEGADERMA* GEOFFROY, 1810

Megaderma richardsi n. sp.

(Pl. 1-2)

Holotype: Queensland Museum F23619, a right maxillary fragment with C^1 and P^4.

Etymology: The species is named after Greg Richards, one of Australia's foremost bat researchers, whose help in interpreting aspects of Riversleigh's complex fossil bat faunas is greatly appreciated.

Paratypes (from type locality): QM F23620, a right C^1; QM F23621, a left C^1.

Referred material (from type locality): QM F23598, a right M^1; QM F23599, a right M^2; QM F23600, a left M_1.

Type locality, lithology and **age:** The type locality, 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, and has been described by Hand (submitted). 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 Pliocene in age. It contains abundant plesiomorphic murids (at least 13 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: The Rackham's Roost deposit contains the remains of crustaceans, fish, frogs, lizards, small crocodiles, snakes, birds, dasyurids, peramelids, a pseudocheirid, an extinct macropodid and potoroid, at least 13 murids, two emballonurids *(Taphozous* spp), four hipposiderids, four vespertilionids and the large megadermatid *Macroderma gigas* (Archer *et al.* 1991, Hand submitted). 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 that species. Boids, the emballonurids, hipposiderids and vespertilionids probably cohabited the megadermatid roost; the macropodid may have camped near the cave's entrance.

Diagnosis: *Megaderma richardsi* differs from living species of *Megaderma* (i.e. *M. spasma* and *M. lyra*) in its loss of P^2.

It differs from most species of *Megaderma* in its very small size. However, it is similar in size to the Tertiary *M. jaegeri* and *M. lopezae*.

Megaderma richardsi differs from *M. jaegeri* SIGÉ, 1976 of the middle Miocene Beni Mellal deposit in Morocco in, among other features, its slightly smaller size, C^1 with taller anterior accessory cusp, taller posterior accessory cusp less separated from the main cusp, M^1 with shorter postmetacrista, smaller parastyle, less lingually displaced mesostyle, posteriorly opening protofossa, M_1 lower crowned with less sinuous buccal cingulum, trigonid and talonid subequal in length, more anteriorly extended pre-entocristid, and smaller and less posteriorly displaced hypoconulid so that there is little inflexion in the hypocristid.

Megaderma richardsi differs from *M. lopezae* SEVILLA, 1990 of the late Oligocene Carrascosa del Campo locality, Spain, in its M^1 with more lingually displaced mesostyle, posteriorly opening protofossa, and more posteriorly directed heel, and M_1 having a more laterally compressed trigonid, less sinuous buccal cingulum, anteriorly extended pre-entocristid, the metaconid contribution to the cristid obliqua less reduced, and the hypoconulid less well-developed and less posteriorly-situated so that it is less distinct from the entoconid and there is little inflexion in the hypocristid.

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Description

The right maxillary fragment retains C^1 and P^4. There is no sign of an alveolus for P^2 either in the tooth row or lingually (as in *M. spasma* and *M. lyra*). The anterobuccal shelf of P^4 rests on a small posterobuccal cingular shelf in C^1.

C^1 is known from three specimens, QM F23619, QM F23620 and QM F23621. It is massively-rooted and recurved posteriorly with a tall, slender, dominant main cusp. In basal outline the tooth is semicircular, flattened on the lingual side. There is a narrow cingulum around the whole tooth. It has a large posterior accessory cusp, occuring within the cingular rim, that is poorly separated from the paracone and rises to more than half the paracone's height. It has a well-developed anterolingual cingular cusp. The antero- and posterolingual corners of the paracone are defined by vertical crests. The anterior vertical crest intersects the crown base just buccal to the anterolingual cingular cusp. The posterolingual vertical crest extends to the anterior base of the posterior crown cusp. On the flattened lingual face of the paracone is a vertical crest which is attenuated towards the base and apex of the cusp. There is a slight indentation in the buccal cingulum immediately buccal to the junction of the paracone and posterior cusp, a small cingular cusp at the most posterior point of the crown, and immediately buccal to this a small cingular shelf on which the anterobuccal shelf of P^4 rests.

P^4 is known from the holotype QM F23619. In occlusal view the crown is subtriangular. There is one main cusp, the paracone, which occurs midway along its length and slightly buccal to the crown's centre. There is a short, narrow, posterolingually directed heel on its lingual margin. The heel is surrounded by a thin continuous cingulum that is thickest and deepest around the heel. The buccal cingulum is relatively thick but is interrupted by the flank of the paracone about midway along the tooth's buccal length. Anteriorly there is a relatively tall cingular cusp. The preparacrista is convex in profile and runs anteriorly from the paracone's apex towards the anterior cingular cusp from which it is separated by a narrow valley that extends buccally and lingually. The postparacrista, which is slightly concave occlusally and in profile, runs towards the posterior margin of the tooth before dropping vertically immediately before reaching the cingulum.

QM F23600, LM_1, QM F23598, RM^1, and QM F23599, RM^2, are referred to *M. richardsi*. They are of an appropriate size to belong to this taxon and exhibit features typically found in megadermatids.

M_1 is nyctalodont with a laterally-compressed trigonid, reduced paraconid with the paracristid longer than the metacristid, twinned entoconid and hypoconulid, reduced pre-entocristid such that the talonid opens lingually, and continuous but relatively poorly developed anterior, buccal and posterior cingula. The trigonid and talonid are approximately equal in length but the talonid is much wider than the trigonid which is very laterally compressed. The trigonid is not much taller than the talonid. Thus the protoconid is taller than the metaconid which is taller than the entoconid (and broken hypoconid) which is taller than the reduced paraconid. The paraconid contribution to the paracristid is very short. The angle made by the para- and metacristids is very wide, being approximately 160 degrees. The cristid obliqua is much longer than the paracristid and sweeps up the posterior flank of the metaconid almost to its apex. The hypocristid is also long but shorter than the cristid obliqua. The hypoconulid is located

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on the lingual margin of the crown close to the small (worn) entoconid. The angle formed between the the cristid obliqua and hypocristid is relatively small, being approximately 60 degrees. From the entoconid, a pre-entocristid extends anteriorly only a short distance. There is a slight inflexion in the buccal cingulum where the trigonid and talonid join.

M^1 is longer than wide. The tooth is worn. The metacone is the tallest and most massive cusp and is taller than the paracone which is taller than the protocone. The postmetacrista is much longer than the subequal premetacrista and postparacristae which are longer than the preparacrista. The mesostyle is tall, being the same topographic height as the small parastyle and the metastyle, and is slightly lingually displaced. There is a very small parastyle. There is no posterior cingulum, but a very

QM F no		23619	23620	23621	23598	23599	23600
C^1–P^4	L	3.24					
C^1	L	2.00	1.77	1.92			
	I	1.08	0.97	1.13			
	Hi	2.64	--	2.80			
	He	2.79	--	2.87			
	Hi'	1.63	1.33	1.62			
	He'	1.75	1.44	1.74			
P^4	L	1.44					
	I	1.31					
	Hi	1.89					
	He	1.63					
M^1	L				1.88		
	Ll				1.81		
	Li				1.43		
	I				1.93		
M^2	L					2.08	
	Ll					1.85	
	Li					1.32	
	I					2.13	
M_1	L						1.98
	LT						1.01
	Lt						0.97
	IT						1.35
	It						1.30

Table 1.— Measurements (mm) of the holotype (QM F23619), paratypes (QM F23620-23621) and referred specimens (QM F23598-23600) of *Megaderma richardsi* n. sp. from the Pliocene Rackham's Roost Site, Riversleigh Station, northwestern Queensland, Australia.

Measurements and abbreviations follow Sigé (1968): L, length; Li, internal length, Ll, lingual length; I, width; Hi, internal height; He, external height; Hi', internal height of posterior accessory cusp; He', external height of posterior accessory cusp; LT, trigonid length; Lt, talonid length; IT, trigonid width; It, talonid width.

faint anterior cingulum on the buccal half of the tooth and a separate cingular swelling anterolingual to the base of the paracone. The lingual cingulum extends from the base of the metacone (posterior to the base of the protocone) and encloses the very posteriorly directed heel. The heel cingulum is more robust posteriorly than lingually and thickest at the most posterolingual corner of the heel. The protocone is a conical, puncturing cusp that is topographically quite low, particularly with respect to the metacone. The preprotocrista is initially directed anterobuccally towards the base of the the paracone, a short curved crest (paraloph) extending the preprotocrista a short distance up the posterolingual flank of the paracone. The postprotocrista runs posterobuccally then almost immediately vertically and posterolingually onto the heel but does not meet the lingual cingulum to which it briefly runs parallel.

M^2 is very worn but is basically similar to M^1 except as follows. There is less difference in size between the paracone and metacone, the preparacrista is only just shorter than the postmetacrista, and the mesostyle is perhaps lower. As in M^1, there is no posterior cingulum, a very feint anterior cingulum, and a separate anterolingual cingular swelling between the para- and protocones. The protocone structure is very similar to that in M^1 but the tooth is more worn and this accentuates the curve in the postprotocrista. The heel is rounder, there being no elaboration or thickening of the cingulum at the posterolingual corner of the heel.

Measurements of the teeth of *Megaderma richardsi* n. sp. are given in table 1.

COMPARISONS WITH OTHER MEGADERMATIDS

FOSSIL FORMS

Megaderma richardsi n. sp. has been compared with all adequately described fossil species of *Megaderma*, with the following exceptions. Comparable material has not been reported for: *Megaderma* sp. from the late Oligocene of St Victor la Coste, France (Sigé 1967); *M. janossyi* of the Pliocene of Hungary (Topal 1974); and *M. watwat* of the Pleistocene of Palestine (Bate 1937). A mandible and maxilla representing an undescribed Pliocene species of *Cardioderma* (Butler & Greenwood 1965; *Megaderma sensu* Sigé 1976) from Olduvai Gorge, East Africa were not examined.

Among fossil forms examined, *Megaderma richardsi* appears most similar to four taxa: the late Oligocene *Megaderma lopezae* from Carrascosa del Campo, Spain (Sevilla 1990); *M. jaegeri* from the middle Miocene Beni Mellal fauna of Morocco (Sigé 1976); *M. lugdunensis* from the early Miocene Vieux-Collonges deposit, France (Guérin & Mein 1971), middle Miocene of Neudorf, Czechoslavakia (Zapfe 1950) and late Miocene of Lissieu, France (Mein 1964); and *M. vireti* of the middle Miocene La Grive St-Alban, France (Guérin & Mein 1971), late Miocene of Lissieu, France (Mein 1964) and Kohfidisch of Austria (Bachmayer & Wilson 1970).

Megaderma lopezae and *M. richardsi* share: almost identical P^4 morphology; M^1

with similar sized heel, tall mesostyle not greatly displaced lingually, no posterior cingulum, possibly a paraloph; a relatively low crowned M_1 with trigonid and talonid approximately equal in length and hypoconulid not greatly buccally displaced. *Megaderma lopezae* differs from *M. richardsi* (in addition to the features noted above in the diagnosis) in its M^1 with buccally projecting mesostyle, unreduced postparacrista and premetacrista, general protocone morphology and small, closed protofossa. C^1 and M^2 are not known in *M. lopezae*.

Megaderma jaegeri and *M. richardsi* share: similar general proportions of M^1, height of mesostyle (which is slightly more lingually displaced in *M. jaegeri*), reduced postparacrista and premetacrista, heel direction and size, anterolingual cingulum (though very faint); relatively low crowned M_1, with lingual hypoconulid, similar lateral and anteroposterior trigonid compression and lateral talonid compression (with more anteroposterior compression in *jaegeri*). In addition to the differences noted above in the diagnosis, *Megaderma jaegeri* differs from *M. richardsi* in its: proportionately longer C^1 with thicker buccal cingulum and more massive root; M^1 protocone morphology and weak paraloph development; M_1 with trigonid longer than talonid, hypoconulid and entoconid more distinct and buccally displaced, and reduced metaconid contribution to the cristid obliqua. P^4 and M^2 are not known for *M. jaegeri*.

Megaderma lugdunensis and *M. richardsi* share: M^1 with posteriorly directed heel and similar heel cingulum, very similar parastyle development, relative size of paracone and metacone, mesostyle height; M^2 with postparacrista and premetacrista only moderately reduced and heel posteriorly directed; M_1 with well developed pre-entocristid, and lingually and posteriorly situated hypoconulid. It differs from *M. richardsi* in: its C^1 with buccal vertical crest; P^4 with slimmer heel, shorter anterior cingular cusp, broader and buccally deeper anterior cingular shelf, anteriorly poorly defined buccal cingulum; M^1 with longer and broader heel, no paraloph, more lingually displaced mesostyle; M^2 with more reduced postparacrista and premetacrista, broader stylar shelf and much lower, more lingual mesostyle; M_1 with trigonid less laterally compressed and reduced metaconid contribution to the cristid obliqua.

Megaderma vireti and *M. richardsi* share: similar C^1 morphology including separation of a blade-like posterior cusp, presence of posterior cingular cusp, cingulum development, relative cusp heights; similar P^4 morphology; M^1 with posteriorly directed heel and large difference between size of paracone and metacone; M^2 with similar relative proportions, heel, cingulum, anterolingual cingulum and paraloph. Differences include: lack of tall anterior cingular cusp in P^4; M^1 with large, narrow heel, protocone morphology; M^2 protocone morphology, mesostyle much lower and lingually situated, postparacrista and premetacrista more reduced; long, narrow M_1 with stronger lateral compression of talonid and trigonid, hypoconulid more anteriorly and buccally placed, reduced pre-entocristid and metaconid contribution to cristid obliqua.

Megaderma richardsi appears to be less similar to: *Megaderma brailloni* from the French early Miocene Bouzigues (Sigé 1968) and Serre de Verges (Meurisse *et al.* 1969) localities; *M. franconica* from the early Miocene of Wintershof-West of Eichstätt, Germany (Ziegler 1993); *M. gaillardi* from the middle Miocene sites of La Grive St-Alban, France (Guérin & Mein 1971), Beni Mellal, Morocco (Sigé 1976) and Escobosa, Spain (Sesé 1986); and *M. mediterraneum* from the late Pliocene of Sète,

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southern France (Sigé 1974). Similarities, however, include: with *brailloni*, the degree of separation of the posterior accessory cusp from the paracone in C^1, in M^1 general morphology of the buccal part of the crown (stylar shelf, paracone and metacone), and in M_1 the degree of lateral compression of the trigonid and anteroposterior compression of the talonid; with *gaillardi*, C^1 morphology of the posterior accessory cusp, anterior accessory cusp development and vertical lingual crest, M^2 heel size; with *franconica*, at least M^2 heel size and probably (as in *gaillardi*) C^1 morphology of the posterior accessory cusp, anterior accessory cusp development and vertical lingual crest; and with *mediterraneum*, in C^1 separation of the blade-like (but short) posterior cusp, well defined buccal cingulum, pronounced lingual vertical crest and marked indentation in the buccal crown.

Megaderma brailloni differs from *M. richardsi* in its: C^1 with posterior cusp relatively short and conical (rather than blade-like), no posterior cingular cusp, vertical buccal crest; M^1 with broader stylar shelf and shorter and more lingually situated mesostyle, paracone and metacone subequal in height, lingually directed heel, different protocone morphology, no paraloph, parastyle relatively well developed; M_1 with sinuous buccal cingulum on trigonid, more laterally compressed talonid, more anteriorly and buccally located hypoconulid, more robust cingulum, greater difference in trigonid and talonid heights, and reduced metaconid contribution to the cristid obliqua.

Megaderma gaillardi differs from *M. richardsi* in its: taller crowned teeth; C^1 with poorly defined buccal cingulm, buccal vertical crest; M^2 with reduced postparacrista and premetacrista, broader stylar shelf, much lower, more lingual mesostyle, no paraloph, more lingually directed heel, lingual elaboration of heel cingulum, very different protocone (although the protofossa does open posteriorly slightly), lack of anterolingual cingulum; M_1 with very buccally situated hypoconulid, laterally compressed trigonid, little difference between talonid and trigonid widths, very sinuous buccal cingulum. (Note that in M_2 the cristid obliqua is not greatly reduced, there is a greater difference in talonid and trigonid heights, the pre-entocristid is not as anteriorly developed, the hypoconulid more buccally and posteriorly situated and the hypoconid cingulum is elaborated.) *Megaderma franconica* differs from *M. richardsi* in at least its: P^4 heel morphology, M^{1-2} protocone morphology, and M_1 cristid obliqua and buccal cingulum morphology.

Megaderma mediterraneum differs from *M. richardsi* in its: C^1 with buccal vertical crest, no posterior cingular cusp although the cingulum may rise there very slightly; high crowned lower molars (as represented by M_2) and, by extrapolation from M_2, posteriorly situated hypoconulid so that there might be an inflexion in the hypocristid.

LIVING TAXA

Among living taxa, *Megaderma richardsi* is most similar to *Megaderma spasma* and *Cardioderma cor*.

Megaderma richardsi and *M. spasma* share: similar overall P^4 morphology; M^1

shape and proportions, heel direction, a posteriorly-opening protofossa (slightly in *M. spasma*); M^2 shape and proportions, heel direction and cingulum, relatively low protocone. *Megaderma spasma* differs in having: a weakly developed or absent anterior accessory cusp in C^1; broader and shorter P^4 heel; in M^{1-2}, more lingual and lower mesostyle, reduced postparacrista and premetacrista, a posterior cingulum, more continuous anterior cingulum; in M^1 slightly broader heel, better developed parastyle, no posterior elaboration of heel cingulum, no paraloph; M^2 with longer heel, protofossa not as open; M_1 with more laterally compressed trigonid and talonid.

Cardioderma cor shares with *M. richardsi*: in C^1, a tall, blade-like posterior accessory cusp little separated from the paracone, posterior cingular cusp and buccal cingulum; loss of P^2; in P^4, heel size, shape and direction, paracone position; in M^{1-2}, heel size, little lingual displacement of mesostyle, only moderately reduced postparacrista and premetacrista; in M_1, posterior postion of hypoconulid and unreduced metaconid contribution to the cristid obliqua. It differs from *M. richardsi*: in C^1, lacking an anterior accessory cusp, less separation of the posterior accessory cusp from the paracone; P^4 without anterior cingular cusp (replaced by posterior cingular cusp on C^1), shallow anterobuccal cingulum; M^1 with broader and lingually directed heel, no posterior elaboration of cingulum, protofossa closed, no anterior or posterior cingulae; M^2 with more lingually directed heel, protofossa closed, anterior cingulum but no anterolingual cingulum.

Lavia frons shares with *M. richardsi*: in M^{1-2} the relatively buccal position of the mesostyle, an anterolingual cingulum (also anterior cingulum); in M_1, degree of lateral and anteroposterior compression of talonid, little difference between trigonid and talonid lengths and heights, position of hypoconulid (posterior and lingual), unreduced metaconid contribution to the cristid obliqua. It differs from *M. richardsi*: in C^1 with short posterior accessory cusp well separated from the paracone; P^4 morphology very distinct, with very curved postparacrista from central paracone, small, indistinct anterior cingular cusp, but with broad anterior (=anterolingual) shelf and deep anterobuccal cingular shelf, broad and long heel that is very different from other taxa; M^1 and M^2 protocone morphology different again with buccal cingulum sweeping up protocone, continuous posterior and heel cingula; in M_1, pre-entocristid unreduced, extending anteriorly to metaconid.

Megaderma (Lyroderma) lyra and *M. richardsi* share: in C^1 a blade-like posterior accessory cusp; in M^{1-2}, lack of posterior cingulum; and in M_1, degree of lateral and anteroposterior compression of the trigonid. *Megaderma lyra* differs in: being high crowned; in C^1 the posterior accessory cusp relatively short and better separated; P^4 with no anterior cingular cusp, much slimmer heel (which appears to be posteriorly displaced), poorly developed buccal cingulum; in M^{1-2}, more lingual and low mesostyle, closed protofossa, better developed parastyle, reduced postparacrista and premetacrista, heel longer and slimmer (lingually directed in M^1), better developed posterior cingulum, more continuous anterior cingulum, no paraloph; in M_1, more laterally and anteroposteriorly compressed talonid, greater difference in trigonid and talonid heights and lengths, little difference in widths, buccal position of hypoconulid, sinuous buccal cingulum and reduced metaconid contribution to the cristid obliqua.

Megaderma richardsi shares with *Macroderma gigas*: loss of P^2; P^4 with

anterior cingular cusp and posterolingually directed heel; M^{1-2} with no posterior cingulum; and in M_1, similar degrees of lateral and anteroposterior compression of the trigonid. *Macroderma gigas* differs from *Megaderma richardsi* in: being high crowned; in C^1 with well separated, short and conical posterior cusp; P^4 with buccal paracone, no buccal cingulum, tall anterior cingular cusp, waisted, elongated heel, pronounced vertical drop from posterior end of relatively curved postparacrista to cingulum; M^{1-2} with broad buccal shelf and low, lingual mesostyle, more reduced postparacrista and premetacrista, closed protofossa, long, posterolingually directed heel, no posterior elaboration of heel cingulum, no paraloph; M_1 with strong lateral and anteroposterior compression of talonid.

Overall, *Megaderma richardsi* appears to be most similar (phenetically) to *M. lopezae*, *M. jaegeri*, *M. lugdunensis* and *M. vireti* among fossil forms and *M. spasma* and *Cardioderma cor* among living species. It is perhaps significant that these taxa are mostly small to medium-sized megadermatids, with very large taxa such as *Megaderma brailloni*, *M. gaillardi* and *Macroderma gigas* being most dissimilar (see Discussion).

PHYLOGENETIC RELATIONSHIPS

A subset of the shared features noted in the comparisons above appear to provide preliminary phylogenetic information. Polarities of character states were determined by outgroup comparison (using nycterids, hipposiderids and rhinolophids; see Hand 1985) and/or commonality within the family Megadermatidae. A list of characters surveyed for phylogenetic information is given in Appendix.

Potentially phylogenetically useful characters include the degree of lingual displacement of the mesostyle of M^{1-2}, lateral and anteroposterior compression of the trigonid and talonid of M_1 and buccal displacement of its hypoconulid (see also Sigé 1976, Hand 1985, Sevilla 1990). Other features, such as M^{1-2} heel direction, presence/absence of paralophs, development of cingula and probably the presence/absence of P^2, are extremely difficult to interpret phylogenetically. Many appear to represent homoplasies that provide little phylogenetic information.

Because so few unambiguously useful characters are evident in the material of *M. richardsi* it is possible only to make preliminary remarks about its phylogenetic relationships.

With respect to *Lavia frons*, *Megaderma richardsi* appears to be more apomorphic in its more lingually displaced and lower M^{1-2} mesostyle, reduced postparacrista and premetacrista, elongated postmetacrista, transversely compressed M_1 trigonid and talonid, and reduced pre-entocristid.

In its lingually displaced and lower M^{1-2} mesostyle, shorter postparacrista and premetacrista, longer postmetacrista and more laterally compressed M_1 trigonid, *M. richardsi* also appears to be more apomorphic than *M. lopezae*.

Megaderma jaegeri exhibits a further lingual displacement of the M^1 mesostyle, and more derived stylar shelf as well as a longer trigonid than talonid (resulting from anteroposterior compression of the talonid), and is interpreted here to be generally more

apomorphic than *M. richardsi.*

Megaderma brailloni, M. vireti, M. lugdunensis, M. spasma and *Cardioderma cor* are also generally more apomorphic, exhibiting a more derived M^{1-2} morphology (i.e. stylar shelf), greater difference between M_1 trigonid and talonid heights and lengths, greater anteroposterior and lateral compression of the talonid and buccal displacement of the hypoconulid. *Megaderma vireti* and *M. lugdunensis* share some features with *M. richardsi* that could be potential apomorphies, such as the posterior (rather than posterolingual) heel direction in M^{1-2} and a much larger metacone than paracone.

Megaderma gaillardi, M. franconica, M. lyra and fossil and Recent species of *Macroderma* appear more derived than other megadermatids (including *M. richardsi*) in their greater M^{1-2} heel development, large size, high crowns and further lateral and anteroposterior talonid compression in M_1. *Megaderma lyra* and species of *Macroderma* also share a taller P^4 with better developed heel and more buccally placed paracone. Because comparisons between *M. richardsi* and *M. mediterraneum* were limited to C^1 characters, the phylogenetic relationship of these taxa could not be satsfactorily assessed.

In essence, *Megaderma richardsi* appears to be more apomorphic than *Lavia frons* and *Megaderma lopezae* but more plesiomorphic than all other species of *Megaderma, Cardioderma* and *Macroderma.*

DISCUSSION

ASSIGNMENT TO *MEGADERMA*

The taxon described here as *Megaderma richardsi* exhibits a number of features that together characterise species of *Megaderma*. These features include a pronounced reduction of the M_1 paraconid and lateral compression of the trigonid, a simple P^4 with small heel and central paracone, and M^{1-2} with small heel. It also lacks a number of features usually found in *Macroderma* species such as high crowns, strong lateral and anteroposterior compression of talonids, C^1 with a well separated, relatively short and conical posterior accessory cusp, P^4 and M^{1-2} with enlarged heels, tall P^4 with buccally situated paracone, M^{1-2} with broad buccal shelf and markedly lingually displaced mesostyle.

Assignment of this Australian Pliocene species to the genus *Megaderma* remains tentative. Unlike living *Megaderma* species, in which the tiny P^2 is extruded lingually from the tooth row, the Riversleigh fossil megadermatid lacks P^2. However, although this tooth is present in *M. spasma* and *M. lyra*, few Tertiary *Megaderma* species preserve this region of the tooth row, and P^2 is known to have been independently lost in some megadermatid lineages (i.e. *Macroderma* spp) and apparently from others. Australian Oligo-Miocene species of *Macroderma* (e.g. *M. godthelpi* and *M. malugara*) contain a P^2 which has been lost in the Pliocene-Recent *M. gigas*. The tooth

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has also been lost, apparently independently, in the living African species *Lavia frons* and *Cardioderma cor*, between which no close phylogenetic relationship has been established (Sigé 1976, Hand 1985, Griffiths *et al.* 1992). The tooth was large and within the tooth row in the oldest megadermatid, the late Eocene *Necromantis adichaster* WEITHOFER, 1887. In the Miocene *Megaderma vireti* MEIN, 1964, it was evidently small though less extruded than in living *Megaderma* species.

Loss of P^2 within the *Macroderma* lineage has been correlated by Hand (submitted) with a general trend to shorten the face (thereby apparently increasing the power of the canines). This trend can be traced from the Oligo-Miocene *M. godthelpi* to the middle Miocene *M. malugara*, the early Pliocene *M. koppa* and Pliocene and Recent specimens of *M. gigas*. Also possibly associated with this shortening of the face is a gradual change in the nature of the posterior accessory cusp of C^1: from a discrete and well-separated, conical cusp in Miocene *Macroderma* taxa to a less separated (but still relatively short and conical) cusp in Recent *Macroderma gigas* (Hand submitted). The close proximity of the blade-like posterior accessory cusp to the paracone in the C^1 of *Megaderma richardsi* has been interpreted here to be a feature shared symplesiomorphically with other species of *Megaderma*, and the absence of P^2 interpreted to be autapomorphic loss. However, it is also possible that these features represent two of few apomorphies shared with some (but not all) species of *Macroderma*.

A relatively tall, blade-like posterior accessory cusp in C^1, little separated from the paracone, is interpreted here to be plesiomorphic within the Megadermatidae. Rhinolophids and nycterids lack a posterior accessory cusp in C^1, but a secondary cusp is variably present within the family Hipposideridae. For example, species of *Hipposideros (Brachipposideros)*, *Syndesmotis*, *Asellia*, *Cloeotis*, *Triaenops*, *Coelops* and *Rhinonicteris* have relatively tall posterior accessory cusps on C^1. Species of *H. (Hipposideros)* variably have a secondary posterior cusp, which in some taxa tends to be low and sometimes blunt. Species of *H. (Pseudorhinolophus)*, *Palaeophyllophora*, *Anthops* and *Aselliscus* lack (or exhibit a very reduced or incipient) posterior accessory cusp. Within the Megadermatidae, a tall, blade-like (versus conical) posterior accessory cusp is present in *M. richardsi*, *M. gaillardi*, *M. vireti*, *M. spasma* and *Cardioderma cor* and variably in *M. lugdunensis*. This condition appears to occur in hipposiderids and megadermatids irrespective of size, diet or presence of P^2.

Although the three known upper canines of *Megaderma richardsi* show little variation in absolute size or cusp morphology (tab. 1, pl. 1-2), some megadermatid taxa exhibit considerable variation in C^1 morphology, including in the degree of separation and form of the posterior accessory cusp. A sample of seven upper canines of *Megaderma lugdunensis* from the early Miocene Vieux-Collonges locality (Guérin & Mein 1971) show striking differences in height and length, with smaller, more gracile teeth tending to have more blade-like posterior accessory cusps. In the Vieux Collonges sample, however, the accessory cusp remains low with respect to the paracone (unlike in *Megaderma richardsi* in which the secondary cusp rises to more than half the height of the paracone). Less variation in C^1 morphology is displayed by a sample of six upper canines of *Megaderma vireti* from the late Miocene Lissieu locality (Mein 1964) and in

a sample of eight *Macroderma gigas* canines from Rackham's Roost (QM F23591-6, QM F23851-2). Sexual dimorphism, which has been documented in the dentition of some Tertiary molossids (Engesser 1972, Rachl 1983), may explain the observed variation in the *M. lugdunensis* canine sample. Sexual segregation within or between roosts could enhance or, equally, mask the extent of morphological variation exhibited by small random samples of extinct megadermatids.

The two upper molars from Rackham's Roost referred here to *Megaderma richardsi* exhibit features that in combination generally characterize megadermatids (i.e. reduced paracone, massive metacone, lingually displaced mesostyle and elongated postmetacrista) but their protocone morphology is quite different. In most megadermatids, the preprotocrista and postprotocrista extend towards (if not touch) the bases of the paracone and metacone respectively, thereby enclosing a relatively small protofossa. In *M. richardsi*, the short postprotocrista drops vertically so that the protocone basin or protofossa opens broadly posterolingually (in *M. jaegeri* the protofossa opens slightly posteriorly). The moderately broad buccal shelf and lingually displaced mesostyle of M^{1-2} are similar to those seen in species of *Megaderma*.

Assignment of the small Australian megadermatid to the genus *Megaderma* has been based primarily on its lack of most of the apomorphies that appear to characterise *Macroderma* species. At the same time, it is recognised that the genus *Megaderma* probably represents a paraphyletic group (see e.g. Hand 1985). Because of its unique M^{1-2} protocone morphology, the Rackham's Roost animal could conceivably be placed in yet another monotypic megadermatid genus. However, the overall affinities of *M. richardsi* appear to lie with species in the *Megaderma* complex and its referral to that group probably most aptly reflects its relationships.

INTRAGENERIC RELATIONSHIPS

Sigé (1976) envisaged three possible lineages of Tertiary *Megaderma*: one essentially European and represented by taxa such as *M. lugdunensis, M. vireti* and *M. mediterraneum*; a second Euroafrican lineage represented by *M. gaillardi*; and a third, northwest African lineage represented by the small but already specialized *M. jaegeri*. It was suggested that the latter two lineages may have arisen from earlier stock morphologically similar to the very large and relatively unspecialized European early Miocene *M. brailloni*. Which if any of these lineages gave rise to extant species is not clear (Sigé 1976). In 1990, Sevilla described the very small *M. lopezae* from late Oligocene sediments of Carrascosa del Campo, central Spain, suggesting that it may be closely related to *M. jaegeri* and that its many primitive features could place it close to the base of the megadermatid radiation proposed by Hand (1985). In that hypothesis, phylogenetic relationships within the *Megaderma* complex could not be confidently resolved but it was suggested that *Megaderma spasma, lugdunensis* and *jaegeri* (at least) might be closely related. Ziegler (1993) considered the German *M. franconica* to be a possible ancestor or close relative of *M. gaillardi*.

Megaderma richardsi is distinguished from most *Megaderma* species by its small size, with the exception of the comparably small *Megaderma lopezae*, and *M. jaegeri*. The two tiny non-Australian taxa share a conspicuous feature not present in

other *Megaderma* species: a strong inflexion in the hypocristid half way along its length (Sevilla 1990). This feature is not present in *M. richardsi* nor does there appear to be any special relationship between the small Australian and non-Australian taxa.

Nevertheless, as noted above, *M. lopezae* and *M. jaegeri* are among taxa that seem to be most similiar to *M. richardsi*, along with the Miocene forms *M. lugdunensis* and *M. vireti* and living species *M. spasma* and *Cardioderma cor*. These are all small to medium-sized megadermatids and it is possible that size rather than phylogenetic relationship might be reflected in these apparent similarities. Further, these taxa have been interpreted to represent various megadermatid lineages (see Sigé 1976, Hand 1985) and it is likely that many similarities with *M. richardsi*, particularly in C^1 and P^4 morphology and in M_1 talonid and M^{1-2} stylar shelf morphology, represent shared plesiomorphies.

Overall, the little Australian bat exhibits an enigmatic mixture of plesiomorphic and autapomorphic features. Some points, however, can be made. Although referred here to the genus *Megaderma*, *M. richardsi* appears to have no special relationship to the living *M. spasma* and *M. lyra*. Its autapomorphies (e.g. loss of P^2 and unique protocone structure) exclude it from being ancestral to any living taxon, or to the Australian *Macroderma* lineage. Its retained plesiomorphic features suggest it may be close to ancestral ?Asian *Megaderma* stock that also gave rise to the late Oligocene Spanish *M. lopezae*, Miocene Moroccan *M. jaegeri* and European *M. lugdunensis-M. vireti* lineage.

PALAEOBIOGEOGRAPHY AND PALAEOECOLOGY

Sigé (1976) has suggested that because early Tertiary megadermatids appear sporadically in the European fossil record, their centre of dispersal was probably outside Europe. Species of *Megaderma* appeared later in Europe, towards the end of the Oligocene, and radiated in an area including Europe during the rest of the Tertiary before disappearing by the Pleistocene. Concurrent Tertiary radiations evidently occurred in the Asian-Australian region to produce the *Macroderma* and *Megaderma richardsi* lineages, both apparently separating from other megadermatid lineages by the late Oligocene.

It is possible that *Megaderma richardsi* was a descendant of poorly represented and poorly understood Oligo-Miocene Riversleigh taxa such as the Dwornamor Variant (Hand 1985) or Henk's Hollow megadermatid (Hand submitted). Unfortunately, little evidence of such a lineage exists. The Australian fossil mammal record is very poor between the middle Miocene and early Pliocene, with only three mammal-bearing deposits of late Miocene age (Alcoota, Ongeva and Beaumaris Local Faunas) being recognised (Woodburne *et al.* 1985, Murray & Megirian 1992), none of which has produced small mammmals.

Alternatively, *M. richardsi* could be the descendant of a late Miocene-early Pliocene Asian immigrant. Its occurrence in the Australian Pliocene coincides with the first occurrence of other allochthronous taxa such as emballonurids and murids. The latter, which now comprise almost a quarter of Australia's native non-marine mammal

fauna, appear to have first colonised Australia from southeast Asia during the late Miocene or earliest Pliocene (Archer *et al.* 1991), and it is possible that emballonurids and the ancestors of *M. richardsi* also arrived at this time. Murids, at least, appear to have entered Australia via the dry woodland corridors of late Tertiary Indonesia and northwestern Australia, rather than the wetter route through New Guinea and eastern Australia (Godthelp in prep.). No megadermatids, fossil nor living, are known from Papua New Guinea, and no emballonurids are endemic to that landmass (Flannery 1990).

During the late Miocene, Australian rainforests declined and drier woodlands spread in northern and central Australia (Archer *et al.* 1991). The Pliocene Rackham's Roost Local Fauna is believed to have been culled from a dry sclerophyl forest or woodland, probably not unlike the dominant vegetation now present in the Riversleigh area. In semi-arid and desert areas of northern Australia today, the most common mammalian remains in the feeding roosts of *M. gigas* have been found to be rodents, dasyurids and small bats (Douglas 1967, Schulz 1986), a balance also characteristic of the Rackham's Roost deposit.

Among the Rackham's Roost bat remains are hipposiderids, vespertilionids and two species of *Taphozous*, all of which probably shared the cave with and/or were victims of *Macroderma gigas*. The small Tertiary megadermatids *M. lopezae* and *M. jaegeri* are believed to have lived in caves and *Megaderma richardsi* was probably a cave-dweller too; living *Megaderma* species usually roost in small groups in caves, pits, buildings and hollow trees (Brosset 1966, Nowak & Paradiso 1983). All three tiny fossil megadermatids are known from deposits interpreted to have accumulated in warm but probably dry habitats in the Oligocene, Miocene and Pliocene respectively (Sevilla 1990, Sigé 1976, Archer *et al.* 1991).

Megaderma richardsi is a very small megadermatid, being approximately one half to two-thirds the size (based on tooth lengths) of the smallest living megadermatid *M. spasma* (av. weight 23-25 g; Nowak & Paradiso 1983). It occurs in the Rackham's Roost deposit with the Ghost Bat *Macroderma gigas*, the largest living megadermatid (weight 140-65 g; Richards 1983) and the predator believed largely responsible for accumulation of the fragmentary bones comprising the deposit. Thus, two very differently sized megadermatids occur together in the deposit, making it difficult to determine what the diet of *Megaderma richardsi* might have been. Of living megadermatids, *Megaderma spasma* is closest in size and dental morphology to *M. richardsi*, if not phylogenetic relationship, and is probably its closest ecological analogue. It is less carnivorous than either *Macroderma gigas* or its living sympatric congener *Megaderma lyra*, eating small vertebrates but favouring grasshoppers and moths for which it forages among trees and undergrowth (Lekagul & McNeely 1977).

ACKNOWLEDGEMENTS

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APPENDIX

Characters surveyed for phylogenetic information were:

- C^1 anterior accessory cusp development, shape, height and separation of posterior accessory cusp with respect to the paracone;

- presence or absence of P^2;

- paracone position in P^4, development of buccal cingulum, heel size and shape;

- M^{1-2} postmetacrista length, reduction of postparacrista and premetacrista, mesostyle height and degree of lingual displacement, presence/absence of paraloph, heel size and direction;

- M_1 trigonid and talonid compression (transverse and anteroposterior), relative heights, lengths and widths of trigonid and talonid, pre-entocristid development, buccal displacement of hypoconulid, hypocristid inflexion (posterior displacement of hypoconulid), metaconid contribution to cristid obliqua;

- high crowns.

LEGENDS OF PLATES

PLATE 1

Megaderma richardsi n. sp. from Rackham's Roost Site, Riversleigh Station, northwestern Queensland, Australia.

Holotype, QM F23619, right maxillary fragment with C^1 and P^4: A-A', stereopairs, occlusal view.

QM F23598, RM^1: B-B', stereopairs, occlusal view; C-C', stereopairs, oblique-occlusal view.

QM F23599, RM^2: D-D', stereopairs, occlusal view; E-E', stereopairs, oblique-occlusal view.

Scale = 1 mm.

PLATE 2

Megaderma richardsi n. sp. from Rackham's Roost Site, Riversleigh Station, northwestern Queensland, Australia.

QM F23620, RC^1: A, buccal view; B, lingual view; C-C', stereopairs, occlusal view.

QM F23600, LM_1: D-D', stereopairs, occlusal view; E, buccal view; F, lingual view.

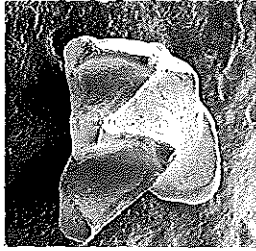Holotype, QM F23619, right maxillary fragment with C^1 and P^4: G, lingual view; G', buccal view.
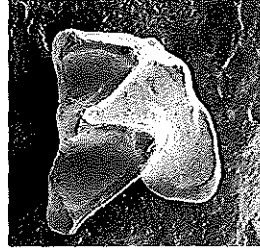
Scale = 1 mm.

PLATE 1

PLATE 2