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Macroderma koppa, a new Tertiary species of false vampire bat (Microchiroptera: Megadermatidae) from Wellington Caves, New South Wales

SUZANNE HAND, LYNDALL DAWSON & MICHAEL AUGEE

School of Zoology, University of New South Wales,
Kensington, NSW 2033, Australia

ABSTRACT. A new late Tertiary false vampire bat, *Macroderma koppa*, is described from the Big Sink doline of Wellington Caves, eastern central New South Wales. The new species appears to be the sister-group of the living Australian Ghost Bat, *Macroderma gigas*. Morphological features that distinguish the new species from *M. gigas* appear to be plesiomorphies shared with most other megadermatids.

Until recently, all Australian fossil megadermatids had been identified as conspecific with (or very close to) the only living Australian megadermatid, the Ghost Bat *Macroderma gigas*. These fossils come from late Pleistocene and Holocene deposits in south-western Western Australia, the Flinders Range in southern central South Australia, north-eastern Queensland and north-eastern and eastern central New South Wales (see Molnar *et al.*, 1984; Fig. 1). Recently, the remains of Miocene species of the Australian endemic genus *Macroderma* have been recovered from limestone sediments on Riversleigh Station, north-western Queensland (Hand, 1984, 1985, 1987). In this paper a new late Tertiary species of *Macroderma* from New South Wales is described.

Fossil specimens described here were collected from breccia in the Big Sink, one of a complex of cave deposits occuring in Wellington Caves, New South Wales. These caves are formed in limestones of the Devonian Garra Formation which outcrops in low hills 1 km east of the Bell River approximately 7 km south of the town of Wellington (32° 35'S, 148° 59'E). They comprise at least five natural caves which have been expanded and greatly disturbed by fossil collection and phosphate mining over a period of 150 years. The history of fossil collection and mining from this locality has been described in detail by Dawson (1985). Cave nomenclature used here follows Dawson (1985, fig. 2).

Recent geological studies of the Wellington cave fills (Frank, 1971; Osborne, 1983) have indicated their considerable stratigraphic complexity. Osborne (1983) has hypothesised a depositional sequence for various stratigraphic units in the Wellington Caves system but the absolute ages of the units have not been determined. Osborne (1983), following Frank (1971), Francis (1973) and others, suggests that the oldest deposits within the caves could have been laid down in the Miocene. He cites faunal evidence suggesting that deposition of bone breccia occurred throughout the Pleistocene at least (Osborne, 1983).

Stratigraphically controlled excavations in the caves were made by the School of Zoology of the University of New South Wales in 1982-1987. Some preliminary results of this collection have been reported by Dawson (1985). Material described here was collected in October 1982 by M. Archer and students of the School of Zoology, University of New South Wales, from the Big Sink doline as part of a pilot study.

The species recovered from the Big Sink doline include : the macropodine *Protemnodon* sp. cf. *P. devisi* (the most abundant species); a plesiomorphic macropodine allied to *Wallabia* spp.; *Macroderma koppa* n.sp.; *Thylacinus* sp.; *Thylacoleo crassidentatus*; *Petauroides stirtoni* (a pseudocheirid otherwise known from the Hamilton local fauna of Victoria); several small dasyurids which are either
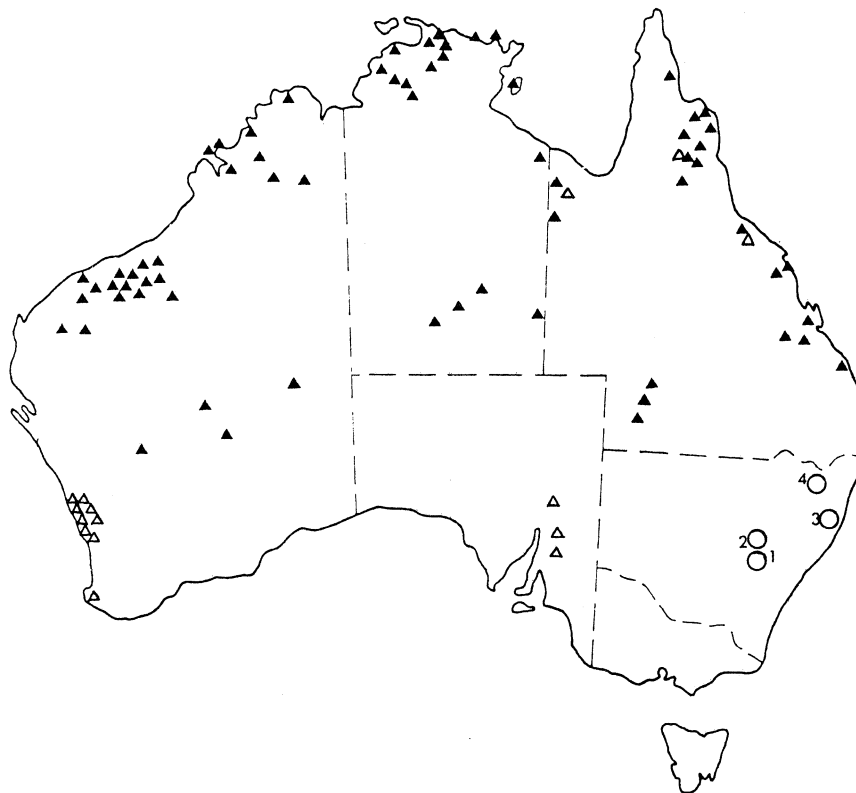
Fig.1. Map of Australia showing the distribution of *Macroderma* (solid triangles, extant populations of *M. gigas*; open triangles, fossil and subfossil remains). Open circles on map represent localities discussed in the text: 1, Cliefden Caves; 2, Wellington Caves; 3, Yessabah Caves; and, 4, Ashford Cave. (After Molnar *et al.*, 1984.)

new species or species otherwise poorly known from late Tertiary deposits (e.g. *Antechinus* sp. comparable to that described from the Floraville local fauna, Queensland by Archer 1982); a small bandicoot which probably represents a new Tertiary genus; a burramyid; and a new pseudomyine rodent. The non-mammalian fauna includes a species of *Tiliqua*, a scincid. The fauna is believed to be early to middle Pliocene in age (see Discussion) and is being described by L. Dawson (in prep.).

Institutional abbreviations used here are as follows: AM F — Australian Museum Fossil Collection; AM M — Australian Museum Mammal Collection (see Fig. 4); BMNH — British Musem (Natural History); UNSW WC — University of New South Wales, Zoology Museum, Wellington Caves Fossil Collection; WAM — Western Australian Museum (see Fig. 3).

CHIROPTERA Blumenbach, 1779

MICROCHIROPTERA Dobson, 1875

RHINOLOPHOIDEA Gray, 1825

MEGADERMATIDAE Allen, 1864

Macroderma Miller, 1907

Macroderma koppa n.sp.

Type material. HOLOTYPE (Fig. 2): the holotype (AM F69070) is a partial skull with associated dentaries. It contains a complete dentition, i.e. $I_{1,2}$, C^1_1, $P^4_{2,4}$, M^{1-3}_{1-3}. PARATYPES: a number of specimens have been selected as paratypes because each serves to illustrate features not represented in the holotype. The paratypes are : UNSW WC171, a skull fragment preserving the cheek, palate and part of the nasal regions; UNSW WC153, fragment with M^{1-3} and the maxillary base of the zygomatic arch; UNSW WC159 fragment preserving the back of the palate and P^4–M^3; UNSW WC158, fragment with P^4–M^3; UNSW WC170, maxillary fragment preserving the cheek region and P^4–M^2; UNSW WC173, 174 and 175, fragments of right C^1s; UNSW WC176, fragment of left C^1; UNSW WC156, associated dentaries with I_1–M_3; UNSW WC173, dentary preserving P_4–M_3, alveoli for C_1 and P_2 and base of ascending ramus; UNSW WC152 dentary fragment preserving M_{1-3} and base of ascending ramus; UNSW WC165, M_{1-3}; UNSW WC177, a right C^1; UNSW WC178, a fragment of a left C_1; and UNSW WC179, a juvenile dentary without teeth. Other referred specimens are also lodged in the Zoology Museum at the University of New South Wales.

Diagnosis. The new species is referred to the megadermatid genus *Macroderma* which currently includes two species: the living Australian Ghost Bat *Macroderma gigas* and the extinct *M. godthelpi* of the Miocene of north-western Queensland (Hand, 1985). Species of *Macroderma* may be distinguished from other megadermatids (of the genera *Lavia, Cardioderma, Megaderma, Lyroderma* and the extinct monotypic *Necromantis*) by, among other features, their large size, enlarged heels of P^4–M^2,
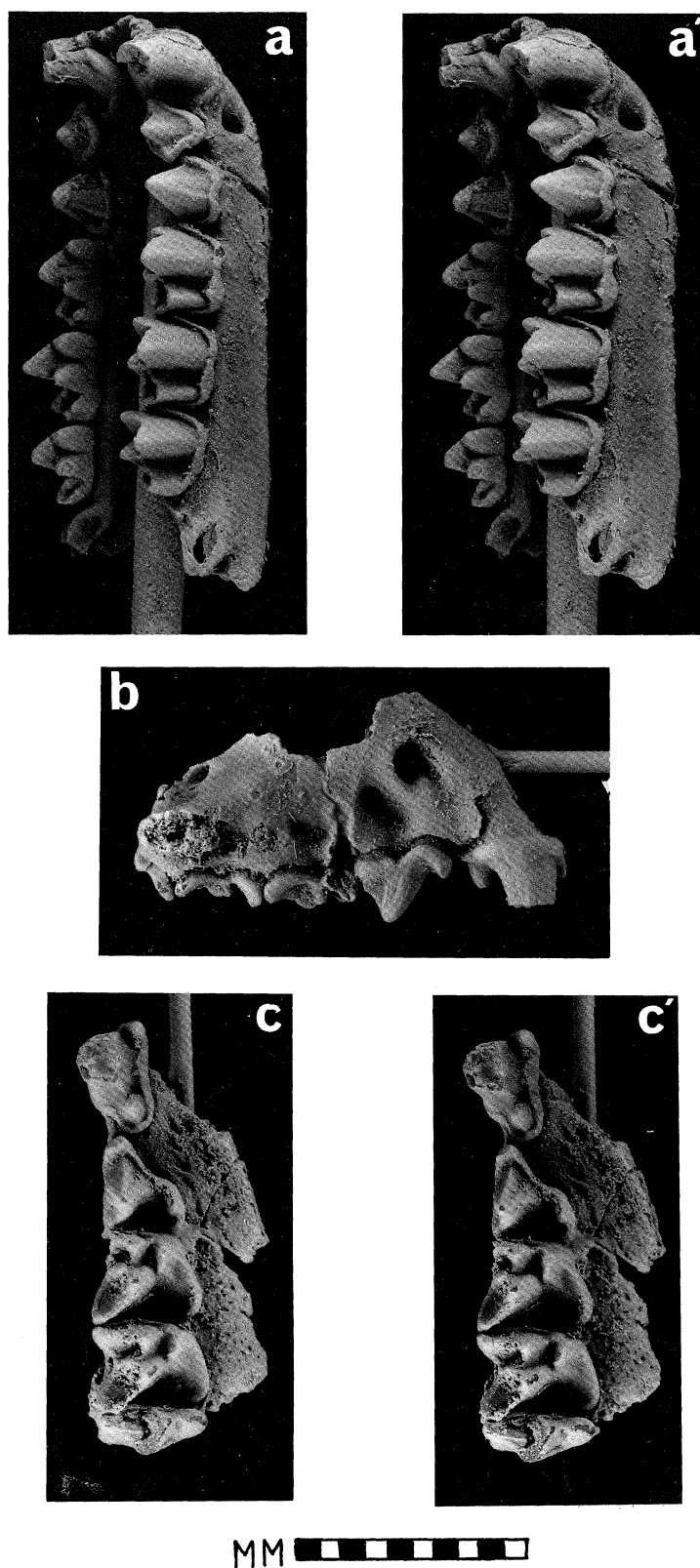
Fig.2. *Macroderma koppa* n.sp., AM F69070 (holotype), partial skull with associated dentaries and complete dentition. a–a^1, stereopairs, buccal-oblique view of mandibles with I$_1$, I$_2$, C$_1$, P$_2$, P$_4$, M$_1$, M$_2$, M$_3$; b, buccal view, right maxillary fragment; and, c–c^1, stereopairs, occlusal-oblique view, right maxillary fragment with C^1, P^4, M^1, M^2 and M^3. Photos by R. Oldfield.

more prominent paracone of C^1 and more robust buccal cingula of the lower molars (Hand, 1985).

The fossil species differs from the living *Macroderma gigas* in its retention of two infraorbital foramina, its poorly-developed nose-shield, its larger incisors and premolars, its less laterally compressed P_4, its lower-crowned and more posteriorly recurved P^4, and in its proportionately longer anterior tooth row.

Macroderma koppa differs from the Australian Miocene species *M. godthelpi* in its much larger size, relatively larger posterior infraorbital foramina, loss of P^2, well-developed P^4 heel, its higher crowns and its more reduced pre-entocristids.

Type locality, lithology and age. The described material was collected from the southern wall of the Big Sink doline at Wellington Caves, NSW. Breccia from this position was identified by Osborne (personal communication, 1982) as part of the Big Sink Unit, the upper stratigraphic member of the Phosphate Mine Beds (Osborne, 1983). It consists of carbonate-cemented osseous sandstones interbedded with thin layers of structureless mud (Osborne, 1983). The unit is hypothesised to be older than (i.e. stratigraphically below) the breccia of the nearby bone-rich Bone Cave, identified by Osborne (1983) as belonging to the Mitchell Cave Beds. The Bone Cave fauna contains many species typical of Pleistocene deposits of eastern Australia (Dawson, 1985). Correlation of associated fauna with taxa otherwise known from better-dated deposits in Queensland and Victoria suggests that the Big Sink deposit from which the holotype was obtained is probably early Pliocene in age.

Description (based on the holotype and paratypes). Because the new species is clearly the closest sister-group of *Macroderma gigas* (see Discussion), it is described only in so far as it differs from *M. gigas*.

Maxillary fragments of *M. koppa* preserve cheek and orbital regions and part of nasal region; no sutures visible. In contrast to *M. gigas*, with single infraorbital foramen, 2 infraorbital foramina exhibited by this species (Fig. 3). Larger, anterior foramen opens onto face within fossa developed above anterior end of P^4. Second, smaller foramen penetrates maxilla, possibly for lateral branch of trigeminal (facial) nerve, occurs within fossa developed above posterior end of P^4. Larger fossa directed more anteriorly towards what would have been noseleaf; smaller fossa is directed anteroventrally towards lips or cheeks.

Nasal region of maxilla rises at approximately same angle as that of *M. gigas* (i.e. about 45° with respect to tooth row), is similarly gently concave. However, at least anterior part of nose-shield differs markedly from *M. gigas* in lack of bony lateral eminences (Fig. 4). Posterior (dorsal) region of nose-shield not preserved.

In their teeth, there is a great deal of morphological overlap between the two species. However, a combination of features in the anterior dentition distinguishes *M. koppa* from *M. gigas*. These features of *M. koppa* are described below.

C^1, represented by 6 specimens, semicircular in basal outline with buccal side convex. Base of tooth posterobuccally swollen with marked notch separating base of paracone from base of large posterolingual accessory cusp. Latter cusp appears to be more discrete or isolated in *M. koppa* than *M. gigas*, being smaller in cross-sectional area and rising more steeply from base of crown. Posterolingually, tall but narrow cingulum commonly surrounds entire tooth but does not always enclose posterolingual accessory cusp. C^1 of *M. koppa* is comparable in size to C^1 of large specimens of *M. gigas* but lacks marked anteroposterior compressional flexure in base of lingual cingulum which characterises *M. gigas*.

P^4 is represented by 5 specimens which are comparable in width to, but much longer than, those of *M. gigas*. Difference in length appears due to elongation anterior to paracone so that principal cusp situated far more posteriorly along buccal edge of tooth than in *M. gigas*, accentuated by posteriorly recurved shape of paracone in *M. koppa*, shallow-angled rise of anterior crest of paracone from anterior cingulum and overall lower crown height of tooth. Anterior cingulum more pronounced in *M. koppa* with a cingular swelling occurring at its highest point. In lingual cingulum of broad heel, a distinct cingular cusp is developed which is also variably present within populations of *M. gigas*.

The morphology of M^1, M^2 and M^3 appears to fall within the range of variation observed in *M. gigas*.

Lower incisors of *M. koppa*, known from holotype and UNSW WC156, far more robust than those of *M. gigas*, being at least one and one half times larger in crown area. Of what is known of incisors, their shape aparently similar to those of *M. gigas* with lateral incisors being much larger than inner incisors.

C_1, represented by 6 specimens, similar in both size and shape to those of large individuals of *M. gigas*. Some intraspecific variation in *M. koppa*, however, appears to occur at lowest posterobuccal point of tooth (i.e. base of buccal edge of posteriorly flattened face of protoconid) where there is sometimes a break in otherwise high buccal cingulum.

P_2, represented by 3 specimens, show considerable variation in depth and height of buccal cingulum. Tooth much wider and longer than in *M. gigas*, being markedly longer posterior to protoconid, so that in *M. koppa* protoconid occurs approximately midway along length of tooth.

P_4, represented by 5 specimens, noticeably more robust than in *M. gigas* (Hand, 1985, fig. 12), being longer, wider, markedly less laterally compressed in area of protoconid. Longitudinal crest linking tip of protoconid to point on posterior cingulum appears to
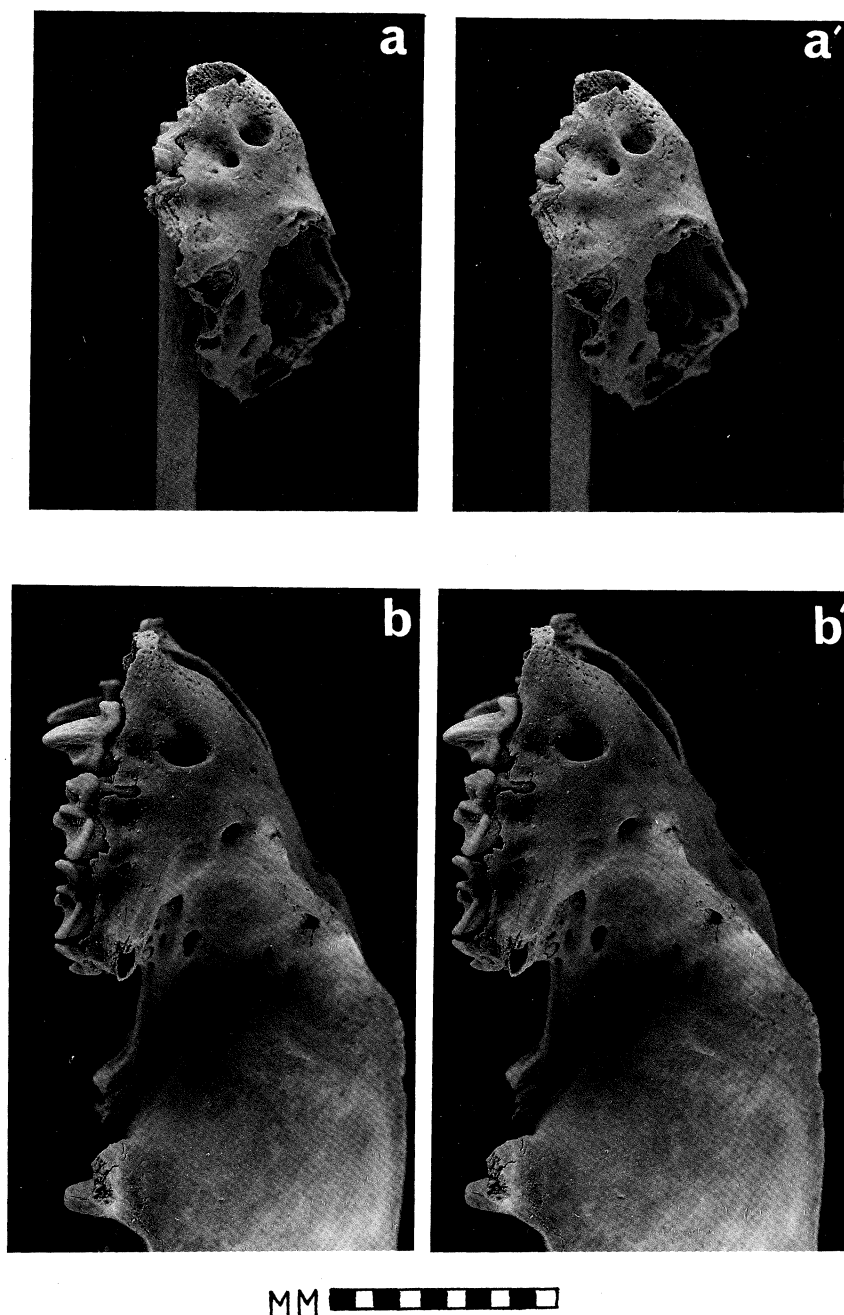
Fig.3. Comparison of the maxillas and number of infraorbital foramina in: a–a¹ (stereopairs), *Macroderma koppa* n.sp. (UNSW WC171); and b–b¹ (stereopairs), *Macroderma gigas* (WAM 65.12.191). Photos by R. Oldfield.

be more pronounced in *M. koppa*, often changes angle at base of protoconid. On either or both sides of crest (i.e. posterolingually and/or posterobuccally) depressions may be developed.

Morphology of M_1, M_2 and M_3 (represented by minimum of 7 specimens each) appears to fall within range of variation in morphology observed in *M. gigas* (Hand, 1985, figs 13–15). In M_1 and M_2,

however, buccal cingulum swollen and ornate at point just anterior to protoconid. This feature, which occurs variably in populations of *M. gigas* (e.g. Hand, 1985, fig. 14), appears to be fixed in this population of *M. koppa* (but see below).

Table 1 gives measurements of the holotype, paratypes and refered specimens made to the nearest 0.1mm using a Wild MMS235 Digital Length-
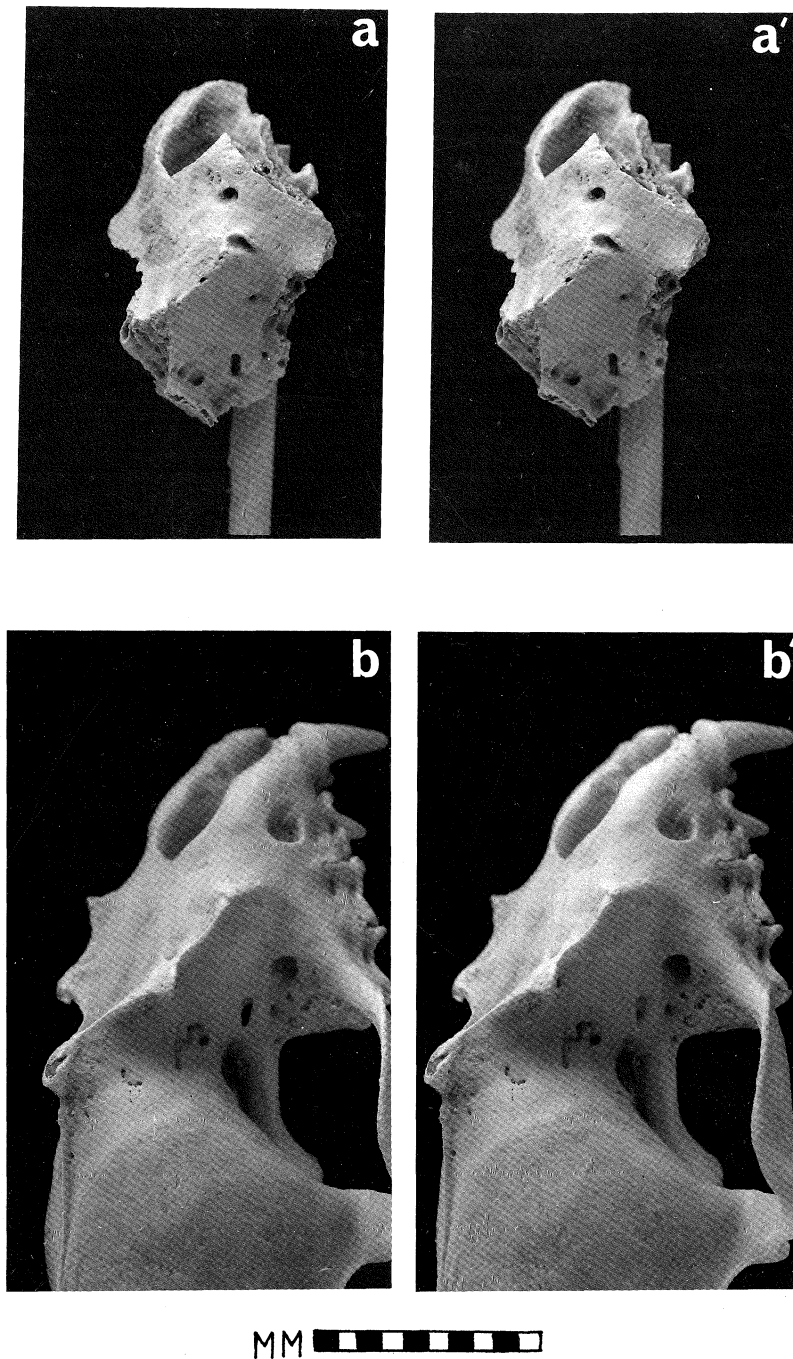
Fig.4. Comparison of the development of the bones comprising the frontal nose-shield in: a–a[1] (stereopairs), *Macroderma koppa* n.sp. (UNSW WC171); and, b–b[1] (stereopairs), *Macroderma gigas* AM M10190). Photos by R. Oldfield.

Measuring Set attached to a Wild M5A Stereomicroscope (see Hand, 1985, figs 9–10 for further explanation of measures).

Further comparisons. Other large specimens of *Macroderma* examined in this study include a dentary fragment from Australian Museum fossil collections (AM F47021; see Molnar *et al.*, 1984, fig. 3) collected from an unknown locality in the

Wellington Caves system. The specimen was probably collected last century or early this century and originally housed in the Mining Museum, Sydney before transfer to the Australian Museum (see Dawson, 1985).

Features of AM F47021 shared with *M. koppa* include its large size, lack of lateral compression of P_4 and its pronounced crest on P_4 running from the tip

of the protoconid to the posterior cingulum. For these reasons, the dentary fragment AM F47021 is tentatively referred to *M. koppa* n.sp. This specimen does not, however, exhibit a particularly swollen or ornate buccal cingulum on M_{1-2}.

Another specimen from "Wellington Caves", BMNH 42670b, discussed by Molnar *et al.* (1984) and housed in the British Museum, was not examined in this study.

Large Quaternary specimens of *Macroderma* from Yessabah Caves in north-eastern New South Wales and Cliefden Caves in eastern central New South Wales (see Fig. 1) are currently refered to *M. gigas* (Molnar *et al.*, 1984). Although larger than most specimens of *M. gigas*, because they are represented only by isolated dentaries lacking anterior teeth their identity remains in doubt.

The maxilla of a recently described partial skull recovered from Ashford Cave, north-eastern New South Wales (see Fig. 1) (*Macroderma sp.* of Molnar *et al.*, 1984, figs 1,2) exhibits a single infraorbital foramen which excludes it from *M. koppa*. The lingual shape of the M^3 protocone, the feature singled out by Molnar *et al.* as being different, does not appear to differ significantly from larger samples of *M. gigas* and it is therefore refered to that species.

Etymology. The species is named after "Koppa", the mythological spirit believed by Australian Aborigines to have inhabited Wellington Caves (Lane & Richards, 1963). The reference to a spirit or ghost alludes to this species' close phylogenetic relationship with the living Ghost Bat, *Macroderma gigas*. Of the Big Sink fossil species so far identified, *M. koppa*, like its mythological counterpart, is probably the only one that actually inhabited the cave.

Table 1. Measurements of upper and lower teeth of the holotype (AM F69070), paratypes and referred specimens of *Macroderma koppa* n.sp. from Wellington Caves, New South Wales. In mm. (See Hand, 1985, figs 9–10 for further explanation of measures.)

Character	Holotype AM F69070	UNSW WC152	UNSW WC162	UNSW WC161	UNSW WC163	UNSW WC154	UNSW WC158	UNSW WC153	UNSW WC164	UNSW WC156	UNSW WC159	UNSW WC170	AM F47021
Length C^1–M^3	16.7												
Length P^4–M^3	13.1										12.8		
Length M^1–M^3	9.4												
P^4 buccal length	4.1					4.2					3.7	4.0	
M^1 buccal length	4.1					4.1	4.0				4.2		
M^2 buccal length	3.8			3.6		3.8	3.9					4.2	
M^3 buccal length	2.0						1.9						
P^4 lingual length	4.1											4.2	
M^1 lingual length	4.0												
M^2 lingual length	3.6			3.9								3.6	
P^4 width	3.5											3.2	
M^1 width	4.4					4.3	4.1						
M^2 width	4.5			4.4		4.5	4.6					4.1	
M^3 width	4.3					4.5							
Dentary depth below M_2 protocomid	4.2	4.5								4.4			
Length C_1–M_3	19.7												
Length P_4–M_3	15.0												
Length M_1–M_3	12.1												
P_4 length	3.4	3.2									3.1		3.6
P_4 anterior cingulum to protoconid length	1.4										1.4		1.9
M_1 length (in situ)	4.2	3.7									3.9		3.8
M_2 length (in situ)	4.2	4.1									4.0		3.9
M_3 length (in situ)	4.0												
M_1 trigonid length	2.7	2.3	2.5	2.2							2.6		2.5
M_1 talonid length	1.5	1.5	1.4	1.6							1.4		1.4
M_2 trigonid length	2.5	2.4		2.3					2.3		2.5		2.4
M_2 talonid length	1.6	1.6		1.3					1.6		1.5		1.5
M_3 trigonid length	2.5					2.5			2.2	2.5			
M_3 talonid length	1.4					1.4			1.7				
P_4 width	2.3		2.0								2.1		2.1
M_1 trigonid width	2.4	2.3	2.3	2.1							2.4		2.2
M_1 talonid width	2.5	2.4	2.3	2.2							2.5		2.4
M_2 trigonid width	2.8	2.4		2.4					2.4		2.6		2.5
M_2 talonid width	2.6	2.3		2.2					2.3		2.5		2.5
M_3 trigonid width	2.5					2.2			2.4				2.6
M_3 talonid width	2.1					1.6			1.9				

Discussion

Recent geological studies by Frank (1971, 1972, 1975), Francis (1973) and Osborne (1983) have shown that bone-bearing stratigraphic units in Wellington Caves are not contemporaneous. Osborne (1983) suggests that they represent a minimum of three periods of deposition ranging from at least the Pliocene to late Pleistocene. The Big Sink Unit has been identified as being the upper member of the Phosphate Mine Beds (Osborne, 1983) and, on the basis of faunal evidence, is hypothesised to have been deposited during the early to middle Pliocene.

This faunal evidence is provided by a number of studies in progress involving stage-of-evolution comparisons with mammalian taxa from the stratigraphically higher (i.e. younger) Bone Cave sediments, as well as other better-dated Australian Pliocene and Pleistocene fossil mammal assemblages. For example, the dominant macropodine of the Big Sink local fauna, *Protemnodon* sp. cf. *P. devisi*, differs only slightly

(Dawson, 1985) from *P. devisi* which is known only from the early Pliocene-aged Chinchilla Sand fauna of south-eastern Queensland (Bartholomai, 1973). A Pliocene age is also supported by the presence of *Thylacoleo crassidentatus* and, among the small marsupials, *Petauroides stirtoni* and a unique peramelid which are otherwise known only from the early Pliocene Hamilton local fauna of Victoria. A Pliocene age is also indicated by the conspicuous absence of many species which are typically found in Pleistocene deposits (e.g. species of *Macropus, Procoptodon, Diprotodon optatum, Sthenurus atlas,* several rodent and dasyurid species, etc.) and which are abundantly present in the Bone Cave deposits of Wellington Caves (Dawson, 1985).

The Big Sink's *Macroderma koppa* is clearly distinguished from all known modern and Pleistocene specimens of *M. gigas* by the retention of two infraorbital foramina on the facial side of the maxilla. The double foramen state is a plesiomorphic (or primitive) condition present in most megadermatids (Hand, 1985) with the exception of
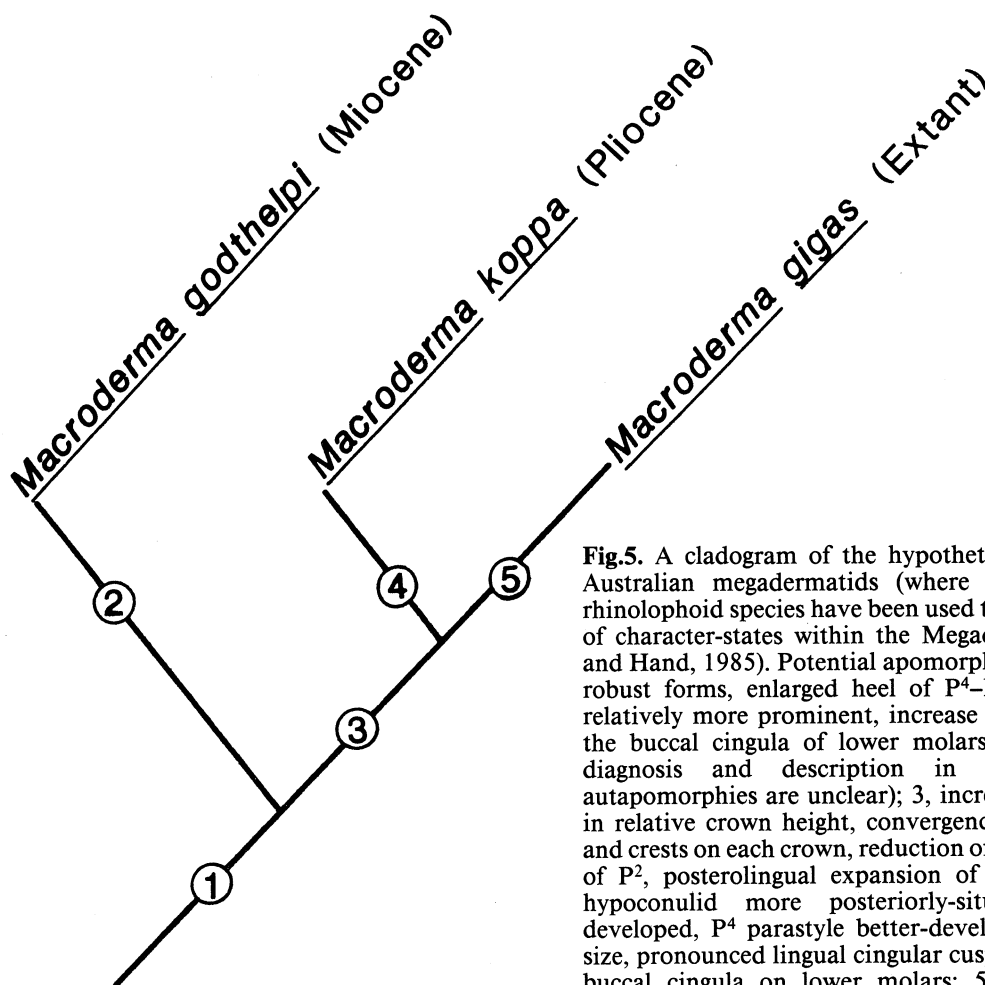

Fig.5. A cladogram of the hypothetical relationships of Australian megadermatids (where nycterid and other rhinolophoid species have been used to determine polarity of character-states within the Megadermatidae; see text and Hand, 1985). Potential apomorphies are as follows: 1, robust forms, enlarged heel of P^4–M^2, paracone of C^1 relatively more prominent, increase in the robusticity of the buccal cingula of lower molars; 2, (see systematic diagnosis and description in Hand, 1985; but autapomorphies are unclear); 3, increase in size, increase in relative crown height, convergence of principle cusps and crests on each crown, reduction of preentocristids, loss of P^2, posterolingual expansion of the heel of P^4, M_2 hypoconulid more posteriorly-situated and better-developed, P^4 parastyle better-developed; 4, increase in size, pronounced lingual cingular cusp on P^4, more robust buccal cingula on lower molars; 5, single infraorbital foramen, relative shortening of the anterior tooth row, elaboration of frontal nose-shield, lateral compression of P_4, higher crowned and less posteriorly recurved P^4.

species of the French early Tertiary genus *Necromantis* (Revilliod, 1922) and all specimens of *M. gigas*. *Necromantis adichaster* and *M. gigas* exhibit a single infraorbital foramen. Because *N. adichaster* lacks most of the derived features that *M. gigas* shares with other living and fossil megadermatids (e.g. loss of P_3, a posteriorly extended palate, well-developed heels on P^4–M^2 and an expanded paroccipital shelf) and exhibits a number of striking autapomorphies (e.g. a conspicuously flattened skull, shortened face and inclined rectilinear sagittal crest), the shared state of the single foramen in *N. adichaster* and *M. gigas* is interpreted to be the result of evolutionary convergence (Hand, 1985).

Macroderma koppa and *M. gigas* appear to be very closely related. *Macroderma gigas* appears to be a relatively recent offshoot from an ancestral population of the kind represented by *M. koppa*. A phylogenetic hypothesis involving these species and the Australian Miocene *M. godthelpi* is given in Fig. 5. Determination of the polarity of character-states in this phylogenetic analysis has been facilitated by common recognition (following Miller, 1907) of a Megadermatidae-Nycteridae sister-group relationship within the Rhinolophoidea (see Hand, 1985).

Features that distinguish *M. koppa* from *M. gigas* include its relatively poorly-developed nose-shield, more robust incisors and premolars, less laterally compressed P_4, lower crowned but larger P^4 and its proportionately longer anterior tooth row. In these plesiomorphic features, *M. koppa* more closely resembles the Australian Miocene species *Macroderma godthelpi* than the living *M. gigas* (Fig. 5).

Macroderma koppa is the second fossil megadermatid to be described from Australia. Four new but as yet undescribed Miocene megadermatids and a tiny Pliocene species have been recently recovered from deposits on Riversleigh Station (Hand, 1987). This diversity indicates that *M. godthelpi*, *M. koppa* and *M. gigas* are representatives of what was once an extensive Australian radiation of false vampires, second only, perhaps, to that of the European Tertiary.

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