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A New Species of Extinct False Vampire Bat (Megadermatidae: Macroderma) from the Kimberley Region of Western Australia

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Abstract. A new species of False Vampire Bat (Megadermatidae), Macroderma handae sp. nov., is described from dental, dentary and maxillary fragments recovered from limestone deposits at Dingo Gap, Oscar Range, in the Kimberley region of Western Australia. This material is likely to be of Pliocene age, or early Pleistocene, based on biocorrelation within the same sample. The absence of the P3 indicates that it is more derived than Miocene taxa including Macroderma malugara and M. godthelpi, but its phylogenetic position relative to M. koppa could not be determined. It appears to be slightly smaller than M. gigas and M. koppa based on the size of M1 and M2. It can be distinguished from M. gigas by the lesser degree of fenestration in the maxilla; and from all other species of Macroderma by the shape of the protofossa of the M1, plus the M2 protoconid relatively high and of proportionally greater area within the trigonid. Other material collected, but not identified completely or described, includes several lower canines from a species of emballonurid, and a dentary with M1, representing a vesperilionid bat. Given the wear striations observed on the M2 of the newly-described Macroderma species, we suggest that it was a predator of small vertebrates, including possibly the chiropteran co-inhabitants of the cave. This new species of Macroderma is the sixth species recognized in the genus so far, and the second from the Pliocene.

Introduction

The family Megadermatidae (False Vampire Bats) has a long history that began in the mid-Eocene with its divergence from the Craseonycteridae c. 44–43 Ma, based on molecular dating methods (95% credibility interval 47–39 Ma; Teeling et al., 2005; Foley et al., 2015). Until recently, the oldest known megadermatid fossil was considered to be Necromantis adichaster Weithofer, 1887, represented in the Quercy Phosphorites Formation, France, but this genus is now accepted to be part of a distinct family (Necromantidae; Sigé, 2011; Ravel et al., 2016; Hand & Sigé, 2018). Early megadermatid lineages are represented by modern extant taxa in the genera Lavia and Cardioderma, based on their inferred phylogenetic position (Hand, 1985; but see Kaňuch et al., 2015). The oldest megadermatid fossils, however, are: Saharaderma pseudovampyrus Gunnell et al., 2008 from early Oligocene deposits in Egypt (33.9–28.4 Ma), which shows similarities to Cardioderma and Lavia, and with which it may form a distinct African clade (Gunnell et al., 2008); and Megaderma lopazaev Sevilla, 1990 from early Oligocene deposits in Spain. The remaining eight described Afro-European species of extinct Macroderma are represented in deposits that range from the Kimberley Region of Western Australia. In Papers in Honour of Ken Aplin, ed. Julien Louys, Sue O’Connor, and Kristofer M. Helgen. Records of the Australian Museum 72(5): 161–174. https://doi.org/10.3853/j.2201-4349.72.2020.1732

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† Ken Aplin 1958–2019, deceased
in age from the early Miocene (e.g., *Megaderma brailloni* Sigé, 1968 from the Aquitanian) to the Pleistocene (e.g., *Megaderma watwat* Bate, 1937) (reviewed in Sigé, 1976; Sevilla, 1990; Ziegler, 1993).

Australia has excellent representation of megadermatid fossil taxa, beginning from the mid-Cenozoic and extending to subfossil recent material (Molnar *et al.* 1984; Hand, 1996). Most have been discovered in the freshwater limestone deposits of Riversleigh World Heritage Area, northwestern Queensland, which has a rich diversity of bat species from the families Mystacinidae (Hand *et al.*, 1998), Emballonuridae (Archer *et al.*, 2006; King, 2013), Rhinonycteridae (Sigé *et al.*, 1982; Hand, 1997a; Hand & Archer, 2005), Hipposideridae (Hand, 1997b; Hand, 1998a, 1998b), Molossidae (Hand, 1990; Hand *et al.*, 1997), and Vespertilionidae (Menu *et al.*, 2002).

The genus *Megaderma* is thought to have entered Australia after the middle Miocene, and the small-sized *Megaderma richardi* from the early Pleistocene Rackham’s Roost Site at Riversleigh is its only known representative in Australia (Hand, 1995; Woodhead *et al.*, 2016). Four extinct Australian megadermatid taxa have been referred to the endemic genus *Macroderma*—*M. godthelpi* Hand, 1985 from the early Miocene Microsite and middle Miocene Gag Site, Riversleigh; *M. malugara* Hand, 1996 from the middle Miocene Gotham City Site, Riversleigh; an unnamed species of *Macroderma* from the middle Miocene Henk’s Hollow Site, Riversleigh (Hand, 1996); and *M. koppa* Hand, Dawson & Augee, 1988 from the Pliocene deposits of Big Sink, Wellington Caves, New South Wales (Hand *et al.*, 1988). The remaining two extinct megadermatid taxa from Australia have not been given a formal binomial name—Dwornamor Variant from the middle Miocene Gag Site, Riversleigh (Hand, 1985); and *Macrodermatidae indet.* from the middle Miocene Henk’s Hollow Site, Riversleigh (Hand, 1996).

The extant *Macroderma gigas* (Dobson, 1880) is currently distributed across northern Australia, from the Pilbara and Kimberley regions of Western Australia, through the Top End of the Northern Territory and part of the Gulf Coastal and Mt Isa Inlier bioregions of the Northern Territory and northwestern Queensland, to Cape York, Queensland (Worthington Wilmer *et al.*, 1999; Churchill, 2008). It contracted from areas further south in the Holocene (Molnar *et al.*, 1984), and has declined further since the arrival of Europeans (Churchill & Helman, 1990; Churchill, 2008; Woinarski *et al.*, 2014; Augusteyn *et al.*, 2018; Armstrong *et al.*, 2019). This taxon is also represented in the early Pleistocene deposit of Rackham’s Roost, Riversleigh (Hand, 1996; Woodhead *et al.*, 2016), as well as many sites of Pleistocene and Holocene age around Australia (Molnar *et al.*, 1984). In Western Australia, fossil and subfossil bat material has been discovered in very few localities, though *M. gigas* is a conspicuous presence in numerous limestone caves in the south-west corner (reviews in Cook, 1960; Bridge, 1975; Baynes *et al.*, 1975; Molnar *et al.*, 1984; Armstrong & Anstee, 2000), and few of these caves are now used by bats of any species (Armstrong *et al.*, 2005). Megadermatid fossils have also been discovered further north on Barrow Island and the Monte Bello Islands off the Pilbara coast (Ken Aplin, unpublished observations).
More recently, a limestone deposit from Dingo Gap in the Kimberley region, north-west of Fitzroy Crossing (Fig. 1), has produced material from a range of fossil mammals, which includes at least three species of bat. One of these is clearly a megadermatid, which is described here as a new species. The other bat species are not sufficiently well represented for identification or formal description, but they do provide context for the occurrence of the megadermatid bones and teeth.

Methods

Scanning electron micrographs were taken with a Jeol JSM6606B microscope. Holotype and paratype material was examined and illustrated in comparison with a specimen of *M. gigas* from the CSIRO Australian National Wildlife Collection (ANWC), Canberra (CM568, male, collected from Mt Etna, Queensland), as well as material in the Western Australian Museum (WAM; three dentaries from *M. gigas* specimens M3415, M18284 and M18575; all from the Pilbara region of Western Australia). Descriptions are made in comparison with information in Hand (1985, 1995, 1996) and Hand et al. (1988). Measurements were made from SEM images using the software ImageJ (Rasband, 1997–2005; Abramoff et al., 2004). Measurements of the newly described species made for direct comparison with *M. gigas* correspond to a subset of those in Hand (1985) and are numbered accordingly (Fig. 2). Additional measurements made for descriptive purposes are indicated by letters (Table 1). Higher level systematics follow Simmons & Cirranello (2014). Anatomical terminology follows Hand (1985, 1996).

Systematics

Chiroptera Blumenbach, 1779

Yinpterochiroptera Springer, Teeling, Madsen, Stanhope & de Jong, 2001

Rhinolophoidea Gray, 1825

Megadermatidae H. Allen, 1864

*Macroderma* Miller, 1906

*Macroderma handae* sp. nov. Aplin and Armstrong

Figs 3–8

Holotype. Fragment of left dentary containing a mostly intact M\(^2\), broken P\(^4\), M\(_1\), and M\(_2\), and alveoli of single-rooted P\(_2\) and C\(_1\) (WAM 2020.4.1; Figs 3A,B and 4A,C,E,G). Paratypes. A second fragment of left dentary with alveoli of incisors, C\(_1\), P\(_2\) and P\(_4\), and first two molars (WAM 2020.4.2; Fig. 3D,E); a third fragment of left dentary containing a worn M\(_1\), and one alveolus of M\(_2\) (WAM 2020.4.3; Fig. 3C); palatal fragment of left maxilla with lingual alveoli of P\(_4\) and M\(_1\) (WAM 2020.4.4; Fig. 5B,C); fragment of right maxilla with alveoli of C\(_1\) and P\(_4\) (WAM 2020.4.5; Fig. 5A); right M\(_1\) (WAM 2020.4.6; Fig. 6A,C); right M\(^2\) fragment (WAM 2020.4.10; Fig. 6E); anterior portion of right C\(_1\) (WAM 2020.4.7; Fig. 7A); right C\(_1\) with broken paracone (principal cusp, sensu Hand, 1985; WAM 2020.4.9; Fig. 7C,D); left P\(_2\) (WAM 2020.4.8; Fig. 8A,B,D); left M\(_3\) in poor condition (WAM 2020.4.11; Fig. 4I); left P\(_4\) with damaged paracone (principal cusp; WAM 2020.4.12; Fig. 8E–H). All type material is lodged in the Western Australian Museum.

Type locality, lithology, and age. Material was collected from a cemented accumulation of bone material that formed on the floor of a cave in a carbonate-rich stratigraphic sequence at Dingo Gap, Oscar Range, Kimberley region, Western Australia (17°40’S 125°13’E, Fig. 1). The location is part of the marginal reef slope and basinal facies of the northern face of the Oscar Range (Stephens & Sumner, 2003). This range forms the northern edge of the Canning Basin, and is the remnant of an Upper Devonian marine reef complex.

The bone accumulation was in a hard limestone matrix and consisted of teeth and small bone fragments of mammals, particularly rodents (Muridae: Hydromyini (*sensu* Smissen & Rowe, 2018); *Rattus* was absent). Further details of the fauna in this collection are not yet available. It is more likely to be an accumulation from a cave floor beneath a megadermatid bat roost site rather than a pellet accumulation from an owl given that larger jaw fragments were absent. Dental material from other bats was also present, including an unknown species of bat (Fig. 9A–D), canines from an emballonurid (probably *Taphozous* sp.; Fig. 9E–L), and a lower row of molars from an unidentified vespertilionid (Fig. 9M,N). Given the absence of *Rattus*, which is thought to have reached Australia by at least the mid-Pleistocene (Rowe et al., 2019), the material is aged tentatively as Pliocene or early Pleistocene.

Diagnosis. Referred to the genus *Macroderma* Miller, 1906 on the basis of the large size of the M\(^1\)–3 (within the lower part of the size range of *M. gigas* and *M. koppa*; Table 1; cf. Hand, 1995: 52), the M\(^3\) with elongated heel, and markedly lingually displaced mesostyle (cf. *Megaderma richardsi*; Hand, 1995: 66); M\(_3\); parasistis (*sensu* Hand, 1995, 1996; = protocristid *sensu* Hand, 1985, who used both terms) longer than metacristid; M\(_{3,1}\); reduced metaconid contribution to the cristid obliqua; M\(_{3,3}\) robust and continuous anterior, labial (= buccal) and posterior cingula (see Hand, 1996: 373).

Compared with *Macroderma gigas*—Maxilla fenestrated (Fig. 5B,C), but not to the degree seen in *M. gigas* (cf. Hand, 1985: 31); anterior part of dentary thickened, though relatively gracile compared with that of *M. gigas* (dentine depth below M\(_1\) protoconid less in *M. handae*; Table 1; Fig. 3A,F); most molar measurements smaller than the average for *M. gigas*, or within the lower part of the size range (Table 1); the shape of the M\(^4\) protofossa (whose edges are defined by the preprotocrista and postprotocrista) is rounded rather than triangular (Fig. 6A–D); M\(_3\) paracristid lower, and protruding less anteriorly past the protoconid (trigonid less expanded anteriorly than in *M. gigas*); M\(_3\) protoconid relatively high and of proportionally greater area within the trigonid (more than half in occlusal view (Fig. 4A,B); and M\(_2\) talonid proportionally larger with respect to the trigonid (Fig. 4A,B). No protostyle cusp on P\(_4\), which is obvious in *M. gigas* (Fig. 8E,F).

Compared with *M. koppa* (see Hand et al., 1988: 344–346)—Anterior upper tooth row relatively shorter in *M. handae*, alveoli of C\(_1\) and P\(_4\) indicating overlap of crowns...
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**Table 1.** Measurements (mm; Fig. 2) of the holotype dentary and M₂ (WAM 2020.4.1), and the paratypes M₁ (WAM 2020.4.6) and C₁ (WAM 2020.4.7) of *Macroderma handae* sp. nov., in comparison with *M. gigas* and *M. koppa*, values and character numbers are from Hand, 1985: 23,25; Hand et al., 1988: 349; mean and range in parentheses; RR indicates measurements from *M. gigas* in Rackham’s Roost, see Hand, 1996: 370; letters in the first column represent measurements made in the present study only; * measurement from paratype WAM 2020.4.2).

<table>
<thead>
<tr>
<th></th>
<th><em>M. handae</em></th>
<th><em>M. gigas</em></th>
<th><em>M. koppa</em></th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>holotype dentary and M₂</strong></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>3 Dentary depth below M₂ protoconid</td>
<td>3.5, 3.42*</td>
<td>3.92 (3.40–4.90) RR: 3.45</td>
<td>4.2 (4.4–4.5)</td>
</tr>
<tr>
<td>10 M₁ length (sum measurements 14 + 15)</td>
<td>3.21</td>
<td>3.78 (3.41–4.17) RR: 3.27</td>
<td>4.2 (3.9–4.1)</td>
</tr>
<tr>
<td>14 M₂ trigonid length</td>
<td>1.73</td>
<td>2.41 (1.91–2.79) RR: 2.10</td>
<td>2.5 (2.3–2.5)</td>
</tr>
<tr>
<td>15 M₂ talonid length</td>
<td>1.48</td>
<td>1.41 (1.00–1.88) RR: 1.19</td>
<td>1.6 (1.3–1.6)</td>
</tr>
<tr>
<td>21 M₂ trigonid width</td>
<td>2.36</td>
<td>2.38 (2.05–2.68)</td>
<td>2.8 (2.4–2.6)</td>
</tr>
<tr>
<td>22 M₂ talonid width</td>
<td>2.16</td>
<td>2.31 (1.86–2.85)</td>
<td>2.6 (2.2–2.5)</td>
</tr>
<tr>
<td>27 M₂ paracristid length</td>
<td>1.44</td>
<td>1.72 (1.38–1.92)</td>
<td>—</td>
</tr>
<tr>
<td>28 M₂ metacristid length</td>
<td>1.04</td>
<td>1.25 (0.98–1.65)</td>
<td>—</td>
</tr>
<tr>
<td>A M₂ protoconid height (not illustrated)</td>
<td>3.19</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>B Mental foramen width (not illustrated)</td>
<td>0.53, 0.55</td>
<td>—</td>
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<thead>
<tr>
<th><strong>paratypes M₁ and C₁</strong></th>
<th><em>M. handae</em></th>
<th><em>M. gigas</em></th>
<th><em>M. koppa</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>14 M₁ labial (buccal) length</td>
<td>3.53</td>
<td>3.93 (3.36–4.40) RR: 3.36, 3.52</td>
<td>4.1 (4.0–4.2)</td>
</tr>
<tr>
<td>18 M₁ lingual length</td>
<td>3.13</td>
<td>4.24 (3.60–4.76) RR: 3.59, 3.85</td>
<td>4.0</td>
</tr>
<tr>
<td>21 M₁ width</td>
<td>3.95</td>
<td>4.15 (3.65–4.63) RR: 3.43, 3.94</td>
<td>4.4 (4.1–4.3)</td>
</tr>
<tr>
<td>25 M₁ metacone apex to metastyle</td>
<td>2.15</td>
<td>2.73 (2.36–2.88)</td>
<td>—</td>
</tr>
<tr>
<td>28 M₁ paracone to heel</td>
<td>2.43</td>
<td>3.20 (2.29–3.66)</td>
<td>—</td>
</tr>
<tr>
<td>30 M₁ heel inflexions</td>
<td>1.49</td>
<td>2.34 (1.84–3.54)</td>
<td>—</td>
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<tr>
<td>32 M₁ length through protocone</td>
<td>1.70</td>
<td>2.44 (2.08–2.90)</td>
<td>—</td>
</tr>
<tr>
<td>C M₁ protofossa width</td>
<td>1.20</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>D M₁ heel width</td>
<td>1.37</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>E C₁ height (not illustrated)</td>
<td>4.29</td>
<td>—</td>
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![Figure 2](image-url)  
**Figure 2.** Dental measurements taken from the left M₂ and the right M₁, based on Hand (1985).

(Fig. 5A; cf. Hand et al., 1988: 345, fig. 2b,c); the shape of the M₁ protofossa (with edges defined by the preprotocrista and postprotocrista) is rounded rather than triangular; molar measurements smaller than the values for *M. koppa* (Table 1; cf. Hand et al., 1988: 349); anterior part of dentary relatively gracile compared with that of *M. koppa* (dental depth below M₂ protoconid less in *M. handae*; Table 1); M₂ paraconid relatively low, and protruding less anteriorly past the protoconid due to anterior compression of the trigonid (Fig. 4C,E; cf. Hand et al., 1988: 345, fig. 2a); M₂ paraconid relatively high and of proportionally greater area within the trigonid (more than half in occlusal view; Fig. 4A); entoconid smaller than hypoconulid (Fig. 4E,G; cf. Hand et al., 1988: 345, fig. 2a); the P₂ is of a similar shape in both species (Fig. 8A,B,D; cf. Hand et al., 1988: 345, fig. 2a).

Compared with *M. malugara* Hand, 1996—P₂ absent in *M. handae*; slightly smaller size of M₁ and M₂ (Table 1; cf. Hand, 1996: 368); the shape of the M₁ protofossa (whose edges are defined by the preprotocrista and postprotocrista) is rounded rather than triangular; M₁ paraconid relatively low, and protruding less anteriorly past the protoconid due to anterior compression of the trigonid (Fig. 4A,C,P; cf. Hand, 1996: 366–367, pl. 48k–m); M₂ protoconid relatively high and of proportionally greater area of the trigonid (more than
Figure 3. Scanning electron micrographs of holotype and paratype material of *Macroderma handae* sp. nov. (A) lateral view of the left dentary of holotype WAM 2020.4.1 with mostly intact M$_2$, broken P$_4$, M$_1$ and M$_3$, and alveoli of single-rooted P$_2$ and C$_1$; (B) occlusal view of the holotype WAM 2020.4.1 anterior to the M$_2$; (C) occlusal view of a fragment of left dentary, paratype WAM 2020.4.3; (D, E) lateral and occlusal view of a fragment of left dentary, paratype WAM 2020.4.2; (F) digital photograph of the left dentary of *M. gigas* WAM M18284. Scale bars 1 mm.
Figure 4. Scanning electron micrographs of holotype and paratype material of Macroderma handae sp. nov. (A, C, E, G) occlusal, lingual, labial, and labial-oblique views of the left M2 from the holotype WAM 2020.4.1; (B, D, F, H) corresponding views of the left M2 of M. gigas ANWC CM568; (I) occlusal view of left M3, paratype WAM 2020.4.11; (J) left M3 of M. gigas ANWC CM568. Scale bars 1 mm.
Figure 5. Scanning electron micrographs of paratype material of *Macroderma handae* sp. nov. (A) fragment of the right maxilla with alveoli of the C1 and P4, paratype WAM 2020.4.5; (B) palatal fragment of left maxilla with lingual alveoli of P4 and M1, paratype WAM 2020.4.4; (C) detail of the blood vessel fenestrations in paratype WAM 2020.4.4; (D) probable wear striations on the M3, paratype WAM 2020.4.11; (E) wear striations from *M. gigas* ANWC CM568. Scale bars 1 mm, except where indicated otherwise.
Figure 6. Scanning electron micrographs of paratype material of Macroderma handae sp. nov. (A, C) occlusal-oblique views of a right M1, paratype WAM 2020.4.6; (B, D) corresponding views of the right M1 of M. gigas ANWC CM568; (E) occlusal view of a fragment of a right M2, paratype WAM 2020.4.10; (F) corresponding view of the right M2 of M. gigas ANWC CM568. Scale bars 1 mm.
Description. The anterior part of the dentary is thickened, though relatively gracile and shallower in depth compared to *M. koppa* and *M. gigas*, with likely two lower incisors per side (paratype WAM 2020.4.2; anterior detail not shown in Fig. 3A,B,D,E). Two premolars are present—P2 and P4, in addition to the M1–2 (Fig. 3A,B), and the M3 (Fig. 4I). There is marked extension posterolingually of the C1, similar to *M. gigas* (Fig. 7A–D). The P2 has a proportionally large cingulum, as can be seen in occlusal view, which gives the tooth the appearance of a “witches hat” when viewed from either the labial or lingual side (Fig. 8A,B,D).

The M1 is shorter than, or equal in length to, the tall-crowned M2 (Fig. 3A). The paracristid of the M2 is longer than the metacristid (Fig. 4A). There is relatively little contribution of the M2 metaconid to the cristid obliqua (Fig. 4A). The M2 hypoconulid is situated posteriorly (Fig. 4A). The anterior, labial, and posterior cingula are robust and continuous (Fig. 4A,E,G). There is no development of the entostylid (Fig. 4A).

The maxilla is rugose and fenestrated, with grooves of blood vessels along the surface (Fig. 5B,C). The condition of the infraorbital foramen (a key feature separating *M. 
Figure 8. Scanning electron micrographs of paratype material of *Macroderma handae* sp. nov. (A, B, D) lingual, labial and occlusal views of a left P$_2$, paratype WAM 2020.4.8; (C) labial view of the left P$_2$ of *M. gigas* ANWC CM568; (E, G, H) occlusal, lingual-oblique, and posterior views of a damaged left P$_4$, paratype WAM 2020.4.12; (F) occlusal view of a left P$_4$ of *M. gigas* ANWC CM568. Scale bars 1 mm.
Figure 9. Scanning electron micrographs of other unidentified and undescribed bat material recovered from the same deposit at Dingo Gap. (A–D) WAM 2020.4.13; (E–G) right C₁ of an emballonurid, WAM 2020.4.14; (H) right C₁ of an emballonurid, WAM 2020.4.15; (I, J) left C₁ of an emballonurid, WAM 2020.4.16; (K, L) left C₁ of an emballonurid, WAM 2020.4.17; (M, N) lingual and occlusal views of a fragment of dentary of a vespertilionid containing M₁–M₃ (M₁ is on the right in both views), WAM 2020.4.18. Scale bars 1 mm.
koppa [two foramina] and M. gigas [one foramen]; Fig. 5A) cannot be observed.

The P2 is absent, as indicated by the absence of an alveolus between those of the canine and P4 (paratype WAM 2020.4.5; Fig. 5A). The alveolus of C1 and anterobuccal/anterolabial alveolus of P4 indicate that the crowns of these teeth overlapped in the tooth row (Fig. 5A). The heel of the P4 is broad, and the posterior edge is at right angles to the paracone (it is angled close to 45° lingually in M. gigas; Fig. 8E–H). There is no protostyle cusp, which is obvious in M. gigas (Fig. 8E,F).

The M1 has a broad labial (buccal, sensu Hand, 1996) shelf, though narrower than that of M. gigas (Fig. 6A,B), and a markedly lingually displaced mesostyle (cf. Megaderma richardsi; Hand, 1995). The preprotocrista and postprotocrista are curved, giving the protofossa a rounded shape, which contrasts with the more triangular form of other Macroderma species (Hand et al., 1988: 345, fig. 2c; Hand, 1985: 10, fig. 3c, 1996: 366–367, pl. 48d), and also Megaderma richardsi (Hand, 1995: pl. 1b,c). Both the M1 and M2 have tall crowns, and appear to be slightly compressed anteroposteriorly relative to Macroderma gigas (Fig. 6A–F).

Unidirectional wear striations are observable on the left M2, which resemble those found on the teeth of the predatory M. gigas that crush the bones of prey (Fig. 5D,E).

**Etymology.** Named in honour of Professor Suzanne (“Sue”) J. Hand of the University of New South Wales, in recognition of her previous extensive work on fossils of this family, and her extraordinary, sustained, and ongoing work on fossils that has helped piece together the rich history of the Australasian mammal fauna.

**Discussion**

**Phylogenetic relationships**

The phylogenetic position of *Macroderma handae* relative to most megadermatids can be estimated based on the presence of various synapomorphies that characterize subclades within the family (character sets 1–5 listed in Hand, 1996: 373) (Fig. 10). It displays the following apomorphic conditions: (a) Characterizing it as part of the *Megaderma–Macroderma* clade: M1 shorter than or equal in length to M2. (b) Distinguishing it from the *Megaderma* clade: M1 with elongated heel, and markedly lingually displaced mesostyle (cf. *Megaderma richardsi*; Hand, 1995); in the M2: the paracristid longer than metacristid, reduced metaconid contribution to the cristid obliqua; robust, continuous anterior, labial and posterior cingula. (c) Distinguishing it from *Macroderma godthelpi*: large-sized, tall-crowned teeth; M2 with robust and broad anterior cingulum. (d) Distinguishing it from *M. malugara*: P2 absent; C1 markedly posterolingually-extended; M1,2 larger and more posteriorly-situated hypoconulid; and preentocristid further reduced. The phylogenetic position of *M. handae* relative to *M. koppa* and *M. gigas* could not, however, be determined unambiguously based on the material from Dingo Gap because the condition of the infraorbital foramen (one or two foramina) and some other diagnostic features could not be observed.

**Australian Pliocene megadermatid diversity**

The new species *M. handae* represents the second Pliocene species of *Macroderma* discovered to date, together with
M. koppa. The age of the Big Sink Site of Wellington Caves in New South Wales has also been estimated as Pliocene, though it has not been dated other than on the basis of biocorrelation with better-dated faunas (reviews in Hand, 1996; Dawson et al., 1999), and the inferred plesiomorphic condition of M. koppa (Dawson et al., 1999: 284). Both sites lack Rattus material, though they have representatives of the Old Endemic murid radiation (Hydromyini, sensu Smisien & Rowe, 2018), so their likely age is at least somewhere between the first Australian murid radiations and the invasion of Rattus (Aplin, 2006; Rowe et al., 2019). The species M. handae and M. koppa might have been contemporaneous, or alternatively they could have arisen at slightly different ages sometime from the late Miocene to early Pliocene. While M. handae appears slightly smaller on the basis of a few molar measurements, it is not markedly so. Thus, it might have been an earlier or allopatric taxon. A proposed common name for M. handae is the Kimberley False Vampire Bat.

Chiropteran assemblage

Several other bat species were recovered from the same assemblage that contained M. handae (Fig. 9). The lack of molars, or those in an unbroken condition, precluded identification to species, or species description. But on the basis of canine morphology (the position of cingular cusps), an emballonurid species, most likely representing the genus Taphozous, is present. A small vespertilionid species was also present. Based on the wear striations on the M1 of M. handae (Fig. 5D), probably derived from crushing the bones of vertebrates, these smaller bat species might well have been prey, as well as co-inhabitants of the roost. Body parts of the species Taphozous georgianus, Rhinonicteris aurantia and Vespadelus finlaysoni have all been observed in the prey accumulations of modern M. gigas in the Pilbara region of Western Australia and Northern Territory (Churchill, 2008; K. N. Armstrong personal observations).

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References


