The Eocene *Protohierodula crabbi* Ross, 2019 cannot be reliably assigned to Manteidae (Insecta: Mantodea)

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ABSTRACT: The late Eocene mantis genus and species *Protohierodula crabbi* can be attributed to the extant clade Artimantodea *incertae sedis* sit. nov., but its original placement in the Manteidae is not supported. It remains the oldest reliable described Artimantodea.

KEY WORDS: Artimantodea, Priabonian, revision.

Mantodea Burmeister, 1838 are a small order of insects with a very poorly known fossil record. While fossils of stem Dictyoptera Leach, 1818 (the super-order that comprises Blattodea and Mantodea) and Blattodea Latreille, 1810 are very common and found in all geological stages from the mid-Carboniferous to the present (Zhang *et al*. 2013), those of Mantodea are more rarely found and the oldest reliable fossils date from the mid-Cretaceous (Grimaldi 2003). The Jurassic family Juramantidae Vršanský, 2002 is based on a fragment of the cubito-anal area of a Dictyoptera, too incomplete and insufficient to be accurately attributed to the Mantodea (Vršanský 2002, figs 6 and 7; Grimaldi 2003). Moreover, there is no crown Mantodea fossil known from the Mesozoic period, and they are very rare in the Cenozoic (see Cui *et al*. 2018).

In this context, the discovery of a crown Mantodea is very important because it greatly helps in dating the clade. Ross (2019) described a new genus and species of Mantodea, *Protohierodula crabbi*, from the latest Eocene of the Isle of Wight (UK), and assigned it to the Manteidae (=Mantidae; see Carpenter 1992) family, the largest family of Mantodea with more than half of extant mantises species. Svenson & Whiting (2009) considered the family polyphyletic. This new fossil was assigned to the Manteidae on the basis of the general shape of the forewing, which is very close to that of some extant genera in this family (Ross 2019). As mentioned by Ross, there is no forewing character allowing an attribution of a mantis to the Manteidae, not only because the current classification is mainly based on foreleg spines but also because the forewings of the crown mantises are very similar in their venations.

The general shape of the wings of *P. crabbi*, with a 'coarse archaedictyon' and 'gently curved' subcostal (Sc) vein and radial (R) vein that diverge in the basal half of the wing (Ross 2019), can be found in a large number of Mantodea, including non-Manteidae mantises, such as Hymenopodidae (Fig. 1). However, this fossil wing is not similar to those of the Chaeteessidae Fig. 2a), where the area between Sc and R (*sensu* Ross 2019) is broader and with numerous crossveins. It

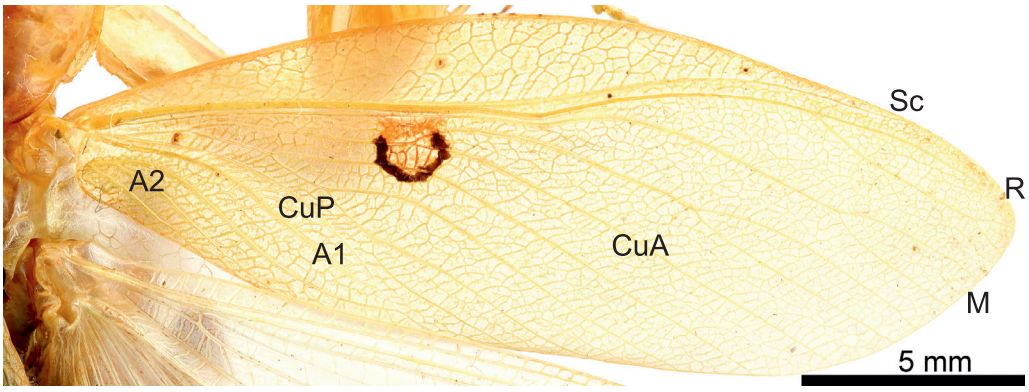


Figure 1 Right forewing of extant *Chloroharpax modesta* (Gerstaecker, 1883) (Artimantodea: Hymenopodidae) in dorsal view (Muséum national d'Histoire naturelle (MNHN), Paris). Abbreviations: Sc = subcostal vein; R = radial vein; CuA = cubitus anterior vein; CuP = cubitus posterior vein; M = median vein; A1 = first anal vein; A2 = second anal vein.

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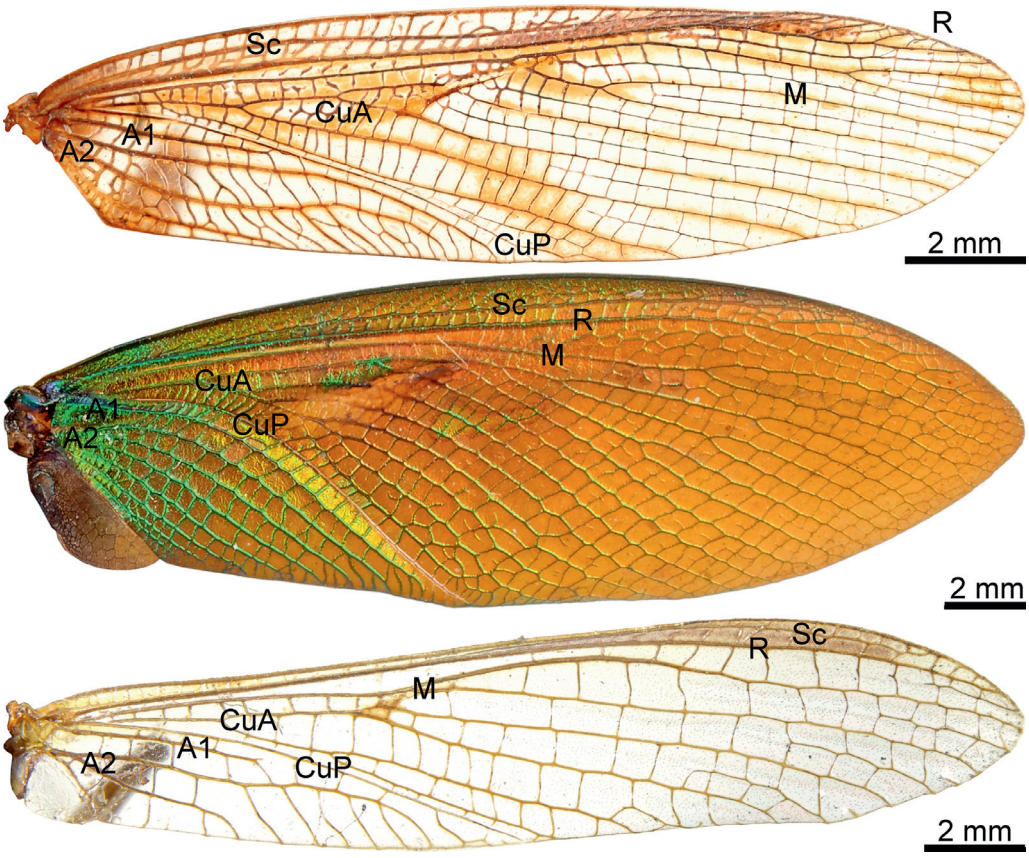


Figure 2 Forewings of non-Artimantodea extant Mantodea: (a) *Chaeteessa valida* Perty, 1883; (b) *Metallyticus violaceus* Burmeister, 1838; (c) *Mantoida brunneriana* Saussure, 1871 (MNHN collection). Abbreviations: Sc = subcostal vein; R = radial vein; CuA = cubitus anterior vein; CuP = cubitus posterior vein; M = median vein; A1 = first anal vein; A2 = second anal vein.

is also not similar to those of the Mantoidae (Fig. 2c), which are thinner, smaller and with fewer branches in all areas; and to those of Metallyticidae (Fig. 2b), which have no archaedictyon and possess a clearly higher number of A2 branches. Due to these facts, this wing could reliably be assigned to Artimantodea (see Svenson & Whiting 2009), as we find that its attribution to Manteidae is not supported by any synapomorphy. Thus, we consider *P. crabbi* as an Artimantodea *incertae sedis* sit. nov.

Despite the fact that this identification is less precise, *P. crabbi* remains one of the oldest, if not the oldest, known Artimantodea fossil. A few Mantodea are recorded from the Middle Eocene Baltic amber, but none are correctly described (von Spahr 1992). As a consequence, this fossil is very important and interesting to clarify the evolution of all the order.

1. References

Carpenter, F. M. 1992. Superclass Hexapoda. *In* Moore, R. C. & Kaesler, R. L. (eds) *Treatise on invertebrate paleontology*, Volume **3/4**, 142–43. Boulder, CO: The Geological Society of America and the University of Kansas, Arthropoda 4, xxii + 655 pp.

Cui, Y., Evangelista, D. A. & Béthoux, O. 2018. Prayers for fossil mantis unfulfilled: *Prochaeradodis enigmaticus* Piton, 1940 is a cockroach (Blattodea). *Geodiversitas* **40**, 355–62.

Grimaldi, D. A. 2003. A revision of Cretaceous mantises and their relationships, including new taxa (Insecta, Dictyoptera, Mantodea). *American Museum Novitates* **3412**, 1–47.

Ross, A. J. 2019. The Blattodea (cockroaches), Mantodea (praying mantises) and Dermaptera (earwigs) of the Insect Limestone (late Eocene), Isle of Wight, including the first record of Mantodea from the UK. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh* **110**, 301–11. DOI: 10.1017/S1755691018000440.

Svenson, G. J. & Whiting, M. F. 2009. Reconstructing the origins of praying mantises (Dictyoptera, Mantodea): the roles of Gondwanan vicariance and morphological convergence. *Cladistics* **25**, 468–514.

von Spahr, U. 1992. Ergänzungen und Berichtigungen zu R. Keilbachs Bibliographie und liste der Bernsteinfossilien, Klasse Insecta (Ausgenommen: 'Apterygota', Hemipteroidea, Coleoptera, Hymenoptera, Mecopteroidea). *Stuttgarter Beiträge zur Naturkunde (B)* **182**, 1–102.

Vršanský, P. 2002. Origin and the early evolution of mantises. *AMBA Projekty* **6**, 1–16.

Zhang, Z.-J., Schneider, J. W. & Hong Y.-C. 2013. The most ancient roach (Blattodea): A new genus and species from the earliest Late Carboniferous (Namurian) of China, with a discussion of the phylomorphogeny of early blattids. *Journal of Systematic Palaeontology* **11**, 27–40.

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