

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

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**ABSTRACT:** I accept Schubnel & Nel's (2019) opinion that *Protohierodula* belongs to the clade Artimantodea, that it cannot be reliably assigned to the family Manteidae and should be regarded as family *incertae sedis*.

**KEY WORDS:** Artimantodea; Insect Limestone; Isle of Wight; Mantoidea; praying mantis; Priabonian.



I welcome the Schubnel & Nel (2019) discussion on the placement of *Protohierodula crabbi* Ross, 2019. I would like to clarify my reasons for the initial placement and continue the discussion.

My placement of *Protoheirodula* was based on a closest match to extant Mantodea in the collection at the Natural History Museum (NHM), London. The broad shape of the wing indicated it was a female and a combination of the form of the venation, coarse archidictyon, smooth stigma and broad costal area looked closest to members of the Manteidae, though I accept these characters are not unique to the family. Unfortunately many species in the NHM collection were only represented by male specimens, and of course the collection is not comprehensive. So although my decision was based on what could be viewed at the time, I accept that it was not a comprehensive comparative study and that the placement was therefore tentative. Although a fragmentary hindwing is also present I realised that the origin of the median vein can be variable within extant taxa so was not useful taxonomically.

Schubnel & Nel (2019) pointed out that the Manteidae are polyphyletic according to Svenson & Whiting (2009). However the four extant genera cited in Ross (2019) that I considered to be most similar to *Protoheirodula*, all belong to the same clade (see Svenson & Whiting 2009, p. 483) which falls within the strict sense of Manteidae as used by Svenson & Rodrigues (2017) in their time-calibrated phylogeny. Svenson & Rodrigues (2017) also suggested that the Manteidae in their strict sense originated in the Late Cretaceous, so the possibility of *Protoheirodula* belonging to the Manteidae is not unreasonable.

Schubnel & Nel considered the combination of 'a "coarse archidictyon" and "gently curved" subcostal (Sc) vein and radial (R) vein that diverge in the basal half of the wing, can be found in large number of Mantodea.' Many of the extant females in the NHM collection had a straight Sc and R for most of their length and the divergence commenced at or near the middle of the wing. I agree that the specimen of *Chloroharpax modesta* (Hymenopodidae) that Schubnel &

Nel use to support their argument has a gently curved Sc and R, but the curve and their divergence commences just before the mid-wing causing the costal area to narrow rapidly, which is different from *Protoheirodula*. Perhaps I should have used 'basal third' instead of 'basal half' in the diagnosis but that is a mute point. When I examined the extant taxa I noted that a coarse archidictyon and curved Sc and R, which diverge in the basal half of the wing also occurs in *Idolomantis* in the family Empusidae, so I agree these characters can be found in other taxa, but were not observed in a 'large number' of female Mantodea. The Empusidae, Hymenopodidae and Manteidae comprised the superfamily Mantoidea (see Grimaldi 2003), however given that the Manteidae is now considered to be polyphyletic, it may be worth redefining the Mantoidea to represent the clade of Hymenopodidae + Empusidae + Danuriinae + Manteidae s.s. + Deroplatyinae as presented by Svenson & Rodrigues (2017). *Protoheirodula* could then be tentatively placed in this superfamily, but I'll leave it for other researchers to decide if that is a reasonable suggestion.

Schubnel & Nel considered that *Protohierodula*'s 'attribution to Manteidae is not supported by any synapomorphy' which I accept; however, this is the case for many fossil insects which are known only from wings yet the classification of their extant relatives is often based primarily on other characters. This should not stop palaeoentomologists from attempting to place them in extant families based on what characters are available (or placing them in extinct families if they are sufficiently different from extant taxa).

Rivera & Svenson (2016) considered that the 'polymorphic earless praying mantises' belong to the superfamily Acanthopoidea and are only found in the neotropics—old world taxa were rejected from the clade. This superfamily plus the Cernomantodea constitute the Artimantodea. Svenson & Rodrigues (2017) went on to suggest that the Acanthopoidea diverged from the Cernomantodea in the Early Cretaceous during the break up of Gondwana. Given that *Protohierodula* is from the old world and Eocene in age, it could be argued that it could not possibly belong to the Acanthopoidea and therefore

belongs to the clade Cernomantodea. However, there is a potential problem. Like with any phylogenetic study based only on extant biogeographic distributions, fossils can throw metaphorical ‘spanners in the works’. Species in the past may not have lived where their living relatives do today. The classic example is the archaic termite *Mastotermes*, which although it lives in Australia today (and introduced to other countries by human activity) has been found as fossils in new-world amber and European deposits, including the Insect Limestone of the Isle of Wight, where *Protohierodula* came from (see Jarzembowski 1980). There are also examples of taxa in Baltic amber where their nearest living relatives live in the southern hemisphere and/or new world today (see Ross *et al.* 2000). As Schubnel & Nel indicate, there are Mantodea known from Baltic amber which are not described. They considered Baltic amber to be of middle Eocene in age; however, it is most likely to be late Eocene (Priabonian) (see Grimaldi & Ross 2017, Seyfullah *et al.* 2018), similar in age to the Insect Limestone. Ehrmann (1999) produced a summary of the records of Mantodea in amber and copal and listed Chaeteessidae, Mantoididae, Liturgisidae and Mantidae as occurring in Baltic amber, and Zompro (2005) described a species of Mantoididae. The possible presence of the Liturgisidae in Baltic amber is very interesting as this is one of the families included in the Acanthoidea. Ehrmann also recorded this family as present in Dominican amber, Dominican copal, Colombian copal and Madagascan copal. If these are correctly identified then it would suggest that this family had a much wider palaeogeographic distribution until relatively recently and casts doubt on Svenson & Rodrigues (2017) hypothesis that the Acanthoidea and Cernomatodea diverged with the break-up of Gondwana. Careful re-examination and description of the amber and copal specimens is required though given that the specimens are probably nymphs then reliable identifications may be difficult.

To conclude, I accept Schubnel & Nel’s view that *Protohierodula* belongs to the clade Artimantodea and that it cannot be reliably assigned to the family Manteidae. My comparison with extant taxa was not comprehensive and therefore it should be regarded as family *incertae sedis*. It will be for future researchers to decide if the further classification of *Protohierodula* is possible.

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