

Evolutionary Relic or a Curious Coincidence? A Mantisfly Emerging from a Mud-Dauber Nest.

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Abstract

Mantispoidea exhibit a remarkably diverse morphology and life history for a relatively small group of insects, in part, complicating our understanding of its evolutionary history. Dietary specialisation of the larvae, however, seems to have played an important evolutionary role in this group. Symphrasinae (Rhachiberothidae) larvae are thought to be predators of aculeate Hymenoptera brood, while Mantispinae (Mantispidae) larvae are predators of spider eggs. Herewith the first observation of a Mantispinae adult emerging from the nest of a mud-dauber wasp (Sphecidae) is described. This is also the first genus record of *Afromantispa* Snyman & Ohl from the Oriental Region, including three new name combinations. The curious coincidence of a Mantispinae emerging from an aculeate wasp nest, the food source of a related taxon, is discussed in the light of our current understanding of Mantispoidea classification.

Background

Mantispoidea is a relatively small group of lacewings (Insecta: Neuroptera) with a remarkable range of interesting biology and morphology (Ardila-Camacho et al. 2021; Snyman et al. 2021). The group comprise three families, the Berothidae, Rhachiberothidae and Mantispidae (Winterton et al. 2018; Ardila-Camacho et al. 2021). Our understanding of the relationships among the families and subfamilies within Mantispoidea has been the cause of much debate and discussed in detail elsewhere (Winterton et al. 2018; Lu et al. 2020; Ardila-Camacho et al. 2021; Snyman et al. 2021). Based on a recent study, the Berothidae is thought to be sister to a monophyletic Rhachiberothidae + Mantispidae. Rhachiberothidae comprise a monophyletic Rhachiberothinae + Symphrasinae and a monophyletic Mantispidae in turn comprise three subfamilies, the Mantispinae sister to a monophyletic Drepanicinae + Calomantispinae (Figure 1) (Ardila-Camacho et al. 2021).

The biology of the group was recently compiled and discussed in detail (Snyman et al. 2021). The Rhachiberothidae and the Mantispidae possess raptorial forelegs and an elongated prothorax, convergent in structure and function to those present in Mantodea. Although it has not been recorded in the Rhachiberothinae and thought to be no longer present in the Calomantispinae, larvae of these groups undergo parametamorphic ontogeny, an accentuated metamorphic cycle nearly comparable to the hypermetamorphosis seen in meloid beetles (Snyman et al. 2021). The larval diet of insect pupae is also seen as a plesiomorphic characteristic, with only the Mantispinae transitioning to a different diet consisting only of spider eggs (Snyman et al. 2021).

Punctuated Dietary Specialisation Of Mantispoidea Larvae

The reigning hypothesis is that the campodeiform planidium larvae of the Mantispoidea ancestrally exhibited a fossorial lifestyle, capable of producing aggressive allomones that subdue and/or preserve their prey (Johnson and Hagen 1981; Dorey and Merritt 2017; Badano et al. 2021). Subsequent divergence into terrestrial habitats seems to coincide with the dietary specialisation of the larvae (Figure 1: A & B).

The Berothidae larvae became predators of subterranean eusocial insects, producing an aggressive allomone that subdue termites so that uninterrupted feeding can commence. The remaining members probably evolved into specialist predators of insect pupae as is still displayed by the Symphrasinae (Maia-Silva et al. 2013) and Calomantispinae (Macleod and Redborg 1982) as well as the hypothesised situation in Drepanicinae (Dorey and Merritt 2017). It is not known how the allomone, which is likely present, is used by members of these subfamilies, but it has been shown to preserve and hinder the development of spider eggs in the Mantispinae (Redborg 1983). It is therefore likely that the allomone hinders the development of the pupae while preserving it, yielding increased feeding opportunity to the larval predator.

The Symphrasinae larvae subsequently evolved into predators of aculeate hymenopteran brood (Figure 1: C) (Maia-Silva et al. 2013; Snyman et al. 2021). While there are fragmented reports of possible deviations from this diet, Snyman *et al.* (2021) noted that evidence generally support symphrasines as specialist brood predators targeting aculeate hymenopterans, rather than being generalist brood parasites. Most aspects of the biology, including its larval diet, of the Rhachiberothinae unfortunately remains a mystery.

The final dietary specialisation evolved in the Mantispinae: these larvae are specialist predators of spider eggs (Figure 1: D). Mantispinae larvae gain access to the spider eggs by actively searching for egg-sacs and penetrating the silken enclosure, or by boarding a spider (phoresy) and entering the egg-sac during construction. Some species are obligate “spider boarders” or “egg-sac penetrators”, but species exhibiting facultative behaviours are common. It is not known which of these behaviours are ancestral with arguments supporting both scenarios (Snyman et al. 2021).

The Hymenoptera Connection

Apart from the Symphrasinae larvae being specialist predators of hymenopteran pupae, mimicry of Hymenoptera adults is present in both Symphrasinae and Mantispinae (Opler 1981; Rasmussen and Ardila-Camacho 2021; Snyman et al. 2021). Mimesis in the Symphrasinae is seemingly more diverse and complex than what is observed in the Mantispinae (Dejean and Canard 1990; Maia-Silva et al. 2013; Rasmussen and Ardila-Camacho 2021). Mimicking in Mantispinae is common and seemingly always based on an aculeate wasp model, especially aggressive vespids equipped with a painful sting. The evolutionary reasoning for developing the mimesis is a straightforward case for Batesian mimicry: it is beneficial to resemble something dangerous when harmless (Opler 1981; Ohl 2004a).

In the Symphrasinae, mimicking wasps are rare and only reported for a single species (Rasmussen and Ardila-Camacho 2021). Mimicking bees are however more common in the Symphrasinae and several species are mimics of stingless bee species, especially members of *Ptilotrigona* Moure, 1951 or *Trigona* Jurine, 1807. While these bees are stingless, they are both aggressive and unpalatable, making them ideal models in Batesian mimicry systems (Rasmussen and Ardila-Camacho 2021). The bees are also a food source of Symphrasinae larvae, and the mimesis may therefore provide adult symphrasines entry into the nests and thus access to a food source. There is even circumstantial evidence of chemical

camouflage in Symphrasinae, where adults could easily penetrate a host nest without difficulty, despite not looking the part (Dejean and Canard 1990).

Observation Report

Sceliphron coromandelicum (Lepeletier, 1845) (Hymenoptera: Sphecidae) is a solitary mud-dauber wasp commonly encountered in the Orient (Anagha et al. 2021). Like most *Sceliphron* species, the female *S. coromandelicum* constructs mud nests which she provisions with spiders as a food source for the enclosed immatures. The spiders are generally Araneidae and in some cases terricolous Salticidae (Coville 1987; Polidori et al. 2005).

The *Sceliphron coromandelicum* mud nest, reported here, was attached to the adaxial surface of a wooden cabinet in the house of the second author [INDIA: Kerala, Kozhikode district, Elathur (lat. 11.325644°; lon. 75.741754°, alt. 23m above mean sea level). Coll. C. Binoy] (Figure 2A). The nest was initiated on the 8th of May 2021 and completed on the 12th of May 2021. The nest comprised eight separate subcylindrical cells, each provisioned with approximately five spiders and an egg attached to one of the spiders.

Six adult wasps (5♂ & 1♀) emerged from the nest on the 10th of June 2021, while one of the eggs laid by the wasp was nonviable with the provisions in the cell untouched. Five days prior to the emergence of the last wasp offspring, an adult female mantispine emerged from another one of the cells harbouring a wasp larva and five provisioned spiders. An oval mantispine cocoon (~5 x ~3 mm) made of loosely woven silken threads was observed and attached to the wall of the cell. Embedded in the cell wall were four stalked mantispine eggs of which one was seemingly non-viable, but typical of Mantispidae (Minter 1990) (Figure 2B). Three disfigured and dismembered mantispine larvae (Figure 2C) were also retrieved from the nest, all dry and desiccated. Some of the spiders present in the cell were partially eaten, presumably by the wasp larva and mantispinae larvae have straight piercing mouthparts (Minter 1990). The poor state of both the mantispine larvae and wasp larva made it difficult to assess if it was fed upon.

Morphology Of *Afromantispa Neptunica* (Navás, 1914), New Combination

The nomenclature of three species is affected and amended during the course of the identification reported on here. The mantispinae was identified as *Afromantispa neptunica* by inspecting photos of the type specimen. Two other species, *Afromantispa coomani* (Navás, 1930) **new comb.** and *Afromantispa tonkinensis* (Navás, 1930) **new comb.** are morphologically very similar and perhaps synonyms of *A. neptunica*, but require closer inspection. The amended taxonomic detail of each name is summarised below (amended from Ohl's catalogue (Ohl 2004b)).

All three species have the characteristic pale bands in the distal third of the flagella, a granulated prothorax and a truncated bicoloured pterostigma (Snyman et al. 2012, 2015) confirming the species as an *Afromantispa* Snyman & Ohl 2012 species (Figure 2: D1-D6). The colouration of the tergites of the three species are distinctive and unique. Prominent yellow patches are seen on the lateral aspect of the tergites consisting of a small apicolateral yellow margin of tergite III onwards merged with basolateral patches present on tergite VI (iii in Figure 2: D7). These patches along with a pair of yellow centrolateral spots on tergites VI & V (iv in Figure 2: D7) are deemed characteristic and sufficient for confidently identifying the specimen as a member of *A. neptunica*.

To date, *Afromantispa* was known only from the Afrotropical Region, and the adjacent Arabian and Iberian peninsulas (Snyman et al. 2015, 2018). *Afromantispa* is thus reported here for the first time as present in the Oriental region. The specimen is deposited in the National Zoological Collections of Zoological Survey of India (ZSIK), Western Ghat Regional Centre, Kozhikode, Kerala India with accession and catalogue as ZSIK Regd. No. ZSI/WGRC/I.R.-INV. 19037.

Discussion

It can only be speculated exactly what occurred in the cell where the mantispine larva developed into an adult. What is clear is that the larva did not have access to its established preferred food source, spider eggs, but had access to the wasp larva, the immobilised spiders and its kin. While maintenance feeding of mantispine larvae on the haemolymph of spiders has been reported, development to the adult is not realised (Redborg and Macleod 1983). It is also worth noting that larvae tend to board spiderlings that emerge before the mantispine can commence with feeding rather than attacking the spiderlings (Redborg 1985). Cannibalism is unlikely as several reports of gregarious behaviour and multiple larvae boarding a single spider and sharing the host without malicious behaviour (Snyman et al. 2021). The mantispine could also perhaps have fed on the wasp larva. The wasp larva was recovered dead, perhaps lending the possibility of the mantispine feeding and killing the larvae through predation or perhaps producing an allomone that negatively affected the ontogeny of the wasp resulting in its death. Finally, spiders collected by wasps are often female (pers. comm. M. Ohl 2021). Since the wasp larva partially fed on the spider provisions, it is possible that a pregnant female spider could have been left partially eaten with eggs exposed and available to the mantispine larva.

The presence of the Mantispinae eggs on the nest also lends interesting interpretations. At first thought, it supports non-random ovipositing behaviour by the adult females. It can easily be argued that the female mantispine somehow realised the presence of suitable hosts, i.e., spiders. By ovipositing close to a potential “food source” will likely increase the chances of her minute offspring locating it. On the other hand, if females keep mistakenly ovipositing near wasp nests due to the presence of spiders but not spider eggs, the larvae will be at a disadvantage. Such a mechanism will likely not be favoured and will not evolve.

The events reported on here can probably be dismissed as an anomaly or mistake. Curiously, however, the mistake involved a nest-building hymenopteran. Such hymenopterans not only serve as mimicry models for other Mantispinae species, but also serve as a source of food for the larvae of a closely related taxon, the Symphrasinae.

Snyman et al. (2021) favoured a single origin of aculeate hymenopteran mimicry in Mantispoidea. The authors argued that the specialist diet of spider eggs probably originated by 'proto' mantispine larvae boarding wasps to gain access to its food source, hymenopteran pupae. Since spiders, a substantial source of food of various wasp species, would often be encountered in wasp nests, boarding spiders might also increase the chances of the 'proto' mantispine larvae to gain access to hymenopteran pupae, its food source. By boarding spiders, a plausible switch to spider eggs can thusly be postulated. A more random scenario of changing diet from pupa to spider eggs, generally protected by a protective silken sac, is however, not as easily explained (Snyman et al. 2021).

While the single origin idea proposed by Snyman et al. (2021) is appealing, this is seemingly not the case and mimicry probably evolved twice, once in Symphrasinae and once in Mantispinae. The mimicry in Symphrasinae possibly evolved, at least in part, to gain access to food as well as benefiting from being a Batesian mimic. In Mantispinae, however, the characteristic is probably a derived one and evolved in a Batesian system only, where the mimics frequents flowers as hunting platforms, the same flowers utilised by the model wasps for maintenance feeding (Pascarella et al. 2001). Even though mimicry seems to be quite plastic, once present in a species, it is not easily lost (Prudic and Oliver 2008). In times of an allopatric existence between the mimic and model the mimesis might wane without going extinct, and return once the model and mimic occurs in sympatry again (Prudic and Oliver 2008). So perhaps a "mimicry predisposition" can at least serve as a tenuous connection between aculeate Hymenoptera and both Symphrasinae and Mantispinae. Reverting to a far-removed ancestral food source, after the establishment of a specialised diet, proves more difficult to explain and is thought to be governed by both ecological and phylogenetic determinants (Pekár et al. 2011). This will also assume that the ancestral diet of the raptorial Mantispoidea was aculeate hymenopteran brood. Reverting to an ancestral food source occurs due to an apparent residual capacity to use ancestral hosts, at least in phytophagous insects (Ikonen et al. 2003; Gassmann et al. 2006). This pattern might even be more common than to establish a new host association due to novel barriers that may be involved in moving to a new host (Gassmann et al. 2006). This might then imply that the host preference of Rhachiberothinae, Drepanicinae and Calomantispinae should likely also be brood of Hymenoptera. Rare reports such as this, should however, be interpreted with caution as it might lend itself to be "over-interpreted". Nevertheless, the association described here certainly warrants closer inspection and elucidating variation in mantispinae larval diet should perhaps be revisited using choice and no-choice experiments.

In conclusion, the occurrence of *Afromantispa* now includes the Oriental region. The evolution of the Mantispoidea is complex and despite being on the receiving end of multiple recent studies, still not well understood. Perhaps a better understanding of the dietary range of Rhachiberothinae, Drepanicinae and

Calomantispinae will elucidate the curious connection between taxa within Mantispoidea and the aculeate Hymenoptera.

Declarations

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Tables

Table 1: Summary of taxonomic information pertaining to three affected Mantispinae species

New combination	Original designation	Holotype detail	Remarks
<i>Afromantispa neptunica</i> (Navás, 1914)	<i>Mantispa neptunica</i> Navás, 1914	Sex: Unknown Origin: Vietnam BMNH (NHMUK)	Sex cannot be determined from the images, apex of abdomen covered in mould
<i>Afromantispa coomani</i> (Navás, 1930)	<i>Mantispilla coomani</i> Navás, 1930	Sex: Male Origin: Malaysia MNHN	Specimen in good state at time of imaging
<i>Afromantispa tonkinensis</i> (Navás, 1930)	<i>Mantispa tonkinensis</i> Navás, 1930	Sex: Male Origin: Vietnam MNHN	Sex determined by R Hall, 1985, terminus of abdomen removed, in a vial pinned alongside specimen

Figures

Series of photos documenting the wasp nest (A1-2); Mantispinae eggs (B1-3); larvae (C); and adult mantispine (D1-7) that emerged from the nest.