*Review*

# A review of the biology and biogeography of Mantispidae (Neuroptera)

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**Abstract**

Adult Mantispidae are general predators of arthropods equipped with raptorial forelegs. The three larval instars display varying degrees of hypermetamorphic ontogeny. The larval stages exhibit a remarkable life history ranging from specialised predators of nest-building hymenopteran larvae and pupa, to specialised predators of spider-eggs, to possible generalist predators of immature insects. Noteworthy advances in our understanding of the biology of Mantispidae has come to light over the past two decades which are compiled and addressed in this review. All interactions of mantispids with other arthropods are tabled and their biology critically discussed and compared to the current classification of the taxon. Additionally, the ambigous systematics within Mantispidae and between Mantispidae and its sister groups, Rhachiberothidae and Berotidae, is reviewed. Considering the biology, systematics, distribution of higher taxonomic levels and the fossil record, the historical biogeography of the group is critically discussed with Gondwana as the epicenter of Mantispidae radiation.

**Keywords**

mantis-flies; mantidflies; life history; spider-insect interactions; mimesis

## Overview

Neuroptera are a relatively small order of holometabolous insects that are thought to have originated during the Permian Period (Engel et al. 2018; Winterton et al. 2018). Larvae of Neuroptera are generally predators, while adults are either predacious or pollen-feeders, thereby fulfilling vital roles in the functioning of natural ecosystems (Mansell 2010). The ecological separation of adults and larvae, which occupy a wide

range of habitats (e.g. arboreal, psammophilous, semi-aquatic, aquatic, inquilines) and exhibit many different life history strategies, make them ideal insect models for ecosystem health as well as environmental indicators (Aspöck 1992). Despite their great ecological importance, many families are comparatively poorly studied and knowledge of their taxonomy, biology, phylogeny, biogeography and conservation status, are inadequate (Ohl 2004, 2005).

Mantispidae are one of the neglected families of Neuroptera. Mantispids are easily recognised by their raptorial front legs, similar to those of the praying mantis. Mantispidae currently comprise four extant subfamilies, Symphrasinae, Drepanicinae, Calomantispinae and Mantispinae, with the biology of the most diverse subfamily, Mantispinae, best studied (Lambkin 1986a; Willmann 1990; Liu et al. 2015). The classification of the family, however, remains unsettled, with a recent phylogenomic study by Winterton et al. (2018), which included Berothidae, rendering Mantispidae paraphyletic. The authors suggested reviewing the status of Berothidae, Rhachiberothidae and Mantispidae as separate families. Here we do not suggest any changes to the status of Berothidae, Rhachiberotidae and Mantispidae and merely use the family status as it is widely accepted. The proposal from Winterton et al. (2018) may be accepted in time, but the authors did not present a formal breakdown of the classification and we therefore follow the findings of Liu et al. (2015).

Mantispid larvae are predators of either insect pupae (mainly from the orders Coleoptera, Lepidoptera and Hymenoptera) or, as in the case with the largest subfamily, Mantispinae, of spider eggs (Lambkin 1986b; Ohl 2011; Redborg 1998; Redborg & Macleod 1985). Some of the Mantispinae larvae display phoretic behaviour and board spiders to locate spider eggs (Haug et al. 2018; Ohl 2011; Redborg & Macleod 1983). While being transported on the spider, the larvae of some species may take blood meals and can therefore be considered as ectoparasites. Other members mimic wasps of the families Vespidae, Eumenidae and Sphecidae (various authors; Supplementary Table S1). It is possible that they use flowers as a platform for locating prey (Snyman et al. 2012). These platforms might make them vulnerable targets to predators and they may benefit by mimicking wasps that are equipped with a sting (Beck 2005; Hoffman 1992; O'Donnell 1996; Kauppinen & Mappes 2003; Rashed et al. 2005). This however, remains to be tested and clarified.

The behavioural ecology of Mantispidae and its associations with other taxa are also well worth looking into. Most of the reports published on this topic are only fragmented information. No studies have yet aimed to resolve the interspecific differences using comparative studies. It is unclear what cues mantispid larvae follow (olfactory or other) to reach their hosts. The same is true for the adult oviposition behaviour. The long suspected pheromonal release by adult males has also not been studied and might provide valuable information into mantispid behaviour and evolution (Batra 1972; Eltringham 1932; McKeown & Mincham 1948; Redborg & Macleod 1985). The positions adopted by the planidial larvae on spiders as well as the ecological guild occupied by the spiders that are attacked, might have interspecific differences. This can provide interesting partitioning behaviour between sympatric species and result in a better understanding of the general ecology of mantispids. The mimicry present in several taxa

is also only superficially understood. Thus far, only Opler (1981) demonstrated the evolutionary and ecological significance of mimicry in this enigmatic family.

The biology of Mantispidae was last reviewed two decades ago (Redborg 1998). Since then, significant publications have elucidated key aspects of life-histories, behaviour and interactions with other Arthropoda. Significant fossil finds have also been reported with new subfamilies, genera and species recently described (Jepson 2015). The historical biogeography is, however, not well understood and the unconventional distribution of extant subfamilies and general lack of fossil data adds to the complexity.

This review aims to sumarise the biology of Mantispidae, review the fossil record and critically discuss the historical biogeography of Mantispidae in light of the current ambiguous classification of Mantispidae, Rhachiberothidae and Berothidae.
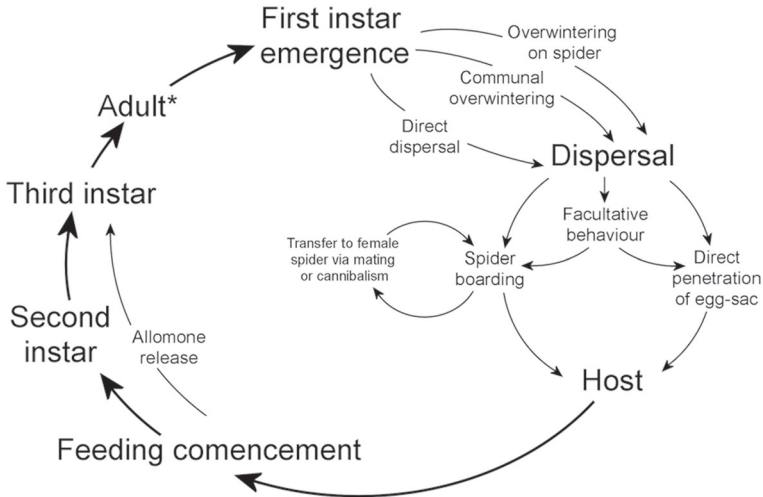
## The life-history of Mantispidae

### *Mantispinae* (Figs 1, 2)

The life history of the Mantispinae, compared to the other subfamlies, is well recorded, despite it being based on only a few species. Many fragmented reports from various authors are summarised in the supplementary material (Table 1) with initial noteworthy reports come from the studies of Brauer (1852, 1855, 1869, 1887). Brauer explored the life history of *Mantispa styriaca* and subsequently deduced that spidereggs might be the obligatory food for mantispines. Thereafter McKeown & Mincham (1948) completed a detailed study on the life-cycle of the Australian mantispid *Campion australasiae* (then cited as *Mantispa vittata*) which provided foundational insights into the gregarious nature and overwintering behaviour of the first instar larvae. McKeown & Mincham (1948) also provided rearing techniques for mantispids in lab conditions, which were later improved by Davidson (1958) and Brushwein & Culin
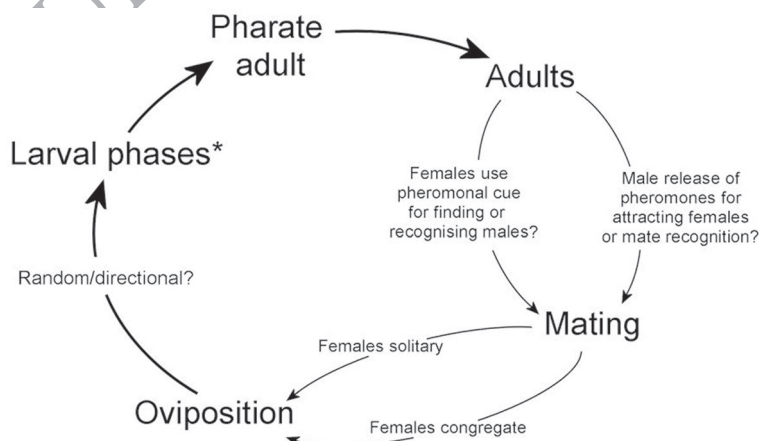


**Fig. 1.** Behavioural diagram of the life-history of Mantispinae adults. The larval phase, indicated in the figure with an "*", is presented in Fig. 2. Unsubstantiated hypotheses are denoted by a "?".

**Fig. 2.** Behavioural diagram of the life-history of Mantispinae larvae. The adult phase, indicated in the figure with an "*", is presented in Fig. 1.

**Table 1.** Distribution of extant subfamilies belonging to Mantispidae, Rhachiberothidae and Berothidae. (AFRO = Afrotropics; AUS = Australasia; NEA = Nearctic; NEO = Neotropics; ORT = Orient PAL = Palearctic).

|  | AFRO | AUS | NEA | NEO | ORT | PAL |
|---|---|---|---|---|---|---|
| Calomantispinae |  | • | • | • |  |  |
| Drepanicinae |  | • | • | • | • |  |
| Mantispinae | • | • | • | • | • | • |
| Symphrasinae |  |  | • | • |  |  |
| Berothinae | • | • | • | • | • | • |
| Cyrenoberothinae | • |  |  | • |  |  |
| Nosybinae | • |  |  | • |  |  |
| Nyrminae |  |  |  | • |  | • |
| Protobiellinae |  | • |  |  |  |  |
| Trichomatinae |  | • |  |  |  |  |
| Rhachiberothidae | • |  |  |  |  |  |
| Mantispidae subfamilies | 1 | 3 | 3 | 4 | 2 | 1 |
| Rhachiberothidae | 1 |  |  |  |  |  |
| Berothidae subfamilies | 3 | 3 | 1 | 4 | 1 | 2 |
| **Total subfamilies present** | 5 | **6** | **4** | **8** | **3** | **3** |

(1991). Bissett & Moran (1967) in turn documented the life history of a South African mantispid, *Afromantispa cf. nana*, laying emphasis on the cocoon spinning behaviour of the third instar. More recently, studies by Redborg (1982, 1983, 1985), Redborg & Macleod (1983a, b) and Hoffman & Brushwein (1989, 1992) added considerably to our understanding of mantispine behaviour, habitat and chemical ecology. A great deal of the life history of Mantispidae can be deduced from published works over the last two centuries as well as aspects that require further scrutiny.

As far as is known, female mantispines lay batches of elongate stalked eggs approximately 70-90 hours after copulation (Batra 1972; Minter 1990; Redborg & Macleod 1985). The eggs of some species have distinct anterior micropylar "caps" present that probably play a role in larval emergence (Batra 1972; Kuroko 1961; Minter 1990; Redborg & Macleod 1985). The batches can be circular (Bisset & Moran 1967) or square-like when composed of regular rows or completely irregular in form (McKeown & Mincham 1948). The size and number of batches laid by a single female exhibits great variation. McKeown & Mincham (1948) reported 100-3000 eggs laid by a single female for *Campion australasiae*. Reports for *Dicromantispa sayi* suggest eggs per female to be in the range of 2000 (Smith 1934), whereas *Dicromantispa interrupta* range from 1300-2400 with averages closer to 1500 per female (Hungerford 1939; Viets 1941). Bissett & Moran (1967) reported a mean of 836 eggs per batch with the maximum at 1650 and minimum at 214 eggs per batch (n = 16 batches) for *A. cf. nana*. Unfortunately, the authors did not record the mean number of batches laid by a single female. The number of eggs laid by female *Climaciella* spp. seem to be quite varied with reports ranging from 250-3340 (Batra 1972; Hoffmann 1936). Kuroko (1961) recorded the variable number of eggs for *Tuberonotha strenua* (as *Climaciella magna*) females, laying anywhere between 1791 and 8121 eggs in one or two batches: with an average of 3994 eggs per female (n = 5) and an average of around 2852 per batch (n = 7). *Mantispilla japonica* (as *Mantispa japonica*) in turn laid 956-1553 eggs in one to four batches with an average of about 1384 eggs per female (n = 8) and an average of around 503 per batch (n = 22). Eggs generally hatch 9-16 days after oviposition takes place (Bissett & Moran 1967; Davidson 1958; Kuroko 1961; Smith 1934). However, the study by Kuroko (1961) indicated that hatching times can be greatly altered by temperature fluctuations. Under a constant temperature of 27°C, eggs of *T. strenua* hatched within 15-16 days. However, under a fluctuating range of temperatures (10.4-28.7°C), eggs only hatched after 25-27 days (Kuroko 1961). Without reporting specific temperatures, eggs only hatched 45 days after oviposition under "natural temperature conditions". Under the same "natural temperature conditions" *M. japonica* eggs in turn hatched after 13-28 days but took only 7-9 days to hatch with a constant temperature of 27°C (Kuroko 1961). It can therefore be assumed that the time to hatching will not only be species specific, but be subject to environmental conditions as well.

A planidium, campodeiform larvae emerges from the eggs. Some authors have erroneously referred to the first instar of mantispids as triungulin and campodeiform. The term triungulin was derived from the Latin "tri", meaning three and "ungula", meaning claw. It specifically refers to the first instar of the Meloidae (Coleoptera) which possesses three tarsal claws. The term "planidium", however, (derived from Greek "planos", meaning roaming) refers to a highly sclerotised, flattened and mobile parasitoid larvae searching for hosts. It therefore includes the first instar of meloids as well as mantispids, whereas triungulin excludes mantispid larvae which possess a single tarsal claw. The newly emerged larvae either disperse or display gregarious behaviour. Brauer (1869), and later McKeown & Mincham (1948), observed the lack of dispersion when larvae hatch before the coming of winter and suggested that the larvae "hibernate" on, or close to, the egg mass in large numbers and in a gregarious nature. It should,

however, be noted that "hibernate" is probably not the correct term. Mantispids are probably ectotherms and therefore cannot hibernate. There is a general lack of physiological evidence in mantispines to clearly define the process, and "overwintering" is therefore probably more accurate. Some larvae have an overwintering period of 5-6 months before finally dispersing (McKeown & Mincham 1948). Dispersion of the gregarious larvae could be induced by warming them in the sun or with artificial heat such as lightbulbs (McKeown & Mincham 1948). This opposes the hypothesis that stalked eggs, as found in Chrysopidae (Neuroptera), evolved to reduce cannibalism (Fréchette et al. 2006). The gregarious nature of first instars has also been observed in Ascalaphinae (Neuroptera: Myrmeleontidae) which produce sessile eggs (pers. comm. M.W. Mansell). An argument can, therefore, be made that the stalked eggs probably evolved as a defensive response to predation and not to reduce cannibalism (Hayashi & Nomura 2014).

All mantispine larvae need spider eggs for hypermetamorphic development to the second and finally third instar stages (Bissett & Moran 1967). Redborg (1998) expressed concern with respect to the term "hypermetamorphosis" in relation to mantispid ontogeny as described by Brauer (1869b). Understandably, the hypermetamorphism expressed by mantispids is not as pronounced as that which is exemplified by the Meloidae beetles with their unique coarctate stage. However, neither is the ontogeny exhibited by other taxa such as the dipteran families Acroceridae, Bombilidae and Nemestrinidae, the order Stresiptera and the parasitic wasp family, Eucharitidae. The metamorphosis found in these taxa is certainly more pronounced than what is found in the non-hypermetamorphic citrus swallowtail (*Papilio demodocus*). These taxa are "lost" between the complex "true" hypermetamorphic Meloidae ontogeny and the non-hypermetamorphic swallowtail.

Redborg's (1998) concerns about the feeding mechanisms are somewhat validated. The feeding mechanisms differ in meloid ontogeny but not in any of the other hypermetamorphic taxa mentioned. However, the larval "microhabitat" and lifestyle differ significantly between the first and second plus third instars in mantispids. Hypermetamorphosis remains an analogous characteristic and not a homologous one. Meloidae beetles are obviously unique and hypermetamorphosis is expressed best by them. In order to resolve this, "parametamorphosis" or "parametamorphic ontogeny" could be useful terminology to describe the taxa between "normal" metamorphosis and the true hypermetamorphic ontogeny exhibited by meloids.

Redborg & Macleod (1985) described two main strategies utilised by the first instar larvae for locating spider eggs: (1) actively searching for spider egg-sacs deposited in the environment and penetrating the wall of the sac, or (2) by boarding a spider and entering the egg-sac while the sac is under construction by the spider. Facultative penetrators or facultative boarders are the most common behaviour exhibited and probably the ancestral state. The larvae can thus employ both strategies, depending if an egg sac or a spider is encountered first. However, specialists occur on both sides with obligate penetrators as well as obligate spider boarders. *Zeugomantispa virescens*, *Mantispa styriaca* as well as *Campion australasiae* seem to be obligate penetrators and display no interest in spiders in confined spaces and have also not been found on spiders in the field

(Brauer 1869b; McKeown & Mincham 1948; Redborg & Macleod 1985). *Climaciella brunnea* is an example of an obligate spider boarder which exhibit specilised behaviour to facilitate boarding. First instar *C. brunnea* larvae assumes a phoretic position before a spider is boarded (Redborg & Macleod 1983a). The larvae use a caudal sucker on the apex of the abdomen (discussed below) which it can attach to a substrate to lift its body from the ground. In this vertical position, with legs outstretched and swaying slightly, the larvae waits for a spider to run past or over it so that it can attach itself to the spider (Redborg & Macleod 1983a). It is not known if other mantispines employ a similar strategy. *Dicromantispa sayi* and *D. interrupta* are both facultative spider boarders and, so far, have not been recorded exhibiting the phoretic posture. Several other notes published on mantispine behaviour are inadequate to assign them to either of these groups (Supplementary material, Table 1).

Once inside the egg sac, feeding commences. Similar to several other basal members of Neuroptera, grooved maxillae and mandibles are united into a straight sucking tube (Winterton et al. 2018). The mouthparts are simply inserted into the egg by piercing the chorion where extracellular digestion allows the larva to ingest a liquid. The above-mentioned caudal sucker, if present, can then be used to grip the spider eggs during feeding (McKeown & Mincham 1948). Hoffmann (1936) was the first to describe a caudal sucker on the first instar of *Climaciella brunnea* var. *occidentalis*. Subsequent studies by Batra (1972) and Redborg & Macleod (1983) described the importance of the caudal sucker as a mechanism for boarding spiders. However, McKeown & Mincham (1948) described a caudal sucker on the abdomen of *Campion australasiae*, a mantispid that is thought of as an obligate egg-sac penetrator. Instead of using the sucker for attaching the larva to a substrate to assume the "phoretic position" as with *C. brunnea*, both *Campion australasiae* and *A. cf. nana* seem to use it for attaching the larvae to the smooth surface of the eggs while feeding. Contradicting accounts from Bissett & Moran (1967) and Minter (1990) add to this. Bissett & Moran described an *Afromantispa cf. nana* with a caudal sucker, whereas Minter (1990) described an *A. capeneri* with the terminal segment as bifid. Hoffman & Brushwein (1992) did not mention a caudal sucker in their descriptions of some Nearctic mantispid larvae, however, from their figures, abdominal segment X seem similar to the suckers described by Brauer (1869), McKeown & Mincham (1948) and Bissett & Moran (1967). These authors described the caudal sucker as important during both the emergence from the egg as well as feeding whilst inside the egg-sac instead of a specialised structure for spider boarding behaviour. An indepth morphological comparison of the caudal suckers will prove valuable and might resolve these conflicting reports. One might argue that the structure is a pleisomorphic one, evolved for either emergence or feeding and an example of a behavioural exaptation in the case of *C. brunnea*.

It is apparent that the time it takes for the first campodeiform instar to moult into the second more sluggish and less mobile second instar differs greatly among mantispid species (Bissett & Moran 1967; McKeown & Mincham 1948; Redborg & Macleod 1985). Moulting also seems to be a difficult transitional period for larvae, and death occurs frequently during the moulting phases (McKeown & Mincham 1948). After commencement of feeding, the first instar of *Campion australasiae* moults into

the second instar larva after approximately 24 days (McKeown & Mincham 1948). The first moult in *A. cf. nana* Bissett & Moran (1967) occurs approximately five to nine days after commencement of feeding. *Dicromantispa sayi* (cited as *Mantispa uhleri*) moults after an average of 7.4 ± 0.3 days (Redborg & Macleod 1985).

The growth during the second instar is rapid and the second moult occurs quite soon after the first. *Afromantispa cf. nana* almost double in width during the two to five days before moulting to the final instar (Bissett & Moran 1967). *Campion australasiae* moults to the third instar after five days (McKeown & Mincham 1948) and *D. sayi* takes 2.3 ± 0.1 days to moult to the third instar (Redborg & Macleod 1985). A few hours before the moult, the larva stops feeding, the cuticle becomes visibly sticky and peristaltic movements follow until the larva can exit the exuviate head first. It is known that second and third instar larvae will mortally wound each other, and even feed on each other if the egg-sac contains several larvae, but not enough food for all to mature (McKeown & Mincham 1948).

The final instar is creamy white, grub-like with legs that are basically functionless and very small. Additionally, it seems clear that the third and final immobile and scarabaeiform (referred to as eruciform by Cannings & Cannings 2006) instar exhibit the highest growth rate. Larvae measured by Bissett & Moran (1967) more than doubled in width in two to six days and started spinning a cocoon when the food was depleted. Redborg & Macleod (1985) divided the time into 2.5 ± 0.2 days for pre-spinning and 5.7 ± 0.1 for post-spinning based on observations of *Dicromantispa sayi* (as *M. uhleri*).

By the end of the third instar, the parametamorphosis is complete. A spherical, sometimes oval, silken cocoon is spun before pupation inside the spider egg sac. The colour ranges from light cream to light green to yellow. Cocoon spinning behaviour may be divided into an "initial phase", an "ntermediate phase" and a dominant "final phase" (Bissett & Moran 1967; Redborg & Macleod 1985). The cocoon is composed of a series of layers that are spun by the larvae following a "figure of eight" motion. Bissett & Moran (1967) described the spinning behaviour of *A. cf. nana* in great detail and Redborg & Macleod (1985) did not record any variation for *Dicromantispa sayi* (As *M. uhleri*). In *A. cf. nana* a period of 9-15 days quiescence follows, after which the pupa forms and the imago emerges 20-28 days later (Bissett & Moran 1967).

### *Symphrasinae* (Fig. 3)

It has been suggested that the symphrasine larvae are generalist predators of insect pupa. This is mainly due to several no-choice feeding experiments from a single study (Macleod & Redborg 1982) as well as isolated instances where cocoons were found in proximity of pupal exuviae from insects other than Hymenoptera (Woglum 1935; Werner & Butler 1965) (Supplementary Table S2). Apart from these cases, the majority of evidence supports a very close relationship with nest-building Hymenoptera (Supplementary Table S2). Most of the evidence indicates a strong relationship where the mantispids (pupal predators) feed on Hymenoptera (hosts). Mimesis is not as apparent in this subfamily as in some mantispine members and if present, the mantispid is the mimic and the hymenopteran the model (Penny & Da Costa 1983; Machado 2018).
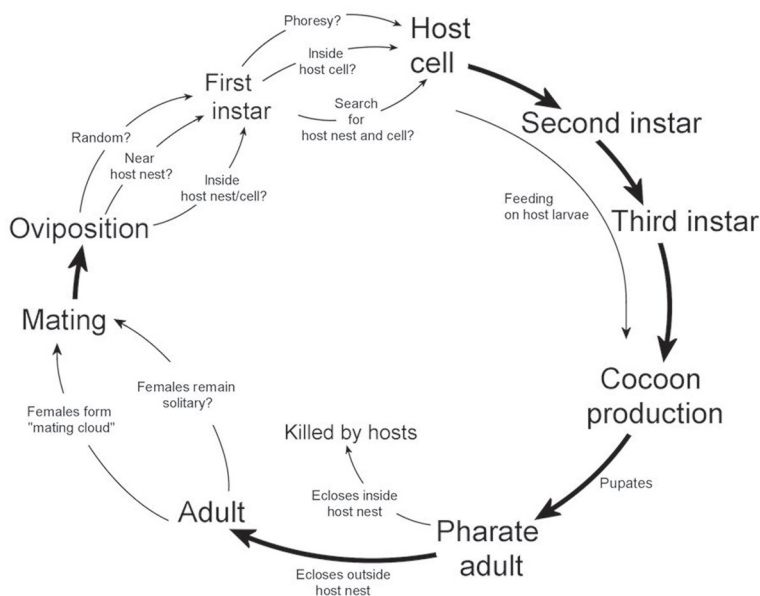
**Fig. 3.** A behavioural diagram of the life-history of Symphrasinae adapted from Maia-Silva et al. (2013). Unknown phases or behaviours are indicated by a "?".

Similar to the mantispines, the symphrasines undergo parametamorphic ontogeny over three larval instars, followed by spinning a cocoon inside the host nest. The duration of the instars as well as the development is unknown. The *Plega* cocoon is generally oval in shape, whereas the cocoon of *Anchieta* seems to be elongated or cylindrical (Buys 2008; Maia-Silva et al. 2013). Due to the tight-fitting cocoon spun in the hymentoteran brood cell, the oval or cylindrical shape is probably due to the shape of the brood cell, and not indicative of the spinning behaviour of the symphrasine larva (see Maia-Silva et al. 2013: Fig. 1).

Maia-Silva et al. (2013) suggested three possible life-cycle strategies in Symphrasinae: (1) larval phoresy, (2) larval nest entry and (3) adult nest entry (Fig. 3).

The first involves a random ovipositioning site (probably on plant surfaces). Each larva subsequently searches for a suitable phoretic host which can transport the it back into the nest of the host. Once inside the host's nest, the larva dismounts the phoretic host and searches for a brood cell. With the second strategy, the female has directional choice during ovipositioning, and will choose a site close to the nest of the host. The larvae can then disperse and enter the nest and subsequently a brood cell without any assistance. The third strategy involves the adult female entering the nest of a host and ovipositing inside, either the nest, or a brood cell.

Unfortunately, few studies have explored any of these strategies and all can be viewed as equally likely. Dejean & Canard (1990) and Dejean et al. (1998) recorded adult *Trichoscelia santareni* flying near the eusocial wasps *Polybia diguetana* and *Polybia scrobalis surinama* (Vespidae). Even though no symphrasine has been observed entering a host nest, Dejean & Canard (1990) described more than 40 adult males and females

of *Trichoscelia santareni* congregated outside the nest of *Polybia diguetana.* After mating, the females groom themselves and can enter the nests of the wasps undetected. The authors could not comment on the time the symphrasines spent in the nest, due to the fall of darkness and it is unknown if ovipositing occured. Similarly, Dejean et al. (1998) reported "parasitic mantispids" flying in the vicinity of two nests of *Polybia scrobalis surinama* in the Neotropics. Not much was discussed in the report except that the mantispids also entered the nest after mating. This conforms to the third strategy proposed by Maia-Silva et al. (2013). The presence of an ovipositor in symphrasines suggests that it might be used to lay eggs inside the brood of the hymenopteran hosts.

In contrast to these reports, Maia-Silva et al. (2013) studied *Plega hagenella* mass-infesting colonies of the eusocial stingless bee *Melipona subnitida* in Brazil. The authors made their observations from already infested bee-colonies and could therefore not report on the mating or oviposition behaviour of adults, nor the first instar larvae, but only on the second, third and adult phases. Even though the adults were observed close to, or even on the nest of the bees, all adults entering the nests were attacked and killed by the worker bees. The second and third instars were found feeding on pupa inside the brood cells of the bees and subsequently spun silken cocoons inside the cells. The large number of cells containing *Plega hagenella* larvae in each of the two nests suggests that many larvae emerged quite close to the colony and could gain access without the female having to enter the bee nest. Hook et al. (2010) found *Plega hagenella* eggs attached to a mud nest of the crabronid wasp *Trypoxylon manni* being reused by *Hylaeus (Hylaeopsis)* sp. (Colletidae). The egg chorions were found as clusters inserted into crevices formed by the mud nest. It is, therefore, reasonable to argue that the adults find nests of suitable hosts, and lay eggs on the nests of the host leaving the larva to find the entrance to the nest and brood cells by themselves. The authors suggested that *Hylaeus* should be regarded as a novel food source and target species for the larvae of *P. hagenella.*

The report by Hook et al. (2010) is difficult to interpret and subsequently may support any of the hypotheses presented by Maia-Silva et al. (2013). *Trypoxylon* is a possible host genus of *Plega* as reported by Parker & Stange (1965), Macleod & Redborg (1982) and Penny (1982), but so are bees from Apidae (Linsley & MacSwain 1955; Maia-Silva et al. 2013) and Megachilidae (Parker & Stange 1965). If the arguments of Hook et al. (2010) are correct, and *P. hagenella* target nests of Colettidae and not *Trypoxylon* (Crabronidae), then the larval nest entry strategy is favoured, despite the presence of an ovipositor on female *P. hagenella.*

Notwithstanding the well-rounded argument from Hook et al. (2010), it is possible that the gravid female could have mistakenly identified the nest as occupied by *Trypoxylon manni*, but could not penetrate the hardened mud shell with her ovipositor. This might have resulted in the ovipositing of eggs deep in crevices, mistaken for successfully penetrating the brood cell of *T. manni*. This, in turn, will fit with the third strategy, where adult mantispids enter host nests.

Different from the mantispines, motile pharate adults (an adult insect prior to emerging from the pupa but prior to the final ecdysis) seem to play an important part in both Symphrasinae and Drepanicinae. In mantispines, motile pharate adults emerge from the cocoon and eclose some distance from the cocoon (Maia-Silva et al. 2013). However, if *Plega hagenella* ecloses in the eusocial host nest, the imago adult

(an adult insect post-emergence from the pupa or following final ecdysis) is killed, as the pharate adult is motile, it will either exit the nest on its own or will be removed by the eusocial host (Maia-Silva et al. 2013). The final ecdysis occurs after the pharate adults exit the bee nest. When a pharate adult was placed in an enclosed petri dish with worker bees, the bees ignored the mantispid. However, when an imago was placed in the petri dish with worker bees, the mantispid was immediately recognised, attacked and killed by the bees. Motile adults are not uncommon in lacewings. Dorey & Merritt (2017) describe motile adults emerging from the soil and moving, probably using negative geotaxis and/or sight, to climb a substrate, only to undergo final ecdysis well above ground level. This strategy is quite common in Neuroptera and is shared by the closely related Berothidae as well as members of Hemerobiidae, Myrmeleontidae and the snakefly, *Raphidia bicolor* (Aspöck et al. 2012; Brushwein 1987; Dorey & Merritt 2017; Kovarikl et al. 1991).

In conclusion, the life history of Symphrasinae requires further elucidation before making robust hypotheses. Currently, symphrasines might be actively seeking out eusocial and social bees, rather than being a brood parasite of any nest building hymenopteran (Supplementary Table S2). Furthermore, the presence of the ovipositor remains somewhat of a mystery if the female symphrasines soley need to deposit sessile eggs in proximity to a host nest, unless the ancestral behaviour is as was observed by Dejean & Canard (1990) and females regularly enter the nest of a host undetected.

### *Drepanicinae* (Fig. 4)

The life history of Drepanicinae is the least known of all the sub-families. A recent study by Dorey & Merritt (2017) reported the first substantial record on the life history of
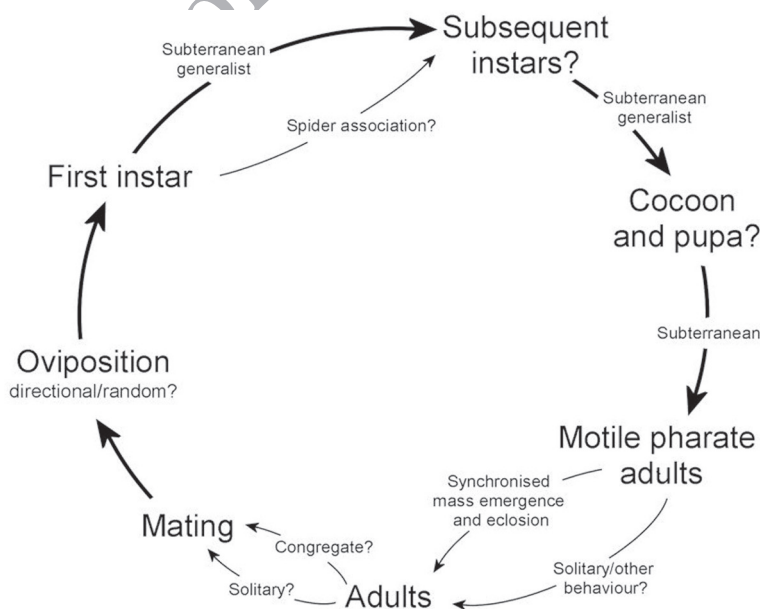


**Fig. 4.** A behavioural diagram of the life-history of Drepanicinae. Unknown phases or behaviours are indicated by a "?". Information largely based on Dorey & Merritt (2017).

the subfamily based on observations of *Ditaxis biseriata*. The authors described an apparent annual synchronisation event (n = 2 years) of mass emergence of motile pharate adults in a *Macadamia* orchard in proximity to subtropical rain forests in New South Wales, Australia. The pharate adults emerge from the soil, presumably after emerging from a subterranean cocoon, climb up/onto a tree trunk, or other vertical structures, and eclose, similar to Cicadidae (Hemiptera). After wing inflation, the adults fly to the canopy, presumably for mating. The authors did not report on any mating rituals, but pregnant females were collected at the sites during the annual emergence event. Females lay clusters of ±120 (n = 1) lime-green elliptical eggs, suspended from a cord of diffuse silken threads. The planidium, campodeiform first instars emerge and after clinging to the empty egg-cases for a while, drop to the ground and burrow into the soil. It seems as if all the larval stages are subterranean, since the pharate adults also emerge from the soil.

Currently, the only known larval association of Drepanicinae was published by Austin (1985). The author merely reports on an interaction between an unidentified *Theristria* (cited as *Theristia* sp. (M) [sic]) and *Achaearanea* (Theridiidae) species in Australia. The study only refers to the interactions as "parasitoids and predators recorded as feeding on spider eggs in Australia" without any additional information.

Apart from these two reports, nothing is known from the life history of Drepanicinae. If the subterranean lifestyle of Drepanicinae is true for all species, Dorey & Merritt (2017) rightly suggested that it might be the reason for the general lack of information regarding the larval phase of Drepanicinae.

### *Calomantispinae*

Our knowledge of the Calomantispinae life cycle is limited to a report by Macleod & Redborg (1982) which involved rearing *Nolima pinal* under lab conditions (Supplementary Table S3). The authors managed to rear first instars to adulthood using spiders (eggs and paralysed spiders obtained from a sphecid nest), insect pupa (Coleoptera, Diptera and Lepidoptera) and insect larvae (Coleoptera and Hymenoptera). Furthermore, the larvae did not undergo the characteristic parametamorphic ontogeny like the Mantispinae, and remained ambulatory in both the second and third instars.

## Mating and oviposition

### *Mating*

The mating ritual of Mantispinae is relatively well understood (Batra 1972; Eltringham 1932; McKeown & Mincham 1948; Redborg & Macleod 1985). Eltringham (1932) was first to describe a possible pheromonal release by male mantispines via an extrusible organ between the abdominal tergites (usually tergites V & VI). It is now understood that the organ as well as the pheromonal release mechanism might vary between taxa (Hoffman 1992). *Mantispa styriaca* has a large "sac" that is extruded during the mating ritual. *Afromantispa* seems to have the same structure (Snyman et al. 2012).

Other taxa have a reduced "sac" accompanied with pores on the anterior tergal margins (Hoffmann 1992; Machado & Rafael 2010; Snyman et al. 2018). It is thought that these pores are used for pheromonal release (Hoffman 1992).

Males approach females with caution since cannibalism has been observed in both sexes (Redborg 1998). When the female notices the male, wing fluttering by the male can be observed in accordance with a pulsating abdomen (and if present, extrusible gland). It has been suggested that the fluttering of the wings distributes the pheromone (Eltringham 1932). This is also supported by the omission of fluttering in the Symphrasinae which do not have a glandular structure. Both sexes then extend a raptorial leg to full length and close the tibia onto the femur again (also referred to as leg folding). This movement is identically copied by the other leg and afterwards reciprocated by the opposite sex. Some species, such as *Zeugomantispa virescens*, include scissor-like movements with the tibia and femur.

Copulation occurs side by side. The male twists its abdomen through 180 degrees to initiate copulation. After copulation is achieved, the male turns away from the female. The final orientation is when both sexes face away from each other. Copulation time among species varies considerably: with *M. styriaca* recorded as taking an hour or less, *Campion austarasiae* taking up to three hours and *Climaciella brunnea* taking approximately 24 hours (Batra 1972; Dejean & Canard 1990; McKeown & Mincham 1948). Post-copulation, a whitish, globular spermatophore is seen attached to the female terminalia. The spermatophore is completely absorbed after 24 to 48 hours. *C. austarasiae* oviposit five to seven days after copulation (McKeown & Mincham 1948) and *C. brunnea* three to four days (Batra 1972).

The most detailed Symphrasinae mating ritual recorded is based on *Trichoscelia santareni* by Dejean & Canard (1990) (n = 9). Prior to mating, males approach females in what the authors refered to as a mantispid "cloud", or loose swarming of females. These "clouds" are apparently found outside of a suitable Hymenoptera host nest.

A male and female "pair" in the cloud and land nearby. The female is reported to land first and sit motionless. The male lands soon after and cautiously approaches her, antennating. When near to the female, reciprocating leg extension and folding between the sexes commences, much like mantispines. Since the symphrasine males do not have any pheromonal gland, the fluttering of the wings is omitted (Lambkin 1986a). Copulation then occurs venter to venter. After approximately two to five minutes, the pair rotates until facing away from one another, remaining attached to one another for 40 to 60 minutes. Dejean & Canard (1990) did not comment on the spermatophore absorption, but it seems to take much less time than mantispines. After grooming for 4-9 minutes, the female flies into the wasp nest, presumably for egg-laying.

The mating rituals of both Drepanicinae and Calomantispinae are currently unknown.

### *Oviposition*

The cues involved in chosing an oviposition site by female mantispids for oviposition are unknown. The excessively large number of eggs produced by females suggests

that only a small number of larvae survive to find a food source. It is therefore likely that the oviposition sites chosen by females must be somewhat non-random or directional. The surface itself need not be anything specific: leaves, rocks, buildings, poles, walls and tree trunks have all been recorded as surfaces chosen for oviposition sites. Wild caught females readily oviposit in vials or paper, if so contained. The eggs of the *Afromantispa cf. nana* (aptly named "the chestnut mantispid" by Bissett & Moran 1967) are apparently only deposited on the adaxial surface of leaves of Cape Chestnut trees (*Calodendrurn capense*) in circular batches. The close relationship between this mantispid species and the Cape chestnut remains unsubstantiated needs to be further investigated. *Campion australasiae* females oviposit on trees, buildings and telephone poles, and apparently only when there were trees with foliage in approximation of the structures (McKeown & Mincham 1948). The authors also noted that eggs are found higher on the trunks due to the presence of ants closer to the ground. This finding has not been substantiated by experimentation and remains merely an observation. The authors mentioned the presence of wolf spider burrows found in the area, most notably *Lycosa perinflata* (Lycosidae). However, if the oviposition sites are found high in order to avoid predation by ants, the larvae will eventually have to cross paths with the ants in order to reach the ground and in-so-doing the lycosid host. Thus, the reason for choosing the high ovipositioning sites is still unclear. McKeown & Mincham (1948) also described mass oviposition or communal oviposition behaviour exhibited by female *C. australasiae* on telegraph poles in Australia. Rice (1986) described a similar phenomenon in *D. sayi* (cited as *M. fuscicornis*) on picnic shelters in Texas, USA. The latter study postulated that the communal behaviour is due to the large number of spiders found on the wooden shelters and that the mantispids choose the sites to give an advantage to the larvae. Hirata & Ishii (1995) postulated that *E. harmandi* and *M. japonica* oviposit in sites where host spiders occur in large numbers and that oviposition is therefore non-random. It should be mentioned that this hypothesis was not tested and is merely based on observational data. Whether mantispid females lay eggs to avoid predators or in approximation of suitable spider hosts, remains a mystery: one that will hopefully soon attract the attention of entomologists.

**Specificity of larval hosts in Mantispidae**

The larvae of mantispids certainly exhibit high levels of specificity when choosing a suitable host. Even though *C. brunnea* have been observed boarding Hymenoptera under lab conditions (Batra 1972) and a single study reporting a single *L. pulchella* larva that was recovered from an adult caddisfly, *Oecetis inconspicua* (Trichoptera, Leptoceridae) (Hoffman & Hamilton 1988a), the accounts can be regarded as rare anomalies. Hoffman & Hamilton (1988) described the accounts as exploratory boarding and that mantispines need to be in contact with potential hosts before their suitability can be determined. The vast majority of the records show an obvious relationship between mantispines and spiders, and these boarding "mistakes" are not made often (Supplementary Table S1).

### Neuroptera feeding on social insects

Neuroptera larvae that feed on the adults or immatures of social insects are quite rare. Principi (1943) described an association between the *Italochrysa italica* (then cited as *Nothochrysa italica*) (Chrysopidae). The larvae of the chrysopid apparently live inside the nests of the ant *Crematogaster scutellaris* Olivier (Formicidae). It is unknown if the larvae feeds on adults or immatures. Berothidae are probably specialist termitophagous insects. Minter (1990) successfully reared larvae to the second instar of *Podallea manselli* (Berothidae) by feeding them immobilised worker caste termites. Möller et al. (2006) successfully reared *P. manselli* larvae to the third instar but did not successfully rear adults by feeding the larvae *Cubitermes* sp. (Termitidae). Möller et al. (2006), however, successfully reared *Podallea vasseana* adults from eggs using the same *Cubitermes* sp. as a food source. North American Berothidae species such as *Lomamyia latipennis* and *L. hamata* are also termitophagous (Dejean & Canard 1990). Both species lay eggs outside of the host nests, sometimes near the nest to facilitate the larvae in entering the nest. Larvae that emerge from the eggs are neonate and enter the host nest unfacilitated.

### Larval hosts: preference and prevalence

#### *Mantispinae*

Aside from our knowledge that mantispines attack spiders belonging to the suborder Araneomorphae, we know little else. This is mainly due to the fragmented reports that are summarised in Table 1 in the supplementary material. Since the review by Redborg (1998), little substantial additional information has come to light and our view on the host ranges of mantispines remains the same.

Our knowledge of the preference and prevalence of mantispine hosts' is biased, since most studies only mention spiders associated with larvae and not spiders caught without larvae. Studies that did include all preference and prevelance data are limited to Rice (1986), Rice & Peck (1991) and Redborg & Redborg (2000).

Rice (1986) and Rice & Peck (1991) conducted studies along the eastern coast of Texas (USA) including spiders with and without mantispids as well as spiders with different ecological guilds. Prevalence ranges were recorded from 12-77%, with Salticidae being the most prominent target group of the mantispid *Dicromantispa sayi*. Redborg & Redborg (2000) conducted a study in a woodland in Illinois, USA, focussing on larval prevalence on spiders in four microhabitats (bark, foliage, leaf litter, grass field). A frequency of 75%, 26%, and 27% was recorded for *D. sayi* (as *M. uhleri*) on *Philodromus vulgaris* (Philodromidae), *Metacyrba undata* (Salticidae) and *Hibana gracilis* (as *Aysha gracilis*) (Anyphaenidae) respetively. A lower level of infestation was recorded for *C. brunnea*, with a frequancy of 19% on the lycosid genus *Schizocosa*.

Host records indicate that *Zeugomantispa virescens* favour web-dwelling spiders, most prominently Araneidae species. It is thought that *Campion australasiae* and *Mantispa styriaca* will possibly exhibit the same preference, however, nothing certain is

known from the literature (Redborg 1998). As suggested by Redborg (1998), egg-sac penetrators are likely to attack web-dwelling spiders and spider boarders, in turn, will most likely attack ground dwelling spiders.

Redborg & Macleod (1985) found 16 *D. sayi* (as *M. uhleri*) larvae associated with ground dwelling spiders of the superfamilies Lycosoidea and Clubionoidea. In contrast, no larvae were found on almost 3000 specimens of mostly plant and web-dwelling spiders. This is contrasted in a later study by Redborg & Redborg (2000) where *D. sayi* (as *M. uhleri*) was found on the plant dwelling spiders of the families Philodromidae, Salticidae and Anyphaenidae as well as on the ground dwelling lycosid *Rabidosa punctulata*.

Redborg (1998) erroneously suggested that *C. brunnea* has a narrow host range that is confined to Lycosidae, subsequently supported by findings in Redborg & Redborg (2000). However, Agelenidae and Salticidae, web-dwelling and plant-dwelling spiders, respectively are also recorded as hosts for *C. brunnea* (Redborg & Macleod 1983a).

What should be considered is that ovipositioning sites chosen by females might play a role in the host selection of the larvae. If the eggs are oviposited on a leaf for example, the first spiders that the larvae will likely encounter will probably be plant or web-dwelling spiders. In contrast, if the female prefers rocks or old logs, ground-dwelling spiders will be the likely host.

So far, we have thus only started to understand the host selection of mantispines. Holistic ecological studies that can elaborate on ovipositioning, host range and prevalence of different mantispine species are in dire need to further our understanding.

### Symphrasinae

Werner & Butler (1965) hypothesised that *Plega banksi* is a generalist predator of subterranean insects. The hypothesis is based on two cocoons found in association with scarab pupae found in the soil in Arizona, USA. One scarab cocoon also contained the remnants of a robber fly (Asilidae) pupa, apparently also devoured by the symphrasine larva. Beyond their study, the majority of the available literature have reported a close relationship between Symphrasinae and Hymenoptera, most notably, aculeate Hymenoptera (Supplementary Table S2). Both records of *Anchieta* indicate a relationship with aculeate hymenopterans as well as reports indicating possible mimicry of hymenopterans. *Plega* have the broadest range of hosts but are still mostly confined to aculeate Hymenoptera with Apidae, Colletidae, Crabronidae, Megachilidae, Sphecidae and Vespidae all reported hosts. All records of *Trichoscelia* are restricted to members of *Polybia* (Vespidae), except for the report of Woglum (1935) which cited *Trichoscelia* larvae feeding on and pupating in Lepidoptera exuviae during an apparent citrus cutworm, *Xylomyges curialis*, outbreak. The Woglum (1935) report is only ten written lines and thus holds very little information. The collected larvae were antlion like and the cocoons disk-shaped. After 14 months a mantispid emerged from one of the cocoons and was identified as *Symphrasis signata* by a Mr. E.P. van Duzee. Unfortunately, the mantispid was not reported to be deposited in any science collection facility and can thus not be reviewed for accuracy of identification. If the rest of the literature is

accurate, *Polybia* (Vespidae) are the general hosts of *Trichoscelia.* If the Woglum (1935) specimen was correctly identified, it is possible that the opportunistic behaviour exhibited by *Trichoscelia* was only due to the abundance of *X. curialis* pupae available during the outbreak, which is an important observation as well.

## *Drepanicinae and Calomantispinae*

Aside from the single report of a *Theristria* (Drepanicinae) larva on an *Achaearanea* spider by Austin (1985) and the Dorey & Merrit (2017) hypothesis postulating that *Ditaxis biseriata* are generalist predators of subterranean arthropods, nothing is known from the prey or hosts of drepanicine larvae.

In the case of Calomantispinae, the same is true. Apart from no choice experiments on *Nolima pinal* larvae in a laboratory environment, nothing is known from the prey or hosts of calomantispine larvae (Macleod & Redborg 1982). The no choice experiments suggested that calomantispine larvae are generalist predators of sedentary arthropods, possible pupae, since the ambulatory larvae could not immobilise moving prey. Unfortunately, this valuable report is not necessarily indicative of their true prey or hosts in the field.

## **Position of first instar larvae on spiders**

Hirata & Ishii (1995) documented a preference for the pedicel as a position for first instar larvae of *Mantispilla japonica* (cited as *Mantispa japonica*). The larvae, without exception, wrapped dorsally around the pedicel, leaving little room for more than one larva per spider. This is possibly the reason why multiple larvae on a host have not been found in this species (see Hirata & Ishii 1995: fig. 1B). In contrast, larvae from *Eumantispa harmandi* were never found on the pedicel and most often encountered on the anterior part of the abdomen or the posterior part of the carapace. The Hirata & Ishii (1995) study is the first study that indicates a partitioning between both host selection and position on the spider by two associated mantispid species, *M. japonica* and *E. harmandi*. Both species showed no preference for the developmental phase or gender of the spider hosts. Both *M. japonica* and *E. harmandi* may be facultative boarders/penetrators due to several larvae found in a single egg sac of a clubionid spider (Kishida 1929; McKeown & Mincham 1948). Hirata & Ishii (1995), however, did express some degree of scepticism regarding the little information provided by Kishida (1929) and subsequent identification of the larvae by Esaki (1949). Hirata and Ishii (1995) suggested more investigation before claiming that either species are facultative in boarding and or penetrating. Redborg & Redborg (2000) reported similar results, *D. sayi* larvae also showed a preference for the pedicel with 93% of larvae attaching to the pedicel of *P. vulgaris*. The authors report that 87.5% of larvae are found alone on *P. vulgaris* specimens, leaving only 12.5% of boarded spiders with multiple larvae, but never exceeding three. Redborg & Macleod (1983a) found that in all their observations of *C. brunnea* on wild caught spiders, the larvae, without exception, positioned themselves on either the posterior or anterior carapace. When multiple larvae board a

single spider, the abdomen and legs were observed as alternate positions, however, all larvae moved to the edge of the carapace after a day. It is apparent that the position adopted on the spider host, post-boarding, is worth investigating and may lead to clear partitioning between sympatrically occurring mantispid species. Similar results for *C. brunnea* larva positioning were observed in the Redborg & Redborg (2000) study.

### Spider behaviour

It seems that some spider species show a response to being attacked by mantispine larvae whereas others do not. Guarisco (1998) noted that a female Lycosidae ignored her egg sac approximately a week before the emergence of the mantispid *M. interrupta*. The author noted that the spider, *Gladicosa gulosa*, detached the egg sac from the spinnerets and did not approach it again, apparently unconventional behaviour for lycosids. Similarly, *Lycosa perinflata* egg sacs containing the Australian mantispid, *C. australasiae* were discarded outside the spider-burrow (McKeown & Mincham 1948). Fink (1987) reported contradicting results with a study of the green lynx spider, *Peucetia viridans* (Oxyopidae). Lynx spiders tend to guard egg sacs against ant predation and possible dislodgement from vegetation in a predictable fashion but continued to guard the egg sacs even after the mantispid larva within became visible to the human eye. According to Fink (1987), it is not known if lynx spiders abandon eggs sacs that are parasitised by taxa other than mantispids. Given the relatively high investation levels (7-32 % of egg sacs were attacked over three sites in Florida, USA), the author questioned why no anti-mantispid behaviour was seen. She attributed the behaviour to the hypotheses present at the time that postulated that lynx spiders were thought to be more closely related to web-dwellers than ground dwellers such as lycosids. Dissimilarity in behaviour might therefore be expected. It is now believed that Oxyopidae are in fact higher lycosids and closely related to the above mentioned Lycosidae species that abandon infested egg sacs (Coddington 2005).

### Adult behaviour: vision, flight, food and fecundity

Generally, mantispids are thought of as weak-flying nocturnal insects. Ohl (2004), however, described opposite behaviour with the description of *Euclimacia horstaspockii* from Thailand. It is thought that this mantispid is an active, fast flying, diurnal insect. These findings are similar to several articles on *C. brunnea* which have been found on flowers during day time. *C. brunnea* visited flowers in Florida (Pascarella et al. 2001) and were found on *Helianthus* spp. sunflowers (Redborg & Macleod 1983a) as well as yellow-spined thistle (Banks 1912). *C. brunnea* probably uses flowers as a platform for capturing prey, similar to praying mantids (Mantodea) and crab spiders (Thomisidae). Communications with Simon van Noort, from Iziko Museum in Cape Town, RSA are also in agreement with much of what is described in the Ohl (2004) study. Van Noort described observations (pers. comm.) of the Afrotropical endemic genus, *Pseudoclimaciella*, gathering on indigenous flowers in dense vegetation in Tanzania.

Meticulous work by Kral (1989, 1990, 2013), with the focus on the eye morphology and function of some diurnal mantispids, may be in support of the diurnal activity of mantispids. Generally, nocturnal insects are equipped with superpositional eyes and not appositional eyes. However, *Mantispa styriaca* and *M. scabricollis* are equipped with refracting superpositional eyes that are modified for diurnal vision. A special tapetal layer at the base of the compound eye, consisting of flattened air-filled tracheoles (tapetum lucidum) in each ommatidium isolates it from the rest of the ommatidia. This structure improves the light-sensitivity or photon catch of the eyes. The resolution of this type of diurnal superpositional eyes are somewhat comparable to phototopic appositional eyes but with higher light sensitivity (Kral 2013). This type of eye might be present in several other diurnal mantispid species and has also been described in Ascalaphinae (Schneider *et al.* 1978) and Chrysopidae (Horridge & Henderson 1976; Yang *et al.*, 1998), both lacewing families (Neuroptera).

New & Haddow (1973) conducted a light trapping study in Entebbe, Uganda, trying to elucidate the nocturnal flying patterns of mantispids. A mercury-vapour light trap was used from one hour before sunset (±17h00) to one hour after sunrise (±07h00). The authors reported that most of the mantispids were caught before midnight and that mantispid activity peaks around 21h00. All the mantispids were caught and preserved, presumebly to avoid pseudoreplication. However, by removing all mantispids in a given area, it is difficult to conclude that the mantispid activity decreased after midnight. It is just as plausible that the activiy would have continued throughout the night if all mantispids were not caught. The reduction in mantispids caught after midnight might therefore be solely due to the decreasing numbers of uncaught mantispids. The study does not document the "true" nocturnal flying patterns of mantispids, but rather just the number of mantispids caught in Entebbe, Uganda.

McKeown & Mincham (1948) recorded two periods of increased adult activity during the year where adults were found in high numbers. The first was late spring (October and November in Australia) and again in autumn (March and April in Australia). This is likely because mantispids are secondary predators and need spiders to mate before they can reach adulthood. The first peak might be due to emerging pupae from the previous season. The second peak in early autumn might be due to the lagging effect while spiders mature, mate and produce egg sacs. Alternatively, it might be bivoltine behaviour, mantispids producing two broods per season. It should be noted however, that overwinterting of mantispines as larvae and pupae are well documented as discussed earlier. Lastly, the perceived bivoltinity might be due to the ability of matispid larvae to either shorten or extend their delevopment inside an egg-sac and emerge when conditions are favourable. Redborg (1983) described the presence of an allomone produced by feeding mantispine larvae. Interestingly, another "aggressive" allomone has been described in the sister group of mantispids, Berothidae. Johnson & Hagen (1981) described *Lomamyia latipennis* larvae immobilising termite workers (*Reticulitermes hesperus*) with an allomone before feeding commenced. In the case of mantispids, the allomone is thought to prevent the spider eggs from hatching and turn the predatory larva into possible spider prey (Redborg 1983). However, the presence of such an allomone might just as well describe the perceived bivoltinity mentioned

by McKeown & Mincham (1948). Alternatively, the allomone is produced to ensure that the feeding larva sustains its food availibility in order to complete metamorphosis.

A detailed monograph by Redborg & Macleod (1985) theorised that a direct relationship between the amount of food ingested by the third instar larva and the body size of the adult exists. *Dicromantispa sayi* (cited as *M. uhelri*) that had food *ad libitum* resulted in adults nearly double the size of those that were fed only 50 *Achaearanea* eggs. In addition, the authors stated that third instar mantispid larvae, with limited food, will pupate as soon as all the eggs have been ingested and ignore all food presented to it after spinning is initiated. It was also proposed that the amount of food ingested by a female mantispid during the larval phase will not only affect size, but also fecundity. This hypothesis was tested by Hirata & Ishii (2001) in another mantispid species, *Eumantispa harmandi*. Females that were fed more often had a positive correlation with both higher number of eggs laid as well as higher number of batches, whilst body size affected neither. The authors also noted a negative correlation between size and longevity but failed to provide a possible explanation of the correlate.

## Biogeography: origins of Mantispidae and the break-up of Pangea

Mantispidae are currently divided into four extant subfamilies: Symphrasinae, Drepanicinae, Calomantispinae and Mantispinae (Lambkin 1986a; b; Lambkin & New 1994). Symphrasinae is generally regarded as the most pleisiomorphic subfamily and sister to the remaining subfamilies (Lambkin 1986a; b; Willman 1990; Lambkin & New 1994; Liu et al. 2015). The most apomorphic subfamilies, Calomantispinae and Mantispinae form a monophyletic group, with Drepanicinae as their sister clade (Lambkin 1986a, b; Lambkin & New 1994; Liu et al. 2015). There is a single extinct subfamily formally described, namely Mesomantispinae and the possibility of an additional extinct subfamily comprising the genus *Doratomantispa* (Poinar & Buckley 2011) (Fig. 5). This arrangement was recently disputed in a phylogenomic study by Winterton et al. (2018) using anchored hybrid enrichment data. The phylogeny generated recovered Symphrasinae as sister to Rhachiberothidae and Berothidae as sister to the remaining Mantispidae. Due to the ambiguous results, the authors suggested the recognition of a single family, Mantispidae, with the berothids, rhachiberothids and dipteromantispids as specialised lineages within the family.

Jepson (2015) reviewed the fossils currently thought to belong to Mantispidae, and in so doing highlighted the current classification problems regarding fossil mantispids. The ancient *Liassochrysa stigmatica* (Liassochrysidae) is thought to be part of Mantispidae, however, the relationship is not clear (Jepson 2015; Liu et al. 2015; Shi et al. 2019; Wedmann & Makarkin 2007). The type species and genus of Liassochrysidae, *Liassochrysa stigmatica* was erroneously placed in Chrysopidae (Ansorge & Schlüter 1990) and later elevated to a monotypic family status with the possibility of being sister to mantispids. *Liassochrysa stigmatica* dates to the lower- and mid-Jurassic period and is regarded as the earliest fossil along with the closely related *Promantispa similis* from the upper Jurassic period (Jepson 2015). Similarly, Winterton et al. (2010, 2018), using
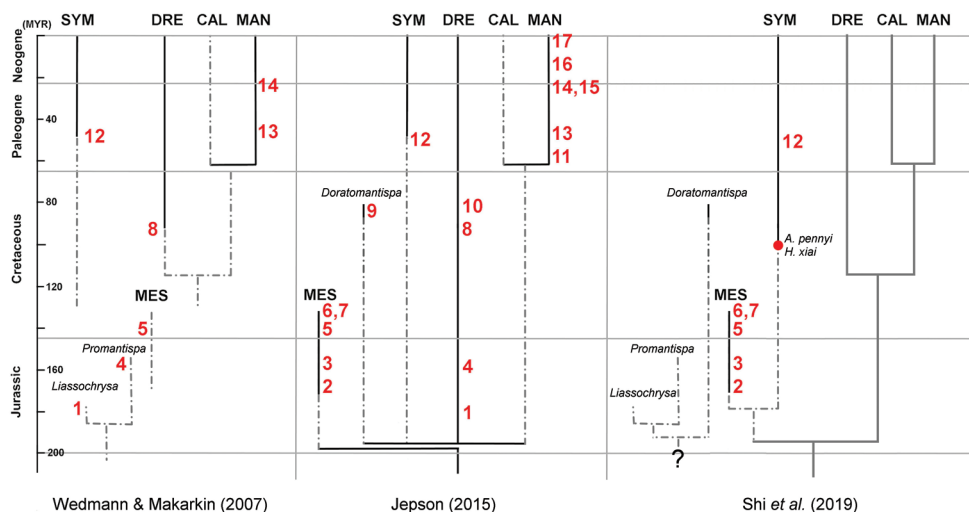
**Fig. 5.** Phylogenetic and divergence time hypotheses based on fossil data of Wedmann & Makarkin (2007), Jepson (2015) and Shi et al. (2019). Numbers indicate the fossils included by the various authors following Jepson (2015). (1) *Liassochrysa stigmatica*, (2) *Clavifemora rotundata* (3a) *Karataumantispa monstruosa* (3b) *Karataumantispa carnaria* (4) *Promantispa similis* (5) *Mesomantispa sibirica* (6a) *Archaeodrepanicus acutus* (6b) *Archaeodrepanicus nuddsi* (6c) *Archaeodrepanicus* sp. (7) *Sinomesomantispa microdentata* (8) *Gerstaeckerella\* asiatica* (9) *Doratomantispa burmanica* (10) *Micromantispa cristata* (11) Unidentified larvae (12) *Symphrasites eocenicus* (13) *Vectispa relicta* (14) *Prosagittalata oligocenia* (15) *Climaciella\*(?) henrotayi* (16a) *Dicromantispa\* electromexicana* (16b) *Dicromantispa\* moronei* (17) *Feroseta prisca.*. Shi et al. (2019) did not specify Mesomantispinae species in their analysis, here all Mesomantispinae fossils are indicated on the phylogeny. \*Extant genera; solid black lines: age of lineages supported by fossils; dash grey line: inferred range/relationship; solid grey line: extant taxa used for analysis.

*Liassochrysa stigmatica* as a crown calibration for molecular divergence time analysis, found the age of Mantispidae to be approximately 150-200 million years ago (Mya). Wedmann & Makarkin (2007) postulated that the diversification of Mantispidae was probably during the Jurassic period, but that the origin of the family might have occurred during the end of the Triassic period and was certainly around by the early Jurassic, with Laurasia as the epicentre of mantispid evolution. The phylogenetic analysis by Liu et al. (2015) from multistate morphology evidence changed this framework in that it led to the transference of *Liassochrysa* and *Promantispa* to the Drepanicinae. This transference increased the age of Drepanicinae, thought to have originated in the upper Cretaceous period (Wedmann & Makarkin 1990), pushing it back to the estimated origin of Mantispidae in the lower Jurassic period (Jepson 2015). The authors unfortunately did not include a divergence time estimate analysis in support of their hypothesis. It should be noted that of the 74 morphological characters used in the Liu et al. (2015) study, 58 (78%) and 60 (81%) of those characters were missing for *Liassochrysa stigmatica* and *Promantispa similis*, respectively. Most recently, Shi et al. (2019) discovered and described two fossil Symphrasinae species from Burmese amber, *Archaeosymphrasis pennyi* and *Habrosymphrasis xiai*. The authors generated a phylogeny

from 19 morphological characters and included 11 taxa, both extant and extinct but excluded *Liassochrysa* and *Promantispa* from their analysis due to the uncertainty of placement within Mantispoidea (Fig. 5). The cascade of changes due to the placement of these taxa within Drepanicinae is drastic lacking substantial evidence and therefore requires careful review of both *Liassochrysa stigmatica* and *Promantispa similis*. The fossil was previously thought to be a separate family, Liassochrysidae (Nel et al. 2005) but was transferred to Mantispidae by Wedman & Makarkin (2007) due to morphological similarities with *Promantispa similis*. This fossil, in turn, was also regarded as being in a monotypic family, Promantispidae (Panfilov, 1980), and transferred to Mantispidae by Lambkin (1986a), who could not determine a relationship with the remaining members of the family. Willman (1994) suggested a stem relationship with Mantispidae. Currently both fossils are considered drepanicines and are being used as calibration fossils for phylogenetic analysis that require certainty, something that should potentially be reconsidered. What should be regarded as important is that both *Liassochrysa stigmatica* and *Promantispa similis* are only known from wing impressions, greatly reducing the number of available morphological characters for phylogenetic analysis. Prior to the Liu et al. (2015) and Winterton et al. (2018) papers, authors suspected convergence with Drepanicinae but not necessarily placement within the subfamily (Jepson 2015; Shi et al. 2015; Wedmann & Makarkin 2007). Furthermore, identification from only wing venation between Mesozoic Berothidae and Mantispidae is challenging at best, not to mention subsequent intrafamilial placements (Makarkin 2015).

It has been suggested that the general neuropteran fauna has long since surpassed its biodiversity high-point and that the taxa left are only remnants of a previously megadiverse group (Liu et al. 2015; Wedmann & Makarkin 2007). Both the age and the former diversity of Neuroptera, and thus also Mantispidae, complicates tracing the steps back to the origin of the group. Distribution of extant diversity is not necessarily indicative of former distribution of taxa and the general lack of fossils closely related to extant fauna adds to the difficulty (Wedmann & Makarkin 2007). Fossils of taxa with uncertain placement may not necessarily help with current classification, in fact it may distort it. Most mantispid related fossils have been discovered in the Palearctic, however, unequal efforts for locating fossils on all the continents might provide a false impression of historical diversity deduced from the fossil record (Jepson 2015) (Fig. 6). For example, can we argue that South America was recolonised by members of all four mantispid subfamilies because no fossils have been found there? Wedmann & Makarkin (2007), using mostly fossil data, hypothesised that Mantispidae had an Asian or Eurasian origin and the extant diversity has no bearing on the past distribution. The recent discovery of two Symphrasinae fossils in Burmese amber, dating to the mid/upper Cretaceous could be considered as supporting the Eurasian origin hypothesis and dispersal took place via a Thulean route, at least to the Nearctic (Shi et al. 2019). However, Burmese amber, in turn, might have a Gondwanan origin, which further complicates matters (Shi et al. 2019). Extant Symphrasinae is known from the southern Nearctic, Neotropics and Australasia (Table 1). Apart from the above-mentioned Symphrasinae fossils, an additional Symphrasinae fossil, *Symphrasites eocenicus* (Wedmann & Makarkin, 2007), has been collected in the Palearctic (Fig. 6). The fossil was
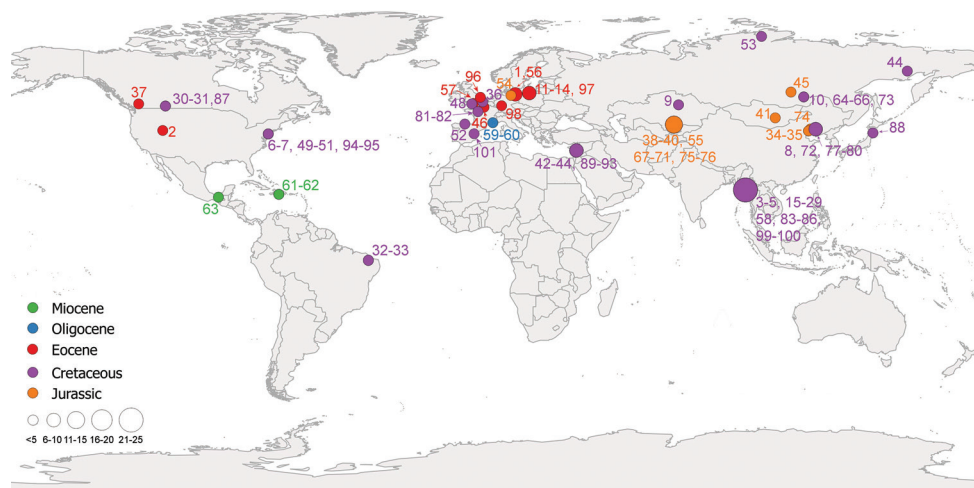
**Fig. 6.** Localities of the fossil Berothidae, Dipteromantispidae, Mantispidae and Rhachiberothidae. Berothinae: 1-2; Dipteromantispidae: 3-8; Drepanicinae: 9, 101; Berothidae *incetae sedis*: 10-53; Liassochrysidae: 54-55; Mantispinae: 56-63; Mesithoninae: 64-72; Mesomantispinae: 73-80; Paraberothinae: 81-95; Rhachiberothidae: 96-97; Symphrasinae: 98-100. Number on map corresponds to fossils in Table 2.

found as an impression in Messel (Germany) dating back to the Eocene, approximately 47 Mya (Liu et al. 2015; Shi et al. 2015; Wedmann & Makarkin 2007), certainly not old enough to postulate that Symphrasinae was also present during the Jurassic. If Burmese amber has a Gondwanan origin, it is also plausible to argue that Symphrasinae colonised the Palearctic from Gondwana and subsequently became extinct since the holarctic was intact during the Paleogene (Winterton 2010).

The extant distribution of higher groupings of Mantispidae, Rhachiberothidae and Berothidae are clearly more diverse on the landmasses that formed part of Gondwana (Table 1). The hypothesis provided by Wedmann & Makarkin (2007) cannot therefore accurately provide evidence for the skewed extant distribution (Fig. 5). It is understandable that one cannot use extant species level distribution for historical patterns, but the presence of all higher-level sister-taxa in Gondwana will prove difficult to explain. Jepson (2015) simply stated that it is possible that during the early Jurassic, drepanicines and symphrasines had a world-wide distribution from the Jurassic until the Neogene.

Fossils, other than *Liassochrysa stigmatica* and *Promantispa similis*, assigned to Drepanicinae are also not without controversy. *Micromantispa cristata* has dissimilar wing venation, but similar fore femurs (Jepson 2015; Shi et al. 2015) when compared to the aforementioned fossils. Shi et al. (2015), expected a close phylogenetic relationship between *Doratomantispa* and *Micromantispa*, and not Drepanicinae. There was even a suggestion that the fossil should be transferred to Paraberothinae (Berothidae) and removed from Mantispidae (Makarkin 2015). The most recent assignment of

*Micromantispa* are also to Drepanicinae by Jepson (2015). The author mentions that the slender fore-femur is unique to Drepanicinae, and the specimen should be regarded as part of the "stem-group" of Drepanicinae, sister to Drepanicinae. Since there is no such classifiecation platform in place, the genus was placed within Drepanicinae. Similarly, the recently discovered fossil from Cretaceous Spanish amber, *Aragomantispa lacerata* Pérez-de la Fuente & Peñalver, 2019, was placed in Drepanicinae due to the diagnostic characters excluding the remaining subfamilies (Pérez-de la Fuente & Peñalver 2019). The authors did, however, state that the placement into Drepanicinae is not without uncertainty and that several characters, such as the presence of trichosors and shape of the scape (Pérez-de la Fuente & Peñalver 2019). This is perhaps reaffirmation of the need to revisit the fossils currently placed in Drepanicinae.

There is no doubt that due to the poor state of fossil specimens and the low numbers available it is challenging to place fossils into an existing classification system. As it currently stands, a previously megadiverse fauna is consistently superimposed on a less diverse classification of extant species. Here we argue that instead of creating a more robust classification, it is increasingly confusing and more difficult to explain or understand. It is plausible to consider a split in the proto-mantispids following the break-up of Pangea during the Jurassic. The mantispids that remained on Gondwana diversified into the extant fauna which might explain the disjunct distribution between the Neotropics and Australasia. In turn, the mantispids that remained on Laurasia also diversified, some at least in convergence with drepanicines. Convergence might explain why a robust hypothesis of classification and clear understanding of the historical biogeography is so difficult to achieve. Pronounced weight on convergence might be a slightly tenuous argument, but to argue that all subfamilies had a worldwide distribution since the Jurassic and became extinct is just as tenuous (Wedman & Makarkin 2007; Jepson 2015).

The Afrotropical endemic Rhachiberothidae have a rather unsettled history (Fig. 7): some authors prefer to place them as a subfamily of the berothids (Tjeder 1959; MacLeod & Adams 1968; Makarkin 2015; Makarkin & Kupryjanowicz 2010) (Fig. 7A), some prefer to place them within the mantispids (Willmann 1990) (Fig. 7B) and some authors suggest that they should form a separate family as either sister to Berothidae (Aspöck & Mansell 1994) or as sister to Mantispidae (Liu et al. 2015) (Fig. 7C). Initially, molecular evidence and integrative evidence points to them being a separate family sister to Mantispidae (Liu et al. 2015). This changed when more in-depth molecular evidence placed them in a monophyletic clade with the Symphrasinae, with Berothidae rendering Mantispidae paraphyletic (Winterton et al. 2018) (Fig. 7D). This is not only supported by the relatively close morphological connection between Symphrasinae and Rhachiberothidae (synapomorphies include a left mandibular tooth, raptorial forelegs, and modified foretarsus in the male) (Willmann 1990; Aspöck & Mansell 1994; Makarkin & Kupryjanowicz 2010), but has been supported with molecular evidence as well (Liu et al. 2015; Winterton et al. 2018). Isolation of Rhachiberothidae in Africa might be the reason for the genetic "distance" from the rest of the berothids or, in turn, mantispids as well as the confusing morphology.
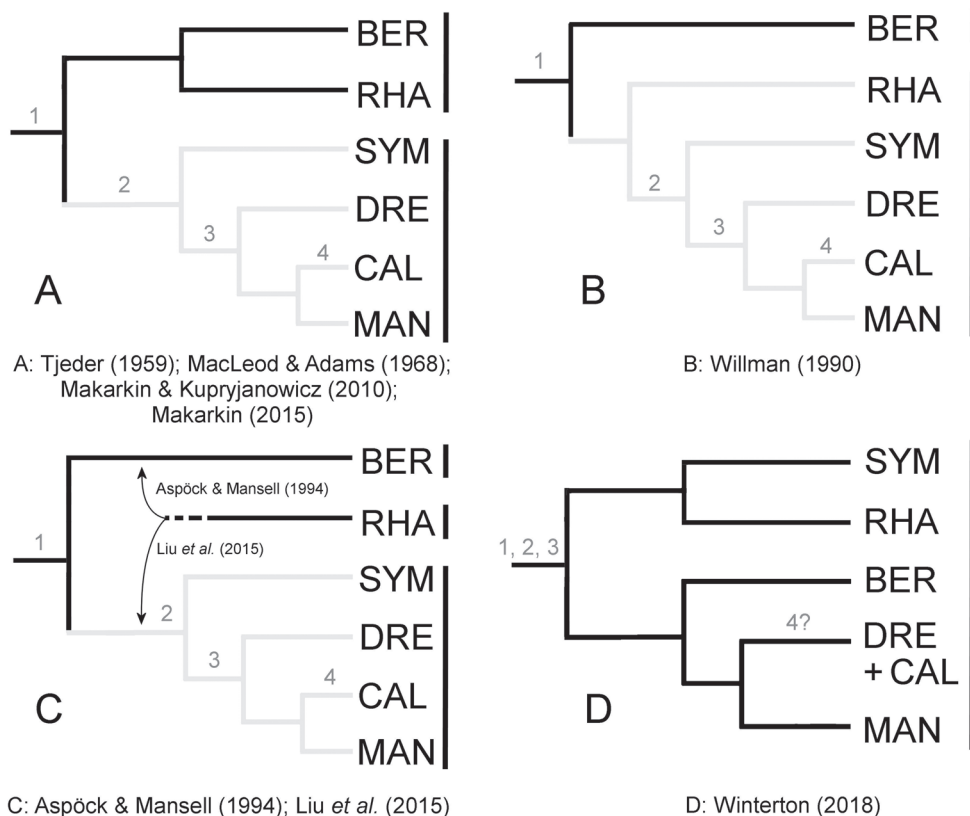
**Fig. 7.** Contrasting views of the phylogenetic relationships of Berothidae, Rhachiberothidae and Mantispidae. Black vertical lines on the right denote family recognition. A. Mantispidae and Berothidae (+Rhachiberothinae) as families. B. Mantispidae (+Rhachiberothinae) and Berothidae as families. C. Mantispidae, Berothidae and Rhachiberothidae as families. D. Only Mantispidae as a family with Berothidae and Rhachiberothidae as specilised lineages. Numbers indicate selected apomorphies. 1. Origin of planidium larvae feeding on social insects and the advent of raptorial forelegs. 2. Origin of wasp mimesis and parametamorphic ontogeny. 3. Spider eggs as a food source. 4. Loss of parametamorphic ontogeny.

The sister-grouping of *Mucroberotha* (Rhachiberothidae) and *Ormiscocerus* (Nyrminae) (Winterton et al. 2010: fig 5) also indicates a Gondwanan origin. Cyrenoberothinae, sister to the Nyrminae, occurs in both the Neo- and Afrotropics with Rhachiberothidae endemic to the Afrotropics, whereas Nyrminae occurs in the Neotropics and the northeastern mediterranean surrounding the Arabian Peninsula. Even though berothids and rhachiberothids had a near cosmopolitan distribution during the Cretaceous, as seen from fossil evidence, the extant Afrotropical Rhachiberothidae are more closely related to the Gondwanan Berothidae, and not members from the Laurasian taxa. Mesoberothidae (now Berothidae) known from compressions in Asia are thought to be either the stem taxon for berothids or possibly all "Mantispoidea" (Winterton et al. 2018). If some members of proto-Mantispoidea remained on Laurasia and some

isolated on Gondwana during the pangean break, it could complicate deducing phylogeny during the following time periods, due to the possbility of parallelism despite genetic isolation, especially given a small sample size such as fossil records tend to be. Unfortunately, no basal berothid members were included in the Winterton et al. (2018) study and a similar study more focussed on including a higher number of taxa in the Mantispoidea could elucidate aspects of these relationships.

The extant diversity of higher taxon groups of Berothidae, Mantispidae and Rhachiberothidae indicates that a "historical diversity" surrounds continents originally part of Gondwana (Table 1). This is not uncommon for taxa with a Gondwana origin (Li & Zhou 2007). The plant genus *Nothofagus* have a very similar distribution pattern, also thought to have originated on Gondwana (Li & Zhou 2007). The loss of other Mantispidae lineages on Africa might be due to several postulates. Firstly, other subfamilies might have been present, but were outcompeted by derived Mantispinae that comparatively recently "recolonised" the Afrotropics from the Palearctic region and became extinct. The other subfamilies went extinct in the Afrotropics, and only Mantispinae remained. The last scenario, similar to *Nothofagus*, is that Mantispidae never colonised central Gondwana and remained on what is today known as South America, Antarctica, India and Australia (Li & Zhou 2007). Rhachiberothidae could have colonised central Gondwana with diversification from Berothidae and Mantispidae occurring after the breakup of Gondwana. These timelines fit with the break-up of Pangea occuring around the same time (200 Mya) as the origin and diversification of Rhachiberothidae, Berothidae and Mantispidae (Jepson & Penney 2007).

Lastly, our understanding of the Mantispidae, Berothidae and Rhachiberothidae phylogeny would drastically improve if the subfamilial level of fossil berothids receive treatment. When considering the Berothidae fossil record, currently thought to comprise 69 taxa, more than 60% of these taxa remain unclassified beyond family level (various authors, see Table 2). The taxa that have been assigned to a subfamily tend to receive more scrutiny and are subsequently moved within the classification more often. This has been true of members of Paraberothinae such as, *Micromantispa cristata* (Shi et al. 2015; Makarkin 2015a, b; Nakamine & Yamamoto 2018), *Retinoberotha stuermeri* (Engel 2004; McKellar & Engel 2009, Makarkin *et al.* 2011; Makarkin 2015a, b; Nakamine & Yamamoto 2018) and *Raptorapax terribilissima* (Petrulevicius et al. 2010; Makarkin et al. 2011; Makarkin 2015a, b; 2018; Nakamine & Yamamoto 2018).

In conclusion, the historical biogeography of Mantispidae and sistergroups, Berothidae and Rhachiberothidae are, at best, not well understood. The disjunct Gondwanan distribution of higher taxon levels is currently also not well explained. Here it is proposed that the following require elucidation in order to improve our understanding of their historical biogeography:

1. Increased fossil data are needed, particularly from regions other than the Palearctic and especially from the Neo- and Afro-tropics.
2. The placement of *Gerstaeckerella asiatica*, *Liassochrysa stigmatica*, *Promantispa similis* and *Micromantispa cristata* should be revisited.

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**Table 2.** Fossil Berothidae, Dipteromantispidae, Mantispidae and Rhachiberothidae. Numbers correspond to those on figures 6. * denotes extant genera.

| Map Ref. | Higher classification | Genus and species | Locality | Age | Reference |
| --- | --- | --- | --- | --- | --- |
| 1 | Berothinae | *Elektroberotha groehni* | Baltic amber | Late Eocene | (Makarkin & Ohl 2015) |
| 2 | Berothinae | *Xenoberotha angustialata* | Green River Formation, USA | Early Eocene | (Makarkin 2017) |
| 3 | Dipteromantispidae | *Halteriomantispa grimaldii* | Burmese amber, Myanmar | Middle/Upper Cretaceous | (Liu et al. 2016) |
| 4 | Dipteromantispidae | *Burmodipteromantispa jiaxiaoae* | Burmese amber, Myanmar | Middle/Upper Cretaceous | (Liu et al. 2017) |
| 5 | Dipteromantispidae | *Mantispidipterella longissima* | Burmese amber, Myanmar | Middle/Upper Cretaceous | (Liu et al. 2017) |
| 6 | Dipteromantispidae | *Mantispidiptera enigmatica* | East USA, Turonian amber | Middle/Upper Cretaceous | (Grimaldi 2000; Wedmann & Makarkin 2007) |
| 7 | Dipteromantispidae | *Jersimantispa henryi* | East USA, Turonian amber | Middle/Upper Cretaceous | (Grimaldi 2000; Wedmann & Makarkin 2007, Liu et al. 2017) |
| 8 | Dipteromantispidae | *Dipteromantispa brevisubcosta* | Yixian for., China | Lower Cretaceous | (Makarkin et al. 2013) |
| 9 | Drepanicinae | *Gerstaeckerella* asiatica* | Kzyl-Zhar, Kazakhstan | Upper Cretaceous | (Makarkin 1990) |
| 10 | *incertae sedis* (Berothidae) | *Pseudosisyra minima* | Baisa, Siberia | Lower Cretaceous | (Makarkin 1999; Khramov 2015) |
| 11 | *incertae sedis* (Berothidae) | *Berothidae* indet. | Baltic amber | Late Eocene | (Bachofen-Echt 1949) |
| 12 | *incertae sedis* (Berothidae) | *Berothidae* indet. | Baltic amber | Late Eocene | (Weitschat & Wichard 1998) |
| 13 | *incertae sedis* (Berothidae) | *Berothidae* indet. | Baltic amber | Late Eocene | (Macleod & Adams 1967) |
| 14 | *incertae sedis* (Berothidae) | *Berothidae* indet. | Baltic amber | Late Eocene | (Janzen 2002) |
| 15 | *incertae sedis* (Berothidae) | *Doratomantispa burmanica* | Burmese amber, Myanmar | Upper Cretaceous | (Poinar & Buckley 2011) |
| 16 | *incertae sedis* (Berothidae) | *Maculaberotha nervosa* | Burmese amber, Myanmar | Upper Cretaceous | (Yuan et al. 2016) |
| 17 | *incertae sedis* (Berothidae) | *Magniberotha recurrens* | Burmese amber, Myanmar | Upper Cretaceous | (Yuan et al. 2016) |
| 18 | *incertae sedis* (Berothidae) | *Haploberotha carsteni* | Burmese amber, Myanmar | Mid Cretaceous | (Makarkin 2018) |
| 19 | *incertae sedis* (Berothidae) | *Protoberotha minuta* | Burmese amber, Myanmar | Mid Cretaceous | (Huang et al. 2019) |
| 20 | *incertae sedis* (Berothidae) | Berothidae indet. (larva) | Burmese amber, Myanmar | Lower Cretaceous | (Engel & Grimaldi 2008) |
| 21 | *incertae sedis* (Berothidae) | *Dasyberotha eucharis* | Burmese amber, Myanmar | Lower Cretaceous | (Engel & Grimaldi 2008) |
| 22 | *incertae sedis* (Berothidae) | *Ethiroberotha elongata* | Burmese amber, Myanmar | Lower Cretaceous | (Engel & Grimaldi 2008) |
| 23 | *incertae sedis* (Berothidae) | *Haploberotha persephone* | Burmese amber, Myanmar | Lower Cretaceous | (Engel & Grimaldi 2008) |
| 24 | *incertae sedis* (Berothidae) | *Iceloberotha kachinensis* | Burmese amber, Myanmar | Lower Cretaceous | (Engel & Grimaldi 2008) |

**Table 2.** (*Cont.*)

| Map Ref. | Higher classification | Genus and species | Locality | Age | Reference |
|---|---|---|---|---|---|
| 25 | *incertae sedis* (Berothidae) | *Iceloberotha simulatrix* | Burmese amber, Myanmar | Lower Cretaceous | (Engel & Grimaldi 2008) |
| 26 | *incertae sedis* (Berothidae) | *Jersiberotha myanmarensis* | Burmese amber, Myanmar | Lower Cretaceous | (Engel & Grimaldi 2008) |
| 27 | *incertae sedis* (Berothidae) | *Jersiberotha tauberorum* | Burmese amber, Myanmar | Lower Cretaceous | (Engel & Grimaldi 2008) |
| 28 | *incertae sedis* (Berothidae) | *Systenoberotha magnillae* | Burmese amber, Myanmar | Lower Cretaceous | (Engel & Grimaldi 2008) |
| 29 | *incertae sedis* (Berothidae) | *Telistoberotha libitina* | Burmese amber, Myanmar | Lower Cretaceous | (Engel & Grimaldi 2008) |
| 30 | *incertae sedis* (Berothidae) | *Berothidae indet.* | Canadian amber | Upper Cretaceous | (Engel & Grimaldi 2008) |
| 31 | *incertae sedis* (Berothidae) | *Plesiorobius canadensis* | Canadian amber | Upper Cretaceous | (Klimaszewski & Kevan 1986) |
| 32 | *incertae sedis* (Berothidae) | *Araripeberotha fairchildi* | Crato Formation, Brazil | Lower Cretaceous | (Martins-Neto & Vulcano 1990) |
| 33 | *incertae sedis* (Berothidae) | *Caririberotha martinsi* | Crato Formation, Brazil | Lower Cretaceous | (Martins-Neto & Vulcano 1990) |
| 34 | *incertae sedis* (Berothidae) | *Sinosmylites fumosus* | Daohugou, China | Middle Jurassic | (Makarkin et al. 2011) |
| 35 | *incertae sedis* (Berothidae) | *Sinosmylites rasnitsyni* | Daohugou, China | Middle Jurassic | (Makarkin et al. 2011) |
| 36 | *incertae sedis* (Berothidae) | *Epimesoberotha parva* | Durlston Bay, England | Lower Cretaceous | (Jepson et al. 2012) |
| 37 | *incertae sedis* (Berothidae) | *Microberotha macculloughi* | Hat creek amber, Canada | Early Eocene | (Archibald & Makarkin 2004) |
| 38 | *incertae sedis* (Berothidae) | *Krokhathone parva* | Karatau, Kazakhstan | Upper Jurassic | (Khramov 2015) |
| 39 | *incertae sedis* (Berothidae) | *Krokhathone tristis* | Karatau, Kazakhstan | Upper Jurassic | (Khramov 2015) |
| 40 | *incertae sedis* (Berothidae) | *Sinosmylites karatavicus* | Karatau, Kazakhstan | Upper Jurassic | (Khramov 2015) |
| 41 | *incertae sedis* (Berothidae) | *Sinosmylites botgoricus* | Khoutiyn-Khotgor, Mongolia | Upper Jurassic | (Khramov 2015) |
| 42 | *incertae sedis* (Berothidae) | *Banoberotha enigmatica* | Lebanese amber | Lower Cretaceous | (Whalley 1980) |
| 43 | *incertae sedis* (Berothidae) | *Berothidae indet.* (larva) | Lebanese amber | Lower Cretaceous | (Whalley 1980) |
| 44 | *incertae sedis* (Berothidae) | *Sibelliberotha rihanensis* | Lebanese amber | Lower Cretaceous | (Azar & Nel 2013) |
| 45 | *incertae sedis* (Berothidae) | *Sibithone dichotoma* | Novospasskoe, Russia | Lower/Mid Jurassic | (Ponomarenko 1984; Khramov 2015) |
| 46 | *incertae sedis* (Berothidae) | *Oisea celinea* | Oise amber, France | Early Eocene | (Nel et al. 2005) |
| 47 | *incertae sedis* (Berothidae) | *Plesiorobius sibiricus* | Ola for, Siberia | Upper Cretaceous | (Makarkin 1994) |
| 48 | *incertae sedis* (Berothidae) | *Epimesoberotha parva* | Purbeck Limestone, England | Lower Cretaceous | (Jepson et al. 2012) |
| 49 | *incertae sedis* (Berothidae) | *Jersiberotha luzzii* | Raritan Amber, USA | Upper Cretaceous | (Grimaldi 2000) |
| 50 | *incertae sedis* (Berothidae) | *Jersiberotha similis* | Raritan Amber, USA | Upper Cretaceous | (Grimaldi 2000) |
| 51 | *incertae sedis* (Berothidae) | *Nascimberotha picta* | Raritan Amber, USA | Upper Cretaceous | (Grimaldi 2000) |
| 52 | *incertae sedis* (Berothidae) | *Berothidae indet.* | Spanish amber | Lower Cretaceous | (Peñalver & Delclòs 2010) |

| | | | | | |
|---|---|---|---|---|---|
| 53 | *incertae sedis* (Berothidae) | *Plesiorobius* cf. *canadensis* | Yantardakh, Siberia | Upper Cretaceous | (Makarkin 1994) |
| 54 | Liassochrysidae? | *Liassochrysa stigmatica* | Dobbertin, Germany | Lower Jurassic | (Ansorge & Schlüter 1990; Wedmann & Makarkin 2007) |
| 55 | Liassochrysidae? | *Promantispa similis* | Karatau, Kazakhstan | Upper Jurassic | (Panfilov 1980; Wedmann & Makarkin 2007) |
| 56 | Mantispinae | Unidentified larvae on spider | Baltic amber | Mid Eocene | (Ohl 2011a) |
| 57 | Mantispinae | *Vectispa relicta* | Bembridge Marls, UK | Upper Eocene | (Cockerell 1921; Jarzembowski 1980; Wedmann & Makarkin 2007) |
| 58 | Mantispinae | Unidentified larvae on spider | Burmese amber, Myanmar | Upper Cretaceous | (Haug et al. 2018) |
| 59 | Mantispinae | *Prosagittalata oligocenia* | Céreste, France | Upper Oligocene | (Nel 1989) |
| 60 | Mantispinae | *Climaciella*(?) *henrotayi* | Daupin, France | Upper Oligocene | (Nel 1989) |
| 61 | Mantispinae | *Dicromantispa* moronei* | Dominican amber | Miocene | (Engel & Grimaldi 2007) |
| 62 | Mantispinae | *Feroseta prisca* | Dominican amber | Miocene | (Poinar 2006) |
| 63 | Mantispinae | *Dicromantispa* electromexicana* | Mexican amber | Miocene | (Engel & Grimaldi 2007) |
| 64 | Mesithoninae | *Mesithone maculosa* | Baisa, Siberia | Lower Cretaceous | (Makarkin 1999; Jepson 2015) |
| 65 | Mesithoninae | *Mesithone proberotha* | Baisa, Siberia | Lower Cretaceous | (Makarkin 1999; Jepson 2015) |
| 66 | Mesithoninae | *Mesithone angusta* | Baisa, Siberia | Lower Cretaceous | (Makarkin 1999; Jepson 2015) |
| 67 | Mesithoninae | *Berothone protea* | Karatau, Kazakhstan | Upper Jurassic | (Panfilov 1980; Khramov 2015) |
| 68 | Mesithoninae | *Berothone gracilis* | Karatau, Kazakhstan | Upper Jurassic | (Panfilov 1980; Khramov 2015) |
| 69 | Mesithoninae | *Mesithone maculata* | Karatau, Kazakhstan | Upper Jurassic | (Panfilov 1980; Jepson 2015) |
| 70 | Mesithoninae | *Mesithone magna* | Karatau, Kazakhstan | Upper Jurassic | (Panfilov 1980; Jepson 2015) |
| 71 | Mesithoninae | *Mesithone grandis* | Karatau, Kazakhstan | Upper Jurassic | (Panfilov 1980; Jepson 2015) |
| 72 | Mesithoninae | *Oloberotha sinica* | Yixian for., China | Lower Cretaceous | (Ren *et al.* 1995) |
| 73 | Mesomantispinae | *Mesomantispa sibirica* | Biassa, Russia/E Siberia | Lower Cretaceous | (Makarkin 1996; Wedmann & Makarkin 2007) |
| 74 | Mesomantispinae | *Clavifemora rotundata* | Jiulongshan for., China | Mid-upper Jurassic | (Jepson et al. 2013) |
| 75 | Mesomantispinae | *Karataumantispa carnaria* | Karatau, Kazakhstan | Upper Jurassic | (Khramov 2013; Jepson 2015) |
| 76 | Mesomantispinae | *Karataumantispa monstruosa* | Karatau, Kazakhstan | Upper Jurassic | (Khramov 2013; Jepson 2015) |
| 77 | Mesomantispinae | *Archaeodrepanicus acutus* | Yixian for., China | Lower Cretaceous | (Jepson et al. 2013) |

(*Continued*)

**Table 2.** (*Cont.*)

| Map Ref. | Higher classification | Genus and species | Locality | Age | Reference |
|---|---|---|---|---|---|
| 78 | Mesomantispinae | *Archaeodrepanicus nuddsi* | Yixian for., China | Lower Cretaceous | (Jepson et al. 2013) |
| 79 | Mesomantispinae | *Archaeodrepanicus sp.* | Yixian for., China | Lower Cretaceous | (Jepson et al. 2013) |
| 80 | Mesomantispinae | *Sinomesomantispa microdentata* | Yixian for., China | Lower Cretaceous | (Jepson et al. 2013) |
| 81 | Paraberothinae | *Alloberotha perrulentii* | Archingeay, France | Lower Cretaceous | (Nel et al. 2005; Makarkin 2015) |
| 82 | Paraberothinae | *Retinoberotha stuermeri* | Bezonnais, France | Upper Cretaceous | (Schlüter 1978; Makarkin 2015) |
| 83 | Paraberothinae | *Creagroparaberotha groehni* | Burmese amber, Myanmar | Lower Cretaceous | (Makarkin 2015) |
| 84 | Paraberothinae | *Eorhachiberotha burmitica* | Burmese amber, Myanmar | Lower Cretaceous | (Engel 2004; Makarkin 2015) |
| 85 | Paraberothinae | *Micromantispa cristata* | Burmese amber, Myanmar | Upper Cretaceous | (Shi et al. 2014) |
| 86 | Paraberothinae | *Scoloberotha necatrix* | Burmese amber, Myanmar | Lower Cretaceous | (Engel & Grimaldi 2008; Makarkin 2015) |
| 87 | Paraberothinae | *Albertoberotha leuckorum* | Canadian amber | Upper Cretaceous | (McKellar & Engel 2009;Makarkin 2015) |
| 88 | Paraberothinae | *Kujiberotha teruyukii* | Kuji amber, Japan | Upper Cretaceous | (Nakamine & Yamamoto 2018) |
| 89 | Paraberothinae | *Chimerhachiberotha acrasarii* | Lebanese amber | Lower Cretaceous | (Nel et al. 2005; Makarkin 2015) |
| 90 | Paraberothinae | *Paraberotha acra* | Lebanese amber | Lower Cretaceous | (Nel 2005; Whalley 1980; Makarkin 2015) |
| 91 | Paraberothinae | *Paraberotha ! acra* | Lebanese amber | Lower Cretaceous | (Whalley 1980; Makarkin 2015) |
| 92 | Paraberothinae | *Raptorapax terribilissima* | Lebanese amber | Lower Cretaceous | (Petrulevicius et al. 2010; Makarkin 2015) |
| 93 | Paraberothinae | *Spinoberotha mickaelacrai* | Lebanese amber | Lower Cretaceous | (Nel et al. 2005; Makarkin 2015) |
| 94 | Paraberothinae | *Rhachibermissa phenax* | Raritan Amber, USA | Upper Cretaceous | (Grimaldi 2000; Makarkin 2015) |
| 95 | Paraberothinae | *Rhachibermissa splendida* | Raritan Amber, USA | Upper Cretaceous | (Grimaldi 2000; Makarkin 2015) |
| 96 | Rhachiberothidae | *Whalfera venatrix* | English amber | Late Eocene | (Whalley 1983) |
| 97 | Rhachiberothidae | *Whalfera wisznieuskii* | Baltic amber | Late Eocene | (Makarkin & Kupryjanowicz 2010) |
| 98 | Symphrasinae | *Symphrasites eocenicus* | Messel, Germany | Mid Eocene | (Wedmann & Makarkin 2007) |
| 99 | Symphrasinae | *Archaeosymphrasis pennyi* | Burmese amber, Myanmar | Upper Cretaceous | (Shi et al. 2019) |
| 100 | Symphrasinae | *Habrosymphrasis xiai* | Burmese amber, Myanmar | Upper Cretaceous | (Shi et al. 2019) |
| 101 | Drepanicinae? | *Aragomantispa lacerata* | Spanish Amber | Mid Cretaceous | (Pérez-de la Fuente & Peñalver 2019) |

3. A revision of the 40 plus fossil taxa currently assigned as Berothidae *incertae sedis* may drastically improve our understanding of the historical biogeography of the group.
4. A robust molecular (or total evidence) phylogeny of Mantispoidea, including divergence time estimates is greatly needed.

## The evolution of mantispids: larval behaviour, mimesis & radiation

Redborg (1985) suggested that proto-mantispids were general predators of sedentary arthropods e.g. pupa. Some members would have then started feeding on spider eggs in which an exclusive niche was realised. Spider boarding, consequently, evolved when the mantispid larvae reached mature spider eggs with spiderlings that had started to hatch. It should be noted that at the time Redborg (1985) proposed his hypotheses, the classification of mantispids was still divided into a primitive Platymantispinae (including Calomantispinae) and derived Mantispinae (Penny 1982b). Much of what Redborg (1985) suggested was based on studies of *Nolima pinal* (Macleod & Redborg 1982) which is now classified as Calomantispinae, sister to Mantispinae and thus derived (Lambkin 1986a; Liu et al. 2015). The phoresy behaviour in mantispines is thus derived and the egg-sac penetrating behaviour ancestral (Macleod & Redborg 1982). If proto-mantispids were generalist predators of arthropod pupae, it would suggest that symphrasines preying on hymenopteran pupa and mantispines mimicking hymenopterans are unrelated and evolved independently.

Most, if not all, *Euclimacia* species are wasp mimics (Ohl 2004). *Euclimacia* might exhibit similar species complexes found in *Climaciella*, most notably *C. brunnea* which have no less than five colour morphs, each mimicking a different wasp (Opler 1981; Ohl 2004; Bhattacharjee et al. 2010). *Euclimacia nodosa* probably mimics *Vespa (Vespa) tropica tropica* (Vespidae) because of the similar colouration of adults (Bhattacharjee et al. 2010). Both *Tuberonotha* and *Pseudoclimaciella* and possibly *Austroclimaciella*, *Entatoneura*, *Nampista* and *Paramantispa*, exhibit very similar colouration found in many *Polistes* wasp species (Hoffman 1992; Snyman et al. 2018). The evolution of mimesis in mantispids is certainly worth investigating as a character shared by several genera of mantispines, and coincidentally, the symphrasines, which are predators of Hymenoptera.

Thus far wasp mimesis has not been described in symphrasines, yet it would make more sense, evolutionary wise, for symphrasinae to evolve wasp mimesis. The mimesis might facilitate gaining access to the host nest without being detected. Dejean & Canard (1990) suggested that *Trichoscelia santareni* might be using chemical camouflage since they gain such easy access to well-guarded nests. However, the hypothesis remains untested. Similarly, *Euclimacia horstaspoecki* was observed flying amongst *Polistes* species (cf. *P. stigma*) without malicious behaviour from either (Ohl 2004). If chemical camouflage is present, mimesis could be considered moot and the coincedental Hymenopteran connection as both larval food source, and mimic

models, unconnected. The diurnal "sit-and-wait" predatory behaviour of *Climaciella, Euclimacia* (Banks 1912; Redborg & Macleod 1983a; Pascarella et al. 2001; Ohl 2004) and *Pseudoclimaciella* observed in Tanzania can then be considered a platform for the evolution on mimesis in one of two ways: (1) either the self-protecting sting possessed by wasps, which is known to protect them from predation (O'Donnell 1996; Kauppinen & Mappes 2003; Rashed et al. 2005) serves as the driver, or (2) mantispids use flowers as a platform for hunting, and thereby gain access to unsuspecting pollinators as a food source (Pascarella et al. 2001).

It does, however, seem unlikely that mantispines evolved from social parasites and secondarily evolved wasp mimesis (Fig. 7). Proto-mantispids probably exhibited a similar life style to what is seen in symphrasines today. Mimesis can allow the mimic to live in close proximity to its model and food source without malicious behaviour from the host, thereby increasing the likelihood of obtaining food. If mimicking behaviour increased the organisms' likelihood of obtaining food, it would surely have been favoured by evolution. Maintaining the mimesis as seen in mantispines is plausible because of the danger wasps hold for several predatory taxa such as Odonata (O'Donnell 1996; Kauppinen & Mappes 2003; Rashed et al. 2005).

It is well understood that the basal subfamily Symphrasinae did not undergo a recent radiation as exhibited by Mantispinae after the divergence of the taxa (Lambkin 1986a, b). It is therefore likely that the behaviour of Symphrasinae did not undergo drastic changes and the life history exhibited today is similar to what it was in the past. The larvae of both Berotidae and Symphrasinae prey on social insects (termites and hymenopterans respectively) with the food source of rhachiberothid larva remaining unknown. Mantispinae, however, must have undergone some sort of drastic change in the evolutionary past to have radiated significantly more than their closely related sister groups. A change in diet might be a plausible explanation. If the proto-mantispines switched from hymenopteran larvae to spider eggs – a novel niche to exploit – a radiation event could be the consequence.

The dietary change from wasps to spiders is not a difficult change. Several studies indicate the importance of spiders as a food source of vespids. After Lepidoptera, Coleoptera and Diptera, Araneae seems to be the preferred food source, especially during autumn when the other arthropod orders presumably pupate and are inaccessible to vespids (Harris & Oliver 1993; Richter 2000; Sackmann et al. 2000). Even though we do not know with certainty that symphrasines have a planidium first instar larvae, it is highly likely that they do. Berothidae, Rhachiberothidae, Calomantispinae, Drepanicinae and Mantispinae all have planidium larvae that actively search for food. The fossilised first instar mantispine larvae described by Ohl (2011) and Haug et al. (2018) from Baltic and Burmese amber respectively, is indicative that boarding of spiders has at least been around since the upper Cretaceous (±100 Mya).

Planidium larvae would have to gain access to such a food source by (1) searching for a nest or (2) search for and board a wasp and gain access to the nest phoretically. If proto-mantispinae planidium larvae started boarding wasps in order to phoretically gain access to nests, boarding of spiders and or other arthropods hunted by wasps, might be a logical next step. Additionally, this will explain both the specialist behaviour

of Mantispinae, and the generalist predatory behaviour exhibited by Calomantispinae larvae. By boarding spiders, access to spider eggs is easier to obtain for an active planidium larvae in stead of adventitiously start penetrating silken egg-sacs in order to obtain eggs. The silk barrier is a very effective protective barrier between the environment and eggs, as explained by Hieber (1992). If Calomantispinae are in fact a generalist insect pupa predator, this hypothesis also explains the evolution thereof. After proto-Calomantispinae larvae board insects that pupate, they will have three options: (1) dismount the pupa and look for alternative food sources; (2) overwinter on the pupa and board the imago; or (3) feed on the pupa.

In conclusion the following is hypothesised:

1. Proto-mantispids radiated in accordance with the radiation of the predatory behaviour in wasps.
2. Mimesis is possibly an ancestral state in Mantispinae, and likely evolved in order to obtain hymenopteran immatures as food.
3. Proto-mantispines radiated in accordance with the radiation of Araneomorphae spiders.
4. Phoresy is possibly the ancestral state in mantispines, and egg-sac penetrators the derived state.

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## Disclosure

All authors declare no conflict of interest.

## Supplementary material

Supplementary material is available online at:
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