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The early stages of *Miomantis binotata* and their bearing on the question whether ant mimicry is a larval feature of first stage praying mantises (Mantodea: Mantidae)

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Abstract
Ant mimicry, i.e., the mimicking of ant workers by another organism, is a widespread phenomenon among different groups of Euarthropoda, including spiders and different insect species. One example of ant mimicry occurs among praying mantises (Mantodea); here the first stage nymphs have been recorded to perform ant mimicry. In this study, we investigated different nymphal instars of *Miomantis binotata* for possible morphological similarities to ants. The different instars were compared as stages supposed to perform ant mimicry would differ morphologically from those stages not supposed to resemble ants. The specimens were investigated under different microscopic settings and measurements were performed. Our results do not show significant differences concerning morphological measurements or shape of structures between the different nymphal instars of *M. binotata.* One prominent difference between stage one nymphs and later stages occurs in the colouration of the body, which is very dark in the earliest nymph. This difference might explain why young nymphs of *Miomantis binotata* are interpreted as ant-mimicking, despite the apparent lack of other morphological resemblances.

Key words: Mantodea, nymph, ontogeny, convergence, colouration.

Introduction

Mimicry
Mimicry is the phenomenon of one organism imitating another organism (or part of it), usually in order to deceive a third type of organism. There are numerous different evolutionary explanations of the advantage of this phenomenon and different aspects of an organism that can be imitated. Evolutionary advantages of mimicry include passive aspects, such as protection by repelling a possible predator, or active ones, such as easier access to a food source by attracting possible prey.

Among the different types of mimicry, optic imitation is probably the most widespread known category, i.e. deceiving the optical senses, or vision, of the organism to be deceived. Other types of mimicry will affect other senses, for example, chemical mimicry will deceive olfactory sensation (e.g., Dettner & Liepert 1994; Akino et al. 1999). Although optical mimicry might appear more trivial, it is in practice not too easy to clearly nail down cases of optical mimicry, or in other words: how can we indeed identify a case of optical mimicry? This is most likely more of a philosophical problem, or better a problem of our recognition (see discussion in Scholtz 2014 for the construct of mind issue). How similar should one organism resemble another one to be accepted as a case of mimicry, and what does 'similar' in this case mean?

Mimicry has been treated as a sub-category of convergent evolution (e.g., McGhee 2011). This is understandable from the point of view that two not closely related organisms evolve a very similar type of morphology. Yet, the evolutionary pressures behind mimicry are most likely very different from those in other cases of convergent evolution: in "normal" cases of convergent evolution two organisms evolve a similar morphology independent of each other, while in cases of mimicry the mimicry-performing organism evolves its morphology depending on the organism it imitates. Still, the recognition of mimicry as a kind of convergence has an important implication. Recently, the philosophical weakness behind the concept of convergent evolution has been pointed out (McGhee 2011). It can be boiled down to the question 'how similar is similar'; hence we would need to quantify similarity. For 'normal' convergence this is for sure of interest, especially when considering predictability of the evolution of convergence.

Yet, for mimicry there is a simple threshold. The degree

of similarity required for successful mimicry certainly depends on the resolution capabilities of the organism to be deceived. To test these capabilities, it would be necessary to perform choice experiments with the organism to be deceived. However, such experiments have usually not been performed for most cases of supposed mimicry, and furthermore, it is often not clear which organism should be deceived by the supposed mimicry. Instead, usually the senses of the researcher are used to evaluate possible cases of mimicry, which is rather subjective and hence unfortunate.

While the theoretical background of mimicry may still be not strictly formulated, we can think of simple criteria that we could use for identifying cases of optical mimicry:

1. Similarity in size: The organism (or part of it) to be imitated and the imitating organism it should be in a similar size. A significant deviation will most likely not successfully deceive the organism to be deceived, although a certain variation in size should be acceptable.
2. Similarity in outline or silhouette: The imitating organism should resemble the organism (or part of it) to be imitated at least in rough outline. It remains difficult to clearly express how large this similarity is. Well-known cases of optical mimicry show well that this aspect generally remains on a rather coarse level of similarity. Flies imitating wasps have a rather coarse similarity concerning the exact outline, but resemble the organism they imitate more in other aspects.
3. Similarity in colour: If the organism to be deceived is capable of colour vision, we should expect also similarities in colour. At least similar patterns of darker and brighter areas should produce a comparable pattern. Here flies and wasps provide a strong example, with similarly striped posterior trunks (abdomina) in black and yellow in both cases (e.g., Marchini et al. 2017).

Ant mimicry

An organism that a variety of terrestrial arthropods are imitating is an ant worker. The phenomenon is therefore addressed as ant mimicry or myrmecomorphy (e.g. McIver & Stonedahl 1993). Not only other insect groups are known to perform ant mimicry, also non-insect euarthropods (the group including all modern forms of segmented organisms with jointed appendages) such as spiders have been interpreted as mimicking ant workers (e.g., Cushing 2012). A larger number of those insects mimicking ants are mantodeans, the praying mantises. At first sight mantodeans have a quite different body outline in comparison to ants. This is especially true for the often highly aberrant-appearing adult mantodeans such as species of *Creobroter*. Yet, ant mimicry seems to be restricted to early nymphal instars, i.e. the small early stages of development shortly after hatching. More precisely, only the first nymphal stage appears to be specialised in this way.

Mantodean larvae?

Mantodeans are non-holometabolous insects (the generally used term "hemimetaboly" is unfortunate as referring to a convergently evolved pattern, see discussion in Haug et al. 2016). Holometabolous insects have early post-embryonic stages addressed to as 'larvae' that appear quite different from their corresponding adults. In non-holometabolous insects the early stages are referred to as nymphs (at least in Anglo-American terminology; in German tradition the term 'nymph' is restricted to the last stage before the adult). Nymphs are generally more similar to their corresponding adults than holometabolous larvae to their adults. Still some nymphs have been accepted to possess true larval specialisations (e.g. Beutel et al. 2014). These specialisations are in many cases related to aquatic life styles of these forms, for example, in dragonflies and damselflies (Odonatoptera), mayflies (Ephemeroptera) or stoneflies (Plecoptera). Yet, if ant mimicry is indeed restricted to the very first nymphs of mantodeans, this specialisation could represent another example of a true larval specialisation of non-holometabolous insects.

As an example we present here observations on early stages of the mantodean *Miomantis binotata*. First stage nymphs of *Miomantis* species have been reported to perform ant mimicry (Edmunds 1972). We discuss, based on our observations, in how far stage one nymphs are specialised to resemble ants.

Material and methods

Material

Specimens of *Miomantis binotata* used in the study came from the private breedings of one of the authors (MI). Both the ootheca from which the nymphs hatched and the nymphs themselves were kept at room temperature in a terrarium. The air humidity in the terrarium was kept stable by spraying water with a spray bottle from time to time. The nymphs were regularly fed with small flies (*Drosophila* sp.).

In total, ten specimens were available for study (Fig. 1). Specimens could be differentiated according to colour and size already with the naked eye. Six specimens are rather small and of a dark brownish colour. Three specimens are larger and significantly paler, almost white in colour. One specimen is a special case, showing aspects of both types of specimens.

Specimens will be deposited in the Zoological State Collection Munich (ZSM).

Documentation methods

Specimens were documented under different microscopical setups, including autofluorescence and white-light settings. For autofluorescence, epifluorescence on a Keyence BZ-9000 microscope was performed for overview images and confocal laser-scanning microscopy on a Leica TCS SP2 microscope for detail images (e.g., Haug et al. 2011a). White-light imaging was performed under reflected cross-

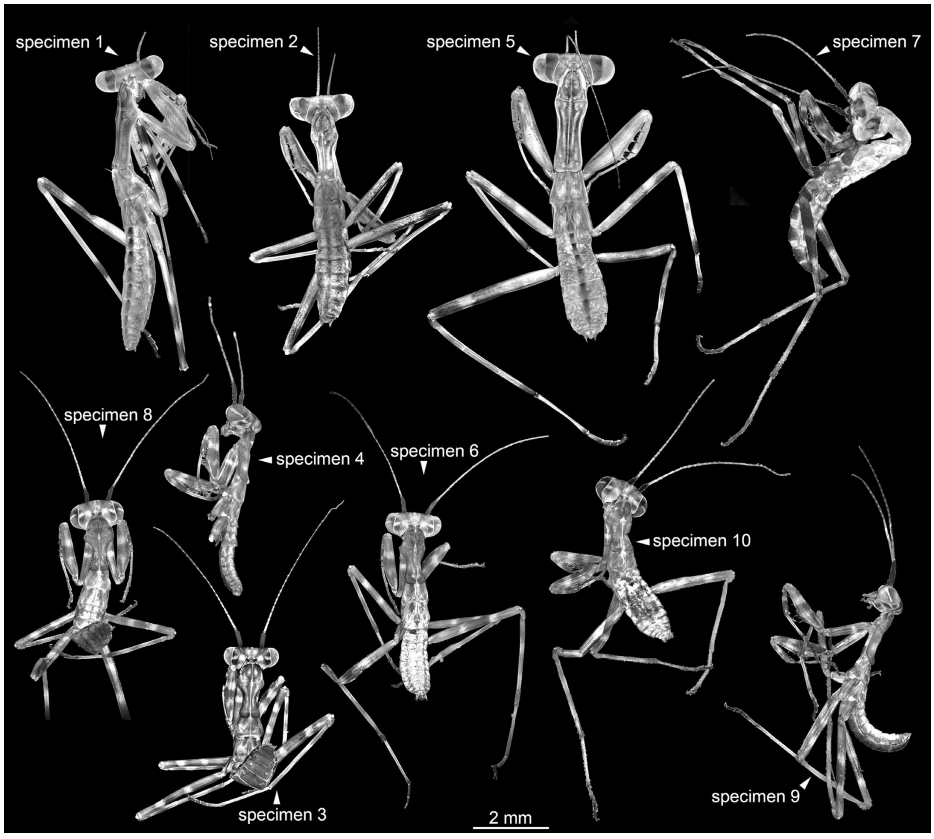

Fig. 1 – Entire material investigated in this study.

polarised light for overview images and under brightfield conditions for detail images, both on a Keyence BZ-9000 microscope (e.g., Haug et al. 2011b). Composite imaging was applied, which means that several image stacks of adjacent image details are recorded to enhance the field of view and depth of field (e.g., Haug et al. 2008).

Image processing
Image stacks recorded with epifluorescence or reflected white light were fused to one sharp image with CombineZP. Image stacks recorded with cLSM were Z-projected (maximum intensity projection) with ImageJ. For image stacks recorded with brightfield, 'find edges' was performed in ImageJ, followed by a Z-projection (maximum intensity projection); the resulting image was colour inverted. The differently fused or projected images were stitched to high-resolution compound images with Adobe Photoshop CS 3 or Adobe Photoshop Elements 11 (e.g., Haug et al. 2008, 2009).

Drawings
Drawings were made with Adobe Illustrator CS 2.

Measurements
The lengths of different morphological structures were measured. These included the femora of the legs (excluding a regenerated leg in one of the specimens), the tergites of the thoracic segments, and the width of the head (Fig. 2).

Predictions
As lain out in the introduction, the concepts of distinguishing cases of mimicry from those that are no mimicry are so far only weakly developed. A similar case in fact accounts for the question when we should call an early post-embryonic stage a larva and when not. Due to the lack of a well-accepted concept we see here the necessity to formulate specific expectations that will be tested by the observations.

1. Difference between nymphal stage one and older stages. If the first nymphal instar is indeed specialised to resemble ants, while later stages are not, we should expect significant recognisable differences in morphology between the stages. Later stages would not have the same selective pressures. As the adult morphology differs in ratios of lengths of structures, a stepwise allometric growth should be expected.
2) Similarities between "original and copy" higher than between others. Nymphs of *Miomantis* have been interpreted to imitate ant workers of the groups *Pheidole* and *Tetramorium* (Edmunds 1972). If this should be indeed the case, the similarity between these ant workers and the mantodean nymph should be higher than the similarity of all three to another ant worker.

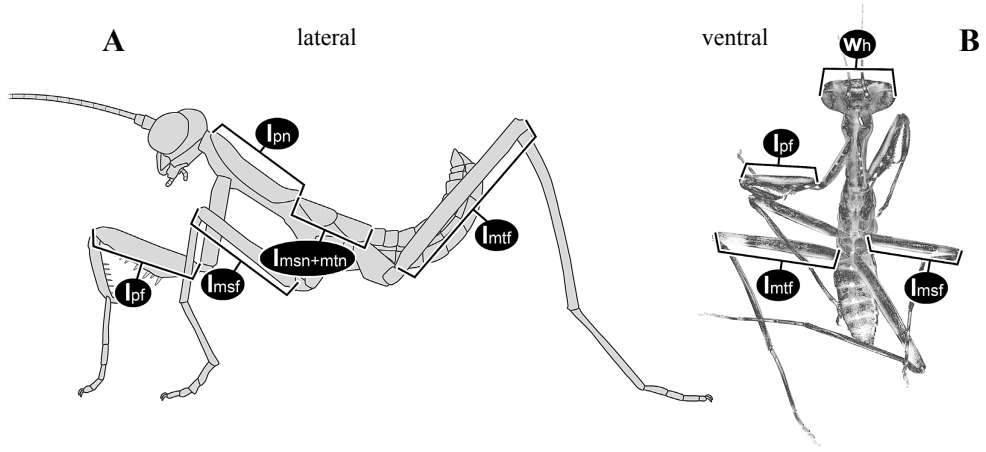

Fig. 2 – Performed measurements in lateral (A) and ventral aspect (B). Abbreviations: lmsf = length mesofemur; lmsn+mtn = length mesonotum plus metanotum; lmtf = length metafemur; lpf = length profemur; lpn = length pronotum; wh = width head.

Results

Identifying stages

As mentioned previously, the specimens of *Miomantis binotata* can already at first sight be separated into two distinct groups:

1. smaller specimens which are of a very dark colour;
2. larger specimens that are significantly paler.

Specimens of both groups possess a general mantodean nymph-type of morphology: The body is subdivided into 20 segments (not all externally visible), six head segments (ocular segment plus post-ocular segment 1–5), followed by a trunk with fourteen segments. The anterior three trunk segments, or thorax segments (post-ocular segment 6–8), each bear a pair of walking appendages (thoracopods). Of the 11 posterior trunk segments, or abdominal segments (insect-type abdomen; post-ocular segments 9–19), only the last one bears a pair of appendages, the cerci. Leg elements 3 (femur) and 4 (tibia) of post-ocular segment 6 are specialised as a sub-chelate raptorial claw.

Measurements on all specimens and simple scatter plots support the initial differentiation (Fig. 3A–C). All smaller, darker specimens cluster together. These are interpreted to represent first instar nymphs. The three larger specimens could indeed represent two distinct clusters, i.e. could represent nymphal instar two and three. Yet, due to the small sample size this cannot be further corroborated as it is unclear how large the maximal size gain per moult is possible in this species. Therefore, size difference between the three specimens could reflect true size diversity within one stage.

Hence, two clear stages can be differentiated by size and colour. Stage one is smaller and dark in colour, stage two is larger and significantly paler (Fig. 4).

Especially the colour difference between the stages can directly be recognised in specimen 7. This specimen represents an animal right in the act of moulting, in which the old outer cuticle of stage one is much darker than the inner cuticle of the following stage two (Fig. 5). Yet, one needs to keep in mind that the new cuticle is usually very pale when hatching and this might slightly overemphasise the contrast between old and new cuticle.

Further differences between stages

A further difference between stages one and two can be recognised in shape. Stage one specimens hold their abdomen in an upward curled position (Fig. 4B), while stage two specimens have their abdomen rather straight (Fig. 4D). This is naturally apparent in lateral view, but in fact also in dorsal and ventral view, as it is almost impossible to straighten out the abdomen in stage one specimens.

We found only minor allometric changes leading to different ratios of morphological lengths. Ratios of measured lengths of thorax sclerites and appendages change only slightly on first and second pair of walking legs from stage one to stage two (Fig. 3D). More precisely, the femoral lengths become relatively shorter from stage one to stage two in relation to the thorax length and with this to overall body length.

Mouthpart morphology is very similar in both stages, no significant changes of relative lengths of structures nor number of elements is apparent (Fig. 6).

Tarsus morphology shows some minor changes in relative lengths of individual elements. The ultimate tarsal element is slightly more elongated in stage two than in stage one. Also the pre-tarsal claw shows some relative changes; it appears relatively smaller in stage two (Fig. 7).

Discussion

Prediction 1: Difference between nymphal stage one and older stages

Do the observed data support or reject prediction 1? Somehow they do both. In fact there are astonishingly few dif-

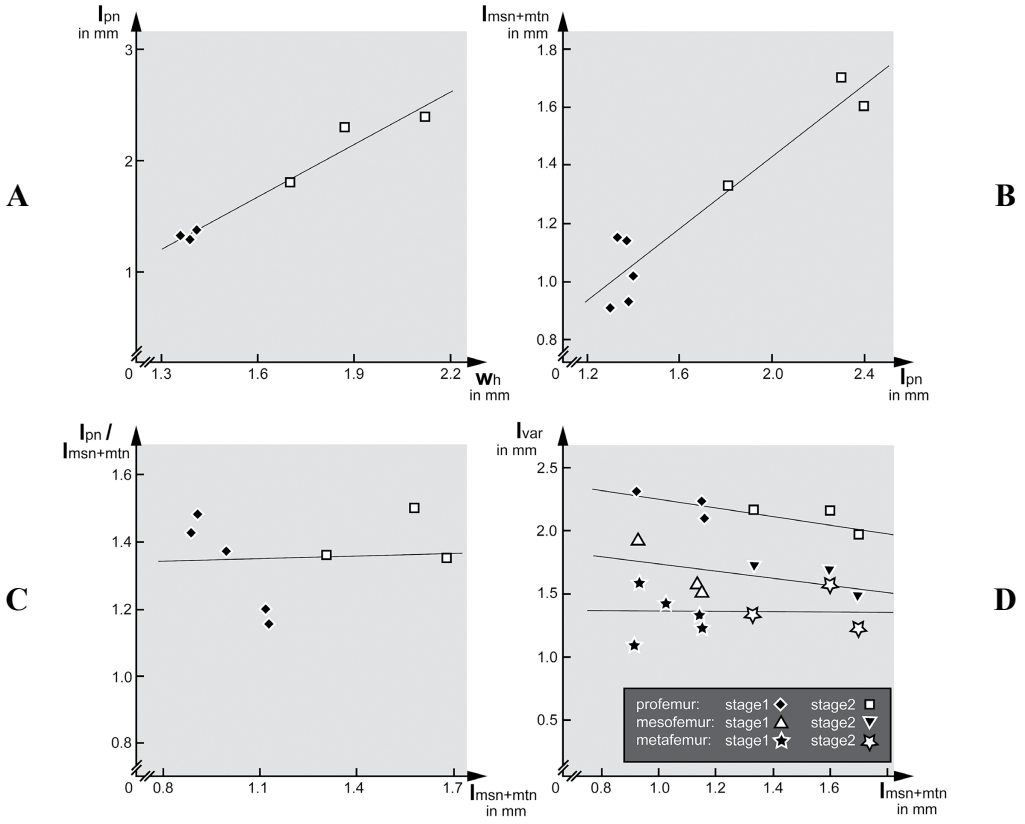

Fig. 3 – Scatter plots of different lengths measured on the specimens. **A–C**, Black diamonds indicate supposed stage 1 specimens, white squares indicate supposed stage 2 (or later) specimens. **D**, Femoral lengths on the different specimens of supposed stage 1 and 2 specimens in comparison. Abbreviations: lmsn+mtn = length mesonotum plus metanotum; lpn = length pronotum; lvar = various lengths; wh = width head.

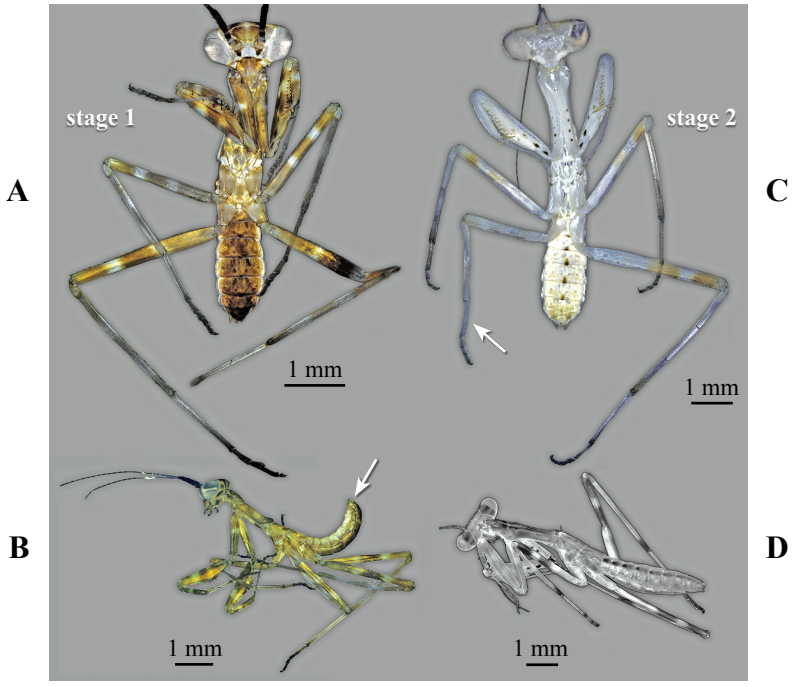

Fig. 4 – Comparison of stage 1 and stage 2 specimens; note the strong colour difference. **A**, Stage 1, ventral view. **B**, Stage 1, lateral view; arrow points to dorsally bent abdomen. **C**, Stage 2, ventral view; arrow points to regenerated leg. **D**, Stage 2, dorso-lateral view.

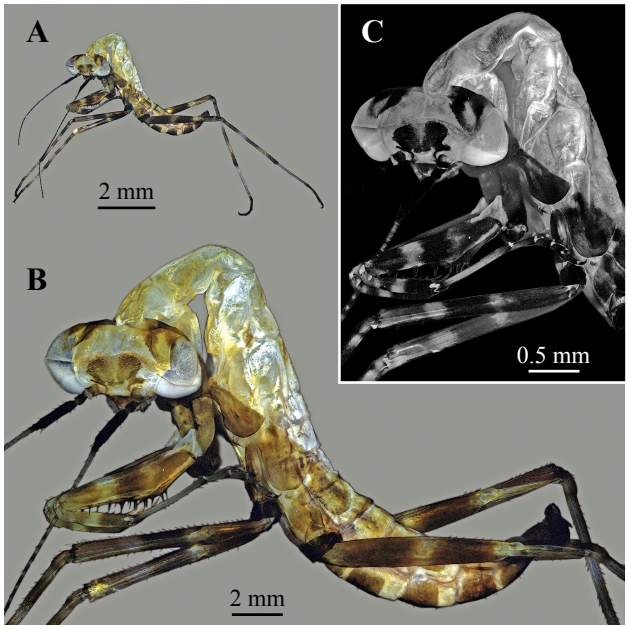

Fig. 5 – Specimen 7 in detail; the animal died in the act of moulting. **A**, **B**, Under white light conditions, the colour difference is clearly visible. **C**, Under fluorescence settings, the differences between inner and outer cuticle are also obvious.

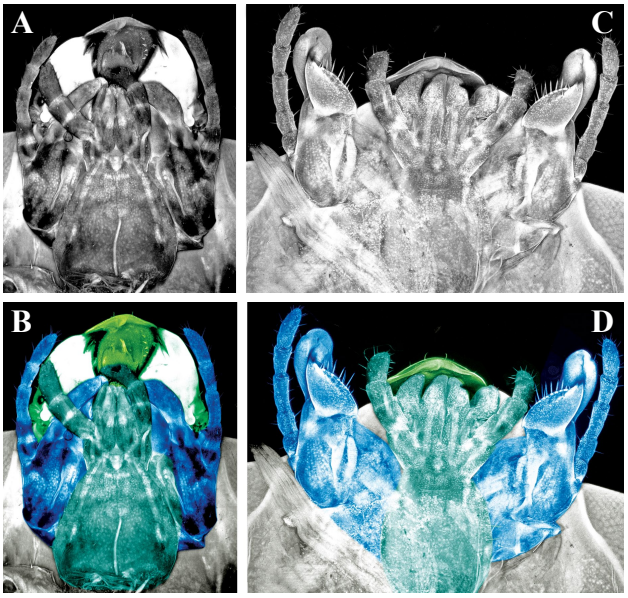

Fig. 6 – Details of the mouthparts, posterior view, confocal laser-scanning microscopy. **A**, **B**, Stage 1 (B colour-marked). **C**, **D**, Stage 2 (D colour-marked). Colour code: green = labrum; blue = maxillae; cyan = labium.

ferences between stages one and two. There is a subtle shape difference due to the curled position of the abdomen in stage one versus the straight position in stage two. Also the rather dark colour is a significant difference to the quite pale colour in stage two specimens.

Yet, it is partly surprising that we find only small allometric effects. The prothorax of adults of *Miomantis binotata* is significantly more elongate than that of the first stage nymphs (see Fig. 8A, C for comparison with an adult of a different *Miomantis* species). Also the legs are much shorter in adults compared to the body length than in first stage nymphs. Hence stepwise increase in the relative length of the prothorax and the legs should have been expected.

Also the absence of (significant) differences in mouthpart and tarsus morphology is partly surprising. Stage two nymphs are significantly larger than stage one specimens, hence relative changes in size of such structures should have been expected. Also if stage one specimens indeed need to employ ant mimicry, a generally rather different behaviour should occur, and it should be expected that this is partly reflected in the morphology. We could expect adaptations to a different substrate (reflected in different tarsus morphology) or different feeding habits (reflected in different mouth part morphology). Yet, this seems not to be the case. While absence of morphological specialisation does not exclude different behaviour, it does clearly not support it.

The morphology between stage one and two specimens is in conclusion less drastically expressed than it should be expected if we would have a strongly expressed case of ant mimicry in stage one specimens.

Prediction 2: Similarities between "original and copy" higher than between others

So in how far does the morphology of stage one nymphs of *M. binotata* match that of workers of the ant group *Pheidole* or *Tetramorium*? There are workers of *Pheidole* that are rather large, at least the majors. They are clearly in the same size range as stage one nymphs of *M. binotata* (Fig. 8A, B) unlike most specimens of *Tetramorium*. Also the darker colour of stage one nymphs resembles the darker colour of ant workers. A major factor of difference between stage one nymphs of *M. binotata* and ant workers is for sure relative leg length. The thoracic appendages of stage one nymphs of *M. binotata* are significantly longer than those of ants in general, i.e. the legs are too long.

Compared to other ant-mimicking arthropods the similarity between stage one nymphs of *M. binotata* and ant workers is in fact rather low. Many other arthropods achieve a much better fit to the shape of a worker. Especially a very similar leg length and gaster shape have been achieved (McIver & Stonedahl 1993). Surprisingly not only insects that have "attempted" to copy ants do better than the stage one nymphs, but even non-insects such as spiders achieve a significantly better match concerning body shape and leg length (McIver & Stonedahl 1993).

Concerning the overall similarities of stage one nymphs to *Pheidole* workers we have to state that any ant worker is more similar to a *Pheidole* worker. Hence this hypothesis is rejected. If stage one nymphs of *Miomantis* species

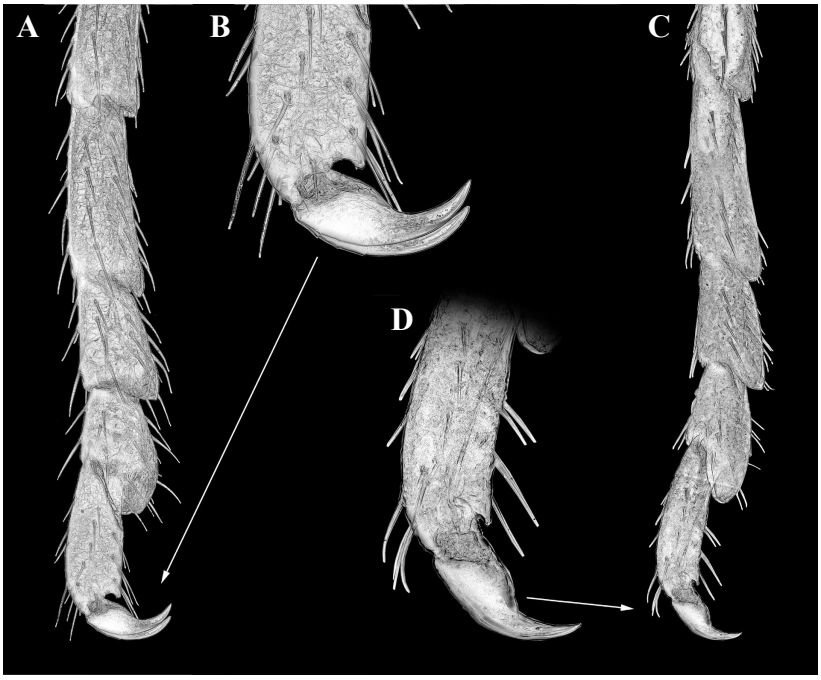

Fig. 7 – Details of the walking legs. **A**, **B**, Stage 1 overview and detail. **C**, **D**, Stage 2 overview and detail.

perform ant mimicry it must be considered as more general and less specific, i.e. not specific to species of *Pheidole* or *Tetramorium*.

Do stage one nymphs of Miomantis binotata show ant mimicry?

As pointed out above, whether an optical resemblance leads to a deceived organism heavily depends on the optical capabilities of the organism to be deceived. We can make relative statements (see discussion in Haug & Haug 2013 for relative vs. absolute statements in evolutionary frameworks): The match between outline of a stage one nymph and an ant is less good than in other euarthropods mimicking ants.

Yet, the question remains, if it is already good enough, i.e. is the threshold of similarity reached? To answer this question we would need to identify the organism to be deceived. So far the literature is almost completely devoid of any hint which type of mimicry the here discussed case could fall into and which organism could be deceived.

Edmunds (1972) suggests that the supposed ant mimicry of stage one nymphs is a defensive mechanism, but does not state against which aggressor. We can speculate that the aggressor is represented by the ants themselves and the nymphs would pretend to be one of them in order not to be attacked. In such a case we should additionally expect especially chemical mimicry as ant recognition is in fact dominated by olfaction.

If it is not the ants that should be deceived, but instead a third organism, how does mimicking ants provide protection? Do the nymphs hide within the ant nest (but then the main aspect would again be deceiving the ants)? Are ants a threat to the potential predator and the nymphs are able to scare it off? If this would be the case we have to ask further: is a single individual enough to scare a potential predator off? If such a strategy is employed, it could be suspected that aggregating in groups would be beneficial for stage one nymphs. Aggregation of nymphs is not unusual for species of Dictyoptera or even Polyneoptera of which Mantodea is an ingroup. Yet, such aspects have not been reported.

Lastly, we could speculate that the potential predator

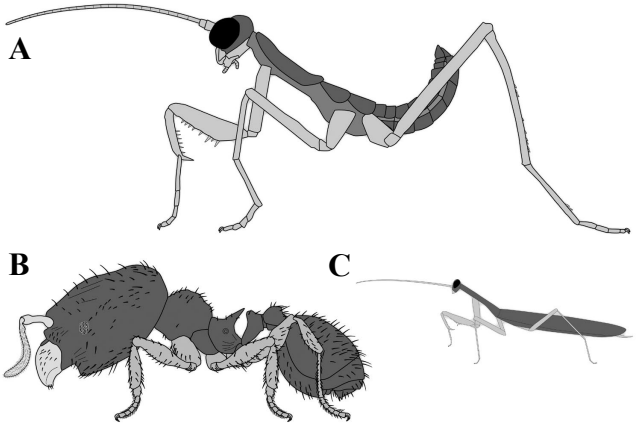

Fig. 8 – Comparison with different ant species. **A**, Stage 1 specimen as observed in this study. **B**, Worker of *Pheidole caldwelli*, modified after Fischer et al. (2016). **C**, Adult of *Miomantis paykullii*, modified after Marabuto (2014).

of stage one nymphs does not like the taste of ants. Also this aspect is quite difficult to evaluate, but would require a predator eating small mantodeans which avoids eating ants.

As a summary:

1. It seems largely accepted that stage one nymphs of different mantodean species perform ant mimicry, especially among private breeders (pers. comm.).
2. The specialisations to be expected of the stage one nymphs remain minimal. Pigmentation appears to be the only one recognisable.
3. Given the last statement, the match to ants is less good than in many other ant-mimicking arthropods. It is certainly less specific than suspected so far.
4. The exact type or function of the supposed mimicry is unclear.

Is this type of mimicry a larval specialisation?

Differences between stages one and two appear to be minor. Still the strong pigmentation of stage one nymphs needs to be further discussed. This difference cannot be simply explained by an underdeveloped state of an early stage. Usually earlier stages tend to be paler than later ones (for example, in the closely related cockroaches; see, e.g., Hörnig et al. 2016). Therefore, the strongly pigmented state of stage one nymphs is indeed unusual and should be coupled to a specific function. Independent whether this function is indeed ant mimicry, this specialisation could be interpreted as a larval specialisation.

Although non-holometabolous insects are generally not considered to have larval forms, numerous groups have evolved early developmental forms that qualify for being recognised as larvae for most (if not all) available criteria. The early post-embryonic developmental stages of dragonflies, damselflies, mayflies and stoneflies, for example, fulfil various such criteria, such as 1) differing significantly from the adult, 2) having specialised organs which will be reduced later in ontogeny (in most cases the gills), or 3) living in a very different ecological realm than their corresponding adults. Despite the terminological trick of calling such forms naiads in entomology, most non-entomologists address these forms as 'larvae'. Hence as other authors have stated (e.g. Beutel et al. 2014) also among non-holometabolous insects we find early post-embryonic stages that represent larvae.

So what about the stage one nymphs?

1. The stronger pigmentation is a specialisation that makes it appear different from the later stages.
2. The pigmentation is reduced later in ontogeny.
3. It remains unclear whether there is any ecological differentiation of the stage one nymphs.

Therefore, also here it remains somehow unclear how to read the observations. For the moment, stage one nymphs of *Miomantis* species should be considered candidates of possibly representing specialised larvae.

Summary and Outlook

The observations and considerations provide a mixed result. It seems that there is a specialisation of the stage one nymphs in which they differ from later stages. This may be understood in the framework of ant mimicry. Yet, we see no support for a more specific mimicry beyond generally resembling ants. Although ant mimicry seems to be well accepted among mantodean breeders, the data are less clear than anticipated.

As the summary provides no clear picture, investigations of other species appear urgently necessary. Most important we would need additional information of observations in the field. Often behavioural studies are focussed on adults, observations on earlier stages remain rare. In general, studies on non-adult polyneopterans are rare, but would be extremely valuable for comparative evolutionary approaches (Mashimo et al. 2014). Therefore, also the limited amount of data provided by this study can provide potentially important data for future comparisons. As this case could represent a distinct larval form in a mantodean species, it should be further considered in how far ecology and behaviour of these early forms differ from that of their corresponding adults.

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