

New details of *Santanmantis axelrodi* and the evolution of the mantodean morphotype

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Abstract

Mantodea is a group of predatory insects that is an ingroup of Dictyoptera, as are roaches and termites. Dictyopterans possess a long-ranging fossil record, the majority being ‘roachoid’ dictyopterans; yet specimens of Mantodea are very rare. *Santanmantis axelrodi* GRIMALDI, 2003, is the only formally described mantodean species from the Lower Cretaceous Crato Formation in Brazil. The original description was based on eight specimens, but on all the raptorial appendages are incompletely preserved or lacking. We present a ninth specimen, showing new details of this species, especially of the raptorial appendages, which let us complement the description of *S. axelrodi*. The raptorial appendages are more specialized than assumed before, but the spinose appearance of the meso- and metathoracic legs appears to be more ancestral. The phylogenetic relationship within the dictyopterans and the evolution of the mantodean morphotype is currently not conclusively resolved. We discuss possible new implications and the relevance of oothecae for reconstructing early mantodean and dictyopteran evolution. The scarce fossil record of oothecae is supplemented by two additional specimens from the Crato Formation.

Key words: Dictyoptera; Mantodea; Cretaceous; Raptorial appendages; Ootheca; Morphotype evolution

1. Introduction

Mantodeans are predatory representatives of Neoptera. The group includes about 2,300 species worldwide, with a main distribution in the tropics. One of the most prominent characteristics of mantodeans is a pair of raptorial appendages.

Mantodea is assigned to Dictyoptera together with Blattodea (including Isoptera). There are several hypotheses about the phylogenetic relationships within Dictyoptera (see below); therefore, they are currently not conclusively clarified (DJERNAES et al. 2012 and references therein), especially the inclusion of early fossil representatives appears to be challenging (BÉTHOUX et al. 2009).

The dictyopterans feature a corpotentorium in the head with perforation through which the ganglionic connectives pass (KLASS & EULITZ 2007), strongly curved Cubitus posterior (CuP) of the forewings, and opener muscles of the abdominal spiracles inserting on the paratergites (KLASS 1999). Females have a subgenital plate, formed by abdominal sternite 7, with flexible terminal lobes distally and a vestibular sclerite dorsally (KLASS 1998). A hinge-like joint is developed between the gonangulum and the paratergite of the ninth abdominal segment (KLASS 1998; BOHN & KLASS 2003; DETTNER & PETERS 2003; KLASS et al. 2012). A very notable autapomorphy for Dictyoptera is that they deposit their eggs in a kind of package, a so-called ‘ootheca’ that is made of secretions from (morphologically and biochemically) asymmetrical true accessory glands of abdominal segment IX (e.g., BOHN & KLASS 2003; GRIMALDI & ENGEL 2005).

Presumably, the early dictyopteran morphotype was roach-like (e.g., SELLARDS 1904; GARWOOD & SUTTON 2010; HAUG J. T. et al. 2013 a), thus the specialized characteristics of Mantodea are highly derived. To understand the evolution and the development of specialized morphologies, it is essential to include fossils into consideration (e.g., DONOGHUE M. J. et al. 1989; RUST 2006; EDGEcombe 2010; HAUG J. T. et al. 2010, fig. 8; HAUG J. T. et al. 2012 a, fig. 11). Overall about 34 species of Mantodea have been described based on fossils by, e.g., SHAROV (1962), GRAT-SHEV & ZHERIKHIN (1993), NEL & ROY (1996), VRŠANSKÝ (2002), GRIMALDI (2003), BÉTHOUX & WIELAND (2009), and BÉTHOUX et al. (2010). Among these are 17 Cretaceous species from New Jersey/USA, Siberia/Russia, Myanmar, Lebanon, Mongolia, Kazakhstan and finally from the Crato Formation in Brazil (GRIMALDI 2003).

The Lower Cretaceous (Aptian) limestones of the Crato Formation in Brazil are well known for the exceptionally good fossil preservation (MARTILL et al. 2007), but specimens of Mantodea are very rare. Only three species are known, of which only one was formally described: *Santanmantis axelrodi* GRIMALDI, 2003 (GRIMALDI 2003, 2007). GRIMALDI (2003) assumed that this could be the sister species of Neomantodea (all other mantodeans). Based on this phylogenetic position and the age of this species, it is likely to provide important insights into early mantodean character evolution and the evolution of the mantodean morphotype.

The original description of *S. axelrodi* was based on eight specimens, but the raptorial appendages are incompletely preserved or lacking (GRIMALDI 2003). During a

visit to the palaeontological collection of the Royal Ontario Museum (ROM), Toronto, a ninth specimen was discovered. It has a well-preserved raptorial appendage that shows new details of this species and complements the description of *S. axelrodi*.

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2. Material and methods

The specimens described or depicted herein originate from the Cretaceous Crato Formation, Brazil (for details of the Crato Formation, see MARTILL et al. 2007). This formation has formerly been addressed to as part of the Santana Formation (MARTILL et al. 2007). They are part of the collection of the Axelrod Institute, University of Guelph, Canada, on long term loan to the ROM with the collection numbers AI 292, AI 444, AI 1736, and AI 3208. Material from the Crato Formation is preserved in a limestone assigned to the Aptian (dated 115 million years; GRIMALDI 2003). Specimen AI 1736 was determined as *Santanmantis axelrodi* GRIMALDI, 2003, specimen AI 444 and AI 3208 as *Mesoblattina cf. limai* PINTO & PURPER, 1986. Specimen AI 292 was identified as roach or roachoid, but could not be allocated to a species.

Specimens were photographed with a Canon Eos Rebel T3 i, equipped with a MP-E 65 mm objective and a MeiKe LED Macro Ring Flash FC 100. To reduce reflections, the light was cross-polarized (e.g., HAUG C. et al. 2011; HAUG J. T. et al. 2011; KERP & BOMFLEUR 2011). Image sections were stitched with the photomerge function of Adobe Photoshop CS3.

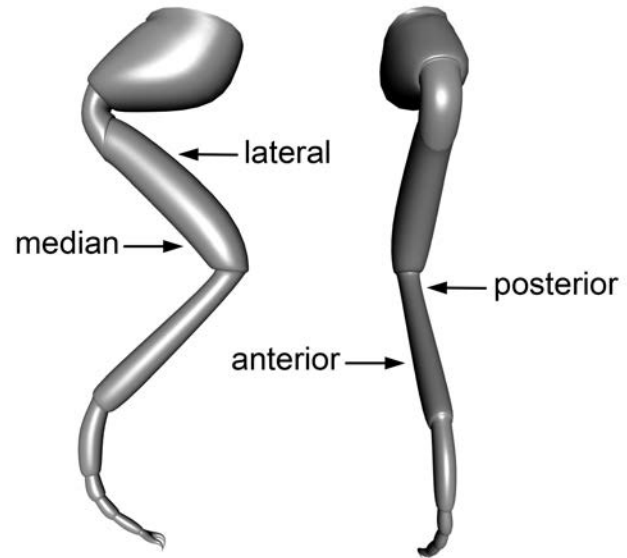


Fig. 1. Positional terms of appendages used in this study.

A reconstruction of *S. axelrodi* was created with Adobe Photoshop CS3 and Adobe Illustrator CS3 (see COLEMAN 2003 for details). It was based on GRIMALDI (2003) and modified after our observation.

The terminology for describing different positions on arthropod legs differs significantly among authors (HAUG J. T. et al. 2013 b), the here applied terminology is shown in Fig. 1.

3. Supplementary description of *Santanmantis axelrodi*

Based on specimen AI 1736; compared to the description in GRIMALDI (2003), we can add details of the raptorial appendages and the mesothoracic legs.

Body. – Specimen AI 1736 is preserved in a lateral position (Fig. 2A). Head and thorax are incomplete. The wings protrude beyond the abdomen significantly. The body length of the specimen is 12.5 mm, including the cerci.

Prothoracic appendages: Prothoracic (presumably raptorial) appendages are prominent. Femur and tibia of one foreleg are well preserved (Fig. 2B, C). Coxa, trochanter, and tarsus are not visible.

The femur is proportional to the body very massive, with 2.9 mm length and 0.6 mm width (posterior view), lateral side slightly curved, distal end narrower than proximal part. The median surface is equipped with two rows of spines, one appears more anterior, one more posterior. Of the supposed anterior row 11 spines are preserved, of the

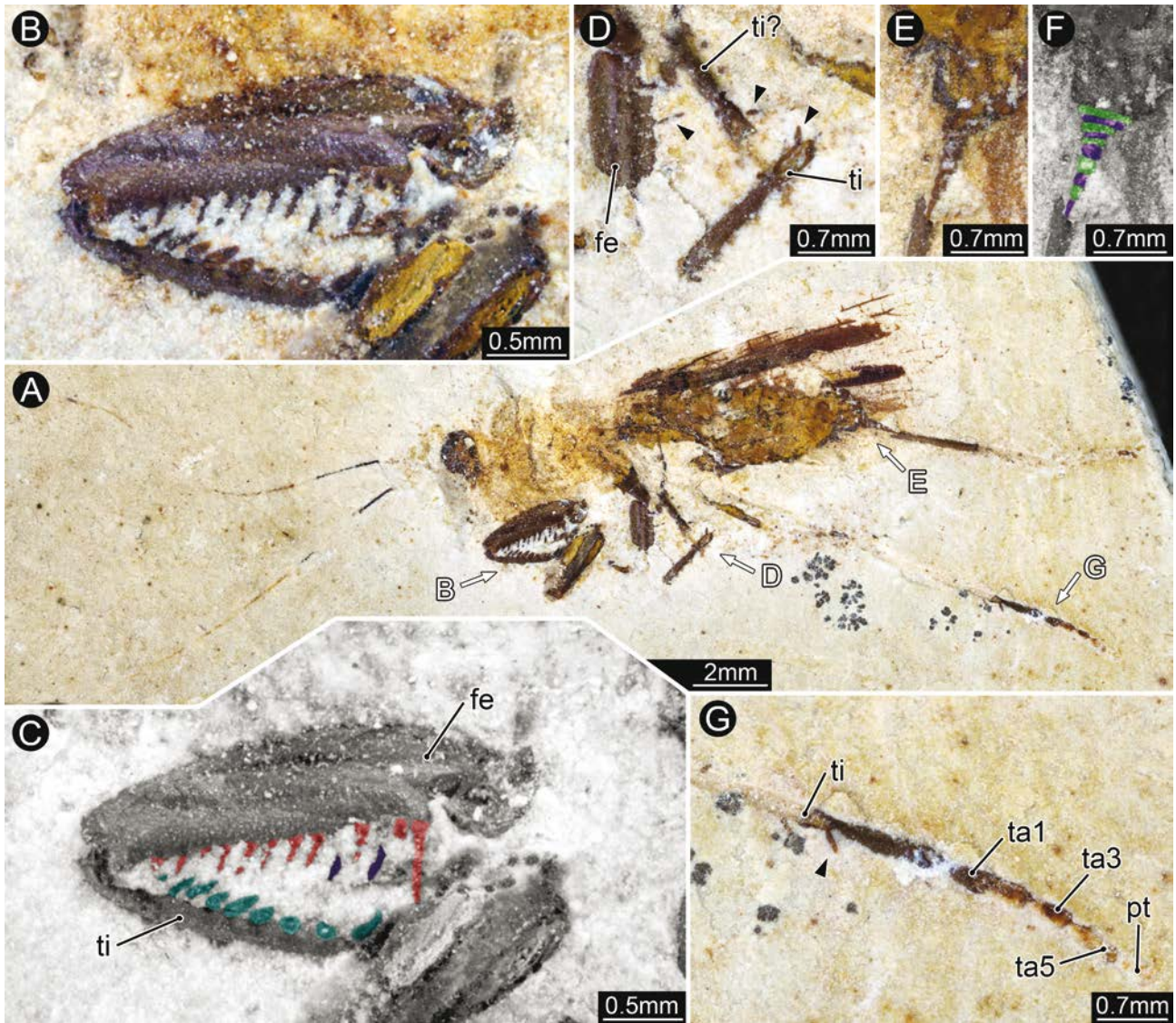


Fig. 2. Specimen AI 1736, identified as *Santanmantis axelrodi* GRIMALDI, 2003, Crato Formation, Brazil; **A:** Overview; **B:** Detailed view of one raptorial appendage; **C:** Colour-marked version of B, red: supposed anterior row of femur with 11 spines, purple: supposed posterior row of femur with two spines, green: tibial row of eight spines; **D:** Mesothoracic legs with preserved spines (arrows); **E:** Cercus; **F:** Colour-marked version of E, indicating subdivision; **G:** Part of tibia and tarsus of a metathoracic leg with one spine (arrow). Abbreviations: ce = cercus, fe = femur, pt = pretarsus, ta = tarsus, ta1–5 = tarsal elements 1–5, ti = tibia.

supposed posterior row 2 spines. Presumably there were more such spines originally in the posterior appearing row. It remains unclear whether there is a groove between the two rows and thus if the posterior-appearing spines are truly posterior. The spines are differentiated in size along the series. The most proximal spine of the more anterior series is the largest one; it measures 0.5 mm in length and is more than twice as long as the most distal one.

The tibia is 1.8 mm long and 0.2 mm wide. On the median surface one row of nine spines is apparent. This might represent an anterior row covering a possible pos-

terior one, but this cannot be verified. The visible spines have a slightly bulging shape and appear quite robust. The maximal length is 0.23 mm. The terminal spine at the distal end (apex) of the tibia is slightly curved with a length of 0.26 mm.

Mesothoracic appendages. – Incompletely preserved (Fig. 2D). Preserved part of femur 1.3 mm long, 0.6 mm wide (incomplete, certainly longer originally). One thin and sharp spine, 0.25 mm long, is visible medially. It is situated about half way along the proximal-distal axis.

The tibia is 1.7 mm long and 0.2 mm wide. It bears several spines close to the distal end medially and laterally, but just one median spine (0.2 mm long) is well preserved; up to 5 more spines are indicated by faint outlines.

Metathoracic appendages. – Incompletely preserved, but the overall appearance is very long and slender (Fig. 2A, G). The distal and proximal ends of femur and tibia cannot be detected, therefore the lengths of the individual elements are non-determinable. The entire length of the metathoracic legs is at least 12 mm. Three distal tibial spines with a maximal length of 0.26 mm are preserved.

The tarsi of the metathoracic legs are about 3 mm long and subdivided into six elements, five tarsomeres and the pretarsus (Fig. 2G). The first proximal element of the tarsus is elongated, about twice as long as the succeeding ones.

Cerci. – One cercus is visible, 1.1 mm long (Fig. 2E, F), 0.26 mm wide at the base and tapering to a finely pointed apex, giving the entire cercus a cone-shaped appearance. The cercus is composed of ten elements. The proximal elements are relatively short and stout. Further distally the elements are more elongate and slender.

4. Discussion

4.1. Ascription of the described specimen

The here described specimen represents a relatively small-sized winged insect. In many cases, fossil insects are ascribed to specific groups based on their wing venation (e.g., BÉTHOUX & WIELAND 2009; BÉTHOUX 2012 and references therein). Yet, in the here described specimen the wings appear partly folded and the venation is not that well-preserved, prohibiting an ascription based on wing venation details. Also other aspects of the specimen are less well-preserved, thus we cannot follow a simple “determination key” strategy.

The most prominent structure is the foreleg with the strong spines, which is reminiscent of the raptorial appendage of a mantodean (Dictyoptera) or mantispid (Neuropteroidea). Yet, similar appearing appendages also occur in other insects, for example, in predatory cockroaches (Dictyoptera) but also in nymphal treehoppers (Auchenorrhyncha; details of the spination of the foreleg on AI 1736 are discussed further below).

A structure arguing for dictyopteran affinities of the specimen are the cerci. These are well-developed, but relatively short. The cerci have a general cone-shaped outline and appear to be composed of ten rather stout elements. Such cerci are found in dictyopterans.

In many eumetabolan groups cerci are reduced, while they are plesiomorphically in insects quite long and composed of many elements (as for example in Arachaeognatha, Zygentoma, Ephemeroptera or Plecoptera; GRIMALDI

& ENGEL 2005). In many polyneopterans the cerci are derived in various conditions. They form pincers in Dermaptera (nymphs of certain species retain the elongate, multi-element state; SHIMIZU & MACHIDA 2011, fig. 1 C); in Orthoptera the cerci range from short to long, but lack subdivisions. Also in Phasmatodea the cerci lack such a subdivision (e.g., ZOMPRO 2005). In Embioptera the cerci comprise only two elongate elements (e.g., POOLPRASERT et al. 2011). In Notoptera (Mantophasmatodea and Grylloblattodea) the cerci are longer than those of Dictyoptera, elongate, more tube-shaped than cone-shaped and are composed of few, elongate elements (e.g., BAI et al. 2010).

Thus, the cercus morphology of AI 1736 is best compatible with a dictyopteran affinity. More precisely, the morphology of the cercus resembles that of mantodeans, or blattodeans, while termites have relatively tiny cerci. The known blattodeans from the Crato Formation have comparably shorter wings than the here described specimens, hardly extending beyond the terminal end of the abdomen; the spination of forelegs is quite different (see below) as is the spination of the mid- and hindlegs. Also blattodeans are characterised by a pronounced pronotum, which is lacking in specimen AI 1736. Hence, AI 1736 is unlikely to represent a blattodean.

Three species of mantodeans are known from the Crato Formation. One unnamed species was described by GRIMALDI (2003), a second one was depicted by LEE (2011). The only formally described species is *Santanmantis axelrodi* (GRIMALDI 2003).

Santanmantis axelrodi has been described possessing the following attributes: a “primitive” (quotation marks added by the present authors) type of mantis with a body length between 9.5 and 11.3 mm and long wings that protrude beyond the abdomen by more than one third of the entire length of the wings. Meso- and metathoracic legs are long and thin with a medial (in GRIMALDI 2003 ‘ventral’) row of spines on the femur. The cerci are well developed, with a length of 1.05–1.37 mm and ten visible elements (GRIMALDI 2003).

These attributes are in accordance with the observed structures of specimen AI 1736. The relatively small body size, the cerci, the long legs and especially the long wings, are shared by AI 1736 and *S. axelrodi*.

Other attributes that were shown by GRIMALDI (2003), such as detailed characteristics of the wings, thorax and head (including the eyes) cannot be compared with specimen AI 1736 because of the incomplete preservation respectively the orientation of the specimen. The few aspects observable of the wing venation in AI 1736 appear to be also similar to the pattern described for other specimens ascribed to *S. axelrodi*.

It could be argued that AI 1736 represents a new species. But there are no structures determined on specimen AI 1736 that contradict an ascription to *S. axelrodi*, i.e., that

could be used to differentiate it from the known species. It is in our view therefore most parsimonious to ascribe the specimen to the already formally described species *S. axelrodi* instead of erecting a new species.

4.2. The foreleg morphology

The foreleg morphology of AI 1736 is of further reaching interest and provides additional support for the mantodean affinities of the specimen. The spination differs significantly from that of a blattodean. In the latter, the

anterior spine row of the femur comprises similar-sized, relatively short spines (e.g. Fig. 4B). In mantodeans these spines are usually significantly more pronounced and differentiated in size (e.g., WIELAND 2008), i.e. the more proximal spines are larger than the further distal ones. Such more pronounced spines are also present in AI 1736, and as in modern mantodeans, the proximal spines on the femur are the largest ones.

Also the spines on the tibia of the foreleg differ from that of blattodeans. Firstly, there are usually only four or five spines in a row on a blattodean foreleg (Fig. 4B). In mantodeans more than five spines occur in one row (e.g.,

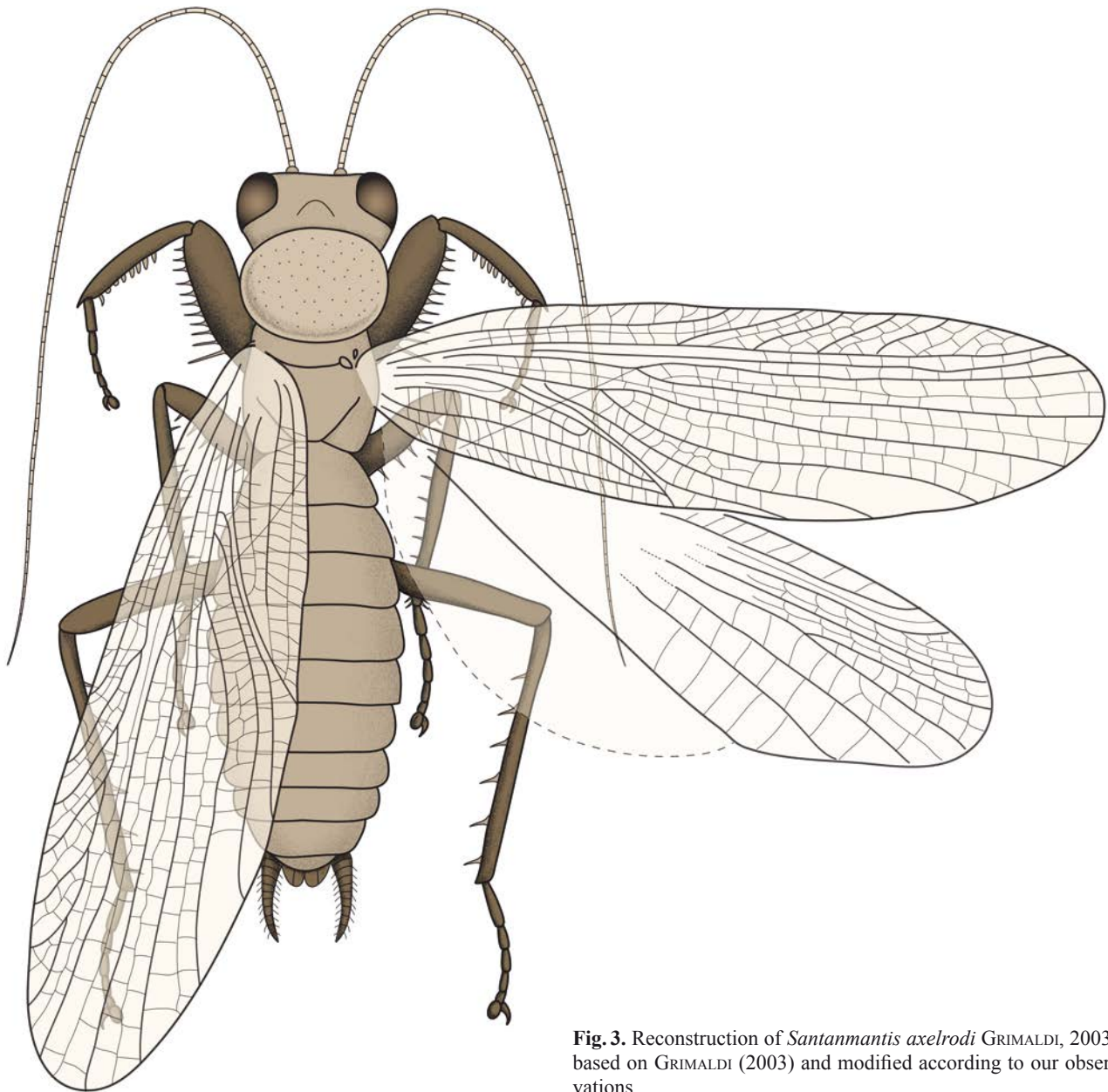


Fig. 3. Reconstruction of *Santanmantis axelrodi* GRIMALDI, 2003, based on GRIMALDI (2003) and modified according to our observations.

WIELAND 2008, 2013), and this is also the case in AI 1736. Secondly, the orientation of the tibial spines in blattodeans is relatively distally, pointing distally about 30° off the main tibial axis. In mantodeans and AI 1736 the spines are oriented further medially about 60° off axis. Thirdly, the shape of the spines in blattodeans is rather slender and elongate, while in AI 1736 and mantodeans these spines appear more massive.

Hence, the raptorial appendage of AI 1736 shows several specializations of a mantodean raptorial appendage. This further supports the interpretation that AI 1736 is a mantodean and a representative of *S. axelrodi*, and indicates that the raptorial foreleg was already highly specialized in this species.

4.3. New details of *Santanmantis axelrodi*

GRIMALDI'S (2003) description of *S. axelrodi* was based on eight specimens from the collections of the American Museum of Natural History, New York, USA (AMNH) and the Staatliches Museum für Naturkunde, Stuttgart, Germany (SMNS). In all eight specimens the forelegs are incompletely preserved or lacking. On specimen AI 1736 the raptorial appendages are well preserved (Fig. 2B); therefore we can amend certain details to the description of *S. axelrodi* (Fig. 3).

Compared to the reconstructions of GRIMALDI (2003) and GRIMALDI & ENGEL (2005) the raptorial appendages in specimen AI 1736 evoke, proportional to body and the meso- and metathoracic legs, a distinctly more massive impression. The presence of spines was just suggested by investigations with HRCT (high-resolution computed tomography) in GRIMALDI (2003). Two rows of sharp spines on the femur of one raptorial appendage of specimen AI 1736 are clearly recognizable; 11 such spines on the posterior row and two on the anterior row, but the lower number in this row is most likely preservational (Fig. 2B, C). In addition, there are also eight massive spines on the tibia (probably representing the original condition).

It remains unclear whether the most distal of the nine spines represents a 'mantid tibial claw' or 'tibial spur'. The term is usually applied for a large and elongated spine on the distal end of the tibia of the raptorial appendage (GRIMALDI & ENGEL 2005; WIELAND 2010). The tibial claw is developed in, e.g., *Ambermantis woźniaki* GRIMALDI, 2003, species of *Mantoida* NEWMAN, 1838 and *Metallyticus* WESTWOOD, 1835, and most other extant mantodeans. In species of *Chaeteessa* BURMEISTER, 1838 the tibial claw is not evident, and it is under consideration whether the absence is the plesiomorphic condition. It has been argued that *Chaeteessa* could therefore be the sister group to all other extant mantodeans (WIELAND 2010 and references therein). *Cretomantis larvalis* GRASHEV & ZHEREKHIN,

1993, and species of *Jersimantis* GRIMALDI, 1997, and *Burmamantis* GRIMALDI, 2003, are listed in the matrix of taxa and characters for cladistic analysis of GRIMALDI (2003) without tibial claw, but with a large apical, articulated spine. Both terms appear to address the same structure in a slightly different degree of specialisation.

It was presumed, that *S. axelrodi* is the sistergroup to most other known mantodeans, Neomantodea, which includes all previously mentioned groups. GRIMALDI (2003) assumed that *S. axelrodi* has also a tibial claw, but there was no direct evidence for this. The terminal spine at the distal end (apex) of the tibia of specimen AI 1736 is slightly longer and more curved than the proximal spines (Fig. 2B, C). It could be interpreted as claw-like, but the proximal end of the tibia, as well as the proximal region of the tarsus are not well visible, so it cannot be determined as a tibial claw with confidence. It needs to be further discussed how early in mantodean evolution this structure occurred.

4.4. Evolution of the mantodean morphotype

The new details about the shape of the raptorial appendages and their spines are important for the reconstruction of the evolution of mantodeans. Earlier reconstructions assumed a less pronounced armature of the forelegs in early mantodeans (e.g., RASNITSYN & QUICKE 2002). The raptorial appendage of *S. axelrodi* as a Cretaceous representative demonstrates that at this time the forelegs were already further specialised in having a significantly more pronounced and differentiated spination, comparable to those of modern species.

On the other hand, *S. axelrodi* retained more plesiomorphies than assumed by GRIMALDI (2003), especially concerning spines on the femur and tibia on the meso- and metathoracic legs (Fig. 2A, D). This condition is also found in extant blattodeans and Palaeozoic early dictyopterans (e.g., SELLARDS 1904), and blattodeans from the Crato Formation (e.g., "*Mesoblattina*" cf. *limai*; Fig. 4A, B). Spiny middle- and hindlegs, thus, represent the plesiomorphic state, while most mantodeans have virtually no spines on the middle- and hindlegs, except species of *Chaeteessa* and *Cretomantis larvalis* (BEIER 1968; GRATSHEV & ZHEREKHIN 1993; GRIMALDI 2003). Thus, the character combination exhibited by *S. axelrodi* marks an important evolutionary step towards modern mantodeans, which was not reconstructed in this specific way before. The former scenario might be described as "mid- and hindleg first", indicating first a loss of spines in these, while not yet having developed the specialised spination of the raptorial appendages. The new details indicate a "foreleg first", i.e., a specialisation of a raptorial appendage before reducing the spination of the mid- and hindlegs.

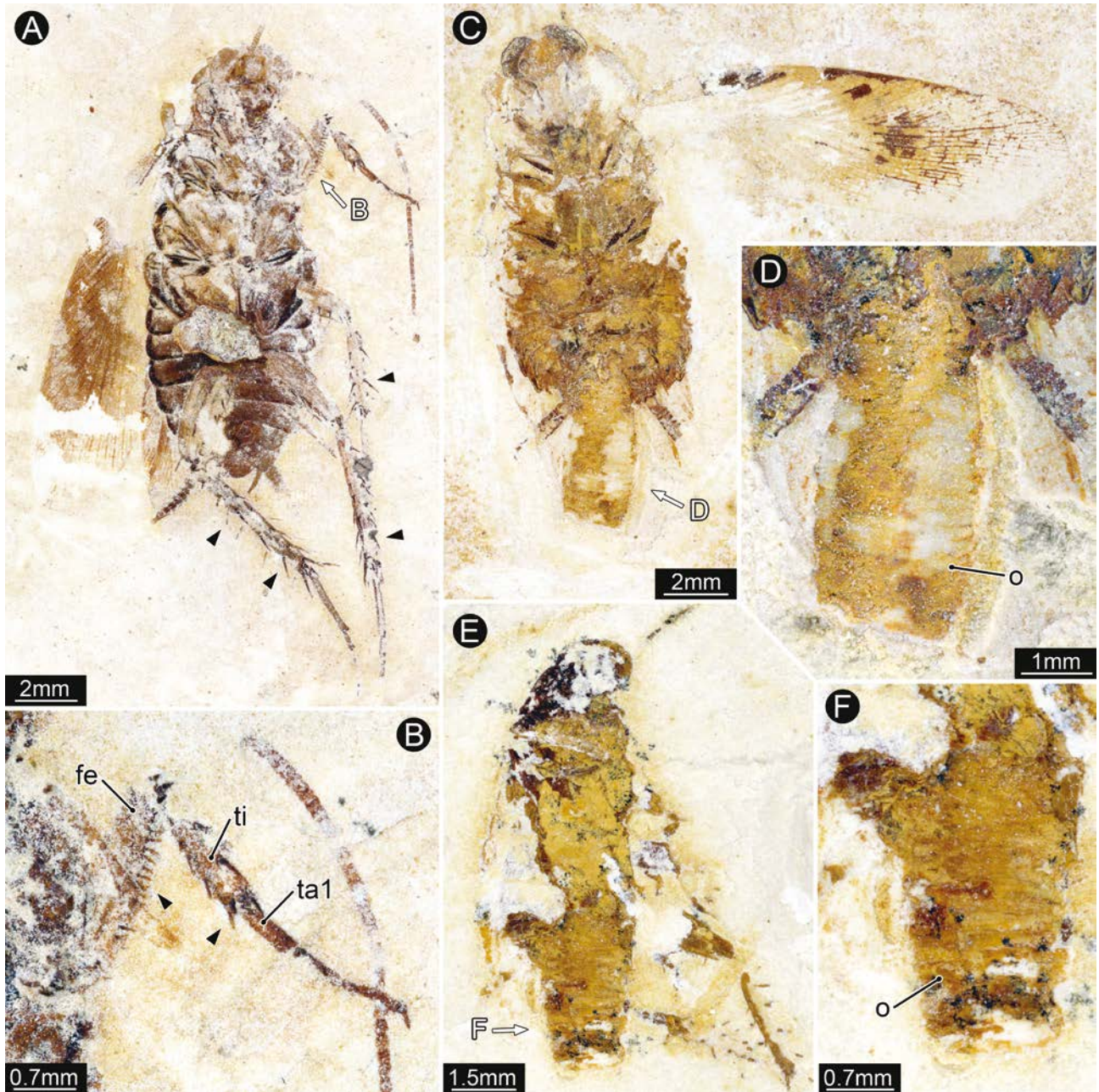


Fig. 4. Cretaceous roaches from the Crato Formation, Brazil; **A–D:** “*Mesoblattina*” cf. *limai* PINTO & PURPER, 1986; **A, B:** AI 444; **A:** Overview, setae marked with arrows; **B:** Detailed view of A of a prothoracic leg with setae (arrows); **C, D:** AI 3208; **C:** Overview; **D:** Detailed view of ootheca of C; **E, F:** Undetermined cockroach, AI 292; **E:** Overview; **F:** Detailed view of ootheca of E. A, B, E, and F flipped horizontally. Other abbreviation than before: o = ootheca

4.5. Origin of Mantodea

The state of specialization and retention of ancestral traits in *S. axelrodi* is congruent with the hypothesis that mantodeans evolved in or before the Cretaceous. GRIMALDI (1997, 2003), GRIMALDI & ENGEL (2005), and SVENSON &

WHITING (2009) assumed the origin of the Mantodea in the Late Jurassic.

To date, just one possible Jurassic mantis has been described, *Juramantis initialis* VRŠANSKÝ, 2002, part of the collection of the Paleontological Institute of the Russian Academy of Sciences (VRŠANSKÝ 2002, 2005). Yet, this

species is controversial, because the description has been based exclusively on a fragmentary wing (see discussion in VRŠANSKÝ 2002 vs. GRIMALDI 2003).

Even older possible mantodeans have been described from the Permian (BÉTHOUX et al. 2010) and Carboniferous (BÉTHOUX & WIELAND 2009). The described specimens have been assigned to Strephocladidae (possibly not monophyletic), which have been interpreted as “stem”-mantodeans. This assignment was based on features of the wing venation, as mainly wing parts are preserved in the fossil specimens.

An assumed origin of Mantodea in the Palaeozoic leads to several conflicts between predictions resulting from such an early origin and the observed fossil record. These conflicts have, to our knowledge, not been discussed elsewhere and are therefore briefly outlined here.

A very notable autapomorphy of Dictyoptera sensu stricto (sensu BÉTHOUX et al. 2009) is the deposition of eggs in a kind of package, a so-called ootheca. The oldest direct fossil evidence of an ootheca is a Cretaceous specimen of Blattellidae from the Crato Formation of Brazil, preserved with an ootheca still lodged in the terminalia (GRIMALDI & ENGEL 2005). An additional specimen of “*Mesoblattina*” cf. *limai* PINTO & PURPER, 1986 and an undetermined roach with preserved oothecae from the Crato Formation of Brazil are depicted in this paper (Fig. 4C–F). It is notable that oothecae, despite their apparent robustness, seem to be quite rarely found as fossils. Besides the now three specimens from the Crato Formation only two other definitive oothecae have been reported: one from the late Cretaceous of Israel (ANISYUTKIN et al. 2008) and one specimen in Miocene amber (POINAR 2010). There are reports of Carboniferous oothecae by PRUVOST (1919, 1930) and LAURENTIAUX (1960); yet the interpretation of these fossils has been repeatedly questioned (e.g., RASNITSYN & QUICKE 2002 and discussion therein).

It is generally assumed, that the ability to deposit eggs in roach-like oothecae is linked to a short ovipositor (GRIMALDI & ENGEL 2005). *S. axelrodi* possesses a slightly protrudent external ovipositor, which is short and broad (GRIMALDI 2003) like in modern mantodeans. Preserved ovipositors of dictyopterans which are older than Cretaceous are notably longer (e.g., GRIMALDI & ENGEL 2005). Relatively long ovipositors are likely to be a plesiomorphic condition for pterygotes (GRIMALDI & ENGEL 2005), reduced numerous times. Especially long ovipositors among polyneopterans are developed, e.g., in ensiferan orthopterans. Short dictyopteran ovipositors have not been recorded before the Cretaceous.

Based on these observations, the following conflict arises: If Mantodea evolved in the Carboniferous (BÉTHOUX & WIELAND 2009), we have a significant gap of about 200 million years for the record of the formation of dictyopteran oothecae (direct evidence via oothecae, or indirect

evidence via a short ovipositor). This discrepancy could be explained by the following assumptions:

1.) Representatives of Dictyoptera that produce oothecae (Dictyoptera sensu stricto) had already existed in the Palaeozoic. A direct evidence in form of a fossil ootheca was simply not found yet, or the possible Carboniferous specimens described by PRUVOST (1919, 1930) and LAURENTIAUX (1960) represent indeed oothecae. This argument demands for a reinvestigation of the supposed Palaeozoic oothecae. New documentation methods for fossils from the Carboniferous have been established in recent years (e.g., GARWOOD & SUTTON 2010; HAUG et al. 2012 b, 2013 a). Yet, given the fact that the last claim of Carboniferous ootheca is some time ago and has received quite negative response, it appears likely that these specimens are indeed not oothecae. Even if we would accept that oothecae have simply not been found yet, this still does not explain the lack of short ovipositors.

2.) The ability to deposit eggs in oothecae is not linked to a short ovipositor. Although this seems to be the case in modern blattodeans and mantodeans, the short ovipositor in both groups might have evolved convergently. The way how oothecae are produced in these two groups differs in many aspects; therefore, the exact ancestral mode of the ootheca production is unclear. This ancestral mode could potentially have been performed with a long ovipositor. This assumption will be hard to be tested, but cannot be ruled out.

Yet, we can apply evolutionary argumentation here. Long ovipositors have the advantage that an egg can be deposited inside a substrate (soil, plant, host animal), yet are a disadvantage during “normal life”. In other words, longer ovipositors bring an evolutionary cost, that pays off with the advantage of hiding the egg from possible predators. When producing an ootheca, the advantage of the long ovipositor is lost, only the costs remain. In fact, the costs are raised as laying the eggs into the ootheca will be more complicated with a long ovipositor. Hence their should be a strong selective pressure against a long ovipositor in this case. Thus, there is very likely a direct correlation of a short ovipositor and ootheca production.

3.) Specimens of Dictyoptera with a short ovipositor that are older than the Cretaceous were not found yet. This argument seems to be a weak one, as specimens with long ovipositors, e.g., from the Triassic, are known, and it seems unlikely that these should have a higher potential to be preserved than those with a short ovipositor. Especially fossils from the Crato Formation demonstrate the preservation potential of a short ovipositor (e.g., BECHLY 2007, fig. 11.23 b).

4.) The ability to produce oothecae might have evolved in Blattodea and Mantodea independently. Also this argument seems weak. The arrangement of eggs inside the ootheca appears very similar in Mantodea and Blattodea.

Also certain unusual chemical substances from asymmetrical accessory glands involved in ootheca formation are found in both groups (HACKMAN & GOLDBERG 1960; KLASS & MEIER 2006), also supporting the assumption of a common origin of this structure in the two groups.

5.) Carboniferous and Permian representatives of Strepocladidae are not derivatives of the evolutionary lineage towards Mantodea, and characters shared by Strepocladidae and Mantodea have evolved convergently.

BÉTHOUX & WIELAND (2009) and BÉTHOUX et al. (2010) provided a reasonable argumentation based on wing venation why strephocladidans should represent “stem”-mantodeans, better derivatives of the evolutionary lineage towards Eumantodea. Yet, the central issue of this hypothesis is based on wing venation. While wing venation has repeatedly proven to be a very powerful tool for understanding especially early insects, it appears to be a less useful tool in Dictyoptera and supposedly closely related polyneopterans (HUANG & NEL 2007; BÉTHOUX et al. 2009; CUI 2012). BÉTHOUX et al. (2009) pointed out that within Dictyoptera often wing venation shows a high degree of intraspecific variation and furthermore assumed that homoplasies occurred quite frequently in this group.

Interpreting the position of Strepocladidae and which species belong to this group appears to be quite controversial. Strepocladidae has been alternatively interpreted as an ingroup of Holometabola (KUKALOVÁ-PECK & BEUTEL 2012) or “Grylloblattidae” (STOROZHENKO 1997). Also supposed ingroup species (KUKALOVÁ-PECK & BEUTEL 2012) have been interpreted as non-strepocladidans, but representing holometabolans by others (BÉTHOUX 2009).

Fossil “grylloblattids” are most likely not monophyletic, comprising species that might represent derivatives of various lineages within Polyneoptera. Some could also be related to Notoptera, yet this is still difficult to assess as modern notopterans do not possess wings at all, and, as stated before, wing venation is a commonly used character system for discussing phylogenetic positions of Palaeozoic insects. Despite this uncertainty, it should be pointed out that the foreleg spination of strephocladidans (BÉTHOUX & WIELAND 2009, fig. 23 B) does not resemble that of mantodeans or also blattodeans. The numerous and similar-sized spines could be better compared to those of the raptorial appendages of representatives of the notopteran ingroup Mantophasmatodea (although admittedly strephocladidan spination is only slightly more similar to mantophasmatodean than to mantodean appendages).

In conclusion, we admit that certain characteristics of strephocladidans appear mantodean-like. Yet, the interpretation of these as relatives of Mantodea causes conflicts in interpreting the evolution of ootheca and ovipositor in Dictyoptera. Such a complex character set should be well considered in phylogenetic and evolutionary interpretations. We therefore see it as at least similar parsimonious

that strephocladidans are not directly related to Mantodea and evolved their mantodean-like characters convergently. This would mean that mantodeans did not evolve in the Carboniferous, but not before the mid Mesozoic. This interpretation would solve the conflict of character evolution and appearance of the ootheca and the short ovipositor. We suggest to compare strephocladidan morphology in a wider polyneopteran context, and to use also other characters than only wing venation, to make a more definite conclusion.

4.6. What is a mantodean?

In conclusion, we have to state that currently the reconstruction of mantodean evolution and the timing of the appearance of the mantodean morphotype is challenging, as the identification of mantodeans is often complicated by incomplete preservation and the insufficiently clarified characteristics of early mantodeans. The here described specimen demonstrates this problem: The wings are partly folded and do not preserve many details of the venation; the venation cannot be used for ascribing such a specimen to a definite group. Without preserved cerci, for example, it might be challenging to differentiate a fossil mantodean and a mantispid neuropteran assuredly as both possess raptorial forelegs with pronounced armature.

Another point is that there is no consensus about the “definition” of the mantodean morphotype, i.e., which criteria need to be fulfilled to call a specimen a mantodean, partly touching the entire “stem” versus “crown” concept (see, e.g., discussion in DONOGHUE P. C. J. 2005). So the question is, what should be the crucial characteristics of a mantodean and from when on (in an evolutionary sense) should we use the term “mantodean” (see also discussion in GRIMALDI 2003)?

General characteristics that often are thought to be present in extant mantodeans (Eumantodea sensu GRIMALDI 2003), such as the presence of raptorial appendages, the free mobility of the head and an elongated prothorax are in fact only found in “higher” mantodeans (Mantoidea sensu GRIMALDI 2003). The head of species of *Chaeteessa*, *Mantoida*, and *Metallyticus* (the supposedly “basal” groups within Mantodea) is not equally movable like in “higher” mantodeans (Mantoidea sensu GRIMALDI 2003). WIELAND (2010: 11) concludes that “the free mobility of the head cannot be interpreted as an apomorphy for Mantodea but for a group within Mantodea at most”. Species of *Chaeteessa*, *Mantoida*, and *Metallyticus* also have a rather short prothorax, comparable to that of *S. axelrodi* (GRIMALDI 2003).

Another generally accepted character appears to be that the prothoracic appendages of mantodeans should be raptorial. Tibia and femur are equipped with spines (which

are arranged in a specific pattern in most extant mantodeans) and can be closed against each other to grab a prey item. Yet, raptorial appendages do not only exist in mantodeans within Dictyoptera; there is a group of roaches (or roachoids?), Raphidiomimidae, from the Cretaceous and Jurassic that possessed raptorial legs, too (GRIMALDI & ROSS 2004; GRIMALDI & ENGEL 2005; LIANG et al. 2009). It is generally assumed that plesiomorphically the primary function of the prothoracic legs of Dictyoptera is locomotion and thus grasping forelegs are clearly a derived condition. It is not clear whether the raptorial appendages of Raphidiomimidae and Mantodea have a common origin (see VRŠANSKÝ 2002 vs. BÉTHOUX & WIELAND 2009). If so, raptorial legs could have evolved before the origin of Mantodea and would characterise the group Mantodea + Raphidiomimidae.

More or less the other way round, RASNITSYN & QUICKE (2002) assumed that the ground pattern of early mantodeans included stout, erect setae on femur and tibia of the prothoracic legs, but not strong spines (based on GRIMALDI 2003 and VRŠANSKÝ pers. com. in RASNITSYN & QUICKE 2002). If this was the case, raptorial appendages in the strict sense (i.e., as most people would expect them) would have evolved within Mantodea. Yet, based on our observations of the well-developed spines of tibia and femur of the raptorial appendages of *S. axelrodi* that resemble those of modern mantodeans in arrangement and differentiation, we can at least reject this latter assumption.

It should be pointed out that the problem is reflected in other iconic raptorial morphotypes. The mantis shrimps, which already by name have a certain connection to mantodeans, have provided comparable problems. While the modern representatives are indeed representing a distinct morphotype, including fossil representatives breaks down this very distinct character set into numerous evolutionary steps (HAUG J. T. et al. 2010). Thus, distinct morphotypes such as that of mantodeans or mantis shrimps are a kind of “artefact of survival” as the forms that represented the evolutionary step “in-between” became extinct. This fact emphasises how important fossils are in reconstructing evolutionary patterns of modern groups.

With this, we can state that, although early mantodean evolution remains obscured in many aspects, newly observed features on *S. axelrodi* provide an additional new piece to the complex jigsaw of the evolution of Mantodea.

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