

Raptoblatta waddingtonae n. gen. et n. sp. – an Early Cretaceous roach-like insect with a mantodean-type raptorial foreleg

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Abstract

We present a new fossil roach-like insect from the Lower Cretaceous Crato Formation (Brazil), hence a representative of Dictyoptera s. str. (the group includes the modern groups Mantodea, Blattodea and Isoptera as ingroup of Blattodea). It is interpreted as representing a new species, *Raptoblatta waddingtonae* n. gen. n. sp. The single known specimen is a middle-sized winged insect with wide abdominal segments and dictyopteran-type cerci. The robust first thoracic appendages appear to be adapted for grasping prey. In this respect, the specimen resembles mantodeans, while the overall morphology is roach-like. Detailed similarities of the raptorial appendages of the new species and mantodeans include: 1) a row of massive femoral spines; 2) a row of opposing spines on the tibia; 3) the position of the spines on the femur (only in the distal region); 4) a shortened tibia (in comparison to the femur); 5) the specific shape of the femur with a distal concave region; here the spines arise, and this region is also functionally opposing the tibia. Based on this combination of characters we suggest that *R. waddingtonae* n. gen. n. sp. is the sistergroup to Mantodea, revealing a further step-wise evolution of the mantodean morphotype. *R. waddingtonae* n. gen. n. sp. (still) lacks a prominent curved distal spine on the tibia (tibial spur). The finding of *R. waddingtonae* n. gen. n. sp. supports the idea of the “foreleg first” hypothesis.

Key words: Fossil insect, Mantodea, Dictyoptera s. str., raptorial appendages, character evolution, Crato Formation, Cretaceous.

1. Introduction

Within arthropods, the evolution of grasping appendages was most likely a reason for the successful emergence of active predators within this group. Numerous different kinds of appendages for grasping prey have evolved in different positions along the body in different groups of arthropods. Well-known examples of arthropod groups with such specialised grasping appendages include whip spiders (e.g., WEYGOLDT 2000), water scorpions (true bugs; e.g. GREVEN & BRENNER 2007) or mantis shrimps (e.g., HAUG J. T. et al. 2010 and references therein).

One famous group of predatory insects with prominent grasping appendages is that of praying mantises or mantodeans. Mantodea is an ingroup of Dictyoptera s. str. (sensu BETHOUX et al. 2009) and evolved from cockroach-like ancestors (HÖRNIG et al. 2013; LEE 2014; VRŠANSKÝ & BECHLY 2015). Yet, within dictyopterans raptorial appendages seem not to be restricted to representatives of Mantodea. There are also extinct groups of supposedly carnivorous roach-like insects, such as representatives of Raphidiomimidae VISHNIAKOVA, 1973, known from the Cretaceous and Jurassic (LIANG et al. 2012a).

Dictyopteran insects in general are quite common in the fossil record. Roach-like insects were abundant already in the Carboniferous (e.g. RASNITSYN & QUICKE

2002; BELL et al. 2007). Yet, these are not true blattodeans (as sometimes assumed) but species branching off the lineage towards Dictyoptera s. str.; often these are called ‘roachoids’ (GRIMALDI & ENGEL 2005; BELL et al. 2007). We stick here to the use of ‘roach-like insect’.

One may tend to think of early fossil representatives as very generalised, “primitive” organisms, but especially Mesozoic predatory roach-like insects appear to have been highly specialised (GRIMALDI & ENGEL 2005). Even if some of these groups seem well studied, still new, unexpected forms are to be found, as recently shown by VRŠANSKÝ & BECHLY (2015) by a very aberrant slender cockroach which was interpreted by the authors as a “predatory cockroach” (unclear if this means ‘blattodean’ as these authors used ‘cockroach’ also for roach-like insects).

Besides Raphidiomimidae and the recently described slender roach-like insect of VRŠANSKÝ & BECHLY (2015) also other fossil groups of dictyopterans have been interpreted as predatory; it thus seems likely that predatory forms evolved independently among dictyopterans. Still, at least one of these forms may represent the sister group to Mantodea (see discussion in HÖRNIG et al. 2013), as supposed early forms of mantodeans appear to have possessed already specialised grasping appendages (e.g., VRŠANSKÝ 2002; GRIMALDI 2003; HÖRNIG et al. 2013). Hence, less specialised but already predatory cockroaches can potentially

inform us about the early evolution towards Mantodea, also allowing us to reconstruct a finely graded character evolution.

Here we present a new roach-like fossil insect interpreted as representing a new species, *Raptoblatta waddingtonae* n. gen. n. sp. The fossil comes from the Lower Cretaceous Crato Formation (Brazil). For a general introduction on dictyopterans from this Lagerstätte see BECHLY (2007). We discuss the impact of this new find on our understanding of the evolution of specializations for raptorial habits in dictyopteran ingroups.

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2. Material and methods

The specimen described in this study originates from the Cretaceous Crato Formation, Brazil, which has formerly been addressed to as part of the Santana Formation (for details see MARTILL & HEIMHOFER 2007). The specimen is part of the collection of the Axelrod Institute, University of Guelph, Canada, and currently on long-term loan to the Royal Ontario Museum, Toronto (ROM) with the collection number ROM63698 (specimen number AI514). Material from the Crato Formation is preserved in a limestone assigned to the late Aptian (dated about 115 million years; MARTILL & HEIMHOFER 2007).

The specimen was photographed with a Canon EOS Rebel T3i camera equipped with a MP-E 65 mm macro lens and a MeiKe LED Macro Ring Flash FC 100. To reduce reflections, the light was cross-polarised (e.g., HAUG C. et al. 2011; HAUG J. T. et al. 2011; KERP & BOMFLEUR 2011). Image sections were stitched with the photo-merge function of Adobe Photoshop CS3 (e.g. HÖRNIG et al. 2013). Further image processing was performed with Adobe Photoshop CS2. Drawings were produced in Adobe Illustrator CS3.

3. Systematic palaeontology

Dictyoptera s. str. (sensu BETHOUX et al. 2009)

Raptoblatta n. gen.

Etymology: ‘Rapto’ derivates from the Latin word *raptare* and means “drag violently off” or “ravage”; ‘Blatta’ (Latin) means any insect that shuns the light and is an often used term for roaches or cockroaches.

Type species: *Raptoblatta waddingtonae* n. sp.

Diagnosis: As for the species.

Raptoblatta waddingtonae n. sp.

Etymology: After JANET WADDINGTON, former assistant curator at the ROM, who kindly supported our work in the collections.

Holotype: ROM63698, curated under a long-term loan from the Axelrod Institute, University of Guelph, Canada (specimen number AI514). A complete adult insect, possibly a male (due to lack of female external structures).

Type locality: Cretaceous Crato Formation, Brazil. This formation has formerly been addressed to as part of the Santana Formation.

Type horizon: Material from the Crato Formation is preserved in a limestone assigned to the Aptian, dated about 115 million years.

Diagnosis: Medium-sized, roach-like, winged insect with wide abdominal segments and dictyopteran-type cerci; most prominent structure is the foreleg with the row of femoral and tibial spines; the median side of the distal region of the femur is concave; only this concave region is equipped with small spines; this region has nearly the same length as the tibia; the pronotum is trapeziform in dorsal view, with laterally rounded edges and strongly enlarged laterally expansions; not entirely covering the head; overhangs the head capsule only in its very posterior region.

Description: Body: Measurable body length without head appendages is about 21.7 mm (post-ocular segments 6–19; including cerci). The head, ocular segment and post-ocular segments 1–5 of the specimen are twisted laterally next to post-ocular segment 6 (first thoracic segment) (Fig. 1A, D, E). Therefore, the length of the head is not included in the total body length.

Head: The ocular segment and post-ocular segments 1–5, which are dorsally contributing to the head capsule, form the head. The head appears to be originally twisted sideways. As it still appears to be attached to the body and the preserved position appears artificial, the head was at least orthognathous originally or even directed forward (prognathous). Dorso-laterally on the head capsule a very large compound eye is present (second one inferred) (Fig. 1A, D, E). Post-ocular segment 1 carries a well-developed antenna, from which only the first antennomere (scapus) is preserved (Fig. 1A, D, E). The scapus is club-shaped, about 0.7 mm long and about 0.2 mm wide. The intercalary segment cannot be identified as such. Mouthparts are not preserved in detail.

Anterior trunk (thorax): Post-ocular segments 6–8 form the anterior region of the trunk, traditionally called thorax. Each of the segments bears a pair of elongate walking-type appendages (Figs. 1A, 2, 3B).

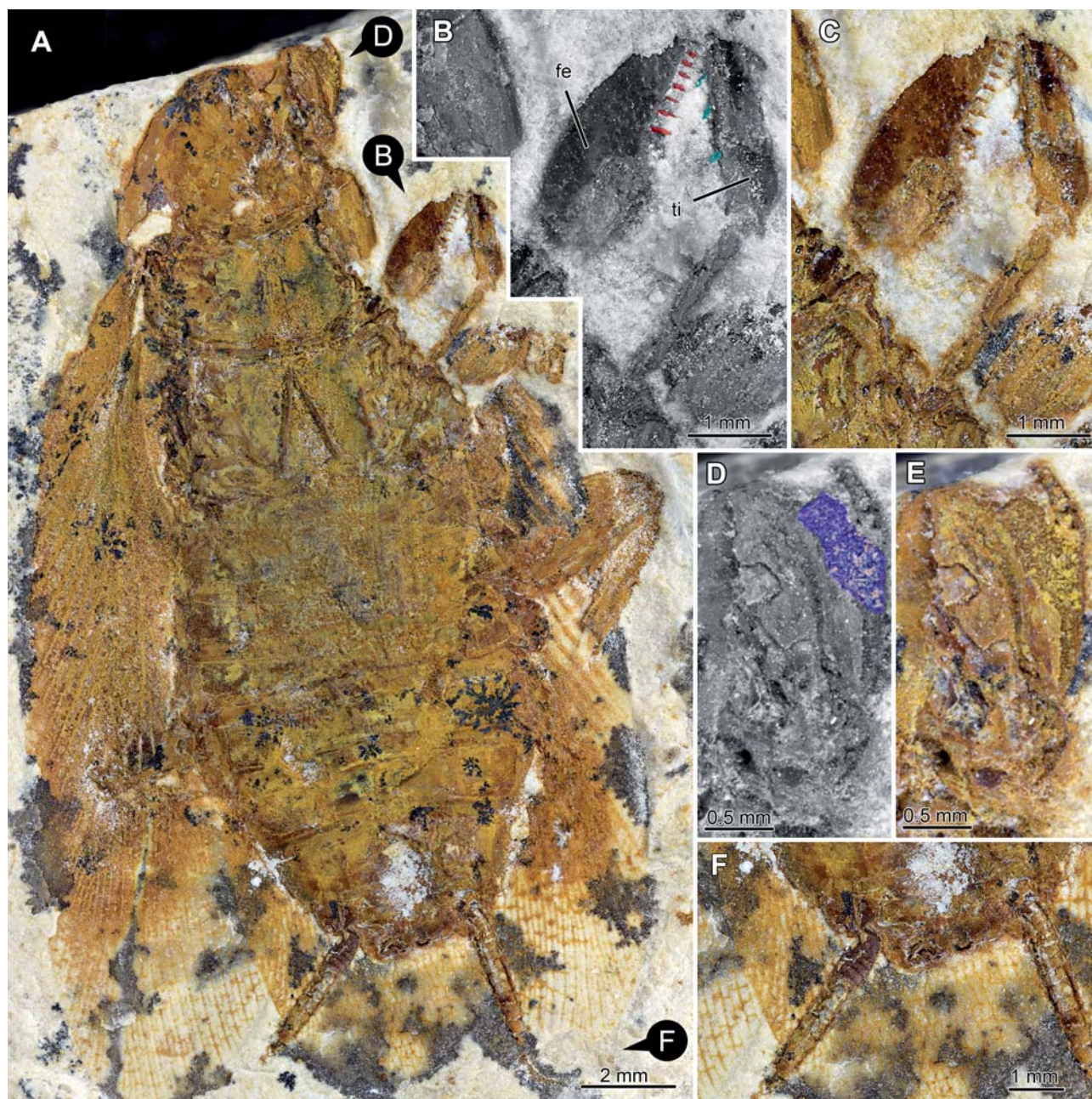


Fig. 1. *Raptoblatta waddingtonae* n. gen. n. sp., ROM63698 (specimen number AI514), Crato Formation, Brazil. **A:** Overview; **B:** Colour-marked detailed view of one raptorial appendage; red: supposed row of femur with seven spines, green: tibial row of three spines; **C:** Detailed view of one raptorial appendage; **D:** Colour-marked detailed view of the head; purple: compound eye; **E:** Detailed view of the head; **F:** Cerci; Abbreviations: fe = femur, ti = tibia.

Post-ocular segment 6 forms dorsally a well-sclerotised tergite (pronotum). The tergite is slightly trapeziform in dorsal view with laterally rounded edges and strongly enlarged lateral expansions; it partly overhangs the head capsule, but only its very posterior region. The widest part of the pronotum is dorsally to the insertion of the appendages of this segment. The maximum width of the pronotum is about 1.7 times of the length.

Post-ocular segment 7 forms dorsally a well-sclerotised tergite (mesonotum). The tergite is trapeziform in dorsal view, tapering anteriorly. It is about 1.3 times as long as wide. Antero-dorsally forewings arise; details of the wing articulation are unknown due to preservation.

Post-ocular segment 8 forms dorsally a well-sclerotised tergite (metanotum). The tergite is rectangular in dorsal view and

about 2.1 times as wide as long. Antero-dorsally hind wings arise; details of the wing articulation are unknown due to preservation.

The fore- and hindwings are slender and covering nearly the entire abdomen (when folded back) including the cerci. They are not strongly sclerotised or intensively colored. Major parts of the wings cannot be observed either. While the main veins appear clearly visible, the exact areas where they are expected to meet cannot be clearly seen. This prohibits a reliable reconstruction of the exact pattern of wing venation.

Appendages of post-ocular segment 6 (thoracic segment 1): The prothoracic (presumably raptorial) appendages are very prominent (Fig. 1A, B, C). Most proximal element (coxa) only partially preserved. It is about 2.5 mm long and about 1.2 mm wide (posterior view). Element 2 (trochanter) cannot be observed. Elements 3 and 4 (femur, tibia) of the right body half are well preserved. The femur is about 2.7 mm long and 1.2 mm wide, lateral side slightly curved, distal end narrower than proximal part. The disto-median side is concave and posterior-distally equipped with one visible row of very massive spines. Seven spines of this row are preserved. All spines have nearly the same size. The tibia is about 2.0 mm long and 0.5 mm wide, tube-shaped and also equipped posteriorly with a row of 3 spines. These spines are long and thin compared to the femoral spines. Femur and tibia are preserved in an opposing position to each other. The preserved part of the tarsus is about 2.7 mm long and 0.2 mm wide and further subdivided into at least two elements.

Appendages of post-ocular segment 7 (thoracic segment 2): The mesothoracic appendages are incompletely preserved (Figs. 1A, 3B). Coxa and trochanter cannot be observed. The femur is tube-shaped, about 1.8 mm long and 1.2 mm wide. The tibia is tube-shaped and about 0.8 mm long and 1.0 mm wide. The tarsus cannot be observed.

Appendages of post-ocular segment 8 (thoracic segment 3): The metathoracic appendages are incompletely preserved (Figs. 1A, 3B). Coxa and trochanter cannot be observed. The femur is tube-shaped, very massive, about 3.5 mm long, at least about 1.8 mm wide and equipped with setae. The tibia is tube-shaped, at least about 3.2 mm long and about 0.7 mm wide. The tarsus cannot be observed.

Posterior trunk (abdomen): Post-ocular segments 9–19 form the posterior region of the trunk, traditionally called abdomen. The abdomen is about 9.8 mm long and 7.3 mm wide, nine tergites and the cerci can be observed (Fig. 1A, F). The cerci are about 2.8 mm long and 0.5 mm wide and composed of 12–15 elements, proximal elements are relatively short and stout. Further distally the elements are more elongate.

4. Discussion

A roach-like insect: The here described specimen represents a medium-sized, roach-like winged insect (Figs. 1A, 2, 3B). The identification as a dictyopteran is based on the general habitus, the wide pronotum, the elongate coxae and the morphology of the cerci. Further reaching systematic ascriptions are more challenging.

A raptorial appendage: The most prominent structure is the foreleg with the strong spines, which

is reminiscent of the raptorial appendage of mantodeans (Figs. 1A–C, 2, 3A). This concerns:

- A row of massive femoral spines
- A row of opposing spines on the tibia
- The position of the spines on the femur (only in the distal region)
- A shorter tibia (in comparison to the femur)
- The specific shape of the femur with a distal concave region; here the spines arise, and this region is also functionally opposing the tibia

All these specific characters are also found in mantodean raptorial appendages; we therefore interpret this appendage as a raptorial one. One might argue that in a lot of species of fossil dictyopteran spines or very massive spine-like setae can be found on the appendages, without directly implying raptorial habits (see discussion in e.g. HÖRNIG et al. 2013, fig. 4A, B). However, as laid out above not only the spines are indicating that the first appendages of *Raptoblatta waddingtonae* were used for grasping prey. In addition, the specific shape of the femur is important here (Figs. 1A–C, 2). In contrast to other non-raptorial dictyopterans which have very tube-shaped femurs and spines or setae along the entire length, the appendage described herein is very similar to the sub-chela of modern mantodeans, which oppose the tibia against the femur to catch their prey (Fig. 3A). Moreover, the position of the appendage in the fossil and its articulations indicate that the forelegs were held in front and folded as in most modern mantodeans.

Other raptorial dictyopterans: Raptorial appendages and raptorial life habits within dictyopterans are not restricted to mantodeans. As mentioned above, there is a group of roach-like insects, Raphidiomimidae, with representatives from the Cretaceous and Jurassic that share several features with mantodeans and might be related to these (HÖRNIG et al. 2013). Their first pair of thoracic appendages has been interpreted as raptorial. Yet, the morphology appears more “simplistic” compared to most mantodeans, i.e. the femur is more tube-shaped, the tibia is as long as the femur and the spines appear almost like “normal” leg spines (Fig. 3A). Furthermore, the pronotum shape of raphidiomimidans differs from the “typical” dictyopteran one, being narrow, slightly elongated and somewhat trapezoidal (in dorsal view); yet it is also not discoid and not covering the head, as supposed for early mantodeans (GRIMALDI & ROSS 2004). An argument for raptorial life habits may be the prognathous position of the head.

Also the pronotum of the here described specimen is trapeziform in dorsal view with laterally rounded edges and relatively strongly enlarged lateral expansions; it is also covering the head only partly in its very posterior region. Both groups share a prognathous head (e.g., LIANG et al. 2009, 2012), although this is less simple to tell for the here described fossil.

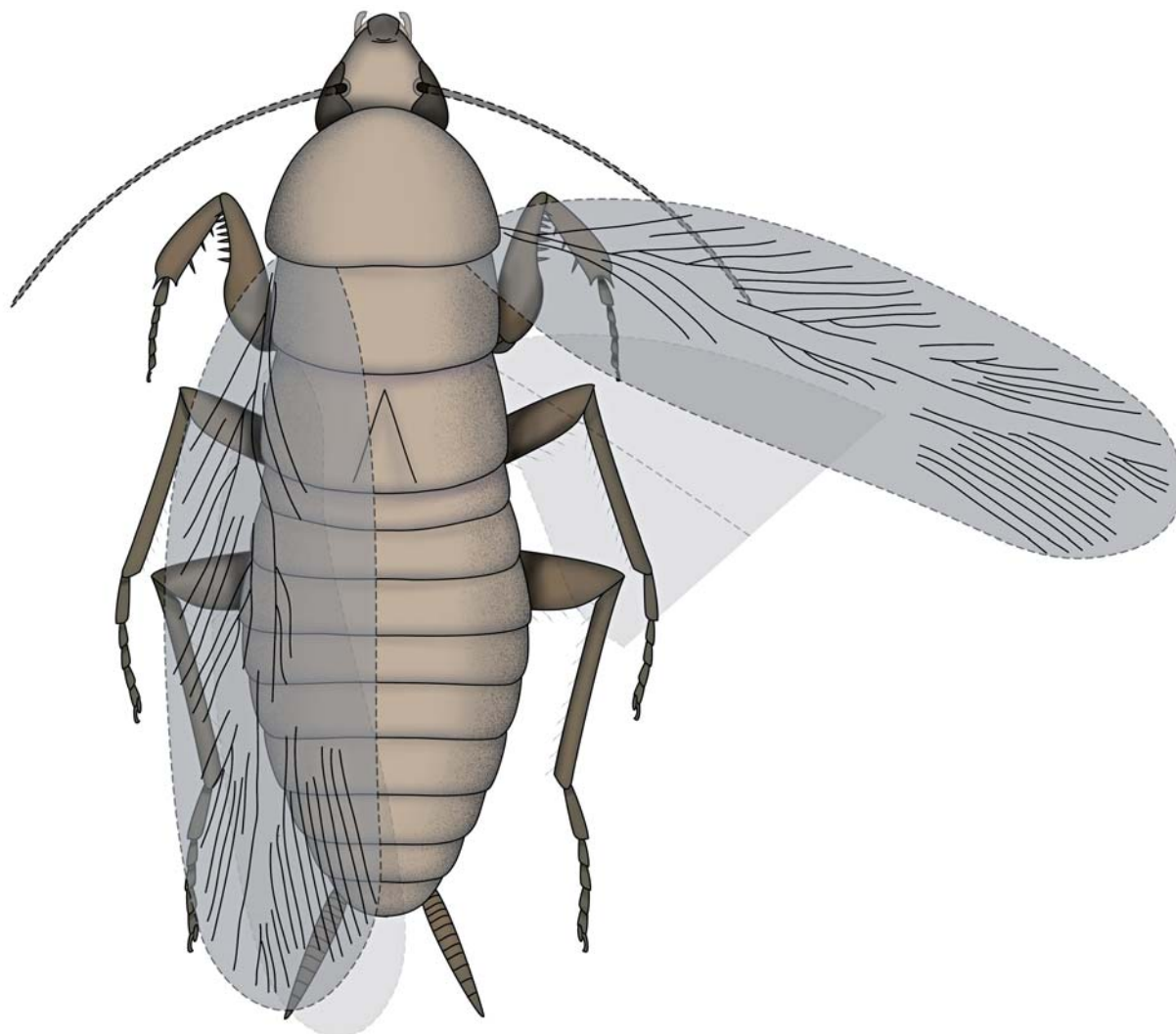


Fig. 2. Reconstruction of *Raptoblatta waddingtonae* n. gen. n. sp. in dorsal view. Length of antennae and exact shape of wings as well as mouthparts unclear, estimated.

Yet, even if some details, like the shape of the pronotum or the prognathous head, are very similar, other morphological aspects of *R. waddingtonae* are quite different from species of Raphidiomimidae. Comparing, for example, the raptorial appendages of the raphidiomimidans *Raphidiomimula burmitica*, *Fortiblatta cuspicolor* or *Divocina noci* shows that the first pair of thoracic appendages in this group is longer and more slender and possesses less spines or hairs (e.g., GRIMALDI & ROSS 2004; LIANG et al. 2009, 2012, figs. 1b, 2d) or is simply less specialised than the appendages of the here described specimen. Many species descriptions of raphidiomimidans are mostly based on the wing venation, which makes it dif-

ficult to compare the first pairs of appendages of further species (e.g., HANDLIRSCH 1938; LIANG et al. 2012).

Manipulator modificaputis is another presumed roach-like insect strongly resembling raphidiomimidans, yet has been interpreted to be not closer related to these (VRŠANSKÝ & BECHLY 2015). Compared to our specimen, *M. modificaputis* shows similar differences as to raphidiomimidans. Here the proportion of femur and tibia are non-differentiated as well, the elements are tube-shaped and spines are not prominent (Fig. 3A).

Another group of raptorial roach-like insects, which according to VRŠANSKÝ (2010) represents the sister group of mantodeans (VRŠANSKÝ 2010, fig. 2) is Eadiidae.

A

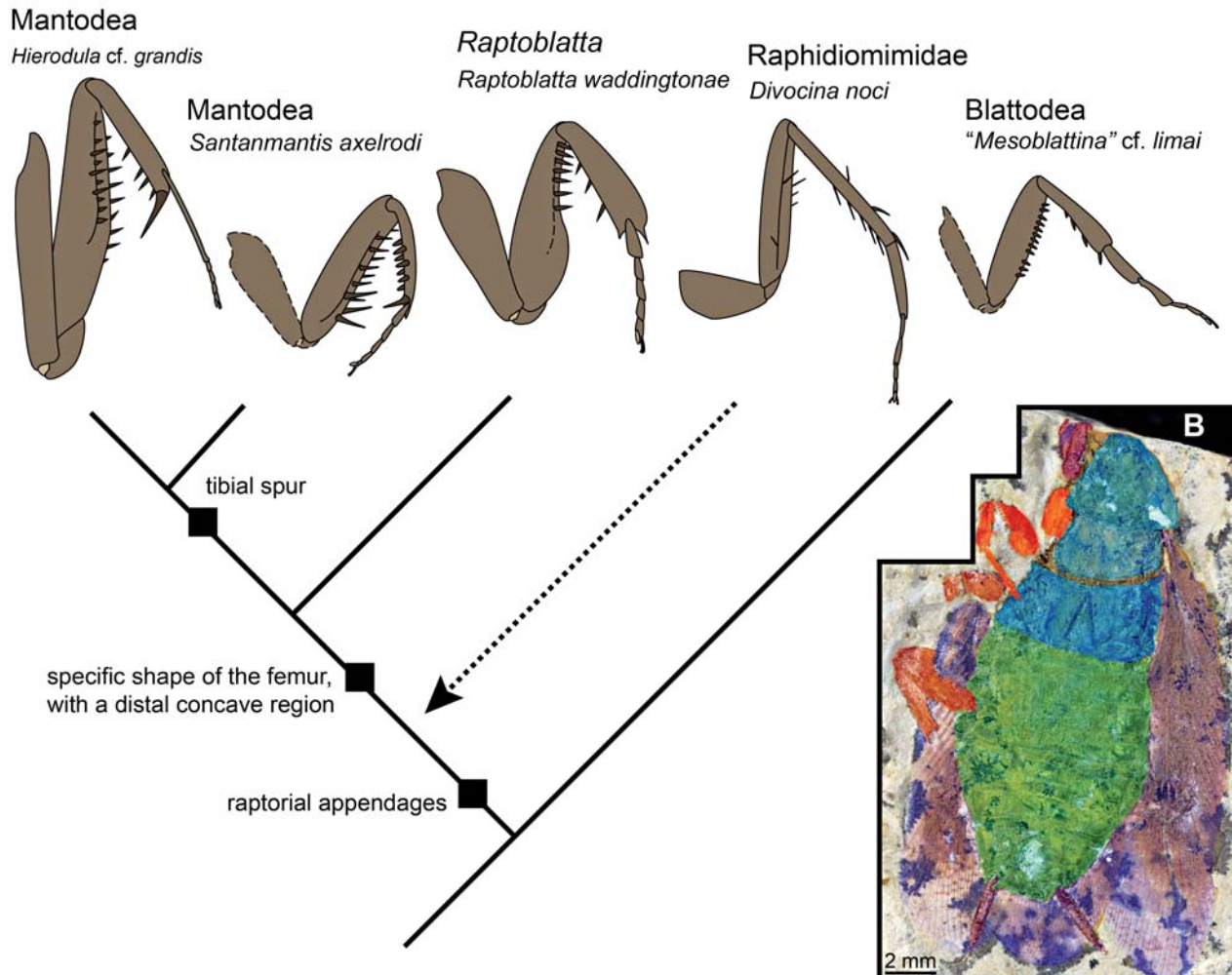


Fig. 3. A: Amended phylogeny of Dictyoptera with an evolutionary scenario; reconstruction of the evolutionary transformation of the raptorial forelegs (for details see text). **B:** Colour-marked specimen, ROM63698 (specimen number AI514), described as *R. waddingtonae* n. gen. n. sp., Crato Formation, Brazil. For a better comparability the image was mirrored.

According to this author, this group includes *Eadia aidae* (VRŠANSKÝ 2009) and *Raphidiomimula burmitica*, but the latter was interpreted as an ingroup of Raphidiomimidae by GRIMALDI & ROSS (2004; see also above). The only known specimens of *R. burmitica* is clearly a nymphal stage. Nymphs, while important (especially those of fossils, e.g. HAUG J. T. 2013, early view), are currently still difficult to interpret in systematic approaches due to the lack of data from extant forms, especially for polyneopteran insects (MASHIMO et al. 2014). We therefore cannot further elaborate on eadiideans in our discussion, besides having to state that their presumed representatives have forelegs, which appear relatively unspecialised and not strongly adapted for grasping prey.

There are two more groups, which have been interpreted as raptorial roach-like insects: Caloblattinidae (VRŠANSKÝ 2008) and Mutoviidae (VRŠANSKÝ, pers. com.). Mutoviidae seems to be only based on wing details (e.g., VRŠANSKÝ & ARISTOV 2012); therefore, it is impossible to make a statement about the characteristics of their forelegs.

The first appendages of the caloblattinid *Decomposita triocella* resembles that of non-raptorial cockroaches and other roach-like insects (e.g., Fig. 3A): it is tube shaped, the tibia has nearly the same length as the femur, only few spines are apparent (VRŠANSKÝ 2008, figs. 1, 2, 5). The first pair of appendages of *Decomposita triocella* do not show any of the upper discussed specifics seen in *R. waddingtonae*.

Evolutionary interpretation: The phylogenetic relationship within the dictyopterans and the evolution of the mantodean morphotype is currently not conclusively resolved (see e.g. discussion in HÖRNIG et al. 2013). While traditionally the wings are used as a primary source of information for identifying relationships in fossil insects, this is seen as problematic in the current case for the following reasons:

- 1) The preservation of the wing venation in the here described specimen is very incomplete. While the distal regions of the veins appear well preserved, the proximal areas, where the veins join each other, is not well enough preserved to allow a reliable and objective reconstruction of the exact pattern.
- 2) Especially within Dictyoptera the wing venation pattern can be extremely variable, and it is to be expected that we have numerous convergencies (e.g., BÉTHOUX et al. 2009), hence lowering the applicability of this character complex. Therefore, alternative characters, such as specializations of the legs, should be taken into account.
- 3) As an emphasise on the last point as well as pointing out the challenges of interpreting fossil wing venation, the following case should be considered: BÉTHOUX & WIELAND (2009) and BÉTHOUX et al. (2010) argued convincingly that strephocladidans are dictyopterans (although they may not be directly branch off the lineage towards modern mantodeans as originally suggested, see discussion in HÖRNIG et al. 2013). Based on the exact same wings, KUKALOVÁ-PECK & BEUTEL (2012) argued that strephocladidans are holometabolous insects, together with a species identified by others as a beetle (BÉTHOUX 2009 and references therein). A third interpretation is that of STOROZHENKO (1997), who considered strephocladidans as “grylloblattids”. This demonstrates that the application of wing venation within dictyopterans bases on the correct interpretation of the identity of the veins. Combined with the rather problematic preservation in the here described specimen, we think that using these characters in the present case would be highly subjective.

Given the points above, characters of the wings are unlikely to resolve the phylogenetic position of *Raptoblatta waddingtonae*. Instead, the distinct morphology of the grasping appendages is used here as a basis for supporting systematic hypotheses of certain groups.

Based on the similarity of their first pair of thoracic appendages we interpret *Raptoblatta waddingtonae* as possible sister group of Mantodea (Fig. 3A). The similarities listed above are interpreted here as synapomorphies shared between the two. Proceeding further from this assumption, we suppose that this specific type of grasping appendage did not evolve several times among dictyopterans, but only once. While we can never exclude convergent evolution; in the present case the similarities sum up to a rather complex set of characters that is not known in

distinct separate lineages, making convergent evolution at least less likely.

Santanmantis axelrodi has been considered to represent a very early mantodean (GRIMALDI 2003; GRIMALDI & ENGEL 2005). Here the morphology of the femur is different to some degree (Fig. 3A). It is very massive in proportion to the body; its lateral side is slightly curved, the distal end is narrower than the proximal part and equipped with two rows of spines (HÖRNIG et al. 2013). It therefore differs from the morphology seen in *R. waddingtonae* and other mantodeans in the absence of a pronounced concave region and the fact that the spines reach further proximally.

R. waddingtonae appears still more roach-like in its overall habitus than *Santanmantis axelrodi*, but shares the specific morphology of the raptorial appendage with further derived ingroup representatives of Mantodea (as well as other supposedly “basal” forms such as *Ambermantis wozniaki*; GRIMALDI 2003). We therefore interpret the morphology of *S. axelrodi* as autapomorphically derived in this species. We should not forget that presumed “basal” groups or species can possess specializations of their own as well.

Alternatively, one could argue that *R. waddingtonae* is even closer related to modern mantodeans than *S. axelrodi*. Yet, *S. axelrodi* shares important characters with modern mantodeans which are absent in *R. waddingtonae*. First, the overall habitus of *S. axelrodi* is already less roach-like, while *R. waddingtonae* indeed could be described as a “cockroach with raptorial forelegs” (Fig. 2). In addition, *S. axelrodi* possesses a tibial spur, a more prominent curved spine distally on the tibia. In *R. waddingtonae* the distal spines are undifferentiated and resemble similar spines in more “normal” roach-like insects (Fig. 3A).

Raphidiomimidae (or also other raptorial roach-like insects) could branch off earlier from the lineage towards Mantodea, with still less specialised raptorial appendages (Fig. 3A). Yet, we cannot further resolve the position of this group.

The finding of *R. waddingtonae* further supports the idea of the “foreleg first” hypothesis put forward by HÖRNIG et al. (2013). Apparently still strongly roach-like forms such as *R. waddingtonae* already evolved highly specialised raptorial forelegs. Other specializations of the mantodean morphotype appear to have evolved later.

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