

Redescription and phylogenetic placement of the Cretaceous wasp *Parviformosus wohlrabeae* (Hymenoptera: Proctotrupomorpha)

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ABSTRACT

The Early Cretaceous fossil *Parviformosus wohlrabeae* Barling et al., 2013, has been described as the oldest known member of the chalcidoid family Pteromalidae. However, its phylogenetic placement has raised doubts, highlighting the necessity for a proper revision. A redescription as well as a re-interpretation of morphological characters is presented here and differences to the original description of Barling et al. (2013) are discussed. Phylogenetic placement of *P. wohlrabeae* is critically examined. We did not find any synapomorphies shared with Chalcidoidea nor any other superfamily and therefore place the fossil as Proctotrupomorpha *incertae sedis*. Despite its unclear phylogenetic position, *P. wohlrabeae* remains a significant fossil as it provides a very rare example of a member of Proctotrupomorpha from the Lower Cretaceous Crato Formation of Brazil.

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INTRODUCTION

Parasitoid wasps are extremely important in our terrestrial ecosystems and significantly influence their host populations (Quicke, 1997). They constitute over three-fourths of all known parasitoid insect species and include some of the most diverse insect groups (Eggleton and Belshaw, 1992; Heraty, 2009). The origin of hymenopteran parasitoids is dated to be between the Permian-Triassic boundary, about 247 m.y.a. (Peters et al., 2017) and the Triassic-Jurassic boundary, 210 m.y.a. (Grimaldi and Engel, 2005), followed by an unprecedented megaradiation leading to the species richness we observe today (Huber, 2009). One of these groups are the Proctotrupomorpha (sensu Rasnitsyn, 1988), which include species-rich but minute parasitoid taxa. The oldest proctotrupomorphan fossils date back 165 m.y.a., excavated from deposits in China (Shih et al., 2011), but most of the fossil diversity appeared more recent as documented by Cretaceous and Palaeogene deposits (Grimaldi and Engel, 2005; Penney, 2010; Rasnitsyn and Kühnle, 2019). With an estimated age of approximately 110 m.y., the limestone compression fossil *Parviformosus wohlrabeae* Barling et al., 2013, is currently one of the oldest representatives of the proctotrupomorphan superfamily Chalcidoidea. Besides *P. wohlrabeae*, few other chalcidoid wasps have been recorded or even described from that time (Grimaldi and Engel, 2005; Kaddumi, 2005; Penney, 2010; Poinar and Huber, 2011; Gumovsky et al., 2018; Haas et al., 2018).

The superfamily Chalcidoidea, with about 22,000 described and 500,000 estimated species (Heraty, 2009; Noyes, 2019), is probably the largest proctotrupomorphan superfamily. Despite numerous morphological and molecular phylogenetic studies (Gibson, 1986; Gibson et al., 1999; Munro et al., 2011; Heraty et al., 2013; Peters et al., 2018), the phylogenetic relationships of Chalcidoidea are not satisfactorily resolved. Fossils often offer valuable information for such phylogenetic studies, by providing a minimum age for their divergence and the possibility to trace back morphological or even biological shifts, which are necessary to understand evolutionary patterns. Appropriate comprehensive description and conclusive phylogenetic placement of those few fossils is therefore imperative for untangling chalcidoid evolution. *Parviformosus wohlrabeae* has been described as the oldest member of the family Pteromalidae (Chalcidoidea), which would make it a key fossil of this group. As Pteromalidae is a polyphyletic

assemblage of unrelated chalcidoid subfamilies (Munro et al., 2011; Heraty et al., 2013), any phylogenetic placement of fossils in “Pteromalidae” needs to consider its various subfamilies.

The possibility of a precisely identified early Cretaceous fossil of Pteromalidae would be highly intriguing for the purposes of determining the timing of chalcidoid diversification relative to the diversification of flowering plants and potential insect host lineages. However, the description and phylogenetic placement of *Parviformosus wohlrabeae* has been followed by some doubts, even in the original study. Barling et al. (2013) already mentioned in their description that “Familial placement for *P. wohlrabeae* is extremely difficult due to the lack of three key taxonomic structures; the legs, wings and antennae.” Moreover, Farache et al. (2016) were also skeptical about the phylogenetic positioning of *P. wohlrabeae* and even questioned whether it should be placed in Chalcidoidea. Even Barling (2018) questioned the validity of the placement of *P. wohlrabeae*. Here we present a redescription of *P. wohlrabeae* and revise its phylogenetic position.

MATERIAL AND METHODS

Specimen

As described by Barling et al. (2013), the female holotype of *Parviformosus wohlrabeae* is preserved in fine-grained laminated limestone, originating from the Crato Formation of the Chapada do Araripe tableland in Brazil, probably from an area of active quarrying between Santana do Cariri, Nova Olinda and Tatajuba, with its quarry of origin unknown. It is dated to the Early Cretaceous (Aptian) period. The specimen is preserved within a circular slab of limestone, which was etched in 10% hydrochloric acid and subsequently sputtered with carbon and gold (Barling et al., 2013). Barling et al. (2013) mentioned that the specimen was damaged, so that parts of the head are missing from its original conservational state (Barling et al., 2013, figure 3B). The specimen is deposited in the Stuttgart State Museum of Natural History (SMNS) under the accession number “SMNS 700902”.

Imaging

New scanning electron microscopic images were taken using a Zeiss EVO LS 15 microscope. Measurements and high resolution images for the digital drawing were taken using a Keyence VHX 5000 digital microscope. Adobe Illustrator CS4 (Version: 14.0.0) was used to create the drawing

based on digital images and to assemble the figure plates.

Terminology

Terminology and abbreviations follow Gibson et al. (1997) and the Hymenoptera Anatomy Ontology (HAO) (Yoder et al., 2010).

SYSTEMATIC PALAEOONTOLOGY

Order HYMENOPTERA Linnaeus, 1758
Suborder APOCRITA Gerstaecker, 1867
Infraorder PROCTOTRUPOMORPHA sensu
Rasnitsyn, 1988, incertae sedis

Type. *Parviformosus wohlraebeae* Barling et al. 2013 (Figures 1-3), holotype female

Diagnosis. Pronotum large, almost as long as half of mesoscutum (Figure 1.1-2). Metanotum medially long, about half as long as propodeum (Figure 1.1-2) and submedially overlapping propodeum (Figure 2.2). Propodeum smooth with distinct median carina ending posteriorly in transverse adpetiolar strip (Figure 2.2). Propodeal spiracle large, kidney-shaped with distinct rim (Figure 2.1). Petiole small, transverse. Metasoma with vaguely indicated segmentation, metasoma length subequal to mesosoma (Figure 1.1, 1.3). Ovipositor elongate and ventrally curved (Figure 1.1).

Specimen condition. The antennae are missing. The left fore- and midleg are embedded under the specimen and are not visible. Other legs are preserved only in part (see description). Wings are poorly preserved, being at most represented by small remnants in their sockets, except for a large piece of wing membrane on the right side of the body. The specimen itself is heavily deformed from possible dorsolateral force effect, either through taphonomy or before fossilization. The head and ventral metasoma suffered severe breakage, with the head being only partly preserved and metasomal sterna not discernable. The ovipositor is embedded within a small limestone ridge, which has partly been broken, seemingly by scratches with a tool.

Redescription. Total body length excluding ovipositor 3.5 mm; ovipositor length about 2.8 mm. Head: Height about 0.68 mm, severely damaged and distorted (Figure 1.1), at least right and frontal part of head missing. Left eye partly identifiable. Left mandible distinguishable, broad, with three teeth, ventral tooth broadest with ventral margin straight. Inner structure, possibly pharynx, visible. Antennal insertion as described in Barling et al. (2013) not recognizable. Left labial palp mentioned

by Barling et al. (2013) visible, covered by setae, but identity not certain.

Mesosoma: Length 1.3 mm, without sculpture, appearing smooth, dorsolaterally depressed from right side (Figure 1.2). Pronotum long, with moderately long collar, posterolateral corner distinctly overlapping mesopleuron (Figure 1.6). Right procoxa partly visible at lateroventral pronotal margin. Mesoscutum with right notaulus faint, but straight and solid, reaching posterior mesoscutal margin. Axilla reaching transscutal articulation mesad of notaulus. Mesoscutellum deformed but convex. Metanotum about one-third the length of propodeum as indicated on the left side by straight suture (Figure 2.2-4), overlapping propodeum submedially (Figure 2.2). Metanotal area on right side submedially very strongly deformed and forced in. Metascutellum probably large. Propodeum about one-fourth the length of mesosoma, smooth, with distinct median carina ending posteriorly in transverse adpetiolar strip (Figure 2.2), partly cracked and distorted (Figure 1.2), original form hardly assessable, lateral and hind margin bordered by strong carina. Right spiracle situated close to anterior propodeal margin, kidney-shaped with distinct rim (Figure 2.1). Mesopleuron concave, smooth to lightly sculptured, dorsally marked by deep and broad groove, possibly mesopleural line. On both sides area adjacent to postalar process marked by deep mesoscutellar trough, delimited posteriorly by broad posterior mesoscutellar arm (Figure 2.1). Only fore wing articulation most probably preserved, marked by small remnant of (probably) wing membrane attached to mesosoma (Figures 2.1, 3, rfw?). Large piece of seemingly detached wing membrane located at left hindwing articulation, folded over right meso- and metapleuron, identity uncertain (Figure 2.1, 3, wf). Remnant of left meso- or metatibia located between propodeum and metasoma (Figures 2.3, 3, lti_{2/3}). Right metafemur and trochanter bent forwards over metapleural area (Figures 2.1, 3).

Metasoma: Length 1.6 mm, without sculpture, smooth (Figure 1.3), with at least seven vaguely indicated separate terga, artificially dorsolaterally depressed from right side, tip broken. Petiole small, transverse. Mt₂₋₄ (Figures 1.3, 3) subequal in length, Mt₅ occupying one-third of metasoma, Mt₆ damaged posteriorly, Mt₇ indicated by a visible layer of cuticle at the breakage point (Figure 1.5). All terga not emarginated medially. Ovipositor curved, partly broken, traceable on limestone and encompassed in limestone ridge (Figure 1.4), apex not clearly delimited. Piece of ovipositor mounted

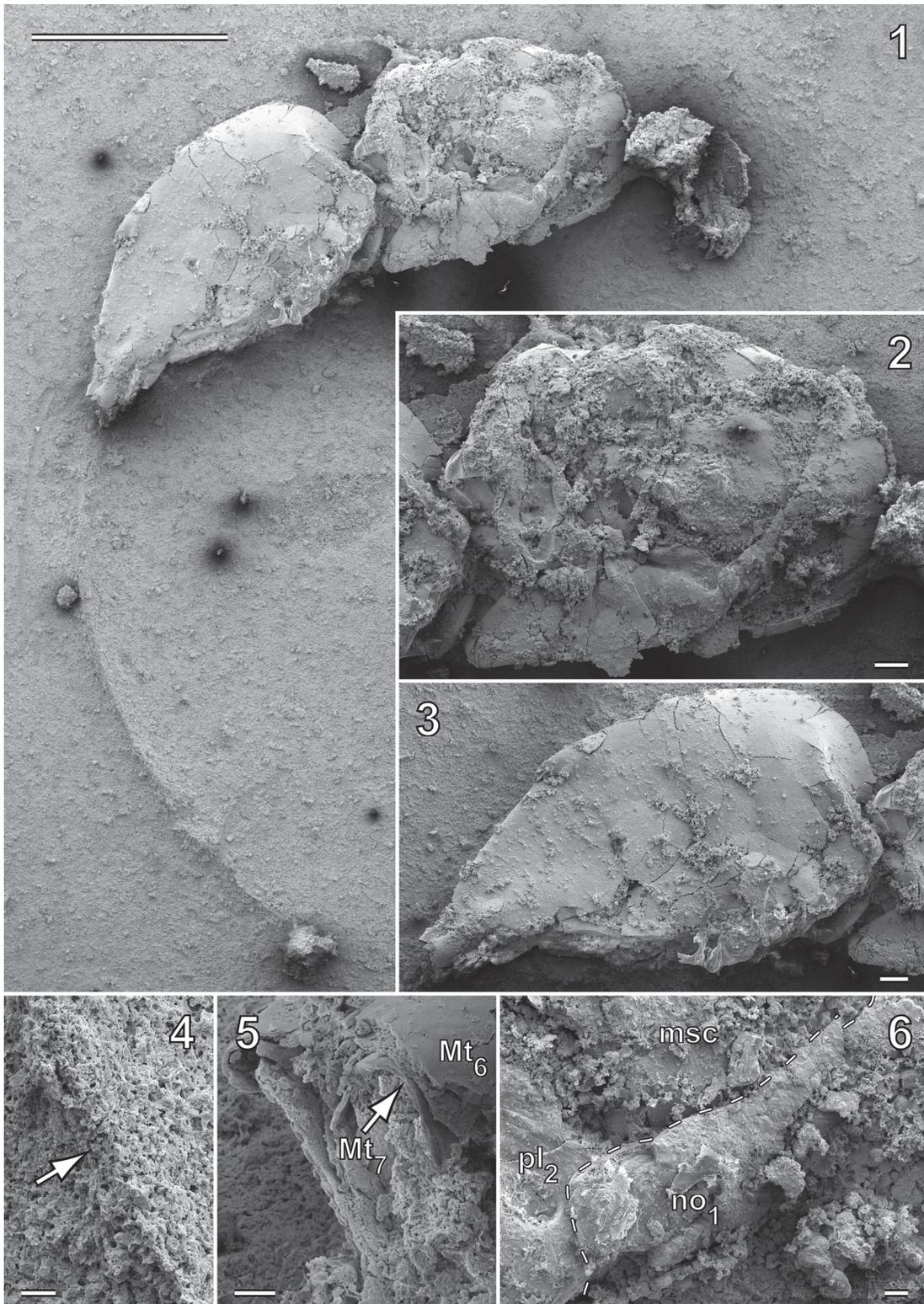


FIGURE 1. Scanning electron microscopic images of *Parviformosus wohlraabeae* Barling et al., 2013. (1) Complete habitus. (2) Mesosoma. (3) Metasoma excluding ovipositor. (4) Ovipositor (arrow) engulfed in mineral ridge. (5) Metasoma, broken posterior tip with individual layers of Mt₇ and Mt₈ (arrow) visible. (6) Anterolateral view of mesosoma, head to right, dashed line marks posterior margin of pronotum. Scales (1) 1 mm; (2, 3) 0.1 mm; (4–6) 0.02 mm. Abbreviations: msc = mesoscutum, Mt_{6/7} = metasomal tergite 6/7, no₁ = pronotum, pl₂ = mesopleuron.

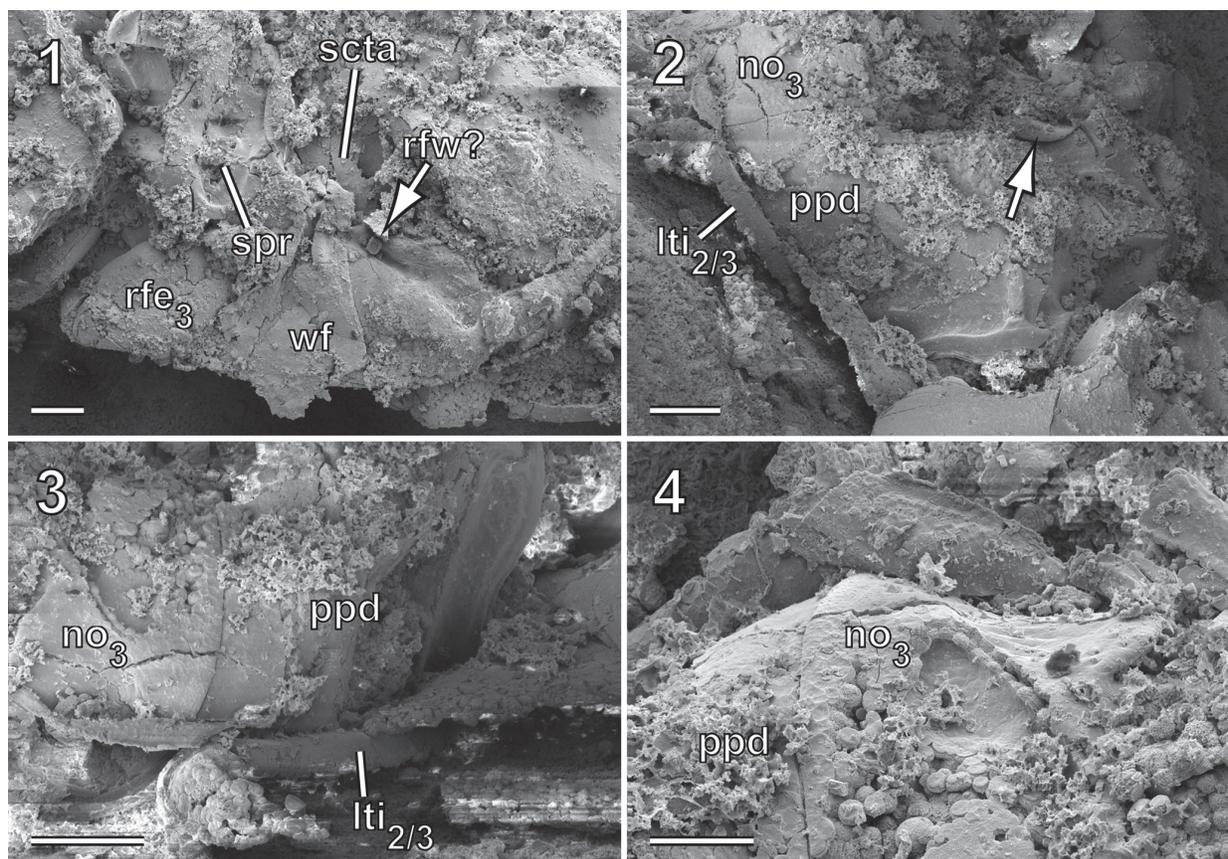


FIGURE 2. Scanning electron microscopic images of the mesosoma of *Parviformosus wohlraabeae*. (1) Posterior part of mesosoma with potential forewing fragment (arrow), right lateral view. (2–4) Metanotum and propodeum, (2) dorsal view, arrow indicates metanotum submedially overlapping propodeum; (3) left dorsolateral view; (4) right dorsolateral view. Scales (1–3) 0.1 mm; (4) 0.05 mm. Abbreviations: lti_{2/3} = left meso- or metatibia, no₃ = metanotum, ppd = propodeum, rfe₃ = right metafemur, rfw? = probably remnant of right forewing, scta = mesoscutellar arm, spr = spiracle, wf = wing fragment.

on a second SEM stub mentioned by Barling et al. (2013) not present.

DISCUSSION

In the light of our new morphological interpretation, the original diagnosis of the genus *Parviformosus* by Barling et al. (2013) needs to be modified. Comparing our morphological interpretation with the interpretation of Barling et al. (2013), it is apparent, that many structures, especially those from the mesosoma, have to be re-interpreted.

Species Diagnosis

The petiole is partly visible in between the propodeum and the first gastral tergite, contrasting Barling et al. (2013) who misinterpreted part of the propodeum as part of the petiole. The described dorsal “lip” on the fourth metasomal segment appears to result from severe deformation of the

metasoma and is therefore considered as an artefact. Total length of ovipositor is difficult to assess, because the distal portion is missing from the holotype, but its length is indicated on the limestone slab by a diffuse marking. In addition to those characters mentioned by Barling et al. (2013), we found a number of additional diagnostic characters. These include a broad mandible with three distinct teeth; an unusually deep and long groove on the mesopleuron, probably representing the mesopleural sulcus; a rather broad metanotum, overlapping the propodeum and a smooth propodeum, which is laterally and posteriorly delimited by a broad shiny rim and bears a distinct median carina.

Family Placement

In the original description, Barling et al. (2013) argued that the posterior end of the metasoma as well as the shape and morphology of the ovipositor

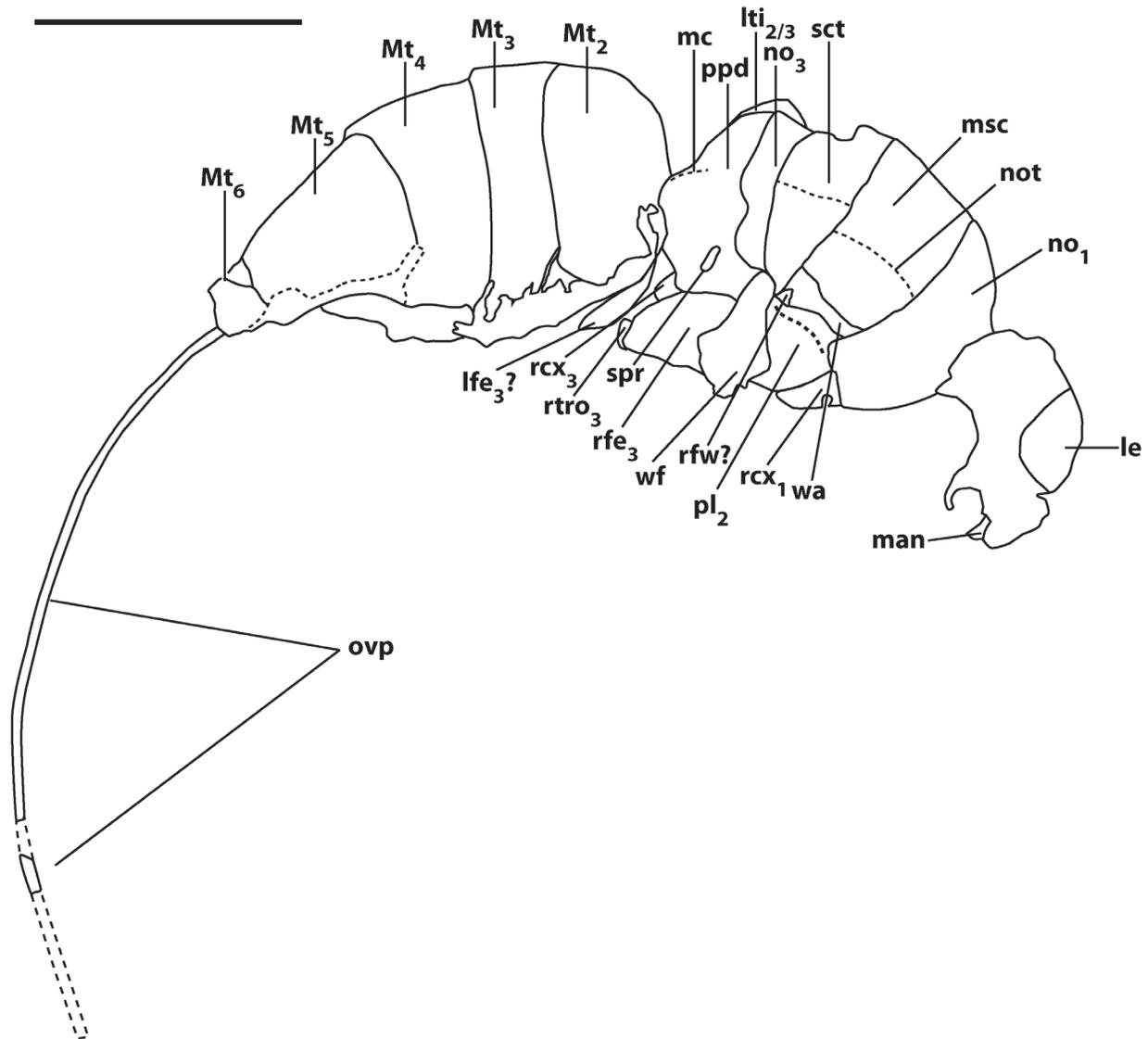


FIGURE 3. *Parviformosus wohlraabeae*, habitus, lateral view; Abbreviations: le = left eye, lfe₃? = probable left metafemur, lti_{2/3} = left meso- or metatibia, man = mandible, mc = median carina, msc = mesoscutum, Mt = metasomal tergite, no₁ = pronotum, no₃ = metanotum, not = notaulus, ovp = ovipositor, pl₂ = mesopleuron, ppd = propodeum, rcx₁ = right procoxa, rcx₃ = right metacoxa, rfe₃ = right metafemur, rfw? = probably remnant of right forewing, rtr₃ = right metatrochanter, sct = mesoscutellum, spr = spiracle, wa = wing articulation, wf = wing fragment; Scale: 1 mm.

allow placement within the Pteromalidae. Principally, offering a solid and universally accepted morphological definition of Pteromalidae is not possible because the group is polyphyletic (Heraty et al., 2013) and therefore lacks synapomorphic characters (Graham, 1969; Bouček and Rasplus, 1991; Grissell and Schauff, 1997). Therefore, a phylogenetic placement of pteromalid lineages makes only sense on the subfamily level. Barling et al. (2013) claimed that because of 1) the “length and shape of the ovipositor”, 2) the “height relative to width of

the gaster”, 3) the “short pronotum”, 4) the “shortened head” and 5) the “apically expanding ovipositor sheath” the specimen might belong to the pteromalid subfamily Sycophaginae, now placed in Agaonidae (Heraty et al., 2013). None of the abovementioned characters is diagnostic nor represents a synapomorphy for any pteromalid or chalcidoid subfamily. The two defining apomorphies of Sycophaginae, i.e., the presence of grooves framing the mesoscutellum and a deeply sinuated margin of the eighth metasomal tergite,

leading to a thumbnail-like medial flap (Cruaud et al., 2011) are not visible on the specimen. Placement of *Parviformus wohlrabeae* in Sycophaginae would also have challenged the current and well-established view that the age of this subfamily and their association with figs (*Ficus*, Moraceae) are of post-Gondwanan origin (Cruaud et al., 2011) and therefore roughly 60 m.y. younger than the fossil. Based on Rønsted et al. (2005) the evolutionary root of figs might lay at the boundary of the Early to the Late Cretaceous, about 100 m.y.a., establishing a time frame of 60 – 100 m.y. for the first development of the mutualism between figs and their chalcidoid pollinators. More recently, the origin of this mutualism was narrowed down to roughly 75 m.y.a. (Cruaud et al. 2012). It is therefore highly unlikely, that *P. wohlrabeae*, with an age of about 110 m.y., had any association with figs.

Superfamily Placement

As *Parviformus wohlrabeae* possesses a deeply incised wasp waist and discernable wing articulations with fragments of wings attached, it can therefore be classified as an apocritan Hymenoptera. Furthermore, possession of a long exerted ovipositor sheath eliminates the possibility of placement in Aculeata. Positioning of the metasoma excludes the parasitoid superfamilies Evanioidea and Stephanoidea. The superfamilies Trigonoidea and Megalyroidea can also be dismissed by the structure of the pronotum, which is dorsally extremely shortened in the mentioned superfamilies. Additionally, the metasoma of these groups has more apparent sterna than that of *P. wohlrabeae*, where the observable part of the metasoma is largely covered by terga. Due to severe damage, the metasomal sterna of *P. wohlrabeae* are hardly discernable, let alone countable. Metasomal characters also contradict placement in the Ichneumonoidea, which possess a metasoma that is usually elongate and petiolate with spiracular openings on each tergum. The metasoma in Ceraphronoidea is also quite different with their first tergite covering most of its length. Moreover, the structure of the mesosoma in *P. wohlrabeae*, like the notauli and the pronotum, does not agree with the morphological features presented in Ceraphronoidea. The only remaining alternative is a placement within the infraorder Proctotrupomorpha, sensu Rasnitsyn (1988), which is comprised mostly of minute parasitoids, being morphologically highly diverse and species rich. Extant superfamilies included in Proctotrupomorpha are the Cynipoidea, Platygastroidea, Chalcidoidea,

Mymarommatoidea, Diaprioidea, and Proctotrupomorpha with addition of the fossil groups Serphitoidea, Cretacoformicidae incertae sedis, and the genus *Koonwarrus* incertae sedis. A more precise phylogenetic placement of *P. wohlrabeae* is highly speculative due to its preservational state. Reliable evidence would arise from detectable synapomorphic characters. Such characters, however, are not visible, missing, or subject to vague interpretation, because of distortion and damage.

As it was described as a member of Pteromalidae, *Parviformus wohlrabeae* should exhibit the synapomorphies of its superordinate superfamily, the Chalcidoidea. Those include 1) possession of a free prepectus, separating the pronotum from the tegula, 2) the position of the mesothoracic spiracle (Gibson, 1985, 1999; Gibson et al., 1999), 3) morphologically unique multiporous plate sensillae on the flagellar segments (Barlin and Vinson, 1981; Gibson, 1986; Basibuyuk and Quicke, 1999). As Barling et al. (2013) state, the prepectus cannot be identified in the fossil (Figure 1.2, 1.6). Barling et al. (2013) further hypothesize that the prepectus "... is probably internalized, as in many pteromalid subfamilies." Internalization of the prepectus is so far not reported in Pteromalidae, although miniaturization might occur, e.g., Macromesinae (Gibson, 1986). This miniaturization also appears in other chalcidoid families and is often linked to a small body size, sometimes leading to an almost fully reduced prepectus (Gibson, 1986). Only the chalcidoid family Rotoitidae was reported to completely lack a visible prepectus (Bouček and Noyes, 1987), but subsequent examination revealed a very slender, independent prepectus, which might be concealed by the pronotum if it is directly adjacent to the mesepisternum (Gibson and Huber, 2000). In *P. wohlrabeae*, the posterolateral corner of the pronotum is distinctly overlapping the mesopleuron, with no indication of a hidden prepectus underneath (Figure 1.6). Evaluating the position of the mesothoracic spiracle is not possible due to the poor conservational state of the specimen. Presence or absence of multiporous plate sensilla on the flagellar segments cannot be assessed as well, because the antennae are missing. Conclusively, none of the aforementioned synapomorphies of Chalcidoidea can be used for placing the fossil in this superfamily. The long ovipositor is the most obvious feature of the fossil and represents a character state that is common in various chalcidoid lineages but it does not unequivocally support placement in this superfamily, with many parasitoid groups including taxa with an exerted ovipositor.

Based on the limited morphological evidence, we propose to treat *Parviformosus wohlraabeae* as *Proctotrupomorpha incertae sedis*. Placement in Chalcidoidea is tempting, mostly due to the lack of satisfactory alternative options, but based on the poor preservation and the absence of any synapomorphies, a reliable superfamily placement of the fossil is not possible. Considering the morphological diversity observed in proctotrupomorphan wasps, *P. wohlraabeae* might as well belong to a yet unknown "morphotype", not bearing an exact

resemblance to any known representative of this clade.

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