

Taxonomic revision of the infraorder Proctotrupomorpha (Hymenoptera)

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Abstract

The authors revise the taxonomy of infraorder Proctotrupomorpha. Although this revision is not meant as being complete, it is based on the most important structures of the infraorder. A new taxon in Proctotrupomorpha is being erected, Microprocta, **taxon nov.**, as a new informal group (clade), comprising the superfamilies Chalcidoidea, Platygastroidea, Diaprioidea, Serphitoidea, and Mymarommatoidea, and families Jurapriidae, Trupochalcididae, and Chalscelionidae, **fam. nov.**, based on five synapomorphic characters of their wing venation.

Keywords: Hymenoptera, Proctotrupomorpha, Microprocta, Cretacoformicidae, Proctotrupeidea, Cynipoidea, Chalcidoidea, Platygastroidea, Diaprioidea, Serphitoidea, Mymarommatoidea, Bipetiolarida

Introduction

The infraorder Proctotrupomorpha Latreille, 1802 was proposed by Rasnitsyn (1988) to harbor the superfamilies Proctotrupeidea, Cynipoidea, and Chalcidoidea. Since then, this definition has been generally accepted. Some authors then changed the definitions of the component superfamilies. Superfamilies were added, in particular Platygastroidea (Goulet & Huber, 1993), Diaprioidea (Sharkey, 2007), Serphitoidea and Mymarommatoidea (Grimaldi & Engel, 2005), and clade Bipetiolarida (to encompass the two latter superfamilies, Engel, 2005). Some authors additionally introduced superfamily Ceraphronoidea into Proctotrupomorpha (e.g., Ronquist *et al.*, 1999; Grimaldi & Engel, 2005). This last addition however was questioned based on morphological observations (Rasnitsyn, 2002; Vilhelmsen & Turrissi, 2011) and phylogenomic results (Heraty *et al.*, 2011; Sharkey *et al.*, 2012; Klopstein *et al.*, 2013; Payne *et al.*, 2013; Mao *et al.*, 2015; Peters *et al.*, 2017), and is currently abandoned.

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In contrast to its volume, the internal topology of the infraorder is in a chaotic state. Several possible topologies are outlined in the following, however still giving an incomplete picture (phylogenomic results prior to 2010 are not included, clades are in brackets, ‘+’ connects sister groups, and ‘&’ connects clades in unresolved polychotomy):

- Mesoserphidae & (Proctotrupidae + Peleciniidae) & (Roproniidae + Heloridae + (Austroiniidae + (Monomachidae + (Diapriidae + Cynipoidea)))) + ((Jurapriidae + Chalcidoidea) + (Platygastroidea + Serphitidae? + Mymarommatoidea)) (simplified from Rasnitsyn, 1988, fig. 3, intuitive cladistics) (Fig. 1A).
- Proctotrupeidea + (Diapriidae & Monomachidae & Chalcidoidea & Platygastroidea & Cynipoidea & Ceraphronoidea) (simplified from Quicke & Basibuyuk in Rasnitsyn, 2006b, fig. 7B, numerical cladistics) (Fig. 1B).
- Roproniidae + (Heloridae + ((Austroiniidae + Monomachidae) + ((Peleciniidae + Proctotrupidae) + ((Diapriidae + Cynipoidea) + ((Chalcidoidea + Mymarommatoidea) + (Platygastroidea + Ceraphronoidea))))) (simplified from Ronquist *et al.*, 1999, fig. 7, numerical cladistics) (Fig. 1C).
- Proctotrupeidea incl. Diapriidae, Monomachidae & Cynipoidea & (Platygastroidea incl. Serphitidae, Mymarommatoidea + Chalcidoidea) (simplified from Rasnitsyn, 2002, fig. 331, intuitive cladistics) (Fig. 1D).
- (Chalcidoidea + (Mymarommatoidea + Maamingidae)) + (Monomachidae + ((Diapriidae + Cynipoidea) + (Roproniidae + (Platygastroidea + Proctotrupeidea)))) (simplified from Vilhelmsen & Turrissi, 2011, fig. 14, numerical cladistics) (Fig. 1E).
- Platygastroidea & Cynipoidea & (Proctotrupeidea + (Mymarommatoidea + (Diaprioidea incl. Monomachidae, Maamingidae) + Chalcidoidea)) (simplified from Heraty *et al.*, 2011, phylogenomics) (Fig. 1F).
- (Platygastroidea + Cynipoidea) + (Proctotrupeidea + (Diaprioidea incl. Monomachidae, Maamingidae + Chalcidoidea)) (simplified from Sharkey *et al.*, 2012, fig. 2, total evidence) (Fig. 1G).
- (Platygastroidea + Cynipoidea) + (Proctotrupeidea +

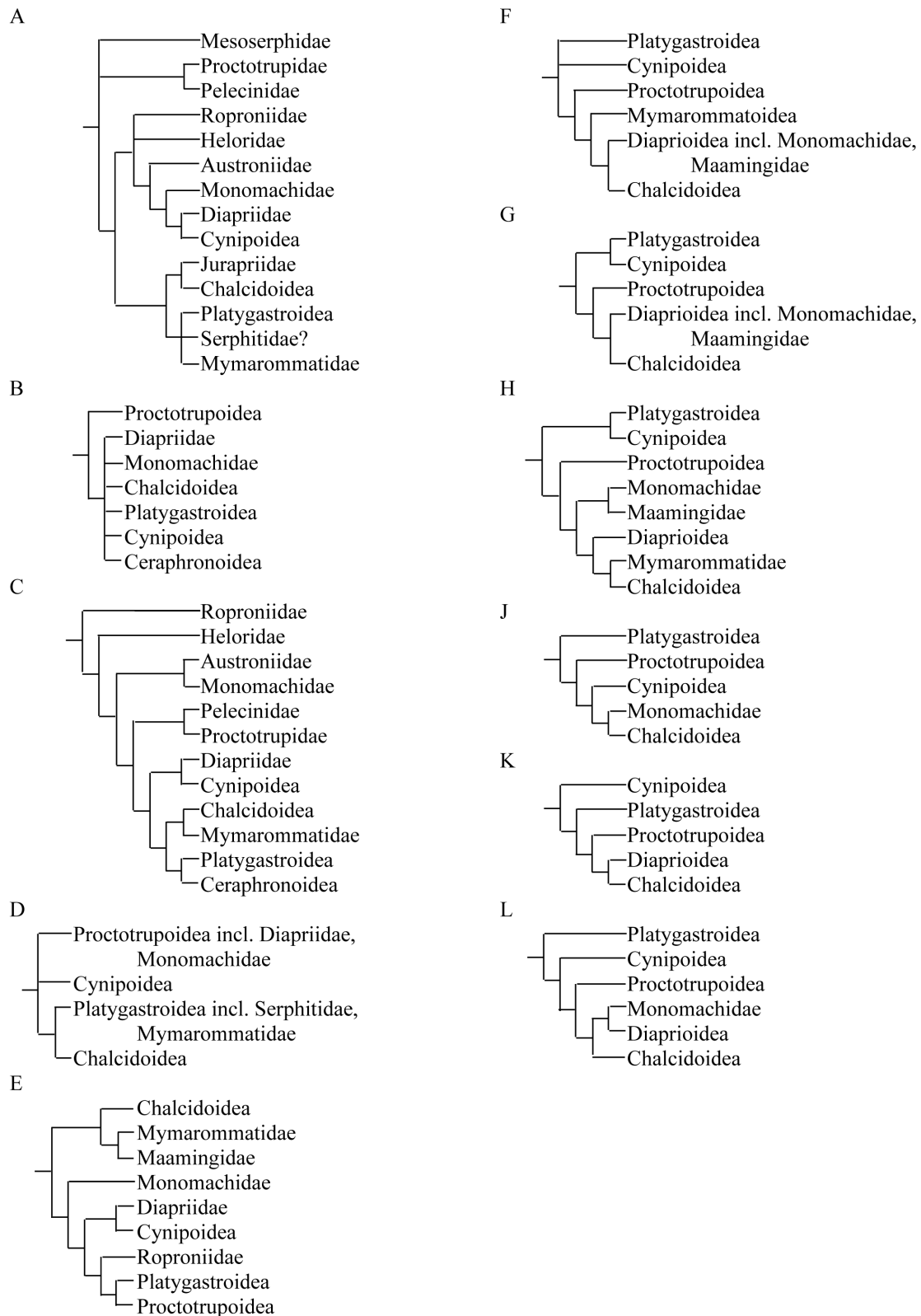


FIGURE 1. Cladograms of Proctotrupomorpha. **A**, Simplified from Rasnitsyn, 1988, fig. 3, intuitive cladistics. **B**, Simplified from Quicke & Basibuyuk in Rasnitsyn, 2006b, fig. 7B, numerical cladistics. **C**, Simplified from Ronquist *et al.*, 1999, fig. 7, numerical cladistics. **D**, Simplified from Rasnitsyn, 2002, fig. 331, intuitive cladistics. **E**, Simplified from Vilhelmsen & Turrisi, 2011, fig. 14, numerical cladistics. **F**, Simplified from Heraty *et al.*, 2011, phylogenomics. **G**, Simplified from Sharkey *et al.*, 2012, fig. 2, total evidence. **H**, Simplified from Klopstein *et al.*, 2013, fig. 2, total evidence. **J**, Simplified from Mao *et al.*, 2015, fig. 4, phylogenomics. **K**, Simplified from Peters *et al.*, 2017, fig. 1, phylogenomics. **L**, Simplified from Tang *et al.*, 2019, fig. 4, phylogenomics.

- ((Monomachidae + Maamingidae) + (Diaprioidea + (Mymarommatoidea + Chalcidoidea))) (simplified from Klopstein *et al.*, 2013, fig. 2, total evidence) (Fig. 1H).
- Platygastridae + (Proctotrupidae + (Cynipoidea + (Monomachidae + Chalcidoidea))) (simplified from Mao *et al.*, 2015, fig. 4, phylogenomics) (Fig. 1J).
- Cynipoidea + (Platygastridae + (Proctotrupidae + (Diaprioidea + Chalcidoidea))) (simplified from Peters *et al.*, 2017, fig. 1, phylogenomics) (Fig. 1K).
- Platygastridae + (Cynipoidea + (Proctotrupidae + ((Monomachidae + Diaprioidea) + Chalcidoidea))) (simplified from Tang *et al.*, 2019, fig. 4, phylogenomics) (Fig. 1L).

These eleven examples clearly demonstrate that all cladograms are essentially different, and that no clade appears consistently in more than three cladograms, except for Monomachidae (with or without Maamingidae), being monophyletic with Diapriidae in cladograms by Heraty *et al.* (2011), Sharkey *et al.* (2012), Klopstein *et al.* (2013) and Tang *et al.* (2019). Exceptions are the results by Sharkey *et al.* (2012) and Klopstein *et al.* (2013), which are similar in their dates, authors, material and methods as well. This certifies that, at least at the present state of phylogenetics, none of the available methods is better

than the others and uniquely preferable. Instead, all of them require cross-checking in order to improve their results (*cf.* Rasnitsyn, 2006a, b, 2010). This concerns intuitive cladistics as well which we have applied in the current study, based on new morphological characters. We consider this legitimate, since the result is meant as a hypothesis, which is to be tested in the future.

Material and methods

This publication is entirely based on published material, except for some of the illustrations. The applied method, intuitive cladistics, was previously described in detail (English versions: Rasnitsyn, 1996, 2006a) and widely applied and tested for decades (Rasnitsyn, 1969, 1980, 1988, 2002; Rasnitsyn & Zhang, 2010).

Results

The inferences below are based on characters that were

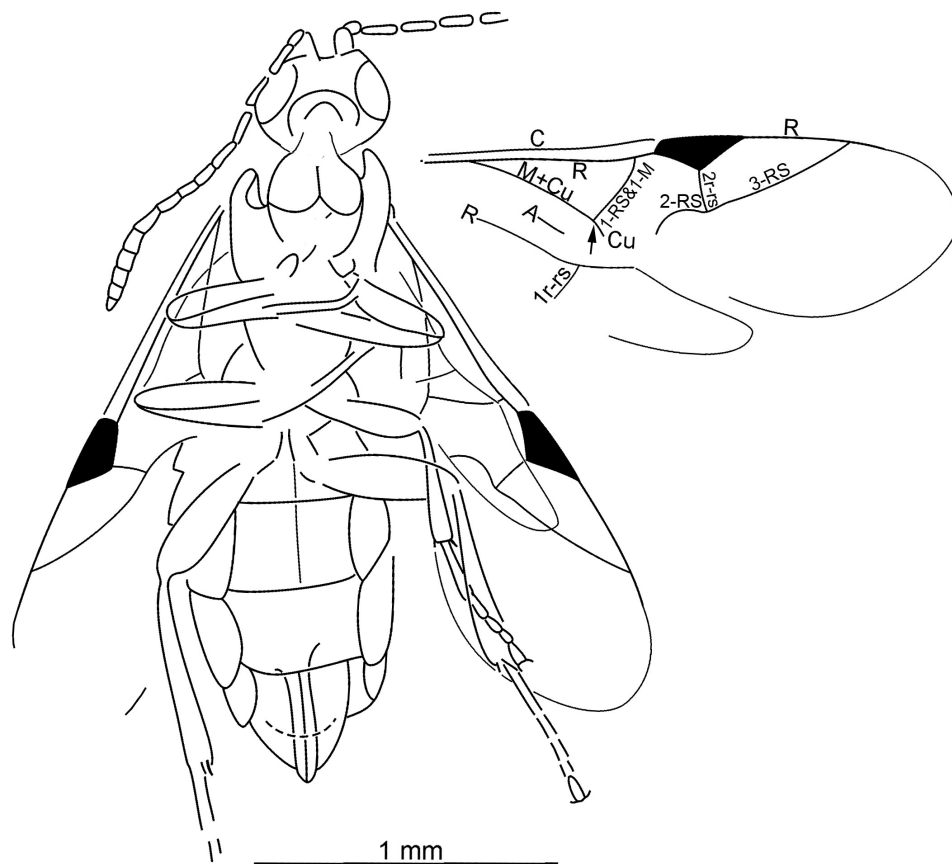


FIGURE 2. *Jurapria sibirica* Rasnitsyn, 1983, holotype, general view and wing venation; Upper Jurassic, Uda fossil site, Uda River, Transbaikalia (modified from Rasnitsyn & Brothers, 2007, by permission from the KwaZulu-Natal Museum Council). Arrow shows position of Cu bend. Venational symbols standard in all figures.

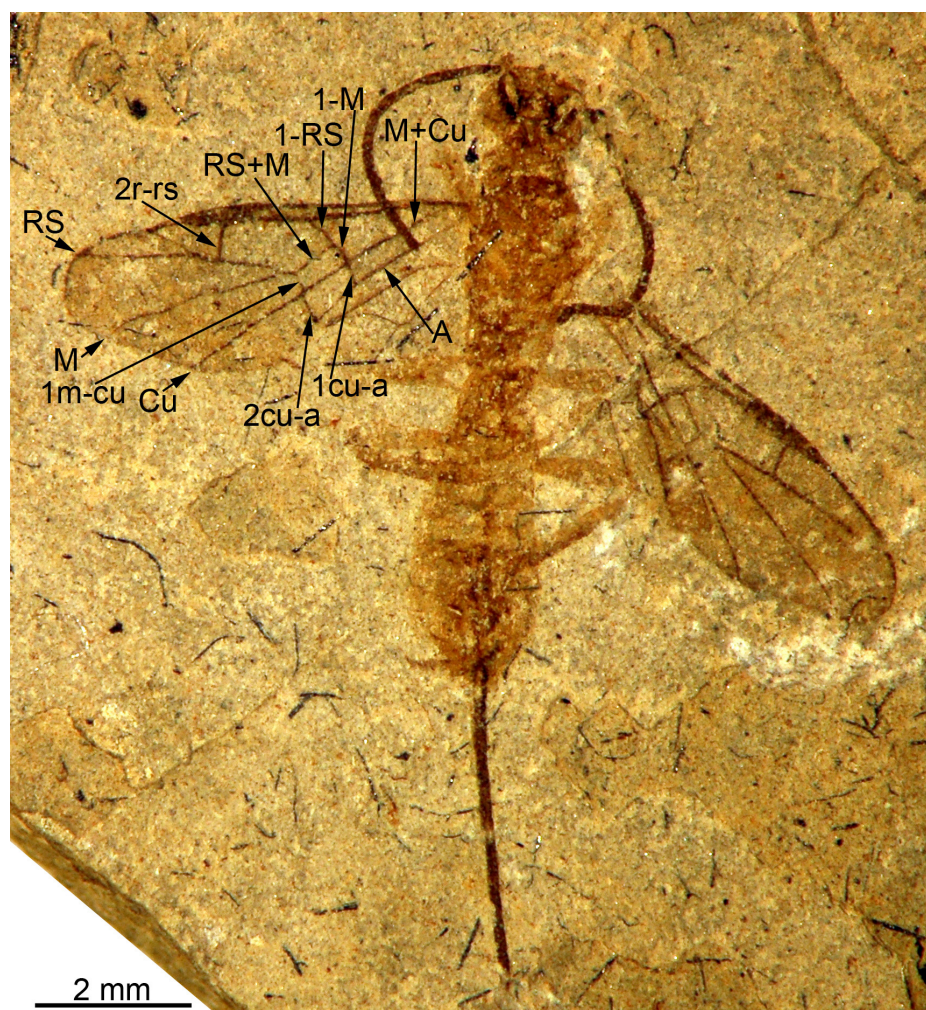


FIGURE 3. *Mesoserphus karatavicus* Kozlov, 1968, holotype, general view; Upper Jurassic, Karatau, S. Kazakhstan (orig., photo by APR).

mentioned earlier (Rasnitsyn, 1983) but not yet correctly defined and sufficiently evaluated. The most important of these characters was described as “Cu bent at its forking with M” (op. cit., p. 93) (Fig. 2). Proctotrupomorpha are known to have Cu, when sufficiently complete, straight, more or less throughout, from the wing base up to 2cu-a and beyond, and in particular lacking any long bending behind (toward wing hind margin) either at M+Cu fork or at its junction with 1m-cu (Fig. 3). This putative synapomorphy of the infraorder (Rasnitsyn, 1980: p. 83) is recorded since the earliest appearance of Mesoserphidae, the stem family of Proctotrupoidea, in the Middle Jurassic of Daohugou, China (Li *et al.*, 2016: fig. 1). The apomorphic posterior bend of Cu was first demonstrated in *Jurapria* Rasnitsyn, 1983 from the Late Jurassic, and later (Rasnitsyn *et al.*, 2004) was found to occur in Serphitidae (Fig. 4), Trupochalcidoidea (Fig. 5), and basal Chalcidoidea (Fig. 6) as well. Currently, it is possible to confirm a posterior bend of Cu also in more old and less advanced taxa of Diaprioidea (Fig. 7; cf. also Fujiyama, 1994, fig. 6; Perrichot & Nel, 2008, fig. 2;

Engel *et al.*, 2013, fig. 9B; Krogmann *et al.*, 2016: fig. 1; Kim *et al.*, 2018: figs 1, 2). The case of Platygastroidea is somewhat controversial, because the most basal family, Proteroscelpidae, shows Cu straight (Talamas *et al.*, 2019: fig. 15) whilst some Scelionidae (e.g., Talamas *et al.*, 2017: fig. 6, and particularly Talamas & Buffington, 2015: fig. 37) show Cu bent at the M+Cu fork. At the same time, it is evident that the posterior bend of Cu is a subject of putative homoplasy, e.g., in Roproniidae, Monomachidae, and Proctotrupidae (Naumann & Masner, 1985: figs. 55, 56, 58), even though the character is subject of variation and not necessarily part of the ground plan of these families as follows from their phylogeny by Rasnitsyn (1988, 2002) (e.g., Townes, 1948: fig. 12; Naumann, 1991: fig. 42.22K; Musetti & Johnson, 2004; Garrouste *et al.*, 2016). Equally, the posterior bend of Cu was lost in the majority of those Platygastroidea and Chalcidoidea, which retain visible Cu.

Because of the above reversals, the posterior bend of Cu at the fork of M+Cu by itself is not a reliable diagnostic character. However, it is accompanied by other characters

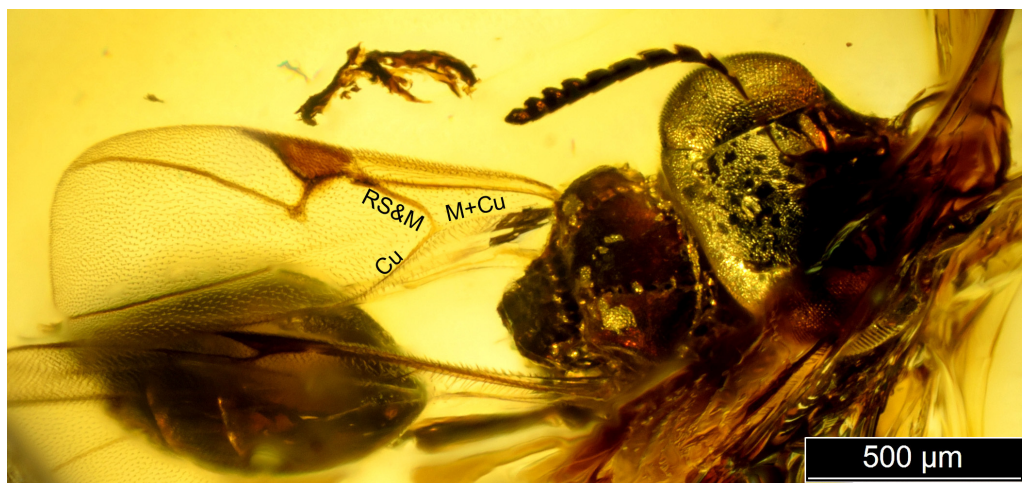


FIGURE 4. *Supraserphites vorontsovi* Rasnitsyn & Öhm-Kühnle, 2020, holotype, oblique upper view; mid-Cretaceous Burmese amber (modified from Rasnitsyn & Öhm-Kühnle, 2020, photo by Dmitry D. Vorontsov).

that jointly form a complex of putative apomorphies sufficient to delimit the taxa concerned, as follows:

- Crossvein cu-a shifted distad from M+Cu fork at least for 1cu-a length (unless lost): a character state apparently known in no other Proctotrupomorpha;
- Cu distinctly bent posteriorly at M+Cu fork (either angularly or gradually so) and so aligned with basal vein (1-RS&1-M, RS&M) (putatively lost in majority of Diaprioidea but not in their basal taxa referred to above, and in Platygastroidea but not in *Duta* Nixon, 1933 and in some other genera, see above). The posterior bend occurs in some Roproniidae, Proctotrupidae and Monomachidae (see above, the first paragraph of this chapter) as well, but it does not result in its alignment with basal vein in examples available for authors.
- Crossvein 2cu-a lost (a slight angular bend of Cu usually persists at its place);
- RS+M lost without trace;
- Crossvein 1m-cu lost without trace.

The hypothesis proposed herein is that the above five characters represent synapomorphies of the clade comprising the superfamilies Diaprioidea, Platygastroidea, Serphitoidea, Mymarommatoidea, Chalcidoidea, and the three families Jurapriidae, Trupochalcididae (=Cretacoformicidae, **syn. nov.**), and Chalscelionidae **fam. nov.** (see below).

Systematic palaeontology

Informal group (clade) Microprocta Rasnitsyn & Öhm-Kühnle, taxon nov.

Type superfamily. Chalcidoidea Spinola, 1811 (by priority).

Etymology. A shortened version of

‘Microproctotrupomorpha’, a name that would be more correct, but too long for a group of predominantly tiny parasitic wasps.

Diagnosis. Proctotrupomorph wasps with: crossvein cu-a if traceable (*e.g.*, as a kink of Cu at its former place) shifted distad from M+Cu fork at least for 1cu-a length; Cu often distinctly bent posteriorly at M+Cu fork and aligned with basal vein (1-RS&1-M); RS+M and 1m-cu traceless lost, 2cu-a lost.

Taxa included. Chalcidoidea Spinola, 1811, Diaprioidea Haliday, 1833 (not including Monomachidae Szépligeti, 1889 and Maamingidae Early *et al.*, 2001), Platygastroidea Westwood, 1840, Bipetiolarida Engel, 2005 (an informal group embracing Serphitoidea and Mymarommatoidea), and unplaced families Jurapriidae Rasnitsyn, 1983, Trupochalcididae Kozlov, 1975 and Chalscelionidae **fam. nov.**

Remarks. The remaining families of Proctotrupomorpha, namely Mesoserphidae, Peleciniidae, Proctotrupidae (including Vanhorniidae), Roproniidae (including Proctorenixidae), Heloridae (including Peradeniidae), Austroniidae, Monomachidae, and Maamingidae, are left comprising the superfamily Proctotrupeoidea, in the hopes that further research will elucidate their relationships and improve this preliminary choice.

It is possible to preliminarily evaluate the taxonomic structure of Microprocta based on two characters that are frequently being employed for the taxonomy of Proctotrupomorpha. These are (i) presence and number of petiolar (tube- or ring-shaped) segments of metasoma (none in Platygastroidea and Jurapriidae, one in Diaprioidea, Chalcidoidea and Trupochalcididae, and two in Bipetiolarida) and (ii) length of scape (short in Jurapriidae and Trupochalcididae and long in all

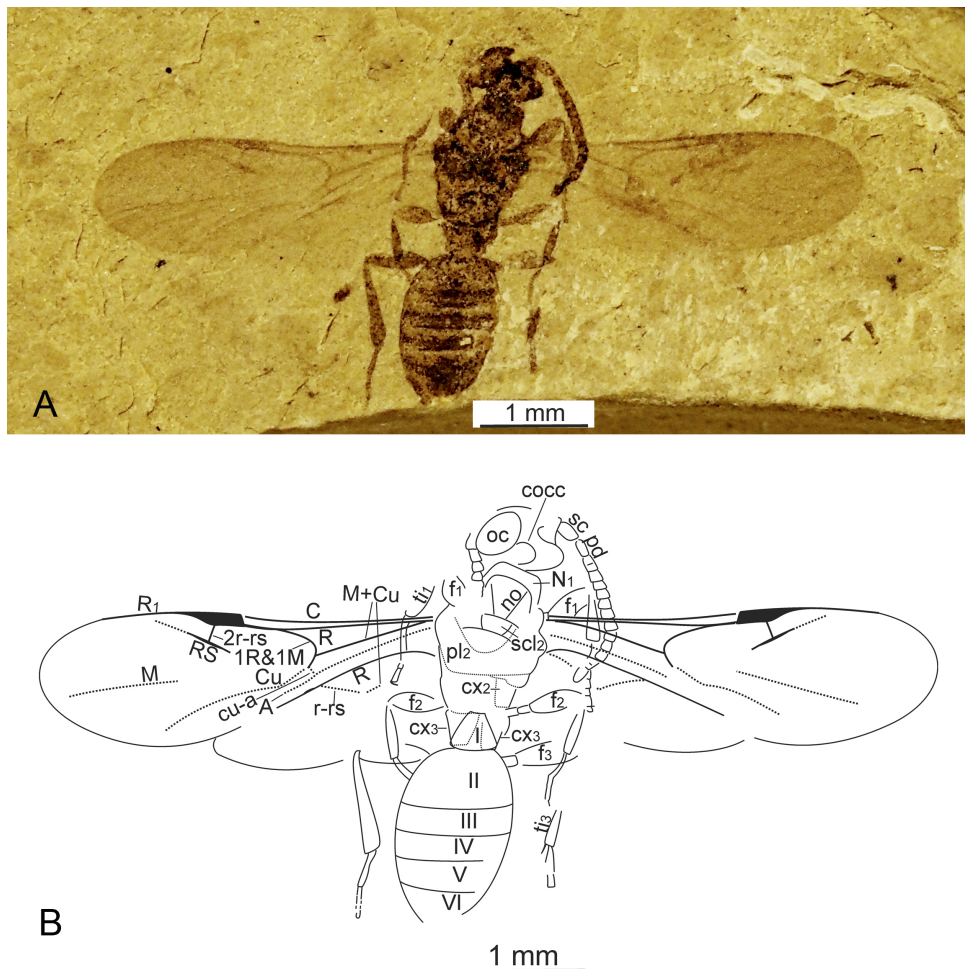


FIGURE 5. *Cretacoformica explicata* Jell & Duncan, 1986, holotype, general view; mid-Lower Cretaceous, Koonwarra fossil site, Victoria, Australia (from Rasnitsyn & Öhm-Kühnle, 2019, by permission). **A**, Upper view. **B**, Interpretation. Symbols: cocc, occipital carina, cx₂, cx₃, mid and hindcoxa, f₁, f₂, f₃, fore, mid and hind femur, N₁, pronotum, no. notaulus, oc, eye, pd, pedicel, pl₂, mesoventropleuron, sc, scape, scl₂, mesoscutellum, ti₁, ti₃, fore and hind tibia, I–VI, metasomal tergites; forewing: 1RS&1M, basal vein (aligned first sections of RS and M), other venational symbols are standard.

other Microprocta). This contradictory combination of characters suggests two alternative models based either on short vs. long scape (Jurapriidae + Trupochalcididae) + (Platygastridae + Diaprioidea + Chalcidoidea + Bipetiolarida + Chalscelionidae), or number of petiolar segments (Platygastridae + Jurapriidae + Chalscelionidae) + (Diaprioidea, Chalcidoidea and Trupochalcididae) + Bipetiolarida. Both models are possible but neither is convincing, because these character states (with the only exception for double petiolar segments) are known to appear independently within Proctotrupoidea as well (petiolar segment in Roproniidae, Heloridae, Austroniidae, Monomachidae and Cynipoidea, long scape in Monomachidae and Maamingidae) and still more often in taxa other than Proctotrupoidea. Equally, we are aware of no other reliable characters to support (or disprove) the above taxonomic structure of Microprocta. The taxonomic positions of the unplaced families

Jurapriidae, Chalscelionidae, and Trupochalcididae cannot be identified with certainty. Jurapriidae and Trupochalcididae could easily be joined in one superfamily based on short scape but this character are putatively plesiomorphic (characteristic of all Symphyta, a vast majority of non-proctotrupoidean Apocrita as well as in otherwise less advanced Proctotrupoidea (Mesoserphidae, Proctotrupoidea, Pelecinidae). To include Jurapriidae in Platygastridae based on a non-petiolar metasoma and Trupochalcididae in Diaprioidea based on a one-segmented petiole would result in radical impoverishing of diagnoses of both superfamilies: up to a single and weak (prone to multiple homoplastic origins) apomorphy, the one-segmented petiole in the case of Diaprioidea, and up to the absence of any apomorphy in the case of Platygastridae. In the case of Chalscelionidae, it can be ascribed neither to Platygastridae because of its supposedly unique chalcid-like pronotum, nor to

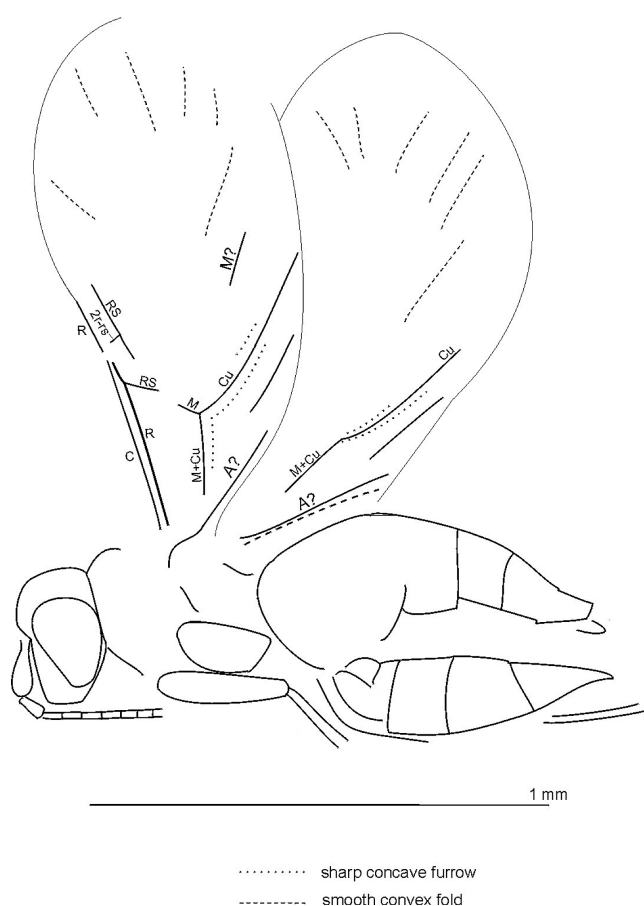


FIGURE 6. *Khutelchalcis gobiensis* Rasnitsyn, Basibuyuk & Quicke, 2004, holotype, general view; Lower Cretaceous, Khutel-Khara fossil site, East Gobi Aymag, Mongolia (modified from Rasnitsyn & Brothers, 2007, by permission from the KwaZulu-Natal Museum Council).

Chalcidoidea because of the absence of petiolar segments and presence of tightly closed metasomal apex. The last alternative, a creation of three monotypic superfamilies is still less appropriate because of the by far too incomplete knowledge of the three families. Therefore, leaving them unplaced is the best choice for now.

Superfamily Chalcidoidea Spinola, 1811

Type family. Chalcididae Spinola, 1811.

Diagnosis. Antenna attached distant from clypeus, geniculate, with long scape and flagellum of 12 segments or less, with at least some segments bearing multiporous plate sensilla. Fore mesosomal spiracle at dorsal (not posterior) pronotal margin, pronotum not reaching tegula. Metasoma with first segment forming ring- or tube-like petiole (sometimes small and not visible externally), with apical external tergum and sternum not completely fitting and so metasomal apex not tightly closed, with genitalia normally visible externally. Position of antennal attachment is of unknown phylogenetic

meaning because of its variability in other Apocrita (apomorphic in comparison with Symphyta). Character states of metasomal apex and genitalia are putatively plesiomorphic (agreeing with those in majority of other Proctotrupoidea and of Hymenoptera in general. Other character states are putatively apomorphic because of their absence in a vast majority of non-proctotrupoidean Hymenoptera and of many Proctotrupoidea.

Families included. Twenty-three families listed by Aguiar *et al.* (2013), plus the extinct Diversinitidae (Haas *et al.*, 2018). Distribution worldwide from the earliest Cretaceous (Rasnitsyn *et al.*, 2004) up to the present. Ecto- and endo-parasites of various Arthropoda, sometimes phytophagous (mainly frugivorous).

Superfamily Diaprioidea Haliday, 1833

Type family. Diapriidae Haliday, 1833.

Diagnosis. Antenna attached far above clypeus (usually on a distinct shelf), with long scape and flagellum of 13 segments or less, with no multiporous plate sensilla. Fore mesosomal spiracle under posterior (not at dorsal) pronotal margin, pronotum reaching tegula. Metasoma with one distinct petiolar segment, with apical external tergum and sternum fitting and closing metasomal apex tightly, with genitalia normally not visible externally. Phylogenetic interpretation of position of antennal attachment is not clear (as above). Long scape, oligomeric antenna, presence of specialized petiolar segment and metasomal apex tightly closed at rest are putatively apomorphic being uncommon in other Proctotrupoidea and rare in other Hymenoptera, particularly in Symphyta. Other character states are putatively plesiomorphic being widespread in other Proctotrupoidea and Hymenoptera in general.

Families included. Diapriidae Haliday, 1833, Ismaridae Thomson, 1858, Spathiopterigidae Engel & Ortega-Blanco, 2013 (possibly including *Cretapria* Fujiyama, 1994). Distribution worldwide, possibly since earliest Cretaceous (Rasnitsyn *et al.*, 1998), certainly since later Early Cretaceous (Engel *et al.*, 2013). Endoparasites predominantly of Diptera (Diapriidae) or hyperparasites of Dryinidae (Hymenoptera) on Homoptera (Ismaridae).

Remarks. Monomachidae Szépligeti, 1889 and Maamingidae Early *et al.*, 2001 are excluded from Diaprioidea based on 1cu-a either complete or rudimentary, retained at or near the apex of M+Cu (Early *et al.*, 2001: fig. 1; Johnson & Musetti, 2012: figs. 7, 13).

Superfamily Platygastroidea Haliday, 1833

Type family. Platygastriidae Haliday, 1833.

Diagnosis. Antenna attached close to clypeus, with long scape and flagellum of 13 segments or less, with



FIGURE 7. *Ismarus dorsiger* Haliday, 1831, fore wing (orig. photo by Victor Kolyada).

no multiporous plate sensilla. Fore mesosomal spiracle under posterior (not at dorsal) pronotal margin, pronotum reaching tegula. Metasoma with no petiolar segment, with apical external tergum and sternum fitting and closing metasomal apex tightly, with genitalia normally not visible externally. Phylogenetic interpretation of the above character states is similar to that in Diaprioidea except that the absence of specialized petiolar segment is putatively plesiomorphic because this character state is characteristic of the vast majority of Hymenoptera including all Symphyta and also known in Proctotrupomorpha (Mesoserphidae, Proctotrupidae, Pelecinidae).

Families included (according to Talamas *et al.*, 2019). Platygastriidae Haliday, 1833, Scelionidae Haliday, 1839, Nixonidae Masner, 1976, and Proterosceliopsidae Talamas *et al.*, 2019, distributed worldwide since earliest Cretaceous (Rasnitsyn *et al.*, 2004) until today. Endoparasites (mainly on Diptera) or egg parasites of various arthropods.

Informal group (clade) Bipetiolarida Engel, 2005

Diagnosis. Antenna attached more or less distant above clypeus, with long scape and flagellum of 12 segments or (usually) less, with no multiporous plate sensilla. Fore mesosomal spiracle under posterior (not at dorsal) pronotal margin, pronotum variable in reaching tegula. Metasoma with two distinct petiolar segments, with apical external tergum and sternum not completely fitting and so not closing metasomal apex tightly, with genitalia normally visible externally. Phylogenetically the position of antennal attachment is equivocal, scape long and antenna oligomeric are putatively apomorphic, and pronotum reaching tegula is putatively plesiomorphic for the same reasons as in Diaprioidea, and metasomal apex not tightly closed at rest is putatively plesiomorphic for the same

reason as in Chalcidoidea. The double petiolar segments of Bipetiolarida is putatively apomorphic because it is unknown in any other Hymenoptera.

Superfamilies included. Serphitoidea Brues, 1937 (with families Serphitidae Brues, 1937 and Archaeoserphitidae Engel, 2016) and Mymarommatoidea Debauche, 1948 (with families Mymarommatidae Debauche, 1948, Gallorommatidae Gibson *et al.*, 2007, Alavarommatidae Ortega-Blanco *et al.*, 2011, and Dipterommatidae Rasnitsyn *et al.*, 2019). Mainly Cretaceous (known since Barremian, early-mid Cretaceous), abundant through Cretaceous starting from Barremian, widespread geographically but rare in species and family count in Cenozoic (until today) where only Mymarommatidae are found. Biology unknown, but egg-parasitism could be hypothesized because of always small body size.

Superfamily incertae sedis

Family Jurapriidae Rasnitsyn, 1983

Type genus. *Jurapria* Rasnitsyn, 1983.

Diagnosis. Antenna with short scape and flagellum of 13 segments, with no visible multiporous plate sensilla, place of antennal attachment on head capsule not clear. Metasoma with no petiolar segments, with apical external tergum and sternum apparently not completely fitting and metasomal apex not closed tightly, with genitalia normally visible externally. The short scape is putatively plesiomorphic because it is characteristic of the majority of Hymenoptera including all Symphyta and many Proctotrupomorpha (Mesoserphidae, Proctotrupidae, Pelecinidae, Heloridae, Roproniidae, Austroniidae). A 13-segmented flagellum is a maximum number and putatively plesiomorphic character state within Microprocta and putatively apomorphic in wider context. Indeed, a majority of Mesozoic non-aculeate Apocrita including many Cretaceous and particularly Jurassic Proctotrupomorpha (Mesoserphidae, Pelecinidae, Heloridae, Roproniidae; cf. Rasnitsyn, 1980, 1990a) have polymerous flagellum (more than 14-segmented). Metasoma with no specialized petiolar segment and with apex not tightly closed at rest are putatively plesiomorphic for the reasons discussed above (the cases of Platygastroidea and Chalcidoidea, respectively).

Genera included. Type only. Late Jurassic and, undescribed, earliest Cretaceous of Transbaikalia.

Remarks. Originally Jurapriidae have been placed in Diaprioidea, which however have been treated in a too wide a manner at that time (Rasnitsyn, 1983).

Chalscalio Rasnitsyn & Brothers, 2007 was originally described in Jurapriidae, but it differs in many aspects from that family, which is why we place it in a family of its own (see below).

As explained above, Jurapriidae can be placed in no existing superfamily. Creating an own superfamily in order to house Jurapriidae is not reasonable as well yet, because of the still insufficient knowledge of the family.

Family Trupochalcididae Kozlov in Rasnitsyn, 1975

Type genus. *Trupochalcis* Kozlov in Rasnitsyn, 1975.

= Cretacoformicidae Rasnitsyn & Öhm-Kühnle, 2019, **syn. nov.**

Type genus, *Cretacoformica* Jell & Duncan, 1986.

Diagnosis. Antenna attached distinctly above clypeus, with scape short and flagellum of 13 segments, with no multiporous plate sensilla. Fore mesosomal spiracle probably under posterior (not at dorsal) pronotal margin, pronotum reaching tegula. Metasoma with one distinct petiolar segment, with apical external tergum and sternum not completely fitting and so metasomal apex not fully closing, with genitalia visible externally. The phylogenetic interpretation of the above diagnostic characters is essentially the same as in case of above taxa and for the same reasons: antennal attachment is equivocal, short scape, absence of multiporous plates, pronotum reaching tegula and with spiracle under its posterior margin, metasomal apex open at rest and so not concealing genitalia are putatively plesiomorphic, flagellum 13-segmented is putatively apomorphic for Hymenoptera but a ground plan character state within Microprocta, and the first metasomal segment modified into petiole is the only putative synapomorphy of the family.

Genera included. Two above-listed type genera. Possibly widespread in the Cretaceous but insufficiently known (recorded from Aptian (early-mid) Cretaceous of Australia, 'mid'-Cretaceous of Burmese amber and Santonian (mid-late) Cretaceous of North Siberia; Kozlov, 1975; Zhang *et al.*, 2018, Rasnitsyn & Öhm-Kühnle, 2019). Unknown in the Cenozoic.

Remarks. Trupochalcididae have been described as a member of Proctotrupoidea and placed next to Austroniidae (Kozlov, 1975) to which it later was attributed (Rasnitsyn, 1980). Now this placement looks erroneous because of a different wing venation (Cu straight and 1cu-a at the base of basal vein in *Austronia* Riek, 1955) and no other apparent synapomorphies. As Jurapriidae, Trupochalcididae can neither be included in any existing superfamily nor it is worth to create a superfamily of its own because of the still insufficient knowledge of the family. That is why there is no reasonable choice other than to leave the family unplaced, but still included in the clade Microprocta.

Description of Cretacoformicidae (Rasnitsyn & Öhm-Kühnle, 2019) was incorrect. *Cretacoformica* originally was described as an ant (Jell & Duncan, 1986) and later

transferred to Diapriidae (Rasnitsyn, 1990a) which was subsequently questioned by Naumann (1993) who however was not able to identify a proper taxonomic position of the genus. Rasnitsyn & Öhm-Kühnle (2019) agreed that *Cretacoformica* did not fit diagnosis of Diapriidae and proposed a new family unplaced within Proctotrupomorpha. They refer to similarities of *Cretacoformica* to Diapriidae, Serphitidae, Khutelchalcididae, and Jurapriidae, and missed a closer similarity to Trupochalcididae. Rasnitsyn & Öhm-Kühnle (2019) included *Iberopria* Engel *et al.*, 2013 in Cretacoformicidae. However, the latter genus displays an antenna attached to a distinct shelf and with characteristically elongate scape and so has to be left in Diaprioidea (see above).

Family Chalscelionidae Rasnitsyn & Öhm-Kühnle, fam. nov.

Type genus. *Chalscelio* Rasnitsyn & Brothers, 2007.

Diagnosis. Antenna with attachment place obscure except that not on a shelf, with long scape and with number of flagellar segments possibly more than 11, with clava and apparently bent twice (like in females of many Platygastroidea). Pronotum long centrally and short laterally, not reaching tegula. Metasoma with no petiolar segment, with apical tergum and sternum fitting to close metasomal apex tightly, with genitalia not visible externally. Phylogenetically long scape is putatively apomorphic for the same reason as in case of Chalcidoidea, Diaprioidea and Platygastroidea, pronotum not reaching tegula the same as in case of Chalcidoidea, and closed metasomal apex as in case of Platygastroidea. Female antenna with distinct clava and with double bend so as clava directed upward is putatively apomorphic because it is a comparatively rare character state known mainly in Platygastroidea. Clavate antenna *per se* appears more often in various Hymenoptera but is not characteristic of Symphyta (except some advanced Tenthredinoidea such as Cymbicidae and some Pergidae) and lower Apocrita. Metasoma lacking specialized petiolar segment is putatively plesiomorphic being characteristic of all Symphyta and majority of Apocrita including some Proctotrupomorpha (Mesoserphidae, Proctotrupidae, Pelecimidae, Platygastroidea).

Genera included. Type only, known from Turonian (earlier Late Cretaceous) of Botswana, S. Africa.

Remarks. The genus *Chalscelio* originally has been described (Rasnitsyn & Brothers, 2007) in the family Jurapriidae, based on venational features (which are now considered to be ground plan characters of Microprocta) and in appreciation of its similarities to both Platygastroidea (in structure of antenna and metasoma) and Chalcidoidea (in the form of their pronotum). These two superfamilies show no putative synapomorphies and

so hardly can be hypothesized as forming a monophylum. This does not permit to refer to *Chalscelio* as a member of any of them or as representing their stem group. Equally, the genus does not fit the refined diagnosis of Jurapriidae. As a result, it can be only treated as a member of an unplaced family of its own, however part of the clade Microprocta, at least until more information is available about this unusual insect.

Conclusion

The revision of the infraorder Proctotrupomorpha results in the understanding that a number of its most advanced families form a clade whose members display a syndrome of venational synapomorphies concerning predominately the (M+)Cu system and adjacent crossveins. Named Microprocta, **taxon nov.**, this clade encompasses four main subclades, namely the superfamilies Chalcidoidea, Platygastroidea, and Diaprioidea, the clade Bipetiolarida (with superfamilies Serphitoidea and Mymarommatoidea), as well as three otherwise unplaced families Jurapriidae, Trupochalcididae, and Chalscelionidae. A more detailed internal structure of Microprocta is certainly a subject for further study, but at the moment it still is possible to note that, among the existing phylogenetic hypotheses listed in the introduction, one (the intuitive one by Rasnitsyn, 2002) agrees well with the clade structure as described herein.

Additionally, it can be noticed that through time the known fossil record of Microprocta as described (not using that word) by Rasnitsyn (1980, 2002; Rasnitsyn & Brothers, 2007; Rasnitsyn *et al.*, 2018; Zhang *et al.*, 2018; Rasnitsyn *et al.*, 2019; Rasnitsyn & Öhm-Kühnle, 2019, 2020) starts with the appearance of Jurapriidae at the end of the Jurassic and continues during the Cretaceous explosion, showing rapid diversification of Platygastroidea and Bipetiolarida. The groups then suffered subsequent decrease (almost up to extinction in the case of Bipetiolarida) since the beginning of Cenozoic. In contrast, the fossil record of Chalcidoidea and Diaprioidea (by the above sources and Rasnitsyn *et al.*, 2004) apparently displays their slow start during the Cretaceous and then a strong Cenozoic diversification. Unlike these, there are several still unplaced and enigmatic families, which as well are witnesses of the dawn of Microprocta.

Acknowledgements

We offer our sincere gratitude to the reviewers for their valuable comments. We appreciate with thanks permission by Mr. Viktor A. Kolyada to publish his photograph. For

APR, this research was supported by the program of the Presidium of the Russian Academy of Sciences “Problems of the Origin of Life and Formation of the Biosphere”.

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