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Geometric morphometric analysis of Ichneumonidae (Hymenoptera: Apocrita) with two new Mesozoic taxa from Myanmar and China

Longfeng Li^{a*}, Peter J. M. Shih^{b,c}, Dmitry S. Kopylov^{d,e*}, Daqing Li^a and Dong Ren^{c*}

^aInstitute of Vertebrate Paleontology, College of Life Science and Technology, Gansu Agricultural University, Lanzhou City 730070, Gansu Province, PR China; ^bAcademy for Allied Health Sciences, 1776 Raritan Road, Scotch Plains, NJ 07076, USA;

^cCollege of Life Sciences, Capital Normal University, 105 Xisanhuanbeilu, Haidian District, Beijing 100048, PR China;

^dPaleontological Institute, Russian Academy of Sciences, Profsoyuznaya street, 123, Moscow 117997, Russia; ^eCherepovets State University, Lunacharskogo 5, Cherepovets, Vologda Region, 162600 Russia

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A new genus and species of Labenopimplinae (Ichneumonidae), *Heteropimpla megista* Li, Shih, Kopylov & Ren gen. et sp. nov., is erected based on a specimen in mid-Cretaceous Myanmar (Burmese) amber. A key to genera of Labenopimplinae is provided. In addition, a new species, *Amplicella abbreviata* Li, Shih, Kopylov & Ren (Tanychorinae) from the Lower Cretaceous Yixian Formation is described. Geometric morphometric analysis (GMA) was applied to study forewing venation of 24 Cretaceous species of Ichneumonidae and the results are presented for the first time. The GMA results not only confirm the taxonomic position of new taxa and relationships among these genera consistent with subfamily classifications, but also clarify the methodological differences between classical taxonomy and the GMA.

<http://zoobank.org/urn:lsid:zoobank.org:pub:DC98459D-45C1-4B78-B59E-F32787B787F1>

Keywords: new taxa; taxonomy; amber; parasitoid; Yixian Formation

Introduction

Ichneumonidae is one of the most diverse hymenopteran families in many modern ecosystems, comprising approximately 60,000 extant species, and is distributed around the globe (Gauld & Bolton 1988; Wahl & Sharkey 1993; Huber 2009; Engel & Krombein 2012; Yu *et al.* 2012). Members of Ichneumonidae are parasitoids of Lepidoptera, Hymenoptera, Diptera, Coleoptera and, rarely, of spiders and other arthropod groups (Townes 1969). The first findings of fossil ichneumonids came from Lower Cretaceous (Neocomian) deposits (Khasurty in Transbaikalia, Russia and the Yixian Formation in Liaoning Province, China). In the Cretaceous, ichneumonids were neither diverse nor abundant. Hitherto, 59 species belonging to 26 genera of Mesozoic Ichneumonidae have been reported (Li *et al.* 2017a; Kopylov *et al.* 2018; this study) and classified into five subfamilies: Tanychorinae Rasnitsyn, 1980, Labeninae Ashmead, 1900, Palaeoichneumoninae Kopylov, 2009, Labenopimplinae Kopylov, 2010b and Novichneumoninae Li, Kopylov, Shih & Ren, 2017 (Townes 1973a, b; Rasnitsyn 1975, 1980; Zhang 1991; Zhang & Rasnitsyn 2003; Kopylov 2009, 2010a,b;

2011, 2012a, 2012b; Kopylov *et al.* 2010; McKellar *et al.* 2013; Kopylov & Zhang 2014; Li *et al.* 2017a).

Cretaceous ichneumonids are rather well studied: most of the known collections have been described, with just a few undescribed species to be documented from Bon-Tsagaan and Taimyr amber (in the Paleontological Institute, Moscow) and Burmese amber (in the Nanjing Institute of Geology and Paleontology). Conversely, Cenozoic ichneumonids are very diverse and numerous, but much less well studied. More than 200 species are known from the Cenozoic and many more remain undescribed (Kopylov *et al.* 2018). As mentioned in the literature, fossil ichneumonids can be placed in families with certainty based on their unique forewing venation, but it is very difficult to assign them to extant subfamilies and genera (Spasojevic *et al.* 2018). Three main reasons for this have been suggested: 1) living ichneumonids are very diverse, with more than 1500 genera in 45 subfamilies currently recognized (Yu *et al.* 2012); 2) ichneumonid morphology has extensive host-related homoplasy, so that similar character states usually appear separately in different parts of the phylogeny, and many key characters are not preserved in the process of fossilization (Gauld & Mound 1982); and 3)

*Corresponding authors. Emails: fenger4499@163.com (L.F. Li); rendong@cnu.edu.cn (D. Ren); aeschna@yandex.ru (D.S. Kopylov)

to date, no complete phylogeny of Ichneumonidae has been available to shed light on the age of the groups and to help distinguish crown- and stem-group representatives (Spasojevic *et al.* 2018). Therefore, it is necessary to consider all of the evidence and acknowledge uncertainty when taxonomic studies on fossil ichneumonids are carried out.

In this report, we describe two new ichneumonids: *Heteropimpla megistus* Li, Shih, Kopylov & Ren from mid-Cretaceous Myanmar (Burmese) amber and *Amplipicella abbreviata* Li, Shih, Kopylov & Ren from the Lower Cretaceous Yixian Formation of north-eastern China. In recent years, many well-preserved hymenopteran fossils have been reported from Myanmar amber, including Evanioidea (Li *et al.* 2015, 2018; Shih *et al.* 2019), Peleciniidae (Guo *et al.* 2016), Stephanoidea (Li *et al.* 2017b), Ichneumonidae (Li *et al.* 2017a), Myanmarinidae (Li *et al.* 2018; Zhang *et al.* 2018a) and Panguidae (Li *et al.* 2019). More specifically, Zhang *et al.* (2018b) reviewed the hymenopteran records from mid-Cretaceous Burmese amber in the collections of the Nanjing Institute of Geology and Paleontology. The Myanmar amber deposit is located in Kachin (Hukawng Valley), northern Myanmar, approximately 100 km south-west of the village of Tanai (Li *et al.* 2018), and an earliest Cenomanian age (98.79 ± 0.62 Ma) has recently been established for this material (Cruikshank & Ko 2003; Shi *et al.* 2012). The Yixian Formation is an important source for the Jehol entomofauna of north-eastern China and is considered to be Lower Cretaceous in age (late Barremian–earliest Aptian), with an absolute age estimate of approximately 125 Ma based on $^{40}\text{Ar}/^{39}\text{Ar}$ and SHRIMP $^{206}\text{Pb}/^{238}\text{U}$ dating (Wang *et al.* 2005; Walker *et al.* 2013; Li *et al.* 2018; Ren *et al.* 2019).

Materials and methods

The fossil specimens described herein are housed in the Key Laboratory of Insect Evolution and Environmental Changes, in the College of Life Sciences, Capital Normal University, Beijing, China (CNUB). The specimens were examined and photographed under a Nikon SMZ 25 dissecting microscope with an attached Nikon DS-Ri2 digital camera system. The figures were drawn using CorelDraw v. 12.0 and Adobe Photoshop CS5. The venational terminologies used here are based on Rasnitsyn (1969, 1980), with the addition of abscissa number in front of vein names.

Geometric morphometric analysis (GMA) has been applied widely to the studies of phenetic relationships (without consideration of evolutionary relationships)

among extant and fossil insects and/or their associations with plants (Perrard *et al.* 2012; Bai *et al.* 2013; Lin *et al.* 2016; Shih *et al.* 2017, 2019). Adobe Photoshop CS5 was used to re-draw the wings and venation of the ichneumonid specimens used in the GMA, based on new photos or previously published figures. The JPEG images were then exported to tps-UTILS (Rohlf 2006a) and converted into TPS files. Using tps-DIG (Rohlf 2006b) we selected 19 landmarks for 24 ichneumonid forewings representing key points on the wing veins (Fig. 1). The positions of the landmarks were used as data inputs for tps-SPLIN (Rohlf 2004) and a global least squares (GLS) reference was calculated. The program generated a table containing the Procrustes distances of all 24 specimens in relation to each other (Supplementary material, Table S1). These data were then analysed using the NTSYSp package (Rohlf 2007) with the unweighted pair-group method using the arithmetic averages (UPGMA) to create a tree showing the phenetic relationships among these specimens.

In GMA, landmarks are selected to identify wing shape, important veins and the positions of key venational points, such as the relative positions and shapes of the veins, branching points and/or cells. For a set of GMA, all specimens must have the same number of landmark points defining the same positions. The application of GMA in this study has revealed its effectiveness but also some drawbacks. One pitfall of this methodology is that absent landmarks for a specimen are not allowed, in contrast to using the ‘unknown’ or ‘unavailable’ conditions for missing character states in a phylogenetic analysis. For this study, we did not select landmarks on the intersections of the Rs, M, Cu and A with the wing margin and 1cu-a and 2cu-a intersecting with vein A, because some fossil forewings do not have these veins well preserved. Since it is quite common for fossil specimens to miss some of the preserved parts that are essential for determining landmarks, to proceed with the GMA we might need to assume landmark positions based on inferences from other related or similar fossils (Shih *et al.* 2017). In some cases we also needed to use assumptive landmarks for evolutionarily lost venation features: e.g. point 18 (M and 1m-cu junction, when 1-Rs + M is completely lost and 1m-cu & 2Rs + M have no bend), points 19 and 11 (r-m junctions with Rs and M, when r-m is lost). The assumptions incorporated into our analyses are clearly marked using dotted lines on the wing outlines, as shown in Figure 1.

For the GMA, all landmarks chosen were considered to be of equal weight, in contrast to the option of using weighting factors for individual characters in phylogenetic analyses. To accommodate for this issue,

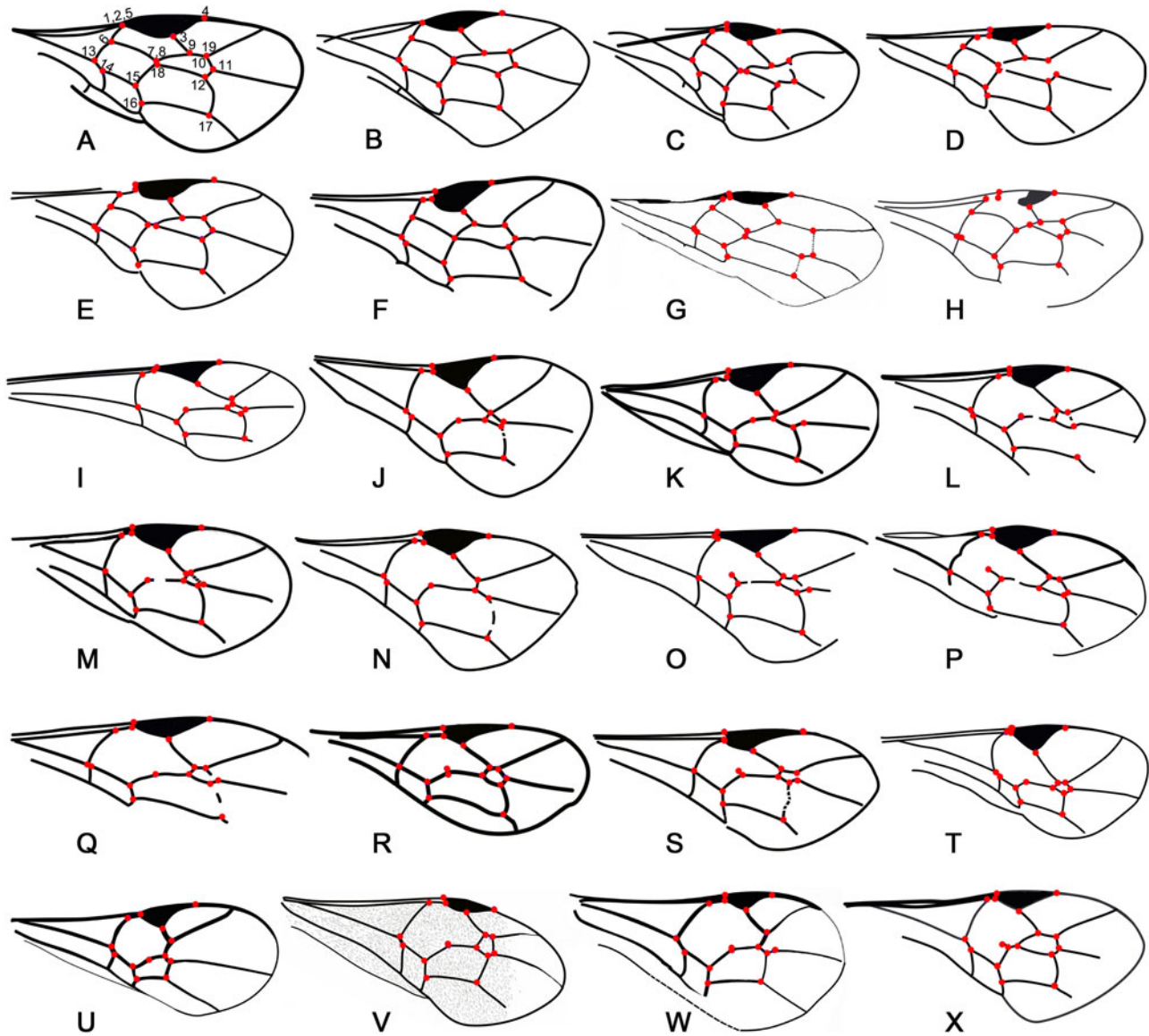


Figure 1. Landmark positions of the 24 forewing samples of Ichneumonidae: **A**, *Amplicella beipiaoensis*; **B**, *Amplicella abbreviate* sp. nov.; **C**, *Sinchora distorta*; **D**, *Khasurtella buriatica*; **E**, *Tanychora petiolate*; **F**, *Megachora sibirica*; **G**, *Cretobraconus mongolensis*; **H**, *Paratanychora mongoliensis*; **I**, *Agapteron popovi*; **J**, *Agapia sukatcherae*; **K**, *Urotryphon baikurensis*; **L**, *Dischysma maculate*; **M**, *Rugopimpla vulgaris*; **N**, *Tryphopimpla xoidoptera*; **O**, *Ramulimonstrum intermedium*; **P**, *Rudimentifera mora*; **Q**, *Micropimpla lucida*; **R**, *Palaeoichneumon freja*; **S**, *Labenopimpla orapa*; **T**, *Catachora minor*; **U**, *Caloichneumon perrarus*; **V**, *Heteropimpla megista* gen. et sp. nov.; **W**, *Novichneumon longus*; **X**, *Tanychorella dubia*.

we might select more landmarks in areas deemed to host ‘important’ characters. Conversely, if judged as ‘not important’ (e.g. features that typically show intraspecific variation), we may not select any landmarks for that area. One advantage of GMA is that this methodology can handle landmarks on a continuum basis, in contrast to the discrete character states in phylogenetic analyses. Furthermore, GMA takes an overarching approach to make comparisons based on all landmarks, e.g. by calculating the ‘Procrustes distance’ (i.e. the square root of the sum of all squares of the

distances between sample landmarks versus references in all axes) for each specimen (Shih *et al.* 2017).

Systematic palaeontology

Family **Ichneumonidae** Latreille, 1802
Subfamily **Labenopimplinae** Kopylov, 2010b

Type genus. *Labenopimpla* Kopylov, 2010b (by original designation).

Composition. *Catachora* Townes, 1973a, *Eubaeus* Townes, 1973a, *Urotryphon* Townes, 1973a, *Armanopimpla* Kopylov, 2010b, *Labenopimpla* Kopylov, 2010b, *Micropimpla* Kopylov, 2010b, *Ramulimonstrum* Kopylov, 2010b, *Rugopimpla* Kopylov, 2010b, *Agapia* Kopylov, 2012b, *Agapteron* Kopylov, 2012b, *Heteropimpla* gen. nov.

Genus *Heteropimpla* Li, Shih, Kopylov & Ren
gen. nov.

Etymology. The generic name is a combination of the Greek ‘hetero-’ meaning different and the genus name *Pimpla* Fabricius, 1804. Gender feminine.

Type species. *Heteropimpla megista* sp. nov.

Diagnosis. Mesonotum with notauli converging, forming a fan-shape, longitudinal sculpture absent. Forewing with areolet pentagonal, almost as long as wide, 2-Rs and 2 + 3-M nearly equal in length, and with nearly 90° angle between them, 2-Rs longer than 3-Rs, 2 + 3-M distinctly longer than 4-M, r-m subvertical; 1-Rs&1-M issuing from C + Sc + R with distinct distance to pterostigma base; ramulus present; 1cu-a strongly postfurcal, 1-Cu about 1/3 length of cu-a; 3-Cu slightly longer than 2cu-a. Hind wing with 1-Rs distinctly shorter than r-m, 1-Cu and cu-a nearly equal in length, free endings of Rs, M, Cu and A reaching wing margin. Propodeum with strong longitudinal and minority transverse carinae. Ovipositor short, slightly protrudes beyond metasomal apex, ovipositor tip serrated.

Composition. Type species only.

Remarks. The new genus differs from other genera of the subfamily in its forewing with broad pentagonal areolet with 2-Rs and 2 + 3-M nearly equal in length and subvertical r-m (*Labenopimpla* and *Armanopimpla* also have broad areolet with subvertical r-m and *Armanopimpla* has 2-Rs and 2 + 3-M nearly equal in length, but in these genera areolet is 1.5–3.0 times as long as wide), 1cu-a strongly displaced distad. More detailed differences among the genera of Labenopimplinae are provided in the key (Appendix 1).

Heteropimpla megista Li, Shih, Kopylov & Ren
sp. nov.
(Figs 2–4)

Etymology. The specific name is derived from the Latin word *megista*, meaning large, referring to the broad areolet with long 2-Rs and 2 + 3-M and r-m.

Diagnosis. As for the genus, by monotypy.

Type material. Holotype, CNU-HYM-MA-2018101, female, well preserved except for the antennae (Fig. 2).

Locality and horizon. Hukawng village, Kachin State, northern Myanmar; mid-Cretaceous, earliest Cenomanian.

Description. Body length 6.6 mm (excluding ovipositor and antennae). Head oval in lateral view with compound eyes large (Fig. 3B), ocelli prominent, forming equilateral triangle in dorsal view (Fig. 3C); antennae with scape slightly wider than pedicel, only several flagellomeres as preserved; chewing mouthparts visible, maxillary palp with four segments and labial palp with four segments preserved (Fig. 3B). Mesosoma 2.5 mm long and 1.7 mm in height, pronotum like a broad triangle in lateral view, and two sides contacting the mesoscutum and mesopleuron, respectively; mesoscutum long and arched in lateral view; mesopleuron a broad irregular rectangle; propodeum sculptured (Fig. 3A). Legs completely preserved, elongate, hind legs distinctly longer and wider than fore and middle legs, tarsi pentamerous. Metasoma 3.4 mm long, with seven metasomal segments; the base of first metasomal segment distinctly narrowed, formed like a short petiole in lateral view, but the apical of first metasomal segment transversally broad in dorsal view; the second and third metasomal segments nearly equal in length, with rough tergites; remaining segments gradually shortened in length, with smooth tergites (Fig. 3D, E). Ovipositor short, exposed to metasoma about 1.2 mm long.

Forewing (4.4 mm long by 1.8 mm wide) with pterostigma 3.6 times as long as wide; 1-Rs & 1-M issuing from the C + Sc + R have a short distance (0.3 mm) to pterostigma base; ramulus short; areolet pentagonal, 2-Rs 1.1 times as long as 2 + 3-M, and with nearly 90° angle between them, 2-Rs 1.9 times as long as 3-Rs, 2 + 3-M 1.9 times as long as 4-M, r-m developed; r-rs issuing from the middle of pterostigma, strongly inclined; 1cu-a strongly postfurcal, 2-Cu 2.5 times as long as 1-Cu; 1cu-a 1.1 times as long as 2-Cu, 3-Cu 1.1 times as long as 2cu-a; 2m-cu 2.5 times as long as r-m, present and well-developed. Hind wing (3.4 mm long by 0.8 mm wide) with 1-Rs 0.5 times as long as r-m; 1-M 2.3 times as long as r-m; M + Cu slightly curved; 1-Cu 1.1 times as long as cu-a, A completely present (Fig. 4).

Subfamily **Tanychorinae** Rasnitsyn, 1980

Type genus. *Tanychora* Townes, 1973b (by original designation).

Composition. *Tanychora* Townes, 1973b, *Tanychorella* Rasnitsyn, 1975, *Paratanychora* Zhang & Rasnitsyn, 2003, *Ampllicella* Kopylov, 2010a, *Megachora* Kopylov,

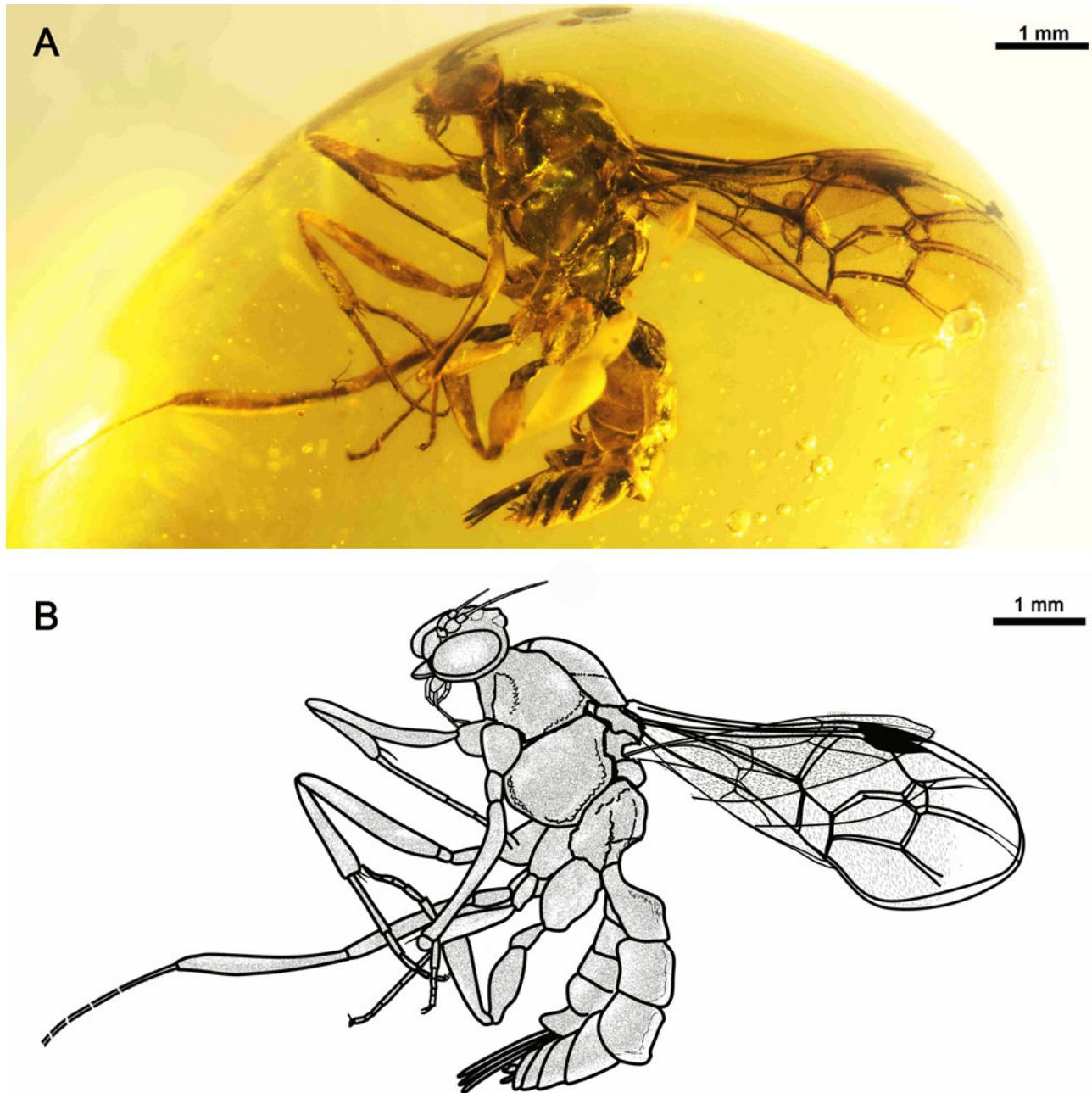


Figure 2. *Heteropimpla megista* gen. et sp. nov. Holotype (CNU-HYM-MA-2018101). **A**, photograph of habitus; **B**, line drawing of whole body.

2010a, *Khasurtella* Kopylov, 2011, *Sinochora* Kopylov & Zhang, 2014.

Genus *Ampllicella* Kopylov, 2010a

Type species. *Ampllicella sessilis* (Townes, 1973b).

Ampllicella abbreviata Li, Shih, Kopylov & Ren
sp. nov.
(Fig. 5)

Etymology. The specific name is derived from the Latin word *abbreviata*, meaning abbreviated, referring to both the forewing and hind wing with r-m abbreviated, shorter than 4-M and 1-Rs.

Diagnosis. Large body size with forewing longer than 6.5 mm. Forewing with 1-Rs shorter than 1-M, 1cu-a distinct postfurcal, 4-M longer than r-m. Hind wing with 1-Rs 2 times as long as r-m.

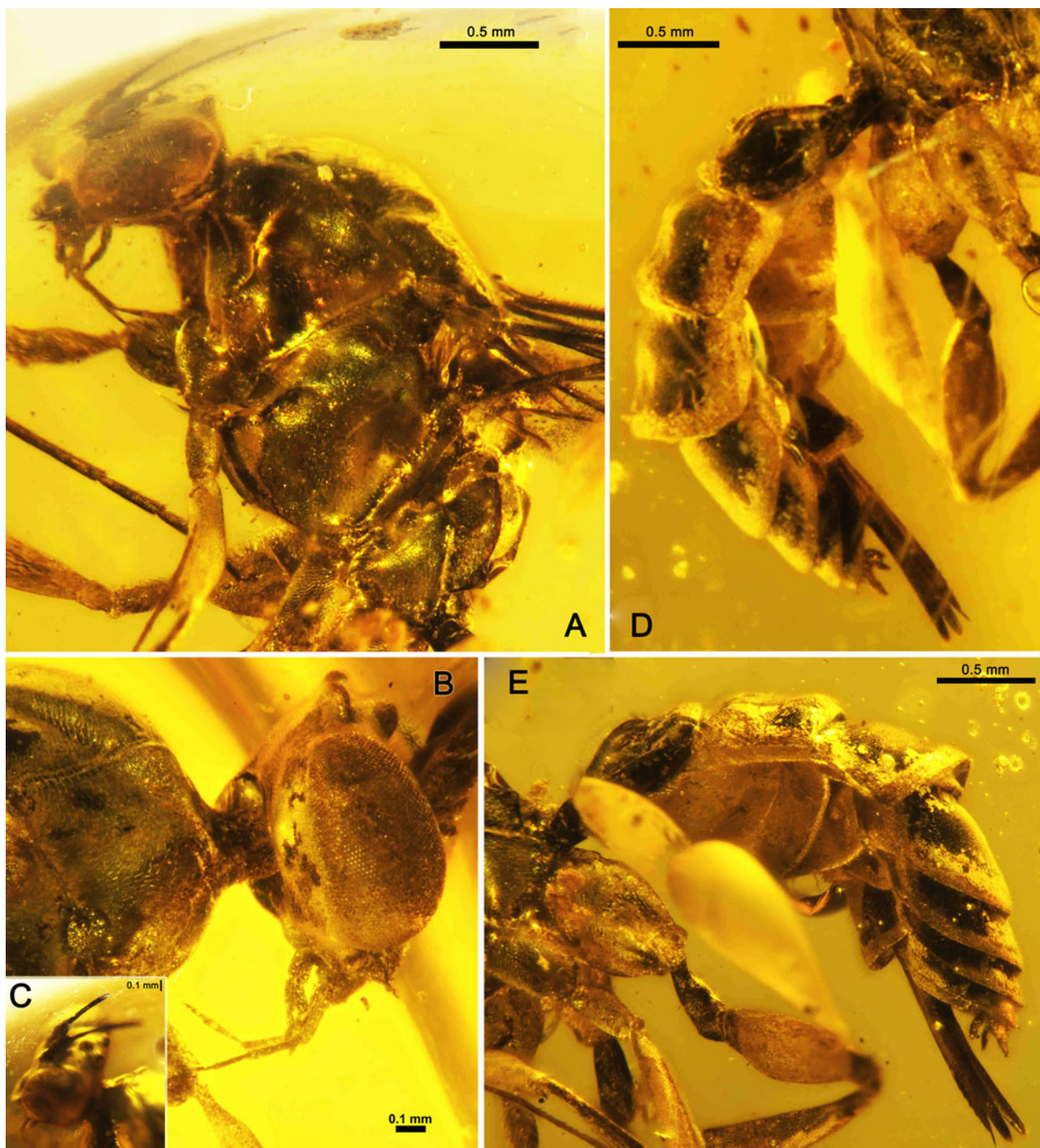


Figure 3. *Heteropimpla megista* gen. et sp. nov. Holotype (CNU-HYM-MA-2018101). **A**, mesosoma; **B**, part of head in lateral view; **C**, part of head in dorsal view; **D**, **E**, metasoma.

Type material. Holotype, CNU-HYM-LB-2018101, female, well preserved except for the mesosoma being compressed badly (Fig. 5).

Locality and horizon. Yixian Formation, Huangbanjigou, Beipiao City, Liaoning Province, China; Lower Cretaceous (Barremian).

Description. Body length 10.3 mm (excluding ovipositor and antennae). Head transversely elongate in lateral view (Fig. 5A), 1.9 mm long by 1.3 mm high. Antenna preserved about 5.6 mm long, with scape broader than pedicle. Mesosoma 3.5 mm long and 1.8 mm high. Legs partly preserved. Metasoma

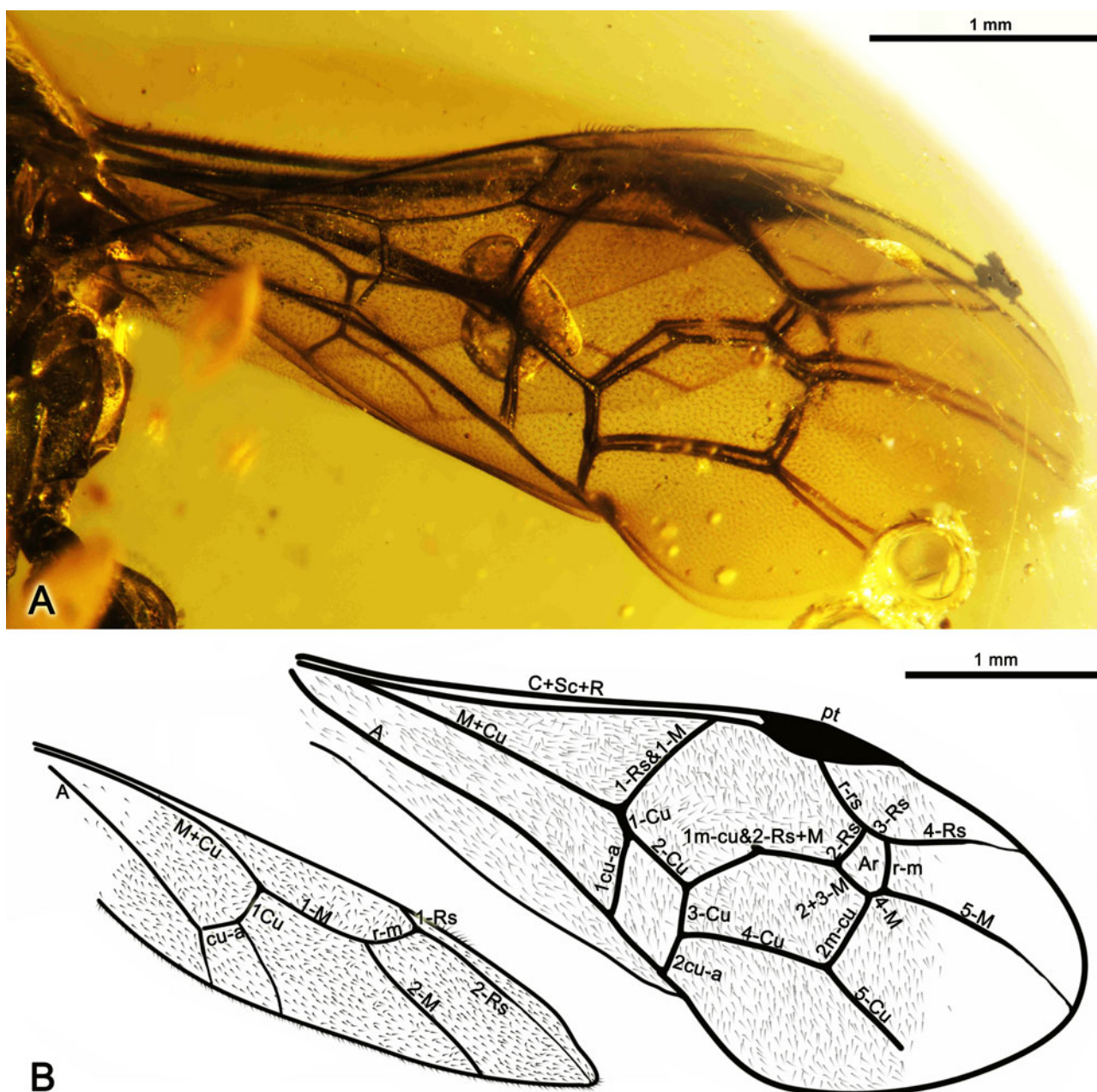


Figure 4. *Heteropimpla megista* gen. et sp. nov. Holotype (CNU-HYM-MA-2018101). **A**, photograph of wings; **B**, line drawing of wings.

5.9 mm long with eight metasomal segments. Ovipositor long, exposed to metasoma about 5.4 mm long.

Forewing (6.6 mm long \times 1.8 mm wide) with pterostigma 1.9 mm long by 0.5 mm wide; 1-Rs issuing from the base of pterostigma and about 0.7 times as long as 1-M; r-rs strongly inclined, issuing beyond the middle of pterostigma, 1.1 times as long as 2-Rs; areolet pentagonal, r-m 0.8 times as long as 4-M and with 90° angle between both of them; 2-Rs and 3-Rs nearly in a straight line and 2-Rs 1.2 times as long as 3-Rs; 3-M

2.5 times as long as 4-M; 1cu-a strongly postfurcal; length of 1-Cu: 2-Cu: 3-Cu: 4-Cu is 0.3: 0.9: 0.4: 1.3; 1m-cu straight, 2m-cu curved; a1-a2 and A present as well. Hind wing with 1-Rs 2.5 times as long as r-m; 1-M 4.5 times as long as r-m.

Remarks. The new species differs from other species of *Amplipella* in having a forewing with **4-M distinctly longer than r-m** (except for *A. townesi* and *A. flagellate*). In *A. abbreviata* the r-rs is longer than 2-Rs, in contrast to *A. townesi* and *A. flagellata* that have r-rs shorter than

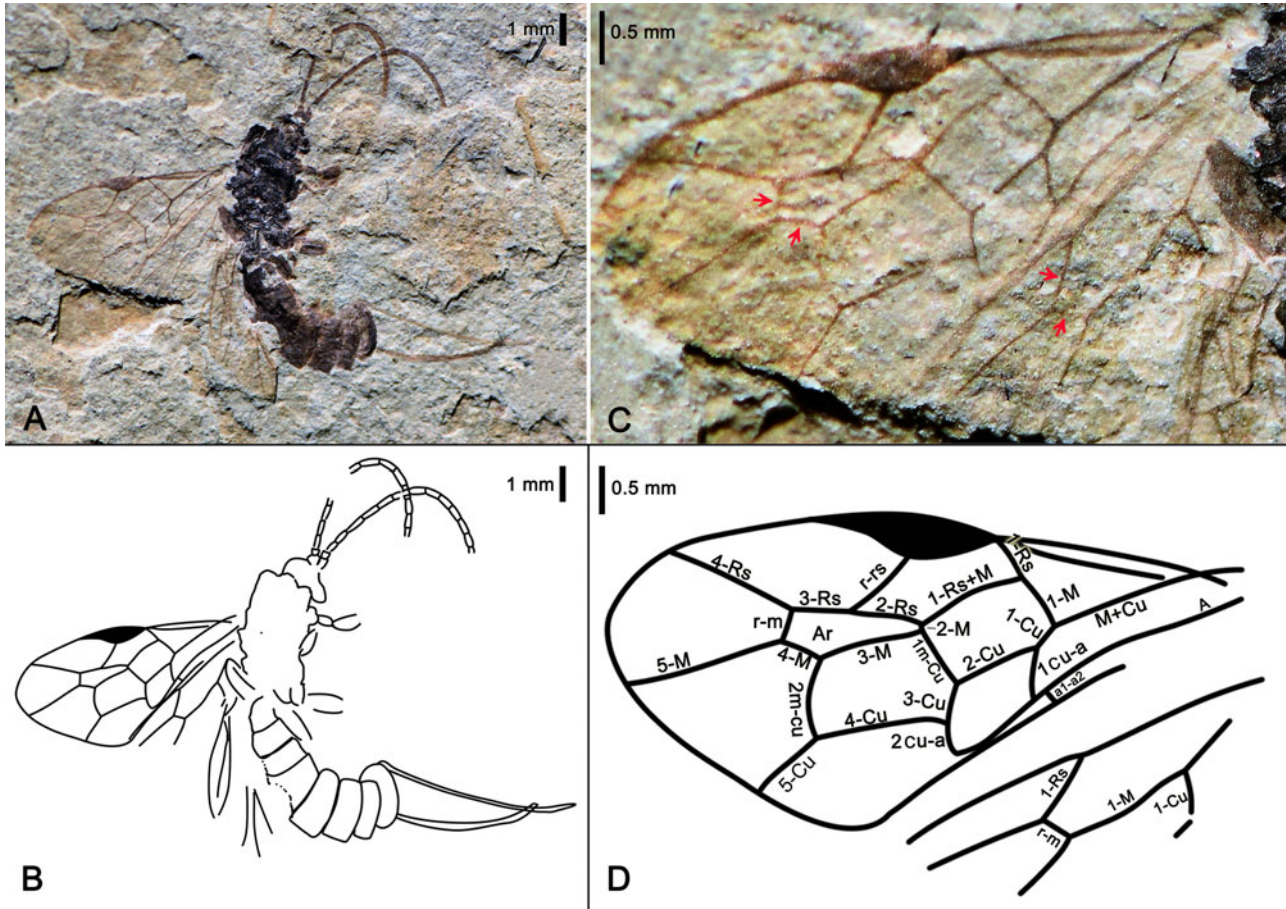


Figure 5. *Amplicella abbreviata* sp. nov. Holotype (CNU-HYM-LB-2018101). Photographs of **A**, habitus and **C**, wings. Line drawings of **B**, whole body and **D**, wings.

2-Rs. The hind wing of *A. abbreviata* has 1-Rs much longer than r-m, differing from all other species except *A. shcherbakovi*.

Discussion

Based on the ‘Procrustes distances’ of all 24 ichneumonid species relative to each other (Supplemental material, Table S1), we obtained a tree showing their phenetic relationships (Fig. 6) and between-species similarity patterns (Fig. 7). These results confirm the following observations:

1. *Amplicella beipiaoensis* (A.be^T) (Fig. 1A) and *Amplicella abbreviata* (A.ab^T) (Fig. 1B) are very similar, with a short Procrustes distance of 0.09, suggesting that the *A. abbreviata* should belong to *Amplicella*, which is consistent with traditional taxonomy.

2. *Cretobraconus mongolensis* (C.mo^E) (Fig. 1F), as a representative of Eoichneumoninae in Braconidae (Perrichot *et al.* 2009), has venational characters intermediate between those of Braconidae and Ichneumonidae (Rasnitsyn & Sharkey 1988). *Cretobraconus mongolensis* (C.mo^E) and another seven species in six genera (*Amplicella*, *Sinchora*, *Khasurtella*, *Tanychora*, *Megachora* and *Paratanychora*: Fig. 1A–H) in Tanychorinae belong to the first large clade and have Procrustes distances <0.21, indicating that Eoichneumoninae is much more similar to Tanychorinae than the other subfamilies. Moreover, Rasnitsyn (1975, 1980) proposed that Tanychorinae occupies a basal position and that it is probably ancestral to all other Ichneumonidae and Braconidae based on morphological characters. Therefore, the GMA results further support the proposal that tanychorines with complete 1-Rs + M are precursor taxa to other ichneumonids. *Tanychorella dubia* (T.du^T) (Fig. 1X)

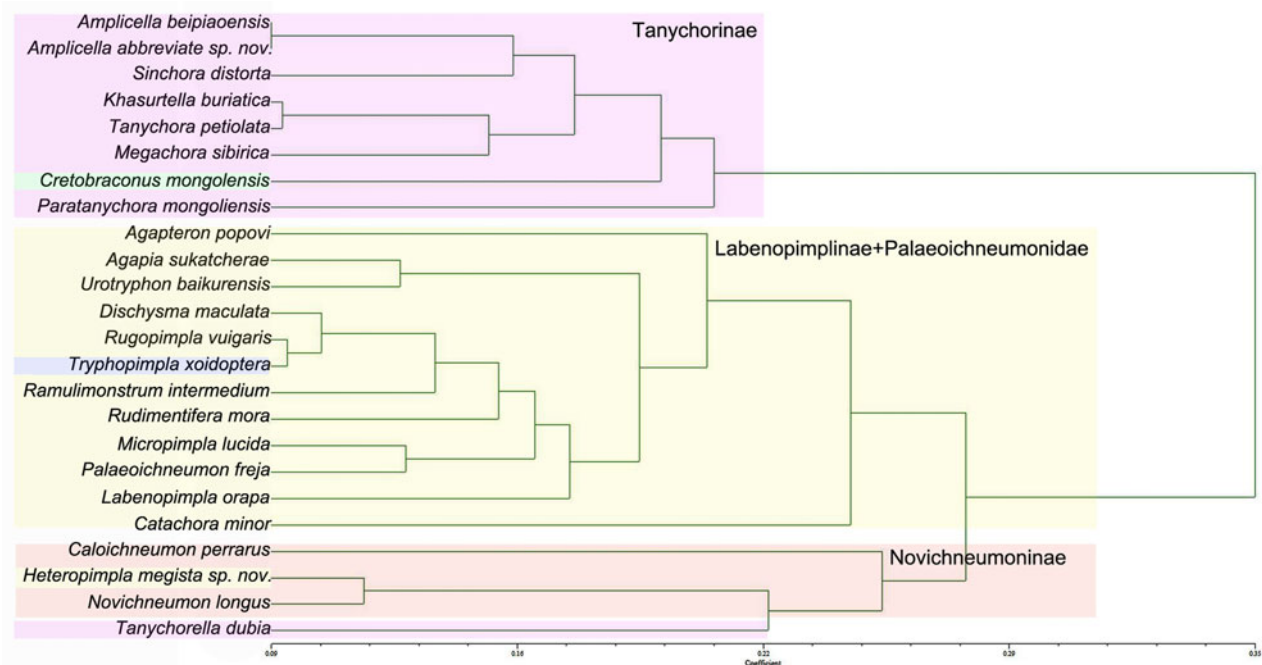


Figure 6. Tree resulting from GMA showing the phenetic relationships for 24 species of Ichneumonidae.

is exceptional, located outside of the plots of Tanychorinae + Eoichneumoninae, and is generally isolated from all other taxa with Procrustes distances >0.27 , which is due mainly to its forewings having 1-Rs + M that are much reduced.

- To date, only three species of ichneumonid have been described from Myanmar amber, *Caloichneumon perrarus* (C.pe^N) (Fig. 1U), *Heteropimpla megista* (H.me^L) (Fig. 1V) and *Novichneumon longus* (N.lo^N) (Fig. 1W), representing a Mesozoic occurrence of this family in a tropical climate regime (Li *et al.* 2017a; this study). More importantly, these three species each have much longer Procrustes distances than the other ichneumonids shown in this tree. In particular, *Caloichneumon perrarus* (C.pe^N) has much longer Procrustes distances (>0.27) than the other two species. However, H.me^L and N.lo^N have a very short Procrustes distance of 0.12 between them. H.me^L has cross-vein r-m present and areolet closed, which are important characters for distinguishing Labenopimplinae and Novichneumoninae, and which suggest that distinct similarities and differences between species at the same locality were present at the same time.
- Eight genera of Labenopimplinae (*Agapteron*, *Agapia*, *Urotryphon*, *Rugopimpla*, *Ramulimonstrum*, *Micropimpla*, *Labenopimpla* and *Catachora*) and three genera of Palaeoichneumoninae (*Dischysma*,

Rudimentifera and *Palaeoichneumon*) form the second big clade and have Procrustes distances <0.25 indicating venational similarity of these two subfamilies (Fig. 1I–T) in contrast to those in Tanychorinae (Fig. 1A–H). This does not contradict the current taxonomy of the family, because these two subfamilies are defined generally on body characters. It is worth noting that the genus *Tryphopimpla* (T.xo^{is}), of uncertain subfamilial position, also belongs to this clade and has a particularly short Procrustes distances (<0.13) with the labenopimplines *Rugopimpla* (R.vu^L) and *Ramulimonstrum* (R.in^L), which suggests that *Tryphopimpla* should be placed in Labenopimplinae instead of erecting a new subfamily.

Conclusions

As discussed above, two new Mesozoic ichneumonids from Myanmar and China are described. Based on GMA analysis, we propose: that Tanychorinae with 1-Rs + M complete are precursor taxa to other ichneumonids; that the three species of Mesozoic ichneumonids in Myanmar amber represent tropical climate occurrences that differ markedly from most other taxa but are similar to each other; and that *Tryphopimpla* should be placed in Labenopimplinae instead of erecting a new subfamily.

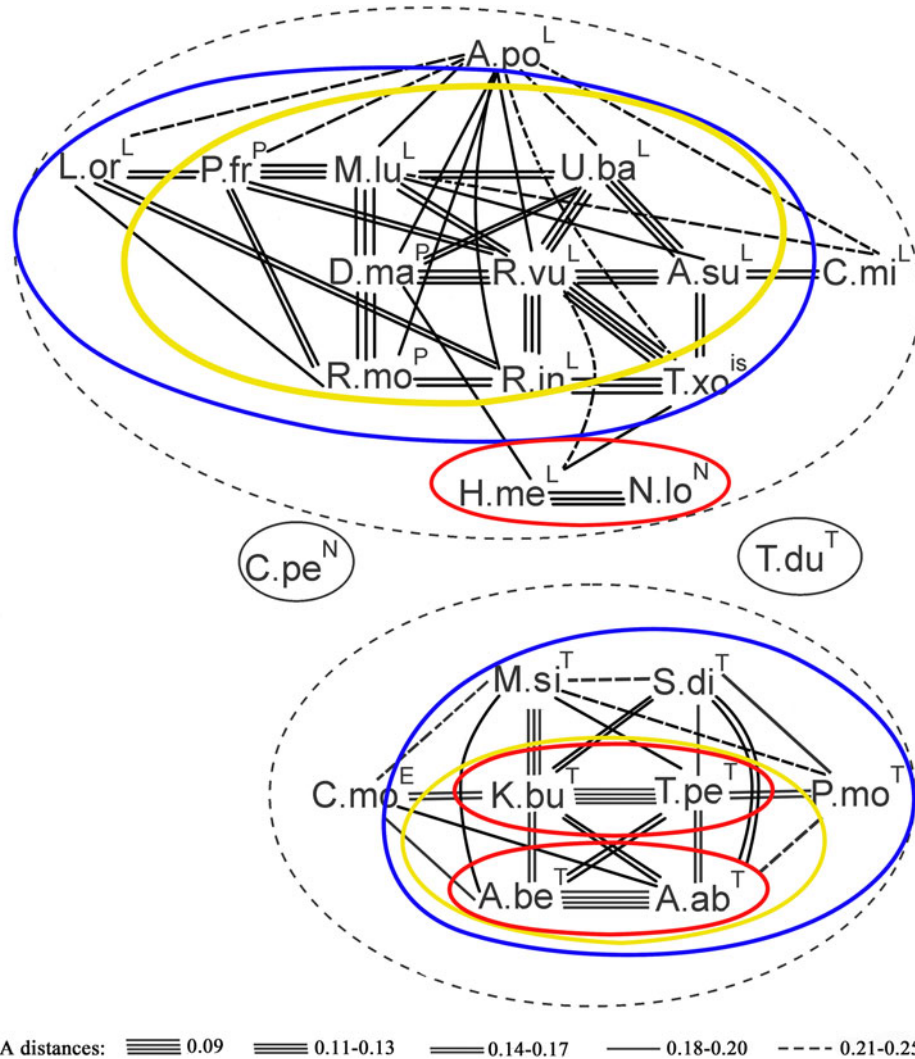


Figure 7. Between-species similarity for forewing venations as revealed by GMAs and Procrustes distances. Four lines mean the shortest distance, from 0.09–10, three lines mean the next shortest intervals, from 0.11–0.13, and so on. These intervals form classes of similarity, so the differences within the class are considered irrelevant, and only those between classes are considered. **Abbreviations:** **A.ab**, *Amplipella abbreviate*; **A.be**, *Amplipella beipiaoensis*; **A.po**, *Agapteron popovi*; **A.su**, *Agapia sukatchevae*; **C.mo**, *Cretobraconus mongolensis*; **C.pe**, *Caloichneumon perrarus*; **D.ma**, *Dischisma maculate*; **H.me**, *Heteropimpla megista*; **K.bu**, *Khasurtella buriatica*; **L.or**, *Labenopimpla orapa*; **M.lu**, *Micropimpla lucida*; **M.si**, *Megachora sibirica*; **N.lo**, *Novichneumon longus*; **P.fr**, *Palaeoichneumon freja*; **P.mo**, *Paratanychora mongoliensis*; **R.in**, *Ramulimonstrum intermedium*; **R.mo**, *Rudimentifera mora*; **R.vu**, *Rugopimpla vulgaris*; **S.di**, *Sinchora distorta*; **T.du**, *Tanychorella dubia*; **T.pe**, *Tanychora petiolate*; **T.xo**, *Tryphopimpla xoridoptera*; **U.ba**, *Urotryphon baikurensis*. Subfamily symbols (superscripts): ^EEoichneumoninae; ^LLabenopimplinae; ^NNovichneumoninae; ^PPalaeoichneumoninae; ^TTanychorinae; ^{is}incertae subfamiliae.

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References

- Ashmead, W. H. 1900. Report upon the Aculeate Hymenoptera of the islands of St. Vincent and Grenada, with additions to the parasitic Hymenoptera and a list of the described Hymenoptera of the West Indies. *Transactions of the Entomological Society of London*, **1900**, 207–367.
- Bai, M., Beutel, R. G., Shih, C. K., Ren, D. & Yang, X. K. 2013. Septiventeridae, a new and ancestral fossil family of Scarabaeoidea (Insecta: Coleoptera) from the Late Jurassic to Early Cretaceous Yixian Formation. *Journal of Systematic Palaeontology*, **11**, 359–374. doi:10.1080/14772019.2012.660995
- Cruickshank, R. D. & Ko, K. 2003. Geology of an amber locality in the Hukawng Valley, northern Myanmar. *Journal of Asian Earth Sciences*, **21**, 441–455. doi:10.1016/S1367-9120(02)00044-5
- Engel, M. S. & Krombein, K. V. 2012. Hymenoptera. Pp. 787–798 in *McGraw-Hill encyclopedia of science and technology*. McGraw-Hill, New York.
- Fabricius, J. C. 1804. Systema Piezatorum: secundum ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus. *Carolus Reichard, Brunsvigae*, 439 + 32 pp.
- Gauld, I. D. & Bolton, B. 1988. *The Hymenoptera*. Oxford University Press, Oxford. 332pp.
- Gauld, I. D. & Mound, L. A. 1982. Homoplasy and the delineation of holophyletic genera in some insect groups. *Systematic Entomology*, **7**, 73–86. doi:10.1111/j.1365-3113.1982.tb00127.x
- Guo, L. C., Shih, C. K., Li, L. F. & Ren, D. 2016. New peleciniid wasps (Hymenoptera: Peleciniidae) from Upper Cretaceous Myanmar amber. *Cretaceous Research*, **61**, 151–160. doi:10.1016/j.cretres.2016.07.003
- Huber, J. T. 2009. Biodiversity of Hymenoptera. Pp. 303–323 in R. Foottit & P. Adler (eds) *Insect biodiversity: science and society*. Wiley-Blackwell, Oxford.
- Kopylov, D. S. 2009. A new subfamily of ichneumonids from the Lower Cretaceous of Transbaikalia and Mongolia (Insecta: Hymenoptera: Ichneumonidae). *Paleontological Journal*, **43**, 83–93. doi:10.1134/S0031030109010092
- Kopylov, D. S. 2010a. Ichneumonids of the subfamily Tanychorinae (Insecta: Hymenoptera: Ichneumonidae) from the Lower Cretaceous of Transbaikalia and Mongolia. *Paleontological Journal*, **44**, 180–187. doi:10.1134/S0031030110020097
- Kopylov, D. S. 2010b. A new subfamily of ichneumon wasps (Insecta: Hymenoptera: Ichneumonidae) from the Upper Cretaceous of the Russian Far East. *Paleontological Journal*, **44**, 422–433. doi:10.1134/S003103011004009X
- Kopylov, D. S. 2011. Ichneumon wasps of the Khasurty Locality in Transbaikalia (Insecta, Hymenoptera, Ichneumonidae). *Paleontological Journal*, **45**, 406–413. doi:10.1134/S0031030111040058
- Kopylov, D. S. 2012a. New species of Praeichneumonidae (Hymenoptera, Ichneumonoidea) from the Lower Cretaceous of Transbaikalia. *Paleontological Journal*, **46**, 66–72. doi:10.1134/S0031030112010078
- Kopylov, D. S. 2012b. New Ichneumonidae (Hymenoptera) from the Upper Cretaceous Ambers of the Taimyr Peninsula. *Paleontological Journal*, **46**, 383–391. doi:10.1134/S0031030112040041
- Kopylov, D. S., Brothers, D. J. & Rasnitsyn, A. P. 2010. Two new labenopimpline ichneumonids (Hymenoptera: Ichneumonidae) from the Upper Cretaceous of southern Africa. *African Invertebrates*, **51**, 423–430. doi:10.5733/afin.051.0211
- Kopylov, D. S. & Zhang, H. C. 2014. New ichneumonids (Insecta: Hymenoptera: Ichneumonidae) from the Lower Cretaceous of north China. *Cretaceous Research*, **52**, 591–604. doi:10.1016/j.cretres.2014.03.012
- Kopylov, D. S., Spasojevic, T. & Klopstein, S. 2018. New ichneumonids (Hymenoptera, Ichneumonidae) from the Eocene Tadushi Formation, Russian Far East. *Zootaxa*, **4442**, 319–330. doi:10.11646/zootaxa.4442.2.8
- Latreille, P. 1802. Histoire naturelle, générale et particulière des crustacés et des insectes. Ouvrage faisant suite à l'histoire naturelle générale et particulière, composée par Leclerc de Bu on, et rédigée par C. S. Sonnini, membre de plusieurs sociétés savantes. *Familles naturelles des genres. Tome troisième, F. Dufart, Paris*, xii + 467 pp.
- Li, L. F., Rasnitsyn, A. P., Shih, C. K. & Ren, D. 2015. A new genus and species of Praeaulacidae (Hymenoptera: Evanioidea) from Upper Cretaceous Myanmar amber. *Cretaceous Research*, **55**, 19–24. doi:10.1016/j.cretres.2015.01.007
- Li, L. F., Kopylov, D. S., Shih, C. K. & Ren, D. 2017a. The first record of Ichneumonidae (Insecta: Hymenoptera) from the Upper Cretaceous of Myanmar. *Cretaceous Research*, **70**, 152–162. doi:10.1016/j.cretres.2016.11.001
- Li, L. F., Rasnitsyn, A. P., Labandeira, C. C., Shih, C. K. & Ren, D. 2017b. Phylogeny of the Stephanidae (Hymenoptera, Apocrita) with a new genus from Upper Cretaceous Myanmar amber. *Systematic Entomology*, **42**, 194–203. doi:10.1111/syen.12202
- Li, L. F., Shih, C. K., Rasnitsyn, A. P., Labandeira, C. C., Buffington, M., Li, D. Q. & Ren, D. 2017c. Phylogeny of the Evanioidea (Hymenoptera, Apocrita) with a new genus from Upper Cretaceous Myanmar amber. *Systematic Entomology*, **43**, 810–842. doi:10.1111/syen.12315
- Li, L. F., Rasnitsyn, A. P., Shih, C. K., Li, D. Q. & Ren, D. 2018. A new wasp of Myanmarinidae (Hymenoptera: Stephanidae) from the Mid-Cretaceous Myanmar amber. *Cretaceous Research*, **86**, 33–40. doi:10.1016/j.cretres.2018.02.009
- Li, L. F., Rasnitsyn, A. P., Shih, C. K., Li, D. Q. & Ren, D. 2019. Two new rare wasps (Hymenoptera: Apocrita: Panguidae and Burmusculidae) from mid-Cretaceous amber of northern Myanmar. *Cretaceous Research*, doi:10.1016/j.cretres.2019.104220
- Lin, X. D., Shih, M. J. H., Labandeira, C. C. & Ren, D. 2016. New data from the Middle Jurassic of China shed light on the phylogeny and origin of the proboscis in the Mesopsychidae (Insecta: Mecoptera). *BMC Evolutionary Biology*, **16**, 1. doi:10.1186/s12862-015-0575-y
- McKellar, R. C., Kopylov, D. S. & Engel, M. S. 2013. Ichneumonidae (Insecta: Hymenoptera) in Canadian Late Cretaceous amber. *Fossil Record*, **16**, 217–227. doi:10.5194/fr-16-217-2013

- Perrard, A., Villemant, C., Carpenter, J. M. & Baylac, M. 2012. Differences in caste dimorphism among three hornet species (Hymenoptera: Vespidae): forewing size, shape and allometry. *Journal of Evolutionary Biology*, **25**, 1389–1398. doi:10.1111/j.1420-9101.2012.02527.x
- Perrichot, V., Nel, A. & Quicke, D. L. J. 2009. New braconid wasps from French Cretaceous amber (Hymenoptera, Braconidae): synonymization with Eoichneumonidae and implications for the phylogeny of Ichneumonoidea. *Zoologica Scripta*, **38**, 79–88. doi:10.1111/j.1463-6409.2008.00358.x
- Rasnitsyn, A. P. 1969. Origin and evolution of the lower Hymenoptera. *Transactions of the Paleontological Institute, Academy of Sciences of the USSR*, **123**, 1–196. [In Russian]
- Rasnitsyn, A. P. 1975. Hymenoptera Apocrita of Mesozoic. *Transactions of the Paleontological Institute, Academy of Sciences of the USSR*, **147**, 1–134. [In Russian]
- Rasnitsyn, A. P. 1980. The origin and evolution of Hymenoptera. *Transactions of the Paleontological Institute, Academy of Sciences of the USSR*, **174**, 1–192. [In Russian, with English translation: Rasnitsyn, A.P. (1981). The origin and evolution of Hymenoptera. Department of the Secretary of State Translation Bureau, Ottawa, 1–329]
- Rasnitsyn, A. P. & Sharkey, M. 1988. New Eoichneumonidae from Early Cretaceous of Siberia and Mongolia (Hymenoptera: Ichneumonoidea). *Advances in Parasitic Hymenoptera Research*, **1988**, 169–197.
- Ren, D., Shih, C. K., Gao, T. P., Wang, Y. J. & Yao, Y. Z. 2019. *Rhythms of insect evolution: evidence from the Jurassic and Cretaceous in northern China*. Wiley-Blackwell, New Jersey, 710 pp.
- Rohlf, F. J. 2004. *tps-SPLIN, File utility Program. Version 1.20 (software and manual)*. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook. Available from: http://www.flywings.org.uk/MorphoJ_page.htm
- Rohlf, F. J. 2006a. *tps-UTIL, File utility Program. Version 1.38 (software and manual)*. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook. Available from: http://www.flywings.org.uk/MorphoJ_page.htm
- Rohlf, F. J. 2006b. *tps-DIG, File utility Program. Version 1.38 (software and manual)*. Department of Ecology and Evolution, State University of New York at Stony Brook, Stony Brook. Available from: http://www.flywings.org.uk/MorphoJ_page.htm
- Rohlf, F. J. 2007. *NTSYS-pc: numerical taxonomy and multivariate analysis system, Version 2.20 for Windows (software and manual)*. Exeter Software, New York. Available from: http://www.flywings.org.uk/MorphoJ_page.htm
- Shi, G. H., Grimaldi, D. A., Harlow, G. E., Wang, J., Wang, J., Yang, M. C., Lei, W. Y., Li, Q. L. & Li, X. H. 2012. Age constraint on Burmese amber based on U-Pb dating of zircons. *Cretaceous Research*, **37**, 155–163. doi:10.1016/j.cretres.2012.03.014
- Shih, J. M. P., Li, L. F., Li, D. Q. & Ren, D. 2019. Application of geometric morphometric analyses to confirm three new wasps of Evaniidae (Hymenoptera: Evanioidea) from mid-Cretaceous Myanmar amber. *Cretaceous Research*, 2019.104249. doi:10.1016/j.cretres
- Shih, M. J. H., Li, L. F. & Ren, D. 2017. Application of geometric morphometric analyses to confirm two new species of Karatavidae (Hymenoptera: Karatavitoidea) from northeastern China. *Alcheringa*, **41**, 499–508. doi:10.1080/03115518.2017.1316872
- Spasojevic, T., Broad, G. R., Bennett, A. M. R. & Klopstein, S. 2018. Ichneumonid parasitoid wasps from the early Eocene Green River Formation: five new species and a revision of the known fauna (Hymenoptera, Ichneumonidae). *Paläontologische Zeitschrift*, **92**, 35–63. doi:10.1007/s12542-017-0365-5
- Townes, H. 1969. The genera of Ichneumonidae. Part 1. *Memoirs of the American Entomological Institute*, **11**, 1–301.
- Townes, H. 1973a. Two ichneumonids (Hymenoptera) from the Early Cretaceous. *Proceedings of the Entomological Society of Washington*, **75**, 216–219.
- Townes, H. 1973b. Three Tryphoninae ichneumonids from Cretaceous amber (Hymenoptera). *Proceedings of the Entomological Society of Washington*, **75**, 282–287.
- Wahl, D. B. & Sharkey, M. J. 1993. Superfamily Ichneumonoidea. Pp. 358–509 in H. Goulet & J. T. Huber (eds) *Hymenoptera of the world: an identification guide to families*. Agriculture Canada Research Branch Monograph 1894/E, Ottawa.
- Walker, J. D., Geissman, J. W., Bowe, S. A. & Babcock, L. E. 2013. The Geological Society of America geologic time scale. *Geological Society of America Bulletin*, **125**, 259–272. doi:10.1130/B30712.1
- Wang, W. L., Zhang, L. J., Zheng, S. L., Ren, D., Zheng, Y. J., Ding, Q. & Yang, F. L. 2005. The age of the Yixian stage and the boundary of Jurassic-Cretaceous – the establishment and study of stratotypes of the Yixian stages. *Geology Reviews*, **51**, 234–242.
- Yu, D. S., Achterberg, C. von & Horstmann, K. 2012. *Taxapad 2012, Chalcidoidea 2001*. Database on flash-drive. Ottawa, Ontario. Available from: <http://www.taxapad.com> (accessed 1 May 2018).
- Zhang, H. C. & Rasnitsyn, A. P. 2003. Some ichneumonids (Insecta, Hymenoptera, Ichneumonoidea) from the Upper Mesozoic of China and Mongolia. *Cretaceous Research*, **24**, 193–202. doi:10.1016/S0195-6671(03)00031-4
- Zhang, J. F. 1991. A new species of *Tanychora* Townes (Hymenoptera, Ichneumonidae). *Acta Palaeontologica Sinica*, **30**, 502–504. [In Chinese, English abstract]
- Zhang, Q., Rasnitsyn, A. P., Wang, B. & Zhang, H. C. 2018a. Myanmarinidae, a new family of basal Apocrita (Hymenoptera: Stephanoidea) from mid-Cretaceous Burmese amber. *Cretaceous Research*, **81**, 86–92. doi:10.1016/j.cretres.2017.09.015
- Zhang, Q., Rasnitsyn, A. P., Wang, B., Zhang, H. C. 2018b. Hymenoptera (wasps, bees and ants) in mid-Cretaceous Burmese amber: a review of the fauna. *Proceedings of the Geologists' Association*, **129**, 736–747. doi:10.1016/j.pgeola.2018.06.004

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Appendix

Key for the genera of Subfamily Labenopimplinae Kopylov, 2010b

1. Forewing with r-m present (may be partly desclerotized), shorter than or equal to 3-Rs2
 - Forewing with r-m distinctly longer than 3-Rs or absent4
2. Areolet 3 times as long as wide, with 2 + 3M as long as 4 M *Armanopimpla* Kopylov, 2010b
 - Areolet less than 2 times as long as wide, 2 + 3M longer than 4 M3
3. r-m subvertical, shorter than 3-Rs*Labenopimpla* Kopylov, 2010b
 - r-m oblique, as long as 3-Rs*Catachora* Townes, 1973b
4. Rs + M furcates after r-rs, areolet absent*Eubaeus* Townes, 1973b
 - Rs + M furcates before r-rs, areolet usually present ..5
5. Areolet petiolate (r-rs joins Rs after r-m)*Agapteron* Kopylov, 2012b
 - Areolet normally shaped (r-rs joins Rs before or next to r-m)6
6. 2-Rs as long as 2 + 3-M, r-m subvertical*Heteropimpla* gen. nov.
 - 2-Rs shorter than 2 + 3-M, r-m oblique7
7. Areolet with 3-Rs longer than 2-Rs; ramulus very long*Ramulimonstrum* Kopylov, 2010b
 - Areolet with 3-Rs shorter or, rarely, as long as 2-Rs; ramulus absent or present, but never very long8
8. 1cu-a & 2-Rs + M bent, usually with short ramulus9
 - 1cu-a & 2-Rs + M gently curved, without ramulus .10
9. Antenna with more than 20 flagellomeres; hind wing with 1-Rs as long as or longer than r-m; forewing longer than 3 mm*Rugopimpla* Kopylov, 2010b
 - Antenna with 15 flagellomeres; hind wing with 1-Rs shorter than r-m; forewing shorter than 2 mm*Agapia* Kopylov, 2012b
10. Hind wing with free ending of Cu present*Micropimpla* Kopylov, 2010b
 - Hind wing with free ending of Cu absent*Urotryphon* Townes, 1973b