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Torymidae (Hymenoptera, Chalcidoidea) revised: molecular phylogeny, circumscription and reclassification of the family with discussion of its biogeography and evolution of life-history traits

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Running title: Phylogeny and classification of Torymidae

Abstract

A phylogeny of the Torymidae (Chalcidoidea) is estimated using 4734 nucleotides from 5 genes. Twelve outgroups and 235 ingroup taxa are used, representing about 70% of the recognized genera. Our analyses do not recover Torymidae as monophyletic and we recognize instead two families: Megastigmidae (**stat. rev.**) and Torymidae *s.s.* (**stat. rev.**). Within Torymidae *s.s.*, we recognize 6 subfamilies and 6 tribes, including Chalcimerinae, Glyphomerinae and Microdontomerinae **(subf. nov.)**, and two new tribes: Boucekinini and Propalachiini **(trib. nov.)**. Seven unclassified genera (i.e. *Cryptopristus*, *Echthrodape*, *Exopristoides*, *Exopristus*, part of *Glyphomerus*, *Thaumatorymus*, *Zaglyptonotus*) are assigned to tribes within our new classification. Five genera are restored from synonymy, *Ameromicrus* and *Didactyliocerus* from under *Torymoides* (**stat. rev.**), *Iridophaga* and *Iridophagoides* from under *Podagrionella* (**stat. rev.**) and *Nannocerus* from under *Torymus* (**stat. rev.**), and three genera are synonymized, *Allotorymus* under *Torymus* **syn. nov.**, *Ditropinotus* under *Eridontomerus* **syn. nov.** and *Pseuderimerus* under *Erimerus* **syn. nov.** A Palaearctic or Eurasian origin for Torymidae is proposed. The ancestral area of Megastigmidae is indicated as the Australian region. The most probable ancestral life strategy for Torymidae *s.s.* is ectoparasitism on gall-forming Cynipidae. The life strategy and putative hosts of the common ancestor of Megastigmidae remain uncertain.

Introduction

Within Hymenoptera, Chalcidoidea is an extremely diverse superfamily. More than 22,500 species have been described and their overall diversity is estimated at more than 500,000 species (Heraty, 2009; Noyes, 2017). Although the number of recognized chalcid families has varied substantially, most recently 22 families have been recognized (Aguiar et al., 2013; Heraty et al., 2013). Their morphological disparity and enormous species diversity are also reflected by their biological and feeding strategies. Most Chalcidoidea are parasitoids and thus are important natural enemies of insects. Despite their functional importance in natural ecosystems, the taxonomy, biology and phylogeny of most chalcidoid families are poorly known (Huber, 2009). Until now, only a few comprehensive phylogenetic studies of families or subfamilies of Chalcidoidea have been published. Most of these studies are based on morphology (Gibson, 1989 - Eupelmidae, 1995 - Eupelminae; Grissell, 1995 - Toryminae; Heraty, 2002 - Eucharitidae; Lotfalizadeh et al., 2007 - Eurytominae), and only a few have used molecular characters (Owen et al., 2007 - Trichogrammatidae; Cruaud et al., 2010, 2012 - Agaonidae *s.s.*; Cruaud et al., 2011a, b - Agaonidae, Sycophaginae; Cruaud et al., 2013 - Pteromalidae, Sycoecinae; Burks et al., 2011 - Eulophidae; Segar et al., 2012 - Pteromalidae, Sycoryctinae; Murray et al., 2013 - Eucharitidae).

Torymidae, as recognized until now, is one of the mid-sized families of Chalcidoidea that included 69 valid extant genera and about 1100 described species (Grissell, 1995; Janšta et al., 2013). Monophyly of the family was supported in analyses that included only adult morphological characters (Grissell, 1995; Gibson et al., 1999; Heraty et al., 2013). Although, each of these authors acknowledged the monophyly of Torymidae, they emphasized the lack of unique synapomorphies for the family. Bouček (1988) summarized the classification history of Torymidae and proposed five morphological features defining the family. Grissell (1995) questioned all of the characters stated by Bouček (1988) and interpreted them as synapomorphies of the family. He also suggested that the family was monophyletic based on a combination of the same five character states. In contrast, the monophyly of Torymidae based only on molecular or larval characters, has never been recovered (Campbell et al., 2000; Gómez et al., 2008; Munro et al., 2011).

The infrafamilial classification of Torymidae has been revised several times since the family was first described (Walker, 1833). Several subfamilies within Torymidae were created: Idarninae, Megastigminae, Monodontomerinae, Ormyrinae, Toryminae (all Ashmead, 1899), Podagrioninae (Ashmead, 1904), Erimerinae (Crawford, 1914), Epichrysomallinae and Sycophaginae (Hill, 1967), and Thaumatoryminae (Peck et al., 1964). Some of them are now classified in other families (Idarninae and Sycophaginae in Agaonidae, Epichrysomallinae in Pteromalidae, and Ormyrinae in Ormyridae) (Heraty et al., 2013), whereas the remaining subfamilies (Megastigminae, Monodontomerinae, Toryminae, Podagrioninae, Erimerinae and Thaumatoryminae) remained in Torymidae. The first tribal classification (excluding Idarnini) was established by Bouček (1976) who created Palachiini and Podagrionini within Podagrioninae (Torymidae). Later, Bouček (1978) included the former Podagrioninae as a tribe of Monodontomerinae (along with Palachiini and Podagrionini) and created several other tribes within the subfamily (Chalcimerini, Chrysochalcissini, and Monodontomerini). Bouček (1988) reduced Erimerinae to a tribe of Monodontomerinae and decreased the number of subfamilies of Torymidae to Megastigminae, Monodontomerinae, Thaumatoryminae, and Toryminae, with the latter divided into two tribes, Torymini and Odopoiini.

Grissell (1995) conducted a comprehensive phylogenetic analysis of the Torymidae based on 24 morphological characters and 46 taxa. He classified Torymidae and recognized only two subfamilies, Megastigminae and Toryminae (including Monodontomerinae, Thaumatoryminae and Toryminae *sensu* Bouček, 1988), and hypothesized the monophyly of both groups. Toryminae were divided into seven tribes consisting of 49 genera (Fig. S1) and 890 extant species: Chalcimerini included 1 genus and 1 species (i.e. 1/1), Microdontomerini

(9/112), Monodontomerini (13/78), Palachiini (3/29), Podagrionini (7/140), Torymini (10/420) and Torymoidini (6/110) (Grissell, 1995; Noyes, 2017). *Odopoia* was placed in Torymini, however Grissell (1995) did not explicitly withdraw Odopoiini. Some genera were treated as *incertae sedis* with respect to tribal classification in Toryminae and remained unplaced: *Cryptopristus* (3 species), *Echthrodape* (2), *Exopristoides* (2), *Exopristus* (1), *Glyphomerus* (9), *Stenotorymus* (1), *Thaumatorymus* (1), and *Zaglyptonotus* (3) (Grissell, 1995; Noyes, 2017).

Grissell's classification of Torymidae was only partly adopted by Zerova and Seryogina (1999) and Zerova et al. (2003), who recognized only two subfamilies (Megastigminae and Toryminae) and only three tribes within Toryminae (Podagrionini *sensu* Bouček, 1978, Monodontomerini (=Monodontomerinae *sensu* Bouček, 1988 excluding Podagrionini), and Torymini *sensu* Grissell, 1995). Nothing was stated about Thaumatoryminae.

What was previously classified as the subfamily Megastigminae is composed of 206 species in 12 genera (Bouček, 1988; Noyes, 2017). There has not been a rigorous phylogenetic study of this group based on either morphological or molecular characters. Munro et al. (2011) and Heraty et al. (2013) recovered Megastigminae as monophyletic, however with only 3 and 4 included genera, respectively.

Most torymid genera (45) are distributed in the Old World (Grissell, 1995; Janšta et al., 2013; Noyes, 2017), with only a few cosmopolitan genera shared with the New World: *Cryptopristus*, *Eridontomerus*, *Glyphomerus*, *Idiomacromerus*, *Megastigmus*, *Microdontomerus*, *Monodontomerus*, *Palmon*, *Podagrion*, *Pseuderimerus,* and *Torymus*. Only a few genera are endemic to the Neotropical and the Nearctic regions, including *Boucekinus* and *Platykula* (Torymoidini), *Zaglyptonotus* (Toryminae *incertae sedis*), *Chileana*, *Perissocentrus* and *Zdenekius* (Monodontomerini), *Physothorax* and *Plesiostigmodes* (Torymini), and *Neopalachia* (Palachiini).

The biology of torymid species is still largely unknown but a few well-defined patterns are apparent. Most larvae of Torymidae *s.s.* (Chalcimerinae, most of Microdontomerinae, Toryminae) are ectoparasitoids of various gall makers, mainly Cynipidae and Cecidomyiidae. At least two species of Palachiini and most species of Podagrionini (Grissell 1995) as well as *Microdontomerus iridis* are reported as parasitoids of mantid eggs. Most Monodontomerinae are ectoparasitoids on larvae of bees or endoparasitoids of eggs of Heteroptera and of pupae of Lepidoptera or Symphyta (Grissell, 1995). Only a few species of Torymini are phytophagous. As far as is known, species of nearly all megastigmine genera are ectoparasitoids of various gall makers or phytophagous in plant seeds (Grissell, 1999).

Little is known about the larval morphology of Torymidae. There are several individual studies concerning larval morphology and descriptions of various immature stages (Askew, 1961, 1966, 2002; Sellenschlo, 1982, 1983, 1984, 1989; Skrzypczyńska and Roques, 1987; Askew et al., 2004, 2007; Nieves-Aldrey et al., 2007), but none have discussed larval characters in a phylogenetic framework. The only phylogenetic analysis based on characters of the terminal-instar larvae was done by Gómez et al. (2008). In that study, larval morphology did not support the monophyly of Torymidae as postulated in other studies (Grissell, 1995; Heraty et al., 2013), but instead suggested that Megastigminae and Toryminae were two unrelated lineages.

No fossil of Megastigmidae and only a few fossils of Torymidae *s.s.* have been documented so far. The oldest described torymid fossils are in Baltic amber - 44 Myr (*Monodontomerus primaveus* Brues, 1923), but they are also known from Dominican amber (15-25 Myr, Cruaud et al., 2010) and Eocene-Oligocene shales (Grissell, 1976, 1995). Two extinct genera are known from Dominican amber (Grissell, 1980), *Gummilumpus bouceki* (Grissell, 1980) which is assigned to Palachiini, and *Zophodetus woodruffi* Grissell, 1980 which appears to be closely related to Microdontomerini (Grissell, 1995). The extinct genus *Paleotorymus* and extant species of *Torymus* were documented also from the Eocene-Oligocene boundary of Florissant shales in Colorado (Grissell 1976, 1995) and from Miocene compression fossils in Spain (Peñalver and Engel, 2006; Heraty and Darling, 2009). While Grissell (1995) questioned the inclusion of some fossil species of *Paleotorymus* in Torymidae, the species described by Peñalver and Engel (2006) is correctly placed (Heraty and Darling, 2009). Several new amber fossils (mostly from Dominican and Baltic amber) of undetermined Toryminae have been recorded (Krogmann - pers. comm.). Surprisingly, the oldest fossil, which is, however, not unambigously placed within Toryminae (Krogmann and Janšta - pers. comm.), comes from Burmese amber (mid-Cretaceous, latest Albian, ca. 100 Myr).

Historically, several families or subfamilies (i.e. Ormyridae, Agaonidae: Agaoninae and Sycophaginae, Pteromalidae: Epichrysomallinae) have been proposed to be sister to Torymidae *sensu* Grissell (1995) based either on intuitive analysis (Noyes, 1990) or on convergences (Cruaud et al., 2010, 2011b), but without any morphological support. Bouček (1988) mentioned that Ormyridae could be closely related to Torymidae based on shape of the occipital carina. The same hypothesis was also proposed by Noyes (1990) in his intuitive cladogram that groups together Torymidae plus Ormyridae and Agaonidae plus Ormocerinae (Pteromalidae). Grissell (1995) added Pteromalidae, but not Ormyridae, as outgroups to his phylogenetic analysis of the Toryminae. Gibson et al. (1999) noted that relationships and the proper classification of Torymidae, Ormyridae and Agaonidae are one of the more perplexing issues of chalcidoid classification. Because of variable results, no sister group was proposed for Torymidae as a result of the comprehensive phylogenetic analyses of Chalcidoidea using molecular (Munro et al., 2011) or combined molecular and morphological data (Heraty et al., 2013). However, this latter analysis repeatedly placed Torymidae in a clade with Ormyridae and Colotrechninae (Pteromalidae).

The main aims of our study are to (i) test the monophyly of the family based on molecular data using broad taxon sampling, (ii) propose the first phylogenetic hypothesis for Torymidae based on molecular data, (iii) compare the phylogeny of Torymidae to previous morphological results and revise the current classification accordingly, (iv) test the monophyly of most genera, (v) assess the biogeography of the family, subfamilies and tribes, and (vi) discuss the origin of various host specializations.

Material and methods

Taxon sampling

A total of 235 ingroup taxa (about 70% of the known genera) were used for this study. The chosen taxa represent the Megastigmidae and all tribes previously recognized in Torymidae *s.s.* To test the monophyly of Torymidae *sensu* Grissell (1995), we included in our analysis species of two taxa that were hypothesized as closely related lineages to Torymidae by Heraty et al. (2013): Ormyridae (*Ormyrus* spp. and *Ormyrulus* sp.) and Colotrechninae (Pteromalidae: *Zeala walkerea*) as well as Sycophaginae (Agaonidae: *Sycophaga gigas*, *Sycophaga* sp.) and Epichrysomallinae (Pteromalidae: *Odontofroggatia* spp.) that were sometimes historically included in the Torymidae (Bouček, 1988; Grissell, 1995; Gibson et al., 1999). We also included Eurytomidae (*Eurytoma gigantea*, *Ficomila* sp.), which are considered phylogenetically as more distant taxa (Heraty et al., 2013). Thus, a total of 12 outgroup species belonging to four families were used (Table S1).

Most specimens sampled were initally preserved in 70 or 96% EtOH, although a few extracts were made from dry, card-mounted specimens (Table S1). Specimen vouchers and extracts are deposited in the Center for Biology and Management of Populations, INRA, Montferrier-sur-Lez, France (CBGP); Charles University, Faculty of Science, Department of Zoology, Prague, Czech Republic (CUPC); Department of Entomology, University of California, Riverside, CA, USA (UCR); and the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA (USNM) (Table S1).

Molecular methods

DNA extraction either followed a modified Chelex protocol (CP) (Walsh et al., 1991) or isolation using the Qiagen DNeasy® kit (QP) following the manufacturer's protocol. If we had more than one specimen from a specific taxon and locality, we used destructive DNA extraction (D) to obtain a higher quantity of genomic DNA. We used non-destructive DNA extraction (N) for rare taxa or for taxa that belong to taxonomically difficult groups (Table S1).

Five loci were sequenced: two nuclear protein coding genes, the *F2 copy of elongation factor-1α* (*EF-1α*, 516 bp) and *Wingless* (*Wg*, 402bp); two ribosomal nuclear genes, *18S rDNA* (*V3-V5 expansion region*, ~809bp) and *28S rDNA* (*D2* and *D3-D5 expansion regions*, ~1555bp); and mitochondrial *cytochrome c oxidase subunit I* (*barcode fragment* and *C1-J-2183* (*Jerry*) - *TL2-N-3014* (*Pat*) fragment, 1452bp). Primer sequences and amplification protocols followed Cruaud et al. (2010) for *COI* (barcode fragment) and *Wg*, Cruaud et al. (2011a) for *EF-1α,* Munro et al. (2011) for *18S rDNA* and *28S rDNA*, and Weiblen (2001) for *COI* (*C1-J-2183* (*Jerry*) - *TL2-N-3014* (*Pat*) fragment).

PCR products were either sent as non-purified products to Macrogen Inc. for purification and sequencing, or purified using the QIAquick PCR Purification Kit®, and then sequenced using the BigDyeTerminator v3.1® kit (Applied Biosystems) and an 3130xl Genetic Analyzer at Charles University in Prague, an ABI3730XL sequencer at Genoscope, Evry, France, or sequenced at the San Diego State University Microchemical Core Facility or the UCR Genomics Core Facility. All sequences are deposited in GenBank. All regions sequenced for specific taxa and GenBank accession numbers are listed in Table S1.

Alignment

Contigs were assembled and subsequently edited using the software Geneious version 7.1.7® (Kearse et al., 2012). All gene regions were aligned using MAFFT (Katoh and Standley, 2013) version 7.110 using the E-INS-i strategy for ribosomal genes and L-INS-i strategy for coding genes. Alignments of protein-coding sequences (*EF-1α*, *Wg*, *COI*) were translated into amino acids using Geneious 7.1.7 to detect stop-codons that may indicate pseudogenes or misalignments. Possible substitution saturation for each protein-coding gene and nucleotid composition, respectively, was checked using DAMBE (Xia, 2013). We also plotted the number of transitions (Ts) and transversions (Tv) vs an F80 model of genetic distance.

Phylogenetic analyses

Parsimony and probalistic methods were used to infer trees. Maximum parsimony analyses (MP) were conducted under TNT ver. 1.1 (Goloboff et al., 2003, 2008, updated version of June 18, 2015). Analyses were performed under New Technology methods using 1000 random addition sequences (RAS), random sectorial search (RSS) (with a global swap every 40 changes in sectors of size below 75 and every 100 changes in sectors of size above 75; 60 drifting cycles for selections of size above 75 and 30 starts for selections of size below 75), tree-drifting of 100 cycles, and tree-fusing of 100 rounds. A final swapping of the most parsimonious trees was performed using the bbreak option and the Tree Bisection Reconnection (TBR) method. Character states were considered unordered, equally weighted and non-additive, all substitutions were equally weighted. Gaps were treated as missing data. Nodal supports were calculated using 100 standard bootstrap replicates under the same search criteria except for the number of RAS, which was set to 100. Bootstrap percentage (BP) ≥ 70% were regarded as strong nodal support (Felsenstein and Kishino, 1993). For both Bayesian (BA) and maximum likelihood (ML) analyses, Partition Finder v1.1.1 (Lanfear et al., 2012) was used to calculate best-fit partitioning schemes and nucleotide substitution models of evolution for individual genes under the Bayesian Akaike Information Criterion (BIC). ML analyses were implemented in RAxML 8.1.24 using GTRCAT approximation with 1000 bootstrap replicates (Stamatakis, 2006). Bootstrap percentages (BP) ≥ 70% were considered as strong nodal support. For Bayesian Analyses (BA), a parallel version of MrBayes 3.2.3 (Huelsenbeck et al., 2001; Ronquist and Huelsenbeck, 2003) was used. Parameter values for the partitioning strategy were initiated with default uniform priors and branch lengths estimated using default exponential priors. The heating parameter was set to 0.02 in order to allow swap frequencies from 20 to 70% as recommended by the manual of MrBayes. We ran two independent runs of 30 million generations, sampling every 1,000. For the determination of burn-in, we examined the plot of overall model likelihood against generation number using Tracer v1.6 (Rambaut et al., 2014) to find the convergence point where the likelihood started to fluctuate around a constant value. The points sampled prior to convergence of the chains were then discarded. Posterior probabilities (PP) ≥ 0.95 were considered as strong support, PP < 0.90 as weak. All ML and BA analyses were conducted on the CIPRES Science Gateway (Miller et al., 2010).

Philosophy of a new classification

A new classification of Torymidae was established based on our results and in combination with morphological features (mostly published by Grissell, 1995). A major shift in the classification of Torymidae *s.s.* was required to coincide with the revised family classification of Megastigmidae, and our new phylogenetic hypothesis. The subfamiles of Torymidae *s.s.* that we propose herein meet both the criteria that they are demonstrably monophyletic in our analyses, and that they can be characterized by morphological data. Our proposed subfamilies and tribes are further supported by molecular, morphology, biogeography and biology-based features.

Character mapping and ancestral state reconstruction

To infer biogeography history and evolution of life-history strategies of parasitoid larvae, we conducted MP and ML ancestral state reconstruction using Mesquite 2.75 (Maddison and Maddison, 2011). All reconstructions were performed on the resulting RAxML (ML) tree. For ML optimization, we used a stochastic Markov model of evolution (Mk1). The Likelihood Decision Threshold was set to 2 loglikelihood units. We assembled a matrix (see Table S1) of two characters, 1) species distribution and 2) host assotiation of parasitoid larvae, from our own collecting data or several literature sources (Hanson, 1992; Grissell, 1995; Gómez et al., 2008; Noyes, 2017). All character states are discrete and unordered. For species distribution character we identified six states: (0) Oriental, (1) Afrotropical, (2) Australian, (3) Palaearctic, (4) Neotropical, and (5) Nearctic region. Genera that are distributed in more than one biogeographical region were represented in the dataset by taxa/species originated from all known regions to cover the entire area of the specific genus distribution.

We defined parasitoid larvae life-history by the following character states: (0) parasitoids feeding on larvae of gall-forming Cynipidae (Hymenoptera: Cynipoidea), (1) parasitoids feeding on larvae of gall-forming Cecidomyidae (Diptera), (2) parasitoids feeding on larvae of gall-forming Eurytomidae (Hymenoptera: Chalcidoidea), (3) parasitoids feeding on larvae of gall-forming Tephritidae (Diptera), (4) parasitoids feeding on boring or gall-forming Lepidoptera, (5) parasitoids feeding on larvae or pupae of Tephritidae (Diptera) or Curculionidae (Coleoptera) in flowerheads of Asteraceae, (6) parasitoids feeding on larvae of Aculeate Hymenoptera in their nests (Hymenoptera: Aculeata), (7) parasitoids feeding on pupae of Lepidoptera or larvae of free-living Symphyta (Hymenoptera: Tenthredinoidea) [including facultative secondary parasitism of their primary parasitoids (Diptera: Tachinidae, Hymenoptera: Ichneumonoidea etc.)], (8) parasitoids feeding on eggs of Mantodea, (9) (endo)parasitoids feeding on Heteroptera eggs, (10) figs associates [parasitoids on larvae of gall-forming Cecidomyidae or Agaonidae (Chalcidoidea) in figs], (11) parasitoids feeding on larvae of Bruchidae (Coleoptera) or Eurytomidae (Chalcidoidea) in seeds of Fabaceae, (12) phytophagous species feeding in plant ovaries/seeds or buds, (?) unknown host association.

Torymidae are biologically extremely diverse and include fundamentally different host associations, even at the genus level. In cases where we did not have enough biological information to summarize host association (i.e. for species whose hosts are unknown or for those parasitoids we were not able to determine to species level), we generalized it based on genus-level characteristics obtained from the literature. Thus, for the few cases where species were known to attack more than one taxon, they were scored as polymorphic, with only one taxon (*Idiomacromerus*) scored for a maximum of three character states to represent the most common host associations for that particular genus. Moreover, as *Microdontomerus* has exceptionally broad host ranges at the species level (parasitic on various life-stages of Lepidoptera, Tephritidae, Apoidea, Coleoptera or Mantodea as well as hyperparasite of Hymenoptera within Lepidoptera and Coleoptera larvae), we assigned state "?" to undetermined species of *Microdontomerus*.

Furthermore, to minimize the number of states for this character, we provided some complex states that contain unrelated host taxa (i.e. state 5, 7, 10 or 11). However, all these states are defined as discrete traits with respect to a specific parasitoid group (mostly genus level) or niche where their hosts are living, and, in general, their complexity do not affect estimation of the ancestral host association. For example, state 5 is used for some species of *Microdontomerus*, *Torymoides* and *Zaglyptonotus* (belonging to three different tribes), which are parasitoids of larvae and pupae of Tephritidae (Diptera) or Curculionidae (Coleoptera) in flowerheads of Asteraceae; state 7 reflects host associations of some *Monodontomerus* or *Perissocentrus* species (both Monodontomerini) which are known as parasitoids (or hyperparasitoids) of Lepidoptera and Symphyta pupae; state 11 is used for species ovipositing into pods or seeds of Fabaceae infected by larvae of Bruchidae (Coleoptera) or *Bruchophagus* (Hymenoptera: Eurytomidae) and for which we do not have reliable observations of the exact host.

However, because several taxa are considered in our dataset as parasitoids of more than one host, and because Mesquite requires unique character states for ML analyses of the ancestral state, we defined 8 “extra” states: (C) 0&11, (D) 0&1&11, (E) 4&5, (F) 6&7, (G) 0&1, (H) 1&2, (J) 1&3, (K) 5&11. Then, for graphic visualization (pie plots in trees, Figs 1a-d, Figs. S5-S6) and host estimation of the character states over the tree, we added to the particular character state the probability of the aforementioned “extra” states as a weighted ratio (ratio of extra state probability to sum of state probabilities which are parts of the extra state multiplied by the particular character state probability).

Results

Alignment and phylogenetic analyses

A total of 4734 bp was used for our analysis: *18S rDNA* = 809bp, *28S rDNA* = 1555bp (722bp + 833bp), *EF-1α* = 516, *COI* = 1452 (654bp + 798bp) and *Wg* = 402. Under parsimony analyses with gaps treated as missing, there were 3025 constant, 1709 variable and 1347 informative characters. Alignment of protein coding genes revealed no stop codons or frame shifts. For the mitochondrial locus (*COI*) and nuclear (*Wg* and *EF-1α*), the third codon position (nt3) showed a high bias in base composition (A+T 92% in *COI*, C+G 72% in *Wg* and 60% in *EF-1α*) and high level of transition (for *COI*) and transition and transversion (for *Wg* and *EF-1α*) saturation of the third codon position compared to the first and second position (Fig. S2). To decrease the saturation level and base heterogeneity of nt3 in all three genes we decided to recode all adenine (A) and guanine (G) in nt3 nucleotide positions as purines (R) and all cytosine (C) and thymine (T) as pyrimidines (Y) (Phillips and Penny, 2003).

As suggested by Partition Finder, the dataset was separated into six partitions: *18S rDNA (V3-V5)* (1) + *28S rDNA (D2)* (2) + *28S rDNA (D3-D5)* (3) + *COI (barcode fragment* and *C1-J-2183 (Jerry) - TL2-N-3014 (Pat))* (4) + *EF-1α* (5) + *Wg* (6). Models choosen for these partitions for BA were K80+I+G (for 1), SYM+I+G (for 2, 3), GTR+I+Γ (for 4) and SYM+G (for 5, 6).

Maximum Likelihood (ML) and Bayesian (BA) analyses yielded almost similar topology (Figs 1a-d, S3a-d). The parsimony analysis (MP) of the entire unpartitioned dataset resulted in 32 most parsimonious trees with a tree length of 17,136 steps (CI =0.142, RI=0.581). The strict consensus tree of all most parsimonious trees is presented in Figs S4a-c (BP values > 50 at nodes). The topology from MP analysis is slightly different when compared to the ML and BA topologies. Deviations of topology under different phylogenetic approaches are discussed below.

Monophyly of Torymidae sensu Grissell (1995)

In all our analyses, Torymidae *sensu* Grissell (1995) (i.e. Megastigminae + Toryminae=Megastigmidae + Torymidae *s.s.* in our sense, for details see Discussion) was never recovered as a monophyletic group. Instead, a monophyletic Torymidae *s.s.* was recovered that was sister to most included outgroups (excluding Eurytomidae for ML and BA and Eurytomidae and Sycophaginae for MP) + Megastigmidae (node support ML/BA/MP 92/1.00/-) (Figs 1a-d, S3a-d, S4a-c).

Phylogeny of Megastigmidae

Megastigmidae were recovered as monophyletic (100/1/99) (=clade 1, Figs 1a, S3a, S4a) and with the exception of *Bootanomyia* (part 1 and part 2) all included genera were monophyletic, mostly with high or very high support (> 97/0.98/92). *Malostigmus*, *Megastigmus* and *Neomegastigmus* had lower support in ML and BA analyses and very low or none in MP analyses. The relationships among genera across all analyses were different. ML and BA (Figs 1a, S3a) analyses recovered *Bootanomyia* part 1 (*Bootanomyia dorsalis* and *B. stigmatizans*) as sister to all other Megastigminae (with support only in BA - 0.99) while MP analysis (Fig. S4a) recovered *Paramegastigmus* as sister to the rest of Megastigmidae (with no bootstrap support).

Phylogeny of Torymidae s.s.

Nodal support for a monophyletic Torymidae *s.s.* (= Toryminae *sensu* Grissell, 1995) was high in all analyses (98/1/92). All analyses recovered a monophyletic *Thaumatorymus* + (*Chalcimerus* + *Exopristoides*) (Chalcimerinae, clade 2, Figs 1b, S3b) with high support (100/1/100). This clade was recovered sister to all other Torymidae *s.s.* (90/1/93). In ML and BA analyses, Torymoidini + Torymini *sensu* Grissell (1995) (Toryminae, clades 3-5; 75/1/-, Figs 1b, S3b) were recovered sister to all other Torymidae (Microdontomerinae, Monodontomerinae, Podagrioninae, and rest of genera treated by morphology as *incertae sedis* with respect to tribal classification in Toryminae *sensu* Grissell, 1995) (clades 6-11, 73/1/-, Figs 1c-d, S3c-d). MP analysis recovered a different topology (support <50) with Torymoidini + Torymini *sensu* Grissell (1995) nested within Torymidae (Fig. S4b). Torymoidini *sensu* Grissell (1995) was paraphyletic in all analyses (clades 3 and 4, Figs 1b, S3b, S4b), with *Boucekinus* + (*Platykula* + one undescribed genus from Chile) (clade 3) (99/1/80) sister to a monophyletic (67/0.98/-) group containing all other Torymoidini (clade 4) (74/1/-) + Torymini (clade 5) (100/1/91). Torymoidini (clade 4) is monophyletic and the sister group of Torymini in both ML and BA (Figs 1a, S3b) analyses, with Holarctic *Pseudotorymus* (subclade 4a) (i.e., excluding French Guiana *cf. Pseudotorymus* - PJAN1056) (99/1/98) sister to a strongly supported clade (90/1/-) including *Torymoides* (subclade 4b) and subclade 4c, which consists of a Neotropical species of *cf. Pseudotorymus* (PJAN1056) and species included in *Ameromicrus, Didactyliocerus* and *Senegalella* that previously were classified in *Pseudotorymus* or *Torymoides* (see further below). Torymoidini (clade 4) was paraphyletic in the MP analysis (Fig. bS4b) with Holarctic *Pseudotorymus* (subclade 4a) sister to Torymini (clade 5, support <50).

The tribe Torymini (clade 5, Figs 1b, S3b, S4b) was recovered as monophyletic in all analyses (100/1/91), but with different ingroup topologies. The genus *Torymus* was polyphyletic and divided into two major and a few minor clades. In all analyses, most New World species of *Torymus* and all New World species of *Physothorax* as well as the subgenus *Nannocerus* of *Torymus* were clustered into a poorly supported clade (subclade 5a; 51/0.72/-). The second major clade (subclade 5b) included most Old World species and a few Nearctic species (88/1/58) of *Torymus*. The position of species belonging to the genus *Diomorus*, as well as the genus *Ecdamua* and one species of *Torymus* sp. from Chile, were unstable and recovered in multiple positions in the different reconstructed topologies.

In ML and BA analyses, the remaining Torymidae *s.s.* (73/1.00/-) were subdivided into two clades (Figs 1c-d, S3c-d). A poorly supported clade (48/0.76/-) included several species of *Glyphomerus* (clade 6) + Microdontomerinae (clade 7) and a well supported clade (71/1/-) grouping all Monodontomerinae (clade 8), *Propalachia* spp. (clade 9), *Palachia* spp. (clade 10) and Podagrionini (clade 11). MP analysis (Figs S4a-c) resulted in different topologies with Microdontomerinae always sister to Glyphomerinae + (Toryminae + (Monodontomerinae + Podagrioninae)). In MP analysis, bootstrap values supporting these lineages were always <50.

Glyphomerus was always recovered as paraphyletic. Three species of *Glyphomerus* (including the type species, *G. stigma* from Europe, and two undescribed species from Canada) grouped in a strongly supported clade (clade 6) (100/1/100), while three other species of *Glyphomerus* (subclade 7a) formed a well-supported clade that was nested within all species of Microdontomerinae (subclade 7a) (100/1/99). The position of clade 6 varied in the different analyses. Clade 6 was recovered sister to tribe Microdontomerinae (clade 7) (some ML and all BA analysis, <50/0.76/-, Figs 1c, S3c), sister to (Monodontomerinae (clade 8) + (*Propalachia* spp. (clade 9) + (Palachiini (clade 10) + Podagrionini (clade 11))) (some ML analyses, <50/-/-) or sister to (Torymoidini (clade 4) + Torymini (clade 5)) + (Monodontomerinae (clade 8) + (*Propalachia* spp. (clade 9) + (Palachiini (clade 10) + Podagrionini (clade 11))) (in MP analysis, -/-/<50, Figs S4b-c).

Within Microdontomerinae (clade 7, 100/1.00/99), all of the genera were monophyletic, and strongly supported with the exception of *Eridontomerus, Idiomacromerus* and *Pseuderimerus*. *Eridontomerus* was rendered paraphyletic by the type species of *Ditropinotus, D. aureoviridis,* whereas *Pseuderimerus* was rendered paraphyletic by *Erimerus,* and *Idiomacromerus* was polyphyletic in all analyses (Figs 1c, S3c, S4a). Several genera previously classified as *incertae sedis* relative to tribal placement were placed in our clade 7 with high support, namely *Cryptopristus*, *Echthrodape, Exopristus*, and *Glyphomerus* in part. *Echthrodape* was recovered as sister to the rest of Microdontomerinae.

Monodontomerinae (clade 8) were monophyletic (91/1.00/83) and included *Zaglyptonotus* (unplaced to tribe by Grissell, 1995). Monodontomerinae were subdivided into three subclades in all analyses. *Zdenekius* (subclade 8a) was recovered sister to all other Monodontomerinae (67/-/53), and all other Monodontomerinae were subdivided into subclade 8b (predominantly Old World species, 100/1/99) and subclade 8c (New World species, 88/1/73) with strong support values. *Monodontomerus* (51/0.99/-) was rendered paraphyletic by *Rhynchoticida maai* in all analyses (Figs 1d, S3d, S4c). Although the support for this topology was always low (<50 in all analysis), it is necessary to test these relationships in future studies using broader taxon sampling and more markers.

In all analyses, *Propalachia* spp., *Palachia* spp. (Palachiini *sensu* Grissell, 1995), and Podagrionini formed a monophyletic clade (74/0.98/-) within Torymidae *s.s*. *Propalachia* spp. (clade 9) was sister (98/1.00/-) to *Palachia* spp. (clade 10) + Podagrionini (clade 11) (Figs 1d, S3d, S4c).

Podagrionini (clade 11) was always recovered as monophyletic (73/1.00/75), as well as most of the Podagrionini genera (*Propachytomoides* (79/0.96/64), *Palmon* (100/1.00/97), *Mantiphaga* (100/1.00/100), *Podagriomicron* (85/0.98/68), and *Podagrion* (99/1.00/83)). *Podagrionella* was polyphyletic in all analyses. The support values of the backbone of Podagrionini were always low and topologies varied across analyses.

Character mapping

Biogeographical history

While the biogeographical origin of Torymidae *s.s.*and those of most tribes remained equivocal using parsimony reconstruction, the common ancestor of Megastigmidae was shown to have an Australasian origin (Fig. S5a). Similarly, maximum likelihood favored an Australian over a Palaearctic origin of the Megastigmidae (proportional likelihoods of 0.79 and 0.19, respectively). The most likely ancestral area of Torymidae *s.s.* was the Palaearctic region (proportional likelihood of 0.90). Within Torymidae *s.s.*, only the ancestral areas of Chalcimerinae, clade 3 (*Boucekinus*, *Platykula* and one undescribed genus from Chile), and clade 9+(10+11) (*Propalachia* spp., *Palachia* spp. and Podagrionini) were identified using a maximum parsimony approach. These areas were the Palaearctic for Chalcimerinae (proportional likelihoods of Palaearctic origin was 0.96), the Neotropics for clade 3 (proportional likelihoods of Neotropical origin was 0.8 over 0.15 for Palaearctic origin), and the Afrotropical region for clade 9+(10+11) (proportional likelihoods of Afrotropical origin was 0.67 over 0.23 for Palaearctic origin) (see Figs 1, S5 and Table S2).

Parasitoid larvae life-history

Both ML (proportional likelihood of 0.97) and MP analyses suggested that the ancestral biology of Torymidae *s.s.* was ectoparasitism on larvae of gall-forming Cynipidae (see Figs 1, S6). This was also the case for the common ancestor of Chalcimerinae, of clade 6 (*Glyphomerus*) and of Microdontomerinae (proportional likelihood of 0.99, 0.99 and 0.89 respectively). The MP ancestral biology of clades 3, 4 and 5 was ectoparasitism on larvae of gall-forming Cecidomyidae (Diptera). However, ML analysis estimated states 0, 1 and 11 as almost equiprobable for clades 4+5 (proportional likelihood of 0.34, 0.33 and 0.30 respectively), states 1 and 11 for clade 4 (proportional likelihood of 0.5, and 0.48 respectively), and it highly favored state 0 for clade 5 (proportional likelihood of 0.90). The ancestral biology of *Palachia* spp. and Podagrionini was estimated to be parasitism of Mantodea eggs using both MP and ML approaches (see Figs 1, S6 and Table S3).

Discussion

The monophyly of Torymidae *sensu* Grissell (1995) (i.e. Megastigminae + Toryminae) was not supported by our analyses, which contradicts most previous studies based on morphology (e.g., Bouček, 1988; Grissell, 1995; Heraty et al., 2013), but see Campbell et al. (2000) and Munro et al. (2011). Grissell (1995) discussed all characters previously used for the definition of Torymidae and pointed out that Torymidae could be defined by the concomitant presence in females of an occipital carina (character 1 in Grissell (1995) dataset), an exserted cercus (char. 23), a flap-like and articulated metasomal tergite 9 (Mt_9) separated from Mt_8 (char. 24), the construction of Mt_8 and position of the cercus (part of char. 23 in Grissell (1995) dataset), and a hypostomal bridge, constituted by the fusion of the hypostomal carina ventrad to the occipital foramen (not used in Grissell (1995) dataset). However, as Grissell (1995) stated, because of character variability within the family, there is no unique synapomorphy to define

Torymidae. Furthermore, these characters are homoplastic and are partly found in several other Chalcidoidea lineages.

Using a combination of molecular and morphological evidence, Heraty et al. (2013) recovered Torymidae as monophyletic. The authors specified the following character states as putative synapomorphies of Torymidae: sulci extending from tentorial pits (46: 1), mesepimeron with posterior margin notched (110: 1), fore wing with basal lobe present (141: 1), fore wing with Rs absent (159: 3), basitarsus with ordinary setae (186: 2), Mt_{8-9} articulating (211: 0, character 24 in Grissell (1995); also define Agaonidae), cercus arising from membranous area (217: 1, character 23 in Grissell (1995); also define Agaonidae) and valvifers without sclerotized bridge between them (224: 0). However, these hypothesized character state polarities were established using the most parsimonious explanation of character transformation based on position of Torymidae with respect to other chalcidoid taxa; in some cases (for example characters 46 and 110) they are likely symplesiomorphies rather than synapomorphies. No unique character state defines Torymidae as most occur, at least partly, in other Chalcidoidea families. In Heraty et al. (2013), Ormyridae and *Colotrechnus* (Pteromalidae: Colotrechninae) formed the sister group of a monophyletic Torymidae, however with poor support values. This relationship is morphologically corroborated by the presence of a sulcus extending from the posterior tentorial pits (46: 1 in Heraty et al., 2013), the broad metanotal scutellar arm (124: 0) and the presence of a setal line defining the cubital vein (144: 3, reversed in *Ormyrulus* and *Echthrodape*).

In our ML and BA analyses, Megastigmidae is nested within a clade that also includes Ormyridae, some Pteromalidae (Colotrechninae: *Zeala walkerae* and Epichrysomallinae: *Odontofroggatia* spp.) and Agaonidae (MP results in similar topology but Agaonidae are excluded from the clade). However, using the characters of Heraty et al. (2013), there are again no synapomorphies defining this clade (except Agaonidae + Megastigmidae in ML and BA analysis - characters 211: 0, 217: 1). Based on our analyses, Megastigmidae always appear more closely related to Ormyridae, Pteromalidae (Colotrechninae and Epichrysomalinae), and possibly also to Agaonidae, than to Torymidae. This result is supported by an analysis of the morphology of the last larval instar (Gómez et al., 2008), which failed to recover a monophyletic Torymidae *sensu* Grissell (1995) and suggested instead that Megastigminae and Toryminae were not related. In their study, the authors showed that larvae of *Megastigminae* have bare body segments (bare or only with very short setae), mandibles with four or five teeth and labrum divided into several small lobes. In contrast, larvae of Toryminae have hairy body segments, mandibles with a single tooth and an undivided labrum (Gómez et al., 2008; Nieves-Aldrey et al., 2008). Gómez et al. (2008) also suggested that Toryminae and Eupelmidae (using *Eupelmus* only) could be closely related. All other included taxa (Pteromalidae, Eulophidae, Ormyridae and Megastigminae) differed from Toryminae + Eupelmidae by having very short setae or no setae on the abdominal segments. However, as Gómez et al. (2008) stated, Megastigminae, Ormyridae and Eurytomidae do not appear to be closely related, as they differ significantly in several other morphological characters of the larva.

We propose here to elevate Toryminae and Megastigminae (*sensu* Grissell, 1995) to family rank (namely Torymidae *s.s.* and Megastigmidae). Within Torymidae *s.s.*, we also recognize six subfamilies, namely Monodontomerinae, Toryminae, Podagrioninae (both **stat. rev**.), and Chalcimerinae, Glyphomerinae, Microdontomerinae (all **subf. nov.**), and the tribes Palachiini, Torymoidini (both ***sensu*** **nov.**), and Boucekinini and Propalachiini (both **trib. nov.**).

Megastigmidae stat. rev.

Diagnosis. Excluding five morphological features (symplesiomorphies) shared with Torymidae, Megastigmidae are defined as follows: body yellow with dark parts (less frequently with metallic color); clypeus either bilobed, deeply incised medially, or margin produced as a broad angle or median tooth; head and dorsal part of mesosoma with only a few, usually dark and symmetrically distributed long setae; pronotum dorsally elongate, usually almost as long as mid lobe of mesoscutum; marginal vein often shorter than postmarginal vein; stigmal vein always developed, branching off most commonly at almost right angle with marginal vein, and accentuated by knobbed stigma, the stigma usually higher than wide, with height subequal to or greater than height of costal cell (some species with only moderate size stigma, but these with considerably long stigmal vein), stigma often surrounded by infuscated area; basal setal line usually well pigmented, in some genera developed into basal vein that posteriorly is curved outwards; hind coxa relatively short, not more than two times length of mid coxa (Bouček, 1988; Grissell, 1995, 1997).

Although Megastigmidae are distributed worldwide, most of their diversity (9 of 12 genera) has been reported from the Australian region (Bouček, 1988). However, the diversity in other regions, especially on angiosperm plants, appears to be underestimated (Roques et al. 2016) and many species remain to be described. Many species are parasitoids of various plant gallers, whereas others are phytophagous (feeding on seeds or as gall makers, e.g. *Bortesia*) (Bouček, 1988). Several phytophagous species of Megastigmidae are considered as serious pests (Roques et al. 2010, Auger-Rozenberg & Roques 2012).

Discussion. The monophyly of Megastigmidae (as Megastigminae) has never been questioned (Bouček, 1988; Grissell, 1995). However, no phylogenetic classification of Megastigmidae has been proposed and our analysis is the first to include a significant number of genera. In all of our analyses Megastigmidae is monophyletic with very high support though the relationships between the genera remain unresolved. ML analysis favours an ancestral feeding strategy phytophagy (*Bootanomyia dorsalis* and *B. stigmatizans*), and zoophagy appears to have originated at least twice independently in the genera *Bootanomyia* part 1 and *Neomegastigmus*. Our analyses also highlight that the phytophagous *Megastigmus* is the last lineage to diverge.

In our analyses, the metallic Palaearctic species of *Bootanomyia* (*Bootanomyia* part 1, that are zoophagous and were historically included within *Megastigmus*) do not group with the Australian species of the genus (*Bootanomyia* part 2) (Figs 1a, S3a) as advocated by Doğanlar (2011a) and should be excluded from that genus. Indeed, in addition to the metallic coloration of adults, the larvae of *Bootanomyia* have a medial pit on the frons (Askew, 1966) that is not present in phytophagous *Megastigmus* (Nieves-Aldrey et al., 2008). However, the larvae of species belonging to *Bootanomyia* part 2 are unknown and support for these two groups is high only in BA analysis. Until the adult morphology is more thoroughly studied, we do not yet want to assign *Bootanomyia* part 1 to a new genus.

Torymidae stat. rev.

Diagnosis. Torymidae are defined by having: body of most taxa with metallic coloration, rarely only yellow; clypeus not bilobed (in marginal cases with deep emargination only); setation of head and dorsal part of mesosoma irregular, not symmetrically distributed, often dense and adjacent; pronotum dorsally usually not elongate, transverse, noticeably shorter than mid lobe of mesoscutum; marginal vein usually obviously longer than, rarely subequal in length to postmarginal vein, stigmal vein branching off at an acute angle (usually about 45°) with marginal vein, and stigma subquadrate or wider than high, its height less than height of costal cell; hind coxa elongated, at least about 2.5 times length of mid coxa (Bouček, 1988; Grissell, 1995, 1997).

Biology and distribution is discussed in detail within specific tribes.

Discussion. The monophyly of Torymidae *s.s.* (as Toryminae) has been demonstrated by several studies based on both molecular and morphological characters (Grissell, 1995; Campbell et al., 2000; Munro et al., 2011; Heraty et al., 2013) and is corroborated by our results. However, no unique synapomorphy defines the clade, and the group is instead defined by a combination of five character states shared in part by other chalcid families, including Megastigmidae (Bouček, 1988; Grissell, 1995). Our analyses also corroborate the monophyly of nearly all tribes morphologically defined by Grissell (1995). However, the relationships between the tribes differ from those proposed by Grissell (1995) (Figs 1b-d, S1, S3b-d, S4).

Chalcimerinae subf. nov.

Diagnosis. Malar space long, more than 0.5 times height of eye; antennal clava without micropilosity area; occipital carina dorsally arched, nearer posterior ocelli than occipital foramen, lateral margins not nearly reaching upper half of hypostomal carina; posterior tentorial sulci elongate; marginal vein as long as postmarginal vein (except in *Thaumatorymus*) and 2 times longer than stigmal vein; metasomal terga not emarginate.

All three genera have similar distributions (restricted to the West Palaearctic region) and share similar biologies (parasitoids of Aylacini gallwasps, Cynipidae).

Discussion. Chalcimerinae **(subf. nov.)** (clade 2) is sister to all other subfamilies of Torymidae. This clade includes *Chalcimerus* and two genera that were previously unclassified to tribe: *Exopristoides* and *Thaumatorymus*. *Chalcimerus* was formerly treated as Chalcimerini (*sensu* Bouček, 1978) and the sister group of Podagrionini (Grissell, 1995). This relationship was supported by several putative morphological synapomorphies (enlarged hind leg with toothed femora and curved tibia bearing only one apical tibial spur). However, these features appear to be homoplastic across Chalcidoidea (Heraty et al., 2013), and consequently the hypothesis of synapomorphy and proposed relationship between Podagrionini and *Chalcimerus* is likely based on convergence. Our inclusion of the three genera in Chalcimerinae is mostly based on our molecular results, corroborated also with some morphological character states (see above) suggesting their close relationship and enabling a differential diagnosis of the tribe. However, some of diagnostic states defined by Grissell (1995, p. 141) cannot be assumed for Chalcimerinae because they characterize only *Chalcimerus*. Synapomorphies of Chalcimerinae are now considered only to be shape of the occipital carina and posterior tentorial sulci.

Toryminae stat. rev.

Diagnosis. Occipital carina present, dorsally arched, closer to posterior ocelli than to occipital foramen and with its ventrolateral edges extending at least below ventral margin of occipital foramen, often reaching an imaginary line drawn horizontally across dorsum of hypostoma; metepisternum with anterior edge of propodeal foramen located about midway between anterior and posterior margins of hind-coxal foramen, metepisternal area transversely narrowed to strip half as long as diameter of propodeal foramen, without metepisternal shelf; marginal vein most often relatively long, most often 3 to 7 times length of postmarginal vein and at least 6 times length of stigmal vein, latter sessile or subsessile; hind femur usually simple, though sometimes angulate or with single or double teeth; hind tibia usually straight, at most slightly curved (in some *Diomorus*), apex truncate (margins at right angle), and with 2 spurs at ventral corner; Mt_2 not emarginate laterally, usually dorsomedially emarginate.

Discussion. Members of clades 3, 4 and 5 (Toryminae) share only one hypothesized synapomorphy, the *Torymus*-like wing venation as defined above (Grissell, 1995, Fig. 42 - character 8, state Tory; Janšta et al., 2011). Other character states mentioned above are present randomly in other tribes. Torymoidini *sensu* Grissell (1995) is subdivided into two clades, Boucekinini (clade 3) and Torymoidini (clade 4). The latter is sister to Torymini.

Boucekinini trib. nov.

Diagnosis. Metepimeron (lateral panel of metapleuron) with anterior margin straight; marginal vein very long, about 4.5-8 times as long as postmarginal vein and 11-16 times as long as stigmal vein, stigmal vein sessile (Grissell, 1995; Janšta et al., 2011).

Boucekinini comprises only New World members, *Boucekinus,* one undescribed genus from Chile, and *Platykula*. The biology is only known for *Boucekinus,* which is parasitoid of gall-forming Cecidomyidae (Janšta et al. 2011).

Discussion. Except for character states mentioned above, there has been no morphological characterization of taxa in this tribe until now. As previously noticed (Janšta et al., 2011), based on wing venation *Boucekinus* appears to be morphologically similar to *Platykula*. However, based on our analyses we propose a new tribe (**Boucekinini trib. nov**.) to include all species in clade 3.

Torymoidini *sensu* nov.

Diagnosis. Metepimeron with anterior margin straight; marginal vein very long, but at most 3.5-8 times as long as postmarginal vein and 8 times as long as stigmal vein, stigmal vein at least short subsessile; hind femur simple or with subapical angle ventrally (Grissell, 1995).

Members of this tribe are distributed throughout the world with most species in the Palaearctic and Australian regions. Torymoidini are mostly parasitoids of larvae of gall-forming Cecidomyiidae, Cynipidae and Tephritidae in various plant families, or parasitoids feeding on larvae of Bruchidae (Coleoptera) or Eurytomidae (Chalcidoidea) in seeds of Fabaceae (Grissell, 1995).

Discussion. In our analyses, Torymoidini (clade 4) is restricted to *Torymoides* and *Pseudotorymus.* The genera *Ameromicrus, Didactyliocerus* and *Senegalella*, that we recognize here, were previously synonymized under *Torymoides* and *Pseudotorymus*. The Palaearctic species of *Pseudotorymus* (subclade 4a) is sister to the rest of Torymoidini. Subclade 4b includes only species of *Torymoides*. The species from Australia and New Zealand are the sister group to the Palaearctic (*Torymoides kiesenwetteri*) and African species within this clade. Subclade 4c constitutes the rest of Torymoidini. This clade contains several lineages that previously had been synonymized under either *Torymoides* or *Pseudotorymus* (Figs 1b, S3b), and one undescribed genus (*cf. Pseudotorymus*) from French Guiana. The latter is morphologically similar to other *Pseudotorymus* species (subclade 4a and part of subclade 4c - i.e. *Senegalella*), but molecularly separated. We could not find any evident morphological character that would differentiate these two taxa.

Torymoides violaceus was described in *Ameromicrus* (Nikol'skaya and Kjao, 1954) but was transferred to *Torymoides* by Grissell (1995). *Ameromicrus* has marginal vein shorter (only about 6 times stigmal vein length vs 8 times) than *Torymoides* (subclade 4b) and Grissell (1995) did not consider that it should warrant generic status. *Torymoides dispar* was described in *Didactyliocerus* (Masi, 1916) and was later synonymized by Bouček (1988). Bouček (1988) did not consider that absence of a mesepimeral dividing groove in females (but present in males) of *D. dispar* was enough to separate the two different genera. However, because these two species stand far away from all other species belonging to clade 4b (contains only *Torymoides*), and furthermore have some morphological differences, we propose to restore the two generic names (i.e. *Ameromicrus violaceus* and *Didactyliocerus dispar* **stat**. **rev**.).

Risbec (1951) described the Afrotropical genus *Senegalella*, which differs from *Pseudotorymus* only by the absence of setae on the dorsal surface of the hind coxa in combination with a hind femur lacking a tooth. Grissell (1995) discovered undescribed species of *Senegalella* in the Oriental region, northern Africa and southern Europe, and based on these distribution records synonymized *Senegalella* with *Pseudotorymus*. The crown group of subclade 4c was comprised only of Afrotropical species of *Pseudotorymus* with bare hind coxae, and this group was strongly supported in almost all analyses. Therefore, *Senegalella* (with bare hind coxa dorsally and unmodified hind femur lacking a tooth) appears to be a valid genus, sister to *Didactyliocerus dispar,* and should be restored (**stat**. **rev**.).

Torymini *sensu* Grissell (1995)

Diagnosis. The diagnosis, distribution and biology of Torymini is the same as stated in Grissell (1995, p. 98).

Discussion. Torymini (clade 5, Figs 1b, S3b) is well supported in our analyses and is corroborated morphologically by members having metepimeron with anterior margin sinuate (Grissell, 1976, p. 105, fig. 1, cited as "sinuate metapleural margin"). However, relationships within Torymini are still unresolved. *Torymus* forms a polyphyletic assemblage with different topologies across all analyses. Subclades 5a-c are the only clades consistantly recovered and relatively well supported in all analyses (support of 5a and 5b in MP analysis were > 50). Subclade 5a includes some New World species of *Torymus* (including the subgenus *Nannocerus sensu* Bouček, 1993) and *Physothorax*. The biology of almost all *Torymus* species belonging to this clade is unknown, however species of *Physothorax* and *Torymus* (*Nannocerus*) are associated with figs. Bouček (1993) reported *Physothorax bidentulus* as parasitic on larvae of gall-forming Cecidomyiidae within *Ficus* syconia. From our results, we infer that most species of *Physothorax* and *Torymus* (*Nannocerus*) develop as parasitoids of Cecidomyiidae or other gall-forming fig wasps. Moreover, these species are only known from the neotropics (with a few species reaching Florida, i.e. *P. bidentulus*). The morphological differences between *Physothorax* and *Torymus* (*Nannocerus*) are: 1) the number of ventral teeth on the hind femur (one in *T.* (*Nannocerus*) and two or sometimes more than two in *Physothorax*), and 2) the presence of winged males in *Physothorax* versus apterous males in *T.* (*Nannocerus*) (Ashmead, 1904; Bouček, 1993). Torymini is the only known group of Torymidae containing species with apterous males. Apterism probably evolved as an answer to the association with figs as previously observed in several other fig wasps (Cruaud et al., 2010, 2011b; Segar et al., 2012). Based on such evidence (high bootstrap support in all analyses and clear morphological and biological traits), we propose that *Nannocerus* should be ranked as a genus (**stat. rev.**) as originally established by Mayr (1885) rather than as a subgenus of *Torymus*.

Subclade 5b includes part of the formerly recognized genus *Diomorus*, which has been repeatedly synonymized under *Torymus* (Graham and Gijswit, 1998; Zerova et al., 2000; Zavada, 2003) and resurrected to genus level (Zerova et al., 2003). Within this clade, larvae of *Diomorus armatus* and *D. cupreus* are ectoparasitic on larvae of aculeate wasps, a biology also shared with *Ecdamua* species (Graham and Gijswit, 1998; Zerova et al., 2003) and *D. orientalis* (pers. observ.). However, the position of *Ecdamua* and *D. orientalis* varies across our analyses and there is no evidence to suggest this strategy evolved only once in Torymini, thus rendering *Diomorus* a paraphyletic genus.

Subclade 5c cosists of a majority of the *Torymus* species included in our analyses, plus *Torymus splendens* **comb. n.** *Torymus splendens*, the type species of *Allotorymus,* differs from other species of *Torymus* by its elongate pronotum and a strongly clavate flagellum, but other character states are shared with species from the *Torymus laetus* species-group (Grissell, 1976; Graham and Gijswit, 1998; Zavada, 2003). Therefore, we propose synonymy of *Allotorymus* under *Torymus* (**syn. nov.**).

Our sampling of Torymini is not representative of the overall diversity of the tribe (only five of the ten genera), therefore we do not make other taxonomic changes until the relationships are confirmed by an analysis including more genera.

Toryminae (clades 3-5) is sister to Glyphomerinae (clade 6) + Microdontomerinae (clade 7) and Monodontomerinae (clade 8) + Podagrioninae (clade 9 (Propalachiini) + (clade 10 (Palachiini) + clade 11 (Podagrionini)).

Glyphomerinae subf. nov.

Diagnosis. Occipital carina present and arched dorsally along entire length, situated midway between the posterior ocelli and dorsal margin of occipital foramen; lateral edges of occipital carina at level of occipital foramen, situated midway between posterior tentorial sulci and posterior margin of eye; ventrally occipital carina almost reaching hypostomal carina above base of maxillolabial complex; marginal vein about as long as postmarginal vein and twice as long as stigmal vein; metasomal terga not emarginate.

Glyphomerinae have a Holarctic distribution with many species undescribed in the Nearctic region. Where known, all are parasitoids of gall-forming Cynipidae on *Rosa* spp. (Grissell, 1995).

Discussion. The position of clade 6 (part of *Glyphomerus* species, Figs 1c, S3c, S4b) varies in our analyses and support values are always low. Based on the study of *G. stigma*, Grissell (1995) included *Glyphomerus* as *incertae sedis* within Toryminae and placed it in a basal multifurcation. He found no morphological support to allocate *Glyphomerus* to any of the torymid tribes and defined the genus on a combination of several plesiomorphic character states. In our analyses, *Glyphomerus* appears polyphyletic. While *Glyphomerus stigma*, the type species of *Glyphomerus*, and two other undescribed species from Canada are members of clade 6, *G. aylax* and *G. tibialis* are part of clade 7 (Microdontomerini). *Glyphomerus stigma* and two species not included in our analyses, *G. carinatus* and *G. montanus,* as well as two undescribed Canadian species, differ from all other *Glyphomerus* species (including *G. aylax* and *G. tibialis*) by a more expanded occipital carina and long malar space up to 0.33 length of an eye (Stojanova, 2005). Both groups contain species associated with gall wasps on *Rosa* spp., but some species of the last group develop also on larvae of Aylacini (Cynipidae) gall wasps on herbs (Noyes, 2017). Consequently we propose limiting *Glyphomerus* to those species in clade 6 and recognize this clade as the subfamily Glyphomerinae (**subf. nov.**). This clade does not link within any other subfamilies of Torymidae *s.s.* as they are defined herein and is itself well supported. The species previously classified in *Glyphomerus* and now excluded from the genus form a clade within the new subfamily Microdontomerinae (subclade 7a, see below).

Microdontomerinae subf. nov.

Diagnosis. Occipital carina absent, vaguely indicated or, if present, with ventrolateral edges not extending below imaginary line drawn horizontally across ventral margin of occipital foramen, and dorsally nearer to posterior ocelli than occipital foramen; metepisternum with anterior edge of propodeal foramen placed about midway between anterior and posterior margins of hind-coxal foramen; metepisternal area transversely narrowed to strip half as long as diameter of propodeal foramen, without metepisternal shelf; marginal vein 1.5 to 2.8 times length of postmarginal vein and 2-4.5 times length of stigmal vein; hind femur simple, serrate, enlarged or toothed; metasomal terga not emarginate or Mt_{2-3} dorsomedially deeply emarginate.

Microdontomerini have a mostly Holarctic distribution with a few exceptions reaching into the Afrotropical, Neotropical, Oriental and Australian regions (*Echthrodape*, *Eridontomerus*, *Erimerus*, *Idiomacromerus*, *Microdontomerus*). The members of this tribe exhibit diverse biologies. They mostly parasitize gall-forming Cynipidae, Eurytomidae (Hymenoptera) and Tephritidae (Diptera). Their larvae can also be ectoparasitic on larvae of Eurytomidae in seeds of Fabaceae (*Idiomacromerus*), of aculeate Hymenoptera (*Echthrodape*, *Microdontomerus*), or, in other *Microdontomerus* species, are parasitoids of various life stages of Lepidoptera (including eggs), eggs of beetles, and Mantodea eggs (Grissell, 1995; Janšta et al. 2016).

Discussion. We classify the monophyletic clade 7 (Figs 1c, S3c, S4a) as the Microdontomerinae (***subf. nov***.). *Echthrodape* was not included in previous phylogenetic analyses and was not placed to tribe by Grissell (1995). Indeed, *Echthrodape* is morphologically outstanding within Torymidae and is ectoparasitic on pupae of different *Braunsapis* species (Apidae: Allodapini) (Grissell, 2007). In our analyses, *Echthrodape* is sister to all other Microdontomerini. For the time being we consider the genus as part of Microdontomerinae because they share several character states with other members of this subfamily. The other nodes in clade 7 without *Echtrodape* have generally lower support and we cannot be sure that *Echtrodape* is really sister taxa to the rest of clade 7 or might be included. This is confirmed also by shape of the occipital carina, which is similar to that of *Exopristus* or *Cryptopristus*, and the same organization of the metepisternum as is known for the rest of Microdontomerinae. Moreover, Microdontomerinae are biologically diverse and bee parasitism is known at least also within *Microdontomerus*. As stated above, Microdontomerinae also includes some genera (*Cryptopristus* and *Exopristus*) previously not assigned to tribe by Grissell (1995) as well as some species currently classified in *Glyphomerus*. The relationships of *Glyphomerus s. l.* are discussed above. Grissell (1995) considered *Cryptopristus* and *Exopristus* to be related to Monodontomerinae or a clade consisting of Chalcimerinae, Palachiini and Podagrionini because they share the same modification of the hind femora; however, as stated above, this character is homoplastic. Following *Echthrodape*, *Exopristus* is sister to all other Microdontomerinae. *Cryptopristus* is sister to the genus *Idarnotorymus*. Both genera have the hind margin of the metasomal tergites distinctly emarginate, Microdontomerinae-like occipital carina, and distinctive morphology of the metepisternum; they are respectively parasitoids of gall-forming Eurytomidae in stems of Poaceae and of gall-forming Aylacini (Cynipidae) in herb stems (Grissell, 1995; Zerova et al., 2008).

The genera *Microdontomerus* and *Adontomerus sensu* Grissell (1995) are monophyletic. However, *Pseuderimerus* is paraphyletic with respect to *Erimerus*. *Pseuderimerus* and *Erimerus* share two common character states: 1) a single apical spur on the hind tibia and 2) males of some species with reduced eyes (Grissell, 1995; Burks and Redak, 2004). Therefore we synonymize *Pseuderimerus* under *Erimerus* (**syn. nov.**). *Eridontomerus* is also paraphyletic with respect to *Ditropinotus aureoviridis*, although *Eridontomerus* and *Ditropinotus* were considered as distinct genera by Grissell (1995). However, all the character states that discriminate these genera appear to be homoplastic and there is no synapomorphy that reliably characterizes them (Janšta - pers. obs.). Moreover, the species belonging to these genera share the same biology, recurrently reported as larval parasitoids of Eurytomidae (Chalcidoidea) in grass stems (Grissell, 1995; Janšta and Bouček, 2006). Consequently we synonymise *Ditropinotus* under *Eridontomerus* (**syn. nov.**). *Idiomacromerus sensu* Grissell (1995) is polyphyletic, with most species forming a well-supported clade within Microdontomerinae, but with two species as separate clades within *Adontomerus* + *Erimerus*.

Idiomacromerus arcus, which was described in *Liodontomerus* by Bouček (1969) but transferred to *Idiomacromerus* by Grissell (1995), is recovered as sister to *Adontomerus* species in all analyses (Figs 1c, S3c). Grissell (1995) could not find any feature differentiating *Idiomacromerus* and *Liodontomerus* and consequently synonymized them. However, a few characters appear to discriminate *Idiomacromerus* (*sensu* Grissell, 1995) and *Adontomerus*, such as relative length of the marginal and postmarginal veins to the length of the fore wing and the presence of one vs two anelli. However, as mentioned above, these characters are not reliable to discriminate genera within Torymidae. Moreover, some of the *Adontomerus* species analysed here exhibit two anelli (PEJ_1243). Therefore the transfer of some *Idiomacromerus* (*Liodontomerus*) species to *Adontomerus* is needed.

Monodontomerinae stat. rev.

Diagnosis. Antenna with only one anellus; occipital carina well developed, dorsally flat, closer to occipital foramen than posterior ocelli, with ventrolateral edges reaching hypostomal carina at its median point (except *Chileana* and *Zaglyptonotus* - in which occipital carina does not abut hypostomal carina, dorsum of occipital carina being located midway between posterior ocelli and occipital foramen; and *Oopristus* - where occipital carina is lacking); anterior edge of propodeal foramen closer to posterior edge of hind coxal foramen than anterior edge; inner coxal carinae joining medial edge of propodeal foramen and continuing to anterior margin of plate; metepisternal area longitudinally narrowed, subequal to diameter of propodeal foramen in length; marginal vein 2-3 times as long as postmarginal vein and 4-6 times as long as stigmal vein; hind femur with single tooth distally, or medially placed tooth with or without additional femoral modifications, or enlarged with 1 or 2 rows of teeth; hind tibia straight or curved, always with apex truncate and bearing two spurs; metasomal terga not laterally emarginate, dorsomedially truncate in most genera, except *Chileana*, *Oopristus* and *Zaglyptonotus*, with $Mt_{2\text{-}4}$ emarginate (Grissell, 1995; Janšta et al. 2013).

About half of Monodontomerinae species are Holarctic, with the rest distributed in other zoogeographic regions. Members of this subfamily parasitize predominantly Lepidoptera pupae, larvae of aculeate wasps and bees, and sawflies and larvae of their hyperparasitoids. This is the only group of Torymidae that attack eggs of Heteroptera and Orthoptera. Some species (genus *Zaglyptonotus*) lay eggs into galls caused by various groups of insects (Grissell, 1995).

Monodontomerinae (clade 8, Figs 1d, S3d) are monophyletic in all our analyses. The subfamily is well defined by the morphological characters proposed by Grissell (1995), although *Chileana* and *Zaglyptonotus* each bear a distinct occipital carina not known in other Monodontomerinae (Janšta et al., 2013). Both *Zdenekius* and the Neotropical genus *Rhynchodontomerus* were considered to be basal monodontomerines by Grissell (1993, 1995). Our results (ML and MP analyses) place *Zdenekius* (subclade 8a) as sister to all other Monodontomerinae, whereas *Rhynchodontomerus* is nested within the clade, sister to *Zaglyptonotus* (ML analyses) or to *Chileana* and one undescribed New World genus of Monodontomerinae (MP and BA analyses).

Beyond *Zdenekius*, Monodontomerinae are segregated into two geographically defined subclades. Subclade 8b includes mostly Old World genera (*Monodontomerus, Anneckeida* and *Rhynchoticida*) plus the Holarctic *Monodontomerus*. In our results, *Monodontomerus* is paraphyletic with respect to *Rhynchoticida*, however this relation could be artefactual as we failed to sequence most genes for *Rhynchoticida* (only 28S rDNA is sequenced) (Table S1 and Figs 1d, S3d). Morphologically, *Rhynchoticida* (small bodied with an unusually short ovipositor) is similar to *Anneckeida* and a few other Monodontomerinae (not included here) that are egg parasitoids of Heteroptera or Orthoptera, which is a peculiar biology for Monodontomerinae. The third subclade (8c) includes the New World genera *Chileana*, *Perissocentrus*, *Zaglyptonotus*, and two undescribed genera. *Zaglyptonotus* was treated as *incertae sedis* by Grissell (1995) because it shares features with Torymoidini. Recently, Janšta et al. (2013) described *Chileana*, which shares several features (e.g. long hind tibial spurs, incision of hing margin of metasomal tergites) with *Zaglyptonotus*, and this close relationship is supported here by our molecular results.

Podagrioninae stat. rev.

Diagnosis. Antenna with clava formed of 3 flagellomeres, which in females are frequently indistinctly delimited ventrally by sutures and with large area of micropilosity ventrally over entire length of clava (except in some genera like *Mantiphaga*, *Neopalachia*, *Iridophaga*, where clava formed 3 well separated flagellomeres with very small or no micropilosity area); occipital carina dorsally arched, nearer to posterior ocelli than to dorsum of occipital foramen, ventrolaterally expanded, joining hypostomal carina near base of mandibles; metepisternal shelf always present, but with metepisternum variable, either with propodeal foramen adjacent to hind-coxal foramen (some *Palachia*) or placed well beyond bases of hind coxae, lateral carina connecting propodeal and hind-coxal foramen present (Grissell, 1995); petiole with a distinct and often long posterior projection strongly attached to basal sternite (Delvare & Janšta, pers. observ.).

Discussion. Podagrioninae can be easily defined by two apomorphic states (shape of occipital carina joining hypostomal carina near base of mandibles, and posterior projection of petiole). This is the only subfamily where all of the species with known biology are adapted for parasitizing Mantodea eggs in egg cases, which is mirrored by their general habitus (usually long ovipositor, usually hind femur enlarged with many small teeth, and claval segments usually almost fused with distinct micropilosity area). Based on our analysis, morphological features and the biological specialization presented mostly by Grissell (1995), we distinguish within Podagrioninae three tribes and leave two genera as *incertae sedis*.

Propalachiini *trib. nov.*

Diagnosis. Head and dorsum of mesosoma with distinct though not long and subdecumbent pilosity; colors generally dull, not contrasting; flagellum of females distinctly clavate, with no visible annulation within segments and with large area of micropilosity; occipital carina joining hypostomal carina in its upper half, but abruptly turning downward towards base of mandible; pronotal collar anteriorly rounded; propodeal foramen placed well beyond bases of hind coxae, lateral carina connecting propodeal and hind-coxal foramen present; propodeum posteriorly produced into short neck; fore wing with marginal vein less than 4 times as long as stigmal vein; hind femur moderately thickened, ventrally in distal half with a row of teeth, 2 of them usually prominent; hind tibia only slightly curved, with truncate apex and 2 apical spurs; metasoma laterally not depressed, terga entire or rarely dorsally emarginate (Grissell, 1995; Bouček 1978; 1998).

There are only three described and a few undescribed species, all known only from the Old World tropics. We do not have information about biology (Bouček, 1998) but based on their general habitus we can expect Propalachiini are parasitoids of Mantodea or other Polyneoptera eggs in oothecae.

Discussion. *Propalachia* (clade 9, Figs 1d, S3d, S4c) is monophyletic and sister to *Palachia* + Podagrionini in all analyses, although the MP support is low. Based on morphology, *Propalachia* was historically classified within Palachiini, together with the extant genera *Palachia* and *Neopalachia* and the extinct genus *Gummilumpus* (Bouček, 1978; Bouček, 1998; Grissell 1995). As discussed by Bouček (1978), *Propalachia* exhibits rather plesiomorphic character states (widespread pubescence, shape of wing venation, pronotum and metasoma) and was considered basal to *Palachia*. Taking into account our results as well as the aforementioned discussions, we proposed to classify this genus into a new tribe **Propalachiini (trib. nov.**).

Palachiini *sensu nov.*

Diagnosis. Head and dorsum of mesosoma at most with indistinct or extremely short pilosity; body with contrasting colored regions; flagellum of females distinctly clavate, with clava one-segmented and large area of micropilosity; occipital carina joining hypostomal carina in its upper half, but abruptly turning downward towards base of mandible; pronotal collar anteriorly usually forming right-angular collar; propodeal foramen adjacent to hind-coxal foramen, lateral carina connecting propodeal and hind-coxal foramen present; fore wing with marginal vein at least 7 times as long as stigmal vein, which is very short or only rudimentary; hind femur moderately thickened, in distal half ventral edge with a row of teeth, 2 of them usually prominent; hind tibia slightly curved, with truncate apex and 2 apical spurs; metasoma laterally depressed, Mt_{2-4} usually dorsally emarginate (Grissell, 1995; Bouček 1978; 1998). The tribe is only distributed in the Old World tropics (Bouček, 1998). Two species are known to be mantid egg parasitoids in oothecae (Narendran, 1984, Delvare unpubl.)

Discussion. Palachiini was considered closely related to Podagrionini by Bouček (1976). Palachiini (*sensu* Bouček, 1976, 1998; Grissell, 1995) differs from Podagrionini in having a shorter hind coxa, slender hind femur bearing relatively few small teeth, a truncate hind tibia bearing two apical spurs, occipital carina appearing to join hypostomal carina in upper half, but abruptly turned downward towards base of mandible, and Mt_2 without lateral emargination (Bouček, 1978; Grissell, 1995). However, as shown above, Palachiini (based on *Propalachia* and *Palachia*) is paraphyletic in all our analyses and *Palachia* (clade 10, Figs 1d, S3d, S4c) is sister to Podagrionini. *Propalachia* is sister to *Palachia* and differs in many morphological features. Therefore we propose the lineage, which includes only the extant genus *Palachia*, as Palachiini ***sensu nov.***

Podagrionini

Diagnosis. Ventral part of clava bearing an area of micropilosity (in some species clava formed by 3 well separated flagellomeres with very small or no micropilosity area); occipital carina completely encircling back of head, ventrolaterally expanded and meeting hypostomal carina slightly above base of mandible; propodeal foramen placed well beyond bases of hind coxae, lateral carina connecting propodeal and hind-coxal foramen present; marginal vein 4-9 times longer than postmarginal vein and 3-9 times longer than stigmal vein; enlarged hind femur with numerous ventral teeth; hind tibia curved with apex prolonged into spine; single hind tibial spur; Mt_{2-5} laterally and dorsolaterally emarginate.

Although worldwide in distribution, the majority of species are pan-tropical occurring in the Neotropical, Afrotropical, Oriental and Australian regions and reported as parasitoids of mantid egg cases (Grissell, 1995).

Discussion. Grissell (1995) defined several synapomorphies for Podagrionini (see above) which are monophyletic in all our analyses with high support, and five (out of seven) genera of Podagrionini are also monophyletic (*Mantiphaga*, *Palmon*, *Podagriomicron*, *Podagrion*, and *Propachytomoides*). *Micropodagrion* is not included in our analyses. *Podagrionella* (*sensu* Grissell, 1995) appears polyphyletic, but forms several monophyletic groups that roughly reflect the previously accepted genera, i.e. *Iridophagoides*, *Iridophaga* and *Podagrionella* (Bouček, 1976; Girault, 1913). Furthermore, *Iridophaga* and *Iridiophagoides* (*sensu* Bouček, 1976) are clades supported based several morphological characters (Bouček, 1976, Delvare unplubl.) as well. Hence we prefer to split some of *Podagrionella* groups into distinct genera and resurrect some of the previously known genera (i.e. *Iridophaga* **stat. rev.** and *Iridophagoides* **stat. rev.**). However, the rest of *Podagrionella* lineages have low nodal supports and require deeper morphological study to clarify their generic status.

The inclusion of *Neopalachia* (only known in Neotropics) and fossil *Gummilumpus* (Dominican amber) in Podagrioninae is questionable as they differ morphologically in several traits from *Palachia* and *Propalachia* (see Grissell, 1995) (*Neopalachia* and *Gummilumpus* have the antennal club 3-segmented without micropilosity and are known from the Neotropics; moreover, *Neopalachia* has the hind femur with a comb of fine, regular teeth, and the hind tibia curved and diagonally truncate (character 11, Grissell, 1995), and *Gummilumpus* has a frenal line, elongated stigma vein, and no elongated submarginal bristles). Their inclusion within the newly defined tribes requires a thorough morphological analysis of *Gummilumpus* and new sampling and sequencing of the rare *Neopalachia*. Therefore we propose to keep *Neopalachia* and *Gummilumpus* as ***incertae sedis*** relative to tribal placement, but with apparent close relationships to Propalachiini, Palachiini and Podagrionini.

Reconstruction of biogeographical history

The areas of origin of Megastigmidae and Torymidae have never been hypothesized. The highest diversity of Megastigmidae, both in terms of genera and species [including many undescribed species (Janšta, pers. obs.)] is in the Australian region (Bouček, 1988), with only *Megastigmus* and *Bootanomyia* found outside of this biogeographical region (Bouček, 1988; Doğanlar, 2011a, 2011b). Here, we included seven of the twelve described genera of

Megastigmidae, four of which are endemic to Australia. The five genera not included in our analysis are all distributed in Australia, with a few species reaching the Oriental region. Although *Bootanomyia* clade 1, which is distributed in the Palaearctic region, is sister to the rest of Megastigmidae, all of our analyses proposed the Australian region as the ancestral area of Megastigmidae. However, the backbone of the Megastigmidae is poorly resolved and several key taxa need to be included before reaching a definitive conclusion. With more comprehensive sampling, two scenarios could be tested in future analyses: (1) the common ancestor of Megastigmidae has an Australian origin with at least two subsequent dispersal events (*Bootanomyia* part 1, *Megastigmus*), or (2) Megastigmidae originated in the northern hemisphere and subsequently colonized the Australian region where it diversified into multiple lineages, and possibly (at least for *Megastigmus*) recolonized the rest of world. Based on our limited outgroup analysis, we cannot identify a definitive sister group to Torymidae, and this prevents proposing a robust biogeographic hypothesis for the family. Consequently, the ancestral area reconstruction analysis is either unresolved (using MP approach) or favors a Palaearctic origin for Torymidae and for most of the included tribes (ML approach). Considering fossil evidence from Burmese amber (not yet unambiguously placed within Toryminae, Janšta - pers. obs.), Baltic amber (*Monodontomerus primaveus,* Brues, 1923, undetermined Microdontomerini, Janšta - pers. observ.) and ML analyses, we propose a Palaearctic or a Eurasian origin for Torymidae with subsequent dispersals to all other regions (Afrotropical, Nearctic, Neotropical and the Australian regions).

It was difficult to identify areas of origin for most of the torymid tribes, however the Boucekinini are indicated to have a Neotropical origin, Chalcimerini a Palaearctic origin and the most derived tribes (Propalachiini, Palachiini and Podagrionini) appear to have originated in the Afrotropical region with subsequent dispersals to the New World, Australian, and Oriental regions (see Fig. S5). The relatively recent dispersal of Palachiini and Podagrionini to the New World is corroborated by fossils found in Dominican amber (*Gummilupus bouceki* (Grissell, 1980)), which are the only fossils known from these tribes (Grissell, 1995).

Evolution of life strategies

Because most Megastigmidae have phytophagous larvae, phytophagy was hypothesized as the putative ancestral strategy for that family by Grissell (1995) with a subsequent shift in biology to parasitizing insects developing in seeds and finally to attacking gall makers. The sister relationship of “*Bootanomyia* part 1” to all other Megastigmidae may indicate a different ancestral biology for Megastigmidae. Indeed, “*Bootanomyia* part 1” is known to be ectoparasitic on gall-forming Cynipidae, and MP ancestral reconstruction analysis yields an ambiguous evolutionary pattern. Furthermore, our knowledge of the biology of many genera of Megastigmidae is still fragmentary and all outgroup species included in our analysis have unknown biology (parasitic or phytophagous). To better assess the ancestral biology of Megastigmidae, we need to know more about the biology of "*Bootanomyia* part 2" and to identify the closest group to Megastigmidae (as well as its biology), which is still unknown (Munro et al., 2011, Heraty et al., 2013). Although the ancestral biology of Megastigmidae remains unknown, our results strongly suggest that zoophagy (i.e. ectoparasitism on gall-forming Cynipidae or Cecidomyidae) evolved at least two times independently within Megastigmidae. Indeed, "*Bootanomyia* part 1" and *Neomegastigmus* are two unrelated genera that are zoophagous. In contrast, phytophagy may have evolved once in the clade including the three genera whose larvae develop on plant tissues, namely *Megastigmus*, *Bortesia*, and *Botanelleus*.

Both ML and MP analyses suggest that ectoparasitism on larvae of gall-forming Cynipidae is the ancestral biology for Torymidae. Several lineages of Torymidae are then presumed to have switched hosts, becoming ectoparasitoids of the larvae of other gall-makers, including Cecidomyidae, Eurytomidae, Tephritidae, and also in larvae of Bruchidae or Eurytomidae in seeds of Fabaceae, which may simulate the gall environment. Our results propose several additional switches, and even reversals, of biology during the evolution of Torymidae (see Fig. S6), including ectoparasitism on larvae of Aculeata in twigs or endoparasitism on pupae of Lepidoptera or Symphyta. We do not know if recurrent exploitation of similar hosts by Torymidae is correlated with convergent morphological adaptation, but most extant and extinct Torymidae have long ovipositors to oviposit on concealed host larvae. Therefore we can presume that a long ovipositor is a pre-disposition for exploiting hosts that developed in concealed situations to protect against parasitoids (Bailey et al., 2009).

Some Torymidae are known to be endoparasitic or oophagous (parasitism of eggs) (Grissell, 1995). With the exception of Mymaridae and Trichogrammatidae, oophagy is rare within Chalcidoidea and has been observed only in some species of Aphelinidae, Eupelmidae, Eulophidae, Eurytomidae, Pteromalidae, Signiphoridae, Tetracampidae, and Torymidae (Heraty et al., 2013). Grissell (1995) suggested that oophagy was a derived strategy that evolved several times independently in Torymidae. Oophagy has been observed for all studied species of Podagrionini and Palachiini, two species of Microdontomerini and several species of Monodontomerinae (Grissell, 1995). Grissell also suggested that oophagy and endoparasitism were two closely related biologies. The proximity of these two biological strategies could explain why a majority of Monodontomerinae are either endoparasitoids of pupae of Lepidoptera/Symphyta or oophagous. However, some studies (Parker, 1924 - for *Podagrion pachymerum*; Delvare, 2005 - for Podagrionini; Janšta et al., 2016 - for *Microdontomerus iridis*) have suggested that a few cases of endoparasitic life styles (endoparasitoids of mantid eggs in oothecea) are in fact special cases of ectoparasitism, where the parasitoid larvae fed on the host eggs within the ootheca, but not within the eggs. Therefore oophagy in Torymidae could be only a special case of ectoparasitism. We clearly need accurate investigations in other oophagous Torymidae.

Our results strongly suggest that parasitism of the eggs of Mantodea was the ancestral biology for *Palachia* (Palachiini) and Podagrionini. However, there are only two biological observations for *Palachia* (Narendran, 1984, Delvare unpubl.) and generalizing this biology to the entire tribe could be inadequate. The biology of *Propalachia* (Propalachiini) is unknown. However, Palachiini, Podagrionini and Propalachiini share unique morphological adaptations associated with the parasitism of mantid oothecae (long ovipositor and micropilose area on clava), and we hypothesize that (ecto)oophagy of Mantodea could also be the ancestral biology of Propalachiini, although there is no host record for this group (Bouček, 1998).

Endoparasitism is definitely a derived biological strategy in Torymidae and originated at least once within the family. The same derived pattern for endoparasitism has also been observed within a few other chalcidoid families (e.g. Perilampidae and Eucharitidae) (Heraty and Murray, 2013). In contrast to Megastigmidae, phytophagy is uncommon in Torymidae (Grissell, 1995). Unfortunately, no phytophagous species of Torymidae are included in our analyses. However, because all species of Torymidae known to be phytophagous belong to the genus *Torymus* (Grissell, 1995), we hypothesize that phytophagy is a derived biological strategy within Torymidae.

Conclusion

This study did not support monophyly of the family Torymidae *sensu* Grissell (1995). Rather, our broad taxonomic sampling and large amount of sequence data indicates Torymidae *sensu* Grissell is a polyphyletic group that necessitates treating Toryminae and Megastigminae at a family rank, i.e. Torymidae *s.s.* and Megastigmidae. Based on both molecular data and morphological data from immatures, Megastigmidae and Torymidae are two unrelated families within Chalcidoidea. Although subdivision of the family Torymidae into 6 subfamilies and 6 tribes is repeatedly corroborated regardless of analytical methods, the position of some subfamilies (namely Glyphomerinae, Microdontomerinae, and Monodontomerinae) is not well supported and needs further investigation. The ancestral area of Megastigmidae is indicated as the Australian region. Torymidae is indicated to have originated in the Palaearctic region with subsequent dispersals to all other regions. While the ancestral hosts for Megastigmidae remain uncertain, the most probable ancestral life strategy for Torymidae is ectoparasitism on larvae of gall-forming Cynipidae with several derived traits throughout the torymid phylogeny. However, to resolve the pattern of host association and biogeographical events within these two families, tribes and genera will need further collecting of taxa including host data. Last, but not least, additional sequencing and detailed morphological analysis of all lineages including fossil records are urgently needed to test evolutionary history of these two families properly.

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Figure captions

Figure 1a. Phylogram of Megastigmidae and Torymidae relationships (outgroups and Ormyridae) based on RaxML with 1000 bootstrap (BP) replications. If no support values indicated, BP maximum likelihood and maximum parsimony <50 and posterior probablities <0.75. Shaded areas highlight supported monophyletic genera. Upper pie charts at main nodes show the likelihood of ancestral state of different geographic areas of origin, lower pie charts are likelihood of ancestral state of life strategies as inferred by Mesquite. Bars on terminal branches indicate host association, icons after taxon names indicate biogeographical region of specific taxa distribution (color legend for bars and icons below tree). Clades are labelled using the new classification of Megastigmidae and Torymidae as proposed in text.

Figure 1b. Phylogram of Torymidae relationships (Chalcimerinae and Toryminae: Boucekinini, Torymoidini and Torymini) based on RaxML with 1000 bootstrap (BP) replications. If no support values indicated, BP maximum likelihood and maximum parsimony <50 and posterior probablities <0.75. Shaded areas highlight supported monophyletic genera. Upper pie charts at main nodes show the likelihood of ancestral state of different geographic areas of origin, lower pie charts are likelihood of ancestral state of life strategies as inferred by Mesquite. Bars on terminal branches indicate host association, icons after taxon names indicate biogeographical region of specific taxa distribution (color legend for bars and icons below tree). Clades are labelled using the new classification of Torymidae as proposed in text.

Figure 1c. Phylogram of Torymidae relationships (Glyphomerinae and Microdontomerinae) based on RaxML with 1000 bootstrap (BP) replications. If no support values indicated, BP maximum likelihood and maximum parsimony <50 and posterior probablities <0.75. Shaded areas highlight supported monophyletic genera. Upper pie charts at main nodes show the likelihood of ancestral state of different geographic areas of, lower pie charts are likelihood of ancestral state of life strategies origin as inferred by Mesquite. Bars on terminal branches indicate host association, icons after taxon names indicate biogeographical region of specific taxa distribution (color legend for bars and icons below tree). Clades are labelled using the new classification of Torymidae as proposed in text.

Figure 1d. Phylogram of Torymidae relationships (Monodontomerinae and Podagrioninae: Propalachiini, Palachiini and Podagrionini) based on RaxML with 1000 bootstrap (BP) replications. If no support values indicated, BP maximum likelihood and maximum parsimony <50 and posterior probablities <0.75. Shaded areas highlight supported monophyletic genera. Upper pie charts at main nodes show the likelihood of ancestral state of different geographic areas of origin, lower pie charts are likelihood of ancestral state of life strategies as inferred by Mesquite. Bars on terminal branches indicate host association, icons after taxon names indicate biogeographical region of specific taxa distribution (color legend for bars and icons below tree). Clades are labelled using the new classification of Torymidae as proposed in text.

Supplementary material:

Figure S1. Phylogeny of Torymidae sensu Grissell (1995) based on morphological characters (modified from Grissell 1995).

Figure S2. Saturation plots for transitions (s) and transversions (v) of entire fragment sequenced (a), first (b), second (c) and third (c) codon positions for *COI* (1), *EF-1α* (2) and *Wg* (3). Matrix based uncorrected p-distances on y-axis versus K80 distances on x-axis.

Figure S3a-d. Phylogram of Megastigmidae and Torymidae relationships based on RaxML with 1000 bootstrap (BP) replications. Support values indicate in order: BP maximum likelihood ≥ 50, posterior probablities (PP) ≥0.75, BP maximum parsimony ≥ 50. Letters (a-g) behind name of each taxa specify gene regions sequenced (i.e. *18S rDNA*, *28S rDNA D2*, *28S rDNA D3-5*, *EF-1α*, *COI barcode fragment*, *COI Jerry -Pat*, *Wg*, respectively), asterisks indicate only part of gene region sequenced. Shaded areas highlight supported monophyletic genera. Clades are labelled using the new classification of Torymidae as proposed in text.

Figure S4a-c. The strict consensus tree of all most parsimonious trees of Megastigmidae and Torymidae founded in the TNT analysis, gaps were treated as missing data (L= 17199, CI=0.142, RI=0.579). Bootstrap support values >50 at nodes. Letters (a-g) behind name of each taxa specify gene regions sequenced (i.e. *18S rDNA*, *28S rDNA D2*, *28S rDNA D3-5*, *EF-1α*, *COI barcode fragment*, *COI Jerry -Pat*, *Wg*, respectively), asterisks indicate only part of gene region sequenced. Shaded areas highlight supported monophyletic genera. Clades are labelled using the new classification of Torymidae as proposed in text.

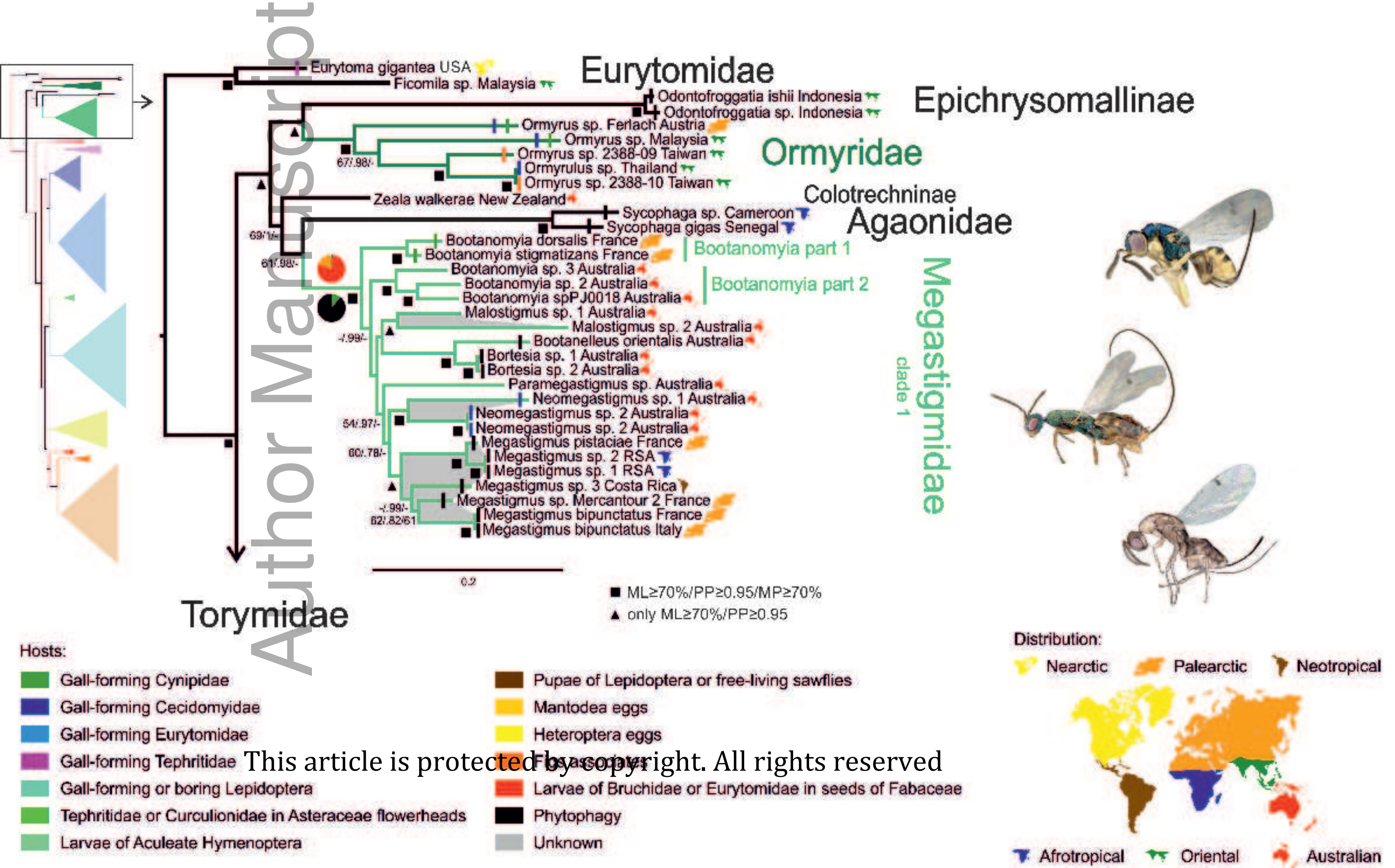
Figure S5a-b. Maximum parsimony and maximum likelihood ancestral state reconstruction of biogeographical history of Megastigmidae and Torymidae. Ancestral states were mapped onto the RAxML tree topology using Mesquite. Color of background indicates the tribal/subfamiliar or familiar affiliation as in Figs S3-S4. Pie charts at main nodes show the likelihood, branch colors show the most parsimonious ancestral state of different geographic areas of origin as inferred by Mesquite (see “Materials and Methods” section), exact likelihood of all values at all nodes in Supporting Material (Table S2). Clades are labelled using the new classification of Torymidae as proposed in text.

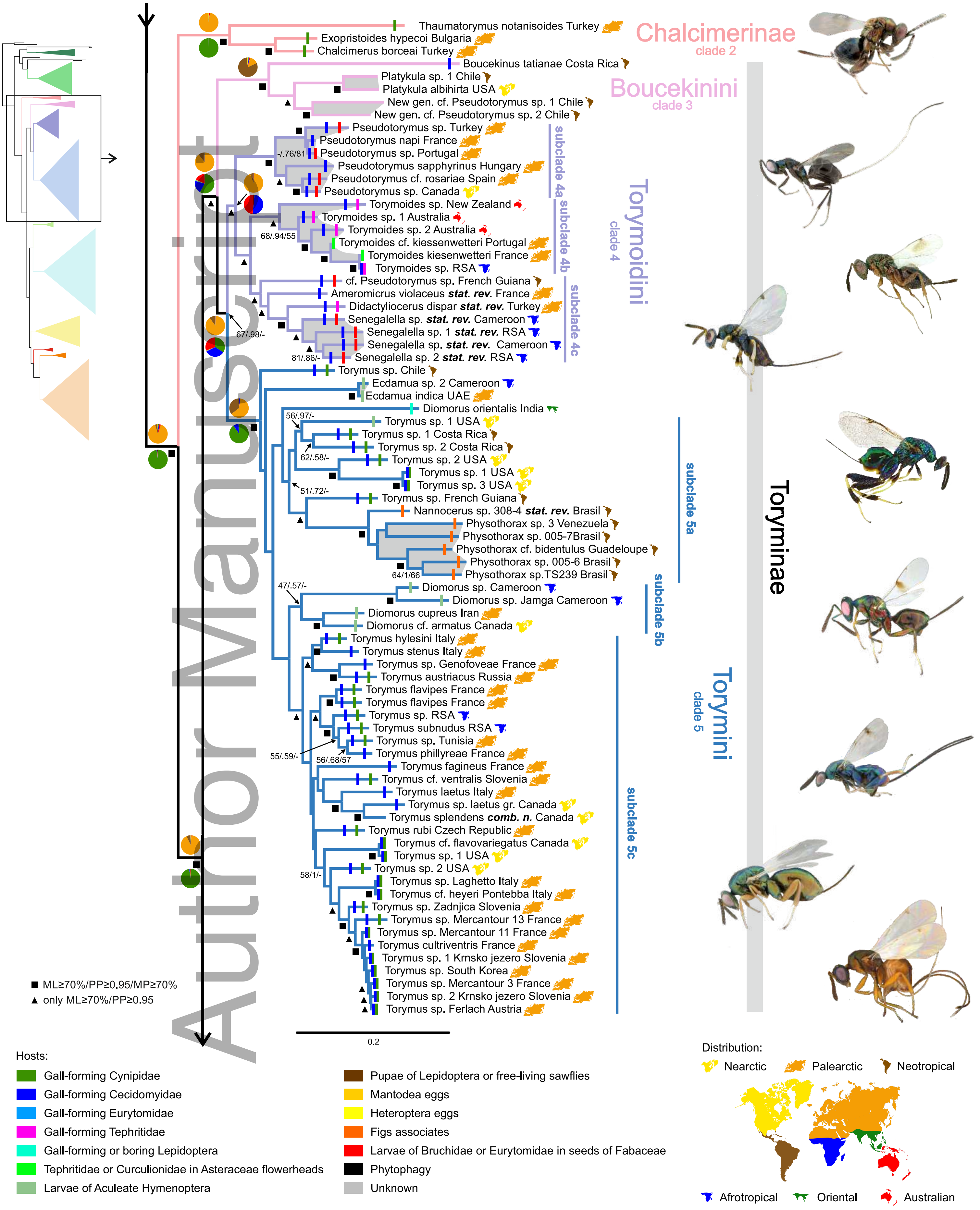
Figure S6a-b. Maximum parsimony (a) and maximum likelihood (b) ancestral state reconstruction of parasitoid larvae life-history strategies of Megastigmidae and Torymidae . Ancestral states were mapped onto the RAxML tree topology using Mesquite. Color of background indicates the tribal/subfamiliar or familiar affiliation as in Figs S3-S4. Pie charts at main nodes show the likelihood, branch colors show the most parsimonious ancestral state of different larvae life-history strategies as inferred by Mesquite (see “Materials and Methods” section), exact likelihood of all values at all nodes in Supporting Material (Tab. S3). Clades are labelled using the new classification of Torymidae as proposed in text.

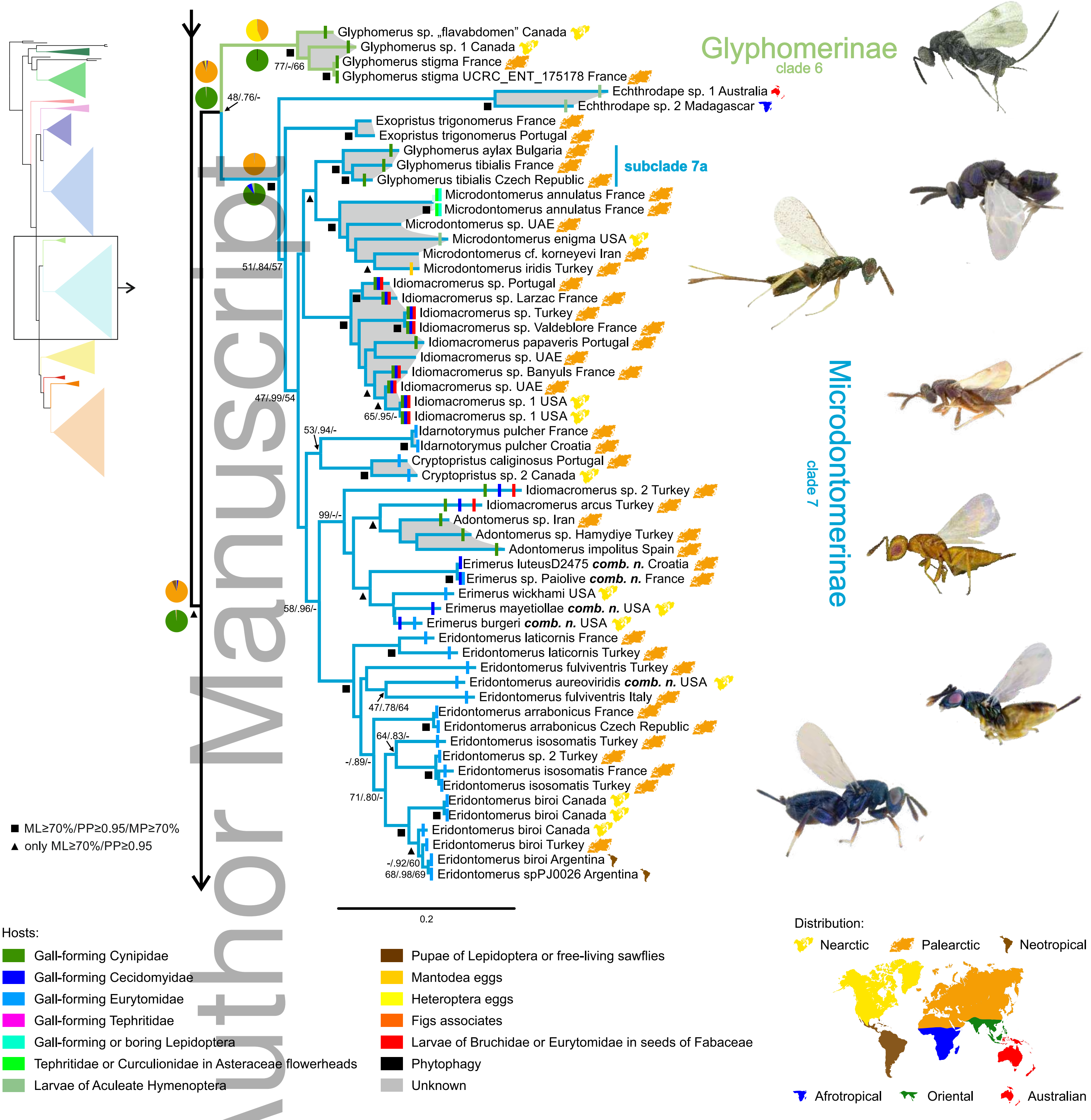
Table S1. Specimen voucher information and GenBank accession numbers (AGS - Agaonidae: Sycophaginae, EU - Eurytomidae, OR - Ormyridae, PTC - Pteromalidae: Colotrechninae, PTE - Pteromalidae: Epichrysomallinae, MEG - Megastigmidae, TOC - Torymidae: Chalcimerinae, TOM - Torymidae: Microdontomerinae, TON - Torymidae: Monodontomerinae, TOO - Torymidae: Podagrioninae: Podagrionini, TOP - Torymidae: Podagrioninae: Palachiini, TOR - Torymidae: Podagrioninae: Propalachiini, TOB - Torymidae: Toryminae: Boucekinini, TOT - Torymidae: Toryminae: Torymini, TOY - Torymidae: Toryminae: Torymoidini; Extraction: D - destructive, N - non-destructive, P - partly destructive, QP - Quaigen protocol, CP - Chelex protocol; Voucher prior condition: 96/70 - in 96/70% EtOH, D - dryed and mounted; Voucher museum repositories abbreviations and all character states for species distribution and host association are listed in M&M. Outgroups species names are bolded).

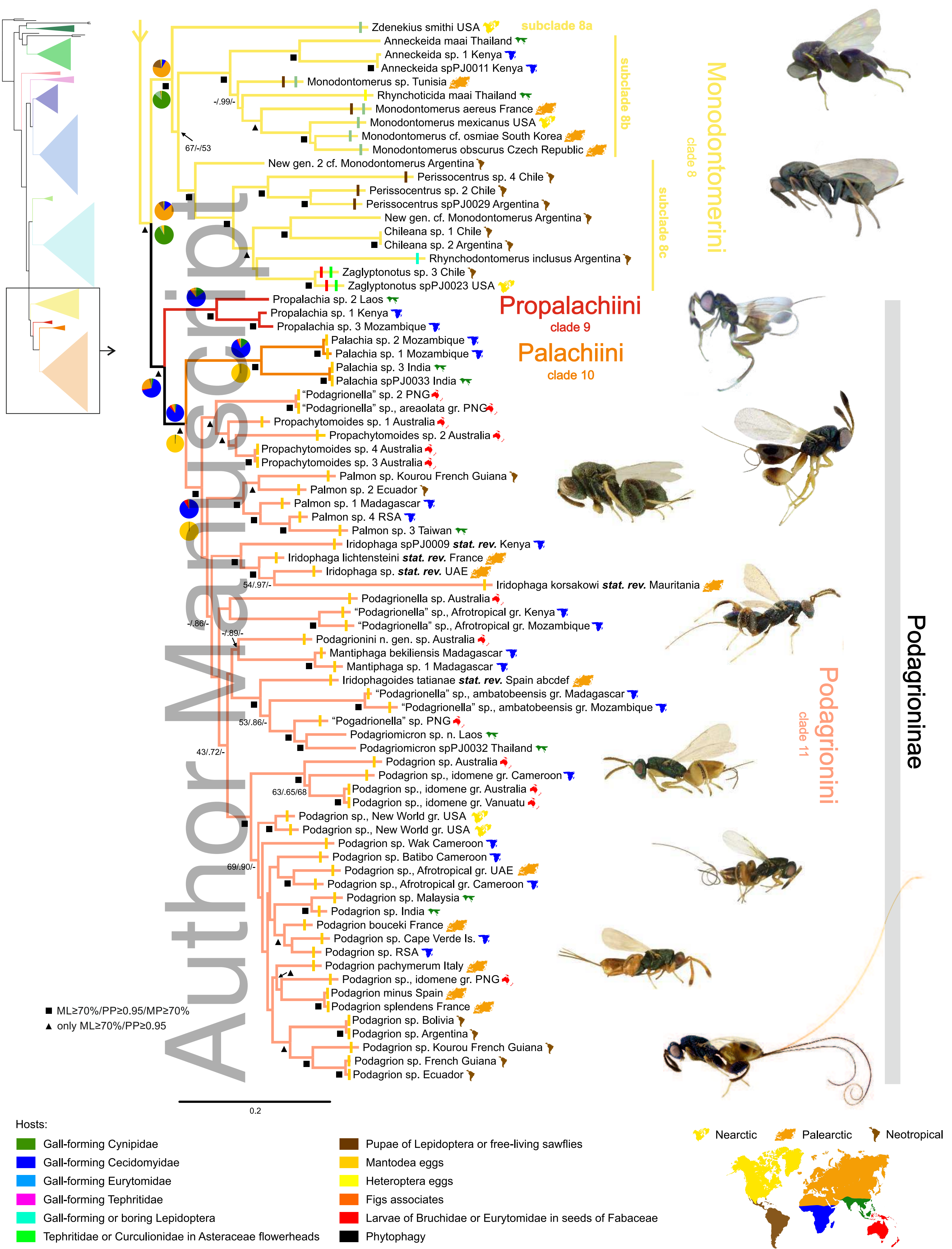
Table S2. Likelihood values of biogeographical history ancestral state reconstruction of Megastigmidae and Torymidaeat all nodes mapped onto the RAxML tree topology using Mesquite.

Table S3. Likelihood values of parasitoid larvae life-history strategies ancestral state reconstruction of Megastigmidae and Torymidaeat all nodes mapped onto the RAxML tree topology using Mesquite.


Eurytoma gigantea USA
Ficomila sp. Malaysia
Eurytomidae
Odontofroggatia ishii Indonesia
Odontofroggatia sp. Indonesia
Epichrysomallinae
Ormyrus sp. Ferlach Austria
Ormyrus sp. Malaysia
Ormyrus sp. 2388-09 Taiwan
Ormyrulus sp. Thailand
Ormyrus sp. 2388-10 Taiwan
Ormyridae
67/.98/-
Zeala walkerae New Zealand
Colotrechninae
Sycophaga sp. Cameroon
Sycophaga gigas Senegal
Agaonidae
69/1/-
61/.98/-
Bootanomyia dorsalis France
Bootanomyia stigmatizans France
Bootanomyia part 1
Bootanomyia sp. 3 Australia
Bootanomyia sp. 2 Australia
Bootanomyia spPJ0018 Australia
Bootanomyia part 2
Malostigmus sp. 1 Australia
-/.99/-
Malostigmus sp. 2 Australia
Bootanelleus orientalis Australia
Bortesia sp. 1 Australia
Bortesia sp. 2 Australia
Paramegastigmus sp. Australia
Neomegastigmus sp. 1 Australia
54/.97/-
Neomegastigmus sp. 2 Australia
Neomegastigmus sp. 2 Australia
Megastigmus pistaciae France
60/.78/-
Megastigmus sp. 2 RSA
Megastigmus sp. 1 RSA
Megastigmus sp. 3 Costa Rica
-/.99/-
Megastigmus sp. Mercantour 2 France
62/.82/61
Megastigmus bipunctatus France
Megastigmus bipunctatus Italy
Megastigmidae
clade 1
0.2
Torymidae
■ ML≥70%/PP≥0.95/MP≥70%
▲ only ML≥70%/PP≥0.95
Hosts:
Gall-forming Cynipidae
Gall-forming Cecidomyidae
Gall-forming Eurytomidae
Gall-forming Tephritidae
Gall-forming or boring Lepidoptera
Tephritidae or Curculionidae in Asteraceae flowerheads
Larvae of Aculeate Hymenoptera
Pupae of Lepidoptera or free-living sawflies
Mantodea eggs
Heteroptera eggs
Fig wasps
Larvae of Bruchidae or Eurytomidae in seeds of Fabaceae
Phytophagy
Unknown
Distribution:
Nearctic
Palearctic
Neotropical
Afrotropical
Oriental
Australian


Thaumatorymus notanisoides Turkey
Exopristoides hypecoi Bulgaria
Chalcimerus borceai Turkey
Chalcimerinae
clade 2
Boucekinus tatianae Costa Rica
Platykula sp. 1 Chile
Platykula albihirta USA
New gen. cf. Pseudotorymus sp. 1 Chile
New gen. cf. Pseudotorymus sp. 2 Chile
Boucekinini
clade 3
Pseudotorymus sp. Turkey
Pseudotorymus napi France
-/.76/81
Pseudotorymus sp. Portugal
Pseudotorymus sapphyrinus Hungary
Pseudotorymus cf. rosariae Spain
Pseudotorymus sp. Canada
subclade 4a
Torymoides sp. New Zealand
Torymoides sp. 1 Australia
68/.94/55
Torymoides sp. 2 Australia
Torymoides cf. kiessenwetteri Portugal
Torymoides kiesenwetteri France
Torymoides sp. RSA
subclade 4b
Torymoidini
clade 4
cf. Pseudotorymus sp. French Guiana
Ameromicrus violaceus stat. rev. France
Didactyliocerus dispar stat. rev. Turkey
Senegalella sp. stat. rev. Cameroon
67/.98/-
Senegalella sp. 1 stat. rev. RSA
Senegalella sp. stat. rev. Cameroon
81/.86/-
Senegalella sp. 2 stat. rev. RSA
subclade 4c
Torymus sp. Chile
Ecdamua sp. 2 Cameroon
Ecdamua indica UAE
Diomorus orientalis India
56/.97/-
Torymus sp. 1 USA
Torymus sp. 1 Costa Rica
62/.58/-
Torymus sp. 2 Costa Rica
Torymus sp. 2 USA
Torymus sp. 1 USA
Torymus sp. 3 USA
51/.72/-
Torymus sp. French Guiana
Nannocerus sp. 308-4 stat. rev. Brasil
Physothorax sp. 3 Venezuela
Physothorax sp. 005-7Brasil
Physothorax cf. bidentulus Guadeloupe
Physothorax sp. 005-6 Brasil
64/1/66
Physothorax sp.TS239 Brasil
subclade 5a
Toryminae
47/.57/-
Diomorus sp. Cameroon
Diomorus sp. Jamga Cameroon
Diomorus cupreus Iran
Diomorus cf. armatus Canada
subclade 5b
Torymus hylesini Italy
Torymus stenus Italy
Torymus sp. Genofoveae France
Torymus austriacus Russia
Torymus flavipes France
Torymus flavipes France
Torymus sp. RSA
Torymus subnudus RSA
Torymus sp. Tunisia
55/.59/-
56/.68/57
Torymus phillyreae France
Torymus fagineus France
Torymus cf. ventralis Slovenia
Torymus laetus Italy
Torymus sp. laetus gr. Canada
Torymus splendens comb. n. Canada
Torymus rubi Czech Republic
Torymus cf. flavovariegatus Canada
Torymus sp. 1 USA
58/1/-
Torymus sp. 2 USA
Torymus sp. Laghetto Italy
Torymus cf. heyeri Pontebba Italy
Torymus sp. Zadnjica Slovenia
Torymus sp. Mercantour 13 France
Torymus sp. Mercantour 11 France
Torymus cultriventris France
Torymus sp. 1 Krnsko jezero Slovenia
Torymus sp. South Korea
Torymus sp. Mercantour 3 France
Torymus sp. 2 Krnsko jezero Slovenia
Torymus sp. Ferlach Austria
Torymini
clade 5
subclade 5c
■ ML≥70%/PP≥0.95/MP≥70%
▲ only ML≥70%/PP≥0.95
0.2
Hosts:
Gall-forming Cynipidae
Gall-forming Cecidomyidae
Gall-forming Eurytomidae
Gall-forming Tephritidae
Gall-forming or boring Lepidoptera
Tephritidae or Curculionidae in Asteraceae flowerheads
Larvae of Aculeate Hymenoptera
Pupae of Lepidoptera or free-living sawflies
Mantodea eggs
Heteroptera eggs
Figs associates
Larvae of Bruchidae or Eurytomidae in seeds of Fabaceae
Phytophagy
Unknown
Distribution:
Nearctic
Palearctic
Neotropical
Afrotropical
Oriental
Australian


Glyphomerus sp. „flavabdomen" Canada
Glyphomerus sp. 1 Canada
Glyphomerus stigma France
Glyphomerus stigma UCRC_ENT_175178 France
77/-/66
Glyphomerinae
clade 6
Echthrodape sp. 1 Australia
Echthrodape sp. 2 Madagascar
48/.76/-
Exopristus trigonomerus France
Exopristus trigonomerus Portugal
Glyphomerus aylax Bulgaria
Glyphomerus tibialis France
Glyphomerus tibialis Czech Republic
subclade 7a
Microdontomerus annulatus France
Microdontomerus annulatus France
Microdontomerus sp. UAE
Microdontomerus enigma USA
Microdontomerus cf. korneyevi Iran
Microdontomerus iridis Turkey
51/.84/57
Idiomacromerus sp. Portugal
Idiomacromerus sp. Larzac France
Idiomacromerus sp. Turkey
Idiomacromerus sp. Valdeblore France
Idiomacromerus papaveris Portugal
Idiomacromerus sp. UAE
Idiomacromerus sp. Banyuls France
Idiomacromerus sp. UAE
Idiomacromerus sp. 1 USA
Idiomacromerus sp. 1 USA
47/.99/54
65/.95/-
53/.94/-
Idarnotorymus pulcher France
Idarnotorymus pulcher Croatia
Cryptopristus caliginosus Portugal
Cryptopristus sp. 2 Canada
Idiomacromerus sp. 2 Turkey
Idiomacromerus arcus Turkey
99/-/-
Adontomerus sp. Iran
Adontomerus sp. Hamydiye Turkey
Adontomerus impolitus Spain
Erimerus luteusD2475 ***comb. n.*** Croatia
Erimerus sp. Paiolive ***comb. n.*** France
Erimerus wickhami USA
Erimerus mayetiollae ***comb. n.*** USA
Erimerus burgeri ***comb. n.*** USA
58/.96/-
Eridontomerus laticornis France
Eridontomerus laticornis Turkey
Eridontomerus fulviventris Turkey
Eridontomerus aureoviridis ***comb. n.*** USA
Eridontomerus fulviventris Italy
47/.78/64
Eridontomerus arrabonicus France
Eridontomerus arrabonicus Czech Republic
64/.83/-
Eridontomerus isosomatis Turkey
Eridontomerus sp. 2 Turkey
-/.89/-
Eridontomerus isosomatis France
Eridontomerus isosomatis Turkey
71/.80/-
Eridontomerus biroi Canada
Eridontomerus biroi Canada
Eridontomerus biroi Canada
Eridontomerus biroi Turkey
Eridontomerus biroi Argentina
-/.92/60
68/.98/69
Eridontomerus spPJ0026 Argentina
Microdontomerinae
clade 7
■ ML≥70%/PP≥0.95/MP≥70%
▲ only ML≥70%/PP≥0.95
0.2
Hosts:
Gall-forming Cynipidae
Gall-forming Cecidomyidae
Gall-forming Eurytomidae
Gall-forming Tephritidae
Gall-forming or boring Lepidoptera
Tephritidae or Curculionidae in Asteraceae flowerheads
Larvae of Aculeate Hymenoptera
Pupae of Lepidoptera or free-living sawflies
Mantodea eggs
Heteroptera eggs
Figs associates
Larvae of Bruchidae or Eurytomidae in seeds of Fabaceae
Phytophagy
Unknown
Distribution:
Nearctic
Palearctic
Neotropical
Afrotropical
Oriental
Australian



subclade 8a
Zdenekius smithi USA
Anneckeida maai Thailand
Anneckeida sp. 1 Kenya
Anneckeida spPJ0011 Kenya
Monodontomerus sp. Tunisia
Rhynchoticida maai Thailand
Monodontomerus aereus France
Monodontomerus mexicanus USA
Monodontomerus cf. osmiae South Korea
Monodontomerus obscurus Czech Republic
subclade 8b
-/.99/-
67/-/53
New gen. 2 cf. Monodontomerus Argentina
Perissocentrus sp. 4 Chile
Perissocentrus sp. 2 Chile
Perissocentrus spPJ0029 Argentina
New gen. cf. Monodontomerus Argentina
Chileana sp. 1 Chile
Chileana sp. 2 Argentina
Rhynchodontomerus inclusus Argentina
Zaglyptonotus sp. 3 Chile
Zaglyptonotus spPJ0023 USA
subclade 8c
Monodontomerini
clade 8
Propalachia sp. 2 Laos
Propalachia sp. 1 Kenya
Propalachia sp. 3 Mozambique
Propalachiini
clade 9
Palachia sp. 2 Mozambique
Palachia sp. 1 Mozambique
Palachia sp. 3 India
Palachia spPJ0033 India
Palachiini
clade 10
"Podagrionella" sp. 2 PNG
"Podagrionella" sp., areaolata gr. PNG
Propachytomoides sp. 1 Australia
Propachytomoides sp. 2 Australia
Propachytomoides sp. 4 Australia
Propachytomoides sp. 3 Australia
Palmon sp. Kourou French Guiana
Palmon sp. 2 Ecuador
Palmon sp. 1 Madagascar
Palmon sp. 4 RSA
Palmon sp. 3 Taiwan
Iridophaga spPJ0009 stat. rev. Kenya
Iridophaga lichtensteini stat. rev. France
Iridophaga sp. stat. rev. UAE
Iridophaga korsakowi stat. rev. Mauritania
54/.97/-
Podagrionella sp. Australia
"Podagrionella" sp., Afrotropical gr. Kenya
"Podagrionella" sp., Afrotropical gr. Mozambique
-/.86/-
-/.89/-
Podagrionini n. gen. sp. Australia
Mantiphaga bekiliensis Madagascar
Mantiphaga sp. 1 Madagascar
Iridophagoides tatianae stat. rev. Spain abcdef
"Podagrionella" sp., ambatobeensis gr. Madagascar
"Podagrionella" sp., ambatobeensis gr. Mozambique
"Pogadrionella" sp. PNG
53/.86/-
Podagriomicron sp. n. Laos
Podagriomicron spPJ0032 Thailand
43/.72/-
Podagrion sp. Australia
Podagrion sp., idomene gr. Cameroon
Podagrion sp., idomene gr. Australia
Podagrion sp., idomene gr. Vanuatu
63/.65/68
Podagrion sp., New World gr. USA
Podagrion sp., New World gr. USA
Podagrion sp. Wak Cameroon
Podagrion sp. Batibo Cameroon
69/.90/-
Podagrion sp., Afrotropical gr. UAE
Podagrion sp., Afrotropical gr. Cameroon
Podagrion sp. Malaysia
Podagrion sp. India
Podagrion bouceki France
Podagrion sp. Cape Verde Is.
Podagrion sp. RSA
Podagrion pachymerum Italy
Podagrion sp., idomene gr. PNG
Podagrion minus Spain
Podagrion splendens France
Podagrion sp. Bolivia
Podagrion sp. Argentina
Podagrion sp. Kourou French Guiana
Podagrion sp. French Guiana
Podagrion sp. Ecuador
Podagrionini
clade 11
Podagrioninae
■ ML≥70%/PP≥0.95/MP≥70%
▲ only ML≥70%/PP≥0.95
0.2
Hosts:
Gall-forming Cynipidae
Gall-forming Cecidomyidae
Gall-forming Eurytomidae
Gall-forming Tephritidae
Gall-forming or boring Lepidoptera
Tephritidae or Curculionidae in Asteraceae flowerheads
Larvae of Aculeate Hymenoptera
Pupae of Lepidoptera or free-living sawflies
Mantodea eggs
Heteroptera eggs
Figs associates
Larvae of Bruchidae or Eurytomidae in seeds of Fabaceae
Phytophagy
Unknown
Nearctic
Palearctic
Neotropical
Afrotropical
Oriental
Australian