Phylogeny and classification of the leafhopper subfamily Eurymelinae (Hemiptera: Cicadellidae) inferred from molecules and morphology

QINGQUAN XUE 1 , CHRISTOPHER H. DIETRICH 2 and YALIN ZHANG 1

¹Key Laboratory of Plant Protection Resources and Pest Management, Ministry of Education, Entomological Museum, College of Plant Protection, Northwest A&F University, Yangling, China and ²Illinois Natural History Survey, Prairie Research Institute, University of Illinois at Urbana-Champaign, Champaign, IL, U.S.A.

Abstract. Phylogenetic analysis of the globally distributed arboreal leafhopper subfamily Eurymelinae was conducted based on DNA sequence data from three nuclear and two mitochondrial genes in addition to 86 discrete morphological characters. The analysis included 89 species representing 61 genera from all major biogeographic regions including six species from outgroups, Megophthalminae and Ulopinae. Trees resulting from partitioned Bayesian and maximum likelihood analyses of the combined data were well resolved and largely congruent, differing mainly in the relationships among the earliest diverging lineages. The results are consistent with an expanded concept of Eurymelinae, including tribes Austroagalloidini and Macropsini. Six monophyletic groups are recognized as new tribes, Balocerini, Chiasmodolini, Chileanoscopini, Idioceroidini, Kopamerrini and Nesocerini, tribe n., and the previously recognized tribes Eurymelini, Idiocerini and Megipocerini are redefined. A new synonym, Busonini Zhang & Li, 2015 syn.n. is proposed here for Megipocerini Isaev, 1988. Molecular divergence time estimates were calibrated using two fossil taxa and suggested that the earliest divergences occurred in the Lower Cretaceous and that most major lineages of this group arose during the Cretaceous. Reconstruction of ancestral areas revealed considerable continental-scale biogeographical structure. The place of origin of Eurymelinae is equivocal but major lineages arose in the Neotropical, Australian and Afrotropical regions. A key to tribes and a checklist of genera showing current tribal placements are provided.

Introduction

Cicadellidae is the largest and one of the most economically important families of Hemiptera. Recent phylogenetic studies have begun to reveal the status and relationships of the family and its major lineages (Dietrich *et al.*, 2001, 2005, 2017; Jones & Deitz, 2009; Zahniser & Dietrich, 2010; Krishnankutty *et al.*, 2016; Du *et al.*, 2017; Wang *et al.*, 2017). Most recently, Dietrich *et al.* (2017) used the anchored hybrid enrichment phylogenomic approach to reconstruct relationships

Correspondence: Yalin Zhang, Key Laboratory of Plant Protection Resources and Pest Management, Ministry of Education, Entomological Museum, College of Plant Protection, Northwest A&F University, Yangling, Shaanxi 712100, China. E-mail: yalinzh@nwsuaf.edu.cn

among Membracoidea (leaf- and treehoppers), showing that Cicadellidae, as currently defined, is paraphyletic with respect to the treehopper lineages (Aetalionidae, Membracidae and Melizoderidae). Their analysis recovered many of the currently recognized cicadellid subfamilies as monophyletic but was unable to resolve the relationships among these major lineages with confidence. The analyses (Dietrich *et al.*, 2017) indicated that Idiocerinae (sensu Oman *et al.*, 1990) is paraphyletic with respect to Eurymelinae, which is consistent with previous studies (Dietrich *et al.*, 2001, 2005) and also recovered Macropsinae as sister to Eurymelinae + Idiocerinae with strong maximum likelihood (ML) bootstrap support in the analysis of concatenated data. Based on these results, Dietrich & Thomas (2018) proposed an expanded concept of Eurymelinae, including Idiocerini and Macropsini as tribes.

Eurymelinae is one of the largest lineages of arboreal leafhoppers. Species of this group feed on a wide variety of trees and shrubs, including several of economic importance with some considered agricultural pests (Fletcher & Dangerfield, 2002; Gnaneswaran *et al.*, 2007). This group is distributed worldwide and includes more than 1300 species in 174 genera. Some species of this group are unusual among leafhoppers in exhibiting gregarious behaviour, ant mutualism and/or parental care (Dietrich & McKamey, 1990).

Most recent research on this subfamily has consisted of taxonomic descriptions of new genera and species (e.g. Hamilton, 1980a,b, 1983; Webb, 1983a,b; Maldonado-Capriles, 1985; Freytag, 2006; Viraktamath, 2007; Lozada, 2010; Zhang & Li, 2012; Li et al., 2014; Xue et al., 2016; Yang et al., 2016). Krishnankutty & Dietrich (2011) conducted the first explicit morphology-based phylogenetic analysis of this subfamily, focused on the endemic Madagascar genus *Nesocerus* Freytag & Knight. Krishnankutty (2012) conducted a molecular phylogenetic analysis focusing on eurymeline leafhoppers in Madagascar in her unpublished PhD dissertation using sequence data from two nuclear genes (28S and histone H3). Previous phylogenetic studies have not sampled taxa or characters sufficiently large in size to resolve the classification and phylogenetic relationships within Eurymelinae.

To explore the relationships in Eurymelinae, we conducted phylogenetic analyses based on DNA sequence data and morphological characteristics with worldwide representatives. Based on these phylogenetic results, the classification of Eurymelinae is revised and the biogeography of this group explored, and the divergence times are estimated for various lineages using fossil calibrations.

Materials and methods

Taxon sampling and DNA sequencing

Adult specimens preserved in 95% or anhydrous ethanol were selected from collections maintained at Northwest A&F University (NWAFU) (Yangling, Shaanxi, China) and the Illinois Natural History Survey (INHS) (Champaign, USA). Specimens were identified taxonomically based on morphological characters and vouchers are deposited in the permanent collections of these institutions. The dataset included 89 species from all biogeographic realms representing 61 genera and all previously recognized tribes. Table S1 gives a checklist of specimens with the depository institutions, collecting localities, voucher codes and GenBank accession numbers. The concatenated alignment used in the analyses, with data partitions indicated, is available from the Illinois Data Bank at https://doi.org/10.13012/B2IDB-3573054_V1. One taxon (Megipocerus mordvilkoi Zachvatkin) represented only by morphological data was included because of its importance as the type genus of the Megipocerini Isaev. The taxon sample also included outgroups representing Ulopinae (one species) and Megophthalminae (five species) based on the phylogenetic results of Dietrich et al. (2017).

We obtained nucleotide sequences for three nuclear [28S D2] (c. 700 bp), H3 (349bp) and H2A (315 bp)] and two mitochondrial [16S (c. 550 bp), COI (658 bp)] gene fragments. These genes have previously been utilized to reconstruct phylogenetic relationships within Hemiptera (e.g. Cryan, 2005; Cryan & Svenson, 2010; Cryan & Urban, 2012; Bell et al., 2014; Evangelista et al., 2017). Genomic DNA was extracted either from the abdomen or thoracic muscles using Qiagen DNEasy Kits (Qiagen, Valencia, CA, U.S.A.). Fragments of H2A, H3 and 28S D2 were amplified by PCR in 25 µL reaction volumes with the following cycling protocol: 3 min at 94°C, then 30 cycles of 1 min at 94°C, 1 min at 52-57°C, 1.5-2 min at 72°C, ending with 7 min incubation at 72°C. COI was amplified as follows: 3 min at 94°C; five cycles of 1 min at 94°C, 1.5 min at 45°C and 1.5 min at 72°C; 35 cycles of 1 min at 94°C, 1 min at 52-55°C and 1 min at 72°C; 5 min at 72°C. 16S was amplified as follows: 5 min at 94°C; 11 cycles of 1 min at 92°C, 1 min at 48°C and 1.5 min at 72°C; 30 cycles of 1 min at 92°C, 35 s at 54-56°C and 2 min at 72°C; 7 min at 72°C. PCR primers are listed in Table S2. Some unpublished sequences from Krishnankutty (2012) were obtained directly from the author. Total genomic DNA was stored at -20°C prior to PCR and Sanger sequencing using the same primer pairs.

Sequences were assembled and edited with MEGA 6 (Tamura et al., 2013). Sequences were aligned in MAFFT 7. 037 (Katoh & Standley, 2013) using the G-INS-i algorithm. Molecular and morphological datasets were merged using SEQUENCEMATRIX 1.7.8 (Vaidya et al., 2011).

Morphological characters

The morphological dataset comprised 86 characters, 74 binary and 12 multistate (Tables S3, S4). Character states were scored by examining specimens under a stereomicroscope. The dissected genitalia were stored in a microvial with fresh glycerol and pinned below the specimen from which the abdomen was removed. The terminology follows Zhang (1990) and Dietrich (2005). Morphological data were compiled using MESQUITE v. 3.31 (Maddison & Maddison, 2017). Inapplicable characters were indicated as '–' and unobserved states with '?'. All characters were treated as unordered and of equal weight.

Phylogenetic analysis

Phylogenetic analyses were conducted with partitioned Bayesian (BI) analyses using MRBAYES 3.2.6 (Ronquist *et al.*, 2012) and IQ-TREE 1.6.5 (Nguyen *et al.*, 2015) for ML analyses. BI analyses were performed using MRBAYES 3.2.6 (analyses on CIPRES Science Gateway) (Miller *et al.*, 2010), with PARTITIONFINDER 2 used to determine the best-fitting nucleotide model for each gene (Lanfear *et al.*, 2016). The best-fitting models were GTR+I+G for all molecular data partitions. The morphology dataset was run under the standard discrete model. Six chains were included in two runs of 10 million generations, sampled every 1000 generations with a burn-in of

0.25. The average standard deviation of split frequencies was < 0.01, suggesting that runs converged. The convergence of runs was monitored using TRACER v.1.7 (Rambaut et al., 2018). After the first 25% of trees were discarded as burn-in, posterior probability values (PP) were calculated for the majority-rule consensus tree. For the ML analyses, IQ-TREE selected the model for each gene using the Bayesian information criterion (BIC). The GTR + F + I + G4 model was specified for 16S, COI and H2A, GTR + F + R4 for 28S, TIM3 + F + I + G4 for H3, and the MK model for morphology. IQ-TREE executed the following tests to determine node support for the ML analysis: 1000 bootstrap pseudoreplicates (BS), 5000 replicates for ultrafast bootstrap approximation (UFB) and 1000 replicates for the Shimodaira-Hasegawa approximate likelihood ratio test (SH-aLRT).

Divergence time estimation

Divergence times were inferred using BEAST 1.8.4 (Drummond & Rambaut, 2007) on CIPRES using the GTR + I + Γ model with four gamma categories. The analysis assumed a Yule speciation process and used an uncorrelated normal relaxed clock. Markov chain Monte Carlo (MCMC) chains were run for 10 million generations with parameters sampled every 1000 generations. TRACER 1.7 assessed convergence of the chains and effective sample size for each parameter, which were all > 300. The first 25% of trees were discarded as 'burn-in', and node ages with upper and lower 95% posterior density (HPD) were calculated using TREEANNOTATOR v.1.8.4.

Based on previous molecular divergence time estimates for major lineages of Membracoidea (Dietrich et al., 2017), the node including Ulopsina szwedoi Dai et al., Anaceratagallia venosa Fourcroy, Anaceratagallia sp., Dryodurgades lamellaris Vilbaste, Japanagallia sp. 1 and Japanagallia sp. 2 was calibrated to have a mean age of 146 Ma with a normal prior. In addition, the fossil taxa Eoidiocerus emarginatus Dietrich & Thomas and Archipedionis obscurus Dietrich & Thomas, both from Baltic amber dated to 37-44 Ma, were used as minimum age estimates for the origins of Idiocerini and Macropsini, respectively, both with a log-normal prior.

Biogeographical analyses

For inferring the distribution history of Eurymelinae, we adopted the classical zoogeographical regions with Wallace's line (Wallace, 1876). However, Madagascar was given particular attention as a specific region with high levels of species richness and endemism (Krishnankutty, 2012). The following biogeographic regions were assigned to extant taxa based on known distributions: (A) Oriental, (B) Palaearctic, (C) Nearctic, (D) Neotropical, (E) Australian, (F) Afrotropical, and (G) Madagascar. Ancestral area probabilities were estimated in RASP v.4.0 (Yu et al., 2015) using the Bayesian binary MCMC (BBM) method and default parameter settings. The consensus tree inferred from the Bayesian analysis was used to infer ancestral ranges.

Results

Phylogenetic analyses

The matrix included 2590 aligned sites (28S D2, 707 bp; 16S, 561 bp; COI, 658 bp; H2A, 315 bp; H3, 349 bp) and 86 morphological characters. Of the 2590 molecular characters, 1252 were variable, among which 1055 were parsimony-informative and 197 were uninformative.

The result of the Bayesian analysis is shown in Fig. 1; ML (BS, SH-aLRT and UFB) scores are shown on individual nodes. Most received moderate to high support (Bayesian PP = 0.9-1/ BS = 70-100/SH-aLRT = 80-100/UFB = 95-100) (Hillis & Bull, 1993; Trifinopoulos & Bui, 2018), but several deep internal nodes were poorly supported in some analyses.

Austroagalloidini was recovered as sister to Eurymelini + Idiocerini (sensu lato) in both analyses (ML and BI) of combined morphological and molecular data with moderate support (PP = 0.87/BS < 50/SH-aLRT = 69.5/UFB = 83). This lineage was sister to Macropsini with moderate branch support (0.91/-/60.5/79). Both analyses (BI and ML) recovered Eurymelini + Idiocerini (sensu lato) as monophyletic with strong branch support (1/95/99.9/100), and this lineage included nine well-supported clades.

The endemic Madagascar genus Nesocerus was placed as sister to the remaining members of the clade. The morphologically aberrant Oriental genus Idioceroides Matsumura (Fig. 4C), was sister to the rest of the clade, excluding Nesocerus, but the branch separating it from the adjacent nodes received poor support. The remaining taxa grouped into two major lineages, one comprising taxa from the Neotropical, Oriental and Australian regions, the other including mostly taxa from the Afrotropical, Madagascar, Oriental and Holarctic regions. Clade 3 comprising most of the endemic South American genera received strong support (1/99/100/100) and was sister to a clade comprising all included Australian taxa, a single genus from Chile, and two taxa from China. The Chilean genus Chileanoscopus Freytag & Morrison grouped with the Australian genus Wiloatma Webb (clade 4) with moderate support (1/-/-/82), but its relationship to neighbouring clades was poorly resolved. The remaining Australian taxa previously included in Idiocerini (except Wiloatma) were placed in a clade with the Australian and Oriental genera Balocerus Freytag & Morrison and Balocha Distant (clade 5) with high support (1/100/99.7/100). Eurymelini (clade 6) was recovered as monophyletic with high support (1/100/100/100). In the remaining major lineage, comprising Afrotropical, Madagascar, Oriental and Holarctic genera, a clade (clade 7) comprising Afrotropical taxa Kopamerra Webb and Rotifunkia China received strong support (1/100/99.8/100). The widespread Palaeotropical genus Chunra Distant (represented by five species from China, Madagascar, Malaysia and Cameroon) was placed in a moderately well-supported (1/73/100/100) clade 8 with Megipocerus Zakhvatkin and Busonia Distant, but Chunra was not recovered as monophyletic and relationships within this clade are poorly resolved. Clade 9, including Holarctic, Oriental, Madagascar and Afrotropical taxa, received moderate to high support (1/62/95.9/99).

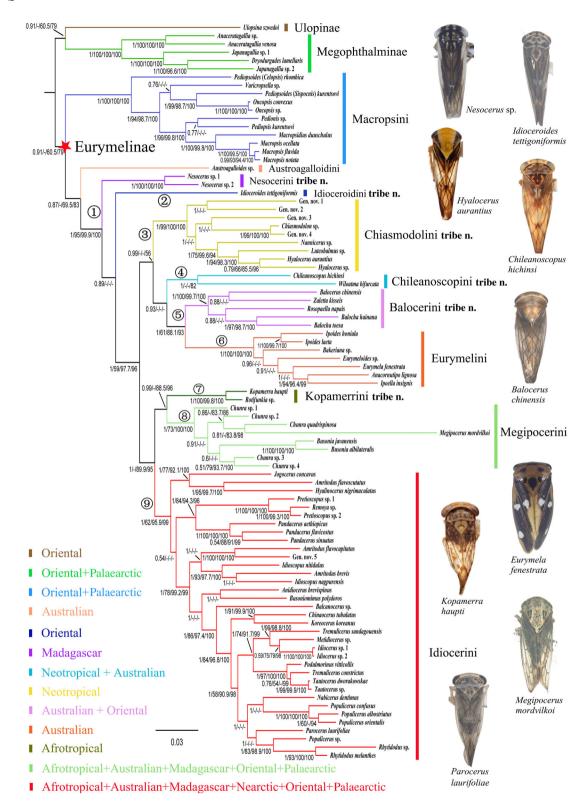


Fig. 1. Bayesian consensus tree from analysis of combined morphological and molecular data. Numbers below branches are Bayesian posterior probability (PP), bootstrap pseudoreplicates (BS), Shimodaira–Hasegawa-like approximate likelihood ratio test (SH-aLRT) and ultrafast bootstrap (UFB) from maximum likelihood analysis. '-' indicates clade not recovered in ML analysis or with support values <50%. [Colour figure can be viewed at wileyonlinelibrary.com].

Some relationships differed between BI and ML results, but these conflicting topologies received low branch support in one or both analyses. Clade 1 was recovered as sister to the rest of Eurymelinae in the BI tree (Fig. 1), excluding Austroagalloidini and Macropsini, but the positions of clades 1 and 2 are reversed in the ML tree (Fig. S1). The BI analyses placed clade 4 as sister to clade (5+6), but in the ML tree, clade 4 is sister to clade (3+5+6). Both trees indicated that the Old World clade (7+8+9) is a sister group to the New World clade (3+4+5+6), clade 5 is sister to clade 6, and clade 9 is sister to clade 7 + 8.

Analyses of molecular data alone (without morphology) yielded topologies largely the same as those obtained from analyses of combined morphological and molecular data. However, the BI analysis (Fig. S2) united Eurymelinae sensu lato in one clade, with the relationships among them unresolved. The ML analysis yielded a consensus tree (Fig. S3) supporting Macropsini as sister to Eurymelini, and this lineage as sister to Austroagalloidini. In the ML topology, *Idioceroides* and Nesocerus formed a clade sister to the remaining members of Eurymelinae, except for Austroagalloidini and Macropsini. The ML topology also did not unite Chileanoscopus and Wiloatma in one clade, instead placing Chileanoscopus as sister to clade 3 and Wiloatma as sister to clade 5. However, these branches received only low to moderate support.

Divergence time estimates

Molecular divergence time estimates (Fig. 2) indicate that Eurymelinae diverged from other Cicadellidae during the Lower Cretaceous at c. 144 Ma. The tribe-level lineages of Eurymelinae are estimated to have diverged between the Lower and Upper Cretaceous (73-137 Ma).

Biogeographic analyses

Inferred ancestral areas are summarized in Fig. 3. The most likely ancestral region for Eurymelinae was recovered as Oriental (98%) and subsequently for Eurymelinae (without Austroagalloidini and Macropsini) (84%), clade 7 + 8 + 9 (92%), clade 7 + 8 (62%), clade 8 (69%) and clade 9 (98%). The most likely ancestral region for clade 3+4+5+6 was reconstructed as Neotropical (51%), as well as clade 3 (99%). The Australian region is recovered as the most likely ancestral area for clade 4 + 5 + 6 (84%), clade 5 + 6 (97%), clade 4 (70%), clade 5 (98%)and clade 6 (99%). Clade 7 is estimated to have originated in the Afrotropical region (78%).

Discussion

Phylogeny of Eurymelinae

The present results provide a well-resolved phylogenetic framework for Eurymelinae and confirm that this subfamily is monophyletic. In agreement with previous analyses

(Krishnankutty, 2012; Dietrich et al., 2017), our results indicate that Idiocerinae (sensu Oman et al., 1990) is paraphyletic with respect to Eurymelinae (sensu stricto). Based on the phylogenomic analysis of Dietrich et al. (2017), Dietrich & Thomas (2018) broadened the concept of Eurymelinae to include Macropsini. Our results are consistent with the inclusion of Austroagalloidini as a tribe of Eurymelinae (sensu lalto), although the position of the latter tribe was unresolved by the analysis of Dietrich et al. (2017). Our taxon sample here included outgroups from only two other cicadellid subfamilies (Ulopsinae and Megophthalminae) and therefore did not thoroughly test the monophyly of this broader concept of Eurymelinae sensu Dietrich & Thomas (2018). Additional analyses with denser sampling of both taxa and characters will be needed to fully test these hypotheses and further validate the proposed broader concept of Eurymelinae.

Overall, our analyses of Eurymelinae recovered 11 clades with moderate to strong branch support and each of these clades is diagnosable using morphological characters, so we propose a new tribal classification here with 11 tribes, including the monobasic tribe Austroagalloidini.

Eurymelini was formerly treated as a separate family (Evans, 1966) or subfamily (Oman et al., 1990) but our analysis shows that it is the sister of Balocerini tribe n. (see later) and merits tribal status. The three formerly recognized tribes of Eurymelinae, Eurymelini (sensu stricto) and Ipoini were not recovered as monophyletic. Specimens of Pogonoscopini, species of which live in ant nests, were not available for our study, so more detailed analyses with a larger taxon sample is needed to elucidate the relationships within Eurymelini.

Webb (1983b) previously noted that *Kopamerra* shared some unique morphological traits with Rotifunkia (e.g. male abdomen dorsal apodeme strut-like, male pygofer with a protuberance on posterior margin and a heavily sclerotized area at the inner dorsal margin of the male pygofer). Based on our phylogeny, which placed these two genera in a well-supported clade, we propose a new tribe, Kopamerrini tribe n.

Clade 5, comprising genera from the Australian and Oriental regions (Rosapaella, Zaletta, Balocerus and Balocha), also received strong branch support and is morphologically characterized by the male style having a preapical lobe and ventrally serrate apical process. A new tribe Balocerini tribe n. is here established for this group.

Isaev (1988) established Megipocerini based on the type genus Megipocerus from the Palaearctic region but also included all the known endemic Neotropical genera and several Australian, Afrotropical and Oriental genera in this tribe. However, Wei et al. (2010) suggested that the morphological characters proposed as diagnostic for Megipocerini are unreliable. Zhang & Li (2015) established Busonini based on the type genus Busonia and included another nine Oriental genera in the tribe. Our phylogenetic analysis did not support a close relationship between Megipocerus and the Neotropical genera included in Megipocerini by Isaev (1988). On the other hand, our results do support including Chunra (also included in the tribe by Isaev) and Busonia (not previously included) in Megipocerini. Thus, we recognize Busonini syn.n. as a junior synonym

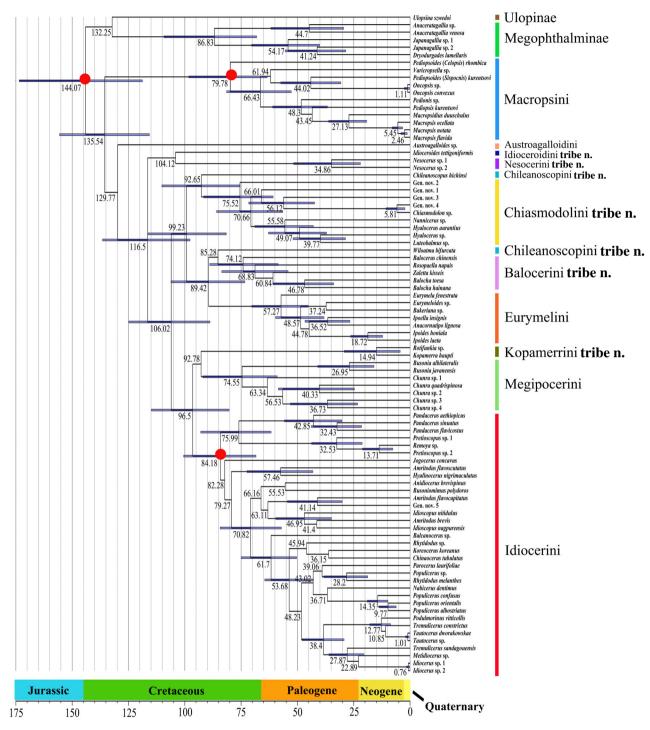


Fig. 2. Chronogram of Eurymelinae with divergence times estimated from the BEAST analysis. The blue bars represent 95% posterior density intervals for the node age. Placement of two fossil calibrations and one secondary (root node) calibration are indicated by red circles. [Colour figure can be viewed at wileyonlinelibrary.com].

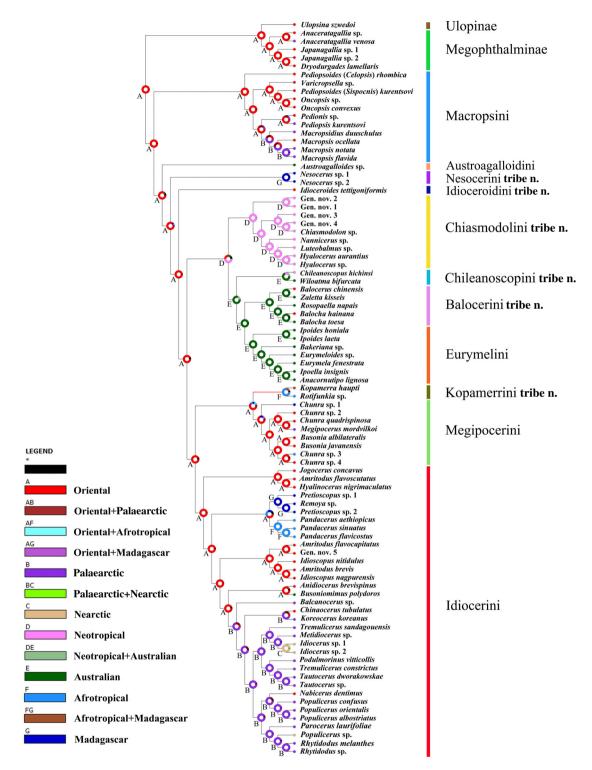


Fig. 3. Ancestral area reconstructions for Eurymelinae as inferred using the Bayesian binary Markov chain Monte Carlo analysis (exported from RASP). Pie diagrams show the ancestral distribution estimated for internal nodes, with the most likely state displayed outside of the centre. [Colour figure can be viewed at wileyonlinelibrary.com].

of Megipocerini. Megipocerini is redefined here to comprise Afrotropical, Australian, Madagascar, Oriental and Palaearctic taxa. Based on the placement of most Neotropical genera in a separate clade with high support, a new tribe, Chiasmodolini **tribe n.** is here established for this clade.

Chileanoscopus, endemic to Chile (Freytag & Morrison, 1969; Heller, 1969; Xue et al., 2017), differs from other endemic Neotropical genera in several respects (e.g. subgenital plates not broadened in ventral view; style apophysis longer than apodeme; apophysis broad in lateral view; apex not hook-shaped and not curved ventrally) but is similar to Wiloatma Webb (distributed in Australia and the western Pacific) in the structure of the hind leg and male genitalia (e.g. hind femur with 2+1 apical macrosetae; segment X with pair of slender and elongate processes; subgenital plates broadened in lateral view). In our analysis, Chileanoscopus and Wiloatma grouped together with moderate to strong branch support, but their relationship with other clades was not well resolved. We propose a new tribe, Chileanoscopini tribe n., for these two genera.

Our results indicate that Idiocerini, as previously defined, is paraphyletic, so we redefine this tribe to correspond with clade 9 (Fig. 1), with other previously included genera transferred to Balocerini **tribe n.**, Chileanoscopini **tribe n.**, Idioceroidini **tribe n.**, Kopamerrini **tribe n.**, Nesocerini **tribe n.** and Megipocerini, Idiocerini now includes genera from the Afrotropical, Australian, Madagascar, Oriental and Holarctic regions. Within this group, our analysis recovered a clade of Afrotropical and Madagascar genera with strong support (1/84/94.3/96). Otherwise, the Idiocerus group (including Balcanocerus, Chinaocerus, Idiocerus, Koreocerus, Metidiocerus, Nabicerus, Parocerus, Podulmorinus, Populicerus, Rhytidodus, Tautocerus and Tremulicerus) of Idiocerini is widely distributed in the Holarctic region (e.g. Freytag, 1965; Hamilton, 1985; Kwon, 1985; Isaev, 1988), and was recovered as monophyletic with mostly strong support in our results (1/86/97.4/100).

Although our results from BI and ML analyses are very similar, there is some discordance in higher-level relationships within Eurymelinae. In the BI topology, Nesocerus subtends Idioceroides but the positions of these two genera are reversed in the ML topology. Idioceroides has been difficult to classify based on morphology because it shares certain traits (e.g. anteclypeus swollen in male; ocelli high on the face and forewing appendix narrow) with Macropsini and Megophthalminae. Although *Idioceroides* was originally placed in Eurymelinae by Matsumura (1912), Maldonado-Capriles (1976) transferred it to Agallinae (now in Megophthalminae) based on the narrow forewing appendix and the ocelli high on the face. Zhang & Viraktamath (2009) returned Idioceroides to Eurymelinae. Moreover, the swollen male anteclypeus, emarginate gena, and obsolete lateral frontal sutures in Idioceroides also suggest a possible relationship to Macropsini. Our phylogenetic analyses support placement of Idioceroides in Eurymelinae and its placement as an early-diverging lineage is consistent with its apparent (plesiomorphic) morphological similarity to Macropsini and Megophthalminae. Based on our phylogenetic analysis, two new tribes are established for the two early-diverging groups, Idioceroidini tribe n. and Nesocerini tribe n.

In both BI and ML analyses, the species of *Amritodus* Anufriev failed to form a monophyletic group. Instead, in the ML tree, *Amritodus brevis* Viraktamath grouped with species of *Idioscopus* Baker, forming a well-supported monophyletic group, *Amritodus flavoscutatus* Cai & Shen sister to *Hyalinocerus nigrimaculatus* Zhang & Li, and *Amritodus flavocapitatus* Cai & He grouped with an undescribed genus, indicating that *Amritodus* needs to be systematically revised.

Divergence times and biogeography

Reconstruction of the ancestral areas of major clades indicate a high degree of continental-scale biogeographical structure in Eurymelinae. Genera occurring in the same biogeographical region often group together. Although the ancestral range of the subfamily was reconstructed as Oriental, this result was certainly biased by the inclusion of only Oriental taxa in the outgroup. Considering that two of the earlier-diverging lineages of Eurymelinae occur in the Oriental region (Idioceroides) and Madagascar (Nesocerus) and that the ancestral area of the clade comprising the remaining groups was more equivocal, we consider the ancestral area for the subfamily to be unresolved, although, given the distribution of ancestral areas among the major lineages, a Gondwanan origin seems reasonable. Most of the included taxa grouped into two major lineages (clades 3-6 and clades 7-9 in Fig. 1), one comprising Neotropical and Australian sister clades (clades 3-6), and the other (clades 7-9) with a likely Afrotropical ancestral distribution but including more derived lineages occurring primarily in the Oriental and Holarctic regions. Although the overall pattern suggests a possible Gondwanan vicariant origin for these major lineages, the divergence time estimates for these clades suggest that rare trans-oceanic dispersal events were responsible for the origins of these geographically restricted lineages.

Molecular divergence time estimates indicate that Eurymelinae diverged from other cicadellid subfamilies during the Lower Cretaceous (144 Ma). This is somewhat earlier than the previous estimate (138 Ma) by Dietrich et al. (2017). Within Eurymelinae, divergences among major lineages and tribes are estimated to have occurred mostly between the Lower and Upper Cretaceous. A clade comprising primarily Neotropical and Australian tribes (Balocerini tribe n., Chiasmodolini tribe n., Chileanoscopini tribe n. and Eurymelini) diverged from the remaining tribes distributed mainly in the Afrotropical, Oriental and Holarctic regions (Kopamerrini tribe n., Megipocerini and Idiocerini) at c. 89-125 Ma (in Cretaceous). Divergence of Australian tribes Eurymelini and Balocerini **tribe n.** appears to have occurred during 73-106 Ma. Divergence of the Neotropical endemic tribe Chiasmodolini tribe n. from Australian Eurymelini + Balocerini **tribe n.** occurred c. 82–116 Ma (in Cretaceous). Kopamerrini tribe n. + Megipocerini diverged from Idiocerini c. 80-115 Ma. These divergence time estimates should be interpreted with caution, given the sparse fossil record of Eurymelinae. The two fossils used to calibrate the root nodes of Macropsini and Idiocerini could possibly be placed more precisely within these groups through further comparative morphological study of the type specimens (Dietrich & Thomas, 2018) and by adding morphological data for the fossils to the present data matrix. This might be expected to shift the divergence time estimates slightly backward in time.

Taxonomy

Subfamily Eurymelinae Amyot & Serville

Revised diagnosis. Head wider than pronotum, rarely equal in width (Fig. 5A, B); crown short, usually evenly rounded to face; face usually wider than long, rarely slightly narrower; ocelli on face well below crown margin; antenna sometimes expanded apically or subapically; lateral frontal sutures usually developed; lorum broad, rarely narrow (Fig. 5C, D); pronotum lateral margin shorter than medially; forewing without granulose texture (Fig. 5E-M); hind femur with setal formula 2+0 or 2+1; first valvula of ovipositor usually with dorsal sculpturing strigate (Fig. 5N, O); second valvula of ovipositor usually with several dorsal teeth (Fig. 5P, O); male subgenital plates free and usually elongate (Fig. 6A-C); male style apex linear, not cheliform (Fig. 6E-G).

The new classification proposed for the tribes of Eurymelinae is summarized in Table S5.

Key to tribes of Eurymelinae

- 1. Pronotum strongly produced, anterior margin extended anterad of eyes in dorsal view (Fig. 4B); proepisternum large, not concealed by gena; hindwing vein R_{2+3} absent, submarginal vein not extended along costal margin basad
- Pronotum not produced anterad of eyes in dorsal view (Fig. 4C-I); proepisternum small, mostly or entirely concealed by gena; hindwing vein R₂₊₃ present and extended
- 2. Head with short but well-delimited crown, transition from crown to face delimited by transverse carina (Fig. 4A) Austroagalloidini
- Head with transition from crown to face rounded, not delimited by transverse carina (Fig. 4C–I)...................3
- 3. Lateral frontal sutures absent or very weakly delimited; ocelli distinctly above mid-height of eyes in anterior view, closer to eyes than to midline (Fig. 5D); forewing appendix narrow (Fig. 5F) Idioceroidini tribe n.
- Lateral frontal sutures usually well delimited or, if not, ocelli not distinctly above mid-height of eyes and closer to midline than to eyes (Fig. 5C); forewing appendix broad (Fig. 5M)......4
- 4. Forewing with crossvein r-m1 elongate and connected between R_{2+3} and R_{4+5} (Fig. 5J) $\ldots\ldots$. Eurymelini
- Forewing without crossvein r-m1, if present, short and
- Style attached to subgenital plate, apex hook-like and curved ventrally (Fig. 6F) Chiasmodolini tribe n.

- Style not attached to subgenital plate, linear or gradually curved, apex not hook-like and not curved ventrally (Fig. 6G).....6
- 6. Subgenital plate ventral margin with prominent macrosetae (Fig. 6B)......Nesocerini tribe n.
- Subgenital plate without macrosetae, long and fine setae may be present (Fig. 6A, D)......7
- Style with preapical lobe, apical process serrate along ventral margin (Fig. 6E)......Balocerini tribe n.
- Style without preapical lobe, apical process not serrate (Fig. 6G).....8
- 8. Forewing appendix bordering three apical cells (Fig. 5L) Megipocerini
- Forewing appendix bordering two apical cells (Fig. 5H, K).....9
- 9. Male abdominal segment X with pair of slender, elongate
- Male abdominal segment X without such processes (Fig. 6A, D)......10
- 10. Male pygofer posterior margin with protuberance and heavily sclerotized area on inner dorsal margin
 - Male without such protuberance and sclerotized area (Fig. 6D)......Idiocerini

Austroagalloidini Evans, stat. rev.

Austroagalloidinae Evans, 1938: 41.

Type genus: Austroagalloides Evans, 1935: 70.

Diagnosis. Medium-sized; head with crown well delimited and usually depressed, crown-face transition angulate in profile; face above antennal ledge forming angle with lower part of face; lateral frontal suture extended to ocellus; gena narrow; pronotum not extended anterad of eye in dorsal view; forewing appendix narrow.

Notes. This tribe includes only the type genus, which was placed between Macropsini and the remaining Eurymelinae in the phylogenetic results. It was recognized as a separate subfamily by Oman et al. (1990) but the present results support including it as a tribe within Eurymelinae. The phylogenomic analysis of Dietrich et al. (2017) placed Austroagalloides as sister to the endemic Chilean genus Chibala Linnavuori & DeLong (Neobalinae) with 100% ML bootstrap support, but the position of this clade relative to other leafhoppers was unresolved.

Distribution. Australian.

Balocerini Xue, Dietrich & Zhang tribe n.

Type genus: Balocerus Freytag & Morrison, 1969: 41, here designated.

http://zoobank.org/urn:lsid:zoobank.org:act:DD975CE8-A 109-47A5-89BD-9A370DBD6DC4.

Diagnosis. Small to medium-sized; crown and pronotum striate; lateral frontal suture long, usually extended 1/2-2/3 distance to corresponding ocellus; hind femur macrosetal formula 2+0 (except Quilopsus Webb and Tumocerus Evans); forewing



Fig. 4. Representatives of Eurymelinae. (A) Austroagalloides grisea Evans (Austroagalloidini), New South Wales (NSW), Australia; (B) Pedionis garuda (Distant) (Macropsini), Guangxi, China; (C) Idioceroides tettigoniformis Matsumura (Idioceroidini), Taiwan, China; (D) Eurymeloides sp. (Eurymelini), NSW, Australia; (E) Rotundicerus sp. (Chiasmodolini), Roraima, Brazil; (F) Rosopaella magnata Webb (Balocerini), Queensland, Australia; (G) Busoniomimus polydoros (Kirkaldy) (Idiocerini), Queensland, Australia; (H) Populicerus suturalis (Fitch) (Idiocerini), Illinois, U.S.A.; (I) Chinaocerus sp. (Idiocerini), Shaanxi, China. Photographs are by C.H. Dietrich. [Colour figure can be viewed at wileyonlinelibrary.com].

with two subapical cells (except *Musgraviella* Evans with small third subapical cell), appendix developed and bordering two apical cells; segment X with pair of arms; subgenital plate expanded distally in lateral view, with fine setae on dorsal and ventral margin; style with preapical lobe, apical process serrate distally on ventral margin; connective Y-shaped; aedeagal shaft curved ventrally, broadened in lateral view, dorsal apodeme absent, preatrium developed, gonopore apical.

Notes. This tribe includes nine genera: Balocerus Freytag & Morrison, Balocha Distant, Balocharella Webb, Bharinka Webb, Musgraviella Evans, Quilopsus Webb, Rosopaella Webb, Tumocerus Evans and Zaletta Metcalf.

Distribution. Australian and Oriental.

Chiasmodolini Xue, Dietrich & Zhang tribe n.

Type genus: *Chiasmodolon* Dietrich, 1990 in Dietrich & McKamey, 1990: 217, here designated.

http://zoobank.org/urn:lsid:zoobank.org:act:83191074-CC57-41BF-ADD8-77815448FDE3.

Diagnosis. Medium-sized; crown and pronotum usually shagreen; lateral frontal suture long, usually reaching or nearly

reaching the corresponding ocellus; hind femur macrosetal formula 2+0; forewing with two subapical cells, appendix developed and bordering two apical cells; segment X with pair of arms; subgenital plates fused at base, broadened in ventral view; style attached to subgenital plate, apophysis as short as or shorter than apodeme, apex hook-like and curved ventrally; connective usually V- or U-shaped, stem very short; aedeagal shaft elongate, dorsal apodeme usually undeveloped, preatrium usually developed, gonopore apical or subapical.

Notes. This tribe includes 17 Neotropical genera (Aduchunroides Maldonado-Capriles, Barolineocerus Freytag, Bolivianoscopus Lozada, Chiasmodolon Dietrich, Chunroides Evans, Corymbonotus Maldonado-Capriles, Hyalocerus Maldonado-Capriles, Isolineocerus Freytag, Jamacerus Freytag, Luteobalmus Maldonado-Capriles, Maynacerus Lozada, Nannicerus Maldonado-Capriles, Optocerus Freytag, Parachunroides Maldonado-Capriles, Pseudoidioscopus Maldonado-Capriles, Rotundicerus Maldonado-Capriles and Tomopennis Maldonado-Capriles), most of which were previously included in Megipocerini. Chiasmodolini tribe n. is restricted to the Neotropical region and is sister to a clade comprising Australian genera.

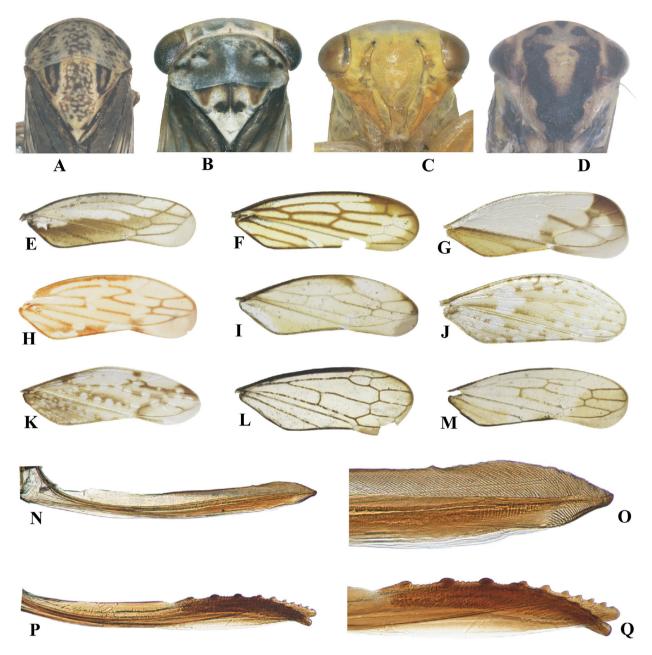


Fig. 5. (A, B) Head and pronotum, dorsal view: (A) Megipocerus mordvilkoi Zakhvatkin; (B) Parocerus laurifoliae (Vilbaste). (C, D) Face: (C) Parocerus laurifoliae (Vilbaste); (D) Idioceroides petaliformis Xue & Zhang. (E-M) Forewing: (E) Nesocerus sp.; (F) Idioceroides tettigoniformis Matsumura; (G) Hyalocerus aurantius Maldonado-Caprilesi; (H) Chileanoscopus hichinsi (Heller); (I) Balocerus chinensis Freytag & Morrison; (J) Ipoides honiala (Kirkaldy); (K) Kopamerra haupti (Melichar); (L) Megipocerus sp.; (M) Parocerus laurifoliae (Vilbaste). (N-Q) Parocerus laurifoliae (Vilbaste): (N) first valvula; (O) apex of first valvula; (P) second valvula; (Q) apex of second valvula. [Colour figure can be viewed at wileyonlinelibrary.com].

Distribution. Neotropical.

Chileanoscopini Xue, Dietrich & Zhang tribe n.

Type genus: Chileanoscopus Freytag & Morrison, 1969: 285, here designated.

http://zoobank.org/urn:lsid:zoobank.org:act:262EA680-267 B-458D-AF2C-F4C47C0BD307.

Diagnosis. Small to medium-sized; crown striate; lateral frontal suture extended to 1/2 distance from antennal ledge to corresponding ocellus; hind femur with 2+1 apical macrosetae; forewing with two subapical cells, appendix developed and bordering two apical cells; segment X with pair of slender and elongate processes; subgenital plate broadened in lateral view; style curved dorsally, without preapical lobe; connective

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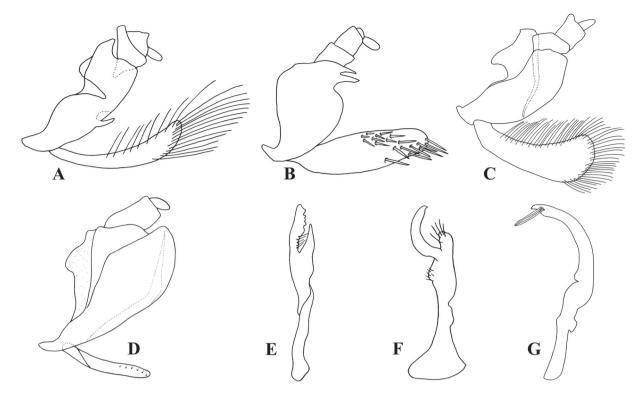


Fig. 6. (A–D) Male pygofer, anal tube and subgenital plate, lateral view: (A) Kopamerra haupti (Melichar); (B) Nesocerus tulearensis Krishnankutty & Dietrich; (C) Chileanoscopus hichinsi (Heller); (D) Amritodus brevis Viraktamath. (E–G) style, lateral view: (E) Balocerus chinensis Freytag & Morrison; (F) Hyalocerus sp.; (G) Populicerus albostriatus Cai & Shen.

Y-shaped, with medial longitudinal keel; aedeagal shaft elongate, dorsal apodeme well-developed, preatrium undeveloped; gonopore subapical.

Notes. This tribe only includes the type genus *Chileanoscopus* Freytag & Morrison and *Wiloatma* Webb.

Distribution. Australian and Neotropical.

Eurymelini Amyot & Serville

Eurymelini Amyot & Serville, 1843: 554. Type genus: *Eurymela* Le Pelletier & Serville, 1825: 603, original designation.

Diagnosis. Medium-sized; forewing with crossvein r-m1 elongate, resembling a longitudinal vein and connected between R_{2+3} and R_{4+5} ; appendix developed but short, bordering one apical cell; subgenital plate dorsoventrally flattened; connective not present between styles; style attached to subgenital plate; aedeagal basal apodeme situated dorsally.

Notes. Eurymelini is restricted to the Australian region and includes all genera previously included in Eurymelinae (sensu Oman et al., 1990), 33 genera, they are Aloeurymela Evans, Aloipo Evans, Anacornutipo Evans, Australoscopus China, Bakeriana Evans, Citripo Evans, Cornutipo Evans, Dremuela Evans, Eurymelella Evans, Eurymela Le Peletier & Serville, Eurymelessa Evans, Eurymelita Evans, Eurymeloides Ashmead, Eurymelops Kirkaldy, Eurypella Evans, Ipolo Ev

Iposa Evans, Katipo Evans, Lasioscopus China, Malipo Evans, Myrmecoscopus Evans, Nanipoides Evans, Opio Evans, Pauripo Evans, Pauroeurymela Evans, Platyeurymela Evans, Pogonoscopus China, Relipo Evans and Stenipo Evans.

Distribution. Australian.

Idiocerini Baker

Idiocerini Baker, 1915: 317. Type genus: *Idiocerus* Lewis, 1834: 47, original designation.

Diagnosis. Small to medium-sized; crown usually striate; lateral frontal suture usually reaching or nearly reaching the corresponding ocellus; forewing with two or three subapical cells, appendix developed and bordering two apical cells; hind femur with setal formula 2+0 or 2+1; subgenital plate broadened in lateral view, depressed in ventral view; style sickle-shaped, usually without preapical lobe, often with fine or stout preapical setae on dorsal margin; aedeagus tube-like, usually with paired processes, dorsal apodeme usually developed, gonopore on ventral margin apical or subapical.

Notes. Idiocerini includes 59 genera: Acericerus Dlabola, Amritodus Anufriev, Anidiocerus Maldonado-Capriles, Austrocerus Evans, Balcanocerus Maldonado-Capriles, Bharoopra Webb, Bugraia Koçak, Bundabrilla Webb, Burmascopus Viraktamath, Busoniomimus Maldonado-Capriles, Cafixia Webb, Chinaocerus Zhang & Li, Dianica Zhang, Flexocerus

Kuoh & Fang, Grootonia Webb, Hatralixia Webb, Henanocerus Zhang & Wang, Hespericerus Gnezdilov, Hyalinocerus Zhang & Li, Idiocerus Lewis, Idioscopus Baker, Jogocerus Viraktamath, Koreocerus Kwon, Lambirocerus Xue & Zhang, Longicauda Zhang & Wu, Maroopula Webb, Mediocerus Freytag, Metidiocerus Ossiannilsson, Mexicanocerus Freytag, Nabicerus Kwon, Neoidioscopus Huang & Maldonado-Capriles, Nilgiriscopus Viraktamath, Nyndgama Webb, Pandacerus Webb, Paraidioscopus Maldonado-Capriles, Parocerus Vilbaste, Pascoepus Webb, Pedioscopus Kirkaldy, Periacerus Viraktamath & Parvathi, Philippocerus Maldonado-Capriles, Podulmorinus Kwon, Populicerus Dlabola, Pretioscopus Webb, Quartauropa Webb, Remoya Webb, Rhusopus Webb, Rhytidodus Fieber, Sahlbergotettix Zakhvatkin, Sulamicerus Dlabola, Taiwanocerus Huang & Maldonado-Capriles, Tasnimocerus Ghauri, Tautocerus Anufriev, Theronopus Webb, Tinderella Webb, Tremulicerus Dlabola, Undophomorpha Xue & Zhang, Yachandra Webb and Zinislopa Webb. It also includes the recently described fossil genus Eoidiocerus Dietrich & Thomas from the Eocene Baltic amber.

Distribution. Afrotropical, Australian, Madagascar, Nearctic, Oriental and Palaearctic.

Idioceroidini Xue, Dietrich & Zhang tribe n.

Type genus: Idioceroides Matsumura, 1912: 324, here designated.

http://zoobank.org/urn:lsid:zoobank.org:act:714F2475-8 FDA-4F68-AB6A-074ECD9D40D2.

Diagnosis. Medium-sized; crown striate; ocelli very high on face, close to eyes; lateral frontal suture not reaching ocelli; lora narrow and anteclypeus swollen in male; hind femur macrosetal formula 2+1; forewing with three subapical cells, appendix well-developed but narrow, bordering two apical cells; segment X with pair of arms; subgenital plate broadened in lateral view; style slender and elongate; connective T-shaped; aedeagal shaft stout and curved dorsally, preatrium elongate and arcuate, gonopore apical.

Notes. This tribe includes only the type genus, which was recovered as sister to the rest of Eurymelinae except in the ML topology.

Distribution. Oriental.

Kopamerrini Xue, Dietrich & Zhang tribe n.

Type genus: Kopamerra Webb, 1983: 220, here designated. http://zoobank.org/urn:lsid:zoobank.org:act:5FBBED0D-3ECD-4426-839C-393D072B1154.

Diagnosis. Small to medium-sized; crown and pronotum shagreen; lateral frontal suture present, long; hind femur with 2+0 apical macrosetae; forewing with three subapical cells, appendix developed and bordering two apical cells; male abdomen with dorsal apodemes strut-like; male pygofer with protuberance on posterior margin, inner dorsal margin of pygofer with sclerotized region; segment X loosely attached to pygofer; style foot-like, apex curved dorsally; connective Y-shaped, with medial longitudinal keel; aedeagal shaft elongate, with preapical process on lateral surface, dorsal apodeme broadened in lateral view, preatrium undeveloped, gonopore subapical.

Notes. This tribe includes two genera, Kopamerra Webb and Rotifunkia China.

Distribution. Afrotropical.

Macropsini Evans

Macropsinae Evans, 1935: 63. Type genus: Macropsis Lewis, 1834: 49, by subsequent designation.

Diagnosis. Small to medium-sized; crown usually shorter medially than next to eye, rounded to face; lateral frontal sutures usually poorly delimited; gena narrow, exposing large flap-like proepisternum; forewing appendix narrow; hindwing vein R₂₊₃ absent; male subgenital plate slender throughout length; female second valvula elongate and slender.

Notes. This group has been treated as a separate subfamily (Oman et al., 1990) but was recently reduced to tribal status within Eurymelinae (Dietrich et al., 2017; Dietrich & Thomas, 2018). Our phylogenetic results place Macropsini as sister to the remaining Eurymelinae. In addition to the type genus, the following genera are included: Archipedionis Dietrich & Thomas, Galboa Distant, Hephathus Ribaut, Macropsella Hamilton, Macropsidius Ribaut, Macropsis Lewis, Oncopsis Burmeister, Paragalboa Yang, Dietrich & Zhang, Pedionis Hamilton, Pediopsis Burmeister, Pediopsoides Matsumura, Reticopsella Viraktamath, Reticopsis Hamilton, Ruandopsis Linnavuori, Stenopsoides Evans, Stenoscopus Evans, Toropsis Hamilton, Varicopsella Hamilton and Zelopsis Evans.

Distribution. Afrotropical, Australian, Madagascar, Nearctic, Oriental and Palaearctic.

Megipocerini Isaev

Megipocerini Isaev, 1988: 65. Type genus: Megipocerus Zakhvatkin, 1945: 3, original designation.

Busonini Zhang & Li, 2015: 100. syn.n. Type genus: Busonia Distant, 1908: 198.

Diagnosis. Small to medium-sized; head slightly wider or as wide as pronotum; crown and pronotum shagreen (except Dhongariva Webb and Hydabricta Webb with crown and pronotum striate, Eutandra Webb crown striate); lateral frontal suture developed (except Busonia Distant absent); combined length of mesoscutum and scutellum usually longer than pronotum and crown together; hind femur usually with 2+1 apical macrosetae; forewing appendix broadened, extending to the third apical cell; style dorsal margin without setae; connective T- or I-shaped, arm not distinctly broadened in lateral view; aedeagal shaft tube-like, curved dorsad, preatrium present but short, gonopore apical or subapical.

Notes. This tribe, as previously defined by Isaev (1988), included 24 genera from all zoogeographic realms. Our phylogenetic analysis supports a narrower definition of the tribe, which now includes only Old World genera. In addition to the type genus, the following genera are included: Angusticella Maldonado-Capriles, Brachylorus Maldonado-Capriles, Busonia Distant, Candulifera Webb, Ceylonoscopus Viraktamath, Chunra Distant, Dhongariva Webb, Dolichopscerus Maldonado-Capriles, Eutandra Webb, Gressittocerus Maldonado-Capriles, Hensleyella Webb, Hydabricta Webb, Ipocerus Baker, Iposcopus Baker, Kuchingella Wei & Webb, Lankacerus Viraktamath, Maldonadora Webb, Muinocerus Ghauri, Namiocerus Ghauri, Neoscopus Viraktamath, Philippogalla Xue, McKamey & Zhang, Philipposcopus Maldonado-Capriles and Serridiocerus Xue, McKamey & Zhang.

Distribution. Afrotropical, Australian, Madagascar, Oriental and Palaearctic.

Nesocerini Xue, Dietrich & Zhang tribe n.

Type genus: Nesocerus Freytag & Knight, 1966: 82, here designated.

http://zoobank.org/urn:lsid:zoobank.org:act;2EE8DAEF-D317-4719-8890-C8B37079EBD3.

Diagnosis. Small to medium-sized; crown and pronotum shagreen; lateral frontal suture extending to corresponding ocellus; hind femur usually with 2+0 apical macrosetae; forewing with two subapical cells, appendix bordering three apical cells; segment X loosely attached to pygofer; subgenital plate dorsoventrally flattened, with several prominent macrosetae; style without lateral lobe, apex curved dorsad; connective usually V- or U-shaped, stem very short; aedeagal shaft usually tubular and slender, dorsal apodeme developed, preatrium short and broad in lateral view; gonopore apical or subapical.

Notes. This tribe includes only the type genus, an early-diverging lineage of Eurymelinae.

Distribution. Madagascar.

Unplaced genera in Eurymelinae

Six genera were not placed to tribes, because of inadequate information in their descriptions, having only female specimens, or lack of diagnostic morphological characters; these include *Adiaerotoma* Spinola, *Idiocerella* Evans, *Idionannus* Linnavuori, *Meroleucocerus* Maldonado-Capriles, *Metapocirtus* Costa and *Strongylomma* Spinola.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Maximum likelihood (ML) tree estimated from the combined morphological and molecular datasets. Numbers below branches are bootstrap pseudoreplicates (BS), SH-like approximate likelihood ratio test (SH-aLRT) and ultrafast bootstrap (UFB) from maximum likelihood analysis. '–' indicates support values < 50%.

Figure S2. Bayesian consensus tree recovered from Bayesian analysis of molecular datasets (without morphology). Numbers below branches are Bayesian posterior probabilities (PP).

Figure S3. Maximum likelihood (ML) tree estimated from molecular datasets. Numbers below branches are bootstrap pseudoreplicates (BS), SH-like approximate likelihood ratio test (SH-aLRT) and ultrafast bootstrap (UFB) from maximum-likelihood analysis. '-' indicates support values < 50%.

Table S1. List of taxa and DNA sequences included in the study.

Table S2. Primers used in this study.

Table S3. Morphological characters and character state coding.

Table S4. List of morphological characters used in phylogenetic analyses.

Table S5. Proposed New Eurymelinae classification.

Acknowledgements

We sincerely thank J.R. Schrock (Emporia State University) for editing this manuscript. We wish to thank Sindhu Krishnankutty (Xavier University) for sharing unpublished sequences. We are very grateful to the many colleagues who provided specimens for this study and/or facilitated collecting, including L. Lu, L.B. Ma, Y. Wang, L.Y. Yang, W.J. Huang, M. Catalano, M. Cigliano, J. Cryan, M. Irwin, K. Hill, D. Marshall, S. Krishnankutty, N. Penny, R. Rakitov, M. Sharkey, M. Stiller, D. Takiya, M.D. Webb and J. Zahniser. We thank Shaun Winterton and three anonymous reviewers for constructive and insightful suggestions that substantially improved the manuscript. This research was supported by the National Natural Science Foundation of China (31420103911, 31672339, 31801995), the China Postdoctoral Science Foundation (2018M633590), the Ministry of Science and Technology of the People's Republic of China (2015FY210300, 2005DKA21402) and the U.S. National Science Foundation (grants DEB-1239788 and DEB-1639601).

The authors declare that there are no conflicts of interest.

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Accepted 15 January 2020