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Phylogeny of the tribe Empoascini (Hemiptera: Cicadellidae: Typhlocybinae) based on morphological characteristics, with reclassification of the *Empoasca* generic group

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Abstract. A morphology-based phylogenetic analysis of the tribe Empoascini (Hemiptera: Cicadellidae: Typhlocybinae) is presented for 58 of 83 formerly recognized genera based on 99 morphological characters of adults. The results support excluding the New World *Beamerana* generic group from Empoascini. The remaining genera of Empoascini were recovered as a monophyletic sister group of Dikraneurini. Previously recognized tribes Jorumini and Helionini are derived from within Empoascini and are considered synonyms of the latter tribe. Three previously recognized informal generic groups, the *Empoasca* group, *Alebroides* group and *Usharia* group were paraphyletic but the *Ficiana* group was recovered as monophyletic based on five synapomorphies. Genera previously placed in the *Alebroides* group represent at least six independent lineages, indicating that the hind wing character separating this group from the *Empoasca* group (CuA and MP veins free) is highly homoplasious. *Empoasca* (*sensu lato*) is also paraphyletic. Thus, twelve previously recognized subgenera of *Empoasca* are elevated to genus status and five species groups of *Empoasca* from the New World are recognized as separate new genera. *Sikkimasca* Dworakowska, 1993 is treated as synonym of *Marolda* Dworakowska, 1977 based on the phylogeny. Biogeographic analysis suggests that Empoascini most likely first evolved in the Oriental region and spread to other biogeographic realms more recently by multiple independent invasions.

Introduction

With nearly 5000 known species worldwide, Typhlocybinae (microleafhoppers) is currently the second largest cicadellid subfamily (after Deltocephalinae) based on numbers of described species. Members of this subfamily are ubiquitous and abundant in terrestrial ecosystems worldwide where most appear to feed preferentially on leaf parenchyma cell contents. Many species feed on economically important plants and are considered pests, mostly due to direct feeding injury but some have also been shown to transmit plant pathogens (DeLong, 1971; Weintraub & Beanland, 2006). However, this group remains understudied compared to other groups and tropical faunas in particular remain largely undescribed (Dietrich, 2013a). This group is notoriously difficult taxonomically due to its high diversity, the lack of comprehensive identification tools and the existence of some genera comprising hundreds of described species, often indistinguishable based on their external appearance, distributed across multiple continents. Online interactive keys have been developed for some of these groups (Dmitriev &

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Dietrich, 2019) but the status and relationships of most Typhlocybinae have not yet been elucidated through phylogenetic analysis and many taxonomic problems remain to be resolved.

Empoascini is the second largest tribe of Typhlocybinae, currently comprising about 1373 valid species in 83 extant genera (Southern & Dietrich, 2010; Xu *et al.*, 2017a, 2017b; Dmitriev & Dietrich, 2019). Members of the tribe (Fig. 1) are small (2.0–4.0 mm) and widely distributed on every continent except Antarctica, with different regions hosting distinctive regional faunas. The highest genus-level diversity is found in the Oriental region, home to many relatively small apparently endemic genera. In contrast, the New World fauna has very high species richness but only six previously recognized genera, two of which are endemic. Nielson & Knight (2000) speculated that some presently widespread genera of Empoascini originated in the Oriental region based on their intuitive assessment of species distributions but no explicit biogeographic analysis of the tribe has ever been attempted.

Some Empoascini are serious agricultural and forestry pests, including the cotton leafhopper, *Amrasca biguttula* (Ishida) and potato leafhopper *Empoasca fabae* (Harris), both of which cause hopperburn, a plant disease resulting in browning and shriveling of leaves as a result of leafhopper feeding in combination with plant immune response, leading to millions of dollars in crop losses and costs for control yearly (Backus *et al.*, 2005).

The tribe was established by Distant (1908) (as Empoascaria, one of the two divisions of Typhlocybinae), but the status of this and other typhlocybine tribes has long been controversial, with various authors (e.g. McAtee, 1934; Oman, 1949; Young, 1952, 1965; Metcalf, 1964; Mahmood, 1967) disagreeing over its status and composition. For example, in his review of New World Typhlocybinae, Young (1952) recognized a very broad concept of Typhlocybini that included Empoascini but Mahmood & Ahmed (1968) retained Typhlocybini and Empoascini as separate tribes. Dworakowska's (1979) definition of Empoascini included Jorumini (treated as a synonym) but also included the Neotropical genus *Eualebra* Baker, subsequently transferred to Typholocybini (Dietrich, 2013a). Qin *et al.* (2014) and Xu *et al.* (2017b) adopted the classification of Typhlocybinae by Ahmed (1983) and Dietrich (2013a), which recognizes five tribes in the subfamily and distinguishes Empoascini from other Typhlocybinae by the absence of an appendix on the forewing, and the presence of a hind wing submarginal vein apically between the jugal lobe and MP or RM but not extended around the wing apex along the costal margin. Other diagnostic traits include the presence of well-developed ocelli, the characteristically curved distal segment of forewing vein MCu, presence of a longitudinal row or band of numerous macrosetae on the male subgenital plate, and absence of a well-developed preapical lobe on the style (Qin *et al.*, 2014; Xu *et al.*, 2017b).

Although Empoascini is now widely accepted as a valid tribe of Typhlocybinae, its monophyly has not been adequately tested and its phylogenetic relationship to other tribes has still not been adequately elucidated. Young (1952), Mahmood (1967) and Mahmood & Ahmed (1968) suggested a close relationship to Typhlocybini and similarities in the wing venation of Empoascini to some endemic South American genera of Typhlocybini, e.g., *Columbonirvana* Linnavouri, *Eualebra* Baker, *Tahurella* Dietrich appear to support this view. Zhang (1990) considered Empoascini to be closer to Dikraneurini based on the presence of a well-developed submarginal vein in the hind wing of both groups and the Oriental genera, *Rakta* Dietrich, *Albodikra* Dietrich and *Rubiparvus* Xu, Dietrich & Qin, which appear to be morphologically intermediate between these two tribes, support this hypothesis. Phylogenetic analyses of Cicadellidae by Wagner (1951) and Dietrich *et al.* (2017) suggest that Empoascini is closely related to Alebrini. The analysis of Dietrich *et al.* (2017), based on 388 genetic loci, resolved relationships among included Typhlocybinae with strong branch support but the taxon sample included only two representatives of Empoascini. A comprehensive phylogenetic analysis of Empoascini has never been attempted until now.

Within Empoascini, four informal generic groups have been recognized to date, i.e. the *Alebroides* group and the *Empoasca* group which comprises the *Ficiana* and *Usharia* subgroups (Xu *et al.*, 2017b). The status and relationships of these groups, defined based on characters of the hind wing venation and male genitalia, have not been examined using phylogenetic methods. Most genera of Empoascini are relatively small, comprising 1–30 species. However, the largest genus, *Empoasca*, remains poorly defined and comprises hundreds of species distributed worldwide (Mühlethaler *et al.*, 2009; Southern & Dietrich, 2010). This genus has long been a taxonomic dumping ground for the many mostly small, pale green, indistinctly marked species of Empoascini that lack the distinctive morphological traits used to define other genera of the tribe. Until now, *Empoasca* included 8–14 subgenera, mostly accommodating Old World species, with various authors disagreeing over the validity and status of some subgenera. Although *Empoasca* (*Hebata*) DeLong, 1931 was described to accommodate some North American species, DeLong did not refer to this subgenus in his numerous subsequent papers on *Empoasca* and most other authors have also largely abandoned its use (but see Hamilton & Whitcomb, 2010; Chandler & Hamilton, 2017). Its phylogenetic status also remains untested to date.

Recent studies suggest that the characters of the hind wing venation traditionally used to diagnose typhlocybine tribes may not be reliable in all cases (Dietrich, 2013a, 2013b; Xu *et al.*, 2016). Additional characters are needed to provide more robust taxonomic definitions. In this paper, we provide the first morphology-based phylogenetic analysis of Empoascini, testing its status and relationships to other tribes as well as relationships among its included genera. Based on this analysis, we present a re-classification of species hitherto included in *Empoasca* that uses easily observable characters and reflects, to the extent possible, proposed phylogenetic relationships among species. We also use the morphology-based phylogeny to reconstruct biogeographic relationships, inferring the area of origin of the tribe and relationships among regional faunas.

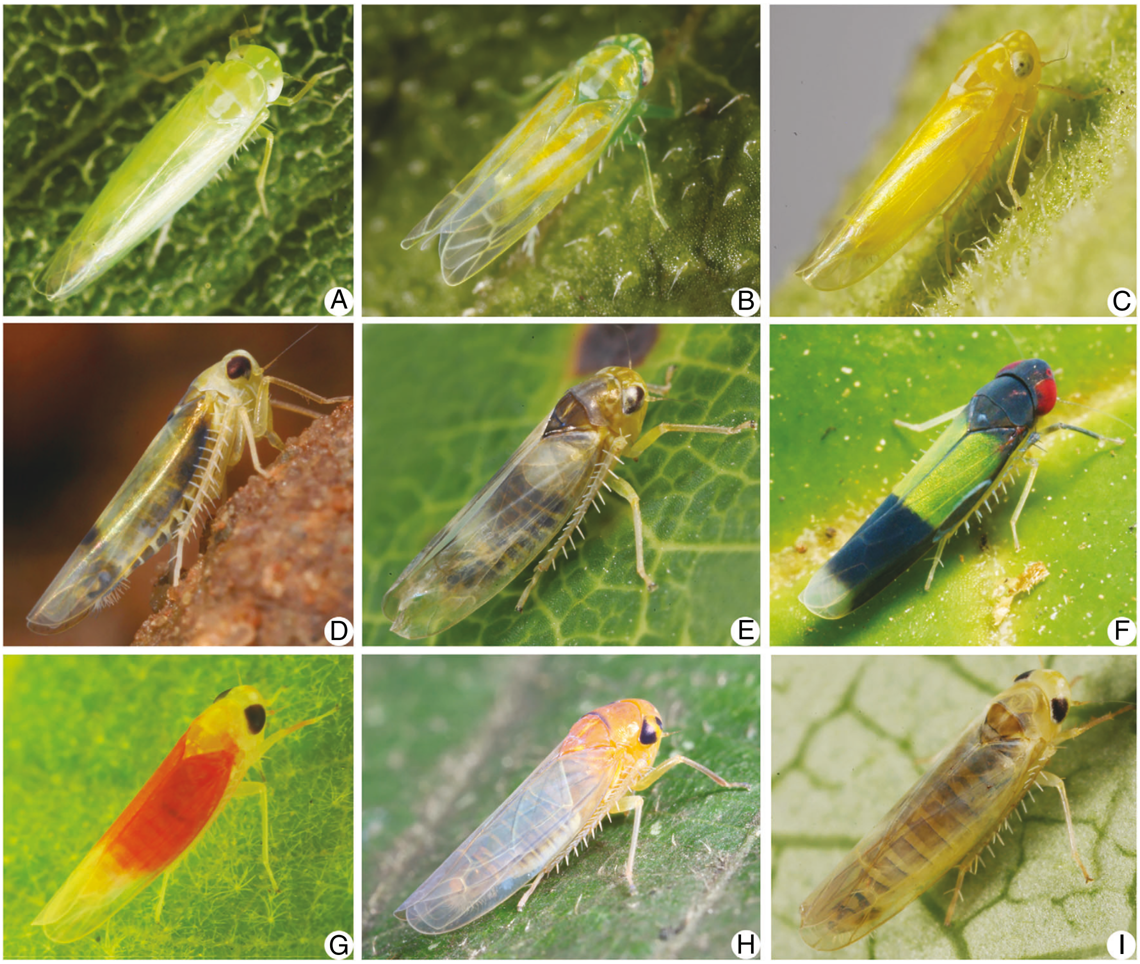

Fig. 1. Representatives of empoascine species. A, C, D. *Empoasca* spp.; B. *Hebata* sp.; E. *Kybos* sp.; F. *Joruma* sp.; G. *Alebrasca actinidiae* Hayashi & Okada; H. *Flaviata* sp.; I. *Alebroides* sp. [Colour figure can be viewed at wileyonlinelibrary.com].

Materials and methods

Specimens studied

Specimens examined are deposited in the following institutions: National Museum of Natural History, Washington DC, U.S.A. (USNM); Illinois Natural History Survey, Champaign, Illinois, U.S.A. (INHS); Entomological Museum, China Agricultural University, Beijing, China (CAU); and Entomological Museum, Northwest A&F University, Yangling, Shaanxi, China (NWAFU).

Terminology and techniques

Morphological terminology (Fig. 2) used in this study mainly follows that of Zhang (1990) except for the abbreviated systems for wing veins and groups of setae of the subgenital plate that follow Dietrich & Dmitriev (2006) and Dworakowska (1994b), respectively. Leg chaetotaxy follows Rakitov (1998) and Dietrich (2005).

The entire male abdomens of the examined specimens were removed and macerated in 10% NaOH solution at approximately 90°C for about 3 min, then rinsed 1–2 times with pure water to clear the digested soft tissues, and subsequently transferred into glycerin for identification and comparative study. Male habitus photos of the specimens were made using a Leica M205A microscope with a Leica DFC camera and processed using the Leica Application Suite (LAS) V3.7. Drawings of male genitalia were made using a drawing tube attached to an Olympus BX40 microscope. Final pictures were edited and improved using Adobe Photoshop CS 8.0.

Taxon sampling and morphological characters

Ninety-nine species belonging to 58 genera of Empoascini (*sensu lato*), representing all generic groups of the tribe, and most species groups of *Empoasca*, were included in the morphological data matrix (Appendix 2). Among these, seven species belong to the *Joruma* group, 10 to the *Beamerana* group, two

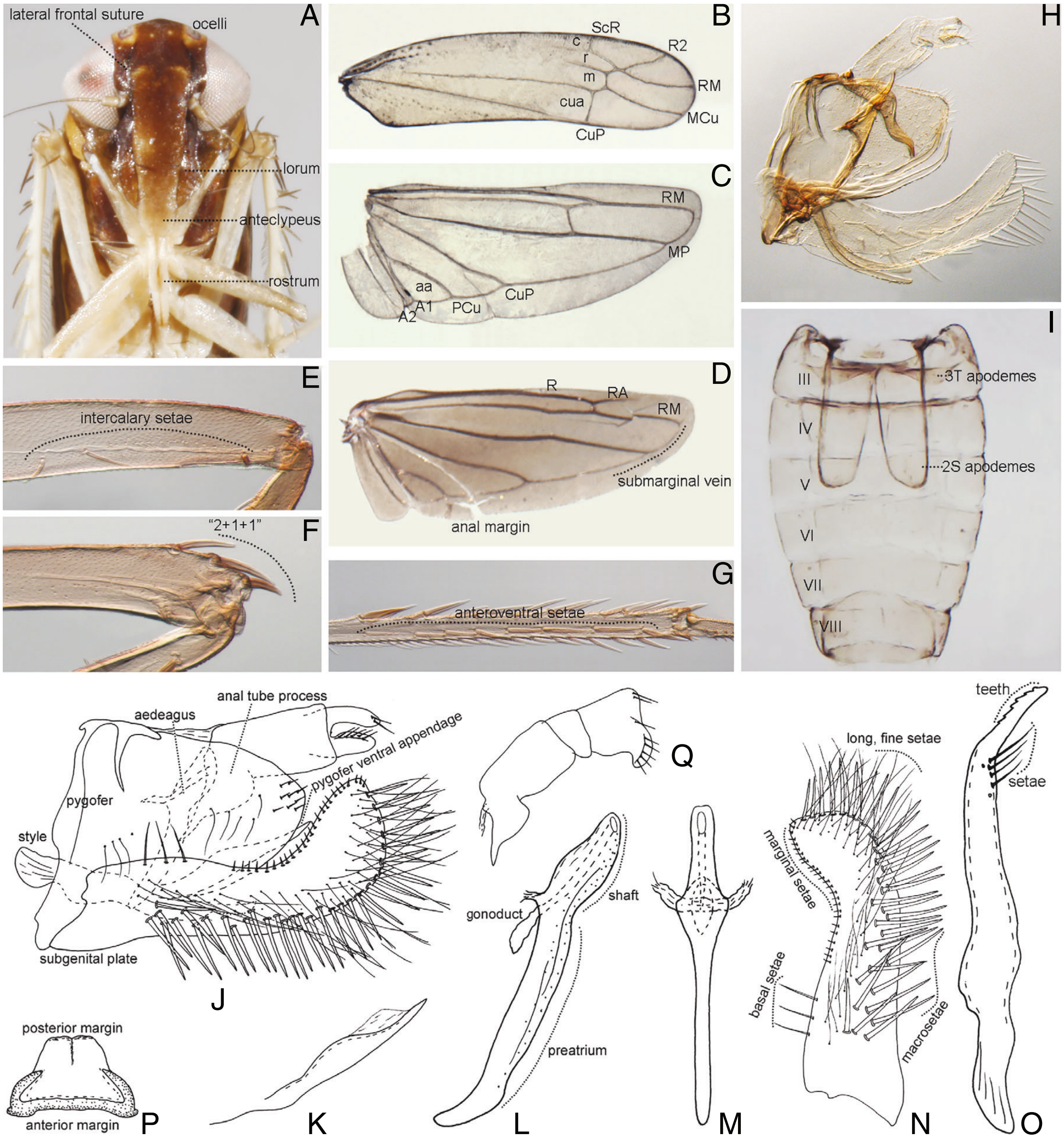

Fig. 2. Empoascini morphology. A, D. *Joruma* sp., face (A) and hindwing (D); B, C, J–Q. *Empoasca fabae* (Harris), forewing (B), hindwing (C), male genitalia, left view (J), pygofer ventral appendage (K), aedeagus, left view (L), aedeagus, dorsal view (M), subgenital plate (N), style (O), connective (P) and anal tube process (Q); E–H. *Concaviasca concava* (Southern), apex of front leg (E), apex of hind femur (F), apex of hind tibia (G) and male genitalia, left view (H); I. *Matsumurasca* (*Solanasca*) *solana* (DeLong), abdominal apodemes. [Colour figure can be viewed at wileyonlinelibrary.com].

to the *Heliona* group, 16 to the *Alebroides* group, four to the *Ficiana* group, four to the *Usharia* group and 42 to the problematic genus *Empoasca*. Some other species not currently assigned to groups were also included in the in-group. Representatives of the '*Empoasca signata* group' (*sensu* Dworakowska) were found to be identical to species of *Empoasca* (*Hebata*) for the included characters and were not included in the matrix. The included taxa represent endemic genera from all biogeographical realms. The out-groups included 11 representatives of the other four recognized tribes of Typhlocybinae, with at least two species of each tribe (see Appendix 2).

Ninety-nine morphological characters of male adults included 35 external structural characters of the body (15 head, 4 leg, 9 forewing and 7 hind wing) and 64 characters of the male genitalia and accessory structures (7 male pregenital abdomen, 10 pygofer, 19 subgenital plate, 9 style, 11 aedeagus, 5 connective and 3 anal tube; see Appendix 1 and File S1). Of these, 76 characters are binary and 23 are multistate. Missing data were coded as '?', and inapplicable data as '-'. All characters were treated as unordered and of equal weight. Eleven species for which specimens were not available were scored for morphology based on published descriptions and illustrations.

Phylogenetic analysis

The data matrix was analysed using TNT ver. 1.5 (Goloboff & Catalano, 2016) initially using the New Technology Search method (using default algorithms: ratchet, sectorial searches, drifting and fusing). For large datasets, the New Technology Search is much more effective than the traditional search (Goloboff *et al.*, 2008). The equal weighting (EW) analysis with 1000 random addition replicates (Init. addaseqs = 100, Random seed = 10) was used to produce the final results, and character changes were mapped using WinClada ver. 1.00.08 (Nixon, 2002). TNT was also used to conduct implied weighting (IW) analyses, which gives greater weight to characters showing less homoplasy after an initial tree search. Separate IW searches were conducted with k values of 5, 10, 20, 50 and 100. Relative support was measured by using TNT to search for suboptimal trees and calculating decay indices (Bremer support) as the difference in length between the original MP trees and the shortest trees incompatible with each resolved branch. A separate maximum likelihood (ML) ultrafast bootstrap analysis was also performed in IQTREE (Nguyen *et al.*, 2015; Hoang *et al.*, 2017) using the MK model for categorical data and empirical character state frequencies with the correction for ascertainment bias applied.

Ancestral biogeographic areas were reconstructed on the most parsimonious trees from analysis of equally weighted characters using the Bayesian Binary MCMC (BBM) and Statistical Dispersal Vicariance (S-DIVA) methods in RASP 4.2 (Yu *et al.*, 2010, 2015) under the default settings. Distribution categories were as follows: A = Nearctic; B = Neotropical; C = Oriental; D = Palearctic; E = Afrotropical; F = Australian. Taxa that occur in multiple realms were assigned multiple states according to known distributions.

Results

The EW analysis of morphological data (Appendix 1) yielded 31 MP trees of length 770, consistency index (CI) of 0.17, and retention index (RI) of 0.63. Maximum likelihood bootstrap analysis yielded a consensus tree (Fig. S1) that was similar in many respects to the MP result but with several topological differences limited to branches with relatively low support in one or both analyses, i.e., <60% bootstrap support or decay index = 1 or less. IW analyses did not substantially reduce the number of trees found and trees resulting from IW analysis were less parsimonious (based on equal character weights) than the original 31 MP trees. To simplify the presentation of results, only one of the MP trees is shown (Fig. 3) with MP decay indices and ML boostrap support indicated for branches that were in agreement between both analyses. Among the original MP trees, this tree shows the best overall agreement with the ML consensus, with the maximum number of resolved branches recovered in both MP and ML analyses. Nevertheless, several, mostly deep internal branches with no support values shown in Fig. 3 collapsed in the strict consensus of all MP trees (Fig. S2) and were also not recovered by ML boostrap analysis (Fig. S1). Although the ML bootstrap consensus tree (Fig. S1) is fully resolved, nearly all deep internal branches are very short with <50% support. Clearly, although many branches supporting taxa previously recognized based on morphological characters are consistently resolved by our analyses of morphological data, more characters will be needed to resolve relationships among these taxa with confidence.

All MP trees, including the tree presented in Fig. 3, are consistent with the previous genus-level classification with the exception of *Empoasca* (*sensu lato*), which is highly polyphyletic and, therefore, a reclassification of this genus is proposed (see below). Two genera segregates from *Empoasca* (*s.l.*), *Hebata* and *Matsumurasca*, are not consistently monophyletic in all analyses; however, the former is consistently recovered by MP analysis and the latter is monophyletic with a bootstrap score of 68 in the ML consensus. Both genera may be diagnosed by unique combinations of apomorphic traits (see below and Fig. 4). Most of the areas of disagreement between MP and ML results are in deep internal branches with short internodes, i.e., indicated by 2 or fewer homoplastic character state changes on Fig. 4. All clades recovered with strong ML support (95% ML bootstrap or higher) were consistently recovered by MP analyses.

Aside from the *Beamerana* group, which is placed as sister to the included representatives of Typhlocybini in the MP trees, Empoascini is consistently recovered as monophyletic, but with low branch support. ML analysis recovers Empoascini including the *Beamerana* group as monophyletic, but with the latter group derived from within the *Joruma* group clade and connected by a long branch. The sister group relationship of Empoascini is also not consistently resolved, with Dikraneurini recovered as sister group in the MP results and Typhlocybini in the ML consensus, both with low branch support. The sister relationship to Dikraneurini is supported by two apomorphies: crown shorter medially than next to eyes (char. 1: 0) and pygofer lobe with a few small rigid distal setae (char. 44: 1).

The monophyly of Empoascini, excluding the *Beamerana* group, is supported by the following apomorphies: 2S apodemes extended beyond posterior margin of sternite IV (char. 36: 3), subgenital plate with MI group of setae (char. 62: 1), style with a few preapical setae (char. 76: 1) and aedeagus with developed preatrium (char. 80: 1). The *Joruma* group and *Heliona* group, both formerly placed in separate tribes, are monophyletic but derived from within Empoascini. Neither the *Alebroides* group nor the *Usharia* group was recovered as monophyletic. The monophyletic *Ficiana* group is the sister to *Dapitana* Dworakowska and is supported by three apomorphies.

The Oriental genus *Rubiparvus* Xu, Dietrich & Qin, morphologically intermediate between Empoascini and the out-groups Typhlocybini and Dikraneurini, is sister to the remaining Empoascini in the MP results. *Empoasca*, as previously

Fig. 3. One of 31 equally parsimonious trees from maximum parsimony analysis of morphological data. Bremer support values are indicated above ML bootstrap scores are indicated below branches that also were recovered in the ML analysis. Unlabelled branches did not appear in all MP trees or were incongruent between MP and ML results. [Colour figure can be viewed at wileyonlinelibrary.com].

defined, is not monophyletic in either MP or ML results. Representatives of the *Empoasca* subgenera *Greceasca* Thapa, *Livasca* Dworakowska & Viraktamath, *Okubasca* Dworakowska from the Oriental Region, *Buhria* Dworakowska, *Marolda* Dworakowska, *Ociepa* Dworakowska from Afrotropical Region and *Hebata* DeLong from the New World are scattered across multiple independent branches of the tree and grouped with various other genera of the tribe. Most of the subgenera represented by more than one species are recovered as monophyletic but many did not group with the nominotypical subgenus. Several other groups of New World species previously included in *Empoasca* also represent lineages separate from members of the nominotypical subgenus.

Instability in the trees resulting from phylogenetic analysis make it difficult to draw firm conclusions about global biogeographic patterns based on our present results. Thus, results of biogeographic analysis from the BBM (Fig. 5) and S-DIVA (Fig. S3) methods based on the MP tree in Fig. 3 represent

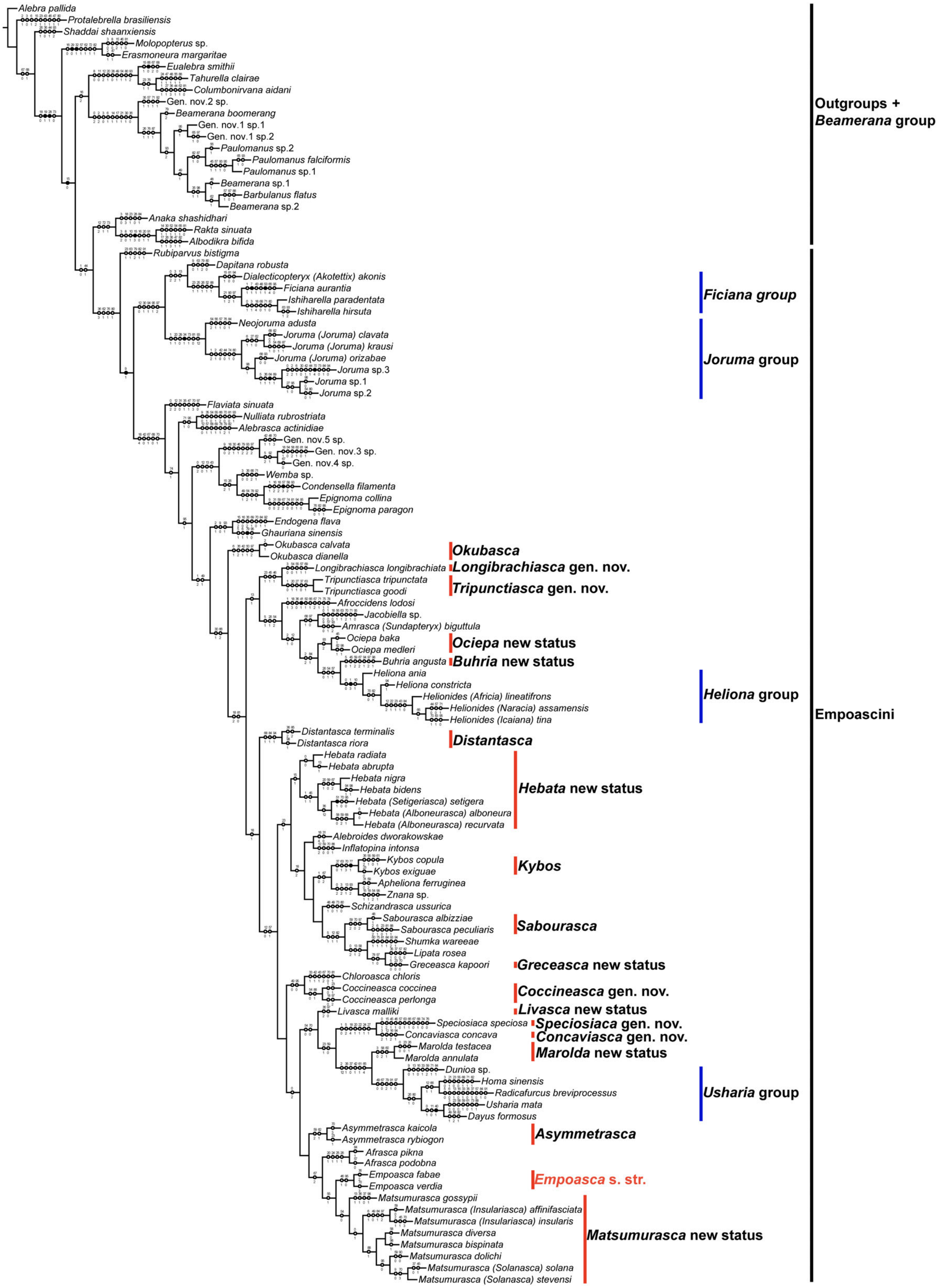

Fig. 4. Phylogenetic hypothesis for the tribe Empoascini from Fig. 3 showing character state changes. Numbers above the circles refer to characters and those below refer to character state. Filled and open circles represent synapomorphies and homoplasious character changes, respectively. [Colour figure can be viewed at wileyonlinelibrary.com].

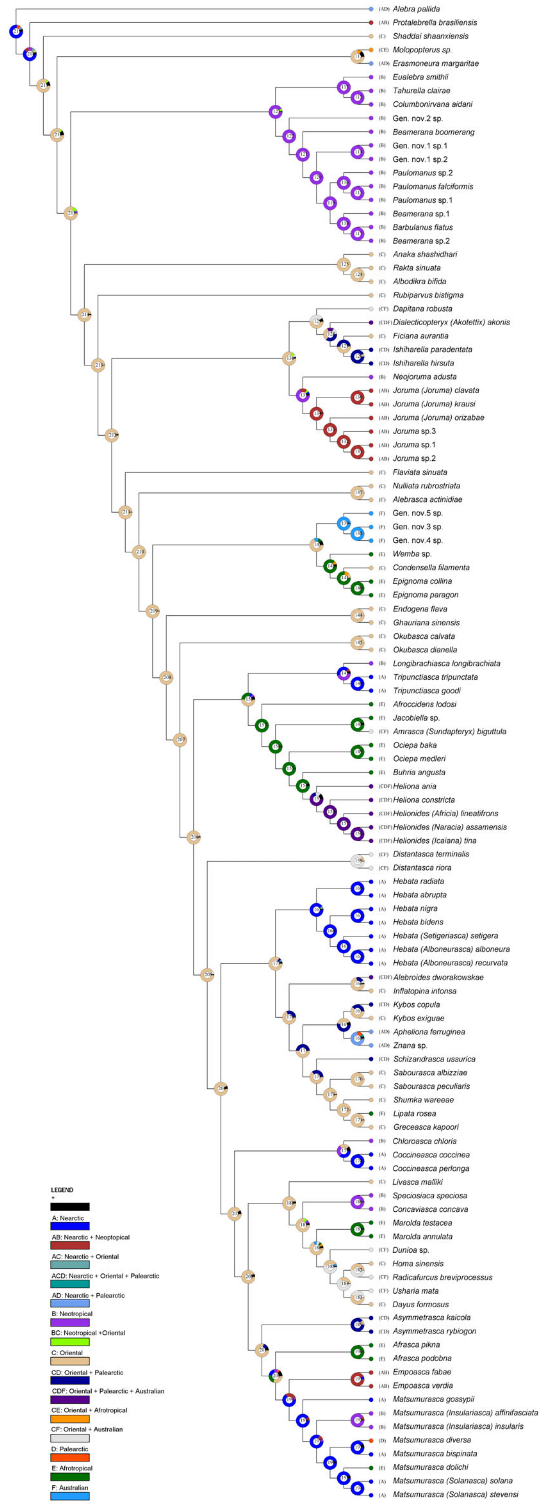

Fig. 5. Bayesian Binary MCMC reconstruction of biogeographic associations using the consensus of the two original MP trees. Distribution categories are as follows: A = Nearctic; B = Neotropical; C = Oriental; D = Palearctic; E = Afrotropical; F = Australian. Some taxa were assigned multiple states. [Colour figure can be viewed at wileyonlinelibrary.com].

only one of many possible scenarios, particularly with regard to relationships among lineages restricted to particular continents or biogeographic realms. Nevertheless, several lineages that were consistently recovered in MP and ML analyses are restricted to particular regions, suggesting that Empoascini show a high level of continental-scale biogeographic structure. Biogeographic reconstructions based on the two methods were similar although ancestral areas in S-DIVA tended to be less decisive. The most likely area of origin of Empoascini appears to be the Oriental region given that several early-diverging lineages occur largely or entirely in this region. The faunas of the Australian, Afrotropical and Neotropical/Nearctic regions all appear to have originated through multiple independent colonizations from other regions, primarily the Oriental region. The membracoid molecular time tree of Dietrich *et al.* (2017) estimated the origin of Empoascini at ca. 112 million years ago (mya) with crown-group diversification commencing at ca. 77 mya. This suggests that the major empoascine lineages occurring in Africa, Australia and the New World originated from rare long-distance dispersal and colonization events followed by diversification.

Discussion

Our investigation represents the first phylogenetic study of Empoascini that includes most known genera and subgenera of the tribe. Phylogenetic analysis of morphological characters (Figs 3, 4) supports the monophyly of Empoascini, excluding *Beamerana* and related Neotropical genera, and generally supports the monophyly of most previously recognized genera and subgenera, but indicates that *Empoasca*, as previously defined, is highly polyphyletic. The sister-group relationship of Empoascini to Dikraneurini is consistent with the hypothesis of Zhang (1990) but this relationship was not recovered in the ML analysis and received low branch support. Thus, the relationships between Empoascini and other Typhlocybinae need to be confirmed by analyses incorporating more data and more representatives of other typhlocybine tribes.

Morphological data provided strong support for the monophyly of several groups here recognized as genera or subgenera but relationships among these groups were poorly resolved overall and inconsistent between MP and ML analyses. Because of this instability in the phylogenetic results, our biogeographic reconstructions should be interpreted with caution. Future analyses including more characters, including molecular data, may provide a more robust reconstruction of relationships among major lineages of Empoascini. Nevertheless, our present results justify some revisions to the classification of the tribe and its included genera. The *Beamerana* group is excluded from Empoascini, and tentatively placed in Typhlocybini based on morphological criteria (see Notes below). Most of our other proposed changes relate to *Empoasca* (*sensu lato*), until now the largest genus of the tribe. The status and composition of this genus have long been controversial. Based on our phylogenetic results, we elevate several previously recognized subgenera of *Empoasca* to the genus level, and diagnoses and notes are given for each of them below. We also restrict the definition of *Empoasca* to comprise only the New World *Empoasca fabae* species group, sensu Ross (1959a, b) and establish several new genera and subgenera, mostly for groups of species previously included in *Empoasca*. These taxa are defined mostly based on characters of the male terminalia, particularly the genital capsule, many of which were neglected by previous authors. Although we were able to include only a few representatives of each genus and subgenus in our phylogenetic analysis, we were able to place, at least tentatively, most of the previously described species based on information available in the literature. A checklist indicating current placements of species previously included in *Empoasca* is provided in Appendix 3 and File S2.

Beamerana group

Diagnosis: This group may be recognized by the following unique combination of apomorphic characters: crown including eyes distinctly wider than maximum width of pronotum (char. 0: 2), crown distinctly longer than width between eyes (char. 2: 2), coronal suture not extended beyond mid-length of crown (char. 3: 0), eyes wider than distance between basomedial angles (char. 6: 1), lorum not visible (char. 14: 1), hind femoral macrosetal formula 2 + 1 + 0 (char. 17: 1), cell c wider than cell r in forewing (char. 21: 1), vein CuA and MP of hind wing are fused (char. 30: 1), and 2S apodemes inconspicuous (char. 36: 0).

Composition: This group includes the following genera: *Beamerana* Young, *Paulomanus* Young and *Barbulanus* Xu, Qin & Dietrich. Samples from eastern Ecuador collected by fogging rainforest canopies, include many new taxa of this group waiting to be described (Xu unpublished data). These phylogenetic results show that *Beamerana boomerang* Coelho *et al.*, 2014, should be excluded from *Beamerana* and placed in a separate new genus.

Notes. Young (1952) included *Paulomanus* and *Beamerana* in Typhlocybini, which he broadly defined also to include other genera more recently placed in Empoascini. The two genera were transferred into Empoascini by Catalano *et al.* (2014) based on the hind wing venation. Phylogenetic analysis of morphological data indicates that the *Beamerana* group is sister to Typhlocybini.

As a whole, this group can be distinguished from Empoascini as follows: ocelli absent; lorum not delimited; hind femur with macrosetal formula 2 + 1 + 0; male 2S apodeme weakly developed; pygofer lobe without microsetae; subgenital plate macrosetae reduced or absent. The group shares some features with Empoascini: forewing without appendix; hind wing submarginal vein extended between apices of veins RA + RM; style with a few preapical teeth, or without teeth; anal tube with pair of well-developed appendages. Wing venation has been used almost exclusively by previous authors to define tribes of Typhlocybinae. Our phylogenetic results suggest that although the hind wing venation of the *Beamerana* group is identical to that of Empoascini, the group is more closely related to Typhlocybini. This relationship is supported by one apomorphy: middle femur with 2 dorsoapical macrosetae (char. 16: 2). Additional analyses including more representatives of Typhlocybini are needed to further elucidate the relationships of this group. For now, we tentatively include the group in Typhlocybini.

Empoascini Distant, 1908

Diagnosis: This tribe is defined based on the following combination of characters: ocelli present; lorum conspicuous, delimited by suture; lateral frontal sutures present; forewing without appendix, without transverse vein basally; hind wing with veins RA + RM confluent (except in *Joruma* and *Neojoruma*), submarginal vein extended between apices of veins RM + MP and MP + CuA, anal vein separated from postcubital vein; hind femoral macrosetae formula 2 + 1 + 1; male 2S apodemes well developed; aedeagus with developed preatrium; subgenital plate with numerous macrosetae, marginal macrosetae (MA) present; style without preapical lobe, usually with a few tiny teeth and preapical setae; anal tube usually with pair of basal appendages.

Composition. This group includes all the species with the forewing lacking an appendix and the hind wing with the submarginal vein terminated at the apex of vein RA, except the *Beamerana* group from the Neotropics (Typhlocybini) and *Rakta* Dietrich from Thailand (Dikraneurini).

Notes: Aside from the *Beamerana* group, here excluded from the tribe, the remaining taxa of Empoascini were recovered as monophyletic, supported by four synapomorphies as mentioned above. Although these four characters are not unique to this tribe and do not occur in all species of Empoascini, they are usually present and represent supplemental diagnostic features. Our phylogenetic results were equivocal with regard to the sister-group relationship of the tribe. The phylogenomic analysis of Dietrich *et al.* (2017) placed Empoascini sister to Alebrini.

Joruma group

Diagnosis: This group may be recognized by the following unique combination of apomorphic characters: crown approximately as long medially as next to eye (char. 1: 1), vein MCu ending near apex of anal margin in forewing (char. 20: 1), hind wing veins MP and CuA not confluent distally (char. 28: 0), hind wing anal margin serrate (char. 34: 1), style apophysis little longer than apodeme (char. 73: 1), aedeagus without dorsal apodeme (char. 81: 0), connective with median lobe on anterior margin or deeply emarginated (char. 93: 1, 2).

Composition: The *Joruma* group includes two known genera: *Joruma* McAtee, 1924 and *Neojoruma* Young, 1952. *Joruma* is represented by two or three subgenera with 29 species restricted to the New World, and *Neojoruma* is monotypic, known only from a single species: *N. adusta* (McAtee, 1924) from Brazil.

Notes: The status of Jorumini has long been controversial. It was recognized as a tribe by McAtee (1926, 1934), Oman (1949), Metcalf (1968), Oman *et al.* (1990) and Gebicki & Szwedo (2006) but treated as a synonym of Typhlocybini or Empoascini by Young (1952), Mahmood (1967), Mahmood & Ahmed (1968), Dworakowska (1979), Ahmed (1983), Ruppel (1987) and Zhang (1990). Most recently, Dietrich (2013a) treated Jorumini as a synonym of Empoascini.

Within Empoascini, the *Joruma* group is sister to the *Ficiana* group + *Dapitana*. The following morphological characters are generally shared by this group and other Empoascini: ocelli well-developed (Fig. 2A), presence of one or two distally closed apical cells in the hind wing formed by veins RM + MP and the submarginal vein (Fig. 2D), subgenital plate with numerous macrosetae, style with a few preapical setae and teeth, and anal tube with a pair of well-developed processes. Some previous authors treated this group as a separate tribe, Jorumini, based on the unique hind wing venation. Our analysis indicates that the group is derived from within Empoascini, so we follow Dworakowska (1979), Ahmed (1983) and Dietrich (2013a) in treating Jorumini as a synonym of Empoascini.

The species in this group are small to medium-sized, often brightly or iridescently coloured with prominent, darkly coloured ocelli. The hind wing venation, with RM free distally, not connected to the submarginal vein and serrate anal margin, are unique. Because most of the diversity is concentrated in South America, we speculate that *Joruma* group originated in South America during its long period of Cretaceous to late Paleogene isolation.

Heliona group

Diagnosis: This group may be recognized by the following combination of characters: crown strongly produced; ocelli well developed; face quite long and narrow; hind wing submarginal vein terminated at apex of vein RM, vein MP and CuA are fused; 2S apodeme well developed, enlarged apically; pygofer lobe with ventral appendage; aedeagus with preatrium well developed, usually with large atrial apodeme, without dorsal apodeme; subgenital plate with numerous macrosetae; anal tube massive.

Composition: This group includes *Heliona* Melichar and *Helionides* Matsumura. *Heliona* includes eight species and *Helionides* includes four subgenera and 37 species. Both genera are distributed in the Old World (Dworakowska, 1981, 1994a, 1997).

Notes: The Old World genus *Heliona* was formerly treated as the type genus of the monobasic tribe Helionini Haupt, 1929, which is characterized by the strongly produced crown with the anterior margin forming an acute angle and the face quite narrow and elongated. This tribe was subsequently treated as a synonym of Empoascini by Dworakowska (1979), Ahmed (1983), Ruppel (1987), Dietrich (2005) and Gebicki & Szwedo (2006). Our phylogenetic results show that this group is derived from within Empoascini, sister to *Helionides*, supporting treatment of Helionini as a synonym of Empoascini.

Our phylogenetic results show that both genera of the group share three apomorphic characters: crown distinctly narrower than maximum width of pronotum (char. 0: 0), crown strongly produced, anterior margin forming acute angle (char. 1: 3) and face with maximum length > 1.5X width across eyes (char. 10: 1). The distinction between the two genera is unclear and a species-level revision is needed.

Alebroides group, *Ficiana* group *and Usharia* group

Although they did not perform a phylogenetic analysis, Xu *et al.* (2017b) suggested that the *Ficiana* and *Usharia* generic groups are monophyletic because they share unique diagnostic morphological characters. In contrast, they suggested that the *Alebroides* group is not monophyletic because it lacks such characters. Our analyses placed members of the *Alebroides* group on six independent branches, indicating that the hind wing character (CuA separate from MP) used to diagnose the group is homoplastic. State 1 of this character (char. 30: 1, fused) is derived at least five times on the phylogeny. The included *Usharia* group genera, which have the aedeagus and connective fused, grouped together with *Radicafurcus*, which has the aedeagus articulated to the connective, indicating that this character is also homoplastic. In contrast, the *Ficiana* group is well supported as a monophyletic group based on the following apomorphies: veins MP and CuA confluent for a short distance preapically in forewing (char. 23: 1), vein R2 arising from m cell in forewing (char. 25: 1), vein RM arising from m cell in forewing (char. 26: 1), male subgenital plates fused at least at base (char. 52: 1) and aedeagus with basal processes (char. 88: 1). This group is sister to *Dapitana* from the Oriental and Australian Regions. Further analyses including more genera may eventually provide support for recognizing some of the informal generic groups.

Rubiparvus Xu, Dietrich & Qin, 2016

Type species: *Rubiparvus bistigma* Xu, Dietrich & Qin, 2016.

The Oriental genus *Rubiparvus*, recovered as sister to the remaining Empoascini, shares five apomorphies with other empoascines: vein MP and CuA confluent for a short distance preapically in forewing (char. 23: 1); marginal microsetae numerous, multiseriate at apex of subgenital plate (char. 63: 1); style base very broad and distinctly bent mesad at point of articulation to subgenital plate (char. 79: 2); aedeagus with distal processes (char. 82: 1); connective fused to base of aedeagus (char. 91: 1). Presence of a single macroseta on the male subgenital plate, absence of apical teeth on the male style and presence of few setae on the style are not common in Empoascini but occur frequently in some of the out-group taxa. The unusual crescent-shaped ocelli of this genus are similar to those commonly found in Erythroneurini. This accounts for the placement of this genus as an early diverging lineage of Empoascini.

Former *Empoasca* subgenera elevated to genus status

Eight to fourteen subgenera were previously recognized within the large, taxonomically complex and cosmopolitan genus *Empoasca*. Over the past several decades, there has been disagreement in the literature over the status of some of these taxa. For example, *Kybos* was treated as a subgenus of *Empoasca* by Ross (1963) and Dworakowska (1982) and this status has been adopted by more recent North American authors (Hamilton & Langor, 1987) but most European authors (e.g., Mühlethaler *et al.*, 2009) now treat this taxon as a separate genus. Ghauri (1974) formally recognized *Solanasca* to include members of the New World *Empoasca solana* species group recognized by previous authors but Southern (1982) continued to include species of this group in *Empoasca*. Dlabola (1958) established *Asymmetrasca* to include members of the *Empoasca decedens* species group, which are, so far, recorded only from the Old World. Dworakowska (1968) initially accepted this genus as valid but later (Dworakowska, 1970) considered it a synonym of *Empoasca*. More recently, Liu *et al.* (2014a) reinstated *Asymmetrasca* as a valid genus.

Our phylogenetic results support separating all of these former subgenera from *Empoasca* as separate genera. *Endeia* McAtee, 1934, described as a subgenus of *Empoasca* based on a female specimen from the Philippines, was not available for study and the holotype appears to be lost; but the original figures of the wings indicate that it does not belong in *Empoasca*.

Asymmetrasca Dlabola, 1958

Type species. *Empoasca decedens* Paoli, 1932.

Diagnosis: This genus superficially resembles *Empoasca* in external morphology but differs as follows: forewing veins R2 and RM free, connected by RP vein; pygofer with single median sclerotized dorsal lobe at base; ventral appendage simple, acuminate; subgenital plate without basolateral lamella; basal group of setae poorly differentiated, situated near midlength of plate; style abruptly narrowed preapically, apex falcate, directed posteroventrad; aedeagus with preatrium short, shaft well-sclerotized, tubular, with long unpaired distal asymmetrical process arising distad of gonopore; basal process of anal tube simple, acuminate, usually with small apical denticuli.

Notes: This genus consists of the *A. decedens* species group of authors, a complex of closely related and in some cases doubtfully distinct species distributed throughout the Palearctic region, distinguished mainly by details of the structure of the aedeagus. *Asymmetrasca* was originally designated as a separate genus but was subsequently treated as a synonym of *Empoasca* by Dworakowska (1970). It was recently reinstated by Liu *et al.* (2014a). This genus includes 22 species distributed in the Oriental and Palaearctic Regions (see Appendix 3 and File S2).

Buhria Dworakowska, 1976, new status

Type species: *Empoasca* (*Buhria*) *angusta* Dworakowska, 1976.

Diagnosis: Morphological characters that distinguish this taxon from *Empoasca* and other empoascines are as follows: forewing cua and m cells each with distinct black spot distally; pygofer lobe strongly sclerotized apically, ventral appendage areolate; connective with well-developed median anterior lobe; style apex bent laterad at 90° angle, foot-like.

Notes. The African genus *Buhria* is sister to the *Heliona* group distributed in the Old World based on three features: vein RM arises from m cell in forewing (char. 26: 0), the length of subgenital plate distinctly longer than 2X maximum width (char. 54: 1), and presence of basal group in subgenital plate (char. 57: 1). Dworakowska (1976) described this taxon as a subgenus of *Empoasca* based on a single species from Cameroon. Characters given in the original description, particularly the presence of a well-developed median anterior lobe on the connective and the foot-like style apex, exclude *Buhria* from the present definition of *Empoasca* and the former is here elevated to separate genus. This genus is known only from the type species.

Distantasca Dworakowska, 1972

Type species: *Empoasca terminalis* Distant, 1918.

Diagnosis. This genus externally resembles *Empoasca* but may be distinguished by the following combination of features: body small and fragile, usually with green or yellowish colour; coronal suture well delimited; forewing rounded apically, second apical cell usually rectangular, R2 and RM arising from r cell and MCu from m cell; hind wing with vein MP and CuA fused; pygofer lobe short, with ventral appendage; macrosetae not reaching tip of subgenital plate, fine setae greatly elongated, divided into distinct basal and distal groups; connective strongly constricted posteriorly; anal tube process well-developed, often ornamented with tiny teeth.

Notes: Dworakowska (1972) described this taxon as a distinct genus, but later, without explanation (Dworakowska & Viraktamath, 1975), reduced its status to a subgenus of *Empoasca*, and more recent authors have followed this latter assignment. More recently, Liu *et al.* (2014b) reinstated it as a valid genus and provided a revised generic diagnosis. This uncertainty regarding the status of *Distantasca* may have been due to the fact that some more recently described species appear to bridge the gap between the type species, *D. terminalis*, and more 'normal' looking *Empoasca*. For example, Dworakowska's (1972) description of *Distantasca* mentions the presence of teeth on the basal processes of anal tube and paired basal processes on the aedeagus as diagnostic features of the genus, but these are lacking in *D. atika* Dworakowska (1982), described from Japan, in which the genitalia more closely resemble *Empoasca* species. Nevertheless, the presence of two distinct groups of elongate slender fine setae on the subgenital plate unites several Old World species and supports the recognition of *Distantasca* as a separate genus.

Our phylogenetic analysis supports this genus as monophyletic and separate from *Empoasca* (*s.s.*), based on three apomorphic characters: macrosetae not reaching tip of subgenital plate (char. 68: 1), presence of process on shaft of aedeagus (char. 84: 1), and connective with lateral margin distinctly constricted (char. 94: 1). Although the previously described species of *Distantasca* are recorded from the Oriental and Eastern Palearctic regions, undescribed species of this genus have been studied from central Africa and Fiji. This genus includes 21 species distributed in the Oriental and Australian Regions (see Appendix 3 and File S2).

Empoasca Walsh, 1862

Type species: *Empoasca viridescens* Walsh, 1862.

Diagnosis. This genus is defined based on the following combination of characters: colour pale green (yellow in preserved specimens) with cream coloured markings (Fig. 1A); head in dorsal view with crown slightly longer medially than next to eye, anterior margin bluntly angulate; forewing veins RM and MCu usually confluent for short distance preapically (Fig. 2B); male sternite VIII with posterior margin usually produced or truncate; pygofer with conspicuous basolateral setal group; distal group scattered, not greatly enlarged; inner face of lobe without setae; ventral appendage broadened near midlength, extended to or slightly beyond apex of lobe, excavated preapically with poorly sclerotized medial extension, apex acuminate (Fig. 2J); male subgenital plate with basolateral lamella present but not greatly enlarged; basal group comprising 2–4 well-differentiated setae; marginal microsetae more or less continuous in distal two-thirds; fine setae numerous, longer than macrosetae (Fig. 2N); aedeagus simple, preatrium long, shaft triangular in cross-section, partially membranous posteriorly, processes and teeth absent (Fig. 2L, M); style with apex curved laterad, bearing several evenly spaced teeth basad of acute tip (Fig. 2O); basal process of anal tube rounded posteriorly with acuminate ventral extension, not extended ventrad of mid-height of genital capsule (Fig. 2Q).

Notes: The two representatives of the *Empoasca fabae* species group included in the phylogenetic analysis grouped together on a clade sister to representatives of four other previously recognized *Empoasca* species groups. Thus, *Empoasca*, as here redefined, corresponds to the *Empoasca fabae* species group (Ross, 1959a, b), which is restricted to the New World and comprises 39 species distributed from Chile and Argentina to Canada (see Appendix 3 and File S2). Most species in this group are very similar in external appearance and in the structure of their male terminalia but may be distinguished by the size and shape of the tergal and sternal apodemes at the base of the male abdomen.

Greceasca Thapa, 1985, new status

Type species: *Empoasca kapoori* Thapa, 1985.

Diagnosis: This genus is defined based on the following combination of characters: head including eyes wider than pronotum; coronal suture extended past vertex midlength; face longer than broad; veins R2 and RM dissociated at bases in forewing; pygofer with ventral appendage large, dagger-like, without microsetae at lower margin; subgenital plate large and narrowing apically; aedeagus with long preatrium, shaft tubular with pair of short terminal processes; style with long rows of sensory setae; anal tube process short.

Notes: *Greceasca* is sister to the African genus *Lipata* in the MP tree, sharing with the latter two apomorphic characters: style preapical setae extended from midlength to tip (char. 78: 1) and male anal tube process weakly developed (char. 97: 0). Only a few other species of Empoascini have the style preapical setae extended from midlength to tip, e.g. *Empoasca speciosa* Young and *Empoasca concava* Southern, both placed in new genera below. *Greceasca* is known only from the type species from Nepal.

Hebata DeLong, 1931, new status

Type species: *Empoasca nigra* Gillette & Baker, 1895.

Diagnosis: This genus differs from other members of the *Empoasca* group in the structure and chaetotaxy of the male subgenital plate, which lacks a basolateral lamella and has the basal group of setae situated on the basal half of the lateral margin. Many species (Fig. 1B) resemble *Empoasca* in external morphology but a large number of North American species, particularly in the southwestern USA and Mexico (here included in the nominotypical subgenus), have distinctive colour patterns including numerous brown spots or larger, symmetrical areas of red, orange and/or fuscous pigment.

Notes: Phylogenetic analysis placed the included species of this genus in a clade sister to a clade comprising several genera of the *Alebroides* group as well as *Kybos* and three other generic segregates of the *Empoasca* group. The subgenera *Hebata* (*s.s.*), *Setigeriasca* and *Alboneurasca* form a branch and share two apomorphies: crown as long medially as next to eye (char. 1: 1), pygofer lobe with a few long, fine setae (char. 45: 1). This genus was established by DeLong (1931) as a subgenus of *Empoasca*, comprising a group of Nearctic species, but DeLong abandoned use of the name *Hebata* and no longer attempted to place New World *Empoasca* species to subgenus in his subsequent papers. Our results support recognizing *Hebata* as a separate genus based on three apomorphic features: forewing vein MCu distinctly curved, ending near apex of anal margin (char. 20: 1), basal group of setae situated on basal half of subgenital plate (char. 59: 0), macrosetae numerous (char. 67: 2). This genus, as here defined, is broader than that proposed for subgenus *Hebata* by DeLong (1931) and comprises three new subgenera in addition to the nominotypical subgenus.

Hebata (*Hebata*) DeLong, 1931

Diagnosis: The nominotypical subgenus is defined based on the following combination of characters: coloration variable, ground colour usually off white with markings consisting of irregular brownish flecks and/or larger symmetrical areas of orange, red, black or brown; forewing inner apical cell shorter than in *Empoasca*, R2 and RM usually confluent for short distance; sternite VIII truncate or emarginate; pygofer without basolateral setal group; ventral appendage simple, attenuate, usually bowed mediad; subgenital plate base narrow, without lateral lamella; basal group of setae absent or poorly differentiated from marginal microsetae, situated near midlength of plate; apex not or only weakly compressed, rounded; aedeagus with preatrium long, shaft tubular, with or without paired basal processes; basal process of anal tube simple, sickle-shaped.

Notes: The subgenus, as here defined, corresponds to *Empoasca* (*Hebata*) of DeLong (1931) and comprises 141 species (see Appendix 3 and File S2), many recorded from *Artemisia* in the southwestern USA and Mexico, as well as a majority of the species recorded from Mexico.

Hebata (*Alboneurasca*) Xu, Dietrich & Qin **subgen. nov.**

Type species: *Empoasca alboneura* Gillette, 1898.

Diagnosis: Body robust; 2S apodemes with lateral margins convergent, medial margins parallel; male pygofer with ventral appendage; subgenital plate without basolateral lamella, basal depressed section elongate, basal group of setae well-differentiated and situated distad of plate midlength; macrosetae not extended to plate apex; connective longer than wide; basal process of anal tube slender, curved posterad, with numerous small teeth distally in some species.

Notes: Our results support *Hebata* (*Alboneurasca*) as a separate subgenus based on three apomorphic characters: basal group of setae poorly differentiated, continuous with marginal microsetae, situated distad of plate midlength (char. 58: 0; char. 59: 2) and macrosetae not reaching tip of subgenital plate (char. 68: 1). This new genus includes 28 species (see Appendix 3 and File S2) and has a close relationship with *Hebata* (*Setigeriasca*).

Etymology. The new subgenus name is derived from its type species name, *Empoasca alboneura* Gillette, 1898, combined with the suffix of the genus *Empoasca*. The gender is feminine.

Hebata (*Setigeriasca*) Xu, Dietrich & Qin **subgen. nov.**

Type species: *Empoasca setigera* Oman, 1936.

Diagnosis: Body small; 2S apodemes weakly developed; pygofer appendage broadened distally with several stout, spur-like macrosetae; subgenital plate without basolateral lamella, basal group of setae well-differentiated and near base of plate; aedeagus simple, without process; basal process of anal tube usually bifurcate.

Notes: *Hebata* (*Setigeriasca*) forms a sister group with *H.* (*Alboneurasca*) due to having the 2S apodemes extended to segment III or IV (char. 36: 1, 2). Its status as a separate subgenus is also supported by three synapomorphies: pygofer ventral appendage with stout spurs (char. 51: 1), fine setae inconspicuous in male subgenital plate (char. 70: 0), and connective posterior margin straight or weakly concave (char. 95: 0). This subgenus includes four species from the Neotropical region (Peru, Puerto Rico and Argentina) (see Appendix 3 and File S2).

Etymology: The new subgenus name is derived from its type species name, *Empoasca setigera* Gillette, 1898, combined with the suffix of the genus *Empoasca*. The gender is feminine.

Hebata (*Signatasca*)*,* Xu, Dietrich & Qin **subgenus. nov.**

Type species: *Eupteryx solani* Curtis, 1846.

Diagnosis: Pygofer with ventral appendage often expanded distally, sometimes serrate or branched; subgenital plate without basolateral lamella but with distinct internal ridge; basal group of setae well differentiated and large, usually situated well basad of plate midlength, fine setae conspicuous and longer than macrosetae, plate apex usually strongly compressed and expanded.

Notes: This subgenus comprises the informal *E. signata* species group and *E. schiemenzi* species group recognized by Dworakowska (1974 and subsequent papers) for numerous Old World species formerly included in *Empoasca*. Dworakowska (1974) apparently based her concept of this group on Dlabola's (1965) incorrect interpretation of *E. signata* Haupt, which was a misidentification of *E. distinguenda* Paoli. Most of the species are restricted to the Old World but several New World species also appear to belong here. Unlike the nominotypical subgenus of *Hebata*, species in this subgenus are generally pale green in colour with symmetrical white markings on the head, as in *Empoasca*. Representatives of this subgenus were not included in the phylogenetic analysis because they appear to be identical to *Hebata* (*Hebata*) for the included characters. Its status and relationships remain to be tested by additional data.

Etymology: The new subgenus name is derived from the species name, *Empoasca signata* (Haupt, 1927), combined with the suffix of the genus *Empoasca*. The gender is feminine.

Kybos Fieber, 1866

Type species: *Cicada smaragdula* Fallén, 1806.

Diagnosis: This genus is defined based on the following combination of characters: body robust, green or yellow; head short and broad; forewing with second apical cell stalked; hind wing with veins MP + CuA fused; 2S and 3T apodemes present; subgenital plate twisted apically; style with thickened preapical section bearing dense tuft of elongate setae, apical teeth well-developed; anal tube short, slender.

Notes: This taxon has variously been treated by previous authors either as a subgenus of *Empoasca* (Ross, 1963; Dworakowska, 1976) or as a separate genus (Dworakowska, 1973; Mühlethaler *et al.*, 2009). Our phylogenetic analysis supports it as a separate genus based on the following four characters: 3T apodemes present (char. 37: 0); subgenital plate with numerous multiseriate marginal microsetae (char. 63: 1); fine setae numerous throughout length of plate, long (char. 70: 3); style with numerous long, hair-like setae preapically (char. 77: 1).

Although the vast majority of *Kybos* species are restricted to the Holarctic, Dworakowska (1976) mentioned some *Empoasca* species groups from other regions that also have a distinctively thickened style with numerous elongate preapical setae. Although as mentioned by Dworakowska (1976) these groups are more similar to *Empoasca* in the structure of the head and other aspects of the male genitalia, their unique (synapomorphic) style structure unites them with *Kybos*. Therefore, we consider the *E. clodia*, *E. remanei*, *E. saopa* and *E. barbistyla* groups, sensu Dworakowska, to belong to *Kybos* and these new combinations are proposed. Here, a checklist with 142 species is provided for this genus (see Appendix 3 and File S2).

Livasca Dworakowska & Viraktamath, 1978, new status

Type species: *Empoasca* (*Livasca*) *malliki* Dworakowska & Viraktamath, 1978.

Diagnosis: Morphological features that distinguish this taxon from *Empoasca* and other empoascines, in the present sense, include the broad, leaf-like subgenital plate and the sclerotized dorsal connective articulated between the atrial rim of the aedeagus and the base of the anal tube. Both of these features are absent in other genera of the *Empoasca* group.

Notes: This genus is known only from the Oriental region, specifically northern India and Thailand. Two autapomorphies, state 2 of character 36 (2S apodemes extended to segment IV) and state 0 of character 97 (anal tube weakly developed), are not unique to *Livasca* but support its status as a separate genus within Empoascini. This genus is known only from the type species.

Marolda Dworakowska, 1977, new status

Type species: *Empoasca* (*Marolda*) *testacea* Dworakowska, 1977a.

= *Sikkimasca* Dworakowska, 1994a, new synonym.

Type species: *Sikimasca annulata* Dworakowska, 1984.

Diagnosis: The following combination of features distinguish this genus from *Empoasca* and other empoascines: coronal suture short, not extended to midlength of crown; 3T apodemes large and strongly divergent; pygofer lobe with distinct dorsoapical concavity; subgenital plate with setae in basal group greatly enlarged and blunt-tipped; style with apex terminating in a retrorse spine.

Notes: *Marolda annulata*, formerly placed in *Sikkimasca*, is sister to the African species *Marolda testacea* based on the coronal suture not extended beyond mid-length of crown (char. 3: 0), basal setae almost the same size as macrosetae on the subgenital plate (char. 58: 2) and basal group with more than eight setae (char. 60: 1), supporting synonymy of *Sikkimasca* with *Marolda*. *Marolda* is closely related to the *Usharia* group + *Radicafurcus*, sharing six apomorphic characters: crown length equal to or distinctly longer than width between eyes (char. 2: 1, 2), absence of 2S apodemes (char. 35: 1), presence of 3 T apodemes (char. 37: 0), pygofer lobe firmly fused to base, dorsal cleft absent (char. 42: 1), apices of setae in basal group blunt in subgenital plate (char. 61: 1), macrosetae uniseriate basally, scattered apically in plate (char. 66: 4). This genus includes two species from the Oriental (Southern China, India and Sri Lanka) and African (Nigeria and Congo) regions (see Appendix 3 and File S2).

Matsumurasca Anufriev, 1973, new status

Type species: *Empoasca diversa* Vilbaste, 1968.

Diagnosis: The following combination of features distinguish this genus from *Empoasca* and other Empoascini: forewing veins R2 and RM usually confluent for short distance preapically; male sternite VIII usually truncate or produced; pygofer without basolateral setal group; distal group scattered, not greatly enlarged; ventral pygofer appendage, if present, extended to or slightly beyond apex of lobe, acuminate, often flattened and bladelike preapically, often with minute serrations and/or pubescence, without excavated membranous area preapically; male subgenital plate with well-developed basolateral lamella; basal group of setae well-differentiated, usually with 2–4 setae; marginal microsetae more or less continuous in distal two-thirds; fine setae numerous, as long as or longer than macrosetae; aedeagus well-sclerotized, preatrium usually as long as or longer than shaft, tubular or compressed in cross-section, without extensive membranous area on posterior surface, often with paired basal processes; style with apex curved laterad, bearing several teeth preapically, apex acute or blunt; basal process of anal tube well-developed, simple or branched, variable in length and orientation.

Notes: Our phylogenetic analysis grouped representatives of *Matsumurasca* in a clade with several other groups of former *Empoasca* species, including the New World *E. insularis* and *E. solana* species groups, and *Empoasca gossypii*, based on the presence of a lamelliform basolateral angle on the male subgenital plate. Anufriev (1973) originally characterized the subgenus based on this feature, in addition to the stalked second apical cell of the forewing, and the presence of paired processes at the base of the aedeagus. This definition comprises many New World species previously placed in *Empoasca*, including a majority of species described from South America, as well as numerous species from tropical Africa (see Appendix 3 and File S2). In addition to the nominotypical subgenus, we recognize two subgenera for the *E. insularis* species group and *E. solana* species group within *Matsumurasca*. Overall, *Matsumurasca* as presently defined is similar to *Empoasca* (*sensu stricto*) in the structure and chaetotaxy of the subgenital plate but differs in lacking a basolateral setal group on the male pygofer and a subapical excavation on the pygofer appendage. It also differs from *Empoasca* in having aedeagus well sclerotized posteriorly, often with basal processes (absent in *Empoasca*) and the larger basolateral lamella of the subgenital plate (weakly developed in *Empoasca*).

Matsumurasca (*Matsumurasca*) Anufriev, 1973

Diagnosis: Members of the nominotypical subgenus may be recognized by the absence of the synapomorphic traits diagnostic for the other two recognized subgenera (described below): pygofer with ventral appendage present and elongate; aedeagal shaft not strongly compressed, preatrium well developed.

Notes: In our phylogenetic results, the nominotypical subgenus, as presently defined, was paraphyletic with respect to the two subgenera included below. More detailed future phylogenetic studies may justify recognition of additional subgenera for the three separate clades here comprising *Matsumurasca* (*Matsumurasca*).

Matsumurasca (*Insulariasca*) Xu, Dietrich & Qin **subgen. nov.**

Type species: *Empoasca affinifasciata* Southern, 1982.

Diagnosis: Eyes as wide as distance between basomedial angles (char. 6: 1), pygofer without ventral appendage (char. 49: 0), aedeagus with paired basal appendages (char. 84: 1), anal tube process well-developed, acute apically (char. 97: 2).

Notes: Southern (1982) noted that this group is similar to the *E. coccinea* species group in lacking a ventral pygofer appendage, but retained both in *Empoasca*. However, our phylogenetic results support erecting a separate genus for the *E. coccinea* species group (see below). Here, we place the *E. insularis* species group in *Matsumurasca* due to the similar subgenital plate structure. This subgenus includes eight species restricted to South America (see Appendix 3 and File S2).

Etymology: The new subgenus name is derived from the species name, *Empoasca insularis* Oman, 1936, combined with the suffix from the genus *Empoasca*. The gender is feminine.

Matsumurasca (*Solanasca*) Ghauri, 1974, new status

Type species: *Empoasca solana* DeLong, 1931.

Diagnosis: Aedeagal shaft strongly compressed, broad in lateral view, with basal process or processes, shaft longer than preatrium.

Notes: *Matsumurasca* (*Solanasca*) was recovered in a monophyletic group with *M. dolichi* and *M*. *deversa* + *M. bispinata* based on presence of basal processes on the aedeagus (char. 88: 1). This group was originally recognized by Young (1953) as the *E. solana* species group of *Empoasca* and later was described as a separate genus by Ghauri (1974). Because our phylogenetic results show that this group is derived from within *Matsumurasca*, we treat Ghauri's taxon as a subgenus. The subgenus includes 30 species that are restricted to the New World (see Appendix 3 and File S2).

Ociepa Dworakowska, 1977, new status

Type species: *Empoasca* (*Oceipa*) *medleri* Dworakowska, 1977.

Diagnosis: Morphological features that distinguish this taxon from *Empoasca* are as follows: head relatively short and broad; forewing with dark maculae near apices of M and brachial cells; 2S apodemes greatly enlarged and extended >3/4 distance to genital capsule, pygofer with distinct vertical ledge near base of lobe, lobe apex acute; subgenital plate relatively long, slender and depressed, macrosetae uniseriate at base and biseriate near midlength; marginal microsetae poorly differentiated; aedeagus quite short, with manubrium and well-sclerotized lateral processes; connective broad, bilobate.

Notes: *Ociepa* is endemic to Africa and derives from the clade consisting of African genus *Buhria*, and the more widely distributed Old World *Heliona* group. This clade is well supported by two apomorphic characters: crown longer than width between eyes (char. 2: 2); aedeagus shaft with process (char. 84: 1). This genus includes two species recorded from the Democratic Republic of Congo and Nigeria (see Appendix 3 and File S2).

Okubasca Dworakowska, 1982

Type species: *Empoasca okubella* Matsumura, 1931.

Diagnosis: The following combination of features places *Okubasca* well outside of *Empoasca* (*s.s.*) and other members of the *Empoasca* group: body somewhat depressed; 2S apodemes extended dorsad at nearly 90° from horizontal; pygofer apex acutely angulate; anal tube with dorsal sclerotized arch extended nearly to apex of segment; subgenital plate with basal depressed section >2X longer than distal, upturned section, marginal microsetae short, stout from near base to apex, group of fine setae strongly reduced, represented by a few sparse setae, apex tapered, and not strongly compressed; style with several long setae arranged in dense group preapically; connective much longer than wide; aedeagus with dorsal apodeme well-developed with pair of lateral arms; preatrium with well-developed unpaired spine near midlength; apex of shaft usually with paired processes.

Notes: Two representative species *O. calvata* and *O. dianella*, grouped together, sharing five apomorphic characters: eyes as wide as distance between basomedial angles (char. 6: 1), 2S apodemes extended to segment IV (char. 36: 2), pygofer lobe firmly fused to base (char. 42: 1), pygofer ventral appendage quite short, vestigial (char. 50: 1) and anal tube appendage well-developed (char. 97: 2). Dworakowska (1982) proposed this taxon as a subgenus of *Empoasca*, noting that the type species is externally similar to *Kybos* but differs in its male genitalia. Both the characters illustrated and described by Dworakowska (1982) and our results seem sufficient to justify treatment of *Okubasca* as a distinct genus. More recently, Yu & Yang (2019) treated it as a separate genus and recorded two new species from China. Thus, this genus now includes five known species from China and Japan (see Appendix 3 and File S2).

Sabourasca Ramakrishan & Menon, 1972

Type species: *Sabourasca peculiaris* Ramakrishana & Menon, 1972.

Diagnosis: The following combination of features places *Sabourasca* well outside the normal range of variation of *Empoasca* and justifies retaining the former as a separate genus: body somewhat depressed; male 2S apodemes extended dorsad at nearly 90° from horizontal; pygofer apex acutely angulate; anal tube with dorsal sclerotized arch extended nearly to apex of segment; subgenital plate with basal depressed section >2X longer than distal, upturned section, group of fine setae strongly reduced, represented by a few sparse setae, apex tapered and not strongly compressed; style with several long setae arranged in dense group preapically; connective much longer than wide; aedeagus with dorsal apodeme well-developed with pair of lateral arms; preatrium with well-developed unpaired spine near midlength; apex of shaft usually with paired processes.

Notes: Ramakrishnan & Menon (1972) described this genus based on the type species from India. Dworakowska (1977b) transferred the species to *Empoasca*, rendering *Sabourasca* a junior synonym of *Empoasca*, but later (Dworakowska, 1994a) reinstated *Sabourasca* as a subgenus of *Empoasca*. Our phylogenetic results support its status as a separate genus based on the following diagnostic characters: basal group of setae distinctly distad of mid-length and fine group absent or inconspicuous on subgenital plate (char. 59: 2, char. 70: 0), and anal tube with elongate process (char. 97: 2). This genus includes nine species from the Oriental Region (India, Thailand, Bangladesh and Pakistan) (see Appendix 3 and File S2).

Five new genera from New World

The Western Hemisphere includes more than 200 species previously placed in *Empoasca*. Most of these species have been inadequately described and illustrated previously. In addition to *Empoasca* (*sensu stricto*), which now includes only New World species, and *Matsumurasca*, *Kybos* and *Hebata*, which now include species from both Eastern and Western Hemispheres, our phylogenetic results support recognition five new genera to include New World species formerly placed in *Empoasca*: *Speciosiaca* Xu, Dietrich & Qin gen. nov., *Concaviasca* Xu, Dietrich & Qin gen. nov., *Coccineasca* Xu, Dietrich & Qin gen. nov., *Longibrachiasca* Xu, Dietrich & Qin gen. nov., and *Tripunctiasca* Xu, Dietrich & Qin gen. nov.

Coccineasca Xu, Dietrich & Qin **gen. nov.**

Type species: *Empoa coccinea* Fitch, 1851.

Diagnosis: Body medium sized; some species with orange or reddish coloration; forewing with R2 and RM confluent basally, arising from r cell; hind wing with fused veins MP + CuA unbranched; 2S apodemes well-developed, reaching segment V; pygofer without basolateral setae group, ventral appendage absent; subgenital plate without basolateral lamella; basal group of setae well-differentiated, basad of plate midlength; aedeagus with pair of long processes arising from base of preatrium distant from shaft, preatrium long, shaft simple; connective with caudal margin straight or weakly concave; anal tube process simple.

Notes: *Coccineasca* forms a sister group to the Palaearctic *Chloroasca* due to the absence of a pygofer ventral appendage (char. 49: 0) and the connective caudal margin straight or weakly concave (char. 95: 0). Its genus status is supported by the following characters: subgenital plate with length little if any more than 2X maximum width in lateral view (char. 54: 0) and aedeagus with pair of basal processes (char. 88: 1). Species of this genus are restricted to North America and appear to specialize on *Pinus* spp. (see Appendix 3 and File S2).

Etymology: The new genus name is derived from the type species name, *Empoa coccinea* Fitch, 1851, combined with the suffix of the genus *Empoasca*. The gender is feminine.

Concaviasca Xu, Dietrich & Qin **gen. nov.**

Types species: *Empoasca concava* Southern, 2008.

Diagnosis: Body robust; head including eyes broader than pronotum; coronal suture long, almost extending to face; ocelli separated from eyes by more than one ocellar diameter; anteclypeus strongly convex; forewing R2, RM, MCu confluent basally, arising from r cell; hind wing with fused veins MP + CuA; male pygofer elongate, caudally with a few microsetae, ventral appendage present; subgenital plate with basolateral lamella undeveloped; basal group of setae distinct primarily by location; macrosetae numerous, scattered basally, uniseriate apically; group of fine setae undeveloped; style with setae short and stout, distributed along ventral medial face from near articulation with connective to basal-most teeth; aedeagus with preatrium developed, shaft tubular, without process; anal tube process well-developed.

Notes: Our phylogenetic results strongly support recognizing *Concaviasca* (Fig. 2H) as a genus separate from *Empoasca* and other empoascines based on the following characters: coronal suture extended onto face (char. 3: 2), male anteclypeus strongly convex but not distinctly broadened (char. 12: 1), middle femur with two dorsoapical macrosetae (char. 16: 2), and connective with lateral margin distinctly constricted (char. 94: 1). Southern (2008) placed *C. concava* within *Empoasca* but suggested that it should eventually be moved to a separate genus. This new genus is very similar to *Speciosiaca* in coloration and forewing venation but it can be distinguished from the latter by the diagnosis given above. It also differs from *Speciosiaca* in absence of a basolateral setal group on the pygofer lobe (present in *Speciosiaca*), presence of basal group of setae on subgenital plate (absent in *Speciosiaca*) and in having macrosetae scattered basally, uniseriate apically, reaching the tip of the plate (macrosetae uniseriate, not reaching tip of plate in *Speciosiaca*). This genus is known from the type species from Ecuador.

Etymology: The new genus name is derived from the type species name, *Empoasca concava* Southern, 2008, combined with the suffix of the genus *Empoasca*. The gender is feminine.

Longibrachiasca Xu, Dietrich & Qin **gen. nov.**

Type species: *Empoasca longibrachiata* Southern, 1982.

Diagnosis: Body robust; anteclypeus strongly convex but not distinctly broadened; 2S apodemes well-developed, sternite VIII with posterior margin strongly produced medially; pygofer with posterodorsal margin long, weakly concave, presence of basolateral setal group; ventral appendage long and thin, curved upward; subgenital plate with basolateral lamella, setal group of basal setae poorly differentiated, continuous with marginal microsetae; style relatively straight, dentifer curved weakly upward; aedeagus simple, shaft slightly broader than preatrium; connective trapezoidal.

Notes: *Longibrachiasca* forms a sister with *Tripunctiasca* due to having the vein R2 and RM confluent for short distance preapically in forewing (char. 23: 1), the pygofer with a few long, fine setae and a basolateral setal group (char. 45: 1; char. 46: 1). Its genus status is well supported by five apomorphic characters: coronal suture not extended beyond mid-length of crown (char. 3: 0), male subgenital plate length little if any more than 2X maximum width (char. 54: 0), subgenital plate with basolateral lamella (char. 55: 1), presence of basal group (char. 57: 1) and apices of macrosetae blunt (char. 69: 1). This genus is known only from the type species from Peru. The type species is one of the largest New World Empoascini (about 6 mm long) and sternite VIII has the posterior margin strongly produced medially, which is unique in Empoascini.

Etymology: The new genus name is derived from the type species name, *Empoasca longibrachiata* Southern, 1982, combined with the suffix of the genus *Empoasca*. The gender is feminine.

Speciosiaca Xu, Dietrich & Qin **gen. nov.**

Types species: *Empoasca speciosa* Young, 1953.

Diagnosis: Body robust; head with median anterior black spot; pronotum with anterolateral black spot; scutellum elevated, black laterally; forewing venation unique, vein R2, RM and MCu confluent basally, arising from r cell or m cell; hind wing with fused vein MP + CuA; 2S apodemes extended to segment V, sternite VIII sinuate, produced; pygofer appendage simple, with a few fine basolateral setae; ventral appendage present; subgenital plate with basolateral lamella developed but not produced dorsolaterad; basal group of setae absent; marginal microsetae multiseriate and unusually long distally; macrosetae uniseriate, not extended to apex of plate; style without distal teeth, elongate, narrow, apex abruptly hooked, preapical setae widely spaced along lateral margin over most of length; aedeagus with preatrium long; shaft tubular, curved dorsad; basal process of anal tube simple.

Notes: *Speciosiaca* is sister to *Concaviasca* due to having the crown medially shorter than width between eyes (char. 1: 0), ocelli separated from eyes by more than one ocellar diameter (char. 5: 2), hind tibia setae row AV with 7 macrosetae (char. 18: 4), vein MCu distinctly curved, ending near apex of anal margin in forewing (char. 20: 1), vein RM strongly curved in forewing (char. 22: 1), veins RM and MCu confluent for short distance preapically in forewing (char. 24: 1), and vein MCu arising from r cell (char. 27: 1). The genus status is well supported by eleven apomorphic characters: crown width including eyes subequal to that of pronotum (char. 0: 1), row AV setae subequal or gradually decreasing in size distally in front femur (char. 15: 2), pygofer lobe with a few long, fine setae (char. 45: 1), basolateral setal group present on pygofer (char. 46: 1), basal group of setae absent on male subgenital plate (char. 57: 0), marginal microsetae numerous, multiseriate (char. 63: 1), macrosetae uniseriate, fewer eight, not reaching tip of plate (char. 66: 1; char. 67: 0; char. 68: 1), style without teeth apically (char. 74: 0) and absence of preapical setae on style (char. 76: 0). This genus is known only from the type species from Argentina.

Etymology: The new genus name is derived from the type species name, *Empoasca speciosa* Young, 1953, combined with the suffix of the genus *Empoasca*. The gender is feminine.

Tripunctiasca Xu, Dietrich & Qin **gen. nov.**

Type species: *Empoasca tripunctata* Davidson & DeLong, 1943.

Diagnosis: Body robust; head with three brown spots along anterior margin (sometimes merged with larger area of dark pigmentation on face); forewing with veins R2 and RM confluent basally, vein MCu dissociated at bases, arising from r cell; hind wing with fused veins MP + CuA; 3 T apodemes present; male pygofer with basolateral setal group usually distinct, ventral appendage spatulate distally, with one margin conspicuously serrate; ventral appendage present; subgenital plate without basolateral lamella, with numerous short rigid setae scattered over ventral surface distally, basal group of setae absent or with long setae similar to group of fine setae; aedeagus simple; anal tube well-developed.

Notes: Our results well support *Tripunctiasca* as a separate genus based on the following shared characters: crown shorter medially than next to eye (char. 1: 0), vein MCu distinctly curved, ending near apex of anal margin in forewing (char. 20: 1), vein MCu arising from r cell in forewing (char. 27: 1), 3 T apodemes present (char. 37: 0) and marginal microsetae numerous, multiseriate (char. 63: 1). This new genus includes four species from Mexico (see Appendix 3 and File S2).

Etymology: The new genus name is derived from the type species name, *Empoasca tripunctata* Davidson & DeLong, 1943, combined with the suffix of the genus *Empoasca*. The gender is feminine.

Species incertae sedis.

Numerous other species formerly placed in *Empoasca* are here treated as species incertae sedis within Empoascini (see Appendix 3 and File S2). Further comparative morphological study, particularly of the numerous New World species that have been inadequately illustrated and described in previous literature, are needed to determine whether they can be accommodated within any of the genera defined above or whether additional new genera are needed.

Distribution patterns

The distributional patterns of the genera of Empoascini are summarized in Supplemental File S3. Most known genera are restricted to a single biogeographic realm. The Oriental fauna harbours nearly half of the endemic genera but several general also appear to be endemic to the Ethiopian region. *Empoasca* as here defined is restricted to the New World but some genera previously treated as subgenera of *Empoasca* (*sensu lato*), e.g., *Kybos*, *Matsumurasca* and *Hebata* are distributed across multiple biogeographic realms. Although these groups appear to be well-defined based on morphology, they also and show high levels of morphological diversity and remain poorly studied. Further comparative study of these diverse and widespread groups is needed to determine how species and lineages endemic to different regions are related to each other. A key to adults of known genera is also provided to further justify and characterize the generic classification adopted here (see Appendix 4).

The fossil record of the Typhlocybinae includes an extinct tribe Protodikraneurini (from Middle Eocene Baltic amber, about 44 Ma) and the extant tribe Dikraneurini (from Oligocene/Miocene Dominican amber, about 55 Ma) (Dietrich & Vega, 1995; Gebicki & Szwedo, 2006; Szwedo & Gebicki, 2008). Fossils representing other tribes, including Empoascini remain unknown. Nevertheless, the molecular timetree of Dietrich *et al.* (2017) suggests that this subfamily originated ~138 million years ago (mya) and that Empoascini emerged ~26 million years later, during the Cretaceous. This same analysis indicates that the two included representatives of Empoascini, *Joruma* and *Apheliona*, diverged ~77 mya, consistent with the hypothesis that the endemic New World *Joruma* group first evolved when South America was isolated from other continents. Our biogeographic analyses suggest that Empoascini first evolved in the Oriental region and spread to the New World and other biogeographic realms more recently by multiple independent invasions. This may explain why the Oriental fauna is much more phyletically diverse, while the New World includes relatively few genera but large numbers of species.

Supporting Information

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

Appendix 1. Morphological characters coded in the phylogenetic analysis.

Appendix 2. Data matrix for the phylogenetic analysis with the taxa studied.

Appendix 3. New genera and new combinations proposed in this study.

Appendix 4. Key to adults of known genera of Empoascini (males) worldwide.

File S1. Morphological character matrix in tnt format for the phylogenetic analysis.

File S2. Checklist of *Empoasca* (*s.s.*) and generic segregates of *Empoasca* (*s.l.*).

File S3. Distributional patterns of generic taxa of Empoascini in the world.

Fig. S1. Maximum likelihood bootstrap consensus tree.

Fig. S2. The consensus tree of 31 MP trees in tnt with 100 replications of Find min. length.

Fig. S3. Statistical Dispersal-Vicariance Analysis reconstruction of biogeographic associations using the consensus of the two original MP trees.

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Data availability

The data that support the findings of this study are openly available in Illinois Data Bank at https://doi.org/10.13012/B2IDB-4470290_V1.

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