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The phylogeny and classification of Embioptera (Insecta)

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Abstract. A phylogenetic analysis of the order Embioptera is presented with a revised classification based on results of the analysis. Eighty-two species of Embioptera are included from all families except Paedembiidae Ross and Embonychidae Navás. Monophyly of each of the eight remaining currently recognized families is tested except Andesembiidae Ross, for which only a single species was included. Nine outgroup taxa are included from Blattaria, Grylloblattaria, Mantodea, Mantophasmatodea, Orthoptera, Phasmida and Plecoptera. Ninety-six morphological characters were analysed along with DNA sequence data from the five genes *16S rRNA*, *18S rRNA*, *28S rRNA*, *cytochrome c oxidase I* and *histone III*. Data were analysed in combined analyses of all data using parsimony and Bayesian optimality criteria, and combined molecular data were analysed using maximum likelihood. Several major conclusions about Embioptera relationships and classification are based on interpretation of these analyses. Of eight families for which monophyly was tested, four were found to be monophyletic under each optimality criterion: Clothodidae Davis, Anisembiidae Davis, Oligotomidae Enderlein and Teratembiidae Krauss. Australembiidae Ross was not recovered as monophyletic in the likelihood analysis in which one *Australembia* Ross species was recovered in a position distant from other australembiids. This analysis included only molecular data and the topology was not strongly supported. Given this, and because parsimony and the Bayesian analyses recovered a strongly supported clade including all Australembiidae, we regard this family also as monophyletic. Three other families – Notoligotomidae Davis, Archembiidae Ross and Embiidae Burmeister, as historically delimited – were not found to be monophyletic under any optimality criterion. Notoligotomidae is restricted here to include only the genus *Notoligotoma* Davis with a new family, Ptilocerembiidae Miller and Edgerly, new family, erected to include the genus *Ptilocerembia* Friederichs. Archembiidae is restricted here to include only the genera *Archembia* Ross and *Calamoclostes* Enderlein. The family group name Scelembiidae Ross is resurrected from synonymy with Archembiidae (new status) to include all other genera recently placed in Archembiidae. Embiidae is not demonstrably monophyletic with species currently placed in the family resolved in three separate clades under each optimality criterion. Because taxon sampling is not extensive within this family in this analysis, no changes are made to Embiidae classification. Relationships between families delimited herein are not strongly supported under any optimality criterion with

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a few exceptions. Either Clothodidae Davis (parsimony) or Australembiidae Ross (Bayesian) is the sister to the remaining Embioptera taxa. The Bayesian analysis includes Australembiidae as the sister to all other Embioptera except Clothididae, suggesting that each of these taxa is a relatively plesiomorphic representatative of the order. Oligotomidae and Teratembiidae are sister groups, and Archembiidae (*sensu novum*), Ptilocerembiidae, Andesembiidae and Anisembiidae form a monophyletic group under each optimality criterion. Each family is discussed in reference to this analysis, diagnostic combinations and taxon compositions are provided, and a key to families of Embioptera is included.

Introduction

Among the most poorly known insects, Embioptera, or webspinners, comprise a distinctive, monophyletic group with representatives found throughout warmer regions of the world. Although moderately large in size (5–25 mm), they are rarely encountered, even by experienced entomologists. Reflected in this is the poor knowledge of their diversity. About 400 species have been described, but one prominent Embioptera researcher has estimated at least 1500 undescribed species in his collection alone (Ross, 1991). Their best-known characteristic, and the source of the common name, is their ability to spin silk from unicellular glands in the enlarged protarsomere I, or foreleg basitarsus, which they use to create domiciles. These domiciles may be on tree or rock surfaces, under rocks, in leaf litter, or in certain other habitats depending on taxon. Female embiopterans are wingless and often found in the domicile with their eggs or nymphs. In some species, a single female inhabits a domicile with her offspring. In other cases, many females may live together, and may exhibit varying degrees of sociality (reviewed by Edgerly, 1997). Males are often winged, although they may be wingless; some species are variable with some male specimens winged and others wingless. Usually, mature males are less often collected, because they are not generally found in the domiciles with females and nymphs. This has made studying Embioptera difficult as most of the known characters are found in the male head and terminalia. Males, while difficult to find in the wild, can be reared in the laboratory.

Given the unusual ability of webspinners to spin silk from the protarsi in both nymphs and adults, there is little doubt as to monophyly of Embioptera. Numerous other characters taken together further suggest close relationship among members of the order, including three-segmented tarsi, presence of a gula, absence of ocelli, complex and asymmetrical male genitalia, and absence of a female ovipositor. Relationships between Embioptera and other orders remain unclear (Klass, 2009), but proposals about the Embioptera sister group have included Plecoptera (Boudreaux, 1979; Wheeler *et al*., 2001), Zoraptera (Grimaldi & Engel, 2005; Engel & Grimaldi, 2006; Yoshizawa, 2007, 2011) and Neoptera except Plecoptera (Hennig, 1969, 1981; Beutel & Gorb, 2006). The current best consensus, however, is a sister group relationship between Phasmida and Embioptera (Flook & Rowell, 1998; Thomas *et al*., 2000; Whiting *et al*., 2003; Terry & Whiting, 2005; Kjer *et al*., 2006; Jintsu *et al*., 2010; Ishiwata *et al*., 2011; Wipfler *et al*., 2011).

Most historical taxonomic literature on the group has emphasized descriptions of new species. Relatively few papers have comprehensively addressed the phylogeny or higher classification, and fewer of these have incorporated a more modern philosophy emphasizing cladistics or the naming of demonstrably monophyletic groups. The earliest comprehensive treatments include those by Hagen (1861, 1885) during which time members of Embioptera were recognized as neuropterans, and less than 20 species were recognized in a single family (Hagen, 1885). New species were added only rarely until comprehensive revisions by Enderlein (1903, 1909, 1912) and Krauss (1911) added numerous new species and higher taxa.

Subsequent attempts at formalizing the higher classification include Davis (1940a, b), who, as reviewed thoroughly by Szumik (1996), approached modern methods in his emphasis on multiple characters and techniques similar to cladistics. Davis (1940b) recognized seven families: Clothodidae Enderlein, Embiidae Burmeister, Oligotomidae Enderlein, Oligembiidae Davis, Teratembiidae Krauss, Anisembiidae Ross and Notoligotomidae Davis.

The last 70 years of Embioptera studies have been dominated by a single researcher, E. S. Ross, who contributed the descriptions of very many new species. Because of the expansion of known global diversity, he developed progressively a higher classification summarized especially in Ross (1970) in which he formally recognized most of the families recognized by Davis except Oligembiidae, which was synonomyzed with Teratembiidae, and Australembiidae Ross, which he had erected earlier (Ross, 1963). Furthermore, he proposed a number of additional hypothetical suborders, families and subfamilies which he left unnamed. Some of Ross's informally recognized family-rank groups have been described recently (Ross, 2006, 2007), but others have not. Ross's interpretation of the group was based in large part on an authoritarian approach that was criticized heavily by Szumik (1996) and Szumik *et al*. (2008) who subjected the group to careful cladistic analysis.

Szumik's (1996, 2004) and Szumik's *et al*. (2008) contributions have been significant in examining the homology of numerous morphological features, reconstructing the phylogeny of the group based on cladistic methods, and revising the classification to better reflect the evolutionary history. Despite these recent advances, a comprehensive treatment of the phylogeny of Embioptera using both morphological and molecular data and a critical examination of the classification in light of that phylogeny appears warranted. The goal of this project is such an analysis.

Material and methods

Taxon sampling

Ingroup

Embioptera are difficult to collect and require rearing to acquire males upon which the classification is based. Once collected, specimens are often difficult to identify or represent undescribed taxa making taxon sampling more challenging than many other taxa. The ingroup includes 82 Embioptera species. All currently recognized extant families of Embioptera (Miller, 2009) are represented with the exception of Embonychidae Navás and Paedembiidae Ross, which are represented by a few very rare species. Three families – Anisembiidae, Archembiidae and Embiidae – comprise the largest number of genera in Embioptera. Of these, Embiidae is not as well represented in the analysis as the others because many of these groups occur in Africa and Southeast Asia making their collection difficult because of the challenging logistics of collecting in those regions. Only a single species of Andesembiidae (*Andesembia banosae* Ross) is included, so monophyly of that family was not tested. See Table S1 for a list of included taxa. Not all species were identified beyond genus, and three species of Embiidae from Africa were not identified to genus. Each of these appear to be undescribed taxa. Vouchers of extracted and sequenced Embioptera are deposited in the Division of Arthropods, the Museum of Southwestern Biology, the University of New Mexico (MSBA, K.B. Miller, curator).

Outgroup

The outgroup includes nine species from the polyneopteran taxa Grylloblattodea, Blattodea, Mantophasmatodea, Orthoptera, Mantodea and Phasmida. Sequences were downloaded from GenBank. See Appendix for a list of outgroup species and GenBank numbers of the sequences used in the analysis.

Data

DNA

DNAs were extracted using the Qiagen DNEasy kit (Valencia, CA, U.S.A.) and the animal tissue protocol. For each specimen an incision was made along the lateral margin of the thorax using a sharp razor and the specimen was placed in extraction buffer. After incubation for several hours or overnight, the specimen was retrieved from the extraction buffer and retained for vouchering purposes.

Five genes were used in the analysis: *cytochrome oxidase I* (COI, 1282 bp), *16S rRNA* (16S, ∼580 bp), *28S rRNA* (28S, ∼2800 bp), *18S rRNA* (18S, ∼1800 bp) and *histone III* (H3, 328 bp). Most methods, including primers used for amplification and sequencing are the same as in Miller & Edgerly (2008) except primers for 18S from Whiting (2002). Primers are shown in Table S2 and amplification conditions in Table S3. DNA fragments were amplified using PCR with *TaKaRa Ex Taq* (Takara Bio Inc., Otsu, Shiga, Japan) on an Eppendorf Mastercycler ep gradient S Thermal Cycler (Eppendorf, Hamburg, Germany) and visualized by gel electrophoresis. PCR purification was done using ExoSAP-IT (USB-Affymetrix, Cleveland, OH, USA) and cycle-sequenced using ABI Prism Big Dye v3.1 (Fairfax, VA, USA) with the same primers used for amplification. Sequencing reaction products were purified using Sephadex G-50 Fine (GE Healthcare, Uppsala, Sweden) and sequenced with an ABI 3130xl Genetic analyzer (Molecular Biology Facility, UNM). All gene regions were sequenced in both directions, and sequences were edited using Sequencher (Genecodes, 1999). For reasons that are unclear, Embioptera were difficult to amplify and/or sequence, even with taxon-specific primers. For this reason, entire gene regions or portions of genes are missing for some taxa (see Table S1).

Morphology

Morphological characters were derived primarily from Szumik *et al*. (2008), the most comprehensive dataset published to date. However, character codings were re-evaluated as were state assignments for taxa. Some characters were omitted, for several reasons (see Table S4). Differences in taxon sampling here rendered some original or reassessed characters of Szumik *et al*. (2008) uninformative, and they were excluded. Some characters were removed because they exhibited considerable ambiguity among the included taxa. In other cases, characters were removed as we were less convinced of their validity either because of apparent ambiguity in homology assessment, the seemingly gradational nature of the character states in question, or simply a disagreement in our observations. In addition, the additivity of numerous characters were reassessed because many multistate characters presented by Szumik *et al*. (2008) were coded as additive, although not always in a way with which we could agree. Characters were examined also for alternative coding schemes that might better reflect our assessment of primary homology. Our choice of characters is determined partly because of lack of illustration or thorough explanation by Szumik *et al*. (2008), and we emphasized characters that have been used traditionally in the classification or have been illustrated in previous works. Many of the included characters are illustrated and discussed more fully by Ross (2001, 2003a, b, 2006, 2007, and especially Ross, 2000). Despite our refinements in these characters, we acknowledge numerous remaining problems, and this character matrix should be considered provisional and subject to further careful reinterpretation. We note also that in some cases we use morphological terminology that reflects historical use in the Embioptera literature, even though some of these terms are not now used as generally across other taxa. Until Embioptera characters can be more thoroughly evaluated, this consistency will aid future researchers in tracking their continuity between this study and earlier ones. The characters, as reassessed, are discussed in the Appendix. A few new characters applicable to differences between outgroup taxa and Embioptera are added.

Character state scoring mainly reflects that presented by Szumik *et al*. (2008) whenever taxon sampling overlaps at the species level, although a few taxa were assessed differently and recoded (see above and Appendix). Females of many taxa were not examined, and these were coded either as in Szumik *et al*. (2008) or coded as ambiguous in species not included by Szumik *et al*. (2008). One included terminal is from a species or, possibly, a population (*Haploembia solieri* Rambur) that is parthenogenetic, and male characters were all coded as inapplicable. Females and males in Embioptera are structurally quite different with females typically appearing neotenous with wings absent and, except for paragenital sclerites, female reproductive tract, size and coloration, other features similar to nymphal instars (Ross, 2000). For this reason, many of the characters included refer only to males or only to females. Outgroup taxa are coded as inapplicable for most characters because many are specific to Embioptera and difficult to homologize. Morphological data are shown in Table S5 and are available as a nexus file in the Supporting Information.

Analysis

Alignment

Alignments of H3 and COI were based on conservation of codon reading frame. These sequences evidently are not length variable and are aligned easily by eye. 16S, 18S and 28S exhibit considerable length variability in the included taxa and were aligned using the program Muscle (Edgar, 2004) with the default settings. The bulk of the alignment-ambiguous regions in 18S and 28S are the result of inclusion of outgroups rather than alignment ambiguity within Embioptera. Gaps in this analysis are treated as missing data in all analyses. Aligned data are available as nexus files in the Supporting Information.

Parsimony

A combined equal-weights parsimony analysis was conducted using the program NONA (Goloboff, 1995) as implemented by WinClada (Nixon, 2002). The 'Ratchet' option was implemented using 800 iterations/rep, 1 tree held/iteration, 734 (about 10%) characters sampled, amb-poly, and 10 random constraint. The resulting trees then were resubmitted to NONA and TBR branch swapping was executed to search for additional equally parsimonious trees. Branch support (bootstrap) was calculated in NONA using 1000 replications, 10 search reps, 1 starting tree per replication, don't do max*, and save consensus of each replication. Because of considerable change to a published morphological dataset (see above) the morphological data were analysed independently to examine differences in the topology as compared with results of Szumik *et al.* (2008). These data were analysed using parsimony similar to the strategy for the combined analysis.

Likelihood

A bootstrap likelihood analysis was conducted using RaxML v7.2.6 (Stamatakis, 2006). Morphology was not included. The model used was GTR-MIX (general time reversal mixed model incorporating rate variation among sites) partitioning by gene (9 partitions) and 2000 bootstrap replications.

Bayesian

A partitioned Bayesian analysis of both molecular and morphological data was conducted using Mr Bayes v3.1.2 (Huelsenbeck & Ronquist, 2001). The molecular data were partitioned by gene with a six parameter model, invariant sites and gamma rate distribution. Morphology was included and modelled with the MK1 default model. Four Markov Chain Monte Carlo runs were conducted for 40 000 000 generations sampled every 2000th generation. The first 1 000 000 generations were discarded in each run as burn-in with the remaining trees pooled and summarized to find the topology with the highest posterior probably, and to calculate clade support values as the frequency of each clade among the pooled trees.

Results

Analysis of the morphological data by itself resulted in excess of 10 000 parsimony trees, the consensus of which is shown in Fig. 1 (length = 412, CI = 29, RI = 82). This result is much less resolved than the combined analysis (see below) and the analysis of a much larger morphological dataset by Szumik *et al*. (2008). Because of considerable ambiguity in the scoring of many characters used in that analysis (see above), data used here represent only a subset of that much larger dataset, which is probably reflected in the lack of resolution. However, several groups are supported by these data including Embioptera, Clothodidae, Australembiidae, Archembiidae (except *Archembia* and *Calamaclostes*), Teratembiidae + Oligotomidae (and Teratembiidae within this group), and numerous genera. Some historically recognized groups are not monophyletic in this analysis including Anisembiidae, Notoligotomidae, Oligotomidae and Embiidae. Although not represented in the consensus tree because of topological conflict (Fig. 1), a sister relationship between Clothodidae and the other Embioptera is represented in some of the most parsimonious solutions.

The parsimony analysis of the combined data resulted in 16 equally parsimonious trees, with the well-resolved strict consensus shown in Fig. 2. Support values are relatively strong for family-level groupings and within families, but among-family relationships are not well supported, in general (Fig. 2). The likelihood analysis resulted in one most likely tree shown in Fig. 3 (final ML optimization likelihood = −94079.519732). Bootstrap support across the tree is not strong for among-family level relationships, but, like the parsimony analysis, is

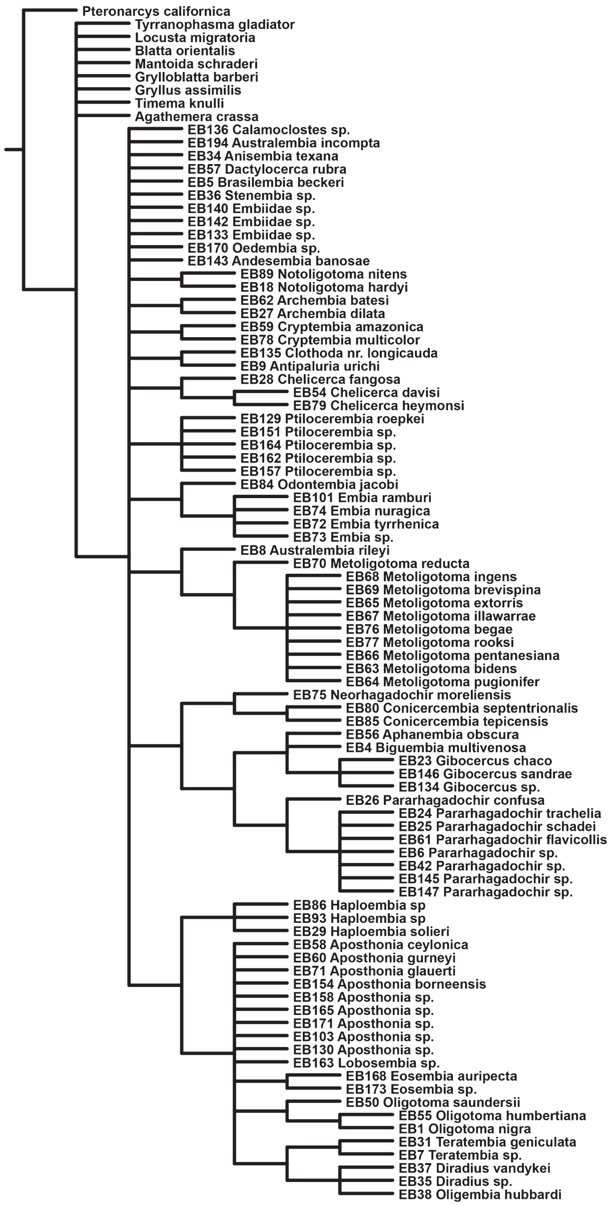

Fig. 1. Consensus cladogram of >10 000 equally parsimonious trees resulting from analysis of Embioptera using morphological data alone.

relatively strong for family groups and within families (Fig. 3). The Bayesian analysis resulted in a well-resolved tree with strong support values across the topology at all levels of relationships (Fig. 4).

Results across optimality criteria are not strongly congruent regarding interfamilial relationships, although in each analysis family groups are monophyletic with the exception of Embiidae, Notoligotomidae and Archembiidae, which are not monophyletic under any optimality criterion (Figs 2–5). Australembiidae is not monophyletic in the likelihood analysis. Teratembiidae, Oligotomidae, Clothodidae and Anisembiidae (each as defined traditionally) are monophyletic under each criterion. Andesembiidae includes only a single terminal exemplar and was not tested for monophyly. Other clades congruent between optimality criteria include Teratembiidae + Oligotomidae, *Oedembia* + *Ptilocerembia*, and Archembiidae (s.s., see below) + Notoligotomidae (s.s., see below) + Anisembiidae + Andesembiidae.

Classification

Although taxon sampling is inadequate to examine the question comprehensively, the sister group to Embioptera based on this analysis is resolved as Phasmida in the parsimony analysis (Fig. 2) and Phasmida + Grylloblattaria in the likelihood and Bayesian analyses (Figs 3, 4), corroborating, in part, previous analyses that recognize close relationship between Embioptera and Phasmida (Flook & Rowell, 1998; Thomas *et al*., 2000; Whiting *et al*., 2003; Terry & Whiting, 2005; Kjer *et al.*, 2006; Ishiwata *et al*., 2011; Wipfler *et al*., 2011).

Family-group classification of Embioptera has changed considerably in the past 15 years as a result of several papers by Ross (2000, 2001, 2003a, b, 2006, 2007), Szumik (1996, 2004) and Szumik *et al*. (2008). The current family-group classification was summarized recently by Miller (2009). Of 11 families currently recognized (Miller, 2009), five were retrieved as monophyletic in this analysis (including Australembiidae despite evidence from the likelihood analysis, see below); one family, Andesembiidae, was represented by a single terminal taxon and, thus, not tested for monophyly, and two families, Embonychidae and Paedembiidae, were not included. Each family is discussed below in relation to results from this analysis.

Clothodidae Enderlein, 1909

Clothodinae Enderlein, 1909:175; as subfamily of Embiidae Burmeister, 1839, elevated to family by Davis (1940a); type genus: *Clothoda* Enderlein, 1909.

Discussion. This family was erected (Enderlein, 1909) to include the genus *Clothoda* Enderlein and, later (Enderlein, 1912), *Antipaluria* Enderlein was described in the family. Most recently, in a revision of the group, Ross (1987) added additional genera. Members of the family are Neotropical mainly in lowland forests with domiciles on tree and rock surfaces (Ross, 1987). Other aspects of their biology are discussed by Ross (1987).

Because of seemingly generalized morphology of the head, wings and male genitalia, members of this group usually have been regarded as sister group to the remaining taxa (Davis, 1940a; Ross, 1970, 1987; Szumik, 1996; Grimaldi & Engel, 2005; Szumik *et al*., 2008). In a study of the female postabdomen in five diverse embiopteran species Klass & Ulbricht's (2009) showed that this body part exhibits the overall most plesiomorphic morphology in *Metoligotoma* (Australembiidae), whereas in *Clothoda* it is most derived. This rather suggests australembiids to be the sister group

Fig. 2. Consensus cladogram derived from 12 equally parsimonious trees resulting from analysis of Embioptera using the combined data. Numbers at branches are bootstrap values. Small tree inset is 1 of 12 equally parsimonious trees chosen at random to depict branch lengths mapped under 'fast' parsimony optimization in WinClada with grey section comprising Embioptera.

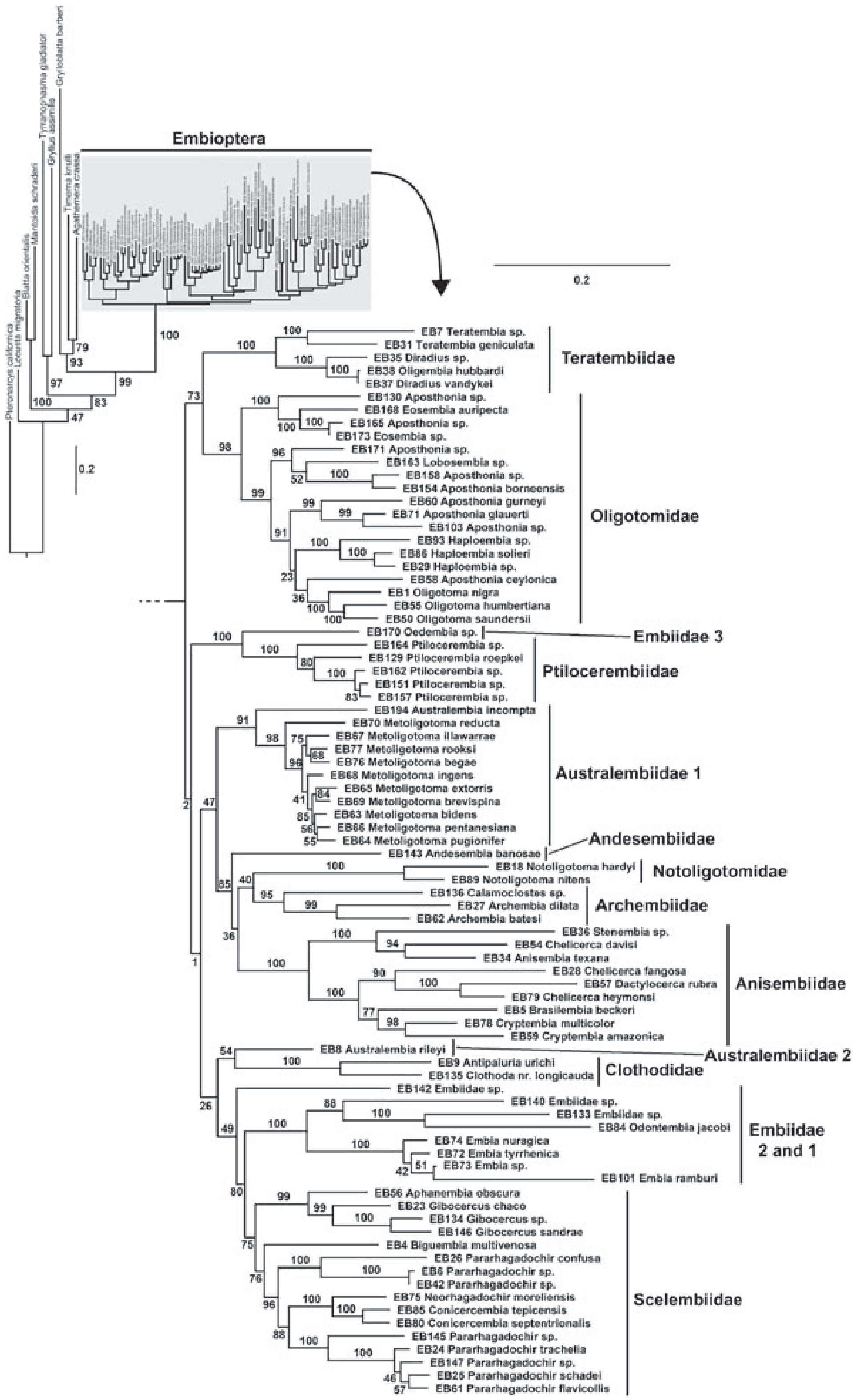

Fig. 3. Tree resulting from likelihood bootstrap analysis of Embioptera using molecular data alone. Numbers at branches are bootstrap values.

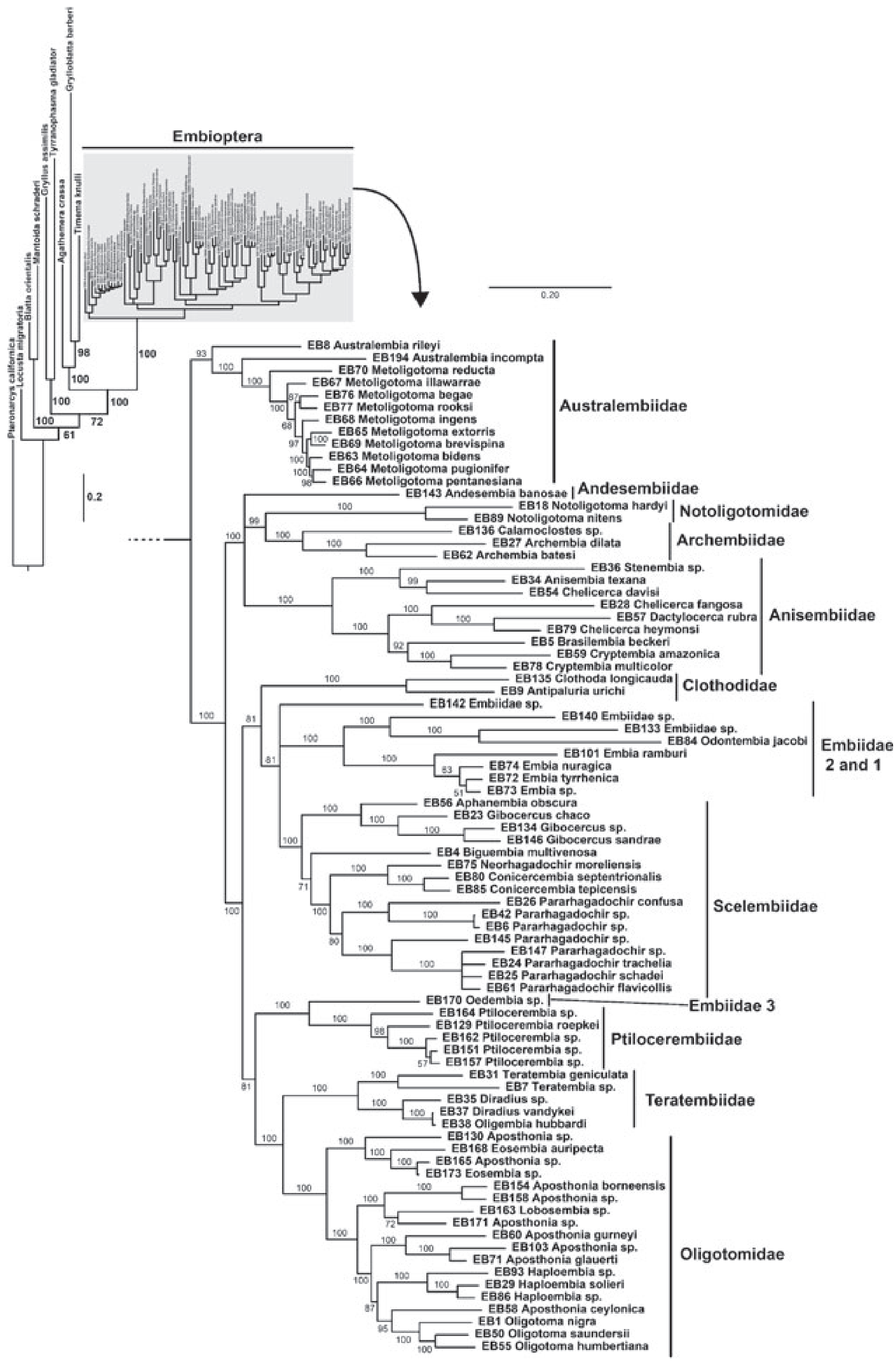

Fig. 4. Tree resulting from Bayesian analysis of Embioptera using combined data. Numbers at branches are posterior probability values.

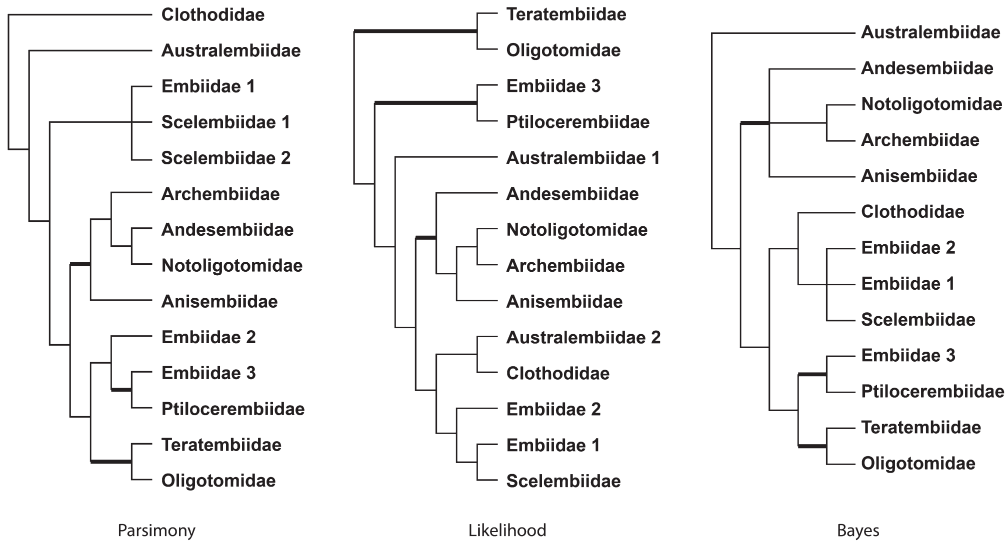

Fig. 5. Comparsion of family-group relationships among Embioptera from each of three optimality criteria. Thickened branches are monophyletic groups of families common to each optimality criterion. Family groups represented by terminals are monophyletic in each optimality criterion except Australembiidae which is polyphyletic in the likelihood analysis and Embiidae which is not monophyletic in any trees.

of the remaining embiopterans. In recent cladistic analyses (e.g. Szumik, 1996; Szumik *et al*., 2008), no non-Embioptera outgroup taxa were included and resulting cladograms were rooted using clothodids. There have been no comprehensive analyses of Embioptera that tested the assumption that clothodids actually are the sister group to the rest of the order. And our analysis is the first to test this assumption explicitly.

Our results indicate a monophyletic Clothodidae (including species in *Clothoda* and *Antipaluria* but with the other described genera, *Cryptoclothoda* Ross and *Chromatoclothoda* Ross, not included). However, placement is ambiguous with respect to optimality criteria. Parsimony resolved Clothodidae as sister to the remaining members of the order, but with low support (Fig. 2), but the Bayesian analysis and likelihood analyses (this last excluding the morphological data) found Clothodidae nested well within the remaining Embioptera taxa, with better support (Figs 3, 4). Placement of this taxon as sister to the remaining Embioptera taxa has been based on authoritative assumptions about the polarity of certain characters without testing them adequately. Although results from this analysis are inconclusive, care should be taken not to assume placement of Clothodidae as sister to the rest of the order. Australembiids, instead, may represent the sister-group to the remaining Embioptera (see below, Fig. 4 and Klass & Ulbricht, 2009).

Diagnosis. Clothodidae is characterized by males with relatively, but not entirely, symmetrical male genitalia with tergite X not medially divided, the left cercomeres elongate and similar to the right cercomeres, and wing venation extensive with most major veins bifurcated and with numerous crossveins.

Taxon content. Clothodidae currently includes the following four genera:

Antipaluria Enderlein, 1912
Clothoda Enderlein, 1909
Chromatoclothoda Ross, 1987.
Cryptoclothoda Ross, 1987

Australembiidae Ross, 1963

Australembiidae Ross, 1963:124; as family of Embioptera; type genus: *Australembia* Ross, 1963 (= *Metoligotoma* Davis, 1936, new synonymy).

Discussion. Australembiids are restricted to the east coast of Australia in dry, sclerophyll forests where typically they create domiciles in leaf litter in which the entirely apterous males can often be found with females and nymphs (Davis, 1936a, b, 1938; Ross, 1963; Miller & Edgerly, 2008). Australembiidae, including the genera *Australembia* Ross and *Metoligotoma* Davis, generally has been regarded as monophyletic since the family was erected by Ross (1963) for taxa placed previously along with *Notoligotoma* Davis in the family Notoligotomidae. Davis (1938) and a recent paper by Miller & Edgerly (2008) described the morphology, natural history and biogeography of australembiids, and their ecology and ecophysiology were explored by Edgerly & Rooks (2004) and Edgerly *et al*. (2007).

This analysis resulted in a monophyletic Australembiidae although *Australembia* is paraphyletic with respect to *Metoligotoma*, corroborating Szumik *et al*. (2008), and the topology within *Metoligotoma* largely reflecting the results of Miller & Edgerly (2008) (Figs 2–4). Exceptional to this is the likelihood analysis, which finds a polyphyletic Australembiidae with one species, *A. rileyi* Davis weakly supported as sister to Clothodidae in a different part of the tree. This untenable result probably can be disregarded based on a wealth of morphological evidence (Miller & Edgerly, 2008) as well as parsimony (Fig. 2) and Bayesian (Fig. 4) analyses of combined data. The parsimony analysis recovered Australembiidae sister to Embioptera except Clothodidae (Fig. 2), and the Bayes analysis recovered Australembiidae sister to all other Embioptera (including Clothodidae) (Fig. 4). Neither of these results have been proposed extensively in other literature, although Klass & Ulbricht (2009) found evidence for *Metoligotoma* being sister to the remaining Embioptera (and Clothodidae nested higher within the group), which accords well with the Bayes analysis. Clothodidae has been regarded as the sister to the remaining Embioptera based especially on the relatively symmetrical male genitalia, extensive wing venation compared with other Embioptera, and general features of the male head, each of which has been assumed to be plesiomorphic. Australembiids have highly modified, extremely asymmetrical male genitalia suggesting that relative symmetry of these structures within clothodids may be derived. Australembiids lack wings entirely (both females and males) and their wing venation cannot be assessed. The australembiid male head also is modified compared with other Embioptera that have enlarged palpi and characteristic robust mandibles, presumably for grasping females during courtship or mating, but perhaps also for feeding; these are among the few adult male Embioptera that are known to feed, a possibly plesiomorphic feature, as well. They are not particularly similar to Clothodidae in many features, and relationships between Australembiidae, Clothodidae and the remaining Embioptera taxa need further study.

Diagnosis. Australembiidae are characterized by males apterous, robust and heavily sclerotized (some males are neotenous in some cases according to Ross (1963, 2000)), the left cercomeres fused and curved, and the right basal cercomere robust and short. Other male genitalic features are also unique and complex (see Miller & Edgerly, 2008).

Taxon content. Because of clear evidence of paraphyly of *Australembia* with respect to *Metoligotoma*, as defined currently, in this analysis (Figs 2, 4) and in previous analyses (Szumik *et al*., 2008), these two genera are synonymized formally here. *Metoligotoma* Davis, 1936 has priority over *Australembia* Ross, 1963, so the valid name of the taxon is *Metoligotoma* Davis, 1936 (new synonymy). Thus, as currently defined, the family includes only the genus *Metoligotoma* Davis. This has no affect on the family-group name, however, which remains Australembiidae Ross, 1963.

Anisembiidae Davis, 1940

Anisembiidae Davis, 1940:537; as family of Embioptera; type genus: *Anisembia* Krauss, 1911.

Discussion. With 24 genera (Miller, 2009) and over 100 species (Ross, 2003b), Anisembiidae represents one of the largest diversifications in the Embioptera. The group is restricted to the New World from the southern Nearctic throughout lowland Central and South America and can be found in a great many different habitats. The group was treated completely by Ross (2003b) who discussed the natural history and biogeography of the group and mentioned numerous additional species remaining to be described in his collection. Although among the most diverse groups of Embioptera and geographically restricted to the New World, this group is well supported as monophyletic (Figs 2–4). The clade differs in its resolution with respect to other families depending on optimality criterion, but always groups with Archembiidae (s.s., see below), Notoligotomidae (s.s., see below) and Andesembiidae (Figs 2–4).

Diagnosis. The main morphological features uniting Anisembiidae include vein M_A not bifurcated, a single bladder on the hind basitarsus, and the male mandibles sickle-shaped and apically not conspicuously dentate.

Taxon content. This taxon includes 24 currently recognized genera (Miller, 2009). The various genera were assigned to tribes and subfamilies by Ross (2003b), but many are invalid because they were not properly erected (Engel & Grimaldi, 2006; Miller, 2009). The nomenclature of this large family needs to be revisited. The following genera are assigned to Anisembiidae:

Anisembia Krauss, 1911
Aporembia Ross, 2003
Brasilembia Ross, 2003
Bulbocerca Ross, 1940
Chelicerca Ross, 1940
Chorisembia Ross, 2003
Cryptembia Ross, 2003
Dactylocerca Ross, 1940
Ectyphocerca Ross, 2003
Exochosembia Ross, 2003
Glyphembia Ross, 2003
Isosembia Ross, 2003
Mesembia Ross, 1940
Microembia Ross, 1944
Oncosembia Ross, 2003
Pelorembia Ross, 1984
Phallosembia Ross, 2003
Platyembia Ross, 2003
Pogonembia Ross, 2003
Poinarembia Ross, 2003
Saussurembia Davis 1940
Schizembia Ross, 1944
Scolembia Ross, 2003
Stenembia Ross, 1972

Andesembiidae Ross, 2003

Andesembiidae Ross, 2003:1; as family of Embiidina; type genus: *Andesembia* Ross, 2003.

Discussion. This is a recently described family circumscribed to include two genera and seven species (Ross, 2003a). Its members are small and characteristic of high elevations in the neotropics. Their morphology and natural history are discussed by Ross (2003a).

A single species, *Andesembia banosae* Ross, was included in this analysis, and, therefore, monophyly of the family was not tested. It is resolved under each optimality criterion with Notoligotomidae (s.s., see below), Archembiidae (s.s., see below) and Anisembiidae, although its relationship with any one of these families is ambiguous and not well supported under any optimality criterion (Figs 2–4).

Diagnosis. Andesembiidae is characterized by having vein M_A not furcated, tergite X divided to the base, the mandibles large, robust and with distinct apical incisor teeth, the left basal cercomere apically expanded with distinct medial echinulations, and the hind basitarsus long, slender and with only a single, apical bladder.

Taxon content. Andesembiidae includes the two genera *Andesembia* Ross, 2003 and *Bryonembia* Ross, 2003.

Archembiidae Ross, 2001

Archembiinae Ross, 2001:3; as subfamily of Embiidae Burmeister, 1839, elevated to family rank by Szumik (2004); type genus: *Archembia* Ross, 1971.

Discussion. This family was described as a subfamily of Embiidae (Ross, 2001) to include two genera, *Archembia* Ross and *Calamoclostes* Enderlein. Subsequently, Szumik (2004) elevated the subfamily to family rank and expanded the definition well beyond the original two genera to include all Neotropical and an African genus placed historically in Embiidae. In this context, Archembiidae was defined based on tergite X with a large basal membranous region separating 10R and 10L except for a slender connection and the mandibles relatively short and with well-differentiated incisor and molar teeth regions on the mandibles (Szumik, 2004).

Based on this analysis, Archembiidae, as defined by Szumik (2004), is not monophyletic (Figs 2–4). Rather, results support a monophyletic group corresponding to Ross's (2001) limits on the subfamily definition, that is, the genera *Archembia* and *Calamoclostes* together (Figs 2–4). All other Neotropical Archembiidae *sensu* Szumik (2004) are together monophyletic, but not related to the *Archembia* + *Calamoclostes* clade (Figs 2–4). The *Archembia* + *Calamoclostes* clade does correspond to Szumik's (2004) 'Group A'. Because of the seemingly clear evidence of monophyly of *Archembia* + *Calamoclostes* (Figs 2–4), historical emphasis on close relationship between these taxa (e.g. Ross, 2001), other phylogenetic analyses grouping these taxa in their own clade (e.g. Szumik, 2004) and evidence that this clade is not closely related to other Archembiidae *sensu* Szumik (2004), the family Archembiidae is here restricted to include only the genera *Archembia* and *Calamoclostes*. All other Archembiidae *sensu* Szumik (2004) are transferred to a different family concept (Scelembiidae, see below). The family, as so defined, is found in lowland Neotropical forests (*Archembia*) and higher elevations in the Andes (*Calamoclostes*). Archembiidae, as defined here, belongs to a clade along with Notoligotomidae (s.s., see below), Anisembiidae and Andesembiidae (Figs 2–4).

Diagnosis. Archembiidae, as restricted here, is characterized by an expanded anal region of the wings, M_A bifurcated (though at least some specimens in each genus with M_A not furcated), the basal left cercomere with a prominent medial process that is echinulate, 10LP large and conspicuous, the anterior margin of the clypeus evenly curved (without processes), and either the medial flap (MF) elevated or with a prominent sclerite in the posterior marginal membrane of tergite IX.

Taxon content. As defined here, Archembiidae includes the two genera *Archembia* Ross, 1971 and *Calamoclostes* Enderlein. This is consistent with the original composition of Archembiinae as a subfamily of Embiidae (Ross, 2001) but differs considerably from a later concept of the family-group by Szumik (2004).

Notoligotomidae Davis, 1940

Notoligotomidae Davis, 1940:536; as family of Embioptera; type genus: *Notoligotoma* Davis, 1936.

Discussion. As originally conceived, Notoligotomidae included taxa currently in Australembiidae (Davis, 1940b). Ross (1963) redefined the group and restricted it to include only the eastern Australian genus *Notoligotoma* Davis and the Southeast Asian genus *Ptilocerembia* Friederichs with only few species. Members of *Notoligotoma* are relatively conspicuous elements of the Australian Embioptera fauna. The two currently recognized species may represent several more (Ross, 1963). Their natural history was discussed by Ross (1963) and Edgerly & Rooks (2004).

As defined here, the family Notoligotomidae comprises only a monophyletic *Notoligotoma* (Figs 2–4). The other genus placed historically in this group, *Ptilocerembia*, is not closely related to *Notoligotoma* (Figs 2–4, see below under Ptilocerembiidae). Notoligotomidae is resolved in a clade together with Andesembiidae, Anisembiidae and Archembiidae (s.s., see above) (Figs 2–4). Of this clade, Notoligotomidae is the only group that is not Neotropical. This Australian/Neotropical relationship suggesting an ancestral Gondwanian distribution of ancestral taxa is the only one like it in Embioptera.

Diagnosis. Members of this group have the left cercomeres fused (apomorphic) and males that are either apterous or winged with vein M_A not bifurcate and with tergite X completely divided to the base with each hemitergite separated by a broad membrane.

Taxon content. Under the definition used here, Notoligotomidae includes only the extant genus *Notoligotoma* Davis, 1936. An extinct genus, *Burmitembia* Cockerel, 1919 has been placed in this family in its own subfamily, Burmitembiinae Engel and Grimaldi, 2006.

Embiidae Burmeister, 1839

Embiidae Burmeister, 1839:768, as family ('Embidae') of Tribus Corrodentia; type genus: *Embia* Latreille, 1925.

Discussion. This family has been one of the most problematic from the standpoint of classification, probably because it is the original family in the group and over time distinctive groups have been carved out of it leaving behind a loose assemblage of taxa without convincing synapomorphies. The main subdivision in recent years was the removal of numerous taxa placed into the family Archembiidae Ross (Szumik, 2004), which was erected originally as a subfamily of Embiidae to include most of the New World species (Ross, 2001). This resulted in a major reduction in the overall number of taxa in Embiidae restricting it to several genera in the Mediterranean region, throughout Africa, and in South and Southeast Asia. Members of the group are diverse in morphology and natural history which has been discussed to a limited extent by Ross (2001) and Szumik (2004). Some members of the group are parthenogenetic (Ross, 1960).

As defined historically, the family Embiidae is not monophyletic in this analysis under any optimality criterion (Figs 2–4). Embiidae has been defined as Embioptera with males having vein M_A bifurcate (in alate males), the left basal cercomere apically clavate or with a medial process and bearing echinulations, and tergite X entirely divided medially (e.g. Davis, 1940a). Each of these conditions occur in other currently recognized families, however, suggesting that Embiidae is not well-established based on morphology. In our analyses, Embiidae is separated distinctly into three groups. *Embia* (the type genus), *Odontembia* and two African species (EB133 and EB140) are resolved in a distinct clade. An additional African species (EB142) is isolated with an ambiguous placement in each separate analyses (Figs 2–4). Our single included species of *Oedembia* is resolved in a clade with *Ptilocerembia* (Figs 2–4). *Oedembia* is a Southeast Asian group which, although well-supported as sister group to *Ptilocerembia*, shares no unambiguous morphological synapomorphies with that group. Given that Embiidae has experienced considerable historical change in taxon composition, it is unsurprising that the group is not monophyletic. Because relatively few taxa currently placed in the family were included in this analysis, and the few that were are not monophyletic, no changes to the classification are made here. Although it is tempting to expand the definition of Ptilocerembiidae to include *Oedembia*, as no unambiguous synapomorphies were found for this clade and there appears to be other additional Southeast Asian taxa possibly related to *Oedembia* (Ross, 2007) which were not included here, we take a conservative approach and refrain from doing so. Placement of *Oedembia* and the African 'Embiidae' (EB142) suggest that there may well be additional, currently unrecognized family-group clades in the Embioptera. Additional taxon sampling will be required to test the limits of Embiidae adequately and establish formally these other family groups.

Diagnosis. This family has the most problematic definition in Embioptera because many of the diagnostic features have similar corresponding features in other taxa, and the group evidently is not monophyletic (Figs 2–4). As currently defined, the family has males with vein M_A bifurcate (in alate males), the left basal cercomere apically clavate or with a medial process and bearing echinulations, and tergite X entirely divided medially.

Taxon content. Although now more restricted in its taxon content than historically, and still probably not monophyletic, Embiidae includes numerous genera. Given the problems with the phylogeny of this group, a thoroughgoing phylogenetic analysis with much deeper taxon sampling will result in more changes to the content of this taxon. Along with the extinct genus *Electroembia* Ross 1956, the following extant genera are assigned currently to Embiidae:

Acrosembia Ross, 2006
Apterembia Ross, 1957
Arabembia Ross, 1981
Berlandembia Davis, 1940
Chirembia Davis, 1940
Cleomia Stefani 1953
Dihybocercus Enderlein, 1912
Dinembia Davis, 1939
Donaconethis Enderlein, 1909
Embia Latreille, 1825
Enveja Navás, 1916
Leptembia Krauss, 1911
Machadoembia Ross, 1952
Macrembia Davis, 1940
Metembia Davis, 1939
Odontembia Davis, 1939
Oedembia Ross, 2007
Parachirembia Davis, 1940
Parembia Davis, 1939
Parthenembia Ross, 1960
Pseudembia Davis, 1939

Ptilocerembiidae Miller and Edgerly, new family

Ptilocerembiidae Miller and Edgerly, new family: type genus: *Ptilocerembia* Friederichs, 1923.

Discussion. This group includes usually large embiopterans in Southeast Asia that make large sheets of silk on trees as domiciles in the wet season when they breed. In the dry season, they appear to reside in silk retreats in leaf litter. The single genus, *Ptilocerembia* Friederichs, has been placed in Notoligotomidae for much of its history, although Ross (2007) implied that the genus should be placed in a new family. Evidence from this anlaysis indicates that *Ptilocerembia* is not closely related to *Notoligotoma* (Figs 2–4), the other extant genus historically placed in Notoligotomidae. Instead, *Ptilocerembia* is resolved in a clade with taxa placed currently in Embiidae (Figs 2–4). In addition to *P. roepkei* Friederichs, specimens that appear to represent other species of *Ptilocerembia* are included in this analysis (Figs 2–4). Although it is possible that *Oedembia*, sister to *Ptilocerembia*, should be placed here, we take a conservative approach to this problem and leave *Oedembia* in Embiidae (see under Embiidae for further explanation).

Diagnosis. Ptilocerembiidae is characterized by M_A bifurcated, antennal segments generally with long setae, tergite X obliquely divided into two unequal sclerites with the area between the hemitergites depressed, HP relatively long (longer than the length of H), and the left cercomeres fused, sometimes with the suture between the cercomeres indistinctly visible.

Taxon content. Ptilocerembiidae is erected here to include only the genus *Ptilocerembia* Friederichs, 1923.

Scelembiidae Ross, 2001, new status

Scelembiinae Ross, 2001:24; as subfamily of Embiidae Burmeister, 1839; type species: *Scelembia* Ross, 1960 (= *Rhagadochir* Enderlein 1912); synonymy by Szumik (2004).

Pachylembiinae Ross 2001:81; as subfamily of Embiidae Burmeister 1839; type species: *Pachylembia* Ross 1984a; new synonymy.

Discussion. Ross (2001) recognized four subfamilies of American Embiidae, Archembiinae Ross, Scelembiinae Ross, Pachylembiinae Ross and Microembiinae Ross. Szumik (2004) reclassified this group placing Microembiinae in synonymy with Anisembiidae and placing all other American taxa and the African genus *Rhagadochir* Enderlein in the family Archembiidae without subfamily divisions, thereby synonymizing Scelembiinae and Pachylembiinae with Archembiidae. Results from our analysis indicate that Archembiidae should be redefined to reflect more closely the composition recognized originally by Ross (2001) (see Archembiidae s.s. above). The remaining taxa represented in this analysis are from Ross's (2001) concept of Scelembiinae, and they are together monophyletic (Figs 3–4) except in the parsimony analysis where *Biguembia* is in an unresolved position with sister to the other scelembiids one parsimonious solution. Pachylembiinae comprises a single genus, *Pachylembia* Ross, which is not represented in this analysis.

Because of convincing evidence presented here that Archembiidae *sensu* Szumik (2004) is polyphyletic, a new family group name is required for the monophyletic group of taxa not related to *Archembia* + *Calamoclostes* (Figs 2–4). All the taxa included here belong to the historically recognized subfamily Scelembiinae Ross (2001), although the type genus, *Scelembia* Ross (= *Rhagadochir* Enderlein), is not included. *Pachylembia* (the only genus in the historical Pachylembiinae Ross) is not included in the analysis and its relationships therefore were not examined. Based on the description by Ross (2001) it appears that members of this genus are more closely related to Scelembiinae than Archembiidae s.s., although absence of a medial lobe on the basal left cercomere in *Pachylembia* makes placement of this taxon in Scelembiinae problematic and worthy of further investigation. Of the two available names for this taxon, Scelembiinae Ross, 2001 and Pachylembiinae Ross, 2001, each has equal priority, but the first name includes the bulk of the known diversity in the clade. Further, as no members assigned to Pachylembiinae were included in this analysis, the name Scelembiinae Ross, 2001 is resurrected and elevated here to family rank within Embioptera to include *Scelembia*, *Pachylembia* and related genera (see list below), new status. Pachylembiinae Ross, 2001, previously in synonymy with Archembiidae Ross, 2001, is moved to synonymy with Scelembiidae Ross, 2001, new synonym. Under each optimality criterion, Scelembiidae is closely associated with a clade of Embiidae found in the Mediterranean region (including the genus *Embia*) and Africa (Figs 2–4). Scelembiidae (represented by *Pararhagadochir*) was included in the analysis by Szumik *et al.* (2008) where similarly it was not associated with the clade containing *Archembia*.

Diagnosis. Scelembiidae is characterized by a reduced anal region of the wings, M_A bifurcated (some specimens with M_A not bifurcated), the basal left cercomere with a prominent medial process that is echinulate (though this is variable, especially in some *Pararhagadochir*, is not echinulate in *Conicercembia* and is absent entirely in *Pachylembia*), the anterior margin of the clypeus evenly curved (without processes), and the medial flap not elevated and without a sclerite in the posterior membrane of tergite IX.

Taxon content. This is a large family of mostly New World genera and the African genus *Rhagadochir* Enderlein. Under this new definition, this subfamily includes the following genera:

Ambonembia Ross, 2001
Biguembia Szumik, 1997
Conicercembia Ross, 1984
Dolonembia Ross, 2001
Ecuadembia Szumik, 2004
Embolyntha Davis, 1940
Gibocercus Szumik, 1997
Litosembia Ross, 2001
Malacosembia Ross, 2001
Neorhagadochir Ross, 1944
Ochrembia Ross, 2001
Pachylembia Ross, 2984
Pararhagadochir Davis, 2940

Rhagadochir Enderlein, 1912
Xiphosembia Ross, 2001

Teratembiidae Krauss, 1911

Teratembiidae Krauss, 1911:33; as family of Embiidina; type genus: *Teratembia* Krauss, 1911.

Discussion. This is a group of four genera found in the New World. Ross (1970) has indicated, however, that the greatest diversity in the group actually is found in Africa with other species in India and Thailand, although none of this diversity has been described formally. The known taxa are among the smallest Embioptera. Their biology and natural history has been little investigated.

The taxa included here, which may be a small representation of the actual diversity (see Ross, 1970) are monophyletic and sister to Oligotomidae (Figs 2–4), a result consistent with historical assumptions about relationships between these two families (Krauss, 1911; Davis, 1940a; Ross, 1944) and recent cladistic analyses (Szumik, 1996; Szumik *et al*., 2008).

Diagnosis. As currently delimited, Teratembiidae is characterized by having vein M_A bifurcated, the hind basitarsus with a single, apical bladder, tergite X incompletely divided longitudinally, but divided transversely to the right margin and with the anterior margin of tergite X extended ventrad under the posterior margin of tergite IX. The species generally are small. An undescribed African species assigned by Ross (1970) to Teratembiidae apparently have M_A not furcated.

Taxon content. Teratembiidae includes four genera currently, though Ross (1970) has indicated that most of the diversity of the group remains undescribed, and presumably many new taxa will be added to the family in the future. Currently included genera are:
Diradius Freiderichs, 1934
Oligembia Davis, 1939
Paroligembia Ross, 1952.
Teratembia Krauss, 1911

Oligotomidae Enderlein, 1909

Oligotomidae Enderlein, 1909:175; as family of Embiidina; type genus: *Oligotoma* Westwood, 1837.

Discussion. This family has had a similar composition since its inception over a century ago (Enderlein, 1909; Ross, 1970), with three historically recognized genera: *Oligotoma* Westwood, *Aposthonia* Krauss and *Haploembia* Verhoeff. Three additional genera were described from Southeast Asia (Ross, 2007). Members of the group are endemic to the Mediterranean regions (*Haploembia*, although some additional taxa from other regions of the world are ambiguously placed in this genus, see Ross, 1966) and Central and Southeast Asia and Australia (all other genera). Members of the group have been introduced throughout the world, however, and several species are now among the most commonly encountered Embioptera. The genus *Haploembia* includes both sexual and parthenogenetic taxa, as discussed in numerous papers by Stefani (1953, 1954, 1955a, b, 1956, 1960).

Of the six currently valid genera, five were included in this analysis. The group appears to be demonstrably monophyletic based on other analyses (Szumik, 1996; Szumik *et al*., 2008), and is also monophyletic in this analysis under each optimality criterion (Figs 2–4). The genus *Aposthonia*, however, appears not to be monophyletic (Figs 2–4) with each of the other included genera nested within this genus. Others already have proposed the possible paraphyly of *Aposthonia* (Ross, 2007), and there appear to be large numbers of undescribed taxa (Ross, 2007) suggesting that a thorough phylogenetic revision within the family will be required to provide for a more natural classification.

Oligotomidae is resolved as the sister group to Teratembiidae in this analysis under each optimality criterion (Figs 2–4). These two families, though mutually monophyletic, have been closely associated historically (Krauss, 1911; Davis, 1940a; Ross, 1944), and have been resolved together as monophyletic in previous analyses (Szumik, 1996; Szumik *et al*., 2008).

Diagnosis. Oligotomidae are characterized by lacking medial echinulations on the left basal cercomere (whether lobed or not), tergite X incompletely divided longitudinally, but divided transversely to the right margin, and wing vein M_A not bifurcated (when alate).

Taxon content. Six genera are currently assigned to Oligotomidae:
Aposthonia Krauss, 1911
Bulbosembia Ross, 2007
Eosembia Ross, 2007
Haploembia Verhoeff, 1904
Lobosembia Ross, 2007
Oligotoma Westwood, 1837

Embonychidae Navás, 1917

Embonychidae Navás, 1917:16; as family of Embioptera; type genus: *Embonycha* Navás, 1917.

Discussion. This family is represented by a single species, *Embonycha interrupta* Navás, known only from northern Vietnam (Navás, 1917). Poorly known, this taxon has been proposed as a close relative to Notoligotomidae or *Ptilocerembia* (Davis, 1940a; Ross, 1970). The family is unrepresented in our analysis.

Diagnosis. The description is inadequate to comprehensively diagnose the family, but according to Ross (2007) it can be diagnosed by having vein M_A bifurcated, the left cercomeres fused, at least partially, the antennae without long setae, and the wings with white maculae.

Taxon content. Embonychidae includes only the genus and species *Embonycha interrupta* Navás, 1917.

Paedembiidae Ross, 2006

Paedembiidae Ross, 2006:786; as family of Paedembiamorpha; type genus: *Paedembia* Ross, 2006.

Discussion. This, the most recently described family, was erected for two new genera and species from Central Asia (Gorochov & Anisyutkin, 2006; Ross, 2006). At least one species is unusual for being entirely subterranean, and both have males that are strikingly neotenous. Ross (2006) found the unusual biology and morphology of these species to be so compelling he erected not only a new family, but also a new infraorder, Paedembiamorpha Ross. Szumik *et al*. (2008) thought then either to be sister to all embiopterans except *Clothoda* or sister to all embiopterans. The main feature supporting this is the nearly symmetrical condition of the male genitalia, but this may not be plesiomorphic within the order (see under Clothodidae above). Because paedembiids were not included in our analysis, its relationships were not tested here. The natural history of the group was discussed by Ross (2006).

Diagnosis. Males of Paedembiidae are wingless and strongly neotenous with highly reduced male genitalia that are nearly symmetrical. As such, they are somewhat similar to Clothodidae but differ in lacking wings.

Taxon content. Paedembiidae includes the genera *Paedembia* Ross, 2006 and *Badkhyzembia* Gorochov and Anisyutkin, 2006.

Key to the extant families of Embioptera (males only)

Embiopterans are difficult to key and difficult to identify to family. Although there are a few characters that might be used to identify females, males are the only life stage that can be reliably and consistently identified based on current knowledge, which makes identification of the several parthenogenetic taxa particularly problematic. The best key characters are general features of the wings, male genitalia and number of bladders on the hind basitarsus, each of which requires some special knowledge of Embioptera morphology. The best single comprehensive reference for Embioptera morphology is an excellent work by Ross (2000) which should be consulted for explanation of the characters included in this key. Characters in the following key refer to males.

1. Male terminalia approximately symmetrical, tergite X not medially divided; hind basitarsus with two bladders 2
– Male terminalia strongly asymmetrical, tergite X medially completely or incompletely divided; hind basitarsus with one or two bladders 3
2. Alate; adult males not neotenous; Neotropical . . . . Clothodidae
– Apterous; adult males neotenous with simplified terminalia; central Palaearctic . . . . Paedembiidae
3. Left cercomeres completely fused and distinctly curved; right basal cercomere broad and short; males always apterous; eastern Australian . . . . Australembiidae
– Left cercomere fused or not; right basal cercomere elongate and slender; males apterous or alate 4
4. Mandibles sickle-shaped, apically pointed and not dentate or with small denticles; vein M_A not bifurcated; hind basitarsus with a single bladder; Nearctic and Neotropical . . . . Anisembiidae
– Mandibles robust, not sickle-shaped, generally with prominent teeth; vein M_A bifurcate or not; hind basitarsus with one or two bladders 5
5. Tergite X incompletely divided longitudinally, with distinct sclerotized basal connection between hemitergites, (in Archembiidae and Scelembiidae comprised of only slender basal connection) 6
– Tergite X completely divided longitudinally with distinct membranous area between hemitergites 9
6. Tergite X nearly completely divided with only slender basal connection between hemitergites; basal left cercomere in most species with prominent medial process bearing small echinulations (lobe variable in *Pararhagadochir*, prominent but not echinulate in *Conicercembia* and absent in *Pachylembia*) 7
– Tergite X with broad connection between hemitergites 8
7. Anal region of wings not expanded; medial flap of tergite X not elevated and without a sclerite in posterior membrane of tergite IX; Neotropical and Afrotropical . . . . . Scelembiidae
– Anal region of wings moderately expanded; medial flap of tergite X elevated or with a distinct sclerite in posterior membrane of tergite IX; Neotropical . . . . Archembiidae
8. Vein M_A with single branch; cosmopolitan . . . . Oligotomidae
– Vein M_A bifurcate; Neotropical (with numerous undescribed taxa apparently Afrotropical and Oriental) . . . . . Teratembiidae
9. Vein M_A with single branch 10
– Vein M_A bifurcate 11
10. Left cercomeres fused, sometimes incompletely with suture visible between cercomeres; with two bladders on hind basitarsus; Australian . . . . Notoligotomidae
– Left cercomeres not fused; with one bladder on hind basitarsus; Neotropical . . . . Andesembiidae
11. Left cercomeres fused, sometimes incompletely with suture visible between cercomeres; basal cercomere without echinulations 12
– Left cercomeres not fused (a few rare taxa fused); basal cercomere clavate or with distinct medial lobe bearing small echinulations; Palaearctic, Afrotropical and Oriental . . . . Embiidae
12. Antennae with elongate setae; wings without maculae; Oriental . . . . Ptilocerembiidae

– Antennae without elongate setae; wings with white maculae; Oriental . . . . Embonychidae

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/j.1365-3113.2012.00628.x

Table S1. Taxon sampling, voucher codes, collecting data and GenBank numbers. Taxonomy follows classification prior to changes introduced in text.

Table S2. Primers used for amplification and sequencing.

Table S3. Amplification conditions used in PCR reactions.

Table S4. Characters included by Szumik *et al*. (2008) but excluded in this analysis with explanations.

Table S5. Morphological characters analysed for Embioptera and outgroups. Characters marked with '+' are treated as additive. $ = polymorphic, states 0,1; ? = unknown; − = inapplicable.

Nexus files. All data including morphology and aligned molecular data. Morphology, 16S, 18S, 28S, CO1, H3.

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Appendix

Morphological characters analysed in the cladistic analysis of Embioptera. Number in parentheses refer to corresponding character numbers in Szumik *et al*. (2008). Characters in Szumik *et al*. (2008) not included here are presented in Table S4 along with an explanation for the exclusion. See further discussion under Morphology section above.

General

0(0). Male development. (0) not neotenous; (1) neotenous. Males of some species seemingly have, especially, the head and thorax under-developed relative to males in other species.

1(2). Ecdysial longitudinal white band on thorax and abdomen. (0) absent; (1) present.

Head

2(3). Male mandible shape. (0) with incisor and molar areas not differentiated; (1) with incisor and molar areas well differentiated. Szumik *et al*. (2008) coded this with three states, but their states 1 and 2 did not appear to be adequately differentiated in the taxa to which the states were assigned, and these two states were combined into state 1.

3(4). Male mandible shape. (0) not elongate and sickle-shaped, apex with multiple teeth. (1) elongate, sickle-shaped, apex acute without multiple teeth.

4(6). Number of molar teeth on left and right mandibles of males (additive). (0) 3–2; (1) 2–1; (2) 1–1.

5(8). Incisor position on mandibles. (0) not concentrated at apex of mandible; (1) concentrated at apex of mandible.

6(11). Convexity on the lateral margin of mandibles. (0) absent; (1) present.

7(14). Anterior margin of clypeus in males (additive). (0) concave; (1) straight; (2) convex.

8(15). Anterior margin of clypeus in females. (0) concave; (1) straight.

9(16). Epistomal sulcus in males. (0) medial discontinuous externally; (1) continuous. Szumik *et al*. (2008) referred to the ‘episomal’ sulcus, but presumably meant ‘epistomal’.

10(17 in part). Ecdysial suture in males. (0) absent; (1) present. The condition of this suture was coded in a single additive character by Szumik *et al*. (2008). It is included here as two characters because the state ‘absent’ in this character is not logically homologous with the various conditions of the ‘present’ state relegated to the following character.

11(17 in part). Ecdysial suture in males. (0) carinate; (1) a pigmented line. Those taxa without an evident ecdysial suture in character 10 are scored as inapplicable for this character.

12(18 in part). Ecdysial suture in females. (0) absent; (1) present. Szumik *et al*. (2008) presented this character as a single additive character. See character 10 for a description of the treatment of that similar character in males.

13(18 in part). Ecdysial suture in females. (0) prominent and distinctly carinate; (1) not prominent, represented by a pigmented line. See character 12.

14(21 in part). Length proportions of scape and pedicel. (0) scape = pedicel; (1) scape > pedicel. This character and the following were combined into one additive character by Szumik *et al*. (2008), but this does not appear justifiable from the standpoint of homology and it is not treated as additive here. 0, 1 and 2.

15(21 in part). Length proportions of flagellomere I and pedicel. (0) flagellomere I = pedicel; (1) flagellomere I > pedicel. 0 = 0, 1 = 1, 2 = 0

16(22). Apical antennomeres in males. (0) not pigmented; (1) pigmented, similar to other antennomeres.

17(23). Apical antennomeres in females. (0) not pigmented; (1) pigmented, similar to others.

18(26). Male mentum. (0) not sclerotized; (1) sclerotized.

19(27). Male submentum, anterior margin. (0) membranous, not well defined; (1) straight; (2) concave; (3) convex. Szumik *et al*. (2008) used a complicated cost matrix for this character, although it is not clear that such a matrix is warranted. It is treated here as a single, multistate, nonadditive character.

20(28). Male submentum, width of base. (0) broader than anterior margin; (1) subequal to anterior margin.
21(31). Male submentum, surface. (0) with two deep concavities, or fovea, one on each side; (1) with one shallow concavity; (2) without concavity. Szumik *et al*. (2008) treated this character as additive, but it is not clear that the homology assessment justifies additivity, and it is not treated as additive here.

Thorax

22(32). Male prothorax. (0) not pigmented; (1) pigmented.
23(33). Female prothorax. (0) not pigmented; (1) pigmented.
24(34). Female mesoprescutum. (0) not divided into two sclerites; (1) divided into two sclerites, one on each side.
25(35). Mesoacrotergite (additive). (0) undivided; (1) partially divided medially; (2) completely divided medially into two sclerites, one on each side.

Legs

26(36). Medial bladder (pulvilli) on hind basitarsus in males. (0) absent; (1) present.
27(37). Medial bladder on hind basitarsus in females. (0) absent; (1) present.
28(38). Medial bladder size in males. (0) large, $>0.5 \times$ width of basitarsus; (1) small, $<0.4 \times$ width of basitarsus.
29(40). Medial bladder position in males (additive). (0) basal; (1) medial, (2) apical.
30(41). Medial bladder position in females (additive). (0) basal; (1) medial, (2) apical.
31(49). Coxal pigmentation in males. (0) absent; (1) present.

Wings (only in male)

32(51). Wings. (0) absent; (1) present. This character was coded with three states by Szumik *et al*. (2008) who included a state for brachyptery. Because that state seemingly grades into full-sized wings across the group (and within a species, in some cases), we have coded brachyptery and fully winged as simply 'wings present'. A number of taxa (e.g. *Embia* species, *Anisembia* species) were coded incorrectly for this by Szumik *et al*. (2008) because they are polymorphic for wings present and absent. These were recoded for this analysis. Those taxa with wings absent (but not those that are polymorphic) were coded as ambiguous for all the following wing characters.
33(52). Anal area in both anterior and posterior wings. (0) not expanded; (1) expanded.
34(54). M_A. (0) not bifurcated; (1) bifurcated.
35(56). Cu. (0) not furcated; (1) bifurcated.
36(59). R_1–$R_S + M_A$ cross-veins. (0) absent; (1) present.
37(61). R_S–M_A cross-veins. (0) absent; (1) present.
38(62). R_S–M_{A1} cross-veins. (0) absent; (1) present.
39(63). M_A–M_P cross-veins. (0) absent; (1) present.
40(64). M_{A1}–M_{A2} cross-veins. (0) absent; (1) present.
41(65). M_{A2}–M_P cross-veins. (0) absent; (1) present.
42(66). M_P–Cu_A cross-veins. (0) absent; (1) present.
43(68). Cu–A cross-veins. (0) absent; (1) present.

Abdomen

44(81). Abdominal laterotergites on I–VIII in males. (0) comprised of a single sclerite per side; (1) divided into two sclerites, on anterior and one posterior.
45(82). Abdominal laterotergite in females. (0) comprised of a single sclerite; (1) divided into two sclerites.
46(83). Abdominal lateral white band in males. (0) absent; (1) present.
47(84). Abdominal lateral white band in females. (0) absent; (1) present.

Female terminalia

48(85). First valvifers. (0) well developed and clearly separated from medial sclerite; (1) well developed and partially separated from medial sclerite; (2) differentiated from medial sclerite by two emarginations on posterior margin; (3) inconspicuous, differentiated from medial sclerite only by difference in pigmentation. Szumik *et al*. (2008) coded this character as additive, but here it is coded as nonadditive. Outgroup taxa were coded based in large part on explanations by Klass (2008), Klass *et al.* (2003) and Klass & Ulbricht (2009).
49(87 in part). Posterior margin of medial sclerite. (0) convex; (1) straight. This character was coded with three additive states by Szumik *et al*. (2008), but here we have divided their character into what appears to be a more logical two characters. Character 49 emphasizes the states 'convex'or 'straight' and character 50 includes only the convex state which may be 'not emarginate' or 'emarginate' but which is ambiguous for those taxa coded 'straight' for this character.
50(87 in part). Posterior margin of medial sclerite. (0) not emarginate; (1) emarginate. See discussion under character 49.
51(88). Posterior margin of second valvifers (ninth sternum, Ross, 2000). (0) bilobed; (1) convex, (2) straight. Szumik *et al*. (2008) coded this character as additive, but this does not necessarily follow from the states involved, and the character is not treated as additive here.

Male terminalia

52(90). Apical cercomere. (0) not pigmented; (1) pigmented.
53(91). Basal cercomere. (0) not strongly curved, (1) strongly curved.
54(93 in part). Ratio between lengths of basal and apical left cercomeres (additive). (0) apical cercomere length > basal cercomere length; (1) lengths subequal; (2) apical cercomere length $= 0.5$–$0.9 \times$ basal

cercomere length; (3) apical cercomere length much shorter, <0.5 × length of basal cercomere. This character and the following were coded as the same character with additive states by Szumik *et al*. (2008). It is not clear, however, that cercomere fusion is logically related to the ratio of lengths of the cercomeres in taxa with two clear segments, so this character was divided into two independent characters for this analysis with fusion incorporated into character 55. Taxa coded for state 1 in character 55 (see below) were coded as inapplicable for this character.

55(93 in part). Left cercomeres. (0) not fused; (1) fused. See character 54. Szumik *et al*. (2008) coded both partial fusion and complete fusion as separate states (in their character 93, see our character 54). However, they did not, in fact, code any taxa as completely fused (their state 5 of character 93), possibly as an oversight because there are numerous taxa that have the cercomeres entirely fused with no evidence of a suture between them (such as australembiids). Relatively fewer taxa (such as notoligotomids) have the cercomeres apparently fused with a moderately distinct suture remaining between them. This condition is difficult to assess, however, and only the clearly unfused or relatively clearly fused condition is coded here (regardless of whether a vague suture is visible or not).

56(97). Medial process on left basal cercomere. (0) absent; (1) present. Szumik *et al*. (2008) are not particularly clear or precise about which process on the left basal cercomere is referenced in their various characters. In many taxa there is a more-or-less distinctive prominence or process along the medial surface of the left basal cercomere which occurs roughly at midlength or more apically along the cercomere (see character 58). There may also be another process located more proximally along the cercomere (see character 59). Characters 56 to 58 refer to the more apically- or medially-located process. We assume homology between these, but not between these and the proximal processes. There are some taxa with both processes.

57(99). Length of medial process on left basal cercomere. (0) < width of cercomere; (1) > width of cercomere.

58(100). Position of medial process on left basal cercomere. (0) apical; (1) at midlength.

59(105). Proximal process on left basal cercomere. (0) absent; (1) present.

60(111). 10° tergite condition. (0) one sclerite; (1) partially divided longitudinally into two subequal sclerites; (2) completely divided longitudinally into two subequal plates; (3) obliquely divided into two unequal sclerites; (4) divided medially with division extending transversely to right side. Szumik *et al*. (2008) coded this character as additive. Whereas some in the series might be justifiably additive, it is not clear that the entire series of states is justifiably so, and this character is not treated as additive here. The condition of tergite 10 will require considerably more investigation to develop better coding and scoring in Embioptera. This character, as coded here, should be considered provisional.

61(117). LPP. (0) not fused to HP; (1) fused to HP.

62(118). EP. (0) not fused to 10RP2; (1) fused to 10RP2.

63(119). 10RP2. (0) absent, (1) present. Szumik *et al*. (2008) coded the conditions of 10RP2 as separate states in this character (which would more defensively be included in a separate character), but those conditions (‘present as a small node’ versus ‘well developed’) appear to be relatively gradational in the included taxa and are not coded here. The previous character and the following three characters are scored as inapplicable for taxa with the absent state for this character.

64(120). 10RP2 shape. (0) broad; (1) slender. This wording is a reinterpretation of Szumik’s *et al*. (2008) states, but seems to be accurate. Szumik *et al*. (2008) coded several taxa with state 2, but did not describe a state 2. Those taxa coded with state 2 by Szumik *et al*. (2008) should apparently be coded as state 1.

65(121). Microtrichiae on 10RP2. (0) absent; (1) present.

66(123). Longitudinal and laminate keels on 10RP2. (0) absent; (1) present.

67(126). Small, echinulate process on medial margin of 10R. (0) absent; (1) present.

68(127). Anteromedial angle of 10L. (0) not excavated; (1) excavated.

69(128). Posterior margin of 10L (additive). (0) convex; (1) straight; (2) concave.

70(135). 10LP origination (additive). (0) at posteromedial angle; (1) medially along posterior margin of 10L; (2) at anteromedial angle. This character was coded by Szumik *et al*. (2008) as additive, but with states 0 and 1 reversed with respect to our coding which seems more defensible with respect to additive coding.

71(136). 10LP apex. (0) not expanded; (1) expanded.

72(140 in part). Longitudinal carina on 10LP1. (0) absent; (1) present. This character and the following were included in one additive character by Szumik *et al*. (2008), but it is here divided into two characters to reflect absence/presence and differences in the present condition (character 73).

73(140 in part). Longitudinal carinae on 10LP1. 0) one; (1) many. See character 72. This character is coded as ambiguous for those coded ‘absent’ in character 72.

74(141). Surface between 10LP and 10L. (0) not depressed; (1) depressed.

75(149). Longitudinal keel on 10RP1. (0) absent; (1) present.

76(152). Microtrichiae on 10RP1. (0) absent; (1) present.

77(155). LPP and RPP. (0) each well developed and subequal; (1) RPP reduced. Szumik *et al*. (2008) included an additional state for this character, but this seemed ambiguous and their states 1 and 2 were merged into a single state (1) for this analysis.

78(156). Small process with microtrichiae between LC1 and 10L. (0) absent; (1) present.

79(158). LPP sclerotization (additive). (0) entirely membranous; (1) partially membranous and partially sclerotized; (2) completely sclerotized.

80(160). Posteromedial angle of LPP. (0) without a process; (1) with a thornlike process; (2) with a prominent node; (3) with a flat hook. Szumik *et al*. (2008) coded these states as additive, but it is not clear that these states are logically additive and are treated as nonadditive in this analysis.

81(161). Small process on anterolateral angle of LPP. (0) absent; (1) present.

82(162). Microtrichiae on LPP. (0) absent; (1) present.

83(163). RPP sclerotization (additive). (0) entirely membranous; (1) partially membranous and partially sclerotized; (2) completely sclerotized. Szumik *et al*. (2008) included an additional state (3) refering to degree of sclerotization of RPP, but this state appeared indifferentiable from state 2 and was merged with state 2 in this analysis.

84(164). HP. (0) conspicuous, originates medially on H; (1) inconspicuous, arising more-or-less medially; (2) distinctly originating from right margin of H; (3) distinctly originating from left margin of H. Szumik *et al*. (2008) developed a complex cost matrix for this character that was not adopted for this analysis.

85(165). HP length. (0) $<$ length of H; (1) $>$ length of H.

86(167). Transversal carinae on HP. (0) absent; (1) present.

87(169). Microtrichiae on EP. (0) absent; (1) present.

88(170). EP shape. (0) inconspicuous; (1) broad and sclerotized; (2) narrow and sclerotized; (3) narrow and sclerotized with caudal apex expanded. Szumik *et al*. (2008) treated these states as additive, but we treat the states as nonadditive for this analysis.

89(175). Microtrichia on 10RP2. (0) absent; (1) present.

90(178). Medial basal area of 10T. (0) without triangular sclerite; (1) with a triangular sclerite.

91(180). RC1 shape. (0) not robust, short and broad; (1) robust, short and broad.

New characters not included in Szumik et al. (2008)

92. Silk glands on prothoracic basitarsus. (0) absent; (1) present.
93. Bladders on mesothoracic tarsi. (0) absent; (1) present.
94. Females. (0) not neotenous; (1) neotenous. See explanation above under ‘Morphology’.