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Phylogeny of embiopterans (Insecta)

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Abstract

A cladistic analysis of embiopterans, based on 157 species (representing 70% of the known genera) and 186 morphological characters, is presented, as well as a molecular analysis for 22 taxa using genes encoding 16S, 18S and 28S rDNA and COI. Species of all known families are included, except Andesembiidae Ross (specimens of which are in a private collection). The evidence presented supports the monophyly of four of the families (Australembiidae, Oligotomidae, Teratembiidae, and Anisembiidae). Notoligotomidae is paraphyletic and included within the Afro-neotropical family Archembiidae (which is also paraphyletic). The genera *Embia*, *Cleomia*, *Macrembia*, and *Dihybocercus* (Embiidae) form, together with Australembiidae, a group strongly supported by morphology; the position of the remaining genera of Embiidae has two quite different resolutions. Almost 80% of the genera of Anisembiidae recently described appear as either paraphyletic or polyphyletic. Contrary to the opinion of other specialists, the major groups as well as the monophyly of some families are supported by features which have been ignored in classical approaches to the systematics of Embioptera, such as the ovipositor and cephalic and leg structures, characters with an almost perfect fit.

The morphology of the male terminalia is the best documented structure in the literature on Embioptera; most of the groups in the order have been created and recognized almost solely on this basis. Needless to say, the male terminalia has a wide variety of processes—modified for copulation—which are so conspicuous that they have kept other potentially informative structures almost completely ignored in the traditional classification of Embioptera. Most of the current families and genera were described not only overestimating the value of just one structure but also on the basis of dubious theoretical justifications. New taxa that are extremely different from those belonging to families or genera already described (i.e. with relatively apomorphic character states with regard to their counterparts) are often used to erect new families or genera (e.g. Ross, 1984; the new genus *Pelorembia*, p. 41; Ross, 2003a; the new family Andesembiidae, p. 2), resulting in one or both groups being paraphyletic. Thus, there is no reason to believe that currently recognized groups are monophyletic units. In a preliminary cladistic study on the classification of the order (Szumik, 1996; which constituted the first attempt to understand the higher classification of the Embioptera), using 36 characters and 41 taxa, only two families—Anisembiidae and Australembiidae—appeared as monophyletic. That study and subsequent analyses at the family level (Szumik, 1994, 1998, 2004) revealed that many of the currently recognized genera are not monophyletic.

This paper reanalyses the problem of embiopteran phylogeny considering many more taxa and morphological characters, in order to test the current classification and analyse how new and old traits adjust to the resulting trees. Even with numerous recent additions to the alpha taxonomy of American Embioptera (Ross, 2001, 2003a,b), which raise the number of species from 280 to almost 400, the group is still small enough to attempt a study of comparative morphology encompassing essentially the whole group. Thus, an analysis using 157 taxa, which represent 70% of the genera and almost 40% of the known species (Table 1), is presented

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here. Many of the morphological traits used include characters potentially useful but rarely used before in the systematics of the Embioptera. Such is the case of female terminalia, wing venation, cephalic structures, and other thoracic and abdominal structures of females and males. Additionally, an analysis using 2672 aligned positions for 22 of the 157 taxa is also presented (see Table 1), as well as a comparison between the hypotheses obtained from the molecular and morphological data.

Materials and methods

Cladistic analysis

There is wide agreement in cladistics that all the available evidence—regardless of the source—should ideally be analysed in a combined way. However (as argued by Goloboff et al., 2008), computational or algorithmic limitations may make such combined analyses difficult or impossible to perform. In the present case, the morphological data—owing to high levels of homoplasy in some characters—are best analysed under implied weights (Goloboff, 1993), while the molecular data—owing to unequal sequence lengths—are best analysed under direct optimization (Wheeler, 1996). However, the direct optimization approach implemented in the program POY ver. 4 (Varon et al., 2007) does not include implied weighting (although POY ver. 3 has a very rudimentary version of this method). Thus, molecular and morphological data are here analysed separately, and the discussion is focused on both results.

Tree searches for the morphological data were made using implied weighting (implemented in TNT ver. 1.1, Goloboff et al., 2003b) under four different concavity values (see Table 2 for the cost of adding extra steps under each of the concavities used). This concavity sample means that the characters were weighted against their homoplasy during the search, varying from strongly to lightly. Thus, the resolution of the consensus should indicate to what extent the results depend on whether homoplastic characters are down-weighted strongly or mildly. The tree search for these analyses consisted of a combination of tree-drifting, sectorial search, and tree-fusing (Goloboff, 1999). To make sure that optimal trees had been obtained, the run continued until the minimum score was hit 20 times. WinClada (Nixon, 2002) was used to display the synapomorphies in common to the optimal trees of each concavity (although these synapomorphies were calculated with TNT; WinClada does not calculate them).

Table 1
Number of genera described for each family of the order and the number included here for the morphological (71%) and molecular study (19%), number of species described, and the number included in the morphological (40%) and molecular study (6%)

	Genera			Species		
Family	Known	Morph.	Mol.	Known	Morph.	Mol.
Clothodidae	4	3	2	17	10	2
Anisembiidae	24	13	3	111	32	3
Archembiidae	20	17	4	68	46	7
Embiidae	20	13	–	80	24	–
Teratembiidae	4	4	2	44	24	4
Andesembiidae	2	–	–	7	–	–
Oligotomidae	3	3	2	48	12	3
Australembiidae	2	2	1	17	6	2
Notoligotomidae	2	2	1	3	3	1
Total	81	57	15	395	157	22

Table 2
Character cost according to the number of extra steps (s) for the four concavity values (K)

$s\backslash K$	4	5	6	7
0	1.0	1.0	1.0	1.0
1	0.67	0.71	0.75	0.78
2	0.48	0.54	0.58	0.62
3	0.36	0.42	0.47	0.51
4	0.28	0.33	0.38	0.42
5	0.22	0.27	0.32	0.36
6	0.18	0.23	0.27	0.31
7	0.15	0.19	0.23	0.27
8	0.13	0.16	0.20	0.23
9	0.11	0.14	0.18	0.21
10	0.10	0.13	0.15	0.18
11	0.08	0.11	0.14	0.16
12	0.07	0.10	0.12	0.15
13	0.07	0.09	0.11	0.13
14	0.06	0.08	0.10	0.12
15	0.05	0.07	0.09	0.11
16	0.05	0.06	0.08	0.10
17	0.04	0.06	0.08	0.09
18	0.03	0.05	0.07	0.09
19	0.03	0.05	0.06	0.08
20	0.03	0.05	0.06	0.07
21	0.03	0.04	0.06	0.07
22	0.03	0.04	0.05	0.06
23	0.03	0.04	0.05	0.06
24	0.02	0.03	0.05	0.06
25	0.02	0.03	0.04	0.05
26	0.02	0.03	0.04	0.05
27	0.02	0.03	0.04	0.05
28	0.02	0.03	0.04	0.04
29	0.02	0.02	0.03	0.04
30	0.02	0.02	0.03	0.04
31	0.02	0.02	0.03	0.04
32	0.02	0.02	0.03	0.04
33	0.01	0.02	0.03	0.03
34	0.01	0.02	0.03	0.03
35	0.01	0.02	0.02	0.03
36	0.01	0.02	0.02	0.03
37	0.01	0.02	0.02	0.03
38	0.01	0.02	0.02	0.03
39	0.01	0.02	0.02	0.03
40–46	0.01	0.01	0.02	0.02
47–54	0.01	0.01	0.01	0.02

Tree search for the molecular data was performed by parsimony analysis under direct optimization and applied to a combined dataset including all sequence fragments. Six cost matrices were used, with the following costs for gap(extension):substitution equal to 2(2):1, 1(1):1, 2(1):2, 4(1):2, 6(1):2 and 8(1):2. The tree search protocol consisted of 40 cycles of TBR (Tree Bisection Reconnection) keeping two trees per replicate, manually stopping the run when the minimal length was hit more than eight times.

Finally, as molecular and morphological data were analysed separately, a semi-strict supertree (Goloboff and Pol, 2002) was calculated in order to determine which groups are supported by both the molecular and the morphological phylogenetic hypotheses. The semi-strict supertree was calculated by using the original trees from each analysis, given that combining strict consensus trees instead of the original trees may produce misleading results for combinable components (see Nixon and Carpenter, 1996; Goloboff and Pol, 2002).

Three types of support measures were applied to the morphological data: Bremer support (Bremer, 1994), relative Bremer support (Goloboff and Farris, 2001), and symmetric resampling (Goloboff et al., 2003a). The Bremer supports were calculated from about 30 000 suboptimal trees, found in two rounds, first applying TBR from the optimal trees saving up to 15 000 trees a fit up to 1 unit worse, and then another 15 000 trees up to 1.5 units worse (searching suboptimal trees in stages precludes overestimation of supports for weakly supported groups). Each replication (500 altogether) of the symmetric resampling was done with five random addition sequences, each followed by TBR, random and exclusive sectorial searches, and five rounds of tree-drifting, keeping the final tree for each random addition sequence. The support for each group was measured with the GC value, which is the difference in frequency between the group and the most frequent contradictory group (Horovitz, 1999; Goloboff et al., 2003a).

Support measures for the molecular data were calculated using the Jackknife method as implemented in POY ver. 4 (Varon et al., 2007).

Taxon sampling

The morphological data set includes 157 species from 57 genera in eight families (see Table 1). All the species were scored using as many specimens as possible (type and common specimens), with the exception of 12 species which were scored solely on the basis of the original description (see supplementary Appendix S1), given that specimens of those species were not available. The molecular data includes 22 species (see Table 1, Appendix S3). Although the species sequenced are only a fraction of the number of terminals in the morphology-based analysis, the terminals to be sequenced were chosen carefully so that all the major groups would be represented (with the exception of Embiidae *sensu lato* for which fresh specimens were not available).

Clothoda (Clothodidae) was selected as an outgroup because the genus is widely considered to be the most primitive form in the order (for discussion, see Ross, 1987; Szumik, 1996, 2004). Hence, the monophyly of Clothodidae is not tested here.

The family Andesembiidae (Ross, 2003a) is not included here as types and common material are deposited in Ross's private collection, which is not publicly available. Based on the brief original description, it seems that Andesembiidae is closely related to the genus *Microembia* (Anisembiidae); both families are distinguishable—according to Ross—only by the male mandibles (Ross, 2003a, p. 2).

Also excluded from the analysis are 11 genera of Anisembiidae (Ross, 2003b) and seven genera of Embiidae *sensu lato* (Ross, 2001). These taxa are undistinguishable from those presented here, at least for the characters used here; most of them are monotypic and present only in Ross's private collection.

Morphological data

In total, 186 morphological characters (Appendix S1) have been scored (see Appendix S2 for a more detailed description of characters and states). Most of these 186 characters (such as wings or female terminalia) are not commonly used in the alpha taxonomy of Embioptera. Three of the characters depict general features: adult or neotenic features in males, sexual dimorphism, and presence or absence of an ecdysial white band on the thorax and abdomen. Cephalic characters comprise from the most common structures described in species diagnoses—e.g. number of mandibular teeth—to traits poorly or never described, such as antennomere shape, mandibular shape, cephalic sulci, and sutures.

The presence or absence of a middle bladder on the hind basitarsus is the only leg character previously used by other authors (e.g. Ross, 1970). The distribution of the setae is included, as well as the shape and position of the bladder (for more discussion, see Szumik, 1996, 2004).

The origin of veins RS + Ma and Mp was described and applied only in a cladistic framework (Szumik, 1994, 1996, 2004), and this character appeared to be highly informative within the major groups of the order. Other wing characters included here are the position of cross-veins and some features of the longitudinal veins (forked vs. unforked, their degree of development, etc.).

Female Embioptera have a rudimentary ovipositor which consists of a central plate (8°St), two lateral bands (1°Vfs) and one posterior unsclerotized band (2°Vfs) (terminology as in Ross, 2000). Except for the work of Szumik (1996, 2004, and others), female terminalia had been completely ignored in lower and higher taxonomy

of Embioptera; perhaps this was obscured by the huge number of characters in its counterpart, the male terminalia. In fact, the female terminalia has a low variation within Embioptera but this variation—only four general features, divided here into seven characters—is potentially useful because it seems to correlate very well with the major lineages.

There are 95 characters depicting male terminalia; this means that 50% of the morphological characters used in this analysis come from this structure.

Molecular data

The molecular data set consists of gene sequences for 16S, 18S and 28S rDNA and COI for 22 taxa (Table 1) with a total of 2672 aligned positions (Appendix S3).

Results

The semi-strict supertree (Fig. 1) of the trees from the molecular data (six types of step matrices) and the morphological data (four concavity values) displays four families, Australembiidae, Anisembiidae, Oligotomidae, and Teratembiidae, as well as the groups formed by Teratembiidae + Oligotomidae, Archembiidae + Notoligotomidae, and Australembiidae + Embiidae (in part).

The sister group of Clothodidae—the cladograms were rooted with Clothodidae as monophyletic—appears as a large basal polytomy. First, this lack of resolution is not due to the morphological trees, which show Oligotomidae + Teratembiidae as sister group to the rest of Embioptera, but to multiple molecular trees, each of which proposes a different resolution (see consensus of molecular trees in Fig. 2), among which is included (in part) the resolution displayed by the morphologhy trees. Secondly, some taxa (*Archembia dilata*, *Biguembia multivenosa*, and *Notoligotoma hardyi*) float among different positions in the molecular trees; when these three taxa are removed from the cladograms—not from the data matrix—some additional groups are recovered (Fig. 3).

The molecular hypotheses do show some groupings consistent with the morphological trees; for example, the groups of Teratembiidae + Oligotomidae, Australembiidae, Anisembiidae, and *Pararhagadochir* are recovered (Fig. 3). Finally the agreement subtree of the molecular trees retains only half of the taxa analysed, where *Pararhagadochir*, Oligotomidae, and Teratembiidae appear monophyletic (see Fig. 4).

Morphological trees

The strict consensus of the most parsimonious trees from the four concavities (Fig. 5) is well resolved and the main groups are recovered. There are either partial polytomies at the base of some families (e.g. Embiidae, Fig. 5; Anisembiidae, Fig. 9; and Archembiidae, Fig. 16) or complete polytomies for other families (e.g. Oligotomidae is fully unresolved, Fig. 6); in general, this kind of inconsistency is a problem of rooting of the family, with polytomies resulting from only two very different rootings (see below).

Hitherto, the idea that male terminalia is the only valid trait to differentiate embiopterans has been very common. However, the resolution of the major groups obtained here is supported by other traits as well, such as the rudimentary ovipositor, and cephalic and leg structures. One of the features is the ovipositor, whose level of fusion between the 1st valvifers and the 8th sternite, and the shape of the 2nd valvifers, adjusts almost perfectly to the cladograms and defines several major groups (Fig. 5). There are two striking apomorphies, one onto the most basal group of the order, the genus *Clothoda* (Fig. 5), where the rudimentary ovipositor is almost absent; additionally, this may be correlated with the simplicity of the male terminalia. The other apomorphy is present in Australembiidae (Fig. 5), where the well-defined valvifers appear to be the most primitive condition. According to Ross (2000) the australembiid ovipositor is a case of neoteny and should be related to the general neotenic condition of the males of Australembidae.

Male mandibles are one of the most complex structures, with a great variety of shapes, used to retain the female during copulation. Because of their complexity, the mandibles provided many characters, supporting some groups. Just a few characters of male terminalia adjust well to the cladograms (e.g. the cleavage of 10T, the level of plate fusion, and the shape of some processes). The male terminalia synapomorphies shown in Fig. 5 clearly reflect the gradual transformation from a perfectly symmetric terminalia (*Clothoda*) into an increasingly asymmetric one.

Colour characters (degree of pigmentation) have been used in alpha taxonomy to distinguish genera or species (Ross, 1960, 2001). Coloration characters are doubtfully reliable because of their extremely high variability (even with age, for the same individual). In the cladistic analysis of Archembiidae (Szumik, 2004) these characters seemed to exert little influence in the classification. In the present analysis, these characters again have a poor fit to the tree(s), and receive very low weights (thus, a similar topology is obtained when these characters are excluded).

Major lineages of Embioptera

Teratembiidae and Oligotomidae are a well-supported group in the present analysis (Table 3). Ross (1970) had grouped these two families in his suborder 'C', but

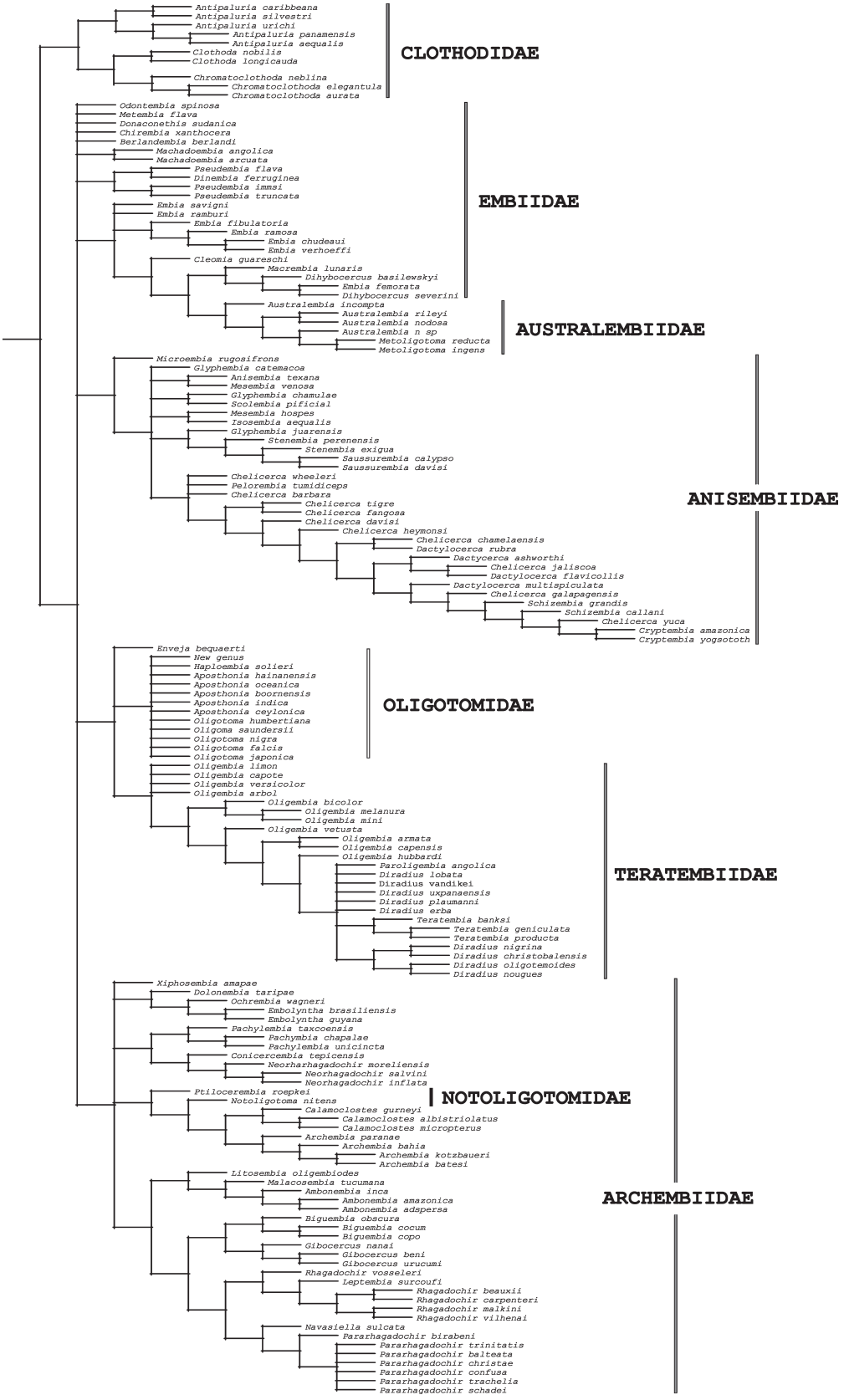


Fig. 1. Semi-strict consensus of the optimal trees of the molecular and morphological data (rooting in Clothodidae).

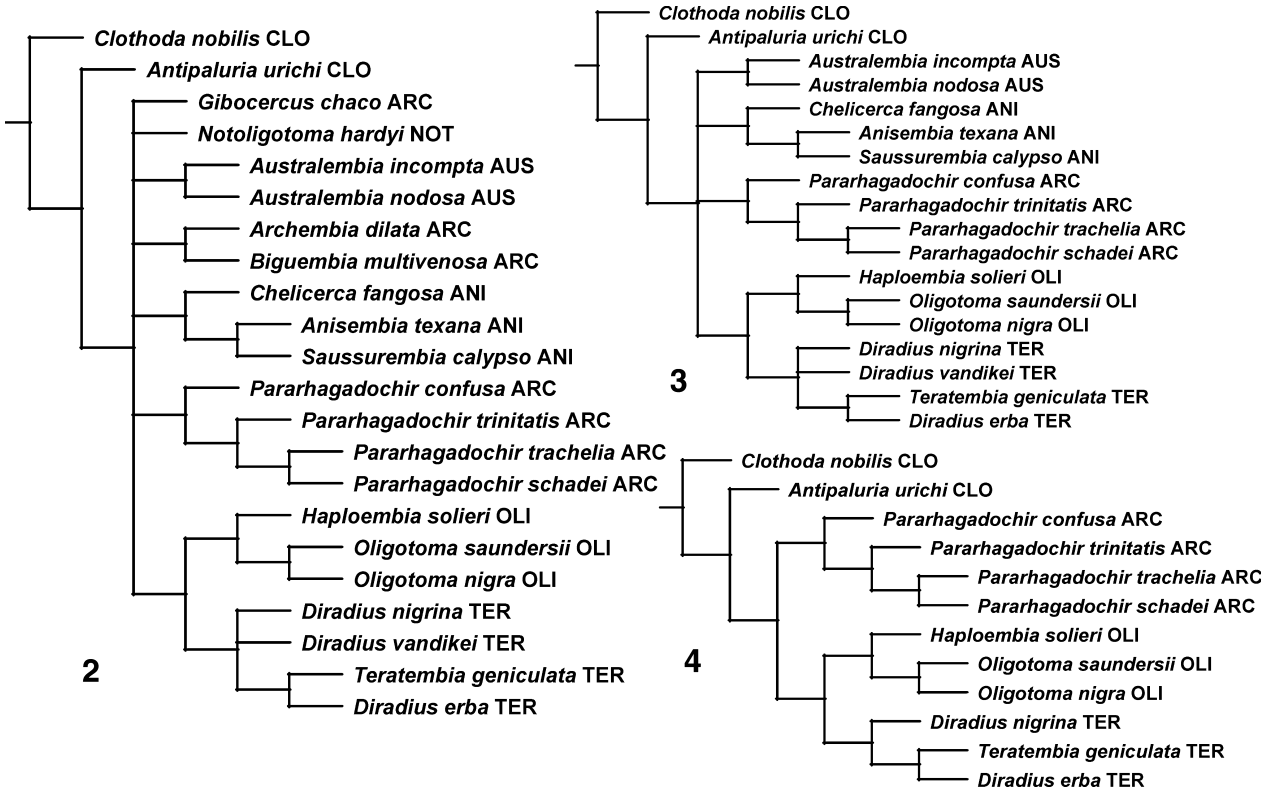


Fig. 2. Strict consensus of the optimal trees of molecular data.
Fig. 3. Strict consensus of the optimal trees of molecular data with *Archembia dilata*, *Biguembia multivenosa*, and *Notoligotoma hardyi* deactivated.
Fig. 4. Agreement subtree of the optimal trees of molecular data. CLO, Clothodidae; AUS, Australembiidae; ANI, Anisembiidae; ARC, Archembiidae; NOT, Notoligotomidae; TER, Teratembiidae; OLI, Oligotomidae.

provided no justification for this. Davis (1940), by contrast, held that Teratembiidae and Oligotomidae were not closely related, arguing that their shared characters were parallelisms. Since the earliest cladistic analyses of embiopterans (Szumik, 1994) to the present one, these two families have always formed a monophyletic group, thus supporting Ross's conclusion, rather than Davis's. Unlike previous analyses, both families are monophyletic here (Fig. 6). The genus *Enveja* [included as an Embiidae by Davis (1940) and included as the only member of 'Suborder B' by Ross (1970)] now appears in two possible positions, as the sister group of either Teratembiidae or Oligotomidae + Teratembiidae (Fig. 6). The group of *Enveja* plus these two families has high support (Table 3) and is defined by several synapomorphies (see Fig. 6).

As demonstrated in previous analyses (Szumik, 1994, 1996), the generic limits proposed on the basis of geographical distribution by Ross (1970) for *Oligotoma* and *Aposthonia* (two very species-rich genera, Figs 7 and 8) are not supported by morphological evidence.

The monophyly of the Afro-american Teratembiidae (Fig. 7) is well supported (Table 3), mostly by male traits. Although the groups which include *Teratembia* + *Diradius* + *Paroligembia*, as well as the monophyly of *Teratembia* and *Diradius*, are recovered here and in previous analyses (Szumik, 1994, 1996), only the genus *Teratembia* has high support. Because *Oligembia* was traditionally defined on the basis of plesiomorphic traits (which in fact define the family Teratembidae), it appears paraphyletic as in a previous analysis (Szumik, 1994).

After the recent alpha-taxonomic work of Ross (2003b), Anisembiidae seems to be the richest and most diverse family of Embioptera. This exclusively American family (Fig. 10) now contains 24 genera, 19 of which seem to have been proposed only because they are so differentiated from the others as to justify a separate group. More than half of those new genera are included here (represented by two or more species) and, as shown in the consensus (Fig. 9), none of them appears as a monophyletic group. Actually, a fuller analysis of Anisembiidae, while desirable, is impossible at the present time, given that all these new species are deposited in Ross's private collection, and are out of reach. In contrast to their constituent genera, the monophyly of Anisembiidae itself is consistent and has high support (see Table 3). Szumik (1996) considered *Dactylocerca* and *Pelorembia* as junior synonyms of *Chelicerca*; Ross (2003b) resurrected *Dactylocerca* and

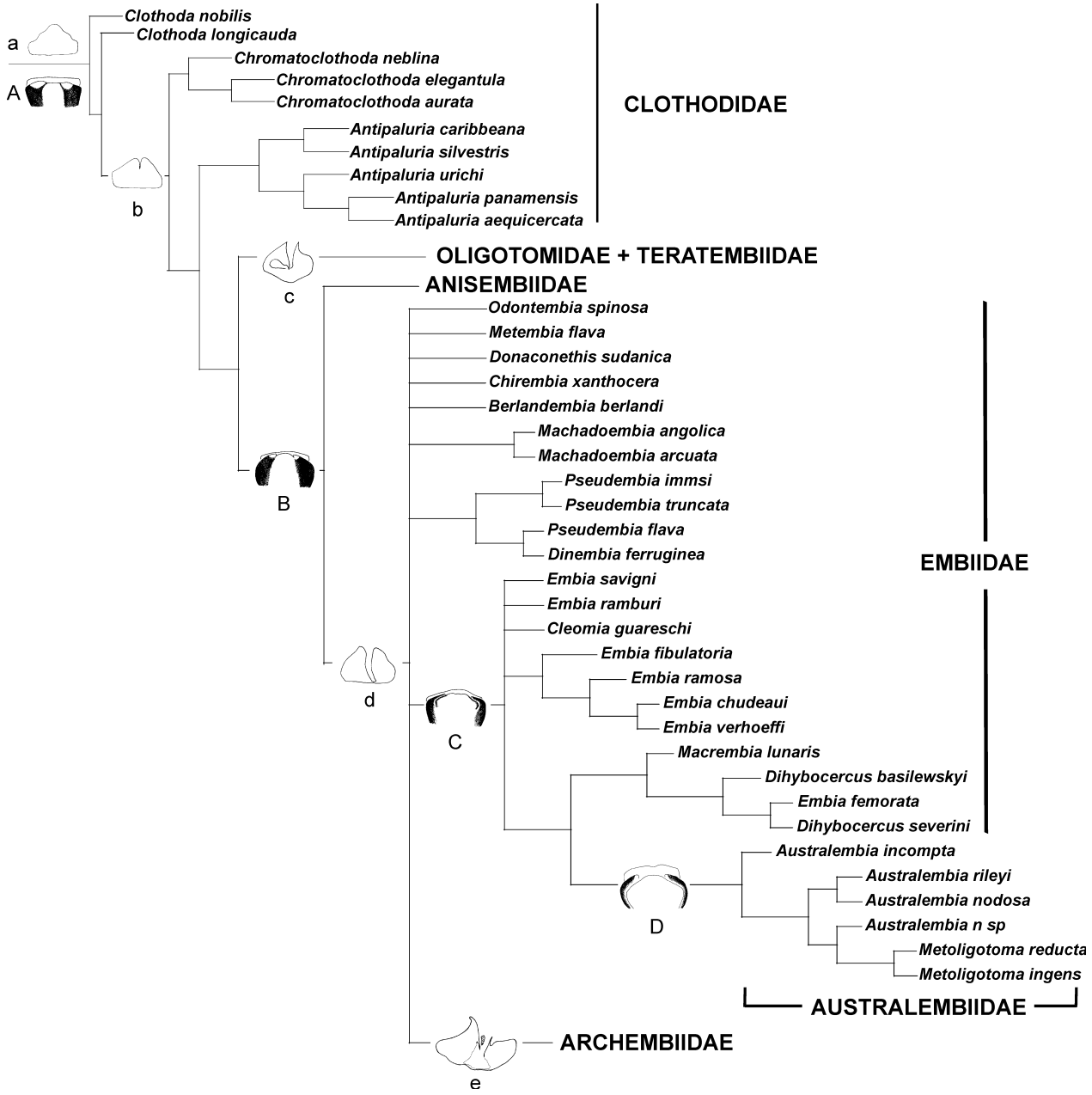


Fig. 5. Strict consensus of the optimal trees of morphological data (rooting in *Clothoda nobilis*). (a–e) Male terminalia (10° tergite shape): (a) one plate; (b) partially divided into two subequal plates; (c) longitudinal and transverse divided; (d) totally and longitudinal divided into two subequal plates; (e) longitudinal and oblique divided into two different plates. (A–D) Female terminalia (1st valvifers): (A) inconspicuous, differentiated from central plate by degree of pigmentation; (B) differentiated from central plate by two notches on caudal margin; (C) partially separated from central plate; (D) well developed and clearly separate from central plate.

Pelorembia, and added *Schizembia* and *Cryptembia*; not surprisingly, with the addition of new characters and species, these five genera continue forming a well-supported monophyletic group (Fig. 9, Table 3) with some synapomorphies with almost no homoplasy, such as hypandrium process shape, whose state transformation is perfectly adjusted to the cladogram. A further analysis of the family should probably take us back to the idea of the *Chelicerca* group (as proposed by Szumik, 1996). The same applies to the *Stenembia* and *Saussurembia* (Fig. 11) groups.

Historically, Embiidae has been defined by features—e.g. a bladder in the hind basitarsus, a furcated medial vein, and a setose apical process of the left cercus—which are convergences or synapomorphies of a larger group of Embioptera (Szumik, 2004). On the

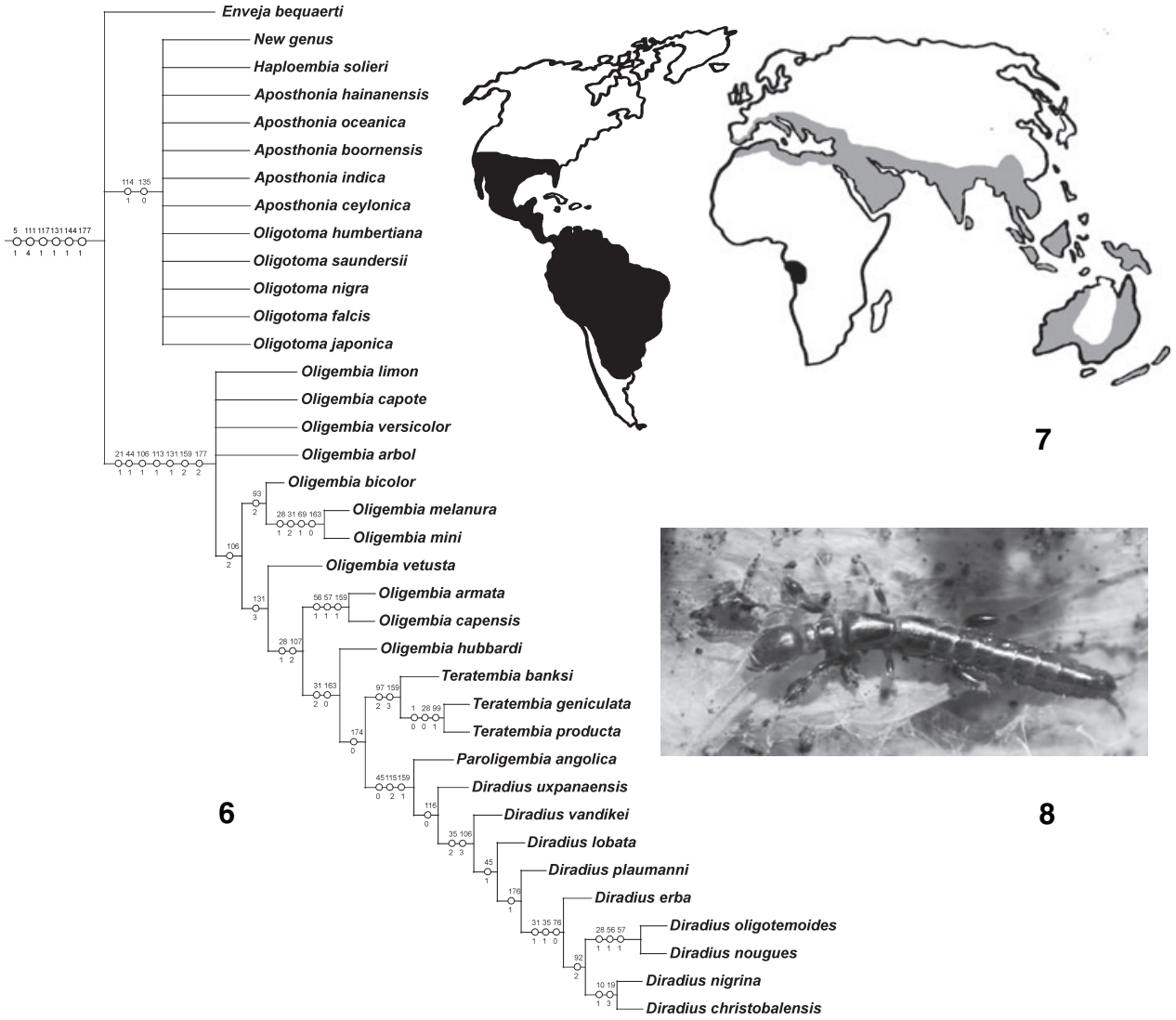


Fig. 6. Oligotomidae and Teratembiidae, resolution according to morphological data.
Fig. 7. Distribution map of Teratembiidae (black) and Oligotomidae (grey).
Fig. 8. *Oligotoma nigra*, female (photographed by J. Edgerly).

other hand, Australembiidae Ross 1963 was the result of dividing the well-known genus *Metoligotoma* into two genera: the new one *Australembia*—with two plesiomorphic species—and the remaining *Metoligotoma*. As in the preliminary analysis of the order (Szumik, 1996), the type genus *Australembia* appears paraphyletic in terms of *Metoligotoma*. In the present analysis, the poor resolution of Embiidae is due to the fact that there are two resolutions: one where Embiidae is paraphyletic in terms of Australembiidae (Fig. 12; see Fig. 13 for general distribution of both families), the other in which some genera of Embiidae are the sister group to Australembiidae and other genera are the sister group to Archembiidae (Fig. 14). These quite different resolutions may be due in part to the fact that most of their species are known only by the types, and very few females are known (Fig. 15).

Archembiidae was recently revised and some genera were re-delimited or synonymized (Szumik, 2004). The nomenclatorial changes (as well as familial synapomorphies) proposed in that work are consistent with the current cladogram. Szumik (2004) holds that some African genera of Embiidae should probably be transferred to Archembiidae; here only the monotypic genus *Leptembia* (Fig. 16) appears within Archembiidae. Actually, the main difference compared with the previous analysis lies in Notoligotomidae being part of the Afro-neotropical Archembiidae (Figs 16–18). In previous analyses (Szumik, 1996) genera of the Notoligotomidae were basically two floating terminals that

Table 3
Bremer support (BS), relative Bremer support (RBS) and symmetric resampling (SM) within each concavity (*K*) in the major groups (i.e. relationships between families, families themselves, and some internal groups)

	BS				RBS				SM			
Group*K*	4	5	6	7	4	5	6	7	4	5	6	7
A	0.66	0.99	0.72	0.65	77	80	86	79	96	96	96	97
B	1.49	1.40	0.73	0.64	100	100	78	77	99	97	94	90
C	0.19	0.20	0.19	0.21	24	30	33	41	17	36	42	43
D	0.43	0.36	0.33	0.31	41	40	38	34	76	71	69	68
E	1.40	1.40	1.40	1.40	100	100	100	100	99	94	92	91
F	0.86	0.78	0.96	0.88	76	76	88	89	97	97	98	97
G	0.64	0.57	0.72	0.68	59	60	70	70	89	87	88	88
H	0.54	0.47	0.44	0.33	45	48	47	50	69	73	71	67
I	0.30	0.26	0.33	0.16	35	34	39	40	29	27	26	21
J	0.68	0.61	0.61	0.56	70	68	67	67	66	77	79	80

A, non-Clothodids; B, *Enveja* + Oligotomidae + Teratembiidae; C, Anisembiidae + Australembiidae + Embiidae + Archembiidae + Notoligotomidae; D, Oligotomidae; E, Teratembiidae; F, Anisembiidae; G, *Chelicerca*; H, Australembiidae + Embiidae + Archembiidae + Notoligotomidae; I, *Dihybocercus* + Australembiidae; J, Archembiidae + Notoligotomidae.

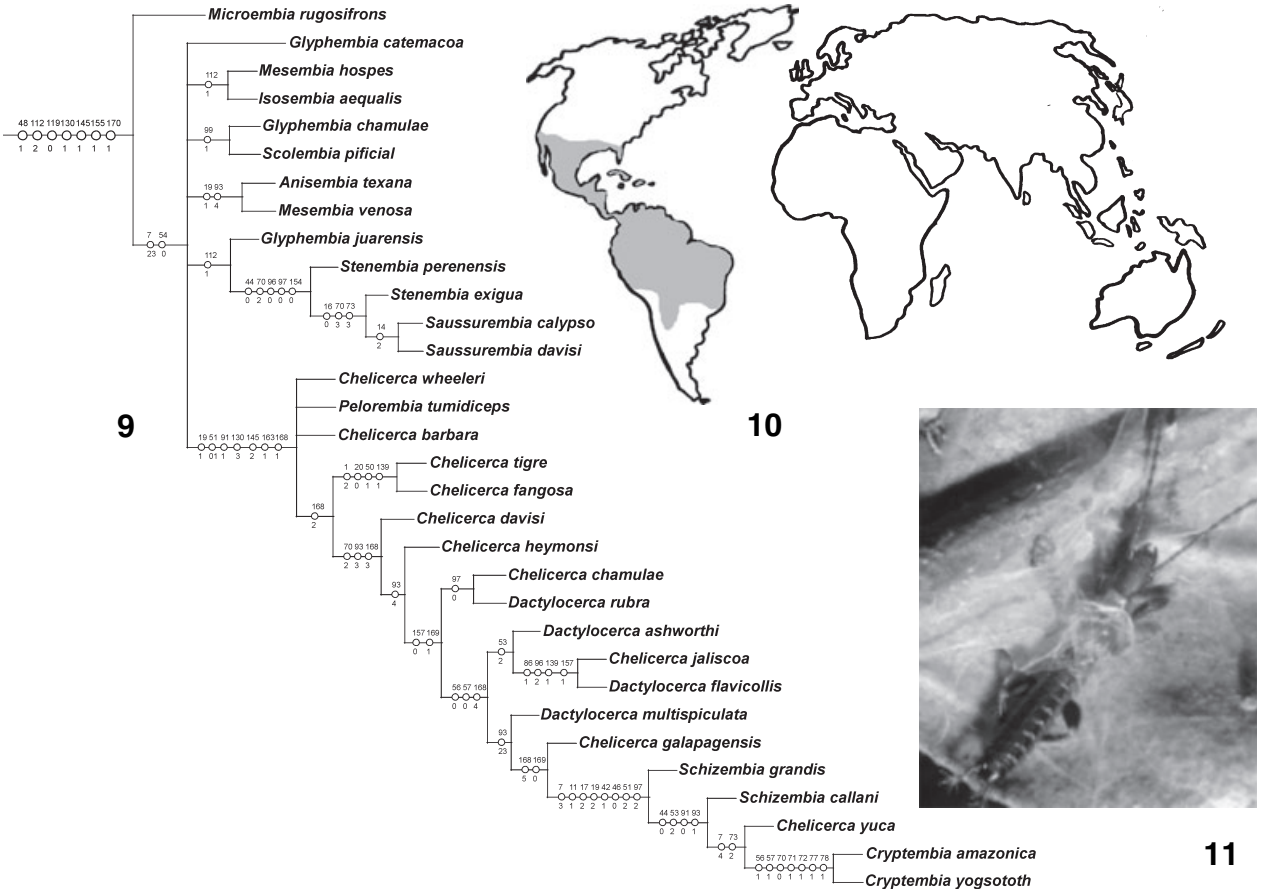
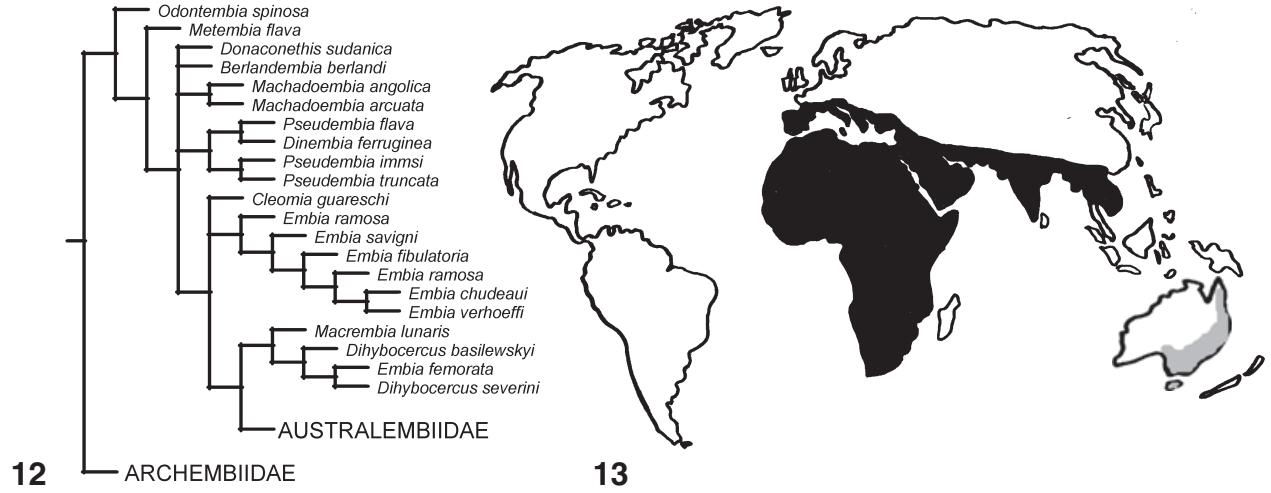


Fig. 9. Anisembiidae resolution according to morphological data.
Fig. 10. Distribution map of Anisembiidae.
Fig. 11. *Saussurembia davisi*, male (photographed by J. Edgerly).



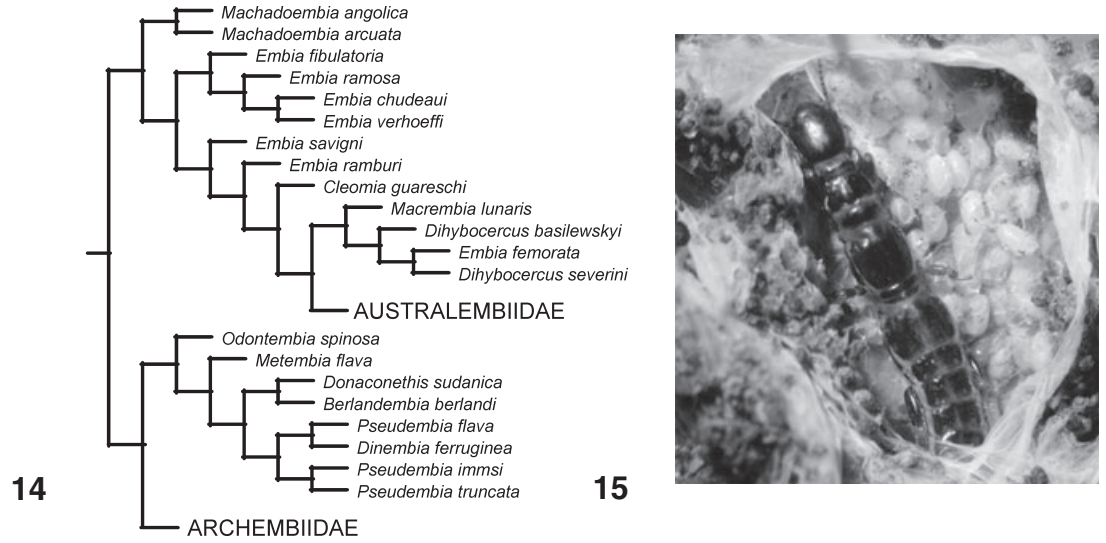


Fig. 12. Resolutions of the Embiidae + Australembiidae.
Fig. 13. Distribution map of Embiidae (black) and Australembiidae (grey).
Fig. 14. Resolutions of the Embiidae + Australembiidae.
Fig. 15. *Metoligotoma brevispina*, female (photographed by J. Edgerly).

could not be placed elsewhere. Now, its current placement is strongly supported by sharing cephalic, wing, and terminalia characters with Archembiidae (see Fig. 16) and is paraphyletic in terms of *Calamoclostes* + *Archembia*. These families should probably be synonymized.

Final comments

The aim of the present study was to include all the evidence available so that the current classification of Embioptera could be tested as stringently as possible. Thus, the analysis included not only a large taxon sampling but also features that are used commonly to distinguish species (e.g. used in alpha taxonomy) and traits used to distinguish higher groups (some of them already applied in a cladistic framework). The high resolution of the morphological strict consensus indicates that these results do not depend on the concavity values used. Instead, the inconsistency between the molecular trees—from six different cost matrices—indicates that the taxon sampling is not sufficiently large to resolve the basal relationships of the order.

Two recent papers have proposed new subordinal divisions of the Embioptera. Ross (2006) described a new species (*Paedembia afghanica*), highly neotenic and very different from any other group in the order, for which he created a new family and infraorder (Paedembiidae, Paedembiamorpha). In the same year, Engel and Grimaldi (2006) described a species (*Sorellembia*

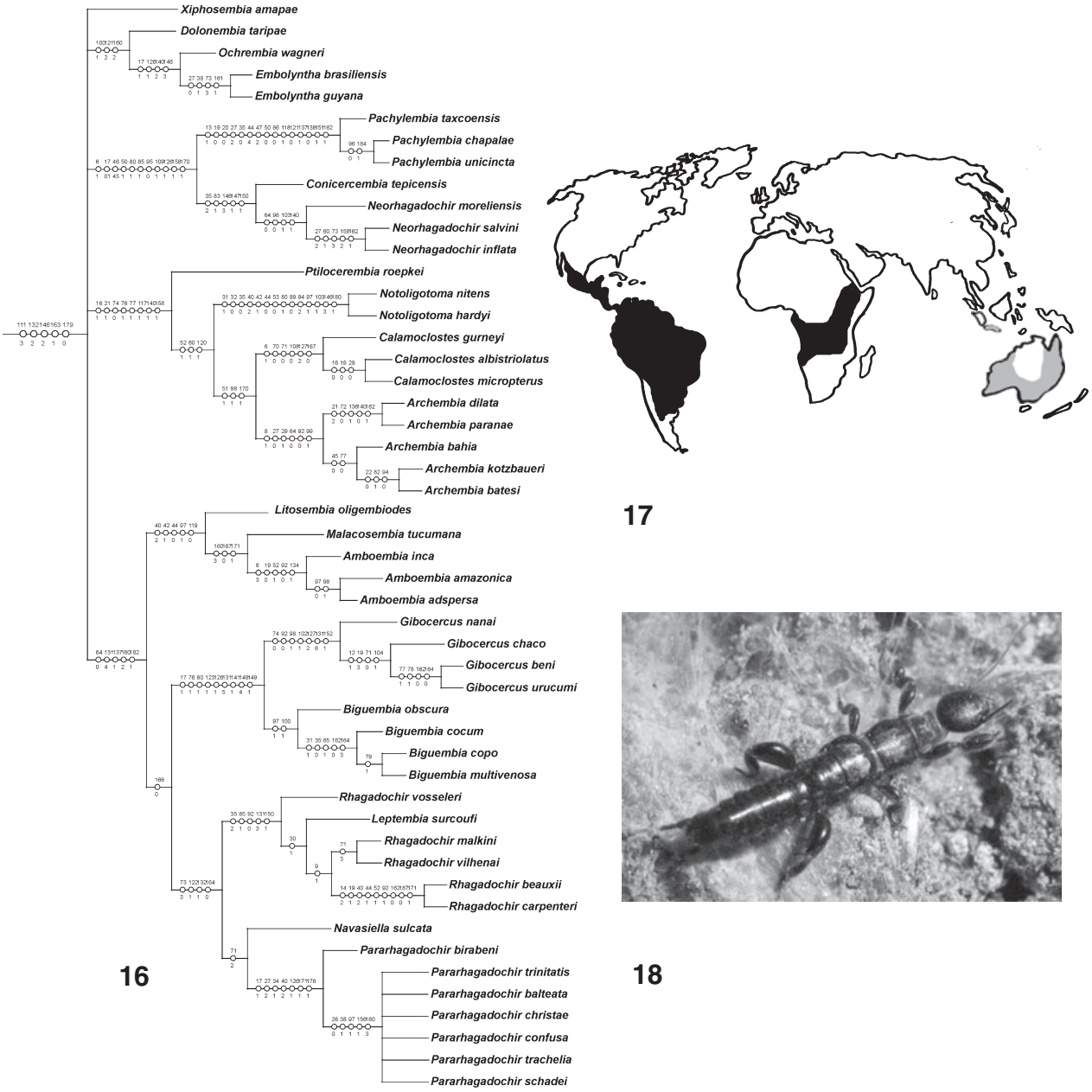


Fig. 16. Archembiidae resolution according to the morphological data.
Fig. 17. Distribution map of Archembiidae (black) and Notoligotomidae (grey).
Fig. 18. *Pararhagadochir trachelia*, female (photographed by C. Szumik).

estherae) from mid-Cretaceous amber with plesiomorphies so conspicuous that they created a monotypic family (Sorellembiidae), which they consider less plesiomorphic than Clothodidae; they proposed to include Sorellembidae as a basal group of a new suborder (Neoeoembiodea) including all non-clothodid embiopterans.

Neither Ross (2006) nor Engel and Grimaldi (2006) performed detailed cladistic analyses, nor provided an ample description of phylogenetically useful characters. The few characters each of the papers reports were included in the morphological matrix, as a first test of their proposed placements.

The suborder Paedembiamorpha appears in two possible positions, depending on where the cladogram is rooted, either as sister group of all embiopterans except *Clothoda*, or as sister group of all embiopterans. Its position is strongly supported by the near-symmetrical condition of the male terminalia, the female terminalia similar to that of some clothodids,

and the two convex surfaces (Ross, 2006, p. 787) instead of the medial bladder of the hind basitarsus which is characteristic of Embioptera. This is hardly conclusive, as many characters could not be scored on the basis of Ross's description (and Ross tends to emphasize the characters which do support his proposed placement, not commenting on the others).

The fossil family Sorellembiidae appears as sister group of *Conicercembia* and *Neorhagadochir*, which belong to a basal group of Archembiidae. Its position is clearly supported by the typical wing characters of Archembiidae, the process of the right hemitergite, and the shape of the left cercus. It is beyond the scope of the present study to propose synonymies between these taxa, but it is evident that in future *Sorellembia* will have to be assigned to Archembiidae.

The next step in this research will be aimed to increase the amount of molecular data as well as other sources of potentially useful evidence (e.g. behaviour, traits from other stages such as eggs, microsculpture, and internal morphology; Edgerly et al., 2007).

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Supporting information

Additional supporting information may be found in the online version of this article.

Appendix S1. Morphological data matrix.

Appendix S2. List of morphological characters.

Appendix S3. Molecular data matrix.

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