

# Phylogenetic systematics of Archembiidae (Embiidina, Insecta)

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**Abstract.** A cladistic analysis of the American genera of Embiididae is presented, using fifty-seven representative taxa and ninety-four morphological characters. The results support the elevation (and significant re-delimitation) of the subfamily Archembiinae to family level; as delimited here, Archembiidae, revised status, includes the genera *Ecuadembia* n.gen., *Calamoclostes* Enderlein, *Archembia* Ross, *Embolynta* Davis, *Xiphosembia* Ross, *Ochrembia* Ross, *Dolonembia* Ross, *Conicercembia* Ross, *Neorhagadochir* Ross, *Pachylembia* Ross, *Rhagadochir* Enderlein, *Litosembia* Ross, *Navasiella* Davis, *Ambonembia* Ross, *Malacosembia* Ross, *Biguembia* Szumik, *Gibocercus* Szumik and *Pararhagadochir* Davis. The results also indicate that some genera recently proposed are unjustified and therefore they are synonymized: *Argocercembia* Ross (a junior synonym of *Embolynta*), *Brachypterembia* Ross (*Neorhagadochir*), *Scelembia* Ross (*Rhagadochir*), *Ischnosembia* Ross (*Ambonembia*) and *Aphanembia* Ross (*Biguembia*); all new synonymy. The new genus *Ecuadembia* is described (type species *Archembia arida* Ross). *Ischnosembia surinamensis* (Ross) is returned to the genus *Pararhagadochir*. The following species synonymies are established: *Archembia lacombea* Ross 1971 = *Archembia kotzbaueri* (Navas 1925), *Archembia peruviana* Ross 2001 = *Archembia batesi* (MacLachlan 1877), and *Conicercembia septentrionalis* (Mariño & Márquez 1988) = *Conicercembia tepicensis* Ross 1984; all new synonymy. The family Archembiidae, and all its constituent genera, are diagnosed and described. The genus *Microembia* Ross (originally described as an Embiididae) is transferred to Anisembiidae. Pachylembiinae, Scelembiinae, and Microembiinae proposed by Ross are unsupported by the present cladistic analysis.<sup>1</sup>

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<sup>1</sup>Note from the editors: We are aware that several taxa reviewed in this manuscript have not been examined by the author, and proposed synonymy and character states scored for the matrix have been derived from publication(s) alone. Although this is unsound taxonomic practice, we accept that in this case it is unavoidable. The specimens, which reside in the Embiidina collection curated by Ross at the California Academy of Sciences, over more than a decade have not been made available for loan to the author (requests and refusal correspondence viewed by P. S. Cranston). Furthermore, type specimens purportedly deposited in the Smithsonian Institution and Natural History Museum (London) had not been received there by mid-2003 (letters to editor Cranston, 2003).

According to Recommendation 72F.3 (‘Institutional responsibility’) of the International Code for Zoological Nomenclature, ‘Every institution in which name-bearing types are deposited should . . . make them accessible for study’. We are aware of the problems managers and curators of collections may have with individual recalcitrant researchers, but feel that this footnote is a necessary explanation for aspects of this manuscript that may seem deficient.

## Introduction

Embiidae, with forty-two genera and 150 described species, contains almost half the known species of the order Embiidina and is the only family present on more than one continent (four) and in more than one biogeographical region (four). Historically, Embiidae has been defined by the possession of a bladder in the hind basitarsus, the medial vein of the anterior wing being furcate, and the apical process of the left cercus setose. All these features, however, are either convergences, or define a larger group of Embiidina. The very wide distribution and numerous species in the family therefore reflect more artefact than reality. Davis (1938, 1940c,d) had already noted the lack of naturalness in the family, considering Embiidae as polyphyletic; Szumik (1996) corroborated Davis' ideas in a phylogenetic analysis of the order. In that study (Szumik, 1996), even the American genera of Embiidae appeared as a nonmonophyletic group, although they do possess some characters which might indicate monophyly. Thus, in a subsequent analysis (Szumik, 1998b) including a larger number of representatives, the American genera grouped with the African genera *Scelembia* Ross, *Rhagadochir* Enderlein and *Navasiella* Davis, in a relationship stable to the subsequent addition of more taxa and characters (Szumik, 2000a,b). The placement of *Microembia* (originally described as Embiidae) was also stable, as sister group of *Chelicerca* Ross (Anisembiidae).

The studies by Szumik (1996, 1998b) represented only a first approximation to the problem. The other recent contribution to the American Embiidae is that of Ross (2001), who concentrated only on the alpha-level taxonomy of the group. Ross (2001) added nine new genera (seven of which were monotypic) to the ten American genera previously described for Embiidae, and divided the American Embiidae into four subfamilies, Archembiinae, Microembiinae (monotypic), Scelembiinae and Pachylembiinae (monotypic). However, the results of Szumik (1996, 1998b) suggest that some of the subfamilies or genera Ross recognized may not be monophyletic; in some cases taxa erected by Ross simply reflect the tradition of erecting new groups for highly autapomorphic or plesiomorphic conditions of pre-existing taxa.

Given this situation, evidently a phylogenetic analysis of the American Embiidae including all characters relevant to the group is desirable. Few of these characters are discussed by Ross (2001) who focused more on the species-level treatment, and therefore concentrated on putative species-level characters (coloration, male terminalia). Thus, using previous studies of the order as a framework, a more complete cladistic analysis of the Embiidae is undertaken here, including outgroup taxa appropriate to test monophyly. On the basis of the cladistic analysis presented here, the subfamily Archembiinae is elevated to familial status and includes all American Embiidae (with the exception of *Microembia*), plus the African genera *Rhagadochir* (= *Scelembia*) and *Navasiella*. Cladistic analyses show that the subfamilies Scelembiinae and Pachylembiinae proposed by Ross (2001), as well as certain genera, are delimited incorrectly. The Peruvian genus *Microembia* is transferred to Anisembiidae.

## Materials and methods

The material used in this study was generously lent by the following people and institutions: Randall T. Schuh, The American Museum of Natural History, New York, U.S.A. (AMNH); John E. Rawlins, The Carnegie Museum of Natural History, Pittsburgh, U.S.A. (CMNH); Enrique Mariño, Instituto de Biología, Universidad Autónoma de México, Mexico (IBUNAM); Axel O. Bachmann, Museo Argentino de Ciencias Naturales, Buenos Aires, Argentina (MACN); Stephan P. Cover, Museum of Comparative Zoology, Massachusetts, U.S.A. (MCZ); Jean Legrand, Muséum National d'Histoire Naturelle, Paris, France (MNHN); Adriano Kury, Museo Nacional de Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Eliane De Coninck, Musée Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC); Alcide Costa, Museu de Zoologia, São Paulo, Brazil (MZSP); Arno A. Lise, Pontificia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil (PUC-RS); David A. Nickle, United States National Museum of Natural History, Washington, U.S.A. (USNM); Jürgen Deckert, Museum für Naturkunde, Humboldt Universität, Berlin, Germany (ZMB). The material collected by the author is deposited in the Instituto and Fundación Miguel Lillo, Tucumán, Argentina (IFML).

The following abbreviations have been used: Mm, mentum; Sm, submentum; wing base union (Szumik, 1996): type A, Rs+Ma and Mp fork together from Cu, a broader cross-vein present between Rs+Ma and R<sub>1</sub>; type B, Rs+Ma and Mp start separately from a cross-vein between R<sub>1</sub> and Cu; type C, Rs+Ma and Mp start fused from a cross-vein between R<sub>1</sub> and Cu; 1°Vfs, rudiments of valvifers one; Ep, epiproct; Lpp, left paraproct; Rpp, right paraproct; H, hypandrium or ninth sternite; Hp, process of the hypandrium; LC1, basal left cercus; LC1dp, distal process of LC1; LC1bp, basal process of LC1; LC2, apical left cercus; 10T, tenth tergite; 10L, tenth left hemitergite; 10R, tenth right hemitergite; 10Lp1, caudal process of the left hemitergite; 10Rp1, caudal process of the right hemitergite; 10Rp2, anterior process of the right hemitergite.

### Cladistic analysis

The choice of trees was made using the implied weighting method of Goloboff (1993a), implemented in the program PEE-WEE version 2.9 (Goloboff, 1993b). The search algorithm used for the data matrix with ninety-four morphological characters and fifty-seven taxa (Appendix 1) was the 'parsimony ratchet' of Nixon (1999), with thirty replications of a random addition sequence, each followed by fifty iterations of tree bisection-reconnection (TBR)-ratchet (thus totalling 1500 ratchet iterations). The group support was measured with a jackknifing procedure modified from Farris *et al.* (1996), where in each replication (500 in total) a more exhaustive search is done (three random addition sequences, each followed by TBR, saving up to 500 trees). The support for each group was measured as the GC value, which is the

difference in frequency for the group, and the most frequent contradictory group (Horovitz, 1999; Goloboff *et al.*, 2003).

### Taxa

Ten taxa of the families Clothodidae and Embiidae were selected as outgroups (see Appendix 2); as long acknowledged (and supported and discussed in Szumik, 1996, 1998b, 2002), the genera of Clothodidae form the most basal branches of the order. The analysis included all the American genera of Archemiidae, with the exception of *Microembia* (transferred to Anisemiidae) and six of the seven species in the African genera *Rhagadochir* (= *Scelembia*) and *Navasiella*. Of the fifty-seven species included in the analysis, fifteen were scored on the basis of the original descriptions, as material was not available; the remaining forty-two (see Appendix 2) were scored on the basis of type and common specimens with the exception of eight taxa. For the choice of included taxa, many more species were studied, but they represented no significantly different character combinations, and would thus have added minimally to the analysis.

### Characters

Ninety-four morphological characters were used; only brief comments are included here; a more detailed description of the characters and states is provided in Appendix 3.

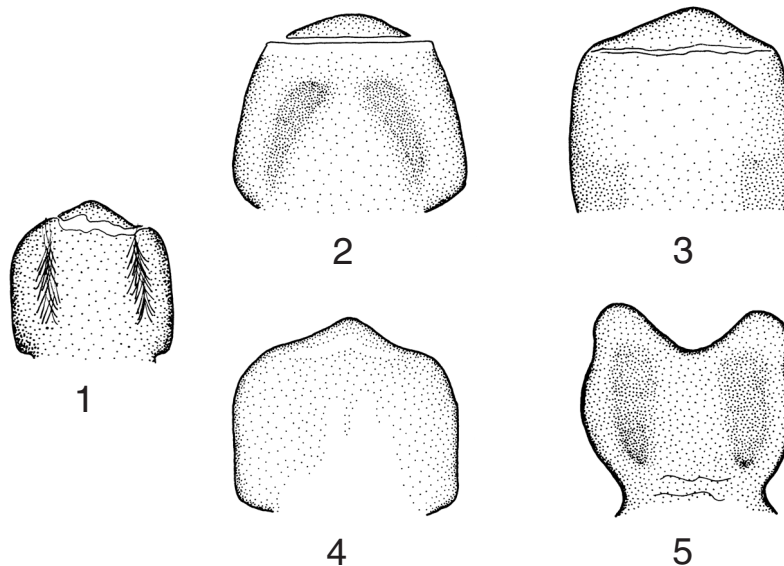
*Coloration* (six characters, both sexes). Colour characters have sometimes been used to recognize genera of Embiina

(e.g. Ross, 1960 distinguished *Scelembia* from *Rhagadochir* only on the basis of colour differences; Ross, 2001 continues explicitly to defend the use of coloration). I have observed colour characters (such as the degree of pigmentation) to vary in specimens of the same nest, in different seasons, and with the time elapsed since the last moult; this casts doubt on the use of such characters for higher groups. Although these characters are doubtful, it seemed better to include them in the analysis, so that their reliability could be checked against the distribution of other characters.

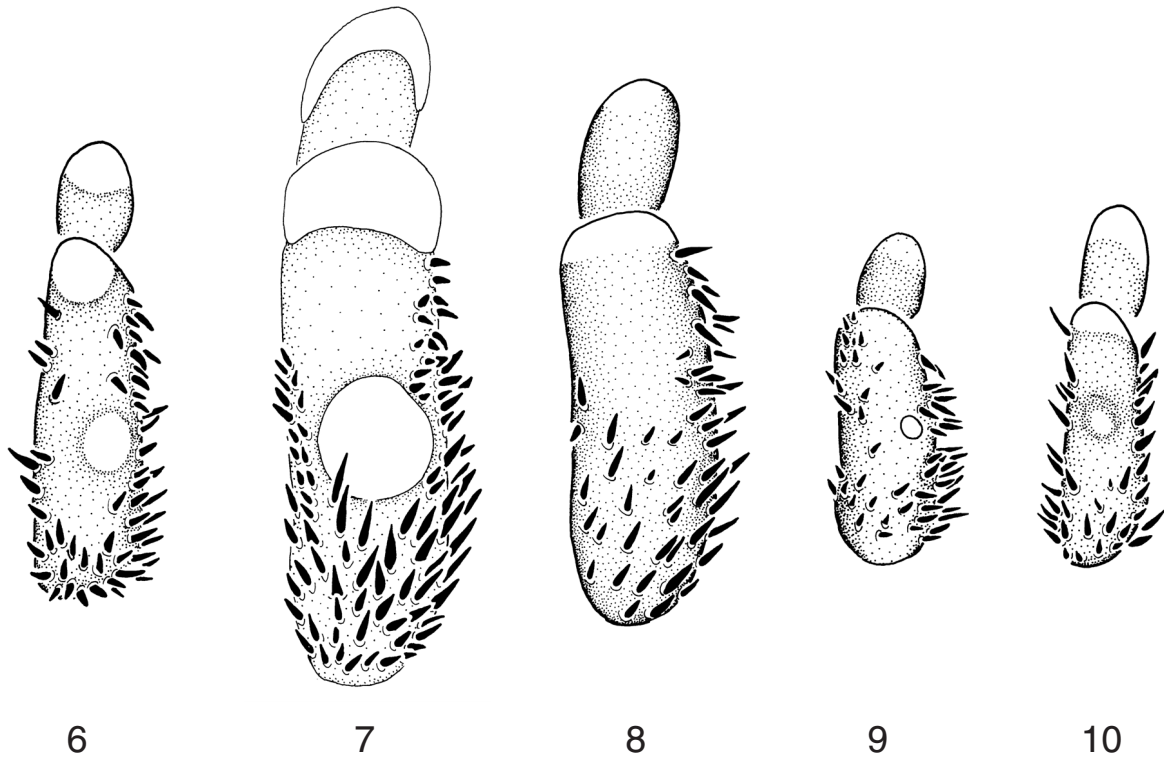
The three basic colour conditions recorded here have been observed to vary independently in males and females; thus, the male and female characters are considered as independent.

*Head* (seven characters, males). The head characters most often used in systematics concern the male mandibles. Other informative male characters have been found in the mouthparts and cephalic capsule. The shape of the mentum and submentum is easy to observe (Figs 1–5) and the presence of no less than seventeen possible states in the order makes their utilization potentially useful. However, homologizing all the possible conditions in the shape of the mentum and submentum is a difficult task; only the most relevant differences were used here.

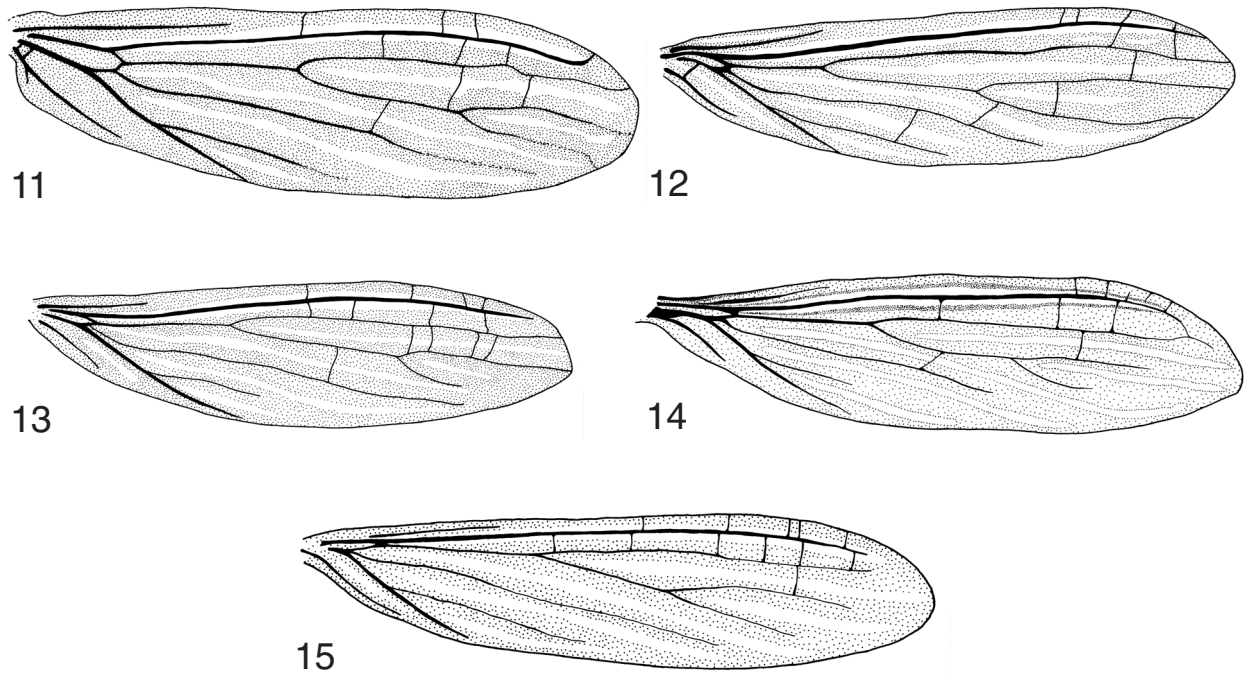
*Hind basitarsus* (six characters, males and females). This article seems to be used as anchorage over the silk layer of the gallery. Of the several basitarsal characters, the only one used in the literature to distinguish families (and sometimes genera) is the presence or absence of a medial bladder. Other characters (used previously in Szumik, 1994, 1996) were included here, such as the



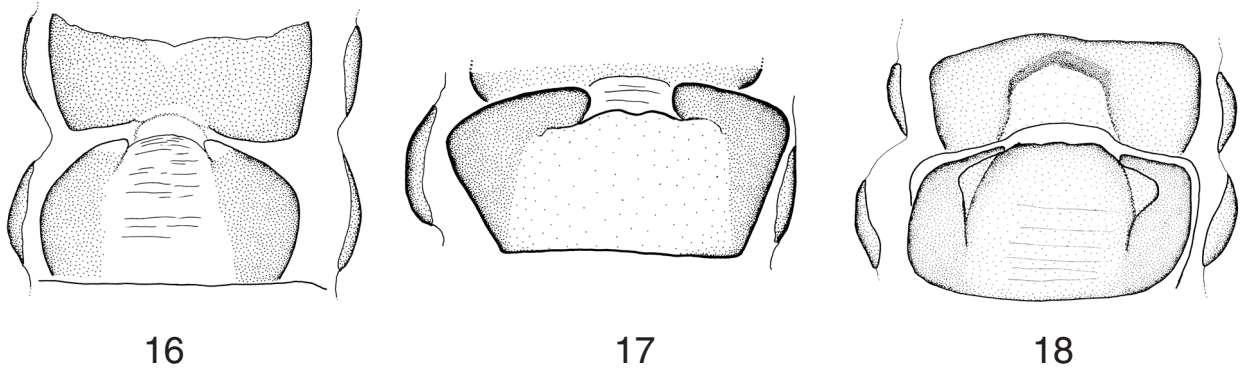
**Figs 1–5.** Mentum + submentum. 1, *Archembia kotzbaurei*; 2, *Archembia* spB; 3, *Ochrembia wagneri*; 4, *Biguembia copo*; 5, *Pararhagadochir schadei*.



**Figs 6–10.** Hind basitarsus, male. 6, *Archembia batesi*; 7, *Gibocercus urucumi*; 8, *Pararhagadochir flavicollis*; 9, *Pararhagadochir christae*; 10, *Malacosembia tucumana*.



**Figs 11–15.** Wing. 11, *Archembia kotzbaurei*; 12, *Biguembia copo*; 13, *Gibocercus urucumi*; 14, *Pararhagadochir confusa*; 15, *Malacosembia tucumana*.



**Figs 16–18.** Female terminalia, eighth and ninth sternites. 16, *Biguembia copo*; 17, *Pachylembia taxcoensis*; 18, *Archembia kotzbaurei*.

setae, apical bladder, and the position of the medial bladder (Figs 6–10).

*Wings (nineteen characters, males).* Wing venation (Figs 11–15) has in general been poorly studied in Embiidina. The wing characters most often mentioned in descriptions are the absence or presence of wings, and whether the Ma and Cu veins are forked or simple.

The number of transversal veins is often variable at the population level (Ross, 2000, 2001; pers. obs.), and even between the wings of the same individual (pers. obs.). Although the exact number of veins is variable, the presence or absence of a type of vein is much less variable or not variable at all. For example, the origin of the Rs + Ma and Mp veins described in Szumik (1996) distinguishes major groups of Embiidina and presents almost no variation. Several venation characters of this type were therefore included in the present analysis: the degree of development of longitudinal veins, whether they reach wing margins, and the presence or absence of transversal veins.

Some characters used here refer to the absence of certain transversal veins; it must be noted that this varies independently of the general reduction of longitudinal veins, thus suggesting that the two types of character are not correlated.

*Terminalia (fifty-five male characters, one female character).* The Embiidina lack an ovipositor; the eighth sternite is in general partly divided caudally into two small lateral lobes (called first valvifers) and between them there is a slightly corrugated plate, centrally not pigmented and with two strongly pigmented lateral bands. This is the condition common to most Embiidina, and to all Archembiidae. The lateral lobes of Archembiidae can vary in their degree of fusion with the central plate (Figs 16–18).

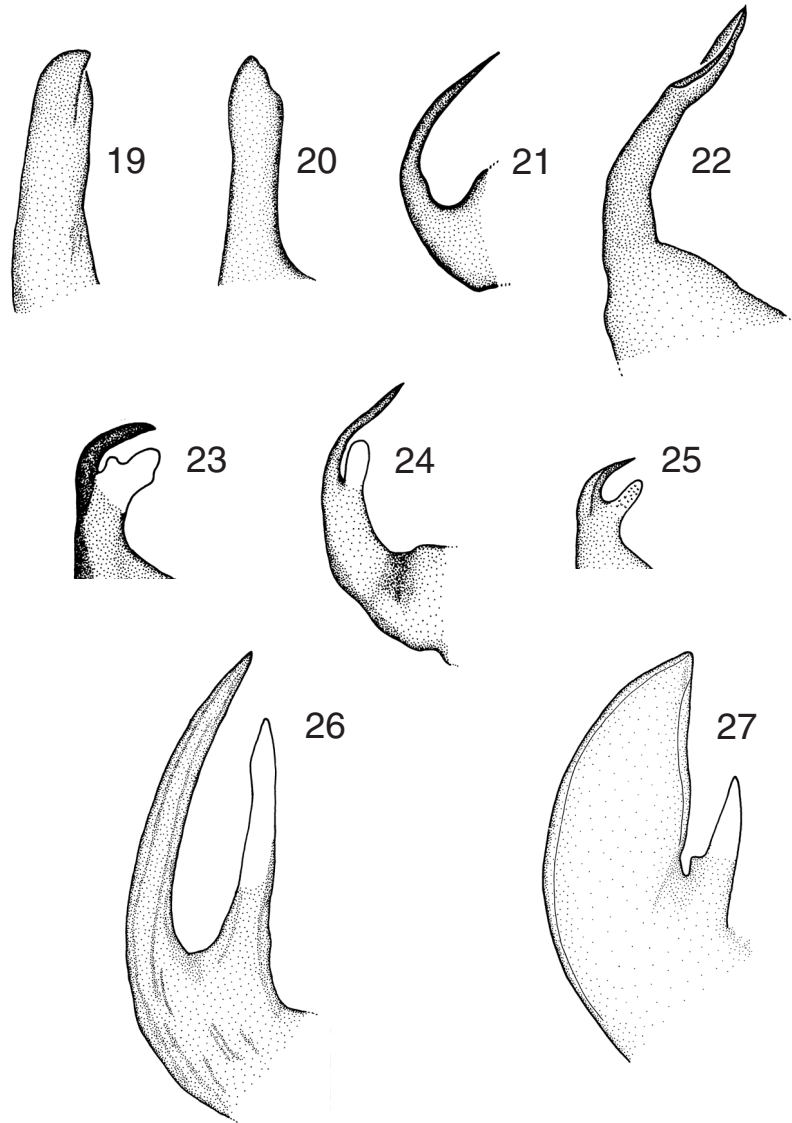
Given how copulation is achieved, the male terminalia have a great variety of processes and structures which hold the female abdomen and open the genital opening of the female (Figs 19–42). Most of the ordinal classification is based on these characters.

## Results

PEE-WEE found two optimal trees (strict consensus in Fig. 43); of the 1500 ratchet iterations (see Materials and methods), 488 found the optimal trees. These trees have a fit of 500.0 (36% of rescaled fit, and 540 steps long). Given that fifteen of the fifty-seven species analysed here have been scored only on the basis of the literature (thus having a significant proportion of missing entries and doubtful scorings), some artefacts could be introduced into the analysis. To make sure that this is not the case, those fifteen taxa were eliminated from the matrix; the results of analysing such a reduced matrix were almost identical to the results for the full data (Fig. 44 shows the strict consensus for the taxa shared in both datasets).

The American and some African genera form a monophyletic group (Fig. 43), grouped by eight synapomorphies (discussed below, in the family description); the group has a very high support (Fig. 45).

Ross (2001) stated that some characters (wing venation and the hind basitarsus) are too variable to be used in either the lower or higher classification of Embiidina. To ensure that those potentially misleading characters were not affecting the results, the data matrix was also run excluding all those characters. Optimal trees found without basitarsal characters were almost identical to trees for the full data, differing only in the position of *Malacosembia* and *Ischnosembia surinamensis* (with *Malacosembia* as the sister group of *Pararhagadochir* and *Ischnosembia surinamensis* as the sister group of *Aphanembia* + *Biguembia* + *Gibocercus*). The only two groups differing in the analyses including and excluding those 'variable' characters have very low support under jackknifing (Fig. 45), and therefore the difference is trivial. When the wing characters were excluded instead, some optimal trees had the same resolution as the trees for the full data, others differed only in having *Litosembia* as the sister group of *Rhagadochir* (again, the position of *Litosembia* is very weakly supported; Fig. 45). Finally, the influence of the colour characters was evaluated



**Figs 19–27.** Caudal process of the left hemitergite. 19, *Archembia kotzbaurei*; 20, *Archembia* spA; 21, *Conicercemia tepicensis*; 22, *Ochrembia wagneri*; 23, *Pararhagadochir birabeni*; 24, *Pararhagadochir trachelia*; 25, *Malacosembia tucumana*; 26, *Biguembia cocum*; 27, *Gibocercus urucumi*.

by excluding them; some of the resulting trees were identical to the trees for the full data, others differed only in the apical resolution of *Gibocercus* (with *Gibocercus chaco* as the sister of *Gibocercus urucumi*).

**Archembiidae, new status**

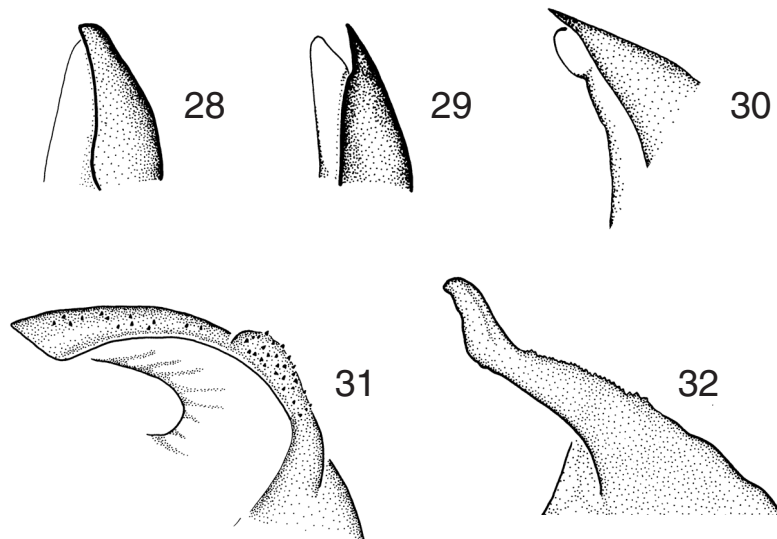
*Diagnosis*

Archembiidae is distinguished from the remaining families by the 10T with a membranous area occupying the base and centre of the sclerite and most of the base of the 10R, the 10R and 10L connected by a thin basal bar;

10Rp2 present, bar-shaped and well sclerotized. It is distinguished from Embiidae by the depressed mandibles, with incisive and molar areas clearly differentiated (instead of concentrated apically; note that the molars can be lost in some species of *Rhagadochir*).

*General features*

Medium to large sized individuals (6–18 mm total length). Hind basitarsus robust, medial bladder generally present (absent in *Pararhagadochir flavicollis* (Enderlein), *Ambo-nembia amazonica* (Ross), *Pararhagadochir surinamensis* Ross, and males of *Litosembia* Ross), apical bladder more



**Figs 28–32.** Caudal process of the right hemitergite. 28, *Pachylembia taxcoensis*; 29, *Conicercemia tepicensis*; 30, *Pararhagadochir trachelia*; 31, *Biguembia cocum*; 32, *Gibocercus urucumi*.

or less developed. Hind basitarsus chaetotaxy: one to two rows in retrolateral face, one to six rows in pro-lateral; no setae around middle bladder or between middle and apical bladders.

#### Males

Mandibles more or less robust, incisives 3–2, molars 2–1 or 1–1. Mm normally sclerotized, Sm with anterior margin straight (Fig. 2) or concave (Fig. 5). Winged; apterism at the population level (as in *Pararhagadochir trachelia* (Navas) or *Neorhagadochir salvini* (Mac Lachlan)) or generic level (i.e. *Pachylembia* Ross). Ma forked (except in *Archembia arida* Ross and *Calamoclostes albistriolatus* Enderlein), Cu simple or forked; cross-veins more or less numerous (Figs 11–15). 10Rp1 and 10Lp1 present, with apex simple (Figs 19–22) or forked (Figs 23–27). Epiproct rodlike (but some differences in shape are present), free (fused to the 10Rp2 only on *Archembia*, *Calamoclostes*, *Ecuadembia* gen.n. and *Litosembia*). Lpp well developed, partially (Fig. 33) or totally (Figs 34, 35) sclerotized, microtrichia present or not, sometimes with a nodule or a carinate hook in the inner caudal angle of the sclerite (Figs 34, 35). Rpp reduced and mostly fused to the Hp. Hp well developed, carinae normally present; some genera like *Pararhagadochir* Davis, *Rhagadochir*, *Gibocercus* Szumik, *Biguembia* Szumik, etc., Hp is rectangular, centred and with the caudal margin membranous (Figs 34, 35). LC1 and RC1 cylindrical, except in *Neorhagadochir* Ross where LC1 is conical (Fig. 36). LC1dp present (absent in *Neorhagadochir* and some species of *Pachylembia*), with variable shape (Figs 37–42), with numerous setae (absent in the Mexican genera, Figs 37, 38). LC1bp normally absent, present in some species of

*Pachylembia*, *Biguembia* and *Gibocercus* (Fig. 41, see Szumik, 1998b: 142).

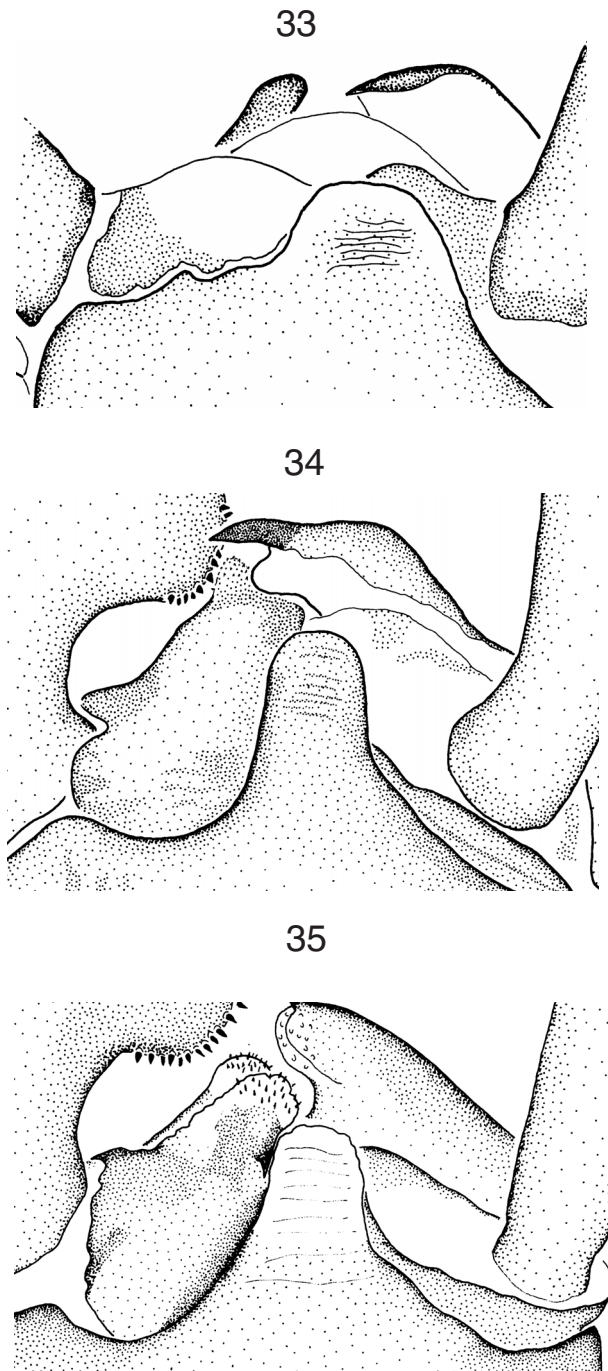
#### Females

Commonly the 1°Vfs are differentiated from the central plate by two notches on the caudal margin and by the degree of pigmentation (Fig. 16); in the Mexican taxa, the 1°Vfs are well-developed lobes (Fig. 17); also in some females of *Archembia* the 1°Vfs are well differentiated of the central plate (Fig. 18).

#### Relationships

The monophyly of Archembiidae is supported (Fig. 43) by the depressed mandibles, with molar and incisive teeth well differentiated (character 2), the Cua diffuse (character 25), cross-veins absent between Ma1 and Ma2 (character 35), the LC1 with setae on the apical area (character 40), the 10T divided into two subdistinct plates (character 49), the 10Lp shaped as a flat bar (character 54), the 10R with a small membranous base (character 67), and the 10Rp2 bar-shaped (character 79); some of these characters have a medium or high fit (Appendix 4).

Within Archembiidae, three main groups can be distinguished. One group has *Archembia* and *Calamoclostes* ('A' in Fig. 43), with very high support (Fig. 45); *Archembia* appears as paraphyletic in terms of *Calamoclostes*. The second group ('B' in Fig. 43) has medium support (Fig. 45) and is defined by the 10Lp1 simple, curved and externally laminate (character 56, see Appendix 4). This group comprises nine genera (seven of which are monotypic); eight of



**Figs 33–35.** Male terminalia, ventral view, process of the hypandrium and left paraproct. 33, *Archembia kotzbaurei*; 34, *Pararhagadochir confusa*; 35, *Pararhagadochir trachelia*.

these genera belong to Ross' (2001) Scelembiinae and the ninth genus (*Pachylembia*) constitutes, according to Ross, the monotypic subfamily Pachylembiinae. The genus *Pachylembia* has very high support (Fig. 45); Ross (2001) elevated the genus to subfamily because of its numerous

autapomorphies, but the genus also has characters which clearly ally it with other Mexican genera, such as *Neorhagadochir* and *Conicercebmbia* Ross. The third and last group ('C' in Fig. 43), with high support (Fig. 45), comprises nine genera, which share the shape of the 10Lp1 (characters 53, 54, 55), and rectangular and centred Hp (Figs 34, 35; character 83). Two genera in this group appear as nonmonophyletic: *Scelembia* is paraphyletic in terms of *Rhagadochir* (Fig. 43); the paraphyly of *Scelembia* is strongly supported by the data (Fig. 45) and, therefore, *Scelembia* is proposed as a junior synonym of *Rhagadochir*. The other nonmonophyletic genus is *Ischnosembia* Ross, with its type species, *Ischnosembia amazonica*, more closely related to *Ambonembia* Ross than to *Ischnosembia surinamensis*; *Ischnosembia* is therefore proposed as a junior synonym of *Ambonembia* and *Ischnosembia surinamensis* transferred back to *Pararhagadochir*.

Given that most groups in the present analysis are very stable, the name Archembiidae, new status, is proposed; the composition of the Archembiidae, however, is quite changed from Ross' concept. The three subfamilies proposed by Ross (2001) are rejected, because they bear no possible correspondence with the groups of Archembiidae.

#### *Distribution and composition*

The family includes eighteen genera, with sixty-nine species (in America and Africa). In America they are found from central Mexico to central Argentina; some genera have a very restricted distribution (*Pachylembia*, exclusively Mexico) and others have a wider distribution (*Pararhagadochir*, present in most of South America). These data, however, are not very reliable, as many species are known only from the type locality, and there are vast regions where the order has not been collected. The African genera *Rhagadochir* and *Navasiella* occur in Tanzania, Uganda, Angola and Congo. Three other African genera of Embiidae (*Chirembia* Davis from Ethiopia, *Parachirembia* Davis from Nigeria, and *Macrembia* Davis from Congo), will possibly have to be transferred to Archembiidae when additional material becomes available.

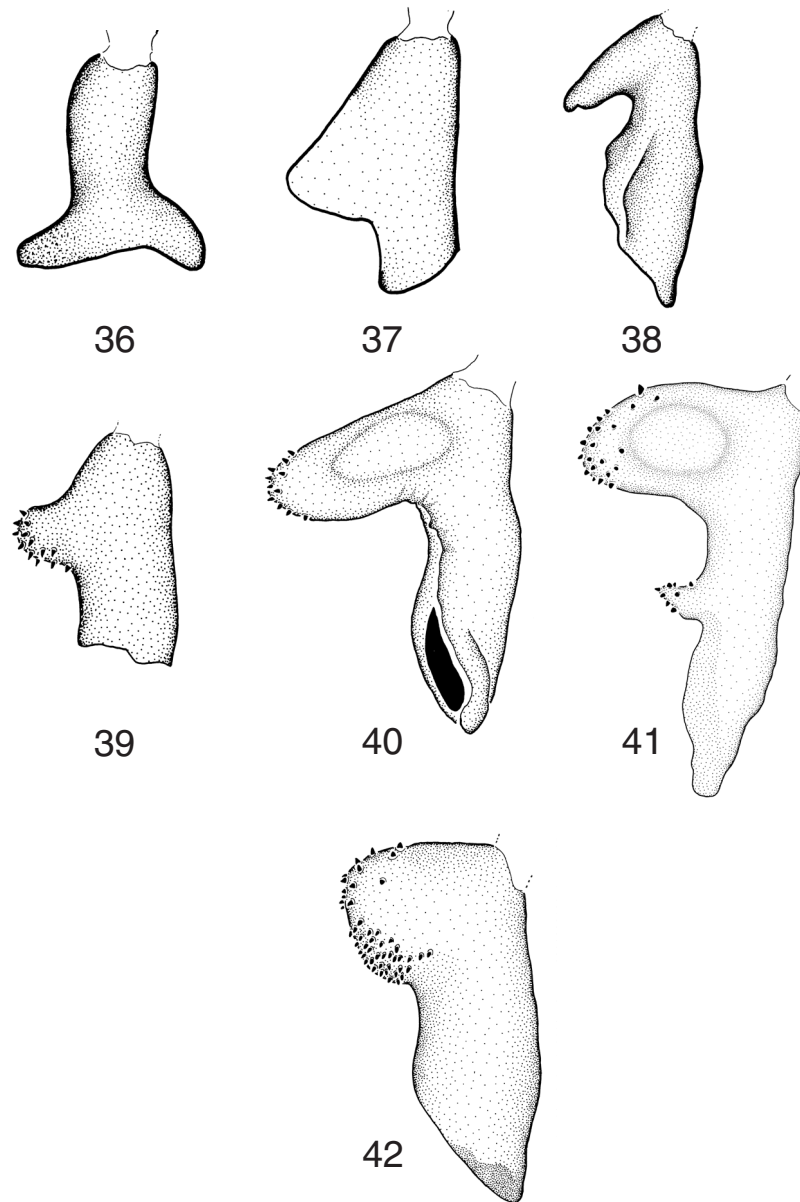
*Archembia* Ross, 1971 (Figs 1, 2, 6, 11, 18–20, 33, 39)

*Archembia* Ross, 1971: 30, 2001: 4; Szumik, 1996: 51, 1998a: 34, 1998b: 141, 2002: 444. Type species: *Archembia lacombea* (syn.n. of *Embia kotzbaurei* Navas, 1925).

**Diagnosis.** Differs from *Calamoclostes* and *Ecuadembia* by having the incisive teeth concentrated in the apex of the mandible (character 4), the apical cercus segments longer than the basal segments (character 38), and the medial LC1dp (Fig. 39; character 42).

**Relationships.** Ross (1971) originally included *Archembia* in Embiidae, although considering it as 'closer to





**Figs 36–42.** Basal left cercus. 36, *Neorhagadochir salvini*; 37, *Pachylembia taxcoensis*; 38, *Conicercemia tepicensis*; 39, *Archembia kotzbaurei*; 40, *Gibocercus nanai*; 41, *Gibocercus urucumi*; 42, *Ochrembia wagneri*.

Clothodidae' (Ross, 1970, 1971, 2001) than to Embiidae. The characters shared between Clothodidae and *Archembia* are actually plesiomorphies (as discussed elsewhere; Szumik, 1996, 1998b). The group formed by *Archembia* and *Calamoclostes* (Fig. 43) is distinguished clearly by the type B vein origin (Fig. 11; character 20), the large anal region (Fig. 11; character 21), the straight 10Lp1 with a spatulate apex (Figs 19, 20; character 58), and the Ep fused to the 10Rp1. Excepting *Archembia arida*, both *Archembia* and *Calamoclostes* are well-defined genera, and therefore *Archembia arida* is excluded from *Archembia* (see under *Ecuadembia*).

*Composition and distribution.* Until recently, *Archembia* had only three species, *A. kotzbaurei*, *A. lacombea*, and *A. batesi* (MacLachlan), known only from their type localities in Brazil. Ross (1971) transferred *Embia kotzbaurei* Navas (described on the basis of a male from Rio de Janeiro) to *Archembia*, based on the original description (the type is lost). Ross (1971: 32) also described type species of *Archembia*, *A. lacombea*, from Rio de Janeiro, mentioning that two species coexist in Rio de Janeiro, the lighter-coloured *lacombea* and a darker one, possibly *kotzbaurei*. These two are distinguishable only by the degree of pigmentation, but given the individual variability in the pigmentation (see

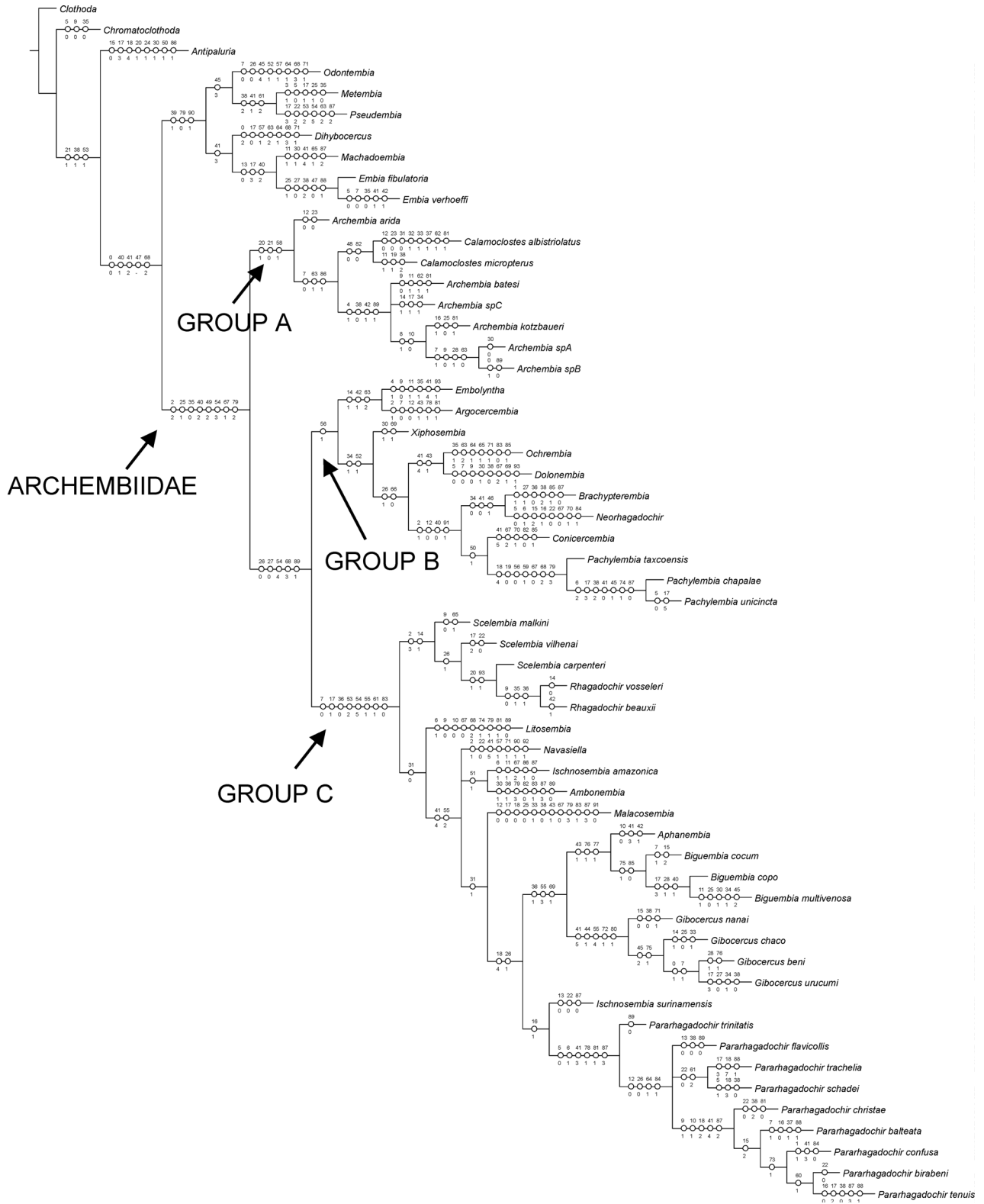


Fig. 43. Consensus of the two optimal trees.

discussion of 'Characters'), the distinction of a new species on the basis of this character alone seems unjustified. Having studied specimens of *Archembia lacombea* (paratypes) and other specimens recently collected in Rio de Janeiro and São Paulo, I conclude that there is only one species in the area, and therefore synonymize *Archembia lacombea* with *Archembia kotzbaueri*. Ross (2001) has recently described another six species, *A. boliviana* (Bolivia), *A. peruviana* (Peru), *A. bahia*, *A. dilata*, *A. paranae* (Brazil),

and *A. arida* (Ecuador). Here again, two species, *Archembia peruviana* and the long known *Archembia batesi*, are distinguished solely by coloration. Having studied the type of *Archembia batesi*, as well as specimens from Peru matching Ross' description of *Archembia peruviana*, I found no difference and synonymize *Archembia peruviana* with *Archembia batesi*. The cladistic analysis includes three species of *Archembia* (identified as spA, spB and spC), which could perhaps be *A. boliviana*, *A. bahia*, *A. dilata* or *A. paranae* (all

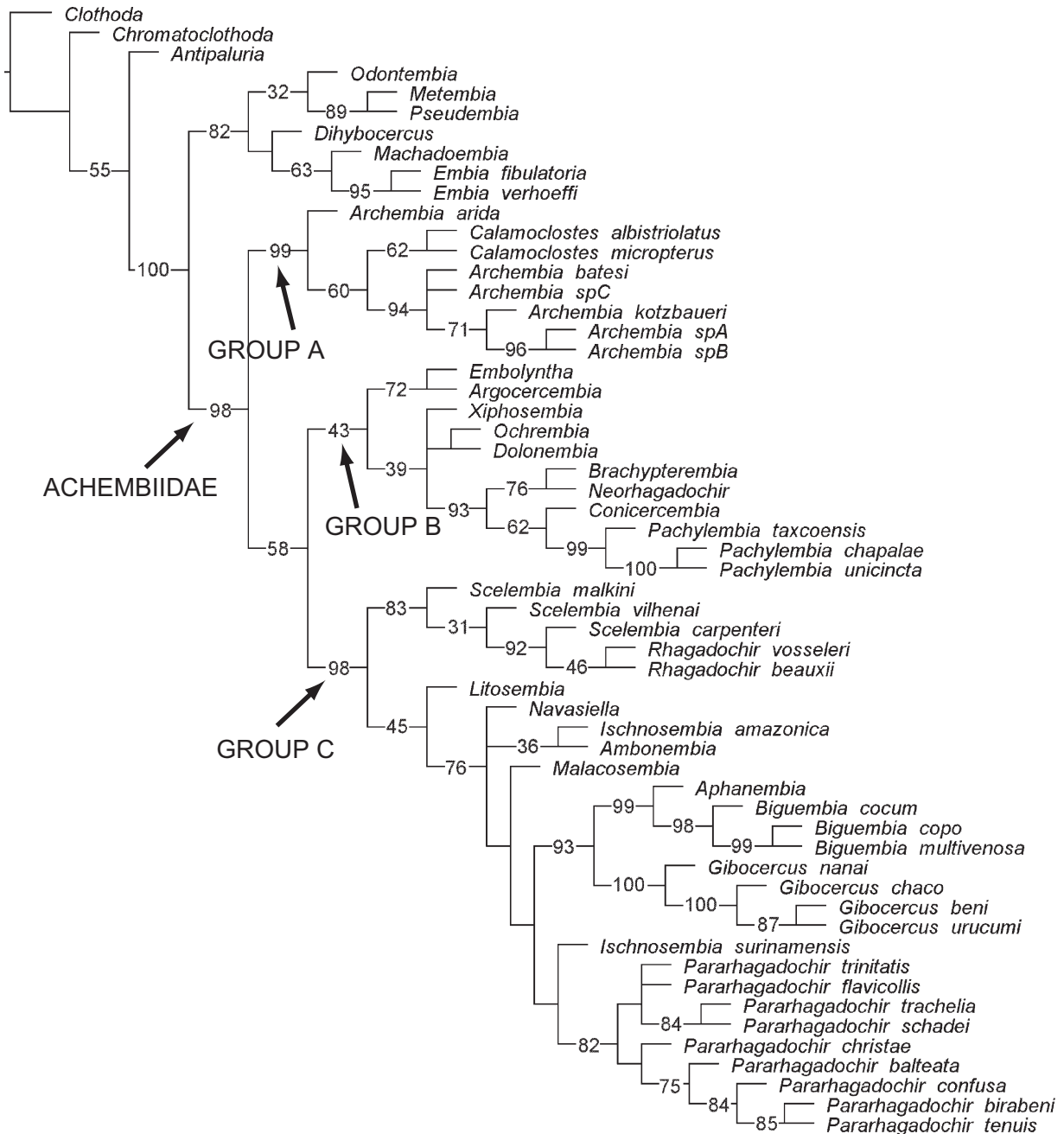
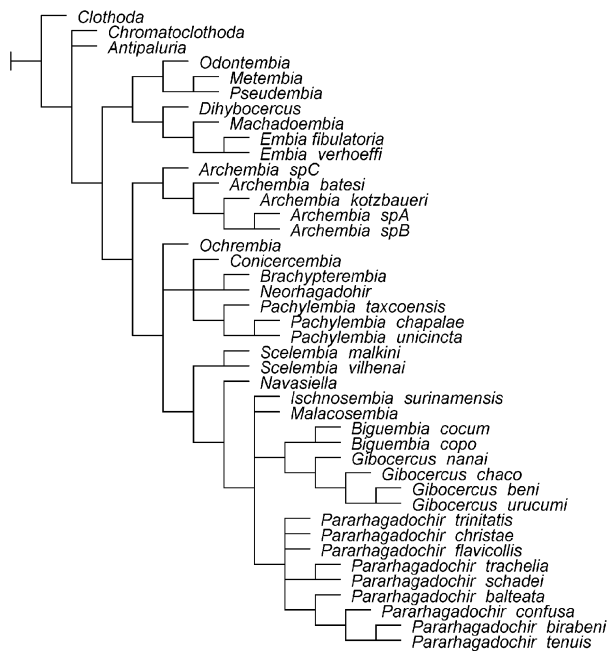


Fig. 44. Jackknifing tree (see methods), unnumbered nodes have support below 30.



**Fig. 45.** Consensus of the optimal trees with and without the fifteen taxa scored on the basis of the literature.

described by Ross, 2001); these species were not illustrated, and the description provides data only on coloration. Based on geographical distribution alone, spB is possibly *Archembia dilata*, and spA and spC may be *Archembia bahia* and *Archembia paranae*, respectively. The distribution of *Archembia* is poorly understood, as all the species are known from one or two localities, but it seems likely that (as conjectured by Ross, 1971) it occurs in the Amazon area, eastern Brazil, and tropical forests of Peru and northeastern Argentina.

#### *Calamoclostes* Enderlein, 1909

*Calamoclostes* Enderlein, 1909: 188, 1912: 27; Krauss, 1911: 73; Navas, 1918: 94; Davis, 1940a: 189; Ross, 1944: 414; 2001: 17. Type species: *Calamoclostes albistriolatus*.

**Diagnosis.** *Calamoclostes* can be distinguished from *Archembia* and *Ecuadembia* by having the sclerotic discoidal area on the 9T (character 48), the tip of the 10Lp1 strongly curved and acute. *Calamoclostes* differs from *Archembia* by having the LC1dp apical (medial in *Archembia*).

**Relationships.** Because *Calamoclostes* is a uniform genus, only two species (*C. albistriolatus* and *C. micropterus*) were used to test the monophyly and the relationships with *Archembia*. Ross (2001) claimed that the species of *Calamoclostes* are derived from the genus *Archembia* because, according to him, *Archembia* has more plesiomorphic morphological and behavioural characters. Although Ross states that there is only one female per

nest in *Calamoclostes*, and more than one in *Archembia*, only one female was observed per nest in *Archembia* spB from Argentina (Szumik, pers. obs.). In the cladistic analysis, *Calamoclostes* is supported as monophyletic (Fig. 43) by having the sclerotic discoidal area on the 9T (character 48) and the Hp without transversal keels (character 82), with high and medium fit, respectively (Appendix 4).

**Composition and distribution.** *Calamoclostes* contains six species: *C. albistriolatus* Enderlein, *C. auriceps* Ross, *C. micropterus* Ross, *C. silvestris* Ross (Ecuador), *C. gurneyi* Ross and *C. oculus* Ross (Colombia); all species are known from the type locality only (Ross, 2001).

#### *Ecuadembia* n.gen.

Type species: *Archembia arida* Ross.

**Diagnosis.** *Ecuadembia* can be distinguished from *Archembia* and *Calamoclostes* by having the Lpp completely sclerotized and the 10Lp1 tip without any carinae; *Ecuadembia* differs from *Archembia* by having the incisive teeth well developed and not concentrated on the apex, the LC1dp with apical position (medial in *Archembia*), apical and basal cerci with the same length (apical cerci longer than basal cerci in *Archembia*) and apical antennal segments of the females coloured (not pigmented in *Archembia*).

**Relationships.** *Ecuadembia* lacks the numerous synapomorphies which define the genus *Archembia* and the resultant grouping of (*Calamoclostes* + *Archembia*). *Ecuadembia* justifies the new genus for *Archembia arida* to avoid paraphyly of *Archembia*.

**Composition and distribution.** Contains just one species *Ecuadembia arida* (Ross) from Ecuador.

#### *Embolynta* Davis, 1940

*Olyntha* Gray, 1832: 347. Type species: *Olyntha brasiliensis* Gray.

*Embius* Gray, 1832: 786.

*Embolynta* Davis, 1940b: 344 (*Embius* and *Olyntha* preoccupied names); Ross, 1944: 412, 1971: 29, 2001: 26; Szumik, 1998a: 34, 1998b: 141.

*Argocercembia* Ross, 2001: 63. syn.n. Type species: *Argocercembia guyana*.

**Diagnosis.** *Embolynta* can be distinguished from other Archembiidae by having the 10Lp1 simple and starting at the inner caudal angle of the 10L (at the inner anterior angle in *Xiphosembia*, some species of *Ochrembia* and the Mexican genera), the 10Lp1 leaflike with many longitudinal carinae.

**Relationships.** *Embolynta brasiliensis* and the monotypic genus *Argocercembia* are grouped by sharing the 10Lp1

shape (see diagnosis, character 63), the medial bladder on males small (character 14) and the LC1dp with medial position (character 42, a condition also present in *Archembia*), these synapomorphies have low fit (Appendix 4) but the group has high support (Fig. 45). Because the differences between *Embolynta* and *Argocercemia* are insignificant and because the group is well supported, *Embolynta* should now be considered a senior synonym of *Argocercemia*.

*Composition and distribution.* *Embolynta* has two species: *Embolynta brasiliensis* from Brazil (without any specific location) and *Embolynta guyana* (Ross) from Guyana (Ross, 2001).

#### Xiphosembia Ross, 2001

*Xiphosembia* Ross, 2001: 28. Type species: *Xiphosembia amapae*.

*Relationships.* As no material was made available to be examined, data were derived from Ross (2001). Ross did not mention a possible association of *Xiphosembia* with other genera; the diagnosis was purely descriptive. *Xiphosembia* has a character combination such that one possible placement would be between the group of (*Archembia* + *Calamoclostes*) and the grouping of the Mexican genera (*Neorhagadochir* (*Conicercemia Pachylembia*)). This genus shares with *Neorhagadochir* and *Conicercemia* the shape of the 10Lp1 and with *Archembia* the form of the LC1dp. In the analysis, *Xiphosembia* is the sister group of ((*Ochrembia Dolonembia*) (*Conicercemia* (*Neorhagadochir* (*Pachylembia*))))), by having the 10Lp1 starting from the inner anterior angle of the 10L (character 52), synapomorphy with maximum fit (Appendix 4).

*Composition and distribution.* The monotypic genus comes from one locality of the state of Amapa (Brazil) from the Amazon Basin.

#### Ochrembia Ross, 2001 (Figs 3, 22, 42)

*Ochrembia* Ross, 2001: 73. Type species: *Embia wagneri* Navas.

*Diagnosis.* Can be differentiated from other genera by having the 10Lp1 tubular with the tip acute and excavate (Fig. 22) and the 10Rp2 inconspicuous.

*Relationships.* *Ochrembia* is grouped with *Dolonembia* – another monotypic genus of Ross – by sharing the LC1dp squared and depressed (Fig. 42; characters 41 and 43), a condition also present in *Embolynta guyana*, *Malacosembia* and *Biguembia*. Some synapomorphies of *Ochrembia*, like the depression between the 10Lp1 and 10L (character 64), the internal anterior angle of the 10L excavated (character 65)

and the Hp centred, lobed, with margins not sclerotized (character 83), are also present in the most apical group of the cladogram (*Rhagadochir*, *Pararhagadochir*, etc.).

*Composition and distribution.* *Ochrembia* is a monotypic genus known from three localities of the dry Chaco of the northwest of Argentina (Szumik, pers. obs.).

#### Dolonembia Ross, 2001

*Dolonembia* Ross, 2001: 30. Type species: *Dolonembia tapirape* Ross.

*Relationships.* As no material was made available to be examined, data were derived from Ross (2001). Ross (2001: 30) distinguished the males of *Dolonembia* from the ‘distant’ *Xiphosembia* by the larger size (but the male of *Xiphosembia* has 8–12 mm total length and the unique male of *Dolonembia* has 11.5 mm total length) and by having dark coloration, the mandibles robust (also in *Xiphosembia*), the caudal margin of the 10L convex and the 10Lp starting at the posterior inner angle of the 10L (also in *Xiphosembia*). In consequence *Dolonembia* can be differentiated from *Xiphosembia* only by coloration and by the shape of the caudal margin of the 10L. *Dolonembia* groups with *Ochrembia* (Fig. 43) by bearing the LC1dp depressed (character 43), a character with medial fit (Appendix 4), but this group has no support under jackknifing (Fig. 45). Both *Dolonembia* and *Xiphosembia* were scored as ambiguous for many characters, and probably the position of these genera will change in the future.

*Composition and distribution.* The unique species of *Dolonembia* was described from one locality in Mato Grosso, Brazil.

#### Neorhagadochir Ross, 1944 (Fig. 36)

*Neorhagadochir* Ross, 1944: 418, 1984: 4, 2001: 75; Szumik, 1996: 55, 1998b: 141, 2002: 444. Type species: *Neorhagadochir inflata*.

*Brachypterembia* Ross, 1984: 7, 2001: 76; Szumik, 1998b: 141, 2002: 444. syn.n. Type species: *Brachypterembia moreliensis*.

*Diagnosis.* *Neorhagadochir* can be differentiated from the other genera of Archembiidae by having the LC1 base conical and with microtrichiae.

*Relationships.* *Neorhagadochir* forms, together with the monotypic genus *Brachypterembia*, a well-supported group (Fig. 43); one of the most striking synapomorphies is the LC1 conical (Fig. 36; character 46). Both genera differ only in small details and *Brachypterembia* is proposed here as a junior synonym of *Neorhagadochir*.

*Neorhagadochir* is the sister group of *Conicercemia* and *Pachylembia* (Fig. 43) by bearing the poorly conspicuous

molar teeth (character 2); the female with apical antennal segments coloured (character 12); the LC1 setae absent (character 40) and the Ep broad, sclerotized plate shape (character 91); these synapomorphies have medium fit (Appendix 4).

*Composition and distribution.* The central American genus contains three species: *Neorhagadochir inflata* Ross (Guatemala), *Neorhagadochir salvini* (MacLachlan) known from south of Mexico to Costa Rica (Ross, 1984; Szumik, 2002) and *Neorhagadochir moreliensis* (Ross), new combination (known from a single locality in Michoacan, Mexico).

*Conicercemia* Ross, 1984 (Figs 21, 29, 38)

*Conicercemia* Ross, 1984: 10, 2001: 6; Szumik, 1996: 55, 1998b: 141, 2002: 444. Type species: *Conicercemia tepicensis*.

*Diagnosis.* *Conicercemia* can be distinguished from *Neorhagadochir* by having the LC1 tubular (conical in *Neorhagadochir*), the LC1dp (absent in *Neorhagadochir*) long and acute with a notch on the apex and without setae (Fig. 38), the basal area of the 10R membranous and well defined (reduced in *Neorhagadochir*). *Conicercemia* can be differentiated from *Pachylembia* by having the 10Rp1 (Fig. 29) forked and acute, and the ventral tip of the 10Rp1 well developed (longer than the dorsal tip).

*Relationships.* *Conicercemia* has many autapomorphies not included in the analysis because they are not informative at this level (see diagnosis). *Conicercemia* is the sister group of *Pachylembia* (Fig. 43), sharing the 10T pilose (character 50), a character with high fit (Appendix 4).

*Composition and distribution.* Ross (1984) described this Mexican genus for *Conicercemia tepicensis* Ross; Mariño & Márquez (1988) subsequently described the same species with the name *Clothoda septentrionalis* in the family Clothodidae. Ross (2001) transferred *septentrionalis* to the genus *Conicercemia*, and considered that *septentrionalis* differs from his type species *tepicensis* (Ross, 2001: 76). In studying types for both species I found no difference, and therefore propose *C. tepicensis* as the senior synonym of *C. septentrionalis* (Szumik, 2002). The genus is known from four localities in four states of Mexico: Michoacan, Jalisco, Colima and Nayarit (Ross, 1984).

*Pachylembia* Ross, 1984 (Figs 17, 28, 37)

*Pachylembia* Ross, 1984: 13, 2001: 81; Szumik, 1996: 55, 1998b: 141, 2002: 444. Type species: *Pachylembia chapalae*.

*Diagnosis.* *Pachylembia* can be differentiated from other Mexican genera by having the basal area of the 10R inconspicuous (character 56); the 10Lp1 tiny, hooklike, shorter than half the width of the 10L (character 59); the 10Rp1 simple with apex truncate (Fig. 28; character 68); the 10Rp2 obsolete (character 79) and males wingless (character 19).

*Relationships.* The monophyletic genus *Pachylembia* has the maximum support in this study (Fig. 45). The species are grouped by many synapomorphies (Fig. 43, many of those included in the diagnosis). *Pachylembia chapalae* and *Pachylembia uncinata* (Fig. 43) share the Sm with anterior margin w-like (character 6), the apical cerci reduced (character 38), the LC1 without setae and with a basal node on the inner side (character 45, absent in *Pachylembia taxcoensis*, but this species has a medial LC1dp, Fig. 37), and the absence of processes on the Lpp (character 87).

*Composition and distribution.* Exclusive to Mexico, the genus includes five species: *Pachylembia chapalae*, *P. taxcoensis*, *P. uncinata*, *P. colimae* and *P. autlanae*. The genus is known only from seven localities in Jalisco, Michoacan, Colima and Guerrero (Ross, 1984, 2001; Szumik, 2002).

*Rhagadochir* Enderlein, 1912

*Rhagadochir* Enderlein, 1912: 54; Friederichs, 1934: 406; Davis, 1938: 267, 1940a: 171, 1940c: 533, 1940d: 679; Ross, 1944: 420, 1952: 46, 1960: 301. Type species: *Embia vosseleri* Enderlein.

*Scelembia* Ross, 1960: 300; Szumik, 1996: 51, 1998b: 141. syn.n. Type species: *Rhagadochir malkini* Ross.

*Diagnosis.* *Rhagadochir* can be differentiated from other Archembiidae by having the tips of the 10Lp1 completely fused and the external margin of the 10Rp1 with a strong notch. It can also be distinguished from *Pararhagadochir* by having the anterior margin of the Sm straight (not concave), the incisive teeth acute (medial ones tiny), and just one molar tooth per mandible (small and inconspicuous).

*Relationships.* Ross (1960) transferred all but two species of *Rhagadochir* to his new genus *Scelembia*; these changes were supported only by differences in coloration. In this analysis, *Scelembia* appears paraphyletic in terms of *Rhagadochir* and is well supported (Fig. 45). Because the group is clearly homogeneous, *Scelembia* must be considered a junior synonym of *Rhagadochir*.

*Composition and distribution.* *Rhagadochir* contains six species: *Rhagadochir vosseleri* (Enderlein), *R. carpenteri* Davis [Tanzania], *R. beauxii* Davis [Uganda], *R. malkini* Ross, *R. villenai* Ross [Angola] and *R. virgo* (Ross) [Congo]; all the species are known only from the type locality.

*Litosembia* Ross, 2001

*Litosembia* Ross, 2001: 58. Type species: *Litosembia oligembiodes*.

*Relationships.* As no material was made available to be examined, data were taken from Ross (2001). This genus has a combination of characters that places it between *Rhagadochir* and *Pararhagadochir*. Many of the characters given by Ross (2001: 58) in his diagnosis of *Litosembia* are also found in other related genera; the characters actually distinguishing *Litosembia* are the anterior margin of the Sm concave, the small 10Rp2, the Ep free and reduced, the 10Lp1 with the tips fused, the Lpp without any structure and the absence of the middle bladder of the hind basitarsus. *Litosembia* shares with *Rhagadochir* and *Pararhagadochir* the absence of cross-veins between Rs and Ma1 (character 31).

*Composition and distribution.* *Litosembia* contains only one species, *L. oligembioides*, known only from Belem, Brazil (Ross, 2001).

#### Navasiella Davis, 1940

*Navasiella* Davis, 1940a: 177. Type species *Oligotoma sulcata* Navas.

*Diagnosis.* *Navasiella* can be distinguished by having the LC1dp tubular (character 41) with the setae concentrated on the tip, the laminate carinae on the inner tip of the 10Lp1 (character 57), the ventral tip of the 10Rp1 sclerotized (character 71). It can also be distinguished from *Pararhagadochir* and *Rhagadochir* by the well-developed Rpp (character 90), the fused Ep and 10Rp2 (character 92), and the well-differentiated molar teeth (character 2).

*Relationships.* The position of *Navasiella* is well supported (Fig. 45); it is clear that this genus possesses numerous characters to be a member of Archemiidae closely related to *Rhagadochir* and *Pararhagadochir*.

*Composition and distribution.* This genus contains only one species, *Navasiella sulcata*, described from a single locality in Congo.

#### Ambonemia Ross, 2001

*Ambonemia* Ross, 2001: 66. Type species: *Ambonemia incae*.

*Ischnosembia* Ross, 2001: 32. syn.n. Type species: *Ischnosembia amazonica*.

*Diagnosis.* *Ambonemia* can be distinguished from *Biguemia*, *Gibocercus* and *Pararhagadochir* (the most closely related genera) by having the 10L diagonally elevated and the 10Lp1 with the tips not well separated (as in Teratemiidae).

*Relationships.* *Ambonemia* and *Ischnosembia amazonica* Ross are grouped by having the 10L diagonally elevated (character 51, a synapomorphy with the highest fit; Appen-

dix 4); both also share the apex of the Ep elevated and the shape of the 10Lp1 (see diagnosis). In spite of the clear similarity between *Ambonemia* and *Ischnosembia*, Ross did not comment on their likeness, but compared each one of these genera with a different genus (*Ambonemia* with *Malacosembia* and *Ischnosembia* with *Pararhagadochir*). Here, I propose *Ischnosembia* as the junior synonym of *Ambonemia*.

*Composition and distribution.* *Ambonemia adspersa* (Enderlein) from Bolivia, *Ambonemia incae* Ross from Peru, and *Ambonemia amazonica* (Ross) from Brazil; all species known only for the type locality from the Amazon Basin.

#### Biguemia Szumik, 1998 (Figs 4, 12, 16, 26, 31)

*Biguemia* Szumik, 1998b: 149, 2002: 444; Ross, 2001: 60. Type species: *Biguemia copo*.

*Aphanemia* Ross, 2001: 64. syn.n. Type species: *Aphanemia obscura*.

*Diagnosis.* *Biguemia* is a genus clearly distinguishable by having the 10Lp1 with both tips longer (longer than the 10L) and equal (Fig. 26), with the inner tip more sclerotized, the LC1dp depressed (character 43), the 10Rp1 with a longitudinal carinae (character 76) and the presence of a convexity on the 10Rp1 (Fig. 31; character 77).

*Relationships.* The monotypic genus *Aphanemia* is grouped with *Biguemia* (Fig. 43) by bearing all the characters mentioned in the diagnosis; this group has the highest support under jackknifing (Fig. 45). The only species of *Aphanemia* has no distinctive characters to justify its exclusion from *Biguemia* and, therefore, I propose *Biguemia* as a senior synonym of *Aphanemia*.

*Biguemia* and *Gibocercus* form a well-supported group (Fig. 45) by having the 10Rp1 with the dorsal tip well developed and the ventral tip very inconspicuous (character 69) and the 10Lp1 with both tips longer (character 55, both characters have minimal homoplasy). These genera are also grouped by the presence of cross-veins between Ma and Mp (Fig. 12; character 36), but this condition is also present in other groups of Embioptera.

*Composition and distribution.* Originally described for two species, *Biguemia copo* and *Biguemia cocum* from Argentina and Brazil, respectively (Szumik, 1998b); the genus now includes *Biguemia multivenosa* Ross and *Biguemia obscura* (Ross), both from Brazil.

#### Gibocercus Szumik, 1998 (Figs 7, 13, 27, 32, 40, 41)

*Gibocercus* Szumik, 1998b: 141, 2002: 444; Ross, 2001: 35. Type species: *Gibocercus chaco*.

**Diagnosis.** *Gibocercus* can be distinguished easily by many exclusive characters, such as the tubular form of the LC1dp (Figs 40, 41; character 41), the convexity on the dorsal face of the LC1dp (Figs 40, 41; character 44), the inner tip of the 10Lp1 beaklike and larger, the external tip of the 10Lp1 conic, unsclerotized and smaller (Fig. 27; character 55), the external face of the 10Rp1 strongly depressed (character 72) and the 10Rp2 broad with a discoidal apex (character 80).

**Relationships.** With the exception of character 41, all the synapomorphies mentioned in the diagnosis have little or no homoplasy (Appendix 4) and the monophyly of the genus is well supported (Fig. 45). *Gibocercus nanai* is a sister group of the other species of *Gibocercus* by not having the basal process of the LC1 (Fig. 41), otherwise an autapomorphy of the genus (Szumik, 1998b).

**Composition and distribution.** *Gibocercus* was described originally (Szumik, 1998b) with four species: *G. chaco*, *G. urucumi*, *G. nanai* and *G. beni* from Argentina, Brazil, Peru and Bolivia, respectively. Recently Ross (2001) described another five species: *G. peruvianus*, *G. flavipes* [Peru], *G. magnus* [Bolivia], *G. sandrae* and *G. napoa* [Ecuador].

*Pararhagadochir* Davis, 1940 (Figs 5, 8, 9, 14, 23, 24, 30, 34, 35)

*Pararhagadochir* Davis, 1940a: 181, 1942: 114; Ross, 1944: 420, 2001: 43; Szumik, 1996: 51, 1998a: 34, 1998b: 141, 2002: 444. Type species: *Embia trinitatis* De Saussure.

**Diagnosis.** *Pararhagadochir* can be distinguished from other Archembiidae by having the anterior margin of the Sm strongly concave (Fig. 5; character 6), the 10Lp1 forked with the internal tip (hook) and the external tip (flat lobe) separated, with both tips always shorter than the width of the 10L (Figs 23, 24). Also, it can be differentiated by the presence of a sclerotized node between the 10L and the base of the LC1 (character 84) and the 10Rp2 with more than one longitudinal laminate keel (character 78).

**Relationships.** The position of *Pararhagadochir surinamensis* as a sister group of the other species of *Pararhagadochir* is not well supported (Fig. 45); in addition, slightly suboptimal trees have this species excluded from the genus *Pararhagadochir*. Many groups inside the genus have no support because those resolutions are defined by highly homoplastic mandible or wing characters. Only three groups have some degree of support: all the species excluding *P. surinamensis*, is supported by the characters mentioned in the diagnosis, *Pararhagadochir birabeni* (Navas) + *Pararhagadochir tenuis* (Enderlein) by having the external tip of the 10Lp1 bilobed (Fig. 23; character 60), and *Pararhagadochir trachelia* + *Pararhagadochir schadei* by having the 10Lp1 base longer (Fig. 24; character 61).

**Composition and distribution.** The genus is known from Colombia to south of Buenos Aires (Argentina). It includes thirteen species: *Pararhagadochir trinitatis* (de Saussure) from Trinidad and Venezuela, *P. bicingillata* (Enderlein), *P. christae* Ross, *P. balteata* Ross, *P. minuta* Ross from Brazil, *P. flavicollis* (Enderlein), *P. tenuis* (Enderlein) from Bolivia, *P. schadei* Ross from Paraguay, *P. birabeni* (Navas), *P. trachelia* (Navas), *P. confusa* Ross, *P. pallida* Ross from Argentina and *P. picchua* Ross from Peru. Although *Pararhagadochir* is the genus with the most species of Archembiidae, many of these species are known only from type locality; a manuscript in preparation considerably enlarges the distribution of many known species.

*Malacosembia* Ross, 2001 (Figs 10, 15, 25)

*Malacosembia* Ross, 2001: 70. Type species: *Malacosembia tucumana*.

**Diagnosis.** *Malacosembia* can be distinguished from *Pararhagadochir*, the genus most closely related to it, by having the Ep and 10Rp2 inconspicuous; the dorsal tip of the 10Rp1 like a depressed hook, well developed, with two or three longitudinal carinae, and the anterior margin of the Sm straight and membranous.

**Relationships.** Although *Malacosembia* appears in both optimal trees as the sister group of *Pararhagadochir* + (*Biguembia* + *Gibocercus*), the relationship has low support (Fig. 45).

**Composition and distribution.** The genus contains two species: *Malacosembia tucumana* from Argentina and *Malacosembia yungae* from Bolivia. The nests of *Malacosembia tucumana* are 10–39 cm in diameter, with numerous tubes crossing over, all covered with a shiny layer of web (Szumik, pers. obs.).

## Acknowledgements

This work was supported by grants PIP CONICET no. 4973 and PICT98 no. 01–04347. The criticisms of Pablo Goloboff, James Carpenter, Fernando Navarro and an anonymous reviewer are deeply appreciated.

## References

- Davis, C. (1938) Studies in Australian Embioptera. Part III: Revision of the genus *Metoligotoma*, with descriptions of new species, and other notes on the family Oligotomidae. *Proceedings of the Linnean Society of New South Wales*, **63**, 226–272.
- Davis, C. (1940a) Taxonomic notes of order Embioptera. Part XV: The genus *Rhagadochir* Enderlein, and genera convergent to it. *Proceedings of the Linnean Society of New South Wales*, **65**, 171–191.



- Davis, C. (1940b) Taxonomic notes on the order Embioptera. Part XVII: A new neotropical genus previously confused with *Embia* Latreille. *Proceedings of the Linnean Society of New South Wales*, **65**, 344–352.
- Davis, C. (1940c) Taxonomic notes of order Embioptera. Part XX: The distribution and comparative morphology of the order Embioptera. *Proceedings of the Linnean Society of New South Wales*, **65**, 533–542.
- Davis, C. (1940d) Family classification of the order Embioptera. *Annals of the Entomological Society of America*, **33**, 676–682.
- Davis, C. (1942) Report on a collection of Embioptera from Trinidad and Guyana. *Proceedings of the Royal Entomological Society of London B*, **11**, 111–119.
- Enderlein, G. (1909) Die klassifikation der Embiidinen, nebst morphologischen und phisiologischen Bemerkungen, besonders über das Spinnen derselben. *Zoologischen Anzeiger*, **35**, 166–191.
- Enderlein, G. (1912) Embiidinen. *Collections Zoologiques du Baron Longchamps, Catalogue Systematique et Descriptif, Bruxelles*, **3**, 1–121.
- Farris, J.S., Albert, V.A., Källersjö, M., Lipscomb, D. & Kluge, A.G. (1996) Parsimony jackknifing outperforms neighbor-joining. *Cladistics*, **12**, 99–124.
- Friederichs, K. (1934) Das Gemeinschaftsleben der Embiiden und Näheres zur Kenntnis der Arten. *Archiv für Naturgeschichte*, **3**, 405–444.
- Goloboff, P.A. (1993a) Estimating character weights during tree search. *Cladistics*, **9**, 83–91.
- Goloboff, P.A. (1993b) *Pee-Wee: Parsimony and Implied Weights*, version 2.7. San Miguel de Tucuman, Tucuman.
- Goloboff, P.A., Farris, J.S., Källersjö, M., Oxelmann, B., Ramirez, M. & Szumik, C.A. (2003) Improvements to resampling measures of group support. *Cladistics*, **19**, 324–332.
- Gray, G.R. (1832) *The Animal Kingdom of Cuvier* (ed. by E. Griffith and E. Pidgeon), pp. 346–347. Whittaker, London.
- Horovitz, I. (1999) A report on 'One day symposium on numerical cladistics'. *Cladistics*, **15**, 177–182.
- Krauss, H.A. (1911) Monographie der Embien. *Zoologica Stuttgart*, **23**, 1–78.
- Mariño, E. & Márquez, C. (1988) Embiopteros de Mexico. IV. Descripción de una nueva especie del genero *Clothoda* Enderlein, 1909. *Anales del Instituto de Biología de la Universidad Nacional Autónoma de México, Serie Zoológica*, **58**, 63–68.
- Navas, L. (1918) Embiopteros (Ins.) de America Meridional. *Broteria, Serie Zoológica*, **16**, 85–110.
- Nixon, K. (1999) The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics*, **14**, 407–414.
- Ross, E.S. (1944) A revision of the Embioptera or web-spinners, of the New World. *Proceedings of the Entomological Society of Washington*, **94**, 401–504.
- Ross, E.S. (1952) The Embioptera of Angola. *Publicações Culturais da Companhia de Diamantes de Angola*, **14**, 41–54.
- Ross, E.S. (1960) Parthenogenetic African Embioptera. *Wasmann Journal of Biology*, **18**, 297–304.
- Ross, E.S. (1970) Biosystematics of the Embioptera. *Annual Review of Entomology*, **5**, 157–172.
- Ross, E.S. (1971) A new neotropical genus and species of Embioptera. *Wasmann Journal of Biology*, **29**, 29–36.
- Ross, E.S. (1984) A classification of the Embiidina of Mexico with descriptions of new taxa. *Occasional Papers of the California Academy of Sciences*, **140**, 1–56.
- Ross, E.S. (2000) Origin, relationships and integumental anatomy of the insect order Embiidina. *Embia*, Part 1. *Occasional Papers of the California Academy of Sciences*, **149**, 1–53.
- Ross, E.S. (2001) The Embiidae of the Americas (order Embiidina). *Embia*, Part 3. *Occasional Papers of the California Academy of Sciences*, **150**, 1–86.
- Szumik, C.A. (1994) *Oligembia vetusta*, a new fossil Teratemiid (Embioptera) from Dominican amber. *Journal of the New York Entomological Society*, **102**, 67–73.
- Szumik, C.A. (1996) The higher classification of the order Embioptera: a cladistic analysis. *Cladistics*, **12**, 41–64.
- Szumik, C.A. (1998a) Embioptera. *Biodiversidad de artropodos argentinos* (ed. by S. Coscaron and J. J. Morrone), pp. 32–37. Ediciones del Sur, Argentina.
- Szumik, C.A. (1998b) Two new Neotropical genera of Embiidae (Embioptera, Insecta). *Journal of the New York Entomological Society*, **105**, 140–153.
- Szumik, C.A. (2000a) The Embiopteran classification (Insecta). Presented at the XIX Hennig Meeting of the Willy Hennig Society, 28 May–2 June 2000, Leiden.
- Szumik, C.A. (2000b) Phylogeny of Embioptera (Insecta) revisited. Presented at the XXI International Congress of Entomology/ XVIII Brazilian Congress of Entomology, 20–26 August 2000, Foz do Iguazú.
- Szumik, C.A. (2002) Embioptera. *Biodiversidad, taxonomia y biogeografía de artropodos de México: hacia una síntesis de su conocimiento* (ed. by J. Llorente Bousquets and J. J. Morrone), pp. 441–448. Universidad Nacional Autónoma de México, México.

Accepted 25 August 2003

Appendix 1. Data matrix: ninety-four characters × fifty-seven taxa. Polymorphism: A = 01.

	1	2	3	4	5	6	7	8	9	
	0	1	2	3	4	5	6	7	8	9
<i>Clothoda</i>	11000111010101023200310011111	A100111110000	--003100000	--0	03100000	--0	-----0	-----	--1101000000--	-----
<i>Chromatoclothoda</i>	21000011001110102320011001111	10101010000	--003110000	--0	03110000	--0	-----01010000000000	0001001	1010000110	-----
<i>Antipaluria</i>	210001101111000342112110111	11011110000	--003111000	--00000	00000000	000000	00000000000000	0001001	10110000110	-----
<i>Machadoemia</i>	0-000101000--10--03-201110011	111100011A	112400002	1100012	00000000	0001102	000000000000	000001101	1020001200	-----
<i>Dityrocercus</i>	2-10111010--000200-201110011	110100111130000	--1100012	000002	103000000	000000	0000010300010000	000001101	101001200	-----
<i>Odontembia</i>	0-00110010--000202-201110000	0100011A	11200040	--1100112	00000000	000001000	000000000000	0000101	101001200	-----
<i>Metembia</i>	0-01000101--10101-20111011	00100102	1100030	--1100012	--000020	00000000	000000000000	0000101	101001200	-----
<i>Pseudembia</i>	0-000010101--110103-20121001	111101001112	11100030	--1100025	--000020	000102000000	000000000001	101	102001200	-----
<i>Embia</i>										
<i>fibulatoria</i>	0-01010101--00--03-20111011	00100100	11102123	0000000	1100012	0000000000	000000000000	00000101	1010101200	-----
<i>verhoeffi</i>	0-01001001--00--03-20111011	001001A	100000102	121100000	1100012	000000000000	000000000000	0000101	1010101200	-----
<i>Archembia</i>										
<i>kozbauei</i>	012011001110010112221011001	10111000A	1000221	0000012	000130000	10--0010011	2000000000	00002011	10110010110	-----
<i>batesi</i>	01201100001110102221011011	101A	10000100	02210000	12000130000	10--0110011	2000000000	00002011	10110010110	-----
<i>nspA</i>	0-20110110--010102-21011011	11101000100	02210000	--1200013	00010--000011	20000000	0000000000	00002011	10110010110	-----
<i>nspB</i>	1120110101010232101101111	11100001A	002210000	12000130000	10--000011	20000000	0000000000	00002011	10110000110	-----
<i>nspC</i>	0-20110001--011101-21011011	101A	10010100	2210000	12000130000	10--010011	2000000000	00002011	10110010110	-----
<i>arida</i>	00200101010101--210-A-	-----1-100--	--1-102	200000	--12000130000	10--0000011	2000000000	00002011	10000000110	-----
<i>Calamoclostes</i>										
<i>albitriola</i>	00200100010101----21010011	--011011001110	2200000	--0200013	00010--0110011	2000000000	0000000000	00002010	10010000110	-----
<i>micropterus</i>	01200100011111----110110--	--111000102	200000	--0200013	00010--0010011	2000000000	0000000000	00002000	10010000110	-----
<i>Ochrembia</i>	0-20010101--010201-20111010	10010110	102401000	--1200114	01000--0021103	0010000000	0000000000	00002000	100102000200	-----
<i>Embolyntha</i>	00201101001111--2011101000	A01000	A110241000	--1200014	01000--0020011	3000000000	0000000000	00002001	10002010201	-----
<i>Argocerambia</i>	001001000101011--2-1101000	--0100010102	311000	--1200014	01000--0020011	3000000000	0000000000	00002011	10000010200	-----
<i>Xiphosombia</i>	0020010110010102-2--110100	1110010102	200000	--1200114	01000--0000011	3000000000	0000000000	00002001	10000010200	-----
<i>Dolonembia</i>	0020000001001--2--2--11100	1010002	401000	--1200114	01000--000002	3000000000	0000000000	00002001	10002000201	-----
<i>Conicerambia</i>	00100101000010102310111001	00100100A	1010050000	1210114	01000--000002	3000000000	0000000000	00002000	10112000100	-----
<i>Brachypterembia</i>	0110010101010231011001101	1010000002	2000--01112001	1401000	--000001	3000000000	0000000000	00002001	10110000100	-----
<i>Neorhagadochir</i>	0010000110101021232010101	100101000A	101000	--001112001	1401000	--000000	00000030	1000000000	0000200111002010100	-----
<i>Pachylembia</i>										
<i>chaptale</i>	0-10012101--010103-0---	1-----	-----	-----	2000--	01011210114	000001--00000002	00000000	00003001	10010000100
<i>taxcoensis</i>	001001010101010240---	1-----	-----	-----	100210000	1210114	000001--00000002	00000000	00003001	10012010100
<i>unicincta</i>	00100021010101010550---	1-----	-----	-----	2000--	1011210114	000001--00000002	00000000	00003001	10010010100
<i>Ischnosombia</i>										
<i>amazonica</i>	00200010011111A-----	2---1-1000	--00000000	102300000	--120102520	0000010000	123000000000	00000000	00002001	100110010201
<i>surinamensis</i>	0-20010000--00--11-20101011	001000000102	400000	--120002520	0000010001	1230000000	0000000000	00002001	100100010201	-----
<i>Litosembia</i>	0020001000100A--1-2--11010	1000--00000000	102300000	--120002510	0000010000	10200000	0000000000	0000101	100102000200	-----
<i>Ambonembia</i>	0-20000001--0102---	2--11101010000	1000001010240	00000	--120102520	0000010000	113000000000	00000000	00003000	10103000201

	1	2	3	4	5	6	7	8	9
	0123456789012345678901234567890123456789012345678901234567890123								
<i>Pararhagadochir</i>									
<i>trinitatis</i>	0020001000100111124201110110010100000010230000021200025200000100011130000000001201100103000201								
<i>trachelia</i>	0020001000000111137201010100001010000001023000002120002520000020011123000000001201101103110201								
<i>schadei</i>	0020011000000111123201010-0001010000A0002300002120002520000200111300000001201101103010201								
<i>balteata</i>	00200011010102012201110100001110240000212000252000010011123000000001201101102110201								
<i>christae</i>	002000100101011112220101010000A020240000212000252000010011113000000001200101102010201								
<i>birabeni</i>	002000100101010211122010101000010102400002120002520000110011123000010001201101102010201								
<i>tenuis</i>	0-20001001--010202-201110100001010000100240000-120002520000110011123000010001201101103110201								
<i>confusa</i>	012000100101011220111010001A100001010230000212000252000010011123000010001201100102010201								
<i>flavicollis</i>	00200010000000--114201110-0001010000002300000-1200025200001001112300000001201101103000201								
<i>Malacosembia</i>	0020010001010102000201110000010101A00000240100021200025200001000110300000000300110103010001								
<i>Navasiella</i>	0-10010001--010101-201010-00010000000102500000-120002520100010001113001000000200100102011210								
<i>Scelembia</i>									
<i>malkini</i>	0-30010000--0111111-201110100001010000001023000002120002510000010001123000000000200100102010200								
<i>carpenteri</i>	0-30010001--0111111-2111101100101000000102300000-12000251000001000-11300000000020-100-030-0201								
<i>vilhenai</i>	0-30010001--0111102-2010101100101001000102300000-12000251000001000012300000000000200100002010200								
<i>Rhagadochir</i>									
<i>vosseleri</i>	00300100000101010-321111011001010011101023000002-200025100000100--1-3000000-000200-0--30-0201								
<i>beauxii</i>	--30010000--0111111-211110110010100110102310000-120002510000100--11300000-00-20--0-0020-0201								
<i>Aphanembia</i>									
<i>Biguembia</i>	00200100011001-----2-----1-----102311000-1200025300000100011131000000110200100102010201								
<i>cocum</i>	0-20010100-010202-21111011001010000AA102401000-1200025300000100111131000001110200100002010201								
<i>copo</i>	0020010001-101010352111011110100011110140100021200025300000100111131000001110200100002010201								
<i>multivenosa</i>	0020010001111010352111100111-1100111110140102021200025300000100111131000001110200100002010201								
<i>Gibocercus</i>									
<i>nanai</i>	0-20010000--110001-20111011101010000A0002500100-1200025400000100111131011000000210100102010201								
<i>beni</i>	1120010100-1110102320110111101000A101-25001202-200025400000100111131001001100210100102010201								
<i>chaco</i>	012001000011011102520111001101101AA1010250012021200025400000100111131001001000210100102010201								
<i>urucumi</i>	1-20010100--110103--01111011001110010101A002500120-1200025400000100111131001001000210100102010201								

**Appendix 2**

List of species studied for the cladistic analysis.

*Outgroup*

*Clothoda nobilis* (Gerstaecker) BRAZIL: paratypes (USNM)  
*Antipaluria urichi* (De Saussure) TRINIDAD: common material (CU, USNM, AMNH)  
*Antipaluria silvestris* Ross VENEZUELA: paratypes (USNM)  
*Chromatoclothoda aurata* Ross PERU: paratypes (USNM)  
*Chromatoclothoda elegantula* Ross BRAZIL: paratypes (USNM)  
*Odontembia spinosa* (Navas) CONGO R.D.: holotype (MRAC)  
*Embia verhoeffi* Friederichs MOZAMBIQUE: holotype (ZMB)  
*Embia fibulatoria* Enderlein CAMEROON: paratypes (ZMB)  
*Machadoembia angolica* Ross ANGOLA: paratypes (MCZ, USNM)  
*Machadoembia arcuata* Ross CONGO R.D.: holotype (MRAC)  
*Dihyboecercus basilewskyi* Ross BURUNDI: holotype (MRAC)  
*Dihyboecercus severini* Enderlein CONGO R.D.: holotype (MRAC)  
*Pseudembia truncata* Davis INDIA: holotype (MCZ)  
*Pseudembia ferox* (Davis) INDIA: holotype (MCZ)  
*Pseudembia immsi* (Davis) INDIA: holotype (MCZ)  
*Metembia flava* Davis INDIA: holotype (MCZ)

*Ingroup*

*Archembia kotzbaueri* (Navas) BRAZIL: common material (MNRJ, MZSP, USNM *lacombea* paratypes)  
*Archembia batesi* (MacLachlan) BRAZIL, PERU: common material (USNM, AMNH)  
*Biguembia cocum* Szumik BRAZIL: holotype and paratypes (MZSP)  
*Biguembia copo* Szumik ARGENTINA: holotype and paratypes (IFML)  
*Brachypterembia moreliensis* Ross MEXICO: paratypes (USNM)  
*Conicerembia tepicensis* Ross MEXICO: paratypes (USNM)  
*Gibocercus chaco* Szumik ARGENTINA: holotype, common material (IFML)  
*Gibocercus urucumi* Szumik BRAZIL: holotype (MZSP)  
*Gibocercus beni* Szumik BOLIVIA: holotype and paratypes (MCZ)  
*Gibocercus nanai* Szumik PERU: holotype (USNM)  
*Malacosembia tucumanensis* Ross ARGENTINA: common material (IFML)

*Neorhagadochir salvini* (McLachlan) MEXICO, EL SALVADOR, HONDURAS: common material (IBUNAM, USNM, CMNH)  
*Ochrembia wagneri* (Navas) ARGENTINA: holotype (MNHN), common material (IFML)  
*Pachylembia chapalae* Ross MEXICO: paratypes (USNM)  
*Pachylembia taxcoensis* Ross MEXICO: paratypes (USNM)  
*Pachylembia uncinata* Ross MEXICO: paratypes (USNM)  
*Pararhagadochir trinitatis* (De Saussure) TRINIDAD, COLOMBIA: common material (AMNH, CU, USNM, MCZ)  
*Pararhagadochir balteata* Ross BRAZIL: paratypes (USNM), common material (MZSP)  
*Pararhagadochir birabeni* (Navas) ARGENTINA: common material (MACN, IFML)  
*Pararhagadochir christae* Ross BRAZIL: paratypes (USNM)  
*Pararhagadochir confusa* Ross PARAGUAY, ARGENTINA: paratypes (MCZ), common material (IFML)  
*Pararhagadochir tenuis* (Enderlein) BOLIVIA: holotype (HUBN), common material (IFML)  
*Pararhagadochir trachelia* (Navas) ARGENTINA: common material (IFML, MACN)  
*Pararhagadochir flavicollis* (Enderlein) BOLIVIA: common material (USNM, IFML)  
*Pararhagadochir schadei* Ross PARAGUAY, ARGENTINA: paratypes (MCZ), common material (IFML)  
*Pararhagadochir surinamensis* Ross SURINAM: holotype (CU)  
*Rhagadochir malkini* Ross ANGOLA: paratype (MCZ)  
*Rhagadochir vilhenai* Ross ANGOLA: paratype (MRAC)  
*Navasiella sulcata* (Navas) CONGO R.D.: holotype (MNHN)

**Appendix 3**

List of characters used in the cladistic analysis.

*Head*

- Interocular elliptical area not pigmented (males)*: (0) no; (1) yes; (2) yes, but in a prominent elevation (in some Clothodidae).
- Interocular elliptical area not pigmented (females)*: (0) no; (1) yes; (2) yes, in a prominent elevation.
- Number of molar teeth on left and right mandibles (males)*: (0) 2–1, teeth strong, as well defined as incisive teeth; (1) 2–1, teeth strong, but less defined than incisive teeth; (2) 2–1, same as (1) but one of the left molar teeth inconspicuous; (3) 1–1, just one molar tooth.
- Mandibles*: (0) depressed; (1) tubular.
- Incisive teeth concentrated on tip of mandibles*: (0) no; (1) yes.
- Mm sclerotized*: (0) no (Fig. 5); (1) yes (Figs 1–4).

6. *Anterior margin of Sm*: (0) straight and well defined (Figs 2, 3); (1) concave (Fig. 5); (2) W-like (2 small concavities).
7. *Sm, base*: (0) narrow, same width as anterior margin (Figs 1, 5); (1) broad, wider than anterior margin (Figs 2–4).
8. *Sm pilose*: (0) no; (1) yes (Fig. 1).
9. *Prothorax pigmented (male)*: (0) no; (1) yes.
10. *Prothorax pigmented (female)*: (0) no; (1) yes.
11. *Apical antennal segments pigmented (male)*: (0) yes; (1) no.
12. *Apical antennal segments pigmented (female)*: (0) yes; (1) no.

#### *Hind basitarsus*

13. *Middle bladder*: (0) absent (Fig. 8); (1) present (Figs 6, 7, 9, 10).
14. *Shape of middle bladder*: (0) large (more than 50% of width of basitarsus; Figs 6, 7); (1) small (less than 40% of width of basitarsus; Figs 9, 10).
15. *Position of middle bladder*: (0) basal; (1) medial (Figs 6, 7); (2) apical (Fig. 10).
16. *Shape of apical bladder*: (0) large (Figs 6, 7); (1) small (Figs 8, 9).
17. *Number of prolateral rows (male)*: (0) one; (1) 2; (2) 3; (3) 4; (4) 5; (5) 6.
18. *Number of prolateral rows (female)*: (0) one; (1) 2; (2) 3; (3) 4; (4) 5; (5) 6; (6) 7; (7) 8.

#### *Wings*

19. *Wings*: (0) absent; (1) reduced; (2) present.
20. *Wing base union* (Szumik, 1996): (0) 'type A', Rs + Ma and Mp start together from Cu, and a broad cross-vein present between Rs + Ma and R<sub>1</sub> (Figs 14, 15); (1) 'type B', Rs + Ma and Mp start separately from R<sub>1</sub> and Cu (Fig. 11); (2) 'type C', Rs + Ma and Mp start fused from R<sub>1</sub> and Cu.
21. *Anal region*: (0) large (Fig. 11); (1) small (Figs 12–15).
22. *Cu forked*: (0) no; (1) yes, with 2 veins (Figs 11–15); (2) yes, with 3 veins; (3) yes, with 4 veins.
23. *Ma forked*: (0) no; (1) yes (Figs 11–15).
24. *Anal forked*: (0) no; (1) yes (Fig. 11).
25. *Cua*: (0) conspicuous; (1) diffuse.
26. *Ma1 finished on the wing edge*: (0) no (Figs 14, 15); (1) yes (Figs 12, 13).
27. *Ma2 finished on the wing edge*: (0) no (Figs 14, 15); (1) yes (Fig. 12).
28. *Mp finished on the wing edge*: (0) no (Figs 11–15); (1) yes.
29. *Cross-veins present between C and R<sub>1</sub>*: (0) no; (1) yes (Figs 11–15).
30. *Cross-veins present between Rs and Ma*: (0) no (Figs 12–15); (1) yes (Fig. 11).

31. *Cross-veins present between Rs and Ma1*: (0) no; (1) yes (Figs 11–15).
32. *Cross-veins present between R<sub>1</sub> and Rs + Ma*: (0) no; (1) yes.
33. *Cross-veins present between Rs + Ma and Mp*: (0) no; (1) yes.
34. *Cross-veins present between Ma2 and Mp*: (0) no (Figs 11, 13–15); (1) yes (Fig. 12).
35. *Cross-veins present between Ma1 and Ma2*: (0) no (Figs 11, 13–15); (1) yes (Fig. 12).
36. *Cross-veins present between Ma and Mp*: (0) no (Figs 12, 15); (1) yes (Figs 11, 13, 14).
37. *Cross-veins present between Mp and Cua*: (0) no (Figs 11, 13–15); (1) yes (Fig. 12).

#### *Terminalia*

38. *Longitudinal ratio between basal and apical cerci*: (0) apical cerci longer than basal; (1) both the same length; (2) apical cerci shorter; (3) apical cerci very short, less than half length of basal cerci.
39. *Internal face of LC1 depressed*: (0) no; (1) yes.
40. *LC1, setae distribution*: (0) absent; (1) present, on apical and medial area; (2) present, on apical area.
41. *LC1dp, shape*: (0) absent (Fig. 36); (1) dome-shaped process; (2) conical process, where caudal and anterior margins are oblique to longitudinal axis of LC1 (Fig. 37); (3) semiglobose process, caudal margin oblique and anterior margin perpendicular to longitudinal axis of LC1; (4) square process, caudal and anterior margins perpendicular to longitudinal axis of LC1 (Fig. 42); (5) tubular, same as (4) but process is longer than width of LC1 (Fig. 41).
42. *LC1dp, position*: (0) apical (Figs 38, 40–42); (1) medial (Figs 37, 39).
43. *LC1dp, depressed*: (0) no; (1) yes.
44. *Semiglobose convexity on dorsal face of LC1dp*: (0) no; (1) yes (Figs 40, 41).
45. *LC1, basal node*: (0) absent; (1) present, internal and without setae; (2) present, internal with setae (Fig. 41); (3) present, dorsal with setae; (4) present, ventral with setae.
46. *LC1, base*: (0) narrow (LC1 tubular); (1) broad (LC1 conical, Fig. 36), this condition is only present in *Neorhagadochir* (= *Brachypterembia*).
47. *1° Vfs (female)*: (0) well developed, well separated from central plate (Fig. 18); (1) well developed, partially separated from central plate (Fig. 17); (2) differentiated from central plate by 2 notches on caudal margin (Fig. 16); (3) inconspicuous, differentiated from central plate by degree of pigmentation.
48. *9T*: (0) with a discoidal area sclerotized on middle of tergite, only present in *Calamoclostes*; (1) uniformly sclerotized.
49. *10T shape*: (0) one plate; (1) 2 subequal plates; (2) 2 different plates.
50. *10T pilose*: (0) no; (1) yes.

51. *10L diagonally elevated*: (0) no; (1) yes.
52. *10Lp1 start in inner anterior angle*: (0) no; (1) yes.
53. *Tip of 10Lp1*: (0) absent; (1) simple (Figs 19–22); (2) forked (Figs 23–27).
54. *10Lp1 shape*: (0) absent; (1) small lobe; (2) sharp hook; (3) straight and flat stick (Figs 19, 20); (4) curved and flat stick (Fig. 21); (5) stick with an internal hook and external laminate lobe (Figs 23–27).
55. *10Lp1 forked*: (1) internal tip (hook) and external tip (flat lobe) fused (present in *Rhagadochir* (= *Scelembia*)); (2) same as (1), tips separated (e.g. *Pararhagadochir*, Figs 23–25); (3) internal and external tips longer and conical (*Biguembia*, Fig. 26); (4): same as (3) but internal tip broad (*Gibocercus*, Fig. 27).
56. *Internal face of 10Lp laminate*: (0) no; (1) yes.
57. *Laminate carina on 10Lp1*: (0) no; (1) yes.
58. *10Lp with apex expanded*: (0) no; (1) yes.
59. *10Lp1 reduced to a small hook*: (0) no; (1) yes, only present in *Pachylembia*.
60. *Shape of external tip of 10Lp1*: (0) lobed; (1) bilobed (Fig. 23). Exclusive of some species of *Pararhagadochir*.
61. *10Lp1 base*: (0) absent; (1) shorter; (2) longer.
62. *External margin of 10Lp1*: (0) regular; (1) irregular.
63. *Longitudinal carinae on 10Lp1*: (0) absent; (1) one (Fig. 19); (2) many.
64. *Depression between 10Lp and 10L*: (0) absent; (1) present; (2) same as (1) but more depressed.
65. *Internal anterior angle of 10L excavated*: (0) no; (1) yes.
66. *Caudal margin of 10L*: (0) convex; (1) concave.
67. *Basal area of 10R membranous*: (0) no; (1) yes, but only a smaller area; (2) yes, but a larger area (half the plate).
68. *Caudal process of 10R (10Rp1)*: (0) absent; (1) a small and rounded lobe; (2) a small and sharp tip; (3) a forked process (Figs 29, 30), with a dorsal tip (hooklike, well sclerotized) and a ventral tip (unsclerotized lobe).
69. *10Rp1, dorsal tip well developed*: (0) no; (1) yes (Figs 31, 32).
70. *10Rp1, ventral tip well developed*: (0) no; (1) yes.
71. *10Rp1, ventral tip sclerotized*: (0) no; (1) yes.
72. *10Rp1 strongly depressed on external margin*: (0) no; (1) yes.
73. *Base of 10Rp1 prolonged, longer than length of 10R*: (0) no; (1) yes.
74. *Apex of 10Rp1 truncated*: (0) no, (1) yes (Fig. 28).
75. *Microtrichiae in 10Rp1*: (0) no; (1) yes (Fig. 31).
76. *10Rp1 with a longitudinal keel*: (0) no; (1) yes.
77. *Convexity on base of 10Rp1*: (0) no; (1) yes (Fig. 31).
78. *Anterior process of 10R (10Rp2) with longitudinal laminate keels*: (0) no; (1) yes.
79. *10Rp2, shape*: (0) lateral flap extended over 10Lp1, parallel to 10R; (1) incipient lobe; (2) rodlike, longer, oblique to 10R; (3) same as (2) but diffuse.
80. *10Rp2, broad and discoidal*: (0) no; (1) yes.
81. *Microtrichiae in 10Rp2*: (0) no; (1) yes.
82. *Hp with transversal keels*: (0) no; (1) yes (Figs 33–35).
83. *Hp centred, lobed, with unsclerotized margins*: (0) yes (Figs 34, 35); (1) no (Fig. 33).
84. *Node with microtrichiae between LC1 and 10L*: (0) no; (1) yes.
85. *Lpp fused to H*: (0) no; (1) yes.
86. *Lpp partially membranous*: (0) no (Figs 34, 35); (1) yes (Fig. 33).
87. *Internal caudal angle of Lpp*: (0) without a process; (1) with a thornlike process; (2) with a prominent node (Fig. 34); (3) with a flat hook (Fig. 35).
88. *Node on external anterior angle of Lpp*: (0) no; (1) yes.
89. *Microtrichiae in Lpp*: (0) no; (1) yes.
90. *Rpp*: (0) reduced; (1) well developed.
91. *Shape of Ep*: (0) inconspicuous; (1) broad sclerotized plate; (2) narrow sclerotized band.
92. *Ep–10Rp2 fused*: (0) no; (1) yes, condition present in Anisembiidae, in some species of Clothodidae, and in *Archembia* and *Calamoclostes*.
93. *Ep elevated caudally*: (0) no; (1) yes.

**Appendix 4.** Character number, fit, steps and extra steps for the optimal trees.

Character	Fit	Steps	Extra steps	Character	Fit	Steps	Extra steps
0	3.7	7	5	47	5.0	6	3
1	3.7	6	5	48	10.0	1	0
2	5.0	6	3	49	10.0	2	0
3	6.0	3	2	50	7.5	2	1
4	7.5	2	1	51	10.0	1	0
5	2.5	10	9	52	7.5	2	1
6	2.7	10	8	53	7.5	3	1
7	2.5	10	9	54	5.0	7	3
8	10.0	1	0	55	10.0	4	0
9	1.7	15	14	56	7.5	2	1
10	3.0	8	7	57	6.0	3	2
11	2.3	11	10	58	10.0	1	0
12	3.3	7	6	59	10.0	1	0
13	6.0	3	2	60	10.0	1	0
14	3.0	8	7	61	6.0	4	2
15	2.7	10	8	62	7.5	2	1
16	3.0	8	7	63	2.7	10	8
17	1.4	23	18	64	3.7	6	5
18	2.1	18	11	65	4.2	5	4
19	6.0	4	2	66	6.0	3	2
20	5.0	4	3	67	2.0	14	12
21	7.5	2	1	68	4.2	7	4
22	2.7	11	8	69	6.0	3	2
23	7.5	2	1	70	7.5	2	1
24	–	–	–	71	4.2	5	4
25	2.7	9	8	72	10.0	1	0
26	3.7	6	5	73	10.0	1	0
27	3.0	8	7	74	7.5	2	1
28	3.3	7	6	75	7.5	2	1
29	–	–	–	76	7.5	2	1
30	2.5	10	9	77	10.0	1	0
31	6.0	3	2	78	7.5	2	1
32	6.0	3	2	79	5.0	6	3
33	6.0	3	2	80	10.0	1	0
34	2.3	11	10	81	3.3	7	6
35	3.0	8	7	82	6.0	3	2
36	3.7	6	5	83	5.0	4	3
37	3.7	6	5	84	6.0	3	2
38	1.8	15	13	85	3.0	8	7
39	10.0	1	0	86	4.2	5	4
40	4.2	6	4	87	1.2	24	21
41	1.2	27	22	88	5.0	4	3
42	3.7	6	5	89	2.3	11	10
43	5.0	4	3	90	7.5	2	1
44	10.0	1	0	91	4.5	6	4
45	3.7	9	5	92	6.0	3	2
46	10.0	1	0	93	5.0	4	3