

ORIGINAL ARTICLE

# New insights into the systematics of Entomobryoidea (Collembola: Entomobryomorpha): first instar chaetotaxy, homology and classification

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**Abstract** The largest superfamily Entomobryoidea is one of the key groups in Collembola. However, incorrect recognition of chaetotaxic homology within Entomobryoidea severely impedes the accurate species comparison of adults and phylogenetic reconstruction. Traditional classification of the superfamily at suprageneric level is disputable in the light of recent advances. Transformational homology of tergal chaetotaxy was traced and revised based on 38 species of first instar and partial early instars. Morphological phylogenetic reconstructions were reconstructed mainly relying on first instar characters using both parsimony and likelihood-based algorithms. Outgroup selection and several rogue taxa impacted on resolution and support of otherwise well-supported clades. Integrating published molecular phylogeny, a revised classification of three families and nine subfamilies was presented: Orchesellidae, Entomobryidae and Paronellidae. Orchesellidae includes all basal taxa having a short fourth abdominal segment. Cyphoderidae and Microfalculidae taxa were sunk into Paronellidae. New Paronellidae was divided into two subfamilies: Paronellinae (Paronellini + Cyphoderini + Bromacanthini) and Salininae (Cremastocephalini + Callyntrurini). Microfalculidae (*Microfalcula*) was closer to *Salina* and *Akabosia* and thus transferred into Cremastocephalini. This study erected a new classification framework for Entomobryoidea based upon comprehensive phylogenies. Chaetotaxic homologization across a wide range provided a standardized, comparable, powerful tool for taxonomy.

**Key words** Phylogeny, chaetotaxic homologization, Orchesellidae, Entomobryidae, Paronellidae.

## 1 Introduction

Entomobryoidea is the largest superfamily in Collembola, with more than 2,000 species in the world (Bellinger *et al.*, 1996–2019). Its members have long appendages (antennae, legs, furcula *etc.*), body macrochaetae multilaterally ciliate and cylindrical with tip usually truncate or broadened (Fig. 1A), hind trochanter bearing a variable set of smooth pointed chaetae (trochanteral organ), and a unique bothriotricha pattern on dorsal head and terga. They are usually very active aboveground and rarely euedaphic. Entomobryoidea, Tomoceroidea and Isotomoidea constitute Entomobryomorpha, one of the four orders in Collembola (Deharveng, 2004; Soto-Adames *et al.*, 2008).

Classification history of Entomobryoidea has been recently reviewed by Soto-Adames *et al.* (2008) and Zhang *et al.*

(2015). Börner (1913), Absolon & Kseneman (1942), Yosii (1961), Szeptycki (1979), Yoshii & Suhardjono (1989), and Soto-Adames *et al.* (2008) made great contributions to the suprageneric classification. These systems have no essential differences although those taxa were often treated as families, subfamilies or tribes by different authors (Table 1). Entomobryoidea was traditionally classified using the morphology of below characters: dens, mucro, ratio of abdominal segments III/IV, scales (presence or absence and shape), antennal segments, and trochanteral organ. Whereas, most of them were demonstrated to be of less phylogenetic signals (Zhang *et al.*, 2015) and possibly to be unavailable for suprageneric classification (Zhang & Deharveng, 2015). The traditional definition cannot strictly separate Paronellidae (dens smooth) from Entomobryidae (dens crenulate). Genera *Akabosia*, *Metacoelura* and *Yosii* within Paronellidae have distinct crenulations on dens as those in Entomobryidae.

Relationships within Entomobryoidea have rarely been subjected to rigorous phylogenetic analyses. Szeptycki (1979) discussed the phylogeny based on tergal chaetotaxy, hypothesizing that Microfalculidae was apart from other Entomobryoidea. He also stated that chaetotaxy of Cyphoderidae and Paronellidae was distinctly related to the higher Entomobryidae although relationships of the Entomobryidae, Cyphoderidae and Paronellidae remained obscure. Zhang *et al.* (2015, 2017) presented molecular phylogenies of Entomobryoidea, indicating that Paronellidae and Cyphoderidae were ingroups within Entomobryidae and the Paronellidae was polyphyletic; they also discovered the strong phylogenetic signals of tergal specialized chaetae (S-chaetae).

However, the phylogenetic hypotheses of Entomobryoidea lack comprehensive evidence, particularly morphological support. Several difficulties impede the accurate phylogenetic reconstruction. The first is the insufficient taxa sampling in known analyses. In Szeptycki's book, only two species were examined for non-Entomobryidae taxa; even *Akabosia* having crenulate dens was an atypical paronellid species. Zhang *et al.* (2015) sampled nine species of Paronellidae, whereas few taxa were analyzed for Bromacanthini and Paronellini; two years later two more Paronellidae species were sampled with similar results. None of them examined Microfalculidae. Another difficulty is accurate recognition of chaetotaxic homology across suprageneric taxa particularly those of adults. Chaetotaxy (number, nature and position of chaetae) has been the most important external morphological character in the modern taxonomy of Entomobryoidea. Robust homology hypotheses haven't been applied in a wider range within Entomobryoidea, although Szeptycki (1969, 1972, 1979) erected the basic criteria of homology recognition and related nomenclature system. Some mistakes of Szeptycki's homology hypotheses were discovered by later studies (Soto-Adames, 2008; Zhang *et al.*, 2011).

Theoretically, chaetotaxic homology should be established according to their transformation from a common ancestor. For collembologists, these transformations, which are chaetotaxic correspondences in different species, are operationally determined and hence named by their relative positions (Agolin & D'Haese, 2009). This recognition process is often very difficult for adults because of a gradual differentiation of chaetae during development in epimetabolic Collembola, which includes the development of a whole set of secondary chaetae and modification of first instar elements. Empirical diagnosis of homology in adults is often controvertible without any reference knowledge. Jordana & Baquero (2005) proposed a nomenclature system for *Entomobrya* and its related genera based on only empirical observation of adults, but its accuracy has never been justified. Ontogenetic observation advanced by Szeptycki (1969, 1979) is powerful to strictly trace chaetotaxic correspondences (transformation) between instars and between species. First instar (primary) chaetotaxy, easier to establish homology compared to those of adults, is thus the key groundwork for the establishment of homology hypotheses and also of great phylogenetic significance (Szeptycki, 1979). Up to date, complete primary tergal chaetotaxy of 19 species has been described within Entomobryoidea (Szeptycki, 1969, 1979; Barra, 1975; Soto-Adames, 2008, 2015, 2016; Pan *et al.*, 2011; Zhang *et al.*, 2011; Zhang & Deharveng, 2015). Some important groups have never been documented, such as Cremastocephalini, Callyntrurini, Microfalculidae.

In this study, we investigated first instar tergal chaetotaxy of 35 Entomobryoidea species and related juvenile chaetotaxy, revised Szeptycki's chaetotaxic homology and nomenclature system based upon a wide sampling, and reconstructed a morphological phylogeny using parsimony and likelihood algorithms. Integrative known molecular phylogeny, a new classification framework for Entomobryoidea was presented. A key to the suprageneric taxa and new diagnoses were also provided.

## 2 Materials and methods

### 2.1 Taxa sampling and preparation

Forty-three Entomobryoidea species, covering all four families *sensu* Szeptycki, 1979 and main subfamilies and tribes,

were examined. Among them, first instar larvae of 35 species were collected from cultured populations or directly from alcohol material. One Tomoceridae and two Isotomidae species were selected for homology comparison across Entomobryomorpha and as outgroups for phylogenetic analyses (Table S1). Specimens, including juveniles and adults, were mounted in Marc André II solution after clearing in lactic acid and were studied using Leica DMLB and Nikon E80i microscopes. Photographs were taken using a Hitachi S4800 scanning electron microscope (SEM). Illustrations were enhanced with Photoshop CS2 ® (Adobe Inc.). All material was deposited at the collections of the Department of Entomology, College of Plant Protection, Nanjing Agricultural University (NJAU), P. R. China, the Museum National d'Histoire Naturelle (MNHN), Paris, France, and the Department of Entomology, University of Illinois (UI), USA. The taxonomical hierarchy in below text follows the new definitions defined in this study if no special reference.

## 2.2 Homologization and nomenclature of tergal chaetae

To easily compare homology hypotheses between different systems, homologization criteria and nomenclature of tergal chaetae strictly follow Szeptycki (1979) in the present study. Recognizing primary (first instar) chaetae is crucial for the homologization of secondary (after first instar) chaetae and the final chaetotaxy. Main homologization criteria are shown below:

1. Primary chaetotaxy is very similar within Entomobryomorpha, particularly Entomobryoidea (Szeptycki, 1972). Sockets and sizes of primary chaetae are often somewhat larger than those of secondary ones around them.

2. Besides the position of chaetae in relation to each other, invariable elements, such as bothriotricha, pseudopores, middle line of the body, and margins of terga, are easier to establish homology and thus help to determine the homology of the chaetae in relation to these elements.

3. Looking for species with the intermediate status of the arrangement of chaetae helps to resolve some puzzling cases.

4. If the position of chaetae differs slightly between species, the displacement of a homologous chaeta is more probable than its reduction together with the origin of a new non-homologous one.

5. If the number of chaetae differs between species, the absence of some secondary chaetae is more probable than that of the primary one.

Nomenclature of the ordinary chaetae is designated using the combination of letters and numbers. Primary chaetae on each tergum are designated with a letter and a number. The letter (a—anterior, m—median, p—posterior) indicates the row in which the chaeta locates except those on the fourth abdominal tergite. The number means the relative position to the middle line (1 the closest, 7 the farthest). Secondary chaetae are designated with the symbol of the nearest primary/secondary chaeta and a letter (a—anterior, p—posterior, i—internal, e—external) representing their position in relation to this primary chaeta. For example, a1 represents a most internal primary chaeta in anterior row, ali represents a secondary chaeta internal to a1, a1ip represents a secondary chaeta posterior to ali. Multiplets consisting of rows of macrochaetae close to each other are named by the largest (main) macrochaeta preceded by the letter m, e.g., m.a1a. Groups of some chaetae which are connected by broken lines are named by the characteristic chaeta and the symbol +, e.g. set m5+. Tergal S-chaetae are designated following Zhang & Deharveng (2015).

## 2.3 Phylogenetic analyses

A matrix comprising 38 taxa and 153 morphological characters, mainly drawn from primary chaetotaxy (Appendix 1), was generated for phylogenetic analyses. One Tomoceridae and two Isotomidae species were selected as the outgroups. The distant outgroup taxa represent long branches and often work as an attractor of long branched ingroup taxa (Bergsten, 2005). In addition, errors possibly occur in homologization between outgroup and Entomobryoidea taxa. Subsequent phylogenetic analyses were performed with and without the outgroup. When the outgroup taxa excluded, the trees were re-rooted using the (Orchesellinae + Heteromurinae) taxa, which have been demonstrated to be the basal group within Entomobryoidea (Szeptycki, 1979; Zhang *et al.*, 2015, 2017) and within Entomobryidae (Zhang *et al.*, 2014, 2016). Maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) criteria were employed for reconstructions.

MP-analyses were performed in TNT v1.1 (Goloboff *et al.*, 2008) with all characters unweighted and character status unordered. New technology search was applied to the tree search, with 100 random addition sequences and four search methods (sectorial searches, ratcheting, tree-drifting, and tree-fusing) under default settings. Node support was calculated using symmetric resampling, 1,000 pseudoreplicates, 10 random-addition replicates, and tree bisection reconnection (TBR) branch swapping.

Likelihood-based methods using the Mk model (Lewis, 2001) outperform parsimony for estimation of phylogeny from discrete morphological data (Wright & Hillis, 2014; O'Reilly *et al.*, 2016; Puttick *et al.*, 2017). ML-analyses were performed

**Table 1. Suprageneric classification systems used in Entomobryoidea.**

Börner, 1913	Absolon & Kseneman, 1942	Yosii, 1961	Szeptycki, 1979	Yoshii & Suhardjono, 1989	Soto-Adames <i>et al.</i> , 2008	Zhang & Deharveng, 2015	This study
<b>Entomobryidae</b>	<b>Entomobryidae</b>	<b>Entomobryidae</b>	<b>Entomobryidae</b>	<b>Orchesellidae</b>	<b>Entomobryidae</b>	<b>Entomobryidae</b>	<b>Orchesellidae</b>
Entomobryinae	Orchesellinae	Orchesellinae	Orchesellinae	<b>Entomobryidae</b>	Capbryinae	Nothobryinae	Nothobryinae
Orchesellini	Orchesellini	Entomobryinae	Entomobryinae	Entomobryiformes	Orchesellinae	Orchesellinae	Nothobryini
Entomobryini	Entomobryinae	Seirinae	Seirinae	Entomobryini	Nothobryini	Orchesellini	Capbryini
Paronellinae	Entomobryini	Paronellinae	Lepidocyrtinae	Siraeformes	Orchesellini	Corynothrichini	Orchesellinae
Cyphoderinae	Lepidocyrtinae	<b>Cyphoderidae</b>	<b>Paronellidae</b>	Willowsiini	Corynothrichini	Heteromurinae	Orchesellini
Troglopedetini	Heteromurini		<b>Cyphoderidae</b>	Lepidocyrtiformes	Heteromurini	Heteromurini	Corynothrichini
Cyphoderini	Lepidocyrtini		<b>Microfalculidae</b>	Seirini	Mastigocerini	Mastigocerini	Bessoniellinae
	Siraini			Lepidocyrtini	Bessoniellini	Bessoniellinae	Heteromurinae
	<b>Paronellidae</b>			<b>Paronellidae</b>	Entomobryinae	Entomobryinae	Heteromurini
	Paronellinae			<b>Cyphoderidae</b>	Entomobryini	Seirinae	Mastigocerini
	Paronellini				Willowsiini	Lepidocyrtinae	<b>Entomobryidae</b>
	Troglopedetini				Seirini	<b>Paronellidae</b>	Entomobryinae
	Salininae				Lepidocyrtini	Paronellinae	Seirinae
	Salinini				<b>Paronellidae</b>	Bromacanthini	Lepidocyrtinae
	<b>Cyphoderidae</b>				Paronellinae	Callyntrurini	<b>Paronellidae</b>
	Cyphoderinae				Bromacanthini	Cremastocephalini	Paronellinae
	Cyphoderini				Callyntrurini	Paronellini	Paronellini
	Oncopodurinae				Cremastocephalini	Troglopedetini	Cyphoderini
	Oncopodurini				Paronellini	Cyphoderinae	Bromacanthini
					Troglopedetini	<b>Microfalculidae</b>	Salininae
					Cyphoderinae		Cremastocephalini
					<b>Microfalculidae</b>		Callyntrurini

in raxmlGUI 1.3 (Stamatakis, 2006; Silvestro & Michalak, 2012) with the MULTIGAMMA+Mk model and 1,000 rapid bootstrap replicates.

Bayesian reconstructions were conducted in MrBayes 3.2.6 (Ronquist *et al.*, 2012) with four chains (three heated, one cold) ran, Mk model, and only variable characters sampled. Twenty million generations were executed for the total analysis, with the chain sampled every 2,000 generations and the burn-in value as 25%. To confirm convergence, the average standard deviation of split frequencies and the potential scale reduction factor values were visualized in MrBayes, and evaluating effective sample size values were checked in Tracer 1.5 (Rambaut & Drummond, 2007).

The presence of unstable (rogue, or floating) taxa, which assume different positions in the tree set (typically bootstrap replicate trees), may decrease the resolution and support of the consensus. To obtain reliable results, four methods were performed to detect unstable taxa. Leaf stability index (Thorley & Wilkinson, 1999), taxonomic instability index (Maddison & Maddison, 2009), and RogueNaRok-algorithm (Aberer & Stamatakis, 2011) were conducted on online RogueNaRok tool (Aberer *et al.*, 2013) with the defaults. The bootstrap trees for RogueNaRok analyses were drawn from previous ML-analyses. The fourth algorithm was performed using the command “prunnelsen” in TNT. Unstable species in this study were designated as taxa simultaneously accepted by at least two algorithms and severely impacting on the topology of deep nodes. Previous phylogenetic reconstructions were re-analyzed after pruning unstable species.

## 2.4 Abbreviations

Th. I–III—thoracic segment I–III;  
 Abd. I–VI—abdominal segment I–VI;  
 mac—macrochaeta, -ae;  
 mes—mesochaeta, -ae;  
 mic—microchaeta, -ae;  
 ms—S-microchaeta, -ae (microsensillum, -a);  
 sens—ordinary S-chaeta, -ae on terga;  
 PAO—post-antennal organ.

## 3 Results

### 3.1 First instar chaetotaxy on terga

Tergal elements consist of macrochaetae, mesochaetae, microchaetae, scales, bothriotricha, pseudopores, S-microchaetae and ordinary S-chaetae (Figs 1A–F). Mesochaetae, sometimes longer than macrochaetae, are essentially slightly thicker microchaetae but of very long length and with acuminate apex. Symbols of each element used in figures are also illustrated (Fig. 1G). First instar chaetotaxy of 38 Entomobryomorpha species, 35 Entomobryoidea, 1 Tomoceridae and 2 Isotomidae, were examined in this study, most of them presented in Figs 2–13.

Primary chaetotaxy on Th. II follow the hypothesis of 7-7-6 chaetae in a-m-p horizontal (transversal) rows. In the a-row, 6 chaetae occur in 5 species, a1 is absent in *Tomocerus minor* (Fig. 2A) and two *Salina* species (Figs 13B–C), while a2 is absent in two isotomid species (Figs 2B–C). Chaetae a1–6 are mostly mac in Entomobryoidea, with exception of *Entomobrya proxima* (a1 as mic) (Fig. 5B), *Salina* spp. (a1 absent, a5 or a5–6 as mic) and *Microfalcula* sp. (only a6 as mac) (Fig. 13). Such chaetae become the anterior collar of macrochaetae in several adult forms of Entomobryoidea. Chaeta a7 is mic in all sampled taxa. In the m-row, the complete set (m1–7) is observed in *T. minor* and *Isotomurus palustris* (Fig. 2A, C) with m5 duplicated in the former (am5); chaeta m2 is a scale in most Lepidocyrtinae species (Figs 10–11, 12A); m3 is absent in *Isotoma anglicana* (Fig. 2A) and all Entomobryoidea taxa; m1, m5 and m7 are absent in *Salina* (Figs 13B–C); m4 is only absent in *Microfalcula* (Fig. 13A). Chaeta m6 is mac in *Isotoma anglicana* (Fig. 2B) and all Entomobryoidea spp. while m1 and m4 are also mac in most Entomobryoidea, except to *Heteromurus nitidus*, *Entomobrya nivalis* and *Coecobrya aokii* (m1 as mic) (Figs 4A, 5A, 7A), *Entomobrya proxima* (both as mic) (Fig. 5B), *Microfalcula* sp. (m1 as mic, m4 absent) (Fig. 13A) and *Salina* spp. (m1 absent, m4 as mic) (Figs 13B–C). In the p-row, incomplete sets are found in 3 species, p2 and p4 absent in *Salina* (Figs 13B–C), p4 absent in *Microfalcula* (Fig. 13A). Chaeta p5 is duplicated in *T. minor* (Fig. 2A). Chaeta p3 is mac in *Isotoma anglicana* (Fig. 2A) and all Entomobryoidea spp. except for *Microfalcula* sp. (as mic) (Fig. 13A). Chaetae p4 and p6 are always mic in all studied taxa in which both are present. More than two sens occur in tomocerid and isotomid species. In Entomobryoidea, sens acc.p6 within the p-row is only present in Orchesellidae and Entomobryinae, internal to

p6 in *Orchesellides* (Fig. 3B) but external to p6 in others. Lateral ms and one accessory sens (al, internal or external to ms) are present in all sampled species.

Primary chaetae on Th. III also follow the hypothesis of 7-7-6 in a-m-p rows. In the a-row, chaetae a1, a3 and a4 are transformed into scales in *Cyphoderus* (Fig. 12C). Chaetae a2, a4 and a5, as well as m1–5, m7 and p4–5, are absent in *Salina* (Figs 13B–C). Chaetae a3 and a5 are absent in *Isotoma* (Fig. 2B). Chaeta a5 is absent in *Isotomurus* (Fig. 2C), Lepidocyrtinae and Paronellinae species. Chaeta a7 is mic in all studied taxa, while a1–6 can be mic or mac when present. In the m-row, complete set occurs only in *Isotomurus* (Fig. 2C); m2 and m3 are absent in Entomobryoidea; m4 is absent in *Tomocerus*, as well as m5 (Fig. 2A), and only three chaetae (m5–7) are present in *Microfalcula* (Fig. 13A). Chaetae m1, m4–5 and m7 are always mic in Entomobryoidea taxa which present them, except for m1 in *Trogolaphysa* and *Cyphoderus albinus* (as scale) (Figs 12B–C). Chaeta m6 is mac in *Isotoma* (Fig. 2B) and most Entomobryoidea except for *Coecobrya aokii* (Fig. 7C), the Lepidocyrtinae (Figs 10–11, 12A) and *Cyphoderus* (Fig. 12C). In the p-row, p4 is absent in *Microfalcula* (Fig. 13A) and p4–5 are absent in *Trogolaphysa* (Fig. 12B). Chaetae p1–3 are mostly mac in Entomobryoidea except for *Cyphoderus* and *Microfalcula* (all as mic) (Figs 12C, 13A), *Salina* (p1 as mic) (Figs 13B–C) and *Entomobrya proxima* (p1–2 as mic) (Fig.

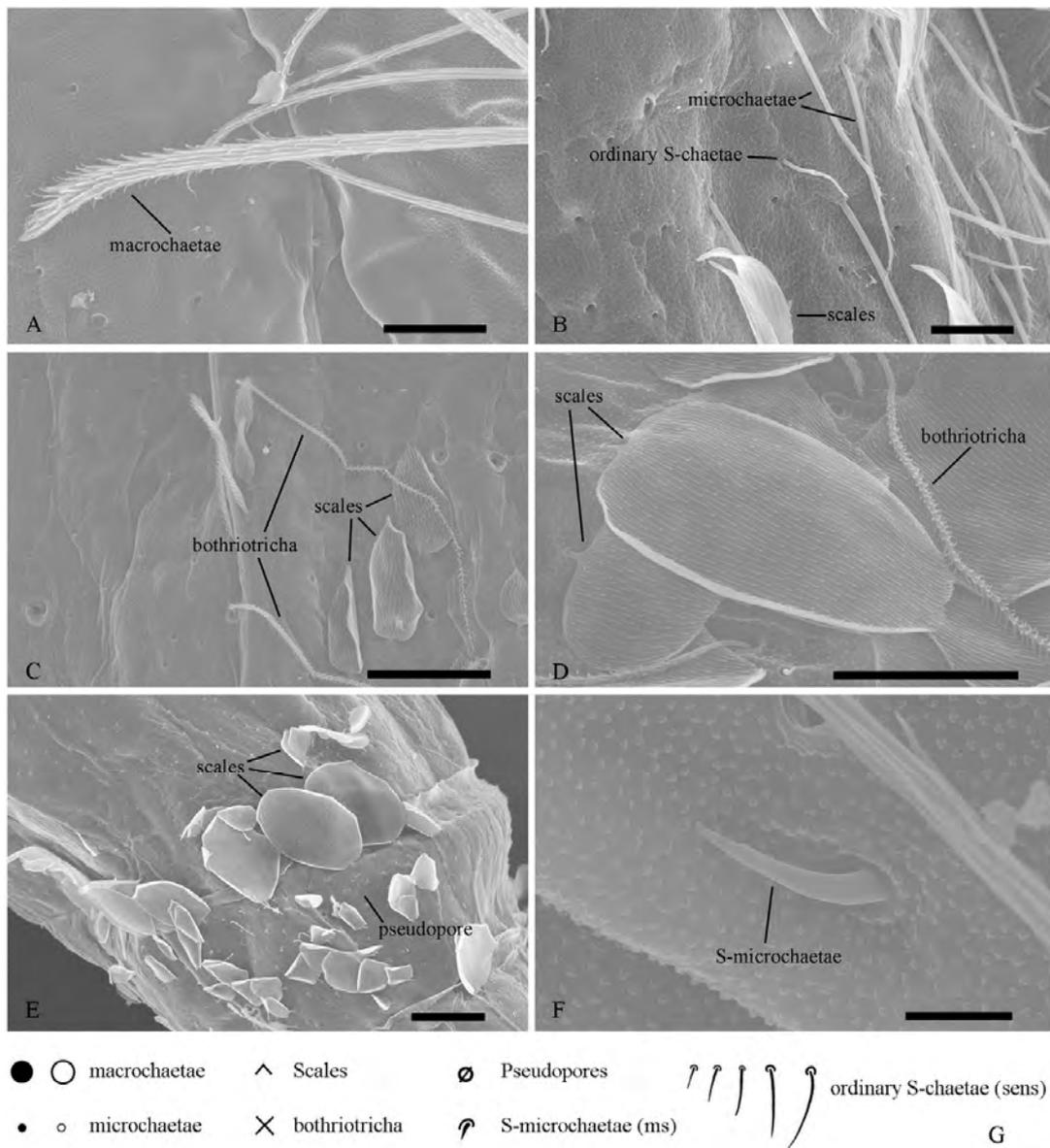


Figure 1. Tergal elements and their symbols used in this study. Solid and hollow circles represent primary and secondary chaetae, respectively. A. Macrochaeta in *Willowsia japonica*. B. Abd. IV in *Willowsia neocaledonica*. C. Abd. IV in *Willowsia* sp. D. Abd. III in *Lepidocyrtus absens*. E. Abd. III–IV in *Lepidonella* sp. F. Ms on Th. II in *Sinhomidia bicolor*. G. A diagram of element symbols. Scale bars: A–B, D=100 µm; C, E=300 µm; F=20 µm.

5B). Chaetae p4–6 are always mic in all Entomobryoidea species which have them. As for sens on Th. III, more than two sens occur in tomocerid and isotomid species, while Entomobryoidea present two lateral sens (al and acc.p6) such as Orchesellinae, Heteromurinae and Entomobryinae. Sens acc.p6 is absent in Seirinae, Lepidocyrtinae, and Paronellidae as well as *Microfalcula* which lacks both sens (Fig. 13A). Sens around m7 is external to m7 in Lepidocyrtinae and Cyphoderini, but internal to m7 in others. Chaetae a2 and m1 in Lepidocyrtinae and Paronellinae correspond to m2 and a2 in Szeptycki's system respectively (Table 2).

**Table 2. Homology revision of tergal chaetae and correspondence among three nomenclature systems. All names of Soto-Adames (2008) only refer to Seirinae.**

Tergum	Szeptycki, 1979	Soto-Adames, 2008	This study
Th. II	a3e after 1st instar	a3e	a4
	a4 after 1st instar	a4	a4e
	a4e after 1st instar	a4e	a4e2
	a4p2	a5i	a5i
	-	m5p	m5e
Th. III	a2 in Lepidocyrtinae	-	m1
	m2 in Lepidocyrtinae	-	a2
	m6e	m6p	m6e
Abd. I	a5 in <i>Sinella</i> , <i>E. muscorum</i> , <i>E. puncteola</i> , <i>Drepanosira</i> , <i>Homidia hjesanica</i> , <i>Himalanura kangbachensis</i> , <i>Himalanura pamirensis</i> , <i>Seira lusitanica</i> , <i>Seira arenaria</i>	-	m4
	a5i in <i>Sinella</i> , <i>E. muscorum</i> , <i>E. puncteola</i> , <i>Drepanosira</i> , <i>Homidia hjesanica</i> , <i>Himalanura kangbachensis</i> , <i>Himalanura pamirensis</i>	-	m4i
	m4 in <i>Sinella</i> , <i>E. muscorum</i> , <i>E. puncteola</i> , <i>Drepanosira</i> , <i>Homidia hjesanica</i> , <i>Himalanura kangbachensis</i> , <i>Himalanura pamirensis</i> , <i>Seira lusitanica</i> , <i>Seira arenaria</i>	-	m4p
	-	m4i	m4p
Abd. III	p4	p3	p3
	mac p7 after 1st instar	p7i	p6pe
Abd. IV	A1-2-3-6 in <i>Orchesella</i>	-	A2-3-5-6
	B1-2-3-5 in <i>Orchesella</i>	-	B2-3-5-6
	A1-2-3-6 in <i>Heteromurus</i>	-	B2-A2-B5-A6
	B1-5 in <i>Heteromurus</i>	-	C1-B6
	E2 in <i>Orchesella</i> and <i>Heteromurus</i>	-	E3
	A4 at 1st instar in Entomobryinae	-	A5
	C1 at 1st instar in <i>Entomobryoides</i> and Lepidocyrtinae	C1	T1
	B3 at 1st instar in Lepidocyrtinae	B2	C1
	B2 at 1st instar in Lepidocyrtinae	B1	B2
	A2p after 1st instar	-	A3
	A3 after 1st instar	-	Si
	B3p after 1st instar	-	B3
	single mac B3 or C1 after 1st instar	-	Sm
	mac C1 and B3 after 1st instar	-	Sm, B4
two mac E2a and E2 after 1st instar	-	E2, E2p	
Abd. V	m5e	-	a6
	a6 after 1st instar	-	a6a

Primary chaetae also follow the pattern of 6-6-6 on Abd. I and 7-7-7 on Abd. II–III. On Abd. I, 7–13 primary chaetae occur. In the a-row, a4 is only present in *Isotomurus*, with only a1 always occurring (Fig. 2C). Chaeta a1 is transformed into scales in Paronellini (Fig. 12B) and Cyphoderini, a2 and a3 of the latter also as scales (see fig. 164 in Szeptycki 1979). Chaeta a2 is only absent in *Salina* (Figs 13B–C), a3 only absent in *Pseudosinella* sp.B (Fig. 12A). Chaetae a5 and a6 are

often absent in some species of Entomobryoidea as well as a6 is absent in *Tomocerus* and isotomids (Figs 13B–C). Chaetae of a-row are all mic (or scales) in most sampled taxa, excluding the Orchesellinae in which *Orchesella* sp. presents a2 as mac and *Orchesellides sinensis* presents a2–3 as mac (Figs 3A–B). Five chaetae (m2–6) usually occur in m-row, with m5 absent in Tomoceridae, Isotomidae, *Pseudosinella decipiens* and *Trogolaphysa* (Figs 2, 12B). Chaetae m2–4 are the three main mac of several Entomobryoidea, Tomoceridae and *Isotoma*, but in *Heteromurus nitidus* m4 is mic (Fig. 4A), in *Entomobrya proxima* m2–3 are mic (Fig. 5B), in *Coecobrya*, *Sinella umesaoi* and *Salina* m2 is mic (Figs 6B, 7B–C, 13B–C), in *Trogolaphysa* m2 and m4 are mic (Fig. 12B) and in *Microfalcula* all three are mic (Fig. 13A). Chaetae m5 and m6 are mic in all taxa which present them. In the p-row, two chaetae (p5, p6) occur in most Entomobryoidea, with a single chaeta p6 in *Heteromurus*, *Trogolaphysa jataca* and *Microfalcula* (Figs 4A, 12B, 13A) while p-row is entirely absent in *Pseudosinella* sp.B, *Cyphoderus* and *Salina* (Figs 12A, 13B–C). Only the non Entomobryoidea taxa present p1–2 and p4 chaetae (p1 missing in *Isotoma*) (Fig. 2), while only the Entomobryoidea can present p6. All chaetae on p-row of all studied taxa are mic. S-microchaeta is only absent in *Tomocerus minor* (Fig. 2A). Sens are abundant in Tomoceridae and Isotomidae, absent in Seirinae, Lepidocyrtinae, Paronellidae, while there is one lateral sens (acc. p6) in Orchesellinae, Heteromurinae and Entomobryinae.

On Abd. II, 12–16 primary chaetae occur. Chaetae a5 and m2 are transformed into bothriotricha in Entomobryoidea and only in this group there can be a7, m7 and p7. Chaeta a1 is a scale in Paronellini and Cyphoderini (Fig. 12B) and a mic in all other taxa. Chaeta a4 is only present in Isotomidae while m5 and p7 are absent (Figs 2B–C). Chaeta a2 is mac in Orchesellinae, Seirinae, Lepidocyrtinae, *Homidia cingula* (Fig. 8A) and *Callyntrura guangdongensis* (Fig. 9B) while it is mic in other taxa. Chaetae a3, a6–7 are mic in most Entomobryoidea, but in *Orchesellides sinensis* a3 is mac (Fig. 3B) and some taxa may lose a6 and/or a7. Chaeta m4 is absent in *Heteromurus*, *Trogolaphysa* and *Salina* and in other Entomobryoidea it is a mic. Chaeta m7 is often absent as in *Coecobrya*, *Pseudosinella* sp.B and Salinae (Figs 6B, 7C, 9B, 12A, 13B–C). Chaeta m3 is mac in almost all Entomobryoidea except for *Microfalcula* (Fig. 13A). Chaeta m5 is also mac in most Entomobryoidea except for Heteromurinae (Fig. 4A, B), *Entomobrya proxima* (Fig. 5B) and *Trogolaphysa* (Fig. 12B). Chaeta m6 is mic in all species except for *Pseudosinella* sp.B (absent) (Fig. 12A). In the p-row, p1–3 are absent, and p4, p6 and p7 are always present as mic in Entomobryoidea with p5 mic lacking in several species. Sens are more than three in Tomoceridae, Isotomidae and Orchesellinae, three (as, acc.p3, acc.p6) in Heteromurinae, one (as) in Lepidocyrtinae and Paronellinae, none in *Microfalcula* and *Salina* (Fig. 13), and two (as, acc.p6) in others. Lateral S-microchaeta (ms) is only present in isotomids (Figs 2B–C).

Some additional chaetae on Abd. III often occur externally to 7-7-7 putative chaetae and are not named here. In the a-row, chaeta a2 is a scale in *Campylothorax* (Soto-Adames, 2016) and absent in *Tomocerus*; a4 is only present in *Isotoma* (Fig. 2B); a5 is a mic in Isotomidae but a bothriotrichum in others. Chaetae a1–3 and a6–7 are all mic in isotomids and most Entomobryoidea, except for Orchesellinae (a2 is mac), *Trogolaphysa* (a1 is mac) and *Pseudosinella* sp.B (a7 missing) (Figs 3A–B, 12C). In the m-row, m2 and m5 are bothriotricha in Entomobryoidea with only m2 as a bothriotrichum in *Isotomurus*; m6 is duplicated in *Tomocerus* and Entomobryoidea, anterior one designated as am6. Chaeta m1 is absent in all taxa, m6 is duplicated (am6+pm6) in Entomobryoidea, and m7 can be rarely absent as in *Pseudosinella* sp.B (Fig. 12A). Chaeta m3 is the main central mac of most Entomobryoidea, except for *Microfalcula* and *Salina* (Fig. 13). Chaeta pm6 are commonly as mac as in Orchesellinae, *Heteromurus*, part of Entomobryinae (*Entomobrya nivalis*, *Homidia* sp.), Seirinae, Lepidocyrtinae, Paronellinae and *Microfalcula*. In the p-row, p1, p2 and p4 are absent in Entomobryoidea; p5 is absent in *Trogolaphysa*, *Microfalcula* and *Salina* (Fig. 13). Chaetae p3, p5 and p7 are mic all species which present them and p6 can be mic or mac. Sens are more than three in Tomoceridae, Isotomidae and Orchesellinae, three (as, acc.p3, acc.p6) in Heteromurinae, one (as) in Lepidocyrtinae, Paronellinae and *Salina*, none in *Microfalcula*, and two (as, acc.p6) in others. S-microchaeta (ms) is widely present in most Entomobryoidea, but can be absent as in some *Coecobrya* spp. (Figs 6B, 7B).

On Abd. IV, the complete pattern of 7-7-7 of a-m-p rows occurs in *Tomocerus* and *Isotomurus* except p3 and p7 absent in *Isotoma* (Fig. 2). Bothriotricha are a2 and a5 in *Tomocerus* and a4 in *Isotomurus*. Nomenclature in Entomobryoidea accepts a different system of longitudinal rows and chaetae are homologized with a-m-p system exemplified in *Tomocerus minor* (Fig. 2A). Chaetae A1, A4, B1, B3, C3, T3, T5 and D1 are absent in tomocerids and isotomids. Within Entomobryoidea, series A–C are strongly reduced in *Salina* with only A6, B4–6 and C4 present (Figs 13B–C), and are moderately reduced in Heteromurinae with 4 or 3, 3 or 2, 1 (C1) chaetae in Series A–C, respectively (Figs 4A–B, 13B–C). Chaetae A2 and B2 are scales in Paronellini (Fig. 12B). Chaetae A1, B1 and E2 are often absent. Chaeta A4 is observed only in *Lepidocyrtus curvicolis*, *Pseudosinella impediens*, *Cyphoderus*, *Microfalcula* and *Callyntrura* (Figs 9B, 12D, 13A). Additional chaetae between rows B and C are present in Orchesellinae and *Microfalcula* (Figs 3A–B, 13A). A total of 16–17 chaetae occur externally to row C, 7, 3, 4 or 3, 3 chaetae respectively in rows T, D, E, F. Chaeta E2 is only present in Seirinae, Lepidocyrtinae and *Trogolaphysa*. E4 is a bothriotrichum in *Callyntrura* (Fig. 9C). Chaetae B5 and E3 are mac in most



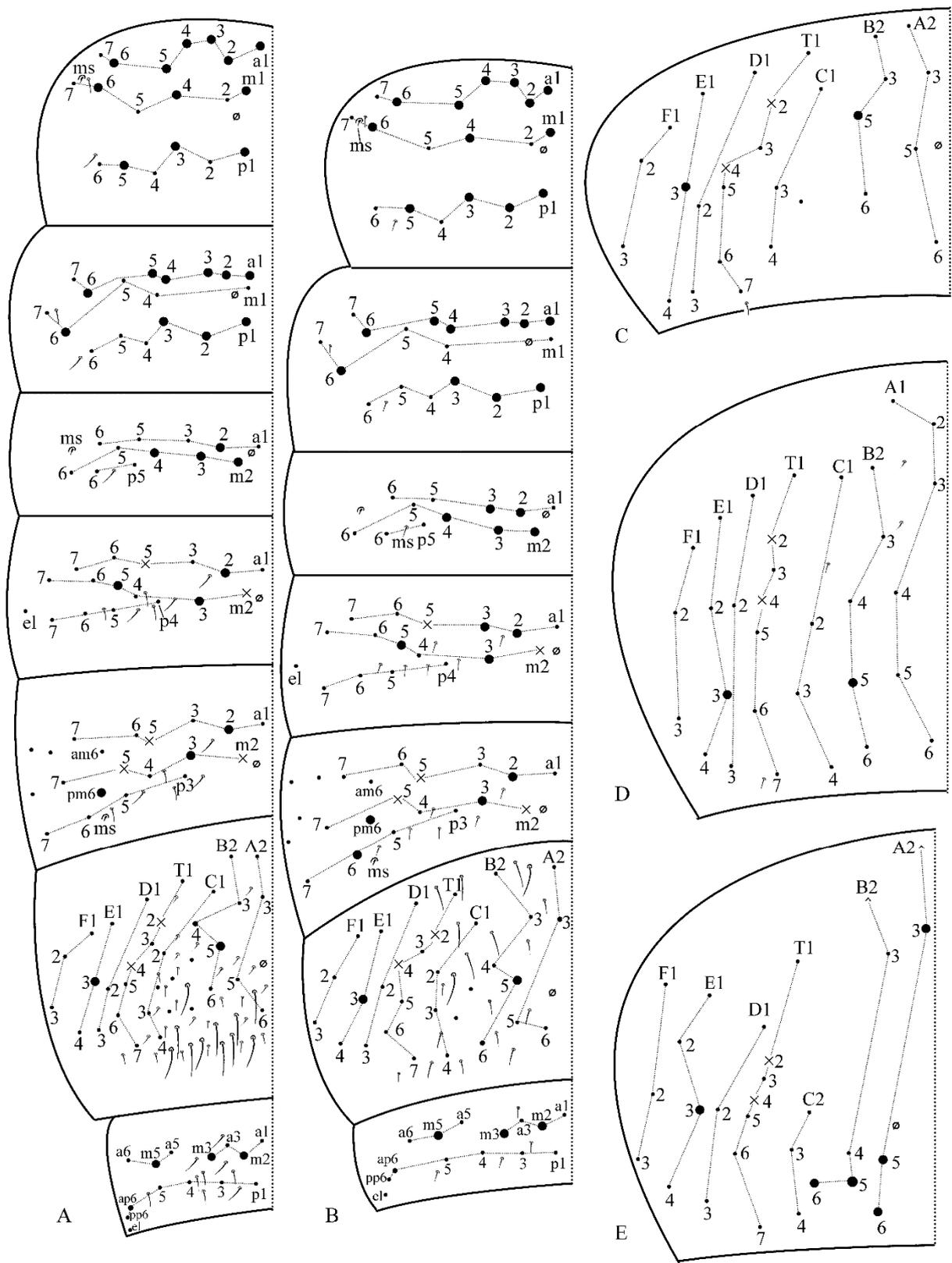


Figure 3. First instar dorsal chaetotaxy of Th. II to Abd. V in Orchesellinae. A. *Orchesella* sp. B. *Orchesellides sinensis*. C. Abd. IV of *Orchesella flavescens* (Orchesellinae, redrawn from Szeptycki, 1979). D. Abd. IV of *Lepidocyrtus curvicollis* (Lepidocyrtinae, redrawn from Szeptycki, 1979). E. Abd. IV of *Campylothorax sabanus* (Paronellinae, redrawn from Soto-Adames, 2016).

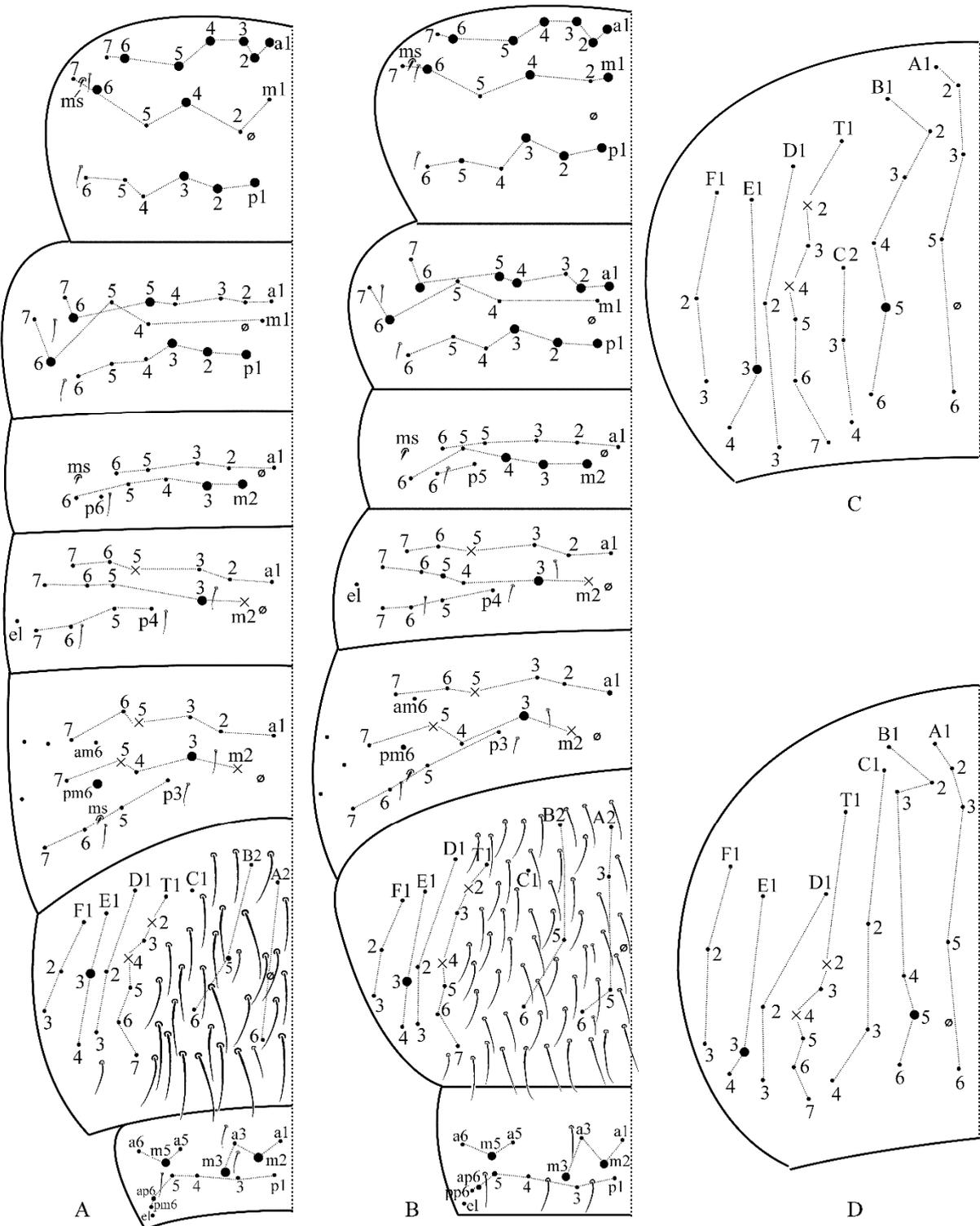


Figure 4. First instar dorsal chaetotaxy of Th. II to Abd. V in Heteromurinae. A. *Heteromurus nitidus*. B. *Dicranocentrus wangi*. C. Abd. IV of *Entomobryoides myrmecophila* (Entomobryinae, redrawn from Szeptycki, 1979). D. Abd. IV of *Homidia jordanai* (Entomobryinae).

Primary chaetae on Abd. V have fewer variations. This segment lacks pseudopores in Entomobryoidea and there are usually four (a1-3-5-6) in a-row, four (m2-3-5-6) in m-row, five (p1, p3–6) chaetae in p-row. Chaetae ap6 and pp6 in Entomobryoidea are homologous to m6 and p6 respectively in Isotomidae and Tomoceridae. Chaeta a1 is only absent in *Salina celebensis* (Fig. 13B) and *Cyphoderus*. Two additional chaetae are found around p5 in tomocerids (Fig. 2A) while most Entomobryoidea presents extra el near pp6. Chaetae m2–3 and m5 are the main mac of Abd. V in several taxa, except

for part of Entomobryinae (as *Entomobrya proxima* with m5 as mic and ap6 is mac, *Sinella umesaoui* with m3 and m5 as mic, and *Coecobrya aokii* with m5 as mic), *Callyntrura* (m3 is mic), *Pseudosinella* sp.A (m5 as mic) and *Microfalcula* (m2 is mic) (Figs 5B, 7B–C, 9B, 11B, 13A). Sens are usually more than three in Tomoceridae, Isotomidae and Orchesellinae, three or four in Heteromurinae, one (acc.p5) in *Microfalcula* and three (as, acc.p4, acc.p5) in others.

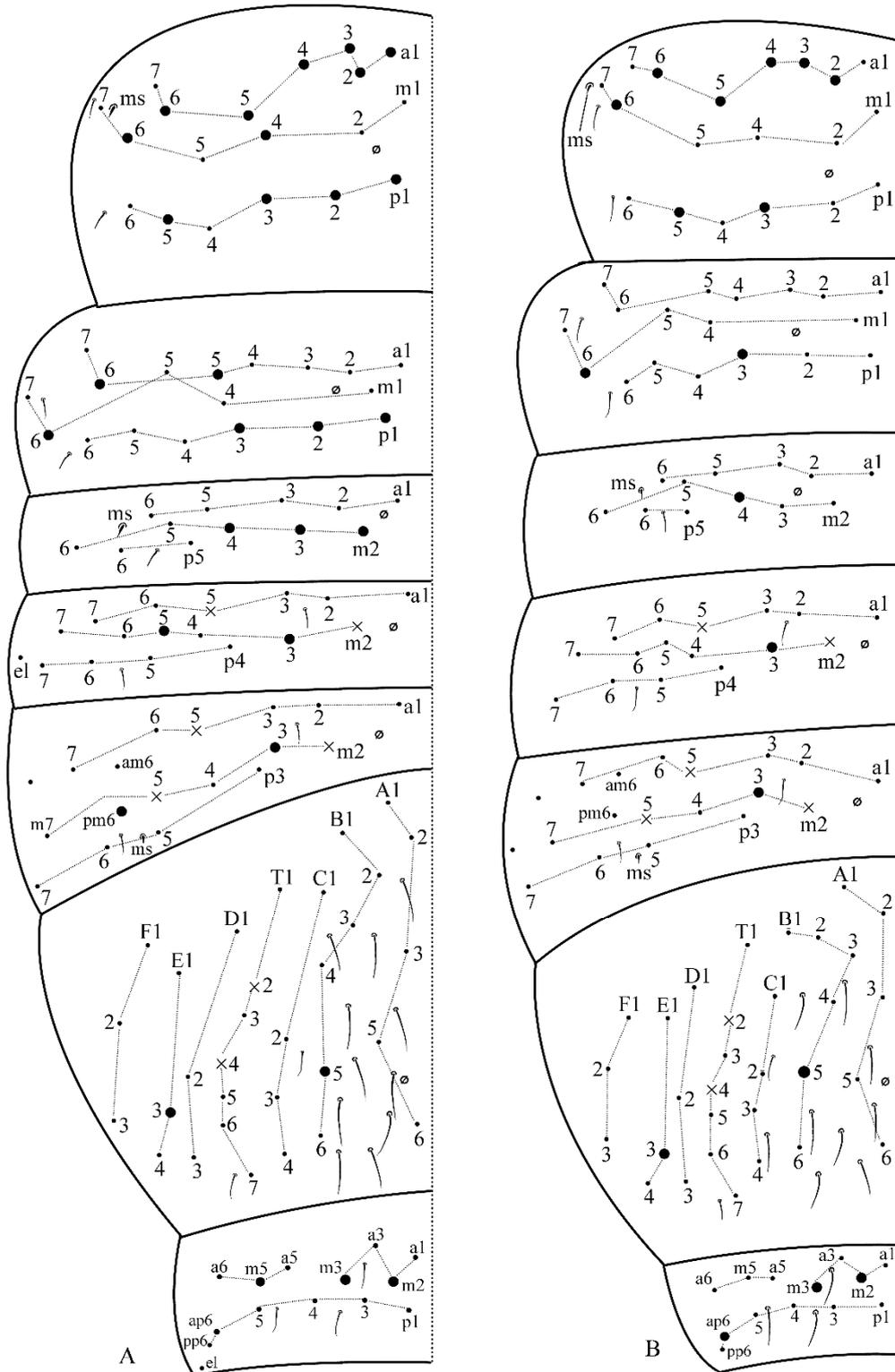


Figure 5. First instar dorsal chaetotaxy of Th. II to Abd. V in Entomobryinae. A. *Entomobrya nivalis*. B. *Entomobrya proxima* (B1 present or absent).

### 3.2 Homology during postembryonic development

Most homology hypotheses of secondary chaetae, which are identical with Szeptycki (1979), are not repeated in detail here. Homology revisions across a wider sampling are highlighted (Table 2). During the postembryonic development of Entomobryoidea some primary chaetae can change states, and some mic can become mes or mac, mac can become mic and

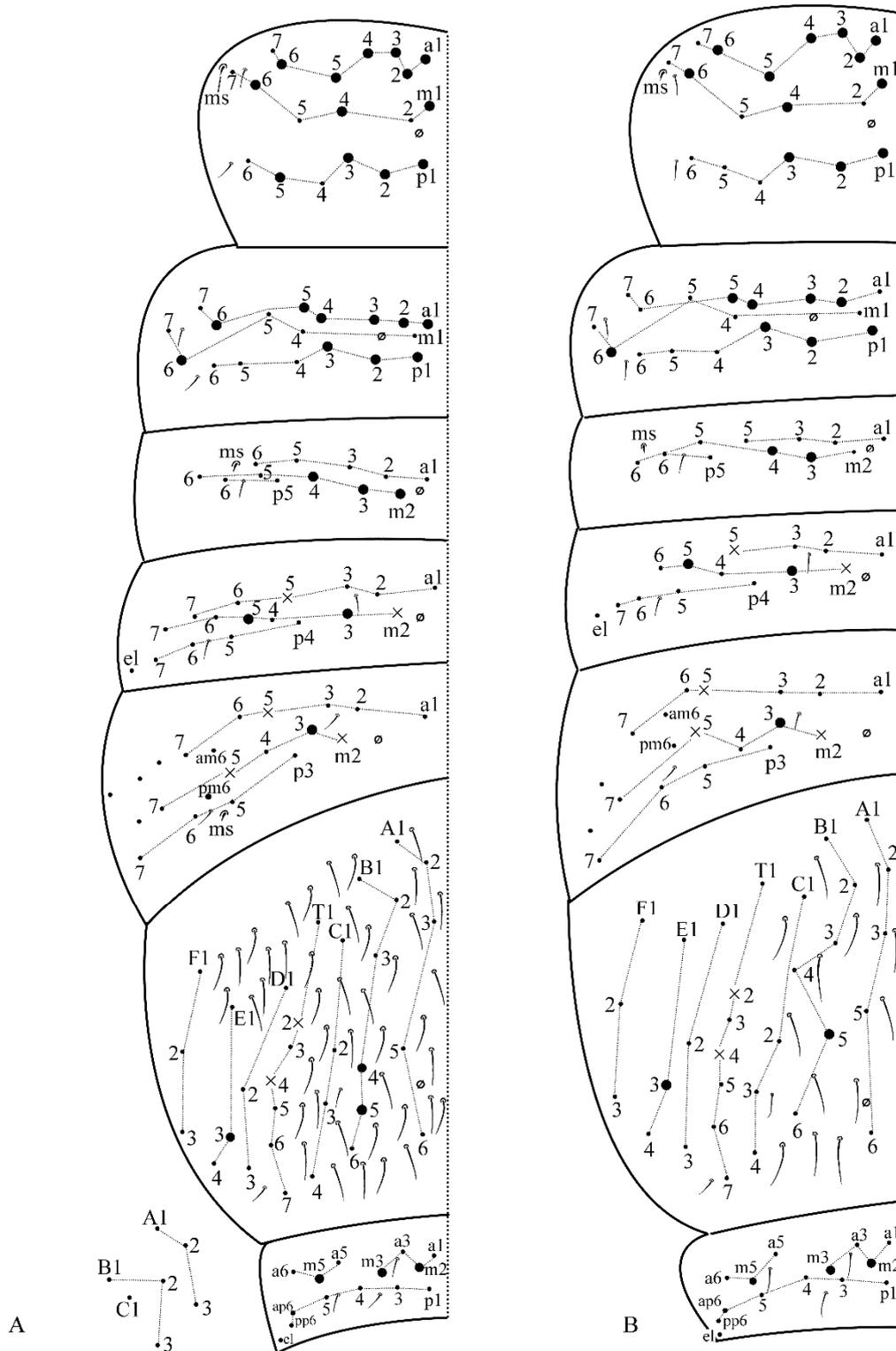


Figure 6. First instar dorsal chaetotaxy of Th. II to Abd. V in Entomobryinae. A. *Entomobrya* sp. B. *Coecobrya tenebricosa* (redrawn from Zhang *et al.*, 2011).

few elements as mic or scales can be completely lost or hardly tracked among the secondary chaetae, which includes a dense cover of scales or other chaetae in adults. Bothriotricha, pseudopores, ms and sens are otherwise stable.

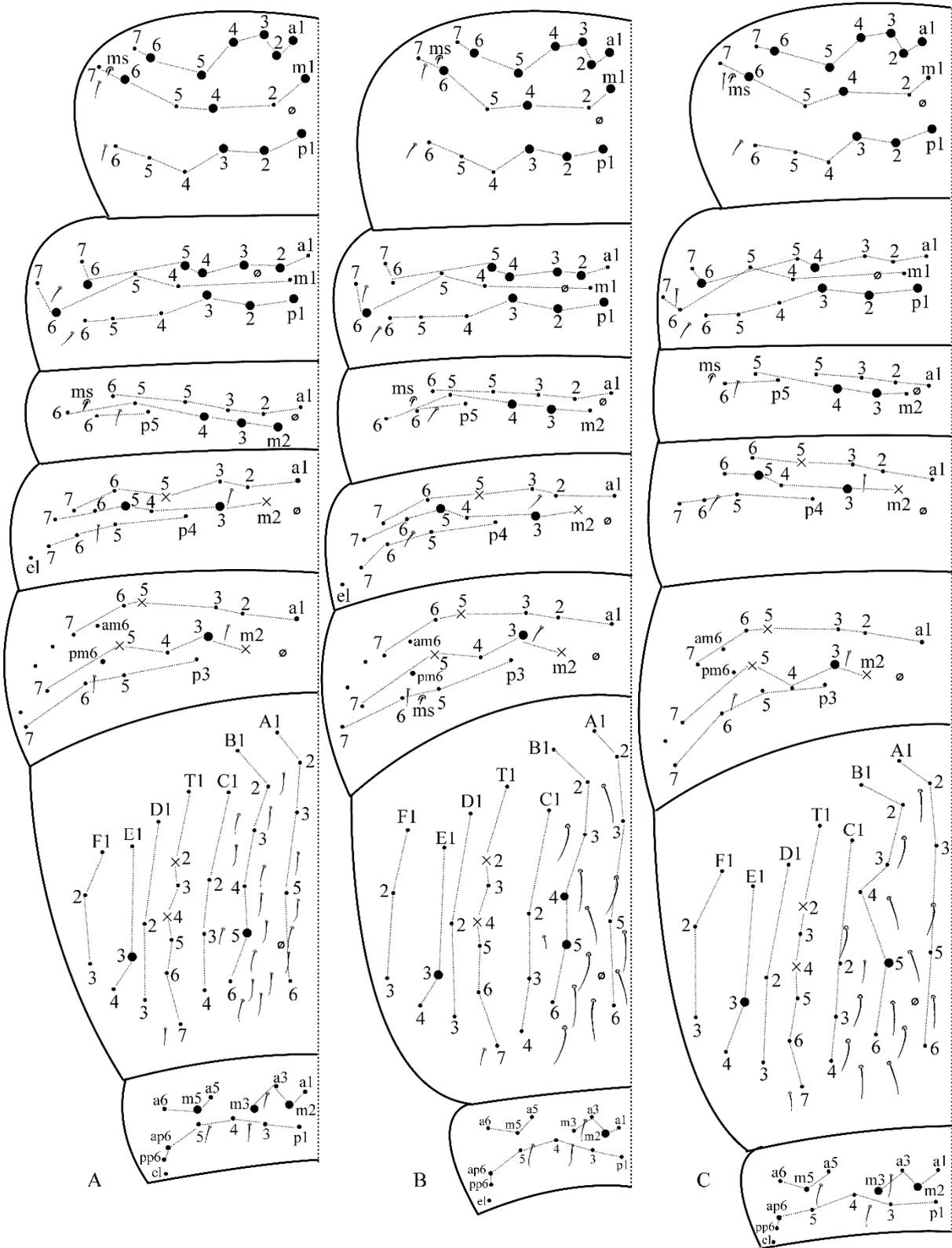


Figure 7. First instar dorsal chaetotaxy of Th. II to Abd. V in Entomobryinae. A. *Sinella curviseta* (redrawn from Zhang *et al.*, 2011). B. *Sinella umesaoui* (redrawn from Zhang & Deharveng, 2015). C. *Coecobrya aokii* (redrawn from Zhang *et al.*, 2011).

On Th. II (Figs S1–3), there are usually two (a4e, a4e2) secondary mac external to the line connecting a4 and a5 at 2nd instar (Figs S1A, S2); thus, a4, a4e, a4e2 correspond to “a3e, a4, a4e” in Szeptycki’s system. A mac, which is posterior to the multiplet a4e and usually appears at 3rd instar (2nd instar in *Entomobryoides*), is designated as a5i. A mic, external to m5 and named as “m5p” in Soto-Adames (2008), is designated as m5e (Fig. S2). Several multiplets of posterior chaetae are commonly seen in subadults and adults of Orchesellinae and part of Entomobryinae (Figs S1C–D, S3A, C).

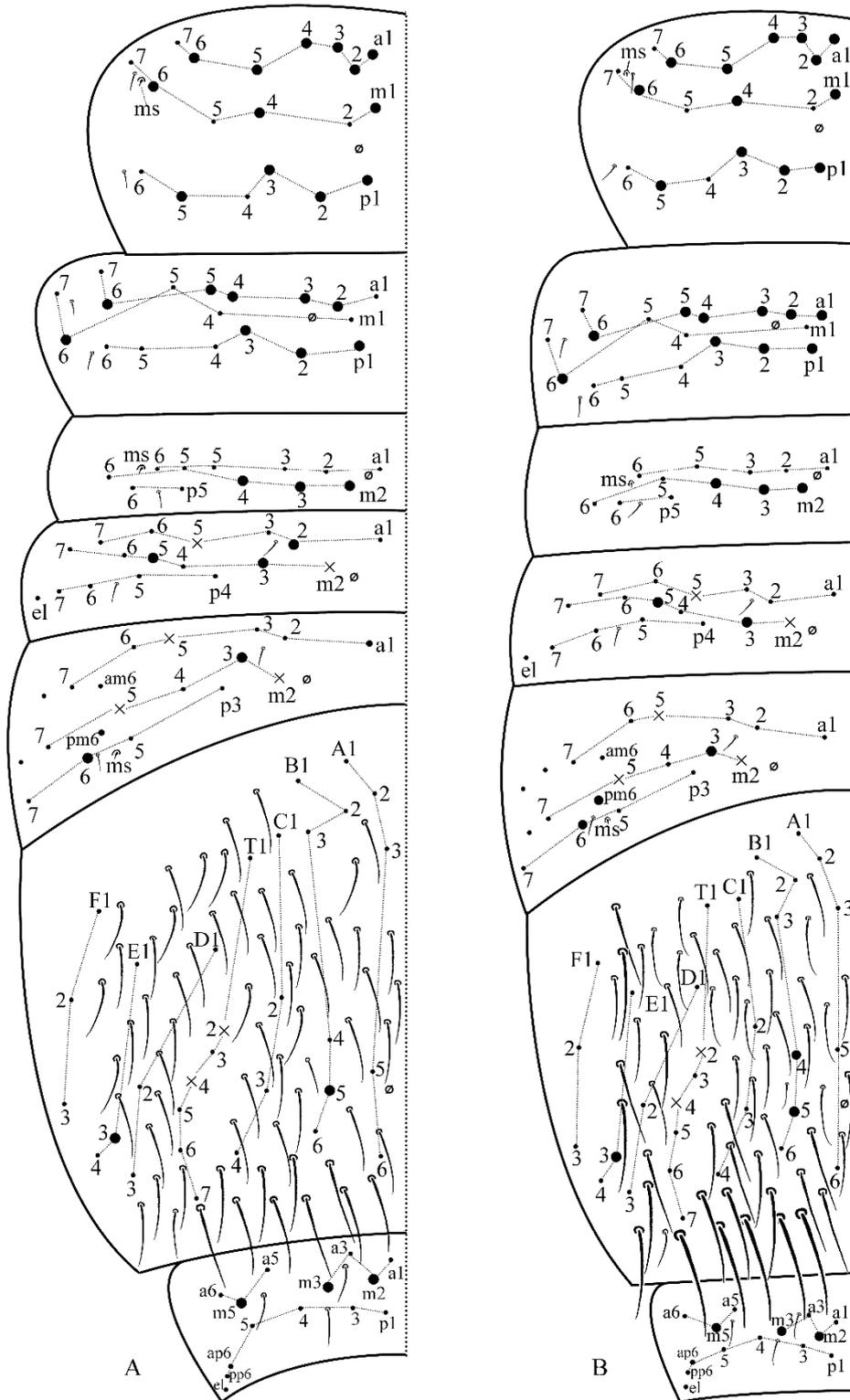


Figure 8. First instar dorsal chaetotaxy of Th. II to Abd. V in Entomobryinae. A. *Homidia cingula*. B. *Homidia* sp.

On Th. III (Figs S4–5), a secondary chaeta, external to m6 at 2nd instar and designated as m6e, corresponds to m6p in Soto-Adames (2008). A high number of multiplets of posterior chaetae are present in subadults and adults of Orchesellinae and part of Entomobryinae as well (Figs S4B, D, F–G, S5G) while Seirinae can present multiplets of p1-2 chaetae plus p3p

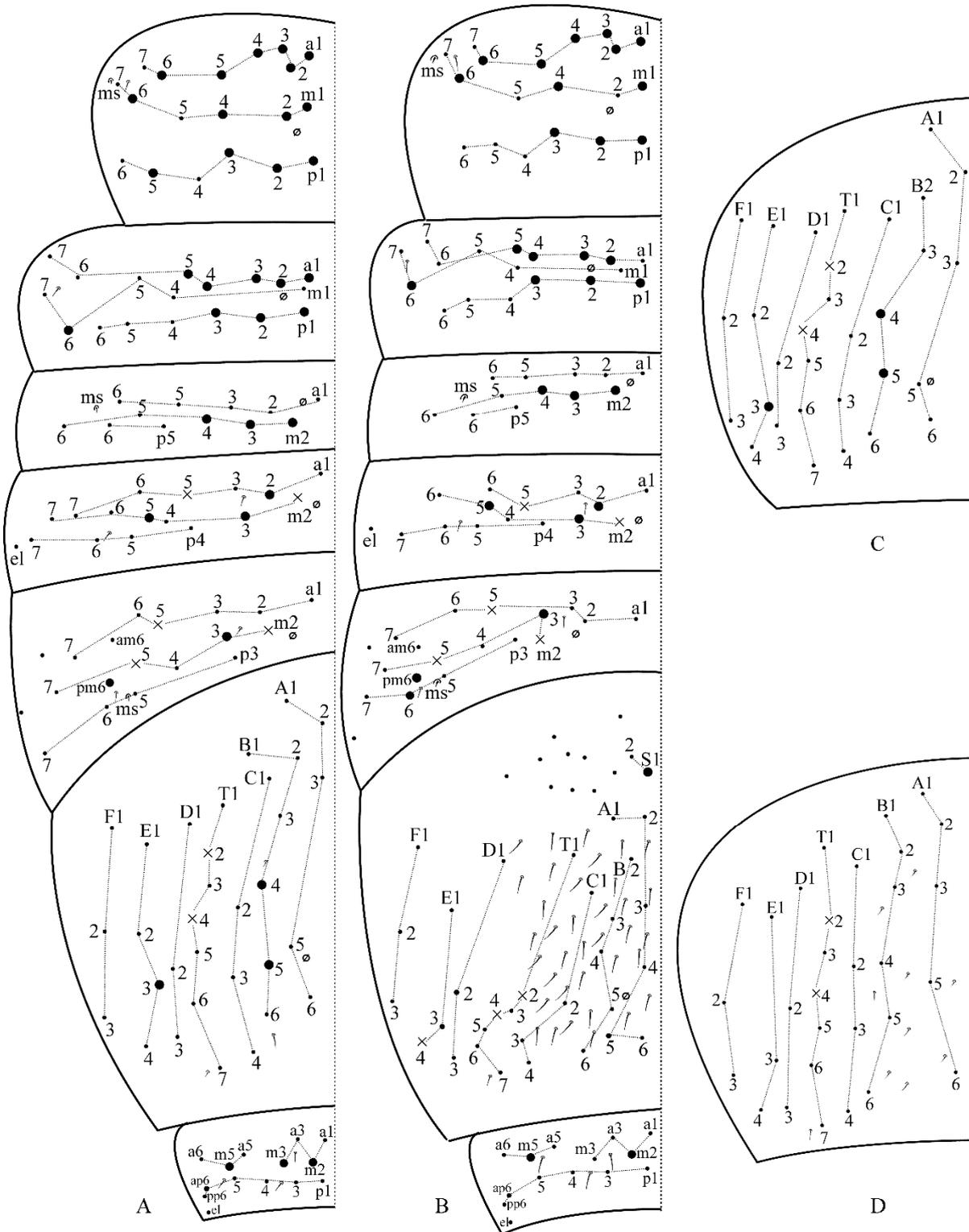


Figure 9. First instar dorsal chaetotaxy of Th. II to Abd. V. A. *Seira barnardi* (Seirinae). B. *Callyntrura guangdongensis* (Saliniinae). C. Abd. IV of *Seira dowlingi* (Seirinae, redrawn from Soto-Adames, 2008). D. Abd. IV of *Willowsia buskii* (Entomobryinae, redrawn from Szeptycki, 1979).

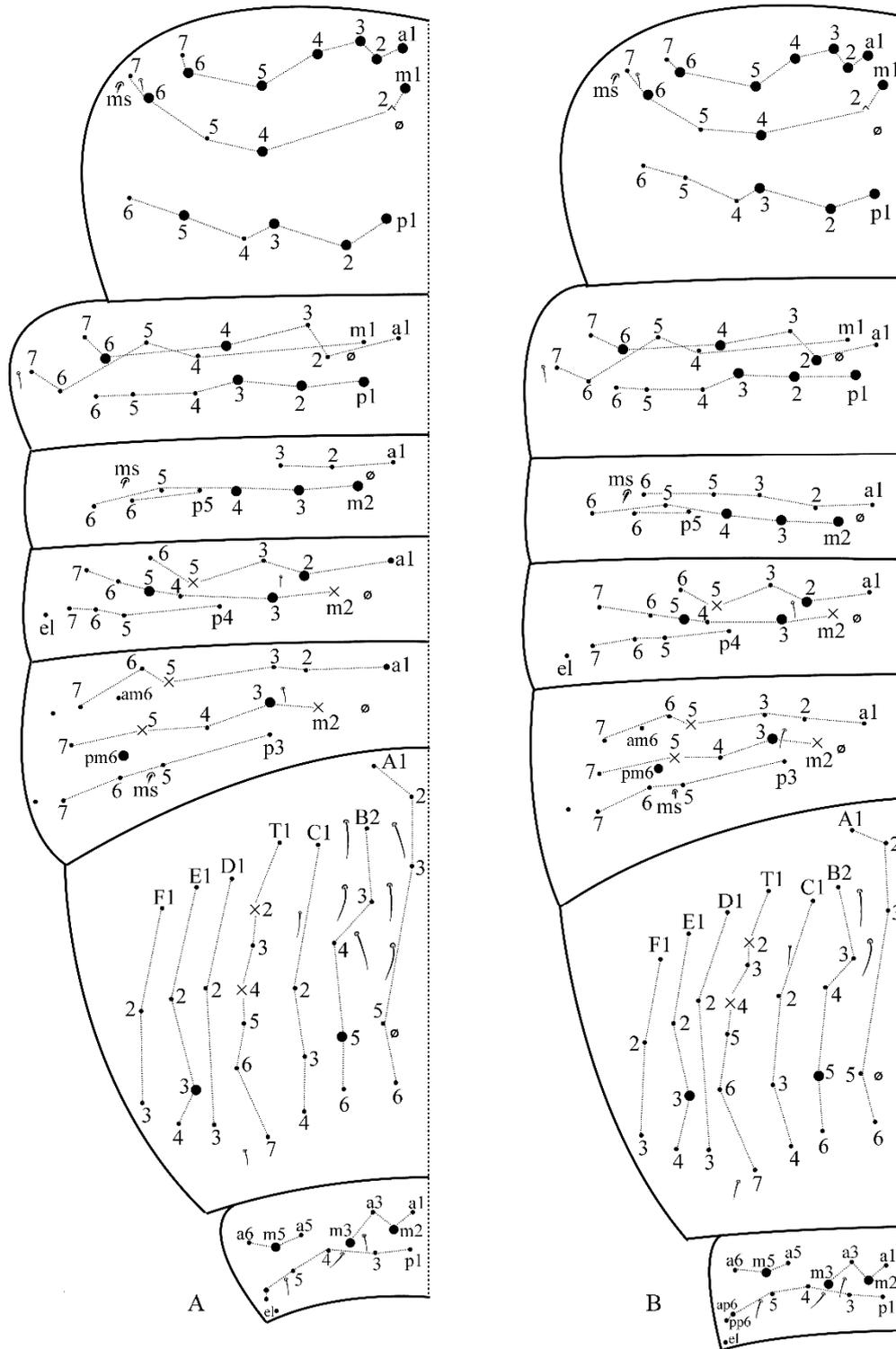


Figure 10. First instar dorsal chaetotaxy of Th. II to Abd. V in Lepidocyrtinae. A. *Lepidocyrtus cyaneus*. B. *Leidocyrtus* sp.

and other Entomobryoidea present some punctual or none secondary chaetae associated to p-row.

On Abd. I (Figs S6–7), a secondary chaeta (often as mac) postero-internal or internal to m4 usually occurs at 2nd or 3rd instar in Orchesellidae, Entomobryinae and Seirinae and is designated as m4p (Table 2). Another chaeta m4i antero-internal to m4 occurs later than m4p with its socket usually smaller than m4p (Figs S6D, G, S7A). In adults of Orchesellinae there can be several multiplets of a1–3, a5 and m2–4, while other taxa present few or no secondary multiplets of chaetae.

On Abd. II (Figs S8–9), a secondary chaeta m3e is sometimes present in several taxa after the 2nd instar (Figs S8, S9A–D) and may become more multiplets in some groups (as in Orchesellinae, Seirinae and *Entomobrya*). Multiplets other than m3 sets are present in *Orchesella* subadults and adults (a1–3) (Fig. S9A).

On Abd. III (Figs S10–11), two secondary chaetae at 2nd instar occur posteriorly to p6, p6pi internal to p6 and p6pe external to p6. Chaeta m7a, which can occur after the 2nd instar, often develops into mac in adults (Figs S10D, G). Multiplets

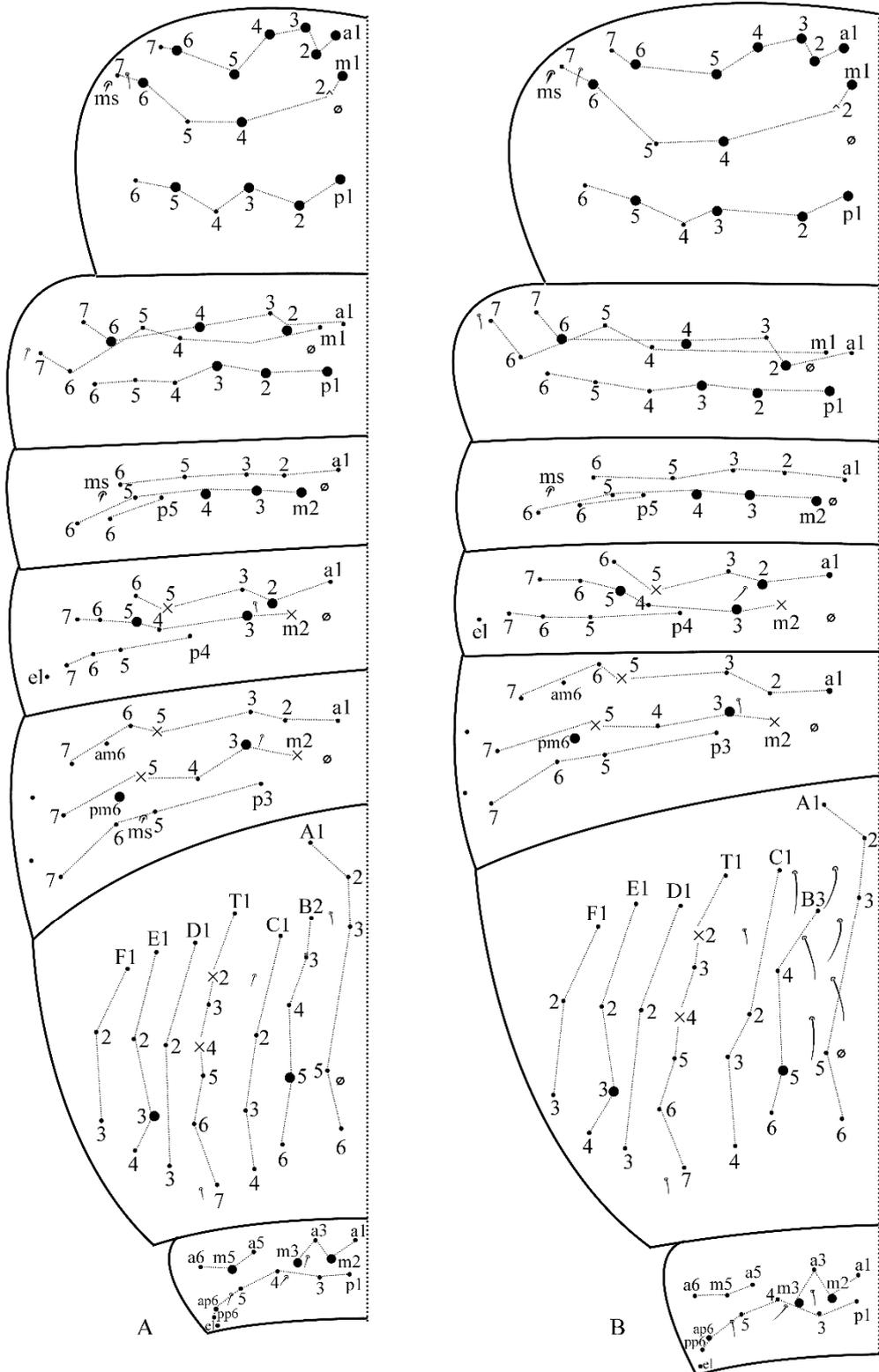


Figure 11. First instar dorsal chaetotaxy of Th. II to Abd. V in Lepidocyrtinae. A. *Pseudosinella alba*. B. *Pseudosinella* sp.A.

of a1–3 can be present in subadults and adults of Orchesellinae and rarely Entomobryinae (as a2ea).

On Abd. IV (Figs S12–16), there are usually two or one secondary antero-medial chaetae (mac or larger mic) occurring at 2nd instar in Entomobryidae (Figs S12–16). Internal Si locates postero-externally to A3, which mostly remains mic during

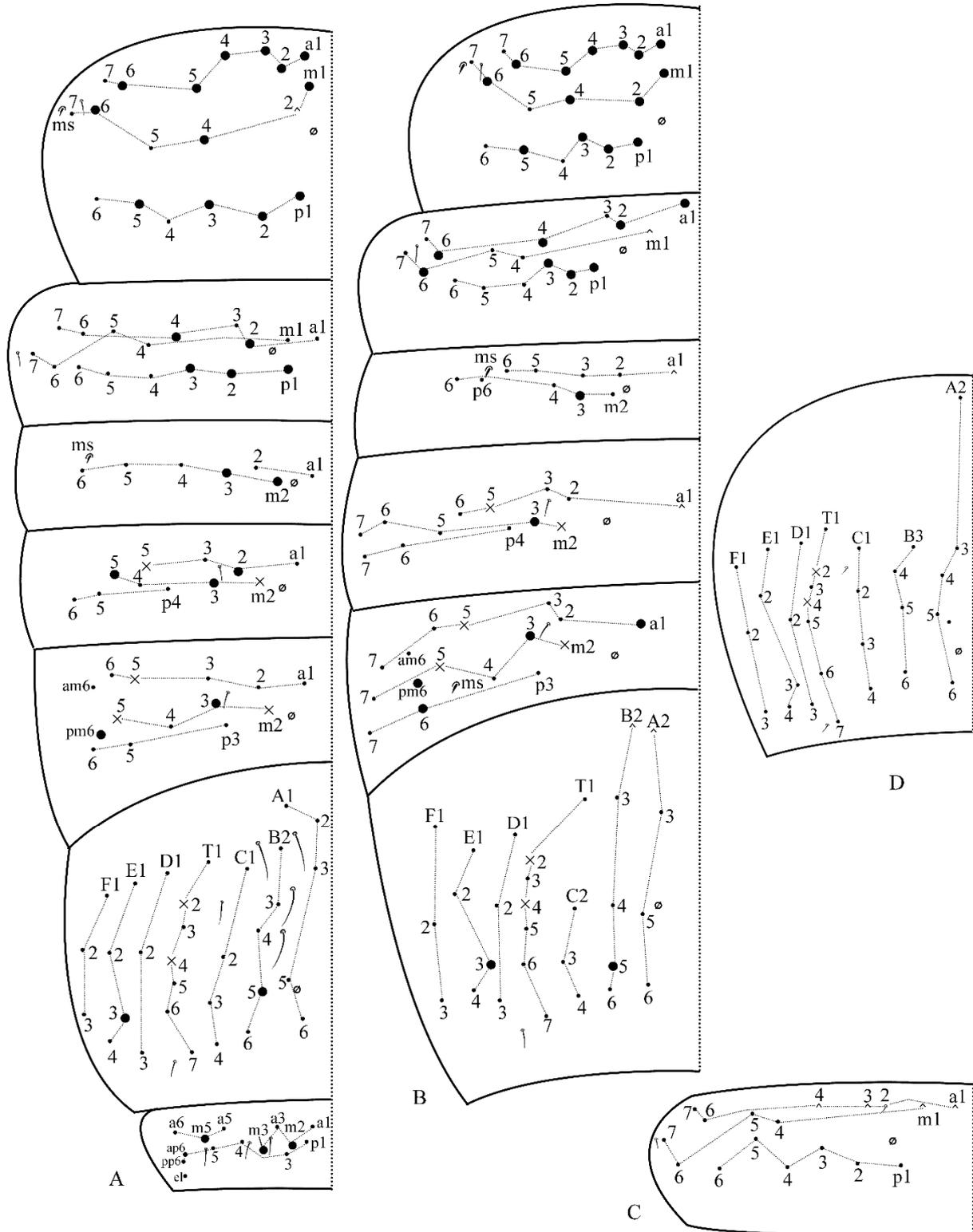


Figure 12. First instar dorsal chaetotaxy of Th. II to Abd. V. A. *Pseudosinella* sp.B (Lepidocyrtinae). B. *Trogolaphysa jataca* (Abd. V omitted, Paronellinae, redrawn from Soto-Adames, 2015). C. Th. III of *Cyphoderus albinus* (Paronellinae, redrawn from Szeptycki, 1979). D. Abd. IV of *Cyphoderus albinus* (Paronellinae, redrawn from Szeptycki, 1979).

development. External Sm is usually external to series B, internal to bothriotrichum T2, and posterior to C1; it is often incorrectly recognized as B3 or C1. There are only two mac locate between E1 and E3, they are homologous to E2 and E2p rather than “E2a and E2”.

On Abd. V (Figs S17–18), three relatively large secondary mic anterior to the set m5+ (a5–m5–a6) are designated as a5a–m5a–a6a respectively (Figs S17B–G, S18).

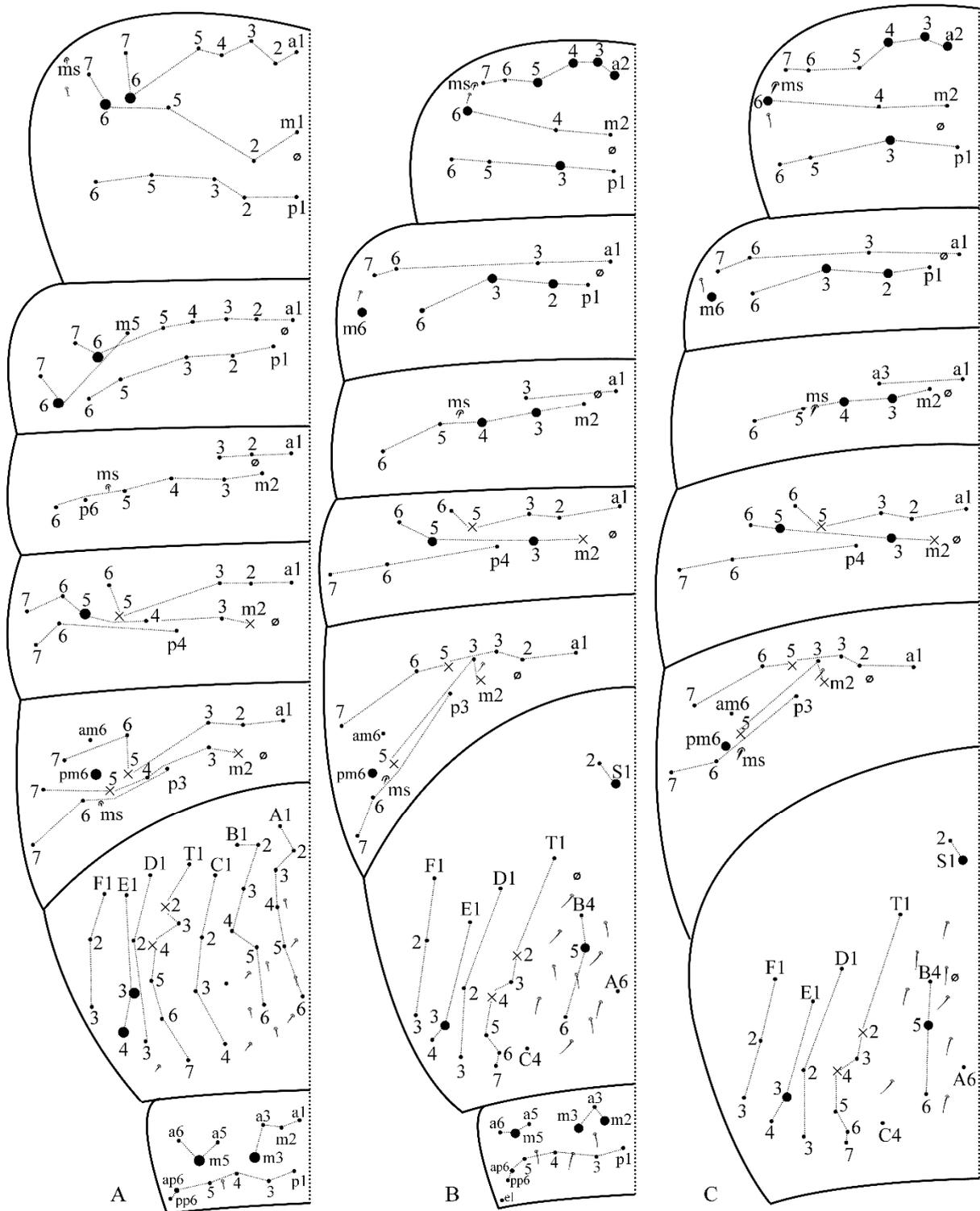


Figure 13. First instar dorsal chaetotaxy of Th. II to Abd. V in Saliniinae. A. *Microfalcula* sp. (pseudopore not clearly seen). B. *Salina celebensis*. C. *Salina tristani* (Abd. V omitted).

**Table 2. Homology revision of tergal chaetae and correspondence among three nomenclature systems. All names of Soto-Adames (2008) only refer to Seirinae.**

Tergum	Szeptycki, 1979	Soto-Adames, 2008	This study
Th. II	a3e after 1st instar	a3e	a4
	a4 after 1st instar	a4	a4e
	a4e after 1st instar	a4e	a4e2
	a4p2	a5i	a5i
	-	m5p	m5e
Th. III	a2 in Lepidocyrtinae	-	m1
	m2 in Lepidocyrtinae	-	a2
	m6e	m6p	m6e
Abd. I	a5 in <i>Sinella</i> , <i>E. muscorum</i> , <i>E. puncteola</i> , <i>Drepanosira</i> , <i>Homidia hjesanica</i> , <i>Himalanura kangbachensis</i> , <i>Himalanura pamirensis</i> , <i>Seira lusitanica</i> , <i>Seira arenaria</i>	-	m4
	a5i in <i>Sinella</i> , <i>E. muscorum</i> , <i>E. puncteola</i> , <i>Drepanosira</i> , <i>Homidia hjesanica</i> , <i>Himalanura kangbachensis</i> , <i>Himalanura pamirensis</i>	-	m4i
	m4 in <i>Sinella</i> , <i>E. muscorum</i> , <i>E. puncteola</i> , <i>Drepanosira</i> , <i>Homidia hjesanica</i> , <i>Himalanura kangbachensis</i> , <i>Himalanura pamirensis</i> , <i>Seira lusitanica</i> , <i>Seira arenaria</i>	-	m4p
	-	m4i	m4p
Abd. III	p4	p3	p3
	mac p7 after 1st instar	p7i	p6pe
Abd. IV	A1-2-3-6 in <i>Orchesella</i>	-	A2-3-5-6
	B1-2-3-5 in <i>Orchesella</i>	-	B2-3-5-6
	A1-2-3-6 in <i>Heteromurus</i>	-	B2-A2-B5-A6
	B1-5 in <i>Heteromurus</i>	-	C1-B6
	E2 in <i>Orchesella</i> and <i>Heteromurus</i>	-	E3
	A4 at 1st instar in Entomobryinae	-	A5
	C1 at 1st instar in <i>Entomobryoides</i> and Lepidocyrtinae	C1	T1
	B3 at 1st instar in Lepidocyrtinae	B2	C1
	B2 at 1st instar in Lepidocyrtinae	B1	B2
	A2p after 1st instar	-	A3
	A3 after 1st instar	-	Si
	B3p after 1st instar	-	B3
	single mac B3 or C1 after 1st instar	-	Sm
	mac C1 and B3 after 1st instar	-	Sm, B4
two mac E2a and E2 after 1st instar	-	E2, E2p	
Abd. V	m5e	-	a6
	a6 after 1st instar	-	a6a

### 3.3 Phylogeny

Phylogenetic analyses were conducted with or without the outgroup/unstable taxa (Figs 14–15, S19–26). The detection of unstable taxa with or without the outgroup achieved consistent results. Four unstable species, which severely impacted on the topology of deep nodes, were recognized by at least two approaches (Tables S2–3).

Both outgroups and unstable species sharply impacted the topology and the supports of nodes (Fig. 14, Table 4). All analyses support the polyphyly of Paronellidae under traditional definitions with three Szeptycki's families Paronellidae, Cyphoderidae, and Microfalculidae as ingroups of Entomobryidae (Figs 14–15, S19, S21, S23, S24). Orchesellinae and (Entomobryidae + Paronellidae), were recovered with high supports in most reconstructions. With the outgroup excluded, the monophyly of several more taxa was recovered: Entomobryidae and (Entomobryinae + Cremastocephalini) in MP- and

ML-analyses, and Entomobryinae in BI-analyses; partial node supports were significantly increased, Heteromurinae in MP- and BI-analyses, Entomobryidae and Entomobryinae in ML-analyses (Table 4). When the unstable taxa excluded, the monophyly of two taxa was recovered, Entomobryinae in MP-, ML- and BI-analyses, Seirinae in ML- and BI-analyses.

**Table 3. Unstable taxa detected using leaf stability index (lsi), taxonomic instability index (tii), RogueNaRok-algorithm and TNT\*.**

Taxa	lsi	tii	RogueNaRok	TNT
<i>Microfalcula</i> sp.	+	+		+
<i>Salina celebensis</i>	+			+
<i>Salina tristani</i>	+			+
<i>Callyntrura guangdongensis</i>		+	+	

\*Plus sign (+) represents the unstable taxa supported by the algorithm.

**Table 4. Monophyletic groups supported by different tree optimality criteria and taxa selection strategies. Molecular phylogeny was drawn from Zhang *et al.* (2015, 2017), other analyses from this study. Sign “\*” represents the high node supports (MP>70, ML>70, BI>0.95). Sign “-” indicates Cremastocephalini is excluded from the analyses. Abbreviation: M—molecular phylogeny; a—d—taxa selection strategies (a—all 38 species; b—35 species without the outgroup taxa; c—34 species without the unstable taxa; d—31 species without the outgroup and the unstable taxa).**

Taxa	M	MP				ML				BI			
		a	b	c	d	a	b	c	d	a	b	c	d
Orchesellinae	+	+	+	+	+	+	+	+	+	+	+	+	+
Heteromurinae	+	+	+	+	+		+		+	+	+	+	+
Orchesellidae		+	+	+			+		+	+	+	+	+
(Entomobryidae+Paronellidae)	+		+		+	+	+	+	+		+		+
(Entomobryinae+Cremastocephalini)			+	-	-	+	+	-	-		+	-	-
Entomobryinae					+			+	+				+
Cremastocephalini	+	+	+	-	-	+	+	-	-	+	+	-	-
(Seirinae+Lepidocyrtinae+Paronellinae)		+	+	+	+	+	+	+	+	+	+	+	+
Seirinae	+	+	+	+	+			+		+	+	+	+
(Lepidocyrtinae+Paronellinae)	+	+	+	+	+	+	+	+	+	+	+	+	+
Lepidocyrtinae		+	+	+	+	+	+	+	+	+			
Paronellinae		+	+	+	+	+	+	+	+				

## 4 Discussion

### 4.1 Revision of homology recognition

In principle, homology hypotheses should be established on the basis of thorough observation of the postembryonic instars among all the species. However, it is very difficult to trace all the instars of all species, even genera. Plenty of information of important instars (early instars) presented in this study provided robust, comparable evidence for the homology recognition. Many Szeptycki’s hypotheses were revised across a wide of taxa sampling within Entomobryoidea.

Homology of a4 and several chaetae around it on Th. II was revised. At 2nd instar, there are three chaetae anterior to a5 in most species, with one primary a4 and other two secondary (Figs S1A, S2). The difficulty is correctly recognizing a4, the inner one or the middle one? Length of chaetae and size of their sockets have no distinct differences between them in most species. The occurrence of two secondary chaetae in *Microfalcula* (Fig. S2H) provides a comprehensive case supporting the hypothesis of two external secondary chaetae. In *Microfalcula*, the positions of a4 and a5 are peculiar with a5 antero-external to a4. At the 2nd instar, a4 is transformed into mac but its relative position has no change in the area; two secondary chaetae appear antero-external to a4 and a5, and their positions are farther than those in other species, distinctly separated from a4 and a5. The two secondary chaetae are thus named as a4e and a4e2 with the most inner chaeta as a4.

On Th. III, there are always four chaetae (or scales) anterior to p1-p2, designated as a1-a2-a3-m2 in Lepidocyrtinae and a1-a2-a3-m1 in others following Szeptycki (1979). Alternatively, the four elements could be homologous to a1-m1-a2-a3 across all taxa from the central to the lateral side (Figs 3–12, S4–S5). Chaeta m1 moves anteriorly and thus within the line

connecting a1 and a2 in Lepidocyrtinae, and locates posteriorly to a1-a2 in other taxa. In *Seira*, m6p is usually posterior to m6 and m6e is external to m6, therefore a chaeta external to m6 in Soto-Adames’ drawings are corrected as m6e rather than m6p.

On Abd. I, a secondary chaeta m4p (often as mac) appears postero-internally or internally to m4 at 2nd or 3rd instar. Chaetae m4 and m4p often develop into mac in polymacrochaetotic species (Figs S6–S7). If a5 is a mac in adults, its transformation from mic to mac usually occurs later than m4 and m4p. The largest socket of chaeta m4 often helps to recognize its homology.

On Abd. III, there is only one chaeta internal to p5 in the p-row. Szeptycki (1979) designated it as p3 (posterior to m3) in Lepidocyrtinae and p4 (external to m3) in others. However, its position is very similar in *Entomobrya*, *Sinella*, *Coecobrya*, *Homidia* and *Pseudosinella* sp.A (Figs 5–8, 11B), with the chaeta posterior-external to m3. Therefore, we believe this chaeta is homologous in all taxa and designate it as p3. Szeptycki (1979) also named a chaeta external to p6 as p7. Actually, p7 is much farther from p6 than this chaeta (Figs S10, S11A–D), which is supposed to be homologous to p6pe in this study.

Lateral primary chaetae (columns T, D, E, F) of Abd. IV have few variations within Entomobryoidea, 17 (E2 present) in Seirinae, Lepidocyrtinae and Paronellinae and 16 (E2 absent) in others. When three chaetae are present in column E, the middle one is a mac in Orchesellidae, as well as most taxa having elongate Abd. IV. The middle chaeta “E2” for Orchesellidae in Szeptycki’s book is homologous to E3 in other taxa (Table 2). To easily compare lateral chaetae between taxa, we keep the complete seven chaetae (T1–7) in column T when the most anterior chaeta is difficult to determine as T1 or C1. Therefore, the most anterior chaetae of column C, as well as columns A and B, are supposed to be possible absent in this study. In the aM (antero-medial) area defined by Szeptycki, a maximum of eight chaetae are included: A1–3, B1–3, C1 and T1. The presence of A1 and B1 in Entomobryidae indicates that the elongation of Abd. IV may result in the occurrence of the two

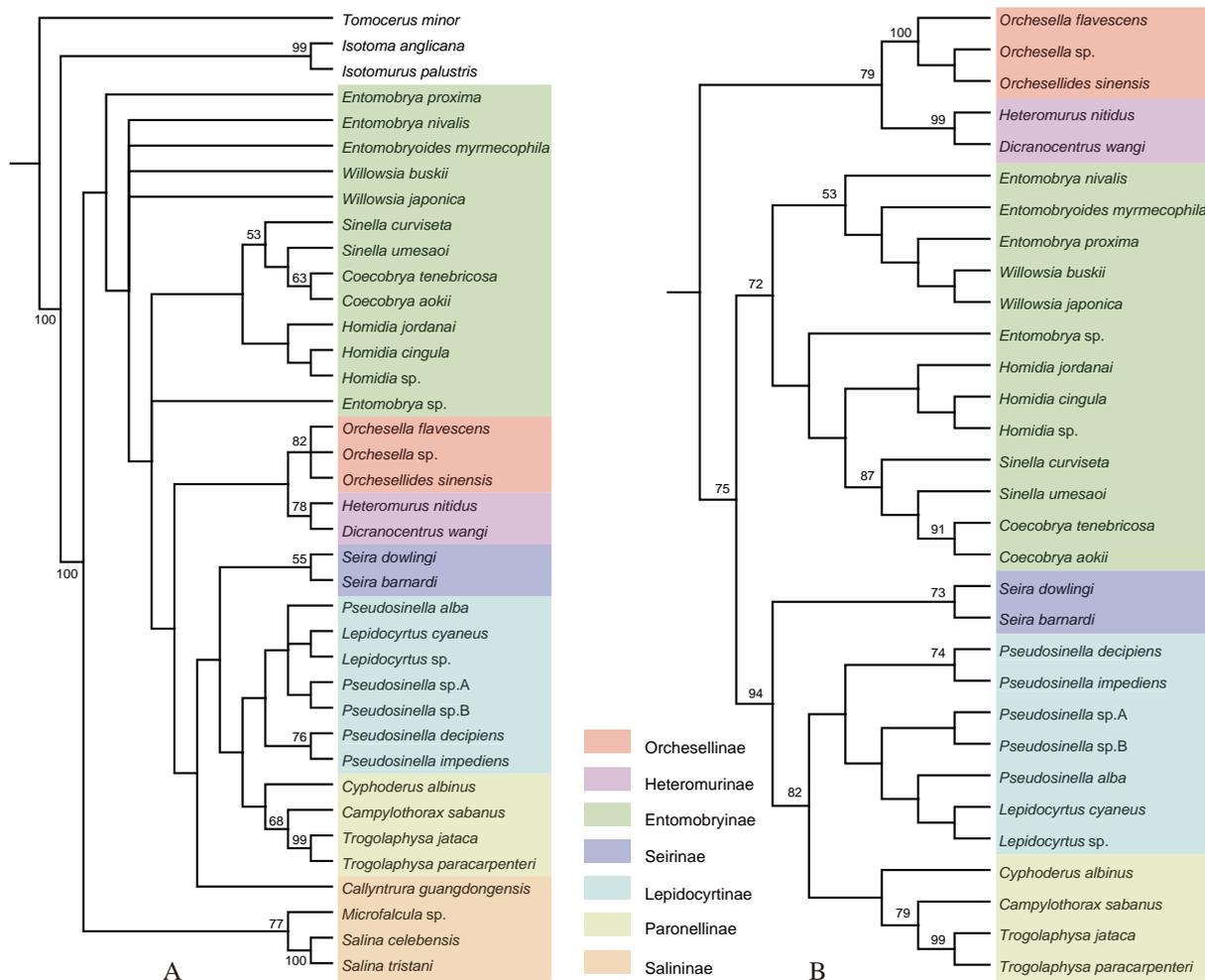


Figure 14. Phylogeny of Entomobryoidea using maximum parsimony. The bootstrap values greater than 50 are given on the nodes. A. Strict consensus of ten equally parsimonious trees with all 38 species included. B. Strict consensus of two equally parsimonious trees with the outgroup and unstable species excluded.

chaetae, which never occur in Orchesellidae, as well as Tomoceridae and Isotomidae, so such chaetae should be interpreted as derived characters within the Entomobryoidea, which may be lost in some lineages as *Salina* and *Trogolaphysa* (Figs 12C, 13B–C). Homology hypotheses in the area aM are a bit complicated for Seirinae and Lepidocyrtinae. Mistakes were possibly generated from *Pseudosinella alba*, in which B3 is absent the Szeptycki’s drawings but is present in one side of our material (Fig. 11A); thus, Szeptycki incorrectly designated C1 and T1 as “B3” and “C1”, respectively. Actually, B3 always locates within or internally to the line connecting B2 and B4, never externally to the line as shown in Szeptycki’s figures. Similarly, B3 in *Lepidocyrtus curvicollis* (Fig. 3D) was unnamed with C1 and T1 incorrectly named in Szeptycki’s book (p. 211). Soto-Adames (2008, p. 22) included the chaeta C1 (“B2” in his figure) in column B, resulting in the incorrect designation of B2, C1 and T1 (Fig. 9C). In the postero-medial (pM) area, there are usually 2 chaetae present in column A, which are supposed to be A5 and A6. The homology of most anterior two chaetae in *Salina* is possible to be supposed as A1 (mic) and A2 (mac) (Figs 13B–C). However, the complete columns A, B and C posterior the mac in *Callyntrura* indicate that the two most anterior chaetae are supplementary to other primary chaetae and thus are named as S1 and S2.

Among the secondary chaetae on Abd. IV, the most important revisions are the two chaetae (Si, Sm) occurring after the 1st instar in several taxa (Figs S12–16). They were often respectively named as A3 and B3/C1 in adults. Some chaetae were

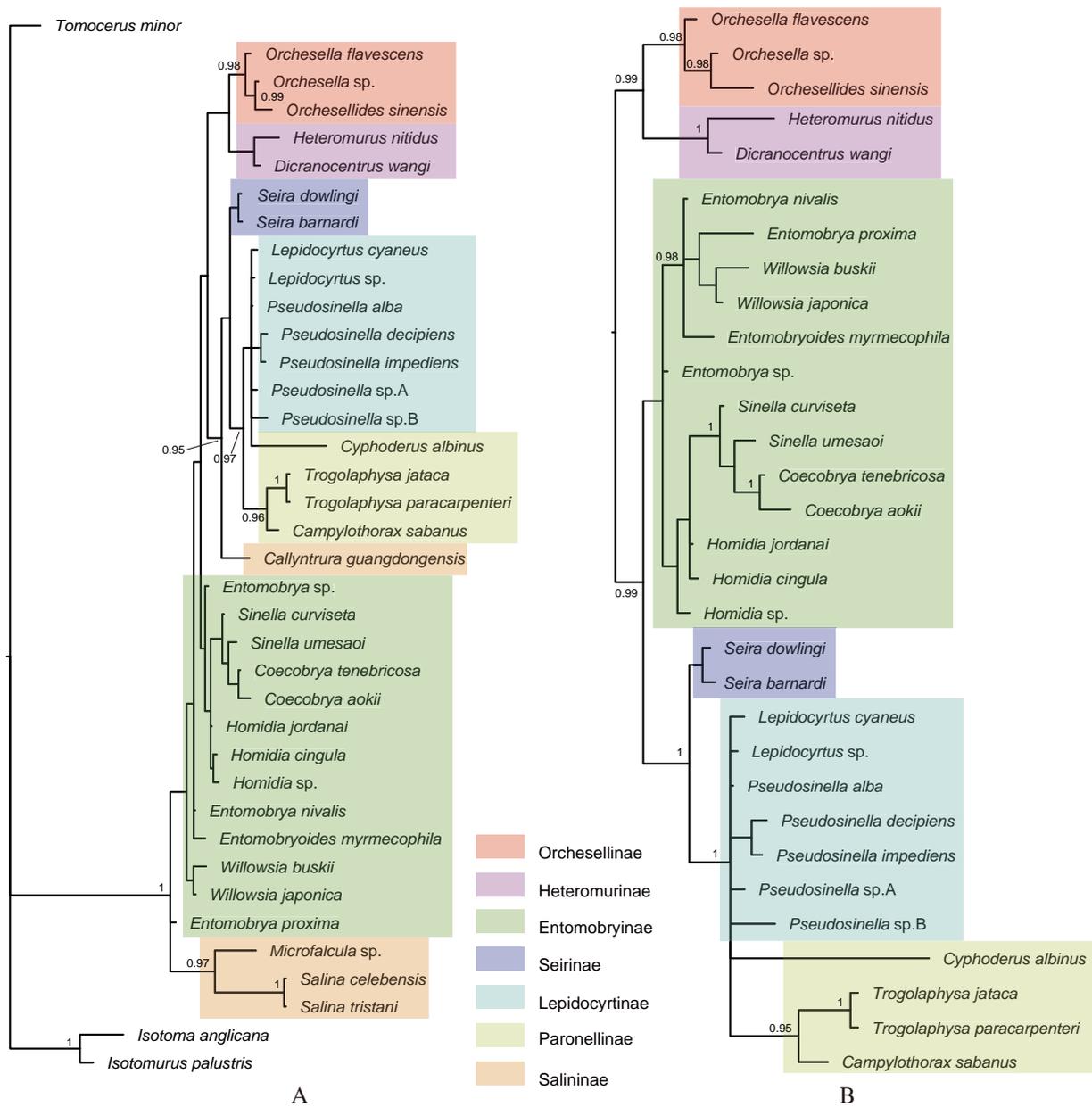


Figure 15. Bayesian phylogeny of Entomobryoidea. Posterior probability values greater than 0.95 are shown on the nodes. A. Consensus tree of all 38 species included. B. Consensus tree of 31 species with the outgroup and unstable species excluded.

considered to sharply displace with the development (Szeptycki, 1979; Soto-Adames, 2008). According to our observation, the displacement of the chaetae, as well as the position of the chaetae relative to their around chaetae, is very conservative with the development, particularly the adjacent instars. Macrochaetae are supposed to be more possible to develop from primary than secondary chaetae, and therefore the two chaetae (often as mac) near A3/B3/C1 appearing at the 2nd instar were named as primary chaetae. For example, A3, as well as A2, is closest to the midline. At the 2nd instar, a chaeta appears postero-externally to A3; when the chaeta (often as mac or its socket larger than other mic) is and not far from A3 (Figs S15A, C–D, S16A–B), it is considered to be “A3” by Szeptycki (1979) and Soto-Adames (2008). However, the long distance of the two chaetae in other taxa (Figs S12–14, S15B, S16C) indicates that the antero-internal chaeta is primary A3 and the posterior one is secondary (Si). Another secondary chaeta Sm appearing at 2nd instar usually locates internally to bothriotrichum T2 (Figs S12–16).

The present study mainly revises the homology hypotheses of primary chaetae and important secondary chaetae of early instars. Many groups, such as Bessoniellinae, Salininae, Paronellini, Bromacanthini, Cyphoderini *etc.*, lack the adequate chaetotaxic information concerning the postembryonic development. Besides comparison among taxa, chaetotaxic variations within species or both sides of the individual should be carefully estimated. For example, asymmetric chaetotaxy (position and size) on both sides are often seen in polymacrochaetotic species (Fig. S13D). Recent literature has shown polymorphic characters on adult Entomobryoidea are quite common, which suggests a wider number of studied specimens in the same species is important to truly understand its chaetotaxy patterns.

## 4.2 Systematics of Entomobryoidea

Three outgroup species, two *Salina* and one *Microfalcula* representing long branches, are grouped at the root (Fig. 14A). Indeed, likelihood-based methods (ML, BI) and the exclusion of those taxa reduce the long-branch attraction (LBA) and improve the tree resolution (Table 4, Figs 14B, 15B). Integrating published molecular phylogeny (Zhang *et al.*, 2015, 2017) and phylogenies reconstructed in this study, a revised classification of three families and nine subfamilies is presented for Entomobryoidea (Table 1). The new classification partially differs from the traditional classification mainly relying on the furcula (dens plus mucro), in which straight non crenulate dens and non-claw-like mucro possibly had multiple independent origins (Zhang *et al.*, 2015). Taxa having short Abd. IV are included in Orchesellidae. Other taxa having elongated Abd. IV constitute the Entomobryidae and Paronellidae, the latter including the traditional Szeptycki's (1979) families Paronellidae, Cyphoderidae and Microfalculidae. Microfalculidae (*Microfalcula*) is transferred into Cremastocephalini. Bromacanthini, Paronellini and Cyphoderini constitute the new Paronellinae. The remaining two tribes of Paronellidae (Callyntrurini and Cremastocephalini) constitute the Salininae.

Orchesellidae. Taxa of short Abd. IV have been demonstrated to be the basal group within Entomobryoidea by molecular evidence (Zhang *et al.*, 2015, 2017) and ML-phylogenies. These taxa were widely treated as Orchesellini (Börner, 1913; Stach, 1960) or Orchesellinae (Absolon & Kseneman, 1942; Yosii, 1961; Szeptycki, 1979; Soto-Adames *et al.*, 2008), and further divided on the basis of the number of antennal segments (Mari-Mutt, 1980). The earliest familial status was used by Yosii (1966, 1971, 1977). Soto-Adames *et al.* (2008) excluded Capbryinae from Orchesellinae based on the reduced trochanteral organ. Within them, monophyly of scaled Heteromurinae and unscaled Orchesellinae is highly supported in this study (Table 4, Fig. 14), again confirming previous molecular results. Considering their basal positions and the primitive trait (Abd. IV not elongated), these taxa are excluded from Entomobryidae and treated as a distinct family, Orchesellidae. Two subfamilies Heteromurinae and Orchesellinae are not upgraded as familial status because their relationships with other Entomobryoidea taxa remain completely unresolved. Molecular phylogeny favoured the hypothesis of (Orchesellinae + (Heteromurinae + remaining taxa)), but the hypothesis of monophyly of Orchesellidae *s. l.* was not rejected by likelihood CONSEL tests (Zhang *et al.*, 2015). The single clade of Orchesellidae *s. l.* in this study is recovered in MP- and BI-trees with weak supports when the outgroup was included (Table 4). Heteromurinae species does not form a monophyletic clade but locates at the most basal position in ML-analyses when the outgroup was included (Figs S23, S25). Systematic discussions of other two small subfamilies within Orchesellidae see Zhang & Deharveng (2015): Nothobryinae is closely related to other Orchesellinae (it can be possibly an ingroup of Orchesellinae), which is supported by overall dorsal chaetotaxy (Barra, 1999; Baquero *et al.*, 2004; Silveira & Mendonça, 2016; Nunes & Bellini, 2019). *Capbrya* and *Hispanobrya* (Capbryini) also present a remarkably similar chaetotaxy compared to other Orchesellinae, specially *Nothobrya* (Nothobryini), but this group shows a very different S-chaetotaxy: 1,1|0,2–3,2 (Table 5). Nevertheless, morphology supports both genera belong to Nothobryinae and such S-chaetotaxy is quite possibly and autapomorphy. The position and status of *Bessoniella* (Bessoniellinae) remains unclear without a molecular phylogenetical approach, but due to its unique absence of tergal ms and reduced S-chaetotaxy (1, 1|0, 2, 4) we consider its status as a subfamily for now, as proposed in Zhang & Deharveng (2015).

Dismissal of Microfalculidae. Microfalculidae (*Microfalcula*) was characterized by the absence of mucro, enlarged tenent hairs and reduced claw. Actually, *Salina* and *Akabosia* also have enlarged tenent hairs compared to other taxa. Besides, the three genera share unilobed antennal bulb, discrete eyes, and reduced tergal S-chaetae from Th. II to Abd. III (10|000 in *Microfalcula*, 11|000 in *Akabosia*, 11|001 in *Salina*). Concerning 1st instar dorsal chaetotaxy, absence of p4 in Th. II, reduction of chaetae in m-row on Th. III (m1 and m4 lacking), in a-row on Abd. I (a5–6 lost), absence of a7 on Abd. II and m3 as mic on Abd. III were also shared by the studied species of *Salina* and *Microfalcula* (Fig. 13). Crenulate dens in *Microfalcula* are also similar to *Akabosia*. Trees reconstructed here always cluster the three genera together with high node supports (Table 4, Fig. 14A). In the light of weak phylogenetic signal of dens and mucro at high levels (Zhang *et al.*, 2015), Microfalculidae (*Microfalcula*) is transferred into Cremastocephalini.

(Entomobryidae + Paronellidae). The monophyly of taxa having elongate Abd. IV is strongly supported by molecular phylogeny (Zhang *et al.*, 2015, 2017) and morphological reconstructions when the outgroup excluded (Table 4). Compared to Orchesellidae, these taxa have four antennal segments (plesiomorphy), elongate Abd. IV (apomorphy), less tergal S-chaetae (apomorphy), variable scale distribution and surface sculpture, and variable dens and mucro. However, (Entomobryidae + Paronellidae) has strong conflicts on further divisions observed among phylogenies, whatever between molecular and morphological ones or within morphological ones (Table 4). Monophyly of Entomobryidae and Paronellidae is never supported in phylogenetic analyses, and taxa of two families are always mixed upon trees. Three clades can be roughly recognized in molecular and partial morphological phylogenies: Seirinae, (Entomobryinae + Salininae), and (Lepidocyrtinae + Paronellini + Cyphoderini) (the latter two named as “Entomobryinae” and “Lepidocyrtinae” respectively in previous papers); only “Lepidocyrtinae” is absolutely supported in almost all phylogenies.

Furthermore, these phylogenetic divisions greatly differ from the traditional classification of Entomobryidae and Paronellidae. Diversified dens and mucro simultaneously occur in “Entomobryinae” and “Lepidocyrtinae”. Even S-chaetotaxic pattern and its high phylogenetic potentials (Zhang & Deharveng, 2015; Zhang *et al.*, 2015) is difficult to be fully compatible with above phylogenies. For Cremastocephalini and Callyntrurini, each has two S-chaetotaxic patterns (Table 5), of which patterns 2, 2|1, 2, 2 and 1, 1|0, 2, 2 are identical with that of Entomobryinae and Seirinae, respectively. Molecular phylogenies (Zhang *et al.*, 2015, 2017) always clustered *Callyntrura* with Cremastocephalini than Seirinae. At the current stage, no perfect solution can be found to eliminate these conflicts because details of many groups, particularly those of Paronellidae, are still unknown. Therefore, we here retain the traditional concepts of Entomobryidae (dens crenulate) and Paronellidae (dens straight and smooth). Phylogenomic tool and more group sampling are expected to give more reliable results, especially for those anomalies in the genera *Akabosia*, *Microfalcula*, *Metacoelura* and *Yosiia*.

Morphology supports the proximity of Lepidocyrtinae *s. str.* and part of Paronellidae *sensu* Soto-Adames *et al.* (2008). The clearly reduced macrochaetotaxy seen in *Paronella*, *Lepidonella*, *Trogolaphysa*, *Troglopedetes*, *Campylothorax* and *Cyphoderinae sensu* Soto-Adames *et al.* (2008), plus the presence on adults of several primary chaetae as mic, strongly contrast with other groups of Paronellinae *sensu* Soto-Adames *et al.* (2008), like Salininae and *Pseudoparonella*-group. The scales morphology of the first taxa is different and it is more similar to Lepidocyrtinae *s. str.*, which is devoid of coarsely ribs (Mitra, 1992, 1993; Soto-Adames *et al.*, 2008, 2014; Soto-Adames & Bellini, 2015; Bellini & Cipola, 2017; Deharveng *et al.*, 2018; Nunes & Bellini, 2018). Thus Paronellini, Troglopedetini (a very likely synonym to Paronellini as discussed in Soto-Adames *et al.*, 2014), Bromacanthini and Cyphoderini are potentially related to Lepidocyrtinae, which is supported by molecular data as well (Zhang *et al.*, 2015, 2017). Such groups also share a similar S-chaetotaxy formula (1, 1|0, 1, 1) (Table 5). Consequently, the straight dens lacking crenulations may have arisen more than one time among the Entomobryoidea. For instance, potential secondary absence of dens crenulations in Entomobryomorpha is reported to different subfamilies of Isotomidae (as seen in *Appendisotoma*, *Archisotoma*, *Folsomides*, *Pachyotoma*, *Tetracanthela* among several other genera) (Potapov, 2001) and molecular phylogenies point to a similar process within Entomobryoidea (Zhang *et al.*, 2015, 2017).

Seirinae as proposed by Zhang & Deharveng (2015) holding species only with falcate mucro lacking mucronal spine is the most stable group of Entomobryoidea, and it is supported by all previous molecular studies (Zhang & Deharveng, 2015; Zhang *et al.*, 2015, 2016, 2017; Nunes *et al.*, 2019). However, the systematic position of Seirinae, *i.e.* closer to Entomobryinae-like (Entomobryinae + Cremastocephalini) or Lepidocyrtinae-like (Lepidocyrtinae + Paronellinae) taxa, is still unclear. The traditional view of (Seirinae + “Lepidocyrtinae”) is supported by morphological evidence (Table 4, Soto-Adames, 2008) and molecular phylogeny from three ribosomal markers (Zhang *et al.*, 2014). When one extra marker (COI) is applied in analyses (Zhang *et al.*, 2015, 2016, 2017), or it is the single mitochondrial marker used (Nunes *et al.*, 2019), molecular phylogenies support alternative hypothesis. Actually, CONSEL topology tests can accept both hypotheses (Zhang *et al.*, 2015). In morphology, Seirinae also shares characteristics to various groups: polymacrochaetotaxic chaetotaxy and 2, 2 sens on Abd. II–III with Entomobryinae, 1, 1|0, 2, 2, ?, 3 tergal sens with *Callyntrura*, scale shape and distribution and 1, 1|0 sens on Th. II–Abd. I with Lepidocyrtinae and Paronellinae. So Seirinae may represent a transitional group between

Entomobryinae-like and Lepidocyrtinae-like taxa. This condition was curiously observed by Lubbock (1873) in the description of *Seira*, which literally meant to him “a link in a chain” (in Greek more precisely “a sequence”) between scaled (*Lepidocyrtus*) and unscaled (*Entomobrya*) Entomobryidae.

Paronellidae. Five main groups sensu Soto-Adames *et al.* (2008, 2014) are retained but re-combined into two subfamilies in this study (Table 1). The two subfamilies are completely separated in morphology and phylogeny. Bromacanthini, Paronellini and Cyphoderini have rounded scales and reduced mac while others have scales pointed or absent and abundant mac. The familial status of *Cyphoderus*-like taxa is usually emphasized by its morphological classification (presence of fringed dental scales) rather than phylogeny. Many recent studies (Soto-Adames *et al.*, 2008; Soto-Adames & Bellini, 2015; Zhang *et al.*, 2015, 2017; Zeppelini & Oliveira, 2016) and the present study highlighted its closer relationships with Paronellini and Bromacanthini. As early as 1913, Börner pointed out the closer relationship between Cyphoderini and Troglapedetini (now Paronellini) and placed them into Cyphoderinae. All phylogenies well support the monophyly of this subfamily with high node values (Table 4). Therefore, the new Paronellinae is defined in the light of tergal sens 11|011 on Th. II–Abd. III, few tergal mac, and scale morphology (ribless, finely denticulate, mostly apically rounded). Among three tribes of Paronellinae, Bromacanthini is considered to be closer to Lepidocyrtinae (Mari-Mutt, 1987) and the basal group within Paronellinae (Soto-Adames & Bellini, 2015).

We group Cremastocephalini and Callyntrurini into Salininae, a concept presented by Absolon & Kseneman (1942). Their separation is simply defined by the presence/absence of scales. Zhang *et al.* (2017) doesn’t support the monophyly of any tribe, and body scales are again demonstrated to be of independent origins among Salininae as those in Entomobryinae; new discovered *Zhuqinia* cannot be assigned to either tribe. Three clades in phylogenies also match the three S-chaetotaxic patterns (Table 5). Mucro morphology also provides positive evidence for the separation of three sampled groups: mucronal teeth at least five in *Callyntrura*, 2–3 in Cremastocephalini and *Pseudoparonella/Zhuqinia*; mucro sharply separated from dens in *Callyntrura* and Cremastocephalini but weakly separated from dens in *Pseudoparonella/Zhuqinia*. However, at least one-half of genera lack information of important morphological characters particularly S-chaetae. In addition, Salininae taxa are clustered with Entomobryinae in molecular and partial morphological phylogenies as above stated. Resolving systematic position of Salininae needs more sampling, particularly genera from Oceanian fauna.

The revised classification just gets his foot in the door for the fundamental framework of Entomobryoidea integrating molecular and morphological phylogenies. It may be imperfect with many problems unresolved, such as relationships between families/subfamilies, monophyly of Paronellidae and Salininae *etc.* Advances in future indeed rely on molecular phylogeny or phylogenomics by sampling more representative taxa and sequencing more markers, and morphological evidence based on a wider sampling of first instar larvae, as well as adults. Revision of poorly defined or described genera also could substantially improve our understanding.

**Table 5. Known sens patterns of Th. II–Abd. III and corresponding groups within Entomobryoidea.**

Sens	Taxa
2, 2 1, >3, >3	Most Orchesellinae
2, 2 1, 6, 6	Nothobryini
1, 1 0, 2–3, 2	Capbryini
2, 2 1, 3, 3	Heteromurinae
2, 2 1, 2, 2	Most Entomobryinae, <i>Pseudoparonella</i> , <i>Plumachaetas</i> , <i>Metacoelura</i> , <i>Zhuqinia</i> , <i>Paronellides</i>
1, 1 0, 2, 4	Bessoniellinae
1, 1 0, 2, 2	Seirinae, <i>Callyntrura</i>
1, 1 0, 1, 1	Lepidocyrtinae, Bromacanthini, Paronellini, Cyphoderini
1, 0 1 0, 0, 0 1	<i>Salina</i> (1, 1 0, 0, 1), <i>Akabosia</i> (1, 1 0, 0, 0), <i>Microfalcula</i> (1, 0 0, 0, 0)

**Key to the suprageneric classification of Entomobryoidea.**

1. Abd. IV less than 2.0 times Abd. III in length at middle line (**Orchesellidae**)..... 2  
 Abd. IV more than 2.0 times Abd. III in length at middle line..... 7
2. Body scales absent; tergal sens formula not as 2, 2|1, 3, 3 ..... 3  
 Body scales present; tergal sens formula as 2, 2|1, 3, 3 (**Heteromurinae**) ..... 6
3. Mucro tridentate; tergal ms absent ..... **Bessoniellinae**  
 Mucro falcate or bidentate; tergal ms present..... 4
4. PAO present; mucro falcate.....**Nothobryinae**  
 PAO usually absent; mucro bidentate (**Orchesellinae**) ..... 6

5. Six antennal segments; tergal sens formula as 2, 2|1, 6, 6..... **Nothobryini**  
 Four antennal segments; tergal sens formula as 1, 1|0, 2–3, 2..... **Capbryini**
6. Antennae with four segments; tenaculum with four chaetae..... **Corynothricini**  
 Antennae with 5–6 segments; tenaculum with 0–2 or 5–15 chaetae..... **Orchesellini**
7. Scales fusiform, apically pointed, absent on antennae and legs..... **Mastigocerini**  
 Scales apically rounded or truncate, present on antennae and legs..... **Heteromurini**
8. Dens crenulate and tapering, mucro always present (**Entomobryidae**)..... 9  
 Dens usually smooth and cylindrical, mucro present or rarely absent (**Paronellidae**)..... 11
9. Bothriotricha 2, 3, 3 on Abd. II–IV; tergal sens formula as 1, 1|0, 2, 2; mucro falcate without basal spine and lamella; scales present..... **Seirinae**  
 Bothriotricha 2, 3, 2 on Abd. II–IV; tergal sens formula not as 1, 1|0, 2, 2; mucro falcate or bidentate; scales present or absent..... 10
10. Tergal sens formula on Th. II–Abd. III as 1, 1|0, 1, 1; tergal mac reduced; scales ribless, finely denticulate, mostly apically rounded..... **Lepidocyrtinae**  
 Tergal sens formula on Th. II–Abd. III as 2, 2|1, 2, 2; tergal mac abundant; scales present or absent; if present, scales with coarse ribs..... **Entomobryinae**
11. Tergal sens formula on Th. II–Abd. III as 1, 1|0, 1, 1; tergal mac reduced; scales ribless, finely denticulate, mostly apically rounded (**Paronellinae**)..... 12  
 Tergal sens formula on Th. II–Abd. III not as 1, 1|0, 1, 1; tergal mac usually abundant; scales present or absent; if present, scales with coarse ribs (**Salininae**)..... 14
12. Dens with dorsal fringed scales..... **Cyphoderini**  
 Dens without dorsal fringed scales..... 13
13. Bothriotricha 2, 3, 2 on Abd. II–IV..... **Bromacanthini**  
 Bothriotricha 2, 3, 3 on Abd. II–IV..... **Paronellini**
14. Scales present..... **Callyntrurini**  
 Scales absent..... **Cremastocephalini**

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**Appendix 1. Character coding and character matrix in “nex” format.****Character coding used for phylogenetic analyses.**

1. Subdivision of Ant. I in adults: (0) absent; (1) present.
2. Subdivision of Ant. II in adults: (0) absent; (1) present.
3. Scales on body in adults: (0) present; (1) absent.
4. Scales on dens in adults: (0) absent; (1) present.
5. Dental spines of adults: (0) absent; (1) present.
6. Mucronal basal spine of adults: (0) absent; (1) present.
7. Ratio of Abd. IV/III: (0) <2; (1) >2.
8. Ant. IV apical bulb: (0) absent; (1) unilobed; (2) bilobed.
9. Number of eyes: (0) 8; (1) <8.
10. Prelabral chaetae: (0) ciliate; (1) smooth.
11. Labial chaeta M: (0) ciliate; (1) smooth.
12. Labial chaeta M: (0) ciliate; (1) smooth.
13. Tenent hairs on legs: (0) clavate; (1) pointed.
14. The first (median) unpaired unguual inner tooth: (0) absent; (1) present.
15. The second unpaired unguual inner tooth: (0) absent; (1) present.
16. A large outer tooth on unguiculus: (0) normal; (1) larger.
17. Dens dorsally: (0) smooth; (1) crenulate.
18. Apical teeth on mucro: (0) 2; (1) 1; (2) >2; (3) 0.
19. Cephalic postocellar bothriotricha: (0) absent; (1) present.
20. Longitudinal row ia of tibiotarsal primary chaetae: (0) absent; (1) present.
21. Longitudinal row a of tibiotarsal primary chaetae: (0) absent; (1) present.
22. Primary chaeta a1 on Th. II at 1st instar: (0) mic (Fig. 2B); (1) mac (Fig. 3A); (2) absent (Fig. 2A).
23. Primary chaeta a2 on Th. II at 1st instar: (0) mic (Fig. 13A); (1) mac (Fig. 3A); (2) absent (Fig. 2B).
24. Primary chaeta a3 on Th. II at 1st instar: (0) mic (Fig. 2B); (1) mac (Fig. 3A).
25. Primary chaeta a4 on Th. II at 1st instar: (0) mic (Fig. 2B); (1) mac (Fig. 3A).
26. Primary chaeta a5 on Th. II at 1st instar: (0) mic (Fig. 2B); (1) mac (Fig. 3A).
27. Primary chaeta a6 on Th. II at 1st instar: (0) mic (Fig. 2B); (1) mac (Fig. 3A).
28. Primary chaeta m1 on Th. II at 1st instar: (0) mic; (Fig. 2A) (1) mac (Fig. 3A); (2) absent (Fig. 13B).
29. Primary chaeta m2 on Th. II at 1st instar: (0) mic (Fig. 3A); (1) mac (Fig. 9A); (2) scale (Fig. 10).
30. Primary chaeta m3 on Th. II at 1st instar: (0) mic (Fig. 2A); (1) absent (Fig. 3A).
31. Primary chaeta m4 on Th. II at 1st instar: (0) mic (Fig. 2A); (1) mac (Fig. 3A); (2) absent (Fig. 13A).
32. Number of antero-lateral sens on Th. II at 1st instar: (0) extra sens, as well as al, present (Fig. 2A); (1) only al present (Fig. 3A).
33. Primary chaeta p1 on Th. II at 1st instar: (0) mic (Fig. 2A); (1) mac (Fig. 3A).
34. Primary chaeta p2 on Th. II at 1st instar: (0) mic (Fig. 3A); (1) mac (Fig. 3B); (2) absent (Fig. 13B).
35. Sens between p2 and p3 on Th. II at 1st instar: (0) absent (Fig. 3A); (1) present (Fig. 2C).
36. Primary chaeta p3 on Th. II at 1st instar: (0) mic (Fig. 2A); (1) mac (Fig. 3A).
37. Primary chaeta p4 on Th. II at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 13).
38. Primary chaeta p5 on Th. II at 1st instar: (0) mic (Fig. 2B); (1) mac (Fig. 3A); (2) duplicated (Fig. 2A).
39. Sens acc.p5 between p5 and p6 on Th. II at 1st instar: (0) absent (Fig. 3A); (1) present (Fig. 2C).
40. Sens around p6 (acc.p6) on Th. II at 1st instar: (0) absent (Fig. 9A); (1) outer to p6 (Fig. 3A); (2) inner to p6 (Fig. 3B).
41. Primary chaeta a1 on Th. III at 1st instar: (0) mic (Fig. 2A); (1) mac (Fig. 3A); (2) scale (Fig. 12B).
42. Primary chaeta a2 on Th. III at 1st instar: (0) mic (Fig. 2A); (1) mac (Fig. 3A); (2) absent (Fig. 13B).
43. Primary chaeta a3 on Th. III at 1st instar: (0) mic (Fig. 2A); (1) mac (Fig. 3A); (2) scale (Fig. 12B); (3) absent (Fig. 2B).
44. Primary chaeta a4 on Th. III at 1st instar: (0) mic (Fig. 2B); (1) mac (Fig. 3A); (2) scale (Fig. 12C); (3) absent (Fig. 13B).
45. Primary chaeta a5 on Th. III at 1st instar: (0) mic (Fig. 2A); (1) mac (Fig. 3A); (2) absent (Fig. 2B).
46. Primary chaeta a6 on Th. III at 1st instar: (0) mic (Fig. 2A); (1) mac (Fig. 3A).
47. Primary chaeta m1 on Th. III at 1st instar: (0) mic (Fig. 3A); (1) scale (Fig. 12B); (2) absent (Fig. 13).
48. Primary chaeta m2 on Th. III at 1st instar: (0) mic (Fig. 2A); (1) absent (Fig. 3A).
49. Primary chaeta m3 on Th. III at 1st instar: (0) mic (Fig. 2A); (1) absent (Fig. 3A).
50. Primary chaeta m5 on Th. III at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 2A).
51. Primary chaeta m6 on Th. III at 1st instar: (0) mic (Fig. 2A); (1) mac (Fig. 3A).
52. Sens al on Th. III at 1st instar: (0) inner to m7 (Fig. 3A); (1) outer to m7 (Fig. 10); (2) absent (Fig. 13A).
53. Primary chaeta p1 on Th. III at 1st instar: (0) mic (Fig. 2B); (1) mac (Fig. 3A).
54. Primary chaeta p2 on Th. III at 1st instar: (0) mic (Fig. 2B); (1) mac (Fig. 3A).
55. Sens acc.p2 between p2 and p3 on Th. III at 1st instar: (0) absent (Fig. 3A); (1) present (Fig. 2B).
56. Primary chaeta p3 on Th. III at 1st instar: (0) mic (Fig. 2C); (1) mac (Fig. 3A).

57. Primary chaeta p4 on Th. III at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 13).
58. Sens acc.p4 between p4 and p5 on Th. III at 1st instar: (0) absent (Fig. 3A); (1) present (Fig. 2C).
59. Sens acc.p5 between p5 and p6 on Th. III at 1st instar: (0) absent (Fig. 3A); (1) present (Fig. 2C).
60. Sens acc.p6 (external to or posterior to p6) on Th. III at 1st instar: (0) absent (Fig. 9A); (1) present (Fig. 3A).
61. Primary chaeta a1 on Abd. I at 1st instar: (0) mic (Fig. 3A); (1) scale (Fig. 12B).
62. Primary chaeta a2 on Abd. I at 1st instar: (0) mic (Fig. 2A); (1) mac (Fig. 3A); (2) scale (Fig. 12C); (3) absent (Fig. 13B).
63. Primary chaeta a3 on Abd. I at 1st instar: (0) mic (Fig. 3A); (1) mac (Fig. 3B); (2) scale (Fig. 12C); (3) absent (Fig. 12A).
64. Primary chaeta a5 on Abd. I at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 12A).
65. Primary chaeta a6 on Abd. I at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 12A).
66. Primary chaeta m2 on Abd. I at 1st instar: (0) mic (Fig. 2C); (1) mac (Fig. 3A).
67. Primary chaeta m3 on Abd. I at 1st instar: (0) mic (Fig. 2C); (1) mac (Fig. 3A).
68. Primary chaeta m4 on Abd. I at 1st instar: (0) mic (Fig. 2C); (1) mac (Fig. 3A).
69. Primary chaeta m5 on Abd. I at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 2A).
70. Primary chaeta p1 on Abd. I at 1st instar: (0) mic (Fig. 2A); (1) absent (Fig. 3A).
71. Primary chaeta p2 on Abd. I at 1st instar: (0) mic (Fig. 2A); (1) absent (Fig. 3A).
72. Sens associated to p2 on Abd. I at 1st instar: (0) present (Fig. 2A); (1) absent (Fig. 3A).
73. Sens associated to p4 on Abd. I at 1st instar: (0) present (Fig. 2A); (1) absent (Fig. 3A).
74. Primary chaeta p4 on Abd. I at 1st instar: (0) mic (Fig. 2A); (1) absent (Fig. 3A).
75. Number of sens between p4 and p5 on Abd. I at 1st instar: (0) 1 (Fig. 2B); (1) 2 (Fig. 2A); (2) 0 (Fig. 3A).
76. Primary chaeta p5 on Abd. I at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 4A).
77. Sens acc.p6 between p5 and p6 on Abd. I at 1st instar: (0) present (Fig. 3A); (1) absent (Fig. 9A).
78. Primary chaeta p6 on Abd. I at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 13).
79. Primary chaeta a1 on Abd. II at 1st instar: (0) mic (Fig. 3A); (1) scale (Fig. 12B).
80. Primary chaeta a2 on Abd. II at 1st instar: (0) mic (Fig. 4A); (1) mac (Fig. 3A).
81. Sens as between a2 and a3 on Abd. II at 1st instar: (0) absent (Fig. 13); (1) present (Fig. 3A).
82. Primary chaeta a4 on Abd. II at 1st instar: (0) mic (Fig. 2B); (1) absent (Fig. 3A).
83. Primary chaeta a5 on Abd. II at 1st instar: (0) mic (Fig. 2); (1) bothriotrichum (Fig. 3A).
84. Primary chaeta a7 on Abd. II at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 7).
85. Primary chaeta m2 on Abd. II at 1st instar: (0) mic (Fig. 2C); (1) bothriotrichum (Fig. 3A); (2) mac (Fig. 2A).
86. Sens associated (antero-internal) to m4 on Abd. II at 1st instar: (0) absent (Fig. 5); (1) present (Fig. 3A).
87. Primary chaeta m4 on Abd. II at 1st instar: (0) mic (Fig. 3A); (1) mac (Fig. 2B); (2) absent (Fig. 4A).
88. Primary chaeta m5 on Abd. II at 1st instar: (0) mic (Fig. 2A); (1) mac (Fig. 3A); (2) absent (Fig. 2B).
89. S-microchaeta (ms) on Abd. II at 1st instar: (0) present (Fig. 2B); (1) absent (Fig. 3A).
90. Primary chaeta m7 on Abd. II at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 2).
91. Primary chaeta p1 on Abd. II at 1st instar: (0) mic (Fig. 2A); (1) absent (Fig. 3A).
92. Primary chaeta p2 on Abd. II at 1st instar: (0) mic (Fig. 2A); (1) absent (Fig. 3A).
93. Sens acc.p2 between p2 and p3 on Abd. II at 1st instar: (0) absent (Fig. 5A); (1) present (Fig. 2B).
94. Sens acc.p3 between p3 and p4 on Abd. II at 1st instar: (0) absent (Fig. 5A); (1) present (Fig. 2B).
95. Number of sens between p4 and p5 on Abd. II at 1st instar: (0) 1 (Fig. 2B); (1) 2 (Fig. 3A); (2) 0 (Fig. 5A).
96. Primary chaeta p5 on Abd. II at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 12B).
97. Sens acc.p6 between p5 and p6 on Abd. II at 1st instar: (0) absent (Fig. 10); (1) present (Fig. 3A).
98. Primary chaeta p7 on Abd. II at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 12A).
99. Primary chaeta a1 on Abd. III at 1st instar: (0) mic (Fig. 3A); (1) mac (Fig. 12B); (2) scale.
100. Primary chaeta a2 on Abd. III at 1st instar: (0) mic (Fig. 2B); (1) mac (Fig. 3A); (2) absent (Fig. 2A).
101. Sens as between a2 and a3 on Abd. III at 1st instar: (0) absent (Fig. 13A); (1) present (Fig. 3A).
102. Primary chaeta a5 on Abd. III at 1st instar: (0) mic (Fig. 2B); (1) bothriotrichum (Fig. 3A).
103. Primary chaeta m3 on Abd. III at 1st instar: (0) mic (Fig. 2C); (1) mac (Fig. 3A).
104. Sens internal to m4 on Abd. III at 1st instar: (0) absent (Fig. 4A); (1) present (Fig. 3A).
105. Primary chaeta m5 on Abd. III at 1st instar: (0) mic (Fig. 2); (1) bothriotrichum (Fig. 3A).
106. Primary chaeta am6 on Abd. III at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 2B).
107. Primary chaeta pm6/m6 on Abd. III at 1st instar: (0) mic (Fig. 2); (1) mac (Fig. 3A).
108. Primary chaeta p1 on Abd. III at 1st instar: (0) mic (Fig. 2C); (1) absent (Fig. 3A).
109. Sens acc.p1 between p1 and p2 on Abd. III at 1st instar: (0) absent (Fig. 3A); (1) present.
110. Primary chaeta p2 on Abd. III at 1st instar: (0) mic (Fig. 2); (1) absent (Fig. 3A).
111. Sens acc.p2 between p2 and p3 on Abd. III at 1st instar: (0) absent (Fig. 5); (1) present (Fig. 3A).
112. Primary chaeta p4 on Abd. III at 1st instar: (0) mic (Fig. 2A); (1) absent (Fig. 3A).
113. S-microchaeta (ms) between p4 and p5 on Abd. III at 1st instar: (0) absent (Fig. 3A); (1) present (Fig. 2C).
114. Sens between p4 and p5 on Abd. III at 1st instar: (0) present (Fig. 3A); (1) absent (Fig. 4A).

115. Primary chaeta p5 on Abd. III at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 12B).  
 116. S-microchaeta (ms) between p5 and p6 on Abd. III at 1st instar: (0) present (Fig. 3A); (1) absent (Fig. 2).  
 117. Sens between p5 and p6 on Abd. III at 1st instar: (0) absent (Fig. 2A); (1) present (Fig. 3A).  
 118. Primary chaeta p6 on Abd. III at 1st instar: (0) mic (Fig. 3A); (1) mac (Fig. 3B).  
 119. Primary chaeta S1 on Abd. IV at 1st instar: (0) absent (Fig. 3A); (1) present (Fig. 13B).  
 120. Primary chaeta A1 on Abd. IV at 1st instar: (0) mic (Fig. 5); (1) absent (Fig. 3A).  
 121. Primary chaeta A2/a1 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 13B); (2) scale (Fig. 3E).  
 122. Primary chaeta A3/m1 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) mac (Fig. 3E); (2) absent (Fig. 13B).  
 123. Primary chaeta A4 on Abd. IV at 1st instar: (0) mic (Fig. 3D); (1) absent (Fig. 3A).  
 124. Primary chaeta A5 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 4A); (2) mac.  
 125. Primary chaeta B1 on Abd. IV at 1st instar: (0) mic (Fig. 4C); (1) absent (Fig. 3A).  
 126. Primary chaeta B2/a2 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) bothriotrichum (Fig. 2A); (2) absent (Fig. 12D); (3) scale (Fig. 3E).  
 127. Primary chaeta B3 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 4A).  
 128. Primary chaeta B4/m3 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) mac (Fig. 6A); (2) absent (Fig. 4A).  
 129. Primary chaeta B5 on Abd. IV at 1st instar: (0) mic (Fig. 4A); (1) mac (Fig. 3A).  
 130. Primary chaetae between row B and C at 1st instar: (0) present (Fig. 3A); (1) absent (Fig. 5).  
 131. Primary chaeta C1/a3 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 3E).  
 132. Primary chaeta C2/m4 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 4A).  
 133. Primary chaeta C3 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 4A).  
 134. Primary chaeta C4/p3 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 4A).  
 135. Primary chaeta T3 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 2).  
 136. Primary chaeta T4/m5 on Abd. IV at 1st instar: (0) mic (Fig. 2); (1) bothriotrichum (Fig. 3A).  
 137. Primary chaeta T5 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 2).  
 138. Primary chaeta D1 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 2).  
 139. Primary chaeta E2 on Abd. IV at 1st instar: (0) mic (Fig. 10); (1) absent (Fig. 3A).  
 140. Primary chaeta E3/m6 on Abd. IV at 1st instar: (0) mic (Fig. 9D); (1) mac (Fig. 3A).  
 141. Primary chaeta F2 on Abd. IV at 1st instar: (0) mic (Fig. 3A); (1) absent (Fig. 2B).  
 142. Primary chaeta a1 on Abd. V at 1st instar: (0) mic (Fig. 3A); (1) absent.  
 143. Sens antero-lateral to a3 on Abd. V at 1st instar: (0) absent (Fig. 2); (1) present (Fig. 3A).  
 144. Primary chaeta m2 on Abd. V at 1st instar: (0) mic (Fig. 13A); (1) mac (Fig. 3A).  
 145. Primary chaeta m3 on Abd. V at 1st instar: (0) mic (Fig. 7B); (1) mac (Fig. 3A).  
 146. Sens as on Abd. V at 1st instar: (0) absent (Fig. 3B); (1) present (Fig. 3A).  
 147. Sens between p1 and p3 on Abd. V at 1st instar: (0) absent (Fig. 4A); (1) present (Fig. 3A).  
 148. Primary chaeta m5 on Abd. V at 1st instar: (0) mic (Fig. 5B); (1) mac (Fig. 3A).  
 149. Sens between p3 and p4 on Abd. V at 1st instar: (0) absent (Fig. 4A); (1) present (Fig. 3A).  
 150. Sens between p4 and p5 on Abd. V at 1st instar: (0) absent (Fig. 3A); (1) present (Fig. 2B).  
 151. Sens between p5 and p6 on Abd. V at 1st instar: (0) absent (Fig. 5); (1) present (Fig. 3A).  
 152. Additional sens on Abd. V at 1st instar: (0) absent (Fig. 5); (1) present (Fig. 3A).  
 153. Primary chaeta ap6/m6 on Abd. V at 1st instar: (0) mic (Fig. 3B); (1) mac (Fig. 2A).

**Character matrix in 'nex' format.**

#NEXUS

BEGIN TAXA;

TITLE Taxa;

DIMENSIONS NTAX=38;

TAXLABELS

Tomocerus\_minor Isotoma\_anglicana Isotomurus\_palustris Orchesella\_flavescens Orchesella\_sp Orchesellides\_sinensis  
 Heteromurus\_nitidus Dicranocentrus\_wangi Entomobrya\_nivalis Entomobrya\_proxima Entomobrya\_sp Entomobryoides\_myrmecophila  
 Sinella\_curviseta Sinella\_umesaoi Coecobrya\_tenebricosa Coecobrya\_aokii Homidia\_jordanai Homidia\_cingula Homidia\_sp  
 Willowsia\_buskii Willowsia\_japonica Seira\_dowlingi Seira\_barnardi Lepidocyrtus\_cyaneus Lepidocyrtus\_sp Pseudosinella\_alba  
 Pseudosinella\_decipiens Pseudosinella\_impediens Pseudosinella\_spA Pseudosinella\_spB Cyphoderus\_albinus Trogolaphysa\_jataca  
 Trogolaphysa\_paracarpenteri Campylothorax\_sabanus Microfalcula\_sp Salina\_celebensis Salina\_tristani Callyntrura\_guangdongensis ;  
 END;

BEGIN CHARACTERS;

TITLE Character\_Matrix;

DIMENSIONS NCHAR=153;

FORMAT DATATYPE = STANDARD GAP = - MISSING = ? SYMBOLS = " 0 1 2 3";

MATRIX

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110001000100111010110011101110100110111011

*Isotomurus\_palustris*

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*Orchesella\_flavescens*

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*Orchesella\_sp*

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0110001001001010001000000100110011111110111

*Orchesellides\_sinensis*

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*Heteromurus\_nitidus*

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0111001001001112120101110100110011110100100

*Dicranocentrus\_wangi*

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0111001001001010120101110100110011101110100

*Entomobrya\_nivalis*

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0111001000001000001100000100110001110111000

*Entomobrya\_proxima*

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*Entomobrya\_sp*

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0111001000001000011100000100110001110111000

*Entomobryoides\_myrmecophila*

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*Sinella\_curviseta*

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*Sinella\_umesaoi*

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0111001000001000011100000100110001010011000

*Coecobrya\_tenebricosa*

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*Coecobrya\_aokii*

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0111011000001000001100000100110001110011000

*Homidia\_jordanai*

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*Homidia\_cingula*

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*Homidia\_sp*

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*Willowsia\_buskii*

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*Willowsia japonica*

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*Seira dowlingi*

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*Seira barnardi*

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*Lepidocyrtus cyaneus*

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*Lepidocyrtus sp*

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*Pseudosinella alba*

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*Pseudosinella decipiens*

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0111000000011010001100000100010001110110100

*Pseudosinella impediens*

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0111000000010000001100000100010001110110100

*Pseudosinella spA*

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*Pseudosinella spB*

0001011010000101101011111112111110101000101200110011101000000311110011111211101111110011111002001001110101101  
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*Cyphoderus albinus*

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0111000001000012000100000100000100010010100

*Trogolaphysa jataca*

000110101000011002101111111111111010100110121111010110100001000001011111211010111110201011002100101110101101  
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*Trogolaphysa paracarpenteri*

000110101000011002101111111111111010100110121111010110110001000001011111201010111110201011002100101110101101  
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*Campylothorax sabanus*

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*Microfalcula sp*

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01111000000000000000000000000000100110000100100000

*Salina celebensis*

00100011000001100210121111020101020111000203202111100101100003011011011111211100011110211111002100001110101101  
0111100011121112101111100100110101110110000

*Salina tristani*

00100011000001100210121110020101020111000203202111100101100003011011011111211100011110211111002100001110101101  
0111100011121112101111100100110????????????

*Callyntrura guangdongensis*

00000010000001100210111111101111101000001110011010110100000000011101111201001111110011111002010001110101101  
011100111000000000100000100100001010110000;

END;

**Table S1. Species, reference, and their numbers examined in this study.**

Species	Reference	Juveniles	Adults
<i>Tomocerus minor</i> (Lubbock, 1862)*	This study	1	0
<i>Isotoma anglicana</i> Lubbock, 1862*	Fjellberg, 2003	-	-
<i>Isotomurus palustris</i> (Müller, 1776)*	Deharveng, 1979	-	-
<i>Orchesella flavescens</i> (Bourlet, 1939)*	Szeptycki, 1979	-	-
<i>Orchesella cincta</i> (Linnaeus, 1758)	This study	1	4
<i>Orchesella</i> sp.*	This study	3	0
<i>Orchesellides sinensis</i> (Denis, 1929)*	This study	2	0
<i>Orchesellides boraai</i> Bonet, 1930	This study	0	2
<i>Heteromurus nitidus</i> (Templeton, 1839)*	This study	2	1
<i>Dicranocentrus wangi</i> Ma & Chen, 2007*	This study	2	5
<i>Entomobrya nivalis</i> (Linnaeus, 1758)*	This study	4	5
<i>Entomobrya proxima</i> Folsom, 1924*	This study	5	4
<i>Entomobrya huangi</i> Chen & Ma, 1998	This study	2	1
<i>Entomobrya koreana</i> Yosii, 1965	This study	0	2
<i>Entomobrya</i> sp.*	This study	4	2
<i>Entomobryoides myrmecophila</i> (Reuter, 1886)*	Szeptycki, 1979	-	-
<i>Sinella curviseta</i> Brook, 1882*	Zhang <i>et al.</i> , 2011	-	-
<i>Sinella umesaoi</i> Yosii, 1940*	Zhang & Deharveng, 2015	-	-
<i>Coecobrya tenebricosa</i> (Folsom, 1902)*	Zhang <i>et al.</i> , 2011	-	-
<i>Coecobrya aokii</i> (Yoshii, 1995)*	Zhang <i>et al.</i> , 2011	-	-
<i>Homidia jordanai</i> Pan, Shi & Zhang, 2011*	Pan <i>et al.</i> , 2011	-	-
<i>Homidia cingula</i> Börner, 1906*	This study	1	0
<i>Homidia</i> sp.	This study	3	1
<i>Willowsia buskii</i> (Lubbock, 1869)*	Szeptycki, 1979	-	-
<i>Willowsia japonica</i> (Folsom, 1897)*	This study	2	3
<i>Willowsia cassagnai</i> Zhang, 2015	This study	3	1
<i>Americabrya arida</i> (Christiansen & Bellinger, 1980)	This study	0	5
<i>Janetschekbrya himalica</i> Yosii, 1971	This study	2	2
<i>Seira dowlingi</i> Wray, 1953*	Soto-Adames, 2008	-	-
<i>Seira barnardi</i> (Womersley, 1934)*	Zhang and Deharveng, 2015	-	-
<i>Lepidocyrtus cyaneus</i> Tullberg, 1871*	This study	3	1
<i>Lepidocyrtus curvicollis</i> (Bourlet, 1839)	Szeptycki, 1979	-	-
<i>Lepidocyrtus</i> sp.*	This study	1	0
<i>Pseudosinella alba</i> (Packard, 1873)*	This study	3	1
<i>Pseudosinella decipiens</i> Denis, 1924*	Barra, 1975	-	-
<i>Pseudosinella impediens</i> Gisin & da Gama, 1969*	Barra, 1975	-	-
<i>Pseudosinella</i> sp.A*	This study	1	0
<i>Pseudosinella</i> sp.B*	This study	1	0
<i>Cyphoderus albinus</i> Nicolet, 1842*	Szeptycki, 1979	-	-
<i>Trogolaphysa jataca</i> (Wray, 1953)*	Soto-Adames, 2015	-	-
<i>Trogolaphysa paracarpenteri</i> Soto-adames, 2015*	Soto-Adames, 2015	-	-
<i>Campylothorax sabanus</i> (Wray, 1953)*	Soto-Adames, 2016	-	-
<i>Salina celebensis</i> (Schäffer, 1898)*	This study	1	2
<i>Salina tristani</i> Denis, 1931*	This study	1	0
<i>Callyntrura guangdongensis</i> Ma, 2012*	This study	1	1
<i>Microfalcula</i> sp.*	This study	3	0

\*First instar larvae of the species examined.

**Table S2. Assessments of unstable taxa on the dataset with the outgroups included using leaf stability index, taxonomic instability index, RogueNaRok-algorithm and TNT. Unstable taxa are marked with reddish or label U (TNT).**

Species	Leaf stability index	Taxonomic instability index	RogueNaRok	TNT
<i>Isotomurus palustris</i>	0.582421	118510.3		
<i>Isotoma anglicana</i>	0.582421	118441.2		
<i>Heteromurus nitidus</i>	0.639887	155041.9		
<i>Dicranocentrus wangi</i>	0.639708	155023.9		
<i>Orchesella flavescens</i>	0.66028	133974.3		
<i>Orchesellides sinensis</i>	0.661359	130505.9		
<i>Orchesella</i> sp	0.661727	123209.2		
<i>Entomobrya nivalis</i>	0.606165	135923.4	0.037	
<i>Entomobrya proxima</i>	0.611813	146815.8	0.624	
<i>Willowsia japonica</i>	0.622492	133367.7		
<i>Willowsia buskii</i>	0.619068	141482.9		
<i>Entomobrya</i> sp	0.572817	150376.3	0.52	
<i>Homidia jordanai</i>	0.657217	118361.4		
<i>Sinella curviseta</i>	0.67923	117540.4		
<i>Sinella umesaoi</i>	0.678123	110759.5		
<i>Coecobrya aokii</i>	0.680591	96602.59		
<i>Coecobrya tenebricosa</i>	0.681558	91584.52		
<i>Entomobryoides myrmecophila</i>	0.590708	163163.4	0.038	
<i>Homidia</i> sp	0.632854	139320	0.24	
<i>Homidia cingula</i>	0.657874	120776.7		
<i>Pseudosinella impediens</i>	0.717381	123363.3		
<i>Pseudosinella decipiens</i>	0.71736	122452.2		
<i>Pseudosinella</i> spB	0.710191	136483.7		
<i>Pseudosinella</i> spA	0.715298	128564.6		
<i>Pseudosinella alba</i>	0.711337	120356.2		
<i>Lepidocyrtus cyaneus</i>	0.696616	149626.2	0.081	
<i>Lepidocyrtus</i> sp	0.70217	140751	0.591	
<i>Microfalcula</i> sp	0.470537	178274.4		U
<i>Salina celebensis</i>	0.493284	144843.7		U
<i>Salina tristani</i>	0.493284	144892.1		U
<i>Campylothorax sabanus</i>	0.725625	133604.7		U
<i>Trogolaphysa jataca</i>	0.728688	107501.4		U
<i>Trogolaphysa paracarpenteri</i>	0.728657	107457.1		U
<i>Cyphoderus albinus</i>	0.642245	170479.5	1.556	U
<i>Seira dowlingi</i>	0.67945	142570.4		
<i>Callyntrura guangdongensis</i>	0.621612	182398.1	1.076	
<i>Seira barnardi</i>	0.678739	142635.3		
<i>Tomocerus minor</i>	0.582421	146062.3		

**Table S3. Assessments of unstable taxa on the dataset with the outgroups excluded using leaf stability index, taxonomic instability index, RogueNaRok-algorithm and TNT. Unstable taxa are marked with reddish or label U (TNT).**

Species	Leaf stability index	Taxonomic instability index	RogueNaRok	TNT
<i>Heteromurus nitidus</i>	0.697353	122276.2		
<i>Dicranocentrus wangi</i>	0.697353	122207.3		
<i>Callyntrura guangdongensis</i>	0.651095	173567.2	1.059	
<i>Entomobrya</i> sp	0.625517	145090.2	0.066	
<i>Homidia jordanai</i>	0.724774	109385		
<i>Homidia cingula</i>	0.724049	112932.8		
<i>Homidia</i> sp	0.694788	132752.8	0.777	
<i>Sinella umesaoi</i>	0.7511	98991.7		
<i>Coecobrya tenebricosa</i>	0.756591	73311.01		
<i>Coecobrya aokii</i>	0.756575	73331.2		
<i>Sinella curviseta</i>	0.753381	103496.3		
<i>Entomobrya proxima</i>	0.679403	130007.4	0.629	
<i>Willowsia japonica</i>	0.688096	124616.9		
<i>Microfalcula</i> sp	0.484167	174147.1		U
<i>Salina tristani</i>	0.53494	139420.7		U
<i>Salina celebensis</i>	0.53494	139416.6		U
<i>Willowsia buskii</i>	0.68548	129478		
<i>Entomobryoides myrmecophila</i>	0.657191	155110.6	0.08	
<i>Entomobrya nivalis</i>	0.673939	127616	0.062	
<i>Seira barnardi</i>	0.698464	135595.4		
<i>Seira dowlingi</i>	0.701314	133941	0.008	
<i>Pseudosinella decipiens</i>	0.7411	114443		
<i>Pseudosinella impediens</i>	0.74124	115460.1		
<i>Cyphoderus albinus</i>	0.66751	161945.9	1.606	U
<i>Lepidocyrtus cyaneus</i>	0.714157	143312.8	0.084	
<i>Lepidocyrtus</i> sp	0.721291	132445.6	0.606	
<i>Pseudosinella</i> spB	0.733279	128574.3		
<i>Pseudosinella</i> spA	0.740553	120871.3		
<i>Pseudosinella alba</i>	0.734384	113674.1		
<i>Campylothorax sabanus</i>	0.749782	127887.8		U
<i>Trogolaphysa jataca</i>	0.753335	103716.1		U
<i>Trogolaphysa paracarpenteri</i>	0.753303	104130.2		U
<i>Orchesellides sinensis</i>	0.746631	114099		
<i>Orchesella</i> sp	0.746726	106100.3		
<i>Orchesella flavescens</i>	0.746024	116111		

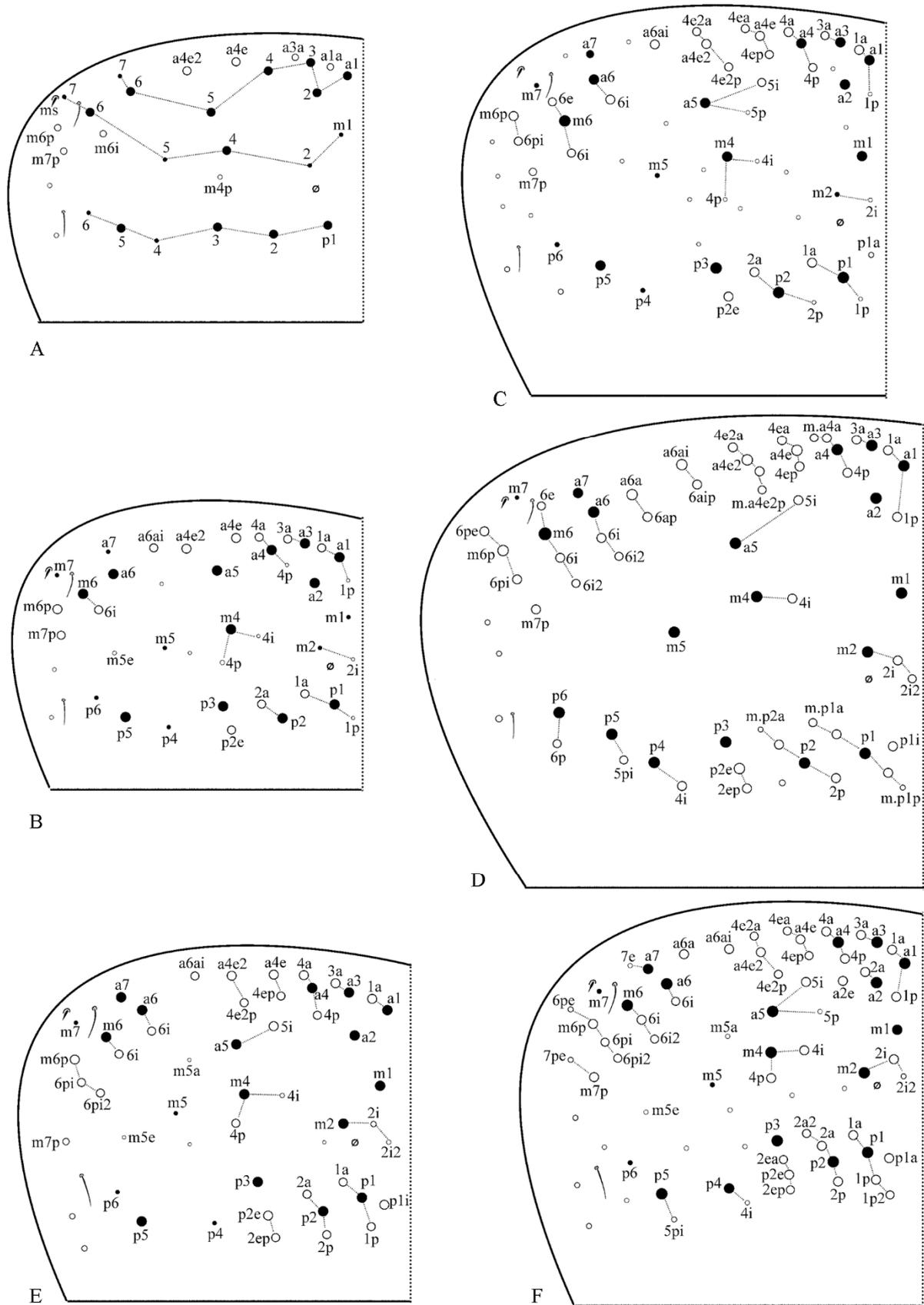


Figure S1. Development of dorsal chaetotaxy of Th. II in Entomobryinae. A–D. *Entomobrya nivalis*. A. 2nd instar. B. 3rd instar. C. 4th instar. D. Adult. E–F. *Entomobrya* sp. E. 3rd instar. F. 4th instar.

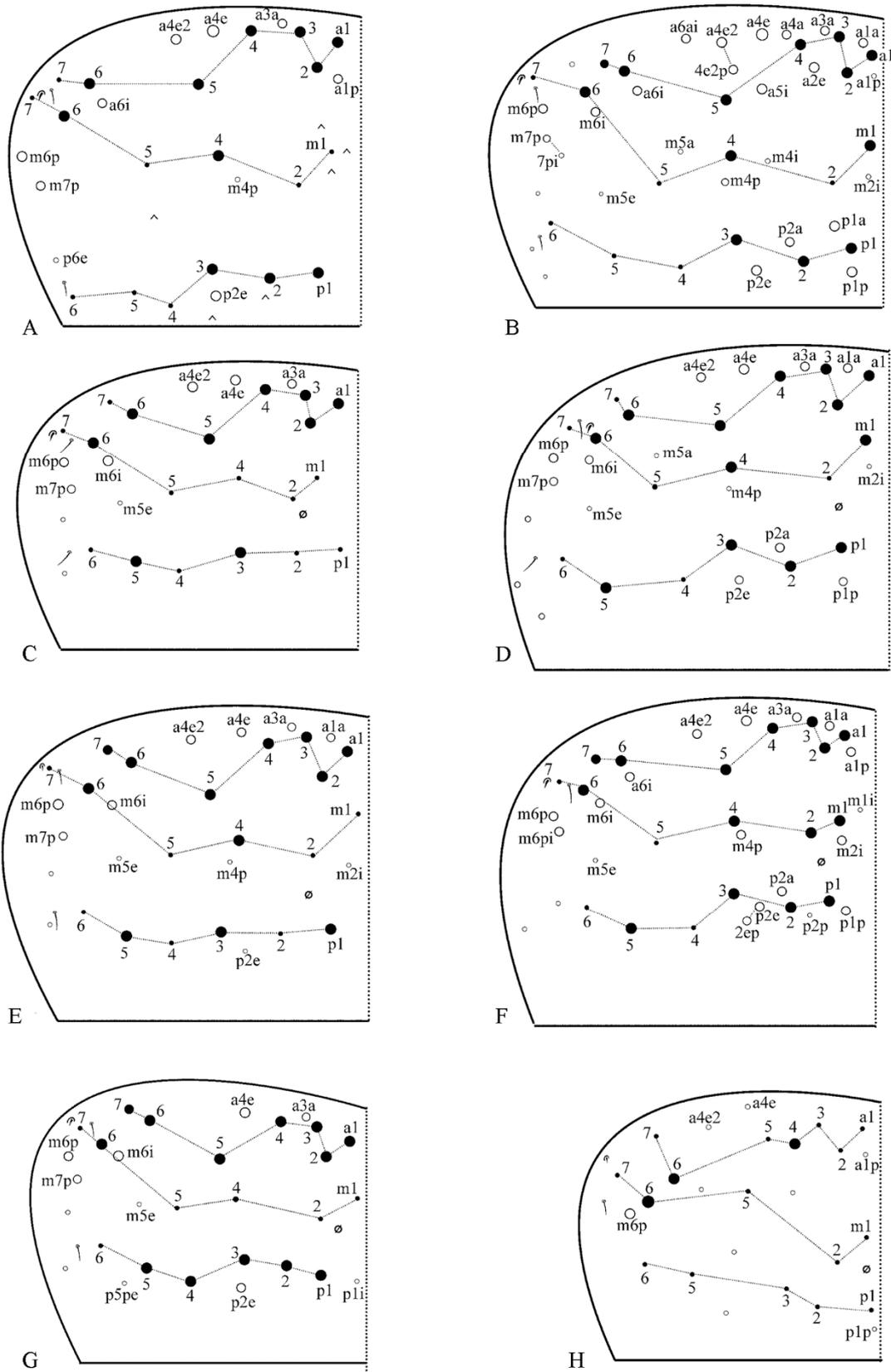


Figure S2. Development of dorsal chaetotaxy of Th. II (2nd instar). A. *Heteromurus nitidus* (Orchesellinae). B. *Entomobryoides myrmecophila* (Entomobryinae). C. *Entomobrya huangi* (Entomobryinae). D. *Homidia* sp. (Entomobryinae). E. *Willowsia japonica* (Entomobryinae). F. *Seira dowlingi* (Seirinae). G. *Janetschekbrya himalica* (Entomobryinae). H. *Microfalcula* sp. (Salininae).

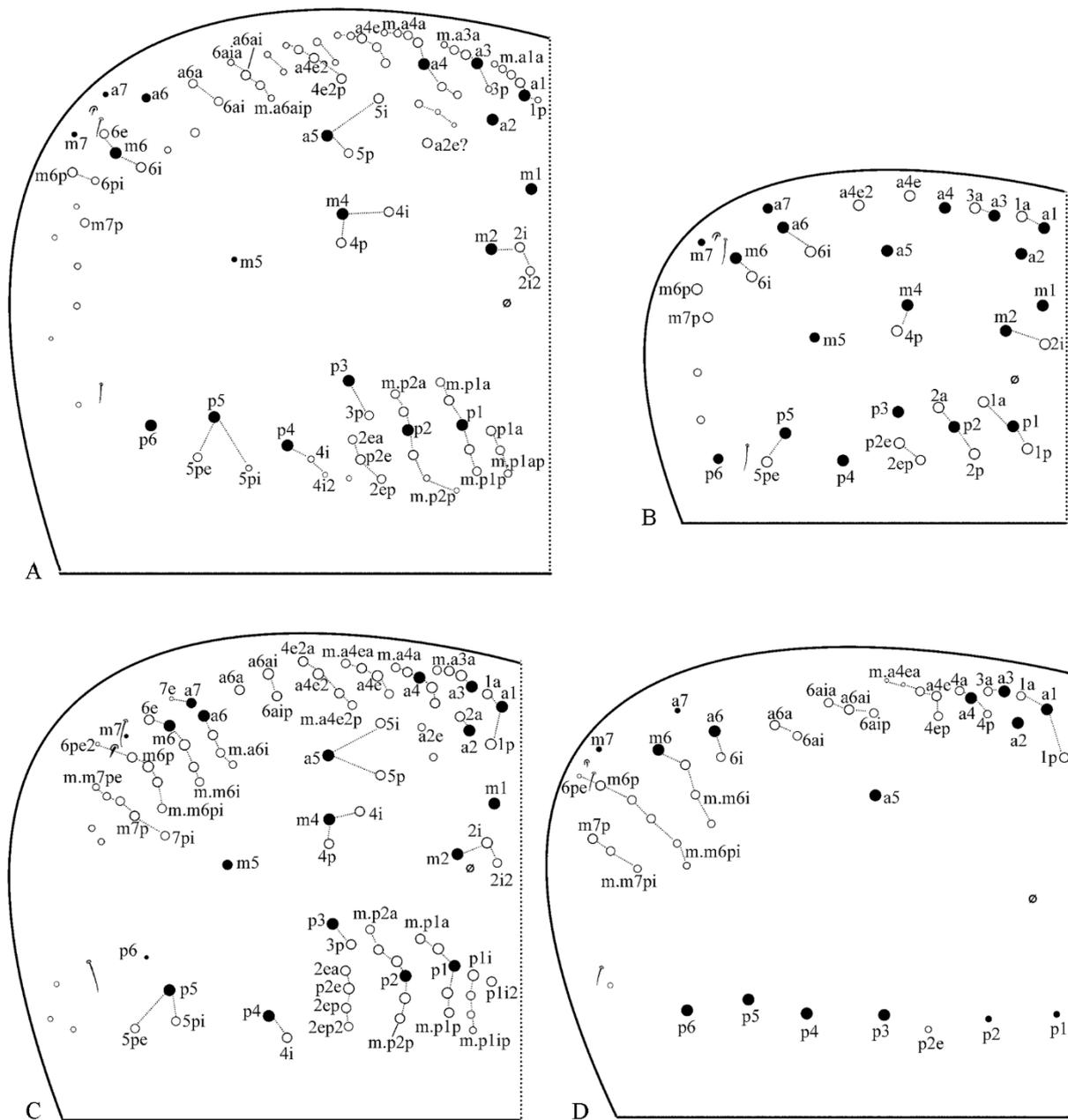


Figure S3. Development of dorsal chaetotaxy of Th. II. A. *Orchesella cincta* (subadult, Orchesellinae). B. *Orchesellides boraai* (juvenile, Orchesellinae). C. *Entomobrya* sp. (adult, Entomobryinae). D. *Americabrya arida* (adult, Entomobryinae).



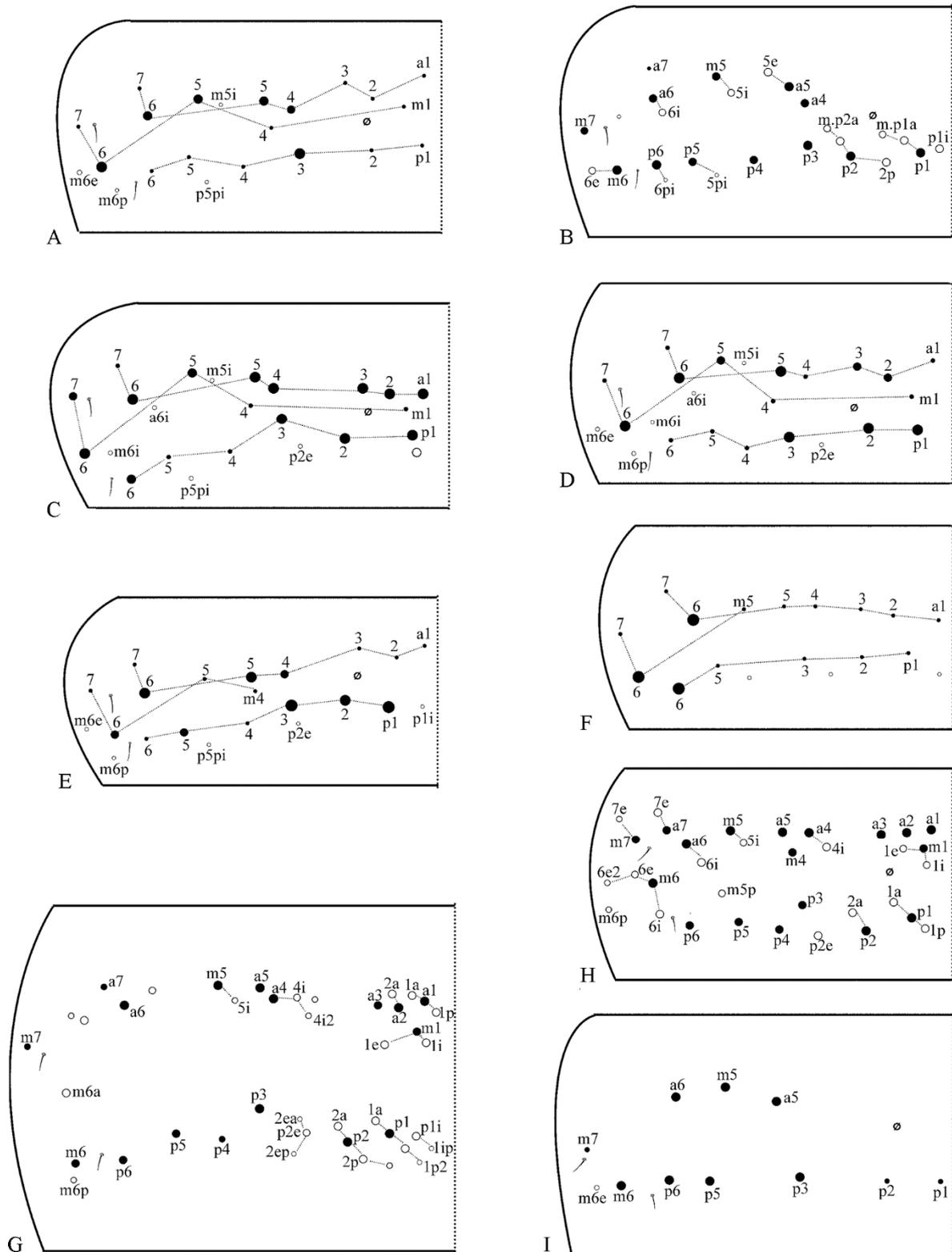


Figure S5. Development of dorsal chaetotaxy of Th. III. A–B, *Entomobrya huangi* (Entomobryinae). A. 2nd instar. B. Adult. C. *Homidia* sp. (2nd instar, Entomobryinae). D. *Willowsia japonica* (2nd instar, Entomobryinae). E. *Janetschekbrya himalica* (2nd instar, Entomobryinae). F. *Microfalcula* sp. (2nd instar, Saliniinae). G. *Orchesella cincta* (subadult, Orchesellinae). H. *Orchesellides boraai* (juvenile, Orchesellinae). I. *Americabrya arida* (adult, Entomobryinae).

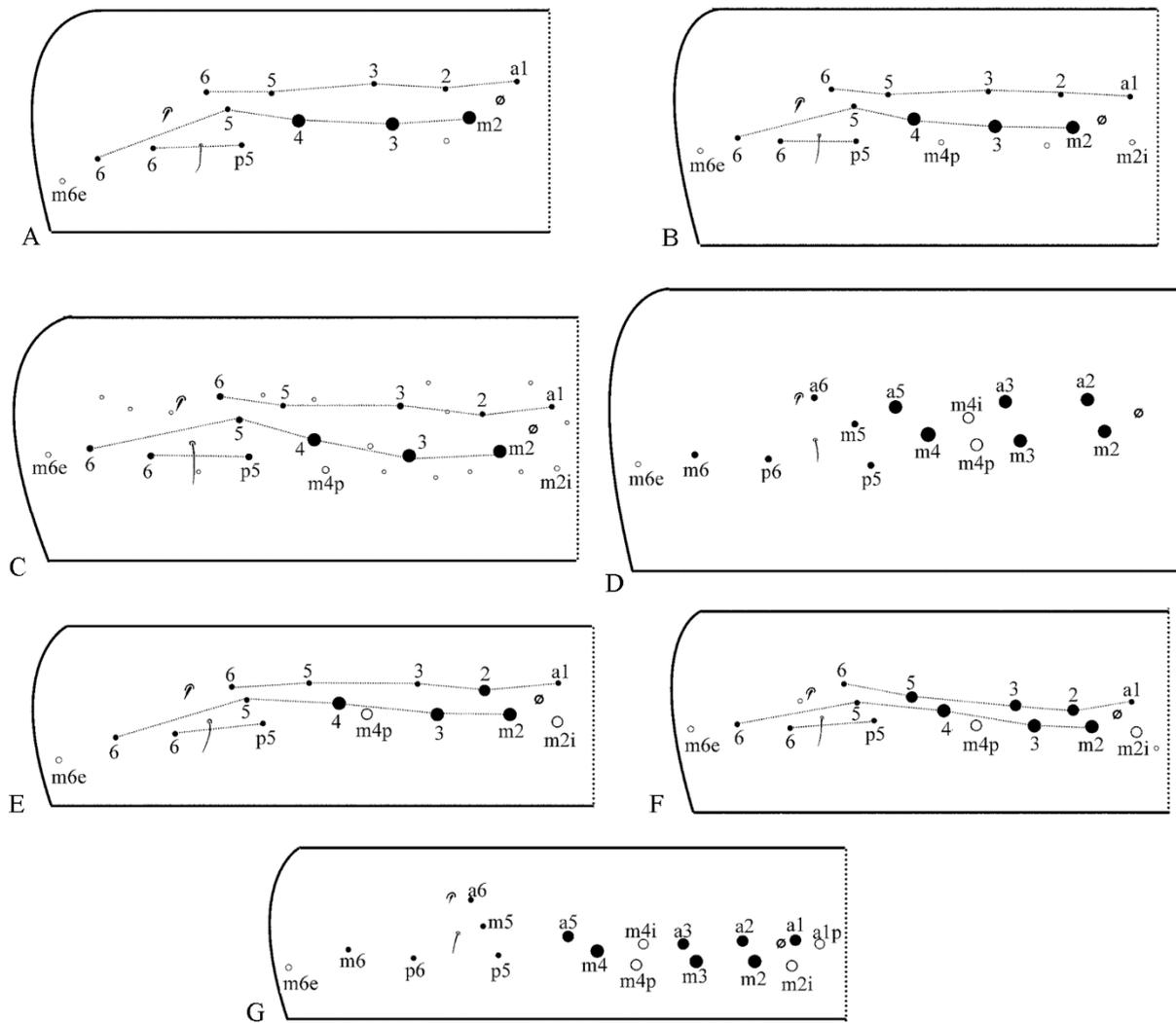


Figure S6. Development of dorsal chaetotaxy of Abd. I in Entomobryinae. A–D. *Entomobrya nivalis*. A. 2nd instar. B. 3rd instar. C. 4th instar. D. Adult. E–G. *Entomobrya* sp. E. 3rd instar. F. 4th instar. G. Adult.

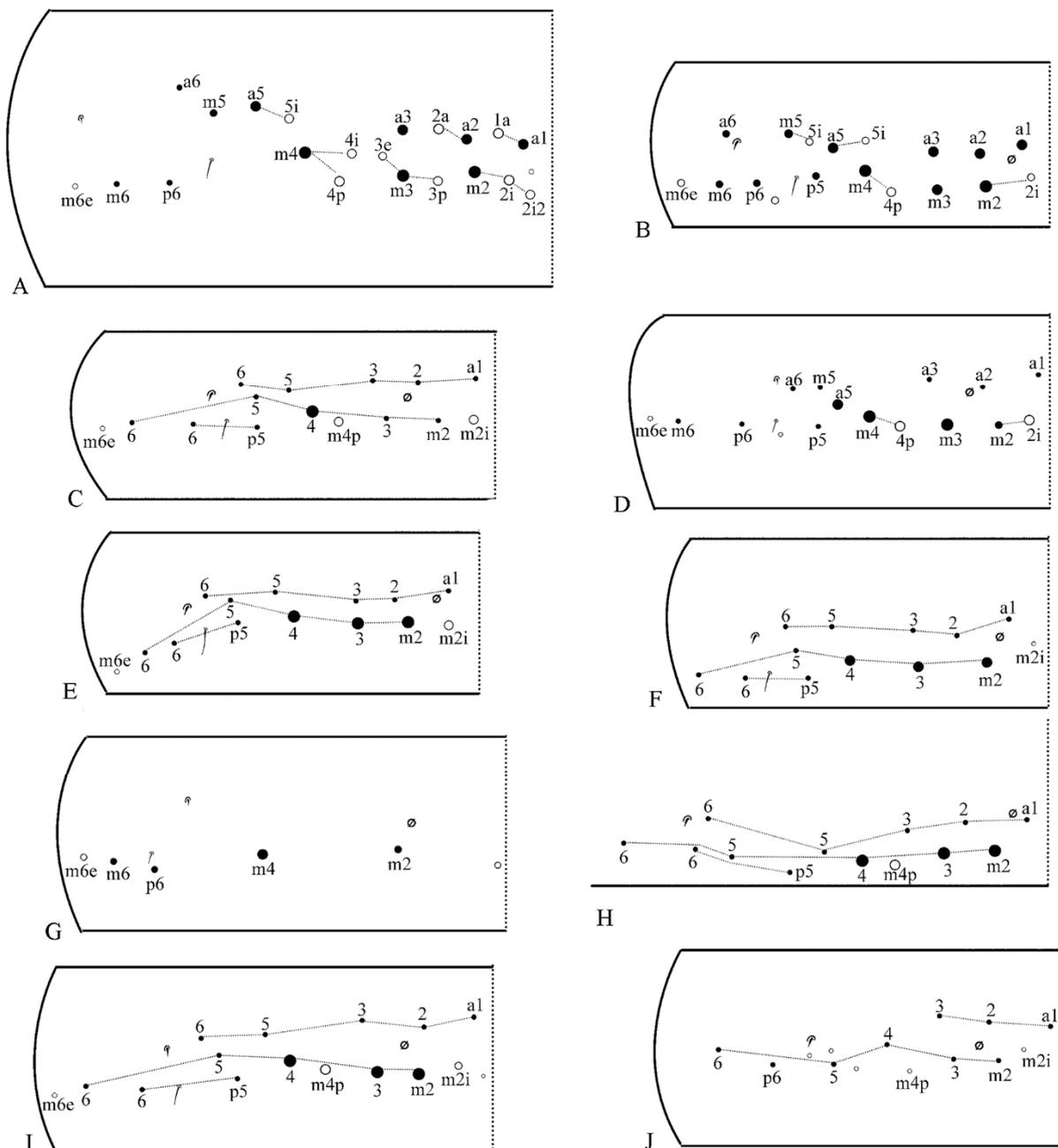


Figure S7. Development of dorsal chaetotaxy of Abd. I. A. *Orchesella cincta* (subadult, Orchesellinae). B. *Orchesellides boraoui* (juvenile, Orchesellinae). C–D. *Entomobrya huangi* (Entomobryinae). C. 2nd instar. D. Adult. E. *Homidia* sp. (2nd instar, Entomobryinae). F. *Willowsia japonica* (2nd instar, Entomobryinae). G. *Americabrya arida* (adult, Entomobryinae). H. *Seira dowlingi* (2nd instar, Seirinae). I. *Janetschekbrya himalica* (2nd instar, Entomobryinae). J. *Microfalcula* sp. (2nd instar, Salininae).

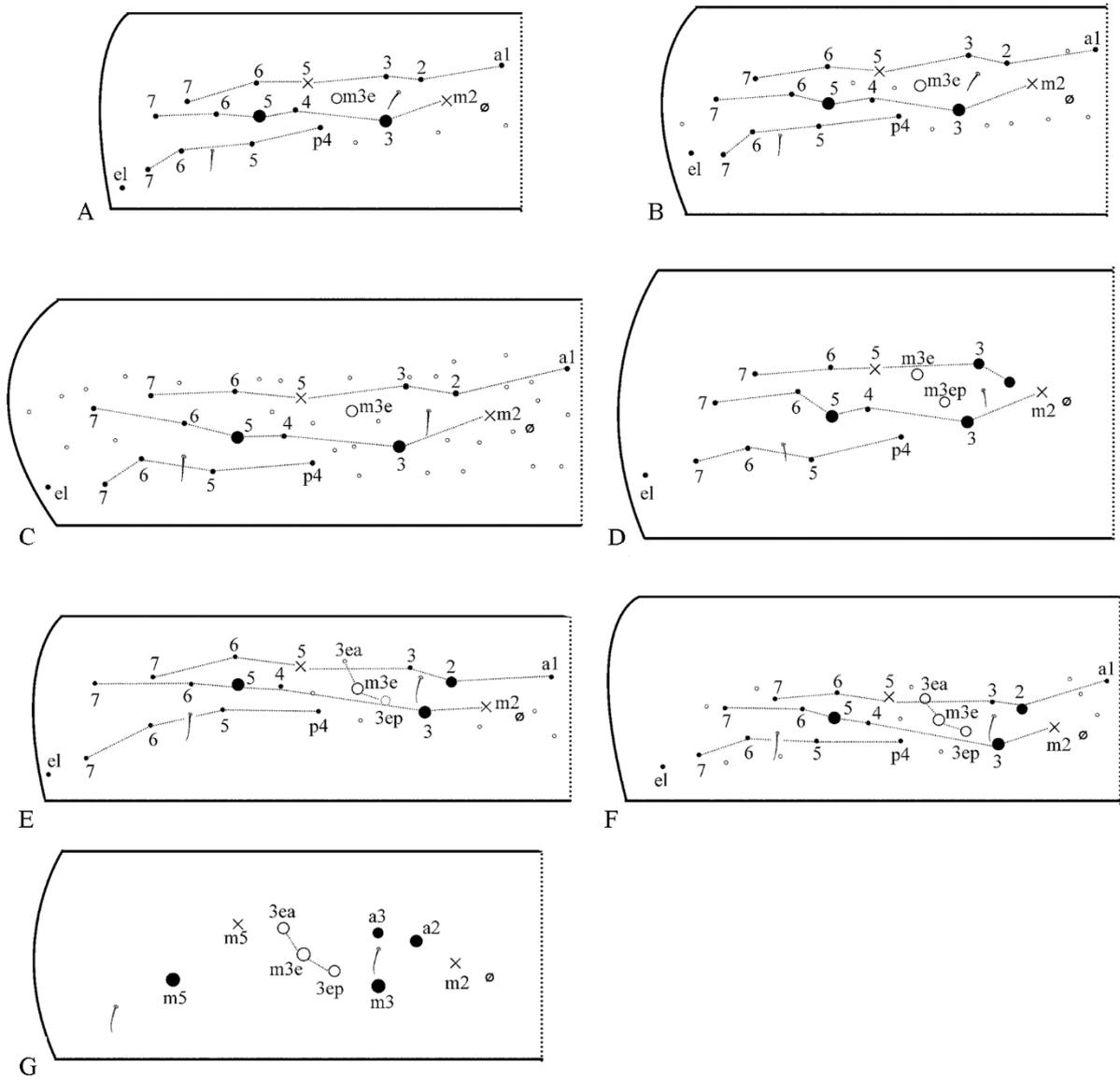


Figure S8. Development of dorsal chaetotaxy of Abd. II in Entomobryinae. A–D. *Entomobrya nivalis*. A. 2nd instar. B. 3rd instar. C. 4th instar. D. Adult. E–G. *Entomobrya* sp. E. 3rd instar. F. 4th instar. G. Adult.

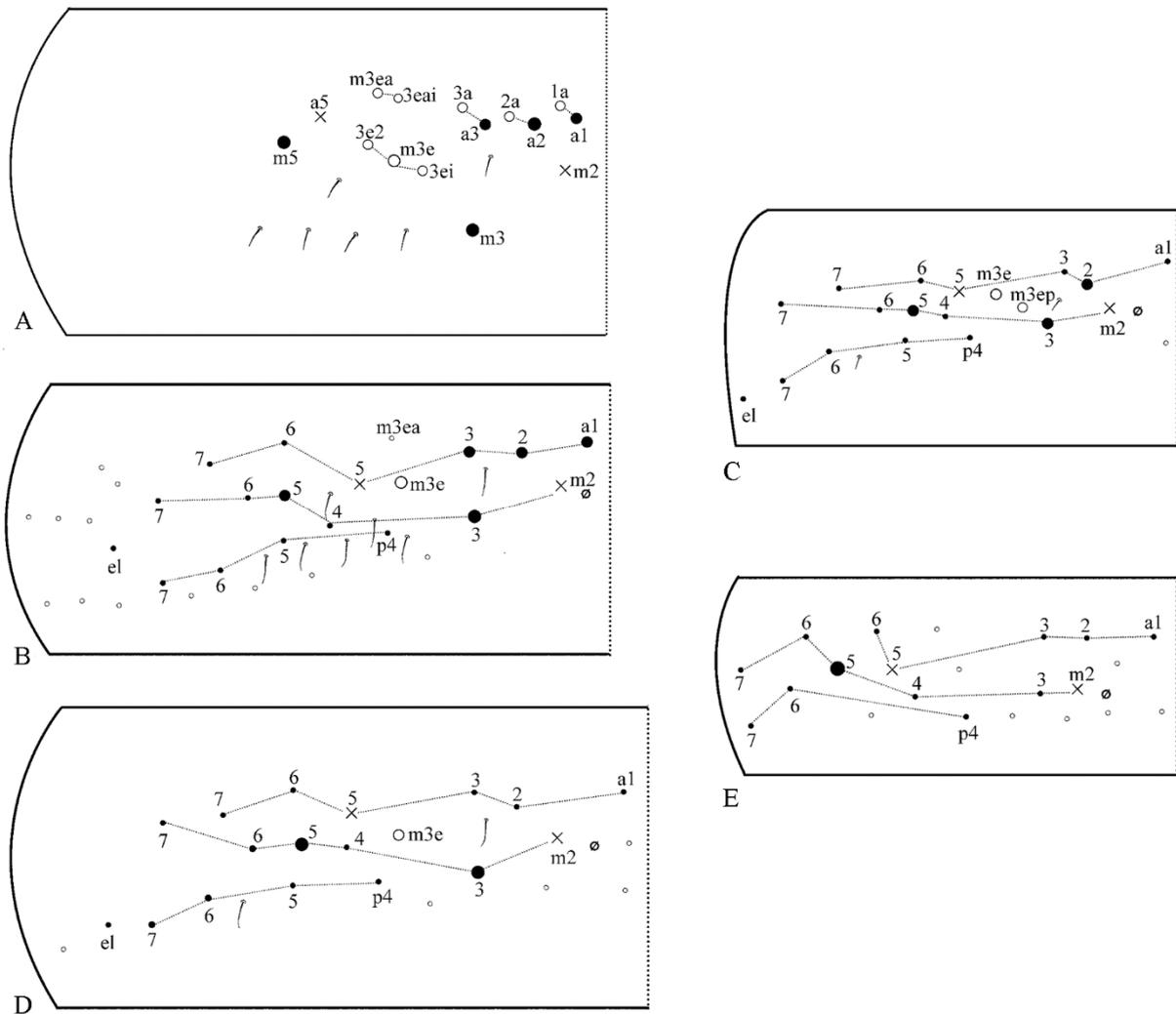


Figure S9. Development of dorsal chaetotaxy of Abd. II. A. *Orchesella cincta* (subadult, Orchesellinae, external chaetae not represented). B. *Orchesellides boraai* (juvenile, Orchesellinae). C. *Entomobrya huangi* (2nd instar, Entomobryinae). D. *Willowsia japonica* (2nd instar, Entomobryinae). E. *Microfalcula* sp. (2nd instar, Salininae).

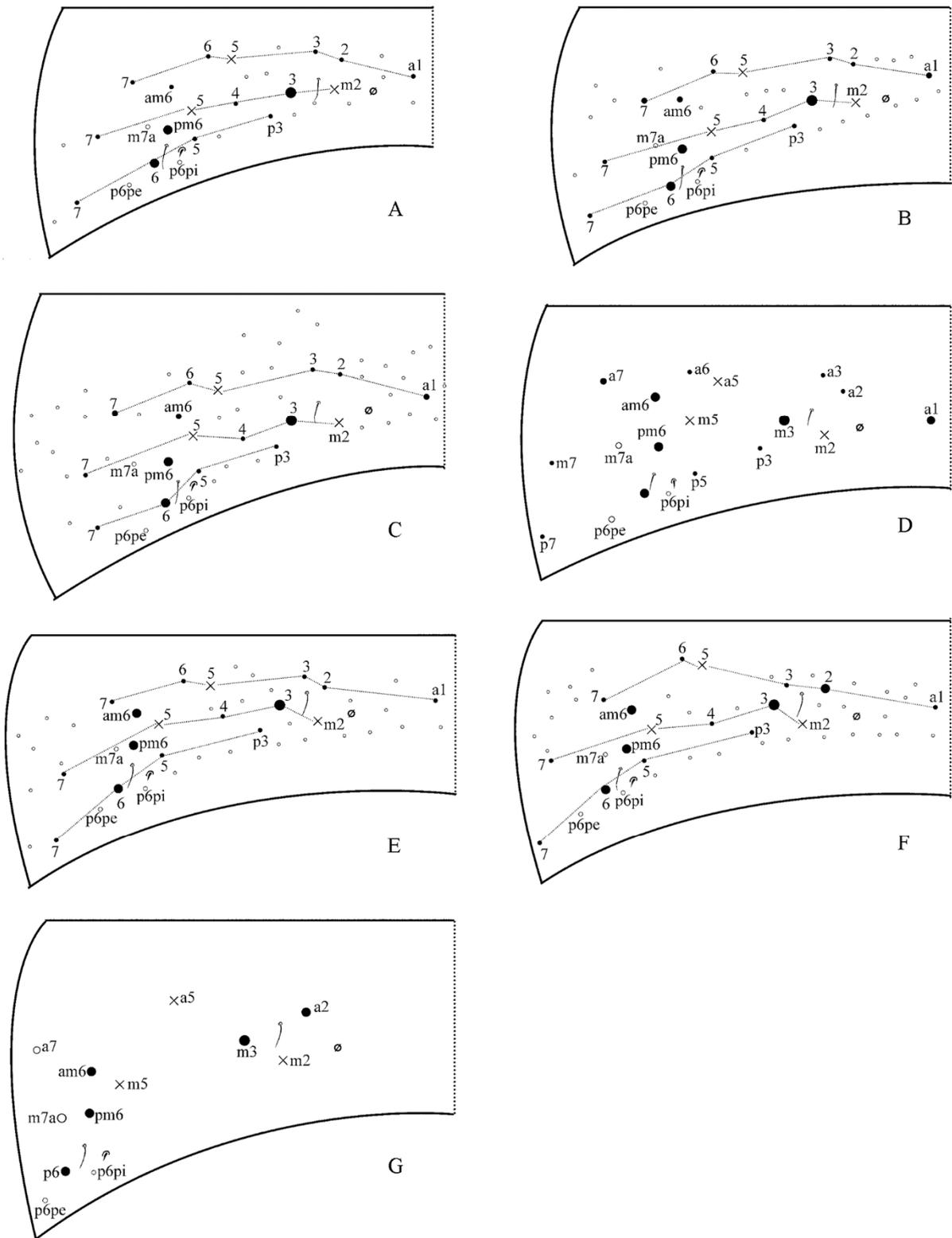


Figure S10. Development of dorsal chaetotaxy of Abd. III in Entomobryinae. A–D. *Entomobrya nivalis*. A. 2nd instar. B. 3rd instar. C. 4th instar. D. Adult. E–G. *Entomobrya* sp. E. 3rd instar. F. 4th instar. G. Adult.

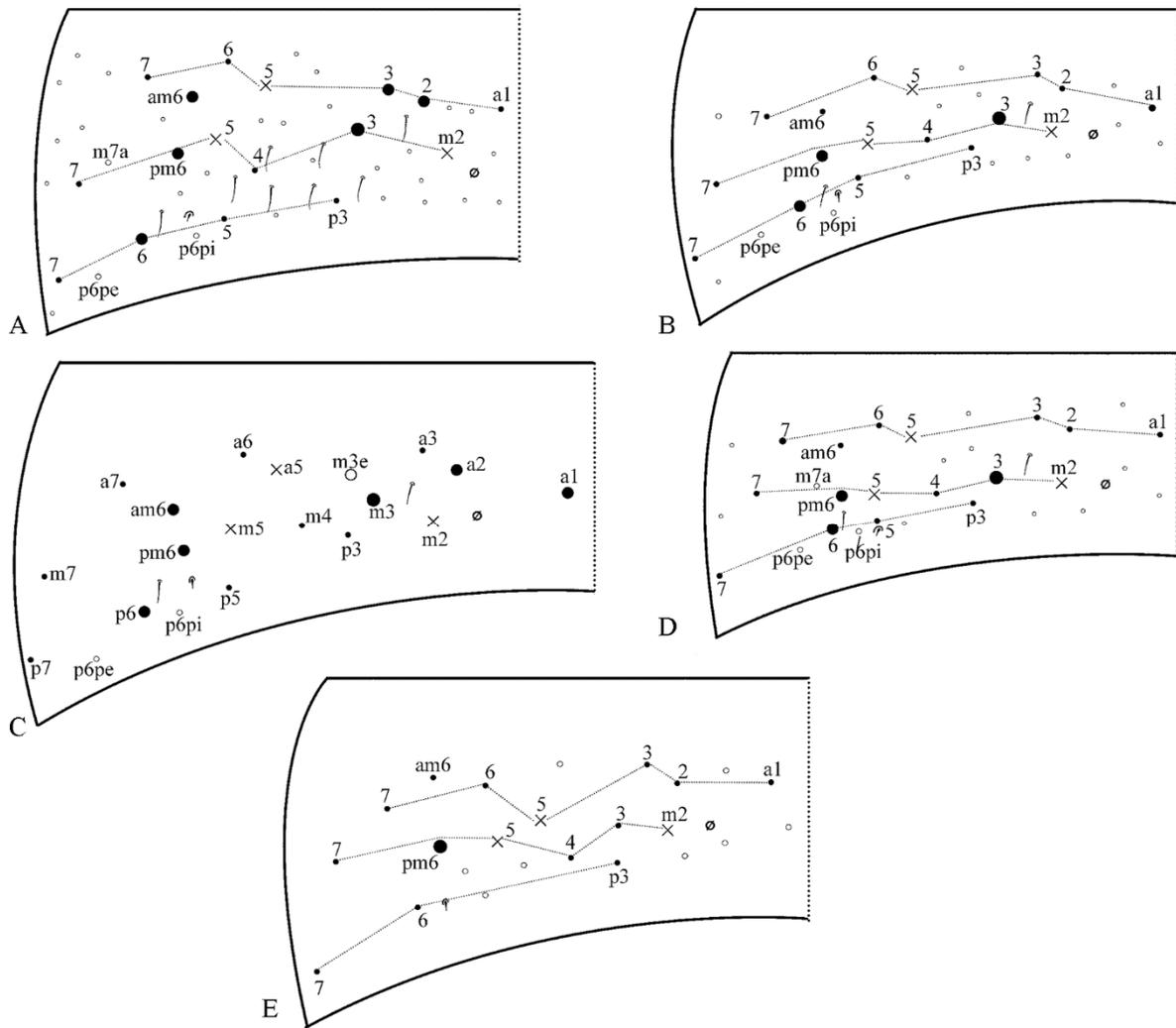


Figure S11. Development of dorsal chaetotaxy of Abd. III. A. *Orchesellides boraai* (juvenile, Orchesellinae). B–C, *Entomobrya huangi* (Entomobryinae). B. 2nd instar. C. adult. D. *Willowsia japonica* (2nd instar, Entomobryinae). E. *Microfalcula* sp. (2nd instar, Salininae).

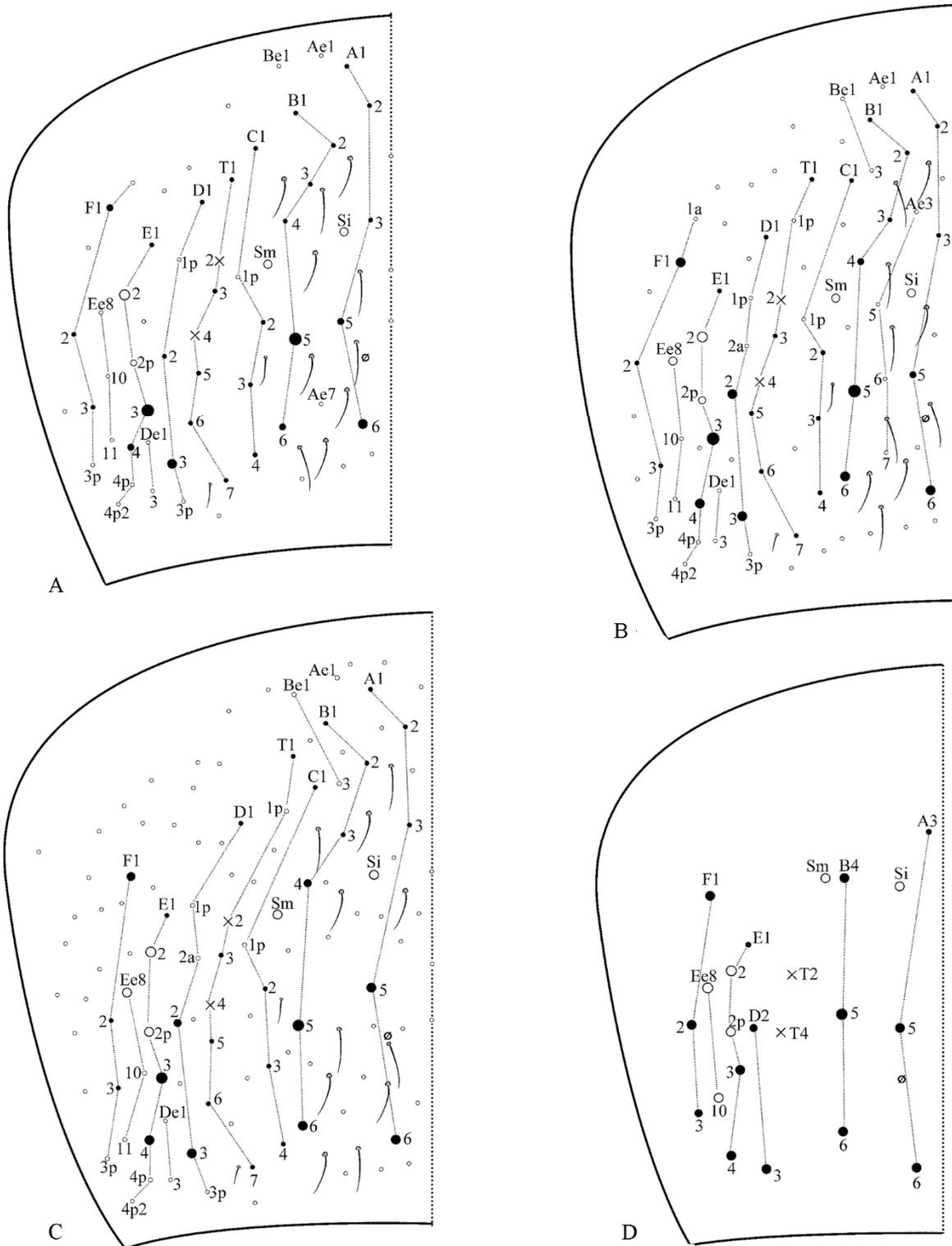


Figure S12. Development of dorsal chaetotaxy of Abd. IV in *Entomobrya nivalis* (Entomobryinae). A. 2nd instar. B. 3rd instar. C. 4th instar. D. Adult.



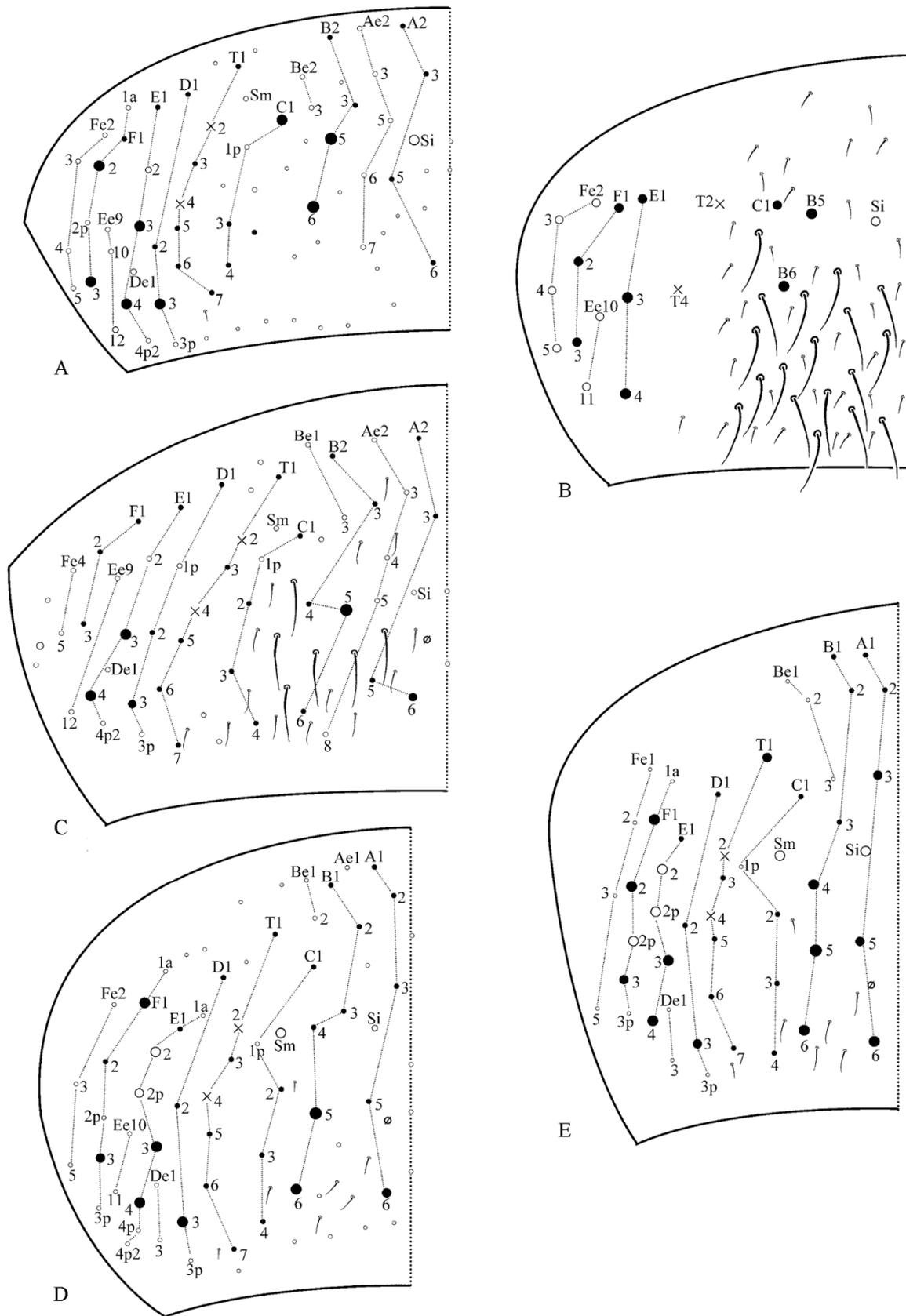


Figure S14. Development of dorsal chaetotaxy of Abd. IV. A. *Orchesella flavescens* (2nd instar, Orchesellinae). B. *Orchesella cincta* (subadult, Orchesellinae). C. *Orchesellides boroai* (juvenile, Orchesellinae). D–E. *Entomobrya huangi* (Entomobryinae). D. 2nd instar. E. Adult.

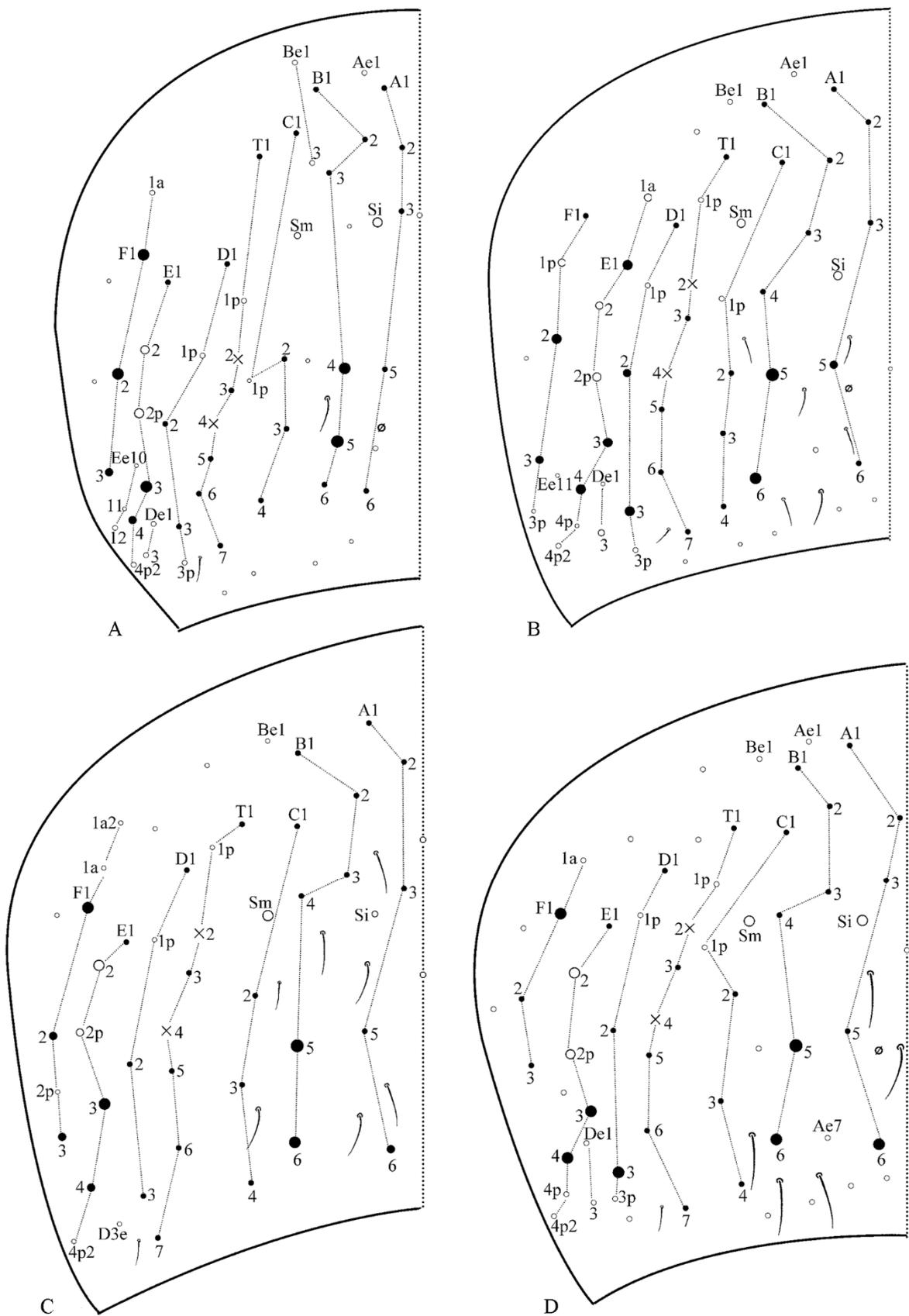


Figure S15. Development of dorsal chaetotaxy of Abd. IV in Entomobryinae (2nd instar). A. *Homidia* sp. B. *Willowsia japonica*. C. *Willowsia cassagnau*. D. *Janetschkebrya himalica*.

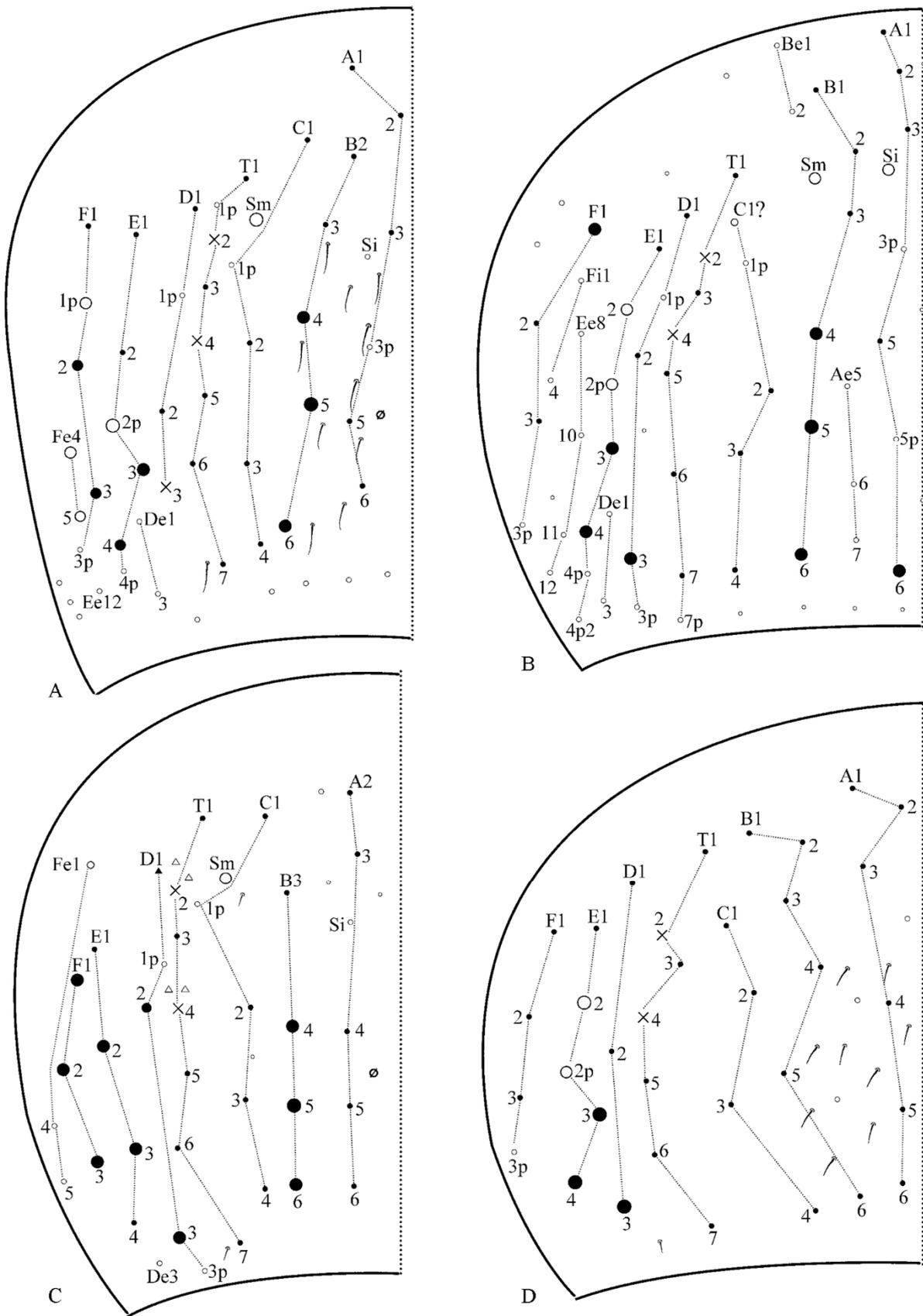


Figure S16. Development of dorsal chaetotaxy of Abd. IV (2nd instar). A. *Seira dowlingi* (Seirinae). B. *Entomobryoides myrmecophila* (Entomobryinae). C. *Lepidocyrtus curvicollis* (Lepidocyrtinae). D. *Microfalcula* sp. (Saliniinae).

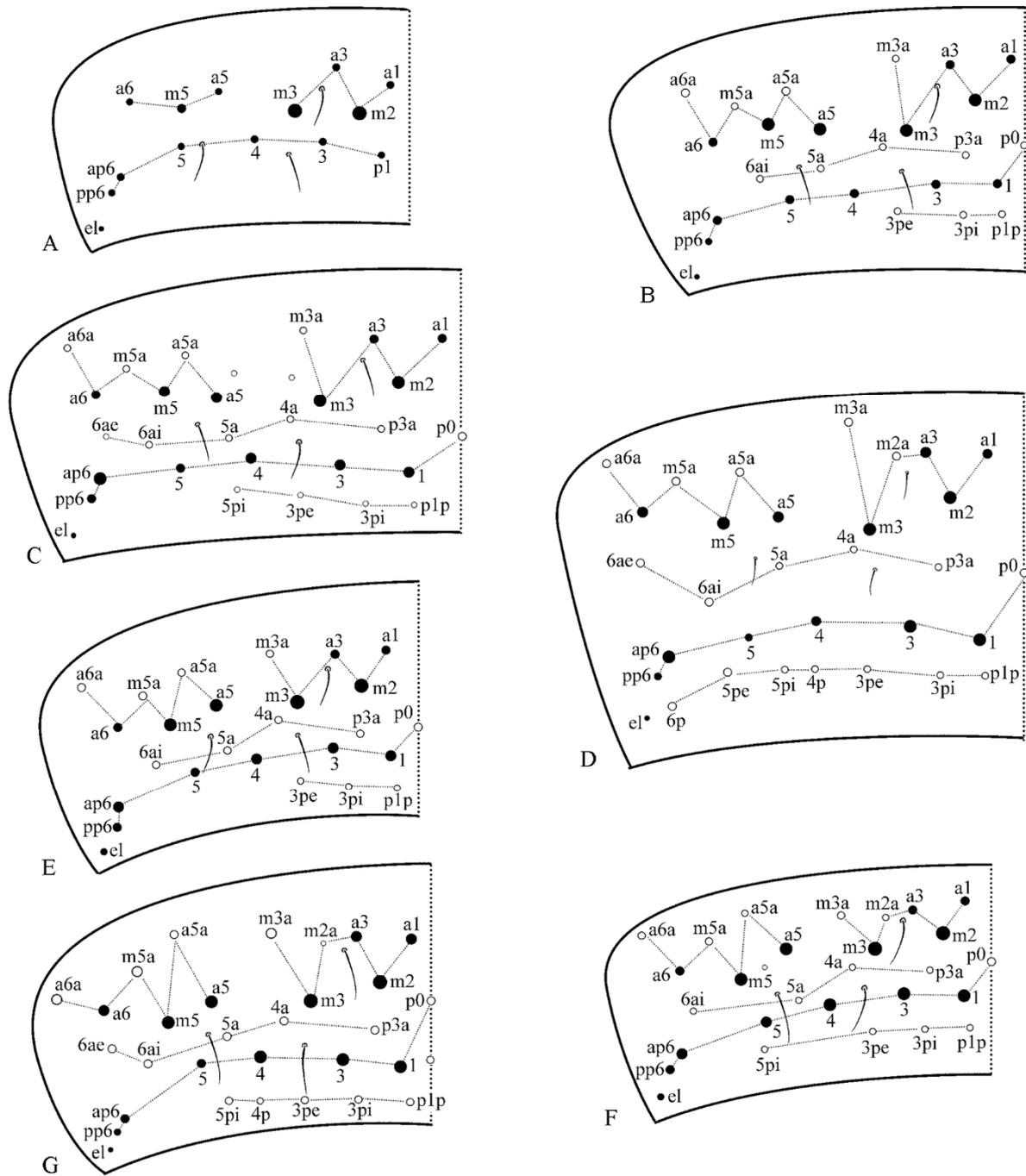


Figure S17. Development of dorsal chaetotaxy of Abd. V in Entomobryinae. A–D. *Entomobrya nivalis*. A. 2nd instar. B. 3rd instar. C. 4th instar. D. Adult. E–G. *Entomobrya* sp. E. 3rd instar. F. 4th instar. G. Adult.

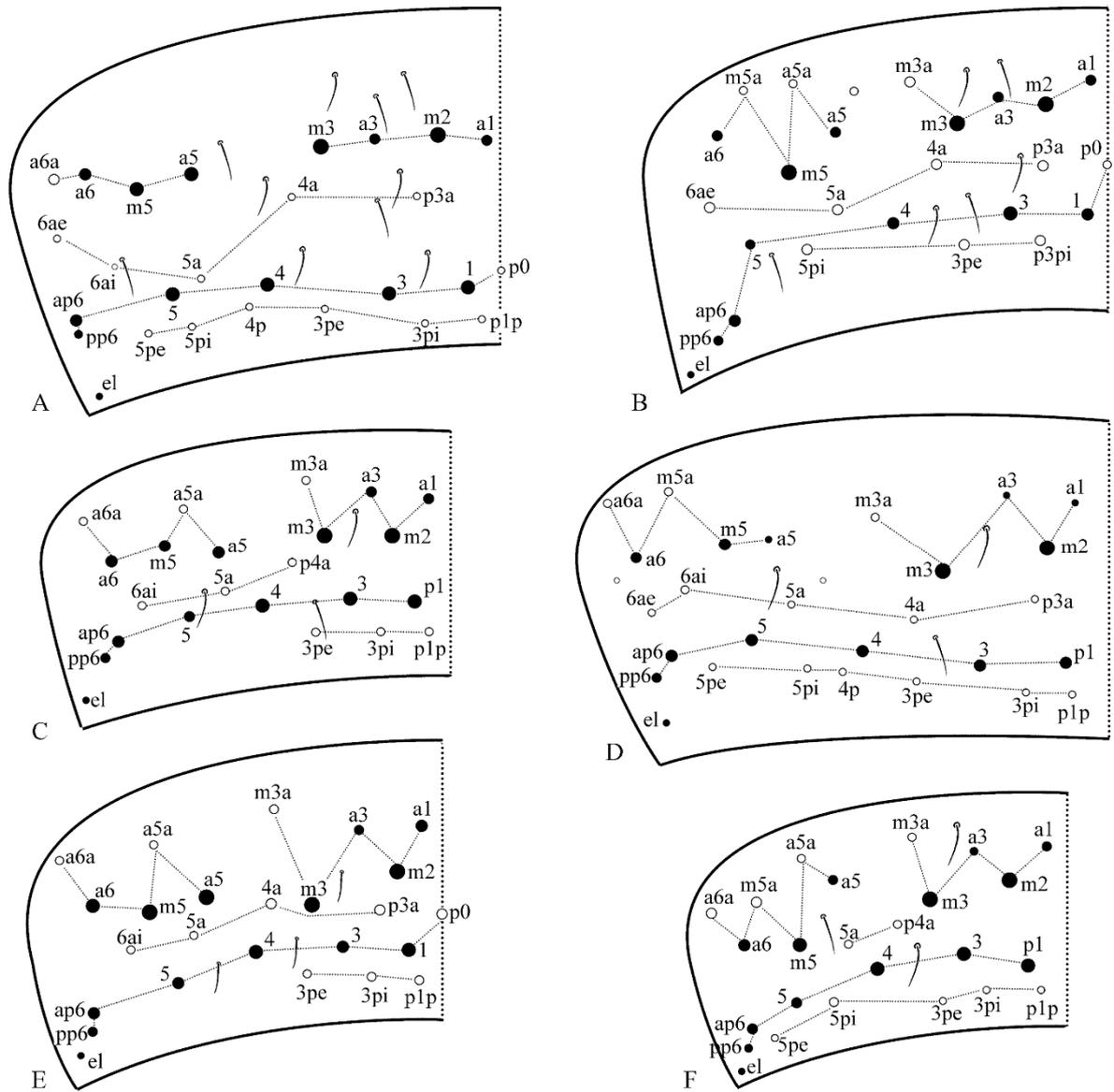


Figure S18. Development of dorsal chaetotaxy of Abd. V. A. *Orchesella cincta* (subadult, Orchesellinae). B. *Orchesellides boraoi* (juvenile, Orchesellinae). C. *Willowsia japonica* (2nd instar, Entomobryinae). D. *Americabrya arida* (adult, Entomobryinae). E. *Janetschekbrya himalica* (2nd instar, Entomobryinae). F. *Homidia* sp. (2nd instar, Entomobryinae).

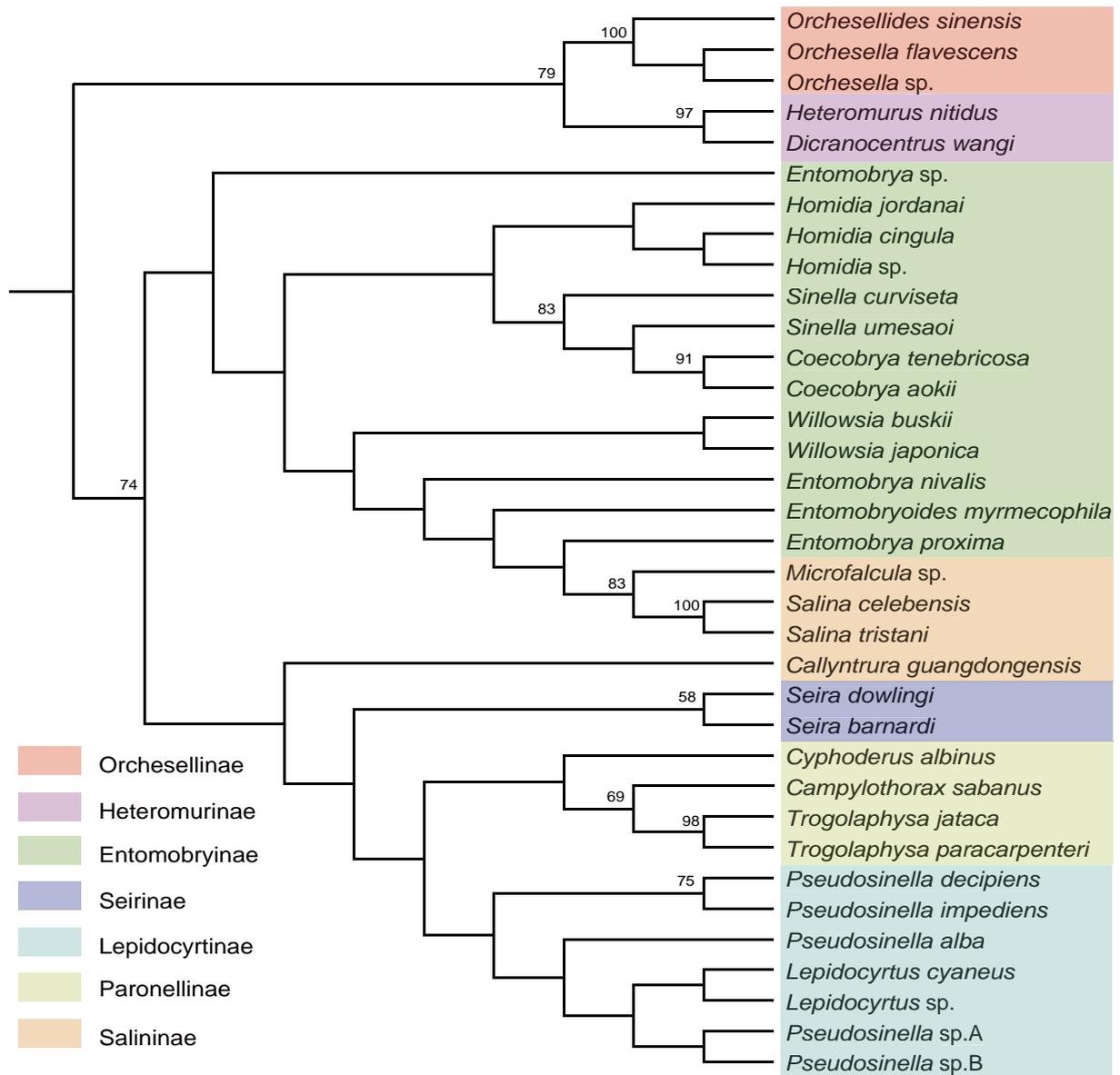


Figure S19. Consensus tree of Entomobryoidea using maximum parsimony with 35 species included (the outgroup species excluded). The bootstrap values greater than 50 are given on the nodes.

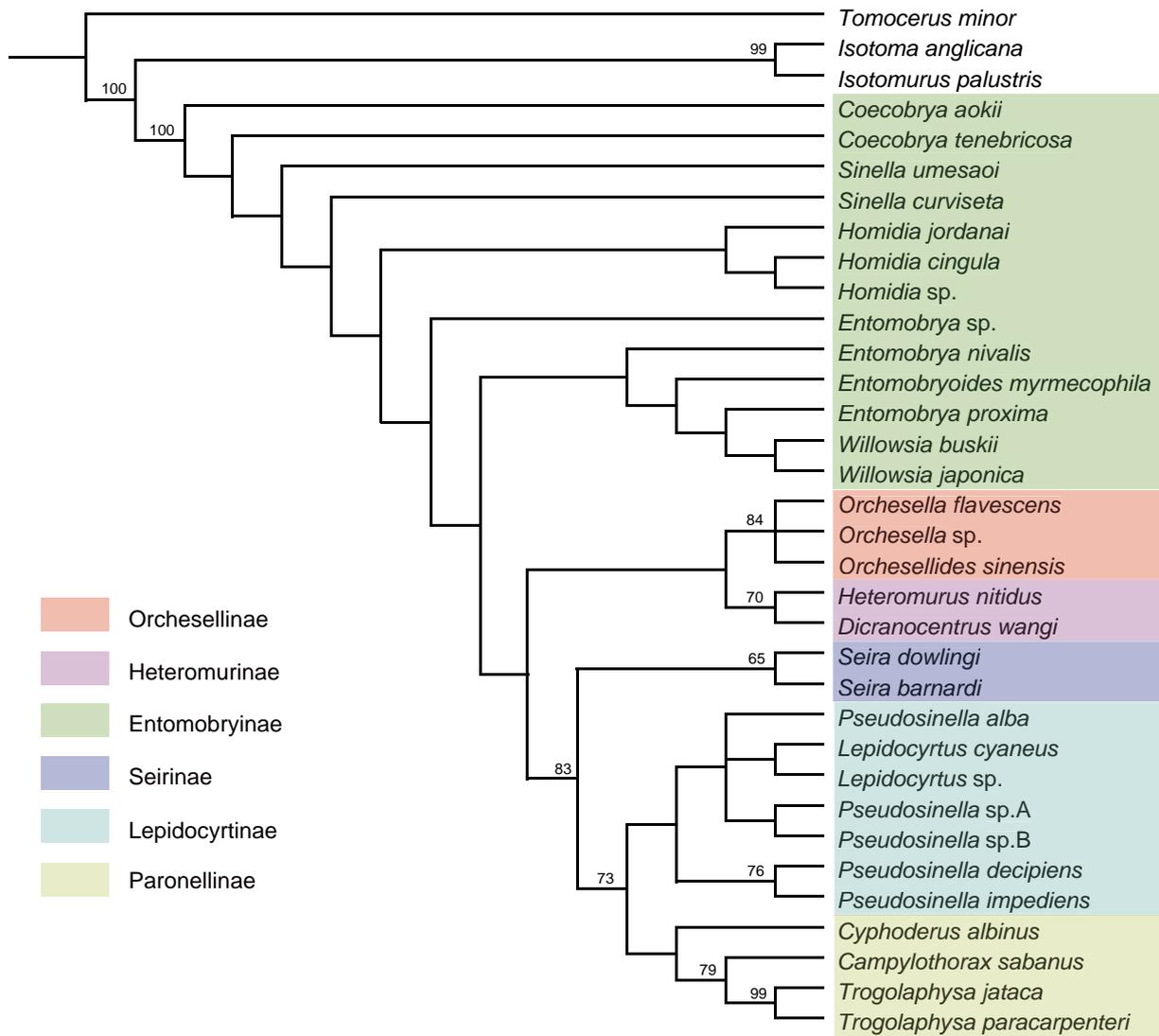


Figure S20. Consensus tree of Entomobryoidea using maximum parsimony with 34 species included (the outgroup species excluded). The bootstrap values greater than 50 are given on the nodes.

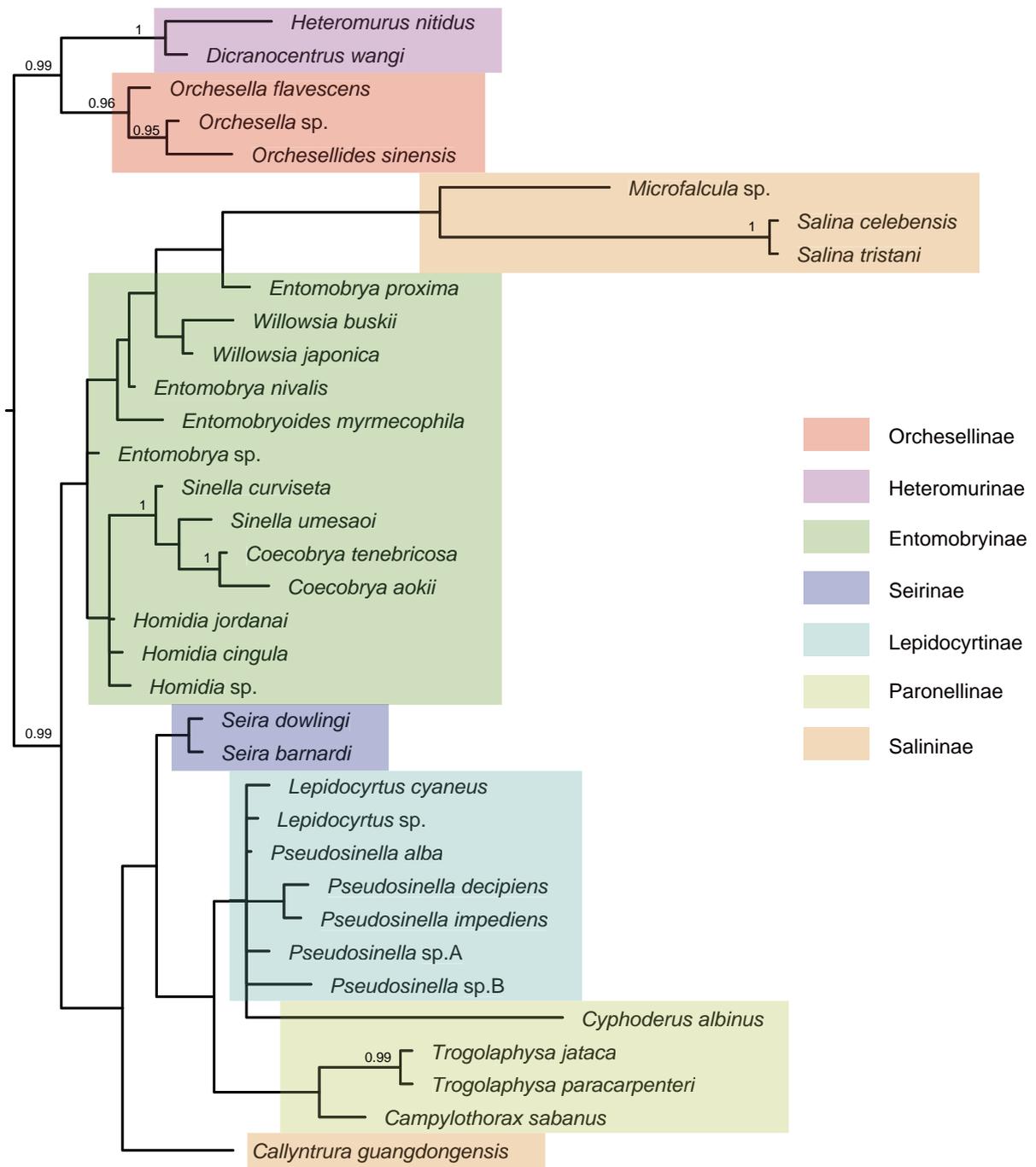


Figure S21. Consensus tree of Entomobryoidea using Bayesian inference with the outgroup species excluded. Posterior probability values greater than 0.95 are shown on the nodes.

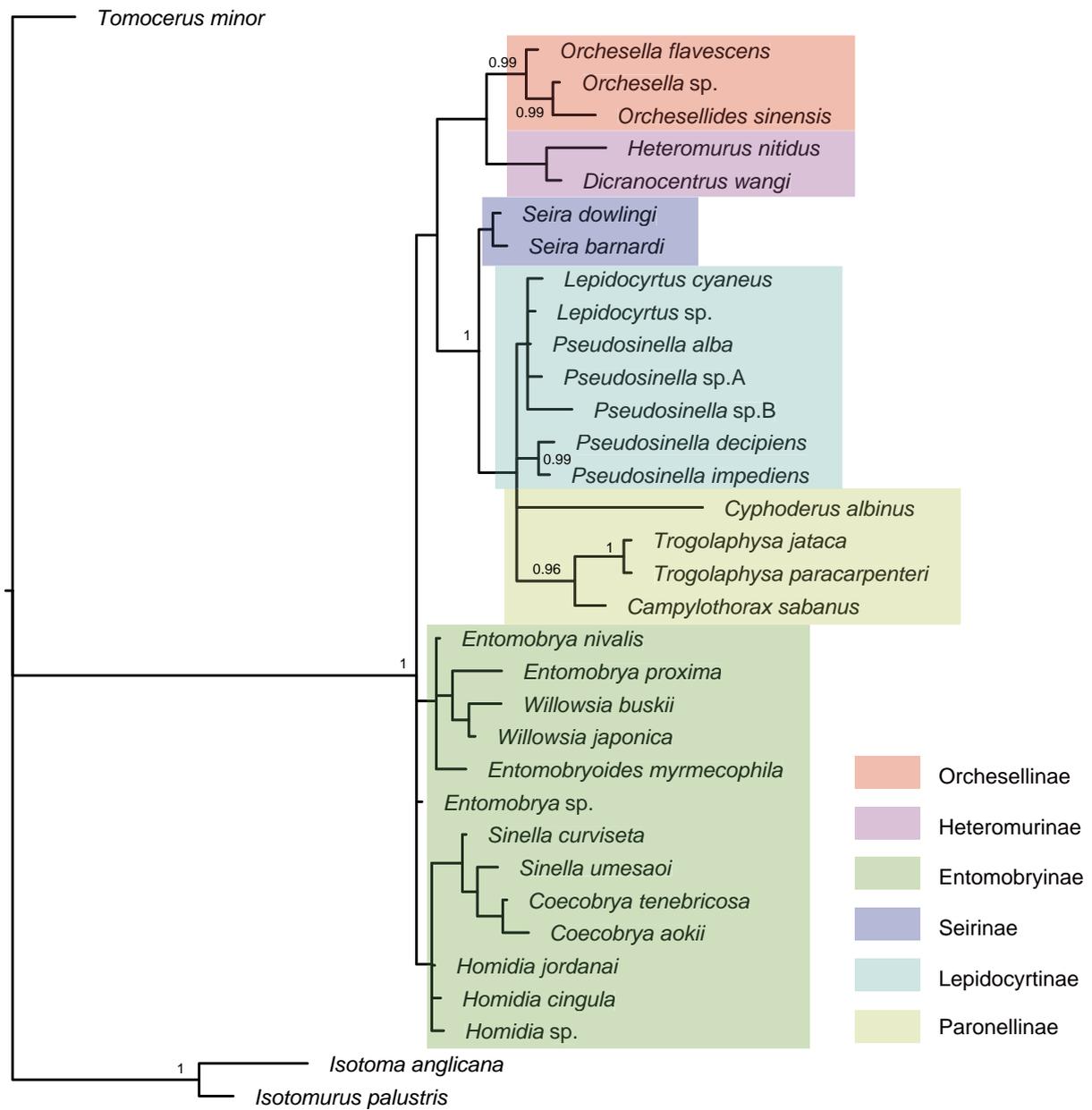


Figure S22. Consensus tree of Entomobryoidea using Bayesian inference with the unstable species excluded. Posterior probability values greater than 0.95 are shown on the nodes.

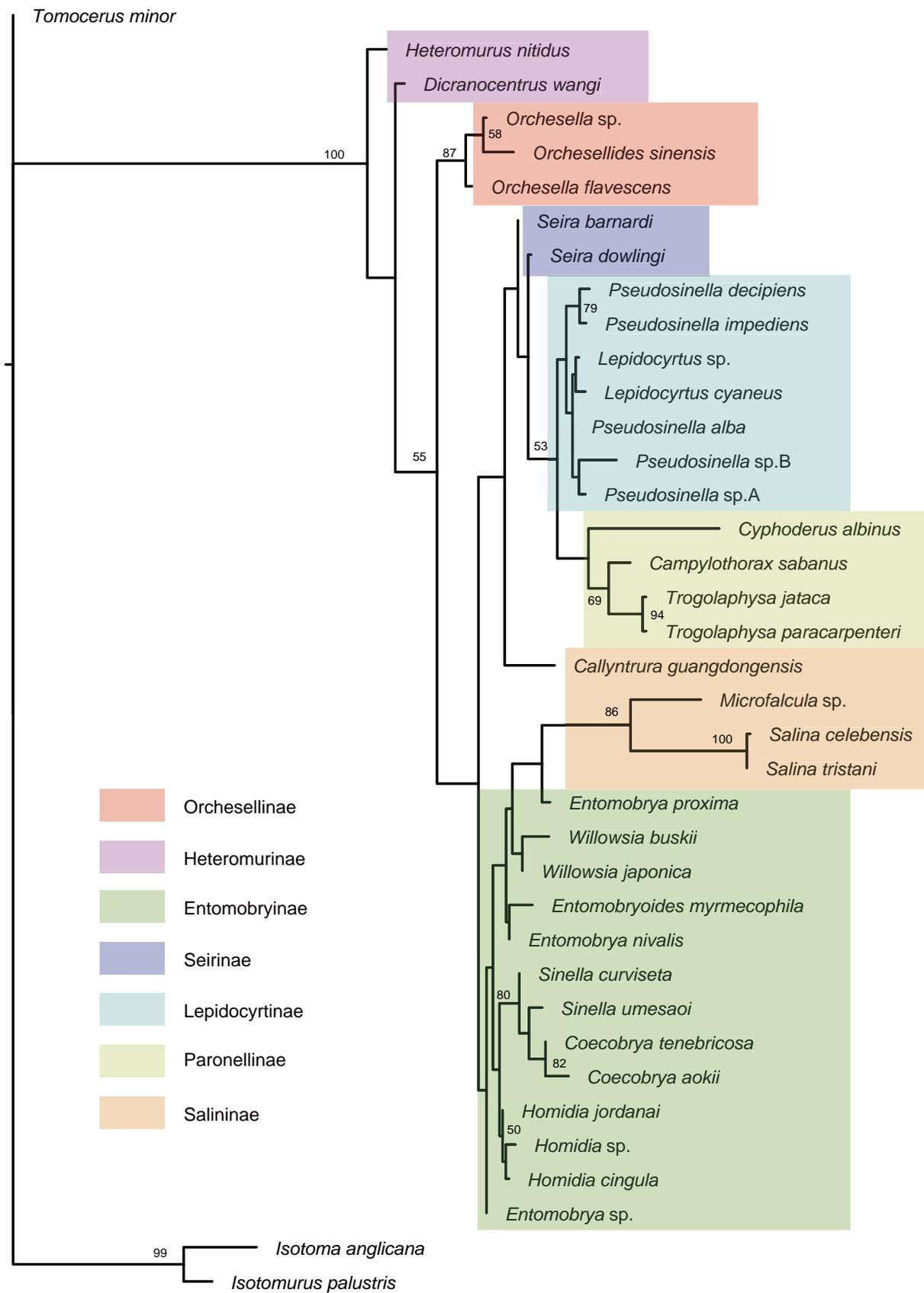


Figure S23. Phylogeny of Entomobryoidea using maximum likelihood with all 38 species included. Bootstrap values greater than 50 are shown on the nodes.

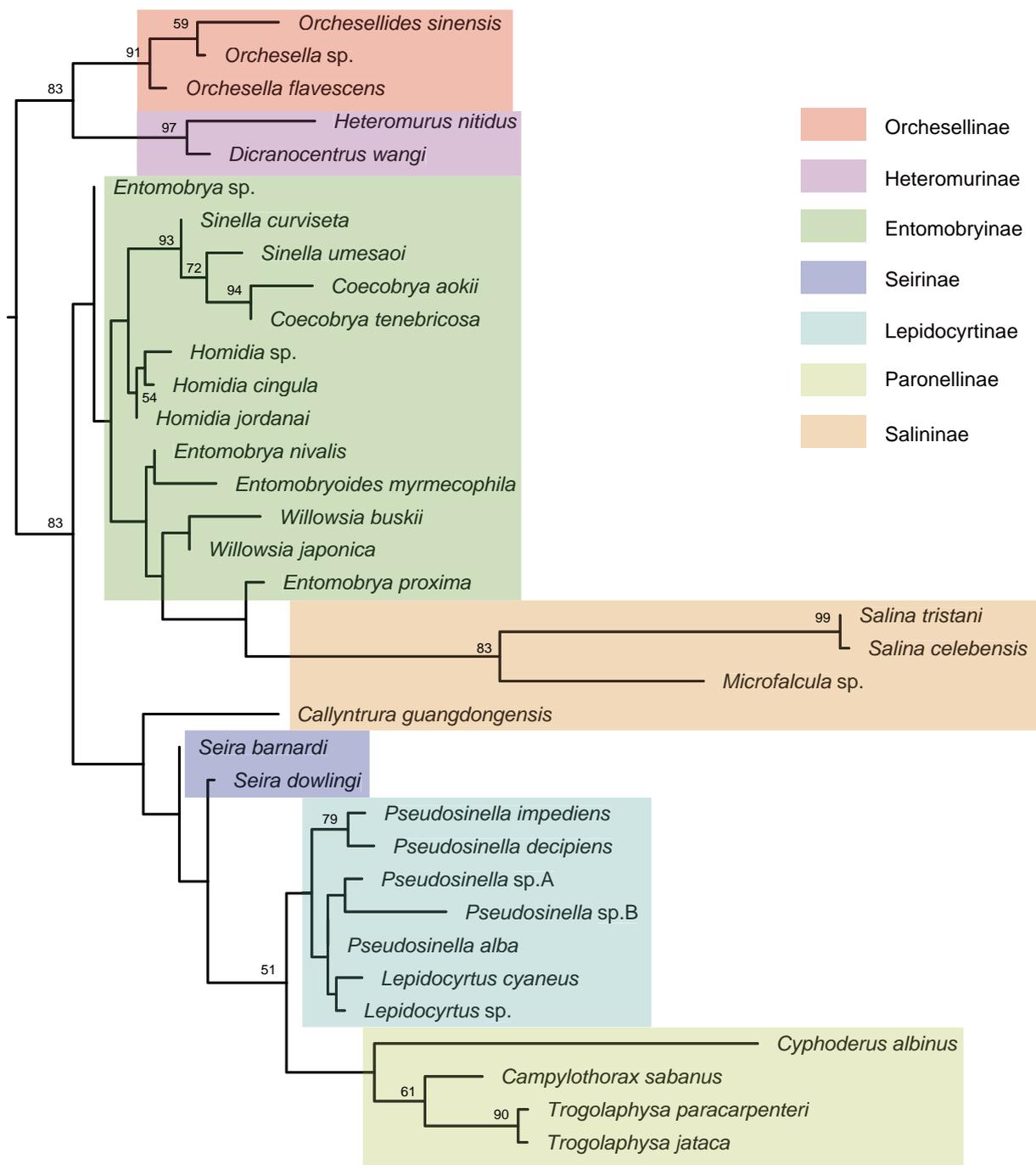


Figure S24. Phylogeny of Entomobryoidea using maximum likelihood with the outgroup species excluded. Bootstrap values greater than 50 are shown on the nodes.

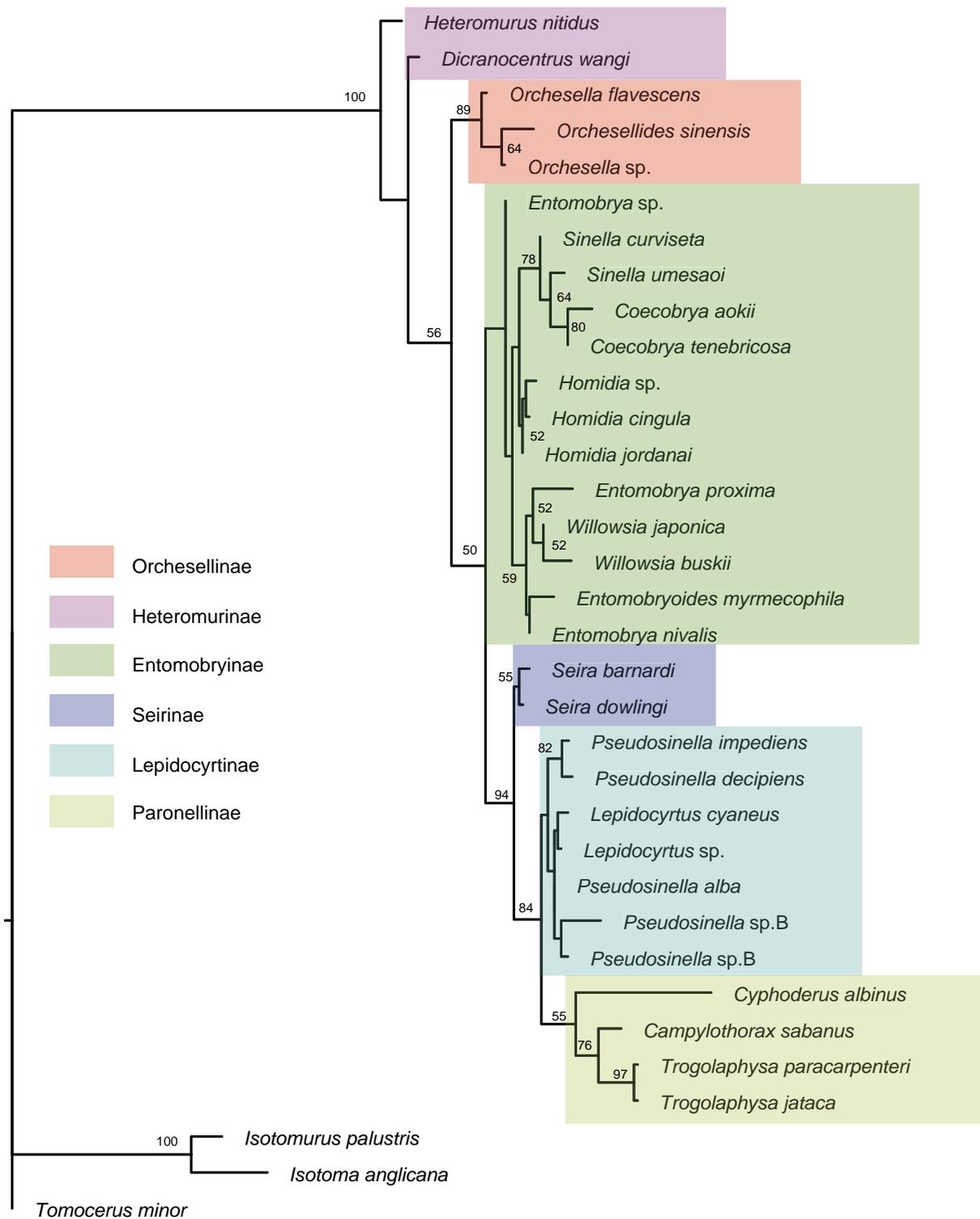


Figure S25. Phylogeny of Entomobryoidea using maximum likelihood with the unstable species excluded. Bootstrap values greater than 50 are shown on the nodes.

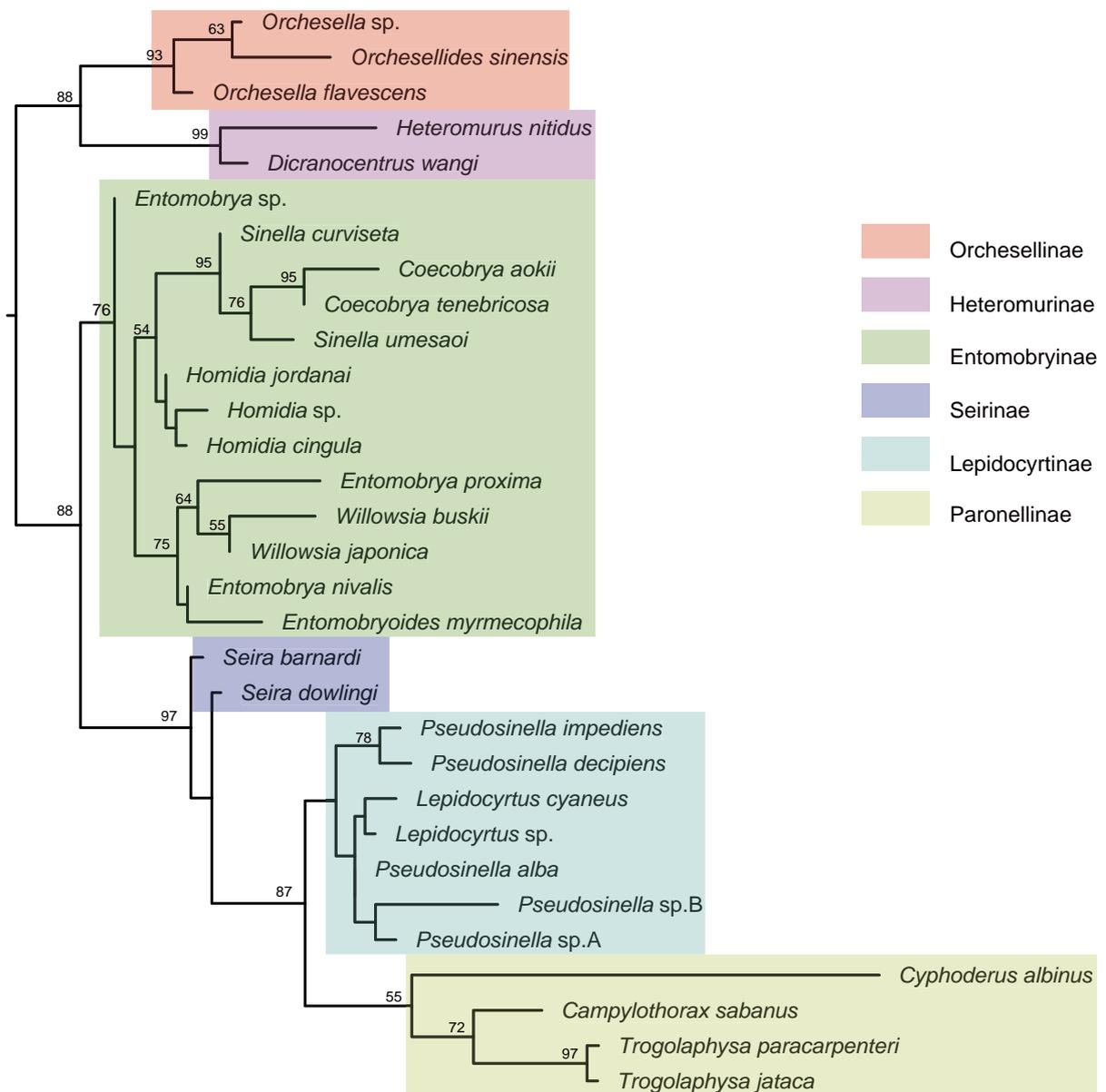


Figure S26. Phylogeny of Entomobryoidea using maximum likelihood with both the outgroup and the unstable species excluded. Bootstrap values greater than 50 are shown on the nodes.