Comparative Analysis of the Dorsal Chaetotaxy of Troglopedetes, Trogolaphysa, and Campylothorax Supports the Synonymization of Tribes Paronellini and Trogolopedetini (Collembola: Paronellidae)

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ABSTRACT. Genera in subfamily Paronellinae have been grouped into five tribes, in part based on chaetotaxy. Tribes Bromacanthini, Paronellini, and Trogolopedetini are characterized by having rounded scales and reduced or no macrochaetae, and although Bromacanthini harbors two well-differentiated genera, the core genera in tribes Paronellini and Trogolopedetini form a homogeneous group where even generic diagnoses were, until recently, unclear. The genus Absolon traditionally placed in Trogolopedetini (Troglopedetes Absolon, Trogolaphysa Mills, and Cyphoderopsis Carpenter) harbor many species with reduced eyes number, whereas the tribe Paronellini (genera Paronella Schött, Dicranocentruca Wray and Campylothorax Schött) includes species with 6–8 eyes. Recent analyses of the chaetotaxy of Troglopeda and Cyphoderopsis suggest that these genera represent specialized forms related to species in Paronellini. The taxonomy of Troglopedetes, the type genus of Trogolopedetini, is based almost exclusively on claw and micro shape and dorsal macrochaetae pattern, and few details of the complete dorsal chaetotaxy of the species are known. This contribution presents a comparative analysis of the complete dorsal chaetotaxy of two species of Troglopedetes from Spain (one new to science), two new species of Troglopeda from the Dominican Republic and Martinique, and Campylothorax sabanus with the purpose of identifying aspects of the chaetotaxy that could provide diagnostic characters for the separation of Troglopeda and Troglopedetes, and a new diagnosis for tribe Trogolopedetini. The analysis shows that neither the number of chaetae nor its organization or pattern of macrochaeta provides diagnostic differences between Troglopeda and Troglopedetes. It is also concluded that the separation of Paronellini and Trogolopedetini is not justified. Trogolopedetini is here synonymized with Paronellini, and a new diagnosis for Paronellini is provided.

Key Words: Spain, Dominican Republic, Martinique, Cyphoderopsis, entomobryoidea

The genus Troglopedetes Absolon comprises some 35 species distributed throughout the temperate and tropical regions of Eurasia (Bellinger et al. 1996–2013). Most temperate species are restricted to caves, but tropical forms are found both in caves and surface habitats (Deharveng 1987).

The relationship and taxonomic status of Troglopedetes with respect to similar genera (Troglopeda Mills, Dicranocentruca Wray, Cyphoderopsis Carpenter, Trogonella Delamare-Deboutteville, and Troglopedetina Delamare-Deboutteville) has been an object of controversy (Deharveng 1987, Mari Mutt 1987, Yoshii 1988). Thibaud and Najt (1988) reviewed a significant number of species assigned to the genera listed above and proposed new diagnoses for Troglopeda, Troglopedetes, and Cyphoderopsis, and the synonymization of Dicranocentruca, Troglopedetina, and Trogonella, under each of the firstly cited genera, respectively. Thibaud and Najt (1988) restricted Troglopedetes to species with fourth antennal segment subdivided, labial chaeta 1 reduced, 0–3 eyes, and mucro relatively long, whereas Troglopeda grouped species with the fourth antennal segment undivided, labial chaetae 1 normal, 0–8 eyes, and short mucro with 3–5 teeth. Mitra (1993) supported the separation of Troglopedetes, Troglopeda, Cyphoderopsis, and Dicranocentruca and placed the first three genera in the tribe Trogolopedetini Börner, whereas Dicranocentruca was allocated to Paronellini Börner, based on the presence of the extra ocular structure (EOS; Mitra 1972). Mitra (2002) reiterated his placement of all species with 6–6 or more eyes and an EOS in Dicranocentruca.

Soto-Adames and Taylor (2013) studied the dorsal chaetotaxy of two species of Troglopeda and three species originally assigned to Dicranocentruca and, in agreement with Thibaud and Najt (1988), concluded that there are no differences in the organization of the chaetotaxy to justify the separation of the genera. The synonymization of Dicranocentruca and Troglopeda has further implications for classification. The genus Troglopeda was traditionally placed in tribe Troglopedetini, whereas Dicranocentruca was placed in Paronellini (Mitra 1993, 2002). The chaetotaxy organization reported by Soto-Adames and Taylor (2013) suggested Troglopeda should be placed in Paronellini. Likewise, recent work by Jantanit et al. (2013) shows that the idiochaetotaxy (i.e., all chaetae distinct from the basic chaeta; in the species under scrutiny, the basic chaetotaxy is formed by scales) of Cyphoderopsis does not differ in organization from that of Troglopeda. Transferring Troglopeda and Cyphoderopsis to Paronellini would leave tribe Trogolopedetini harboring only the genus Troglopedetes and in need of a new diagnosis.

The taxonomy of Troglopedetes is based almost exclusively on claw shape and dorsal macrochaetae pattern (Deharveng and Gers 1993), and few other aspects of the morphology are included in species descriptions. As a result, most of the dorsal chaetotaxy Troglopedetes remains undescribed.

The purpose of this study is to determine whether dorsal chaetotaxy provides diagnostic characters for the separation of Troglopeda and Troglopedetes, and a new diagnosis for tribe Trogolopedetini. This contribution presents a comparative analysis of the complete dorsal chaetotaxy of two species of Troglopedetes from Spain and two species of Troglopeda from the Dominican Republic and Martinique. The chaetotaxy of these four species, and the six species treated by Soto-Adames and Taylor (2013), is compared with the chaetotaxy of Campylothorax sabanus (Wray 1953), a member of tribe Paronellini. This study concludes that the dorsal chaetotaxy in Troglopeda and Troglopedetes is
similarly organized and does not provide additional diagnostic characters to separate the genera. Furthermore, the similarity in chaetotaxy organization in *Campylotothorax*, *Trogolaphysa*, *Troglopedetes*, and *Cyphoderopsis* indicates that there is no justification for retaining tribe *Troglopedetini*, hence *Troglopedetes* and *Cyphoderopsis* are transferred to tribe *Paronellini*.

**Materials and Methods**

Selected specimens were cleared in Nesbitt’s solution, mounted in Mark André’s (Mari Mutt 1979) on glass slides, and examined under a compound microscope with phase-contrast. Drawings were made using a drawing tube, with final illustrations completed using Microsoft Power Point v14.3.5 Redmond, WA.

Throughout the descriptions, the abbreviations Ant., Th., and Abd. stand for antennal, thoracic, and abdominal segments, respectively. The formula for the labial chaetotaxy follows Christiansen and Bellinger (1998), where upper case represents macrochaetae, lower case microchaetae, underscore ciliate chaetae, and without underscore smooth chaetae. Repositories of material studied are the Illinois Natural History Survey at the University of Illinois, Champaign, IL (INHS); National Museum of Natural Sciences, Madrid, Spain (MNCN); National Museum of Natural History, Paris, France (MNHN); Natural Science Museum of Barcelona (MCNB); Museum of Zoology, University of Navarra, Pamplona, Spain (MZNA); and Carnegie Museum of Natural History, Pittsburgh, PA (CMNH).

Nomenclature of head and body chaetotaxy follow the systems of Jordana and Baquero (2005), Soto-Adames (2008, 2010), and Szeptycki (1979). The nomenclature of head chaetae is based on a combination of assumptions about which chaetae are primary (Barra 1975, Soto-Adames 2008, Pan et al. 2011) and their insertion relative to other chaetae and head landmarks (e.g., eye patch and dorsal sulcus). Head chaetae can be divided into anterior (series A, M, S, and Ps) and posterior (series Pm, Pm, and Pp). In the genera under consideration, most anterior head chaetae can be unambiguously identified following the model in Figs. 11 and 55. The only chaetae open to interpretation are those lateral to series A, which may be interpreted as either A5 or A5. Following Soto-Adames (2008) and Pan et al. (2011), A5 is a primary macrochaeta, whereas A4 is a secondary microchaeta, hence the external macrochaeta in *C. sabanus* is identified as A5. Other chaeta associated to series A are unstable and were not identified. Posterior chaetae are often difficult to identify due to inadequacies of the mounting technique. Row Pa includes only four chaetae, which are identified as Pa3, Pa3, Pa4, and Pa5. Chaeta Pa4 is always a trichobothrium, and Pa5 is often transformed into a macrochaeta. The number of chaetae in rows Pm and Pp in adults is unclear, but one or two members of these rows are often modified into macrochaetae. The anterior macrochaeta was identified as Pa1, as it is almost invariably inserted directly below Pa1 or between Pa2 and Pa3, and the posterior one as Pp3. Macrochaeta Pp3 is common in *Troglopedetes* spp. (Deharveng 1988, 1990; Deharveng and Gers 1993), including the two species studied here.

Dorsal body chaetotaxy follows Szeptycki (1979), but chaeta identification is based on the relative position of each element in a general model with a full complement of chaetae. The idiochaetotaxy of the species considered here is reduced in comparison with other scaled Entomobryoidea and identification of many elements is subjective. The criteria used to identify chaeta of uncertain homology are discussed below.

**Mesothorax.** The anterior chaetae associated with the pseudopore belong to series m2. In most species, there is a single chaeta displaced externally to the pseudopore, which is identified as m2e. A chaetae is identified as m2 only when inserted directly or almost directly above the pseudopore; the chaeta internal and near to the pseudopore is m2i, whereas the element internal to the pseudopore, but closer to the pseudopore is m1. Among species with known chaetotaxy, only *Trogolaphysa jacobyi* Soto-Adames and Taylor 2013 has more than one chaeta in series m2, and under the present interpretation they were identified as m2 and m2i.

First Abdominal Segment Chaeta p6. The insertion of the latero-posterior chaeta on this segment appears to shifts from left to right and back in interspecific comparisons. The identification of the lateral chaetae as p6 is based on the observation that when a6 is present, the two chaetae are aligned.

Third Abdominal Segment. The chaetotaxy of the lateral trichobothrial complexes is difficult to homologize with the chaetotaxy of Entomobryoidea. Several possible interpretations of the lateral chaetotaxy were explored, but in the absence of clear and strong evidence to support any of them, it was decided to adopt the interpretation presented in Fig. 22.

Fourth Abdominal Segment. Determination of the identity of chaetae in columns A and B is problematic because of pervasive anterior, posterior and lateral displacement of the elements in interspecific comparisons. To achieve a degree of objectivity, the system of Jordana and Baquero (2005) and Jordana (2012) was adopted, which divides the inner section of the segment into five (four in *Troglopedetes* and *Trogolaphysa*) zones delimited by more or less stable landmarks. In summary (Figs. 22 and 56), zones 6–7 are the fields above the anterior trichobothria; zone 8 is the field between the anterior and medial trichobothria; zone 9 is the area...
ciliate and smooth setae, respectively. (11) Dorsal chaetotaxy of head. (6) Pleural setae and setae of outer circles, macrochaetae; close circles, microchaetae; open squares with sublobular plate. (8) Chaetotaxy of labial palp Papilla E. (9) Labial inserted anterior to B6 and somewhat internal to the pseudopore (Figs. 38). (10) Ventral chaetotaxy of head, open and black circles are ciliate and smooth setae, respectively. (11) Dorsal chaetotaxy of head.

between the posterior trichobothrium and a line running from the pseudopore to chaeta T6; and zone 10 is the area below the pseudopore and T6. Chaetae in columns A–B inserted in zones 6–7 belong to row 3; chaetae in zone 8 are part of row 4; in zone 9 one finds rows 4–5, whereas zone 10 includes row 6, sometimes row 5, and more rarely row 4. Chaetae in column A inserted in zone 10 are called A6, A12, or A17 depending on their relative insertion: A6 is inserted close to the posterior margin of the segment, at the same level as B6, which is almost always present; chaeta A12 is inserted anterior to B6 and somewhat internal to the pseudopore (Figs. 38 and 45); A17 is anterior to A12 and inserted between columns A and B. The most posterior chaeta in column B was interpreted as B6p, and the chaeta anterior to that as B6.

Results

Species Level Diagnostic Characters in Troglopedetes and Trogalaphysa. A list of characters used to diagnose species of Troglopedetes and Trogalaphysa is presented below. Characters are divided in two groups: primary characters are considered sufficient by themselves, or in combination with one other character, to diagnose species; secondary characters are those that provide support for interspecific discontinuities suggested by primary characters but that by themselves are not thought of as providing sufficient evidence of population isolation. Primary characters typically are easy to observe, discrete, and show very little intrapopulation variation. Secondary characters may be difficult to observe consistently across a number of slide-mounted specimens, show continuous variation, or show varying levels of intrapopulation variation in different species. Characters considered secondary may prove to be, after analysis of a larger sample of species, as useful in species delimitation and identification as primary characters. It is recommended that at a minimum, all primary characters be described and illustrated for all species. However, a proper species description should provide information for all the characters listed below, irrespective of whether they are listed as primary or secondary. Characters below are listed in morphological order from anterior to posterior. Characters considered primary are followed by (P), whereas secondary characters are identified by (S).

1. Scale distribution (S)—The distribution of scales in these two genera is of little diagnostic utility. All species have distally rounded scales (Fig. 34) present on Ant. I–II, head, body, and ventral face of furcula. A few species have basal scales on the dorsal face of Ant. III, but these scales often fall off and evidence of their presence is not always clear.

2. Relative length of antennae to head length (S)—The head length is measured from the cervix to the interantennal area.

3. Subapical sense organ Ant. IV (S)—Typically, there is a short capitate or rod-like sensillum inserted in a shallow pit (Fig. 5), accompanied by a guard sensillum. The capitate sensillum seems to be always present, but in some species, like Trogalaphysa sau-ron n. sp., it is small and translucent, and it may appear to be absent. The guard chaeta is always present and rather conspicuous. Most of the unambiguous interspecific variation is found in the shape, relative size, and thickness of the guard sensillum.

4. Subdivision of Ant. IV (P)—The presence of a subdivision on Ant. IV (Fig. 5) distinguishes Troglopedetes from Trogalaphysa. Unfortunately, the fourth antennomere is often lost in cave forms with long antennae that are collected in pitfall traps or those that have to be dragged out of caves through narrow passages.

5. Sense organ of Ant. III (S)—Sensilla 2–3 (sensu Chen and Christiansen 1993) are, in general, rod-like in surface species and flat and laterally expanded in cave forms. Some species (Figs. 4 and 26) have additional distal sensilla on Ant. II.

6. Eye number (P)—The number varies from 0 to 8. This character is considered primary, but it should be noticed that eyes G and H are always reduced, sometimes to such extent that even when present they are difficult to see in regular mounts, and species with eight eyes are reported as having only six eyes. For this reason, eye number is good diagnostic character when fewer than six are present. Another caveat is that in large species with reduced number of eyes (e.g., T. jacobyi), the EOS is large enough to be confused with an eye. The EOS is typically found between chaetae Ps8 and Pa8 (Figs. 39 and 60), and any eye-like structure observed in this area should be tentatively reported as EOS, until examination under polarized light or SEM can be arranged.

7. Number of chaetae in eye valley (S)—The number of chaetae in the eye valley varies from 3 to 6. This character can be scored only when eyes E and F are present. This character is stable and useful to distinguish Trogalaphysa jataca (Wray 1953) from Trogalaphysa geminata (Mari Mutt 1987), but many more species need to be evaluated before it can be considered primary.

8. Number of chaetae along the dorsal base of the antennae (S)—The row of chaetae along the dorsal base of the antennae, denominated An, includes macro- and mesochaetae with large sockets. The number chaetae shows intraspecific variation related to post-embryonic development, but the range of chaetae in adults can be used to separate groups of species.

9. Dorsal head chaetotaxy (P)—Most species level variation is found in the number of macrochaetae in series A, M, and S. The two
most common posterior macrochaeta are Pa₅, Pm₃, and, in Troglopedetes, Pp₃.

10. Prelabral chaetae ornamentation (P)—All species have four prelabral chaetae. Most species have ciliate prelabral chaetae, but in T. jacobyi and a few other species, the chaetae are smooth. This character seems to be very stable within species, but it is often left out of species descriptions.

11. Labral chaetae (S)—All species have 554 chaetae on the basal (A), medial (B), and distal (C) rows, respectively (Ojeda and Palacios-Vargas 1983). There is species-specific variation in the relative size of chaetae in row B. In some species, all chaetae in row B are subequal to each other but ostensibly more delicate than chaetae in rows A and C. Other species show differences in the size among elements in row B, usually chaetae B₂ are shorter than B₀ and B₁. This character is often difficult to score, unless the labrum lays flat on the preparation.

12. Ornamentation of labral margin (P)—The distal margin of the labrum may bear 1 + 1 spine-like projections or it may be smooth. The spines may be completely separated or may show different levels of basal fusion, such that they may look Y-shaped.

13. Number of appendages on the sublobal plate of the maxillary palp (S)—The number of appendages is usually 2, but some species have a smooth plate. This character is also very stable within species, but it is often difficult to score.

14. Labial chaetae (P)—The number of posterior chaetae is M₁M₂r(R)EL₁L₂(l₂), but the ornamentation is informative for species identification. In some species, all chaetae, except r, are ciliate, whereas in others, the chaetae are smooth. In addition, L₂ can be a ciliate macrochaeta or smooth microchaeta.

15. Number of chaetae along ventral head groove and postlabial scales (P)—Most species have a uniform cover of scales on the postlabial area, there are few postlabial chaetae, and up to + + 4 chaetae along the ventral groove. In species with few or no postlabial scales, the area is polychaetotic, and the number of chaetae along the groove is greater than + + 4. In almost all species, the posterior chaeta along the ventral groove is inserted far away from the anterior chaetae.

16. Dorsal macrochaeta of body (P)—All interspecific variation in the number of macrochaetae in the species evaluated is limited to the Th. II–III and the inner columns of the Abd IV. The lateral macrochaetae of Abd. IV are of limited diagnostic utility, as the stable chaetae (anterior elements in series D–F) are almost invariant, and the externo-posterior macrochaetae appear to vary according to size or instar of the individual. The chaetae (including macrochaetae) on Abd. II–III show little to no variation between species. The possible exceptions are some chaetae lateral to the trichobothrial complexes, but these chaetae are difficult to score consistently across individuals.

17. Relative position of lateral sensillum and microsensillum on Th II (S)—In most Trogolophysa, the lateral sensillum is inserted...
anterior to the microsensillum, but in Trogolaphysa belizeana Palacios-Vargas and Thibaud and T. jacobyi, the microsensillum is anterior and the sensillum posterior. This character has not been described for most species, and its diagnostic utility beyond the two species mentioned above is unclear.

18. Presence or absence of chaeta a6 on Abd I (S): This chaeta may be present or absent. There is some intraspecific variation in some species, but the presence or absence of the chaeta is stable in most species examined.

19. Number of posterior chaetae of Abd IV (S)—These chaetae are variable and informative. In the Trogolaphysa examined, species have either 7 or up to 13–15 per side.

20. Trochanteral organ (S)—This is a continuous character, and unless the legs are properly and cleanly dissected, the actual number of spines is often difficult to ascertain.

21. Claw complex (P)—This is one of the most important character systems used to diagnose species in Trogolaphysa and Troglopedetes. The claw complex show interspecific variation in the shape of the tenent hair, shape, and number of teeth on the unguiculus, and number, shape, and distribution of teeth on the unguis. Describing the shape of the teeth is often challenging, and an illustration of the claw should always be included with descriptions.

22. Number of distal macrochaetae on anterior face of collophore (S)—These macrochaetae are relatively easy to observe, but smaller or younger individuals have fewer macrochaetae than larger adults.

23. Dens spines (S)—The number of rows of spines on the dens is either 1 or 2 depending on the species; in Troglopedetes, there is a single row, whereas in most Trogolaphysa species there are two rows of spines. The number of spines and their ornamentation is often reported and may be useful to delimit species, but this number varies intraspecifically with specimen size, and the ornamentation appears to vary from smooth to ciliate within individuals along the length of the dens.

24. Mucro (P)—The number of teeth and relative length of the mucro are usually species specific, although in some species both characters show intraspecific variation. The relative length of the mucro is sometimes expressed as a proportion of the length of the dens, but many older descriptions do not report this proportion. Most old descriptions provide figures of the mucro, from which we can derive the relative length of the mucro as the ratio of its length to its width (measured at the juncture with the dens). Using this measure, Trogolaphysa has a relatively short and wide mucro, whereas in Troglopedetes, the mucro is long and narrow. Mucronal teeth have different general distribution in Trogolaphysa and Troglopedetes. Trogolaphysa typically have


3–5 teeth, more or less equally distributed along the length of the mucro, but in *Troglopedetes*, there are 2–11 teeth forming basal and distal groups.

**Species Description.** Genus *Troglopedetes* Absolon, 1907, sensu Thibaud and Najt, 1988

Type species *Troglopedetes pallidus* Absolon, 1907

Scales present on Ant I–II, head, body, and ventral face of furcula; Ant IV subdivided; eyes 0–3; labial setae 12 reduced to a cone; dens with a single row of spines; micro elongate, with distinct groups of basal and distal teeth.

*Troglopedetes absolonii* Bonet, 1931

(Figs. 1–22, Table 1)

**Type Material.** Holotype, slide labeled as “*Troglopedetes absolonii* Bonet 1931; 554N Mina del Capellat, Calpe. Tipo. 29.VIII.1930. F. Bonet; Cat. MNCN Cat. Tipos 9775; MNCN Ent No. Cat. 61163”; locality: Calpe (Alicante), Spain; deposited at MNCN (Madrid, Spain).

**Additional Material.** Spain: Cueva de la Fajara (Canillas de Aceituno, Sierra de Tejeda, Málaga); sample no. 3 (28.IX.2009), 7 specimens in ethanol; sample no. 4 (28.IX.2009), 5 specimens in ethanol; sample no. 5 (06.IX.2009), 15 specimens slide mounted; sample no. 5 (28.IX.2009), 1 specimen slide mounted; sample no. 9 (06.IX.2009), 3 specimens in ethanol; sample no. 11 (06.IX.2009), 2 specimens slide mounted; sample no. 15 (28.IX.2009), 15 specimens in ethanol; sample 142, 1 specimen slide mounted and 16 in ethanol (28.IX.2009); all samples GES-SEM leg. Cueva del Far: sample 2011 08 FT51; A. Sendra leg. All material deposited in MZNA (Pamplona, Spain).

**Distribution.** In addition to the type locality, the species has been reported from eastern reaches of the Prebetico (Jaen and Alicante), la Cova de les Ratetes in the Serra de Corbera (Valencia), and Cova de les Meravelles de Llombai, this last one at the northeastern edge of the Plataforma del Caroig (Valencia) (Gamza 2005). This work extends the distribution of this species between the provinces of Malaga and Cordoba.

**Size.** 1.0–1.8 mm (n = 18); holotype 1.6 mm.

**Color Pattern.** White, without trace of pigment (Fig. 6).

**Scale Distribution.** Ant. I–II, head, body, and ventral face of furcula.

**Head.** Antennae 0.45× as long as body. Ant IV subdivided into two subsegments, without apical bulb, chaetae not forming whorls. Length antennal segments I–IVab as 50 μm, 130 μm, 140 μm, 104 μm, and 116 μm, respectively. Number of clubbed sensilla on antennal segments: 3–5 on Ant I, 15 on Ant II, 15 on Ant III, and 3–6 on distal area on Ant IVa (Figs. 1–5). Eyes absent. Head dorsally (Fig. 11) with six anterior (A0, A2, A3, S1, S2, and S5) macrochaetae; chaetae A2a enlarged. Prelabral chaetae ciliate; labial chaetae smooth; distal margin of labrum smooth. Maxillary palp with subapical and papillate apical chaetae smooth; sublobal plate with two appendages (Fig. 7).

Lateral appendage of labial papilla E as in Fig. 8. Labial triangle (Fig. 9) with M1, M2, EL1, A1, S, M1, E, and L1 ciliate and subequal; r and l2 short and smooth. All postlabial chaetae ciliate (Fig. 10), column I with four chaetae; with seven chaetae between columns I and O (group bound by hatched line in Fig. 10); ventral cervical chaetae 6–7 + 6–7.
Body. Dorsal body chaetotaxy as in Fig. 22. Th. II with four anterior (m1, a5, m2e, and m4) and six posterior (p3 complex) macrochaetae. Th. III with four macrochaetae (a2, p2, p3, and m4). Abd. I chaeta a6 absent, with four posterior microchaetae, probably homologous to m2, m3, m4, and p6. Abd. II with four ciliate chaetae, two macrochaetae (m3 and m5), and one sensillum associated with macrochaeta m3. Abd. III with four macrochaetae (m3, am6, pm6, and p6); chaetae associated with trichobothria smooth or distally ciliate: trichobothrium a2 with two anterior, ciliate chaetae, trichobothrium a5 with one smooth and one ciliate anterior chaetae, trichobothrium m5 with one anterior ciliate seta; sensilla as and d2 present; five additional ciliate chaetae external to lateral trichobothrial complex arranged as in Fig. 22. Abd. IV with two inner macrochaetae (B4, zone 8 and B6, zone 10) and mesochaeta B6p; large lateral macrochaetae correspond to D1, E2, F1, F2, and F3; small lateral macrochaetae as in Fig. 22; lenticular organs rounded, present (3 + 3) in all specimens examined; posterior chaetae absent.

Male Genital Plate. Circinate, without modified chaetae (Fig. 21).

Legs. Trochanteral organ (Fig. 14) with 5–6 medium and 10–11 small, smooth straight chaetae, arranged in “V,” distal chaeta largest. Metathoracic claw complex as in Figs. 12 and 13. Tenent hair acuminate or weakly spatulate (as in holotype), 0.8–0.9 times as long as claw. Unguis thick, with 3–4 inner teeth; paired internal teeth at 55–60% (proximal wings); proximal unpaired tooth at 65–70% inner unguale edge; distal unpaired tooth, when present (as in holotype, and in one leg of one specimen from Malaga), at 75% of inner unguale edge; one external tooth at 25–30%, and lateral teeth at 30% from claw base. Unguiculus lanceolate, with outer margin serrated.

Ventral Tube. Anterior face with 2+2 distal macrochaetae (Fig. 15). Lateral flaps with 5 + 5 chaetae (distal chaeta three smooth and one ciliate, all proximal chaeta ciliate). Posterior face with 9 + 9 long, coarsely ciliate chaetae, and 2 + 2 small spines at posterior area.

Tenaculum. Basally with a single coarsely ciliate chaeta; rami with four teeth (Fig. 16).

Furcula. Proportion manubrium:dens:mucro length = 1:0.85:0.14 (n = 3) (450 μm, 320 μm, and 50 μm, respectively, in holotype). Dorsal face of manubrium with many ciliate chaetae (Fig. 18). Dens (Fig. 19) slightly tapering, with 1 dorsal row of 16–22 smooth, stout spines, and intercalated chaetae following the pattern: 5–11/i/2/i/1/i/1/i/1/1/i/1/i/1/i/1/2–i, with a maximum of 22 spines (chaetae in subscript) (22 in holotype), and 2 external rows of chaetae 3× as long as spines (Fig. 17). Mucro (Fig. 20) stout, basally with 1 large and 2–4 small teeth, sometimes accompanied by minute lateral basal serrations; distally with 3 blunt teeth.
Remarks. The small differences observed between the specimens from Valencia and Malaga do not justify the recognition of a different species. The group of blind *Troglolopedetes* comprises 26 species, of which 13 have a single row of dental spines. This group is further reduced to seven species, if only species having more than three basal mucronal teeth are considered. Among the seven species with more than three basal mucronal teeth, three have three distal teeth: *Trogl. absoloni*, *Troglopedetes machadoi* Delamare-Deboutteville 1946 (Portugal) and *Troglopedetes orientalis* Cassagnau and Delamare-Deboutteville 1955 (Lebanon). The unguiculus of *Trogl. absoloni* is externally serrate, whereas in the other two species, it is smooth. In addition, *Trogl. orientalis* carries 27–30 dental spines.

*Troglopedetes ildumenensis* Soto-Adames, Jordana and Baquero n. sp. (Figs. 23–38, Table 1)

**Etymology.** The name of the species refers to Ildum, the original roman name for the municipality of Cabanes, near where the cave in which the new species was collected is located.

**Type locality.** Spain: L’avenç del Mas de la Cova, Cabanes (Castellón). Coordinates (ED 50): 31T0251173/4445105, (GSW84: N 40.11951 E 0.08001), 304 m.

**Material Examined.** Spain: Holotype, one female on slide, 27.XII.2011, code Ta-1-13-3(2); two paratypes on slides, codes Ta-1-13-3(1) and Ta-1-13-3(3); and 21 paratypes in ethanol, sample Ta-1-13-3; F. Fadrique leg. All specimens, except for two paratypes deposited in the MCNB (Barcelona, Spain), are deposited in MZNA (Pamplona, Spain).

**Size.** 1.1–1.5 mm.

**Color Pattern.** White, without trace of pigment.

**Scale Distribution.** Ant. I, head, body, and ventral face of furcula.

**Head.** Antennae 0.42× as long as body. Ant IV subdivided into two subsegments (Figs. 23 and 27), without apical bulb, chaetae not forming whorls. Length Ant. I–IV (Fig. 23) as 80 μm, 170 μm, 130 μm, 110 μm, and 150 μm, respectively, total 640 μm (holotype). Ant. I–III with 2–5, 25–30, and 25–30 blunt sensilla, respectively (Figs. 24–26).
Eyes absent. Head dorsally (Fig. 28) with seven anterior (A₀, A₂, A₃, S₁, S₂, S₃, and S₅) and six posterior (Pa₂, Pa₃, Pa₅, Pₚ₃, Pₚ₄, and Pₚ₅) macrochaetae. Microchaetae distributed as in Fig. 28. Prelabral chaetae ciliate; labral chaetae smooth; distal margin of labrum smooth. Maxillary palp with subapical and papillate apical chaetae smooth; sublobal plate with 1 appendages. Lateral appendage of labial papilla E as in Fig. 29. Labial triangle with M₁,M₂,E,L₁; M₁, M₂, E, and L₁ ciliate and subequal; r and l₂ short and smooth (Fig. 30). All postlabial chaetae ciliate. Postlabial column I with 6 chaetae, field between columns I and O with 18 chaetae (Fig. 31); ventral cervical chaetae 4+4.

**Body.** Dorsal body chaetotaxy as in Fig. 38. Th. II with four anterior (a₅, m₁, m₂, and m₄) and six posterior (p₁ complex) macrochaetae. Posterior microchaetae normal. Th. III with four macrochaetae (a₂, p₂, p₃, and m₄); scale rounded, about 40 μm in wide (Fig. 34). Abd. I chaeta a₀ absent, with three posterior microsetae (m₁, m₄, and p₃). Abd. II with five ciliate chaetae, two macrochaetae (m₁ and m₃) and one sensillum associated with macrochaeta m₃. Abd. III with four macrochaetae (m₁, am₆, pm₆, and p₉); chaetae associated with trichobothria smooth or distally ciliate: trichobothrium a₂ with three ciliate chaetae; trichobothrium a₃ with one smooth and three ciliate anterior chaetae, trichobothrium m₁ with one ciliate anterior seta; sensillum as present, sensillum d₂ and chaeta p₂ absent. Abd. IV with two inner macrochaetae (B₄, zone 9 and B₆, zone 10) and mesochaeta B₆p; large lateral macrochaetae correspond to E₂, E₃, F₁, F₂, and F₃; small lateral macrochaetae as in Fig. 38; lenticular organs oval, present (3 + 3) in all specimens examined; posterior chaetae absent.

**Legs.** Trochanteral organ (Fig. 33) with 11 spines in “V” formation and 6 other small spines. Metathoracic claw complex as in Fig. 32. Tenent hair weakly spatulate (as in holotype), 0.5–0.8 times as long as claw. Unguis thick, with three inner teeth; paired internal teeth at 45–50% (proximal wings), basal teeth enlarged, asymmetric, longest basal tooth reaching unpaired tooth; unpaired tooth at 65–70% of inner ungual edge, almost as large as smallest of basal teeth; external and lateral teeth present. Unguiculus lanceolate, with outer margin serrated.

Figs. 45–50. Tragolaphysa quisqueyana n. sp. Open circles, macrochaetae; close circles, microchaetae; open square with dot, bothriotricha; black squares, fan-shaped setae; open circles with cross bar, pseudopores. (45) Complete dorsal chaetotaxy of fourth abdominal segment. (46) Detail of chaetae near anterior bothriotrichal complex. (47) Lateral chaetotaxy of fourth abdominal segment in another individual. (48) Outer maxillary lobe and pleural setae. (49) Metathoracic leg claw complex. (50) Two aspects of mucro.
Ventral Tube. Anterior face with 3 ± 3 distal macrochaetae. Distal lateral flaps with 4 ± 4 chaetae (three smooth and one ciliated distally). Posterior face with 18–19 long, coarsely ciliate chaetae.

Tenaculum. As in *Trogl. absoloni*.

Furcula. Proportion manubrium:dens:mucro length = 1:1.16:0.22. Dorsal face of manubrium with ciliate chaetae (Fig. 37). Dens tapering slightly, ventrally scaled, with a dorsal row of 13–16 smooth, stout spines with intercalated chaetae following the pattern: \(4-5/1 `/1 `/1 `/1 `/1 `/1 `/1 `/1 `/1 `/1 `/1 `/1 `/1 `/1 `/1 `/1 `/1 `/1 `/2 \) (chaetae in subscript), and large chaetae, becoming larger distally (Fig. 35). Mucro elongate, with three distal and two basal external subequal blunt teeth (Fig. 36).

Remarks. *Trogl. ildumensis* n. sp. belongs to the same group as *Trogl. absoloni*, in lacking eyes and having a single row of spines. Only *Troglopedetes cavernicola* Delamare-Debouteville 1944 (Portugal), *Cyphoderopsis nepalensis* (Wilson 1982) (Nepal), *Cyphoderopsis nayakensis* (Stach 1960) (Afghanistan), *Troglopedetes pallidus* Absolon 1907 (Austria), and *Troglopedetes rasendranis* Bhattacharjee 1985 (India) have a mucro similar to the new species. The poor quality of the descriptions, by current standards, for the species listed above yield few diagnostic characters. *Trogl. ildumensis* n. sp. is similar to *C. nayakensis* and *Trogl. pallidus*, in having a relatively short mucro (dens/mucro ratio > 4), but it can be distinguished from all other member of the group by the presence of a clearly serrate unguiculus.

Genus *Trogolaphysa* Mills, 1938 sensu Thibaud and Najt, 1988

Type species *Trogolaphysa maya* Mills, 1938

Scales present on Ant I-II, head, body and ventral face of furcula; Ant IV not subdivided; eyes 0–8; labial setae L2 normal acuminate; dens with 1–2 rows of spines; mucro rectangular short or elongate, with teeth evenly distributed.

*Trogolaphysa quisqueyana* Soto-Adames, Jordana and Baquero n. sp. (Figs. 39–50, Table 1)

Etymology. The epithet refers to Quisqueya, the native-American (Taino) name for the island of Hispaniola.
Type locality. Dominican Republic: Independencia, Sierra de Bahoruco, Loma del Toro, 5.3 km SW El Aguacate, N 18.28778, W 71.71278, 2,316 m, Pinus L. and Garrya Douglas montane forest, DR43273, 29–30 March 2004, C. Young, R. Davidson, J. Rawlins. Holotype, slide mounted, deposited at CMNH.

Material Examined. Dominican Republic: Independencia, Sierra de Bahoruco, north slope, 13.5 km SE Puerto Escondido, N 18.25221, W 71.55471, 1,789 m, ecotonal Pinus grassland, DR41173, 24–26 March 2004, R. Davidson, J. Rawlings, C. Young, C. Núñez, M. Rial, 3 on slides, 5 in alcohol. La Vega, Cordillera Central, Valle Nuevo Station, 5.2 km ESE Valle Nuevo, N 18.78151, W 70.61192, 2,288 m, slope on open pine forest, DR23172, 23 May 2003, C. Young, J. Rawlins, C. Núñez, R. Davidson, P. Acevedo, 3 on slides. Independencia, Sierra de Bahoruco, north slope, 13.5 km SE Puerto Escondido, N 18.20907 W 71.53011, 1,807 m, broad leaf Pinus dens woodland, DR41273, 24–26 March 2004, R. Davidson, J. Rawlings, C. Young, C. Núñez, M. Rial, 2 on slides, 18 in alcohol. Two paratypes deposited at INHS, all other material deposited at CMNH.

Size. Up to 2.2 mm.

Color Pattern. Background color creamy white (Fig. 43), brownish purple pigment uniformly distributed on antennae, mouth cone, whole


Fig. 65. Campylotborax sabanus. Chaetotaxy of third abdominal segment.

Legs. Trochanteral organ with up to 28 spine-like chaetae. Metathoracic claw complex as in Fig. 49. Tenent hair spatulate, proportion inner edge of claw: tenent hair = 0.83. Smooth posterior chaetae on metathoracic legs 0.83× (0.78–0.87) as long as unguiculus. Unguis with four inner teeth: basal teeth asymmetric, one larger, larger basal tooth inserted at 43% of inner unguinal edge; proximal unpaired tooth shorter than basal paired teeth, inserted at 67% of inner edge; distal unpaired tooth smallest of all inner teeth, inserted at 85% of inner edge. Outer tooth ending on basal quarter of outer unguinal edge. Unguiulus lanceolate, with outer margin smooth.

Ventral Tube. Anterior face with 2+2 distal macrochaetae, other chaetae not seen.

Tenaculum. As in Trogol. absoloni

Furcula. Proportion manubrium:dens:muacro length = 1:1:0.07 (n = 7).

Dens with 2 rows of ciliate spines: inner row with 35–42 spines; outer row with 25–28 spines. Muacro with four short, stout teeth (Fig. 50), basal outer tooth reaching to at least half the length of basal inner tooth; macro 3.1–3.5× as long as width of dens tip.

Remarks. T. quiquevyna n. sp. is unique among species with 6–8 eyes and spatulate tenent hair in having six anterior dorsal head macrochaeta, four chaetae in eye valley, and outer and lateral unguinal teeth ending on basal fourth of outer margin. Among species for which the dorsal chaetotaxy is known, the new species is most similar to Trogolaphysa riopedrensis (Mari Matt 1987), from which it can be distinguished by the characters listed above, and by having the basal mucronal teeth almost aligned instead of sequential.

Trogolaphysa carpenteri (Denis 1925), Trogolaphysa berlandi (Denis 1925), Trogolaphysa separata (Denis 1933), Trogolaphysa distinguisenda (Denis 1931), and Trogolaphysa hirtipes (Handschi 1924) have been reported as having 6–8 eyes and spatulate tenent hair, but they are otherwise so poorly described by current standards that separation from the new species is provisional. T. carpenteri seems to differ from the new species in having only three inner teeth on the unguis and, if Yoshii’s (1988) material from Mexico actually represents T. carpenteri, by having only two anterior dorsal head macrochaeta (A0 and A2) and lacking mesothoracic macrochaetae. Trogolaphysa berlandi has only one row of dental spines; T. separata has the outer and lateral teeth of the unguis inserted on the distal half the dorsal margin, whereas T. hirtipes has the basal unguinal teeth inserted near the basal quarter of the claw and the manubrium ostensibly longer than the dens.

Trogolaphysa sauron Soto-Adames, Jordana and Baquero n. sp.

(Figs. 51–59, Table 1)

Etymology. Refers to the resemblance of the dorsal pattern on the fourth abdominal segment with the helmet of Sauron, the character in Lord of the Rings, as represented in Peter Jackson’s 2001 film.


Material Examined. Martineau: same as holotype, 3 on slides, and 40 (mostly small juveniles) in alcohol. Two paratypes deposited at INHS, all other material deposited at MNHN.

Size. Up to 1.9 mm.

Color Pattern. Background color light yellow to white, purple pigment distributed according to two general patterns, one dark, one light (Figs. 51 and 52). Pattern in light individuals clearly representing a subset of pattern in dark individuals and not a fundamentally different pattern.

Scale Distribution. Ant. I–II and base of Ant. III, head, body, and ventral face of furcula.

Head. Antennae up to 0.66× as long as body. Ant. IV not subsegmented, with well-organized whorls of chaetae on dorsal face, ventrally whors indistinct; subapical organ inserted very close to tip of segment, sensillum capitato, but small, almost without pedicel, and translucent, seemingly absent in most mounted specimens; guard sensillum apically

Scale Distribution. Ant. I–II and base of Ant. III, head, body, and ventral face of furcula.

Head. Antennae up to 0.66× as long as body. Ant. IV not subsegmented, with well-organized whorls of chaetae on dorsal face, ventrally whors indistinct; subapical organ inserted very close to tip of segment, sensillum capitato, but small, almost without pedicel, and translucent, seemingly absent in most mounted specimens; guard sensillum apically

legs and most of Abd. 4. Pigment most intense on coxae and posterior margin of Abd. 4.

Scale Distribution. Ant. I–II and base of Ant. III, head, body, and ventral face of furcula.

Head. Antennae up to 0.66× as long as body. Ant. IV not subsegmented, with well-organized whorls of chaetae on dorsal face, ventrally whors indistinct; subapical organ inserted very close to tip of segment, sensillum capitato, but small, almost without pedicel, and translucent, seemingly absent in most mounted specimens; guard sensillum apically
constricted. Sense organ of Ant. III normal rods. Eyes 8+8, but appearing as 6+6 (Fig. 55), eyes G and H greatly reduced and often not visible, even at high magnification; eye valley with 4 ciliate chaetae, as in T. quisqueyana (Fig. 39). EOS not seen. Head dorsally (Fig. 55) with three anterior (A 0, A 2, and M 2) and one posterior (P a2) macrochaetae. Prelabral chaetae ciliate. Labral chaetae smooth. Distal margin of labrum with 1+1 small seta-like spines. Basal pleural chaeta coarsely ciliate, distal pleural chaetae short and smooth as in T. quisqueyana n. sp. (Fig. 48). Maxillary palp with subapical and papillate apical chaetae smooth; sublobal plate with two appendages. Labial triangle as M, M 0, EL, L, A 1, 5; anterior chaetae smooth; all posterior chaetae, except r, ciliate; r stout and smooth as in Troglo. absoloni (Fig. 9); L 2 as long as or slightly shorter than E. All postlabial chaetae ciliate. Postlabial column I with four chaetae, ventral cervical chaetae four; with eight chaetae in field between columns I and O.

**Body.** Thoracic chaetotaxy as in Fig. 53: Th. II with one anterior (a 0) and three posterior (p 1 complex) macrochaetae; Th. III without macrochaetae. Abd. I chaeta a 0 present; four posterior microchaetae present (m 2, m 3, m 4, and p 6). Abd. II with two macrochaetae (m 3 and m 4) and one sensillum associated with macrochaeta m 3; trichobothria m 2 and a 5; ciliate chaetae. In Abd. III with four macrochaetae (m 2, m 13, m 14, and p 6) associated with trichobothrial complexes fan shaped; trichobothrium m 2 with two anterior chaetae, trichobothrium a 5 with six anterior chaetae, trichobothrium m 3 with three anterior seta; sensilla as and d 2 present; additional ciliate chaetae external to lateral trichobothria. In Abd. IV (Fig. 56) with three inner macrochaetae (A 0, zones 6–7, A 0, zone 9; B 0, zone 10) mesochaeta B 0 present; column Te with 1 microchaetae and 1–2 macrochaetae external to lateral trichobothrial complex arranged as typical for Troglophyss (cf. Soto-Adames and Taylor 2013, Fig. 16).

**Male Genital Plate.** Circinate, as in Trogol. absoloni.

**Legs.** Trochanteric claw complex as in Fig. 58. Tenent hair spatulate, proportion inner edge of claw: tenent hair = 1:0. Unguis with four inner teeth: basal teeth asymmetric, one tooth longer and more slender than other (Fig. 59), longest tooth inserted at 25% of inner ungual edge; unequal teeth minute and subequal, proximal unpaired tooth often present as a simple mound, without a discernible tooth; proximal unpaired tooth inserted at 51% of inner edge, distal unpaired tooth inserted at 84% of inner edge. Outer tooth ending on basal quarter of outer ungual edge, lateral teeth ending on basal half. Unguiculus truncate (Fig. 57), outer margin smooth or with 2–3 small teeth, inner margin with one tooth.

**Ventral Tube.** Anterior face with 3+3 distal macrochaetae, other chaetae not seen.

**Tenaculum.** As in Trogol. absoloni.

**Furcula.** Proportion manubrium:dens:muco length = 1:1:0.07 (n = 3). Dens with 2 rows of ciliate spines: inner row with 32–38 spines; outer row with 20–23 spines. Mucro with 4 short, stout teeth (Fig. 54), mucro 2× as long as width of dens tip.

**Remarks.** T. sauron n. sp. can be distinguished from all other members of the genus by its unique color pattern and combined presence of a truncate unguiculus, three mesothoracic macrochaetae, and needle-shaped paired ungual teeth. Among species with known chaetotaxy only T. jacobyi, T. belizeana, Troglophyss bessoni Thibaud and Najt 1989 and Troglophyss cotopaxiana Thibaud and Najt 1989 have three posterior macrochaetae on Th. II: the first three species are troglo-morphs, with acuminate tenent hair and without eyes or pigments, whereas T. cotopaxiana is white, without pattern, has a single row of dental spines, a five-toothed mucro and small fin-like inner ungual teeth. Among species for which the chaetotaxy is unknown, Troglophyss sauron n. sp. is similar to Troglophyss haitica (Palacios-Vargas et al. 1985), in having needle-shaped inner ungual teeth, but the two species differ in almost all other general morphological characters. Troglophyss millsi Arlé 1939 and Troglophyss tijucana Arlé and Guimarães 1979 are the only other members of the genus with truncate unguiculus, but they differ from T. sauron n. sp. in color pattern, in having only two eyes and in that the paired ungual teeth are fin shaped.

**Dorsal Chaetotaxy of Troglopedetes, Trogolaphysa, and Campylothorax.** The discussion that follows is based on observations of species described above (Table 1), those described by Soto-Adames and Taylor (2013), and when possible, Deharveng (1987, 1988, 1990), and Deharveng and Gers (1993). Miura and Dallai (1980) and Miura (1993, 2002) present drawings for Campylothorax and Troglophyss, but these data were not incorporated because the stylized drawings make it difficult to determine homologies, even in comparisons with C. sabanus and T. jataca. In the descriptions below, we first identify conserved elements followed by elements unique to each genus.

**Head (Figs. 11, 28, 55, and 60).** When compared with other scaled Entomobryoidea, the three genera have a reduced chaetotaxy. All species lack chaeta M 6, S 0, but most characteristically, P 3 is also absent. The dorsal chaetotaxy of the head has the same organization in Troglophyss and Troglopedetes, whereas in Campylothorax, some aspects of the organization of elements in series A are different.

In the three genera, chaeta A 1 is always an acuminate, coarsely ciliate microchaeta, but all other members of the series can develop into macrochaetae. In Troglopedetes and Troglophyss, chaetae A 2 and A 3 are inserted well posterior to A 0 and A 2, more or less in line with the most posterior chaeta in row an, whereas in Campylothorax, chaetae A 0, 3 form a compact group near the point of inflection of row an (cf. Figs. 11, 55, and 60). Campylothorax has 1+1 macrochaetae external to A 3 that could be interpreted as either A 4 or A 5. Troglophyss and Troglopedetes also have microchaetae that can be interpreted as A 4 or A 5, whereas in Troglopedetes, these chaetae appear to be stable and identifiable, and in Troglophyss they are unstable, varying between individuals and asymetrically within individuals.

In Troglophyss and Troglopedetes, series M includes up to two chaetae here considered homologous to M 2–3. Chaeta M 2 is often developed into a macrochaeta. Series M is absent in Campylothorax.

All species have at least four posterior chaetae in series S (S 2–5). Troglophyss and Troglopedetes also carry anterior chaeta S 1, which is absent in C. sabanus (Fig. 60), but lacking chaeta S 0, which is present in that species. The pattern of macrochaetae differs in the three genera. In Troglophyss, only S 1 and S 4 are transformed into macrochaetae, and in Troglopedetes S 1, S 2, S 4 (some species from Thailand only), and S 5 can be macrochaetae, whereas in Campylothorax, all posterior members of the series, except S 0, are transformed into macrochaetae. Microchaeta S 0 in C. sabanus may represent a posteriorly displaced M 1.

Series P 5 of all species considered here includes chaetae P 5 and P 8, whereas P 3 is absent. Row Pa in Troglophyss and Troglopedetes includes chaetae P 5, P 3, P 8, and P a5, but in Camylothorax, only macrochaetae P 1 and bothriotrix P a5 remain. P 2 and P 3 are macrochaetae in all Troglopedetes but microchaetae in Troglophyss. Chaeta P m 3 is the only member of row Pm present in Troglophyss and Troglopedetes, and it is often transformed into a macrochaeta in both genera. The number of chaetae in row Pp is unclear, but P 3 appears to be a microchaeta in Troglophyss and a macrochaeta in Troglopedetes.

**Mesothorax (Figs. 22, 38, 42, 53, and 61).** Only chaetae P 1–3 are conserved in the same general spatial distribution in the three genera. In Troglophyss and Troglopedetes, the homology of chaetae a 5, m 2, m 4, and the p 3 complex seems uncontroversial. In the species studied, p 3 forms a complex of either three or six macrochaetae, similarly arranged in both genera, and p 1 appears to be absent. It is likely that the p 3 complex includes p 1–3. The six macrochaetae could be explained by a duplication of p 1–3 (as p 1, p 1i, p 2, p 2i, p 3, and p 3i). The presence of
microchaetae p1–2 in Trogolaphysa giordanoae, which has six macrochaetae in the p3 complex, seems to invalidate the previous conclusion. However, Soto-Adames and Taylor (2013) have suggested that microchaetae that p1–2 in T. giordanoae is secondary. Clarification of the homology of these chaetae requires further analysis. In C. sabanus (Fig. 61), the inner posterior complex includes seven (rarely eight) macrochaetae in a peculiar arrangement and their homology is uncertain. Assuming that the chaetae conserved in Trogolaphysa and Troglopedetes are also conserved in C. sabanus, it is possible that the inner macrochaetae in the posterior complex comprise six chaetae in the p1 complex plus a posteriorly displaced m2s.

Unique conditions of the mesothoracic chaetotaxy include the presence in Troglopedetes from Spain of chaeta m1, transformed into a macrochaeta associated with the mesothoracic collar; presence of m2, in T. jacobyi; and absence of a1 and m1 in C. sabanus.

Metathorax (Figs. 22, 38, 42, 53, and 61). The chaetotaxy of the three genera is considerably reduced. All species have only four inner postero medial chaetae, but their relative insertion varies according to whether they are micro- or macrochaetae, and the real identity of the elements is unclear. Following Soto-Adames and Taylor (2013), in species like T. quisqueyana n. sp. and T. sauron n. sp., which carry only microchaetae, the chaetae appear to correspond to a2, p2, p3, and m4 (Fig. 43). This arrangement is retained when only one chaeta (usually p1) is transformed into a macrochaeta. When three inner chaetae are macrochaetae, as in the two species of Troglopedetes, T. giordanoae and T. belizeana, the two posterior chaetae move closer together and the anterior migrates posteriorly to form a triangle (Fig. 22). In Troglopedetes, the triangular pattern is retained even when putative m4 is transformed into a macrochaeta. Campylothorax (Fig. 61) carries four macrochaetae, but they are arranged into a column. The identification of macrochaetae in C. sabanus is suggested by the arrangement of macrochaetae in Trogl. idludensis n. sp. (Fig. 38).

A lateral posterior chaeta is present in Trogl. absoloni and all Troglophysis studied. This chaeta is absent in Trogl. idludensis n. sp. and C. sabanus.

First Abdominal Segment (Figs. 22, 38, and 63). The chaetotaxy of this segment is reduced to such extent that the identity of the chaetae is a matter of speculation. All species have three posterior chaetae probably homologous to m3, m4, and p4. Most species, including C. sabanus, also have m2 (Fig. 63). Most species of Troglophysis also have a8 inserted near the lateral microsensillum (Fig. 59 in Soto-Adames and Taylor 2013).

Second Abdominal Segment (Figs. 22, 38, and 64). The chaetotaxy of this segment is also considerably reduced. The chaetae associated with trichobothrium m2 are the same in the three genera, but the chaetae external to trichobothrium a8 differ. Chaetae a1, m3c, p4, and m4 are absent. Chaetae associated with m2 are 2–3 fan-shaped or ciliate supplementary chaetae, sensillum as and macrochaeta m3. The chaetae associated to trichobothrium a8 are the 2–4 anterior supplementary fan-shaped chaetae and macrochaeta m3. In all Troglophysis and Trogl. absoloni (Fig. 22), the chaetae external to a8 are a8, m6c, and p4, but in Trogl. idludensis n. sp. (Fig. 38) and C. sabanus (Fig. 64), homologies are unclear.

Third Abdominal Segment (Figs. 22, 38, and 65). All species have the same chaetotaxy: trichobothrium a2 complex has two fan-shaped supplementary chaetae, sensillum as and macrochaeta m1; trichobothria a3 and m3 complex have 4–9 fan-shaped supplementary chaetae and three latero-posterior macrochaetae. All species, except T. jacobyi, have sensillum d3 inserted at the level of the middle macrochaeta. There are two other columns of chaetae of uncertain homology lateral to the macrochaetae; the inner column includes three microchaetae in Trogolaphysa and Troglopedetes and two in C. sabanus (Fig. 65), the outer column includes three meso- or small macrochaetae in all species.

Fourth Abdominal Segment (Figs. 22, 38, 44, 56, and 62). The chaetotaxy of Abd. 4 includes three (A, B, and C) more or less organized columns internal to the bothriotrichal complex (column T) and three (D, E, and F) columns external to the complex. Common elements to the three genera are the presence of macrochaetae B3, D3, E3, F1, and F2. Trogolaphysa and Troglopedetes share secondary posterior mesochaeta B6p and secondary trichobothrium D4. Campylothorax (Fig. 62) lacks chaeta B6p and the secondary trichobothrium appears homologous to T6. In addition, C. sabanus differs from Trogolaphysa and Troglopedetes in having a column of, presumably, secondary chaetae running along the middle of the segment, ending anteriorly on the medial unpaired macrochaeta, and in having all macrochaetae in columns A and B displaced toward the posterior margin of the segment and inserted in zone 10.

In Troglopedetes and Trogolaphysa, the determination of the actual number of normal microchaetae in the central area of the segment (area between bothriotrichal complexes) is difficult. The central area carries many sensilla-like chaetae with sockets indistinguishable from those of normal chaeta, and without the shaft, it is usually impossible to categorize the organ. Most sensilla are inserted near a scale, whereas chaetae are not, but this is not always the case. This problem is particularly acute in zone 7, where microchaetae are very short and their placement seems to be determined by the anterior elongation of the segment in each species.

Inner columns A, B, and C comprise 3–4, 2–4, and 4 chaetae, respectively, whereas in each of the three external columns (D, E, and F), only the three anterior elements can be unambiguously identified. Most of the variation in the number of chaetae in columns A and B is attributable to the troglomorphic species. All surface species and T. giordanoae (collected in a cave but not troglomorphic) have three chaetae in columns A and B, whereas the two troglomorphic Trogolaphysa from Belize have 3, 2 chaetae and the Troglopedetes from Spain have 3, 4, and 4, 3 chaetae.

Most inner chaetae in Trogolaphysa and Troglopedetes show considerable lateral and antero-posterior displacement in interspecific comparisons. There is a trend in members of these two genera for chaetae to be displaced toward the posterior margin of the segment. This trend is most evident in Trogolaphysa, where, e.g., A5 is a macrochaeta inserted in zone 10, whereas in the two species of Troglopedetes, A5 is a microchaeta inserted in zone 9.

Discussion
Homology and Nomenclature of Chaetotaxy in Troglopedetes, Trogolaphysa, and Campylothorax. Nomenclature systems developed by Szepytki (1979) and Soto-Adames (2008) for head and body chaetotaxy of Entomobryidae were predicated on the basis of putative homology of the elements, as determined by studies of the postembryonic development. Three factors confuse homology determination of individual elements: plurichaetosis, extreme reduction in element number, or extensive insertion displacement. It is evident that the nomenclature systems become difficult to apply as the number of chaetae departs in either direction from the number found in the first instar. As the number of elements of the idiochaetotaxy increases, the insertion of each individual chaeta is displaced until it becomes impossible to identify basic elements. This is the condition found in most genera lacking scales such as those in tribes Orchesellini, Entomobryini, Cremastocephalini, and Callyntrini (e.g., Mari Mutt 1979, Mitra 1993, Potapov and Kremenitsa 2008, Jordana 2012). At the other extreme are species with dense scale cover and such reductions in idiochaetotaxy of some segments that appropriate landmarks are lacking to identify the elements that remain. This is evident in the genera Trogolaphysa, Troglopedetes, and Campylothorax and in some Lepidocyrtini (Metaspinella, some Pseudosinella, Mari Mutt and Grinia 1983, Mari Mutt 1986, Soto-Adames 2002), some Lepidosira (Seirini, F.N.S.A., unpublished data), and Cyphoderus (Cyphoderini, Szepytki 1979). Displacement of individual elements introduces ambiguity in homology determination because it is unclear if the displaced element represents precisely that or if it represents a secondary chaeta sprouted during postembryonic development.
In the genera of Paronellidae considered here, ambiguity in homology determination is brought about by extreme reduction and displacement of idiochaetotaxy. The effect of the interaction between these factors is most evident on the inner fields of the meso- and metathorax, and first and fourth abdominal segments. The inner chaetotaxy of the second and third abdominal segments is reduced to such extent that there is little to homologize. The number of chaetae is greatly reduced in all species, and when transformed into macrochaetae, individual elements are displaced to form clusters.

The chaetotaxy of the fourth abdominal segment is particularly interesting, as some elements seem to be missing in some species, whereas others are displaced along longitudinal and transversal tracks in interspecific comparisons. Soto-Adames and Taylor (2013) assumed that fourth abdominal segment inner secondary chaetae are rare and considered the eighth posterior chaetae in columns A and B to be primary. Based on these assumptions, Soto-Adames and Taylor (2013) named chaetae sequentially, from posterior to anterior, irrespective of relative insertion position. This study follows Jordana and Bagues (2005) and Jordana (2012) in assuming that secondary chaetae are common and homology is determined by insertion location not by simple sequence in a series. Determination of which of these two systems more faithfully reflects the evolution of chaetotaxy in Paronellidae and Entomobryidae will require additional analysis. Diptera taxonomists have dealt with problems of homology determination by studying patterns of chaeta nerve connection changes during postembryonic development (Belkin 1960, Harbach 1991, Craig 2005). Research on patterns of nerve connections may also prove valuable to reach consensus on a nomenclature system for entomobryoid springtails. However, irrespective of whether the homology of individual chaetotaxy elements can be established unambiguously, their diagnostic value is unquestionable. The current lack of nomenclature consensus makes evident that descriptions referring to chaetae by name only are incomplete if not accompanied by illustrations displaying the precise spatial organization of the chaetae.

**Trogopedetes and Trogolaphysa Have the Same Chaetotaxy Organization.** The distinction between Trogolaphysa and Trogopedetes hinges on the presence or absence of a median division on the fourth antennal segment and micro morphology (Thibaud and Najt 1988). It was suggested (Mitra 1993, Soto-Adames and Taylor 2013) that chaetotaxy could provide additional diagnostic characters to separate these genera, but the data presented here indicate otherwise. Neither the number of chaetae nor the pattern of body macrochaeta displays diagnostic differences between the genera. Only the presence of head macrochaetae Pa2 and Pa3 in Trogopedetes and their absence in Trogolaphysa appears to be diagnostic, but this observation needs to be confirmed by examination of more species from each genus.

**Trogopedetini Is a Junior Synonym of Paronellini.** Genera in subfamily Paronellinae have been grouped into five tribes, in part based on common aspects of the chaetotaxy (Mitra 1993). Members of tribe Cremastocephalini differ from other genera in having scales, members of Callyntrurini have fusiform scales and abundant macrochaetotaxy, whereas members of Bromancanthini, Paronellini, and Trogloopetini have rounded scales and reduced or no macrochaetotaxy. The tribe Bromancanthini is an amalgam of seemingly unrelated genera and probably does not withstand detailed phylogenetic scrutiny (Mitra 1993). Paronellini and Trogopedetini, on the other hand, form a homogeneous group where even generic diagnoses have been, until recently, unclear (Thibaud and Najt 1988, Soto-Adames and Taylor 2013).

Soto-Adames et al. (2008) included seven genera in Trogopedetini, but three genera have been synonymized: Thibaud and Najt (1988) synonymized Dicranocentruge with Trogolaphysa and Trichorypha with Paronella, whereas Deharveng and Bedos (1995) synonymized Microparonella Carpenter with Trogopedetes. These nomenclatorial acts leave only Trogopedetes, Trogolaphysa, Cypheotheropsis, and Troglobius Palacios-Vargas and Wilson 1990, assigned to Trogolophedi. Troglobius is a small genus of cave-adapted species with uncertain phylogenetic affinities, characterized by peculiar macro and absence of spines on dens. Tribe assignment for Troglobius will have to await detailed description of the dorsal chaetotaxy of the species. The other three genera assigned to Trogopedetini sensu Mitra (1993) harbor Paronella-like species with reduced eye number, many of which are troglomorphic, whereas the three genera in tribe Paronellini sensu Mitra (1993) include species with 6–8 eyes-most of which live in surface habitats and lack adaptations to subterranean life. Analysis of species in these tribes (Soto-Adames and Taylor 2013) suggests that Trogopedetini represents a group of specialized forms related to species in Paronellini, the same way Pseudosinella Shaffer relates to Lepidocyrtus Bourel or Sinella Brook to Entomobrya Rondani (Yoshii, 1988).

Evidently, separation of Trogopedetes and Trogolaphysa in two different tribes is unnecessary and makes Trogopedetini polyphyletic. The synonymization of Dicranocentruge with Trogolaphysa (Thibaud and Najt 1988) based on characters of the antennae and furcula was the first step in the fusion of the tribes. Soto-Adames and Taylor (2013) provided additional evidence for the synonymy of Dicranocentruge and Trogolaphysa by showing that species assigned to both genera have EOS and identical chaetotaxy organization. Jantarit et al. (2013) have also shown that the organization and level of reduction of the chaetotaxy in Cypheotheropsis is almost identical to that in Trogolaphysa. The analysis presented here adds evidence in support of a common origin and close relationship between Trogopedetes, Trogolaphysa, and Cypheotheropsis by highlighting the similarity in chaetotaxy organization in these three genera when compared with Campylothorax.

On the basis of the evidence presented above, we propose the synonymization of Trogopedetini and Paronellini, with a new circumscription of Paronellini as follows:

**Diagnosis of Paronellini.** Paronellinae with 0–8 eyes, basic chaetotaxy composed of hyaline, denticulate, apically rounded scales present dorsally on head, body, and ventrally on manubrium and dens; idiochaetotaxy reduced, head chaeta P5A absent, metathorax with four inner chaetae, first abdominal segment with 2–3 inner chaetae; second and third abdominal segments each with one inner macrochaeta and one inner sensillum, without inner microchaetae in addition to supplementary chaetae associated with trichobothria; fourth abdominal segment with three trichobothria.

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4 While this article was in press, Zeppellini et al. (2014) transferred the genus Troglobius to subfamily Cyphoderininae.