

Article

Synopsis of Neotropical *Trogolaphysa* Mills, 1938 (Collembola: Paronellidae) with Reduced Eye Number, and Description of Two New Troglobiontic Species from Belize [†]

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[†] urn:lsid:zoobank.org:pub: urn:lsid:zoobank.org:pub:883DCD4E-0503-4D27-BAF3-64C04A0987F7;
urn:lsid:zoobank.org:act: urn:lsid:zoobank.org:act:0DDCFF02-87B2-4C3F-9F39-6F5E1F753765,
urn:lsid:zoobank.org:act:486DDBFC-1658-439A-BF70-FDD58B1AC22F.

Abstract: The genus *Trogolaphysa* comprises 81 described species distributed across the Neotropical and Afrotropical regions. In the Americas, just over half of the species found in subterranean habitats have a reduced eye number (0–5 eyes). Subterranean species are of interest as models to study the evolution of morphological adaptations. Many subterranean species of *Trogolaphysa* were described before the introduction of chaetotaxy as a diagnostic tool and thus remain incompletely described and diagnosed. To identify gaps in descriptions and facilitate the identification of newly collected forms, we provide standardized summary descriptions, species diagnoses, diagnostic tables, and a dichotomous key to the 33 Neotropical species of *Trogolaphysa* with reduced eye number. As a result of this synthesis, we describe two new troglobiontic species, *Trogolaphysa reneau* n. sp. and *Trogolaphysa welchi* n. sp. from Belizean caves.

Keywords: chaetotaxy; Mexico; Brazil; species diagnosis; morphology; caves; leaf litter; identification key



Citation: Soto-Adames, F.; Daly, K.M.; Wynne, J.J. Synopsis of Neotropical *Trogolaphysa* Mills, 1938 (Collembola: Paronellidae) with Reduced Eye Number, and Description of Two New Troglobiontic Species from Belize. *Taxonomy* **2024**, *4*, 199–236. <https://doi.org/10.3390/taxonomy4010011>

Academic Editor: Antonio Carapelli

Received: 24 November 2023

Revised: 1 February 2024

Accepted: 17 February 2024

Published: 5 March 2024



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1. Introduction

Trogolaphysa Mills, 1938 is a medium size genus of Paronellidae (Hexapoda: Collembola) characterized by the presence of apically rounded or truncate scales covering the head, body, and ventral face of the furcula, three bothriotricha on the fourth abdominal segment, one or two rows of spines dorsally on the dens, and a relatively short mucro with three to five teeth. The genus is restricted to the Americas and Africa. The 81 described species are unevenly distributed between biogeographic regions, with 13 species restricted to Africa [1] and the remaining 68 found in the Neotropics [2,3]. The African fauna is poorly known, and all described species are surface forms with color patterns and six to eight eyes. The Neotropical fauna is significantly more morphologically diverse. The 68 New World species are commonly found in leaf litter and subterranean habitats. Just over half of the Neotropical species (36) are restricted to subterranean habitats; most (30) are colorless or, if pigmented, lack a color pattern, and are either eyeless or have fewer than six eyes [2–7].

Subterranean *Trogolaphysa* are of general evolutionary interest because many species exhibit morphological adaptations to hypogean life [4]. Contrary to *Pseudosinella* Schäfer, which has diversified mostly in temperate subterranean habitats ([8] but see [9]), all troglomorphic and troglobiontic *Trogolaphysa* are found in the tropics. This provides a system to potentially tease apart subterranean environments from latitudinal effects.

During a recent visit to caves in the Belize District, Belize, Central America, junior author JJW collected several specimens of colorless and eyeless springtails. This material

appeared to represent two new species in the genus *Trogolaphysa*. While comparing the new material to previously described species, it became clear that most subterranean forms with reduced eye number remain poorly and/or unevenly described. Few descriptions before the work by Mari Mutt [10] referred to chaetotaxy and the only characters of diagnostic utility consistently described were eye number, labial chaetotaxy, claw complex, and mucro.

To facilitate the comparison between described species and specimens from Belize, and to call attention to gaps in diagnostic character descriptions across species, we present summary descriptions, diagnostic tables, and a species-level identification key for all Neotropical species of *Trogolaphysa* with fewer than six eyes. We also describe two new troglobiotic species from Runaway Creek Nature Reserve in central Belize.

2. Materials and Methods

2.1. Study Area

Runaway Creek Nature Reserve (RCNR) is a 2428-hectare private reserve located on the east side of the Coastal Highway, approximately 16 km south by southeast of La Democracia, Belize, Central America (N 17.3185, W 88.4457). Vegetation is characterized as pine savanna in the lowlands and broadleaf forest in the karst hills [11,12]. RCNR is nestled within the Sibun River and Northern and Southern Lagoon watersheds [13] and the key biodiversity area of the Peccary Hills [14], while the surrounding coastal plain is considered an important bird conservation area [15]. All caves are in the karst hills.

2.2. Field Sampling

From 22 through 30 July 2019, four caves were sampled within the RCNR boundary. Arthropods were collected via direct intuitive searches within cave deep zones and opportunistically while traversing the length of each cave [16]. Three observers spent four hours collecting arthropods within each cave. RCNR personnel and JJW searched for arthropods on flood detritus, mud floors, bat guano, other mammal scat, animal carcasses, and along the edges of pools.

During the sampling period, the region experienced a widespread drought. With the exceptions of several small subterranean pools, the caves were muddy but rapidly becoming desiccated. In subsequent site visits, JJW observed three of the four study caves as largely flooded from the entrance to the deep zone.

2.3. Analysis and Preparation

Specimens were cleared in Nesbitt's fluid and mounted using Marc André II fluid [17]. Slides were studied with an Eclipse E400 phase/contrast Nikon microscope. Habitus photographs were produced with an Axiocam HRC camera attached to a Zeiss Discovery V-20 dissection microscope. Photographs were enhanced using Adobe Photoshop Elements (v.19). Original drawings were made using a Y-IDT drawing tube attached to the Nikon microscope. New line drawings and new renditions of previously published hind claws were inked using Microsoft Power Point (v.16).

2.4. Morphological Description Conventions

The traditional macrochaeta formula proposed by Gisin and others [18] displays the number of macrochaetae on the thorax and abdomen in the form of Th. 2, Th. 3/Abd. 1, Abd. 2, Abd. 3, Abd. 4 element C1 + Abd. 4 macrochaetae in column B. A modified version of this formula can also be used to describe the dorsal macrochaetae in *Trogolaphysa* and in all other Paronellini sensu [19]. We propose two versions of the formula: (1) the long, or complete, formula with structure as follows: anterior head macrochaetae (rows A, M, S, Ps), posterior head macrochaetae (rows Pa and Pm)/Th. 2 (a5 and number of macrochaetae in the p3 complex), Th. 3/Abd. 1, Abd. 2, Abd. 3, Abd. 4 inner macrochaetae (columns A and B, including B6), Abd. 4 outer macrochaetae (columns D, E, and F) + Abd. 4 meso-/microchaetae along posterior margin of segment; and (2) the short macrochaeta formula, which includes only the paired macrochaetae of the head, mesothorax, metathorax

and Abd. 4, and Abd. 4 posterior margin chaetae. The short version of the formula is proposed because, for all neotropical *Trogolaphysa* in which the chaetotaxy is known, variation in macrochaetae number is limited to the paired macrochaetae of the head, thorax, and Abd. 4, whereas Abd. 1–3 are invariably carrying zero, two (m3 and m5), and four (m3, am6, pm6, p6) macrochaetae, respectively. Thus, for *Trogolaphysa welchi* n. sp., the long and short formulae are 42/72/02435 + 13–14 and 32/72/35 + 13–14, respectively. The short formula is used in individual species diagnosis and in the diagnostic tables.

Nomenclature and homology of the chaetotaxy on Abd. 4 are according to [20]. The homology of lateral elements on Abd. 4 in [3] differs from that in [20,21]. Provided that homologies in [20,21] are based on evaluation of primary chaetae that agree in all relevant points, we report the macrochaeta of species described in [3] using the homologies accepted by [20,21]. In any case, the chaetotaxy of the lateral section of Abd. 4 (external to column T) is complex. Multiple supplementary elements develop into macrochaetae in different species, especially near the postero-lateral margin of the segment. Homology of most postero-lateral supplementary elements is unclear; for that reason, we do not include them in the formula or description. Thus, we only report the condition of macrochaetae in columns D, E, and F. The only exception is element Te3, which in *Trogolaphysa sotoadamesi* Ferreira, Oliveira and Zeppelini, 2022 [3] is developed into a large macrochaeta. Macrochaetae with large sockets are short, thick, and blunt, whereas macrochaetae with small (relatively speaking) sockets are long, slender, and acuminate. In the descriptions below, macrochaetae with large sockets are represented by upper-case letters and macrochaetae with small sockets are represented by lower-case letters.

The labial formula follows [8], in which upper-case letters represent long chaetae, lower-case represents short chaetae, underscored letters represent ciliate chaetae, and non-underscored letters smooth chaetae. Nomenclature of post-labial chaetae follows [21] as adapted to *Trogolaphysa* by [22].

As the hind claw complex has been the most important character system for diagnosing *Trogolaphysa* species, we provide simplified renderings of the hind claw complex for all species with fewer than six eyes described before 2022. Drawings of the claw of the 11 species recently described in [3] are not reproduced, but these species are included in the identification key, diagnostic tables, summary descriptions, and abbreviated diagnosis. Differences in unguis inner teeth origin distribution, relative length, and shape are the main features described. Tooth origin distribution (Figure 1A) is calculated as the distance between the origin of the inner edge of the unguis and the tooth's origin, divided by the total length of the inner edge, multiplied by 100. The term "subequal" is used if the teeth are of similar size. Description of relative length of a tooth is qualitative and described as small (Figures 2I and 3A), well-developed or -marked (Figure 2A), or enlarged (Figure 2E). Basal teeth are referred to as symmetric when they are the same general shape and asymmetric when they differ in shape (e.g., *T. maya* Mills, 1938 [23] has asymmetric basal teeth, Figure 3B, as one tooth is acuminate and elongate, and the other is wedge-shaped).

Measurements from published drawings were standardized as follows: tenent hairs were measured from tip to the base of the chaeta itself, not including the socket; the unguiculus was measured from its origin on the tarsus to the most distal point (Figure 1A); the length of the inner edge of the unguis was linear and did not account for the curvature of its distal half; the insertion of the inner teeth was measured to the approximate middle of the curvature of the tooth's origin as shown in Figure 1A. The width of the mucro was measured at the origin of the basal tooth, while the mucronal length was measured from the tip to the midpoint of contact with the dens (Figure 1B). Mucrones with a length-to-width proportion smaller than 2.49 are described as paraquadrangle, those with proportions between 2.5 and 2.9 are sub-rectangular, and they are rectangular if the proportion is ≥ 3.0 .

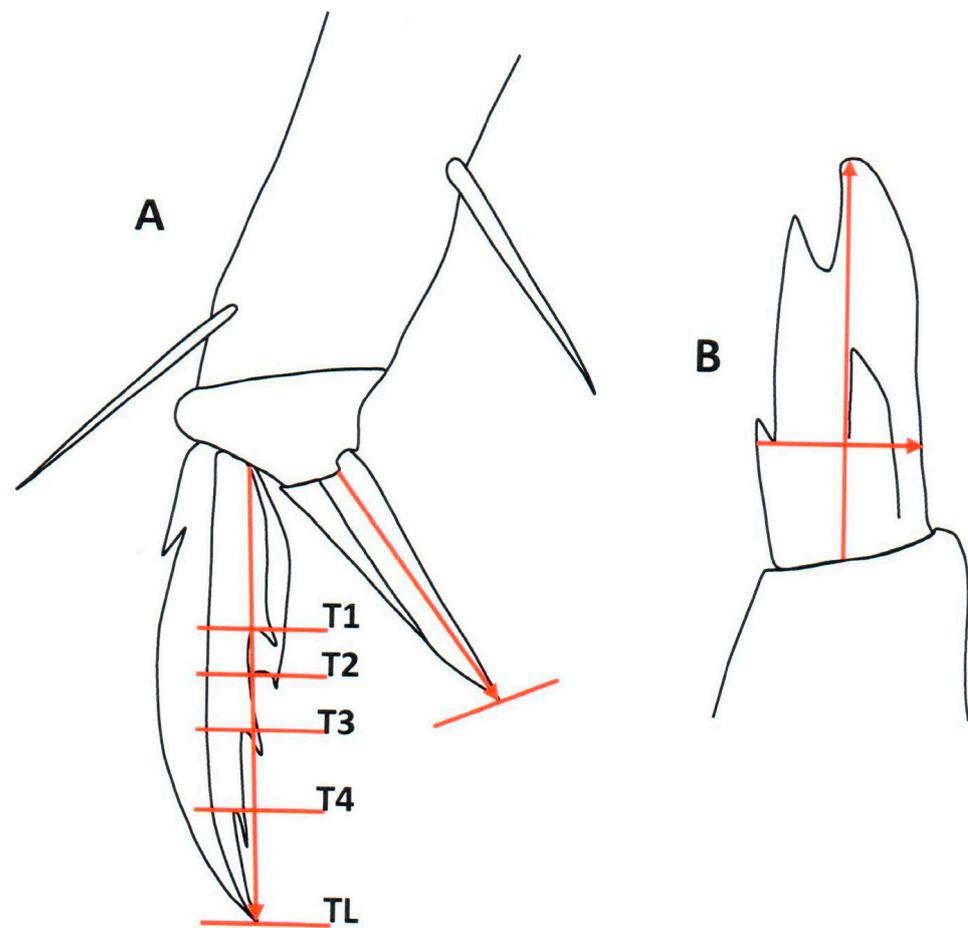


Figure 1. Measurement standardization: (A) unguis inner teeth origin spread and unguiculus length and (B) mucro shape index.

In the descriptions, size refers to the combined length of head and trunk, excluding antennae and furcula.

Some caves in Mexico and South America are well known, and coordinates for entrances can be easily found by an online search. The actual location for other collecting sites could not be determined based on original descriptions. Therefore, coordinates for cave locations should be treated as approximations, within 1 km distance from the entrance.

Abbreviations used in the text, tables, and figure captions are as follows: Abd. for abdomen; Ant. for antenna(e), BT for basal paired teeth of unguis, Mc for macrochaeta, and Th. for thorax.

2.5. Annotated Checklist of Neotropical Trogolaphysa with 0–5 Eyes

All measurements for previously described species were obtained from published drawings. Complete descriptions are provided for the new species. For already described species, we present abbreviated descriptions comprising characters most often included in the original descriptions. Abbreviated descriptions include body size, color, eye number, dorsal chaetotaxy (when available), prelabral chaetae ornamentation, labial triangle chaetotaxy, claw complex morphology, and mucro shape, and number of teeth. Dorsal macrochaetotaxy is summarized using the short formula proposed above. The macrochaetotaxy of several species is only partially described and the gaps in knowledge are represented in the short formula by question marks (e.g., ??/40/3 + 3 means the state of the dorsal macrochaetae of the head is unknown). The claw complex is illustrated for all species described before 2022.

A few other useful diagnostic characters are not included in the short descriptions because they have been reported for only a handful of recently described species. The excluded diagnostic characters are presence/absence and shape of distal labral papillae, number of appendages on the sublobal plate of the outer maxillary lobe, shape of the lateral appendage on labial papilla E, and number of lenticular organs on the intersegmental membrane between Abd. 4 and Abd. 5. The number of ocellar setae appears to be useful for diagnosing species with 6–8 eyes, but it is not included because the absence of eyes makes it almost impossible to determine the actual number and homology of chaetae. The relative size of chaetae on the proximal row of the labrum may also contain good diagnostic information, but it is rarely reported. All these characters should be revisited and reported for all species. A more extensive discussion of the diagnostic value of additional character systems can be found in [3,19,20,22].

Synonymies are not exhaustive; they are limited to changes in nomenclature, new distributional records, identification keys, and redescriptions. Citations of new combinations in the synonymy follow the current convention of author publication year: page where species is mentioned, and brief explanation of citation context. All other references in the synonymy are cited as authors (publication year): page.

All species were collected in caves, unless otherwise noted.

2.6. Type Material Repository

Holotypes and one paratype of each new species are deposited at the Florida State Collection of Arthropods (FSCA). All other type material is deposited at the Northern Arizona University (NAU) collection.

3. Results

3.1. Species Account

1. *Trogolaphysa aelleni* Yoshii, 1988 [5]

(Figure 2M, Table 1)

Trogolaphysa aelleni Yoshii, 1988 [5]: 453–455, figure 3A–G. Soto-Adames & Taylor (2013) [2]: 37, list of Neotropical species. Bellini and Cipola (2017) [24]: 176, *Trogolaphysa* from Brazilian Atlantic Forest and Caatinga. Silva and Bellini (2015) [25]: 57, compared to *T. formosensis*. Nunes and Bellini (2018) [26]: 94, key to Brazilian species *Trogolaphysa*. Zeppelini et al. (2022) [3]: 19, table 2, diagnostic table.

Description. Size to 1.5 mm. Head, body, and appendages white. Antennae 2.4× longer than head. Eyes 2 + 2 on individual pigmented spots. Dorsal chaetotaxy not described. Prelabral chaetae ciliate. Labial formula $\underline{M1M2rEL1L2}$ A1–5. Tenent hair acuminate and shorter (0.45×) than unguiculus. Unguis (Figure 2M) with three small, wedged-shaped inner teeth distributed as 37, 37, 61; basal teeth symmetrical and subequal, not reaching unpaired tooth. Unguiculus lanceolate and uniquely narrow, 0.82× as long as inner edge of unguis. Mucro paraquadrate, 2.11× longer than wide, with four teeth.

Remarks. *Trogolaphysa aelleni* is probably a troglobiont and the only white member of the genus with 2 + 2 individually pigmented eyes, ciliate prelabral chaetae, three inner unguis teeth, and a long and narrow lanceolate unguiculus.

Distribution. Brazil, Sao Paulo, Grutas das Areias, S 24.5894, W 48.7019

2. *Trogolaphysa barroca* Brito and Zeppelini, 2022 [3]

(Table 2)

Trogolaphysa barroca Brito and Zeppelini in Zeppelini et al. (2022) [3]: 2, table 1; 12, identification key; 19, table 2; 31–33, description; 36–38, figures 30–32.

Description. Size to 2.13 mm. White, without dark pigment. Proportion Ant./Head not reported. Eyes absent. Summary dorsal chaetotaxy formula as 21/60/46 + ?. Head dorsally with two anterior (A2, A3) and one posterior (Pa5) macrochaetae. Prelabral chaetae weakly ciliate. Labial formula $\underline{M1M2rEL1L2}$ A1–5. Mesothorax p3 complex with five macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with

four inner (A3, B4, B5, B6) and six outer (D3, E2, e3, e4, F1, F3) macrochaetae. Tenent hair acuminate and subequal ($1.00\times$) to unguiculus. Unguis with two teeth distributed as 22, 22: basal teeth paired, well-developed, subequal, symmetric and lunate. Unguiculus lanceolate and basally weakly swollen, $0.66\times$ as long as inner edge of unguis. Mucro rectangular, $3.03\times$ as long as wide, with four teeth.

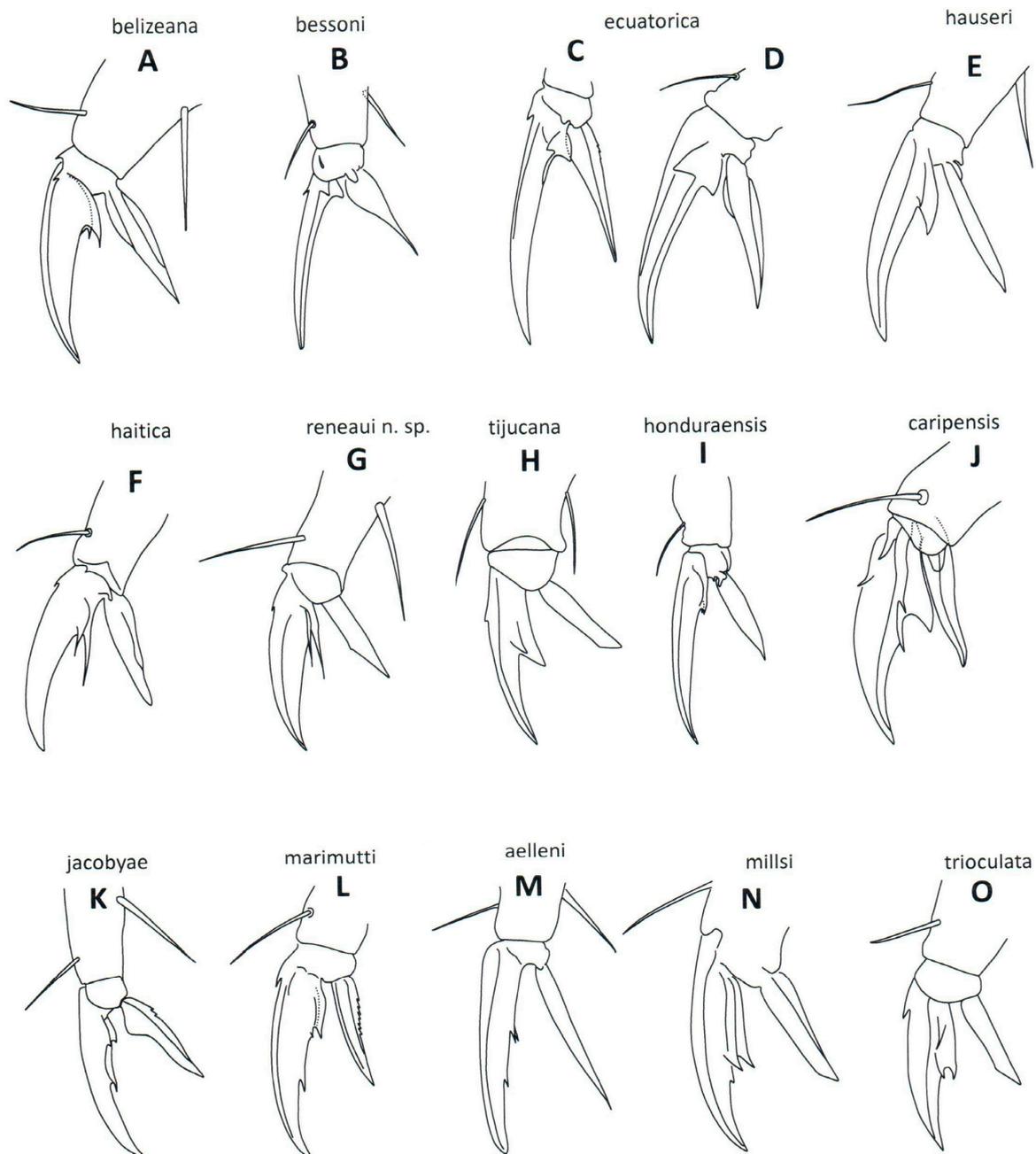


Figure 2. Hind claw complex (unless otherwise noted) modified from the literature. (A) *T. belizeana* [2]. (B) *T. bessoni* [27]. (C,D) *T. ecuatorica*, fore and hind claw, respectively [7]. (E) *T. hauseri* [5]. (F) *T. haitica* [7]. (G) *T. reneai* n. sp. (H) *T. tijucana* [28]. (I) *T. honduraensis* [7]. (J) *T. caripensis* [6]. (K) *T. jacobyi* [2]. (L) *T. marimutti* [7]. (M) *T. aelleni* [5]. (N) *T. millsi* [29]. (O) *T. trioculata* [20].

Table 1. Diagnostic table for Neotropical species of *Trogolaphysa* with fewer than six eyes and unguis with three inner teeth; BT = paired basal teeth of unguis; Mc = macrochaetae.

Species	Eye Number	Smooth Labial Setae	Tenent Hair Tip	Unguis Teeth Spread	Unguis BT Relative Size	Unguis BT Relative Shape	Unguiculus Shape	Mucro Teeth Number	Mucro Shape	Summary Mc Formula
<i>T. aelleni</i>	2	r	acuminate	37, 37 61	small subequal	symmetric wedge	lanceolate narrow	4	2.1× square	?
<i>T. caripensis</i>	0	r	acuminate	39, 43 55	enlarged one much larger	asymmetric lunate>> wedge	lanceolate triangular	4	3.5× rectangular	2??2?/70/56 + ?
<i>T. crystallensis</i>	0	r	acuminate	35, 35 65	well-marked subequal	symmetric wedge	lanceolate wide	4	3.2× rectangular	12/60/56 + ?
<i>T. epitychia</i>	0	r	acuminate	36, 36 69	well-marked one tooth slightly larger	symmetric wedge	lanceolate wide	4	3.3× rectangular	12/40/46 + ?
<i>T. gisbertae</i>	0	r	acuminate	23, 23 54	well-marked subequal	symmetric wedge	lanceolate wide	4	3.9× rectangular	22/60/46 + ?
<i>T. jacobyi</i>	0	M2, r, E, L1, L2	acuminate	26, 26 58	small subequal	symmetric lunate	basally swollen	3	3.2× rectangular	52/41/47 + 6–7
<i>T. maricurieae</i>	0	r	spatulate	30, 30 35	well-marked subequal	symmetric wedge	lanceolate wide	4	4.4× rectangular	12/40/36 + ?
<i>T. marimutti</i>	0	M2, r, E	acuminate	27, 27 59	small subequal	symmetric weakly lunate	lanceolate wide	4	2.5× sub- rectangular	?
<i>T. millsi</i>	2	?	acuminate	48, 48 65	enlarge subequal	symmetric wedge	truncate	4	3.0× rectangular	?
<i>T. strinatii</i>	5	r	spatulate	40, 40 73	small subequal	symmetric wedge	lanceolate	4	2.3× paraquadrate	?
<i>T. trioculata</i>	3	r	acuminate	18, 43 43	small one larger	asymmetric wedge> lunate	truncate	4	3.4× rectangular	12/60/44 + 9–10

Table 2. Diagnostic table for Neotropical species of *Trogolaphysa* with fewer than six eyes and unguis with two inner teeth; BT = paired basal teeth of unguis; Mc = macrochaetae.

Species	Eye Number	Smooth Posterior Labial Setae	Tenet Hair Tip	Unguis Teeth Spread	Unguis BT Relative Size	Unguis BT Relative Shape	Unguiculus Shape	Mucro Teeth	Mucro Shape	Short Dorsal Mc Formula
<i>T. barroca</i>	0	r	acuminate	22, 22	well-marked subequal	symmetric lunate	lanceolate weakly swollen basally	4	3.0× rectangular	21/60/46 + ?
<i>T. belizana</i>	0	M2, r, E, L1, L2	acuminate	22, 22	well-marked subequal	symmetric lunate	lanceolate weakly swollen basally	3	3.0× rectangular	52/43/47 + 7
<i>T. bessonii</i>	0	r	acuminate	4, 4	well-marked subequal	symmetric wedge	swollen basally, drop-shaped	5	3.8× rectangular	??/40/34 + ?
<i>T. dandarae</i>	0	r	spatulate	39, 39	well-marked subequal	symmetric wedge	lanceolate wide	3	3.6× rectangular	22/73/46 + ?
<i>T. ecuatorica</i>	0	r	acuminate	20, 20	well-marked subequal	symmetric wedge	lanceolate/weakly swollen basally	5	3.1× rectangular	?
<i>T. haitica</i>	0	r	acuminate	24, 29	enlarged one larger	symmetric long acuminate	lanceolate wide	4	2.9× sub-rectangular	?
<i>T. hauseri</i>	0	r	acuminate	18, 24	enlarged one much larger	asymmetric lunate>> wedge	lanceolate narrow	4	3.0× rectangular	?
<i>T. honduraensis</i>	4	r	acuminate	21, 21	small subequal	symmetric lunate	lanceolate wide	4	2.7× sub-rectangular	?
<i>T. sotoadamesi</i>	0	r	acuminate	18, 18	well-marked subequal	asymmetric lunate wedge	lanceolate wide	4	2.6× sub-rectangular	12/60/37 + ?
<i>T. tijucana</i>	2	?	acuminate	43, 43	enlarged one much larger	symmetric wedge	truncate	4	3.2× rectangular	?
<i>T. reneaui</i> n. sp.	0–1	M2, E	acuminate	18, 19	enlarged one larger	symmetric long acuminate	lanceolate/weakly truncate	4	2.4× paraquadrate	42/42/45 + 7

Remarks. This troglobiont is the only eyeless species with two-toothed unguis, four-toothed rectangular mucro, only one posterior macrochaeta dorsally on the head, and lacking Abd. 4 macrochaeta F2. *Trogolaphysa barroca* is most similar to *T. beliziana* Palacios-Vargas and Thibaud, but the two species differ in the number of mucronal teeth (four in *T. barroca*, three in *T. beliziana*), number of smooth chaetae in the labial triangle (one in *T. barroca*, five in *T. beliziana*) and in summary chaetotaxy formula (21/60/46 in *T. barroca*, 52/43/47 in *T. beliziana*). *Trogolaphysa honduraensis* (Palacios-Vargas, Ojeda and Christiansen) is also similar to *T. barroca*, but the Honduran species has four eyes and the unguiculus is not swollen basally.

Distribution. Brazil, Minas Gerais, cave ALFA-0003, S 20.1519, W 43.4897.

3. *Trogolaphysa bellinii* Oliveira, Lima and Zeppelini, 2022 [3]

(Table 3)

Trogolaphysa bellinii Oliveira, Lima and Zeppelini in Zeppelini et al. (2022) [3]: 2, table 1; 12, identification key; 19, table 2; 15–17, description; 16–18, figures 12–14.

Description. Size to 1.8 mm. White, without dark pigment. Proportion Ant./Head not reported. Eyes 0 + 0 or 2 + 2. Summary dorsal chaetotaxy formula as 12/40/56 + 7. Head dorsally with one anterior (A2) and two posterior (Pa5, Pm3) macrochaetae. Prelabral chaetae ciliate. Labial formula M1M2rEL1L2 A1–5. Mesothorax p3 complex with three macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with five inner (A3, A5, B4, B5, B6) and six outer macrochaetae (D3, E2, E3, e4, F1, F3). Tenent hair spatulate and subequal (0.93×) to unguiculus. Unguis with four teeth distributed as 31, 31, 72, 92: basal teeth paired, well-developed, subequal, and wedge-like, not reaching proximal unpaired tooth; proximal tooth well-developed, distal tooth minute. Unguiculus lanceolate wide, posterior edge with few basal serrations, 0.74× as long as inner edge of unguis. Mucro with four teeth, sub-rectangular, 2.9× as long as wide.

Remarks. *Trogolaphysa bellinii* is a troglobiont and the only member of the genus with 0–2 eyes, four inner unguis teeth, and spatulate tenent hair. *Trogolaphysa bellinii* is most similar to *T. chapelensis* Lima, Oliveira and Zeppelini, *T. lacerta* Lima, Oliveira and Zeppelini, and *T. zampauloi* Lima, Oliveira and Zeppelini, but differs from these species in having a spatulate tenent hair and in macrochaeta formula (see Table 3).

Distribution. Brazil, Minas Gerais, caveMDIR-0028, next to Mina de Brucutu, S 19.8802, W 43.4397.

4. *Trogolaphysa belizeana* Palacios-Vargas and Thibaud, 1997 [30]

(Figure 2A, Table 2)

Trogolaphysa belizeana Palacios-Vargas and Thibaud, 1997 [30]: 326, 327, 328, figures 8–14. Soto-Adames and Taylor (2013) [2]: 36–37, 42, 47, 53, 54, figures 45–52, re-description based on two paratypes, diagnostic table, compared to *T. jacobyi*. Soto-Adames et al. (2014) [19]: 13, compared to *T. sauroni*.

Description. Size to 2.6 mm. Unpigmented. Antennae 4.0× longer than head. Eyes absent. Summary dorsal chaetotaxy formula as 52/43/47 + 7. Head dorsally with five anterior (A2, A3, M2, S3, S5) and two posterior (Pa5, Pm3) macrochaetae. Prelabral chaetae smooth. Labial formula M1M2rEL1L2 A1–5. Mesothorax p3 complex with three macrochaetae. Metathorax with three macrochaetae. Fourth abdominal segment with four inner (A4, A5, B5, B6) and seven outer macrochaetae (D3, E2, E3, E4, F1, F2, F3). Tenent hair acuminate and shorter (0.57×) than unguiculus. Unguis with two teeth distributed as 22, 22: basal teeth paired, well-developed, subequal, and lunate. Unguiculus lanceolate, weakly swollen basally, 0.73 to 0.76× as long as inner edge of unguis. Mucro with three teeth, rectangular, 3.00× as long as wide.

Remarks. This troglobiont is the only eyeless *Trogolaphysa* with two inner unguis teeth, three toothed mucro, and summary macrochaetae formula 52/43/47 + 7. *Trogolaphysa beliziana* is most similar to *T. barroca*; the differences between the two species are detailed in the remarks to *T. barroca*. *Trogolaphysa jacobyi* Soto-Adames and Taylor is also similar to *T. beliziana*, but they differ in the number of metathoracic macrochaetae (three in

T. beliziana, one in *T. jacobyi*), the number of inner unguual teeth (three in *T. jacobyi*, two in *T. beliziana*) and in the shape of the unguiculus (swollen basally in *T. jacobyi*, widely lanceolate in *T. beliziana*).

Distribution. Belize, Cayo, Actun Chapat Cave, N 17.0465, W 89.1338.

5. *Trogolaphysa bessoni* Thibaud and Najt, 1988 [27]

(Figure 2B, Table 2)

Trogolaphysa bessoni Thibaud and Najt, 1988 [27]: 724–726, figures 1–5. Soto-Adames and Taylor (2013) [2]: 37, 47; list Neotropical species; diagnostic table. Soto-Adames, et al. [19]: 13 compared to *T. sauroni*. Cipola et al. (2022) [22]: 289 compared to *T. quinquedentomucronata*.

Description. Size to 1.4 mm. White. Antennae $2.7\times$ longer than head. Eyes absent. Summary dorsal chaetotaxy formula as 10/40/?? + ?. Head apparently with only paired macrochaeta, A2. Prelabral chaetae smooth. Labial formula M1M2rEL1L2 A1–5. Mesothorax p3 complex with three macrochaetae. Metathorax without macrochaetae. Homology of Abd. 4 macrochaetae intractable. Tenent hair acuminate and shorter ($0.35\times$) than unguiculus. Unguis with two wedge-shaped teeth, distributed as 4, 4. Unguiculus basally swollen, tear shaped, $0.58\times$ as long as inner edge of unguis. Mucro rectangular, $3.83\times$ as long as wide, with five teeth.

Remarks. This presumed troglobiont is the only eyeless species with two inner teeth inserted on basal quarter of unguis and basally swollen, tear-shaped unguiculus. Based on claw shape, *T. bessoni* is most similar to *T. equatorica* (Palacios, Ojeda and Christiansen) but whereas in *T. bessoni* the unguiculi on all legs are of similar shape, in *T. equatorica* the fore and hind leg unguiculi are different (Figure 2C, D). In addition, the hind leg unguiculus is much shorter ($0.58\times$ unguis) in *T. bessoni* than in *T. equatorica* ($0.72\times$ unguis).

The original description states that the dorsal macrochaetotaxy of *T. bessoni* is similar to that in *Trogolaphysa cotopaxiana* Thibaud and Najt, but the rendering of the general distribution of macrochaetae for that species lacks the detail needed to infer the homology of elements on Abd. 4.

Distribution. Ecuador, Napo Province, Gruta de San Bernardo, S 0.9492, W 77.7923.

6. *Trogolaphysa caripensis* (Gruia, 1987) [6]

(Figure 2J, Table 1)

Troglopedetes caripensis Gruia, 1987 [6]: 153–155; figures 1–3, 5–9 and 14a,b.

Trogolaphysa caripensis Thibaud and Najt, 1988 [27]: 723, new combination. Soto-Adames and Taylor (2013) [2]: 37; list Neotropical species.

Description. Size to 1.8 mm. White. Antennae $3.0\times$ longer than head. Eyes absent. Summary dorsal chaetotaxy formula as 22/70/56 + ? Homology of dorsal head chaetotaxy uncertain, possibly with four macrochaetae, two anterior (A2, A3) and two posterior (Pa5, Pm3). Prelabral chaetae not described. Labial formula M1M2rEL1L2 A1–5. Mesothorax p3 complex with six macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment apparently with four (A3, A5, B5, B6) inner and six (D3, E2, E3, F1, F2, F3) outer macrochaetae. Tenent hair acuminate and shorter ($0.78\times$) than unguiculus. Unguis with three inner teeth distributed as 39, 43, 55: basal teeth asymmetric and unequal, lunate tooth evidently larger than wedge-shaped tooth; lunate tooth approaching but not reaching unpaired tooth. Unguiculus lanceolate to triangular, $0.65\times$ as long as inner edge of unguis. Mucro rectangular, $3.46\times$ as long as wide, with four teeth.

Remarks. The Venezuelan species is a troglobiont unique among eyeless species with three inner unguual teeth in having the basal teeth asymmetric and unequal, with the lunate tooth much larger than the wedge-shaped tooth. All other eyeless species with three inner unguual teeth have subequal or marginally unequal size teeth.

Distribution. Venezuela, Monagas, Cueva del guácharo, N 10.1717, W 63.556.

7. *Trogolaphysa chapelensis* Lima, Oliveira and Zeppelini, 2022 [3]

(Table 3)

Trogolaphysa chapelensis Lima, Oliveira and Zeppelini in Zeppelini et al. (2022) [3]: 2, table 1; 12, identification key; 19, table 2; 21–23, description; 24–26, figures 18–20.

Description. Size to 2.22 mm. White, without dark pigment. Proportion Ant./Head not reported. Eyes absent. Summary dorsal chaetotaxy formula as 12/50/56 + ?. Head dorsally with one anterior (A2) and two posterior (Pa5, Pm3) macrochaetae. Prelabral chaetae ciliate. Labial formula M1M2rEL1L2 A1–5. Mesothorax p3 complex with four macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with five inner (A3, A5, B4, B5, B6) and six outer (D3, E2, E3, e4, F1, F3) macrochaetae. Tenent hair acuminate and subequal (0.97×) to unguiculus. Unguis with four teeth distributed as 48, 48, 71, 93: basal teeth symmetric, well-marked, subequal, and wedge-like, not reaching proximal unpaired tooth; proximal unpaired tooth well-developed, distal tooth minute. Unguiculus lanceolate wide, posterior edge with few basal serrations, 0.69× as long as inner edge of unguis. Mucro rectangular, 3.23× as long as wide, with four teeth.

Remarks. Among eyeless species with four inner unguis teeth, this is the only troglobiont with basal unguis teeth subequal and symmetric, four macrochaetae in the p3 complex of the mesothorax, with Abd. 4 macrochaeta A5 and more than 70 external spines on the dens. *Trogolaphysa chapelensis* is most similar to *T. lacerta* Lima, Oliveira and Zeppelini, but the later species carries six macrochaetae in the p3 complex of the mesothorax and lacks macrochaeta A5 on Abd. 4. *Trogolaphysa zampauloi* Lima, Oliveira and Zeppelini is also similar to *T. chapelensis* in claw structure, but that species has four macrochaetae in series A on the head, whereas in *T. chapelensis* series A has only one macrochaeta. *Trogolaphysa bellinii* is also similar to *T. chapelensis*, but in the later species the tenent hair is acuminate.

Distribution. Brazil, Minas Gerais, Rio Acima municipality, gruta-2d7 next to Morro do Chapéu, S 20.1281, W 43.9089.

8. *Trogolaphysa crystallensis* Oliveira, Lima and Zeppelini, 2022 [3]

(Table 1)

Trogolaphysa crystallensis Oliveira, Lima and Zeppelini, in Zeppelini et al. (2022) [3]: 2, table 1; 12, identification key; 19, table 2; 23–26, description; 27–29, figures 21–23.

Description. Size to 1.68 mm. White, without other pigment. Proportion Ant./Head not reported. Eyes absent. Summary dorsal chaetotaxy formula as 12/60/56 + ?. Head dorsally with one anterior (A2) and two posterior (Pa5, Pm3) macrochaetae. Prelabral chaetae ciliate. Labial formula M1M2rEL1L2 A1–5. Mesothorax p3 complex with five macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with five inner (A3, A5, B4, B5, B6) and six (D3, E2, e3, e4, F1, f3) outer macrochaetae. Tenent hair acuminate and subequal (0.94×) to unguiculus. Unguis with three teeth distributed as 35, 35, 65: basal teeth, symmetric, well-marked, subequal, and wedge-like, not reaching unpaired tooth; unpaired tooth well-developed. Unguiculus lanceolate wide, smooth, 0.78× as long as inner edge of unguis. Mucro rectangular, 3.23× as long as wide, with four teeth.

Remarks. This troglobiont is the only eyeless species with acuminate tenent hair and three inner unguis teeth which also carries five macrochaetae in the p3 complex of the mesothorax and five inner macrochaetae on Abd. 4. *Trogolaphysa crystallensis* is most similar to *T. epitychia* Oliveira, Lima and Zeppelini and *T. gisbertae* Brito and Zeppelini but the three species differ in summary macrochaetae formula as shown in Table 1.

Distribution. Brazil, Minas Gerais, Mariana municipality, cave LOC-0090, near Cachoeira Crystal, S 20.3407, W 43.4074.

9. *Trogolaphysa dandarae* Brito and Zeppelini, 2022 [3]

(Table 2)

Trogolaphysa dandarae Brito and Zeppelini in Zeppelini et al. (2022) [3]: 2, table 1; 12, identification key; 19, table 2; 41–44, 50, description; 48–50, figures 42–44.

Description. Size to 1.75 mm. White. Proportion Ant./Head not reported. Eyes absent. Summary dorsal chaetotaxy formula as 22/73/46 + ?. Head dorsally with two anterior (A2, S5) and two posterior (Pa5, Pm3) macrochaetae. Prelabral chaetae ciliate. Labial formula

M1M2rEL1L2 A1–5. Mesothorax p3 complex with six macrochaetae. Metathorax with three macrochaetae. Fourth abdominal segment with four inner (A3, B4, B5, B6) and six outer (D3, E2, e3, e4, F1, f3) macrochaetae. Tenent hair spatulate and subequal (1.00×) to unguiculus. Unguis with two inner teeth distributed as 39, 39: teeth well-marked, subequal, and wedge-like. Unguiculus lanceolate wide, smooth, 0.66× as long as inner edge of unguis. Mucro rectangular, 3.57× as long as wide, with three teeth

Remarks. This troglobiont is the only eyeless species with spatulate tenent hair, two inner unguis teeth and three mucronal teeth. This is a distinctive species not easily confused with other described species.

Distribution. Brazil, Pará, Parauapebas municipality, cave N4WS-0018/48, near Serra Norte, S 6.0762, W 50.1963.

10. *Trogolaphysa ecuatorica* (Palacios-Vargas, Ojeda and Christiansen, 1985) [7]

(Figure 2C,D, Table 2)

Troglopedetes ecuatoricus Palacios-Vargas, Ojeda and Christiansen, 1985 [7]: 21, 22, 24; figure 8C–E (erroneously referred to figure 9C–E in the description).

Trogolaphysa ecuatorica Thibaud and Najt, 1988 [27]: 723, new combination, compared to *T. bessoni*. Soto-Adames and Taylor (2013) [2]: 37, 47; list Neotropical species; diagnostic table.

Description. Size to 1.5 mm. White. Antennae 2.3× longer than head. Eyes absent. Dorsal chaetotaxy not described. Prelabral chaetae smooth. Labial formula M1M2rEL1L2 A1–5. Tenent hair acuminate and much shorter (0.53×) than unguiculus. Unguis with two large wedge-shaped and subequal inner teeth distributed as 20, 20. Unguiculus on fore and middle legs somewhat triangular, wide at base and tapered; hind legs unguiculus lanceolate, widest near middle, broadly acuminate, 0.72× as long as inner edge of unguis. Mucro rectangular, 3.1× as long as wide, with five teeth.

Remarks. This troglobiont is the only eyeless species with large, paired teeth inserted on the basal quarter of the unguis, lacking unpaired teeth, and having heteromorphic unguiculi. Claw shape is most similar to *T. bessoni*, also from Ecuador, but in *T. ecuatorica* the fore and hind unguiculi are different shape and neither of them approach the basally swollen, tear-shaped unguiculus present in *T. bessoni*.

Distribution. Ecuador, Morona-Santiago, Los Tayos, Cueva Comando/Cueva de Los Tayos, S 3.0515, W 78.2025.

11. *Trogolaphysa epitychia* Oliveira, Lima and Zeppelini, 2022 [3]

(Table 1)

Trogolaphysa epitychia Oliveira, Lima and Zeppelini in Zeppelini et al. (2022) [3]: 2, table 1; 12, identification key; 19, table 2; 33–36, description; 39–41, figures 33–35.

Description. Size to 1.35 mm. White. Proportion Ant./Head not reported. Eyes absent. Summary dorsal chaetotaxy formula as 12/40/46 + ?. Head dorsally with one anterior (A2) and two posterior (Pa5, Pm3) paired macrochaetae. Prelabral chaetae ciliate. Labial formula M1M2rEL1L2 A1–5. Mesothorax p3 complex with three macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with four inner (A3, A5, B5, B6) and six outer macrochaetae (D3, E2, e3, e4, F1, f3). Tenent hair acuminate and subequal to slightly longer (1.07×) than unguiculus. Unguis with three teeth distributed as 36, 36, 69: basal teeth well-marked, subequal or one slightly larger, and wedge-like, not reaching unpaired tooth; unpaired tooth well-developed. Unguiculus lanceolate wide, smooth, 0.77× as long as inner edge of unguis. Mucro rectangular, 3.33× as long as wide, with four teeth.

Remarks. This troglobiont is unique among eyeless species with an acuminate tenent hair and three inner unguis teeth in having three macrochaetae on the mesothoracic p3 complex and four inner macrochaetae on Abd. 4. This form is part of a complex that includes *T. crystallensis* and *T. gisbertae*, and only can be distinguished using chaetotaxy (see Table 1).

Distribution. Brazil, Minas Gerais, Mato Dentro municipality, cave CSS-0118 near São Sansebastião do Bom Sucesso, S 18.9739, W 44.1056.

12. *Trogolaphysa gisbertae* Brito and Zeppelini, 2022 [3]

(Table 1)

Trogolaphysa gisbertae Brito and Zeppelini in Zeppelini et al. (2022) [3]: 2, table 1; 12, identification key; 19, table 2; 38–41 description; 45–47, figures 39–41.

Description. Size to 1.23mm. White. Proportion Ant./Head not reported. Eyes absent. Summary dorsal chaetotaxy formula as 22/60/46 + ?. Head dorsally with two anterior (A2, A3) and two posterior (Pa5, Pm3) paired macrochaetae. Prelabral chaetae ciliate. Labial formula M1M2rEL1L2 A1–5. Mesothorax p3 complex with five macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with four inner (A3, B4, B5, B6) and six outer macrochaetae (D3, E2, e3, e4, F1, f3). Tenent hair acuminate and shorter (0.86×) than unguiculus. Unguis with three teeth distributed as 23, 23, 54: basal teeth paired, well-marked, subequal and wedge-like, not reaching unpaired tooth; unpaired tooth small and wedge-like. Unguiculus lanceolate wide, with a few posterior teeth basally, 0.72× as long as inner edge of unguis. Mucro rectangular, 3.85× as long as wide, with four teeth.

Remarks. This presumed troglobiont is the only eyeless form with three well-marked inner unguual teeth, two anterior head macrochaetae and lacking Abd. 4 macrochaeta A5. *Trogolaphysa gisbertae* is most similar to *T. crystallensis* and *T. epitychia*, but they can be reliably distinguished using dorsal chaetotaxy (see Table 1).

Distribution. Brazil, Pará, Parauapebas municipality, cave N1N8-N8-017, near Serra Norte, S 6.1692, W 50.16308.

13. *Trogolaphysa guacharo* Yoshii, 1988 [5]

(Figure 3E, Table 3)

Trogolaphysa guacharo Yoshii, 1988 [5]: 455–456, figure 4A–E. Soto-Adames and Taylor (2013) [2]: 37; list Neotropical species.

Description. Size to 1.7 mm. White. Antennae 2.71× longer than head. Without eyes. Dorsal chaetotaxy incompletely described, 2?/??/? + ?. Head dorsally with two anterior (A2, A3) and apparently no posterior paired macrochaetae. Prelabral chaetae ciliate. Labial formula M1M2rEL1L2 A1–5, with L2 displaced laterally and away from L1. Tenent hair acuminate and much shorter (0.48×) than unguiculus. Unguis (Figure 3E) with four inner teeth distributed as 26, 29, 32, 42: basal teeth symmetric, wedge-shaped, but unequal, with one tooth much larger, unpaired teeth larger than smaller basal tooth, largest basal tooth overlapping both unpaired teeth. Unguiculus lanceolate and narrow, 0.81× as long as inner edge of unguis. Mucro square 1.93× as long as wide, with four teeth.

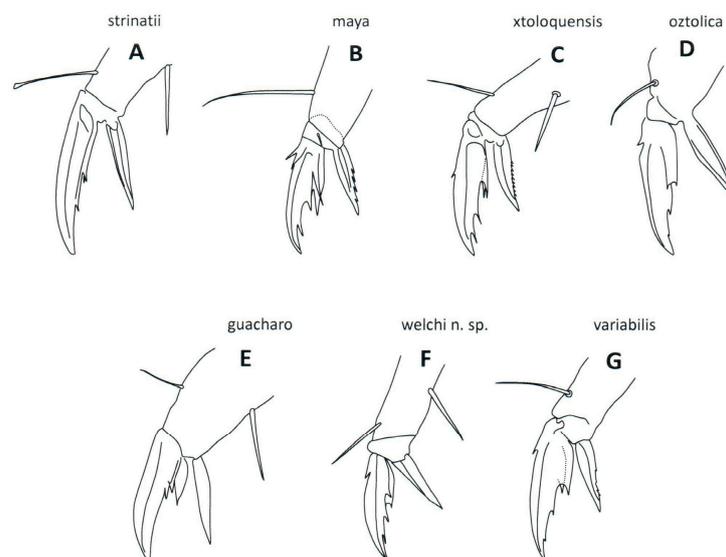


Figure 3. Hind claw complex modified from the literature. (A) *T. strinatii* [5]. (B) *T. maya* [23]. (C) *T. xtoloquensis* [7]. (D) *T. oztolica* [31]. (E) *T. guacharo* [5]. (F) *T. welchi* n. sp. (G) *T. variabilis* [7].

Remarks. This presumed troglobiont is the only eyeless species with four inner unguual teeth in which one basal tooth is much larger than the other and overlaps both unpaired teeth (Figure 3E). No other species with a four-toothed unguis approaches this morphology.

Distribution. Venezuela, Miranda, Cueva Alfredo Jahn, N 10.4767, W 66.2719; Venezuela, Monagas, Cueva del guácharo, N 10.1717, S 63.556.

14. *Trogolaphysa haitica* (Palacios-Vargas, Ojeda and Christiansen, 1985) [7]

(Figure 2F, Table 2)

Troglopedetes haiticus Palacios-Vargas, Ojeda and Christiansen, 1985 [7]: 10, 16, figure 6E, key to New World species of *Troglopedetes*, original description.

Trogolaphysa haiticus Thibaud and Najt, 1988 [27]: 723, new combination.

Trogolaphysa haitica Soto-Adames and Taylor, 2013 [2]: 37, 47, list Neotropical species; diagnostic table. Soto-Adames et al. (2014) [19]: 13, compared to *T. sauron*.

Description. Size to 2.7 mm. White. Antennae $2.7\times$ longer than head. Without eyes. Dorsal chaetotaxy not described. Prelabral chaetae smooth.

Labial formula M1M2rEL1L2 A1–5. Tenent hair acuminate and shorter ($0.62\times$) than unguiculus. Unguis (Figure 2F) with two inner teeth distributed as 24, 29: teeth acuminate, elongate, sharply tapered and unequal, one tooth clearly longer. Unguiculus lanceolate wide, $0.76\times$ as long as inner edge of unguis. Mucro sub-rectangular, $2.88\times$ as long as wide with four teeth.

Remarks. This troglobiont is the only eyeless member of the genus with two elongate and sharply acuminate unguual teeth, labial chaeta M2 ciliate and chaeta 'r' smooth. *Trogolaphysa haitica* is most similar to *T. reneau* n. sp. and the differences between the two forms are discussed in the remarks to the new species. *Trogolaphysa sauron* Soto-Adames, Baquero and Jordana has a similar claw morphology but differs from *T. haitica* in having 8 + 8 eyes and a distinctive color pattern.

Distribution. Haiti, Département du Sud, Grotto Counoubais, N 18.324, W 73.8679.

15. *Trogolaphysa hauseri* Yoshii, 1988 [5]

(Figure 2E, Table 2)

Trogolaphysa hauseri Yoshii, 1988 [5]: 457–458, figure 5A–E, original description. Soto-Adames and Taylor (2013) [2]: 37; list Neotropical *Trogolaphysa*. Silva and Bellini [25]: 57, compared to *T. formosensis*. Bellini and Cipola [24]: 176, list *Trogolaphysa* species reported from Brazilian Atlantic Forest. Nunes and Bellini [26]: 93, key to Brazilian species *Trogolaphysa*. Cipola et al. [22]: 290, key to Brazilian species *Trogolaphysa*.

Description. Size to 1.5 mm. White. Antennae $1.7\times$ longer than head. Eyes absent. Dorsal chaetotaxy not described. Prelabral chaetae ciliate. Labial formula M1M2rEL1L2 A1–5. Tenent hair acuminate and shorter ($0.60\times$) than unguiculus. Unguis (Figure 2E) with two inner teeth distributed as 18, 24: teeth asymmetric and unequal, with lunate tooth much larger than wedge-shaped tooth. Unguiculus lanceolate narrow (Figure 2E), $0.79\times$ as long as inner edge of unguis. Mucro rectangular, $3.0\times$ as long as wide, with four teeth.

Remarks. This troglobiont is the only eyeless species with two inner unguual teeth, one of which is lunate and much larger than the other, and a long narrow unguiculus. All other eyeless species with two markedly unequal basal unguual teeth (i.e., *T. haitica* and *T. reneau* n. sp.) have acuminate inner teeth and wide lanceolate unguiculi.

Distribution. Brazil, Sao Paulo, Gruta da Tapagem, S 24.6258, W 48.4047.

16. *Trogolaphysa hondurasensis* (Palacios-Vargas, Ojeda and Christiansen, 1985) [7]

(Figure 2I, Table 2)

Troglopedetes hondurasensis Palacios-Vargas, Ojeda and Christiansen, 1985 [7]: 9, 24, 25; figure 10A,B, key New World *Troglopedetes*, original description

Trogolaphysa hondurasensis Thibaud and Najt, 1988 [27]: 723, new combination. Soto-Adames and Taylor [2]: 37; list Neotropical species.

Description. Size to 2.64 mm. Head and body blue. Proportion Ant./Head not reported (all types lack intact antennae). Eyes 4 + 4. Dorsal chaetotaxy not described.

Prelabral chaetae smooth. Labial formula $\underline{M1M2rEL1L2}$ A1–5. Tenent hair acuminate and shorter ($0.71\times$) than unguiculus. Unguis (Figure 2I) with two inner teeth distributed as 21, 21: basal teeth unusually small, subequal and lunate. Unguiculus smooth, lanceolate, wider in the middle than at base, short, $0.50\times$ as long as inner edge of unguis. Mucro sub-rectangular $2.7\times$ as long as wide, with four teeth.

Remarks. This troglophile is the only *Trogolaphysa* species with four eyes, two minute lunate basal unguis teeth and wide lanceolate unguiculus. No other species has a similar combination of unguiculus and unguis morphology.

Distribution. Honduras, Cueva Peña Águila (location unknown).

17. *Trogolaphysa jacobyi* Soto-Adames and Taylor, 2013 [2]

(Figure 2K, Table 1)

Trogolaphysa jacobyi Soto-Adames and Taylor (2013) [2]: 47, figures 24–43, original description. Soto-Adames et al. [19]: 13, compared to *T. sauroni*.

Description. Size to 2.0 mm. Yellow when alive, white in alcohol. Eyes absent. Short chaetotaxy formula as 52/41/47 + 6–7. Head with five anterior (A2, A3, M2, S3, S5) and two posterior (Pa5 and Pm3) paired macrochaetae. Prelabral chaetae smooth. Labial formula $\underline{M1M2rEL1L2}$ A1–5. Mesothorax p3 complex with three macrochaetae. Metathorax with one macrochaeta. Fourth abdominal segment with four inner (A5, B4, B5, B6) and seven outer macrochaetae (D3, E2, E3, E4, F1, F2, and F3). Tenent hair acuminate and shorter ($0.67\times$) than unguiculus. Unguis (Figure 2K) with three inner teeth, all small and distributed as 26, 26, 58: basal teeth lunate, symmetric, not overlapping unpaired tooth. Unguiculus basally swollen, with a few basal teeth on posterior margin, $0.72\times$ as long as inner edge of unguis. Mucro rectangular, $3.2\times$ as long as wide, with three teeth.

Remarks. This troglobiont is the only eyeless species with tridentate unguis, basally swollen unguiculus and all labial triangle chaetae, except M1, smooth. Among species for which the dorsal chaetotaxy is known, this is the only form with summary formula 52/41/47 + 6–7. *Trogolaphysa jacobyi* is most similar to *T. marimutti* (Ojeda, Palacios and Christiansen) from Mexico and *T. beliziana*. The Mexican species has a four-toothed mucro (three teeth in *T. jacobyi*), labial chaetae L1 and L2 ciliate (both smooth in *T. jacobyi*) and the unguiculus is lanceolate (basally swollen in *T. jacobyi*). The differences between *T. jacobyi* and *T. beliziana* are detailed in the remarks of *T. beliziana*.

Distribution. Belize, Toledo District, Yok Balum Cave, N 16.2083, W 89.0759.

18. *Trogolaphysa lacerta* Lima, Oliveira and Zeppelini, 2022 [3]

(Table 3)

Trogolaphysa lacerta Lima, Oliveira and Zeppelini in Zeppelini et al., 2022 [3]: 3, table 1; 12, identification key; 20, table 2; 18, 20–21, description; 21–23, figures 15–27.

Description. Size to 1.86 mm. White. Eyes 0 + 0 or 3 + 3. Summary dorsal chaetotaxy formula as 12/70/46 + ?. Head dorsally with one anterior (A2) and two (Pa5, Pm3) posterior paired macrochaetae. Prelabral chaetae smooth. Labial formula $\underline{M1M2rEL1L2}$ A1–5. Mesothorax p3 complex with six macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with four inner (A3, B4, B5, B6) and six outer (D3, E2, E3, e4, F1, F3) macrochaetae. Tenent hair acuminate and shorter ($0.79\times$) than unguiculus. Unguis with four inner teeth distributed as 49, 49, 72, 93: basal teeth well-marked, subequal, and wedge-like, not reaching proximal unpaired tooth; proximal tooth well-developed; distal tooth minute. Unguiculus lanceolate wide, smooth, $0.67\times$ as long as inner edge of unguis. Mucro rectangular, $3.23\times$ as long as wide, with four teeth.

Remarks. This troglobiont is the only species with 0–3 eyes, acuminate tenent hair, four well-marked unguis teeth and smooth lanceolate unguiculus that also bears six macrochaetae in the mesothoracic p3 complex and lacks Abd. 4 macrochaeta A5. *Trogolaphysa lacerta* is most similar to *T. chapelensis*, but this last species has a serrated unguiculus and a different summary macrochaetae formula (see Table 3).

Distribution. Brazil, Minas Gerais, Rio Acima municipality, cave GAND-115, near Lapa do Calango, S 20.0708, W 43.679.

Table 3. Diagnostic table for Neotropical species of *Trogolaphysa* with fewer than six eyes and unguis with four inner teeth. All species also have 4-toothed mucro; BT = paired basal teeth of unguis; Mc = macrochaetae.

Character Species	Eye Number	Smooth Labial Setae	Tenant Hair Tip	Unguis Teeth Spread	Unguis BT Relative Size	Unguis BT Relative Shape	Unguiculus Shape	Mucro Shape	Summary Mc Formula
<i>T. bellinii</i>	0–2	r	spatulate	31, 31, 72, 92	well-marked subequal	symmetric wedge	lanceolate wide	2.9× sub-rectangular	12/40/56 + 7
<i>T. chapelensis</i>	0	r	acuminate	48, 48 71, 93	well-marked subequal	symmetric wedge	lanceolate wide	3.2× rectangular	12/50/56 + ?
<i>T. guacharo</i>	0	r	acuminate	26, 29 32, 42	small/enlarged, one much larger	symmetric wedge	lanceolate narrow	1.9× square	20?/??/? + ?
<i>T. welchi n. sp.</i>	2	(r), E	acuminate	35, 43 57, 74	well-marked one slightly larger	asymmetric lunate > wedge	lanceolate triangular	2.3× paraquadrate	32/72/35 + 13–14
<i>T. lacerta</i>	0–3	r	acuminate	49, 49 72, 93	well-marked subequal	symmetric wedge	lanceolate wide	3.2× rectangular	12/70/46 + ?
<i>T. maya</i>	0	r	acuminate	24, 38 51, 78	enlarged one much larger	asymmetric wedge >> acuminate	lanceolate wide	2.3× paraquadrate	53/60/45 + ?
<i>T. oztolica</i>	0	r	acuminate	43, 43, 67, 85	small subequal	Symmetric wedge	lanceolate weakly excavate	3.0× rectangular	?
<i>T. variabilis</i>	4–6	M2, r	acuminate	34, 34 63, 86	well-marked subequal	symmetric wedge	lanceolate	2.5× sub-rectangular	?
<i>T. xtoloquensis</i>	0	r, E, L1, L2	acuminate	36, 36 67, 81	enlarged subequal	symmetric acuminate short	lanceolate	3.2× rectangular	?
<i>T. zampauloi</i>	0–4	R	acuminate	29, 29 65, 88	well-marked subequal	symmetric wedge	lanceolate wide	3.5× rectangular	42/60/56 + ?

19. *Trogolaphysa mariecurieae* Ferreira, Oliveira and Zeppelini, 2022 [3]

(Table 1)

Trogolaphysa mariecurieae Ferreira, Oliveira and Zeppelini in Zeppelini et al., 2022 [3]: 3, table 1; 12, identification key; 20, table 2; 28–31, description; 33–35, figures 27–29.

Description. Size to 1.49 mm. White. Eyes absent. Summary dorsal chaetotaxy formula as 12/40/36 + ?. Head dorsally with one anterior (A2) and two posterior (Pa5, Pm3) paired macrochaetae. Prelabral chaetae ciliate. Labial formula M1M2rEL1L2 A1–5. Mesothorax p3 complex with three macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with three inner (A5, B5, B6) and six outer (D3, E2, E3, e4, F1, f3) macrochaetae. Tenent hair spatulate and longer (1.21×) than unguiculus. Unguis with three teeth distributed as 30, 30, 35: basal teeth symmetric, wedge-like, well-marked, subequal, completely overlapping unpaired tooth; unpaired tooth much smaller than paired teeth. Unguiculus lanceolate wide, smooth, 0.73× as long as inner edge of unguis. Mucro rectangular, 4.35× as long as wide, with four teeth.

Remarks. This troglobiont is the only eyeless species with the tenent hair spatulate and longer than the unguiculus, and three-toothed unguis in which the basal teeth completely overlap the unpaired tooth. *Trogolaphysa mariecurieae* is also unique among species with three-toothed unguis in having only three inner macrochaetae on Abd. 4.

Distribution. Brazil, Minas Gerais, Mato Dentro, cave MSS 10/11, near Pico do Soldado, S 19.0093, W 43.4015.

20. *Trogolaphysa marimutti* (Palacios-Vargas, Ojeda and Christiansen, 1985) [7]

(Figure 2L, Table 1)

Trogolapedetes marimutti Palacios-Vargas, Ojeda and Christiansen, 1985 [7]: 10, 24–26, figure 10C,D, identification key, original description.

Trogolaphysa marimutti Thibaud and Najt, 1988 [27]: 723, new combination.

Description. Size to 2.3mm. White. Eyes absent. Chaetotaxy not described. Prelabral chaetae ciliate. Labial formula M1M2rEL1L2 A1–5. Tenent hair acuminate and shorter (0.82×) than unguiculus. Unguis (Figure 2L) with three inner teeth, all small and distributed as 27, 27, 59: basal teeth weakly lunate, symmetric, small, subequal not reaching unpaired tooth, unpaired tooth well-developed, wedge-like. Unguiculus lanceolate, 0.64× as long as inner edge of unguis, posterior margin serrate. Mucro sub-rectangular, 2.5× as long as wide, with four teeth.

Remarks. This troglobiont is the only eyeless species with acuminate tenent hair, three unguis teeth where the basal teeth are symmetric, the unguiculus is lanceolate and serrated, and labial triangle chaetae E is smooth. Five other species, *T. caripensis*, *T. crystallensis*, *T. epitychia*, *T. gisbertae*, and *T. jacobyi*, are eyeless, have acuminate tenent hair and three-toothed unguis; however, all of them have clearly rectangular mucrones (between 3.2 and 4.4 times as long as wide in other species and 2.5 times in *T. marimutti*), and in all, except in *T. jacobyi*, labial triangle chaetae M2 and E are ciliate (smooth in *T. marimutti*). *Trogolaphysa jacobyi* has a basally swollen unguiculus and three-toothed mucro, whereas in *T. marimutti*, the unguis has four teeth and the unguiculus is lanceolate. *Trogolaphysa oztolica* Ojeda and Palacios-Vargas, may be confused with *T. marimutti* if the minute distal unpaired tooth is overlooked. However, in *T. oztolica* labial chaetae E is coarsely ciliate and the inner membrane of the unguiculus is weakly excavate (see Figures 2L and 3D).

Distribution. Mexico, Veracruz, Grutas de Atoyac, N 18.9215, W 96.7678.

21. *Trogolaphysa maya* Mills, 1938 [23]

(Figure 3B, Table 3)

Trogolaphysa maya Mills, 1938 [23]: 184, 186; figures 13–16. Wilson [31]: 215, generic placement. Soto-Adames and Taylor [2]: 37, 39, 66, list Neotropical species.

Trogolapedetes maya Bonet, 1942 [32]: 59, new combination.

Trogolapedetes delamarei Massoud and Gruia, 1974 [33]: 339, figure 7E–H; Mari Mutt [34]: 282. Gruia [6]: 153, 154, figure 4a,b, 10–13, 15, descriptive notes.

Trogolaphysa delamarei Wilson, 1982 [35]: 215, new combination; Thibaud and Najt [27]: 723, new junior synonym of *T. maya*.

Description. Size to 2.9 mm. White. Eyes absent. Short chaetotaxy formula 53/60/45 + ? (Cuban population). Head with five anterior (A2, A3, M2, S2, S3) and four (Pa5, Pa2, Pa3, Pm3) posterior paired macrochaetae. Prelabral chaetae not reported. Labial formula $\underline{M1M2rEL1L2 A1-5}$. Mesothorax p3 complex with five macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with four inner (A3, A5, B5, B6) and five outer (D3, E3, E4, F1, F2) macrochaetae. Tenent hair acuminate and longer (1.62×) (Mexican population) or shorter (0.87×) (Cuban population) than unguiculus. Unguis (Figure 3B) with four inner teeth, all well-developed and distributed as 24, 38, 51, 78: basal teeth large, asymmetric, largest wedge-shaped, smaller elongate and sharply acuminate, both overlapping proximal unpaired tooth; both unpaired teeth well-developed, distal tooth longer and more slender than proximal. Unguiculus lanceolate, posterior margin serrate, 0.64× as long as inner edge of unguis. Mucro paraquadrate, 2.3× as long as wide, and four teeth.

Remarks. This is the only eyeless species with four large inner unguis teeth where the basal teeth are asymmetric and overlap the proximal unpaired tooth, the tenet hair is longer than the unguiculus, and the mucro is short and almost square.

Trogolaphysa delamarei was described from individuals collected at a single cave in Cuba and according to the original description, it differs from *T. maya* in the shape and relative size of the basal teeth of the unguis and in having a smooth unguiculus. Gruia [6] provided details of the dorsal and labial chaetotaxy of *T. delamarei* based on type material from Cuba. In support of Massoud and Gruia's [33] justification for recognizing *T. delamarei*, the original description shows a claw complex with unequal but symmetric basal teeth, a smooth and broadly lanceolate unguiculus, and tenent hair shorter (0.87×) than the unguiculus. However, Thibaud and Najt [27] examined the type specimens of *T. delamarei* and affirmed that there were no differences in claw structure between the holotype of *T. delamarei* and the illustrations accompanying the original description of *T. maya*. Mari Mutt [33] also reported *T. maya* (as *T. delamarei*) from a cave in the Dominican Republic, potentially extending the range of the species to the neighboring island of Hispaniola.

It seems unlikely that the Mexican and Cuban/Hispaniolan populations of such a specialized form are conspecifics. An alcohol preserved syntype of *T. maya* deposited at the Illinois Natural History Survey is in poor condition and little information on chaetotaxy would likely be drawn for it. Therefore, in the absence of information on the dorsal chaetotaxy in the population from Yucatan, and until fresh material from Mexico is obtained, and the morphological and genetic relatedness of the Mexican, Cuban and Dominican populations is examined, we accept the synonymy proposed by Thibaud and Najt [27].

The combination of external macrochaetae on Abd. 4 illustrated by Gruia [6] is unusual in suggesting that lateral macrochaetae E3 and E4 are present but E2 is absent. Since all other species reported here carry E2 it seems possible that either the specimen Gruia chose to illustrate was not typical or that the macrochaeta was left out of the drawing by mistake. Either way, we accept the description as stated.

This is the only species treated here having surface and subterranean populations, suggesting it is a troglophile.

Distribution. Mexico, Yucatan, Chichen Itzá, under rocks, N 20.6813, W 88.569; Balaam Canche, N 20.8902, W 88.1460, and Xkyc, N 20.5371, W 90.0318, caves. Cuba, cueva La Majana, (location information unavailable). Dominican Republic, Distrito Nacional, cueva Cofresí (location information unavailable).

22. *Trogolaphysa millsii* Arlé, 1939 [29]

(Figure 2N, Table 1)

Trogolaphysa millsii Arlé, 1939 [29]: 28, figures 14–16. Wilson [35]: 215, generic placement. Soto-Adames and Taylor [2]: 37, list Neotropical species. Soto-Adames, et al. [19]: 13, compared to *T. sauron*. Silva and Bellini [25]: 57, compared to *T. formosensis*. Bellini and Cipola [24]: 176, list of *Trogolaphysa* species reported from Brazilian Atlantic

Forest. Nunes and Bellini [26]: 94, key to Brazilian species *Trogolaphysa*. Cipola, et al. [22]: 290, key to Brazilian species *Trogolaphysa*.

Troglopedetes millsii Bonet, 1942 [32]: 59, new combination.

Troglopedetina millsii Delamare-Deboutteville, 1951 [36]: 293, new combination.

Description. Size to 0.6 mm. White with traces of red pigment all throughout head and body. Eyes 2 + 2. Dorsal chaetotaxy not described. Labral and labial chaetotaxy undescribed. Tenent hair acuminate and shorter (0.76x) than unguiculus. Unguis (Figure 2N) with three inner teeth distributed as 48, 48, 65: basal teeth well-developed, subequal, symmetric, wedge-shaped, nearly reaching unpaired tooth; unpaired tooth much smaller than basal teeth. Unguiculus truncate, smooth, 0.68x as long as inner edge of unguis. Mucro rectangular, 3.0x as long as wide, with four teeth.

Remarks. This is the only species with 2 + 2 eyes, three inner unguis teeth and truncate unguiculus. *Trogolaphysa aelleni* also has 2 + 2 eyes and three unguis teeth, but the basal teeth are minute and do not reach the unpaired tooth, and the unguiculus is lanceolate and slender. Nine other species have three inner unguis teeth (Table 1), but they either lack eyes or have a different number of eyes. This is an epigeal species.

Distribution. Brazil, Distrito Federal, Represa dos Ciganos, S 22.977, W 43.3662.

23. *Trogolaphysa oztolica* (Ojeda and Palacios-Vargas, 1984) [31]

(Figure 3D, Table 3)

Troglopedetes oztolicus Ojeda and Palacios-Vargas, 1984 [31]: 1, 6–20, figures 1–14. Palacios-Vargas et al. [7]: 10, 28, identification key, descriptive notes.

Trogolaphysa oztolica Thibaud and Najt, 1988 [27]: 723, new combination. Soto-Adames and Taylor [2]: 37, list Neotropical species.

Description. Size to 3.0 mm. White. Eyes absent. Dorsal chaetotaxy not described. Prelabral chaetae smooth. Labial formula $\overline{M1M2rEL1L2}$ A1–5. Tenent hair acuminate and shorter (0.66x) than unguiculus. Unguis (Figure 3D) with four inner teeth distributed as 43, 43, 67, 85: basal teeth small, subequal, symmetric, wedge-shaped, not reaching proximal unpaired tooth; proximal unpaired tooth smaller than basal teeth; distal unpaired tooth minute. Unguiculus lanceolate to weakly excavate, with minute serrations on inner edge, 0.70x as long as inner edge of unguis. Mucro with four teeth, rectangular, 3.0x as long as wide.

Remarks. This troglobiont is the only eyeless species with four small, wedge-shaped inner unguis teeth, basal teeth symmetric, and a weakly excavate lanceolate unguiculus. Six other eyeless species have four inner unguis teeth and acuminate tenent hair, but all have distinct claws with well-marked inner teeth (Table 3).

Distribution. Mexico, Guerrero, Gruta de Juxtahuaca, on guano, N 17.4414, W 99.1607.

24. *Trogolaphysa reneaui*, n. sp. Soto-Adames, Daly and Wynne

urn:lsid:zoobank.org:act:0DDCFF02-87B2-4C3F-9F39-6F5E1F753765

(Figures 4A, 5, 6 and 7, Table 2)

Etymology. This species is named for Stevan Reneau, former Director of Environmental Education at Runaway Creek Nature Reserve. Reneau is also an accomplished field biologist and cave explorer.

Material examined. Holotype female, microscope slide mounted, accession # FSCA00051050. BELIZE, Belize District, Runaway Creek Nature Reserve, Crocodile Cave 1 (17.3071, –88.4802) deep zone, 24.vii.2019, J.J. Wynne, leg. Paratypes all mounted on microscope slides, two adult females (FSCA00000114, FSCA00000115) on individual slides and one adult male mounted together with one immature female on the same slide (FSCA00000116), with same collection information as holotype, but Crocodile Cave 2 (N 17.3075, W 88.434).

Description. Size to 3.3 mm. Scales present on Ant. 1–2, absent from all other antennal and leg segments, and colophore. Complete dorsal macrochaetae formula (Figure 5A,B) 52/42/02445 + 7; summary formula 42/42/45 + 7.

Color pattern. White, with yellowish tinge (Figure 4A).

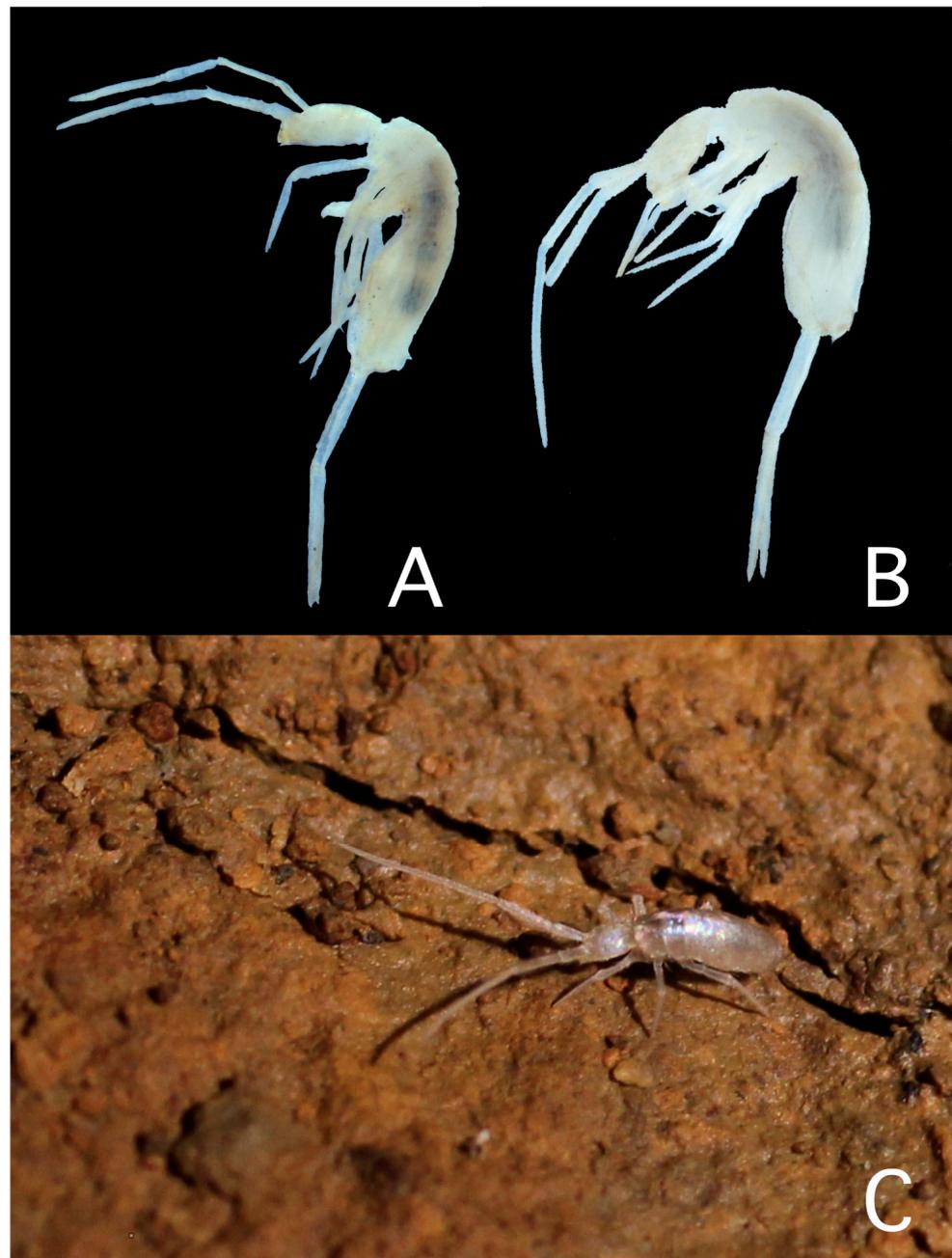


Figure 4. *Trogolaphysa* habitus of (A) *T. reneaui* n. sp. and (B,C) *T. welchi* n. sp.

Head. Antennae up to $3.0\times$ as long as head (Figure 4A). Antennal segments 3–4 lost in all specimens during slide making process. Eyes 1 + 1 (Figure 5C), sometimes seemingly eyeless. Extra ocular structure not seen. Number of ocellar chaetae unclear. Dorsal chaetotaxy of head as in Figure 5A,C: series An3 with two macrochaeta, An3p absent; with one unpaired (A0), and six paired (A2, A3, M2, S5, Pa5, Pm3) macrochaetae. Prelabral and labral chaetae formula 4/5,5,4, all smooth. Labral chaetae as in Figure 5D: proximal row with element p2 gradually tapered and appreciably longer than p0 and p1; medial row chaetae m1 longest, m2 shortest; chaetae on distal row subequal. Distal margin of labrum (Figure 5E) without spines but with minute paired medial carinae; ventral face of labrum with bilobed bulb covered with minute spines. Basal pleural chaeta coarsely ciliate, distal pleural chaeta short and smooth, spine-like. Outer maxillary lobe as in *T. welchi* n. sp. (Figure 8F), with basal seta smooth and subequal to slightly shorter than apical appendage; sublobal plate smooth, without appendages. Lateral appendage of

labial papillae E (Figure 5F) long, blunt, thin walled, curving dorsally and not reaching tip of papilla. Proximal labial chaetae smooth. Labial triangle (Figure 5I) formula as $M1M2rEL1L2$ A1–5: chaetae M subequal, M1 ciliate, M2 smooth; r reduced and coarsely ciliate; E smooth, not differentiated from A2; chaeta A2 displaced posteriorly, almost aligned with chaetae E on posterior row. All post-labial chaetae ciliate: cephalic groove with three anterior and two posterior marginal chaetae separated by large scales (2–3, and 1) as in Figure 6A–D; rows G, H and J with 4, 4, and 3 chaetae, respectively; chaeta Xp present; 4–5 medial chaetae posterior to row J (arrows in Figure 6B–D), 2–4 other chaeta latero-posterior to J present. Ventral cervical chaetae 5(6) + 5(6) anterior and 6 + 6 posterior in a row (Figure 6A).

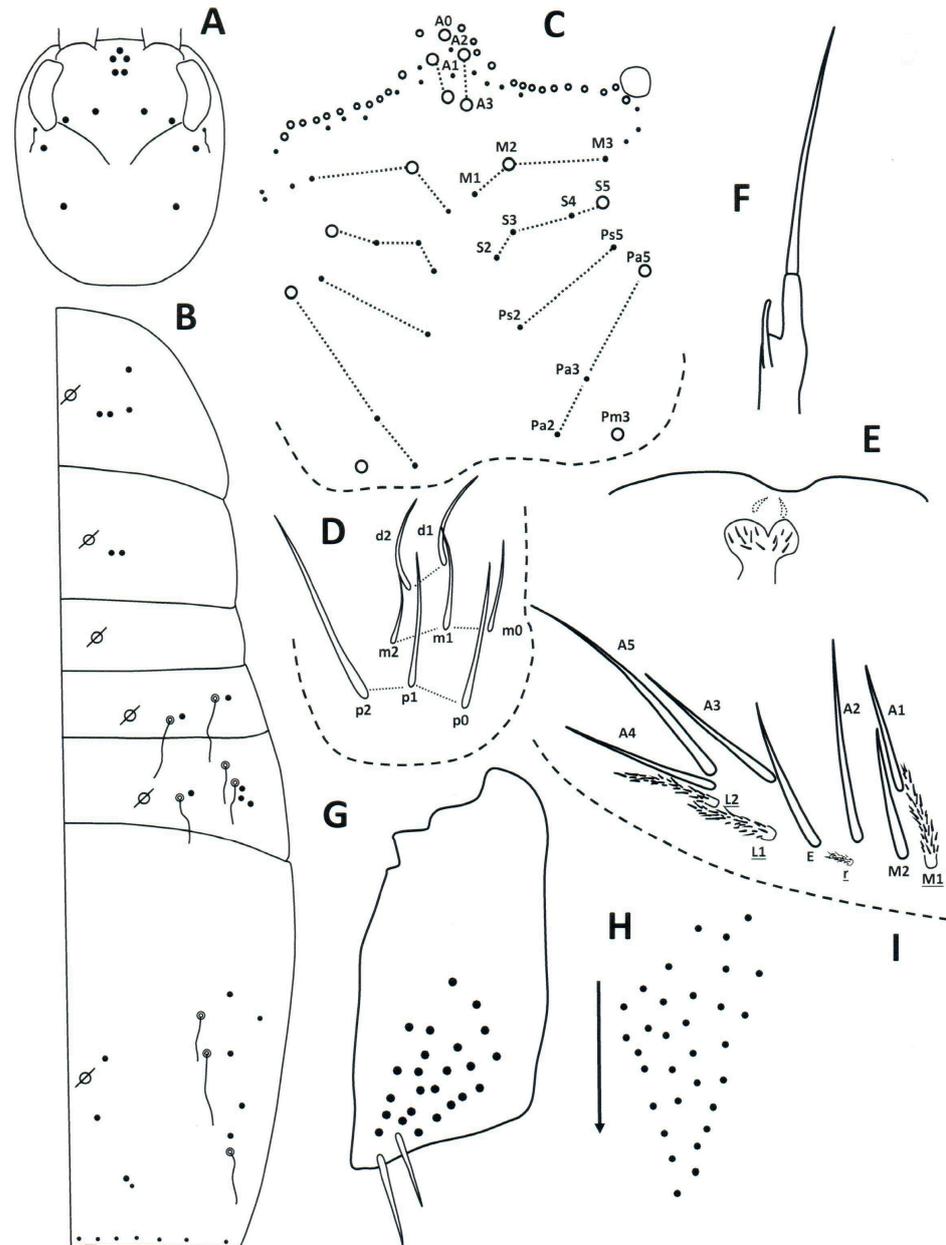


Figure 5. *Trogolaphysa reneauui* n. sp. (A) Head macrochaetae map. (B) Trunk macrochaetae map. (C) Detail of head chaetotaxy. (D) Labral chaetotaxy, left side. (E) Distal margin of labrum. (F) Lateral appendage on labial papilla E. (G,H) Distribution of setae on hind leg trochanteral organ, arrow points towards distal end. (I) Labial triangle chaetotaxy.

Body. Mesothorax with one anterior (a5) and three posterior (p3 complex) macrochaeta, external macrochaeta of p3 complex characteristically separated from inner macrochaetae (Figures 5B and 6E). Metathorax (Figures 5B and 6E) with two (p2, p3) macrochaetae. Abdominal segment 1, chaeta a6 absent; Abd. 2 with two (m3, m5) macrochaetae; Abd. 3 with four (m3, am6, pm6, p6) macrochaetae. Fourth abdominal segment (Figure 6F,G) with four inner (A4, A5, B5, B6) and five large outer macrochaetae (D3, E2, E3, F1, F2); elements A3 and A6 unmodified microchaetae; outer section with additional long and slender macrochaetae sometimes present (Figure 6F,G and Figure 7A); posterior chaetae 7 + 7; Abd. 4–5 inter segmental membrane usually with five lenticular organs (only three visible in holotype). Distribution of macrochaetae on Abd. 5 as in Figure 6H.

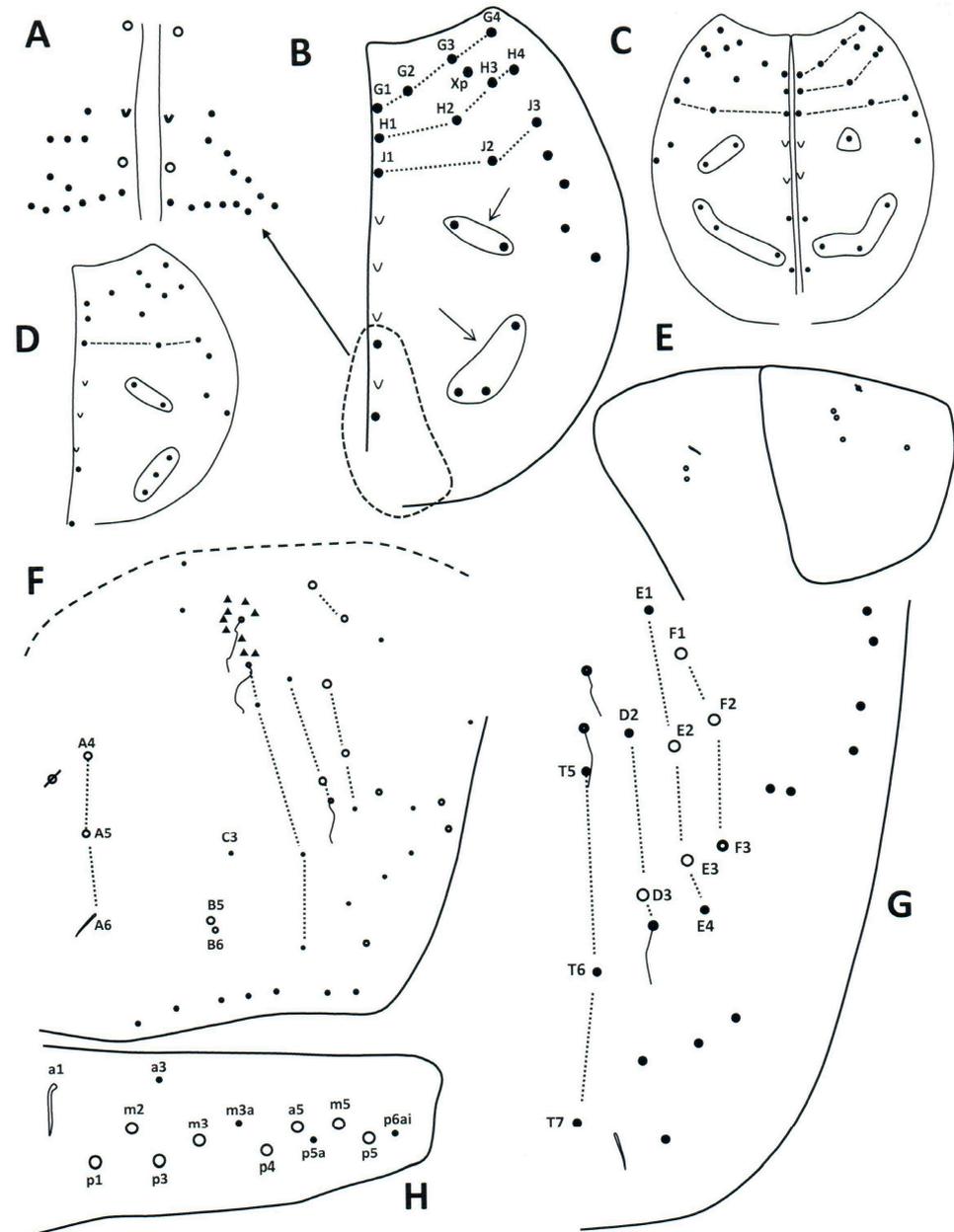


Figure 6. *Trogolaphysa reneai* n. sp. Symbols as in Figure 5. (A) Detail ventral cervical chaetotaxy. (B–D) Variation in post-labial setae distribution. (E) Distribution of thoracic macrochaetae. (F) Fourth abdominal segment dorsal chaetotaxy. (G) Fourth abdominal segment, detail of dorso-lateral chaetotaxy in a different individual. (H) Dorsal chaetotaxy of fifth abdominal segment.

Legs. Trochanteral organ trapezoidal, with up to 33 chaetae (Figure 5G,H). Hind claw complex as in Figure 7B,C: tenent hair acuminate, subequal to unguiculus, proportion tenent hair/unguiculus = 0.93–1.08; claw with two well-developed sharply acuminate unequal inner teeth (Figure 7C,D); teeth spread 18, 19. Unguiculus lanceolate (Figure 7B,E) to weakly truncate (Figure 7C), 0.62–0.70x as long as inner edge of unguis, posterior edge smooth.

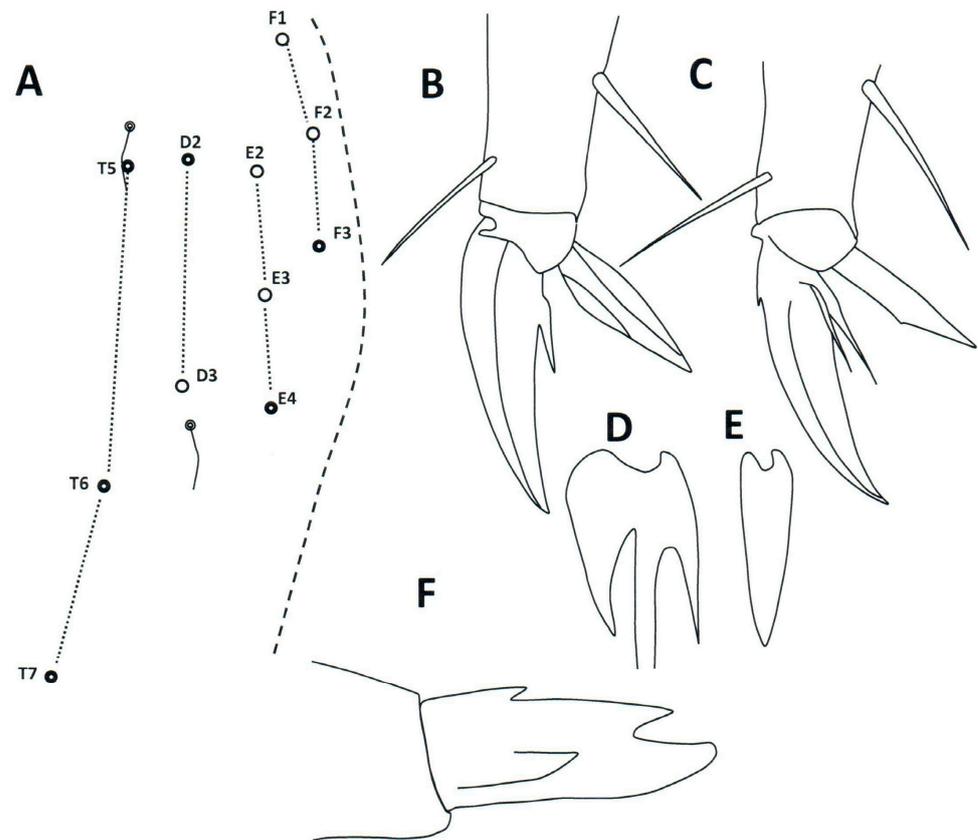


Figure 7. *Trogolaphysa reneai* n. sp. (A) Fourth abdominal segment, arrangement of dorso-lateral chaetotaxy in a different individual. (B,C) Hind claw complex in female and male, respectively, tooth shown in (B) is homologous to left tooth in (C). (D) Ventral view of basal teeth. (E) Different perspective of hind unguiculus in female. (F) Mucro.

Furcula. Dens with two rows of ciliate spines, inner row with up to 54 spines, outer row with 50 spines. Mucro paraquadrated, 2.44 times as long as wide, with four teeth (Figure 7F).

Remarks. *Trogolaphysa reneai* n. sp. is the only member of the genus with summary chaetotaxy formula 42/42/45 + 7. In addition, the new species is the only form with 0 + 0 to 1 + 1 eyes, inner edge of hind claw with two teeth, tenent hair acuminate and subequal in length to the unguiculus, and labial microchaeta r ciliate. Four other species (*T. barroca*, *T. haitica*, *T. hauseri* and *T. sotoadamesi*) are eyeless, carry two inner unguis teeth and have a four-toothed mucro. The species most similar to *T. reneai* n. sp. is *T. haitica*, which shares the same general shape of the hind unguis. However, the two species differ in that the tenent hair is shorter (0.62x) relative to the unguiculus in *T. haitica* (up to 1.08x in *T. reneai* n. sp.), and in having labial triangle chaeta M2 ciliate and r smooth (chaeta M2 smooth and chaeta r coarsely ciliate in *T. reneai* n. sp.). *Trogolaphysa hauseri* also has only two inner unguis teeth, but they are asymmetric (symmetric in the new species) and the unguiculus is lanceolate narrow (lanceolate wide or weakly truncate in the new species). *Trogolaphysa barroca* and *T. sotoadamesi* also have two-toothed unguis but they have five macrochaetae in the p3 complex on Th. 2 and do not carry macrochaetae on Th. 3,

whereas in the new species the p3 complex on Th. 2 carries three macrochaetae and Th. 3 carries two macrochaetae.

Table 2 provides diagnostic characters for all Neotropical species with two inner unguual teeth and fewer than six eyes.

25. *Trogolaphysa sotoadamesi* Ferreira, Oliveira and Zeppelini, 2022 [3]

(Table 2)

Trogolaphysa sotoadamesi Ferreira, Oliveira and Zeppelini in Zeppelini et al., 2022 [3]: 12, identification key; 20, table 2; 26–28, description; 30–32, figures 24–26.

Description. Size to 1.81 mm. White. Eyes absent. Summary dorsal chaetotaxy formula as 12/60/37 + ?. Head dorsally with one anterior (A2) and two posterior (Pa5, Pm3) paired macrochaetae. Prelabral chaetae ciliate. Labial formula M1M2rEL1L2 A1–5. Mesothorax p3 complex with five macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with three inner (B4, B5, B6) and seven outer macrochaetae (Te3, D3, E2, e3, e4, F1, F3). Tenent hair acuminate and subequal (0.97×) to unguiculus. Unguis with two teeth distributed as 18, 18: basal teeth well-marked, subequal, and lunate. Unguiculus lanceolate wide, smooth, 0.76× as long as inner edge of unguis. Mucro sub-rectangular, 2.56× as long as wide and with four teeth.

Remarks. This troglobiont is the only eyeless species with two well-marked asymmetric inner unguual teeth, four mucronal teeth, and Abd. 4 with macrochaeta Te3. *Trogolaphysa sotoadamesi* is most similar to *T. barroca*, but whereas in the latter form the basal unguual teeth are asymmetric (one wedge-like and one lunate), in the former species both basal teeth are lunate.

Distribution. Brazil, Minas Gerais, Mariana, ALEA 0003 cave near Mina de Alegria, S 20.1519, W 43.48712.

26. *Trogolaphysa strinatii* Yoshii, 1988 [5]

(Figure 3A, Table 1)

Trogolaphysa strinatii Yoshii, 1988 [5]: 452–453, figure 2A–F. Soto-Adames and Taylor [2]: 37, list of Neotropical species.

Description. Size to 2.0 mm. White with dusky diffused pigment all over. Eyes 5 + 5. Dorsal chaetotaxy not described. Prelabral chaetae ciliate. Labial formula M1M2rEL1L2 A1–5. Tenent hair capitate and subequal (0.94×) to unguiculus. Unguis (Figure 3A) with three inner teeth distributed as 40, 40, 73: basal teeth small, subequal, symmetric, wedge-shaped, not reaching unpaired tooth; unpaired tooth smaller than basal teeth. Unguiculus smooth, narrowly lanceolate, tapering apically, 0.69× as long as inner edge of unguis. Mucro sub-square 2.31× as long as wide and with four teeth.

Remarks. This troglophile is the only species of *Trogolaphysa* with 5 + 5 eyes, spatulate tenent hair and three small unguual teeth. None of the other species with reduced eye number approaches *T. strinatii*. According to Yoshii [5], *T. strinatii* is similar to Mexican populations of what he identified as *T. carpenteri* (Denis), however, *T. carpenteri* has 8 + 8 eyes and smooth prelabral chaetae, whereas *T. strinatii* has 5 + 5 eyes and ciliate prelabral setae.

Distribution. Mexico, Guerrero, Sima del Borrego and Resumidero de Xocomanatlán, N 17.5436, W99.63.

27. *Trogolaphysa tijucana* (Arlé and Guimarães, 1979) [28]

(Figure 2H, Table 2)

Paronella tijucana Arlé and Guimarães, 1979 [28]: 213–216, figures 1–10. Thibaud and Najt (1988) [26]: 723, uncertain generic placement.

Troglopedetes tijucana Palacios-Vargas et al., 1985 [7]: 9, new combination, identification key.

Trogolaphysa tijucana Mari Mutt and Bellinger, 1990 [37]: 123, new combination, catalog. Soto-Adames and Taylor [2]: 37, list Neotropical species. Soto-Adames et al. [19]: 13, compared to *T. sauron*. Silva and Bellini [25]: 57, compared to *T. formosensis*. Bellini and Cipola [24]: 176, list of *Trogolaphysa* species of the Brazilian Atlantic Forest. Nunes and

Bellini [26]: 94, identification key Brazilian *Trogolaphysa*. Cipola et al. [22]: 290, key to Brazilian *Trogolaphysa*. Zeppelini et al. [3]: 12, identification key; 20, diagnostic table.

Description. Size to 0.8 mm. Background color yellowish or whitish with dark pigment on Ant. 3–4, Th. 2–Abd. 2, coxae, trochanters, and colophore. Eyes 2 + 2. Dorsal chaetotaxy not described. Prelabral and labial chaetotaxy not described. Tenent hair acuminate and subequal ($0.90\times$) to unguiculus. Unguis (Figure 2H) with two inner teeth distributed as 43, 43: basal teeth wedge-shaped, symmetric but unequal, one much larger. Unguiculus smooth, truncate, about $0.62\times$ as long as inner edge of unguis. Mucro rectangular, $3.19\times$ as long as wide, with four teeth.

Remarks. No other Neotropical member of *Trogolaphysa* has 2 + 2 eyes, two unequal inner unguis teeth, and truncate unguiculus. Only *T. millsii* and *T. trioculata* Soto-Adames also have a clearly truncate unguiculus, but both species have three inner unguis teeth.

The presence of color pattern and collection location suggest this is a troglophile. The species was collected in leaf litter in a cave and in surface forest.

Distribution. Brazil, Rio de Janeiro, Maciço da Tijuca, in an unnamed grotto and in surface forest leaf litter, S 22.9521, W 43.2907.

28. *Trogolaphysa trioculata* Soto-Adames, 2015 [20]

(Figure 2O, Table 1)

Trogolaphysa trioculata Soto-Adames, 2015 [20]: 35, figures 3G, 20A–F, diagnostic table 5; original description.

Description. Size to 1.1 mm. White. Eyes 3 + 3. Short chaetotaxy formula 12/60/44 + 9–10. Head dorsally with one anterior (A2) and two posterior (Pa5, Pm3) paired macrochaetae. Prelabral chaetae ciliate. Labial formula $\underline{M1M2rEL1L2}$ A1–5. Mesothorax p3 complex with five macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with four inner (A3, A5, B5, B6) and four outer (D3, E2, E3, F1) macrochaetae. Tenent hair acuminate and shorter ($0.75\times$) than unguiculus. Unguis with three inner teeth distributed as 18, 43, 43: basal teeth asymmetric, proximal basal tooth wedge-shaped and larger than distal lunate one, distal basal tooth overlapping unpaired tooth. Unguiculus truncate, smooth, $0.71\times$ as long as inner edge of unguis. Mucro rectangular $3.38\times$ as long as wide, with four teeth.

Remarks. This is the only species of *Trogolaphysa* with three unguis teeth, 3 + 3 eyes and truncate unguiculus. The species is also unique in the peculiar asymmetry and distal displacement of one basal unguis tooth (Figure 2O). *Trogolaphysa millsii* is the only other member of the genus with three unguis teeth and (weakly) truncate unguiculus, but the basal teeth are paired, subequal, and considerably larger than the proximal unpaired tooth (Figure 2N).

Trogolaphysa trioculata was collected in surface leaf litter and despite having a reduced number of ocelli it is not associated with subterranean habitats.

Distribution. Mexico, Chiapas, Cacahuatan, N 14.9954, W 92.1865.

29. *Trogolaphysa variabilis* (Palacios-Vargas, Ojeda and Christiansen, 1985) [7]

(Figure 3G, Table 3)

Trogolapedetes variabilis Palacios-Vargas, Ojeda and Christiansen, 1985 [7]: 18–20, figure 7C–E, original description.

Trogolaphysa variabilis Thibaud and Najt, 1988 [27]: 723, new combination. Soto-Adames and Taylor [2]: 37, list Neotropical species.

Description. Size to 2.8 mm. Dark pigment only on eye patch, otherwise unpigmented. Eyes 4 + 4–6 + 6. Dorsal chaetotaxy not described. Prelabral chaetae ciliate. Labial formula $\underline{M1M2rEL1L2}$ A1–5. Tenent hair acuminate and subequal ($0.95\times$) to unguiculus. Unguis (Figure 3G) with four inner teeth distributed as 34, 34, 63, 86: basal teeth well-developed, subequal, wedge-shaped to weakly lunate, not reaching proximal unpaired tooth; proximal and distal unpaired teeth small, wedge-like. Unguiculus lanceolate, tapering distally, posterior margin serrated, $0.63\times$ as long as inner edge of unguis. Mucro sub-rectangular $2.5\times$ as long as wide, with four teeth.

Remarks. This is the only species with 4 + 4 to 6 + 6 eyes, labial chaetae r and E smooth, acuminate tenet hair, and four inner unguual teeth with a distal unpaired tooth much shorter than the proximal unpaired tooth. It is generally similar to *T. welchi* n. sp. in claw morphology, but the number of eyes, ornamentation of unguiculus (serrated in *T. variabilis*, smooth in *T. welchi* n. sp.) and shape of distal unpaired tooth (short wedge in *T. variabilis*, elongate in *T. welchi* n. sp.) will easily distinguish them.

The presence of a pigmented eye patch with 4–6 ocelli suggests this is a troglophile.

Distribution. Mexico, Veracruz, Cueva de Ungurria, N 18.548, W 96.7568.

30. *Trogolaphysa welchi*, n. sp. Soto-Adames, Daly and Wynne

urn:lsid:zoobank.org:act:486DDBFC-1658-439A-BF70-FDD58B1AC22F

(Figure 4B,C, Figures 8 and 9, Table 3)

Etymology. This species is named for Gilroy “Nico” Welch, Director of Health and Safety at Runaway Creek Nature Reserve, Belize. Welch is also an accomplished field biologist and cave researcher.

Material examined. Holotype male, slide mounted, accession # FSCA00051049. BELIZE, Belize District, Runaway Creek Nature Reserve, BatSub Cave (N 17.3071, W 88.4802), right passage, deep zone, 30.vii.2019, J.J. Wynne, leg. Paratypes, slide mounted, one immature male (FSCA00000113), and one adult female (FSCA00000112; furcula missing) with same information as holotype.

Description. Size up to 2.2 mm (holotype = 1.6 mm). Scales present on Ant. 1 and basal 1/4 of Ant. 2, absent from all other antennal segments, legs, and collophore. Complete dorsal macrochaetae formula (Figure 8A,B) 42/72/02435 + 13–14; summary formula 32/72/35 + 13–14

Color pattern. Alcohol preserved specimens unpigmented (Figure 4A).

Head. Antennae up to 4.7× as long as head (Figure 4B,C). Middle section of Ant. 4 with weakly defined subsegments, dorsally each subsegment carries chaetae arranged in a single row, ventral chaetae arranged into two or three rows, rendering ventral sub-segmentation indistinct. Subapical sense organ not seen. Sensilla on Ant. 3 sense organ heteromorphic, one a normal rod, one clubbed (Figure 8C). Eyes 2 + 2 (Figure 8D), only A and B present. Extra ocular structure not seen. Number of ocellar chaetae unclear. Dorsal chaetotaxy of head as in Figure 8A,D series An3 with two macrochaetae, An3p absent; with one unpaired (A0), and five paired (A2, A3, S5, Pa5, Pm3) macrochaetae. Prelabral and labral chaetae smooth (Figure 8E): proximal row of labral chaetae with element p2 longest; chaetae in medial row representing three size classes (Figure 8E); chaetae in distal row subequal. Distal margin of labrum smooth, without spines. Basal pleural chaeta coarsely ciliate, distal pleural chaeta short, and smooth, spine-like. Outer maxillary lobe (Figure 8F) with basal chaeta smooth and subequal to apical appendage; sublobal plate without appendages. Lateral appendage of labial papillae E (Figure 8G) long, blunt, thin walled, curving dorsally, and not reaching tip of papilla. Proximal labial chaetae smooth. Labial triangle (Figure 8H) formula in females as $M1M2rEL1L2 A1-5$: r reduced but coarsely ciliate; E smooth, not differentiated from A2; labial chaeta L2 shorter than L1 and inserted farther from L1 than usual; chaeta A2 displaced posteriorly, almost aligned with chaetae on posterior row; males (holotype) with similar arrangement but chaeta r smooth (Figure 8I). All post-labial chaetae ciliate: cephalic groove with 4–5 marginal chaetae, three anterior and 0–1 posterior separated by three large scales (Figure 9A,B); rows G, H and J with 4, 4, 3 chaetae, respectively, supplementary chaeta Xp present, two medial and 3–4 lateral chaetae posterior to row J; medio-posterior chaetae absent (Figure 9A). Ventral cervical chaetae (Figure 9B) forming two clusters, an anterior group with 5 + 5 elements and a posterior row with 9 + 9 elements.

Body. Distributions of trunk macrochaetae as in Figure 8A: mesothorax with one anterior (a5) and six posterior (p3 complex) macrochaeta; metathorax with two macrochaetae (p2, p3), socket of chaeta a4 enlarged in holotype. First abdominal segment chaeta a6 absent; Abd. 2 with macrochaetae m3 and m5; Abd. 3 with macrochaetae m3, am6, pm6 and p6. Fourth abdominal segment (Figure 9C) with inner macrochaetae A4, B5 and B6;

elements A3, A5 and A6 unmodified microchaetae; lateral macrochaetae D3, E2, E3, F1, and F2 present; posterior chaetae 13–14 + 13–14. Intersegmental membrane between Abd. 4 and 5 with 4–6 + 4–6 lenticular organs. Distribution of macrochaetae on Abd. 5 as in Figure 9D.

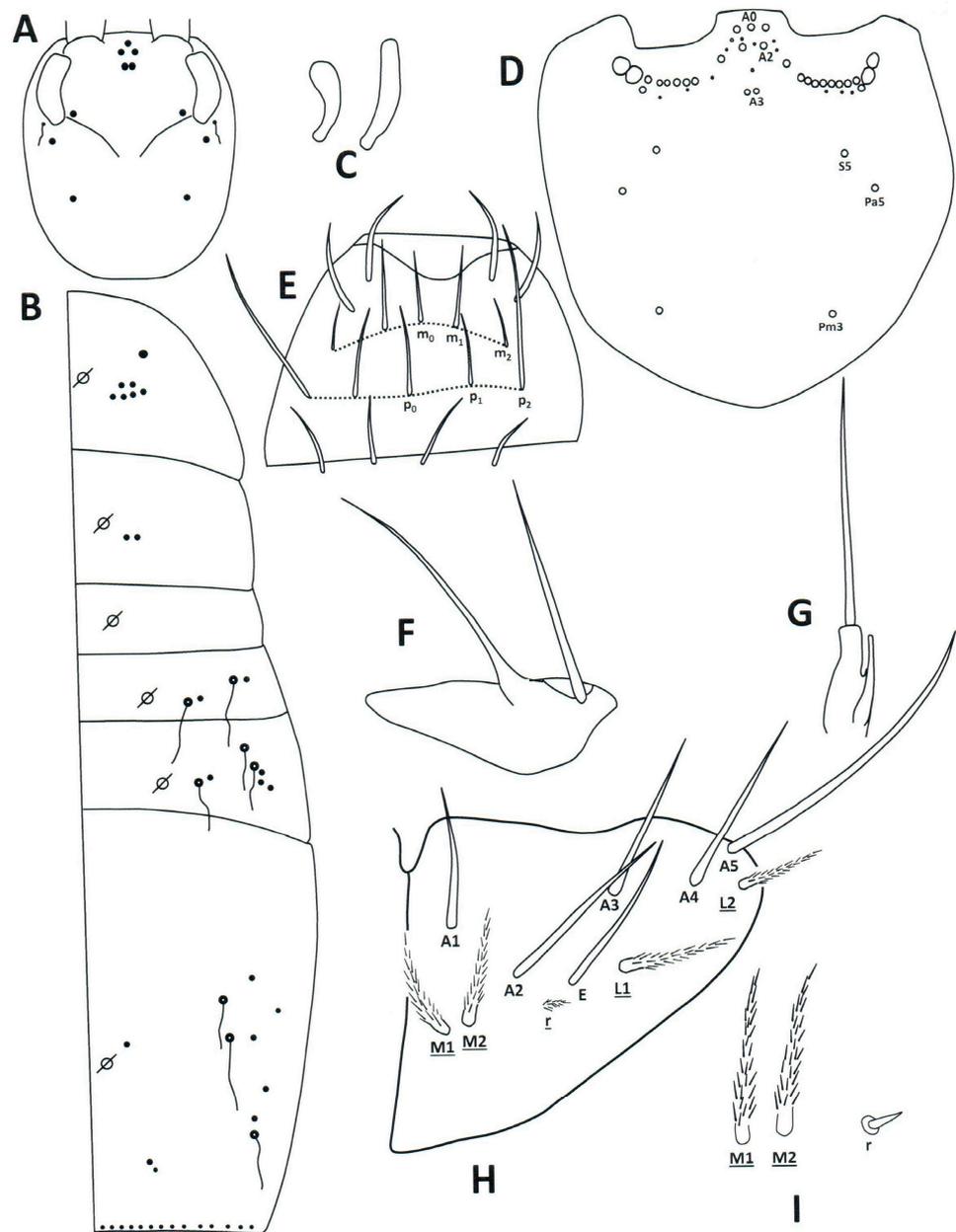


Figure 8. *Trogolaphysa welchi* n. sp. (A) Head macrochaetae map. (B) Trunk macrochaetae map. (C) Ant. 3 sense organ sensilla. (D) Detail of head macrochaetae. (E) Prelabral chaetae and labral chaetotaxy. (F) Outer maxillary lobe. (G) Lateral appendage on labial papilla E. (H) Female labial chaetotaxy. (I) Detail of inner posterior labial chaetae in males.

Legs. Trochanteral organ V-shaped, with at least 23 chaetae (Figure 9E). Metathoracic claw complex as in Figure 9F,G: tenent hair acuminate, subequal to unguiculus, proportion tenent hair/unguiculus = 1.00; claw with four well-developed inner teeth, basal teeth offset, making one tooth seem larger than other, one sub-lunate, other wedge-shaped; proximal unpaired tooth well-marked, distal unpaired tooth relatively long but following curvature of unguis tightly rather than projecting; inner teeth spread in male as 35, 43, 57, 74 (spread could not be measured in females available). Outer teeth (Figure 9G) ending on basal

quarter of unguis; dorsal tooth minute, barely projecting beyond edge of basal tunica; lateral teeth thick. Unguiculus lanceolate, posterior edge smooth.

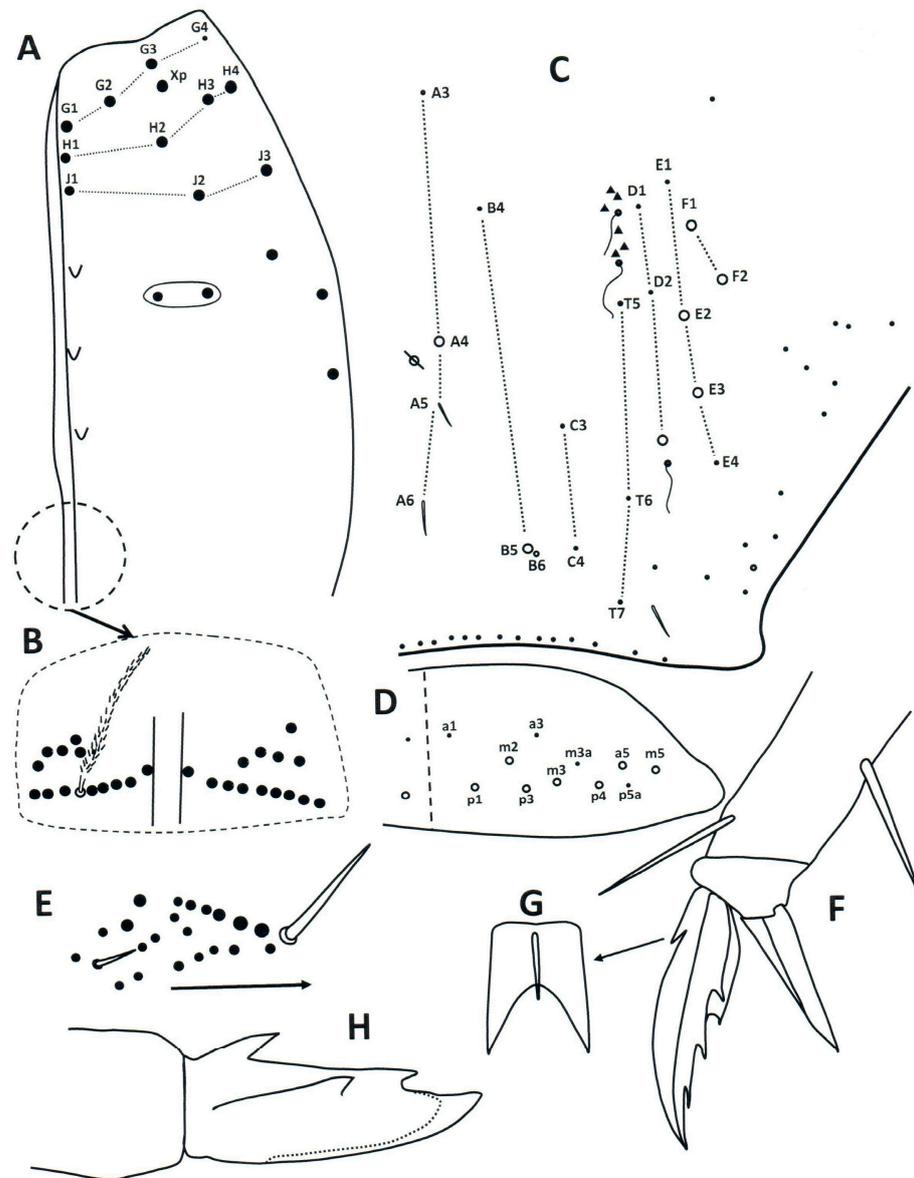


Figure 9. *Trogolaphysa welchi* n. sp. (A) Post-labial chaetotaxy, large dots, small dots and 'V' represent ciliate mesochaetae, microchaetae, and scales, respectively. (B) Detail of ventral cervical chaetae. (C) Dorsal chaetotaxy of fourth abdominal segment, dots as in (A), open circles represent macrochaetae, triangles represent fan-shaped microchaetae. (D) Dorsal chaetotaxy of fifth abdominal segment. (E) Hind leg trochanteral organ, arrow point towards distal end. (F) Hind leg claw complex. (G) Dorsal view of outer teeth on hind unguis. (H) Mucro.

Furcula. Dens with two rows of ciliate spines, in males both rows with up to 33 spines; largest female with 44 inner and 34 outer spines. Mucro paraquadrangle, $2.26\times$ as long as wide, with four sequential teeth (Figure 9H).

Remarks. No other species of *Trogolaphysa* has two eyes, unguis with four inner teeth, two metathoracic macrochaetae, and acuminate tenent hair. In addition, *T. welchi* n. sp. is the only member of the genus with the summary macrochaetae formula $32/72/35 + 13-14$. *Trogolaphysa bellinii* from Brazil is the only other Neotropical species with $2 + 2$ eyes and four inner unguis teeth, but the Brazilian species has spatulate tenent hair (acuminate

in *T. welchi* n. sp.), lacks metathoracic macrochaetae (two in the new species) and has seven posterior chaetae on Abd. 4 (13–14 chaetae in the new species).

The reduced number of eyes, pigment, the relative length of the antennal, and the fact that it was collected deep in the dark zone indicate this species is a troglobiont.

31. *Trogolaphysa xtolokensis* (Palacios-Vargas, Ojeda and Christiansen, 1985) [7]

(Figure 3C, Table 3)

Trogolapedetes xtolokensis Palacios-Vargas, Ojeda and Christiansen, 1985 [7]: 8, 10–12; figures 1, 2A–F and 3A–E, original description.

Trogolaphysa xtolokensis Thibaud and Najt, 1989 [27]: 723, new combination. Soto-Adames & Taylor [2]: 37, list Neotropical species.

Description. Size to 2.6 mm. White. Eyes absent. Dorsal chaetotaxy not described. Prelabral chaetae smooth. Labial formula $\underline{M1M2rEL1L2}$ A1–5. Tenent hair acuminate and subequal ($0.91\times$) to unguiculus. Unguis with four inner teeth distributed as 36, 36, 67, 81: all teeth well-developed, acuminate and elongate; basal teeth subequal, not reaching proximal unpaired tooth; proximal and distal unpaired teeth subequal. Unguiculus lanceolate, tapering distally, posterior margin serrated, $0.67\times$ as long as inner edge of unguis. Mucro rectangular, $3.2\times$ as long as wide, with four teeth.

Remarks. This troglobiont is the only eyeless member of the genus with serrated unguiculus, all unguis teeth acuminate and elongate, and labial chaetae r, E, L1 and L2 smooth. The organization of inner unguis teeth in *T. xtolokensis* is similar to that in *T. variabilis*, but the shape and size of the teeth is quite distinct (see Figure 3C,G). Only *T. maya* has unpaired unguis teeth as well-developed as in *T. xtolokensis*, but they differ in shape (in *T. maya* three teeth are wedge-shaped, whereas in *T. xtolokensis* all are acuminate); in addition, the basal teeth in *T. maya* are asymmetric and reach the proximal unpaired tooth whereas in *T. xtolokensis* the basal teeth are symmetric and do not reach the unpaired teeth.

Distribution. Mexico, Yucatan, Cueva del Cenote Xtolok, N 20.6803, W 88.5715.

32. *Trogolaphysa zampauloi* Lima, Olivieri and Zeppelini, 2022 [3]

(Table 3)

Trogolaphysa zampauloi Lima, Olivieri and Zeppelini in Zeppelini et al., 2022 [3]: 3, table 1; 12, identification key; 20, table 2; 36–38, description; 42–44, figures 36–38.

Description. Size to 1.91 mm. White. Eyes 0 + 0 to 4 + 4. Summary dorsal chaetotaxy formula as 42/60/56 + ?. Head dorsally with four anterior (A2, A3, A4, A5) and two posterior (Pa5, Pm3) macrochaetae. Prelabral chaetae ciliate. Labial formula $\underline{M1M2rEL1L2}$ A1–5. Mesothorax p3 complex with five macrochaetae. Metathorax without macrochaetae. Fourth abdominal segment with five inner (A3, A5, B4, B5, B6) and six outer macrochaetae (D3, E2, E3, E4, F1, F3). Tenent hair acuminate and subequal ($0.93\times$) to unguiculus. Unguis with four teeth distributed as 29, 29, 65, 88: basal teeth well-marked, symmetric, subequal and wedge-like, not reaching proximal unpaired tooth; proximal unpaired tooth well-developed, wedge-like; distal unpaired tooth minute. Unguiculus lanceolate wide, smooth, $0.88\times$ as long as inner edge of unguis. Mucro rectangular, $3.45\times$ as long as wide, with four teeth.

Remarks. This troglobiont is the only species with four inner unguis teeth in which the basal teeth are symmetric, subequal and well-marked, there are four anterior head macrochaetae and the mesothoracic p3 complex has five macrochaetae. The general morphology of the unguis in *T. zampauloi* is similar to that in *T. bellini*, *T. chapelensis*, *T. lacerta*, *T. oztolica*, and *T. variabilis*, but *T. bellini* has a spatulate tenent hair (acuminate in *T. zampauloi*), *T. oztolica* has an excavate unguiculus (lanceolate in *T. zampauloi*), *T. variabilis* has a smooth M2 in the labial triangle (ciliate in *T. zampauloi*), and *T. chapelensis* and *T. lacerta* have only one anterior head macrochaeta (four in *T. zampauloi*).

Distribution. Brazil: Sao Paulo, Ribeira, cave MTD-13, near Serra Pontalhao, S 24.6471, W 48.9665.

3.2. Character Analysis

1. Ratio antennal length to head diagonal. This is a continuous character and as such difficult to use for diagnosis. Partitions are arbitrary, and only useful to diagnose species with ratios at the ends of the distribution (antennae either much longer or much shorter than the average). The problem is compounded because head measurements may not be consistent across authors. Head diagonal is typically measured on a sideview of the head, from its posterior margin to the tip of mouth cone; however, some authors measure the head on flattened, slide-mounted specimens, which consistently yields shorter head lengths. Some authors (e.g., [2,3,22]) calculate the antennal ratio with respect to trunk length, instead of head length. Although this new ratio may be more consistent than the traditional ratio, it prevents comparisons with most published data.

Additionally, it is unclear that in *Trogolaphysa* long antennae is a result of adaptation to cave habitats, as many surface species also have long antennae (see [20,22]).

2. Eye Number. All states, from 0 + 0 to 5 + 5, are represented in the species included here, but the most common character state is absence of eyes (in 20 species). Four species have been reported as having a variable number of eyes per side (e.g., *T. zampauloi* with 0 or four, *T. bellini* with 0 or three, *T. lacerta* with 0 or two, and *T. reneau* n. sp. 0 or one); the appearance of variability may be an artifact of the slide mounting process. It is possible that in some specimens the eyes were over cleared during the digestion process, thus giving the appearance of being eyeless when they are not. This matter may be settled by the examination of several specimens under a scanning electron microscope.

Eye number is considered a character that responds readily to adaptive pressure in subterranean systems [38], but it is not clear if eye reduction is the direct result of selective pressure to subterranean life or a preadaptation derived from living in soil. Typical soil forms have relatively short appendages, irrespective of eye number, whereas cave-adapted species tend to have long antennae, legs, and furcula [4,38]. If most of the reduction in eye number took place in the soil, before the species colonized caves, we would expect incongruence between eye number and the level of adaptation to subterranean life in other characters. This should be further evaluated.

3. Paired Dorsal Macrochaetae of the Head. There is complete information for 19 species, whereas for 13 species the information is incomplete or totally absent. Eleven paired macrochaetae are variable in comparisons between species; a twelfth macrochaeta, A2, is always present. The order in which macrochaeta are added in comparisons between species is not fixed beyond the observation that all species with three macrochaetae carry A2, Pa5, and one other macrochaeta, and all species with four macrochaeta have A2, Pa5, Pm3, and one other macrochaeta. Macrochaeta A3 is always present when there are five or more macrochaeta, and M2 is always present if there are more than seven macrochaetae. There are 10 patterns of macrochaetae; the most common pattern is the presence of three macrochaetae in the combination of A2, Pa5, and Pm3, and is shared by eight species. All other patterns are present in one or two species.

4. Ornamentation of Prelabral Chaetae. All species have four prelabral chaetae and they are either ciliate or smooth. This character has been reported for all species except *T. mills*, *T. tijucana*, *T. caripensis*, and *T. maya*.

5. Labral Chaetae. All reported species fit the formula 554. Characters derived from the labral chaetae are not included in the summary description because the chaetae are smooth in the 27 species for which we have information. There are other potentially diagnostic characters to be found on the labral chaetae, but they have not been reported for most species. For example, the external chaetae of the proximal row maybe shorter (chaeta B2 in figure 27 in [2]), subequal (chaeta C2 in figure 4B in [28]) or much longer (chaeta p2 in Figures 5D and 8E here) than the inner chaetae. This character system merits further evaluation.

6. Labral Papillae. This character has been reported for 17 of the 33 species treated here. Only two character states are found among the species reported: the papillae are either

absent or independent and unfused. This contrasts with surface species which display several levels of fusion and papilla shape transformations (e.g., [2,20]).

7. Labial Triangle Chaetotaxy. This character is almost always reported and is described for 30 of the 32 species. The only states scored are whether the chaetae are smooth or ciliate. All chaetae on the anterior row are smooth and variation is limited to the posterior row. Chaeta M1 is invariably ciliate, but all other chaetae can be either ciliate or smooth. There are eight patterns of chaetae but the most common pattern, present in 21 species, is **M1M2rEL1L2**, (all chaetae ciliate, except r). Two patterns are shared by two species each and the other five patterns are autapomorphic.

8. Number of Chaetae Along Cephalic Groove. As circumscribed here, this character only refers to the number of chaetae inserted along the section of the ventral groove found on the head. This character has been reported for 18 species. The number of chaetae varies from 3 to 8 but most species have 4 chaetae. The number of chaetae along the ventral groove (and anywhere else on the post-labium) seems to be related to the density of scales on the ventral face of the head. Species with a less dense scale cover tend to have more chaetae (e.g., *T. jacobyi*, see [2]). This may be one of the few chaetotactic characters that reflects adaptation to subterranean life. However, the density of scales on the ventral surface of the head has been poorly reported in the literature and the meaning of the variation observed in the number of chaetae along the ventral groove is unclear.

9. Number of Macrochaetae in p3 Complex of the Mesothorax. This character refers to the number of setae with enlarged sockets forming a cluster on the medio-posterior area of Th. 2 (Figures 5B and 8B). Macrochaetae in the p3 complex almost invariably fall off during the mounting process, and their condition is derived from the relative size of the sockets. This character has been reported in 19 species and is present in three states: three, five, or six macrochaetae. The distribution of the states among species is even, with two groups of seven species each having three or five macrochaetae, and a group of five species with six macrochaetae.

10. Number of Metathoracic Macrochaetae. This character has been reported for 19 species and there are four character states: 14 species lack macrochaetae, one species has one macrochaeta, two species carry two macrochaeta, and two species bear three macrochaetae.

11. Fourth Abdominal Segment Inner Macrochaetae. There is complete information for 18 species. In *T. bessoni*, the homology of the chaetae is intractable from the information provided in the original description. For 13 species, no information is available.

Across species, the number of macrochaetae varies from three to five. Macrochaetae B5 and B6 are fixed and present in all species and macrochaeta A3, A5, and B4 are variable. The pattern of macrochaeta addition is not fixed: species with three macrochaetae carry B5, B6, and either A5 or B4, whereas species with four macrochaetae have B5, B6, plus two others in any combination of A3, A5, or B4. As a result, there are six patterns of macrochaetae. The most common number of macrochaetae is four (ten species), but the most common pattern is the combination of all five macrochaetae.

There are two other sources of variation in this system, the shape of the macrochaetae, and their insertion relative to other components of the chaetotaxy. Macrochaetae can be relatively short and parallel sided or strongly tapered and long. That difference is not clearly reflected by the sockets in this system and could be scored only if the macrochaeta cover remains intact on the mounted specimens. Thus, the diagnostic utility of macrochaeta shape in this system may remain unfulfilled. Exploration of the relative position of the macrochaetae as a source of diagnostic information may prove more fruitful.

The traditional characters scored for the dorsal chaetotaxy of Abd. 4 are the number of macrochaetae, their combination, and shape. However, there is also considerable variation among species in macrochaetae insertion with respect to each other, to the pseudopore, and the bothriotricha complex. This information is easily extracted from drawings of the specimens. It is recommended that drawings of actual chaetae distributions (e.g., Figure 9C) be published, even if maps of macrochaetae distribution are also included with

the descriptions (e.g., Figure 8B). The spatial distribution of macrochaetae is not considered here but will be further examined in a future study.

12. Fourth Abdominal Segment Outer Macrochaetae. There is complete information on this system for 18 species. The homology of chaetae in *T. bessoni* is not discernable from the original drawings, and information is lacking for 13 species.

This system is more difficult to circumscribe than the inner macrochaetae because there are differences in the number, arrangement, and relative shape of the elements, all of which are reflected by the sockets. For the purpose of this study, we have restricted the observations to the subset of primary outer macrochaetae: D3, E1, E2, E3, E4, F1, F2, and F3. The only secondary macrochaeta considered here is Te3 because it is inserted close to D3 and is unlikely to be missed if elements in series E and F are illustrated. Other secondary macrochaeta, such as Fe2 and Fe3, are often well-developed, but they are external to column F and may be omitted from illustrations; thus, they are not considered here. The discussion that follows is then limited to the number of primary elements and their combination patterns.

The number of macrochaetae varies from four to seven, with most species (eleven) carrying six. There are seven combinations of the eight macrochaetae, and no single species carries all macrochaetae. Elements D3, E3, and F1 are invariably present; D3 and F1 are always parallel-sided macrochaetae with large sockets, whereas in six species E3 is a long, strongly tapered chaeta with the socket distinctly smaller than that of D3 and F1. Element E2 is only absent in *T. maya*, but the drawing provided by [6] is difficult to interpret and, in fact, the missing element may be E4. Most of the variation is attributable to the presence or absence of F2, F3, and E4 and to the relative size of E3 and E4. Presence or absence of F2 is unambiguous in all species and the most useful diagnostic character of the lateral chaetotaxy. Macrochaeta Te3 is present only in *T. sotoadamesi*.

13. Number of Posterior Chaetae on the Fourth Abdominal Segment. This character is included because in species with six to eight eyes, the number of chaetae is variable and diagnostic. However, this character has been reported in only four of the 32 species included here. Three species have seven chaetae, and the fourth species has 13–14 chaetae.

14. Shape and Relative Length of Tenent Hair. All original descriptions have illustrations of the tenent hair of the hind legs or provide explicit descriptions of the characters considered here. Variation in the tenent hair can be coded into two characters: the relative size of the chaeta and the shape of its tip. A third character, whether the chaeta is smooth or ciliate, is not included here because all species with 0 + 0 to 5 + 5 eyes have smooth tenent hair. The shape of the tip is a discrete character with two states, the tip can be either acuminate or capitate spatulate. In species where the spatula is small, the tip of the chaeta appears to be rounded on side views. However, dorsoventral views invariably show the tip to be spatulate. The relative size of the chaeta is reported in relation to the length of the unguiculus. The size of the chaeta is continuous, from less than half the length of the unguiculus to longer than the unguiculus. Tenent hairs with acuminate tips span the range of sizes, from less than half to subequal to the unguiculus. Species with spatulate tips invariably have tenent hairs subequal to, or longer than, the unguiculus.

15. Number, Shape, and Spread of Inner Teeth on Hind Legs. The hind claw complex has been illustrated or described for all species. There are at least seven characters that can be derived from unguis morphology, but here we consider only four: number of teeth; inner teeth spread; inner teeth shape; and inner teeth relative size.

The number of inner teeth varies from two to four. Teeth may originate anywhere along the inner edge of the unguis, but the basal pair (BT) are never inserted on the distal half (the most distal BT origin is 49, in *T. lacerta*) whereas the two unpaired teeth are usually inserted on the distal half. The number of teeth and their spread are not correlated, although when only the BT are present, they are most likely inserted on the basal quarter of the inner edge. The two exceptions to this generality are *T. dandarae* with the BT originating at 39, and *T. tijucana*, with BT at 43. Otherwise, the spread of teeth is diagnostic, even if the continuous nature of the states makes it difficult to apply.

In most species, teeth take one of three distinct shapes: they can be lunate (Figure 2A), acuminate (Figure 2F), or wedge-shaped (Figure 2N). The shape of at least one tooth in *T. barroca*, *T. hauseri*, and *T. caripensis* is difficult to assign to either of the three classes, but seems to be transitioning between wedge and lunate, and they have been designated as transitional lunate. In most species, the BT are the same shape, and are referred to as symmetric. However, in *T. trioculata*, *T. maya*, and *T. caripensis*, each basal tooth is a different shape, and thus, the teeth are asymmetric. The size of teeth also varies across species; in some species, the BT are of different size. We describe as minute those teeth barely visible at 400× (Figures 2I and 3D); teeth are small when they do not project much (Figure 2M,K), developed teeth are projected (Figure 2A,D), and well-developed teeth are relatively large (Figures 2F and 3B,C). The term enlarged is used only for the largest tooth in uneven-sized BT, and the enlarged tooth is usually wedge- or transitional-lunate-shaped (Figure 2E,J and Figure 3E). The proximal unpaired tooth is never larger than the BT and the distal unpaired tooth is most often minute or absent.

16. Unguiculus Shape. The unguiculus has been illustrated for all species. Three general shapes are represented across species: lanceolate, basally swollen, or truncate. Three species (*T. tijucana*, *T. millsii*, and *T. trioculata*) have truncate unguiculus; the unguiculus is clearly basally swollen in *T. bessoni*, and *T. jacobyi*, and weakly swollen in *T. beliziana* and *T. ecuatorica*; whereas all other species show variations in shape that can be generally described as lanceolate. The term lanceolate fails to address variation that encompasses unguiculi that are very narrow (*T. aelleni* and *T. hauseri*), asymmetrically convex (*T. marimutti*, *T. ecuatorica*, and most other species), or symmetrically convex (*T. honduraensis*).

17. Number of Teeth and Mucro Shape. The mucro has been reported for all species. The number of teeth varies from three to five, but the vast majority carries four teeth. *Trogolaphysa beliziana*, *T. jacobyia*, and *T. dandarae* have three teeth, whereas *T. ecuatorica* is the only species with five real teeth.

The shape ratio length/width varies from 1.93 to 4.35. Seventeen species have rectangular mucrones (shape ratio of ≥ 3.00), in six species the mucro is sub-rectangular (2.50 to 2.99), and in five species it is paraquadrate (shape ratio 2.00 to 2.49). Only *T. guacharo* has an almost square mucro. All species with three or five teeth have rectangular mucrones.

3.3. Identification Key to Neotropical Species of *Trogolaphysa* with 0 + 0 to 5 + 5 Eyes ^a

Thirty-three species of Neotropical *Trogolaphysa* have been described as having a reduced eye number (Tables 1–3). The complete dorsal chaetotaxy is known for seventeen species; for one species, drawings were so diagrammatic that no homology of elements was possible; there was partial information on three other species. No chaetotaxy information was available for thirteen species. Given the information gap on dorsal chaetotaxy, the key below is based on eye number, labial triangle chaetotaxy, hind claw complex, and mucro morphology. Dorsal chaetotaxy is used to separate only a few of the most recently described species.

- 1a. Hind unguis with 2 inner teeth2
- 1b. Hind unguis with 3–4 inner teeth13
- 2a. Eyes present3
- 2b. Eyes absent5
- 3a. Eyes 4 + 4; basal unguis small, subequal and lunate (Figure 2I); unguiculus lanceolate*T. honduraensis*
- 3b. Eyes 1 + 1 or 2 + 2; basal unguis enlarged, one tooth clearly larger and either wedge-shaped or acuminate; unguiculus weakly (Figure 2G) or strongly truncate (Figure 2H)4
- 4a. Eyes 1 + 1; basal unguis acuminate, elongated (Figure 2G), needle-shaped and arising on basal 1/5 of inner edge, unguiculus weakly truncate*T. reneauui* n. sp.
- 4b. Eyes 2 + 2; basal unguis wedge-shaped (Figure 2H) and arising near middle of inner edge;

unguiculus strongly truncate <i>T. tijucana</i>	
5a. Mucro with 3 teeth	6
5b. Mucro with 4–5 teeth	7
6a. Unguiculus acuminate; head with 7 paired macrochaetae	<i>T. belizana</i>
6b. Unguiculus spatulate; head with 4 paired macrochaetae	<i>T. dandarae</i>
7a. Inner unguis teeth acuminate elongate, needle-like, symmetric (Figure 2F)	8
7b. Inner unguis teeth wedge-shaped or lunate	9
8a. Labial chaetae M2 and E smooth, chaeta r ciliate; Unguiculus weakly truncate (Figure 2G)	<i>T. reneai</i> n. sp.
8b. Labial chaetae M2 and E ciliate, chaeta r smooth; unguiculus lanceolate (Figure 2F)	<i>T. haitica</i>
9a. Mucro with 4 teeth	11
9b. Mucro with 5 teeth	10
10a. All unguiculi greatly expanded basally, flame-shaped (Figure 2B)	<i>T. bessoni</i>
10b. Fore and middle unguiculi triangular (Figure 2C), hind unguiculus lanceolate and marginally swollen basally (Figure 2D)	<i>T. ecuatorica</i>
11a. Unguis basal teeth unequal, one much larger (Figure 2E); unguiculus lanceolate narrow	<i>T. hauseri</i>
11b. Unguis basal teeth subequal; unguiculus lanceolate wide	12
12a. Head macrochaeta Pm3 present; Abd. 4 macrochaeta A3 absent	<i>T. sotoadamesi</i>
12b. Head macrochaeta Pm3 absent; Abd. 4 macrochaeta A3 present	<i>T. barroca</i>
13a. Eyes present	14 ^c
13b. Eyes absent	22
14a. Eyes 2 + 2	15
14b. Eyes 3 + 3 to 6 + 6	19
15a. Unguis with 4 inner teeth	16
15b. Unguis with 3 inner teeth	17
16a. Tenet hair acuminate; labial chaeta E smooth	<i>T. welchi</i> n. sp.
16b. Tenet hair spatulate; labial chaeta E ciliate	<i>T. bellini</i>
17a. Tenet hair spatulate	<i>T. bellini</i>
17b. Tenet hair acuminate	18
18a. Basal teeth small, not reaching proximal unpaired tooth (Figure 2M); unguiculus lanceolate, narrow	<i>T. aelleni</i>
18b. Basal teeth enlarged, nearly reaching proximal unpaired tooth (Figure 2N); unguiculus truncate	<i>T. millsi</i>
19a. Eyes 3 + 3; unguiculus truncate; basal unguis teeth not paired (Figure 2O)	<i>T. trioculata</i>
19b. Eyes 4 + 4 or 5 + 5; unguiculus lanceolate; basal unguis teeth paired	20
20a. Eyes 5 + 5; tenet hair spatulate; unguis with 3 teeth	<i>T. strinatii</i>
20b. Eyes 4 + 4; tenet hair acuminate; unguis with 4 teeth	21
21a. Labial chaeta M2 smooth; unguiculus serrate	<i>T. variabilis</i>
21b. Labial chaeta M2 ciliate; unguiculus smooth	<i>T. zampauloi</i>
22a. Unguis with 3 inner teeth	23 ^b
22b. Unguis with 4 inner teeth	29
23a. Labial chaetae M2 and E ciliate	24
23b. Labial chaetae M2 and E smooth	28

- 24a. Basal unguual teeth unequal and asymmetric, lunate tooth much larger than wedge-shaped tooth (Figure 2J); mesothorax p3 complex with 6 macrochaetae*T. caripensis*
- 24b. Basal unguual teeth subequal, symmetric and wedge-like; mesothorax p3 complex with 3–5 macrochaetae25
- 25a. Tenent hair spatulate; basal unguual teeth overlapping proximal unpaired tooth; mucro more than 4.0× as long as wide*T. mariecurieae*
- 25b. Tenent hair acuminate; basal unguual teeth not reaching proximal unpaired tooth; mucro less than 3.9× as long as wide26
- 26a. Unguiculus serrate and triangular; head macrochaeta A3 present*T. gisbertae*
- 26b. Unguiculus smooth and lanceolate; head macrochaeta A3 absent27
- 27a. Mesothorax p3 complex with 5 macrochaetae; Abd. 4 macrochaeta A4 present*T. crystallensis*
- 27b. Mesothorax p3 complex with 3 macrochaetae; Abd. 4 macrochaeta A4 absent*T. epitychia*
- 28a. Mucro with 3 teeth; unguiculus basally swollen (Figure 2K); labial chaetae L1 and L2 smooth*T. jacobyi*
- 28b. Mucro with 4 teeth; unguiculus lanceolate (Figure 2L); labial chaetae L1 and L2 ciliate*T. marimutti*
- 29a. Unguis basal inner teeth unequal30
- 29b. Unguis basal inner teeth subequal31
- 30a. Largest basal unguual tooth reaching distal unpaired tooth (Figure 3E); unguiculus lanceolate, narrow and smooth*T. guacharo*
- 30b. Basal unguual teeth not reaching distal unpaired tooth (Figure 3B); unguiculus lanceolate, wide, and serrate*T. maya*
- 31a. Labial chaetae E, L1 and L2 smooth; basal unguual teeth well-developed acuminate (Figure 3C); distal unpaired tooth well-marked elongated*T. xtoloquensis*
- 31b. Labial chaetae E, L1 and L2 ciliate; basal unguual teeth small, wedge-shaped; distal unpaired tooth minute32
- 32a. Unguiculus serrated; tenent hair subequal (0.90–1.10×) to unguiculus33
- 32b. Unguiculus smooth; tenent hair shorter (<0.80×) than unguiculus34
- 33a. Tenent hair spatulate; mesothorax p3 complex with 3 macrochaetae*T. bellinii*
- 33b. Tenent hair acuminate; mesothorax p3 complex with 4 macrochaetae*T. chapelensis*
- 34a. Unguiculus weakly excavated; basal unguual teeth arising well proximal (at 43) of middle of inner edge (Figure 3D)*T. oztolica*
- 34b. Unguiculus lanceolate; basal unguual teeth arising on middle (at 49) of inner edge*T. lacerta*
- a. According to Thibaud and Najt [26], *T. delamarei* is a junior synonym of *T. maya* and therefore it is not included in the key. See additional comments under the remarks to *T. maya*.
- b. Specimens of *T. oztolica* will key out here if the minute distal unpaired tooth is not seen clearly. However, in *T. oztolica* all labial chaetae are ciliate, except r, the basal inner

teeth are wedge-shaped, subequal and small, and the inner membrane of the unguiculus is weakly excavate.

4. Discussion

The independent evolution of cave systems in different geographic regions, with the concomitant development of unique underground assemblages derived from local surface communities, provide the ideal experimental conditions to study the evolution of morphological adaptations. The genus *Trogolaphysa* is one of several springtail genera that have radiated extensively in subterranean environments across the Americas [4]. Other genera with many specialized subterranean species, like *Pseudosinella* and *Pygmarrhopalites* Vargovitsh, have centers of diversification in temperate North America and Eurasia, whereas *Trogolaphysa* has diversified in the neotropics, a region that has received relatively little attention. Factors that have discouraged the study of *Trogolaphysa* include the absence of a clear understanding of the morphology and character systems that reflect species-level discontinuities; access to the scattered scientific literature necessary to identify cave-adapted *Trogolaphysa*; and a lack of synthetic treatment of described species. A series of recent papers [10,19,21] have helped to circumscribe character systems that consistently identify independent lineages.

The main goal of this contribution was to synthesize available diagnostic information about all species of *Trogolaphysa* with 0 to 5 + 5 eyes. The purpose of early descriptions was to diagnose putative new forms from the few other forms already known. Descriptions were not intended to provide data to evaluate phylogenetic relationships between species or adaptive evolutionary pathways. Hence, species descriptions were incomplete by current standards. Although the breadth of characters included in descriptions gradually increased over time (compare the transition from [23,28] through [7] and [5]), it was not until [10] that descriptions began to include explicit statements of the dorsal chaetotaxy. Mari Mutt [10] further expanded descriptions to include characters of the chaetotaxy routinely reported for two genera of scaled Entomobryidae with similarly reduced macrochaetotaxy (*Lepidocyrtus* and *Pseudosinella*), but never explored in *Trogolaphysa*.

Soto-Adames et al. [19] presented a list of 24 character systems found to provide information useful for species identification. The evaluation of 32 species in the present study reaffirms the diagnostic value of classical characters and confirms the diagnostic utility of chaetotaxy. All species for which chaetotaxy has been reported (19 of 32) can be diagnosed using the combined distributions of macrochaetae on the head, thorax, and fourth abdominal segments—that is, the information synthesized in the summary macrochaetae formula. The diagnosis of species differing even by a single macrochaeta on the head or trunk is supported by other characters of the chaetotaxy (i.e., condition of prelabral chaetae, the number of post-labial chaetae, etc.) and/or structural characters (i.e., number of eyes, claw and mucro shape, and claw teeth pattern). In addition to the evident value of a larger number of characters, chaetotaxy provides an independent set of characters to evaluate hypotheses about the evolution of subterranean adaptations. Among *Trogolaphysa* with 0 to 5 + 5 eyes, classical diagnostic characters (eye number, morphology of hind leg claw complex, and mucro) show strong response to adaptive evolution [4,38], whereas the chaetotactic characters evaluated here were largely uncorrelated to the level of adaptation to the subterranean environment. This is consistent with a previous phylogenetic analysis of a limited number of species showing that chaetotactic characters supported clades of species congruent with geographic distribution, whereas structural characters supported clades congruent with habitat distribution (Soto-Adames and Taylor [2]). The polarity of putative subterranean adaptive characters must be evaluated as part of a larger data set that also includes surface species. A cursorial review of surface forms shows that large antennal length/head diagonal and mucro shape ratios are not an exclusive characteristic of cave-adapted species (see [20,22,39] for some examples). The condition of some structural characters in several surface lineages may be the reason for the success of *Trogolaphysa* colonizing deep cave habitats.

In summary, we synthesize all the relevant morphological information available for species of *Trogolaphysa* with 0 to 5 + 5 eyes, thus providing the foundation for future studies on the phylogeny of the genus and the evolution of adaptive characters in neotropical subterranean species.

Author Contributions: Conceptualization, F.S.-A. and J.J.W.; methodology, F.S.-A.; formal analysis, F.S.-A. and K.M.D.; field investigation, J.J.W.; data curation, F.S.-A. and K.M.D.; writing—original draft preparation, F.S.-A.; writing—review and editing, F.S.-A., J.J.W. and K.M.D.; funding acquisition, J.J.W. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Belize Zoo Neotropical Conservancy, Runaway Creek Nature Reserve, Belize Zoo & Tropical Education Center, Cave Research Foundation, and the National Speleological Society's Research Grant and International Exploration funds.

Data Availability Statement: All data generated during the study is include in the publication.

Acknowledgments: We would like to thank Ray Cal, Michael Cal, Stevan Reneau, and Gilroy Welch for their assistance during fieldwork, and to Quinton Redmond and Dana Headman for their assistance with arthropod sorting and identification. We also would like to thank Rosanna Giordano (Florida International University), and Samuel Bolton and Paul Skelley (Florida State Collection of Arthropods) for valuable comments on the manuscript.

Conflicts of Interest: The authors declare no conflicts of interest.

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