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REVISÃO DE *TROGOLAPHYSA* MILLS, 1938 (COLLEMBOLA,
ENTOMOBRYOMORPHA, PARONELLIDAE), COM A DESCRIÇÃO DE NOVAS
ESPÉCIES DE CAVERNAS, DOMÍNIO CAATINGA, BRASIL

PAOLLA GABRYELLE CAVALCANTE DE SOUZA

Dissertação de Mestrado
Natal/RN, Fevereiro de 2021

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Orientador: Dr. Bruno Cavalcante Bellini

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(COLLEMBOLA, ENTOMOBRYOMORPHA, PARONELLIDAE) FROM

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RESUMO

Trogolaphysa Mills (Paronellidae) é amplamente distribuído em regiões tropicais, com 65 espécies descritas em todo o mundo. As espécies neotropicais de *Trogolaphysa* são melhor conhecidas que as afrotropicais; porém, há grandes lacunas de conhecimento para várias espécies nas duas regiões, que são reconhecidas principalmente pelos padrões de coloração, número de olhos, morfologia do complexo empodial e da fúrcula. Muitas espécies de *Trogolaphysa* apresentam troglomorfismos evidentes, como redução ou ausência de olhos, corpo sem pigmentos e antenas alongadas. As cavernas possuem um papel importante para compreensão dos processos biológicos devido à sua estabilidade ambiental, mas também são relevantes para mineração brasileira, sendo a extração de calcário a principal atividade econômica nos municípios que possuem cavernas de rochas carbonáticas no Rio Grande do Norte (RN). Estudos anteriores demonstraram que *Trogolaphysa* é o gênero dominante de Collembola presente em cavernas do RN. Este gênero abriga espécies com *status* questionáveis e o seu estudo taxonômico pode auxiliar em políticas de conservação. Por isso, este trabalho apresenta uma revisão taxonômica com base em bibliografia de *Trogolaphysa*, com uma diagnose revisada e um resumo da morfologia geral do gênero, diagnoses detalhadas para todas as espécies, tabelas comparativas, chave de identificação para todos os táxons do gênero e descrições de duas novas espécies do gênero presentes em cavernas do RN. As espécies novas foram coletadas com aspiradores entomológicos e pincéis, fora e dentro de 10 cavernas calcárias inseridas no bioma Caatinga. A sugestão de *species inquirendae* considerou descrições taxômicas pouco informativas, características taxonômicas duvidosas e/ou localização pouco informativa ou imprecisa. Foram identificadas 14 *species inquirendae*: *T. berlandi*, *T. carpenteri*, *T. fuelleborni*, *T. ghesquieri*, *T. guacharo*, *T. hauseri*, *T. hirtipes*, *T. innominata*, *T. lamottei*, *T. maya*, *T. millsi*, *T. nigromaculata*, *T. separata* e *T. strinatii*; e foi desconsiderada a sinonímia de *T. delamarei* com *T. maya*. Foi apresentada uma síntese da morfologia geral do gênero, com as variações na quetotaxia e em suas principais estruturas. A descrição de duas novas espécies de *Trogolaphysa* amplamente distribuídas nas cavernas do RN em conjunto com a revisão do gênero proporcionam dados mais precisos no diagnóstico de espécies, aumentam o conhecimento sobre a fauna mundial de *Trogolaphysa* e podem auxiliar políticas de conservação de cavernas no RN.

Palavras-chave: diagnoses; fauna de cavernas; quetotaxia; Região Neotropical; taxonomia.

ABSTRACT

Trogolaphysa Mills (Paronellidae) is widely distributed in tropical regions, with 65 species described worldwide. Neotropical species of *Trogolaphysa* are better understood than the Afrotropical ones; however, there are large gaps in knowledge for several species from the two regions, which are mainly recognized by color patterns, number of eyes, empodial complex and furcula morphologies. Many species of *Trogolaphysa* have evident troglomorphisms such as the reduction or absence of eyes, body lacking pigmentation and elongated antennae. Caves provide an important role for biological processes due to the unique environmental stability, but they also have an important economic role in Brazilian mining, with limestone extraction being the main economic activity in municipalities that share carbonate rock caves in the Rio Grande do Norte (RN). Previous surveys have shown that *Trogolaphysa* is the dominant Collembola genus in RN caves. This genus has species with questionable status and its taxonomic study may assist in conservation policies. For this reason, this work presents a taxonomic review based on *Trogolaphysa* bibliography, with a revised diagnosis and a summary of the general morphology of the genus, detailed diagnoses for all species, comparative tables, key for all taxa of the genus and the description of two new species of *Trogolaphysa* from RN caves. The new species were collected with entomological aspirators and brushes, outside and inside of 10 limestone caves from the Caatinga biome. We suggested as *species inquirendae* taxa which status was considered uncertain due to uninformative diagnoses, dubious taxonomic characteristics and/or inaccurate data on distribution. Fourteen *species inquirendae* were identified: *T. berlandi*, *T. carpenteri*, *T. fuelleborni*, *T. ghesquieri*, *T. guacharo*, *T. hauseri*, *T. hirtipes*, *T. innominata*, *T. lamottei*, *T. maya*, *T. millsii*, *T. nigromaculata*, *T. separata* and *T. strinatii*; also the synonym of *T. delamarei* and *T. maya* was disregarded, considering *T. delamarei* as a different species, revalidating its species status. A synthesis of the general morphology of the genus was also presented, summarizing the variations in the chaetotaxy and other main structures. The description of two new species of *Trogolaphysa* widely distributed in RN caves, along with the genus revision, provide more accurate data in the species diagnoses and increases the knowledge to the world fauna of *Trogolaphysa* which can assist in the conservation policies of caves in the RN.

Keywords: diagnoses; cave fauna; chaetotaxy; Neotropical Region; taxonomy.

1 Introdução Geral

Colêmbolos são microartrópodes abundantes em quase todos os ambientes terrestres, estando presentes desde desertos polares até florestas tropicais quentes (Lukić 2019; Potapov *et al.* 2020). Eles também são encontrados em ambientes subterrâneos, sendo a sua abundância importante para a base da teia alimentar dentro de cavernas (Lukić 2019).

As cavernas representam ambientes relativamente estáveis que podem ser modelos para o estudo de processos biológicos (Mammola *et al.* 2020; Poulson & White 1969). No início dos anos 1960, questionamentos sobre a biologia de animais subterrâneos resultaram em estudos sobre a morfologia, ecologia, comportamento e evolução de animais cavernícolas, incluindo os Collembola (Barr 1967; Christiansen 1961, 1965; Culver & Pipan 2015).

O ambiente subterrâneo (ambiente hipógeo) e o ambiente externo (ambiente epígeo) são diferenciados quanto à exposição à luz, estabilidade do ambiente e variação de temperatura e umidade (Poulson & White 1969; Trajano 2012). A região subterrânea é caracterizada pela redução ou ausência de luz, restrição de organismos fotoautotróficos e tendência à escassez de alimento (Trajano 2012). O aporte de matéria orgânica dentro das cavernas é realizado especialmente através de corpos de água, chuvas ou pela ação de animais, como aves e morcegos (Trajano 2012). Tendo em vista as particularidades do ambiente cavernícola, animais dependentes de cavernas sofrem pressões seletivas e por isso apresentam características morfofisiológicas distintas daqueles do ambiente epígeo.

As adaptações morfofisiológicas dos animais ao ambiente subterrâneo foram muitas vezes explicadas por ideias lamarckistas de “uso e desuso”. Até mesmo Darwin considerou explicações desta natureza para espécies sem olhos encontradas em cavernas da Eslovênia (Culver & Pipan 2015; Trajano *et al.* 2010). Em seu livro “A Origem das Espécies”, Darwin menciona: “É sabido que certos animais, pertencentes às mais diversas classes que habitam as cavernas da Carniola e Kentucky, são cegos [...]. Como é difícil imaginar que os olhos, embora inúteis, possam, de alguma forma, ser nocivos aos animais que vivem no escuro, sua perda pode ser atribuída ao desuso”(Darwin 1859, pg. 167).

Christiansen (1961, 1965) estudou a redução/ausência de olhos em colêmbolos cavernícolas, sua locomoção sobre superfícies úmidas ou alagadas e as diferenças morfológicas que as espécies subterrâneas poderiam apresentar. Christiansen cunhou o termo troglomorfo para se referir a adaptações evolutivas regressivas ou progressivas

em animais que habitam cavernas e como elas poderiam explicar a morfologia, fisiologia e o comportamento destes animais.

A família Paronellidae pertence à maior e mais diversificada ordem de Collembola, Entomobryomorpha, e possui ao menos 45 espécies troglóbias em vários gêneros, que se diversificaram dentro de cavernas (Lukić 2019). Embora muitas espécies do gênero *Trogolaphysa* Mills, 1938 estejam presentes na serapilheira do solo, algumas possuem afinidade ao ambiente subterrâneo, podendo também serem troglomórficas (Soto-Adames & Taylor 2013).

As espécies do gênero *Trogolaphysa* estão distribuídas nas regiões Neotropical e Afrotropical, e as espécies neotropicais são morfologicamente melhor caracterizadas que as afrotropicais (Nguyen & Soto-Adames 2018; Soto-Adames 2015; Soto-Adames & Taylor 2013). Porém, há grandes lacunas de conhecimento a respeito de várias espécies em ambas as regiões. As espécies normalmente são caracterizadas principalmente por padrões de coloração, número de olhos, morfologia do complexo empodial e da fúrcula, porém, esses caracteres se mostraram insuficientes para distinguir espécies de Collembola de acordo com as revisões mais recentes (Nguyen & Soto-Adames 2018).

Existem, ao menos, dois grupos de espécies com incertezas taxonômicas evidentes: um na região Afrotropical, contendo ao menos as espécies *Trogolaphysa nigromaculata* (Schött, 1903) e *T. fuelleborni* (Börner, 1903), e outro na região Neotropical, com ao menos as espécies *T. jataca* (Wray, 1953), *T. geminata* (Mari-Mutt, 1987) e *T. luquillensis* (Mari-Mutt, 1987). As espécies dentro desses grupos, além de compartilharem características semelhantes, muitas vezes possuem distribuição ampla, como por exemplo *T. nigromaculata*, que pode ser encontrada do oeste ao leste da África. Essas espécies necessitam de revisões taxonômicas detalhadas, como a realizada por Mitra (2002b), que a partir da análise do material tipo de *T. nigromaculata* descreveu uma espécie nova distinta, *T. wahgreni* (Mitra, 2002).

Oito espécies de *Trogolaphysa* foram descritas/registradas para o Brasil, são elas: *T. aelleni* Yoshii, 1988, *T. ernesti* Cipola & Bellini, 2017, *T. formosensis* Silva & Bellini, 2015, *T. hauseri* Yoshii, 1988, *T. hirtipes* (Handschin, 1924), *T. millsii* (Arlé, 1939), *T. piracurucaensis* Nunes & Bellini, 2018 e *T. tijucana* (Arlé & Guimarães, 1979). Três dessas espécies, *T. aelleni*, *T. hauseri* e *T. hirtipes*, foram encontradas em cavernas da Região Sudeste com características troglomórficas evidentes, como: redução de dentes no complexo empodial, ausência de pigmentação e redução do número de olhos (Arlé 1939; Arlé & Guimarães 1979; Thibaud & Najt 1988).

A extração de calcário é a principal atividade econômica nos municípios que possuem cavernas de rochas carbonáticas no estado do Rio Grande do Norte (RN), e juntamente com a visitação irregular, são as maiores ameaças aos ambientes cavernícolas na região (Cruz *et al.* 2010). As cavernas do Brasil estão ameaçadas por empreendimentos de mineração, cujas atividades podem impactar permanentemente cavernas próximas, uma vez que a retirada de vegetação do entorno resultará no aumento da temperatura e diminuição da umidade no interior das cavernas, além de limitar o aporte de matéria orgânica no meio subterrâneo, comprometendo a sobrevivência de espécies cavernícolas. Além disso, detonações de explosivos podem afetar a estrutura das cavernas, provocando desabamentos e alterando o meio físico. A extração de calcário no estado do Rio Grande do Norte já resultou em danos às cavernas Capoeira de João Carlos e Caverna do Macaco, localizadas nos municípios de Apodi e Governador Dix-Sept Rosado, respectivamente (Cruz *et al.* 2010).

Estudos anteriores em cavernas do RN demonstraram grande abundância e ampla distribuição de *Trogolaphysa* (Bento 2011). O gênero também possui espécies com descrições imprecisas e a revisão taxonômica de suas espécies, mesmo baseada apenas na bibliografia, pode auxiliar políticas de conservação, bem como no manejo das cavernas na área inventariada do RN, por exemplo, facilitando a estimativa do número de espécies em uma determinada área. Por isso, este trabalho se propõe a apresentar uma revisão taxonômica de *Trogolaphysa*, baseada em dados publicados, com um resumo da morfologia geral do gênero, diagnoses detalhadas para todas as suas 65 espécies, tabelas comparativas, uma chave para todos os táxons do gênero e a descrição de duas novas espécies de *Trogolaphysa* provenientes de cavernas do RN.

2 Objetivos Gerais e Específicos

Revisar e compilar dados taxonômicos das espécies do gênero *Trogolaphysa* e inventariar e descrever espécies do gênero em cavernas da região mesoeste do Rio Grande do Norte.

- Caracterizar e ilustrar os padrões morfológicos do gênero *Trogolaphysa*, e apresentar uma diagnose revisada para o gênero (capítulo 1);
- Apresentar dados comparativos de todas as espécies de *Trogolaphysa* através de tabelas e diagnoses específicas (capítulo 1);
- Descrever duas novas espécies de *Trogolaphysa* provenientes de cavernas da região mesoeste potiguar (capítulo 2).

3 Referências bibliográficas

- Arlé, R. (1939) Collemboles nouveaux de Rio de Janeiro.
- Arlé, R. & Guimarães, A.É. (1979) Nova espécie do gênero *Paronella* Schött, 1893 do Rio de Janeiro (Collembola). *Revista Brasileira de Entomologia* 23, 213–217.
- Barr, T. (1967) Observations on the ecology of caves. *The American Naturalist*, 101, 475–491.
- Bellini, B.C. & Cipola, N.G. (2017) The Neotropical genera of Paronellinae (Collembola, Entomobryoidea, Paronellidae) with description of two new species and redescription of *Campylothorax mitrai*. *Zootaxa* 4300, 151. <https://doi.org/10.11646/zootaxa.4300.2.1>
- Bento, D. de M. (2011) Diversidade de invertebrados em cavernas calcárias do oeste potiguar: Subsídios para a determinação de áreas prioritárias para conservação. Dissertação de Mestrado em Biodiversidade - Universidade Federal do Rio Grande do Norte, Natal, 2011. 162 pp.
- Börner, C. (1903) Über neue Altweltliche Collembolen, nebst Bemerkungen zur Systematik der Isotominen und Entomobryinen. *Gesellschaft naturforschender Freunde*, 129–182.
- Christiansen, K. (1961) Convergence and parallelism in cave Entomobryinae. *Evolution* 15, 288–301. <https://doi.org/10.2307/2406229>
- Christiansen, K. (1965) Behavior and form in the evolution of cave Collembola. *Evolution* 19, 529. <https://doi.org/10.2307/2406249>
- Cruz, J.B., Bento, D.M., Bezerra, F.H.R., Freitas, J.I. & Campos, U.P. (2010) Diagnóstico espeleológico do Rio Grande do Norte. *Revista Brasileira de Espeleologia* 1, 1–24.
- Culver, D.C. & Pipan, T. (2015) Shifting paradigms of the evolution of cave life. *Acta Carsologica* 44, 415–425. <https://doi.org/10.3986/ac.v44i3.1688>
- Darwin, Charles. 1859. On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life. / Tradução Carlos Duarte e Anna Duarte. 1 ed. São Paulo: Martin Claret, 2014.
- Handschin, E. (1924) Neue myrmecophile und termitophile Collembolenformen aus Süd-Amerika. *Neue Beiträge zur systematischen Insektenkunde* 3, 13–28.
- Lukić, M. (2019) Collembola. *Encyclopedia of Caves*, 308–319. <https://doi.org/10.1016/b978-0-12-814124-3.00034-0>

- Mammola, S., Amorim, I.R., Bichuette, M.E., Borges, P.A.V., Cheeptham, N., Cooper, S.J.B., Culver, D.C., Deharveng, L., Eme, D., Ferreira, R.L., Fišer, C., Fišer, Ž., Fong, D.W., Griebler, C., Jeffery, W.R., Jugovic, J., Kowalko, J.E., Lilley, T.M., Malard, F., Manenti, R., Martínez, A., Meierhofer, M.B., Niemiller, M.L., Northup, D.E., Pellegrini, T.G., Pipan, T., Protas, M., Reboleira, A.S.P.S., Venarsky, M.P., Wynne, J.J., Zagamajster, M. & Cardoso, P. (2020) Fundamental research questions in subterranean biology. *Biological Reviews* 95, 1855–1872. <https://doi.org/10.1111/brv.12642>
- Mitra, S.K. (2002) Status of *Dicranocentrua* Wray, 1953 With the Description of a New Species (Collembola: Entomobryidae). *Records Zoological Survey of India* 100, 105–116.
- Nguyen, M. & Soto-Adames, F.N. (2018) Annotated checklist of Afrotropical *Trogolaphysa* Mills, 1938 (Hexapoda: Collembola: Paronellidae) and description of a new species from Madagascar. *Zoosystema* 40, 179–196. <https://doi.org/10.5252/zoosystema2018v40a10>
- Nunes, R.C. & Bellini, B.C. (2018) Three new species of Entomobryoidea (Collembola: Entomobryomorpha) from Brazilian Caatinga-Cerrado transition, with identification keys to Brazilian *Cyphoderus*, *Pseudosinella* and *Trogolaphysa* species. *Zootaxa* 4420, 71. <https://doi.org/10.11646/zootaxa.4420.1.4>
- Potapov, A., Bellini, B.C., Chown, S.L., Deharveng, L., Janssens, F., Kováč, Ľ., Kuznetsova, N. & Ponge, J. (2020) Towards a global synthesis of Collembola knowledge – challenges and potential solutions. 92, 161–188. <https://doi.org/10.25674/so92iss3pp161>
- Poulson, T.L. & White, W.B. (1969) The cave environment. *Science* 165, 971–981.
- Schött, H. (1903) Über zwei Gattungen der apterygoten Insecten. Redogorelse, für Allmanna Laroverken I. Linköping. *Ekso och Vadstena. Underlasaret*, 3–16.
- Silva, D.D. da, Bellini, B.C., da Silva, D.D. & Bellini, B.C. (2015) *Trogolaphysa formosensis* sp. nov. (Collembola: Paronellidae) from Atlantic Forest, Northeast Region of Brazil. *Zoologia* 32, 53–58. <https://doi.org/10.1590/S1984-46702015000100008>
- Soto-Adames, F.N. (2015) The dorsal chaetotaxy of first instar *Trogolaphysa jataca*, with description of twelve new species of neotropical *Trogolaphysa* (Hexapoda: Collembola: Paronellidae). *Zootaxa* 4032, 1–41. <https://doi.org/10.11646/zootaxa.4032.1.1>

- Soto-Adames, F.N. & Taylor, S.J. (2013) The dorsal chaetotaxy of *Trogolaphysa* (Collembola, Paronellidae), with descriptions of two new species from caves in Belize. *ZooKeys* 323, 35–74. <https://doi.org/10.3897/zookeys.323.4950>
- Thibaud, J. & Najt, J. (1988) Collemboles (Insecta) de l'Équateur IV. Paronellidae avec rérevision de quatre genres. *Bull. Mus. natn. Hist. nat.* 10, 719–730.
- Trajano, E. (2012) Ecological Classification of Subterranean Organisms. *Encyclopedia of Caves*. Elsevier Inc., 275–277 pp. Available from: <http://dx.doi.org/10.1016/B978-0-12-383832-2.00035-9>
- Trajano, E., Bichuette, M.E. & Kapoor, B.G. (2010) *Biology of Subterranean Fishes*. E. Trajano, M. E. Bichuette, and B. G. Kapoor (Eds). CRC Press, 478 pp.
- Yoshii, R. (1988) Paronellid Collembola from caves of Central and South America collected by P. Strinati. *Revue suisse de zoologie*. 95, 449–459. <https://doi.org/10.5962/bhl.part.82022>

Chapter 1: Review of *Trogolaphysa* Mills, 1938 (Collembola, Entomobryomorpha, Paronellidae)

1 Introduction

According to the most recent systematic revision of the Entomobryoidea (Zhang *et al.* 2019), the subfamily Paronellinae is subdivided in three tribes: Paronellinae, Cyphoderini and Bromacanthini. The Paronellinae present well-developed appendages, elongated fourth abdominal segment (Abd. IV), dens smooth and straight and trunk sens formula on the second thoracic segment to the fifth abdominal segment as 1, 1 | 0, 1, 1,+,3 (Zhang *et al.* 2019; Bellini & Cipola 2017). The members of Paronellinae also share rounded scales and reduced macrochaetatoxy, lacking most of the secondary and some of the primary chaetae (Soto-Adames *et al.* 2014; Zhang *et al.* 2019). The reduced chaetotaxy in these tribes can lead to ambiguity in the identification of homologies in some characters due to inaccuracy in the determination if primary chaetae are displaced in different areas of distinct taxa or secondary chaetae emerged independently in different lineages, even if the species are closely related (Soto-Adames *et al.* 2014). Several studies and revisions of the dorsal chaetotaxy were made by Soto-Adames *et al.* (2013, 2014, 2015) to determine the main diagnostic characters of the genera of Paronellini.

Mills (1938) described the genus *Trogolaphysa* to hold *T. maya* Mills, 1938, an eyeless cave paronellid species found in Mexico. In the description, Mills presented *Paronella* Schött, 1893 as the most similar genus to *Trogolaphysa*, in the same way to the comparisons made between *Pseudosinella* Schäffer, 1897 and *Lepidocyrtus* Bourlet, 1839, or *Sinella* Brook, 1982 and *Entomobrya* Rondani, 1861 (see Mills, 1938, p. 184). He indicated that *Trogolaphysa* was remarkably similar to *Paronella* but devoid of eyes. Mills' delimitation of *Trogolaphysa* was based on a single cave species. Many of its diagnostic features for the genus were based on potential troglomorphisms: the absence of eyes, pigments, the fourth antennal segment with plenty of modified chaetae and ungues with modified inner teeth. Such morphological features are common to several cave species placed in the genus, but not to the epiedaphic taxa (as in Palacios-Vargas *et al.* 1985, Thibaud & Najt 1988; Soto-Adames & Taylor 2013, Soto-Adames 2015).

According to the most recent revisions, new characters have been added to the diagnosis, thus *Trogolaphysa* is defined by having: fourth antennal segment annulated or smooth - but never subdivided, **L2** chaeta of labium normal and not reduced, eyes 0–8,

Abd. IV with 3 bothriotracha, manubrium lacking spines, dens with spines and mucro square or rectangular, with 3 to 5 teeth (a detailed diagnosis is presented in the results topic) (Soto-Adames & Taylor 2013; Soto-Adames 2015; Bellini & Cipola 2017; Nguyen & Soto-Adames 2018).

Trogolaphysa has a Neotropical and Afrotropical distribution, but the majority of the species was recorded from the Neotropical Region (Nguyen & Soto-Adames 2018). The morphology of Neotropical species is more detailed than the African ones, due to research effort; however, there are many gaps in the knowledge for both regions. The species are mostly diagnosed only by colour patterns, the number of eyes and empodial complex and furca morphology (Nguyen & Soto-Adames 2018). Here we provide a review of *Trogolaphysa* species, presenting a revised diagnosis and a summary of the general morphology of the genus, in addition to detailed diagnoses to all 65 species, comparative tables and a key to all *Trogolaphysa* taxa.

2 Material and methods

2.1 Taxonomic data and status analysis

The status analysis of the *Trogolaphysa* species, as well as the production of new diagnoses, were based on previous studies of the genus, especially Soto-Adames (2013, 2014, 2015) and Nguyen & Soto-Adames (2018). A survey of all 65 species and their distribution was based on several sources, which are referenced under the results and discussion. The suggestion of *species inquirendae* was assigned to species with ambiguous and mostly overlapping diagnoses considering the current taxonomy of Entomobryoidea, with uncertain taxonomic characteristics and/or inaccurate or conflicting distribution data. The diagnoses of several species were updated and additions, corrections and remarks were provided based on this review.

2.2 Terminology

The shape of the mucro in *Trogolaphysa* is usually described as square (or short) and rectangular (or elongate). However, there are no clear parameters for this distinction. Therefore, clearer morphometric parameters to characterize the mucro shape were proposed. A “square mucro” in the descriptions means that the width: length ratio is at most 1:1.5; a “subrectangular mucro” means a ratio of 1:1.6–2.0; and a “rectangular mucro” means a ratio of 1:2.1 or more (Fig. 1.1).

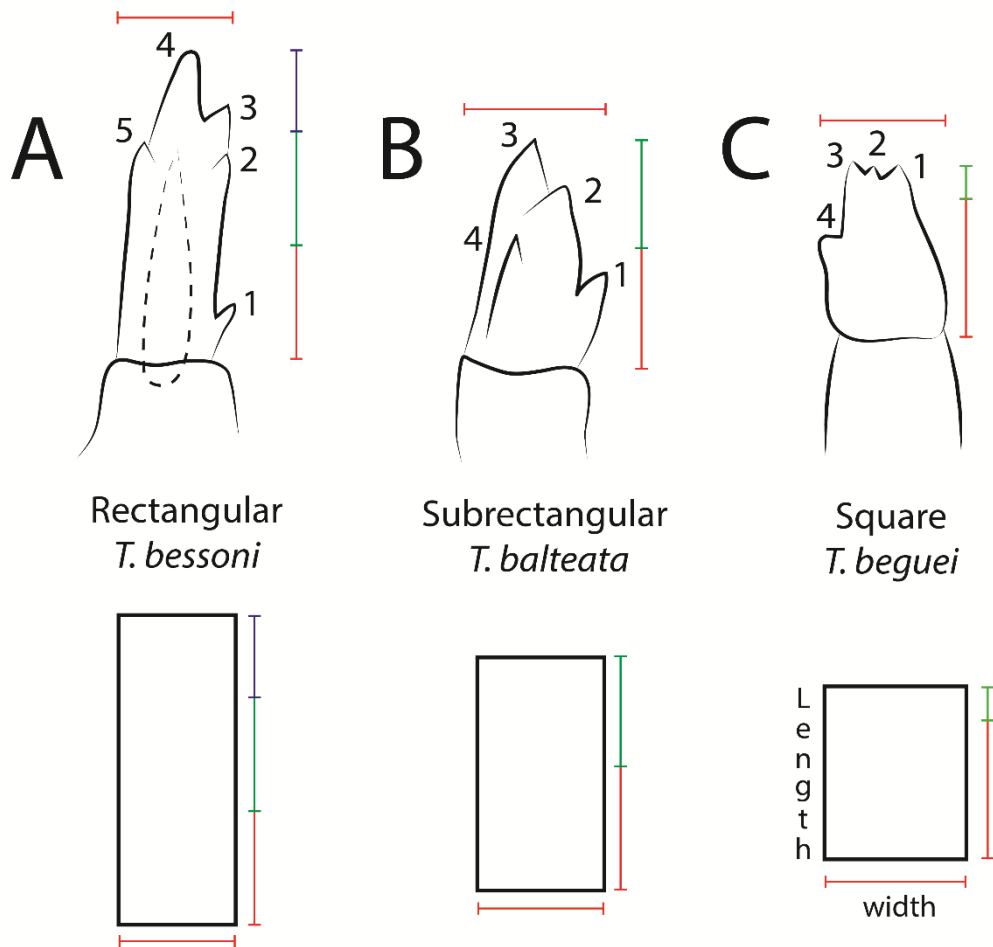


Figure 1.1. Mucronal shapes. A, rectangular mucro (elongate); B, subrectangular mucro (elongate); and C, square mucro (short). The external coloured lines of the geometric shapes represent the width and length, red lines represent width dimensions.

Some cave species have been described as having reduced tenant hairs, as *T. bessoni* Thibaud & Najt, 1988, which has the ratio unguis: tenent-hair approximately 1: 0.37. Considering this species as a parameter, whenever the ratio unguis: tenent-hair was < 0.5 , it is described as reduced tenent-hair. In cases in which measurements of the tenent-hair were not included in the original descriptions, this proportion was obtained based on the original drawings. The same was applied to measurements of the mucro, thorax II vs. III, and antennae vs. head or body of some species.

The dorsal trunk microsensilla (**ms**) formula (Th. II–Abd. V) is indicated by a formula in which its numbers are the quantity of **ms** present by half segment. For example, a **ms** formula 10 | 10100 the values before the vertical bar indicate that the second thoracic segment has one sensillum and the third segment has no sensilla, (since the Entomobryoidea lack the pronotum); the values after the vertical bar correspond to the

abdominal segments, sequentially, up to the fifth abdominal segment (Fig. 2.1) (Zhang & Deharveng 2015). The dorsal trunk sensilla (sens) formula (Th. II–Abd. V) is similar to the **ms** formula; however, a plus sign “+” is used for the fourth abdominal segment, which bears several sensilla that are often overlooked. Therefore, the formula 11 | 011+2–3 indicates there is one sensillum on the second and one on the third thoracic segments; after the vertical bar, the first abdominal segment lacks sensilla, the second and third abdominal segments have one sensillum, the fourth segment presents several (+), and the fifth presents two or three (Fig. 2.1) (Zhang & Deharveng 2015).



Figure 2.1. Example of microsensilla and sensilla formulae.

The labial formula follows the Gisin’s system (1967), with additions of Mari-Mutt (1986), in which the letters represent the anterior (a), medial (m), reduced (r), external (e) and lateral (l) chaeta. Uppercase letters indicate ciliated chaetae and lowercase indicate smooth chaetae. Figure 3.1 shows an example of the labial formula M1–2rEL1–2a1–5.

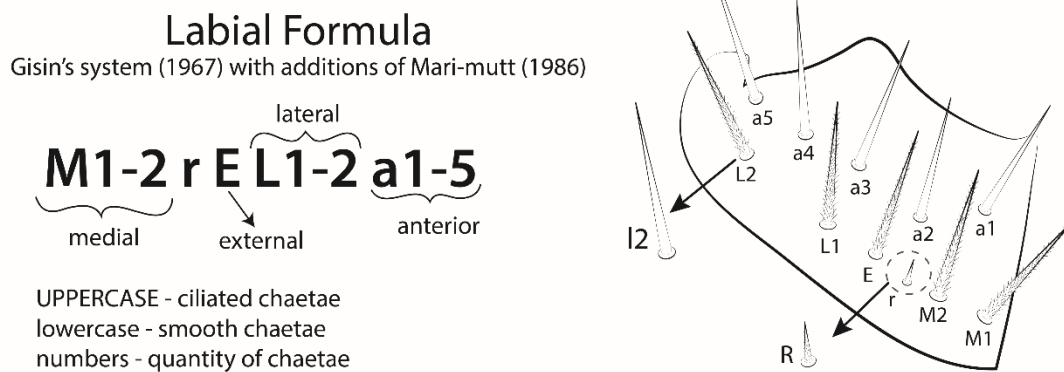


Figure 3.1. Example of the labial formula based on Gisin’s System (1967) with Mari-Mutt’s additions (1986).

The nomenclature of structures used in the diagnoses mainly follows Gisin (1967) and Mari-Mutt (1986) for labial chaetotaxy, as previously noted; Fjellberg (1999) for labial palp papillae; Cipola *et al.* 2014 for labral chaetotaxy; Mari-Mutt (1979) modified by Soto-Adames (Soto-Adames 2015; Soto-Adames *et al.* 2008) for dorsal head

chaetotaxy; Szeptycki (1979), Zhang & Deharveng (2015) and Soto-Adames (2015) for dorsal chaetotaxy. Chaetae of uncertain homology are followed by a question mark (?).

Abbreviations used in diagnoses are: mac = macrochaeta(e); mic = microchaeta(e); mes = mesochaeta(e); Ant. = antennal segment(s); Th. = thoracic segment(s); Abd. = abdominal segment(s); sensila(s) = sens; trunk microsensilla = ms.

3 Results and Discussion

3.1 Taxonomic Summary of the Genus *Trogolaphysa*

Order Entomobryomorpha Börner, 1913

Superfamily Entomobryoidea Womersley, 1934

Family Paronellidae Börner, 1906 *sensu* Zhang *et al.* 2019

Subfamily Paronellinae Börner, 1906 *sensu* Zhang *et al.* 2019

Tribe Paronellini Börner, 1906 *sensu* Soto-Adames *et al.* 2014

Genus *Trogolaphysa* Mills, 1938

Diagnosis. Pigmentation variable, dark to devoid of pigments (cave forms). Hyaline ciliate scales distributed on Ant. I–II (at least), head (dorsally and ventrally), dorsal trunk and ventral face of manubrium and dens. Ant. IV not subsegmented, slightly annulated or smooth, apical bulb absent. Labrum lacking outer papillae, internal papillae, if present, mostly spine-like, rarely fringed; prelabral chaetae smooth or ciliate. Eyes 0–8. Dorsal head with anterior bothriotrichum, lateral to Ant. I, **Ps3** mic absent. Labial chaetae **L1** and **L2** subequal, **L2** never reduced. Post-labial basal region usually with several chaetae organized in one or two transversal rows. Chaetotaxy of Th. II–III and Abd. I in adults mostly reduced. Dorsal trunk (Th. II–Abd. V) with **ms** and sens formulae respectively: 10|10100 and 11|011+2–3. Abd. IV with 3 bothriotricha. Manubrium without clear spines like the ones on dens. Dens with one or two rows of ciliate spines; mucro square (shorter), subrectangular or rectangular (longer), with 3–5 teeth (Mills 1938; Soto-Adames *et al.* 2014; Soto-Adames 2015; Bellini & Cipola 2017; Nguyen & Soto-Adames 2018).

Type species: *Trogolaphysa maya* Mills, 1938

3.2 Diagnoses of the worldwide *Trogolaphysa* species

3.2.1 *T. aelleni* Yoshii, 1988

Original description: *Trogolaphysa aelleni* Yoshii (1988: p. 453)

Type locality: Gruta das Areias, São Paulo, Brazil.

Known distribution: Brazil.

Type material: 12 specimens (sex not indicated).

Diagnosis. Body length about 1.5 mm. Specimens whitish; eyepatches weakly pigmented. Antennae up to 2.4 times longer than head length. Ant. IV annulated. Eyes 2. Prelabral chaetae weakly ciliate, 2 anterior labral spines present, normal and separated. Dorsal head chaetotaxy with at least 9 **An** mac, **A0** and **A2** as mac, others unknown. Labial formula: **M1–2rEL1–2a1–2** (**a3–5** possibly present and smooth). Mesothorax longer than the metathorax in the midline. Trochanteral organ with about 18 spine-like chaetae. Ungues narrow with 3 internal teeth: 2 small paired symmetrical basal and 1 small unpaired medial; unguiculi narrow and lanceolate, with postero-external lamella smooth; tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.82: 0.46. Ventral tube lateral flap with about 10 smooth chaetae. Dens with 2 rows of spines weakly developed. Mucro rectangular (ratio width: length of the drawing about = 1: 2.4), with 4 teeth.

Remarks. This subterranean species is similar to other cave taxa with reduced number of eyes. There are only three species of *Trogolaphysa* with 2 eyes: *T. aelleni*, *T. millsii* and *T. tijucana*, all recorded from Brazil. *T. aelleni* is the only one completely white, with two rows of dental spines and with lanceolate unguiculi, while the other two species have some pigmentation over the body, truncate unguiculi and *T. tijucana* has only one row of dental spines (Arlé 1939; Arlé & Guimarães 1979; Soto-Adames 2015).

References: Yoshii (1988); Soto-Adames (2015).

3.2.2 *T. balteata* Soto-Adames, 2015

Original description: Soto-Adames (2015: p. 27)

Type locality: Monte Diablo, Saint Ann Parish, Jamaica.

Known distribution: Jamaica.

Type material: 1 female, 2 paratypes on slides and 12 specimens in alcohol (sex not indicated).

Diagnosis. Body length up to 1.9 mm. Specimens with dark blue pigment on Ant. II–IV, frontal and post-ocular region of the head, lateral Th. II–Abd. II, central and latero-posterior Abd. IV, coxae II–III; tibiotarsi light blue; eyepatches black. Antennae up to 2.6 times longer than head length; Ant. III sense rods normal, not swollen. Eyes 6–8. Prelabral chaetae ciliate (serrate), 2 anterior labral spines present, normal and separated. Dorsal head chaetotaxy with 12 **An** mac, **A0**, **A2**, **S3**, **Pa5** and **Pm3** as mac; 4 interocular chaetae,

none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax shorter than metathorax in the midline; Th. II with **a5** plus 6 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with about 22 spine-like chaetae. Ungues wide with 4 internal teeth: 2 small paired basal asymmetrical (one tooth slight larger), 1 unpaired medial as large as the shortest paired basal tooth and 1 apical smaller; unguiculi narrow, lanceolated to weakly truncate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hairs about = 1: 0.88–0.92: 0.88. Abd. I with **a6** mic; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 3 inner mac (**A3**, **A5** and **B5**), **B6** as mes; 6 lateral mac and 12–13 posterior chaetae. Dens with 2 rows of spines, internal with 32–33 and external with 21 spines. Mucro subrectangular (ratio width: length of the drawing about = 1: 2.0), with 4 teeth.

Reference: Soto-Adames (2015).

3.2.3 *T. beguei* (Delamare-Deboutteville, 1951)

Original description: *Paronella beguei* Delamare-Deboutteville (1951, p. 1072)

Type locality: Le Banco, Ivory Coast.

Known distribution: Ivory Coast.

Type material: 10 specimens (sex not indicated).

Diagnosis. Body length about 2 mm. Specimens with dark blue pigments on Ant. III and IV, as lateral bands from post-ocular region to Th. II and Abd. IV; Th. III to Abd. II completely pigmented; eyepatches black. Antennae about 2 times longer than head length. Eyes 8. Mesothorax longer than metathorax in the midline. Ungues narrow or wide with 3–4 internal teeth: 2 paired basal, 1 unpaired longer, 1 apical small or absent; unguiculi truncate to excavate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.5–0.7: 1.1–1.5. Dens with 2 rows of spines. Mucro square to subrectangular (ratio width: length of the drawing about = 1: 1–2), with 4 teeth.

Remarks. Delamare-Deboutteville (1951) mentioned an internal row of “smooth” dental spines and an external row of large chaetae, similar to spines; therefore, we considered that the species bears 2 rows of dental spines. Nguyen & Soto-Adames (2018) mention this species has a unique colour pattern among the African *Trogolaphysa*, as well as the presence of a distinctive truncate unguiculus, this last feature is only shared with *T.*

penicillata. Our revision of the original drawings indicates such structure is slightly excavated (see Delamare-Deboutteville 1951, p. 1074, fig. 8). Some of the type specimens were found in association with *Amitermes evuncifer* termites.

References: Delamare-Deboutteville (1951); Nguyen & Soto-Adames (2018).

3.2.4 *T. belizeana* Palacios-Vargas & Thibaud, 1997

Original description: *Trogolaphysa belizeana* Palacios-Vargas & Thibaud (1997: p. 326)

Type locality: Cave Actun Chapal, Cayo District, Belize.

Known distribution: Belize.

Type material: 1 female and 5 specimens (sex not indicated).

Diagnosis. Body length up to 2.6 mm. Specimens lacking pigmentation on body, appendages and eyepatches. Antennae about 4 times longer than head length; Ant. IV apparently not annulated. Eyes absent. Prelabral chaetae smooth. Dorsal head chaetotaxy with at least 10 **An** mac, **A0**, **A2–3**, **M2**, **S3**, **S5**, **Pa5** and **Pm3** as mac. Labial formula: **M1–2rel1–2a1–5** (**L2** ciliate or smooth, others smooth – see the remarks), **r** reduced. Mesothorax and metathorax subequal in the midline. Th. II with **a5** plus 2–4 mac on **p3** complex; Th. III with 3 inner mac near to each other. Trochanteral organ with about 18 spine-like chaetae. Ungues narrow with 2 internal paired basal asymmetrical teeth, unpaired teeth absent; unguiculi lanceolated with postero-external lamella serrate (unguiculus I) or smooth (unguiculi II–III); tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.62: 0.41. Abd. I apparently lacking **a6** mic. Abd. IV with 3 inner mac (**A4–5**, **B5**), **B6** as mes. Ventral tube anterior face with 2+2 distal mac; lateral flap with 5 smooth chaetae. Dens with 2 rows of spines, internal and external with about 30 spines. Mucro rectangular (ratio width: length of the drawing about = 1: 3.6), with 3 teeth.

Remarks. The paratypes analyzed by Soto-Adames & Taylor (2013) have the labial chaetae **l2** smooth (ciliate in the original description) and Th. II with only 2 mac, which could be due to post-embryonic development.

References: Palacios-Vargas & Thibaud (1997); Soto-Adames & Taylor (2013).

3.2.5 *T. berlandi* (Denis, 1925)

Original description: *Paronella carpenteri* Denis (1925: p. 262)

Type locality: Camopi, French Guiana.

Known distribution: French Guiana and Argentina.

Type material: 4 specimens (sex not indicated).

Diagnosis. Body length about 9.1 mm (without antennae and furcula). Specimens uniformly pale yellow; eyepatches black. Eyes 8. Antennae 2.6 times longer than the head length. Ungues wide with 3–4 internal teeth: 2 paired basal symmetrical, 1 unpaired medial and 1 apical smaller present or absent; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.5–0.6: 0.9–1.0. Dens with 1 row of spines with about 13–19 spines. Mucro rectangular (ratio width: length of the drawing about = 1: 3.6–3.8), with 4 teeth.

Remarks. Although Denis' original description of *T. berlandi* outlines a species with a body length of 9.1 mm, this is very unlikely since no other *Trogolaphysa* species is clearly larger than 3 mm. Denis' notes on this species morphology do not discuss such feature as an uncommon condition, as well as Cassagnau (1963), who recorded *T. berlandi* from Argentina. It is possible this data was mistyped by Denis and it was actually 1.9 mm. Cassagnau's specimens of *T. berlandi* were identified mostly based on the shape of the mucro, which is elongate with 4 teeth. However, such feature is not remarkably different from other taxa with rectangular mucro, and Cassagnau's specimens had a slightly different number of dental spines, 15–19 (vs. 13 of the original description). Due to the distance of Camopi, French Guiana (type locality) from Tucuman province, Argentina (Cassagnau's specimens), and the very brief morphological data provided by the authors to *T. berlandi*, it is possible the populations of Argentina and French Guiana represent two distinct species. Even if the dental spines could be used to distinguish this species from others, we opted to consider *T. berlandi* as a *species inquirenda* due to the uncertainty about the individual size, as well as other data in the original description, at least until a redescription is published. *T. beguei* specimens from French Guiana were also found associated with termites (Denis 1925).

References: Denis (1925); Cassagnau (1963); Thibaud & Najt (1988).

3.2.6 *T. bessoni* Thibaud & Najt, 1988

Original description: *Trogolaphysa bessoni* Thibaud & Najt (1988: p. 724)

Type locality: Cueva San Bernardo, Archidona, Napo province, Ecuador.

Known distribution: Ecuador.

Type material: 4 specimens (sex not indicated).

Diagnosis. Body length about 1.4 mm. Specimens lacking pigmentation on body, appendages and eyepatches. Antennae about 2.7 times longer than head length; Ant. IV annulated. Ant. III senses rods normal, not swollen. Eyes absent. Prelabral chaetae

smooth, 2 anterior labral spines absent. Labial formula: **M1–2rEL112a1–5**. Th. II with 3 central mac (possibly **a5** plus two central **p**); Th. III lacking mac (*sensu* Soto-Adames & Taylor, 2013). Trochanteral organ with 19 spine-like chaetae. Ungues narrow with 2 internal paired basal symmetrical teeth, median and distal teeth absent; unguiculi basally swollen, leaf-shaped with postero-external lamella smooth; tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.62: 0.37. Abd. IV apparently with 3 central mac (**A5**, **B4–5**). Dens with 2 rows of spines, internal and external with 20 and 25 spines, respectively. Mucro rectangular (ratio width: length of the drawings about = 1: 3.1–3.6) with 4–5 teeth.

References: Thibaud & Najt (1988); Soto-Adames & Taylor (2013).

3.2.7 *T. caripensis* (Gruia, 1987)

Original description: *Troglopedetes caripensis* Gruia (1987: p. 155)

Type locality: Cueva del Guacharo, Monagas, Venezuela.

Known distribution: Venezuela.

Type material: 6 specimens (sex not indicated).

Diagnosis. Body length about 1.6–1.8 mm. Specimens lacking pigmentation on body and eyepatches. Antennae about 3 times longer than head length. Ant. IV with a single annulation. Eyes absent. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced; **L2** longer. Dorsal head chaetotaxy with 9–12 **An**, **A0**, **A2**, **M1–2**, **S2–3**, **S5**, **Pa5** and **Pm3** as mac; post-labial basal chaetae 1+4. Mesothorax slightly longer than the metathorax in the midline. Th. II with **a5** plus 6 mac on **p3** complex. Th. III lacking mac. Trochanteral organ with about 21 spine-like chaetae. Ungues with 3 internal teeth: 2 paired basal asymmetrical and 1 unpaired medial as large as the smallest basal tooth; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.6: 0.5. Abd. II–III with 2 and 4 mac respectively, **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III. Abd. IV with 4 inner mac, apparently **A3**, **A5**, **B4–5**; with at least 6 lateral mac. Dens with 2 rows of spines, internal and external with 30–35 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 2.5–3.6), with 4 teeth.

Reference: Gruia (1987).

3.2.8 *T. carpenteri* (Denis, 1925)

Original description: *Paronella carpenteri* Denis (1925: p. 261)

Type locality: Bas Carsevenne, French Guiana.

Known distribution: French Guiana, Mexico, Costa Rica and Venezuela.

Type material: 2 specimens (sex not indicated).

Diagnosis. Body length about 1.8–2 mm. Colour pattern variable, with specimens mostly pale with Ant. III–IV pigmented, or with body laterally pigmented on Th. II to Abd. I and Abd. III–V, proximal legs and furca dark pigmented, or even specimens with diffused pigments all over the trunk and antennae entirely dark pigmented; eyepatches black. Antennae about 1.8–3 times longer than head length. Ant. IV annulated. Eyes 8. Prelabral chaetae smooth, 2 anterior labral spines present, normal and separated. Dorsal head chaetotaxy with 11 **An** mac, **A0** and **A2** as mac, **A3** possibly as mic, others unknown. Labial formula: **M1–2rEL1–2a1–2 (a3–5** possibly as smooth chaetae), **r** reduced. Mesothorax longer than the metathorax in the midline. Trochanteral organ with more than 60 spine-like chaetae. Ungues wide with 3–4 internal teeth: 2 paired basal symmetrical, 1 unpaired medial as large as the paired basal teeth and 1 minute apical teeth present or absent; unguiculi lanceolate with postero-external lamella smooth or slightly serrated; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.66: 0.64 (*sensu* Yoshii's 1988 drawings). Ventral tube anterior face apparently lacking distal mac, lateral flap with about 15 smooth chaetae. Dens with 2 rows of spines, internal and external with 24–29 and 16–25, respectively. Mucro rectangular (ratio width: length of the drawing about = 1: 2.4–2.8), with 4 teeth.

Remarks. Most of the diagnostic characters for *T. carpenteri* listed here were described by Yoshii (1988), including the anterodorsal aspects of the head, and chaetotaxy of the labrum, labium and ventral tube. Our diagnosis is a consensus of the three descriptions based on materials from four different countries, two from Central America and two from South America. Denis' original description (1925) was based on specimens from French Guiana, but some features were amended by the same author in 1931, after the analysis of specimens from Costa Rica. Two of his additions were the inclusion of the apical unpaired tooth of unguis and discrete serrations on one of the two posterior lamellae of the unguiculus (Denis 1931, p. 152). Yoshii's more detailed description (1988) was based on material from Mexico and Venezuela. However, Yoshii's description of *T. carpenteri* does not entirely match Denis' 1931 redescription, as it lacks information on the apical tooth of the unguis and serrations of the unguiculus. Besides, Denis (1925, 1931) and Yoshii (1988) report different colour patterns for the same species. It is likely that the different populations of *T. carpenteri* represent two or more species, with similar

characters. However, since several features of the type material are unknown or unclear, we opted to consider *T. carpenteri* as a *species inquirenda*, with widespread distribution of similar morphotypes. Further data on the type material (or at least topotypical) are needed to clarify this issue.

References: Denis (1925); Denis (1931); Yoshii (1988).

3.2.9 *T. clarencei* Soto-Adames, 2015

Original description: *Trogolaphysa clarencei* Soto-Adames (2015: p. 21)

Type locality: Volcan San Martin, Veracruz, Mexico.

Known distribution: Mexico.

Type material: 2 specimens on slides and 7 specimens in alcohol (sex not indicated).

Diagnosis. Body length up to 3 mm. Specimens with light blue pigments scattered all over the body; antennae, distal femurs and tibiotarsi uniformly light blueish; furca pale; eyepatches black. Antennae up to 2.6 times longer than head length; Ant. III sense rods normal, not swollen. Eyes 6, G and H lenses unclear, possibly absent. Prelabral chaetae ciliate, 2 anterior labral spines absent. Dorsal head chaetotaxy with 12–16 **An** mac, **A0**, **A2–3**, **M2**, **S3**, **Pa5** and **Pm3** as mac; 4 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 6 mac on **p3** complex; Th. III with 3 inner mac near to each other, forming a triangle (**a2?**, **p2–3**). Trochanteral organ with up to 38 spine-like chaetae. Ungues wide with 3 internal teeth: 2 small paired basal asymmetrical (one slightly larger) and 1 unpaired medial as long as the shortest paired tooth; unguiculi lanceolated with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hairs about = 1: 0.78: 0.74. Abd. I with **a6** mic; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 4 inner mac (**A3**, **A5**, **B4** and **B5**), **B6** as mes; 7 main lateral mac (**D3**, **E2–4** and **F1–3**) and up to 20 posterior chaetae. Dens with 2 rows of spines, internal and external with 30 and 24 spines, respectively. Mucro rectangular (ratio width: length of the drawing about = 1: 2.4), with 4 teeth.

Reference: Soto-Adames (2015).

3.2.10 *T. cotopaxiana* Thibaud & Najt, 1988

Original description: *Trogolaphysa cotopaxiana* Thibaud & Najt (1988: p. 726)

Type locality: Province de Cotopaxi, Latacunga, Ecuador.

Known distribution: Ecuador.

Type material: 3 specimens (sex not indicated).

Diagnosis. Body length about 1.5–1.75 mm. Specimens pale with antennae and head slightly pigmented; eyepatches dark. Antennae about 2 times longer than head length. Ant. IV annulated. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines absent. Dorsal head apparently with about 12 **An**, **A0**, **A2** as mac, with 4 interocular chaetae. Labial formula: **M1–2rEL1–2a1–5**. Mesothorax slightly longer than the metathorax in the midline. Th. II with 3 mac on **p3** complex; Th. III lacking mac. Ungues wide with 4 internal teeth: 2 paired basal symmetrical, 1 medial and 1 apical smaller; unguiculi lanceolated with postero-external lamella apparently smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.7: 1.0. Abd. II with 2 mac (**m3** and **m5**), Abd. III with at least 2 mac (homologies uncertain, possibly mistakenly represented). Abd. IV with 3 inner mac; with at least 4 lateral mac. Ventral tube anterior face with 2+2 distal mac. Dens with 1 row of internal spines, with 20–24 spines. Mucro (ratio width: length of the drawing about = 1: 3.2), rectangular with 4–5 teeth.

Reference: Thibaud & Najt (1988).

3.2.11 *T. delamarei* (Massoud & Gruia 1973)

Original description: *Troglopedes delamarei* Massoud & Gruia (1973: p. 339)

Type locality: Cueva la Majana, Cuba.

Known distribution: Cuba.

Type material: 5 specimens (sex not indicated).

Diagnosis. Body length about 2.9 mm. Specimens lacking pigmentation on body, appendages and eyepatches. Antennae about 3.7 times longer than head length; Ant. IV annulated. Eyes absent. Dorsal head chaetotaxy with 14 **An** mac, **A0**, **A2**, **A5**, **M2**, **S2-3**, **Pa5** and **Pm3** as mac, **Pa2** apparently as mac. Labial formula: **M1–2rEL1–2A1–5**, **r** reduced; post-labial basal chaetae 5(4)-6+5(4)-6. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 5 mac on **p3** complex; Th. III lacking mac. Ungues wide with 4 internal teeth: 2 paired basal asymmetrical, 1 unpaired medial slightly smaller than the smaller basal tooth and 1 apical minute tooth; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.63: 0.50. Abd. II–III with 2 and 4 mac respectively, **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III. Abd. IV with 4 inner mac, apparently **A3**, **A5**, **B4-5**; with at least 5 lateral mac. Dens with 2 rows of spines. Mucro rectangular (ratio width: length of the drawings about = 1: 2.5), with 4 teeth.

Remarks. Gruia (1987) provided a detailed set of features for *T. delamarei*: dorsal and ventral chaetotaxy for the head, dorsal chaetotaxy for the trunk and labial morphology. One year later, Thibaud & Najt (1988) examined *T. delamarei*'s holotype and noted that the serrations on unguiculus were similar to *T. maya*, proposing the synonymy, apparently disagreeing with Gruia's redescription and notes on *T. delamarei*. The new characters described by Gruia (1987) for *T. delamarei*, along with the differences in antennal size, the morphology of the empodial complex (clearly troglomorphic in *T. maya*) and the distance between the type-localities of the two cave species strongly support the hypothesis that *T. delamarei* and *T. maya* are two different taxa. Therefore, we revalidate here the name *T. delamarei* as a distinct species of *T. maya* (see also remarks under *T. maya*).

References: Massoud & Gruia (1973); Gruia (1987); Thibaud & Najt (1988).

3.2.12 *T. dimorphica* Soto-Adames, 2015

Original description: *Trogolaphysa dimorphica* Soto-Adames (2015: p. 14)

Type locality: Cacahoatán, Chiapas State, Mexico.

Known distribution: Mexico.

Type material: 2 females and 1 male on slides and 11 juveniles in alcohol.

Diagnosis. Body length up to 2.3 mm. Specimens with light blue pigments on head, Th. III–Abd. III and tibiotarsi and dark blue pigments on distal Ant. I, Ant. II–IV and hind coxae; eyepatches black. Antennae up to 3 times longer than head length; Ant. III sense rods normal, not swollen. Eyes 6–8 (possibly 8). Prelabral chaetae ciliate, 2 anterior labral spines present, reduced and separate. Dorsal head chaetotaxy with about 13 **An** mac, **A0**, **A2–3**, **M2**, **S3**, **Pa5** and **Pm3** as mac, one individual with only **A0** and **A2** as mac; 4 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 5–6 mac on **p3** complex; Th. III with 3 inner mac near to each other, forming a triangle (**a2?**, **p2–3**). Trochanteral organ with at least 18 spine-like chaetae. Ungues wide with 3 internal teeth: 2 small paired basal (one slightly larger) and 1 unpaired medial as long as the shortest paired tooth; unguiculi lanceolated with postero-external lamella serrated proximally in females or smooth in males; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.63: 0.85. Abd. I with **a6** mic; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 4 inner mac (**A3**, **A5**, **B4–5**), **B6** apparently as mes, **B4** absent in male specimens, 5–7

lateral mac and 14–15 posterior chaetae. Dens with 2 rows of spines, internal and external with 24–30 and 18–23 spines, respectively. Mucro rectangular (ratio width: length of the drawing about = 1: 2.7), with 4 teeth.

Remarks. *Trogolaphysa dimorphica* shows a remarkable sexual dimorphism on unguis teeth, postero-external lamella of the unguiculus and internal and external chaetotaxy of Abd. IV (Soto-Adames 2015). However, it should be noted that the number of available specimens for analysis (only 3 adults) may obscure the fact that such polymorphisms could occur in both sexes, or represent two different species. The very dissimilar chaetotaxy of one specimen (sex unknown), lacking most centro-anterior mac, supports the second hypothesis.

Reference: Soto-Adames (2015).

3.2.13 *T. distinguenda* (Denis, 1931)

Original description: *Paronella distinguenda* Denis (1931: p. 152)

Type locality: San José, Faldas volcano Irazú, Puente de las Mulas and Puente de las Apilas, Costa Rica.

Known distribution: Costa Rica.

Type material: 11 specimens (sex not indicated).

Diagnosis. Body length up to 2.2 mm. Specimens pale with violet pigment on antennae, legs (darker over the coxae) and lateral trunk; eyepatches black. Antennae about 2 times longer than head length. Ant. IV not annulated. Mesothorax and metathorax subequal in the midline. Ungues narrow with 4 internal teeth: 2 paired basal symmetrical, 1 unpaired medial as large as the paired basal teeth and 1 apical smaller; unguiculi lanceolate with postero-external lamella smooth, with one basal tooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.43–0.64: 0.78–0.93. Dens with 2 rows of spines, internal and external with 15–25 and 10–20, respectively. Mucro rectangular (ratio width: length of the drawing about = 1: 3.1–3.3), with 5 teeth.

Remarks. Denis (1931) collected specimens of *T. distinguenda* from San José, Costa Rica, and from three different localities apparently in its vicinities. *T. carpenteri* was also recorded from Puente de las Mulas, and it shows a very similar colour pattern to *T. distinguenda*. Both species also have overlapping morphological characters, such as the shape of the unguis and the number of dental spines. However, even if *T. carpenteri* was considered a *species inquirenda*, *T. distinguenda* can still be readily distinguished from *T. carpenteri* due to the presence of a basal tooth on unguiculus and 5 mucronal teeth,

which is an uncommon feature in most species of the genus. Therefore, even if many chaetotaxy features could not be characterized here, we believe there is sufficient data to consider *T. distinguenda* as a valid species.

References: Denis (1931); Soto-Adames & Taylor (2013).

3.2.14 *T. ecuatorica* (Palacios-Vargas, Ojeda & Christiansen, 1985)

Original description: *Troglopedetes ecuatorica* Palacios-Vargas, Ojeda & Christiansen (1985, p. 22)

Type locality: Cueva Comando, Los Tayos (Andes Mountain), Ecuador.

Known distribution: Ecuador.

Type material: 3 specimens (sex not indicated).

Diagnosis. Body length about 1.5 mm. Specimens lacking pigmentation on body and eyepatches. Antennae about 2.3 times longer than head length. Ant. IV not annulated. Eyes absent. Prelabral chaetae smooth; 2 anterior labral spines absent. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Trochanteral organ with about 12 spine-like chaetae. Ungues narrow with 2 internal paired basal symmetrical teeth, apical and medial teeth absent, unguis III slightly wider than II, with larger basal teeth; unguiculi lanceolated with postero-external lamella smooth (unguiculus II with 3 small proximal teeth); tenent-hairs reduced and acuminate; ratio unguis: unguiculus: tenent-hair about = 1: 0.58: 0.31. Dens with 2 rows of spines, internal and external rows with about 45 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 2.3), with 5 teeth.

Remarks. The single illustration plate in the original description (Palacios-Vargas *et al.* 1985). is misnumbered. We considered it as figs 8C–E (p. 21) since they fit the description text and do not suit any other species described in the paper.

Reference: Palacios-Vargas *et al.* (1985).

3.2.15 *T. entreriosensis* Soto-Adames, 2015

Original description: *Troglophysa entreriosensis* Soto-Adames (2015: p. 23)

Type locality: El Palmar National Park, Entre Rios, Argentina.

Known distribution: Argentina.

Type material: 1 specimen on slide (sex not indicated).

Diagnosis. Body length about 1.4 mm. Specimens pale with scattered pigment on head and trunk; distal Ant. I, Ant. II, lateral edges of Th. II–III and coxae dark pigmented; eyepatches black. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines present, normal and separated. Dorsal head chaetotaxy with 14 **An mac**, **A0**, **A2–3**, **S5**, **Pa5** and **Pm3** as

mac; 3–4 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 6 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with 16 spine-like chaetae. Ungues wide with 4 internal teeth: 2 paired basal symmetrical, 1 unpaired medial and 1 apical smaller; unguiculi lanceolated with postero-external lamella smooth or weakly serrate; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.67: 0.60. Abd. I with **a6** mic; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 3 inner mac (**A3**, **B4** and **B5**), **B6** as mes; 6 lateral mac and 7 posterior chaetae. Dens with 2 rows of spines, internal and external with 19 and 15 spines, respectively. Mucro rectangular (ratio width: length of the drawing about = 1: 3.0–3.3), with 4 teeth.

Reference: Soto-Adames (2015).

3.2.16 *T. ernesti* Cipola & Bellini, 2017

Original description: *Trogolaphysa ernesti* Cipola & Bellini (2017: p. 170)

Type locality: Geopark Araripe, Ceará. Brazil.

Known distribution: Brazil.

Type material: 6 males and 2 females on slides.

Diagnosis. Body length about 2.5 mm. Specimens pale with dark blue pigment on distal Ant. I–IV, lateral Th. II–III, distal femurs I–II to half tibiotarsi; eyepatches black. Antennae about 2.2 times longer than head length. Ant. IV annulated. Ant. III sense rods swollen. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines present, normal and separated. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Dorsal head chaetotaxy with 16 **An** mac, **A0**, **A2–3**, **M2**, **S3**, **S5**, **Pa5** as mac, **Pm3** as mes; 4 interocular chaetae, none as mac; post-labial basal chaetae 0+6. Mesothorax longer than metathorax in the midline. Th. II with **a5** plus 6 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with about 49 spine-like chaetae. Ungues wide with 4 internal teeth: 2 paired basal symmetrical, 1 unpaired medial as large as the paired basal teeth and 1 apical smaller; unguiculi lanceolated with postero-internal lamella entirely serrate; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.62: 0.97. Abd. I with **a6** mic. Abd. II with 2 (**m3** and **m5**) and Abd. III with 5 (**m3**, **am6**, **pm6**, **p6–7**) mac, respectively; Abd. IV with 4 inner mac (**A3**, **A5**, **B4** and **B5**), **B6** as mes; 10 lateral mac and 10 posterior chaetae. Ventral tube anterior face with 4+4 distal mac (3+3 on the distal row); lateral flap with 12 chaetae: 9 ciliate and 3 smooth; posterior face lacking smooth chaetae. Dens

with 2 rows of spines, internal row with 23–30 and external with 21–27. Mucro subrectangular (ratio width: length of the drawing about = 1: 2), with 4 teeth.

Reference: Bellini & Cipola (2017).

3.2.17 *T. formosensis* Silva & Bellini, 2015

Original description: *Trogolaphysa formosensis* Silva & Bellini (2015: p. 53)

Type locality: Reserva Privada Mata Estrela, Baía Formosa, Brazil.

Known distribution: Brazil.

Type material: 5 females and 3 males on slides.

Diagnosis. Body length about 1.4 mm. Specimens pale with dark blue pigment on Ant. I–IV, frontal head, lateral Th. II to Abd. III, posterior Abd. III and almost half of Abd. IV (as a transversal band); eyepatches black. Antennae about 3.1 times longer than head length. Ant. IV not annulated; Ant. III sens rods normal. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines absent. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Dorsal head chaetotaxy with 8–10 **An** mac, **A0**, **A2**, **M2**, **M4** (also as mes), **S3**, **S5** and **Pa5** as mac; 5 interocular chaetae, none as mac. Mesothorax shorter than metathorax in the midline; Th. II with **a5** and **p4** plus 6 mac on **p3** complex; Th. III with **a2**, **p2** and **p3** as mac. Trochanteral organ with about 12 spine-like chaetae. Ungues wide with 4 internal teeth: 2 paired basal symmetrical, 1 unpaired medial smaller than the basal teeth and 1 minute apical tooth; unguiculi truncate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.62: 0.87. Abd. I with **a6** mic; Abd. II–III with 2 and 4 mac respectively, **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 4 inner mac (**A3**, **A4**, **B4** and **B5**), **B6** as mes; 7 lateral mac. Dens with 2 rows of spines. Mucro rectangular (ratio width: length of the drawing about = 1: 2.2), with 4 teeth, with a crest-like projection almost forming a fifth tooth.

Remarks. See remarks under *T. tijucana*.

Reference: Silva & Bellini (2015).

3.2.18 *T. fuelleborni* (Börner, 1903)

Original description: *Paronella fuelleborni* Börner (1903: p. 143)

Type locality: Tukungu (Langenburg, former German colony), Tanzania.

Known distribution: Tanzania, Madagascar (uncertain)

Type material: 3 specimens (sex not indicated).

Diagnosis. Body length up to 2.4 mm. Specimens pale with light blue pigment on Ant. I–II; dark blue pigment on Ant. III–IV, lateral trunk, coxae; head anteriorly darker. Eyes 8. Ungues wide with 4 internal teeth: 2 paired basal asymmetrical, 1 medial unpaired shorter than the basal teeth and 1 apical subequal to the medial tooth; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.66: 0.96 (*sensu* Nguyen & Soto-Adames 2018). Dens with 1 row of 20–44 spines. Mucro square with 4 teeth.

Remarks. The short diagnosis provided by Börner (1903) resulted in confusion regarding the identity of *T. fuelleborni*, which was already considered a synonym of *T. nigromaculata*, which is currently considered to be a species complex (Nguyen & Soto-Adames, 2018). Womersley (1934) published a list of species from Africa and reported the species from Madagascar. However, the record of *T. fuelleborni* in the island is still uncertain because the author did not provide descriptive information about the species (Nguyen & Soto-Adames, 2018). Because the generic and brief diagnosis lacks sufficient features to distinguish the species, and considering its likely similarity with *T. nigromaculata*, we herein consider *T. fuelleborni* as a *species inquirenda*.

References: Börner (1903); Nguyen & Soto-Adames (2018).

3.2.19 *T. geminata* (Mari-Mutt, 1987)

Original description: *Dicranocentrua geminate* Mari-Mutt (1987: p. 402)

Type locality: Maricao, Puerto Rico.

Known distribution: Puerto Rico.

Type material: 3 specimens on slides and 16 specimens in alcohol (sex not indicated).

Diagnosis. Body length up to 2.0 mm. Colour pattern as in *T. jataca*, but all specimens with Ant. I–IV pigmented. Ant. IV annulated. Eyes 6. Prelabral chaetae ciliate; 2 anterior labral spines present. Dorsal head chaetotaxy with 15–16 **An** mac, **A0**, **A2**, **M2**, **S3**, **Pa5** and **Pm3** as mac; 3 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline. Th. II with **a5** mac plus 6 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with up to 25 spine-like chaetae. Ungues wide with 3–4 internal teeth: 2 large paired basal asymmetrical, and 1 unpaired medial as large as the smallest basal tooth and 1 minute distal, present or absent; unguiculi lanceolated with postero-external lamella serrated; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.73: 0.76. Abd. I with **a6** mic. Abd. II–III with 2 and 4 mac respectively, **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III.

Abd. IV with 3 inner mac (**A4, A5, B5**), **B6** as mes; 7 main lateral mac (**Te2, D3, E2–3, F1–3**) and 13–14 posterior chaetae. Ventral tube anterior face with 3+3 distal mac. Dens with 2 rows of spines, internal and external rows with up to 22 spines each. Mucro subrectangular with 4 teeth.

Remarks. The original description of *T. geminata* was strongly based on the redescription of *T. jataca* by Mari-Mutt (1987). The author pointed out two main differences between the two species: the absence of **S5** dorsal head mac (following Soto-Adames & Taylor 2013, present in *T. jataca*), and one additional interocular chaeta in *T. jataca*. Soto-Adames & Taylor (2013) also mentioned the presence of **a6** mic on Abd. I in *T. geminata* (absent in *T. jataca*). *Trogolaphysa geminata* belongs to *T. jataca* species complex, and its variable morphology may be an indication of the existence of cryptic species (see also remarks under *T. luquillensis* and *T. riopedrensis*).

References: Mari-Mutt (1987); Soto-Adames & Taylor (2013).

3.2.20 *T. ghesquierei* (Marlier, 1945)

Original description: *Paronella ghesquierei* Marlier (1945: p. 260)

Type locality: Eala, Mbandaka, Republic of Congo.

Known distribution: Republic of Congo.

Type material: 8 specimens (sex not indicated).

Diagnosis. Body length about 1.5 mm. Specimens uniformly yellowish with brown pigments on legs and Ant. II apically, Ant. III–IV totally violet pigmented; eyepatches black. Antennae shorter than body. Ungues with 4 internal teeth: 2 paired basal symmetrical, 1 unpaired subequal to the basal teeth and 1 apical smaller; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.53: 0.92. Dens with 1 row with 16 spines. Mucro subrectangular (ratio width: length of the drawing about = 1: 1.7), with 4 teeth.

Remarks. According to Nguyen & Soto-Adames (2018), *T. ghesquierei* is apparently the only African species presenting an uniformly yellowish trunk and 4 internal teeth on the ungues. However, its very brief diagnosis and generic morphology are insufficient to clearly separate this species from all other *Trogolaphysa*, and therefore we place *T. ghesquierei* as a *species inquirenda*.

References: Marlier (1945); Nguyen & Soto-Adames (2018).

3.2.21 *T. giordanoae* Soto-Adames & Taylor 2013

Type locality: Blue Creek cave, Toledo District, Belize.

Known distribution: Belize.

Type material: 1 female plus 6 specimens on slides and 85 on alcohol (sex not indicated).

Diagnosis. Body length up to 2.1 mm. Colour pattern unknown, eyepatches dark. Antennae about 2–2.5 times longer than head length; Ant. IV not annulated; Ant. III sense rods swollen (leaf-like). Eyes 6. Prelabral chaetae ciliate, 2 anterior labral spines present, normal and basally fused. Dorsal head chaetotaxy with 13–14 **An** mac, **A0**, **A2**, **M2**, **Pa5** and **Pm3** as mac; 4–6 interocular chaetae, none as mac. Labial formula: **M1–2REL1–2a1–5**, **R** reduced; post-labial basal chaetae 3+6. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 6 mac on **p3** complex; Th. III with 3 inner mac near to each other, forming a triangle (**a2?**, **p2–3**). Trochanteral organ with up to 36 spine-like chaetae. Ungues wide with 4 internal teeth: 2 small paired basal symmetrical, 1 unpaired medial (larger than the others) and 1 unpaired apical; unguiculi lanceolated with postero-external lamella serrated (entirely); tenent-hairs weakly capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.61: 0.59. Abd. I with **a6** mic; Abd. II–III with 2 and 4 mac respectively, **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 4 inner mac (**A3**, **A5**, **B4–5**), **B6** apparently as mes, 9 lateral mac and 19–21 posterior chaetae. Ventral tube anterior face with 3–4 distal mac. Dens with 2 rows of spines, internal row with 35–42 and external with 25–28 spines, respectively. Mucro subrectangular (ratio width: length of the drawings about = 1: 2.0), with 4 teeth.

Reference: Soto-Adames & Taylor (2013).

3.2.22 *T. grassei* (Delamare-Deboutteville, 1952)

Original description: *Paronella grassei* Delamare-Deboutteville (1952: p. 241)

Type locality: Le Banco, Ivory Coast.

Known distribution: Ivory Coast.

Type material: 1 specimen (sex not indicated).

Diagnosis. Specimen pale with violet pigmentation on Ant. II–IV, lateral Th. II to Abd. II, legs I–III, distal half of Abd. IV and ventral manubrium; eyepatches black. Eyes 8. Mesothorax longer than metathorax in the midline. Ungues wide with 3 internal teeth: 2 paired basal symmetrical and 1 unpaired medial shorter than the basal teeth; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis:

unguiculus: tenent-hair about = 1: 0.43: 0.55. Dens with 2 rows of spines. Mucro rectangular (ratio width: length of the drawing about = 1: 2.45–3.64), with 3 teeth.

Remarks. *Trogolaphysa grassei* is the only African species with 3 mucronal teeth (Nguyen & Soto-Adames 2018); it is also the only species in the genus with 8 eyes and unguis with 3 internal teeth.

References: Delamare-Deboutteville (1952); Nguyen & Soto-Adames (2018).

3.2.23 *T. guacharo* Yoshii, 1988

Original description: *Trogolaphysa guacharo* Yoshii (1988: p. 455)

Type locality: Cueva Alfredo Jahn, Miranda; Cueva del Guacharo, Mongas, Venezuela.

Known distribution: Venezuela and Costa Rica.

Type material: 5 specimens (sex not indicated).

Diagnosis. Body length about 1.7 mm. Specimens lacking pigmentation. Antennae about 2.7 times longer than head length. Ant. IV annulated; Ant. III sense rods normal, not swollen. Eyes absent. Prelabral chaetae weakly ciliate, 2 anterior labral spines present, normal and separated. Dorsal head chaetotaxy with at least 8 **An** mac, **A0** and **A2–3** as mac, others unknown. Labial formula: **M1–2rEL1–2**. Th. II–III lacking mac. Trochanteral organ with about 40 spine-like chaetae. Ungues wide with 3 internal teeth: 2 paired basal larger asymmetrical and 1 unpaired medial with the same size of the smaller basal tooth; unguiculi lanceolated with postero-external lamella smooth; tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.78: 0.38. Abd. I–IV lacking mac. Ventral tube lateral flap with about 8–10 smooth chaetae. Dens with 2 rows of spines with about 25 spines each. Mucro subrectangular (ratio width: length of the drawing about = 1: 2.0), with 4 teeth.

Remarks. The original description indicates *T. guacharo* lacks mac on dorsal trunk, similarly to *T. strinatii* in Yoshii (1988). As discussed under *T. strinatii*, this is unlikely and must be better investigated, since at least Abd. II–IV usually hold few mac, not only in *Trogolaphysa* but in Entomobryoidea as a whole. Therefore, we placed *T. guacharo* as *species inquirenda* until the dorsal chaetotaxy can be redescribed.

Reference: Yoshii (1988).

3.2.24 *T. haitica* (Palacios-Vargas, Ojeda & Christiansen, 1985)

Original description: *Troglopedetes haiticus* Palacios-Vargas, Ojeda & Christiansen (1985, p. 16)

Type locality: Gruta Counoubais, Camp-Perrin, Haiti.

Known distribution: Haiti.

Type material: 4 specimens (sex not indicated).

Diagnosis. Body length about 2.7 mm. Specimens lacking pigmentation on body, appendages and eyepatches. Antennae 2.3 times longer than head length. Ant. III sens rods swollen. Ant. IV annulated. Eyes absent. Prelabral chaetae smooth; 2 anterior labral spines absent. Labial formula: **M1–2reL1–2a1–5**, **r** reduced. Th. II–III lacking mac (*sensu* Soto-Adames & Taylor, 2013). Trochanteral organ with approximately 22 spine-like chaetae. Ungues wide with 2 internal paired basal asymmetrical teeth, medial and apical teeth absent; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs reduced and acuminate, ratio unguis: unguiculus ; tenent-hair about = 1: 0.71 ; 0.47. Abd. IV lacking internal mac (*sensu* Soto-Adames & Taylor, 2013). Dens with 2 rows of spines, internal and external rows with 30–38 spines. Mucro rectangular (ratio width: length of the drawing about = 1: 2.7), with 4 teeth.

Remarks. Despite the similarities shared by the eyeless cave species, *T. haitica* can be distinguished from other subterranean species by the combination of Ant. IV morphology, prelabral and labial **e** chaetae smooth and overall empodial complex morphology. *T. haitica* is also the sole eyeless species of the genus recorded from Haiti.

References: Palacios *et al.* (1985); Soto-Adames & Taylor (2013).

3.2.25 *T. hauseri* Yoshii, 1988

Type locality: Gruta da Tapagem, São Paulo, Brazil.

Known distribution: Brazil.

Type material: 2 specimens (sex not indicated).

Diagnosis. Body length about 1.5 mm. Specimens lacking pigments. Antennae about 1.6 times longer than head length. Ant. IV not annulated. Eyes absent. Prelabral chaetae ciliate, 2 anterior labral spines present. Dorsal head chaetotaxy with **A0** as mac, **A2** and **A3** apparently as mic, others unknown. Labial formula: **M1–2rEL1–2**. Th. II–III lacking mac. Trochanteral organ with about 15 spine-like chaetae. Ungues narrow with 2 internal paired basal asymmetrical teeth, medial and distal teeth absent; unguiculi narrow and lanceolated with postero-external lamellae smooth; tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.80: 0.48. Abd. I–IV lacking mac. Ventral tube anterior face apparently lacking distal mac. Dens with 2 rows of spines, internal and external with about 30 and 14, respectively. Mucro rectangular (ratio width: length of the drawing about = 1: 2.7), with 4 teeth.

Remarks. The absence of dorsal trunk mac in *T. hauseri* is quite uncertain unlikely, as noted also for *T. strinatii* and *T. guacharo*. Therefore, we considered *T. hauseri* as a *species inquirenda* until the dorsal chaetotaxy is redescribed.

Reference: Yoshii (1988).

3.2.26 *T. hirtipes* (Handschin, 1924)

Type locality: Blumenau, Santa Catarina, Brazil.

Known distribution: Brazil and Argentina.

Synonym: *Paronella hirtipes*.

Type material: 3 specimens (sex not indicated).

Diagnosis. Body length about 1.5–2.5 mm. Specimens pale with frontal head and antennae light purple, Ant. II–IV distally dark pigmented, Th. II and III lateral edges and subcoxae II and III dark blue, ventral tube with light blue pigment. Antennae about 1.5–2.0 times longer than head length. Ant. IV annulated. Eyes 8. Mesothorax longer than metathorax in the midline. Ungues wide with 4 internal teeth: 2 basal larger possibly subequal, 1 unpaired medial smaller than the basal teeth and 1 apical as long as the medial; unguiculi lanceolated with postero-external lamella apparently smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.54: 0.79. Dens with 1 row of spines (apparently the inner row). Mucro rectangular (ratio width: length of the drawing about = 1: 2.4–2.7), with 4 teeth.

Remarks. We considered the ungues internal basal teeth as a pair, not as a single tooth as in the original description, based on the illustrations by Cassagnau (1963) and Mendonça (1981), who indicated the paired basal teeth on ungues. According to Cassagnau (1963) and Thibaud & Najt (1988), this species may be identical to *T. carpenteri* (Denis, 1925), but *T. hirtipes* apparently has only one row of spines on dens, while *T. carpenteri* has 2 rows. Even so, due to such brief and generic diagnosis, we consider *T. hirtipes* as a *species inquirenda*. This species was collected in association with termites, inside nests of *Eutermes arenarius* (Handschin 1924).

References: Handschin (1924); Cassagnau (1963); Mendonça (1981); Thibaud & Najt (1988).

3.2.27 *T. hondurasensis* (Palacios-Vargas, Ojeda & Christiansen, 1985)

Original description: *Troglopedetes hondurasensis* Palacios-Vargas, Ojeda & Christiansen (1985: p. 24)

Type locality: Cueva Peña del Aguila, Honduras.

Known distribution: Honduras.

Type material: 2 specimens (sex not indicated).

Diagnosis. Body length about 2.6 mm. Body pigmented, eyepatches black. Eyes 4. Prelabral chaetae smooth, 2 anterior labral spines present. Labial formula: **M1–2rEL1–2a1–5, r** reduced. Ungues narrow with 2 small internal basal symmetrical paired teeth, median and apical teeth absent; unguiculi lanceolated with postero-external lamella smooth; tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.47: 0.42. Dens with 2 rows of spines, internal and external rows with about 30–36 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 3.0), with 4 teeth.

Remarks. *Trogolaphysa hondurasensis* and *T. variabilis* (Palacios-Vargas, Ojeda & Christiansen, 1985) are the only species of the genus that have 4 eyes (4 or 6 in *T. variabilis*). Such species can be separated from each other by the anterior labral spines, ciliated in *T. variabilis* (smooth in *T. hondurasensis*); and morphology of the unguis and unguiculus, as *T. variabilis* has a wide unguis with 4 internal teeth and unguiculi postero-external lamella serrated, while *T. hondurasensis* has a narrow unguis with only 2 small internal paired teeth and smooth unguiculi postero-external lamella.

Reference: Palacios-Vargas *et al.* (1985).

3.2.28 *T. innominata* (Denis, 1933)

Original description: *Paronella innominata* (CRI, CRII and CRIII) Denis (1933: p. 263)

Type locality: La Palma and Apaicán, Costa Rica.

Known distribution: Costa Rica.

Type material: 3 specimens (sex not indicated)

Diagnosis. Body length about 0.7–1.1 mm. Ungues wide with 3–4 internal teeth: 2 paired basal symmetrical, 1 medial unpaired shorter tooth and 1 minute apical tooth, present or absent; unguiculi lanceolate or truncate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.55–0.68: 1.1. Dens with 1–2 rows of spines, internal with 10–20 and external with 13. Mucro rectangular (ratio width: length of the drawing about = 1: 4.4), with 4 teeth.

Remarks. Denis (1933) described three morphotypes of *T. innominata* based mostly on measurements, empodial complex and dental morphology. The author provided very few

notes on their morphology and questioned the specific value of such morphotypes, which made him name them as “*innominata*” (nameless) forms. Apparently, all three specimens were also juveniles (Thibaud & Najt 1988). Therefore, we consider *T. innominata* as a *species inquirenda*.

Reference: Denis (1933).

3.2.29 *T. jacobyi* Soto-Adames & Taylor 2013

Original description: *Trogolaphysa jacobyi* Soto-Adames & Taylor (2013: p. 47)

Type locality: Yok Balum Cave, Toledo District, Belize.

Known distribution: Belize.

Type material: 1 female plus 4 specimens on slides and 6 specimens in alcohol (sex not indicated).

Diagnosis. Body length up to 2 mm. Live specimens pale yellow discretely pigmented on mesothorax, specimens in alcohol lacking pigments; small eyepatches brownish. Antennae longer than body, about 5.8 times longer than head length; Ant. IV not annulated, but with an incomplete constriction at middle; Ant. III apical organ sense rods swollen. Eyes absent. Prelabral chaetae smooth; 2 anterior labral spines absent. Dorsal head chaetotaxy with 9–13 **An** mac, **A0**, **A2–3**, **M2**, **S3**, **S5**, **Pa5** and **Pm3** as mac, others as mic; post-labial basal chaetae 1–2+5. Labial formula: **M1m2rel1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline. Th. II with **a5** plus 1–3 mac on **p3** complex; Th. III with 1 inner mac (**p3**). Trochanteral organ with up to 25 spine-like chaetae. Ungues narrow with 3 internal teeth: 2 small paired basal symmetrical and 1 larger medial tooth; unguiculi basally swollen, lanceolated with postero-external lamella weakly serrated (proximally); tenent-hairs acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.50–0.68: 0.59–0.45. Abd. I lacking **a6** mic; Abd. II with 2 (**m3** and **m5**) and Abd. III with 4 (possibly **m3**, **am6**, **pm6**, **p6**) mac, respectively. Abd. IV with 3 inner mac (**A5**, **B4**, **B5**), **B6** apparently as mes, with 5 main lateral mac (**D3**, **E2–3**, **F1–2**) and 6–7 posterior chaetae. Ventral tube anterior face with 2+2 distal mac. Dens with 2 rows of spines, internal row with at least 36 spines. Mucro rectangular (ratio width: length of the drawing about = 1: 3.0), with 3 teeth.

Reference: Soto-Adames & Taylor (2013).

3.2.30 *T. jamaicana* (Palacios-Vargas, Ojeda & Christiansen, 1985)

Original description: *Troglopedetes jamaicanus* Palacios-Vargas, Ojeda & Christiansen (1985, p. 19)

Type locality: Saint Ann Bambrider Cave, Jamaica.

Known distribution: Jamaica.

Type material: 4 specimens (sex not indicated).

Diagnosis. Body length about 2.7 mm. Specimens with dark pigmentation on antennae; body apparently lacking other pigments; eyepatches black. Antennae about 2.3 times longer than head length. Ant. IV annulated. Eyes 6 or 8. Prelabral chaetae ciliate, labral row **p** with longer chaetae; 2 anterior labral spines absent. Dorsal head chaetotaxy with 13 **An** mac, **M** and **S** series apparently lacking mac, other chaetae unclear. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Ungues wide with 3 internal teeth: 2 internal paired basal symmetrical teeth and 1 unpaired medial slightly smaller than the basal pair; unguiculi lanceolated with postero-external lamella smooth; tenent-hairs acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.64: 0.51. Dens with 2 rows of spines, internal and external rows with about 34–38 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 2.2), with 5 teeth.

Remarks. The illustration plate for *T. jamaicana* original description is misnumbered in Palacios-Vargas *et al.* (1985). As previously noted by Mari-Mutt & Bellinger (1990), we interpreted it as figures 8A–B (p. 21) since they fit the description text and do not match any other species described in that paper.

Reference: Palacios-Vargas *et al.* (1985).

3.2.31 *T. jataca* (Wray, 1953)

Original description: *Dicranocentruga jataca* Wray (1953, p. 143)

Type locality: Quebradillas, Guajataca, Puerto Rico.

Known distribution: Puerto Rico and Jamaica.

Type material: 1 neotype plus 3 specimens on slides and 2 specimens in alcohol (sex not indicated) sensu Mari-Mutt 1987.

Diagnosis. Body length about 1.3–2 mm. Specimens with antennae and legs pigmented; head and trunk laterally weakly pigmented; posterior Abd. IV–VI darkly pigmented; some specimens almost entirely pigmented, some specimens lacking pigments on Ant. II. Antennae about 1.5 times longer than head length. Ant. IV annulated or smooth; Ant. III apical organ with two sensory rods and two guard sensilla. Eyes 6. Prelabral chaetae ciliate; 2 anterior labral spines present. Dorsal head chaetotaxy with 14–17 **An** mac, **A0**, **A2**, **M2**, **S3**, **S5**, **Pa5** and **Pm3** as mac; 4 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline. Th. II with **a5** mac plus 6 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with

approximately 10–25 spine-like chaetae. Ungues wide with 3–4 internal teeth: 2 large paired basal asymmetrical, and 1 unpaired medial as large as the smallest basal tooth and 1 minute distal, present or absent; unguiculi lanceolated with postero-external lamella smooth or serrated; tenent-hairs acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.60: 0.73. Abd. I lacking **a6** mic; Abd. II–III with 2 and 4 mac respectively, **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 3 inner mac (**A4**, **A5**, **B5**), **B6** as mes; 7 main lateral mac (**Te2**, **D3**, **E2–3**, **F1–3**) and 13–14 posterior chaetae. Ventral tube anterior face with 3+3 or 2+2 distal mac. Dens with 2 rows of spines, internal and external rows with 15–22 spines each. Mucro subrectangular (ratio width: length of the drawing about = 1: 2.0), with 4–5 teeth.

Remarks. The broad scope of morphologies indicated for Ant. IV (annulated or smooth), trochanteral organ range of spines, ventral tube chaetotaxy and empodial complex morphologies reported in the literature (Palacios-Vargas *et al.* 1985, Mari-Mutt 1987 and Soto-Adames & Taylor 2013) suggests *T. jataca* is probably a complex of very similar species (see also remarks under *T. luquillensis* and *T. riopedrensis*).

References: Wray (1953); Palacios-Vargas *et al.* (1985); Mari-Mutt (1987); Soto-Adames & Taylor (2013).

3.2.32 *T. judithnajtae* Nguyen & Soto-Adames, 2018

Original description: *Trogolaphysa judithnajtae* Nguyen & Soto-Adames (2018: p. 184)

Type locality: Nosy Be Réserve naturelle intégrale de Lokobe, Province d'Antsiranana, Madagascar.

Known distribution: Madagascar.

Type material: 1 female plus 4 specimens on slides and 8 in alcohol (sex not indicated).

Diagnosis. Body length about 2.3–2.6 mm. Specimens pale with dark blue pigment on Ant. I–IV, clypeal area, legs (darker on coxae), manubrium and proximal ventral tube; head and body almost entirely light bluish; eyepatches black. Antennae 2.7 times longer than head length. Ant. III sense rods swollen. Eyes 8. Prelabral chaetae ciliate, anterior labral spines absent. Dorsal head chaetotaxy with about 16 **An** mac, **A0**, **A2–3**, **A5**, **M2**, **S3–S5**, **Pa5** and **Pm3** as mac; **M2** and **S4** present or absent; 5–7 interocular chaetae, none as mac. Labial formula: **M1–2rEL1-2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline. Th. II with **a5** plus 5–7 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with up to 39 spine-like chaetae. Ungues wide with 3–4 internal teeth: 2 paired basal symmetrical to slightly asymmetrical, 1 medial unpaired shorter than the basal pair and 1 minute apical tooth, present or absent; unguiculi lanceolate with

postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.64: 0.67–0.82. Ventral tube anterior face with 3+3 distal mac. Abd. I lacking **a6** mic; Abd. II with 2 (possibly **m3** and **m5**) and Abd. III with 4 (possibly **m3**, **am6**, **pm6**, **p6**) mac, respectively. Abd. IV with 4 inner mac (**A3**, **A5**, **B4**, **B5**), **B6** as mes, with 7–8 main lateral mac (**D2–3**, **E2–E4**, **F1–F3**; **D2** mac or mic) and 10 posterior chaetae. Ventral tube anterior face with 3+3 distal mac, lateral flap with up to 14 chaetae, at least 4 of them smooth. Dens with 2 rows of spines, internal row with up to 28 spines and external with up to 18. Mucro rectangular (ratio width: length of the drawing about = 1: 2.3–2.6), with 4 teeth.

References: Nguyen & Soto-Adames (2018).

3.2.33 *T. lamottei* (Delamare-Deboutteville, 1950)

Original description: *Paronella lamottei* Delamare-Deboutteville (1950: p. 43)

Type locality: Monte Nimba, Guinea.

Known distribution: Guinea, Camaroon (uncertain).

Type material: 2 specimens (sex not indicated).

Diagnosis. Specimens pale with dark blue pigments on Ant. II–IV; front head and lateral Th. II–Abd. I; violet pigments on tibiotarsi I–III; eyepatches dark. Antennae about 3.7 times longer than head length. Eyes 8. Ungues wide with 4 internal teeth: 2 paired basal symmetrical, 1 medial unpaired tooth subequal to the basal teeth and 1 apical smaller; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus about = 1: 0.55. Dens with 2 rows of spines. Mucro square to subrectangular (ratio width: length of the drawing about = 1: 1.5–1.8), with 2–4 teeth.

Remarks. According to Nguyen & Soto-Adames (2018), this species resembles *Trichorypha atrofasciata* Schött, 1893 due to the manubrium longer than dens and presence of long antennae. In fact, *T. lamottei* shares several characters with *T. atrofasciata*, from Cameroon: pale body with lateral margins of Th. II at least to Abd. I and tibiotarsi with blue pigmentation, Ant. II to Ant. IV with dark blue pigmentation; unguis slender with 4 internal teeth, tenent-hair capitate; and mucro with 4 teeth (Schött 1903). In this scenario it is possible that *T. lamottei* may represent a junior synonym of *Paronella atrofasciata*. Although Nguyen & Soto-Adames (2018) transferred it to *Trogolaphysa* based on the shape of the mucro and absence of manubrial spines, Delamare-Deboutteville (1950) did not describe the manubrium in detail, nor mentioned the absence of manubrial spines, so the generic placement of this species remains

uncertain. In the face of its uncertain genus placement and very brief and generic description, we hereby place *T. lamottei* as a *species inquirenda*.

References: Schött (1893); Schött (1903); Delamare-Deboutteville (1950); Mitra (2002a); Nguyen & Soto-Adames (2018).

3.2.34 *T. laterolineata* Soto-Adames, 2015

Original description: *Trogolaphysa laterolineata* Soto-Adames (2015: p. 16)

Type locality: Ocosingo, Chiapas State, Mexico.

Known distribution: Mexico.

Type material: 4 specimens on slides and 11 specimens in alcohol (sex not indicated).

Diagnosis. Body length up to 2.1 mm. Specimens with dark blue pigments on distal Ant. I, Ant. II–V, coxae, trochanters, femurs and proximal colophore, lateral Abd. IV (as large bands); eyepatches black. Antennae about 2.7 times longer than head length; Ant. III sense rods normal, not swollen. Eyes 6–8. Prelabral chaetae ciliate, 2 anterior labral spines present, normal and base fused. Dorsal head chaetotaxy with 12–13 **An mac**, **A0**, **A2–3**, **M2**, **Pa5** and **Pm3** as mac; 4–5 interocular chaetae, none as mac. Labial formula: **M1–3rEL1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 6 mac on **p3** complex; Th. III lacking mac. Ungues wide with 3–4 internal teeth: 2 small paired basal symmetrical, 1 unpaired medial smaller than the proximal ones and 1 unpaired minute distal (present or absent); unguiculi lanceolated with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.59–0.63: 0.70–0.90. Abd. I lacking **a6**; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 4 inner mac (**A3**, **A5**, **B4** and **B5**), **B6** as mes; 6 lateral mac and 12 posterior chaetae. Dens with 2 rows of spines, internal with 23 and external with 9 spines. Mucro rectangular (ratio width: length of the drawing about = 1: 2.6) with 4 teeth.

Reference: Soto-Adames (2015).

3.2.35 *T. luquillensis* (Mari-Mutt, 1987)

Original description: *Dicranocentrua luquillensis* Mari-Mutt (1987: p. 402)

Type locality: El Yunque National Park, Luquillo, Puerto Rico.

Known distribution: Puerto Rico.

Type material: 6 specimens on slides and 14 specimens in alcohol (sex not indicated).

Diagnosis. Body length up to 2 mm. Colour pattern as in *T. jataca*, but all specimens with Ant. I–IV pigmented. Ant. IV annulated. Eyes 6. Prelabral chaetae ciliate; 2 anterior labral

spines present. Dorsal head chaetotaxy with about 15 **An** mac, **A0**, **A2**, **S5**, **Pa5** and **Pm3** as mac; 4 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline. Th. II with **a5** mac plus 5 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with up to 25 spine-like chaetae. Ungues wide with 3 internal teeth: 2 paired basal asymmetrical and 1 unpaired medial smaller; unguiculi lanceolated with postero-external lamella smooth; tenent-hairs acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.74: 0.52. Abd. II–III with 2 and 4 mac respectively, **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III. Abd. IV with 3 inner mac (**A4**, **A5**, **B5**). Ventral tube anterior face with 3+3 distal mac. Dens with 2 rows of spines, internal and external rows with up to 22 spines each. Mucro subrectangular with 4 teeth.

Remarks. This species also belongs to the *T. jataca* species complex, as *T. geminata* and *T. riopedrensis* (see also remarks for these species). *Trogolaphysa luquillensis* can be separated from the other two species by: the absence of the cephalic mac **M2** and **S3** (both present in *T. jataca* and *T. geminata*), presence of cephalic mac **S5** (absent in *T. geminata*), **p3** complex with 5 mac (6 in the other two), and unguiculus postero-external lamella smooth (serrate in *T. geminata*, variable in *T. jataca*). Nevertheless, their similar distribution and congruence in several morphological features may indicate they are closely related or constitute a species complex, as well as *T. subterranea* and *T. riopedrensis* (Soto-Adames & Taylor 2013).

Reference: Mari-Mutt (1987); Soto-Adames & Taylor (2013).

3.2.36 *T. marielouiseae* Soto-Adames, 2015

Original description: *Trogolaphysa marielouiseae* Soto-Adames (2015: p. 19)

Type locality: Cacahuatan, Chiapas state, Mexico.

Known distribution: Mexico.

Type material: 1 male, 2 females on slides and 3 juveniles in alcohol.

Diagnosis. Body length up to 2 mm. Specimens almost entirely dark, distal femurs and tibiotarsi light blue or whitish; eyepatches black. Eyes 6–8. Antennae about 1.9 times longer than head length; Ant. III sense rods apparently not swollen. Prelabral chaetae ciliate, 2 anterior labral spines present, normal and base fused. Dorsal head chaetotaxy with 15 **An** mac, **A0**, **A2**, **M2**, **S3**, **Pa5** and **Pm3** as mac; 4–5 interocular chaetae, none as mac. Labial formula: **M1–3rEL1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 5 mac on **p3** complex; Th. III lacking mac. Trochanteral

organ with at least 23 spine-like chaetae. Ungues wide with 2–3 internal teeth: 2 small paired basal asymmetrical, 1 unpaired medial as long as the shortest paired tooth (present only on leg III); unguiculi lanceolated with postero-external lamella smooth; tenent-hairs acuminate (leg I–II) or capitate (leg III), ratio unguis: unguiculus: tenent-hairs about = 1: 0.70–0.73: 0.66–0.70. Abd. I with **a6** mic; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 3 inner mac (**A3**, **A5** and **B5**), **B6** as mes; 5 lateral mac and 18–19 posterior chaetae. Dens with 2 rows of spines, internal with 25–30 and external with 16–24. Mucro subrectangular (ratio width: length of the drawing about = 1: 2.0), with 4 teeth.

Reference: Soto-Adames (2015).

3.2.37 *T. marimutti* (Palacios-Vargas, Ojeda & Christiansen, 1985)

Original description: *Troglopedetes marimutti* Palacios-Vargas, Ojeda & Christiansen (1985, p. 24)

Type locality: Grutas de Atoyac, Veracruz, Mexico.

Known distribution: Mexico.

Type material: 9 specimens (sex not indicated).

Diagnosis. Body length about 2.3 mm. Specimens lacking pigmentation on body and eyepatches. Antennae about 2.5 times longer than head length. Ant. IV not annulated. Eyes absent. Prelabral chaetae ciliate; 2 anterior labral spines absent. Labial formula: **M1–2reL1–2a1–5**, **r** reduced. Trochanteral organ with about 15 spine-like chaetae. Ungues wide with 3 internal teeth: 2 small internal paired basal teeth apparently asymmetrical and one medial slightly larger than the basal pair, apical tooth absent; unguiculi lanceolated with postero-external lamella serrated (proximally); tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.58: 0.47. Dens with 2 rows of spines, internal and external rows with about 50 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 2.2), with 4 teeth.

Reference: Palacios-Vargas *et al.* (1985).

3.2.38 *T. maya* Mills, 1938

Original description: *Trogolaphysa maya* Mills (1938, p. 184)

Type locality: Cueva Balancanché, Chichen Itza and cueva Xkyc, Calcehtok, Yucatan, Mexico.

Known distribution: Mexico and Dominican Republic.

Type material: 1 specimen from cueva Balancanché cave and 1 specimen from cueva Xkyc (sex not indicated).

Diagnosis. Body length about 1.7 mm. Specimens lacking pigmentation on body, appendages and eyepatches. Antennae 4.5 times longer than head length. Ant. IV annulated. Eyes absent. Mesothorax longer than metathorax in the midline. Ungues wide with 4 internal teeth: 2 paired basal asymmetrical (one tooth elongated), 1 unpaired medial smaller than the smaller basal tooth and 1 apical developed tooth; unguiculi lanceolate with postero-external lamella serrate in the distal half; tenent-hairs acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.63: 1. Dens with 2 rows of spines, internal and external with about 35–40 each. Mucro rectangular (ratio width: length of Mills' drawing about = 1: 2.9), with 4 teeth.

Remarks. Thibaud & Najt (1988) considered *T. delamarei* Massoud & Gruia, 1973 from Cuba as a synonym of *T. maya* from Mexico, and corrected a few features imprecisely described by Massoud & Gruia (1973). The main differences between *T. delamarei* and *T. maya* are the antennal length and the unguiculi postero-external lamella. *T. maya* has the antennae about 4.5 times longer than the head and the postero-external lamella smooth, while in *T. delamarei* this ratio is 3.7 times and the postero-external lamella serrated. However, both species lack eyes, pigmentation on body, have long antennae, and were collected in caves, which strongly suggests they may be troglobiont. It is unlikely that the Cuban and Mexican populations belong to the same species. *T. delamarei* was redescribed in detail by Gruia (1987) and there is enough data to separate it from *T. maya* and to circumscribe it among other Neotropical *Trogolaphysa* (see also the remarks under *T. delamarei*). On the other hand, in the absence of several data concerning the morphology of *T. maya*, its small type series with only two cave specimens from different localities, and in the lack of clear diagnostic features which can separate it from other Neotropical troglomorphic taxa, we herein place *T. maya* as a *species inquirenda* until a revision and redescription of the species is published.

References: Mills (1938); Massoud & Gruia (1973); Thibaud & Najt (1988); Soto-Adames & Taylor (2013).

3.2.39 *T. mills* Arlé, 1939

Original description: *Trogolaphysa mills* Arlé (1939: p. 28)

Type locality: Represa dos ciganos, Rio de Janeiro, Brazil.

Known distribution: Brazil.

Type material: 2 specimens (possibly juveniles).

Diagnosis. Body length about 0.6 mm. Specimens mostly pale with light red pigment irregularly distributed over the body; eyepatches black. Antennae about 1.5 times longer than head length. Eyes 2. Mesothorax and metathorax subequal in the midline. Ungues wide with 3 internal teeth: 2 paired basal slightly asymmetrical, 1 unpaired smaller median, distal tooth absent, without lateral teeth; unguiculi truncate with postero-external lamella smooth; tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.54: 0.49. Dens with 2 rows of spines. Mucro subrectangular (ratio width: length of the drawing about = 1: 2.0), with 4 teeth.

Remarks. Arlé's description of *T. millsii* was likely based on 2 juveniles (see Arlé, 1939, p. 29), based on the small body, with about 0.6 mm, and the habitus drawing (see Arlé, 1939, plate III, fig. 14) with large head and somehow short appendages. Also, there is very little information on this species, especially regarding its chaetotaxy; therefore, we hereby place *T. millsii* as *species inquirenda*. The type material for *T. millsii* was destroyed in the fire of the National Museum in Rio de Janeiro in 2018, so that a redescription would require the collection of fresh topotypical material.

Reference: Arlé (1939).

3.2.40 *T. monomaculata* (Barra, 1969)

Original description: *Paronella (Microparonella) monomaculata* Barra (1969: p. 212)

Type locality: Ipassa, Makokou, Gabon.

Known distribution: Gabon.

Type material: 4 specimens (sex not indicated).

Diagnosis. Body length about 1.5 mm. Specimens pale with light blue pigment uniform over all the antennae, ventral head, lateral and ventral trunk and ventral tube and legs; with a large dark blue trapezoid band on posterior Abd. IV; eyepatches black. Antennae about 1.9 times longer than head length; Ant. IV not annulated; Ant. III sens rods swollen. Eyes 8. Dorsal head chaetotaxy with about 6 **An** mac, **A0**, **A2**, **Ps5** and **Pm3** as mac; apparently 3 interocular chaetae, none as mac. Labial formula: **M1EL1a1–2**, others unknown. Mesothorax longer than metathorax in the midline. Ungues wide with 3 internal teeth: 2 paired basal asymmetrical and 1 unpaired medial tooth smaller than the basal teeth; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.51–0.68: 0.68–0.71. Ventral tube anterior face with 2+2 distal mac; lateral flap with 11 chaetae. Dens with 2 rows of spines,

internal and external with up to 19 and 14, respectively. Mucro rectangular (ratio width: length of the drawing about = 1: 3.4–4.6), with 5 teeth.

Remarks. See remarks under *T. vivieni*.

References: Barra (1969); Nguyen & Soto-Adames (2018).

3.2.41 *T. nacionalica* (Palacios-Vargas, Ojeda & Christiansen, 1985)

Original description: *Troglopedetes nacionalicus* Palacios-Vargas, Ojeda & Christiansen (1985: p. 18)

Type locality: Gruta de Monteflor, Oaxaca, Mexico.

Known distribution: Mexico.

Type material: 12 specimens (sex not indicated).

Diagnosis. Body length about 2.1 mm. Specimens weakly pigmented, eyepatches black. Antennae about 1.6 times longer than head length. Ant. IV annulated; Ant. III sense rods normal, not swollen. Eyes 6. Prelabral chaetae smooth, labral row p with longer chaetae; 2 anterior labral spines absent. Dorsal head chaetotaxy **A3**, **A5**, **M** and **S** series and **Pa5** as mic, **Pm3** apparently as mac, others unclear. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Trochanteral organ with approximately 26 spine-like chaetae. Ungues wide with 3 internal teeth: 2 internal paired basal slightly asymmetrical teeth and 1 unpaired medial larger; unguiculi lanceolated with postero-external lamella smooth; tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.55: 0.49. Dens with 2 rows of spines, internal and external rows with about 29–34 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 2.7), with 4 teeth.

Remarks. The plate in the original description is misnumbered in Palacios-Vargas *et al.* (1985). It is actually on page 23, and its captions are on page 21.

Reference: Palacios-Vargas *et al.* (1985).

3.2.42 *T. nigromaculata* (Schött 1903)

Original description: *Paronella nigromaculata* Schött (1903: p. 7)

Type locality: Bonge, Cameroon.

Known distribution: Cameroon, Ivory Coast, Rwanda, Burundi, Tanzania, Ethiopia and Kenya.

Type material: 19 specimens and 30 syntypes in alcohol (sex not indicated).

Diagnosis. Body length 1.5–2.0 mm. Specimens pale with dark blue pigment on Ant. I–IV and coxae; eyepatches black. Antennae shorter than body. Antennae 2.3 times longer than head length. Eyes 8. Dorsal head chaetotaxy with **A2**, **A5**, **M2**, **S3** and **S5** as mac;

Pa5 absent. Ungues wide with 3–4 internal teeth: 2 paired basal, 1 unpaired medial, apical tooth present or absent; unguiculi lanceolate or truncate with postero-external lamella smooth; tenent-hairs capitate; ratio unguis: unguiculus: tenent-hair about = 1: 0.64: 0.89. Mucro rectangular (ratio width: length of the drawing about = 1: 2.6), with 4 teeth.

Remarks. This is possibly the most widespread species of *Trogolaphysa* in Africa, and its distribution covers disjunct localities in the continent. It is likely to be a species complex based on the diversity of environments, variable colour patterns and variation of the internal unguis teeth and shape of unguiculi according to localities samples (Mitra 2002c, Nguyen & Soto-Adames, 2018). Schött (1927) revisited his biological material from Debundscha (Cameroon) and described pigmented and pale specimens of *P. nigromaculata* (Mitra 2002b). However, the type locality for this species is “Bonge” and the descriptions in Schött (1927) do not seem to represent *T. nigromaculata* based on the variation in colour patterns and shape of unguiculus (Nguyen & Soto-Adames, 2018). Delamare-Deboutteville (1952) described the subspecies *T. nigromaculata pallida* from Ivory Coast, which is characterized by blue scattered pigmentation spots but retains the morphological characters originally described for *T. nigromaculata* by Schött (1903). The absence of a formal description of this subspecies made Nguyen & Soto-Adames (2018) consider it as a *nomen nudum*. Since several features of *T. nigromaculata* are unknown or unclear, it is considered a widespread species, but previous literature already pointed it as a species complex with variable morphotypes. We herein consider *T. nigromaculata* a *species inquirenda*, and further data on the type material (or material from the type locality) are needed to clearly circumscribe it.

References: Schott (1903); Schött (1927); Mitra (2002b); Nguyen & Soto-Adames (2018).

3.2.43 *T. ocellata* Soto-Adames, 2015

Original description: *Trogolaphysa ocellata* Soto-Adames (2015: p. 25)

Type locality: Ocosingo Valley, Chiapas, Argentina.

Known distribution: Mexico.

Type material: 3 specimens on slides and 4 specimens in alcohol (sex not indicated).

Diagnosis. Body length up to 2.1 mm. Specimens with blue pigment on Ant. II–IV, lateral margin of thorax, coxa II, trochanter III, femur III, Abd. II–III and central Abd. IV; eyepatches black. Antennae about 3.1 times longer than head length; Ant. III sense rods normal, not swollen. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines present,

normal and separated. Dorsal head chaetotaxy with 8–9 **An** mac, **A0**, **A2–3**, **M2** and **Pa5** as mac; 3–4 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced; post-labial basal chaetae 1+6. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 5–6 mac on **p3** complex. Th. III lacking mac. Trochanteral organ with up to 30 spine-like chaetae. Ungues wide with 3–4 internal teeth: 2 paired basal symmetrical, 1 unpaired medial smaller than the proximal ones and 1 minute apical (absent on leg III); unguiculi lanceolated narrow or normal with external lamella smooth; tenent-hairs capitate, reduced or normal, ratio unguis: unguiculus: tenent-hair about = 1: 0.77–0.95: 0.45–0.85. Abd. I with **a6** mic; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 4 inner mac (**A3**, **A5**, **B4** and **B5**), **B6** as mes; 7 lateral main mac (**D3**, **E2–4**, **F1–3**) and 14–16 posterior chaetae. Dens with 2 rows of spines, internal and external with 50 and 27 spines, respectively. Mucro subrectangular (ratio width: length of the drawing about = 1: 1.9–2.5), with 4 teeth.

Reference: Soto-Adames (2015).

3.2.44 *T. octosetosa* Soto-Adames, 2015

Original description: *Trogolaphysa octosetosa* Soto-Adamese (2015: p. 32)

Type locality: Chichen Itza, Yucatan, Mexico.

Known distribution: Mexico.

Type material: 1 female, 3 specimens on slides and 73 specimens in alcohol (sex not indicated).

Diagnosis. Body length up to 2 mm. Specimens with light blue pigment all over the body, slightly darker on coxae and lighter on head; eyepatches black. Antennae up to 2.1 times longer than head length; Ant. III sense rods swollen. Eyes 6. Prelabral chaetae weakly ciliate, 2 anterior labral spines present, normal and separated. Dorsal head chaetotaxy with **A0**, **A2**, **Pa5** and **Pm3** as mac; 3 interocular chaetae. Labial formula: **M1–2rEL1–2a1–5** or with **m1–2** independently smooth, **r** reduced. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 5 mac on **p3** complex; Th. III with 3 inner mac (**a2**, **p2** and **p3**). Trochanteral organ with up to 28 spine-like chaetae. Unguis III wide with 4 internal teeth: 2 small paired basal asymmetrical, 1 unpaired medial smaller than basal tooth, 1 unpaired distal minute; unguiculi lanceolated, narrow or normal, with external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.86: 0.66. Abd. I lacking **a6** mic; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 3 inner mac

(**A3**, **A5** and **B5**), **B6** as mes; 6 lateral mac and 9–10 posterior chaetae. Dens with 2 rows of spines, internal with up to 23 and external with 19 spines. Mucro subrectangular (ratio width: length of the drawing about = 1: 2.1–2.3), with 4 teeth.

Reference: Soto-Adames (2015).

3.2.45 *T. oztotlica* (Ojeda & Palacios-Vargas, 1984)

Original description: *Troglopedetes oztotlicus* Ojeda & Palacios-Vargas (1984, p. 16)

Type locality: Gruta de Juxtlahuaca, Guerrero State, Mexico.

Known distribution: Mexico.

Type material: 8 specimens (sex not indicated).

Diagnosis. Body length about 2–3 mm. Specimens lacking pigmentation on body and eyepatches. Antennae about 3 times longer than head length. Ant. IV annulated; Ant. III sense rods normal, not swollen. Eyes absent. Prelabral chaetae ciliate, labral row **p** with longer chaetae; 2 anterior labral spines absent. Dorsal head chaetotaxy with **A3**, **A5**, **M** and **S** series as mic, **Pa5** and **Pm3** as mac; with 3 interocular chaetae. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Trochanteral organ with approximately 12 spine-like chaetae. Ungues wide with 4 internal teeth: 2 small paired basal symmetrical, 1 unpaired medial and 1 unpaired apical smaller than the medial; unguiculi lanceolated with postero-external lamella weakly serrated; tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.6: 0.4. Abd. I with **a6** mic; Abd. II–III with 2 and 4 mac respectively, **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV apparently with a single inner mac (homology unclear). Ventral tube anterior face with 4+4 distal mac; lateral flap with about 20 chaetae. Dens with 2 rows of spines, internal and external rows with 35–40 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 2.7–3.0), with 4 teeth.

References: Ojeda & Palacios-Vargas (1984); Palacios-Vargas *et al.* (1985).

3.2.46 *T. palaciosi* Soto-Adames, 2015

Original description: *Troglophysis palaciosi* Soto-Adames (2015: p. 32)

Type locality: Cueva Arroyo Seco, Oaxaca, Mexico.

Known distribution: Mexico.

Type material: 4 specimens on slides (sex not indicated).

Diagnosis. Body length up to 2.3 mm. Colour pattern unknown. Ant. III sense rods swollen. Eyes 8. Prelabral chaetae smooth, 2 anterior labral spines absent. Dorsal head chaetotaxy with 14 **An** mac, **A0**, **A2**, **Pa5** and **Pm3** as mac; 4 interocular chaetae, none

as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 3 mac on **p3** complex; Th. III with 1–2 mac (**p2–3**, **p2** as mac or mic). Trochanteral organ with up to 26 spine-like chaetae. Unguis III wide or narrow with 2–3 internal teeth: 2 paired basal symmetrical and 1 unpaired medial as long as the basal tooth (if present); unguiculi basally swollen or weakly truncated with postero-external lamella mostly smooth, with 1 small tooth on antero-external or on postero-external lamella; tenent-hairs acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.62–0.90: 0.60. Abd. I with **a6** mic; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 4 inner mac (**A3**, **A5**, **B4** and **B5**), **B6** as mes; 6 lateral mac and 12 posterior chaetae. Dens with 2 rows of spines, internal with about 22–25 and external with about 32–36 spines. Mucro rectangular (ratio width: length of the drawing about = 1: 2.3), with 4 teeth.

Remarks. The polymorphism of the empodial complex in specimens from the different localities, along with the variation on Th. III macrochaetotaxy and the low number of type specimens analyzed may suggest *T. palaciosi* could represent more than one species. It is unclear if the Th. III with 1 or 2 mac are followed by the polymorphism on the empodial complex, with two morphotypes: one with narrow unguis lacking the medial tooth and unguiculus with one tooth on antero-external lamella, other with wide unguis with the medial tooth and unguiculus with one tooth on postero-external lamella. More specimens need to be studied to better circumscribe its morphology, since this polymorphism could also represent ontogenetic differences, as discussed by Soto-Adames (2015).

Reference: Soto-Adames (2015).

3.2.47 *T. paracarpenteri* Soto-Adames, 2015

Original description: *Trogolaphysa paracarpenteri* Soto-Adames (2015: p. 29)

Type locality: Ocosingo Valley, Chiapas, Mexico.

Known distribution: Mexico.

Type material: 1 male, 2 specimens on slides and 20 specimens in alcohol (sex not indicated).

Diagnosis. Body length up to 1.9 mm. Specimens with pale blue pigments on frontal head, Ant. II distally, Ant. III–IV entirely pigmented, Ant. I without pigments; dark blue pigments over the body and legs, Abd. IV with longitudinal lighter stripes; eyepatches black. Antennae up to 2.9 times longer than head length; Ant. III sense rods swollen. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines present, normal and base fused. Dorsal

head chaetotaxy with 15 **An** mac, **A0**, **A2**, **Pa5** and **Pm3** as mac; 4–5 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax slightly larger than metathorax in the midline; Th. II with **a5** plus 5 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with at least 15 spine-like chaetae. Ungues wide with 3 internal teeth: 2 projected needle-shaped paired basal asymmetrical and 1 unpaired medial as large as the shorter paired basal tooth; unguiculi lanceolated with external lamella smooth or very weakly serrate; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hairs about = 1: 0.61: 0.64. Abd. I **a6** mic apparently absent; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 3 inner mac (**A3**, **A5** and **B5**), **B6** as mes; 6 lateral mac. Dens with 2 rows of spines, internal and external with about 21 and 17, respectively. Mucro subrectangular (ratio width: length of the drawing about = 1: 2.0), with 4 teeth.

Reference: Soto-Adames (2015).

3.2.48 *T. penicillata* (Schött, 1927)

Original description: *Paronella penicillata* Schött (1927, p. 29)

Type locality: Debundscha, Cameroon.

Known distribution: Cameroon, Ivory Coast and Gabon.

Type material: 6 syntypes on slides (sex not indicated).

Diagnosis. Specimens pale in alcohol with light blue pigmentation on Ant. I, dark blue pigment on Ant. II–IV, laterally on Th. II–Abd. I, transversal band on anterior half of Abd. IV; eyepatches black. Antennae shorter than body. Ant. IV not annulated. Eyes 8. Ungues wide with 4 internal teeth: 2 paired basal, 1 unpaired medial and 1 apical; unguiculi truncate with postero-external lamella smooth; tenent-hairs long and capitate; ratio unguis: unguiculus: tenent-hair about = 1: 0.55: 1. Dens with 1 row of spines, modified distally in paintbrush-like structures. Mucro rectangular (ratio width: length of the drawing about = 1: 3.0–3.8), with 4 teeth.

Remarks. Delamare-Deboutteville (1952) described the subspecies *T. penicillata pallida* from Ivory Coast based on variation of the colour pattern: the subspecies *pallida* is pale without pigments laterally on Th. II, and only spots on Abd. IV. Although *T. penicillata* needs to be redescribed, since several features are unknown, it is unique among *Trogolaphysa* taxa by its distal dens spines modified into paintbrush-like structures (see Schött 1927, plate II, fig. 19) (Nguyen & Soto-Adames 2018).

References: Schött (1927); Delamare-Deboutteville (1952); Mitra (2002b); Nguyen & Soto-Adames (2018).

3.2.49 *T. piracurucaensis* Nunes & Bellini, 2018

Original description: *Trogolaphysa piracurucaensis* Nunes & Bellini (2018, p. 87)

Type locality: Sete Cidades National Park, Piracuruca, Piauí, Brazil.

Known distribution: Brazil.

Type material: 3 females, 1 male and 1 juvenile on slides.

Diagnosis. Body length about 2.23–2.64 mm. Specimens pale with blue pigment on antennae, lateral Th. II–III and Abd. I–III, proximal subcoxae and tibiotarsi I–III; eyepatches black. Antennae about 2.3 times longer than head length. Ant. III sense rods normal, not swollen. Ant. IV annulated; Ant. III sense rods swollen. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines present. Dorsal head chaetotaxy with 16–18 **An** mac, **A0**, **A2–3**, **M2**, **S3–5**, **Pa5** and **Pm3** as mac; **S4** as mac or mic; 4 interocular chaetae. Labial formula: **M1–3rEL1–2a1–5**, **r** reduced; **M3** chaeta present or absent; post-labial basal chaetae 0–2+1–5. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 6 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with about 35–40 spine-like chaetae. Ungues wide with 4 internal teeth: 2 paired basal symmetrical, 1 unpaired medial as large as the paired basal tooth and 1 apical smaller; unguiculi lanceolate with postero-external lamella smooth or slightly serrate; tenent-hairs capitate; ratio unguis: unguiculus: tenent-hair about = 1: 0.63: 0.65. Abd. I with **a6** mic; Abd. II–III with 2 and 4 mac respectively, **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 4 inner mac (**A3**, **A5**, **B4** and **B5**), **B6** as mes; 14 lateral mac and 10 posterior chaetae. Ventral tube anterior face with 3+3 distal mac; lateral flap with 14 chaetae: 7 ciliate and 7 smooth; posterior face lacking smooth chaetae. Dens with 2 rows of spines, internal with 25–29 and external row with 21–27 spines, respectively. Mucro subrectangular (ratio width: length of the drawing about = 1: 2.5), with 4 teeth.

Remarks. Here we add to the diagnosis of *T. piracurucaensis* the unguiculus posterior edge smooth or slightly serrated, based on the analysis of the type material.

Reference: Nunes & Bellini (2018).

3.2.50 *T. quisqueyana* Soto-Adames, Jordana & Baquero, 2014

Original description: *Trogolaphysa quisqueyana* Soto-Adames, Jordana & Baquero (2014, p. 10)

Type locality: Loma del Toro, Independencia, Dominican Republic

Known distribution: Dominican Republic.

Type material: 8 specimens on slides and 23 in alcohol (sex not indicated).

Diagnosis. Body length up to 2.2 mm. Specimens pale with purple pigment on antennae, frontal head and legs, darker on Abd. IV and coxae; eyepatches black. Antennae shorter than body (0.60x). Ant. IV not annulated; Ant. III sense rods normal, not swollen. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines present. Dorsal head chaetotaxy with 15 **An** mac, **A0**, **A2–3**, **M2**, **S3**, **S5**, **Pm3** and **Pa5** as mac; 4 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced, post-labial basal chaetae 0+5. Mesothorax longer than metathorax in the midline. Th. II with **a5** plus 6 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with up to 28 spine-like chaetae. Ungues with 4 internal teeth: 2 paired asymmetrical basal, 1 unpaired medial as large as the smaller basal tooth and 1 minute apical; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.72: 0.76. Abd. I **a6** mic present or absent. Abd. II with 2 (**m3** and **m5**) and Abd. III with 4 (**m3**, **am6**, **pm6**, **p6**) mac, respectively; Abd. IV with 4 inner mac (**A3**, **A5**, **B4** and **B5**), **B6** as mes, with 6 main lateral mac (**D3**, **E2–3**, **F1–3**) and 12–14 posterior chaetae. Ventral tube anterior face with 2+2 distal mac. Dens with 2 rows of spines, internal with 35–42 and external rows with 25–28, respectively. Mucro rectangular (ratio width: length of the drawing about = 1: 2.1–2.6), with 4 teeth.

References: Soto-Adames *et al.* (2014).

3.2.51 *T. relictus* (Palacios-Vargas, Ojeda & Christiansen, 1985)

Original description: *Troglopedetes relictus* Palacios-Vargas, Ojeda & Christiansen (1985: p. 26)

Type locality: Grutas de Acuitlapán, Guerrero, Mexico.

Known distribution: Mexico.

Type material: 17 specimens (sex not indicated).

Diagnosis. Body length about 1.4 mm. Specimens with body and antennae bluish; eyepatches black. Antennae about 1.6 times longer than head length. Ant. IV not annulated. Eyes 6. Prelabral chaetae ciliate, 2 anterior labral spines present, normal and fused. Dorsal head chaetotaxy with **A0**, **A2**, **Pa5** and **Pm3** mac, **M** and **S** series without mac; 3 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Th. II with **a5** plus 5 mac on **p3** complex. Th. III lacking mac. Trochanteral organ with about 15 spine-like chaetae. Ungues wide with 3–4 internal teeth: 2 large basal paired and one medial slightly smaller, small apical tooth present only on unguis III; unguiculi lanceolated with external lamella serrated (proximally); tenent-hairs capitate, ratio

unguis: unguiculus: tenent-hairs about = 1: 0.73: 0.67. Abd. I lacking **a6** mic. Abd. IV with 2 inner mac (**A3**, **B5**), **B6** apparently as mes; 5 lateral mac and 10 posterior chaetae. Dens with 2 rows of spines, internal and external rows with about 25 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 3–3.3), with 4 teeth.

Remarks. *T. relictata* was originally described without labral spines and unguis III with 3 internal teeth. Soto-Adames (2015) examined the type material, correcting these observations and described chaetotaxic information.

References: Palacios-Vargas *et al.* (1985); Thibaud & Najt (1988); Soto-Adames (2015).

3.2.52 *T. riopedrensis* (Mari-Mutt, 1987)

Original description: *Dicranocentrua riopedrensis* Mari-Mutt (1987, p. 403)

Type locality: Rio Piedras, San Juan, Puerto Rico.

Known distribution: Puerto Rico.

Type material: 4 specimens on slides and 3 specimens in alcohol (sex not indicated).

Diagnosis. Body length up to 1.5 mm. Colour pattern as in *T. jataca*, but all specimens with Ant. I–IV pigmented. Ant. IV annulated. Eyes 6. Prelabral chaetae ciliate; 2 anterior labral spines present. Dorsal head chaetotaxy with 14–15 **An** mac, **A0**, **A2–3**, **S3**, **S5**, **Pa5** and **Pm3** as mac, **A2** also as mic; 6 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Th. II with **a5** mac plus 5 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with up to 25 spine-like chaetae. Ungues wide with 4 internal teeth: 2 large paired basal asymmetrical, 1 unpaired medial as large as the smaller basal tooth and 1 unpaired minute distal; unguiculi lanceolated with postero-external lamella serrated (distally); tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.45: 0.66. Abd. I with **a6** mic. Abd. II–III with 2 and 4 mac respectively, **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III. Abd. IV with 4 inner mac (**A4**, **A5**, **B4**, **B5**), **B6** as mes, 7 main lateral mac (**D3**, **E2–3**, **F1–3**, **Fe3**) and 17 posterior chaetae. Ventral tube anterior face with 4+4 distal mac. Dens with 2 rows of spines, internal and external rows with up to 22 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 3.4), with 4 main teeth plus up to 2 smaller accessory teeth.

Remarks. This is the most distinctive species in the *T. jataca* species complex, and its main diagnostic feature being the presence of 4 internal mac on Abd. IV, while *T. jataca*, *T. geminata* and *T. luquillensis* have only 3 mac (Mari-Mutt 1987; Soto-Adames & Taylor

2013). The information on dorsal head and trunk chaetotaxy provided by Soto-Adames & Taylor (2013) for *T. riopedrensis* species was based on individuals from Aguadilla (Puerto Rico) and Saint Thomas (USA Virgin Island). However, the dorsal head chaetotaxy of Soto-Adames & Taylor's description (2013) conflicts with the original description, as the samples from St. Thomas seem to have the anterior mac **A2** as mic, while this chaeta is a mac in Aguadilla's individuals and in the original description.

References: Mari-Mutt (1987); Soto-Adames & Taylor (2013).

3.2.53 *T. sauron* Soto-Adames, Jordana & Baquero, 2014

Original description: *Trogolaphysa sauron* Soto-Adames, Jordana & Baquero (2014: p. 12)

Type locality: Plateau Concorde, Martinique.

Known distribution: Martinique.

Type material: 4 specimens on slides and 40 juveniles in alcohol (sex not indicated).

Diagnosis. Body length up to 1.9 mm. Specimens pale yellow with dark or light purple pigments on Ant. I–III (apically always dark), Ant. IV lighter, lateral Th. II–III, proximally on coxae III, centrally on Abd. III, Abd. IV pigments W-shaped, or only as a small spot on lateral Th. III plus other spots on distal and lateral Abd. III–IV; eyepatches black. Antennae shorter than body (0.66). Ant. IV not annulated; Ant. III sense rods normal, not swollen. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines present. Dorsal head chaetotaxy with **A0**, **A2**, **M2** and **Pa5** as mac, others as mic; 4 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline. Th. II with **a5** plus 3 mac on **p3** complex. Th. III lacking mac. Trochanteral organ with up to 24 spine-like chaetae. Ungues wide with 4 internal teeth: 2 basal paired asymmetrical, 1 unpaired medial smaller than the basal teeth and 1 minute apical; unguiculi truncate, postero-external lamella smooth basally with 1–2 teeth on leg III; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.64: 1.0. Abd. I with **a6** mic. Abd. II with 2 (**m3** and **m5**) and Abd. III with 4 (**m3**, **am6**, **pm6**, **p6**) mac, respectively; Abd. IV with 3 inner mac (**A3**, **A5**, **B5**), **B6** as mes, with 6 main lateral mac (**D3**, **E2–3**, **F1–3**) and 13–14 posterior chaetae. Ventral tube anterior face with 3+3 distal mac. Dens with 2 rows of spines, internal with 28–32 and external rows with 20–23 spines, respectively. Mucro subrectangular (ratio width: length of the drawing about = 1: 1.8–2.0), with 4 teeth.

References: Soto-Adames *et al.* (2014).

3.2.54 *T. separata* (Denis, 1933)

Original description: *Paronella separata* Denis (1933, p. 262)

Type locality: La Palma, Costa Rica.

Known distribution: Costa Rica.

Type material: 8 specimens (sex not indicated).

Diagnosis. Body length about 1.1–1.3 mm. Specimens pale yellow. Antennae 1.6–2.0 times longer than head length. Ungues wide with 4 internal teeth: 2 paired basal symmetrical or slightly asymmetrical, 1 unpaired medial as large as the paired basal teeth and 1 apical smaller; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.51–0.66: 0.7–0.72. Dens with 2 rows of spines, internal with 15–22 and external with 11–19, respectively. Mucro rectangular (ratio width: length of the drawing about = 1: 3.2), with 4 teeth.

Remarks. The short diagnosis lacks clear diagnostic features to separate *T. separata* from other *Trogoalphysa* species with 4 internal teeth on ungues, unguiculus smooth, capitate tenent-hair and rectangular mucro with 4 teeth; therefore, we herein place *T. separata* as a *species inquirenda*.

Reference: Denis (1933).

3.2.55 *T. stannardi* Soto-Adames, 2015

Type locality: Chichen Itza, Yucatan, Mexico.

Known distribution: Mexico.

Type material: 1 male plus 2 specimens on slides and 10 juveniles in alcohol (sex not indicated).

Diagnosis. Body length up to 2.6 mm. Specimens with blue pigments on distal Ant. I, Ant. II–IV, hind coxae, lateral margin of Abd. I., tibiotarsi weakly pigmented; eyepatches black. Antennae up to 2.6 times longer than head length; Ant. III sense rods normal, not swollen. Eyes 6. Prelabral chaetae ciliate, 2 anterior labral spines present, normal and base fused, smooth or abnormally ciliate. Dorsal head chaetotaxy with at least 7–8 **An** mac, **A0**, **A2–3**, **M2**, **S3**, **S5** and **Pa5** as mac; 4–5 interocular chaetae, none as mac. Labial formula: **M1–4rEL1–2a1–5**, **r** stout and reduced. Mesothorax longer than metathorax in the midline; Th. II with **a5** plus 4–5 mac on **p3** complex; Th. III with 2 inner mac (**p2** and **p3**). Trochanteral organ with up to 27 spine-like chaetae. Ungues wide with 4 internal teeth: 2 small paired basal symmetrical, 1 unpaired apical smaller than the basal ones and 1 apical inconspicuous; unguiculi lanceolated, narrow in females, normal in males, with postero-external lamella serrated (in males) or smooth (in females); tenent-hairs capitate,

ratio unguis: unguiculus: tenent-hairs about = 1: 0.74: 0.93. Abd. I lacking **a6** mic; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 4 inner mac (**A3**, **A5**, **B4–B5**), **B6** as mes; 6 lateral mac and 10–11 posterior chaetae. Dens with 2 rows of spines, internal and external rows with up to 33 and 25 spines, respectively. Mucro subrectangular (ratio width: length of the drawing about = 1: 2.0), with 4 teeth.

Reference: Soto-Adames (2015).

3.2.56 *T. strinattii* Yoshii, 1988

Original description: *Trogolaphysa strinattii* Yoshii (1988, p. 452)

Type locality: Cave Sima del Borrego, Guerrero, Mexico.

Known distribution: Mexico.

Type material: 15 specimens (sex not indicated).

Diagnosis. Body length up to 2 mm. Specimens entirely pale or mostly pale with diffused dark pigments on antennae and body; eyepatches black. Antennae about 1.7 times longer than head length. Ant. IV annulated. Eyes 5. Prelabral chaetae ciliate, 2 anterior labral spines present, normal and separated. Dorsal head chaetotaxy with at least **A0** and **A2** as mac, others unknown. Labial formula: **M1–2rEL1–2**, **r** reduced. Mesothorax longer than metathorax in the midline; Th. II and Th. III lacking mac. Trochanteral organ with about 40 spine-like chaetae. Ungues wide with 4 internal teeth: 2 paired basal symmetrical, 1 unpaired medial as large as the paired basal teeth, and 1 minute apical tooth; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.58: 0.58. Abd. I–IV lacking mac. Ventral tube lateral flap with about 12 smooth chaetae. Dens with 2 rows of spines, internal and external with about 35 spines. Mucro subrectangular (ratio width: length of the drawing about = 1: 1.8), with 4 teeth.

Remarks. Yoshii's description reports 5 eyes for *T. strinattii*, however its drawings suggests the presence of 2 extra lenses (Yoshii 1988, p. 453, fig. 2C–D), possibly vestigial. Since in the text the author outlines a variation in the arrangement of the eyes in different specimens, it is possible that this species actually has at least 7 eyes. Yoshii (1988) also mentioned the complete absence of dorsal mac, with the exception of the mesothorax anterior collar. This feature is unlikely as at least the Abd. II–IV must present dorsal mac. Considering these uncertainties, we considered *T. strinattii* as a *species inquirenda* until a redescription can be published.

Reference: Yoshii (1988).

3.2.57 *T. subterranea* (Mari-Mutt, 1987)

Original description: *Dicranocentrua subterranean* Mari-Mutt (1987, p. 403)

Type locality: Aguas Buenas Cave, Puerto Rico.

Known distribution: Puerto Rico.

Type material: 4 specimens on slides and 6 specimens in alcohol (sex not indicated).

Diagnosis. Body length up to 2.5 mm. Colour pattern as in *T. jataca*, but all specimens with Ant. I–IV pigmented. Ant. IV annulated. Eyes 6. Prelabral chaetae ciliate, anterior labral spines absent. Dorsal head chaetotaxy with about 15 **An** mac, **A0**, **A2** as mac, **M** and **S** series lacking mac, **Pa5** and **Pm3** as mac; 4 interocular chaetae, none as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax longer than metathorax in the midline. Th. II with 6 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with up to 25 spine-like chaetae. Ungues with 3 internal teeth: 2 paired basal asymmetrical and 1 unpaired medial smaller than the basal teeth; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.60: 0.57. Abd. II–III with 2 and 4 mac respectively, **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III. Abd. IV with 3 inner mac (**A3**, **A5**, **B5**, *sensu* Soto-Adames 2015). Ventral tube anterior face with 3+3 distal mac. Dens with 2 rows of spines, internal and external with about 31 spines. Mucro rectangular (ratio width: length of the drawing about = 1: 2.6), with 4 teeth.

Remarks. This species is similar to other Puerto Rican taxa described by Mari-Mutt (1987). The complete absence of cephalic **M** and **S** series mac of *T. subterranea* clearly separate it from the *T. jataca* species complex. The species was described as “*T. subterranean*” by Mari-Mutt (1987), but in other parts of its paper the author used “*T. subterranea*”, as well as in his first supplement to the Neotropical catalog of springtails (Mari-Mutt 1996). Thus, we considered *T. subterranean* as a *lapsus calami* (article 32.5 of the International Code of Zoological Nomenclature – ICZN 2021), and the name of the species actually as *T. subterranea*, as seen in other literature as Soto-Adames & Taylor (2013) and Soto-Adames (2015).

References: Mari-Mutt (1987); Soto-Adames (2015).

3.2.58 *T. tijucana* (Arlé & Guimarães, 1979)

Original description: *Paronella tijucana* Arlé & Guimarães (1979, p. 213)

Type locality: Três Rios, Rio de Janeiro State, Brazil.

Known distribution: Brazil.

Type material: 7 specimens (sex not indicated).

Diagnosis. Body length up to 0.8 mm. Specimens ground colour pale, dark pigmented Ant. IV, frontal head, lateral edges of thorax and Abd. I–II, ventral tube and proximal legs (coxae and trochanters) light pigments on anterior Ant. II–III, mouth, dorsal Th. II to anterior Abd. III; eyepatches black. Antennae about 1.4 times longer than head length; Ant. IV apparently not annulated. Eyes 2. Mesothorax smaller than metathorax in the midline. Ungues wide with 2 internal paired basal asymmetrical teeth, median and distal teeth absent; unguiculi truncate with postero-external lamella smooth; tenent-hairs acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.56: 0.61. Dens with 1 row with 5–6 proximal spines. Mucro rectangular (ratio width: length of the drawing about = 1: 3), with 4 teeth.

Remarks. Thibaud & Najt (1988) reported *T. tijucana* as presenting 3 eyes instead the 2 described by Arlé & Guimarães (1979). Apparently this was a lapsus as there is no indication the former authors revised the type specimens. The reduced size, large metathorax compared to mesothorax, unguiculi morphology and partial colour pattern suggests *T. tijucana* may be related to *T. formosensis*. The latter species resembles *Campylothorax* Schött, 1893 in some features, and the presence of proximal spines which become slender longer chaetae more distally on dens in *T. tijucana* is reported for *Campylothorax* spp. as well in *C. mitrai* Bellini & Meneses, 2012 (Bellini & Cipola, 2017).

References: Arlé & Guimarães (1979); Palacios-Vargas *et al.* (1985); Thibaud & Najt, (1988); Soto-Adames & Taylor (2015).

3.2.59 *T. toroi* (Palacios-Vargas, Ojeda & Christiansen, 1985)

Original description: *Troglopedetes toroi* Palacios-Vargas, Ojeda & Christiansen (1985: p. 12)

Type locality: Cueva Encantada, Chiapas, Mexico.

Known distribution: Mexico.

Type material: 8 specimens (sex not indicated).

Diagnosis. Body length about 1.5 mm. Specimens with light purple pigments diffused throughout the body; eyepatches black. Antennae about 2 times longer than head length. Ant. IV annulated. Eyes 6. Prelabral chaetae ciliate, labral row **p** with longer chaetae; 2 anterior labral spines present, normal and separated. Dorsal head chaetotaxy with 17 **An** mac, **A3**, **A5** and **M4** as mic, others unknown. Labial formula: **M1–2rEL1–2a1–5, r**

reduced. Trochanteral organ with approximately 20 spine-like chaetae. Ungues wide with 4 internal teeth: 2 internal paired basal symmetrical and 2 unpaired, medial tooth smaller than the basal pair, apical smaller than medial; unguiculi lanceolated with postero-external lamella serrated (proximally); tenent-hairs acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.57: 0.59. Dens with 2 rows of spines, internal and external rows with about 40 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 2.1), with 4 teeth.

Reference: Palacios-Vargas *et al.* (1985).

3.2.60 *T. trioculata* Soto-Adames, 2015

Original description: *Trogolaphysa trioculata* Soto Adames (2015: p. 35)

Type locality: Cacahuatan, Chiapas, Mexico.

Known distribution: Mexico.

Type material: 2 specimens (sex not indicated).

Diagnosis. Body length up to 1.1 mm. Body colour pattern unclear; eyepatches black. Antennae shorter (0.83) or slightly longer than head length. Ant. III sense rods normal, not swollen. Eyes 3. Prelabral chaetae ciliate, 2 anterior labral spines absent. Dorsal head chaetotaxy with at least 8 **An mac**, **A0**, **A2**, **Pa5** and **Pm3** as mac. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Mesothorax slightly longer than metathorax in the midline. Th. II with **a5** plus 5 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with up to 14 spine-like chaetae. Ungues wide with 2 internal paired basal asymmetrical teeth; unguiculi basally swollen or weakly truncated with external lamella smooth; tenent-hairs acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.66: 0.53. Abd. I lacking **a6** mic; Abd. II–III with 2 and 4 mac respectively, possibly **m3** and **m5** on Abd. II and **m3**, **am6**, **pm6** and **p6** on Abd. III; Abd. IV with 3 inner mac (**A3**, **A5**, **B5**), **B6** apparently as mes; 4 lateral mac and 10 posterior chaetae. Dens with 2 rows of spines, internal and external with about 15 and 12 spines, respectively. Mucro rectangular (ratio width: length of the drawing about = 1: 2.6), with 4 teeth.

Remarks. In the original description of *T. trioculata* the antennae size is described as 0.83 times the head length, but the photograph of one species shows it longer (see Soto-Adames 2015, p. 10, fig. 3G). In addition, the unguis morphology apparently is mistakenly presented (p. 38, fig. 20C), since it possibly presents one of the lateral teeth as internal and more proximal compared to the basal pair. Such data were corrected here.

Reference: Soto-Adames (2015).

3.2.61 *T. variabilis* (Palacios-Vargas, Ojeda & Christiansen, 1985)

Original description: *Troglopedetes variabilis* Palacios-Vargas, Ojeda & Christiansen (1985: p. 18)

Type locality: Cueva de Ungurria, Veracruz, Mexico.

Known distribution: Mexico.

Type material: 6 specimens (sex not indicated).

Diagnosis. Body length about 2.8 mm. Eyepatches black, body apparently lacking other pigments. Antennae about 2.7 times longer than head length. Ant. IV annulated. Eyes 4+4 or 6+6. Prelabral chaetae ciliate, labral row **p** with longer chaetae; 2 anterior labral spines absent. Labial formula: **M1–2reL1–2a1–5**, **r** reduced. Trochanteral organ with approximately 32 spine-like chaetae. Ungues wide with 4 internal teeth: 2 paired basal symmetrical, 1 unpaired medial smaller than the proximal, and 1 apical smaller than the medial; unguiculi lanceolated with postero-external lamella serrated (distally); tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.54: 0.47. Dens with 2 rows of spines, internal and external rows with about 31–39 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 2.5), with 4 teeth.

Reference: Palacios-Vargas *et al.* (1985).

3.2.62 *T. vivieni* (Barra, 1969)

Original description: *Paronella vivieni* Barra (1969, p. 207)

Type locality: Ipassa, Makokou, Gabon.

Known distribution: Gabon.

Type material: 11 specimens (sex not indicated).

Diagnosis. Body length up to 1.7 mm. Specimens pale with dark blue pigment on Ant. IV, proximal Ant. II–III, trochanter III; Abd. I–III weakly pigmented; eyepatches black. Antennae about 2.7 times longer than head length; Ant. IV annulated; Ant. III sense rods swollen. Eyes 8. Dorsal head chaetotaxy with about 10 **An** mac, **A2**, **M2**, **S3** and **Pa5** as mac, **Pm3** and others as mic; 3 interocular chaetae, none as mac. Labial formula: **M1–2rEa1–2**, **r** reduced, others unknown. Mesothorax longer than metathorax in the midline. Ungues wide with 3 internal teeth: 2 paired basal symmetrical and 1 unpaired medial as large as the paired basal teeth; unguiculi lanceolate with postero-external lamella weakly serrate with a proximal tooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.78: 0.57–0.68. Ventral tube anterior face with 4+4 distal mac; lateral flap with 13 smooth chaetae. Dens with 2 rows of spines, internal and external with 13–32

each. Mucro rectangular (ratio width: length of the drawing about = 1: 2.9–3.1), with 5 teeth.

Remarks. This is one of the few species of *Trogolaphysa* with 5 teeth on the mucro. Among the African taxa, *T. vivieni* and *T. monomaculata* are the only ones with such morphology, and both species are from Gabon. However, *T. vivieni* has the entire Ant. IV, proximal Ant. II–III and trochanter III dark pigmented (only distal Abd. IV in *T. monomaculata*), dorsal head with about 10 **An** mac, **M2**, **S3** and **Pa5** mac, and **Ps5** as mic (about 6 **An** mac, **M2**, **S3** and **Pa5** as mic and **Ps5** as mac in *T. monomaculata*), labium with **M2** and **r** chaetae (both absent in *T. monomaculata*) and ventral tube with 4+4 distal mac and 13 chaetae on lateral flap (2+2 and 11 respectively in *T. monomaculata*). Apparently, *T. vivieni* can live nearby or maybe even associate to termite nests (Barra 1969).

References: Barra (1969); Nguyen & Soto-Adames (2018).

3.2.63 *T. wahlgreni* (Mitra, 2002b)

Original description: *Dicranocentrua wahlgreni* Mitra (2002b, p. 109)

Type locality: Meru, Kenya.

Known distribution: Kenya.

Type material: holotype on slide and 111 paratypes in alcohol (sex not indicated).

Diagnosis. Body length about 3 mm. Specimens uniformly white or yellow; eyepatches black. Ant. IV annulated. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines present. Dorsal head chaetotaxy with **A0**, **A2**, **A3**, **A5**, **M2**, **S3**, **S5** and **Pa5** present, about 8 interocular chaetae. Mesothorax longer than metathorax in the midline; Th. II with 6 mac on **p3** complex; Th. III lacking mac. Trochanteral organ with about 66 spine-like chaetae. Ungues wide with 3 internal teeth: 2 paired basal symmetrical, 1 unpaired medial; unguiculi lanceolate with postero-external lamella smooth; tenent-hairs long and capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.70: 0.77. Ventral tube anterior face with 4+4 distal mac. Abd I without mac; Abd. II with 1 central mac (**m3**), lateral **m5** mac apparently missing; Abd. III with 1 central (**m3**) and 7 lateral mac; Abd. IV with 6 central and 14 lateral mac. Dens with 1 row of spines (at least 26). Mucro rectangular (ratio width: length of the drawing about = 1: 2.2), with 4 teeth.

Remarks. As observed by Mitra (2002b), the material of Schött (1903) and Wahlgren (1908) descriptions represent different species from *T. nigromaculata* species-complex.

Here we took into consideration the note by Nguyen & Soto-Adames (2018) about pseudopore symbols mistakenly used in abdominal segments to represent mac by Mitra (2002c), and counted 6 central mac on Abd. IV. Such chaetae are possibly **A1, A3–4, B4–6**. The 7 lateral mac on Abd. III of this species are possibly **a7i(or a6)–7, am6, pm6, m7i–7, p6**.

Reference: Wahlgren (1908); Mitra (2002b); Nguyen & Soto-Adames (2018).

3.2.64 *T. xtolokensis* (Palacios-Vargas, Ojeda & Christiansen, 1985)

Original description: *Troglopedetes xtolokensis* Palacios-Vargas, Ojeda & Christiansen (1985: p. 10)

Type locality: Cueva del Cenote Xtolok, Yucatan, Mexico.

Known distribution: Mexico.

Type material: 13 specimens (sex not indicated).

Diagnosis. Body length about 2.6 mm. Specimens lacking pigmentation on body and eye patches. Antennae about 2.5 times longer than head length. Ant. IV annulated; Ant. III sense rods normal, not swollen. Eyes absent. Prelabral chaetae smooth, labral row **p** with longer chaetae; 2 anterior labral spines present, normal and separated. Dorsal head chaetotaxy with 14 **An** mac, **A0, A2, Pa5** as mac (**Pm3** unclear), **S2** apparently as a short mac, **M** series and other **S** chaetae as mic; 4 interocular chaetae, none as mac. Labial formula: **M1–2rel1–2a1–5, r** reduced. Mesothorax slightly longer than metathorax in the midline. Trochanteral organ with approximately 20 spine-like chaetae. Ungues wide with 4 internal teeth: 2 paired basal symmetrical and 2 unpaired apical, all with similar sizes; unguiculi lanceolated with postero-external lamella serrated (distally); tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.45: 0.40. Ventral tube anterior face apparently with 3+3 distal mac. Dens with 2 rows of spines, internal and external rows with 41–69 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 3.2), with 4 teeth.

Reference: Palacios-Vargas *et al.* (1985).

3.2.65 *T. yoshii* (Palacios-Vargas, Ojeda & Christiansen, 1985)

Original description: *Troglopedetes yoshiius* Palacios-Vargas, Ojeda & Christiansen (1985: p. 14)

Type locality: Cueva del Guayabo, Oaxaca, Mexico.

Known distribution: Mexico.

Type material: 7 specimens (sex not indicated).

Diagnosis. Body length about 2.6 mm. Specimens with eyes pigmented, body apparently lacking pigments. Antennae about 2.3 times longer than head length. Ant. IV annulated; Ant. III sense rods normal, not swollen. Eyes 6. Prelabral chaetae smooth, labral row **p** with longer chaetae; 2 anterior labral spines absent. Dorsal head chaetotaxy with at least 9 **An** mac, **M** and **S** series apparently lacking mac, other chaetae unclear. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Trochanteral organ with approximately 26 spine-like chaetae. Ungues wide with 3 internal teeth: 2 paired basal larger symmetrical and 1 unpaired medial smaller, apical tooth absent; unguiculi apically blunt with postero-external lamella weakly serrated (proximally); tenent-hairs reduced and acuminate, ratio unguis: unguiculus: tenent-hair about = 1: 0.55: 0.38. Ventral tube anterior face apparently with 3+3 distal mac; lateral flap with 12 ciliate and 3 smooth chaetae, posterior face apparently lacking smooth chaetae. Dens with 2 rows of spines, internal and external rows with about 30–39 spines each. Mucro rectangular (ratio width: length of the drawing about = 1: 2.1), with 4 teeth.

Reference: Palacios-Vargas *et al.* 1985.

3.3 Phylogenetic relationships

Among the Paronellinae, genera like *Troglopedetes* Joseph, 1872 and *Cyphoderopsis* Carpenter, 1917 are morphologically closer to *Trogolaphysa*. *Cyphoderopsis* was established placed as a junior synonym of *Troglopedetes* (Bonet 1931; Wilson 1982) and posteriorly the genera *Trogolaphysa*, *Dicranocentruga* Wray, 1953 and *Paronella* Schött, 1893 were considered as potential synonyms to *Troglopedetes* species based on reduction of eyes and pigmentation (Palacios-Vargas *et al.* 1985). However, Yoshii (1988) highlighted the reduction of the antennae as diagnostic of *Cyphoderopsis* as well as the Ant. IV subdivided in *Troglopedetes* (Yoshii 1988). After Thibaud & Najt (1988), the species with 1+1 rows of manubrium spines were placed under *Paronella*; species without such spines but with subdivided Ant. IV, as *Troglopedetes*; and those without manubrial spines and with Ant. IV entire, as *Trogolaphysa*; while *Dicranocentruga* was synonymized under *Trogolaphysa* based on morphological features of the antennae and furcula. Mitra (1992) revised the types of *Paronella fusca* (Schött 1893) and confirmed the manubrial and dental spines features, however, he described two rows of spines on each distal arm of the manubrium, which differs of the Thibaud & Najt's (1988) first observation.

Mitra (1992; 2002) demonstrated the presence of the extra-ocular structure (EOS) behind the eyepatches in *Dicranocentruga* species (currently a synonym of *Trogolaphysa*); EOS is also present at least in *Paronella* and *Campylothorax* Schött, 1893 (Mitra 1992, 2002b). After revising several genera of Paronellinae, Mitra (2002b) delimited *Dicranocentruga* as holding the EOS, with 8+8 eyes; while related species lacking the EOS, with 6+6 or less eyes belong to *Troglopedetes* (with Ant. IV subdivided) or *Trogolaphysa* (with Ant. IV entire). However, Soto-Adames & Taylor (2013) reported that *Trogolaphysa jacobyi* and the syntype of *T. maya* both show the EOS. Several species of *Trogolaphysa* have 8+8 eyes; hence, they kept *Dicranocentruga* as a junior synonym of *Trogolaphysa* as firstly proposed by Thibaud & Najt (1988).

The dorsal trunk chaetotaxy of the Paronellinae genera (i.e. *Trogolaphysa*, *Cyphoderopsis*, *Paronella*, *Lepidonella* Yosii, 1960, *Bromachantus* Schött, 1925 and *Troglopedetes*) and Lepidocyrtinae (i.e. *Lepidocyrtus* Bourlet, 1839 and *Pseudosinella* Schäffer, 1897) are insufficient to separate genera or even species, although both subfamilies share the tergal S-chaetotaxy formula: 1, 1 | 0, 1, 1 from Th. II to Abd. III (Zhang *et al.* 2015). Molecular phylogenies have shown a close relationship among

Cyphoderus, *Cyphoderopsis*, *Campylothorax* and *Trogolaphysa* with Lepidocyrtinae genera, which suggests Entomobryidae and Paronellidae may be artificial (Zhang *et al.* 2015; Zhang & Deharveng 2015; Zhang *et al.* 2019). On the other hand, the colour pattern (pigmented or white), antennal size (shorter or longer than body), the subdivision on Ant. IV, number of eyes (0–8), number of bothriotracha on Abd. IV (2–3), number of the inner teeth on unguis (0–4), presence or absence of manubrial spines, chaetae type on dens (spines or feathered), number of spines rows on dens (1 or 2) and the shape of mucro (elongate or short) are important features to distinguish the Paronellinae genera (Tab. 1).

Table 1.1 Main diagnostic features of the genera of Paronellidae

Genera Type species	<i>Campylothorax</i> <i>C. longicornis</i> ³	<i>Cyphoderopsis</i> <i>C. kempfi</i> ⁴	<i>Cyphoderus</i> <i>C. albinus</i> ¹	<i>Paronella</i> <i>P. fusca</i> ³	<i>Trichorypha</i> <i>T. atrofasciata</i> ³	<i>Troglopedetes</i> <i>T. albus</i> ²	<i>Trogolaphysa</i> <i>T. maya</i> ⁷	<i>Bromachantus</i> <i>B. handschini</i> ⁶	<i>Lepidonella</i> <i>L. tokiokai</i> ⁸
Colour Pattern	Usually pigmented ⁹	White or weakly pigmented ¹³	White ^{15,16}	Pigmented ¹⁰	Pigmented ¹¹	Usually white ^{14,20}	White or pigmented ¹⁴	Devoid of dark pigmented ¹²	White or pigmented ¹⁸
Thorax shape	Humped ⁹	Normal ¹³	Normal ^{15,16}	Normal ¹⁰	Normal ¹¹	Normal ^{14,20}	Normal ¹⁴	Convex? ¹²	Humped ^{12,18}
Antennae size	Longer than body ⁹	Shorter than body ¹³	Shorter than body?	Shorter than body ¹⁰	Longer than body ¹¹	Shorter or longer than body ^{14,20}	Shorter or longer than body ¹⁴	Shorter or subequal to body ¹²	Shorter or longer than body ^{12,18}
Ant. IV subdivided	No	No ¹³	No	No	No	Yes ^{14,20}	No ¹⁴	No	No
Eyes	8 ⁹	0–6 ¹³	0 ^{15,16}	8 ¹⁰	8 ¹¹	0–3 ^{14,20}	0–8 ¹⁴	8 ¹²	3–8 ^{12,18}
Abd. IV bothriotricha	3 or 4 ¹⁷	3 ¹³	3 ^{15,16}	2 ¹⁰	2?	3 ^{14,20}	3 ¹⁴	2 ¹²	2 ¹⁸
Ungues inner teeth	2–4 ^{9,17}	0–2 ¹³	3–4 ^{15,16}	2–3 ¹⁰	4 ¹¹	0–2 ^{14,20}	2–4 ¹⁴	4 ¹²	2–3 ¹⁸
Manubrial spines	Absent ⁹	Absent?	Absent?	Present ¹⁰	Absent ¹¹	Absent ^{14,20}	Absent ¹⁴	Present (distally) ¹²	Absent ¹⁸
Dens chaetae type	Spines ^{9,17}	Spines?	Feathered ^{15,16}	Spines ¹⁰	Spines ¹¹	Spines ^{14,20}	Spines	Spines ¹²	Spines ¹⁸
Rows of dental spines	1 ⁹ or 2 ¹⁴	1 or 2 ¹³	2 ^{15,16}	1 or 2 ¹⁰	1 ¹¹	1 ¹⁴ or 2 ²⁰	1 or 2 ¹⁴	1 ¹²	2 ¹⁸
Mucro shape and teeth	Elongate, 4–6 teeth ¹⁴	Short, 3 main teeth ¹³	Elongate, 3 or more teeth ^{15,16}	Short, 3–4 teeth ¹⁰	Short, 4 teeth ¹¹	Variable length, 3–5(6) teeth ²⁰	Short/Elongate, 3–5 teeth ¹⁴	2 teeth ¹²	Short, 3–4 teeth ¹⁸

References: ¹ Nicolet 1842; ² Joseph 1872; ³ Schött 1893; ⁴ Carpenter 1917; ⁶ Schött 1925; ⁷ Mills 1938; ⁸ Yosii 1960; ⁹ Mitra & Dallai 1980; ¹⁰ Mitra 1992; ¹¹ Mitra 2002a; ¹² Mitra 2003; ¹³ Jantarit *et al.* 2013; ¹⁴ Soto-Adames *et al.* 2014; ¹⁵ Jantarit *et al.* 2014; ¹⁶ Zeppelini & Oliveira 2016; ¹⁷ Bellini & Cipola 2017; ¹⁸ Deharveng *et al.* 2018; ²⁰ Jantarit *et al.* 2020.

3.4 General morphology

Among the 65 species of *Trogolaphysa* surveyed in this study, 14 were here considered to be *species inquirendae*: *T. berlandi*, *T. carpenteri*, *T. fuelleborni*, *T. ghesquieri*, *T. guacharo*, *T. hauseri*, *T. hirtipes*, *T. innominata*, *T. lamottei*, *T. maya*, *T. millsii*, *T. nigromaculata*, *T. separata* and *T. strinatii* (Tab. 2.1). The absence of information on several features for African species prevents an effective comparison with Neotropical species. However, only four African species were classified as *species inquirenda*, while 10 Neotropical species have a questionable status. After this survey, 51 species have clearer diagnoses, even if lacking important data on chaetotaxy.

The general habitus of *Trogolaphysa* is typical of Lepidocyrtinae: species have the head and body dark or lightly pigmented (epigean species) or completely white, without pigments (hypogean species). *Trogolaphysa* species have antennae longer than head length but Ant. I shorter than head, with Ant. IV entire, smooth or annulate (Fig. 4.1A–B); however, *T. caripensis* and *T. jacobyi* show an incomplete constriction on Ant. IV. On Ant. IV there are at least two types of chaetae (blunt and ciliate) and 1 apical shallow sensory organite (pseudopore-like) which could be present or absent, and may present a sensilla. The Ant. III sensory organ is mostly typical, usually with two sense rods, normal or swollen, and usually three surrounding guard sensilla (Fig. 4.1C–D). Ant. II ventrally can bear at least 3 types of sensilla: pin, blunt and swollen sensilla at the apex, and Ant. I show at least 3 smooth pointed sens at the base (Fig. 5.1).

The majority of *Trogolaphysa* species have ciliate prelabral chaetae, but few species hold smooth chaetae (*T. belizeana*, *T. bessoni*, *T. ecuatorica*, *T. haitica*, *T. hondurasensis*, *T. jacobyi*, *T. nacionalica*, *T. palaciosi*, *T. xtlokensis* and *T. yoshii*) (Fig. 4.1E–F). Posterior labral chaetae (**p** row) are mostly longer than others, but at least few species show them as subequal to the other rows (**a** and **m**) (Fig. 4.1E–F). The species could have labral spines smooth (often called "normal spines" in the literature) or rarely ciliate, separated at the base (normal) or fused (Y-shape). However, several species do not present such spines (*T. bessoni*, *T. clarencei*, *T. cotopaxiana*, *T. ecuatorica*, *T. formosensis*, *T. haitica*, *T. jacobyi*, *T. jamaicana*, *T. judithnajtae*, *T. marimutti*, *T. nacionalica*, *T. oztolica*, *T. palaciosi*, *T. subterranea*, *T. trioculata*, *T. variabilis* and *T. yoshii*) (Fig. 4.1G–I). The labial chaetae **M1–2**, **R** and **L2** can be ciliated or smooth; **M3–4**, rarely present, are ciliate; **L1** is always ciliate and **a1–5** are mostly smooth (Fig. 4.1J–K).

The dorsal head chaetotaxy could vary on the number of mac/mic on antennal (**An**), anterior (**A**), medial (**M**) and sutural (**S**) series, and apparently only postoccipital (**Ps**) series is conserved in the genus (Fig. 5A). The posterior region includes the series postoccipital anterior (**Pa**), medial (**Pm**), posterior (**Pp**) and external (**Pe**), and this region is more stable than the anterior head, i.e. **Pa5** as mac and **Pa6** as bothriotricum, however the chaeta **Pm3** could be mac or mic and some mic could be present or absent (Fig. 5.1A). A synthesis of adult head chaetotaxy is represented in Fig. 5.1A. Concerning the eyes, most species show 6–8 eyes (epigean forms) or a complete absence of eyes (cave forms), but few species have 2–4 eyes (*T. aelleni*, *T. hondurasensis*, *T. tijucana*, *T. trioculata* and *T. variabilis*). The putative homology of eye lenses is presented in Fig. 5.1B.

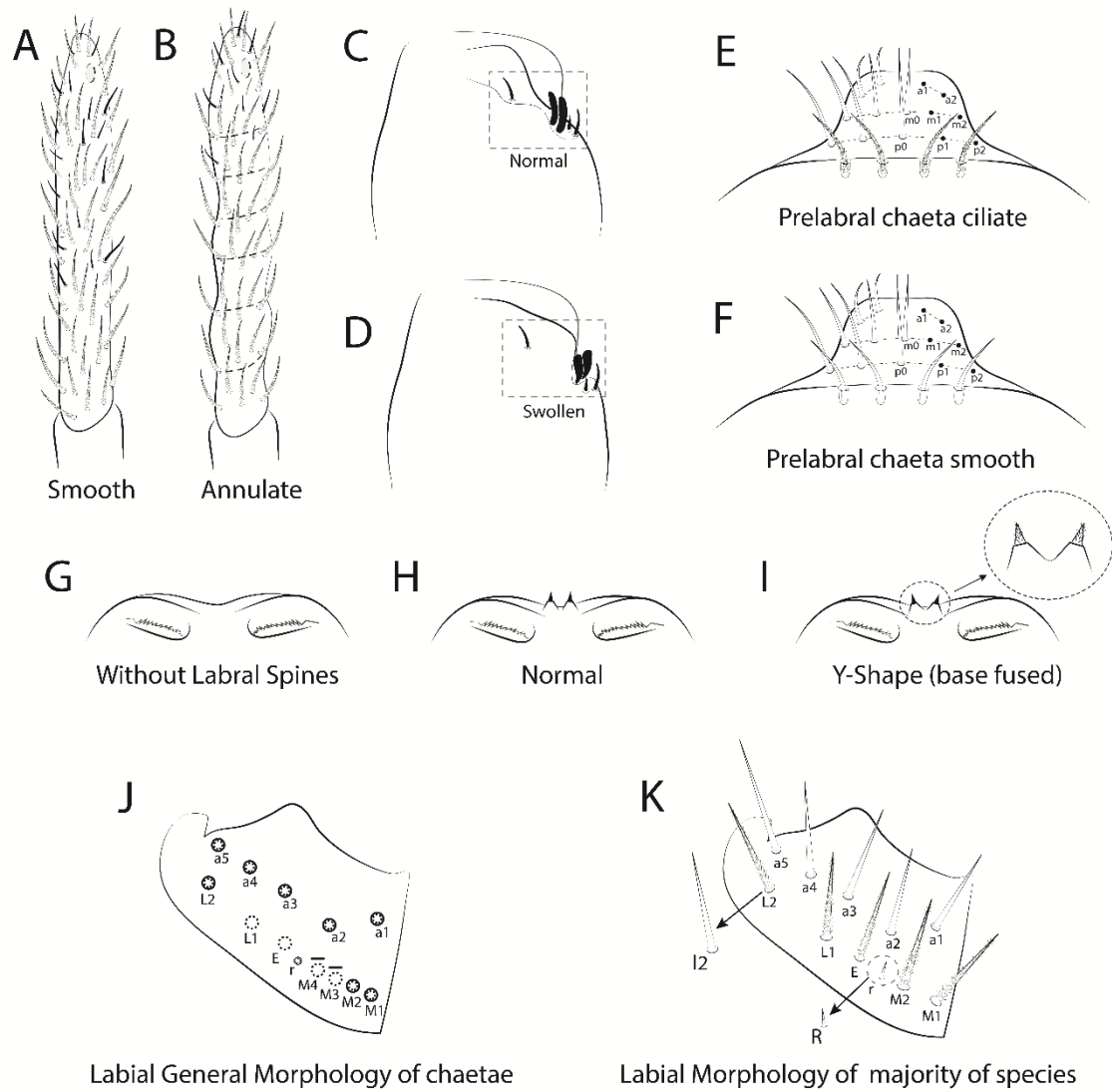
The dorsal trunk chaetotaxy is quite similar among the species, but variations in macrochaetotaxy are often observed in Th. II–III and Abd. IV–V (Fig. 6.1–7.1). The Th. II has several sets of 3 to 7 chaetae on **p3** complex, while **p4** mac is rarely present. Th. III may have 0 (most often) to 3 central mac. The mac on Abd. II (**m3** and **m5**) and Abd. III (**m3**, **am6**, **pm6** and **p6**) are conserved, while the accessory scales and lateral chaetae can variate (Fig. 6.1). Abd. IV usually is represented with 3–4 central mac, but may have six central mac (*T. wahlgreni* Mitra, 2002b) or none (*T. haitica sensu* Soto-Adames & Taylor 2013) (Fig. 7.1A). Abd. V usually has **as** sens present and 1–2 accessory sensilla (**acc.p4** and **acc.p5**), the postero-anterior series is the most variable in Abd. V, while the anterior, medial and posterior series, at least in the central area, are frequently stable (Fig. 7.1B). A synthesis of adult trunk chaetotaxy is represented in Figs. 6.1–7.1.

The empodial complex can be separated in three main structures, as in other Entomobryoidea: unguis, unguiculus and tenent-hair. The unguis can be wide (normal) (Fig. 8.1A–B) or narrow (Fig. 8.1C), and it can have 2 to 4 internal teeth and 1 to 3 external teeth (Fig. 8.1A–C); the basal internal teeth can be symmetrical (Fig. 8.1A–B) or asymmetrical (Fig. 8.1C). The unguiculi can be lanceolate (Fig. 8.1A–B) or truncate (Fig. 8.1C), basally normal or swollen, with external or internal lamellae smooth or serrate (Fig. 8.1A–C). The tenent-hair can be acuminate (Fig. 8.1A) or capitate (Fig. 8.1B–C), normal sized or reduced. The shape of mucro is classified in three types: rectangular, subrectangular and square as previously explained under the “materials and methods”, and can present 3 to 5 teeth. The different shapes and number of teeth on the mucro are shown in Fig. 9.1.

Table 2.1 Summarized information of taxonomic notes for status of the *species inquirendae*

Species	Synonyms	Distribution	Reason for placement as <i>species inquirendae</i>	References
<i>T. berlandi</i> (Denis, 1925)	<i>Paronella berlandi</i>	French Guiana Argentina	<ul style="list-style-type: none"> • Original description with insufficient diagnostic characters to distinguish from others <i>Trogolaphysa</i>; • Unusual body size (9.1 mm); • Large distribution with different features. 	Denis (1925); Cassagnau (1963); Thibaud & Najt, (1988)
<i>T. carpenteri</i> (Denis, 1925)	<i>Paronella carpenteri</i>	French Guiana Mexico Costa Rica Venezuela	<ul style="list-style-type: none"> • Original description with insufficient diagnostic characters to distinguish from others <i>Trogolaphysa</i>; • Large distribution with different features. 	Denis (1925); Denis (1931); Yoshii (1988)
<i>T. fuelleborni</i> (Börner, 1903)	<i>Paronella fuelleborni</i>	Tanzania Madagascar (unverified)	<ul style="list-style-type: none"> • Original description with insufficient diagnostic characters to distinguish from others <i>Trogolaphysa</i>; • Already considered <i>T. nigromaculata</i>; 	Börner (1903); Nguyen & Soto-Adames (2018)
<i>T. ghesquierei</i> (Marlier, 1945)	<i>Paronella ghesquierei</i>	Republic of Congo	<ul style="list-style-type: none"> • Original description with insufficient diagnostic characters to distinguish from others <i>Trogolaphysa</i>; • Know only for its colour pattern, empodial complex and dens. 	Marlier (1945); Nguyen & Soto-Adames (2018)
<i>T. guacharo</i> Yoshii, 1988	-	Venezuela Costa Rica	<ul style="list-style-type: none"> • Absence of dorsal trunk mac in original description, a common features for <i>Trogolaphysa</i> and Entomobryoidea species. 	Yoshii (1988)
<i>T. hauseri</i> Yoshii, 1988	-	Brazil	<ul style="list-style-type: none"> • Absence of dorsal trunk mac in original description, a common features for <i>Trogolaphysa</i> and Entomobryoidea species. 	Yoshii (1988)
<i>T. hirtipes</i> (Handschin, 1924)	<i>Paronella hirtipes</i> .	Brazil Argentina	<ul style="list-style-type: none"> • Descriptions with insufficient diagnostic characters to distinguish from others <i>Trogolaphysa</i>. 	Handschin (1924); Cassagnau (1963); Mendonça (1981); Thibaud & Najt (1988)
<i>T. innominata</i> (Denis, 1933)	<i>Paronella innominata</i> (CRI, CRII and CRIII)	Costa Rica	<ul style="list-style-type: none"> • Original notes with insufficient diagnostic characters to distinguish from others <i>Trogolaphysa</i>; 	Denis (1933)

			<ul style="list-style-type: none"> The authors already questioned the specific value of the morphotypes; 	
<i>T. lamottei</i> (Delamare-Deboutteville, 1950)	<i>Paronella lamottei</i> <i>Paronella atrofasciata?</i>	Guinea Cameroon (unverified)	<ul style="list-style-type: none"> Descriptions with insufficient diagnostic characters to distinguish from others <i>Trogolaphysa</i>; Perhaps a junior synonym of <i>Paronella atrofasciata</i> (Nguyen & Soto-Adames 2018) 	Schött, (1893); Schött, (1903); Delamare-Deboutteville (1950); Mitra (2002a); Nguyen & Soto-Adames (2018)
<i>T. maya</i> Mills, 1938	Previously synonymized as <i>T. delamarei</i> by Thibaud & Najt 1988	Mexico Dominican Republic	<ul style="list-style-type: none"> Descriptions with insufficient diagnostic characters to distinguish from others subterranean <i>Trogolaphysa</i> species; After additional features provided by Gruia 1987 for <i>T. delamarei</i>, this allowed the separation between <i>T. delamarei</i> and <i>T. maya</i>. 	Mills (1938); Thibaud & Najt (1988; Massoud & Gruia (1973); Gruia (1987); Soto-Adames & Taylor (2013)
<i>T. millsii</i> Arlé, 1939	-	Brazil	<ul style="list-style-type: none"> The drawings of the original description seem to indicate that the description was based in 2 juveniles, which have small body (0.6 mm) with large head and short appendages. 	Arlé (1939)
<i>T. nigromaculata</i> (Schött 1903)	<i>Paronella nigromaculata</i>	Cameroon Ivory Coast Rwanda Burundi Tanzania Ethiopia Kenya	<ul style="list-style-type: none"> Original description with insufficient diagnostic characters to distinguish from other African forms of <i>Trogolaphysa</i>; Large distribution with variable or different morphological features; Possibly a species complex (Nguyen & Soto-Adames 2018) 	Schott (1903); Schött (1927); Mitra (2002b); Nguyen & Soto-Adames (2018)
<i>T. separata</i> (Denis, 1933)	<i>Paronella separata</i>	Costa Rica	<ul style="list-style-type: none"> Descriptions with insufficient diagnostic characters to distinguish from others subterranean <i>Trogolaphysa</i> species; 	Denis (1933)
<i>T. strinatii</i> Yoshii, 1988	-	Mexico	<ul style="list-style-type: none"> Absence of dorsal trunk mac, a common feature for <i>Trogolaphysa</i> and Entomobryoidea species. Yoshii's descriptions report 5 eyes while his drawings suggest 2 extra lenses. 	(1988)



- L Symbols:**
- Smooth chaeta
 - ⊙ Ciliate chaeta
 - ⊗ Smooth or ciliate chaeta
 - Chaeta present or absent

Figure 4.1. General morphology of Ant. III-IV (A-D); prelabral and labral chaetae (E-F); distal labrum and spines (G-I); and labial basomedium and basolateral chaetotaxy (J-K); L, symbols used to describe the labial chaetae.

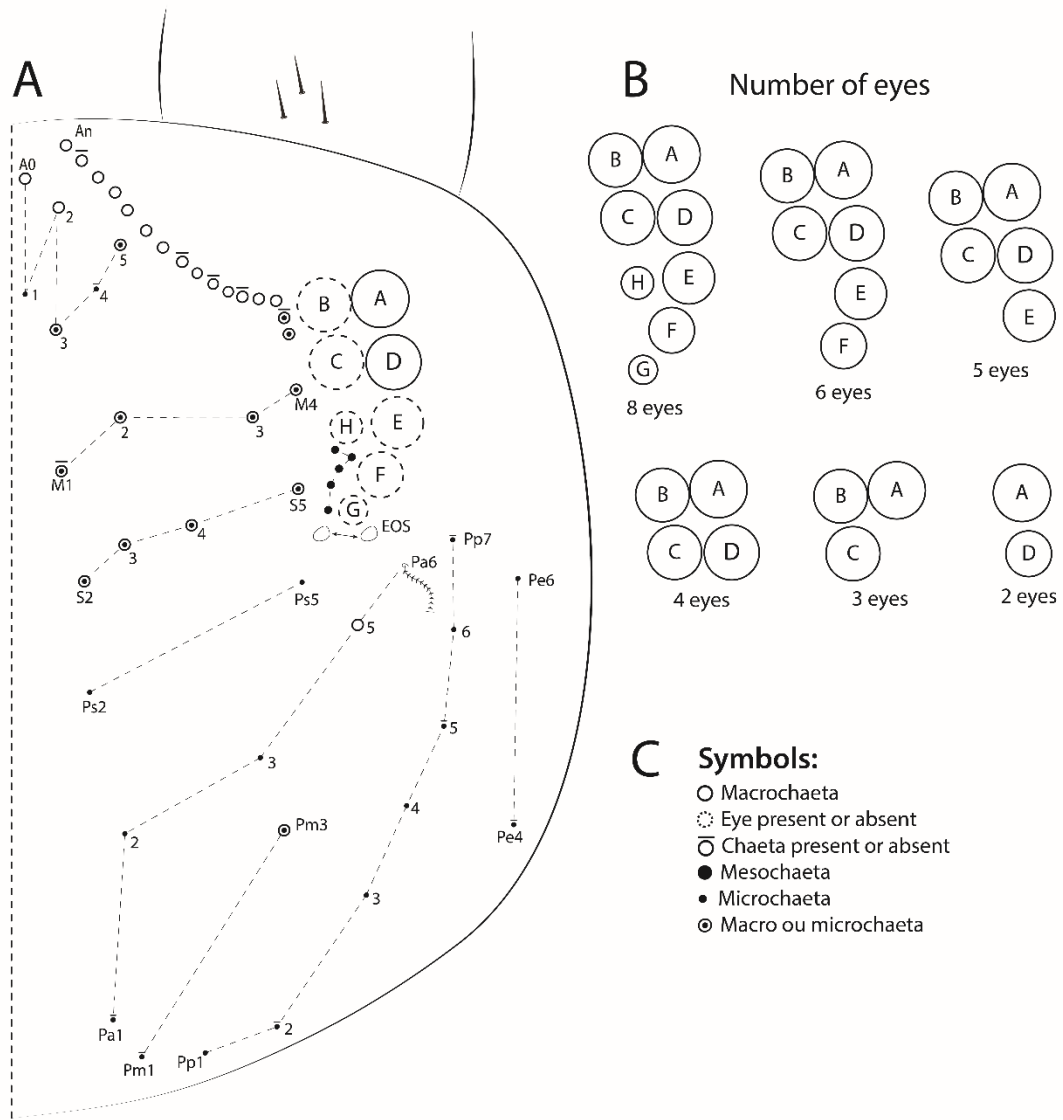


Figure 5.1. Dorsal head chaetotaxy of *Trogolaphysa* (A) and eyes homology (B); Symbols used to describe the chaetotaxy (C).

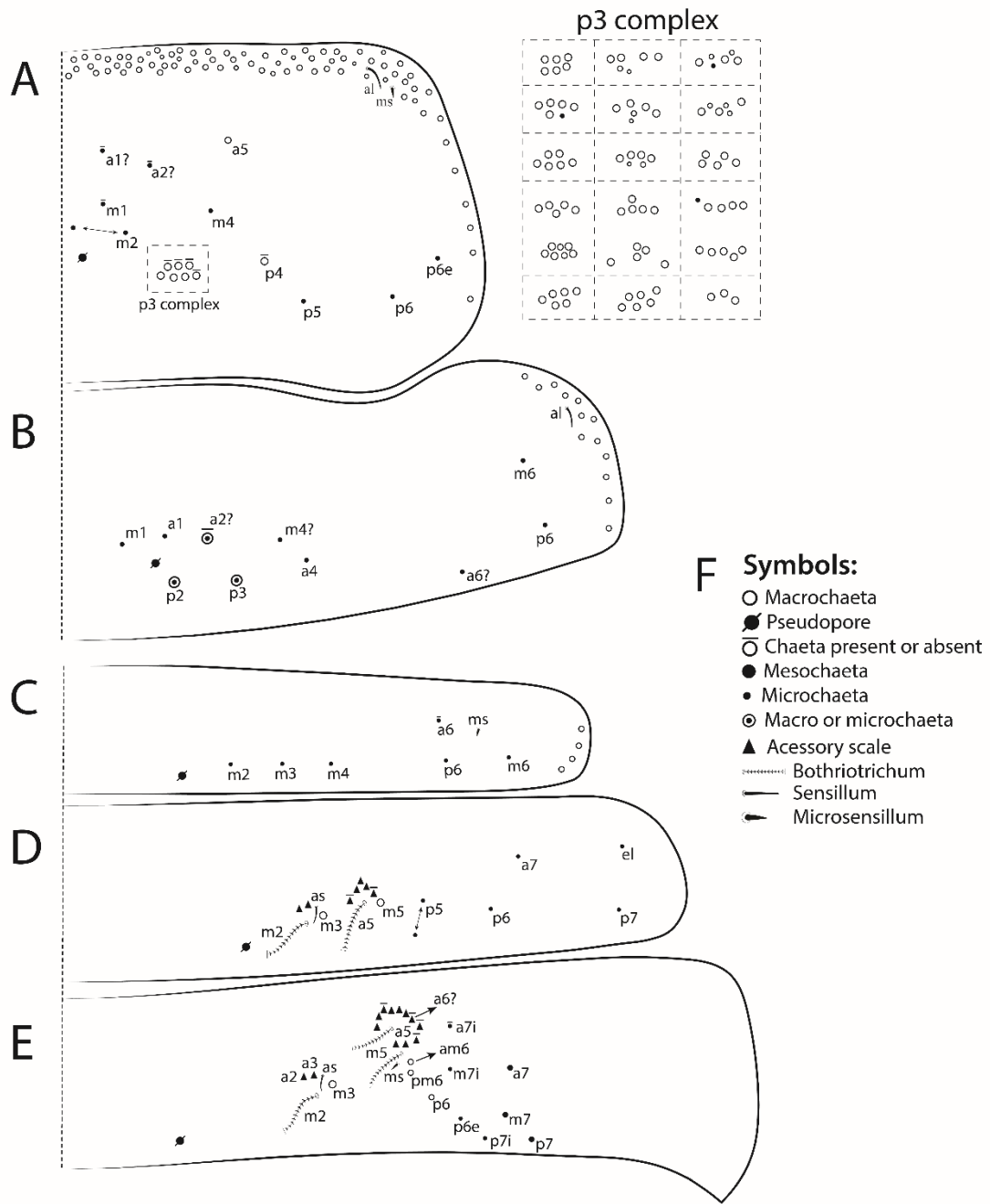


Figure 6.1. Dorsal trunk chaetotaxy. A, Th. II and p3 arrangements; B, Th. III; C, Abd. I; D, Abd. II; E, Abd. III; F, Symbols used to describe the chaetotaxy.

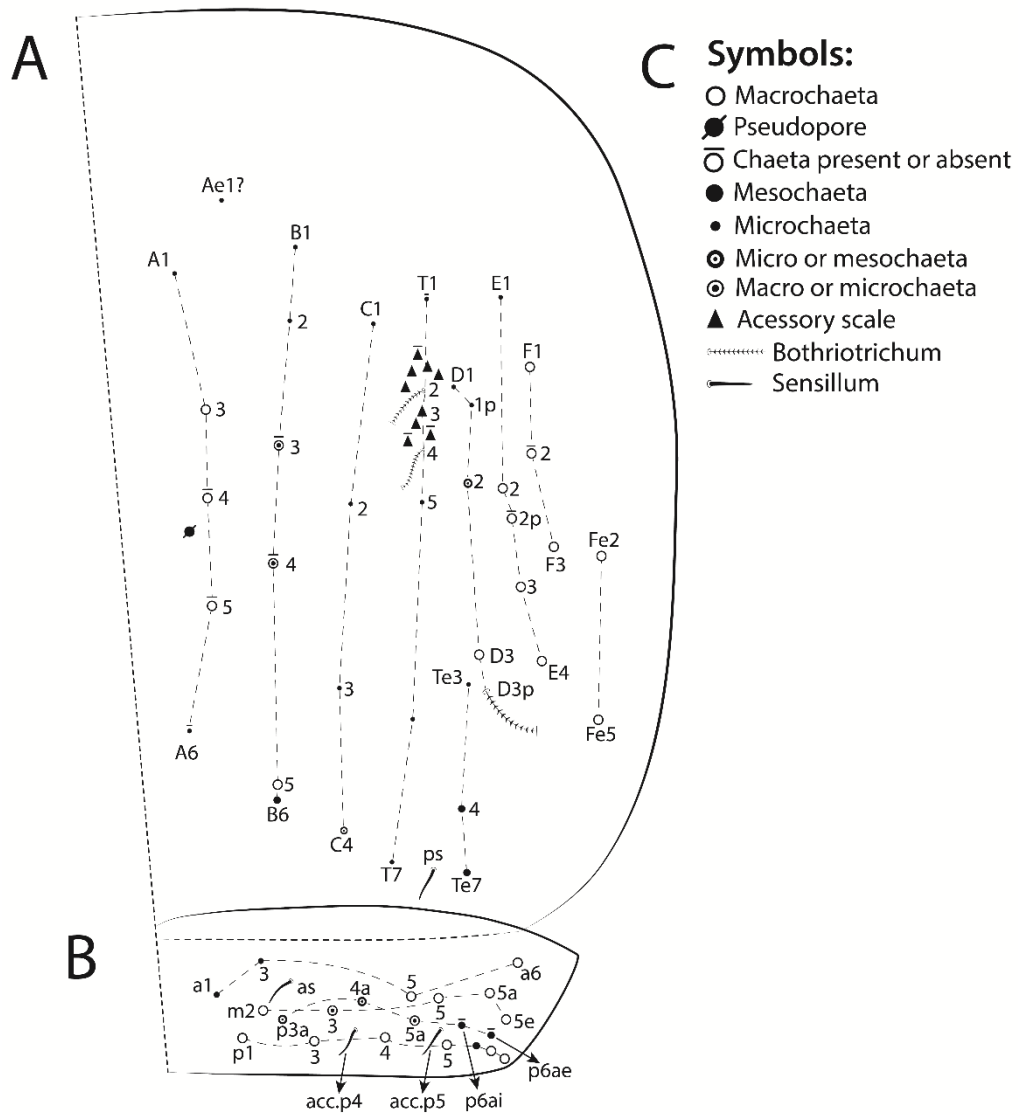


Figure 7.1. Dorsal trunk chaetotaxy. A, Abd. IV (regular sens omitted); B, Abd. V; C, Symbols used to describe the chaetotaxy.

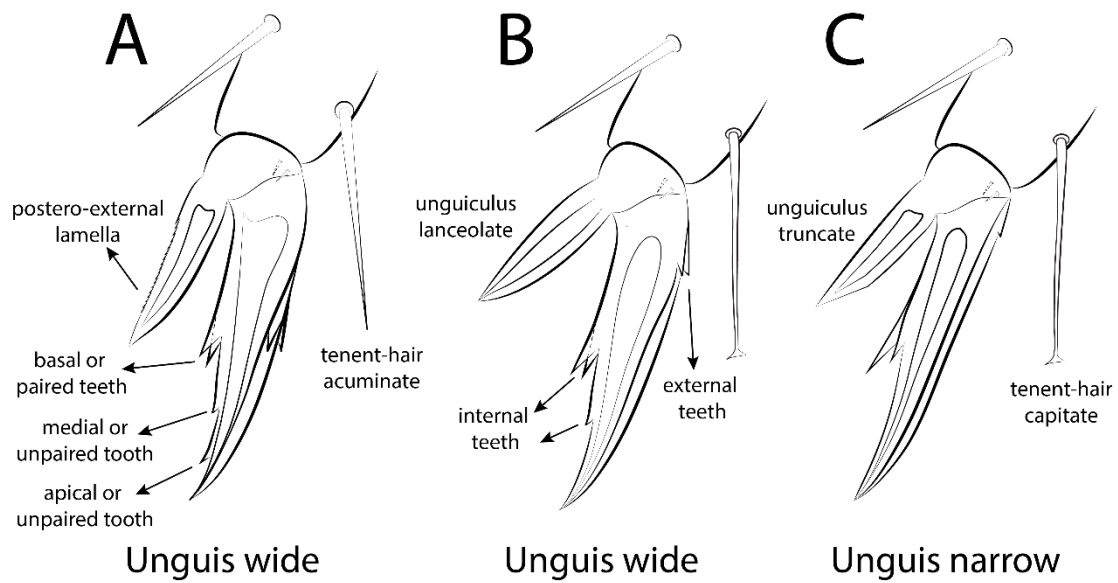


Figure 8.1. Morphology of the empodial complex in *Trogolaphysa*. A, Unguis wide with 4 internal and 2 external teeth, unguiculus lanceolate with postero-external lamella slightly serrate and tenent hair acuminate; B, Unguis wide with 3 internal and 2 external teeth, unguiculus lanceolate with postero-external lamella smooth and tenent hair capitate; C, Unguis narrow with 2 internal and 1 external teeth, unguiculus truncate with postero-external lamella smooth and tenent hair capitate.

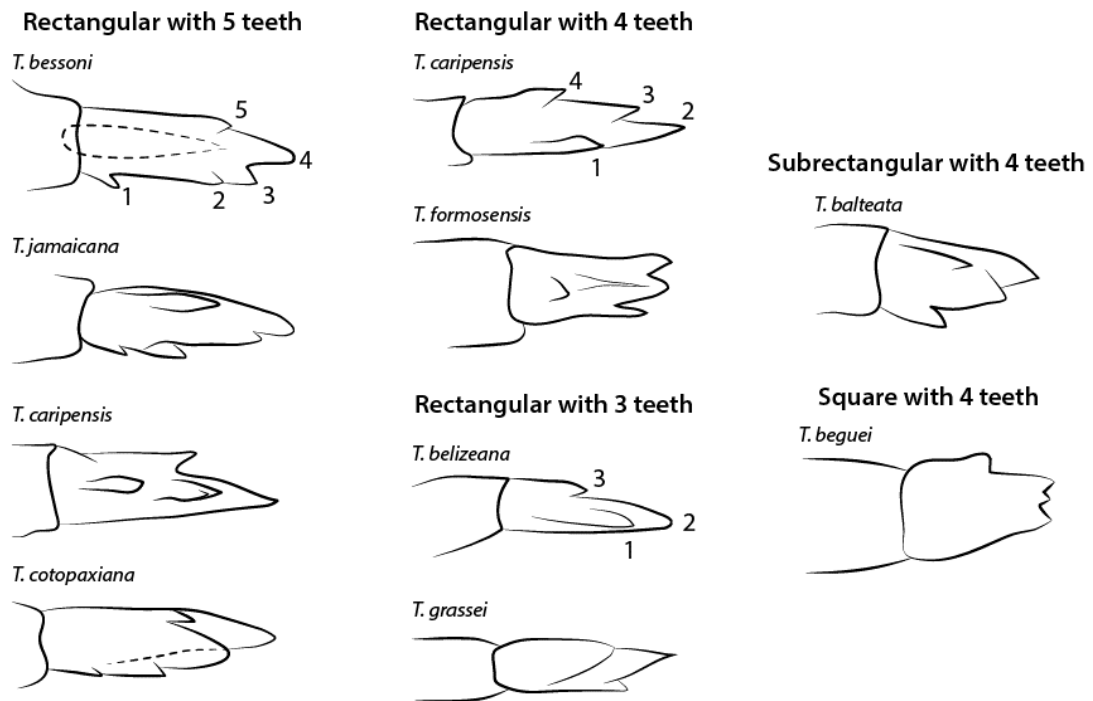


Figure 9.1. Different shapes and numbers of mucronal teeth in *Trogolaphysa* species.

3.4.1 Remarks on general morphology

About half of the *Trogolaphysa* species (25 species) have 6–8 eyes and 2–4 central mac on Abd. IV (internal rows **A** and **B**), and an average body size of 2.4 mm, with 1.5 to 3.1 mm size variation (Tab. 3.1–4.1). Almost all species with 6–8 eyes and 2–4 mac on Abd. IV has prelabral chaetae ciliate, only *T. palaciosi* has smooth chaetae (Soto-Adames 2015). Six species have distinctive labial formulae: *T. laterolineata*, *T. marielouiseae* and *T. piracurucaensis* share the formula **M1–3rEL1–2a1–5** (**M3** present or absent), while *T. stannardi* has **M1–4rEL1–2a1–5**, *T. giordanoae* has **M1–2REL1–2a1–5** and *T. delamarei* has **M1–2rEL1–2A1–5** (Nunes & Bellini 2018; Soto-Adames 2015; Soto-Taylor 2013); all other species present **M1–2rEL1–2a1–5** (Tab. 3.1–4.1). The labral spines are present in all species with 6–8 eyes, except in *T. subterranea* (Mari-Mutt 1987) (Tab. 3.1; Fig. 4.1G).

Despite the oligochaetotaxy seen in Paronellinae, *Trogolaphysa* could be partially distinguished by the macrochaetotaxy of dorsal head, thorax and Abd. IV (Fig. 5.1–7.1). The species with 6–8 eyes usually share the cephalic anterior chaetae **A0**, **A2**, **M2**, **S3**, **Ps5** and **Pm3** as mac (Tab. 3.1–4.1). Th. II frequently has chaeta **a5** as mac and 3–7 mac on **p3** complex (Fig. 6.1A). Often Th. III lacks mac, but when present, the species have 1–3 central mac. The **a6** mic on Abd. I is usually present among species with 6–8 eyes (Tab. 3.1–4.1). Most species with 6–8 eyes have 4 central mac on Abd. IV, only one species has 2 mac (*T. relictata* with **A3** and **B5**) (Soto-Adames 2015); and 10 to 11 species have 3 mac (Tab. 3.1–4.1). Species with 4 internal mac on Abd. IV usually have the chaetae **A3**, **A5**, **B4**, **B5**; species with 3 internal mac usually have **A4**, **A5**, **B5** or **A3**, **B4**, **B5** (Tab. 3.1–4.1). The **B4** and **B5** mac are present in all species with 6–8 eyes and 4 central mac on Abd. IV, and the set of mac in most of these species is **A3**, **A5**, **B4** and **B5**. Only two species differ, *T. riopedrensis* with **A4**, **A5**, **B4** and **B5** and *T. formosensis* with **A3**, **A4**, **B4** and **B5** (Tab. 4.1).

From 21 species described from caves, 11 species are blind or have 2 eyes (as *T. aelleni*), and in these species the apical tooth of unguis is usually absent and the tenent-hairs are reduced (Tab. 5.1). This condition probably indicates that cave *Trogolaphysa* have adaptive features to live in this kind of habitat, such as reduction of body pigmentation and eyes, elongated appendages and several types of sensilla on antennal segments. *Trogolaphysa* species from distant caves show similar morphologies, but troglomorphisms may result of convergent evolution. Christiansen (1961) demonstrated several characteristics of convergences and parallelism in the evolution of cave-

dependent Entomobryidae (Entomobryoidea). The adaptations for new cave dwellers, such as the modification of the empodial complex improves the locomotion on wet surfaces using the surface tension of the water (Christiansen 1961, 1965). The ungal elongation, reduction of the internal teeth and swollen base of unguiculus may represent the last stage of the adaptation to move in cave substrate (Fig. 10.1A–C). Such morphology is shown by *T. bessoni*, for instance (Fig. 10.1C). A synopsis of the main morphological features of all *Trogolaphysa* species is presented in Tables 3–6.

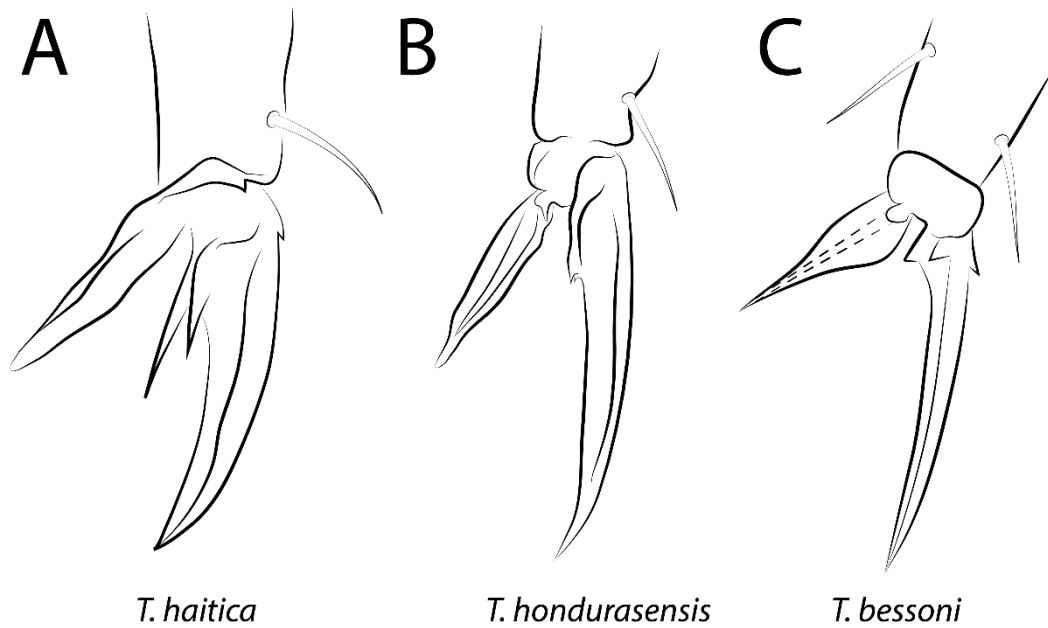


Figure 10.1. Troglomorphic empodial complex of three cave species of *Trogolaphysa*. A, unguis of *Trogolaphysa haitica* with 2 basal asymmetrical teeth and unguiculus lanceolate; B, unguis of *Trogolaphysa hondurasensis* with 2 minute basal symmetrical teeth and unguiculus lanceolate; C, the most troglomorphic unguis, *Trogolaphysa bessoni*, with 2 basal symmetrical teeth and unguiculus basally swollen, lanceolate.

Table 3.1 Main diagnostic features of *Trogolaphysa* species with 6–8 eyes and 2–3 mac on Abd. IV.

	<i>T. balteata</i>	<i>T. entretiosensis</i>	<i>T. geminata</i>	<i>T. jataca</i>	<i>T. luquillensis</i>	<i>T. marielouiseae</i>	<i>T. octosetosa</i>	<i>T. paracarpenleri</i>	<i>T. relicta</i>	<i>T. sauron</i>	<i>T. subterranea</i>
Body size	1.9	1.4	2.0	1.3-2.0	2.0	2.0	2.0	1.9	1.4	1.9	2.5
Ratio Ant/Head	2.6	?	?	1.5	?	1.9	2.1	2.9	1.6	?	?
Ant. IV annulations	?	?	An	An/ Sm	An	?	?	?	Sm	Sm	An
Prelabral chaetae	Ci	Ci	Ci	Ci	Ci	Ci	Ci	Ci	Ci	Ci	Ci
Labral Spines	+	+	+	+	+	+	+	+	+	+	–
Labial Formula	M1–2rEL1–2a1-5	M1–2rEL1–2a1-5	M1–2rEL1–2a1-5	M1–2rEL1–2a1-5	M1–2rEL1–2a1-5	M1–3rEL1–2a1-5	M1–2*rEL1–2a1-5	M1–2rEL1–2a1-5	M1–2rEL1–2a1-5	M1–2rEL1–2a1-5	M1–2rEL1–2a1-5
Eyes	6-8	8	6	6	6	6-8	6	8	6	8	6
Head dorsal mac	A0, A2, S3, Pa5, Pm3	A0, A2-3, S5, Pa5, Pm3	A0, A2, M2, S3, Pa5, Pm3	A0, A2, S3, S5, Pa5, Pm3	A0, A2, S5, Pa5, Pm3	A0, A2, S5, Pa5, Pm3	A0, A2, S5, Pa5, Pm3	A0, A2, Pa5, Pm3	A0, A2, Pa5, Pm3	A0, A2, Pa5, Pm3	A0, A2, Pa5, Pm3
Th. II mac	7	7	7	7	6	6	6	6	6	4	6
Th. III mac	0	0	0	0	0	0	3	0	0	0	0
Abd. I a6 mic	+	+	+	–	?	+	–	–	–	+	?
Ungues inner teeth	4	4	3-4	3-4	3	2-3	4	3	3-4	4	3
Unguiculi shape	L/T	L	L	L	L	L	L	L	L	T	L
Unguiculi lamella	Sm	Sm/Se	Se	Sm/Se	Sm	Sm	Sm	Sm/↓Se	Se (←)	Sm	Sm
Tenent-hair	Ca	Ca	Ca	Ac	Ac	Ac/Ca	Ca	Ca	Ca	Ca	Ca
Dens inner row	32-33	19	22	15-22	22	25-30	</=23	21	25	28-32	31

Dens outer row	21	15	22	15-22	22	16-24	</=19	17	25	20-23	31
Mucro shape	Sub	Rec	Sub	Sub	Sub	Sub	Sub	Sub	Rec	Sub	Rec
Mucro teeth	4	4	4	4-5	4	4	4	4	4	4	4
Habitat	Leaf mould	Leaf litter	Leaf litter	Leaf litter	Leaf litter	Leaf mould	Leaf mould	Leaf litter?	Cave	Leaf litter?	Cave
Type locality	Jamaica	Argentina	Puerto Rico	Puerto Rico	Puerto Rico	Mexico	Mexico	Mexico	Mexico	Martinique	Puerto Rico

Legend: +: Present; -: Absent; An: Annulated; Sm: Smooth; Ci: Ciliate; Se: Serrate; Ca: Capitate; Ac: Acuminate; Sy: Symmetrical; As: Asymmetrical; ↓: Weakly; /: or; ←: proximally; Rec: Rectangular; Sub: Subrectangular; L: Lanceolate; T: Truncate; </=: up to; ?: uncertain or lacking information. .

Table 4.1 Main diagnostic features of *Trogolophysa* species with 6–8 eyes and 4 mac on Abd. IV.

	<i>T. clarencei</i>	<i>T. cotopaxiana</i>	<i>T. dimorphica</i>	<i>T. ernesti</i>	<i>T. formosensis</i>	<i>T. giordanoae</i>	<i>T. judithmajtae</i>	<i>T. latereolineata</i>	<i>T. ocellata</i>	<i>T. palaciosi</i>	<i>T. piracurucaensis</i>	<i>T. quisqueyana</i>	<i>T. riopedrensis</i>	<i>T. stannardi</i>
Body size	3.0	1.5-1.7	2.3	2.5	1.4	2.1	2.3-2.6	2.1	2.1	2.3	2.2-2.6	2.2	1.5	2.6
Ratio Ant/Head	2.6	2.0	3.0	2.2	3.1	2-2.5	2.7	2.7	3.1	?	2.3	?	?	2.6
Ant. IV annulations	?	Sm	?	An	Sm	Sm	?	?	?	?	An	Sm	An	?
Prelabral chaetae	Ci	Ci	Ci	Ci	Ci	Ci	Ci	Ci	Ci	Sm	Ci	Ci	Ci	Ci
Labral Spines	-	-	+	+	-	+	-	+	+	-	+	+	+	+
Labial Formula	M1-2rEL1-2a1-5	M1-2rEL1-2a1-5	M1-2rEL1-2a1-5	M1-2rEL1-2a1-5	M1-2rEL1-2a1-5	M1-2REL1-2a1-5	M1-2rEL1-2a1-5	M1-3rEL1-2a1-5	M1-2rEL1-2a1-5	M1-2rEL1-2a1-5	M1-3**rEL1-2a1-5	M1-2rEL1-2a1-5	M1-2rEL1-2a1-5	M1-4rEL1-2a1-5
Eyes	6	8	6-8	8	8	6	8	6-8	8	8	8	8	6	6

Head dorsal mac	A0, A2, A3, M2, S3, Pa5, Pm3	A0, A2	A0*, A2*, A3, M2, S3, Pa5, Pm3	A0, A2, A3, M2, S3, S5, Pa5	A0, A2, M2, M4, S3, S5, Pa5	A0, A2, M2, Pa5, Pm3	A2, A3, A5, M2, S3, S4, S5, Pa5, Pm3	A0, A2, A3, M2, Pa5, Pm3	A0, A2, A3, M2, Pa5	A0, A2, Pa5, Pm3	A0, A2, A3, M2, S3, S4, S5, Pa5, Pm3	A0, A2, A3, M2, S3, S5, Pm3, Pa5	A0, (A2), A3, S3, S5, Pa5, Pm3	A0, A2, A3, M2, S3, S5, Pa5
Th. II mac	7	3	6-7	7	8	7	6-8	7	6-7	4	7	7	6	5-6
Th. III mac	3	0	3	0	3	3	0	0	0	1-2	0	0	0	2
Abd. I a6 mic	-	?	+	+	+	+	-	-	+	+	+	+/-	+	-
Ungues inner teeth	3	4	3	4	4	4	3-4	3-4	3-4	3-4	4	4	4	4
Unguiculi shape	L	L	L	L	T	L	L	L	L	↓T	L	L	L	L
Unguiculi lamella	Sm	Sm	Sm/Se	Se	Sm	Se	Sm	Sm	Sm	1 teeth	Sm/Se	Sm	Se(→)	Sm/Se
Tenent-hair	Ca	Ca	Ca	Ca	Ca	Ca	Ca	Ca	Ca	Ac	Ca	Ca	Ca	Ca
Dens inner row	30	1 row of spines with 20-24	24-30	23-30	+	35-42	</= 28	23	50	22-25	25-29	35-42	22	33
Dens outer row	24		18-23	21-27	+	25-28	</= 18	9	27	32-36	21-27	25-28	22	25
Mucro shape	Rec	Rec	Rec	Sub	Rec	Sub	Rec	Rec	Sub	Rec	Sub	Rec	Rec	Sub
Mucro teeth	4	4-5	4	4	4	4	4	4	4	4	4	4	4**	4
Habitat	?	?	Leaf mould	Leaf litter	Leaf litter	Cave	Soil of forests	Leaf litter	Leaf litter?	Cave	Leaf litter	Forest	Leaf litter?	Leaf mould
Type locality	Mexico	Ecuador	Mexico	Brazil	Brazil	Belize	Madagascar	Mexico	Mexico	Mexico	Brazil	Dominica n Republic	Puerto Rico	Mexico

Legend: +: Present; -: Absent; An: Annulated; Sm: Smooth; Ci: Ciliate; Se: Serrate; Ca: Capitate; Ac: Acuminate; ↓: Weakly; /: or; Red: Reduced; →: distally; Rec: Rectangular; Sub: Subrectangular; L: Lanceolate; T: Truncate; </=: up to; ?: uncertain or lacking information. *One individual with only 2 anterior mac: A0 and A2; ** One specimen with M3 present or absent; *** 4 main teeth with 2 smaller accessory teeth.

Table 5.1 Main diagnostic features of *Trogolaphysa* species with 0–3 eyes.

	<i>T. aelleni</i>	<i>T. belizeana</i>	<i>T. bessoni</i>	<i>T. caripensis</i>	<i>T. delamarei</i>	<i>T. ecutorca</i>	<i>T. haitica</i>	<i>T. jacobyi</i>	<i>T. marimutti</i>	<i>T. ozotolica</i>	<i>T. tijucana</i>	<i>T. trioculata</i>	<i>T. xtlokensis</i>
Body size	1.5	2.6	1.4	1.6-1.8	2.9	1.5	2.7	2.0	2.3	2.0	0.8	1.1	2.6
Ratio Ant/Head	2.4	4	2.7	3	3.7	2.3	2.3	5.8	2.5	3	1.4	0.83	2.5
Ant. IV annulations	An	Sm	An	One An	An	Sm	An	One An	Sm	An	Sm	?	An
Prelabral chaetae	Ci	Sm	Sm	?	?	Sm	Sm	Sm	Ci	Ci	?	Ci	Sm
Labral Spines	+	?	–	?	?	–	–	–	–	–	?	–	+
Labial Formula	M1-2rEL1-2a1-5	M1-2rEL1-2*a1-5	M1-2rEL112a1-5	M1-2rEL1-2a1-5	M1-2rEL1-2a1-5	M1-2rEL1-2a1-5	M1-2reL1-2a1-5	M1m2reL1-2a1-5	M1-2reL1-2a1-5	M1-2rEL1-2A1-5	?	M1-2rEL1-2a1-5	M1-2rel1-2a1-5
Eyes	2	0	0	0	0	0	0	0	0	0	2	3	0
Head dorsal mac	A0, A2	A0, A2-3, M2, S3, S5, Pa5, Pm3	?	A0, A2-3, M1-2, S2-3, S5, Pa5, Pm3	A0, A2, A5, M2, S2-3, Pa5, Pm3	?	?	A0, A2-3, M2, S3, S5, Pa5, Pm3	?	Pa5, Pm3	?	A0, A2, Pa5, Pm3	A0, A2, Pa5
Th. II mac	?	3-5	3	7	6	?	0	2-4	?	?	?	6	?
Th. III mac	?	3	0	0	0	?	0	1	?	?	?	0	?
Abd. I a6 mic	?	–	?	?	?	?	?	–	?	+	?	–	?
Abd. IV mac	?	A4, A5, B5	A5, B4, B5	A3, A5, B4, B5	A3, A5, B4, B5	?	0	A5, B4, B5	?	1?	?	A3, A5, B5	?
Ungues inner teeth	3	2	2	3	4	2	2	3	3	4	2	2	4
Unguiculi shape	L	L	Leaf-shaped	L	L	L	L	L	L	L	T	T**	L

Unguiculi lamella	Sm	Sm/Se	Sm	Sm	Sm	Sm**	Sm	Se (←)	Se (←)	↓Se	Sm	Sm	Se (→)
Tenent-hair	Ac	Ac, Red	Ac, Red	Ac	Ac	Ac, Red	Ac, Red	Ac	Ac, Red	Ac, Red	Ac	Ac	Ac, Red
Dens inner row	+	30	20	30-25	+	45	30-38	>/= 36	50	35-40	1 row of spines	15	41-69
Dens outer row	+	30	25	30-25	+	45	30-38	+	50	35-40		12	41-69
Mucro shape	Rec	Rec	Rec	Rec	Rec	Rec	Rec	Rec	Rec	Rec	Rec	Rec	Rec
Mucro teeth	4	3	4-5	4	4	5	4	3	4	4	4	4	4
Habitat	Cave	Cave	Cave	Cave	Cave	Cave	Cave	Cave	Cave	Cave	Leaf litter	Leaf mold	Cave
Type locality	Brazil	Belize	Ecuador	Venezuela	Cuba	Ecuador	Haiti	Belize	Mexico	Mexico	Brazil	Mexico	Mexico

Legend: +: Present; -: Absent; An: Annulated; Sm: Smooth; Ci: Ciliate; Se: Serrate; Ac: Acuminate; ↓: Weakly; /: or; Red: Reduced; →: distally; ←: proximally; Rec: Rectangular; L: Lanceolate; >/=: at least; One An: one incomplete annulation; ?: uncertain or lacking information. * L2 ciliate or smooth; ** unguiculus II with 3 small proximal teeth;

Table 6.1 Main diagnostic features of *Trogolaphysa* species with 4–8 eyes and absence of data on trunk chaetotaxy.

	<i>T. beguei</i>	<i>T. distiguenda</i>	<i>T. grassei</i>	<i>T. hondurasensis</i>	<i>T. jamaicana</i>	<i>T. minomaculata</i>	<i>T. nacionalica</i>	<i>T. penicillata</i>	<i>T. toroi</i>	<i>T. variabilis</i>	<i>T. vivieni</i>	<i>T. walgreni</i>	<i>T. yoshiii</i>
Body size	2	2.2	?	2.6	2.7	1.5	2.1	?	1.5	2.8	1.7	3	2.6
Ratio Ant/Head	2	2	?	?	2.3	1.9	1.6	?	2	2.7	2.7	?	2.3
Ant. IV annulations	?	Sm	?	?	An	Sm	An	Sm	An	An	An	An	An
Prelabral chaetae	?	?	?	Sm	Ci	?	Sm	?	Ci	Ci	?	Ci	Sm
Labral Spines	?	?	?	+	-	?	-	?	+	-	?	+	-

Labial Formula	?	?	?	M1-2rEL1-2a1-5	M1-2rEL1-2a1-5	M1EL1a1-2	M1-2rEL1-2a1-5	?	M1-2rEL1-2a1-5	M1-2reL12a1-5	M1-2rEa1-2	?	M1-2EL1-2a1-5
Eyes	8	?	8	4	6/8	8	6	8	6	4/8	8	8	6
Head dorsal mac	?	?	?	?	?	A0, A2, Ps5, Pm3	A3, A5, Pm3	?	?	?	A2, M2, S3, Pa5	A0, A2, A3, A5, M2, S3, S5, Pa5	?
Th. II mac	?	?	?	?	?	?	?	?	?	?	?	6	?
Th. III mac	?	?	?	?	?	?	?	?	?	?	?	0	?
Abd. I a6 mic	?	?	?	?	?	?	?	?	?	?	?	?	?
Abd. IV mac	?	?	?	?	?	?	?	?	?	?	?	?	?
Ungues inner teeth	3-4	4	3	2	3	3	3	4	4	4	3	3	3
Unguiculi shape	T	L	L	L	L	L	L	T	L	L	L	L	Blunt
Unguiculi lamella	Sm	Sm	Sm	Sm	Sm	Sm	Sm	Sm	Se (←)	Se (→)	↓Se	Sm	Se (←)
Tenent-hair	Ca	Ca	Ca	Ac, Red	Ac	Ca	Ac, Red	Ca	Ac	Ac, Red	Ca	Ca	Ac, Red
Dens inner row	+	15-25	+	30-38	34-38	19	29-34	*	40	31-39	13-32	1 row of spines	30-39 30-39
Dens outer row	+	10-20	+	30-38	34-38	14	29-34		40	31-39	13-32	13-32	
Mucro shape	Sqr/Sub	Rec	Rec	Rec	Rec	Rec	Rec	Rec	Rec	Rec	Rec	Rec	Rec
Mucro teeth	4	5	3	4	5	5	4	4	4	4	5	4	4
Habitat	Near termites	?	Leaf litter	Cave	Cave	Over mosses	Cave	?	Cave	Cave	?	?	Cave
Type locality	Ivory Coast	Costa Rica	Ivory Coast	Honduras	Jamaica	Gabon	Mexico	Cameroon	Mexico	Mexico	Gabon	Kenya	Mexico

Legend: +: Present; -: Absent; An: Annulated; Sm: Smooth; Ci: Ciliate; Se: Serrate; Ac: Acuminate; ↓: Weakly; /: or; Red: Reduced; →: distally; ←: proximally; Rec: Rectangular; L: Lanceolate; >/: at least; One An: one incomplete annulation; ?: uncertain/uncertain or lacking information. * 1 row with paintbrush-like structures; ** Unguiculi truncante basally swollen.

3.5 Habitat and Distribution

So far, *Trogolaphysa* species were found on leaf litter, over mosses, in soil of tropical forests, over and under rocks or associated to guano and food debris of birds in caves, and nearby or inside termite nests. Most of the 51 species with valid diagnoses were collected from leaf litter (15 species) or mould (6 species), while 22 species were found in subterranean environments. For example, *Trogolaphysa beguei* was found next to termites and *T. caripensis* in food debris of the cave bird *Steatornis caripensis* (Delamare-Deboutteville 1951; Gruia 1987).

Trogolaphysa is widely distributed in the Neotropical and Afrotropical Regions, and Nguyen & Soto-Adames (2018) proposed the origin of the taxon between 160 and 120 mya, with the diversification of the genera *Campylothorax* and *Trogolaphysa* taking place after the fragmentation of Gondwana in its Western and Eastern halves (Soto-Adames 2016). The central-eastern Neotropical and central-western Afrotropical region have in common the equatorial climate (A) with dry winter (w) (Kottek *et al.* 2006). Outside the Neotropical Region, *Trogolaphysa* species are mainly present in western Africa, where an equatorial climate (Aw) similar to the neotropics is found, while the northern and southern Africa are more arid with desert and steppe climates (BWh and BSh), which may have reduced the genus expansion into these areas.

3.6 Identification key to worldwide *Trogolaphysa* species*

1. Species with 0–3 eyes.....	2
1'. Species with 4–8 eyes	13
2. Species with 0–2 eyes.....	3
2'. Species with 3 eyes	<i>T. trioculata</i> Soto-Adames, 2015 (Mexico)
3. Species with 2 eyes.....	4
3'. Species without eyes	5
4. Ant. IV smooth	<i>T. tijucana</i> (Arlé & Guimarães, 1979) (Brazil)
4'. Ant. IV annulated	<i>T. aelleni</i> Yoshii, 1988 (Brazil)
5. Unguiculi lanceolate	6
5'. Unguiculi basally swollen (leaf-shaped)	<i>T. bessoni</i> Thibaud & Najt 1988 (Ecuador)
6. Less than four teeth on mucro	7

6'. Four or more teeth on mucro.....	8
7. Th. III with 3 central mac; Abd. IV with A4, A5 and B5 ... <i>T. jacobyi</i> Soto-Adames & Taylor 2013 (Belize)	
7'. Th. III with 1 central mac; Abd. IV with A5, B4 and B5 ... <i>T. belizeana</i> Palacios-Vargas & Thibaud 1997 (Belize)	
8. Unguiculi posterior lamella smooth	9
8'. Unguiculi posterior lamella serrate or weakly serrate.....	11
9. Labial formula M1–2rEL1–2a1–5	10
9'. Labial formula M1–2reL1–2a1–5 <i>T. haitica</i> (Palacios-Vargas, Ojeda & Christiansen, 1985) (Haiti)	
10. Dorsal head with 10 mac (A0, A2, A3, M1, M2, S2, S3, S5, Pa5, Pm3); Th. II with 7 mac (p3 complex plus a5); Ungues with 3 asymmetrical basal teeth... <i>T. caripensis</i> (Gruia, 1987) (Venezuela)	
10'. Dorsal head with 8 mac (A0, A2, A5, M2, S2, S3, Pa5, Pm3); Th. II with 6 mac (p3 complex plus a5); Ungues with 4 asymmetrical basal teeth..... <i>T. delamarei</i> (Massoud & Gruia 1973) (Cuba)	
11. Prelabral chaetae ciliate; labral spines absent.....	12
11'. Prelabral chaetae smooth; labral spines present..... <i>T. xtlokensis</i> (Palacios-Vargas, Ojeda & Christiansen, 1985) (Mexico)	
12. Labial formula M1–2reL1–2a1–5 <i>T. marimutti</i> (Palacios-Vargas, Ojeda & Christiansen, 1985) (Mexico)	
12'. Labial formula M1–2rEL1–2A1–5 <i>T. oztolica</i> (Ojeda & Palacios-Vargas, 1984) (Mexico)	
13. Species with 4 or 5 mucronal teeth.....	14
13'. Species with 3 mucronal teeth..... <i>T. grassei</i> (Delamare-Deboutteville, 1952) (Ivory Coast)	
14. Species with rectangular mucro.....	15
14'. Species with square or subrectangular mucro	37
15. Ungues with 3 or 4 internal teeth.....	16

15'. Ungues with 2 internal teeth... <i>T. hondurasensis</i> (Palacios-Vargas, Ojeda & Christiansen, 1985) (Honduras)	
16. Unguiculi truncate or weakly truncate.....	17
16'. Unguiculi lanceolate or blunt	19
17. Dens with 2 rows of spines.....	18
17'. Dens with 1 row of spines..... <i>T. penicillata</i> (Schött, 1927) (Cameroon, Ivory Coast and Gabon)	
18. Prelabral chaetae ciliate; 6–7 dorsal mac (A0, A2, M2, M4**, S3, S5 and Pa5); mesothorax shorter than metathorax in the midline; Th. II with 8 mac (a5, p4 plus p3 complex).....	<i>T. formosensis</i> Silva & Bellini, 2015 (Brazil)
18'. Prelabral chaetae smooth; 4 dorsal mac (A0, A2, Pa5, Pm3); mesothorax longer than metathorax in the midline; Th. II with 4 mac (a5 plus p3 complex).....	<i>T. palaciosi</i> Soto-Adames, 2015 (Mexico)
19. Unguiculi lanceolate	20
19'. Unguiculi blunt..... <i>T. yoshii</i> (Palacios-Vargas, Ojeda & Christiansen, 1985) (Mexico)	
20. Species with 1 row of dental spines.....	21
20'. Species with 2 row of dental spines	22
21. Ungues with 4 internal teeth; 2 anterior labral spines absent; Th. II with 3 mac (p3 complex); Abd. IV with 3 central mac.....	<i>T. cotopaxiana</i> Thibaud & Najt, 1988 (Ecuador)
21'. Ungues with 3 internal teeth; 2 anterior labral spines present; Th. II with 6 mac (p3 complex); Abd. IV with 6 central mac	<i>T. wahgreni</i> (Mitra, 2002b) (Kenya)
22. Mucro with 5 teeth.....	23
22'. Mucro with 4 teeth	26
23. Ungues wide with 3 internal teeth	24
23'. Ungues narrow with 4 internal teeth.....	<i>T. distiguenda</i> (Denis, 1931) (Costa Rica)
24. Ant. IV annulated	25

24'. Ant. IV smooth.....	<i>T. monomaculata</i> (Barra, 1969) (Gabon)	
25. Unguiculli postero-lamella smooth; tenent hair acuminate; 6 or 8 eyes; specimens with pigmented antennae and body lacking pigments.....	<i>T. jamaicana</i> (Palacios-Vargas, Ojeda & Christiansen, 1985) (Jamaica)	
25'. Unguiculli postero-lamella weakly serrate; tenent hair capitate; 8 eyes; specimens pale with pigmented antennae and body.....	<i>T. vivieni</i> (Barra, 1969) (Gabon)	
26. Prelabral chaetae ciliate		27
26'. Prelabral chaetae smooth.....	<i>T. nacionalica</i> (Palacios-Vargas, Ojeda & Christiansen, 1985) (Mexico)	
27. Labial formula M1-2rEL1-2a1-5 or M1-3rEL1-2a1-5		28
27'. Labial formula M1-2reL1-2a1-5.....	<i>T. variabilis</i> (Palacios-Vargas, Ojeda & Christiansen, 1985) (Mexico)	
28. Labial formula M1-2rEL1-2a1-5		29
28'. Labial formula M1-3rEL1-2a1-5	<i>T. laterolineata</i> Soto-Adames, 2015 (Mexico)	
29. Labral spines absent.....		30
29'. Labral spines present.....		32
30. Abd. IV with 4 central mac (A3, A5, B4, B5).....		31
30'. Abd. IV with 3 central mac (A3, A5, B5)	<i>T. subterranea</i> (Mari-Mutt, 1987) (Puerto Rico)	
31. Six eyes; dorsal head with 7 mac (A0, A2, A3, M2, S3, Pa5 and Pm3); Th. III with 3 mac (a2?, p2-3).....	<i>T. clarencei</i> Soto-Adames, 2015 (Mexico)	
31'. Eight eyes; dorsal head with 8 mac (A2, A3, A5, M2, S3, S4, Pa5 and Pm3); Th. III lacking mac.....	<i>T. judithnajtae</i> Nguyen & Soto-Adames, 2018 (Madagascar)	
32. Th. III lacking mac		33
32'. Th. III with 3 mac (a2?, p2-3	<i>T. dimorphica</i> Soto-Adames, 2015 (Mexico)	
33. Species with 6 eyes.....		34
33'. Species with 8 eyes	<i>T. entreriosensis</i> Soto-Adames, 2015 (Argentina)	

34. Tenent hair capitate	35
34'. Tenent hair acuminate.....	<i>T. toroi</i> (Palacios-Vargas, Ojeda & Christiansen, 1985) (Mexico)
35. Abd. IV with 4 central mac (A3 or A4, A5, B4 and B5).....	36
35'. Abd. IV with 2 central mac (A3, B5).....	<i>T. relictata</i> (Palacios-Vargas, Ojeda & Christiansen, 1985) (Mexico)
36. Th. II with 8 mac (A0, A2, A3, M2, S3, S5, Pm3, Pa5); Abd. IV with 4 central mac (A3, A5, B4, B5); unguiculli postero-external lamellae smooth.....	<i>T. quisqueyana</i> Soto-Adames, Jordana & Baquero, 2014 (Dominican Republic)
36'. Th. II with 6–7 mac (A0, (A2), A3, S3, S5, Pa5, Pm3); Abd. IV with 4 central mac (A4, A5, B4, B5); unguiculli postero-external lamellae serrate (distally)	<i>T. riopedrensis</i> (Mari-Mutt, 1987) (Puerto Rico)
35. Abd. IV with 4 central mac (A3 or A4, A5, B4 and B5).....	36
35'. Abd. IV with 2 central mac (A3, B5)...	<i>T. relictata</i> (Palacios-Vargas, Ojeda & Christiansen, 1985) (Mexico)
36. Th. II with 8 mac (A0, A2, A3, M2, S3, S5, Pm3, Pa5); Abd. IV with 4 central mac (A3, A5, B4, B5); unguiculli postero-external lamellae smooth.....	<i>T. quisqueyana</i> Soto-Adames, Jordana & Baquero, 2014 (Dominican Republic)
36'. Th. II with 6–7 mac (A0, (A2), A3, S3, S5, Pa5, Pm3); Abd. IV with 4 central mac (A4, A5, B4, B5); unguiculli postero-external lamellae serrate (distally).....	<i>T. riopedrensis</i> (Mari-Mutt, 1987) (Puerto Rico)
37. Unguiculi truncate	38
37'. Unguiculi lanceolate.....	39
38. Ungues with 2 asymmetrical basal teeth.....	<i>T. sauron</i> Soto-Adames, Jordana & Baquero, 2014 (Martinique)
38'. Ungues with 2 symmetrical basal teeth.....	<i>T. beguei</i> (Delamare- Deboutteville, 1951) (Ivory Coast)
39. Th. III with 3 or 2 mac.....	40
39'. Th. III lacking mac	42
40. Th. III with 3 mac	41

40'. Th. III with 2 mac (p2, p3)	<i>T. stannardi</i> Soto-Adames 2015 (Mexico)
41. Dorsal head with 5 mac (A0, A2, M2, Pa5, Pm3); Abd. I with a6 mic; Abd. IV with central 4 mac (A3, A5, B4, B5).....	<i>T. giordanoae</i> (Soto-Adames & Taylor 2013) (Belize)
41'. Dorsal head with 4 mac (A0, A2, Pa5, Pm3); Abd. I lacking a6 mic; Abd. IV with 3 central mac (A3, A5, B5).....	<i>T. octosetosa</i> Soto-Adames, 2015 (Mexico)
42. Abd. IV with 4 central mac	43
42'. Abd. IV with 3 central mac	45
43. More than 5 dorsal head mac.....	44
43'. Five dorsal head mac (A0, A2, A3, M2, Pa5)... <i>T. ocellata</i> Soto-Adames, 2015 (Mexico)	
44. Dorsal head with 7 mac (A0, A2, A3, M2, S3, S5, Pa5); labial formula M1–2rEL1–2a1–5 ; trochanteral organ with 49 spines.....	<i>T. ernesti</i> Cipola & Bellini, 2017 (Brazil)
44'. Dorsal head with 9 (A0, A2, A3, M2, S3, S4, S5, Pa5, Pm3); labial formula M1–3rEL1–2a1–5*** ; trochanteral organ with 35–40 spines... <i>T. piracurucaensis</i> Nunes & Bellini, 2018 (Brazil)	
45. Abd. IV with A3, A5 and B5	46
45'. Abd. IV with A4, A5 and B5	48
46. Labial formula M1–2rEL1–2a1–5	47
46'. Labial formula M1–3rEL1–2a1–5 ... <i>T. marielouiseae</i> Soto-Adames, 2015 (Mexico)	
47. Dorsal head mac with A0, A2, S3, Pa5 and Pm3 ; Th. II with 7 mac (a5, p3 complex); Abd. I with a6 mic.....	<i>T. balteata</i> Soto-Adames, 2015 (Jamaica)
47'. Dorsal head mac with A0, A2, Pa5 and Pm3 ; Th. II with 6 mac (a5, p3 complex); Abd. I lacking a6 mic	<i>T. paracarpenteri</i> Soto-Adames, 2015 (Mexico)
48. Th. II with 7 mac (a5, p3 complex).....	49
48'. Th. II with 6 mac (a5, p3 complex)... <i>T. luquillensis</i> (Mari-Mutt, 1987) (Puerto Rico)	

49. Dorsal head mac **A0**, **A2**, **M2**, **S3**, **Pa5** and **Pm3**; Abd. I with **a6** mic; Tenent hair capitate.....*T. geminata* (Mari-Mutt, 1987) (Puerto Rico)
- 49'. Dorsal head mac **A0**, **A2**, **S3**, **S5**, **Pa5** and **Pm3**; Abd. I lacking **a6** mic; Tenent hair acuminate..... *T. jataca* (Wray, 1953) (Puerto Rico and Jamaica)

* *Species inquirendae* were omitted from the key.

Dorsal head chaetae **M4 of *T. nacionalica* can be mac or mes.

***Chaeta **M3** of the labial formula of *T. piracurucaensis* can be present or absent.

4 Conclusions

In this study, we indicated 14 *species inquirendae*, which makes it evident the need for a redescription of several species using approaches based on the most recent taxonomy of Entomobryoidea and methods combining morphology, distribution and, if possible, molecular data (integrative taxonomy). Such methods should be applied mainly in complex of species to make clearer the identities of these taxa. We hope that this revision and compilation of the taxonomic data of *Trogolaphysa* will help to better understand the morphological patterns in the group, which can favor a better estimate of the number of species in a protected area, facilitate new species descriptions and other comparative studies within the genus and among the Paronellinae.

5 References

- Arlé, R. (1939) Collemboles nouveaux de Rio de Janeiro.
- Arlé, R. & Guimarães, A.É. (1979) Nova espécie do gênero *Paronella* Schött, 1893 do Rio de Janeiro (Collembola). *Revista Brasileira de Entomologia* 23, 213–217.
- Barra, J.-A. (1969) Collemboles du Gabon. *Biologia Gabonica* 5, 189–216.
- Bellini, B.C. & Cipola, N.G. (2017) The Neotropical genera of Paronellinae (Collembola, Entomobryoidea, Paronellidae) with description of two new species and redescription of *Campylothorax mitrai*. *Zootaxa* 4300, 151. <https://doi.org/10.11646/zootaxa.4300.2.1>
- Bonet, F. (1931) Estudios sobre los Colémbolos cavernícolas con especial referencia a los de la fauna española. *Memorias de la Sociedad Española de Historia Natural* 14, 362–365.

- Börner, C. (1903) Über neue Altweltliche Collembolen, nebst Bemerkungen zur Systematik der Isotominen und Entomobryinen. *Gesellschaft naturforschender Freunde*, 129–182.
- Börner, C. (1906) Das System der Collembolen nebst Beschreibung neuer Collembolen des Hamburger Naturhistorischen Museums. *Mitteilungen aus dem Naturhistorischen Museum* 23, 147–188.
- Börner, C. (1913) Die Familien der Collembolen. *Zoologischer Anzeiger* 41, 315–322.
- Bourlet, A. (1839) Mémoire sur les Podures. *Mémoires de la Société des Sciences de l'Agriculture de Lille* 1, 377–417.
- Carpenter, G.H. (1917) Zoological results of the Abor Expedition 1911–12: Collembola. *Records of the Indian Museum* 8, 561–568.
- Cassagnau, P. (1963) Collemboles D'amérique du Sud.
- Cipola, N.G., De Morais, J.W. & Bellini, B.C. (2014) Two new species of Seira Lubbock (Collembola, Entomobryidae, Seirini) from South Brazil. *Zootaxa*. <https://doi.org/10.11646/zootaxa.3793.1.7>
- Deharveng, L., Jantarit, S. & Bedos, A. (2018) Revisiting *Lepidonella* Yosii (Collembola: Paronellidae): character overview, checklist of world species and reassessment of *Pseudoparonella doveri* Carpenter. *Annales de la Societe Entomologique de France* 54, 381–400. <https://doi.org/10.1080/00379271.2018.1507687>
- Delamare Deboutteville, C. (1950) Deux nouvelles espèces de collemboles du Mont Nimba (Guinée Française) récoltées par M. Maxime Lamotte. *Extrait du Bulletin de la Société Zoologique de France* 1, 43–45.
- Delamare Deboutteville, C. (1951) Nouveaux Paronelliens de la Côte-d'Ivoire. *Bulletin Inst.Française d'Afrique Noire* 13, 1072–1075.
- Delamare Deboutteville, C. (1952) Trois nouvelles espèces de collemboles de la Côte D'Ivoire. *Revue Française d'Entomologie* 19, 240–243.
- Denis, J.R. (1925) Sur le Collemboles du Museum de Paris (2er Partie). *Annales de la Société Entomologique de France* 93, 261–290.
- Denis, J.R. (1931) Collemboles de Costa Rica avec une contribution au species de l'ordre. *Bollettino del Laboratorio di zoologia generale e agraria della R. Scuola superiore d'agricoltura in Portici* 23, 69–170.
- Denis, J.R. (1933) Bollettino del Laboratorio di Zoologia Generale e Agraria. *Bollettino del Laboratorio di Zoologia Generale e Agraria*, Portici XXV, 222–322.
- Fjellberg, A. (1999) The Labial Palp in Collembola. *Zoologischer Anzeiger*.

- Gisin, H. (1967) Espèces nouvelles et lignées évolutives de *Pseudosinella* endogés. *Memórias e Estudos do Museu Zoológico da Universidade de Coimbra* 301, 5–25.
- Gruia, M.M. (1987) Deux nouvelles espèces de Collembola du Venezuela. Fauna hipógea y hemiedáfica de Venezuela. *Ed.Acad.Rep.Social. Romania Bucaresti*, 151-.
- Handschin, E. (1924) Neue myrmecophile und termitophile Collembolenformen aus Süd-Amerika. *Neue Beiträge zur systematischen Insektenkunde* 3, 13–28.
- ICZN – International Commission on Zoological Nomenclature. (2021) International Code of Zoological Nomenclature. Available online at <https://www.iczn.org/>, accessed in 07 April 2021.
- Jantarit, S., Satasook, C. & Deharveng, L. (2013) The genus *Cyphoderopsis* Carpenter (Collembola: Paronellidae) in Thailand and a faunal transition at the Isthmus of Kra in Troglopedetinae. *Zootaxa* 3721, 49–70. <https://doi.org/10.11646/zootaxa.3721.1.2>
- Jantarit, S., Satasook, C. & Deharveng, L. (2014) *Cyphoderus* (Cyphoderidae) as a major component of collembolan cave fauna in Thailand, with description of two new species. *ZooKeys* 368, 1–21. <https://doi.org/10.3897/zookeys.368.6393>
- Jantarit, S., Surakhamhaeng, K. & Deharveng, L. (2020) The multiformity of antennal chaetae in *Troglopedetes* Joseph, 1872 (Collembola, Paronellidae, Troglopedetinae), with descriptions of two new species from Thailand. *ZooKeys* 2020, 1–40. <https://doi.org/10.3897/zookeys.987.54234>
- Joseph, G. (1872) Beobachtungen über die Lebensweise und Vorkommen den in den Krainer Gebirgsgrotten einheimischen Arten der blinden Gattungen Machaerites, Leptodirus, Oryotus und Troglorrhynchus. *Jahres-Bericht der Schlesischen Gesellschaft für Vaterländische Cultur* 49, 171–182.
- Kottek, M., Grieser, J., Beck, C., Rudolf, B. & Rubel, F. (2006) World map of the Köppen-Geiger climate classification updated. *Meteorologische Zeitschrift* 15, 259–263. <https://doi.org/10.1127/0941-2948/2006/0130>
- Mari-Mutt, J.A.. (1986) Puerto Rican species of *Lepidocyrtus* and *Pseudosinella* (Collembola: Entomobryidae). *Caribbean Journal of Science* 22, 43–47.
- Mari-Mutt, J.A. (1979) A revision of the genus *Dicranocentrus* Schött (Insecta: Collembola: Entomobryidae). *Agricultural Experiment Station Bulletin* 259, 1–79.
- Mari-Mutt, J.A. (1987) Puerto Rican Species of Paronellidae (Insecta: Collembola). *Caribbean Journal of Science* 23, 400–416.
- Marlier, G. (1945) Collemboles du Congo belge. *Revue de zoologie et de botanique africaines* 38, 252–264.

- Massoud, Z. & Gruia, M.M. (1973) Collemboles Arthropléones de Cuba récoltés en par la mission cubano-roumaine. In: *Résultat des expéditions biospéologiques cubano-roumaines à Cuba*. pp. 327–343.
- Mendonça, M.C. de (1981) Contribuição para o conhecimento de Collembola Entomobryomorpha (Insecta) do Parque Nacional da Tijuca, Rio de Janeiro, Brasil.
- Mills, H.B. (1938) Collembola from Yucatan Caves. In: *Fauna of the caves of Yucatan*, 183–190.
- Mitra, S.K. (1992) Fixation of the concept of *Paronella* Schött, 1893 [Collembola: Entomobryidae]. *Records of the Zoological Survey of India* 92, 211–224.
- Mitra, S.K. (2002a) Resuscitation of *Trichorypha* Schott 1893 (Collembola: Entomobryidae). *Records of the Zoological Survey of India* 100, 99–104.
- Mitra, S.K. (2002b) Status of *Dicranocentruga* Wray, 1953 With the Description of a New Species (Collembola : Entomobryidae). *Records Zoological Survey of India* 100, 105–116.
- Mitra, S.K. (2003) On *Lepidonella* Yosii, 1960 and *Bromacanthus* Schött, 1925 complex (Collembola : Entomobryidae : Paronellinae). *Records Zoological Survey of India* 101, 67–86.
- Mitra, S.K. & Dallai, R. (1980) Studies of the Genus *Campylothorax* Schött, 1893 (Collembola Entomobryidae Paronellinae) with the description of a new species from Zaire. *Monitore Zoologico Italiano. Supplemento* 13, 273–321. <https://doi.org/10.1080/00269786.1980.11758554>
- Nguyen, M. & Soto-Adames, F.N. (2018) Annotated checklist of Afrotropical *Trogolaphysa* Mills, 1938 (Hexapoda: Collembola: Paronellidae) and description of a new species from Madagascar. *Zoosystema* 40, 179–196. <https://doi.org/10.5252/zoosystema2018v40a10>
- Nicolet, H. (1842) Recherches pour servir à l’Histoire des Podurelles. *Nouveaux Mémoires de la Société helvétique des Sciences naturelles* 6, 1-88.
- Nunes, R.C. & Bellini, B.C. (2018) Three new species of Entomobryoidea (Collembola: Entomobryomorpha) from Brazilian Caatinga-Cerrado transition, with identification keys to Brazilian *Cyphoderus*, *Pseudosinella* and *Trogolaphysa* species. *Zootaxa* 4420, 71. <https://doi.org/10.11646/zootaxa.4420.1.4>
- Ojeda, M. & Palacios-Vargas, J.G. (1984) A new species of *Troglopedetes* (Collembola: Paronellidae) from Guerrero, Mexico. *Entomological news* 95, 16–20.

- Palacios-Vargas, J., Ojeda, M. & Christiansen, K. (1985) Taxonomía y biogeografía de *Troglopedetes* (Collembola: Paronellidae) en América, con énfasis en las especies cavernícolas. *Folia entomologica mexicana*, 3–35.
- Palacios-Vargas, J.G. & Thibaud, J.M. (1997) New cave Collembola from Mexico and Belize. *Southwestern Entomologist* 22, 323–329.
- Schäffer, C. (1897) Apterygoten. *Hamburger Magalhaensische Sammelreise*, 1–48.
- Schott, H. (1925) Collembola from Mount Murud and Mount Dulit in Northern Sarawak. *Sarawak Museum Journal* 3, 107–127.
- Schött, H. (1893) Beiträge zur Kenntnis der Insektenfauna von Kamerun. I. Collembola. *Bihang till Kongliga Svenska Vetenskaps, Akademien Handlingar* 19, 1–28.
- Schött, H. (1903) Über zwei Gattungen der apterygoten Insecten. Redogörelse, für Allmanna Laroverken I. Linköping. *Ekso och Vadstena. Underlasaret*, 3–16.
- Schött, H. (1927) Kamerunische Collembolen. *Medd. Linköpings Högre Allmänna Läroverk redogörelse*, 1–39.
- Silva, D.D. & Bellini, B.C., da Silva, D.D. & Bellini, B.C. (2015) *Trogolaphysa formosensis* sp. nov. (Collembola: Paronellidae) from Atlantic Forest, Northeast Region of Brazil. *Zoologia* 32, 53–58. <https://doi.org/10.1590/S1984-46702015000100008>
- Soto-Adames, F. (2008) Postembryonic development of the dorsal chaetotaxy in *Seira dowlingi* (Collembola, Entomobryidae); with an analysis of the diagnostic and phylogenetic significance of primary chaetotaxy in *Seira*. *Zootaxa* 1683, 1–31. <https://doi.org/10.5281/zenodo.180444>
- Soto-Adames, F.N. (2015) The dorsal chaetotaxy of first instar *Trogolaphysa jataca*, with description of twelve new species of Neotropical *Trogolaphysa* (Hexapoda: Collembola: Paronellidae). *Zootaxa* 4032, 1–41. <https://doi.org/10.11646/zootaxa.4032.1.1>
- Soto-Adames, F.N., Jordana, R. & Baquero, E. (2014) Comparative analysis of the dorsal chaetotaxy of *Troglopedetes*, *Trogolaphysa*, and *Campylothorax* supports the synonymization of tribes Paronellini and Troglopedetini (Collembola: Paronellidae). *Journal of Insect Science* 14, 278–278. <https://doi.org/10.1093/jisesa/ieu140>
- Soto-Adames, F.N. & Taylor, S.J. (2013) The dorsal chaetotaxy of *Trogolaphysa* (Collembola, Paronellidae), with descriptions of two new species from caves in Belize. *ZooKeys* 323, 35–74. <https://doi.org/10.3897/zookeys.323.4950>

- Szeptycki, A. (1979) Chaetotaxy of the Entomobryidae and its phylogenetical significance - Morpho-systematic studies on Collembola IV. *Polska Akademia Nauk, Zakład Zoologii Systematycznej i Doświadczalnej* 4, 213.
- Thibaud, J. & Najt, J. (1988) Collemboles (Insecta) de l'Équateur IV. Paronellidae avec rérision de quatre genres. *Bull. Mus. natn. Hist. nat.* 10, 719–730.
- Wahlgren, E. (1908) Wissensh Ergebn. der Schwed. Zoolog. Exped. nach dem Kilimandjaro dem Meru, 1905-1906. Unter Leitung von Prof. Ygve Sjöstedt. *Apterygogenea I. Collembola*, pt. I 18, 1–10.
- Wilson, J.M. (1982) A review of world Troglopedetini (Insecta, Collembola, Paronellidae) including an identification table and descriptions of new species. *Cave Science - Transactions British Cave Research Association* 9, 210–226.
- Womersley, H. (1934) A preliminary account of the Collembola — Arthropleona of Australia II (Entomobryoidea). *Transactions of the Royal Society of South Australia* 58, 86–138.
- Wray, D.L. (1953) New Collembola from Puerto Rico. *The Journal of Agriculture of the University of Puerto Rico* 37, 140–150.
- Yoshii, R. (1988) Paronellid Collembola from caves of Central and South America collected by P. Strinati. *Revue Suisse de Zoologie* 95, 449–459. <https://doi.org/10.5962/bhl.part.82022>
- Yosii, R. (1960) On some Collembola of New Caledonia, New Britain and Solomon Islands. *Bulletin of the Osaka Museum of Natural History* 12, 9–38.
- Zeppelini, D. & Oliveira, J.V.L.C. (2016) Chaetotaxy of Neotropical *Cyphoderus caetetus* sp. nov. with comments on the taxonomic position of Cyphoderinae within Paronellidae (Collembola, Entomobryoidea). *Zootaxa* 4098, 560–570. <https://doi.org/10.11646/zootaxa.4098.3.8>
- Zhang, F., Bellini, B.C. & Soto-adames, F.N. (2019) New insights into the systematics of Entomobryoidea (Collembola: Entomobryomorpha): first instar chaetotaxy, homology and classification. *Zoological Systematics* 44, 249–278. <https://doi.org/10.11865/zs.201926>
- Zhang, F. & Deharveng, L. (2015) Systematic revision of Entomobryidae (Collembola) by integrating molecular and new morphological evidence. *Zoologica Scripta* 44, 298–311. <https://doi.org/10.1111/zsc.12100>
- Zhang, F., Sun, D.D., Yu, D.Y. & Wang, B.X. (2015) Molecular phylogeny supports S-chaetae as a key character better than jumping organs and body scales in classification

of Entomobryoidea (Collembola). *Scientific Reports* 5, 1–12.
<https://doi.org/10.1038/srep12471>

Chapter 2: Two new species of *Trogolaphysa* Mills, 1938 (Collembola, Entomobryomorpha, Paronellidae) from caves in Caatinga of Rio Grande do Norte State, Brazil

1 Introduction

Springtails are abundant microarthropods found in almost all terrestrial environments, from cold deserts in polar regions to warm and highly diverse tropical rainforests (Lukić 2019; Potapov *et al.* 2020). They are also found in subterranean environments, where they serve as the basis of food chains encompassing arthropod predators (Lukić 2019). Entomobryomorpha is the most diverse higher taxon of Collembola in subterranean habitats, and also the largest order. One of the families, Paronellidae, includes 45 troglomorphic species distributed in several genera (Lukić 2019). Among them, the genus *Trogolaphysa* Mills, 1938 holds 64 species with troglomorphic cave forms and non-troglomorphic species. About 40% (26 spp.) of *Trogolaphysa* species were found in subterranean environments, and at least the troglophiles or troglonexes taxa can maintain semipermanent populations in caves.

Trogolaphysa is found in the Neotropical and Afrotropical regions, where 54 and 11 species have been recorded, respectively (Bellinger *et al.* 2021; Mari-Mutt & Bellinger 1990; Nguyen & Soto-Adames 2018; Soto-Adames & Taylor 2013). Two different general morphological groups can be recognized in *Trogolaphysa* species. The epigeic taxa usually have the antennae, head and body pigmented, eyes present (mostly 6–8 eyes) and empodial complex with 3–4 teeth, whereas the hypogean species frequently have reduced number or complete absence of eyes and body colour, reduced number of teeth in empodial complex and unguiculi, and elongated appendages.

Caves play an important role for biological processes due to their unique environmental stability (Poulson & White 1969), but economic activities such as mining can disturb its environmental stability (Cruz *et al.* 2010; Gomes *et al.* 2001). Limestone extraction is the main economic activity in municipalities which have carbonate caves in Rio Grande do Norte (RN) State, Brazil (Cruz *et al.* 2010). The National Cave Research and Conservation Center (CECAV) registered at least four incidents in caves involving the extraction of minerals before 2010. For instance, the damages caused by the extraction of limestone to the caves of Capoeira de João Carlos and Macaco, in the municipalities of Apodi and Governador Dix-sept Rosado, RN, respectively, was described by Cruz *et*

al. (2010). Rio Grande do Norte also has a representative production of oil and natural gas and nowadays is the sixth largest in Brazil of both resources (Agência Nacional do Petróleo 2019). Approximately 90% of natural cavities in the state are located within areas where mineral extraction is legally allowed. These activities can further impact the cave environments in RN and efforts to identify, describe, evaluate and preserve the natural populations of hypogean invertebrates are in need to delimit priority areas for wildlife conservation. Previous studies in RN caves demonstrated a large abundance and richness of Collembola (Bento 2011), and such data demonstrate a wide distribution of *Trogolaphysa* in the RN caves. This paper describes two new species that were found in caves of western RN, adding to the known diversity the first *Trogolaphysa* species recorded from this region.

2 Methodology

2.1 Sampling

The biological material was collected on July 21 to 26, 2019 from caves in western Rio Grande do Norte, located in the municipalities of Baraúna, Felipe Guerra and Governador Dix-sept Rosado (Fig. 1.2; Tab. 1.2). All sampled caves are located within the Caatinga biome, in the Jandaíra Formation of the Potiguar Basin. The specimens were collected from the superficial (epigeal) environment (near the entrance of caves), with entomological aspirators, while samples of the subterranean environment (hypogean) were collected with painting brushes soaked in alcohol in the euphotic zones and aphotic zones. Specimens collected in disphotic zones (transitional-twilighted region) were grouped with those from the euphotic region. The specimens were stored in plastic centrifuge tubes with ethanol (100%) and kept refrigerated. The specimens were prepared following the protocols for optical microscopy (Bellinger et al. 1996-2021). The main bibliographies used for identification of the specimens were Soto-Adames & Taylor (2013), Soto-Adames (2015), Bellini & Cipola (2017) and Nunes & Bellini (2018).

The new species were frequently found near water puddles, under and over rocks, over guano and cave soil. These cavities are located in Caatinga Domain, characterized for climate marked long dry season and typical vegetation. The climate of the region is considered as Aw, with a main equatorial climate with desert-like annual precipitation (Kotteck et al. 2006).

The terminology used in the descriptions follows mainly: Gisin (1967) and Mari-Mutt (1986) for labial chaetotaxy; Fjellberg (1999) for labial palp papillae; Cipola *et al.* 2014 for labral chaetotaxy; Mari-Mutt (1979) modified by Soto-Adames (Soto-Adames 2015; Soto-Adames *et al.* 2008) for dorsal head chaetotaxy; Szeptycki (1979) for dorsal chaetotaxy with additions of Zhang & Deharveng (2015) and Soto-Adames (2015). The notations for chaetae of uncertain homology are followed by a question mark (?).

Abbreviations used in the descriptions are: mac = macrochaeta(e); mic = microchaeta(e); mes = mesochaeta(e); Ant. = antennal segment(s); Th. = thoracic segment(s); Abd. = abdominal segment(s); sens = sensilla; ms = trunk microsensilla; l.p. = lateral process.

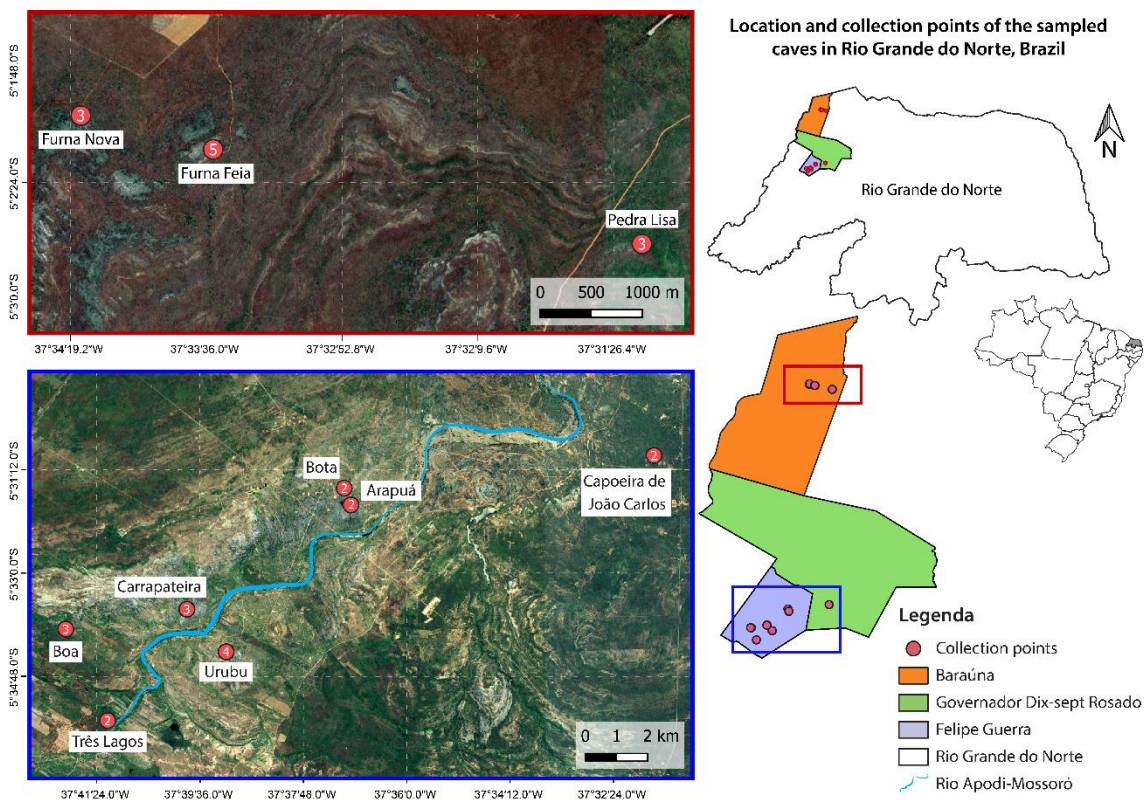


Figure 1.2 Caves sampled in the Caatinga domain of western Rio Grande do Norte, Brazil. Numbers inside the red points represent the total of samples collected inside and outside each cave.

Table 1.2 Location of the sampled caves, western Rio Grande do Norte, northeastern Brazil.

Municipality	Cave	Area (m ²)	Latitude (S)	Longitude (W)
Baraúna	Pedra Lisa	501.9	05° 02' 44"	37° 31' 18.72"
	Furna Nova	701.2	05° 02' 03.8"	37° 34' 15.8"
	Furna Feia	4891	05° 02' 13.38"	37° 33' 35.24"
Governador Dix-Sept Rosado	Capoeira de João Carlos	169.9	05° 30' 57"	37° 31' 42"

Felipe Guerra	Boa	2940.4	05° 33' 58"	37° 41' 58.4"
	Urubu	1796.6	05° 34' 23"	37° 39' 08.7"
	Três Lagos	329.9	05°35' 34.4"	37° 41' 12.7"
	Carrapateira	838.9	05° 33' 38"	37° 39' 49.65"
	Bota	129.1	05° 31' 30.9"	37° 37' 05.3"
	Vale	121.9	05° 31' 50.6"	37° 36' 58.3"
	Arapuá	570	05° 31' 48.2"	37° 36' 58.5"

3 Results

The analysis of the sampled material resulted in the identification of two species of *Trogolaphysa*, both new to science. Their descriptions are presented below. Further information on the collected material is presented in the discussion topic (4).

Order Entomobryomorpha Börner, 1913

Superfamily Entomobryoidea Womersley 1934

Family Paronellidae Börner, 1906 *sensu* Zhang *et al.* 2019

Subfamily Paronellinae Börner, 1906 *sensu* Zhang *et al.* 2019

Tribe Paronellini Börner, 1906 *sensu* Soto-Adames *et al.* 2014

Genus *Trogolaphysa* Mills, 1938

3.1 *Trogolaphysa* sp. nov. 1



Figure 2.2 *Trogolaphysa* sp. nov. 1, habitus, lateral view, specimen in ethanol (100%).

Type material. Holotype female on slide, Brazil, Rio Grande do Norte State, Baraúna municipality, Parque Nacional da Furna Feia, Furna Feia cave, euphotic zone (05°02'13.38"S; 37°33' 35.24"W). 22/VII/2019, P.G.C Souza, D. M. Bento, B.C. Bellini, G.M. Silva coll. Paratypes on slides, one male and seven females, same data as holotype. Other material examined: BRAZIL, RN, Baraúna municipality, Furna Nova cave (05°02'03.8"S; 37°34'15.8"W), euphotic zone, 21/VII/2019, P.G.C Souza, D. M. Bento, B.C. Bellini, G.M. Silva coll. Paratypes on slides: one male, one juvenile and two specimens (sex unknown); BRAZIL, RN, Baraúna municipality, Pedra Lisa cave (05°02'44.0"S; 37°31'18.72"W), aphotic zone, 21/VII/2019, P.G.C Souza, D. M. Bento, B.C. Bellini, G.M. Silva coll. Paratypes on slides: two males, one juvenile and two specimens (sex unknown); BRAZIL, RN, Baraúna municipality, Boa cave (05°33'59.5"S; 37°41'52.4"W), euphotic zone, 23/VII/2019, P.G.C Souza, D. M. Bento, B.C. Bellini, G.M. Silva coll. Paratypes on slides: four females and 2 specimens (sex unknown); BRAZIL, RN, Felipe Guerra municipality, Três Lagos cave (05°35'34.4"S; 37°41'12.7"W), euphotic zone, Felipe Guerra municipality, 25/VII/2019, P.G.C Souza, D. M. Bento, B.C. Bellini, G.M. Silva coll. Paratypes on slides: six females. Specimens

will be deposited at the Collembola Collection of Centro de Biociências of Universidade Federal do Rio Grande do Norte (CC/UFRN).

Diagnosis. Body length about 1.4 mm (0.6–2.7). Specimens pale with blue pigmentation distally on Ant. I, Ant. II–IV entirely pigmented; legs with scattered pigment; eyepatches black. Antennae about 2.1 times longer than head length. Ant. IV smooth with 1 apical shallow sensory organite. Ant. III sense rods normal. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines present, normal and separated. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Dorsal head chaetotaxy with 14 **An** mac, **A0**, **A2**, **S5**, **Pa5** and **Pm3** as mac; 4 interocular chaetae, none as mac; post-labial basal chaetae 0–1+5–7. Mesothorax longer than metathorax in the midline. Th. II with **a5** plus 3 mac on **p3** complex; Th. III lacking mac. Abd. I with **a6** mic. Abd. II with 2 (**m3** and **m5**) and Abd. III with 3 (**m3**, **am6**, **pm6**) mac, respectively; Abd. IV with 4 central mac (**A3**, **A5**, **B4** and **B5**), **B6** as mes; 9–14 posterior chaetae. Trochanteral organ with about 23–28 spine-like chaetae. Ungues with 4 inner teeth, 2 paired basal symmetrical, 1 medial subequal to the basal pair and 1 minute apical tooth; unguiculi lanceolated with postero-external lamella entirely serrate or smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.46–0.70: 0.42–0.91. Ventral tube anterior face with 2+2 distal mac; lateral flap with 10–14 chaetae: 5–8 ciliate and 5–6 smooth. Dens with 2 rows of ciliate spines, internal row with 22–41 and external with 17–33. Mucro rectangular (ratio width: length of mucro about = 1: 2.5–4.5), with 4 teeth.

Description. Total length (head + trunk) of type series between 1.8–2.4 mm (holotype 2 mm). Habitus typical of Lepidocyrtinae. Specimens pale to yellowish with blue light pigmentation distally on Ant. I, Ant. II–IV entirely pigmented; legs with scattered pigment; head and body without clear pigments (Fig. 2.2). Heavily ciliate apically rounded scales covering Ant. I–II, Ant. III (proximally), dorsal and ventral head, dorsal trunk and ventrally on manubrium and dens. Legs and ventral tube without scales.

Head (Fig. 3.2A–I). Antennae about 2.1 times longer than the head length (1.7–2.6 mm), antennal average ratio I:II:III:IV = 1: 1.4: 1.2: 2.6. Ant. IV smooth without apical bulb and with 1 apical shallow sensory organite (pseudopore-like) and at least two types of chaetae: blunt sens and ciliated chaetae (Fig. 3.2A). Ant. III sense organ typical with two sense rods normal and three surrounding guard sensilla, one ventro-lateral reduced (Fig. 3.2B). Ant. II dorsally with 3 types of sens: pin, blunt and swollen sensilla at the apex (Fig. 3.2C). Four prelabral ciliated chaetae. Labral formula 4 (**a1–2**), 5 (**m0–**

2) and 5 (**p0–2**), all smooth chaetae, **p** chaetae longer than the others, **a** chaetae slightly thicker than others (Fig. 3.2D); two normal labral spines on individualized papillae (Fig. 3.2E). Labial palp papillae (and guard chaetae) formula as **H(2)**, **A(0)**, **B(5)**, **C(0)**, **D(4)**, **E(4)** + **l.p.**; **l.p.** not reaching the apex of papilla **E** (Fig. 3.2F). Outer maxillary lobe with basal and distal chaetae subequal and smooth; sublobal plate with 2 smooth appendages (Fig. 3.2G). Labial basolateral and basomedial fields with **M1–2**, **r** reduced, **E**, **L1–2** ciliated, **a1–5** smooth. Ventral postlabial chaetotaxy with **G1–4**, **H1–4** and **J1–2**; cephalic groove with 3+3 anterior, 1+1 medial and 0–1+5–7 posterior basal chaetae (Fig. 3.2H). Eyes 8+8, A-F lenses subequal, G and H smaller; 4 interocular chaetae, none as mac (Fig. 3.2I). Dorsal chaetotaxy with 15 antennal (**An**), 4–5 anterior (**A0**, **A1–3** and **A5**, **A1** present or absent or as a scale), 4 medial (**M1–4**), 4 sutural (**S2–5**), 2 postoccipital (**Ps2** and **Ps5**), 4 postoccipital anterior (**Pa2–3**, **Pa5**, **Pa6** as the postocular bothriotrichum), 2 postoccipital medial (**Pm1** and **Pm3**), 6 postoccipital posterior (**Pp1–4**, **Pp6–7**) and 2 postoccipital external chaetae (**Pe4** and **Pe6**) (Fig. 3.2I).

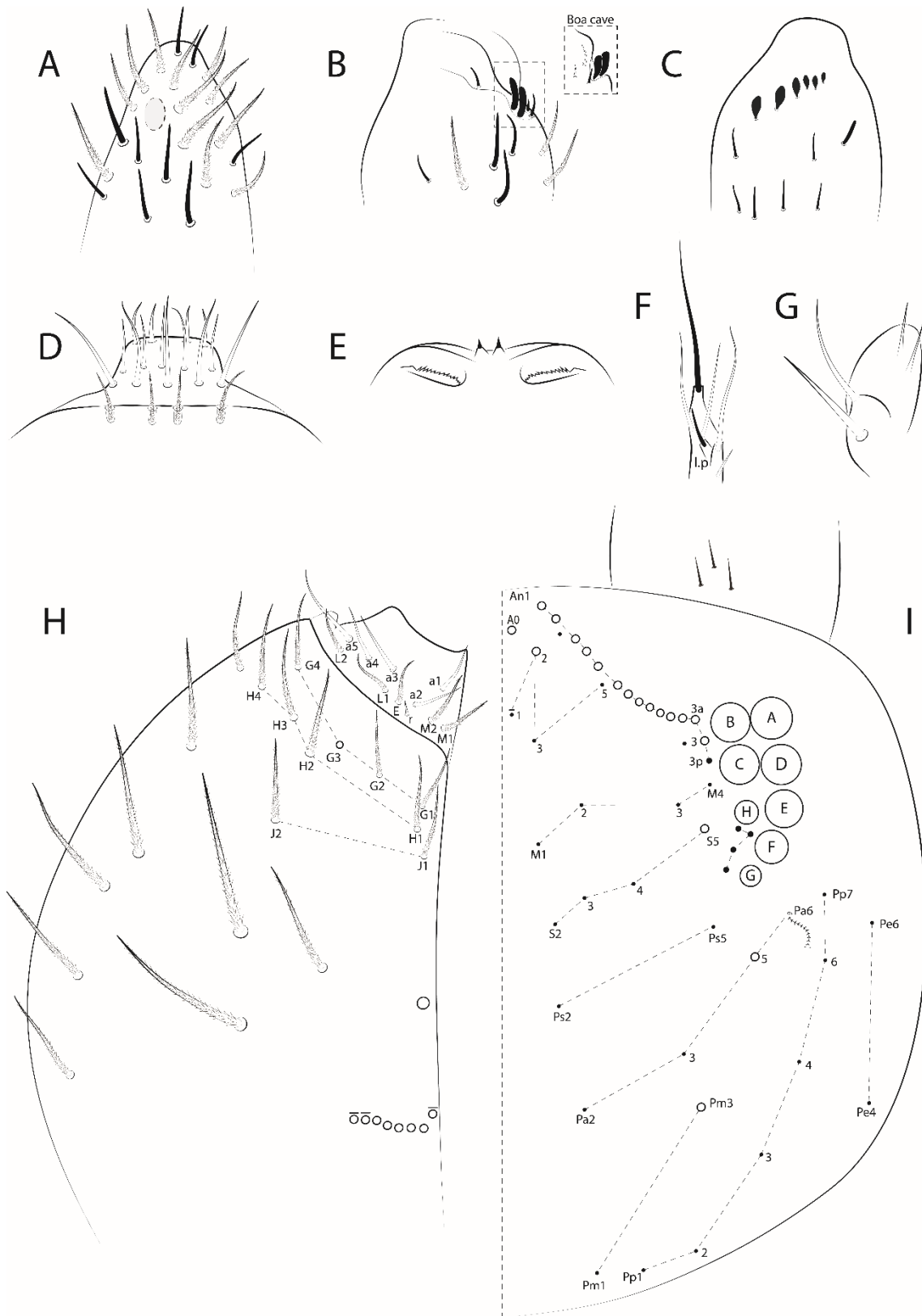


Figure 3.2 *Troglaphysa* sp. nov. 1. A, apex of the Ant. IV; B, Ant. III sense organ (swollen sens in Boa cave specimens); C, Ant. II sens (dorsal side); D, prelabral chaetae and labral chaetae; E, anterior labral spines; F, labial papilla; G, outer maxillary lobe and sublobal plate; H, post-labial ventral head; I, dorsal head chaetotaxy.

Trunk chaetotaxy (Fig. 4.2A–G). Central mac formula from Th. II to Abd. IV: 4, 0 / 0, 2, 4, 4. Th II with 1 S-microchaeta (**ms**), 1 anterolateral sens (**al**), 1 anterior (**a5** mac), 1–2 medial (**m2**, **m4**; **m2** present or absent) and 6 posterior chaetae (**p3 complex** with 3 mac plus **p5**, **p6–6e** as mic) (Fig. 4.2A). Th. III with 1 **al**, 2–3 anterior (**a1–2**, **a4** as mic, **a2** present or absent), 1 medial (**m6** as mic) and 3 posterior chaetae (**p2–3** and **p6** as mic) (Fig. 4.2B). Abd. I with 1 **ms**, 1 anterior (**a6**), 4 medial (**m2–4** and **m6**) and 1 posterior chaetae (**p6**) (Fig. 4.2C). Abd. II with 1 anterosubmedial sens (**as**), 4 anterior (**a2–3** as accessory scales, **a5** as bothriotrichum and **a7** as mic), 3 medial (**m2** as bothriotrichum, **m3** and **m5** as mac) and 3 posterior chaetae (**p5–7** as mic); **el** chaeta present (Fig. 4.2D). Abd. III with 1 **ms**, 1 **as**, 4 anterior (**a2–3** as accessory scales, **a5** as bothriotrichum and **a7** as mes), 6 medial (**m2** and **m5** as bothriotricha, **m3**, **am6** and **pm6** as mac, and **m7** as mes) and 4 posterior chaetae (**p6** as mac, **p7i** and **p6e** as mic and **p7** as mes); **el** present as mic (Fig. 4.2E). Abd. IV with 1 posterior (**ps**) and at least 10 median sens; chaetae formula as 4 ‘A’ (**A1**, **A3**, **A5–6**), 1 ‘Ae’ (**Ae1**), 5 ‘B’ (**B1**, **B3–6**), 4 ‘C’ (**C1–4**), 6 ‘T’ (**T2–7**), 3 ‘Te’ (**Te3–4**, **Te7?**), 5 ‘D’ (**D1–3p**), 4 ‘E’ (**E1–4**), 3 ‘F’ (**F1–3**) and 2 ‘Fe’ (**Fe2**, **Fe5**) (Fig. 4.2F); 9–14 posterior chaetae and 5–6 pseudopores (lenticular organs). Abd. V with 1 sens (**as**), 1 accessory sens (**acc.p5**), 4 anterior (**a1**, **a3**, **a5–6**), 5 medial (**m2–3**, **m5–5e**), 3 postero-anterior (**p3a–5a**) and 5 posterior main chaetae (**pp1**, **p3–5**) (Fig. 4.2G).

Legs (Fig. 5.2A–E). Subcoxa I with 2 chaetae and 2 pseudopores (Fig. 5.2A); subcoxa II ‘a’ row with 7–9 chaetae and ‘p’ row with 9 chaetae (Fig. 5.2B); subcoxa III with 4–5 plus 5–8 main anterior chaetae and 2 pseudopores (Fig. 5.2C). Trochanteral organ with 23–28 spine-like chaetae (Fig. 5.2D). Ungues with 3–4 inner teeth, 2 paired basal symmetrical, 1 medial subequal to the basal pair of teeth and 1 minute apical tooth, present or absent; outer side with 3 teeth, one unpaired dorsal and 2 paired lateral teeth. Unguiculi lanceolated with postero-external lamella serrated (entirely) or smooth (Fig. 5.2E). Tenent-hairs capitate, mean ratio unguis: unguiculus: tenent-hair = 1: 0.58: 0.65, with minimum and maximum values as 1: 0.46–0.70: 0.42–0.91 (Fig. 5.2E).

Ventral tube (Fig. 5.2F–G). Anterior side with 2+2 distal mac plus 6–8 normal ciliate chaetae (Fig. 5.2F). Lateral flap with about 5–8 ciliated and 5–6 smooth chaetae (Fig. 5.2G). Posterior side not seen.

Furca (Fig. 5.2H–J). Manubrium without clear spines. Manubrial plate (dorsal side) with 4–7 chaetae and 2–4 pseudopores (Fig. 5.2H). Manubrium ventrally with 1+1 apical chaetae and 7–8 subapical scales (Fig. 5.2I). Dens dorsally with inner row with 22–

41 robust ciliated spine-like mac (holotype with 36) and outer row with 17–33 spines (holotype with 32). Muco rectangular (ratio width: length about = 1: 2.5–4.5), with 4 teeth, 3 apical and 1 basal (Fig. 5.2J).

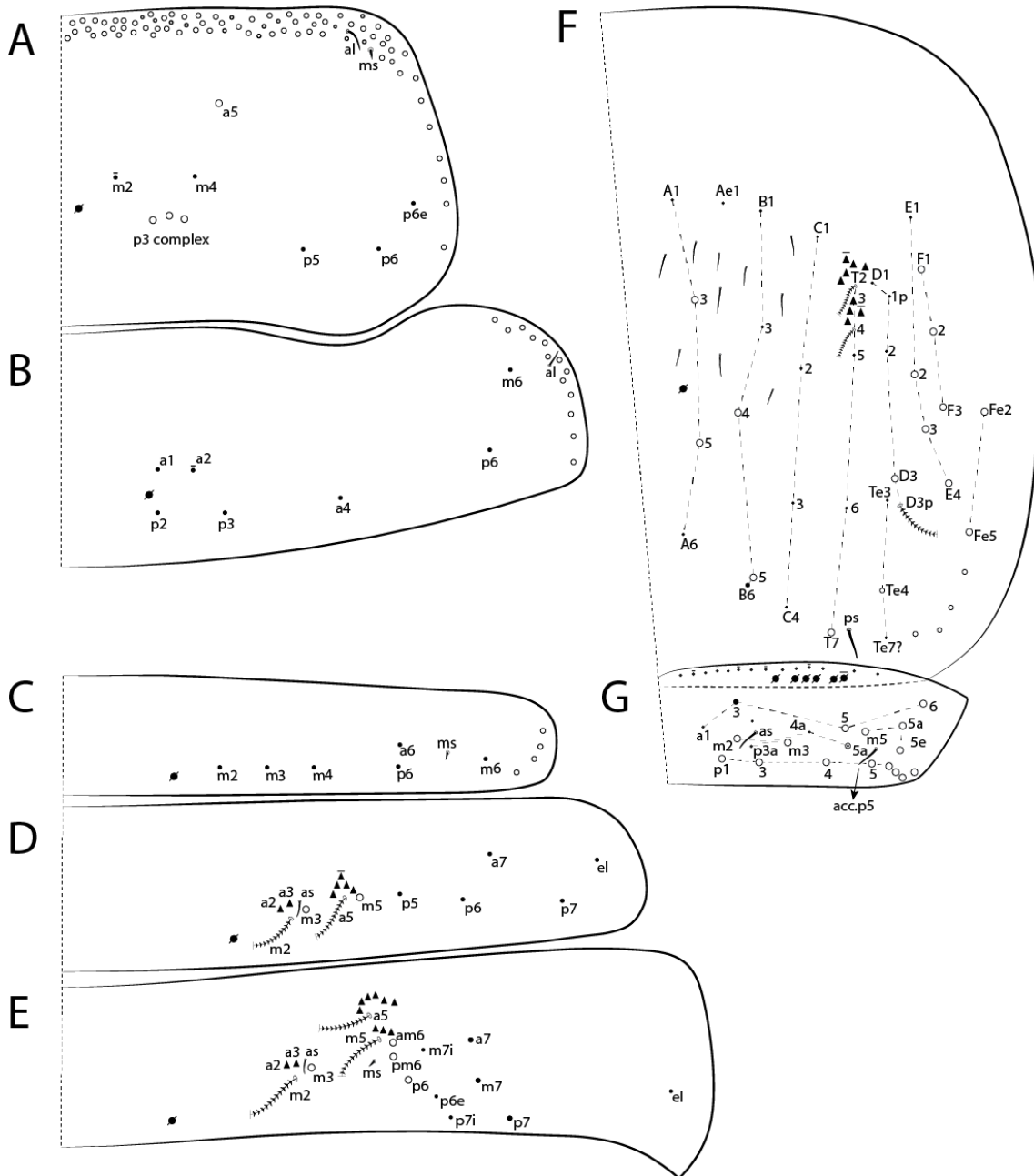


Figure 4.2 *Trogolaphysa* sp. nov. 1. A–G, Dorsal chaetotaxy of trunk, right side; A, Th. II; B, Th. III; C, Abd. I; D, Abd. II; E, Abd. III; F, Abd. IV; G, Abd. V.

Distribution and habitat. *Trogolaphysa* sp. nov. 1 was collected from caves in western Rio Grande do Norte State, Brazil. *Trogolaphysa* sp. nov. 1 is found in Furna Feia cave complex (Furna Feia National Park), Furna Nova, Pedra Lisa, Três Lagos and Boa cave (Fig. 1.2; Tab.1.2).

Remarks. *Trogolaphysa* sp. nov. 1 is similar to other Neotropical taxa of the genus, especially *T. piracurucaensis*, *T. formosensis* and *T. palaciosi* since they all share: 8 eyes, **a6** mic on Abd. I, 4 inner mac on Abd. IV and 4 teeth on mucro. However, the new species has Ant. IV smooth, while *T. piracurucaensis* and *T. palaciosi* have Ant. IV annulated. The Ant. III sense organ in specimens from Boa cave shows swollen sens, while others specimens from others localities have normal sens. *Trogolaphysa* sp. nov. 1, *T. formosensis* and *T. palaciosi* share 2 anterior mac on dorsal head (**A0**, **A2**), while *T. piracurucaensis* has 3 mac (**A0**, **A2–3**); *Trogolaphysa* sp. nov. 1 and *T. formosensis* have the medial **M4** chaeta as mac, *T. piracurucaensis* has the medial chaeta **M2**; only *Trogolaphysa* sp. nov. 1 has 1 sutural mac (**S5**), *T. formosensis* has 2 sutural mac (**S3** and **S5**) and *T. piracurucaensis* has 3 sutural mac (**S3–S5**); *T. piracurucaensis*, *T. formosensis*, *T. palaciosi* and the new species have 1 postoccipital anterior mac (**Pa5**), but *T. piracurucaensis*, *T. palaciosi* and *Trogolaphysa* sp. nov. 1 also have 1 postoccipital medial mac (**Pm3**).

All species cited above differ on trunk central mac formula mainly on Th. II and Th. III. *Trogolaphysa* sp. nov. 1 has 4 (**a5** plus 3 **p3**) on Th. II and no mac on Th. III; *T. piracurucaensis* has 7 and none mac, respectively; *T. formosensis* has 8 and 3 mac, respectively; and *T. palaciosi* has 4 and 1–2, respectively. On Abd. IV, they share 4 central mac, but *T. formosensis* differs in chaetae homology, with **A3**, **A4**, **B4** and **B5** as mac, while the others have **A3**, **A5**, **B4** and **B5** as mac. *Trogolaphysa* sp. nov. 1, *T. sp. nov. 2*, *T. piracurucaensis*, *T. marielouiseae* and *T. paracarpenteri* have lanceolate unguiculi, while *T. palaciosi* and *T. formosensis* have truncate unguiculi.

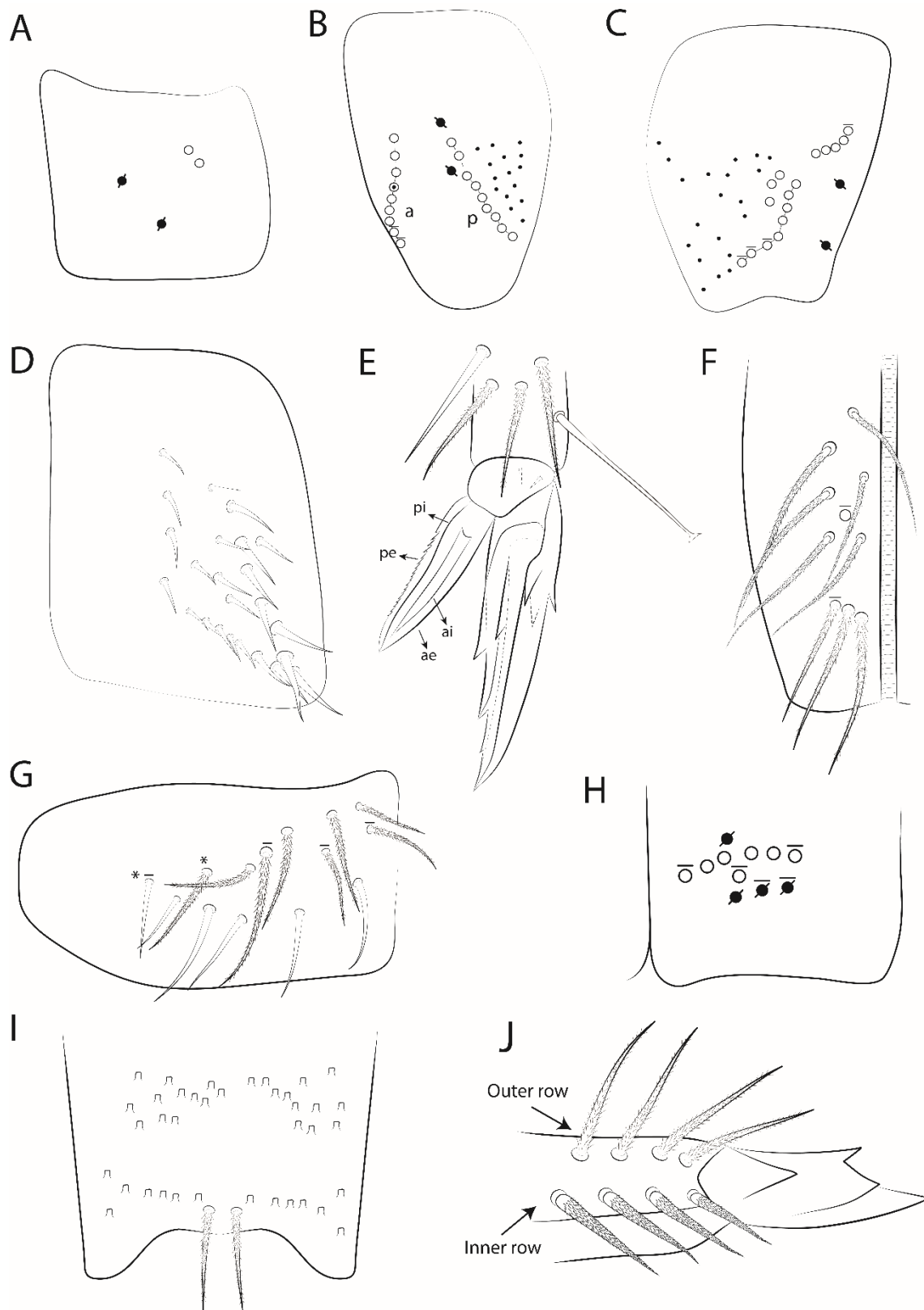


Figure 5.2 *Trogolaphysa* sp. nov. 1. A, subcoxa I external face; B, subcoxa II external face; C, subcoxae III external face; D, trochanteral organ; E, distal tibiotarsus and empodial complex; F, antero-lateral view of colophore chaetotaxy; G, lateral-flap chaetae (*ciliated or smooth chaeta); H, manubrial plate; I, dental chaetotaxy; J, dorsal-internal view of mucro.

3.2 *Trogolaphysa* sp. nov. 2



Figure 6.2 *Trogolaphysa* sp. nov. 2, habitus, lateral view, specimen in ethanol (100%).

Type material. Holotype female on slide, BRAZIL, Rio Grande do Norte State, Felipe Guerra municipality, Urubu cave, aphotic zone (05°34'21.7"S; 37°39'08"W). 24/VII/2019, P.G.C Souza, D. M. Bento, B.C. Bellini, G.M. Silva coll. Paratypes on slides, 3 females and 3 specimens (sex unknown). Other material examined: BRAZIL, RN, Felipe Guerra municipality, Bota cave (05°31'30.9"S; 37°37'05.3"W), euphotic zone, 26/VII/2019, P.G.C Souza, D. M. Bento, B.C. Bellini, G.M. Silva coll. Paratypes on slides: two females and two specimens (sex unknown); BRAZIL, RN, Felipe Guerra municipality, Carrapateira cave (05°33'38.01"S; 37°39'49.65"W), aphotic zone, 25/VII/2019, P.G.C Souza, D. M. Bento, B.C. Bellini, G.M. Silva coll. Paratypes on slides: two females and one specimens (sex unknown); BRAZIL, RN, Felipe Guerra municipality, Arapuá cave (05°31'48.2"S; 37°36'58.5"W), aphotic zone, 23/VII/2019, P.G.C Souza, D. M. Bento, B.C. Bellini, G.M. Silva coll. Paratypes on slides (sex not indicated); BRAZIL, RN, Felipe Guerra municipality, Capoeira de João Carlos cave

(05°30'57.0"S; 37°31'42.0"W), euphotic zone, 23/VII/2019, Governador Dix-sept Rosado municipality, P.G.C Souza, D. M. Bento, B.C. Bellini, G.M. Silva coll. Paratypes on slides: two male, two females and two specimens (sex unknown). Specimens will be deposited at the Collembola Collection of Centro de Biociências of Universidade Federal do Rio Grande do Norte.

Diagnosis. Body length about 1.5 mm (0.7–2.2). Specimens pale with blue light pigments distally on Ant. I, Ant. II–IV entirely pigmented; legs with scattered pigment; head and body without pigments; eyepatches black. Antennae about 2.1 times longer than head length. Ant. IV smooth with 1 apical shallow sensory organite with a short swollen sensillum. Ant. III sense rods swollen. Eyes 8. Prelabral chaetae ciliate, 2 anterior labral spines present, normal and separated. Labial formula: **M1–2rEL1–2a1–5**, **r** reduced. Dorsal head chaetotaxy with 11–14 **An** mac, **A0**, **A2**, **S5**, **Pa5** and **Pm3** as mac; 5 interocular chaetae, none as mac; post-labial basal chaetae 0–1+5–6. Mesothorax longer than metathorax in the midline. Th. II with **a5** plus 3 mac on **p3** complex; Th. III lacking mac. Abd. I with **a6** mic. Abd. II with 2 (**m3** and **m5**) and Abd. III with 3 (**m3**, **am6**, **pm6**) mac, respectively; Abd. IV with 3 inner mac (**A3**, **A5** and **B5**), **B6** as mes; 12 posterior chaetae. Trochanteral organ with about 16–21 spine-like chaetae. Ungues with 4 inner teeth, 2 paired basal symmetrical, 1 medial subequal to the basal pair of teeth and 1 minute apical tooth; unguiculi lanceolated with postero-external lamella entirely serrate or smooth; tenent-hairs capitate, ratio unguis: unguiculus: tenent-hair about = 1: 0.6: 0.7. Ventral tube anterior face with 2+2 or 3+3 distal mac; lateral flap with 10–13 chaetae: 5–7 ciliated and 5–6 smooth chaetae. Dens with 2 rows of ciliated spines, internal row with 15–57 and external with 16–51. Mucro rectangular (ratio width: length of mucro about = 1: 2.1–3.8), with 4 teeth.

Description. Total length (head + trunk) of type series between 1.4–2.6 mm (holotype 2.6 mm). Habitus typical of Lepidocyrtinae. Specimens pale to yellowish with blue light pigments distally on Ant. I, Ant. II–IV entirely pigmented; legs with scattered pigment; head and body without clear pigments (Fig. 6.2). Heavily ciliate apically rounded scales covering Ant. I-II, Ant. III (proximally), dorsal and ventral head, dorsal trunk and ventrally on manubrium and dens. Legs and ventral tube without scales.

Head (Fig. 7.2A–I). Antennae about 2 times longer than head length (ratio Ant: Head = 1:1.8–2.2 mm), antennal average ratio I: II: III: IV = 1: 1.4: 1.1: 2.1. Ant. IV smooth without apical bulb with 1 apical shallow sensory organite with a short swollen

sensillum inside, and at least with other two types of chaetae: blunt sens and ciliated chaetae (Fig. 7.2A). Ant. III sense organ typical with two sense rods swollen and three surrounding guard sensilla, the ventro-lateral one reduced (Fig. 7.2B). Ant. II dorsally with 3 types of sens: pin, blunt and swollen sensilla at the apex (Fig. 7.2C). Four prelabral ciliated chaetae (Fig. 7.2E). Labral formula 4 (**a1–2**), 5 (**m0–2**) and 5 (**p0–2**), all smooth chaetae, **p** chaetae longer than the others, **a** chaetae slightly thicker than others (Fig. 7.2E); two normal labral spines on individualized papillae (Fig. 7.2D). Outer maxillary lobe with basal and distal chaetae subequal and smooth; sublobal plate with 2 smooth appendages (Fig. 7.2F). Labial palp papillae (and guard chaetae) formula as **H(2)**, **A(0)**, **B(5)**, **C(0)**, **D(4)**, **E(4)** + **l.p**; **l.p.** reaching the apex of papilla **E** (Fig. 7.2G). Labial basolateral and basomedial fields with **M1–2**, **r** reduced, **E**, **L1–2** ciliated, **a1–5** smooth. Ventral postlabial chaetotaxy with **G1–4**, **H1–4** and **J1–2**; cephalic groove with 3+3 anterior, 1+1 medial and 0–1+5–6 posterior basal chaetae (Fig. 7.2H). Eyes 8+8, A-F lenses subequal, G and H smaller; 5 interocular chaetae. Dorsal chaetotaxy with 11–14 antennal (**An**), 4 anterior (**A0–3** and **A5**), 4 medial (**M1–4**), 4 sutural (**S2–5**), 2 postoccipital (**Ps2** and **Ps5**), 4 postoccipital anterior (**Pa2–3**, **Pa5**, **Pa6** as the postocular bothriotrichum), 2 postoccipital medial (**Pm1** and **Pm3**), 6 postoccipital posterior (**Pp1–4**, **Pp6–7**) and 2 postoccipital external (**Pe4** and **Pe6**) chaetae (Fig. 7.2I).

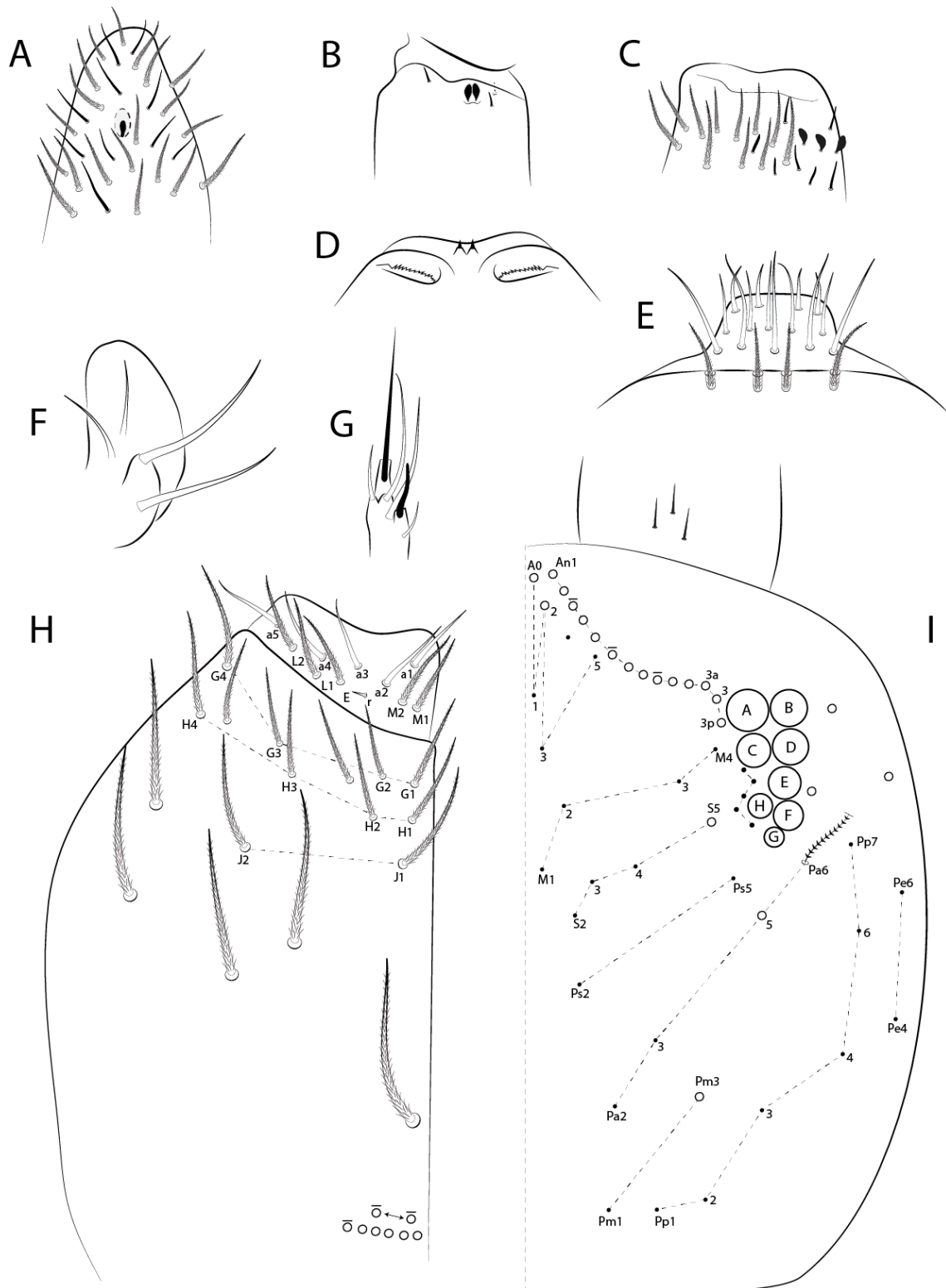


Figure 7.2 *Trogolaphysa* sp. nov. 2. A, Apex of Ant. IV; B, Ant. III sense organ and surrounding chaetae; C, Ant. II's swollen sens; D, anterior labral spines; E, prelabral chaetae and labral chaetae; F, outer maxillary lobe and sublobal plate; G, labial papilla E; H, post-labial ventral head; I, dorsal head chaetotaxy.

Trunk chaetotaxy (Fig. 8.2A–G). Central mac formula from Th. II to Abd. IV: 4, 0 / 0, 2, 4, 3. Th II with 1 S-microchaeta (**ms**), 1 anterolateral sens (**al**), 1 anterior (**a5** as mac), 2 medial (**m2** and **m4**) and 6 posterior (**p3 complex** with 3 mac plus **p5**, **p6-6e** as

mic) chaetae (Fig. 8.2A). Th. III with 1 **al**, 2 anterior (**a2** and **a4** as mic), 1 medial (**m6** as mic) and 3 posterior (**p2-3** and **p6** as mic) chaetae (Fig. 8.2B). Abd. I with 1 **ms**, 1 anterior (**a6**), 4 medial (**m2-4** and **m6**) and 1 posterior (**p6**) chaetae (Fig. 8.2C). Abd. II with 1 anterosubmedial sens (**as**), 4 anterior (**a2-3** as accessory scales, **a5** as bothriotrichum and **a7** as mic), 3 medial (**m2** as bothriotrichum, **m3** and **m5** as mac) and 3 posterior (**p5-7** as mic) chaetae; **el** chaeta present (Fig. 8.2D). Abd. III with 1 **ms**, 1 **as**, 4 anterior (**a2-3** as accessory scales, **a5** as bothriotrichum, and **a7** as mes), 6 medial (**m2** and **m5** as bothriotrichum, **m3**, **am6** and **pm6** as mac and **m7** as mes) and 4 posterior (**p6** as mac, **p7i** and **p6e** as mic and **p7** as mes) chaetae; **el** present as mic (Fig. 8.2E). Abd. IV with 1 anterosubmedial (**as**), 1 posterior (**ps**) and at least 8 median sens; Chaetae formula as 3-4 'A' (**A1**, **A5-6**, **A6** present or absent), 5 'B' (**B2**, **B3-6**), 4 'C' (**C1-4**), 6 'T' (**T2-7**), 3 'Te' (**Te3-4**, **Te7?**), 5 'D' (**D1-3p**), 4 'E' (**E1-4**), 3 'F' (**F1-3**) and 2 Fe (**Fe2** and **Fe5**) chaetae (Fig. 8.2F); 12 posterior chaetae and 4-6 pseudopores (lenticular organs). Abd. V with 1 sens (**as**), 1 accessory sens (**acc.p5**), 4 anterior (**a1**, **a3**, **a5-6**), 5 medial (**m2-3**, **m5-5e**), 2 postero-anterior (**p3a**, **p5a**) and 4 posterior (**p1**, **p3-5**) main chaetae (Fig. 8.2G).

Legs (Fig. 9.2A-C). Subcoxa I with 4 chaetae and 2 pseudopores (Fig. 9.2A); subcoxa II with 'a' row with 7-9 chaetae and 'p' row with 6-7 chaetae (Fig. 9.2B); subcoxa III with 4-5 plus 7-8 main chaetae and 1 pseudopore (Fig. 9.2C). Trochanteral organ with 16-21 spine-like chaetae (Fig. 9.2D). Ungues with 3-4 inner teeth, 2 paired basal symmetrical, 1 medial subequal to the basal pair of teeth and 1 minute apical tooth, present or absent; outer side with 3 teeth, one unpaired dorsal and 2 paired lateral teeth. Unguiculi lanceolated with postero-external lamella serrated (entirely) or smooth. Tenent-hairs capitate, mean ratio unguis: unguiculus: tenent-hair about = 1: 0.6: 0.7, with minimum and maximum values as 1: 0.43-0.73: 0.61-0.91 (Fig. 9.2E).

Ventral tube (Fig. 9.2F-G). Anterior side with 2+2 or 3+3 distal mac plus 4-13 ciliate chaetae (Fig. 9F). Lateral flap with about 5-7 ciliated and 5-6 smooth chaetae (Fig. 9.2G). Posterior side not seen.

Furca (Fig. 9.2H-J). Manubrium without clear spines. Manubrial plate (dorsal side) with 5 chaetae and 4 pseudopores (Fig. 9.2H). Manubrium ventrally with 1+1 apical chaetae and 7-10 subapical scales (Fig. 9.2I). Dens dorsally with inner row with 15-57 robust ciliated spine-like mac (holotype with 28-47) and inner row with 16-51 spines (holotype with 30-44). Mucro rectangular (ratio width: length about = 1: 2.1-3.8), with 4 teeth, 3 apical and 1 basal (Fig. 9.2J).

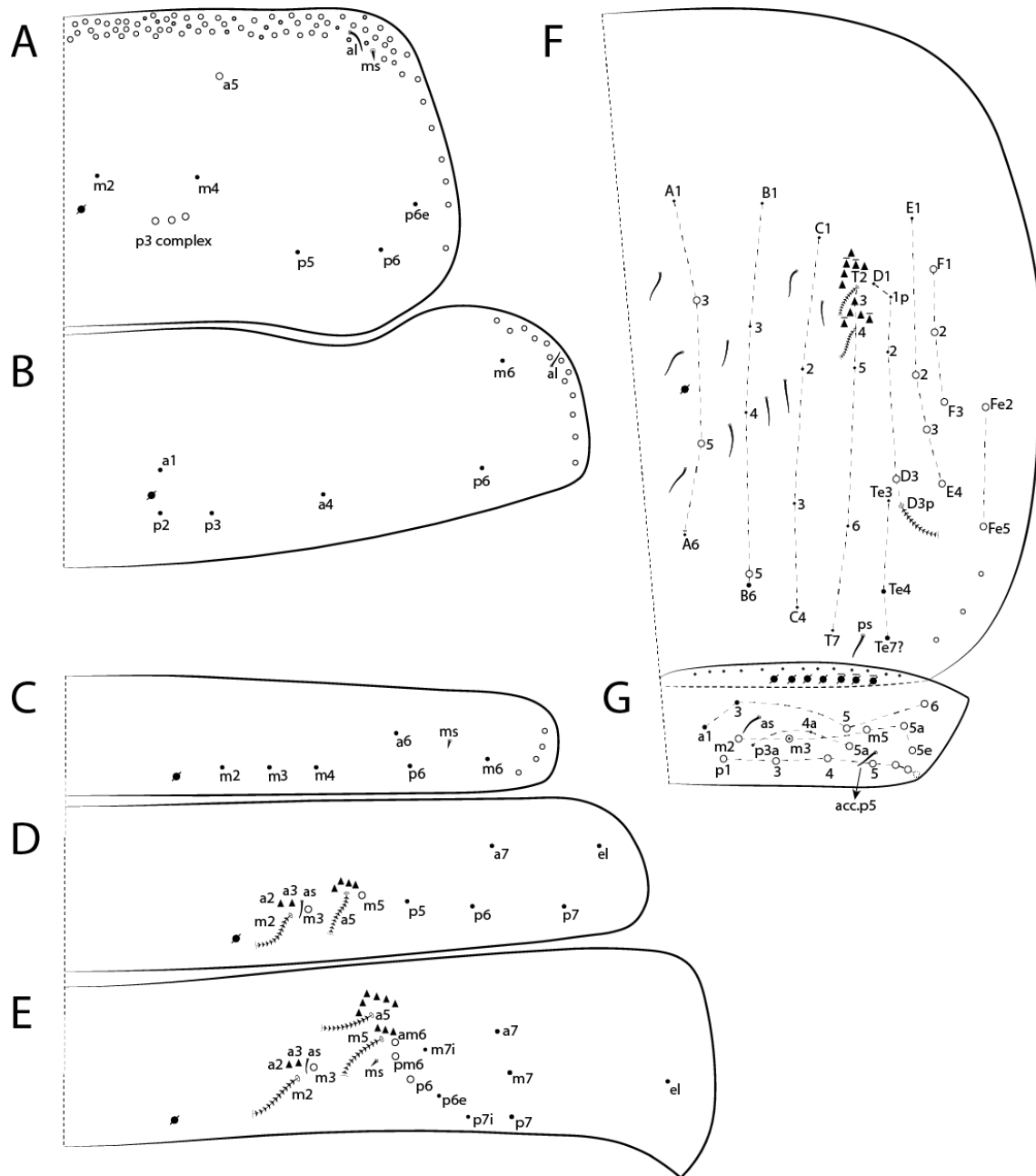


Figure 8.2 *Trogolaphysa* sp. nov. 2. A–G, Dorsal chaetotaxy of trunk, right side; A, Th. II; B, Th. III; C, Abd. I; D, Abd. II; E, Abd. III; F, Abd. IV; G, Abd. V.

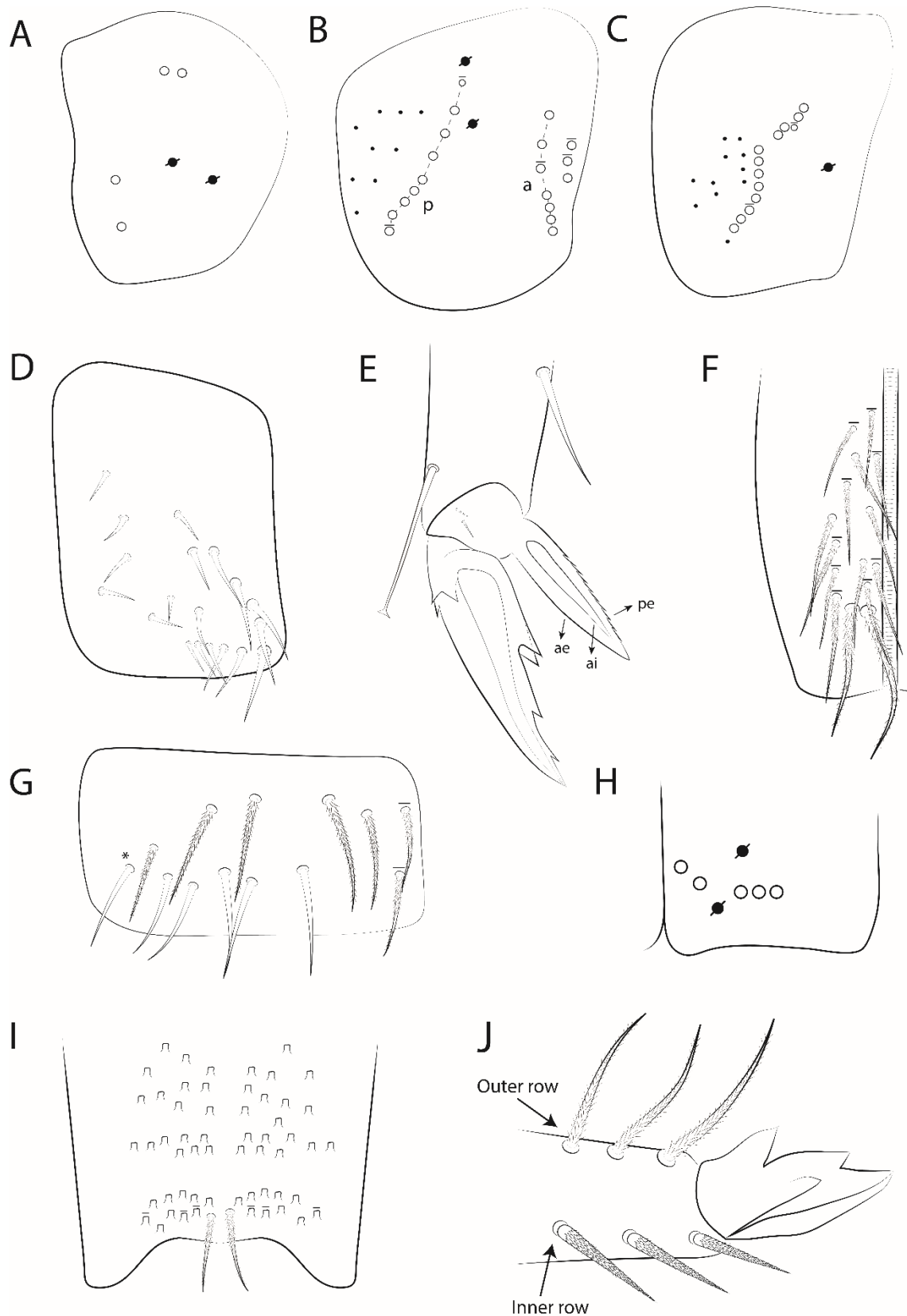


Figure 9.2 *Trogolaphysa* sp. nov. 2. A, subcoxa I external face; B, subcoxa II external face; C, subcoxae III external face; D, trochanteral organ; E, distal tibiotarsus and empodial complex; F, antero-lateral view of colophore chaetotaxy; G, lateral-flap chaetae (*ciliated or smooth chaeta); H, manubrial plate; I, dental chaetotaxy; J, dorsal-internal view of mucro.

Distribution and habitat. *Trogolaphysa* sp. nov. 2 is found in the caves: Urubu, Capoeira de João Carlos, Carrapateira, Bota and Arapuá (Fig. 1.2, Tab. 1.2). The new species were frequently found near water puddles, under and over rocks, over guano and cave soil.

Remarks. *Trogolaphysa* sp. nov. 2 resembles *Trogolaphysa* sp. nov. 1 in several characters, such as the habitus, smooth Ant. IV, 8 eyes, head macrochaetotaxy with **A0**, **A2**, **S5**, **Pa5** and **Pm3**, same central mac formula on Th. II to Abd. III: 4, 0 / 0, 2, 4, unguis with 3–4 internal teeth, unguiculi postero-external lamella serrate or smooth and rectangular mucro with 4 teeth. Also the chaeta **m2** on Th. II and chaeta **a2** on Th. III may be present or absent in *Trogolaphysa* sp. nov. 1, but absent in *Trogolaphysa* sp. nov. 2. The main difference between the species are on Abd. IV: *Trogolaphysa* sp. nov. 1 has 4 internal mac (**A3**, **A5**, **B4** and **B5**), while *Trogolaphysa* sp. nov. 2 has 3 internal mac (**A3**, **A5** and **B5**).

Among the Neotropical species, *Trogolaphysa* sp. nov. 2 resembles most *T. paracarpenteri*, *T. balteata* and *T. marielouiseae*. They all have 6–8 eyes, prelabral chaetae ciliate, Th. III lacking mac, Abd. IV with 3 inner mac (**A3**, **A5** and **B5**) and mucro with 4 teeth. *Trogolaphysa* sp. nov. 2, *T. paracarpenteri* and *T. marielouiseae* also share the same labial formula, **M1–2rEL1–2a1–5**, while *T. balteata* has **M1–3rEL1–2a1–5**. On dorsal head, all species have 2 anterior mac (**A0**, **A2**), but only *T. marielouiseae* has 1 medial mac (**M2**); sutural mac **S3** is present in *T. marielouiseae* and *T. balteata*, while *Trogolaphysa* sp. nov. 2 has the sutural mac **S5**; all species has postoccipital anterior (**Pa5**) and medial chaetae (**Pm3**).

The above cited species differ on trunk central mac formula on Th. II, *Trogolaphysa* sp. nov. 2 has 4 mac (**a5** plus 3 mac on **p3** complex), *T. balteata* has 7 mac (**a5** plus 6 mac on **p3** complex), *T. marielouiseae* and *T. paracarpenteri* has 6 mac (**a5** plus 5 mac on **p3** complex). All species have **a6** mic on Abd. I, except for *T. paracarpenteri*. Finally, in an ecological point of view, the new species and *T. palaciosi* were found in subterranean environments, while *T. piracurucaensis*, *T. formosensis*, *T. paracarpenteri*, *T. balteata* and *T. marielouiseae* were found associated to leaf litter or mould over the soil.

Table 2.2 Comparative table of species similar to *Trogolaphysa* sp. nov. 1 and *T.* sp. nov. 2.

	<i>Trogolaphysa</i> sp. nov. 1	<i>Trogolaphysa</i> sp. nov. 2	<i>T. balteata</i> ¹	<i>T. marielouiseae</i> ¹	<i>T. formosensis</i> ²	<i>T. paracarpenteri</i> ¹	<i>T. piracurucuensis</i> ³	<i>T. palaciosi</i> ¹
Body Size	1.8–2.7	1.7–2.6	1.9	2.0	1.4	1.9	2.2–2.6	2.3
Ratio Ant/Head	2.1	2.0	2.6	1.9	3.1	2.9	2.3	?
Ant. IV	Sm	Sm	?	?	Sm	?	An	?
Pre labral chaetae	Ci	Ci	Ci	Ci	Ci	Ci	Ci	Sm
Labral Spines	+	+	+	+	–	+	+	–
Labial Formula	M1–2rEL1–2a1–5	M1–2rEL1–2a1–5	M1–2rEL1–2a1–5	M1–3rEL1–2a1–5	M1–2rEL1–2a1–5	M1–2rEL1–2a1–5	M1–3*rEL1–2a1–5	M1–2rEL1–2a1–5
Eyes	8	8	6–8	6–8	8	8	8	8
Head dorsal mac	A0, A2, S3, Pa5, Pm3	A0, A2, S3, Pa5, Pm3	A0, A2, S3, Pa5, Pm3	A0, A2, S5, Pa5, Pm3	A0, A2, M2, M4, S3, S5, Pa5	A0, A2, Pa5, Pm3	A0, A2, A3, M2, S3, S4, S5, Pa5, Pm3	A0, A2, Pa5, Pm3
Th. II mac	4	4	7	6	8	6	7	4
Th. III mac	0	0	0	0	3	0	0	1–2
Abd. I a6 mic	+	+	+	+	+	–	+	+
Ungues inner teeth	3–4	3–4	4	2–3	4	3	4	3–4

Unguiculi shape	L	L	L/T	L	T	L	L	↓T
Unguiculi lamella	Sm/Se	Sm/Se	Sm	Sm	Sm	Sm/↓Se	Sm/Se	1 teeth
Tenent-hair	Ca	Ca	Ca	Ac/Ca	Ca	Ca	Ca	Ac
Dens inner row	15–57	18–41	32-33	25-30	+	21	25-29	22-25
Dens outer row	16–51	17–34	21	16-24	+	17	21-27	32-36
Mucro shape and teeth	Rec	Rec	Sub	Sub	Rec	Sub	Sub	Rec
Mucro teeth	4	4	4	4	4	4	4	4
Habitat	Cave	Cave	Mould	Mould	Leaf litter	Leaf litter (?)	Leaf littter	Cave
Country type locality	Brazil	Brazil	Jamaica	Mexico	Brazil	Mexico	Brazil	Mexico

Meaning of symbols: +: Present; -: Absent; An: Annulated; Sm: Smooth; Ci: Ciliate; Se: Serrate; Ca: Capitate; Ac: Acuminate; /: or; Red: Reduced; Rec: Rectangular; Sub: Subrectangular; L: Lanceolate; T: Truncate; </=: up to; ↓: weakly; ?: uncertain or missing information. * M3 present or absent.

References: ¹ Soto-Adames 2015; ² Silva & Bellini 2015; ³ Nunes & Bellini 2018.

4 Discussion

The earliest descriptions of *Trogolaphysa* used simpler characters to differentiate species, such as mucro and unguis morphology (i.e. Mills 1938). These characters plus the colour patterns have become insufficient to distinguish species in the light of modern taxonomy of springtails (Soto-Adames et al. 2014). They also obscure the real identities of several species considered widely distributed, such as *T. nigromaculata*, registered from several localities from Africa and *T. hirtipes*, described from caves in Brazil, but also found in Argentina, which is unlikely for both species (Cassagnau 1963; Mendonça 1981; Nguyen & Soto-Adames 2018). Hardly differentiated only by the dorsal macrochaetotaxy, *Trogolaphysa* species can be better diagnosed using a set of primary or secondary characters, such as those used in recent descriptions and herein (Bellini & Cipola 2017; Nguyen & Soto-Adames 2018; Nunes & Bellini 2018).

Cave species usually share morphological adaptations to thrive in such environments (troglomorphisms). Populations of subterranean collembolans frequently have decreased amount of pigmentation on body, reduction of eyes, elongation of sensory structures (i.e. antennae and chaetae) and unguis (Christiansen 1961, 1965). Only 12 specimens of *Trogolaphysa* were collected outside in epigeal samples, while 688 specimens were found in euphotic or aphotic zones inside caves (Fig. 10.2). Most collected specimens were identified as *Trogolaphysa*, followed by 126 *Cyphoderus* Nicolet, 1842, another genus of Entomobryoidea usually found in caves. On the other hand, in epigeal samples the Seirinae were the dominant euedaphic specimens (Fig. 10.2).

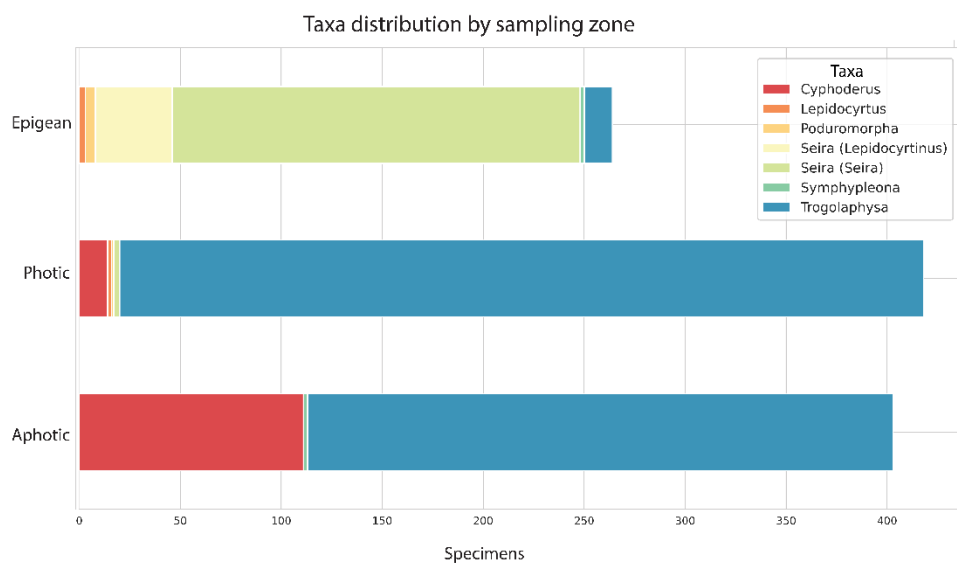


Figure 10.2 Graph with taxa distribution by sampling region (outside, euphotic and aphotic).

In spite of their large populations within caves, both new species of *Trogolaphysa* do not show any clear troglomorphisms such as reduction of pigmentation and eyes, elongate appendages or changes on the empodial complexes; however they are probably troglophiles, as they were found mostly inside caves (blue bars of the graph of the euphotic and aphotic zones vs. epigeal zone in fig.10.2) (Trajano, 2012; Trajano & Bessi, 2017). Based on this observation and the descriptions of the worldwide species of genus, it can be suggested that *Trogolaphysa* has a biological association with the subterranean environment, since about 40% of the species were collected inside caves regardless of their morphology (Palacios-Vargas *et al.* 1985; Soto-Adames & Taylor 2013; Soto-Adames 2015).

The lack of clear troglomorphisms in *Trogolaphysa* sp. nov. 1 and *Trogolaphysa* sp. nov. 2 perhaps can be explained by a recent colonization of the subterranean habitat by their populations, considering a geological time scale. Another hypothesis is the genetic flow between surface and subterranean populations, that can occur if the surface population actively migrates the caves during the day. This migration of Collembola throughout the day to shallow subterranean habitats is possible through surface cracks and fissures (also known as *Milieu Souterrain Superficiel* - MSS), which usually occurs when superficial environment conditions are not favourable (Rendoš *et al.* 2020). The Caatinga caves, as well as MSS, can act as climatic refuges to springtails, specially the troglophiles ones. Perhaps the subterranean habitat in the Caatinga can be considered an oasis in a desert for invertebrates that need to escape from the heat and sun exposure. Nevertheless, further studies on the ecology and genetics of the cave populations must be conducted to better understand the dynamics and evolution of *Trogolaphysa* lineages in the Caatinga domain.

5 Conclusion

The two new species described here increase the number of nominal *Trogolaphysa* species registered in Brazil to 10. *Trogolaphysa* sp. nov. 1 is protected at least in one cave within the Furna Feia National Park, and the description of the species could provide additional support for the environmental management plan of the park. Understanding the subterranean habitat and the distribution of species is important to promote conservation actions in environments already affected by human activities, such as the Caatinga.

6 References

- Agência Nacional do Petróleo, G.N. e B. (2019) Boletim da Produção de Petróleo e Gás Natural. Superintendência de Desenvolvimento e Produção, 1–38.
- Bellinger, P.F., Christiansen, K.A. & Janssens, F. (1996-2021) Checklist of the Collembola of The World. 1996. Available from: <http://www.collembola.org>
- Bento, D. de M. (2011) Diversidade de invertebrados em cavernas calcárias do oeste potiguar: Subsídios para a determinação de áreas prioritárias para conservação. Dissertação de Mestrado em Biodiversidade - Universidade Federal do Rio Grande do Norte, Natal, 2011. 162 pp.
- Börner, C. (1906) Das System der Collembolen nebst Beschreibung neuer Collembolen des Hamburger Naturhistorischen Museums. *Mitteilungen aus dem Naturhistorischen Museum* 23, 147–188.
- Börner, C. (1913) Die Familien der Collembolen. *Zoologischer Anzeiger* 41, 315–322.
- Cassagnau, P. (1963) Collemboles D'amérique du Sud.
- Christiansen, K. (1961) Convergence and Parallelism in Cave Entomobryinae. *Evolution* 15, 288–301. <https://doi.org/10.2307/2406229>
- Christiansen, K. (1965) Behavior and Form in the Evolution of Cave Collembola. *Evolution* 19, 529. <https://doi.org/10.2307/2406249>
- Cruz, J.B., Bento, D.M., Bezerra, F.H.R., Freitas, J.I. & Campos, U.P. (2010) Diagnóstico Espeleológico do Rio Grande do Norte. *Revista Brasileira de Espeleologia* 1, 1–24.
- Gomes, F.T. de M.C., Lopes Ferreira, R. & Maria Jacobi, C. (2001) Comunidade de artrópodes de uma caverna calcária em área de mineração: composição e estrutura. *Revista Brasileira de Zoociências* 3.
- Lukić, M. (2019) Collembola. *Encyclopedia of Caves*, 308–319. <https://doi.org/10.1016/b978-0-12-814124-3.00034-0>
- Mari-Mutt, J.A.. & Bellinger, P.F. (1990) Catalog of the Neotropical Collembola. *Flora & Fauna Handbook* 5, 1–237.
- Mendonça, M.C. de (1981) Contribuição para o conhecimento de Collembola Entomobryomorpha (Insecta) do Parque Nacional da Tijuca, Rio de Janeiro, Brasil.

- Mills, H.B. (1938) Collembola from Yucatan Caves. In: Fauna of the caves of Yucatan. Carnegie Institution of Washington Publication, pp. 183–190.
- Nguyen, M. & Soto-Adames, F.N. (2018) Annotated checklist of Afrotropical Trogolaphysa Mills, 1938 (Hexapoda: Collembola: Paronellidae) and description of a new species from Madagascar . *Zoosystema* 40, 179–196. <https://doi.org/10.5252/zoosystema2018v40a10>
- Nunes, R.C. & Bellini, B.C. (2018) Three new species of Entomobryoidea (Collembola: Entomobryomorpha) from Brazilian Caatinga-Cerrado transition, with identification keys to Brazilian *Cyphoderus*, *Pseudosinella* and *Trogolaphysa* species. *Zootaxa* 4420, 71. <https://doi.org/10.11646/zootaxa.4420.1.4>
- Palacios-Vargas, J., Ojeda, M. & Christiansen, K. (1985) Taxonomía y biogeografía de Troglopedetes (Collembola: Paronellidae) en América, con énfasis en las especies cavernícolas. *Folia Entomologica Mexicana*, 3–35.
- Potapov, A., Bellini, B.C., Chown, S.L., Deharveng, L., Janssens, F., Kováč, Ľ., Kuznetsova, N. & Ponge, J. (2020) Towards a global synthesis of Collembola knowledge – challenges and potential solutions. 92, 161–188. <https://doi.org/10.25674/so92iss3pp161>
- Poulson, T.L. & White, W.B. (1969) The cave environment. *Science* 165, 971–981.
- Rendoš, M., Miklisová, D., Ľubomír, K. & Mock, A. (2020) Dynamics of Collembola (Hexapoda) in a forested limestone scree slope, Western Carpathians, Slovakia. *Journal of Cave and Karst Studies*, 18–29. <https://doi.org/10.4311/2018LSC0140>
- Silva, D.D. da, Bellini, B.C., da Silva, D.D. & Bellini, B.C. (2015) *Trogolaphysa formosensis* sp. nov. (Collembola: Paronellidae) from Atlantic Forest, Northeast Region of Brazil. *Zoologia* 32, 53–58. <https://doi.org/10.1590/S1984-46702015000100008>
- Soto-Adames, F.N. (2015) The dorsal chaetotaxy of first instar *Trogolaphysa jataca*, with description of twelve new species of neotropical *Trogolaphysa* (Hexapoda: Collembola: Paronellidae). *Zootaxa* 4032, 1–41. <https://doi.org/10.11646/zootaxa.4032.1.1>

- Soto-Adames, F.N., Jordana, R. & Baquero, E. (2014) Comparative Analysis of the Dorsal Chaetotaxy of *Troglopedetes*, *Trogolaphysa*, and *Campylothorax* Supports the Synonymization of Tribes Paronellini and Troglopedetini (Collembola: Paronellidae). *Journal of Insect Science* 14, 278–278. <https://doi.org/10.1093/jisesa/ieu140>
- Soto-Adames, F.N. & Taylor, S.J. (2013) The dorsal chaetotaxy of *Trogolaphysa* (Collembola, Paronellidae), with descriptions of two new species from caves in Belize. *ZooKeys* 323, 35–74. <https://doi.org/10.3897/zookeys.323.4950>
- Trajano, E. (2012) Encyclopedia of Caves. In: Ecological classification of subterranean organisms. Elsevier Inc., pp. 275–277.
- Trajano, E. & Bessi, R. (2017) The Schiner-Racovitza classification of subterranean organisms: a critical analysis, difficulties of application and conservation. *Espeleo-Tema* 28, 87–102.
- Womersley, H. (1934) A preliminary account of the Collembola — Arthropleona of Australia II (Entomobryoidea). *Transactions of the Royal Society of South Australia* 58, 86–138.
- Zhang, F., Bellini, B.C. & Soto-adames, F.N. (2019) New insights into the systematics of Entomobryoidea (Collembola: Entomobryomorpha): first instar chaetotaxy, homology and classification. *Zoological Systematics* 44, 249–278. <https://doi.org/10.11865/zs.201926>