2012 Belize Biospeleology Expedition

submitted to:

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2012 Belize Biospeleology Expedition

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Introduction

In our 2011 expedition report (Taylor et al. 2011) we provided a review and summary of the state of knowledge on the cave fauna of Belize, and detailed preliminary findings from our 2011 fieldwork. That information will not be presented again here, instead we highlight new findings from 2012.

Material & Methods

For 2012, we fielded a team of seven researchers, visiting caves in the Toledo District of Belize between 28 April and 7 May, 2012. Sampling methods remained the same as in our 2011 expedition report (Taylor et al. 2011), with hand-collecting being our primary means of obtaining data, supplemented with measurements of temperature and humidity. No baited well sampling was attempted.

Goals & Scope

In 2012 we continued to make progress on several of the goals of our ongoing work in Belize:

- Identify study areas suited to cave ecology research
- Identify potential in-country collaborators, contacts, and bases of operation
- Preliminary documentation and assessment of biodiversity in select Belizean caves
- Collect data suitable for publication in peer reviewed journals
- Publish popular articles achieving outreach and education objectives related to subterranean ecology

Cover: A cave-adapted pseudoscorpion, *Mexobisium*? sp., from a Toledo District cave, likely an undescribed species. Photo © Jean Krejca.
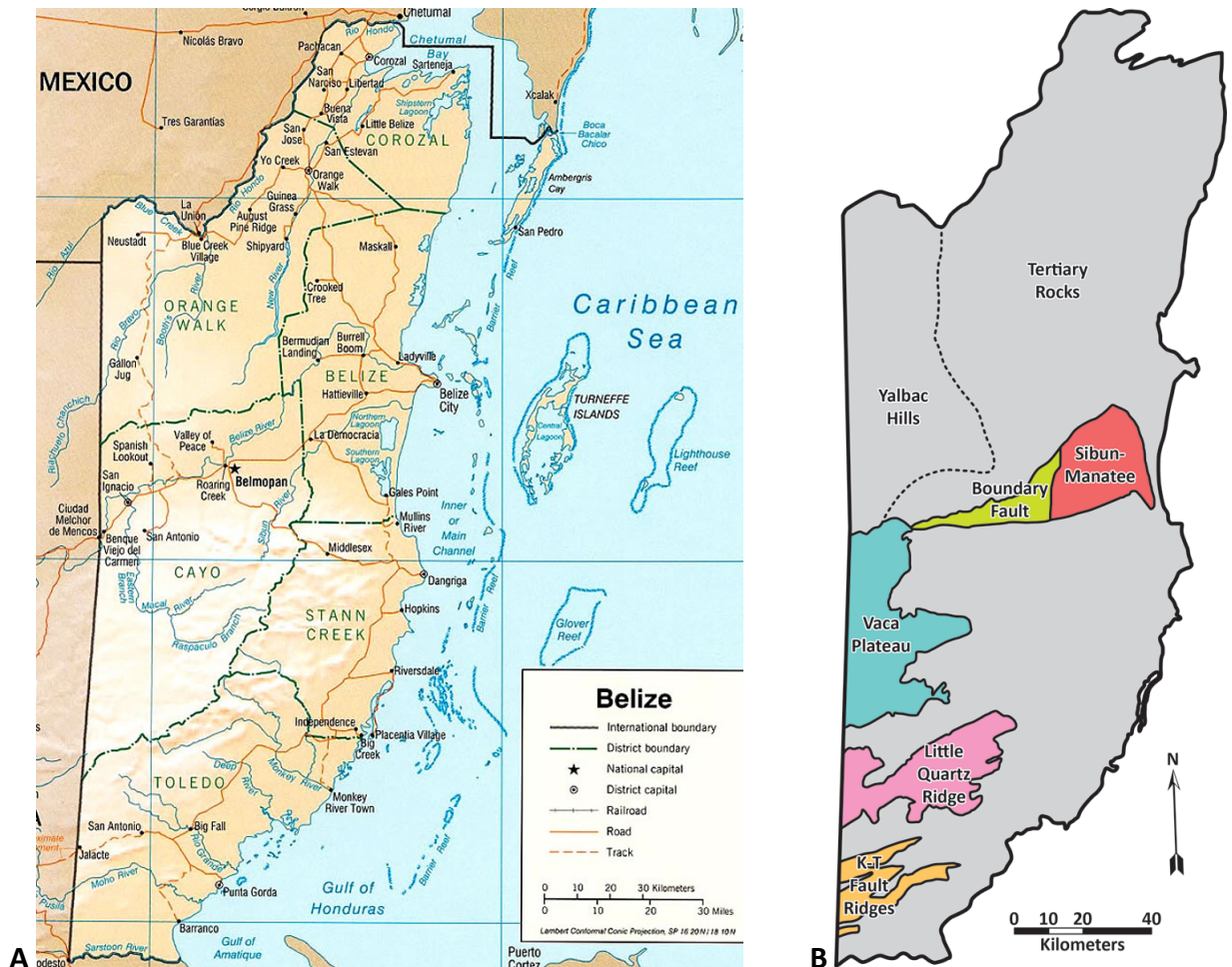
Figure 1. Maps of Belize showing: **A.** Districts, major towns, & roads. Our 2012 studies took place in the general vicinity of the communities of Big Fall, Punta Gorda, and San Antonio, in the far south of the Toledo District. **B.** The five primary mainland karst areas of Belize. Map by Steve Taylor, modified after Miller (1996).

Study Area

We have focused all of our efforts on the Toledo District, in the far south of Belize (**Figure 1**). Nearly all of the previous cave biology research in Belize has focused on the more accessible caves of the Cayo District.

Permits

Appropriate permits were secured from Institute of Archaeology, Archaeology Museum & Research Centre (Culvert Road, Belmopan City, Belize C.A.) and Forest Department (Ministry of Natural Resources and the Environment, Forest Drive, Belmopan City, Belize C.A.). In addition, we worked closely with a customs broker in Belize and US Fish & Wildlife Service personnel to complete appropriate paperwork to get material legally into the United States. Requests for specific cave locations from the present study should be directed to the Belize Institute of Archeology (Belmopan).

Results & Discussion

Nine caves were visited during the 2012 expedition. These include:

- Tiger Cave
- Indian Creek Cave #1
- Indian Creek Cave #2
- Charles Borland Cave (= Lester Quarry Cave)
- Rash Ha Cave
- Bat Cave
- Pueblo Creek Cave
- "Cave nearest the Agucate River"
- Rash Tzul Cave

At these sites, we recorded 1739 specimens. Except for site records, the collected specimens from 2012 have been shipped to the laboratory at the University of Illinois, where they are being sorted, identified and curated (labeling and storing in appropriate museum quality vials). In some cases, specimens will be shipped to taxonomic experts for species-level identification. We recorded two phyla (Arthropoda, Mollusca) and eight classes (Arachnida, Chilopoda, Diplopoda, Hexapoda, Malacostraca, Bivalvia, Gastropoda, & Turbellaria) of animals. In total, the field work for 2012 represents 357.5 person hours of effort.

Tiger Cave

This site was visited 30 April 2012 by Steven J. Taylor, JoAnn Jacoby, Aimee E. Beveridge, Geoffrey B. Hoese, Jean K. Krejca, and Kristina D. Hager, and on 4 May 2012 by Aimee E. Beveridge, Geoffrey B. Hoese, Jean K. Krejca, Kristina D. Hager. A primary objective was to collect additional specimens of the new species of millipedes found in 2011, to facilitate proper description of these species. In addition, an arachnid specialist, Jason Bond (Auburn University), was interested in additional material of the trap door spider recorded in 2011. These additional collections were successfully made, along with select collections of other material.

Indian Creek Caves #1 & #2

These two caves, only a short walk from one another in the same bluff face, were visited on 1 May 2012 by Steven J. Taylor, JoAnn Jacoby, Aimee E. Beveridge, Geoffrey B. Hoese, Jean K. Krejca, Kristina D. Hager, Manuel Bolon, Martin Chiquin, and Ernando Pap. Indian Creek Cave #2 was richer in cave-limited fauna, likely due to a well developed dark zone with significant moisture. Indian Creek Cave #1 has two entrances on opposite sides of a hill, and the air flow through the passage results in drier conditions.

Charles Borland Cave (= Lester Quarry Cave)

This site was visited on 2 May 2012 by Steven J. Taylor, Sam W. Heads, JoAnn Jacoby, Aimee E. Beveridge, Geoffrey B. Hoese, Jean K. Krejca, Kristina D. Hager, Manuel Bolon, and Solomon Coleman.

Rash Ha Cave

This site was visited on 3 May 2012 by Steven J. Taylor, Sam W. Heads, JoAnn Jacoby, Aimee E. Beveridge, Geoffrey B. Hoese, Jean K. Krejca, Kristina D. Hager, Manuel Bolon, and Samuel Tzui.

Bat Cave

The entrance area of this cave was briefly revisited on 4 May 2012 by Steven J. Taylor and Sam W. Heads.

Pueblo Creek Cave

This remote cave was visited on 5 May 2012 by Aimee E. Beveridge, Geoffrey B. Hoese, Jean K. Krejca, Kristina D. Hager, Gregorio Coc, and Mark Choc.

"Cave nearest the Aguacate River"

We were unable to determine a name for this cave, which we were taken to in place of one of the caves we had intended to visit. The site was visted by Steven J. Taylor, JoAnn Jacoby, Aimee E. Beveridge, Geoffrey B. Hoese, Jean K. Krejca, Kristina D. Hager, Abraham Kan, Salvador Ical, and Sachanias Ical on 6 May 2012. Though small, the cave has a relatively rich cave fauna.

Rash Tzul Cave

This cave was visited on 7 May 2012 by Steven J. Taylor, Sam W. Heads, JoAnn Jacoby, Aimee E. Beveridge, Geoffrey B. Hoese, Vicente Sackal, Jean K. Krejca, and Kristina D. Hager.

Invertebrate Inventories

Table 1 provides a summary of the invertebrates collected during the 2012 expedition.   Many of the taxa obtained in 2012 are the same as those recorded in 2011, and a detailed discussion of each taxon will not be repeated here. However, several notable taxa were collected. Perhaps the most interesting animal discovered during the expedition is a probably undescribed pseudoscorpion of the genus *Mexobisium* (Neobisoidea, Bochicidae; **Figure 2**).   This animal, a predator, exhibits morphological characteristics typical of a true troglobite – loss of pigmentation and extremely narrow, elongated appendages.   Other notable taxa include very large cockroaches (**Figure 3**), which may represent a new record for Belize. We also documented a number of spiders (**Figures 4, 5**), more schizomids (**Figure 6**) and terrestrial snails (**Figure 7**).

In spite of intensive collecting in 2011, we still found new species in 2012 indicating that we had not yet fully sampled the fauna of caves in southern Belize. Nonetheless, many of the animals we saw during 2012 were the same species, occurring in the same habitats. In the future, more work on microgeographic distributions and trophic positions is needed. We are only at the beginning of developing an understanding of the distribution of the species within the caves, species co-occurrence, trophic structure, and nutrient sources. More scientific study in the caves of Belize is needed before we can begin to fully understand these unique ecosystems.

We hope to return soon to continue our work, including more sampling of above-ground invertebrates to provide additional context for interpretation of the observed subterranean biodiversity.

Table 1. Summary of invertebrates collected during the 2012 Belize Biospeleology Expedition to the Toledo District.

Phylum	Class	Order	Family	Count
Unidentified invertebrates (invert eggs, etc.)				25
Arthropoda	Arachnida	Acari		22
Arthropoda	Arachnida	Amblypygi		52
Arthropoda	Arachnida	Araneae		275
Arthropoda	Arachnida	Ixodida		57
Arthropoda	Arachnida	Opiliones		16
Arthropoda	Arachnida	Pseudoscorpiones		9
Arthropoda	Arachnida	Schizomida		15
Arthropoda	Arachnida	Scorpiones		5
Arthropoda	Arachnida	Thelyphonida		1
Arthropoda	Chilopoda			6
Arthropoda	Diplopoda			244
Arthropoda	Hexapoda	Blattodea		14
Arthropoda	Hexapoda	Coleoptera		67
Arthropoda	Hexapoda	Coleoptera	Carabidae	3
Arthropoda	Hexapoda	Coleoptera	Cerambycidae	10
Arthropoda	Hexapoda	Coleoptera	Chrysomelidae	1
Arthropoda	Hexapoda	Coleoptera	Curculionidae	2
Arthropoda	Hexapoda	Coleoptera	Histeridae	1
Arthropoda	Hexapoda	Coleoptera	Lampyridae	2
Arthropoda	Hexapoda	Coleoptera	Psephenidae	5
Arthropoda	Hexapoda	Coleoptera	Scarabaeidae	2
Arthropoda	Hexapoda	Coleoptera	Staphylinidae	20
Arthropoda	Hexapoda	Coleoptera	Tenebrionidae	5
Arthropoda	Hexapoda	Collembola		136
Arthropoda	Hexapoda	Dermaptera		2
Arthropoda	Hexapoda	Diplura		12
Arthropoda	Hexapoda	Diptera		33
Arthropoda	Hexapoda	Diptera	Culicidae	2
Arthropoda	Hexapoda	Diptera	Mycetophilidae	1
Arthropoda	Hexapoda	Diptera	Phoridae	1
Arthropoda	Hexapoda	Diptera	Psychodidae	1
Arthropoda	Hexapoda	Diptera	Sciaridae	9
Arthropoda	Hexapoda	Diptera	Tabanidae	1
Arthropoda	Hexapoda	Diptera	Tachinidae	1
Arthropoda	Hexapoda	Diptera	Tipulidae	4
Arthropoda	Hexapoda	Hemiptera		20
Arthropoda	Hexapoda	Hemiptera	Cercopidae	6
Arthropoda	Hexapoda	Hemiptera	Cicadellidae	5
Arthropoda	Hexapoda	Hemiptera	Coreidae	2
Arthropoda	Hexapoda	Hemiptera	Cydnidae	2
Arthropoda	Hexapoda	Hemiptera	Gerridae	2
Arthropoda	Hexapoda	Hemiptera	Lygaeidae	2
Arthropoda	Hexapoda	Hemiptera	Pentatomidae	1

(Continued on following page)

Table 1. Continued.

Phylum	Class	Order	Family	Count
Arthropoda	Hexapoda	Hemiptera	Reduviidae	50
Arthropoda	Hexapoda	Hemiptera	Veliidae	12
Arthropoda	Hexapoda	Hymenoptera	Formicidae	59
Arthropoda	Hexapoda	Hymenoptera		1
Arthropoda	Hexapoda	Isoptera		12
Arthropoda	Hexapoda	Lepidoptera		39
Arthropoda	Hexapoda	Lepidoptera	Nymphalidae	1
Arthropoda	Hexapoda	Lepidoptera	Tineidae	13
Arthropoda	Hexapoda	Lepidoptera	Tortricidae	1
Arthropoda	Hexapoda	Neuroptera	Myrmeleontidae	1
Arthropoda	Hexapoda	Orthoptera		3
Arthropoda	Hexapoda	Orthoptera	Acrididae	16
Arthropoda	Hexapoda	Orthoptera	Gryllidae	161
Arthropoda	Hexapoda	Orthoptera	Gryllidae: Hapithinae	8
Arthropoda	Hexapoda	Orthoptera	Gryllidae: Nemobiinae	11
Arthropoda	Hexapoda	Orthoptera	Gryllidae: Pentacentrinae	2
Arthropoda	Hexapoda	Orthoptera	Gryllidae: Phalangopsinae	21
Arthropoda	Hexapoda	Orthoptera	Ripipterygidae	2
Arthropoda	Hexapoda	Orthoptera	Tetrigidae	2
Arthropoda	Hexapoda	Orthoptera	Tettigoniidae	5
Arthropoda	Hexapoda	Orthoptera	Tettigoniidae: Copiphorinae	2
Arthropoda	Hexapoda	Orthoptera	Tettigoniidae: Phaneropterinae	4
Arthropoda	Hexapoda	Orthoptera	Tettigoniidae:Conocephalinae	4
Arthropoda	Hexapoda	Orthoptera	Thericleidae	1
Arthropoda	Hexapoda	Orthoptera	Tridactylidae	1
Arthropoda	Hexapoda	Orthoptera	Tridactylidae: Tridactylinae	10
Arthropoda	Hexapoda	Plecoptera		3
Arthropoda	Hexapoda	Protura		8
Arthropoda	Hexapoda	Thysanura		7
Arthropoda	Hexapoda			20
Arthropoda	Malacostraca	Decapoda	Trichodactylidae	1
Arthropoda	Malacostraca	Decapoda: Brachyura		2
Arthropoda	Malacostraca	Decapoda: Caridea		1
Arthropoda	Malacostraca	Isopoda		85
Arthropoda	Malacostraca	Isopoda	Ostracoda	20
Arthropoda				2
Mollusca	Bivalvia	Unionoida	Unionidae	25
Mollusca	Gastropoda			20
Platyhelminthes	Turbellaria	Tricladida	Geoplanidae	1
			TOTAL	**1739**

Figure 2. *Mexobisium*? sp. from a Toledo District cave, likely an undescribed species of pseudoscorpion (also pictured on report cover). Photo © Jean Krejca.

Figure 3. A large, but still immature, cockroach in a cave just outside of Punta Gorda, Toledo District. Photo ©Aimee Beveridge.

Figure 4. A female spider carrying her eggs. This pale species appears to be cave adapted. The irridescence visible on the legs is likely caused by structural refraction of light. Photo © Jean Krejca.

Figure 5. A commonly encountered cave-inhabiting spider. This female is holding her egg case with already-hatched young spiderlings. Photo © Jean Krejca.

Figure 6. This impressive schizomid (Arachnida) appears not to be a cave-limited species. Photo © Jean Krejca.

Figure 7. A tiny terrestrial snail, possibly cave adapted, a the tip of collecting forceps. Photo © Geoff Hoese.

Environmental Data

Temperature, humidity, and light data have been collected at all caves visited during the 2011 & 2012 expeditions. Those data are presented here (**Table 2, Figures 8-11**). Air and 2 cm soil temperatures are strongly positively correlated (best fit linear regression: SoilTemp = 0.3622xAirTemp + 15.203, R^2 = 0.45003) (**Figure 8**), with air temperatures varying more widely than soil temperatures. As expected, temperatures were less variable in the twilight and dark zones.   Because we only sampled near the end of the dry season (due to logistical considerations), the data do not show the full range of variation in surface temperatures.   We use soil temperature as a more representative measure of temperature when comparing to light and humidity data, below.

The 2 cm soil temperature and relative humidity were negatively correlated (best fit linear regression: SoilTemp = -0.1086xRH + 33.386, R^2 = 0.33404), with higher humidities associated with lower temperatures (**Figure 9**). Twilight and dark zone humidities, were above 80%, while surface and entrance zone humidities varied more widely.

The 2 cm soil temperature was consistently below 25 ˚C when light levels were low (below 1 Lux), which generally correlated with the dark & twilight zones (**Figure 10**), at higher temperatures, generally in the entrance zone and on the surface, the soil temperature was generally positively correlated with available light. Similarly, relative humidity was highest at the lowest light levels, which generally correlated with the dark & twilight zones (**Figure 11**), at

higher light levels, generally in in the entrance zone and on the surface, relative humidity was lower and negatively correlated with available light.

More data are needed to allow correlation of habitat data with the distributions of individual invertebrate taxa, but note that Soto-Adames & Taylor (2013, pg 69, Figs 66-69), using data from our Belize collections, found that patterns of microclimatic data correlated well with degree of cave adaptation for two newly described springtail species (see **Appendix 1**).

Peer-reviewed papers

Our fieldwork has resulted in a number of discoveries that are in various stages of publication. Four papers have been published thus far, including the description of a new species of tridactyloid orthopteran (Heads & Taylor 2012), a new species of spider (Bond & Taylor 2013), two new species of springtails (Soto-Adames & Taylor 2013), and a new country record for a silverfish (Espinasa et al. 2013). Various other publications are in preparation. Published, peer-reviewed works are included in **Appendix 1**.

Relevance

Our work fits well with Belize's national Environmental and Natural Resources Research Agenda (ERI 2010). Specifically, our work addresses terrestrial research priority needs delineated by ERI (2010):

> *Determine the impacts, including cumulative impacts, of different land-use practices on Belize's natural resources and hydrology.*

> *Determine the ecosystems, and associated species, in Belize that are of national and international conservation concerns and assess their status.*

Providing local, regional and national decision makers with better information on the interconnectedness of subterranean communities and above ground land use practices will lead to better management of natural resources.
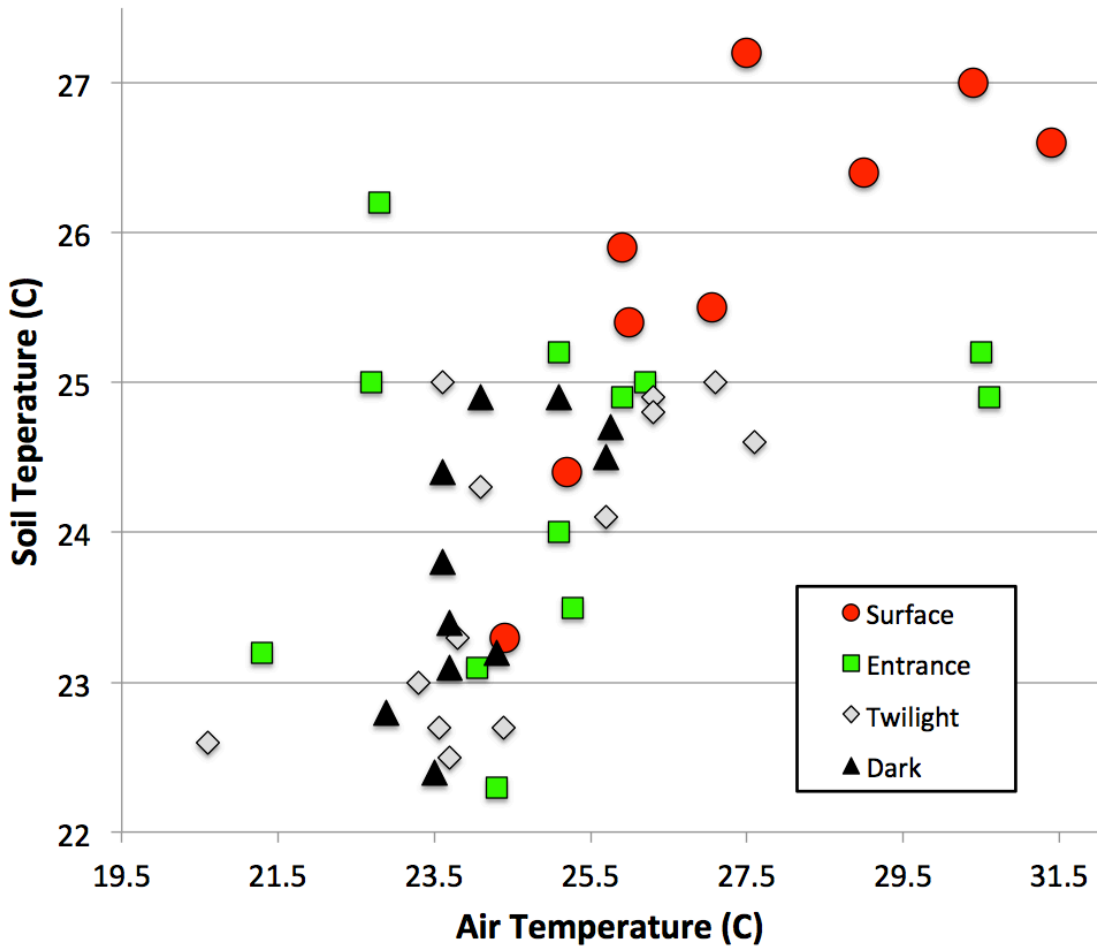
Figure 8. Soil and Air temperature data from caves sampled in 2011 (9-16 April) and 2012 (30 April - 7 May) in the Toledo District of Belize. Cave zone (Surface, Entrance, Twilight, Dark) was determined during site visit. Air temperature collected with an ExTech probe, 2 cm soil temperature collected with a Check Temp probe.
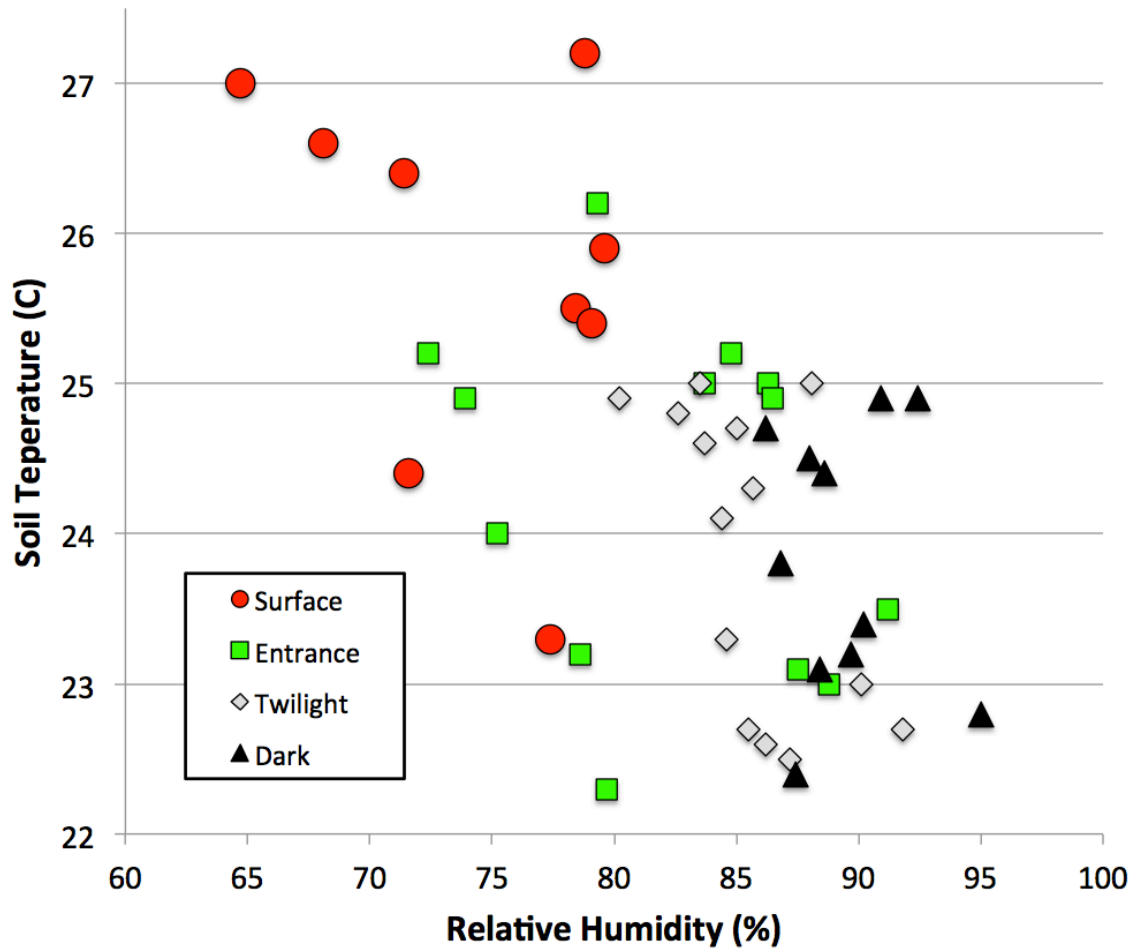
Figure 9. Soil temperature and humidity data from caves sampled in 2011 (9-16 April) and 2012 (30 April - 7 May) in the Toledo District of Belize. Cave zone (Surface, Entrance, Twilight, Dark) was determined during site visit. Relative humidity data collected with an ExTech probe, 2 cm soil temperature collected with a Check Temp probe.

Figure 10. Soil temperature and light data from caves sampled in 2011 (9-16 April) and 2012 (30 April - 7 May) in the Toledo District of Belize. Cave zone (Surface, Entrance, Twilight, Dark) was determined during site visit. Light levels measured with an ExTech light meter which does not register light below 0.1 lux - lower light levels were thus coded as 0.01 lux, and complete absence of light was coded as 0.001 lux to allow visualization by plotting on a Log_{10} scale, 2 cm soil temperature collected with a Check Temp probe.
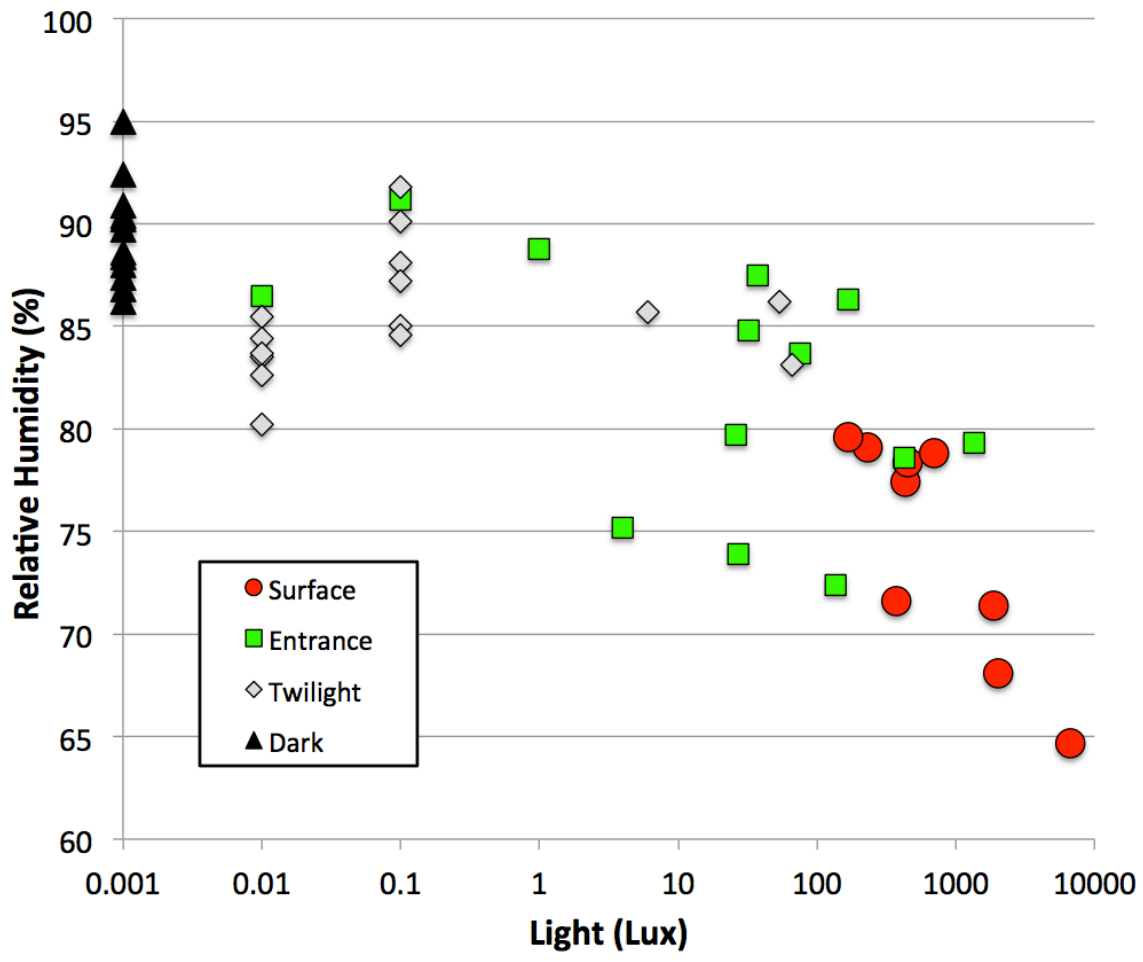
Figure 11. Humidity and light data from caves sampled in 2011 (9-16 April) and 2012 (30 April - 7 May) in the Toledo District of Belize. Cave zone (Surface, Entrance, Twilight, Dark) was determined during site visit. Light levels measured with an ExTech light meter which does not register light below 0.1 lux - lower light levels were thus coded as 0.01 lux, and complete absence of light was coded as 0.001 lux to allow visualization by plotting on a Log_{10} scale, Relative humidity data collected with an ExTech probe.

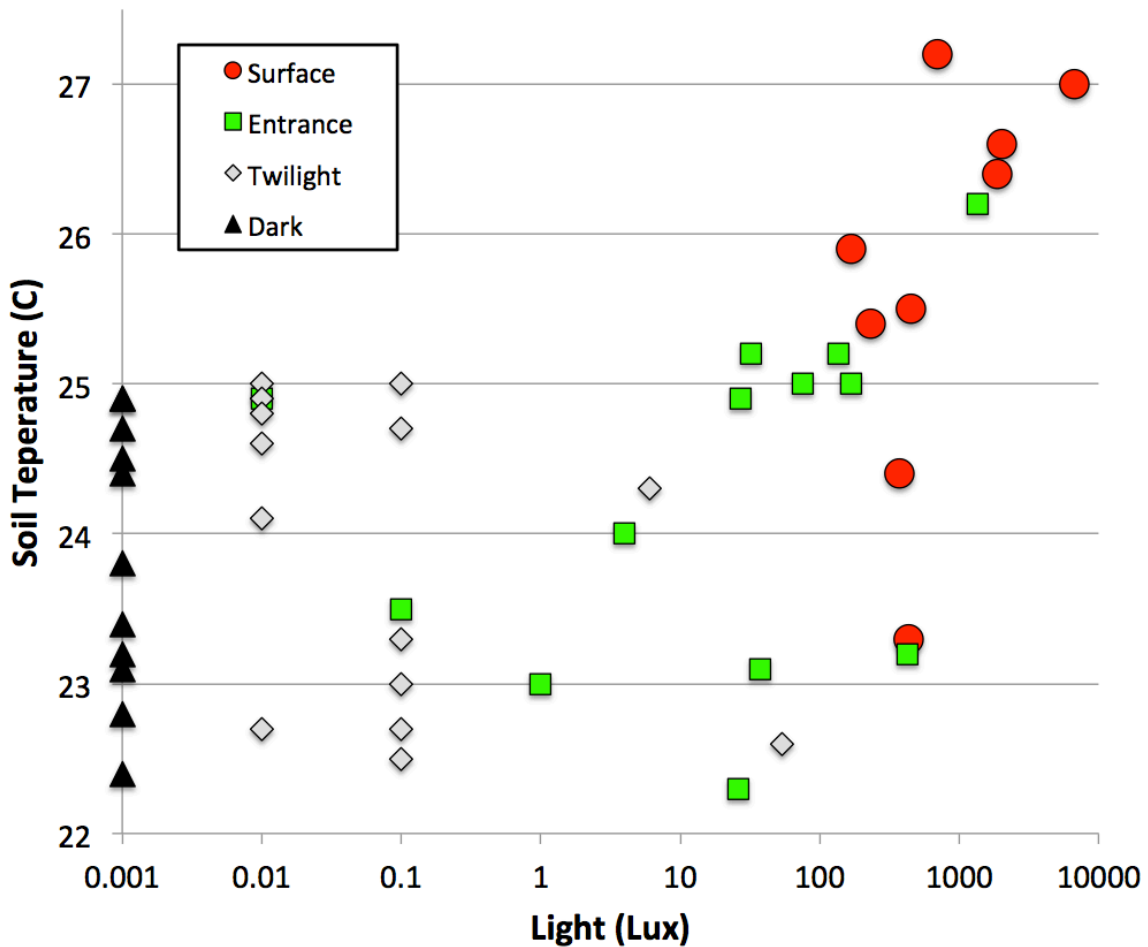**Table 2**. Environmental parameters from caves sampled in 2011 (9-16 April) and 2012 (30 April - 7 May) in the Toledo District of Belize. Cave zone (Surface, Entrance, Twilight, Dark) was determined during site visit. Light levels measured with an ExTech light meter which does not register light below 0.1 lux - lower light levels were thus coded as 0.01 lux, and complete absence of light was coded as 0.001 lux to allow visualization by plotting on a Log_{10} scale. Relative humidity data collected with an ExTech probe. Air temperature collected with an ExTech probe. 2 cm soil temperature were collected with a Check Temp probe.

Year	Meter Num.	Zone	Cave	Light (lux)	RH (%)	Air Temp (C)	Soil Temp (C)
2011	8999	Surface	Tiger Cave				
2011	9000	Entrance	Tiger Cave	425	78.6	21.3	23.2
2011	9001	Twilight	Tiger Cave	54	86.2	20.6	22.6
2011	9002	Twilight	Tiger Cave	0.1	88.1	23.6	25
2011	9003	Twilight	Tiger Cave	0.1	87.2	23.7	22.5
2011	9004	Dark	Tiger Cave	0	87.4	23.5	22.4
2011	9005	Dark	Tiger Cave				
2011	9008	Twilight	Bat Cave	66.6	83.1	25.6	
2011	9009	Surface	Blue Creek	6690	64.7	30.4	27
2011	9010	Entrance	Blue Creek	27	73.9	30.6	24.9
2011	9011	Twilight	Blue Creek	0.1	85		24.7
2011	9012	Dark	Blue Creek	0	86.2	25.8	24.7
2011	9013	Surface	Yok Balum	373	71.6	25.2	24.4
2011	9014	Entrance	Yok Balum	4	75.2	25.1	24
2011	9015	Dark	Yok Balum	0	89.7	24.3	23.2
2011	9016	Dark	Yok Balum	0	90.2	23.7	23.4
2011	9017	Dark	Yok Balum	0	90.4	23.7	
2011	9018	Entrance	Yok Balum				
2011	9019	Twilight	Yok Balum				
2011	9020	Surface	Okebal Ha	429	77.4	24.4	23.3

Table 2. Continued.

Year	Meter Num.	Zone	Cave	Light (lux)	RH (%)	Air Temp (C)	Soil Temp (C)
2011	9021	Entrance	Okebal Ha	26	79.7	24.3	22.3
2011	9022	Twilight	Okebal Ha	0.1	84.6	23.8	23.3
2011	9023	Dark	Okebal Ha	0	88.4	23.7	23.1
2011	9024	Dark	Small cave near Okebal Ha	0	86.8	23.6	23.8
2011	9025	Twilight	Small cave near Okebal Ha	0.1	90.1	23.3	23
2011	9026	Entrance	Small cave near Okebal Ha	1	88.8		23
2011	9027	Dark	Cave near Pueblo Creek Cave	0	95	22.9	22.8
2011	9028	Twilight	Cave near Pueblo Creek Cave	0.1	91.8	23.6	22.7
2011	9029	Entrance	Cave near Pueblo Creek Cave	0.1	91.2	25.3	23.5
2012	9040	Surface	Tiger Cave	453	78.4	27.1	25.5
2012	9041	Entrance	Tiger Cave	37	87.5	24.1	23.1
2012	9042	Twilight	Tiger Cave	0.01	85.5	24.4	22.7
2012	9043	Surface	Indian Creek Cave # 2	1884	71.4	29.0	26.4
2012	9044	Entrance	Indian Creek Cave # 2	1340	79.3	22.8	26.2
2012	9045	Twilight	Indian Creek Cave # 2	0.01	84.4	25.7	24.1
2012	9046	Dark	Indian Creek Cave # 2	0	88	25.7	24.5
2012	9047	Dark	Indian Creek Cave # 2	0	88.6	23.6	24.4
2012	9048	Entrance	Indian Creek Cave # 1	168	86.3	22.7	25
2012	9049	Twilight	Indian Creek Cave # 1	6	85.7	24.1	24.3
2012	9050	Surface	Charles Borland Cave (= Lester Quarry Cave)	233	79.1	26.0	25.4
2012	9051	Entrance	Charles Borland Cave (= Lester Quarry Cave)	32	84.8	25.1	25.2
2012	9052	Surface	Rash Ha Cave	167	79.6	25.9	25.9

Table 2. Continued.

Year	Meter Num.	Zone	Cave	Light (lux)	RH (%)	Air Temp (C)	Soil Temp (C)
2012	9053	Entrance	Rash Ha Cave	0.01	86.5	25.9	24.9
2012	9054	Dark	Rash Ha Cave	0	90.9	24.1	24.9
2012	9055	Dark	Rash Ha Cave	0	92.4	25.1	24.9
2012	9056	Surface	Cave nearest to the Aguacate River	2024	68.1	31.4	26.6
2012	9057	Entrance	Cave nearest to the Aguacate River	135	72.4	30.5	25.2
2012	9058	Twilight	Cave nearest to the Aguacate River	0.01	83.5	27.1	25
2012	9059	Twilight	Cave nearest to the Aguacate River	0.01	83.7	27.6	24.6
2012	9060	Surface	Rash Tzul Cave	696	78.8	27.5	27.2
2012	9061	Entrance	Rash Tzul Cave	75	83.7	26.2	25
2012	9062	Twilight	Rash Tzul Cave	0.01	80.2	26.3	24.9
2012	9063	Twilight	Rash Tzul Cave	0.01	82.6	26.3	24.8

Figure 12. 2012 Belize Biospeleology Expedition members: L Manuel Bolon (local guide), Jean Krejca, Geoff Hoese, Amy Beveridge, Kristina Hager, Steve Taylor, JoAnn Jacoby, and Sam Heads.

Acknowledgements

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Appendix 1

**Published, peer-reviewed works
based on our fieldwork in
southern Belize**

RESEARCH ARTICLE

A new species of *Tarsonops* (Araneae, Caponiidae) from southern Belize, with a key to the genera of the subfamily Nopinae

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Abstract

A new species of Caponiidae, *Tarsonops irataylori* **sp. n.** is described from southern Belize, and a key to the genera of the subfamily Nopinae is provided.

Keywords

Spider, *Tarsonops*, new species, Belize

Introduction

Comprising 84 species parceled among 15 genera (Platnick 2012), the spider family Caponiidae is widely distributed but not currently known from Australia or Europe. Petrunkevitch (1939) divided the Caponiidae into two subfamilies, Caponiinae and Nopinae, the latter of which is characterized by subsegmented tarsi and has a New World distribution with 53 species described from North, South, and Central America and numerous species known from the Caribbean. While recent authors have ques-

tioned the monophyly of the Caponiinae, citing a lack of synapomorphies (Jiménez et al. 2011), the Nopinae is generally regarded as a valid group with subsegmented tarsi as a distinguishing feature. However, Platnick (1994) suggests that caponine taxa with fewer than eight eyes may be more closely related to nopines.

The genus *Tarsonops*, the subject of this paper, was erected by Chamberlin (1924) to accommodate the species, *Nops sternalis*, originally described by Banks (1898). At the time, Chamberlin (1924) also described, on the basis of female specimens, three additional species, *Tarsonops clavis, Tarsonops sectipes,* and *Tarsonops systematicus,* all collected in Mexico adjacent to the Gulf of California. He also provided a key to species based on female anatomy, with an emphasis on leg morphology. Subsequently, Gertsch (1935) published additional records for *Tarsonops systematicus*, collected in southern Texas, and Ubick (2005) reports that this species also occurs in California and Arizona and illustrates the male pedipalp (figure 18.10). Although numerous new species have been described in the family Caponiidae, including its subfamily Nopinae since the 1930s, no new species of *Tarsonops* have been described.

The primary purpose of this paper is to describe a new species of *Tarsonops* collected from Belize and to provide a key for the nopine genera. Unfortunately, this newly discovered species is known from only a single specimen. While a large of number of new species are described only from single specimens, greater than 1/6th of all species (Lim et al. 2012), it is with some trepidation that we propose a new taxon on the basis

Table 1. Character states for genera of Nopinae (Caponiidae) compared to *Tarsonops irataylori* sp. n.

Character	Taxon						
	Cubanops	*Nops*	*Nopsides*	*Nyetnops*	*Orthonops*	*Tarsonops* (all other species)	*Tarsonops irataylori* sp. n.
Number of eyes	2	2	4	2	2	2	2
Ventral translucent keel on the anterior metatarsi and translucent extension of the membrane between the anterior metatarsi and tarsi	yes	yes	no	no	yes	yes	no
Distally expanded endites	no	no	yes	yes	no	no	no
Patterned carapace	yes	no	no	yes	no	no	no
Dorsally extended inferior claw	no	yes	yes	no	no	no	no
Wide labium	yes	no	no	no	no	no	no
Bisegmented metatarsi IV	yes	yes	?	no	no	no	no
Palpal bulb longer than cymbium, distinction evident between bulb and embolus only by differences in cuticular surface	no	no	no	yes	no	no	no
Anterior tarsus with a distinct suture dividing it into two, the distal of which is shorter (versus anterior tarsus with several false sutures, most distinct of which is proximal	yes	yes	yes	yes	yes	no	no

of a single unique specimen. However, the morphological uniqueness of the species, the extension of the genus distribution, and recognition of important species level and morphological diversity serves as the impetus despite any misgivings. Moreover, it may very well be, given the combination/absence of characteristics (Table 1) for this species, that it may ultimately represent a new genus or species group, however, its palpal morphology closely resembles that described for *T. systematicus* by Ubick (2005). Although two of the nopine genera are monotypic (*Nopsides* Chamberlin 1924 and *Nyetnops* Platnick and Lise 2007) it is our opinion that the description of a new genus should be postponed until more material, including the female, and potential other species become available.

Key to the genera of the subfamily Nopinae (Caponiidae)

1   4 eyes...***Nopsides* Chamberlin, 1924**
1'   2 eyes...**2**
2   Palpal endites (both sexes) expanded anteriorally, broadest at anterior apex of labium (see Platnick and Lise 2007); palpal bulb longer than cymbium, distinction between bulb and emobolus not evident except by sculpturing ...
        .... ***Nyetnops* Platnick & Lise, 2007**
2'   Palpal endites (both sexes) not broadest anterior to apex of labium; normal palpal bulb with distinct embolus **3**
3   Anterior tarsus with distinct suture that divides article into two distinct sub-segments **4**
3'   Anterior tarsus with several false sutures, lacking distinct suture, not divided into two distinct sub-segments...................... ***Tarsonops* Chamberlin, 1924**
4   Metatarsus IV divided into two distinct subsegments..................................**5**
4'   Metatarsus IV entire ....***Orthonops* Chamberlin, 1924**
5   Tarsus I with inferior claw extended dorsally between superior claws; carapace generally lacking distinct patterning....................***Nops* MacLeay, 1839**
5'   Tarsus I with inferior claw not extending dorsally between superior claws; carapace patterned .... ***Cubanops* Sánchez-Ruiz et al., 2010**

Materials and methods

All measurements were taken with a Leica MZ16.5 stereomicroscope equipped with a 10× ocular and ocular micrometer scale. We measured the left appendage, usually in retrolateral view, using the highest magnification possible. Legs I-IV (femur, patella, tibia, metatarsus, tarsus) and palp article lengths (femur, patella, tibia, cymbium) given in order of proximal to distal. Illustrations were prepared using a Visionary Digital Imaging System (Ashland, VA). Photographs were recorded in multiple focal planes and assembled using the Zerene Stacker software package (Zerene Systems

LLC, Richland, WA). The habitus illustration was constructed from whole body images that were bisected, copied, and reflected in Adobe Photoshop (Adobe Systems, Inc.) to produce a roughly symmetrical image (technique described in Bond 2012). Measurements in millimeters.

Taxonomy

Tarsonops irataylori sp. n.
urn:lsid:zoobank.org:act:4B93D052-EA8C-43E7-A5D4-28A52FE05DBE
http://species-id.net/wiki/Tarsonops_irataylori
Map 1, Figs 1–7

Type material. Holotype male from BELIZE: **Toledo District**: Cave near Pueblo Creek Cave: 37 km WNW of Punta Gorda, 16°12'N, 89°08'W (Figure 1): 16 April 2011: sjt11-018: Coll. Michael E. Slay, Jean K. Krejca, Christy M. Slay, Geoffrey B. Hoese, Germano Coe. Sample# 253, Specimen# 0222. On dry flowstone in entrance zone, 0.1 lux, air temperature 25.7 °C, soil temperature 23.5 °C, relative humidity 91.2%. Deposited in the Auburn University Museum of Natural History collection.

Etymology. The specific epithet honors the contributions of Mr. Ira W. Taylor to the study of subterranean ecosystems.
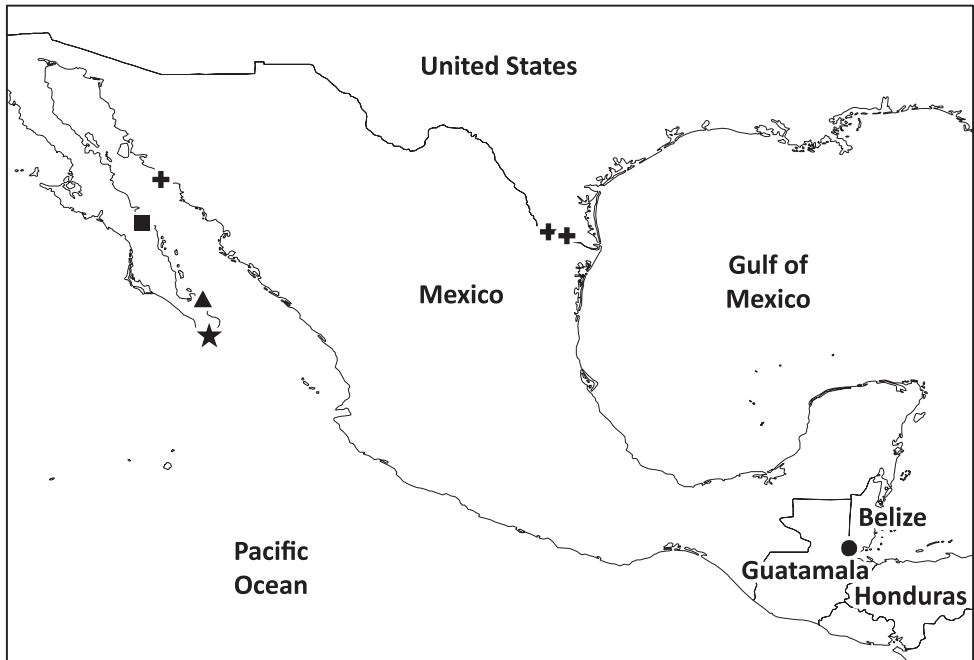
Map 1. Distribution of *Tarsonops* species: *T. sternalis* (star), *T. sectipes* (triangle), *T. clavis* (square), *T. systematicus* (crosses, also recorded from California and Arizona, see Ubick *et al.* [2005]), *T. irataylori* sp. n. (circle).
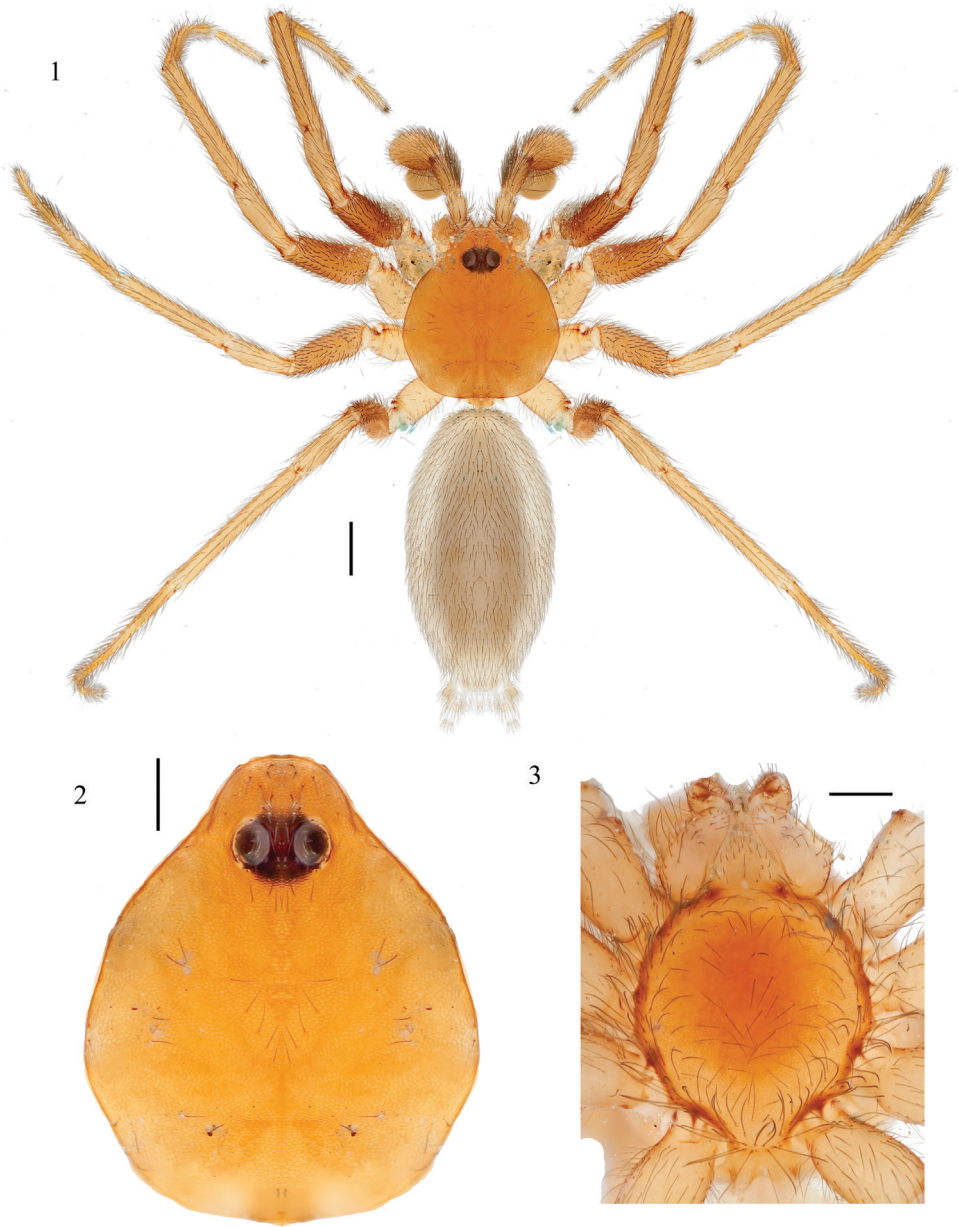
Figures 1–3. *Tarsonops irataylor* sp. n., male holotype **1** habitus, dorsal view **2** carapace, dorsal view **3** cephalothorax, ventral view. Scale bar = 0.50 mm (Fig. 1); 0.25 mm (Figs 2, 3)

Diagnosis. *Tarsonops irataylori* sp. n. differs from all known species of *Tarsonops* by the absence of a ventral translucent keel on the anterior metatarsi and a highly reduced translucent extension of the membrane between the anterior metatarsi and tarsi.

Description of male holotype. *Specimen preparation and condition.* Specimen collected live, preserved in 70% ethanol. Coloration may be faded. Pedipalp, leg I left
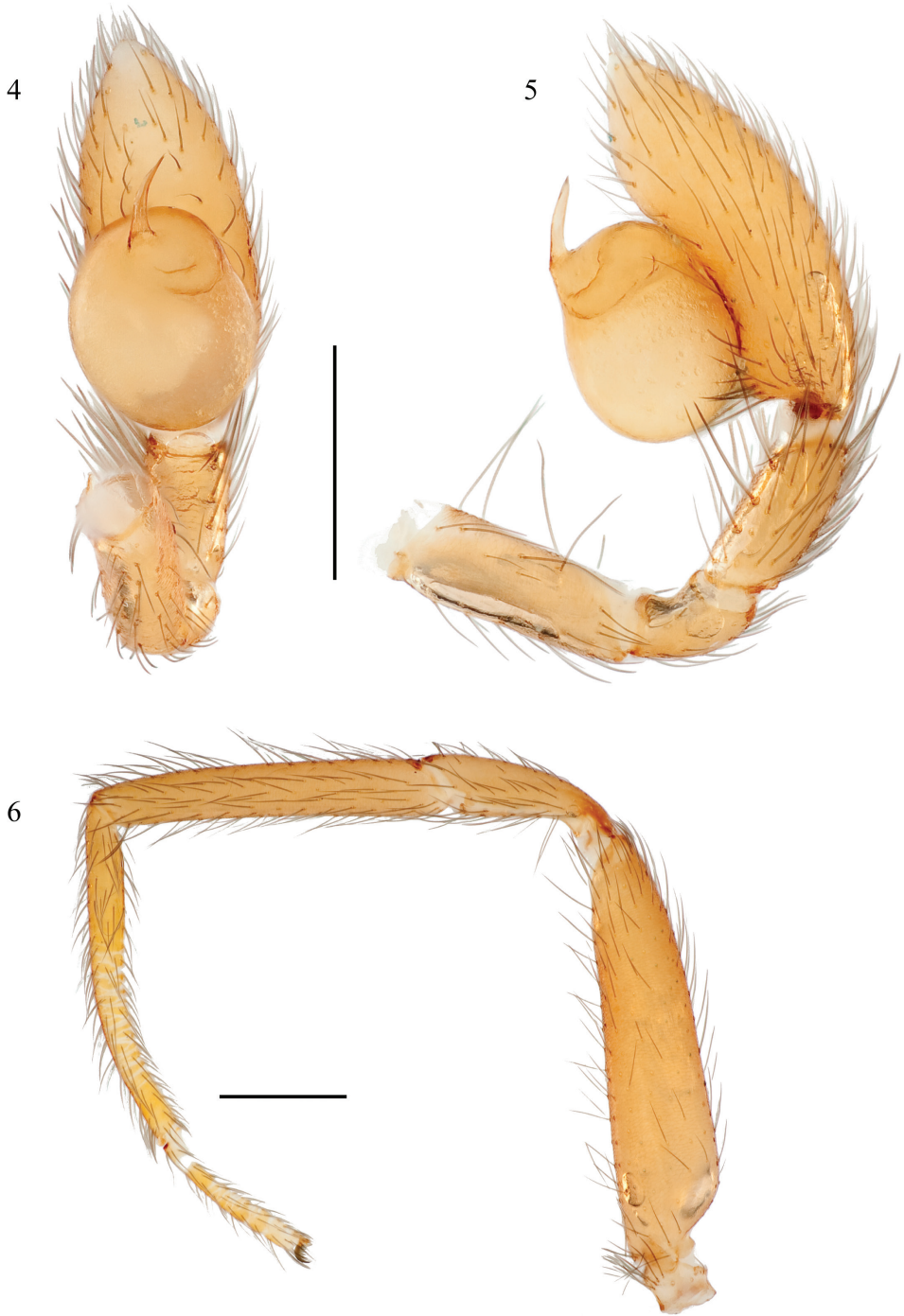
Figures 4–6. *Tarsonops irataylor* sp. n., male holotype. **4** left pedipalp, ventral view **5** left pedipalp, retrolateral view **6** leg I, retrolateral view. Scale bars = 0.50 mm.

side removed and stored in vial with specimen. *General coloration.* Carapace, chelicerae, legs light orangish red (Figs 1, 2). Abdomen uniform very pale grayish brown dorsally. No dorsal carapace or abdominal patterning. *Cephalothorax.* Carapace 1.56 long, 1.40 wide, with sparse thin setae, surface lightly granular (Fig. 3), pars cephalica elevated slightly. Clypeus height 1.5× eye diameter. Two eyes, eyes separated by distance equal to radius. Sternum lightly setose, widest between coxae II, III (Fig. 4). Sternum length 1.12, width 1.00. Palpal endites rectangular, anterior margin rounded, extending slightly beyond anterior margin of labium (Fig. 4). Labium width 0.348, length 0.244. *Legs.* Leg I: 1.67, 0.740, 1.34, 1.41, 0.626; Leg II: 1.672, 0.751, 1.335, 1.485, 0.568; Leg III: 1.401, 0.600, 1.120, 1.404, 0.720; Leg IV: 1.814, 0.663, 1.509, 2.000, 1.028. Legs I-IV metatarsi and tarsi subsegmented distally (Fig. 7). Superior tarsal claw, Leg I with 5 teeth; inferior tarsal claw not extending dorsally between superior tarsal claws. Tarsus I with two trichobothria. Metatarsus I with 4 trichobothria, arranged along dorsal midline, lacking a ventral translucent keel, translucent extension of the membrane between the anterior metatarsus I and tarsus I greatly reduced, barely evident on close examination as wrinkled bump. Leg I illustrated in Figure 7. *Pedipalp.* (Figs 5, 6): 0.522, 0.270, 0.357, 0.940; bulb total length 0.618. Dense group of setae on prolateral tibial surface. Embolus short, less than 1/4th length of bulb, tapering to sharp single point, bulb sub-spherical.

Discussion

Although this species was taken from just inside a cave, it does not exhibit any obvious troglomorphies, and may be accidental in this habitat. The description of *Tarsonops irataylori* sp. n. extends the range of the genus 9 degrees east and 6.8 degrees south from the previously known range. A number of undescribed species of *Tarsonops* are known from collections in Mexico (Platnick, pers. comm. 31 October 2011).

   Tarsonops irataylori sp. n. is the first species of *Tarsonops* described which lacks a ventral translucent keel on the anterior metatarsi and marked translucent extension of the membrane between the anterior metatarsi and tarsi. Chamberlin's (1924) diagnoses of the genus does not list these characters, thus we have taken the conservative approach of placing the species in this genus. As discussed above, future studies in which more specimens are examined, may further warrant the establishment of a new genus to accommodate this somewhat unusual species.

Acknowledgements

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A new record for *Nicoletia phytophila* (Nicoletiidae: Zygentoma: Insecta) from a cave in Belize

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Nicoletia phytophila Gervais, 1844 (=*Nicoletia meinerti* Silvestri, 1905) was first described from specimens collected in a greenhouse in Paris (Gervais 1844). It has a vast geographical distribution of primarily tropical localities in the Old and New World as well as greenhouses in Europe (Wygodzinsky and Hollinger 1977). This species is of particular interest because all populations consist exclusively of parthenogenetic females (Wygodzinsky and Hollinger 1977) that reproduce clonally, with the exception of Hawaii (Silvestri 1912) and the Galapagos Islands (Palct 1976), where there are males.

Although populations from Venezuela and Hawaii (Silvestri 1905, 1912) initially were described as a separate species, *N. meinerti*, Wygodzinsky (1980) considered them to be conspecific, and thus synonymous with *N. phytophila*. According to Mendes (1988), the subfamily Nicoletinae includes a single species, *N. phytophila*, which is also the type species of the type genus of the family Nicoletiidae.

In contrast to Wygodzinsky and Mendes' findings, when Espinasa et al. (2011) sequenced the 16S rRNA gene from a Puerto Rico cave population, its 16S rRNA sequences were considerably different from populations from Mexico, Cuba, and the Grenadine Islands, revealing that divergence was more consistent with an origin millions of years ago. Espinasa et al. (2011) rejected the hypothesis that *Nicoletia's* cosmopolitan distribution was the result of recent indirect human action, such as the transporting of garden soil from one area to another. Espinasa et al. (2011) proposed

that while perhaps most of the world populations of *Nicoletia* belong to a single clonal phyletic line (*N. phytophila sensu stricto*) whose dispersal could in part be associated with human activities, there may be other "wild" populations of parthenogenetic *Nicoletia* with a more ancient and independent origin which would warrant classification as a distinct species.

Nicoletia phytophila is known to inhabit caves. They have been reported from the first chamber of Culebrones Cave, near the Mata de Plátano Field Station and Nature Reserve (Puerto Rico) (Espinasa et al. 2011) and from volcanic caves in Hawaii such as in Kula Kai (Howarth 1981). We report *N. phytophila* from a cave in Belize, and analyze the 16SrRNA sequence of the Belize specimen. We compare its DNA sequence to other populations of *Nicoletia* to determine if it shares close relationship to the Puerto Rico population, to the nearby Mexican populations, or to an altogether independent group.

The entrance, twilight zone, and dark zone of 14 caves in the Toledo District of Belize were surveyed for invertebrates in 2011 (9–16 April) and 2012 (30 April–7 May). Temperature, light, and humidity were recorded with handheld probes. Samples were hand collected into ethanol, and returned to the laboratory for sorting and distribution to taxonomic experts.

Genomic DNA was extracted using Qiagen's DNEasy® Tissue Kit by digesting a leg in lysis buffer. Amplification and sequencing of the 16S rRNA fragment was done as in Espinasa and Giribet (2009), following standard protocols and primers for the 16S rRNA fragment used in the past for nicoletiids. Chromatograms obtained from the automated sequencer were read and contigs made using the sequence editing software Sequencher™ 3.0. External primers were excluded from the analyses. Sequence data from the Belize specimen were compared to all nicoletiids where 16S rRNA has been sequenced, including *Nicoletia phytophila* from Central America, the Caribbean, and Malaysia. Sequences were aligned and a neighbor-joining analysis was performed using ClustalW.

Out of more than 2,000 specimens of various invertebrate species recorded from the 14 caves in Belize, only a single *Nicoletia phytophila* specimen was collected (**Figure 1**), with locality and habitat data as follows: Belize: Toledo District: Rash Tzul Cave (**Figure 2**): 15.7 km WNW of Punta Gorda: 7 May 2012: sjt12-032: S.J. Taylor, S.W. Heads, J. Jacoby, A.E. Beveridge, G.B. Hoese, J.K. Krejca, K.D. Hager, V. Sackal: Sample# 399. Habitat: leaf litter and guano with fungus on dry soil floor; twilight zone light <1 lux; air temperature 26.3°C; soil temperature 24.9°C; relative humidity 80.2%.

The *Nicoletia phytophila* specimen from Rash Tzul Cave is a 5.5 mm long female with ovipositor fully developed (**Figure 1**). It is assigned to *N. phytophila* based on morphology (Espinasa et al. 2011). The 16S rRNA fragment with primers excluded was 498 bp long (GeneBank No. KF110747). Its sequence was identical to a specimen from Lake Catemaco (GeneBank No. KF110742, Catemaco, Veracruz, Mexico 18°25'43"N,

95°05'27"W, 340 masl). The Belize/Catemaco specimens differed from specimens from Actopan (GeneBank No. KF110743, Veracruz, Mexico; 19°29'47.72"N, 96°34'59.61"W, 198 masl) by only one bp (0.2%). The Belize/Mexico specimens differed from Cuba specimens (GeneBank No. KF110744, Topes de Collantes; 21°55'N, 80°01'W) by 2–3 bp (0.4–0.6%), from Saint Vincent and the Grenadine Islands (GeneBank No. KF110745, Mustique Island; 12°53'15"N, 61°11'20"W) by 5–6 bp (1–1.2%) and from the Puerto Rican specimens (GeneBank No. KF110746, Culebrones Cave; 18°25'N, 66°43'W) by 77–78 bp (15.4–15.6%).

There is evidence to suggest that the cosmopolitan *N. phytophila* is actually a complex of species (Espinasa et al. 2011). DNA data indicate that a cave population from Puerto Rico belongs to a different species than surface populations from Mexico, and the Caribbean islands of Cuba and Mustique. Could it be that cave populations of *Nicoletia* belong to different species than surface *Nicoletia*? In this study we report on a new population of *N. phytophila* that was found at Rash Tzul Cave, in Belize. To our knowledge, this is the first record of *N. phytophila* within Belize. Its 16S rRNA sequence failed to support that it was from an independent line and therefore, a new species. The sequence from the Belize specimen was identical to surface populations from Mexico, consistent with the Belize cave population belonging within the same species of *Nicoletia* that is found throughout Mexico and many islands of the Caribbean, at the exclusion of the Puerto Rico cave example.

Figure 1. *Nicoletia phytophila* (Nicoletiidae) from Rash Tzul Cave, Toledo District, Belize. Scale bar = 1.0 mm.

Members of *Nicoletia* inhabit a large array of habitats such as under rocks, under logs, in ant nests, and under bark, where they are hidden from direct sunlight. Based on specimens collected from Raz Tzul Cave in Belize and Culebrones Cave in Puerto Rico, similar habitats in the entrance and twilight zones of caves may also be colonized by both described clades of *Nicoletia*.

Figure 2. Looking out of the entrance of Rash Tzul Cave, Toledo District, Belize. Photographer (not present in photograph) was standing near to where the *Nicoletia phytophila* specimen was collected. Photograph by Steven J. Taylor.

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RESEARCH ARTICLE

A new species of *Ripipteryx* from Belize with a key to the species of the Scrofulosa Group (Orthoptera, Ripipterygidae)

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Abstract

A new species of the genus *Ripipteryx* (Orthoptera: Tridactyloidea: Ripipterygidae) from the Toledo District of southern Belize is described and illustrated. *Ripipteryx mopana* **sp. n.** is placed in the Scrofulosa Group based on its elaborately ornamented frons and is readily distinguished from its congeners by the fusion of the superior and inferior frontal folds to form a nasiform median process, the epiproct with both anterior and posterior margins emarginate, the subgenital plate with distinct lateroapical depressions either side of the median line, the basal plate of the phallus strongly bilobed apically, and the development of well-demarcated denticular lobes in the dorsal endophallic valves. A preliminary key to the species of the Scrofulosa Group is provided.

Keywords

Introduction

Neotropical tridactyloids are both diminutive and cryptic, and being collected only rarely, are also underrepresented in collections. The tridactyloid fauna of Central

America in particular is extremely diverse and yet simultaneously poorly documented. Indeed, only 19 tridactyloid species are recorded from Mesoamerica compared to over 100 known from South America (Otte 1997; Günther 1980; Eades et al. 2011). Work on Mesoamerican tridactyloids began with Saussure's (1859) description of *Ripipteryx mexicana* from Oaxaca, Mexico and continued with his contribution to *Biologia Centrali-Americana* (Saussure 1896) in which he described 17 additional species. These taxa were subsequently revised by Günther (1969, 1975–1977, 1989) who added several species to the fauna and synonymized others. Despite Günther's work however, chronic under-sampling in the region means that very little is known about tridactyloid diversity in Mesoamerica and even less about their biology.

The genus *Ripipteryx* Newman, 1834 is exclusively Neotropical, with some 44 species distributed throughout South and Central America (Günther 1969, 1980; Heads 2010). The majority of *Ripipteryx* species known from Mesoamerica belong to the Scrofulosa Group, a presumably monophyletic group comprised of small, variegated species characterized by their peculiar and elaborately ornamented frons and tuberculate or denticulate dorsal endophallic valvulae (Heads 2010). Here, we provide for the first time, a key to the Scrofulosa Group and describe a distinctive new species as the first record of the family Ripipterygidae from Belize.

Material and methods

The holotype is deposited in the Entomology Collection of the Illinois Natural History Survey (INHS), Prairie Research Institute, University of Illinois, and was studied using an Olympus SZX12 zoom stereomicroscope with 1× and 2× objectives. Drawings were produced with the aid of a *camera lucida*. Photomicrographs were made using a digital SLR camera and 65 mm macro lens. To examine the terminalia and phallic complex, the abdomen was removed using Vannas' scissors and cleared in warm 10% KOH. The phallus was then dissected and subsequently stored together with the terminalia under glycerin in a glass microvial pinned beneath the specimen. Terminology generally follows that of Heads (2010) with modifications concerning structures associated with the highly modified male paraproct. In most tridactyloids, the paraproct bears two distinctive processes: [1] a well-sclerotized proximal hook-like structure, herein termed the *uncus* ("Hakensklerit" of Günther 1969); and [2] an elongate, cercus-like structure, herein termed the *brachium* ("Paraproctfortsatz" of Günther 1969).

Systematics

Genus *Ripipteryx* Newman, 1834
Scrofulosa Group *sensu* Heads, 2010

***Ripipteryx mopana* Heads & Taylor, sp. n.**
urn:lsid:zoobank.org:act:93A6697D-C161-4275-B1D7-6FC0F9D3245F
urn:lsid:orthoptera.speciesfile.org:TaxonName:73795
http://species-id.net/wiki/Ripipteryx_mopana
Figs 1–5

Diagnosis. The new species is readily separated from other small, variegated *Ripipteryx* by the elaborately ornamented frons characteristic of Scrofulosa Group species. From other members of the Scrofulosa Group the new species is distinguished by [1] fusion of the superior and inferior frontal folds forming a nasiform median process; [2] the emarginated anterior and posterior margins of the epiproct; [3] the subgenital plate with distinct lateroapical depressions either side of the median line; [4] the strongly bilobed apex of the basal plate of phallus; and [5] the presence of well-demarcated denticular lobes in the dorsal endophallic valves.

    Description. *Male*: Body form small (length 4.54 mm from frons to apex of subgenital plate) and compact with coloration highly variegated (Figs 1–2). Vertex largely black, with crescent-shaped pale cream patches circumscribing the anterodorsal margins of the compound eyes. Interocular distance 0.73 mm. Compound eyes broadly subovoid, 0.86 mm high. Lateral ocelli very small, situated very close to the medial margin of the compound eyes. Median ocellus absent. Frons largely pale cream fringed with reddish brown and bearing numerous elaborate folds and lobes; comprising a central nasiform process formed through fusion of the superior and inferior folds, flanked by deep, sinuous furrows themselves bordered by broad ridges and lobes; frontoclypeal lobe present (Fig. 1). Antennae ten segmented, moniliform, inserted directly beneath the compound eyes. Scape twice as long as pedicel; flagellomeres densely pubescent and wider apically than at their base. Scape, pedicel and flagellomeres 1 and 2 pale cream dorsally and black ventrally; flagellomere 3 almost entirely black; flagellomere 4 with triangular-shaped pale cream patch dorsally and black ventrally; flagellomere 5 almost entirely pale cream; remaining flagellomeres entirely black. Pronotum somewhat tectate anteriorly (Fig. 2), 1.77 mm long, broadly rounded posteriorly; black with broad, pale cream lateral and posterior margins and a prominent orange-brown median patch dorsally that is obovate anteriorly and rhombiform posteriorly. Tegmen entirely black, 2.38 mm long. Hind wing remigium entirely black; posterior fan cream. Profemora 1.18 mm long, black to dark brown dorsally and pale brown to cream ventrally. Protibiae claviform and largely black with a pale cream longitudinal stripe. Mesofemora 1.91 mm long, subquadrate in section, black dorsally and pale cream ventrally. Mesotibiae black with a prominent pale cream longitudinal stripe along the dorsolateral margin. Metafemora large and robust, 3.28 mm long, reddish brown medially with broad pale
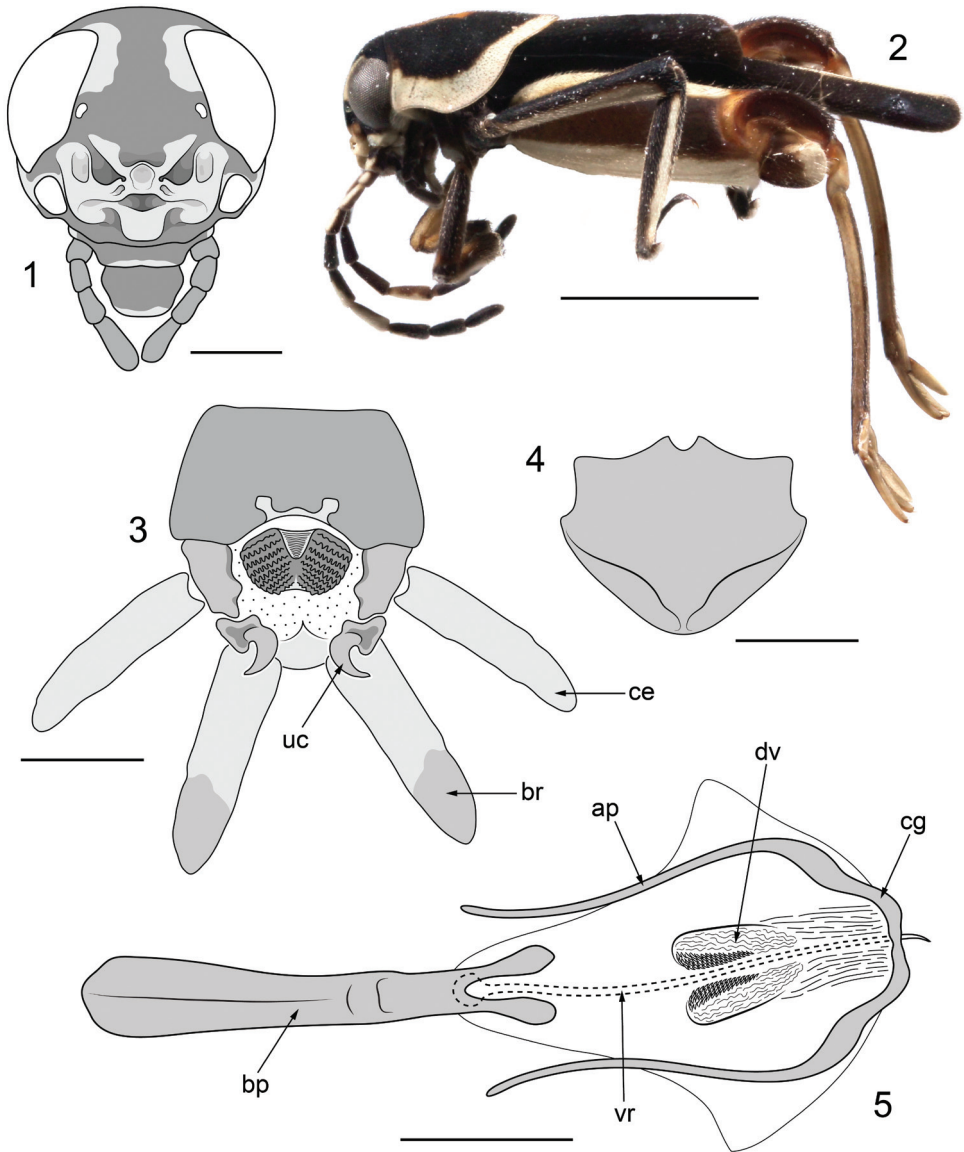
Figures 1–5. Holotype ♂ of *Ripipteryx mopana* Heads & Taylor, sp. n. **1** frontal view of head capsule with antennae omitted (scale bar 0.5 mm) **2** lateral habitus (scale bar 2.0 mm) **3** dorsal view of terminalia with setae omitted for clarity (scale bar 0.25 mm) **4** ventral view of subgenital plate with setae omitted for clarity (scale bar 0.25 mm) **5** dorsal view of phallic complex (scale bar 0.25 mm). Abbreviations: **ap** apodemes of cingulum; **bp** basal plate; **br** brachium; **ce** cercus; **cg** cingulum; **dv** dorsal valve; **uc** uncus; **vr** virga.

cream bands dorsally and ventrally; geniculae well-developed, dark reddish brown with pale cream apices. Metatibiae 3.14 mm long, pale yellowish brown with prominent darker dorsal carinae; apical metatibial spurs blade-like with prominent apical hooks, more than twice as long as subapical spurs. Metatarsus sublanceolate, 0.66 mm long,

marginally shorter than the apical metatibial spurs. Posterior margin of abdominal tergite 10 broadly emarginate with prominently bilobed membranous median region (Fig. 3). Epiproct with large, densely reticulate lateral lobes and emarginate anterior and posterior margins. Cerci fusiform, bearing numerous long and evenly spaced setae. Paraprocts with large, well-sclerotized and strongly hooked uncuses and robust, apically thickened brachia bearing numerous strong ventroapical setae; brachia only marginally longer than cerci (Fig. 3). Subgenital plate broadly rounded with prominent lateroapical depressions either side of the median line; densely pubescent apically (Fig. 4). Phallus with basal plate strongly bilobed apically; cingulum broad and furcate, thickened laterally and bearing elongate, gently curved apodemes; dorsal valves of the endophallus forming flexible lobes armed with numerous denticles; virga filiform with an uncinate basal articulating process (Fig. 5).

Female: Unknown.

Holotype. ♂: Belize, Toledo District, hand collected on shore of Rio Grande at night, approx. 2 hrs after sunset, 28.1 km NNW of Punta Gorda, 16.31739°N, 88.93442°W, 15 April 2011, sjt11-016, coll. S. J. Taylor, sample # 231, specimen # 0338 (INHS).

Etymology. The specific epithet honors the Mopan, a Mayan people that live primarily in the southern part of Belize where the new species was collected. There is considerable ethno-historic and toponymic evidence to suggest that the Mopan have lived in this region since before the Spanish conquest (Jones 1998; Wainwright 2009). The Mopan people are recognized by their eponymous language (a form of Yucatec Mayan), spoken by 11,800 people in Belize and Guatemala (Lewis 2009). The gender of the epithet is feminine.

Remarks. Ordinarily, we would hesitate to describe a new species based on a single specimen. However, given the number of robust morphological apomorphies there can be no doubt that *R. mopana* is a distinct species. Within the Scrofulosa Group, *R. mopana* is most similar to *R. biolleyi* Saussure, 1896 sharing with this species the loss of the median ocellus and the distinctive nasiform frontal process. The nasiform process in *R. biolleyi* is formed by the upturned apex of the inferior fold strongly overlapping that of the superior fold. *Ripipteryx mopana* differs in that the apex of the inferior fold is completely fused to the underlying superior fold (Fig. 1). The frontal ornament of *R. mopana* further differs from that of *R. biolleyi* in the presence of carinulated pits on the lateral lobes of the inferior fold and deep, sinuous furrows (rather than ovoid cavities as in *R. biolleyi*) flanking the nasiform process. Both species possess a furcate cingulum with long, slender apodemes, though the apex of the basal plate is strongly bifurcated in *R. mopana* and undivided in *R. biolleyi*. Together, *R. biolleyi* and *R. mopana* appear to be most closely related to *R. saltator* Saussure, 1896 and *R. saussurei* Günther, 1969 sharing with these species a deep invagination of the inferior fold above the frontoclypeal lobe and the development of well-sclerotized denticles in the dorsal valves of the endophallus. These denticles are directed posteriorly and arranged in rows along valvular axial lobes, which are particularly well developed in *R. mopana* (Fig. 5). Denticular lobes are not present in *R. mediolineata* Saussure, 1896, *R. mexicana* Saussure, 1859,

R. scrofulosa Günther, 1969 and *R. tricolor* Saussure, 1896 all of which instead possess rows of weakly sclerotized, tubercle-like rugosities (Günther 1969). Of these species, *R. mediolineata* and *R. scrofulosa* are apparently the most primitive of the group having the frontal folds poorly developed and lacking a frontoclypeal lobe.

Preliminary key to species of the Scrofulosa Group

1   Frontal folds poorly-developed; frontoclypeal lobe absent; uncus reduced with retrograde apex; brachium long, about twice the length of the cercus...........**2**

–   Frontal folds well-developed; frontoclypeal lobe present; uncus large with either retrograde or dorsolaterally directed apex; brachium almost equal in length to slightly longer than cercus..**3**

2   Inferior frontal fold pale cream or white with two small black spots; pronotum black with broad yellowish white margins; brachium strongly claviform ....***R. scrofulosa* Günther**

–   Inferior frontal fold entirely pale cream or white, lacking black spots; pronotum black with broad yellowish white margins and a distinctive median yellow stripe with black spots in anterior half; brachium fusiform................ .... ***R. mediolineata* Günther**

3   Inferior frontal fold with shallow depression above the frontoclypeal lobe; dorsal valves of endophallus with weakly sclerotized tubercle-like rugosities.......**4**

–   Inferior frontal fold with deep invagination above the frontoclypeal lobe; dorsal valves of endophallus with more or less developed lobes bearing well-sclerotized rows of posteriorly directed denticles **5**

4   Frontal depression lenticular and flanked by two small black spots; posterior margin of abdominal tergum 10 with median membranous region unilobate .... ***R. tricolor* Saussure**

–   Frontal depression ovoid and lacking black spots; posterior margin of abdominal tergum 10 with median membranous region bilobed...................... .... ***R. mexicana* Saussure**

5   Median ocellus nascent or entirely lost; lateral lobes of inferior frontal fold with prominent rounded callosities or pits; frontoclypeal lobe well-developed **6**

–   Median ocellus present; lateral lobes of inferior frontal fold with a shallow longitudinal sulcus; frontoclypeal lobe weakly developed (Fig. 6).................. .... ***R. saussurei* Günther**

6   Median ocellus entirely lost; apices of superior and inferior folds strongly overlapped or fused forming a nasiform process; subgenital plate broadly rounded **7**

–   Median ocellus nascent; apices of superior and inferior folds closely approximated but not overlapping (Fig. 7); subgenital plate paraboliform ....***R. saltator* Saussure**
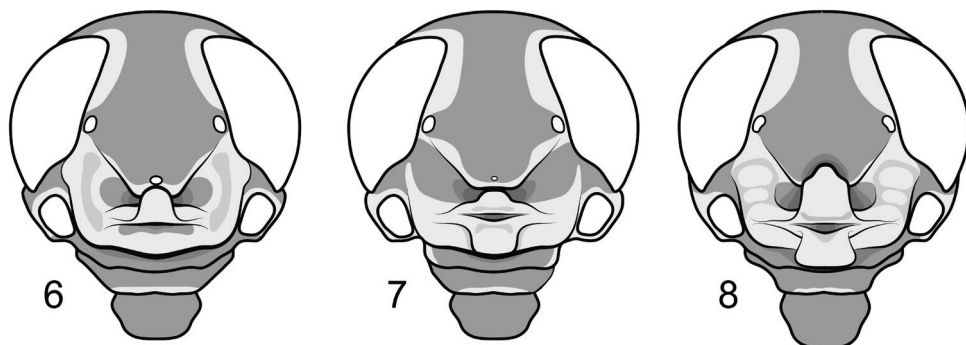
Figures 6–8. Head capsules of representative Scrofulosa Group species. **6** *Ripipteryx saussurei* Günther (Mexico); **7** *Ripipteryx saltator* Saussure (Costa Rica) **8** *Ripipteryx biolleyi* Saussure (Costa Rica).

7   Nasiform process formed from strongly overlapping apex of inferior frontal fold and flanked by deep, ovoid cavities; lateral lobes of inferior frontal fold with two swollen callosities, the dorsalmost at least twice as large as the ventral (Fig. 8); apex of basal plate undivided; dorsal valves of endophallus with poorly-developed denticular lobes...................................***R. biolleyi* Saussure**
–   Nasiform process formed from fused apices of the superior and inferior frontal folds and flanked by deep sinuous furrows; lateral lobes of inferior frontal folds with large outer and smaller inner pits each bordered by very weak carinulae; apex of basal plate strongly bifurcate; dorsal valves of endophallus with well-developed denticular lobes..............***R. mopana* Heads & Taylor, sp. n.**

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The dorsal chaetotaxy of *Trogolaphysa* (Collembola, Paronellidae), with descriptions of two new species from caves in Belize

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Abstract

Species diagnosis in *Trogolaphysa* has been based, until now, almost exclusively on number of eyes and shape of claws and mucro. Chaetotaxy, a character system important to diagnose species in other genera of scaled Entomobryoidea, has been described only for a few *Trogolaphysa* species. Here the complete dorsal chaetotaxy of six species of *Trogolaphysa* is described using the AMS and Szeptycki's systems for head and body, respectively. A morphology-based parsimony analysis was performed to evaluate whether chaetotaxic characters overcome the influence of putatively cave adaptive convergent characters to resolve species level relationships, and to evaluate the evolution of the dorsal macrochaetae of the head. Phylogenetic analysis using only putative cave-adaptive characters support clades of unrelated taxa, but the addition of chaetotaxy overcomes the influence of convergent characters. A phylogeny based on all characters supports a trend towards reduced head macrochaetae number. Head macrochaetae are lost beginning with A3 and followed, in order, by S5, S3 and M3. In addition, a checklist of New World *Trogolaphysa* is provided and two new species, *Trogolaphysa giordanoae* **sp. n.** and *Trogolaphysa jacobyi* **sp. n.**, are described on the basis of material collected in six caves in southern Belize.

Keywords

Puerto Rico, *Dicranocentruga*, phylogeny, cave-adaptive characters

Introduction

The collembolan fauna of Belize is among the least known of any Central American country. The Catalogue of Neotropical Collembola (Mari Mutt and Bellinger 1990) and subsequent updates (Mari Mutt and Bellinger 1996, Mari Mutt et al. 2009) list one species, the troglomorphic *Trogolaphysa belizeana* Palacios-Vargas & Thibaud, 1997, for Belize. A recent biospeleological expedition to the Toledo District of Belize yielded several new springtail species, including two new species in the genus *Trogolaphysa*.

What is understood about the evolution of morphological adaptations to cave habitats in entomobryoid springtails is derived from northern temperate members of the genera *Pseudosinella* and *Sinella* (Christiansen 1961, Gama 1984). The evolution of troglobiont species in tropical *Trogolaphysa* (Palacios Vargas et al. 1985[1986]) and *Troglopedetes* (Deharveng 1987, Deharveng and Gers 1993), could provide important independent information to test hypotheses about the direction of character evolution in Entomobryoidea. The characters utilized in the descriptions of most of the 33 species of *Trogolaphysa* reported from the New World (Mari Mutt and Bellinger 1990, Mari Mutt et al. 2009; Table 1) are limited to claw complex and mucronal shape (e.g., Palacios-Vargas et al. 1985[1986]), two character systems prone to convergent evolution in cave habitats (Christiansen 1961, Christiansen and Culver 1987). Chaetotaxy is known for few species (Gruia 1987, Mari Mutt 1987[1988], Thibaud and Najt 1988[1989]), and is limited to the number of macrochaetae. While convergence itself is of interest in understanding evolution in caves (Derkarabetian et al. 2010, Hedin and Thomas 2010), distinguishing convergent characters adaptive for subterranean life from characters that better reflect phylogenetic history has proven to be important in a variety of groups of animals (e.g., Wiens et al. 2003).

The relationships between the genera *Paronella*, *Troglopedetes*, *Trogolaphysa*, and *Dicranocentruga* has been a source of confusion. Thibaud and Najt (1988[1989]) evaluated morphological characters of these genera and provided clear diagnoses for all of them: *Paronella* was retained for species with 1+1 rows of external spines on the manubrium; *Troglopedetes* was restricted to species with a single subdivision of the fourth antennal segment; *Trogolaphysa* was circumscribed to include *Paronella*-like species with Ant. 4 not subdivided, manubrium without spines and a short mucro (in relation to dens) with 3-5 teeth; whereas *Dicranocentruga* was placed as a junior synonym of *Trogolaphysa*. Thibaud and Najt (1988 [1989]) did not consider the presence of EOS (extra ocular structure) as a diagnostic character. Mitra (1992, 1993, 2002) argued that species without manubrial spines but sharing the presence of an EOS and 8+8 (or apparently 6+6) eyes should be placed in the genus *Dicranocentruga*, whereas species with fewer than 6+6 eyes and without EOS should be allocated to *Trogolaphysa* or *Troglopedetes*. Mitra (1993) suggested that further observations of the chaetotaxy would furnish characters to support this separation, but until now, the complete dorsal chaetotaxy of these taxa remained undescribed.

Here we present complete descriptions of the dorsal chaetotaxy of the head and trunk for the two new species of *Trogolaphysa* and for *T. belizeana,* and compare their

Table 1. Check-list of the species of *Trogolaphysa sensu* Thibaud and Najt (1988[1989]) of the New World, with distribution by country (given as ISO 3166–1 alpha-3 code).

Species	Distribution
Trogolaphysa aelleni Yoshii, 1988	BRA
Trogolaphysa belizeana Palacios-Vargas and Thibaud, 1997	BLZ
Trogolaphysa berlandi (Denis, 1925)	ARG, GUF
Trogolaphysa bessoni Thibaud & Najt, 1989	ECU
Trogolaphysa caripensis (Gruia, 1987)	VEN
Trogolaphysa carpenteri (Denis, 1925)	CRI, GUF, MEX, VEN
Trogolaphysa cotopaxiana Thibaud & Najt, 1989	ECU
Trogolaphysa distinguenda (Denis, 1931)	CRI
Trogolaphysa ecuatorica (Palacios-Vargas, Ojeda & Christiansen, 1986)	ECU
Trogolaphysa geminata (Mari Mutt, 1988)	PRI
Trogolaphysa giordanoae Soto-Adames & Taylor sp. n.	BLZ
Trogolaphysa guacharo Yoshii, 1988	CRI, VEN
Trogolaphysa haitica (Palacios-Vargas, Ojeda & Christiansen, 1986)	HTI
Trogolaphysa hauseri Yoshii, 1988	BRA
Trogolaphysa hirtipes (Handschin, 1924)	ARG, BRA, VEN
Trogolaphysa hondurasensis (Palacios-Vargas, Ojeda & Christiansen, 1986)	HND
Trogolaphysa jamaicana (Palacios-Vargas, Ojeda & Christiansen, 1986)	JAM
Trogolaphysa jataca (Wray, 1953)	JAM, PRI
Trogolaphysa jacobyi Soto-Adames & Taylor sp. n.	BLZ
Trogolaphysa luquillensis (Mari Mutt, 1988)	PRI
Trogolaphysa marimutti (Palacios-Vargas, Ojeda & Christiansen, 1986)	MEX
Trogolaphysa maya Mills, 1938	CUB, DOM, MEX
Trogolaphysa millsi Arlé, 1939	BRA
Trogolaphysa nacionalica (Palacios-Vargas, Ojeda & Christiansen, 1986)	MEX
Trogolaphysa oztotlica (Ojeda & Palacios-Vargas, 1984)	MEX
Trogolaphysa relicta (Palacios-Vargas, Ojeda & Christiansen, 1986)	MEX
Trogolaphysa riopedrensis (Mari Mutt, 1988)	PRI
Trogolaphysa separata (Denis, 1933)	CRI
Trogolaphysa strinatii Yoshii, 1988	MEX
Trogolaphysa subterranea (Mari Mutt, 1988)	PRI
Trogolaphysa tijucana (Arlé & Guimarães, 1979)	BRA
Trogolaphysa toroi (Palacios-Vargas, Ojeda & Christiansen, 1986)	MEX
Trogolaphysa variabilis (Palacios-Vargas, Ojeda & Christiansen, 1986)	MEX
Trogolaphysa xtolokensis (Palacios-Vargas, Ojeda & Christiansen, 1986)	MEX
Trogolaphysa yoshiia (Palacios-Vargas, Ojeda & Christiansen, 1986)	MEX

chaetotaxy to that of *T. jataca* (Wray, 1953), *T. geminata* (Mari Mutt, 1987[1988]) and *T. riopedrensis* (Mari Mutt, 1987[1988]), three surface species from Puerto Rico. Finally, we present a morphology-based phylogenetic analysis to assess the value of chaetotaxy in elucidating species relationships in this genus, and to evaluate the evolution of some elements of the dorsal chaetotaxy of the head.

Materials and methods

Springtails were collected with aspirators and preserved in 70% ethanol. Samples were associated with substrate characterizations and field-collected measurements of temperature, light intensity and humidity.

Selected specimens were cleared in Nesbitt's solution, mounted in Mark André II (Mari Mutt 1979) on glass slides, and examined under a compound microscope with phase contrast. The extra-ocular structure (EOS) was examined under polarized light. Drawings were made using a drawing tube, with final illustrations completed using Adobe Illustrator CS5, version 15.0.2.

Abbreviations used for structures are: antennae (Ant.), thorax (Th.) abdomen (Abd.), extra ocular structure (EOS). Abbreviations used for names are: Avelardo Canti (AC), Gabriel Chaco (GaC), Germano Coe (GeC), William R. Elliott (WRE), Geoff B. Hoese (GBH), JoAnn Jacoby (JJ), Jean K. Krejca (JKK), Bruno K. Kuppinger (BKK), C. Marcela Ospina (CMO), Rosalio Sho (RS), Christy M. Slay (CMS), Michael E. Slay (MES), Felipe N. Soto-Adames (FSA), and Steven J. Taylor (SJT).

To protect vulnerable sites, latitude and longitude are not provided for the Belize material. These locations are controlled by, and may be requested from, the Institute of Archaeology, Belmopan, Belize (see Acknowledgements). Holotypes and paratypes of the new species are deposited in the Illinois Natural History Survey Insect Collection (INHS).

Here we describe only elements of the chaetotaxy that are modified into microchaetae, macrochaetae or sensilla (i.e., idiochaetotaxy, Szeptycki 1979). We follow the nomenclature of Szeptycki (1979) for the body and the AMS system (Jordana and Baquero 2005, Soto-Adames 2008, 2010) for the head. Mitra (1993) proposed a system for the chaetotaxy of the head in Paronellidae, but it has not been widely embraced, whereas the AMS system has been applied to entomobryoids since the 1970's (Szeptycki 1973, Mari Mutt 1979) and allows evaluation of homologies between families of Entomobryoidea.

The idiochaetotaxy of *Trogolaphysa* is reduced, and in naming body setae we assume it represents the remnant of primary chaetotaxy. The setae closest to the mesothoracic pseudopore (Figs 12, 32, 53) are identified as m1 and m2, even though they occupy positions that in entomobryoids with more abundant idiochaetotaxy might be assigned to setae m2i and m2e, respectively. The nomenclature of setae on the fourth abdominal segment follows Szeptycki's system (Soto-Adames 2010): setae in columns A and B are named sequentially from posterior to anterior, irrespective of their relative insertion. Columns A and B have a maximum of four setae, and when all are present they are always setae 3-6 (e.g., A3, A4, A5 and A6). In the species described below, setae A3, A6, B3 and B6 are always present, and it is assumed that setae A4 and B4 are always suppressed before A5 and B5.

For the labial chaetotaxy, upper case letters represent macro- or mesosetae and lower case represent microsetae, an underscore in the formula identifies ciliate setae.

The eye patch of a generalized springtail comprises a group of 5 anterior and 3 posterior simple eyes, we refer to the space between these two groups of eyes as the 'eye patch well' to distinguish it from the inter-ocular space, which is the gap between the eye patches on either side of the head.

The formula of the dorsal macrochaetae of head and trunk is based on Gisin's (1967) model, but we consider all macrochaetae associated with the bothriotricha on abdominal segments 2-4, instead of only those found between the bothriotrichal complexes. The number of macrochaetae on the head is presented as two digits; the first digit refers to macrochaetae anterior to the head sulcus (series A, M and S), the second to the posterior macrochaetae (series Ps, Pa and Pm). The macrochaetae on abdominal segment 4 are represented by three digits separated by plus (+) symbol, where the first, second and third numbers refer to the inner (series A and B), medial (assumed, in Szeptycki's system, to be series C) and outer macrochaetae (series T, D, E, F and Fe). The last number in the macrochaeta formula may be represented by a range because the number of outer macrochaetae may be variable, as some macrochaetae external to series F appear to be added as individuals grow older. The formula is based on the relative size of the sockets and includes all macrochaetae, irrespective of whether they are large (i.e., short, thick and blunt) or small (long, slender and acuminate).

Phylogenetic trees were estimated using parsimony as implemented in PAUP 4.0* (Swofford 2002).

The habitat parameters substrate temperature, air temperature, light, and relative humidity were measured with hand held meters. Differences in abiotic parameters between habitats occupied by the two new species were tested using a Wilcoxon rank sum test in R 2.15.2 (R Developmental Core Team 2012), with continuity correction.

Results

Genus *Trogolaphysa* Mills, 1938 *sensu* Thibaud and Najt (1988[1989])
http://species-id.net/wiki/Trogolaphysa

Diagnosis. Paronellidae with finely denticulate scales covering dorsum of head and body, and ventral face of furcula; Ant. 4 sometimes annulated, never subdivided in two; labial seta L2 normal, not reduced; eyes 0-8; EOS present; Abd. 2-4 with 2, 3, 3 bothriothricha; manubrium without spines, dens with 1-2 rows of spines; mucro short, with 3-5 more or less evenly spaced teeth.

Remarks. As currently circumscribed (Thibaud and Najt 1988 [1989]), the absence of a subdivision on Ant. 4 in *Trogolpahysa* is the only character that distinguishes this genus from *Troglopedetes*.

It is not known if the type species of the genus, *T. maya* Mills, 1938, has EOS, but the presence of this structure in all species discussed below, including the two troglomorphic forms, suggests it is likely also present in that species.

Trogolaphysa giordanoae Soto-Adames & Taylor, sp. n.
http://zoobank.org/3C37791A-056D-496F-87E2-58D72A355B4B
http://species-id.net/wiki/Trogolaphysa_giordanoae
Figs 1–21; Figs 22–23 (habitat)

Type locality. BELIZE: Toledo District: 29 km WNW of Punta Gorda, Blue Creek Cave, Hokeb Ha entrance, 11.IV.2011, SJT, MES, JJ, CMS, GBH & RS, coll.

Type material: Holotype, female on microscope slide preparation, INHS Collection Number 579,406; Paratypes: BELIZE: Toledo District: 29 km WNW of Punta Gorda, Blue Creek Cave, Hokeb Ha entrance, 11.IV.2011, (3 in alcohol), SJT, MES, JJ, CMS, GBH & RS, coll.; 37 km WNW of Punta Gorda, cave near Pueblo Creek Cave, 16.IV.2011, (4 in alcohol-one headless), MES, JKK, CMS, GBH & GeC, coll.; 28 km NNW of Punta Gorda, Tiger Cave, 9.IV.2012, (1 on slide, 33 in alcohol), SJT, MES, JJ, CMS, GBH, BKK & GaC, coll.; 28 km NNW of Punta Gorda, Bat Cave, 10.IV.2011, (2 on slides, 29 in alcohol—some in poor condition, one headless), SJT, MES, JJ, CMS & GBH, coll.; 31 km WNW of Punta Gorda, Okebal Ha, 14.IV.2011, (3 on slides, 16 in alcohol), SJT, MES, JJ, CMS, GBH, BKK & RS, coll.

Diagnosis. *Trogolaphysa giordanoae* sp. n. is unique among species with 6–8 eyes in having 5 dorsal head macrochaetae, 3 metathoracic macrochaetae and 4 inner macrochaetae on Abd. 4. Among species with known dorsal chaetotaxy, the new species is most similar to *T. riopedrensis*, but the two species are easily distinguished by the combination of characters given above and by the presence of a relatively shorter mucro in the new species (Table 2). Additional diagnostic characters distinguishing the new species from all other New World *Trogolaphysa* with 6–8 eyes and capitate/spatulate tenent hair are presented in Table 2. Among the species described before the introduc-
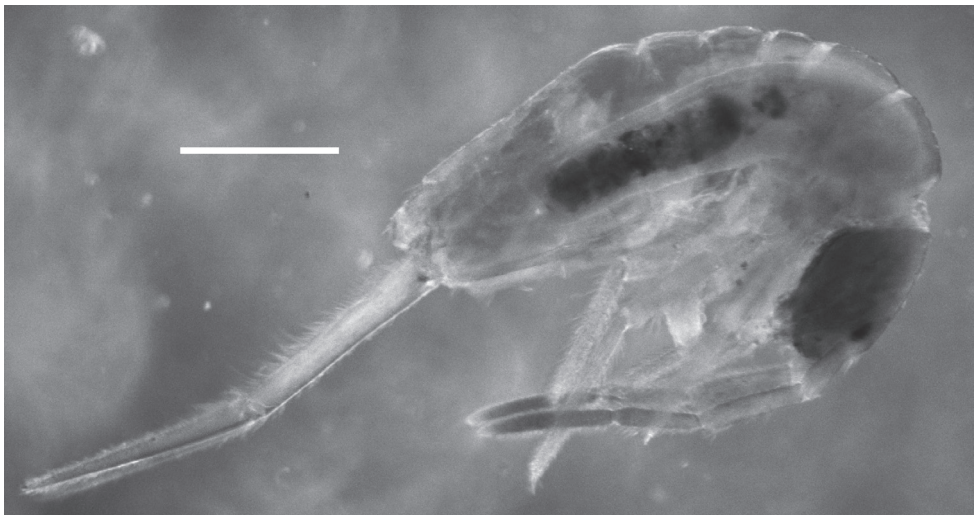

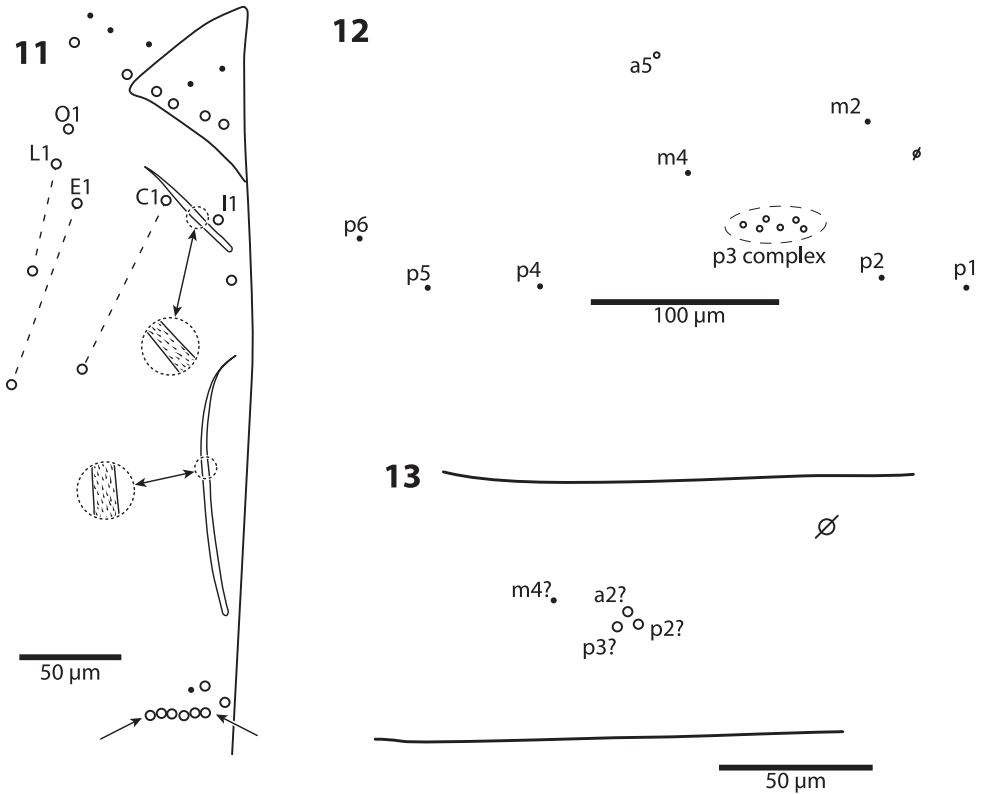**Figure 1.** *Trogolaphysa giordanoae* sp. n. habitus, scale=0.5 mm.

Table 2. Diagnostic table for species of *Trogolaphysa* with 6–8 eyes and capitate or spatulate tenent hair.

Species	Mucronal teeth	Mucro length/ Width dens apex	Inner ungual teeth	Dorsal head macrochaetae	Th. 2 Macrochaetae	Th. 3 Macrochaetae	Abd. 4 Inner large macrochaetae
T. giordanoae sp. n.	4	1.8	4	5	7	3	4
T. riopedrensis	4	2.9	4	7	7	0	4
T. geminata	4	2.2	4	6	7	0	3
T. jataca	4	2.9	4	7	7	0	3
T. carpenteri †	4	3.5	3	2	0	0	0
T. relicta	4	2.7	3	0	0	0	0
T. subterranea	4	2.7	3	3	7	0	3
T. cotopaxiana	5	3.6	4	2	3	0	3
T. distinguenda	5	3.3	4	?	?	?	?

† Most characters based on Yoshii (1988).
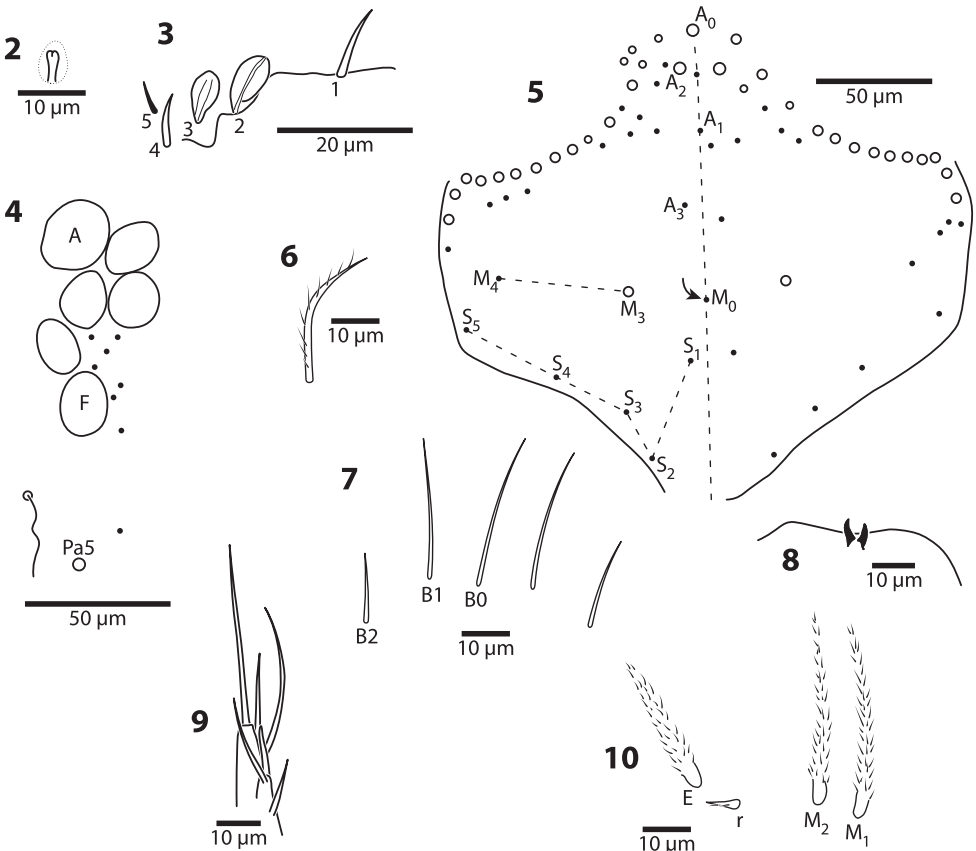
Figures 2–10. *Trogolaphysa giordanoae* sp. n., circles are macrochaetae, filled circles are ciliate microchaetae **2** Antennal segment 4, subapical sensillum **3** Antennal segment 3, sense organ **4** Eyepatch and associated setae, **5** Head dorsal chaetotaxy, line represents dorsal sulcus **6** Prelabral seta **7** Labral row B setae **8** Distal margin of labrum **9** Labial papilla E **10** Posterior setae of labial triangle.

Figures 11–13. *Trogolaphysa giordanoae* sp. n. **11** Postlabium, circles are ciliate setae, filled circles are smooth setae, arrows point at ventral cervical setae **12** Mesothorax, dorsal chaetotaxy, circles are macrochaetae, filled circles are microchaetae **13** Metathorax, dorsal chaetotaxy, circles are macrochaetae, filled circles are microchaetae, seta a6 present but not shown.

tion of chaetotaxy, the new species is most similar to *T. distinguenda* (Denis, 1931), but the two species can be separated by the presence of a relatively long mucro with 5 teeth in *distinguenda*, and a 4-toothed short mucro in *T. giordanoae* sp. n. *Trogolaphysa belizeana* is the only other New World *Trogolaphysa* with 3 metathoracic macrochaetae. However, *T. belizeana* is a troglobiont (*sensu* Sket 2008, Culver and Pipan 2009)—blind, with long antennae and modified ungues.

Description. Size. Body length up to 2.1 mm.

Color. Pattern, if any, obscured by green dye present in the alcohol in which specimens were preserved (Fig. 1).

Scale distribution. Scales dark brown, present on Ant. 1-2 and base of Ant. 3, more abundant on dorsal face than on ventral face of segment. Scales absent from ventral tube, legs and dorsal face of manubrium.

Head. Antenna/cephalic diagonal ratio 2.0–2.5 (Fig. 1). Apical bulb of Ant. 4 absent; subapical sensillum capitate (Fig. 2), fully contained in circular depression; guard sensillum absent. Sense organ of Ant. 3 (Fig. 3) with sensilla 1 and 4 acumi-

14

a6

50 µm

15

m5

p5

m3

50 µm

16

a7?

am6?

m7e?

pm6   /d2

m7

p6

m3

p7

50 µm
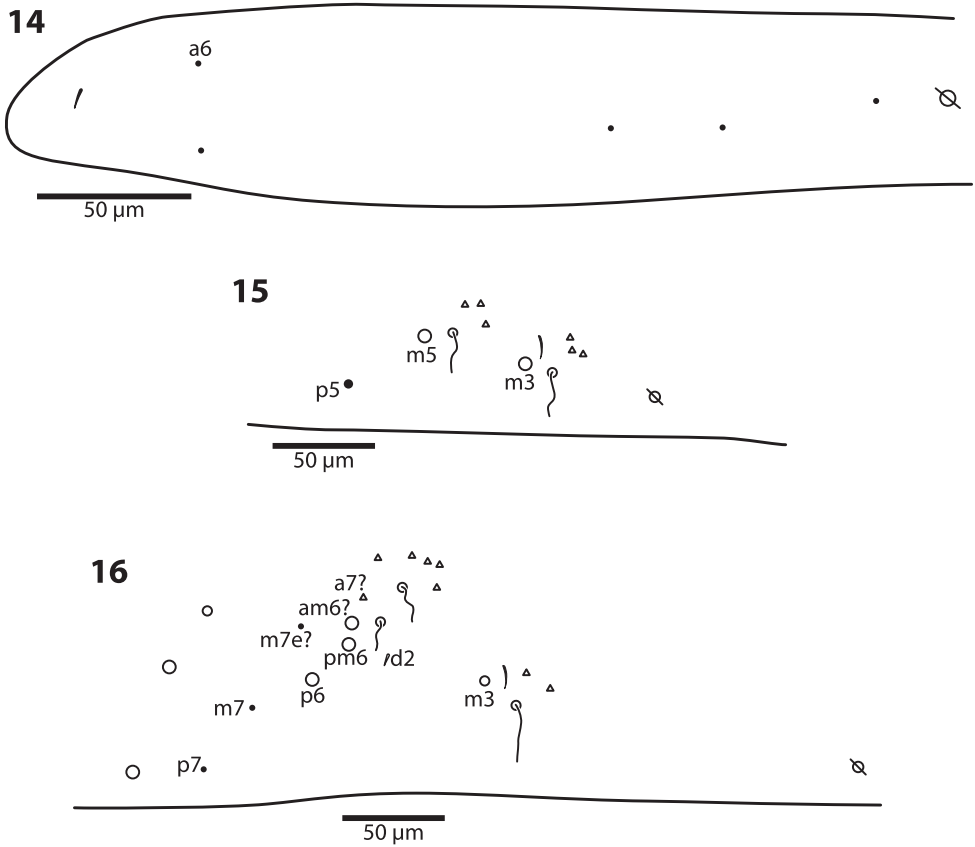
Figures 14–16. *Trogolaphysa giordanoae* sp. n. Dorsal chaetotaxy of abdominal segments 1–3, triangles are fan-shaped setae, circles are macrochaetae, filled are circles ciliate microchaeta **14** First abdominal segment **15** Second abdominal segment **16** Third abdominal segment.

nate, thin-walled and translucent; sensillum 5 acuminate, dark (light dense), shorter than 1 and 4; sensilla 2–3 wide, leaf-like, resting in shallow grooves. Eyes 6+6 (Fig. 4), chaetotaxy of eyepatch well with 4, sometimes 6 ciliate setae, and 1 seta posterior to eye F. Head dorsally with 5 macrochaetae (A0, A2, M3, Pa5 and Pm3— Figs 4–5). Series M with 2 setae (M3–4); series S with 5 setae (S1–5); seta M0 seen only in one individual; S0 absent. Prelabral setae serrate (Fig. 6). Labral setae smooth: setae in rows A and C subequal; seta B2 distinctly shorter than setae B0 and B1 (Fig. 7). Distal margin of labrum with 1+1 medial hooks, papillae absent (Fig. 8). Apical and subapical setae of maxillary palp smooth; sublobular plate with 2 seta-like appendages. Lateral process of labial papilla E weakly bent dorsally, barely reaching apex of papilla (Fig. 9). Labial triangle setae as <u>M1M2rEL1–2</u>A1–5 (Fig. 10); r short, stout and sparsely ciliate; L1 inserted close to E and distant from L2 when compared to other entomobryoids (Fig. 11). Postlabium covered by setae and scales, all postlabial setae ciliate, modified setae absent. Columns ICELO with 42221 setae (Fig. 11): col-
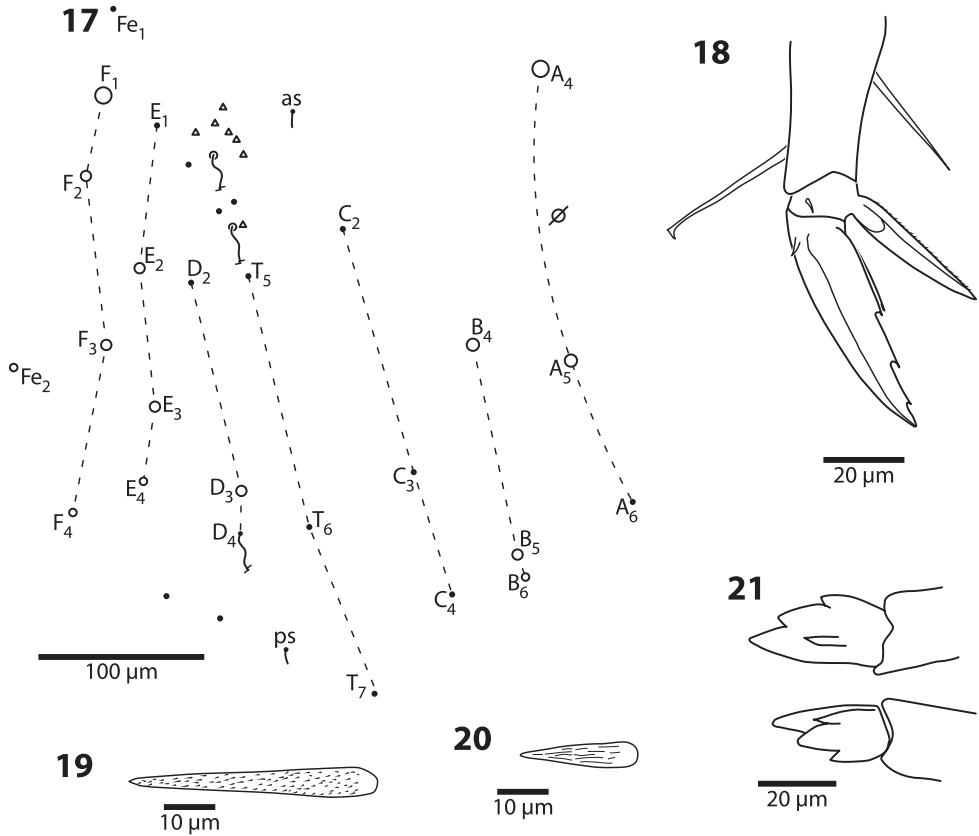
Figures 17–21. *Trogolaphysa giordanoae* sp. n. **17** Fourth abdominal segment dorsal chaetotaxy, diameter of circle is approximately proportional to size of macrochaeta **18** Metathoracic claw complex **19** Dens basal spine, outer row **20** Dens basal spine, inner row **21** Mucro.

umn I with posterior seta detached from main group and much longer than anterior setae. Ventral cervical setae usually 8+8.

Body. Mesothoracic hood not developed. Complete dorsal macrochaetae as 32/73/0245+0+9. Mesothorax with 1 anterior (a5) and 6 posterior (p3 complex) macrochaetae arranged as is typical for genus (Fig. 12); microchaetae m2, m4, p1, p2, p4, p5 and p6 present. Inner chaetotaxy of metathorax with 3 macro- and 1 microchaetae (Fig. 13). First abdominal segment with 1 anterior (a6) and 4 posterior setae arranged in a single row (Fig. 14). Second abdominal segment (Fig. 15) inner bothriotrix with 3 fan-shaped setae, one microsensillum and macrochaeta m3; outer bothriotrix with 3 fan-shaped setae and macrochaeta m5; setae a6, m6 and p5 present. Third abdominal segment (Fig. 16) inner bothriotrix complex with 2 fan-shaped setae, 1 sensillum, and macrochaeta m3; external bothriotricha with 7 fan-shaped setae, and macrochaetae am6, pm6 and p6; sensillum d2 present, inserted near pm6. Fourth abdominal segment with 5 inner and 9 outer macrochaetae (Fig. 17): large inner macrochaetae A4, A5, B4, and B5 present; B6 a small macrochaeta;

Figure 22. *Trogolaphysa giordanoae* sp. n. paratype habitat Okebal Ha entrance/twilight zone. Specimens were collected from a small pile of fruit bat guano near the researchers in the foreground, below a bat roost site. Sample site was much darker than it appears in this enhanced image. Photo courtesy of MES.

large outer macrochaetae D3, E2, E3, F1, F2, and F3 present; macrochaetae E4, F4 and one other seta probably homologous to Fe4, small. Anterior and medial bothriotricha with 7 and 3 fan-shaped supplementary setae, respectively. Posterior bothriotrix, corresponding to D4, without associated supplementary setae. Posterior setae 19–21+19–21. Intersegmental membrane between Abd. 4–5 with 4–10 lenticular organs (as in *T. riopedrensis*, Fig. 60).

Legs. Trochanteral organ with up to 36 setae. Metathoracic claw complex as in Fig. 18. Tenent hair weakly spatulate. Smooth posterior setae on metathoracic legs 0.76× as long as unguiculus. Unguis with 4 inner teeth: 1 basal tooth sometimes ap-

Figure 23. *Trogolaphysa giordanoae* sp. n. on old feces in Tiger Cave. Photo courtesy of GBH.

pearing slightly larger than other, both paired teeth ending near middle of inner edge; proximal unpaired tooth as large as basal paired teeth, ending on distal half of inner edge; distal unpaired tooth smallest of all inner teeth and ending on distal fourth of inner edge. Outer tooth ending on basal quarter of outer ungual edge. Unguiculus lanceolate, with outer margin serrate.

Ventral tube. Anterior face with 3+3 or 4+4 distal macrochaetae; lateral and posterior setae not seen clearly.

Furcula. Dens with 2 rows of ciliate spines: inner row with 35–42 spines; outer row with 25–28 spines. Basal outer spines longest (Figs 19–20). Mucro with 4 short, stout teeth (Fig. 21), ratio mucro length/width of dens tip 1.2–1.8×; basal outer tooth reaches to at least half length of basal inner tooth.

Etymology. This species is dedicated to Rosanna Giordano, the senior author's wife, for her years of support and contributions to science.

Distribution. The species is known only from Belize

Habitat. *Trogolaphysa giordanoae* sp. n. is a guanophile, recorded from entrance, twilight (Fig. 22) and dark zones of caves (6.7, 53.3 & 40.0 % of 15 collections, respectively), often in association with fruit bat or other guano (Fig. 23) (noted for 40% of 15 collections). It was commonly found on the floor of caves (76.9% of 13 collections where position was noted), but also on cave walls (23.1% of 13 collections where position was noted).

Trogolaphysa jacobyi Soto-Adames & Taylor, sp. n.

http://zoobank.org/5F865EE9-B5E0-4844-8482-902F8E9EA2B2
http://species-id.net/wiki/Trogolaphysa_jacobyi
Figs 24–43; Fig. 44 (habitat)

Type locality. BELIZE: Toledo District: 32 km WNW of Punta Gorda, Yok Balum Cave, 13.IV.2012, SJT, MES, JJ, CMS, GBH & AC, coll.

Type material. Holotype, female on microscope slide preparation, INHS collection number 579,407; BELIZE: Toledo District: 32 km WNW of Punta Gorda, Yok Balum Cave, 13.IV.2012, SJT, MES, JJ, CMS, GBH & AC, coll.; Paratypes: BELZE: Toledo District: 32 km WNW of Punta Gorda, Yok Balum Cave, 13.IV.2012, (2 adults & 1 juvenile on slides, 3 adults or subadults & 3 juveniles in alcohol), SJT, MES, JJ, CMS, GBH & AC, coll.; 37 km WNW of Punta Gorda, cave near Pueblo Creek Cave, 16.IV.2011, (1 adult on slide—without legs), MES, JKK, CMS, GBH & GeC, coll.

Diagnosis. *Trogolaphysa jacobyi* sp. n. is the only member of the genus that is blind, has 3-toothed mucro and unguis, and has a single macrochaeta on the metathorax. *Trogolaphysa belizeana* is the only other New World *Trogolaphysa* lacking eyes and having a 3-toothed mucro, but it differs from *T. jacobyi* sp. n. in having 3 metathoracic macrochaetae (1 in *T. jacobyi* sp. n.), in the arrangement and identity of inner macrochaetae on Abd. 4 (cf. Figs 38, 49 see discussion below), in having few postlabial scales (absent in *T. jacobyi* sp. n.) and setae (many in *T. jacobyi* sp. n., cf. Figs 30, 46), in the presence of sensillum d2 on Abd. 3 (absent in *T. jacobyi* sp. n.), in the absence of unpaired ungual teeth (1 tooth in *T. jacobyi* sp. n.) and in having a typical lanceolate unguiculus (basally swollen in *T. jacobyi* sp. n.). Table 3 provides a list of characters that distinguish *T. jacobyi* sp. n. from all other New World *Trogolaphysa* lacking eyes and having paired basal ungual teeth inserted near the basal fourth of the inner edge.

Description. Size. Body length up to 2.0 mm.

Color. Living specimens yellowish, with pigment only on a small eyepatch and mesothorax (Fig. 24). Specimens in alcohol white, without trace of pigment.

Table 3. Diagnostic table for blind species of *Trogolaphysa* with basal paired ungual teeth originating on basal fourth of inner edge of claw.

| Species	Mucronal teeth	Inner ungual teeth	Unguiculus shape	Mesothorax macrochaetae	Metathorax macrochaetae	4th Abdominal segment large inner macrochaetae
T. jacobyi sp. n.	3	3	basally swollen	4	1	A5, B4, B5
T. belizeana	3	2	lanceolate	4	3	A4, A5, B5
T. haitica	4	2	lanceolate	0	0	0
T. ecuatoriana	5	2	basally swollen	0	0	0
T. bessoni	5	2	basally swollen	3	0	apparently A5, B4, B5

Figure 24. *Trogolaphysa jacobyi* sp. n. habitus, photographed in Yok Balum Cave.

Scale distribution. Scales transparent, present on Ant. 1–2. Scales absent from postlabial region of head, ventral tube, legs and dorsal face of manubrium.

Head. Antenna/cephalic diagonal ratio up to 5.8 (Fig. 24). Fourth antennomere with incomplete but clear constriction near middle, with many shallow whorls of setae (Fig. 25); apical bulb absent; subapical sensillum not seen. Sense organ of Ant. 3 with sensilla 1 and 4 short, acuminate, thin-walled and translucent; sensillum 5 acuminate, dark and shorter than 1 and 4; sensilla 2–3 broad, leaf-like, resting in shallow grooves. Eyes not seen on slide-mounted specimens, but 1–2 pigment patches visible in life (Fig. 24). Head dorsally with 8 macrochaetae (A0, A2, A3, M3, S3, S5, Pa5 and Pm3—Fig. 26). Seta M4 displaced laterally towards cephalic sulcus. Series S with setae S1–5; S0 absent, macrochaeta S3 displaced anteriorly, away from cephalic sulcus (cf. Figs 5, 26). Prelabral and all labral setae smooth: setae within row A and C subequal; seta B2 shorter than B0 and B1 (Fig. 27). Distal margin of labrum smooth, papillae absent. Apical and subapical setae of maxillary palp smooth; sublobular plate without seta-like appendages. Lateral process of labial papilla E weakly bent dorsally and not nearly reaching apex of papilla (Fig. 28). Labial triangle setae as M1M2rEL1–2A1–5 (Fig. 29), seta M1 ciliate, all others smooth; r short; A2 close to r, L1 close to E and distant
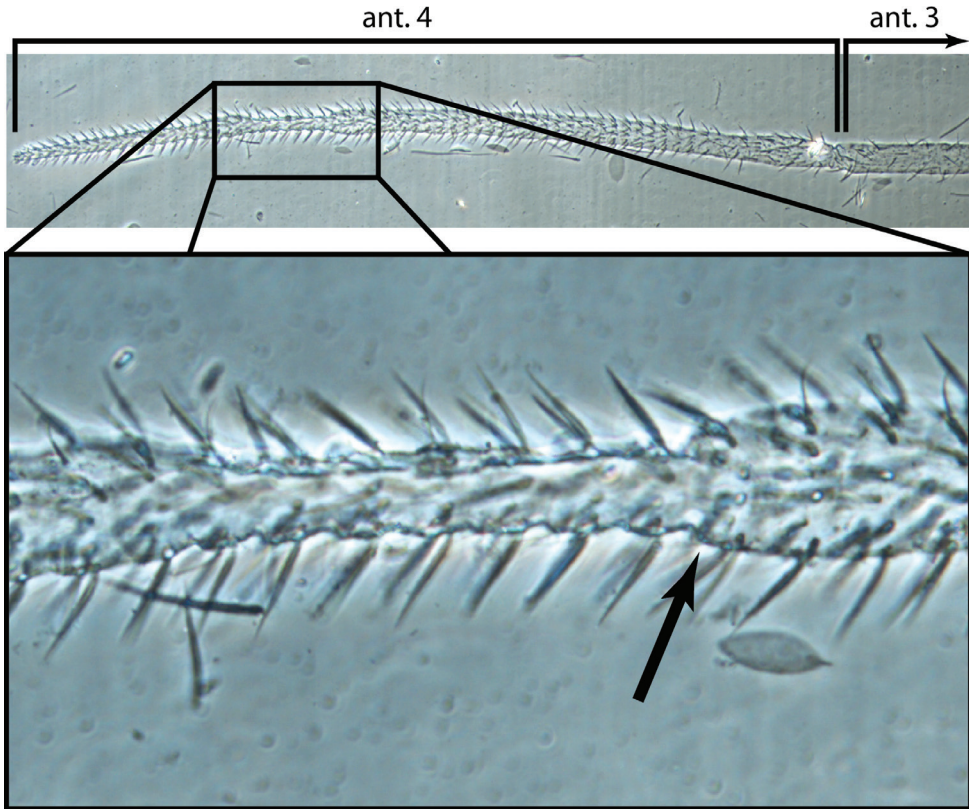
Figure 25. *Trogolaphysa jacobyi* sp. n. Fourth antennal segment showing constriction and incomplete suture (arrow).

from L2. Postlabium without scales, polychaetotic, uniformly covered with many large and small, weakly ciliate or smooth setae (Fig. 30); modified setae absent. Columns ICELO ill defined due to polychaetosis. Ventral cervical setae usually 6+6.

    Body. Mesothoracic hood not developed. Complete dorsal macrochaetae as 62/41/0244+0+9-11. Mesothorax with 1 anterior (a5) and usually 3 posterior (p1–3) macrochaetae forming an arch (Fig. 31); some individuals with only mesothoraxic macrochaeta p2 (Fig. 32); microchaetae m1, m2, m4, p4 and p5 present. Metathorax with 1 macro- and 5 microchaetae (Fig. 33). First abdominal segment seta a6 absent; 4 posterior setae arranged in a single row (Fig. 34–36). Inner bothriotrix complex of Abd. 2 with 3 fan-shaped setae, one microsensillum and macrochaeta m3; outer bothriotrix with 3 fan-shaped setae and macrochaeta m5; setae a6, m6 and p5 present. Inner bothriotrix complex of Abd. 3 with 3 fan-shaped setae, one sensillum and macrochaetae m3; external bothriotrichal complex (Fig. 37) with 6–7 fan-shaped setae, macrochaetae am6, pm6 and p6; sensillum d2 absent. Fourth abdominal segment with 4 inner (Fig. 38) and 9–11 outer (Fig. 39) macrochaetae: inner macrochaetae A5, B4, and B5 large, B6 small; B5 displaced towards A6 instead of B6; (Fig. 38). Outer
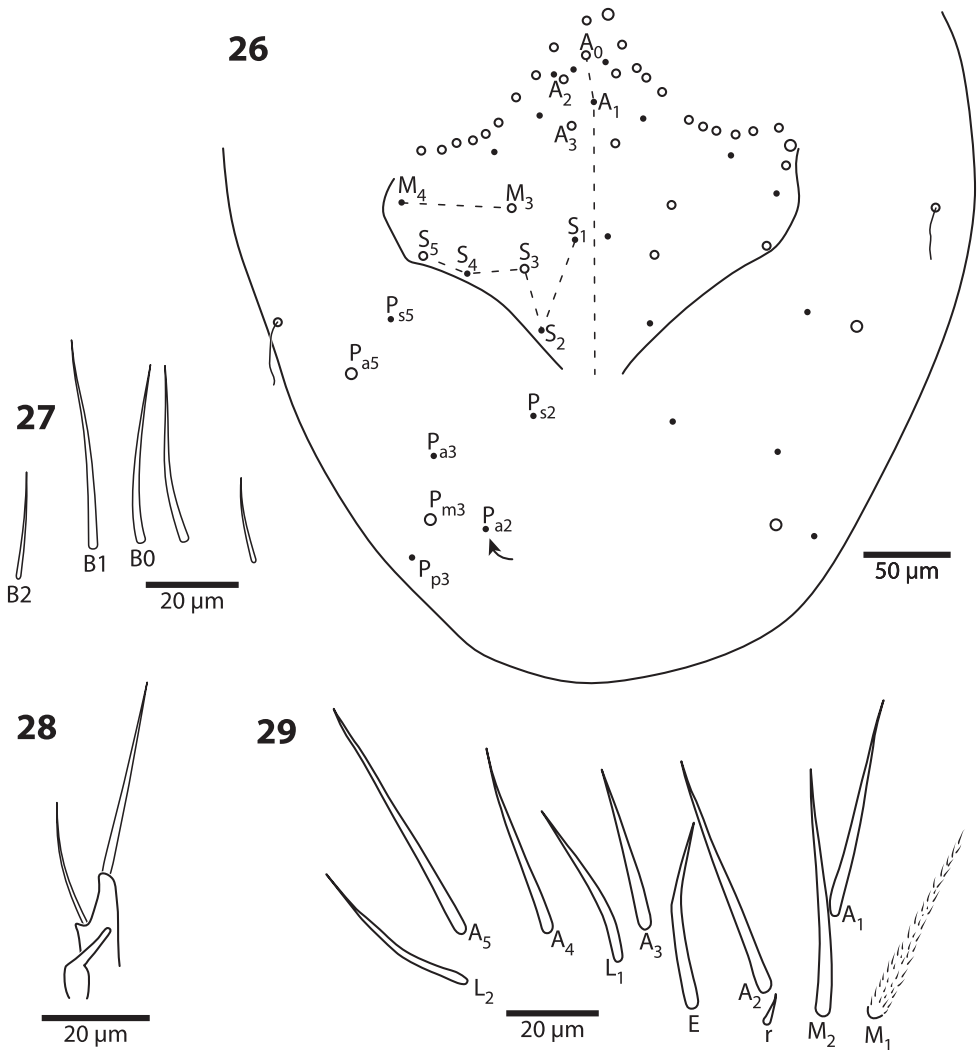
Figures 26–29. *Trogolaphysa jacobyi* sp. n. **26** Head dorsal chaetotaxy **27** Labral setae on row B **28** Lateral process of labial papilla E **29** Labial triangle.

macrochaetae D3, E2, E3, F1, and F2 large; small outer macrochaetae E4, F3, F4 and 3 others probably belonging to series Fe present. Abd. 4 anterior and medial bothriotricha with 4 and 2 fan-shaped supplementary setae, respectively (Fig. 39). Posterior bothriotrix corresponds to D4, without associated supplementary setae. Posterior setae 6–7+6–7. Intersegmental membrane between Abd. 4–5 with 4–7 lenticular organs.

Legs. Trochanteral organ with up to 25 setae. Claw complex as in Figs 41–42. Tenent hair acuminate, longer on L1 than L3. Smooth posterior setae on metathoraxic legs as long as unguiculus. Unguis with 3 inner teeth: basal teeth small, subequal and ending on basal fourth of inner edge; unpaired tooth distinctly larger than basal
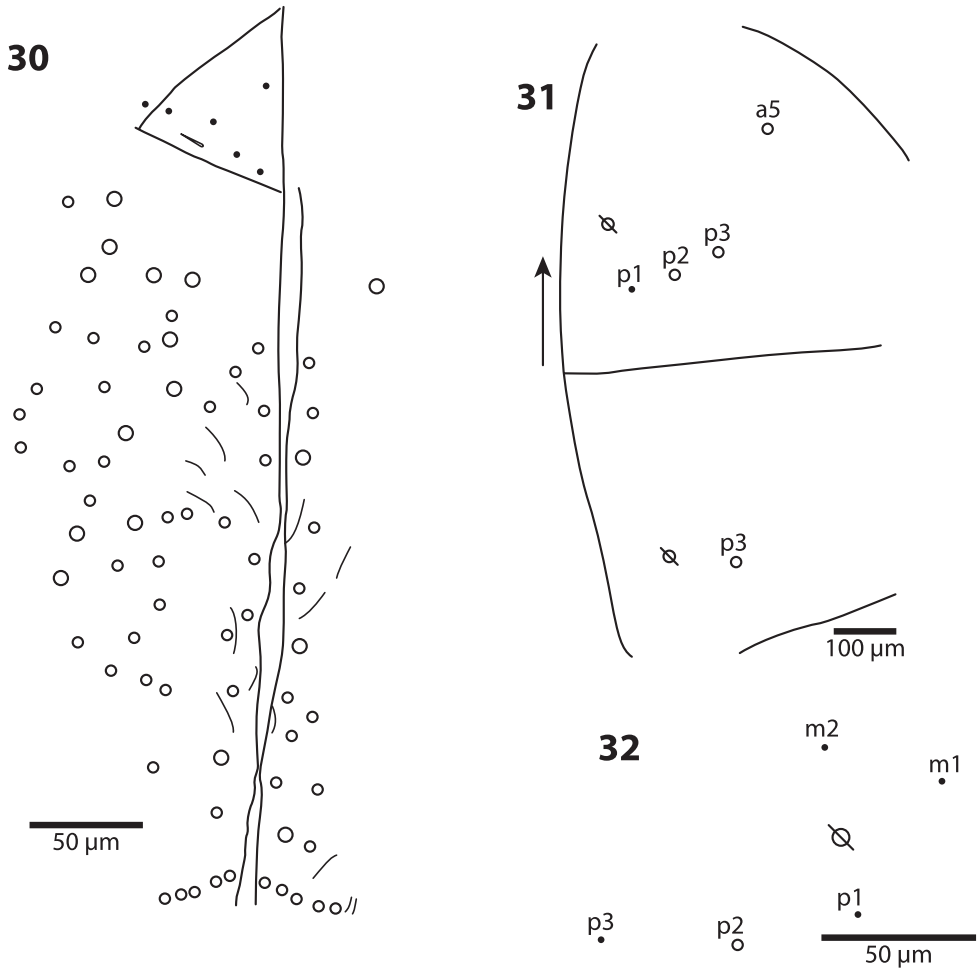
Figures 30–32. *Trogolaphysa jacobyi* sp. n. **30** Labial triangle and postlabium, open and filled circles represent ciliate and smooth setae, respectively **31** Thorax macrochaetae **32** Mesothorax, detail of inner chaetotaxy on a different individual.

teeth, ending near middle of inner ungual edge. Outer tooth absent on all claws; lateral teeth present only on pro- and mesothoracic legs, and ending on basal quarter of outer edge of unguis (Fig. 41). Unguiculus basally swollen, with basal fifth of outer margin weakly serrate.

Ventral tube. Anterior face with 2+2 distal macrochaetae; lateral and posterior setae not seen.

Furcula. Dens with 2 rows of finely ciliate spines, number of spines per row unclear on all specimens examined, but inner row with at least 36 spines. Mucro elongate and slender, with 3 teeth, basal inner tooth absent (Fig. 43): ratio mucro length/width of dens tip 2.3–2.8 (mode=2.4).
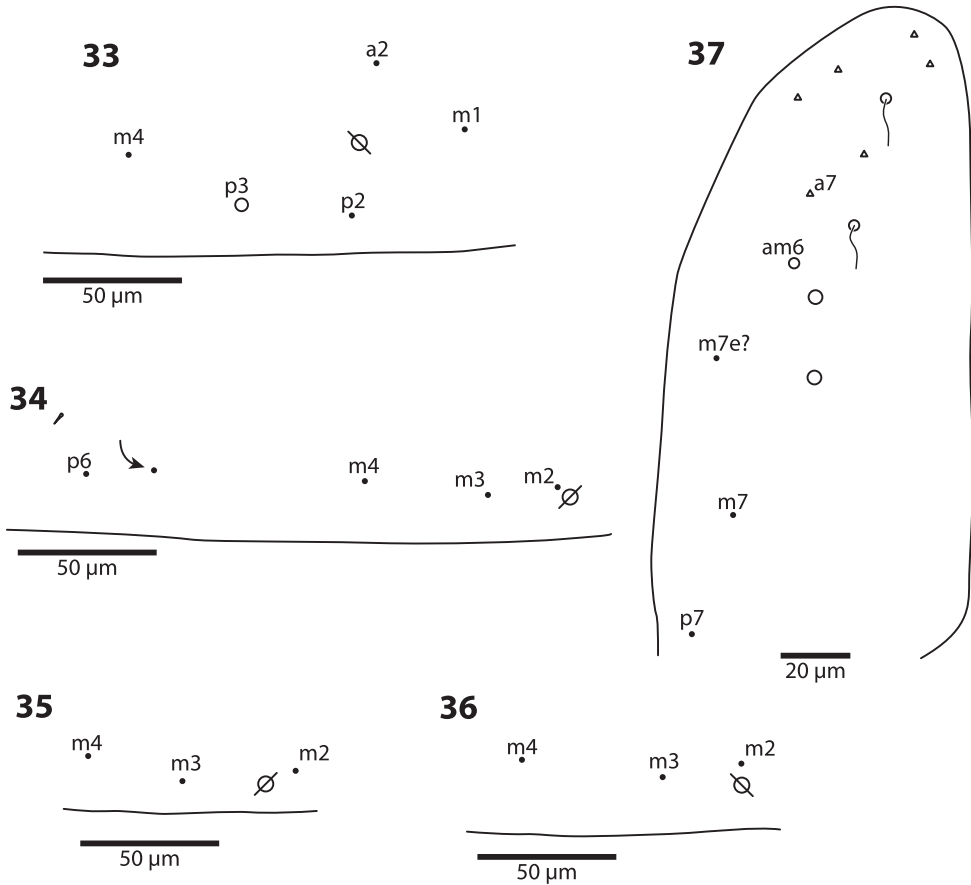
Figures 33–37. *Trogolaphysa jacobyi* sp. n., open and filled circles represent macro- and microchaetae, respectively, triangles represent fan-shaped microchaetae. **33** Metathorax, detail of inner chaetotaxy, seta a6 present but not shown **34** First abdominal segment, chaetotaxy, arrow points at seta seen in a single individual **35–36** First abdominal segment, alternative insertions of seta m2 **37** Third abdominal segment, setae associate with lateral bothriotricha.

Distribution. The species is known only from caves in southern Belize

Remarks. *Trogolaphysa jacobyi* sp. n. is a troglobiont (*sensu* Sket 2008, Culver and Pipan 2009). Living specimens seem to have eye pigment (Fig. 24), but we were unable to identify corneas on specimens examined. The only structure resembling a cornea corresponds to the EOS.

It could be argued that the constriction of the fourth antennomere places this species in *Troglopedetes*. However, the presence of a well-developed ciliate labial seta L2, the incomplete nature of the constriction on Ant. 4, and the similarity with *T. belizeana* (presumably with complete, unconstricted Ant. 4, and therefore an uncontested *Trogolaphysa*) suggest that *T. jacobyi* sp. n. should be retained in *Trogolaphysa*.
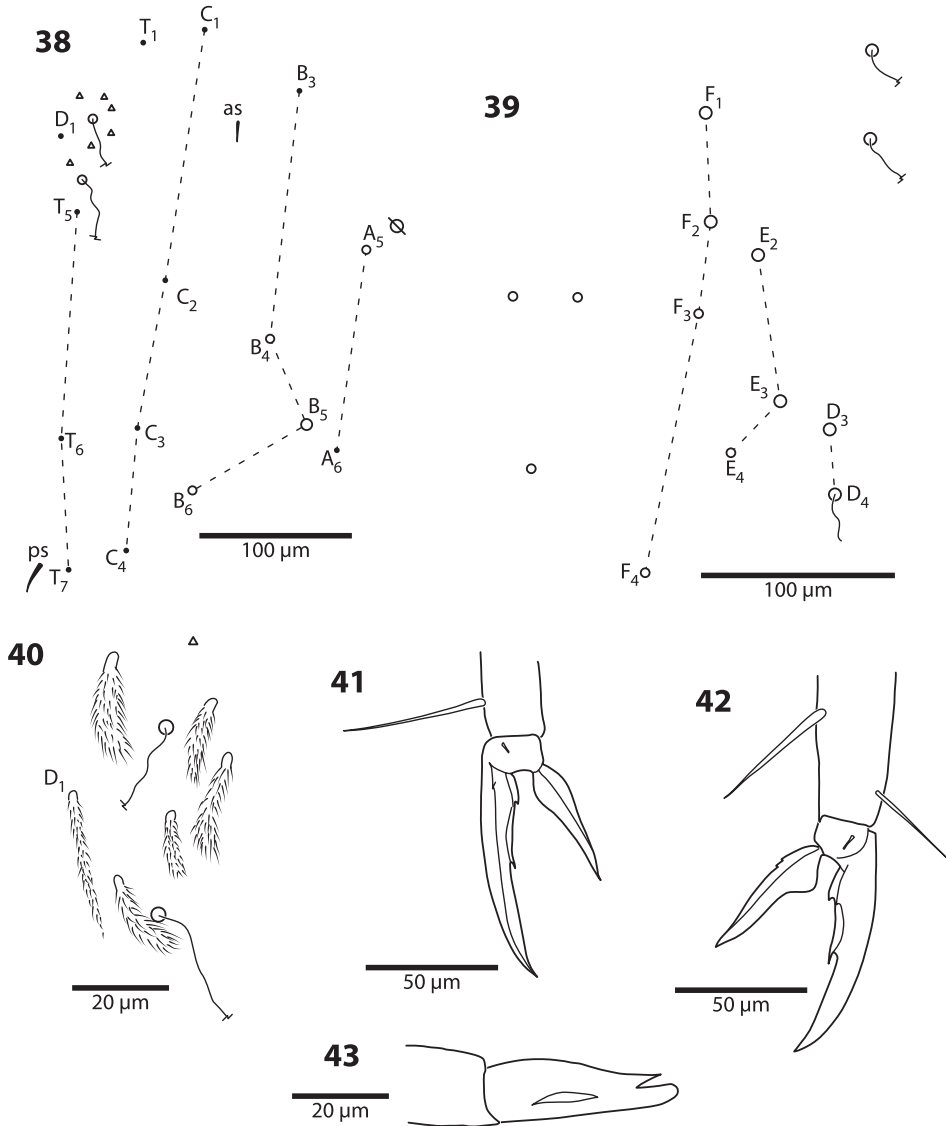
Figures 38–43. *Trogolaphysa jacobyi* sp. n., symbols as in previous plate. **38** Fourth abdominal segment, inner chaetotaxy **39** Fourth abdominal segment, outer macrochaetae **40** Fourth abdominal segment anterior bothriotrichal complex **41** Prothoracic claw complex **42** Metathoracic claw complex **43** Mucro.

Additionally, the fact that all other *Troglopedetes* species are restricted to the Old World have prompted us to retain the new species in *Trogolaphysa*.

Etymology. This species is dedicated to JoAnn Jacoby, the junior author's wife, in gratitude for her enthusiasm and assistance in the planning and execution of field-work in the caves of Belize and in many earlier excursions.

Figure 44. Type locality for *Trogolaphysa jacobyi* sp. n. in the dark zone of Yok Balum. Photo courtesy of MES.

Habitat. This species is a troglobiont, and all 5 collections (11 individuals) were taken in the dark zone (0 lux) on the floor (Fig. 44), often (80% of collections) in wet conditions associated with flowstone or calcite and drip pools, sometimes with scattered cricket droppings.

Trogolaphysa belizeana Palacios-Vargas & Thibaud, 1997

http://species-id.net/wiki/Trogolaphysa_belizeana
Figs 45–52

Material examined. Two paratypes; Belize: Cayo District, Actun Chapal cave, 7 km SE of Benque Viejo del Carmen, 10.XII.1992, W.R. Elliott.
Additions to the original description.

Head. Dorsal chaetotaxy of the head identical to that of *T. jacobyi* sp. n., with macrochaetae A0, A2, A3, M3, S3, S5, Pa5 and Pm3. Labral margin smooth. Sublobular plate of outer maxillary lobe without setae-like appendages. Labial papilla E with lateral appendage reaching tip of papilla; 5 proximal smooth labial setae present, seta z (Soto-Adames 2010) longest. Labial triangle formula as M1M2rEL1L2A1-5 (Fig. 45): M1 ciliate, shorter but thicker than M2; r short, stout, apically acuminate; A2 close to r. Postlabium with few scales; columns ICEL with 7732 setae (Fig. 46); seta L2 shortest; ventral cervical setae 6+6.

Body. Dorsal macrochaeta formula as 62/3–43/0343+0+11. Mesothorax with macrochaetae p2, p3 and a5, and microchaetae m4 and p5 clearly visible; setae p1,
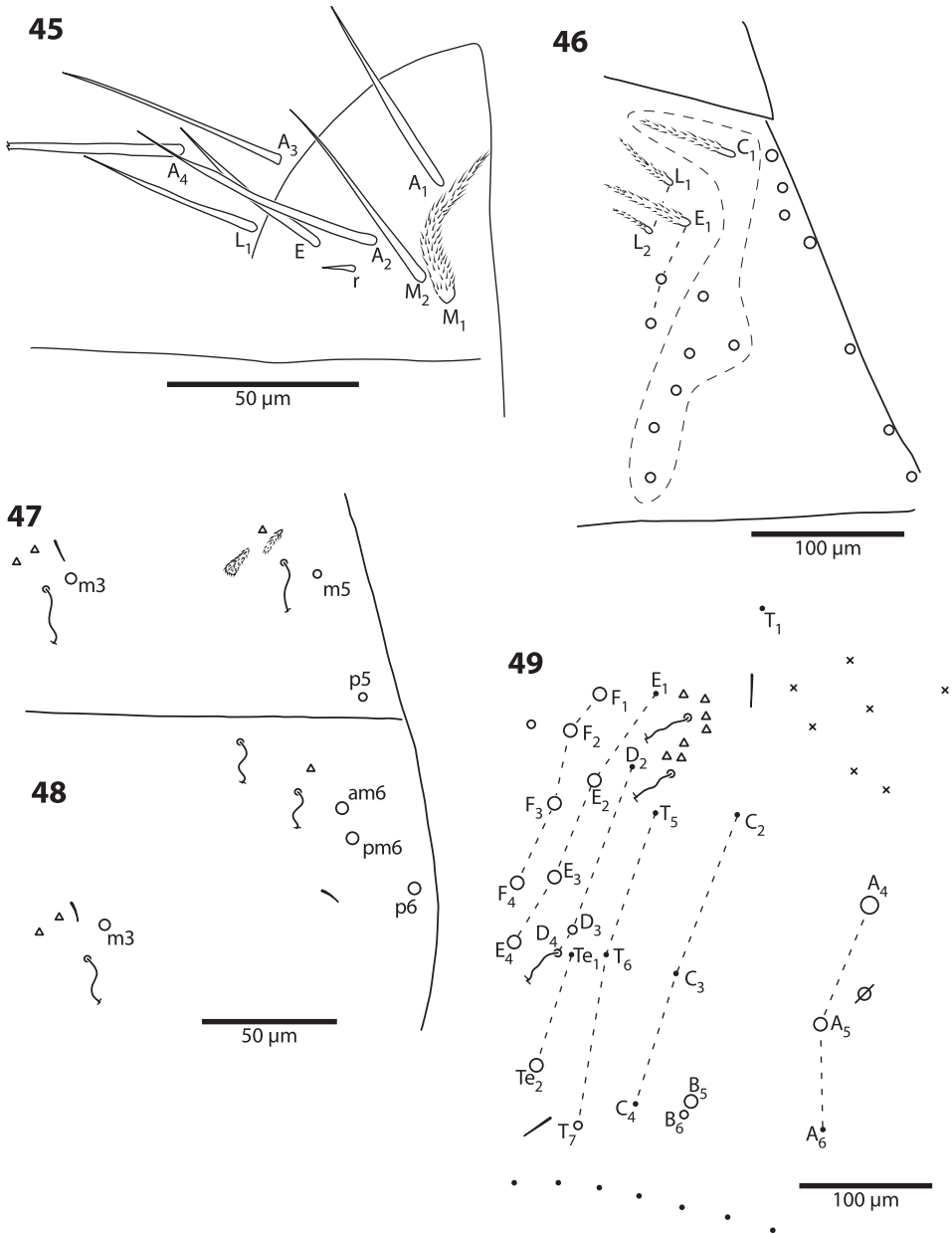
Figures 45–49. *Trogolaphysa belizeana* **45** Labial triangle **46** Postlabial chaetotaxy **47** Chaetotaxy of second abdominal segment **48** Chaetotaxy of third abdominal segment **49** Complete chaetotaxy of fourth abdominal segment, x represent sensilla-like setae.

m2 and p6 obscured. Metathorax with 3 macro- and 1 microchaetae arranged as in *T. giordanoae* sp. n. (Fig. 13). Abd. 1 with at least three inner microchaetae, apparently without a6, but lateral field of segment not clearly visible. Abd. 2 chaetotaxy normal
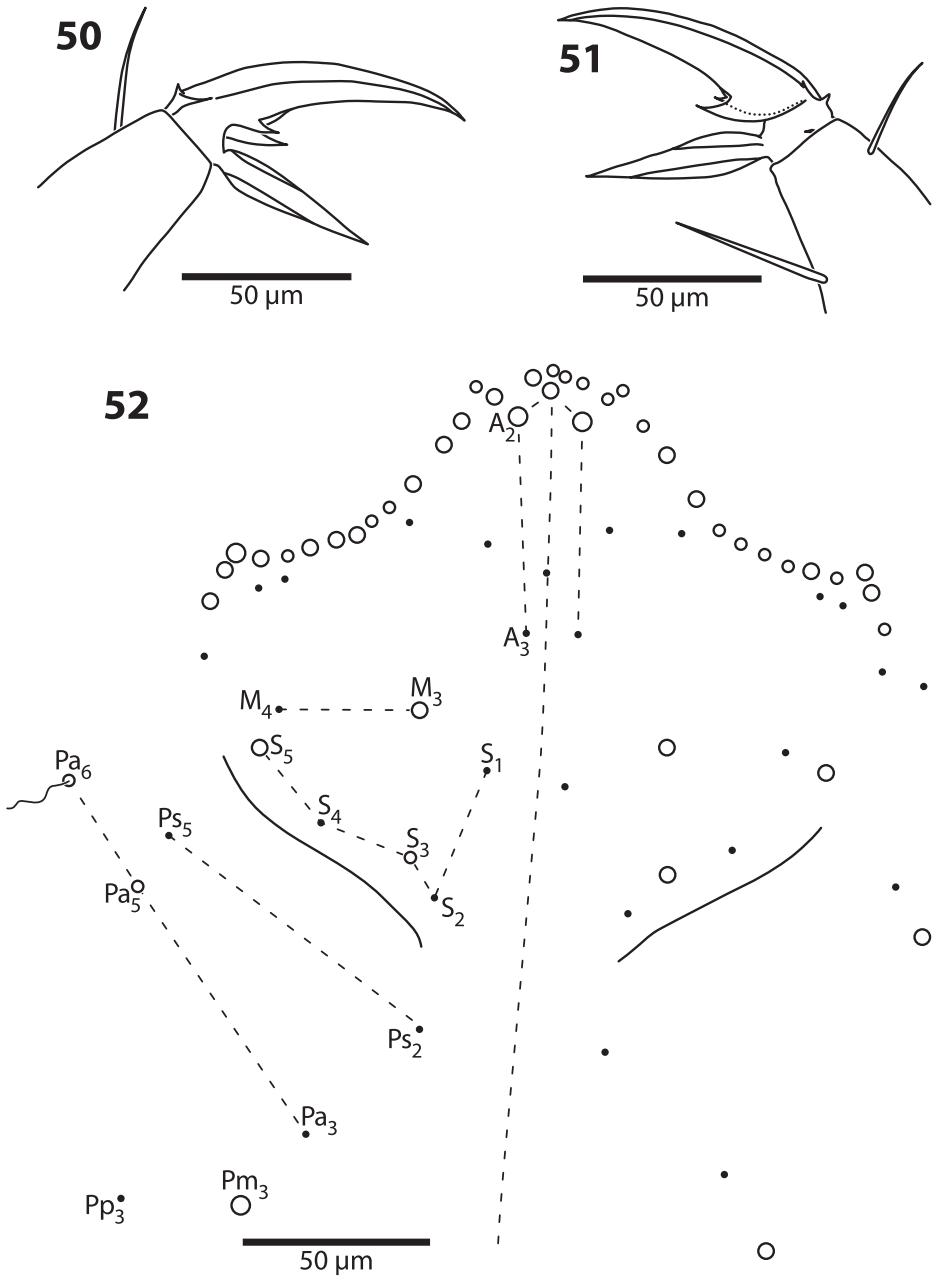
Figures 50–52. *Trogolaphysa belizeana* (**50**, **51**) and *Trogolaphysa jataca* (**52**) **50** Prothoracic claw **51** Metathoracic claw **52** Dorsal chaetotaxy of head.

(Fig. 47): with bothriotricha m2 and a5, sensillum as, macrochaetae m3 and m5, setae a6, m6 and p5, and fan-shaped supplementary setae around bothriotrichal complexes. Abd. 3 (Fig. 48) with insertion of bothriotricha m2, a5 and m5, macrochaetae m3,

a7, pm6 and p6, and sensillum d2 normally placed. Chaetotaxy of Abd. 4 as in Fig. 49: inner macrochaetae A4, A5, B5 and B6 present, B6 smallest; outer macrochaetae T7, D3, E2, E3, E4, F1, F2, F3, F4, one member of series Fe and one posterior setae of unclear homology present; relative position of bothriotricha normal; microchaeta B4 absent, microchaeta Te1 present. Posterior setae 7+7. Intersegmental membrane between Abd. 4–5 with at least 4 lenticular organs, actual number of organs unclear due to folding of membrane.

Legs. Claw complex of pro- and metathoracic legs as in Figs 50–51. Tenent hair acuminate. Outer and lateral unguis teeth small, inconspicuous; inner paired teeth with one tooth slightly, but clearly larger, unpaired teeth absent. Unguiculus lanceolate.

Ventral tube. With 2+2 distal macrochaetae on anterior face.

Remarks. The paratypes examined differ from the original description of the species in having labial seta L2 smooth instead of ciliate, in having only 2 posterior mesothoraxic macrochaetae, in the claws having lateral teeth and in the number of bothriotricha on Abd. 2 and Abd. 4.

Variation in the number of mesothoraxic macrochaetae is also seen in *T. jacobyi* sp. n and may be related to post-embryonic development. The chaetotaxy of Abd. 2 in fig. 12 of Palacios-Vargas and Thibaud (1997) suggests a composite of the chaetotaxy of Abd. 2 and 3, whereas the bothriotrichal complex of Abd. 4 shown in Palacios-Vargas and Thibaud (1997, fig. 13) seems based on an aberrant specimen.

Trogolaphysa jataca (Wray, 1953)
http://species-id.net/wiki/Trogolaphysa_jataca
Fig. 53–55

Material examined. Puerto Rico: Isabela, Guajataca Commonwealth Forest, Rd. 446, 18.41263°N, 66.96887°W, top of mogote at crossroad between trails 6, 25 & 26, leaf litter, 15.V.2009, F. Soto (2 specimens); Cayey, Rd. 4471, Km 4.1, leaf litter, 18.VI.1998, F. Soto (1 specimen); Mayagüez, University of Puerto Rico, secondary forest east of Biology Building, 18.21350°N, 67.13774°W, royal palm (*Roystonea borinquena* O.F. Cook) leaf litter, III.2009, M. Ospina (3 specimens).

Additions to the original description.

Head. Dorsal chaetotaxy as in Fig. 52: macrochaetae A0, A2, M3, S3, S5, Pa5 and Pm3 present; 1+1 microchaetae inserted near A1. Postlabium with all setae ciliate; columns ICELO with 41232; posterior setae on column I detached from anterior group.

Body. Mesothorax (Fig. 53) with one anterior (a5) and six posterior macrochaeta; microchaetae m2, m4, p5 and p6 present; microchaetae p1 and p2 absent. Metathorax with 4 inner microchaetae, as in *T. riopedrensis* (Fig. 58). Abd. 1 with 4 posterior setae; seta a6 absent. Abd. 2 and 3 as in *T. giordanoae* sp. n. (Figs 15, 16); Abd. 2 seta p5 fusiform, with enlarged socket (Fig. 54). Abd. 4 as in Fig. 55: inner macrochaetae A4, A5, B5 and B6 present; macrochaetae Te2, D3, E2, E3, F1–3 present; 4 other lateral
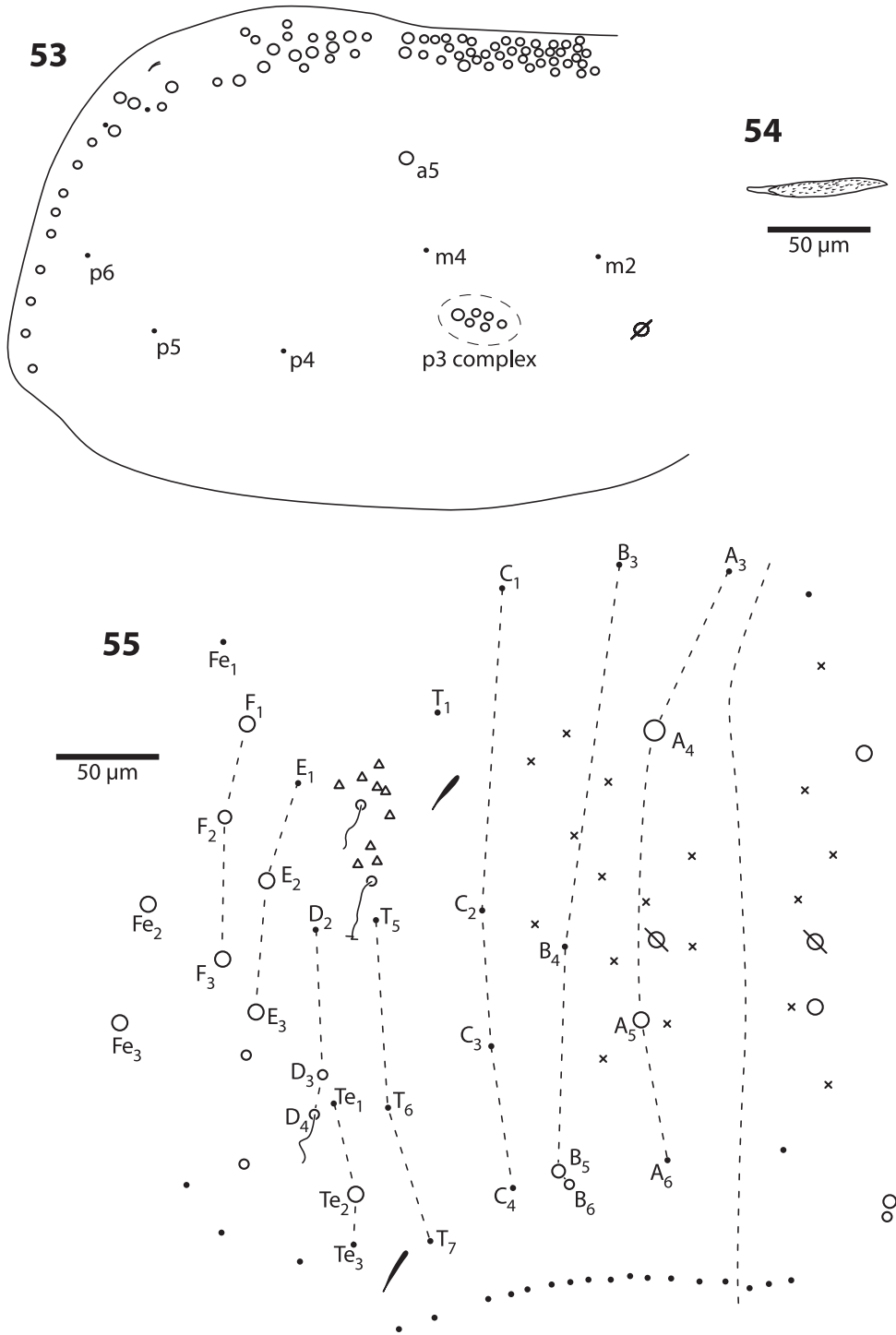
Figures 53–55. *Trogolaphysa jataca* **53** Mesothorax chaetotaxy **54** Second abdominal segment seta p5 **55** Complete chaetotaxy of fourth abdominal segment.

and posterior small macrochaetae present. Posterior setae 13–14+13–14. Intersegmental membrane between Abd. 4–5 with 4 lenticular organs.

Ventral tube. Anterior face with 3+3 distal macrochaetae; smaller individuals with 2+2 macrochaetae.

Trogolaphysa geminata (Mari Mutt, 1988)
http://species-id.net/wiki/Trogolaphysa_geminata
Fig. 56

Material examined. Puerto Rico: Maricao, Maricao Commonwealth Forest, near observation tower on Rd. 120, 18.14444°N, 66.97962°W, leaf litter, 8.VI.1998, F. Soto (1 specimen); Mayagüez, University of Puerto Rico, secondary forest east of Biology Building, 18.21350°N, 67.13774°W, royal palm (*R. borinquena*) leaf litter, III.2009, M. Ospina (3 specimens).

Additions to the original description.

Head. Dorsal chaetotaxy as in Fig. 56: macrochaetae A0, A2, M3, S3, Pa5 and Pm3 present. Postlabium with all setae ciliate; columns ICELO with 41232; posterior setae on column I detached from anterior group.

Body. Mesothorax as in *T. jataca* (Fig. 53). Metathorax as in *T. riopedrensis* (Fig. 58). Abd. 1 as in *T. riopedrensis* (Fig. 59) with one anterior (a6) and 4 posterior setae. Abd. 2 and 3 as in *T. giordanoae* sp. n. (Figs 15, 16); Abd. 2 seta p5 fusiform as in *T. jataca*. Abd. 4 as in *T. jataca* (Fig. 55): inner macrochaetae A4, A5, B5 and B6 present; macrochaetae Te2, D3, E2, E3, F1, F2, F3 present; 4 other lateral and posterior small macrochaetae present. Posterior setae 13–14+13–14. Intersegmental membrane between Abd. 4–5 with 4–6 lenticular organs.

Ventral tube. Anterior face with 3+3 distal macrochaetae.

Trogolaphysa riopedrensis (Mari Mutt, 1988)
http://species-id.net/wiki/Trogolaphysa_riopedrensis
Fig. 57–60

Material examined. Puerto Rico, Aguadilla, Caimital Alto, Villa Grajales, 18.44058°N, 67.11840°W, moist mown lawn, 9.VII.1999, F. Soto (1 specimen); USA Virgin Islands, St. Thomas, 18.35348°N, 64.93520°W, wet leaf litter, patch of forest along Rd. 33 near intersection with Rd. 40, 28.VI.2000, F. Soto (1 specimen).

Additions to the original description.

Head. Dorsal chaetotaxy as in Fig. 57: macrochaetae A0, (A2), A3, S3, S5, Pa5 and Pm3 present. Postlabium with all setae ciliate; columns ICELO with 41232; posterior setae on column C detached from anterior group.

Body. Mesothorax as in *T. jataca* (Fig. 53). Metathorax as in (Fig. 58). Abd. 1 with 1 anterior (a6) and 4 posterior setae (Fig. 59). Abd. 2 and 3 as in *T. giordanoae*
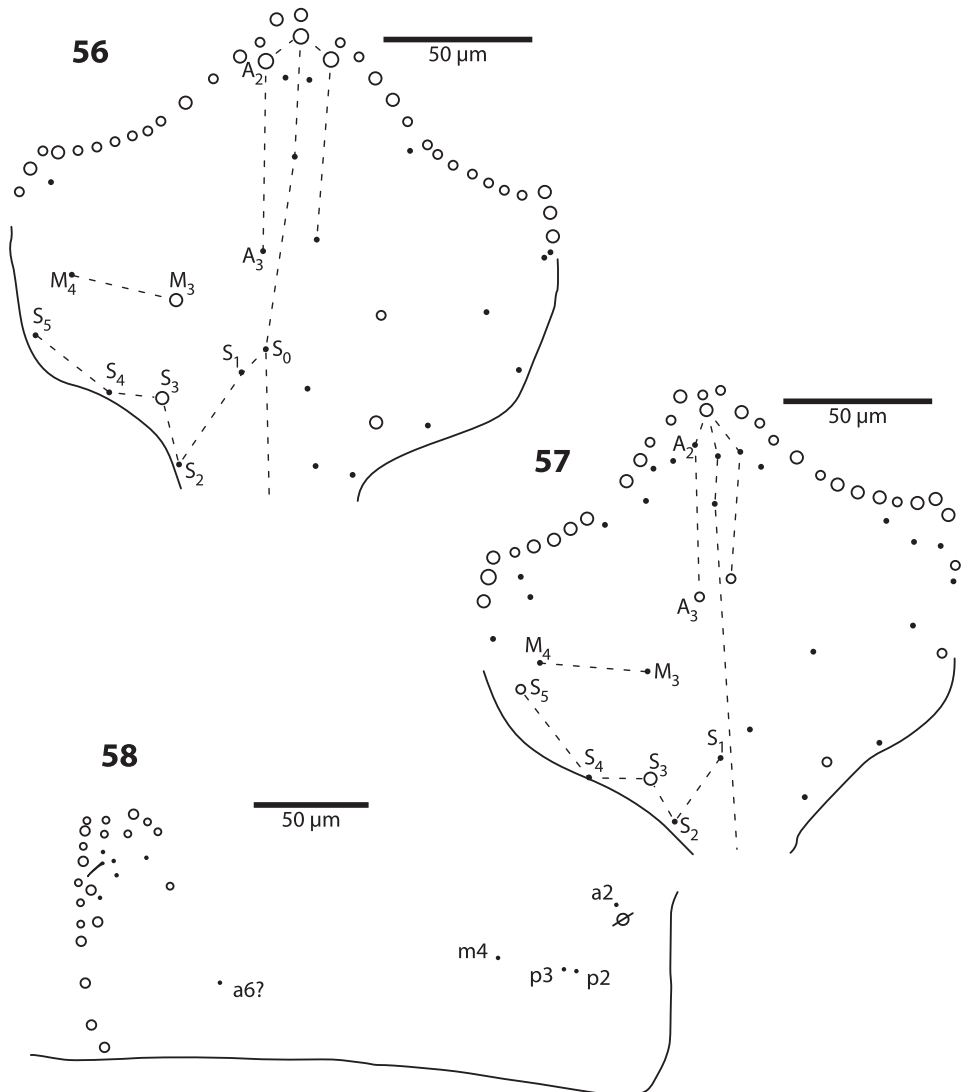
Figures 56–58. *Trogolaphysa geminata* (**56**) and *Trogolaphysa riopedrensis* (**57, 58**) **56** Head dorsal chaetotaxy **57** Head dorsal chaetotaxy **58** Metathorax chaetotaxy.

sp. n. (Figs 15, 16). Abd. 4 as in Fig. 60: inner macrochaetae A4, A5, B4, B5 and B6 present; outer macrochaetae D3, E2, E3, F1, F2, F3, Fe3 present; at least one other outer macrochaeta present. Posterior setae 17+17. Intersegmental membrane between Abd. 4–5 with 4–6 lenticular organs (Fig. 60).

Ventral tube. Anterior face with 4+4 distal macrochaetae.

Remarks: The individual from St. Thomas lacks head macrochaetae A2. In the individual from Aguadilla the dorsal and outer teeth of the unguis end on the basal fourth of the claw instead of the distal half.
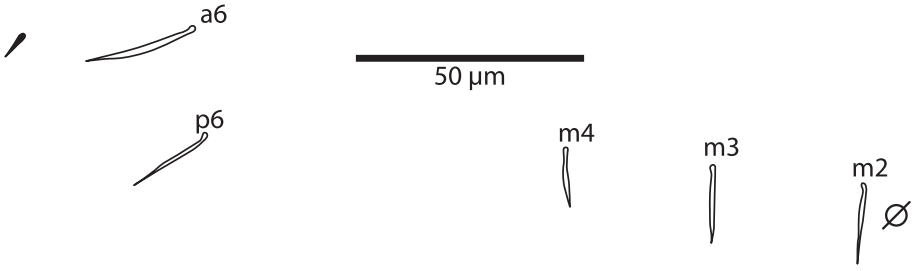
Figures 59, 60. *Trogolaphysa riopedrensis* **59** Chaetotaxy of first abdominal segment **60** Complete chaetotaxy of fourth abdominal segment, arrows identify the lenticular organs.

Discussion

Dorsal chaetotaxy

The dorsal chaetotaxy of *Trogolaphysa* has not been fully described in the context of the AMS (Soto-Adames 2010) and Szeptycki (1979) systems of nomenclature. The notes presented below are based on the study of *T. jataca*, *T. geminata* 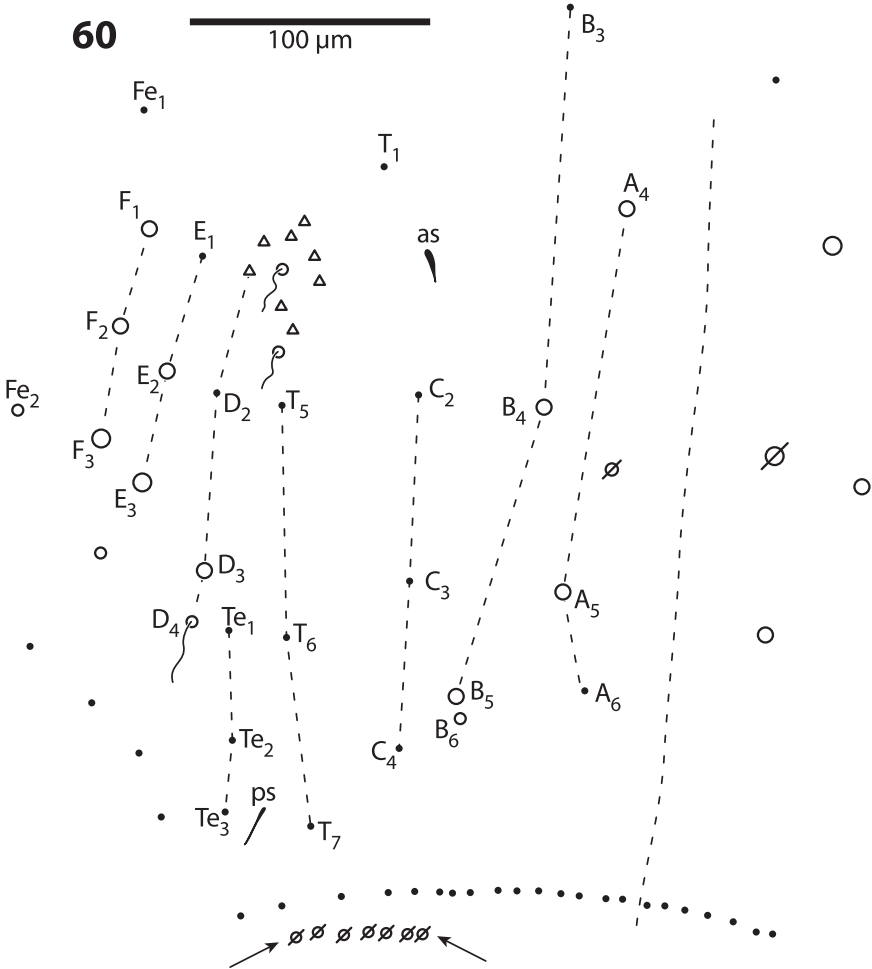and *T. riopedrensis*, three surface species from Puerto Rico, in addition to the three species of cave *Trogolaphysa* from Belize.

Head. The dorsal chaetotaxy of the head is reduced when compared to other genera of scaled Entomobryidae (e.g., *Seira, Pseudosinella*; cf. Fig. 26 here to fig. 1 in Soto-Adames [2008] and fig. 4 in Soto-Adames [2010]). In the species studied, series A includes setae A0-3. Some species have additional microchaetae that can be construed as belonging to this series (e.g., *T. jataca*, Fig. 52) but only A0–3 are present in all species examined. Seta A1 is always a normal, coarsely ciliate microchaeta, all other members of the series can develop into macrochaetae.

Series M includes 2 setae, probably homologous to M3–M4. In most species the lateral seta in series M is internal to S5, but in troglomorphs *T. jacobyi* sp. n. and *T. belizeana* the seta is inserted external to S5 and just internal to the dorsal cephalic suture. M0 is absent (seen only in one individual of *T. giordanoae* sp. n.), whereas M3 is often developed into a macrochaetae. Series S includes setae S1–5, S0 is absent (seen only in one individual of *T. geminata*). Among the species examined only setae S3 and S5 are modified into macrochaetae. Most setae in series S are inserted along the dorsal cephalic sulcus; the exceptions are S1, which is anterior to all others, and seta S3 when it is modified into a macrochaeta (cf., *T. giordanoae* sp. n. [Fig. 5] versus *T. jacobyi* sp. n. [Fig. 26]).

There is a pattern in the addition of macrochaetae on the interocular region of the head for species with 3–4 macrochaetae, but the pattern in not retained for species with five macrochaetae: whenever three macrochaetae are present they are always A0, A2 and M3; the species with four macrochaetae carries A0, A2 and M3 plus S3; the species with five macrochaetae have A0, A2, S3, S5, and either A3 or M3.

Series Ps includes only two setae (Ps2 and Ps5) whereas series Pa has four setae (Pa2, 3, 5 and bothriotrix Pa6), and series Pm and Pp has one seta each (Pm3 and Pp3). Posterior setae Pa5 and Pm3 are often modified into macrochaetae.

Mesothorax. The chaetotaxy of the mesothorax is reduced, as in scaled Entomobryidae (e.g., *Seira, Pseudosinella* [Soto-Adames 2008, 2010]), the closest group of Entomobryoidea for which detailed information about chaetotaxy is available. All *Trogolaphysa* species share the presence of macrochaetae a5 and p3, and microchaetae m2, m4, p4, p5, and what we provisionally call p6. Setae p1 and p2 are present in the three species from Belize but either absent or integrated in the p3 macrochaetae complex in the three surface species from Puerto Rico (Fig. 53)

The homologies of the posterior macrochaetae across the species examined are unclear. The presence of setae p1 and p2 in *T. giordanoae* sp. n. suggests that the cluster of six posterior macrochaetae represent a multiplication of seta p3; whereas the transfor-

mation of p1 and p2 into macrochaetae in *T. jacobyi* sp. n. and *T. belizeana*, and their absence in the surface species *T. jataca*, *T. geminata* and *T. riopedrensis* suggest that the three setae have been integrated (and duplicated) into the macrochaetal complex. We propose three hypotheses to explain the evolution of posterior macrochaeta: the macrochaetae evolved independently more than once in the genus, either as 1) a duplication of p1–3 or as 2) multiplication of p3 alone; 3) the cluster evolved only once, a duplication of p1–3, and the setae we have identified as p1 and p2 in *T. giordanoae* sp. n. are secondary and not homologous to those present in *T. jacobyi* sp. n. and *T. belizeana*. A study of the postembryonic development of these setae or molecular phylogenetic analysis may provide evidence in support one of the hypotheses proposed above.

Metathorax. The chaetotaxy of this segment is reduced to five setae (e.g., *T. geminata*, Fig. 58). The homologies of these setae are uncertain, and names provided in Fig. 58 are based on comparison with the general organization of the chaetotaxy in first instar *Seira dowlingi* (Wray, 1953), *Heteromurus nitidus* (Templeton, 1835) and *Willowsia buskii* (Lubbock, 1870) (Soto-Adames 2008, Szeptycki 1979). The single macrochaeta present in *T. jacobyi* sp. n. appears to be homologous to p3, whereas the three macrochaetae present in *T. giordanoae* sp. n. and *T. belizeana* appear to be homologous to a displaced a2, p2 and p3.

Abdomen 1. This segment also has a reduced chaetotaxy, carrying not more than six setae (Figs 14, 59). The homologies proposed are based on comparisons with first instar *S. dowlingi, H. nitidus* and *W. buskii* (Soto-Adames 2008, Szeptycki 1979). Seta a6 is present in *T. giordanoae* sp. n., *T. geminata* and *T. riopedrensis* and absent in *T. jacobyi* sp. n. and *T. jataca.*

Abdomen 2–3. The chaetotaxy of these segments was previously described by Mari Mutt (1987[1988]) and the species examined here, including *T. belizeana,* conform to that description. These two segments do not carry inner microchaetae beyond those associated with the bothriotichal complexes. The macrochaetae on Abd. 2 are homologous to m3 and m5. Lateral setae a6, m6 and p5 appear to be present in all species, although a6 and m6 are often difficult to see. The socket of p5 is enlarged, macrochaeta-like, but this seta falls off in most slide-mounted individuals, it was observed in *T. jacobyi* sp. n, where it is a ciliate mesochaeta and in *T. jataca*, where it is enlarged and fusiform (Fig. 54).

The macrochaetae on Abd. 3 appear to be homologous to m3, am6, pm6 and p6 (Fig. 16). Sensillum d2 is absent in *T. jacobyi* sp. n. (Fig. 37), in *T. belizeana* it is inserted posterior to macrochaeta pm6 (Fig. 48), whereas in *T. giordanoae* sp. n., *T. jataca*, *T. geminata* and *T. riopedrensis* it is inserted anterior to or forming a row with pm6 (Fig. 16).

Abdomen 4. The chaetotaxy of Abd. 4 is similar to that in scaled Entomobryidae and setae modified in, for example, *Seira* or *Lepidocyrtus*, can also be modified in *Trogolaphysa*. The chaetotaxy displays some unique peculiarities. For example, what appears to be seta B6 is, in most species, a meso- or small macrochaeta inserted just posterior to B5 (Fig. 17). In addition, the posterior bothriotrix corresponds to D4 (D3 in *Seira,* Soto-Adames 2008). The number, identity and relative insertion of inner

macrochaetae varies between *Trogolaphysa* species. *Trogolaphysa giordanoae* sp. n. and *T. riopedrensis* share the same inner macrochaetae (A4, A5, B4, B5), but the insertion of B4 in relation to the pseudopore and seta C2 differ between these two species (cf., Figs 17, 60). *Trogolaphysa geminata*, *T. jataca* and *T. belizeana* have three inner macrochaetae and share macrochaetae A5 and B5, but whereas in *T. jacobyi* sp. n. the third macrochaetae is B4, in the other two species it is A4. *Trogolaphysa jacobyi* sp. n. is also unusual in having macrochaeta B5 displaced towards A6 instead of C4 (Fig. 38).

The external macrochaetae in the first three rows of columns D, E and F are stable in the species of examined. All species have macrochaetae D3, E2, E3, F1 and F2. Macrochaeta F3 is present in all species except *T. jacobyi* sp. n. The number of macrochaetae external to column F and posterior to row 3 varies intra- and interspecifically. However, the lateral and posterior fields are often difficult to see in regular preparations and it is possible that some of the apparent differences are simply incomplete observations.

The number of posterior setae (per side) on Abd. 4 also varies between species: 6–7 in *T. belizeana* and *T. jacobyi* sp. n., 13–14 in *T. jataca* and *T. geminata*, 17 in *T. riopedrensis* and 19–21 in *T. giordanoae* sp. n.

Chaetotaxy and phylogenetic analysis of cave-adapted species

The morphological information for surface species *T. luquillensis* (Mari Mutt 1987[1988]), cave species *T. subterranea* (Mari Mutt 1987[1988]) and the six species treated here was coded into 69 characters (Appendix 1). The data matrix (Appendix 2) includes character systems identified (Christiansen 1961, 1965; Gama 1984) as most responsive to adaptation to cave habitats (i.e., eye number, claw complex morphology), but most characters (60) refer to chaetotaxy. *Campylothorax sabanus* (Wray, 1953) was designated as outgroup.

Phylogenetic analysis based on all characters supports two equally parsimonious trees (Figs 61–64) in which the two troglobiontic species from Belize form a monophyletic group and *T. giordanoae* sp. n. is placed at the base of the species from Puerto Rico. The parsimony trees support the sister species relationship between *T. subterranea* and *T. luquillensis*, but relationships between the other three species from Puerto Rico are unresolved, as *T. riopedrensis* is placed as sister to either *T. jataca* or to a clade that includes all other island species.

The apparently rare occurrence of metathoracic macrochaetae in the three Belizean species suggests a close relationship between them, but the parsimony trees show the troglobiontic species diverging before the separation of *T. giordanoae* sp. n. from the ancestor of the island species. The lack of support for the monophyly of Belizean species may be an artifact of a disproportionate contribution of characters under strong cave habitat selection to the final topology of the tree. However, parsimony analysis based only on chatotactic characters results in a single shortest tree (Fig. 63), which also supports the monophyly of troglobiontic species while retaining *T. giordanoae* sp. n. at the base of the island species clade.
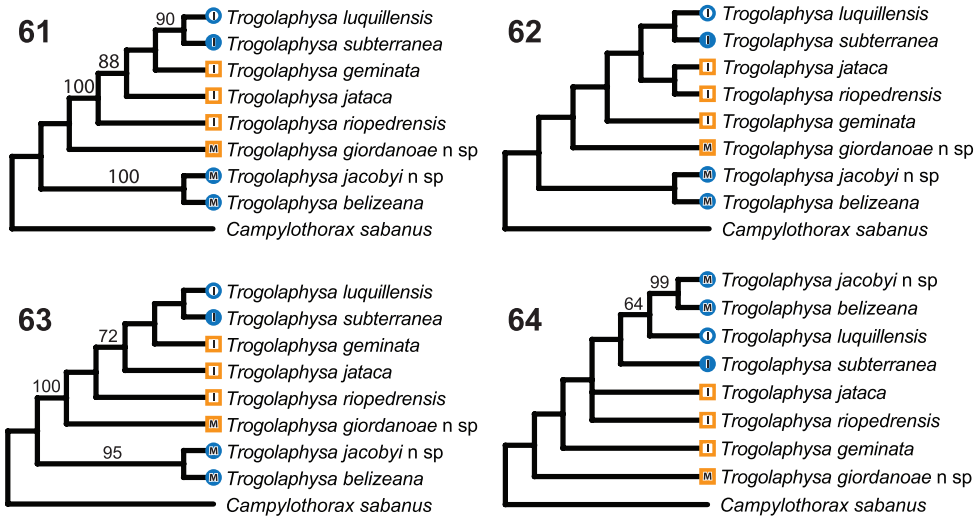
Figure 61–64. Cladograms. Branch lengths are arbitrary. All searches performed using branch and bound, including the bootstrap analyses. Numbers above branches are bootstrap values based on 5000 pseudoreplicates. Circles: taxa with troglomorphies, squares-not troglomorphic. Solid symbols recorded only from caves, open symbols recorded from surface. M, mainland species: I, island species **61–62** The two shortest trees found when all characters are included in the analysis **63** Shortest tree found when only chaetotactic characters are analyzed **64** Shortest tree found when only eye number, characters related to claw complex morphology and mucro are analyzed.

To assess whether putative adaptive characters provide support for alternative relationships, we conducted a phylogenetic analysis using only eye number, ornamentation of labral papilla, and claw and mucro morphology. These characters support a single tree (Fig. 64) that places most surface forms at the base of the tree while supporting a clade comprising the cave species (*T. jacobyi* sp. n., *T. belizeana*, *T. subterranea*) and *T. luquillensis*. *Trogolaphysa luquillensis* is endemic to the tropical rainforest and is unique among surface species examined here in having an acuminate tenent hair and three inner ungual teeth close to each other and inserted in the basal half of the claw. These characters of the claw have been identified as adaptations to walking on water surface or other, permanently wet, surfaces such as those found in rainforest leaf litter and caves (Christiansen 1961, 1965).

Evaluation of the direction of evolution of head chaetotaxy using trees in Fig. 61 and Fig. 62 supports a trend towards a reduction in number of macrochaetae. However, the pattern is equivocal because some macrochaetae may be lost independently through out the tree, depending on tree topology. For example, S5 might have been lost once and regained or it might have been lost twice independently. What is clear from this analysis is that A3 is the first macrochaetae to be lost, followed by S5, S3 and M3 (Table 4). *Trogolaphysa riopedrensis* is the only species in which this pattern seems to be disrupted: under either tree this species is hypothesized to have lost M3 and gain A3 independently.

Table 4. Distribution of head macrochaetae in eight species of New World *Trogolaphsya.*

Species	Macrochaetae number	Macrochaeta identity					
T. jacobyi sp. n.	6	A0	A2	A3	M3	S3	S5
T. belizeana	6	A0	A2	A3	M3	S3	S5
T. riopedrensis	5	A0	A2	A3	—	S3	S5
T. jataca	5	A0	A2	—	M3	S3	S5
T. geminata	4	A0	A2	—	M3	S3	—
T. luquillensis,	3	A0	A2	—	M3	—	—
T. giordanoae sp. n.	3	A0	A2	—	M3	—	—
T. subterranea	2	A0	A2	—	—	—	—

## Taxonomic status of *Dicranocentruga* and *Trogolaphysa*

The character used by Mitra (1993, 2002) to diagnose genera *Trogolaphysa* and *Dicranocentruga* can be difficult to apply. The presence of EOS is difficult to ascertain using phase contrast or DIC light microscopy. The retention of *Dicranocentruga* as a valid genus hinges on whether *Trogolaphysa maya*, the type species of *Trogolaphysa*, carries the EOS. As pointed out above, the presence of EOS in the two troglomorphic species considered here suggests that this structure is also present in *T. maya*. We examined the single alcohol preserved syntype of *T. maya* deposited at the Illinois Natural History, but the condition of the specimen is such that confirmation of the presence of the EOS is impractical.

It is possible, as proposed by Mitra (1993), that a more extensive analysis of idiochaetotaxy may provide diagnostic characters for these two genera that are easier to see and interpret. The present study does not support this idea. The organization of the idiochaetotaxy is the same in all the species studied. Changes in the distribution of setae, as in the case of the metathorax, are related to the morphology of the elements (whether macro- or microsetae), and not to the presence of EOS, number of eyes, or other cave adaptive characters. Until such time as the presence of EOS can be reliably determined, or other diagnostic characters are found, we retain all New World *Dicranocentruga* in the genus *Trogolaphysa*, as proposed by Thibaud and Najt (1988[1989]).

Morphological characters and phylogeny

The genus *Trogolaphysa* has diversified in the New World from where now 35 species have been named (Table 1, Fig. 65), many of which are troglobionts or at least eutroglophiles (*sensu* Sket 2008, Culver and Pipan 2009). Phylogenetic studies of species-level relationships have not been published for this genus, perhaps as a result of the scarcity and quality of the characters available for analysis. Most described species, es-
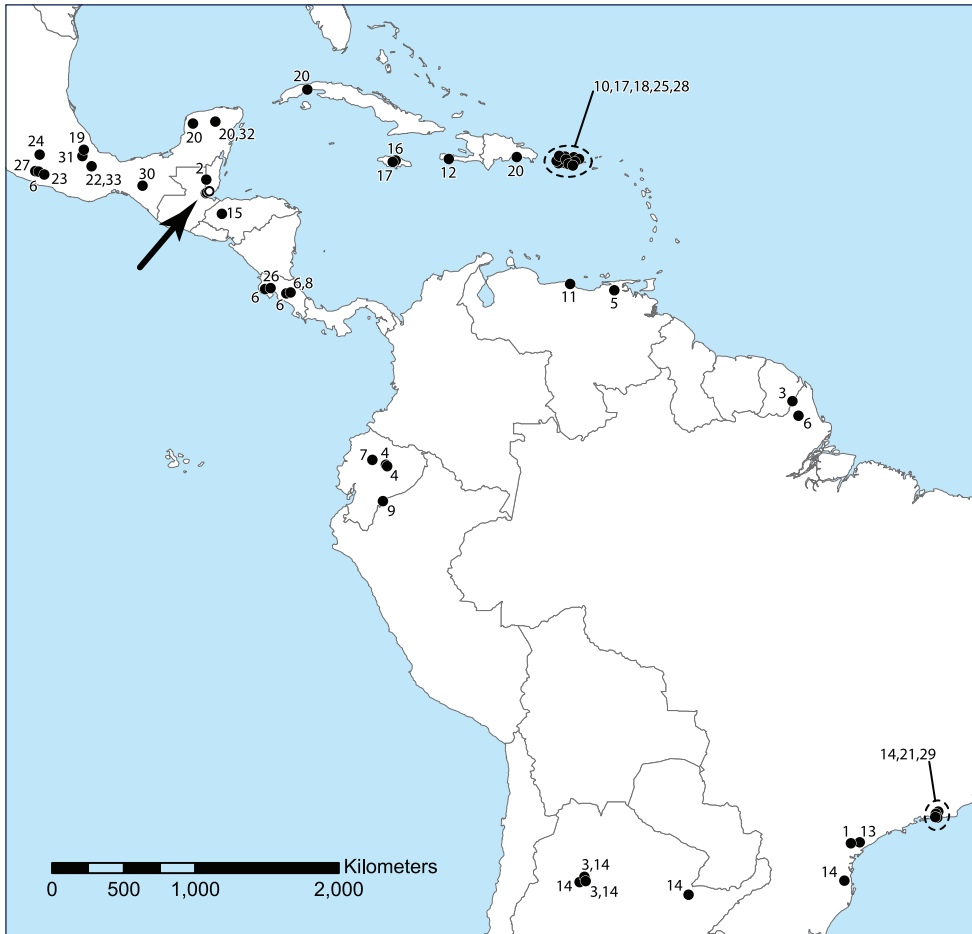
Figure 65. Central and South America and the Caribbean Islands, showing the published distributions of described New World species of the genus *Trogolaphysa*. Open circles (arrow): *Trogolaphysa jacobyi* sp. n., *Trogolaphysa giordanoae* sp. n. Closed circles: **1** *T. aelleni* Yoshii, 1988 **2** *T. belizeana* **3** *T. berlandi* (Denis, 1925) **4** *T. bessoni* Thibaud & Najt, 1989 **5** *T. caripensis* (Gruia, 1987) **6** *T. carpenteri* (Denis, 1925) **7** *T. cotopaxiana* Thibaud & Najt, 1989 **8** *T. distinguenda* (Denis, 1931) **9** *T. ecuatorica* (Palacios-Vargas, Ojeda & Christiansen, 1986) **10** *T. geminata* **11** *T. guacharo* Yoshii, 1988 **12** *T. haitica* (Palacios-Vargas, Ojeda & Christiansen, 1986) **13** *T. hauseri* Yoshii, 1988 **14** *T. hirtipes* (Handschin, 1924) **15** *T. hondurasensis* (Palacios-Vargas, Ojeda & Christiansen, 1986) **16** *T. jamaicana* (Palacios-Vargas, Ojeda & Christiansen, 1986) **17** *T. jataca* **18** *T. luquillensis* **19** *T. marimutti* (Palacios-Vargas, Ojeda & Christiansen, 1986) **20** *T. maya* **21** *T. millsi* Arlé, 1939 **22** *T. nacionalica* (Palacios-Vargas, Ojeda & Christiansen, 1986) **23** *T. oztotlica* (Ojeda & Palacios-Vargas, 1984) **24** *T. relicta* (Palacios-Vargas, Ojeda & Christiansen, 1986) **25** *T. riopedrensis* **26** *T. separata* (Denis, 1933) **27** *T. strinatii* Yoshii, 1988 **28** *T. subterranea* **29** *T. tijucana* (Arlé & Guimarães, 1979) **30** *T. toroi* (Palacios-Vargas, Ojeda & Christiansen, 1986) **31** *T. variabilis* (Palacios-Vargas, Ojeda & Christiansen, 1986) **32** *T. xtolokensis* (Palacios-Vargas, Ojeda & Christiansen, 1986) **33** *T. yoshiia* (Palacios-Vargas, Ojeda & Christiansen, 1986).

pecially cave forms, have been diagnosed almost exclusively based on characters of the claw complex, mucronal shape and development of the antennae, characters identified as malleable under selective pressures (Christiansen 1961). A new set of characters or character systems, would be needed to perform more reliable phylogenetic analyses. Most other studies addressing the evolution of morphological convergence in cave-adapted arthropods have used molecular data (e.g., Trontelj et al. 2012) to generate phylogenies for hypothesis testing. However, many troglobiontic springtail species are known only from a few individuals from few, seldom visited localities (as is evident from the small number of records reported in Mari Mutt and Bellinger 1990, 1996, and Mari Mutt et al. 2009), which are not suitable or available for molecular analysis. For these species only morphological information can be used to evaluate the evolution of other morphological characters.

Ever since the publication of Gisin's (1967) "systématique ideal," collembolan systematists have assumed that ideochaetotaxic characters are non-adaptive characters that evolve neutrally, are less prone to convergence and, therefore, more valuable for phylogenetic analysis. However, this assumption has never been tested in a phylogenetic context. The simple test performed here supports the traditional view of chaetotaxy as less vulnerable to directional convergence than characters related to claw structure. Analysis based exclusively on putative cave-adaptive characters support a clade comprising cave species from Puerto Rico and Belize, whereas analysis of chaetotaxy alone supports the placement of cave species from Puerto Rico and Belize in independent clades. Despite the clear difference in signal in the character partitions it should be noted that analysis of the complete character set results in higher bootstrap values for what is basically the chaetotaxy-only tree, than when only chaetotactic characters are analyzed. It is clear that some putative adaptive characters retain phylogenetic information concordant with chaetotaxy characters, an observation which argues in favor of the retention of all characters in the analysis. The simple test preformed here has to be expanded to include many more species, to determine if the result obtained are consistent or just an artifact of the sparse taxon sampling. It is unclear if chaetotaxy will provide sufficient characters to resolve relationships in an analysis that includes all species. In any case, there are problems related to the evolution and homology of some chaetotactic characters (e.g., posterior macrochaetae on the meso- and metathorax, and the inner macrochaetae on the fourth abdominal segment) that may be intractable on morphology-based datasets, and will require the use of putatively independent molecular characters.

Habitats

The two new species were found in conditions of similar substrate (*T. jacobyi* sp. n. mean=23.0 °C; *T. giordanoae* sp. n. mean=23.1 °C; W=11, p=0.7200) (Fig. 66) and air temperatures (*T. jacobyi* sp. n. mean=23.7 °C; *T. giordanoae* sp. n. mean=24.3 °C; W=23.5, p=0.3947) (Fig. 67), but *T. jacobyi* sp. n. was found only in complete
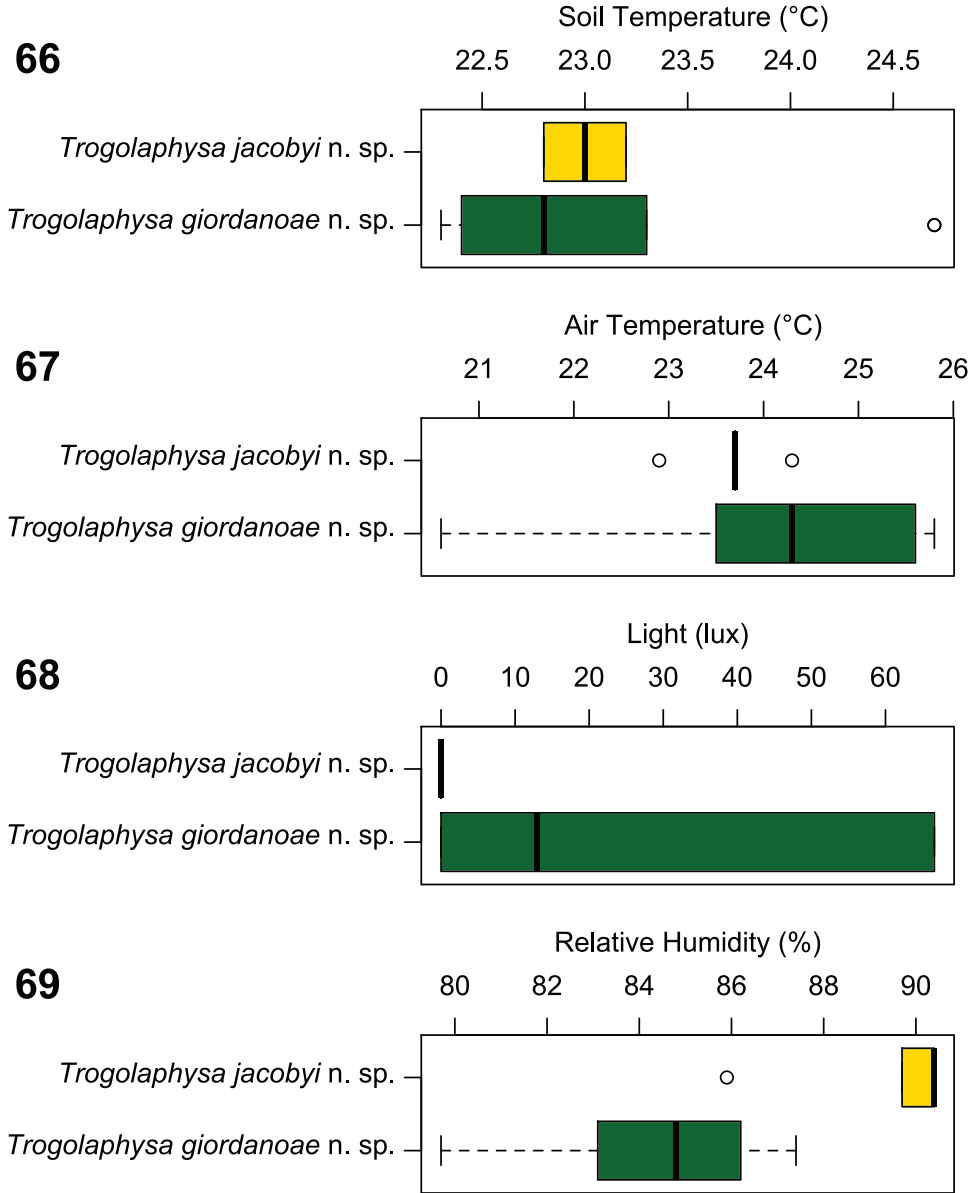
Figure 66–69. Boxplot comparisons of environmental parameters for collections of *Trogolaphysa jacobyi* sp. n. and *Trogolaphysa giordanoae* sp. n. **66** Soil temperature **67** Air temperature **68** Light **69** Relative humidity.

darkness (Fig. 68), whereas *T. giordanoae* sp. n. was found at significantly brighter and varying light conditions, typically in twilight (*T. jacobyi* sp. n. mean=0.0 lux; *T. giordanoae* sp. n. mean=29.5 lux; W=12.5, p=0.0260). *T. jacobyi* sp. n. also was found primarily under conditions of significantly elevated humidity, whereas *T. giordanoae* sp. n. was more varied in the humidity levels at which it was found (*T. jacobyi* sp. n.

mean=89.36 %; *T. giordanoae* sp. n. mean=84.56 %; W=65, p=0.0056) (Fig. 69). In addition, *T. giordanoae* sp. n. was frequently associated with fruit bat guano or other scat (Fig. 23). These observations support our classification of *T. jacobyi* sp. n. as a troglobiont and *T. giordanoae* sp. n. as a guanophile.

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Appendix I

Character and character states as circumscribed for phylogenetic analysis. (doi: 10.3897/zookeys.323.4950.app1) File format: Microsoft Word document (doc).

Citation: Soto-Adames FN, Taylor SJ (2013) The dorsal chaetotaxy of *Trogolaphysa* (Collembola, Paronellidae), with descriptions of two new species from caves in Belize. ZooKeys 323: 35–74. doi: 10.3897/zookeys.323.4950 Character and character states as circumscribed for phylogenetic analysis. doi: 10.3897/zookeys.323.4950.app1

Appendix II

Data matrix of morphological characters used in the phylogenetic analysis. (doi: 10.3897/zookeys.323.4950.app2) File format: Microsoft Word document (doc).

Citation: Soto-Adames FN, Taylor SJ (2013) The dorsal chaetotaxy of *Trogolaphysa* (Collembola, Paronellidae), with descriptions of two new species from caves in Belize. ZooKeys 323: 35–74. doi: 10.3897/zookeys.323.4950 Data matrix of morphological characters used in the phylogenetic analysis. doi: 10.3897/zookeys.323.4950.app2

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