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Endogean beetles (Coleoptera) of Guatemala: deep soil sampling and illustrated DNA barcode library

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Abstract

We document the diversity of endogean beetles discovered by us in the deep soil in Guatemala. They belong to eight families: Carabidae, Histeridae, Jacobsoniidae (first record for the country), Ptiliidae, Staphylinidae (subfamilies Aleocharinae, Leptotyphlinae, Osoriinae, Paederinae, Pselaphinae, Scydmaeninae, Staphylinidae), Scarabaeidae, Tenebrionidae, and Curculionidae. In total, we took 26 soil samples, each 20–40 litres in volume, and extracted from them 444 endogean adult beetles. To facilitate further studies of these poorly known organisms, often belonging to unnamed species and/or genera, we provide an open access online DNA barcode library containing 78 representative specimens (dx.doi.org/10.5883/DS-VGDS26). This is the first dedicated study highlighting the diversity of wingless and often eyeless beetles inhabiting the deep soil in Central America.

Keywords Coleoptera | beetle | endogean | deep soil | Guatemala

1. Introduction

Endogean beetles form a polyphyletic assemblage of coleopterans adapted for life in the minute hollows and crevices of the deep soil. Like many habitat-specific and distantly related organisms (e.g., soil-adapted caecilians, earthworms, and leptotyphlopid snakes), endogean beetles display a common set of convergent, adaptive morphological features such as the reduction or absence of eyes and hind wings, as well as relatively small and uniformly pale bodies. Due to their small size and cryptic habitat, endogean beetles are rarely encountered and grossly understudied. In this respect, endogean beetles might be considered terrestrial analogues to the inhabitants of the oceanic abyss (Jamieson & Weston 2023), in other words, rarely seen and inadequately known. In both cases, dedicated and labour-intensive sampling, if efficiently applied, is likely to result in significant findings. Examples of such deep soil beetle surveys are not numerous and are mainly limited to southern Europe, e.g., Fancello et al. (2009) for Italy and Bekchiev & Guéorguiev (2014) for Bulgaria. No dedicated deep soil beetle sampling has been reported from Central America. Guatemala, the spatial focus of our work, has a few records of eyeless endogean beetles suggestive, however, of much greater diversity. Examples include the ten congeneric species of anilline ground beetles (Sokolov & Kavanaugh 2014), one species of leptotyphline rove beetles (Gusarov 2003), and one unnamed lymantine weevil (Grebennikov & Anderson 2022). The main goal of our work is to provide a preliminary overview of endogean beetles from Guatemala, a grossly under sampled region.

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2. Material and Methods

2.1 Soil sampling and specimen extraction

We extracted endogean beetles from a total of 26 deep soil samples taken by us between May 7 and 17, 2022, in Guatemala (Tab. 1, Figs 1, 2A–C, Supplementary online material Figs 1–4). We targeted five types of forest (Tab. 1). Cloud forests are evergreen, montane, moist forests characterized by a frequent cloud cover sustaining Lauraceae, Ericaceae, Bromeliaceae, and Orchidaceae plants, along with mosses and ferns. Oak forests are dominated by the genus *Quercus*, with the admixture of pines. Dry forests have low precipitation ranging between 400 and 1000 mm per year; its deciduous trees shed leaves during the dry season and include those of the genera *Bursera*, *Ceiba*, *Caesalpinia*, *Cochlospermum*, *Cordia*, *Enterolobium*, *Ficus*, *Guaiacum*, *Haematoxylon*, *Leucaena*, *Plumeria*, *Zanthoxylum*, as well as cacti. The lowland tropical rainforest has high temperatures and humidity, distinct wet and dry seasons, and annual precipitation ranging between 1,000 and 2,000 mm, with a large variety of evergreen broadleaf trees dominated by *Swietenia* and *Ceiba*. Perturbed montane forest is an agricultural matrix with remnants of forest on steep terrain composed if broadleaf trees with the admixture of pines.

The herein reported specimens are currently stored in the Canadian National Collection of Insects, Arachnids, and Nematodes (Ottawa); different taxa will likely be distributed among collaborating taxonomic experts and stored elsewhere, depending on the subsequent work to this initial report. We used the floatation technique (Figs 2D–E) to extract the organic fraction from the deep soil samples. After completing the sampling stage, we conducted the Sun-driven specimen extraction in the town of Zacapa selected for its relatively hot and sunny climate. In almost all methodological details, we followed our earlier protocol, including site selection, deep soil sampling, soil flotation (= soil washing), sample storage and transportation, Sun-driven extraction of live specimens on thermoeclectors, and the transfer of specimens into vials (Andújar & Grebennikov 2021).

Learning from our previous experience, we introduced three methodological novelties. Firstly, our Sun-heated thermoeclectors were of a new lightweight aluminium design (Figs 2G–H) with an extraction surface twice as large as the older plastic design (Andújar & Grebennikov 2021). We used commercially available aluminium steam table pans 53.34 × 33.02 × 7.62 cm in size (21 × 13 × 3 inches) as water receptacles, while the floated soil sample was placed on top of the pans supported by a rectangle of chicken wire (Figs 2G–I). Unlike our earlier method (Andújar & Grebennikov 2021), a single setup consisted of one pan (not two, as before). Secondly, rapid fungal growth in the water beneath the samples had to be constantly battled; therefore, we harvested fallen specimens every day (not once in two days, as before) to prevent any damage caused by quickly growing fungi. We did not use detergents to reduce the surface tension because this would have resulted in rapid drowning and dying of specimens. Our goal was to keep small organisms floating alive on the water surface for a few extra hours, thus lessening the time to sink, die,

Figure 1. Map of the southern part of Guatemala showing the localities of the 26 deep soil samples.

and decay. When refilling water into each pan daily, we vigorously scrubbed and cleaned the internal wet surface of all aluminium pans to remove any quickly forming fungal growth. Thirdly, correlating with the twice as large extraction surface of the new eclectors and starting with sample 18, we increased the soil sample volume from approximately 20 litres (Figs 2A, B) to approximately 40 litres (Fig. 2C).

Floating deep soil samples frequently contained fully winged and eyed beetles from the soil surface or canopy. We disregarded such records and sampled only specimens with signs of morphological adaptations for the endogean lifestyle, which form the focus of the present study. In a few instances, however, a subjective decision had to be made on whether a litter- or soil-inhabiting specimen should be considered a deep soil inhabitant or not. For example, the Staphylinidae subfamilies Osoriinae, Pselaphinae, and Scydmaeninae include species with notably depigmented bodies and with eyes variously reduced in size. These beetles likely inhabit the border zone between the forest litter and underlying soil, thus being present in both. In such cases, we considered specimens with notably smaller eyes as those from the deep soil, although this criterion is subjective and difficult to define.

2.2 Generating and analysing DNA data

Identification of poorly known endogean beetles from our Guatemala deep soil samples was hampered by their inadequate taxonomy. None of the herein reported beetles could be identified by us to a named species and some of them not even to a named genus or tribe. This is in part due to our inability to use existing taxonomic names without establishing their identity by performing labour-intensive taxonomic revisions (e.g., Leptotyphlinae), or to the presence of likely unnamed taxa in our samples, either species or perhaps genera (e.g., some scydmaenine

Figure 2. Sampling methods of the deep soil Guatemala beetles. (**A–C**) pits producing samples GT12, GT16, and GT25, respectively (note that sample GT16 is from an extremely dry habitat, while sample GT25 is twice as large in volume); (**D**) a floating soil sample in a barrel with water; (**E**) scooping floating organic foam containing live beetles on a fine mesh; (**F**) wet samples prior to specimen extraction; (**G**) two aluminium thermoeclectors of the novel larger and lighter design; (**H**) thermoeclectors exposed to the Sun.

Table 1. List of 26 Guatemala localities and 444 endogean adult beetles sampled in May 2022 using deep soil flotation technique. **Hab**. – Habitat, **Lat**. – latitude, **Lon**. – longitude, **Alt**. – altitude. Two letter habitat abbreviations are **CF** – Cloud Forest, **DF** – Dry Forest, **OF** – Oak Forest, **PM** – Perturbed Montane Forest, **TR** – Tropical Rain Forest. Three-letter abbreviations of families are **Car**. – Carabidae, **His**. – Histeridae, **Jac**. – Jacobsoniidae, **Pti**. – Ptiliidae, **Sca**. – Scarabaeidae, **Ten**. – Tenebrionidae, and **Cur**. – Curculionidae. Four-letter abbreviations of Staphylinidae subfamilies are **Aleo**. – Aleocharinae, **Lept**. – Leptotyphlinae, **Osor**. – Osoriinae, **Paed**. – Paederinae, **Psel**. – Pselaphinae, **Scyd**. – Scydmaeninae, and **Stap**. – Staphylininae. Larvae were detected for Carabidae (two in GT21, one in GT22) and Leptotyphlinae (one in each GT09 and GT10).

##	Region	Hab.	Lat.	Lon.	Alt.	Date	Car.	His.	Jac.	Pti.	Staphylinidae							Sca.	Ten.	Cur.	Σ
											Aleo.	Lept.	Osor.	Paed.	Psel.	Scyd.	Stap.				
GT01	Chichicastenango	OF	14,9199	-91,1061	2015	7.v	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GT02	Nebaj	CF	15,3718	-91,1319	2598	8.v	14	0	0	3	0	0	5	0	0	2	0	0	0	0	24
GT03	Nebaj	CF	15,3698	-91,1302	2571	8.v	61	0	0	0	0	8	0	1	0	0	4	0	0	0	74
GT04	Nebaj	CF	15,3791	-91,1323	2378	8.v	15	0	0	0	0	4	0	0	0	0	0	0	0	0	19
GT05	Nebaj	CF	15,4428	-91,1406	1939	8.v	20	1	0	0	0	0	0	0	0	0	0	0	0	0	21
GT06	Nebaj	CF	15,3705	-91,1142	2536	9.v	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3
GT07	Nebaj	CF	15,3655	-91,1036	2559	9.v	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GT08	volc. Zunil	CF	14,7726	-91,4795	2209	9.v	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GT09	volc. Zunil	CF	14,7461	-91,4843	2666	10.v	7	0	0	0	0	4	0	0	0	0	0	0	0	0	11
GT10	volc. Zunil	CF	14,7456	-91,4782	2650	10.v	0	0	0	0	0	2	0	0	0	0	0	0	0	0	2
GT11	volc. Zunil	CF	14,747	-91,4803	2585	10.v	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3
GT12	volc. Sta. María	CF	14,7702	-91,5466	2994	11.v	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
GT13	volc. Sta. María	CF	14,7782	-91,553	2705	11.v	6	0	0	1	0	0	0	0	0	0	0	0	0	0	7
GT14	Quetzaltenango	OF	14,8947	-91,5862	2699	11.v	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
GT15	Quetzaltenango	OF	14,8915	-91,5848	2571	11.v	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
GT16	Zacapa	DF	14,8604	-89,7858	541	12.v	0	0	1	0	0	0	0	0	0	0	0	0	1	3	5
GT17	Zacapa	DF	14,8669	-89,7774	484	12.v	0	0	0	0	0	0	0	0	0	0	0	0	2	1	3
GT18	Chiquimula	DF	14,6009	-89,4525	769	13.v	0	0	0	4	0	0	4	0	3	10	0	0	1	0	22
GT19	Zacapa	PM	14,9478	-89,41	1101	13.v	0	0	0	1	0	1	0	0	0	0	0	0	0	0	2
GT20	Zacapa	PM	14,9678	-89,4091	767	13.v	0	0	0	0	7	2	0	0	1	3	0	0	0	0	13
GT21	S. de las Minas	CF	15,0833	-89,9409	2597	15.v	20	0	0	0	0	0	0	0	0	1	0	0	0	0	21
GT22	S. de las Minas	CF	15,0835	-89,944	2574	15.v	29	0	0	22	4	0	0	0	0	0	0	0	0	0	55
GT23	S. de las Minas	CF	15,0725	-89,9506	2166	15.v	12	0	0	0	0	10	0	0	0	8	0	0	0	0	30
GT24	Cerro San Gil	TR	15,6483	-88,8279	597	17.v	11	0	0	0	0	1	0	0	8	3	0	0	0	1	24
GT25	Cerro San Gil	TR	15,6483	-88,8277	598	17.v	10	0	0	0	0	0	0	0	0	2	0	6	0	2	20
GT26	Cerro San Gil	TR	15,6388	-88,8296	399	17.v	6	0	0	0	0	0	47	0	14	0	0	7	0	8	82
						Σ	220	1	1	31	11	32	56	1	26	29	4	13	4	15	**444**

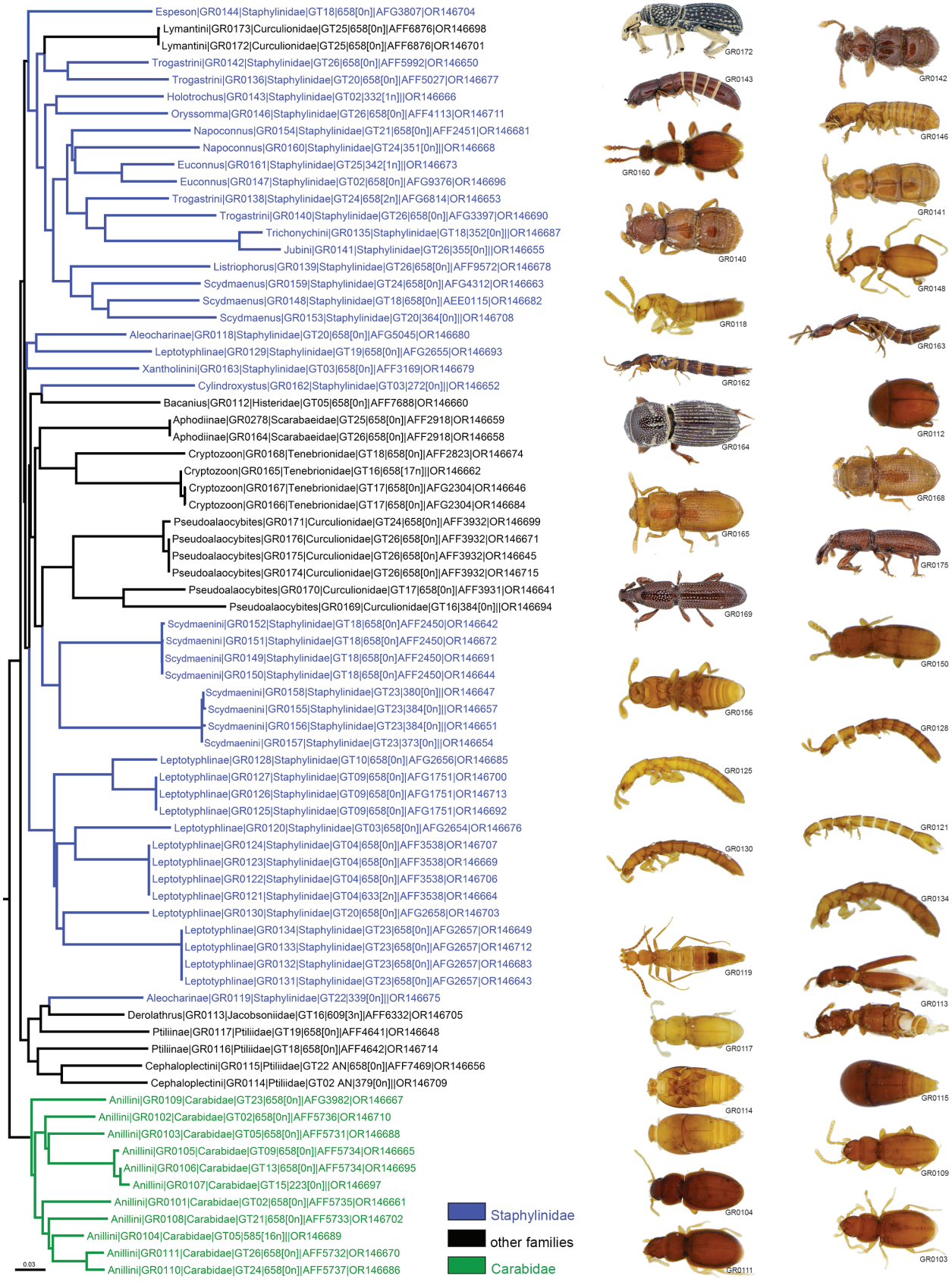

Figure 3. Neighbour Joining DNA barcode tree of 75 endogean beetles from Guatemala. Terminal names consist of the most detailed current taxonomic identification (genus, tribe, or subfamily), followed by specimen number, family name, sample number, length of the DNA barcode fragment [with the number of ambiguously read bases in square brackets], BIN number, and GenBank accession number.

rove beetles and lymantine weevils). To bypass this taxonomic peril and provide unambiguous references to the biological identity of our specimens, we used the DNA barcoding approach, i.e, sequencing the standardized part of the cytochrome oxidase mitochondrial gene (Hebert et al. 2003). From among 444 deep soil Guatemala beetles detected in our samples, we selected 78 specimens, which best represent the morphological and geographical diversity discovered. From these, 75 specimens were successfully sequenced for the DNA barcode fragment longer than 200 bp, and 59 of them had the DNA barcode sequence longer than 600 bp. The three specimens not responding to DNA barcode were a pselaphine and an osoriine rove beetles (specimens GR0137 and GR0145, respectively) and a molytine weevil (GR0177). We grouped DNA barcodes into Barcode Index Numbers (BINs, Ratnasingham & Hebert 2013) and treated them as candidate species in lieu of presently inaccessible Linnaean names. Specimen images and geographical data for these 78 specimens are publicly accessible on the Barcode of Life Data system (BOLD) web portal (at dx.doi.org/10.5883/DS-VGDS26; Ratnasingham & Hebert 2007). GenBank accession numbers and BINs of 75 successfully sequenced specimens are shown in Fig. 3. The herein implemented DNA analysis used 75 DNA barcodes and the standard Neighbour Joining (= NJ) clustering algorithm implemented in the online BOLD tree-building engine under the link 'Sequence Analysis: taxon ID tree' using the default parameters (e.g., the Kimura 2 model of nucleotide substitutions) and selecting 'BOLD Aligner' for the 'Align Sequences' parameter.

3. Results

In total, we collected 444 adult and five larval specimens of endogean beetles in 26 Guatemala soil samples (Tab. 1). These beetles belong to eight families: Carabidae, Histeridae, Jacobsoniidae, Ptiliidae, Staphylinidae (subfamilies Aleocharinae, Leptotyphlinae, Osoriinae, Paederinae, Pselaphinae, Scydmaeninae, Staphylinidae), Scarabaeidae, Tenebrionidae, and Curculionidae. The number of specimens per sample varied between zero (samples GT01, GT07, GT08, GT14) and 82 (sample GT26), with an average of 17 (Tab. 1). The NJ tree of the DNA barcodes obtained from the 75 specimens is shown in Fig. 3.

Carabidae were represented by the tribe Anillini. In total, 220 adults were found in 16 samples (Tab. 1), which is half of all deep soil beetles sampled by us in Guatemala (444). The taxonomy and diversity of this tribe in Central America are inadequately documented (Cicchino & Roig-Juñent 2001). The genus *Geocharidius* Jeannel, 1963, is the only one recorded from Guatemala (Sokolov & Kavanaugh 2014), where it is common and widespread, although species of the recently described Mexican genus *Zapotecanillus* Sokolov, 2013, are known from localities a mere 100–150 km from our westernmost samples (Sokolov 2013).

Histeridae were represented by a single specimen of the nearly cosmopolitan genus *Bacanius* LeConte, 1853 (Tab. 1). The eyeless species of this genus are not necessarily endogean and are also found under bark (Cornell 1972). The majority of small-bodied and eyeless Histeridae are either troglodytic and/or associated with rotten wood, rather than free-living in the deep soil (Kovarik & Caterino 2016), although the North American *Geocolus caecus* Wenzel, 1944, might be a true endogean (Caterino & Harden 2022).

Jacobsoniidae were represented by a single specimen of the genus *Derolathrus* Sharp, 1908 (Tab. 1). This minute (about 1 mm) beetle was damaged because of rapid fungal growth occurring in the hot water of the thermoeclector (despite being in the water for a maximum of 24 hours). This is the first record of the genus (and the family) in both North and South America outside of Florida (Peck 2010, Théry 2023). Remarkably, the sample containing the specimen was taken in an extremely hot and dry habitat, formed by a seasonal, dry riverbed (Fig. 2B).

Ptiliidae were represented by 31 specimens found in four samples (Tab. 1). Those in samples GT03, GR13, and GT22 belong to the obligate myrmecophilous ptiliine tribe Cephaloplectini (Polilov et al. 2019), formerly known as the family 'Limulodidae' (e.g., Seevers & Dybas 1943). The only record of cephaloplecine ptiliids from Guatemala is that of *Cephaloplectus trilobitoides* Mann, 1926 (Seevers & Dybas 1943). We do not know whether our specimens were collected from the belowground nests of their ant hosts (and thus not meeting the definition of 'endogean'; which is not applicable to social parasites) or not; the ants were not particularly abundant in the same samples. The remaining ptiliids from samples GT18 and GT19, likely belong to the ptiliine tribe Ptiliini.

Staphylinidae: Aleocharinae were represented by 11 specimens found in samples GT20 and GT22 (Tab. 1) and resembling those of the tribes Homalotini and Falagriini (Hoebeke 1985), respectively. Leptotyphlinae were represented by 32 unidentified specimens from eight samples (Tab. 1); the single reported country record is that of *Cubanotyphlus guatemalae* Gusarov, 2003 (Gusarov 2003), while *Mayatyphlus carltoni* Gusarov, 2003, was described from nearby Belize (Asenjo et al. 2019). Osoriinae were represented by 56 specimens from three samples (Tab. 1), likely belonging to the

following genera: *Holotrochus* Erichson, 1839 (GT02), *Espeson* Schaufuss, 1882 (GT18), *Geotrochopsis* Irmler, 2016 (GT26), and *Oryssomma* Notman, 1925 (GT26). Paederinae were represented by a single specimen of the genus *Cylindroxystus* Bierig, 1943 (Żyła et al. 2021). Pselaphinae were represented by 26 specimens from four samples and included species of the tribes Goniacerini, Jubini, Trichonychini, and Trogastrini. Scydmaeninae were represented by 29 specimens from seven samples and included species from the following genera: *Euconnus* Thomson, 1859, *Napoconnus* Franz, 1957, and *Scydmaenus* Latreille, 1802. Extremely small (approximately 0.8 mm in body length) and eyeless specimens from samples GT19 and GT23 are not assigned to a genus, however resemble those of the Southeast Asian genus *Liliputella* Jałoszyński, 2016, as well as *Blefuscudia* Jałoszyński, 2017 from Papua New Guinea (Jałoszyński 2016, 2017). Staphylininae were represented by four specimens from a single sample all belonging to an unidentified species of the tribe Xantholinini, resembling those of the genus *Somoleptus* Sharp, 1885 (Irmler 2022).

Scarabaeidae were represented by 13 conspecific specimens found in two samples (Tab. 1), likely belonging to an unnamed species (and perhaps a genus) of the aphodiine tribe Odontolochini (Skelley 2007).

Tenebrionidae were represented by four eyeless specimens found in three samples (Tab. 1). All of them likely belong to the genus *Cryptozoon* Schaufuss, 1882 (Diaperinae: Gnathidiini: Anopidiina) or two other genera with 11 antennomeres and a tarsal formula 5–5–4: *Menimopsis* Champion, 1896, and *Caecophloeus* Dajoz, 1972 (Spiessberger & Ivie 2020). The taxonomic validity of the latter two genera with respect to the *Cryptozoon* is, however, uncertain (Erich Spiessberger, personal communication).

Curculionidae were represented by 15 specimens from five samples (Tab. 1) belonging to two genera of the tribe Lymantini, however, likely non-monophyletic (Grebennikov & Anderson 2022). Two eyed conspecific specimens from sample GT25 resemble those of the genus *Devernodes* Grebennikov, 2018, which consists of five species restricted to Southern China, Vietnam, and Malaysia (Grebennikov 2018). All remaining specimens are likely congeneric, or perhaps conspecific, with an eyeless specimen tentatively assigned to the genus *Pseudoalaocybites* Osella, 1980, by Grebennikov & Anderson (2022) (fig. 33 and voucher code #10842 in Grebennikov & Anderson 2022). Remarkably, our deep soil sampling detected no eyeless Brachycerinae, although forest litter sifting samples taken within meters from samples GT02, GT21, and GT22 contained specimens of an unnamed genus of the tribe Raymondionymini.

4. Discussion

Results of our sampling in Guatemala are consistent with our original hypothesis that application of the specialized deep soil sampling method is likely to uncover a significant number of scientific novelties among previously almost undocumented endogean beetles of the country. The following detections appear particularly noteworthy. Firstly, our record of a member of the family Jacobsoniidae is the third for the continental Americas and the first outside of Florida. Secondly, our record of endogean Scydmaeninae is the first from the Americas and likely attributable to an unnamed genus. Thirdly, our detection of lymantine weevils morphologically similar to the genus *Devernodes* (the only non-American member of the tribe) is novel and biogeographically intriguing. As we continue studying the collected endogean specimens, new discoveries are likely to be made.

5. Acknowledgements

Preliminary identification of the endogean beetles from Guatemala was pivoted on the taxonomic opinions solicited by us from our colleagues based on specimen photographs. The herein reported names are based on our critical evaluation of all available evidence. All correct identifications, therefore, should be attributed to the people listed below, while all possible misidentifications are ours: Histeridae: Alexey K. Tishechkin (Sacramento, CA, USA); Jacobsoniidae: Michael A. Ivie (Bozeman, MT, USA); Ptiliidae & Staphylinidae (except the subfamilies listed below): Alfred F. Newton (Chicago, IL, USA); Staphylinidae: Aleocharinae: Igor Orlov (Tyumen, Russia); Staphylinidae: Paederinae: Adam Brunke (Ottawa, Canada); Staphylinidae: Pselaphinae: Peter Hlaváč (Prague, Czech Republic); Staphylinidae: Scydmaeninae: Paweł Jałoszyński (Wroclaw, Poland); Scarabaeidae: Showtaro Kakizoe (Tokyo, Japan) and Paul E. Skelley (Gainesville, FL, USA); Tenebrionidae: Erich L. Spiessberger (Tübingen, Germany).

6. Supplementary online material

Figures 1–4. 26 soil samples in Guatemala.

7. References

Andújar, C. & V. V. Grebennikov (2021): Endogean beetles (Coleoptera) of Madagascar: deep soil sampling and illustrated overview. – Zootaxa **4963**: 317–334 [https://doi.org/10.11646/zootaxa.4963.2.4].

Asenjo, A., U. Irmler, J. Klimaszewski, D. S. Chandler, H. E. Fierros-López & J. S. Vieira (2019): Staphylinidae (Insecta: Coleoptera) in Latin America: synopsis, annotated catalog, diversity and distribution. – Zootaxa 4621: 1–406 [https://doi.org/10.11646/zootaxa.4621.1.1].

Bekchiev, R. & B. Guéorguiev (2014): First purposive study of beetles (Coleoptera) from endogean environments in Bulgaria: collection sites and preliminary results. – Biodiversity Journal **5**: 327–340.

Caterino, M. S. & C. W. Harden (2022): Unseeing and unseen: on the distribution, morphology, and larva of one of North America's rarest histerid beetles, *Geocolus caecus* Wenzel (Coleoptera: Histeridae). – The Coleopterists Bulletin **76**: 191–205 [https://doi.org/10.1649/0010-065X-76.2.191].

Cicchino, A. C. & S. Roig-Juñent (2001): Description and relationships of *Paranillopsis* new genus, two new species from Argentina, and a key to the Neotropical genera of the subtribe Anillina (Coleoptera: Carabidae: Bembidiini). – The Coleopterists Bulletin **55**: 185–193 [https://doi.org/10.1649/0010-065X(2001)055[0185:DAROPN]2.0.CO;2].

Cornell, J. F. (1972): The eyeless beetles of North Carolina with notes on their ecology and evolution (Insecta: Coleoptera). – Journal of the Elisha Mitchell Scientific Society **88**: 260–264.

Fancello, L., Hernando, C. & P. Leo (2009): The endogean beetle fauna of the Marganai-Oridda-Valle del Leni area (SW Sardinia), with description of seven new species of Staphylinidae Leptotyphlinae (Coleoptera). – Zootaxa **2318**: 317–338.

Grebennikov, V. V. (2018): Discovery of Lymantini weevils (Coleoptera: Curculionidae: Molytinae) outside the Americas: *Devernodes*, a new genus for five new species from Southeast Asia. – Zootaxa **4500**: 363–380 [https://doi.org/10.11646/zootaxa.4500.3.4].

Grebennikov, V. V. & R. S. Anderson (2022): Phylogeny, diversity and biogeography of flightless amphi-Pacific lymantine weevils (Coleoptera: Curculionidae: Molytinae). – Acta Entomologica Musei Nationalis Pragae **62**: 411–442 [https://doi.org/10.37520/aemnp.2022.023].

Gusarov, V. I. (2003): *Cubanotyphlus guatemalae*, a new species of leptotyphline staphylinid from Guatemala (Insecta: Coleoptera: Staphylinidae). – Studies on Neotropical Fauna and Environment **38**: 125–128.

Hebert, P. D. N., S. Ratnasingham & J. R. DeWaard (2003): Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. – Proceedings of the Royal Society B: Biological Sciences **270**: 96–99 [http://dx.doi.org/10.1098/rsbl.2003.0025].

Hoebeke, E. R. (1985): A revision of the rove beetle tribe Falagriini of America north of Mexico (Coleoptera: Staphylinidae: Aleocharinae). – Journal of the New York Entomological Society **93**: 913–1018 [https://www.jstor.org/stable/25009456].

Irmler, U. (2022): The Neotropical species of the genus *Somoleptus* Sharp, 1885 (Coleoptera: Staphylinidae: Staphylininae: Xantholinini). – Contributions to Entomology **72**: 123–178 [https://doi.org/10.3897/contrib.entomol.72.e87211].

Jałoszyński, P. (2016): *Liliputella*, a new genus of microscopic, wingless and blind Scydmaenini of the Bismarck Islands (Coleoptera, Staphylinidae, Scydmaeninae). – Zootaxa **4093**: 135–142 [https://doi.org/10.11646/zootaxa.4093.1.9].

Jałoszyński, P. (2017): Subterranean Scydmaeninae of Southeast Asia (Coleoptera: Staphylinidae). – Annales Zoologici **67**: 713–723 [https://doi.org/10.3161/00034541ANZ2017.67.4.008].

Jamieson, A. J. & J. N. J. Weston (2023): Amphipoda from depths exceeding 6,000 meters revisited 60 years on. – Journal of Crustacean Biology 43: 1–28 [https://doi.org/10.1093/jcbiol/ruad020].

Kovarik, P. W. & M. S. Caterino (2016): Histeridae Gyllenhall, 1808. – In: Beutel, R. G. & R. A. B. Leschen (eds): Handbook of Zoology: Coleoptera, Beetles. – Volume 1. 2-nd edition. – De Gruyter, Berlin: 281–315.

Peck, S. B. (2010): *Derolathrus cavernicolus* n. sp., a beetle family new for North America (Coleoptera: Jacobsoniidae). – Annals of the Entomological Society of America **103**: 1–6 [https://doi.org/10.1603/008.103.0101].

Polilov, A. A., I. Ribera, M. I. Yavorskaya, A. Cardoso, V. V. Grebennikov & R. G. Beutel (2019): The phylogeny of Ptiliidae (Coleoptera: Staphylinoidea) – the smallest beetles and their evolutionary transformations. – Arthropod Systematics and Phylogeny **77**: 433–455 [https://doi.org/10.26049/ASP77-3-2019-4].

Ratnasingham, S. & P. D. N. Hebert (2007): BOLD: the barcode of life data system. – Molecular Ecology Notes **7**: 355–364 [https://doi.org/10.1111/j.1471-8286.2007.01678.x].

Ratnasingham, S. & P. D. N. Hebert (2013): A DNA-based registry for all animal species: The Barcode Index Number (BIN) system. – PLoS ONE **8**(8): e66213 [https://doi.org/10.1371/journal.pone.0066213].

Seevers, C. H. & H. S. Dybas (1943): A synopsis of the Limulodidae (Coleoptera): a new family proposed for myrmecophiles of the subfamilies Limulodinae (Ptiliidae) and Cephaloplectinae (Staphylinidae). – Annals of the Entomological Society of America **36**: 546–586 [https://doi.org/10.1093/aesa/36.3.546].

Skelley, P. E. (2007): New South American taxa of Odontolochini Stebnicka and Howden (Coleoptera: Scarabaeidae: Aphodiinae). – Insecta Mundi **22**: 15 pp.

Sokolov, I. M. (2013): A new genus and eight new species of

the subtribe Anillina (Carabidae, Trechinae, Bembidiini) from Mexico, with a cladistic analysis and some notes on the evolution of the genus. – ZooKeys **352**: 51–92 [https://doi.org/10.3897/zookeys.352.6052].

Sokolov, I. M. & D. H. Kavanaugh (2014): The integripennis species group of *Geocharidius* Jeannel, 1963 (Carabidae, Bembidiini, Anillina) from nuclear Central America: a taxonomic review with notes about biogeography and speciation. – ZooKeys **443**: 61–118 [https://doi.org/10.3897/zookeys.443.7880].

Spiessberger, E. L. & M. A. Ivie (2020) A new genus and fourteen new species of Anopidiina (Coleoptera: Tenebrionidae: Diaperinae: Gnathidiini) from the West Indies. – The Coleopterists Bulletin **74**: 667–695 [https://doi.org/10.1649/0010-065X-74.4.667].

Théry, T. (2023): Description of *Derolathrus foveiceps* n. sp. from Florida (Coleoptera: Jacobsoniidae). – Faunitaxys **11** (36): 1–4.

Żyła, D., A. Bogri, T. A. Heath, & A. Solodovnikov (2021): Total-evidence analysis resolves the phylogenetic position of an enigmatic group of Paederinae rove beetles (Coleoptera: Staphylinidae). – Molecular Phylogenetics and Evolution **157**: 1–30 [https://doi.org/10.1016/j.ympev.2020.107059].