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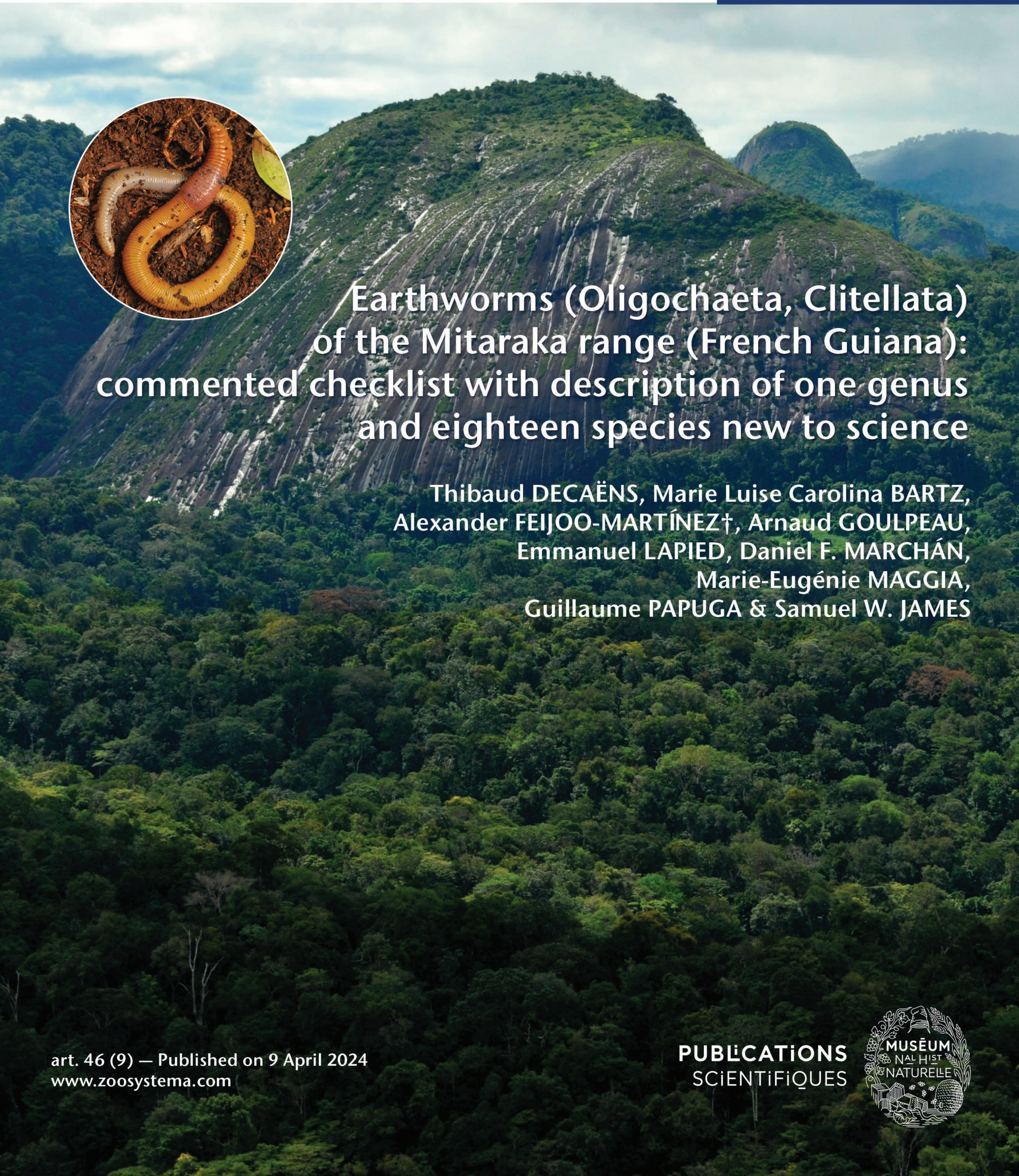

Earthworms (Oligochaeta, Clitellata) of the Mitaraka range (French Guiana): commented checklist with description of one genus and eighteen species new to science

Thibaud DECAËNS, Marie Luise Carolina BARTZ, Alexander FEIJOO-MARTÍNEZ†, Arnaud GOULPEAU, Emmanuel LAPIED, Daniel F. MARCHÁN, Marie-Eugénie MAGGIA, Guillaume PAPUGA & Samuel W. JAMES

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The Mitaraka Massif, French Guiana. In medallion: holotype of *Martiodrilus* (*Botaria*) *flavus* Decaëns & Bartz, n. sp.

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ABSTRACT

Intensive sampling of earthworms in French Guiana has been carried out for several years. The first published results have highlighted a very high regional diversity, a considerable geographical turnover in the composition of communities, as well as a very high proportion of species new to science. However, the work of describing these new species had not been undertaken until now. In this work, we present the results of the sampling carried out in March 2015 during the "Our Planet Reviewed" terrestrial expedition in the Mitaraka Range. We used an integrative taxonomy approach combining the use of DNA barcodes and morpho-anatomical characters, which allowed the identification of 31 species, nine of which were represented in our samples only by juveniles, and four of which corresponded to already known species (*Nouraguesia parare* Csuzdi & Pavlícek, 2011, *Pontoscolex corethrurus* (Müller, 1856), *Dichogaster andina* Cognetti de Martiis, 1904 and *Dichogaster bolaui* (Michaelsen,1891)). The remaining 18 species were new to science and are described in this work. They belong to the genera *Andiorrhinus* Cognetti de Martiis, 1908 (one species), *Martiodrilus* Michaelsen, 1936 (nine species), *Urobenus* Benham, 1886 (one species), *Atatina* Righi, 1971 (one species), *Neogaster* Cernosvitov, 1934 (two species), *Omodeoscolex* Csuzdi, 1993 (three species), and a new genus of *Ocnerodrilidae* Beddard, 1891 which we describe as *Guianodrilus* Bartz & Decaëns, n. gen. We then discuss the Linnaean deficit that characterizes the earthworm fauna of French Guiana and the taxonomic implications of our results.

KEY WORDS
Earthworms,
Martiodrilus,
Andiorrhinus,
Urobenus,
Atatina,
Neogaster,
Omodeoscolex,
French Guiana,
new genus,
new species.

RÉSUMÉ

Les vers de terre (Oligochaeta, Clitellata) du massif du Mitaraka (Guyane) : liste commentée avec description d'un genre nouveau et de dix-huit espèces nouvelles pour la science.

Un échantillonnage intensif des vers de terre de Guyane est en cours depuis plusieurs années. Les premiers résultats publiés ont mis en évidence une diversité régionale très importante, un turnover géographique considérable dans la composition des communautés, ainsi qu'une proportion très importante d'espèces nouvelles pour la science. Cependant le travail de description de ces espèces nouvelles n'avait pas été entrepris jusqu'à maintenant. Dans ce travail, nous présentons les résultats de l'échantillonnage réalisé en mars 2015 à l'occasion de la mission terrestre de la « Planète Revisitée » dans le massif du Mitaraka. Nous avons pour cela utilisé une approche de taxonomie intégrative combinant l'utilisation de codes-barres ADN et de caractères morpho-anatomiques. Nous avons ainsi identifié la présence de 31 espèces, dont neuf ne sont représentées dans nos échantillons que par des juvéniles, et quatre correspondent à des espèces d'ores et déjà connues (*Nouraguesia parare* Csuzdi & Pavlícek, 2011, *Pontoscolex corethrurus* (Müller, 1856), *Dichogaster andina* Cognetti de Martiis, 1904 et *Dichogaster bolaui* (Michaelsen, 1891)). Les 18 espèces restantes se sont révélées nouvelles pour la science et sont décrites dans ce travail. Elles appartiennent aux genres *Andiorrhinus* Cognetti de Martiis, 1908 (une espèce), *Martiodrilus* Michaelsen, 1936 (neuf espèces), *Urobenus* Benham, 1886 (une espèce), *Atatina* Righi, 1971 (une espèce), *Neogaster* Cernosvitov, 1934 (deux espèces), *Omodeoscolex* Csuzdi, 1993 (trois espèces), et un nouveau genre d'Ocnerodrilidae Beddard, 1891 que nous décrivons sous le nom de *Guianodrilus* Bartz & Decaëns n. gen. Nous discutons ensuite le déficit linnéen qui caractérise les vers de terre de Guyane ainsi que les implications taxonomiques de nos résultats.

MOTS CLÉS
Vers de terre,
Martiodrilus,
Andiorrhinus,
Urobenus,
Atatina,
Neogaster,
Omodeoscolex,
Guyane,
espèces nouvelles,
genre nouveau.

INTRODUCTION

Earthworms are recognised for the ecological functions they perform in terrestrial ecosystems and the support they provide for the production of important ecosystem services. They are defined as ecosystem engineers, capable of physically modifying their edaphic environment by altering its physico-chemical properties, thereby modifying soil fertility, plant production and the living conditions of the species with which they coexist (Lavelle *et al.* 2016). Despite this undeniable importance for the functioning of soils and terrestrial ecosystems, earthworms are relatively poorly known from a taxonomic point of view, particularly in little-studied and difficult-to-access tropical regions (Decaëns *et al.* 2013). French Guiana is emblematic of this paradox. Indeed, in the early 2000s, slightly less than fourty named species were cited there, some of which described recently (Csuzdi & Pavlicek 2011), which was far below the diversity expected for a tropical region of this size (Brown & Fragoso 2007; Pavlicek & Csuzdi 2012; Brown *et al.* 2013).

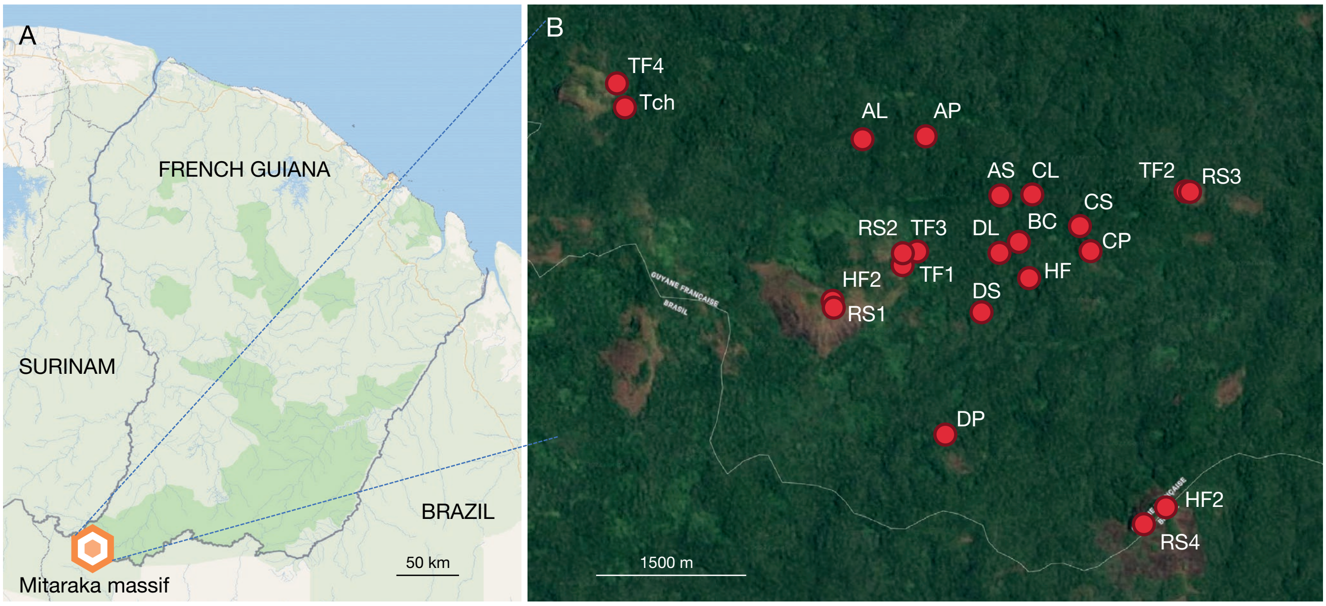

FIG. 1. — **A**, **B**, Localisation of the sampling sites in the Mitaraka Massif, French Guiana. Site codes are the same as in Table 1. Dark green areas in **A**, represent conservation areas.

Since 2010, several sampling campaigns focussing on biodiversity assessment and including earthworms have been carried out in different parts of French Guiana. Decaëns *et al.* (2016) published a first contribution to the knowledge of earthworm diversity in the Nouragues Nature Reserve. Using an integrative taxonomy approach based on the combined use of morphological characters and DNA barcodes, they found a total of 48 species in this locality, and suggested that up to 60 species might be present. Although they suggested on the basis of their observations that most of the species sampled might be new to science, the authors of this work did not go as far as to formally describe these taxa. Recently, Maggia *et al.* (2021) extended this approach to six localities and re-estimated the regional diversity to nearly 120 operational taxonomic units (OTUs) delimited from DNA barcodes. Goulpeau *et al.* (2022) then used a larger dataset allowing them to delineate nearly 300 OTUs. Considering the high turnover of species between localities and habitats, Maggia *et al.* (2021) suggest that the number of species present in the whole territory of French Guiana could reach several hundred. However, this estimate is based on OTUs used as species proxies without further taxonomic assignments. Generally speaking, these first articles highlight the remarkable species diversity of earthworms in French Guiana, and the need to develop an effective taxonomic approach to describe the multitude of taxa that have already been sampled or that will be discovered in future field campaigns.

In this work, we publish a list of species collected during the "Our Planet Reviewed" expedition in the Mitaraka range (Touroult *et al.* 2018), southern French Guiana. We used the DNA barcodes of Maggia *et al.* (2021) and performed morphological diagnoses for each of the OTUs delineated by these authors. Based on the morpho-anatomical diagnoses and molecular data, we describe *Guianodrilus* Bartz & Decaëns, n. gen. in the family Ocnerodrilidae Beddard, 1891, and 18 species new to science in the genera *Martiodrilus* Michaelsen, 1936 (nine species), *Andiorrhinus* Cognetti de Martiis, 1908 (one species), *Urobenus* (one species), *Atatina* Righi, 1971 (one species), *Guianodrilus* Bartz & Decaëns, n. gen. (one species), *Neogaster* Cernosvitov, 1934 (two species) and *Omodeoscolex* Csuzdi, 1993 (three species). We further discuss the Linnaean deficit that characterises the earthworm fauna of French Guiana, and taxonomic implications of our results.

MATERIAL AND METHODS

STUDY SITE AND EARTHWORM SAMPLING

Earthworms were sampled in March 2015 in the Mitaraka Massif, a largely unknown and currently uninhabited area in the extreme south-western corner of French Guiana (Touroult *et al.* 2018). The region belongs to the Tumuc-Humac mountain chain, extending east in the Amapá region of Brazil and west in southern Surinam (Fig. 1A). Local landscape essentially consists in an alternance of tropical rainforest ecosystem on slope and plateau positions, periodically flooded forests in lowlands, and scattered inselbergs, i.e., isolated granitic rocky outcrops that stand above the forest cover (Fig. 2A, B). Vegetation on the inselbergs includes rocky savannahs (i.e., open formations dominated by terrestrial bromeliads; Fig. 2D, G), and transition to hilltop forests (Fig. 2C). The entire area is situated in the core of the protected Parc Amazonien de Guyane.

The base camp was located near the Alama river, at coordinates 2°14'2"N, 54°27'1"W, and at an altitude of 330 m a.s.l. Around this central point, the main characteristic eco-

Table 1. — List of the study plots where earthworms were sampled in the Mitaraka Massif.

Codes	Site description	Coordinates	Altitude	Habitat	Microhabitats
BC	Mitaraka base camp	2°14'2"N, 54°27'1"W	331	Plateau forest	soil, decaying trunks, epiphytes
AL	A trail / Lowland	2°14'36"N, 54°27'52"W	327	Lowland forest	soil, decaying trunks, litter
AS	A trail / Slope	2°14'17"N, 54°27'7"W	344	Slope forest	soil, decaying trunks
AP	A trail / Plateau	2°14'37"N, 54°27'31"W	371	Plateau forest	soil, decaying trunks, epiphytes
HF	*Heliconia* forest	2°13'50"N, 54°26'57"W	351	Plateau forest	soil, decaying trunks
CL	C trail / Lowland	2°14'17"N, 54°26'56"W	310	Lowland forest	soil, decaying trunks
CS	C trail / Slope	2°14'7"N, 54°26'41"W	377	Slope forest	soil, decaying trunks
CP	C trail / Plateau	2°13'59"N, 54°26'37"W	449	Plateau forest	soil, decaying trunks
DL	D trail / Lowland	2°13'58"N, 54°27'7"W	318	Lowland forest	soil, decaying trunks
DS	D trail / Slope	2°13'39"N, 54°27'13"W	339	Slope forest	soil, decaying trunks
DP	D trail / Plateau	2°12'58"N, 54°27'25"W	381	Plateau forest	soil, decaying trunks
HF1	Hilltop forest #1 ("Sommet en Cloche")	2°13'42"N, 54°28'2"W	638	Hilltop forest	soil, decaying trunks
HF2	Hilltop forest #2 ("Borne 1")	2°12'35"N, 54°26'12"W	600	Hilltop forest	soil, decaying trunks
TF1	Transition forest #1 ("Sommet en Cloche")	2°13'54"N, 54°27'39"W	401	Transition forest	soil, decaying trunks, litter
TF2	Transition forest #2 ("Layon C")	2°14'19"N, 54°26'6"W	389	Transition forest	decaying trunks
TF3	Transition forest #3 ("Sommet en Cloche")	2°13'59"N, 54°27'34"W	395	Transition forest	soil
TF4	Transition forest #4 ("Tchoukouchipan")	2°14'54"N, 54°29'12"W	405	Transition forest	soil
TCH	Transition forest #5 ("Tchoukouchipan")	2°14'46"N, 54°29'10"W	329	Transition forest	cave
RS1	Rocky savannah #1 ("Sommet en Cloche")	2°13'40"N, 54°28'1"W	623	Rocky savannah	soil, roots
RS2	Rocky savannah #2 ("Sommet en Cloche")	2°13'58"N, 54°27'39"W	427	Rocky savannah	roots
RS3	Rocky savannah #3 ("Layon C")	2°14'18"N, 54°26'5"W	401	Rocky savannah	roots
RS4	Rocky savannah #4 ("Borne 1")	2°12'29"N, 54°26'20"W	585	Rocky savannah	roots

systems of the region were sampled according to a replicated sampling design and using a standardised protocol (Fig. 1B). The list of surveyed sites, the corresponding ecosystems and their geographical location is given in Table 1.

The detailed sampling protocol is given in Maggia *et al.* (2021). Briefly, each site consisted in a 1 ha area plot, where earthworms were collected by combining 1) digging and hand-sorting three blocks of soil, each 25 × 25 × 20 cm (length × width × depth); 2) digging and handsorting an additional area of 1 m^2 to a minimum depth of 30-40 cm in an area with large earthworm casts; and 3) micro-habitat sampling by visually inspecting all available micro-habitats (such as sandy to muddy sediments of stream banks, leaf litter accumulations, decaying trunks and epiphytic soils) for a standardised period of time. In addition, a number of specimens were collected opportunistically by teams working on other taxonomic groups during the expedition. Earthworms of all life stages (adults, juveniles and cocoons) were collected and kept in 100% ethanol. Ethanol was changed after 24 h to ensure optimal fixation.

DNA barcoding, OTU delimitations and phylogenetic analyses

The collected specimens were first sorted according to their external morphology, and up to five specimens per sampling unit and per morpho-group were selected for DNA analysis. A small tissue fragment was taken from each of them for DNA analysis at the Canadian Centre for DNA Barcoding. Lab work followed standardized protocols of the International Barcode of Life (see Maggia *et al.* [2021]) for details). Sequences, supporting information and GenBank accession codes are available in the Barcode of Life Datasystems (BOLD) database (Ratnasingham & Hebert 2007) in the dataset "Earthworms from the Mitaraka Massif, French Guiana" (DS-EWMITK, https://doi.org/10.5883/DS-EWMITK).

Sequences were further used to delimit operational taxonomic units (OTUs) using the Automatic Barcode Gap Discovery method (ABGD, Puillandre *et al.* 2012) as described in Maggia *et al.* (2021). We further aligned sequences with MAFFT v.7 (Katoh & Standley 2013) with default settings, and collapsed them into unique haplotypes in FaBox 1.61 (Villesen 2007). The best fitting evolutionary model (GTR + I + G) was selected with jModelTest v. 2.1.3 (Darriba *et al.* 2012) by applying the Akaike information criterion (AIC; Akaike 1973), and Bayesian information criterion (BIC; Schwarz 1978). Bayesian Inference of the phylogeny was estimated with MRBAYES v.3.1.2 (Ronquist & Huelsenbeck 2003) as implemented in the CIPRES Science Gateway V. 3.3. Parameters were set to 50 million generations and sampled every 5000th generation (10 000 trees). Two independent runs each with four chains were performed and 20% of the trees were discarded as burn-in. The remaining trees were combined and summarized on a 50% majority-rule consensus tree. Separate phylogenetic trees were inferred for Rhinodrilidae Benham, 1890 plus Glossoscolecidae Michaelsen, 1900, Benhamiidae Michaelsen, 1897 and Ocnerodrilidae, using *Hirudo medicinalis* Linnaeus, 1770 (Genbank accession HQ333519) as outgroup in each case. Uncorrected average pairwise genetic distances within and between species were calculated in MEGA 11 (Tamura *et al.* 2021).

Fig. 2. — (next page) The Mitaraka Massif: **A**, general view of the inselberg landscape from "Borne 1", with "Sommet en Cloche" in the foreground, followed by "Tchoukouchipan" and "Mitaraka"; **B**, *Astrocaryum* forest plateau near Base Camp; **C**, transitional forest (TF1) on the slopes of the "Sommet en Cloche"; **D**, Rocky savannah (RS3) showing terrestrial bromeliad (*Pepinia* sp.) and transitional forest (TF2) in the background; **E**, a specimen of *Martiodrilus* (*Botaria*) *tchoukouchipan* Decaëns & Bartz n. sp. in the root mat of terrestrial bromeliads in a rocky savannah (RS2); **F**, the holotype of *Martiodrilus* (*Botaria*) *flavus* Decaëns & Bartz n. sp. in a transitional forest (TF2); **G**, detail of the terrestrial bromeliad beds in the rocky savannah RS3 (all photos by T. Decaëns).


A
B
C
D
E
F
G

Morpho-anatomical descriptions and integrative taxonomy approach

When available, at least three adult specimens (i.e., specimens presenting a differentiated clitellum) per OTUs were selected for complete morpho-anatomical examinations, and additional specimens were considered for external morphology only and described following a similar approach to that described in Decaëns *et al.* (2016). For external morphology, we measured body size and weight and counted the number of segments, recorded external data on setal relations (distance between setal lines in postclitellar segments), shape of prostomium, pigmentation, location and shape of clitellum, visible genital pores, modified setae, and genital markings (including tubercula pubertatis if appropriate). For internal characters, we recorded locations and form of calciferous glands, number and position of muscular hearts, shape and size of the gizzard, muscularity of anterior septa, spermathecal characters, condition of male reproductive organs, location of the intestinal starting point, form and position of typhlosole (a dorsal inward extension of the intestinal wall), presence and number of caecal pouches when relevant. For the family Benhamiidae, we recorded the numbers and form of nephridia, and the characteristics of the acanthodriline male fields represented. Explanations of these morphological characters are available in Csuzdi (2010) and Righi (1995). We did not consider other characters that can be used in descriptions within certain genera (e.g. genital setae in *Martiodrilus*), as we considered that they did not provide significant diagnostic information in addition to those already used in combination with molecular information. For each new species, we provide a description based on what we considered relevant diagnostic characters, and an additional diagnosis in the "remarks" paragraph. Although this is more than the minimal work recommended by the International Code of Zoological Nomenclature, we are aware that this may be seen by some readers as a shortcoming. However, considering the number of new species to be described in French Guiana (Maggia *et al.* 2021), we have resolutely adopted a "turbotaxonomy" approach (*sensu* Butcher *et al.* 2012) in which we try to maximise the quality of the original descriptions while trying to reduce the time cost. Colleagues interested in describing more characters for future taxonomic revisions will still be able to study the type material for their own needs.

We then followed the following integrative approach: 1) when two OTUs presented consistent differences in more than one morpho-anatomical character traditionally deemed of specific value, we considered them as two distinct species; 2) when two OTUs were morphologically indistinguishable, we still considered them as distinct species (in this case cryptic species) when they were clearly separated in the phylogenetic tree (i.e., did not form a monophyletic group); and 3) when two OTUs were morphologically indistinguishable, and closely related in the phylogenetic tree (i.e., forming a monophyletic group), we considered them as conspecific cryptic lineages.

Diversity patterns and species number estimates

The species diversity at the scale of the Mitaraka range was analysed by plotting rarefaction and extrapolation curves. We used incidence-based rarefaction curve to highlight species number accumulation as a function of the number of sampled plots within the study area, and abundance-based rarefaction curves to highlight species number accumulation as a function of the number of earthworm individual sampled within each main types of habitats and microhabitats. We also calculated the Chao index, which estimates the lower bound for the expected asymptotic species richness (Gotelli & Chao 2013). All these analyses were done using the 'iNEXT' package for R (Hsieh *et al.* 2019; R Core Team 2019).

Community-scale species richness was estimated as the accumulated number of species observed at the scale of a 1 ha plot. We tested the overall habitat effect using Kruskal-Wallis rank sum test with the 'kruskal.test' function of R, and pair wise differences among habitats using pairwise Wilcoxon rank sum tests with the 'pairwise.wilcox.test' function of R.

Automated species descriptions

For each of the species recognised by the integrative taxonomy approach described above, we compared the morpho-anatomical characters to those reported in the literature for already known species in the genera concerned. To do this, we first reviewed already available keys, and then looked at original species descriptions for the ones that were closest to our own species based on key diagnostic characters. When a species differed from the known species by at least one morpho-anatomical character of specific diagnostic value, we considered it as a species new to science and proceeded to its formal description.

We then compiled two tables: 1) a first one containing the collection data of all the specimens collected for each species and specifying which are holotype, paratypes or "other material"; 2) a second one describing the morpho-anatomical characters of each species. We then created a script for R Markdown (Allaire *et al.* 2021) that automatically generates the list of specimens we designated as holotypes, paratypes and other material and corresponding collection data, as well as a standardised description of the external morphological characters and internal anatomy of each species new to science. This automated approach allowed us to save a considerable amount of time on the description writing phase (i.e., less than one day to generate the whole manuscript once the character tables have been completed). The advantage of using R Markdown is that it is an open source program, and that the codes used to generate the text blocks can thus be adapted "à la carte" to produce specimen lists conforming to the format of the target journal, and to adjust the automated descriptions to the specifics of any given taxa. The data tables and the R scripts, including an annotated example explaining how to use them step by step, are available on GitHub as a Supplementary Material of this article (https://github.com/tdecaens/Turbotaxonomy).

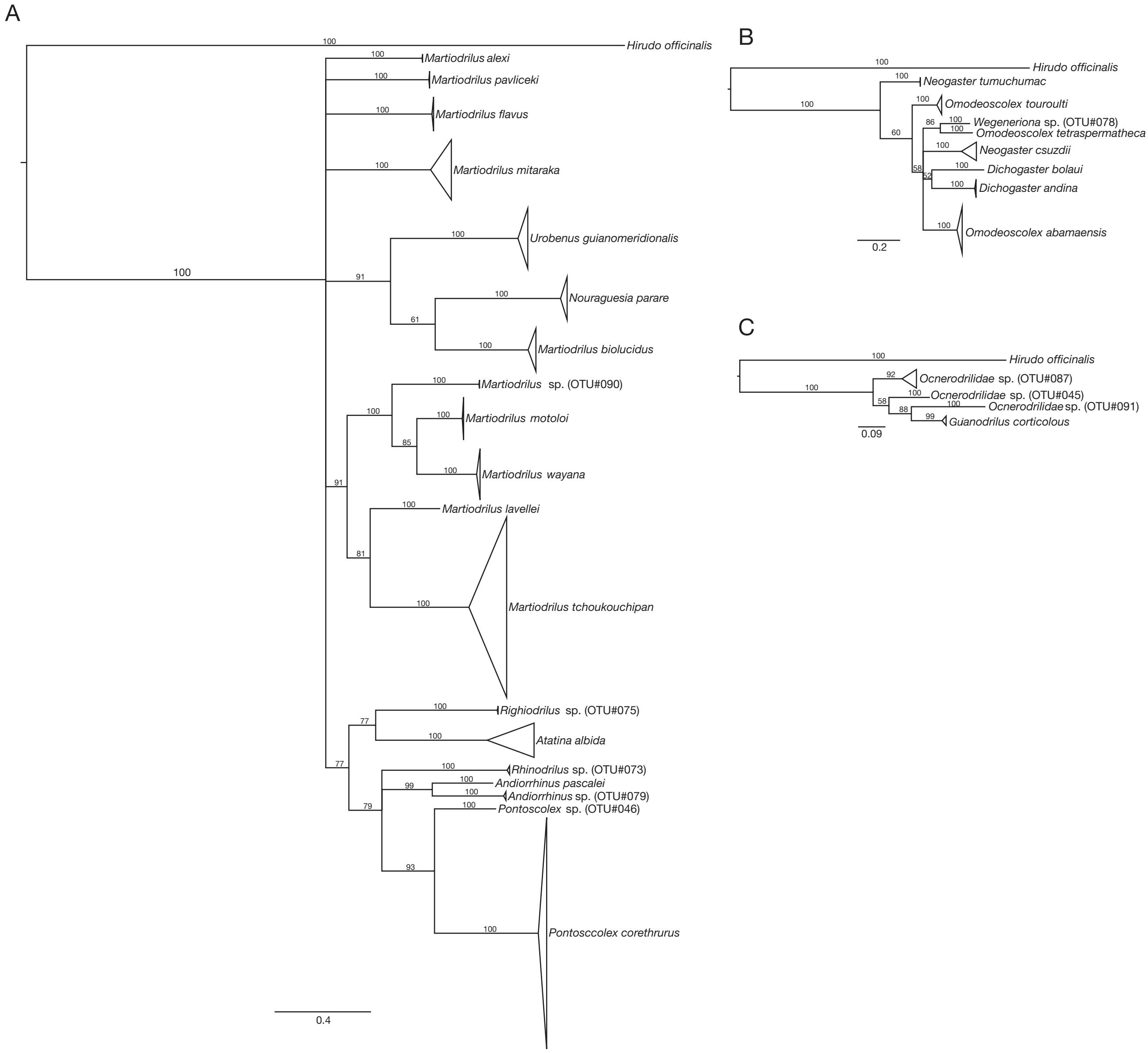

Fig. 3. — Bayesian Inference of the phylogeny of species of **A**, Rhinodrilidae Benham, 1890 and Glossoscolecidae Michaelsen, 1900; **B**, Benhamiidae Michaelsen, 1897; **C**, Ocnerodrilidae Beddard, 1891 based on the sequence of COI. In all of them *Hirudo officinalis* Linnaeus, 1758 was included as outgroup. Clades corresponding to species were collapsed, with depth of the triangles representing intraspecific genetic divergence and height representing intraspecific haplotype diversity.

Collection abbreviations and specimen identifiers

CEFE Centre d'écologie fonctionnelle et évolutive, Montpellier;
MNHN Muséum national d'Histoire naturelle, Paris.

The BOLD Sample ID mentioned in the material lists are also used as collection ID in both CEFE and MNHN collections.

RESULTS

Our study produced 348 COI barcodes, which clustered into 31 OTUs belonging to the families Rhinodrilidae, Glossoscolecidae, Benhamiidae and Ocnerodrilidae (Fig. 3). All these OTUs are supported by bootstarp values above 99%, except for one Ocnerodilidae with had a bootstrap of 92% (Fig. 3). All of them also presented average pairwise genetic distances well above the 14% threshold usually recognised of species-level significance for earthworms (Decaëns *et al.* 2013), even within single genus or closely related genus (Tables 2; 3).

Of these OTUs, nine were represented only by juveniles or fragments that could only be identified to genus or family levels (i.e., one *Andiorrhinus* sp., one *Martiodrilus* sp., one *Pontoscolex* sp., one *Rhinodrilus* sp., one *Righiodrilus* sp, one *Wegeneriona* sp. and three Ocnerodrilidae sp.), and four corresponded to already described species (*Nouraguesia parare* Csuzdi and Pavlícek, 2011, *Pontoscolex corethrurus* (Müller, 1856), *Dichogaster andina* Cognetti de Martiis, 1904 and *Dichogaster bolaui* (Michaelsen, 1891)). The remaining

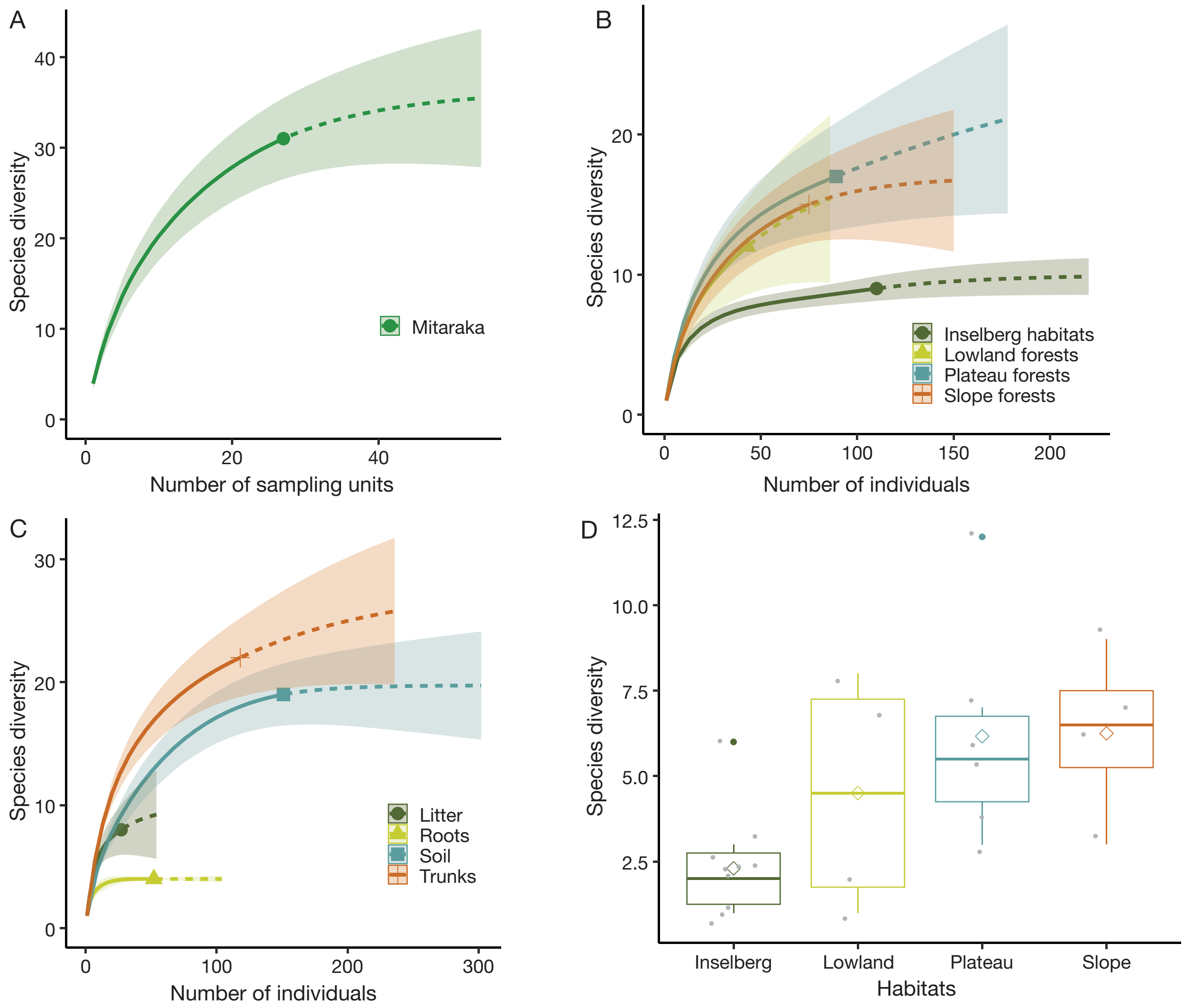

Fig. 4. — Earthworm species diversity in the Mitaraka range: **A**, incidence–based rarefaction and extrapolation curve showing species number accumulation as a function of the number of plots sampled within the study area; **B**, abundance–based rarefaction and extrapolation curves showing species number accumulation as a function of the number of earthworm individuals sampled within four main types of habitats (Inselberg habitats include rocky savannahs, transition and hilltop forests); **B**, abundance–based rarefaction and extrapolation curves showing species number accumulation as a function of the number of earthworm individuals sampled within four main types of microhabitats (**Litter**, litter accumulations on granitic rocks; **Roots**, root mat of terrestrial bromeliads; **Soil**, organo-mineral soil and sediments; **Trunks**, decaying trunks and associated termite mounds); **D**, box–plots of community-scale species richness for the four main type of habitats (as in **B**). In **A**-**C**, solid curves: rarefaction curves; dotted curves: extrapolation curves. In **D**, diamond symbol: mean; coloured dots: outliers; grey dots: individual values.

18 OTUs were found to be new to science after morpho-anatomical examination and are described herein. They belong to the genera *Andiorrhinus* (one species), *Martiodrilus* (nine species), *Urobenus* (one species), *Atatina* (one species), *Neogaster* (two species), *Omodeoscolex* (three species), and a new genus of Ocnerodrilidae described as *Guianodrilus* Bartz & Decaëns, n. gen.

The rarefaction curves indicate that the sampling effort deployed in our study was enough to identify a significant proportion of earthworm diversity at the scale of the study site. Indeed, the incidence-based rarefaction curve shows an inflection (Fig. 4A), and the Chao index indicates that at least 36 species could be present in this region of the Mitaraka mountains, which is not far from the 31 species found in our study. Most of species diversity was recovered in the plateau, slope and lowland forests, whereas inselberg habitats (i.e., transition and hilltop forests, rocky savannahs) were comparatively less diversified (Fig. 4B). Regarding microhabitats, most of the species diversity was found in decaying trunks and associated termite mounds, followed by the organo-mineral soil (Fig. 4C).

The average community-level richness (alpha diversity) was 4.3 species observed per ha, with the highest value observed in a plateau forest where 12 species were sampled, and the lowest in a lowland forest and some inselberg habitats where only one species was found (Fig. 4D). Overall, plateau and slope forests had similarly diversified communities (6.2 species observed per ha in average), lowland forests were slightly less diversified (4.5 species observed per ha in average), and inselberg habitats showed the lowest values (2.3 species

Table 2. — Uncorrected average pairwise genetic distances within (diagonal) and between species (under diagonal) of *Martiodrilus* Michaelsen, 1936 included in this work.

Species	Mfla	Mtch	Mlav	Mway	Mmot	OTU.090	Mpav	Mmit	Malexi	Mlumi
M. flavus Decaëns & Bartz n. sp.	0.09	–	–	–	–	–	–	–	–	–
M. tchoukouchipan Decaëns & Bartz n. sp.	21.23	3.86	–	–	–	–	–	–	–	–
M. lavellei Decaëns & Bartz n. sp.	18.72	16.85	0.00	–	–	–	–	–	–	–
M. wayana Bartz & Decaëns, n. sp.	20.41	20.62	17.53	0.52	–	–	–	–	–	–
M. motoloi Bartz & Decaëns, n. sp.	20.17	19.62	17.62	12.97	0.12	–	–	–	–	–
M. OTU#090	20.84	20.12	16.55	16.75	15.70	0.00	–	–	–	–
M. pavliceki Bartz & Decaëns, n. sp.	20.03	21.20	17.83	20.04	19.19	20.32	0.05	–	–	–
M. mitaraka Decaëns & Bartz n. sp.	21.39	20.67	19.91	21.51	20.29	21.71	19.44	3.71	–	–
M. alexi Bartz & Decaëns, n. sp.	19.63	21.23	19.41	19.50	19.73	20.72	20.12	20.09	0.00	–
M. luminescens Decaëns & Bartz n. sp.	20.36	20.53	20.83	21.69	22.56	21.75	21.40	22.65	21.94	1.21

Table 3. — Uncorrected average pairwise genetic distances within (diagonal) and between species (under diagonal) of Benhamiidae Michaelsen, 1897 included in this work.

Species	Ncsu	Otou	Oaba	OTU.078	Otet	Ntum	Dand	Dbol
Neogaster csuzdii Bartz & Decaëns, n. sp.	5.45	–	–	–	–	–	–	–
Omodeoscolex touroulti Decaëns & Bartz, n. sp.	16.91	1.87	–	–	–	–	–	–
Omodeoscolex abamaensis Bartz & Decaëns, n. sp.	17.18	16.18	1.61	–	–	–	–	–
Wegeneriona OTU#078	18.45	17.09	17.01	0.00	–	–	–	–
Omodeoscolex tetraspermatheca Decaëns & Bartz, n. sp.	18.20	18.16	17.71	14.31	0.00	–	–	–
Neogaster tumuchumac Bartz & Decaëns, n. sp.	20.00	16.73	18.54	17.73	19.19	0.00	–	–
Dichogaster andina Cognetti de Martiis, 1904	18.42	18.03	17.33	17.92	19.88	19.86	0.51	–
Dichogaster bolaui (Michaelsen, 1891)	20.64	18.06	18.91	19.03	17.89	19.43	18.76	0.00

observed per ha in average). The effect of main habitat types on community-scale species richness was significant (Kruskal-Wallis test; p-value = 0.02) and was mainly explained by the lower species richness in inselberg habitats compared to plateau and slope forests (Wilcoxon rank sum test; p-values = 0.006 and 0.014, respectively). Other pairwise comparisons among habitats were not significant.

TAXONOMY

Phylum ANNELIDA Lamarck, 1802
Class CLITELLATA Michaelsen, 1919
Sub-class OLIGOCHAETA Grube, 1850
Order CRASSICLITELLATA Jamieson, 1988
Family Rhinodrilidae Benham, 1890

Genus *Andiorrhinus* Cognetti de Martiis, 1908

Andiorrhinus Cognetti de Martiis, 1908: 511. — Michaelsen 1918: 198. — Cordero 1945: 2. — Righi 1971: 31; 1986: 124; 1993: 126. — Zicsi 1995: 592. — Feijoo *et al.* 2017: 57.

Type species. — *Andiorrhinus salvadorii* Cognetti de Martiis, 1908.

Diagnosis. — Setae arranged in four pairs of regular longitudinal lines. Intra-clitellar male pores. Gizzard in VI. Three pairs of calciferous glands in VII-IX, with lamellar structure. Lateral hearts in VII-IX (Cognetti de Martiis 1908; Righi 1993; Feijoo *et al.* 2017). Testes in X-XI within teste sacs. Two pairs of seminal vesicles in XI-XII. Spermathecae in pre-testicular segments, sometimes missing. Ovaries in XIII.

Five sub-genera are recognized, which differ from each other according to the number and position of intestinal hearts:
Andiorrhinus (*Turedrilus*) Righi, 1993 has the last pair of hearts in XI;
Andiorrhinus (*Andiorrhinus*) Cognetti de Martiis, 1908 has two pairs of intestinal hearts, with the last pair in XII;
Andiorrhinus (*Quibario*) Feijoo, Borwn & James, 2017 has three pairs of intestinal hearts, with the last pair in XII;
Andiorrhinus (*Meridrilus*) Righi, 1993 has two pairs of intestinal hearts, with the last pair in XIII;
Andiorrhinus (*Amazonidrilus*) Righi, 1993 has three pairs of intestinal hearts, with the last pair in XIII.

Diversity and Distribution. — *Andiorrhinus* comprises 47 valid species (not including the new species described here), which are distributed in Venezuela (22 species), Brazil (17 species), Bolivia (four species), Colombia (three species), Guyana (one species), Paraguay (one species) (http://taxo.drilobase.org/; Brown *et al.* 2023; Misirlioğlu *et al.* 2023).

Andiorrhinus (*Turedrilus*) *pascalei* Bartz & Decaëns, n. sp. (Fig. 5)

urn:lsid:zoobank.org:act:9E3C409B-0CD2-4876-9D94-EAF68E2D2C52

Type material. — **Holotype. French Guiana** • Adult (with posterior regeneration); Tumuc-Humac, Mitaraka Massif, plateau forest at base camp, in the soil; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0174; MNHN.
Paratypes. French Guiana • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0176; CEFE.

Other material examined. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0177; MNHN.

Etymology. — This species is named in acknowledgment to Olivier Pascal, who organised the "Our Planet Reviewed" in the Mitaraka Massif.

Ecology. — *Andiorrhinus* (*T.*) *pascalei* Bartz & Decaëns, n. sp. was found in the organo-mineral soil at the base camp of the expedition in a plateau forest ecosystem (Fig. 5D, E).

Distribution. — *Andiorrhinus* (*T.*) *pascalei* Bartz & Decaëns, n. sp. is known from the Mitaraka Massif.

Description

External morphology (Fig. 5A)

Body shape cylindrical. Body pigmentation absent. Body length: 196 mm in the holotype, 158 mm in the paratype, after ethanol fixation. Body mass: 11.90 g after ethanol fixation in the holotype, 5.51 g in the paratype. Diameter: 8 to 9 mm in the preclitellar region, 10 to 12 mm in the clitellum, 9 to 11 mm in the postclitellar region. Number of segments: 244 in the holotype, 230 in the paratype. Prostomium proepilobic. Setae closely paired, *ab* beginning in III and *cd* in IV, *ab* ventral and *cd* mid-lateral to dorsal. Postclitellar setal arrangement *aa:ab:bc:cd:dd* = 16:1:11:1:33. Clitellum in (dorsal XIII) XIV-XXI (dorsal XXII, XXIII), saddle-shaped. Genital markings in IX to XI, intraclitellar in XVII-XX (*ab* position). Tubercula pubertatis linear in ¼XV-¾ XX. Male pores not recognised, and ovipores not visible. Spermathecal pores in 6/7, 7/8 and 8/9. Nephridial pores begining in III, in *D* line.

Internal anatomy (Fig. 5B, C)

Septa: strongly thickened in 6/7 to 13/14, otherwise membranous. Gizzard: muscular and well developed in VI, with an average size (width × length) of 3.45 × 4.45 mm. Calciferous glands: three pairs in VII-IX, with lamellar structure (Fig. 5B). Esophagus-intestine transition in XX; intestine without caeca. Typhlosole abruptly begining in XX/XXI, structured as a long thick folded lamella occupying all the lumen. Intestinal hearts: two pairs of large hearts in X-XI, more developed in XI than in X. Excretory system holoic. Testes sacs: in X and XI containing the two pairs of testes and funnels, ventrally attached to septa 9/10 and 10/11. Seminal vesicles: two pairs in XI-XII, forming very small white mass under the alimentary canal, the pair in XI slightly smaller than in XII, both at least three times smaller than the hearts. Spermathecae: three pairs in VII to IX, very small and round spatula-shaped, attached to septa 6/7, 7/8 and 8/9, without diverticula (Fig. 5C).

Remarks

Andiorrhinus (*T.*) *pascalei* Bartz & Decaëns, n. sp. is attached to the subgenus *Turedrilus* by the position of the last pair of intestinal hearts in XI. Within *Turedrilus* it is close to *Andiorrhinus* (*Turedrilus*) *royeroi* Drachenberg, 1991, *Andiorrhinus* (*Turedrilus*) *samuelensis* Righi, 1986, *Andiorrhinus* (*Turedrilus*) *baniwa* Righi & Nemeth, 1983, and *Andiorrhinus* (*Turedrilus*) *brunneus* (Michaelsen, 1892), all of which have three pairs of spermathecae. It differs from *A.* (*T.*) *royeroi* by the position of the spermathecae in VII-IX instead of VI-VIII, and from all species mentioned by the unique position of its clitellum and tubercula pubertatis (Hernández-García *et al.* 2018a). This species corresponds to OTU#084 in Maggia *et al.* (2021).

Genus *Martiodrilus* Michaelsen, 1936

Martiodrilus Michaelsen, 1936: 1172. — Righi 1971: 4; 1995: 512. — Zicsi & Csuzdi 1997: 82. — Zicsi 2001: 113. — Csuzdi & Pavlíček 2011: 57.

Thamnodrilus – Michaelsen 1900: 434. — Černosvitov 1935: 18.

Thamnodrilus (*Thamnodrilus*) (part.) — Michaelsen 1918: 86. — Černosvitov 1934: 53. — Fragoso & Brown 2007: 59.

Thamnodriloides – Csuzdi & Pavlíček 2011: 58.

Type species. — *Hypogaeon heterostichon* Schmarda, 1861.

Diagnosis. — Setae arranged in eight regular longitudinal lines. One pair of intra-clitellar male pores. Five to eight pairs of calciferous glands in segments VII-XI, XII, XIII, XIV of tubular structure or alveolar structure. Genital apparatus holandric and metagynous. Seminal vesicles generally short, limited to one segment. Spermathecae in pre-testicular segments (Righi 1971). Ovaries in XIII.
Four sub-genera are separated depending on the type of anterior septa, the type of nephridia and the number of spermathecae (Csuzdi & Pavlicek 2011):
Martiodrilus (*Martiodrilus*) Michaelsen, 1936 has strongly thickened septa after the gizzard and nephridia with a single nephrostome;
Martiodrilus (*Cordilleroscoloex*) Zicsi & Csuzdi, 1997 has strongly thickened septa after the gizzard and nephridia with multiple nephrostomes;
Martiodrilus (*Botaria*) Zicsi, 1998 has membranous septa after gizzard, nephridia with a single nephrostome and two to three pairs of spermathecae;
Martiodrilus (*Maipure*) Righi, 1995 membranous septa after gizzard, nephridia with a single nephrostome and four to six pairs of spermathecae.

Distribution. — *Martiodrilus* comprises 85 valid species (not including the new species described here) distributed in South and Central America: Ecuador (57 species), Colombia (22 species), French Guiana (seven species), Peru (six species), Brazil (three species), Surinam (three species), Panama (two species) and Guyana (one species) (http://taxo.drilobase.org/; Misirlioğlu *et al.* 2023; Brown *et al.* 2023).

Martiodrilus (*Botaria*) *flavus* Decaëns & Bartz, n. sp. (Figs 2F; 6)

urn:lsid:zoobank.org:act:72B28D19-6D97-473A-924C-8053998DF36F

Type material. — **Holotype. French Guiana** • Adult (with posterior regeneration); Tumuc-Humac, Mitaraka Massif, transition forest on DIADEMA project C trail, in decaying trunk; 2°14'19"N, 54°26'6"W; 389 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0001; MNHN.
Paratypes. French Guiana • 3 adult specimens; Tumuc-Humac,

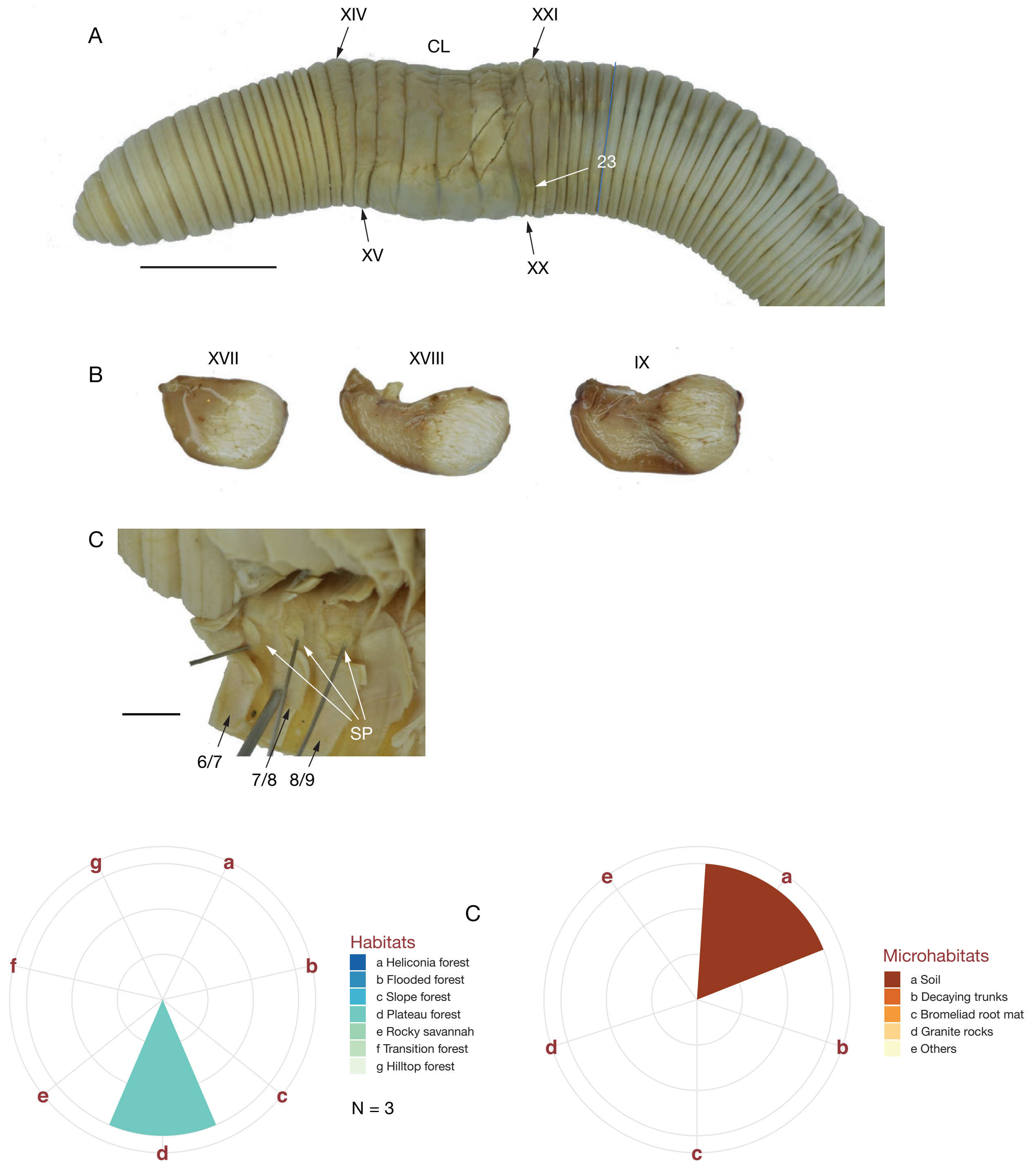

Fig. 5. — *Andiorrhinus* (*Turedrilus*) *pascalei* Bartz & Decaëns n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position on the dorsal side, and of the tubercula pubertatis on the ventral side); **B**, detail of the calciferous glands after being extracted from the dissection; **C**, detail of the dissection showing the spermathecae; **D**, habitat preferences; **E**, microhabitat preferences. All images from the holotype specimen: **CL**, clitellum; **SP**, spermathecae; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset. Scale bars: A, 10 mm; C, 2.5 mm.

Mitaraka Massif, plateau forest on DIADEMA project D trail; 2°12'57"N, 54°27'25"W; 381 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0008, EW-MI15-0009, EW-MI15-0010; CEFE • 2 adult specimens; Tumuc-Humac, Mitaraka Massif, slope forest on trail to Sommet en Cloche Inselberg; 2°14'6"N, 54°27'11"W; 352 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0358, EW-MI15-0359; MNHN.

Other material examined. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0175; MNHN • 1 juvenile specimen, 8 cocoons; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project D trail; 2°12'57"N, 54°27'25"W; 381 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample

ID: EW-MI15-0024, EW-MI15-0028, EW-MI15-0012, EW-MI15-0013, EW-MI15-0014, EW-MI15-0015, EW-MI15-0016, EW-MI15-0017, EW-MI15-0018; MNHN.

Etymology. — This species is named in reference to the remarkable yellow pigmentation of the body observed in most adult specimens.

Ecology. — *Martiodrilus* (*B.*) *flavus* Decaëns & Bartz, n. sp. was predominantly found in plateau forests (81.25% of specimens) and other well-drained habitats such as slope forests (12.5%) and transition forest at the edge of rocky savannah (6.25%) (Fig. 6G). It preferentially inhabits under large decaying trunks fallen at the soil surface (81.25%), but was also occasionally found within the soil (18.75%) (Fig. 6H). Cocoons are tan yellow, spherical, 15-20 mm in diameter, with marked mucrons at the anterior and posterior ends.

Distribution. — *Martiodrilus* (*B.*) *flavus* Decaëns & Bartz, n. sp. is known from the Mitaraka Massif.

Description

External morphology (Fig. 6A, B)

Body shape cylindrical. Body pigmentation yellow when alive (Fig. 2F) sometimes with a transition to grey toward the tail and in regerating parts of the body, clitellum pink when alive, dark beige after ethanol fixation. Body length: 285 mm in the holotype, 265 to 300 mm in the paratypes (average: 283.3 mm; n = 3), after ethanol fixation. Body mass: 21.32 g after ethanol fixation in the holotype, 15.45 to 23.70 g in the paratypes (average: 20.56 g; n = 3). Diameter: 9.3 to 12.5 mm in the preclitellar region, 12.2 to 13 mm in the clitellum, 10.5 to 13 mm in the postclitellar region. Number of segments: 234 in the holotype, 245 to 264 in the paratypes (average: 254.7; n = 3). Prostomium proepilobic. Setae closely paired, *ab* and *cd* beginning in III or IV. Setal arrangement *aa:ab:bc:cd:dd* = 10:1:12:1:34. Clitellum in (½ XIII) XIV-½ XXVI, saddle-shaped (Fig. 6A). Genital markings in V-XIII, intraclitellar in XIV-XXIV (*ab* position). Tubercula pubertatis linear in XIX-XXV (Fig. 6B). Male pores not recognised, and ovipores in XIV, anterior and slightly dorsal to *b*. Spermathecal pores in 5/6, 6/7 and 7/8, in line of *ab*. Nephridial pores begining in III-IV, in *D* line.

Internal anatomy (Fig. 6C-F)

Septa: membranous, slightly thickened in 9/10 to 13/14. Gizzard: muscular and well developed in VI, but displaced to X, XI, with an average size (width × length) of 6.15 × 8.05 mm. Calciferous glands: eight pairs in VII-XIV, yellow bean-shaped with a brown round distal appendix in VII-XII, deprived of appendix and kidney-shaped in XIII-XIV; all with composite tubular structure. Esophagus-intestine transition in XIX; intestine without caeca. Typhlosole abruptly begining in XXV, structured as a large folded tissue (Fig. 6E, F). Hearts: six pairs, the two intestinal pairs well developed in X-XI, enclosed in the testes sacs. Excretory apparatus holoic, nephridia with simple nephrostome. Testes sacs: midventral or hypoesophagic in X and XI. Seminal vesicles: two pairs in XI-XII, short and flat lobulated, and respectively inserted ventrally in X and XI by a tube passing through the septa. Spermathecae: three pairs, VI, VII and VIII, without diverticula (Fig. 6D).

Remarks

Of the *Martiodrilus* species found in French Guiana, *M.* (*B.*) *flavus* Decaëns & Bartz, n. sp. is easily distinguished by its relatively large size and yellow to grey skin pigmentation. The presence of three pairs of spermathecae links it to *Botaria*, however it differs from the other 22 species in the subgenus by their position in 5/6-7/8 instead of 6/7-8/9. It is similar in the position of the clitellum to *Martiodrilus* (*Botaria*) *vassae* Zicsi & Czusdi, 1999 and *Martiodrilus* (*Botaria*) *gara* Righi, 1995, but differs in the position of the tubercula pubertatis in XIX-XXV instead of XXI-XXV in *M.* (*B.*) *vassae* or XIX-XXIII, ½XXIV in *M.* (*B.*) *gara*. It also differs from *M.* (*B.*) *gara* by its larger size (265 to 300 mm, instead of 50 to 100 mm), and from both species by its yellow to grey pigmentation, instead of green in *M.* (*B.*) *vassae* and reddish-violet in *M.* (*B.*) *gara*. *Martiodrilus* (*B.*) *flavus* Decaëns & Bartz, n. sp. is clearly separated from the other *Martiodrilus* species of the Mitaraka Massif by its COI barcode (Table 2). This species corresponds to OTU#064 in Maggia *et al.* (2021).

Martiodrilus* (*Botaria*) *lavellei
Decaëns & Bartz, n. sp.
(Fig. 7)

urn:lsid:zoobank.org:act:AFE58CB8-CEE3-46FE-8576-0259AAF5E274

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, tropical rainforest on DIADEMA project A trail, in the soil; 2°14'27"N, 54°27'15"W; 359 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0105; MNHN.

Etymology. — This species is named in honour of Patrick Lavelle, in acknowledgement to his contribution for the study of tropical earthworm ecology.

Ecology. — This species is only known from the holotype specimen, which has been collected in the organo-mineral soil of a plateau forests (Fig. 7D, E).

Distribution. — *Martiodrilus* (*B.*) *lavellei* Decaëns & Bartz, n. sp. is only known from the Mitaraka Massif.

Description

External morphology (Fig. 7A, B)

Body shape cylindrical. Body pigmentation dorsally light brown, ventrally beige. Body length: 56 mm after ethanol fixation. Body mass: 0.19 g after ethanol fixation. Diameter: 3.4 mm in the preclitellar region, 4.2 mm in the clitellum, 2.5 mm in the postclitellar region. Number of segments: 131. Prostomium proepilobic. One pair of longitudinal grooves going anterior to posterior through segment I in line of nephridial pores. Setae closely paired, *ab* beginning in II, *cd* in III. Setal arrangement *aa:ab:bc:cd:dd* = 8:1:10:2:34. Clitellum in (dorsal XV) XVI-XXV, saddle-shaped (Fig. 7A). Genital markings in V-XXIII, intraclitellar in XV-XXV (*ab* position). Tubercula pubertatis linear in

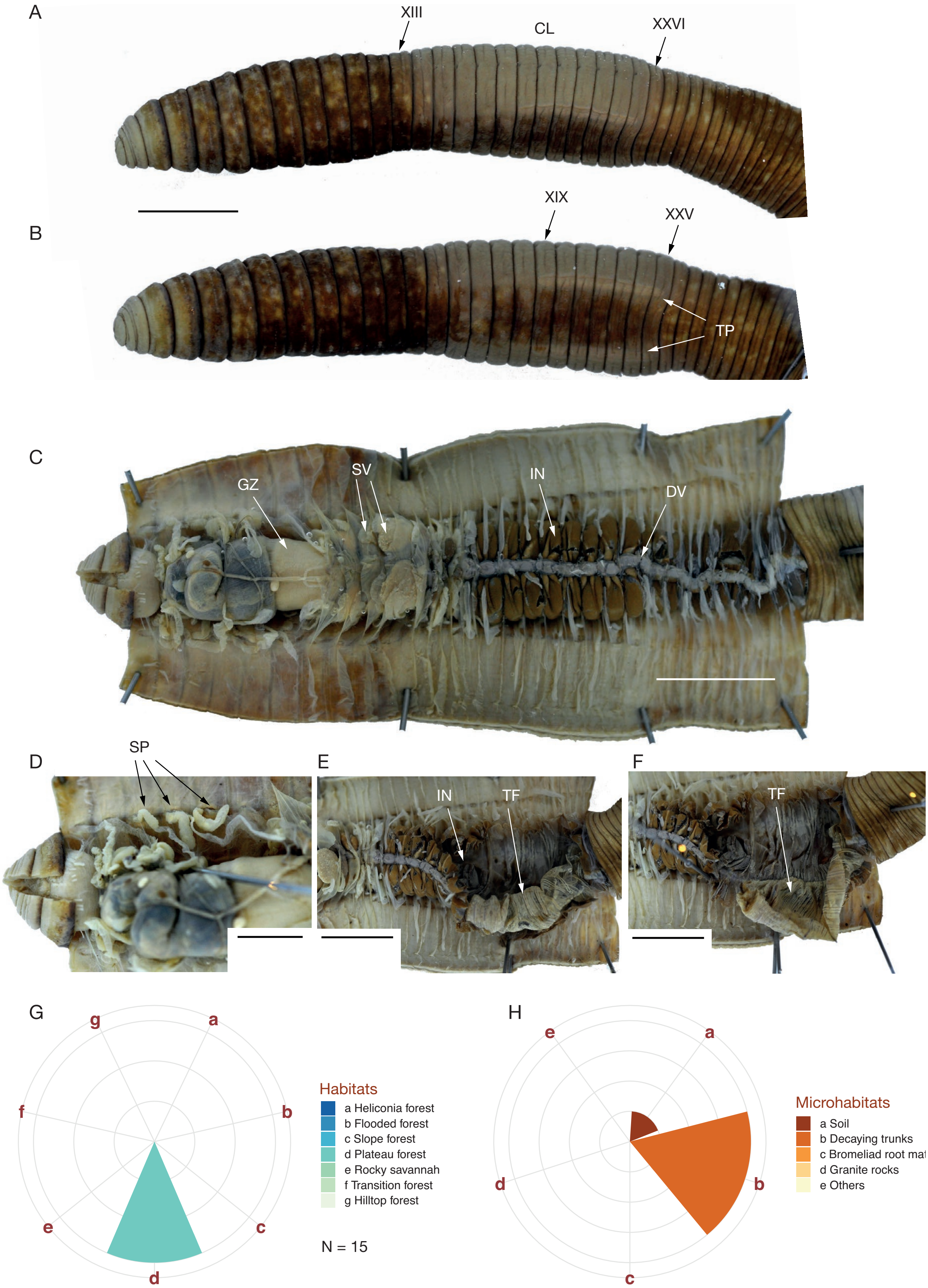

Fig. 6. — *Martiodrilus* (*Botaria*) *flavus* Decaëns & Bartz n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and semi-ventral view of the anterior body (**arrows** indicate the position of the tubercula pubertatis); **C**, dorsal dissection showing anterior internal anatomy; **D**, detail on the spermathecae; **E**, detail on the typhlosole when rolled up; **F**, detail on the typhlosole when unrolled; **G**, habitat preferences; **H**, microhabitat preferences. All images from the holotype specimen: **CL**, clitellum; **DV**, dorsal vessel; **GZ**, gizzard; **IN**, intestine; **SP**, spermathecae; **SV**, seminal vesicles; **TF**, typhlosole; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset. Scale bars: A-C, E, F, 10 mm; D, 5 mm.

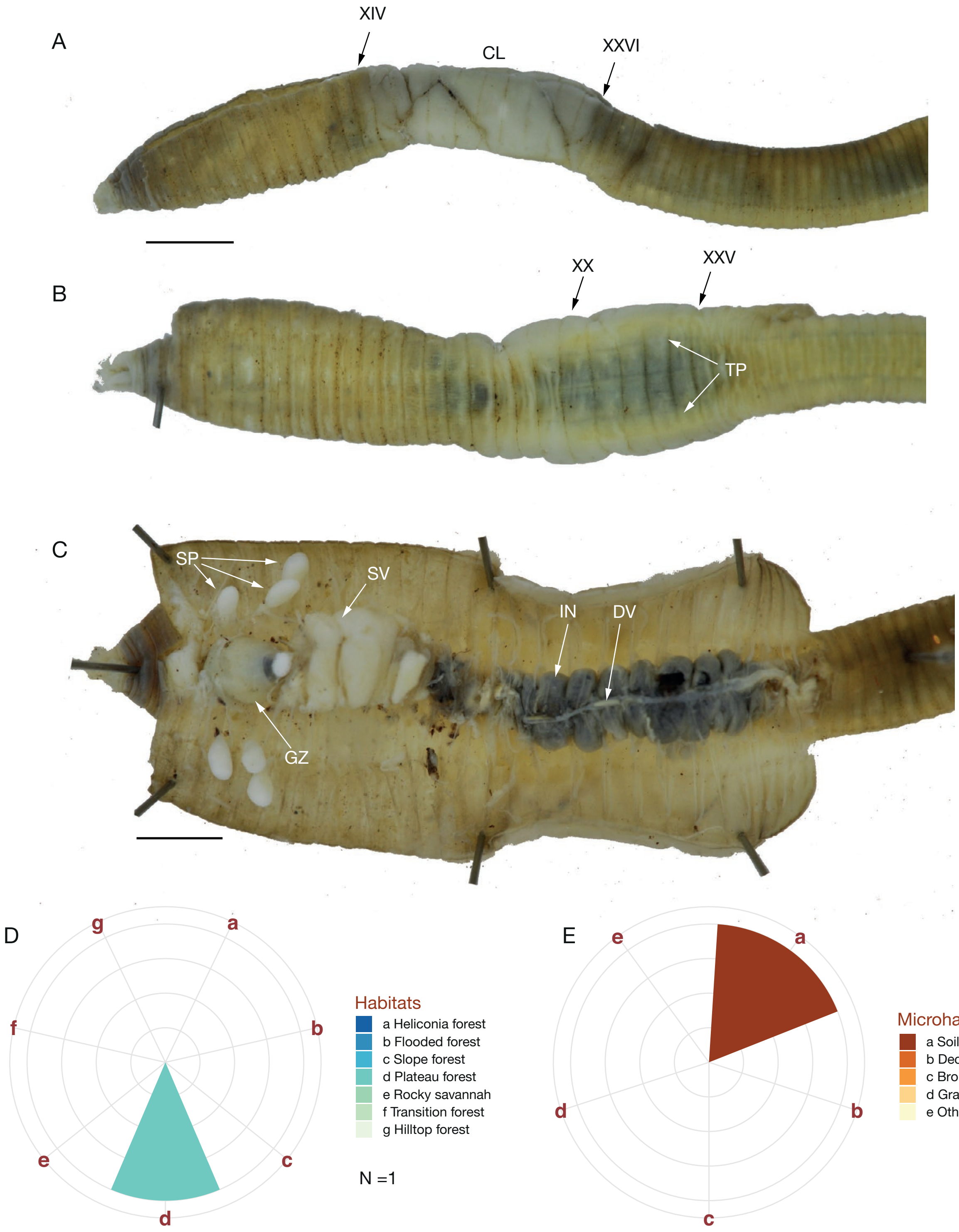

Fig. 7. — *Martiodrilus* (*Botaria*) *lavellei* Decaëns & Bartz n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the position of the tubercula pubertatis); **C**, dorsal dissection showing anterior internal anatomy; **D**, habitat preferences; **E**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **DV**, dorsal vessel; **GZ**, gizzard; **IN**, intestine; **SP**, spermathecae; **SV**, seminal vesicles; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset. Scale bars: 2.5 mm.

¼ XX-½ XXV (Fig. 7B). Male pores not recognised, and ovipores not visible. Spermathecal pores in 5/6, 6/7 and 7/8, near nephridial pore. Nephridial pores begining in III, in *CD* line.

Internal anatomy (Fig. 7C)

Septa: membranous. Gizzard: muscular and well developed in VI, 1.80 × 2.30 mm (width × length). Calciferous glands: eight pairs, in VII-XIV with tubular composite structure.

Esophagus-intestine transition in XVIII/XIX; intestine without caeca. Typhlosole abruptly begining in XXVI, structured as a long thin folded lamella occupying all the lumen. Hearts: five pairs, the two intestinal pairs well-developed in X-XI. Excretory apparatus holoic, nephridia with simple nephrostome. Testes sacs: semi-periesophageal in X and XI, enclosing basal part of hearts, calciferous glands and seminal vesicles. Seminal vesicles: two pairs in XI-XII, small lobulated occupying their segments only. Spermathecae: three pairs, VI, VII, VIII; ovoid elongated without diverticula.

Remarks

Martiodrilus (*B.*) *lavellei* Decaëns & Bartz, n. sp. belongs to the subgenus *Botaria* because of the presence of three pairs of spermathecae. It differs from the majority of species in the subgenus by its clitellum beginning in XVI, a position which it shares only with the two Guyanese species *Martiodrilus* (*Botaria*) *dewynteri* Csuzdi & Pavlicek, 2011 and *Martiodrilus* (*Botaria*) *helleri* (Michaelsen, 1918). Although this needs to be confirmed on a larger number of specimens, the clitellum of *M.* (*B.*) *lavellei* Decaëns & Bartz, n. sp. seems less extended posteriously than in these two species, ending in XXV in the holotype specimen instead of XXVI to ½ XXVI. The position of tubercula pubertatis also differs among these species: ¼ XX-½ XXV in *M.* (*B.*) *lavellei* Decaëns & Bartz, n. sp. instead of ½ XXI-½XXVI in *M.* (*B.*) *dewynteri* and XX-½ XXVI in *M.* (*B.*) *helleri.* Furthermore, *M.* (*B.*) *lavellei* Decaëns & Bartz, n. sp. is significantly smaller than *M.* (*B.*) *helleri*, and appears to have a lighter body pigmentation than *M.* (*B.*) *dewynteri* (light brown instead of brown-violet). *Martiodrilus* (*B.*) *lavellei* Decaëns & Bartz, n. sp. is clearly separated from other species of *Martiodrilus* from the Mitaraka Massif by its COI barcode (Table 2). This species corresponds to OTU#080 in Maggia *et al.* (2021).

Martiodrilus* (*Botaria*) *motoloi Bartz & Decaëns, n. sp. (Fig. 8)

urn:lsid:zoobank.org:act:5A2277F5-F203-4A95-8D39-A17776BC4D7A

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project A trail, in decaying trunk; 2°14'34"N, 54°27'54"W; 327 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0245; MNHN.

Paratypes. French Guiana • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project A trail; 2°14'34"N, 54°27'54"W; 327 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0240; CEFE • 1 adult specimen; same data as for preceding; EW-MI15-0246; MNHN.

Other material examined. — **French Guiana** • 1 fragment, 2 juvenile specimens; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project A trail; 2°14'34"N, 54°27'54"W; 327 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0241, EW-MI15-0227, EW-MI15-0250; MNHN.

Etymology. — This species is named after the word 'motoloi', which means earthworm in the language of the Wayana Amerindian people.

Ecology. — *Martiodrilus* (*B.*) *motoloi* Bartz & Decaëns, n. sp. has been found in lowland forests (Fig. 8D), in decaying trunks (50% of specimens), organo-mineral soil (16.67% of specimens), and in litter accumulation on granite rocks in decaying trunks (33.33% of specimens) (Fig. 8G).

Distribution. — *Martiodrilus* (*B.*) *motoloi* Bartz & Decaëns, n. sp. is only known from the Mitaraka Massif.

Description

External morphology (Fig. 8A, B)

Body shape cylindrical. Body pigmentation dorsally dark red-brown, ventrally light brown. Body length: 52 mm in the holotype, 42 to 56 mm in the paratypes, after ethanol fixation. Body mass: 0.19 g after ethanol fixation in the holotype, 0.14 to 0.21 g in the paratypes. Diameter: 3 to 3.6 mm in the preclitellar region, 3.1 to 3.9 mm in the clitellum, 2.8 to 3.4 mm in the postclitellar region. Number of segments: 120 in the holotype, 106 to 115 in the paratypes. Prostomium proepilobic. One pair of longitudinal grooves going anterior to posterior through segment I in line of nephridial pores. Setae closely paired, *ab* beginning in II, *cd* begining in III. Setal arrangement *aa:ab:bc:cd:dd* = 6:1:8:1:26. Clitellum in (dorsal XIV) XV-½ ½XXVI, saddle-shaped (Fig. 8A). Genital markings variable in V-XIII, intraclitellar in XIV-XXIII and then continuing in XXVI-XXVIII (*ab* position). Tubercula pubertatis linear in ⅓XX-½XXV (Fig. 8B). Male pores not recognised, and ovipores not visible. Spermathecal pores in 5/6, 6/7 and 7/8, near nephridial pore. Nephridial pores begining in II, in *D* line.

Internal anatomy (Fig. 8C)

Septa: membranous. Gizzard: muscular and well developed in VI, with an average size (width × length) of 1.35 × 2.25 mm. Calciferous glands: eight pairs in VII-XIV, with X and XI smaller than the others; all kidney-shaped with lobular distal appendix and composite tubular structure. Esophagus-intestine transition in XVII; intestine without caeca. Typhlosole abruptly begining in XXIV/XXV, structured as a long thin folded lamella occupying all the lumen. Hearts: five pairs in VII-XI, the two intestinal pairs in X-XI larger. Excretory apparatus holoic, nephridia with simple nephrostome. Testes sacs: mid-ventral or hypoesophagic in X and XI, enclosing the seminal vesicles. Seminal vesicles: two pairs in XI-XII, forming large lobulated masses; the first pair enclosed in septa with hearts, calciferous glands and testes sacs in X, and forming a wing extending anteriously up to IX-X; the second pair extending posteriously up to XIII/XV. Spermathecae: three pairs, VI, VII, VIII; elongated sacs little wavy, without diverticula.

Remarks

Martiodrilus (*B.*) *motoloi* Bartz & Decaëns, n. sp. belongs to the subgenus *Botaria* because of the presence of three pairs of spermathecae. It resembles other species of this subgenus which share a clitellum in XV-XXVI, including *Martiodrilus* (*Botaria*) *benhami* (Cognetti de Martiis, 1904), *Martiodri-*

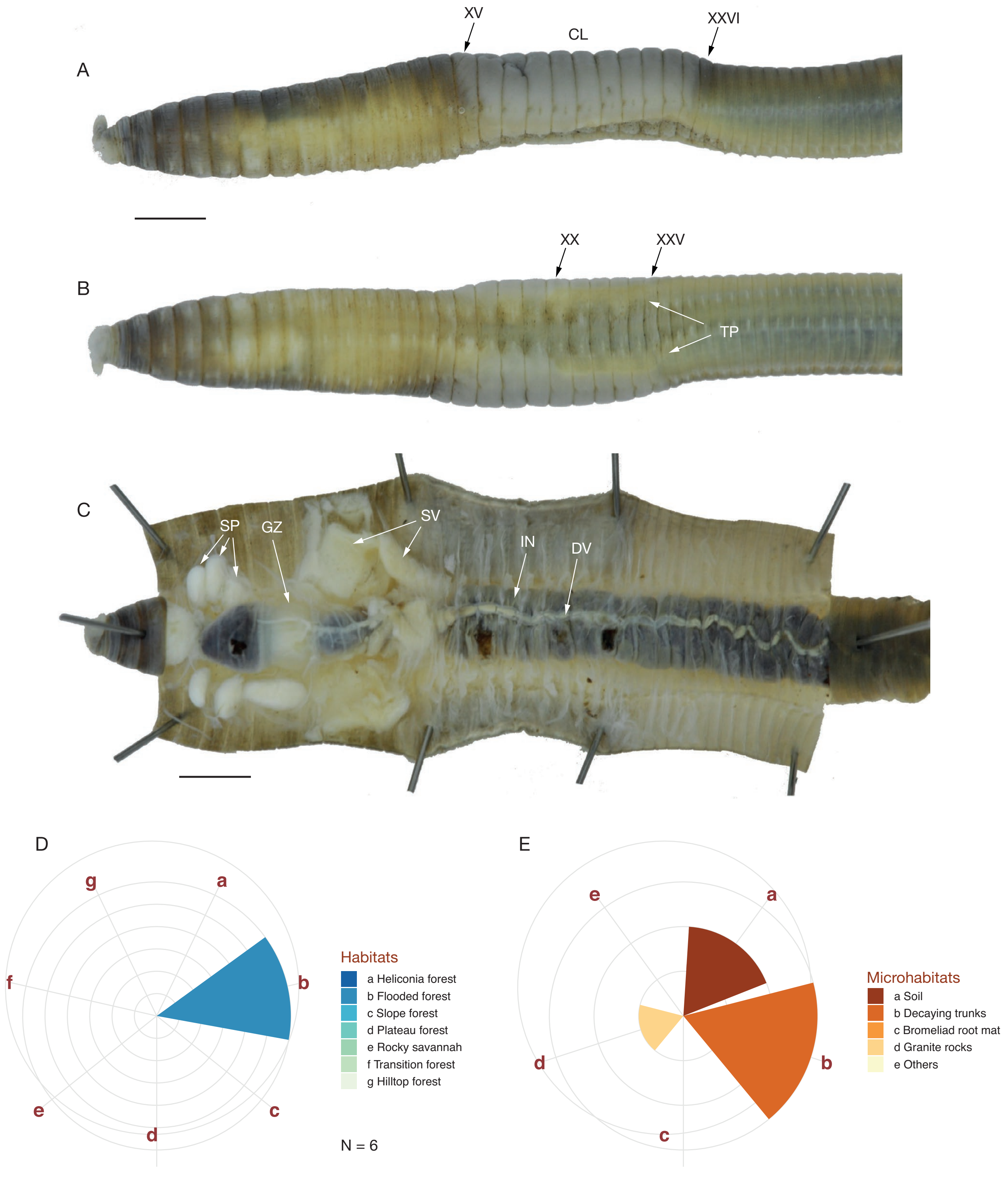

Fig. 8. — *Martiodrilus (Botaria) motoloi* Bartz & Decaëns n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the position of the tubercula pubertatis); **C**, dorsal dissection showing anterior internal anatomy; **D**, habitat preferences; **E**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **DV**, dorsal vessel; **GZ**, gizzard; **IN**, intestine; **SP**, spermathecae; **SV**, seminal vesicles; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset. Scale bars: 2.5 mm.

lus (*Botaria*) *feijooi* Zicsi, 1998, *M.* (*B.*) *gara*, *Martiodrilus* (*Botaria*) *gravis* (Cognetti de Martiis, 1904), *Martiodrilus* (*Botaria*) *pano* Righi, 1992, *M.* (*B.*) *vassae* and *Martiodrilus* (*Botaria*) *wayana* Bartz & Decaëns, n. sp. It differs from all these species but *M.* (*B.*) *gravis* and *M.* (*B.*) *benhami* by the position of its tubercula pubertatis in ⅓XX-½XXV. It can be distinguished from both *M.* (*B.*) *gravis* and *M.* (*B.*) *benhami* by its smaller size (42 to 56 mm instead of more than 90 mm and 170 mm, respectively), and by its darker pigmentation. *Martiodrilus* (*B.*) *motoloi* Bartz & Decaëns, n. sp. is clearly separated from other species of *Martiodrilus* from the Mitaraka Massif by its COI barcode (Table 2). This species corresponds to OTU#088 in Maggia *et al.* (2021).

Martiodrilus (*Botaria*) *pavliceki* Bartz & Decaëns, n. sp. (Fig. 9)

urn:lsid:zoobank.org:act:F97CD986-B5A0-42ED-B68F-277EC269F565

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp, in the soil; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0283; MNHN.

Other material examined. — **French Guiana** • 3 juvenile specimens; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project C trail; 2°14'5"N, 54°26'42"W; 377 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0058, EW-MI15-0059, EW-MI15-0060; MNHN.

Etymology. — This species is named in honour of Tomas Pavlicek, in acknowledgement to his contribution for the study of earthworms in French Guiana and in other regions of the World.

Ecology. — *Martiodrilus* (*B.*) *pavliceki* Bartz & Decaëns, n. sp. has been found in slope forests (75% of specimens) and in plateau forests (25%) (Fig. 9D). All specimens were collected in the organo-mineral soil (Fig. 9E).

Distribution. — *Martiodrilus* (*B.*) *pavliceki* Bartz & Decaëns, n. sp. is only known from the Mitaraka Massif.

Description

External morphology (Fig. 9A, B)

Body shape cylindrical, with flattened tail. Body pigmentation dorsally yellow-brown before clitellum, brown after clitellum with anterior to posterior gradient, ventrally beige, clitellum light grey. Body length: 95 mm after ethanol fixation. Body mass: 1.08 g after ethanol fixation. Diameter: 4 mm in the preclitellar region, 5.2 mm in the clitellum, 4.4 mm in the postclitellar region. Number of segments: 156. Prostomium proepilobic. One pair of longitudinal grooves going anterior to posterior through segment I in line of nephridial pores. Setae closely paired, *ab* beginning in II, *cd* in III. Setal arrangement *aa:ab:bc:cd:dd* = 5:1:6:1:20. Clitellum in (dorsal XIV) XV-XXV (dorsal XXVI), saddle-shaped (Fig. 9A). Genital markings in V-XVIII, intraclitellar in XVIII-XXIV (*ab* position). Tubercula pubertatis linear in XIX-⅟nXXV (Fig. 9B). Male pores not recognised, and ovipores not visible. Spermathecal pores not recognised. Nephridial pores begining in II, in *C* line.

Internal anatomy (Fig. 9C)

Septa: membranous, slightly thickened in 9/10 to 16/17. Gizzard: muscular and well developed in VI, with an average size (width × length) of 2.70 × 2.90 mm. Calciferous glands: eight pairs, the first five pairs (VII-XI) small and globular to pear-shaped, the three next pairs (XII-XIV) two times larger and kidney-shaped; all with a lobular distal appendix. Esophagus-intestine transition in XVIII; intestine without caeca. Typhlosole abruptly begining in XXV, structured as a long thin folded lamella occupying all the lumen. Hearts: five pairs in VII-XI, the two intestinal pairs in X-XI larger and enclosed to testes sacs. Excretory apparatus holoic, nephridia with simple nephrostome. Testes sacs: periesophageal in X and XI, enclosing seminal vesicles, heart and calciferous gland. Seminal vesicles: two pairs in XI-XII; first pair extending to X and forming lobes in XI; second pair lobular extending to XIV without perforating septa. Spermathecae: three pairs in VII to IX, formed by a thin duct terminated by a round and flattened sac; last pair larger than the two first ones.

Remarks

Martiodrilus (*B.*) *pavliceki* Bartz & Decaëns, n. sp. resembles species of subgenus *Botaria* which share a clitellum in XV-XXV, including *Martiodrilus* (*Botaria*) *tchoukouchipan* Decaëns & Bartz, n. sp., *Martiodrilus* (*Botaria*) *bicolor* (Michaelsen, 1913), *Martiodrilus* (*Botaria*) *euzonus* (Cognetti de Martiis, 1904), *M.* (*B.*) *gara*, *M.* (*B.*) *gravis*, *Martiodrilus* (*Botaria*) *minoriformis* Zicsi, 1998, *Martiodrilus* (*Botaria*) *poncei* Zicsi, 1998 and *Martiodrilus* (*Botaria*) *tutus* (Cognetti de Martiis, 1904). It differs from all these species, by the unique position of its tubercula pubertatis in XIX-⅟nXXV. It is also noticeably larger than *M.* (*B.*) *tchoukouchipan* Decaëns & Bartz, n. sp. (95 mm vs 55-75 mm in the latter), and has flattened sac-like spermathecae whereas they are elongated in *M.* (*B.*) *tchoukouchipan* Decaëns & Bartz, n. sp. *Martiodrilus* (*B.*) *pavliceki* Bartz & Decaëns, n. sp. is clearly separated from other species of *Martiodrilus* from the Mitaraka Massif by its COI barcode (Table 2). This species corresponds to OTU#076 in Maggia *et al.* (2021).

Martiodrilus (*Botaria*) *tchoukouchipan* Decaëns & Bartz, n. sp. (Figs 2E;10)

urn:lsid:zoobank.org:act:D2235D38-95FC-44C7-8FDE-CD45AC4F308F

Type material. — **Holotype. French Guiana** • Adult specimen; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project C trail, in the soil; 2°13'58"N, 54°26'38"W; 449 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0289; MNHN.

Paratypes. French Guiana • 2 adult specimens; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0285, EW-MI15-0303; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project C trail; 2°13'58"N, 54°26'38"W; 449 m a.s.l.; III.2015;

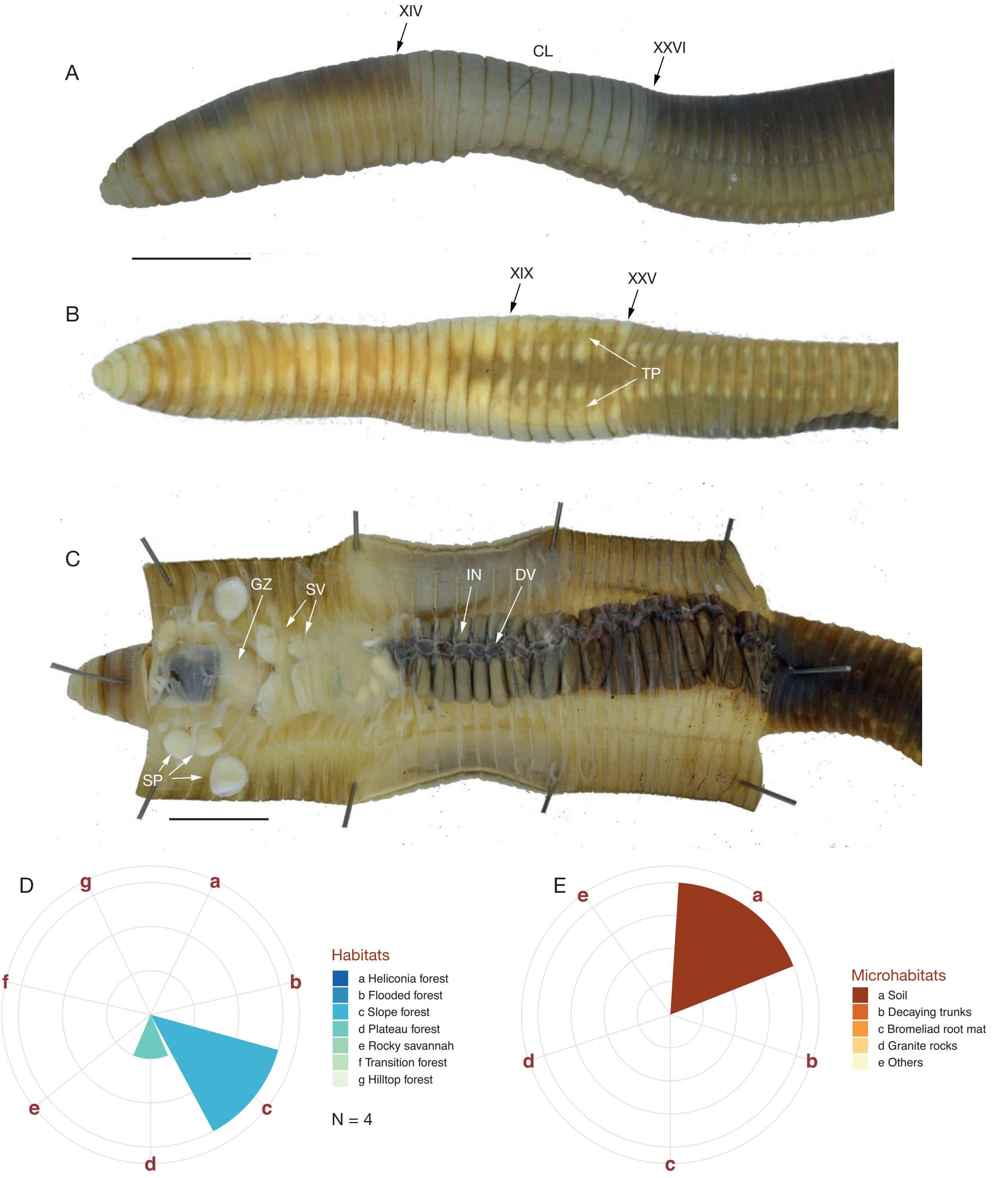

Fig. 9. — *Martiodrilus (Botaria) pavliceki* Bartz & Decaëns n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the position of the tubercula pubertatis); **C**, dorsal dissection showing the internal anatomy of the anterior body; **D**, habitat preferences; **E**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **DV**, dorsal vessel; **GZ**, gizzard; **IN**, intestine; **SP**, spermathecae; **SV**, seminal vesicles; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset. Scale bars: 5 mm.

T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0298; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, rocky savannah #1 on Sommet en Cloche Inselberg; 2°13'40"N, 54°28'1"W; 623 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0362; CEFE • 3 adult specimens; Tumuc-Humac, Mitaraka Massif, rocky savannah #2 on Sommet en Cloche Inselberg; 2°13'58"N, 54°27'39"W; 427 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0324, EW-MI15-0379, EW-MI15-0157; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, transition forest # 1 Sommet en Cloche Inselberg;

2°13'54"N, 54°27'39"W; 401 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; EW-MI15-0336; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, transition forest on Tchoukou Chipan Inselberg; 2°14'54"N, 54°29'12"W; 405 m a.s.l.; III.2015; C. Baraloto leg.; BOLD Sample ID: EW-MI15-0108; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, tropical rainforest on crowned mountain; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0127; MNHN.

Other material examined. — **French Guiana** • 3 adult specimens; Tumuc-Humac, Mitaraka Massif, hilltop forest on Sommet en Cloche Inselberg; 2°13'42"N, 54°28'2"W; 638 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0152, EW-MI15-0153, EW-MI15-0154; MNHN • 4 juvenile specimens; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project C trail; 2°13'58"N, 54°26'38"W; 449 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0287, EW-MI15-0288, EW-MI15-0290, EW-MI15-0292; MNHN • 13 juvenile specimens; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project D trail; 2°12'57"N, 54°27'25"W; 381 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0020, EW-MI15-0021, EW-MI15-0022, EW-MI15-0092, EW-MI15-0093, EW-MI15-0095, EW-MI15-0096, EW-MI15-0097, EW-MI15-0098, EW-MI15-0101, EW-MI15-0102, EW-MI15-0103, EW-MI15-0104; MNHN • 4 adult specimens, 3 juvenile specimens, 5 cocoons; Tumuc-Humac, Mitaraka Massif, rocky savannah #1 on Sommet en Cloche Inselberg; 2°13'40"N, 54°28'1"W; 623 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0155, EW-MI15-0156, EW-MI15-0158, EW-MI15-0159, EW-MI15-0165, EW-MI15-0166, EW-MI15-0167, EW-MI15-0168, EW-MI15-0169, EW-MI15-0160, EW-MI15-0162, EW-MI15-0163; MNHN • 3 adult specimens, 4 juvenile specimens, 2 cocoons; Tumuc-Humac, Mitaraka Massif, rocky savannah #2 on Sommet en Cloche Inselberg; 2°13'58"N, 54°27'39"W; 427 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0320, EW-MI15-0322, EW-MI15-0323, EW-MI15-0331, EW-MI15-0332, EW-MI15-0325, EW-MI15-0326, EW-MI15-0327, EW-MI15-0328; MNHN • 4 juvenile specimens; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project D trail; 2°13'40"N, 54°27'14"W; 339 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0265, EW-MI15-0266, EW-MI15-0267, EW-MI15-0268; MNHN • 1 adult specimen, 2 juvenile specimens, 1 fragment; Tumuc-Humac, Mitaraka Massif, transition forest # 1 Sommet en Cloche Inselberg; 2°13'54"N, 54°27'39"W; 401 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0313, EW-MI15-0354, EW-MI15-0314, EW-MI15-0338; MNHN • 4 adult specimens; Tumuc-Humac, Mitaraka Massif, transition forest # 2 Sommet en Cloche Inselberg; 2°13'59"N, 54°27'34"W; 395 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0110, EW-MI15-0111, EW-MI15-0112, EW-MI15-0113; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, tropical rainforest on crowned mountain; NA/NA; NA m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0129; MNHN.

Etymology. — This species is named in reference to the Tchoukou Chipan inselberg near which the holotype specimen was collected.

Ecology. — *Martiodrilus* (*B.*) *tchoukouchipan* Decaëns & Bartz, n. sp. has been found in a wide range of well-drained habitats, with a marked preference for rocky savannahs of the inselbergs (38.46% of specimens), plateau forests (32.31%) and inselberg transition forests (15.38%) (Fig. 10D). Most specimens were collected under terrestrial bromeliads covering rocky savannahs (38.46% of specimens), in the organo-mineral soil (38.46%) and a lower proportion in decaying trunks (16.92%) and in litter accumulating on large granite rocks (6.15%) (Fig. 10E). Cocoons are tan yellow, spherical, 4.5-5.5 mm in diameter, with two mucrons at the anterior and posterior ends.

Distribution. — *Martiodrilus* (*B.*) *tchoukouchipan* Decaëns & Bartz, n. sp. is only known from the Mitaraka Massif.

Description

External morphology (Fig. 10A, B)

Body shape cylindrical. Body pigmentation dorsally yellow-brown, ventrally yellow. Body length: 56 mm in the holotype, 55 to 75 mm in the paratypes (average: 76.3 mm; n = 6), after ethanol fixation. Body mass: 0.32 mm after ethanol fixation in the holotype, 0.31 to 0.82 g in the paratypes (average: 0.54 g; n = 6). Diameter: 3 to 5.5 mm in the preclitellar region, 3.9 to 5.5 mm in the clitellum, 3.2 to 4.7 mm in the postclitellar region. Number of segments: 96 in the holotype, 101 to 145 in the paratypes (average: 128.3; n = 6). Prostomium proepilobic. One pair of longitudinal grooves passing through segment I in line of nephridial pores in II. Setae closely paired, *ab* and *cd* beginning in III or IV. Setal arrangement *aa:ab:bc:cd:dd* = 6:1:9:1:31. Clitellum in (dorsal XIV) XV (XVI)-½ XXV, saddle-shaped (Fig. 10A). Genital markings variable in V-VIII and in X-XII, and intraclitellar in XV-XVIII (*ab* position). Tubercula pubertatis linear in ¼XX-⅓XXV (Fig. 10B). Male pores not recognised externally, internally open in 19/20, and ovipores not visible. Spermathecal pores in 5/6, 6/7 and 7/8. Nephridial pores begining in II, in *CD* line.

Internal anatomy (Fig. 10C)

Septa: membranous. Gizzard: muscular and well developed in VI, but displaced to X, XI, with an average size (width × length) of 2.60 × 3.38 mm. Calciferous glands: eight pairs in VII-XIV, those in X and XI slightly smaller; all kidney-shaped with a terminal appendix and tubular composite structure. Esophagus-intestine transition in XVII/XVIII; intestine without caeca. Typhlosole abruptly begining in XXVI, structured as a long-folded lamella occupying all the lumen. Hearts: six pairs, the two intestinal pairs in X-XI and well developed. Excretory apparatus holoic, nephridia with simple nephrostome. Testes sacs: midventral or hypoesophagic in X and XI, enclosing seminal vesicles. Seminal vesicles: two pairs in XI-XII: first pair enclosed in septa extending to IX and X; second pair going until XVII, lobulated with division in the segments and attached to the dorsal body wall. Spermathecae: three pairs, VI, VII and VIII, elongated without diverticula.

Remarks

Martiodrilus (*B.*) *tchoukouchipan* Decaëns & Bartz, n. sp. belongs to the subgenus *Botaria* because of the presence of 3 pairs of spermathecae. It resembles a group of species sharing a clitellum positioned on XV-XXV, including *M.* (*B.*) *pavliceki* Bartz & Decaëns, n. sp., *M.* (*B.*) *bicolor*, *M.* (*B.*) *euzonus*, *M.* (*B.*) *gara*, *M.* (*B.*) *gravis*, *M.* (*B.*) *minoriformis*, *M.* (*B.*) *poncei* and *M.* (*B.*) *tutus*. However, it differs from these species in the position of the tubercula pubertatis in ¼XX-⅓XXV which is only compatible with the description of *M.* (*B.*) *gravis* and *M.* (*B.*) *tutus*. It is finally distinguished from the latter two species by its significantly smaller size (55-75 mm,

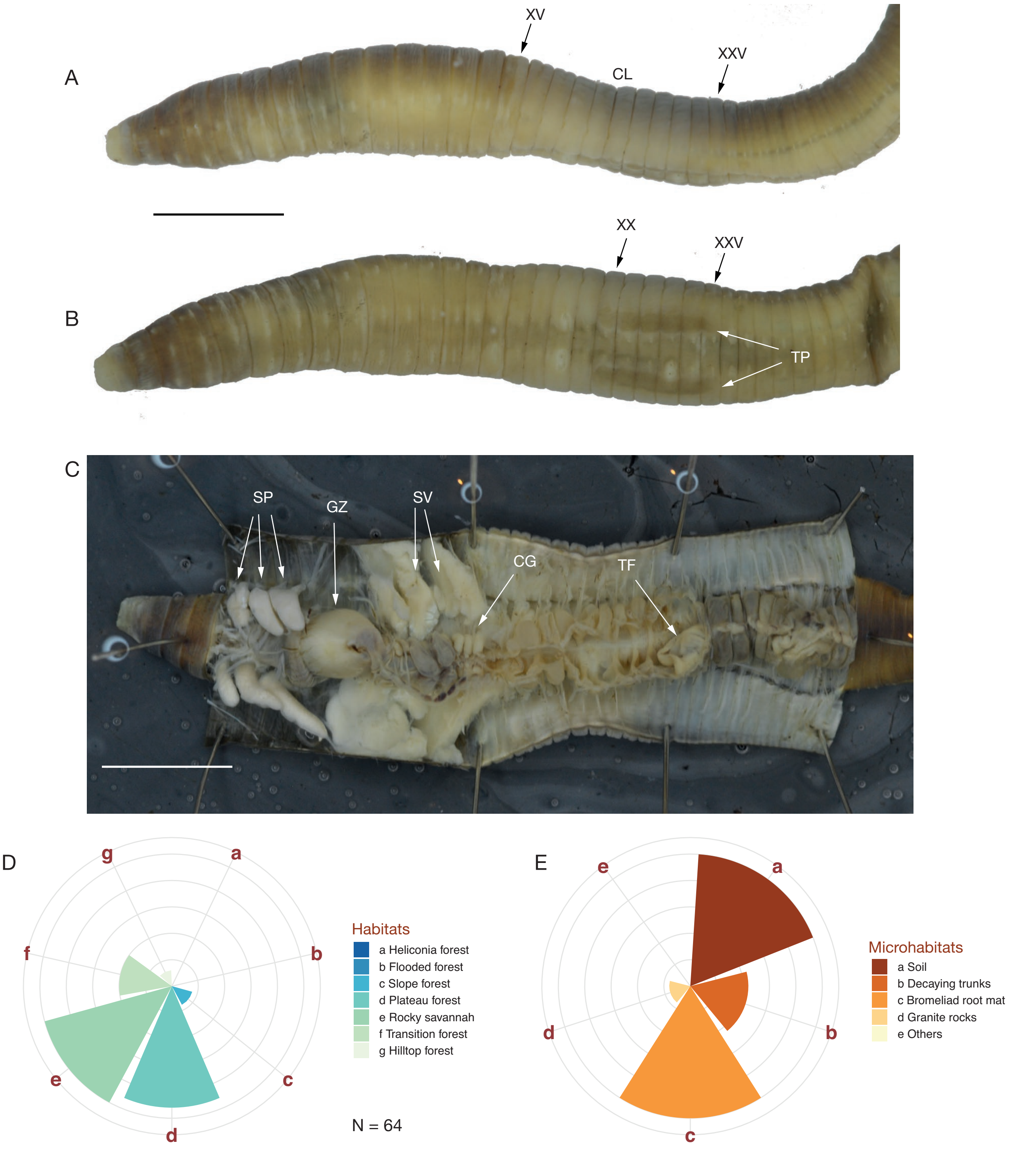

FIG. 10. — *Martiodrilus (Botaria) tchoukouchipan* Decaëns & Bartz n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the position of the tubercula pubertatis); **C**, dorsal dissection showing anterior internal anatomy; **D**, habitat preferences; **E**, microhabitat preferences. All images from the holotype; **CG**, calciferous glands; **CL**, clitellum; **GZ**, gizzard; **SP**, spermathecae; **SV**, seminal vesicles; **TF**, typhlosole; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset. Scale bars: 5 mm.

whereas *M.* (*B.*) *gravis* and *M.* (*B.*) *tutus* are larger than 90 mm and 100 mm, respectively). *Martiodrilus* (*B.*) *tchoukouchipan* Decaëns & Bartz, n. sp. is clearly separated from the other species of *Martiodrilus* from the Mitaraka Massif by its COI barcode (Table 2). This species corresponds to OTU#071 in Maggia *et al.* (2021).

Martiodrilus (*Botaria*) *wayana* Bartz & Decaëns, n. sp. (Fig. 11)

urn:lsid:zoobank.org:act:DE41C1ED-7C4B-46C2-B48B-7029D3D57299

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, rocky savannah on Borne 1 Inselberg, in terrestrial bromeliad roots; 2°12'29"N, 54°26'20"W; 585 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0134; MNHN.
Paratypes. French Guiana • 3 adult specimens; Tumuc-Humac, Mitaraka Massif, rocky savannah on Borne 1 Inselberg; 2°12'29"N, 54°26'20"W; 585 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0378, EW-MI15-0136, EW-MI15-0137; CEFE • 3 adult specimens; same data as for preceding; BOLD Sample ID: EW-MI15-0133, EW-MI15-0135, EW-MI15-0138; MNHN.

Other material examined. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, hilltop forest on Borne 1 Inselberg; 2°12'35"N, 54°26'12"W; 600 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0220; MNHN • 10 juvenile specimens; Tumuc-Humac, Mitaraka Massif, rocky savannah on Borne 1 Inselberg; 2°12'29"N, 54°26'20"W; 585 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0140, EW-MI15-0141, EW-MI15-0142, EW-MI15-0143, EW-MI15-0144, EW-MI15-0145, EW-MI15-0146, EW-MI15-0147, EW-MI15-0148, EW-MI15-0149; MNHN.

Etymology. — This species is named after the Wayanas Amerindian people who inhabited this region of French Guiana and have left multiple petroglyphs and stone assemblages on the Borne 1 inselberg (Fleury *et al.* 2021).

Ecology. — *Martiodrilus* (*B.*) *wayana* Bartz & Decaëns, n. sp. has been found essentially in inselberg rocky savannahs (94.44% of specimens) (Fig. 11D), where it inhabits the root mat of terrestrial bromeliad formations (Fig. 11G).

Distribution. — *Martiodrilus* (*B.*) *wayana* Bartz & Decaëns, n. sp. is only known from the Borne 1 inselberg, at the frontier between French Guiana and Brazil, in the Mitaraka Massif.

Description

External morphology (Fig. 11A, B)
Body shape cylindrical. Body pigmentation dorsally dark brown, ventrally yellow. Body length: 74 mm in the holotype, 55 to 70 mm in the paratypes (average: 60.7 mm; n = 3), after ethanol fixation. Body mass: 0.50 g after ethanol fixation in the holotype, 0.11 to 0.48 g in the paratypes (average: 0.23 g; n = 3). Diameter: 3.2 to 5 mm in the preclitellar region, 3.5 to 4.5 mm in the clitellum, 3.4 to 5 mm in the postclitellar region. Number of segments: 140 in the holotype, 104 to 141 in the paratypes (average: 123; n = 3). Prostomium proepilobic. One pair of longitudinal grooves going anterior to posterior through segment I in line of nephridial pores in II. Setae closely paired, *ab* beginning in II, *cd* in III or IV. Setal arrangement *aa:ab:bc:cd:dd* = 4:1:5:1:19. Clitellum in (dorsal XIII, XIV) XV-(XXV) XXVI, saddle-shaped (Fig. 11A). Genital markings in variable in III-X, intraclitellar in XIV-XXIII (*ab* position). Tubercula pubertatis linear in XX-½ XXVI (Fig. 11B). Male pores not recognised, and ovipores in XIV, almost in the border of 13/14, in diagonal to *b*. Spermathecal pores in 5/6, 6/7 and 7/8, inter segmental near nephridial pore. Nephridial pores begining in II, in *CD* line.

Internal anatomy (Fig. 11C)
Septa: membranous. Gizzard: muscular and well developed in VI, displaced to X, with an average size (width × length) of 2.25 × 2.78 mm. Calciferous glands: eight pairs in VII-XIV, those in X and XI twice smaller than the others; all with peduncula attaching the inner middle of the gland to esophagus, kidney-shaped with lobular distal appendix, and composite tubular structure. Esophagus-intestine transition in XVIII/XIX; intestine without caeca. Typhlosole abruptly begining in XXV/XXVIII, structured as a long-folded lamella, occupying all the lumen. Hearts: six pairs, the two intestinal pairs in X-XI and well developed. Excretory apparatus holoic, nephridia with simple nephrostome. Testes sacs: midventral or hypoesophagic in X and XI, enclosing seminal vesicles. Seminal vesicles: two pairs in XI-XII; the first pair enclosed in septa, strap-shaped extending anteriously up to IX/X; the second pair extending to XIII, lobulated and attached to dorsal body wall. Spermathecae: three pairs, VI, VII and VIII, spatula-shaped without diverticula, of increasing size from VI to VIII.

Remarks

Martiodrilus (*B.*) *wayana* Bartz & Decaëns, n. sp. belongs to the subgenus *Botaria* because of the presence of three pairs of spermathecae. It resembles other species of this subgenus which share a clitellum in XV-XXVI, including *M.* (*B.*) *benhami*, *M.* (*B.*) *feijooi*, *M.* (*B.*) *gara*, *M.* (*B.*) *gravis*, *M.* (*B.*) *pano*, *M.* (*B.*) *vassae* and *M.* (*B.*) *motoloi* Bartz & Decaëns, n. sp. It differs from all these species but *M.* (*B.*) *pano*, by the position of its tubercula pubertatis in XX-½ XXVI, instead of XX-XXV in *M.* (*B.*) *benhami*, ½ XIX-½ XXVI in *M.* (*B.*) *feijooi*, XIX, ⅔XIX-XXIII, ½ XXIV in *M.* (*B.*) *gara*, XX, ¾XX- ½XXV in *M.* (*B.*) *gravis*, XXI-XXV in *M.* (*B.*) *vassae* and ⅓XX-½ XXV *M.* (*B.*) *motoloi* Bartz & Decaëns, n. sp. It further differs from *M.* (*B.*) *pano* by its smaller size (55 to 74 mm instead of 85 mm), by its brown instead of violet body pigmentation, and by the more anterior transition between esophagus and intestine. *Martiodrilus* (*B.*) *wayana* Bartz & Decaëns, n. sp. is clearly separated from other species of *Martiodrilus* from the Mitaraka Massif by its COI barcode (Table 2). This species corresponds to OTU#083 in Maggia *et al.* (2021).

Martiodrilus (*Maipure*) *luminescens* Decaëns & Bartz, n. sp. (Fig. 12)

urn:lsid:zoobank.org:act:C0B6F2F4-F011-4CE0-B842-3D05A0D4CA27

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, rocky savannah #2 on Sommet en Cloche Inselberg, in terrestrial bromeliad roots; 2°13'58"N, 54°27'39"W; 427 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0319; MNHN.
Paratypes. French Guiana • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, rocky savannah #2 on Sommet en Cloche Inselberg; 2°13'58"N, 54°27'39"W; 427 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0318;

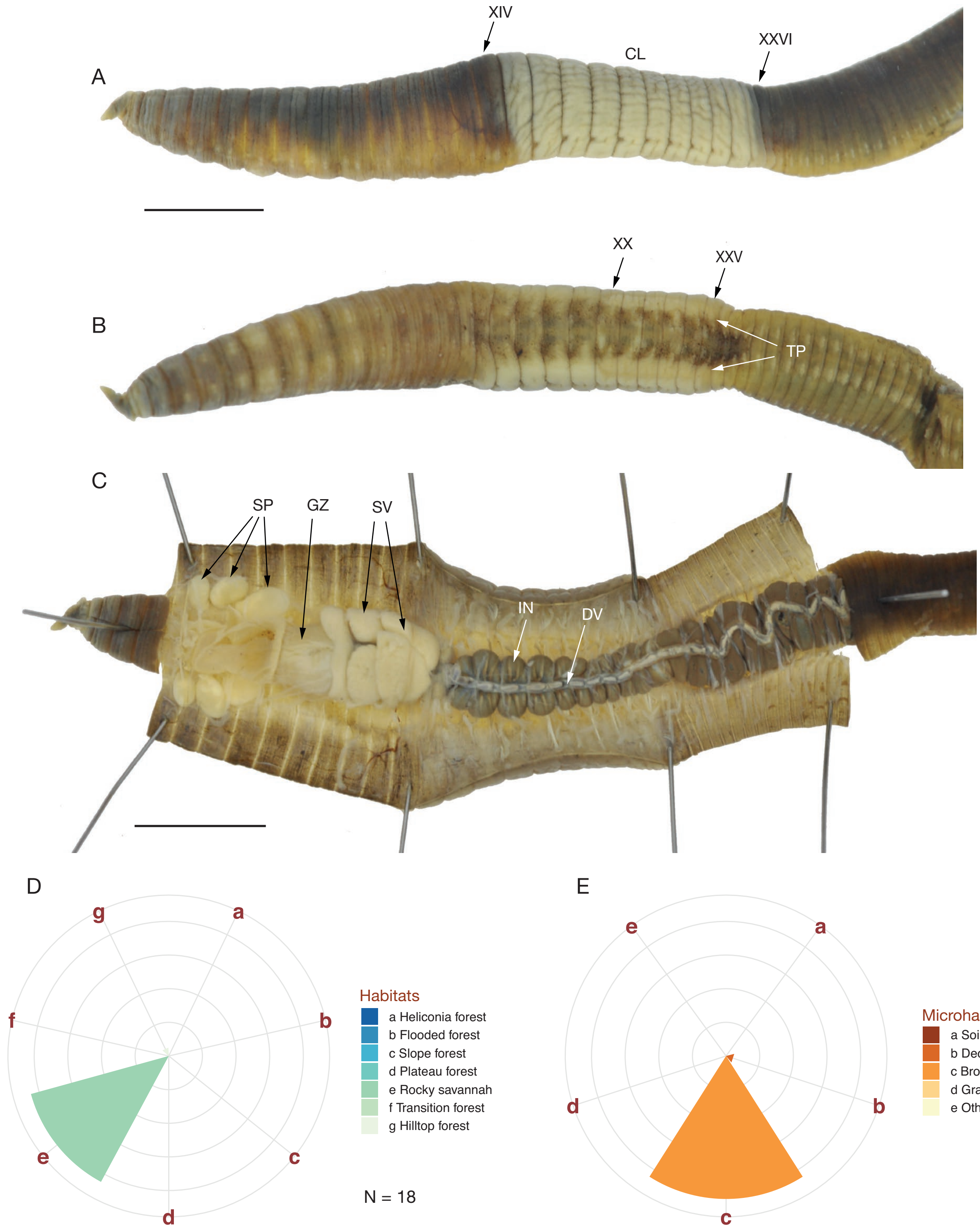

FIG. 11. — *Martiodrilus* (*Botaria*) *wayana* Bartz & Decaëns n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the position of the tubercula pubertatis); **C**, dorsal dissection showing anterior internal anatomy; **D**, Habitat preferences; **E**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **DV**, dorsal vessel; **GZ**, gizzard; **IN**, intestine; **SP**, spermathecae; **SV**, seminal vesicles; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset. Scale bars: 5 mm.

CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project D trail; 2°13'40"N, 54°27'14"W; 339 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0254; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, slope forest on trail to Sommet en Cloche Inselberg; 2°14'6"N, 54°27'11"W; 351 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0194; MNHN.

Other material examined. — **French Guiana** • 2 juvenile specimens; Tumuc-Humac, Mitaraka Massif, rocky savannah #2 on Sommet en Cloche Inselberg; 2°13’58”N, 54°27’39”W; 427 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0329, EW-MI15-0330; MNHN • 2 juvenile specimens; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project A trail; 2°14’16”N, 54°27’7”W; 344 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0202, EW-MI15-0209; MNHN • 3 juvenile specimens, 1 cocoon; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project D trail; 2°13’40”N, 54°27’14”W; 339 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0263, EW-MI15-0264, EW-MI15-0269, EW-MI15-0276; MNHN • 4 juvenile specimens; Tumuc-Humac, Mitaraka Massif, transition forest # 1 Sommet en Cloche Inselberg; 2°13’54”N, 54°27’39”W; 401 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0337, EW-MI15-0339, EW-MI15-0340, EW-MI15-0376; MNHN • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, tropical rainforest on crowned mountain; unknown; unknown; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0132; MNHN.

Etymology. — The name of the species refers to the bioluminescent character observed on one of the type specimens during field sampling.

Ecology. — *Martiodrilus* (*M.*) *luminescens* Decaëns & Bartz, n. sp. has been found mostly in slope forests (41.18% of specimens) and in inselberg rocky savannahs (23.53%) and transition forests (23.53 (Fig. 12F). Most specimens were collected in decaying trunks (35.29%), in litter accumulations on granite rocks (23.53%) and in the root mat of terrestrial bromeliads (23.53%) (Fig. 12G). Cocoons are tan yellow, spherical, 10 mm in diameter, with two mucrons at the anterior and posterior ends. A specimen moving at night on the surface of the ground was observed producing a green bioluminescence.

Distribution. — *Martiodrilus* (*M.*) *luminescens* Decaëns & Bartz, n. sp. is only known from the Mitaraka Massif.

Description

External morphology (Fig. 12A, B)

Body shape cylindrical, slightly flattened after clitellum. Body pigmentation dorsal grey-brown, ventral light-brown. Body length: 109 mm in the holotype, 105 to 170 mm in the paratypes (average: 139 mm; n = 3), after ethanol fixation. Body mass: 1.87 after ethanol fixation in the holotype, 1.84 to 5.38 g in the paratypes (average: 3.90 g; n = 3). Diameter: 5.3 to 7 mm in the preclitellar region, 9 to 10.3 mm in the clitellum, 6.5 to 8 mm in the postclitellar region. Number of segments: 108 in the holotype, 85 to 136 in the paratypes (average: 118.3; n = 3). Prostomium proepilobic. Setae closely paired, *ab* and *bc* beginning in IV. Setal arrangement *aa:ab:bc:cd:dd* = 7:1:14:1:42. Clitellum in (XIV) ½ XV-XXVI, saddle-shaped (Fig. 12A). Genital markings in in V-IX, intraclitellar in XVI, XIX and XXIV (*ab* position). Tubercula pubertatis linear in XXI-XXVII (Fig. 12B). Male pores not recognised, and ovipores not visible. Spermathecal pores invisible. Nephridial pores begining in II, in *CD* line.

Internal anatomy (Fig. 12C-E)

Septa: membranous. Gizzard: muscular and well developed in VI, but displaced to X, XI and XII, with an average size (width × length) of 4.27 × 5.40 mm. Calciferous glands: eight pairs in VII-XIV, yellow bean-shaped with a brown round distal appendix, and composite tubular structure (Fig. 12E). Esophagus-intestine transition in XVII; intestine without caeca. Typhlosole absent. Hearts: six pairs, the two intestinal pairs in X-XI well developed and enclosed in the testes sacs. Excretory apparatus holoic, nephridia with simple nephrostome. Testes sacs: periesophageal in X and XI, but sac enclosing calciferous glands, heart and seminal vesicles. Seminal vesicles: two pairs in XI and XII-XVI, lobulated (Fig. 12E). Spermathecae: four pairs, VI, VII, VIII and IX, without diverticula (Fig. 12D).

Remarks

Martiodrilus (*M.*) *luminescens* Decaëns & Bartz, n. sp. belongs to the subgenus *Maipure* due to the presence of four pairs of spermathecae. It is related to other species sharing a clitellum in XV-XXVI, such as *Martiodrilus* (*Maipure*) *micrurus* Cognetti de Martiis, 1904, *Martiodrilus* (*Maipure*) *potarensis* Rosa, 1895, *Martiodrilus* (*Maipure*) *ophioides* (Cognetti de Martiis, 1904) and *Martiodrilus* (*Maipure*) *rigeophilus* Cognetti de Martiis, 1904. It differs from the first two species in the position of the tubercula pubertatis in XXI-XXVII instead of ½ XX-½ XXV in *M.* (*M.*) *Micrurus*, XXI-XXVI in *M.* (*M.*) *potarensis*, XX-XXVI in *M.* (*M.*) *ophioides* and XX-½ XXVI in *M.* (*M.*) *rigeophilus*. *Martiodrilus* (*M.*) *luminescens* Decaëns & Bartz, n. sp. is also significantly smaller than *M.* (*M.*) *potarensis* (109-170 mm instead of 380 mm), and larger than *M.* (*M.*) *rigeophilus* and *M.* (*M.*) *ophioides* which have body sizes ranging from 70 to 80 mm and from 100 to 120 mm, respectively. Furthermore, both of these two last species are known from high-altitude montane ecosystems (above 4000 and 2500 m a.s.l., respectively) which are quite different from the type habitat in which *M.* (*M.*) *luminescens* Decaëns & Bartz, n. sp. was found. This species corresponds to OTU#082 in Maggia *et al.* (2021).

Martiodrilus* (*Maipure*) *mitaraka
Decaëns & Bartz, n. sp.
(Fig. 13)

urn:lsid:zoobank.org:act:DC414303-8A7E-4399-8E0B-F8048B5490FC

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, slope forest on trail to Sommet en Cloche Inselberg, in the soil; 2°14’6”N, 54°27’11”W; 352 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0360; MNHN.

Paratypes. **French Guiana** • 9 adult specimens; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14’2”N, 54°27’1”W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0173, EW-MI15-0178, EW-MI15-0179, EW-MI15-0196, EW-MI15-0361, EW-MI15-0365, EW-MI15-0366, EW-MI15-0367, EW-MI15-0180; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project C trail; 2°13’58”N, 54°26’38”W; 449 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0297; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project C trail; 2°14’5”N, 54°26’42”W; 377 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0369; CEFE • 2 adult specimens; Tumuc-Humac, Mitaraka Massif, transition forest # 1 Sommet en Cloche Inselberg; 2°13’54”N,

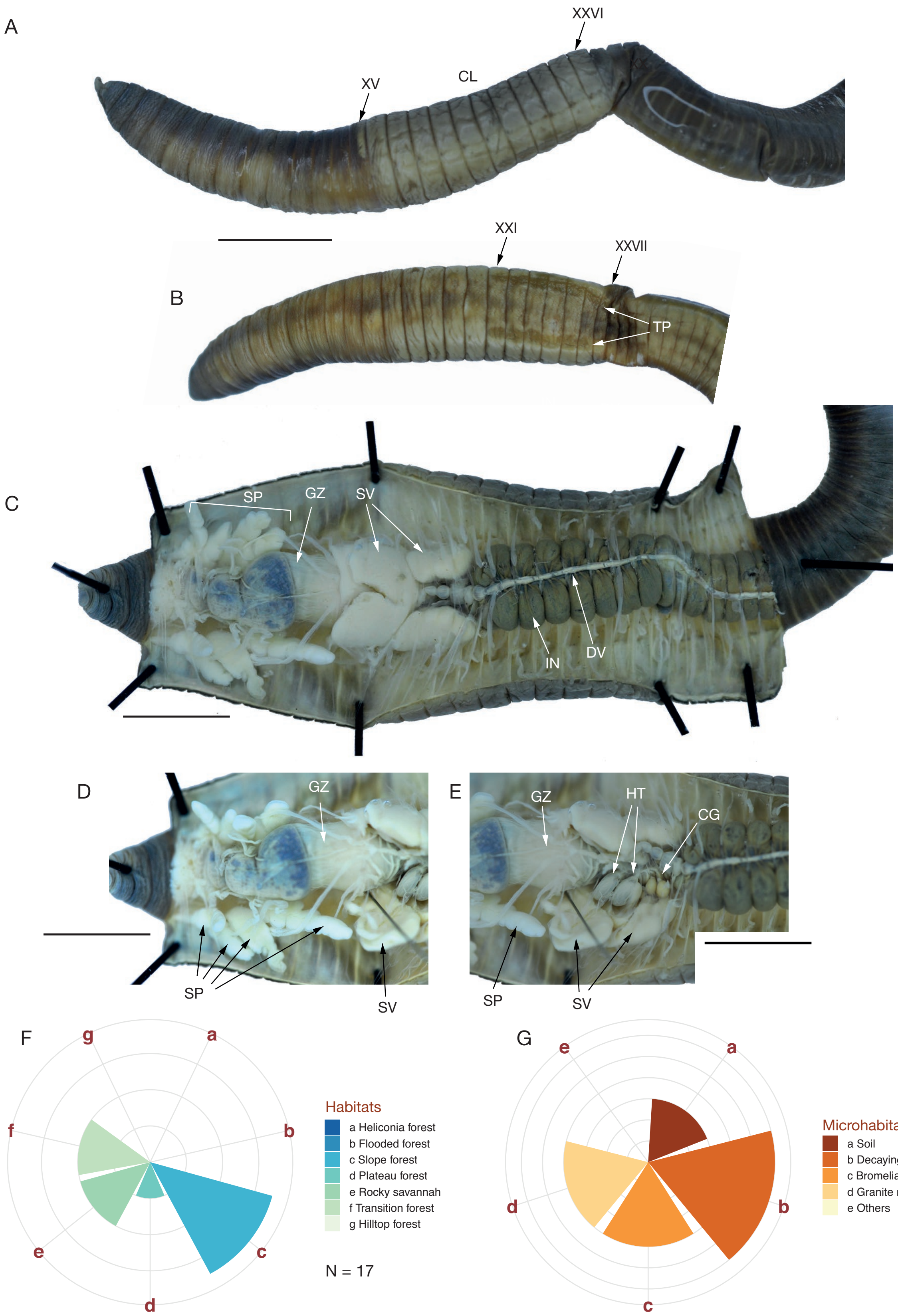

Fig. 12. — *Martiodrilus (Maipure) luminescens* Decaëns & Bartz n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the position of the tubercula pubertatis); **C**, dorsal dissection showing anterior internal anatomy; **D**, detail of the anterior part of the dorsal dissection showing the spermathecae; **E**, detail of the dorsal dissection showing the seminal vesicle and the calciferous glands; **F**, habitat preferences; **G**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **CG**, calciferous glands; **DV**, dorsal vessel; **GZ**, gizzard; **HT**, intestinal hearts; **IN**, intestine; **SP**, spermathecae; **SV**, seminal vesicles; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset. Scale bars: 10 mm.

54°27'39"W; 401 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0335, EW-MI15-0334; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, tropical rainforest on crowned mountain; unknown; unknown; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0128; MNHN.

Other material examined. — **French Guiana** • 1 cocoon; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0371; MNHN • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project C trail; 2°13'58"N, 54°26'38"W; 449 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0293; MNHN • 3 juvenile specimens; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project A trail; 2°14'16"N, 54°27'7"W; 344 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0210, EW-MI15-0211, EW-MI15-0212; MNHN • 3 juvenile specimens, 1 cocoon; Tumuc-Humac, Mitaraka Massif, transition forest # 1 Sommet en Cloche Inselberg; 2°13'54"N, 54°27'39"W; 401 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW- EW-MI15-0333, EW-MI15-0341, MI15-0350, EW-MI15-0377; MNHN • 2 juvenile specimens; Tumuc-Humac, Mitaraka Massif, tropical rainforest on crowned mountain; NA/NA; NA m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0130, EW-MI15-0131; MNHN.

Etymology. — This species is named in reference to the Mitaraka Massif where the type material has been collected.

Ecology. — *Martiodrilus* (*M.*) *mitaraka* Decaëns & Bartz, n. sp. has been found mostly in plateau forests (61.54% of specimens) and in inselberg transition forests (23.08%) (Fig. 13E). Most specimens were collected in the organo-mineral soil (61.54%) and to a lower extent in litter accumulation on granit rocks (19.23%) and in decaying trunks (19.23%) (Fig. 13F). Cocoons are tan yellow, spherical, 7-10 mm in diameter, with two mucrons at the anterior and posterior ends.

Distribution. — *Martiodrilus* (*M.*) *mitaraka* Decaëns & Bartz, n. sp. is only known from the Mitaraka Massif.

Description

External morphology (Fig. 13A, B, D)

Body shape cylindrical, slightly flattened after clitellum. Body pigmentation dorsally red-brown, ventrally light brown. Body length: 130 mm in the holotype, 100 to 140 mm in the paratypes (average: 116.7 mm; n = 3), after ethanol fixation. Body mass: 2.13 g after ethanol fixation in the holotype, 1.59 to 2.04 g in the paratypes (average: 1.74 g; n = 3). Diameter: 5 to 6.7 mm in the preclitellar region, 6.5 to 7.6 mm in the clitellum, 5.9 to 6 mm in the postclitellar region. Number of segments: 173 in the holotype, 107 to 167 in the paratypes (average: 137; n = 3). Prostomium proepilobic. One pair of longitudinal grooves going anterior to posterior through segment I in line of nephridial pores (Fig. 13D). Setae closely paired, *ab* beginning in II, *cd* in III or IV. Setal arrangement *aa:ab:bc:cd:dd* = 7:1:9:1:25. Clitellum in (dorsal ½ XIII, XIV) XV (XVI)-XXV, saddle-shaped to annular (Fig. 13A). Genital markings variable in V-VIII and in X, intraclitellar in XV and XXIII (*ab* position). Tubercula pubertatis linear in (XIX) XX-(XXV) XXVI (Fig. 13B). Male pores not recognised, and ovipores in XIV, pre-clitellar diagonally to *b*. Spermathecal pores in 4/5, 5/6, 6/7 and 7/8. Nephridial pores begining in II, in *CD* line.

Internal anatomy (Fig. 13C)

Septa: membranous, slightly thickened in 6/7 to 16/17. Gizzard: muscular and well developed in VI, but displaced to X, XI, with an average size (width × length) of 4.50 × 4.90 mm. Calciferous glands: eight pairs in VII-XIV, the last three pairs two to three times the size of the others; all kidney-shaped with a lobular distal appendix and tubular composite structure. Esophagus-intestine transition in XVIII; intestine without caeca. Typhlosole abruptly begining in XXV/XXVII, structured as a long thin folded lamella occupying all the lumen. Hearts: six pairs, the two last intestinal pairs in X-XI well developed and enclosed in the testes sacs. Excretory apparatus holoic, nephridia with simple nephrostome. Testes sacs: periesophageal in X and XI. Seminal vesicles: two pairs in XI-XII; first pair enclosed in septa with hearts, calciferous glands and testes sacs in X, and forming a wing extending anteriously up to IX; the second pair going until XV/XVI. Spermathecae: four pairs, V, VI, VII, VIII; without diverticula.

Remarks

M. (*M.*) *mitaraka* Decaëns & Bartz, n. sp. belongs to the subgenus *Maipure* due to the presence of four pairs of spermathecae. It is similar to the species of this subgenus whose clitellum is in XV-XXV: *Martiodrilus* (*Maipure*) *ecuadoriensis* (Benham, 1892), *Martiodrilus* (*Maipure*) *palmirus* Zicsi & Feijoo,1994, and *M.* (*M.*) *ophioides*. It also shares with the latter the position of the tubercula pubertatis in XX-XXVI. It differs from these three species, however, in the position of spermathecal pores in 4/5-7/8, instead of in this species 5/6-8/9 in the others. This species corresponds to OTU#081 in Maggia *et al.* (2021).

***Martiodrilus* (*Maipure*) *alexi* Bartz & Decaëns, n. sp. (Fig. 14)**

urn:lsid:zoobank.org:act:6E1A80C3-5EA9-4309-8D46-65175597C61B

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp, in the soil; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0284; MNHN.
Paratypes. **French Guiana** • 2 adult specimens; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0181, EW-MI15-0195; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, tropical rainforest on DIADEMA project C trail; 2°14'4"N, 54°26'54"W; 323 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0364; MNHN.

Etymology. — This species is dedicated to our late friend and colleague Alexander Feijoo-Martínez, who passed away prematurely in December 2023. Alex was a great specialist in Neotropical earthworm taxonomy, and was particularly interested in the genus *Martiodrilus*, to which the species we are dedicating to him belongs.

Ecology. — *Martiodrilus* (*M.*) *alexi* Bartz & Decaëns, n. sp. has been found essentially in the organo-mineral soil of plateau forest ecosystems (Fig. 14D, E).

Distribution. — *Martiodrilus* (*M.*) *alexi* Bartz & Decaëns, n. sp. is only known from the Mitaraka Massif.

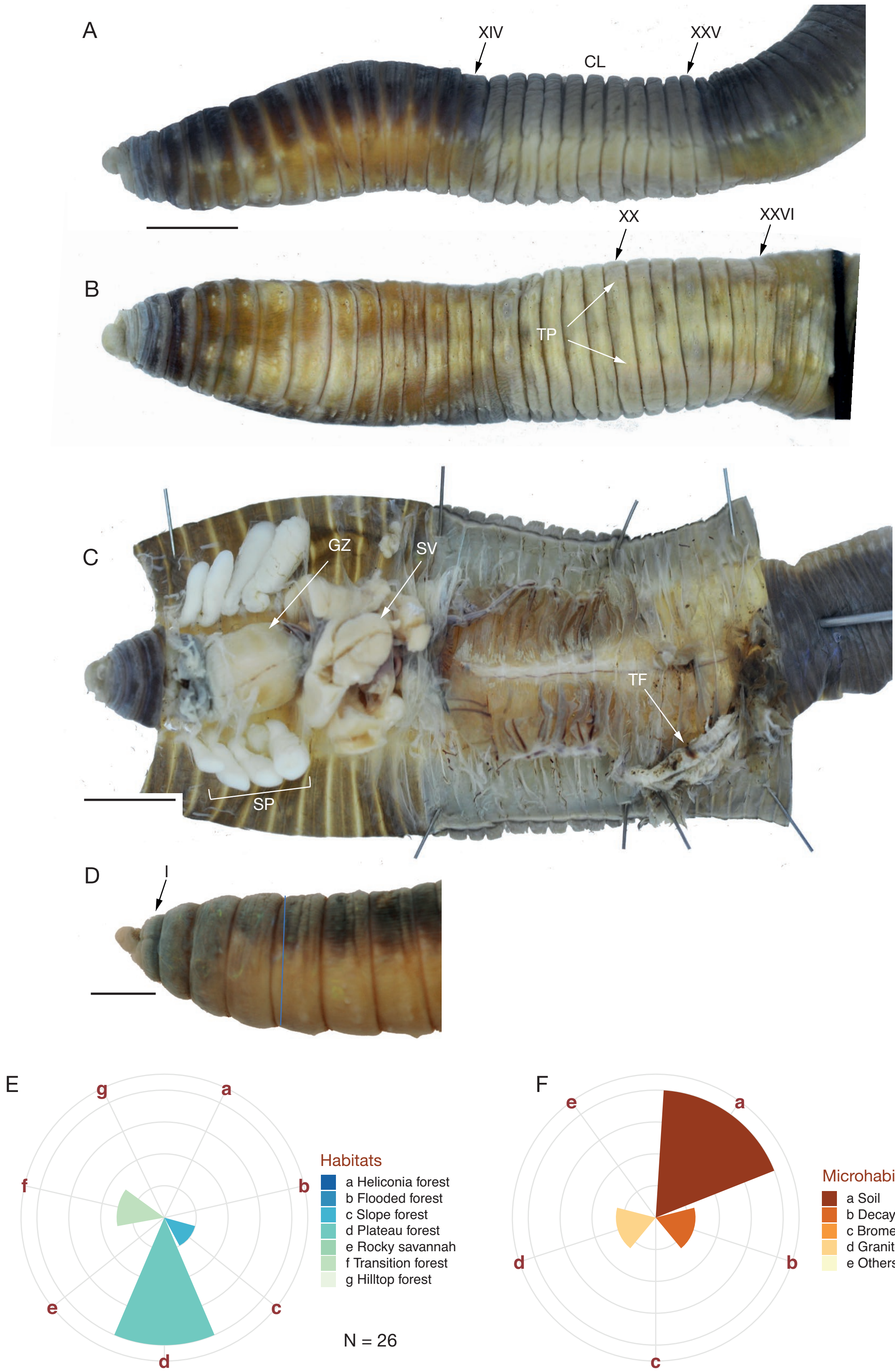

Fig. 13. — *Martiodrilus* (*Maipure*) *mitaraka* Decaëns & Bartz n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the position of the tubercula pubertatis); **C**, dorsal dissection showing anterior internal anatomy; **D**, detail of anterior segments (external lateral view); **E**, habitat preferences; **F**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **GZ**, gizzard; **SP**, spermathecae; **SV**, seminal vesicles; **TF**, tiphlosole; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset. Scale bars: A-C, 5 mm; D, 2.5 mm.

Description

External morphology (Fig. 14A, B)
Body shape cylindrical, slightly flattened after clitellum. Body pigmentation dorsally beige to brown, with antero-posterior gradient, ventrally beige. Body length: 225 mm in the holotype, 170 to 197 mm in the paratypes (average: 183.5; n = 2), after ethanol fixation. Body mass: 6.67 g after ethanol fixation in the holotype, 4.63 to 6.38 g in the paratypes (average: 5.5; n = 2). Diameter: 7.5 to 8 mm in the preclitellar region, 9.5 to 10.2 mm in the clitellum, 7.7 to 8.8 mm in the postclitellar region. Number of segments: 139 in the holotype, 149 to 164 in the paratypes (average: 156.5; n = 2). Prostomium proepilobic. Setae closely paired, beginning in II. Setal arrangement *aa:ab:bc:cd:dd* = 5:1:10:1:28. Clitellum in ⅟nXIV-XXV (⅓XXVI), saddle-shaped (Fig. 14A). Genital markings variable in V-XIII, intraclitellar in XIV, XVII-XXI in *ab*. Tubercula pubertatis linear in XX-XXVI (Fig. 14B). Male pores not recognised externally, internally open in 20/21, and ovipores not visible. Spermathecal pores in 4/5, 5/6, 6/7 and 7/8. Nephridial pores begining in II, in *D* line.

Internal anatomy (Fig. 14C)
Septa: thickened in 9/10 to 14/15, otherwise membranous. Gizzard: muscular and well developed in VI, displaced to X-XI, with an average size (width × length) of 6.37 × 7.40 mm. Calciferous glands: eight pairs in VII-XIV, with XII, XIII and XIV twice larger than the others; gland in VII-IX with kidney shape, otherwise globular to pear-shaped; all with lobular distal appendix and composite tubular structure. Esophagus-intestine transition in XVII/XVIII; intestine without caeca. Typhlosole abruptly begining in XXV/XXVIII, structured as a long thin folded lamella occupying all the lumen. Hearts: five pairs in VII-XI, the two intestinal pairs in X-XI larger and enclosed in testes sacs. Excretory apparatus holoic, nephridia with simple nephrostome. Testes: periesophageal in X and XI, enclosing seminal vesicles, hearts and calciferous glands. Seminal vesicles: two pairs in XI-XII; the first pair extending to X and lobulated in XI; the second pair lobulated extending to XV without perforating septa. Spermathecae: four pairs in V, VI, VII and VIII; elongated with edge lobulated.

Remarks

Martiodrilus (*M.*) *alexi* Bartz & Decaëns, n. sp. belongs to the subgenus *Maipure* due to the presence of four pairs of spermathecae. It is quite similar to *M.* (*M.*) *luminescens* Decaëns & Bartz, n. sp. and *M.* (*M.*) *mitaraka* Decaëns & Bartz, n. sp. regarding the position of clitellum and tubercula pubertatis (Table 4). It can however be separated from *M.* (*M.*) *luminescens* Decaëns & Bartz, n. sp. by the position of spermathecae (in V-VIII instead of VI-IX), the position of the tubercula pubertatis of one segment more anterior (XX-XXVI instead of XXI-XXVII), and its slightly larger body size (170 to 225 mm instead of 109 to 170 mm). It further differs from *M.* (*M.*) *mitaraka* Decaëns & Bartz, n. sp. by its larger size (*M.* (*M.*) *mitaraka* Decaëns & Bartz, n. sp. ranging from 100 to 130 mm), its lighter pigmentation, by the presence of thickened septa in 9/10 to 14/15 and the absence of distal appendix in calciferous glands. The three species are clearly separated by their DNA barcodes. *Martiodrilus* (*M.*) *alexi* Bartz & Decaëns, n. sp. is also similar to *M.* (*M.*) *ophioides* which may also have a clitellum in XIV-XXV and has tubercula pubertatis in XX-XXVI. *Martiodrilus* (*M.*) *alexi* Bartz & Decaëns, n. sp. is however much larger in body size than this species (which ranges from 100 to 120 mm), from which it also differs in the position of the spermathecal pores in 4/5-7/8 instead of 5/6-8/9. Furtheremore, *M.* (*M.*) *alexi* Bartz & Decaëns, n. sp. occurs in a radically different habitat from the Andean forests from which *M.* (*M.*) *ophioides* is known. This species corresponds to OTU#085 in Maggia *et al.* (2021).

Genus *Urobenus* Benham, 1886

Urobenus Benham, 1886: 82; 1890: 255. — Beddard 1895: 661. — Righi 1985: 247.

Anteus – Rosa 1896: 90.

Rhinodrilus – Michaelsen 1900: 430, 1918: 165. — Stephenson 1930: 894. — Cordero 1945: 8. — Righi 1971: 10. — Jamieson 1971: 738.

Rhinodrilus (*Rhinodrilus*) – Cognetti de Martiis 1906: 174.

Type species. — *Urobenus brasiliensis* Benham, 1886.

Diagnosis. — Setae arranged in eight regular longitudinal lines. One pair of intra-clitellar male pores. Gizzard in VI. Three pairs of calciferous glands in VII-IX, those of VII and VIII wholly or mostly of tubular-paniculated structure, those of IX saccular, with thin wall and wide cavity endowed with irregular and sparse folds. Hearts in VII-XI. Genital apparatus holandric and metagynous. Seminal vesicles short. spermathecae in pre-testicular segments. Ovaries in XIII (Righi 1985).

Distribution. — *Urobenus* comprises seven valid species (not including the new species described here) distributed in Brazil (6 species) and Venezuela (one species), with *Urobenus brasiliensis* (Benham, 1886) also reported from Paraguay (http://taxo.drilobase.org/; Righi 1985; Misirlioğlu *et al.* 2023; Brown *et al.* 2023).

Urobenus guianomeridionalis Bartz & Decaëns, n. sp. (Fig. 15)

urn:lsid:zoobank.org:act:5582A14C-A215-41DD-9F1B-10D090EEB1B9

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project C trail, in decaying trunk; 2°14'5"N, 54°26'42"W; 377 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0078; MNHN.
Paratypes. French Guiana • 2 adult specimens; Tumuc-Humac, Mitaraka Massif, hilltop forest on Borne 1 Inselberg; 2°12'35"N, 54°26'12"W; 600 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0218, EW-MI15-0219; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, hilltop forest on Sommet en Cloche Inselberg; 2°13'42"N, 54°28'2"W; 638 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0106; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project A trail; 2°14'38"N,

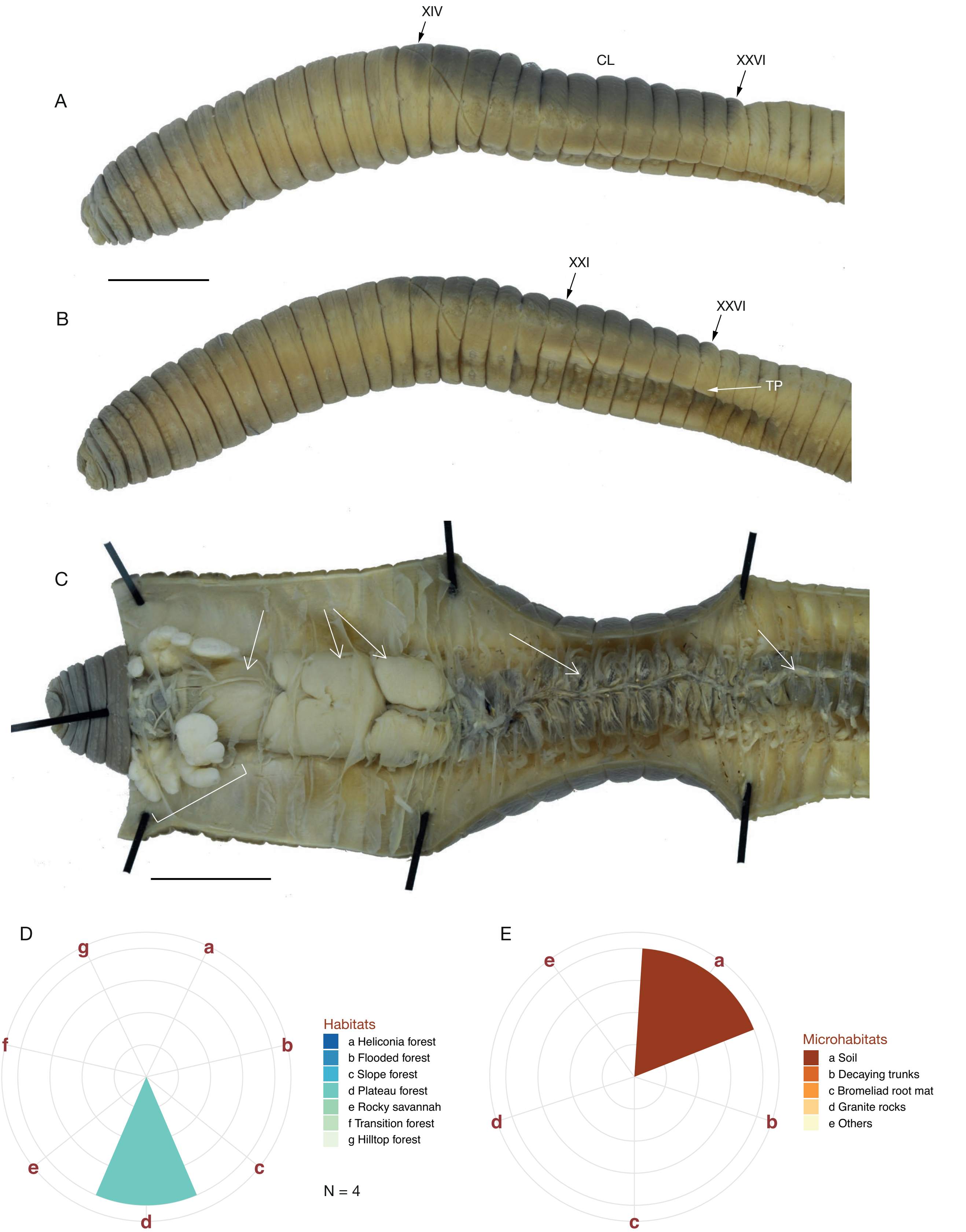

Fig. 14. — *Martiodrilus* (*Maipure*) *alexi* Bartz & Decaëns n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the position of the tubercula pubertatis); **C**, dorsal dissection showing anterior internal anatomy; **D**, habitat preferences; **E**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **DV**, dorsal vessel; **GZ**, gizzard; **IN**, intestine; **SP**, spermathecae; **SV**, seminal vesicles; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset.

54°27'32"W; 371 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0084; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project D trail; 2°12'57"N, 54°27'25"W; 381 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0019; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project D trail; 2°13'40"N, 54°27'14"W; 339 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0262; MNHN.

OTHER MATERIAL EXAMINED. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, hilltop forest on Sommet en Cloche Inselberg; 2°13'42"N, 54°28'2"W; 638 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0107; MNHN • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project A trail; 2°14'38"N, 54°27'32"W; 371 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0087; MNHN • 2 juvenile specimens; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project C trail; 2°13'58"N, 54°26'38"W; 449 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0301, EW-MI15-0302; MNHN • 2 juvenile specimens; Tumuc-Humac, Mitaraka Massif, transition forest # 1 Sommet en Cloche Inselberg; 2°13'54"N, 54°27'39"W; 401 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0342, EW-MI15-0343; MNHN.

ETYMOLOGY. — This species is named in reference to the type locality situated in the south of French Guiana.

ECOLOGY. — *Urobenus guianomeridionalis* Bartz & Decaëns, n. sp. has been found in plateau forests (38.46% of specimens), in inselberg hilltop and transition forests (46.15% of specimens), and in slope forests (15.38% of specimens) (Fig. 15D). It is a specialist of epigeic microhabitats such as decaying trunks and litter accumulations on granite rocks (Fig. 15G).

DISTRIBUTION. — *Urobenus guianomeridionalis* Bartz & Decaëns, n. sp. is only known from the Mitaraka Massif.

DESCRIPTION

External morphology (Fig. 15A, B)

Body shape cylindrical. Body pigmentation dorsally dark grey, ventrally beige to yellow. Body length: 35 mm in the holotype, 35 to 41 mm in the paratypes (average: 37.1 mm; n = 3), after ethanol fixation. Body mass: 0.11 g after ethanol fixation in the holotype, 0.10 to 0.14 g in the paratypes (average: 0.11 g; n = 3). Diameter: 1.2 to 2.8 mm in the preclitellar region, 3.4 to 4 mm in the clitellum, 2.7 to 3 mm in the postclitellar region. Number of segments: 87 in the holotype, 96 to 113 in the paratypes (average: 98.7; n = 3). Prostomium proepilobic. One pair of longitudinal grooves through segments I-II in line of nephridial pores. Setae closely paired, *ab* beginning in II and *cd* in III. Setal arrangement *aa:ab:bc:cd:dd* = 3:1:4:1:13. Clitellum in XV-XXIV, saddle-shaped (Fig. 15A). Genital markings absent. Tubercula pubertatis linear in ¼XIX (½XIX)-XXIII (Fig. 15B). Male pores not recognised externally, internally open in 19/20, and ovipores in XIV, almost in the border of 13/14, in diagonal to *b*. Spermathecal pores in 6/7, 7/8 and 8/9. Nephridial pores begining in II.

Internal anatomy (Fig. 15C)

Septa: membranous. Gizzard: muscular and well developed in VI, with an average size (width × length) of 1.87 × 2.07 mm. Calciferous glands: three pairs in VII-IX, of tubular paniculated structure and bean-shaped without appendix in VII-VIII, and sacs/trabecular and slightly curved oval shape in IX. Esophagus-intestine transition in XVII; intestine without caeca. Typhlosole abruptly begining in XXIII/XXV, laminar, long-folded lamella, occupying all the lumen. Hearts: two pairs of large intestinal hearts in X-XI, enclosed in the testes sacs. Excretory apparatus holoic. Testes sacs: in X and XI. Seminal vesicles: two pairs in XI-XII, small and lobulated, occupying only one segment; the pair in XI enclosed in septum and testes sac and the pair in XII free and slightly larger. Spermathecae: three pairs in VII to IX, small elongated without diverticula.

REMARKS

Urobenus guianomeridionalis Bartz & Decaëns, n. sp. is close to *Urobenus brevis* (Omodeo, 1955) and *U. brasiliensis* in the position of the clitellum in XV-XXIV (Benham 1886; Omodeo 1955). It differs mainly from the two species in its much smaller size (35 to 41 mm in length and 1.2 to 2.8 mm in anterior diameter, compared to 90 mm and 8 mm in *U. brevis*, respectively), the setal ratio (3:1:4:1:13, compared to 9:1:10:1:38 in *U. brevis*) and spermathecae lacking seminal chambers in *U. guianomeridionalis* Bartz & Decaëns, n. sp. (Righi 1985). This species corresponds to OTU#052 in Maggia *et al.* (2021).

Genus *Atatina* Righi, 1971

Atatina Righi, 1971: 34.

TYPE SPECIES. — *Atatina puba* Righi, 1971.

DIAGNOSIS. — Setae arranged in eight regular longitudinal lines. One pair of intra-clitellar male pores. Gizzard in VI. Four to five pairs of calciferous glands in segments IX-XIV, of trabecular structure, sacculiform and opening widely into the esophagus. Genital apparatus metandric and metagynous. Seminal vesicles long, extended posteriously across many segments. spermathecae in pre-testicular segments. Ovaries in XIII (Righi 1971; Righi *et al.* 1978).

DISTRIBUTION. — *Atatina* comprises two species from Brazil (not including the species described here) (http://taxo.drilobase.org/; Misirlioğlu *et al.* 2023; Brown *et al.* 2023).

Atatina albida Bartz & Decaëns, n. sp.
(Fig. 16)

urn:lsid:zoobank.org:act:A7BC66DF-5196-4FC2-9D83-3029CDEF9D45

TYPE MATERIAL. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project D trail, in decaying trunk; 2°13'40"N, 54°27'14"W; 339 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0271; MNHN.
Paratypes. French Guiana • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, *Heliconia* forest near plateau forest at base camp; 2°13'50"N, 54°26'57"W; 351 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0052; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project C trail; 2°14'16"N, 54°26'56"W; 310 m a.s.l.; III.2015;

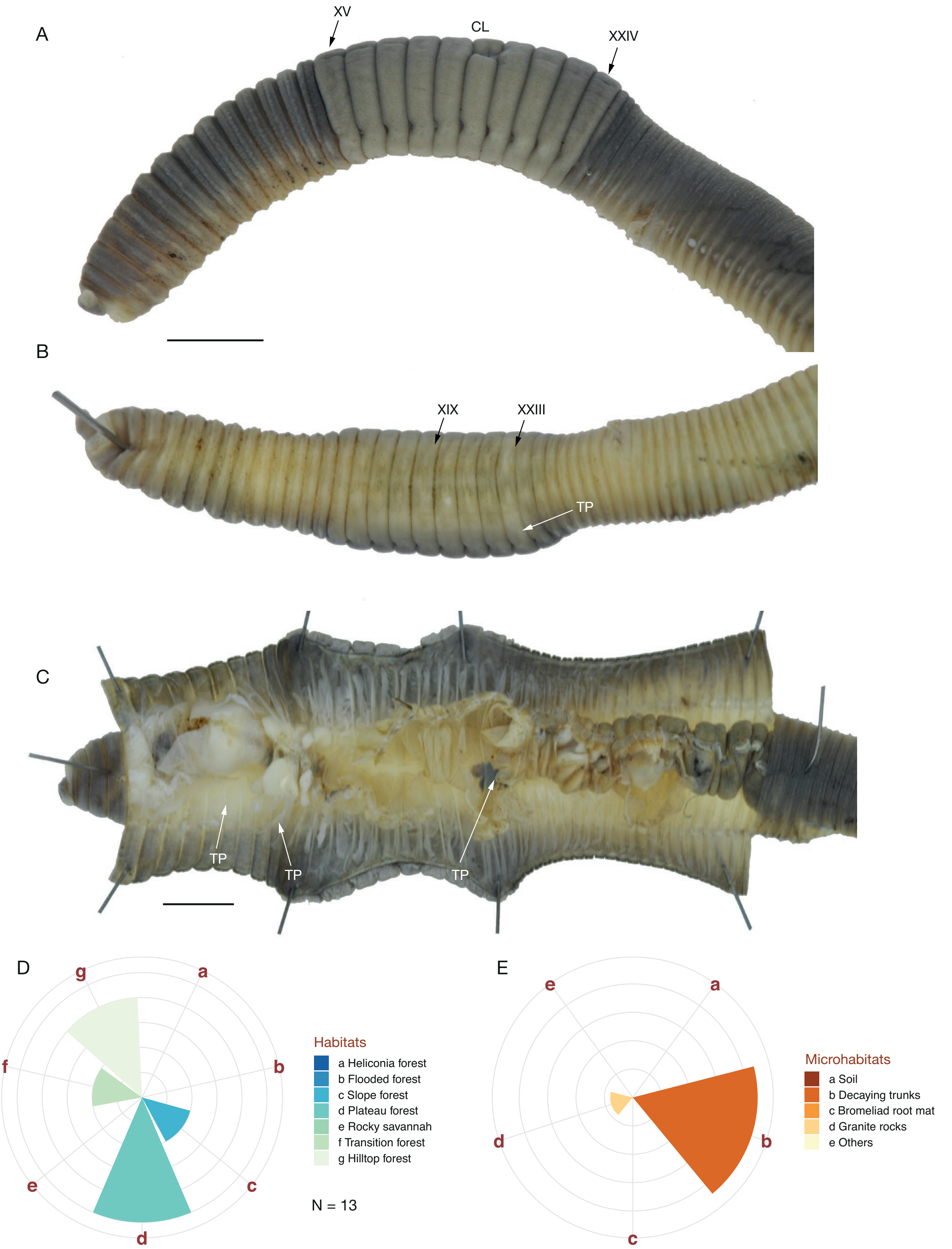

Fig. 15. — *Urobenus guianomeridionalis* Bartz & Decaëns n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the position of the tubercula pubertatis); **C**, dorsal dissection showing anterior internal anatomy; **D**, habitat preferences; **E**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **GZ**, gizzard; **SP**, spermathecae; **SV**, seminal vesicles; **TF**, typhlosole; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset. Scale bars: 2.5 mm.

T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0226; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project D trail; 2°13'58"N, 54°27'7"W; 318 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0306; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0368; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project D trail; 2°13'40"N, 54°27'14"W; 339 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0270; MNHN • 5 adult specimens; Tumuc-Humac, Mitaraka Massif, transition forest # 2 Sommet en Cloche Inselberg; 2°13'59"N, 54°27'34"W; 395 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0121, EW-MI15-0122, EW-MI15-0123, EW-MI15-0124, EW-MI15-0125; MNHN.

OTHER MATERIAL EXAMINED. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, transition forest # 2 Sommet en Cloche Inselberg; 2°13'59"N, 54°27'34"W; 395 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg. (1 specimens); BOLD Sample ID: EW-MI15-0126; MNHN.

ETYMOLOGY. — This species is named after its lack of pigmentation.

ECOLOGY. — *Atatina albida* Bartz & Decaëns, n. sp. has been found in a range of ecosystems including lowland, slope, plateau, transition and *Heliconia* forests (Fig. 16D). It has been observed in the organo-mineral soil (75% of specimens) and in decaying trunks (25% of specimens) (Fig. 16G).

DISTRIBUTION. — *Atatina albida* Bartz & Decaëns, n. sp. is only known from the Mitaraka Massif.

DESCRIPTION

External morphology (Fig. 16A, B)

Body shape cylindrical. Body pigmentation absent. Body length: 25 mm in the holotype, 24 to 41 mm in the paratypes (average: 31.3 mm; n = 3), after ethanol fixation. Body mass: 0.07 mm after ethanol fixation in the holotype, 0.06 to 0.15 g in the paratypes (average: 0.11 g; n = 3). Diameter: 1.5 to 2.0 mm in the preclitellar region, 1.5 to 2.1 mm in the clitellum, 1.5 to 2.4 mm in the postclitellar region. Number of segments: 167 in the holotype, 119 to 299 in the paratypes (average: 194; n = 3). Prostomium proepilobic. One pair of longitudinal grooves passing through segments I-II in line of nephridial pores. Setae widely paired. Setal arrangement *aa:ab:bc:cd:dd* = 2:1:3:1:12. Clitellum in XV-XXIV, saddle-shaped (Fig. 16A). Genital markings observed in some specimens in VII to VIII (*ab* position). Tubercula pubertatis linear XVII-XXIV (Fig. 16B). Male pores, ovipores, and spermathecal pores not recognised. Nephridial pores begining in XIV in *CD* line.

Internal anatomy (Fig. 16C)

Septa: slightly thickened in 6/7 to 9/10, otherwise membranous. Gizzard: muscular and well developed in VI, with an average size (width × length) of 1.30 × 1.03 mm. Calciferous glands: four pairs forming simple expansions of the esophageal walls in IX-XII, apparently of glandular structure but not isolated from the gut lumen by having a distinct connecting duct. Esophagus-intestine transition in XVIII. Typhlosole begining in XXII, small folded lamella. Hearts: last two intestinal pairs in IX and X. Excretory apparatus holoic. Testes: in XI; mid-ventral metandric. Seminal vesicles: one pair in XI, extending posteriously to XXXX-LX. Spermathecae: two pairs in VIII and IX.

REMARKS

Atatina albida Bartz & Decaëns, n. sp. differs from *Atatina gatesi* (Righi & Ayres, 1978) and *Atatina puba* (Righi, 1971), the only other known species in the genus, in the position of the clitellum and tubercula pubertatis, as well as in the presence of two pairs of spemathecae instead of one in these two relatives (Righi 1971; Righi *et al.* 1978). It shares with *A. gatesi* the presence of four pairs of calciferous glands, but their position is different (at IX-XII in *A. albida* Bartz & Decaëns, n. sp. vs. XI-XIV in *A. gatesi*). It also shares with *A. puba* the presence of a single pair of seminal vesicles in XI. This species corresponds to OTU#074 in Maggia *et al.* (2021).

Family BENHAMIIDAE Michaelsen, 1897

Genus *Neogaster* Cernosvitov, 1934

Neogaster Cernosvitov, 1934: 51. — Righi & Caballero 1970: 94. — Righi 1988: 351.

TYPE SPECIES. — *Neogaster americanus* Cernosvitov, 1934.

DIAGNOSIS. — Setae arranged in eight regular longitudinal lines. Clitellum extending from segments XIII to XX. Weak gizzard in VI. Excretory system meronephric. Two pairs of calciferous glands in XIV-XV, of lamellar type and opening in the esophagus through a common duct. Genital apparatus acanthodriline. Spermathecae in pre-testicular segments, paired and without diverticula (Cernosvitov 1934; Csuzdi 2010).

DISTRIBUTION. — *Neogaster* comprises four Neotropical species (not including the new species described here), all known from the state of Amapá in Brazil (Cernosvitov 1934; Righi & Caballero 1970; Righi 1988; Brown *et al.* 2023).

Neogaster csuzdii Bartz & Decaëns, n. sp.
(Fig. 17)

urn:lsid:zoobank.org:act:E45DE917-168A-44C4-8374-1DAA3D857F34

TYPE MATERIAL. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project A trail, in decaying trunk; 2°14'16"N, 54°27'7"W; 344 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0205; MNHN.

Paratypes. French Guiana • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project D trail; 2°13'58"N, 54°27'7"W; 318 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0304; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, transition forest # 1 Sommet en Cloche Inselberg; 2°13'54"N, 54°27'39"W; 401 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0344; MNHN.

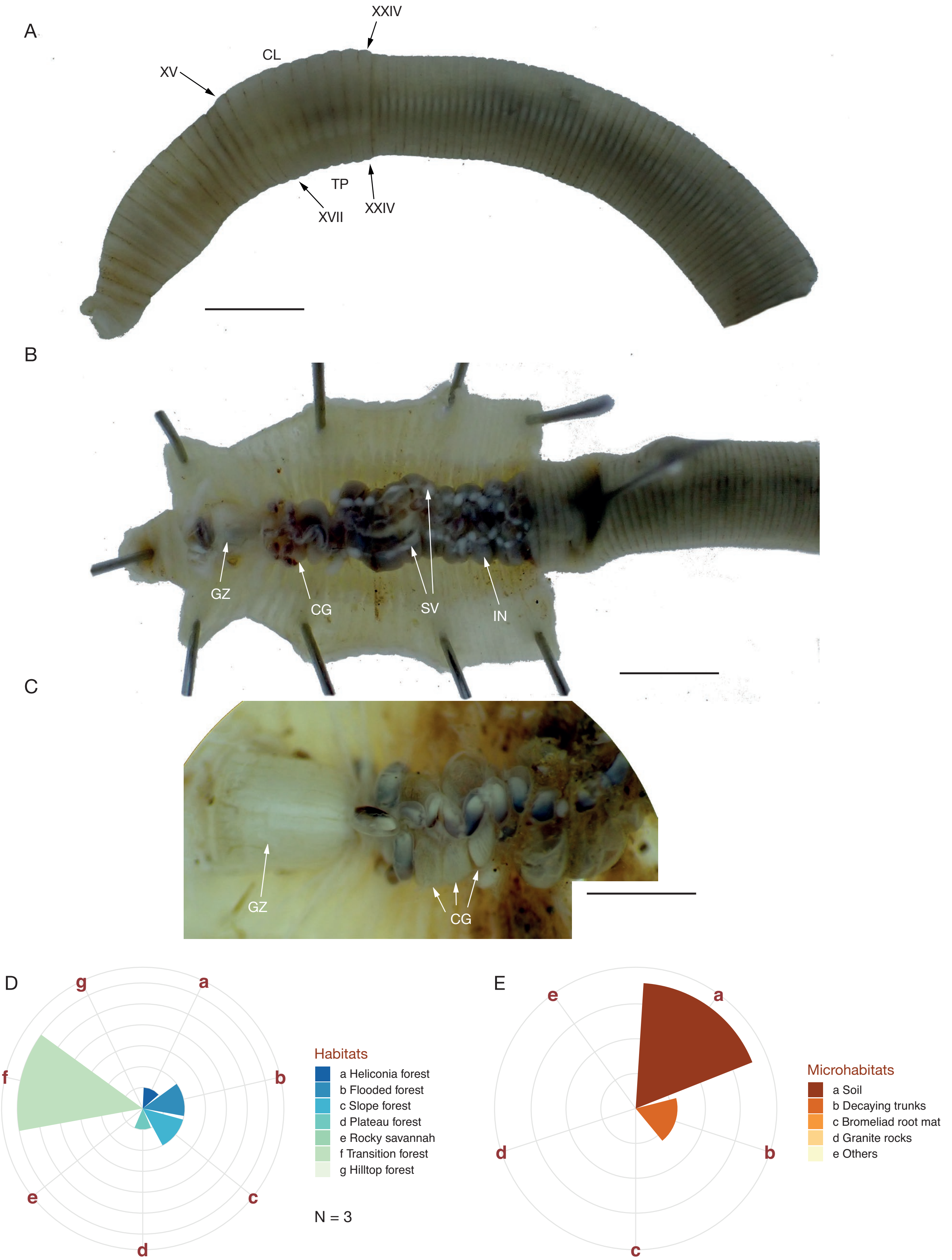

FIG. 16. — *Atatina albida* Bartz & Decaëns n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum and tubercula pubertatis positions); **B**, dorsal dissection showing anterior internal anatomy; **C**, detailed view of the dorsal dissection showing the calciferous glands; **D**, habitat preferences; **E**, microhabitat preferences. All images from the holotype, except **C**, (Paratype EW-MI15-0121); **CG**, calciferous glands; **CL**, clitellum; **GZ**, gizzard; **IN**, intestine; **SV**, seminal vesicles; **TP**, tubercula pubertatis; **N**, total number of specimens in the dataset. Scale bars: A, B, 2 mm; C, 1 mm.

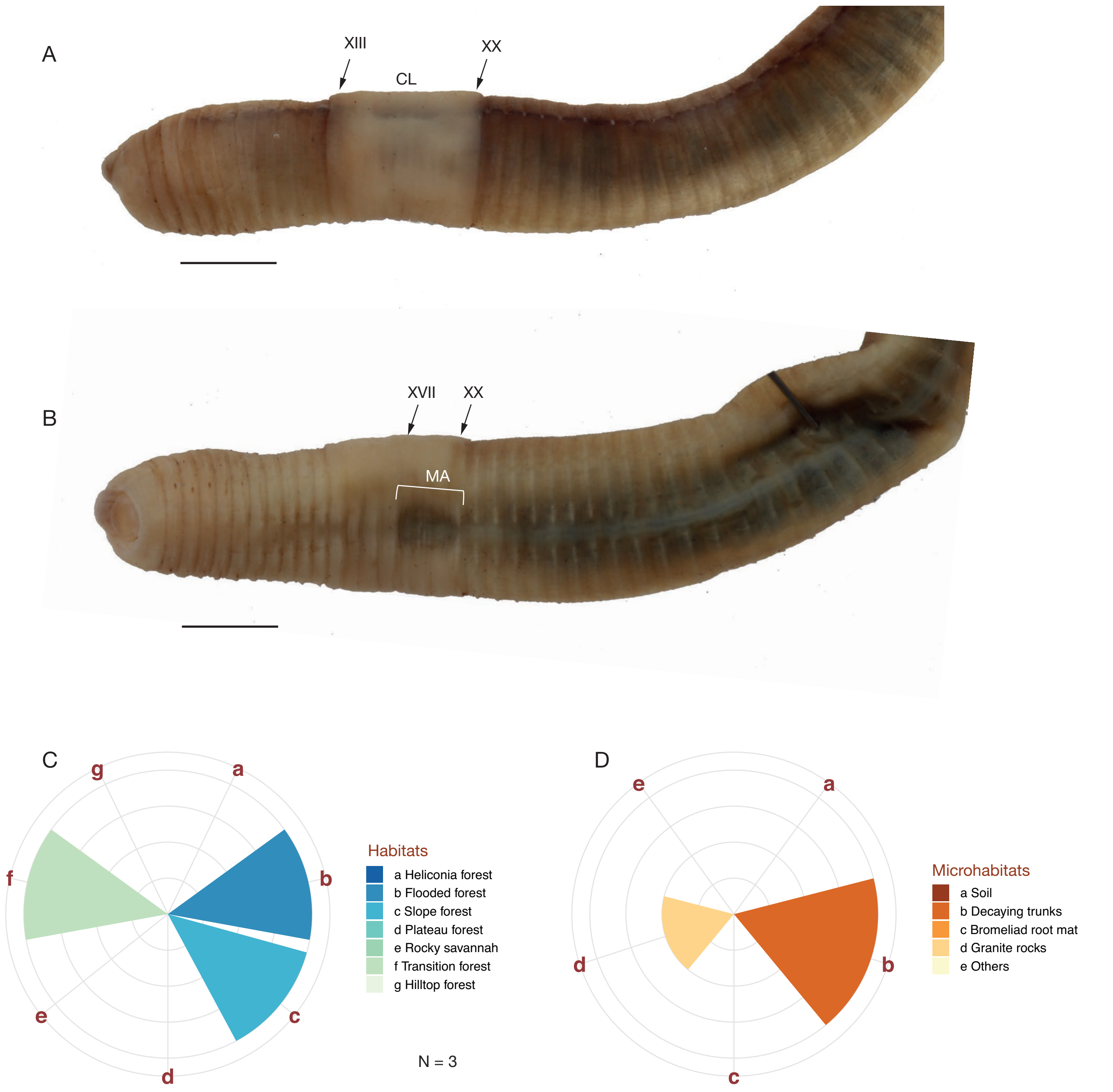

FIG. 17. — *Neogaster csuzdii* Bartz & Decaëns n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the clitellum male field); **C**, habitat preferences; **D**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **MF**, male field; **N**, total number of specimens in the dataset. Scale bars: 1 mm.

ETYMOLOGY. — This species is named in homage to Csaba Csuzdi, in recognition for his involvement in the study of the Benhamiidae family, and his contribution to the description of new earthworm species for French Guiana.

ECOLOGY. — The three known specimens of *N. csuzdii* Bartz & Decaëns, n. sp. have been found in a lowland, a slope and a transition forests (Fig. 17C), two in decaying trunks and one in the litter accumulating on a granite rock (Fig. 17D).

DISTRIBUTION. — *Neogaster csuzdii* Bartz & Decaëns, n. sp. is only known from the Mitaraka Massif.

DESCRIPTION

External morphology (Fig. 17A, B)

Body shape cylindrical, slightly flattened posteriously. Body pigmentation dorsally light yellow-brown, lighter ventrally. Body length: 20 mm in the holotype, 30 mm in one paratype, after ethanol fixation. Body mass: 0.02 g after ethanol fixation in the holotype, 0.04 g in the paratype. Diameter: 1.3 to 1.5 mm in the preclitellar region, 1.4 to 1.9 mm in the clitellum, 1.7 to 1.9 mm in the postclitellar region. Number of segments: 79 in the holotype to 99 in the paratype. Prostomium tanylobic.

Table 4. — Main morpho-anatomical characteristics of the new Rhinodrilidae Benham, 1890 species from the Mitaraka range.

Species	Pigmentation	Size (mm)	Clitellum	*Tubercula pubertatis*	Calciferous glands	Spermathecae	Testes
Andiorrhinus pascalei Bartz & Decaëns, n. sp.	Absent	158 to 196	(dorsal XIII) XIV-XXI (dorsal XXII-XXIII)	$^1/_4$XV-$^3/_4$XX	Three pairs in VII-IX, lamellar structure	Three pairs in VII-IX, very small spatula-shaped	Two pairs of testes and funnels in X -XI
Martiodrilus flavus Decaëns & Bartz, n. sp.	Yellow to grey, clitellum pink	265 to 300	(½ XIII) XIV-½ XXVI	XIX-XXV	Eight pairs in VII-XIV, tubular composite structure	Three pairs in VI-VIII, small elongated	Midventral or hypoesophagic in X-XI
Martiodrilus tchoukouchipan Decaëns & Bartz, n. sp.	Dorsally yellow-brown, ventrally yellow	55 to 75	(dorsal XIV) XV (XVI)- ½ XXV	$^1/_4$XX-$^3/_4$XXV	Eight pairs in VII-XIV, tubular composite structure	Three pairs in VI-VIII, elongated	Periesophageal in X-XI, enclosing SV
Martiodrilus pavliceki Bartz & Decaëns, n. sp.	Dorsally yellow-brown to brown, ventrally beige	95	(dorsal XIV) XV-XXV (dorsal XXVI)	XIX-$^1/_n$XXV	Eight pairs in VII-XIV, tubular composite structure	Three pairs in VII-IX, thin duct terminated by a round and flattened sac	Periesophageal in X-XI, enclosing SV, heart and CG
Martiodrilus lavellei Decaëns & Bartz, n. sp.	Dorsally light brown, ventrally beige	56	(dorsal XV) XVI-XXV	$^1/_4$ XX-½XXV	Eight pairs in VII-XIV, tubular composite structure	Three pairs in VI-VIII, ovoid elongated	Periesophageal in X-XI, enclosing SV, heart and CG
Martiodrilus mitaraka Decaëns & Bartz, n. sp.	Dorsally red-brown, ventrally light brown	100 to 130	(dorsal ½XIII, XIV) XV (XVI)-XXV	(XIX) XX-(XXV) XXVI	Eight pairs in VII-XIV, tubular composite structure	Four pairs in V-VIII, elongated	Periesophageal in X-XI
Martiodrilus luminescens Decaëns & Bartz, n. sp.	Dorsal grey-brown, ventral light brown	109 to 170	(XIV) ½XV-XXVI	XXI-XXVII	Eight pairs in VII-XIV, tubular composite structure	Four pairs in VI-IX, elongated	Periesophageal in X-XI, sacs attached in XIV/XV
Martiodrilus wayana Bartz & Decaëns, n. sp.	Dorsally dark brown, ventrally yellow	55 to 74	(dorsal XIII, XIV) XV-(XXV) XXVI	XX-½XXVI	Eight pairs in VII-XIV, tubular composite structure	Three pairs in VI-VIII, spatula-shaped	Periesophageal in X-XI, enclosing SV
Martiodrilus alexi Bartz & Decaëns, n. sp.	Dorsally beige to brown, ventrally beige	170 to 225	$^1/_n$XIV-XXV ($^1/_3$XXVI)	XX-XXVI	Eight pairs in VII-XIV, tubular composite structure	Four pairs in V-VIII, elongated	Periesophageal in X-XI, enclosing SV, heart and CG
Martiodrilus motoloi Bartz & Decaëns, n. sp.	Dorsally dark red-brown, ventrally light brown	42 to 56	(dorsal XIV) XV-½XXVI	$^1/_3$XX-½XXV	Eight pairs in VII-XIV, tubular composite structure	Three pairs in VI-VIII, elongated	Periesophageal in X-XI, enclosing SV, heart and CG
Urobenus guianomeridionalis Bartz & Decaëns, n. sp.	Dorsally dark grey, ventrally beige to yellow	35 to 41	XV-XXIV	$^1/_4$XIX (½XIX)-XXIII	Three pairs, tubular paniculated structure in VII-VIII and trabecular structure in IX	Three pairs in VII-IX, small elongated	Two pairs in X and XII
Atatina albida Bartz & Decaëns, n. sp.	Absent	25 to 41	XV-XXIV	XVII-XXIV	Four pairs intestinal, intra-mural in IX-XII	Two pairs in VIII and IX	Midventral metandric in XI

Dorsal pores begining in 5/6. Setae closely paired, beginning in II, *ab* ventral and *cd* sub-ventral. Setal arrangement *aa:ab:bc:cd* = 4:2:4:1, *dd* > ½ Ø. Clitellum in XIII-XX, annular. Genital markings: paired papillae in VIII to XII (*bc* position), intraclitellar in XIII to XVI (*ab* position); acanthodriline male field forming an ovoid depression in XVII-XX. A pair of ventral male pores in XVIII, and ovipores not visible. Spermathecal pores not visible. Nephridial pores not visible.

Internal anatomy

Septa: membranous. Gizzard: absent. Calciferous glands: two pairs in XIV and XV, with lamellar structure, kidney-shaped and attached through the middle inside. Esophagus-intestine transition in XVI. Typhlosole absent. Hearts: five pairs, last three intestinal bigger and last pair in XII. Excretory apparatus meronephridial with two pairs of nephridia per segment. Prostatic glands: two pairs in XVII and XIX, elongated lingulate. Ovaries: one pair in XIII. Testes: two pairs of testes sacs in X and XI. Seminal vesicles: one pair in XII, small. Spermathecae: one pair in IX, sac-shaped without diverticulum.

Remarks

Neogaster csuzdii Bartz & Decaëns, n. sp. is closely related to *Neogaster tumuchumac* Decaëns & Bartz, n. sp. with which it shares small body size, the absence of a gizzard and the entirely membranous septa in the anterior part of the body

(Table 5). It is distinguished from all other *Neogaster* by the presence of a single pair of spermathecae in IX, whereas the other species have two (in *N. tumuchumac* Decaëns & Bartz, n. sp.), three (in *Neogaster angeloi* Righi, 1988 and *Neogaster americanus* Cernosvitov, 1934), four (in *Neogaster gavrilovi* Righi & Caballero, 1970) or five (in *Neogaster aidae* Righi, 1975). In *N. csuzdii* Bartz & Decaëns, n. sp., we observed only one pair of seminal vesicles in XII, whereas two pairs are usually present in other species except in *N. aidae* in which no seminal vesicle has been seen (but see remarks on *N. tumuchumac* Decaëns & Bartz, n. sp.). *Neogaster csuzdii* Bartz & Decaëns, n. sp. is smaller than most of the other species (20-30 mm compared to over 40 mm in *N. americanus*, *N. aidae* and *N. gavrilovi*), and differs from the equally small *N. angeloi* by the presence of skin pigmentation, which the latter lacks (Cernosvitov 1934; Righi & Caballero 1970; Righi 1975, 1988). *Neogaster csuzdii* Bartz & Decaëns, n. sp is clearly separated from *N. tumuchumac* Decaëns & Bartz, n. sp. from its COI barcode (Table 3). This species corresponds to OTU#009 in Maggia *et al.* (2021).

Neogaster tumuchumac Decaëns & Bartz, n. sp. (Fig. 18)

urn:lsid:zoobank.org:act:F77F9096-722E-473A-AC3F-7706BD642410

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project C trail, in decaying trunk; 2°14'5"N, 54°26'42"W; 377 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0081; MNHN.
Paratypes. French Guiana • 2 adult specimens; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0280, EW-MI15-0281; CEFE • 2 adult specimens; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project A trail; 2°14'38"N, 54°27'32"W; 371 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0085, EW-MI15-0086; MNHN • 3 adult specimens; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project A trail; 2°14'16"N, 54°27'7"W; 344 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0206, EW-MI15-0207, EW-MI15-0208; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project C trail; 2°14'5"N, 54°26'42"W; 377 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg. (1 specimens); BOLD Sample ID: EW-MI15-0080; MNHN.

Other material examined. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project C trail; 2°13'58"N, 54°26'38"W; 449 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0300; MNHN • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project A trail; 2°14'16"N, 54°27'7"W; 344 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0213; MNHN.

Etymology. — This species is named in reference to the Tumuc Humac mountains to which the Mitaraka Massif belongs to.

Ecology. — *Neogaster tumuchumac* Decaëns & Bartz, n. sp. has been found in decaying trunks in both slope (54.55% of specimens) and plateau forests (45.45% of specimens) (Fig. 18C, D).

Distribution. — *Neogaster tumuchumac* Decaëns & Bartz, n. sp. is only known from the Mitaraka Massif.

Description

External morphology (Fig. 18A, B)
Body shape cylindrical, slightly flattened posteriously. Body pigmentation dorsally light yellow-brown, ventrally lighter. Body length: 12 mm in the holotype, 12 to 17 mm in the paratypes (average: 14.7 mm; n = 3), after ethanol fixation. Body mass: 0.002 g after ethanol fixation in the holotype, 0.002 to 0.008 g in the paratypes (average: 0.006 g; n = 3). Diameter: 1.0 to 1.3 mm in the preclitellar region, 1.0 to 1.1 mm in the clitellum, 0.9 to 1.3 mm in the postclitellar region. Number of segments: 76 in the holotype, 81 to 91 in the paratypes (average: 86; n = 3). Prostomium tanylobic. Dorsal pores begining in 5/6. Setae closely paired, beginning in II, *ab* ventral and *cd* sub-ventral. Setal arrangement *aa:ab:bc:cd* = 4:1:4:1, *dd* > ½ Ø. Clitellum in XIII-XX, annular. Genital markings in in some specimens in IV to VI (*bc* position) and VII to X (*ab* position); acanthodriline male field in XVII-XIX, delimited posteriously by a transversal lip in XIX. One pair of ventral male pores in XVIII, and ovipores not visible. Spermathecal pores not visible. Nephridial pores not visible.

Internal anatomy
Septa: membranous. Gizzard: absent. Calciferous glands: two pairs in XIV and XV, with lamellar structure, kidney-shaped and attached through the middle inside. Esophagus-intestine transition in XVII. Typhlosole absent. Hearts: five pairs, last three intestinal bigger and last pair in XII. Excretory apparatus: not easy to observe due to the minute size of the species, probably meronephridial. Prostatic glands: two pairs in XVII and XIX, elongated spatula or folded tube-shaped. Ovaries: one pair in XIII. Testes: two pairs of testes sacs in X and XI, the one in X less developed. Seminal vesicles: one or two pairs in XI (in some specimens) and XII. Spermathecae: two pairs in VIII and IX, sometimes an additional smaller pair or a single one in VII, all bowling pin-shaped, sometimes crossing the septa with the ental ampulla displaced to next segment.

Remarks

As previously stated, *N. tumuchumac* Decaëns & Bartz, n. sp. is closely related to *N. csuzdii* Bartz & Decaëns, n. sp due to the absence of gizzard and the membranous anterior septa (Table 5). It is the smallest known species within the genus, with body size not exceeding 17 mm in the material examined. It differs from other *Neogaster* by the presence of two pairs of spermathecae in VIII-IX, whereas other species have one (in *N. csuzdii* Bartz & Decaëns, n. sp.), three (in *N. angeloi* and *N. americanus*), four (in *N. gavrilovi*) or five (in *N. aidae*) (Cernosvitov 1934; Righi & Caballero 1970; Righi 1975, 1988). *Neogaster tumuchumac*, Decaëns & Bartz, n. sp. is clearly separated from *N. csuzdii* Bartz & Decaëns, n. sp. from its COI barcode (Table 3). This species corresponds to OTU#077 in Maggia *et al.* (2021).

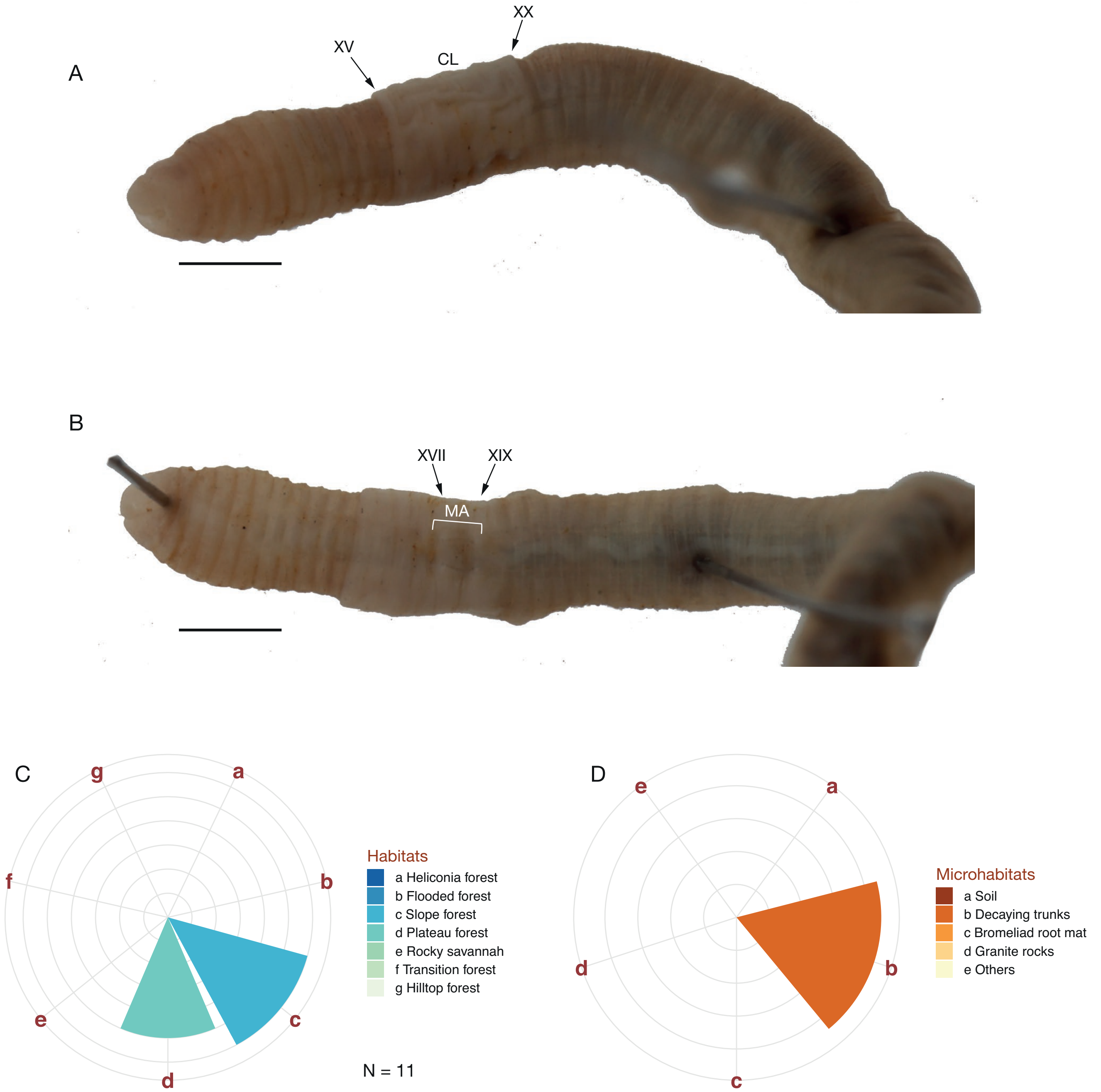

FIG. 18. — *Neogaster tumuchumac* Decaëns & Bartz n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the clitellum male field); **C**, habitat preferences; **D**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **MF**, male field; **N**, total number of specimens in the dataset. Scale bars: 1 mm.

Genus *Omodeoscolex* Csuzdi, 1993

Omodeoscolex Csuzdi, 1993: 67; 2010: 105.

TYPE SPECIES. — *Notiodrilus divergens* Cognetti de Martiis, 1905.

DIAGNOSIS. — Setae arranged in eight regular longitudinal lines. Clitellum extending from segments XIII to XX. Gizzard usually absent. Excretory system holoic. Two pairs of calciferous glands in XIV-XV, of lamellar type and opening in the esophagus separately. Spermathecae in pre-testicular segments, paired and without diverticula (Csuzdi 1993, 2010).

DISTRIBUTION. — *Omodeoscolex* comprises two Neotropical species (not including the new species described here): *Omodeoscolex divergens* (Cognetti de Martiis, 1905) is reported from Brazil, Ecuador, French Guiana and Panama (http://taxo.drilobase.org/), while *Omodeoscolex tocaya* (Righi, Ayres & Bittencourt, 1978) is known from Brazil (Amazonas) (Righi *et al.* 1978).

Omodeoscolex touroulti Decaëns & Bartz, n. sp. (Fig. 19)

urn:lsid:zoobank.org:act:7B7FC13C-8E11-411F-9047-3FCFFC7A0EC4

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project A trail, in termite nest; 2°14'34"N, 54°27'54"W; 327 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0235; MNHN.
Paratypes. French Guiana • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0282; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project C trail; 2°14'5"N, 54°26'42"W; 377 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0079; MNHN.

Etymology. — This species is named in acknowledgment to Julien Touroult, co-organisator of the "Our Planet Reviewed" in the Mitaraka Massif.

Ecology. — The three specimens of *O. touroulti* Decaëns & Bartz, n. sp. were found in decaying trunks and termite nest in a lowland, a slope and a plateau forest (Fig. 19C, D).

Distribution. — *Omodeoscolex touroulti* Decaëns & Bartz, n. sp. is only known from the Mitaraka Massif.

Description

External morphology (Fig. 19A, B)
Body shape cylindrical, slightly flattened posteriously. Body pigmentation dorsally reddish-brown, ventrally light yellow-brown. Body length: 25 mm in the holotype, 18 mm one paratype, after ethanol fixation. Body mass: 0.04 g after ethanol fixation in the holotype, 0.015 g in the paratype. Diameter: 1.2 to 1.5 mm in the preclitellar region, 1.3 to 1.6 mm in the clitellum, 1.2 to 1.5 mm in the postclitellar region. Number of segments: 92 in the holotype, 86 in the paratype. Prostomium tanylobic. Dorsal pores begining in 4/5. Setae closely paired, beginning in II, *ab* ventral and *cd* sub-ventral. Setal arrangement *aa:ab:bc:cd* = 4:1:4:1, *dd* > ½ Ø. Clitellum in XIII-XX, annular. Genital markings in two transversal lips in XVII and XX, delimiting a rectangular acanthodriline male field. One pair of ventral male pores in XVIII, and ovipores one pair in XIV. Spermathecal pores not visible. Nephridial pores not visible.

Internal anatomy
Septa: membranous. Gizzard: absent. Calciferous glands: two pairs in XIV and XV, with lamellar structure, kidney shape and attached through the middle inside part. Esophagus-intestine transition in XVI. Typhlosole weak. Hearts: five pairs, last three intestinal bigger and last pair in XII. Excretory apparatus holoic. Prostatic glands: two pairs in XVII and XIX, spatula-shaped. Ovaries: one pair in XIII, grape-shaped. Testes: two pairs of testes sacs in X and XI. Seminal vesicles: two pairs in XI and XII, very small and weak. Spermathecae: three unpaired midventral in VI to VIII, spherical.

Remarks

O. touroulti Decaëns & Bartz, n. sp. is different from the two previously described species of *Omodeoscolex* by the presence of unpaired instead of paired spermathecae. Despite this strong difference, we provisionally assign the species to the genus *Omodeoscolex* because of lack of a gizzard and of the holonepridial type of its excretory system. This species corresponds to OTU#012 in Maggia *et al.* (2021).

Omodeoscolex abamaensis Bartz & Decaëns, n. sp. (Fig. 20)

urn:lsid:zoobank.org:act:1FE90ABA-30AB-4AC1-AE8D-35CBD888435C

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project A trail, in decaying trunk; 2°14'34"N, 54°27'54"W; 327 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0248; MNHN.
Paratypes. French Guiana • 2 adult specimens; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project A trail; 2°14'34"N, 54°27'54"W; 327 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0247, EW-MI15-0249; CEFE • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project D trail; 2°13'58"N, 54°27'7"W; 318 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0305; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project C trail; 2°13'58"N, 54°26'38"W; 449 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0299; MNHN.

Other material examined. — **French Guiana** • 1 fragment; Tumuc-Humac, Mitaraka Massif, *Heliconia* forest near plateau forest at base camp; 2°13'50"N, 54°26'57"W; 351 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0035, MNHN • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project D trail; 2°13'58"N, 54°27'7"W; 318 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0310; MNHN.

Etymology. — The name of the species refers to the Abama River along which the expedition base camp was located.

Ecology. — The three specimens of *O. abamaensis* Bartz & Decaëns, n. sp. were found in decaying trunks and termite nest in a lowland, a slope and a plateau forest (Fig. 20C, D).

Distribution. — *Omodeoscolex abamaensis* Bartz & Decaëns, n. sp. is only known from the Mitaraka Massif.

Description

External morphology (Fig. 20A, B)
Body shape cylindrical, slightly flattened posteriously. Body pigmentation dorsally light yellow-brown, ventrally lighter. Body length: 18 mm in the holotype, 14 to 21 mm in two of the paratypes, after ethanol fixation. Body mass: 0.03 g after ethanol fixation in the holotype, 0.02 to 0.03 g in two of the paratypes. Diameter: 1.4 to 1.5 mm in the preclitellar region, 1.0 to 1.6 mm in the clitellum, 1.0 to 1.6 mm in the postclitellar region. Number of segments: 109 in the holotype, 95 to 122 in two of the paratypes. Prostomium tanylobic. Dorsal pores begining in 4/5. Setae closely paired, beginning in II, *ab* ventral and *cd* sub-ventral. Setal arrangement *aa:ab:bc:cd* = 4:1:4:1, *dd* > ½ Ø. Clitellum in XIII-XX, annular. Genital markings in acanthodriline male field in XVII-XIX, delimited anteriously and posteriously by two

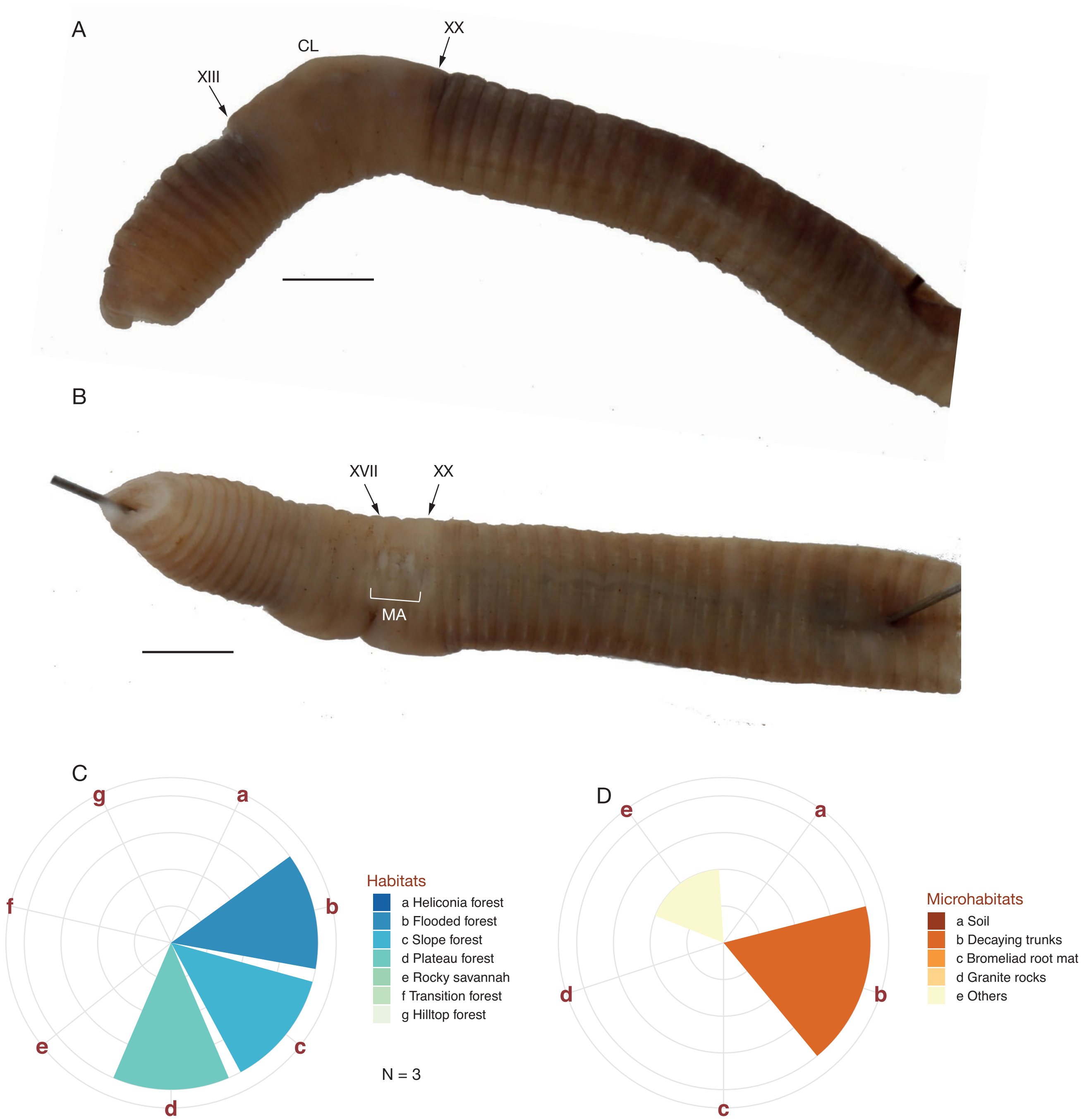

FIG. 19. — *Omodeoscolex touroulti* Decaëns & Bartz n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the clitellum male field); **C**, habitat preferences; **D**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **MF**, male field; **N**, total number of specimens in the dataset. Scale bars: 1 mm.

transversal lips in ¾ XVII and ¼ XX, respectively. One pair of ventral male pores in XVIII, and ovipores one pair in XIV, presetal, internally diagonal to *a*. Spermathecal pores not visible. Nephridial pores not visible.

Internal anatomy

Septa: membranous. Gizzard: absent. Calciferous glands: two pairs in XIV and XV, with lamellar structure, kidney-shaped and attached through the middle inside. Esophagus-intestine transition in XVI. Typhlosole absent. Hearts: five pairs, last three intestinal bigger and last pair in XII. Excretory apparatus holoic. Prostatic glands: two pairs in XVII and XIX, short. Ovaries: one pair in XIII, small sacs containing ovules. Testes: two pairs of testes sacs in X and XI. Seminal vesicles: one pair in XII, small. Spermathecae: three unpaired midventral in VII to IX, spherical.

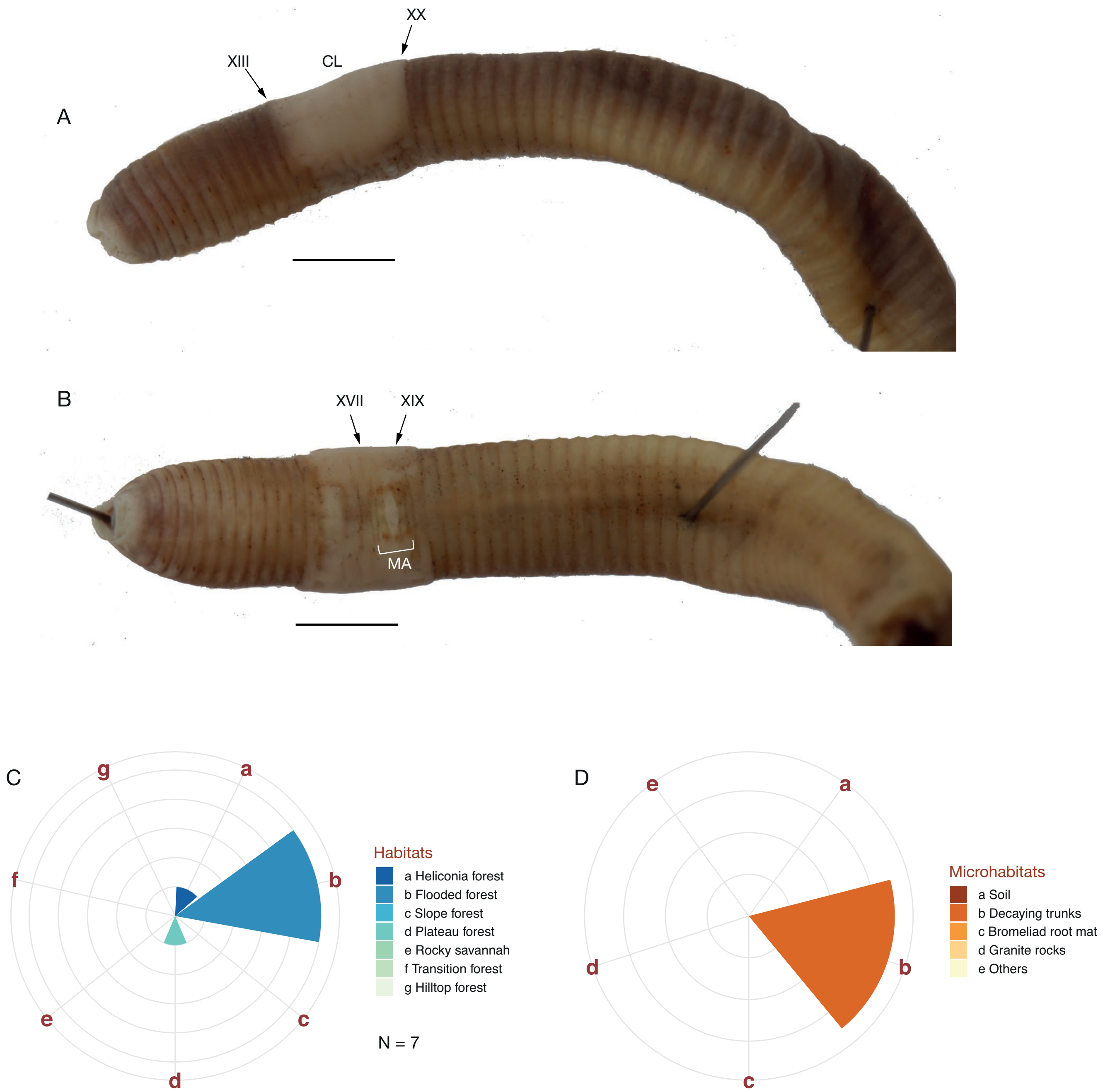

FIG. 20. — *Omodeoscolex abamaensis* Bartz & Decaëns n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the clitellum male field); **C**, habitat preferences; **D**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **MF**, male field; **N**, total number of specimens in the dataset. Scale bars: 1 mm.

REMARKS

Omodeoscolex abamaensis Bartz & Decaëns, n. sp. is close to *O. touroulti* Decaëns & Bartz, n. sp. in presence of three unpaired spermathecae (Table 5). It however differs from this species by its DNA barcode (mean pairwise divergence > 16% with these species; Table 3), and by the position of spermathecae (i.e., in VII to IX instead of VI to VIII in *O. touroulti* Decaëns & Bartz, n. sp.). This species corresponds to OTU#072 in Maggia *et al.* (2021).

Omodeoscolex tetraspermatheca Decaëns & Bartz, n. sp. (Fig. 21)

urn:lsid:zoobank.org:act:ECE72D9E-C9DB-48FC-B69C-A4676C1DE816

TYPE MATERIAL. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project A trail, in decaying trunk; 2°14'16"N, 54°27'7"W; 344 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0203; MNHN.

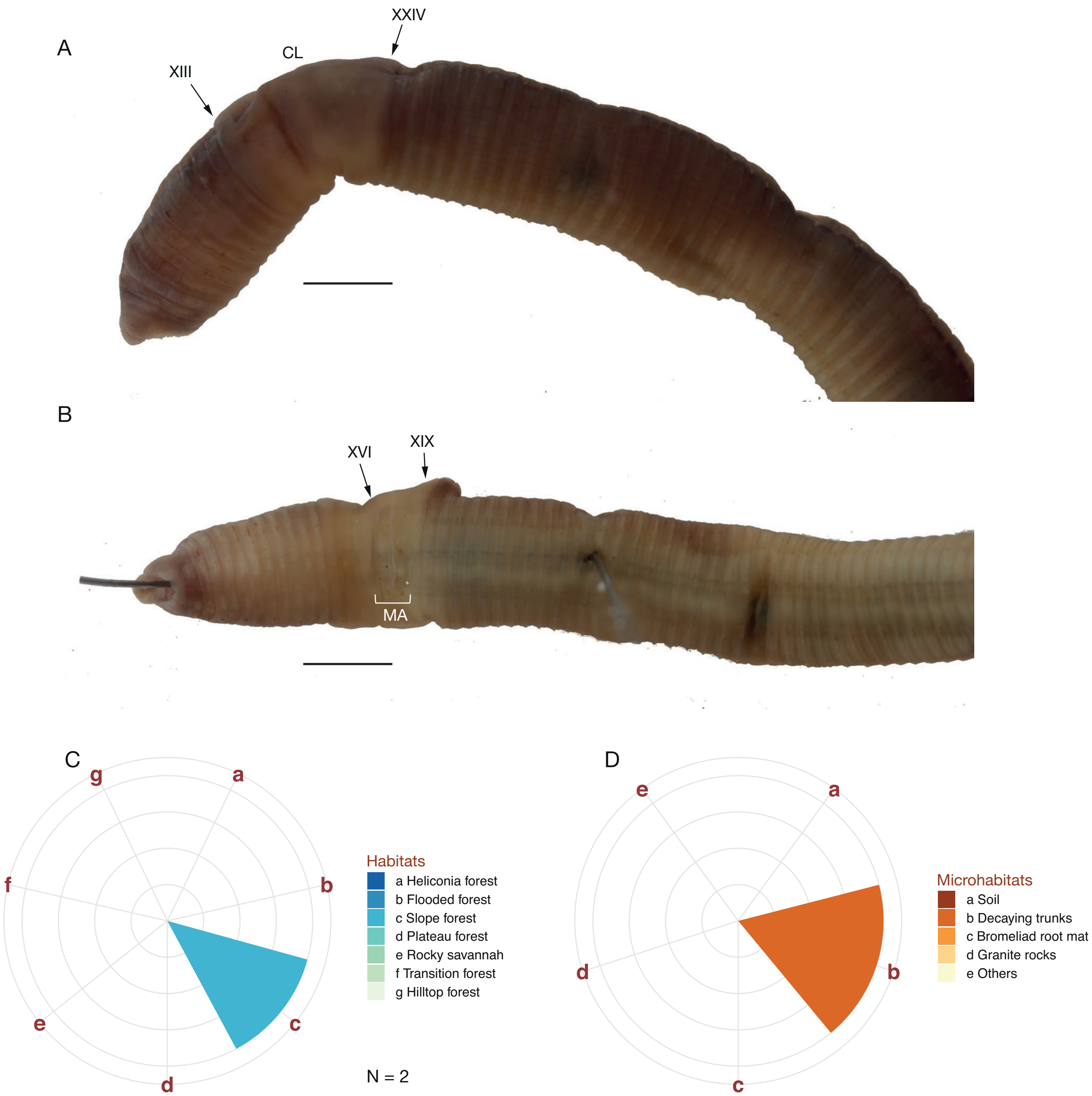

Fig. 21. — *Omodeoscolex tetraspermatheca* Decaëns & Bartz n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the clitellum position); **B**, external and ventral view of the anterior body (**arrows** indicate the clitellum male field); **C**, habitat preferences; **D**, microhabitat preferences. All images from the holotype; **CL**, clitellum; **MF**, male field; **N**, total number of specimens in the dataset. Scale bars: 1 mm.

Paratypes. French Guiana • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project A trail; 2°14'16"N, 54°27'7"W; 344 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0204; CEFE.

Etymology. — The species name refers to the presence of four unpaired spermathecae.

Ecology. — The two known specimens of *O. tetraspermatheca* Decaëns & Bartz, n. sp. have been collected in a decaying trunk in a slope forest (Fig. 21C, D).

Distribution. — *Omodeoscolex tetraspermatheca* Decaëns & Bartz, n. sp. is only known from the Mitaraka Massif.

Description

External morphology (Fig. 21A, B)

Body shape cylindrical, slightly flattened posteriously. Body pigmentation dorsally reddish-brown, ventrally light yellow-brown. Body length: 18 mm in the holotype, 26 mm in the paratype, after ethanol fixation. Body mass: 0.04 g after ethanol fixation in the holotype, same in the paratype.

Diameter: 1.6 to 1.8 mm in the preclitellar region, 1.5 to 2.6 mm in the clitellum, 1.4 to 2.5 mm in the postclitellar region. Number of segments: 117 in the holotype, 122 in the paratype. Prostomium tanylobic. Dorsal pore: begining in 4/5. Setae closely paired, beginning in II, *ab* ventral and *cd* sub-ventral. Setal arrangement *aa:ab:bc:cd* = 5:1:5:1, *dd* > ½ Ø. Clitellum in XIII-XX, annular. Genital markings in two transversal lips in ¾ XVI and ¼ XX, delimiting a rectangular acanthodriline male field. Male pores one ventral pair in XVIII, and ovipores one pair in XIV, presetal, internally diagonal to *a*. Spermathecal pores not visible. Nephridial pores in line of *C*.

Internal anatomy

Septa: membranous. Gizzard: absent. Calciferous glands: two pairs in XIV and XV, with lamellar structure, kidney-shaped and attached through the middle inside. Esophagus-intestine transition in XVI. Typhlosole absent. Hearts: five pairs, last three intestinal bigger and last pair in XII. Excretory apparatus holoic. Prostatic glands: two pairs in XVII and XIX, irregular lobulated shape. Ovaries: one pair in XIII, grape bunch-shaped. Testes: two pairs in X and XI. Seminal vesicles: one pair, very small in XII, attached to septum 11/12. Spermathecae: four unpaired midventral in VI to IX, round-ball-sac-shaped.

Remarks

Omodeoscolex tetraspermatheca Decaëns & Bartz, n. sp. is characterized by the presence of four unpaired spermathecae in VI-IX, whereas in the other known species of the genus with unpaired spermathecae there are three (*O. touroulti* Decaëns & Bartz, n. sp. and *O. abamaensis* Bartz & Decaëns, n. sp.) (Table 5). It also differs from the two previously described species by its COI-barcode (Table 3). This species corresponds to OTU#086 in Maggia *et al.* (2021).

Family Ocnerodrilidae Beddard, 1891

Genus *Guianodrilus* Bartz & Decaëns, n. gen.

urn:lsid:zoobank.org:act:9EDD9660-EE46-4B62-A54C-A58FC0D860E8

Etymology. — The name of the genus refers to the Guianan Center of endemism (Cardoso Da Silva *et al.* 2005) in which is located the type locality of the type species.

Type species. — *Guianodrilus corticolous* Bartz & Decaëns, n. sp.

Diagnosis. — Setae eight per segment, closely paired. Dorsal pores absent. Gizzard absent. Esophagus with extramural calciferous glands in segment IX. Holandric and holonephridial. Last hearts in XII. Intestine begining in XIV. Male pores in XVII. Prostatic pore and tubular prostates in XVII. Bidiverticulate spermathecae in IX.

Distribution. — To date, the genus is only known from the type locality of *G. corticolous* Bartz & Decaëns, n. sp.

Guianodrilus corticolous Bartz & Decaëns, n. sp. (Fig. 22)

urn:lsid:zoobank.org:act:8F945CA5-277B-42BD-9502-5CA745DAF6D3

Type material. — **Holotype. French Guiana** • Adult; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project D trail, in decaying trunk; 2°13'58"N, 54°27'7"W; 318 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0307; MNHN.

Paratypes. French Guiana • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project A trail; 2°14'34"N, 54°27'54"W; 327 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg. (1 specimen); BOLD Sample ID: EW-MI15-0251; CEFE

Etymology. — The name of the species refers to the microhabitat where the type specimens have been collected.

Ecology. — The two known specimens of *G. corticolous* Bartz & Decaëns, n. sp. have been found in decaying trunks in a lowland forest (Fig. 23).

Distribution. — *Guianodrilus corticolous* Bartz & Decaëns, n. sp. is only known from the Mitaraka Massif.

Description

External morphology (Fig. 22)

Body shape cylindrical, slightly flattened posteriously. Body pigmentation absent. Body length: 19 mm in the holotype, 21 mm in the paratype, after ethanol fixation. Body mass: 0.01 g after ethanol fixation in the holotype, same in the paratype. Diameter: 1.0 mm in the preclitellar region, 1.0 mm in the clitellum, 1.0 to 1.2 mm in the postclitellar region. Number of segments: 87 in the holotype, 81 in the paratype. Prostomium proepolobic. Dorsal pores: absent. Setae closely paired. Setal arrangement *aa:ab:bc:cd* = 5:1:5:1, *dd* > ½ Ø. Clitellum in XIV-⅔XVIII, saddle-shaped. Genital markings absent. Male pores one pair in XVII, like papillae and with ejected material, and ovipores in XIV, almost in the border of 13/14, in diagonal to *b*. Spermathecal pores not visible. Nephridial pores in line of *C*.

Internal anatomy (Fig. 22)

Septa: 6/7 to 8/9 membranous but thicker than the others. Gizzard: absent. Calciferous glands: one pair in IX, peanut-shaped, attached by the bottom and projected laterally with internal united lamella. Esophagus-intestine transition in XIV. Typhlosole absent. Single dorsal blood vessel. Hearts: three last pair in X-XII (latero-esophageal) and VIII and IX (lateral). Excretory apparatus holoic. Prostatic glands: one pair in XVII, short duct forming long elongated tubes (tubular) folded and tangled with irregular directions for each tube in the ventral part, about 1.5 to 2.0 mm long. Ovaries: one pair in XIII. Testes and funnels: two pairs of brushy testes and iridescent male funnels, free, in X and XI. Seminal vesicles: two pairs in XI and XII, occupying a single segment with lobular-globular shape. Spermathecae: one pair in IX, big folded sac with very short duct and two iridescent diverticula baseball-bat-shaped (bidiverticulate), one projected ventral side and other dorsal side, ental to the duct.

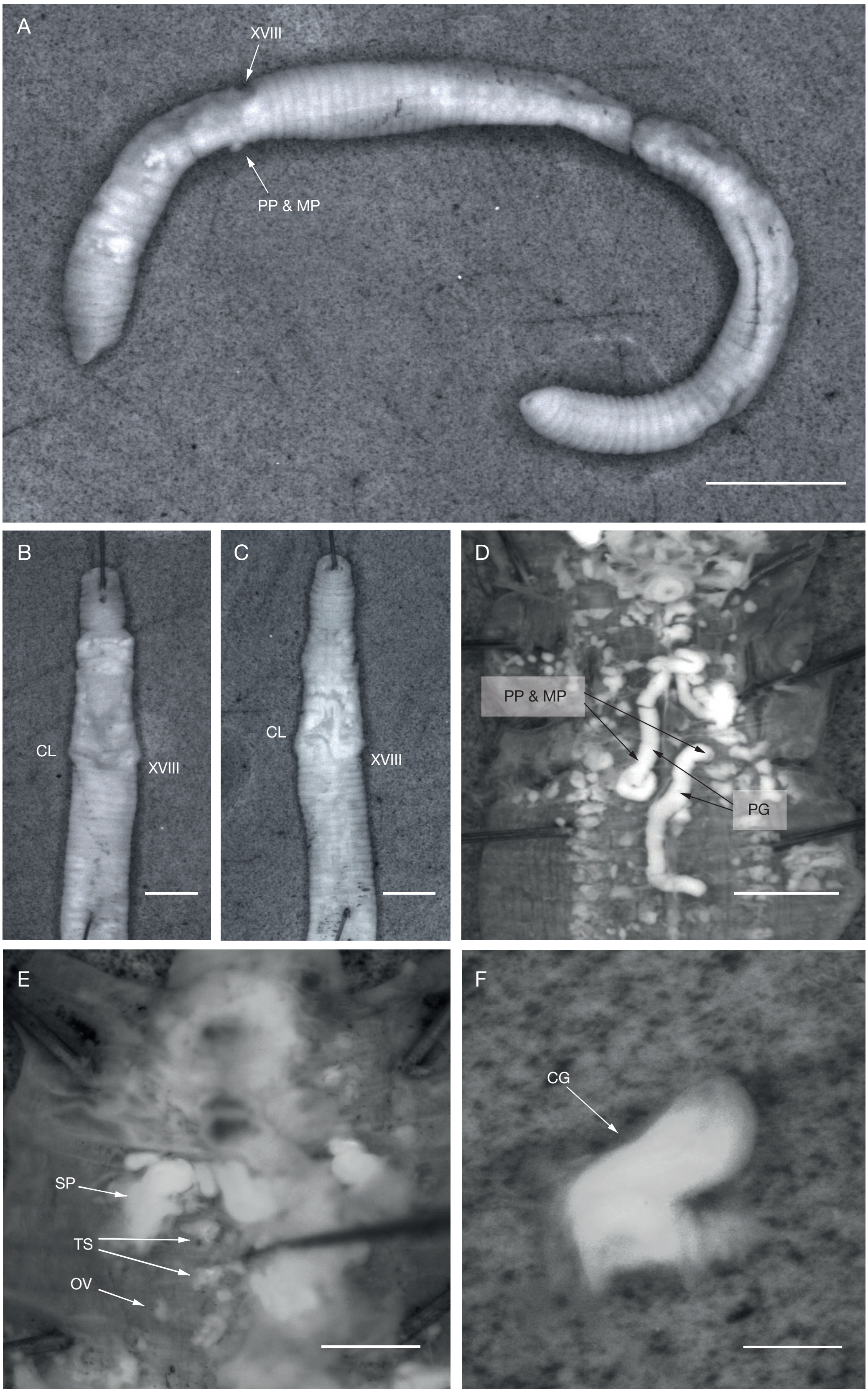

Fig. 22. — *Guianodrilus corticolous* Bartz & Decaëns n. sp.: **A**, external and lateral view of the anterior body (**arrows** indicate the end of clitellum and male and prostatic pore position); **B**, external and dorsal view of the anterior body (segment number indicate the end of clitellum); **C**, external and ventral view of the anterior body (**arrows** indicate the clitellum and male field); **D**, Internal view indicating the pair of prostates and male and prostatic pore; **E**, internal view indicating male and female strutures; **F**, detail of a calciferous gland after being extracted from the dissection. All images from the holotype; **CG**, calciferous gland; **CL**, clitellum; **MP**, male pore; **PP**, prostate pore; **PG**, prostatic gland; **SP**, spermathecae; **TS**, testes; **OV**, ovaries; **CG**, calciferous gland. Scale bars: A, 2 mm; B, D, 1 mm; e, 0.5 mm; F, 200 µm.

TABLE 5. — Main morpho-anatomical characteristics of the new Benhamiidae Michaelsen, 1897 species from the Mitaraka range.

Species	Pigmentation	Size (mm)	Clitellum	*Tubercula pubertatis*	Calciferous glands	Spermathecae	Testes
Neogaster csuzdii Bartz & Decaëns, n. sp.	dorsally light yellow-brown, lighter ventrally	20 to 30	XIII-XX, annular	absent	two pairs in XIV-XV, lamellar structure	one pair in IX	two pairs in X-XI
Neogaster tumuchumac Bartz & Decaëns, n. sp.	dorsally light yellow-brown, ventrally lighter	12 to 17	XIII-XX, annular	absent	two pairs in XIV-XV, lamellar structure	two pairs in VIII-IX	two pairs in X-XI
Omodeoscolex touroulti Bartz & Decaëns, n. sp.	dorsally reddish-brown, ventrally light yellow-brown	18 to 25	XIII-XX, annular	absent	two pairs in XIV-XV, lamellar structure	three unpaired in VI-VIII	two pairs in X-XI
Omodeoscolex abamaensis Bartz & Decaëns, n. sp.	dorsally light yellow-brown, ventrally lighter	14 to 21	XIII-XX, annular	absent	two pairs in XIV-XV, lamellar structure	three unpaired in VII-IX	two pairs in X-XI
Omodeoscolex tetraspermatheca Bartz & Decaëns, n. sp.	dorsally reddish-brown, ventrally light yellow-brown	18 to 26	XIII-XX, annular	absent	two pairs in XIV-XV, lamellar structure	four unpaired in VI-IX	two pairs in X-XI

REMARKS

This species corresponds to OTU#089 in Maggia *et al.* (2021). It is the first species described from its genus. We determined it to be new based on the summary of genus characters implicit in the keys of Hernández-García *et al.* (2018b) and Fragoso & Rojas (2009). *Guianodrilus* Bartz & Decaëns, n. gen. is similar to *Pygmaeodrilus* Michaelsen, 1890 by the absence of the gizzard, calciferous glands paired in IX, male and female reproductive system holandric and metagynous, respectively, diverticulate spermathecae, and dorsal pores absent (Michaelsen 1890). The principal difference between the new genus and *Pygmaeodrilus* are the last hearts in XII in *Guianodrilus* Bartz & Decaëns, n. gen. instead of XI in *Pygmaeodrilus*; and intestinal origin in XIV (*Guianodrilus* Bartz & Decaëns, n. gen.) instead of XII (*Pygmaeodrilus*). The seminal vesicles of *Guianodrilus* Bartz & Decaëns, n. gen. are in XI and XII, but in IX and XII in *Pygmaeodrilus*. The prostates of *Guinanodrilus* Bartz & Decaëns, n. gen. have a relatively thick glandular parts and short ducts, compared to the thinner glands and relatively long ducts of *Pygmaeodrilus*. Both genera have more than one diverticulum on the spermathecae. The Brazilian species *Pygmaeodrilus amapaensis* Righi, 1988 differs from its African congeners in having a more posterior intestinal origin (XIII) but has last hearts in XI. It has a longer clitellum (XIII-XX) than *G. corticolus* Bartz & Decaëns, n. sp., and has genital markings near the combined male and prostatic pores, which are on elevated papillae. However, the two share the elevated papillae of the male pores. One could consider transferring *P. amapaensis* to *Guianodrilus* Bartz & Decaëns, n. gen. but that would remove all but one distinction, the posterior intestinal origin. It might be better to await the discovery of further members of both genera in South America.

OTHER SPECIES COLLECTED

Family RHINODRILIDAE Benham, 1890

Nouraguesia parare Csuzdi & Pavlícek, 2011

Nouraguesia parare Csuzdi & Pavlícek, 2011: 1764.

MATERIAL EXAMINED. — **French Guiana** • 1 adult specimen, 6 juvenile specimens; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project A trail; 2°14’34”N, 54°27’54”W; 327 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0231, EW-MI15-0236, EW-MI15-0237, EW-MI15-0238, EW-MI15-0239, EW-MI15-0242, EW-MI15-0244; MNHN • 1 adult specimen, 2 juvenile specimens; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project C trail; 2°13’58”N, 54°26’38”W; 449 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; EW-MI15-0294, EW-MI15-0295, EW-MI15-0296; CEFE • 1 adult specimen, 5 cocoons; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project D trail; 2°12’57”N, 54°27’25”W; 381 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0011, EW-MI15-0029, EW-MI15-0030, EW-MI15-0031, EW-MI15-0032, EW-MI15-0033; CEFE • 1 adult specimen, 4 juvenile specimens, 1 cocoon; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project A trail; 2°14’16”N, 54°27’7”W; 344 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0197, EW-MI15-0214, EW-MI15-0198, EW-MI15-0199, EW-MI15-0200, EW-MI15-0201; MNHN • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project C trail; 2°14’5”N, 54°26’42”W; 377 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0077; MNHN • 5 juvenile specimens; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project D trail; 2°13’40”N, 54°27’14”W; 339 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0253, EW-MI15-0258, EW-MI15-0259, EW-MI15-0260, EW-MI15-0261; MNHN • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, transition forest on Tchoukou Chipan Inselberg; 2°14’46”N, 54°29’10”W; 329 m a.s.l.; III.2015; C. Baraloto leg.; BOLD Sample ID: EW-MI15-0172; MNHN.

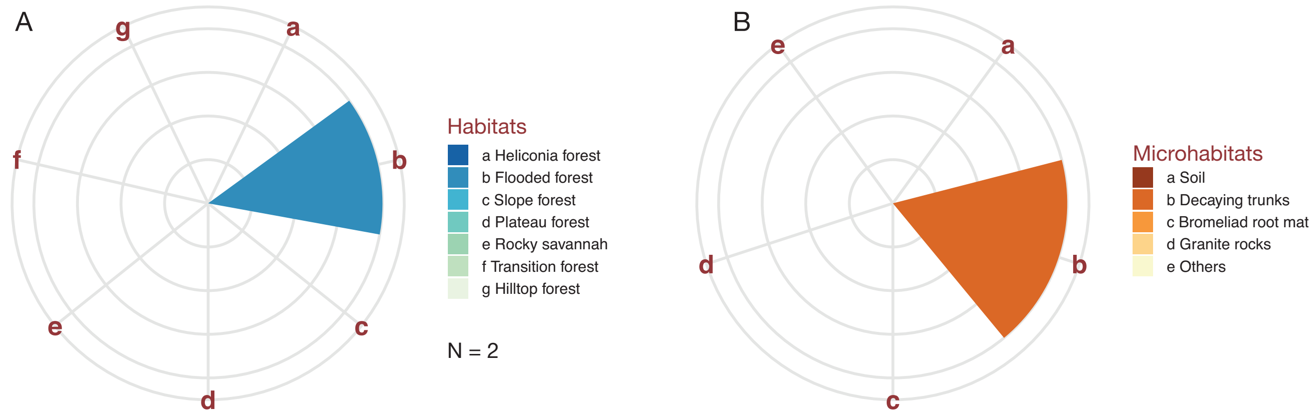

FIG. 23. — *Guianodrilus corticolous* Bartz & Decaëns n. sp.: **A**, habitat preferences; **B**, microhabitat preferences. **N**, total number of specimens in the dataset.

REMARK

This species corresponds to OTU#028 in Maggia *et al.* (2021).

Pontoscolex corethrurus (Müller, 1856)

Lumbricus corethrurus Müller, 1856: 113.

MATERIAL EXAMINED. — **French Guiana** • 4 adult specimens, 5 juvenile specimens, 4 cocoons; Tumuc-Humac, Mitaraka Massif, *Heliconia* forest near plateau forest at base camp; 2°13'50"N, 54°26'57"W; 351 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0037, EW-MI15-0038, EW-MI15-0039, EW-MI15-0040, EW-MI15-0041, EW-MI15-0042, EW-MI15-0043, EW-MI15-0044, EW-MI15-0045, EW-MI15-0046, EW-MI15-0047, EW-MI15-0048, EW-MI15-0050; MNHN • 2 adult specimens, 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, hilltop forest on Borne 1 Inselberg; 2°12'35"N, 54°26'12"W; 600 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0221, EW-MI15-0222, EW-MI15-0223; MNHN • 3 adult specimens; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project A trail; 2°14'34"N, 54°27'54"W; 327 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0232, EW-MI15-0233, EW-MI15-0234; CEFE • 5 adult specimens, 5 juvenile specimens; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project D trail; 2°13'58"N, 54°27'7"W; 318 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0183, EW-MI15-0184, EW-MI15-0185, EW-MI15-0186, EW-MI15-0187, EW-MI15-0188, EW-MI15-0189, EW-MI15-0190, EW-MI15-0191, EW-MI15-0192; MNHN • 1 adult specimen, 1 fragment; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0182, EW-MI15-0370; MNHN • 1 adult specimen, 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project A trail; 2°14'38"N, 54°27'32"W; 371 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0090, EW-MI15-0091; MNHN • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, rocky savannah #1 on Sommet en Cloche Inselberg; 2°13'40"N, 54°28'1"W; 623 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0150; MNHN • 5 adult specimens, 1 cocoon; Tumuc-Humac, Mitaraka Massif, rocky savannah on DIADEMA project C trail; 2°14'18"N, 54°26'5"W; 401 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0002, EW-MI15-0003, EW-MI15-0004, EW-MI15-0005, EW-MI15-0006, EW-MI15-0007; MNHN • 2 adult specimens, 1 cocoon; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project A trail; 2°14'16"N, 54°27'7"W; 344 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0215, EW-MI15-0216, EW-MI15-0217; MNHN • 3 adult specimens, 10 juvenile specimens, 1 cocoon; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project C trail; 2°14'5"N, 54°26'42"W; 377 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0055, EW-MI15-0056, EW-MI15-0057, EW-MI15-0062, EW-MI15-0063, EW-MI15-0064, EW-MI15-0065, EW-MI15-0072, EW-MI15-0073, EW-MI15-0074, EW-MI15-0075, EW-MI15-0076, EW-MI15-0082, EW-MI15-0083; MNHN • 1 adult specimen, 9 juvenile specimens; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project D trail; 2°13'40"N, 54°27'14"W; 339 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0273, EW-MI15-0255, EW-MI15-0256, EW-MI15-0257, EW-MI15-0272, EW-MI15-0274, EW-MI15-0275, EW-MI15-0277, EW-MI15-0278, EW-MI15-0279; MNHN • 4 adult specimens, 5 juvenile specimens; Tumuc-Humac, Mitaraka Massif, transition forest # 1 Sommet en Cloche Inselberg; 2°13'54"N, 54°27'39"W; 401 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0345, EW-MI15-0346, EW-MI15-0347, EW-MI15-0351, EW-MI15-0355, EW-MI15-0348, EW-MI15-0349, EW-MI15-0352, EW-MI15-0353; MNHN • 5 adult specimens, 2 juvenile specimens; Tumuc-Humac, Mitaraka Massif, transition forest # 2 Sommet en Cloche Inselberg; 2°13'59"N, 54°27'34"W; 395 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0114, EW-MI15-0115, EW-MI15-0116, EW-MI15-0117, EW-MI15-0118, EW-MI15-0119, EW-MI15-0120; MNHN • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, tropical rainforest on DIADEMA project D trail; 2°13'26"N, 54°27'20"W; 317 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0315; MNHN.

REMARK

This species corresponds to OTU#026 in Maggia *et al.* (2021).

Pontoscolex sp.

MATERIAL EXAMINED. — **French Guiana** • 1 fragment; Tumuc-Humac, Mitaraka Massif, stream bank on DIADEMA project D trail; 2°13'26"N, 54°27'20"W; 316 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0171; MNHN.

REMARK

This species corresponds to OTU#046 in Maggia *et al.* (2021).

Andiorrhinus (*Turedrilus*) sp.

Material examined. — **French Guiana** • 1 damaged adult specimen; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0363; MNHN • 2 juvenile specimens; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project D trail; 2°12'57"N, 54°27'25"W; 381 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0094, EW-MI15-0100; MNHN.

Remark

This species corresponds to OTU#079 in Maggia *et al.* (2021).

Martiodrilus sp.

Material examined. — **French Guiana** • 2 juvenile specimens; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project C trail; 2°13'58"N, 54°26'38"W; 449 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0286, EW-MI15-0291; MNHN.

Remark

This species corresponds to OTU#090 in Maggia *et al.* (2021).

Rhinodrilus sp.

Material examined. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, *Heliconia* forest near plateau forest at base camp; 2°13'50"N, 54°26'57"W; 351 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0036; MNHN • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project C trail; 2°14'5"N, 54°26'42"W; 377 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0036; MNHN.

Remark

This species corresponds to OTU#073 in Maggia *et al.* (2021).

Family Glossoscolecidae Michaelsen, 1900

Righiodrilus sp.

Material examined. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, *Heliconia* forest near plateau forest at base camp; 2°13'50"N, 54°26'57"W; 351 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0053; MNHN • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, slope forest on DIADEMA project C trail; 2°14'5"N, 54°26'42"W; 377 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0071; MNHN.

Remark

This species corresponds to OTU#075 in Maggia *et al.* (2021).

Family Benhamiidae Michaelsen, 1897

Dichogaster andina Cognetti de Martiis, 1904

Dichogaster andina Cognetti de Martiis, 1904: 4.

Material examined. — **French Guiana** • 1 adult specimen; Tumuc-Humac, Mitaraka Massif, *Heliconia* forest near plateau forest at base camp; 2°13'50"N, 54°26'57"W; 351 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0034; CEFE • 1 adult specimens, 3 juvenile specimens; Tumuc-Humac, Mitaraka Massif, plateau forest at base camp; 2°14'2"N, 54°27'1"W; 331 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0312, EW-MI15-0193, EW-MI15-0316, EW-MI15-0317; MNHN.

Remark

This species corresponds to OTU#035 in Maggia *et al.* (2021).

Dichogaster bolaui (Michaelsen, 1891)

Benhamia bolaui Michaelsen, 1891: 9.

Material examined. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project D trail; 2°13'58"N, 54°27'7"W; 318 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0311; MNHN.

Remark

This species corresponds to OTU#048 in Maggia *et al.* (2021).

Wegeneriona sp.

Material examined. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, plateau forest on DIADEMA project A trail; 2°14'38"N, 54°27'32"W; 371 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0088; MNHN.

Remark

This species corresponds to OTU#078 in Maggia *et al.* (2021).

Family Ocnerodrilidae Beddard, 1891

Ocnerodrilidae sp. 1

Material examined. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project D trail; 2°13'58"N, 54°27'7"W; 318 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0308; MNHN.

Remark

This species corresponds to OTU#045 in Maggia *et al.* (2021).

Ocnerodrilidae sp. 2

Material examined. — **French Guiana** • 2 juvenile specimens; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project A trail; 2°14'34"N, 54°27'54"W; 327 m a.s.l.; III.2015; T.

Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0229, EW-MI15-0252; MNHN • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project C trail; 2°14'16"N, 54°26'56"W; 310 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0224; MNHN.

Remark

This species corresponds to OTU#087 in Maggia *et al.* (2021).

Ocnerodrilidae sp. 3

Material examined. — **French Guiana** • 1 juvenile specimen; Tumuc-Humac, Mitaraka Massif, lowland forest on DIADEMA project D trail; 2°13'58"N, 54°27'7"W; 318 m a.s.l.; III.2015; T. Decaëns, E. Lapied leg.; BOLD Sample ID: EW-MI15-0309; MNHN.

Remark

This species corresponds to OTU#091 in Maggia *et al.* (2021).

DISCUSSION

In this work, we identified 31 species of earthworms from the material collected during a single expedition in the Mitaraka Massif. Our analyses further predict that 36 species could compose the regional species pool. The overall rarefaction curve (Fig. 2A) shows that the sampling effort was probably sufficient to detect the majority of the species present in the study area. However, it can also be predicted that intensified sampling would necessarily lead to the discovery of some additional taxa, especially in decaying trunks and in the best drained habitats (mainly plateau and slope forests). This places Mitaraka second only to the Nouragues Reserve in terms of regional earthworm diversity, and among the most diverse sites on a worldwide scale (Decaëns *et al.* 2016; Maggia *et al.* 2021).

In general, the levels of local diversity (alpha diversity) observed in our study range from one to 12 species per community. This is higher than the prediction by Phillips *et al.* (2019), but also lower than some of the values cited by James *et al.* (2021). The finding of higher alpha diversity values than predicted by Phillips *et al.* (2019) meta-analysis has already been highlighted by Maggia *et al.* (2021), and can be explained by the added value of using DNA barcoding and qualitative sampling, compared to most of the studies on which the Phillips *et al.* model relies. The lower values than those reported by James *et al.* (2021) may be explained by differences in scale between some studies where both the alpha and beta components may have been integrated in species richness calculations. By opposition, sampling effort in our work was well circumscribed spatially and designed to strictly sample community-scale species diversity. Generally speaking, we found alpha diversity values of the same order of magnitude as those observed by Maggia *et al.* (2021) at several study sites in French Guiana, and also substantially similar to what is commonly reported for temperate regions (Decaëns *et al.* 2008; Decaëns 2010).

We also observe a significant turnover in the composition of the assemblages, since only four species found in Mitaraka (*N. parare*, *P. corethrurus*, *D. bolaui* and *D. andina*) seem to be shared with the Nouragues fauna (Decaëns *et al.* 2016). This high beta diversity is linked to a high proportion of local endemics in the species pools, which suggests that there could be a very large number of earthworm species at the scale of the whole French Guiana (Decaëns *et al.* 2016; Maggia *et al.* 2021). This result is also in line with the conclusions of Phillips *et al.* (2019) who showed that despite the absence of a latitudinal gradient of alpha diversity, tropical areas are globally characterised by a high geographical turnover, and consequently by higher levels of regional diversity, than in temperate regions.

Our results also provide new insights into the distribution of earthworm diversity at the local scale. In particular, we observe differences in community diversity between the main ecosystem types sampled. The fact that plateau and slope forests host the most diverse earthworm communities can be explained by the fact that they are the least environmentally constrained habitats. In comparison, lowland forests and inselberg habitats present stronger hydric constraints (periodic flooding in the former, or on the contrary xeric conditions in the latter), which can act as environmental filters and limit the composition of the communities to the better adapted fraction of the regional species pool. We also observe that the species assemblage is dominated by pigmented forms, with a high diversity of "epigeic" species inhabiting decaying trunks and other surface micro-habitats. This trend, already highlighted by Decaëns *et al.* (2016) for the Nouragues fauna, can be explained by the oligotrophic nature of Guyanese soils, which are not very conducive to the activity of endogeic earthworms, and which would have led to a strong adaptation for the use of above-ground sources of organic matter. In other tropical regions such as Meso-America and sub-Saharan Africa, the more nutrient-rich soils host communities largely dominated by endogeic species (Fragoso & Lavelle 1992).

From a taxonomic point of view, our work represents a quite remarkable contribution to the knowledge of the diversity of earthworms in French Guiana. Indeed, the description of 18 species new to science represents a near doubling of the number of species cited for this territory, since only 37 species were previously cited in the region (Brown *et al.* 2013). This of course underlines the extent of the taxonomic deficit that characterises tropical earthworms, and which has already been mentioned before (Decaëns 2010).

We describe nine new species of *Martiodrilus*, in a genus that previously comprised 89 species (http://taxo.drilobase.org/), i.e., an increase of nearly 10% in the number of known species. Beyond this re-evaluation of the number of species within this genus, our results modify the vision we had of its geographical distribution. Indeed, whereas most of the species known until now had been described from the north of the Andean Range, our work moves west this diversity barycentre, suggesting the possible existence of another centre of diversity in the Oriental Guiana Shield. It will be interesting in the future to carry out a complete phylogenetic analysis of this genus, in order to highlight the evolutionary relationships between the different subgenera that compose it, and try to reconstruct its biogeographic history in the north of the South American continent.

With the exception of *Andiorrhinus*, which had 45 species before our work, the other new species described here concern genera where few species were known until now (i.e., *Atatina*, *Urobenus*, *Neogaster* and *Omodeoscolex*). Decaëns *et al.* (2016) had already assigned some OTUs sampled in the Nouragues Nature Reserve to these same genera (i.e., one in *Atatina*, one in *Urobenus*, and seven in *Neogaster*), but their DNA barcodes suggest that they are different species from the one described here. It is therefore reasonable to assume that more species may be described in the future in these genera, which may thus appear to be much more diverse in French Guiana than originally thought. This may simply reflect the fact that these groups, which are essentially made up of small species, have attracted little attention from taxonomists to date or, alternatively, that the Guiana Shield may represent a centre of diversity for them.

The particular cases of the genera *Neogaster* and *Omodeoscolex* deserve special attention. Indeed, their phylogenetic proximity to other genera of Benhamiidae distributed on the South American and African continents makes them an interesting illustration of how the splitting of Gondwana landmass may have influenced macroevolutionary processes in earthworms around 100 million years ago (Csuzdi 1993, 2010). Thus, species with a meronephridic excretory system (i.e., genera *Wegeneriona* and *Neogaster*) evolved on the South American continent and species with a holonephridic excretory system (i.e., genera *Wegeneriella* Michaelsen, 1933 and *Pickfordia* Omodeo, 1958) evolved in Africa. *Omodeoscolex* is an exception in this scheme, as species within this genus are the only ones with holonephridia and a Neotropical distribution. It is important to emphasise here that the three new species of *Omodeoscolex* described in this work have unpaired spermathecae, which distinguishes them from previously known species and calls into question the validity of this character as a criterion for generic distinction. As the topology of barcode trees cannot be reliably used as a proxy for the phylogenetic relationships of *Omodeoscolex*, *Neogaster*, *Wegeneriona* and *Dichogaster* species (Fig. 3B) a multi-locus study will be necessary to clarify the respective positioning of the different Neotropical representatives of the family Benhamiidae.

This work is the first in a series of taxonomic publications in which we aim to study all the OTUs delineated by Maggia *et al.* (2021) and Goulpeau *et al.* (2022) in order to explore more fully the diversity of earthworms in French Guiana. This is a considerable task considering the nearly 300 OTUs delineated by Goulpeau *et al.* (2022) at the scale of this territory. In order to make this objective achievable, we have adopted an approach combining "turbotaxonomy" (*sensu* Butcher *et al.* 2012) and "integrative taxonomy" (*sensu* Dayrat 2005). Turbotaxonomy is the rapid description of many species in "fast papers", thanks in particular to automated procedures and to the increased use of molecular tools for species differentiation and diagnosis (Fernandez-Triana 2022). The combined use of morphological characters and molecular information also defines integrative taxonomy (Padial *et al.* 2010), although papers adopting this integrative approach are not necessarily produced in the fast-paced manner as sought by turbotaxonomy (Fernandez-Triana 2022).

In our case adopting such an approach implies that we do not provide as detailed a description of new species as might be expected in morphological taxonomy. This may seem imperfect and we understand that some readers may regret the absence of certain characters in the descriptions that could be useful for example for future taxonomic revisions. However, our work clearly falls within the scope of alpha taxonomy (*sensu* Mayr & Ashlock 1991), the aim of which is to identify and name new taxa. In this context, the nomenclature code clearly stipulates that "in order to be validly published, a name of a new taxon must be accompanied by a description or diagnosis of the taxon.." (Turland *et al.* 2018; Article 38.1). In accordance with this article and consistently with our objectives, we only provide for each named species a succinct description and a diagnosis that non-equivocally allows it to be positioned at a generic level and separated from related species already known. We consider that this approach is reasonable and necessary given the extraordinary diversity of earthworms in French Guiana.

Supplementary material

The supplementary material of this article is available on the github repository (https://github.com/tdecaens/Turbotaxonomy or https://doi.org/10.5852/zoosystema2024v46a9_s1). It contains an annotated example of the R scripts that were used to generate the automated descriptions and the scripts of Figure 4. The folder '1_Datasets', contains the tables of the paper, the list of specimens with collecting data and other metadata, and a table with the characters used in the descriptions.

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