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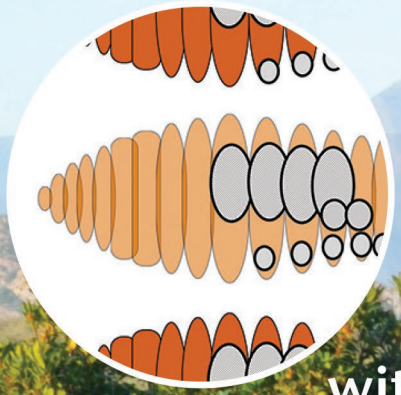

The cradle of giants: insights into the origin of *Scherotheca* Bouché, 1972 (Lumbricidae, Crassiclitellata) with the descriptions of eight new species from Corsica, France

Daniel Fernández MARCHÁN, Jorge DOMÍNGUEZ, Mickaël HEDDE & Thibaud DECAËNS

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Mediterranean chaparral dominated by *Arbutus unedo* L., 1753 at Santo-Pietro-di-Tenda (Haute Corse). In medallion: Schematic representation of the morpho-anatomical features of some of the newly described species.

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The cradle of giants: insights into the origin of *Scherotheca* Bouché, 1972 (Lumbricidae, Crassiclitellata) with the descriptions of eight new species from Corsica, France

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ABSTRACT
Scherotheca Bouché, 1972 is a highly diverse genus of Lumbricidae Rafinesque-Schmaltz, 1815, broadly distributed from Northern Italy and Corsica Island to the Pyrenees and Northeastern Iberian Peninsula. A recent survey of earthworm species diversity in Corsica resulted in the identification of 12 operational taxonomic units (OTU) within *Scherotheca* and the closely related genus *Eumenescolex* Qiu & Bouché, 1998, based on both morphological characters and COI barcodes. In this work, we complete molecular analyses to provide a dataset including four DNA markers (COI, 16S, 28S and ND1) and analyze it through Bayesian phylogeny reconstruction and barcode gap analysis. Our results highlight the existence of eight phylogenetically and morphologically distinct species, new for science, which we described herein as *Scherotheca altarocca* Marchán, Decäens & Domínguez, n. sp., *Scherotheca marceli* Marchán, Decäens & Domínguez, n. sp., *Scherotheca darioi* Marchán, Decäens & Domínguez, n. sp., *Scherotheca boccaverghju* Marchán, Decäens & Domínguez, n. sp., *Scherotheca qiui* Marchán, Decäens & Domínguez, n. sp., *Scherotheca litoralis* Marchán, Decäens & Domínguez, n. sp., *Scherotheca capcorsana* Marchán, Decäens & Domínguez, n. sp. and *Scherotheca mausoleana* Marchán, Decäens & Domínguez, n. sp. The diversity of the genus in Corsica has thus increased from four to 12 species. In addition, *Eumenescolex emiliae* Qiu & Bouché, 1998 appears phylogenetically nested within the Corsican *Scherotheca*, justifying amendment of the name to *Scherotheca emiliae* (Qiu & Bouché, 1998) n. comb. leading to 13 Corsican species in the genus. We further discuss diversity patterns, phylogenetic relationships and biogeographical history of the genus in the Corsica Island.

KEY WORDS
Oligochaeta, Lumbricidae, *Scherotheca*, *Eumenescolex*, Corsica, molecular phylogeny, new combination, new species.

RÉSUMÉ
Le berceau des géants : aperçu de l'origine du genre Scherotheca *Bouché, 1972 (Lumbricidae, Crassiclitellata) et description de huit nouvelles espèces de Corse, France.*
Scherotheca Bouché, 1972 est un genre très diversifié de Lumbricidae Rafinesque-Schmaltz, 1815, largement distribué depuis le nord de l'Italie et la Corse jusqu'aux Pyrénées et au nord-est de la péninsule Ibérique. Un inventaire récent de la diversité spécifique des vers de terre en Corse a permis d'identifier, au sein du genre *Scherotheca* et du genre étroitement apparenté *Eumenescolex* Qiu & Bouché, 1998, 12 unités taxonomiques opérationnelles (OTU) soutenues à la fois par leurs caractères morphologiques et leurs code-barres ADN (gène COI). Dans ce travail, nous complétons ces analyses afin de produire un jeu de données comprenant quatre marqueurs moléculaires (COI, 16S, 28S et ND1), et nous analysons ces données par le biais d'une reconstruction phylogénétique bayésienne et d'une analyse de barcode gap. Nos résultats mettent en évidence l'existence de huit espèces phylogénétiquement et morphologiquement distinctes, nouvelles pour la science, que nous décrivons ici sous les noms de *Scherotheca altarocca* Marchán, Decäens & Domínguez, n. sp., *Scherotheca marceli* Marchán, Decäens & Domínguez, n. sp., *Scherotheca darioi* Marchán, Decäens & Domínguez, n. sp., *Scherotheca boccaverghju* Marchán, Decäens & Domínguez, n. sp., *Scherotheca qiui* Marchán, Decäens & Domínguez, n. sp., *Scherotheca litoralis* Marchán, Decäens & Domínguez, n. sp., *Scherotheca capcorsana* Marchán, Decäens & Domínguez, n. sp. et *Scherotheca mausoleana* Marchán, Decäens & Domínguez, n. sp. La diversité du genre en Corse passe ainsi de quatre à 12 espèces. Par ailleurs, l'espèce *Eumenescolex emiliae* Qiu & Bouché, 1998 s'avère phylogénétiquement nichée au milieu des représentants corses du genre *Scherotheca*, ce qui justifie la modification de son nom en *Scherotheca emiliae* (Qiu & Bouché, 1998) n. comb. et porte à 13 le nombre d'espèces du genre en Corse. Nous discutons également des patrons de diversité, des relations phylogénétiques et de l'histoire biogéographique du genre *Scherotheca* dans l'île de Corse.

MOTS CLÉS
Oligochaeta,
Lumbricidae,
Scherotheca,
Eumenescolex,
Corse,
phylogénie moléculaire,
combinaison nouvelle,
espèces nouvelles.

INTRODUCTION

Lumbricidae Rafinesque-Schmaltz, 1815 is the most diverse earthworm family in the Palearctic, with at least 668 species distributed in more than 63 genera (Csuzdi & Zicsi 2003). A number of new genera and species have been described within the family in the last 20 years (e.g. Csuzdi *et al.* 2011; Szederjesi *et al.* 2014, 2021; Díaz Cosín *et al.* 2014; Domínguez *et al.* 2017; Marchán *et al.* 2020, 2021; Jiménez *et al.* 2021). Among these, *Scherotheca* Bouché, 1972 shows remarkable taxonomic diversity with 41 recognized species and subspecies to date. *Scherotheca* is distributed from Northeastern Italy (including the Tuscan Archipelago) and Southern France (including Corsica) to the Northeastern Iberian Peninsula. The species inhabiting Corsica constitute a homogeneous and distinct group. Qiu & Bouché (1998a) created the subgenus *Corsicadrilus* Qiu & Bouché, 1998 for these species, excluding *Scherotheca brevisella* Bouché, 1972, which they placed together with continental species in the subgenus *Rosanus* Qiu & Bouché, 1998. The Corsican *Scherotheca* are mainly mid-sized endogeic earthworms (generally geophagous, non- to slightly pigmented and horizontal burrowers), unlike most *Scherotheca* species from the continent, which are often large to giant-sized anecics (strongly pigmented, litter-feeding and vertical burrowers). No standardized size classification has been established for earthworms, but for French fauna small earthworms are generally under 5 cm and 0.5 grams, mid-sized earthworms range between 5-10 cm and 0.5-5 grams, large-sized earthworms between 10-30 cm and 5-20 grams, and giant earthworms exceed those sizes (up to 1 metre long and 100 grams in weight).

The evolutionary and biogeographical history of the genus remains unknown. It is possible that *Scherotheca* colonized the Corsican terrane from mainland France, or the genus may have originated in the Corsican terrane and expanded into the continent – most likely before the separation of the island in the Oligocene-Miocene (Oudet *et al.* 2010). The Corsican origin appears to be supported by a previous molecular phylogenetic analysis of the relationships among Lumbricidae (Domínguez *et al.* 2015), which showed three Corsican *Scherotheca* species branching earlier than continental species. However, the diversity of the genus was not fully represented, and further analyses considering a more comprehensive sample will be necessary to support this hypothesis.

The taxonomy of the Corsican *Scherotheca* is further complicated by the specific case of *Scherotheca corsicana* (Pop, 1947) whose original description is a matter of discussion. Indeed, Pop (1947) described this species based on material from four different localities, with none of them explicitly stated as the type locality. In addition, the diagnosis comprised an unusual range of morphological variability in external and internal characters, and for all of the studied populations information about one of the key characters is missing (position of the clitellum, position of the *tubercula pubertatis* or number and position of the spermathecae). Bouché (1972) included several additional populations and described two varieties and a subspecies (*Scherotheca corsicana albomaculata* Bouché, 1972), but he did not designate any type locality nor did he address the question of the morphological heterogeneity within *Sc. corsicana corsicana* (Pop, 1947). Qiu & Bouché (1998a) revised the material available and described two new species:

Scherotheca portonana Qiu & Bouché, 1998 and *Scherotheca omodeoi* Qiu & Bouché, 1998. They also elevated *Sc. corsicana albomaculata* to species level and the varieties *magna* and *popi* to subspecies level. However, the taxonomic status of *Sc. corsicana corsicana* remained uncertain.

Adding further uncertainty to the taxonomy of the Corsican *Scherotheca* and their phylogenetic relationships, the mysterious genus *Eumenescolex* Qiu & Bouché, 1998 partially shares its range and a remarkable morphological similarity with some Corsican *Scherotheca* (besides some internal anatomical details). This has led to suggestions of a close phylogenetic relationship between the two genera (Qiu & Bouché 1998b; Marchán *et al.* 2022b), although this hypothesis has not been formally tested.

During a sampling survey conducted within the Our Planet Reviewed program ("La Planète Revisitée", coordinated by the Muséum national d'Histoire naturelle, Paris, MNHN), specimens assigned to *Scherotheca* and *Eumenescolex* were collected from 25 localities in March-April 2021. Morphological characters and DNA barcoding were used to study the material, and eight *Scherotheca* species putatively new to science were identified (Marchán *et al.* 2022a). In this work, we describe these new taxa and present the results of an integrative morpho-molecular analysis that was performed with the following objectives: 1) to test the hypothesis that Corsica is the evolutionary and biogeographic origin of *Scherotheca*; 2) to clarify the taxonomy and systematics of the Corsican *Scherotheca*; and 3) to establish the phylogenetic relationships between Corsican *Scherotheca* and *Eumenescolex*.

MATERIAL AND METHODS

Specimens, sampling and morphological description

The specimens described in this study were collected during a sampling survey carried out on the island of Corsica in March-April 2021. A total of 185 specimens belonging to the genera *Scherotheca* and *Eumenescolex* were found in 25 localities. The complete list of localities and species is reported in Marchán *et al.* (2022a).

Earthworms were collected by digging and hand-sorting the soil, then rinsed with water and fixed in 70% in order to obtain relaxed (as opposed to excessively retracted) specimens. The earthworms were subsequently transferred to 100% ethanol to enable further molecular analyses. Species classification and morphological diagnoses were conducted using the same set of external and internal morphological characters reported by Qiu & Bouché (1998a).

The following main external morphological characters were considered: mean length, mean number of segments, mean weight, pigmentation, type of prostomium, position of papillae, position of first dorsal pore, position of spermathecal pores, position of clitellum and position of *tubercula pubertatis*. The following main internal anatomical characters were considered: position of oesophageal hearts, position of thickened septa, position and morphology of calciferous glands, position of crop, position of gizzard, type of typhlosole, shape of nephridial bladders, number and position of seminal vesicles, and number and position of spermathecae.

Note that pigmentation is known to be partially lost in fixed earthworms, but it can be still compared between specimens collected around the same time (as the degradation is similar). Unpigmented earthworms can be distinguished from pigmented earthworms regardless of fixation, and slight/moderate pigmentation can be well differentiated with specimens side-by-side (and the use of pictures of alive specimens if necessary).

DNA sequencing and phylogenetic analyses

COI sequences covering all specimens of *Scherotheca* and *Eumenescolex* are reported in Marchán *et al.* (2022a) and are available, together with GenBank accession numbers and associated metadata, in the "Earthworms from Corsica" dataset (DS-EWCORS; https://doi.org/10.5883/DS-EWCORS) of the Barcode of Life Data systems; BOLD; Ratnasingham & Hebert 2007). These sequences were first used to perform a barcode gap analysis based on the uncorrected average pairwise distances to test the relevance of the molecular operational taxonomic units (MOTU) outlined in Marchán *et al.* (2022). Twelve MOTUs were supported by this analysis and were subsequently considered as "putative species". This was done using the "barcode gap analysis" function of BOLD.

The molecular analysis was completed for additional markers. Total genomic DNA was extracted from ventral integument samples, of approximate size 5 × 5 mm, with the DNeasy Blood & Tissue Kit (Qiagen) from two representative specimens of each putative species. Regions of the nuclear 28S rRNA and mitochondrial 16S rRNA, NADH dehydrogenase (ND1) and COI were amplified by polymerase chain reaction (PCR), with the primers and conditions described in Pérez-Losada *et al.* (2009, 2015). PCR products were purified and sequenced by the C.A.C.T.I Genomics service (University of Vigo). The DNA sequences are available in Genbank, under accession numbers ON100588-ON100605, ON133895-ON133912 and ON133915-ON133932.

Sequences from representatives of most of the Lumbricidae genera and an outgroup (Oligochaeta, Haplotaxida, Criodrilidae), were downloaded from Genbank and used as a reference data set. The species included are listed in Appendix 1.

Sequences were aligned with MAFFT v.7 (Katoh & Standley 2013) with default settings. As no significant topological incongruence was detected between the different markers, they were concatenated with BioEdit (Hall 1999), resulting in a matrix of 2970 bp (COI: 606 bp; 16S: 654 bp; ND1: 890 bp; 28S: 820 bp). The best fitting evolutionary model for each partition was selected with jModelTest v. 2.1.3 (Darriba *et al.* 2012) by applying the Akaike information criterion (AIC; Akaike 1973) and the Bayesian information criterion (BIC; Schwarz 1978). GTR + I + G was selected as the best-fitting evolutionary model for COI, 28S and ND1 and HKY+I+G was selected for 16S.

Bayesian inference of the phylogeny was estimated with MRBAYES v.3.1.2 (Ronquist & Huelsenbeck 2003) as implemented in CIPRES Science Gateway V. 3.3. The best-fitting models for each partition were specified independently. Para-

TABLE 1. — Morphological characters of the newly described species of Corsican *Scherotheca* Bouché, 1972 and their closest relatives. Length in millimetres; weight in grams; 1st D.P., position of first dorsal pore. Symbols: *, according to Pop (1947): composite between the different populations included in the original description; **, according to Bouché (1972).

Species	Av. length	Av. # segments	Av. weight	Pigmentation	Papillae	1st D.P.
Sc. albomaculata Bouché, 1972	98-118	110-236	2.07 (1.3-3.06)	Moderate	14, 17, (18, 19), 41-44	11/12
Sc. altarocca Marchán, Decäens & Domínguez, n. sp.	80 (66-95)	149 (135-156)	1.26 (0.81- 1.78)	Absent	(10, 11) 12-16, (29, 30), 31, 32, 37, 38 (39-42).	10/11
Sc. boccaverghju Marchán, Decäens & Domínguez, n. sp.	109 (93-125)	189 (187-191)	1.66 (1.34-1.99)	Slight	28, 30, 35, 36	–
Sc. brevisella Bouché, 1972	198	212	2.76 (1.47-3.55)	Moderate	10, 11, 26-28, 38, 40	11/12
Sc. capcorsana Marchán, Decäens & Domínguez, n. sp.	87 (80-90)	168 (165-171)	1.78 (1.77-1.78)	Moderate	10-16, 17, 27-29, (35)36, 37	–
*Sc. corsicana** (Pop, 1947)	80-150	155-180	?	Absent	?	?
*Sc. corsicana***	90-140	177-215	2-3.5	Slight-moderate	9-11, 27-37	8/9-10/11
Sc. corsicana popi Bouché, 1972	100	155	1.20	Slight	12, 13, (14), 15, 16, 40, 42	10/11
Sc. darioi Marchán, Decäens & Domínguez, n. sp.	75 (65-85)	169 (159-178)	1 (0.76-1.25)	Slight	10-16, 27, 28, 34, 35(36)	9/10
Sc. emiliae (Qiu & Bouché, 1998) n. comb.	93-105	156-161	0.71 (0.29-1.24)	Absent	10,14,27,33,38	9/10(10/11)
Sc. litoralis Marchán, Decäens & Domínguez, n. sp.	71	160	0.82	Moderate	10-16, 17, 27-29 (30), 35, 36	9/10
Sc. marceli Marchán, Decäens & Domínguez, n. sp.	56 (50-62)	150 (127-172)	0.65 (0.61-0.68)	Slight	10-16, 17, 26-28, (35) 36	–
Sc. mausoleana Marchán, Decäens & Domínguez, n. sp.	–	–	–	Moderate	11-14, 16, 28-30, 35, 36	–
Sc. portcrosana Marchán & Decäens, 2020	80 (75-85)	163 (160-166)	2.13 (1.89-2.36)	Slight	11, 12, 14, 27, 29, 34-38	5/6
Sc. portonana Qiu & Bouché, 1998	78-165	193-208	1.8 (1.45-3.4)	Slight	11, 14, 34, 35	8/9
Sc. qiui Marchán, Decäens & Domínguez, n. sp.	74 (64-89)	138 (119-152)	0.92 (0.60-1.4)	Absent	11-14, 16, (26)27, 28, (29), 34-36	(9/10)10/11
Sc. targionii (Baldasseroni, 1906)	15	–	–	Moderate	–	(10/11)11/12

metres 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.

ABBREVIATIONS

Eco&Sols Eco&Sols collection, Montpellier;
MNHN Muséum national d'Histoire naturelle, Paris.

RESULTS

PHYLOGENETIC ANALYSES

The barcode gap analysis (Appendix 2) revealed mean intraspecific distances of between 0 and 5.69%, with an average mean of 1.75%. All maximum intraspecific distances were less than 9% except for *Scherotheca qiui* Marchán, Decäens & Domínguez, n. sp. (9.44%). Interspecific distances (to the nearest neighbour) ranged between 9.27% and 14.13% (mean, 11.37%). When outliers which cause a small overlap were removed (*Sc. quiui* and the *darioi-capcorsana* species pair), a clear barcode gap (8.66%-9.88%) was observed, with interspecific distances within the usual interval observed in other earthworm groups. Together with the morphological differences (Fig. 2; Tables 1; 2), this supports the status of 12 OTUs as different species, of which eight are described as new species below.

The Bayesian phylogenetic analysis recovered all of the studied species of *Scherotheca* within a well-supported clade (Fig. 1; Appendix 3), which also included *Eumenescolex emiliae* Qiu & Bouché, 1998. *Scherotheca albomaculata* Bouché, 1972, representatives of mainland France *Scherotheca* and the other Corsican *Scherotheca* (plus *Scherotheca portcrosana* Marchán & Decaëns, 2020, *Scherotheca targionii* (Baldasseroni, 1906) and *Eu. emiliae*) were recovered as three well-supported clades in a polytomy. The Corsican clade was further divided in two subclades: the first one comprised species from Northern and Central Corsica plus the Tuscan *Sc. targionii*, while the second included species from Southern Corsica and *Sc. portcrosana* from the Hyères archipelago. The representatives of the different putative novel species of *Scherotheca* were all separated by long branches.

TAXONOMY

Phylum ANNELIDA Lamarck, 1802
Class CLITELLATA Michaelsen, 1919
Sub-class OLIGOCHAETA Grube, 1850
Order CRASSICLITELLATA Jamieson, 1988
Sub-order LUMBRICINA De Blainville, 1828
Family LUMBRICIDAE Rafinesque-Schmaltz, 1815

Genus *Scherotheca* Bouché, 1972

Scherotheca Bouché, 1972: 279.

TYPE SPECIES. — *Lumbricus gigas* Dùges, 1828.

DIAGNOSIS. — Lumbricidae of medium to giant size, post-clitellar trapezoidal section. Pigmentation ranging from absent to dark brown. Prostomium epilobous, closed. Longitudinal furrows in the

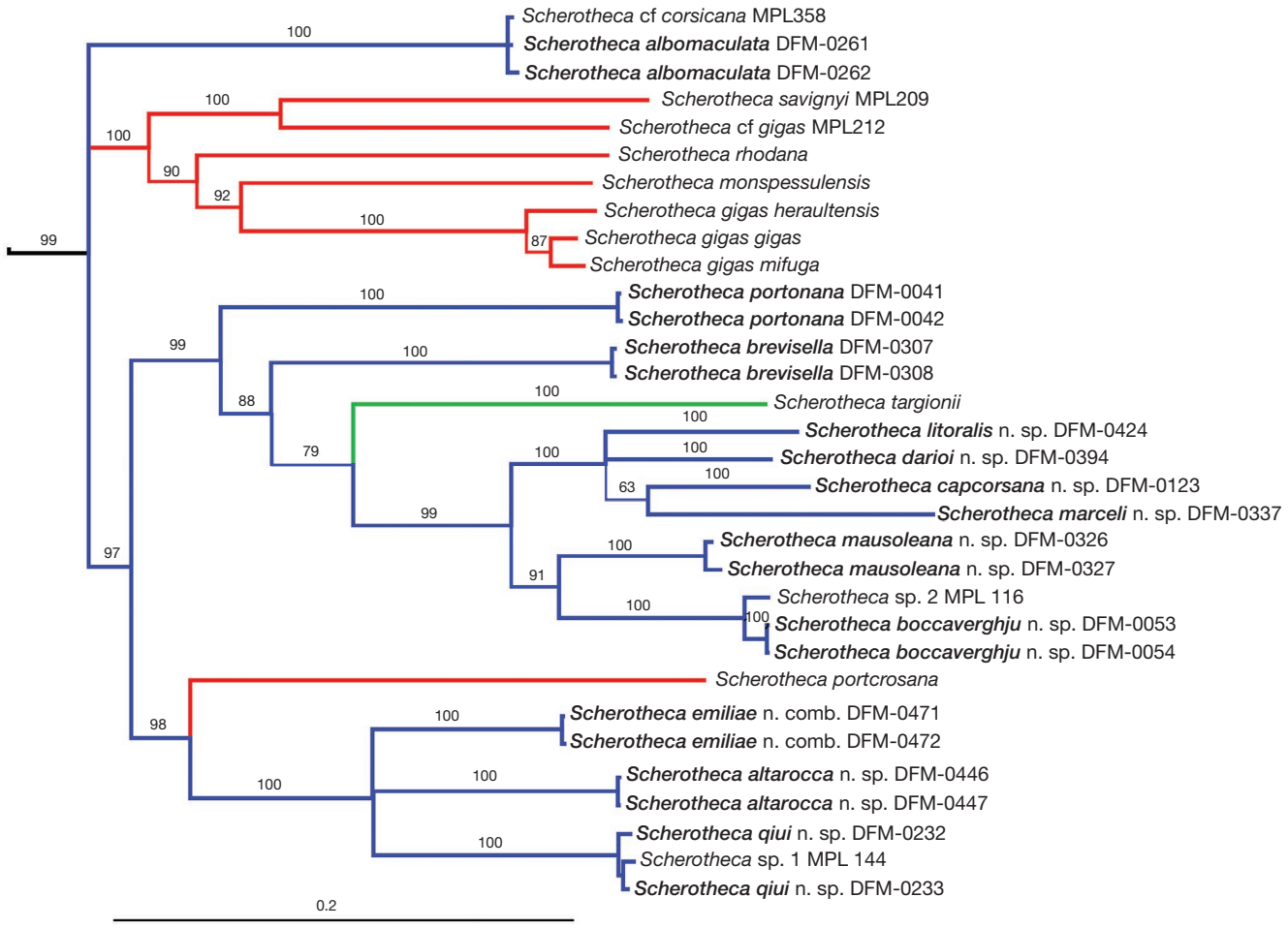

FIG. 1. — Detail of the phylogenetic tree obtained by Bayesian phylogenetic analysis of the concatenated sequence of molecular markers COI, 16S, ND1 and 28S (see full tree in Appendix 3). The species sequenced in this work are shown in **bold**. **Blue branches** indicate Corsican species, **red branches** indicate species from mainland France (and the Hyères archipelago) and **green branches** indicate Tuscan (Italian) species. Posterior probability support values are shown above the corresponding branches; branch thickness is proportional to branch support. Codes besides species names are their BOLD Sample IDs (only for the species sequenced in this study).

peristomium. Nephridial pores "en solfège" (irregularly distributed). Spermathecal pores in at least two intersegments, between 9/10 and 13/14, or 12/13 and 18/19, sometimes multiple. Anterior septa strongly thickened. Male pores in ½ 15, usually with porophores. Gizzard in 17-20 (21, 22). Typhlosole pinnate. Two or four pairs of seminal vesicles in (9, 10) 11, 12.

DISTRIBUTION. — The genus *Scherotheca* is known (from the eastern to the western limits of its range) from Northeastern Italy, Tuscan Archipelago, Corsica Island, Mediterranean continental France and Spanish Catalonia, Southwestern France and part of the Spanish Cantabrian mountains.

Scherotheca altarocca
Marchán, Decäens & Domínguez, n. sp.
(Fig. 3A)

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TYPE MATERIAL. — **Holotype. Corsica** • Adult; Corse du Sud, Zicavo, Castellu d'Ornucciu; 41°52'22"N, 9°9'17"E; 1422 m a.s.l.; 3.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0446; MNHN.

Paratypes. Corsica • 3 adult specimens; Corse du Sud, Olivese (D26 road); 41°50'45"N, 9°4'55"E; 1051 m a.s.l.; 6.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0512, DFM-0513, DFM-0514; MNHN • 3 adult specimens; Corse du Sud, Olivese (D69 road); 41°50'13"N, 9°5'45"E; 1178 m a.s.l.; 6.IV.2021; T. Decaëns, D. Fernández Marchán leg.; Eco&Sols; BOLD Sample ID: DFM-0266, DFM-0267, DFM-0268) • 2 adult specimens, 12 juvenile; same data as for preceding; BOLD Sample ID: DFM-0269, DFM-0270, DFM-0271, DFM-0272, DFM-0274, DFM-0275, DFM-0276, DFM-0277, DFM-0278, DFM-0279, DFM-0280, DFM-0281, DFM-0282, DFM-0283; MNHN • 6 adult specimens; Corse du Sud, Zicavo, Castellu d'Ornucciu; 41°52'22"N, 9°9'17"E; 1422 m a.s.l.; 3.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0447, DFM-0448, DFM-0449, DFM-0450, DFM-0451, DFM-0452; MNHN • 3 adult specimens; Corse du Sud, Zicavo, Ponte di Valpine; 41°52'33"N, 9°7'58"E; 1248 m a.s.l.; 03.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID:, DFM-0443, DFM-0444, DFM-0445; MNHN.

ETYMOLOGY. — The species name is derived from the natural region of Altarocca where the type specimens have been collected (name in apposition).

TABLE 2. — Reproduction-related morphological characters of the newly described species of Corsican *Scherotheca* Bouché, 1972 and their closest relatives. Abbreviations: **Sperm. pores**, position of spermathecal pores; **S.V.**, position of seminal vesicles; **T.P.**, position of *tubercula pubertatis*. Symbols: *, according to Pop (1947): composite between the different populations included in the original description; **, according to Bouché (1972).

Species	Sperm. pores	Clitelum	T.P.	S.V.	Spermathecae
Sc. albomaculata Bouché, 1972	11/12-13/14 multiple	(26)27-37(38)	30-38	9,10,11,12	Multiple 11,12,13
Sc. altarocca Marchán, Decäens & Domínguez, n. sp.	(11/12)12/13, 13/14 simple	(29)30-36(37)	(½ 32)33-36(37)	11,12	Simple (11),12,13
Sc. boccaverghju Marchán, Decäens & Domínguez, n. sp.	12/13, 13/14 multiple	27-36	31-34(½ 35)	9,10,11,12	Multiple 12,13
Sc. brevisella Bouché, 1972	9/10-13/14 simple	½ 27-37	30-37	(10)11,12	Simple 9,10,11,12,13
Sc. capcorsana Marchán, Decäens & Domínguez, n. sp.	12/13, 13/14 simple	(27)28-35(36)	½ 30-34	9,10,11,12	Simple 12,13
*Sc. corsicana** (Pop, 1947)	12/13,13/14 simple/ double/triple	27-35,36 26-34	31-34 30,31-34,35 29-32	9,10,11,12	Simple/double/ triple 12,13
*Sc. corsicana***	12/13, 13/14 simple	(1/2 26)1/2 27-1/2 36(36)	(1/2 30)31-1/2 34(34)	9,10,11,12	Simple 12,13
Sc. corsicana popi Bouché, 1972	12/13, 13/14 simple	30-1/2 37	(33)34-1/2 37	9,10,11,12	Simple 13, 14
Sc. darioi Marchán, Decäens & Domínguez, n. sp.	12/13, 13/14 simple	26-35	29-33	9,10,11,12	Simple 12,13
Sc. emiliae (Qiu & Bouché, 1998) n. comb.	12/13, 13/14 simple	26-35	28-32(33)	11,12	Simple 12,13
Sc. litoralis Marchán, Decäens & Domínguez, n. sp.	12/13, 13/14 simple	27-36	30-34(35)	9,10,11,12	Simple 12,13
Sc. marceli Marchán, Decäens & Domínguez, n. sp.	12/13, 13/14 simple	26-35	(29)30-33	9,10,11,12	Simple 12,13
Sc. mausoleana Marchán, Decäens & Domínguez, n. sp.	12/13, 13/14 simple	(26)27-36(37)	30-34(35)	9,10,11,12	Simple 12,13
Sc. portcrosana Marchán & Decäens, 2020	12/13, 13/14 simple	26-35(½ 36)	30-33	9,10,11,12	Simple 12,13
Sc. portonana Qiu & Bouché, 1998	12/13, 13/14 simple	(25)26-35	(28)29-32(33)	9,10,11,12	Simple 12,13
Sc. qiui Marchán, Decäens & Domínguez, n. sp.	12/13, 13/14 simple	(26)27-35(36)	30-33(1/n 34)	*11,12	Simple 12,13
Sc. targionii (Baldasseroni, 1906)	11/12,12/13 simple/double	(26)27-40	27-40	11,12	Simple/double 11,12

DIAGNOSIS. — *Scherotheca altarocca* Marchán, Decäens & Domínguez, n. sp. can be distinguished from all of the other species of *Scherotheca* (except *Sc. corsicana popi* Qiu & Bouché, 1998) by the position of the clitellum in segments (29)30-36(37) and *tubercula pubertatis* in segments (½ 32)33-36(37) (Tables 1; 2; Figs 2; 3A). Although *Sc. altarocca* Marchán, Decäens & Domínguez, n. sp. resembles *Scherotheca corsicana popi* Qiu & Bouché, 1998 in characters such as the clitellum and *tubercula pubertatis*, it does not exactly fit the description made by Qiu & Bouché (1998a), differing significantly in internal characters such as position of spermathecae and number of seminal vesicles (spermathecae in (11)12, 13 vs 13, 14 and 2 pairs of seminal vesicles in *Sc. altarocca* Marchán, Decäens & Domínguez, n. sp. vs 4 pairs in *Sc. corsicana popi*).
COI uncorrected average pairwise distances and topology of multilocus molecular phylogenetic trees supports the status of *Sc. altarocca* Marchán, Decäens & Domínguez, n. sp. as independent from other morphologically related species for which sequences are available.

DISTRIBUTION AND ECOLOGY. — *Scherotheca altarocca* Marchán, Decäens & Domínguez, n. sp. has been found in the municipality of Olivese and Zicavo, in the natural region of Altarocca, Corse du Sud (Fig. 4A), in *Fagus sylvatica* L. forests and alpine grasslands at moderately high elevations (1051 to 1258 m).

DESCRIPTION

External morphology

Body pigmentation absent. White-beige in fixed specimens (Fig. 3A). Average length, 80 mm (66-95 mm, *n* = 12 adults); body cylindrical in cross-section; average number of segments 149 (135-156 mm, *n* = 11 adults; 135 segments in the holotype). Average weight (fixed specimens), 1.26 g (0.81-1.78 g, *n* = 14 adults). Prostomium epilobous, closed. Longitudinal furrows in segments 1 and 2. First dorsal pore at intersegmental furrow 10/11. Nephridial pores "en solfège" (irregularly distributed). Spermathecal pores at intersegmental furrows (11/12) 12/13 and 13/14 in setal line *c*. Male pores in segment 15, surrounded by a well-developed porophore. Female pores in segment 14. Clitellum saddle-shaped in segments (29)30-36(37). *Tubercula pubertatis* in segments (½ 32)33-36(37). *Chaetae* small and closely paired. Genital papillae in segments (10,11)12-16, (29,30)31,32,37,38(39,40,41,42).

Internal anatomy

Septa 5/6-10/11 thickened and muscular. Hearts in segments 6-11, oesophageal. Calciferous glands in segments 10-14, with diverticula in segment 10. Crop in segments 15-16, gizzard in segments 17-19. Typhlosole pinnate. Male sexual system holandric, testes and funnels (not enclosed in testes sacs, but with sperm present) located ventrally in segments 10 and 11. Two pairs of reniform seminal vesicles in segments 11 and 12; in one individual very inconspicuous, vestigial seminal vesicles present in segments 9 and 10. Ovaries and female funnels in segment 13, ovarian receptacles (ovisacs) in segment 14. Two or three pairs of small globular spermathecae in segments (11), 12 and 13 (intersegments 11/12, 12/13, 13/14). Nephridial bladders U-shaped, reclinate in segment 30.

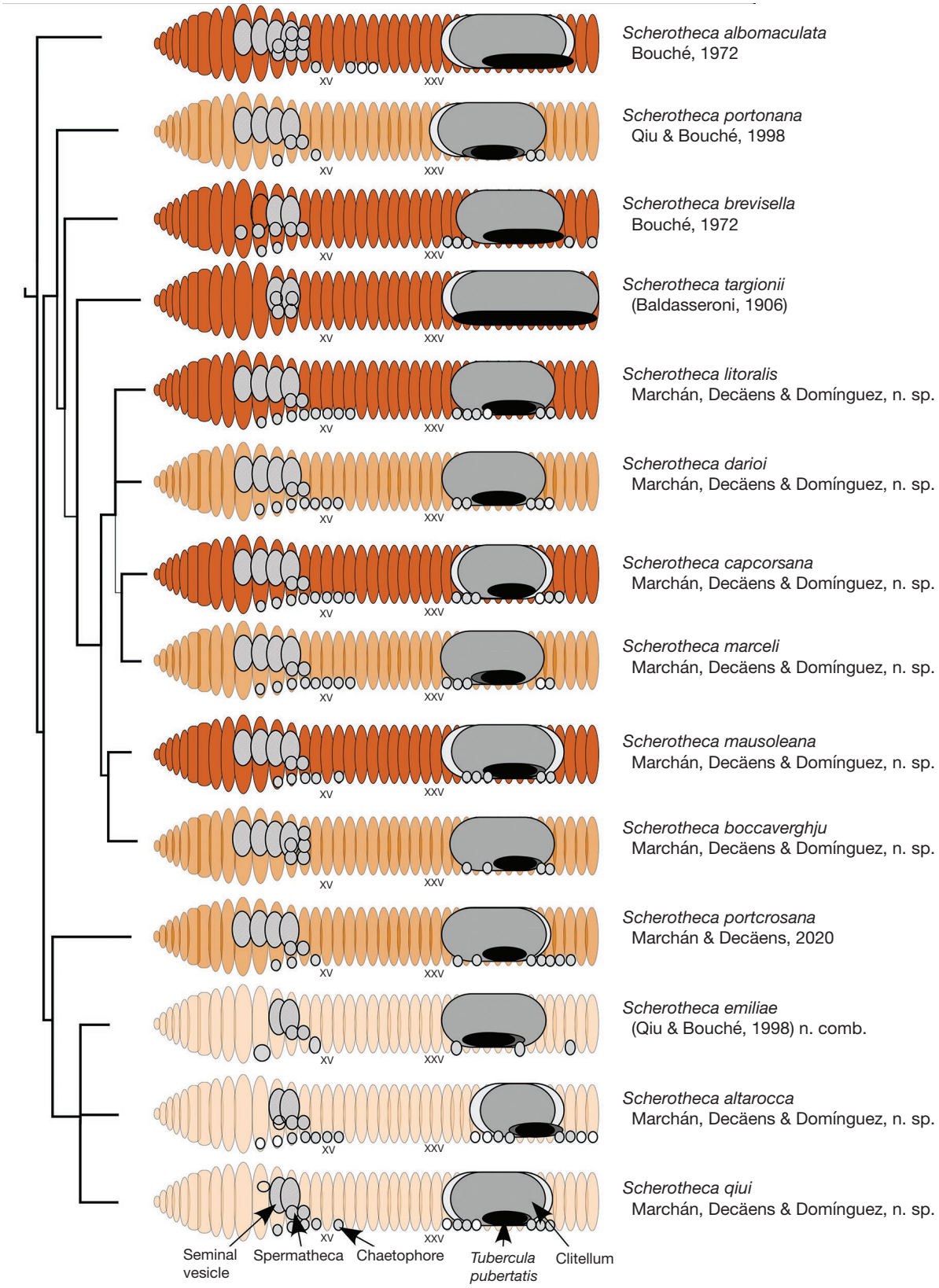

FIG. 2. — External and internal morphological differences between the newly described species of Corsican *Scherotheca* Bouché, 1972 and their closest relatives. The three different shades represent absent, slight and moderate pigmentation. Open circles represent structures that only appear in some individuals. Structures shown in light and dark shades (genital papillae, clitellum and *tubercula pubertatis*) represent the maximum and minimum extension of these characters, respectively. Phylogenetic relationships are the same as those shown in Figure 1.

Remarks

This species displays some degree of morphological variability, with different combinations of extension of clitellum and *tubercula pubertatis*, position of genital papillae and spermathecae. These different morphotypes do not show any clear association with genetic lineages, and therefore they do not appear to correspond to differentiated taxa within the species described here.

This species corresponds to *Sc. corsicana* L6 in the checklist of Corsican earthworms of Marchán *et al.* (2022a).

Scherotheca marceli
Marchán, Decäens & Domínguez, n. sp.
(Fig. 3B)

urn:lsid:zoobank.org:act:65734D0A-192D-4C03-9F9F-DCFE59FE6C64

Type material. — **Holotype**. **Corsica** • Adult; Haute-Corse, Santo-Pietro-di-Tenda, Camping La Canardière; 42°38'56"N, 9°14'9"E; 304 m a.s.l.; 29.III.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0337; MNHN.
Paratypes. **Corsica** • 1 adult specimen; Haute-Corse, Santo-Pietro-di-Tenda, Camping La Canardière; 42°38'56"N, 9°14'9"E; 304 m a.s.l.; 29.III.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0338; Eco&Sols.

Etymology. — This species is named in honour of the well-known taxonomist Marcel Bouché, in recognition of his major contribution to the knowledge of the genus *Scherotheca* and in appreciation of his positive and always constructive comments on the research of the authors of this paper.

Diagnosis. — *Scherotheca marceli* Marchán, Decäens & Domínguez, n. sp. can be distinguished from non-Corsican species of *Scherotheca* by the shorter and more anterior clitellum. It resembles *Scherotheca darioi* Marchán, Decäens & Domínguez, n. sp., *Sc. portonana* and *Sc. portcrosana*, but differs from them by the smaller average length, number of segments and weight, the position of genital papillae and a lighter pigmentation (Tables 1; 2; Figs 2; 3B).
COI uncorrected average pairwise distances and topology of multilocus molecular phylogenetic trees support the status of *Scherotheca marceli* Marchán, Decäens & Domínguez, n. sp. as independent from other morphologically similar species.

Distribution and ecology. — *Scherotheca marceli* Marchán, Decäens & Domínguez, n. sp. was found in a single locality in Santo-Pietro-di-Tenda, Haute Corse (Fig. 4A), in a Mediterranean chaparral at low elevation (304 m).

Description

External morphology

Body pigmentation faint brown. White-beige with brownish colour in the cephalic region in fixed specimens (Fig. 3B). Average length, 56 mm (50-62 mm, *n* = 2 adults); body cylindrical in cross-section; average number of segments 150 (127-172, *n* = 2 adults; 172 segments in the holotype). Average weight (fixed specimens), 0.65 g (0.61-0.68 g, *n* = 2 adults). Prostomium epilobous, closed. Longitudinal furrows in segments 1 and 2. First dorsal pore not seen. Nephridial pores "en solfège" (irregularly distributed). Spermathecal pores in intersegmental furrows 12/13 and 13/14 in setal line *c*. Male pores in segment 15, surrounded by a well-developed porophore. Female pores in segment 14. Clitellum saddle-shaped in segments 26-35. *Tubercula pubertatis* in segments (29)30-33. *Chaetae* small and closely paired. Genital *papillae* in segments 10-16, 17, 26-28, (35) 36.

Internal anatomy

Septa 5/6-10/11 thickened and muscular. Hearts in segments 6-11, oesophageal. Calciferous glands in segments 10-14, with diverticula in segment 10. Crop in segments 15-16, gizzard in segments 17-19. Typhlosole pinnate. Male sexual system holandric, testes and funnels (not enclosed in testes sacs, but with sperm present) located ventrally in segments 10 and 11. Four pairs of reniform seminal vesicles in segments 9, 10, 11 and 12, with the latter two pairs being larger. Ovaries and female funnels in segment 13, ovarian receptacles (ovisacs) in segment 14. Two pairs of small globular spermathecae in segments 12 and 13 (intersegments 12/13, 13/14). Nephridial bladders U-shaped, reclinate in segment 30.

Remark

This species corresponds to *Sc. portonana* L1 in the checklist of Corsican earthworms of Marchán *et al.* (2022a).

Scherotheca darioi
Marchán, Decäens & Domínguez, n. sp.
(Fig. 3C)

urn:lsid:zoobank.org:act:ACEE54C6-DECC-47DC-B0E1-013B83518F75

Type material. — **Holotype**. **Corsica** • Adult; Haute-Corse, Murato, Cagnanozza; 42°33'39"N, 9°18'14"E; 715 m a.s.l.; 1.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0393; MNHN.
Paratypes. **Corsica** • 2 adult specimens; Haute-Corse, Murato; 42°34'12"N, 9°18'21"E; 536 m a.s.l.; 1.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0401, DFM-0402; MNHN • 4 adult specimens; Haute-Corse, Murato, Cagnanozza; latitude/longitude, 42°33'39"N, 9°18'14"E; elevation, 715 m a.s.l.; 1.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0391, DFM-0392, DFM-0393, DFM-0394, DFM-0395; MNHN • 1 adult specimen, 1 juvenile specimen; Haute-Corse, Volpajola; 42°30'54"N, 9°20'52"E; elevation, 313 m a.s.l.; 1.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0143, DFM-0150; MNHN • 2 adult specimens; same data as for preceding; BOLD Sample ID: DFM-0148, DFM-0149; Eco&Sols.

Etymology. — This species is named in honour of Prof. Darío J. Díaz Cosín, renowned earthworm taxonomist and mentor of several earthworm researchers including the first author of this paper.

Diagnosis. — *Scherotheca darioi* Marchán, Decäens & Domínguez, n. sp. can be distinguished from non-Corsican species of *Scherotheca* by the shorter and more anterior clitellum. It resembles *Sc. marceli* Marchán, Decäens & Domínguez, n. sp., *Sc. portonana* and *Sc. portcrosana*, but differs from *Sc. marceli* Marchán, Decäens & Domínguez, n. sp. in the average length, number of segments, weight and position of the genital papillae; it also differs from *Sc. portonana* and *Sc. portcrosana* by the smaller average length, number of segments and weight, the position of genital papillae, and a lighter pigmentation (Tables 1; 2; Figs 2; 3C).

FIG. 3. — External morphology of the newly described species of Corsican *Scherotheca* Bouché, 1972: **A**, *Scherotheca altarocca* Marchán, Decäens & Domínguez, n. sp.; **B**, *Scherotheca marceli* Marchán, Decäens & Domínguez, n. sp.; **C**, *Scherotheca darioi* Marchán, Decäens & Domínguez, n. sp.; **D**, *Scherotheca boccaverghju* Marchán, Decäens & Domínguez, n. sp.; **E**, *Scherotheca qiui* Marchán, Decäens & Domínguez, n. sp.; **F**, *Scherotheca litoralis* Marchán, Decäens & Domínguez, n. sp.; **G**, *Scherotheca capcorsana* Marchán, Decäens & Domínguez, n. sp.; **H**, *Scherotheca mausoleana* Marchán, Decäens & Domínguez, n. sp. Left side, lateral view; right side, ventral view. Scale bars: 1 cm.

COI uncorrected average pairwise distances and topology of multilocus molecular phylogenetic trees support the status of *Scherotheca darioi* Marchán, Decäens & Domínguez, n. sp. as an independent species from other morphologically similar species.

DISTRIBUTION AND ECOLOGY. — *Scherotheca darioi* Marchán, Decäens & Domínguez, n. sp. was found in the regions of Murato and Volpajola, Haute Corse (Fig. 4A), in Mediterranean chaparral, *Quercus suber* open wood and ripicolous grasslands, indicating a remarkable ecological plasticity.

DESCRIPTION

External morphology

Body pigmentation faint brown. Beige with white-beige clitellum in fixed specimens (Fig. 3C). Average length 75 mm (65-85 mm, *n* = 6 adults); body cylindrical in cross-section; average number of segments 169 (159-178, *n* = 5 adults; 168 segments in the holotype). Average weight (fixed specimens), 1 g (0.76-1.25 g, *n* = 6 adults). Prostomium epilobous, closed. Longitudinal furrows in segments 1 and 2. First dorsal pore in intersegmental furrow 9/10. Nephridial pores "en solfège" (irregularly distributed). Spermathecal pores in intersegmental furrows 12/13 and 13/14 in setal line *c*. Male pores in segment 15, surrounded by a well-developed porophore. Female pores in segment 14. Clitellum saddle-shaped in segments 26-35. *Tubercula pubertatis* in segments 29-33. Chaetae small and closely paired. Genital papillae in segments 10-(14)16,27,28,34,35(36).

Internal anatomy

Septa 5/6-10/11 thickened and muscular. Hearts in segments 6-11, oesophageal. Calciferous glands in segments 10-14, with diverticula in segment 10. Crop in segments 15-16, gizzard in segments 17-19. Typhlosole pinnate. Male sexual system holandric, testes and funnels (not enclosed in testes sacs, but with sperm present) located ventrally in segments 10 and 11. Four pairs of reniform seminal vesicles in segments 9, 10, 11 and 12, with the latter two pairs being larger. Ovaries and female funnels in segment 13, ovarian receptacles (ovisacs) in segment 14. Two pairs of small globular spermathecae in segments 12 and 13 (intersegments 12/13, 13/14). Nephridial bladders U-shaped, reclinate in segment 30.

REMARK

This species corresponds to *Sc. portonana* L2 in the checklist of Corsican earthworms of Marchán *et al.* (2022a).

Scherotheca boccaverghju
Marchán, Decäens & Domínguez, n. sp.
(Fig. 3D)

urn:lsid:zoobank.org:act:5A5CAD1F-B242-418D-856E-3646F3D64BD7

TYPE MATERIAL. — **Holotype. Corsica** • Adult; Haute-Corse, Albertacce, Col de Vergio; 42°17'27"N, 8°52'44"E; 1450 m a.s.l.; 28.III.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0054; MNHN.
Paratypes. Corsica • 1 adult specimen; Haute-Corse, Albertacce, Col de Vergio; 42°17'27"N, 8°52'44"E; 1450 m a.s.l.; 28.III.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0053; Eco&Sols • 1 juvenile specimen; same data as for preceding; BOLD Sample ID: DFM-0057; MNHN.

ETYMOLOGY. — The species name is derived from the Corse name of the type locality (Bocca à Verghju, Col de Vergio). Name in apposition.

DIAGNOSIS. —*Scherotheca boccaverghju* Marchán, Decäens & Domínguez, n. sp. can be distinguished from all the other species of *Scherotheca* by the combination of position of the clitellum in segments 27-36, *tubercula pubertatis* in segments 31-34(½ 35) and multiple spermathecae in segments 12 and 13 (Table 1; 2; Figs 2; 3D). COI uncorrected average pairwise distances and topology of multilocus molecular phylogenetic trees support the status of *Scherotheca boccaverghju* Marchán, Decäens & Domínguez, n. sp. as independent from other morphologically similar species.

DISTRIBUTION AND ECOLOGY. —*Sc. boccaverghju* Marchán, Decäens & Domínguez, n. sp. was found in Col de Vergio, Albertacce (Fig. 4A), in an alpine grassland at a relatively high elevation (1450 m).

DESCRIPTION

External morphology

Body pigmentation faint brown. White-beige with dorsal brownish mid-segment brown bands in fixed specimens (Fig. 3D). Average length, 109 mm (93-125 mm, *n* = 2 adults); body cylindrical in cross-section; average number of segments, 189 (187-191, *n* = 2 adults; 187 segments in the holotype). Average weight (fixed specimens), 1.66 g (1.34-1.99 g, *n* = 2 adults). Prostomium epilobous, closed. Longitudinal furrows in segments 1 and 2. First dorsal pore in unknown intersegmental furrow. Nephridial pores "en solfège" (irregularly distributed). Spermathecal pores in intersegmental furrows 12/13 and 13/14 in setal line *c*, multiple. Male pores in segment 15, surrounded by a well-developed porophore. Female pores in segment 14. Clitellum saddle-shaped in segments 27-36. *Tubercula pubertatis* in segments 31-34(½ 35). Chaetae small and closely paired. Genital papillae in segments 28,30,35,36.

Internal anatomy

Septa 5/6-10/11 thickened and muscular. Hearts in segments 6-11, oesophageal. Calciferous glands in segments 10-14, with diverticula in segment 10. Crop in segments 15-16, gizzard in segments 17-19. Typhlosole pinnate. Male sexual system holandric, testes and funnels (not enclosed in testes sacs, but with sperm present) located ventrally in segments 10 and 11. Four pairs of reniform seminal vesicles in segments 9, 10, 11 and 12, with the latter two pairs being significantly larger. Ovaries and female funnels in segment 13, ovarian receptacles (ovisacs) in segment 14. Multiple small globular spermathecae in segments 12 and 13 (intersegments 12/13, 13/14). Nephridial bladders U-shaped, reclinate in segment 30.

REMARK

This species corresponds to *Sc. corsicana* L1 in the checklist of Corsican earthworms of Marchán *et al.* (2022a).

Scherotheca qiui
Marchán, Decäens & Domínguez, n. sp.
(Fig. 3E)

urn:lsid:zoobank.org:act:78F07B1F-8F87-4BC8-A454-5E7E3096EC24

TYPE MATERIAL. — **Holotype. Corsica** • Adult; Corse du Sud, Zonza; 41°44'34"N, 9°11'42"E; 785 m a.s.l.; 4.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0235; MNHN. **Paratypes. Corsica** • 1 juvenile specimen; Corse du Sud, Olivese (D69 road); 41°50'13"N, 9°5'45"E; 1178 m a.s.l.; 6.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0273; MNHN • 2 adult specimens; Corse du Sud, Zicavo, Ponte di Valpine; 41°52'33"N, 9°7'58"E; 1248 m a.s.l.; 3.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0441, DFM-0442; MNHN • 3 adult specimens; Corse du Sud, Zonza; 41°44'34"N, 9°11'42"E; 785 m a.s.l.; 4.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0230, DFM-0232, DFM-0233; Eco&Sols • 4 adult specimens, 1 juvenile specimen; same data as for preceding; BOLD Sample ID: DFM-0234, DFM-0236, DFM-0237, DFM-0238, DFM-0248; MNHN • 4 adult specimens, 7 juvenile specimens; Corse du Sud, Zonza, Pacciunituli (D368 road); 41°43'26"N, 9°12'10"E; 940 m a.s.l.; 4.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0159, DFM-0160, DFM-0161, DFM-0162, DFM-0163, DFM-0164, DFM-0165, DFM-0166, DFM-0167, DFM-0168, DFM-0169; MNHN • 2 adult specimens; Corse du Sud, Zonza, Pacciunituli (D67 road); 41°44'9"N, 9°10'51"E; 813 m a.s.l.; 03.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0434, DFM-0435; MNHN • 5 adult specimens; Corse du Sud, Zonza, Samulaghia; 41°45'43"N, 9°13'8"E; 975 m a.s.l.; 4.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0483, DFM-0484, DFM-0485, DFM-0486, DFM-0487); MNHN.

ETYMOLOGY. — This species is named after Prof. Jianping Qiu, in recognition to its significant contribution to the taxonomic knowledge of the genus *Scherotheca*.

DIAGNOSIS. — *Scherotheca qiui* Marchán, Decäens & Domínguez, n. sp. can be distinguished from non-Corsican species of *Scherotheca* by the shorter and more anterior clitellum. It resembles *Scherotheca litoralis* Marchán, Decäens & Domínguez, n. sp. and *Scherotheca mausoleana* Marchán, Decäens & Domínguez, n. sp., from which it differs by the absence of pigmentation, the number of seminal vesicles (2 pairs instead of 4 pairs in its close relatives) and by the shorter *tubercula pubertatis* (30-33($^{1}/_{n}$ 34) instead of 30-34(35) (Table 1; 2; Figs 2; 3E).
COI uncorrected average pairwise distances and topology of multilocus molecular phylogenetic trees support the status of *Sch. qiui* Marchán, Decäens & Domínguez, n. sp. as separate from other morphologically similar species.

DISTRIBUTION AND ECOLOGY. —*Scherotheca qiui* Marchán, Decäens & Domínguez, n. sp. was found in several localities in the region of Zonza and Zicavo, Corse du Sud (Figure 4a), mainly in *Pinus laricio* forests at moderate elevations (785 to 1248 m), with some individuals found in *Fagus sylvatica* forests and shrublands.

DESCRIPTION

External morphology

Body unpigmented. White-beige in fixed specimens (Fig. 3E). Average length, 74 mm (64-89 mm, *n* = 13 adults); body cylindrical in cross-section; average number of segments, 138 (119-152, *n* = 11 adults; 142 segments in the holotype). Average weight (fixed specimens), 0.92 g (0.60-1.4 g, *n* = 2 adults). Prostomium epilobous, closed. Longitudinal furrows in segments 1 and 2. First dorsal pore in intersegmental furrow (9/10)10/11. Nephridial pores "en solfège" (irregularly distributed). Spermathecal pores at intersegmental furrows 12/13 and 13/14 in setal line *c*. Male pores in segment 15, surrounded by a well-developed porophore. Female pores in segment 14. Clitellum saddle-shaped in segments (26)27-35(36). *Tubercula pubertatis* in segments 30-33($^{1}/_{n}$ 34). Chaetae small and closely paired. Genital papillae in segments 11-14,16, (26)27, 28, (29)34, 35, 36.

Internal anatomy

Septa 5/6-10/11 thickened and muscular. Hearts in segments 6-11, oesophageal. Calciferous glands in segments 10-14, with diverticula in segment 10. Crop in segments 15-16, gizzard in segments 17-19. Typhlosole pinnate. Male sexual system holandric, testes and funnels (not enclosed in testes sacs, but with sperm present) located ventrally in segments 10 and 11. Two pairs of reniform seminal vesicles in segments 11 and 12, sometimes with one or two pairs of vestigial seminal vesicles in segments 9 and 10. Ovaries and female funnels in segment 13, ovarian receptacles (ovisacs) in segment 14. Two pairs of small globular spermathecae in segments 12 and 13 (intersegments 12/13, 13/14). Nephridial bladders U-shaped, reclinate in segment 30.

REMARKS

This species corresponds to *Sc. corsicana* L2 in the checklist of Corsican earthworms of Marchán *et al.* (2022a).

Scherotheca quiui n. sp. displayed a level of intraspecific genetic divergence which was slightly above the expected threshold (around 9%), which could indicate the existence of cryptic genetic linages.

Scherotheca litoralis
Marchán, Decäens & Domínguez, n. sp.
(Fig. 3F)

urn:lsid:zoobank.org:act:B9F4D51C-0A1A-49E9-B7C7-C9275C9E9B01

TYPE MATERIAL. — **Holotype. Corsica** • Adult; Haute-Corse, Ghisonaccia, Marais de Cattolica; 42°1'15"N, 9°28'12"E; 8 m a.s.l.; 2.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0425; MNHN.
Paratypes. Corsica • 2 adult specimens; Haute-Corse, Ghisonaccia, Marais de Cattolica; 42°1'15"N, 9°28'12"E; 8 m a.s.l.; 2.IV.2021; T. Decaëns, D. Fernández Marchán leg.; Eco&Sols; BOLD Sample ID: DFM-0424, DFM-0426 • 2 adult specimens; same data as for preceding; MNHN; BOLD Sample ID: DFM-0427, DFM-0428).

ETYMOLOGY. — The species name is derived from the habitat in which it was found, a littoral pine forest located immediately behind the dune line in the Marais de Cattolica.

DIAGNOSIS. —*Scherotheca litoralis* Marchán, Decäens & Domínguez, n. sp. can be distinguished from non-Corsican species of *Scherotheca* by the shorter and more anterior clitellum. It resembles *Sc. qiui* Marchán, Decäens & Domínguez, n. sp. and *Sch. mausoleana* Marchán, Decäens & Domínguez, n. sp. It can be distinguished from *Sc. qiui* n.sp. by the presence of pigmentation, the number of seminal vesicles (4 pairs instead of 2 pairs) and by the longer *tubercula puberta-*

tis (30-34(35) instead of 30-33(1/n 34)), and from *Sc. mausoleana* Marchán, Decäens & Domínguez, n. sp. by the position of genital papillae and the shorter clitellum (27-36 instead of (26)27-36(37)). The specimens also presented a more developed male porophore than found in both closely related species (Tables 1; 2; Figs 2; 3f). COI uncorrected average pairwise distances and topology of multilocus molecular phylogenetic trees supports the status of *Sc. litoralis* Marchán, Decäens & Domínguez, n. sp. as independent from other morphologically similar species.

DISTRIBUTION AND ECOLOGY. — *Scherotheca litoralis* Marchán, Decäens & Domínguez, n. sp. was found in a single locality in Ghisonaccia, Haute-Corse (Fig. 4A), in a pine forest on sandy soil, at almost sea level (8 m a.s.l) and close to the sea (200 m).

DESCRIPTION

External morphology

Body pigmentation brown. Beige with dorso-ventral and antero-posterior brownish gradients and white-beige clitellum in fixed specimens (Fig. 3F). Average length, 71 mm (n = 1 adult); body cylindrical in cross-section; average number of segments, 160 (*n* = 2 adult). Average weight (fixed specimens), 0.82 g (*n* = 1 adult). Prostomium epilobous, closed. Longitudinal furrows in segments 1 and 2. First dorsal pore in intersegmental furrow 9/10. Nephridial pores "en solfège" (irregularly distributed). Spermathecal pores in intersegmental furrows 12/13 and 13/14 in setal line *c*. Male pores in segment 15, surrounded by a greatly developed porophore. Female pores in segment 14. Clitellum saddle-shaped in segments 27-36. *Tubercula pubertatis* in segments 30-34(35). Chaetae small and closely paired. Genital papillae in segments 10-16,17,27-29(30),35,36.

Internal anatomy

Septa 5/6-10/11 thickened and muscular. Hearts in segments 6-11, oesophageal. Calciferous glands in segments 10-14, with diverticula in segment 10. Crop in segments 15-16, gizzard in segments 17-19. Typhlosole pinnate. Male sexual system holandric, testes and funnels (not enclosed in testes sacs, but with sperm present) located ventrally in segments 10 and 11. Four pairs of reniform seminal vesicles in segments 9, 10, 11 and 12, with the latter two pairs being larger. Ovaries and female funnels in segment 13, ovarian receptacles (ovisacs) in segment 14. Two pairs of small globular spermathecae in segments 12 and 13 (intersegments 12/13, 13/14). Nephridial bladders U-shaped, reclinate in segment 30.

REMARK

This species corresponds to *Sc. corsicana* L3 in the checklist of Corsican earthworms of Marchán *et al.* (2022a).

Scherotheca capcorsana
Marchán, Decäens & Domínguez, n. sp.
(Fig. 3G)

urn:lsid:zoobank.org:act:3B68DEE3-DC36-4DF7-92A5-CBE738CE13D6

TYPE MATERIAL. — **Holotype. Corsica** • Adult; Haute-Corse, Cagnano; 42°52'33"N, 9°26'6"E; 150 m a.s.l.; 31.IV.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0123; MNHN.

Paratypes. Corsica • 1 adult specimen, 1 juvenile specimen; Haute-Corse, Cagnano; 42°52'33"N, 9°26'6"E; 150 m a.s.l.; 31.III.2021; T. Decaëns, D. Fernández Marchán leg.; Eco&Sols; BOLD Sample ID: DFM-0124, DFM-0135 • 1 adult specimen, 2 juvenile specimens; same data as for preceding; BOLD Sample ID: DFM-0125, DFM-0136, DFM-0138); MNHN.

ETYMOLOGY. — The species name is derived from Cap Corse, the region where the type populations were discovered.

DIAGNOSIS. — Specimens of *Scherotheca capcorsana* Marchán, Decäens & Domínguez, n. sp. can be distinguished from all the other species of *Scherotheca* by the position of the clitellum in segments (27)28-35(36) and *tubercula pubertatis* in segments ½ 30-34 (Tables 1; 2; Figs 2; 3G).
COI uncorrected average pairwise distances and topology of multilocus molecular phylogenetic trees support the status of *Scherotheca capcorsana* Marchán, Decäens & Domínguez, n. sp. as separate from other morphologically similar species.

DISTRIBUTION AND ECOLOGY. — *Sc. capcorsana* Marchán, Decäens & Domínguez, n. sp. is only known from the type locality in the municipality of Cagnano, Haute-Corse (Fig. 4A), where it has been found in a *Quercus suber* woodland.

DESCRIPTION

External morphology

Body pigmentation brown. Beige with dorso-ventral brownish gradients and white-beige clitellum in fixed specimens (Fig. 3G). Average length, 87 mm (80-90 mm, *n* = 3 adults); body cylindrical in cross-section; average number of segments, 168 (165-171, *n* = 3 adults; 171 segments in the holotype). Average weight (fixed specimens), 1.78 g (1.77-1.78 g, *n* = 2 adults). Prostomium epilobous, closed. Longitudinal furrows in segments 1 and 2. First dorsal pore in unknown intersegmental furrow. Nephridial pores "en solfège" (irregularly distributed). Spermathecal pores in intersegmental furrows 12/13 and 13/14 in setal line *c*. Male pores in segment 15, surrounded by a well-developed porophore. Female pores in segment 14. Clitellum saddle-shaped in segments (27)28-35(36). *Tubercula pubertatis* in segments ½ 30-34. Chaetae small and closely paired. Genital papillae in segments 10-16,17,27-29,(35)36,37.

Internal anatomy

Septa 5/6-10/11 thickened and muscular. Hearts in segments 6-11, oesophageal. Calciferous glands in segments 10-14, with diverticula in segment 10. Crop in segments 15-16, gizzard in segments 17-19. Typhlosole pinnate. Male sexual system holandric, testes and funnels (not enclosed in testes sacs, but with sperm present) located ventrally in segments 10 and 11. Four pairs of reniform seminal vesicles in segments 9, 10, 11 and 12, with the latter two pairs being larger. Ovaries and female funnels in segment 13, ovarian receptacles (ovisacs) in segment 14. Two pairs of small globular spermathecae in segments 12 and 13 (intersegments 12/13, 13/14). Nephridial bladders U-shaped, reclinate in segment 30.

REMARK

This species corresponds to *Sc. corsicana* L4 in the checklist of Corsican earthworms of Marchán *et al.* (2022a).

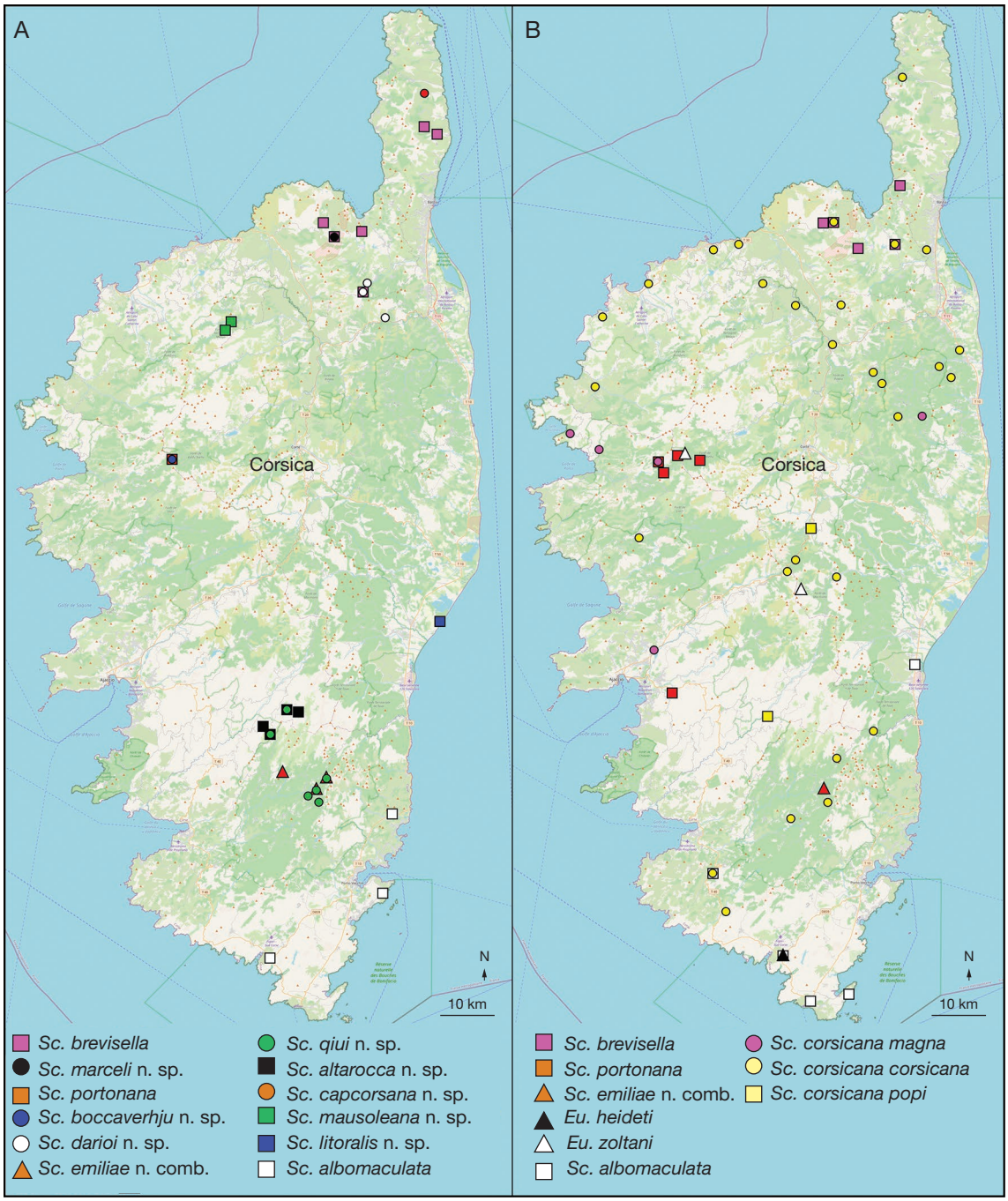

FIG. 4. — Distribution of the genus *Scherotheca* Bouché, 1972 in Corsica: **A**, localities documented in this work of the newly described species and other *Scherotheca* species sampled during this work; **B**, distribution of Corsican species of *Scherotheca* and *Eumenescolex* Qiu & Bouché, 1998 according to Bouché (1972), Qiu & Bouché (1998) and Szederjesi *et al.* (2021).

Scherotheca mausoleana
Marchán, Decäens & Domínguez n. sp.
(Fig. 3H)

urn:lsid:zoobank.org:act:6F27625A-7EA2-44DC-A22D-3FB3A1B1A1B2

TYPE MATERIAL. — **Holotype. Corsica** • Adult; Haute-Corse, Olmi-Cappella, Mausoleo, Tartagine; 42°29'38"N, 8°59'45"E; 779 m a.s.l.; 28.III.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0327; MNHN.

Paratypes. Corsica • 1 juvenile specimen; Haute-Corse, Mausoleo; 42°30'14"N, 9°0'14"E; 635 m a.s.l.; 28.III.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0516; MNHN • 2 adult specimens; Haute-Corse, Olmi-Cappella, Mausoleo, Tartagine; 42°29'38"N, 8°59'45"E; 779 m a.s.l.; 28.III.2021; T. Decaëns, D. Fernández Marchán leg.; BOLD Sample ID: DFM-0326, DFM-0328; Eco&Sols • 1 adult specimen; same data as for preceding; BOLD Sample ID: DFM-0329; MNHN.

ETYMOLOGY. — The species name is derived from the municipality of Mausoléo where the type population has been discovered.

DIAGNOSIS. —*Scherotheca mausoleana* Marchán, Decäens & Domínguez, n. sp. can be distinguished from non-Corsican species of *Scherotheca* by the shorter and more anterior clitellum. It resembles *Sc. qiui* Marchán, Decäens & Domínguez, n. sp. and *Sc. litoralis* Marchán, Decäens & Domínguez, n. sp. It differs from *Sc. qiui* Marchán, Decäens & Domínguez, n. sp. by the presence of body pigmentation, the number of seminal vesicles (4 pairs instead of 2 pairs) and by the longer *tubercula pubertatis* (30-34(35) instead 30-33($^1/_n$ 34)). It can further be distinguished from *Sc. litoralis* Marchán, Decäens & Domínguez, n. sp. by the position of genital papillae and the longer clitellum ((26)27-36(37) instead of 27-36) (Tables 1; 2; Fig. 3H).
COI uncorrected average pairwise distances and topology of multilocus molecular phylogenetic trees support the status of *Sc. mausoleana* Marchán, Decäens & Domínguez, n. sp. as separate from other morphologically similar species.

DISTRIBUTION AND ECOLOGY. — *Sc. mausoleana* Marchán, Decäens & Domínguez, n. sp. is known only from the type locality in the municipality of Mausoleo, Haute-Corse (Fig. 4A), where it has been found in *Pinus laricio* forest and Mediterranean chaparral at moderate elevation (635-779 m).

DESCRIPTION

External morphology

Body pigmentation brown. Beige with antero-posterior brownish gradients and white-beige clitellum in fixed specimens (Fig. 3H). Average length unknown (no complete specimens available) body cylindrical in cross-section; average number of segments unknown (no complete specimens). Average weight (fixed specimens) unknown (no complete specimens). Prostomium epilobous, closed. Longitudinal furrows in segments 1 and 2. First dorsal pore unknown. Nephridial pores "en solfège" (irregularly distributed). Spermathecal pores in intersegmental furrows 12/13 and 13/14 in setal line *c*. Male pores in segment 15, surrounded by a moderately-developed porophore. Female pores in segment 14. Clitellum saddle-shaped in segments (26)27-36(37). *Tubercula pubertatis* in segments 30-34(35). *Chaetae* small and closely paired. Genital papillae in segments 11-14,16,28-30,35,36.

Internal anatomy

Septa 5/6-10/11 thickened and muscular. Hearts in segments 6-11, oesophageal. Calciferous glands in segments 10-14, with diverticula in segment 10. Crop in segments 15-16, gizzard in segments 17-19. Typhlosole pinnate. Male sexual system holandric, testes and funnels (not enclosed in testes sacs, but with sperm present) located ventrally in segments 10 and 11. Four pairs of reniform seminal vesicles in segments 9, 10, 11 and 12, with the latter two pairs being larger. Ovaries and female funnels in segment 13, ovarian receptacles (ovisacs) in segment 14. Two pairs of small globular spermathecae in segments 12 and 13 (intersegments 12/13, 13/14). Nephridial bladders U-shaped, reclinate in segment 30.

REMARK

This species corresponds to *Sc. corsicana* L5 in the checklist of Corsican earthworms of Marchán *et al.* (2022a).

Scherotheca emiliae
(Qiu & Bouché, 1998), n. comb.

Eumenescolex emiliae Qiu & Bouché, 1998: 5.

REMARKS

Based on its position in the molecular phylogenetic trees and on its morphology, *Eumenescolex emiliae* Qiu & Bouché, 1998 is clearly nested within a clade of Corsican *Scherotheca* with two pairs of seminal vesicles (*Sc. altarocca* Marchán, Decäens & Domínguez, n. sp. and *Sc. qiui* Marchán, Decäens & Domínguez, n. sp.). We consequently propose to transfer this species into the genus *Schecotheca* under the new combination *Scherotheca emiliae* n. comb. Other species currently assigned to *Eumenescolex* (i.e., *Eumenescolex pereli* (Bouché, 1972), *Eumenescolex heideti* Qiu & Bouché, 1998, *Eumenescolex gabriellae* Qiu & Bouché, 1998, *Eumenescolex simplex* (Zicsi, 1981) and *Eumenescolex zoltani* Szederjesi, Pavlíček & Csuzdi 2021) should be included in molecular phylogenetic analyses before a full synonymy of *Eumenescolex* and *Scherotheca* can be proposed.

DISCUSSION

SYSTEMATIC IMPLICATIONS

The diversity of the Corsican *Scherotheca* was previously established at four species and three subspecies after Qiu & Bouché (1998a): *Sc. albomaculata*, *Sc. brevisella*, *Sc. portonana*, *Sc. corsicana*, with the last species being subdivided into three subspecies, i.e., *Sc. corsicana corsicana*, *Sc. corsicana magna* Bouché, 1972 and *Sc. corsicana popi*. The current study has increased the number of species to 12, by adding eight new species which do not correspond to any of the previously known taxa.

Two of the new species described in our study (i.e., *Sc. marceli* Marchán, Decäens & Domínguez, n. sp. and *Sc. darioi* Marchán, Decäens & Domínguez, n. sp.) are compatible in their general diagnostic characters with *Sc. portonana*, from which they differ due to their smaller size and lighter pigmentation. In addition, the distinction between both new species and *Sc. portonana* is clearly supported by DNA barcodes as well as by the relative phylogenetic position of the three species (Fig. 1). *Scherotheca altarocca* Marchán, Decäens & Domínguez, n. sp. shows some similarities with *Sc. corsicana popi*, with which it probably shares at least part of its geographical range (Fig. 4). However, the separation of these two taxa is clearly supported by significant differences in morpho-anatomical characters of high diagnostic value.

Scherotheca boccaverghju Marchán, Decäens & Domínguez, n. sp. and *Sc. qiui* Marchán, Decäens & Domínguez, n. sp. both fit with the external morphology of *Sc. corsicana corsicana* as described by Bouché (1972), but their internal morphology is not compatible with this species from which they differ in the number of seminal vesicles and spermathecae. Finally, three species (*Sc. litoralis* Marchán, Decäens & Domínguez, n. sp., *Sc. capcorsana* Marchán, Decäens & Domínguez, n. sp. and *Sc. mausoleana* Marchán, Decäens & Domínguez, n. sp.) also

appear to be compatible with the diagnosis of *Sc. corsicana corsicana* reported by Bouché (1972). Nonetheless, none of them fully matches the original description by Pop (1947). The closest one appears to be *Sc. litoralis* Marchán, Decäens & Domínguez, n. sp., but it differs from Pop's description by the presence of cutaneous pigmentation, and the fact it was found in a remarkably different habitat compared with those prevailing at the type localities of *Sc. corsicana*. Additionally, there are reasonable doubts about the conspecificity of the different populations which constitute the syntypes of *Sc. corsicana corsicana*, as at least one of them presents characteristics similar to *Sc. portonana.* For these reasons we considered reasonable to regard *Sc. litoralis* Marchán, Decäens & Domínguez, n. sp. as a different species than *Sc. corsicana*.

Interestingly, no population compatible with *Sc. corsicana magna* was found during this study. This is not wholly surprising given that we did not carry out intensive sampling in the Western region of Corsica where this subspecies has been reported (Fig. 4). Further field sampling in this area will be necessary in order to include this taxon in molecular phylogenetic analysis and to confirm its possible status as an additional species. *Sc. omodeoi*, which inhabits Maddalena Island (northeastern Sardinia) also remains to be sampled and analyzed, as it has been suggested to be a synonymous of *Sc. corsicana corsicana* by Omodeo & Rota (2004) despite clear morphological differences.

Scherotheca albomaculata was recovered as an independent long branch in the phylogenetic tree. This confirms the accuracy of its elevation to species level from its original status as *Sc. corsicana albomaculata* by Qiu & Bouché (1998a). As the continental species *Scherotheca dugesi* (Rosa, 1895) could not be included in this work, a similar evaluation could not be performed for *Sc. brevisella*, which was originally considered a subspecies of *Sc. dugesi*. However, its recovery within the Corsican *Scherotheca* clade suggests that *Sc. brevisella* is more closely related to these than to other continental species.

Overall, considering the general lack of overlap between the locations of the newly described species and the previously known species (Fig. 4), and the large areas that remain unsampled, we expect that intensifying sampling in Corsica will inevitably result in the discovery of other previously undescribed species. This includes the discovery of new species nested within the populations assigned by Bouché (1972) to *Sc. corsicana corsicana* as well as new species in unsampled regions. This expectation is supported by the results of Marchán *et al.* (2022a), who highlighted that sampling remained unsaturated at the scale of the island, and predicted, through Chao's asymptotic index that increasing sampling effort could result in the discovery of around 20 more endemic species.

Another highlight of our study refers to the phylogenetic relationships among species within the genus *Scherotheca*. According to the phylogenetic tree, the subgenus *Corsicadrilus* in its original conception (i.e., including *Sc. albomaculata*, *Sc. portonana*, *Sc. corsicana* and *Sc. omodeoi*) appears to be paraphyletic, unless all the other members of *Scherotheca* studied (*Scherotheca savigny* Bouché, 1972, *Scherotheca rhodana* (Bouché, 1972), *Scherotheca monspessulensis* Bouché, 1972, *Scherotheca gigas* (Duges, 1828) and *Sc. targionii*) are included. This would make the subgenus redundant, as it would comprise representatives of all the other subgenera (i.e., *Scherotheca*, *Opothedrilus* Bouché, 1972 and *Rosanus*). This highlights the need for a comprehensive systematic revision of the genus.

Biogeography and evolution of *Scherotheca*

The existence of two independent lineages of Corsican *Scherotheca* intermixed with an equally long-branched clade of mainland species can only be explained by initial diversification of the genus while the Corso-Sardinian terrane and Southeastern France were still a continuous land mass. If the divergence of Corsican and continental *Scherotheca* had occurred during or after the separation of Corsica (in the Oligocene-Miocene; Oudet *et al.* 2010), two clearly separated clades would be expected. A pre-rifting origin is supported by the phylogenetic position of *Sc. portcrosana* (from the island of Port-Cros, 8.4 km from the French coast), which is deeply nested within one of the Corsican clades instead of being related to other far more geographically close species in the mainland. Given the higher diversity of *Scherotheca* in Corsica when compared to the area to which it was attached before rifting (Provence), the most likely location of the initial center of diversification of the genus would be the pre-rift Corsica terrane. A small subsample of the ancestral Corsican fauna would have inhabited the periphery of their range (current day Provence) and diversified independently after the separation of the terranes. In order to obtain more robust support for this evolutionary scenario, comprehensive sampling of Provencal *Scherotheca* (and *Eumenescolex*) species will be necessary for inclusion in time-calibrated phylogenetic trees.

Within the *Scherotheca* fauna of Corsica (including the eight newly described species) many species (six out of 13) can be assigned to the ecological category of endogeics (*sensu* Bottinelli *et al.* 2020) according to their absent or faint pigmentation, their small body size and their non-flattened body, or to endo-anecics (three species out of 13; similar but with stronger pigmentation), with only *Sc. albomaculata* and *Sc. brevisella* belonging to the anecics (*sensu* Bottinelli *et al.* 2020). This suggests that even if an evolutionary trend towards the anecic lifestyle had already started within the Corsican fauna, most of the associated traits such as large body size, dark pigmentation and swollen/flattened tail further evolved and became dominant in the mainland clade. Until further research is conducted, it is not clear whether this evolutionary trend is related to different environmental pressures in both regions, or to biotic interactions having led to niche differentiation. Interestingly, the Corsican *Scherotheca* showed strikingly similar morphologies to those of most species of *Aporrectodea s.s.* (Orley, 1885) (e.g. *Aporrectodea trapezoides* (Dugès, 1828) and its closest relatives), from which they are barely distinguishable without studying their internal anatomy. In addition, Marchán *et al.* (2022a) found that the only *Aporrectodea* species inhabiting Corsica are cosmopolitan lineages likely introduced recently by human action. Thus, it appears that both earthworm groups evolved convergently in Corsica and mainland France (even though the center of

diversification of *Aporrectodea s.s.* remains to be identified). Alternatively, this could be a result of shared ancestral character states due to a close phylogenetic relationship between the two genera. Such similarity could have fueled competitive evasion through niche differentiation when both lineages made contact (as *Scherotheca* expanded further into the continent), which would explain the evolutionary trend towards anecic strategy in mainland *Scherotheca* species.

In *Scherotheca*, two internal anatomical characters (i.e., the number of seminal vesicles and the number and position of spermathecae) have been used to differentiate species and to group them in subgenera (Qiu & Bouché 1998a). The same characters were also used to justify considering *Eumenescolex* a separate genus (Qiu & Bouché 1998b). Phylogenetic relationships recovered from molecular data showed that these characters may not be as reliable as previously thought for such purpose. Although character states usually remained stable within populations and species, they often varied between closely related species (for example *Sc. portonana* and *Sc. brevisella*, *Sc. mausoleana* Marchán, Decäens & Domínguez, n. sp. and *Sc. boccaverghju* Marchán, Decäens & Domínguez, n. sp. or *Sc. portcrosana* and its closest Corsican relatives). A similar observation has already been reported for *Eumenescolex* (Qiu & Bouché 1998b), species of which either display four pairs of seminal vesicles and one pair of spermathecae or two pairs of seminal vesicles and two pairs of spermathecae. Beyond systematic implications, this observation reveals an unusual evolutionary plasticity of these characters within the genera *Scherotheca* and *Eumenescolex* (potentially synonymous – see also Marchán *et al.* [2022b]). Such plasticity is not common in other crown group Lumbricidae genera such as *Eisenia* Malm, 1877, *Aporrectodea*, *Lumbricus* Linnaeus, 1758, *Bimastos* Moore, 1893 or *Eisenoides* Gates, 1969, but is rather common within *Dendrobaena* Eisen, 1873 or *Octodrilus* Omodeo, 1956. The evolutionary significance of these characters and the adaptive value of their different character states are poorly known and deserve to be the focus of comparative research across the family.

Acknowledgements

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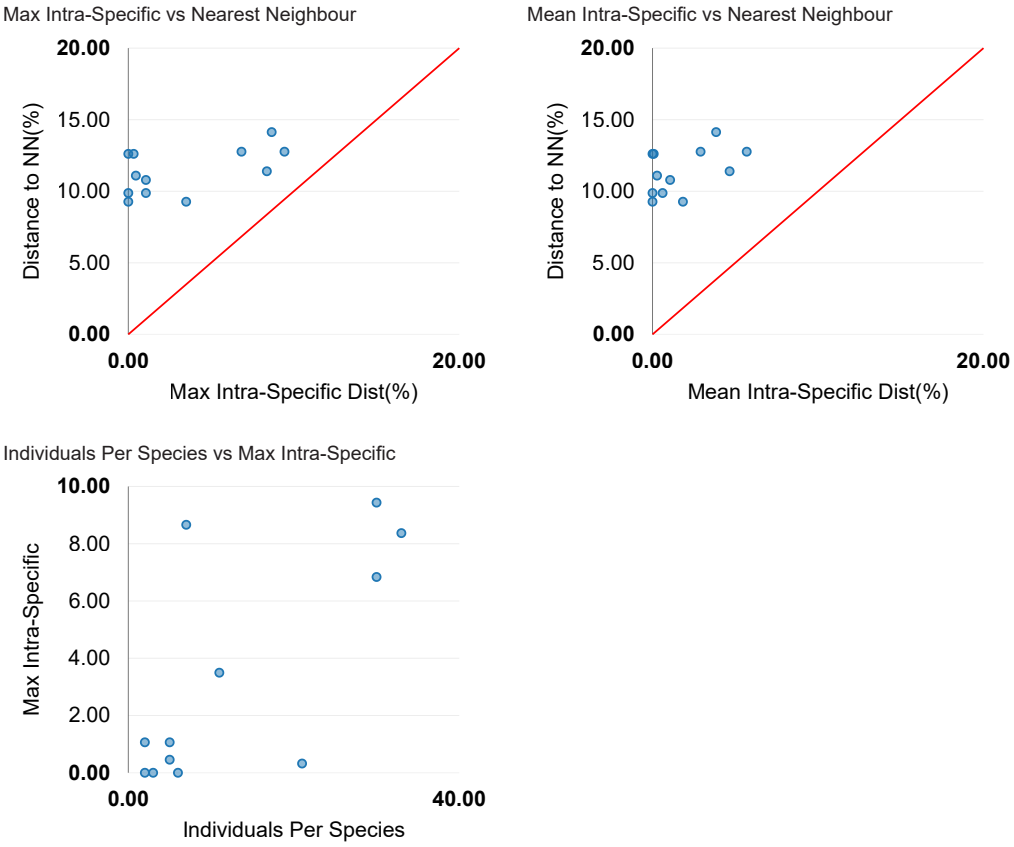
APPENDICES

Appendix 1. — Species included in the phylogenetic trees and publications in which the sequences were made available.

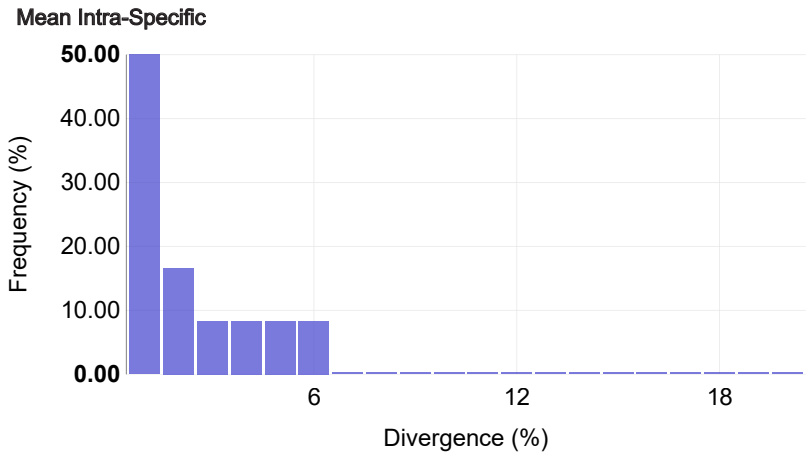
Species	Publication
Allolobophora bartolii Bouché, 1970	Marchán *et al.* 2021b
Allolobophora chlorotica (Savigny, 1826)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Cernosvitovia robusta (Rosa, 1895)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Aporrectodea jassyensis (Michaelsen, 1891)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Aporrectodea limicola (Michaelsen, 1890)	Pérez-Losada *et al.* 2009, 2015; Domínguez *et al.* 2015
Aporrectodea rosea (Savigny, 1826)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Avelona ligra (Bouché, 1969)	Marchán *et al.* 2021b
Castellodrilus ibericus (Trigo, Mariño and Diaz Cosin, 1988)	Jiménez *et al.* 2021
Cataladrilus edwarsi Qiu and Bouché, 1998	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Cernosvitovia dudichi Zicsi and Sapkarev, 1982	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Compostelandrilus bercianus Dominguez *et al.* 2017	Domínguez *et al.* 2015
Criodrilus lacuum Hoffmeister, 1845	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Dendrobaena byblica (Rosa, 1893*)*	Csuzdi *et al.* 2017
Dendrobaena octaedra (Savigny, 1826)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Diporodrilus pilosus Bouche 1972	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Eisenia fétida (Savigny, 1826 *)*	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Eiseniella tetraedra (Savigny, 1826)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Eiseniona albolineata Diaz Cosin, Trigo & Mato, 1989	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Eisenoides lonnbergi (Michaelsen, 1894)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Eophila tellinii (Rosa, 1888)	Paoletti *et al.* 2016; De Sosa *et al.* 2019
Ethnodrilus zajonci Bouche, 1972	Jiménez *et al.* 2021
Galiciandrilus morenoe (Diaz Cosin, Calvin & Mato, 1985)	Pérez-Losada *et al.* 2011, 2015; Domínguez *et al.* 2015
Gatesona rutena Bouché, 1972	Marchán *et al.* 2021b
Helodrilus oculatus (Hoffmeister, 1845)	Marchán *et al.* 2021a
Helodrilus patriarcalis (Rosa, 1893)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Kritodrilus calarensis (Tetry, 1944)	Marchán *et al.* 2021a
Lumbricus rubellus Hoffmeister, 1843	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Octodrilus complanatus (Duges, 1928)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Octolasion lacteum (Orley, 1885)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Postandrilus majorcanus (Qiu & Bouche, 1998)	Pérez-Losada *et al.* 2011, 2015; Domínguez *et al.* 2015
Proctodrilus antipai (Michaelsen, 1891)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Prosellodrilus pyrenaicus (Cognetti, 1904)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Scherotheca cf. gigas	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Scherotheca cf. corsicana (Pop, 1947)	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Scherotheca gigas gigas (Duges, 1828)	Marchán *et al.* 2020
Scherotheca gigas heraultensis Qiu & Bouché, 1998	Marchán *et al.* 2020
Scherotheca gigas mifuga Qiu & Bouché, 1998	Marchán *et al.* 2020
Scherotheca monspessulensis Bouche, 1972	Marchán *et al.* 2020
Scherotheca rhodana Bouché, 1972	Marchán *et al.* 2020
Scherotheca savignyi Bouche, 1972	Domínguez *et al.* 2015; Pérez-Losada *et al.* 2015
Scherotheca sp. 1	Pérez-Losada *et al.* 2009, 2015; Domínguez *et al.* 2015
Scherotheca sp. 2	Pérez-Losada *et al.* 2009, 2015; Domínguez *et al.* 2015
Vindoboscolex hrabei (Cernosvitov, 1935)	Marchán *et al.* 2021a
Vindoboscolex mrazeki (Cernosvitov, 1935)	Marchán *et al.* 2021a
Zophoscolex atlanticus (Bouché, 1972)	Jiménez *et al.* 2021

APPENDIX 2. — Barcode Gap Analysis Result - LPRCE (155 records selected): **A**, three scatterplots are provided to confirm the existence and magnitude of the Barcode Gap. The first two scatterplots show the overlap of the max; **B**, distance distribution histograms; **C**, details for species comparison; **D**, analysis descriptions.

A Three scatterplots are provided to confirm the existence and magnitude of the Barcode Gap. The first two scatterplots show the overlap of the max and mean intra-specific distances vs the inter-specific (nearest neighbour) distances. The third scatterplot plots the number of individuals in each species against their max intra-specific distances, as a test for sampling bias.



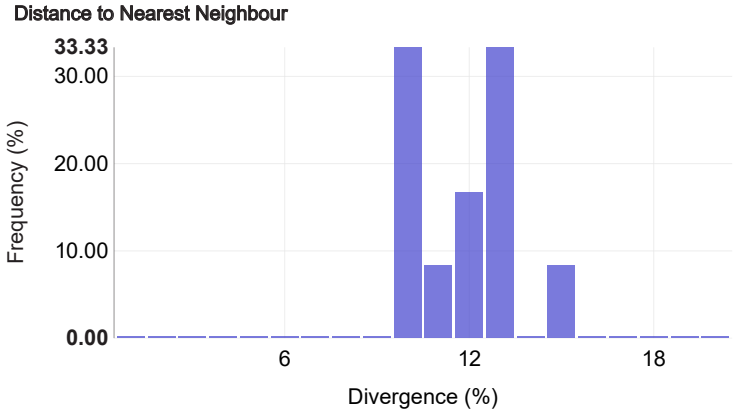
B



Distribution Details

Min:	0	**Mean:**	1.75
Max:	5.69	**SE:**	0.16

Appendix 2. — Continuation.



Distribution Details

Min: 9.27 **Mean:** 11.37

Max: 14.13 **SE:** 0.13

C For each species, the mean and maximum intra-specific values are compared to the nearest neighbour distance in the table below. Where the species is a singleton, N/A is displayed for intra-specific values. Distances are highlighted if the nearest neighbour is less than 2% divergent, or when the distance to the nearest neighbour is less than the max intra-specific distance. Toggle the "Show Warnings Only" button to show only highlighted records.

Order	Family	Species	Mean Intra-Sp	Max Intra-Sp	Nearest Neighbour	Nearest Species	Distance to NN
Haplotaxida	Lumbricidae	Scherotheca albomaculata	3.84	8.66	LPRCE021-21	Scherotheca portonana L3	14.13
Haplotaxida	Lumbricidae	Scherotheca brevisella	4.66	8.37	LPRCE354-21	Scherotheca portonana L2	11.4
Haplotaxida	Lumbricidae	Scherotheca corsicana L1	0	0	LPRCE286-21	Scherotheca corsicana L5	9.88
Haplotaxida	Lumbricidae	Scherotheca corsicana L2	5.69	9.44	LPRCE240-21	Scherotheca corsicana L6	12.77
Haplotaxida	Lumbricidae	Scherotheca corsicana L3	0.27	0.46	LPRCE354-21	Scherotheca portonana L2	11.09

Appendix 2. — Continuation.

Order	Family	Species	Mean Intra-Sp	Max Intra-Sp	Nearest Neighbour	Nearest Species	Distance to NN
Haplotaxida	Lumbricidae	Scherotheca corsicana L4	0	0	LPRCE361-21	Scherotheca portonana L2	9.27
Haplotaxida	Lumbricidae	Scherotheca corsicana L5	0.61	1.06	LPRCE017-21	Scherotheca corsicana L1	9.88
Haplotaxida	Lumbricidae	Scherotheca corsicana L6	2.9	6.84	LPRCE120-21	Scherotheca corsicana L2	12.77
Haplotaxida	Lumbricidae	Scherotheca portonana L1	1.06	1.06	LPRCE361-21	Scherotheca portonana L2	10.79
Haplotaxida	Lumbricidae	Scherotheca portonana L2	1.84	3.5	LPRCE096-21	Scherotheca corsicana L4	9.27
Haplotaxida	Lumbricidae	Scherotheca portonana L3	0	0	LPRCE025-21	Scherotheca portonana L4	12.61
Haplotaxida	Lumbricidae	Scherotheca portonana L4	0.07	0.32	LPRCE021-21	Scherotheca portonana L3	12.61

D

Analysis description

The Barcode Gap Analysis provides the distribution of distances within each species and the distance to the nearest neighbour of each species. Species are tested for the presence of the Barcode Gap.

Distance Model: Pairwise Distance
Marker: COI-5P
Deletion Method: Pairwise Deletion
Minimum Complete Columns: 0
Alignment: MUSCLE (Edgar, 2004)
Filters Applied: ≥ 200bp only

Filter Summary

Data Summary

Appendix 3. — Phylogenetic tree obtained by Bayesian phylogenetic analysis of the concatenated sequence of molecular markers COI, 16S, ND1, and 28S. The species sequenced in this work are shown in bold. Posterior probability support values are shown above the corresponding branches.