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Earthworms (Clitellata, Megadrili) of the world: an updated checklist of valid species and families, with notes on their distribution

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Abstract

In the current paper we present an updated checklist of all the megadrile earthworms (Crassiclitellata: Annelida) in the world, and notes on the distribution of families worldwide. Biogeographic responses to geological phenomena including plate tectonics, as well as to past and present climate and habitat distributions, are the main factors determining the present distribution of earthworm families. A total of ca. 5,738 species/subspecies (5,406 species and 332 unique subspecies; i.e., not counting the nomino-typical subspecies) belonging to 23 families (including one non-crassiclitellate family: Moniligastridae) are currently recognized worldwide, of which three families (Tritogeniidae and Kazimierzidae from Southern Africa and Arecoidae, a new family from Brazil described herein), 35 genera and close to 1200 new taxa (including subspecies) were described in the 21st century. Nonetheless, the large number of still undescribed species will likely increase this value to well over 8,000 species. Ten families are monospecific and/or monogeneric and have a mostly restricted distribution. On the other hand, more than 87 widespread cosmopolitan species have been catalogued, some of them with important invasive potential, belonging mainly to families Lumbricidae, Acanthodrilidae, Benhamiidae, Megascolecidae, Rhinodrilidae and Ocnerodrilidae. Taxonomic housekeeping was performed for the preoccupied Rhinodrilidae genus *Tairona* Righi – herein substituted by *Taironina* nom. nov., and *Guarani camaqua* Rodríguez & Lima was reinstated and removed from synonymy with *Criodrilus lacuum* Hoffmeister, 1845, resulting in a wider definition of the Almidae family. Furthermore, *Amynthas maximalis* nom. nov. is proposed herein as a substitution name for the preoccupied name *Amynthas maximus* Qiu &

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Dong, 2019, and Arecoidae is proposed herein as a new monotypic family for the aquamegadrile species *Areco reco* Righi, Ayres & Bittencourt, 1978.

Key words: Annelida, Biodiversity, Biogeography, Crassiclitellata, Earthworms, Megadriles, Invasive species

Introduction

Megadrile earthworms (Crassiclitellata: Annelida) are a major component of the soil fauna, and often responsible for the majority of the soil animal biomass (Fragoso *et al.* 1999), reaching in some situations, over 1 T ha^{-1} of fresh weight (Phillips *et al.* 2019). Hence, geophagous endogeic (mineral soil dwelling) species may consume considerable amounts of soil (up to more than 400 T ha^{-1}; Lavelle 1988). Earthworms are considered ecosystem engineers (Lavelle *et al.* 1997), and important contributors to soil ecosystem services (Lavelle *et al.* 2006; Blouin *et al.* 2013).

Nonetheless, the distribution of earthworms throughout the world is not uniform. Although they are present in all continents except Antarctica, their abundance and biomass are influenced by factors operating at different spatial and temporal scales (Lavelle *et al.* 1993; Brown & Domínguez 2010; Decaëns 2010). At the largest geographic scale (continents), it is mainly climate and biogeographic history that control their distribution (Michaelsen 1903; Bouché 1983, 2014; Lavelle *et al.* 1993; Phillips *et al.* 2019). Continental drift and the availability of adequate soils and climates in the different land masses of the world promoted diversification and vicariance over millennia, greatly influencing the distribution of earthworm families in the past and present (Omodeo 2000). The current family distributions result in a great part, from these phenomena (Michaelsen 1922).

At regional scales (countries, biomes), climate is also important, but habitat and soil types also begin to play an important role in earthworm distributions (Lavelle 1996), as well as in their abundance and biomass (Phillips *et al.* 2019). However, human activities, both present and past are also extremely important, since they can affect both local and regional climate conditions, as well as habitat availability (Lavelle 1996). Furthermore, humans are major dispersers of earthworms, particularly the anthropochores – cosmopolitan species associated with human activities (Hendrix *et al.* 2008).

However, the overall diversity of earthworm species in the world is not currently known, and there are only a few sources which can be accessed in order to obtain a full listing of the known described species. Just over ten years ago, Csuzdi (2012) first launched the searchable database on "Earthworm species", which can be accessed online (http://earthworm.uw.hu/index.php), and is regularly updated by the author. A couple years later, the DriloBase Taxo project (DriloBase 2022) – was initiated and is still maintained by Emmanuel Lapied. This site provides a list upon demand, and includes over 5,357 names, but has not been updated since 2018. The Integrated Taxonomic Information System (ITIS 2022) also provides a list (prepared by Samuel James in 2014), but it has not been updated since its release. Finally, the Nomenclatura Oligochaetologica first published in 1976 (Reynolds & Cook 1976) and followed by three printed supplements (Reynolds & Cook, 1981, 1989, 1993), is now available online as the second edition (Reynolds & Wetzel 2022), and includes all the oligochaete taxa described (valid and invalid), and is regularly updated. In the present paper, we provide an updated list of the valid megadrile earthworm taxa described up to December 2022, and some notes on the current distribution of earthworm families in the world, making a distinction, when possible, of the main cosmopolitan species, i.e., the widespread peregrine or exotic taxa within each family (if present).

Material and Methods

The available literature on earthworm species distributions at worldwide, regional and country level were reviewed, and combined with personal databases of the authors, as well as the data available in DriloBase (2022), ITIS (2022), Nomenclatura Oligochaetologica (Reynolds & Wetzel 2022), the Earthworm species database (Csuzdi 2012) and Blakemore (2008a).

These data were then used to produce a full list of species, which is available for download from the EU's open access repository Zenodo (Brown *et al.* 2023). The family classification chosen for the present paper is based on that of James and Davidson (2012) and James (2012), expanded by Anderson *et al.* (2017) and Erséus *et al.*

(2020), mainly based on multilocus DNA analyses. Moniligastridae in the Order Moniligastrida – although not Crassiclitellata – was included here as it is part of the Megadrili. Syngenodrilidae and Alluroididae were excluded from the list as they have been tentatively placed into the Order Alluroidida, mainly because we still lack genetic sequence data needed to make a more informed decision as to their placement (Schmelz *et al.* 2021). The list is recognizably not exhaustive and may be missing some species which were not caught in the senior author's searches. If any mistakes are encountered, kindly reach out to the authors to update the list online.

Results and Discussion

More than 6,000 species of megadrile earthworms have been described worldwide (Csuzdi 2012; Reynolds & Wetzel 2022), although the number of valid species is approximately 5,406 (with a total of around 332 unique subspecies; i.e., not counting the nomino-typical subspecies), belonging to 382 genera and 23 families (**Table 1**). Of this total, 1,201 we taxa described in the 21st century: 716 Megascolecidae, 121 Acanthodrilidae, 77 Lumbricidae, 58 Rhinodrilidae, 46 Benhamiidae, 34 Glossoscolecidae, 29 Moniligastridae, 27 Microchaetidae, 21 Ocnerodrilidae, 19 Almidae, 16 Eudrilidae, 13 Hormogastridae, 10 Kynotidae, 6 Tritogenidae, 5 Kazimierzidae, 2 Tumakidae, and 1 Sparganophilidae species/subspecies. Furthermore, three new families and 35 genera were described since 2000 (Brown *et al.* 2023). Nevertheless, numerous, as yet-undescribed taxa are held in many earthworm collections worldwide (including in the authors' institutions), and we acknowledge the highly uneven distribution of earthworm sampling worldwide (e.g., Phillips *et al.* 2019) – with many gaps in important biodiverse hotspots, especially in the tropics. Hence, it is likely that an equally large or larger number of taxa will probably be found with further sampling efforts in the next few decades, though descriptions will continue to lag behind discoveries due to the taxonomic "impediment" (Evenhuis 2007; Magalhães *et al.* 2021). Hence, the total richness of earthworms worldwide is probably well over 8,000 species.

In the following pages, we provide a list of the main families and the number of species/subspecies and genera in each family, as well as some notes on their worldwide distribution, focusing particularly on native species and endemic taxa, but also highlighting some of the main widespread cosmopolitan earthworms, i.e., the anthropochores *sensu* Gates (1972, p. 318), corresponding to the widespread peregrine earthworm species (Lee 1987; Blakemore 2009). The subspecies counts provided are those of unique subspecies, not counting the nomino-typical subspecies.

Acanthodrilidae Claus, 1880

The Acanthodrilidae is the second most speciose earthworm family – 746 species and 48 subspecies in 68 genera. Csuzdi (1996) divided it into three subfamilies: Acanthodrilinae, Octochaetinae and Benhamiinae, but the molecular work of James and Davidson (2012) provided evidence that suggested raising the Behamiinae to family level (Benhamiidae). Hence, we consider Benhamiidae as a separate family here. Diplocardinae Michaelsen 1899 has been proposed, but differently defined. The African, Central and South American, and Austral-Asian octochaetine worms surely belong to Acanthodrilinae (Buckley *et al.* 2011; James & Davidson 2012). Various other subfamilies were proposed by Blakemore (2013), but to date there has been limited acceptance of these subfamilies due to unresolved taxonomic issues and disagreement, and pending further molecular work within the Acanthodrilidae (see Fragoso & Rojas 2016, 2019).

The endemic taxa of Acanthodrilinae can be found throughout the southern continents (South America, South Africa, Madagascar, Australia, New Zealand, New Caledonia and the Antarctic Islands), as well as in the USA, Mexico and the Caribbean Islands (Fragoso & Rojas 2016, 2019; Buckley *et al.* 2011). However, they are completely missing from Europe and the Northern part of Asia (the Palearctic Region). This widely distributed Gondwanan subfamily includes 41 genera and ca. 580 species (updated from Fragoso & Rojas 2016). From continental Central America and the Caribbean Islands and Mexico, we know 14 genera (*Balanteodrilus*, *Borgesia, Diplocardia, Diplotrema, Exxus, Kaxdrilus*, *Larsonidrilus*, *Lavellodrilus*, *Mayadrilus*, *Protozapotecia*, *Neotrigaster, Trigaster, Zapatadrilus, Zapotecia*) and around 120 species (Fragoso & Rojas 2016, 2018, 2019; Cervantes *et al.* 2016). Further endemic genera are found in Eastern African countries and in Madagascar (*Howascolex* and *Vazimbascolex*, with four and one species, respectively; Csuzdi *et al.* 2016; Hong *et al.* 2019).

In USA and Mexico there are over 50 species of *Diplocardia*, and in Mexico, the following additional native genera can be found: *Balanteodrilus* (3 species), *Diplotrema* (6 species), *Kaxdrilus* (3 species), *Larsonidrilus* (2 species), *Lavellodrilus* (3 species), *Mayadrilus* (1 species), *Microscolex* (3 species), *Protozapotecia* (4 species), and *Zapotecia* (2 species) (Reynolds 2020; Fragoso & Rojas 2016, updated with new species). In Central America and the Caribbean, there are the following native genera: *Balanteodrilus* (1 sp.), *Diplotrema* (4 species), *Kaxdrilus* (4 species), *Parachilota* (2 species), *Protozapotecia* (3 species) and *Zapotecia* (1 sp.), while in South America, we find mostly *Chilota* (26 species), *Diplotrema* (9 species), *Microscolex* (10 species) and *Yagansia* (21 species) in the Andean and Pampean regions of Chile and Argentina (Fragoso & Rojas 2016, 2018; Cervantes & Fragoso 2018). *Exxus* is of unknown provenance, but suspected to be Caribbean or Central American.

TABLE 1: Updated list of earthworm families in the world and the number of genera and unique species/subspecies in each, and the number of the most common cosmopolitan (peregrine or widespread) species. For further information, please see dataset available online (Brown *et al.* 2023).

Families	Genera	Species	Subspecies	Cosmopolitan species
Acanthodrilidae	68	746	48	3
Almidae	7	64	4	0
Arecoidae	1	1	0	0
Benhamiidae	20	351	6	6
Biwadrilidae	1	1	0	0
Criodrilidae	1	2	0	1
Diporodrilidae	1	3	2	0
Eudrilidae	45	305	21	2
Glossoscolecidae	6	156	9	1
Hormogastridae	9	37	3	0
Kazimierzidae	1	25	0	0
Komarekionidae	1	1	0	0
Kynotidae	1	22	0	0
Lumbricidae	47	615	74	33
Lutodrilidae	1	1	0	0
Megascolecidae	85	2,208	127	27
Microchaetidae	3	81	6	0
Moniligastridae	5	185	19	3
Ocnerodrilidae	37	172	4	9
Rhinodrilidae	38	376	7	1
Sparganophilidae	1	12	2	1
Tritogeniidae	2	39	0	0
Tumakidae	1	3	0	0
Totals: 23	**382**	**5,406**	**332**	**87**

In Africa, the Acanthodrilinae are distributed mainly in South Africa comprising 5 genera (*Chilota, Eodriloides, Microscolex, Parachilota* and *Udeina*) and ca. 110 species (Plisko & Nxele 2015). In Australia, native acanthodrilinae include six native genera (*Diplotrema, Kayarmacia, Microscolex, Neodiplotrema, Rhododrilu*s and *Torresiella*) and approximately 120 species (expanded from Fragoso & Rojas 2016). However, the genus *Diplotrema* is in need of further work (particularly molecular) within the Acanthodrilinae, which will probably end up splitting off the Neotropical species present in Mexico from those in Oceania (Fragoso & Rojas 2019).

At least two Acanthodrilinae species – *Microscolex dubius* (Fletcher), and *M. phosphoreus* (Dugés), probably originally from Southern South America (Argentina) – are cosmopolitan, although they tend to be more common in subtropical and temperate climate regions (Rota *et al.* 2018b). These species were described from specimens collected outside their native range, and have been widely reported from North American and European countries (e.g., Portugal, Spain, France, Italy, Hungary, Serbia, Bulgaria, Albania and Greece), Australia, New Zealand and South Africa. The species *M. phosphoreus* is a well-known widespread bioluminescent worm, but recent work has shown the need for more detailed analysis of its taxonomy (both morphology and genetics) and questioned the identity of samples deposited throughout the world, due to the presence of cryptic morphs that may be different species (Rota *et al.* 2018b). However, this high morphological plasticity and deep genetic differentiation can also be due to its well-known parthenogenetic reproduction mode (as in many peregrine species) (Gates 1972).

Almidae Duboscq, 1902

Together with Acanthodrilidae this is the most widely distributed family of earthworms (excluding exotic species), being found in tropical Africa, South-East Asia, South America and the Caribbean. It includes 64 species and four subspecies in seven genera. The genera *Alma* (16 spp.) and *Callidrilus* (3 spp.) are exclusively African, while the monospecific genus *Progizzardus* is unique to its type locality in India (Nair *et al.* 2010). The genus *Glyphidrilus* (36 spp.) is found mainly in Southeast Asia (Myanmar, Laos, Cambodia, Thailand, Indonesia, China, Singapore, India, Sri Lanka), with one species *G. stuhlmanni* Michaelsen, present in Africa (Tanzania). In South America and the Caribbean there are three genera present: *Drilocrius*, with seven species spread from Costa Rica to Southeastern Brazil, *Glyphidrilocrius* (1 sp.) in Amazonia, and *Guarani* (1 sp.; see below) in southernmost Brazil and probably Uruguay (Grosso & Brown 2007).

Omodeo (2000) suggested restricting Almidae to *Alma*, moving African *Callidrilus* and Asian *Glyphidrilus* to the Glyphidrilidae, which also included the South American *Drilocrius*, *Glyphidrilocrius* and *Areco*, but *Guarani* does not fit into either of his family definitions (Lima & Rodríguez 2007). *Areco* also does not fit with the Glyphidrilidae as defined by Omodeo (2000). Furthermore, Omodeo placed *Criodrilus, Lutodrilus*, *Sparganophilus*, *Biwadrilus*, and *Komarekiona* in an expanded Criodrilidae, but all of those latter are phylogenetically well-separated from *Criodrilus* (James & Davidson 2012) and each is the sole genus in their respective monogeneric families. At present we cannot clarify phylogenetic relationships among the genera either now or historically assigned to Almidae and/or Glyphidrilidae, because no single phylogenetic analysis includes adequate representation. For now, Almidae are placed between Glossoscolecidae s.s. and Rhinodrilidae in molecular phylogenies; where *Alma* and *Guarani* are present in the same analysis, they are sister taxa (James & Davidson 2012; Anderson *et al.* 2017). Will additional genera from South America (Steffen *et al.* 2018; Ferreira *et al.* 2023) change the picture? Preliminary indications say no.

Taxonomic housekeeping note:

Guarani camaqua Rodríguez & Lima, had been placed by its authors in Criodrilidae (Lima & Rodríguez 2007), but genomic-scale molecular data placed *Guarani* very close to the Almidae (James & Logsdon, unpublished data), to which it is here transferred. Furthermore, cytochrome oxidase-1 (CO1) barcoding of specimens collected in the type locality by two of the authors (James & Brown, unpublished data) in 2012, confirmed the erroneous synonymy (without consultation of the type material for confirmation) of *G. camaqua* with *Criodrilus lacuum* Hoffmeister, by Blakemore (2008b). Finally, evaluation of a specimen from the Knäpper collection (catalog number 5183) at the Universidade do Rio dos Sinos (São Leopoldo, Brazil), seems to indicate that reports of *C. lacuum* by Knäpper (1976) and Knäpper & Porto (1979) from Rio Grande do Sul actually referred to *G. camaqua*, now known from several locations in the state (Ferreira *et al.* 2023), besides its type locality (Camaquã). The inclusion of *Guarani* in Almidae, however, requires expanding the diagnosis of the family to embrace species both with and without spermatophores.

Arecoidae James, Csuzdi & Brown, 2023 Fam. nov.

Type genus: *Areco* Righi, Ayres & Bittencourt, 1978

Diagnosis: Crassiclitellata with quadrangular body, and dorsal post-clitellar groove. Four pairs of closely-paired, regularly distributed hook-shaped setae. Dorsal pores present. Genital pores microscopic. Long muscular esophagus, but no gizzard. No calciferous glands, no prostates or copulatory pouches. Intestine begins in XXXVII, typhlosole present. Pretesticular spermathecae, ovaries in XIII. Moniliform hearts in segments VIII to XI. No subneural vessel. Nephridia holoic, without bladders. Metandric, with one pair of testicles and seminal funnels in segment XI. Seminal vesicles in XII to XV.

Etymology: This new family name derives from the genus name *Areco* which with the species name *reco* is derived from "arecoreco", originally in the Tupi indigenous language, meaning to confuse or to mix something up (Drumond 1952).

Considerations: The intriguing aqua-megadrile (*sensu* Jamieson 1988) species *Areco reco* was described by Righi *et al.* (1978) from four specimens collected at the Reserva Ducke near Manaus, Amazonas (Brazil) in 1975. Type specimens are deposited in the Instituto Nacional de Pesquisas da Amazonia (INPA) collection in Manaus. The authors placed the species tentatively in Sparganophilidae, but emphasized that the exact position of *Areco* was uncertain. They claimed similarity with *Glyphydrilocrius* by shape of body and organization of digestive system, and with *Sparganophilus* by presence of pretesticular spermathecae, though this is a feature shared with several other South American families (e.g., Glossoscolecidae, Rhinodrilidae). Furthermore, *Sparganophilus* and *Glyphydrilocrius* are holandric, while *Areco* is metandric. Additional *Areco* specimens were collected at the type locality by S. James and S. Tapia-Coral in 2012 (Erséus *et al.* 2020), and molecular phylogenomic analyses revealed it to be sister to Rhinodrilidae, and far from Sparganophilidae and other semi-aquatic families (Erséus *et al.* 2020). Nonetheless, Arecoidae shows important genetic divergence and major morphological differences with Rhinodrilidae, lacking gizzard and calciferous glands, so we propose here the erection of this new monotypic family to accommodate its only species and genus.

Benhamiidae Michaelsen, 1897

Native species of the Benhamiidae (351 species and 6 subspecies in 20 genera) are mainly restricted to sub-Saharan Africa, Oceania, Central America and northern South America (Csuzdi 2010). However, a few *Dichogaster* (including the type species of the genus) are also known from the Pacific islands of Fiji and Samoa (Easton 1984; James & Davidson 2012). In Africa, the native Benhamiidae are present mainly in the tropical region with 16 genera (*Afrogaster*, *Agastrodrilus*, *Benhamia*, *Benhamiona*, *Dichogaster*, *Dudichiodrilus*, *Guineoscolex*, *Loksaia*, *Millsonia*, *Monogaster*, *Monothecodrilus*, *Omodeona*, *Pickfordia*, *Pickfordiella*, *Reginaldia* and *Wegeneriella*) and ca. 250 species. From the Neotropics, i.e., the Caribbean islands, Central America, Mexico, and Northern South America we know five genera (*Dichogaster*, *Eutrigaster*, *Neogaster*, *Omodeoscolex*, and *Wegeneriona*) and around 100 species, mainly of *Dichogaster* and *Eutrigaster*, many of which show high endemism rates, particularly on the Caribbean islands. The diversity of the minute South-American species is certainly underestimated due to a lack of sampling, especially in Amazonia, where recent work (in French Guyana), revealed several new species, that are presently being described.

Several species in the family Benhamiidae, particularly in the genus *Dichogaster*, are widespread anthropochores in the tropics, as their native ranges were probably originally in Central and Eastern Africa (Gates 1972; Csuzdi 2010). These species were probably widely dispersed during the centuries of commercial product exchanges between Africa and other continents, where ships could have transported soil in planted pots containing these generally parthenogenetic species. More recent transport with manure piles or agricultural equipment may also have led to the abundance of *Dichogaster gracilis* (Michaelsen), *Dichogaster bolaui* (Michaelsen), *Dichogaster saliens* (Beddard), and *Dichogaster affinis* (Michaelsen) in many no-tillage sites in Southern and Central Brazil, where they may reach abundances well over 100 individuals m^{-2} (Bartz *et al.* 2009; Bartz *et al.* 2014; Santos *et al.* 2018). Although *Dichogaster* spp. are generally restricted to warm and humid tropical regions, several species have been reported from greenhouses in temperate climates and at least one species (*D. bolaui*) was considered a *domicole* (adapted to human homes) species, as it was found in bathtubs, showers and sewage pipes in Hungary, Ireland, Finland, Sweden and Israel (Terhivuo 1991; Erséus *et al.* 1994; Rota & Schmidt 2006; Csuzdi *et al.* 2008). In fact, the type locality of *D. bolaui* is Hamburg, where it was found in fermenting bark at a factory (Michaelsen 1891). *Dichogaster annae* (Horst) is an epigeic species, common in vermicomposting ventures in tropical countries such as Brazil (James & Guimarães 2010), but its distribution is probably much wider than presently known or reported, due to the lack of recognition by worm composters, and the little knowledge of its life-cycle and biology. *Dichogaster modiglianii*

(Rosa) is an epi-endogeic species also with wide distribution (Africa, Southeast Asia, Australia, Oceania, Central America, Caribbean, Southern North America (Blakemore 2010), and was recently found in several Amazonian sites, associated with Pre-Columbian human activities (Conrado 2018). Specimens of *D. bolaui* were also recently reported from a remote and human-free Amazonian rainforest area in Southern French Guyana, highlighting the potential of these cosmopolitan species to establish stable populations that persist centuries after original introduction by humans (Maggia *et al.* 2021).

Biwadrilidae Jamieson, 1971

This monogeneric family includes only one species, *Biwadrilus bathybates* (Stephenson), known only from the Lake Biwa region in Japan. It was originally described as a *Criodrilus* species, and Blakemore (2008b) transferred it back to Criodrilidae based on new material and re-analysis of previously observed material. However, molecular analysis shows this family solidly placed as the sister family to Kynotidae, and therefore quite distant phylogenetically from the Criodrilidae (James & Davidson 2012), hence we maintain it within Biwadrilidae, following Jamieson (1971, 1988).

Criodrilidae Vejdovský, 1884

The Palearctic family Criodrilidae includes mainly aquatic species in a single genus, *Criodrilus* with two valid species, *C. lacuum* from Europe, and *C. ghianae* Qiu & Bouché, from Mediterranean Algeria. The former species, may be among the longest living of earthworms, known to achieve 46 years of age when kept in aquaria (Timm 2020). The species is widely distributed in Europe and common all around the Mediterranean, with its northernmost distribution in Latvia (Smiljkov *et al.* 2005; Blakemore 2008b; Atanacković *et al.* 2013; Valchovski 2013; Mısırlıoğlu 2017; Timm 2020). Outside its native range, *C. lacuum* has only been reported from potted plants in Baltimore (USA) (McKey-Fender & MacNab 1953). Previous reports of this species from Brazil (Knäpper 1976; Knäpper & Porto 1979) actually refer to *G. camaqua*, a species of Almidae (see above, and Ferreira *et al.* 2023).

Diporodrilidae Bouché, 1970

This monogeneric family with three species and two subspecies was erected by Bouché (1970) for specimens collected in the Mediterranean islands of Corsica and Sardinia, from where they are endemic. Recent sampling in Corsica revealed several new lineages and species that must still be described (Marchán *et al.*, 2022b). The validity of this family was also re-affirmed with recent molecular (Anchor-Hybrid Enrichment) analyses, which placed it as sister to the Lumbricidae (Marchán *et al.*, 2022c).

Eudrilidae Claus, 1880

The Eudrilidae is a peculiar earthworm family with internal fertilisation (Clausen 1965; Sims 1969). It consists of 45 genera and 305 species (plus 21 subspecies) distributed in tropical Africa from south of the Sahara to the Kalahari Desert and northern South Africa (Sims 1987). There are only two species in the family regarded as widely introduced peregrines: *Eudrilus eugeniae* (Kinberg) and *Hyperiodrilus africanus* Beddard. The first species, commonly called the "African Nightcrawler" is widespread, found mainly in vermiculture outside its native range (West Africa) throughout the tropics and sub-tropics in Latin America, the Caribbean, Madagascar, Sri Lanka, India, Philippines, Malaysia, Indonesia, Vietnam and Australia (Blakemore 2015). Rarely has this species been found inhabiting soils (Blakemore 2015) and not compost beds, and its survival under these conditions probably requires high moisture and the presence of abundant litter, or organic resources, which are its major food source. The second species, *H. africanus* can also be found frequently in compost-beds and high organic content soils, but its distribution is more restricted, being known from Western (Ivory Coast, Nigeria, Gabon) and Central Africa (Congo, Democratic Republic of Congo, Angola) (Tondoh & Lavelle 2005) and Brazil (Righi 1972; Sousa *et al.* 2020).

Glossoscolecidae Michaelsen, 1900

In its more restricted sense, after the splitting up of the Rhinodrilidae by James (2012), the Glossoscolecidae family is distributed mainly in continental Central and South America from Panama to Northern Argentina and Uruguay. The first species described from Latin America belongs to this family, *Glossoscolex giganteus* Leuckart, a large earthworm from Southeastern Brazil. In fact, the genus contains a relatively large proportion of large-bodied (>30 cm long) species (18 out of 58 known species; Feijoo & Brown 2023). So far, native species are known in the Caribbean Islands only from Guadeloupe (James & Gamiette 2016), but they may likely occur on other islands. The family includes six genera (*Enantiodrilus, Fimoscolex, Glossodrilus, Glossoscolex, Holoscolex*, and *Righiodrilus*) and 156 species (plus 9 subspecies). One widespread species, *Enantiodrilus borellii* Cognetti (with which both *Diaguita* species, *D. vivianae* Righi and *D. michaelseni* Cordero were synonymized by Moreno *et al.* 2005) may constitute a potentially invasive species in the tropics, considering its distribution from Argentina to Venezuela (Fragoso & Brown 2007). As the family occurs in a region with high endemicity (Lavelle & Lapied 2003), there is a large potential to find many new species and possibly genera, with further sampling efforts, particularly in the Andean region and Northern South America, but also in the Atlantic Forest region of Southeastern Brazil (Silva *et al.* 2017).

Hormogastridae Michaelsen, 1900

The family Hormogastridae was recently revised by Marchán *et al.* (2018) using an integrative approach including ecological, morphological and molecular data, and was shown to include nine genera (*Ailoscolex*, *Boucheona*, *Carpetania*, *Diazcosinia*, *Hemigastrodrilus*, *Hormogaster*, *Norana*, *Vignysa*, *Xanina*) and 37 species (plus three subspecies). The genus *Ailoscolex*, with its single known species *Ailoscolex lacteospumosus* Bouché, formerly in the family Ailoscolecidae was basal to all Hormogastridae but kept within the family. The genera show rather restricted distribution and little geographic overlap, with the exception of *Norana* with *Hormogaster* and *Boucheona* (Marchán *et al.* 2018). Overall, the family is restricted to Europe and Northern Africa, being found in Southern France, the Spanish Iberian Peninsula, Corsica, Sardinia, the Tuscan Archipelago, mainland Italy, Sicily, Algeria and Tunisia. So far, no Hormogastridae have been found in Portugal. Given the restricted range of most known species, the future discovery of new taxa in this family is highly probable (see Marchán *et al.* 2023b).

Kazimierzidae Nxele & Plisko, 2016

This recently erected family of earthworms, which includes 25 nominal species all in the single genus *Kazimierzus*, is restricted to the Western Cape and Northern Cape provinces, including the Namaqualand areas, along the Atlantic region of South Africa. This is a hotspot of biodiversity (Myers *et al.* 2000), with considerable topographical and botanic diversity, which will probably still lead to the discovery of new earthworm species, as observed by Nxele *et al.* (2017).

Komarekionidae Gates, 1974

There is only one species in this monogeneric Nearctic family: *Komarekiona eatoni* Gates. It is found only in the mid-Atlantic states west to southern Illinois, USA (Gates 1974; Reynolds 2020). Interestingly, the specimens east of the Smoky Mountains are amphimictic while those west of the Smokies are parthenogenetic (Reynolds 2020).

Kynotidae Jamieson, 1971

This endemic family appears to be restricted to Madagascar (Razafindrakoto *et al.* 2017) and includes a single genus (*Kynotus*) and 22 species. The description of *K. verticillatus* Perrier, was not adequate and it cannot be assigned to any other named species or any other genus or species. It was described as Acanthodrilus "*pas du tout développé et paraissant réduit aux quatre pénis formés de soies courbes caractéristiques jusqu'ici des vers de ce genre*" (Perrier 1872).

Lumbricidae Rafinesque-Schmaltz, 1815

The Lumbricidae is the phylogenetically youngest family in the subclass of Oligochaeta. The family perhaps originated in the Palearctic but there is a well-supported clade native to Eastern North America. Overall, the Lumbricidae family comprises some 615 species and 74 subspecies belonging to 47 genera (Brown *et al.* 2023), although the lumbricid taxonomy is still controversial and not yet settled (Bouché 1972; Mršić 1991; Qiu & Bouché 1998; Csuzdi & Zicsi 2003; Domínguez *et al.* 2015; de Sosa *et al.* 2019; Marchán *et al.* 2022a; Marchán *et al.* 2022c). Around 33 cosmopolitan species of the family are widespread and often invasive in numerous regions (Blakemore 2009), such as North America, Australia, New Zealand, South Africa, Southern South America, and even in equatorial countries at higher elevation (e.g., Zicsi 2007).

In North America there are both native and non-native species and genera. The native genera are *Bimastos* and *Eisenoides* with 15 and two species, respectively. There are 11 genera of non-native invasive lumbricids in North America (Fragoso & Rojas 2014; Reynolds 2020, 2022), and 10 genera of invasives in South America (Fragoso & Brown 2007). In Europe, centers of diversity of lumbricids are situated in the Pyrenees and the Balkan Peninsula, as well as in the Carpathians and the Caucasus (Kvavadze 1985, 1999; Rota & de Jong 2015). The biodiversity of the Balkans is the largest in Europe (Griffiths *et al.* 2004), due to the complex geological history and the specific geographical position with several biogeographical regions, each characterized by specific ecological, climatic and geomorphological conditions, as well as a great variety of habitats (Trakić *et al.* 2016).

For the last 2 million years, repeated glaciations have destroyed the biotas of much of northern and alpine Europe, and on the major mountain ranges such as the Carpathians, Caucasus, and Pyrenees. The present European earthworm fauna consists of the survivors in unglaciated, non-permafrosted areas, and their descendants who colonized the rest of the continent after the end of the last (Würm or Wisconsinan) glaciation. There is no way to know how many species were driven to local or global extinction. Repeated cycles could have contributed to in-refuge speciation by changing vegetation zonation. However, the pre-Pleistocene conditions were probably adequate to support earthworm populations throughout Europe and even into the Arctic, including the North American Arctic, as subtropical vegetation fossils from the Eocene occur on Ellesmere Island (Eberle & Greenwood 2012; Francis 1991).

Today, most earthworm scientists agree that the original lumbricid fauna was significantly destroyed during the glacial period in much of Europe. Today's lumbricid fauna come from various elements, differing both in their historical age and in their origins. Namely, the present faunal elements are fragments of modified fauna from the Tertiary Period, that are thought to have originated in the Paleocene or Eocene. These are species that, due to their adaptability to specific conditions, have survived to this day. Such relic species are now present in the Balkans, the Pyrenees and the Apennine peninsula, the northwestern part of Africa (Maghreb), the southern part of France, Sardinia, Corsica, the southern parts of Switzerland and the Czech Republic, Turkey and the central parts of Asia (Omodeo 1952, 1956, 1961, 1988; Bouché 1972, 1983; Mısırlıoğlu 2017; Mršić & Šapkarev 1988; Mršić 1991; Marchán *et al.* 2020; Marchán *et al.* 2022b). In addition to relic species, there are also "modern" species that are thought to have appeared in the Miocene and later. A greater expansion of new "modern" species occurred during interglacial and postglacial periods, mainly in the Holocene (Mršić 1991).

On the Balkan Peninsula there are 90 endemic species with the largest share in *Dendrobaena* (25) and *Allolobophora* (20) (Trakić *et al.* 2016; Popovic *et al.* 2022), while 39 have been discovered in the basin of the Carpathians, mostly Dacian endemics. Of these, 12 species are of the genus *Octodrilus* whose distribution center is located in the Apuseni Mountains in the southern part of the Carpathians (Csuzdi *et al.* 2011). Other genera appear to be endemic from southern France to the northern Iberian Peninsula. The most speciose is presently *Scherotheca* with 42 species/subspecies recognized to date, though many other species are still expected to be found (e.g., eight new species were recently described from Corsica; Marchán *et al.* 2023a).

The ecologically important Lumbricidae have been explored using various tools by numerous researchers. Despite significant molecular research, there are still many species that do not have a stable taxonomic status, most of which relate to archaic species with unique taxonomic characteristics and disjunctive distributions (Marchán *et al.* 2022c). Answers to some of these questions are expected in the near future, and will certainly lead to a better understanding of many concerns regarding the origin and dynamics of the development of the Lumbricidae family as a whole.

Lutodrilidae McMahan, 1976

There is only one species in this semi-aquatic family, *Lutodrilus multivesiculatus* McMahan, with a distribution restricted to four parishes/counties in eastern Louisiana, USA (McMahan 1976; Anderson *et al.* 2017). It has developed caudal respiration similar to that observed in *Alma* and *Drilocrius* (both in the family Almidae), a special respiratory adaptation to survive in its mostly anaerobic habitat, consisting of areas with large accumulations of fine-textured mud and organic debris along the margins of slow-moving water courses (McMahan 1998).

Megascolecidae Rosa, 1891

The Megascolecidae is the most speciose family of earthworms (2,208 spp. and 127 subspecies) and includes 85 genera. The most speciose genera are *Amynthas* (713 spp./ssp.), *Metaphire* (242 spp./sspp.), *Pheretima* (171 spp./sspp.), and *Megascolex* (104 sp./sspp.). The available molecular studies all support its monophyly and show just slight differentiation inside the family. Therefore, given the contradictory taxonomic divisions (e.g., Jamieson *et al.* 2002; Blakemore 2013) here we do not distinguish subordinate family rank taxa.

The Megascolecidae show a predominantly Australasian distribution being most speciose in Australia (ca. 45 genera and 400 species), New Zealand (8 genera and 50 spp.), Eastern and Southeastern Asia (over 1,500 spp.) (Sims 1980; Jamieson 2000). But interestingly, the North American megascolecids seem to be basal to several modern megascolecid groups such as the Asian *Amynthas* and Australian *Perionychella*, *Megascolides*, and *Diporochaeta* (Buckley *et al.* 2011). These include *Arctiostrotus* (7 species), *Argilophilus* (9 species), *Chetcodrilus* (3 species), *Kincaidodrilus* (1 species), *Macnabodrilus* (2 species), *Nephrallaxis* (2 species) and *Toutellus* (4 species), present mostly in the Pacific Northwestern States of the United States and Southern Canada (near Vancouver), but also in California (Reynolds, 2020, 2022).

At least 27 species in the genera *Amynthas* and *Metaphire,* as well as *Perionyx excavatus* Perrier*, Pithemera bicincta* (Perrier), *Polypheretima elongata* (Perrier)*, Polypheretima taprobanae* (Beddard) and *Pontodrilus litoralis* (Grube) are probably some of the most widely distributed earthworms in the world (Blakemore, 2009). In fact, many of these species were described from specimens collected outside their native ranges in Asia: for instance, *Metaphire californica* (Kinberg) from San Francisco, *Amynthas gracilis* (Kinberg) from Rio de Janeiro, *Amynthas corticis* (Kinberg) from Hawaii, and *P. elongata* from Peru. Therefore, they had been already extensively transported by humans from Asia to other continents even before they were recorded from their home ranges. The presence of parthenogenetic morphs, and wide plasticity in terms of soil and habitat preferences in several of these species means that they are excellent invaders, particularly in subtropical, tropical and even temperate regions (Brown *et al.* 2006; Chang *et al.* 2017). Some species, such as *Pi. bicincta* may have been extensively transported with Polynesians that sailed throughout the Pacific Ocean, as well as in flotsam or sailing ship ballast (Blakemore 2007; James 2011). Several *Amynthas* and *Metaphire* species have invaded cold-temperate regions, including the continental USA, causing extreme alterations in the native ecosystems (Chang *et al.* 2021).

Taxonomic housekeeping note:

***Amynthas maximalis* Brown & James, 2023 nom. nov.** pro *Amynthas maximus* Qiu & Dong, 2019 (in *Zookeys*, 884, 23-42); non *Amynthas maximus* (Cognetti, 1915)

Amynthas maximus Qiu & Dong, 2019 was erected for a species from Guangxi Zhuang Autonomous Region in China (Dong *et al.* 2019), but the name is preoccupied by *Amynthas maximus* (Cognetti), from Irian Jaya in Indonesia. Hence, we propose a substitution name: *Amynthas maximalis* Brown & James, 2023.

Microchaetidae Michaelsen, 1900

The family Microchaetidae is closely related to the two other Microchaetoidea families Tritogeniidae and Kazimierzidae (Plisko 2013; Nxele *et al.* 2016), and consists of three genera (*Geogenia*, *Microchaetus* and *Proandricus*) and 81 species (plus six subspecies) distributed exclusively in temperate and Mediterranean Southern Africa. They are known from Northern South Africa near the vicinity of the Limpopo River down to the southern limit of the continent, in all provinces as well as in Lesotho and Swaziland (Plisko 2013). The three genera appear to have a rather geographically separate distribution, with little overlap. None of the known species have been reported outside of this rather restricted range, although Plisko (2013) predicted that Microchaetidae would also be found in Zimbabwe, Botswana and Mozambique. Interestingly, some of the longest known earthworm species in the world, including *Microchaetus vernoni* Plisko (measuring up to 2.6 m when alive) belong to this family, which contains a reasonably large number of giant (very large or long) earthworm species, some with over 1,000 segments, particularly in the genus *Microchaetus* (Plisko 1992, 2013).

Moniligastridae Claus, 1880

Although moniligastrids are not considered part of the Crassiclitellata since their clitella have only a single layer like the Enchytraeidae, they tend to have much larger individual body size and mass than enchytraeids and are phylogenetically sister to the Crassiclitellata (James & Davidson 2012; Schmelz *et al.* 2021). The family is mainly distributed in the Oriental region from south India east to the Philippines and north to southern Siberia and Japan (Gates 1972; Perel 1997). It includes 185 species (and 19 subspecies), distributed among five genera (*Desmogaster*, *Drawida*, *Eupolygaster*, *Hastirogaster*, *Moniligaster*), of which *Drawida* is the most widely distributed and speciose (162 spp./sspp.). Three species, *Drawida barwelli* (Beddard), *Drawida japonica* (Michaelsen), and *Drawida nepalensis* Michaelsen, are cosmopolitan, but of these, *D. barwelli* is the most widely distributed. It is also sometimes mentioned under its synonymous names *D. bahamensis* (Beddard), or *D. beddardi* (Rosa), being reported from Africa (Csuzdi 2005), Australia, South-East Asia, Mexico, Central America, the Caribbean, and several Pacific Islands (Blakemore *et al.* 2014; Csuzdi *et al.* 2017).

Ocnerodrilidae Beddard, 1891

The widespread Ocnerodrilidae family, with 37 genera and 172 species (plus four subspecies), sister taxon to the Megascolecidae + Acanthodrilidae s.l. clade (James & Davidson 2012), was last reviewed by Fragoso & Rojas (2009) and Hernández-García *et al.* (2018), who provided keys to the genera known until then. Two sub-families (Ocnerodrilinae and Malabariinae) were proposed by Gates (1966) and their definitions expanded by Gates (1972) and Fragoso and Rojas (2009). Ocnerodrilinae is more speciose and wider spread, while Malabariinae includes species only from India, China and Myanmar (Fragoso & Rojas 2009), without extramural glands and internal calciferous lamellae. With the exception of several peregrine species with worldwide distribution, all endemic genera and species of Ocnerodrilinae are confined to South and Central America, sub-Saharan Africa, India (*Curgiona*), and the Seychelles (*Maheina*). A large number of new species and several new genera were recently found in Brazil (James *et al.* 2023; Hernández-García *et al.* 2018), and it is likely that further sampling particularly in Northern South America, and in Brazil's Northeastern region will reveal many more. The majority (27) of the known genera occur in Latin America, while nine genera are known from Africa and five from Asia (India, China and Myanmar). In Latin America, many of the smaller and pigmented ocnerodriles, particularly in the genera *Kerriona* and *Eukerria* inhabit wetlands or bromeliads, and some of them are quite resistant to disturbance, being present in intensively plowed rice or no-tillage row-crop fields in Southern Brazil (Bartz *et al.* 2013; Bartz *et al.* 2014; Ferreira *et al.* 2023; Lima & Rodríguez 2007).

There are nine widespread anthropochorous ocnerodriles: *Eukerria eiseniana* (Rosa), *Eukerria kuekenthali* (Michaelsen), *Eukerria saltensis* (Beddard), *Eukerria stagnalis* (Kinberg), *Gordiodrilus elegans* Beddard, *Gordiodrilus habessinus* Michaelsen, *Gordiodrilus paski* Stephenson, *Nematogenia lacuum* Beddard, and *Ocnerodrilus occidentalis* Eisen, that typically live in wet or saturated soils, generally close to water sources. Some of these are of uncertain origin, being possibly of South America or Africa but, in any case, are of Gondwanan or

Central Pangean origin (Fragoso & Rojas 2009). The presence of many parthenogenetic morphs in some species (e.g., *O. occidentalis*), has resulted in extensive synonymies which must be checked (James *et al.* 2023), although the use of molecular methods may help unravel some of these. The species *Nematogenia panamaensis* Eisen was synonymized with *N. lacuum* by Righi (1984a), because variations between the two species were included in a group of specimens collected at the same location in Mato Grosso do Sul, Brazil. Similar to *O. occidentalis* further work is warranted on these poorly known ocnerodriles, particularly using more detailed genetic methods, in order to confirm the presence of potential cryptic species (Fragoso & Rojas 2009).

Rhinodrilidae Benham, 1890

Recent changes in classification (James & Davidson 2012) moved many genera from Glossoscolecidae to Rhinodrilidae (James 2012). This family now includes 38 genera and some 376 species (plus seven subspecies) including one widespread invasive species, *Pontoscolex corethrurus* (Müller), probably the most widely distributed earthworm in the world (James 2011; Taheri *et al.* 2018b). Native species of this family occur from Argentina (Mischis 2007) up to Mexico (Fragoso & Rojas 2014), including several on Caribbean Islands (Rodríguez *et al.* 2007), although none are known from Chile (Zicsi & Csuzdi 2007). Studies on the genetic diversity of several *Pontoscolex* species highlighted the importance of proper identification of *P. corethrurus*, requiring at least barcoding, to certify species status (Taheri *et al.* 2018a). Species belonging to *P. corethrurus* must conform to the genetic lineage L1, as identified in Taheri *et al.* (2018a) and James *et al.* (2019). The genus *Martiodrilus* with 88 known species and subspecies is the most speciose, occurring from Panama in the north to Peru in the south, and to French Guyana in the east (Fragoso & Brown 2007), with a large number of species still to be found with additional sampling efforts in Amazonia and the Andes region. The following other speciose Rhinodrilidae genera by decreasing order of species richness are: *Rhinodrilus* (52 spp./sspp.), *Andiorrhinus* (48 spp./sspp.) and *Andiodrilus* (40 spp./sspp.). Together with *Rhinodrilus*, *Martiodrilus* is also remarkable for the presence of several very large-bodied earthworm species (Brown & James 2007; Zicsi 2007). One other widespread species of Rhinodrilidae is worth mentioning here: *Urobenus brasiliensis* Benham, found in Paraguay (Brown & Fragoso, 2007) and in Brazil from Manaus in the Amazon (Römbke *et al.* 1999; Zicsi *et al.* 2001) to Pelotas in the Pampa biome (Santos *et al.* 2019). This cryptic species requires further morphological and molecular work in order to separate the many genetic lineages that have little morphological differentiation (da Silva *et al.* 2017). Furthermore, the genus *Alexidrilus* Righi, was recently synonymized with *Urobenus* Benham, and its two species, *A. lourdesae* Righi and *A. littoralis* Ljungström, with *U. brasiliensis* (Ferreira *et al.* 2023).

Taxonomic housekeeping note:

Genus *Taironina* James & Brown, 2023, nom. nov. pro *Tairona* (Type species *T. adrianae*) Righi, 1984 (in *Studies on Neotropical Ecosystems*, v. 2, p. 455-468); non *Tairona* Hebard, 1928, Orthoptera

The genus *Tairona* Righi, 1984, assigned by Righi (1984b) to the species *Tairona adrianae* from the Sierra Nevada de Santa Marta in Colombia, is preoccupied by *Tairona* Hebard, 1928 (Orthoptera: Phalangopsidae). Hence, a replacement name is necessary; we propose *Taironina*, gender feminine, meaning the one coming from *Tairona*, an ancient Indian group inhabiting the region of the type locality. *Taironina adrianae* (Righi) is the type species of this monospecific genus.

Sparganophilidae Michaelsen, 1918

This family native to North America has only one genus (*Sparganophilus*), with 12 species and 2 subspecies (Reynolds 1980, 2008). At least one species, *Sparganophilus tamesis* Benham (*Sparganophilus eiseni* Smith, is a junior synonym of *S. tamesis*; see Rota *et al.* 2016), is cosmopolitan, and found mainly in limicole habitats, throughout the USA (within and outside of its native range), Mexico (Ikeda *et al.* 2020), Canada (Reynolds 2022) and in several European countries including Germany, France, England, Switzerland, Italy and Spain (Rota *et al.* 2018a; Bouché & Qiu 1998).

Tritogeniidae Plisko, 2013

The family Tritogeniidae was erected by Plisko (2013) as part of important housekeeping duties within the Microchaetidae, and includes two genera, *Michalakus* with a single species and the others all belonging to *Tritogenia*. All 39 species are endemic to Southern Africa, with only one species newly described from Botswana (Nxele *et al.* 2018).

Tumakidae Righi, 1995

The monogeneric Tumakidae family has only three known species, *Tumak hammeni* Righi, *Tumak amari* Celis & Rangel-Ch., and *Tumak congorum* Celis & Rangel-Ch., found in relatively drier, lower-elevation forests in Central Colombia and the Caribbean region, along the Magdalena River valley (Righi 1995; Celis & Rangel-Ch. 2015). Given the relatively small amount of remaining forest fragments of its native habitat in Colombia, due primarily to agricultural expansion and pastures for cattle, further efforts are needed to ensure adequate conservation of the few species known. Additional sampling efforts are also needed to discover if there are any other species present along its potential distribution range.

Conclusions and Future Perspectives

Worldwide, there are ca. 5,739 spp./sspp. of megadrile earthworms, of which 5,406 and 332 are unique species and subspecies (i.e., not counting the nomino-typical subspecies), respectively, belonging to 382 genera and 23 families (**Table 1**; Brown *et al.* 2023), including the new Arecoidae family described herein, and the recently resurrected Diporodrilidae (Marchán *et al.* 2022c). Of these families, almost half show very restricted distribution, and a limited number of known genera and/or species, raising concern regarding the conservation of these endemic taxa, particularly in regions with little remaining native vegetation or high anthropic impacts. Further efforts are needed, particularly to assess potential danger of extinction of these species (Philips *et al.* 2017; Eisenhauer *et al.* 2019). Furthermore, some families, particularly the Megascolecidae and Acanthodrilidae require urgent attention and revision. The three most speciose families are the Megascolecidae, Acanthodrilidae and the Lumbricidae, comprising around two-thirds of all known species. A few families, particularly the Lumbricidae and Megascolecidae have anthropochorous cosmopolitan species that are widespread throughout the world, many of which also have important invasion potential (Hendrix *et al.* 2008). Efforts to contain further expansion of these invasives are critical in order to reduce negative impacts to soils and their biodiversity (e.g., Chang *et al.* 2021). Given the dwindling number of earthworm taxonomists, and the immense number of earthworm species still to be found and described, further capacity building in taxonomy is urgently needed, including both traditional morphological and molecular methods (Magalhães *et al.* 2021).

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