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Worldwide distribution of cave-dwelling Chelodesmidae (Diplopoda, Polydesmida)

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Abstract: Chelodesmidae is one of the most species rich families within the Myriapoda. However, little is known regarding their association with caves. We provide a list of all Chelodesmidae taxa reported from caves, map their worldwide distribution, and discuss the troglomorphic features of the group. A total of 25 species and subspecies from 20 genera and 2 subfamilies have been recorded from 59 caves and cave systems in 11 countries. These numbers represent a surprisingly modest proportion (~3%) of the approximately 800 described species in the family. Records of cave-dwelling chelodesmids appear to be geographically biased with most taxa reported from the Neotropics, likely due to the greater diversity of the group in the region. The lack of published records from the Afrotropics can undoubtedly be attributed to low sampling efforts. In addition, many studies focusing on cave invertebrates, especially in the tropics, often fail to identify chelodesmid taxa to the species level, thus precluding their inclusion on checklists. The majority of the Chelodesmidae reported from caves do not display obvious adaptations to a subterranean lifestyle and are not troglomorphic. The five troglobitic taxa indicated in this study may represent relictual lineages suggesting that few, if any, radiations of chelodesmids within caves have occurred in the past. Increased efforts are needed to bridge the gap between our current understanding and the true diversity of the group in these fragile and threatened habitats, which is necessary to allow policy makers to prioritize appropriate and effective conservation efforts, including the protection of environments severely impacted by human activities.

Keywords: Afrotropical, millipedes, Neotropical, troglobitic, troglomorphic, troglomorphisms

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INTRODUCTION

The family Chelodesmidae Cook, 1895 comprises 176 genera and nearly 800 species of medium-sized millipedes commonly found in moist habitats, primarily in the Neotropical and Afrotropical regions of the world (Hoffman, 1980; Bouzan et al., 2019). Members of the family exhibit an impressive degree of morphological variability including a wide range of color patterns, paranotal ornamentations, and gonopodal morphology (Schubart, 1955; Hoffman, 1969, 1976; Pena-Barbosa et al., 2013; Bouzan et al., 2017). The currently accepted classification of the group divides Chelodesmidae into two subfamilies, Chelodesminae Cook, 1895 for the Neotropical species, and Prepodesminae Cook, 1896 for the Afrotropical and Palearctic taxa (Hoffman, 1980). At present, 19 tribes are recognized within the Chelodesminae and 2 in the Prepodesminae with over half of the described species not yet assigned to a tribe (Hoffman, 1980; Pena-Barbosa et al., 2013; Bouzan et al., 2017; Shelley & Smith, 2018).

Although the unusual morphology and biology of cavernicolous animals have long attracted the attention of speleologists and biologist alike, the invertebrate communities of most of the world's cave systems remain understudied and are not well known (Howarth, 1983; Wynne et al., 2019). Millipedes are often found in caves and other subterranean habitats, along with other commonly encountered terrestrial arthropod groups, such as harvestmen, spiders, isopods, springtails, and beetles (Golovatch & Kime, 2009; Culver et al., 2013; Enghoff, 2015; Gallão & Bichuette, 2018; Hal'kova et al., 2020). Despite this fact, cave-dwelling millipedes remain relatively understudied and new taxa are found with regularity.

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This is evidenced by the description of over 40 millipede species from caves in the United States between 2004 and 2016, and approximately 100 species from Chinese caves during the same time period (Lewis, 2005; Shear, 2007, 2008a, 2008b, 2010, 2011; Shear et al., 2009; Liu et al., 2017). In addition, the recent discovery of the previously unknown suborder Dobrodesmidea from a Brazilian cave suggests that even high-level cave-dwelling millipede taxa remain to be discovered (Shear et al., 2016).

The defining feature of the subterranean realm is the permanent absence of light, although different habitats within it exhibit different relationships with light ranging from a light-dark gradient at the boundary of the habitat (e.g., soil, caves) to its complete absence (e.g., epikarst and deep-cave areas). In general, subterranean habitats can be separated into two broad categories - deep (i.e., caves) and shallow. Broadly defined, Shallow Subterranean Habitats (SSH, Culver & Pipan, 2008, 2014) include soil, shallow aquatic interstitial habitats, lava tubes, hypotelminorheic and seepage springs, Milieu Souterrain Superficiel (MSS, Juberthie et al., 1980), epikarst, calcrete aquifers (Culver & Pipan, 2014), and the voids associated with the superficial topmost breccia (canga formation) in ferrugineous landscapes (Ferreira et al., 2018). These habitats, except for some lava tubes, are typically close to the surface and do not extend beyond a few meters in depth. While some subterranean habitats are characterized by large spaces (e.g., caves, lava tubes), others represent intermediate cavities (e.g., MSS) or small voids (e.g., soil) with a corresponding effect on the morphology of the organisms that inhabit them (Culver & Pipan, 2014).

These unusual environments present strong filters acting on the local epigean fauna, thus affecting the colonization and successful establishment of these taxa in subterranean environments (Prous et at., 2004, 2015). Invertebrates adapted for a subterranean existence are, in most cases, morphologically distinct and can be distinguished from their surface-dwelling counterparts by the reduction or loss of eyes and pigment. Other adaptations for subterranean existence may include changes in body size (smaller body size of animals associated with small cavity habitats, e.g., soil), elongation (e.g., caves) or shortening of appendages (e.g., soil), reduction of spinescence (e.g., soil), winglessness and others (Culver & Pipan, 2014; Ortuño & Gilgado, 2010; Wong & Guénard, 2017). It is important to note that not all of these taxa live exclusively in just one of these environments and while the absence of eyeless, depigmented species in the surface realm is rather the norm, the finding of eyed, pigmented species in subterranean habitats is a common occurrence (Martin et al., 2001; Culver & Pipan, 2014).

As with other subterranean habitats, ecological factors such as the absence of light and the reduced availability of food resources restrict the number and types of organisms which can thrive in caves. Troglomorphic taxa (i.e., taxa exhibiting features associated with life in caves) are usually characterized by specialized morphological traits (troglomorphisms), in addition to physiological and behavioral adaptations (which are by no means less biologically relevant). These taxa include troglobionts (obligatory cave-dwelling species with exclusively subterranean populations) and some troglophiles (species with populations in both epigean and subterranean habitats) (Christiansen, 1962; Howarth, 1983; Trajano, 2012). It is important to note that while troglomorphisms can be useful in the description and study of subterranean taxa, it is often difficult to connect them to functional troglobiosis (Sket, 2008).

Classical arthropod troglomorphisms include both regressive and constructive traits. Regressive traits include reduction or loss of eye structures, pigmentation, wings, and thining of the cuticle (Howarth, 1983; Sket, 2008; Romero, 2009). Constructive traits, such as elongation of appendages (i.e., legs and antennae), usually arise as a sensory compensation (i.e., antennae or fish barbels) selected under dark conditions. Many of these troglomorphisms, including elongated, slender legs and/or antennae, depigmentation, and reduction or complete lack of ommatidia, have been found in cave-restricted Diplopoda (Chamberlin, 1942; Enghoff, 1985, 1993; Shear, 1986; Moseley, 2006; Liu et al., 2017; Antić et al., 2022). Modifications unique or nearly unique to millipedes include an enlargement of the Tömösváry organs in some Glomeridesmida (Iniesta et al., 2012) and an adaption of the mouthparts to a seemingly filter-feeding lifestyle (Enghoff, 1985). In the latter group of millipedes, which belong to the families Julidae, Blaniulidae, and Polydesmidae, the mandibles are reduced, and the pectinate teeth are increased in number and length, resembling the baleen plates of some whales, which may allow these millipedes to catch small particulate matter in rivulets of water running down the walls and floors of caves (Enghoff, 1985). Analogous modifications in mouthparts may also be observed in species of Collembola and Coleoptera (Deharveng & Christian, 1984; Perreau & Pavićević, 2008; Malcicka et al., 2017; Jantarit et al., 2019). Body size variation in troglobitic millipedes, as compared to congeneric epigean relatives, may also be indicative of restriction to caves (Liu et al., 2017). In some Neotropical cave-dwelling millipedes, such as *Pseudonannolene* Silvestri, 1895 (Spirostreptida), the adults are smaller than their epigean relatives, while in *Glomeridesmus* Gervais, 1844 (Glomeridesmida) the adults are bigger than congeneric species (Iniesta et al., 2012; Iniesta & Ferreira, 2013a, b). Other troglomorphic traits may include variation in the number of body rings. The troglomorphic *Dobrodesmus mirabilis* Shear, Ferreira & Iniesta, 2016 (Dobrodesmidea) exhibits a remarkable postembryonic development with 39 body rings plus telson in adults, while the typical number of rings in polydesmidans is 19 (usually referred as 19+t) (Shear et al., 2016). A similar postembryonic development (39-43 trunk segments as compared to 21-23 in congeneric species) has been observed in *Scolopendropisis duplicata* Chagas-Jr, Edgecombe &

Minelli, 2008, an epigean centipede restricted to the Cerrado of northern Brazil (Chagas-Jr et al., 2008; Minelli et al., 2009).

As is the case with many other arthropod groups, records of cave chelodesmids are geographically biased and some areas are much better represented in the published literature than others (Wynne et al., 2019). For example, Brazil, especially the southeastern part of the country, is one of the best-explored areas in relation to cavernicolous chelodesmid diversity (Pinto-da-Rocha, 1995; Trajano et al., 2000). On the other hand, the entire African continent, which contains 140 described chelodesmid taxa, has a single species, *Macellolophus rubromarginatus* (Lucas, 1846), recorded from a single cave (d'Aïn Fezza; Algeria). It is important to note that many studies focusing on cave invertebrates, especially in the tropics, often fail to identify taxa to the species level, thus precluding their inclusion on checklists.

The paucity of trained taxonomists and speleologists hinders our ability to understand the taxonomy, biology, and ecology of cave-dwelling millipedes. To facilitate and encourage further studies of cavernicolous millipedes we summarize all published information regarding cave-dwelling Chelodesmidae, focusing on the records presented in the literature at the species level, map their worldwide distribution, and provide a discussion of the troglomorphic features of the group.

MATERIAL AND METHODS

Data on all chelodesmid taxa recorded from caves were extracted through a series of queries using "Chelodesmidae," "Leptodesmidae," "Macellolophidae," and "cave" (in English, French, German, Italian, Portugese, and Spanish) as search terms in CIM LIT - the Online Literature Database for Myriapoda (https://cms.myriapodology.org/index.php) and in MilliBase - a global species catalog of the Diplopoda (https://www.millibase.org/) covering works published up to 2022. Once a species was determined to have been recorded from a cave, or cave system, we expanded our search to include all published records pertaining to that species.

To our knowledge, there have been no studies that have quantified chelodesmid troglomorphisms, as is the case with many other cavernicolous taxa. The difficulty of identifiying and quantifying troglomorphisms within the group is exacerbated by the fact that many early taxonomic studies are largely descriptive, merely providing a narrative of a taxon's morphology and do not include information on quantifiable characters. Moreover, all members of the order Polydesmida, to which Chelodesmidae belongs, lack eyes. Therefore, the reduction or loss of eye structures, a classical, quantifiable, troglomorphic feature often used as a proxy for adaptation to a subterranean existence, cannot be applied to this family. As a result, we relied on existing collection records and on morphological character descriptions as they appear in the published literature to identify troglobitic (*sensu* Sket [2008]) taxa. We classified taxa as troglobitic if they possessed at least one troglomorphic feature and were exclusively recorded from cave environments.

It is important to note that most of the reviewed records lack geographic coordinates. In the case of older works, precise localities are not presented due to the obvious difficulties in obtaining coordinates of a given locality. More recently, however, some authors have chosen not to present coordinates claiming that this approach would help protect the integrity of these fragile habitats. Most of the current species descriptions, however, include coordinates and frequently list specific microhabitats where these taxa occur. Such information is essential for assessing current and future threats to these species. Not providing locality information to avoid impacts to cave habitats has actually proven to be more harmful than useful, as this practice hinders our ability to locate species and assess a species' habitat on a large scale, in the case of threat assessments. We provide verbatim localities as they appear in the published literature and only report geographic coordinates that have been previously published (Supplementary Information). Locality information, such as geographic coordinates, that was not presented in the literature was obtained using Google Earth Pro (Alphabet, California, USA, v.7.3.4). Distribution maps were generated using the free software DIVA-GIS 7.5.0. (Hijmans et al. 2001). Nomenclature and taxonomic terms follow Hoffman (1980) and Bouzan et al. (2019).

RESULTS

We identified a total of 118 records of cave-dwelling Chelodesmidae from 61 published studies representing 25 species and subspecies from 20 genera and 2 subfamilies in 12 countries (Table 1; Supplementary Information). These data include 61 cave records from 59 caves and cave systems (functionally interconnected caves) in 11 countries (Fig. 1; Table 1; Supplementary Information). The single record from Morocco was epigean. There were only two caves with more than a single record each – Cueva del Aura, Cuba (*Amphelictogon couloni* (Humbert & DeSaussure, 1869) and *A. propinquus* Loomis, 1938), and Cueva el Fustete, Cuba (*A. cubanus* Chamberlin, 1918 and *Granmadesmus minor* Pérez-Asso, 1990).

Of the taxa recorded from caves, ten have not been collected from epigean environments and seven of those are known from a single cave (Table 1; Supplementary Information). Twelve species and subspecies have the majority (67-100%) of their records from caves, six species have an equal number of epigean and cave records, and the remaining seven taxa have <50% of their records from caves (see Supplementary Information). Only three taxa were represented by four or more cave records - *M. rubromarginatus* (24 records; 39.3% of all cave records), *Cantabrodesmus lorioli* Mauriès, 1971 (7; 11.5%), and *Leodesmus yporangae* (Schubart, 1946) (4; 6.6%). These three taxa made up more than half (57.4%) of all cave records identified in this study (Supplementary Information). The remainig taxa were represented by two or fewer cave records each.

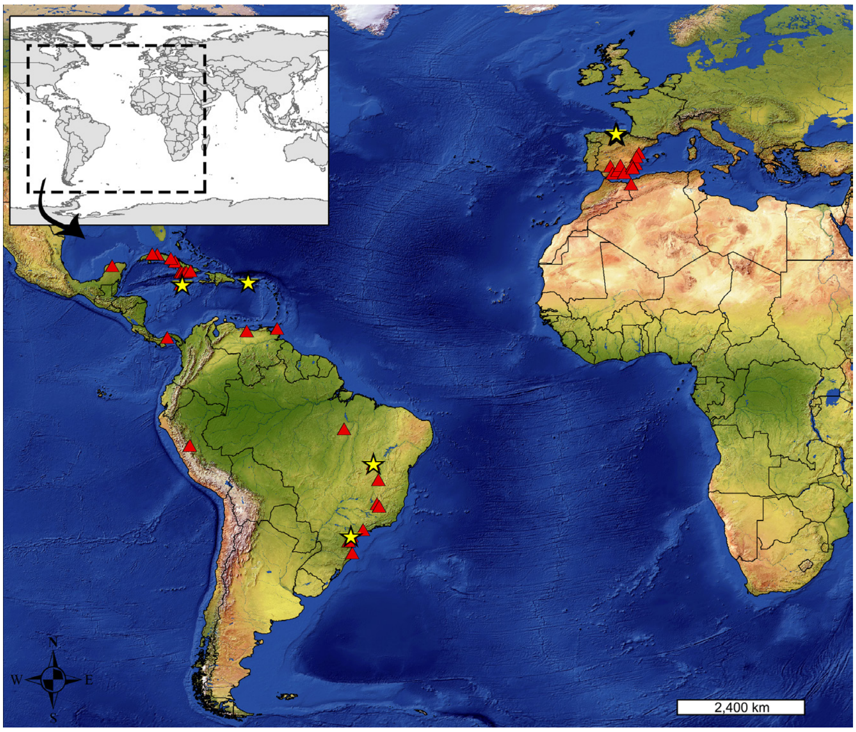

Fig. 1. Map of Chelodesmidae cave records. Troglobitic taxa are represented by yellow stars.

Based on morphological features and collection records, five of the taxa reported from caves are herein considered troglobitic: *L. yporangae*; *Platyurodesmus parallelus* Loomis, 1977; *Ricodesmus uniporus* (Loomis, 1977); *Strongylosomides troglobius* Golovatch, Bouzan & Gallo, 2022; and *C. lorioli*. All of these taxa are only known from caves (Figures 1, 2; Table 1; Supplementary Information).

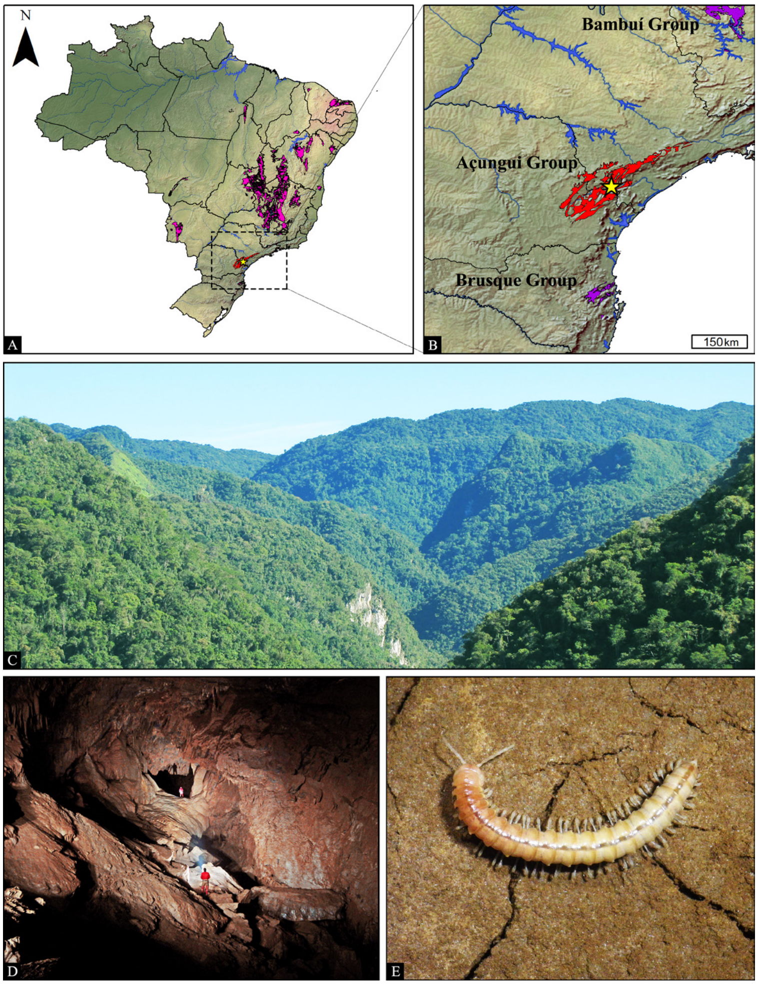

Fig. 2. A: Map of Brazil showing lithostratigraphic units; B: Type locality (yellow star) of *Leodesmus yporangae* in the Açungui Group; C: Atlantic Forest in the Açungui Group; D: Inner cave conduit where *L. yporangae* is found; E: Living specimen of *L. yporangae*. Photos: A–C and E are by R.L. Ferreira, and D is courtesy of D. Menin.

Table 1. Summary of worldwide cave-dwelling Chelodesmidae. Taxa are arranged alphabetically by subfamily, genus, and species. Troglobitic taxa are presented in bold.

Taxon	Country	Troglomorphisms	Remarks
CHELODESMINAE			
Amphelictogon couloni (Humbert & DeSaussure, 1869)	Cuba	---	Original description does not include precise location. Subsequently reported from a cave by Pérez-Asso (1996).
Amphelictogon cubanus Chamberlin, 1918	Cuba	---	Multiple records from epigean environments
Amphelictogon propinquus Loomis, 1938	Cuba	---	The original description includes the single known cave record (Loomis, 1938). Multiple records from epigean environments.
Amphelictogon subterraneus dolius Chamberlin, 1922	Cuba	---	Described from an epigean environment, and later recorded from caves in the region (Pérez-Asso, 1996)
Amphelictogon s. subterraneus (DeSaussure, 1859)	Cuba	"Corps d'un blanc luisant." [shiny, white body] (DeSaussure, 1859)	Described from a cave, and later recorded from epigean environments in the region (Pérez-Asso, 1996).
Brasilodesmus decipiens (Brölemann, 1902)	Brazil	---	Described from an epigean environment, and later recorded from caves in the region (Bouzan et al., 2018a)
Camptomorpha weyrauchi (Chamberlin, 1955)	Peru	---	Known only from a single cave
Caraibodesmus pictus Loomis, 1969	Jamaica	---	Known only from a single cave
Chondrodesmus sabachanus Chamberlin, 1938	Mexico	---	Considered troglobitic by Nicholas (1962) and listed as a troglophile/trogloxene by Reddell (1981). This species displays the typical coloration of the genus and has also been recorded from a single epigean locality (Chamberlin, 1938, 1952)
Curimaguana granulata (Hoffman, 1982)	Venezuela	---	Listed as a troglophile by Hoffman (1982). This species "shows no special modification for cavernicoly" (Hoffman, 1982, p. 648). Known only from a single cave
Granmadesmus minor Pérez-Asso, 1990	Cuba	---	Described from a cave, and later recorded from epigean environments in the region (Pérez-Asso, 1995)
***Leodesmus yporangae* (Schubart, 1946)**	Brazil	Body depigmented, long legs, claws, and antennae (Schubart, 1946a)	Only known from caves
Leptodesmus cordisburgensis Schubart, 1956	Brazil	---	Described from an epigean environment, but also recorded from the photic zone of a cave (Schubart, 1956).
Leptodesmus gilvomelaena Schubart, 1946	Brazil	---	Described from an epigean environment, and later recorded from caves in the region (Trajano et al., 2000)
Lepturodesmus joannae Hoffman, 1975	Trinidad and Tobago	---	Described from a cave, and later recorded from epigean environments in the region (Jeekel, 2009)
Obiricodesmus rupestris Schubart, 1956	Brazil	Some cavernicolous populations depigmented, thin cuticle, long legs (Schubart, 1956)	Listed as a troglophile by Schubart (1956). This species is found in both cave and epigean environments, with cave populations supposedly presenting troglomorphisms (Schubart, 1956)
Parastenonia carajas Bouzan & Iniesta, 2019	Brazil	---	Listed as a probable troglophile by Bouzan et al (2019). Only two specimens were recorded from epigean localities after extensive searching in the surrounding forests (Bouzan et al., 2019)
***Platyurodesmus parallelus* Loomis, 1977**	Jamaica	Body depigmented (Loomis 1977)	Listed as a probable troglophile by Loomis (1977). Only known from caves
***Ricodesmus uniporus* (Loomis, 1977)**	Puerto Rico	Body depigmented, long, slender legs and antennae (Loomis 1977, Pérez-Asso, 2002)	Listed as a probable troglobite by Loomis (1977) and Pérez-Asso (2002). Only known from a single cave
Rotundotergum elevatum Golovatch, Bouzan & Gallo, 2022	Brazil	---	Listed as a troglophile by Golovatch et al. (2022). No apparent adaptations for cavernicoly. Long legs, but no more than related epigean species (Golovatch et al., 2022). Only known from a single cave
Rupidesmus ruber Schubart, 1952	Brazil	---	Described from an epigean environment, and later recorded from caves in the region (Bouzan et al., 2018b)

Table 1. Continued

***Strongylosomides troglobius* Golovatch, Bouzan & Gallo, 2022**	Brazil	Light pigmentation, thin cuticle (Golovatch et al., 2022)	Listed as a probable troglophile by Golovatch et al. (2022). Only known from a single cave
Trichomorpha capillata Loomis, 1964	Panama	---	Although many juveniles were collected from a cave, a number of individuals were also recorded from epigean environments (Loomis, 1964)
PREPODESMINAE			
***Cantabrodesmus lorioli* Mauriès, 1971**	Spain	Body depigmented antennomeres, podomeres, and tarsal claws elongated (Mauriès, 1971, Luque & Labrada, 2017)	Listed as a troglobite by Mauriès (1971). Only known from caves
Macellolophus rubromarginatus (Lucas, 1846)	Algeria, Morocco, Spain	---	Listed as a troglophile by Mauriès et al. (2006). Cave-dwelling populations appear to be scattered randomly over the geographical range of this species

The total number of cave records was highest for Spain (30 records; 2 species), followed by Brazil (13 records; 9 species), Cuba (8 records; 6 species), Jamaica (2 records; 2 species), and Puerto Rico (2 records; 1 species) with the remaining six countries with a single cave record each (Fig. 3). Of the five troglobitic taxa, two (40%) occur in Brazil, with Jamaica, Puerto Rico, and Spain represented by a single species each (Table 1).

The following taxa were not included in the above assessment due to the lack of sufficient information and difficulties of determining discrete taxonomic units (i.e., species and subspecies) and associating cave collections of these taxa with epigean records: Batodesmini Cook, 1896 [undescribed *Alocodesmus* Silvestri, 1896 (Chapman, 1980, Venezuela)], Trichomorphini Hoffman, 1979 [*Trichomorpha* Silvestri, 1897 (Chapman, 1980, Venezuela; Barriga et al., 2019, Colombia)]; Arthrosolaenomeridini Hoffman, 1976 [*Arthrosolaenomeris* Schubart, 1943 and *Gangugia* Schubart, 1947 (Trajano et al., 2000, Brazil)]; Chelodesmini Cook, 1895 [*Eurydesmus* DeSaussure, 1860 (Trajano et al., 2000, Brazil)]; Strongylomorphini Hoffman, 1981 [*Brasilodesmus* Brölemann, 1929 (Trajano et al., 2000, Brazil; Bichuette et al., 2017, Brazil) and *Strongylomorpha* Silvestri, 1897 (Trajano et al., 2000, Brazil)]; Leptodesmini Attems, 1898 [*Leptodesmus* DeSaussure, 1859 (Trajano et al. 2000, Brazil)]; Lepturodesmini Hoffman, 1975 [*Camptomorpha* Silvestri, 1897 (Trajano et al., 2000, Brazil) and *Lepturodesmus* Silvestri, 1898 (Chapman 1980, Venezuela)]; and the genus without tribal position *Henrisaussurea* Hoffman, 1971 (Bichuette et al., 2017, Brazil). It is important to reinforce the idea that many studies focusing on cave invertebrates do not present Chelodesmidae taxa determined to the genus or species level, but only present family-level records (e.g., Ferreira et al., 2010; Simões et al., 2015; Souza-Silva et al., 2020, 2021). Therefore, the actual number of chelodesmid cave records is certainly higher than the one presented in this study, which focused on described and valid taxa.

DISCUSSION

The 25 taxa reported from caves represent 3% of the approximately 800 described species in the Chelodesmidae. This modest proportion holds true for the center of worldwide diversity for the group, Brazil, which although having the highest known chelodesmid diversity of any country in the world, only contains a handful of cavernicolous taxa (see also Trajano et al., 2000). In Brazil, the group is outnumbered in terms of cave-frequenting taxa by far less species rich families such as the polydesmidan Oniscodesmidae (~35 species) and the spirostreptidan Pseudonannolenidae (~90 species) (Trajano et al., 2000).

The five troglobitic species indicated in this study belong to five separate genera, representing 2.8% of the 176 genera in the Chelodesmidae. This is in stark contrast to many other groups, including millipedes, in which troglomorphic taxa are often concentrated within a small number of genera and/or tribes (Trajano et al., 2000; Niemiller et al., 2017; Huber, 2018). For example, the North American genus *Pseudotremia* Cope, 1869 (Chordeumatida: Cleidogonidae) and the East Asian genus *Epanerchodus* Attems, 1901, (Polydesmida: Polydesmidae) both contain a high proportion of the cavernicolous taxa in their respective families. Why this is not the case in the Chelodesmidae remains an open question, but the lack of congeners within cave systems suggests that these troglomorphic taxa may represent relictual lineages, and that few, if any, radiations of chelodesmids within caves has occurred in the past. A similar trend of possibly relictual cavernicolous taxa can be seen in the family Trichopolydesmidae (Antić et al., 2022).

Two hypotheses can be used to explain the apparent rarity of troglomorphic chelodesmids: i) the low number of troglobitic species is due to a paucity of sampling efforts in cave environments in most tropical areas where the family is more diverse or ii) the fact that most members of the family are intertropical, forest-dwelling taxa, and thus the effects of climate changes during the last glacial maximum may have not been sufficiently strong to isolate populations within caves. Both of these hypotheses merit further investigation.

The four countries with the highest number of cave records and cave-frequenting species are Spain (30 records; 2 species), Brazil (13; 9), Cuba (8; 6), and Jamaica (2; 2). The high number of Spanish cave records appears inflated by the presence of the widespread and non-troglomorphic *M. rubromarginatus*, which accounts for nearly 80% of the cave records for that country. The relatively high number of cave records from Brazil, Cuba, and to a lesser extent Jamaica is due to their well-developed cave systems, and undoubtedly due to the historical efforts of biospeleology groups in these countries. Targeted cave faunal surveys have been conducted in Brazil, and in some Central American countries, since the mid-20th century (Schubart, 1946a; Causey, 1966; Loomis, 1969; Trajano, 1987; Pinto-da-Rocha, 1995). In this regard, the presence of a single record from Mexico, a similarly cave-rich country in which there have been multiple studies focused on cave-dwelling millipedes is rather surprising (Chamberlin, 1942; Shear, 1973, 1977, 1986). On the other hand, the presence of a single cave record from Africa can undoubtedly be attributed to low sampling efforts.

Among the troglobitic Chelodesmidae, *C. lorioli* is undoubtedly the most striking. This rarely collected, ornamented, nearly completely depigmented species has elongated legs, antennae, and tarsal claws, and is only found deep within caves of the Alton Asón-Miera basin of Spain, an area known for its high subterranean biodiversity (Luque & Labrada, 2017). *Cantabrodesmus lorioli* is the only cave-restricted Chelodesmidae known from the Palearctic and is likely a relictual species whose ancestors first ventured into caves in the past when the family was likely more widespread in what is now modern day Spain. Several studies have supported the idea that the unfavourable climatic conditions during the Last Glacial Maximum (ca. 20,000 years ago) were one of the main ecological drivers influencing the diversity of troglomorphic species in the Holarctic (Allegrucci et al., 2005; Protas & Jeffery, 2012; Bryson-Jr et al., 2014; Sánchez-Fernández et al., 2016). Nonetheless, little is known regarding the mechanisms of troglomorphic evolution in groups with low vagility, such as millipedes.

The population ecology of *L. yporangae*, known only from the Areias and the Alambri Cave of southeastern Brazil, was studied by Thompson and Moracchioli (1996) who reported high population densities (up to 10 individuals/m^2) in cave sediment banks of the Areias system, along with seasonal fluctuations likely related to periodical movement of individuals between shallower and deeper sediment layers synchronized with the rain cycles. Although no further studies of this species have been conducted, recent observations (R.L. Ferreira, unpublished data) indicate a pronounced reduction of population densities, at least in the Areias system. It is important to note that morphological variations have been observed among distinct populations of this species (Mauriès & Geoffroy, 2000). Considering the lack of detailed work on this species, we cannot exclude the possibility that these populations may eventually turn out to represent distinct cryptic species. A similar situation has been observed in other previously widely distributed troglobitic species, such as amphipods and fish (Niemiller et al., 2013; Chakrabarty et al., 2014, Delić et al., 2017). The remaining three troglobitic taxa have been only rarely collected and appear to be geographically restricted. *Platyurodesmus parallelus* is only known from two collection events in Jackson Bay Cave, south-central Jamaica, made in 1974; *R. uniporus* has been reported from two caves of the Camuy River cave system, in the central and northern regions of Puerto Rico; and *S. troglobius* is only known from the aphotic zone of the Caverna Baixa Fria in eastern Brazil (Loomis, 1977; Peréz-Asso, 2002; Golovatch et al., 2022). Virtually nothing is known regarding the biology and ecology of these taxa.

An interesting case of color dimorphism occurs in the troglomorphic *O. rupestris*, in which epigean populations display a dark coloration while some specimens of cave populations are nearly completely depigmented (Schubart, 1956). Schubart (1956) reported no other noticable differences between these populations including gonopod morphology. This interesting case merits further research, however, this rare species has not been collected or seen since its original discovery in the municipality of Lagoa Santa, Brazil, nearly 75 years ago. It is important to mention that troglomorphic populations of troglophilic species are known for other taxa occurring in caves, such as isopods (Protas et al., 2011) and fishes (Mendes et al., 2019).

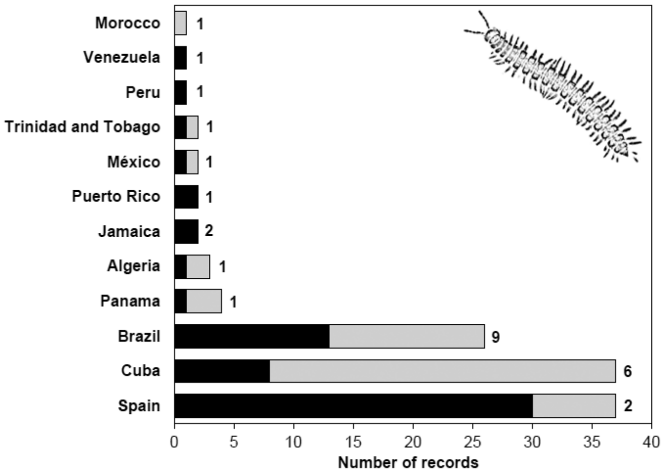

Fig. 3. Number of cave-dwelling Chelodesmidae records by country. Dark shaded portion of bars represents number of cave records; light shaded portion of bars represents number of non-cave records; numbers by each bar represent number of species.

The highest known diversity of cave-dwelling Chelodesmidae is found in the Neotropics, with most species occurring in unprotected areas without conservation policies. Except for *L. yporangae*, there are no studies on the distribution or conservation status of troglomorphic chelodesmids, which could partially explain the scarce information available for these taxa. Although *L. yporangae* occurs in a protected area in Brazil (i.e., Parque Estadual Turístico do Alto Ribeira, PETAR), it is the only troglomorphic chelodesmid species categorized as critically endangered (CR) in a list of Brazilian threatened Myriapoda based on IUCN criteria (Karam-Gemael et al., 2018). The PETAR karst corresponds to carbonate rocks of the Formation Bairro da Serra (geological conformation of Açungui Group), which is primarily composed of marine deposits of an ancient continental margin formed between the Mesoproterozoic and Neoproterozoic. The origin of this system is related to the separation of continents since the Cretaceous (ca. 120 Ma) and remains active in geomorphological terms (Campanha & Sadowski, 1999; Campanha et al., 2008, 2010). It also harbors the cave-dwelling *Yporangiella stygius* Schubart, 1946 (Pyrgodesmidae), the first troglobitic millipede described from Brazil along with *L. yporangae* (Schubart, 1946a). To date, several other troglomorphic invertebrates have been described from the cave system (Trajano & Bichuette, 2010; Souza-Silva & Ferreira, 2016), including the centipede *Cryptops (Trigonocryptops) iporangensis* Ázara & Ferreira, 2013 (Ázara & Ferreira, 2013). The main impacts to PETAR caves are largely a result of tourism management (Lobo, 2015; Lobo et al., 2014, 2015).

The regions where *Rupidesmus ruber* Schubart, 1952, *Leptodesmus cordisburgensis* Schubart, 1956, and *O. rupestris* are found are suffering from uncontrolled tourism, including trampling, garbage, artificial lighting, and impacts related to human activities in the surrounding areas, such as deforestation, agropastoral practices, and construction close to cave entrances (Bouzan et al., 2018b; Souza et al., 2021). In addition, this karst system has suffered from carbonate rock mining, causing environmental alterations with major impacts on cave communities. A similar situation can be seen in *Parastenonia carajas* Bouzan & Iniesta, 2019, a species which is widespread in caves of Serra do Carajás, a landscape composed of large plateaus of ferruginous outcrops located within the Amazon Forest of northern Brazil (Bouzan et al., 2019). The Carajás region contains appoximately 2,000 caves which are threatened by mining operations of its large iron ore deposits (Palheta et al., 2017). Although all Brazilian caves have been integrally protected, a recent presidential decree (decree n°10.935, posted on January 12, 2022) is currently allowing the alteration and destruction of caves, representing a serious threat to Brazilian subterranean biodiversity (Ferreira et al., 2022). There is a pressing need to review the Brazilian policy regarding cave protection, considering both the needs of preserving karst systems due to their biodiversity and endemic species, and the essential ecosystem services they provide.

Unfortunately, little is known regarding non-Brazilian cave-dwelling chelodesmids beyond their original descriptions. Further studies are needed to more fully understand the biological aspects and conservation needs of these taxa. In this regard, a worldwide list of cave-dwelling species is necessary to facilitate research and allow policy makers to prioritize appropriate and effective conservation efforts at the local or national level, including the protection of environments severely impacted by human activities.

Troglomorphisms within the Chelodesmidae

Known, or suspected, troglomorphisms within the Chelodesmidae include depigmentation, thinning of the cuticle, and elongation of appendages. Of these, the most commonly mentioned troglomorphism was depigmentation, followed by elongation of appendages, and thinning of the cuticle. With the exception of the latter, these features present challenges within the framework of the group. The family displays a wide range of colors and color patterns, therefore an assessment of depigmentation as a troglomorphism should be based on a careful quantification of the reduction, or loss, of dark pigments in troglomorphic taxa as compared to close epigean relatives. Many taxa in the family are known to possess elongated legs and antennae supposedly to aid in the navigation of their environments in the absence of eyes. Therefore, these characters must be quantified based on detailed comparisons between troglomorphic taxa and closely related epigean relatives, including comparisons of ratios between appendages and other somatic features (e.g., body ring width, head width, body length). Importantly, the reduction of podomere length (e.g., femur), however, does not necessarily preclude a troglomorphic status. Long legs may not be especially advantageous to a cave-dwelling scavenger, a situation seen in the troglomorphic *P. parallelus* (Loomis, 1977; Hoffman, 1979). For subterranean species restricted to small voids (e.g., shallow subterranean habitats), short legs will be the norm.

In addition to morphophysiological adaptations for subterranean environments, such as metabolic rate and longevity, other potential chelodesmid adaptations may include number and size of eggs, overall body size, number and size of sensory setae, mouthpart modifications, reduction in number and size of ozopores, and changes in the size and/or shape of paranota. Identification and/or quantification of such features, however, will require a dedicated effort including carefully planned and executed field and laboratory studies.

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