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ORIGINAL PAPER

Spots of high diversity of troglobites in Brazil: the challenge of measuring subterranean diversity

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Abstract Subterranean ecosystems are among the most fragile and threatened worldwide. Among organisms living in the subterranean domain, source populations restricted to subterranean habitats are called troglobites, generally distinguished by sets of morphological, physiological, and ecological specializations. The singularities at both systemic (high dark and phylogenetic diversities) and species levels greatly contribute to regional and global biodiversity. However, good descriptive and interpretative knowledge about this diversity, which is important as a basis for effective conservation policies, is lacking especially for tropical areas. We describe and characterize Brazilian karst areas recognized as spots of high diversity of troglobites, highlighting particularly important cave systems. We considered not only taxonomic richness but also indicators of phylogenetic (e.g., presence of relictual taxa) and genetic diversities, the latter based on degree of specialization of individual species, i.e., accumulation of autapomorphies. For this, we used available literature and our own data, both published and unpublished. Only identifications validated by a taxonomist were considered, while all data based on parataxonomy were disregarded. We propose hypotheses based on models of origin of troglobites aiming to explain the differences between karst areas.

Keywords Subterranean diversity · Cave fauna · Evolutionary models · Relicts

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Introduction

The problem of measuring biodiversity in special habitats

Biodiversity is the result of the interaction between evolutionary processes and patterns, expressed in various ways, including, but not restricted to, number of species, known as taxonomic diversity. However, speciation is not the only relevant process producing diversity; differential rates of divergence (for instance, due to bottleneck effects), adaptation to extreme habitats, and extinction are other factors that also result in phylogenetic, functional, and genetic diversities (Wilson 1992; Cianciaruso et al. 2009).

Strong ecological filters distinguish special habitats such as subterranean habitats, sulfur-based ecosystems, deep sea, isolated islands, and high altitudes. Such filters represent selective regimes that highly contrast with regimes where most species evolve. Consequently, taxonomic diversity is low, but divergence rates tend to be higher, leading to higher levels of phenotypical (morphological, physiological, behavioral, and bionomical) disparity. Ecological filters in the subterranean realm restrict effective colonization, i.e., the establishment of subterranean source populations, to organisms that are able to complete their life cycle in permanently dark, generally food poor habitats. Taxa preadapted to the subterranean life include those that are nocturnal, cryptobiotic, predominantly chemo- and/or mechano-oriented animals, detritivores, opportunistic omnivores or generalist carnivores, and able to cope with low nutrient availability. According to Schiner-Racovitza's nomenclature, subterranean source populations that are genetically connected to epigean populations by individuals commuting between these habitats are referred to as troglophiles (Trajano 2012). Individuals able to orient themselves in darkness, but are dependent on epigean (surface) resources to complete their life cycles, for instance, those that leave caves to feed, such as bats, some crickets and harvestmen, are referred to as trogloxenes (Trajano 2012). Because of these filters, even the richest cave system is taxonomically impoverished when compared to the adjacent epigean areas.

On the other hand, the protected nature of the subterranean environment favors the long-term survival of populations that disappear from the surface during phases of adverse climates. Such taxa may remain in hypogean habitats in the condition of relicts, long after their epigean relatives are extinct, regionally or even globally. Due to the relatively frequent presence of relicts, subterranean phylogenetic diversity is generally higher than in adjacent epigean ecosystems.

Low population sizes due to the generally fragmented nature of subterranean habitats, especially in karst areas where most caves develop, are associated with a highly distinctive and selective regime that results in high levels of differentiation in species evolving in isolation in such habitats (troglobites, i.e., species with exclusively subterranean source populations; Trajano 2012), with accumulation of large number of autapomorphies. Those related to the subterranean life are called troglomorphisms (the term was coined in 1962 by Christiansen—Christiansen 2005; in this paper we follow the definition by Trajano 2012). The commonest and most conspicuous troglomorphisms are regressive (reductive) character states, especially those affecting visual structures and dark pigmentation. On the other hand, constructive troglomorphisms include, for example, developed non-visual sensorial systems and mechanisms of energy conservation. Consequently, exclusively subterranean species are highly distinctive, and subterranean faunas show levels of phenotypical disparity much greater than that observed in the related epigean ones (Bichuette et al. 2015a).

Special habitats could be characterized by loss of alpha diversity, and, at least in the case of subterranean habitats, frequent increase in phylogenetic, functional, and, in fragmented areas, beta diversity. In addition to this, a high level of genetic diversity could be expressed because of the immense morphological, physiological, behavioral and ecological disparity in comparison to their surface counterparts. Thus, it is clear that the traditional focus on biodiversity, limited to taxonomic diversity, is far from satisfactory for such special habitats.

As a consequence of their singularities, subterranean systems as an integrated set of components and proprieties, as well as individual species with their unique sets of autapomorphies, greatly contribute to regional and global biodiversity. However, subterranean habitats are among the most threatened in the world, due to their fragility and low resilience, mostly because of such singularities (Trajano 1992; Culver and Pipan 2009). The detection and description of areas with high subterranean diversity, together with the discussion of scientific criteria aiming to recognize and describe this diversity, are fundamental for the establishment of effective conservation policies, including the prioritization of areas for the creation of protected areas.

A most relevant and frequently used modern concept in conservation biology is that of "hotspot" of biodiversity. The notion of a hotspot was first developed for vegetation (Myers 1990), for areas with relatively high number of plant species, such as tropical forests. Worldwide, biodiversity hotspots have been used as a primary criterion to establish priorities for conservation. Nevertheless, one must keep in mind that this concept was proposed for biomes, which were losing diversity, and that the three main criteria to establish a hotspot were as follows: (1) the number of plant species that was originally extant, (2) the number of species remaining today, and (3) the number of species likely to survive into the beginning of the next century (Myers 1990). It is worthwhile to note that the misuse of ecological terms may result in erroneous implications for conservation (Batalha 2011).

Some authors have applied the concept of hotspots for subterranean biodiversity (e.g., Culver and Sket 2000; Deharveng 2005). However, in view of the inadequacy of the concept, we have chosen a more comprehensive approach, based on the various aspects of biodiversity, and not just the numbers of species. Therefore, we adopted herein the concept "spots of high diversity of troglobites".

Spots of high subterranean biodiversity in Brazil

The occurrence of karst areas in South America with high *versus* low diversity of troglobites was predicted by Trajano two decades ago (Trajano 1994, 1995), as she argued for the applicability of the paleoclimatic model, which was originally developed for temperate zones (Barr 1968), to tropical regions as well. Based on data from speleobiological surveys, Trajano (2001) indicated the Alto Ribeira karst area, São Paulo State, and karst areas in Bahia State like Campo Formoso (northern Bahia) that had been subjected to extensive paleoclimatic fluctuations during the Quaternary, as spots of high diversity of troglobites in Brazil. This is in contrast to the São Domingos karst area, Goiás State, a region in South America considered to be rich in troglobitic ichthyofauna, which is situated in the climatically stable Cerrado core area (Bichuette and Trajano 2003a; Rizzato and Bichuette 2014).

Two spatio-temporal levels may be considered in which vicariant events act to produce diversity for subterranean fauna, karst areas, and cave systems. Trajano and Moracchioli (2002) discussed the importance of the Bodoquena karst area, southwestern Brazil, as a spot of high diversity for aquatic troglobites. In a revision of diversity patterns in tropical caves, Deharveng (2005) cited two spots of high troglobitic diversity (more than 10 species) in Brazil: Areias System (6th position among 16 well-studied caves) and Alambari de Cima Cave (10th position), both in the Alto Ribeira karst area, southeastern Brazil, based on information by E. Trajano. More recently, Cordeiro et al. (2014) pointed out the importance of the Serra da Bodoquena karst area, southwestern Brazil, as a spot of high diversity of troglobites, both terrestrial and aquatic, the latter including relictual taxa. As taxonomic studies frequently change suprageneric categories, and epigean surveys regularly bring into light new distributional records, we prefer not to distinguish between geographic and phylogenetic relicts (sensu Holsinger 1988). Furthermore, Gallão and Bichuette (2015) shed light on the high troglobitic diversity for sandstone caves in Bahia state, Brazil, the first spot outside of karst limestones in this country. Recent faunistic surveys have developed into taxonomic, phylogenetic, biogeographic, ecological, biological, and behavioral studies, both in progress and already published (Trajano 2000; Campos-Filho et al. 2014, 2016; Chagas-Jr and BichuetteME 2015; Bichuette and Trajano 2015; Bichuette et al. 2015a; Pinto-da-Rocha et al. 2015; Fernandes et al. 2016; Souza et al. 2016). They have shown the occurrence of several areas with an elevated number of troglobitic taxa, especially in the currently semiarid countryside ("sertão") of northeastern Brazil (M. E. Bichuette pers. obs).

We focused on those among well-studied areas that emerged as spots of high diversity of troglobites, also highlighting some special cave systems, describing these areas and the troglobitic fauna so far recorded there. As aforementioned, diversity is understood not only as taxonomic richness, but also includes indicators of phylogenetic (presence of relictual taxa) and genetic diversities; the latter based on the degree of specialization of individual species, measured by the accumulation of troglomorphisms.

Efficient conservation policies also depend on our ability to predict the most probable location of spots of high subterranean diversity among areas with speleobiological potential. For this, it is necessary to understand the causes of diversity through detection of patterns of distribution of troglobites correlated with available paleoclimatic, geological, topographic, and hydrologic data. We discuss some possible models explaining the origin of these faunas and the current primary threats to the Brazilian subterranean systems.

Our main objective is to describe, the Brazilian karst areas, which appear as spots of high diversity of troglobites. Further, by comparing them, our objective is to postulate models of origin and diversification of the subterranean fauna, aiming to predict new areas that may also be of priority for conservation.

Materials and methods

We used our own published and unpublished data, as well as data from literature when based on identifications undertaken or validated by specialists.We did not consider the literature based on data using parataxonomy sensu Majka and Bondrup-Nielsen (2006) who define sorting into morphospecies as "groupings of similar individuals, categorized by non–experts, relying on features of external morphology", because such data are not reliable and can lead to inaccurate results and wrong conclusions. When testing the utility of parataxonomic sorting in the study of forest beetle communities, Majka and Bondrup-Nielsen (op. cit.) observed a huge variation in sorting errors of four individuals families (ranging from 0 to 200 %, average 38 %). These results confirmed the conclusions of previous studies that sorting errors are not predictable, making it difficult if not impossible to generalize the groups for which a parataxonomic approach is amenable. According to Krell (2004), the use of parataxonomy tends to produce overestimations, with sorting errors that are not only unpredictable but can also be equal to more than 100 %. Therefore, parataxonomic units would provide limited, but adequately accurate, thus useful data only for non-comparative descriptions of species richness of single areas. Bortulus (2008), using the term bad taxonomy, discussed error cascades resulting from identifications that were not done or confirmed by taxonomists. For our purposes, parataxonomic data based conclusions are useless. We considered as evidence of parataxonomy, the lack of reference to a specialist who identified the material.

The numbers herein presented as taxonomic richness are conservative, and must be regarded as minimum values for biodiversity. Sampling efforts are heterogeneous among areas and within areas, hampering quantitative comparative analyses. We describe five Brazilian areas and a cave with their unique troglobitic faunas, which are considered as spots of high diversity of troglobites based on the following criteria: (1) high number of troglobites, when compared to other studied cave areas, (2) presence of higher taxa (families, order) so far not recorded in subterranean habitats elsewhere in Brazil, (3) presence of highly troglomorphic taxa, and (4) presence of phylogenetic relicts (taxa which have no close living relatives, and distributional relicts, whose relatives survived somewhere else sensu Holsinger 1988).

Study sites (Fig. 1)

The areas and caves described below have been intensively studied in the last decades. The first region to be biologically surveyed was the Upper Ribeira River (Alto Ribeira) karst area, in São Paulo State, beginning in the mid 1970's. Systematic collections were started in the early 1990's in Chapada Diamantina, Serra da Bodoquena, São Domingos (not a spot with high diversity of troglobites, but see Discussion), and Olhos d́Água Cave, and in the 2000's in Serra do Ramalho and Toca do Gonçalo in Campo Formoso.

Data on non-karst areas are sparse or too localized, as is the case of caves on igneous rocks (granites) and volcanic (basalts) rocks, or are non-available, or unreliable. Many environmental studies have been carried out in ferruginous areas for mining projects, but the results are in unpublished reports, some bound by contracts of no public disclosure. Because troglomorphic subterranean populations from these areas belong mostly to soil taxa, many of which already presenting troglomorphisms, their troglobitic status is uncertain in the absence of extensive surveying in the epigean environment. This is the case for almost all studies so far carried out in Brazil (Bichuette et al. 2015b). Therefore, we do not indicate any non-karst spot of high diversity of troglobites for Brazil.

Campo Formoso karst area, north State of Bahia, northeastern Brazil (including Caatinga Formation area)

The Campo Formoso karst develops mostly in Proterozoic Una Group carbonates. Surface karst in the area is subdued but there are very extensive cave systems of non-epigenic origin, including the largest in Brazil, Toca da Boa Vista Cave, with 108 km of mapped passageways, and smaller caves opening at the bottom of shallow dolines that are likely to represent segmented portions of much more extensive hypogenic systems (Auler et al.

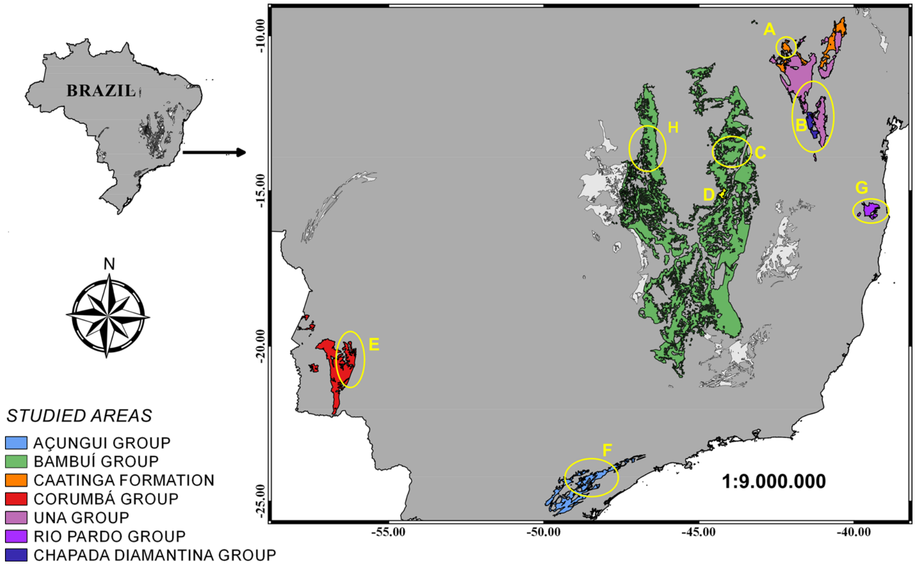

Fig. 1 Main Brazilian karst regions, showing thestudied karst areas (*encircled*): *A* Campo Formoso/ Caatinga Formation (Bahia), locality of Toca do Gonçalo Cave; *B* Chapada Diamantina region (Bahia), Una and Chapada Diamantina Groups; *C* Serra do Ramalho (Bahia); *D* Peruaçu area with Olhos dÁgua Cave (Minas Gerais); *E* Serra da Bodoquena (Mato Grosso do Sul); *F* Alto Ribeira in São Paulo State; *G* Rio Pardo (Bahia); *H* São Domingos (Goiás). Map confection: Diego Monteiro von Schimonsky

2009). Contiguous to the exposed Una carbonates, Salitre Formation, lies a karst area, formed of limestones from the much more recent Quaternary age, referred to as the Caatinga Formation (Auler and Farrant 1996). These limestones were formed by reshaping of the Una limestones due to weathering, erosion, and transportation of sediments during karstification of the Salitre Formation. The latter was exposed at the beginning of the Paleogene, approximately 65 mi years ago, whereas karstification of the Caatinga Formation would have probably begun ca. 2.5 mi years ago (R. Fraga, pers. comm.). Campo Formoso, situated in the Caatinga domain, is characterized by vegetation that is sparse, low arboreal and deciduous scrubland. Climate is semi-arid with mean annual rainfall around 490 mm concentrated between the months of February and May. Mean annual temperature is around 26 °C (Auler et al. 2009a).

Chapada Diamantina area, central State of Bahia, northeastern Brazil

Chapada Diamantina, in the central portion of Bahia, is an extension of Serra do Espinhaço. With an area of ca. 38,000 km^2, its landscapes are dominated by karst landforms formed by carbonatic and, to a lesser extent, siliciclastic rocks. Limestones of Neoproterozoic age, belonging to the Una Geological Group, Salitre Formation, are exposed in two metasedimentary basins separated by much older Mesoproterozoic exposed rocks of the Chapada Diamantina Group, disposed in three layers, two of which are formed by sandstones intercalated by limestones of the Caboclo Formation (Schobbenhaus et al. 1984). The presence of caves in the Chapada Diamantina sandstones indicates karstification of these rocks (Bichuette et al. 2015a). The altitudes vary from 1000 to 1700 m, representing a drainage divide between the São Francisco and the East Basins. The climate is tropical semi-arid, with distinct wet/dry periods (Type “Aw” according to Köeppen 1948) and the mean annual temperature is around 20 °C (Nimer 1989). The region is partly included in the Chapada Diamantina National Park, thus legally protected by law.

Serra do Ramalho karst area, southern State of Bahia, northeastern Brazil

The Serra do Ramalho karst, middle São Francisco River basin, is dominated by a plateau formed by limestone rocks of the Bambuí Group and extending for kilometers. It has two sections, the lower plateau, to the south, and the upper plateau, to the north. There are several important cave systems in the region, some reaching more than 30 km of passageways. The climate is tropical dry (=semiarid), “Aw” type, characterized by dry winters (March to October), with an annual precipitation around 640 mm (Köeppen 1948). The native vegetation is Caatinga (a typical dry forest, with shrubby components), interspersed with Cerrado (savannah-like) vegetation (Bichuette and Rizzato 2012). Serra do Ramalho karst area is not protected by law, being threatened mostly by monoculture plantations and mining projects predicted for the next years (Gallão 2012).

Peruaçu karst area: Olhos d́Água cave, north state of Minas Gerais, southeastern Brazil

The core area of this region is the Peruaçu valley. Caves crossed by streams are quite open, with very large entrances and karst windows. In addition, there are several relatively small upper dry caves. The main interest of this area, justifying the recent creation of a National Park, the Parque Nacional Cavernas do Peruaçu, is archeological, due to the presence of cave paintings, and for tourism, due to the beauty of the landscape. It is situated at the transition between the Cerrado and Caatinga morphoclimatic domains. According to the Koppen-Geiger classification (Peel et al. 2007), the climate is tropical semiarid, with a well-defined dry period between April and September.

The longest cave in Minas Gerais State, Olhos d́Água Cave (ca. 9 km), has its sinkhole in the Peruaçu area, but the resurgence is located in a farm area, near Itacarambi Town. The cave is crossed by a stream, in a conduit with dimensions varying from low passages to some large rooms, and a few upper galleries; the resurgence opens into the São Francisco River lowlands, and the water leaving the cave is canalized for human use. Its resurgence end is not included in the protected area.

Serra da Bodoquena, Mato Grosso do Sul State, southwestern Brazil

Serra da Bodoquena consists of a plateau extending for approximately 200 km in the north–south direction, width between 10 and 70 km, formed by Neoproterozoic limestones of the Corumbá Group. It is an important water divide in the Paraguay Belt, with an altitude around 800 m, related to the development of the Cenozoic Pantanal Basin, which is still subsiding within the limits of the Paraguay Basin. The climate is classified as “Aw,” i.e., tropical with wet summer and dry winter (Köeppen 1948), with rains concentrated in November-February, average precipitation of ca. 1.300 mm per year and a mean annual temperature of 24 °C. The natural vegetation is savanna, in contact with semi-deciduous seasonal forests. Most caves are within the limits of a protected area, the Parque Nacional da Serra da Bodoquena (Cordeiro et al. 2014).

Alto Ribeira karst area, São Paulo State, southeastern Brazil

The Alto Ribeira (Upper Ribeira Valley) karst area is defined geologically by the presence of metasediments, deposited in a Pre-Cambrian tectonically active environment. The lithology consists of crystalline limestones, quartzites, phyllites, metaconglomerates, and metabasites. Discontinuous limestone outcrops are oriented NE-SW, with a width varying from 1000 to 8000 m and reaching up to 20 km of extension; intercalated to limestone outcrops, and insoluble rocks, especially phyllites. These isolate the different cave systems (Fernandes et al. 2013) (Fig. 2). The area is situated in the transition between the Tropical Atlantic and the Araucaria Forest domains, the climate is subtropical humid, without a typical dry season, and the mean annual temperature is around 18–19 °C (Nimer 1989). It represents one of the last continuous remnants of the Brazilian Atlantic forest.

The area is mostly protected by two contiguous conservation units, the Parque Estadual Intervales—PEI, and the Parque Estadual Turístico do Alto Ribeira—PETAR. A third conservation unit, the Parque Estadual de Jacupiranga, in the Médio-Alto Ribeira, was created basically for the Tapagem Cave, also known as Caverna do Diabo (Devil´s Cave), the most famous show cave in São Paulo, which has the first kilometer managed for tourism. Biological surveys have not been undertaken in the other caves in the area.

Results

The numbers of species of troglobitic invertebrates belonging to different orders, which includes already described species and those validated by specialists and awaiting description, that have been recorded in the best studied Brazilian karst areas are shown in Table 1. Plate 1 shows some examples. For comparative purposes, we have included data from São Domingos karst area, where biological surveys have been undertaken since the 1970’s, with the most intensive surveys undertaken in the 2000’s. As aforementioned, sampling efforts were heterogeneous among areas, and hence quantitative analyses were not possible. However, differences in the proportions among orders indicate faunistic differences among areas.

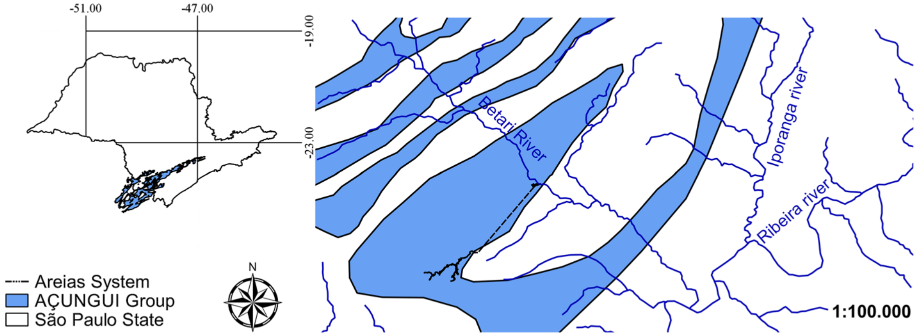

Fig. 2 *Left* Açungui Geological Group (*in blue*), with limits of State of São Paulo, southeastern Brazil. *Right* Detail of Rio Betari Valley, tributary of Rio Ribeira that cross the limestone outcrops (*in blue*) in the Alto Ribeira karst area. Map confection: Diego Monteiro von Schimonsky. (Color figure online)

Table 1 Numbers of troglobitic invertebrates, including described species and those validated by a specialist (awaiting description)

	Chapada Diamantina (sandstone)	Chapada Diamantina (limestone)	Serra do Ramalho	São Domingos	Serra da Bodoquena	Alto Ribeira
Porifera **Haplosclerida**		1				
Platyhelmynthes Tricladida			1		1	1
Annelida **Oligochaeta**					1	
Onychophora					1	
Crustacea						
Bathynellacea					1	
Spelaeogriphacea					1	
Amphipoda		2	3		2	5
Isopoda	2		8		1	6
Decapoda						3
Arachnida						
Scorpiones	1	1				
Acari	2					
Palpigradi	1					1
Amblypygi			2			
Araneae	7	2	1	3	3	2
Opiliones	3	2	2	1	1+	2
Pseudoscorpiones	2	1	1		1	5
Myriapoda						
Diplopoda		1				
Polydesmida		3	1		3	13
Spirostreptida	1					
Chilopoda						
Geophilomorpha						1
Scolopendromorpha	2					1
Lithobiomorpha			1			1
Hexapoda						
Diplura						1
Collembola	4	1			4	15
Insecta						
Blattaria	1	1				
Orthoptera Ensifera		1			1	
Hemiptera			2		1	
Coleoptera	2	1	2	2	1	7
Hymenoptera				1		
Mollusca						
Caenogastropoda			1		1	
Mesogastropoda					1	6
Pulmonata	1					1

Table 1 continued

	Chapada Diamantina (sandstone)	Chapada Diamantina (limestone)	Serra do Ramalho	São Domingos	Serra da Bodoquena	Alto Ribeira
Total	29	17	25	07	25+	71

Taxa recorded from only one among these areas are indicated in bold font

Karst areas

Campo Formoso karst area (sensu Auler and Farrant 1996)

Although taxonomic richness is not particularly high in the Campo Formoso area, the phylogenetic and morphological diversity of troglobites is outstanding. This includes a highly specialized heptapterid catfish, genus *Rhamdiopsis* (Plate 1a), which has been found in Toca do Gonçalo Cave in the Caatinga Formation (Trajano and Bockmann 2000, cited as *Taunayia* sp.); amphipods *Spelaeogammarus trajanoae*, widely distributed in the Campo Formoso karst area; the first Calabozoan isopod described from Brazil, *Pongycarcinia xiphidiouros*, found in Toca do Gonçalo; the oniscidean *Trichorhina guanophila*; a highly troglomorphic scolopendra, *Cryptops (Cryptops) spelaeoraptor*, and a troglomorphic cricket (F.G.A. Mello pers. comm.), both from Toca do Gonçalo; nicoletiid insects (two nominal species were described from the Toca da Boa Vista system, *Anelspistona spelaea* and *Coletinia brasiliensis*, but they are probably synonyms according to Mendes et al. (2009); in this case, the name "*spelaea*" has priority).

Two nominal species of highly troglomorphic carabid beetles, genus *Coarazuphium*, have been reported for the area: *C. formoso* from caves in Una limestones, and *C. caatinga* from Toca do Gonçalo. However, the description of the latter was based on characteristics that are variable withinthe species (S.A. Vanin pers. comm.), and it may be a junior synonym of the former. It is probable that these beetles disperse through deep soil, a hypothesis corroborated by the recent description of an epigean species in Mexico (Ball and Shpely 2013), thus devoid ofa strong biogeographic signal for our purposes.

This area fulfills the criteria for spot of high diversity of troglobites due to the presence of relict species and highly troglomorphic taxa.

Chapada Diamantina, central state of Bahia, northeastern Brazil

Twenty-nine troglobitic species have been recorded in 11 sandstone caves distributed in a small area with ca. 25 km^2 (JE Gallão and ME Bichuette, pers. obs). However, only a few have been described: the opilionid *Discocyrtus pedrosoi*, the catfish *Glaphyropoma spinosum*, the first troglobitic scorpion known for Brazil, *Troglorhopalurus translucidus*, the first troglobitic Mygalomorphae recorded for the country, *Tmesiphantes hypogeus*, and the recently described centipede *Scolopocryptops troglocaudatus*. Among these caves, Parede Vermelha, a 3 km long cave crossed by stream, stands out as a spot of high diversity of troglobites (13, including 11 terrestrial and two fishes), an unexpected number for a sandstone cave. This area holds endemisms on the local, regional and zoogeographical scalesuch as a new species of the troglobitic genus *Verhoeffiella* (Collembola), previously known only from the Paleartic region (Gallão and Bichuette 2015).

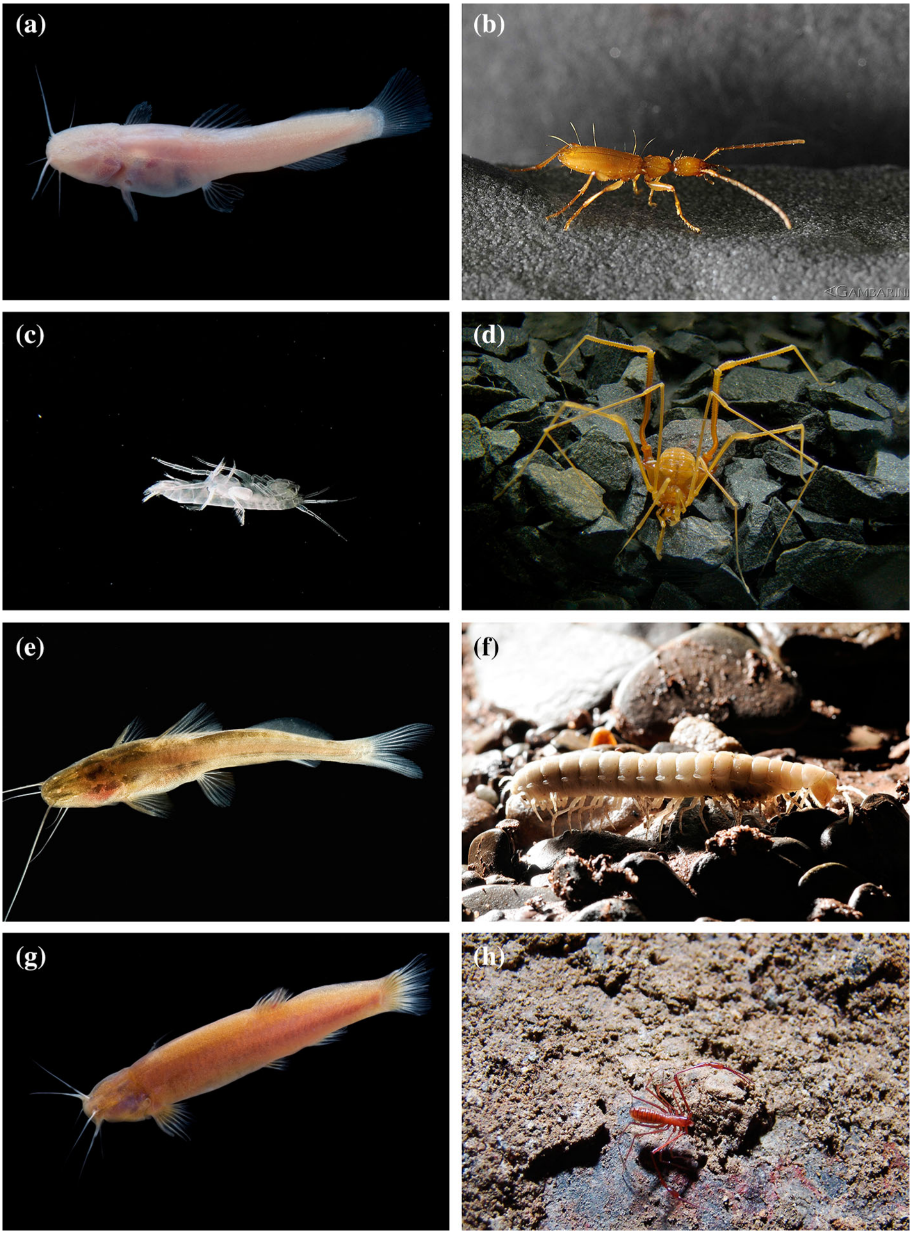

Plate 1 **a** *Rhamdiopsis* sp. (Campo Formoso/Danté Fenolio); **b** *Coarazuphium cessaima* (Chapada Diamantina/Adriano Gambarini); **c** *Spelaeogammarus spinilacertus* (Chapada Diamantina/Adriano Gambarini); **d** *Iandumoema uai* (Peruaçu/Pedro Pereira Rizzato); **e** *Pimelodella kronei* (Alto Ribeira/Danté Fenolio); **f** Polydesmida (Peruaçu/Adriano Gambarini); **g** *Trichomycterus dali* (Serra da Bodoquena/Danté Fenolio); **h** *Spelaeobochica muchmorei* (Alto Ribeira/Maria Elina Bichuette)

The troglobitic fauna from limestone caves is equally remarkable. Its includes the highly troglomorphic catfish *Rhamdiopsis krugi*, which is undergoing differentiation into subpopulations due to geological and hydrological barriers (Bichuette et al. 2015a); the only troglomorphic poriferan so far known for Brazil, *Raceckiela cavernicola* (Demospongiae); species of the exclusively subterranean genus *Spelaeogammarus* (e.g., *S. spinilacertus*—Plate 1c); the first, and so far the only troglobitic cockroach known for Brazil; the highly troglomorphic beetle *Coarazuphium cessaima* (Plate 1b) (type-locality for the genus, the most troglomorphic among Brazilian carabids); the cricket *Endecous apterus*; the Pholcidae spider *Metagonia diamantina*; and *Rhopalurus lacrau*, which, together with *T. translucidus*, are the only troglobitic scorpions from Brazil.

There are 16 troglobitic species described for Chapada Diamantina (11 in limestone caves and 5 in sandstone caves). At least 30 species remain undescribed, and the number is increasing (Gallão and Bichuette 2015). This area is distinguished not only by the richness of troglobites, but also by the high degree of troglomorphism of several species and the presence of representatives of higher taxa not recorded elsewhere in Brazil so far.

Serra do Ramalho karst area

Serra do Ramalho is a spot of high subterranean biodiversity, both aquatic (Bichuette and Trajano 2005; Mattox et al. 2008; Bichuette and Rizzato 2012; Simone 2012) and terrestrial (e.g. Baptista and Giupponi 2002; Pérez and Kury 2002; Trajano and Bichuette 2010; Hattori 2012; Campos-Filho et al. 2014). Seven troglobitic species have been described so far, four of them highly troglomorphic: *Xangoniscus aganju* (cited as *Thailandoniscus* sp. 2 in Trajano and Bichuette 2010), the first amphibian oniscidean isopod known for South America (a putative relictual; the most troglomorphic Brazilian cave amblypygi, *Charinus troglobius*; the opilionid *Giupponia chagasi*; the hemipteran *Iuiuia caeca* and aquatic gastropods, *Spiropokia punctata* (Potamiopsidae), also highly troglomorphic (Hattori 2012; Simone 2012; Bichuette et al. 2013). The region also harbors two species of troglobitic catfishes—*Rhamdia enfurnada* and *Trichomycterus rubbioli* (Bichuette and Trajano 2005; Bichuette and Rizzato 2012). At least nine additional troglobitic species are waiting for description, including planarians, isopods, spiders, hemipterans and fishes.

As is the case for other karst areas in the semiarid countryside of Bahia state, Serra do Ramalho troglobitic fauna is distinguished mostly by a high degree of troglomorphism and presence of relictual species.

Peruaçu karst area: Olhos d́Água Cave

The Olhos d́Água Cave is a spot of high diversity of troglobites, both aquatic and terrestrial, with five troglobitic species described so far. The five species that have been described includes the second troglobitic amblypigid (*Charinus eleonorae*), and the second cricket (*Endecous peruassuensis*) described for Brazil, an opilionid belonging to an exclusively subterranean genus, *Iandumoema uai* (Plate 1d), a pseudoscorpion (*Pseudochthonius biseriatus),* and the catfish (*Trichomycterus itacarambiensis*). The catfish exhibits a unique polymorphism regarding melanic pigmentation, part of the population formed by DOPA(-) individuals (Felice et al. 2008). At least six species await description. This includes a relict opilionid belonging to the Kimulidae family, so far known only from northeastern Brazil (Pérez-Gonzáles et al. 2016), besides an Entomobryomorpha collembolan, a Polydesmida diplopod (Plate 1f), and three oniscidean isopods (Gallão 2012), one of which is an amphibious species.

Olhos d́Água Cave is exceptional because of its taxonomic and morphological diversity, and because of the presence of relictual taxa.

Serra da Bodoquena karst area

Serra da Bodoquena shows 34 troglobitic species, including five catfishes (Trajano and Bichuette 2010; Cordeiro et al. 2013; Borghezan 2013; Cordeiro 2014): *Ancistrus formoso*, endemic of flooded caves of the Formoso system; *Ancistrus* undescribed sp. and *Rhamdia* undescribed species, syntopic and endemic to the Fadas cave system; *Trichomycterus dali*(Plate 1g) and one undescribed catfish, referred as *Trichomycterus* sp.1 by Cordeiro et al. (2014). Among these, *A. formoso* is highly troglomorphic, totally depigmented and without eyes; moreover, *T. dali* features specialized neotenic character state, a retention in the adult of a pre-dorsal adipose fold (Rizzato et al. 2011).

Two relictual invertebrates coexist in several flooded caves of Serra da Bodoquena, widely distributed in the phreatic habitat: the spelaeogriphacean *Potiicoara brasiliensis* and the bogidiellid amphipod *Megagidiella azul*; planarians *Girardia multidiverticulata* and an unidentified oligochaete are usually also found in the same caves (Moracchioli 2002). On the other hand, a new highly troglomorphic stream-dwelling Pomatiopsidae gastropod is known from a single cave (Cordeiro et al. 2014).

Terrestrial troglobites include the first, and until now the only known Brazilian troglomorphic onychophoran (Cordeiro et al. in prep.), different species of *Eusarcus* (Gonyleptidae) opilionids, ctenid and ochyroceratid (*Speocera*) spiders, a chernetid pseudoscorpion (*Spelaeochernes*), a carabid (*Pachytelis*) beetle, a dipsocorid hemipteran, collembolans, Polydesmida diplopods, such as oniscodesmids (*Katantodesmus*, *Crypturodesmus*) and paradoxosomatids. This fauna is unique in combining typically tropical and subtropical elements (Gnaspini and Trajano 1994; Cordeiro et al. 2014).

This area fulfills the criteria we set to identify spots of high diversity of troglobites especially by the relictual nature of the aquatic fauna, high degree of troglomorphisms of species, and occurrence of representatives of higher taxa exclusive to these caves contribute towards this.

Alto Ribeira karst area

The Alto Ribeira lies in a zone where faunas from warm climates in the north (tropical Atlantic Forest) meet those from cooler climates in the south (Araucaria Forest), and is distinguished by its subterranean and epigean biodiversity.

We estimate the number of troglobitic species known for the Alto Ribeira karst area to be 120–150, because there is clearly much hidden diversity to be uncovered. Among aquatic troglobites, there is a nominal species of catfish, *Pimelodella kronei* (Plate 1e); crustaceans, including amphipods, genus *Hyalella*, with two described species, *H. caeca* and *H. epikarstica*, and one to three undescribed ones (the caves in which these populations were found—Gnaspini and Trajano 1994, are located in separated limestone outcrops), and anomuran decapods, genus *Aegla*, with three described and at least four undescribed ones (Fernandes et al. 2013); at least five hydrobiid gastropods, of which only one has been described (*Potamolithus troglobius*) (Bichuette 1998); and a planarian found exclusively in Alambari de Cima Cave in the early 1980s.

The terrestrial invertebrate troglobites include: Oniscidean isopods of several families, such as philosciids (*Benthana* spp.), Platyarthrids (*Trichorhina* spp.) and Styloniscids; Polydesmid diplopods, such as *Leodesmus yporangae* "formes" "type", "acutus" and "alambari" (Mauriès and Geoffroy 2000), *Peridontodesmella alba*, *Yporangiella stygius*, *Katantodesmus* spp., *Cryptodesmus* spp. and *Crypturodesmus* spp.; some chilopods

(Geophilidae, Cryptopidae); symphylans; collembolans: arrhopalitids (e.g., *Arrhopalites* spp.), cyphoderids, entomobryids, hypogastrurids (*Acherontides*), isotomids, onychyurids, paronellids (e.g., *Troglolaphysa* spp.); campodeid diplurans (e.g., *Oncinocampa*); some insects, mostly coleopterans: carabids (*Schizogenius*, *Oxidrepanus*), pselaphids and staphilinids (*Arthmius*); and arachnids, mainly acarians, gonyleptid opilionids (e.g., *Pachylospeleus*), pseudoscorpions (chthoniids, genus *Pseudochthonius*, bochicids, ideoroncids), aside from a few spiders, family Hahniidae (e.g., *Harmiella*), and palpigrads (Trajano and Bichuette 2010).

Areias System This cave system is home to *Pimelodella kronei*, the first troglobitic vertebrate described for South America, as well as *Leodesmus yporangae* morphotype, the first troglobitic invertebrate described for Brazil. It was, together with Gruta da Tapagem, visited by P. Strinati in his speleobiological expedition to South America (Strinati 1971). Strinati made the first comprehensive and reliable biological observations of Brazilian caves, producing a list of 11 invertebrate taxa, including five troglobitic species (four described based on the material he collected; a collembolan would be described in 1988). Gnaspini and Trajano (1994) listed 16 troglomorphic, probably troglobitic invertebrates for this system, the total richness being 17 species; later on, this number was raised to 20 (Trajano 2007). Recently, two new species were described and, in addition, specimens of troglomorphic planarians have been found, elevating the number of species so far recorded for the Areias system to 24, as follows: *Hyalella epikarstica* (cited by Deharveng 2005 as Amphipoda), *Aegla cavernicola*, *Benthana iporanguensis*, *Trichorhina* sp. 1, *Trichorhina* sp. 2, *Pachylospeleus strinatii*, *Spelaeobochica muchmorei* (Plate 1h), *Pseudochtonius strinatii*, Geophilidade gen. sp., *Cryptops* (*Trygonocryptops*) *iporanguensis*, *Leodesmus iporangae* morphotype, *Peridontodesmella alba*, *Crypturodesmus* sp., *Cryptodesmus* sp., *Onicocampa trajanoae*, *Troglolaphysa aelleni*, *Folsomia* sp., Paronellidae gen. sp., Cyphoderidae gen. sp., *Schizogenius ocellatus*, Pselaphinae Brachyglutinigen. sp., *Pothamolithus troglobius*, Dugesiidae sp., *Pimelodella kronei*.

Other cave systems distinguished by the number of troglobites are: Santana Cave (at least 14 species), and Alambari system, formed by Alambari de Cima and the Alambari de Baixo Caves (12+ spp.), in PETAR; Tapagem Cave (Caverna do Diabo; 10+ spp.); Colorida Cave (9+ spp.) in PEI (Bichuette and Trajano 2003b; Trajano and Bichuette 2010; Fernandes et al. 2013; Trajano, Bichuette and Pellegatti-Franco unpubl. report 2010).

The Alambari the Cima troglobitic fauna deserves some comments. Among the three aquatic troglobites recorded, two seem to be locally extinct since the mid 1980s, afterthe occurrence of a pollution event causedby illegal mining activities upstream from the cave, which left unmistakable traces in the cave stream; particularly on the blind catfish, nominal species *Pimelodella kronei* (Trajano 1997) and the first troglomorphic planarians found in Brazil. In spite of intensive collecting efforts, no other catfish was found after 1980s. On the other hand, a relatively abundant population is still found in Gurutuva Cave, formed by a tributary of the Alambari system.

It is noteworthy that the degree of troglomorphism of the troglobites from the Alto Ribeira karst area is generally low to medium. A good example is the blind catfish from Iporanga, *P. kronei*, which exhibits a great deal of intrapopulation variability regarding degree of pigmentation; and about 10 % of individuals of the largest known population, that of Areias de Cima Cave, have asymmetrical vestigial eyes, externally visible (Trajano and Britski 1992). Several troglobitic invertebrates present a mosaic distribution of troglomorphic character states, with more or less developed visual structures but no dark pigmentation and vice versa, as well illustrated by the several troglobitic hydrobiid species. Among the decapods, genus *Aegla*, there are troglobitic species showing all degrees of specialization, with *A. microphthalma* being the most troglomorphic, besides several troglophilic populations.

Even for thiskarst area, the most intensively investigated in Brazil, the numbers herein presented are, as aforementioned, conservative and the real taxonomic diversity is probably much higher.

The Alto Ribeira is a spot of high diversity of troglobites basically in terms of taxonomic diversity (Table 1).

Discussion

Comparison between Brazilian karst areas: understanding the causes of diversity of troglobites

Gibert and Deharveng (2002) discussed the truncated nature of subterranean biodiversity and its implications from functional and evolutionary perspectives. Among the main factors shaping subterranean biodiversity, these authors indicate the strong ecological filtering that occurred when colonization of hypogean habitats first began, whichwould require specific pre-adaptations to overcome the darkness barrier, resulting in low numbers of lineages. Also a main factor islimited speciation by ecological diversification, since relevant non-trophic variables (e.g. air temperature and humidity, physico-chemical water variables) are constrained within narrow ranges. As a consequence, there seems to be a correlation between biodiversityand habitat age and fragmentation due to geological and hydrological processes, as indicated by the high proportion of endemic species and the large number of allopatric vicariant species. Also, the narrow limits of ecological changes in the subterranean realm on the geological time scale favors survival of lineages long after their epigean relatives disappeared. These hypotheses are consistent with data on Brazilian subterranean fauna.

On the scale of karst areas, paleoclimatic fluctuations may function as a primary cause of isolation of whole biotas in subterranean habitats; whereas on the local scale in sedimentary basins or cave systems, other factors like topographic and hydrological barriers may assume more important roles in the fragmentation of populations. In fact, the presence of high diversity spots of troglobites in Bahia and in the Alto Ribeira karst area has been predicted by Trajano (1995, 2001) based on the paleoclimatic model.

Due to the protected nature of the subterranean environment, cave deposits such as chemical sediments (speleothems, travertines) and fossils, serve as good material for dating, providing accurate measures for estimating past climates. Such data has allowed for paleoclimate reconstruction in northern Bahia and southeastern Brazil.

The karst areas in the countryside of Bahia and other states of semiarid northeastern Brazil were exposed to alternating very dry and wet paleoclimates. Wang et al. (2004), based on calcite dating, documented pronounced climatic fluctuations during the last 210,000 years in the currently semi-desertic Campo Formoso. The presence of megafauna fossils (Auler et al. 2006) in Toca da Boa Vista Cave,along with those representing typical forest faunaslike large climbing allouatine monkeys, *Cartelles combrafilhoi* (Halenar and Rosenberger 2013) is testimony of milder climates, respectively open forests or cerrado-like vegetation and forests. In addition, taphonomic studies based on material collected in a cave situated halfwayCampo Formoso and Chapada Diamantina indicated a climate wetter than the present-day prevalent xeric conditions during the Last Glacial Maximum (Castro et al. 2014). However, according to Wang et al. (op. cit.), the wet phases were quite short, representing a small fraction (8 %) of the last 210 kiloyears (kyr) in northern Bahia.

This would explain why the high diversity of troglobites innortheastern Brazil expresses high phylogenetic diversity and high degree of morphologic diversity (in the sense of accumulation of troglomorphisms), but not as much in species richness. Under dry conditions, increased extinction rates are expected in subterranean habitats due to a drastic shortage of nutrient input and other adverse conditions. At the same time, surviving populations would be subject to accelerated differentiation rates due to bottleneck effects, resulting in the observed patterns, as predicted by Trajano (1995, 2001) for northeastern Brazil and northern Patagonia.

The karst areas in the Salitre and Caatinga Formations (Una Group) are herein considered a single biogeographic unit because the presence of ancient relictual taxa, both in caves from Salitre Formation and in Toca do Gonçalo located in Quaternary limestones, indicate a deep phreatic connection between these areas. Since limestones of the Salitre Formation started been exposed at the beginning of the Paleogene, the maximum age of habitable conduits would be 35 Megayears (Myr); on the other hand, karstification of Caatinga limestones began only 2.5 Myr (R. Fraga pers. comm.).Therefore, it is reasonable to hypothesize a subterranean dispersion from the much older subterranean habitats in the Salitre Formation to the young Caatinga habitats. That would be the case of *S. eleonorae*; according to Koenemann and Holsinger (1999), the subterranean genus *Speleogammarus*, endemic of northeastern Brazil, is a basal taxon within the large, cosmopolitan family Bogidiellidae, indicating a very old phylogenetic age. In addition, the presence of synapomorphies unrelated to subterranean life shared by the heptapterid catfishes, *Rhamdiopsis krugi*, from Salitre limestones of Chapada Diamantina, and *Rhamdiopsis* sp. from Toca do Gonçalo (Bockmann and Trajano, in prep.), supports the hypothesis of dispersion from Salitre to Caatinga habitats. The presence of Calabozoan isopods in Toca do Gonçalo cave, another very ancient and clearly relictual taxon (Messana et al. 2002), is further evidence for this hypothesis.

Therefore, although several troglobites from Campo Formoso have been recorded in Toca do Gonçalo, this cave does not qualify as a spot of high diversity of troglobites per se, as there is no good evidence that the aquatic fauna (possibly also the case with at least part of the terrestrial fauna) originated and evolved in isolation in this cave, not even in the karst in which it is located. As a matter of fact, evidence points to an origin and diversification of this fauna in the deep phreatic zone of the Salitre Formation, with dispersion to the Caatinga karst when suitable habitats became available for colonization during the Quaternary. Concentration of troglobites in Toca do Gonçalo may be due to circumstantial factors: the water table is more superficial than in caves in the Salitre Formation, rendering the phreatobic fauna more accessible; and its large entrance room has been used to shelter goats, enriching the cave with organic matter and ammonia. This illustrates the importance of the biogeographical approach in establishing adequate scales when defining spots of high *versus* low troglobitic biodiversity, a first step in detecting patterns for understanding the causes of such diversity.

Speleological studies are relatively recent in Serra do Ramalho, and there is no good paleoclimatic data for this karst area. Drainage is predominantly hypogean, apparently isolating aquatic and hygrophilous riparious fauna in cave systems, since all aquatic and amphibious troglobites—and some terrestrial, namely *Charinus troglobius* (Amblypygi), *Giupponia chagasi* (Opiliones), the hemipterans *luiuia caeca* and an undescribed species (Hydrometridae) and *Xangoniscus aganju* (Styloniscidae)—are endemic of single cave systems.

According to AbŚaber (2000), during the last glacial period (from 18 to 13 Kyr ago), the Ribeira Valley region was occupied by a corridor of open vegetation, a hypothesis supported by the presence of fossils of megafauna discovered in caves from the Alto Ribeira area (Trajano 1995). After learning this evidence, Trajano and Britski (1992) proposed an allopatric model for the origin and evolution of the blind catfish, *Pimelodella kronei*, based on disruption of epigean drainage and differentiation in isolation from its surface ancestors during these dry periods (*P. transitoria* catfish, its putative sister-species, are found in epigean streams, forming troglophilic populations in some caves). Paleoclimatic reconstructions based on speleothem dating have evidenced the occurrence of cold, dry phases in subtropical Brazil over the last 116 Kyr (Cruz et al. 2005). The presence of megafauna fossils and other geomorphological evidence (AbŚaber 1981) points to the existence of dry, open corridors across the Ribeira Valley during such phases, when the troglophilic population would be isolated, extinguished or differentiated, originating troglobites. In fact, this karst area appears to have been a region of climatic instability during the Pleistocene, according to Carnaval and Moritz (2008).

In addition to providing better knowledge, fragmentation also explains the high diversity recorded in the Alto Ribeira karst area. This hilly, humid area is characterized by folded limestone outcrops dissected by insoluble rocks such as phyllites, crossed by streams forming several semi-isolated micro-basins (map in Fernandes et al. 2013). In this case, the high degree of fragmentation would also affect the terrestrial fauna.

On the other hand, the Rio Pardo karst area (Trajano 2000), also in the Atlantic Forest, is a cold spot of troglobitic diversity, with only four troglomorphic, possibly troglobitic taxa recorded. This observation is also consistent with the paleoclimatic model, because Rio Pardo is situated in the Bahia Refuge, which had remained forested during the Pleistocene (Carnaval and Moritz 2008).

The Bodoquena karst area combines different aspects of diversity of troglobites. A widespread, phreatobic fauna (*Girardia* planarians, oligochaetans), including relictual taxa (*Potiicoara* spelaeogriphaceans, *Megagidiella* amphipods) coexists with highly endemic species, such as a Pomatiopsid gastropod, a Bathynellacea crustacean, a *Rhamdia* catfish and two *Ancistrus* armored catfishes, each occurring in a single cave system. At least for fish, typical stream-dwellers such as new, undescribed species of *Rhamdia* and *Ancistrus* catfish from Gruta das Fadas cave system, show a low degree of troglomorphism (Cordeiro et al. 2013), indicating relatively recent isolation in the subterranean habitat (as also observed for the stream-dwellers in São Vicente karst area—Bichuette and Trajano 2004, 2006; Reis et al. 2006, and also *P. kronei*, from Alto Ribeira, and *Rhamdia enfurnada*, from Serra do Ramalho karst area—Bichuette and Trajano 2005).

In contrast, fishes and invertebrates living in flooded caves, which represent the upper phreatic zone connected tothe surface, are highly troglomorphic, as is the case with *Ancistrus formoso*, *Trichomycterus dali* (Rizzato et al. 2011) and the widespread phreatobic invertebrate fauna. In terms of taxonomic richness, the Bodoquena terrestrial invertebrate fauna is intermediate between the Alto Ribeira and the karst areas in Bahia, due to an intermediate degree of geographic fragmentation. Although the limestones are continuous at surface, hydrological barriers to terrestrial troglobites have been formed due to fluvial incision that, in the north plateau, had cut down to non-carbonated rocks. Therefore, four geographic compartments corresponding to micro-basins have been recognized in the Serra da Bodoquena karst area, with phreatobic troglobites widely distributed across them, while those living in base-level streams and in the vadose (aerated) zoneare generally restricted to one of those compartments (Cordeiro et al. 2014). The Bodoquena karst area is an interesting example of superposition of different speleobiological patterns.

Within spots of high diversity of troglobites, certain cave systems stand out when compared to others with similar sizes, habitat heterogeneity and level of knowledge. This is the case of Olhos d́Água Cave in the Peruaçu region, Toca do Gonçalo in Campo Formoso, the Areias system in Alto Ribeira, and Parede Vermelha in Chapada Diamantina. This isprobably related to fine-grained factors, such as fragmentation at a local scale due to geological, geographic and/or hydrological barriers, topographic isolation caused by alluvial down-cutting (see, for instance, Bichuette and Trajano 2004; Reis et al. 2006, for São Domingos karst area, central Brazil), and ecological singularities.

It is noteworthy that several troglobites have been found in caves that are hypogenic according to Auler (2009), such as Toca da Boa Vista and Toca da Barriguda in Campo Formoso, and Dente do Cão in Serra da Bodoquena. Troglomorphic nicoletiids, described in the early 2000s, have been found in deep conduits of Toca da Boa Vista system. So far four troglobitic species were recorded at Dente do Cão Cave (Cordeiro et al. 2014): two spiders, a new *Ctenus* sp. and *Speocera eleonorae*, a new gonyleptid harvestman, genus *Eusarcus*, as well as an onychophoran. This provides evidence against the model by Sendra et al. (2014), which concluded the lack of troglobites in hypogenic caves, based on the study of two caves in Spain and data from the literature. According to these authors, because karstification of hypogenic systems proceeds from confined deep aquifers upwards, such habitats would be available for biological colonization late during this process, when openings to the surface are formed. However, there is no necessary correlation betweenage and the present-day morphology of caves and distribution of troglobites. On one hand, karst processes are dynamic and the great majority of caves dated thus far were formed within the last 10 Myr, many of them in the past million years (Palmer 2007, p. 358). On the other, ancient highly troglomorphic relicts have been found in several Brazilian caves, including localities illuminated by natural or artificial windows that opened late during the karst evolution; these animals clearly did not evolve there, or at least not under the current conditions. This indicates that, especially in the case of highly troglomorphic taxa adapted for survival under harsh conditions, present-day distributions may be achieved by subterranean dispersion, independent of the present openings to the surface, and thatthe Sendra et al. (op. cit.) generalization is not valid.

The problem of measuring subterranean diversity

Annual and infrannual variations have long been reported for subterranean ecosystems, caused not only by reproductive cycles but also, and more frequently, by migrations between caves and the fissure network around them, causing a temporary absence of these animals in the large spaces accessible to direct research (Giachino and Vailati 2010). Fluctuations in the composition of cave communities have been observed in the few long-term studies carried out in Brazil, corroborating the need for several temporal replicas in order to characterize, with some degree of accuracy, such communities. These few examples include the Areias system in the Alto Ribeira karst area, Olhos d́Água Cave in the Peruaçu region (some studies are still in progress), Urubu Rei Cave in Bodoquena karst area, Gruna do Enfurnado in the Serra do Ramalho karst area, Parede Vermelha Cave in Chapada Diamantina and Angélica cave in São Domingos krats area. Nevertheless, Culver and Pipan (2009) state “there is probably not even a single relative species-rich cave, let alone a region for which we can be confident that all cave-limited species (…) have been discovered and described.” Included in this statement are caves in Europe and the U.S.A. that have been investigated since the eighteenth century.

It is widely recognized that taxonomic diversity is not the only measure of diversity. In fact, traditional diversity measures, which only take into account the number of species and their relative contribution, have little predictive power about the functioning of ecosystems. Recent studies have shown that phylogenetic diversity, a measure of species relatedness, and functional diversity that considers functional traits, are more sensitive to detecting responses of communities to environmental changes (Cianciaruso et al. 2009). The presence of relictual taxa increases phylogenetic diversity and may overcome taxonomic diversity in terms of relevance for conservation purposes. Indeed, according to Faith (1992) the emphasis on conservation regards preserving as much of this hierarchical variation as possible, no matter what the taxonomic units involved. Arponen (2012) says that evolutionary potential seems easier to apply when places rather than species are prioritized, as is shown in caves. This adds relevance to the karst areas in Bahia and Mato Grosso do Sul.

Stiassny and Pinna (1994) stressed the scientific relevance of basal taxa, often depauperate in number of species and with very restricted geographic distributions, as is frequently the case of troglobites. Examples are the Brazilian exclusively subterranean bogidiellids, *Megagidiella azul* (a monotypic genus) and *Spelaeogammarus*, the troglobitic catfishes, genus *Rhamdiopsis*, the scorpionid *Troglorhopalurus translucidus* from Bahia, the characid *Stygichthtys typhlops* and Copionodontinae catfishes. Based on their crucial importance in resolving higher and lowerlevel phylogenetic relationships of their respective lineages, basal taxa should be assigned a high conservation priority.

Recently, Trajano (2012), Gallão and Bichuette (2015) and Fernandes et al. (2016) discussed the importance of incorporating dark, functional and phylogenetic diversities in the description of subterranean biodiversity. Among the singularities of subterranean communities, the exclusion of taxa is one of the most conspicuous and ecologically relevant, resulting in increased phylogentic and dark diversities (the latter defined as all species in a determined region that can potentially inhabit those particular conditions—Pärtel et al. 2011). Implications for conservation are clear: phylogenetic, functional and dark diversity may be more important that species richness per se; and the relative contribution ofan individual species, including its putative position in a phylogeny, whether it is a relict or not, its degree of specialization (number of autapomorphies), endemism, complex behavior and physiology, genetic diversification etc., must be considered when discussing conservation issues.

When applied to localities sampled on too few occasions, which is the case of the large majority of Brazilian caves, indexes based on the richness of troglomorphic/troglobitic species have no scientific support and produce biologically meaningless values. When used to set priorities for conservation, as in Souza-Silva et al. (2015), they are not only useless, but harmful, resulting in biased conclusions, with potential to lead to equivocal conservation policies. Therefore, in view of state-of-art speleobiological knowledge in Brazil, it was our decision to point out and describe karst areas that are spots of high diversity of troglobites without establishing priorities, as they are all fragile, singular and raise concern; most caves, even those in protected areas, are threatened in some way.

Final remarks

Brazilian speleobiology developed relatively late, becoming an organized and autonomous field only in 1980. Despite this and the taxonomic impediment that is especially serious in countries with mega-diversity, there is currently, a significant body of knowledge on subterranean fauna that allows for the recognition of spots of high diversity of troglobites. In our conceptual framework, which is integrated with the goals of conservation (preservation of representative samples of biodiversity, its processes and patterns), we take into consideration not only present-day ecological factors (maintenance of general diversity or increase in functional diversity) but also historical factors that increase taxonomic diversity (species richness) by promoting speciation and/or phylogenetic diversity by causing extinction of some taxa.

Therefore, spots of high diversity of troglobites in Brazil have been recognized based not only on species richness, but also on a high proportion of these species in relation to the total subterranean richness, also including troglophiles and trogloxenes. For this reason, karst areas in the semiarid countryside of Bahia state, such as Campo Formoso and Serra do Ramalho, have been considered spots of high diversity of troglobites. These are priority areas for conservation because they represent unique patterns of subterranean evolution.

With progress in speleobiological studies, other spots of diversity will be recognized. The present knowledge that points to the role of paleoclimatic fluctuations, associated with topographic and hydrological factors, allows us to indicate potential areas with high diversity of troglobites. However, the big question remains—will there be time to describe such diversity, for the benefit of humans, before it disappears?

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