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article

Subterranean biodiversity in the Serra da Bodoquena karst area, Paraguay river basin, Mato Grosso do Sul, Southwestern Brazil

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Abstract: We present herein a synthesis of faunistic data from caves in the Serra da Bodoquena karst area, middle Paraguay River basin, Mato Grosso do Sul State. Those include phreatic, submerged and dry caves. Emphasis is given to troglobites (exclusively subterranean species), potentially threatened due to their morphological, physiological and behavioral specializations, associated to generally small distributions. The Bodoquena karst area distinguishes as a spot of high diversity of troglobites, such as trichomycterid and heptapterid catfishes, aquatic planarians and gastropods, arachnids (*Eusarcus* opilionids, ctenid spiders), Polydesmida diplopods, several collembolans, some insects, and Peracarida crustaceans, which include interesting phylogenetic relicts as spelaeogriphaceans. Four geographic compartments corresponding to microbasins, seemingly with biogeographic importance for the subterranean fauna, are recognized. Phreatobic troglobites (*Trichomycterus* catfishes, aquatic peracarids, planarians) distribute widely across these compartments and some well beyond (the spelaeogriphacean *Potiicoara brasiliensis* reaches Mato Grosso state), while those living in base-level streams (*Rhamdia* and *Ancistrus* catfishes) and the terrestrial ones, that live in the vadose (aerated zone) are generally restricted to one compartment. Many subterranean ecosystems in Mato Grosso do Sul are endangered by several threats described here and urgent actions for effective protection are required to guarantee a sustainable use of the land and the karst aquifers.
Keywords: *Subterranean biodiversity, troglobites, distribution, Serra da Bodoquena karst area, Mato Grosso do Sul, Biota-MS Program.*

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Resumo: Neste trabalho, são reunidos dados faunísticos sobre os táxons registrados em cavernas, freáticas, submersas e secas, da área cárstica da Serra da Bodoquena, na bacia do médio Rio Paraguai, Estado do Mato Grosso do Sul. É dada maior ênfase às espécies exclusivamente subterrâneas (troglóbias), potencialmente ameaçadas de extinção devido às especializações morfológicas, fisiológicas e comportamentais, e a distribuição geralmente restrita. A Serra da Bodoquena destaca-se por sua alta diversidade de troglóbios, entre peixes siluriformes, planárias aquáticas e gastrópodes, aracnídeos (opiliões *Eusarcus*, aranhas Ctenidae), diplópodes Polydesmida, diversos colêmbolos e alguns insetos, e crustáceos Peracarida, que incluem destacados relictos filogenéticos, como os crustáceos Speleogriphacea e anfípodes *Megagidiella*. São reconhecidos quatro compartimentos de aparente relevância biogeográfica para cavernícolas, correspondendo a microbacias na área. Troglóbios freáticos (bagres *Trichomycterus*, crustáceos Peracarida aquáticos, planárias) apresentam distribuições amplas através desses compartimentos, atingindo áreas distantes, como o Mato Grosso no caso dos Spelaeogriphacea *Potiicoara brasiliensis*, enquanto as espécies aquáticas que vivem em riachos (siluriformes como *Rhamdia e Ancistrus*) e os terrestres em geral, que vivem na zona vadosa, descontínua, tendem a apresentar distribuições restritas aos respectivos compartimentos. Muitos ecossistemas subterrâneos do Mato Grosso do Sul estão vulneráveis às várias ameaças descritas aqui e ações urgentes de proteção efetiva são necessárias para garantir uma utilização sustentável da terra e dos aquíferos cársticos.
Palavras-chave: *biodiversidade subterranean, troglóbios, área cárstica da Serra da Bodoquena, Mato Grosso do Sul, Programa Biota-MS.*

Introduction

The Serra da Bodoquena karst area has ca. 200 caves so far recorded (Sallun-Filho et al. 2010), with a great variety of subterranean habitats, including phreatic (never exposed at the vadose zone – Ford & Williams 2007) and submerged (found beneath the water level after a period at the vadose zone) cave systems, and dry caves. It distinguishes as a high diversity spot for troglobites (species with exclusively subterranean source populations – Trajano 2012) in South America. Among these, five siluriform fishes and several invertebrates have been recorded, such as spelaegriphaceans and bogidiellid amphipods, planarians, Pomatiopsidae gastropods, polydesmid diplopods, opilionids and onychophorans, including phylogenetic and geographic relicts. In addition, a rich troglophilic (also found in epigean habitats) fauna is observed, which coexists and interacts with the several troglobitic populations. Such diversity points to intricate evolutionary patterns related to the complex geological history of the area, interacting with present-day ecological factors, including the epigean (surface) biodiversity and biomass allowing for a significant input of nutrients into the subterranean realm.

1 History of speleobiology in the Mato Grosso do Sul State

The speleobiological interest in the area started in the mid-1980′s, with the discover, in a submerged cave (the Lago Azul Cave), followed by description of *Potiicoara brasiliensis* Pires 1987, the second known species of living Spelaeogriphacea – the first one was *Spelaeogriphus lepidops* Gordon 1957, from Table Moutains, South Africa (there are recent reports from caves other than the type locality - S. Craven & A.L.F. Guil, pers. comm.). Later on, two other species were found in Australia, confirming the Gondwanic distribution for the taxon and its relictual character. Further studies showed a wide distribution for spelaeogriphaceans in Mato Grosso do Sul, and also brought into light another phylogenetically and biogeographically important crustacean, the *Megagidiella* amphipods.

The period from mid-1990′s to mid-2000′s was marked by cave diving by biologists, who found the first troglobitic fishes from Serra da Bodoquena karst area, Bonito County, in the southern plateau: the armored catfish *Ancistrus formoso* Sabino & Trajano 1997 and *Trichomycterus dali* Rizzato, Costa-Jr., Trajano & Bichuette 2011 (this fish was first collected in 1998, but its description took more than one decade to be published).

In the early 1990′s, extensive biologic surveys were made, focusing mainly on terrestrial cave communities, which resulted in the first comprehensive faunal lists for caves in the southern plateau of the Bodoquena karst area, Bonito, Jardim and Porto Murtinho counties (Gnaspini & Trajano 1994). By then, the high potential for the occurrence of specialized terrestrial and aquatic subterranean animals was clear.

The presence of several spectacular submerged and phreatic caves, for which the Bonito region is notorious worldwide, implied an increasingly strong touristic pressure over the area. Brazilian legislation requires management plans for caves destined for tourism and their surroundings. Hence, environmental studies were designed to base such plans, beginning with the most famous touristic point, the flooded cave Lago Azul, where *Potiicoara brasiliensis* was discovered. Such studies allowed for a better knowledge of the aquatic communities in some caves, such as Mimoso, Buraco das Abelhas, São Miguel and Anhumas, besides the Lago Azul.

In 2002, N. Moracchioli finished her Ph. D. thesis centered on Brazilian spelaeogriphaceans, which proved to be quite abundant and widespread in Serra da Bodoquena, also occurring in Ricardo Franco Cave, Forte Coimbra area, Corumbá Co. (also in Mato Grosso do Sul, but on the opposite margin of the Paraguay river, distant ca. 200 km from Bodoquena), and in Curupira cave, Serra das Araras, Rosário do Oeste County, in Mato Grosso state, to the north of Mato do Grosso do Sul. She also gathered data on *Megadiella* amphipods, which co-occur with spelaeogriphaceans in most localities, including Ricardo Franco, but not Curupira cave. Ricardo Franco Cave is historically important because it was the first Brazilian cave mentioned in a written document, a poem by Dom Aquino Corrêa, from the late 1700′s (Martin 1980) – *Harta figueira à porta. Entrada bruta.*/ *Desço. Horrido hypogeum! Antro sombrio!*/ *Mas, de repente, um mágico arrepio,*/ *À luz das tochas. Tímida, a alma escruta…*/…. In 2000, that big fig tree was still at the cave entrance. As far as we know, this cave was not studied by biologists before their visit.

The studies above were carried out basically by researchers from the Universidade de São Paulo - USP, since there was no autochthonous academic speleobiology in Mato Grosso do Sul. In 2008, L. M. Cordeiro finished her M.Sc. dissertation, presented at the Universidade Federal do Mato Grosso do Sul - UFMS, which significantly enlarged the faunistic knowledge on the Bodoquena subterranean communities, in terms of new records for previously studied caves and new caves visited, including several in the northern plateau, reaching higher altitudes. She also performed the first detailed ecological study on cave terrestrial invertebrate communities in the area. As the result of a joint effort with Rodrigo Borghezan, student at the UNIDERP (MS), two additional new troglobitic fishes were found by these pioneers works on speleobiology in Mato Grosso do Sul, the heptapterid *Rhamdia* Bleecker 1858, (description is in progress) and the second troglobitic *Ancistrus* Kner 1845, known for the area. These species have been first studied by R. Borghezan for his undergraduate monograph (Borghezan 2008) and, later on, for his M.Sc. dissertation at the Universidade de São Paulo (Borghezan 2012).

We present here a synthesis of the faunal knowledge on the subterranean ecosystems in two karst areas of Mato Grosso do Sul, the intensively studied Serra da Bodoquena and the less known Forte Coimbra, based on published and unpublished data from the last two decades, as well as studies in progress, discussing the main threats for this highly relevant fauna.

Study site

The Serra da Bodoquena is one of the most extensive continuous Brazilian karst areas, located in the Mato Grosso do Sul state, in central-western Brazil. It consists of a north-south plateau extending for approximately 200 km, which forms an important water divide with an altitude around 800 m (Figure 1). It is unique in the context of the Brazilian Platform, because tectonic activities have been recognized in the area in the context of the Paraguay Belt and related to the development of the Cenozoic Pantanal Basin, which is still subsiding (Sallun-Filho & Karmann 2009, Campanha et al. 2011). Rains are concentrated in November to February, with a mean average

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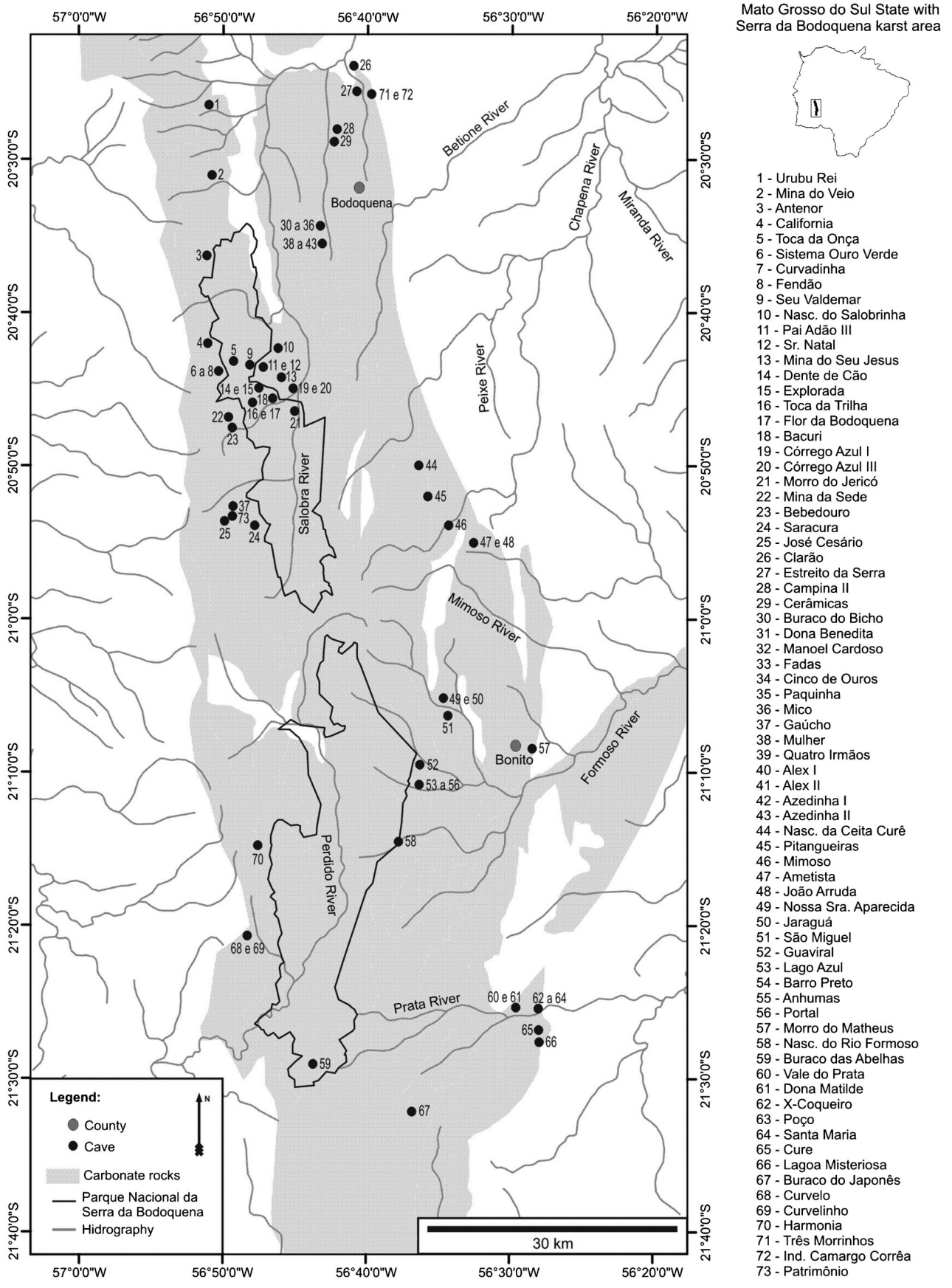

Figure 1. Map of the Serra da Bodoquena karst area, showing the localization of the studied caves (Modified from Bizzi et al. 2001). / Figura 1: Mapa da área cárstica da Serra da Bodoquena com a localização das cavernas estudadas (Modificado de Bizzi et al. 2001).

precipitation of about 1,300 mm per year and a mean annual temperature of 24°C. The natural vegetation consists of savanna in contact with semi-deciduous seasonal forest (Boggiani & Clemente 1999, Scremin-Dias et al. 1999).

At the eastern highland (greater than 500 m a.s.l.) the Bodoquena Plateau is divided into two main compartments, well defined by geomorphological contrasting features: the southern sector (Perdido River area), which has mainly karst landforms; and the northern part (Salobra River area), which has more fluvial characteristics. In the western lowlands (less than 500 a.s.l.), the Miranda river Depression forms exposed karst systems and part of a separate system of subjacent karst (Sallun-Filho & Karmann 2007). Geological evidence indicates that the karst aquifer is recharged mainly by autogenic waters, promoting the intense deposition of carbonates (as tufa deposits) as a consequence of resurgence of saturated waters (Sallun-Filho et al. 2004).

Most caves included in the present study are within the limits of the Parque Nacional da Serra da Bodoquena (PNSB), with 76.481 ha., created in 2000. Four rural settlements have been established in the surroundings of the PNSB at least 20 years ago, where several relevant caves harboring endemic troglobites are located. The livestock is currently the main economic activity in the region, although the tourism, including speleotourism, has an increasing economic importance, especially in Bonito, Bodoquena and Jardim counties.

Methods

Part of the data herein gathered were compiled from the literature, including publications such as the faunistic inventories (Gnaspini & Trajano 1994, Pinto da Rocha 1995, Pinto-da-Rocha & Sossegolo 2001, Galati et al. 2003, Costa-Jr. 2004, Eriksson & Gonçalves 2010) and taxonomy-oriented works (Trajano et al. 2000, Andrade et al. 2001, Mahnert 2001, Labruna & Venzal 2009, Pires-Vanin 2012), in addition to unpublished dissertations (Moracchioli 2002, Cordeiro 2008) and grey literature (Godoy 1986, Gnaspini et al. 1994). Original data came from collections by several speleobiologists in different occasions, including field courses, and more detailed identifications of material cited in the literature. For the sake of simplicity, we did not distinguish the source of data in the tables. Details on geographic coordinates of the caves listed in present work can be accessed at CNC/SBE link (Cadastro Nacional de Cavernas / Sociedade Brasileira de Espeleologia - www.cavernas.org.br/cnc).

In general, terrestrial organisms were collected by hand during visual inspections of all accessible substrates, using small brushes and tweezers. Pitfall-traps were used in some caves (Dente de Cão, Mateus, Córrego Azul I, Córrego Azul III, Sr. Natal, Fadas, Pitangueiras). Aquatic animals were collected with hand nets, bottles and baited minnow traps, from outside the water and during free and scuba diving. Surbers 30 x 30 cm were used for sampling benthonic organism in the Urubu Rei Cave.

Specimens were preserved in the proper solutions and brought to the laboratory for identification. Fishes were killed by over-anesthesia using benzocaine, fixed in formalin 4%, and preserved in alcohol 70%. Some samples were fixed in alcohol 100% for future molecular studies.

We did not use parataxonomy. Morphoespecies, when cited, have been identified by specialists on the taxonomy of the respective groups. Otherwise, the identifications are provided at the lowest level (usually supraespecific) reliable by non-specialists. Therefore, the number of species is probably much higher than shown in the tables.

The collecting efforts were highly heterogeneous. Most caves were sampled on a few occasions, generally during the dry seasons and on different years. A few caves were studied on several, consecutive occasions, both during dry and rainy seasons, such as the Córrego Azul I, Córrego Azul III, Fadas and Sr. Natal caves (4-5 occasions on 2006-2007; Cordeiro 2008); sampling with surber were carried out on eight occasions in the Urubu Rei Cave (2010-2012; L. M. Cordeiro, in progress). Therefore, differences in the number of taxa recorded in the tables do not necessarily reflect differences in biodiversity among caves.

The species/populations were classified according the Schiner-Racovitza system, following definitions in Trajano (2012): 1. **troglobites** correspond to exclusively subterranean source populations (a source populations has excess production and continues to grow if isolated); sink populations (a sink population, if cut off from all other migrants, eventually becomes extinct) may be found in surface habitats; 2. **troglophiles** include source populations both in hypogean and epigean habitats, with individuals regularly commuting between these habitats, promoting the introgression of genes selected under epigean regimes into subterranean populations (and *vice-versa*); 3. **trogloxenes** are instances of source populations in epigean habitats, but using subterranean resources.

Results

The taxa so far recorded for 84 caves visited in the Serra da Bodoquena karst area are presented in tables 1 and 2 (troglobites, found in 43 out of those caves) and in tables 3 to 9 (the remaining taxa); in addition, tables 1, 2 and 8 (Psychodidae dipterans) include caves in the poorly known Corumbá karst area, respectively Ricardo Franco and Forte Junqueira caves, situated ca. 200 km to the northwest of Bodoquena, at the border with Bolivia. The geographic location of studied caves is shown in Figure 1, except for 16 caves, for which there are no coordinates.

The diversity of some taxa, especially mites and ants, is not accurately represented due to taxonomic impediment: only the few identifications below the Order (for Acari) or Family (for the widespread formicids) levels were included in the tables.

As expected, the highest diversities were observed in the most intensively studied caves, in different occasions and seasons, and using different, complementary methods: Córrego Azul I e III, Fadas, Pitangueiras, João Arruda, Nossa Senhora Aparecida, São Miguel e Lago Azul.

Discussion

1 Distribution patterns and diversity

The subterranean fauna from the Bodoquena karst area has a unique taxonomic composition, combining typically subtropical (e.g., oniscodesmid diplopods) and tropical (e.g., Amblypygids, *Eusarcus* opilionids, isopterans, Bogidiellid amphipods), with (so far) exclusive elements (e.g., troglophilic and troglobitic onychophorans), including phylogenetic relicts, such as spelaeogriphaceans and *Megagidiella* amphipods. Geographic relicts include *Trichomycterus* catfish, not found

Table 1. Troglobitic taxa recorded in caves in the Salobra River Basin, Serra da Bodoquena karst area, Mato Grosso do Sul state. * Troglobitic *status* to be confirmed; ** at least six morphospecies recognized by specialists. / Tabela 1. Táxons troglóbios registrados em cavernas na Bacia do Rio Salobra, área cárstica da Serra da Bodoquena. * S*tatus* de troglóbio a ser confirmado; ** pelo menos seis morfoespécies identificadas pelos especialistas.

TAXA	Caves																					
	Salobra River - left margin																Salobra R. - right marg.					
	Urubu Rei	Mina do Vêio	Califórnia	Toca da Onça	S. Valdemar	Pai Adão III	Sr. Natal	M. do Seu Jesus	Dente de Cão	Toca da Trilha	F. da Bodoquena	Bacuri	Morro do Jericó	Mina da Sede	Bebedouro	Saracura	Clarão	Buraco do Bicho	Dona Benedita	Manuel Cardoso	Fadas	Cinco de Ouros
AQUATIC																						
Teleostei Siluriformes																						
Heptapteridae *Rhamdia* sp. n.																				X	X	X
Loricariidae *Ancistrus* sp. n.																					X	
Trichomycteridae *Trichomycterus dali*													X			X						
Trichomycterus cf. *dali*	X	X	X	X	X						X			X	X							
Crustacea																						
Spelaeogriphacea																						
Spelaeogriphidae *Potiicoara brasiliensis*																X		X	X	X	X	X
Amphipoda																						
Bogidiellidae *Megagidiella azul*																	X	X				
Bathynellacea gen. n. sp. n.	X																					
Turbellaria Tricladida																						
Dugesiidae cf. *Girardia*								X										X	X			X
Annelida Oligochaeta																		X	X			
Gastropoda	X																					
Pomatiopsidae cf. *Spiripockia*																						
TERRESTRIAL																						
Onychophora																						
Peripatidae gen. n. sp. n.									X	X		X										
Arachnida																						
Araneae						X			X				X									X
Ctenidae						X			X				X									X
Opiliones																						
Gonyleptidae *Eusarcus* spp.**	X		X						X				X			X				X	X	X
Crustacea																						
Isopoda Oniscoidea	X										X											
Myriapoda																						
Diplopoda Paradoxosomatidae							X	X														
Hexapoda																						
Collembola																						
Paronellidae *Trogolaphysa* sp. n.	X																					
Coleoptera																						
Carabidae Paussinae *Pachytelis* sp.*							X															

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Table 2. Troglobitic taxa recorded in the Ricardo Franco cave, in Corumbá area, and in other microbasins of the Serra da Bodoquena karst area, except Salobra River, both in Mato Grosso do Sul state. * troglobitic *status* to be confirmed. / Tabela 2. Táxons troglóbios registrados na caverna Ricardo Franco, área de Corumbá, e em outras microbacias da área cárstica da Serra da Bodoquena, exceto Rio Salobra, estado do Mato Grosso do Sul. * *Status* de troglóbio a ser confirmado.

TAXA	CAVES																					
	Corumbá	Intermediate					Formoso River					Prata River							Perdido R.		
	Ricardo Franco	Nasc. Ceita Curê	Pitangueiras	Mimoso	Abismo Opossum	Ametista	João Arruda	N. Sra. Aparecida	São Miguel	Lago Azul	Anhumas	N. Rio Formoso	B. das Abelhas	Dona Matilde	X – Coqueiro	Poço	Curê	Lagoa Misteriosa	B. do Japonês	Marcelo	Curvelinho	Harmonia
AQUATIC																						
Teleostei Siluriformes																						
Loricariidae *Ancistrus formoso*												X										
Trichomycteridae *Trichomycterus dali*													X									
Crustacea																						
Spelaeogriphacea																						
Spelaeogriphidae *Potiicoara brasiliensis*	X	X		X	X					X	X	X	X			X		X	X			
Amphipoda																						
Bogidiellidae *Megagidiella azul*		X		X	X					X	X		X			X						
Megagidiella cf. *azul*	X																					
Acari Oribata																						
Hidrozetidae *Hydrozetes* sp.*				X																		
Turbellaria Tricladida																						
Dugesiidae cf. *Girardia*				X	X					X												
Annelida Oligochaeta				X	X					X												
Gastropoda Pomatiopsidae		X										X										
TERRESTRIAL																						
Arachnida																						
Araneae																						
Ochyroceratidae *Speocera eleonorae*															X							X
Pseudoscorpiones																						
Chernetidae *Speleochernes dubius**			X							X	X											X
Myriapoda																						
Diplopoda Polydesmida																						
Oniscodesmidae *Katantodesmus* sp.							X	X	X								X					
Crypturodesmus sp.							X	X	X								X					
Paradoxosomatidae																				X		
Hexapoda																						
Collembola																						
Arrhopalitidae *Pararrhopalites papaveroi*							X			X												
Entomobryidae sp.1										X						X						
Entomobryidae sp.2								X														
Cyphoderidae						X								X			X					X
Paronellidae sp.*									X													
Hemiptera Dipsocoridae																					X	

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Table 3. Non-troglobitic fishes recorded in caves of the Serra da Bodoquena karst area, Mato Grosso do Sul state. S. L. – Salobra River left margin; S. R. – Salobra River right margin; I. – Intermediate area; F. – Formoso river basin; Pr. – Prata river basin. / Tabela 3. Peixes não troglóbios registrados em cavernas da área cárstica da Serra da Bodoquena, estado de Mato Grosso do Sul. S. L. – margem esquerda do Rio Salobra; S. R. – margem direita do Rio Salobra; I – área intermediária; F. – bacia do rio Formoso; Pr. – bacia do Rio da Prata.

Taxa	Caves													
	S. L.		S. R.					I.	F.			Pr.		I.
	Antenor	N. Salobrinha	Nasc. Fadas	Dona Benedita	Manoel Cardoso	Fadas	Cinco de Ouros	Mimoso	Anhumas	N. Rio Formoso	N. Rio Formosinho	B. das Abelhas	Lagoa Misteriosa	B. do Japonês
Teleostei														
Synbranchiformes														
Synbranchidae *Synbranchus marmoratus*											X		X	
Perciformes														
Cichlidae *Bujurquina vittata*					X	X	X				X			
Crenicichla vittata											X			
Characiformes														
Characidae *Astyanax bimaculatus*									X			X	X	
Astyanax lineatus								X	X					
Astyanax fasciatus													X	
Astyanax sp.		X				X								
Jupiaba acanthogaster										X				
Moenkhausia bonita										X				
Hyphessobrycon eques										X				
Crenuchidinae *Characidium* sp.										X		X		
Curimatidae *Steindachneria* sp.										X				
Erythrinidae *Hoplias malabaricus*			X	X	X	X	X			X				
Iguanodectidae *Bryconops* sp.										X				
Gymnotiformes														
Sternopygidae *Sternopygus macrurus*		X									X			
Siluriformes														
Heptapteridae *Rhamdia quelen*	X		X								X	X		
Pimelodella sp.		X												
Loricariidae *Ancistrus* sp.											X	X		X
Hypostomus sp.											X			
Hypostomus cochliodon											X			

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Table 4. Non-troglobitc invertebrates, except Psychodidae dipterans, recorded in caves of the left margin of the Salobra River basin, Serra da Bodoquena karst area, Mato Grosso do Sul state. * at least three species recognized by specialists. / Tabela 4. Invertebrados não troglóbios, exceto dípteros Psychodidae, registrados em cavernas da margem esquerda da bacia do Rio Salobra, área cárstica da Serra da Bodoquena, estado do Mato Grosso do Sul. * Três espécies reconhecidas pelos especialistas.

TAXA	CAVES																			
	Salobra River - left margin																			
	Urubu Rei	Antenor	Califórnia	Califórnia II	Sist. Ouro Verde	Curvadinha	Fendão	Sr. Valdemar	Pai Adão III	Sr. Natal	Mina do Seu Jesus	Dente de Cão	Explorada	Toca da Trilha	F. da Bodoquena	Bacurí	Córrego Azul I	Córrego Azul III	Morro do Jericó	Saracura
Turbellaria Continenticola																				
Turbellaria sp.3											X									
Nematomorpha Gordiacea							X											X		
Mollusca Gastropoda						X	X										X	X	X	
Pulmonata																	X	X		
Stylommatophora												X								
Onychophora																				
Peripatidae gen. n. sp. n.								X						X		X				
Epiperipatus sp.1												X	X	X						
Chelicerata Arachnida																				
Acari																				
Argasidae *Ornithodoros talaje*																	X	X		
Ornithodoros sp.																	X	X		
Ixodidae *Amblyomma cajennense*																		X		
Araneae																				
Araneidae *Alpaida negro*																	X			
Alpaida sp.1										X										
Cyclosa sp.	X																			
Caponiidae *Nops* sp.																		X		
Ctenidae			X		X	X		X				X						X		
Ctenus sp.										X							X	X		
Dipluridae												X								
Hahniidae																	X			
Lycosidae						X											X			
Allocosa sp.			X																	
Linyphiidae															X					
Mimetidae								X												
Ero sp.																	X			
Oonopidae																	X			
Philodromidae																		X		
Pholcidae *Mesabolivar* sp.2																	X			
Mesabolivar sp.3																	X			

Continued on next page

Table 4. Continued.

TAXA	CAVES																				
	Salobra River - left margin																				
	Urubu Rei	Antenor	Califórnia	Califórnia II	Sist. Ouro Verde	Curvadinha	Fendão	Sr. Valdemar	Pai Adão III	Sr. Natal	Mina do Seu Jesus	Dente de Cão	Explorada	Toca da Trilha	F. da Bodoquena	Bacurí	Córrego Azul I	Córrego Azul III	Morro do Jericó	Saracura
aff. *Spermophora*																	X	X		
Salticidae																	X			
Salticidae gen.1 sp.1																		X		
Salticidae gen.2 sp.1																	X			
Cory*thalia* sp.																	X			
Encolpius sp.																	X			
Noegus sp.																	X			
Marma nigritarsis																	X	X		
Segestriidae *Ariadna* sp.								X									X			
Sicariidae		X	X		X	X	X	X	X	X		X			X	X	X	X	X	
Loxosceles sp.1			X					X				X			X	X				
Theridiidae																	X	X		
Theridion sp.																	X	X		
Theridiosomatidae *Plato* sp.		X						X												
Titanoecidae																	X			
Trechaleidae			X				X										X	X		
Opiliones																				
Gonyleptidae *Eusarcus* spp.*			X		X	X	X												X	
Discocyrtus sp.	X		X					X				X		X			X		X	
Cosmetidae			X																	
Pseudoscorpiones																				
Chernetidae *Spelaeochernes* sp.									X								X	X	X	
Cheiridiidae																		X		
Scorpiones																				
Buthidae *Tityus confluens bodoquena*												X								
Amblypygi																				
Prhynidae *Heterophrynus vesanicus*	X	X	X	X	X		X	X		X		X		X	X	X	X	X	X	X
Crustacea																				
Isopoda										X		X					X	X		
Sphaeroniscidae *Circoniscus intermedius*												X								
Copepoda																				
Cyclopidae *Macrocyclops* cf. *albidus*	X																			

Continued on next page

Table 4. Continued.

TAXA	CAVES																				
	Salobra River - left margin																				
	Urubu Rei	Antenor	Califórnia	Califórnia II	Sist. Ouro Verde	Curvadinha	Fendão	Sr. Valdemar	Pai Adão III	Sr. Natal	Mina do Seu Jesus	Dente de Cão	Explorada	Toca da Trilha	F. da Bodoquena	Bacurí	Córrego Azul I	Córrego Azul III	Morro do Jericó	Saracura
Myriapoda																				
Chilopoda			X									X					X			
Diplopoda Spirostreptida																				
Pseudonannolenidae										X		X								
Spirostreptidae				X	X	X	X								X					
Polydesmida																				
Chelodesmidae						X		X				X								
Brasilodesmus sp.										X										
Paradoxosomatidae			X							X	X									
Oxidus gracilis			X																	
Oniscodesmidae	X		X		X	X				X		X			X				X	
Hexapoda																				
Archaeognatha																	X	X		
Blattaria					X		X	X												
Blaberidae aff. *Epilampra* sp.																	X			
Blattellidae *Cariblatta* sp.																	X			
Polyphagidae																	X	X		
Hypercompsa fenestrina																	X	X		
Coleoptera																				
Carabidae																		X		
Cerambycidae																	X	X		
Curculionidae																	X			
Dermestidae																	X	X		
Elateridae																		X		
Nitidulidae										X										
Pselaphidae																		X		
Scarabaeidae																	X			
Scolytidae										X								X		
Staphylinidae										X							X			
Leiodidae *Dissochaetus* sp.																				X
Diptera																				
Chaoboridae										X								X		
Drosophilidae *Drosophila* sp.																	X			

Continued on next page

Table 4. Continued.

TAXA	CAVES																			
	Salobra River - left margin																			
	Urubu Rei	Antenor	Califórnia	Califórnia II	Sist. Ouro Verde	Curvadinha	Fendão	Sr. Valdemar	Pai Adão III	Sr. Natal	Mina do Seu Jesus	Dente de Cão	Explorada	Toca da Trilha	F. da Bodoquena	Bacurí	Córrego Azul I	Córrego Azul III	Morro do Jericó	Saracura
Empididae																		X		
Mycetophilidae																		X		
Phoridae *Conicera* sp.1										X										
Conicera sp.2										X										
Megaselia sp.1																	X			
Megaselia sp.2																	X			
Dermaptera					X															
Orthoptera																				
Gryllidae	X		X	X	X			X			X				X					
Phalangopsidae *Endecous* sp.	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	
Strinatia sp.					X					X										
Ephemeroptera Caenidae	X																			
Hemiptera																				
Cicadellidae																	X			
Cixiidae										X							X	X		
Heteroptera																				
Pyrrhocoridae																	X			
Reduviidae			X		X					X							X	X		
Mepraia sp.																		X		
Hymenoptera																				
Apidae Meliponinae																		X		
Bethylidae																	X			
Chalcidoidea sp.1																		X		
Chalcidoidea sp.2										X										
Ponerinae												X								
Lepidoptera																				
Tineidae	X	X	X		X		X	X				X			X		X	X	X	X
Noctuidae	X		X									X						X	X	
Neuroptera																				
Mantispidae																		X		
Trichoptera																		X		
Polycentropodidae *Polycentropus* sp.															X					
Thysanoptera																	X	X		

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Table 5. Non-troglobitc invertebrates, except Psychodidae dipterans, recorded in caves of the right margin of the Salobra River basin, Serra da Bodoquena karst area, Mato Grosso do Sul state. * at least three species recognized by specialists. / Tabela 5. Invertebrados não troglóbios, exceto dípteros Psychodidae, registrados em cavernas da margem direita da bacia do Rio Salobra, área cárstica da Serra da Bodoquena, estado do Mato Grosso do Sul. * Três espécies reconhecidas pelos especialistas.

TAXA	**Caves**																
	Salobra River - right margin																
	Estreito da Serra	Campina II	Cerâmicas	Buraco do Bicho	Dona Benedita	Manoel Cardoso	Fadas	Cinco de Ouros	Paquinha	Mico	Mulher	Quatro Irmãos	Alex I	Alex II	Azedinha I	Azedinha II
Turbellaria Continenticola																
Turbellaria sp.1						X	X									
Turbellaria sp.2				X												
Nematomorpha Gordiacea								X								
Mollusca Gastropoda						X	X						X			
Onychophora Peripatidae																
Epiperipatus sp.2		X	X		X	X	X		X	X				X		
Chelicerata Arachnida																
Araneae																
Araneidae							X	X								
Alpaida sp.1													X			
Alpaida sp.2								X								
Micrathena sp.								X								
Eustala sp.								X								
Caponiidae *Nops* sp.				X												
Ctenidae			X		X	X	X						X			X
Ctenus sp.							X									
Corinnidae								X								
Linyphiidae													X			
Mimetidae *Ero* sp.							X									
Oonopidae													X			
Pholcidae *Mesabolivar* sp.2											X					
Salticidae *Chira* sp.1													X			
Chira sp.2								X								
Selenopsidae *Selenops* sp.								X								
Sicariidae							X	X					X			
Loxosceles sp.1								X								
Loxosceles sp.3													X			

Continued on next page

Table 5. Continued.

TAXA	Caves																
	Salobra River - right margin																
	Estreito da Serra	Campina II	Cerâmicas	Buraco do Bicho	Dona Benedita	Manoel Cardoso	Fadas	Cinco de Ouros	Paquinha	Mico	Mulher	Quatro Irmãos	Alex I	Alex II	Azedinha I	Azedinha II
Loxoceles gaucho												X				
Sparassidae							X									
Theridiidae							X									
Theridion sp.											X		X			
Thymoites sp.							X									
Theridiosomatidae *Plato* sp.					X	X	X	X					X			
Trechaleidae					X		X									
Uloboridae *Uloborus* sp.													X			
Opiliones																
Gonyleptidae *Eusarcus* spp.*			X								X		X			
Discocyrtus sp.						X		X								X
Cosmetidae						X										
Pseudoscorpiones																
Chernetidae							X									
Scorpiones Buthidae																
Tityus confluens bodoquena			X		X								X			
Amblypygi Phrynidae																
Heterophrynus vesanicus	X		X		X	X	X	X						X		
Crustacea																
Decapoda Palaemonidae																
Macrobrachium brasiliense							X	X								
Myriapoda																
Chilopoda					X			X					X			
Diplopoda																
Spirostreptida																
Pseudonannolenidae				X												
Spirostreptidae						X	X									

Continued on next page

Table 5. Continued.

TAXA	Caves																
	Salobra River - right margin																
	Estreito da Serra	Campina II	Cerâmicas	Buraco do Bicho	Dona Benedita	Manoel Cardoso	Fadas	Cinco de Ouros	Paquinha	Mico	Mulher	Quatro Irmãos	Alex I	Alex II	Azedinha I	Azedinha II
Polydesmida																
Chelodesmidae													X	X		
Paradoxosomatidae					X		X									
Oniscodesmidae			X		X	X	X									
Hexapoda																
Archaeognatha													X			
Coleoptera																
Cerambycidae							X									
Scydmaenidae							X									
Diptera																
Phoridae *Conicera* sp.1							X									
Megaselia sp.1							X									
Megaselia sp.2							X									
Orthoptera																
Gryllidae					X	X								X		
Phalangopsidae																
Endecous sp.						X	X	X	X		X		X		X	X
Ephemeroptera Caenidae						X										
Hemiptera Cixiidae							X									
Heteroptera Reduviidae							X									

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Table 6. Non-troglobitc invertebrates, except Psychodidae dipterans, recorded in caves of the Formoso, Prata and Perdido river basins and intermediate areas of the Serra da Bodoquena karst area, Mato Grosso do Sul state. * Identified as *Blechroscelis* in Pinto-da-Rocha (1995); ** at least three species recognized by specialists. / Tabela 6. Invertebrados não troglóbios registrados em cavernas das bacias dos rios Formoso, Prata e Perdido e áreas intermediárias do carste da Serra da Bodoquena, estado de Mato Grosso do Sul. * Identificado como *Blechroscelis* em Pinto-da-Rocha (1995); ** pelo menos três espécies reconhecidas pelos especialistas.

TAXA	Caves									
	Formoso River									
	N. Sra. Aparecida	São Miguel	Jaraguá	Guaviral	Lago Azul	Barro Preto	Anhumas	Portal	Morro do Mateus	N. Rio Formoso
Annelida Oligochaeta					X					
Mollusca Gastropoda							X			
Pulmonata										
Stylommatophora										
Subulinidae		X								
Camaenidae *Solaropsis* sp.		X								
Megalobulimus cf. *oblongus*		X							X	
Chelicerata Arachnida										
Acari	X	X		X		X				
Argasidae *Carios fonsecai*		X								
Ornithodoros talaje		X	X							
Ornithodoros sp.									X	
Oribatida		X								
Araneae										
Amaurobiidae *Metaltella* sp.		X								
Araneidae				X	X					
Alpaida alto		X								
Ctenidae *Ctenus* aff. *griseolus*			X							
Ctenus sp.	X	X	X		X		X		X	
Isoctenus sp.		X							X	
Nothroctenus sp.		X								
Phoneutria nigriventer		X								
Lycosidae		X								
Mysmenidae *Mysmena* sp.					X					
Oonopidae *Oonops* sp.	X									
Orchestina sp.		X								
Pholcidae			X						X	
Mesabolivar sp.4							X			
Mesabolivar sp.5		X								
Mesobolivar sp.6*		X			X					
Scytodidae				X						
Scytodes globula				X						
Sicariidae	X				X		X		X	
Loxosceles sp.2									X	
Loxoceles gaucho	X	X								
Loxoceles grupo *gaucho*			X							
Loxoceles similis		X			X					
Theridiidae					X					
Achaearanea sp.	X									
Theridiosomatidae *Plato* sp.				X			X			
Titanoecidae		X								
Opiliones										
Gonyleptidae *Eusarcus* spp.**									X	
Parabalta sp.	X	X								
Cosmetidae							X			

Continued on next page

Table 6. Continued.

TAXA	Caves									
	Formoso River									
	N. Sra. Aparecida	São Miguel	Jaraguá	Guaviral	Lago Azul	Barro Preto	Anhumas	Portal	Morro do Mateus	N. Rio Formoso
Pseudoscorpiones										
Chernetidae *Spelaeochernes dubius*					X		X			
Spelaeochernes eleonorae	X	X		X						
Spelaeochernes sp.	X									
Amblypygi										
Prhynidae *Heterophrynus vesanicus*		X								
Crustacea										
Isopoda		X								
Armadillidae *Venezillo* sp.		X		X						
Diplopoda										
Spirostreptida										
Pseudonannolenidae	X			X	X					
Spirostreptidae	X			X						
Orthoporus sp.	X	X		X						
Polydesmida										
Chelodesmidae *Arthrosolaenomeris* sp.		X								
Oniscodesmidae	X				X			X	X	
Crypturodesmus sp.		X					X			
Cryptodesmidae *Cryptodesmus* sp.								X		
Hexapoda										
Collembola	X									
Arrhopalitidae *Arrhopalites* sp.		X								
Entomobryidae							X			
Paronellidae		X			X					
Coleoptera										
Carabidae *Galerita collaris*			X							
Dytiscidae					X					
Cholevidae *Dissochaetus murray*	X	X								
Scarabaeidae *Megasoma* sp.			X							
Staphylinidae	X									
Diptera										
Cecidomyiidae		X								
Chironomidae	X									
Culicidae Subf. Culicinae		X		X						
Drosophilidae *Drosophila eleonorae*	X									
Drosophila sp.				X						
Muscidae		X		X						
Mycetophilidae		X		X						
Keroplatidae				X						
Phoridae		X								
Conicera sp.3	X									
Megaselia sp.3				X						
Sphaeroceridae	X									
Tipulidae		X			X					
Orthoptera										
Phalangopsidae	X		X		X					
Endecous sp.		X					X			
Hemiptera										

Continued on next page

Table 6. Continued.

TAXA	Caves									
	Formoso River									
	N. Sra. Aparecida	São Miguel	Jaraguá	Guaviral	Lago Azul	Barro Preto	Anhumas	Portal	Morro do Mateus	N. Rio Formoso
Cicadellidae		X								
Derbidae		X								
Heteroptera										
Gerridae					X					
Veliidae							X			
Belostomatidae					X					
Coreidae					X					
Reduviidae		X			X					
Emesinae		X								
Hymenoptera										
Braconidae	X									
Ichneumonidae		X								
Solenopsis grupo *geminata*		X		X						
Vespidae	X	X	X							
Polybia ignobilis		X								
Isoptera	X	X			X					
Nasutiterminae *Nasutitermes* sp.		X								
Lepidoptera										
Tineidae	X	X		X	X	X				
Noctuoidea	X	X	X							
Noctuidae		X		X		X				
Psocoptera	X			X	X					
Psyllipsocidae		X								

in epigean water courses until now. Widespread taxa with troglobitic representatives in other karst areas include gastropods, and the several families of Collembola, a very ubiquitous group in caves worldwide. On the other hand, the low diversity of carabid beetles and oniscidean isopods, taxa usually abundant and diversified in most Brazilian caves, is unexpected.

When compared to other karst areas in Brazil, the Bodoquena distinguishes as a spot of high diversity of troglobites, together with the Alto Ribeira, in São Paulo state, and Serra do Ramalho, São Desidério and Chapada Diamantina, in Bahia state.

Among aquatic troglobites (also referred as stygobites), those occurring in the phreatic zone, such as spelaeogriphaceans, amphipods, planarians and *Trichomycterus* catfish, have a wide distribution across the sectors defined by the microbasins, indicating a connection across the aquifer, at least in the past. On the other hand, aquatic species living in base-level streams (for a habitat definition, see Trajano, 2001), such as *Rhamdia* n. sp. and *Ancistrus* n. sp. from Fadas system, and a new gastropod species, which may be the second reported to genus *Spiripockia*, present a locally restricted distribution. As well, terrestrial troglobites generally occur in caves in the same microbasin, probably due to fragmentation of the vadose (aerated) zone.

A higher degree of fragmentation may explain the higher diversity of terrestrial troglobites in the north plateau. Sallun-Filho & Karmann (2007) defined the Salobra River area as a canyons and alluvial plains (CAP). In fact, the Salobra base level already reached the impermeable substrates by the fluvial incision at times cutting down to the noncarbonated rocks (Sallun-Filho & Karmann 2007). This would explain the occurrence of different species of taxa as ctenid spiders, onychophorans and *Eusarcus* opilionids separated by the river valley (mostly a canyon).

As expected, many typically tropical taxa are more frequent in the north plateau, e.g., onychophorans, amblypygids, *Eusarcus* opilionids (also highly diversified in caves from Goiás and Bahia states – M.E. Bichuette, pers. comm., 2012). Troglophilic taxa widespread in Brazilian caves include *Loxosceles*, *Plato*, *Mesabolivar* and ctenid spiders, *Endecous* crickets, *Conicera* and *Megaselia* phorids.

The Serra da Bodoquena may be the southern limit of the distribution area of *Heterophynus vesanicus*, typical Cerrado species (A. Giuponni, pers. comm.). Females with eggs were observed in several caves during the dry season, which seems to correspond to the reproductive peak for the species in the Bodoquena area (Cordeiro 2008); caves are probably an important refuge for this troglophilic species during this period.

Table 7. Non-troglobitc invertebrates, except Psychodidae dipterans, recorded in caves of the Prata and Perdido river basins and intermediate areas of the Serra da Bodoquena karst area, Mato Grosso do Sul state. * Identified as *Blechroscelis* in Pinto-da-Rocha (1995); ** at least three species recognized by specialists./Tabela 7. Invertebrados não troglóbios, exceto dípteros Psychodidae, registrados em cavernas das bacias dos rios Prata e Perdido e áreas intermediárias do carste da Serra da Bodoquena, estado de Mato Grosso do Sul. * Identificado como *Blechroscelis* em Pinto-da-Rocha (1995); ** pelo menos três espécies reconhecidas pelos especialistas.

TAXA	Caves																						
	Intermediate					Prata River								Perd. R.			Indeterminate						
	Pitangueiras	Mimoso	Ametista	João Arruda	Serradinho	B. das Abelhas	Vale do Prata I	Vale do Prata II	Dona Matilde	X – Coqueiro	Poço	Santa Maria	Curê	Curvelo	Curvelinho	Harmonia	Cantagalo	T. do Tamanduá	Pindó	Serrasul	Alto Salobra	Eldorado
Nematomorpha Gordiacea				X																			
Annelida Oligochaeta																							
Hirudinea													X										
Mollusca Gastropoda																							
Pulmonata	X																						
Prosobranchia Thiaridae																							
Melanoides tuberculatus		X																					
Chelicerata Arachnida																							
Acari				X					X	X			X										
Acaroidea	X	X																					
Ixodida																							
Argasidade *Ornithodoros* sp.		X	X				X								X								
Oribata																							
Malaconothridae *Malaconothrus* sp.		X																					
Mesostigmata		X																					
Araneae																							
Araneidae	X	X												X									
Alpaida sp.		X																					
Ctenidae																			X				
Ctenus sp.	X			X							X								X				
Ochyroceratidae *Ochyrocera* sp.														X									
Speocera sp.										X													
Pholcidae	X	X					X			X									X				
Mesabolivar sp.2		X																					
Mesobolivar sp.6*	X										X		X	X	X	X							
Psilochorus sp.												X	X										
Salticidae	X																						
Scytodidae	X																						
Scytodes sp.	X																						

Continued on next page

Table 7. Continued.

TAXA	Caves																					
	Intermediate					Prata River								Perd. R.			Indeterminate					
	Pitangueiras	Mimoso	Ametista	João Arruda	Serradinho	B. das Abelhas	Vale do Prata I	Vale do Prata II	Dona Matilde	X – Coqueiro	Poço	Santa Maria	Curê	Curvelo	Curvelinho	Harmonia	Cantagalo	T. do Tamanduá	Pindó	Serrasul	Alto Salobra	Eldorado
Selenopidae	X																					
Sicariidae *Loxosceles* sp.	X	X	X	X									X			X						
Theridiidae		X								X												
Achaearanea sp.							X															
Chrosiothes sp.							X															
Theridion sp.		X																				
Theridiosomatidae																			X		X	
Plato sp.	X	X	X	X						X		X		X	X							
Thomosidae		X																				
Uloboridae *Ponella fasciata*	X																					
Zoridae		X																				
Opiliones																						
Gonyleptidae *Parabalta* sp.		X		X							X								X			
Cosmetidae	X																					
Pseudoscorpiones											X											
Lechytiidae *Lechytia chthoniiformis*													X									
Chernetidae *Spelaeochernes dubius*	X	X														X						
Spelaeochernes eleonorae		X	X	X			X		X	X	X	X	X					X				
Spelaeochernes sp.																		X				
Zaona cavicola												X										
Scorpiones	X																					
Buthidae *Tityus confluens bodoquena*	X																					
Amblypygi																						
Prhynidae *Heterophrynus* sp.			X	X						X	X	X	X									
Crustacea																						
Isopoda												X										
Armadillidae *Venezillo* sp.							X						X			X						
Sphaeroniscidae *Circoniscus* sp.												X										
Oniscidea *Trichorhina acuta*																		X				
Myriapoda																						
Chilopoda																			X			

Continued on next page

Table 7. Continued.

TAXA	Caves																						
	Intermediate					Prata River								Perd. R.			Indeterminate						
	Pitangueiras	Mimoso	Ametista	João Arruda	Serradinho	B. das Abelhas	Vale do Prata I	Vale do Prata II	Dona Matilde	X – Coqueiro	Poço	Santa Maria	Curê	Curvelo	Curvelinho	Harmonia	Cantagalo	T. do Tamanduá	Pindó	Serrasul	Alto Salobra	Eldorado
Geophilomorpha				X																			
Diplopoda				X					X														
Spirostreptida																							
Pseudonannolenidae	X			X	X		X					X			X					X		
Pseudonannolenidae gen.1 sp.1	X																						
Pseudonannolenidae gen.2 sp.1	X																						
Pseudonannolene sp.	X																						
Spirostreptidae	X			X	X		X	X									X	X					
Orthoporus sp.	X			X	X			X									X	X					
Polydesmida															X				X				
Chelodesmidae *Arthrosolaenomeris* sp.				X					X														
Leptodesmus sp.																	X						
Strongylomorpha sp.																			X				
Paradoxosomatidae *Cantharosoma* sp.	X																						
Mestosoma sp.	X																						
Fuhrmannodesmidae	X																						
Oniscodesmidae		X							X														
Crypturodesmus sp.	X		X									X			X	X	X	X					
Cryptodesmidae *Cryptodesmus* sp.									X														
Hexapoda																							
Collembola																							
Entomobryidae	X	X													X								
Paronellidae	X	X		X			X								X	X							
Archaeognatha															X								
Meinertellidae															X								
Blattaria							X		X														
Blaberidae											X				X								
Epilampra cf. *yersiniana*										X													
Blattellidae *Nyctibora* sp.				X																			
Coleoptera																							
Carabidae	X																						
cf. *Paratachys* sp.		X																					

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Table 7. Continued.

TAXA	Caves																					
	Intermediate					Prata River								Perd. R.			Indeterminate					
	Pitangueiras	Mimoso	Ametista	João Arruda	Serradinho	B. das Abelhas	Vale do Prata I	Vale do Prata II	Dona Matilde	X – Coqueiro	Poço	Santa Maria	Curê	Curvelo	Curvelinho	Harmonia	Cantagalo	T. do Tamanduá	Pindó	Serrasul	Alto Salobra	Eldorado
Polyphaga													X									
Cholevidae *Dissochaetus murray*		X		X												X						
Chrysomelidae													X						X			
Elateridae Pyrophorinae										X												
Ptiliidae Cephaloplectinae											X											
Scarabaeidae *Megasoma* sp.				X																		X
Scraptiidae																X						
Scydmaenidae												X										
Staphylinidae		X																				
Tenebrionidae Alleculinae							X					X										
Histeridae	X																					
Scarabaeidae	X																					
Noteridae	X																					
Leiodidae	X																					
Diptera																						
Drosophilidae	X																					
Fanniidae *Fannia* sp.		X														X						
Milichiidae *Pholeomyia* sp.				X			X						X			X						
Muscidae	X																					
Sciaridae	X						X															
Phoridae *Conicera* sp.3		X	X	X			X															
cf. *Apocephalus* sp.							X															
Dohrniphora sp.																X						
Streblidae				X																		
Tachinidae													X									
Orthoptera																						
Phalangopsidae			X	X																	X	
Endecous sp.	X	X									X											
Hemiptera																						
Cicadellidae																						
Cixiidae				X						X												
Fulgoridae	X			X															X			

Continued on next page

Table 7. Continued.

TAXA	Caves																						
	Intermediate					Prata River								Perd. R.			Indeterminate						
	Pitangueiras	Mimoso	Ametista	João Arruda	Serradinho	B. das Abelhas	Vale do Prata I	Vale do Prata II	Dona Matilde	X – Coqueiro	Poço	Santa Maria	Curê	Curvelo	Curvelinho	Harmonia	Cantagalo	T. do Tamanduá	Pindó	Serrasul	Alto Salobra	Eldorado
Heteroptera	X			X												X							
Cixiidae		X																					
Cydnidae													X										
Dipsocoridae														X									
Emesinae	X										X												
Reduviidae	X	X												X		X							
Hymenoptera																							
Formicidae *Camponotus* sp.												X			X								
Paratrechina sp.	X														X	X							
Acromyrmex sp.							X																
Solenopsis grupo *geminata*		X	X	X			X		X	X			X										
Labidus coecus														X									
Pachycondyla sp.							X																
Isoptera			X	X															X	X			
Nasutiterminae	X																						
Nasutitermes sp.							X								X								
Diversitermes sp.														X									
Syntermes sp.											X												
Lepidoptera																							
Tineidae	X	X	X	X			X					X	X										
Hesperiidae																			X				
Noctuoidea																				X	X	X	
Noctuidae	X													X									
Neuroptera																							
Mantispidae	X	X																					
Psocoptera																							
Psyllipsocidae							X						X										

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Table 8. Psychodidae dipterans recorded in caves of the Serra da Bodoquena karst area, Mato Grosso do Sul state (Modified from Galati et al. 2003). Co. – Corumbá; S.L. – Salobra River left margin; S.R. – Salobra River right margin; I. – Intermediate; F. – Formoso River; Pr. – Prata River; P. – Perdido River./ Tabela 8. Diptera Psychodidae registrados em cavernas da área cárstica da Serra da Bodoquena, Mato Grosso do Sul (Modificado de Galati et al. 2003). Co. – Corumbá; S.L. – margem esquerda do Rio Salobra; S.R. – margem direita do Rio Salobra; I – intermediário; F.R. – Rio Formoso; Pr. – Rio da Prata; P. – Rio Perdido.

TAXA	**CAVES**																				
	Co.	**S.L.**			**S.R.**			**I.**			**F.**					**Pr.**			**P.**	
	Forte Junqueira	José Cesário	Gaúcho	Patrimônio	Três Morrinhos	Estreito da Serra	Indúst. C. Corrêa	Pitangueiras	Mimoso	Ametista	N. Sra Aparecida	São Miguel	Jaraguá	Guaviral	Lago Azul	Buraco das Abelhas	Vale do Prata I	Santa Maria	Curvelo	Harmonia
Diptera Psychodidae									X	X			X	X	X		X	X	X	
Psychodinae																				X
Brumptomyia avellari												X			X					
Brumptomyia brumpti		X	X		X							X			X					
Brumptomyia cunhai			X	X				X				X			X					
Brumptomyia galindoi												X								
Brumptomyia sp.											X				X					
Evandromyia corumbaensis		X	X	X	X	X	X	X			X	X			X					
Lutzomyia almerioi		X	X	X	X	X	X	X			X	X			X					
Lutzomyia longipalpis		X		X	X	X	X	X			X	X			X					
Pintomyia kuscheli		X																		
Sciopemyia sordellii		X	X	X	X	X	X	X			X	X			X					
Sciopemyia sp.								X												
Martinsmyia oliveirai		X		X	X	X	X	X				X			X					
Nyssomyia whitmani		X	X	X	X	X	X	X			X	X			X	X				
Psathyromyia campograndensis															X					
Psathyromyia punctigeniculata		X			X		X					X			X					
Psathyromyia shannoni		X					X					X			X					
Micropygomyia acanthopharynx								X												
Micropygomyia peresi					X	X	X	X			X				X					
Micropygomyia quinquefer	X			X	X	X		X				X			X					

Table 9. Bats recorded in caves of the Serra da Bodoquena karst area, Mato Grosso do Sul state. S.L. – Salobra River left margin; S.R. – Salobra River right margin; I. – Intermediate; F. – Formoso River. / Tabela 9. Morcegos registrados em cavernas da área cárstica da Serra da Bodoquena, estado do Mato Grosso do Sul. S.L. – Rio Salobra margem esquerda; S.R. – Rio Salobra margem direita; I. – intermediário; F. – Rio Formoso.

TAXA	CAVES										
	S.L.			S.R.	I.			F.			
	Sr. Natal	Córrego Azul I	Córrego Azul III	Fadas	Pitangueiras	Mimoso	João Arruda	N. Sra. Aparecida	São Miguel	Anhumas	Morro do Mateus
Mammalia Chiroptera											
Emballonuridae *Peropterix macrotis*									X		X
Phyllostomidae *Chrotopterus auritus*						X		X	X		X
Desmodus rotundus			X		X	X			X	X	X
Anoura geoffroyi						X					
Anoura caudifer	X										
Glossophaga soricina		X	X	X		X			X		
Carolia perspicillata	X		X	X					X		
Plathyrrinus lineatus		X	X								
Phyllostomus hastatus			X			X					
Natalidae *Natalus espiritosantensis*				X			X				X

The largest dry cave in Serra da Bodoquena, Dente de Cão, with more than 2 km of mapped passage ways, harbors a rich troglomorphic fauna, including a new onychophoran species and arthropods such as Ctenidae spiders and *Eusarcus* (Gonyleptidae) opilionids, which, together with troglophilic populations, compose a unique terrestrial cave community. In Toca da Trilha cave, troglobitic velvet-worms are in syntopy with non-troglomorphic peripatids belonging to another new species, which occur at the cave entrance and the twilight zone of several caves; in one occasion, individuals of both species were observed at the same deposit of organic detritus in the twilight zone of Toca da Trilha.

2 Phylogenetically and biogeographically relevant taxa: Spelaeogriphacea, Megagidiella*, Onychophora*

The onychophorans found in caves on the Serra da Bodoquena represent a considerable extension of the distribution area for the Phyllum, and the first record of a troglobitic species for South America. There are only two other described troglobitic species of velvet worms, *Peripatopsis alba* Lawrence 1931, from Wynberg Cave, in the Table Mountains, South Africa, and *Speleoperipatus spelaeus* Peck 1975, from Pedro Great Cave, in Jamaica. Nothing was published after the original descriptions and there is no news about this material. The non-troglomorphic *Epiperipatus* sp. 1 (Table 3) may be troglophile since it was observed both in epigean and in aphotic habitats. It is relevant that, so far, these are the only cases of subterranean (cavernicoles *sensu latu*, herein defined as evolutionary units responding to subterranean selective regimens - Trajano 2012) onychophorans recorded for Brazil.

The distribution of *Megagidiella azul* Koenemann & Holsinger, 1999 and *P. brasiliensis* was extended to the northern plateau, encompassing now all the Bodoquena karst. In general, these species are syntopic, together with the troglomorphic planarians and oligochaetes, suggesting a responding to the same vicariant events by these invertebrates. On the other hand, in general spelaeogriphaceans are absent from caves with *Trichomycterus* catfish, except for Saracura (in the left margin of the Salobra river) and Abelhas (in the Prata River) caves, were the two co-occur. These patterns deserve further studies and we hypothesize that the predator effect on prey may maintain very low densities of *P. brasiliensis* when *Trichomycterus* are present.

The *Megagidiella* species from Ricardo Franco Cave has to be confirmed. On the other hand, the spelaeogriphaceans from this cave, and also from Curupira, in Mato Grosso, more than 700 km far from the type-locality (Lago Azul Cave) are morphological indistinguishable, all included in the nominal species *Potiicoara brasiliensis* (Pires-Vanin 2012). A deep phreatic connection, not demonstrated till now, could explain this exceptionally wide distribution (Pires-Vanin 2012). Other explanation is a former superficial connection, interrupted by the subsidence of the Pantanal basin, associated with a long period of evolutionary stasis, not unexpected for animals living in an exceptionally stable environment. A third hypothesis is dispersion via the hyporheic zone along the Paraguay riverbed.

3 Ecological notes

A marked characteristic of the Cerrado domain is an accentuated variation in the relative humidity of air between the rainy and dry seasons. Values as extreme as 4% of relative humidity in the dry winter to 80-90 % in the rainy summer were recorded outside the entrances of the caves studied by Cordeiro (2008). Several invertebrates concentrate at the entrance and twilight zones during the winter, as is the case with noctuid moths, neuropterans and epigean onychophorans. An increase in faunal richness and abundance was observed in the intensively studied Córrego Azul I and Córrego III caves

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during the dry season, when a migration towards the twilight zone, up to 20 m far from the entrance, was recorded (Cordeiro 2008). This illustrates the importance of caves as refuges for the epigean fauna during the stressful dry and cold seasons.

Exceptionally high population densities for guanophile invertebrates have been recorded at guano deposits, such as *Megagidiella* amphipods reaching densities of hundreds to thousands individuals per m^2 on submerged guano of hematophagous bats in Ricardo Franco Cave (Moracchioli 2002). Oniscodesmid diplopods were also observed in high densities on vampire bat guano in dry caves of the south plateau. However, it is important noting that the large populations of vampire bats in these areas are a response to the increased availability of prey represented by domestic animals, especially cattle, and do not correspond to the original condition. In undisturbed areas, such as Amazonian forests, the population densities of hematophagous bats are low. Consequently, even in caves with huge amounts of insectivorous bat guano, such as those in the Altamira-Itaituba sandstone area, hematophagous guano deposits are small and sparse (Trajano & Moreira 1990). In natural conditions, population booms of guanophilous invertebrates associated to vampire bats would be a rare occurrence, associated to maternity colonies.

Potiicoara brasiliensis also forms very large populations and, in view of its extremely wide distribution, these crustaceans may be among the most abundant aquatic troglobites in the world (copepods excluded), if this is indeed a single species. Although not reaching the exceptional densities shown by *Megagidiella* sp. in Ricardo Franco cave, *P. brasiliensis* may be quite abundant in caves such as Lago Azul – maximum densities of ca. 30 individuals per 400 cm^2 were recorded by Moracchioli (2002), and similar densities were observed by R.B. and L.M.C. in Cinco de Ouros and Buraco do Bicho caves. It is noteworthy that, although much more common in the typically lentic environment of submerged caves, *P. brasiliensis* has also been found in the base-level stream of Fadas cave, on the bottom of a reach with moderate water current, as also observed in the Buraco das Abelhas.

4 Conservation: Main threats to the subterranean biodiversity in the Mato Grosso do Sul karst areas

Subterranean ecosystems pose special problems for conservation due to their intrinsic fragility and the distinctive features of subterranean communities, including a high degree of endemism and morphological, ecological and behavioral specializations of troglobites (Bichuette & Trajano 2010). Subterranean ecosystems in Mato Grosso do Sul, especially in the Serra da Bodoquena karst area, highly relevant in view of its biodiversity, distinguishing as a high diversity spot for troglobites, both vertebrates and invertebrates, are seriously endangered by the inappropriate use of karst landscapes.

Habitat destruction is the main threat to natural environments throughout the globe, and subterranean habitats are not exception. Irreversible habitat loss due to quarrying for cement production is the cause for subterranean biodiversity decline in karst areas, along with building of dams and reservoirs for hydro-electric power plants and water storage for human use (Bichuette & Trajano 2010). In the Serra da Bodoquena karst area, several mining companies are prospecting or requiring licenses for mineral prospection throughout the region, mainly for carbonates and ore (BRASIL 2013). Limestone have been extensively exploited in the Serra da Bodoquena since the 1980′s, including the vicinity of the Parque Nacional da Serra da Bodoquena, without any public environmental studies (it is relevant that caves became fully protected in 1990, by Federal Decree 99.556, which made such studies mandatory for any area with speleological potential; its substitutive, Decree 6640/2008, kept such requirement). In the absence of previous studies, and because the areas where mining is in progress is interdict for speleologists, no information is available for such caves, therefore it is unknown how much diversity has been so far lost due to such activities in Bodoquena and Bonito County. In these cases, the lack of control and law enforcement by the authorities is an important factor responsible for subterranean diversity degradation. A similar situation concerning mining is observed in the Corumbá karst area, but the lack of knowledge (see below) does not allow for evaluation of the real or potential threats for subterranean ecosystems.

Land use in Serra da Bodoquena and Bonito area has intensified since the early 1980′s as relatively small rural settlements and, a decade later, as larger farms in the higher terrains for semi-intensive livestock farming; in the last decade, soybean monoculture has been replacing cattle in the lower terrains, around Bonito Co., with even more catastrophic consequences.

Karst areas are characterized by efficient flow of groundwater through conduit systems originated by the properties of soluble rocks. Therefore, the water usually drains rapidly into the subsurface at recharge zones, through a network of fractures and cave conduits. This groundwater emerges at the surface in discharge zones through springs and wells (Sallum-Filho & Karmann 2012). Removal of the surface vegetation is another global environmental threat, even more in the fragile karst landscapes, due to the predominance of groundwater drainages. This causes decrease in the nutrient input, negatively affecting the subterranean, and changes in hydrological regimes (Bichuette & Trajano 2010).

Intensification of sedimentation, caused by human interference, mainly deforestation and livestock, were recorded during our fieldwork in caves of high hydrological and/or biological relevance, mainly in the Rio Salobra headwaters, where three undescribed troglobitic catfish occur. In Fadas Cave, Campina settlement, where the cave catfish *Rhamdia* and *Ancistrus* populations, endemic to this cave system, have been monitored since 2006, a large deposit of sediment (1.5 m height) was formed after the deforestation of one important sinkhole area located about 300 m upstream this cave. In Califórnia and Beija-Flor caves (systems where *Trichomycterus* cf. *dali* occurs), located in a farm where livestock is expanding, the formation of erosional craters was identified at many upstream points. These caves are major sinkholes and their streams are in advanced stages of sedimentation (Cordeiro et al. 2012)

Pumping of subterranean waters for human and livestock use, another cause for disturbance of subterranean ecosystems due to lowering of water table (Proudlove 2011, Bichuette & Trajano 2010), is common in the Bodoquena and Bonito region as artesian and non-artesian wells; so far, no visible impact has been detected, but this potential threat must be monitored. Introduced species, recognized as a major danger for natural environments around the world, may also become a problem in some areas in the Bodoquena region, where water reservoirs (“açudes”) for cattle use have been build upstream subterranean systems. During rains, fish introduced in these “açudes” enter

caves, such as traíras (Erythrinid characiforms) and cichlids, which are predators of cavefish and other troglobitic organisms.

Alien species are harmful for aquatic indigenous and endemic fauna in fresh waters and can have a deep and pervasive effect on ecosystems that they invade (Strayer 2010). The record of *Melanoides tuberculatus* in Mimoso Cave, where phreatic troglobites as *P. brasiliensis*, *M. azul* and *Girardia* sp. also occur, is the first record of an invasive species in Brazilian groundwaters. *M. tuberculatus* is originally from African continent and have been responsible for total substitution of benthonic communities in surface fresh waters in North and South America (Fernandez et al. 2003, Thiengo et al. 1998). The occurrence of this alien gastropod in Mimoso Cave is recorded ten years after studies on speleogriphaceans made by Morachiolli (2002) in the same site, proving that it is a very recent invasion in this environment. The monitoring and research on population control of *M. turberculatus* is quite urgent for conservation of the endemic phreatic fauna and to understand its potential to damage the groundwater ecosystem.

Pollution of subterranean drainages, another important threat for subterranean ecosystems throughout the world (Proudlove 2001, Bichuette & Trajano 2010), is also concern in the Serra da Bodoquena region. Use of dolines for garbage dumping has been observed in several settlements, such as the Campina. Pollution by detergents, largely used in settlements, may have a deleterious impact on subterranean fish due to interference on their natural behavior (Trajano 1997). Nitrogen derivates, bacteria such as fecal coliforms and chemical residues of drugs used in livestock accumulate in the subsurface. Due to the hydrological characteristics of the karst, pollutants spread fast and widely in groundwaters. In the Bonito County surroundings, the substitution of livestock by soybean monocultures have a great potential to deteriorate even more the quality of underground waters due to the use of large amounts of pesticides, which may contaminate springs and wells, calling for attention and serious actions by the authorities.

Tourism is a major economic activity in the region, especially in Bonito, where caves receive thousands of tourists every year. Therefore, the demand for caves with potential tourist use is increasing and visitation to caves not open to tourism is a recurrent problem. Negative consequences of visitation are: topoclimatic changes, introduction of alien species, including pathogens, and materials (such as metal, cement and treated wood), pollution by items left in caves, soil compacting and trampling of cavernicoles, destruction of specific microhabitats and direct disturbance of fauna (lights, loud noises, handling of specimens) (Trajano 2000). Dente de Cão and Urubu Rei are examples of diversified ecosystems endangered by uncontrolled human visitation.

For a discussion on environmental problems affecting subterranean habitats in Mato Grosso do Sul, see also Cordeiro et al. (2013).

In conclusion, Serra da Bodoquena, the largest and by far the best known karst area in Mato Grosso do Sul, is undoubtedly a priority area for conservation in Brazil, requiring urgent actions for effective protection of its subterranean ecosystems, many of which are endangered. The Park area must be increased, and its limits expanded in order to encompass the headwaters and recharge areas of the main subterranean systems, and, in the occupied areas, other categories of conservation units should be created to guarantee a sustainable use of the land. More attention should be paid to the settlements by the authorities, providing education, health and sanitary conditions adequate to the karst terrain. In addition to environment studies to fulfill the legal requirements in areas of economic interest, and a serious effort by the authorities to enforce such regulations and properly control cave visitation, a responsible attitude by the media is fundamental, in order to broadcast correct information, not distorted by sensationalism, always with the objective of preserving the subterranean biodiversity of Mato Grosso do Sul.

Final considerations

1 Perspectives for speleobiology in Mato Grosso do Sul

The major bottleneck for the progress of the speleobiology in Mato Grosso do Sul, as generally in Brazil, is taxonomic impediment. Therefore, the investment on the formation of taxonomists is of paramount importance.

The faunistic data reunited here allows for a first approach on the taxonomic diversity at the alfa (local) level, in a spatial scale. As a next step to describe the structure and functioning of subterranean ecosystems in the Bodoquena area, long term studies in selected caves are needed in order to detect temporal patterns. In addition, additional collections are needed for taxonomic studies of many taxa. As well, the addition of new caves, especially in the least known southern plateau, will allow to verify the relationship between local and regional species richness.

However, considering only the observed local diversity is not enough because taking into account only the number of species and their relative contribution have little predictive power about the functioning of the communities. A very promising research field is to compare functional and phylogenetic diversity of different types of caves in relation to epigean habitats geographically continuous. Widely distributed nominal species (e.g., *Potiicoara brasiliensis*) or species groups (*Megagidiella*, *Trichomycterus*) are excellent models for phylogeographic analyses associated to detailed morphological studies.

Genera with both troglobitic and troglophilic populations, such as ctenid spiders, *Eusarcus* opilionids and onychophorans, offer good opportunities for comparative studies focusing on genetics, biology, physiology and behavior. On the other hand, the relictual character of several troglobites, specially the aquatic ones, without living epigean relatives in the area, poses difficulties for such studies.

Other cave areas in Mato Grosso do Sul are barely known. Speleobiological studies are lacking in the Corumbá area and the Serra do Amolar, northwestern MS, both with exposed limestones and iron rocks in the vicinity, and in the sandstones of Serra de Maracajú.

2 Main collections:

After study, the material collected in subterranean habitats is send to official collections of institutions registered at the CNPQ – Conselho Nacional de Pesquisa and CGEN – Conselho de Gestão do Patrimônio Genético, mainly the Museu de Zoologia da Universidade de São Paulo – MZUSP, the Museu Biológico do Instituto Butantã, the Museu Nacional do Rio de Janeiro – MNRJ and Coleção do Zoológica da Universidade Federal do Mato Grosso do Sul - ZUFMS.

During studies, the specimens are kept in the institutions of the respective specialists; small reference collections are in the authors' institution for comparison and training.

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