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Diversity of Brazilian subterranean invertebrates, with a list of troglomorphic taxa

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ABSTRACT

The taxonomic diversity of invertebrates found in Brazilian caves and other subterranean habitats is presented, with a brief history of scientific investigations in the country and data on their distribution and biology. Similarities and differences in relation to other tropical and temperate regions are pointed to. An updated list of subterranean troglomorphic taxa is also presented.

Key words: subterranean biodiversity, invertebrates, Brazil, troglomorphic taxa, distribution.

INTRODUCTION

From the description of the first known Brazilian troglobite, the blind catfish, *Pimelodella kronei* Ribeiro, 1907, from the Upper Ribeira karst area, southern Brazil, to the early 1980´s, when organised speleobiology actually started in the country, only scattered data on a few taxa (e.g., harvestmen, diplopods, crickets) or short faunal lists from isolated caves (e.g., Areias and Tapagem caves, briefly visited by P. Strinati on the late 1960´s) were available. Before 1907, one can find some comments on vertebrates observed in association with caves (bats, owls, tracks of mammals such as jaguars and pacas) in the writings of the 19th century naturalists in South America. The most detailed information was provided by P. Lund, the renowned Danish paleontologist and speleologist who spent several years carrying out paleontological excavations in caves of the Lagoa Santa region, State of Minas Gerais. Lund stressed the occurrence of predators such as the barn owl, *Tyto alba*, and extinct carnivores (canids, bears, sabre-toothed “tigers”) regularly inhabiting caves, which were responsible for the introduction of large amounts of bones, that now represent important paleontological sites. By the end of the 19th century, the German topographer, R. Krone, explored several caves in the Upper Ribeira Valley, southern São Paulo State, and found the blind catfish in one of them. Like P. Lund, he had a special interest on paleontology and paid little or no attention to the cave invertebrates (Trajano 1993).

In 1980, the first comprehensive faunistic list encompassing 28 caves from five karst areas was published (Dessen et al 1980) as the result of activities of a few amateur speleological associations. Although identifications were mostly at high taxonomic levels (families or higher), a first glimpse on the Brazilian cave fauna diversity was provided. From that time on, with postgraduate and graduate studies marking the insertion of Speleobiology into the academic world and after systematic efforts to survey the fauna of a representative number of caves throughout the country, a rapidly increasing body of knowledge about Brazilian subterranean fauna was built.

The first thesis on Brazilian cave organisms was by C. Pavan (Pavan 1945; 1946) on *Pimelodella kronei*. However, this renowned geneticist did not proceed with speleobiological investigations, and his PhD thesis is an isolated event in Brazilian speleobiology. Academic work was resumed decades afterwards, with E.Trajano´s M. Sc. dissertation on cave bats (Trajano 1985; 1996) and Ph.D. thesis on *P. kronei*, complementing Pavan´s studies with ecological and behavioural data. Further postgraduate works focusing basically on cave animals include studies on crustaceans, such as anomuran decapods, genus *Aegla* (N.Moracchioli´s M.Sc. thesis, concluded in 1994), peracarid spelaeogriphaceans (N.Moracchioli´s Ph.D. thesis, 2002) and Oniscidean isopods (L.A. Souza-Kury´s Ph.D. thesis, 1997), insects such as beetles (N.M. Godoy´s M.Sc. thesis, 1990; P.Gnaspini Netto´s M.Sc. thesis, 1991; R. Bessi-Pascoaloto´s Ph.D. thesis, 2005), crickets (F. Pellegatti-Franco´s M.Sc. thesis, 1998) and heteropterans (C.F. Lecher´s M.Sc. thesis, 2002), arachnids such as harvestmen (P. Gnaspini-Netto´s Ph.D. thesis, 1993; F.H. Santos´s M.Sc. thesis, 1998), spiders (F. Pellegatti-Franco´s Ph.D. thesis, 2004) and pseudoscorpions (R. Andrade´s M.Sc. and Ph.D. theses, respectively 1999 and 2004), and hydrobiid gastropods (M.E. Bichuette´s M.Sc. thesis, 1998), besides cave fishes (*P. kronei* and others) and bats. More recently, several theses with focus on cave ecology have been concluded (e.g., R.L. Ferreira´s Ph.D. thesis, 2004; L.M. Cordeiro´s M.Sc. thesis, 2008).

In parallel, a series of general and regional faunistic lists has been produced, at first focusing mainly on the Alto Ribeira Valley, southern Brazil, and progressively encompassing a larger number of Brazilian karst areas (e.g., Trajano 1987; Trajano and Gnaspini-Netto 1991; Gnaspini and Trajano 1994; Pinto-da-Rocha 1993; Trajano 2000). Faunistic surveys specific to sandstone karst areas are those by Trajano and Moreira (1991) and Zeppelini-Filho et al (2003). A first synthesis on the Brazilian cave fauna was organized by Pinto-da-Rocha (1995).

In spite of a significant development of Brazilian speleobiology in the last two decades, there is still heterogeneity in the degree of knowledge about different Brazilian karst areas and taxa. Some karst areas have been intensively surveyed and may be considered well known, as it is the case with the Alto Ribeira, in São Paulo and Paraná States, and several karst areas in the States of Minas Gerais (e.g. Peruaçu/Itacarambi, Cordisburgo), Bahia (e.g., Serra do Ramalho, Chapada Diamantina), Mato Grosso do Sul (Serra da Bodoquena and Bonito region) and Goiás (specially São Domingos). For other areas, speleobiological knowledge is still preliminary, gathered during few field trips not covering different seasons and years, but allowing a first view about faunistic patterns (e.g., Rio Pardo, in Bahia; Serra do Araripe, in Ceará; Altamira-Itaituba, in Pará). Others were still the object of very sparse studies or none at all, remaining mostly unknown (e.g., Alto Paraguai, in Mato Grosso; Ubajara, in Ceará). It is noteworthy that, even in the best known Brazilian karst areas, novelties arise every year.

In view of the guano diversity due to the diversity of feeding habits in Neotropical bats, which provides a good opportunity for comparative studies, it is not surprising that several recent studies focused on invertebrate communities associated with this substrate (e.g., Gnaspini-Netto 1989; Ferreira and Martins 1998; Ferreira et al 2000; for a synthesis, see Gnaspini and Trajano 2000).

The greatest present-day difficulty for the progress of Brazilian speleobiology is taxonomic impediment affecting a significant number of taxa. Representatives of several important cave taxa such as mites, collembolans and nematoceran flies, remain identified, mostly, at high taxonomic levels (family or higher). Even among those groups for which there are specialists, the large number of both epigean and hypogean taxa still to be studied, as expected in view of the megadiversity characteristic of many tropical countries as Brazil, is beyond their working capacity, and the description of new species progresses slowly. With the increasing undervaluation of the importance of traditional taxonomy as the most practical, feasible and faster way to access biodiversity, especially in countries with megadiversity and limited resources for scientific research, incompatible with the large application of expensive and slow approaches as the molecular ones, this impediment tends to worsen.

Herein we present data on distribution, habitat, biology and ecology of representative Brazilian subterranean invertebrates, complementing and updating the review by Trajano and Sánchez (1994). We considered all information on truly subterranean invertebrates (i.e., accidentals were excluded) we could assess; grey literature, including unpublished theses and monographs and congress abstracts, is referred as personal communications. Troglomorphic invertebrates so far reported are listed (Table 1), with the main objective of revealing taxonomic patterns concerning the groups with the highest diversity of known putative troglobites. This cannot be considered an exhaustive list, because there is information in non-accessible data bases, such as unpublished reports. For a list of Brazilian subterranean fishes, see Mattox et al (2008) and Trajano & Bichuette (in press 2010).

SUBTERRANEAN INVERTEBRATES

1. Crustacea:

Relatively well-known Brazilian subterranean crustaceans include the peracarids, Amphipoda, Isopoda (especially the terrestrian Oniscidea) and Spelaeogriphacea, and anomuran decapods of the genus *Aegla*.

Two highly troglomorphic bogidiellid (Amphipoda) genera have been reported for phreatic water bodies inside Brazilian caves: *Megagidiella*, with *M. azul* from flooded caves in Bodoquena karst area (Koenemann and Holsinger 1999) and possibly a second, undescribed species (J. Holsinger, pers. comm.) from the Forte Coimbra area, in the opposite margin of the Paraguay River; and *Spelaeogammarus*, widespread in caves from Bahia, with four described species (Koenemann and Holsinger 2000). In addition, *Hyalella* amphipods were found in cave streams of the Alto Ribeira, including a troglomorphic species.

In the mid 1980's, the second known living species of Spelaeogriphacea was discovered in Lago Azul Cave, Serra da Bodoquena karst area, and described as *Potiicoara brasiliensis*. More recently, spelaegriphaceans were found in Australian groundwaters, configurating a typical Gondwanan distribution for the living spelaeogriphaceans. *P. brasiliensis* was studied in detail by Moracchioli (pers. comm. 2002) with focus on distribution, population ecology, biology, morphology and behaviour. These crustaceans have been found in several cave localities within a large area (50 km of radius around Bonito town) in the Bodoquena region, and occur mostly in lentic underwater habitats, from near the surface until deep waters (up to 120 m). Average population densities of 0.36 ind. m^{-2} near the water surface and 28.4 ind. m^{-2} on the bottom were recorded for Lago Azul Cave (Moracchioli pers. comm.), and total populations with hundreds of thousands individuals have been estimated for the area, representing the most abundant and easily accessible populations known for the Order. Moreover, *P. cf. brasiliensis* was found in Ricardo Franco Cave, at Forte Coimbra area. In this cave, the spelaeogriphaceans presented even higher population densities, with 12.5 ind. m^{-2} near the surface and 62.5 ind. m^{-2} on the bottom, where large amounts of submerged vampire bat guano were observed.

It is noteworthy that *P. brasiliensis* is syntopic with *Megagidiella* amphipods in all localities where the latter was recorded, including Ricardo Franco Cave. This provides evidence for the same or parallel vicariant events acting over the two taxa. However, unlike spelaeogriphaceans, these amphipods occur basically near the bottom, showing lower average densities (2.4 ind. m^{-2} in Lago Azul, and 32.5 ind. m^{-2} in Ricardo Franco – Moracchioli pers. comm.) expected in view of their larger size.

The first known Brazilian subterranean aquatic isopods are calabozoids recently found in a cave in the semiarid Campo Formoso karst area, NE Brazil (*Pongicarcinia xiphidiourus*, from Toca do Gonçalo – Messana et al 2002) and in Nobres area, Central Brazil (undetermined species – Moracchioli pers. comm.). These findings greatly increased the distribution of the Calabozoidea, now including three different, largely separated river basins: the Orinoco basin, in Venezuela, encompassing the type-locality of the first described and until recently the only known calabozoid; and the São Francisco and Paraguay basins, in Brazil. In the case of these tiny aquatic organisms, dispersion through hyporheic habitats, in the Amazon basin for instance, is a possibility to be explored. The same applies to *Potiicoara brasiliensis*, for which collections in non-cave habitats may also be hampered by its small size.

On the other hand, terrestrial isopods (Oniscidea) are quite common in Brazilian caves, occurring mainly in humid deposits of sediment, vegetal debris and guano. Several families have been recorded throughout the country (Souza-Kury 1997), most of them including troglomorphic species. Some families are widespread in different karst areas (e.g., Platyarthridae and Styloniscidae, both found in caves from Bahia, Minas Gerais and the Ribeira Valley), others seem to be more frequent and diverse in certain areas (e.g., Phylosciidae, typical of the Ribeira Valley; Armadillidae, more abundant in Bodoquena and Rio Pardo areas; Scleropactidae, in Pará).

Aegla crustaceans are freshwater anomuran decapods that show a typical meridional distribution, occurring in temperate and subtropical headwater streams of southern South America. Accordingly, these omnivorous, night-active crustaceans, highly preadapted to the cave life, are not found to the north of the Ribeira Valley, where they are quite common in both epigean and hypogean streams. Three troglobitic species and several probably troglophilic populations were recorded in these caves. The three troglobitic species are characterised by different degrees of regression of eyes and dark pigmentation, which is complete only in *A. microphthalma*, the most specialized troglobitic *Aegla*. A few other cave populations also present partial depigmentation, but these are probably cases of environmental depigmentation caused by lack of carotenoids in the diet since they became dark in the laboratory, when carotenoids were provided with food.

When compared to troglophilic and epigean relatives, the troglobitic species of *Aegla* may present elongation of antennae and legs (possibly associated with chemo- and mechanosensorial development), smaller chelae (probably in association with the observed reduction of agonistic behaviour) and more delicate bodies, and also a reduction of cleaning behaviour of antenulae (possibly as a consequence of decreased quantity of epibionts in the cave habitat), but a intensification of cleaning behaviour of the antennae and legs, which could maximise the detection of chemical stimuli by the maxillipeds used for cleaning (Moracchioli pers. comm. 1994). Troglophilic populations showed maximum densities reaching 10-20 ind. m^{-2}; in the early 1990's population densities of *A. leptochela* (Paiva Cave) and *A. cavernicola* (Areias de Baixo Cave) were lower, around 2 ind. m^{-2}, but still not so low for troglobites. In the late 2000´s, the population density of both *A. leptochela* and *A. cavernicola* have greatly decreased (Maia and Guil, pers. comm.). Likewise, *A. microphthalma*, relatively frequent in its only locality, Santana Cave, till the 1970´s, is nowadays extremely rare.

There are very few records of copepods and ostracods from Brazilian caves – e.g., *Elaphoidella bidens subterranea* n. subsp. (Harpaticoidea), from a cave in Paraná State (Nogueira 1959); some Cyclopoida (*Paracyclops*, *Tropocyclops*, *Eucyclops*, *Microcyclops*) and Harpacticoidea (*Elaphoidella*) from two caves in the Brasília karst area, Goiás (Reid and José 1987). This certainly represents a tiny portion of their actual diversity in Brazilian karst waters.

2. Myriapoda:

Diplopods are widespread in Brazilian caves, most belonging to the Polydesmida (several families), that encompasses all known Brazilian troglobites, and Pseudonannolenida, with a single genus in caves, *Pseudonannolene*, forming troglophilic populations in different karst areas. Pseudonannolenids show a preference towards animal organic matter and may be very numerous at guano deposits, especially from hematophagous bats. In sediment banks, their population densities are usually lower than those of geophagous chelodesmids (Polydesmida) such as *Leodesmus yporangae*, which presents average densities of 0.1-0.2 ind. m^{-2} in sediment banks inside caves of the Areias system, Alto Ribeira (Thompson and Moracchioli 1996), where they may reach maximum densities of 10 ind. m^{-2}. The troglobitic *Peridontodesmella alba*, from the Ribeira Valley, and *Crypturodesmus* undesc. sp., from the Bodoquena karst area may also attain high population densities at hematophagous bat guano (e.g, 500+ ind. m^2 observed for *Crypturodesmus* sp.). Like opilionids, diplopods are less frequent in warm caves situated in semiarid regions in northeastern Brazil. For a synthesis on Brazilian cave diplopods, see Trajano et al (2000).

Among the large predaceous centipeds, scutigeromorphans, representatives of the genus *Pselliodes* being the most frequent, have been recorded in São Domingos, Chapada Diamantina, São Desidério and Rio Pardo karst areas, and scolopendromorphans were found in Altamira-Itaituba (Cryptopidae – several specimens observed, possibly forming troglophilic populations) and also in the Ribeira Valley (rare). The first Brazilian troglomorphic scolopendromorphan, genus *Cryptops* (Cryptopidae), was recently discovered in iron caves from Carajás area, Pará State. Is notewhorhty that this is the fourth troglobitic species of genus in the world (the other three are from Australia and Cuba) (Amazonas Chagas, com. pess.), pointing to a high potential of iron caves as habitat of troglobitc invertebrates in Brazil, as already shown for Australia.

The typically soil-dwelling lithobiomorphans are uncommon in Brazilian caves, but species living on guano of frugivorous bats in the Alto Ribeira may be observed in relatively large numbers, possibly preying upon cydnid and lygaeid bugs, also typical of this type of guano (Gnaspini and Trajano 2000). Troglomorphic lithobiomorphans were reported for iron caves in Minas Gerais State (R.L.Ferreira, pers. comm.). Geophilomorphans, usually showing troglomorphic traits, have been found in sediment banks, mostly in caves of the Alto Ribeira, but their status as strict troglobites is disputable because all geophilids are eyeless and many epigean litter- and soil-dwelling species are also depigmented (J.-J. Geoffroy, pers. comm.).

There are records of symphylans in Brazilian caves (e.g., Scutigerellidae, from a cave in Rio Pardo karst area; undetermined family, from caves in the Alto Ribeira Valley) most unpublished. Those are typical soil-dwelling myriapods, and troglomorphic traits are of poor use to establish their possible troglobitic status.

3. Insecta:

Omnivorous troglophilic crickets of the genus *Endecous* (Phalangopsidae) are one of the most conspicuous and widespread cave insects throughout Brazil. In some parts of the Ribeira Valey, however, *Strinatia* crickets may establish troglophilic populations in the absence of *Endecous*; otherwise, the latter are restricted to the cave entrances. The same is true for *Eidmanacris* in Rio Pardo, where these crickets form troglophilic populations in euritrophic, bat caves (Trajano 2000), and also in São Desidério karst area. The biology of *Strinatia brevipennis* was investigated in laboratory by F. Pellegatti Franco (Gnaspini and Pellegatti-Franco 2002): when raised together with specimens of the epigean *Endecous itatibensis*, *S. brevipennis* crickets declined in number, while the number of epigean crickets boomed. This suggests that the mutual exclusion of *S. brevipennis* and *Endecous* spp. in caves is due to competition, the latter presenting higher reproductive efficiency – only in the absence of *Endecous* crickets, observed at higher altitudes in the Alto Ribeira, *S. brevipennis* would be able to successfully colonize subterranean habitats. Visual censuses along transects were done for *Endecous* sp. in sandstone bat caves from Altamira-Itaituba, Pará, where these crickets may attain one of the highest average population densities (from 0.17 to 5.15 ind. m^{-2}, Trajano and Moreira 1991) observed for Brazil.

Cockroaches (different families), rare in the subtropical Alto Ribeira, become more frequent in progressively warmer caves to the north of that area, especially in the Amazonia. In typical bat caves of the Altamira-Itaituba sandstone area they may attain very high population densities (up to 100 ind. m^{-2} in passages of Planaltina Cave with high concentrations of ammonia and other gases from insectivorous bat guano, Trajano and Moreira 1991). The first troglobitic species from South America, the blattellid *Litoblatta camargoi*, was recently described (Gutiérrez 2005) from caves in the semiarid Central Bahia and is widely distributed in the area.

Several families of heteropterans were reported for Brazilian caves. Predaceous reduviids, *Zelurus travassosi*, are relatively frequent in the Alto Ribeira, where they prey on harvestmen such as the trogloxenic *Goniosoma spelaeum* (see below), crickets etc. Other species of *Zelurus*, and also undetermined reduviids, were reported for other karst areas throughout the country (Pinto-da-Rocha 1995; E.Trajano and coll., unpubl. data). Other heteropterans recorded in Brazilian caves include veliids (*Velia* and *Rhagovelia*), which are typical components of the neuston (fauna living at the water sufarce), the aquatic naucorids and belostomatids (relatively rare), and the terrestrial cydnids and lygaeids, usually found in guano of frugivorous bats, frequently in association with lithobiomorph chilopods (Gnaspini and Trajano 2000). Enichocephalids have been found in some caves in the Alto Ribeira; potentially troglomorphic species were recently discovered in iron caves in Minas Gerais (R.L. Ferreira, pers. comm., R. Bessi, pers. comm. 2009). Emesine reduviids, usually found as isolated individuals, are typical components of the parietal fauna (animals living on rocky walls and ceilings near cave entrances).

As expected in view of their phytophagous habits, Fulguroidea (mostly cixiid) homopterans have been found near exposed roots in shallow caves, such as those in the Bodoquena karst and, less frequently, in the Alto Ribeira. Troglomophic cixiids and ortheziids have been reported for iron caves in Belo Horizonte region (R.L. Ferreira, pers. comm.).

Beetles are not particularly common in Brazilian caves. As observed abroad, predaceous carabids are among the most frequent and widespread cave beetles, but their diversity seems to decrease northwards. Several species have been recorded in the Ribeira Valley, including two troglobitic ones showing a low degree of troglomorphism. The only highly troglomorphic Brazilian beetles are carabids belonging to the exclusively subterranean genus, *Coarazuphium*, with several species recorded in Bahia, Minas Gerais and Goiás states (Table 1). These species show different degrees of troglomorphism, with a mosaic of character states. The most modified is *C. cessaima* (Bahia), that is completely eyeless (the others have very reduced, but still present eyes), with the most elongated legs, head, pronotum and elytra; *C. pains* (Minas Gerais) has the least reduced eyes among the four species, but is intermediate between *C. cessaima*, by one

Fig. 1 - Brazilian subterranean invertebrates. a. Depigmented Porifera from Chapada Diamantina (photo: Adriano Gambarini); b. Troglobitic gastropod, *Potamolithus troglobius* (Hydrobiidae), from Alto Ribeira karst area (photo: M.E. Bichuette); c. Troglobitic Onycophora from Serra da Bodoquena karst area (photo: L.M. Cordeiro); d. Troglobitic diplopod (Cryptodesmidae) from Alto Ribeira karst area; e. Troglomorphic isopod (Platyarthridae) from Alto Ribeira karst area; f. Troglobitic scorpion, *Troglorhopalurus translucidus*, from Chapada Diamantina (photo: R. L.C. Baptista); g. Troglophilic web-spider, *Plato* sp. (Theridiosomatidae), feeding on a chironomid fly, in the Alto Ribeira karst area; h. Troglobitic harvestman (Gonyleptidae: Pachylinae) from Alto Ribeira karst area. Photos d, f, g, h: F. Pellegatti-Franco.

hand, and *C. tessai* (Bahia) and *C. bezerra* (Goiás), by the other, as regards to the elongation of the body (Gnaspini et al 1998; Alvares and Ferreira 2002). A new species was recently found in iron caves near Belo Horizonte, Minas Gerais State (R.L. Ferreira, pers. comm.).

The detritivorous cholevids (*Dissochaetus* and *Adelopsis*), also relatively frequent, concentrate on animal dead matter as bat guano, other mammals feces and corpses; in contrast to the observed in temperate regions, no troglobitic cholevid has so far been found in Brazil. Other families reported for Brazilian caves include the minute predaceous pselaphids with several putative troglobitic species (Table 1); troglophilic detritivorous ptilodactylids, frequent at and near sediment banks where their larvae live, especially in the Ribeira Valley; the predaceous histerids, that may form large populations in guano piles, as observed in the guano of insectivorous bats in caves from Altamira-Itaituba, Pará State, and Serra da Canastra karst area, Minas Gerais State; detritivorous tenebrionids, also concentrating on guano; staphylinids, observed throughout the country, usually small populations; and the aquatic elmids and dryopids, found in cave streams in the Ribeira Valley, and also in Goiás (São Domingos) and Minas Gerais states.

Nematocera dipterans (especially chironomids), trichopterans (several families) and ephemeropterans (idem), whose juveniles are aquatic, may form flying clouds in stream passages. These clouds are particularly dense during seasons of emergence of adults, when these insects, attracted to the light of speleologists, become a real nuisance. Adult tineid moths, whose living larvae and their abandoned cases are frequently seen in caves, mainly on guano, may join those clouds. Tineids are the only troglophilic lepidopterans regularly observed in Brazilian caves. Other lepidopterans may be frequently found, as is the case with noctuid moths, but always near cave entrances, indicating a trogloxene status; these are typical components of the parietal fauna throughout Brazil.

Small flying insects represent food for web spiders such as *Plato*, pholcids and theridiids, and also for Mycetophilidae keroplatine dipterans. The predaceous larvae of keroplatines (e.g., *Neoditomyia*) may be seen in their webs made of silk threads hanging from the ceiling and walls, usually in humid environments and not far from cave entrances. This is the dipteran family including the glow-worm from New Zeland, *Arachnocampa luminosa*, but no such bioluminescence is present in the Brazilian species. Unlike *A. luminosa*, whose troglophilic status has been already demonstrated, it is not clear whether Brazilian cave keroplatins are troglophiles with very short-lived adults (which are rarely seen in caves) or trogloxenes whose adults leave the caves for some time.

Psychodids, including not only the harmless psychodines but also phlebotomines, leishmaniosis transmitters, have also been found in Brazilian caves; the latter may be quite numerous, especially near cave entrances, representing a potential public health hazard, especially in caves visited by tourists. Larvae of brachyceran flies are found in fresh guano, mostly of hematophagous bats, as is the case with *Drosophila* flies (more common in warmer caves to the north of the Ribeira Valley; e.g., *D. eleonorae*, only known from caves), phorids (*Conicera*, *Megaselia*, *Dohrniphora*, among others), milichiids (*Pholeomyia*), faniids (*Fannia*) and muscids (e.g., *Psilochaeta*) (Gnaspini and Trajano 2000).

Tunnels of termites (*Nasutitermes*) and trails of ants may be observed in shallow, warm caves. Although their status as cavernicoles has been questioned, at least in the case of ants as *Solenopsis* spp. (Myrmicinae), *Pachycondyla* and *Hypoponera* (Ponerinae), that are seen foraging at cave food sources such as owl pellets and other animal remains or prey, it is clear that these insects actively exploit subterranean resources in a more or less regular way and, thus, qualify as cavernicoles. This is in accordance with observations in caves in southeastern Asia, where ants are not rare (Roncin et al. pers. comm. 2001), and may be a characteristic of tropical caves in general.

Among less frequent Brazilian cave insects, one may cite psocopterans (especially Psyllipsocidae); plecopterans (Perlidae and Gripopterygidae); odonatans (dragon- and damselflies), whose nymphae are occasionally found in cave streams – their status as accidentals or trogloxenes has not been established; and non-Formicidae hymenopterans such as the small parasitoid wasps of the families Braconidae, Diapriidae and Scelionidae, and large hunting-wasps with their mud-nests typical of the parietal fauna

Finally, among wingless insects, collembolans are as expected very diversified and widespread in Brazilian caves. Several families have been recorded (e.g., Arrhopalitidae, Cyphoderidae, Entomobryidae, Isotomidae, Paronellidae, Hypogastruridae), including troglomorphic species as shown in Table 1. There are very few specialists dedicating to the taxonomy of neotropical springtails, much below the necessary to describe the epigean and hypogean megadiversity – in fact, this is one of the Brazilian subterranean groups most affected by taxonomic impediment.

The establishment of the troglobitic status for Brazilian collembolans is frequently hampered by the paucity of collections in epigean habitats in most karst areas and also by the possibility of occurrence of troglomorphims in epigean deep-soil living species. For instance, the eyeless and depigmented *Troglobius brasiliensis* (Paronellidae) was recorded in discontinuous, far apart karst areas (the sandstone Altamira-Itaituba area, in the Amazon region, and the limestone Ribeira Valley, in southern Brazil, Palacios-Vargas and Zeppelini 1995). This is probably a case of troglomorphic deep-soil living species widespread in the country, not restricted to hypogean habitats *sensu stricto*, thus not a real troglobite.

An interesting case is that of *Acherontides eleonorae*, a guanobite apparently restricted to hematophagous bat guano (Gnaspini and Trajano 2000), that may reach particularly high population densities on drying guano (hundreds of individuals per cm^{-2}).

Campodeid diplurans have been occasionally found, such as *Oncinocampa trajanoae* from caves in the Alto Ribeira, considered troglobitic, and *Lepidocampa juradii*, from caves in the Rio Pardo karst area, eastern Bahia State (Condé 1997). Troglomorphic japygids and Anajapygids have been reported for iron caves in Minas Gerais State (R.L. Ferreira, pers. comm.).

4. Arachnida:

Probably due to their conspicuousness and frequency in caves favouring their collection and study, arachnids are the best known terrestrial cave invertebrates in Brazil. Among 54 spider families known to occur in the Neotropical region, 33 were recorded until 2001 in Brazilian caves (Rheims and Pellegatti, pers. comm. 2001). The commonest are by far the troglophilic brown-spiders, genus *Loxosceles* (Sicariidae), sedentary spiders that build their irregular, sheet-like webs on sediment banks, between boulders and on corners, sometimes on walls, in which they capture walking arthropods and heavy insects, such as diplopods and beetles; the large wandering Ctenidae spiders (mostly *Isoctenus*), that capture fast, relatively large prey such as crickets; and the small Theridiosomatidae *Plato* spiders, usually found on their orb-webs hanging from rocky ceilings and walls near water bodies and whose rhombohedral egg-sacs may be found in large numbers in stream passages, and which prey on small flying insects such as chironomids and other dipterans, tineid moths and trichopterans. Less frequent, but still widespread in Brazilian caves, are the web-building pholcids (*Mesabolivar* and others), usually found near cave entrances and frequently observed carrying their egg-sacs, and theridiids such as *Nesticodes rufipes* (= *Theridion rufipes*), relatively frequent in tropical caves such as those in Mato Grosso, Bahia and Ceará states, and *Theridion bergi* in the subtropical Ribeira Valley, which may build webs attached to the water surface in slow-moving water bodies (pools in streams), preying on neuston (fauna living on the water surface, such as veliid bugs and some beetles) as well as animals falling by accident on the water (Xavier et al 1995). Semi-aquatic trechaleids (*Trechalea*), that may dive to hunt aquatic prey, are relatively frequent in the Ribeira Valley and São Domingos karst area.

The biology and population ecology of the two ctenid spiders regularly found in caves of the Alto Ribeira karst area, *Ctenus fasciatus* (actually *Isoctenus*, A. Brescovit, pers. comm.) and *Enoploctenus cyclothorax*, was studied in detail by F. Pellegatti-Franco (unpubl. thesis, 2004), who showed that the first species forms troglophilic populations in many caves whereas the latter is trogloxene, using cave entrances for reproduction (like *Goniosoma* harvestmen – see below) – specific biological and behavioral traits, such as eating or not the male after mating and leaving or not the offspring in order to feed during the period of maternal care, explain the different status for these two spiders. The life cycle of cave *Isoctenus* spiders is very long, 3-4 years to attain the maturity in the troglophilic species from the Alto Ribeira, another characteristic that may explain their troglophilic status, as a preadaptive trait. As also observed for cave crickets (F. Pellegatti Franco, pers. comm.), the population density of these ctenids in epigean habitats is extremely low. This is not a surprise, in view of the much higher biodiversity, and consequently higher interspecific competition, observed in tropical epigean regions.

In fully tropical, warmer caves, large mygalomorph theraphosids (e.g., *Lasiodora*) may be found, usually as isolated individuals (their status as trogloxenes or accidentals is difficult to establish), mostly in caves from northeastern and north Brazil. Diplurids have been found from Pará and Bahia (São Desidério region) states; a troglomorphic species was found in iron caves of Belo Horizonte area, Minas Gerais State. The smaller barychelid mygalomorphans may be troglophilic in caves from Altamira-Itaituba karst area, where they are relatively numerous.

Several troglobitic spiders have been reported for Brazil (Table 1), most tiny spiders belonging to forest litter taxa, such as ochyroceratids. On the other hand, the largest Brazilian troglobitic spider is a ctenid known from a single specimen collected in a quartzitic cave. It is worthynote that almost all these records are less than 10 years old.

The fully tropical arachnid Order, Amblypygi, is as expected represented in caves to the north of São Paulo State. Large amblypygids of the genus *Heterophrynus* (Phrynidae) may form troglophilic populations in western and northern Brazil (Pará, Goiás, Mato Grosso, Mato Grosso do Sul), and those of the genus *Trichodamon* (Damonidae) in eastern Brazil (Minas Gerais, Bahia, Ceará). The smaller charinids were recorded in Minas Gerais and Bahia, and include the only troglobitic amblypygids known for Brazil, all belonging to the genus *Charinus* (Table 1). In Brazil, this genus is typical of the Atlantic Forest, and the only species recorded outside its range have been found in caves (the troglomorphic species and a non-troglomorphic one, *C. mysticus* – Baptista & Giupponi 2002), probably as relicts of a formerly widespread forest. Like ctenid spiders, cave amblypygids capture fast, large arthropods such as crickets and cockroaches.

Opilionids are frequent in Brazilian caves, mainly in relatively humid areas, such as the Ribeira Valley, where they are particularly diverse. Most are gonyleptids, including trogloxene, troglophilic and troglobitic species. *Goniosoma spelaeum*, from the Ribeira Valley, was the first Brazilian cave invertebrate shown to be a trogloxene. This species has been exhaustively studied with focus on population ecology, feeding, reproduction and development, behaviour and locomotor activity (Gnaspini 1995, 1996; Gnaspini and Cavalheiro 1998; Santos and Gnaspini 2002; Gnaspini et al 2003); these studies indicated that *G. spelaeum* is an obligatory trogloxene, always reproducing in caves, at or near the entrances – their eggs, usually around 60-80, are attached to rocky substrates and guarded by the female. *G. spelaeum* are, together with *Mesabolivar* spiders and larvae of *Neoditomyia* nematocerans, typical components of the parietal fauna in the Alto Ribeira karst area. When *G. spelaeum* is absent, representatives of other *Goniosoma* species may also be frequent at cave entrances, including limestone, sandstone ands granitic caves in São Paulo State (e.g., *G. longipes*, *G. proximum*); *G.* aff. *badium* was reported for the Ribeira Valley at Paraná State; a new species of *Goniosoma* was recently found at cave entrances in Santa Catarina State (Pinto-da-Rocha 2001); two other species, probably also new, were recently observed living at the entrance of caves from Minas Gerais State. The reproductive biology of *G. longipes* was studied by Machado & Oliveira (1998). Cosmetids of the genus *Paecilaema*, frequently found near cave entrances in Goiás and Altamira-Itaituba, are probably also trogloxenes.

Troglophilic harvestmen would include the gonyleptids *Daguerreia inermes*, studied by Pinto-da-Rocha (1996) and *Pararezendesius luridus*, in the Ribeira Valley; gonyleptids of the genera *Eusarcus* (with two troglomorphic derivatives, respectively in São Domingos and Chapada Diamantina karst areas), in Goiás and Minas Gerais, *Parabalta* in Bodoquena and *Discocyrctus* in Chapada Diamantina karst areas; the stygnid *Verrucastygnus caliginosus*, from Altamira-Itaituba, Pará (Pinto-da-Rocha 2001). Rare opilionids have been found in caves from semiarid regions, as those in Bahia. Troglobitic species, most gonyleptids, have been found in different karst areas (Table 1); the recently created family Escadabiidae probably includes *Spealeoleptes*, originaly in Phalangodidae (Kury and Gonzalez, pers. comm. 2003). In contrast with the observed in temperate regions, Palpatores are very rare in Brazilian caves and restricted to the entrance zone.

Scorpions are rare, usually occurring as isolated individuals or in small numbers in warm caves in the Amazonian region (e.g., sandstone caves in Altamira-Itaituba, Pará, Trajano and Moreira 1991), in the semiarid northeastern Brazil, Bahia and Ceará states, and occasionally in the Bodoquena and Ribeira Valley karst areas, not far from entrances (Pinto-Da-Rocha 1995; Trajano, unpubl. data). The first Brazilian troglobitic species, *Troglorhopalurus translucidus*, was recently discovered in Chapada Diamantina (Baptista et al 2003).

Pseudoscorpions (several families) may be found at different substrates, concentrating in guano piles, including guano of hematophagous, insectivorous and frugivorous bats; the largest population densities (some tens of ind. m^{-2}) have been observed in the latter (Gnaspini and Trajano 2000). The most frequent and widespread are chernetids, apparently all troglophilic. The few troglobitic species are chtoniids or bochicids (Table 1). The biology of cave pseudoscorpions in the Ribeira Valley has been studied by R. de Andrade (Andrade and Gnaspini 2002, 2003). For a synthesis on Brazilian cave pseudoscorpions, see Mahnert (2001).

Palpigrads have recently been found in limestone caves from Alto Ribeira (R. Bessi Pascoaloto, pers. comm.), Arco-Pains (MG; M.E.Bichuette, pers. obs.) and other karst and iron areas in Minas Gerais State (Ferreira, pers. comm. 2004). Palpigrades are relatively common in caves of Pará and Minas Gerais states (L.M .Cordeiro, pers. comm. 2008). Since all palpigrads are blind and depigmented, these animals provide, together with campodeid diplurans, symphylans and geophilomorph chilopods, a good example of difficulty to determine the cave status of population belonging to a troglomorphic soil-dwelling taxon due to the lack of collections in endogeous habitats over the caves.

The diversity of mites in Brazilian caves is certainly greatly underestimated due to the poor collections and difficulties for identification (which discourage collections, in a vicious cycle). Few caves in the Ribeira Valley and in Minas Gerais were object of detailed studies allowing a preliminary view on this diversity. Most collections were made at guano deposits, where several families of Mesostigmata, Prostigmata, Astigmata and Cryptostigmata (Oribatida) have been recorded. In addition, Argasidae ticks such as *Ornithodoros* spp. and *Antricola* spp. (D.M. Barros-Battesti, pers. comm.), ectoparasites of bats, may be very common where bats concentrate. Such is the case of Brejinho Cave, in Chapada do Araripe (Ceará), where hundreds of thousands of ticks almost covered, in a moving mass, the cave floor formed by thick deposits of guano of the frugivorous bat, *Carollia* sp., in the deepest galleries (E. Trajano and M.E. Bichuette, pers. obs. 2004).

5. Onychophora:

Onychophorans are very rare in Brazilian caves, with one report of a specimen observed on the 1980´s in a cave of São Domingos karst area, apparently as an accidental occurrence. Recently, L.M.Cordeiro (unpublished M. Sc. Dissertation, 2008) reported the the occurrence of *Macroperipatus* sp. in some caves of the Bodoquena karst area, forming troglophilic or trogloxenic populations; a highly troglomorphic population belonging to a new genus and species was also found in one of these caves (Dente de Cão), representing the first troglobitic onychophoran for South America. Isolated specimens have also been found in Minas Gerais.

6. Non-arthropod invertebrates:

As observed in other countries, both tropical and temperate, hydrobiid snails are the most prevalent aquatic mollusks in Brazilian cave habitats and include several troglobitic species. These gastropods have been investigated in detail in the Ribeira Valley, where almost every microbasin harbours a distinct population, totaling seven troglophilic and five troglobitic species belonging to the genus *Potamolithus*. In addition, a new troglobitic species was found in the Bodoquena area. Epigean, troglophilic and troglobitic *Potamolithus* gastropods from the Ribeira Valley were compared as regards to morphology, ecology and behaviour (Bichuette and Trajano 1999; 2003). Ancylids (Pulmonata), also aquatic, were recorded in some caves of the Ribeira Valley, São Domingos, and northern Minas Gerais (genus *Gundlachia* or related, in the two latter). Among bivalves, *Pisidium* sp. was found in caves of São Domingos karst area.

Living populations of terrestrial snails, as those of endodontids (Pulmonata) in the Ribeira Valley, are relatively rare in Brazilian caves. The depigmented endodontids from Barra Bonita Cave, at Intervales State Park (Ribeira Valley), are possibly troglobitic. Subulinids are relatively frequent in some caves of the Ribeira Valley at Paraná State (Pinto-da-Rocha 1995).

A few families of Oligochaeta were recorded for Brazil, e.g., the freshwater naidids, and the terrestrial enchytraeids, glossoscolicids and megascolicids. The latter include a common asiatic species introduced in Brazil, *Amynthas hawaianus*, which has already successfully colonised several caves, possibly displacing other, native species.

Few planarians have been found in Brazilian caves. The only large populations, apparently troglophilic, are those of *Dugesia paramensis* from caves in Altamira-Itaituba region (Kawakatsu and Froehlich 1992). Troglomorphic individuals belonging to undescribed species were collected in three caves, one in the Ribeira Valley, one in the Bodoquena karst area and another in the São Desidério karst area (Table 1); the species from Bodoquena is possibly a *Girardia* (Moracchioli pers. comm. 2002).

The cave freshwater sponge, belonging to the genus *Racekiela*, represents the first subterranean species found in cave habitat. This species was discovered in the Lapa dos Brejões, a large cave system (11°00’42,7”S 41°25’59,6”W) at karstic terrains at the northern part of the Chapada Diamantina, State of Bahia, northeast Brazil. Indeed, this is the second species of genus *Racekiela* Bass and Volkmer-Ribeiro, 1998 registered for the Neotropical Region. The finding of *Racekiela* n.sp. inside the Lapa dos Brejões cave system, now the only one in Brazil to shelter a freshwater sponge, comes to be a fresh new argument which adds to the archeological and geological ones in favor of the monitoring and continued conservation of the area.

DISCUSSION

In a very general way, one may distinguish two subterranean faunas in Brazil: a subtropical cave fauna, as observed in the Ribeira Valley and southwards, characterised by the presence of typically subtropical/temperate components such as *Aegla* decapods, *Goniosoma* opilionids, and a diversified fauna of Polydesmida diplopods and Pachyline opilionids; and a tropical one, with components such as Amblypygids, cockroaches, mygalomorph spiders, *Drosophila* flies etc. The Bodoquena subterranean fauna is intermediate, with subtropical (e.g., Polydesmida: Oniscodesmidae: *Crypturodesmus*) and tropical (Amblypygi) components. Some other taxa are found throughout the country, from Amazonia to Santa Catarina, e.g., *Endecous* crickets, *Pseudonannolene* diplopods, ctenid (especially *Ctenus*), pholcid (e.g., *Mesabolivar*), theridiosomatid (*Plato*) and sicariid (*Loxosceles*) spiders. Also widespread are the chironomid and phorid flies, tineid moths, reduviid bugs, cholevid (especially *Dissochaetus*) and carabid (several tribes) beetles. No significant differences were observed between faunas from limestone, sandstone, quartzite and iron caves.

Deharveng and Bedos (2000) pointed to several differences between the tropical southeast Asia and temperate cave faunas. Among these, the following also would apply to Brazil: 1. high diversity of arachnids at all taxonomic levels; 2. general higher group diversity, e.g. Diplopoda, Isopoda Oniscoidea; 3. lower diversity of troglomorphic collembolans; 4**.** relatively poor troglomorphic fauna of Coleoptera. According to these authors, non-troglobitic species are more frequent in SE Asia than in temperate areas, ranging from 66.6 to 81.5 5 of the total richness in the study sites. A large proportion of non-troglobitic species is also a conspicuous characteristic of Brazilian cave faunas.

At least for Brazil, the speleofaunistic differences in relation to temperate zones seem to be more related to characteristics of epigean faunas as source for colonizers, than to ecological differences. Tropical caves have been frequently described as less food-limited than the temperate ones due, in part, to the general presence of large, stable colonies of bats and other trogloxenic vertebrates continuously producing large amounts of guano (e.g., Poulson and Lavoie 2000; Deharveng and Bedos 2000, for southeast Asia). However, such generalisation is not valid for Brazil, where caves with great amounts of guano produced by large, stable colonies of bats are not the rule. In areas with many large caves, bat populations tend to distribute and frequently move between and inside the available shelters, forming relatively small, itinerant colonies (Trajano 1996). Therefore, in many Brazilian caves bat guano piles occupy relatively small areas and are deposited in a more or less irregular, rather unpredictable way, because bats may abandon specific roosts inside caves at any time, sometimes periodically, sometimes not. Only in regions harbouring few, small caves such as sandstone areas (e.g. Serra Geral, in São Paulo; Altamira-Itaituba, in Pará; Chapada do Araripe, in Ceará/Pernambuco) and some carbonate regions as Brasília, Rio Pardo and also Araripe karst areas, bats may concentrate in such caves, forming relatively stable colonies.

As well, the notion that tropical caves in general are less energy-limited also because have more entrances resulting in higher food input (Poulson and Lavoie 2000) does not apply to Brazil. The assumption that speleogenesis proceeds faster in the tropics is based on the notion that tropical regions are always humid (more water, faster speleogenesis), which is not true. There are nowadays extensive dry areas in South America – caatinga,

Table 1. Troglobitic invertebrate taxa reported for Brazilian caves.). * troglomorphic, the status as troglobites is uncertain. (1) L.A. Souza Kury, pers. comm. 1997; (2) R. Pinto da Rocha, pers. comm. 2001; (3) A. Chagas-Jr., pers. comm. 2009; (4) R.L. Ferreira, pers. comm. 2005; (5) R.L.C. Baptista, pers. comm. 2002; (6) C. Rheims, pers. comm. 2004; (7) R. Bessi Pascoaloto, pers. comm. 2007; (8) A. Giuponni & R.L.C. Baptista, pers. comm. 2003; (9) L.M. Cordeiro, pers. comm. 2007; R. Pinto da Rocha, pers. comm.. 2009.

Taxon	Genus or species	**Karst area**
CRUSTACEA		
AMPHIPODA		
Bogidiellidae	*Megagidiella azul* Koenemann & Holsinger, 1999	Bodoquena (MS)
	Megagidiella sp.	Forte Coimbra (MS)
	Spelaeogammarus bahiensis Brum, 1975	Curaçá (BA)
	S. santanensis Koenemann & Holsinger, 2000	Serra do Ramalho (BA)
	S. spinilacertus Koenemann & Holsinger, 2000	Chapada Diamantina (BA)
	S. trajanoae Koenemann & Holsinger, 2000	Campo Formoso/Caatinga (BA)
Hyalellidae	*Hyalella caeca* Pereira, 1989	Alto Ribeira (SP)
ISOPODA		
Calabozoidea	*Pongycarcinia xiphidophorus* Messana, Baratti & Benvenuti, 2002	Campo Formoso (BA)
	indet.	Nobres (MT)
Oniscidea		
Armadillidae	*Venezillo* sp. (1)	Brasília region (DF)
Philosciidae	*Benthana iporangensis* Lima & Serejo, 1993	Alto Ribeira (SP)
Platyarthridae	*Trichorhina* spp. *	Several karst areas (BA/MG/SP/PR) (1) and iron (MG) (4) areas
Scleropactidae	New genus (1)	Altamira-Itaituba (PA)
Styloniscidae	*Pectenoniscus* sp. 1 (1)	Serra do Ramalho (BA) and Lagoa Santa (MG)
	Pectenoniscus sp. 2 (1)	Alto Ribeira (SP/PR)
	Pectenoniscus sp. (2)	Botuverá (SC)
	Thailandoniscus sp. 1 (1)	Peruaçu (MG)
	Thailandoniscus sp. 2 (1)	Serra do Ramalho (BA)
	New genus (1)	Serra do Ramalho (BA) and Itacarambi (MG)
SPELAEOGRIPHACEA	*Potiicoara brasiliensis* Pires, 1987	Bodoquena (MS)
	cf. *P. brasiliensis*	Nobres (MT)
DECAPODA		
Aeglidae	*Aegla cavernicola* Turkay, 1972	Alto Ribeira (SP)
	A. leptochela Bond-Buckup & Buckup, 1994	Alto Ribeira (SP)
	A. microphthalma Bond-Buckup & Buckup, 1994	Alto Ribeira (SP)
CHILOPODA		
Geophilomorpha	Geophilidae, n. genus, n. sp. *	Alto Ribeira (SP)
Scolopendromorpha	Cryptopidae, *Cryptops* n. sp. (3)	Carajás (PA) – iron caves
Lithobiomorpha	Indet.	Minas Gerais – iron caves (4)
DIPLOPODA		
POLYDESMIDA	Indet.	Minas Gerais - iron (4)

Chelodesmidae	*Leodesmus yporangae* (Schubart, 1946)	Alto Ribeira (SP)
Cryptodesmidae	*Cryptodesmus* spp.	Alto Ribeira (SP/PR)
	Peridontodesmella alba Schubart, 1957	Alto Ribeira (SP/PR)
Furhmannodesmidae	*Phaneromerium cavernicolum* Golovatch&Wytwer,2004	Bambui (BA)
Oniscodesmidae	*Crypturodesmus* sp. 1	Bodoquena (MS)
	Crypturodesmus sp. 2	Alto Ribeira (SP/PR)
	Crypturodesmus sp. (2)	Botuverá (SC)
Pyrgodesmidae	*Yporangiella stygius* Schubart, 1946	Alto Ribeira (SP)
SYMPHYLA *	Indet.	Alto Ribeira (SP)
Scutigerellidae	cf. *Hanseniella*	Rio Pardo (BA)
HEXAPODA		
COLLEMBOLA		
Arrhopalitidae	*Arrhopalites amorimi*, *A.gnaspinius*, *A.lawrencei*, *A. wallacei* Palacios-Vargas & Zeppelini, 1995	Alto Ribeira (SP)
	Arrhopalites papaveroi Zeppelini-Filho & Palacios-Vargas, 1999	Bodoquena (MS)
	Arrhopalites spp.	Botuverá (SC) (2), Minas Gerais - iron caves (4)
Cyphoderidae	Several undetermined species	Several karst (BA/MG/GO/MS/SP) and granitic (SP) areas
Entomobryidae	Idem	Several karst (BA/GO/MS/SP/PR) and sandstone (SP) areas
Hypogastruridae	*Acherontides eleonorae* Palacios-Vargas & Gnaspini-Netto, 1993	Alto Ribeira (SP/PR)
	Acherontides spp.	Rio Pardo (BA), Botuverá (SC) (2)
Isotomidae	Several undetermined species	Karst (MG/SP), granitic (SP) and iron (MG)(4) areas
Onychiuridae	Indet.	Alto Ribeira (SP)
Paronellidae	Several indetermined genera/species	Alto Ribeira (SP), Bodoquena (MS)
	Troglolaphysa aelleni, *T. hauseri* Yoshii, 1988	Alto Ribeira (SP)
	Troglopedetes sp. (2)	Botuverá (SC)
DIPLURA		
Campodeidae	*Oncinocampa trajanoae* Condé, 1997	Alto Ribeira (SP)
ZYGENTOMA		
Nicoletiidae	*Cubacubana spelaea* Galán, 2000	Campo Formoso (BA)
BLATTARIA		
Blattellidae	*Litoblatta camargoi* Gutiérrez, 2005	Chapada Diamantina (BA)
HETEROPTERA		
Dipsocoridae	Indet.	Bodoquena (MS)
Enicocephalidae (4)	Indet.	Minas Gerais – iron caves
HOMOPTERA		
Cixiidae, Ortheziidae (4)	Indet.	idem

COLEOPTERA		
Carabidae	*Coarazuphium bezerra* Gnaspini, Vanin & Godoy, 1998	São Domingos (GO)
	C. cessaima Gnaspini, Vanin & Godoy, 1998	Chapada Diamantina (BA)
	C. pains Alvares & Ferreira, 2002	Pains (MG)
	C. tessai Godoy & Vanin, 1990	Serra do Ramalho (BA)
	Coarazuphium sp. (4)	Belo Horizonte área (MG) – iron
	Oxydrepanus sp.	Alto Ribeira (SP)
	Schizogenius ocellatus Whitehead, 1972	Alto Ribeira (SP)
Pselaphidae	*Arthmius* sp.	Alto Ribeira (SP)
	Syrbatus sp.1	Pains (MG)
	Syrbatus sp.2	Serra do Mar (SP) – granitic
	cf. *Strombopsis* sp.	Alto Ribeira (SP)
Tenebrionidae	Indet.	Serra do Mar (SP) – granitic
HYMENOPTERA		
Formicidae	Ponerinae indet.	Brasília (DF)
ARACHNIDA		
SCORPIONES		
Buthidae	*Troglorhopalurus translucidus* Lourenço, Baptista & Giuponni, 2004	Chapada Diamantina (BA) – quartzite
ARANEAE		
Dipluridae	Indet. (4)	Minas Gerais – iron caves
Amaurobiidae	new genus	Bodoquena (MS)
Ctenidae	*Ctenus* n. sp. (5)	Chapada Diamantina (BA) – quartzite
Gnaphosidae	new genus	Ibitipoca (MG)
Hahniidae	Indet.	Alto Ribeira (SP)
Nesticidae	*Nesticus* sp.1	Chapada Diamantina (BA)
	Nesticus sp.2	Lagoa Santa (MG)
Ochyroceratidae	*Speocera eleonorae* Baptista, 2003	Bodoquena (MS)
	Ochyrocera ibitipoca Baptista, Gonzalez & Tourinho, 2008	Ibitipoca (MG) – quartzite
	Ochyrocera sp.1	São Domingos (GO)
	Ochyrocera sp.2	Serra do Mar (RJ) – gnaisse
	new genus 1	Chapada Diamantina (BA) – quartzite
	new genus 2	Serra do Ramalho (BA)
Pholcidae	n. sp. (6)	Chapada Diamantina (BA)
Prodidomidae	*Lygromma ybyguara* Rheims & Brescovit, 2004	Cordisburgo (MG)
AMBLYPYGI		
Charinidae	*Charinus troglobius* Baptista & Giupponi, 2002	Serra do Ramalho (BA)
	Charinus eleonorae Baptista & Giupponi, 2003	Bambuí (MG)
	Charinus n. sp. 1	Serra do Ramalho (BA)
	Charinus n. sp. 2	Central (BA)

PSEUDOSCORPIONES		
Bochicidae	*Spelaeobochica muchmorei* Andrade & Mahnert, 2003	Alto Ribeira (SP)
Chthoniidae	*Pseudochthonius strinati* Beier, 1969	Alto Ribeira (SP)
	Indet.	Minas Gerais – iron caves [4]
PALPIGRADI *	Indet.	Alto Ribeira (SP) [7], Mambai (GO) and karst areas in MG [4]
Eukoenenidae	*Eukoenenia* sp. [4]	Belo Horizonte (MG) – iron caves
OPILIONES		
Gonyleptidae	*Discocyrtus pedrosoi* Kury, 2008	Chapada Diamantina (BA)
	Eusarcus elinae Kury, 2008	Chapada Diamantina (BA)
	Giupponia chagasi Pérez & Kury, 2002	Serra do Ramalho (BA)
	Iandumoema uai Pinto-da-Rocha, 1996	Peruaçu (MG)
	Iandumoema setimapocu Hara & Pinto-da-Rocha, 2008	Montes Claros (MG)
	Pachylospeleus strinatii Silhavy, 1974	Alto Ribeira (SP)
Pachylinae	New genus [10]	Alto Ribeira (SP/PR)
	Indet. [2]	Botuverá (SC)
	Eusarcus sp. 1	Bodoquena (MS)
	Eusarcus sp. 2 [2]	São Domingos (GO)
	Eusarcus elinae Kury, 2008	
	Discocyrtus pedrosoi Kury, 2008	Chapada Diamantina (BA) – quartzite
Tricommatinae	*Spinopilar armatus* Kury & Pérez-González, 2008	Cordisburgo (MG)
Escadabiidae	*Spaeleoleptes spaeleus* Soares, 1966	Cordisburgo (MG)
	Spaeleoleptes n. sp. [8]	Chapada Diamantina (BA)
ONYCHOPHORA		
Peripatidae	New genus, new species [9]	Bodoquena (MS)
GASTROPODA		
Hydrobiidae	*Potamolithus troglobius* Simone & Moracchioli, 1994	Alto Ribeira (SP)
	Potamolithus spp. (at least four undesc. species)	Alto Ribeira (SP)
	cf. *Potamolithus*	Bodoquena (MS)
Endodontidae	Indet.	Alto Ribeira (SP)
TURBELLARIA		
Dugesiidae	cf. *Girardia*	Bodoquena (MS)
	Indet.	Alto Ribeira (SP)
	Indet.	São Desidério (BA)
PORIFERA		
Demospongiae	*Raceckiela* n. sp.	Chapada Diamantina (BA)

chaco, cerrado etc. – and, in coutries such as Brazil and Argentina, most karst areas are located on these more or less dry phytogeographic domains (it is relevant that Amazonia, in great part responsible for that perception of a generally humid, forested South America, encompasses very few and small karst areas).

The degree of openness of a cave system, determined by the extent of contacts with the surface, depends also on other factors such as depth at which the cave develops and the inclination of the rock layers. In Brazil, we find every possible situation, from the less to the most opened systems. Several of our best examples of opened cave systems are found in presently semiarid areas which have been forested in the past (for instance, in northern Minas Gerais and in Bahia). However, such openness is not necessarily due to a past humidity – it is more probably due to the fact that these are horizontal, rather superficial caves. On the other hand, the most important Brazilian karst area currently situated in a wet forest, the Alto Ribeira, in the southern portion of the Brazilian Atlantic forest, is dominated by rather closed systems (mainly resurgences, with relatively few, small upper entrances) due to the inclination of the landscape and distance between water inlets and outlets. Regional uplifting is another less known factor that could influence the fragmentation of caves and which does not follow any tropical versus temperate dichotomy.

The great majority of caves explored in Brazil are oligotrophic, mesotrophic or, in some cases, poecilotrophic; we estimated that no more than 5 % of Brazilian caves may be considered eutrophic (Gnaspini and Trajano 2000). Main food resources for cavernicoles are represented by vegetal debris, relatively small guano piles, and dead and living epigean organisms carried by water (streams, percolating water) or accidentally entering caves.

In order to compare different karst areas with regard to the subterranean biodiversity, it is necessary to distinguish between general diversity (including all cavernicoles, i.e., troglobites, troglophiles and trogloxenes) and diversity of troglobites (Trajano 2001). General diversity is mostly related to present-day ecological aspects such as food availability and diversity of epigean fauna providing potential colonisers. Diversity of troglobites is a consequence of historical factors such as opportunities of isolation in subterranean habitats provided, for instance, by palaeoclimatic fluctuations. As well, hotspots of aquatic diversity may or may not coincide with those of terrestrial diversity. Differences have been found for troglobites, which are probably due to differences in the main isolation events affecting respectively aquatic and terrestrial faunas.

The São Domingos karst area illustrates well such differences. In the presence of fast-running streams, with a high carrying capacity, relatively large amounts of detritus may be accumulated inside caves. As a consequence, these caves are very rich (for Brazilian standards) in both aquatic and terrestrial cavernicoles: 95 terrestrial invertebrate taxa have been recorded in a set of seven caves (C. Rheims and F. Pellegatti-Franco, pers. comm. 2003) and 55 aquatic invertebrate taxa in two caves (A.P. Majer, F.B.Santos and P.A. Basile, pers. comm. 2003). Nevertheless, there are few terrestrial troglobitic invertebrates (and no aquatic invertebrate), as predicted by the model of paleoclimatic fluctuations as a major cause of troglobitic speciation, because there is evidence that São Domingos area is situated in a rather palaeoclimatically stable region (Trajano 1995). On the other hand, with seven species reported for a relatively small area (Mattox et al 2008), this is a hotspot of diversity for troglobitic fish at a worldwide scale. Non-cyclical, progressive topographic isolation (by waterfalls or in perched aquifers), possibly associated with the extinction of related epigean populations in the case of *Ituglanis* and *Pimelodella* catfishes, may explain the origin of such rich troglobitic ichthyofauna (Trajano et al 2004).

Among areas that are hotspots for both terrestrial and aquatic troglobitic biodiversity, one may mention the Alto Ribeira, in São Paulo, the Serra do Ramalho, São Desidério and Chapada Diamantina, in Bahia, and Bodoquena, in Mato Grosso do Sul. Like the observed for troglobitic fishes in São Domingos, troglobites from the Alto Ribeira are not very specialised, usually not showing complete regression of eyes and pigmentation, with a great deal of intra- and interpopulation variation. In contrast, most of the highly specialised Brazilian troglobites are found in currently semiarid regions in Bahia, such as Chapada Diamantina and also Campo Formoso, also in accordance with the palaeoclimatic model (Trajano 1995).

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