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Cave Faunas in the Atlantic Tropical Rain Forest: Composition, Ecology, and Conservation[1]

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ABSTRACT

I present a comparative analysis of the cave fauna composition for two karst areas in the Atlantic tropical rain forest: the extensively studied Ribeira Valley, southeastern Brazil, and the small and poorly known Rio Pardo region, southern Bahia state, northeastern Brazil. These regions also are compared to other Brazilian karst areas. The cave fauna from Rio Pardo appears to be more similar to the fauna of other tropical caves in the Caatinga and Cerrado domains than to the cave fauna of the subtropical Ribeira Valley. Ecological data, including probable trophic relationships, are presented, and special conservation problems related to karst areas, with examples from the Atlantic rain forest cave taxa, are discussed.

RESUMO

No presente trabalho, são comparadas as comunidades cavernícolas das duas principais áreas cársticas situadas na Floresta Tropical Pluvial Atlántica, o extensivamente estudado Vale do Ribeira (São Paulo/Paraná) e a região do Rio Pardo, ao sul de Ilhéus (Bahia). Dados inéditos sobre a fauna de cavernas do Rio Pardo, pela primeira vez estudada, são apresentados, apontando-se as particularidades dessa área. A comparação dessa fauna com a de outras regiões mostra que praticamente todos os táxons compartilhados com o Vale do Ribeira o são também com pelo menos uma região cárstica não situada na Mata Atlântica. Além disso, aparentemente há mais semelhanças entre a fauna das cavernas do Rio Pardo e a de outras cavernas plenamente tropicais, situadas na caatinga e no cerrado, do que em relação a cavernas da Mata Atlântica localizadas mais ao sul no país. Portanto, não parece existir uma unidade bioespeleológica compreendendo as áreas cársticas da Mata Atlântica em oposição áquelas situadas em outros domínios fitogeográficos. Finalmente, são discutidos os problemas especiais relacionados à conservação de ecossistemas cavernícolas e descritas as principais ameaças às comunidades cavernícolas nas diferentes áreas cársticas da Mata Atlântica, com alguns exemplos de espécies que se encontram em risco de extinção.

Key words: *Atlantic rain forest; cave fauna; conservation.*

CAVES—NATURAL CAVITIES IN THE SUBSOIL ACCESSIBLE TO HUMANS, which normally are part of larger systems of interconnecting subterranean spaces—develop mainly in karst areas (*i.e.*, areas geologically characterized by the presence of soluble rocks, such as carbonates [limestones, dolomites] with subterranean drainages through conduits). Six major carbonate and six sandstone karst areas, plus a number of less important and less known karst areas, have been described for Brazil (Fig. 1). The most important areas in geographic extension and speleological activities are the Bambuí Province in Minas Gerais, Bahia, and Goiás states, central–eastern Brazil; the Ribeira Valley in São Paulo and Paraná states, southeastern Brazil; and the Bodoquena Province in Mato Grosso do Sul state, southwestern Brazil.

Two main limestone areas are located in the Atlantic tropical rain forest (*sensu* Veloso *et al.* 1991): the extensively studied Ribeira Valley and the Rio Pardo area, a poorly known, small karst area in southern Bahia state. Granitic caves, formed basically by erosion of sediment deposited between large rocky blocks, present a scattered occurrence between those carbonate provinces.

My purpose is to characterize the cave faunas from Atlantic rain forest localities and compare the taxa frequently found in caves of different Brazilian karst areas, in order to detect qualitative similarities and differences. For this, I present a synthesis of faunistic data available in the literature for the subtropical Ribeira Valley and new data on the tropical Rio Pardo, comparing the composition of these faunas to that of cave faunas found in areas not situated in the Atlantic Forest domain. If more taxa are shared by the two karst areas in the Atlantic Forest than by either of these and other areas, it

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FIGURE 1. Main karst areas situated in the Atlantic rain forest (1 and 2) and other Brazilian phytogeographic domains. 1. Ribeira Valley; 2. Rio Pardo; 3. Bambuí; 4. Una; 5. Ibiapaba; 6. Bodoquena; 7. Alto Paraguai; 8. Altamira-Itaituba; 9. Alto Urubu; 10. Serra Geral.

can be concluded that the present-day distribution of the Atlantic rain forest domain plays a major role in determining cave community composition. Finally, I discuss special conservation problems affecting cave faunas, with an emphasis on species endemic to the subterranean habitat (troglobites).

BIOSPELEOLOGICAL RESEARCH IN THE ATLANTIC FOREST DOMAIN

The first known Brazilian troglobite, the blind pimelodid catfish *Pimelodella kronei* (Ribeiro), was discovered in 1898 in the Ribeira Valley, southern São Paulo state, by R. Krone, the pioneer of speleology in this area. This species was studied in detail by Pavan (1945) and Trajano and colleagues (Trajano 1997). Until the late 1960s, however, Brazilian biospeleology was restricted mainly to isolated records and descriptions of a few taxa such as diplopods (*e.g.*, *Alocodesmus yporangae* Schubart, *Yporangiella stygius* Schubart, and *Peridontodesmella alba* Schubart, all troglobites from the Ribeira Valley).

In 1968, the Swiss biospeleologist P. Strinati visited the Ribeira Valley and carried out a brief but extensive survey in two caves, Tapagem and Areias (type locality of *P. kronei*). This visit resulted in the description of several new species (*e.g.*, Strinati 1975).

From the 1970s on, collecting in Brazilian caves was intensified. Data from São Paulo, and to a lesser extent Goiás and Bahia (Bambuí karst area), were gathered for the first comprehensive faunistic publication (Dessen *et al.* 1980). Subsequently, three other general faunistic surveys were published (Trajano 1987, Trajano & Gnaspini-Netto 1991a, Gnaspini & Trajano 1994), but always with greater emphasis on the intensively studied Ribeira Valley. Only recently, caves from Mato Grosso do Sul (Bodoquena karst area), Minas Gerais, and Bahia (Bambuí) were subjected to systematic biological survey (Gnaspini & Trajano 1994; Trajano, pers. obs.). As well, sandstone and a few granitic caves have been studied in Pará (Trajano & Moreira 1991) and São Paulo (Trajano 1987, Gnaspini & Trajano 1994). Regional faunistic publications include those of Pinto da Rocha (1994) for Paraná state in the Ribeira Valley.

In the meantime, academic work started at the Universidade de São Paulo dealt mainly with cavernicoles found in the Ribeira Valley and focused on the systematics, natural history, and population ecology of taxa as diverse as bats, siluriform fishes, anomuran crustaceans, beetles, opilionids, and gastropods. Therefore, the Ribeira Valley is by far the best known Brazilian karst area from the biospeleological point of view.

At present, the main limitations to biospeleological studies in Brazil are the paucity of specialists for the taxa found in caves, the high number of new species requiring description, and the need for revising several of those groups. For these reasons, detailed faunistic analyses and geographic comparisons are difficult because most identifications are still at the family or generic level. On the other hand, environmental disturbances, including limestone exploitation and uncontrolled visitation, are threatening subterranean ecosystems throughout the country, and require immediate ecological evaluation using the faunistic data available.

CAVE COLONIZATION AND COMMUNITY COMPOSITION

Cave organisms may have different ecological and evolutionary relationships to the subterranean biotope, classified accordingly into: **trogloxenes**—organisms regularly found in caves but which must return periodically to the epigean (surface) habitat

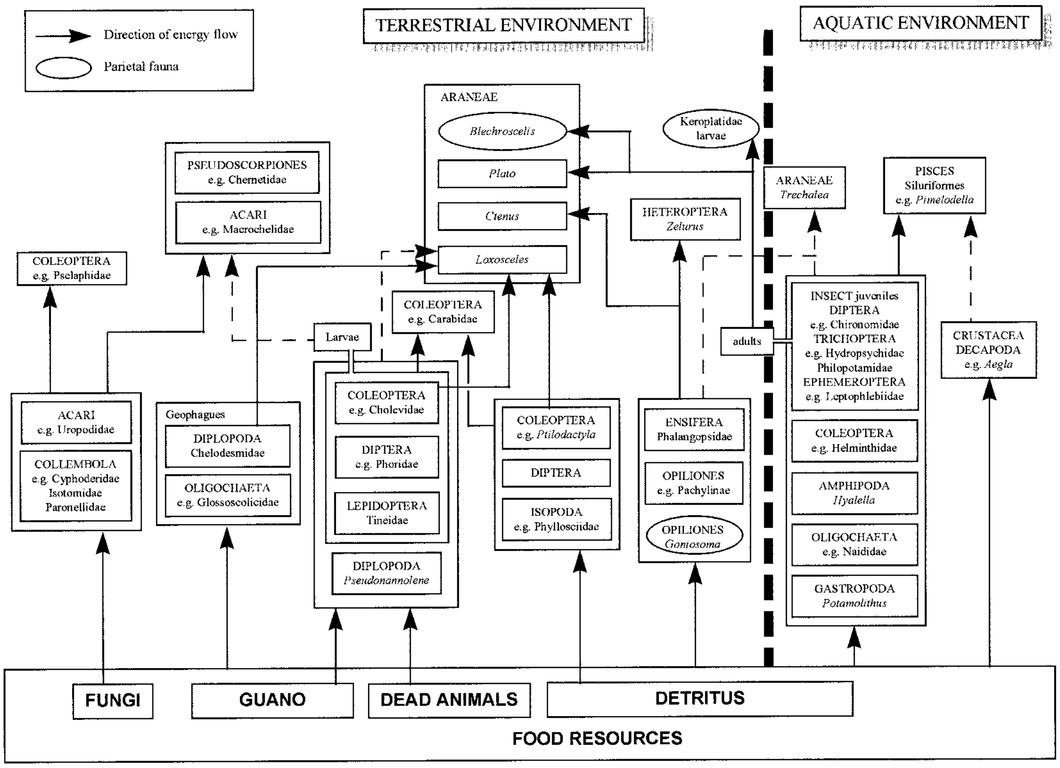

FIGURE 2. Food webs in the Ribeira Valley karst area, southeastern Brazil (modified from Trajano & Gnaspini-Netto 1991b). A: Food web in a generalized cave; B: Guano-based food web.

to complete their life cycles; **troglophiles**—organisms able to complete their life cycles in both the subterranean and the epigean habitats; and **troglobites**—species restricted to the subterranean biotope, and usually distinguished by specializations (troglomorphisms) such as reduction of eyes and pigmentation (Holsinger & Culver 1988). Troglobites originate from troglophilic populations, or directly from epigean populations after some kind of geographic or genetic isolation.

In order to colonize the subterranean habitat effectively, organisms must be able to orient themselves topographically and find food and mates under conditions of permanent absence of light, frequent scarcity of food, and low population densities. Morphological, physiological, and behavioral features of epigean organisms that allow cave colonization are called preadaptations. They correspond to character states developed in relation to lifestyles that by chance resemble the subterranean life—nocturnal activity, cryptobiotic life, opportunistic feeding. The cave communities of a given area will be composed mainly of the preadapted taxa among those epigean groups living at the present or which have lived in the area during the past.

In general, great variation among the taxa occupying a given habitat or substrate in different caves in the same area is not observed. Thus, the faunal composition of caves from a restricted area usually is highly repetitive and predictable. Once one studies in detail a few representative caves (*i.e.*, caves encompassing different kinds of habitats), it is possible to predict the composition of the communities found in the whole set of caves from that area.

THE CAVE FAUNA FROM RIBEIRA VALLEY—A SYNTHESIS

About 360 of 537 invertebrate taxa and 42 of 76 vertebrate taxa, listed by Pinto da Rocha (1995) for Brazilian caves have been recorded for the Ribeira Valley, São Paulo and Paraná states. The maximum number of taxa per cave (*ca* 90) was recorded for the Areias system. Those cave taxa, including troglobites, troglophiles, and trogloxenes, were

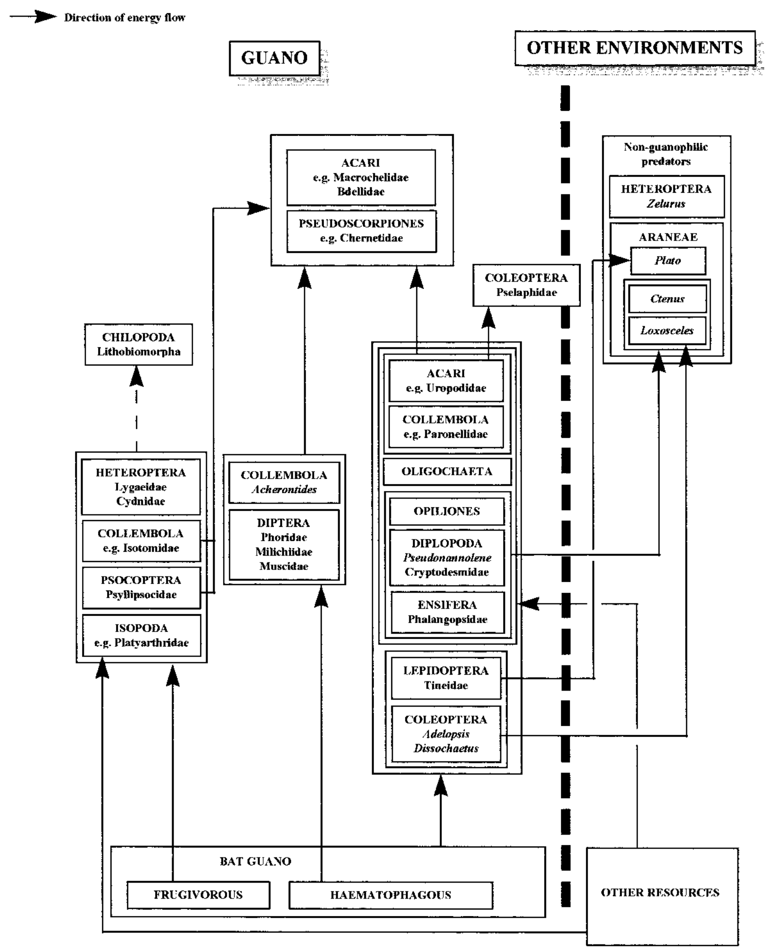

FIGURE 2. Continued.

found exclusively in the Ribeira Valley (including all troglobites) or shared with other Brazilian karst areas. The inclusion rate of new taxa in the Ribeira Valley cave fauna list is leveling off. Most additions today are due to more precise identification of taxa previously sampled. This leveling off indicates that for most taxa, the composition of these communities is well known at the family level, and in many cases, at the generic level.

Faunistic data on the Ribeira Valley are found mainly in Trajano (1987), Trajano and Gnaspini-Netto (1991a, b), and Gnaspini and Trajano (1994). Figure 2 (adapted from Trajano & Gnaspini-Netto 1991b) shows a general food web and a bat guano-based food web for a hypothetical cave in which all main habitats are found, both aquatic (streams with riffles and pools) and terrestrial (rocky substrates, sediment banks, organic matter accumulations). These food webs are based mainly on direct observation of feeding interactions among the commonest cavernicoles in the Ribeira Valley, complemented by data on feeding habits from the literature. The figure provides an overview of the main taxa found in caves of the Ribeira Valley and their most important trophic relationships.

The great majority of families and many genera found in the Ribeira Valley are widely distributed throughout Brazilian caves: *e.g.*, spiders *Loxosceles, Plato, Ctenus,* and *Blechroscelis, Trichorhina* isopods, *Pseudonannolenne* diplopods, *Endecous* crickets, *Zelurus* heteropterans, *Dissochaetus* beetles, *Conicera* and *Dohrniphora* flies. Other genera present a distribution restricted to a few karst areas, such as *Katantodesmus* diplopods in the Ribeira Valley and in the Bodoquena region, and *Goniosoma* opilionids in the Ribeira Valley and the sandstone and granitic caves of São Paulo state.

In other cases, faunistic differences lie in the relative abundances of cave taxa. Keroplatidae dipterans that probably compete with *Plato* and *Blechroscelis* spiders are common in the Ribeira Valley, but are rare elsewhere in caves. In contrast, taxa such as *Drosophila* flies, ants, and cockroaches, are frequent in the typically tropical Brazilian caves but rare in the subtropical Ribeira Valley, where cave temperatures are *ca* 18-20°C. As well, armadillid isopods and histerid beetles may be frequent in other Brazilian karst regions, including the Rio Pardo and the Bodoquena Provinces, but are rare or absent from caves of the RibeiraValley.

The Ribeira Valley is remarkable for its relatively high diversity of diplopods, opilionids, and beetles. Besides the widespread troglophilic Pseudonannolenida diplopods, different families of Polydesmida cave-dwelling millipedes have been recorded in this region. As well, several genera of carabid beetles, the commonest being *Schizogenius*, *Paratachys*, and *Platynus*, and at least seven genera of pselaphid beetles have been recorded in caves of the Ribeira Valley.

The Brazilian fauna of cave opilionids seems to present a high degree of taxonomic specificity according to the geographic location. Different families or genera predominate or are exclusive to each region. Thus, the Ribeira Valley may be characterized by the occurrence of troglophilic *Daguerreia inermes* Soares & Soares and *Pararezendesius luridus* Soares, besides the troglobitic *Pachylospeleus strinatii* Silhavy and the trogloxene *Goniosoma spelaeum* (Mello-Leitão) (Pinto da Rocha 1995).

The Ribeira Valley presents an extremely diversified subterranean aquatic fauna, including several catfish species with heptapterines predominating (the troglobitic *P. kronei* occurs in six caves; Trajano 1997), crustaceans such as *Aegla* decapods (restricted to southern Brazil) and *Hyalella* amphipods, hydrobiid gastropods, planarians, and several species of insects (Trajano & Gnaspini-Netto 1991b).

The Ribeira Valley in São Paulo is remarkable in having a large number of troglobitic species, both aquatic (the catfish *P. kronei*, *Aegla* and *Hyalella* crustaceans, several hydrobiid gastropods, planarians) and terrestrial (several collembolans, carabid and pselaphid beetles, isopods, polydesmid diplopods, the opilionid *P. strinatii*). Among 87 troglomorphic taxa listed in Gnaspini and Trajano (1994), 44 are found in the Ribeira Valley, São Paulo, a high proportion considering the relatively small geographic extension compared to other karst areas such as those of the Bambuí Province. This large number of troglobites could be explained in part by the greater collecting effort applied to the Ribeira Valley caves, which have been surveyed intensively since the 1970s; however, other karst areas also have been studied in recent years, and for terrestrial organisms, the rate of increase in the number of known Brazilian troglobites is not as marked as one might expect. On the other hand, new troglobites are being found in the Ribeira Valley, as is the case with the hydrobiids and planarians not listed by Gnaspini and Trajano (1994). Therefore, in my opinion, even with the intensification of biospeleological activities in other regions, the Ribeira Valley will remain one of the Brazilian karst areas harboring a remarkable diversity of troglobites.

THE CAVE FAUNA FROM RIO PARDO PROVINCE, ILHÉUS REGION, SOUTHEASTERN BAHIA

The Rio Pardo is one of the smallest and less known Brazilian speleological provinces. Cave exploration and mapping in the Ilhéus region began only five years ago. The present report, based on collections made in July and from September to November 1997, represents the first biospeleological study in the area.

All known caves are small (usually not > 200–300 m long), permanently dry and superficial (roots appear in the walls and soil of upper conduits), and harbor relatively large colonies of bats (dozens to hundreds of individuals). The Ilhéus region includes both preserved Atlantic tropical rain forest and "cabrucas" (patches of native forest in which the understory has been cut for cocoa cultivation). It is particularly rich in bat species (D. Faria, pers. comm.) and the availability of shelters represented by those caves may be a factor influencing such richness. Several bat species have been recorded in the caves of the Ilhéus region. The most abundant are the common vampire bat *Desmodus rotundus*, and *Carollia perspicillata*, an ubiquitous and frugivorous (tending to omnivory) species.

Due to the presence of bat colonies that frequently move inside the caves ("itinerant" colonies), the floors of those caves are covered mostly by guano, sometimes forming separated patchs of haematophagous and frugivorous bat guano (but frequently with mixed guano). Apparently, at least for the commonest species, the cave bat populations are relatively stable throughout the year (B. S. Santos, pers. comm.). Thus, there would not be important seasonal variations in the deposition of bat guano and its availability to cavernicoles.

Table 1 shows the taxa recorded in four caves from Pau Brasil county (15°27′S, 39°39′W; *ca* 110 km to the south of Ilhéus), which are among the largest in the area. For comparison, records of these taxa in caves from the Atlantic rain forest of southeastern Brazil (Ribeira Valley and granitic caves in São Paulo) and other karst areas in Bahia also are indicated. The biospeleological survey in Pau Brasil was carried out in July 1997 (a time of less rainfall). Additional material was collected from September to November in Califórnia and Pedra Suspensa Caves (Table 1.) and six other caves (data included in general discussion) within a 80-km radius from Pau Brasil. As expected in a poorly studied region, we found several undescribed taxa, including a new genus and species of a new *Eidmanacris* cricket (F. A. G. Mello, pers. comm.); and a new opilionid species in the genus *Protimesius* (R. Pinto da Rocha, pers. comm.).

The most conspicuous and abundant cavernicoles in Rio Pardo area are the *Eidmanacris* crickets (new species), blattarians, spiders such as *Loxosceles*, *Blechroscelis*, and *Ctenus*, armadillid isopods, and chernetid pseudoscorpions, all probably troglophiles. Pselliophorid chilopods of different ages have been observed in Califórnia Cave, possibly representing the first troglophilic population of scutigeromorphans recorded in Brazilian caves. Less common members of the soil/guano fauna, such as *Dichogaster* earthworms, gastropods, acarians, collembolans, diplurans, and *Trichorhina* isopods, may also be troglophiles.

The cavernicole status is still uncertain for less common, large arthropods such as theraphosid spiders, charinid amblypygids (probably *Charinus*, from Pedra do Sino Cave), diplopods, and flying insects (*e.g.*, dipterans in general), which easily may leave these small caves regularly to feed and/or reproduce (characterizing the trogloxene condition). *Acutisoma* aff. *indistinctum*, with several individuals collected in Pedra do Sino Cave, is probably a trogloxene, as are other Goniosomatinae opilionids in the Ribeira Valley.

Apparently, the Rio Pardo karst area has a low diversity of troglobitic species. Only a few troglomorphic, possibly troglobitic, taxa were recorded: entomobryids and *Acherontides* collembolans, symphylans, and *Trichorhina* isopods.

At family and generic levels, the presently studied fauna does not differ greatly from that of other Brazilian karst areas; practically all taxa from Rio Pardo caves have been recorded in other regions, both in and outside the Atlantic rain forest, such as the Ribeira Valley and the Bambuí Province (Table 1). Some of these taxa correspond to widely distributed groups: *Loxosceles*, *Blechroscelis*, and *Ctenus* spiders, chernetid pseudoscorpions, *Trichorhina* isopods, chironomids, *Dohrniphora* and *Pholeomyia* flies, and tineid moths. Other taxa are more typical of tropical caves to the north of the Ribeira Valley: mygalomorph and *Theridion rufipes* Lucas spiders, amblypygids, armadillid isopods, blattarians, *Nasutitermes* termites, histerid beetles, *Drosophila eleonorae* Tosi *et al.* flies, and ants (Trajano & Gnaspini-Netto 1991a, Gnaspini & Trajano 1994).

The soil fauna living in the substrate composed of sediment and mixed bat guano includes earthworms, chernetid pseudoscorpions, armadillid isopods, spirostreptid diplopods, entomobryid and cyphoderid collembolans, campodeid diplurans, and symphylans. Armadillid isopods were found previously in caves of Mato Grosso do Sul, Goiás, and Minas Gerais, frequently forming large troglophilic populations as they did in Rio Pardo. Campodeids rarely have been recorded in Brazilian caves. The species observed forming relatively large populations in Rio Pardo caves, *Lepidocampa juradii* Silvestri, is widely distributed in epigean/endogean habitats of South America (B. Condé, pers. comm.). Spirostreptidae diplopods also are rare in Brazilian caves. Noteworthy is the presence of feces of minhocuçus (a giant earthworm), *Rhinodrilus motucu* Righi, exposed on the cave floor; this is the first record for these earthworms in Brazilian caves.

Fresh haematophagous bat guano harbored a fauna typical of this niche throughout the country, with many larvae and adults of flies such *Pholeomyia*, *D. eleonorae*, psychodine, phorid, and muscid flies, besides *Acherontides* collembolans and leiodid beetles. This is the first record of *Acherontides* in Brazilian caves outside the Ribeira Valley, where huge populations of *A. eleonorae* Palacios-Vargas & Gnaspini-Netto are found exclusively in haematophagous bat guano. *Trichorhina* isopods and cydnid heteropterans (phytophagous) were found exclusively in frugivorous bat guano, as was observed for the latter in other Brazilian caves (Gnaspini-Netto 1989).

Emesinae heteropterans and noctuid moths are typical of the cave entrance fauna in Brazilian caves. *Blechroscelis* spiders are among the most conspicuous and constant members of this fauna in the Ribeira Valley, along with *Goniosoma* opilion-

TABLE 1. *Taxa recorded in caves from the Rio Pardo Speleological Province (California, Buraco do Galindo, Milagrosa, and Pedra Suspensa Caves), southern Bahia, with the occurrence of these taxa in caves from other regions: Ribeira Valley (V.RIB) and granitic caves (Gran) from the Atlantic Forest and Bambuí Province in Bahia state (BA): (P) = predators; (D) = detritivores (including fungivores, guanophagues, and scavengers); (Phy) = phytophagues; (Ps) = parasites; Tp = troglophile; Tm = troglomorphic; Ent = observed only near or at the cave entrance (max. 10 m deep); G = observed on guano of haematophagous (h) or frugivorous (f) bats; L = only larvae observed; exos = only exoskeletons observed.*

	Rio Pardo						
Karstic areas	Calif	Galin	Milg	Pe.Sus	V.RIB	Gran	BA
Phylum Arthropoda							
CL. ARACHNIDA							
O. Araneae (P)							
Theraphosidae: *Lasiodora* sp.	+						+
Sicariidae: *Loxosceles* spp.					+		+
Loxosceles cf. *laeta*	Tp		Tp				
Theridiidae: *Theridion* spp.					+	+	
T. rufipes		Tp					+
Pholcidae:							+
Blechroscelis sp.		Ent	Tp	Tp	Ent	+	
Ctenidae:				+	+	+	+
Ancylometes sp.	+						
Ctenus group *griseolus*	Tp						
O. Opiliones: Stygnidae: *Protimesius* sp.	+						
O. Pseudoscorpiones: Chernetidae (P)	TP		Tp	Tp	+		+
O. Acari indet.						+	
Mesostigmata spp.		G(f)	G	G(h)	+	+	+
Prostigmata	+				+		+
Ixodida (Ps): cf: *Ornithodoros*	+		+	+	+		
CL. CRUSTACEA							
O. Isopoda (D):							
Armadillidae: *Cubaris* sp.	Tp		Tp	Tp			+
Venezillo sp.	Tp		Tp	Tp			
Platyarthridae: *Trichorhina* sp.		G(f)			+		+
CL. SYMPHYLA					+		+
Scutigerellidae: cf. *Hanseniella*	+						
CL. CHILOPODA: Pselliophoridae	Tp						
CL. DIPLOPODA (D)							
O. Spirostreptida: Spirostreptidae	+			+			
O. Polydesmida: Chelodesmidae	exos	exos	exos	exos	+	+	
CL. HEXAPODA							
O. Collembola (D):							
Cyphoderidae:						+	+
Cyphoderus	+				+		
Entomobryidae	+			G	+		+
Lepidocyrtus		G(f)			+		
Hypogastruridae: *Acherontides*				G(h)	+	+	
O. Diplura: Campodeidae (D):					+	+	+
Lepidocampa juradii	+		Tp				
O. Ensifera: Phalangopsidae (D):					+	+	+
Eidmanacris sp.	Tp	Tp	Tp	Tp			
New genus	+						
O. Blattaria (D): Blattelinae	Tp	+	+	Tp	+	+	
Blaberinae	+				+		
O. Isoptera (D): *Nasutitermes* sp.	+	+		+	+		+
O. Psocoptera (D)	+				+	+	+
O. Heteroptera: Cydnidae (Phy)		G(f)			+		+
Reduviidae Emesinae (P)				Ent	Ent		+
O. Coleoptera:							
Carabidae (P): *Galerita* sp.			+		+		
cf. *Harpalina*		+					
Leiodidae				G(h)			
Staphylinidae Pselaphinae (P)		+			+	+	
Histeridae (P)		+			+		
Lampyridae	L				+		

TABLE 1. *Continued.*

Karstic areas	Rio Pardo				V.RIB	Gran	BA
	Calif	Galin	Milg	Pe.Sus			
Tenebrionidae (D)			+		+		
O. Diptera:							
Psychodidae Psychodinae				G(h)	+	+	
Culicidae	+						
Chironomidae (D)				+	+	+	+
Phoridae (D)	+				+	+	+
Dohrniphora spp.				G(h)			
Megaselia				G(h)			
Sciaridae			+				
Drosophilidae: *Drosophila* spp. (D)					+	+	
D. eleonorae		Ent	+	Ent			+
Milichiidae (D):	+		L				
Milichiella sp.	+						
Pholeomyia sp.	+			+	+		+
Muscidae (D)				LG(h)			
O. Hymenoptera							
Scelionidae (Ps)	+			+	+		
Formicidae:					+		
Ponerinae: *Pachycondyla impressa* (P)				+			
Myrmicinae: *Solenopsis geminata* group	+			+			
O. Lepidoptera:	L			LG(h)			
Noctuidae				Ent	Ent		Ent
Tineidae (D)	+	+		+	+		+
Phylum Annelida: CL. OLIGOCHAETA (D)							
Octochaetidae: *Dichogaster* sp.	Tp	Tp					
Glossoscolecidae: *Rhinodrilus motucu*	+		+				
Phylum Mollusca: CL. GASTROPODA (D)							
Streptaxidae				+			
Subulinidae				+	+		+
Systrophiidae	+			+			

ids. Usually, these spiders are not found far from cave entrances, and they use this habitat for reproduction, probably being trogloxenes limited by the low density of prey inside caves; however, it has been observed that in some bat caves with a high density of potential flying prey, such as in the sandstone caves of Altamira-Itaituba (Pará), *Blechroscelis* spiders colonize the entire cave habitat and establish troglophilic populations (Trajano & Moreira 1991). Such may be the case with *Blechroscelis* in some caves of the Ilhéus region.

Phalangopsid crickets are among the most ubiquitous Brazilian cavernicoles, with *Endecous* species forming troglophilic populations throughout the country. On the other hand, *Eidmanacris* crickets were recorded rarely in Brazilian caves: as members of the entrance fauna in sandstones caves from São Paulo and in a few caves from Goiás, Minas Gerais, and Amazonas states (Pinto da Rocha 1995). The occurrence of abundant troglophilic *Eidmanacris* populations is an interesting peculiarity of Rio Pardo caves, which represents the northernmost record for the genus in the Atlantic Forest (F. A. G. Mello, pers. comm.). As well, the population of *Acutisoma* aff. *indistinctum* found in Pedra do Sino cave represents the northernmost record for Goniosomatinae harvestmen, and the first one for Bahia state.

Feeding interactions similar to that shown in Figure 2 for the Ribeira Valley may be envisaged for Rio Pardo cave communities, with taxa substitutions due to faunistic differences. Few direct observations of predator–prey interactions have been made in Rio Pardo caves, and the following discussion is based partially on analogous trophic relationships of related groups in other cave ecosystems. Such a food web is mainly guano-based and comprises both generalist feeders and strictly guano-associated species, as well as some plant feeders in superficial conduits with exposed roots. Among the generalist macroinvertebrates, one can find crickets, cockroaches, and opilionids, which as observed in other Brazilian caves, would be preyed on by large arachnids such as ctenids and theraphosids, pselliophorid chilopods, amblypygids, and large predaceous ants such as *Pachycondyla impressa* (Roger).

Small detritivorous/guanophagous invertebrates include the generalist armadillids and tineids, as well as acarians, entomobryid collembolans (which concentrate in frugivorous bat guano), diplurans and symphylans (concentrated in soil with roots), and more specialized guano-associated cavernicoles such as cydnids and *Trichorhina* isopods in frugivorous bat guano and *Acherontides* collembolans, phorids, milichiids, and drosophilids in haematophagous bat guano. These organisms probably are preyed on by chernetids, predaceous acarians, beetles such as histerids, carabids, and pselaphines (specialized on acarians), and possibly ants, such as *Solenopsis.*

Flying prey, such as dipterans (psychodids, chironomids), histerids, and tineids are food for web spiders such as *Blechroscelis* sp. and *T. rufipes* (observed preying on histerids). Prey for *Loxosceles* spiders include beetles, young crickets, and cockroaches.

FAUNISTIC COMPARISON BETWEEN KARST AREAS

From Table 1, it is clear that at least at the family and generic levels, there is no greater faunistic similarity between the Ribeira Valley and Rio Pardo area in the Atlantic rain forest, than between the later and other karst areas of Bahia state in the Caatinga domain. As well, comparison to data from the literature indicates that there is no greater similarity between the two karst areas in the Atlantic Forest than between any of these areas and those in the Cerrado, Caatinga, and Amazonian rain forest (Trajano & Gnaspini-Netto 1991a, Gnaspini & Trajano 1994). Almost all cave taxa shared by caves in the Atlantic Forest are shared also with other karst areas and correspond to widely distributed groups.

A close examination even points to a lower faunistic similarity between Rio Pardo and the Ribeira Valley than between Rio Pardo and other typically tropical Brazilian karst areas. On one hand, only *Acherontides* collembolans and goniosomatinae opilionds are typical of caves situated in the Atlantic rain forest. On the other, several taxa such as *Lasiodora* and *T. rufipes* spiders, amblypygids, armadillid isopods, pselliophorid chilopods, blattarians, nasutiterminae termites, histerid beetles, drosophilid flies, and ants found in the Rio Pardo karst area are rare or absent in the Ribeira Valley caves but relatively frequent in Brazilian tropical caves in general.

At the level of the present analysis, the main factor influencing cave fauna composition seems to be the latitudinal distribution of epigean faunas, independent of present-day phytogeographic domains where the caves are located. Apparently, the Atlantic rain forest cave communities do not constitute a faunistic unity distinct from Cerrado or Caatinga cave faunas. Therefore, there is no "Atlantic Forest cave fauna," but rather there is a set of cave faunas from areas situated in the Atlantic Forest realm.

SPECIAL CONSERVATION PROBLEMS: A CASE FOR PROTECTING THE ATLANTIC FOREST CAVE ECOSYSTEMS

Subterranean ecosystems pose special problems for conservation due to their intrinsic fragility and distinctive features of hypogean communities, including a high degree of endemism and morphological, ecological, and behavioral differentiation among troglobites (Culver 1986).

Their fragility is a consequence of the relatively low biological diversity of subterranean ecosystems, their general dependence on nutrients imported from the surface, and the susceptibility of cavernicoles, specially troglobites, to climatic fluctuations, because these animals have evolved in a relatively stable environment. Hence, these ecosystems are influenced strongly by environmental changes in the epigean habitat. Many troglobites have small geographic ranges and low population densities, resulting in small population sizes; frequently, they present a K-selected life history, probably an adaptation to food scarcity. Consequently, their population turnover is very slow and their ability to recover from population losses is decreased compared to epigean taxa. Therefore, these animals generally meet quite well the criteria to receive vulnerable species status.

Unusual features of subterranean faunas also may include the occurrence of morphologically variable populations, with cases of clinal variation related to their distance from the epigean environment; peculiar trophic relationships (*e.g.,* dependence on unusual energy sources such as vertebrate guano and sulfur bacteria); faunal zonation and stratification; cases of exceptionally high population densities of some animals such as bats and collembolans; and occurrence of distributional and phylogenetic relicts. Thus, cave faunas as a whole also meet almost every standard for the establishment of ecosystem conservation policies. The extensively studied Ribeira Valley harbors a large number of endemic and highly differentiated species represented by terrestrial and aquatic troglobites, and their cave communities are composed of a particular set of interacting taxa not found elsewhere.

It is widely recognized that the Atlantic rain forest is one of the most threatened ecosystems in the world due to the accelerated rate of deforestation (Mori *et al.* 1981). In karst areas, other important threats superpose deforestation (Culver 1986, Notenboom *et al.* 1994): limestone quarrying eliminates entire cave systems; pollution from mining and other sources rapidly spreads into the subterranean aquifers due to their limited filter capacity. Even localized disturbance, such as deforestation of small areas for building or agricultural practices, or pollution of a single stream by domestic sewage, may result in rapid extinction of endemic species. As well, human visitation may have an important impact on the fauna due to: topoclimatic changes caused, for instance, by hot light sources and the opening of artificial cave passages during cave exploration and management; introduction of alien epigean organisms and organic matter in general; soil compacting of sediment banks, the easiest pathways inside caves; and direct disturbance and trampling of cavernicoles. Overcollection, easily achieved in view of the small population sizes of cavernicoles, is another not negligible threat.

Most of the karst area in the Ribeira Valley, São Paulo state, is encompassed by conservation units, including three state parks, which at least in theory, would guarantee protection to the majority of the main cave systems of this speleological province: the Parque Estadual Turístico do Alto Ribeira (PETAR; *e.g.*, Santana-Pérolas, Alambari, and Areias Cave systems), comprising most of the Betari and Iporanga River basins, tributaries of the upper Ribeira left margin; the Parque Estadual de Jacupiranga (Tapagem Cave system), situated downstream at the Ribeira right margin; and the recently declared Parque Estadual Intervales, formerly an environmental protection area, which includes the highest karst area at the Ribeira left margin contiguous to the PETAR.

Although decreed in 1958, the PETAR was demarked and regulated only recently; however, the park management plan and zoning regulations still are incomplete, leaving fragile cave ecosystems unprotected against increasingly heavy tourist visitation. Moreover, the protection of a few areas already warranted by law (as is the case with the Areias system in which visitation is prohibited) is enforced poorly due to lack of supervision and failure to educate the local inhabitants who guide unauthorized people to restricted areas (this is a general problem in Brazilian karst areas). Presently, the main threats to the subterranean ecosystems of the PETAR are intense and poorly controlled visitation (including tourism and caving activities), especially in the Betari Valley.

During the 1970s and the beginning of the 1980s when tourism in the PETAR was not as intense and supervision was precarious, mining activities producing water pollution, deforestation (fortunately limited due to the rugged landscape), overcollection, and other disturbances by cavers, resulted in deleterious impacts on the subterranean communities. Although the paucity of previous studies hampers an objective and extended analysis of the consequences, there is strong evidence pointing to real damage to at least some troglobitic populations currently considered as threatened. That is the case with the blind catfish *P. kronei*, with two sets of populations (possibly two separate species) found at opposite margins of the Betari River (Trajano 1997). The populations from the Alambari system, at the left margin, practically disappeared during the 1980s, possibly due to pollution caused by mining activities upstream from the cave system. The most conspicuous population, from the Areias de Cima Cave at the Betari right margin, was subject to a sharp decline due to overcollection by amateurs during the 1970s. This impact was detected in a population study carried out ten years later, by direct observation and estimation of population densities, and also by comparing the distributions of fish sizes before (Pavan 1945) and after the collection events (Trajano & Britski 1992). As expected from life cycle data (Trajano 1991), it took 10–15 years (the estimated mean longevity) for this population to begin recovering from that loss. This represents the best Brazilian example of using hard population data to evaluate the impact on a cave species.

Mining pollution and touristic disturbance also are probable causes of the pronounced population decline of *Aegla microphthalma* Bond-Buckup & Buckup, the most specialized troglobitic aeglid crustacean, found exclusively in Santana Cave. Relatively abundant during the 1970s, these crustaceans have become very rare in the 1990s (Moracchioli 1994).

The terrestrial fauna also is affected by visitation. For instance, *Goniosoma* opilionids, forming large and exposed populations at cave entrances, are disturbed greatly by human passage; these animals are food for cavernicoles such as *Ctenus* spiders, *Zelurus* heteropterans, and the trogloxene marsupial *Philander opossun* (Linnaeus) (Gnaspini-Netto 1996), and a decrease in their populations has predictable consequences for entire communities.

Direct human impact has begun to be a problem in the Intervales region. Since the 1980s, the Intervales area, which is one of the most pristine areas in the Ribeira Valley, has been administrated by the Fundação Florestal de São Paulo, a state foundation that developed a model program of tourist visitation. The consequences of increasing visitation, however, are noticeable already: in Paiva Cave, an important cave harboring many troglobitic species, most soil animals have disappeared from the visited sectors, probably due to trampling.

The exhaustion of many limestone outcrops in the Ribeira Valley attracted the exploiter's attention to undisturbed areas such as Intervales. Currently, a main threat to the area is a project to install a limestone mine and a cement plant just outside the border of Parque Estadual Intervales. The actual extent of the consequences of such enterprises on the subterranean ecosystems situated within and around the park area still are unclear, but certainly not negligible; at least one troglomorphic isopod species (*Alboscia* sp.; L. Souza-Kury, pers. comm.) is found exclusively at one cave that will be affected by the project.

For centuries, the Ilhéus region, southern Bahia, where the Rio Pardo karst area is situated, has been a major area of cocoa plantation, for which the farmers traditionally use "cabrucas" (*i.e.,* areas of native forest in which part of the understory is cut to cultivate the umbrophilous cocoa trees). This marginally invasive agricultural practice contributed greatly to the preservation of the Atlantic Forest in the area. The current depreciation of Brazilian cocoa on the international market, however, is leading many local farmers to change to cattle raising as a viable economic option, and with it, the consequent deforestation for the establishment of pastures represents a major ecological disaster to this otherwise preserved area. Cave ecosystem threats include epigean deforestation and control of haematophagous bats, the guano of which is a major food source for cavernicoles in the area.

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