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Epigean and subterranean ichthyofauna from the São Domingos karst area, Upper Tocantins River basin, Central Brazil

M. E. Bichuette and E. Trajano*

Departamento de Zoologia, Instituto de Biociências da USP, Caixa Postal 11.461, 05422-970, São Paulo, SP, Brazil

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In a survey of epigean and cave streams in the São Domingos karst area, 38 species were present in the stream reaches, including 10 characiforms, 19 siluriforms, seven gymnotiforms and two perciforms. One species of *Astyanax* and the new armoured catfish species *Parotocinclus* were the most common epigean fishes in São Domingos. The most conspicuous non-troglomorphic cave fishes were *Hoplerythrinus unitaeniatus*, *Astyanax* sp., *Brycon* sp. and two species of *Imparfinis*, with *I. hollandi* being the most common fish in most caves. São Domingos karst area has the most diverse and abundant Brazilian cavefish fauna, not only in terms of troglobitic species but also in general fish richness, with 22 non-troglomorphic species recorded in caves in addition to five troglobitic ones. Most fishes examined for stomach contents had at least partially full stomachs. The studied fishes were carnivorous, feeding primarily on aquatic insects. Fishes with developed gonads recorded in caves were *I. hollandi*, *Rhamdia quelen*, *Pseudocetopsis plumbeus*, *Hoplerythrinus unitaeniatus* and *Cichlasoma araguaiensis*, indicating a potential for reproduction in the subterranean habitat.

Key words: central Brazil; distribution; epigean ichthyofauna; feeding habits; subterranean ichthyofauna.

INTRODUCTION

Fishes are important and conspicuous components of aquatic subterranean communities, representing the highest level of predators in many caves, together with decapod crustaceans. The ecological conditions characterizing the subterranean environment, especially those associated with permanent darkness (*e.g.* absence of photoperiods, lack of visual cues and of photoautotrophic organisms and food scarcity) pose limitations to the taxa able to colonize this habitat. Among fishes, the highest potential for hypogean life is shown by nocturnal, generalist carnivores such as many siluriforms.

Fish species richness and abundance in the subterranean biotope are highly variable and dependent on ecological and historical factors, including distribution of the epigean (surface) fish fauna, both present and past, and potential for

*Author to whom correspondence should be addressed. Tel.: +55 11 30917620; fax: +55 11 30917513; email: etrajano@usp.br

adoption of cave life (Dearolf, 1956; Poly & Boucher, 1996; Trajano, 2001*a*). The representation of fishes in caves ranges from accidentally isolated individuals to fish communities composed of several species and of considerable population densities. Organisms regularly found in the subterranean environment, showing a close association with this habitat, may be classified as (1) trogloxenes, which must return periodically to the surface to complete their life cycle, usually because food or other ecological requirements of the species are not fulfilled in the subterranean habitat; (2) troglophiles, able to complete their life cycle both in hypogean and in epigean habitats; (3) troglobites, exclusively subterranean species usually characterized by autapomorphies related to the subterranean life, such as reduction of eyes and pigmentation (Holsinger & Culver, 1988). In addition, some organisms represent transient occurrences in the subterranean habitat, entering caves by accident or in search of a protected, mild environment, not being able to efficiently orient themselves or to establish viable subterranean populations.

This is a meaningful biological classification, but its practical application may be difficult due to the lack of distributional and ecological data for many subterranean taxa. Troglobites in general may be recognized by the presence of those autapomorphic character states which can be related to the subterranean life (troglomorphisms), especially reduction of eyes and pigmentation when compared to their epigean relatives. Distinction between the troglophilic and trogloxenic condition may be more difficult because it requires a knowledge of biology and population dynamics on a case by case basis (Poly & Boucher, 1996). Moreover, the same species may form trogloxene populations in some caves and troglophilic populations in others, depending on food availability in each of these sites. Therefore, as a first approach troglomorphic (probably troglobitic) *v.* non-troglomorphic fishes were considered in the present study.

Understandably, the majority of papers dealing with subterranean fishes have focused on troglobitic species (Romero, 2001). Some species have been investigated in great detail, such as the Mexican tetra characins, genus *Astyanax*, the North American amblyopsids and several Brazilian catfishes. Such studies, focusing on, for example ecology, behaviour, physiology, morphology, genetics, molecular biology and systematics, resulted in many publications. On the other hand, just a few papers have dealt with non-troglomorphic subterranean fishes, and even fewer have used a community approach (Poly & Boucher, 1996).

The relevance of studies on non-troglobitic fishes has been stressed by Poly & Boucher (1996), Poly (2001) and Trajano (2001*a*). First, these are also hypogean fishes, subject to the same ecological constraints as troglobites. In addition, they may coexist and interact with troglobitic fishes, as predators, prey, competitors or simply sharing space. Finally, they illustrate the kind of fish community, originating from troglobitic species, that can be isolated in the subterranean habitat (Dearolf, 1956).

Brazil has a diverse and abundant subterranean ichthyofauna, including at least 18 troglomorphic species occurring in different karst areas throughout the country (Trajano, 1997; unpubl. data). In this aspect, it compares to Mexico, the Caribbean, China and south-east Asia (Weber *et al.*, 1998). As in many other countries, there are sparse records of non-troglomorphic fishes in caves, but few areas have been systematically surveyed for the whole cavefish fauna.

Among Brazilian karst areas, the São Domingos region, State of Goiás, central Brazil, is distinguished by its subterranean ichthyofauna, particularly rich in both troglomorphic and non-troglomorphic species. The aims of the present study were to investigate the ichthyofauna of both epigean and cave streams in the São Domingos karst area, including fish distribution, habitats and relative abundance, and in addition feeding and reproduction of non-troglomorphic fishes found in caves. A comparison between epigean and cave communities allows some inferences about the constraints on the colonization of the subterranean habitat by fishes.

MATERIALS AND METHODS

STUDY SITE

The study area was situated within the limits of the Terra Ronca State Park (46°10′–46°30′ S; 13°30′–13°50′ W), in São Domingos County, eastern State of Goiás, central Brazil, and lies in the Cerrado (the savannah-like Brazilian vegetation) phytogeographical domain. The study area is characterized by a tropical semi-humid climate with four to five dry months per year (Nimer, 1989). São Domingos is a carbonate karst area characterized by the presence of continuous limestone outcrops belonging to the Bambuí Formation. The São Domingos karst area is crossed by several parallel streams running westwards to join the Paranã River, a tributary of the Upper Tocantins River, in the Amazonas Basin. Characteristically, after an epigean reach, each major stream and some of their tributaries enter a cave through a sinkhole, pass hundreds to thousands of metres through subterranean conduits, and surface through a resurgence (Fig. 1). These are typical headwater streams, with transparent and well-oxygenated waters, and rocky bottoms with gravel, pebbles and boulders; reaches with moderate to strong or very strong currents alternate with deep pools with rocky or soft bottoms (mostly in caves). During the rainy period (October to March), floods may render some caves partially or totally inaccessible. Even in the peak of the dry season, however, there is a considerable water volume in the epigean and subterranean drainage. Due to the high carrying capacity of these streams and the fact that the caves in the area represent stream sinkholes, great amounts of organic matter, basically vegetal debris and associated fauna, accumulate inside these caves. Therefore, caves from São Domingos are in general characterized by a high food availability of aquatic organisms.

The following epigean and cave localities were surveyed (Fig. 1): epigean reaches, from north to south, Rio Angélica, upstream of its sinkhole into the homonymous cave and downstream of its confluence Rio Bezerra; Rio Bezerra, downstream of its sinkhole; Rio São Vicente, downstream of its resurgence and at the confluence with Rio Angélica; Córrego Quilombo (tributary of São Vicente); Rio Passa Três (tributary of Rio São Vicente), upstream of its sinkhole into the homonymous cave; Rio São Mateus, upstream of the sinkhole into the homonymous cave and downstream of its resurgence, including two tributaries, São João stream and Grota do Cascudo; Rio da Lapa, upstream of the sinkhole into Terra Ronca Cave (referred as Lap 1), and an epigean reach in a karst window situated 800 m from the sinkhole (referred as Lap 2); Rio São Bernardo, upstream of its sinkhole into the homonymous cave.

Caves (in parenthesis, total cave length, including dry galleries, and approximate cave stream length): Lapa do Angélica (14 100 and 7150 m); Lapa do Bezerra (8250 and 3800 m); Lapa do São Vicente I (10 130 and 8900 m); Lapa do São Vicente II (4670 and 1200 m); Passa Três conduit (2100 and 800 m); Lapa do São Mateus III (10 828 and 6150 m); Lapa da Terra Ronca (750 and 500 m); Lapa do São Bernardo-Palmeiras (3500 and 1100 m). The largest difference in stream size was observed for the Passa Três stream, which was conspicuously smaller than the other studied streams in the São Domingos karst area.

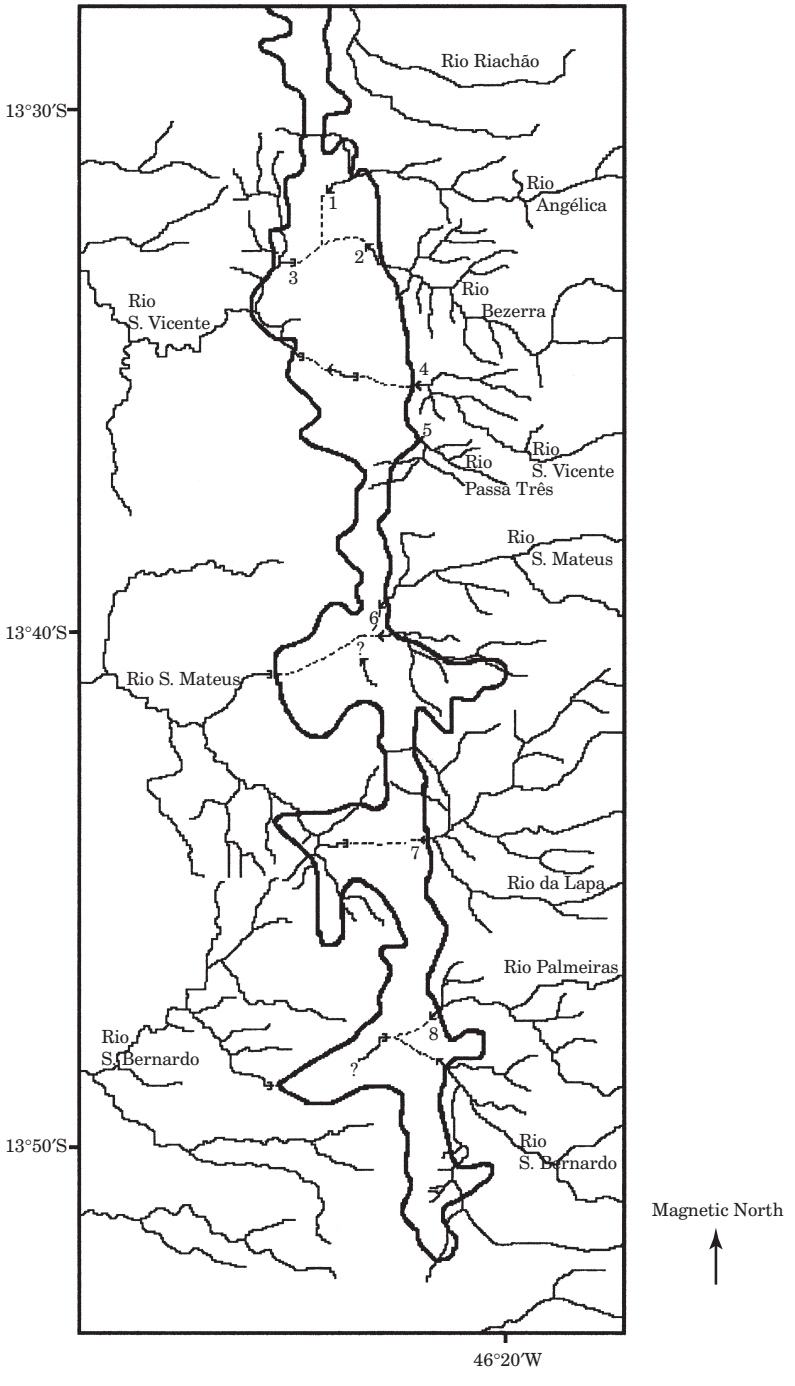

FIG. 1. Map (1 : 100 000) of the Terra Ronca State Park, São Domingos karst area, State of Goiás, central Brazil, showing epigean stream reaches and cave entrances locations (modified from Karmann *et al*., 1984). 1, Angélica Cave; 2, Bezerra Cave; 3, Angélica-Bezerra resurgence; 4, São Vicente system; 5, Passa Três Cave; 6, São Mateus system; 7, Terra Ronca Cave; 8, São Bernardo system; ↘, sinkhole; ⊣, resurgence; **?**, speleological situation not defined; ◢, limestone boundaries.

FISH COLLECTIONS

Ten-day field trips were carried out during the dry seasons from 1999 until 2001, in April, May, July, August and September, totalling eight field trips during the study period. For collections in the epigean streams, different methods were used, including electrofishing, block nets, traps and hand-netting during snorkelling; some records were based only on direct observations during snorkelling. In caves hand-nets were used. A rough estimation of relative abundance was based on the total number of individuals of each species that were captured: very common (>100 individuals), common (50–100), moderate (15–50) and rare (one−15). The fishes were killed by over-anaesthesia in a benzocaine solution, and fixed *in loco* in 10% formalin solution. All fish identifications were confirmed by specialists of the Seção de Peixes (Fish Section) of the Museu de Zoologia da Universidade de São Paulo.

For comparative purposes, environmental variables (water temperature, pH, conductivity, dissolved oxygen and salinity) were measured at least once in each locality with a digital HORIBA apparatus. Measurements in epigean reaches were always made during the morning.

Diet of non-troglomorphic fishes collected in caves was determined through analysis of stomach contents, and expressed as frequency of occurrence and percentage composition of food items (Hynes, 1950; Windell & Bowen, 1978). Reproductive condition based on macroscopic examination of gonads was categorized broadly as: mature (well-developed gonads allowing sex recognition, usually reaching the lateral–ventral body cavity) *v*. non-mature (small gonad and sex not recognizable).

RESULTS

FISH DIVERSITY, DISTRIBUTION AND HABITAT

Water variables were within that expected for a karst drainage (Culver, 1982) (Table I). Waters of epigean stream reaches tended to be lower in pH and conductivity and had a slightly larger range of temperatures than from inside caves. Dissolved oxygen values did not differ between epigean and hypogean reaches with rapids, tending to be higher in larger, swifter streams. The small Passa Três stream was characterized by the lowest temperatures, relatively high pH and conductivity, and salinity above zero both in the hypogean and in the shaded epigean reach upstream of the cave. Phreatic tributaries (travertine basins and side pools) also had salinities >0, and lower values of dissolved oxygen and higher pH and conductivity than in the main cavestreams.

Fish species and their estimated abundance in epigean and cave streams of São Domingos karst area are shown in Table II. Terra Ronca Cave was not included in the table because no fishes were collected in the aphotic zone. A high number of species was present in the studied stream reaches, with 38 species recorded, including 10 characiforms, 19 siluriforms, seven gymnotiforms and two perciforms.

Not surprising for neotropical headwater streams, the ichthyofauna from São Domingos karst area, studied in detail for the first time, included several undescribed and undetermined species. In most cases, for genera such as *Astyanax*, *Brycon* and *Hypostomus*, the taxonomy was unclear and in much need of a broad revision. Species referred to as sp. 1, sp. 2, *etc*. within a given genus correspond to different morphological forms.

The cave ichthyofauna was not just a subsample of the epigean one; it contained several elements which had not been recorded in surface stream

TABLE I. Physico-chemical water variables measured in epigean and cave streams from São Domingos karst area, State of Goiás, central Brazil

Localities, north to south	Date	pH	Conductivity ($ms\,cm^{-1}$)	Dissolved oxygen ($mg\,l^{-1}$)	Temperature (° C);	Salinity
Epigean rivers						
Angélica	May 1999; July 2000; April 2001	7·1; 7·8; 6·9	0·07; 0·01; 0·08	8·6; 8·5; 6·6	24·0; 23·3; 25·3	0; 0; 0
Bezerra	July 2000	5·6	0·06	8·5	22·6	0
São Vicente	May 1999	4·3	0·01	8·3	25·5	0
Passa Três	May 1999; July 2000; April 2001	7·8; 8·2; 7·9	0·31; 0·32; 0·32	8·4; 7·5; 6·4	18·7; 20·8; 21·8	0·01; 0·01; 0·01
Grota do Cascudo	July 2000	7·4	0. 44	6·0	23·6	0
São João	July 2000	5·6	0. 02	6·7	24·5	0
São Mateus	July 2000	5·5	0. 01	7·7	23·1	0
Rio da Lapa (=Terra Ronca)	July 2000	5·4	0. 04	8·1	25·0	0
São Bernardo	May 1999	5·6	0·01	8·0	24·8	0
Caves						
Angélica	May 1999	7·8	0·01	8·5	23·3	0
Bezerra	July 2000	7·2	0·104	8·1	22·0	0
São Vicente II	July 1999; July 2000; April 2001	6·7; 7·8; 6·9	0·02; 0,03; 0·02	8·2; 7·4; 6·9	23·2; 23·4; 24·8	0; 0; 0
Passa Três	May 1999; July 2000; April 2001	7·7; 8·3; 7·9	0·33; 0·33; 0,31	8·9; 6·9; 7·9	19·1; 19·3; 21·7	0·01; 0·01; 0
São Mateus III (main stream)	May 1999	6·8	0·03	9·2	22·0	0
São Mateus III (travertines)	May 1999	7·7	0·71	7·7	24·8	0·03
São Bernardo-Palmeiras (main stream)	May 1999; July 2000; August 2001	6·4; 7·4; 7·4	0·01; 0·02; 0,02	8·7; 7·9; 7·8	23·6; 24·5; 22·8	0; 0; 0
São Bernardo-Palmeiras (small tributary)	May 1999; July 2000; August 2001	6·8–7·5; 7·3	0·35; 0·37; 0,37	5·1; 4·7; 5·4	23·1; 23·0; 22·5	0·01; 0·01; 0·01

TABLE II. Fish species recorded in epigean and cave streams of the São Domingos karst area, Upper Tocantins River Basin. Ang, Rio Angélica, upstream of sinkhole; Bez, Rio Bezerra, upstream of sinkhole; AB, Rio Angélica-Bezerra, downstream of Angélica-Bezerra confluence; Quil, Córrego Quilombo; SVic, Rio São Vicente, downstream of resurgence; PasTr, Rio Passa Três, upstream of sinkhole; Casc, Grota do Cascudo; SJo, Rio São João; SMat1, Rio São Mateus upstream of sinkhole; SMat2, Rio São Mateus, downstream of resurgence; Lap1, Rio da Lapa, upstream of sinkhole; Lap2, Rio da Lapa, karst window; SBern, Rio São Bernardo, upstream of sinkhole; LAng, Lapa do Angélica; LBez, Lapa do Bezerra; LSVicI, Lapa do São Vicente I; LSVicII, Lapa do São Vicente II; LPasTr, Lapa do Passa Três; LSMatIII, Lapa do São Mateus III; LSBern, Lapa do São Bernardo-Palmeiras. *, troglomorphic cave species; +, rare (one−15 individuals collected or observed); ++, moderate (15–50 individuals); +++, common (50–100 individuals); ++++, very common (>100 individuals). In parenthesis, the maximum distance from the nearest cave entrance (sinkhole or resurgence) where each non-troglomorphic species was recorded

	Epigean localities												
Taxa	Ang	Bez	AB	Quil	SVic	PasTr	Casc	SJo	SMat1	SMat2	Lap1	Lap2	SBern
CHARACIFORMES													
HEMIODONTIDAE													
Apareiodon sp.					+							+	
ERYTHRINIDAE													
Hoplerythrinus unitaeniatus								+	+				
CRENUCHIDAE													
Characidium sp.	+										+		+
CHARACIDAE													
Astyanax sp. 1	+++	+	+			++	++	++	+				+
						++	++						
Astyanax sp. 2													+
Bryconamericus sp.	+				+					+			
Brycon undescribed sp.											+	+	
Creagrutus sp.											+	+	
Mylesinus sp.										+			

SILURIFORMES										
CETOPSIDAE										
Pseudocetopsis plumbeus		+						+		
HEPTAPTERIDAE										
Cetopsorhamdia molinae			+							+
Phenacorhamdia tenebrosa	+		+		+	+		+		+
Imparfinis hollandi								+	+	
CALLICHTHYIDAE										
Aspidoras poecilus	+			+	+			+	+	
LORICARIIDAE										
Harttia sp.					+		+			
Spatuloricaria sp.							+			
Parotocinclus			++		+++		++	++	++	
undescribed sp.								++		
Cochliodon sp.							+			
Hypostomus emarginatus							+			
Hypostomus sp. 1							++			
Hypostomus sp. 2			+		++		+	+		
Ancistrus sp.	++	++	+	+				++	+	+
GYMNOTIFORMES										
STERNOPYGIDAE										
Eigenmannia trilineata								+		
APTERONOTIDAE										
Sternarchorhynchus curvirostris			+							

TABLE II. Continued overleaf

Taxa	Epigean localities												
	Ang	Bez	AB	Quil	SVic	PasTr	Casc	SJo	SMat1	SMat2	Lap1	Lap2	SBern
PERCIFORMES													
CICHLIDAE													
Retroculus lapidifer										+			

Taxa	Subterranean localitites						
	LAng	LBez	LSVicI	LSVicII	LPasTr	LSMatIII	LSBern
CHARACIFORMES							
ERYTHRINIDAE							
Hoplerythrinus unitaeniatus	+ (1500 m)				+ (400 m)		
CRENUCHIDAE							
Characidium sp.	+ (300 m)						
CHARACIDAE							
Astyanax sp. 1					++ (100 m)		+ (400 m)
Brycon sp.						+	
Creagrutus sp.							+ (400 m)
SILURIFORMES							
CETOPSIDAE							
Pseudocetopsis plumbeus		+ (300 m)	+ (1500 m)				
HEPTAPTERIDAE							
Cetopsorhamdia molinae	+ (1500 m)	+					
Phenacorhamdia tenebrosa	+ (200 m)						

Imparfinis minutus						+	
I. hollandi	++ (1500 m)						+ (600 m)
Rhamdia quelen	+ (1200 m)						
Pimelodella undescribed sp.*							+++ (400 m)
TRICHOMYCTERIDAE							
*Ituglanis passensis**					+++		
Ituglanis sp. 1*	+++						
Ituglanis sp. 2*						+	+
Ituglanis sp. 3*							
CALLICHTHYIDAE							
Aspidoras poecilus	+ (300 m)						
LORICARIIDAE							
Spatuloricaria sp.				+ (800 m)			+ (600 m)
Hypostomus sp. 2							+ (600 m)
Ancistrus sp.	+ (100 m)						
*A. cryptophthalmus**	+++	++	++		++		
GYMNOTIFORMES							
Sternopygidae							
Archolaemus blax				+ (900 m)			+ (700 m)
*Eigenmannia vicentespelaea**			++	++			
E. trilineata	+ (1200 m)					+	
Sternopygus sp.	+ (1200 m)			+ (500 m)			
APTERONOTIDAE							
Apteronotus albifrons	+					+	

TABLE II. Continued overleaf

Taxa	Subterranean localities						
	LAng	LBez	LSVicI	LSVicII	LPasTr	LSMatIII	LSBern
Sternarchorhynchus curvirostris	+			+ (500 m)		+	
Porotergus ellisi				+ (500 m)		+	
PERCIFORMES							
CICHLIDAE							
Cichlasoma araguaiensis	+ (1500 m)						

reaches. These characteristic elements included troglomorphic and non-troglomorphic species. The latter, including the Heptapteridae (Bockmann & Guazzelli, 2003), *Imparfinis minutus* (Lütken) and most gymnotiforms recorded [*Archolaemus blax* Korringa, *Sternopygus* sp., *Porotergus ellisi* Arámburu and *Apteronotus albifrons* (L.)], are known from other epigean localities (Santos *et al*., 1984). It is noteworthy that the new *Pimelodella* and trichomycterids species, that include four out of the seven troglomorphic cave species in São Domingos, were not recorded in epigean streams of this area. This indicates that the cave populations are indeed isolated in this habitat, corroborating their status as troglobites. On the other hand, no physical barrier exists between epigean populations of *Ancistrus* sp. and populations of *Ancistrus cryptophthalmus* Reis, from Angélica, Bezerra and São Vicente I caves, which are currently parapatric.

Astyanax sp.1 and an undescribed species of *Parotocinclus* were among the most common epigean fishes in São Domingos karst area. On the other hand, *I. minutus*, *Rhamdia quelen* (Quoy & Gaimard) and *A. blax* were rare occurrences in this area. In caves, the troglomorphic species, especially *A. cryptophthalmus* (Trajano, 2001*b*), had the highest population densities. The most conspicuous non-troglomorphic cave fishes were *Hoplerythrinus unitaeniatus* (Spix), *Astyanax* sp. 1, *Brycon* sp. and *Imparfinis* spp.

In the studied area, troglobitic species occurred in two kinds of habitat: riffles with rocky substrata (pebbles, boulders and rocky walls) and swift, well-oxygenated water and slow-moving, soft-bottomed water pools. *Ancistrus cryptophthalmus* had a strong preference for the first type; it was found in large (Angélica Cave) to small (Passa Três Cave) streams (Trajano, 2001*b*). The recently described trichomycterid *Ituglanis passensis* Fernández & Bichuette (2002) was syntopic with *A. cryptophthalmus* in Passa Três Cave, occurring in shallow riffles with moderate water current and rocky and gravelled bottoms, in addition to pools in a small tributary with boulders and silt bottoms. In Angélica Cave, the undescribed troglomorphic trichomycterid, genus *Ituglanis* (M.E. Bichuette, unpubl. data) was found in a tributary of the main stream where there were deep pools alternating with short stretches of the free flowing stream with a silt and clay bottom. Hydrological evidence indicates that this tributary was formed by ground water possibly derived from the epikarst that could encompass the habitats occupied by two other troglobitic trichomycterids, also belonging to the genus *Ituglanis*, from São Mateus III Cave (rimstone dams fed from the ceiling) and São Bernardo-Palmeiras Cave (side pool fed by a small water inlet) respectively.

Most non-troglomorphic fishes recorded in caves were found deep into the aphotic zone, up to distances of several hundred metres from the nearest known entrance (either the sinkhole or the resurgence) (Table II). The heptapterid catfish, *Imparfinis hollandi* Haseman, was the commonest non-troglomorphic fish in caves from São Domingos karst area. This catfish species was consistently found during fieldwork, especially in Angélica Cave, where they have been observed up to 1500 m from the cave entrance. Some catfish of the same size (possibly the same individuals) were spotted several times at the same sites far from any cave entrance, within periods of $\geq$6 months, indicating a medium-term residence in the subterranean habitat. The persistence of this species in

TABLE III. Food items expressed as frequencies of occurrence/percentage composition, for several non-troglomorphic fish species from the São Domingos karst area, central Brazil. Cave, collected in subterranean stream reaches; epigean, collected in epigean stream reaches; *n*, number of stomachs; L_S, standard length; I, immature; A, adult; N, nymph; L, larvae

	H. unitaeniatus, $n = 18$ 134·0-220·0 mm L_S (range), cave	*Characidium* sp., $n = 2$; 54·4 and 56·7 mm L_S, cave	*Astyanax* sp., $n = 2$; 50·0 and 63·5 mm L_S, cave	*P. plumbeus*, $n = 2$; 58·0 and 68·4 mm L_S, cave	*C. molinae*, $n = 7$; 39·6-79·6mm L_S (range), cave	*C. molinae*, $n = 13$; 35·3-59·4 mm L_S (range), epigean	*I. hollandi*, $n = 12$; 77·8-175·4 L_S (range), cave	*I. hollandi*, $n = 4$; 34·8-86·4 mm L_S (range), epigean	*Rhamdia quelen*, $n = 1$; 166·4 mm L_S, cave	*Sternopygus* sp., $n = 2$; 295·1 and 177·3 mm L_S, cave	*S. curvirostris*, $n = 2$; 116·2 and 147·1 mm L_S (range), cave	*Porotergus ellisi*, $n = 1$; 101·1 mm L_S, cave
Nematoda			1/11·1									
Diplopoda	2/14·3											
Arthropoda (not Insecta)							1/3·6					
Insecta	3/21·4		1/11·1		1/10·0	4/23·5	2/7·1	1/16·7	1/25·0	1/9·1		
Insecta I		2/18·2	1/11·1		1/10·0							
Insecta A				1/33·3			2/7·1					
Collembola								1/16·7				
Ephemeroptera N						1/5·9	1/3·6					
Plecoptera N		1/9·1			1/10·0	1/5·9			1/25·0			
Heteroptera Naucoridae							2/7·1					

Neuroptera L					1/10·0								
Coleoptera L		1/9·1											1/25·0
Coleoptera A		1/9·1	1/11·1										
Elmidae L							1/3·6			2/18·2	2/28·4		
Elmidae A							1/3·6	1/16·7		1/9·1	1/14·2		
Dytiscidae A										2/18·2			
Diptera I	2/14·3	2/18·2		1/33·3	2/20·0	1/5·9	3/10·7			2/18·2	1/14·2	1/25·0	
Diptera A			1/11·1	1/33·3									
Chironomidae I		1/9·1			1/10·0	4/23·5	1/3·6		1/25·0		1/14·2		
Simuliidae I						2/11·8	2/7·1		1/25·0		1/14·2		
Trichoptera I		2/18·2	1/11·1		1/10·0	2/11·8	5/17·8	2/33·3		2/18·2		1/25·0	
Lepidoptera						1/5·9							
Nymphiilinae L													
Fish scales			1/11·1										
Animal	3/21·4		1/11·1				3/10·7				1/14·2		
(undetermined).													
Vegetal fragments	1/7·2		1/11·1			1/5·9				1/9·1		1/25·0	
Sand	3/21·4	1/9·1			2/20·0		4/14·3	1/16·7					

Angélica Cave was confirmed by collections made by speleologists 8 years ago. *Imparfinis hollandi* was poorly sampled with electrofishing in epigean streams. These catfish, however, were frequently observed during snorkelling near the sinkhole of Terra Ronca Cave, and were seen to become active at dusk.

The presence of many specimens of the erythrinid, *H. unitaeniatus*, and of tetra characins, *Astyanax* sp., in Passa Três Cave was noteworthy. For about 15 adult individuals of *H. unitaeniatus* were estimated to live in the horizontal conduit downstream of the 5 m high waterfall located 100 m from the cave entrance (stream sinkhole). Specimens of *H. unitaeniatus* were also frequently observed in Angélica Cave. These ambush predators were usually observed in deep, slow-moving water pools but, in Passa Três Cave, they sometimes entered the shallower parts where the troglobitic catfishes, *A. cryptophthalmus* and *I. passensis*, were found. On occasion, erythrinids were observed chasing and occasionally eating dislodged armoured catfishes that entered a pool. Tetra characins were common in the epigean reach upstream of the cave entrance, and large groups were also observed inside the cave upstream of the waterfall. One individual had one of the eyes reduced by half compared with the other eye (R. Borowsky, unpubl. obs.). These tetra fishes seem to be in the cave as accidentals because such groups were always found not far from the cave sinkhole (up to 100 m; Table II), being apparently unable to effectively explore the stream reach downstream of the waterfall. One isolated unpigmented adult specimen, however, was found downstream of the waterfall in the late 1980s (Trajano & Souza, 1994).

An interesting occurrence was the presence of a group of six adult specimens of *Brycon* sp. living in São Mateus III Cave for a long time. Individuals of this species were first noticed in 1980 (R.H. dos Santos, unpubl. obs.). This group was always seen in the same cave site and it was accustomed to the presence of humans. During a visit to this site, the fish approached the light sources and kept swimming nearby; on this occasion, they were observed feeding on crickets that fell onto the water surface.

Most non-troglomorphic fishes captured in caves from São Domingos karst area were in good physical condition, apparently healthy and well-fed, and none showed malformations or other unusual morphological features.

FEEDING AND REPRODUCTION

Food items identified for several non-troglomorphic fish species (four siluriforms, three gymnotiforms and three characiforms), expressed as frequencies of occurrence and percentage compositions, are shown in Table III. The two examined specimens of the cichlid *Cichlasoma araguaiensis* Kullander from Angélica Cave had empty stomachs and were not included in the table. Most specimens had at least partially full stomachs. Relatively large samples, both from caves and epigean stream reaches, were obtained for the siluriforms *I. hollandi* and *Cetopsorhamdia molinae* Milles. For *I. hollandi*, the proportion of stomach with contents was higher in the cave than in the epigean sample, the opposite being observed for *C. molinae*.

The studied fishes were carnivorous, feeding basically on insects. Most food items were aquatic organisms (*e.g.* ephemeropteran and plecopteran nymphs,

naucorid heteropteran, larvae of trichopterans and nematoceran flies, larvae and adults of aquatic beetles and larva of nymphiiline moths). Only three identified items representing rare occurrences corresponded to terrestrial, allochthonous food items eaten by epigean fishes (collembolan, adult dipteran and diplopod). In several cases, however, the taxonomic level of identification did not allow any inference on the original habitat of the food item. The predominant food items were larvae and pupae of trichopterans and dipterans (chironomids and simuliids) and elmid beetles, typical of fast flowing waters.

Scales found in the stomach of one tetra characin (*Astyanax* sp.) may have been the result of active predator behaviour, scavenging or lepidophagy. Although it cannot be considered a food item, the occurrence of sediment (sand grains) was noted as evidence of bottom feeding. Likewise, plant remains found in the stomach of some specimens may have been accidentally ingested during feeding on prey in deposits of vegetal debris.

The results for *H. unitaeniatus* were as follows: 13 specimens with completely or almost empty stomach, sometimes with a few remnants of arthropod exoskeleton, five specimens with partially full stomach. Food items identified were a pseudonannolenid diplopod, insects (dipterans and unidentified), unidentified animal matter, vegetal fragments and sand. Among the 18 specimens of *H. unitaeniatus* examined, four were mature females and one was a mature male.

Individuals with developed gonads in caves were recorded for *I. hollandi* and also for the rarer *R. quelen*, *Pseudocetopsis plumbeus* (Steindachner), *H. unitaeniatus* and *C. araguaiensis*. This could indicate a potential for reproduction of these species in the subterranean habitat. No epigean specimen of *I. hollandi* with developed gonads was observed. On the other hand, reproductive females of *C. molinae* were only observed in epigean streams. No juvenile fishes with less than half the maximum standard length (L_S) recorded for each studied species was collected in caves, except for one *I. hollandi* specimen of 78 mm (maximum $L_S = 175$ mm).

DISCUSSION

The composition of the fish community from São Domingos area is typical of fast-running, headwater streams, with a predominance of siluriforms, especially loricariids and heptapterids, followed by characids, especially tetra characins and *Characidium* spp. (Buck & Sazima, 1995; Castro & Casatti, 1997; Sazima *et al*., 2001). The relatively high diversity of gymnotiforms is a feature of Amazonian fish faunas (Lundberg *et al*., 1987; Campos-da-Paz, 1996). *Pseudocetopsis plumbeus* is a species rarely found elsewhere.

The absence of records of the heptapterid *I. minutus* and of most gymnotiforms in epigean stream reaches is probably due to the collection methods which are less efficient for these elusive fishes, possibly allied to low population densities. It must be noted that visual localization of fish is easier in the exposed cave habitat, in the absence of plants where the animals could hide. Moreover, under the free-running conditions observed in caves, at any time specimens in the resting phases of their activity cycle could be found, when the animals would be less sensitive to disturbance, thus less prone to flee before being located.

São Domingos karst area has by far the most diverse and abundant Brazilian cavefish fauna, not only in terms of troglobitic populations but also in general fish richness, with 22 non-troglomorphic species recorded in caves in addition to seven troglobitic ones. In the intensively studied caves from the Upper Ribeira karst area, a few non-troglobitic siluriforms have been recorded: the most constant are heptapterids, *Pimelodella transitoria* (Miranda-Ribeiro) possibly a troglophile and the sister-species to the troglobitic *Pimelodella kronei* (Miranda-Ribeiro), *R. quelen* and *Rhamdioglanis frenatus* Ihering (=*Imparfinis piperatus* Eigenmann & Norris), with occasional records of loricariids such as *Rineloricaria* sp., and tetra characins, *Astyanax* sp., apparently trapped in caves after floods (Trajano, 1991). Tetra characins occur frequently in Brazilian caves (E. Trajano, pers. obs.). In some cases, these fishes showed clear signs of starvation indicating that they had been trapped in the caves. In others, such as in flooded caves from Serra da Bodoquena karst area, the abundant food represented by troglobitic crustaceans (spelaeogriphaceans and amphipods) would support large, stable groups of healthy tetra characins (E.P. da Costa Jr. & N. Moracchioli, pers. comm.).

In Toca do Gonçalo Cave, northern Bahia, the locality of the troglobitic heptapterid *Taunayia* sp., isolated specimens of *R. quelen* and erythrinids enter the cave during floods, possibly surviving for some time; these are potential predators of the troglobitic catfishes (Trajano & Bockmann, 2000). *Rhamdia quelen* is also common near the entrance of flooded caves in Serra da Bodoquena karst area (E.P. da Costa Jr., pers. comm.). On the other hand, no epigean fish was found in Olhos d'Água Cave, locality of the troglobitic catfish *Trichomycterus itacarambiensis* Trajano & de Pinna.

Like many siluriforms and gymnotiforms which are clearly preadapted to the subterranean habitat due to their nocturnal habits and generalist carnivorous diet, the predaceous erythrinids seem to present a reasonable potential for hypogean life, but only under conditions of high food availability. Besides *H. unitaeniatus* in caves of São Domingos, several specimens of *Erythrinus* sp. were observed in a sandstone cave of Altamira-Itaituba karst area (State of Pará), that is a bat cave with an exceptionally high abundance of terrestrial prey and a moderate abundance of aquatic prey (Trajano & Moreira, 1991). Among four adult specimens of *Erythrinus* sp. collected in this cave, two had normal eye 'sockets' without 'eyeballs'; apart from this malformation, all individuals seemed to be in good condition.

Almost every large cave in São Domingos karst area had one or two troglomorphic species. The only exception was Terra Ronca Cave, relatively short, with several large upper entrances and no upper tributaries, where no troglobitic fishes were found. In other similarly-sized Brazilian karst areas, only one to two troglobitic fish species have been found in each one (Trajano, 1997), as opposed to seven recorded in São Domingos. On the other hand, the degree of specialization to hypogean life, indicated by the degree of reduction of eyes and pigmentation, in the troglomorphic fishes of São Domingos was relatively low when compared, for instance, to the species from karst areas in Bahia and Mato Grosso do Sul.

It is interesting to note that no aquatic troglomorphic inverterbrate has been found in caves from São Domingos karst area, and that terrestrial troglobites

are rare in these caves. Such paucity of invertebrate troglobites is in accordance with the model of palaeoclimatic fluctuations as a major cause of troglobitic differentiation because São Domingos is situated in a relatively stable area. Thus there have been fewer opportunities for isolation due to local elimination of epigean populations (Trajano, 1995). It is clear, however, that this reasoning does not apply to the ichthyofauna, and other evolutionary mechanisms must be sought. The trichomycterids and the new species of *Pimelodella* are geographically isolated in caves, thus subject to allopatric differentiation, although there is no information about the events that could have caused the elimination of their epigean relatives from this area. In the case of *A. cryptophthalmus* and *Eigenmannia vicentespelaea* Triques, parapatric differentiation is a reasonable possibility.

Troglobitic fishes from São Domingos karst area have high population densities when compared to other subterranean fishes throughout the world (Trajano, 2001*b*; unpubl. data). On the other hand, non-troglomorphic fishes are in general far less abundant, as expected for species not specialized to the subterranean way of life. A few exceptions are *Astyanax* sp. and *H. unitaeniatus*, relatively abundant in Passa Três Cave. An immediate interpretation is that *H. unitaeniatus* may be feeding on troglobitic catfishes. Another erythrinid of the same size, *Erythrinus erythrinus* (Bloch & Schneider), was reported as feeding on small fishes in addition to insects (Santos *et al.*, 1984). The numerous troglobitic catfishes in Passa Três could support the small population of predaceous *H. unitaeniatus* living in the cave. Analysis of stomach contents, however, failed to support such an interpretation. There is no evidence of important predation on troglobitic fishes by the non-troglobitic ones in caves of the São Domingos karst area.

The great richness and general abundance of fishes in caves from São Domingos karst area may be explained by the plentiful and relatively constant food availability, mostly represented by large deposits of vegetal debris and associated fauna, and by the absence of physical barriers between epigean and hypogean stream reaches. The fishes found in the subterranean habitat may be actively entering caves, especially those which are predominantly horizontal such as Angélica, Bezerra and São Bernardo, or be introduced by accident, not being able to leave the cave. This seems to be the case with *Astyanax* sp. and *H. unitaeniatus* in Passa Três Cave, where waterfalls downstream of the stream sinkhole (the only direct access to the epigean habitat) would impede exit of fishes washed into the cave.

Several non-troglomorphic fish species from São Domingos were consistently found in the hypogean habitat, *e.g. I. hollandi*, *H. unitaeniatus*, *P. plumbeus*, *Sternopygus* sp. and *Sternarchorhynchus curvirostris* (Boulenger), occurring in different caves and on different occasions. It is noteworthy that some fishes presently recorded in São Mateus III Cave (*Hypostomus* sp., *S. curvirostris*, *A. albifrons*, *Eigenmannia trilineata* Lopez & Castello) were also collected in this cave by speleologists in the mid-1970s (Dessen *et al.*, 1980).

The species mentioned above would qualify as true cavernicoles, *i.e.* species including individuals or populations regularly associated to the hypogean biotope, where they are able to orient themselves. The length of time that the individuals had occupied the caves is generally unknown, although in some

cases (*e.g. Brycon* sp. from São Mateus Cave) it has been shown that they have been in the cave habitat at least for 10 years. Analysis of stomach contents demonstrated that the studied fishes were generally able to find food inside caves.

As expected, fishes found recurrently in caves are generalist carnivores. The most frequently preyed organisms (trichopterans and dipteran larvae) correspond to the most abundant taxa in the cave streams (Majer *et al.*, 2001). This points to opportunistic feeding, as seems to be the rule for subterranean fishes (Trajano, 2001a). Therefore, intra- and interspecific differences in the food items recorded are probably mainly due to differences in food availability, and not to important differences in feeding preferences.

In contrast with Poly (2001), who did not find any evidence of reproduction for nine non-troglomorphic fish species recorded in a cave from West Virginia, individuals with developed gonads, potentially reproductive, were found for several species in caves from the São Domingos karst area. No juveniles of non-troglomorphic fishes, however, were found and thus it cannot be certain that such fishes are able to complete their life cycles without leaving the caves. Consequently, it is not possible to conclude if any of these fishes are troglophiles, *i.e.* organisms able to complete their life cycle both in the epigean habitat and in caves, where they form self-sustained populations which would survive in isolation in the subterranean habitat.

Based on the relatively high number of individuals observed, also at large distances from the cave entrances, and the high proportion of specimens with stomach contents and developed gonads, *I. hollandi* is a candidate for troglophilic status, at least in Angélica Cave (the absence of juveniles for heptapterids is not surprising, as for example very young individuals of the troglobitic catfish *P. kronei* were never found). On the other hand, *C. molinae*, a smaller-sized heptapterid also found in caves from São Domingos karst area, seems to find it difficult to colonize the subterranean habitat, as indicated by the occurrence at shorter distances to cave entrances, relatively low proportion of stomachs with contents and absence of developed gonads in cave specimens.

A situation similar to that of São Domingos karst area is observed in karst areas of Thailand. A rich non-troglomorphic ichthyofauna fauna was recorded in Thai caves which are also crossed by large, strong-current streams with epigean and subterranean reaches. This fauna is composed mainly by cypriniforms such as cyprinids of the genera *Garra*, *Danio*, *Poropuntius* and *Tor*, which may form groups with up to 10 individuals, and balitorids such as *Schistura* (that also includes troglobitic species, but not syntopic with non-troglomorphic fishes), *Homaloptera* and *Balitora*, and, to a lesser extent, siluriforms such as *Glyptothorax* species (Trajano *et al.*, 2002). Therefore, the main faunistic difference between the two countries is the prevalence of siluriforms in Brazilian caves and their relatively low abundance in Thai caves.

Poly (2001) provided a list of non-troglobitic fishes reported from caves worldwide. Around 120 species are listed, from lampreys to soles, most from the U.S.A. This number clearly underestimated the diversity of non-troglobitic fishes in caves, because most speleologists neglect this fauna. For instance, in one cave studied in detail in West Virginia, Poly (2001) recorded nine species, mostly cyprinids and centrarchids. Two of these species, *Semotilus atromaculatus*

(Mitchill) and *Lepomis cyanellus* (Rafinesque), were regularly found in the cave and many individuals were captured at distances varying from 2·4 to 476·0 m from the entrance.

In contrast to reports of malformations such as depigmentation, reduction of eyes and skeletal abnormalities in individuals of epigean species found in caves of North America (Poly & Boucher, 1996), in general non-troglomorphic fishes from caves in the São Domingos karst area seem to be normal. The only exceptions are the unpigmented tetra characin (*Astyanax* sp.) captured in 1988 (Trajano & Souza, 1994) and the one with one reduced eye captured in 2000, also *Astyanax* sp., both in Passa Três cave.

Recurrent records of several species, frequently in the same sectors of the same caves, as is the case with *Brycon* sp. from São Mateus III Cave, *I. hollandi* from São Bernardo and Angélica caves, *H. unitaeniatus* from Passa Três Cave, *P. plumbeus* from São Vicente I Cave and *A. blax* from São Vicente II Cave, among others, are evidence of permanence inside caves for periods varying from weeks to years. Apparently, life under constant darkness does not significantly affect these fishes, which are potential ancestors for troglomorphic populations, at least in a non food-limited environment.

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