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Rediscovery and redescription of the unusual subterranean characiform *Stygichthys typhlops*, with notes on its life history

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The rediscovery of the enigmatic subterranean characiform *Stygichthys typhlops* is reported almost a half-century after the collection of the holotype, the only specimen previously known. Thirty-four specimens were collected in two shallow hand-dug wells at the region of the type locality, *c*. 13 km south-west of the town of Jaíba, Minas Gerais, Brazil. These specimens provide new information on the morphology of this species, and for the first time on its life history. The conservation status of *S. typhlops* is discussed. The species is severely threatened by habitat loss caused by exploitation of the aquifer.

Key words: Characidae; Characiformes; conservation; hypogean fishes.

INTRODUCTION

In 1962, a small, blind and unpigmented fish was brought to the surface during a well-drilling operation at Jaíba, northern Minas Gerais, eastern Brazil. That specimen was later described by Brittan & Böhlke (1965) as a new genus and species, *Stygichthys typhlops* Brittan & Böhlke. Based on external morphology and radiographs, the authors considered the fish as possibly related to the genera *Hyphessobrycon* Durbin and *Hasemania* Ellis in the characiform family Characidae.

No subsequent attempts were made to collect additional specimens of *S. typhlops* for over 40 years, and the species remained known only from the holotype. This species has been regularly included in taxonomic catalogues (Géry, 1977; Lima *et al*., 2003) and essays on troglobitic fishes (Thinès, 1969; Trajano, 1997; Romero

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& Paulson, 2001), but no new information became available. The unusual morphology and habitat make *Stygichthys* one of the most intriguing puzzles in neotropical ichthyology.

Two expeditions to the region of Jaiba in 2004 yielded 34 specimens of *S. typhlops*. This paper reports on the rediscovery of this species, redescribes it based on the new material and provides information on its habitat, behaviour and geographic distribution.

MATERIALS AND METHODS

Specimens were collected in two wells in the município de Jaíba, Minas Gerais, Brazil. Phreatic waters were reached by climbing down open wells using ropes and speleological ladders. Specimens were collected with hand-nets and with minnow-traps baited with commercial fish pellets and dry cat food. Four specimens were collected in a well at Fazenda (farm) do Seu Roque (Fig. 1) in April 2004. Two of these specimens were killed in the field by over-anaesthesia in benzocaine and fixed in 10% formalin (Bichuette & Trajano, 2003). Two were kept alive for behavioural studies, but one died before reaching the laboratory. Twenty-one specimens were collected at a second locality, a well at Fazenda do Lajeado (Fig. 1) in April 2004. Of these, 14 were preserved in the field (as described above) and the remaining seven specimens were kept alive, with one of these specimens dying before reaching the laboratory. Nine additional specimens were collected from Fazenda do Lajeado in September

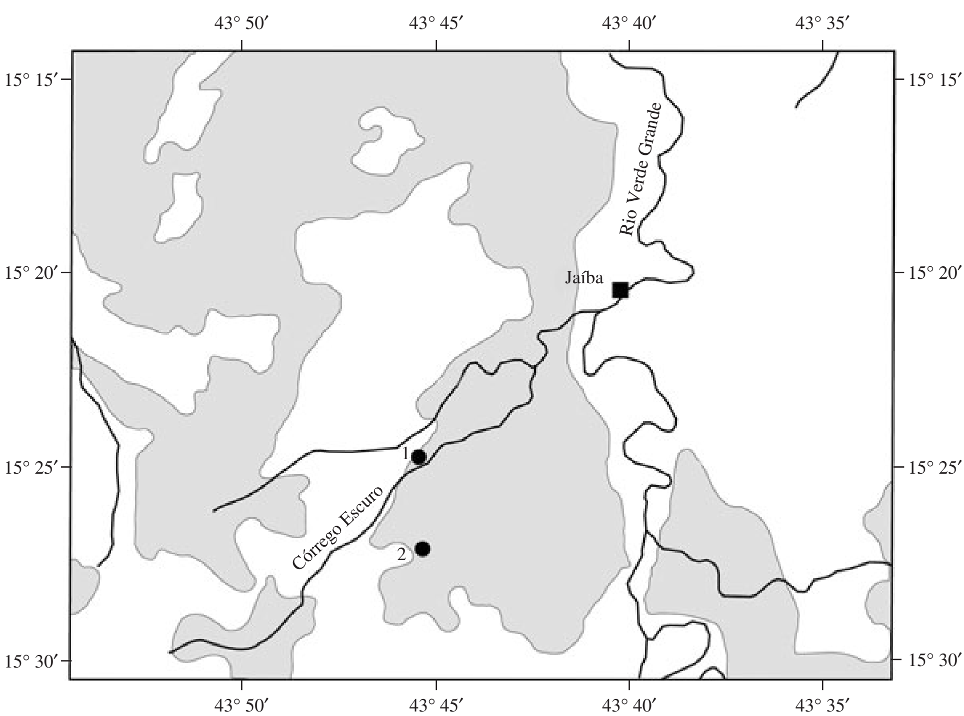

FIG. 1. Distribution of *Stygichthys typhlops*, Minas Gerais, Jaíba, Jaíba karst aquifer: 1, well at the Fazenda do Seu Roque and 2, shallow well at the Fazenda do Lajeado. ☐, the aquifer.

2004, and all kept alive. Conductivity, pH, temperature and salinity were measured using a Horiba, model U-10 water-testing system (www.horiba.com).

Behavioural observations were made in the field (at Fazenda do Lajeado) and on specimens in captivity. Initial laboratory observations were made on the seven specimens collected in April 2004. Those specimens were maintained in three separate 22 l aquaria according to the specimen size (three 39·2–46·0 mm standard length, L_S, specimens; three 25·9–36·5 mm L_S specimens and the one 32·7 mm L_S specimen from Fazenda do Seu Roque) at water temperatures of 19–25° C. None of those specimens survived beyond the second month. Specimens that died in the laboratory were fixed in 10% formalin. The nine specimens (*c*. 30–35 mm L_S) collected from Fazenda do Lajeado in September 2004 were kept in two separate aquaria with six and three specimens, respectively, at 24° C and are still alive at the time of writing. Those specimens are not catalogued.

The redescription of the morphology is based on the holotype and 25 specimens collected in April 2004, except for morphometric data that were taken only from the holotype and 16 specimens preserved in the field. Meristic counts and morphometric measurements follow Fink & Weitzman (1974) and Menezes & Weitzman (1990), except for the gape that was taken transversally between the lateral-most tips of the premaxillae. Longitudinal scales series counts were taken from immediately dorsal to the posterior margin of the opercle, where it meets the subopercle, to the end of hypural plate. All counts were from the left side. Variation of tooth counts between the left and right sides is described in the text. The frequency of each count is provided in parentheses after the respective count, with values for the holotype indicated by an ∗. The numbers of gill rakers, branchiostegal rays and teeth were taken from four cleared and stained specimens (CS), prepared according to Taylor & Van Dyke (1985). Vertebral counts were taken from radiographs of all preserved specimens. The Weberian apparatus was counted as four elements, and the fused preural centrum 1 and ural centrum 1 (PU1+U1) are counted as one. Institutional abbreviations follow Leviton *et al*. (1985).

RESULTS

STYGICHTHYS TYPHLOPS BRITTAN & BÖHLKE

Material

Holotype: ANSP 100891 (23·0 mm L_S) Brazil, Minas Gerais, município de Jaíba. Collector unknown (see under 'Additional information on the holotype collection data'), 16 May 1962.

Non-type specimens: all from Rio Verde Grande system, Rio São Francisco basin, Minas Gerais, município de Jaíba, Brazil. MZUSP 87677 (4: 29·3–39·7 mm L_S) well at Fazenda do Seu Roque, córrego (stream) Escuro, 15° 24′ 41·7″ S; 43° 45′ 19·7″ W, C. Moreira, E. Trajano, M. de Pinna, O. Oyakawa, M. E. Bichuette & F. Passos, 27 April 2004. MZUSP 87678 (21: 22·8–45·8 mm L_S; 4 CS) shallow well at Fazenda do Lajeado (also known as Fazenda do Mandioqueu), córrego Escuro, 15° 27′ 05·8″ S; 43° 45′ 09·2″ W, C. Moreira, M. E. Bichuette, O. Oyakawa, M. de Pinna, E. Trajano & F. Passos, 28 April 2004 (Fig. 2).

Diagnosis

This species can be distinguished from other members of the Characiformes, except for the hypogean species of *Astyanax* by the complete absence of eyes and pigmentation. It can be distinguished from the latter by having seven or eight teeth in the inner row of the premaxilla (*v*. five), eight or more maxillary teeth (*v*. fewer than five) and by the absence of pored scales on the body (*v*. presence).

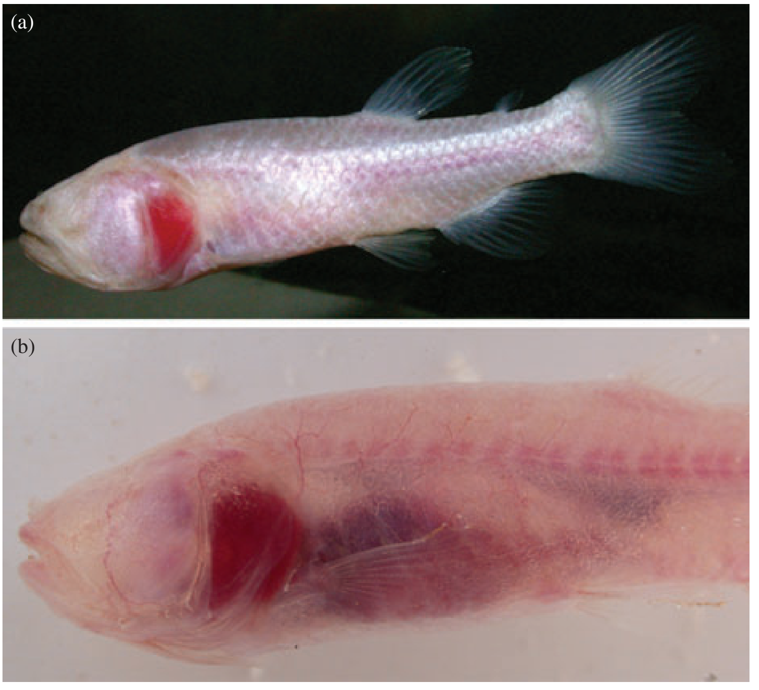

FIG. 2. Live specimens of *Stygichthys typhlops*: (a) MZUSP 87677, 39·7 mm standard length, L_S, live anaesthetized specimen from Fazenda do Seu Roque, just after capture and (b) MZUSP 87678, 45·9 mm L_S, specimen from Fazenda do Lajeado in aquarium 15 days after its collection.

Redescription

Morphometric data are presented in Table I. Body moderately elongate, greatest body depth at vertical located about two-thirds of distance from snout to dorsal-fin origin. Dorsal profile of head slightly convex from tip of snout to posterior limit of ascending process of premaxilla, straight from that point to tip of supraoccipital spine. Predorsal profile of body convex anteriorly to vertical through middle of length of pectoral fin, then straight to dorsal-fin origin. Dorsal-fin base straight, posteroventrally slanted. Dorsal profile from terminus of dorsal fin to adipose fin straight. Dorsal profile of caudal peduncle slightly concave. Anterior margin of dentary straight to slightly convex. Ventral profile of head slightly convex to isthmus. Ventral profile of body straight to slightly convex anterior to anal-fin insertion. Anal-fin base straight, posterodorsally inclined. Ventral profile of caudal peduncle slightly concave.

Head wide, with neuromasts concentrated on region anterior to nares and on anteroventral portion of dentaries. Mouth terminal, lower jaw slightly shorter than upper jaw. Maxilla extending posteriorly beyond ventral wing of lateral ethmoid. Premaxillary teeth in two rows. Outer left row with 6(1), 7(1) or 8(2) uni- to tricuspid teeth, additional lateral cusps very small when present; one specimen with seven teeth on left premaxilla and eight on right premaxilla, and another with eight on left premaxilla and nine on right premaxilla. Inner tooth row with 7(2) or 8(2) teeth on left premaxilla; one specimen with seven teeth on left premaxilla and eight on right premaxilla. Teeth typically tri to pentacuspid, but one specimen with lateral-most

TABLE I. Morphometric data for *Stygichthys typhlops*. Measurements were based on the holotype (ANSP 100891) and recently collected specimens (MZUSP 87677 and MZUSP 87678)

	Holotype	*n*	Minimum	Maximum	Mean ± S.D.
L_S (mm)	23·0	25	22·8	45·9	32·6 ± 6·8
Percentage of L_S					
Depth at dorsal-fin origin	20·6	16	19·6	26·2	23·9 ± 1·8
Snout to dorsal-fin origin	63·2	17	59·0	64·9	62·0 ± 1·4
Snout to pectoral-fin origin	31·9	17	28·3	35·5	33·2 ± 1·8
Snout to pelvic-fin origin	54·9	17	51·1	59·7	55·9 ± 2·0
Snout to anal-fin origin	68·4	17	66·6	73·8	70·6 ± 1·8
Caudal peduncle depth	11·9	17	11·4	13·8	12·6 ± 0·6
Caudal peduncle length	18·6	17	17·1	21·3	18·8 ± 1·1
Pectoral-fin length	16·6	15	14·4	18·3	16·9 ± 1·1
Pelvic-fin length	—	12	12·9	15·6	14·2 ± 0·8
Dorsal-fin base length	9·4	16	8·0	10·8	9·2 ± 0·8
Dorsal-fin height	18·8	15	16·8	22·5	20·4 ± 1·4
Anal-fin base length	13·1	17	10·9	13·9	9·8 ± 0·9
Anal-fin height	15·8	15	15·2	19·3	17·5 ± 1·2
Dorsal-fin origin to caudal-fin origin	39·3	17	39·3	43·2	40·8 ± 1·1
Dorsal-fin origin to adipose fin	24·3	16	22·5	25·9	23·9 ± 1·0
Bony head length	31·8	17	30·0	34·1	32·4 ± 1·3
Percentage of head length					
Upper jaw length	43·2	17	39·9	50·5	43·9 ± 3·1
Gape	35·1	17	29·5	35·9	32·2 ± 2·1

L_S, standard length.

tooth unicuspid. Fourth and fifth lateral-most cusps, when present, much smaller than three central ones, sometimes barely evident. Teeth on left maxilla 9(2) or 10(2); one specimen with nine teeth on left maxilla and 11 on the right maxilla, and another with 10 teeth on the left maxilla and eight on right maxilla. Maxillary teeth uni to tricuspid, with anterior teeth usually tricuspid. Dentary teeth of two morphological types. Medial teeth larger with three to five cusps, with posterior teeth smaller with one to three cusps. Larger medial dentary teeth 7(2) or 8(2). Left posterior dentary teeth 7(3) or 8(1), with one specimen with seven teeth on left dentary and nine teeth on right dentary, and another with seven on left dentary and six on right dentary. Cusps of all teeth in straight line. Cusps of upper jaw approximately straight and cusps of lower jaw teeth slightly angled lingually. Supraorbital absent. Single, probably second, infraorbital present. Laterosensory canal system on head restricted to nasal, frontal, infraorbital, preopercle and dentary.

Dorsal-fin rays ii, 5(1), iii, 5(1), ii, 6(2), iii, 6(11), ii, 7*(5) or iii, 7(1). Dorsal-fin origin located on posterior half of L_S, with dorsal-fin base terminus located approximately at vertical through anal-fin origin. First dorsal-fin pterygiophore inserted immediately posterior to neural spine of 12th*(17) or 13th(7) vertebra. Distal margin of dorsal-fin convex. Adipose fin present and lanceolate, except in one apparently mutilated specimen. Anal-fin rays iii, 7(1), ii, 8(5), iii, 8(1), ii, 9(10), iii, 9*(5) or ii, 10(2). First anal-fin pterygiophore inserted immediately posterior to haemal spine of 17th*(22) or 18th(2) vertebrae. Distal margin of anal fin straight. Pectoral-fin rays i, 8 (6), 9(14) or 10*(2). Tip of pectoral fin falling short of pelvic-fin insertion. Pelvic-fin rays i, 5*(23) or 6(1). Tip of pelvic fin falling short of anal-fin origin. Caudal fin forked, with upper lobe slightly longer than lower lobe. Principal caudal-fin rays 10/9 (21). Nine (2), 10(15) or 11(4) dorsal, and 8(3), 9(15) or 10(3) ventral procurrent caudal-fin rays.

Scales cycloid, with fewer circuli posteriorly and few radii from focus to posterior margin of scale. Scales absent from dorsal and anal-fin bases. No perforated scales along midlateral surface of body. Scales along longitudinal series 27(1), 28*(5), 29(15) or 30(5). Predorsal region with 13(1), 14(2), 15(6), 16(2), 17(2), 18(1) or 19(1) irregularly arranged scales. Scale rows between dorsal-fin origin and pelvic-fin insertion, excluding predorsal scale, 10*(2), 11(14) or 12(5). Scale rows around caudal peduncle 13(4), 14(6), 15(4) or 16*(6).

Vertebrae 30(4), 31*(20) or 32(1). Four(4) branchiostegal rays, with three rays attached to anterior ceratohyal and one to posterior ceratohyal. First gill arch with 5(3) or 6(1) epibranchial, 7(4) ceratobranchial and 1(4) hypobranchial gill rakers. Six supraneurals, very thin, observable with confidence in only one CS specimen.

Sexual dimorphism

No external sexually dimorphic characters were detected.

Colour in alcohol

Body and fins completely devoid of dark pigmentation. Ground colour beige, dark yellowish on trunk and lighter on top of head. Fins hyaline, except for base, which tend to be whitish.

Colour in life

Specimens in field translucent, with overall colouration pinkish [Fig. 2(b)]. Region lateral to vertebral column dark pink, but broken up by thin, anteriorly pointed, lighter-pink chevron marks, aligned along myosepta. Several blood vessels visible through skin and muscles, most noticeably the caudal artery. Gills region deep red. Gut dark red to purple. Adipose and caudal fins with visible blood vessels especially basally. Orbit filled with adipose tissue and visible through skin. Specimens in captivity became noticeably whiter and more opaque than in field, acquiring tint of yellow, mainly on head [Fig. 2(a)]. Physiological tests *in vitro* showed that these fishes are DOPA(+), *i.e.* able to synthesize melanin when L-dopamine provided and, therefore, not true albinos (Trajano & Pinna, 1996).

Distribution and habitat

Stygichthys typhlops was collected from two shallow wells separated by 4·5 km and *c*. 13 km south-west of the town of Jaíba (Fig. 1). The well at Fazenda do Seu Roque is still occasionally used as a source of water for cattle, while the shallow well at Fazenda do Lajeado is abandoned. Both localities have similar physico-chemical characteristics, with the pH and conductivity typical of limestone drainages. Fazenda do Seu Roque: 6·98, 0·683 µsm cm^{-1}, 25·3° C and 0·02; Fazenda do Lajeado: 7·0, 0·647 µsm cm^{-1}, 25·8° C and 0·02% (pH, conductivity, temperature and salinity).

According to local informants, *S. typhlops* occurred in the past in at least two other localities. One, a well, which is now dried up, while the other is a small cave (*c*. 100 m from the well at Fazenda do Seu Roque) with a shallow stream, now filled with soil.

All localities where the species occurs or occurred are associated with a single entirely subterranean drainage, the córrego (stream) Escuro system (Fig. 1). This system is located in a large karstic area (middle São Francisco area; Auler & Farrant, 1996), belonging to the Bambui group. The maximum subterranean depth of circulating water in the aquifer in the area of occurrence of *S. typhlops* is *c*. 50 m (Silva, 1984). This probably corresponds to the potential maximal vertical distribution of the species. The córrego Escuro runs north-east for *c*. 25 km, from its headwaters *c*. 500–600 m above sea level, to its underwater mouth in the Rio Verde Grande (Rio São Francisco basin) in the periphery of the town of Jaíba. The stream had a permanent epigean (surface) water flow at until least 1984 (Silva, 1984). According to local information, such surface flow now only happens during the peak of the rainy season. The region has a tropical savanna climate ('Aw', Köppen, 1948), characterized by a dry winter (May to September), mean annual temperatures of *c*. 23° C (Nimer, 1989) and annual precipitation *c*. 940 mm.

Remarks on collection data of the holotype

According to the original description, the holotype of *S. typhlops* was collected by J. A. Tosi Jr. 30 m below the surface, during a well-drilling operation at Jaíba, on 16 May 1962. This information, however, needs correction. Tosi (1962) mentions that he received the specimen of *S. typhlops* from M. Dias Araújo, Manager of the INIC (Instituto Nacional de Imigração e Colonização, National Institute of Immigration and Colonization), on 16 May 1962. Thus, the date of collection is unknown, since it could have been collected before that date. The specimen was 'brought up in the bucket of one of the communal tube wells drilled for domestic use close by the road leading from the airfield towards Matias Cardoso' (Tosi, 1962), *c*. 2 km away from the Rio Verde Grande. That well had a total depth of 100 m, with permanent water at 18 m, and at 20 m it passed from unconsolidated sedimentary material into limestone bedrock (Tosi, 1962). The type locality information is, therefore, imprecise. The road that Tosi (1962) refers to is north-west from the city of Jaíba and, as such, the possible area of the type locality lies at least 5 km north from the two localities where *S. typhlops* was collected in 2004.

Behaviour

Laboratory and field observations demonstrate that *S. typhlops* is predominantly a midwater swimmer. When undisturbed, it remains almost stationary in midwater, with the body inclined at a 10–40° angle, head facing either up or down, or moving slowly, with the mouth slightly open. This behaviour contrasts with that observed in characids (including the hypogean populations of the genus *Astyanax*; E. Trajano, pers. obs.), which are more active.

Studies on circadian rhythms, using the methods described in Trajano & Menna-Barreto (1995) and Trajano *et al*. (2005) for the locomotor activity in eight specimens monitored in continuous darkness (free-running conditions) for 7 to 10 consecutive days, showed that these fishes are arhythmic, without any significant circadian or ultradian rhythms (Trajano *et al*., 2009). This is consistent with the hypothesis that a population that has undergone a long period of isolation in a very stable environment, such as the phreatic habitat, devoid of zeitgebers (Ali *et al*., 1992) like daily cycles of light and temperature, experiences a regression of time-keeping mechanisms, with loss of circadian components of the locomotor activity.

Stygichthys typhlops is apparently solitary. When in groups (as in the laboratory), they remain indifferent to each other, not schooling. When, by chance, there is contact, it is followed by mutual avoidance movements, usually (but not always) with the smaller individual withdrawing for a short distance. Some intraspecific agonistic biting attempts were observed during feeding.

Specimens that survived in captivity initially accepted only floating dry fish pellets. When fed, their behaviour differs from the behaviour, either in laboratory or in the field, of the blind Mexican tetra, *Astyanax jordani* (Hubbs & Innes), as described by Schemmel (1980). Although the cave populations of *A. jordani* tend to move towards the substratum when fed, *S. typhlops* start exploring the water surface as soon as the food pellets touch the water, positioning themselves near the surface with the head up and the body at a 30–45° angle. The fish touch the water surface with the top of the head, where there is a concentration of superficial neuromasts. After several months in captivity, a change in the feeding behaviour was observed. The fish started to accept live food (brine shrimp *Artemia* sp.) and to feed in midwater.

The surface feeding behaviour in the laboratory of recently captured *S. typhlops*, associated with the fact that phreatic waters are generally food-poor, suggests that in nature these fish concentrate at the upper part of the aquifer. Food input is higher in these sectors, as organic matter washes down from the surface. Ostracods were observed in radiographs of the stomachs of five of the 16 specimens preserved in the field.

Cannibalism in captivity was observed in one instance among the specimens collected at Fazenda do Lajeado in April 2004. These otherwise did not feed in captivity and died of starvation. The largest (45·9 mm L_S) specimen ingested a whole, small specimen (*c*. 27 mm L_S) that was apparently a healthy conspecific. Cannibalism has been reported for a few other subterranean fishes including the Brazilian heptapterid, *Taunayia* sp. (Trajano & Bockmann, 2000) and North American amblyopsids (Poulson, 1969).

During collection with hand-nets in wells, the fish reacted with a quick fleeing movement only when the net was at close range. That, plus the limited responsiveness to live prey as initially observed in the laboratory, indicates a low dependence on mechanosensory systems, probably associated with the loss of the lateral line on the body. There is no clear reaction to light, because they are either insensitive to it or behaviourally unresponsive to light conditions.

DISCUSSION

CONSERVATION STATUS

Information provided by local inhabitants, well-drilling operators, farm owners and workers indicate that *S. typhlops* was quite common and widespread in the Jaíba region until at least the early 1990s, occurring in surface springs, shallow hand-dug wells and also coming out during drilling of artesian wells. This species was nonetheless always associated with the relatively small subterranean drainage restricted to the Jaíba region. The limited distribution of this extremely specialized habitat makes the conservation of this species a major concern. In the past 20 years, extensive irrigation projects for agriculture have been developed in the Jaíba region, mostly drawing on subterranean water. During the early 1980s, the intensity and frequency of utilization of this resource was low, probably one-tenth the recharge capacity of the aquifer (Silva, 1984). At that time, the córrego Escuro system still consisted of both a subterranean drainage and a permanent surface stream fed by numerous springs along its course. During the last decade, the exploitation of subterranean water apparently exceeded the recharge rate. As a consequence, there has been a marked lowering in water table levels, causing the córrego Escuro to become restricted to its subterranean component for most of the year, except during the peak of the rainy season. Several wells and springs have dried out in recent years. This had promoted a shift of human use from traditional hand-dug wells and open springs to artesian wells as a water source, leading to an even faster lowering of the water table. As a consequence, sightings of *S. typhlops* by local people, once common, were not made since 1995, and most of the wells indicated as supporting a population of *Stygichthys* were dry by 2004.

The lowering of the water level results in significant reduction of available habitat and reduces the input of nutrients from the surface, which may lead to a rapid population decline, and as such poses a major threat for the future of *S. typhlops*. Unless unknown deeper hypogean habitat is present, or the human use of subterranean water is severely reduced, it is unlikely that populations of this species will survive. In 2004, *S. typhlops* was included in the official list of threatened species (MMA, 2004), and this action will hopefully aid in the conservation of this species.

We are greatly indebted to the residents of Jaíba who gave us critical information as to where to locate the species (J. Barbosa and G. Maia), and to those who guided us to the localities (M. Farias, A. Vieira, J. Rodrigues and A. da Silva), as well as to landowners and managers who kindly granted us access to their properties (J. Farias, A. da Silva, E. Pedroso and S. Souza). We also acknowledge the sixth member of the *Stygichthys* Expedition, F. Dias Passos, who, even though not an ichthyologist, shared our enthusiasm for the rediscovery of *S. typhlops*, and A. Auler, for geological information. The Böhlke Memorial Endowment Fund supported the visit of C.R.M. to ANSP. We are grateful for the hospitality and assistance of J. Lundberg, M. Sabaj, K. Luckenbill and W. Dahdul during that visit. The manuscript benefited from comments and suggestions from M. I. Landim and R. Vari. Financial support was given by the IB-USP (programme Proap/2004), FAPESP (through CRM 03/01056-8) and Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPQ (M.P., grant no. 305713/2003-5; E.T., grant no. 306066/88-2); IB-USP also provided the vehicle for the field trip.

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