

Pimelodella spelaea: A New Cave Catfish from Central Brazil, with Data on Ecology and Evolutionary Considerations (Siluriformes: Heptapteridae)

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Pimelodella spelaea, new species, is described from a subterranean stream tributary to the São Bernardo River inside the São Bernardo Cave, in the São Domingos karst area, upper Tocantins River basin, central Brazil. The new species can be distinguished from its epigeal (surface) congeners by derived troglomorphic features such as smaller eyes and fainter coloration, which are nevertheless less reduced than in the other known troglobitic (exclusively subterranean) species, *Pimelodella kronei*, from southeast Brazil. Ecological data such as habitat characteristics, population data based on mark-recapture techniques, and distributions of frequencies of standard length, weight, and condition factor, were obtained during the dry season of 2000 (May to September). A relatively high population density (about one individual per m^{-2}) was recorded for the accessible habitat, which is probably much lower in the nonaccessible, phreatic area of distribution. The low condition factor recorded for *P. spelaea*, which tended to decrease along the study period, indicates a regime of severe food limitation, intensifying along the dry season. An allopatric model of differentiation is hypothesized, either because of topographic isolation or because of local extinction of epigeal relatives, or both factors combined. The conservation status of the new species is also discussed.

Pimelodella spelaea, espécie nova, é descrita de um riacho subterrâneo tributário do rio São Bernardo dentro da caverna São Bernardo, na área cárstica de São Domingos, alto rio Tocantins, Brasil. A nova espécie pode ser distinguida dos seus congêneres epígeos (de superfície) por características troglomórficas derivadas tais como olhos e pigmentação reduzidos. Estes são, entretanto, menos reduzidos que na outra espécie troglóbica (exclusivamente subterrânea) conhecida, *Pimelodella kronei*, do sudeste do Brasil. Dados ecológicos tais como características do hábitat, dados de população baseados em técnicas de marcação e recaptura, e distribuição de frequências de comprimento-padrão, peso e fator de condição, foram obtidos durante a estação seca de 2000 (maio a setembro). Uma densidade populacional relativamente alta (cerca de 1 ind. m^{-2}) foi registrada na porção acessível do hábitat da espécie, que é possivelmente muito menor na área freática, não acessível da sua distribuição. Os baixos fatores de condição registrados para *P. spelaea*, que tendem a diminuir ao longo do período de estudo, indicam um regime de severa limitação alimentar, intensificando-se ao longo da estação seca. Um modelo alopatrico de diferenciação é sugerido, seja pelo isolamento topográfico ou pela extinção local de parente epígeos, ou ainda por ambos os fatores combinados. O estado de conservação da nova espécie também é discutido.

THE Neotropical region is remarkable for its rich subterranean ichthyofauna, only comparable to that from China and southeastern Asia. More than 35 among approximately 100 troglobitic (exclusively subterranean) fish species occurring around the world are known from Mexico, Caribbean, Venezuela, Ecuador, Peru, Bolivia and Brazil, including several undescribed taxa (Weber et al., 1998; Romero and Paulson, 2001; ET and MEB, unpubl. data). The great majority are siluriforms belonging to the Heptapteridae (*Rhamdia* and *Pimelodella*, among others), Trichomycteridae (*Trichomycterus* and *Ituglanis*), and Loricariidae (*Ancistrus*). The

prevalence of these groups in the subterranean biotope is an evidence of high potential for colonization of the subterranean habitats, including caves, probably facilitated by their predominantly nocturnal activity and generalized carnivorous (heptapterids, trichomycterids) or detritivorous (*Ancistrus*) diet (Trajano, 2001). Troglobitic species are generally characterized by autapomorphies related to the isolation in the perpetually dark subterranean habitat (troglomorphisms), the most widespread being the reduction or even loss of eyes and pigmentation.

The São Domingos karst area, a limestone re-

gion in Central Brazil crossed by tributaries of the upper Tocantins River, Amazon basin, presents the most diversified cave ichthyofauna in the country. In the course of our studies in this area, we discovered a new cave species of heptapterid catfish, genus *Pimelodella*, living in slow-moving pools in an upper conduit of the São Bernardo Cave. Herein we describe this new species and present data on population ecology gathered during the dry season of 2002. This is the second troglobitic species known for the genus, the first one being *Pimelodella kronei* (Ribeiro, 1907), from southeastern Brazil.

The genus *Pimelodella*, with 71 valid species and a cis- and trans-Andean distribution from Panama to Paraguay and southern Brazil, is the largest among the Heptapteridae (Bockmann and Guazelli, 2003). *Pimelodella* is currently in need of a taxonomic revision being last reviewed by Eigenmann (1917) who diagnosed the genus based on several not unique features but including a few that provide a diagnosis when in combination. These features are "... a long, adnate, adipose fin; caudal fin deeply forked; a frontal and a parietal fontanel, the latter reaching the base of the occipital process, which is narrow and reaches, or nearly reaches the plate in front of the dorsal; and humeral process spine-like . . ." (Eigenmann, 1917:229). More recently, however, Bockmann (1998) presented two characters that may represent synapomorphies for *Pimelodella* or to a subgroup of species within *Pimelodella*. These are (1) the two innermost caudal-fin rays not directly articulating with hypural bones (character 220), and (2) those same rays united by an incomplete caudal-fin membrane (character 223). The new species described below shares the second character but not the first, because the two innermost caudal-fin rays directly articulate with the hypural bones.

MATERIALS AND METHODS

The fieldwork was conducted in May, July, and September 2000 and was restricted to the dry season because of the danger of being caught by floods in the rainy period (October to March). Collections were made with hand nets in May and with funnel-type minnow traps baited with chicken liver in July and September. Baits were kept in small nylon bags to avoid being swallowed by the fish and interfering with weight measurements. Fish were anesthetized in a solution of MS-222 (tricaine-methanesulphonate), measured (standard length, SL) to the nearest 0.1 mm, and weighed with a Pesola dynamometer, 0.1 g precision. Most catfishes were

marked by subcutaneous injection of fluorescent pigments ("Photonics marking," from New West Co.), and released. Association of mark color and position, and fish size, produced individual marks. Some specimens were sacrificed by overanesthesia and preserved in formalin (later transferred to alcohol 70GL) for description. Only eight specimens were preserved to avoid unnecessary mortality in the population, whose total size was unknown.

Mark-recapture data from May to July and from July to September were used separately to estimate the number of individuals in the study section using the Lincoln-Petersen Index (Begon, 1979; Blower et al., 1981). We did not use the whole set of data for a single estimation using a multiple-recapture method (such as the triple-catch) because there is evidence of some loss of marks by pigment reabsorption during our four-month observation period.

Standard length and weight data were used to calculate the allometric condition factors ($K = 100.W.SL^{-b}$; Le Cren, 1951). For these calculations, units of millimeters and grams were used. The power coefficient (b) was estimated from the slope of the regression of log weight on log standard length using the pooled data. Dice-Leraas diagrams (Dice and Leraas, 1936) were used to show tendencies along the study period. Graphs with the distributions of frequencies of size (SL), weight and condition factor (K) in July and in September were built; May was not included here because of the low sample size. July and September samples were compared by two-sample *t*-test, with $\alpha = 5\%$.

For comparison, we estimated the average condition factor for *P. kronei* from the Areias cave, upper Ribeira karst area, in the Atlantic rain forest in southeastern Brazil, based on data gathered between May and September of 1984 and 1985 (ET, unpubl. data), a period of low rainfall locally corresponding to the dry season.

Measurements of preserved fish, taken with electronic calipers (0.1 mm precision), followed basically Lundberg et al. (1991) and Trajano and Britski (1992). In the description, meristic data are followed by number of specimens displaying each count in parentheses. Density of chromatophores was estimated by direct counts under stereomicroscope on a 1-mm² area located immediately posterior of the dorsal-fin origin, midway between the lateral line and the dorsal fin. A cleared-and-stained specimen was prepared according to Taylor and Van Dyke (1985).

No *Pimelodella* species has been described from the upper Tocantins River to date. However, watersheds around the upper Tocantins in-

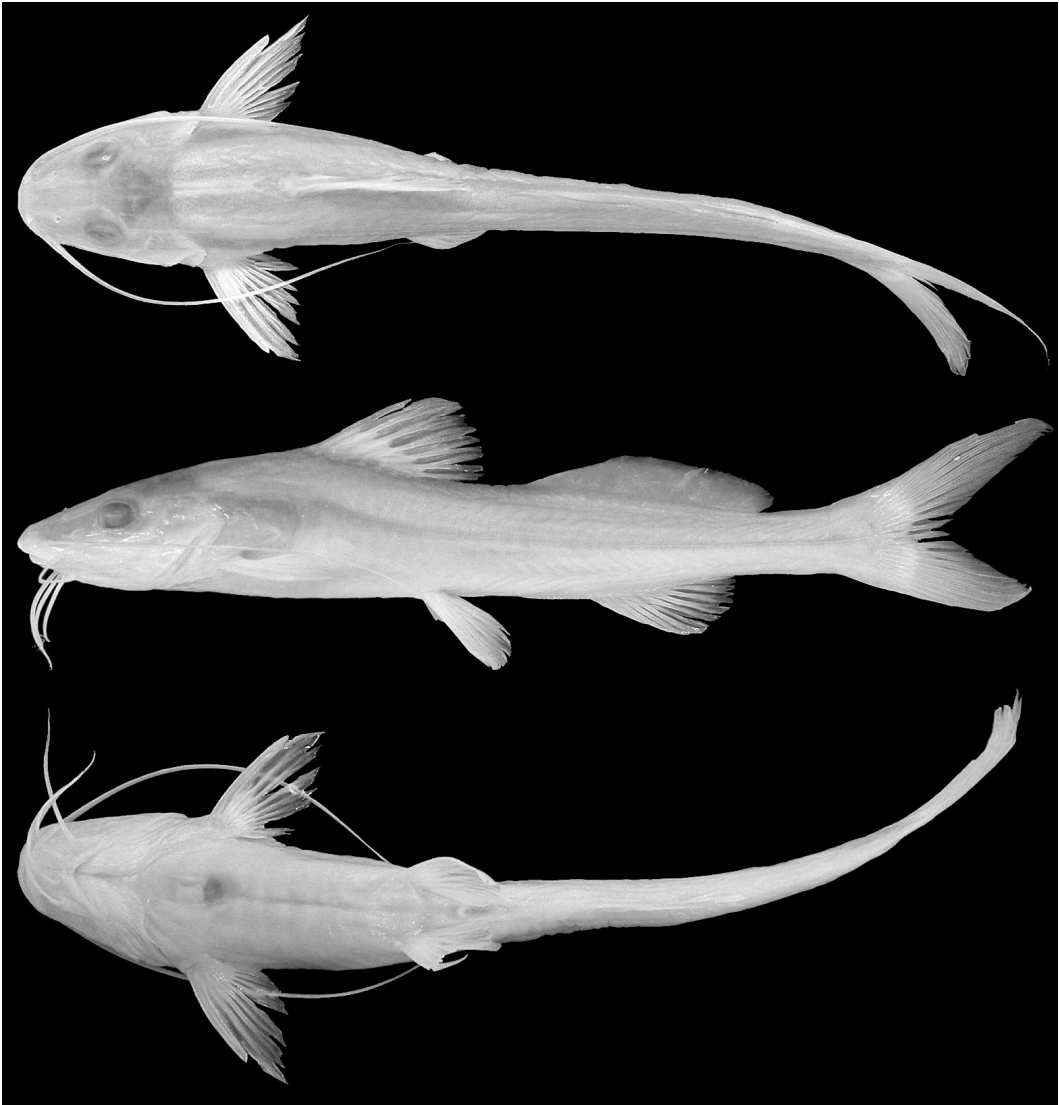


Fig. 1. Holotype of *Pimelodella spelaea*, MZUSP 81726, 80.5 mm SL; Brazil, State of Goiás, São Domingos, upper Tocantins River basin, subterranean stream tributary to São Bernardo River inside São Bernardo Cave. Photograph by Pablo Lehmann.

clude the Araguaia, the São Francisco, and the upper Paraná River basins. Five species were described from these areas: *Pimelodella boschmai*, *Pimelodella meeki*, and *Pimelodella avanhandavae* from the upper Paraná River, and *Pimelodella laurenti* and *Pimelodella vittata* from the São Francisco River. A sixth, unidentified, probably undescribed, species from the upper Tocantins River (MCP 16056) is also included here and listed below as *Pimelodella* sp. 5. *Pimelodella spelaea* is compared to these species below, but because of the confused state of the taxonomy of *Pimelodella*, it was not practical to compare more broadly across the genus.

Pimelodella spelaea new species
Figure 1

Holotype.—MZUSP 81726, 80.5 mm SL, Brazil, State of Goiás, São Domingos, upper Tocantins River basin, subterranean stream tributary to São Bernardo River inside São Bernardo Cave, 13°49'S 46°21'W, 26 July 2000, E. Trajano and M. E. Bichuette.

Paratypes.—Seven specimens, same locality of holotype. MZUSP 81727, 42.8 mm SL, and MCP 31482, 1 + 1 c&s, 47.5–66.7 mm SL, same data of holotype. MZUSP 81728, 47.3 mm SL and

TABLE 1. DESCRIPTIVE MORPHOMETRICS OF *Pimelodella spelaea*. Standard length is expressed in millimeters.

Character	<i>n</i>	Low	High	Mean
Standard length	8	42.8	80.5	61.6
Percents of standard length				
Predorsal length	8	32.5	36.7	34.2
Preanal length	8	64.1	66.7	65.5
Caudal peduncle length	8	21.4	23.8	22.5
Caudal peduncle depth	8	5.1	8.5	7.2
Lower caudal-fin lobe	8	19.6	24.5	22.2
Upper caudal-fin lobe	7	21.6	27.3	24.5
Anal-fin base	8	11.1	13.6	12.4
Urogenital papilla to anal fin	8	8.0	10.3	9.2
Dorsal-fin base	8	12.4	14.4	13.7
Dorsal-fin spine length	7	11.8	18.0	13.7
Longest dorsal-fin ray	8	14.4	20.1	17.0
Dorsal fin to adipose fin	8	10.7	13.7	12.3
Adipose-fin base length	8	26.5	30.2	28.6
Pectoral-fin spine length	8	13.2	18.2	16.1
Pectoral-fin length	8	16.5	20.1	18.2
Pelvic-fin length	8	12.9	15.8	14.0
Body depth	7	12.0	17.1	15.3
Head depth	8	12.1	16.3	13.8
Body width at cleithrum	8	17.1	20.6	18.7
Posterior cleithral process	8	8.6	10.5	9.7
Head length	8	21.7	25.5	23.4
Maxillary barbel length	7	47.6	72.4	61.1
Mentonian barbel length	8	22.5	30.4	27.2
Percents of head length				
Interorbital distance	8	25.0	28.5	27.0
Orbital length	8	23.8	29.1	26.2
Eye ball diameter	8	19.0	21.3	20.1
Snout length	8	38.8	43.0	41.6
Internareal length	8	14.7	16.9	15.6
Internareal distance	8	19.0	21.5	20.1
Mouth width	8	33.6	39.9	37.5

MCP 31483, 59.7 mm SL, 12 July 1999, M. E. Bichuette and R. H. Santos. MZUSP 81729, 2, 72.7–75.8 mm SL, 21 May 1999, F. C. T. Lima.

Diagnosis.—*Pimelodella spelaea* can be distinguished from all of its congeners (except *P. kroniei*) by derived troglomorphic features such as smaller eyes (eyeball diameter 19.0–21.3% HL vs 24.3–34.8% HL in other species, but 20.6–35.9 in *Pimelodella australis*) and fainter coloration with reduced lateral dark band. From *P. kroniei*, it is distinguished by its comparatively larger eyes, which despite being reduced are always visible (vs usually not visible externally in *P. kroniei*).

In addition to smaller eyes and fainter coloration, *P. spelaea* differs from the other species in eastern central Brazil by possessing 10 branched rays in the pectoral fin (vs 8–9 branched rays). From *P. laurenti*, it also differs

by its weakly developed serrae in the posterior margin of dorsal-fin spine (vs serrae well developed in *P. laurenti*); and from *Pimelodella avanhadavae* the new species is further distinguished by lacking the dorsal dark stripe along dorsal and anterior adipose fins (Eigenmann, 1917:pl. 29 fig. 3).

Description.—Morphometric characters given in Table 1. Body very elongate, its highest depth at vertical passing by dorsal-fin origin. Dorsal profile slightly convex and elevating from snout tip to base of dorsal-fin spine; then descending to caudal peduncle, slightly convex at adipose-fin base. Ventral profile of body nearly straight from mouth to caudal peduncle. Body slender in dorsal view, widest at exposed cleithral process. Head broad in dorsal view, lateral margins of supraoccipital process nearly parallel, almost touching the predorsal plate. Mouth slightly in-

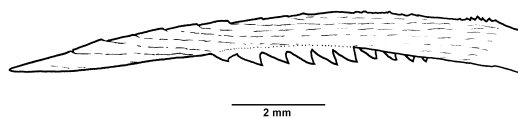


Fig. 2. *Pimelodella spelaea*, pectoral-fin spine, dorsal view. Scale 2 mm.

ferior; small, conic teeth irregularly arranged in plates on dentaries and premaxillae. Eyes reduced in size (19.0–21.3% HL) but apparently functional. Maxillary barbels comparatively short (47.6–72.4% SL), reaching between pelvic-fin insertion and origin of anal fin. Mental barbels short, outer slightly longer, reaching end of pectoral-fin base.

Dorsal fin with one spinelet, one spine and 6 (7) or 7 (1) branched rays, originating approximately above end of pseudotympanum. Dorsal-fin spine smooth, without serrae and comparatively short, its length about three-fourths of first branched ray. Distal margin of dorsal fin slightly convex. Adipose fin comparatively short (26.5–30.2% SL), its origin on vertical through urogenital papilla, and its end slightly posterior to end of depressed anal fin. Adipose fin with slightly convex dorsal margin and very small posterior free lobe. Anal fin short and with convex posterior margin, with 5 (7) or 6 (1) simple and 8 (1), 9 (6), or 10 (1) branched rays. Caudal fin deeply forked, dorsal lobe slightly longer than ventral. Upper lobe with $i+7$ (8) and lower lobe with $i+8$ (8) principal rays.

Pectoral fins with one spine and 10 (8) branched rays (one specimen with 9 branched rays on one side), reaching vertical through third or fourth dorsal-fin ray when depressed. Pectoral-fin spine with weak retrorse serrae occupying up to about two-thirds of posterior margin and very small thorns on anterior margin, restricted to proximal portion (Fig. 2). Serrae on posterior margin of pectoral-fin spine increasing with size, 5–6 in smaller to 11–13 in larger specimens. Bony, pungent portion of spine shorter than first branched ray. Distal margin of dorsal fin slightly convex. Posterior process of cleithrum roughly triangular, concave posterodorsally, ornamented with a series of longitudinal, low bony ridges. Pelvic fin short, reaching midway between urogenital papilla and anal-fin origin, with one unbranched and 5 (8) branched rays. Pelvic fin originating on or slightly posterior of vertical through end of dorsal-fin base.

Color in alcohol.—Overall body coloration pale yellowish, lighter ventrally. Dorsum of body, from top of head to behind adipose fin, slightly

darkened. Eyes dark grey. Concentration of chromatophores on supraoccipital process and predorsal plate smaller than in neighboring skin, making bones lighter than fleshy dorsum. Skin covering dorsal-fin spine and dorsal margin of adipose fin slightly dusker. Chromatophores more concentrated on pseudotympanum and continuing to caudal peduncle around lateral line, forming faint lateral stripe, hardly distinguishable in some specimens.

Color in life.—Dorsal portions of body light gray with a faint lateral stripe. Fins and most of body, especially caudal peduncle highly translucent. When removed from water, skin has slight purple or greenish iridescence.

Etymology.—Specific epithet *spelaea* from the Latin *speleum*, cave, cavern, in allusion to its habitat. An adjective.

Distribution.—Known from its type-locality only, a small upper tributary of the São Bernardo River inside the São Bernardo Cave, upper Tocantins River, São Domingos, State of Goiás, Brazil.

Habitat and ecology.—The type-locality of *P. spelaea* is situated within the limits of the Terra Ronca State Park (13°30'–13°50'S, 46°10'–46°30'W), in São Domingos, eastern State of Goiás. São Domingos is a carbonatic karst area characterized by the presence of continuous limestone outcrops belonging to the Bambuí Formation and crossed by several parallel clear water streams running westward to join the Paranã River, a tributary of the upper Tocantins River. It lies in the Cerrado (the savannah-like Brazilian vegetation) phytogeographic domain and is characterized by a tropical semi-humid climate (Nimer, 1989). This is a seasonal climate with a well-defined dry season from March and April to September and October, and possibility of strong rains in December to February, when caves or cave conduits may be partially or completely flooded depending on conduit dimensions and topography. The São Bernardo Cave (13°49'S, 046°21'W) is part of a cave system (São Bernardo-Palmeiras) with 8000 linear m of development. This particular cave has about 3500 m of linear development and is crossed by a subterranean river with mean width and depth of 5 m and 0.60 m, respectively. There is a small tributary in the left margin where the fishes occur 700 m downstream from the cave entrance. This vadose tributary is in a higher level compared with the main stream and empties into it through a small waterfall. The fishes occur mainly in soft-bottomed pools with very

slow current. About 1500 m downstream from this tributary, the São Bernardo River joins the Palmeiras River inside the cave.

The accessible fish habitat is a slow moving, soft-bottomed pool, 5 m long, 2 m wide and averaging 1.5 m deep, situated 5 m above the mainstream level. Water from the pool forms a shallow water course flowing over a rocky bed along 50 m and discharging into the mainstream through a small waterfall. Access to the fish habitat upstream of the pool requires scuba gear, and the total extent of this habitat is unknown. Just a few *Pimelodella* catfishes were seen in the shallow reach. Four tetra characins (*Crea-grutus* sp.) and a small armored catfish (*Hypostomus* sp.) were found along with *P. spelaea*.

Physico-chemical variables in the *P. spelaea* pool, measured with a digital HORIBA apparatus in May 1999/May 2000/September 2000, are the following: temperature (C) = 24.5/24.8/24.6; pH = 7.31/7.15/7.30; dissolved oxygen (mg l^{-1}) = 7.45/7.65/-; conductivity (ms cm^{-1}) = 0.588/0.607/0.546; salinity (%) = 0.02/0.02/0.02. In the main subterranean river, the environmental variables in May/1999/May/2000/August/2000 were temperature (C) = 23.6/25.7/24.5; pH = 6.36/7.35/7.40; dissolved oxygen (mg l^{-1}) = 8.66/7.67/7.99; conductivity (ms cm^{-1}) = 0.013/0.038/0.024; salinity (%) = 0/0/0. These variables measured in May 1999 in the epigeal reach before the main cave stream sinkhole were temperature (C) = 24.8; pH = 5.63; dissolved oxygen (mg l^{-1}) = 8.03; conductivity (ms cm^{-1}) = 0.010; salinity (%) = 0.

The physico-chemical conditions of water (e.g., pH higher than in base-level streams and typical of slow moving karst waters) and the absence of small epigeal tributaries to the São Bernardo River basin indicate that the hypogean upper tributary where *P. spelaea* lives originates from epikarst waters (the uppermost layer of a karstified rock in which a large proportion of fissures have been enlarged by solutional erosion allowing for a rapid infiltration and storage of large quantities of water; Drew, unpubl.), forming a perched aquifer.

Data on number of captured, marked and recaptured specimens in each date are as follows: 1 May: 13 captured, marked and released (+ 8–9 observed), SL = 49.4–81.7 mm, weight = 1.4–4.5 g; 26 July: 57 captured (including three recaptures), 53 marked and released, SL = 43.7–87.3 mm; weight = 0.9–5.4 g; 8 September: 43 captured (including 24 recaptures, one double), SL = 56.7–77.0 mm; weight = 1.6–4.4 g. The number of individuals in the study section, estimated by Lincoln-Petersen method, is 188.5 (SE = 81.3) for beginning of May, and 95 (SE

= 12) for the end of July (assuming losses but no gains along the study period).

The distributions of frequencies of standard length, weight and condition factor (K) in July and September in the cave habitat are shown in Figure 3. Most specimens examined were very skinny and some were severely underfed. For most specimens recaptured in September (16 of 24 captured fish), the measured values of SL and weight were lower than in July, representing cases of weight loss associated with negative growth in length, that is, these fish shrank (conditions during the measurements, including the caliper used, the person taking the measurements and the degree of fish anesthesia, were similar at all occasions). After a period of 44 days, the differences in standard length (SL in September, SL in May) ranged from -1.0 to $+0.3$ mm (mean = -0.25 mm), and all but one recaptured fish lost weight (differences in weight ranged from 0 to -0.7 g). No specimen showed developed gonads (that would be seen by transparency, if present).

The power coefficient (b) for the pooled data was 2.351. Mean (and standard deviation) for standard length, weight and condition factor were, respectively, May ($n = 13$)–64.7 (8.09), 3.17 (0.86), 4.16 (0.78); July ($n = 53$)–68.1 (7.87), 3.24 (0.88), 4.06 (0.82); and August ($n = 43$)–67.4 (6.30), 2.98 (0.71), 3.79 (0.68). Tendencies in monthly means depicted as Dice-Leraas diagrams are shown in Figure 4A–C. A tendency of decrease in weight and condition factor from July to September is apparent in the graphs (Figs. 3–4), which is in accordance with data from recaptured specimens. Nevertheless, *t*-test failed to show a significant difference between these months: for standard length, $t = 0.423$, $P = 0.673$; for weight, $t = 1.520$, $P = 0.132$; for condition factor (K), $t = 1.713$, $P = 0.090$ (marginally significant). The latter is close to the adopted critical significance value ($P = 0.05$), supporting the idea of a tendency of decrease in condition factor toward the end of the dry season.

For *P. kronei*, the power coefficient (b) was 2.768 for the pooled data (1984 plus 1985; $n = 76$), and 2.806 for 1984 alone ($n = 55$). No difference was observed between consecutive years (Fig. 4D).

Comparison of the length measurements in the field (under anesthesia) and after preservation in alcohol of six specimens of *P. spelaea* revealed differences of 1.2–6.5% of standard length, with values always lower after preservation. Such differences should be taken into account when comparing size distributions of fish samples before and after preservation.

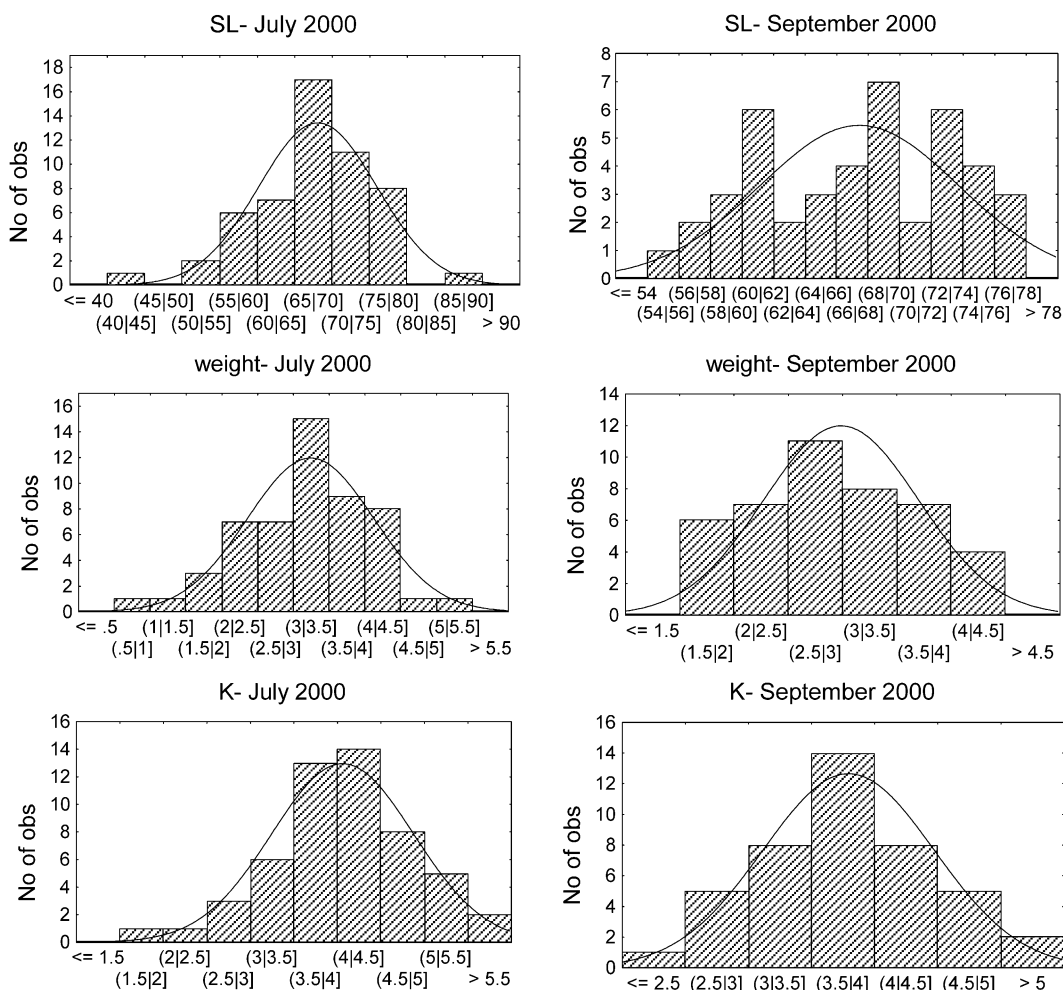


Fig. 3. Distribution of frequencies of size (standard length, SL), weight and condition factor of *Pimelodella spelaea*, in May ($n = 13$), July ($n = 53$) and September 2000 ($n = 43$).

Notes on behavior.—Specimens observed in the habitat were calmly swimming near the bottom, in the midwater and near the surface. However, when approached, they immediately avoided the observer, showing an evident photophobic behavior. As other *Pimelodella* catfishes, these are very elusive fishes, difficult to capture with hand nets.

DISCUSSION

The subterranean ichthyofauna from São Domingos karst area encompasses seven troglomorphic species—the gymnotiform *Eigenmannia vicentespelaea*, the loricariid *Ancistrus cryptophthalmus*, the trichomycterids *Ituglanis passensis*, three undescribed *Ituglanis* species (MEB and ET, unpubl. data), and *P. spelaea*. This is the highest number of troglomorphic fish species

recorded for a single, relatively small karst area in the world. In addition, several nontroglomorphic fishes have been captured in these caves, on a more or less regular basis, including the heptapterids *Rhamdia quelen*, *Imparfinis minutus*, *Imparfinis hollandi*, *Cetopsorhamdia molinae*, a cetopsid, loricariids, gymnotiforms, characiforms and a cichlid (Bichuette and Trajano, 2003).

Five troglomorphic heptapterids are known from Brazil: *P. spelaea*, *P. kroni* (Ribeiro, 1907), from the State of São Paulo, southeastern Brazil, and three undescribed, highly troglomorphic species from the State of Bahia, northeastern Brazil, two of them belonging to the subclade *Nemuroglanis* sensu Ferraris, 1988 (Trajano and Bockmann, 1999) and a new *Rhamdia* (ET and MEB, unpubl. data).

Although smaller than in epigeal relatives,

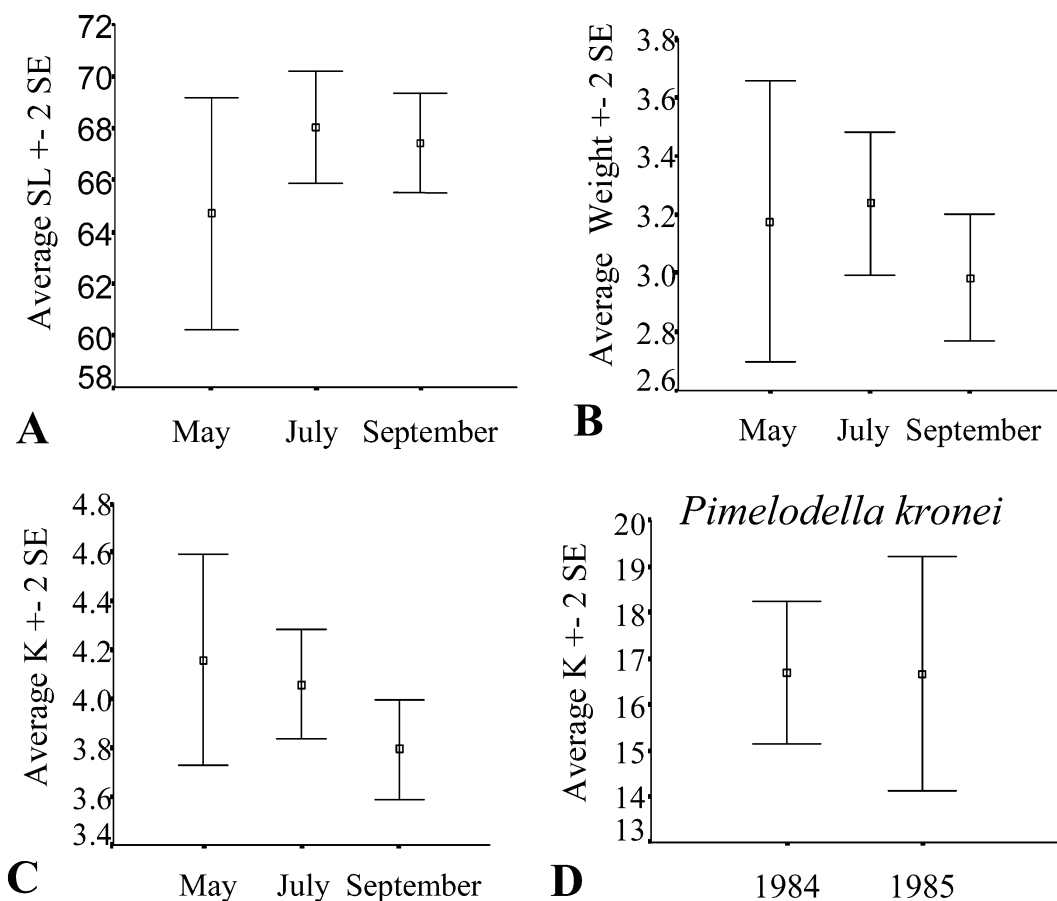


Fig. 4. Dice-Leras diagrams showing tendencies in standard length (A), weight (B), and condition factor (C) of *Pimelodella spelaea*, from Central Brazil, during the dry season of 2000 (May, $n = 13$; July, $n = 53$; September, $n = 43$), and condition factor of *Pimelodella kronei* (D), from southeastern Brazil, during the dry seasons of 1984 and 1985. Central squares = means; vertical bars = \pm standard errors.

the eyes of *P. spelaea* show a low degree of reduction in comparison to other troglotic heptapterids, such as *P. kronei* (the great majority of specimens with eyes not externally visible; Trajano and Britski, 1992), and the heptapterids from Bahia, which are completely eyeless and unpigmented. A great deal of intra- and interspecific variation in eyes development is observed among cave *Rhamdia* species (Weber, 1996), but most have eyes far more reduced than *P. spelaea*.

Pigmentation is also not greatly reduced in *P. spelaea*. Although it is clearly paler than most epigeal relatives, the color pattern typical of *Pimelodella* catfishes is distinguishable in most specimens, with a faint, but generally visible lateral stripe. Paler color may be attributed to the density of chromatophores in *P. spelaea*, that is, lower than in epigeal species. A comparison with an unidentified epigeal species of *Pimelo-*

della (MCP 16056) from the same river basin of *P. spelaea*, the upper Tocantins River, revealed a significant lower density of chromatophores per square millimeter in the latter (*P. spelaea*: 71–110 [$n = 8$, mean 91.5, SD 17.5], *Pimelodella* sp.: 110–220 [$n = 10$, mean 154.8, SD 38.6], $P = 0.008$).

The high recapture rates in *P. spelaea* (53% from July to September) indicate permanence in the study site at least for short periods (44 days). Preference for slow-moving waters with soft-bottom and tendency to sedentariness was also observed for the troglotic *P. kronei* (Trajano, 1991) and its epigeal putative sister-species, *Pimelodella transitoria* (P. Gerhard, unpubl. data).

Comparison with another cave *Pimelodella* catfish, *P. kronei*, studied in seasons corresponding with the study period for *P. spelaea*, emphasizes the low average condition factor observed for

the latter, at least during the dry season. *Pimelodella kronei* clearly is a more robust and better fed cave catfish. This may be partly a species-specific difference, with *P. spelaea* descending from an epigean taxon with a more delicate constitution, and partly caused by differences in food availability along the year in their respective cave habitats. *Pimelodella kronei* lives in base-level cave streams that flow continuously during the dry season, which is not as accentuated and well defined as in *P. spelaea* locality. Therefore, a reasonable amount of food items would be available throughout the year for *P. kronei*.

The low condition factor recorded for *P. spelaea*, which tended to decrease along the study period, indicates a regime of severe food limitation, intensifying along the dry season. The same was reported for the troglobitic trichomycterid *Trichomycterus itacarambiensis*, from eastern Brazil, also with cases of negative growth (shrinkage in length; Trajano, 1997). The cleared-and-stained *P. spelaea* specimen, a very thin, severely underfed individual, showed no skeletal abnormalities, including the vertebrae. Therefore, apparently the shrinkage in length recorded in some of the marked and subsequently recaptured fishes is not explained by alterations in the axial skeleton.

Feeding stress increasing along the dry season is consistent with the decrease in the number of specimens estimated for the study section from May to July, possibly a consequence of loss caused by mortality. However, the density of specimens in the study site (about one individual per m^{-2}) may be considered high for cave (Trajano, 2001) and for epigean standards as well. The higher availability of prey in large, vadose (aerated) conduits, represented by terrestrial food items, explains the concentration of *P. spelaea* in the accessible study area. A much lower population density is expected to occur in the phreatic area of distribution.

The actual extent of *P. spelaea* habitat is not known, but the cave topography, the absence of records in other localities in spite of the intensive collecting effort in the area, and the lack of adaptations to life in small phreatic spaces, indicate a geographically restricted habitat. Therefore, we estimated the total population size of *P. spelaea* in hundreds, possibly reaching 1000 individuals, which is a small population size even for cave fish standards (Trajano, 2001).

The low degree of troglomorphy affecting eyes and melanic pigmentation of *P. spelaea* is consistent with the observed for the other cave fishes from São Domingos karst area. *Eigenmannia vicentespelaea*, from a different cave system,

exhibits a similar low degree of reduction of eyes and pigmentation (MEB, unpubl. data), and a great deal of intra- and interpopulation variation occurs in *Ancistrus cryptophthalmus* (Bessa and Trajano, 2002). The four species of *Ituglanis* have more reduced eyes and pigmentation, but there is still some individual variation and none of these populations is homogeneously anophthalmic and unpigmented (MEB, unpubl. data), unlike troglobitic catfishes found in some other Brazilian karst areas (e.g., the new heptapterids from Bahia, and the loricariid *Ancistrus formoso*, from Mato Grosso do Sul). This indicates relatively short times of isolation in the subterranean habitat for the cave fishes from São Domingos.

The vadose tributary where *P. spelaea* lives is nowadays mostly isolated from the main, base-level drainage, by differences in topographic level, as a consequence of alluvial downcutting resulting in a regional progressive lowering of the water table. Epigean *Pimelodella* ancestors probably lived in water courses at the preterite base level, directly flowing into caves and allowing for the establishment of cave populations. As a consequence of alluvial downcutting, such formerly running-water streams would become perched and fed by infiltration water from the epikarst. Therefore, differences in topographic level may account for (at least partial) isolation of fish populations surviving in perched water bodies. Topographic isolation has been proposed by Borowsky and Mertz (2001) to explain the genetic differentiation between populations of the cave balitorid, *Schistura oedipus*, from Thailand.

However, in spite of intensive collecting efforts in the epigean stream reaches of the area, where other heptapterids (*Imparfinis hollandi*, *Cetopsorhamdia molinae*, *Phenacorhamdia tenebrosa*) have been sampled, no *Pimelodella* catfish was found (Bichuette and Trajano, 2003). It is possible that epigean populations also descending from the ancestor of the troglobitic *Pimelodella* disappeared from this area. We hypothesize that the morphological differentiation resulting in the presently described taxon occurred in allopatry, either because of topographic isolation or because of local extinction of epigean relatives, or both factors combined.

This also applies to the three undescribed troglobitic species of *Ituglanis* from São Domingos region, respectively, from upper vadose tributaries in Angélica and in São Mateus caves and from a side pool in São Bernardo Cave (not syntopic with *P. spelaea*), for which no epigean relatives have been found in the area. However, the model does not fit *A. cryptophthalmus* and *E.*

vicentespelaea, that live in subterranean base-level streams continuous with epigeal reaches where epigeal relatives are currently found. Therefore, the expressive diversity of cave fishes in São Domingos karst area seems to be the result of a combination of different, but all relatively recent, events and processes.

Conservation remarks.—It is well known that subterranean ecosystems are fragile, very vulnerable to disturbance, and several troglotic fishes around the world are currently endangered by threats such as habitat degradation, hydrological manipulations, pollution, and human activities (Proudlove, 2001). In the case of *P. spelaea*, no immediate threat has been identified. Nevertheless, the fact that, in spite of intensive study in the caves of São Domingos karst area, *P. spelaea* was found in only one restricted site inside a single cave, the São Bernardo Cave (high degree of endemism), and the periods of severe food stress to which this species is subject, point to an intrinsic fragility calling for protective measures. The type locality of *P. spelaea* is situated within the boundaries of a State Park, the Parque Estadual de Terra Ronca. However, visitation to caves is poorly controlled, and no management plan has been enforced so far. Enforcement of control of visitation to São Bernardo Cave, with interdiction of access to *P. spelaea* site, is therefore recommended for effective protection of this species.

COMPARATIVE MATERIAL EXAMINED

All localities in Brazil: *Pimelodella australis*, MCP 9349 (48 specimens), Rio Saicã near Cacequi, Rio Grande do Sul. *Pimelodella boschmai*, MZUSP 22932 (8 specimens), Rio Mogi-Guaçu at Emas, São Paulo. *Pimelodella gracilis*, MCP 23140 (10 specimens), Rio Jaguarí near São Francisco de Assis, Rio Grande do Sul. *Pimelodella kronei*, MCP 18312 (2 specimens) Areias de Cima Cave, Iporanga, São Paulo. *Pimelodella lateristriga*, MCP 12574 (10 specimens), Córrego da Posse near Carmo, Rio de Janeiro. *Pimelodella laurenti*, ANSP 69380 (holotype) and ANSP 69381 (2 specimens), Rio São Francisco at Jatobá, Pernambuco, and MZUSP 46454 (5 specimens), Rio Verde at Montes Claros, Minas Gerais. *Pimelodella meeki*, MCP 28519 (1 specimen), Ribeirão Cachoeira near Piracicaba, São Paulo, MCP 28520 (3 specimens), Rio Piracicaba at Piracicaba, São Paulo, and MZUSP 22485 (8 specimens) Rio Corumbataí at Corumbataí, São Paulo. *Pimelodella pappenhaimi*, MCP 16526 (13 specimens), Ribeirão São Luís near Apiúna, Santa Catarina. *Pimelodella transitoria*, MCP

28513 (6 specimens), Rio Ipiranga, near Sete Barras, São Paulo. *Pimelodella vittata*, MCP 16695 (46 specimens), tributary to Rio São Francisco near Bocaiúva, Minas Gerais and MZUSP 47310 (5 specimens), Rio Jequitáí, between Buenópolis e Engenheiro Dolabela, Minas Gerais. *Pimelodella* sp. 1, MCP 25003 (10 specimens), Rio Guamá near São Miguel do Guamá, Pará. *Pimelodella* sp. 2, MCP 15783 (6 specimens), Rio do Bugre, near Porto Esperidião, Mato Grosso. *Pimelodella* sp. 3, MCP 15708 (5 specimens), Rio do Bugre at Barra do Bugre, Mato Grosso. *Pimelodella* sp. 4, MCP 15775 (62 specimens), Rio Paraguay at Cáceres, Mato Grosso. *Pimelodella* sp. 5, MCP 16056 (15 specimens), Riacho Arara near Rosariana, Niquelândia, Goiás.

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