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Multiple-step vertical colonization of the subterranean environment: Brazilian troglobitic catfishes as case studies

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Background

Brazil, a paradise for subterranea fishes

Brazil is distinguished worldwide by a rich subterranean ichthyofauna, composed by many troglophilic populations and 30+ troglobitic species. The latter are distributed throughout the country (Fig 1.), occupying diverse types of habitats (Fig. 2) and present a great deal of intra- and interpopulation variability regarding the degree of troglomorphism (Fig. 3), without a taxonomic correlation (Trajano & Bichuette, 2010). On the other hand, there is a geographic correlation with the degree of troglomorphism.

As a consequence of such diversity, Brazilian subterranean fishes are excelent models for testing evolutionary and ecological models in Biology.

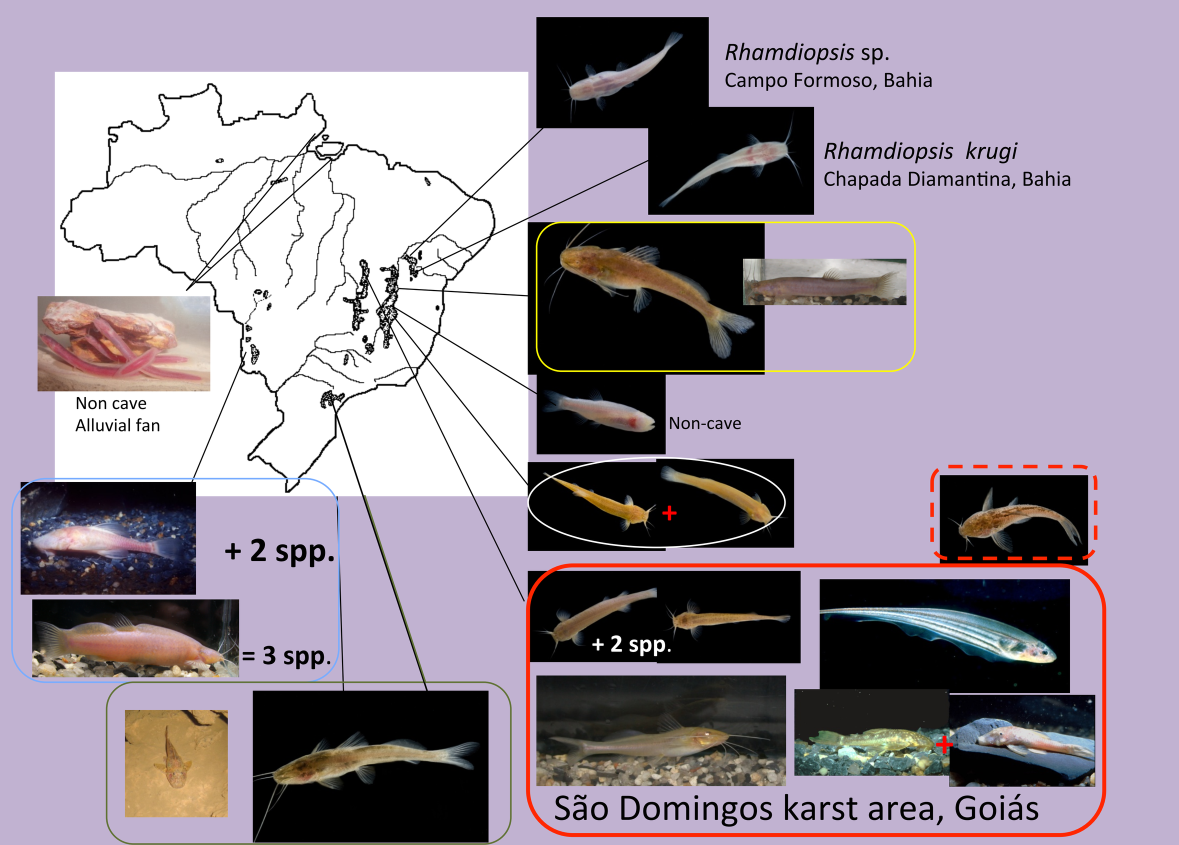
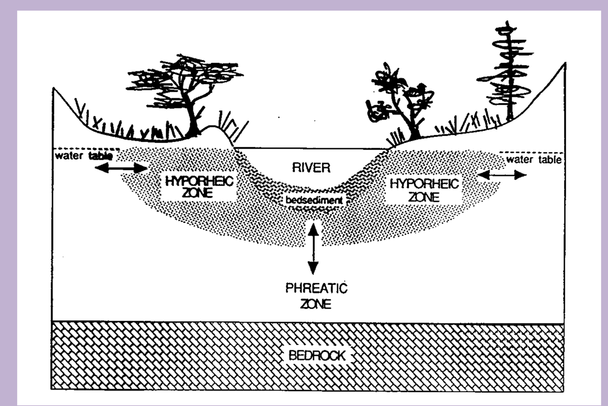
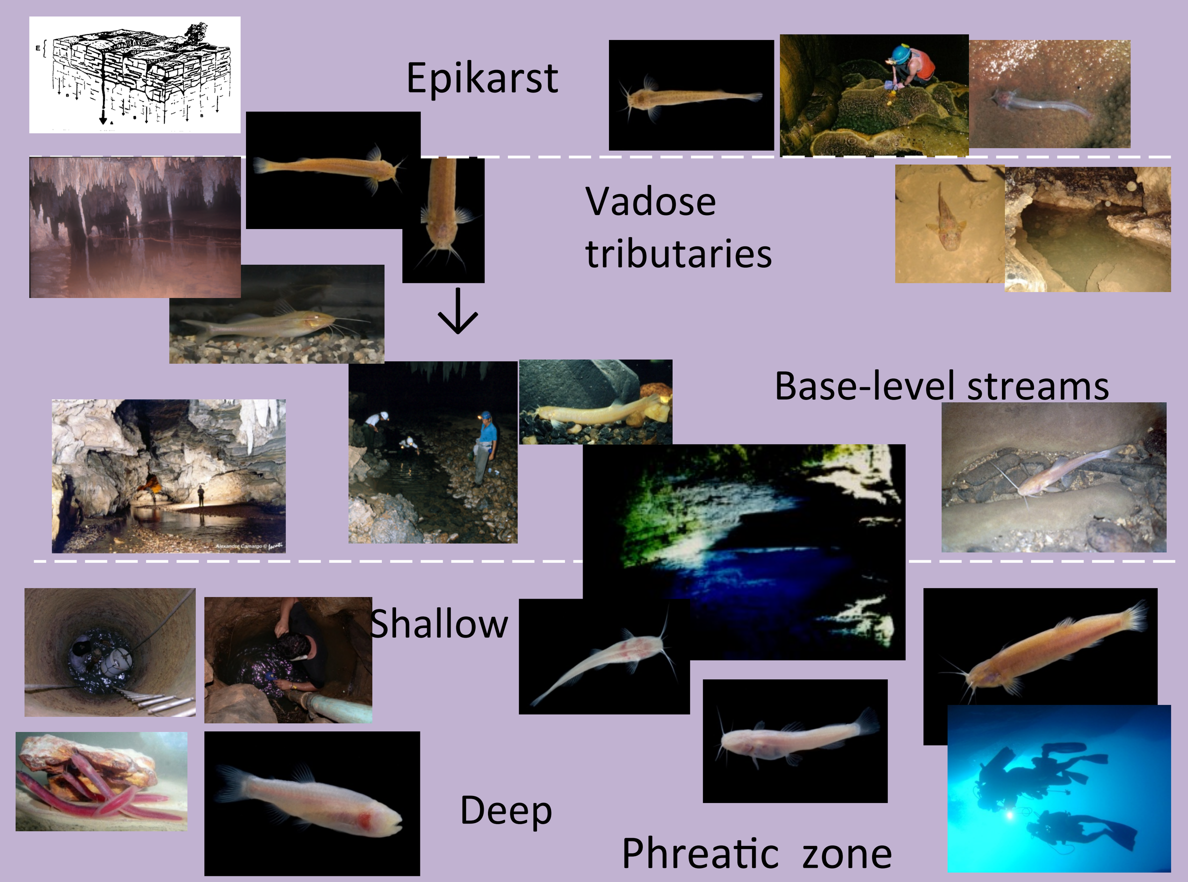
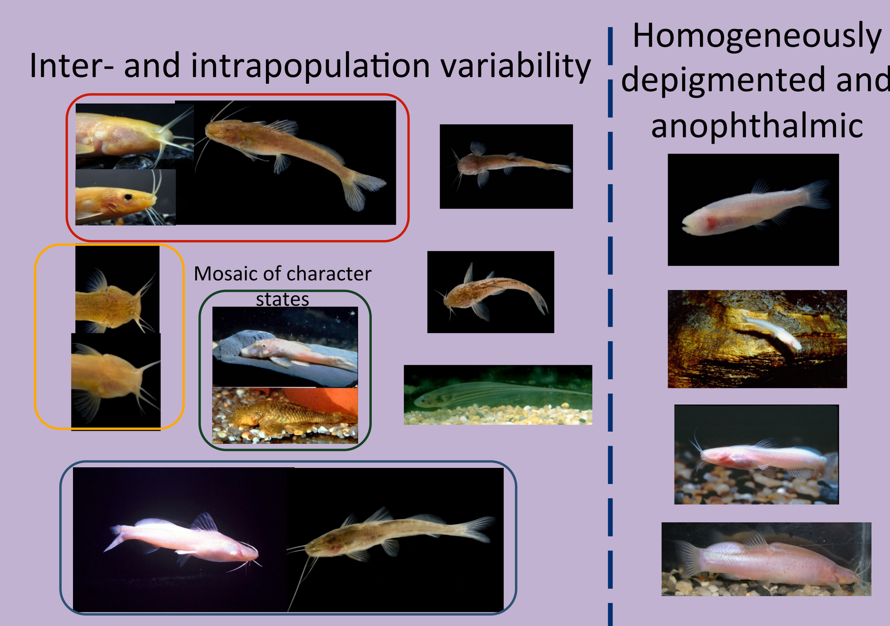


Figure 1. Distribution of troglobitic fishes in Brazil *versus* degree of troglomorphism

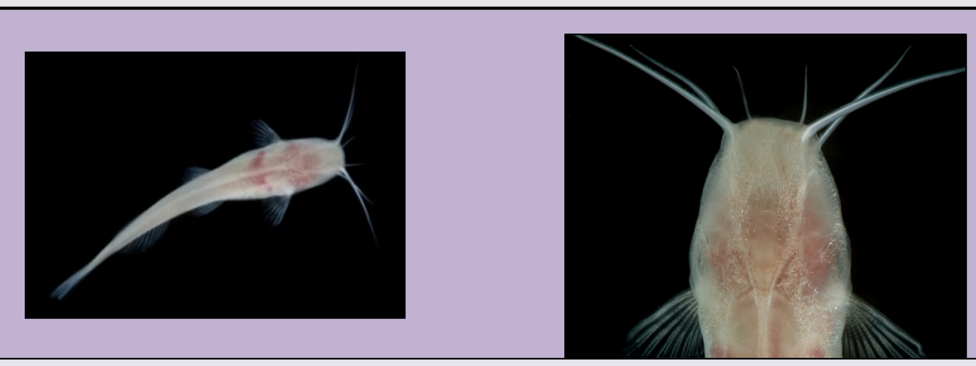


Pathway of colonization of the upper phreatic zone through the hyporheic





Rhadiopsis krugi, a paradox: adaptations for both small and large spaces

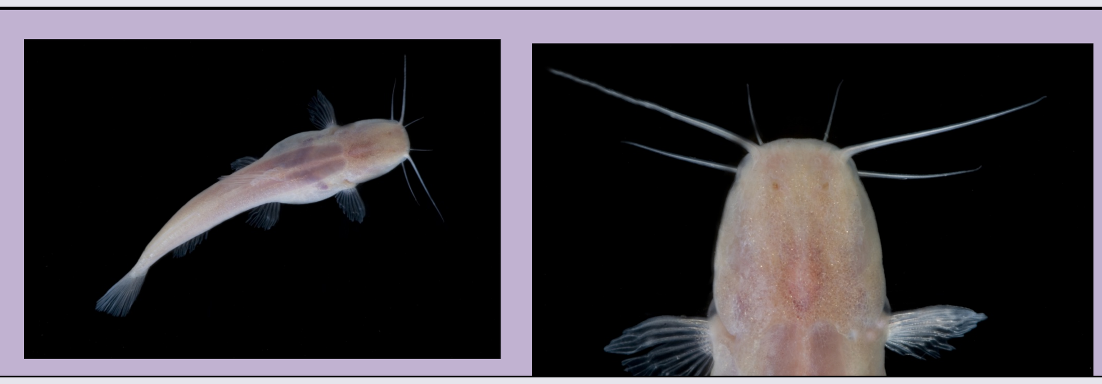


Multiple step vertical colonization of subterranean habitats (Bichuette et al, 2015)

Ω Step 1. (probably during dry paleoclimatic phases). Colonization by typically stream-dwelling *Rhamdiopsis*-like specimens of the hyporheic zone: narrow spaces → **miniaturization** through pedomorphosis; **slender, elongated** and **flexible bod;**, **reduced, very short lateral line in the trunk**; food limitation → **fatty cells** spread throughout the body.

Ω Step 2. Colonization of the hypogean habitat (shallow phreatic zone) → more heterogeneous and larger spaces: **pseudotympanum overdeveloped** (hearing ↑); **broadening of the head and snout** (↑ free neuromasts, taste buds),repositioning of the dorsal and pectoral fins (enhanced stability); frequent activity at midwater.

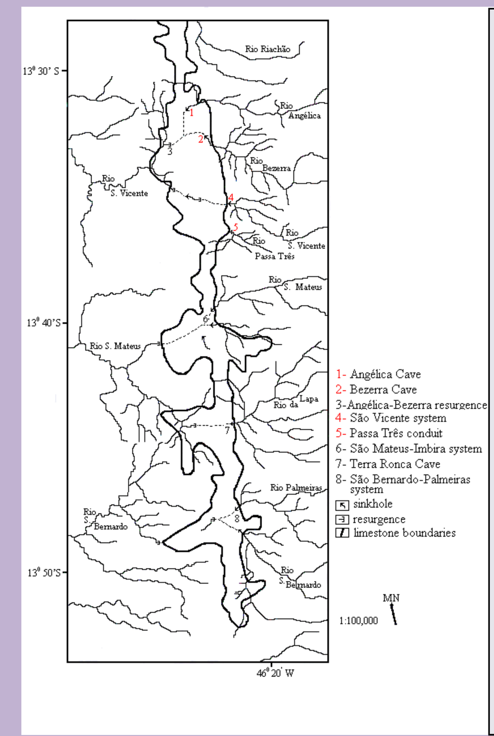
Rhamdiopsis sp. *n.*, another paradox: adaptations for deep phreatic zone, but in shallow water; close to *R. krugi*, but geographically separated in surface



Multiple-step vertical colonization of subterranean habitats, a third step: deep phreatic zone

Ω Step 1 and 2. As in *R. krugi*: **pseudotympanum** widely **exposed** (at least in juveniles) ; **lateral line cannals in the head** are **broad** ; **elongated barbels**; activity at midwater.

Ω Step 3. Adaptations to life in the deep phreatic zone (lower oxygen concentration scarcer food): **head and trunk almost entirely filled by fatty** subcutaneous corpuscles.; **cannibalism**, probably as a density-dependent mechanism of population control; **skin** with **dark pink** coloration when in natural habitat, suggesting facultative cutaneous oxygen uptake.



São Domingos karst area: why so many troglobitic fishes ?

São Domingos karst area harbours a rich fauna of troglophilic fishes and terrestrial invertebrates and a exceptional troglobitic ichthyofauna, with seven nominal species (four *Ituglanis* species), but no troglobitic aquatic invertebrate. (Bichuette & Trajano 2003; Trajano & Bichuette, 2010).

Larger caves are crossed by high-energy allochthnous streams carrying large amounts of organic matter. These streams run parallel from their watershed till the resurgence in non-karst terrain, forming separate cave systems. Each fish species is endemic to one cave system, except *Ancistrus cryptophthalmus.*

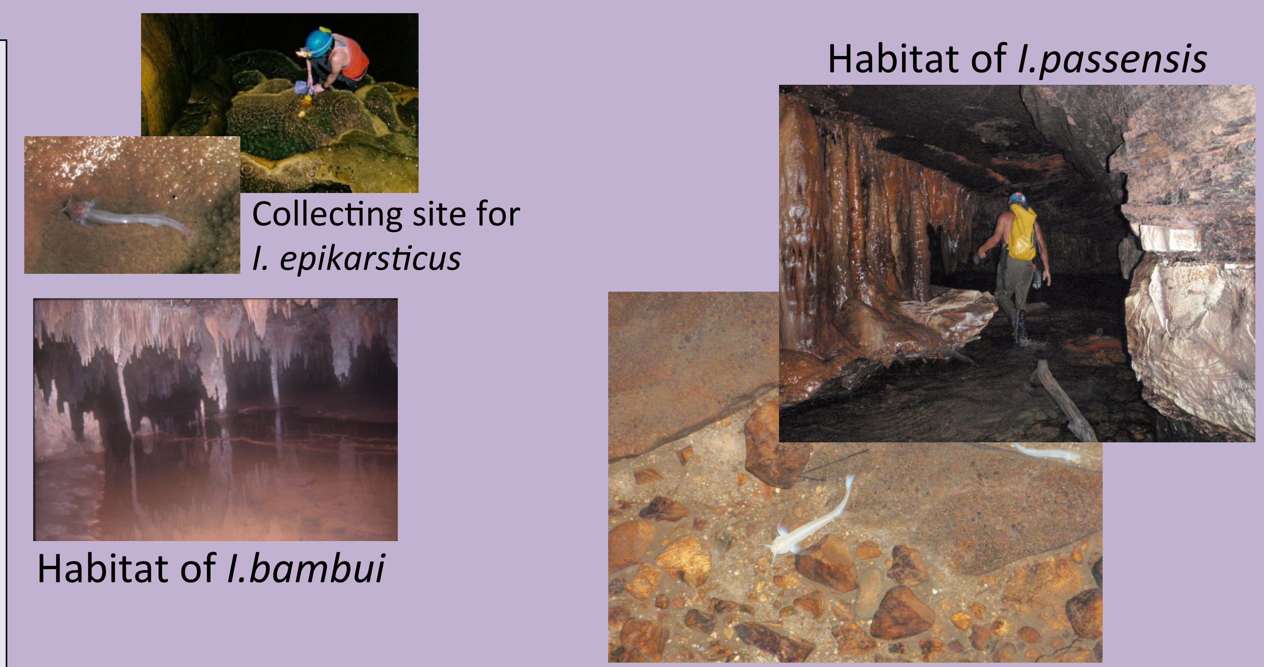
On the other hand, the São Domingos karst area is situated in a paleoclimatically stable region, hence the low number of troglobitic invertebrates.

The case of *Ituglanis* catfishes (Trichomycteridae)

Ituglanis spp. (except *I. passensis*) show adaptations to life in narrow, confined spaces (e.g., small size, reduced number of vertebrae, 36 vs. 38 in epigean species.) and are associated with the epikarst: *I. ramiroi* and *I. bambui* in vadose tributaries fed by epikarst water, *I. epikarsticus* in one permanently wet rimstone pool – its source-population would be in the perched aquifer.

The mosaic distribution of character states and separation of the cave systems indicate an independent origin for these species, from epigean ancestor presently extict.

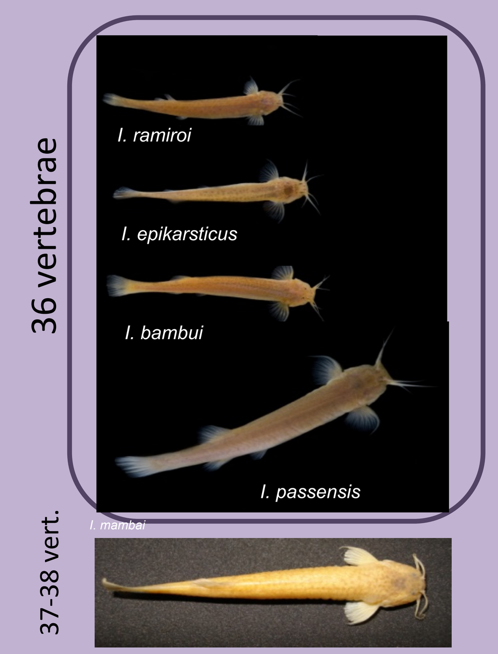
These species would be in **Step 1** according to our model of vertical colonization of karst.



Collecting site for *I. epikarsticus*

Habitat of *I.bambui*

Habitat of *I.passensis*



Troglobitic *Ituglanis* from São Domingos region - comparing number of vertebrae (specimens in the same scale)

I. mambai, from Posse Co.

What about *Ituglanis passensis*?

Ituglanis passensis lives in a open-channel upper tributary, presently a typical lotic habitat. It is an allochthonous stream, carrying large amounts of organic matter through the sinkhol,. It is medium sized for the genus, reaching max. 65 mm standard leghth in the cave (vs. 42 – 122 mm, six described species).

However, *I. passensis* presents traits associated with **Step 1**: lowered number of vertebrae (36 = other 3 spp. from S. Domingos *versus* min. 38 in all described epigean species, including the small sized ones) (Fig. 4) and reduction of the lateral line in the body.

Hence, we propose that *I. passensis* originated from a miniatured ancestor living in a vadose tributary, like *I. bambui* and *I. ramiroi*. When the ceiling collapsed due to erosion, the large opening to the surface became the sinkhole of a small epigean stream, allowing the input of larger amounts of organic matter. Intraspecific competition could account for the selection of larger sizes in the absence of food limitation. This would be the **Step 2*** in a different model.

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