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Gross morphology of the brain and some sense organs of subterranean pencil catfishes of the genus *Ituglanis* Costa and Bockmann, 1993 (Siluriformes, Trichomycteridae), with a discussion on sensory compensation versus preadaptation in subterranean fishes

Pedro P. Rizzato[1] | **Maria Elina Bichuette**[2]

[1]Laboratório de Morfologia, Evolução e Diversidade de Vertebrados, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, Brazil

[2]Laboratório de Estudos Subterrâneos and Instituto Nacional de Ciência e Tecnologia—Biodiversidade e uso Sustentável de Peixes Neotropicais (INCT Peixes), Universidade Federal de São Carlos, São Carlos, Brazil

Correspondence
Pedro P. Rizzato, Laboratório de Morfologia, Evolução e Diversidade de Vertebrados, Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, Rua do Matão, travessa 14, no. 101, São Paulo, SP, Brazil.
Email: rizzatopp@usp.br

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Abstract

Subterranean organisms provide excellent opportunities to investigate morphological evolution, especially of sensory organs and structures and their processing areas in the central nervous system. We describe the gross morphology of the brain and some cephalic sensory organs (olfactory organ, eye, semicircular canals of the inner ear) and the swim bladder (a non-sensory accessory structure) of subterranean species of pencil catfishes of the genus *Ituglanis* Costa and Bockmann, 1993 (Siluriformes, Trichomycteridae) and compare them with an epigean species of the genus, *Ituglanis goya* Datovo, Aquino and Langeani, 2016. We compared qualitatively the size of the different brain regions and sense organs of the subterranean species with those of the epigean one, searching for modifications possibly associated with living in the subterranean environment. Our findings suggest that species of *Ituglanis* exhibit sensory characteristics that are preadaptive for the subterranean life, as only slight modifications were observed in the brains and sense organs of the subterranean species of the genus when compared with the epigean one. Because most subterranean fish species belong to lineages putatively preadapted for subterranean life, our results, discussed in the context of available information on the brain and sense organs of other subterranean species, help identify general trends for the evolution of the brain and sensory organs of subterranean fishes in general.

KEYWORDS
adaptation, cave fish, preadaptation, sensory compensation, sensory evolution, troglomorphism

1 | INTRODUCTION

> *An unusual interest attaches to everything relating to the blind fishes of the caves, partly because of their peculiar deprivation and the compensation for it afforded by the development of special sensory structures more useful to them in their subterranean situation than eyes would be, and partly because the origin of their peculiarities has proved an inviting subject of speculation and discussion with reference to the doctrine of natural selection.*
>
> Forbes, 1882

Subterranean organisms have long attracted the attention of naturalists and biologists interested in understanding how morphology evolves in association with particular characteristics of a given environment (see Culver & Pipan, 2015; Culver & Wilkens, 2000; Juan et al., 2010; Mammola et al., 2020; Protas & Jeffery, 2012; Soares & Niemiller, 2020). Subterranean fishes in particular have been central to such investigations, especially the cave fish *Astyanax mexicanus* (De Filippi, 1853) that represents a model for studies on the evolution of life in caves and other subterranean habitats (e.g., Borowsky, 2008; Gross et al., 2015; McGaugh et al., 2020). The subterranean environment is characterized by ecological features, ultimately related to the permanent absence of light, that contrast drastically with most epigean (i.e., non-subterranean) environments and make it an excellent natural laboratory for investigating morphological evolution (Juan et al., 2010; Langecker, 2000; Poulson & White, 1969; Sánchez-Fernández et al., 2018). These features include, in general, the absence of photosynthesizing organisms, leading to low levels or absence of primary production, resulting in food webs consisting of only a few trophic levels (Culver & Pipan, 2009; Poulson & White, 1969). Subterranean communities are, therefore, usually relatively simple, formed by a smaller number of species than most epigean ones (Poulson & White, 1969), so that fishes, for example, usually represent the highest trophic level of aquatic subterranean communities (Poulson, 2010; Weber, 2000).

The permanent absence of light also represents the impossibility of using vision for sensory perception (Langecker, 2000). This is possibly the most conspicuous feature of subterranean environments from the perspective of humans, for which vision is such an important sensory modality. In the absence of light, subterranean organisms are hypothesized to rely more strongly on other sensory modalities for perception, such as chemoreception and mechanoreception, mediated by hyperdeveloped (e.g., larger, longer) or overelaborated (e.g., more complex) sensory receptor organs or structures, a phenomenon known as sensory compensation (e.g., Hüppop, 1987; Jeffery et al., 2000; Langecker, 2000; Poulson, 1963; Rétaux & Casane, 2013; Schlegel et al., 2009). On the contrary, it is also hypothesized that the conditions experienced in subterranean environments may represent ecological-evolutionary filters, only surpassed by organisms with characteristics, acquired along their evolutionary history, that allow them to survive in conditions similar to those found in the subterranean environment. Those organisms would be, therefore, preadapted for colonizing the subterranean environment (e.g., Langecker, 2000; Pouilly & Miranda, 2003; Romero & Paulson, 2001). Among the possible preadaptive features of subterranean organisms is the capacity of relying mostly or solely on non-visual sensory modalities of perception.

One way to distinguish between sensory compensation and preadaptation is by means of a comparison between subterranean organisms and their closely related epigean taxa, looking for characters possibly associated with living in the subterranean environment that may seem hyperdeveloped or overelaborated in the subterranean organisms, suggesting that these modifications result from sensory compensation. Several subterranean organisms have been studied in an attempt to identify such characters, but among fishes, studies have focused on the cave fish *A. mexicanus* (De Filippi, 1853), a species belonging to a lineage, Characidae, whose members are usually diurnal, visually oriented fishes that swim freely in the water column (e.g., Brejão et al., 2013; Castro et al., 2005) and thus do not appear to be particularly preadapted to the subterranean environment in terms of sensory perception. In *A. mexicanus*, several characteristics (e.g., enlarged and predominantly ventrally spread areas with chemosensory receptors on the head, increased number of taste buds, and neuromasts) have been identified as possibly associated to living in the subterranean environment and hypothesized to result from sensory compensation (e.g., Bibliowicz et al., 2013; Hüppop, 1987; Jeffery et al., 2000; Rétaux & Casane, 2013; Varatharasan et al., 2009; Yamamoto et al., 2009; Yoshizawa et al., 2010). However, the majority of the world's subterranean ichthyofauna belongs to lineages that may be considered preadapted for surviving in the subterranean environment.

One example of a fish lineage whose members may be considered preadapted for survival in subterranean habitats is the catfish family Trichomycteridae, currently the third richest family with respect to the number of known subterranean species (Proudlove, 2023). Members of Trichomycteridae, particularly those of the subfamily Trichomycterinae, are commonly nocturnal, cryptic, generally omnivorous fishes that rely strongly on chemo- and mechanosensory perception, and some species are found burrowing in the bottom of rivers and lakes amid leaves (i.e., in the leaf litter), pebbles, and rocks (Arratia & Huaquin, 1995; Casatti, 2003; Casatti & Castro, 1998; Costa, 1992; Datovo & Bockmann, 2010; De Pinna, 1998; Sazima, 2004; Zanata & Primitivo, 2013). This is true for most species of the genus *Ituglanis* Costa & Bockmann, 1993, which currently includes seven known subterranean species (one of which is still undescribed, Table 1; Figure 1), all of them occurring in the same geographical region in the Paranã River basin, a tributary of the Tocantins River in the northeastern Goiás State, central Brazil (Datovo et al., 2016: fig. 8; Rizzato & Bichuette, 2014: fig. 1). The only epigean species of the genus occurring near the subterranean ones is *Ituglanis goya* Datovo, Aquino and Langeani 2016, which occurs in the upper Tocantins River basin, but only in tributaries in the Paranã River downstream from the region where the subterranean species are found (Datovo et al., 2016: fig. 8). Evidence suggests that, similar to *A. mexicanus*, each subterranean species of *Ituglanis* evolved independently in the subterranean environment (Bichuette & Trajano, 2008; Rizzato & Bichuette, 2014), which makes them excellent models for studying the morphological evolution of subterranean organisms (e.g., Rizzato & Bichuette, 2017).

In the present work, we describe the gross anatomy of the brain and some of the main sense organs (olfactory organ, eye, semicircular canals of the inner ear), and the swim bladder (a non-sensory accessory structure) of all subterranean and one epigean species of *Ituglanis*. The swim bladder is included because it is involved in hearing in otophysan fishes such as catfishes (Chardon et al., 2003; Lechner & Ladich, 2008; Weber, 1820, see Methods). We also compare qualitatively the different brain regions and sense organs of the subterranean species with those of the epigean one (*Ituglanis goya*), looking for modifications possibly associated with living in the subterranean environment. We discuss our findings in the context of available

TABLE 1 Material examined in the present study.

Species	Accession number	Size (mm SL)
Ituglanis epikarsticus	LESCI00300	45.7
Ituglanis bambui	LESCI00034	39.8
	LESCI00151A	45.4
	LESCI00151B	46.7
Ituglanis boticario	LESCI00223	73.5
	LESCI00258A	57.5
	LESCI00258B	69.7
Ituglanis goya[a]	MCP15938	40.8
	DZUFRGS11202	45.0
	DZUFRGS11222	46.4
	DZUFRGS11237A	43.0
	DZUFRGS11237B	43.7
Ituglanis mambai	LESCI00239A	66.4
	LESCI00239B	59.8
	LISDEBE2047	61.5
Ituglanis passensis	LESCI00008A	54.2
	LESCI00008B	55.4
	LESCI00008C	60.1
Ituglanis ramiroi	LESCI00188	41.3
	LESCI00150	42.1
	LESCIuncat.	49.1
Ituglanis undescribed	LESCI00216	47.4
	LESCI00240	45.7
	LESCI00257	42.0

Abbreviations: DZUFRGS, Departamento de Zoologia, UFRGS; LESCI, Ichthyological Collection of Laboratório de Estudos Subterrâneos; LISDEBE, Laboratório de Ictiologia Sistemática, Departamento de Ecologia e Biologia Evolutiva; MCP, Museu de Ciências e Tecnologia, PUC-RS; SL, standard length.

[a] Epigean species.

FIGURE 1 Epigean (top) and subterranean species of *Ituglanis* analysed in the present study, in lateral view (not to scale). Subterranean species organized from those considered less (above) to more troglomorphic. From top to bottom: *Ituglanis goya* (UFRGS11237A, 43.7 mm standard length [SL]), *Ituglanis* undescribed (LESCI00216, 47.4 mm SL), *Ituglanis boticario*, (LESCI00258B, 69.7 mm SL), *Ituglanis mambai* (LISDEBE2047, 61.5 mm SL), *Ituglanis bambui* (LESCI00151A, 45.4 mm SL), *Ituglanis passensis* (LESCI00008A, 54.2 mm SL), *Ituglanis epikarsticus* (LESCI00300, 45.7 mm SL), *Ituglanis ramiroi* (LESCIuncat. 49.1 mm SL).

information on the brain and sense organs of other subterranean fish species in an attempt to investigate if *Ituglanis* may be considered a genus preadapted for living in the subterranean environment, as well as to identify general trends for the evolution of the brain and sensory organs of subterranean fishes in general.

2 | METHODS

We analysed the gross anatomy of the brain and some of the main sense organs (olfactory organ, eye, semicircular canals of the inner ear), and the swim bladder, of one specimen of the subterranean species *Ituglanis epikarsticus* Bichuette and Trajano, 2004 and two specimens of each of the following subterranean species: *Ituglanis bambui* Bichuette and Trajano, 2004, *Ituglanis boticario* Rizzato and Bichuette, 2015, *Ituglanis mambai* Bichuette and Trajano, 2008, *Ituglanis passensis* Fernández and Bichuette, 2002, *Ituglanis ramiroi* Bichuette and Trajano, 2004, and *Ituglanis* undescribed (Table 1). For comparison, we analysed the brain and sense organs of four specimens of the epigean *I. goya*, which also occurs in the Tocantins River basin, geographically close to the area where the subterranean species of *Ituglanis* are found.

The specimens had been previously fixed in 10% formalin solution and then preserved in 70% ethanol solution. Prior to dissection, the specimens were double-stained for bone and cartilage following the protocol described by Datovo and Bockmann (2010). After the specimens were double-stained, the skeleton and different types of soft tissues (e.g., muscles, ligaments, nerves, blood vessels) are easier to distinguish from each other, which facilitates dissection to access the brain cavity without damaging the brain structure. The process of double-staining and dissecting the specimens to expose the brain and main sense organs is illustrated in Figure 2.

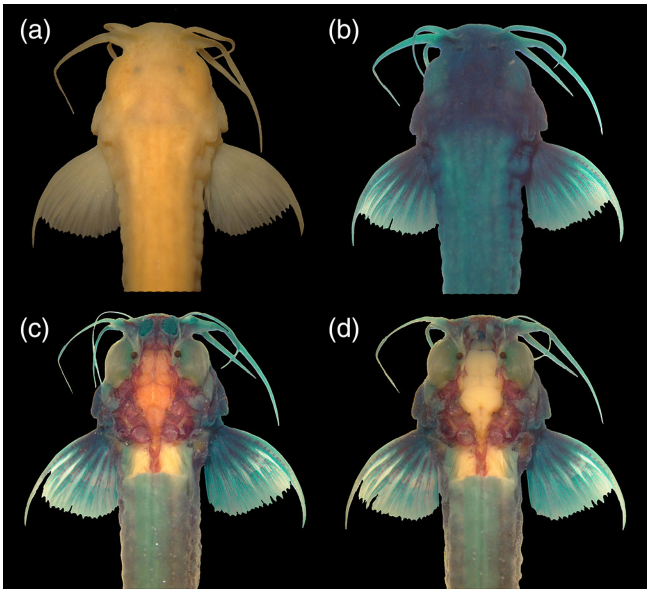

FIGURE 2 Series of photographs of the head and anterior body region of the same specimen of *Ituglanis bambui* (LESCI00034, 39.8 mm standard length [SL]) in dorsal view, showing different stages of the process of double-staining and dissection for exposing the brain and main sense organs: (a) specimen fixed in formalin 10% solution and preserved in ethanol 70% solution, prior to double-staining. (b) After double-staining (the specimen exhibits a blue color as a result of the staining with Alcian blue). (c) After preliminary dissection, with the neurocranium and olfactory organs exposed (notice the bony parts of the skeleton stained in red as a result of the staining with alizarin red, and the contrast with other tissues such as muscles and nerves). The brain can already be seen by transparency at this stage. (d) After dissection, with the brain and sense organs exposed, except for the olfactory organs, which were removed (notice that no damage was caused to the brain structure during the dissection).

After the brain and main sense organs were exposed, the dissected head region was photographed in dorsal view using a digital camera, and standardized illustrations were produced from the photographs using Adobe Illustrator CC. The main brain regions were outlined, checked on the actual specimens with the aid of a stereomicroscope, and compared qualitatively. We follow the assumption, substantiated by several studies (e.g., Kotrschal et al., 1998 and references therein), that the relative size of the brain region associated with processing sensory information from a given sensory modality is a proxy of the relative importance of that particular sensory modality for a given species. In that sense, when comparisons are established between closely related taxa, the difference in the size of a given brain region associated with processing sensory information from a given sensory modality may suggest the relative importance of that particular sensory modality for each taxon (Kotrschal et al., 1998).

We cannot account for allometric or ontogenetic variation in the size of the brain or its regions due to the limited sampling inherent to the fact that only a few specimens of each of the subterranean species of *Ituglanis* are available for dissections. To minimize the influence of allometric and ontogenic variation in comparisons, we attempted to select, whenever possible, specimens of similar sizes (ranging from 39.8 to 73.5 mm standard length [SL]). In addition, we compared the brain regions qualitatively due to the fact that our limited sampling for each species does not allow for robust statistical quantitative analyses. We therefore compared qualitatively the overall size and shape of each brain region, the size and degree of development of the eyes (i.e., degree of formation of the lens and other parts), and the number and general aspect of the olfactory lamellae. All anatomical features were examined on both the left and right sides. The general pattern of the brain, which is the general condition found in all specimens analysed, is described before the comparisons are presented, and compared with data from literature (e.g., Kotrschal et al., 1998). Identification and nomenclature of the different brain regions were based on studies of the brain anatomy of different catfishes, including trichomycterids, available in the literature (Abrahão et al., 2018a; Abrahão et al., 2018b; Abrahão et al., 2021; Abrahão & Shibatta, 2015; Chamon et al., 2018; Espíndola et al., 2018; Kapoor et al., 2003; Langecker & Longley, 1993; Nalbant & Linares, 1987; Northcutt et al., 2000; Pouilly & Miranda, 2003; Pupo & Britto, 2018; Rosa et al., 2020; Trajano, 1994), to facilitate comparisons with other studies on catfish brain anatomy. Besides the different brain regions, we compared the following sense organs: olfactory organ (including the number of olfactory lamellae, which were counted on both sides of the specimens), eye, and semicircular canals of the inner ear, and the swim bladder. The swim bladder, as the name implies, is an internal gas-filled organ mostly related to the control of buoyancy when fishes are stationary or swimming. However, in several fishes it also plays a role in hearing, especially in the so-called hearing specialists that have connections between the swim bladder and the inner ear (Lechner & Ladich, 2008). This is the case of otophysan fishes such as catfishes, in which a series and bones and ligaments named Weberian apparatus allow the transmission of sound pressure between the swim bladder (which functions as a resonating chamber) and the inner ear, improving the hearing capabilities of these fishes (Chardon et al., 2003; Lechner & Ladich, 2008; Weber, 1820). Thus, trichomycterid catfishes have such a connection between the swim bladder and the inner ear, suggesting that the swim bladder in these fishes may be involved in sensory perception; we included the swim bladder as a non-sensory accessory organ in our analysis. The mechanosensory lateral line system of subterranean and epigean species of *Ituglanis* was analysed in a previous paper (Rizzato & Bichuette, 2017), and we did not analyse electroreceptors due to limitations related to the methods required and the material available (e.g., number and condition of specimens for each species).

3 | RESULTS

We first describe the general anatomy of the brain and main sense organs of the subterranean and the epigean species of *Ituglanis* analysed. Then we compare qualitatively the different brain regions and

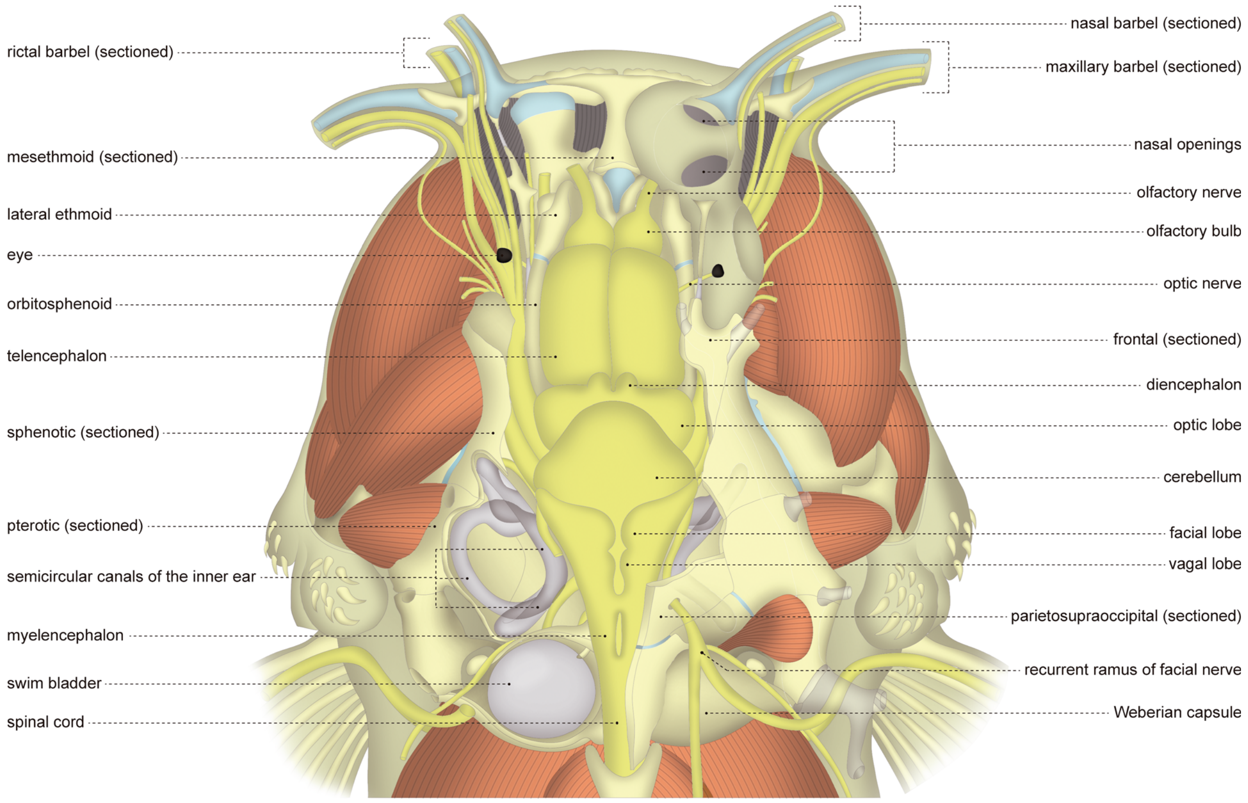

FIGURE 3 Partially dissected head of a specimen of *Ituglanis ramiroi* (LESCI00150, 42.1 mm standard length [SL]), in dorsal view, showing the brain and main bones, cartilages, muscles, nerves, ligaments, and sense organs. On the left side of the specimen more bones were removed to demonstrate internal structures. Notice the asymmetry in the size and position of the eyes.

sense organs of the subterranean species with those of the epigean one.

3.1 | General anatomy of the brain and sense organs

The dissected dorsal region of the head of one specimen of *I. ramiroi* is illustrated in Figure 3 and may be used as a reference for the following descriptions. The brain of *I. goya* and of the subterranean species of *Ituglanis* is according to the general pattern described by Kotrschal et al. (1998) for actinopterygians. The spinal cord is continuous rostrally to the brainstem (myelencephalon or *medulla oblongata*) and *tegmentum* of the mesencephalon and diencephalon. The cerebellum (*corpus cerebelli*) is located dorsally and partially overlaps the diencephalon and optic lobes (*tectum opticum*). The telencephalon is paired and rostrally adjacent to the diencephalon, and the olfactory bulbs (*bulbus olfactorius*) are located rostral to the telencephalon.

The rostral most region of the brain is formed by the olfactory bulb, which is not separated from the telencephalon as in most catfishes (Abrahão et al., 2021; Kapoor et al., 2003; Kapoor & Finger, 2003), but is adjacent and united to it by a short and wide olfactory tract (*tractus olfactorius*). The length of the olfactory tract seems to increase ontogenetically in some fishes (e.g., Abrahão et al., 2021). Indeed, we noticed some intraspecific variation in the length of the olfactory tract in some of the species analysed (e.g., *I. mambai*, *I. boticario*, Figure 4, see below) that may be at least partially explained by the difference in the size of the specimens. The olfactory bulb is covered dorsally by the lateral ethmoid, the anterior portion of the frontal, and by a membrane of connective tissue that extends from the dorsal margins of the lateral ethmoid to the anterior margin of the frontal.

The olfactory nerve (*nervus olfactorius*) extends rostral to the olfactory bulb leaving the neurocranium from a wide anterior opening (i.e., foramen) on the lateral ethmoid, and runs ventrally in the nasal chamber, ramifying into a series of nerve branches that reach the lamellae of the olfactory organ. The olfactory organ is located inside the nasal chamber, which is roughly round in dorsal view and is located dorsal to the flattened main body of the autopalatine. The olfactory organ is feather-like, with several thick lamellae united by a median raphe (Figure 5). The olfactory organ is roughly rostrocaudally oriented, with the base of the raphe adjacent medially to the base of the nasal barbel, and the smaller lamellae located caudally, closer to the posterior nasal opening. The distal portion of each lamella is distinctively deeper than the proximal one. The number of lamellae increases ontogenetically in at least some catfishes (e.g., Abrahão et al., 2021), and we indeed observed larger numbers of lamellae in larger specimens both within and among species.

The telencephalon is located posteriorly to the olfactory bulbs and is well developed, paired, rostro-caudally elongated, with round

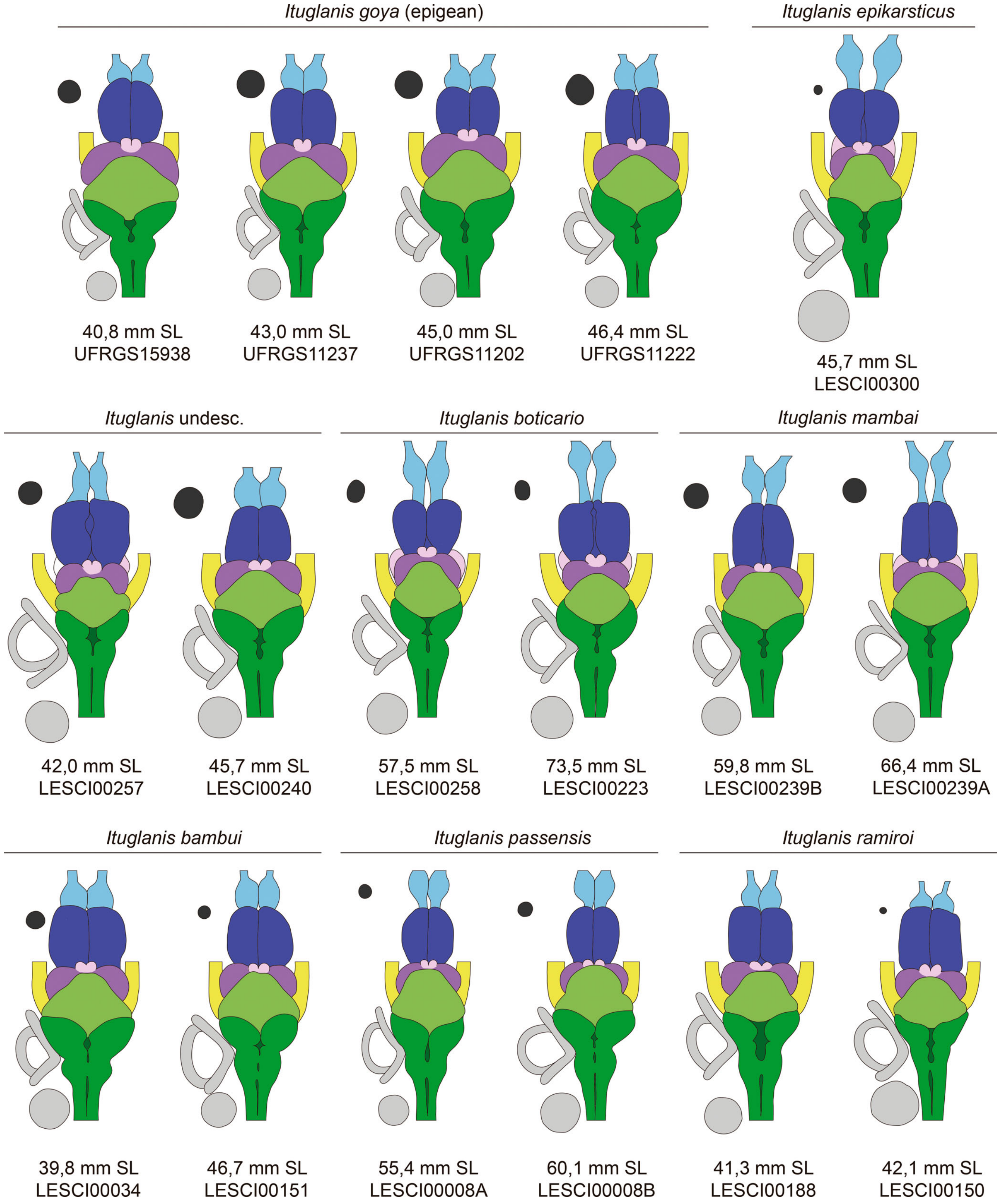

FIGURE 4 Comparison of the brain and main sense organs of epigean (*Ituglanis goya*) and subterranean species of *Ituglanis*. The outlines of the brain, left eye, left semicircular canal, and left swim bladder are shown, scaled to the same size (calculated as the distance between the anterior margin of the diencephalon and the posterior margin of the fourth ventricle) to facilitate comparisons. Specimens of different sizes are illustrated; therefore, the standard length (SL) of each specimen is given below its respective identification number (see Table 1). Main brain regions are distinguished by colors: olfactory bulb in light blue; telencephalon in dark blue; diencephalon in pink; optic lobes in purple; cerebellum in light green; facial lobes, vagal lobes, and myelencephalon in dark green; proximal portion of the common path of the trigeminal and facial nerve in yellow.

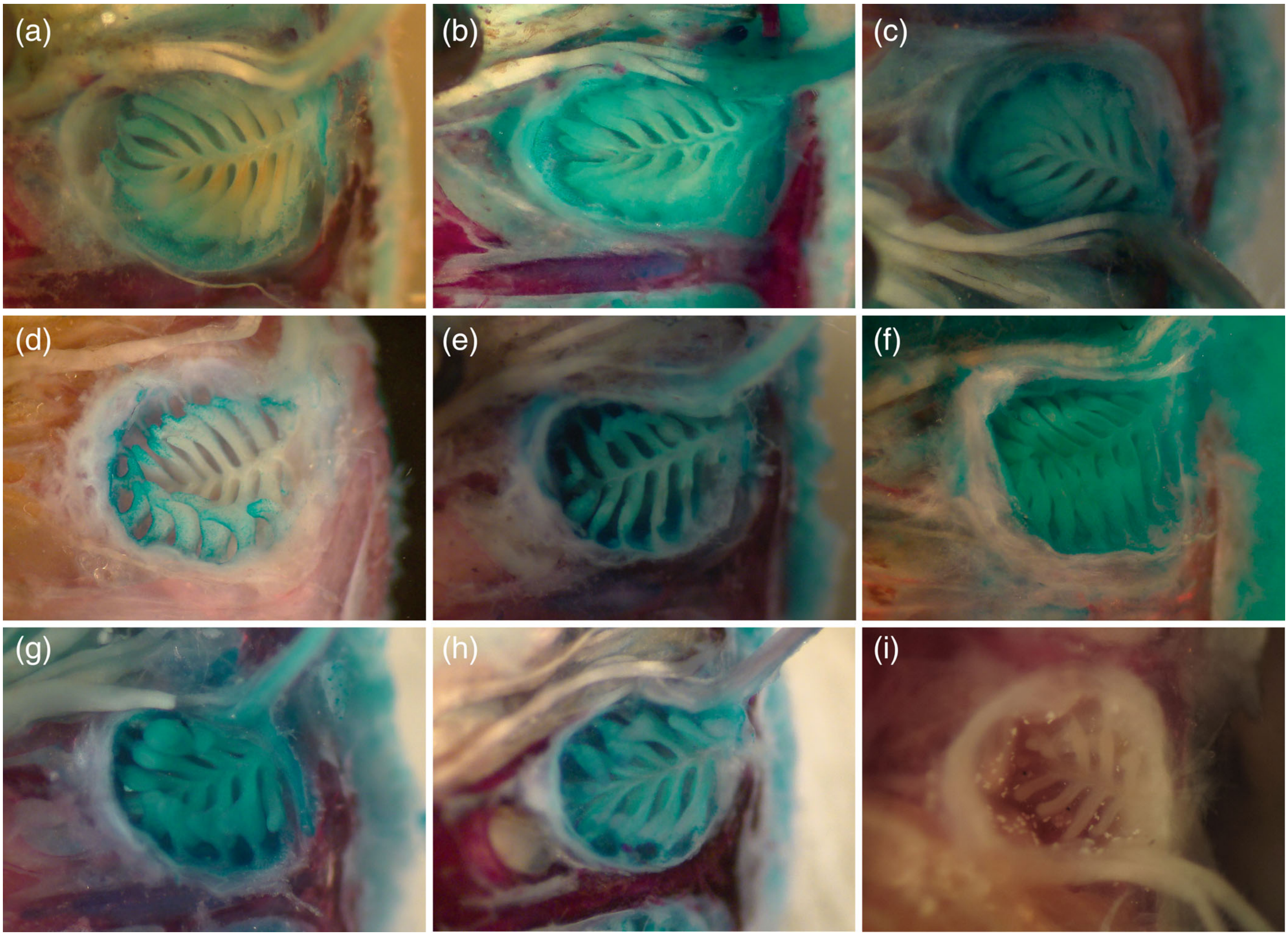

FIGURE 5 Comparison of the nasal organs and number of olfactory lamellae of epigean (*Ituglanis goya*, a–c) and subterranean (d–h) species of *Ituglanis* (not to scale). Tissues stained in blue as a result of the preparation method (see Figure 1). (a) *I. goya*, UFRGS11222, 46.4 mm standard length (SL). (b) *I. goya*, UFRGS11237A, 43.0 mm SL. (c) *I. goya*, UFRGS11202, 45.0 mm SL. (d) *Ituglanis boticario*, LESCI00223, 73.5 mm SL. (e) *Ituglanis* undesc., LESCI00240, 45.7 mm SL. (f) *I. mambai*, LESCI00239, 6.4 mm SL. (g) *I. bambui*, LESCI00151B, 46.7 mm SL. (h) *I. epikarsticus*, LESCI00300, 45.7 mm SL. (i) *I. ramiroi*, LESCI00150, 42.1 mm SL.

anterior margins, covered dorsally by the frontal bones. The telencephalon is continuous with the diencephalon posteriorly and ventrally, but this region is mostly not visible dorsally. The diencephalon is continuous with the bilateral optic lobe, which are relatively poorly developed, round structures located anterolaterally to the border of the cerebellum. Each optic lobe consists of the *tectum opticum*, which forms a dorsal cap over the optic lobe, and the *torus semicircularis*, which is not visible dorsally but occupies a large portion of the internal volume of the optic lobe in catfishes (Nieuwenhuys, 1982).

The cerebellum is the most conspicuous part of the brain in dorsal view. It is a single, median, round structure. The optic lobes are located anterolaterally to the cerebellum and the facial lobes of the hindbrain (*medulla oblongata*) posterolateral to it. The cerebellum is folded anteriorly, covering part of the optic lobes in dorsal view. The cerebellum comprises three parts, macroscopically indistinguishable in the species analysed: (1) the *corpus cerebelli*, which is the main median structure; (2) the *valvula cerebelli*, a ventral structure covered by the anterior folded region of the *corpus cerebelli* (not visible dorsally); and (3) the *lobi vestibulolateralis*, each of which in teleosts forms a compact structure named *eminentia glanularis*, and which in *Ituglanis* occupies the lateral most region of the cerebellum, adjacent to the facial lobes. The cerebellum and the optic and facial lobes are covered dorsally by the frontals and parieto-supraoccipital bones.

Well-developed facial and vagal lobes are located caudally to the cerebellum, the vagal one being part of the *medulla oblongata* (myelencephalon) that is located just rostral to the *foramen magnum* through which the spinal cord (*medulla spinalis*) leaves the cranium. The facial lobes are well-developed paired structures located caudally to the cerebellum and partially covering its posterior portion in dorsal view. In some specimens, the internal margins of the left and right facial lobes contact each other. The well-developed, kidney-shaped vagal lobes are caudally adjacent to the facial ones, and the anterior and posterior internal margins of the left and right vagal lobes contact each other.

The eyes are located laterally, caudal to the olfactory bulb and rostral to the telencephalon. The eye is connected to the brain by a narrow and relatively long optic nerve whose main proximal portion is covered dorsally by the telencephalon. Whereas in the epigean species the eyes are well developed and do not vary much in size, in the subterranean ones there is much variation in the size and degree of development (i.e., degree of formation of the lens and other parts) of the eyes both inter- and intraspecifically, including specimens with asymmetrical eyes (e.g., Figure 3). In some specimens of some of the subterranean species, (e.g., *I. ramiroi*, *I. epikarsticus*), the eyes are present but are not visible externally, being covered by a thick layer of skin. We also observed malformation in the eyes (e.g., the entire organ or at least some of its parts, such as the lens, deformed) of some specimens of the subterranean species analysed, most notably in *I. ramiroi*.

The semicircular canals of the inner ear are located lateral to the facial and vagal lobes. The roughly spherical swim bladder is located caudally to each inner ear and is surrounded by the bony Weberian capsule (modified vertebral elements). Bones and ligaments of the Weberian apparatus connect the swim bladder to the inner ear, allowing the transmission of sound pressure from the former to the latter.

3.2 | Comparisons between the subterranean and the epigean species of *Ituglanis*

The brains and main sense organs of the specimens analysed are illustrated in Figure 4, and the nasal organs are illustrated in Figure 5.

The optic lobes of the subterranean species, especially those with smaller eyes (e.g., *I. epikarsticus*, *I. passensis*, *I. ramiroi*), are slightly smaller than those of the epigean one. The myelencephalon is well developed in all species of *Ituglanis* analysed, notably the facial and the vagal lobes, and we did not find a noticeable difference in the size of the facial and vagal lobes between the subterranean and epigean species of *Ituglanis* analysed. Actually, in some of the subterranean species (e.g., *I. ramiroi*, Figure 4), these structures seem to be less developed than those in the epigean species.

The subterranean species of *Ituglanis* exhibit a slight increase in the area of the cerebellum, which covers dorsally a larger area of the diencephalon. We did not find a noticeable difference in the telencephalon of the subterranean species of *Ituglanis* when compared to the epigean species. Similarly, the olfactory lobes in the subterranean species of *Ituglanis* do not differ from the ones in the epigean species. Actually, an analysis of the internal anatomy of the olfactory organs (Figure 5) showed that the subterranean species usually exhibit a smaller number of olfactory lamellar than the epigean ones.

Regarding the swim bladder, both the subterranean and the epigean species of *Ituglanis* analysed exhibit small, spherical paired swim bladders surrounded by the bony Weberian capsules, but in the subterranean species the swim bladders, as well as the semicircular canals of the inner ear, are slightly larger than those of the epigean species.

4 | DISCUSSION

The general aspect of the brain in the subterranean and the epigean species analysed is very similar, and the occurrence of intraspecific variability associated with the small number of specimens available for analysis makes comparisons difficult. At least part of the variability observed may be due to preservation and preparation artifacts resulting from the way and amount of time passed since the specimens were fixed and preserved, since they were collected separately. Another potential source of intraspecific variability is the fact that some parts of the brain, as well as some sense organs (e.g., the eyes) exhibit allometric growth during ontogeny (e.g., Abrahão et al., 2021; Kotrschal et al., 1998). In fact, we observed variability in the size of different regions of the brain among specimens of the same species, more accentuated in those with more different sizes (e.g., the length of the olfactory tract in the two specimens of *I. mambai* analysed; Figure 4). Regarding the interspecific comparisons, we observed in some cases only slight differences in the size of different parts of the brain in the different species, including when comparing the subterranean with the epigean ones.

Notwithstanding the caveats above, it is still possible to infer, from a comparison of the relative sizes of the different brain regions and main sense organs in the specimens analysed, and in the context of other studies on the brain anatomy of subterranean fishes available in the literature, data on the relative importance of the different sensory modalities associated to them for the subterranean and the epigean species of *Ituglanis* analysed.

We found slightly less-developed optic lobes in the subterranean species of *Ituglanis*, especially those with smaller eyes (e.g., *I. epikarsticus*, *I. passensis*, *I. ramiroi*), than in the epigean one. However, even in the epigean species the optic lobes are poorly developed when compared to other fishes. Less-developed optic lobes are common in catfishes when compared to other teleosts, especially diurnal taxa (Kapoor et al., 2003), suggesting less dependence on visual sensory information in these fishes in general. Regarding Trichomycteridae, except for members of the basal subfamilies Copionodontinae and Trichogeninae that usually have well-developed eyes and exhibit more diurnal habits (Britski & Ortega, 1983; De Pinna, 1992; De Pinna, 1998; De Pinna et al., 2010; Rantin & Bichuette, 2015; Sazima, 2004; Zanata & Primitivo, 2013), other members of the family, especially trichomycterines, commonly have smaller eyes and more cryptic and nocturnal habits (Arratia & Huaquin, 1995; Casatti & Castro, 1998; Costa, 1992; De Pinna, 1998; Sazima, 2004). This suggests that in non-copionodontine, non-trichogenine trichomycterids in general and in trichomycterines in particular there is a trend toward a further reduction (compared to other catfishes) in the relative importance of visual sensory information, associated with the reduction in the size of the eyes and optic lobes.

In subterranean species whose brain anatomy was investigated, reduction in the size of the optic lobes is often reported. In the subterranean species of Amblyopsidae, the volume of the optic lobe decreases based on the degree of troglomorphism (i.e., specialization of taxa to cave life), even considering that, similar to the observed for *Ituglanis*, the epigean species of the family, the swampfish *Chologaster cornuta* Agassiz, 1853, also exhibits reduced eyes and optic lobes, associated to its nocturnal habits (Niemiller & Poulson, 2010; Poulson, 1963). The optic lobes of the blind doctor fish *Garra* *widdowsoni* (Trewavas, 1955) (Cyprinidae) are strongly reduced when compared to those in the epigean doctor fish *Garra rufa* (Heckel, 1843) (Marshal & Thinés, 1958). In the subterranean cave tetra *A. mexicanus* (Hubbs & Innes, 1936), the optic lobes and nerves are considerably less developed than the ones in the epigean species (Riedel, 1997). The optic lobes of the toothless blindcat *Trogloglanis pattersoni* Eigenmann, 1919 and the widemouth blindcat *Satan eurystomus* Hubbs and Bailey, 1947, subterranean catfishes of the family Ictaluridae, are considerably reduced when compared to the optic lobes of epigean species of the family (Langecker & Longley, 1993; Lundberg, 1982). Lundberg (1982) also reported reduction in the optic lobes of the cistern catfish *Phreatobius cisternarum* Goeldi, 1905 (Phreatobiidae) and of the African blind barb *Caecobarbus geertsii* Boulenger, 1921 (Cyprinidae).

However, in the cave astroblepid *Astroblepus pholeter* Collette, 1962, the optic lobes are of a similar size to those of the epigean *A. grixalvii* Humboldt, 1805 (Kapoor et al., 2003). Similarly, when comparing the subterranean heptapterid *Pimelodella kronei* (Miranda Ribeiro, 1907) with the epigean *Pimelodella transitoria* Miranda Ribeiro, 1907, its putative sister-species, Trajano (1994) observed only a slight reduction in the size of the optic lobes. Trajano (1994) argues that this may be explained by the fact that vision is probably a sensory modality of secondary importance for *P. transitoria* (which occurs in epigean environments), and that the secondary importance of vision as a sensory modality is consistent with a hypothesis of preaptation for subterranean life in catfishes in general, and in the genus *Pimelodella* in particular.

Regarding subterranean species of Trichomycteridae whose brain anatomy has been studied so far, Nalbant and Linares (1987) observed well-developed optic lobes in specimens of a subterranean population of *Trichomycterus guianensis* (Eigenmann, 1909). In the subterranean *T. chaberti* Durand, 1968, however, the optic lobes are poorly developed, similar to the ones in the subterranean *Ituglanis* and considerably smaller than those in the epigean species that occurs in the region, *Trichomycterus* cf. *barbouri* (Eingenmann, 1911), according to Pouilly and Miranda (2003: fig. 4b).

In the species analysed in the present work, we observed only a slight difference in the size of the optic lobes of the subterranean species when compared to the epigean one (Figure 4). This suggests that visual sensory information is probably already of lesser importance for epigean species of *Ituglanis*, so that the optic lobes in the subterranean species are not distinctively smaller than those of the epigean species. An alternative explanation is that reduction in the optic lobes does not occur (i.e., the ancestral size is retained) despite the loss of use of visual information. The fact that the eyes of trichomycterines in general are already smaller and less developed when compared to the eyes of the basal subfamilies Copionodontinae and Trichogeninae (Britski & Ortega, 1983; De Pinna, 1992; De Pinna et al., 2010; Sazima, 2004; Zanata & Primitivo, 2013), and that the eyes of species of *Ituglanis* are usually smaller than those of other trichomycterines in general (Costa & Bockmann, 1993), also suggests a trend toward lower importance of the visual sensory information for members of Trichomycterinae in general and of *Ituglanis* in particular, accentuated in the subterranean species of the genus. In this regard, following the same rationale used by Trajano (1994) for *Pimelodella kronei* and *P. transitoria* (Heptapteridae), the lower dependence of visual sensory information in species of *Ituglanis* can be interpreted as a preadaptation for the subterranean life habit.

We also observed in all species of *Ituglanis* analysed a well-developed myelencephalon, notably the facial and the vagal lobes. Facial and vagal lobes are usually well developed in catfishes in general (Nieuwenhuys, 1982), and this is mostly related to the large number of taste buds in these fishes, especially in the barbels (Atema, 1971; Eram & Michel, 2005; Evans, 1931; Herrick, 1906). Atema (1971) demonstrated that there are two functional groups of taste buds in the ictalurid *Ameiurus natalis* (Lesueur, 1819): (1) those innervated by the facial nerve, that are distributed all over the external surface of their skin and are specially concentrated on the barbels, lips, and anterior mouth region; and (2) those innervated by the vagus nerve, that are distributed on the posterior mouth region and gill arches. These two groups are associated with different functional and behavioral responses: those innervated by the facial nerve are more associated with finding food, whereas those innervated by the vagus to accepting and not rejecting food items in the mouth (Atema, 1971; Evans, 1940; Eram & Michel, 2005). Based on the relative importance of each functional type of taste bud, there is a correlated increase in the development of the facial and vagal lobes in the brain of a fish. For example, in species of Catostomidae (Cypriniformes) with more taste buds on the lips, the facial lobes are more developed than the vagal ones, whereas in species of the family with well-developed palatal organs on the roof of the mouth, the opposite is true, the vagal lobes being more developed than the facial ones (Miller & Evans, 1965).

According to Evans (1931), in catfishes the vagal lobes are usually similar to those in other fishes, but the facial lobes are much more developed as a consequence of the higher number of superficial papillae, especially those located in the barbels. Interestingly, in species of Cypriniformes with well-developed barbels, Evans (1931) also observed more developed facial lobes. These observations suggest that there is an intimate relationship between the hyperdevelopment (i.e., enlargement) of the facial lobes and dependence of external taste as a sensory modality especially for finding food, using external taste buds such as those located on the barbels.

Taste is probably a very important source of sensory information for trichomycterids. Behavioral observations of some trichomycterids in laboratory conditions and in the wild provide evidence that these fishes rely strongly on taste to find food. Trichomycterids (including members of the basal subfamilies Copionodontinae and Trichogeninae, Rantin & Bichuette, 2015; Sazima, 2004; Zanata & Primitivo, 2013) usually forage by passing their barbels and mouth over the substrate, sometimes burrowing the snout in it with ondulatory movements of the body, searching for food particles. When stationary or burrowed, they usually extend their barbels to facilitate the passive detection of any chemical and mechanical stimuli (Figure 6).

We did not find a noticeable difference in the size of the facial and vagal lobes between the subterranean and epigean species of

FIGURE 6 Individual of the subterranean species *Ituglanis passensis* kept in aquarium, showing how these fishes usually extend their barbels when resting or burrowing in the substrate to facilitate the detection of chemical and mechanical stimuli.

Ituglanis analysed. Actually, in some of the subterranean species (e.g., *I. ramiroi*), these structures seem to be less developed (i.e., smaller) than those in the epigean species. In an environment characterized in general by the permanent absence of light and by food restriction, the ability to find food using other sensory modalities would be highly advantageous, and we might expect a strong selection toward hyperdevelopment of other sensory modalities such as taste (e.g., proliferation of taste buds) in subterranean organisms in general and fishes in particular in comparison with their epigean relatives.

However, in most of the subterranean fish species analysed so far, the facial and vagal lobes do not exhibit noticeable modifications when compared to those of epigean species. According to Niemiller and Poulson (2010), taste does not represent an important sensory modality in amblyopsids, and the facial and vagal lobes are poorly developed (i.e., small), these regions being even hard to distinguish in the brain of these fishes. Marshal and Thinés (1958) observed that the facial and vagal lobes of *G. widdowsoni* are not markedly more developed (i.e., larger) than those of *Garra rufa* and other epigean species of Cyprinidae, and they attribute this to the low number of taste buds in this species. Among catfishes, Lundberg (1982) and Langecker and Longley (1993) observed a reduction in the facial and vagal lobes of the subterranean catfishes *T. pattersoni* and *S. eurystomus* (Ictaluridae), which suggest, contrary to the expectation, a reduction in the importance of taste as a sensory modality in relation to the epigean species. In *Pimelodella kronei* (Heptapteridae), Trajano (1994) also reported reduced facial and vagal lobes in comparison to *Pimelodella transitoria*. Finally, in *Trichomycterus chaberti*, Pouilly and Miranda (2003) observed only a slight reduction in the size of the facial and vagal lobes in comparison to the epigean *Trichomycterus* cf. *barbouri*.

The fact that the brain regions associated with chemical perception are not noticeably more developed (i.e., larger) in the subterranean species mentioned above does not necessarily mean, however, that this sensory modality is not important for these fishes. Actually, with the exception of the amblyopsids, all species mentioned above belong to two orders, Cypriniformes and Siluriformes, in which taste is already well developed as a sensory modality, especially in association with the presence of barbels in these fishes, and therefore these fishes may be already preapted for surviving in the subterranean environment. This would justify the absence of additional modifications in the brain associated with a further hyperdevelopment of this sensory modality (e.g., elongation or enlargement of barbels) in the subterranean species. In this sense, two interesting counter-examples are the shortfin molly *Poecilia mexicana* Steindachner, 1863 (Poeciliidae) and *A. mexicanus* (Characidae), two subterranean species belonging to groups whose members are predominantly visually oriented. In these species, taste is more developed than in the epigean species, reflected by the increase in the number of taste buds especially in the mouth region (Boudriot & Reutter, 2001; Parzefall, 2001; Schemmel, 1967). These observations suggest that in subterranean fishes not belonging to groups preadapted for life in subterranean habitats, there is a trend toward hyperdevelopment (e.g., enlargement, elongation, proliferation) of sensory structures related to taste, accompanied by hyperdevelopment (e.g., increase in size) of the brain regions associated with processing information from these structures. On the contrary, in subterranean fishes belonging to groups preadapted for life in subterranean habitats, such as catfishes, there is no such a trend as the epigean members of the group already exhibit well-developed (i.e., large) structures and brain regions associated with chemosensory perception.

The cerebellum, which is associated with spatial orientation, proprioception, motor coordination, and eye movement (Kotrschal et al., 1998), is relatively reduced in species of *Ituglanis* in general, correlated with their more benthic life habits. When compared to the epigean species, the subterranean species of *Ituglanis* exhibit a slight increase in the area of the cerebellum, which covers dorsally a larger area of the diencephalon (Figure 4). Because the cerebellum is a center of sensory integration and processing of inputs from several different sensory systems, it is difficult to establish correlations with particular characteristics of these fishes. However, evidence from studies on other fishes suggests that the slight increase in the size of the cerebellum may be related to an increase in exploration of the water column by subterranean species of *Ituglanis*, which was already reported by Bichuette (2003). Similar observations for different subterranean fish species are available in the literature. In amblyopsids, Poulson (1963) and Niemiller and Poulson (2010) observed a significant increase in the size of the cerebellum in the subterranean species when compared to the surface-dwelling *Chologaster cornuta*. In the cave ictalurids *T. pattersoni* and *S. eurystomus*, Langecker and Longley (1993) observed hypertrophy of the cerebellum. In the subterranean *T. chaberti*, according to Pouilly and Miranda (2003), the cerebellum is larger than that in the epigean *T.* cf. *barbouri*. In the subterranean *P. kronei* (Heptapteridae), however, Trajano (1994) reported a smaller cerebellum than that in *P. transitoria*, which also occurs in epigean habitats.

We did not find noticeable differences in the size of the telencephalon of the subterranean species of *Ituglanis* when compared to the epigean species. The telencephalon is responsible for the integration of information coming from virtually all sensory modalities, especially olfaction (Kotrschal et al., 1998), and also for the expression of some species-specific behaviors and learning (Trajano, 1994). This region is highly hypertrophied in the subterranean species of Amblyopsidae (Niemiller & Poulson, 2010; Poulson, 1963) and Ictaluridae (Langecker & Longley, 1993; Lundberg, 1982), as well as in *G. widdowsoni* (Marshal & Thinés, 1958), *T. chaberti* (Pouilly & Miranda, 2003) and *P. kronei* (Trajano, 1994). Trajano (1994) also mentions hypertrophy of the telencephalon in the subterranean *Uegitglanis zammaranoi* Gianferrari, 1923 (Clariidae) and *Garra andruzzi* (Vinciguerra, 1924) (Cyprinidae).

Similarly, the olfactory lobes in the subterranean species of *Ituglanis* do not differ from those in the epigean species. Actually, we found a smaller number of olfactory lamellae in the olfactory organs of the subterranean species than in the olfactory organs of the epigean ones (Figure 5). In addition, the brain region associated with interpreting the olfactory sensory information, the telencephalon, is not more developed in the subterranean species of *Ituglanis* when compared to the epigean. These observations might suggest that there is no increase in the olfactory capabilities of the subterranean species of *Ituglanis*, especially if the number of olfactory lamellae is correlated with, thus an accurate predictor of, the olfactory capability of a given taxon. However, there is so far no evidence of such correlation.

In other subterranean fishes, the importance of olfaction varies, as well as the condition of the olfactory organs and olfactory centers in the brain. In the subterranean species of Amblyopsidae, for example, Niemiller and Poulson (2010) reported an increase in the number of olfactory lamellae and of the area of the olfactory rosettes in the nasal organ, although they did not identify modification in the size of the olfactory lobes. However, the same authors argue that, despite these modifications, apparently there is no increase in the olfactory capabilities of these fishes, and that the most important sensory modality for subterranean amblyopsids is the mechanosensory perception provided by the lateral-line system. For the subterranean *Ituglanis*, however, we found in a previous study (Rizzato & Bichuette, 2017) that at least the lateral-line canals are reduced, suggesting lower reliance on mechanosensory perception, but there is so far no information on their superficial neuromasts and electroreceptors. In subterranean morphs of *A. mexicanus*, Borowsky (2010) and Jeffery and Strickler (2010) observed an increase in the olfactory sensitivity, even though these morphs exhibit a lower number of olfactory lamellae than the epigean morphs (Trajano, 1994; Wilkens, 1988). Langecker and Longley (1993) observed a slight reduction in the size of the olfactory lobes of *S. eurystomus* (Ictaluridae), suggesting a reduction in the importance of olfaction in this species. In *T. pattersoni* (Ictaluridae), however, they observed an increase in the size of the nares and telencephalon, arguing that this could be related to an increase in the importance of olfaction in this species, even though no visible modifications were observed in the olfactory rosette (Lundberg, 1982).

In *G. andruzzi* (Cyprinidae) and *U. zammaranoi* (Clariidae), no modification related to olfaction was detected according to Berti and Messana (2010), despite the hyperdevelopment (enlargement) of the telencephalon (Trajano, 1994), suggesting, according to the authors, that this hyperdevelopment is related to other functions of this brain region. In the golden cave catfish *Clarias cavernicola* Trewavas, 1936 (Clariidae), Berti and Messana (2010) observed a slight reduction of the olfactory apparatus. According to Marshal and Thinés (1958), the olfactory organs are normally developed in *G. widdowsoni* (Cyprinidae), and Trajano (1994) did not observe any structural modification in the olfactory organ of *P. kronei* (Heptapteridae) when compared to *P. transitoria*, except for the number of lamellae, which is lower in the subterranean species. Pouilly and Miranda (2003) did not analyse the olfactory lobes or the internal structure of the nasal organ of *T. chaberti*, but they suggest that the olfaction may be hyperdeveloped (i.e., enhanced) as the telencephalon is hypertrophied.

Regarding the swim bladder, both the subterranean and the epigean species of *Ituglanis* analysed exhibit small, spherical paired swim bladders (see Chardon, 1968) surrounded by the bony Weberian capsules, but in the subterranean species the swim bladders are larger, as well as the semicircular canals of the inner ear are slightly wider and longer than those of the epigean species. In several catfishes, the swim bladder is reduced, and this condition is related to the generally more benthic life style of these fishes (Chardon et al., 2003; Lechner & Ladich, 2008). However, in contrast with other groups of predominantly benthic fishes, in which the swim bladder is completely lost (e.g., Scorpaeniformes, Gobiidae), in benthic catfishes the swim bladder is reduced but still present, suggesting that its retention is due to its participation in hearing (Chardon et al., 2003; Lechner & Ladich, 2008). Lechner and Ladich (2008), for example, demonstrated that, despite the reduction in the size of the swim bladder being associated with reduction in the sensitivity for higher frequency sounds, the auditory capabilities of catfishes with reduced swim bladders is still superior to those of other fishes that do not have a hearing mechanism involving the swim bladder. Furthermore, according to the same authors, the fact that the swim bladder in loricarioid catfishes (including trichomycterids) is encapsulated by bone (forming the Weberian capsule) and closer to the inner ear compensates for the loss of hearing sensitivity to higher frequency sounds as a consequence of the reduction in the volume of the swim bladder (Lechner & Ladich, 2008).

The fact that the subterranean species of *Ituglanis* exhibit larger swim bladders when compared to the epigean one may be related to two possible modifications, not mutually exclusive, associated to their subterranean life habit. The first is an increase in the hearing capability of these species. This condition would represent a mechanism of sensory compensation in the absence of visual sensory information in the subterranean environment. In fact, even though the hearing capability of subterranean species of *Ituglanis* was never experimentally evaluated, field and laboratory observations of live specimens suggest that they exhibit higher sensitivity to sound stimuli (M.E.B., personal observation). However, not much is known about the importance of hearing for subterranean fishes (Soares & Niemiller, 2013).

The second modification is related to a more active exploration of the water column by the subterranean species. Due to the combination of general food scarcity in the subterranean environment, the food being usually scattered through the subterranean habitat, with the absence or scarcity of predators and competitors in the aquatic environment, subterranean fishes would probably need to explore more actively the water column, and this could result in an increase in the size of the swim bladder. This hypothesis is supported by field and laboratory observations that demonstrate that at least some subterranean species of *Ituglanis* spend less time burrowing or stationary and explore more actively the water column (Bichuette, 2003; Neto & Bichuette, 2013). The fact that the semicircular canals of the inner ear, associated with movements in three dimensions during exploration of water column, are also slightly more developed in the subterranean species of *Ituglanis* when compared to the epigean species reinforces this hypothesis.

Few authors investigated the condition of the swim bladder in subterranean fishes. Exceptions are Lundberg (1982) and Langecker and Longley (1993), who noticed that in the subterranean ictalurid catfishes *T. pattersoni* and *S. eurystomus*, the swim bladder is extremely reduced and its position is occupied by fat deposits. Langecker and Longley (1993) argue that the increase in fat accumulation in these species could have been caused by a relaxation of selective pressure in the function of the swim bladder for buoyancy, in combination with the effects of the high hydrostatic pressure in their particular habitat, leading to its extreme reduction. The only other case reported in the literature of reduction of the swim bladder in subterranean fishes is in *A. mexicanus*, and according to Hüppop (1987), this would be also related to increased fat deposits in these fishes.

5 | CONCLUSIONS

By the analysis of the different brain regions and main sense organs of the subterranean species of *Ituglanis* compared with the epigean *I. goya*, and in the context of observations on the brain anatomy of other subterranean fishes, it is possible to make inferences about the relative importance of some sensory modalities and their possible correlation to aspects of living in subterranean environments. The absence of visual sensory information due to the general permanent aphotic conditions of the subterranean environment is correlated with the smaller size of the optic lobes and eyes, even though the reduction on the brain region is not accentuated, as vision is probably already of secondary importance for epigean *Ituglanis* and other trichomycterines in general. Olfaction, contrary to the expected, does not exhibit signs of enhancement in the subterranean species, and there is no evidence of hyperdevelopment (e.g., enlargement) of brain regions associated with chemical information, although this does not necessarily mean that taste is not important as a sensory modality for these fishes. Hearing, on the contrary, may play an important role as a source of sensory information about the environment, as evidenced by the increase in the size of the swim bladder. The hyperdevelopment (enlargement) of the swim bladder may also be related, together with the slight increase in the size of the cerebellum and of the semicircular canals of the inner ear, with more active exploration of the water column, which may be associated with the absence of important predators and competitors in the aquatic environment and with the need to explore more actively the environment to find food. Results of a previous study (Rizzato & Bichuette, 2017) show that at least the mechanosensory lateral-line canals are reduced in the subterranean *Ituglanis*, and there are no data so far regarding their superficial neuromasts and electroreceptors. In general, it may be argued that species of *Ituglanis* exhibit sensory characteristics that are preadaptive for the subterranean life, as only slight modifications were observed in the brains and sense organs of the subterranean species of the genus when compared to the epigean one.

AUTHOR CONTRIBUTIONS

Pedro P. Rizzato and Maria Elina Bichuette contributed equally to the research idea, data generation and analysis, manuscript preparation, and funding.

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ORCID

Pedro P. Rizzato https://orcid.org/0000-0002-6010-5686
Maria Elina Bichuette https://orcid.org/0000-0002-9515-4832

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