Original article

Comparative gross encephalon morphology in Callichthyidae (Teleostei: Ostariophysi: Siluriformes)

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Callichthyidae comprises the subfamilies Callichthyinae and Corydoradinae, both of which are morphologically distinct and monophyletic. Although there is consensus regarding the monophyly of the family, the relationships of about 80% of its species, currently included in the genus *Corydoras*, remain poorly known. Despite the vast amount of osteological information for Teleostei, knowledge regarding the phylogenetic implications of encephalon anatomy is sparse and represents a poorly explored source of potential characters. The present study aims to describe the encephalon morphology in members of the Callichthyidae in order to propose new characters that may help address phylogenetic questions regarding this group. In addition to representatives of Callichthyidae, specimens belonging to the Nematogenyidae, Trichomycteridae, Scoloplacidae, Astroblepidae and Loricariidae were dissected for comparative purposes. Head dissection revealed information on the structure of the *medulla spinalis*, *rhombencephalon*, *mesencephalon*, *diencephalon* and *telencephalon*. The conditions observed on the encephalons examined suggest that representatives of Callichthyidae have great taste perception and processing, while Corydoradinae stand out for visual acuity and Callichthyinae for mechanoreception processing subunits. Our results also indicate that the encephalon has important features for systematic studies of the family bringing greater resolution to current phylogenetic hypotheses.

Keywords: Brain, Comparative Morphology, *Corydoras*, Loricarioidea, Systematics.

Callichthyidae é composto por Callichthyinae e Corydoradinae, ambos morfologicamente distintos e monofiléticos. Apesar do consenso em relação ao mofiletismo da família, as relações de cerca de 80% de suas espécies, atualmente incluídas no gênero *Corydoras*, permanecem pouco conhecidas. Apesar da grande quantidade de informação osteológica sobre Teleostei, o conhecimento sobre as implicações filogenéticas da anatomia do encéfalo é escasso e, por isso, considerado uma fonte inexplorada de caracteres. O objetivo do presente estudo é a descrição morfológica dos encéfalos de Callichthyidae, fornecendo novos caracteres que podem elucidar questões filogenéticas para o grupo. Além dos representantes de Callichthyidae, espécimes pertencentes a Nematogenyidae, Trichomycteridae, Scoloplacidae, Astroblepidae e Loricariidae foram dissecados para fins comparativos. A dissecção do crânio revelou informações sobre a estrutura da *medulla spinalis*, *rhombencephalon*, *mesencephalon*, *diencephalon* e *telencephalon*. As condições observadas nos encéfalos sugerem que representantes de Callichthyidae possuem grande capacidade de percepção e processamento químico, enquanto os Corydoradinae se destacam pela acuidade visual e os Callichthyinae pelas unidades de processamento mecanoreceptoras. Nossos resultados indicam que os encéfalos detêm características importantes para contribuir com estudos sobre a sistemática da família, trazendo maior resolução para as hipóteses atuais de reconstrução filogenética.

Palavras-chave: Cérebro, *Corydoras*, Loricarioidea, Morfologia Comparada, Sistemática.

Introduction

Species of Callichthyidae are easily recognized by the presence of a series of lateral bony plates along the body and a pair of barbels at the junction of the lips (Reis, 1998). They are grouped into eight genera (Ferraris, 2007) distributed throughout all major cis-Andean watersheds, as well as some trans-Andean drainages. The family is the sister-group to a clade composed of Scoloplacidae, Astroblepidae and Loricariidae (de Pinna, 1998). Studies focused on phy-logenetic relationships within Callichthyidae agree with its monophyly and the recognition of two main lineages among its representatives, *i.e.*, Callichthyinae and Corydoradinae (Reis, 1998; Britto, 2003; Shimabukuro-Dias *et al.*, 2004; Alexandrou *et al.*, 2011). However, knowledge about their encephalon morphology remains unknown.

Investigations on the neuroanatomy of Siluriformes date to the end of the 19th century and probably the first attempt to understand the encephalon is the work of Herrick, Herrick (1891) on some species of Ictaluridae. At this time, it was thought that

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siluriform brains are the most specialized among Actinopterygii. Besides the high accurate description, an insight of this contribution include that the encephalon stops to grow at a fish "moderate size" (Herrick, Herrick 1891:212) even if the body continues to gain biomass and independently of the size of the neurocranium. Several studies on the external morphology of the encephalon took place in the middle of the 20th century, followed by many papers published on the anatomy, physiology, cytoarchitecture, hodology and embryology of the encephalon and the peripheral nervous system (Finger, 2000 and references therein). Despite the establishment of phylogenetic systematics as the paradigm for investigating the evolutionary relationships of organisms (Hennig, 1966), few studies have used the central nervous system as sources of characters for vertebrate studies, particularly for fish. Although there is great amount of literature on the nervous system of fish (*e.g.*, Davis, Northcutt, 1983; Northcutt, Davis, 1983), papers relating neuroanatomy to fish Systematics are scarce. The exceptions are the works of Eastman, Lannoo (1995, 1998, 2001, 2003a, 2003b, 2004, 2007, 2008, 2011) and Lannoo, Eastman (1995, 2000, 2006) on the encephalons and sensory systems of Notothenioidei groups; Albert *et al.* (1998) and Albert (2001) on Gymnotiformes. More recently, this subject drew attention of some researchers as the works of Pereira (2014, Characiformes); Rosa *et al.* (2014, miniaturization in *Otothyris*); Abrahão, Shibatta (2015, *Pseudopimelodus bufonius*); Pupo (2015, Loricarioidea) and Pereira, Castro (2016, *Brycon orbignyanus*); Angulo, Langeani (2017, *Rineloricaria heteroptera*); Abrahão *et al.* (2018, Pseudopimelodidae). Wiley, Johnson (2010) reviewed morphological synapomorphies for 118 major monophyletic groups of teleost fishes. This information was summarized by Datovo, Vari (2014: fig 1) in a single chart with only about 1% coming from neuroanatomical data. None of this information had been previously used as a synapomorphy of Siluriformes or even to characterize any of its families. In addition, Kotrschal *et al.* (1998) assigned that both history and ecology fashioned the vast number of encephalon shapes and, as expected, more closely related species share similar patterns of encephalon morphology. Although some homoplasies (manly on highly specialized taxa) can constrain the reliability of characters states, the authors claims that due to the current knowledge on fish brains, a phylogenetic perspective, in addition to purely descriptive, is fundamental to propose testable hypotheses and advance the understanding of how evolutionary forces act on the encephalon.

Accordingly, the aims of the present study is to provide a phylogenetically-oriented description of the encephalon of Callichthyidae, considering representatives of each genus and key groups as found in Reis (1998) and Britto (2003).

Material and Methods

Examination of encephalon gross morphology was performed by the dissection of specimens preserved in 70° GL ethanol under a stereomicroscope. Representatives of all Callichthyidae genera and loricarioid families were sampled. Institutional acronyms are: AUM, Auburn Natural History Museum, Auburn, U.S.A.; CAS, California Academy of Sciences, San Francisco, U.S.A.; DZSJRP, Coleção de Peixes do Departamento de Zoologia e Botânica do Instituto de Biociências, Letras e Ciências Exatas, UNESP, São José do Rio Preto, Brazil; LBP, Laboratório de Biologia e Genética de Peixes, UNESP, Botucatu, Brazil; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MPUJ, Museo Javeriano de Historia Natural Lorenzo Uribe, Bogotá, Colombia; MUSM, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; MZUEL, Museu de Zoologia da Universidade Estadual de Londrina, Londrina, Brazil; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; MZFS, Museu de Zoologia da Universidade Estadual de Feira de Santana, Feira de Santana, Brazil; and UFRGS, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

Nomenclature of encephalon subunits follows International Committee on Veterinary Gross Anatomical Nomenclature (2012) for general vertebrate structures and Meek, Nieuwenhuys (1998) for specific aspects of fish neuroanatomy. All specimens listed at Material examined session were dissected for removal of the encephalon.

Data acquisition. Dissections for the removal of the encephalon were performed according to Abrahão, Pupo (2014), with the following steps: (1) removal of the skin flap on the nostrils; (2) removal of the skin of the head and predorsal area, exposing the skull roof; (3) release of the nasal organ from the olfactory chamber floor by cutting the ligaments between the anterior portion of the organ and the chamber, maintaining its attachment only by the *nervus olfactorius* (N. I); (4) release the *bulbus olfactorius* plus *nervus olfactorius* (N. I) from ligaments posterior to this organ, in the area anterior to the frontal bone; (5) removal of the nuchal plate and three adjacent pairs of dorsolateral plates (in Callichthyidae); (6) removal of the muscle tissue posterior to the head exposing the Weberian apparatus and associated structures; (7) incisions around the supraoccipital bone; (8) incisions between the frontal and sphenotic bones; (9) incisions between the sphenotic and compound pterotic bones; (10) removal of the supraoccipital bone; (11) removal of the dorsal part of the compound pterotic bone on both sides; (12) removal of the dorsal part of sphenotic bone on both sides; (13) removal of the frontal bone; (14) removal of the dorsal surface of the Weberian capsule; (15) removal of the tissue surrounding the encephalon; (16) cross section of the nerve cord (spinal cord) through seventh or eighth vertebra (including those of the Weberian capsule); (17) cross section of the *nervus vagus* (N.X) efferent of *lobus vagus* on both sides; (18) cross section of the group of nerves for the *octavolateralis* area [*nervus trigeminus* (N.V), *nervus facialis* (N.VII), *nervus vestibulocochlearis* (N.VIII), *nervus linea*

lateralis anterior (N.lla), *nervus linea lateralis posterior* (N.llp)] of the *cerebellum* on both sides; (19) cross section of the *nervus opticus* (II) on both sides; and (20) removal of the encephalon with the aid of tweezers. This final step requires special attention because part of the auditory system and the *hypophysis* are ventral to the brainstem.

Figures of encephalon topography were made using a Leica DFC 450 digital camera attached to a Leica M205C auto-stacking multifocus stereomicroscope with the help of Leica Application Suite (version 4.8) software to obtain an "all-in-focus" image. All images were improved using the software Intensify (Macphun Software, San Diego, CA, 2016), Noiseless (Macphun Software, San Diego, CA, 2015) and Pixelmator version 3.6 (UAB Pixelmator team, Vilnius, Lithuania, 2016).

Results

A brief description of the gross morphology of the encephalon and its subunits are addressed below (Figs. 1, 2; Tab. 1). All character states in Tab. 1 refer exclusively to representatives listed in Material examined.

Lobus vagus. Among the representatives of Callichthyidae, the *lobus vagus* tumid with a roughly spherical shape (Figs. 1, 2, LV), and is larger than in other loricarioids (Fig. 3, LV), in which it is not as conspicuous and present a "V" shape. Exceptions of this were found in *Loricaria* and *Loricariichthys*. The anterior margin of the *lobus vagus* is not continuous with *lobus facialis* in Callichthyidae and has an anterior angular expansion positioned above the posterior portion of *lobus facialis* in Corydoradinae (Fig. 1, arrow), and is adjacent rather than dorsal to this lobe in Callichthyinae (Fig. 2). Another pattern was found among Loricariidae (*e.g.*, *Delturus carinotus*, *Hypancistrus* sp., *Hypostomus ancistroides*, *Liposarcus* sp., *Rhinelepis aspera*), roughly pentagonal.

Lobus facialis. In Callichthyidae, the *lobus facialis* (Figs. 2, 4, LF) rises from the floor of the fourth ventricle, with its lateral face detached from the medial face of the ventricle. In other Loricarioidea and several Siluriformes, these lobes are fused with the edge of the fourth ventricle and with the *lobus vagus*. In representatives of Callichthyinae, the *corpus cerebelli* (Fig. 2, CC) is more anterior and the *lobus facialis* is completely exposed in dorsal view, as in other catfish lineages. In specimens of the Corydoradinae (Fig. 1, CC), the *corpus cerebelli* is displaced posteriorly with the *lobus facialis* ventral and almost completely covered by it, in dorsal view. The three divisions of the *lobus facialis* (lateral, intermediate and medial portions) can be seen superficially in Callichthyidae specimens (Figs. 2, 4, LF). The lateral portion varies in shape and can be a dorsal swelling present only in the Callichthyinae (Fig. 2, LF), or a lateral angular expansion which end advances above the *lobus vestibulolateralis*, present in the Corydoradinae (Fig. 4, LF).
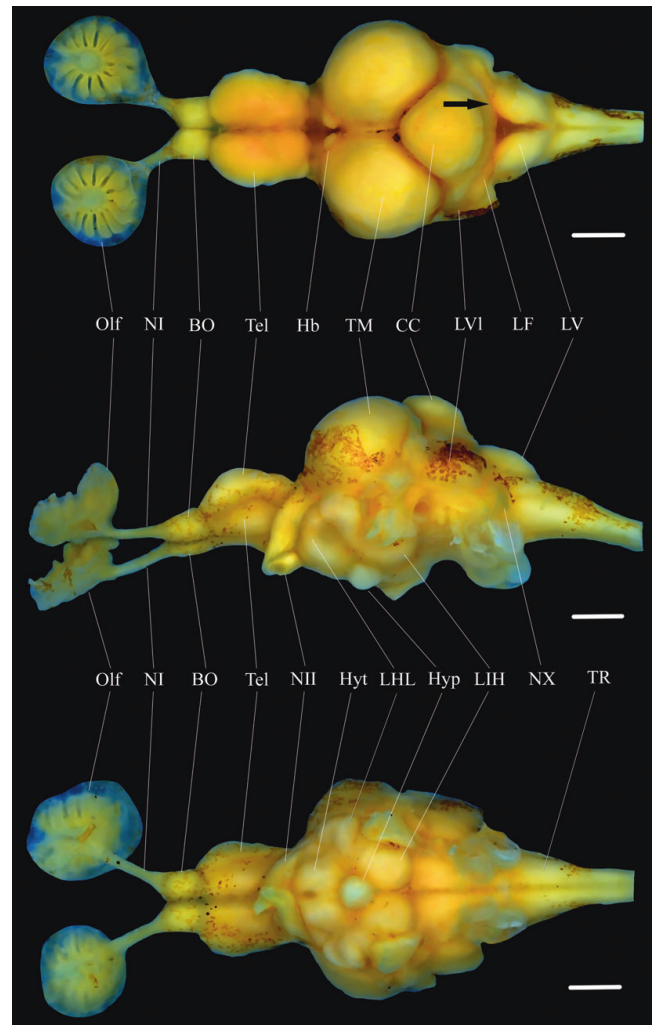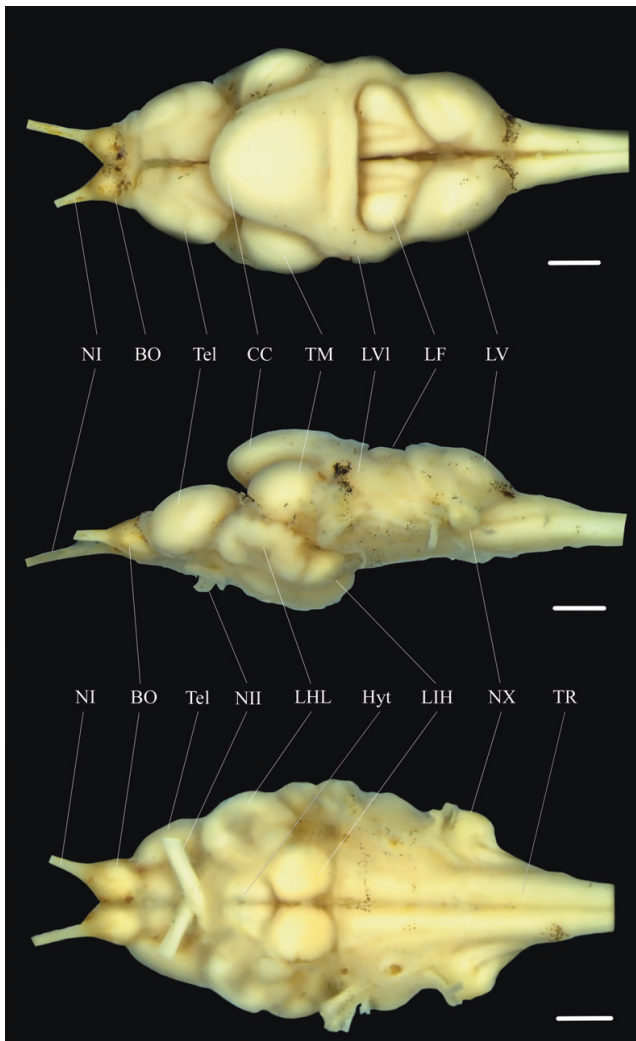

Fig. 1. Encephalon and associated olfactory organ of *Corydoras acutus*, MNRJ 33859, 50.0 mm SL. Dorsal (upper), lateral (middle) and ventral (lower) views. Abbreviations: BO = *bulbus olfactorius*; CC = *corpus cerebelli*; Hb = *ganglion habenulae*; Hyp = *hypophysis*; Hyt = *hypothamalus*; LF = *lobus facialis*; LHL = *lobus hypothalami lateralis*; LIH = *lobus inferior hypothalami*; LV = *lobus vagus*; LVl = *lobus vestibulolateralis*; NI = *nervus olfactorius*; NII = *nervus opticus*; NX = *nervus vagus*; Olf = olfactory organ; Tel = *telencephalon*; TM = *tectum mesencephali*; TR = *tegmentum rhombencephali*. Arrow pointed to the anterior angular expansion of *lobus vagus*. Scale bars = 1.0 mm.

Corpus cerebelli. Modifications of three features of the *corpus cerebelli* were observed among Callichthyidae: shape, volume, and position. In contrast with most of the Loricarioidea, the *corpus cerebelli* in callichthyids is tumid (Figs. 1, 2) and roughly spherical as several non-Siluriformes fishes (Kotrschal *et al.*, 1998), suggesting that this modification could be exclusive to the family. In Corydoradinae, and mainly in representatives of *Corydoras* (Fig. 1, CC), there is a reduction in the volume of this portion of the cerebellum such that it is smaller than the *tectum me-*

Tab. 1. Summary of the characters of gross morphology of the encephalon and its subunits, with its states and respectively taxa.

Structure	Character	States	Taxa
Lobus vagus	Shape, dorsal view	"V" shape	Remaining taxa
		Roughly spherical	Callichthyidae, *Loricaria* and *Loricariichthys*
		Roughly pentagonal	Delturinae, Hypostominae and Rhinelepinae
	Volume	Small	Remaining taxa
		Large	Callichthyidae, *Loricaria* and *Loricariichthys*
	Relation with *lobus facialis*	Fused	Remaining taxa
		Detached	Callichthyidae
	Shape of anterior margin	Straigth	Callichthyinae
		Flap-like	Corydoradinae
	Position of anterior margin	Over *lobus facialis* posterior region	Corydoradinae
		Lateral to *lobus facialis* posterior region	Callichthyinae
Lobus facialis	Position	Exposed	Remaining taxa
		Ventral to *corpus cerebelli*	Corydoradinae
	Shape	Subdivided	Callichthyidae
		No external subdivisions	Remaining taxa
	Shape of *lobus facialis* lateral subdivision	Spherical	Callichthyinae
		With an angulated lateral expansion	Corydoradinae
	Position of *lobus facialis* lateral subdivision	Adjacent to *lobus vestibulolateralis*	Callichthyinae
		Over *lobus vestibulolateralis*	Corydoradinae
	Relation with fourth ventricle medial face	Fused	Remaining taxa
		Detached	Callichthyidae
Corpus cerebelli	Shape of central portion	Depressed	Remaining taxa
		Spherical	Callichthyinae
	Volume of central portion	Larger than *tectum mesencephali*	Callichthyinae
		Equal or smaller than *tectum mesencephali*	Corydoradinae
	Position of anterior margin	Over *telencephalon* posterior margin	Callichthyinae
		Posterior to *telencephalon* posterior margin	Corydoradinae and remaining taxa
Tectum mesencephali	Gauge of *nervus opticus* related to *nervus olfactorius*	Smaller	*Callichthys*, *Lepthoplosternum* and *Astroblepus*
		Larger	Remaining taxa
		More than three times larger	*Corydoras*
Lobus inferior hypothalami	Shape of posterior margin	With invagination	*Corydoras*
		Straight	Remaining taxa
	Shape of lateral margin	Convex	Remaining taxa
		Concave	Callichthyidae, *Delturus* and *Hypancistrus*
		Angular	Trichomycteridae and *Scoloplax*
Bulbus olfactorius	Position	Pedunculated	Remaining taxa
		Sessile	Callichthyidae and miniaturized taxa
Olfactory organ	Shape	Elliptical	Remaining taxa
		Spherical	Callichthyidae
		Oval	Astroblepidae
	Number of lamellae	Less than 15	Callichthyidae
		Between 15 and 45	Remaining taxa
		More than 45	*Delturus*
	Relation between lamella distal and proximal area	Equal	Remaining taxa
		Distal area larger	Callichthyidae
	Shape of lamellae distal area	Laterally sharpen	Remaining taxa
		Depressed	Callichthyinae
		Tumid	Corydoradinae
	Shape of lamella distal area transversal section, lateral view	Straight	Callichthyinae and remaining taxa
		Dorsally curve	Corydoradinae
	Shape of lamella dorsal surface	With dorsal flaps	Corydoradinae and remaining taxa
		Without dorsal flaps	Callichthyinae

Fig. 2. Encephalon of *Megalechis personata*, DZSRJP 8517, 116.4 mm SL, with olfactory organ removed. Dorsal (upper), lateral (middle) and ventral (lower) views. Abbreviations: BO = *bulbus olfactorius*; CC = *corpus cerebelli*; Hyt = *hypothamalus*; LF = *lobus facialis*; LHL = *lobus hypothalami lateralis*; LIH = *lobus inferior hypothalami*; LV = *lobus vagus*; LVl = *lobus vestibulolateralis*; NI = *nervus olfactorius*; NII = *nervus opticus*; NX = *nervus vagus*; Tel = *telencephalon*; TM = *tectum mesencephali*; TR = *tegmentum rhombencephali*. Scale bars = 1.0 mm.

sencephali, while representatives of Callichthyinae display a significant increase in the volume of this region, such that it is greater than the *lobus vagus* or *tectum mesencephali* (Fig. 2). In most of the representatives of Loricarioidea examined in this study the *corpus cerebelli* is positioned in the middle portion of the encephalon with its anterior area between the two mesencephalic *tecta* or even posterior to them. Only in Callichthyinae does the anterior margin of this structure extend anteriorly and is in contact with, or even with a small anterior portion dorsal to, the *telencephalon*. The anterior position of the *corpus cerebelli* of specimens of Callichthyinae is also observed among advanced siluriform families
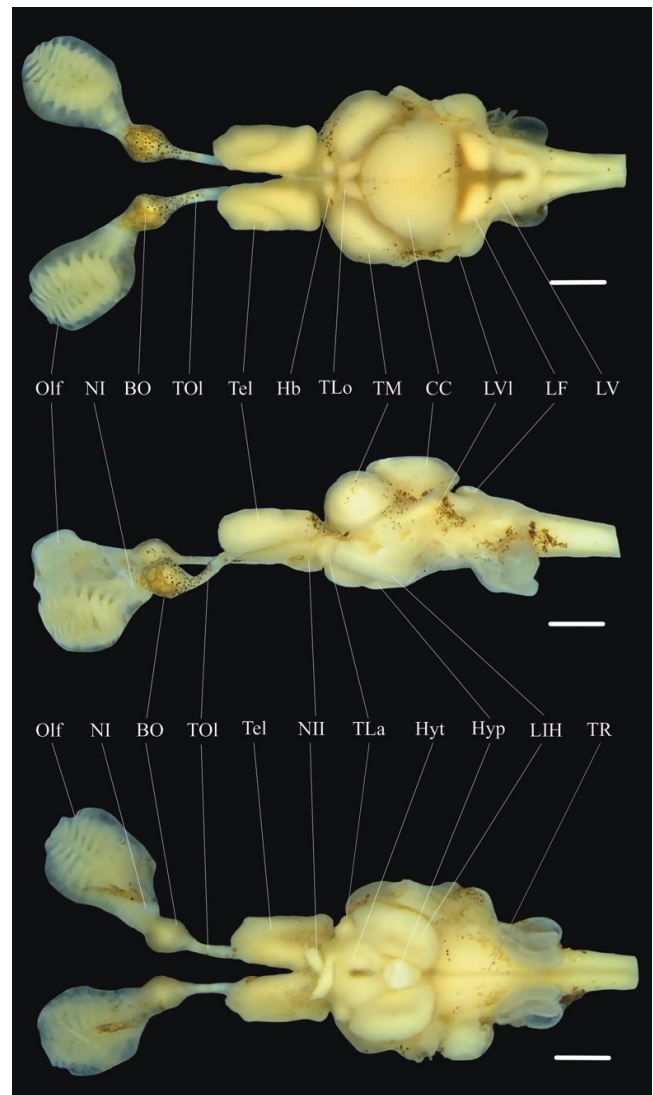
Fig. 3. Encephalon and associated olfactory organ of *Trichogenes longipinnis*, MNRJ 13809, 67.6 mm SL. Dorsal (upper), lateral (middle) and ventral (lower) views. Abbreviations: BO = *bulbus olfactorius*; CC = *corpus cerebelli*; Hb = *ganglion habenulae*; Hyp = *hypophysis*; Hyt = *hypothamalus*; LF = *lobus facialis*; LIH = *lobus inferior hypothalami*; LV = *lobus vagus*; LVl = *lobus vestibulolateralis*; NI = *nervus olfactorius*; NII = *nervus opticus*; Olf = olfactory organ; Tel = *telencephalon*; TLa = *torus lateralis*; TLo = *torus longitudinalis*; TM = *tectum mesencephali*; TOl = *tractus olfactorius*; TR = *tegmentum rhombencephali*. Scale bars = 1.0 mm.

included in clade 5 of Britto (2003: fig. 122: clade 5); in those cases, the *corpus cerebelli* is depressed, not swollen, and straight in lateral view (Pupo, 2015).

Tectum mesencephali. A gradual increase in the absolute size of this structure was noticed among the specimens of Corydoradinae analyzed. *Nervus opticus* (Fig. 1, N.II), could be thinner, equal to, approximately two times thicker, or have the diameter of its cross section three times or grea-
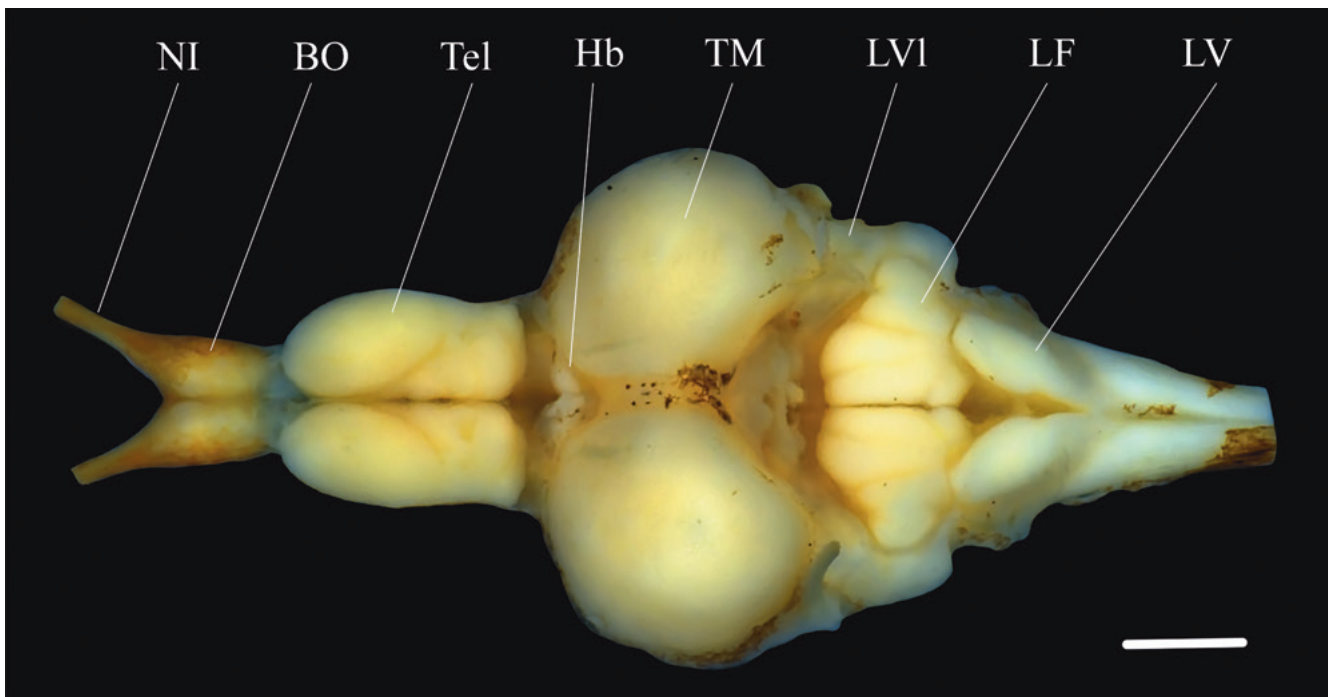
Fig. 4. Encephalon of *Corydoras narcissus*, MNRJ 50365, 64.1 mm SL, with *corpus cerebelli* and olfactory organ removed, showing the lobus facialis in dorsal view. Abbreviations: BO = *bulbus olfactorius*; Hb = *ganglion habenulae*; LF = *lobus facialis*; LV = *lobus vagus*; LVl = *lobus vestibulolateralis*; NI = *nervus olfactorius*; Tel = *telencephalon*; TM = *tectum mesencephali*. Scale bar = 1.0 mm.

ter than of the *nervus olfactorius*. Most of the taxa analyzed exhibited the state "larger". Representatives of *Callichthys*, *Lepthoplosternum* and *Astroblepus* exhibited a thin *nervus opticus*. With regard to Corydoradinae, the optimization of this character in Britto's (2003) hypothesis reveals an exclusive condition within the genus *Corydoras* with the thickness of this nerve being three times greater than the *nervus olfactorius*. This state seems to be positively associated with a gradual but significant increase in the volume of the *tectum mesencephali*, which suggests greater efficiency in visual perception.

Hypothalamus. The *hypothalamus* is the ventral most region of *diencephalon*. It is positioned posterior to the *chiasma opticum*, ventral to the *truncus cerebri* and *tectum mesencephali*, and posterior to the *telencephalon*, in ventral view (Fig. 1, Hyt). It can be divided into the *hypothalamus* itself, the *lobus lateralis hypothalami* and the *lobus inferior hypothalami*. Among the representatives of Loricarioidea, the *lobus inferior hypothalami* possesses an invagination in its posterolateral or posterior margin only in *Corydoras*, suggesting an exclusive condition for the genus. Its lateral margin is concave in Callichthyidae, *Delturus* and *Hypancistrus* while angular in Trichomycteridae and *Scoloplax* and convex in other Siluriformes. The *hypophysis* is rounded in all specimens examined of all families (Fig. 1, Hyp). This structure is anchored anteriorly to the *hypothalamus*.

Telencephalon. Despite the presence of this subunit in all Actinopterygii studied and the numerous studies that have contributed to understanding the organization of this structure, there is no consensus as to the limits of each of its inner *nucleus* and even homology with other vertebrates (Northcutt, Davis, 1983). Some attempts have been successful in determining the dorsomedial (Dm), dorsolateral (Dl), dorsocentral (Dc) and dorsoposterior (Dp) lobes using histology (*e.g.*, Eastman, Lannoo, 2007; 2008; 2011). The telencephalon is the structure with the most variable shape. In general, representatives of Callichthyinae possess a short telencephalon with a rounded lateral edge (Fig. 2, Tel), while among specimens of Corydoradinae this structure is more elongate, has straight lateral margins and is roughly rectangular in shape (Fig. 1, Tel). Other families exhibit a more elongate *telencephalon* (Astroblepidae), and in a few representatives of Trichomycteridae it is even more elongate (*e.g.*, *Stauroglanis goldingi*).

Bulbus olfactorius. Callichthyidae has a sessile *bulbus olfactorius* (Figs. 1, 2, BO), while it is pedunculated in other loricarioids (Fig. 3, BO), in which is connected to the *telencephalon* via the *nervus tractus olfactorius* (Fig. 3, TOl). Some taxa in Loricariidae and Trichomycteridae may possess a greatly reduced *tractus olfactorius*, which is indicative of the presence of the sessile *bulbus* among a few species of these families, mainly the miniatures. The *nervus olfactorius* did not exhibit noticeable superficial variation (Fig. 1, N.I).

Olfactory organ. Within Loricarioidea, only specimens of Callichthyidae possess a circular olfactory organ (Fig. 5), while it is oval in Astroblepidae and elliptical in other Loricarioidea. All examined representatives of Callichthyidae have less than 15 lamellae, while other loricarioids exhibit more than 30. The volume of each lamella of the nasal organ increases in a medial to distal direction (from the center to the edge of rosettes) in Callichthyidae. Also in Callichthyinae, each lamella is flat and attached to the floor of the organ throughout its extension, which differs from Corydoradinae where the distal margin of the lamellae is detached from the chamber floor. In specimens of *Corydoras hastatus*, the olfactory epithelium does not have lamellae, but instead possesses small crests (Fig. 5c).

Discussion

The obtained data of the gross morphology of the encephalon allows some patterns of the organ in Callichthyidae and related families to be discussed. It corroborates Herrick (1891) conclusions about the *cerebellum* that, although its variation, it is suited to characterize families and genera, which means it is phylogenetic informative.

Although the characters presented herein have some limitations in terms of scope, they can help resolve the relationships of groups with uncertain topologies, mainly at the levels of family, subfamily, and genera, as well as raise hypotheses regarding processes of evolutionary convergence. The species *Ochmacanthus alternus* (27.3 mm SL), *Stauroglanis gouldingi* (22.9 mm SL), *Trichomycterus hasemani* (15.1-15.2 mm SL), and *Tridentopsis pearsoni* (19.7 mm SL) possess a reduction in the number of olfactory lamellae (3 to 8) relative to other representatives of Trichomycteridae. *Scoloplax distolothrix* (14.8 mm SL), and *Scoloplax empousa* (12.8 mm SL) bear three lamellae, while *Corydoras hastatus* (15.4 mm SL) lack lamellae altogether but possesses small elevations of the olfactory epithelium (Fig. 5c). These species are considered to be miniature, suggesting that this drastic reduction in lamellae number could be related to the process of miniaturization (*sensu* Weitzman, Vari, 1988).

The following neuroanatomical conditions are unique to Callichthyidae: (1) nasal organ circular in shape in dorsal view; (2) olfactory organ with fewer than 15 lamellae; (3) volume of nasal organ lamellae increasing in a medial-distal direction; (4) sessile positioning of *bulbus olfactorius*; (5) spherical central portion of the *corpus cerebelli*; (6) *lobus facialis* detached from the medial margin of the lateral walls of the fourth ventricle; and (7) swelling of the *lobus vagus*. The monophyly of the two subfamilies of Callichthyidae is also supported by this study. The following conditions are exclusive to Callichthyinae: (1) nasal organ lamellae flattened dorsoventrally; (2) *telencephalon* short with a curved lateral edge; (3) *corpus cerebelli* adjacent or above the posterodorsal margin of the *telencephalon*; (4) increased volume of the *corpus cerebelli*; (5) lateral por-
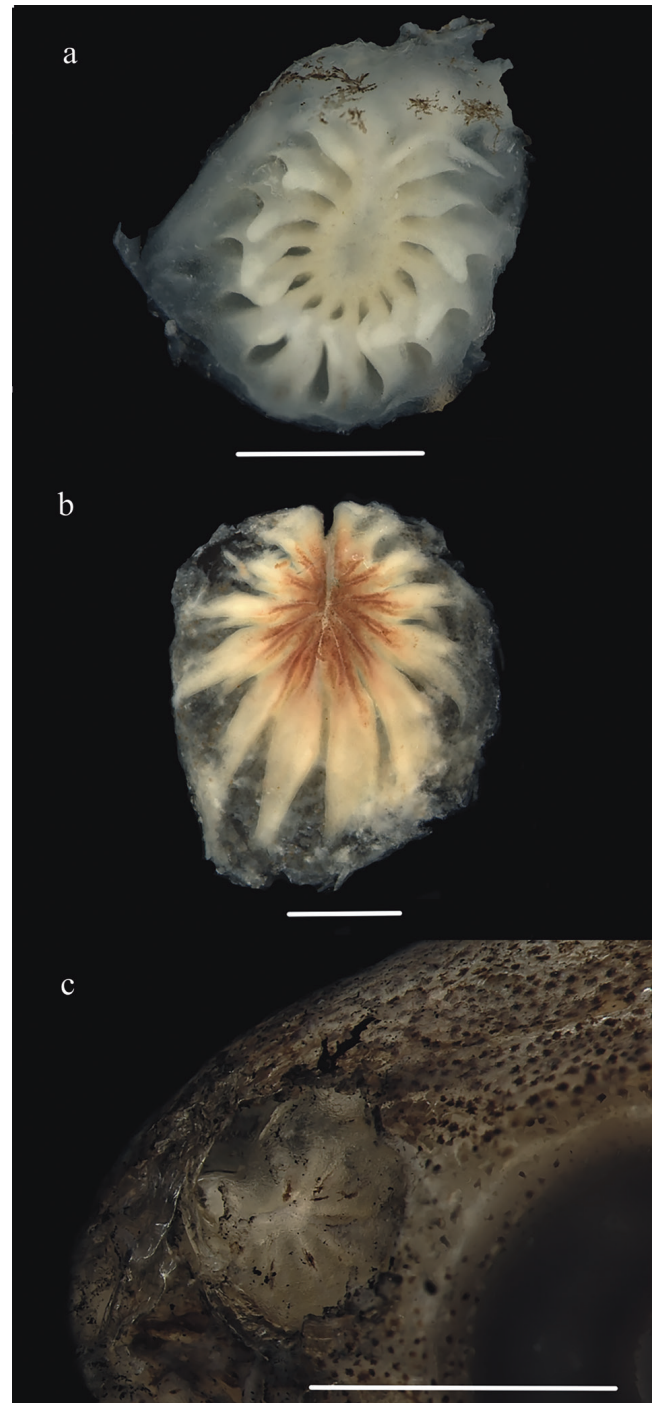
Fig. 5. Olfactory organ of **a.** *Corydoras narcissus*, MNRJ 50365, 64.1 mm SL; **b.** *Dianema urostriatum*, MNRJ 36730, 72.2 mm SL; and **c.** *Corydoras hastatus*, MZUSP 59647, 15.4 mm SL. Scale bars = 1.0 mm.

tion of the *lobus facialis* in the shape of a dorsolateral callosity; and (6) anterior margin of the *lobus vagus* adjacent to the *lobus facialis*. The exclusive features observed in Corydoradinae are: (1) distal area of nasal organ lamellae detached from the nasal chamber floor; (2) *telencephalon* with straight edges and roughly rectangular; (3) increased

size of the *tectum mesencephali*; (4) *corpus cerebelli* posterior to the *tectum mesencephali*; (5) decreased size of the *corpus cerebelli*; (6) *lobus facialis* ventral to *corpus cerebelli*; (7) lateral portion of *lobus facialis* angular, dorsal to the *lobus vestibulolateralis*; and (8) anterior margin of the *lobus vagus* above the posterior portion of the *lobus facialis*. The distributions of these character states support the groups originally proposed by Hoedeman (1952), which were supported by the morphology-based phylogenies proposed by Reis (1998) and Britto (2003) and the molecular-based phylogeny proposed by Shimabukuro-Dias *et al.* (2004) and Alexandrou *et al.* (2011).

According to Britto (2003), most of the species of the subfamily Corydoradinae studied herein are *incertae sedis* within *Corydoras*. The existence of a *nervus opticus* three or more times thicker than the *nervus olfactorius* suggests a group within the genus comprised of *Corydoras polystictus*, *C. julii*, *C. trilineatus*, *C. multimaculatus*, *C. melanistius*, *C. hastatus* and *C. tukano*. Furthermore, the first four belong to lineage 9 of Alexandrou *et al.* (2011), of which lineage 8, including *C. melanistius*, is its sister-group. In fact, a gradual increase in the volume of the *tectum mesencephali* can be observed within *Corydoras*, mainly in these species. This condition also occurs in representatives of *Dianema*. The state in which the *nervus opticus* is thinner than the *nervus olfactorius* occurs in *Callichthys callichthys* and *Lepthoplosternum pectorale*. According to observations of the habit of these animals, species of the genus *Callichthys* are associated with muddy bottoms, while species of *Dianema* occur in the middle of the water column, a behavior also observed for *Corydoras hastatus*. Considering a scenario where a thin nervus opticus constitutes an ancestral condition, and taking into account the topology of Reis (1998), there could be a gradient towards increased thickness of this nerve among the genera of the subfamily Callichthyinae, reflecting adaptation from benthic to mid-water swimming.

One of the most impressive conditions found in the present study involves the shape and position of the *lobus facialis* in Callichthyidae. This structure is considered to be involved in chemoreception because of its connection to taste buds on the surface of the body of catfish, especially on the head, lips and barbels (Butler, Hodos, 2005). Additionally, a significant increase in the *lobus vagus* can be observed in Callichthyidae. This center is responsible for gustatory and tactile senses in the oropharyngeal cavity. These two features suggest, in general, a high capacity for chemical perception of the environment. Kohda *et al.* (1995) recorded an interesting behavior in *Corydoras aeneus* involving females drinking sperm for the fertilization of oocytes. Later, Kohda *et al.* (2002) reported that female *Corydoras aeneus* exhibited no preference for males regarding size or aggressiveness. It is possible that the significant increase of these two encephalon lobes is related to the reproductive mode of this species, such as a chemical role (perhaps through pheromones) instead of a physical or behavioral preference.

Studies of the central nervous system almost invariably lead to issues relevant to animal behavior. More specifically, for those who study patterns, the association between structure and behavior is almost inevitable. Despite the myriad of possible interpretations of the subject, some consensus has been established on the positive relation between the size and efficiency of the encephalon subdivisions (Kotrschal *et al.*, 1998). First, it is hard to imagine that the volume increase of a given portion of the encephalon, especially in fish, would not mean a more complex function of this area for realizing senses or processing information. Examples among teleost fish include: (1) the *lobus vagus* and the sense of taste in the oropharyngeal cavity; (2) *lobus facialis* and the chemoreception on barbels, lips and head surface; (3) *cerebellum* and the receipt and processing of stimuli (mechanical, electrical, motor, proprioceptive, lateral line, etc); (4) *tectum mesencephali* and vision; (5) *telencephalon* and part of olfaction, memory and processing of information from other centers; and (6) *bulbus olfactorius* and the olfactory organ and smell (Davis, Northcutt, 1983; Northcutt, Davis, 1983; Meek, Nieuwenhuys, 1998). In this sense, some questions and possibilities for future work are: (1) to test the relationship between parts of the encephalon and animal behavior, considering a family-level survey whose members have a broad spectrum of body sizes, habitat uses and diets, and with reasonable knowledge about their phylogeny; and (2) test taxonomic and geographic variation in parts of the central nervous system and assess the influence of microhabitat variables.

Material examined. Callichthyidae: *Aspidoras albater* Nijssen, Isbrücker MZUSP 50157, 2 ex., 21.8-26.8 mm SL; *A. microgaleus* Britto MZUSP 86842, 2 ex., 23.8-28.8 mm SL; *A. poecilus* Nijssen, Isbrücker MNRJ 11716, 2 ex., 26.1-27.6 mm SL; *Callichthys callichthys* (Linnaeus) MNRJ 31162, 2 ex., 66.3-68.2 mm SL; *Corydoras acutus* Cope MNRJ 33859, 50.0 mm SL; *C. aeneus* (Gill) MNRJ 27455, 39.4 mm SL; *C. araguaiaensis* Sands MZUSP 86269, 49.6 mm SL; *C. difluviatilis* Britto, Castro MNRJ 26294, 2 ex., 33.0-42.2 mm SL; *C. ehrhardti* Steindachner MNRJ 1095, 43.3 mm SL; MNRJ 26679, 25.5 mm SL; *C. haraldschultzi* Knaack MZUSP 94996, 46.0 mm SL; *C. hastatus* Eigenmann, Eigenmann MZUSP 59647, 15.4 mm SL; *C. julii* Steindachner MNRJ 33869, 26.0 mm SL; *C. melanistius* Regan MZUSP 30844, 41.6 mm SL; *C. multimaculatus* Steindachner MZUSP 57404, 31.9 mm SL; *C. narcissus* Nijssen, Isbrücker MNRJ 50365, 64.1 mm SL; *C. nattereri* Steindachner MNRJ 38120, 37.4 mm SL; *C. paleatus* (Jenyns) MNRJ 27966, 40.5 mm SL; *C.* cf. *polystictus* MZUSP 59452, 23.6 mm SL; *C. splendens* (Castelnau) MNRJ 28913, 52.6 mm SL; *C. trilineatus* Cope MZUSP 30857, 44.0 mm SL; *C. tukano* Britto, Lima MZUSP 92177, 34.2 mm SL; *Dianema longibarbis* Cope MNRJ 37209, 73.9 mm SL; *D. urostriatum* (Miranda-Ribeiro) MNRJ 36730, 68.5 mm; MNRJ 38531, 72.2 mm SL; *Hoplosternum littorale* (Hancock) DZSJRP 2843, 33.4 mm SL; *Lepthoplosternum pectorale* (Boulenger) MZUSP 59388, 2 ex., 29.6-30.4 mm SL; *Megalechis personata* (Ranzani) DZSJRP 8517, 3 ex., 96.2-116.4 mm SL; *Scleromystax barbatus* (Quoy, Gaimard)

MNRJ 27738, 57.7 mm SL; MNRJ 38133, 2 ex., 49.9-53.7 mm SL; *S. macropterus* (Regan) MZUSP 103982, 2 ex., 36.0-36.3 mm SL; *S. prionotos* (Nijssen, Isbrücker) MNRJ 38132, 45.4 mm SL. Astroblepidae: *Astroblepus grixalvii* Humboldt MPUJ 4237, 87.6 mm SL; *A. longifilis* (Steindachner) MNRJ 28436, 76.7 mm SL; *A. rosei* Eigenmann MUSM 1272, 68.6 mm SL; *A. trifasciatus* (Eigenmann) MUSM 1721, 55.6 mm SL; MUSM 44885, 54.7 mm SL. Loricariidae: *Ancistrus brevipinnis* (Regan) MCP 22180, 61.9 mm SL; *Chaetostoma microps* (Günther) MUSM 2367, 70.9 mm SL; *Corumbataia cuestae* Britski MZUEL 4175, 27.9 mm SL; *Curculionichthys insperatus* (Britski, Garavello) DZSJRP 14381, 32.2 mm SL; *Delturus carinotus* (La Monte) MCP 28037, 153.1 mm SL; *Epactionotus bilineatus* Reis, Schaefer MCP 25311, 35.6 mm SL; *Farlowella oxyrryncha* (Kner) MCP 15709, 106.1 mm SL; *Gymnotocinclus anosteos* Carvalho, Lehmann A., Reis UFRGS 11296, 39.8 mm SL; *Harttia punctata* Rapp-Py-Daniel, Oliveira MZUEL 5965, 66.3 mm SL; *H. novalimensis* Oyakawa DZSJRP 11585, 62.7 mm SL; *Hemiancistrus fuliginosus* Cardoso, Malabarba MCP 45900, 72.8 mm SL; *Hemiodontichthys acipenserinus* (Kner) MCP 36442, 99.1 mm SL; *Hemipsilichthys nimius* Pereira, Reis, Souza, Lazzarotto DZSJRP 13916, 89.2 mm SL; *Hisonotus francirochai* (Ihering) DZSJRP 1599, 25.7 mm SL; *H. notatus* Eigenmann & Eigenmann DZSJRP 13852, 27.4 mm SL; *Hypancistrus* sp. MCP 44367, 64.1 mm SL; *Hypoptopoma* sp. MZUEL 7925, 32.6 mm SL; *Hypostomus ancistroides* (Ihering) MZUEL 6269, 2 ex., 80.2-106.6 mm SL; *H. nigromaculatus* (Schubart) MZUEL 1228, 76.7 mm SL; *H. strigaticeps* (Regan) MZUEL 5524, 123.4 mm SL; *Isbrueckerichthys duseni* (Miranda-Ribeiro) MCP 12564, 48.5 mm SL; *Kronichthys subteres* Miranda-Ribeiro MCP 20150, 2 ex., 58.3-58.5 mm SL; *Limatulichthys griseus* (Eigenmann) MNRJ 35692, 2 ex., 155.4-126.4 mm SL; *Lithogenes villosus* Eigenmann AUM 62909, 36.5 mm SL; *Loricaria* sp. MCP 36551, 54.9 mm SL; *Loricariichthys maculatus* (Bloch) MCP 13430, 115.7 mm SL; *L. platymetopon* Isbrücker, Nijssen DZSJRP 4393, 285.0 mm SL; *Neoplecostomus microps* (Steindachner) MNRJ 13683, 77.8 mm SL; *Pareiorhaphis hypselurus* (Pereira, Reis) MCP 23531, 49.8 mm SL; *P. hystrix* (Pereira, Reis) MCP 18741, 64.0 mm SL; *Pareiorhina carrancas* Bockmann, Ribeiro DZSJRP 16154, 37.5 mm SL; *Parotocinclus maculicauda* (Steindachner) DZSJRP 13853, 36.1 mm SL; *Rhinelepis aspera* Spix & Agassiz DZSJRP 4779, 149.0 mm SL; *Rineloricaria steinbachi* (Regan) MCP 41303, 60.9 mm SL; *R. strigilata* (Hensel) MCP 25050, 80.9 mm SL; *Rhinolekos britskii* Martins, Langeani, Costa DZSJRP 5622, 38.7 mm SL. Nematogenyidae: *Nematogenys inermis* (Guichenot) CAS 12692, 303.7 mm SL. Scoloplacidae: *Scoloplax distolothrix* Schaefer, Weitzman, Britski MZUSP 86248, 14.8 mm SL; *S. empousa* Schaefer, Weitzman, Britski MZUEL 5862, 12.8 mm SL. Trichomycteridae: *Bullockia maldonadoi* (Eigenmann) MZUSP 107499, 47.9 mm SL; *Copionodon orthiocarinatus* de Pinna MNRJ 21268, 49.9 mm SL; *Copionodon pecten* de Pinna MZFS 15184, 57.3 mm SL; *Glanapteryx anguilla* Myers MZUSP 36530, 52.7 mm SL; *Hatcheria* sp. MZUSP 107491, 108.7 mm SL; *Ituglanis proops* (Miranda-Ribeiro) MZUSP 70725, 61.2 mm SL; *Listrura camposi* (Miranda-Ribeiro) MNRJ 33031, 30.3 mm SL; *Microcambeva ribeirae* Costa, Lima, Bizerril MNRJ 32443, 33.6 mm SL; *Ochmacanthus alternus* Myers MPUJ 730, 27.3 mm SL; *Pareiodon microps* Kner MNRJ 1165, 102.5 mm SL; *Pseudostegophilus maculatus* (Steindachner) MNRJ 4282, 46.1 mm SL; *Stauroglanis gouldingi* de Pinna MZUSP 86957, 22.9 mm SL; *Stegophilus panzeri* (Ahl) MZUSP 95891, 42.6 mm SL; *Trichogenes longipinnis* Britski, Ortega MNRJ 13809, 67.6 mm SL; *Trichomycterus areolatus* Valenciennes MZUSP 107494, 82.9 mm SL; *T. bahianus* Costa MNRJ 32243, 44.3 mm SL; *T. hasemani* (Eigenmann) LBP 4198, 2 ex., 15.1-15.2 mm SL; *T. zonatus* (Eigenmann) MZUSP 36551, 60.5 mm SL; *Tridentopsis pearsoni* Myers MZUSP 109849, 19.7 mm SL; *Vandellia* sp. MZUSP 17329, 58.8 mm SL.

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