



# Evolutionary trends in encephalic morphology among Geophagini cichlid fish: phylogenetic insights and associations with ecological and behavioral traits

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**Abstract** The gross encephalic morphology of representatives from 17 genera within the Geophagini tribe is comprehensively characterized, compared, and analyzed into a previously proposed phylogenetic hypothesis. Our morphological investigation highlights the prominence of the visual center within the cichlid encephalon. Notably, constrained phylogenetic analysis reveals probable convergent adaptations in two genera, *Cichla* and *Saxatilia*, characterized by diminutive gustatory lobes. In contrast, *Retroculus*, known for its sediment-shifting habits among Geophagini species, exhibits well-developed gustatory lobes. Previous research has established that species engaging in sediment sifting exhibit modifications in

their pharyngeal apparatus and frequently adopt benthivorous feeding strategies, features that appear to be orchestrated by the gustative center in the encephalon. Furthermore, our findings underscore a putative relationship between encephalon morphology and factors such as feeding behavior, environmental conditions (including turbidity and depth), and their association with the studied cichlid species. The neuroanatomical characters proposed in this study hold promise as valuable phylogenetic markers for future analyses and contribute to our understanding of the complex interplay between neuroanatomy, behavior, and ecology within this diverse group of cichlids.

**Keywords** Cichlid · Convergence · Evolution · Neuroanatomy · Sifter feeding

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## Introduction

Cichlidae comprises four subfamilies: Etroplinae (India and Madagascar), Ptychochrominae (Madagascar), Cichlinae (Neotropical region) and Pseudocrenilabrinae (Africa and a few locations in Middle East) (Fricke et al., 2023a), forming a monophyletic group well supported by morphological (Kaufman & Liem, 1982; Stiassny, 1987) and molecular data (Zardoya et al., 1996; Friedman et al., 2013). It is the third most species-rich family in the Neotropical region (Reis et al., 2003; López-Fernández et al., 2010; 2016),

with 571 valid species from a total of 1749 in the family as a whole (Fricke et al., 2023a).

Cichlids have high diversification of the color patterns, feeding habits, breeding, and other behavioral aspects (Parry et al., 2005; Carleton, 2009; Gois et al., 2015; Schneider et al., 2020), and they are a well-studied group. These traits have been the focus of investigation by evolutionary biologists, and some studies have linked morphology to behavior and function (Kotrschal et al., 1998; Arbour & López-Fernández, 2014; Edmunds et al., 2016). In this sense, the encephalon's morphology may provide insight into how the central nervous system coordinates a variety of behavioral features. Studies on Pseudocrenilabrinae, for example, have revealed a significant difference in encephalon morphology, particularly among the three large lakes (Tanganyika, Victoria and Malawi), indicating that environmental factors (e.g. turbidity, depth) and ecological traits (e.g. eating habits) are correlated with evolutionarily neuroanatomic characteristics (van Staaden et al., 1995; Huber et al., 1997).

Besides ecological and behavioral approaches, morphology has been used to generate new phylogenetic hypotheses and for taxonomic purposes. Recently, neuroanatomy has been used characters to generate a phylogenetic hypothesis of Pseudopimelodidae providing useful information in that context, such as synapomorphies and better resolution and support of phylogenetic relationships, as well as information on the evolution of those characters (Abrahão et al., 2018) and a recent neuroanatomical analysis of a cichlid species has brought up information that could be useful in phylogenetic investigations (Oliveira & Graça, 2020). However, few studies analyze fish neuroanatomic characters within the phylogenetic context, with a predominance of osteological characters in such analyses (Datovo & Vari, 2014). Therefore, studies using encephalon morphology in fish phylogenetic systematics are lacking in Neotropical cichlids, we assume.

Allied with morphological analyses, molecular analyses are commonly used in fish phylogenetic systematics. Cichlinae was the only Neotropical subfamily of Cichlidae, now divided into seven tribes: Astronotini, Chaetobranchini, Cichlasomatini, Cichlini, Geophagini, Heroini and Retroculini (Smith et al., 2008; Ilves et al., 2018). Although, some relationships remain ambiguous even in concatenated

trees, such as the divergence between *Geophagus*, *Gymnogeophagus*, and the clade “*Geophagus*” *steindachneri*, Ilves et al. (2018) confirmed the genera belonging to Geophagini.

Geophagini (sensu Ilves et al., 2018) encompasses taxa that exhibit a variety of exterior morphological traits that are linked to their feeding and behavioral patterns (Arbour & López-Fernández, 2014). As a result, they serve as a starting point and model for understanding some aspects of the relationship between the gross anatomy of the central nervous system with respect to some ecological, behavioral and evolutionary characteristics in a phylogenetic framework. The main purposes of our study were: 1) To describe the major encephalon portions and cranial nerves for all Geophagini genera, as well as some Neotropical and African cichlids; and 2) to perform a constrained analysis using neuroanatomical characters from representatives of the Geophagini tribe on the Geophagini phylogeny sensu Ilves et al. (2018), in order to reconstruct the evolution of the different parts of the encephalon and present some putative characters that are synapomorphic to the tribe and subgroups.

## Material and methods

### Morphological analysis

#### Taxonomy

Representative species of all Geophagini genera used by Ilves et al. (2018) were selected to describe the encephalon gross morphology: *Acarichthys heckelii* (Müller & Troschel, 1849), *Apistogramma borellii* (Regan, 1906), *Apistogramma commbrae* (Regan, 1906), *Apistogramma trifasciata* (Eigenmann & Kennedy 1903), *Biotodoma cupido* (Heckel, 1840), *Biotoecus opercularis* (Steindachner, 1875), *Crenicara punctulata* (Günther 1863), *Saxatilia britskii* (Kullander, 1982), *Dicrossus warzeli* Römer et al. (2010), “*Geophagus*” *iporangensis* Haseman, 1911, “*Geophagus*” *steindachneri* Eigenmann & Hildebrand (1922), *Geophagus sveni* Lucinda et al. 2010, *Guianacara dacrya* Arbour & López-Fernández (2011), *Gymnogeophagus balzanii* (Perugia, 1891), *Mazarunia mazarunii* Kullander 1990, *Mikrogeophagus ramirezi* (Myers

& Harry 1948), *Satanoperca acuticeps* (Heckel, 1840), *Satanoperca setepele* Ota et al. 2022, *Taeniacara candidi* Myers 1935, and *Teleocichla proelytus* Kullander 1988. The current taxonomic status of these species follows Fricke et al. (2023b). The classification follows Ilves et al. (2018). The list of examined materials are presented in Supplementary File 1, with their respective institutions and collections.

### *Encephalon nomenclature and preparation*

Encephalons were extracted following Datovo & Vari (2014) with modifications proposed by Oliveira & Graça (2020) for Neotropical cichlids. Neuroanatomic nomenclature and abbreviations of encephalon morphological regions followed Meek & Nieuwenhuys (1998). Photographs were taken with a camera coupled with a stereomicroscope. The encephalon was immersed entirely in 70% ethanol (at a depth of ~1 mm over the surface tissue) to avoid possible refractive problems, according to White & Brown (2015). An ellipsoid model was used to determine the volume of each encephalic region (*i.e.*, dorsal medulla (gustative lobes), *corpus cerebelli*, *tectum mesencephali* plus *torus semicircularis*, *hypothalamus*, *hypophysis*, and *telencephalon*). This method assumes that each region has an idealized elliptical shape (Staadén et al., 1995; Huber et al., 1997; Wagner, 2003; Lisney & Collin, 2006; Pollen et al., 2007; Ullmann et al., 2010; White & Brown 2015; Abrahão et al. 2018). Linear measurements were made based on standardized images of dorsal, lateral and ventral views, using the Opticam Microscopy OPTHD 3.7.8718 software (Opticam, 2003–2017). Measurements of length, width and height of each lobe, including even hemisphere lobes, followed Abrahão et al. (2018). Linear measurement values were converted to volume measurements (V) using the following formula:  $V = 1/6\pi lwh$  (where l=length, w=width and h=height) to calculate each lobe's volume and total encephalon volume, according to Abrahão et al. (2018). Colored illustrations were made using the computer program GIMP, based on photographs and direct stereomicroscopic observations of selected specimens (Table 1).

### Data analysis

#### *Phylogenetic analysis*

A total of 23 characters were used in the phylogenetic hypothesis of Ilves et al. (2018), and are presented in two groups, continuous and discrete (Table 2), in order to facilitate localization they are separated by encephalon structure. The character matrix is presented in Supplementary File 2.

Two constrained phylogenetic analyses were performed using two weighting schemes: equal weighting and implied weighting with K=3,0000. These analyses were conducted using TNT 1.5 software (Goloboff et al., 2008) from a matrix of neuroanatomic characters on the phylogenetic hypothesis proposed by Ilves et al. (2018). Constrained analysis has the purpose of visualizing the distribution of the character states in the phylogenetic tree, reconstructing the putative ancestral states at each node.

Maximum Parsimony (MP) was the optimization criterion. The phylogenetic analysis was performed using “Traditional search” on TNT. The “Random addition sequence” (RAS) algorithm was selected, with 100 replications. The swapping method used was “Tree bisection and reconnection” (TBR). The RAS and TBR technique searches for consistent analysis of up to 100 taxa. Character states were unordered. For resampling data, we used the Bootstrap index, with default replications (100). As the search was performed with 1,000 replications, the total replication number of replications was were 100 times 1000.

## Results

### Geophagini encephalon gross morphology

Cichlid encephalon is divided into four great divisions: *Rhombencephalon*, *Diencephalon*, *Mesencephalon*, and *Telencephalon* (Fig. 1). In all species analyzed, the encephalon is positioned above parasphenoid, prootic and basioccipital and below supraoccipital. *Tectum mesencephali* occupies the main volume of the encephalon (Table 1). All species have different encephalon shapes and sizes. Through subgroups within Geophagini (Fig. 2), encephalon morphology varies more in crenicichlines (Fig. 3a–d) and apistogrammines (Fig. 3e–j), presenting the most

**Table 1** Morphometry of encephalon of Geophagini species and comparative material examined. Total volume of encephalon (EV) is in cubic millimeters; other data are expressed as percentages of EV

Groups	Taxa	N	EV Volume (mm <sup>3</sup> )	GL Volume (mm <sup>3</sup> )	Volume (%)	Cereb Volume (mm <sup>3</sup> )	Volume (%)	TO+TS Volume (mm <sup>3</sup> )	Volume (%)	HI Volume (mm <sup>3</sup> )	Volume (%)	PG Volume (mm <sup>3</sup> )	Volume (%)	Tel Volume (mm <sup>3</sup> )	Volume (%)
Geophagini															
Crenicich- lines	<i>Crenicichla britskii</i>	2	111.69– 117.53	0.43–0.58	0.4–0.5	3.95–4.64	3.4–4.2	22.76– 28.04	20.4–23.9	11.53– 12.03	9.8–10.8	0.11–0.17	0.1–0.2	8.11–8.58	7.3
Crenicich- lines	<i>Teleocichla pro- elytus</i>	1	30.17	0.25	0.8	1.46	4.8	7.36	24.4	2.12	7.0	-	-	2.89	9.6
Crenicich- lines	<i>Acarichthys heckelii</i>	2	58.50– 89.29	0.60–0.87	1.0	2.79–3.47	3.1–5.9	12.78– 14.10	23.3–24.1	3.48–5.30	5.9–6.0	0.05–0.08	0.1	3.94–5.82	6.5–6.7
Crenicich- lines	<i>Biotocucus oper- cularis</i>	1	10.06	0.19	1.9	0.30	3.0	2.90	28.8	0.59	5.9	-	-	0.86	8.5
Apisto- gram- mines	<i>Apistogramma borelii</i>	1	10.71	0.15	1.4	0.26	2.4	2.30	21.4	0.99	9.2	-	-	1.50	14.0
Apisto- gram- mines	<i>Apistogramma combrae</i>	2	13.65– 16.74	0.16–0.20	1.0–1.4	0.50–0.51	3.1–3.7	2.87–3.57	21.0	0.81–1.01	5.9–6.0	-	-	2.11–2.29	13.7–15.5
Apisto- gram- mines	<i>Apistogramma trifasciata</i>	1	13.26	0.15	1.1	0.38	2.8	3.38	25.5	1.21	9.1	0.01	0.1	1.59	12.0
Apisto- gram- mines	<i>Taeniacara candidi</i>	1	9.24	0.03	0.3	0.26	2.8	2.31	25.0	0.88	9.5	-	-	0.69	7.5
Apisto- gram- mines	<i>Satanoperca acuticeps</i>	1	65.99	2.53	3.8	3.16	4.8	14.53	22.0	5.21	7.9	0.08	0.1	2.33	3.5
Apisto- gram- mines	<i>Satanoperca</i> sp.	1	94.00	4.95	5.3	3.12	3.3	16.79	17.9	6.56	7.0	0.17	0.2	6.76	7.2
Guiana- carines	<i>Mazarunia mazarunii</i>	1	61.25	0.61	1.0	3.58	5.8	11.66	19.0	3.64	5.9	0.05	0.1	5.10	8.3
Guiana- carines	<i>Guianacara dacrya</i>	1	85.39	0.54	0.6	4.75	5.6	19.55	22.9	5.30	6.2	0.05	0.1	6.46	7.6
Geophagi- nes	<i>Gymnogeophagus balzanii</i>	1	102.09	3.15	3.1	3.94	3.9	16.00	15.7	7.07	6.9	0.38	0.4	8.25	8.1
Geophagi- nes	<i>Gymnogeophagus meridionalis</i>	1	151.51	2.94	1.9	5.92	3.9	27.85	18.4	10.69	7.1	0.19	0.1	16.98	11.2
Geophagi- nes	" <i>Geophagus</i> " <i>steindachneri</i>	1	82.70	2.32	2.8	3.75	4.5	14.79	17.9	7.32	8.8	0.17	0.2	7.94	9.6

**Table 1** (continued)

Groups	Taxa	N	EV Volume (mm <sup>3</sup> )	GL Volume (mm <sup>3</sup> )	Volume (%)	Cereb Volume (mm <sup>3</sup> )	Volume (%)	TO+TS Volume (mm <sup>3</sup> )	Volume (%)	HI Volume (mm <sup>3</sup> )	Volume (%)	PG Volume (mm <sup>3</sup> )	Volume (%)	Tel Volume (mm <sup>3</sup> )	Volume (%)
Geophagi- nes	<i>Geophagus sveni</i>	2	78.46– 157.20	4.0–4.1	4.0	2.91–6.18	3.7–3.9	14.60– 29.23	18.6	6.08– 12.26	7.8	0.22–0.23	0.1–0.3	8.04–17.21	10.2–10.9
Mikroge- ophagi- nes	<i>Mikrogeophagus ramirezi</i>	1	11.78	0.12	1.0	0.42	3.5	3.20	27.2	0.58	5.0	–	–	1.04	8.8
Mikroge- ophagi- nes	" <i>Geophagus</i> " <i>iporangensis</i>	2	120.73– 245.56	2.38–6.08	2.0–2.5	5.86–10.75	4.4–4.9	22.11– 42.50	17.3–18.3	7.00– 12.16	5.0–5.8	0.21–0.34	0.1–0.2	10.19– 16.19	6.6–8.4
Mikroge- ophagi- nes	<i>Biotodoma cupido</i>	1	38.80	0.37	1.0	0.87	2.2	8.71	22.5	2.22	5.7	0.03	0.1	2.94	7.6
Crenic- aratines	<i>Dicrossus warzelii</i>	1	22.19	0.11	0.5	0.73	3.3	7.20	32.4	2.20	9.9	–	–	2.07	9.3
Crenic- aratines	<i>Crenicara punctu- latum</i>	1	21.11	0.14	0.6	0.60	2.8	5.87	27.8	1.82	8.6	–	–	2.13	10.1
Other Neo- tropical cichlids															
Chaeto- branchini	<i>Chaetobranchius flavescens</i>	1	481.74	7.57	1.6	27.55	5.7	81.18	16.9	36.54	7.6	1.50	0.3	52.64	10.9
Heroini	<i>Amphilophus citrinellus</i>	1	91.16	1.17	1.3	3.23	3.5	16.12	17.7	5.23	5.7	0.29	0.3	5.68	6.2
Heroini	<i>Parachromis managuensis</i>	1	139.13	0.78	0.6	8.31	6.0	25.14	18.1	13.13	9.4	0.47	0.3	10.43	7.5
Cichlaso- matini	<i>Bujurquina vittata</i>	1	86.64	0.68	0.8	2.60	3.0	14.47	16.7	6.63	7.7	0.11	0.1	9.47	10.9
Cichlaso- matini	<i>Acaronia nassa</i>	1	53.74	0.34	0.6	2.14	4.0	13.26	24.7	3.11	5.8	0.06	0.1	3.56	6.6
Cichlaso- matini	<i>Cichlasoma para- naense</i>	1	151.12	1.52	1.0	4.99	3.3	24.88	16.5	10.88	7.2	0.30	0.2	9.34	6.2
Cichlaso- matini	<i>Aequidens plagio- zonatus</i>	1	187.72	2.09	1.1	5.21	2.8	37.11	19.8	14.37	7.7	–	–	15.90	8.5
Retroculini	<i>Retroculinus acher- ontos</i>	1	278.15	5.46	2.0	17.73	6.4	50.74	18.2	19.21	6.9	0.24	0.1	23.16	8.3
Cichlini	<i>Cichla kelberi</i>	1	84.58	0.45	0.5	3.69	4.4	21.80	25.8	4.47	5.3	0.05	0.1	6.25	7.4

Table 1 (continued)

Groups	Taxa	N	EV Volume (mm <sup>3</sup> )	GL Volume (mm <sup>3</sup> )	Volume (%)	Cereb Volume (mm <sup>3</sup> )	Volume (%)	TO+TS Volume (mm <sup>3</sup> )	Volume (%)	HI Volume (mm <sup>3</sup> )	Volume (%)	PG Volume (mm <sup>3</sup> )	Volume (%)	Tel Volume (mm <sup>3</sup> )	Volume (%)
African cichlids															
Haplochromini	<i>Cynotilapia afra</i>	1	47.09	0.41	0.9	2.68	5.7	9.51	20.2	3.10	6.6	0.08	0.2	3.77	8.0
Coptodoni	<i>Coptodon rendalli</i>	1	151.03	1.74	1.2	9.03	6.0	24.14	16.0	9.82	6.5	0.26	0.2	13.46	8.9
Oreochromini	<i>Oreochromis niloticus</i>	1	123.52	1.32	1.1	7.07	5.7	15.75	12.8	6.26	5.1	0.68	0.5	6.29	5.1
Hemichromini	<i>Hemichromis bimaculatus</i>	1	125.21	1.17	0.9	5.00	4.0	25.36	20.3	6.11	4.9	0.38	0.3	9.19	7.3

*Cereb corpus cerebelli*; *GL* gustative lobes; *HI* hypothalamus; *N* number of specimens examined; *PG* pituitary gland; *Tel*, telencephalon; *TM+TS* tectum mesencephali plus torus semicircularis

visible difference in size and shape between homologous structures within each group. Less intra-group variation can be seen among mikrogeophagines (Fig. 4a–c) and guianacarines (Fig. 4d–e) structures. In turn, geophagines (Fig. 4f–i) have the most similar encephalon. In dwarfed species, crenicarines (Fig. 5a–b), *Mikrogeophagus* (Fig. 4c) and *Apistogramma* (Fig. 3f–g), the encephalon almost fills the skull cavity. Among Neotropical (Figs. 5e–c, 6a–b) and African cichlids (Fig. 6c–f), the encephalon also has high variation. Except by *Retroculus*, gustative lobe is less developed in those Neotropical and African species, as discussed below.

### Rhombencephalon

The *rhombencephalon* (Fig. 1) is the most posterior portion, located just anterior to the spinal cord, posterior to the *tectum mesencephali*. The *medulla spinalis* is tubular and passes through the vertebral canal. Anteriorly lies the *medulla oblongata*, which is an intumescent area, larger in its anterior part, tapering posteriorly. There is no visible division between the *medulla spinalis* and the *medulla oblongata* in any of the species studied. They are located above the basioccipital. The *medulla oblongata*, in its anterior portion, lies posterolateral to *lobus vagi*. The latter is located below the posterior part of the supraoccipital process.

In all species analyzed, the gustative lobes (*lobus vagi* and *lobus facialis*) are located in the intermediodorsal rhombencephalic region. The *lobus vagi* is divided into two parts that are symmetrically positioned in the laterodorsal view. The two halves vary among cichlid species, with some having grooves on the dorsal surface, as in *Satanoperca* (Fig. 3h–i), others having a smooth surface. In the dorsal view, the two halves vary among species, forming in some a tubular slot as in *Gymnogeophagus* (Fig. 4h–i), in others a straight one (Figs. 3g, i, 4f–g). The *lobus facialis* is located anterior to the *lobus vagi*, ventral to the *corpus cerebelli* in those species that have a greater caudal prominence, as in *Saxatilia* and *Teleocichla* (Fig. 3c–d). It is not as visible in some species (Fig. 5a–b), but is discernible in others, sometimes being more prominent than the *lobus vagi* (Fig. 5f). Like the *lobus vagi*, the *lobus facialis* is composed of two halves on either side of the intermediodorsal zone of the *rhombencephalon*.

**Table 2** Continuous and discrete characters used for phylogenetic analysis, separated by encephalon structure to facilitate localization

Encephalon Structure	Character	Locator	Variable	States	CI	RI
<i>Continuous characters</i>						
Rhombencephalon	0	Gustative lobes ( <i>lobus vagi</i> and <i>lobus fascialis</i> )	Volume proportion in total encephalon volume	Measurement	0.304	0.398
	1	<i>Cerebellum</i>	Volume proportion in total encephalon volume	Measurement	0.186	0.333
Mesencephalon	2	<i>Tectum mesencephali</i>	Volume proportion in total encephalon volume	Measurement	0.229	0.317
Diencephalon	3	<i>Lobus inferior hypothalami</i>	Volume proportion in total encephalon volume	Measurement	0.156	0.240
	4	<i>Hypophysis</i>	Volume proportion in total encephalon volume	Measurement	0.313	0.313
Telencephalon	5	<i>Telencephalon</i>	Volume proportion in total encephalon volume	Measurement	0.248	0.290
	6	<i>Bulbus olfactorius</i>	Volume proportion in total encephalon volume	Measurement	0.261	0.227
Mesencephalon	7	<i>Tectum mesencephali</i>	Height to length ratio in lateral view	Measurement	0.165	0.200
Telencephalon	8	<i>Telencephalon</i>	Width to length ratio in dorsal view	Measurement	0.223	0.181
<i>Discrete characters</i>						
Rhombencephalon	9	<i>Lobus vagi</i>	Texture	[0] Smooth [1] With grooved areas in dorsolateral view	1.000	1.000
	10	<i>Lobus vagi</i>	Shape of the halves in dorsal view	[0] The halves have a semicircle shape with the concave medial margin forming a tube-shaped space [1] The halves are semi-oval with a concave medial margin forming an ellipsoid space with narrowed anterior and posterior margins [2] The halves are semi-oval, with straight medial margin, forming a straight narrow space anteroposteriorly [3] The halves have a straight medial margin and project anterolaterally, forming a central V-shaped or U-shaped space	0.231	0.333

**Table 2** (continued)

Encephalon Structure	Character	Locator	Variable	States	CI	RI
	11	<i>Lobus vagi</i>	Shape of the halves in lateral view	[0] Rounded [1] Forming a posteriorly-descending slope	0.111	0.000
	12	<i>Lobus vagi</i>	Height in relation to <i>medulla spinalis</i>	[0] Large, greater than the <i>medulla spinalis</i> height [1] medium, approximately the same height as the <i>medulla spinalis</i> [2] Small, lower than <i>medulla spinalis</i> height	0.182	0.500
	13	<i>Lobus fascialis</i>	Anterior to <i>lobus vagi</i>	[0] Distinct [1] Indistinct	0.143	0.250
	14	<i>Lobus fascialis</i>	Height in relation to <i>lobus vagi</i>	[0] Smaller than the <i>lobus vagi</i> [1] Approximately the same height as the <i>lobus vagi</i> [2] Larger than the <i>lobus vagi</i>	0.286	0.545
	15	<i>Cerebellum</i>	Size in relation to <i>tectum mesencephali</i>	[0] Small, <i>cerebellum</i> height does not pass the <i>tectum mesencephali</i> dorsal margin [1] <i>Cerebellum</i> height reaches or passes slightly the <i>tectum mesencephali</i> dorsal margin [2] <i>Cerebellum</i> height clearly passes the <i>tectum mesencephali</i> dorsal margin	0.400	0.500
Mesencephalon	16	<i>Eminentia granularis</i>	In lateral side of <i>cerebellum</i> peduncle	[0] Distinct [1] Indistinct	0.250	0.571
	17	<i>Tectum mesencephali</i>	Projections in dorsal view	[0] Present [1] Absent	0.333	0.000
Diencephalon	18	<i>Hypophysis</i>	Basal margin shape	[0] With a big downward projection [1] With a medium downward projection, forming a small tip [2] Rounded [3] Flattened	0.231	0.167
	19	<i>Hypophysis</i>	position in relation to <i>saccus vasculosus</i>	[0] <i>Hypophysis</i> touches <i>saccus vasculosus</i> [1] <i>Hypophysis</i> does not touch <i>saccus vasculosus</i>	0.167	0.167
	20	<i>Saccus vasculosus</i>	length concerning the <i>Hypophysis</i>	[0] Larger than <i>hypophysis</i> [1] Nearly the same size as the <i>hypophysis</i> [2] Smaller than <i>hypophysis</i>	0.500	0.667
	21	<i>Lobus inferior hypothalami</i>	Shape of posterior part	[0] Without depressed areas, forming an oval margin [1] With depressed, sometimes angled areas, which form an irregular margin	0.250	0.000



**Table 2** (continued)

Encephalon Structure	Character	Locator	Variable	States	CI	RI
	22	<i>Lateral preglomerular nucleus</i>	Width between its boundaries concerning the <i>lobus inferior hypothalami</i> width	[0] Larger than <i>lobus inferior hypothalami</i> width [1] Smaller than <i>lobus inferior hypothalami</i> width	0.200	0.200

CI consistency index and RI retention index

The most anterior part of rhombencephalon is the *cerebellum*, an unpaired lobe with an upwardly directed bulging area called the *corpus cerebelli* (Fig. 1). In some cichlid species, a small bulged area, the *eminentia granularis*, emerges at each side of the *cerebellum* peduncle. The shape of the *corpus cerebelli* varies greatly among the species studied. In dorsal view, it can have a smooth, anteroposteriorly ovate shape (Fig. 5c), or a transversely ovate shape (Fig. 4b, f, h–i), or a rounded shape (Figs. 4a, 6c–f), or irregular borders of different shapes (Fig. 3a–d). The distal part of the *corpus cerebelli* usually has a posterior prominence of varying degree (Figs. 3c–d, 4d–e, h), as if the distal part of the *corpus cerebelli* was bent posteriorly. Furthermore, the *cerebellum* varies in its height in lateral view, in most species its height determines the upper encephalic margin, being higher than height of the *tectum mesencephali*.

Eight pairs of nerves emerge from the rhombencephalon (Fig. 1): *nervus trigeminus* (V), *nervus abducens* (VI), *nervus facialis* (VII), *nervus octavus* (VIII), *nervus glossopharyngeus* (IX), *nervus vagus* (X), *nervus linea lateralis anterior* (Nlla) and *nervus linea lateralis posterior* (Nllp). Nervi V, VII and VIII emerge together from a common stem that is divided into the three nerves. They are located at the anterior mid-lateral part of the rhombencephalon, ventral to the *cerebellum*. Nlla fibers lie anteriorly, passing between the *lobus inferior hypothalami* and the lateral preglomerular nucleus, in the same way as nervi V, VII and VIII, making it sometimes difficult to separate and identify these four nerves. Nllp and *nervus IX* arise in sequence, ventrolateral to *lobus vagi*, the former being anterodorsal to the latter. *Nervus X* is the most posterior encephalic nerve, also arising ventrally to the *lobus vagi*. Unlike nervi V, VII and VIII, *nervus X* is composed of fibers that rise separately and unite to form a common stem. *Nervus X* exits the neurocranium through a foramen situated in the

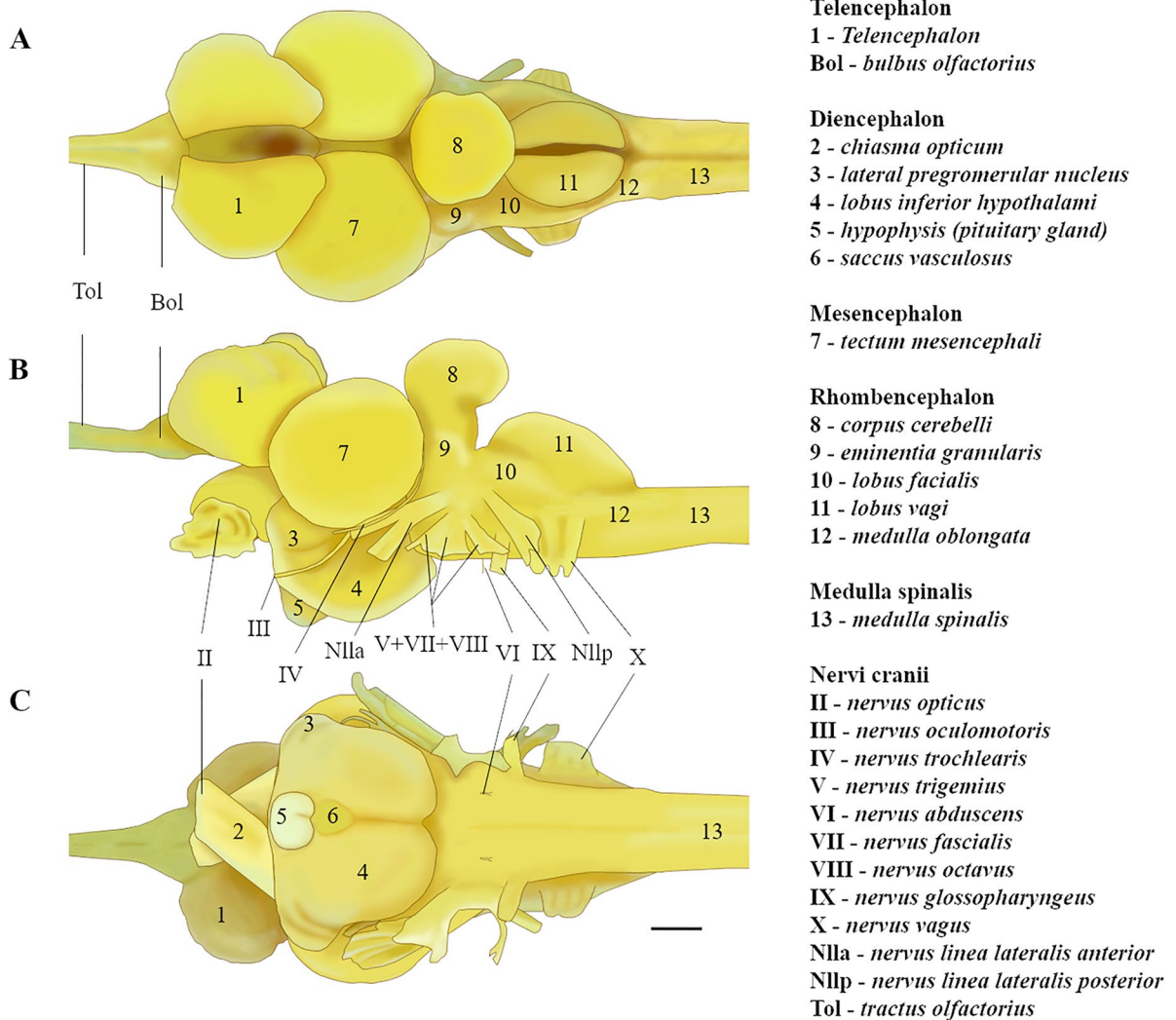
exoccipital. Finally, in the ventral view of the rhombencephalon, *nervus VI* rises, a pair of slender nerves that are difficult to see in most species and are therefore most often damaged during dissection.

### Mesencephalon

The *tectum mesencephali*, the greater part of mesencephalon, is a paired, oval-shaped lobe in lateral view in all species, always with a smooth surface. In some species, it has irregular borders in dorsal view (Fig. 3j). It lies dorsal to the diencephalic structures and is connected to this area by a mass of nervous tissue, the encephalic truncus, and the *torus semicircularis*. *Nervus II* (ophthalmic nerve) (Fig. 1), arises from the anteroventral part of *tectum mesencephali*. This nerve has a chiasma opticum, which is the region where the contralateral ophthalmic nerves cross, one of which runs ventrally to the other. *Nervus III (nervus oculomotoris)* (Fig. 1) is a slender stem rising from the upper part of the *torus semicircularis*, just ventral to the *tectum mesencephali*. *Nervus IV* (Fig. 1) (*nervus trochlearis*) is thin and rises from the mesencephalon posterodorsally to *nervus III*.

### Diencephalon

The *diencephalon* (Fig. 1) is a portion located on the ventral side of the encephalon, consisting mainly of the *hypothalamus* and the pituitary gland or *hypophysis*. In ventral view, the paired *lobus inferior hypothalami* is easily recognizable. In some species it is smooth (Fig. 3c), while in others it forms many bulges and depressions on the posteroventral surface (Fig. 3f, h, j), fitting the sagitta. Viewed from the side, it has a deep groove between the *lateral preglomerular nucleus* and the *lobus inferior hypothalami* (Fig. 1), where nerves V, VII,

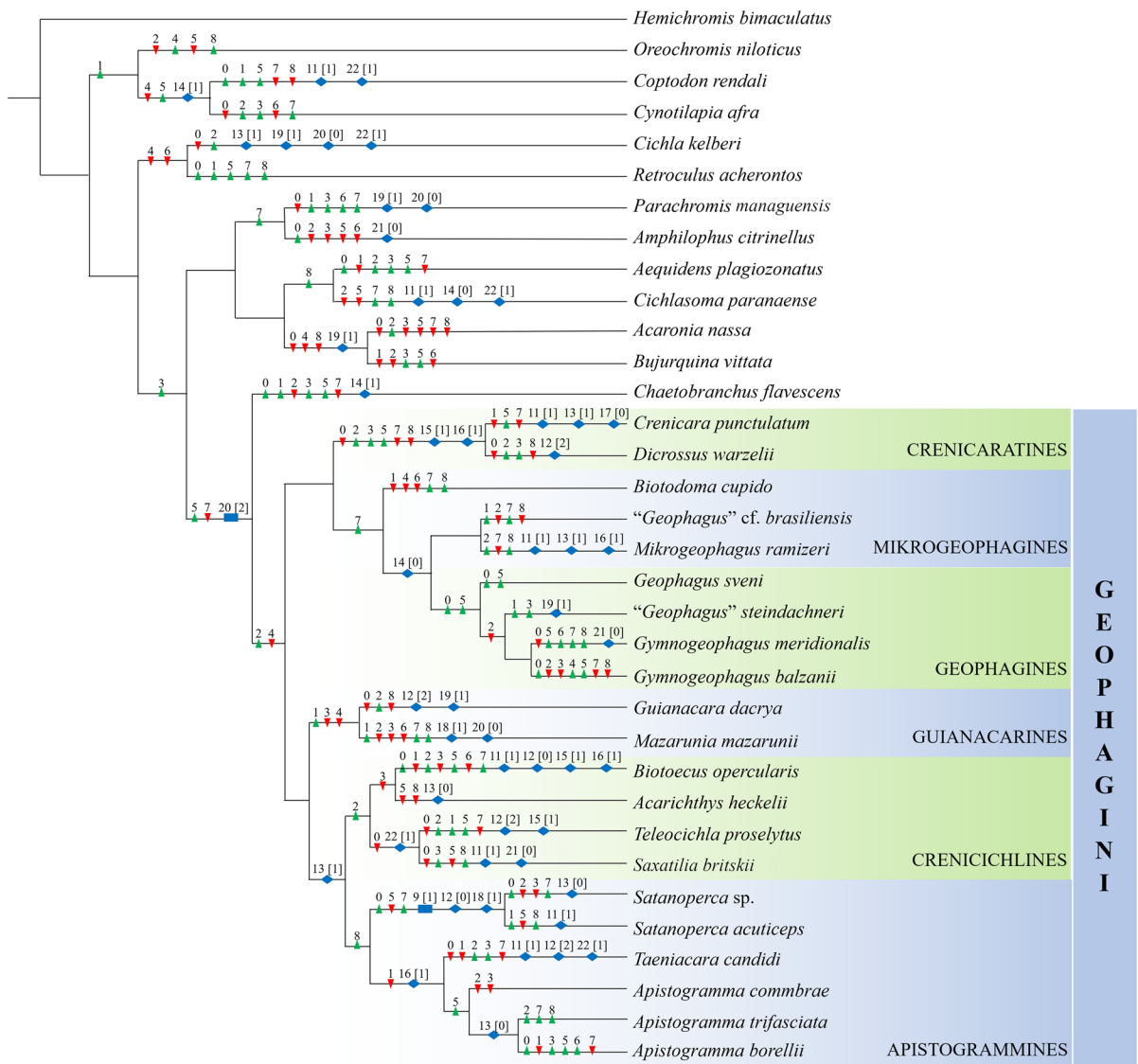


**Fig. 1** Illustration of encephalon gross morphology of *Geophagus sveni* NUP 18979, 120.6 mm standard length, in dorsal (A), lateral (B) and ventral (C) views. Scale bar = 1 mm

VIII and Nlla, coming from the *rhombencephalon*, lie together with nerves III and IV, coming from the *mesencephalon*. The pituitary gland is located ventrally to the *hypothalamus* (Fig. 1) and it varies in shape and size among different taxa. In some species, it is triangle-shaped in lateral view (Fig. 4h), while in others, it is flattened (Fig. 3a) or rounded (Fig. 3c). Posterior to the pituitary gland in ventral view, lies the *saccus vasculosus*, sometimes smaller than the pituitary gland (Fig. 3a), sometimes larger (Fig. 5g, i).

#### *Telencephalon*

The *telencephalon* is the most anterior portion of the encephalon, constituting a paired lobe (Fig. 1) anterior to the *tectum mesencephali*, and varies widely in shape and size both inter- and intraspecifically (Supplementary File 3). In some species it is grooved and triangle-shaped (Fig. 3b, d), while in others it is slender and elongated anteroposteriorly ((Figs. 3a, h, 4b, 5b). From its anterior border, the *nervus I (nervus olfactorius)* arises. In all cichlid species studied, the



**Fig. 2** Synapomorphies derived from encephalic morphology, as recovered by constrained analysis based on the topology by Ilves et al. (2018). Colored clades correspond to subgroups within Geophagini. Green, upward-directed arrowheads represent increases in continuous characters; red, downward-

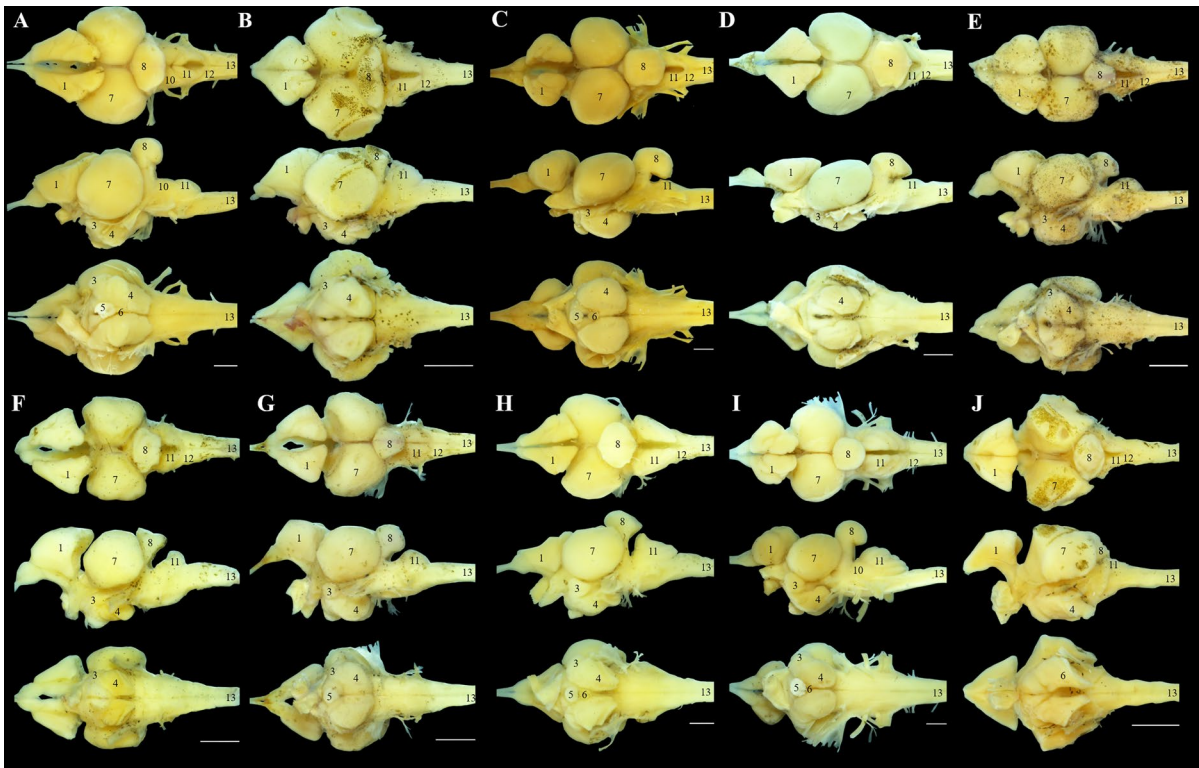
directed arrowheads, a decrease; blue lozenges, synapomorphic discrete character states with parallel acquisitions in other clades; blue rectangles, homoplasmy-free synapomorphic discrete character states

proximal part of this nerve forms the *bulbus olfactorius* (Fig. 1). In dwarf species, most of the encephalon was in direct contact with a thin surrounding neurocranial bone layer. Conversely, in larger species, there is a large space between the encephalon and the skull. Thus, in dwarf species, part of the encephalon case adheres to the encephalon, mostly to the *tectum*

*mesencephali* and *telencephalon*, which were difficult to extract without damage.

Phylogenetic constrained analysis

The minimum score required to obtain the predetermined topology was 97.610 for the unweighted



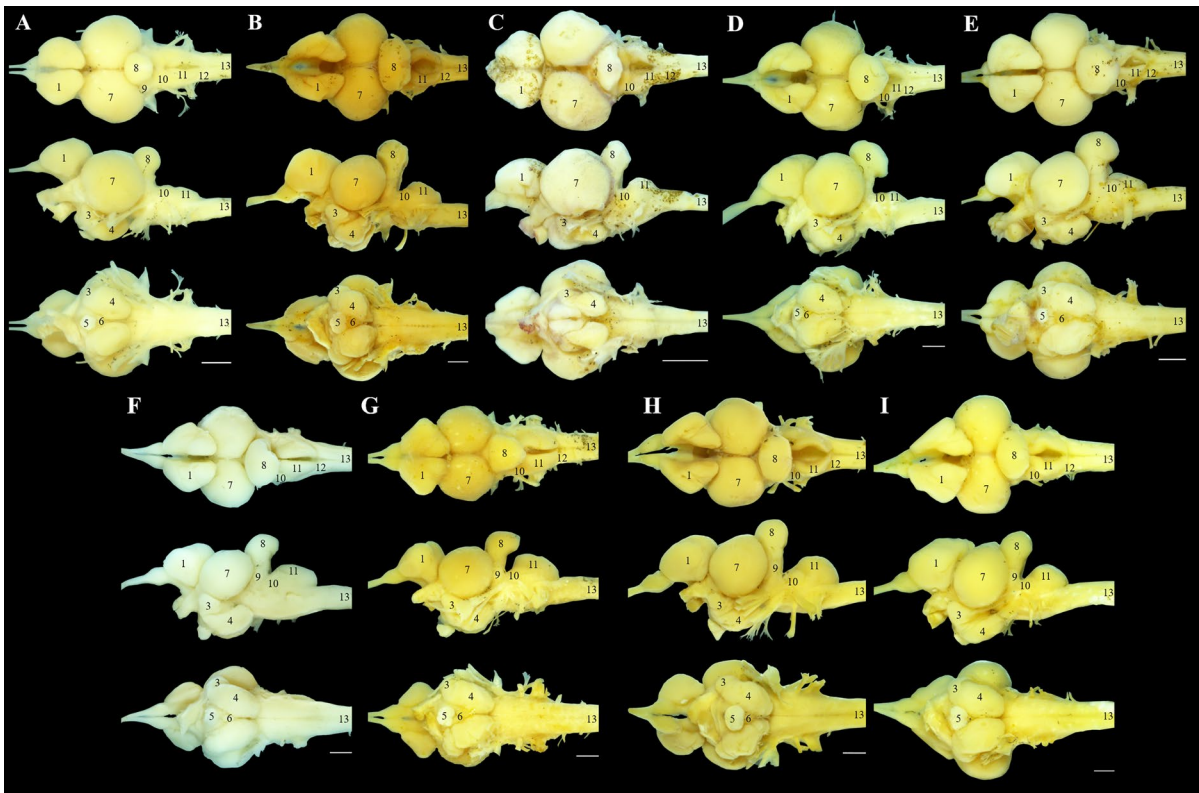
**Fig. 3** **A, B** encephalon gross morphology in dorsal, lateral and ventral view of Crenicichlines: **A**, *Acarichthys heckelii* NUP 4892, 83.85 mm standard length (SL); and **B**, *Biotecus opercularis* UFRO-I 6070, 22.46 mm SL. **C**, *Saxatilia britiskii* NUP 7953, 93.62 mm standard length (SL); and **D**, *Teleocichla proselytus* MZUSP 22017, 16.85 mm SL. **E-G-C** encephalon gross morphology in dorsal, lateral and ventral view of Apistogrammines: **E**, *Apistogramma borellii* NUP 4267, 31.99 mm standard length (SL); **F**, *Apistogramma trifasciata* NUP 16240, 29.5 mm SL; and **G**, *Apistogramma commbrae* NUP 16467,

26.29 mm SL. **H-J**, encephalon gross morphology in dorsal, lateral and ventral view of Apistogrammines: **H**, *Satanoperca acuticeps* NUP 4885, 58.88 mm standard length (SL); **I**, *Satanoperca setepele*, NUP 22313, 97.83 mm SL; and **J**, *Taeniacara candidi* UFRO-I 20710, 27.74 mm SL. 1, telencephalon; 3, lateral preglomerular nucleus; 4, lobus inferior hypothalami; 5, hypophysis; 6, saccus vasculosus; 7, tectum mesencephali; 8, corpus cerebelli; 10, lobus facialis; 11, lobus vagi; 12, medulla oblongata; 13, medulla spinalis. Scale bars = 1 mm

analysis and 8.0960 for the weighted analysis (Fig. 7). See Supplementary File 4 for more details on the changes in each character in the analyzed species.

The continuous character states 2[0.220–0.224] and 4[0.001–0.002] were synapomorphic to Geophagini (Fig. 2; Supplementary File 4, Figs. 3 and 5; Supplementary File 5). Character 2, tectum mesencephali volume, tended to increase in this clade, whereas character 4, volume proportion of hypophysis, tended to decrease in Geophagini. Regarding the subgroups within Geophagini, character state 2[0.238–0.241] were synapomorphic to crenicichlines, consisting of *Saxatilia* plus *Teleocichla* as the sister group to

*Acarichthys* plus *Biotecus* (Fig. 2; Supplementary File 4, Fig. 3; Supplementary File 5), and tended to increase in this group. Character state 8[0.663–0.697] was synapomorphic for apistogrammines, consisting of *Satanoperca* as sister of *Apistogramma* plus *Taeniacara* (Fig. 2; Supplementary File 4, Fig. 9; Supplementary File 5), as the telencephalon width/length ratio increased in this clade. The character states 1 [0.055], 3 [0.062] and 4 [0.000] were synapomorphic to guianacarinae, composed of *Mazarunia* and *Guianacara* (Fig. 2; Supplementary File 4, Figs. 2, 4 and 5; Supplementary File 5). Character 1, cerebellum volume, increased in this clade, being larger than



**Fig. 4** A–C, encephalon gross morphology in dorsal, lateral and ventral view of Mikrogeophagini: **A**, *Biotodoma cupido* NUP 13014, 57.68 mm standard length (SL); **B**, “*Geophagus*” *iporangensis* NUP 3717, 80.52 mm SL; and **C**, *Mikrogeophagus ramizeri* MZUSP 96547, 24.23 mm SL. **D**, **E**, encephalon gross morphology in dorsal, lateral and ventral view of Guianacarines: **D**, *Guianacara dacrya* ROM 96095, 67.21 mm standard length (SL); and **E**, *Mazarunia mazarunii* ROM 89586, 55.37 mm SL. **F**–**I**, encephalon gross morphology in dorsal, lateral and ventral view of Geophagini: **F**,

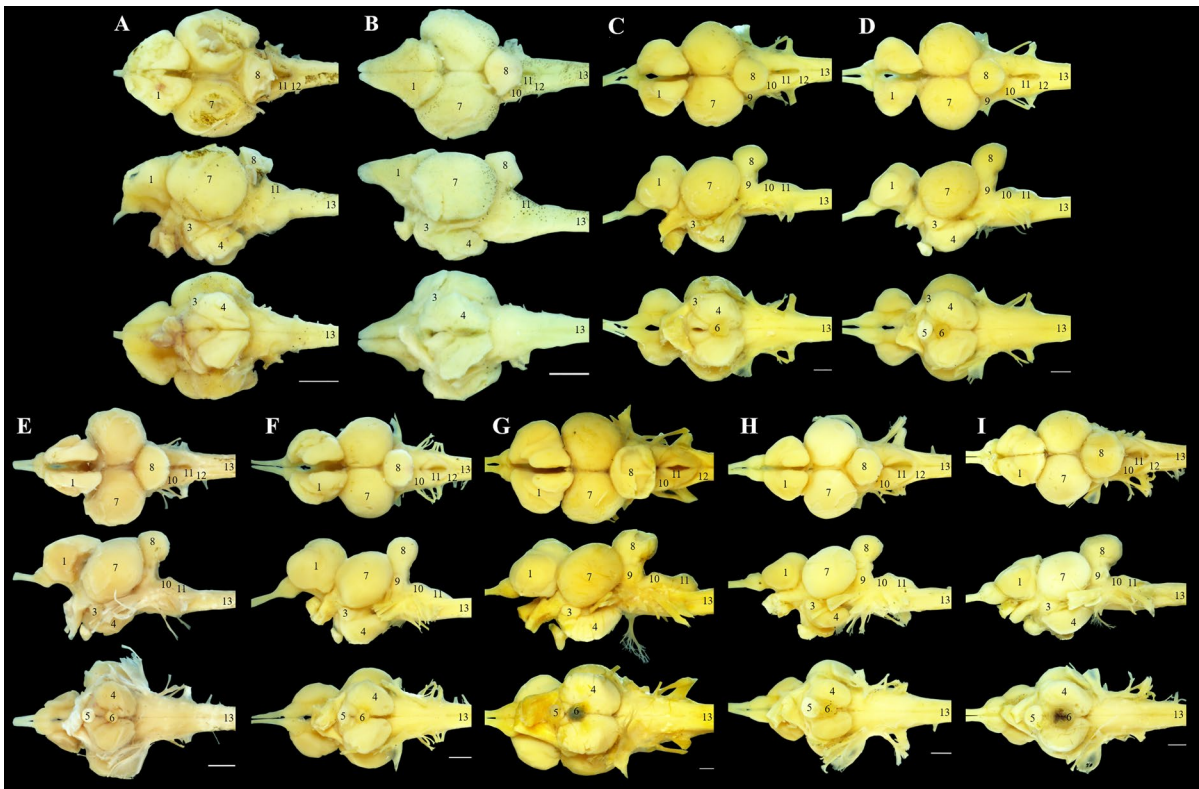
“*Geophagus*” *steindachneri* LBP 18635, 76.73 mm standard length (SL); and **G**, *Geophagus sveni* NUP 18976, 83.93 mm SL. **H**, *Gymnogeophagus balzanii* NUP 3035, 84.34 mm standard length (SL); and **I**, *Gymnogeophagus meridionalis* NUP 18037, 67.29 mm SL. 1, telencephalon; 3, lateral preglomerular nucleus; 4, lobus inferior hypothalami; 5, hypophysis; 6, saccus vasculosus; 7, tectum mesencephali; 8, corpus cerebelli; 9, eminentia granulatis; 10, lobus facialis; 11, lobus vagi; 12, medulla oblongata; 13, medulla spinalis. Scale bars = 1 mm

in all other Geophagini. Character 3, lobus inferior hypothalami volume, tended to decrease in this clade. Character 4, hypophysis volume, was smaller in guianacarines than in other Geophagini.

Here, we will deal first with the characters uniting mikrogeophagini plus geophagini, because it is a monophyletic group indeed. Character state 7[0.903], which deals with the size of the tectum mesencephali in the lateral view, was synapomorphic for this clade (Fig. 2; Supplementary File 4, Fig. 8; Supplementary File 5). However, this character changed several times within the same clade. Considering only the geophagini, character state 2 [0.027] was considered

a synapomorphic for the clade, tending to show lower volumes of the tectum mesencephali (Fig. 2; Supplementary File 4, Fig. 3; Supplementary File 5).

The character states 0[0.006], 2[0.277], 3[0.086], 5[0.093], 7[0.783], 8[0.615], 15[1] and 16[1] were synapomorphic to Crenicaracines, composed of *Dicrossus* and *Crenicara* (Fig. 2; Supplementary File 4, Figs. 1, 3, 4, 6, 8, 9, 16 and 17; Supplementary File 5). All continuous characters showed varied changes along the cladogram. Character 0, gustative lobes volume, decreased in this clade. Character 2, tectum mesencephali volume, increased for this clade. Character 3, volume of the lobus inferior hypothalami, also



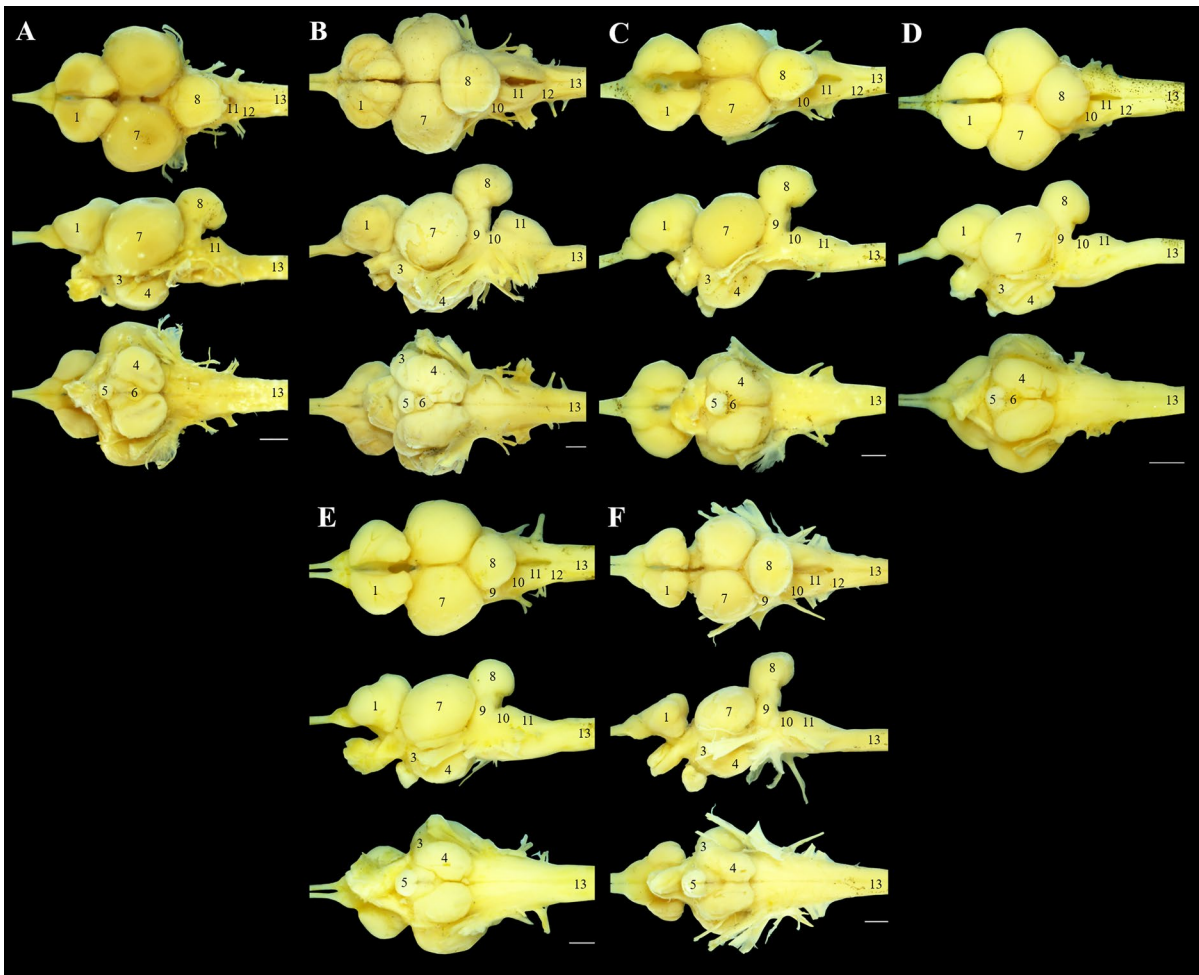
**Fig. 5** A, B, encephalon gross morphology in dorsal, lateral and ventral view of Crenicaratines: **A**, *Crenicara punctulatum* UFRO-I 12763, 27.87 mm standard length (SL); and **B**, *Dicrossus warzelii* MZUSP 25423, 37.53 mm SL. **C**, **D**, encephalon gross morphology in dorsal, lateral and ventral view of Cichlasomatini: **C**, *Aequidens plagiozonatus* NUP 194, 76.65 mm standard length (SL); and **D**, *Cichlasoma paranaense* NUP 1936, 73.41 mm SL. **E**, **F**, encephalon gross morphology in dorsal, lateral and ventral view of Cichlasomatini: **A**, *Acaronia nassa* NUP 17654, 55.23 mm standard length (SL); and **B**, *Bujurquina vittata* NUP 179, 63.03 mm SL. **G**–**I**,

encephalon gross morphology in dorsal, lateral and ventral view of Chaetobranchini (**A**) and Heroini (**B**, **C**): **A**, *Chaetobranchius flavescens* NUP 19495, 150.25 mm standard length (SL); **B**, *Amphilophus citrinellus* NUP 14730, 82.09 mm SL; and **C**, *Parachromis managuensis* NUP 22314, 111.62 mm SL. 1, telencephalon; 3, lateral preglomerular nucleus; 4, lobus inferior hypothalami; 5, hypophysis; 6, saccus vasculosus; 7, tectum mesencephali; 8, corpus cerebelli; 9, eminentia granularis; 10, lobus facialis; 11, lobus vagi; 12, medulla oblongata; 13, medulla spinalis. Scale bars = 1 mm

increased in this clade. Character 5, telencephalon volume, also increased, but presented variation within the clade. Character 7, tectum mesencephali height/length ratio, decreased in this clade, being smaller in *Crenicara*. Character 8, telencephalon width/length ratio, decreases in this clade with variation, being even smaller in *Dicrossus*. Character 15, cerebellum height relative to tectum mesencephali, has a small size 15[1] in *Biotocus*, *Teleocichla* and Apistogrammines. Character 16, distinctiveness of the eminentia granularis, was parallel 16 [1] in *Mikrogeophagus*,

*Biotocus* and the apistogrammines, because it is not visibly distinct.

The continuous character 0 (Fig. 2; Supplementary File 4, Fig. 1; see states for each group/species in Supplementary File 5), gustative lobes volume, underwent several changes along the cladogram. The clades that presented higher volumes of the gustative lobes within Geophagini were mikrogeophagines (except *Mikrogeophagus ramirezi*) plus geophagines, *Satanoperca* (even greater in *Satanoperca* sp.), *Biotocus* and *Apistogramma borellii*. We observed



**Fig. 6** **A, B**, encephalon gross morphology in dorsal, lateral and ventral view of Cichlini (**A**) and Retroculini (**B**): **A**, *Cichla kelberi* NUP 2014, 74.44 mm standard length (SL); and **B**, *Retroculus acherontos* NUP 22315, 122.59 mm SL. **C, D**, encephalon gross morphology in dorsal, lateral and ventral view of Pseudocrenilabrinae: **A**, *Coptodon rendalli* NUP 2000, 78.0 mm standard length (SL); and **B**, *Cynotilapia afra* NUP 14722, 49.59 mm SL. **E, F**, encephalon gross morphol-

ogy in dorsal, lateral and ventral view of Pseudocrenilabrinae: **A**, *Hemichromis bimaculatus* NUP 14724, 75.3 mm standard length (SL); and **B**, *Oreochromis niloticus* NUP2840, 113.99 mm SL. 1, telencephalon; 3, lateral preglomerular nucleus; 4, lobus inferior hypothalami; 5, hypophysis; 6, sacculus vasculosus; 7, tectum mesencephali; 8, corpus cerebelli; 10, lobus facialis; 11, lobus vagi; 12, medulla oblongata; 13, medulla spinalis. Scale bars = 1 mm

convergent values in the outgroup to *Coptodon*, *Retroculus* and *Chaetobranchius*. However, low gustative lobes volume was observed in crenicichlines (even lower in *Saxatilia*), and convergence was observed in the outgroup to *Acaronia* plus *Bujurquina*, *Parachromis*, *Cichla* and *Cynotilapia*.

## Discussion

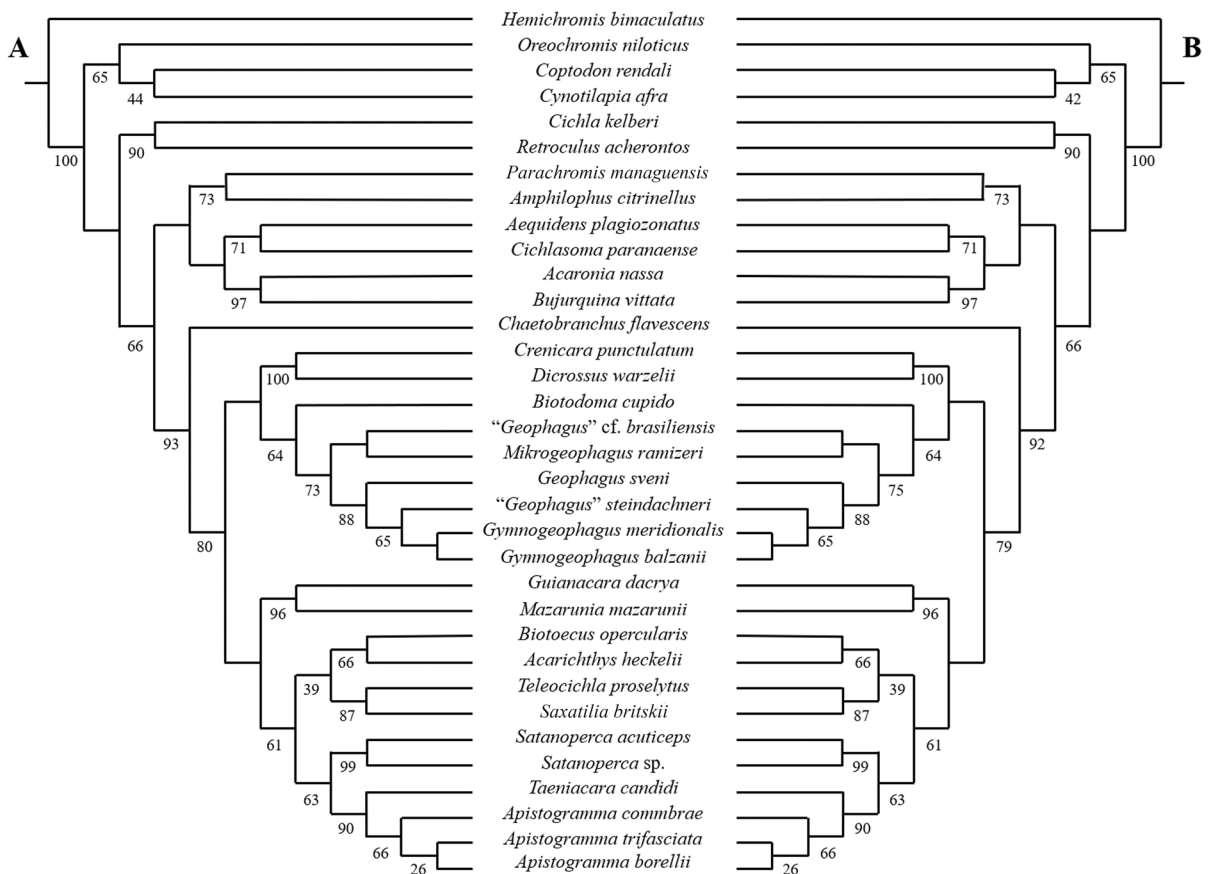
### Encephalon gross morphology

Cichlid encephalon examined herein presents a typical division of a Teleost encephalon, designated from

the posterior to anterior margin in *rhombencephalon*, *diencephalon*, *mesencephalon* and *telencephalon* (see Meek & Nieuwenhuys, 1998). Sutures between neurocranial bones are hardly distinguishable in most cichlids studied herein. Nonetheless, some differences in the relative positions of encephalon parts and skeletal components could be detected when compared to other fish families that had their encephalon gross morphology studied, such as Pseudopimelodidae (Abrahão & Pupo, 2014; Abrahão et al., 2018) and Bathydraconidae (Eastman & Lannoo, 2003). Differently from Pseudopimelodidae, our findings demonstrate that in cichlids the *medulla spinalis* and the *medulla oblongata* are located dorsally to the basioccipital instead of the parasphenoid. *Rhombencephalon* is divided into four main regions, which innervate and receive inputs from viscera: ventral (somatomotor), intermedioventral (visceromotor),

intermediodorsal (viscerosensory) and dorsal zone (somatosensory) (Meek & Nieuwenhuys, 1998). Although Staaden et al. (1995) & Huber et al. (1997) used the term "dorsal medulla" to describe African cichlid rhombencephalon dorsal structures, which is not incorrect due to its location, this portion has specializations such as facial and vagal lobes in the intermedioventral zone (Meek & Nieuwenhuys, 1998).

Our data indicates that *lobus vagi* is well developed in some cichlid species (Table 1; also see Figs. 1–2 in Oliveira & Graça, 2020), but it was shown to be larger in cyprinids, due to the specialized pharyngeal palatal organ in these fishes (Meek & Nieuwenhuys, 1998), a chemosensitive and muscular structure used to select food particles among gravel (Sibbing, 1984; Finger, 1988). Our findings imply that in most of the cichlids, *lobus vagi* is paired, also covering a great portion in the dorsal *rhombencephalon* as Meek &



**Fig. 7** Trees resulting from the constrained unweighted (A) and weighted (B) analysis. Numbers at the base of branches represent bootstrap values. One tree retained, steps = 97.610. Consistency index = 0.237; Retention index = 0.346



Nieuwenhuys, 1998 show for cyprinids. *Lobus facialis* receives sensory input from the facial cranial nerve (VII) and is connected to taste buds in the mouth cavity and external taste buds localized on the lips and body surface. In cichlids, although the *lobus facialis* is discernible in most of the species, it is less developed than in other teleosts, such as ictalurids, because they have an elaborated taste system (Meek & Nieuwenhuys, 1998).

The *cerebellum* is the most anterior portion of the *rhombencephalon*, with a role in processing somatosensory input of lateral line afferent fibers in its posterior part. Our research shows that in cichlids, it is as large as found in most of the other teleosts (Meek & Nieuwenhuys, 1998), but in others, it is greater than in cichlids studied herein, like in Pseudopimelodidae species (Abrahão et al., 2018). According to Meek & Nieuwenhuys (1998) the *cerebellum* comprises three major divisions, a vestibulolateral zone posteriorly, the *corpus cerebelli* in surface and a *valvula cerebelli*. In cichlid species, the *eminentia granularis* and *corpus cerebelli* are easily visible. The vestibulolateral zone is composed of the caudal lobe and *eminentia granularis*. This one is a visible mass of granular cells, involved in lateral line sensory reception. In contrast to cichlids examined in our study, catfish have two sections (Tong & Finger, 1983). The *corpus cerebelli* is a tubular lobe (Meek & Nieuwenhuys, 1998) which may be directed rostrally, as seen in Pseudopimelodidae (Abrahão et al., 2018), or caudally, as seen in Bathydraconidae species (Eastman & Lannoo, 2003), and in cichlids in previously (van Staaden et al., 1995) but in the cichlids analyzed herein, it sometimes appears caudally, sometimes upwardly. Meek (1992) found no functional significance in shape disparity. It is important to know that the afferent centers were found in anterior and posterior to the peduncle of the *cerebellum* (Meek & Nieuwenhuys, 1998) and efferent centers project to several areas of the encephalon (Wullimann & Northcutt, 1988). Finally, the *valvula cerebelli* is a portion located anteriorly to the *cerebellum* (Meek & Nieuwenhuys, 1998).

In cichlids studied herein, nerves are placed in the ventral rhombencephalic, intermedioventral rhombencephalic, and intermediodorsal rhombencephalic zones, as in other teleosts. Meek & Nieuwenhuys (1998) found the *abducens motor nucleus* (VI), whose fibers innervated the *rectus externus*

extra-ocular muscle in the ventral rhombencephalic zone. In the intermedioventral rhombencephalic zone, visceromotor nuclei of nerves V, VII, IX and X have been found innervating striated peripharyngeal muscles of branchial arches (Meijer, 1975). Sensory nuclei of nerves VII, IX and X are distributed in the intermediodorsal rhombencephalic zone (Meek & Nieuwenhuys, 1998). The system of somatosensory region in the dorsal zone is composed of trigeminal sensory nuclei and processes general information of the head, such as touch, temperature and proprioception (Meek & Nieuwenhuys, 1998). According to them, there are acoustic, vestibular, mechanical and electrosensory receptors with cells called “hair cells” in this region, which codify environmental information and are innervated by *nervi* VIII, NIIa and NIIp. Although lateral line receptors are utilized to detect water movements in cichlids, as in other teleosts, there are some groups with electroreception specialized lateral line systems, such as the Gymnotidae and others (Meek & Nieuwenhuys, 1998).

*Mesencephalon* is involved in the motor (ventromedially located *tegmentum*) and sensory (*torus semicircularis*) functions, although there is no rigorous separation of motor and sensory functions, as there is in *rhombencephalon* (Meek & Nieuwenhuys, 1998). The ophthalmic nerve (II) innervates the eyeball in its medial face. Some authors have observed in other teleosts that the oculomotor nucleus has cholinergic neurons (Rhodes et al., 1986; Ekstrom, 1987; Brantley & Bass, 1988). The *nervi* III and IV, along with *abducens* (VI, from *rhombencephalon*), also innervate other extraocular muscles (Meek & Nieuwenhuys, 1998). Motoneurons of trochlear nerve (IV) supply the contralateral *obliquus superior* eye muscle (Luiten & Dijkstra-de Vlieger, 1978; Graf & McGurk, 1985; Szabo et al., 1987). The *Tectum mesencephali*, commonly known as the optic tectum, is paired and occupies a considerable portion of the *mesencephalon* in cichlids analyzed herein. The intertectal commissure connects their halves (Meek & Nieuwenhuys, 1998). Despite its name, the optic tectum does not process only visual inputs, but also integrates visual signs with other sensory information to provide coordination of goal-directed movements (Meek & Nieuwenhuys, 1998). Hence, it is the primary sensorimotor integration center of the teleost central nervous system (Meek & Nieuwenhuys, 1998). In cichlids, the *tectum mesencephali* was shown to be the most

developed region in the encephalon (Kotrschal et al. 1998).

The *diencephalon* is commonly divided into the *epithalamus*, dorsal *thalamus*, ventral *thalamus* and *hypothalamus* zone in cichlids examined herein and the most visible structure is *hypothalamus*, situated beneath the *thalamus*, being the ventral diencephalic area. A pituitary stalk connects it to the *hypophysis* and contains nerve fibers that have a part in neuroendocrine regulation processes (Meek & Nieuwenhuys, 1998). The *lobus inferior hypothalami* is composed by two bulbs visible in ventral view (Meek & Nieuwenhuys, 1998) and *saccus vasculosus* is positioned beneath, posteriorly to the pituitary gland. Jansen (1973) showed that the *saccus vasculosus* is vascularized and contains cerebrospinal fluid in contact with bipolar neurons and cells called coronet.

The *telencephalon* in teleosts is likewise a paired lobe, located anteriorly to other encephalon sections. Compared to other vertebrate groups, the teleost *telencephalon* is everted rather than evaginated (Nieuwenhuys, 1962, 1963), so as in cichlids examined herein. This part includes the olfactory bulb which may be sessile, as in cichlids (herein analyzed and see Kotrschal et al., 1998) and Perciformes (Bathodraconidae in Eastman & Lannoo, 2003), or stalked as in Pseudopimelodidae (Abrahão & Shibatta, 2015) which is connected to the *telencephalon* by secondary fibers through the *tractus olfactorius* (Meek & Nieuwenhuys, 1998). Nonetheless, the forebrain (*telencephalon*) presented the main interspecific variation in size and shape in African cichlids (van Staaden et al., 1995), as well as in our study.

#### Phylogenetic implications in Geophagini

The constrained analysis allowed us to understand the neuroanatomic characters in the phylogeny proposed by Ilves et al. (2018), demonstrating possible adaptive convergences and how these characters are arranged in the evolutionary history of Geophagini. There are two synapomorphies for Geophagini clade by Ilves et al. (2018) characters 2 (*tectum mesencephali* volume percentage) and 4 (*hypophysis* volume percentage). Previous works have also proposed a phylogenetic hypothesis on the cichlid intrarelationships with morphological and molecular data. However, topologies vary among studies. For instance, Kullander (1998) recovered monophyly of Geophaginae

(essentially equivalent to Geophagini of Ilves et al., 2018) using morphological data, but differently from a subsequent study by López-Fernández et al. (2005), *Crenicichla* (we adopt *Crenicichla britskii* belonging to *Saxatilia* Varella et al. 2023) was placed as the sister group of *Cichla*. In the current study, *Cichla* and *Saxatilia* present a convergence in the character 0, represented by a decrease in the volume of gustative lobes, showing that morphological (osteological and neuroanatomical) characters tend to cluster the two genera.

Within Geophagini, character state 2 [0.238–0.241] also is synapomorphic to crenicichlines sensu Ilves et al. (2018), a clade not recovered as monophyletic in Kullander (1998) & López-Fernández et al. (2005). In the total evidence analysis shown in the latter, *Biotocus* and *Saxatilia* were sister groups, while *Acarichthys* was the sister to *Guianacara*.

Character state 8 [0.663–0.697] are synapomorphic to the apistogrammines clade sensu Ilves et al. (2018). In Kullander, these genera were placed within Geophagini (mikrogeophagines and geophagines sensu Ilves et al., 2018), but not as a sister group. Apistogrammines were recovered as monophyletic within the *Satanoperca* clade by López-Fernández's (2005) total evidence analysis. When the authors analyzed only morphological data, they discovered *Taeniacara* and *Apistogramma* with all other small-bodied taxa (*Crenicara*, *Dicrossus*, *Mikrogeophagus* and *Biotocus*), and *Satanoperca* was found in a polytomy formed by *Geophagus*, *Gymnogeophagus* and a clade that includes *Biotodoma* as the sister of *Acarichthys* plus *Guianacara*. Guianacarinae monophyly sensu Ilves et al. (2018) has three synapomorphies, characters 1, 3, and 4. Previous morphological studies (Kullander, 1998; López-Fernández et al., 2005), did not analyze *Mazarunia*, and both recovered *Guianacara* in Acarichthyini, as the sister of *Acarichthys*.

Character state 7 [0.903], height/length ratio of the *tectum mesencephali* are synapomorphic to mikrogeophagines and geophagines sensu Ilves et al. (2018), while character state 2 [0.027] is synapomorphic for geophagines. Kullander's (1998) tribe Geophagini included both mikrogeophagines and geophagines sensu Ilves et al. (2018), as well as *Satanoperca* and *Apistogramma*. Mikrogeophagines, composed of *Mikrogeophagus*, "*Geophagus*" *iporangensis* and *Biotodoma*, do not form a monophyletic clade since

they lack the geophagines species *Gymnogeophagus*, “*Geophagus*” *steindachneri* and *Geophagus sveni* (Fig. 2 and see Ilves et al., 2018). Therefore, both did not have their relationships satisfactorily resolved by Ilves et al. (2018).

Many characters state (0[0.006], 2[0.277], 3[0.086], 5[0.093], 7[0.783], 8[0.615], 15[1] and 16[1]) are synapomorphic to the clade formed by crenicaratines sensu Ilves et al. (2018). *Crenicara* and *Dicrossus* were recovered as sister genera in previous phylogenies (Kullander, 1998; López-Fernández et al., 2005). When just morphological data was analyzed in López-Fernández et al. (2005), these genera were recovered within a clade composed of the small-bodied species, as previously explained.

Character 0, gustative lobes, was important among Geophagini. Gustative lobes tend to increase in *Gymnogeophagus balzanii*, *Gymnogeophagus meridionalis*, “*Geophagus*” *iporangensis*, *Geophagus sveni*, “*Geophagus*” *steindachneri*, *Satanoperca* sp. and *Satanoperca acuticeps*. It is possible to observe convergences in this structure among these taxa and *Retroculus acherontos*. Although *Geophagus*, *Gymnogeophagus*, *Satanoperca* and *Retroculus* do not form a monophyletic group (Ilves et al., 2018), the first three genera were placed together in other morphological phylogenies (Kullander 1998; López-Fernández et al. 2005), and in other studies, *Retroculus* was included in Geophagini (Cichocki, 1976; Landim, 2007).

#### Convergence in Geophagini: an ecological approach

Using the characters proposed herein in the constrained analysis onto the topology of Ilves et al. (2018) is enlightening within an ecological and evolutionary perspective. It is essential to understand the major functions of the encephalon in this context and link them to any behavioral and ecological characteristics of cichlid species.

The primary function of the nervous system is to coordinate the interactions between the organism and the environment via efferent (motor) and afferent (sensorial) systems, of which the latter appears to be more adaptable (Meek & Nieuwenhuys, 1998). Fishes have a variety of sensory organs, namely olfactory, gustatory, visual, acoustic, vestibular and somatosensory, which receive signals from the environment and are connected with the central nervous system by spinal and cranial nerves (Meek & Nieuwenhuys, 1998).

According to the authors, a higher development of a specific region of the encephalon seems to correlate with the presence of specialized organs. For example, groups that are capable of detecting electric current in the environment, such as Mormyridae and Gymnotidae, present a better-developed lateral line system specialized for electroreception than fish that only use the lateral line as a detector of water mechanosensory stimulus (Meek & Nieuwenhuys, 1998), such as cichlids that lack a well-developed lateral-line lobe.

However, even in the absence of specialized organs, highly developed encephalon parts imply that the senses they process are crucial to an individual species' life habits. For example, the rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) has a heightened sense of vision and consequently a high development of the *tectum mesencephali* (Meek & Nieuwenhuys, 1998). In the current study, the vision center has the largest volumes among encephalon parts in all species studied, and the high volume of the *tectum mesencephali* is synapomorphic to Geophagini clade. This agrees with Kotschal et al. (1998), once the vision center, commanded by *tectum mesencephali*, is the most well-developed structure in cichlid encephalon in general.

Once our findings of Cichlid species have established a well-developed vision center, it is critical to comprehend the significance of this center to cichlids in general. First, the encephalon processes vision in all vertebrates via light absorption in the photoreceptors of the retina (cones and rods) (Meek & Nieuwenhuys, 1998). In cichlids, there are seven different genes of cone opsins and one of rod opsin (Carleton et al., 2016), which are expressed in different sets across species (Carleton et al., 2016; Schneider et al., 2020) and along ontogeny (Carleton, 2009), allowing for the absorption of a wide range of light spectra (Carleton et al., 2016; Schneider et al., 2020). In this sense, the evolution of visual sensitivity in cichlids appears to have occurred through altering the expression of these genes, and appears to have been selected mostly for the properties of light incident on the habitat, which vary depending on the water turbidity and depth (Schneider et al., 2020). Thus, this complex vision system and a well-developed *mesencephalon* in Cichlid species found herein, could be linked to visual orientation of cichlids in relation to recognition of conspecific coloration (Schneider et al., 2020), brood guarding behavior and territory defense (Gois

et al., 2015), foraging (Parry et al., 2005) and habitat selection (Carleton, 2009). On the other hand, cichlids are considered microsmatic, *i.e.*, they have a poorly developed olfactory system, therefore their *bulbus olfactorius* is less developed than in other groups, which is consistent with their small olfactory organs (Ridet & Bauchot, 1990).

About feeding habits, some Neotropical cichlid species were discovered to be mostly as benthivorous or piscivorous fishes (López-Fernández et al., 2012). It is difficult to extrapolate feeding habits for all Geophagini genera, because, in that study, there were *CrenicichlaSaxatilia* species which may consume both prey types. Despite this, most of Geophagini have a benthic-feeding behavior, with the exception of *CrenicichlaSaxatilia*, using their protractible jaws to sift the substrate. Geophagini sifters have modifications of the pharyngeal apparatus (weak pharyngeal jaws and the presence of epibranchial 1 lobe), indicating a link between morphology and this feeding behavior (López-Fernández et al., 2012).

Thus, occasionally, it is possible to identify a correlation between encephalon shape and feeding adaptations (Oliveira & Graça, 2020). Our study detected proportionally greater gustative lobes (*lobus facialis* and *lobus vagi*) in sediment-sifting cichlids, such as most mikrogeophagines and geophagines, *Satanoperca* and *Retroculus*, suggesting that taste is important in sorting edible from non-edible particles during winnowing (Fig. 2; Supplementary File 4, Fig. 1; although *Acarichthys*, *Biotodoma*, *Guianacara* and *Mikrogeophagus* present no such increase). Well-developed *lobus vagi* were also found in a previous study conducted with *Geophagus sveni*, which showed a possible relation with adaptations to winnowing (Oliveira & Graça, 2020), and in Cyprinids, which have a specialized pharyngeal palatal organ (Meek & Nieuwenhuys, 1998), and in species that select particles among gravel (Sibbing, 1984; Finger, 1988).

However, in piscivores (*Acaronia*, *Cichla*, *Saxatilia* and *Parachromis*) and in some dwarf species (crenicaratines and *Taeniacara*) the volume of gustative lobes decreased. Perhaps taste is a less important sense in visual predators, which is corroborated by the fact that piscivores have a larger *tectum mesencephali* (van Staaden et al., 1995; Huber et al., 1997). *Bujurquina* and *Guianacara*, which are neither piscivorous nor dwarf species but have a small gustative

lobe volume, and *Biotoecus*, a dwarf species with a large gustative lobe volume, are exceptions to this rule.

Encephalon gross morphology varied among Geophagini and other cichlid species. Encephalon variation may be the reflection of both phylogenetic distance and environmental conditions experienced by fishes throughout time (van Staaden et al., 1995; Huber et al., 1997; Abrahão et al., 2018). Thus, feeding specialization itself does not entirely explain interspecific variation in encephalon morphology, once microhabitat use is also associated with increasing or decreasing in some cichlid encephalon structures between species (van Staaden et al., 1995; Huber et al., 1997). A study conducted in the African lakes, Victoria, Tanganyika and Malawi, revealed that turbidity, depth, and substrate complexity could predict variability, but not causality, of differences in encephalon structures in different cichlids species (Huber et al. 1997). For example, shallow rock environments were associated with small gustatory lobes in the encephalon (*lobus vagi* and *facialis*).

## Conclusion

Geophagini encephalon gross morphology varies interspecifically and the differences provided[ putative characters. In contrast, using neuroanatomic characters on a previous phylogenetic hypothesis we were able to uncover probable adaptive convergences. Four genera analyzed herein (*Acaronia*, *Cichla*, *Saxatilia* and *Parachromis*) that converged to piscivorous habits developed independently smaller gustative lobes in comparison with other taxa investigated, with the exception of some dwarf species (crenicaratines and *Taeniacara*). Conversely, most of the specialized winnowers, namely geophagines, “*Geophagus*” *iporangensis*, *Retroculus* and *Satanoperca* developed large gustative lobes, apparently to facilitate sorting of edible and non-edible particles during sifting. Although it is not quite certain if the ancestor of all Geophagini was a specialized sediment-sifter or not, within the tribe this behavior is correlated to large gustative lobes, with few exceptions, and may represent adaptive convergence. Concurrently, *Retroculus* certainly has developed sifting habits independently from Geophagini, and also possesses

well-developed gustative lobes. Furthermore, the *tectum mesencephali*, which is the largest structure in proportion to the encephalon in all cichlids analyzed herein, is even larger in Geophagini. An increase in its volume is one of the characters that supports the tribe in the constrained analysis. Using encephalon gross morphology to access information under the phylogenetic constrained approach reveals unique characteristics that emphasize the evolution of this structure in Geophagini. In this context, neuroanatomic characters are informative in phylogenetic and ecological studies and they could be used allied to a larger set of other morphological structures, despite their homoplastic nature.

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## Declarations

**Competing interests** The authors have not disclosed any competing interests.

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