Brain morphology of native and invasive *Cichla piquiti*, the blue peacock bass (Cichliformes: Cichlidae), with ecomorphological insights

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The central nervous system (CNS), composed of the encephalon and spinal cord, regulates physiological, motor, and cognitive processes in vertebrates. In Neotropical fishes, however, encephalon morphology and size remain poorly studied, particularly in cichlids. This study describes the encephalon of *Cichla piquiti*, analyzing variations across developmental stages, sex, and native *vs.* invasive populations. The relative proportions of brain structures were distinct, with a marked dominance of the *tectum mesencephali* (54–58%), highlighting strong reliance on visual information. No sexual dimorphism was detected, suggesting similar behavioral patterns between males and females. Juveniles and adults differed in the shape of the *telencephalon*, *lobus inferior hypothalami*, and *cerebellum*, reflecting developmental adjustments in response to sensory and ecological demands. Morphology also varied between populations: juveniles from the native Tocantins population showed faster growth of major brain regions, whereas invasive individuals from Furnas exhibited delayed development, likely associated with contrasting environmental pressures. The encephalization quotient (E_Q) exceeded 1, surpassing typical values reported for Actinopterygii, and the *telencephalon* and *tectum mesencephali* accounted for half of the brain volume, suggesting enhanced cognitive abilities. This work provides the first detailed anatomical account of *Cichla* brain morphology, offering insights into cognitive potential, phenotypic plasticity, and mechanisms underlying the species' invasive success.

Keywords: Central nervous system, Encephalization quotient (E_Q), Encephalon, Morphology.

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O sistema nervoso central (SNC), composto pelo encéfalo e pela medula espinal, regula processos fisiológicos, motores e cognitivos em vertebrados. Em peixes neotropicais, entretanto, a morfologia e o tamanho do encéfalo permanecem pouco estudados, especialmente em ciclídeos. Este trabalho descreve o encéfalo de *Cichla piquiti*, analisando variações entre estádios de desenvolvimento, sexos e populações nativas e invasoras. As proporções relativas das estruturas encefálicas foram distintas, com dominância do *tectum mesencephali* (54–58%), evidenciando forte dependência de informações visuais. Não foi detectado dimorfismo sexual, sugerindo padrões comportamentais semelhantes entre machos e fêmeas. Juvenis e adultos diferiram na forma do *telencephalon*, *lobus inferior hypothalami* e *cerebellum*, refletindo ajustes ontogenéticos relacionados às demandas sensoriais e ecológicas. A morfologia também variou entre populações: juvenis da população nativa do Tocantins apresentaram crescimento mais rápido das principais regiões encefálicos, enquanto indivíduos invasores de Furnas exibiram desenvolvimento mais tardio, provavelmente associado a pressões ambientais contrastantes. O Coeficiente Encefálico (E_Q) superou 1, ultrapassando valores típicos relatados para Actinopterygii, e metade do volume encefálico correspondeu ao *telencephalon* e ao *tectum mesencephali*, sugerindo habilidades cognitivas ampliadas. Este estudo fornece a primeira descrição detalhada do encéfalo de *Cichla*, contribuindo para a compreensão da plasticidade fenotípica, do potencial cognitivo e dos mecanismos de sucesso invasivo.

Palavras-chave: Coeficiente encefálico (E_Q), Encéfalo, Morfologia, Sistema nervoso central.

INTRODUCTION

The vertebrate Central Nervous System (CNS) is a complex anatomical structure that coordinates motor, physiological, behavioral, and endocrine functions (Northcutt, 1984). Its organization reflects the functional and morphological polarization of neurons (Nieuwenhuys, 1966; Butler, Hodos, 2005), enabling the reception, integration, and processing of both internal and external stimuli. Although the brain follows a conserved structural plan comprising the *prosencephalon*, *mesencephalon*, and *rhombencephalon*, it exhibits notable anatomical variation across taxa (Nieuwenhuys, 1966; Meek, Nieuwenhuys, 1998; Nieuwenhuys *et al*., 1998).

Beyond its structural features, the CNS also plays a central role in regulating cognitive processes (Roth, Dicke, 2005). These processes have been extensively investigated in mammals, but are often underestimated in other vertebrates (Brown, 2015). Cognition is generally linked to both absolute and relative brain size (Gignac, Bates, 2017) and neural efficiency (Kandel, Spencer, 1968), with significant ecological and behavioral implications (Ebbesson, Braithwaite, 2012). Among these measures, brain size is one of the most widely applied parameters for evaluating cognitive performance. It is frequently assessed using the Encephalization Quotient (E_Q), a metric that integrates brain size relative to body size (Bauchot, Bauchot, 1978; Jerison, 1985; Bauchot *et al*., 1989a; Lisney, Collin, 2006; Peñaherrera Aguirre *et al*., 2021).

Morphoanatomical variation in the brain is shaped by both ecological and evolutionary factors. In fishes, brain morphology represents a key framework for investigating evolutionary relationships (Pereira, Castro, 2016; Abrahão *et al*., 2018; Rosa *et al*., 2021; Oliveira, Graça, 2024), ecomorphological patterns (Huber *et al*., 1997; Shumway, 2010; Kotrschal *et al*., 2017; Leão-Reis *et al*., 2025), and even the taxonomic description of new species (Chamon *et al*., 2018; Espíndola *et al*., 2018; Abrahão *et al*., 2019). Despite this broad potential, relatively few studies have focused on Neotropical fishes in recent years (Marinho-Nunes *et al*., 2025a). For example, previous research has demonstrated that brain differentiation is linked to functional diversity and sympatric speciation in African cichlids (Huber *et al*., 1997). However, comparable studies remain scarce, particularly for species from the Neotropical region.

Neotropical cichlids have been characterized by behavioral and ecomorphological plasticity (Ribeiro *et al*., 2007; Maan, Sefc, 2013; Novakowski *et al*., 2016; Lehtonen *et al*., 2023), indicating that the group may represent an interesting model to investigate brain structure. Peacock-basses, *Cichla* Bloch & Schneider, 1801, in particular, have shown ecological and morphological shifts under conditions of environmental change (Gilbert *et al*., 2020; Gaspar *et al*., 2024), which enable adjustments in feeding, reproduction, and general behavior (Gomiero, Braga, 2004; Fugi *et al*., 2008; Capra, Bennemann, 2009; Marto *et al*., 2015; Guedes *et al*., 2024). *Cichla* is a group composed of generalist top predators (piscivores) that build nests and exhibit complex parental care (Winemiller *et al*., 2021) usually living in structured environments and forming small aggregations. Species show conspicuous coloration patterns (Pelicice *et al*., 2022) that may serve as social signaling or communication (Reiss *et al*., 2012). These traits, together, have favored the colonization of large reservoirs and other environments across the Amazon basin and elsewhere (Sastraprawira *et al*., 2020; Franco *et al*., 2021; Andrade, Pelicice, 2022; Franco *et al*., 2022a,b), with ecological consequences (Pelicice, Agostinho, 2009; Franco *et al*., 2021; Khaleel *et al*., 2021; Souza *et al*., 2021).

Ecological plasticity in *Cichla* has been associated with its demographic success and invasiveness, but no study has examined the brain morphology of this genus, despite its value for topics such as taxonomy, evolution, behavior, ecology, and cognitive perspectives. Brain variation in fishes has been reported when comparing isolated populations of the same species (Kotrschal *et al*., 2017; Liu *et al*., 2021). Intraspecific morphological differences between males and females are also possible (Angulo, Langeani, 2017; Abrahão *et al*., 2021), as are ontogenetic modifications. Given the taxonomic uncertainties about *Cichla* (Willis *et al*., 2012; Winemiller *et al*., 2021), together with its recognized ecological performance (Carvalho *et al*., 2021; Gaspar *et al*., 2024), the investigation of brain morphoanatomy may provide valuable information and insights about this group. It must also be considered that brain anatomy in Neotropical cichlids remains virtually unstudied, with few published works (Oliveira, Graça, 2020, 2024; Leão-Reis *et al*., 2025).

To fill this gap, this is the first study to characterize brain morphology in *Cichla*. We focused on *Cichla piquiti* Kullander & Ferreira, 2006, a species endemic to the Tocantins-Araguaia basin (Kullander, Ferreira, 2006), but introduced elsewhere (Franco *et al*., 2022b). Specimens from native (*i.e*., Tocantins-Araguaia basin) and non-native populations (*i.e*., Grande River, upper Paraná basin) were described in terms of gross brain morphology and compared to investigate variations in morphology, documenting developmental changes and comparing qualitative and quantitative variation between sexes and populations. Additionally, we calculated the Encephalization Quotient (E_Q) to provide insights into potential associations between cognitive performance and the invasive success of the species. Based on prior research in fish neuroanatomy, we tested two hypotheses: (1) individuals from distinct environments exhibit distinct brain morphology, and (2) *C. piquiti* presents high E_Q values, potentially associated with enhanced behavioral plasticity and invasive success.

MATERIAL AND METHODS

Biological data. Native populations were sampled from two sites: (1) the area influenced by the Luiz Eduardo Magalhães Hydroelectric Plant (UHE Lajeado), Porto Nacional municipality, Tocantins River drainage, 10°42’25”S 48°26’08”W; and (2) the Javaés River, in proximity to the Canguçu Research Center, Araguaia River drainage, 09°58’58”S 50°02’43”W. Non-native populations were collected from (3) the area influenced by the Furnas Reservoir, Grande River, Paraná River drainage, 20°43’59”S 45°44’12”W.

Specimens were euthanized with eugenol diluted in 10% alcohol, fixed in 10% formaldehyde, and subsequently deposited in the Laboratório de Ictiologia Sistemática (Neamb/UFT), where they are catalogued.

A total of 37 specimens of *Cihla piquiti* were analyzed. From the Araguaia River, the sample comprised three adult females, three adult males, and one immature male; from the Furnas Reservoir, eight immature females and eleven immature males; and from the Tocantins River, three immature females and eight immature males. All specimens were measured with a precision caliper (0.01 mm) and weighed on an analytical balance (0.001 g). Standard length (SL), total length (TL), and total weight (TW) were recorded for each individual.

The examined material was deposited in the fish collection at the Laboratório de Ictiologia Sistemática, Universidade Federal do Tocantins (UNT), Porto Nacional, Brazil:

- Area 1: Lajeado Hydroelectric Reservoir, Tocantins River, Tocantins basin (10.706949° S, 48.435552° W): *Cichla piquiti* Kullander & Ferreira, 2006 – UNT 11327 (3: 81.40–100.00 mm SL); UNT 18940 (1: 155.30 mm SL); UNT 19753 (1: 47.50 mm SL); UNT 20100 (3: 87.0–87.90 mm SL); UNT 4543 (1: 58.30 mm SL); UNT 6287 (2: 87.10–97.10 mm SL).
- Area 2: Canguçu Research Center, Pium, Tocantins – Javaés River, Araguaia basin (9.982830° S, 50.045148° W): *Cichla piquiti* Kullander & Ferreira, 2006 – UNT 22471 (2: 252.0–375.0 mm SL); UNT 22472 (5: 250.0–320.0 mm SL); UNT 2397 (1: 124.30 mm SL).
- Area 3: Furnas Hydroelectric Reservoir, Minas Gerais – Grande River, Paraná basin (20.552624° S, 46.814970° W): *Cichla piquiti* Kullander & Ferreira, 2006 – UNT 22487 (7: 90.1–171.7 mm SL); UNT 23004 (12: 95.7–151.4 mm SL).

Anatomical description and comparison. Brain dissection and extraction followed the protocol of Marinho-Nunes *et al.* (2025b). The measurements are presented in different formats because they were obtained using different methods, *i.e.*, brain were weighed using an analytical balance with a precision of 0.0001 g, and morphometric measurements were recorded, including brain weight (BW), total brain length (BL), brain width (BWd), and brain height (BH), using a Leica MC160 stereomicroscope equipped with an attached camera, with a measurement precision of 0.0001 mm. Total brain volume (BV) was estimated using the formula $V = 1/6\ \pi\ H\ W\ L$ (where H = height, W = width, L = length of the brain), commonly referred to as the "half-ellipsoid method" (Huber *et al*., 1997; Van Staaden *et al*., 1995; White, Brown, 2015). The Encephalization Quotient (E_Q) was calculated for each species as the ratio between the actual brain weight and the expected brain weight for an animal of a given body mass, using the formula $E_Q = EaEe^{-1}$, where Ea is the actual brain weight and Ee is the expected brain weight, following the approach of Bauchot, Bauchot (1978) and Bauchot *et al*. (1989b).

For image acquisition, a Leica MC160 stereomicroscope equipped with a multi-capture system (auto-montage) was used to improve image resolution. The brains were immobilized by complete immersion in alcohol gel to prevent displacement during image acquisition. To reduce surface irregularities of the medium and minimize light refraction, 70% ethanol was added to the surface of the alcohol gel, ensuring greater optical uniformity during image recording. Brains were illustrated manually using layered drawings and stippling techniques to depict shading and depth, with Sketchbook® v. 6.0.7. Anatomical nomenclature followed Waibl *et al*. (2012).

Neuroanatomical comparisons and descriptions focused on the following structures: *bulbus olfactorius*, *telencephalon*, *tectum mesencephali*, *hypophysis*, *hypothalamus*, *saccus vasculosus*, *lobus inferior hypothalami*, *cerebellum*, *eminentia granularis*, *lobus vagi*, *lobus gustativus*, *medulla oblongata*, and the *lamellae fossa nasalis*. In adult specimens, the lamellae were stained with Alcian Blue to enhance visualization due to their natural translucency.

The Sturges method was applied to classify standard length (SL) into non-arbitrary categories for comparisons of brain development across size classes (Sturges, 1926). Seven SL classes were defined, although class 6 (300–350 mm) contained no specimens (Tab. 1).

TABLE 1 | Standard length (SL) classes used to determine sample size and size range.

		Locality		
Class	**Range (mm)**	**Araguaia**	**Tocantins**	**Furnas**
1	50–100	-	11	4
2	100–150	2	1	11
3	150–200	-	-	12
4	200–250	1	-	-
5	250–300	3	-	-
6	300–350	-	-	-
7	350–400	1	-	-

Statistical analyses. All statistical analyses were conducted in RStudio v. 2023.01.1 (RStudio Team, 2022). Data normality was assessed using the Shapiro-Wilk test. For analyses involving brain structure volumes, the relative volume (RV) was calculated as $RV = log\ (Volume)\ /\ log\ (Standard\ length)$.

Differences in Encephalization Quotients (E_Q) among populations were tested using Analysis of Variance (ANOVA), with locality as a factor. Differences in E_Q between males and females were tested using a student's t-test (Gotelli, Ellison, 2013).

A Principal Component Analysis (PCA) was performed to investigate variation in brain structures among localities, using the relative volumes of the *bulbus olfactorius*, *telencephalon*, *tectum mesencephali*, *lobus inferior hypothalami*, *cerebellum*, *lobus gustativus*, and *medulla oblongata*. An additional PCA was conducted comparing only specimens from Furnas and Tocantins to minimize potential allometric effects, since the Araguaia specimens were adults and considerably larger. PCA scores were further examined to assess patterns between males and females (Gotelli, Ellison, 2013).

A Permutational Analysis of Variance (PERMANOVA) was conducted to evaluate differences in brain structure among sampling localities and between sexes, using multivariate Euclidean distances as the dissimilarity metric. The coefficient of determination (R^2) was used to quantify the proportion of variation explained by locality, and statistical significance was assessed through permutation-based p-values. To ensure that observed differences were not attributable to unequal within-group dispersion, a test for homogeneity of multivariate dispersions (PERMDISP) was also performed.

To assess potential differences in the number of *lamellae fossa nasalis* among sampled localities, the Kruskal-Wallis test was applied as a nonparametric method to compare medians across three or more groups. When significant differences were detected, Dunn's post hoc test was performed to conduct pairwise multiple comparisons among localities.

RESULTS

Qualitative analysis: morphological descriptions. The brain morphology of *Cichla piquiti* is described comparatively across developmental stages and localities, following an anteroposterior sequence. The descriptions are based on the morphological variation observed between specimens at early developmental stages (Fig. 1) and specimens at advanced developmental stages (Fig. 2) from different sampling localities. We chose not to describe the material by comparing juveniles and adults (based on sexual maturity), as complete brain formation occurs prior to sexual maturation, resulting in juveniles that already exhibit a fully developed brain. The relationship between size (SL) and the development of brain structures is detailed in the subsequent paragraphs.

In early developmental stages, the *lamellae fossa nasalis* form tongue-shaped (linguiform lamellae) projections, which may appear either fully developed or still undergoing development (Figs. 3A–B). In advanced developmental stages, the lamellae assume a leaf-like morphology with a slight invagination, resulting in lateral margins that are elevated relative to the medial margins (Fig. 3C). All lamellae in advanced developmental stages specimens were fully developed.

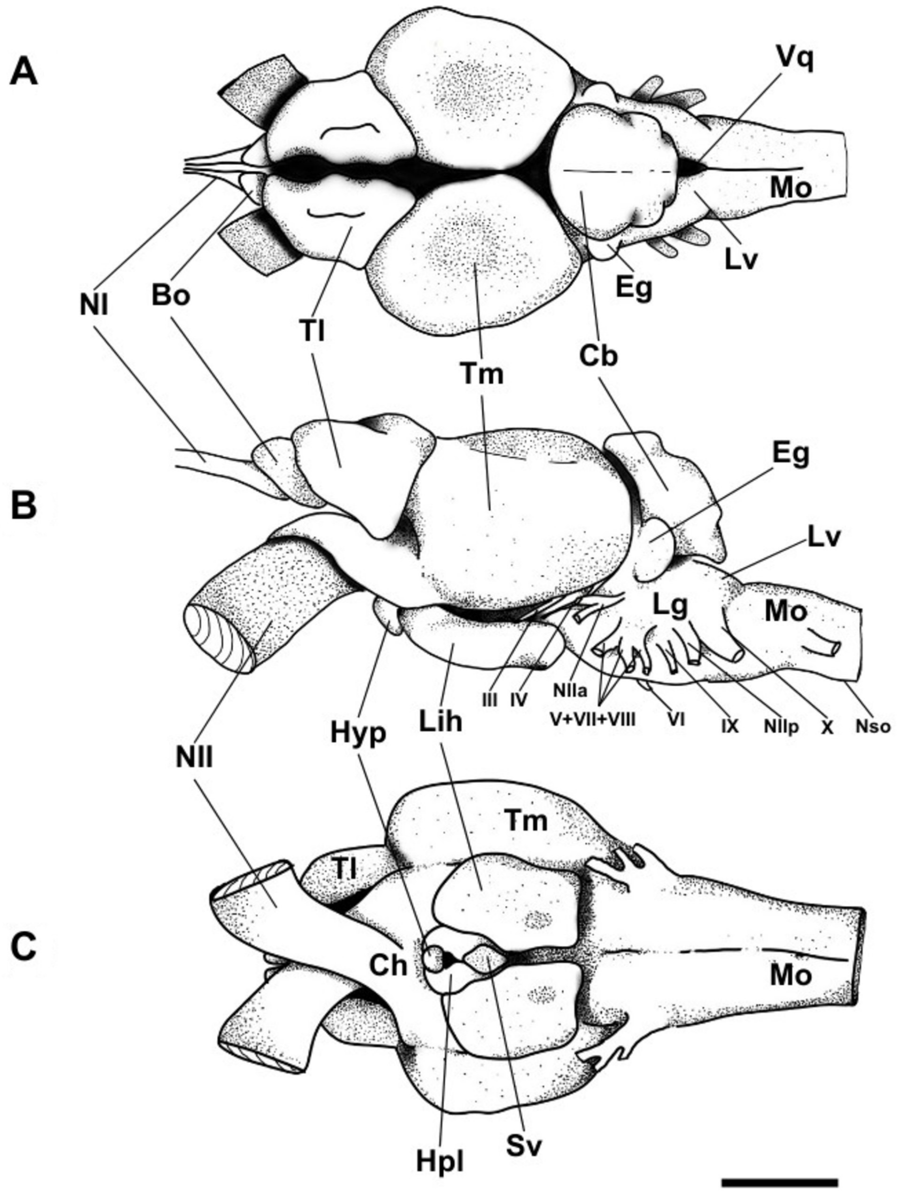

FIGURE 1 | Brain of *Cichla piquiti* in early development stage. **A.** Dorsal view; **B.** Lateral view; **C.** Ventral view. Scale bar = 2 mm. Abbreviations: Bo, *bulbus olfactorius*; Cb, *cerebellum*; Ch, *chiasma opticum*; Eg, *eminentia granularis*; Hyp, *hypophysis*; Hpl, *hypothalamus*; III, *nervus oculomotorius*; IV, *nervus trochlearis*; IX, *nervus glossopharyngeus*; Lg, *lobus gustativus*; Lih, *lobus inferior hypothalami*; Lv, *lobus vagi*; Mo, *medulla oblongata*; NI, *nervus olfactorius*; NII, *nervus opticus*; Nlla, *nervus linea lateralis anterior*; Nllp, *nervus linea lateralis posterior*; Nso, *nervus spino-occipitales*; Sv, *saccus vasculosus*; Tl, *telencephalon*; Tm, *tectum mesencephali*; V, *nervus trigeminus*; VI, *nervus abducens*; VII, *nervus facialis*; VIII, *nervus octavus*; Vq, *Ventriculus quartus*; X, *nervus vagus*.

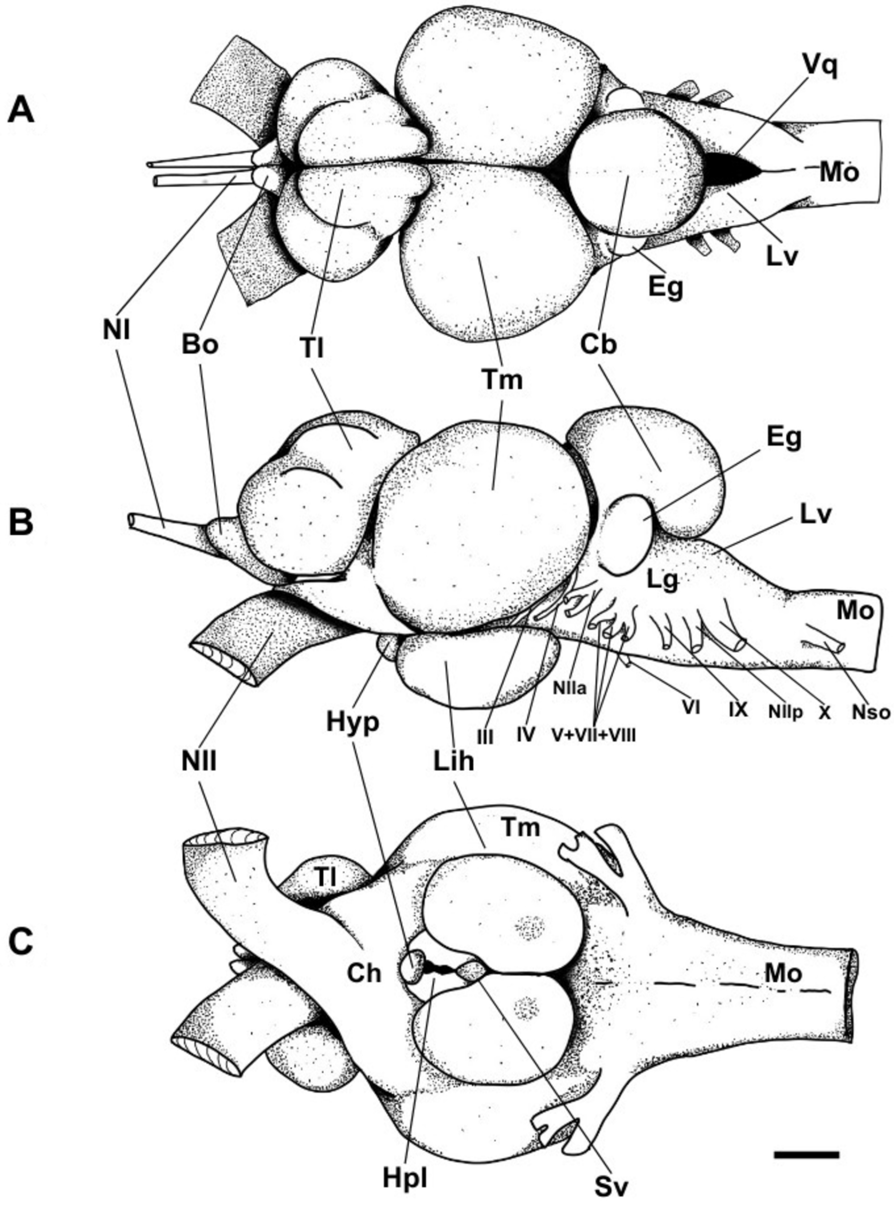

FIGURE 2 | Brain of *Cichla piquiti* in advanced development stage illustrated. **A.** Dorsal view; **B.** Lateral view; **C.** Ventral view. Scale bar = 2 mm. Abbreviations: Bo, *bulbus olfactorius*; Cb, *cerebellum*; Ch, *chiasma opticum*; Eg, *eminentia granularis*; Hyp, *hypophysis*; Hpl, *hypothalamus*; III, *nervus oculomotorius*; IV, *nervus trochlearis*; IX, *nervus glossopharyngeus*; Lg, *lobus gustativus*; Lih, *lobus inferior hypothalami*; Lv, *lobus vagi*; Mo, *medulla oblongata*; NI, *nervus olfactorius*; NII, *nervus opticus*; Nlla, *nervus linea lateralis anterior*; Nllp, *nervus linea lateralis posterior*; Nso, *nervus spino-occipitales*; Sv, *saccus vasculosus*; Tl, *telencephalon*; Tm, *tectum mesencephali*; V, *nervus trigeminus*; VI, *nervus abducens*; VII, *nervus facialis*; VIII, *nervus octavus*; Vq, *Ventriculus quartus*; X, *nervus vagus*.

The number of lamellae in the nasal fossa ranged from 12 to 26, with variation associated with specimen size and sampling locality. In Furnas specimens, lamellae counts varied between 14 and 16, corresponding to Class 2 individuals (100–150 mm SL) and one Class 3 specimen (171 mm SL). Native populations (Tocantins and Araguaia) generally exhibited higher numbers. A single Araguaia specimen from Class 2 (124 mm SL) had 16 lamellae, whereas larger specimens (132–370 mm SL; Classes 2–7) exhibited 21–25 lamellae. Tocantins specimens from Class 1 (n = 9) had 12–17 lamellae, and one Class 3 specimen (155 mm SL) presented 22 lamellae.

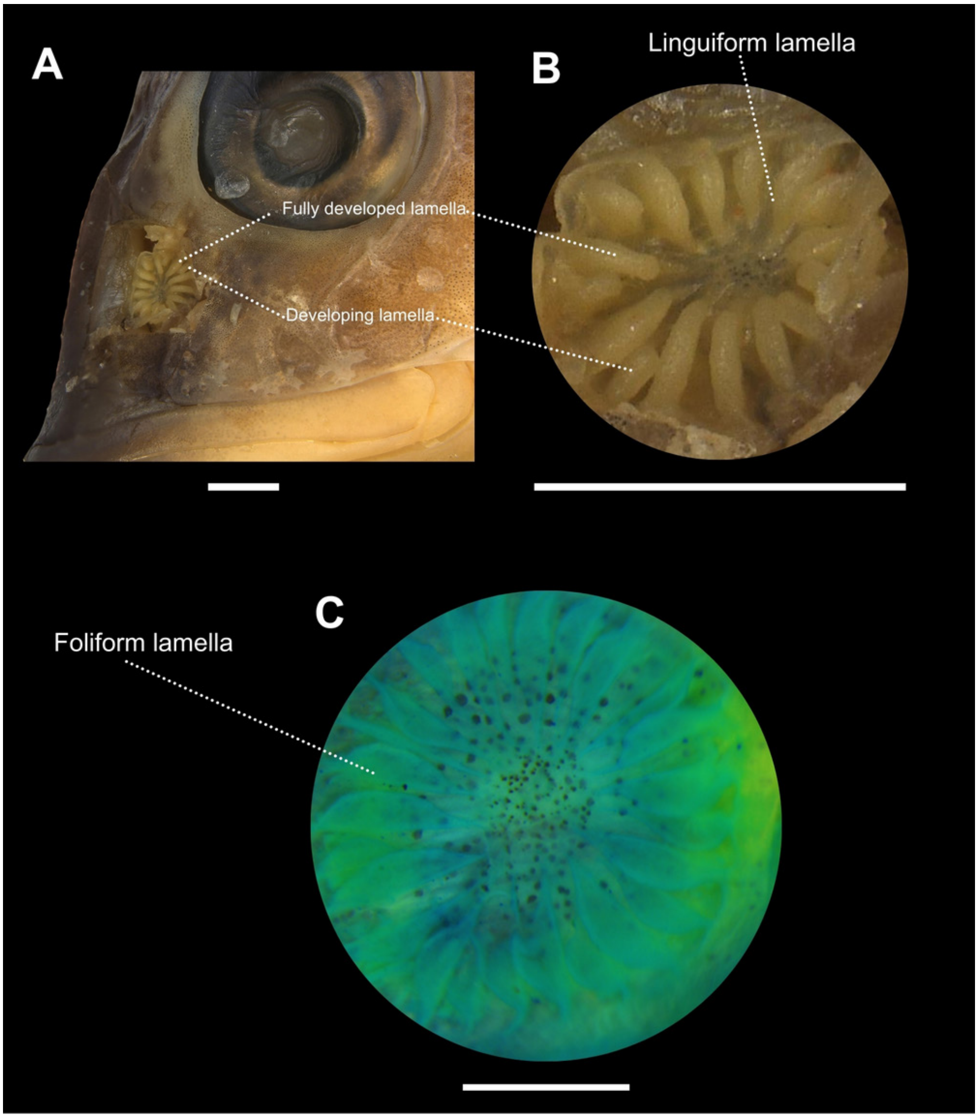

FIGURE 3 | **A.** Nasal lamellae (*lamellae fossa nasalis*) of early development stage *Cichla piquiti* (UNT 22487_2; 116.00 mm SL); **B.** Magnified nasal lamellae of early development stage *Cichla piquiti*; **C.** Nasal lamellae of advanced development stage *Cichla piquiti* (UNT 22471_1; 270.00 mm SL) stained with alcian blue. Scale bars = 2 mm.

***Prosencephalon* and *telencephalon*.** The *bulbus olfactorius* is oval in shape, with an anterior portion that is narrower than the posterior portion, which connects directly to the *telencephalon* (Figs. 4C–D). This structure is relatively small compared with the entire brain, accounting for approximately 1% of total brain volume in adult specimens. In early developmental stages (between 50–200 mm SL), although smaller than all other paired structures, it is proportionally larger, as regions such as the *telencephalon* remain less developed at early stages (Figs. 4A–D).

The morphology of the *telencephalon* differed between early and advanced developmental stages. At early developmental stages (between 50–200 mm SL), according to the defined size classes, the structure is compact, with the two hemispheres clearly separated by a fissure, allowing visualization of the ventral surface (Fig. 4A). In early developmental stages (< 200 mm SL), the dorsal surface of the *telencephalon* exhibits a height comparable to that of the dorsal surfaces of the *tectum mesencephali* and *cerebellum* (Fig. 4C). In advanced developmental stages (> 200 mm SL), the *telencephalon* expands dorsally, the interhemispheric fissure becomes reduced to a shallow sulcus, and the structure assumes a coracoid shape, with the anterior portion wider than the posterior (Fig. 4B). The posterior region is positioned dorsally beyond its own dorsal margin, making the superior surface higher than that of the *tectum mesencephali* (Fig. 4D).

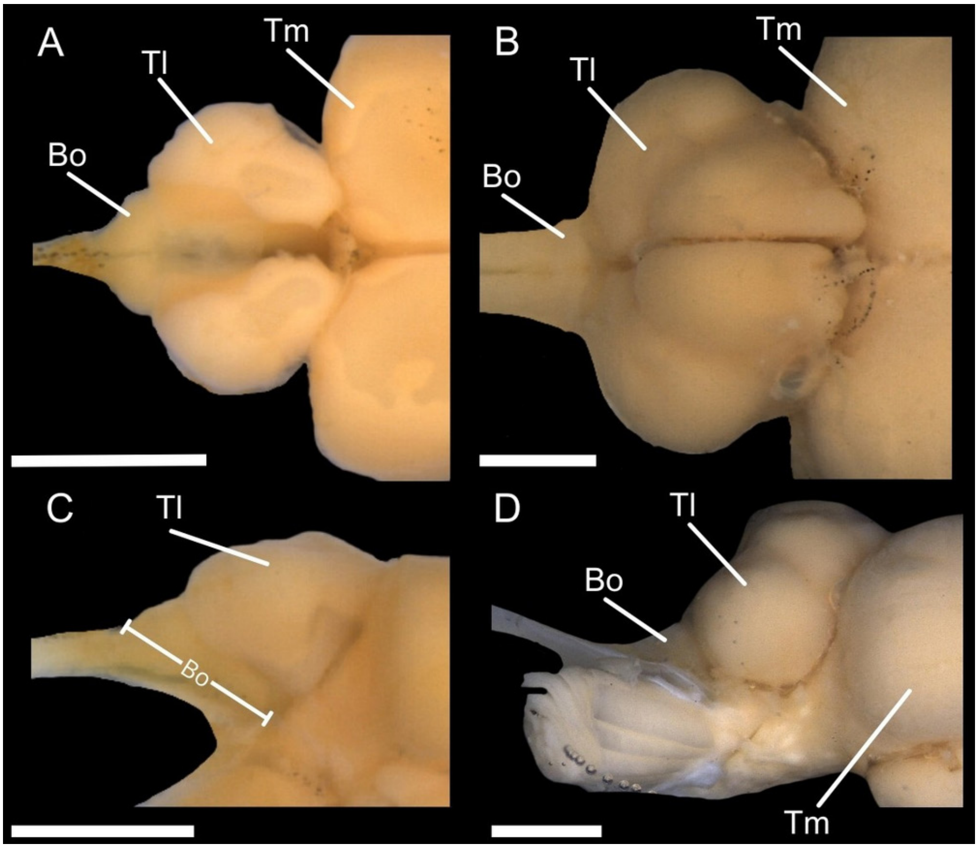

FIGURE 4 | Anterior region of the *Cichla piquiti* encephalon. (**A**, **C**: UNT 4543_1; 58.30 mm SL); (**B**, **D**: UNT 22471_1; 270.50 mm SL); **A.** Dorsal view of early development stage; **B.** Dorsal view of advanced development stage; **C.** Lateral view of early development stage; **D.** Lateral view of advanced development stage. Abbreviations: Bo, *bulbus olfactorius*; Tl, *telencephalon*; Tm, *tectum mesencephali*. Scale bars = 2 mm.

Ontogenetic variation was also observed among localities. In Furnas, all Class 1 and 2 (50–150 mm SL) individuals exhibited an incompletely developed *telencephalon*; only one Class 3 specimen (170 mm SL) displayed a fully developed structure. In contrast, all Araguaia specimens, including juveniles (two Class 2 individuals: 124 mm and 132 mm SL), exhibited a developed *telencephalon*. Among Tocantins specimens, only the smallest individuals (50–81 mm SL) showed the structure in development, whereas from 87 mm SL onwards, including Class 1 and 2 specimens, the *telencephalon* was fully developed.

Diencephalon. The *lobus inferior hypothalami* is a paired structure, with the anterior hemispheres separated by the *hypothalamus* and *saccus vasculosus*, while the posterior portions are connected, forming a sulcus between them (Figs. 5A–B). In early developmental stages specimens, the structure is rectangular in ventral view, with straight anterior and posterior margins (Fig. 5C). In advanced developmental stages, it is reniform. In the lateral view, however, no distinct differences were observed between early and advanced developmental stages (Figs. 5C–D).

Ontogenetic and locality-based variation was also observed. In Furnas, all Class 1 and 2 (50–150 mm SL) individuals exhibited a *lobus inferior hypothalami* still in development, with only one Class 3 specimen (171 mm SL) presenting a fully developed *lobus inferior hypothalami*. In contrast, all Araguaia specimens, including juveniles, showed this structure fully developed. Among Tocantins specimens, individuals exceeding 80 mm SL consistently displayed a developed *lobus inferior hypothalami*.

The *hypophysis*, *hypothalamus*, and *saccus vasculosus* lie on the ventral region of the *diencephalon* (Fig. 6). These structures are relatively small compared with other brain components and exhibited no variation in shape between early and advanced developmental stages or among the populations analyzed. The *hypophysis* has a concave posterior margin, with width exceeding length; it connects to the *chiasma opticum*, although this connection is delicate, making the structure easily detachable. The *hypothalamus* is coracoid in shape, with the anterior portion wider than the posterior, and is visibly divided into two lateral regions by a median fissure. The *saccus vasculosus* is ovoid, located ventrally to the posterior margin of the *hypothalamus*, with its posterior margin in contact with the medial region of the *lobus inferior hypothalami*. Its growth is comparatively reduced relative to other diencephalic structures, such that in advanced developmental stages, the *saccus vasculosus* is proportionally smaller than the other developed components of the *diencephalon*.

Mesencephalon. The *tectum mesencephali* is the most prominent brain structure in *Cichla piquiti*. In early developmental stages (< 200 mm SL), the compact arrangement of the brain within the neurocranium results in a slightly flattened dorsal surface, with a height comparable to that of the dorsal surfaces of the *telencephalon* and *cerebellum* (Fig. 5C). In adults advanced developmental stages (> 200 mm SL), the dorsal surface becomes concave as the structure assumes an oval shape. In the lateral view, the *tectum mesencephali* is diagonally inclined, with the anterior region positioned ventrally relative to the posterior region (Fig. 5D).

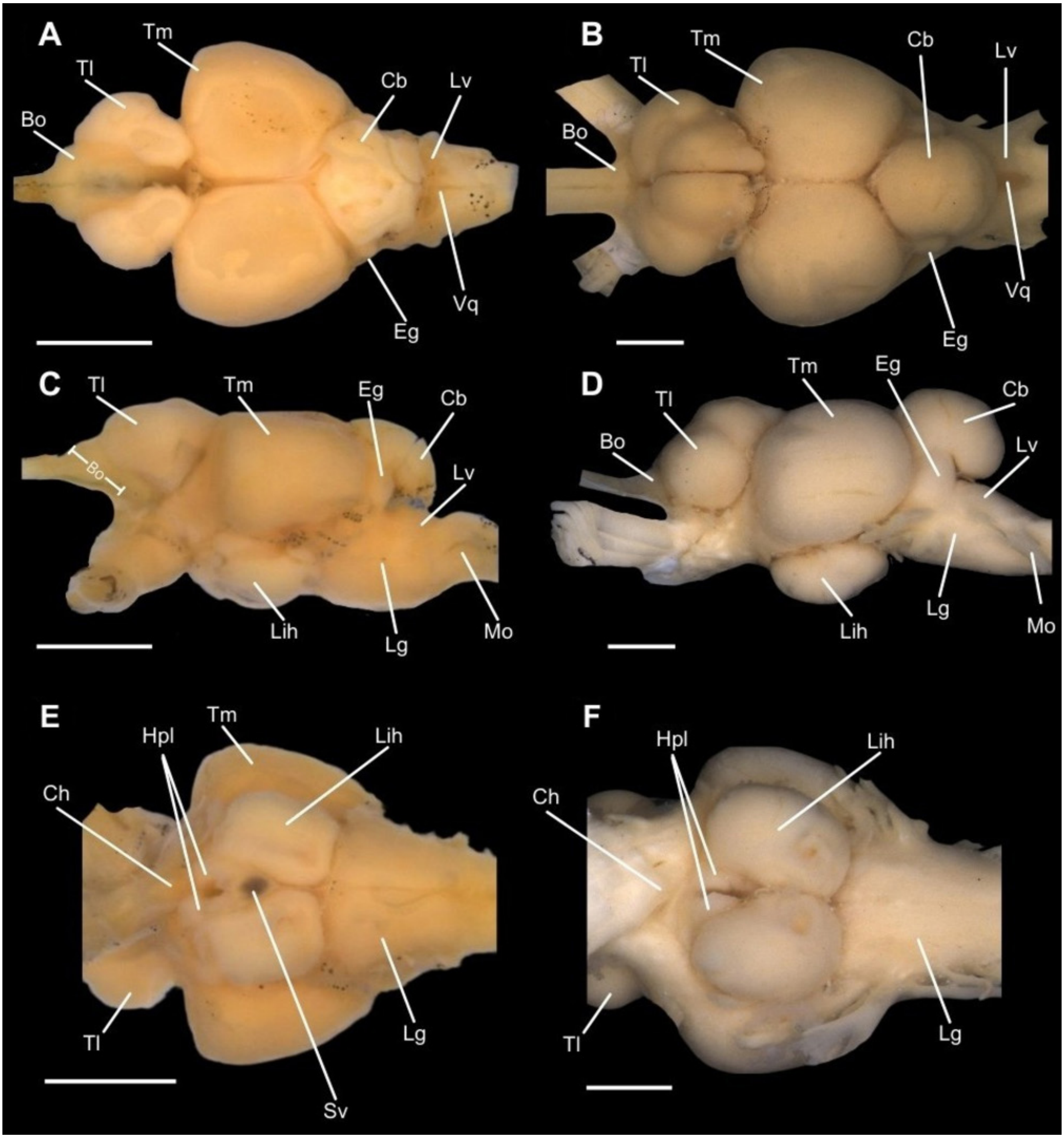

FIGURE 5 | Brain of *Cichla piquiti*. (**A**, **C**, **E**: UNT 4543_1; 58.30 mm SL); (**B**, **D**, **F**: UNT 22471_1; 270.50 mm SL); **A.** Dorsal of early development stage; **B.** Dorsal anterior region of an advanced development stage; **C.** Lateral anterior region of early development stage; **D.** Lateral anterior region of an advanced development stage. Abbreviations: Bo, *bulbus olfactorius*; Cb, *cerebellum*; Ch, *chiasma opticum*; Eg, *eminentia granularis*; Hpl, *hypothalamus*; Lg, *lobus gustativus*; Lih, *lobus inferior hypothalami*; Lv, *lobus vagi*; Mo, *medulla oblongata*; Sv, *saccus vasculosus*; Tl, *telencephalon*; Tm, *tectum mesencephali*; Vq, *Ventriculus quartus*. Scale bars = 2 mm.

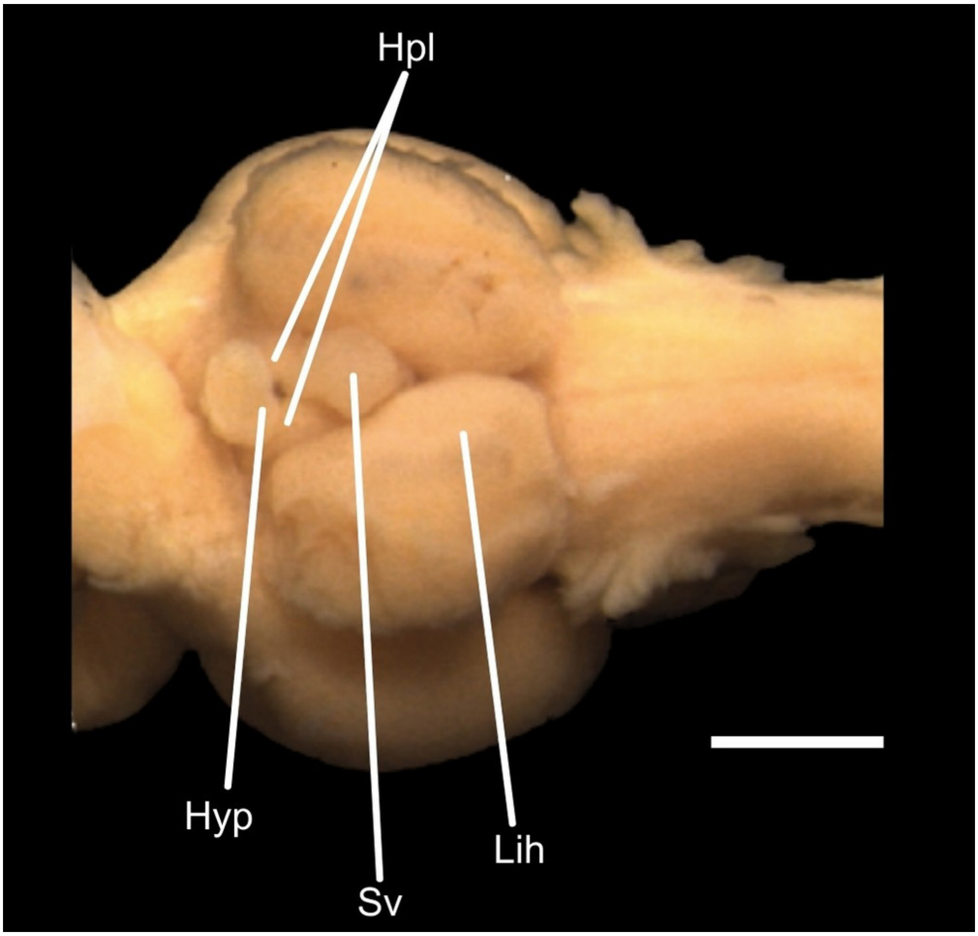

FIGURE 6 | Ventral median region of the brain of early development stage *Cichla piquiti* (UNT 6287_2; 97.00 mm SL. Abbreviations: Hpl, *hypothalamus*; Hyp, *hypophysis*; Lih, *lobus inferior hypothalami*; Sv, *saccus vasculosus*. Scale bar = 2 mm.

***Rhombencephalon*, *metencephalon* and *myelencephalon*.** The *cerebellum* exhibited the greatest morphological variation between early and advanced developmental stages specimens. At early developmental stages (< 200 mm SL), it is compact, with a height of approximately two-fifths of its total length. The lateral margins show two indentations: the first corresponds to a groove formed by an elevated fold, and the second to a lateral compression (Figs. 7A, D). In some Class 1 juveniles (50–100 mm SL), a slight lateral compression is still visible in dorsal view (Fig. 7B). In fully developed specimens, the *cerebellum* becomes oval, with height reaching approximately four-fifths of its total length, and its anteroventral margin connects to the *lobus gustativus* (Figs. 7C, F).

Ontogenetic and population-based differences were also observed. All Araguaia specimens, including Classes 2, 3, and 7 (132–370 mm SL), presented a fully developed *cerebellum*. In Furnas, all individuals except one Class 3 (171 mm SL) specimen exhibited a structure still in development. In Tocantins, only two Class 1 individuals displayed the *cerebellum* in development; from 81 mm SL onward, specimens showed only slight lateral compression, and above 90 mm SL, all individuals had a fully developed *cerebellum*.

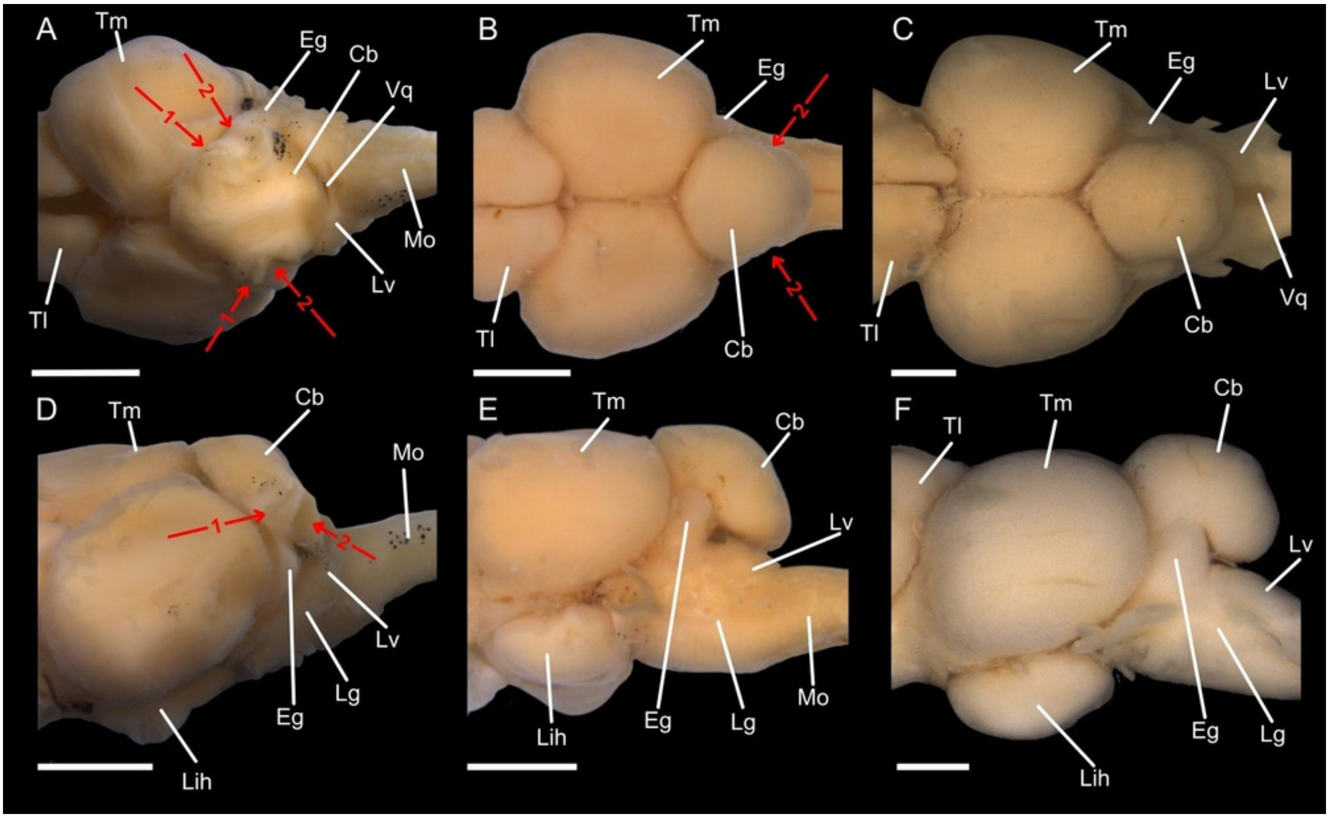

FIGURE 7 | Brain of *Cichla piquiti* (**A**, **D**: UNT 4543_1; 58.30 mm SL); (**B**, **D**: UNT 11327_3; 96.60 mm SL); (**C**, **F**: UNT 22471_1; 270.50 mm SL); arrow 1 = first indentation and arrow 2 = second indentation. **A.** Dorsal view, posterior region of the brain of early development stage rotated 45° to the left; **B.** Dorsal view, posterior region of the brain of early development stage rotated 45° to the left; **C.** Dorsal view, posterior region of the brain of advanced development stage; **D.** Lateral view, posterior region of the brain of early development stage; **E.** Lateral view, posterior region of the brain of a non-reproductive early development stage; and **F.** Lateral view, posterior region of the brain of an advanced development stage. Abbreviations: Cb, *cerebellum*; Eg, *eminentia granularis*; Lg, *lobus gustativus*; Lih, *lobus inferior hypothalami*; Lv, *lobus vagi*; Mo, *medulla oblongata*; Tl, *telencephalon*; Tm, *tectum mesencephali*; Vq, *Ventriculus quartus*. Scale bars = 2 mm.

The *lobus facialis* and *lobus trigeminalis* are inconspicuous. The only structures clearly distinguishable from the *lobus gustativus* are the *lobus vagi* and the *eminentia granularis*. The *eminentia granularis* is oval, with its height approximately twice its length, and is located laterally on the anteroventral region of the *cerebellum* in both developmental stages, but is more conspicuous advanced stages (Figs. 8B–D). The *lobus vagi* is positioned ventral to the *cerebellum*. In early stages, the *Ventriculus quartus* is scarcely visible in the dorsal median region of the *lobus gustativus* (Fig. 8C), but becomes more distinct in advanced developmental stages (> 200 mm SL) (Fig. 8D).

In the ventral region of the *lobus gustativus*, cranial nerves are observed in an anteroposterior sequence: *nervus oculomotorius*, *nervus trochlearis*, *nervus trigeminus*, *nervus abducens*, *nervus facialis*, *nervus octavus*, *nervus glossopharyngeus*, *nervus vagus*, *nervus lineae lateralis anterior*, and *nervus lineae lateralis posterior*. With the exception of the *nervus abducens*, which emerges ventrally from the *metencephalon*, the *nervus olfactorius* (emerging from the anterior region of the *telencephalon*) and the *nervus opticus* (emerging ventrally from the *mesencephalon*), all other cranial nerves emerge laterally from the *metencephalon*.

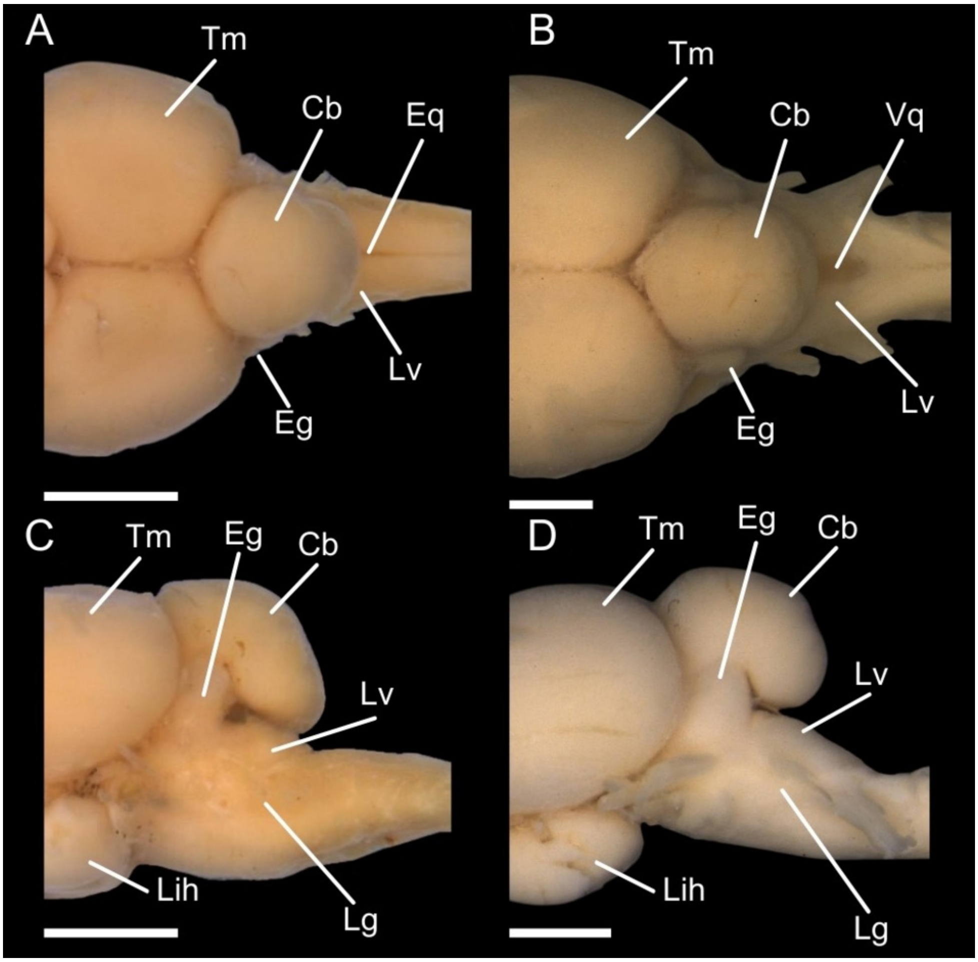

FIGURE 8 | Posterior regions of the brain of *Cichla piquiti*. (**A**, **C**: UNT 11327_3; 96.60 mm SL); (**B**, **D**: UNT 22471_1; 270.50 mm SL); **A.** Dorsal view of early development stage; **B.** Dorsal view of an advanced development stage; **C.** Lateral view of early development stage; **D.** Lateral view of an advanced development stage. Abbreviations: Cb, *cerebellum*; Eg, *eminentia granularis*; Lg, *lobus gustativus*; Lih, *lobus inferior hypothalami*; Lv, *lobus vagi*; Mo, *medulla oblongata*; Tl, *telencephalon*; Tm, *tectum mesencephali*; Vq, *Ventriculus quartus*. Scale bars = 2 mm.

Morphological variation was evident between juveniles in early post-embryonic stages (Classes 1 and 2; 50–150 mm SL), larger juveniles, and adults (Classes 2–7; 150–400 mm SL), particularly in the *telencephalon*, *lobus inferior hypothalami*, and *cerebellum*. Among these structures, the *cerebellum* develops first, although some fully developed specimens still exhibited a slight lateral compression. Development of the *lobus inferior hypothalami* progressed sequentially, with the *telencephalon* reaching maturity finally.

Population-level differences were also observed. Furnas specimens exhibited delayed brain development compared with Tocantins specimens. The only Furnas individual with a fully developed brain measured 171 mm SL; all other individuals between 90–109 mm SL retained the three structures in development, and one specimen at 116 mm SL presented a developed *cerebellum* but with subtle lateral compression. In contrast, Tocantins specimens attained full brain development at smaller sizes. Only three individuals (46–81 mm SL) exhibited three brain structures still under development. In specimens larger than ~81 mm SL, developmental differences were restricted to the *telencephalon*, which remained incompletely developed in some individuals up to 100 mm SL. From approximately 87 mm SL onward, all examined specimens exhibited fully developed brains.

Quantitative analysis. Encephalization quotient (E_Q). The mean Encephalization Quotient (E_Q) values for the sampled localities were: Araguaia = 1.09, Furnas = 1.02, and Tocantins = 0.97. Linear regression analysis revealed a significant positive correlation between body mass and brain size ($p = 0.001$, adjusted $R^2 = 0.67$), indicating that brain size and growth are strongly associated with body mass (Fig. 9A). Analysis of variance (ANOVA) showed no statistically significant differences in E_Q among the three localities ($p = 0.0652$; Fig. 9B). Similarly, a Student's *t*-test revealed no significant differences in E_Q between males and females ($p = 0.1945$).

Relative size of brain structures. The volumes estimated using the half-ellipsoid method are presented in Tab. 2, along with the corresponding height, width, and length measurements of each structure. It should be noted that the calculated volumes (mm^3) do not represent the exact anatomical volumes, as the formula assumes an ideal ellipsoidal shape. Since not all brain structures conform precisely to this geometry, the resulting values should be interpreted as approximations.

The proportional representation of brain structures was generally similar among populations (Fig. 10). The *tectum mesencephali* was consistently the largest structure, while the *bulbus olfactorius* and *eminentia granullaris* remained the smallest across all localities.

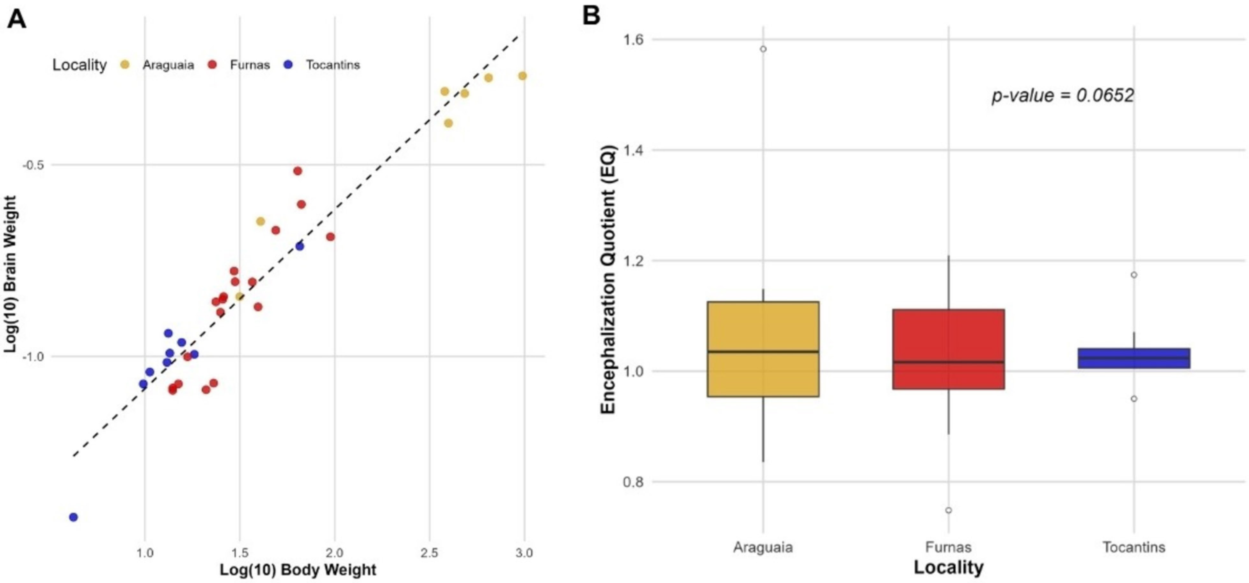

FIGURE 9 | **A.** Linear regression between brain weight and body weight. Variables were log10 transformed; **B.** Analysis of variance comparing the Encephalization Quotient (E_Q) among the three localities.

TABLE 2 | Data on the volumes obtained for each of the examined specimens, where, F: Female; M: Male; SL: Standard length (mm); BW: Body weight (g); EW: Brain weight (g); VE: *Encephalon* volume (mm^3); VBO: Volume of the *bulbus olfactorius* (mm^3); VTM: Volume of the *tectum mesencephali* (mm^3); VCB: Volume of the *cerebellum* (mm^3); VMO: Volume of the *medulla oblongata* (mm^3); VLG: Volume of the *lobus gustativus* (mm^3); VLIH: Volume of the *lobus inferior hypothalami* (mm^3); VEG: Volume of the *eminentia granullaris* (mm^3); and Lam: Number of lamellae in the nasal fossa.

Specimen	Locality	Sex	SL	BW	EW	VE	VBO	VTL	VTM	VCB	VMO	VLG	VLIH	VEG	Lam
UNT17443_1	Araguaia	F	132.00	40.70	0.2250	314.0498	0.6681	34.9685	106.0810	9.7995	5.6586	13.2756	11.6919	0.5414	21
UNT22471_1	Araguaia	F	270.50	647.20	0.5331	866.8127	1.7956	69.8897	166.7444	26.8029	13.0201	41.1602	32.2996	2.7689	24
UNT22471_2	Araguaia	M	370.50	976.70	0.5392	706.5639	0.9027	58.3530	133.5272	18.2135	8.3747	27.8535	26.4143	2.1584	25
UNT22472_2	Araguaia	M	250.00	483.80	0.4852	643.9162	2.0461	59.7834	145.4941	25.9723	11.5899	29.8383	23.7408	2.3792	21
UNT22472_3	Araguaia	F	260.50	397.60	0.4059	601.1100	1.9873	39.7147	140.9538	16.1983	11.0431	24.3979	19.5694	1.2422	26
UNT22472_5	Araguaia	M	260.50	380.00	0.4912	771.2062	2.3943	59.1339	154.0825	24.1190	9.2942	24.8764	25.5258	1.7250	25
UNT2397_1	Araguaia	M	124.30	31.57	0.1432	233.8236	0.3868	15.3822	59.1278	10.4922	2.5141	15.6616	9.8241	0.4717	16
UNT22487_1	Furnas	M	171.70	95.00	0.2051	360.8521	0.7176	18.4394	81.3679	10.6212	3.6547	15.6693	12.7070	1.3759	15
UNT22487_2	Furnas	M	116.20	25.00	0.1304	250.2207	0.4738	11.6626	64.1395	4.7343	5.6138	13.1639	6.4646	0.3725	16
UNT22487_3	Furnas	M	92.40	14.00	0.0827	181.0442	0.3198	11.9274	52.4350	4.3292	2.0701	12.5734	5.7042	0.4154	14
UNT22487_4	Furnas	F	97.40	15.00	0.0848	138.9585	0.5324	12.8472	50.2478	3.7298	2.0780	7.7134	3.7788	0.6261	15
UNT22487_5	Furnas	F	90.10	14.00	0.0816	166.5404	0.1689	9.7745	48.4689	2.1933	2.0202	7.2274	4.0439	0.3047	14
UNT22487_6	Furnas	M	105.70	21.00	0.0819	149.6664	0.1269	9.3760	45.1096	4.9700	5.1044	9.2090	3.6452	0.3201	14
UNT22487_7	Furnas	M	109.90	23.00	0.0852	156.3202	0.5851	7.0204	41.7917	3.9484	5.2582	9.9217	4.5229	0.2081	15
UNT11327_1	Tocantins	F	81.40	9.80	0.0848	178.7991	0.9324	12.6456	49.8993	6.5702	2.0597	7.4576	6.0029	0.2940	15
UNT11327_2	Tocantins	M	100.00	18.21	0.1013	228.9603	0.4163	16.8993	53.8943	6.6648	5.1005	11.5312	6.9151	0.4697	17
UNT11327_3	Tocantins	F	96.60	15.61	0.1088	217.7280	0.7655	17.0919	57.3227	7.4582	2.9101	10.4848	8.0324	0.3280	16
UNT18940_1	Tocantins	M	155.30	65.42	0.1938	324.8040	1.1488	30.3841	112.4101	14.4622	5.7058	15.5893	13.3523	0.7424	22
UNT20100_1	Tocantins	M	87.00	13.28	0.1149	133.6407	0.6518	12.3574	47.1834	6.5024	2.8132	10.5683	8.3157	0.4312	16
UNT20100_2	Tocantins	M	87.90	13.06	0.0965	181.3640	0.6907	14.7925	44.8749	6.1451	3.5338	9.9700	7.0380	0.4208	14
UNT20100_3	Tocantins	M	81.30	10.61	0.0911	164.4040	0.6903	12.1274	40.0302	7.0621	3.0811	7.4965	5.6025	0.5591	15
UNT4543_1	Tocantins	M	58.30	4.20	0.0381	91.4663	0.6126	8.2435	29.4167	5.2747	1.5413	6.8891	3.9618	0.1597	12
UNT6287_1	Tocantins	F	87.10	13.52	0.1020	186.9333	0.8873	14.8906	57.2802	5.4529	2.8843	8.0338	6.4636	0.2929	15
UNT6287_2	Tocantins	M	97.10	16.43	0.7800	174.1208	1.0412	13.4234	38.6533	10.4244	3.6496	11.0913	10.0510	0.4415	16
UNT23004_1	Furnas	F	137.40	47.90	0.1793	302.6809	0.4636	13.0364	82.2626	7.5787	4.9821	17.6945	9.7248	0.6316	18
UNT23004_2	Furnas	F	150.70	63.85	0.3047	508.9405	0.3775	21.2288	101.2495	18.1485	7.9827	24.1430	12.2760	2.1437	17
UNT23004_3	Furnas	F	108.90	23.65	0.1388	265.0994	0.5117	14.7297	61.2870	8.8259	3.6677	12.4148	7.6134	0.6287	15
UNT23004_4	Furnas	M	115.60	29.85	0.1566	274.0925	0.6130	16.9328	71.3619	9.0623	2.1110	11.6522	7.5941	0.6812	14
UNT23004_5	Furnas	M	151.40	66.70	0.2493	441.4521	0.8842	23.8006	112.6752	10.7115	5.2572	11.8835	15.4137	0.6532	16
UNT23004_6	Furnas	F	135.50	48.90	0.2133	306.7103	0.5884	15.6894	82.1979	8.0939	4.4517	15.8642	12.9390	0.7192	15
UNT23004_7	Furnas	M	124.00	36.81	0.1564	287.0161	0.5894	11.7631	59.8831	8.3902	4.6528	6.1632	10.4794	0.7328	15
UNT23004_8	Furnas	M	128.00	39.45	0.1347	253.8859	0.5591	14.2173	61.4636	11.2000	2.1751	11.6995	6.1272	0.9455	15
UNT23004_9	Furnas	F	114.40	29.50	0.1670	241.7730	0.3928	13.6543	50.6332	6.6960	2.9928	10.4543	9.6191	0.6738	13
UNT23004_10	Furnas	F	112.70	25.95	0.1432	230.7820	0.5409	13.3581	52.7963	6.1773	3.0516	9.5426	7.6904	0.2706	15
UNT23004_11	Furnas	M	112.90	25.72	0.1410	278.6862	0.3617	12.4490	66.2134	7.0521	2.7457	9.1057	5.7072	0.5098	16
UNT23004_13	Furnas	M	95.70	16.77	0.0998	201.4605	0.3508	11.3077	47.8728	5.3933	2.1433	12.0324	6.3116	0.9882	15

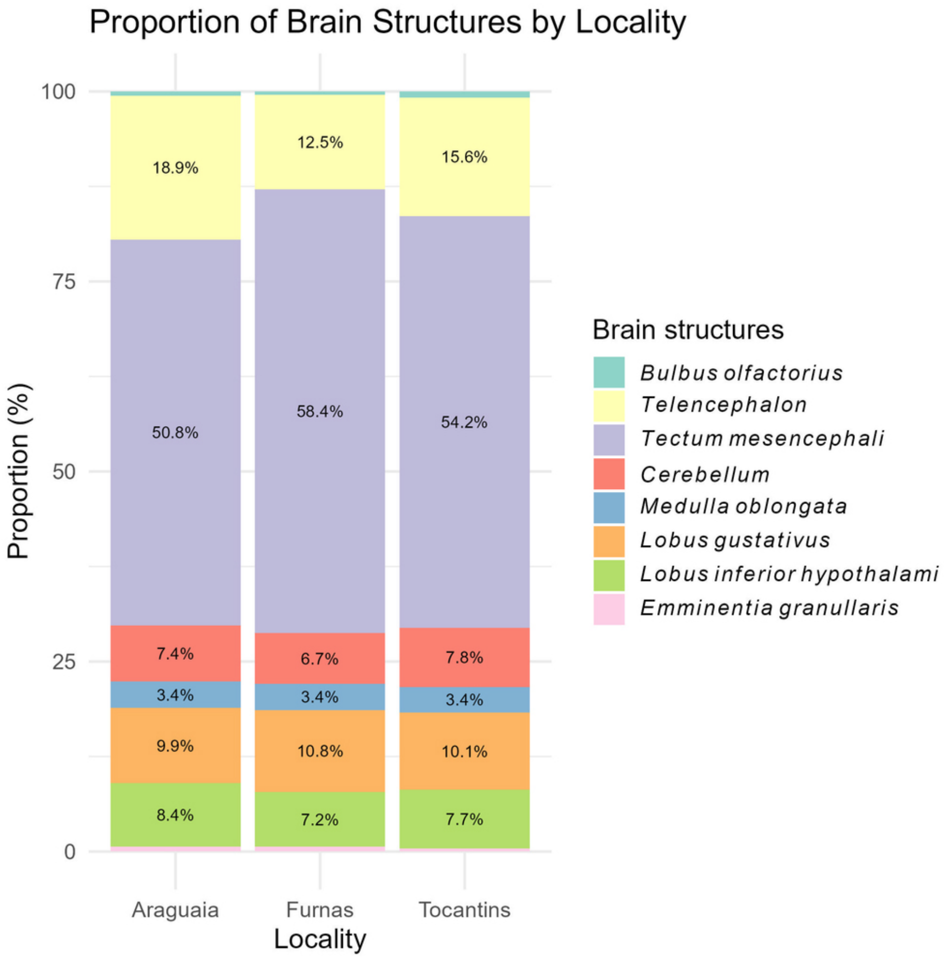

FIGURE 10 | Proportion of brain structure volumes relative to total brain volume.

Among the regions that showed noticeable variation, the *telencephalon* differed the most, corresponding to 18.9% in Araguaia, 12.5% in Furnas, and 15.6% in Tocantins. The *tectum mesencephali* also exhibited moderate variation, ranging from 50.8 to 58.4%. The remaining structures, including the *cerebellum*, *lobus gustativus*, *medulla oblongata*, and *lobus inferior hypothalami*, showed only minor fluctuations among populations.

Population analysis. The Principal Component Analysis (PCA) revealed differences in brain structure among the three localities, with the formation of three groups in the multivariate space (Fig. 11). Larger volumes of the *tectum mesencephali*, *telencephalon*, *lobus inferior hypothalami*, and *cerebellum* were associated with Araguaia, with PC1 accounting for 75.81% of the total variation. PC2 explained 8.68% of the variation, with higher volumes of the *medulla oblongata* and *lobus gustativus* in Furnas, whereas a larger *bulbus olfactorius* volume was associated with Tocantins.

The second PCA, restricted to Furnas and Tocantins specimens, revealed population-level differences only along PC2, which explained 18.23% of the variance (Fig. 12). In this analysis, volume of the *bulbus olfactorius* was positively associated with Tocantins, whereas *medulla oblongata* and *lobus gustativus* volumes were associated with Furnas.

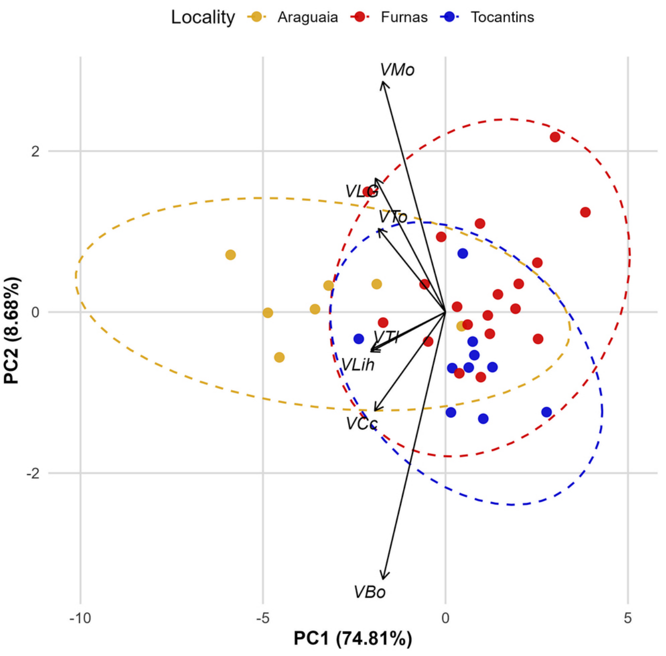

FIGURE 11 | Results of a Principal Component Analysis (PCA) conducted to investigate variation in brain structure among specimens from the three sampled localities. VTo = volume of *tectum mesencephali*; VTl = volume of *telencephalon*; VBo = volume of *bulbus olfactorius*; VCc = volume of *cerebellum*; VLih = volume of *lobus inferior hypothalami*; VLG = volume of *lobus gustativus*; and VMo = volume of *medulla oblongata*.

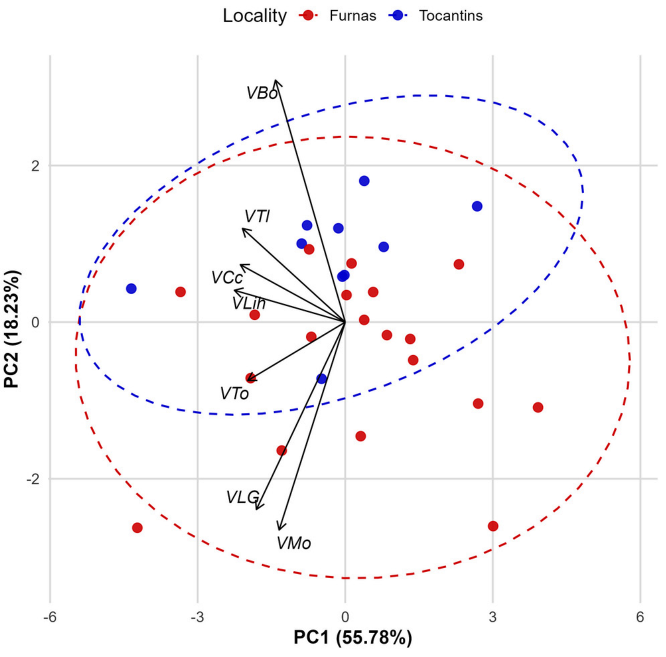

FIGURE 12 | Results of a Principal Component Analysis (PCA) conducted to investigate variation in brain structures among specimens from Tocantins and Furnas. VTo = volume of *tectum mesencephali*; VTl = volume of *telencephalon*; VBo = volume of *bulbus olfactorius*; VCc = volume of *cerebellum*; VLih = volume of *lobus inferior hypothalami*; VLG = volume of *lobus gustativus*; and VMo = volume of *medulla oblongata*.

These results suggest that variation in *telencephalon*, *cerebellum*, *lobus inferior hypothalami*, and *tectum mesencephali* volumes is more strongly influenced by fish size than locality. In both PCA analyses, sex was included as a factor; however, no clustering was observed, with males and females showing extensive overlap in the distribution of data.

The multivariate distances differed significantly among the three sampled localities (PERMANOVA: $R^2 = 0.4206$; $p < 0.01$); when sex was considered, no significant difference was found ($R^2 = 0.00819$; $p = 0.884$). No significant difference in data dispersion was detected among localities (PERMDISP: $p = 0.2960$). Restricting the analysis to Furnas and Tocantins, localities differed with marginal statistical significance (PERMANOVA: $R^2 = 0.0959$; $p = 0.05$), with no significant differences in data dispersion between the two localities (PERMDISP: $p = 0.1120$).

The number of lamellae (*lamellae fossa nasalis*) differed significantly among localities (Kruskal-Wallis: $p < 0.0005$). Differences were found between Araguaia and Furnas (Dunn post-hoc: $p = 0.0003$) and between Araguaia and Tocantins ($p = 0.015$), with a higher number of lamellae observed in the Araguaia population (Fig. 13).

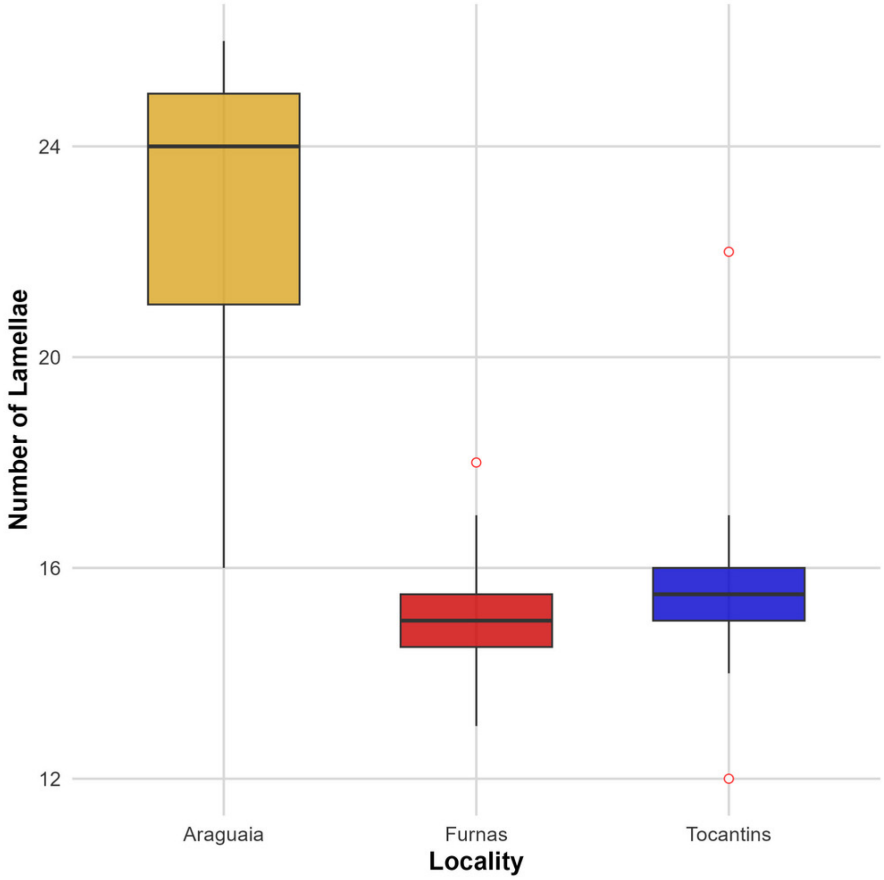

FIGURE 13 | Boxplot comparing the number of *lamellae fossa nasalis* among the three sampled localities.

DISCUSSION

Our analyses provide the first description of the brain of *Cichla piquiti* and its post-larval (*i.e.*, juvenile and adult) developmental changes, revealing a conservative neuroanatomical pattern, particularly in the *telencephalon*, *lobus inferior hypothalami*, and *cerebellum*. Quantitative assessments further revealed neuro-morphological differences among populations from distinct localities. The study also presents data on the Encephalization Quotient (E_Q) of *C. piquiti*, offering insights into the species' cognitive capacities and behavioral performance in novel environments.

The post-larval morphological stages and statistical analyses revealed a developmental pattern in which the *rhombencephalon* structures develop first, followed by the *mesencephalon* and finally, the *prosencephalon*, a sequence observed in most vertebrates (Nieuwenhuys, 1966; Meek, Nieuwenhuys, 1998). The *rhombencephalon* houses structures central to agility, respiration, and motor coordination, such as the *cerebellum* and *medulla oblongata*, which may be particularly important during early developmental stages, when survival and feeding efficiency are critical (Finger, Morita, 1985; Morita, Finger, 1985). Moreover, analyses of ossification patterns in some fishes show that the first bones to develop are functionally related to feeding and respiration, as well as the branchial arches (*e.g.*, Marinho (2023) for *Moenkhausia pittieri* Eigenmann, 1920 (= *Makunaima pittieri*). These structures are coordinated by stimuli originating from the *rhombencephalon*, from which the nerves *nervus trigeminus*, *nervus abducens*, *nervus facialis*, *nervus glossopharyngeus*, and *nervus vagus* project (Meek, Nieuwenhuys, 1998; Striedter, 2005).

The relative proportions of brain structures in *Cichla piquiti* are notably distinct, with the *tectum mesencephali* comprising the largest portion of brain volume (~54–58%), in contrast to the *bulbus olfactorius*, which represents less than 1%. This disproportion suggests that vision plays a dominant role in the sensory processing of these fish, whereas their olfactory system is relatively undeveloped. Species of *Cichla* are visually oriented predators that inhabit the littoral zones of aquatic environments (Fernandes *et al.*, 2025), where conditions favor light incidence and habitat complexity (Winemiller *et al.*, 2021; Andrade, Pelicice, 2022). In such habitats, vision becomes an especially efficient sensory modality, as low turbidity enhances the availability of visual cues, a pattern also observed in other neotropical cichlids (Oliveira, Graça, 2020, 2024; Leão-Reis *et al.*, 2025). Furthermore, *C. piquiti* displays polychromatism, exhibiting changes in body and fin coloration throughout its lifespan (Pelicice *et al.*, 2022). Given that cichlids are tetrachromatic (Carleton, Kocher, 2001; Dalton *et al.*, 2010), it is likely that *C. piquiti* relies on vision not only for foraging but also for social interactions, including intraspecific communication, mate choice, individual recognition, and territory defense or acquisition (Siepen, Caprona, 1986; Carleton *et al.*, 2008; Dalton *et al.*, 2010).

No sexual dimorphism was observed in the brain morphology of the analyzed specimens, considering both the size and the shape of structures. Additionally, no correlations were found between the brain developmental rates and its respective structures across sexes. In *Cichla piquiti*, maturity is similar between males and females (FMP, unpub. data), and reproductive behaviors such as nest building and offspring care are shared by both sexes (Andrade, Pelicice, 2022), indicating that males and females are subject to similar selective pressures on brain function. Differences in the growth rate of brain structures have been reported in *Microglanis garavelloi* Shibatta & Benine, 2005, where females' brains grow faster, as they reach maturity at smaller sizes than males, thus exhibiting faster physiological and morphological maturation (Abrahão *et al*., 2021).

No statistically robust differences were found in the relative size of brain structures among the three sampled populations. However, the Principal Component Analyses formed three distinct groups. Furthermore, when qualitatively assessed, the post-embryonic development of the *telencephalon*, *lobus inferior hypothalami*, and *cerebellum* appeared delayed in the Furnas specimens, as only one individual (171 mm SL) exhibited all brain structures fully developed. Kotrschal *et al*. (2017) reported strong correlations between the volume of specific brain structures and evolutionary pressures, showing that the presence of predators and competitors influenced the relative size of brain structures in isolated populations of *Poecilia reticulata* Peters, 1859. Considering this, the reduced number of predators or competitors for juvenile *Cichla piquiti* in the invaded ecosystem may be related to the delayed development of these structures. In the Furnas Reservoir, only four potential predators or competitors have been recorded: *Salminus hilarii* Valenciennes, 1850; *Hoplias malabaricus* (Bloch, 1794); *Hoplias intermedius* (Günther, 1864); and *Hoplerythrinus unitaeniatus* (Spix & Agassiz, 1829) (Nobile *et al*., 2024), a number considerably lower than the predator diversity reported in the Tocantins and Araguaia rivers (Chamon *et al*., 2022). It is important to note that this hypothesis warrants further investigation, as multiple factors (*e.g*., fish size, food deprivation) may contribute to variation in brain structure.

Our findings support the hypotheses that individuals from populations exposed to distinct environmental conditions exhibit modifications in brain morphology. Differences in brain morphology of *Cichla piquiti* under distinct environmental conditions were observed, as well as a developmental pattern consistently present in juveniles, involving modifications in the *telencephalon*, *lobus inferior hypothalami*, and *cerebellum*. This pattern of structural modifications follows a posteroanterior sequence, indicating that the posterior regions are more relevant during the early developmental stages. It is important to note that statistical differences among populations were influenced by allometric effects related to specimen size, since the exclusion of adult individuals (Araguaia population) reduced the robustness of statistical significance. Nevertheless, qualitative differences among groups were still evident. Future studies with larger sample sizes, encompassing different species and a broader range of environments, are essential to further clarify the evolutionary processes underlying the Central Nervous System diversification in fishes.

The mean Encephalization Quotients (E_Q) of *Cichla piquiti* were 1.09, 1.02, and 0.97 for specimens from Araguaia, Furnas, and Tocantins, respectively; these values exceed the average value of 0.46 estimated for Actinopterygii (Triki *et al*., 2021). High E_Q values are usually associated with small-bodied fishes, because the relationship between brain size and body size in fishes follows a negative allometric pattern, relative brain size decreases as body size increases. Consequently, smaller species tend to exhibit relatively larger brains (higher EQ) than larger-bodied species (Bauchot *et al*., 1977; Peñaherrera Aguirre *et al*., 2021; Triki *et al*., 2021); however, *Cichla piquiti* is a large-sized predator (*i.e*., first maturity between 30 and 40 cm, and maximum total length at 62 cm; FMP, unpub. data). E_Q is strongly related to an organism's cognitive performance, reflecting how the organism responds to environmental cues. Although the use of E_Q to estimate cognitive performance in endothermic taxa has been criticized, it has proven reliable in fishes (Triki *et al*., 2021). Buechel *et al*. (2018) and Triki *et al*. (2022b) associate cognitive performance (defined as the ability to acquire, process, and retain information and act upon it (Shettleworth, 2001) with relative brain size. Brain mass relative to body size reflects the energetic demand of the central nervous system compared to other systems (Jerison, 1973, 1985; Triki *et al*., 2018, 2021, 2022a,b; Peñaherrera Aguirre *et al*., 2021). Some studies suggest that using E_Q alone to assess cognitive investment should be approached with caution, since certain brain regions may have functions more critical for specific organisms and therefore are larger (Peñaherrera Aguirre *et al*., 2021; Triki *et al*., 2021). For example, Elasmobranchii have been reported with E_Q values above 1.0 (Lisney, Collin, 2006); however, a substantial proportion of their brain volume is composed of the *bulbus olfactorius* and *cerebellum*, regions primarily associated with sensory processing and motor coordination rather than integrative or higher-order cognitive functions (Ebbesson, Braithwaite, 2012). In contrast, considering that more than half of *C. piquiti* brain consists of the *telencephalon* and *tectum mesencephali* (Fig. 10), structures fundamental to cognitive processing, brain size can be translated into cognitive performance.

Moreover, some studies indicate that high E_Q values are found in generalist species, both in feeding and reproduction; the ability to adjust diet in response to available resources in a different environment, or to reproduce in a novel habitat, reflects reversal learning enabled by cognitive processes (Sol *et al*., 2005a,b; Ebbesson, Braithwaite, 2012; Pike *et al*., 2018). The cleaner wrasse (*Labroides* sp.) has been used as a model for cognitive studies in fishes, showing high rates of learning and feeding innovations that are associated with relative brain size (Bshary, Grutter, 2002; Wismer *et al*., 2014; Triki *et al*., 2018). Several authors have reported the remarkable success of *Cichla* species as invaders of new environments, characterized by high reproductive rates, and behavioral and ecological adaptations (Neal *et al*., 2017; Khaleel *et al*., 2021; Franco *et al*., 2022a,b; Gaspar *et al*., 2024). It is therefore reasonable to suppose that this invasive success is facilitated by some phenotypic plasticity associated with cognitive performance. In this context, our results support the hypothesis that the phenotypic plasticity of *C. piquiti* may be related to its high E_Q values, thereby enabling the occupation of different ecological niches in habitats under selective pressures that are relatively distinct from those in its native range.

It is important to emphasize that the E_Q of most fish species remains unknown, and therefore, our inferences regarding the cognitive capacity of *Cichla piquiti* are still preliminary. The lack of data on relative brain size in other fish species hampers comparisons between the E_Q of species with high invasion success *vs.* those with lower levels of phenotypic plasticity. Nevertheless, we highlight the risks associated with the introduction of *C. piquiti* into non-native environments, since its high adaptability, probably driven by cognitive performance, confers high invasiveness. Numerous studies have documented severe negative effects caused by the introduction of *Cichla* species, including native population declines, local extinctions, and ecosystem disruption (Pelicice, Agostinho, 2009; Neal *et al*., 2017; Sharpe *et al*., 2017; Valverde *et al*., 2020; Franco *et al*., 2021; Leal *et al*., 2021; Franco *et al*., 2022a,b).

In conclusion, our study provides the first comprehensive description of the brain of *Cichla piquiti*, revealing a conserved neuroanatomical pattern throughout post-larval development and highlighting how environmental conditions may influence neuro-morphological variation among populations. The developmental sequence observed in juveniles, coupled with the predominance of visual-processing structures and the high E_Q values recorded for this species, suggests that cognitive performance and phenotypic plasticity play important roles in its ecological success, particularly in invaded environments. Although statistical differences among populations were affected by allometric variation, qualitative patterns remained evident, indicating that environmental pressures may shape the development of key brain regions. Taken together, these findings advance our understanding of Central Nervous System diversification in Neotropical fishes and underscore the ecological risks associated with the introduction of *C. piquiti*, whose cognitive capacity and adaptability may enhance its invasive potential.

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AUTHORS' CONTRIBUTION

Pedro Henrique Marinho-Nunes: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing-original draft, Writing-review and editing.

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ETHICAL STATEMENT

All procedures were conducted in compliance with ethical and legal requirements, under approval of the Ethics Committee on Animal Use and Experimentation of the Universidade Federal de Tocantins (CEUA/UFT, protocol 23.101.001.818/2019–25) and with collection authorized by ICMBio (license number 270453; responsible researcher: Dr. Paulo H. F. Lucinda).

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author, upon reasonable request.

AI STATEMENT

The authors state that *Copilot* (version GPT-5, Smart Mode) was employed for grammar checking of the manuscript.

COMPETING INTERESTS

The authors declare no competing interests.

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