



UNIVERSIDADE ESTADUAL PAULISTA
“JÚLIO DE MESQUITA FILHO”
Câmpus de São José do Rio Preto

Arturo Angulo Sibaja

**Gross brain morphology of the Loricariinae (Siluriformes:
Loricariidae): Comparative anatomy, ecological implications and
phylogenetic analysis**

São José do Rio Preto
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Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Biologia Animal, junto ao Programa de Pós-Graduação em Biologia Animal, do Instituto de Biociências, Letras e Ciências Exatas da Universidade Estadual Paulista “Júlio de Mesquita Filho”, Câmpus de São José do Rio Preto.

Financiadora: PAEC OEA-GCUB / MICITT – PED-017-2015-1

Orientador: Prof. Dr. Francisco Langeani Neto

São José do Rio Preto
2019

A594g

Angulo, Arturo

Gross brain morphology of the Loricariinae (Siluriformes: Loricariidae): Comparative anatomy, ecological implications and phylogenetic analysis / Arturo Angulo. -- São José do Rio Preto, 2019
227 f. : il., tabs., fotos + 1 CD-ROM

Tese (doutorado) - Universidade Estadual Paulista (Unesp), Instituto de Biociências Letras e Ciências Exatas, São José do Rio Preto
Orientador: Francisco Langeani

1. Zoologia. 2. Ecologia. 3. Peixes de água doce. 4. Cascudo (Peixe). 5. Cérebro. I. Título.

Sistema de geração automática de fichas catalográficas da Unesp. Biblioteca do Instituto de Biociências Letras e Ciências Exatas, São José do Rio Preto. Dados fornecidos pelo autor(a).

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Financiadora: PAEC OEA-GCUB / MICITT –
PED-017-2015-1

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12 de Fevereiro 2019

ACKNOWLEDGEMENTS

To my family, friends, colleagues and teachers (in Brazil and Costa Rica), who supported me and provided me all the necessary tools to successfully complete this academic phase of my life. To Carolina Méndez for her constant support, patience and love in the distance.

To Mark Sabaj, Mariangeles Arce (ANSP), Jonathan Armbruster, Dave Werneke (AUM), Armando Ortega (IMCN), Lucia Rapp Py-Daniel (INPA-ICT), Claudio de Oliveira (LBP), Carlos Lucena, Alejandro Londoño (MCP), Raphael Covain (MHNG), Hernan Ortega (MUSM), Aléssio Datovo, Osvaldo Oyakawa (MZUSP), Carla Pavaneli, Sandra Regina (NUP), Flávio Bockmann, Hertz Santos (LIRP), Myrna López, Ana Ramírez (UCR), Luiz Malabarba, Juliana Wingert (UFRGS), Mónica Rodríguez (UFV), Jeff Williams (USNM), Francisco Severo, Fernando Carvalho (ZUFMS) and Marcelo Loureiro (ZVCP) for the loan/donation of specimens for dissection.

To the authorities and the administrative staff of the IMCN, MZUSP, LIRP, UCR and DZSJRP (IBILCE – UNESP) for the assistance provided and for the use of facilities during my work and visits to the respective collections.

To the Costa Rican Ministerio de Ciencia, Tecnología y Telecomunicaciones (MICITT; PED-017-2015-1) and the Partnerships Program for Education and Training of the Organization of American States in conjunction with the Grupo Coimbra de Universidades Brasileiras (PAEC OEA-GCUB, 2014) for financial support.

To Danilo de Oliveira for reviewing and correcting the format of the references.

RESUMO

A família Loricariidae é a mais diversa dentro do ordem Siluriformes, contendo cerca de 980 espécies válidas. Os membros da família são facilmente reconhecidos por possuírem corpos cobertos por placas dérmicas ossificadas, dentes tegumentares abundantes e um disco oral ventral que facilita a fixação á superfície e a alimentação. A subfamília Loricariinae é a segunda mais diversa dentro de Loricariidae, contendo 31 gêneros e cerca de 243 espécies válidas. Os membros da subfamília são facilmente reconhecidos por ter um pedúnculo caudal alongado e deprimido e por a falta de uma nadadeira adiposa. As espécies de Loricariinae estão amplamente distribuídas pelas principais drenagens da maioria dos rios da América Central e do Sul, sendo geralmente encontradas próximas ao substrato e apresentando uma extraordinária diversidade morfológica e funcional. Tradicionalmente, a maioria dos estudos morfológicos e ecomorfológicos em membros da subfamília e a família, seja sob uma abordagem descritiva/comparativa e/ou cladística, focalizou o uso de caracteres osteológicos. Este estudo descreve e compara a morfologia cerebral superficial dos membros da subfamília e família e explora seu significado ou valor ecológico e filogenético. Mais de 300 espécimes [incluindo representantes de quase todos os gêneros válidos de Loricariinae, bem como de outras sete subfamílias de Loricariidae (Delturinae, Hypoptopomatinae, Hypostominae, Lithogeninae, Neoplecostominae, "Otothyrinae" e Rhinelepininae)] e 89 caracteres foram examinados. Os resultados obtidos sugerem que o tamanho, volume e forma relativa das diferentes estruturas cerebrais examinadas varia principalmente com o comportamento alimentar e o ambiente preferido. Além disso, quando analisados e avaliados em conjunto com hipóteses de relacionamento filogenético, estes resultados podem ser considerados como evidência empírica apoiando o fato de que a diversidade cerebral nos membros atuais da subfamília e a família pode ser o resultado tanto do conservadorismo de nicho filogenético quanto da radiação adaptativa repetida. Finalmente, este trabalho fornece dados adicionais a serem considerados na árvore evolutiva da subfamília e a família, destacando a necessidade de mais estudos integrando informações de diferentes sistemas anatômicos em um contexto filogenético. Além disso, este trabalho representa uma base para futuras investigações sobre as relações entre a anatomia do cérebro e a ecologia dos membros da subfamília, família e ordem em um contexto filogenético.

Palavras-chave: Cascudos. Ecomorfologia. Filogenia. Neuroanatomia. Ontogenia.

ABSTRACT

The family Loricariidae is the most species-rich within the Siluriformes, containing about 980 valid species. Members of the family are easily recognized by having bodies covered by ossified dermal plates, abundant integumentary teeth and a ventral oral disk that facilitates surface attachment and feeding. The subfamily Loricariinae is the second most species rich within the Loricariidae containing 31 genera and about 243 valid species. Members of the subfamily are easily recognized by having an elongate and depressed caudal peduncle and by lacking of adipose fin. Species of the Loricariinae are widely distributed throughout the Central and South American major river drainages, being usually found near the substrate and showing an extraordinary morphological and functional diversity. Traditionally, most of the morphological, and ecomorphological, studies on members of the subfamily and the family, either under a descriptive/comparative and/or cladistic approach, have focused on the use of osteological characters. This study describes and compares the gross brain morphology of the members of the subfamily and the family and explores their ecological and phylogenetic significance. More than 300 specimens [including representatives of almost all valid genera of the Loricariinae, as well as of other seven subfamilies of the Loricariidae (Delturinae, Hypoptopomatinae, Hypostominae, Lithogeninae, Neoplecostominae, "Otothyridae" and Rhinelepidinae)] and 89 characters were examined. The results obtained suggest that the relative size, volume and shape of the different brain structures examined varies mostly with feeding behaviour and preferred environment. Furthermore, when analyzed and evaluated in conjunction with hypotheses of phylogenetic relationships, these results can be considered as empirical evidence supporting the fact that brain diversity in current members of the subfamily, and the family in general terms, could be the result of both phylogenetic niche conservatism and repeated adaptive radiation. Finally, this work provides considerable additional data to the evolutionary tree of the subfamily and the family, highlighting the need of further studies integrating information from different anatomical systems in a phylogenetic context. Moreover, this work could be a basis for further investigations on the relationships between brain anatomy and the ecology of members of the subfamily, family and order in a phylogenetic frame.

Keywords: Ecomorphology. Neuroanatomy. Ontogeny. Phylogeny. Suckermouth armoured catfishes.

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LIST OF ABBREVIATIONS AND ACRONYMS

Ad	<i>Adenohypophysis</i>
Ce	<i>Corpus cerebelli</i>
Ch	<i>Chiasma opticum</i>
Char	Character
De	Delturinae
EG	<i>Eminentia granularis</i>
Hp	<i>Adenohypophysis/Hypoptopomatinae</i>
Hy	Hypothalamus/Hypostominae
I	<i>Nervus olfactorius</i>
II	<i>Nervus opticus</i>
III	<i>Nervus oculomotorius</i>
IV	<i>Nervus trochlearis</i>
IX	<i>Nervus glossopharyngeus</i>
La	Ofactory lamella
LF	Loricariinae, Loricarini, Farlowellina
LH	<i>Lobus inferior hypothalami</i> /Loricariinae, Harttiini
Li	Lithogeninae
LL	Loricariinae, Loricarini, Loricarina
LLA	<i>Nervus linea lateralis anterior</i>
LLP	<i>Nervus linea lateralis posterior</i>
LobVII	<i>Lobus facialis</i>
LobX	<i>Lobus vagi</i>
MO	Alar portion of the <i>medulla oblongata</i>
Me	<i>Medulla spinalis</i>
Ne	Neoplecostominae
OB	Olfactory bulbs
Of	Olfactory organ
OT	Optic tectum
Rh	Rhinelepinae
TC	<i>Truncus cerebri</i>
SL	Standard length
Te	Telencephalon

TG	Taxonomic group
TL	<i>Torus lateralis</i>
Tol	<i>Nervus tractus olfactorius</i>
V	<i>Nervus trigeminus</i>
VI	<i>Nervus abducens</i>
VII	<i>Nervus facialis</i>
VIII	<i>Nervus octavus or vestibulares</i>
X	<i>Nervus vagus</i>

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1. GENERAL INTRODUCTION

The family Loricariidae (suckermouth armoured catfishes, armoured catfishes or plecos) is the most species-rich within the Siluriformes (catfishes), containing about 980 valid species (FRICKEE *et al.*, 2018a) as well as several undescribed forms. Members of the family are easily recognized from other fishes by having bodies covered by ossified dermal plates, abundant integumentary teeth (odontodes) and a ventral oral disk that facilitates surface attachment and feeding (REIS *et al.* 2003; GARG *et al.*, 2010; GEERINCKX *et al.*, 2011; LUJAN *et al.*, 2015). The subfamily Loricariinae is the second most species-rich within the Loricariidae containing 31 genera and about 243 valid species (FRICKEE *et al.*, 2018a) as well as several undescribed forms, corresponding to about 25% of the total known diversity within the family. Members of the Loricariinae are easily recognized from other loricariids by having elongate and depressed caudal peduncles and by lacking of adipose fin, among other distinctive characters (see SCHAEFER, 1987; RAPP PY-DANIEL, 1997; COVAIN & FISCH-MULLER, 2007); they are widely distributed throughout the Central and South American major river drainages, from southern Costa Rica to northern Argentina (REIS *et al.*, 2003; COVAIN & FISCH-MULLER, 2007), showing an extraordinary morphological and functional diversity (see SCHAEFER & LAUDER, 1986; COVAIN & FISCH-MULLER, 2007; COVAIN, 2011; LUJAN & ARMBRUSTER, 2012; LUJAN *et al.*, 2015).

Studies focused on the phylogenetic relationships on members of the Loricariinae, and Loricariidae, in general terms, agree, in some measure, with the monophyly of the subfamily and in the recognition of two major lineages, the tribes Harttiini and Loricariini, whose generic composition varies between authors (see for example the contributions of RAPP PY-DANIEL, 1997; MONTOYA-BURGOS *et al.*, 1998; ARMBRUSTER, 2004; COVAIN & FISCH-MULLER, 2007; COVAIN *et al.*, 2008, 2010, 2016; ROXO *et al.*, 2019). Despite of such studies, and as noted by the same authors, a taxonomic synthesis of the subfamily, and the family, in general terms, is still needed in order to provide a foundation for more detailed studies on its members, considering that (1) at lower taxonomic levels, morphological–molecular discordance and homoplasy is still problematic or has not been appropriately evaluated, (2) synapomorphies for many clades at/below the rank of tribe are relatively scarce and (3) the disagreement about the monophyly and taxonomic

validity of some genera (see RAPP PY-DANIEL, 1997; COVAIN & FISCH-MULLER, 2007; RAPP PY DANNIEL & FICHBERG, 2008; COVAIN, 2011; LONDOÑO-BURBANO, 2012; COVAIN *et al.*, 2016; ROXO *et al.*, 2019).

Most of the morphological, and ecomorphological, studies on members of the Loricariinae, and the Loricariidae, in general terms, either under a descriptive, comparative (*e.g.*, ISBRÜCKER, 1979; RAPP PY-DANIEL, 1997; ARMBRUSTER, 2004; COVAIN & FISCH-MULLER, 2007; LUJAN & ARMBRUSTER, 2012) and/or cladistic approach (*e.g.*, SCHAEFER, 1987; RAPP PY-DANIEL, 1997; ARMBRUSTER, 2004; among others), have focused on the use of osteological characters; this could be understandable given (1) their “pretty well-known” utility for comparative purposes, (2) their relative easy access and (3) the extensive literature available (see for example REGAN, 1904; 1911; LEEGE, 1922; ANGELESCU & GNERI, 1949; ALEXANDER, 1964; 1965; CHARDON, 1968; LUNDBERG & BASKIN, 1969; ISBRÜCKER, 1979; SCHAEFER, 1987; RAPP PY-DANIEL, 1997; COVAIN & FISCH-MULLER, 2007). On the other hand, descriptive, comparative and/or cladistic studies considering alternative body systems, such as the brain anatomy (neuroanatomy), in both members of the Loricariinae and Loricariidae, as well as in other teleost fish taxa, in general terms, have been rarely addressed, and/or when undertaken, rarely carried on in an organized fashion [see FREIHOFER, 1978; HOWES, 1983; RAPP PY-DANIEL, 1997; PUPO, 2011, 2015; DATOVO & VARI, 2014; ROSA, 2015; PEREIRA & CASTRO, 2016; among others (see below), for examples and a more detailed discussion]. This “extensive” exploration of osteological characters demonstrated to be “rather efficient” for the delimitation of most major clades within the Teleostei; however, as noted by DATOVO & VARI (2014) and PEREIRA & CASTRO (2016), among other authors, it also resulted in the “relatively minor attention” of alternative, and (possibly) equally or more informative, anatomical systems.

The first investigations on the neuroanatomy of members of the Siluriformes date to the end of the 19th century (see PUPO & BRITTO, 2018); one of the first attempts was the work of HERRICK & HERRICK (1891) who used members of the family Ictaluridae (bullhead catfishes) as subject of study. In the middle of the 20th century, several studies on the external morphology of the brain took place, followed by many papers published on the general anatomy, physiology, cytoarchitecture, hodology and embryology of the brain and the peripheral nervous system of, mainly,

Nearctic species (see KOTRSCHAL *et al.*, 1998; FINGER, 2000 for an overview). On the other hand, studies on Neotropical fishes, and members of the Siluriformes, specifically, are relatively scarce and have focused only in a few species or supraspecific groups; *e.g.*, members of the Callichthyidae (PUPO, 2011; PUPO & BRITO, 2018), Heptapteridae (TRAJANO, 1994; ABRAHÃO *et al.*, 2018a), Loricariidae (ROSA *et al.*, 2014; ROSA, 2015; ANGULO & LANGEANI, 2017; CHAMON *et al.*, 2018) and Pseudopimelodidae (ABRAHÃO & SHIBATTA, 2015; ABRAHÃO *et al.*, 2018b). Furthermore, in these essentially descriptive (mainly anatomical) contributions, the potential ecological (and phylogenetic) inferences and correlations have been, in most cases, only superficially addressed (see ROSA, 2015; PEREIRA & CASTRO, 2016; ANGULO & LANGEANI, 2017; ABRAHÃO *et al.*, 2018a).

1.1. Aims and dissertation structure

In accordance with the above, the main objective of this work is to describe the general gross morphology of the brain of the armoured catfish subfamily Loricariinae, as a baseline for comparative anatomical, taxonomic, phylogenetic and ecological studies. Moreover, four specific objectives, corresponding each one of them (in general terms) with one or more of the three chapters presented below, were raised. These four specific objectives are: (1) to explore and evaluate (quantitatively and qualitatively) the sexual and ontogenetic (post-larvae) intraspecific variation in the gross brain morphology of members of the Loricariinae (chapter one); (2) to explore and evaluate and describe (quantitatively and qualitatively) the intergeneric (considering the major suprageneric taxonomic divisions) variation in the gross brain morphology in members of the Loricariinae, also comparing it with some external taxa within the Loricariidae, Siluriformes and Ostariophysi (chapter two); (3) to explore and evaluate and discuss the possible correlations between the general brain patterns observed and the sensory and behavioral ecology of the species and supraspecific groups (chapters one and two); and (4) to evaluate the phylogenetic significance of the neuroanatomy, in members of the Loricariinae and the Loricariidae, following a cladistic approach (chapter three).

2. CHAPTER ONE:

GROSS BRAIN MORPHOLOGY OF *Rineloricaria heteroptera* ISBRÜCKER & NIJSSSEN, 1976 AS SPECIES MODEL: A DESCRIPTIVE AND QUANTITATIVE APPROACH

[Article published] Angulo, A. & Langeani, F. (2017). Gross brain morphology of the armoured catfish *Rineloricaria heteroptera* Isbrücker & Nijssen, 1976 (Siluriformes: Loricariidae: Loricariinae): a descriptive and quantitative approach. *Journal of Morphology*, 278, 1689–1705.

2.1. ABSTRACT

The gross morphology of the brain of *Rineloricaria heteroptera* and its relation with the sensory and behavioral ecology of the species is herein described and discussed. The sexual and ontogenetic intraspecific variation in the whole brain length and mass, and within/between the volumes of eight different brain subdivisions is also examined and discussed. Negative allometry on the whole brain length and mass and on the relative growth of the *telencephalon* and the optic tecta was observed. Positive allometry was observed on the relative growth of the olfactory bulbs and the *medulla oblongata*. Univariate and multivariate statistical analyses did not revealed significant differences in the brain subdivisions growth rates among sexes and/or developmental stages, except for the optic tectum, and some portions of the *medulla oblongata*; with juveniles and males showing more developed optic tecta and medullary subdivisions, respectively. Growth rates for each brain subdivision were relatively constant and the slopes of the growth equations were almost parallel, except for the olfactory bulbs and the *medulla oblongata* subdivisions, suggesting some degree of tachyaukinesis against the entire brain. The *corpus cerebelli* was the more voluminous brain subdivision in most specimens (principally adults) and was followed by the optic tectum (the more voluminous subdivision in juveniles), the hypothalamus and the *telencephalon*, in that order.

Differences in the number of lamellae and in the relative size of the olfactory organ also were detected among developmental stages, being more numerous and larger, respectively, in adults. Based on these results, it is possible to infer an ontogenetic shift in the habitat/resources use and behaviors in *R. heteroptera*; were the vision, primarily routed through the optic tectum, could be fundamental in early stages, whereas in adults the olfaction and taste, primarily routed through the olfactory bulbs and the *medulla oblongata*, would play a more important role.

2.2. KEYWORDS

Brain organization, Ontogeny, Sexual dimorphism, Neotropical fish, Teleostei.

2.3. INTRODUCTION

Brain morphology in teleost fishes is diverse and shows a high degree of divergent differentiation hardly comparable to that of other vertebrate groups (NORTHCUTT, 1988; KOTRSCHAL *et al.*, 1998; WAGNER, 2003). Along their evolutionary history, teleost fishes have been subjected to different selective pressures resulting in highly specialized sensory and cognitive capacities, abilities and behaviors (NORTHCUTT, 1988; KOTRSCHAL *et al.*, 1998; WAGNER, 2003; WHITE & BROWN, 2015); such specializations may be directly reflected, by the way of adaptive and exaptive processes, in brain morphology, explaining, in part, the huge taxonomic [about 32500 current known species (FRICKEE *et al.*, 2018a)] and ecological diversity within the group (PARHAR *et al.*, 2001; WAGNER, 2003).

To practical purposes, teleost fish brains can be divided into seven main regions, areas or structures [*i.e.*, olfactory bulbs, *telencephalon*, *diencephalon*, midbrain tectum (often referred as the optic lobe or optic tectum), midbrain tegument, *cerebellum* (including the *corpus cerebelli* and the *valvula cerebelli*) and *medulla oblongata* (including the electrosensory, facial and vagal lobes); see ALBERT *et al.*, 1998], each one of which participates in the control of multiple (*e.g.*, in the case of multimodal integration centers such as the *telencephalon*, midbrain tectum, *cerebellum*, etc.) to very specific (*e.g.*, the olfactory bulbs and the electrosensory, facial and vagal lobes of the *medulla oblongata*) sensory and cognitive functions and/or behaviors (WAGNER, 2002; BUTLER & HODOS, 2005; ULLMANN *et al.*, 2010; WHITE & BROWN, 2015). Most of these brain subdivisions show notable morphological and functional similarities with the respective brain subdivisions of other vertebrate groups (see NORTHCUTT, 2002; WULLIMANN & MUELLER, 2004; BROGLIO *et al.*, 2011; WHITE & BROWN, 2015); in other cases, however, homologies are still largely unresolved (BUTLER & HODOS, 2005).

Earlier investigations on fish brain morphology, functioning and development (*e.g.*, LISSNER, 1923; GEIGER, 1956) demonstrated that the degree of differentiation of the different sensory and cognitive capacities, abilities and behaviors in teleost fishes can be correlated, in many cases, with the morphology of a certain brain subdivision or area, even more than in other vertebrate groups (ITO *et al.*, 2007). As a consequence, brain morphology, in general terms, has been widely utilized, in several teleost fish taxa, as a strong predictor for a species (or species

group) sensory, cognitive and/or behavioral ecology (e.g., BAUCHOT *et al.*, 1989; BRANDSTÄTTER & KOTRSCHAL, 1990; KOTRSCHAL & PALZENBERGER, 1991; HUBER *et al.*, 1997; KOTRSCHAL *et al.*, 1998; WAGNER, 2001, 2002, 2003).

Some systematists also have attempted to use the brain morphology as a source of “new” characters to identify and/or corroborate phylogenetic affinities within some specific teleost fish taxa, in most cases with relative good success (e.g., ALBERT *et al.*, 1998; EASTMAN & LANNOO, 2003A, 2003B, 2004, 2007, 2008, 2011; KHONSARI *et al.*, 2009; PUPO, 2011; ROSA, 2015). This is not surprising because neuroanatomical characters are known to provide strong phylogenetic information (see SVETOVIDOV, 1953; MILLER & EVANS, 1965; FREIHOFFER, 1978; KHONSARI *et al.*, 2009). Despite of this, the brain morphology is still relatively poorly known and under-explored or under-utilized in the vast majority of teleost fish taxa, both in comparative studies and/or as source of characters for taxonomic and phylogenetic studies (PUPO, 2011; ROSA, 2015; PEREIRA & CASTRO, 2016).

In addition to the contribution of the ecological and phylogenetic processes to brain morphology variation and differentiation in teleost fishes, and vice-versa, as briefly mentioned above, some recent studies on brain evolution and development (e.g., ITO *et al.*, 2007; NORTHCUTT, 2004, 2008; GONDA *et al.*, 2009; LECCHINI *et al.*, 2014; SALAS *et al.*, 2015; LISNEY *et al.*, 2017) also have recognized the fundamental role of the ontogenetic processes. This is also not surprising, because it is widely known that the brain, as well as virtually all morphological and physiological features of the organisms, scales allometrically with body size (BAUCHOT *et al.*, 1976; MCMAHON & BONNER, 1983). Most of these studies, however, have used correlative approaches at the interspecific level, being that similar intraspecific studies are usually rare, despite the fact that they could better determine how selection and phenotypic plasticity can influence brain morphology (GONDA *et al.*, 2011; 2013).

Despite of such advances, and considering the huge taxonomic and ecological diversity within the group, little is known on the variation in brain morphology, as well as their evolutionary, sensory, cognitive and behavioral implications, in the vast majority of teleost fish taxa. Moreover, as noted by ABRAHÃO & SHIBATTA (2015), WHITE & BROWN (2015) and PEREIRA & CASTRO (2016), among other authors, more integrative, descriptive and quantitative, approaches, both at the inter- and intraspecific levels, are necessary to increase and promote the understanding on the

diversity, phylogenetic relationships, ecology, physiology and functioning of this rich and complex group of organisms.

Among catfishes, including 39 families and more than 3720 species (FRICKEE *et al.*, 2018a), brain morphology, and its ecologic and phylogenetic correlations and implications, are relatively well known in the north American Ictaluridae, a relatively small family comprised by about 50 species (FRICKEE *et al.*, 2018a); see for example the contributions of ATEMA (1971; 1980), FINGER (1976), KNUSEN (1976), LUNDBERG (1982), TONG & FINGER (1983), LEE & BULLOCK (1984), MORITA & FINGER (1985), KANWAL & CAPRIO (1987), STRIEDTER (1990; 1991), MEEK & NIEUWENHUYS (1998), NORTH CUTT *et al.* (2000), among others. Among the neotropical catfishes, *sensu stricto*, including 14 families and about 2155 species [≈58% of the total known diversity within the order (FRICKEE *et al.*, 2018a)], descriptive and applied studies on brain morphology are, however, absent or relatively scarce; see for example the contributions of TRAJANO (1994), PUPO (2011, 2015), ROSA *et al.*, (2014), ABRAHÃO & SHIBATTA (2015), ROSA (2015), PEREIRA & CASTRO (2016) and ABRAHÃO *et al.* (2018).

With the aim of promoting future studies on the brain morphology of neotropical catfishes, as well as its ecological, evolutionary and phylogenetic correlations and implications, three objectives were raised in the present study using the armoured catfish *Rineloricaria heteroptera* Isbrücker & Nijssen, 1976 (Siluriformes: Loricariidae: Loricariinae) as species model. These objectives were: (1) to describe the gross morphology of the brain of *R. heteroptera*, as basis for comparative studies on brain morphology of members of the Siluriformes and specifically of the Loricariinae and Loricariidae; (2) to explore the sexual and ontogenetic (post-larvae) intraspecific variation in brain (and the different brain subdivisions) size, mass and volume; and (3) comment on the correlation between the brain morphology and the sensory and behavioral ecology of the species.

2.4. MATERIAL AND METHODS

2.4.1. Species of study

Rineloricaria heteroptera (Fig. 1) is a medium sized loricariid, reaching about 133 mm in standard length (SL), restricted to the upper-medium portion of the

Amazon River basin, near Manaus (state of Amazonas), Brazil (FERRARIS, 2003; FROESE & PAULY, 2017), inhabiting mainly small sandy bottom forest streams (RAPP PY-DANIEL & FICHBERG, 2008). As most members of the genus, *R. heteroptera* shows a remarkable external sexual dimorphism as well as benthic habits (ISBRÜCKER & NIJSSEN, 1976, 1992; ABELHA *et al.*, 2001; DELARIVA & AGOSTINHO, 2001; REIS & CARDOSO 2001; LACERDA, 2007; FICHBERG & CHAMON, 2008). The genus *Rineloricaria* Bleeker, 1862, *sensu* COVAIN & FISCH-MULLER (2007), with about 63 valid species (FROESE & PAULY, 2017), is the most species rich genus within the Loricariinae and also shows the largest distribution within the family (from Costa Rica to Argentina), being found in a diverse array of environments (COVAIN & FISCH-MULLER, 2007; FROESE & PAULY, 2017). The choice of *R. heteroptera* as the species subject of study was based mainly in the availability of (museum) specimens, from different developmental stages and from both sexes, for the inevitable and destructive brain removals.

2.4.2. Material examined

Specimens examined (42 in total, 21 males and 21 females; 35.5–114.4 mm SL) are deposited at the fish collection of the Departamento de Zoologia e Botânica of the Universidade Estadual Paulista, campus São José Rio Preto, São Paulo, Brazil (DZSJRP), under the following catalog numbers: 014427, n=3; 014452, n=3; 014549, n=3; 014657, n=4; 014722, n=2; 014771, n=10; 014909, n=2; 016730, n=2; 016982, n=3; 017182, n=6; 017371, n=3; and 017429, n=1 [collection data can be accessed through the “Species link” online database site (<http://splink.cria.org.br/>)]. Total length (TL), standard length, head length (HL) and body mass were measured in all specimens, which were fixed in $\approx 10\%$ formalin and preserved in $\approx 70\%$ ethanol. Measurements were taken with the aim of a digital caliper (± 0.01 mm) and a digital balance (± 0.01 g).

2.4.3. Data acquisition

Brains were dissected and removed following the protocol described by ABRAHÃO & PUPO (2014) as adapted to Loricariidae by ROSA (2015). Nomenclature of brain subdivisions follows MEEK & NIEUWENHUYIS (1998) and

BUTLER & HODOS (2005). Because the brains could not be cut off from the spinal cord at comparable positions in each specimen, the posterior limit of the brain was defined at the posterior end of the alar portion of the *medulla oblongata*, recognizable in all specimens at both dorsal and lateral views, *sensu* MEEK & NIEUWENHUYIS (1998) and PUPO (2011), as a small notch or invagination, representing the transition zone between this structure and the *medulla spinalis* (Fig. 2); all cuts were made posterior to this limit. After removal from the neurocranium the brains were stored in $\approx 70\%$ ethanol.

A digital camera attached to a stereomicroscope was used to capture scaled images of the brain topography of all specimens; dorsal (before and after removal from the neurocranium), lateral (left side) and ventral views were acquired. All photographs were taken while the specimens and brains were submerged in water, covered to exactly the same depth (*i.e.*, all specimens and brains had about 1 mm of water over their surface), and looking straight down onto the brain; therefore, the refractive index should have been about the same for all photos.

Following ABRAHÃO & SHIBATTA (2015) and WHITE & BROWN (2015) a total of twenty-eight brain measurements, including the length, width and height of all major brain subdivisions [*i.e.*, olfactory bulb, *telencephalon*, optic tectum, hypothalamus, *corpus cerebelli* and *medulla oblongata* (see Table 1)], were taken from the scaled images using the image-analysis public domain software IMAGEJ1.49 (RASBAND, 1997). Total brain length was measured, in dorsal view, from the anterior limit of the telencephalon (excluding the *nervus tractus olfactorius*) to the posterior limit of the alar portion of the *medulla oblongata* (see above). The total number of lamellae in each (left and right) olfactory organ, in each specimen, also was recorded.

Volumes of eight major brain subdivisions [*i.e.*, (1) olfactory bulb, (2) *telencephalon*, (3) optic tectum, (4) hypothalamus, (5) *corpus cerebelli* and (6–8, see below) *medulla oblongata* lobes; Fig. 2] were estimated using the half ellipsoid method (modified from VAN STAADEN *et al.*, 1995; HUBER *et al.*, 1997; WHITE & BROWN, 2015). This method assumes that each brain subdivision has the shape of an idealized half ellipsoid and involves obtaining linear measurements for the length (L), width (W) and height (H), converting them into volumetric measures through the following formulae: $1/3 \cdot \pi \cdot L \cdot W \cdot H$ (see VAN STAADEN *et al.*, 1995; HUBER *et al.*, 1997). Despite receiving some criticism [see for example ULMANN *et al.* (2010) and

Table 1. Body length (SL), mass (We) and brain measurements (28) of examined specimens of *R. heteroptera* (n=42); absolute values and percentages of total brain length, head length or total brain volume, as appropriate. Morphometric measurements (-L=length; -W=width, -H=height), numbered from 1 to 28, are expressed in mm, volumes ("-V"s) are expressed in mm³ and masses ("-We"s) are expressed in mg. Linear measurements refer only to the left lobe or counterpart for those bilateral structures; volumes for these bilateral structures were doubled, assuming brain symmetry. Other abbreviations: Ce=*corpus cerebeli*, EG=*eminentia granularis*, Hy=hypothalamus, LobVII=*lobus facialis*, LobX=*lobus vagi*, M=mean, MO=*medulla oblongata* (alar portion), OB=olfactory bulb, OT=optic tectum, T-=total brain (e.g. T-L=total brain length), Te=*telencephalon*, SD=standard deviation.

Measurements	Absolute values			Percentages of total brain length, or total brain volume, as appropriate			Percentages of head length		
	Range	M	SD	Range	M	SD	Range	M	SD
SL	35.48– 114.42	69.32	18.37	–	–	–	–	–	–
We	200–8500	2011.9	1682.8	–	–	–	–	–	–
(1) T-L	4.10–8.11	6.04	0.88	–	–	–	32.90– 66.91	43.91	6.9
(2) T-W	2.26–3.68	3.18	0.37	45.40–59.04	52.86	3.41	14.94– 33.22	23.26	4.11
(3) T-H	1.20–2.77	2	0.34	26.40–36.88	32.87	2.22	11.25– 17.66	14.33	1.66
T-V	3.20–23.74	11.34	4.6	–	–	–	–	–	–

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Measurements	Absolute values			Percentages of total brain length, or total brain volume, as appropriate			Percentages of head length		
	Range	M	SD	Range	M	SD	Range	M	SD
T-We	3.23–23.87	11.39	4.57	–	–	–	–	–	–
(4) OB-L	0.31–0.84	0.58	0.13	6.83–11.58	9.6	1.16	3.12–5.51	4.18	0.58
(5) OB-W	0.21–0.74	0.51	0.12	4.30–10.37	8.45	1.18	2.59–5.17	3.66	0.51
(6) OB-H	0.18–0.72	0.47	0.11	3.69–8.90	7.66	1.07	2.22–4.14	3.31	0.38
OB-V	0.03–0.93	0.33	0.19	0.54–4.21	2.63	0.87	–	–	–
(7) Te-L	0.99–1.78	1.35	0.19	18.71–27.43	22.34	1.98	7.11– 15.20	9.81	1.73
(8) Te-W	0.65–1.15	0.91	0.12	10.47–19.83	15.08	1.55	4.45– 10.53	6.63	1.27
(9) Te-H	0.57–1.04	0.82	0.09	11.12–17.35	13.64	1.18	4.03–9.73	6.02	1.25
Te-V	0.89–4.44	2.15	0.7	12.77–22.97	18.46	1.77	–	–	–
(10) OT-L	1.16–1.96	1.61	0.2	21.21–31.16	27.06	2.11	7.69– 18.72	11.9	2.13
(11) OT-W	0.68–1.08	0.88	0.07	12.56–17.48	14.82	1.34	4.39– 11.31	6.57	1.49
(12) OT-H	0.72–1.29	1	0.14	12.83–20.02	16.49	1.51	5.17– 10.55	7.22	1.19
OT-V	1.32–5.66	3.06	0.92	22.36–32.96	26.5	2.28	–	–	–

Continued on the next page....

Measurements	Absolute values			Percentages of total brain length, or total brain volume, as appropriate			Percentages of head length		
	Range	M	SD	Range	M	SD	Range	M	SD
OT-V	1.32–5.66	3.06	0.92	22.36–32.96	26.5	2.28	–	–	–
(13) Hy-L	1.11–1.69	1.48	0.15	20.56–30.68	24.81	2.74	6.85– 16.49	10.98	2.55
(14) HydW	0.75–1.41	1.15	0.16	15.62–23.36	19.05	1.83	5.14– 11.78	8.34	1.37
(15) Hy-H	0.41–0.87	0.67	0.12	8.68–14.45	11.06	1.26	3.48–7.01	4.84	0.8
Hy-V	0.83–3.96	2.46	0.8	16.35–25.06	20.94	2.15	–	–	–
(16) Ce-L	0.98–1.93	1.52	0.21	21.03–28.18	25.41	1.83	7.81– 15.37	11.15	1.8
(17) Ce-W	1.44–2.64	2.27	0.27	31.66–44.11	37.98	3.12	10.64– 23.90	16.71	3.04
(18) Ce-H	0.63–1.10	0.86	0.11	12.07–17.23	14.4	1.19	4.44–9.89	6.33	1.19
Ce-V	1.00–5.79	3.22	1.05	22.24–34.20	27.49	2.49	–	–	–
(19) EG-L	0.32–0.60	0.45	0.06	6.38–8.81	7.52	0.63	2.37–4.78	3.3	0.56
(20) LobVII-L	0.73–1.34	1.06	0.14	14.80–21.36	17.61	1.3	5.45– 10.72	7.73	1.27
(21) LobVII-W	0.40–0.82	0.66	0.12	8.34–13.90	10.96	1.24	3.34–5.88	4.77	0.63
(22) LobVII-H	0.06–0.27	0.14	0.04	1.32–3.51	2.34	0.47	0.69–1.31	1	0.12

Continued on the next page....

Measurements	Absolute values			Percentages of total brain length, or total brain volume, as appropriate			Percentages of head length		
	Range	M	SD	Range	M	SD	Range	M	SD
LobVII-V	0.04–0.62	0.23	0.12	0.82–2.96	1.84	0.49	–	–	–
(23) LobX-L	0.39–0.91	0.64	0.12	8.32–12.84	10.52	0.97	3.61–6.26	4.58	0.59
(24) LobX-W	0.44–0.91	0.73	0.13	9.17–15.29	12.06	1.36	3.67–6.46	5.25	0.69
(25) LobX-H	0.05–0.24	0.13	0.04	1.20–3.19	2.12	0.43	0.63–1.20	0.91	0.11
LobX-V	0.02–0.41	0.14	0.09	0.42–2.00	1.12	0.37	–	–	–
(26) MO-L	0.41–1.00	0.65	0.15	8.23–13.29	10.68	1.09	3.90–6.06	4.64	0.51
(27) MO-W	0.40–0.81	0.66	0.12	8.28–13.77	10.84	1.22	3.23–5.84	4.72	0.64
(28) MO-H	0.05–0.24	0.13	0.04	1.19–3.13	2.1	0.41	0.62–1.18	0.9	0.1
MO-V	0.02–0.40	0.13	0.08	0.42–1.86	1.01	0.35	–	–	–

references], this method is still in use in the literature and its objectivity, efficacy and utility, in comparative studies, has been corroborated and demonstrated by previous authors (e.g., WAGNER, 2001a, b; LISNEY *et al.*, 2007; GONZALEZ-VOYER & KOLM, 2010; SALAS *et al.*, 2015, and WHITE & BROWN, 2015, among others); given the above, and according to the objectives herein proposed, the use of this methodology, in this particular study, can be justified.

The volume of the olfactory bulb was measured after removal from the *nervus tractus olfactorius*. The *nervus tractus olfactorius*, considered to be part of the telencephalon (see MEEK & NIEUWENHUYS, 1998; LISNEY *et al.* 2017), was not included in the volume estimate of the telencephalon (neither in the total brain volume estimate) given the notable variation in their length throughout growth (see “Results”). The *torus lateralis*, the *hypothalamus* and the *lobus inferior hypothalami*, *sensu* MEEK & NIEUWENHUYS (1998), BUTLER & HODOS (2005) and ABRAHÃO & SHIBATTA (2015; see Fig. 2), were measured as a unit in

the calculation of the hypothalamus volume. *Medulla oblongata* measurements and volumes refer to three different sensory subdivisions: (1) the facial lobe (2), the vagal lobe and the (3) alar portion, *sensu* MEEK & NIEUWENHUYS (1998) and PUPO (2011) (see Fig. 2). Only left lobes, or counterparts, were measured to calculate the olfactory bulb, telencephalon, optic tectum, hypothalamus and *medulla oblongata* subdivisions volumes; for these bilateral structures the values of the volumes were doubled, assuming brain symmetry (see SALAS *et al.*, 2015), for analytical and comparative purposes.

Total brain mass (excluding nerves) was determined using an analytical balance (± 0.0001 g). Before mass measurement, brains were hydrated in ≈ 20 ml of water, room temperature, for about 1 h, in order to avoid variations due to ethanol evaporation. Finally, following SALAS *et al.* (2015), the total brain volume of each specimen was calculated from the total brain mass using the estimated density of the brain tissue [*i.e.*, 1.036 mg/mm^3 ; see STEPHAN (1960)].

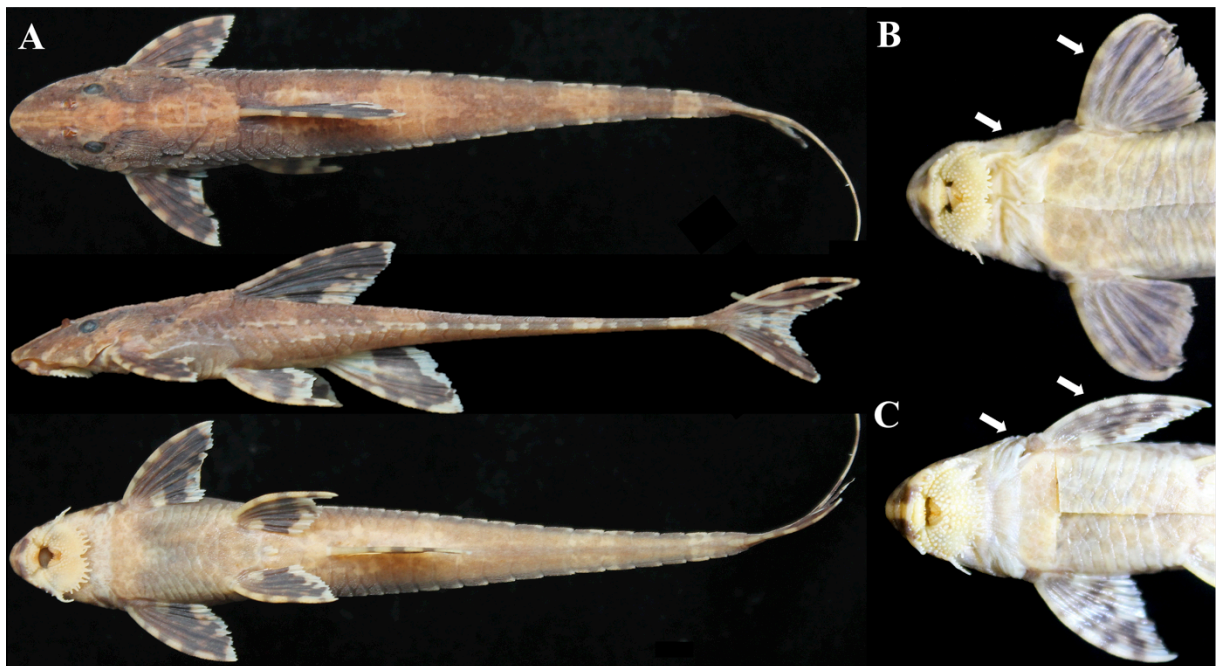


Figure 1. *Rineloricaria heteroptera*; Machado River basin, Madeira River drainage, Rondonia, Brazil; (A) entire specimen (DZSJRP 16730; 75.25 mm SL; female); dorsal (above), lateral (centre) and ventral (below) views; (B, C) ventral detail of head of sexually dimorphic male (B; DZSJRP 14771, 80.15 mm SL) and female (C; DZSJRP 17429, 81.11 mm SL); note the presence (in the male) of shorted, thickened

an curved pectoral-fin spines and numerous small odontodes along the sides of the head and the pectoral-fin spines.

2.4.2. Data analyses

The complete dataset was divided into three subsets, one containing lamellae counts, other containing body and brain lengths and masses and the third containing total brain and brain subdivisions volumes estimates, all of them organized by sex and developmental stage. The sex of each specimen was determined, and corroborated (after observation of external dimorphic characters, in adult specimens), by gonad examination after dissection. For comparative purposes, three developmental stages were defined as follow: 1 [early juvenile; <60.0 mm SL (*i.e.*, 35.0–60.0 mm SL)], 2 (late juvenile; 60.1–80.0 mm SL) and 3 [adult; >80.0 mm SL (*i.e.*, 80.1–115.0 mm SL)]; body size at maturation ($\approx$ 80 mm SL) was defined according to published data for other congeneric species with similar maximum body sizes ($\approx$ 130 mm SL) and life cycles (see ERIC *et al.*, 1982; BARBIERI, 1994; FROESE & PAULY, 2017). A total of seven males and seven females were examined for each developmental stage. Log10 transformations (hereafter LOG) were made on the last two data sets in order to (1) improve normality prior to analysis and to (2) account for an allometric brain size/mass or brain subdivision volume vs. body size/mass or total brain volume relationship (BRANDSTÄTTER & KOTRSCHAL, 1990; WAGNER, 2003; SALAS *et al.*, 2015).

First, a paired sample *t*-test was performed on the first dataset in order to compare the lamellae count values in both left and right olfactory organs in each specimen regardless of sex and developmental stage. Parallel, a two-way analysis of variance (ANOVA) was performed on the same dataset in order to assess whether sex, developmental stage and/or the interaction between them (*i.e.*, sex*developmental stage) have (or not) a significant effect on the number of lamellae on the olfactory organs (calculated as the mean of both left and right olfactory organs values).

Second, Ordinary Least Squares (OLS) linear regressions, were performed on the second dataset in order to assess the scaling relationship between brain and body length and masses, respectively; this was done using LOG total brain length and mass, respectively, as dependent variables and LOG body length and mass,

respectively, as independent variables (see LISNEY *et al.*, 2017). Parallel, two independent two-way analyses of covariance (ANCOVA) were performed on the same dataset in order to assess whether sex, developmental stage or the interaction between them have (or not) a significant influence on the scaling of the overall brain length and mass; this was done, as in the OLSs, using LOG total brain length and mass, respectively, as dependent variables, LOG body length and mass, respectively, as covariates, and sex, developmental stage and the interaction term between them as fixed factors (see LISNEY *et al.*, 2017).

Finally, independent OLS linear regressions also were performed on the third dataset in order to assess the scaling relationships between the volume of each one of the eight major brain subdivisions analyzed [*i.e.*, (1) olfactory bulbs, (2) *telencephalon*, (3) optic tecta, (4) hypothalamus, (5) *corpus cerebelli*, (6) *lobus facialis* (7) *lobus vagi* and the (8) alar portion of the *medulla oblongata*] and the total brain volume; this was done using LOG volume of each brain subdivision as dependent variable and LOG of total brain volume minus the volume of the respective brain subdivision as independent variable [this subtraction was done to account for the bias that exists when a brain subdivision is scaled against the total brain volume or mass (which already includes the subdivision of interest) (see DEACON, 1990; IWANIUK *et al.*, 2010; LISNEY *et al.*, 2017)]. Parallel, eight independent two-way ANCOVAs were performed on the same dataset in order to assess whether sex, developmental stage or the interaction between them have (or not) a significant influence on the scaling of each brain subdivision; this was done, as in the OLSs, using LOG volume of each brain subdivision, as dependent variable, LOG of the total brain volume minus the volume of the respective brain subdivision, as covariate, and sex, developmental stage and the interaction term between them as fixed factors (see SALAS *et al.*, 2015; LISNEY *et al.*, 2017).

Additionally, a principal component analysis (PCA) was performed on the third dataset in order to (1) examine the clustering of the samples in the multidimensional space and to (2) characterize the patterns of brain organization comparing both sexes and developmental stages; this was done using the relative volume of each brain subdivision [calculated as a fraction of the sum of the volume of all eight brain subdivisions measured in each specimen and normalized using an arcsine square root transformation; see SALAS *et al.* (2015)] as correlated variables, and sex and developmental stage as grouping factors; this analysis was performed on an

autocovariance matrix and using the singular value decomposition method for a better numerical accuracy (see SALAS *et al.* 2015). All statistical analyses were carried out using the PAST software version 3.11 (HAMMER *et al.*, 2001).

2.5. RESULTS

2.5.1. Gross brain morphology of *Rineloricaria heteroptera* (Descriptive approach)

Brain subdivisions, and the brain as a whole, are described below in the antero-posterior axis direction according to the scheme implemented by ABRAHÃO & SHIBATTA (2015) and PEREIRA & CASTRO (2016), with modifications. In paired structures only the left lobe or left counterpart is described, unless otherwise stated. The encephalon is slightly elongate and narrow, slightly wider in its middle portion near the *mesencephalon* (optic tectum) and the *diencephalon*, and does not present apparent external hypertrophy of the sensory and/or motor regions *sensu* MEEK & NIEUWENHUYIS (1998) and BUTLER & HODOS (2005). The brain, as a whole, occupies the cranial cavity almost entirely and is, with exception of the olfactory bulbs and part of the anterior portion of the *telencephalon*, completely located ventral to the parietosupraoccipital bone and the posterior portion of the frontal bones, and dorsal to the parasphenoid and the prootic bones, not contacting directly the Weberian apparatus.

Telencephalon

The olfactory organ is located dorsal and anterior to the olfactory bulb, with which it is interconnected via the *nervus olfactorius* (I). The olfactory organ is almost rounded, or oval, in shape in dorsal view and presents a total of 12–24 feather-like lamellae, which are longer and thicker in the posterior portion of the organ (Figs. 2 and 3). In larger specimens (>80.0 mm SL) the olfactory organ was usually larger, with its dorsal surface larger than the dorsal surface of the *telencephalon*, whereas in smaller specimens (<60.0 mm SL) the opposite pattern was observed (Fig. 3). The *nervus olfactorius* is relatively short [usually shorter than the olfactory bulb length, mainly in smaller specimens (<60.0 mm SL)] (Figs. 2 and 3). The olfactory bulb is

positioned at the anterior portion of the brain and is located ventral to the nasal bone, near to the articulation of the lateral ethmoid and the vomer. The olfactory bulb is almost spherical in shape (Figs. 2 and 3) and can be sessile (in smaller specimens) or pedunculated (in larger specimens). The extension of the *nervus tractus olfactorius*, which connect the olfactory bulb with the *telencephalon*, varies in proportion to the total brain length, being that in larger specimens (>80.0 mm SL) its length reaches about 75.0% of the total brain length (T-L; Figs. 2 and 3). The *nervus tractus olfactorius* is inserted directly on the ventral surface of the *telencephalon*.

The *telencephalon*, properly, is located anterior to the optic tectum and the *hypothalamus* and posterior to the olfactory bulb, in both lateral and dorsal views; in smaller specimens (<60.0 mm SL) the distal portion of the *telencephalon* is positioned dorsal to the *hypothalamus*. The *telencephalon* is longitudinally elongated and almost oval in shape, in both lateral and dorsal views; its anterior and posterior margins are rounded, being the anterior one slightly smaller than the posterior one. In lateral view the medial horizontal axis of the *telencephalon* form an angle of about 45° with the medial horizontal axis of the *hypothalamus* (Figs. 2 and 3). The *telencephalon* is divided in two distinct parts: (1) a conspicuous and well-developed *area dorsale* on its dorsal surface, and (2) a small and narrow *area ventrale* on its ventral surface; in the *area dorsale*, two regions, the lateromesial and the posteromesial, are specially prominent and bulging. In most examined specimens, the *telencephalon* is, comparing to the remaining brain subdivisions (e.g., *corpus cerebelli* and optic tectum in that order), smaller and less voluminous (Table 1).

Diencephalon

The hypothalamus is located at the ventral portion of the *diencephalon*, posterior to the *telencephalon* and the *chiasma opticum*, mesial to the *torus lateralis* and the *lobus inferior hypothalami* and anterior to the *adenohypophysis* (Figs. 2 and 3). The *hypothalamus* is longitudinally elongated and almost oval in shape in ventral view; its anterior and posterior margins are rounded, being the posterior margin slightly smaller than the anterior one. The *lobus inferior hypothalami*, located at the outer margin of the *diencephalon*, posterior to the *torus lateralis* and lateral to the *adenohypophysis*, is longitudinally elongated and almost oval in shape (in ventral view); its medial horizontal axis forms, in ventral view, an angle of about 40–50° with

the medial horizontal axis of the *hypothalamus* (Figs. 2 and 3). The *lobus inferior hypothalami* is, in appearance, more voluminous than the *hypothalamus*, but less voluminous than the *telencephalon* and the optic tectum. The *adenohypophysis* is located posterior and ventral to the *hypothalamus*, on its mid axis, and is almost spherical in shape (Fig. 2).

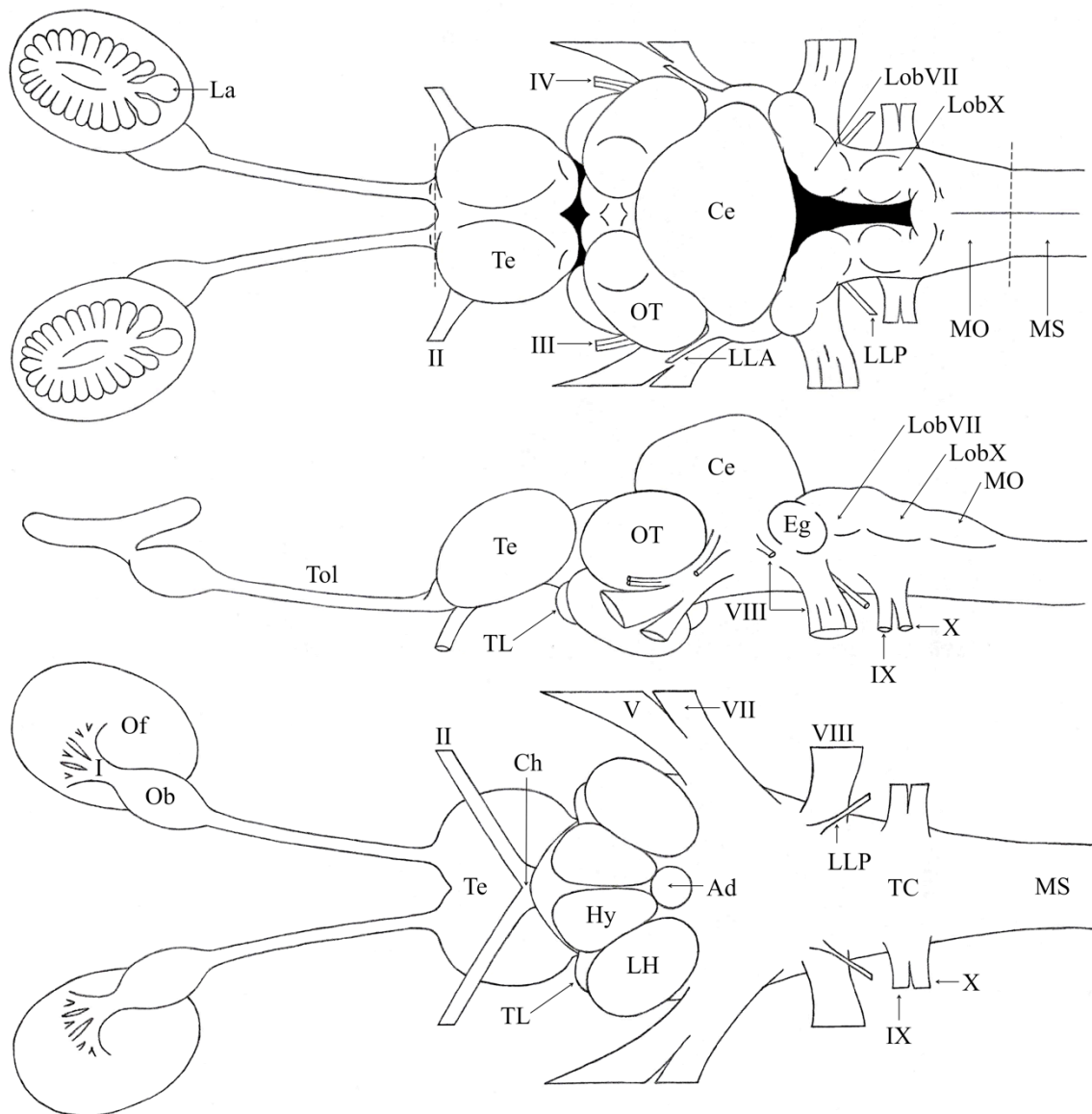


Figure 2. Topographic brain anatomy of *R. heteroptera* (DZSJPR 014771), 114.42 mm SL; Machado River basin, Madeira River drainage, Rondonia, Brazil; (above) dorsal, (centre) lateral (left side) and (below) ventral views. Abbreviations: Ad=adenohypophysis, Ce=corpus cerebelli, Ch=chiasma opticum, EG=eminentia

granularis, Hy=hypothalamus, LH=*lobus inferior hypothalami*, LobVII=*lobus facialis*, LobX=*lobus vagi*, MO=alar portion of the *medulla oblongata*, MS=*medulla spinalis*, I=*nervus olfactorius*, II=*nervus opticus*, III=*nervus oculomotorius*, IV=*nervus trochlearis*, V=*nervus trigeminus*, VI=*nervus abducens*, VII=*nervus facialis*, VIII=*nervus octavus* or *vestibularis*, IX=*nervus glossopharyngeus*, X=*nervus vagus*, La=olfactory lamella, LLA=*nervus linea lateralis anterior*, LLP=*nervus linea lateralis posterior*, OB=olfactory bulbs, Of=olfactory organ, OT=optic tectum, Te=telencephalon, TL=*torus lateralis*, Tol=*nervus tractus olfactorius*, and TC=*truncus cerebri*. Pointed lines indicate the anterior and posterior limits of the brain.

Mesencephalon

The *chiasma opticum*, where the fibers of the *nervus opticus* (II) cross the horizontal midline of the brain, is located ventrally in the *mesencephalon*, at the posterior half of the telencephalon and anterior to the optic tectum (Figs. 2 and 3). The optic tectum is located at the dorsal portion of the *mesencephalon*, anterolateral to the *corpus cerebelli* in dorsal view, about ventral to the *corpus cerebelli* in lateral view, dorsal to the *lobus inferior hypothalami* and the *truncus cerebri* in lateral view and posterior to the *telencephalon* in both dorsal and lateral views (Figs. 2 and 3). The optic tectum is composed by two bilaterally-bean shaped lobes, which contact both the *corpus cerebelli* (dorsally) and the *lobus inferior hypothalami* (ventrally). In dorsal view the medial horizontal axis of the optic tectum forms an angle of about 45° with the medial horizontal axis of the *corpus cerebelli*; in lateral view each lobe appears to be longitudinally elongated and almost oval in shape, with its maximum width at the medial portion (Figs. 2 and 3). In a 71.4% of the examined specimens belonging to the developmental stage 1 (<60.0 mm SL) the optic tectum (considering both lobes) was more voluminous than the *corpus cerebelli*, in medium sized specimens (60.0–80.0 mm SL) the optic tectum was more voluminous only in a 42.8% of the examined specimens, and in all but one specimen (*i.e.*, 92.8%) belonging to the developmental stage 3 (>80.0 mm SL) the *corpus cerebelli* was, on the other hand, the more voluminous brain subdivision (also see the “Quantitative approach”).

Rhombencephalon

The *corpus cerebelli* is located at the dorsal portion of the *rhombencephalon*, posterior to the optic tectum and anterior to the *lobus facialis* in dorsal view; in lateral view its anterior portion is located dorsal to the posterior portion of the optic tectum and its posterior portion is located dorsal to the *eminentia granularis* (Figs. 2 and 3). The *corpus cerebelli* is almost pear-like shaped in dorsal view, with its maximum width (at the posterior portion) almost twice the minimum width (at the anterior portion); in lateral view, its dorsal profile is relatively straight, without undulations; in dorsal view, its lateral and posterior margins are undulated (Figs. 2 and 3). The *eminentia granularis* is usually inconspicuous in smaller specimens (<60.0 mm SL) but conspicuous in larger specimens (>80.0 mm SL; Figs. 2 and 3); it is located at the dorsal portion of the *rhombencephalon*, posterolaterally to the *corpus cerebelli* and lateral (at the outer side) to the *lobus facialis* (Figs. 2 and 3). In lateral view, the *eminentia granularis* is vertically elongated and almost oval in shape, with its vertical middle axis forming an angle of about 60° with the medial horizontal axis of the optic tectum (Figs. 2 and 3). In smaller specimens (<60.0 mm SL) the *eminentia granularis* is located in an anterior position [contrary, in larger specimens (>80.00 mm SL) it is located in a posterior position] and ventral to the *corpus cerebelli* in lateral view (Figs. 2 and 3).

The *lobus facialis* is located at the dorsal portion of the *rhombencephalon*, posterior to the *corpus cerebelli*, anterior to the *lobus vagi*, and mesial to the *eminentia granularis* in dorsal view; in lateral view the *lobus facialis* is located dorsal to the *truncus cerebri* (Figs. 2 and 3). The lobes of the *lobus facialis* are approximately oval in shape, their longitudinal middle axis form an angle of about 160° and they do not contact one another (Figs. 2 and 3). The *lobus vagi*, located immediately posterior to the *lobus facialis*, at the dorsal portion of the *rhombencephalon*, is composed of two “quotation mark” shaped lobes; the anterior portion of each lobe is conspicuously intumescent and their posterior portions are in contact forming a horseshoe-shaped structure (Figs. 2 and 3). The alar portion of the *medulla oblongata*, located immediately posterior to the *lobus vagi*, is composed of two almost oval-shaped structures (in dorsal view) contacting the *medulla spinalis* at the distal margin; the posterior portion of the alar portion of the *medulla oblongata* is slightly smaller than the anterior portion and both are conspicuously intumescent (Figs. 2 and 3).

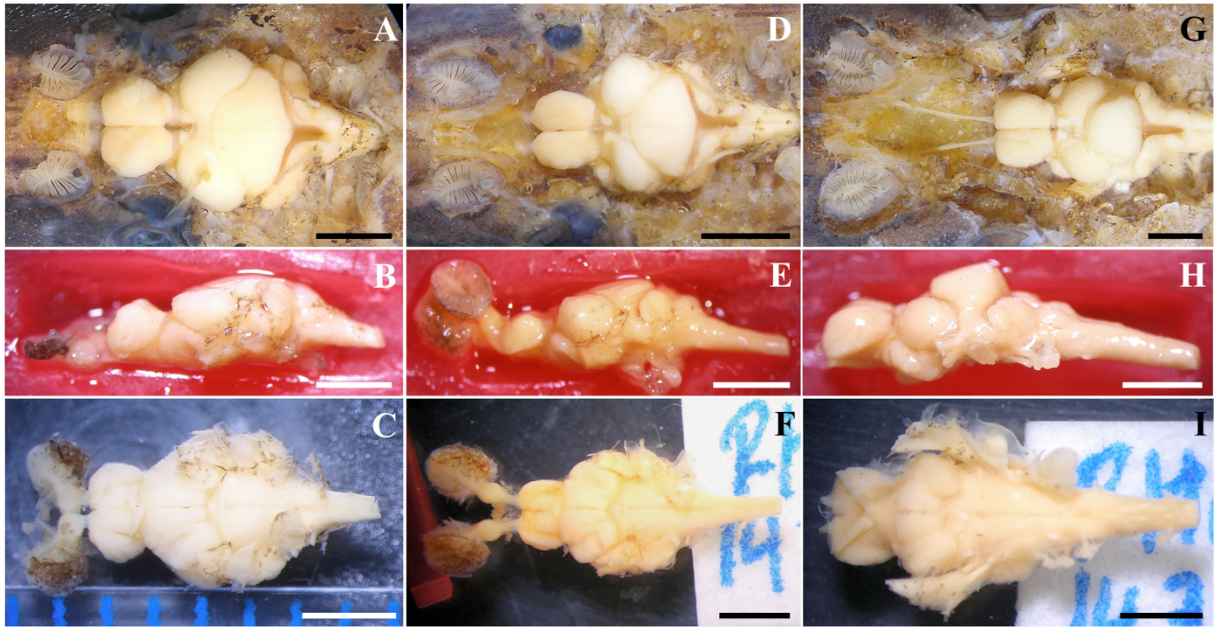


Figure 3. Intraspecific variation on the brain of *R. heteroptera*; Machado River basin, Madeira River drainage, Rondonia, Brazil. (A, B, C) DZSJPR 016730, 38.75 mm SL; (D) dorsal, (E) lateral (left side) and (F) ventral views. (D, E, F) DZSJPR 014771, 54.31 mm SL; (D) dorsal, (E) lateral (left side) and (F) ventral views. (G, H, I) DZSJPR 014549, 97.29 mm SL; (G) dorsal, (H) lateral (left side) and (I) ventral views. Scale bar=2 mm.

The *truncus cerebri* is ventrally located in the brain, between the posterior portion of the *mesencephalon* and the anterior portion of the *medulla spinalis*; it is comprised by both the *mesencephalon* and the *rhombencephalon* (Figs. 2 and 3). Most cranial nerves exit/enter their efferent/afferent fibers, respectively, in this area, except, as detailed above, for the *nervus olfactorius* and the *nervus opticus*. The cranial nerves leaving or entering to the *truncus cerebri* include: the *nervus oculomotorius* (III), the *nervus trochlearis* (IV), the *nervus trigeminus* (V), the *nervus facialis* (VII), the *nervus octavus* or *vestibularis* (VIII), the *nervus glossopharyngeus* (IX), the *nervus vagus* (X) and the *nervus linea lateralis anterior* and *posterior* (Figs. 2 and 3); all these nerves are “unspecialized” and do not present apparent external hypertrophy (Figs. 2 and 3). The nerves III–V and VII and the *nervus linea lateralis anterior* exit/enter their efferent/afferent fibers at the anterior-ventral portion of the *rhombencephalon*, at approximately the mid-point of the *corpus cerebelli*; the *nervus octavus* and the *nervus linea lateralis posterior* enter their afferent fibers at the

medial-ventral portion of the *rhombencephalon*; and the *nervus glossopharyngeus* and the *nervus vagus* exit/enter their efferent/afferent fibers, respectively, at the postero-lateral portion of the *rhombencephalon*, at approximately the mid-point of the *lobus vagi* (Figs. 2 and 3).

2.5.2. Sexual dimorphism and ontogenetic variation in the number of lamellae on the olfactory organs and in the total brain size and mass and brain subdivisions volumes in *Rineloricaria heteroptera* (Quantitative approach)

No significant differences in the number of lamellae between both left and right olfactory organs were recorded in the specimens examined ($t_{41}=0$, $p=1$). On the other hand, significant differences on the average number of lamellae (considering both left and right olfactory organs in each specimen) were recorded between specimens of different developmental stages ($F_{2, 41}=103.60$, $p < 0.05$); *i.e.*, smaller specimens (<60.0 mm SL) presented lower average lamellae counts (12–15, mean 13.7, mode 15), whereas larger specimens (>80.0 mm SL) presented greater average lamellae counts (22–24, mean 22.8, mode 23). Contrary, sex and the interaction between both sex and developmental stage did not show a significant effect on the average number of lamellae ($F_{1, 41}=0.03$, $p=0.85$ and $F_{1, 41}=0.03$, $p=0.97$, respectively); *i.e.*, no differences were observed among sexes, both in general and within each developmental stage.

Both total brain length and mass showed a negative allometric scaling against body length (SL) and mass, respectively (Figs. 4 and 5). Total brain lengths and masses varied from 4.10 mm (in an early juvenile specimen of 35.48 mm SL) to 8.11 mm (in an adult specimen of 114.42 mm SL) and from 3.23 mg (in an early juvenile specimen with a body mass of 200 mg) to 23.87 mg (in an adult specimen with a body mass of 5700 mg; see Table 1); *i.e.*, while largest specimens had a body length and mass that was nearly 3.3 and 28.5 times greater than that of the smallest specimens, over this same range of body lengths and masses the brain length and mass increased only by 2.0 and 7.4 times respectively. The OLS linear regression equations, $\pm$ standard error of mean (SEM), describing these relationships were: $y=0.481\pm0.032 * x - 0.101\pm0.059$ ($r^2=0.84$), for the LOG brain length vs. LOG SL relationship (Fig. 4), and $y=0.441\pm0.027 * x - 2.045\pm0.011$ ($r^2=0.87$), for the LOG brain mass vs. LOG body mass relationship (Fig. 5); in both cases, no differences in

the relative growth of the brain were observed among developmental stages or sexes, both in general and within each developmental stage; *i.e.*, neither of the fixed factors, or the interaction between them, was a significant predictor of the brain length or mass change along growth (Table 2).

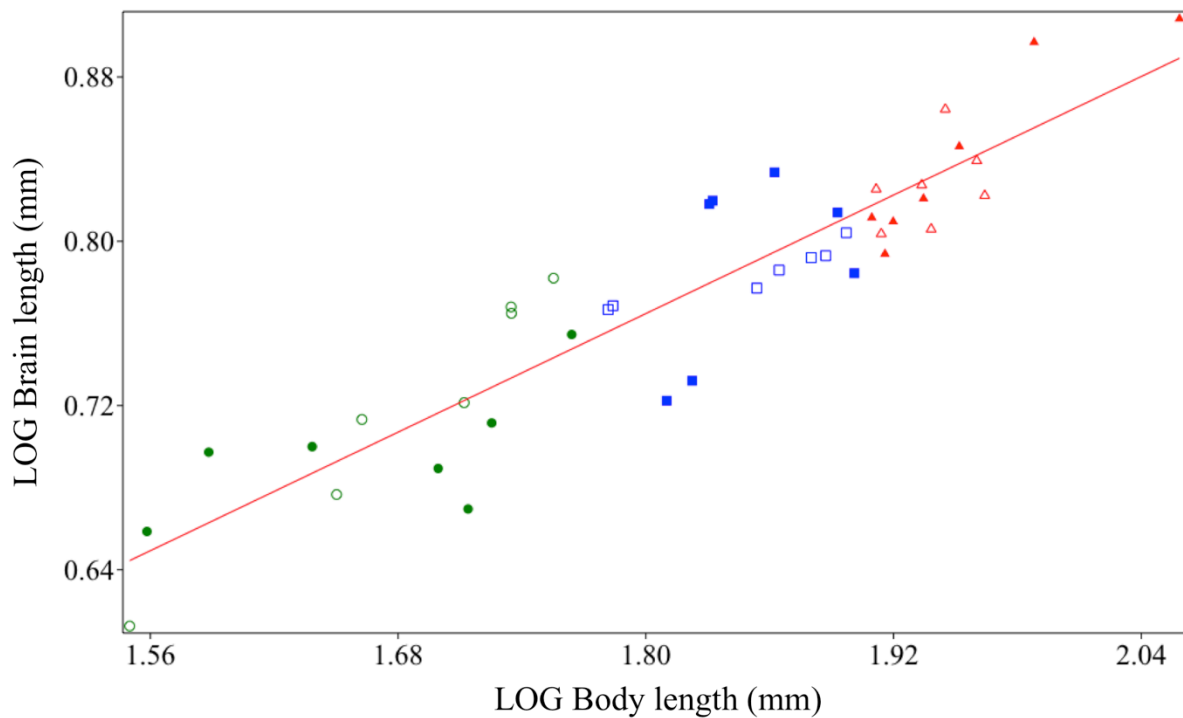


Figure 4. Regression analysis (OLS) of the LOG brain size (length) on the LOG body size (length) in *R. heteroptera*. Developmental stages are denoted with different color symbols (Green=early juveniles, *i.e.* <60.0 mm SL; Blue=late juveniles, *i.e.* 60.1–80.0 mm SL; and Red=adults, *i.e.* >80.0 mm SL); females are represented by closed symbols, males are represented by open symbols.

As previously stated, OLS linear regressions also were used to assess the scaling relationships for each brain subdivision (*i.e.*, olfactory bulbs, *telencephalon*, optic tecta, hypothalamus, *corpus cerebelli*, facial lobe, vagal lobe and alar portion of the *medulla oblongata*), using the corrected total brain volume as independent variable; the resultant regression equations and lines for these relationships are presented and illustrated in the Table 3 and the Figure 6, respectively. The 95% bootstrapped confidence intervals for the allometric coefficient values for each regression equation (see Table 3) revealed that the slopes of the regression lines for

Table 2. Results of the ANCOVAs evaluating the effect of the body length (SL) and the body mass (BW), as the covariates, and the sex, the developmental stage and the interaction between them (*i.e.* sex*developmental stage), as the factors, on the scaling of the overall brain length (T-L) and brain mass (T-W) in *R. heteroptera*. Significant p values are denoted with an asterisk (*).

Brain variable	Specimen variable (SL or BW)		Sex		Developmental stage		Sex*Developmental stage	
	F _{1,35}	p	F _{1,35}	p	F _{2,35}	p	F _{2,35}	p
T-L	202.877	<0.001*	0.018	0.894	0.432	0.653	0.605	0.552
T-W	271.817	<0.001*	0.073	0.787	0.709	0.499	2.032	0.146

Table 3. Slopes or "allometric coefficients" (a) and intercepts or "allometric components" (b), with their respective $\pm$ standard error of mean (SEM) and 95% bootstrapped confidence intervals (CIV; N=1999), and correlation values (r^2), with their respective associated "p" value, of the OLS linear regressions lines for the eighth major brain subdivisions volumes (vs. corrected total brain volumes) in *R. heteroptera*. Other abbreviations: Ce=*corpus cerebeli*, Hy=*hypothalamus*, LobVII=*lobus facialis*, LobX=*lobus vagi*, MO=*medulla oblongata* (alar portion), OB=*olfactory bulb*, OT=*optic tectum*, Te=*telencephalon*.

Brain subdivision	a $\pm$ SEM	CIV	b $\pm$ SEM	CIV	r^2	p
OB	1.9620 $\pm$ 0.1303	(1.5640, 2.2781)	-2.5942 $\pm$ 0.1360	(-2.9471, -2.1596)	0.8500	0.0001
Te	0.8967 $\pm$ 0.0489	(0.7991, 0.9955)	-0.5483 $\pm$ 0.0474	(-0.6455, -0.4558)	0.8935	0.0001
OT	0.8117 $\pm$ 0.0381	(0.7333, 0.8880)	-0.2731 $\pm$ 0.0352	(-0.3422, -0.1978)	0.9191	0.0001

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Brain subdivision	a ± SEM	CIV	b ± SEM	CIV	r ²	p
Hy	0.9926 ± 0.0575	(0.8367, 1.1421)	-0.5722 ± 0.0549	(-0.7200, -0.4217)	0.8816	0.0001
Ce	0.9732 ± 0.0536	(0.8491, 1.1148)	-0.3983 ± 0.0492	(-0.5345, -0.2790)	0.8916	0.0001
LobVII	1.7094 ± 0.0702	(1.5568, 1.8531)	-2.4784 ± 0.0735	(-2.6414, -2.3072)	0.9369	0.0001
LobX	1.8532 ± 0.0880	(1.6613, 2.048)	-2.8578 ± 0.0924	(-3.0743, -2.6417)	0.9172	0.0001
MO	1.8971 ± 0.0837	(1.6996, 2.0604)	-2.9492 ± 0.0880	(-3.1273, -2.7341)	0.9632	0.0001

Table 4. Results of the ANCOVAs evaluating the effect of the corrected total brain volume, as the covariate, and the sex, the developmental stage and the interaction between them (*i.e.* sex*developmental stage), as the factors, on the scaling of each brain subdivision volume in *R. heteroptera*. Significant p values are denoted with an asterisk (*). Abbreviations: Ce=*corpus cerebeli*, Hy=*hypothalamus*, LobVII=*lobus facialis*, LobX=*lobus vagi*, MO=*medulla oblongata* (alar portion), OB=*olfactory bulb*, OT=*optic tectum*, Te=*telencephalon*.

Brain subdivision	Total brain volume		Sex		Developmental stage		Sex*Developmental stage	
	F _{1,35}	p	F _{1,35}	p	F _{2,35}	p	F _{2,35}	p
OB	241.589	<0.001*	2.462	0.126	0.266	0.768	2.316	0.113
Te	304.305	<0.001*	0.185	0.670	0.258	0.774	0.287	0.752
OT	503.107	<0.001*	0.156	0.695	3.610	0.038*	0.943	0.399
Hy	355.804	<0.001*	3.622	0.065	2.334	0.112	2.246	0.121

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Brain subdivision	Total brain volume		Sex		Developmental stage		Sex*Developmental stage	
	F _{1,35}	p	F _{1,35}	p	F _{2,35}	p	F _{2,35}	p
Ce	317.908	<0.001*	1.252	0.271	0.636	0.536	0.564	0.574
LobVII	583.533	<0.001*	1.334	0.256	0.826	0.446	0.665	0.521
LobX	580.415	<0.001*	9.573	0.004*	2.269	0.118	1.624	0.212
MO	661.137	<0.001*	8.115	0.007*	3.759	0.033*	0.436	0.650

Table 5. Results for the first four components (PCs) of the PCA of the relative volume of eight brain subdivisions in *R. heteroptera*. Other abbreviations: Ce=*corpus cerebeli*, Hy=*hypothalamus*, LobVII=*lobus facialis*, LobX=*lobus vagi*, MO=*medulla oblongata* (alar portion), OB=*olfactory bulb*, OT=*optic tectum*, Te=*telencephalon*.

Factor/Brain subdivision	PC 1	PC 2	PC 3	PC 4
Variance explained, proportion (%)	42.49	24.23	18.77	9.04
Variance explained, cumulative proportion (%)	42.49	66.72	85.48	94.53
Relative loadings				
OB	0.621	0.187	0.086	-0.077
Te	-0.092	0.412	0.412	-0.633
OT	-0.456	0.047	0.341	0.567
Hy	0.020	0.385	-0.787	0.096
Ce	0.059	-0.802	-0.135	-0.276

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Relative loadings				
LobVII	0.387	-0.031	0.142	0.183
LobX	0.350	0.000	0.156	0.266
MO	0.347	-0.014	0.156	0.285

Table 6. Results of the PERMANOVA test for statistical significance between groups of the Loricariidae, based on the PCoA using a total of 88 binary or multistate, non-ordered characters describing its gross brain morphology. Pairwise comparisons; F and Bonferroni-corrected p (Bp) values. Abbreviations: TG=Taxonomic group; De=Delturinae; Hp=Hypoptopomatinae; Hy=Hypostominae; LF=Loricariinae, Loricariini, Farlowellina; LH=Loricariinae, Harttiini; Li=Lithogeninae; LL=Loricariinae, Loricariini, Loricariina; Ne=Neoplecostominae; and Rh=Rhinelepininae. Bold numbers denotes a significant difference between groups.

TG (F\Bp)	De	Hp	Hy	LF	LH	Li	LL	Ne	Rh
De	-	0.014	0.306	0.036	0.346	1.000	0.004	0.083	1.000
Hp	1.427	-	0.004	0.004	0.004	1.000	0.004	0.004	1.000
Hy	1.675	1.415	-	0.004	0.004	1.000	0.004	0.004	1.000
LF	1.598	1.481	1.582	-	0.004	1.000	0.004	0.004	1.000
LH	1.595	1.338	1.480	1.446	-	1.000	0.004	0.007	1.000
Li	1.499	1.126	1.363	1.334	1.257	-	1.000	1.000	1.000
LL	1.514	1.530	1.505	1.522	1.448	1.236	-	0.004	1.000
Ne	1.471	1.358	1.419	1.480	1.446	1.208	1.498	-	1.000
Rh	1.379	1.031	1.147	1.161	1.188	1.471	1.101	1.074	-

most of the brain subdivisions (with exception of those from the hypothalamus and the *corpus cerebelli*) were significantly different from zero, indicating allometric growth (vs. isometric growth). The slopes of the regression lines for the olfactory bulbs and the *medulla oblongata* subdivisions were both >1 , indicating that these brain subdivisions grow more quickly than the rest of the brain (*i.e.*, they show a positive allometry), and the slopes of the regression lines for the *telencephalon* and the optic tecta were both <1 , indicating negative allometry. Moreover, comparisons of the confidence intervals for the allometric coefficient values of the different regression equations (see Table 3) revealed that the slopes for the olfactory bulbs and the *medulla oblongata* subdivisions were not significantly different from each other, but they were significantly different from the slopes for all other brain subdivisions, indicating some degree of tachyaukinesis of these subdivisions against the entire brain. The results of the eight independent two-way ANCOVAs, performed on the same dataset, revealed that, as expected, the (corrected) total brain volume was the most significant predictor of the volume of each one of the eight brain subdivisions analyzed (Table 4). In addition, the developmental stage and sex, but not the interaction between them, proved to be significant predictors of the volume of the optic tectum and the alar portion of the *medulla oblongata* and of the vagal lobe and the alar portion of the *medulla oblongata*, respectively (see Table 4). As also mentioned and illustrated below, smaller specimens (<60.0 mm SL) showed proportionally greater (more voluminous) optic tecta and proportionally smaller (less voluminous) *medulla oblongatas* than adults (>80.0 mm SL), whereas, males showed proportionally larger (more voluminous) vagal lobes and alar portions of the *medulla oblongata* than females.

The PCA of the relative volume of the eight brain subdivisions separated relatively well in the multidimensional space the three age groups previously defined; contrary, no apparent differences in the clustering of the samples were recorded considering both sexes, both in general and within each developmental stage (Fig. 7). The relative importance of the first four components and the relative loadings of each variable in each component are showed in Table 5. The first component (PC1), explaining 42.5% of the overall variance, was associated with high loadings for the olfactory bulbs volume, and, secondarily, for the *medulla oblongata* subdivisions volumes (*i.e.*, the facial and vagal lobes and the alar portion), and separated relatively well adults (>80.0 mm SL), which presents relatively large olfactory bulbs

and medullary systems, from early juveniles (<60.0 mm SL), which presents, in contrast, relatively larger optic tecta (showing negative values in PC1; see Table 5). The second component (PC2), explaining 24.2% of the overall variance, was associated with positive loadings for the *telencephalon* and the hypothalamus volumes and with negative values for the *corpus cerebelli* volume; however, the PC2 did not separate juveniles from adults.

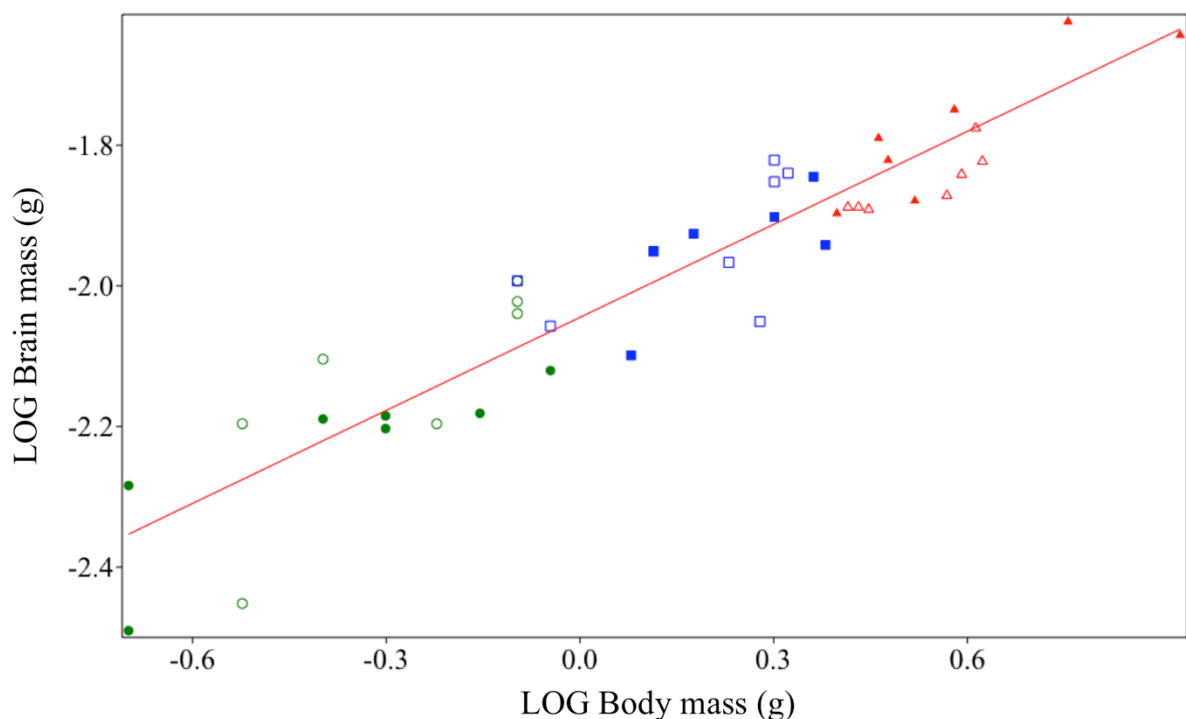


Figure 5. Regression analysis (OLS) of the LOG brain mass on the LOG body mass in *R. heteroptera*. Developmental stages are denoted with different color symbols (Green=early juveniles, *i.e.* <60.0 mm SL; Blue=late juveniles, *i.e.* 60.1–80.0 mm SL; and Red=adults, *i.e.* >80.0 mm SL); females are represented by closed symbols, males are represented by open symbols.

2.6. DISCUSSION

2.6.1. Sexual dimorphism in the brain of *Rineloricaria heteroptera* and its ecological implications

Most species of *Rineloricaria*, including *R. heteroptera*, show a remarkable external sexual dimorphism, characterized by the presence (in males) of thickened and curved pectoral-fin spines as well as of numerous odontodes along the sides of the head, the pectoral-fin spines and the predorsal area (ISBRÜCKER & NIJSSEN, 1976, 1992; RAPP PY-DANIEL & COX-FERNANDES, 2005). These anatomical modifications are usually utilized in agonistic behaviors including intraspecific displays and combats (ISBRÜCKER & NIJSSEN, 1976, 1992), and, as expected, should reflect in brain morphology leading to sexual dimorphism (PARHAR *et al.*, 2001). In contrast to the expected, no sexual dimorphism was found in the relative volume of the most of the examined brain subdivisions along development or independently of this (Figs. 6 and 7). Significant differences in the average volume of the brain subdivisions among sexes, independently of the developmental stage, were detected only for the vagal lobe and for the alar portion of the *medulla oblongata* (see above). Interestingly, other studies examining the gross brain morphology of some species of neotropical catfishes (*e.g.*, PUPO, 2011; ABRAHÃO & SHIBATTA, 2015; ROSA, 2015), cyprinids (Cyprinidae, Cypriniformes; *e.g.*, EVANS, 1931), and cichlids (Cichlidae, Perciformes; *e.g.*, VAN STAADEN *et al.*, 1995), which are known to exhibit a marked external sexual dimorphism, also do not report sex linked differences in most of the examined brain subdivisions along development. These results could suggest, as noted by previous authors (*e.g.*, VAN STAADEN *ET AL.*, 1995; PARHAR *et al.*, 2001; GONZALEZ-VOYER *et al.*, 2009), that sexual external dimorphic characters, and related behaviors, have none or little direct impact on the external brain morphology of these fishes (at least for the great majority of brain subdivisions). On the other hand, as also suggested by previous authors (*e.g.*, LANDE, 1980; VAN STAADEN *et al.*, 1995; GONZALEZ-VOYER *et al.*, 2009), environmental and ecological factors, which are expected to impose similar selective pressures on both sexes, at each different developmental stage, could be more important in shaping brain morphology, explaining in part the absence of sexual dimorphism in most brain subdivisions.

MARTINS & LANGEANI (2011) studied the brain morphology of members of the Hypoptopomatinae (Loricariidae) and reported wider nostrils in males of some genera and species within the subfamily; however, these authors did not mention any difference in the olfactory organs, and/or other related brain subdivision, nor discuss its possible(s) ethological or ecological implications. MARTINS *et al.* (2014) and

ROSA (2015) reported some additional dimorphic neuroanatomical characters in members of the subfamily (*i.e.*, larger olfactory organs and a greater number of olfactory lamellae in males of some species), but, again, they do not refer to other brain subdivision nor discuss its possible(s) ethological or ecological implications. The anatomical differences reported in members of the Hypoptopomatinae by previous authors, which are possibly related to mate location (see GIBBS, 1991; ARIF, 2011), were not observed in *R. heteroptera*. However, as noted above, differences in the average volume of the vagal lobe and of the alar portion of the *medulla oblongata* were observed among sexes.

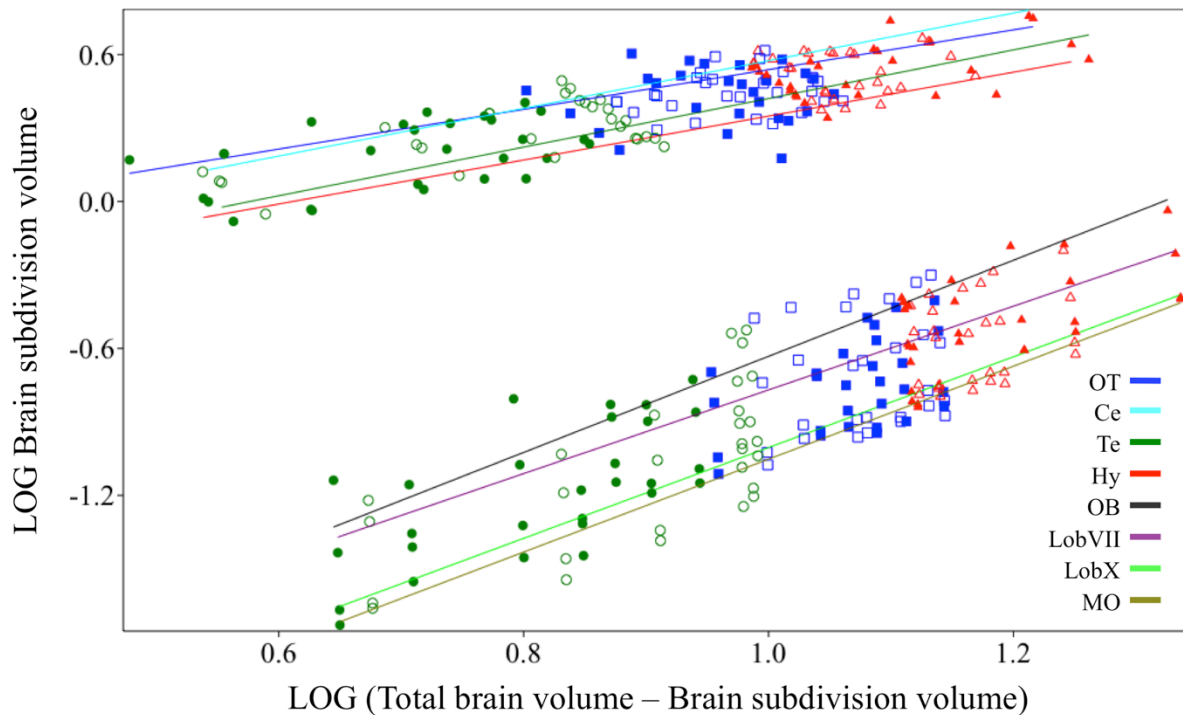


Figure 6. Allometric scaling relationships (volume vs. volume OLS regression lines) for the eighth major brain subdivisions [Ce=*corpus cerebeli*, Hy=*hypothalamus*, LobVII=*lobus facialis*, LobX=*lobus vagi*, MO=*medulla oblongata* (alar portion), OB=*olfactory bulb*, OT=*optic tectum*, Te=*telencephalon*] in *R. heteroptera*. Developmental stages are denoted with different color symbols (Green=early juveniles, *i.e.* <60.0 mm SL; Blue=late juveniles, *i.e.* 60.1–80.0 mm SL; and Red=adults, *i.e.* >80.0 mm SL); females are represented by closed symbols, males are represented by open symbols.

Medulla oblongata subdivisions are usually associated to the gustative perception, receiving sensory information from taste buds present in the barbels, mouth, pharynx and gill arches (MEEK & NIEUWENHUYS, 1998; ABRAHÃO & SHIBATTA, 2015). Differences in the average volume of these medullary subdivisions among sexes can be associated to possible differences in the perception and use of food resources and foraging strategies at the intraspecific level (EVANS, 1931; ATEMA, 1971). In addition, because several species of Loricariidae shows a remarkable “bucal” paternal care, including *R. heteroptera* (see TAYLOR, 1983; GROSS & SARGENT, 1985; MARCUCCI *ET AL.*, 2005; RAPP PY-DANIEL & COX-FERNANDES, 2005), brain modifications on medullary subsystems such as the *lobus vagi* and the alar portion, also could be associated with increased sensitive capacities and/or specialized behaviors related to the care of the progeny [e.g. the males of some species of *Loricaria* and *Loricariichthys* (not being the specific case of *R. heteroptera*) exhibit an accentuated sexual dimorphism during the reproductive season characterized by an increase on the size and structural complexity of some oral structures, such as the lips (see TAYLOR, 1983; RAPP PY-DANIEL & COX-FERNANDES, 2005); additionally, members of these two genera, have massive vagal lobes, generally much more developed than in other members of Loricariidae (Rosa, 2015)]. However, it is difficult to do more than speculate on the factors behind the apparent differences in the volume of some brain subdivisions among sexes considering the absence of both detailed life history data for the species under study as well as information on the role of the senses in both immature and mature specimens, both males and females.

2.6.2. Ontogenetic variation in the brain of *Rineloricaria heteroptera* and its ecological implications

Teleost fish brains grow in a negative allometric relationship to the body (GEIGER 1956; RIDET *et al.*, 1977; BRANDSTÄTTER & KOTRSCHAL, 1990; VAN STAADEN *et al.*, 1995), and, according to the results of this study (see Figs. 4 and 5), *R. heteroptera* is not an exception to this pattern. Brain growth patterns similar to that described here for *R. heteroptera*, i.e., total brain length/mass as dependent variable of total body length/mass, have also been documented in some members of the Cyprinidae (GEIGER, 1956; BRANDSTÄTTER & KOTRSCHAL, 1990;

KOTRSCHAL *et al.*, 1990; 1998; KOTRSCHAL & PALZENBERGER, 1991), Macrouridae (WAGNER, 2003) and even in elasmobranch fishes (LISNEY *et al.*, 2007). Additionally, in most of these published cases, as also found for *R. heteroptera*, the measurements related to the brain as a whole (*i.e.*, total brain length, total brain width and total brain height) as well as those related to the *corpus cerebelli*, optic tectum and the *medulla oblongata*, were usually the most variables. Moreover, the regression lines reported demonstrated that the brain of *R. heteroptera*, as also described for most teleost and non-teleost fish taxa (see KOTRSCHAL *et al.*, 1990; 1998; WAGNER, 2003; LISNEY *et al.*, 2007; 2017; among others), displays an indeterminate growth.

Specific growth rates for each one of the brain subdivisions in *R. heteroptera*, expressed as volume vs. volume relationships, were relatively constant and the slopes of the growth equation for most of them (*i.e.*, telencephalon, optic tectum, hypothalamus and *corpus cerebelli*) were almost parallel (Fig. 6), indicating that functional differentiation, as also occur in most teleost fish taxa (see MILLER & EVANS, 1965; Brandstätter & Kotrschal, 1990; OSSE & VAN DEN BOOGAART, 1999; BUTLER & HODOS, 2005), is nearly complete by hatching. Positive allometric growth was recorded for the olfactory bulbs and the *medulla oblongata* subdivisions; in contrast, the slopes of the regression lines for the *telencephalon* and the optic tecta were both <1 , indicating negative allometry (see Table 3, Fig. 6). These results agree partially with the brain growth patterns described in some species of non-teleost (*e.g.*, LISNEY *et al.*, 2007; 2017; SALAS *et al.*, 2015) and teleost fishes (*e.g.*, WAGNER, 2003) and could suggest ontogenetic shifts in the habitat preference, resources use and/or behavior of the species (see below). Moreover, the slopes of the growth equation for the olfactory bulbs and the *medulla oblongata* subdivisions volumes were significantly higher to those of the remaining brain subdivisions, which indicate some degree of tachauxesis of these structures against the entire brain (see Table 3, Fig. 6).

Because olfaction, which is used primarily for social communication (FINGER, 1988; HUBER & RYLANDER, 1992), is routed through the olfactory bulbs (HUBER & RYLANDER, 1992), and taste, which is used both in locating food and in evaluating it once found (HUBER & RYLANDER, 1992; MEEK & NIEUWENHUYS, 1998), is routed through the dorsal medulla (specifically to the alar portion of the *medulla oblongata* and the sensory nuclei of the *nervus facialis* and the *nervus vagus*;

HUBER & RYLANDER, 1992), the differential development of both structures (olfactory bulb and *medulla oblongata* as a whole) could be correlated, as also found in other teleost (e.g., WAGNER, 2003) and non-teleost fishes (e.g., SALAS *et al.*, 2015; LISNEY *et al.*, 2017), to differences in communication and foraging mechanisms and patterns along the growth. The differences observed in the number of lamellae in the olfactory organ and in the relative size of the olfactory organs between developmental stages, also could support this hypothesis; however, more detailed anatomical, physiological and ecological studies are necessary to corroborate such assumptions.

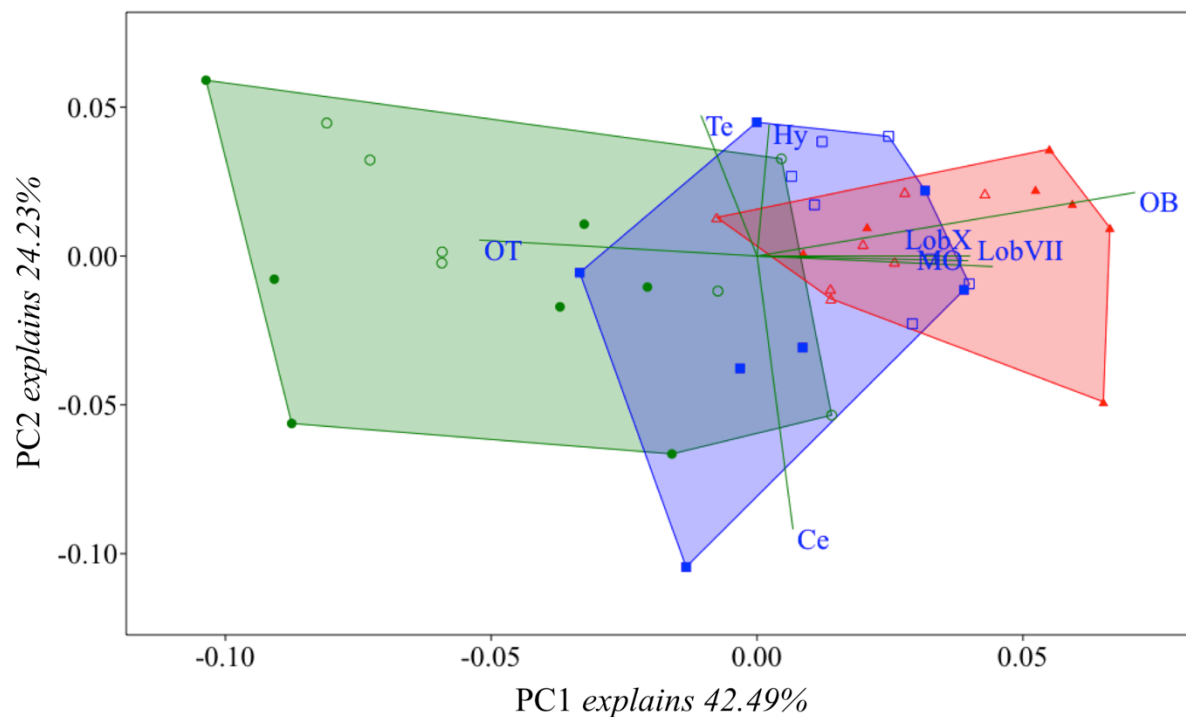


Figure 7. Scatterplot of the PCA (PC1 vs. PC2), representing the major changes in the composition of the brain along development in *R. heteroptera*. Developmental stages are denoted with different color symbols (Green=early juveniles, *i.e.* <60.0 mm SL; Blue=late juveniles, *i.e.* 60.1–80.0 mm SL; and Red=adults, *i.e.* >80.0 mm SL); females are represented by closed symbols, males are represented by open symbols. Abbreviations: Ce=*corpus cerebeli*, Hy=*hypothalamus*, LobVII=*lobus facialis*, LobX=*lobus vagi*, MO=*medulla oblongata* (alar portion), OB=*olfactory bulb*, OT=*optic tectum*, Te=*telencephalon*.

Another factor that could be linked to the presence of enlarged olfactory bulbs in adult specimens of *R. heteroptera* is the reproductive behavior (see LISNEY *et al.*, 2007; 2017). In general terms, hormonal pheromones play a significant role in the reproductive biology of most teleost fishes (see STACEY, 2003; LISNEY *et al.*, 2017) and non-teleost fishes (see PRATT & CARRIER, 2001; CHAPMAN *et al.*, 2003). This fact led some authors (e.g., LISNEY *et al.* 2007; 2017) to suggest that an increased reliance on olfaction in mature specimens could be highly associated with the need to detect reproductive pheromones; assuming that this relationship can also be applied for the studied species, it could also explain at least partially the observed differences. However, as noted by LISNEY *et al.* (2017), further studies, assessing whether the variation in the olfactory bulbs shape, volume and/or ultrastructure is/can be correlated (or not) with possible functional changes in the olfactory capabilities in those fish groups and others, are necessary to corroborate such assumptions.

The *corpus cerebelli* was the larger and more voluminous subdivision of the brain in most of the examined specimens, mainly in adult specimens. This condition, also observed in other catfish species [e.g., *Pseudopimelodus* spp. (ABRAHÃO & SHIBATTA, 2015); *Clarias gariepinus* (Burchell, 1822) and *Pangasius pangasius* (Hamilton, 1822) (CHING *et al.*, 2015); *Diplomystes mesembrinus* (Ringuelet, 1982) (PEREIRA & CASTRO, 2016); members of Loricariidae (Rosa, 2015)] and some members of the Gymnotiformes (PEREIRA & CASTRO, 2016) and the Cypriniformes (BRANDSTÄTTER & KOTRSCHAL, 1990), is relatively common in species inhabiting structurally complex environments, like flowing waters, and is usually related to a high degree of motor coordination during swimming (BAUCHOT *et al.*, 1989; KOTRSCHAL *et al.*, 1998; BUTLER & HODOS, 2005; LISNEY & COLLIN, 2006; ABRAHÃO & SHIBATTA, 2015). The *corpus cerebelli*, as experiments have shown, also is important in various learning and memory processes associated with the spatial orientation (BROGLIO *et al.*, 2003; GONZALEZ-VOYER & KOLM, 2010). Given the results of this study, and considering the habitat use of the adults of *R. heteroptera*, it is possible to conclude, as also stated by previous authors (e.g., BROGLIO *et al.*, 2003; POLLEN *et al.*, 2007; Gonzalez-Voyer & Kolm, 2010; ABRAHÃO & SHIBATTA, 2015), that fish species with larger and voluminous cerebella are favored in structurally complex habitats given the demands on spatial cognition and memory.

In adults of *R. heteroptera*, the optic tectum was the second more important structure (in terms of its relative volume), followed by the *telencephalon*. This condition also observed in other members of the Loricariidae (ROSA, 2015) and some other members of the Siluriformes (ABRAHÃO & SHIBATTA, 2015; PEREIRA & CASTRO, 2016), Gymnotiformes (PEREIRA & CASTRO, 2016) and Cypriniformes (BRANDSTÄTTER & KOTRSCHAL, 1990; PEREIRA & CASTRO, 2016) also has been usually associated with fish species living in spatially structured environments (HUBER *et al.*, 1997; WAGNER, 2003). The optic tectum receives sensory information from the retina through the *nervus opticus*, and is responsible, among other functions, for generating signals that, via its connections to premotor centers, controls eye movements as well as approach and avoidance behaviors (MEEK & NIEUWENHUYS, 1998; BUTLER & HODOS, 2005; ABRAHÃO & SHIBATTA, 2015); in addition, the optic tectum also receives information from the auditory, and somatosensory systems, enabling the animal to create multisensory spatiotopic maps of their environment (BUTLER & HODOS, 2005; ABRAHÃO & SHIBATTA, 2015). The function of the telencephalon, on the other hand, is not well understood (MEEK & NIEUWENHUYS, 1997; WAGNER, 2003); however, as the *corpus cerebelli*, it has been traditionally considered as an important integration center (HUBER *et al.*, 1997; WAGNER, 2003). Therefore, the combination of motor body and eye coordination, promote responses from the *corpus cerebelli*, the optic tectum and the telencephalon being indispensables for behavioral reactions necessary for survival (e.g., location/identification of food items as well as potential predators) and reproduction (MEEK & NIEUWENHUYS, 1998; BROGLIO *et al.*, 2003; Wagner, 2003; BUTLER & HODOS, 2005), which explains the relative importance of these brain subdivisions in relation to the rest of the brain.

In most juveniles of *R. heteroptera*, the optic tectum, in contrast, was the more important structure (in terms of its relative volume), followed by the *corpus cerebelli*. This condition also observed in other members of Loricariidae (ROSA, 2015), some members of the Cypriniformes (BRANDSTÄTTER & KOTRSCHAL, 1989; 1990), most Characiformes (PEREIRA & CASTRO, 2016), Perciformes (HUBER *et al.* 1997; POLLEN *et al.*, 2007) and in some elasmobranch fishes (LISNEY *et al.*, 2007), has been usually associated with fish species that shows high visual dependence at early developmental stages (see NIEUWENHUYS *et al.*, 1998; LISNEY *et al.*, 2007). The differences observed in the proportional volumes of the *corpus cerebelli* and the optic

tectum among developmental stages could indicate, as also inferred from the allometric coefficients, a differential functional development of both brain subdivisions through growth (see below). Some authors (e.g., BRANDSTÄTTER & KOTRSCHAL, 1989; 1990), in contrast, suggest that the characteristic negative allometry of the optic tectum (also applicable for the *telencephalon* volume) is a consequence of initial size constraints in the larvae and the juvenile and a subsequent release from these constraints during development, not necessarily implying a differential functional development. Moreover, the use of the optic tectum size/volume as an indicator of the importance of the vision has been questioned since this structure is, as noted above, a multimodal center that receives inputs from several other modalities (see HUBER *et al.*, 1997; WAGNER, 2003; BODZNICK, 1991; LISNEY *et al.*, 2007); however, the strong correlations between eye size/volume, the number of axons in the *nervus opticus* and the optic tectum size/volume noted in several teleosts fish groups, as well in other fish taxa (i.e., elasmobranch fishes) (see HUBER *et al.* 1997; NIEUWENHUYIS *et al.*, 1998; LISNEY *et al.*, 2007; POLLEN *et al.*, 2007), provide strong evidence for the optic tectum size/volume (as herein measured) being an accurate indicator of visual capabilities, supporting, in part, the hypothesis previously mentioned suggesting the differential functional development of this structure through growth. Additionally, smaller specimens of *R. heteroptera* showed eyes proportionally larger than larger specimens (AA unpublished data), which, based on the above, also can be considered as empirical evidence supporting the idea that vision may be more important in juveniles.

In both juveniles and adults of *R. heteroptera* the *eminencia granularis* was relatively smaller, comparing for example with other catfish species [e.g., EGL=6.38–8.81% T-L vs. 10.10–12.90% T-L in *Pseudopimelodus* spp. (ABRAHÃO & SHIBATTA, 2015)], whereas the *lobus facialis* was relatively larger [LobVII-L=14.80–21.36% T-L vs. 12.8–16.7% T-L in *Pseudopimelodus* spp. (ABRAHÃO & SHIBATTA, 2015)]. The *lobus facialis* and the *lobus vagi*, in general terms, also appear to be more developed in *R. heteroptera* than in species of Ictaluridae (ATEMA, 1971), Siluridae (Siluriformes; ITO *et al.*, 2007) and some members of the Cyprinidae (EVANS, 1931) and the Characiformes (PEREIRA & CASTRO, 2016), whereas that they appear to be equally or less developed than in some species of Callichthyidae (PUPO, 2011, 2015; PUPO & BRITO, 2018; ROSA, 2015) and Cyprinidae (Cypriniformes; EVANS, 1931; ITO *et al.*, 2007). Contrary, the optic tectum, the

corpus cerebelli and the *eminentia granularis* appear to be less developed in *R. heteroptera* than in members of Ictaluridae (ATEMA, 1971), Pimelodidae (Siluriformes; TRAJANO 1994), Siluridae (ITO *et al.*, 2007) and some members of Cyprinidae (EVANS, 1931); being the most common pattern observed in members of Loricariidae (PUPO, 2015; ROSA, 2015; also see “Chapter two”). In this regard, EVANS (1931, 1940), studying the brain morphology in members of Cyprinidae, observed that in species that feed mainly on invertebrates, plant remnants and organic debris, as is the case of *R. heteroptera* (as well as in the vast majority of members of Loricariidae), the *lobus facialis* and the *lobus vagi* are relatively larger, whereas the *eminentia granularis* and the optic tectum are relatively smaller; in contrast, in species that feed primarily on other fishes, as is the case of some members of Pseudopimelodidae, Pimelodidae, Ictaluridae and Siluridae, among others, the opposite pattern was observed. In accordance with the above and considering the alimentary biology of the adults of *R. heteroptera* [mainly composed by aquatic insects (78.00%), algae (14.17%), plant remnants and organic debris (7.33%); see LACERDA (2007)], the results of this study are consistent with the expected and support EVANS’s (1931; 1940) observations.

Given the results of this study, it is possible to infer that, in *R. heteroptera*, the vision (e.g., detection of potential predators) could be fundamental in early stages, whereas in adults the olfaction and taste (e.g., food detection/evaluation and social communication) would play a more important role. This pattern of brain growth do not appear to be confined to this particular species and so an ontogenetic shift in the relative importance of the vision and olfaction may actually be widespread among other armoured catfishes, as well as in other teleost and non teleost fishes (see for example WAGNER, 2003; LISNEY *et al.*, 2007). However, as noted by LISNEY *et al.* (2007), it is difficult to do more than speculate on the factors behind this apparent shift in the absence of both detailed life history data for the majority of teleost fish taxa and information on the role of the senses in both juvenile and adult specimens. Whatever the adaptive significance, the apparent shift in the relative importance of each of the sensory modalities with development and knowing what sensory cues are important to juvenile and adult fishes is important in understanding their ecology and may have management implications, such as the identification of critical habitats and susceptibility to different human impacts (LISNEY *et al.*, 2007). Finally, the results of this study also show that consideration of ontogenetic changes in brain morphology

is necessary for an accurate assessment of neuroanatomical characters in phylogenetic studies, as a possible source of variation.

3. CHAPTER TWO:

GROSS BRAIN MORPHOLOGY OF THE LORICARIINAE: COMPARATIVE ANATOMY AND ECOLOGICAL AND PHYLOGENETIC CONSIDERATIONS

[Manuscript in preparation] A. Angulo, A. Rosa, D. C. Ribeiro & F. Langeani (*in prep.*) Gross brain morphology of the Loricariinae (Siluriformes: Loricariidae): comparative anatomy and ecological and phylogenetic considerations. To be submitted to *Journal of Fish Biology*.

3.1. ABSTRACT

The gross morphology of the brain of the Neotropical catfish subfamily Loricariinae is herein described, illustrated, interpreted and discussed. A comprehensive, qualitative and quantitative, comparison of the relative size, volume, shape and position of all major brain subdivisions (*i.e.*, *telencephalon*, *diencephalon*, *mesencephalon* and *rhombencephalon*), based on a combination of 89 binary or multistate non-ordered characters, is presented for representative species of all valid genera (except *Pterosturisoma*) of the subfamily, as well as for representative species of the other six subfamilies of the Loricariidae. Additional comparisons with species of other phylogenetically related families of the Siluriformes, as well as of other members of the Ostariophysi, provide a broader context for understanding the brain diversity and variation in members of the Loricariinae, Loricariidae and Siluriformes. The possible ecological and phylogenetic correlations and implications given the differences observed between all major brain subdivisions, considering the different taxa evaluated and compared, also are discussed. In general terms, the results of this study suggest that the relative size, volume, shape and position of the different brain subdivisions in members of the Loricariinae, Loricariidae and Siluriformes varies mostly with feeding behaviour and preferred environment. Furthermore, when analyzed and evaluated in conjunction with hypotheses of phylogenetic relationships, the results of this study also can be considered as

empirical evidence supporting the fact that brain diversity in current members of the subfamily and family could be the result of both phylogenetic niche conservatism and repeated adaptive radiation.

3.2. KEYWORDS

Neotropical freshwater fishes; Teleostei; Ostariophysi; neuroanatomy; *encephalon*; morphological disparity.

3.3. INTRODUCTION

Teleost fishes, by far the largest vertebrae group, have developed through the progression of the evolution a wide variety of brains, both in external morphology, size, volume and shape, as well as in internal structure and organization (ITO *et al.*, 2007; WHITE & BROWN, 2015). As in other vertebrate groups, the brain of the teleost fishes can be divided into several main regions, areas or structures [*i.e.*, *telencephalon* (including the olfactory bulbs), *diencephalon* (including the *epithalamus*, *thalamus*, and *hypothalamus*), *mesencephalon* (including the *tectum mecencephali* and the *tegumentum mecencephali*), and the *rhombencephalon* (including the *cerebellum* and the *medulla oblongata*; see NIEUWENHUYS, 1982)], each one of which participates in the control of multiple to very specific sensory and cognitive functions and/or behaviors (see KOTRSCHAL *et al.*, 1998 for an overview). Typical features of the brain of the teleost fishes, comparing with those of other vertebrate groups, include: relatively large olfactory bulbs; relatively small and everted *telencephala*; relatively large *lobi inferior hypothalami*, which are located on the ventral surface of the brain; two pronounced tectal (mesencephalic) halves, which are located dorsal to the *tegumentum mecencephali*; and a relatively large *rhombencephalon*, with a conspicuous *cerebellum* (see NIEUWENHUYS *et al.*, 1998; LECCHINI *et al.*, 2014). As discussed by previous authors (see NIEUWENHUYS *et al.*, 1998 for an overview), these features are usually correlated to different sensory, cognitive and behavioral restrictions, limitations and/or adaptations typical of the aquatic (and semiaquatic) environments.

Despite of the "generalized" pattern described above, the brain of the teleost fishes show a much higher morphological diversity when compared with that of other vertebrate groups (see ITO *et al.*, 2007). Such extraordinary diversity could be explained mainly by the relatively long and complex evolutionary history (phylogeny) of the group, as well as by diverse ecological and behavioral intrinsic and extrinsic factors and selective pressures (including diet and feeding habits, habitat use and complexity and increased sociality, among others) which have modeled or modified, by the way of adaptive and exaptive processes, the overall brain morphology (see KOTRSCHAL *et al.*, 1998; 2012; WAGNER, 2002; LISNEY & COLLIN, 2006; POLLEN *et al.*, 2007; LECCHINI *et al.*, 2014). Given the above and considering that the relative size, volume and shape of a specific brain subdivision typically indicates

the predominance of its function and/or the accuracy of the sense(s) to which it is related, strong ecomorphological correlations (and brain patterns) have been identified and described for some teleost fish taxa [see the contributions of EVANS (1931; 1940), VAN STAADEN *et al.*, (1995), HUBER *et al.* (1997), KOTRSCHAL *et al.* (1998), WAGNER (2002), BUTLER & HODOS (2005), LISNEY & COLLIN (2006), ITO *et al.* (2007), GONDA *et al.* (2011), KOTRSCHAL *et al.* (2012), LECCHINI *et al.* (2014), WHITE & BROWN (2015), among other authors].

For instance, comparative studies on cyprinids (Cyprinidae, Cypriniformes; EVANS, 1931; 1940) and cichlids (Cichlidae, Cichliformes; VAN STAADEN *et al.*, 1995; HUBER *et al.*, 1997), have showed that the relative size, volume and/or shape of the different main brain subdivisions can be related to different qualitative categories of physical environments and feeding strategies; such studies have linked the *telencephalon* size to habitat, the *tectum mecencephali* size to general feeding strategies, and the *medulla oblongata* size to food detection and selection. WAGNER (2002), on the other hand, observed that mesopelagic teleost fishes, including slickheads (Alepocephalidae, Osmeriformes), eels (Anguilliformes) and grenadiers (Macrouridae, Gadiformes), have reduced olfactory bulbs and larger *tecta mecencephali*, comparing with other demersal related species, which would be linked to a greater visual acuity and limited olfaction in mesopelagic environments, contrary to what has been observed in demersal environments. Finally, POLLEN *et al.* (2007), using cichlids as study group, showed that both environmental and social factors can affect in different ways brain morphology and development; the first one showing a broader effect on a wide range of brain subdivisions compared to social factors; *e.g.*, the *telencephalon* size showed a positive correlation with habitat size and complexity, while the *hypothalamus* size showed a positive correlation with monogamy.

Among catfishes (Siluriformes), encompassing about 13% of the total known teleost fish diversity, brain morphology and its ecological (and phylogenetic) correlations and implications have been relatively well studied only in the north American Ictaluridae; see for example the contributions of ATEMA (1971; 1980), FINGER (1976), KNUSEN (1976), LUNDBERG (1982), TONG & FINGER (1983), LEE & BULLOCK (1984), MORITA & FINGER (1985), KANWAL & CAPRIO (1987), STRIEDTER (1990; 1991), MEEK & NIEUWENHUYIS (1998), NORTHCUTT *et al.* (2000), among other authors. Contrary, studies on Neotropical catfishes *sensu stricto* are relatively scarce and have focused only in a few species or supraspecific groups;

e.g., in members of the Callichthyidae (PUPO, 2011; PUPO & BRITTO, 2018), Heptapteridae (TRAJANO, 1994; ABRAHÃO *et al.*, 2018b), Loricariidae (ROSA *et al.*, 2014; ROSA, 2015; ANGULO & LANGEANI, 2017; CHAMON *et al.*, 2018) and Pseudopimelodidae (ABRAHÃO & SHIBATTA, 2015; ABRAHÃO *et al.*, 2018a). Furthermore, in these essentially descriptive (mainly anatomical) contributions, the potential ecological (and phylogenetic) inferences and correlations, derived from such detailed morphological analyses, have been, in most cases, only superficially addressed (see ROSA, 2015; PEREIRA & CASTRO, 2016; ANGULO & LANGEANI, 2017; ABRAHÃO *et al.*, 2018a).

Given the above, and considering the huge taxonomic and ecological diversity within the group, there is still enough to know about variation in brain morphology in the vast majority of Neotropical catfishes (see PUPO, 2015). Consequently, as noted by previous authors (*e.g.*, ABRAHÃO & SHIBATTA, 2015; PUPO, 2015; PEREIRA & CASTRO, 2016; ANGULO & LANGEANI, 2017), more integrative, descriptive and quantitative, approaches, both at the inter- and intraspecific levels, are necessary to counter this problem, increasing and promoting the understanding on the diversity, phylogenetic relationships, ecology, physiology and functioning of this extremely rich and complex group of organisms. In accordance with the above, the aim of this paper is to describe the general, and interspecific (generic and suprageneric), gross morphology of the brain of the armoured catfish subfamily Loricariinae, the most diverse within the Loricariidae, as a baseline for future comparative anatomical, taxonomic, phylogenetic and ecological studies. In addition, the brain of the members of the Loricariinae is, qualitatively and quantitatively, compared with the brain of representatives of all other subfamilies of the Loricariidae, as well as some external taxa (within the Siluriformes and Ostariophysi), in order to evaluate its morphological variation and, in the case of the members of the Loricariidae, its morphological disparity (*i.e.*, the extent of morphospace occupied by its members). Finally, the possible correlations between the general brain morphological patterns observed and the sensory and behavioral ecology of the species and supraspecific groups studied also are evaluated and discussed.

3.4. MATERIAL AND METHODS

3.4.1. Group of study

The subfamily Loricariinae currently comprises 31 genera and 243 valid species (FRICKE et. al, 2018a). Members of the subfamily are widely distributed throughout the Central and South American major river drainages, from southern Costa Rica to northern Argentina (COVAIN & FISCH-MULLER, 2007), being found in an extremely diverse array of environments and showing a great morphological and functional diversity (see COVAIN & FISCH-MULLER, 2007; COVAIN, 2011; LUJAN *et al.*, 2015). Representatives of a total of 30 genera of the Loricariinae (all valid, except *Pterosturisoma*, Isbrücker & Nijssen 1978), including 83 valid species (*i.e.*, about 34% of the total number of current known species within the subfamily), plus seven additional unidentified or undescribed taxa, totalizing 90 taxa, were herein analyzed. Material from different locations throughout the group's whole distribution was included and analyzed. Comparative information from other species of the Loricariidae, including six subfamilies [Delturinae, Hypoptopomatinae in part (including the Otothyridae; see SCHAEFER 1991, 1998; CRAMER *et al.*, 2011; LUJAN *et al.*, 2015), Hypostominae, Lithogeninae, Neoplecostominae (recognized as tribe of the Hypoptopomatinae by LUJAN *et al.*, 2015 and ROXO *et al.*, 2017) and Rhinelepidinae; see FRICKE et. al, 2018a], 34 genera and 50 species, and the Siluriformes, as well as from members of the Characiformes, Cypriniformes and Gymnotiformes, was obtained from specimens examined (see below) and/or from images and descriptions available in the literature (EVANS, 1931, 1940; ALBERT *et al.*, 1998; ITO *et al.*, 2007; PUPO, 2011, 2015; PEREIRA, 2014; ABRAHÃO & SHIBATTA, 2015; ROSA, 2015; PEREIRA & CASTRO, 2016; ABRAHÃO *et al.*, 2018a; b).

3.4.2. Material examined

Material examined is listed in Appendix A; species are listed in alphabetical order; for each species, the following information is provided: lot(s) number(s) examined [institutional abbreviations follow SABAJ (2016); collection data can be accessed through the “Species link” online database site (<http://splink.cria.org.br/>)], number of specimens examined by lot, sex and standard length [SL; distance from the tip of the snout on the upper jaw to the midlateral posterior edge of the hypural plate and taken with the aim of a digital caliper (+/- 0.1 mm)] of examined specimens.

The sex of each specimen was determined, and corroborated (after observation of external dimorphic characters), by gonad examination after dissection. Most specimens examined were adults in order to avoid the “potentially confusing effects” (in the morphological descriptions and comparisons) of the developmental changes (as noted and discussed by HUBER & RYLANDER, 1992; WAGNER, 2003; ROSA *et al.* 2014; ROSA, 2015; ANGULO & LANGEANI, 2017 – also see “Chapter one”). The current taxonomic status of the species examined follows FRICKE *et al.* (2018b).

3.4.3. Data acquisition

Brains were dissected and removed from the preserved specimens following the protocol described by ABRAHÃO & PUPO (2014) as adapted to the Loricariidae by ROSA (2015). As the brains could not be cut off from the spinal cord at comparable positions in each specimen, the posterior limit of the brain was defined at the posterior limit of the alar portion of the *medulla oblongata* (see “Chapter one”) and all cuts were made posterior to this limit. After removal from the neurocranium the brains were stored in ≈70% ethanol. A digital camera attached to a stereomicroscope was used to capture scaled images of the brains of all specimens in dorsal (before and after removal from the neurocranium), lateral (left side) and ventral views. All photographs were taken according to the protocol described in ANGULO & LANGEANI (2017) – see “Chapter one”.

In order to describe, characterize and compare the gross brain morphology of the members of the Loricariinae and Loricariidae, a total of 89 characters were directly examined from the dissected brains, with the help of a stereoscopic microscope, and/or from the scaled photographs with the help of the image-analysis public domain software IMAGEJ1.49 (RASBAND, 1997). Comparative morphological data from other related groups (e.g., other members of the Loricarioidea, Siluriformes and Ostariophysi) were obtained from illustrations, photographs and/or descriptions available in the literature (see above). Characters were chosen to represent all major subdivisions of the brain of members of the Loricariinae and Loricariidae; although these characters include many that may be taxonomically useful at various levels and/or with relatively well known functional significance (see Discussion), presumed taxonomic and/or functional relevance were not used as grounds for character choice; rather, broad coverage and overall description of the gross brain morphology

of the Loricariinae and Loricariidae were the goals. The list of the characters examined, and the correspondent character states, is provided in the Appendix B; the resulting data matrix is provided in the Appendix C.

The different brain subdivisions in members of the Loricariinae, and the brain as a whole, are described in the anteroposterior axis direction according to the scheme implemented by ABRAHÃO & SHIBATTA (2015) and PEREIRA & CASTRO (2016), as presented in ANGULO & LANGEANI (2017) – see “Chapter one”; descriptions are based only on the material examined (see Appendix A). In paired subdivisions only the left lobe or left counterpart are described, unless otherwise stated. Nomenclature of the different brain subdivisions follows NIEUWENHUYS (1982), MEEK & NIEUWENHUYS (1998) and BUTLER & HODOS (2005).

3.4.4. Data analyses

The morphological disparity and occupation of the 90 species of the Loricariinae, plus the 50 additional species, including members of other six subfamilies of the Loricariidae (see Appendices A and C), was examined through a principal coordinate analysis (PCoA; see GOWER, 1966; ZUUR *et al.*, 2007). The PCoA was run using the software PAST, version 3.11 (HAMMER *et al.*, 2001), on the dataset comprising 88 of the 89 binary or multistate non-ordered characters (see Appendices B and C; the character 23 was excluded from the analysis given that all specimens examined shared the same character state condition), which were previously transformed into a Euclidean distance matrix (see FOOTE, 1993; 1996). The morphological disparity and occupation was visualized by generating a scatter-plot based on the first two PCoA components (see YU *et al.*, 2014). The results were explored by studying the PCoA eigenvalues and through a visual inspection of the position of the species and the different supraspecific groups [tribes (Harttiini and Loricariini, with the subtribes Farlowellina and Loricariina comprising the Loricariini) of the Loricariinae and subfamilies of the Loricariidae; see COVAIN *et al.*, 2016; FRICKE *et al.*, 2018a] in the PCoA scatter-plot (morphospace). The possible differences in the disparity and occupation of the groups in the morphospace also were evaluated, and tested, through a non-parametric permutational multivariate analysis of variance (PERMANOVA; see ANDERSON, 2001). The PERMANOVA,

based on a total of 9999 permutations, was run, using the software PAST, on the results (scores) of the PCoA (see XUE *et al.*, 2015).

3.5. RESULTS

3.5.1. Gross brain morphology of the Loricariinae (Descriptive anatomy)

The brain of the Loricariinae is elongate and slightly narrow; its maximum width is at its anteromedial portion, which usually includes the medial portions of the *mesencephalon* and the *diencephalon*, and its maximum height is about at its half-length, on a transversal line that crosses the posterior portions of the *mesencephalon* and the *diencephalon* and the anterior portion of the *rhombencephalon* (Fig. 8). In all examined specimens the brain occupies the cranial cavity almost entirely; on the anteroposterior axis it is usually located between the mesethmoid and the lateral ethmoid (anteriorly) and the third neural arch (posteriorly), usually reaching the anterior portion of the swim bladder [see character (Char.) number 86]; on the dorsoventral axis the brain is located between the frontals and parieto-supraoccipital (dorsally) and the prootics and parasphenoid (ventrally).

Telencephalon

The *telencephalon* (Fig. 8) is the anterior-most subdivision of the brain in most vertebrates, including all teleost fishes (Nieuwenhuys, 1982; Nieuwenhuys *et al.*, 1998), and includes the olfactory bulbs and the *telencephalon*, properly. The olfactory bulbs (Fig. 8) is located anterodorsal to the *telencephalon*, properly, beneath the nasal and near the articulation of the lateral ethmoid and the vomer; in most Loricariinae, it can be drop-shaped (*i.e.*, tapered at the ends) or rounded (*i.e.*, not tapered at the ends; see Char. 11, Fig. 9A), being the last condition the more frequently observed. The olfactory bulb is interconnected to the olfactory organ (not considered part of the *telencephalon*) via the *nervus olfactorius* (NI; Fig. 8) and to the *telencephalon*, properly, via the *nervus tractus olfactorius* (Fig. 8). In most Loricariinae, the *nervus olfactorius* emerges from the posterior portion of the olfactory organ, with its fibers oriented posteriorly towards the olfactory bulbs (vs. inserted in the mesial portion of the olfactory organ, with its fibers oriented obliquely towards the

olfactory bulbs in a few species; see Char. 7) and is usually short and not visible dorsally [except in some species of the *Farlowella* Eigenmann & Eigenmann, 1889 and *Rineloricaria* Bleeker, 1862, in which it is longer and visible dorsally (see Char. 9)]. The *nervus tractus olfactorius* enter/exit its afferent/efferent projections in/from the anteroventral portion of the *telencephalon*, properly; its length is very variable between specimens and species of the Loricariinae [in a few species, e.g., *Crossoloricaria bahuaja* and *Rineloricaria aurata*, the olfactory bulbs appears to be sessile, directly inserted into the *telencephalon*, i.e., the *nervus tractus olfactorius* is short or reduced; in most species, in contrast, the *nervus tractus olfactorius* is variably long (see Char. 13)], appearing to be positively correlated with the ontogenetic stage and the size of the individual (see “Chapter one”).

The olfactory organ (or olfactory rosette; not considered to be part of the brain properly; Fig. 8) is located anterodorsal to the olfactory bulbs and is oval in shape (Figs. 9B, 9F), in dorsal view, in most Loricariinae [except in *Lamontichthys filamentosus* in which it also can be rounded to drop-shaped (see Char. 0)]. The olfactory organ is a “bilateral” structure, composed by a central nervous axis, running anterolaterally from the orbitonasal canal to the posterior wall of the olfactory chamber, and several feather-like, horizontally oriented, lamellae, leaving it; the number, length, thickness and shape of these lamellae vary widely between specimens (even between the right and left sides of each lamellae in a single specimen) and species; i.e., smaller specimens and species (shorter than 100 mm in SL; e.g., most members of the *Farlowella* and *Rineloricaria*), with exception of the members of the *Loricariichthys* Bleeker, 1862, typically showed the lowest lamellae counts (8 to less than 20; see Char. 2); in contrast, larger specimens and species (greater than 100 mm in SL; e.g., members of the *Spatuloricaria* Schultz, 1944, *Sturisoma* Swainson, 1838, and in *Brochiloricaria macrodon*, among others) typically showed the greatest lamellae counts (usually more than 20; see Char. 2). In most Loricariinae, with exception of the members of the *Farlowella* and in *Aposturisoma myriodon*, among others, the olfactory organ presented both external and internal paired lamellae of about the same length (Fig. 9E; vs., external lamellae longer; see Char. 3). On the same way, most species within the subfamily (e.g., members of the *Harttia* Steindachner, 1877, *Loricariichthys* and *Rineloricaria*, among others; see Char. 54) presented the posterior lamellae noticeably more elongated and thickened (vs., posterior lamellae undifferentiated; i.e., all lamellae of similar size and thickness;

see Char. 4). Additionally, dorsal projections can be found in all or only in the posterior lamella (see Char. 5), in its mesial or terminal portion (see Char. 6); in most Loricariinae the dorsal projections are present only in the posterior lamellae and usually located in its posterior portion.

The *telencephalon*, properly (*i.e.*, excluding the olfactory organ, the *nervus olfactorius*, the olfactory bulbs and the *nervus tractus olfactorius*; Fig. 8), is located anterodorsal to the *diencephalon* and anteroventral to the *mesencephalon*. It can be subdivided in two major regions: (1) dorsal and (2) ventral, both of which are widely and closely interconnected (Nieuwenhuys, 1982). In dorsal view, the *telencephalon* can be (1) oval or rectangular (mainly in members of the Harttiini and the Farlowellina; Fig. 9A), or (2) vertically elongated (mainly in members of the Loricariini) (see Char. 14). The greatest width of the *telencephalon* can be approximately at its half-length or at its anterior-most portion (see Char. 16), except in members of the *Hemiodontichthys* Bleeker, 1862, *Limatulichthys* Isbrücker & Nijssen, 1979, *Loricaria* Linnaeus, 1758 and *Pseudoloricaria* Bleeker, 1862, among others, in which its greatest width is usually at its posterior-most portion. In lateral view the *telencephalon* is usually oval to reniform (Fig. 10). The dorsal area of the *telencephalon* in most Loricariinae presented three different circular or semicircular projections or protuberances [*i.e.*, (1) anteromesial, (2) posteromesial, and (3) lateral], with a variable degree of development between species and species groups (see Chars. 19, 20 and 24). The anteromesial projection is well developed in most members of the Loricariinae, except in members of the *Crossoloricaria* Isbrücker, 1979, *Farlowella*, *Hemiodontichthys*, *Rhadinoloricaria* Isbrücker & Nijssen 1974, and some members of the *Rineloricaria*, among others (see Char. 19); the posteromesial projection is well developed in most members of the Loricariinae, except in some members of the *Crossoloricaria*, *Farlowella*, *Hemiodontichthys*, *Rhadinoloricaria*, *Rineloricaria* and in *Cteniloricaria platystoma*, *Furcodontichthys novaesi*, *Pseudoloricaria laeviscula* and *Spatuloricaria tuiira* (see Char. 24); whereas the lateral projection is well developed only in species of the *Harttia*, *Hartiella* Boeseman, 1971, *Loricariichthys*, *Rineloricaria* and *Sturisoma*, among others (see Char. 20). These three projections or protuberances are delimited, according to its degree of development, by furrows, channels or fissures varying in length, arrangement and direction between species and species groups (see Chars. 21 and 25). For example, the fissure that delimits the lateral projection is evident in almost all species of the

Loricariinae, converging anteriorly, towards the mesialmost portion of the *telencephalon* (*vs.*, not converging anteriorly, *i.e.*, parallel to the longitudinal axis of the *telencephalon*, in some species; see Char. 21); whereas the fissure in the region between the lateral and posteromesial projections is evident only in a few species (Char. 25).

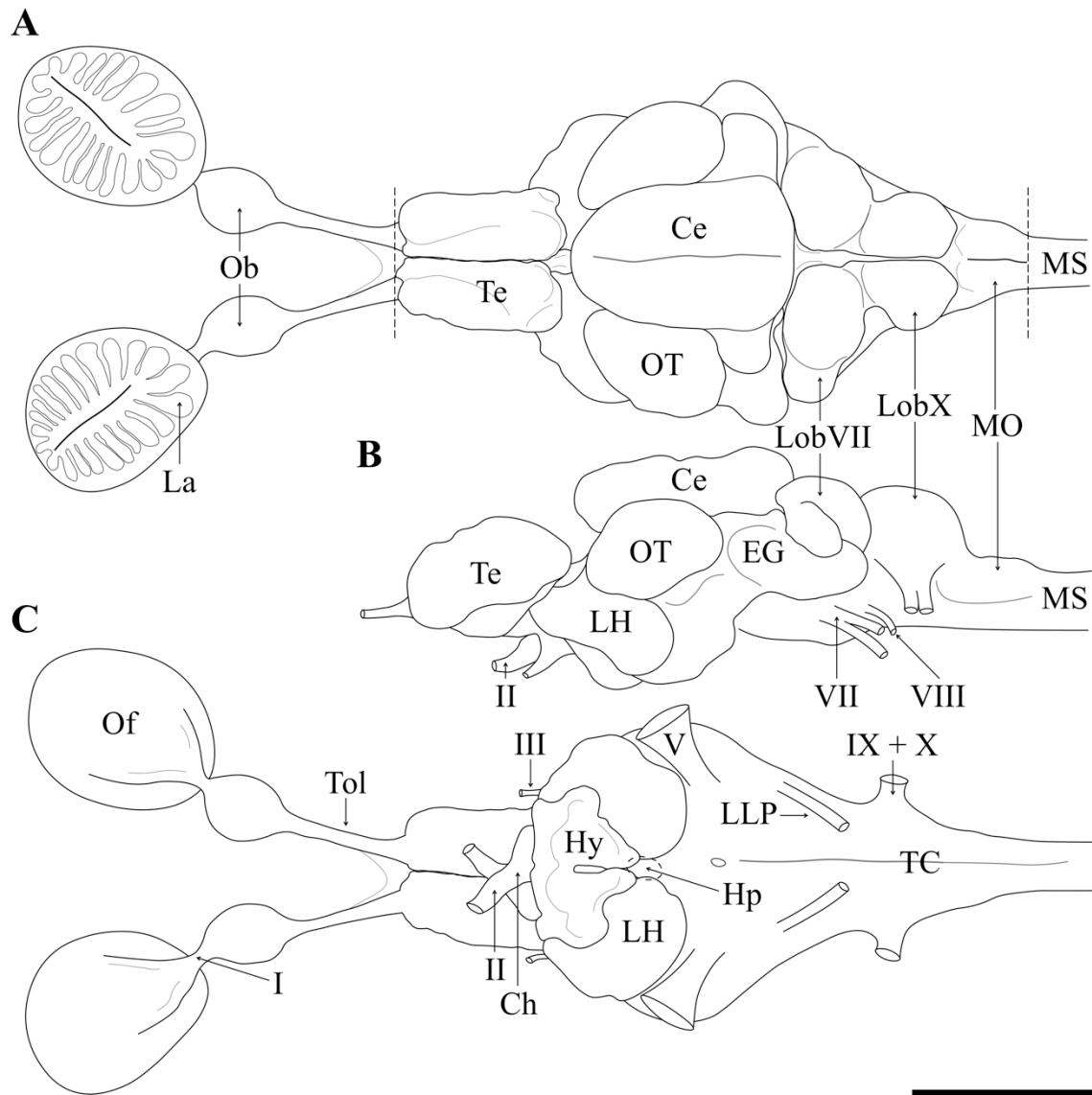


Figure 8. Topographic brain anatomy of a generalized member of the Loricariinae (*L. cataphracta*, type species of the family; MZUSP 014106; 114.70 mm SL); (A) dorsal, (B) lateral (left side) and (C) ventral views. Abbreviations: Ce=*corpus cerebelli*, Ch=*chiasma opticum*, EG=*eminentia granularis*, Hp=*hypophysis*, Hy=*hypothalamus*,

LH=*lobus inferior hypothalami*, LobVII=*lobus facialis*, LobX=*lobus vagi*, MO=alar portion of the *medulla oblongata*, MS=*medulla spinalis*, I=*nervus olfactorius*, II=*nervus opticus*, III=*nervus oculomotorius*, V=*nervus trigeminus*, VII=*nervus facialis*, VIII=*nervus octavus* or *vestibularis*, IX=*nervus glossopharyngeus*, X=*nervus vagus*, La=olfactory lamella, LLP=*nervus linea lateralis posterior*, OB=olfactory bulbs, Of=olfactory organ, OT=optic tectum, Te=telencephalon, Tol=*nervus tractus olfactorius*, and TC=*truncus cerebri*. Pointed lines indicate the anterior and posterior limits of the brain. Scale bar=2 mm.

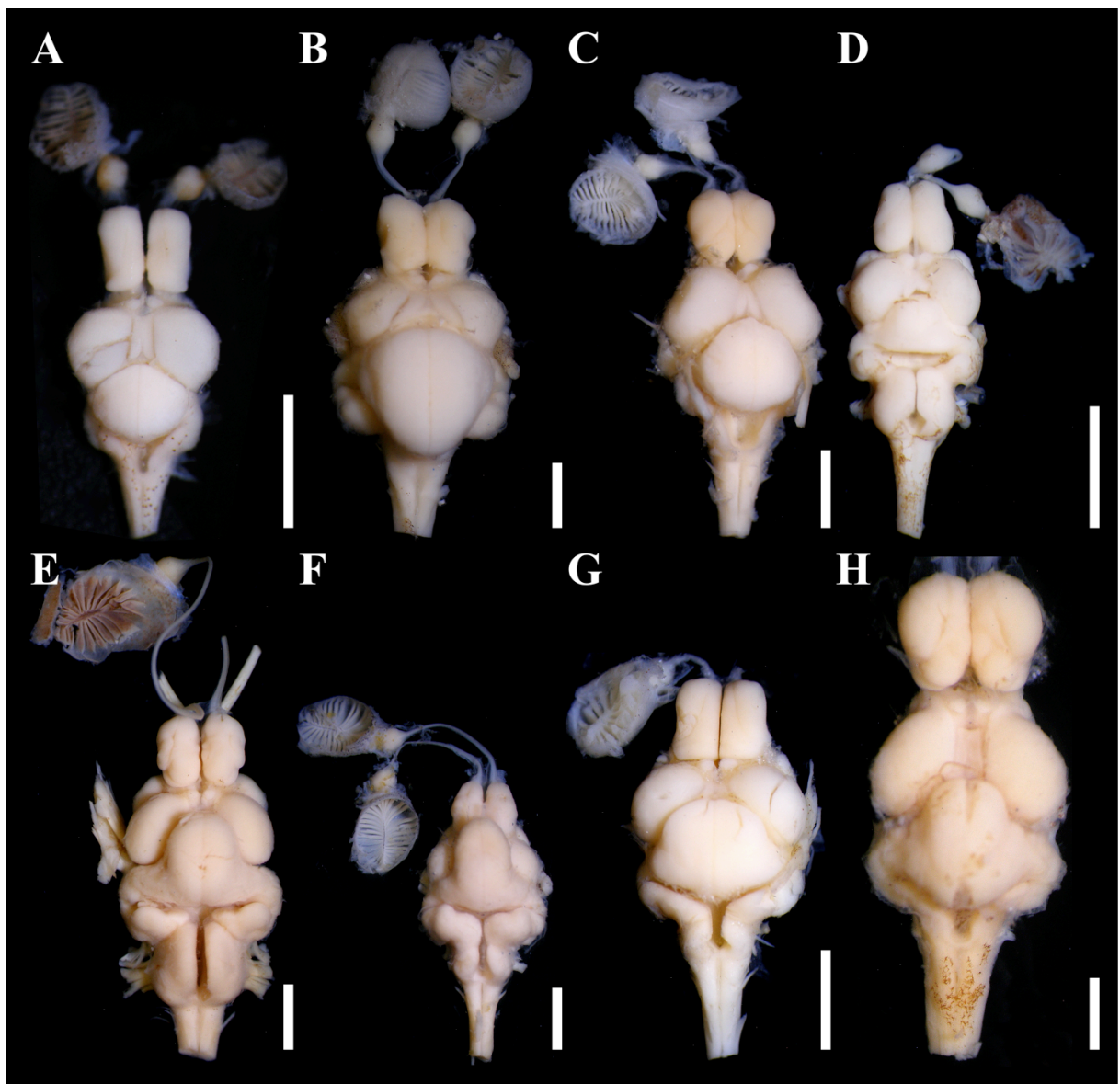


Figure 9. Topographic brain anatomy of members of the Loricariinae, dorsal view; (A) *F. oxyrryncha*, DZSJRP 014920, female, 124.00 mm SL; (B) *F. nanodon*, MUSM

032153, male, 167.98 mm SL; (C) *H. novalimensis*, DZSJRP 01644, male, 102.53 mm SL; (D) *H. acipenserinus*, INPA-ICT 032082, male, 92.34 mm SL; (E) *L. anus*, DZSJRP 010987, female, 158.00 mm SL; (F) *R. macrops*, ZVCP 14035, male, 221.00 mm SL; (G) *R. cubataonis*, DZSJRP 003269, female, 104.53 mm SL; (H) *S. leightoni*, ANSP 084177, male, 118.26 mm SL. Scale bar=2 mm.

Diencephalon

The *diencephalon* is located in the anteroventral portion of the brain, immediately posterior to the *telencephalon*, ventral to the *mesencephalon* [in all examined Loricariinae, except in *Cteniloricaria platystoma* and in some species of the *Harttia*, the anterior limit of the *diencephalon* surpasses the anterior limit of the *mesencephalon* (see Char. 32, Fig. 10)] and anterior to the *rhombencephalon*. In most Loricariinae the length of the *diencephalon*, in lateral view, is usually equal or shorter than the length of the *mesencephalon* (see Char. 30, Fig. 10); whereas its width, in ventral view, is relatively variable, being shorter than, or similar to, the width of the *telencephalon* in species of the *Farlowella*, *Harttia*, *Harttiella*, *Hemiodontichthys*, *Sturisoma*, some species of *Rineloricaria* and in *Aposturisoma myriodon* and *Cteniloricaria platystoma*, vs. greater than the width of the *telencephalon* in the remaining taxa (see Char. 31, Fig. 11). The *diencephalon* can be subdivided in four major regions: (1) the *epithalamus*, including the pineal gland, (2) the *pars dorsalis thalami*, (3) the *pars ventralis thalami*, and (4) the *hypothalamus* (Nieuwenhuys, 1982). The external limits of all these regions are usually inconspicuous in most Loricariinae and, in the case of the dorsal portion of the *epithalamus* and the pineal gland, easily lost during dissections. As inferred from its names, the *epithalamus* and the *pars dorsalis thalami* are located on the dorsal portion of the *diencephalon*, usually arising from grooves between the posterior portion of the *telencephalon* (anteriorly) and the anteromedial portion of the *tecta mesencephali* (posteriorly); the *pars ventralis thalami* and the *hypothalamus*, on the other hand, are located on the ventral portion of the *diencephalon*, posterior to the *chiasma opticum* (see below) and anterior to the *rhombencephalon*.

The *hypothalamus*, being the most conspicuous subdivision of the *diencephalon* in most Loricariinae (and in most teleost fishes), can be subdivided in four major regions: (1) the *hypothalamus*, properly, (2) the *lobus inferior hypothalami*,

(3) the *adenohypophysis* (or pituitary gland), and (4) the *saccus vasculosus* (MEEK & NIEUWENHUYIS, 1998; Fig. 8). The *hypothalamus*, properly, is located in the ventral-most portion of the *diencephalon*, anteromedial to the *lobus inferior hypothalami* and, in most specimens, visibly differentiated from the ventral surface of the lobe in lateral view (see Char. 41). The *hypothalamus*, properly, is about semicircular, with its medial portion almost straight; in some specimens, it is evident, on its anteromedial portion and separating both lobes, a relatively small hole or depression which represents the aperture of the anterior diencephalic ventricle, also known as the third ventricle (see Char. 42, Figs. 11A, 11C, 11E, 11G). The *lobus inferior hypothalami* is located lateral to the *hypothalamus*, properly, and is semicircular to bean-like shaped (mainly in members of the Loricariina; Fig. 11E) or almost rectangular (mainly in members of the Harttiini and the Farlowellina; Fig. 11A) (see Char. 36). In most Loricariinae the lateral and posterior margins of the *lobus inferior hypothalami* are continuous [*i.e.*, without conspicuous invaginations; see Chars. 37 and 40, respectively (Fig. 11E); contrary, in species of the *Farlowella* the lateral margin of the *lobus inferior hypothalami* presents some conspicuous invaginations (Fig. 11A)], and usually presents a ventral expansion (absent in members of the *Farlowella*, *Harttia* and in *Harttiella crassicauda*, among others; see Char. 39, Fig. 10G). In most Loricariinae, the posterior portion of the *lobus inferior hypothalami* expands posteriorly, surpassing the posterior margin of the *hypothalamus* (Figs. 11B, 11C); contrary, in members of the *Farlowella* and *Sturisoma* the posterior margins of both subdivisions are almost at the same level (see Char. 34, Fig. 11A). The *adenohypophysis* is located medially at the ventral surface of the *diencephalon*; posterior to the *hypothalamus*, anterior to the *saccus vasculosus* and mesial to the *lobus inferior hypothalami*. The *adenohypophysis* is relatively well developed in most Loricariinae and can be circular or oval in shape, in ventral view, and about spherical or (dorsoventrally) flattened, in lateral view (see Char. 43). The *adenohypophysis* is interconnected to the *hypothalamus*, and the rest of the brain, via the pituitary stalk, which is composed by a very delicate tissue containing both hypothalamic and preoptic nerve fibers, being usually broken during dissections [by this reason, the *adenohypophysis* was not rescued along with the rest of the brain in most specimens, staying in the concavity of the parasphenoid (where is naturally located) being surrounded by connective tissue and fat]. Finally, the *saccus vasculosus* is located posterior to the *adenohypophysis*, on the posteromedial portion of the

diencephalon and, in most Loricariinae, it is usually of the same size (or slightly smaller) and shape as the *adenohypophysis*.

Mesencephalon

The *mesencephalon* is located in the anterodorsal portion of the brain, immediately posterior to the *telencephalon*, dorsal to the *diencephalon* and anterior to the *rhombencephalon*, being relatively well developed in most Loricariinae. In dorsal view it can be rounded, almost rounded or semi-circular (in most members of the *Farlowella*, *Harttia* and *Sturisoma*, Fig. 9A), or oval, horizontally (in a few species, including some members of the *Rineloricaria*) or vertically elongated (in most Loricariinae; see Char. 44). In lateral view, the *mesencephalon* is usually rounded to horizontally elongated (see Char. 46, Fig. 10); being its volume usually comparable to the volume of the *telencephalon*, properly (see Char. 48). In most Loricariinae, except in *Reganella depressa*, both left and right mesencephalic lobes are not in contact dorsally (see Char. 45, Fig. 9). The *mesencephalon* can be subdivided in four major regions: (1) the *tectum mecencephali* (often referred as the midbrain tectum, optic lobe or *optic tectum*), (2) the *tegmentum mecencephali* (often referred as the midbrain tegmentum), (3) the *torus longitudinalis*, and (4) the *torus lateralis* (MEEK & NIEUWENHUYS, 1998); being the external limits of all these major regions usually inconspicuous in most Loricariinae. The *tectum mecencephali* is located in the dorsal-most portion of the *mesencephalon*, anterolateral to the dorsoanterior portion of the *rhombencephalon*, in dorsal view, and posterior to the *telencephalon* in lateral view (Fig. 8). The *tegmentum mecencephali* is located ventral to the *tectum mecencephali*; it is relatively small and is totally covered by the *tectum mecencephali*, both in dorsal and lateral views. The *torus longitudinalis* is usually inconspicuous (visible only in stained histological preparations or in some specimens as a thin layer of tissue interconnecting both *tecta*; see NIEUWENHUYS, 1982) and is usually located in an anteromedial position; anterior to the *lobus inferior hypothalami* and the anterior portion of *tectum mecencephali*. The *torus lateralis* is usually reduced and is located ventrolaterally on the *mesencephalon*, anterior to the *lobus inferior hypothalami* and the anterior portion of *tectum mecencephali* and anterolateral to the *torus longitudinalis*.



Figure 10. Topographic brain anatomy of members of the Loricariinae, lateral view; (A) *F. oxyrryncha*, DZSJRP 014920, female, 124.00 mm SL; (B) *F. nanodon*, MUSM 032153, male, 167.98 mm SL; (C) *H. novalimensis*, DZSJRP 01644, male, 102.53 mm SL; (D) *H. acipenserinus*, INPA-ICT 032082, male, 92.34 mm SL; (E) *L. anus*, DZSJRP 010987, female, 158.00 mm SL; (F) *R. macrops*, ZVCP 14035, male, 221.00 mm SL; (G) *R. cubataonis*, DZSJRP 003269, female, 104.53 mm SL; (H) *S. leightoni*, ANSP 084177, male, 118.26 mm SL. Scale bar=2 mm.

The *nervus opticus* (II; Fig. 8) emerges from the retina and it is inserted at the anteroventral portion of the *tectum mesencephali*. The afferent and efferent projections of both nerves (left and right) runs throught the region immediately

anterior to the *lobus inferior hypothalami*, commonly referred as the *chiasma opticum* (Fig. 8), which is usually located anterior to the posterior margin of the *telencephalon*. At the *chiasma opticum* both (optic) nerves cross the midline of the brain; this crossing can be oblique (*i.e.*, anteriorly directed, in the form of a “X”; Fig. 11E) or almost parallel (*i.e.*, transversal to the anteroposterior axis of the brain; see Char. 27, Figs. 11C), being the “oblique” arrangement the most frequently observed condition in members of the Loricariinae (the “almost parallel” arrangement was observed only in a few species of the *Farlowella*, *Harttia* and in *Cteniloricaria platystoma*). Fibers mixture may occur, or not, between both right and left nerves at the *chiasma opticum* (see Char. 26), being that most Loricariinae present the “no mixture” condition (*i.e.*, nerves individualized). The thickness of the *nervus opticus* varies little between specimens and species; in most members of the Loricariinae the thickness of the *nervus opticus* is similar to, or slightly greater than, the thickness of the *nervus olfactorius*; in the species *Apistoloricaria ommation* and *Reganella depressa* the opposite patten was observed (*i.e.*, *nervus olfactorius* usually thicker than the *nervus opticus*; see Char. 29). In members of the *Dasylicaria* Isbrücker & Nijssen 1979 can be observed a conspicuous bulge, forming a kind of bulb, on the proximal portion of the *nervus opticus*, after (anterior to) the *chiasma opticum* (see Char. 28).

The *truncus cerebri* (Fig. 8), which comprises the ventral portions of the *mesencephalon* and the *rhombencephalon*, is located in the posteroventral portion of the brain in the region between the posterior portion of the *chiasma opticum* (anteriorly) and the anterior portion of the *medulla spinalis* (posteriorly), above the parasphenoid. In lateral view, the *truncus cerebri* can be almost rectilinear or can present a conspicuous concavity in its anteromedial portion, being the “rectilinear” condition the most frequently observed in members of the Loricariinae (see Char. 51, Fig. 10A). Most cranial nerves enter/exit its afferent/efferent projections from the *truncus cerebri*, with exception of the *nervus olfactorius* and the *nervus opticus* (see above). The cranial nerves entering/leaving the *truncus cerebri* includes: (1) the *nervus oculomotorius* (III), (2) the *nervus trochlearis* (IV), (3) the *nervus trigeminus* (V), (4) the *nervus abducens* (VI), (5) the *nervus facialis* (II), (6) the *nervus vestibulocochlearis* or *octavus* (VIII), (7) the *nervus glossopharyngeus* (IX), (8) the *nervus vagus* (X), (9) the *nervus linea lateralis anterior*, and (10) the *nervus linea lateralis posterior* (Fig. 8).

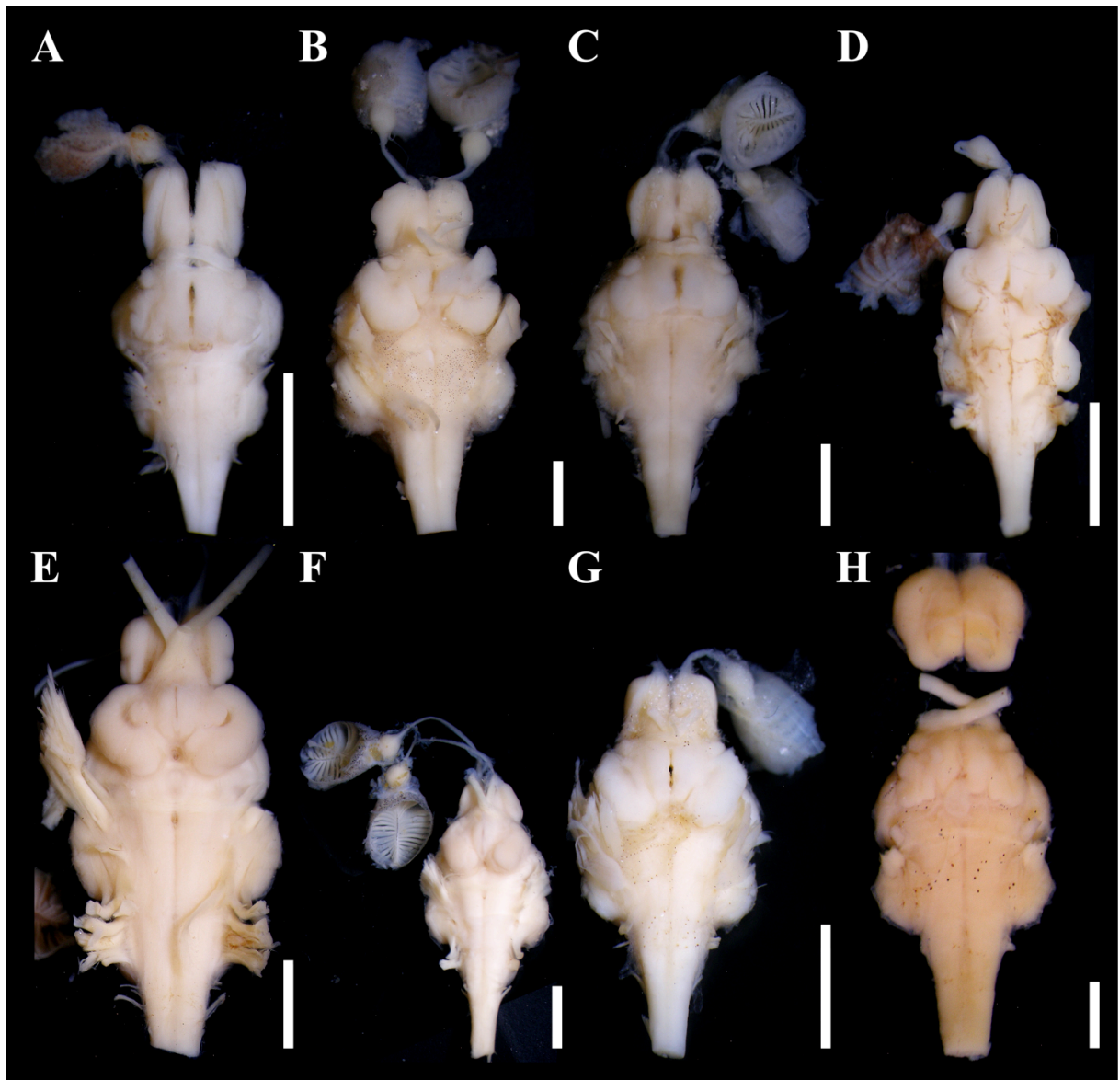


Figure 11. Topographic brain anatomy of members of the Loricariinae, ventral view; (A) *F. oxyrryncha*, DZSJRP 014920, female, 124.00 mm SL; (B) *F. nanodon*, MUSM 032153, male, 167.98 mm SL; (C) *H. novalimensis*, DZSJRP 01644, male, 102.53 mm SL; (D) *H. acipenserinus*, INPA-ICT 032082, male, 92.34 mm SL; (E) *L. anus*, DZSJRP 010987, female, 158.00 mm SL; (F) *R. macrops*, ZVCP 14035, male, 221.00 mm SL; (G) *R. cubataonis*, DZSJRP 003269, female, 104.53 mm SL; (H) *S. leightoni*, ANSP 084177, male, 118.26 mm SL. Scale bar=2 mm.

Rhombencephalon

The *rhombencephalon* is the posterior-most portion of the brain in most vertebrates, including all teleost fishes (NIEUWENHUYS, 1982; NIEUWENHUYS *et al.*, 1998); it is located between the *mesencephalon* (anteriorly) and the *medulla spinalis* (posteriorly; see below; Fig. 8), and can be subdivided in two major regions: (1) ventral and (2) dorsal (NIEUWENHUYS, 1982). The ventral area constitutes, together with the posteroventral portion of the *mesencephalon*, the *truncus cerebri* (see above); the dorsal area, on the other hand, includes (1) the *cerebellum* and (2) the *medulla oblongata* (NIEUWENHUYS, 1982). The *rhombencephalon*, in general terms, is the most prominent, larger and voluminous subdivision of the brain in most Loricariinae [and in most teleost fishes (NIEUWENHUYS, 1982)]; its length, in lateral view, is about equal or greater than the length of the rest of the brain in most members of the Loricariinae (see Char. 49, Fig. 9E); whereas its width is shorter than (Fig. 9A) or about equal to the width of the *tecta mesencephali* in all but some few species (*i.e.*, *Furcodontichthys novaesi*, *Limatulichthys petleyi*, *Loricaria cataphracta* and some species of the *Loricariichthys*; see Char. 50, Fig. 9E) in which it is usually larger.

The *cerebellum* is located in the anterodorsal portion of the *rhombencephalon*, immediately anterior to the *medulla oblongata*, and medial to the *tectum mesencephali*; it is relatively well developed in most Loricariinae and can be subdivided in three major regions: (1) the *valvula cerebelli*, (2) the *corpus cerebelli* and the (3) *lobus vestibulolateralis*. The *valvula cerebelli* is located in the anterior portion of the *rhombencephalon*, anteroventral to the *corpus cerebelli* and posteroventral or medioventral to the *tectum mesencephali*; it occupies most of the mesencephalic ventricle (extending to approximately half the length of the *tecta mesencephali*), being usually inconspicuous or not visibly at simple view in most Loricariinae (see Char. 66). The *corpus cerebelli* (Fig. 8) is usually located posterodorsal or mediodorsal to the *tectum mesencephali* and anterior to the *medulla oblongata* (see below), usually covering the *valvula cerebelli* in the anteromedial portion of the *rhombencephalon*. The *corpus cerebelli* is the most prominent, voluminous (see Char. 56), and variable (both in size and shape) rhombencephalic subdivision in most Loricariinae. In dorsal view it can be about circular or rounded, vertically elongated (oval), horizontally elongated (oval, triangular or rhomboid), or hat-shaped, *i.e.*, (vertically) elongated only in its posterior portion (see Char. 52, Fig. 9); with both margins, anterior and posterior, usually convex (*vs.*, arrow shaped, or

tipped, in a few species; see Chars. 57 and 60, Fig. 9). In lateral view it can be: (1) almost circular to vertically elongated (oval), or (2) horizontally elongated (oval; see Char. 65, Fig. 10); with its dorsal margin usually straight (see Char. 64, Fig. 10) and its maximum height about equal or slightly smaller than the *medulla oblongata* height (measured at the end of the *lobus vagi*, see below; see Char. 63). In most Loricariinae, except in members of the *Loricaria* and *Spatuloricaria*, plus other few species including *Brochiloricaria macrodon*, *Proloricaria prolixa*, *Paraloricaria vetula* and *Ricola macrops* (Fig. 9F), among others, the anterior margin of the *corpus cerebelli* expands on the *tectum mesencephali*, but not reaches its anterior margin (Fig. 9E); contrary, in some members of the *Farlowella* and in *Fonchiiloricaria nanodon* it not expands on the *tectum mesencephali* (see Char. 58, Fig. 9A). Moreover, in most Loricariinae, except in members of the *Loricaria*, plus other few species including *Brochiloricaria macrodon*, *Paraloricaria vetula* and *Ricola macrops* (Fig. 9F), the anterior margin of the *corpus cerebelli* does not expands towards the *telencephalon*, being located posterior to it (see Char. 59, Figs. 9A, 9H). In most Loricariinae, the posterior margin of the *corpus cerebelli* reaches the anterior margin of the *lobus fascialis* (except in members of the *Farlowella* and *Sturisoma*, some species of the *Rineloricaria*, and in *Hemiodontichthys* sp., *Loricaria* sp., *Loricariichthys platymetopon*, *Reganella depressa* and *Sturisomatichthys leightoni*, among others; see Char. 61), but does not reach the anterior margin of the *lobus vagi* (except in *Fonchiiloricaria nanodon* and *Metaloricaria paucidens*; see Char. 62, Fig. 9B). In most Loricariinae the length of the *corpus cerebelli*, in lateral view, is about equal or slightly smaller than the length of the *tectum mesencephali* (except in some members of the *Farlowella*, *Harttia*, *Hemiodontichthys* and *Loricaria*, among others; see Char. 47). In dorsal view the length of the *tectum mesencephali* is usually smaller than its width (except in members of the *Loricaria* and *Spatuloricaria* and in *Brochiloricaria macrodon*, *Dasylicaria latiura*, *Limatulichthys petleyi*, *Metaloricaria paucidens*, *Paraloricaria vetula*, *Proloricaria prolixa*, *Pseudoloricaria laeviscula*, *Pyxiloricaria menezzi* and *Ricola macrops*; see Char. 53), and its width is usually smaller than the width of the *mesencephalon* (see Char. 54) but more than twice the width of the *medulla oblongata* (see Char. 55). The *lobus vestibulolateralis* (Fig. 8) is located in the antero/mediolateral surface of the *rhombencephalon*, being apparently continuous with the *corpus cerebelli* and encompassing (1) the *eminetiae granularis* and the (2) *lobus caudalis* (NIEUWENHUY, 1982; ROSA, 2015); in most

Loricariinae, its length is usually larger (up to two times larger), or about equal in some specimens, than its height (see Char. 69) and larger than the length of the *corpus cerebelli* (see Char. 67); its height, on the other hand, is usually equal or slightly larger than the height of the *medulla oblongata* (measured at the end of the *lobus vagi*, see below; see Char. 68).

The *medulla oblongata* is located in the posterior portion of the *rhombencephalon*, between the *corpus cerebelli* (anteriorly) and the *medulla spinalis* (posteriorly); it is well developed in most Loricariinae and can be divided in four major regions: (1) dorsal, (2) intermediodorsal, (3) intermedioventral and (4) ventral (NIEUWENHUYIS, 1982; D'ANGELO, 2013). The dorsal area encompasses the sensory components of the trigeminal nucleus and the nuclei belonging to the lateral area; the intermediodorsal zone encompasses the *lobi fascialis* (the facial nerve nucleus; Fig. 8) and the *lobi vagi* (the vagal nerve nucleus; Fig. 8); whereas the intermedioventral and ventral zones encompass several visceromotor nuclei, such as the motor components of the *nervi trigeminus*, *abducens* and *glossopharyngeus* (NIEUWENHUYIS, 1982; D'ANGELO, 2013). The *lobus fascialis* is located immediately posterior to the *corpus cerebelli* (fully exposed in all Loricariinae, *i.e.*, not hidden by the posterior portion of the *corpus cerebelli*; see Char. 70, Figs. 8, 9), anterior to the *lobus vagi*, and mesial to the *eminentia granularis* [within the boundaries of the *rhombencephalon*, *i.e.*, not exceeding its lateral margins (see Char. 71)] in dorsal view; in lateral view, it is located dorsal to the *truncus cerebri*. In almost all species of the Loricariinae, with exception of some members of the *Sturisoma* and in *Brochiloricaria* sp., both *lobi fascialis* form an obtuse angulation (see Char. 75, Fig. 9). In all Loricariinae, the *lobus fascialis* is segmented, with two portions, anterior and posterior, well differentiated (see Char. 76, Fig. 9); in most species both portions are of about the same volume (*vs.*, the anterior portion more voluminous in members of the *Harttia*, *Hemiodontichthys*, *Limatulichthys* and in *Cteniloricaria platystoma*, *Furcodontichthys novaesi* and *Harttiella crassicauda*, among others; or, the anterior portion more voluminous in members of the *Brochiloricaria*, *Crossoloricaria*, *Loricaria*, *Rhadinoloricaria*, *Spatuloricaria* and in *Apistoloricaria ommation* and *Lamontichthys filamentosus*, among others; see Char. 77). In most Loricariinae, the *lobus fascialis* is more voluminous than the *lobus vagi* (see Char. 72, Fig. 9); whereas its width is usually about equal to, or larger than, half the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (see Char. 73, Fig. 9). The

lobus vagi is usually located immediately posterior, and medial, to the *lobus fascialis* and anterior to the alar portion of the *medulla oblongata* (Fig. 8) in dorsal view; in lateral view, it is located dorsal to the posterior portion of the *truncus cerebri*. In almost all species of the Loricariinae, except in *Crossoloricaria bahuaja*, *Furcodontichthys novaesi* and *Loricariichthys* sp., the anterior portion of the *lobus vagi* is more voluminous and curved towards the midline of the brain, giving it a boomerang or quotation mark shape (see Char. 79, Figs. 9D, 9F, 9G); moreover, in most Loricariinae, except in members of the *Harttia*, some species of the *Rineloricaria* and in *Harttiella crassicauda*, among others, both *lobi fascialis* form an acute angulation (see Char. 81). In most Loricariinae, the length of the *lobus vagi* is shorter than the length of the *eminentia granularis* (see Char. 82), its width is shorter than half the width of the *medulla oblongata*, measured immediately posterior to the end of the lobes (see Char. 84), and its height is shorter than the height of the *medulla oblongata*, measured immediately posterior to the end of the lobes (see Char. 83). In most Loricariinae, both *lobus vagi* and *facialis* form an obtuse angulation (see Char. 85, Fig. 9). The *medulla spinalis* (Fig. 8), usually not considered part of the *encephalon*, is the most caudal subdivision of the central nervous system of all vertebrates, its origin is located immediately posterior to the *medulla oblongata* (i.e., posterior to the *lobus vagi* and the alar portion of the *medulla oblongata*), above the posterior portion of the parasphenoid and beneath the supraoccipital process, passing through all vertebrae and extending to the caudal portion of the body; it is tubular and almost invariable in diameter along all its extension in all examined exemplars.

3.5.2. Gross brain morphological disparity in the Loricariidae (Quantitative approach)

The empirical morphospace for members of the Loricariinae and Loricariidae, based on the first three principal coordinates (axis; PCos) of the PCoA, explaining about 40% of the total variance (i.e., 23.2, 8.3 and 7.3%, respectively), recovered two major groups (Fig. 12). (1) The first group, occupying the largest area and displaying more disparity among species, included all members of the Loricariinae (with its two tribes and the two subtribes of the Loricariini, relatively well separated in the PCo1), as well as the members of the Delturinae, Hypostominae, Lithogeninae and

Rhinelepinae. Within the Loricariinae, members of the Loricariina occupied exclusively the positive portion of the PCo1, whereas members of the Harttiini, as well as members of the Hypostominae, Lithogeninae and Rhinelepinae, occupied exclusively the negative portion of the PCo1 [except for the species *Harttia loricariformis* and *Megalancistrus parananus* (Peters 1881)]; members of the Farlowellina (and the Delturinae) occupied both the positive and negative portions of the PCo1, with species of the *Aposturisoma* Isbrücker, Britski, Nijssen & Ortega 1983, *Sturisoma*, *Lamontichthys* Miranda Ribeiro, 1939 and *Sturisomaticthys* Isbrücker & Nijssen, 1979 (in the positive portion of the PCo1) more similar to members of the Loricariina, and species of the *Farlowella* (in the negative portion of the PCo1) more similar to members of the Harttiini. Members of the Delturinae, Hypostominae, Lithogeninae and Rhinelepinae occupied exclusively the positive portion of the PCo2; members of the Loricariinae occupied both the positive and negative portions of the PCo2, with all species of the *Farlowella* and *Rineloricaria*, among other genera, in the negative portion of the PCo2. The single representative of the Lithogeninae occupied the positive portion of the PCo3; members of the Farlowellina and Harttiini, as well as the members of the Delturinae, Hypostominae and Rhinelepinae, occupied exclusively the negative portion of the PCo3; members of the Loricariina occupied both the positive and negative portions of the PCo3, with most species in the positive portion of the axis. (2) The second group, including members of the Hypoptopomatinae *sensu lato* and the Neoplecostominae, occupied exclusively the positive portion of the PCo1, showing a relatively strong overlap in its occupation areas. Members of the Hypoptopomatinae *sensu lato* occupied almost exclusively the negative portion of the PCo2 [except for the species *Gymnotocinclus anosteos* Carvalho, Lehmann A. & Reis, 2008 and *Pseudotocinclus tietensis* (Ihering, 1907)], whereas members of the Neoplecostominae were almost restricted to the positive portion of the PCo2, with species of *Pareiorhina* Gosline, 1947 more similar to members of the Hypoptopomatinae *sensu lato*; a similar pattern was observed in relation to the distribution and occupation of these taxa in the PCo3.

Taxa with positive scores in the PCo1 usually shared the following character states and conditions: 13 [2; *i.e.*, olfactory bulbs pedunculated, attached to the *telencephalon* by a *tractus olfactorius* long (larger than the length of the olfactory bulbs)], 27 [0; *i.e.*, optic nerves orientated oblique to the anteroposterior axis of the encephalon (nerves directed anteriorly, intersecting each other in the form of a "X")],

29 (1; *i.e.*, thick of the *nervus opticus* slightly larger than, or similar to, the thick of the *nervus olfactorius*), 34 (2, 3; *i.e.*, margin posterior of the *lobus inferior hypothalami* expanded posteriorly, surpassing the postero-mesial margin of the *hypothalamus*, with the posterior portions of each lobes not very close or clearly surpassing the postero-mesial margin of the *hypothalamus*, with the posterior portions of each lobes very close or in contact), 36 (0; *i.e.*, *lobus inferior hypothalami* semicircular to bean-shaped), 39 (1; *i.e.*, portion lateroposterior of the *lobus inferior hypothalami* ventrally expanded, surface discontinuous with the rest of the lobe), 52 (1, 2, 3; *i.e.*, *corpus cerebelli* hat-shaped, elongated vertically on its posterior portion, oval, circular or rounded), 55 (1; *i.e.*, width of the *corpus cerebelli* more than twice the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi*), 57 (0; *i.e.*, margin anterior of the *corpus cerebelli* circular or rounded, convex), 58 (1, 2; *i.e.*, margin anterior of the *corpus cerebelli* expanded on the *tecta mesencephali* surpassing or not its anterior margin), 66 (1; *i.e.*, *valvula cerebelli* not very conspicuous, extended to approximately the half the length of the *tecta mesencephali*), 67 (1; *i.e.*, length of the *lobus vestibulolateralis* more than, or similar to, half the length of the *corpus cerebelli*), 73 (2; *i.e.*, width of the *lobus facialis* larger than half the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi*), 79 (2, 1; *i.e.*, *lobus vagi* very angled, anterior margins facing to the medial axis), 84 (1; *i.e.*, width of the *lobus vagi* larger than, or similar to, half the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi*), and 85 (2; *i.e.*, angulation between the *lobus vagi* and the *lobus facialis* more than 90°). The PCo2 was “positively correlated” with the following characters and character states (*i.e.*, species and taxa with positive scores in the PCo2 usually shared the following character states): 2 (1, 2; *i.e.*, more than 20 lamellae on the olfactory organ in females), 6 (0; *i.e.*, dorsal projections in the lamellae of the olfactory organ, in females, located on a subterminal position, on the mesial portion of the lamellae), 10 (2; *i.e.*, width of the *nervus olfactorius*, in females, three times or more larger than the width of a single olfactory lamella), 13 [2; *i.e.*, olfactory bulbs pedunculated, attached to the *telencephalon* by a *tractus olfactorius* long (larger than the length of the olfactory bulbs)], 24 [1, 2; *i.e.*, projection postero-mesial of the *telencephalon* present; surface moderately convex (only the posterior margin well delimited) to convex (circular contour well delimited)], 25 (1; *i.e.*, groove or furrow between the lateral and postero-mesial projections of the *telencephalon* present), 40

[0; *i.e.*, posterior margin of the *lobus inferior hypothalami* not continuous, with invagination(s) evident], and 59 (1, 2; *i.e.*, anterior margin of the *corpus cerebelli* not expanded on the *telencephalon*, not expanded on the *telencephalon*, the distance between the anterior margin of the *corpus cerebelli* and the posterior margin of the *telencephalon* is shorter than the minimum width of the *telencephalon* or expanded on the *telencephalon*). On the other hand, the PCo3 was “positively correlated” with the following characters and character states: 4 (2; *i.e.*, lamella of the the olfactory organ symetric, posterior lamellae undifferentiated, all lamellae of similar size and thickness), 16 (0, 1; *i.e.*, *telencephalon* wider in its medial or posterior-most portion), 24 (0; *i.e.*, projection postero-mesial of the *telencephalon* absent or inconspicuous, surface concave or rectilinear), 29 [0; *i.e.*, thick of the *nervus opticus* shorter than the thick of the *nervus olfactorius*], 31 (1; *i.e.*, width of the *diencephalon* larger than the width of the *telencephalon*), 33 (1; *i.e.*, margin anterior of the *lobus inferior hypothalami* expanded anteriorly, clearly surpassing the anterior margin of the lateral portion of the *hypothalamus*), 34 (2, 3; *i.e.*, margin posterior of the *lobus inferior hypothalami* expanded posteriorly, surpassing the postero-mesial margin of the *hypothalamus*, with the posterior portions of each lobes not very close or clearly surpassing the postero-mesial margin of the *hypothalamus*, with the posterior portions of each lobes very close or in contact), 54 (1; *i.e.*, width of the *corpus cerebelli* larger than, or similar to, the width of the *tecta mesencephali*), 79 (0; *i.e.*, *lobus vagi* straight, without angulation) and 85 (0; *i.e.*, angulation between the *lobus vagi* and the *lobus facialis* about 0°, set rectilinear).

The PERMANOVA returned significant results ($F=1.40$; $p<0.001$), indicating overall separation among the group means (centroids). Moreover, significant results for most pairwise comparisons were returned indicating separation between both subtribes of the Loricariini, between both tribes of the Loricariinae and between most subfamilies of the Loricariidae (see Table 6); pairwise comparisons between the subfamilies Delturinae, Lithogeninae and Rhinelepinae vs. almost all other subfamilies or taxonomic groups were non-significant indicating no apparent differences in morphospace occupation (however, such comparisons, as discussed below, requires further scrutiny given the relatively low number of examined representatives for these subfamilies).

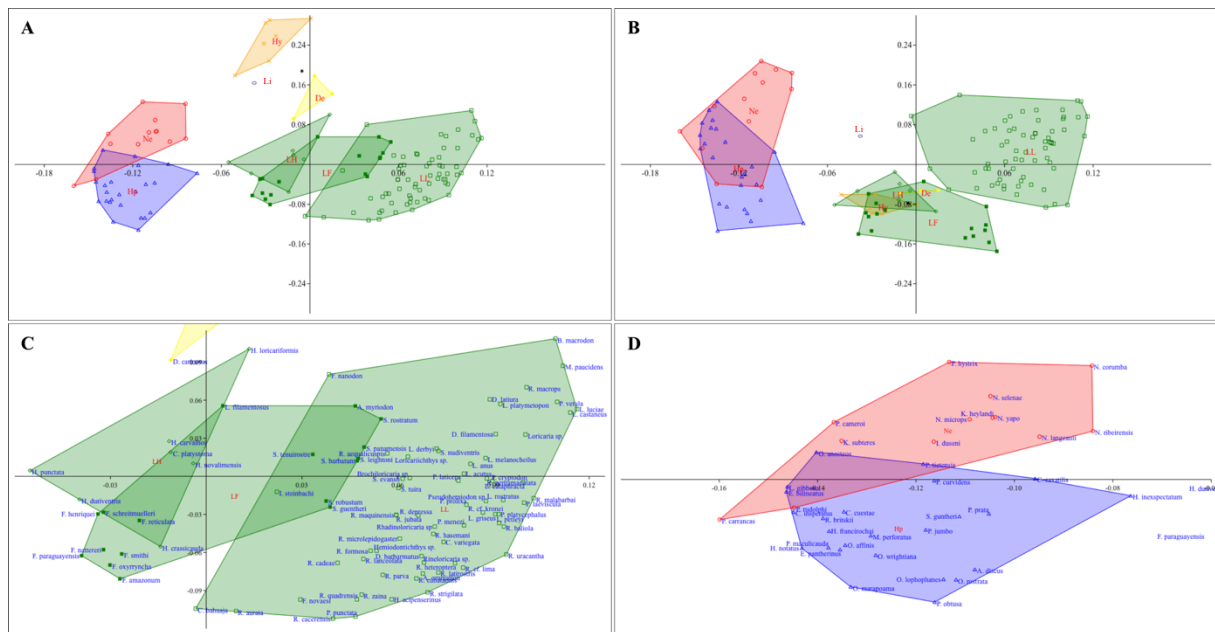


Figure 12. Empirical morphospace for members of the Loricariidae, based on the first three principal coordinates (PCos) of the PCoA using a total of 88 binary or multistate, non-ordered characters describing its gross brain morphology. (A) PCo1 vs. PCo2 empirical morphospace; (B) PCo1 vs. PCo3 empirical morphospace; (C) Detail of the space occupied by members of the Loricariinae in the PCo1 vs. PCo2 empirical morphospace; (D) Detail of the space occupied by members of the Hypoptopomatinae *sensu lato* and the Neoplecostominae in the PCo1 vs. PCo2 empirical morphospace (see complete species names in Appendix C). Yellow symbols represents members of the Delturinae (De); blue symbols represents members of the Hypoptopomatinae (Hp); orange symbols represents members of the Hypostominae (Hy); red symbols represents members of the Neoplecostominae (Ne); green symbols represents members of the Loricariinae [non-filled symbols represents members of the Harttiini (LH); the purple symbol represents the single representative of the Lithogeninae (Li); filled symbols represents members of the Loricariini (LF=Farlowellina, LL=Loricariina)]; the black symbol represents the single representative of the Rhinelepineae.

3.6. DISCUSSION

3.6.1. Comparative anatomy and gross ecological correlations and implications

Members of the Loricariinae and Loricariidae showed a considerable intra and inter-specific variation in the relative size, volume and shape of its different brain subdivisions, which is comparable, in some extent, to what was observed in other teleost fishes (e.g., members of the Characiformes, Cypriniformes and Gymnotiformes; see EVANS, 1931; 1940; HUBER *et al.*, 1997; ALBERT *et al.*, 1998; PEREIRA & CASTRO, 2016; ABRAHÃO *et al.*, 2018a). As previously noted, this (morphological) diversity cannot be explained, necessarily, by simple allometric relationships and/or developmental constraints (see ROSA, 2015; HUBER *et al.*, 1997; ABRAHÃO *et al.*, 2018a – also see “Chapter one”); moreover, ecological and historical (phylogenetic) factors also must be considered, evaluated and analyzed since they may explain an important portion of the total diversity observed (see HUBER *et al.*, 1997; ALBERT *et al.*, 1998; ITO *et al.*, 2007; ABRAHÃO *et al.*, 2018a; among others). Thus, some possible ecological and phylogenetic implications, based on the differences/similarities observed and described in the general brain organization of the members of the Loricariinae and Loricariidae, are discussed below considering individually and grupally, when feasible, all major brain subdivisions as well as most of the major (supraespecific) taxonomic categories evaluated. Additionally, comparisons with members of other related families and orders (as described in previous sections) are provided. Despite the fact that not functional nor phylogenetic analyses were herein conducted, most of the ecological and, to a lesser extent, phylogenetic correlations and implications discussed below have already been empirically tested and proved to be realistic by previous authors using other teleost fish taxa as study groups (see for example EVANS, 1931; 1940; HUBER & RYLANDER, 1992; VAN STAADEN *et al.*, 1995; HUBER *et al.*, 1997; KOTRSCHAL *et al.*, 1998; among others) supporting the interpretations herein exposed; moreover, in such cases, the respective references are cited in the correspondent section(s).

Telencephalon

With some exceptions, the *telencephala* of members of the Loricariinae, Loricariidae and Siluriformes was comparatively larger and more voluminous than most members of the Characiformes (see PEREIRA, 2014; PEREIRA & CASTRO, 2016), comparatively smaller and less voluminous than in most members of the

Cichliformes and some Perciformes (see KOTRSCHAL *et al.*, 1998; POLLEN *et al.*, 2007), and about equally developed comparing with most members of the Cypriniformes and Gymnotiformes (see EVANS, 1931; 1940; ALBERT *et al.*, 1998; PEREIRA & CASTRO, 2016). In relation to this, KOTRSCHAL *et al.* (1998) stated that the relative size of the *telencephalon* may be related, in most teleost fishes, to complex social behaviours and intra and interspecific interactions (e.g., pair formation and communication and interaction), rather than habitat complexity; such affirmation may support, partially, the results obtained here, considering that these (social) behaviours, as several studies have demonstrated, are much more complex and developed in reef fishes and in members of the Cichliformes (see KOTRSCHAL *et al.*, 1998; POLLEN *et al.*, 2007), contrary to what is known for members of the Loricariinae, Loricariidae and Siluriformes, as well as for most members of the Ostariophysi (in which such behaviours are usually less complex). On the other hand, and contradicting partially the exposed by KOTRSCHAL *et al.* (1998), some authors (e.g., VAN STAADEN *et al.*, 1995; HUBER *et al.*, 1997; POLLEN *et al.*, 2007) have correlated the size of the *telencephalon* with habitat size and complexity; such theory would have more sense (and applicability) when analyzing and comparing the relative size of this structure in members of the Loricariinae, Loricariidae and Siluriformes and other Ostariophysi given its habitat use and the “absence” of complex social behaviours. Moreover, as noted by several authors (e.g., FRIEDLANDER, 1983; DAVIS & KASSEL, 1983; HUBER & RYLANDER, 1992; HUBER *et al.*, 1997), the *telencephalon* also appears to be important in the integration of olfactory as well as visual and gustatory stimuli; therefore, the differences and similarities observed in the relative size, volume and shape of this structure in members of the Loricariinae, Loricariidae and Siluriformes, as well as in most Ostariophysi, may be directly linked to differences in habitat size and complexity and olfactory and gustatory capabilities.

Within the Loricariinae, species of the *Brochiloricaria* (*B. macrodon*), *Crossoloricaria*, *Dasylicaria*, *Farlowella* (*F. amazona*, *F. henriquei*, *F. nattereri* and *F. reticulata*), *Fonchiiloricaria*, *Hartiella*, *Hemiodontichthys*, *Loricaria*, *Planiloricaria*, *Pseudohemiodon*, *Rhadinoloricaria*, *Ricola*, *Rineloricaria* (*R. cacerensis*, *R. cadeae*, *R. cf. lima*, *R. formosa*, *R. hasemani*, *R. heteroptera*, *R. jubata*, *Rineloricaria* sp. and *R. uracantha*), *Sturisoma* (*S. barbatum*, *S. guentheri*, *S. rostratum*, *S. tenuirostre* and *S. leightoni*) and *Sturisomatichthys* showed the largest and more voluminous

telencephala; moreover, comparing between subfamilies of the Loricariidae, larger and more voluminous *telencephala* were observed in members of the Loricariinae and the Neoplecostominae (see Chars. 14, 15, 16, 18, 19, 20, 22, 24 and 31). Given the gross ecomorphological correlations anteriorly mentioned, members of these genera, and of the Loricariinae and the Neoplecostominae, in general terms, which showed larger and more developed *telencephala*, could present much more developed olfactory and gustatory capabilities compared to other members of the Loricariinae and Loricariidae, respectively. Interestingly, and different from what was observed in most members of the Loricariina, Loricariinae and Loricariidae, members of the *Farlowella* showed relatively elongated and thin *telencephala* (see Chars. 14 and 15), as also observed in the species *Diplomystes mesembrinus* (Ringuet, 1982; Siluriformes: Diplomystidae; see PEREIRA & CASTRO, 2016); this condition, as noted and discussed by previous authors studying other teleost fishes (e.g., member of the Cypriniformes; see EVANS, 1931; 1940; DAVIS & MILLER, 1967), instead of being correlated to a specific sensory, cognitive and/or behavioral specialization (e.g., increased olfactory and/or gustatory capabilities), may be mostly associated to differences in the snout length and the availability of (cranial) space between both eyes. Interspecific differences in the overall topography of the *telencephalon* were observed in members of the Loricariinae and Loricariidae (see Chars. 11, 14, 16, 18, 19, 20, 22, 23 and 24), as also reported in other teleost fish taxa (see EVANS, 1931; 1940; ALBERT *et al.*, 1998; PEREIRA & CASTRO, 2016; ABRAHÃO *et al.*, 2018a; among others); the degree of development of the different telencephalic areas could indicate, as discussed by HARA (1986), KOTRSCHAL (2000) and DØVING (2007), how the information on the chemical environment be received, analyzed and processed (considering the different sensory strategies, modalities and adaptations), as well as the relative importance of the corresponding behavioural responses; for example, the ventral area of the *telencephalon* is usually related to the physiological regulation of sociality and reproduction, whereas the posterodorsal and laterodorsal areas are usually related to food detection (*i.e.*, foraging; see KOTRSCHAL, 2000).

In most teleost fishes the olfaction, specifically, is used primarily for social communication and, to a lesser extent, for spatial orientation and foraging (see CAPRIO, 1978; FINGER, 1988; HUBER & RYLANDER, 1992; KOTRSCHAL, 2000). Olfactory capabilities, as previous studies have demonstrated (see FINGER, 1988;

HUBER & RYLANDER, 1992; KOTRSCHAL *et al.*, 1998; KOTRSCHAL, 2000), could be directly correlated to the relative size of the olfactory bulbs and the olfactory organ as well as to the number of lamellae in the olfactory organ (in addition to the relative size of the *telencephalon*), being that fishes with larger olfactory bulbs and olfactory organs, as well as greater number of lamellae, have demonstrated increased olfactory abilities (see WAGNER, 2002). In general terms, members of the Siluriformes showed relatively more developed (larger and voluminous) olfactory bulbs and olfactory organs, as well as a greater number of lamellae, comparing, for example, with members of the Characiformes and Cypriniformes (see EVANS, 1931; 1940; PEREIRA & CASTRO, 2016); such results would be in accordance with the expected considering the fact that most members of the Siluriformes, contrary to most members of the Characiformes and Cypriniformes, are primarily nocturnal and/or inhabitants of turbid waters, being oriented mainly by the senses of smell and tact (see CAPRIO, 1978; PEREIRA & CASTRO, 2016; also see the discussion on the “*Mesencephalon*”). Moreover, the sense of smell could be, in the absence of colorful or elaborate coloring patterns (and structural elements for its detention) in most species of Siluriformes, the main responsible in the search for a mate (HARA, 1986; GONZALEZ-VOYER & KOLM, 2010). Members of the Loricariinae showed between 9 and 49 (mean=20, standard deviation=9) lamellae on each olfactory organ, with members of the *Dentectus* Martín Salazar, Isbrücker & Nijssen, 1982, *Pseudohemiodon*, *Spatuloricaria* and *Sturisoma* showing the highest counts (more than 30); within the Loricariidae, members of the Hypostominae stood out for presenting a greater number of lamella (more than 40), whereas members of the Hypoptopomatinae and Otothyirinae presented the lowest counts (usually less than 20; see Char. 2); such results also could be correlated with very fine differences in habitat use, size and complexity and/or behavioural roles or strategies (including, but not limited to social communication and foraging; see FINGER, 1988; HUBER & RYLANDER, 1992; KOTRSCHAL *et al.*, 1998; KOTRSCHAL, 2000; WAGNER, 2002). Finally, significant intraspecific variation on the size, volume and shape of the olfactory organ and the number of lamellae was not observed in the specimens herein examined, however, previous authors (e.g., ROSA *et al.*, 2014; ROSA, 2015 – also see “Chapter one”) have demonstrated both sexual and ontogenetic variation in these structures in members of the Loricariinae, Hypoptopomatinae and Neoplecostominae; such differences, as discussed by these authors, could be linked

to seasonal and/or ontogenetic changes related to mating and the availability of food, as well as to different sensorial and behavioural roles or strategies (also see ATEMA, 1980; HARA, 1986 for a more detailed discussion).

Diencephalon

The *diencephalon*, in general terms, as previous studies in teleost fishes have demonstrated (see NIEUWENHUYS & BODENHEIMER, 1966; DEMSKI & KNIGGE, 1971; SENN, 1981; STRIEDTER, 1990), can be related to the senses of vision and audition, as well as to (the control of) different feeding and aggressive behaviours, the last being usually associated with the reproduction; in members of the Siluriformes, however, the *diencephalon* could be much more related to the senses of audition and taste (see ATEMA, 1971; STRIEDTER, 1990). Electric stimulation of the *lobus inferior hypothalami* in sunfishes (Centrarchidae, Perciformes; see DEMSKI & KNIGGE, 1971), for example, evoked the “snapping up and spitting out gravel” behaviour, which has led to relate this cerebral subdivision with the sense of taste, at least in part; this behaviour (snapping up and spitting out gravel), as noted below, also is present in members of the Loricariina (see MELO *et al.*, 2004; LUJAN & ARMBRUSTER, 2012); interestingly, members of this group (Loricariina) showed relatively more developed *lobus inferior hypothalami*, when comparing with other members of the subfamily and the family, sharing the following unique features: (1) semicircular to bean-shaped configuration, (2) margin lateral continuous, without invagination(s) evident, (3) margin posterior continuous, without invagination(s) evident, and (4) margin posterior expanded posteriorly, surpassing the postero-mesial margin of the *hypothalamus* and with the posterior portions of each lobes very close or in contact (see Chars. 34, 36, 37 and 40), which could be directly related to this specific behavior. On the other hand, studies on members of the Ictaluridae (see Striedter, 1990) have demonstrated that the *hypothalamus* receives and processes auditory and mechanosensory lateral line information (*i.e.*, the sense of hearing). Comparing with other members of the Siluriformes (*e.g.*, members of the Clariidae, Heptapteridae, Ictaluridae, Pseudopimelodidae; see STRIEDTER, 1990; ROSA, 2005; CHING *et al.* 2015; ABRAHÃO *et al.*, 2018a; b), as well as members of the Characiformes and Cypriniformes (see EVANS, 1931; 1940; PEREIRA, 2014; PEREIRA & CASTRO, 2016), members of the Loricariidae showed relatively less

developed *hypothalamus*; considering the above, and the relative importance of the acoustic communication in these fishes (see LADICH, 2004 for a detailed discussion), the results of this study agree with the expected.

Mesencephalon

The *tectum mecencephali*, being the most prominent mecencephalic subdivision, is considered, in all teleost fishes, the main visual center (see NIEUWENHUYS, 1982; MEEK & NIEUWENHUYS, 1998; WAGNER, 2002; NORTHMORE, 2011). In the examined groups, the *tectum mecencephali* showed a considerable variation in its relative size, volume and shape; within the Ostariophysi, for example, members of the Characiformes and Cypriniformes presented relatively more developed *tecta mecencephali* (as well as other optic structures), while members of the Siluriformes and Gymnotiformes usually presented less developed or reduced *tecta mecencephali* and optic structures (also see EVANS, 1931; 1940; ALBERT *et al.*, 1998; PEREIRA, 2014). Within the Loricariidae, members of the Farlowellina (*e.g.*, *Farlowella* and *Sturisomatichthys*), Harttiini, Hypoptopomatinae *sensu lato* and Neoplecostominae (*e.g.*, *Kronichthys* Miranda Ribeiro, 1908) showed relatively more developed *tecta mecencephali*, contrary to the observed in most members of the Loricariina (see Chars. 15, 30, 44, 46, 47 and 48). Considering the above and the fact that most members of these groups, mainly members of the Characiformes and Cypriniformes, are usually found in small streams characterized by clear waters and moderate currents (see EVANS, 1931; 1940; SCHAEFER, 1997; LUJAN & ARMBRUSTER, 2012; PEREIRA & CASTRO, 2016), the results of this study confirms that vision is a dominating sensory modality in such environments (also see GARAMSZEGLI *et al.*, 2002; WAGNER, 2002; HOWLAND *et al.*, 2004; CHING *et al.*, 2015 for a more detailed discussion). Moreover the differences observed between the different taxa in the relative size, volume and shape of the mesencephalic regions, mainly the *tectum mecencephali*, may be related to possible differences in the visual acuity as response to different ecological and/or behavioral factors and selective pressures, including, but not limited to, habitat structure, foraging strategies and mate search (also see WAGNER, 2002; 2003; CHING *et al.*, 2015 for a more detailed discussion).

Rhombencephalon

The *rhombencephalon* is the largest brain subdivision in most fishes, including all teleost fishes, and plays an important role as a center of multimodal coordination and integration (NIEUWENHUYS, 1982; NIEUWENHUYS *et al.*, 1998). In members of the Loricariinae and Loricariidae, as well as in most members of the Siluriformes (see ATEMA, 1971; PUPO, 2011; ABRAHÃO & SHIBATTA, 2015; ABRAHÃO *et al.*, 2018a; among others), Cypriniformes (see EVANS, 1931; 1940; PEREIRA & CASTRO, 2016) and Gymnotiformes (see ALBERT *et al.*, 1998; PEREIRA & CASTRO, 2016) the *rhombencephalon* is comparatively more developed, showing a prominent *corpus cerebelli* and relatively well developed *medulla oblongata* (medullary) subdivisions, differing from the observed in most members of the Characiformes (see PEREIRA & CASTRO, 2016). The *corpus cerebelli* is the largest rhombencephalic subdivision in most orders of the Ostariophysi (see BRANDSTÄTTER & KOTRSCHAL, 1990; ALBERT, 2001; ABRAHÃO & SHIBATTA, 2015; CHING *et al.*, 2015; PEREIRA & CASTRO, 2016; ANGULO & LANGEANI, 2017; ABRAHÃO *et al.*, 2018a); in members of the Loricariinae and Loricariidae (as well as in most members of the Characiformes, Cypriniformes, Gymnotiformes and Siluriformes) its relative size, volume and shape varies considerably between species, genera and suprageneric groups; at one end of this spectrum there are, for example, most members of the Loricariina, Delturiinae, Hypostominae (e.g., *Hypostomus* Lacepède, 1803 and *Megalancistrus* Isbrücker, 1980) and Neoplecostominae (e.g., *Neoplecostomus* Eigenmann & Eigenmann, 1888), as well as members of the Heptapteridae (e.g., *Rhamdia* Bleeker, 1858; see ROSA, 2015; ABRAHÃO *et al.*, 2018b) and Pseudopimelodidae (e.g., *Pseudopimelodus* Bleeker, 1858; see ABRAHÃO & SHIBATTA, 2015; ABRAHÃO *et al.*, 2018a), among others, which present relatively larger and more voluminous *corpus cerebelli*; at the other extreme, there are members of the Farlowellina (*Farlowella*), Hypoptopomatinae (e.g., *Acestridium* Haseman, 1911) and Otothyridae (e.g., *Otocinclus* Cope, 1871 and *Otothyris* Myers, 1927), as well as members of the Callichthyidae (e.g., *Corydoras*; see PUPO, 2011; ROSA, 2015; PUPO & BRITTO, 2018) and most Characiformes and Cypriniformes (see EVANS, 1931; 1940; PEREIRA & CASTRO, 2016), showing relatively small and less voluminous *corpus cerebelli*. Larger *corpus cerebelli*, in general terms, are usually linked to increased motor control while swimming in

structurally complex environments and/or fast currents (see FELLE, 1984; BAUCHOT *et al.*, 1989; HUBER & RYLANDER, 1992; KOTRSCHAL *et al.*, 1998); the *corpus cerebelli*, as experiments have shown, also is important in various learning and memory processes associated with spatial orientation (see BROGLIO *et al.*, 2003; GONZALEZ-VOYER & KOLM, 2010); such theories are in accordance with observations on the habitat and distribution of most of the taxa herein evaluated, especially when comparing most members of the Gymnotiformes and Siluriformes, with most members of the Characiformes and Cypriniformes (see EVANS, 1931; 1940; ALBERT *et al.*, 1998; LUJAN & ARMBRUSTER, 2012; ABRAHÃO & SHIBATTA, 2015; PEREIRA & CASTRO, 2016; ABRAHÃO *et al.*, 2018a). The *corpus cerebelli*, and the lateral lobe of the *rhombencephalon* (see RETHELYI & SZABO, 1973), as previous studies have demonstrated (see SCHLEGEL, 1973), also play an important role in the reception, coding and interpretation of electrical stimuli, qualities or capabilities that are much more developed in members of the Gymnotiformes; in fact, as illustrated in PEREIRA & CASTRO (2016; Fig. 12), members of this order showed, in accordance with the above, much more developed *corpus cerebelli*, with three apparently synapomorphic features: (1) pear-shaped configuration, (2) anterior portion expanded anteriomedially on the mesencephalon and (3) lateral and posterior profiles S-shaped; not found in other members of the Ostariophysi (see Char. 52, 58 and 60).

In members of the Siluriformes, as well as in all other teleost fishes, the medullary subdivisions, including both the *lobi vagi* and *facialis*, are usually associated with gustative perception, receiving sensory information from taste buds present in the barbels, mouth, pharynx and gill arches (see MEEK & NIEUWENHUY, 1998; ABRAHÃO & SHIBATTA, 2015). Previous studies (see ATEMA, 1971; HUBER & RYLANDER, 1992) have demonstrated the existence of two gustatory subsystems in members of the Siluriformes: (1) a “facial subsystem”, which is critical for the localization of food sources, and (2) a “glossopharyngeal-vagal subsystem”, which is critical for the selection and ingestion of food sources once these are inside the mouth. Given the above, the differences observed in the relative size, volume and shape of such brain subdivisions between species and species groups can be associated to differences in the perception and use of food resources and/or foraging strategies (see EVANS, 1931; 1940; ATEMA, 1971 – also see “Chapter one”). Within the Loricariinae, members of the Loricariina (including

members of the *Brochiloricaria* Isbrücker & Nijssen, 1979, *Furcodontichthys* Rapp Py-Daniel, 1981, *Hemiodontichthys*, *Limatulichthys*, *Loricaria*, *Loricariichthys*, *Planiloricaria*, among others) showed more developed medullary subdivisions, including both *lobi vagi* and *facialis*, contrary to most genera and suprageneric groups of the Loricariinae (*i.e.*, members of the Farlowellina and Harttiini) and Loricariidae, which showed less developed medullary subdivisions; moreover, within the Loricariina, members of the *Hemiodontichthys* and *Loricariichthys* showed hypertrophied *lobi vagi*, as also observed in members of the Callichthyidae (Siluriformes; see PUPO, 2011; ROSA, 2015; PUPO & BRITTO, 2018). Members of the Farlowellina and the Harttiini usually forage by scraping food from solid substrates; on the other hand, members of the Loricariina are most commonly associated with sandy substrates, from which they separate and consume small aquatic invertebrates, seeds and other vegetal components, rather than biofilm (see MELO *et al.*, 2004; LUJAN & ARMBRUSTER, 2012); the need to separate discrete food items from loosely aggregated substrates in members of the Loricariina places distinct functional and operational demands on its oral apparatus and associated (brain) medullary subdivisions, explaining the differences herein observed; moreover, the results of this study highlight the importance of the “glossopharyngeal-vagal subsystem” in members of the *Hemiodontichthys* and *Loricariichthys*, among others, as well as in members of the Callichthyidae.

Considering that most members of the Loricariina show bucal paternal care (see TAYLOR, 1983; GROSS & SARGENT, 1985; MARCUCCI *et al.*, 2005; PY-DANIEL & COX-FERNANDES, 2005), brain modifications on some medullary subdivisions, such as the *lobi vagi* and *facialis*, as well as the alar portion of the *medulla oblongata*, also would be related with increased sensitive capabilities and/or specialized behaviours related to the care of the progeny (see “Chapter one”); for example, the males of some species of the *Loricaria* and *Loricariichthys* exhibit an accentuated sexual dimorphism during the reproductive season, which is characterized by an increase in the size and structural complexity of some oral structures, such as the lips (see TAYLOR, 1983; PY-DANIEL & COX-FERNANDES, 2005), parallel, members of these two genera have prominent *lobi vagi* and *facialis* which are much more developed than in most members of the Loricariinae and Loricariidae (see ROSA, 2015 – also see “Chapter one”). Despite that no intra-specific differences in the size, volume and shape of these medullary subdivisions in

species of the Loricariinae and Loricariidae were herein evaluated, the results of previous contributions studying members of this subfamily and family (e.g., ANGULO & LANGEANI, 2017 – see “Chapter one”) may be considered as empirical evidence supporting, in part, these gross ecomorphological correlations, which, moreover, would be extrapolated to other related species showing similar reproductive strategies (e.g., members of the *Furcodontichthys*, *Limatulichthys* and other species of the *Loricaria*, *Loricariichthys*, *Rineloricaria*, among others; see PY-DANIEL & COX-FERNANDES, 2005; ANGULO & LANGEANI, 2017).

On the other hand, as noted by VARI (1985) and PEREIRA & CASTRO (2016), the *lobi vagi* and *facialis* are usually inconspicuous or almost absent in most members of the Characiformes [except in members of the Chilodontidae, Hemiodontidae (e.g., *Bivibranchia* Eigenmann, 1912) and Prochilodontidae], being this one of the first differences observed when comparing with the brain of most members of the Cypriniformes, Gymnotiformes and Siluriformes (see EVANS, 1931, 1940; ALBERT *et al.*, 1998; ABRAHÃO & SHIBATTA, 2015; ROSA, 2015; PEREIRA & CASTRO, 2016; ANGULO & LANGEANI, 2017; ABRAHÃO *et al.*, 2018a). The suite of modifications of the jaws, gill arches, and digestive system characteristic of most members of the Chilodontidae, Hemiodontidae and Prochilodontidae allows them to efficiently gather and process their preferred food items (detritus and aufwuchs; see BOWEN *et al.*, 1984; VARI, 1985; LANGEANI, 1998; CASTRO & VARI, 2004); these anatomical specializations, in some extent, can be comparable to that exhibited by most members of the Loricariinae and Loricariidae and, as discussed above, clearly reflects on brain morphology, explaining some of the similarities observed. Moreover, contrary to members of the Chilodontidae and Prochilodontidae (as well as for most members of the Loricariidae and the Siluriformes), members of the Bryconidae (e.g., *Brycon* Müller & Troschel, 1844 and *Salminus* Agassiz, 1829) and the Characidae (e.g. *Oligosarcus* Günther, 1864; see PEREIRA, 2014), among other Characiformes showing omnivorous to carnivorous habits, present prominent mesencephalic structures (e.g., *tectum mesencephali*), which are much more developed and voluminous compared to the above mentioned medullary subdivisions; this condition, as discussed above, has been widely described by previous authors studying other teleost fishes [e.g., Cypriniformes (see EVANS, 1931, 1940); CICHLIFORMES (see VAN STAADEN *et al.*, 1995; POLLEN *et al.*, 2007)] and is usually correlated to a greater visual acuity (see EVANS, 1931;

1940; NIEUWENHUYNS *et al.*, 1998; WAGNER, 2002; 2003; POLLEN *et al.*, 2007; CHING *et al.*, 2015); such theory makes sense when considering the (usual) foraging habits and strategies, as well as the daily activity cycles, of the groups compared.

3.6.2. Morphological disparity and phylogenetic considerations

The subfamilies Hypoptopomatinae *sensu lato*, Loricariinae and Neoplecostominae occupied the largest areas displaying more disparity among species. Considering that these subfamilies include about 50% of the total number of known species of the Loricariidae (see FRICKE *et al.*, 2018), these results suggest that both (brain) morphological and species diversities are relatively consistent in these groups (see MINELLI, 2015; OYSTON *et al.*, 2015); moreover, these results also correspond to the ecological diversity exhibited by members of these subfamilies, and specially by members of the Loricariinae, which, as noted above, occupies a wide variety of habitats and tropic levels being only comparable to those exhibited, within the Loricariidae, by members of the Hypostominae, the largest subfamily of the Loricariidae (see SCHAEFER & LAUDER, 1986; LUJAN & ARMBRUSTER, 2012; among other authors). The subfamilies Delturinae and Hypostominae (excluding the Lithogeninae and Rhineleporinae, represented in the analysis by a single species each one) occupied the smallest areas in the morphospace projection displaying less disparity among species; these results may be due to two main reasons: (1) the relatively low sampling size, with the consequent underestimation of the "true" (brain) morphological diversity (these two subfamilies were represented in the analysis by three and seven species, respectively; *i.e.*, about 43 and 13%, respectively, of the total number of known species for each subfamily; see FRICKE *et al.*, 2018a), and (2) the conservative (brain) morphology of the groups (see YU *et al.*, 2014 for a more detailed discussion); in this case, considering the taxonomic, morphological and ecological diversity of these groups (see SCHAEFER & LAUDER, 1986; LUJAN & ARMBRUSTER, 2012; LUJAN *et al.*, 2015), the first explanation may be the most feasible for members of the Hypostominae and the second one for members of the Delturinae.

Within the Loricariinae, the three (taxonomic) groups *a priori* defined (*i.e.*, Harttiini, Farlowellina and Loricariina) were well supported statistically; these groups corresponded relatively well with three of the four groups originally established by

IsbrüCKER (1979) (*i.e.*, the tribes Loricariini, Harttiini and Farlowellini), based on a phenetic approach and considering, almost exclusively, osteological and some external morphological characters. Moreover, these three groups, as almost in the same way as they were herein “recovered”, are currently considered, based on molecular information, as monophyletics (see COVAIN *et al.*, 2016), with the Harttiini keeping its category of tribe and the Loricariini, *sensu* ISBRÜCKER (1979; *i.e.*, Loricariina), and the Farlowellini, *sensu* ISBRÜCKER (1979; *i.e.*, Farlowellina), as subtribes of the Loricariini, *sensu* COVAIN *et al.* (2016). Members of the Loricariinae, including both tribes and subtribes of the Loricariini, as in the case of the members of the Hypoptopomatinae *sensu lato* and the Neoplecostominae, occupied adjacent areas in the morphospace projection (Fig. 12); these results, as discussed by previous authors (*e.g.*, WAKE *et al.*, 2011; YU *et al.*, 2014) may indicate (1) shared ancestral character states or (2) homoplasy caused by adaptation to similar ecological conditions; however, considering the proposed phylogenetic relationships for these groups (see COVAIN & FISCH-MULLER, 2007; COVAIN, 2011; ROXO *et al.*, 2014, 2019; LUJAN *et al.*, 2015; COVAIN *et al.*, 2016; among other authors) the first explanation may be the most feasible for this particular case (further analysis, are necessary to corroborate this hypothesis). In the same line, it is notably the relatively strong overlap in the morphospace occupied by members of the subfamilies Hypoptopomatinae *sensu stricto* (including the genera *Acestridium* Haseman, 1911, *Hypoptopoma* Günther, 1868, among others) and Otothyriinae [as defined by CHIACHIO *et al.* (2008); including the genera *Hisonotus* Eigenmann & Eigenmann, 1889, *Otothyris* Myers, 1927, among others] (see Fig. 12), with its group means not significantly different (based on the results of a previous analysis which is not herein showed); these results agree strongly with the phylogenetic hypotheses proposed by ROXO *et al.* (2014, 2019) and LUJAN *et al.* (2015), among other authors, which, based mainly in molecular information, recovered genera of the “Otothyriinae” (and the Neoplecostominae) nested within the Hypoptopomatinae *sensu stricto*, suggesting shared ancestral character states. On the other hand, within the ranges of almost all subfamilies, particularly in the Loricariinae and Neoplecostominae, there were recovered several clusters of species with highly similar (brain) morphologies in the morphospace projection, agreeing with the generic and suprageneric division, classification and relationships proposed and followed for these different groups [*e.g.*, members of the genera *Farlowella*, *Harttia*,

Neoplecostomus, *Rineloricaria* (including members of the former genera *Hemiloricaria* Bleeker, 1862, *Ixinandria* Isbrücker & Nijssen, 1979 and *Fonchiiichthys* Isbrücker & Michels, 2001, current synonyms of *Rineloricaria* see; COVAIN *et al.*, 2016) and *Sturisoma*, among others; see COVAIN & FISCH-MULLER, 2007; COVAIN, 2011; ROXO *et al.*, 2014; LUJAN *et al.*, 2015; COVAIN *et al.*, 2016; Fig. 12). All these results, as noted above and as also demonstrated by previous authors studying other biological groups (e.g., BRIGGS & FORTEY, 2005; BRUSATTE *et al.*, 2008; YU *et al.*, 2014), may suggest that the characters herein analyzed present, besides to its ecological significance, some degree of “phylogenetic signal”, supporting and highlighting the taxonomic and phylogenetic value of the brain morphology for the study of members of this family and order (also see PUPO, 2011, 2015; ROSA, 2015; PEREIRA & CASTRO, 2016; ABRAHÃO *et al.*, 2018a for a more detailed discussion on other taxa of the Siluriformes).

3.6.3. Additional phylogenetic considerations

PEREIRA & CASTRO (2016) proposed two apparently synapomorphic brain features for members of the Siluriformes (based on two species: *Diplomystes mesembrinus* and *Pimelodus maculatus* Lacepède, 1803, Pimelodidae), not found in the examined members of the Characiformes, Cypriniformes and Gymnotiformes [*i.e.*, (1) olfactory organ elongate and well developed (*vs.*, olfactory organ approximately circular and moderately developed); and (2) about 60 olfactory lamellae (*vs.*, less than 30)]; however, as the results of this study demonstrated (see Chars. 0 and 2), these characters are variable and they would not represent valid synapomorphies for the order. Moreover, these authors also proposed six putative synapomorphic brain features for members of the Characiformes, not found in the examined members of the Cypriniformes, Gymnotiformes and Siluriformes [*i.e.*, (1) *tectum mesencephali* horizontally elongate, in contact with the anterior margin of the *corpus cerebelli* (*vs.*, *tectum mesencephali* vertically elongate and not in contact with the anterior margin of the *corpus cerebelli*, or relatively reduced); (2) width of the *rhombencephalon* not exceeding the width of the *mesencephalon*, both in dorsal and ventral views (*vs.*, *rhombencephalon* wider than the *mesencephalon* due to the larger size of the *corpus cerebelli*); (3) *corpus cerebelli* rounded, and elongated vertically (*vs.*, *corpus cerebelli* usually elongated horizontally); (4) *lobus facialis* usually

inconspicuous or visible only as a small oval structure attached to the basis of the *corpus cerebelli* (vs., *lobus facialis* well developed, usually visible dorsally or partial or totally hidden by a large *corpus cerebelli*); (5) *lobus vagi* usually poorly developed (vs., *lobus vagi* relatively well developed); (6) area postrema (*i.e.*, the alar portion of the *medulla oblongata*) shaped as an inverted triangle, wider anteriorly and narrowing posteriorly (vs., area postrema equally narrow throughout its full length, with inconspicuous limits)]; however, as the results of this study also demonstrated, these characters, again, are variable and, as proposed by PEREIRA & CASTRO (2016), they would not represent valid synapomorphies for the order.

4. CHAPTER THREE:

A CONTRIBUTION TO THE PHYLOGENY OF THE LORICARIIDAE, WITH EMPHASIS ON THE LORICARIINAE, USING MOSTLY GROSS BRAIN MORPHOLOGICAL CHARACTERS

[Manuscript in preparation] A. Angulo, A. Rosa & F. Langeani (*in prep.*) A contribution to the phylogeny of the suckermouth armored catfishes (Siluriformes: Loricariidae), with emphasis on the Loricariinae, using mostly gross brain morphological characters. To be submitted to *Zootaxa*.

4.1. ABSTRACT.

A phylogenetic study of the Loricariidae with emphasis on the Loricariinae is herein presented based on a maximum parsimony analysis of 150 phenotypic characters including 89 gross brain morphological (neuroanatomical) characters. The results of this study support previous hypotheses on the monophyly of the Loricariidae, most subfamilies of the Loricariidae [*i.e.*, Delturinae, Hypostominae, Loricariinae, Neoplecostominae and Hypoptomatinae (including the Otothyridae)] and most of the genera (*i.e.*, *Dasylicaria*, *Delturus*, *Farlowella*, *Hemiodontichthys*, *Hypostomus*, *Kronichthys*, *Limatulichthys*, *Loricaria*, *Loricariichthys*, *Neoplecostomus*, *Otothyris*, *Pareiorhaphis*, *Pareiorhina*, *Pseudohemiodon*, *Rineloricaria*, *Spatuloricaria* and *Sturisoma*) and suprageneric groups (*i.e.*, the tribes Harttini and Loricariini, in part, and the subtribe Loricariina, among others) evaluated. This work provides considerable additional data to the evolutionary tree of one of the most diversified vertebrate families, highlighting the need of more studies integrating information from different anatomical systems in a phylogenetic context. Moreover, this work could be a basis for further investigations on the relationships between brain anatomy and the ecology of members of the Loricariinae, Loricariidae and Siluriformes in a phylogenetic frame.

4.2. KEYWORDS

Delturinae, Hypoptopomatinae, Hypostominae, Neoplecostominae,
Neotropical catfishes, Neuroanatomy.

4.3. INTRODUCTION

The family Loricariidae (Siluriformes) comprises a monophyletic group within the Neotropical endemic suborder Loricarioidei (see DE PINNA, 1998; REIS *et al.*, 2003; LUJAN *et al.* 2015), whose members are easily recognized from other fishes by having bodies covered by ossified dermal plates, abundant integumentary teeth (odontodes) and a ventral oral disk (see REIS *et al.*, 2003; GARG *et al.*, 2010; GEERINCKX *et al.*, 2011; LUJAN *et al.* 2015). The Loricariidae currently comprises six to nine subfamilies (*i.e.*, Ancistrinae, Delturinae, Hypoptopomatinae, Hypostominae, Lithogeninae, Loricariinae, Neoplecostominae, Otothyriinae and Rhinelepinae), about 110 genera and about 980 valid species (as well as several undescribed forms), being the most diverse within the Siluriformes and the fifth most diverse within the Vertebrata (see DE PINNA, 1998; SCHAEFER, 2003; ARMBRUSTER, 2004; LUJAN *et al.*, 2015; NELSON *et al.*, 2016; FRICKE *et al.*, 2018a). Members of the Loricariidae are typically small to medium-sized (< 20 cm SL; although some species can reach almost 1 m in total length; see Lujan *et al.*, 2015), obligate freshwater and bottom-feeders fishes, being ecologically important in the regulation of the primary production chain and the nutrient dynamics in many Neotropical rivers (BUCK & SAZIMA, 1995; KNOLL *et al.*, 2009; LUJAN *et al.*, 2011, 2015).

The subfamily Loricariinae, specifically, comprises a monophyletic group within the Loricariidae, whose members are easily recognized from other members of the family by having an elongate and depressed caudal peduncle and by lacking adipose fin (see SCHAEFER, 1987; RAPP PY-DANIEL, 1997; COVAIN & FISCH-MULLER, 2007). The currently accepted hypothesis comprises a total of 31 genera and about 243 valid species (as well as several undescribed forms), converting this subfamily into the second most diverse within the Loricariidae (FRICKE *et al.*, 2018a). Members of the Loricariinae are widely distributed throughout the Central and South American major river drainages, from southern Costa Rica to northern Argentina (REIS *et al.*, 2003; COVAIN & FISCH-MULLER, 2007), being usually found near the substrate, showing a great morphological and functional diversity (see SCHAEFER & LAUDER, 1986; COVAIN & FISCH-MULLER, 2007; COVAIN, 2011; LUJAN & ARMBRUSTER, 2012; LUJAN, *et al.* 2015). Despite of this (great diversity and ecological significance), the evolutionary history and interrelationships of the

members of the subfamily (as well as of the family as a whole) remains relatively poorly understood; in fact, a robust and well-resolved phylogenetic hypothesis is (as noted below) still necessary in order to promote and facilitate future studies on the systematic and evolutionary history of the group (LUJAN *et al.*, 2015).

Studies on the evolutionary history and interrelationships of the members of the Loricariidae, in general terms, started with EIGENMANN & EIGENMANN (1890) and REGAN (1904) who divided it, based on the analysis of morphological characters and under a phenetic approach, into three (Hypoptopomatinae, Loricariinae and Plecostominae) and five (Argiinae, Hypoptopomatinae, Loricariinae, Neoplecostominae and Plecostominae) subfamilies respectively. The first study that employed a cladistic approach to the classification of members of the Loricariidae was published at the end of the 19th century by HOWES (1983), who, based on the analysis of morphological characters (mainly the cranial osteology and myology), divided the family into six subfamilies (Chaetostominae, Hypoptopomatinae, Hypostominae, Lithogeninae, Loricariinae and Neoplecostominae). Since then, there have been published at least 40 studies on relationships within the Loricariidae [divided almost equally between studies based on morphological and molecular characters (see MONTOYA-BURGOS, *et al.*, 1998; LUJAN, *et al.* 2015; PEREIRA & REIS, 2017; for an overview)], which support the monophyly of the family as well as their placement among other five families in the suborder Loricarioidei (see DE PINNA, 1998; REIS, *et al.* 2003), but at the same time disagree in the composition, placement and interrelationships of their major clades (see LUJAN, *et al.* 2015; PEREIRA & REIS, 2017; for an overview).

Studies on the evolutionary history and interrelationships of the members of the Loricariinae, specifically, started with ISBRÜCKER (1979) who recognized a total of 27 genera, classifying them, based on the analysis of morphological characters and under a phenetic approach, into four tribes and eight subtribes [the Loricariini, including 6 subtribes (Loricariina, Planiloricariina, Reganellina, Rineloricariina, Loricariichthyina and Hemiodontichthyina), the Harttiini, including two subtribes (Harttiina and Metaloricariina), the Farlowellini and the Acestridiini]. Subsequently, SCHAEFER (1987), based on the analysis of morphological characters, but at this time under a cladistic approach, established, for the first time, the monophyly of the subfamily and corroborated most of the supra-generic groups proposed by ISBRÜCKER (1979), with exception of the Acestridiini, which was relocated within

the Hypoptopomatinae. Later, RAPP PY-DANIEL (1997) and ARMBRUSTER (2004), based on the analysis of morphological characters and under a cladistic approach, corroborated, again, the monophyly of the subfamily, as well as of the Loricariini *sensu* SCHAEFER (1987), but redefined the Harttiini, which would include the Farlowellini *sensu* ISBRÜCKER (1979) and SCHAEFER (1987); furthermore, these authors divided both tribes into four subtribes, with the Loricariini including the Hemiodontichthyina and the Planiloricariina and the Harttiini including the Harttiina and the Farlowellina. MONTOYA-BURGOS *et al.* (1998), based on the analysis of molecular characters and under a cladistic approach, also corroborated the monophyly of the subfamily, as well as its subdivision into two tribes; however, these authors recovered *Harttia* Steindachner, 1877 (the nominal genus of the Harttiini) as the sister genus of all other Loricariinae [comprising the Farlowellina, part of the Harttiina, *sensu* RAPP PY-DANIEL (1997) and ARMBRUSTER (2004), and the Loricariini], disagreeing, partially, with the results of the previous authors (*i.e.*, SCHAEFER, 1987; RAPP PY-DANIEL, 1997; ARMBRUSTER, 2004). COVAIN & FISCH-MULLER (2007), in their review of the subfamily, listed a total of 30 valid genera and provided a generic identification key and a synopsis for each one of them; in addition, based on the analysis of morphological characters and under a phenetic approach, these authors partly confirmed the division of the subfamily into two tribes [the Harttiini and the Loricariini, *sensu* MONTOYA-BURGOS *et al.* (1998)] and proposed four morphological groups within the Loricariini (the *Loricaria*, *Loricariichthys*, *Pseudohemiodon* and *Rineloricaria* groups). Posteriorly, COVAIN *et al.* (2008, 2010) and RODRIGUEZ *et al.* (2011), based on the analysis of molecular characters and under a cladistic approach, corroborated, again, the monophyly of the subfamily, as usually defined, and its subdivision into two tribes, with the Harttiini restricted to *Harttia* and the Loricariini including the Farlowellina [incorrectly named Sturisomina in COVAIN *et al.* (2008), but corrected in COVAIN *et al.* (2010)] and the Loricariina, agreeing, partially, with the results of previous authors (*i.e.*, MONTOYA-BURGOS *et al.*, 1998; COVAIN & FISCH-MULLER, 2007). Moreover, COVAIN *et al.* (2008, 2010) and RODRIGUEZ *et al.* (2011) corroborated the monophyly of three of the four morphological groups proposed by COVAIN & FISCH-MULLER (2007; *i.e.*, the *Loricaria*, *Loricariichthys* and *Pseudohemiodon* morphological groups), but rejected the monophyly of the *Rineloricaria* group; results that were partially supported by CRAMER *et al.* (2011) and LUJAN *et al.* (2015) in their molecular

phylogenies of the Hypoptopomatinae (including four members of the Loricariinae as the outgroup) and the Hypostominae (including 14 members of the Loricariinae as the outgroup), respectively. Finally, in the most recent phylogeny of the subfamily, COVAIN *et al.* (2016) reaffirmed the subdivision of the Loricariinae into two tribes, with the Harttiini including the genera *Cteniloricaria* Isbrücker & Nijssen, 1979, *Harttia* and *Harttiella* Boeseman, 1971 and the Loricariini including the Farlowellina and the Loricariina, agreeing with the results of ROXO *et al.* (2019). The results of these authors, based on molecular information, however, revealed several incongruences with previous morphological classifications, principally at the generic and suprageneric levels (mainly below the rank of tribe). Given this “confusing/discrepant” scenario, new studies, and more important, new sources of information are fundamental to a better understanding of the group, contributing to the elucidation of the evolutionary history and interrelationships of members of the subfamily and family.

Notably, most of the morphological studies cited above, either under an descriptive, comparative (e.g., ISBRÜCKER, 1979; COVAIN & FISCH-MULLER, 2007; among others) and/or cladistic approach (e.g., HOWES, 1983; SCHAEFER, 1987; RAPP PY-DANIEL, 1997; ARMBRUSTER, 2004; among others), have focused on the use of osteological characters due to their “pretty well-known” utility for comparative porpoises, their relative easy access and the extensive literature available (see REGAN, 1904; 1911; ALEXANDER, 1964; 1965; CHARDON, 1968; LUNDBERG & BASKIN, 1969; ISBRÜCKER, 1979; SCHAEFER, 1987; RAPP PY-DANIEL, 1997; COVAIN & FISCH-MULLER, 2007). On the other hand, descriptive, comparative and/or cladistic studies considering alternative body systems, such as the brain anatomy (see below), in both members of the Loricariinae and the Loricariidae, specifically, as well as in other teleost fish taxa, in general terms, have been rarely addressed, or when undertaken, rarely carried on in an organized fashion (see FREIHOFFER, 1978; HOWES, 1993; PUPO, 2011, 2015; DATOVO & VARI, 2014; ROSA, 2015; PEREIRA & CASTRO, 2016, among others; for examples and a more detailed discussion). The “extensive” exploration of osteological characters demonstrated to be “rather efficient” for the delimitation of most major clades within the Teleostei; however, as noted by DATOVO & VARI (2014) and PEREIRA & CASTRO (2016), it also resulted in the “relatively minor attention” of alternative, and (possibly) equally or more informative, anatomical systems.

In this sense, the relatively few authors that have attempted to use the brain morphology in taxonomic studies on teleost fishes have obtained, in most cases, satisfactory results, which have improved the knowledge about the evolutionary histories of the groups evaluated (see SVETOVIDOV, 1953; MILLER & EVANS, 1965; FREIHOFFER, 1978; YAMAMOTO, 1982; HOWES, 1993; PARENTI, 1993; 2005; EASTMAN & LANNOO, 1995; ALBERT *et al.*, 1998; EASTMAN & LANNOO, 2007, 2008; KHONSARI *et al.*, 2009; PUPO, 2011; ROSA, 2015; ABRAHÃO *et al.*, 2018). For example, SVETOVIDOV (1953) supported the idea that brain patterns, particularly the position of the nasal capsule in relation to the olfactory lobes, could be used as diagnostic characters in an important number of teleost fishes at the intra-familial level, and in some particular cases and with certain precautions, at the inter- and intra-generic levels as well. MILLER & EVANS (1965) pointed out that most differences in the brain of members of the Catostomidae (Cypriniformes), at the subfamily level, reflect an early separation between suprageneric groups; moreover, these authors concluded that the principal benefit of the study of brain pattern lies in the understanding of sensory specializations at the interspecific level. FREIHOFFER (1978) in their study of the cranial nerves of the percoid fish *Polycentrus schomburgkii* Müller & Troschel, 1849 (Perciformes, Nandidae), revealed several anatomical characters of systematic and phylogenetic importance, laying the groundwork for more detailed studies within members of the order. EASTMAN & LANNOO (1995) demonstrated that brain diversification in notothenioids (Perciformes, Notothenioidei) has proceeded at a rate coincident with phyletic diversification at the generic and species levels. More recently, Pupo (2011) described the gross brain morphology of the members of the Callichthyidae (Siluriformes), and using 20 neuroanatomical characters in a cladistics analysis that also included representatives of other families of the Loricarioidea (e.g., Trichomycteridae, Scoloplacidae, Astroblepidae and Loricariidae) corroborated the monophyly of the family as well as of its two subfamilies (i.e., Callichthyinae and Corydoradinae); in addition, this author concluded that the brain of these fishes “has important features to enhance phylogenetic studies, bringing more resolution to current hypotheses about their relationships...” especially at the inter/intra-familial and inter-generic levels. ROSA (2015), studying catfishes of the subfamilies Hypoptopomatinae and Neoplecostominae (Loricariidae), concluded that: “the neuroanatomical characters in these groups can provide a good phylogenetic signal and that they are, indeed, an

important source of new taxonomic characters almost unexplored". Finally, ABRAHÃO *et al.* (2018), studying the gross brain morphology of members of the Pseudopimelodidae (Siluriformes), concluded that "the combination of considerable interspecific modification and restricted intraspecific variation suggests that brain gross morphology provides putative characters for the resolution of supraspecific groups"; moreover these authors also stated that "the morphological patterns shared by species within these groups are indicative of the fact that these characters might be useful in phylogenetic analyses".

Taking the above into consideration, the main objective of this work was to carry out a gross morphological description and characterization of the brain of the members of the Loricariinae and Loricariidae in order to evaluate and provided (possibly) new informative anatomical characters that may help to elucidate some of the phylogenetic questions and incongruences previously mentioned within the group. Moreover, we want to evaluate and analyze, based on our dataset, under a cladistic approach, and comparing with the results of previous studies, the interrelationships among valid genera and suprageneric groups of the Loricariinae, as well as among members of the subfamily with members of other subfamilies and suprageneric groups within the Loricariidae. Finally, in accordance with previous authors (*e.g.*, PUPO, 2011; ABRAHÃO, 2013; PEREIRA, 2014; ABRAHÃO & SHIBATTA, 2015; ROSA, 2015; ABRAHÃO *et al.*, 2018), we also want to promote and encourage the utilization of this relatively "new" approach, as well as the use of underutilized and potentially informative tools and anatomical characters, in more comprehensive evolutionary studies on members of the subfamily and family, specifically, and, in general terms, on members of the order and the group (Teleostei) as a whole.

4.4. MATERIAL AND METHODS

4.4.1. Taxon sampling

The selection of the species was intended to sample most of the morphological and taxonomic diversity within the Loricariinae (and the Loricariidae), including representatives of its two tribes (Harttiini and Loricariini; see above) and most valid genera (there were examined representatives of 30 of the 31 genera that

currently comprises the subfamily, all except *Pterosturisoma*, Isbrücker & Nijssen 1978; see FRICKE *et al.*, 2018b). The taxon sampling also focused in the inclusion of as many species and specimens as possible, considering the availability of material for the inevitably destructive brain removals; with studies of intraspecific variation beyond the scope of the Chapter (for that please refer to the Chapter one). A total of 65 valid species of the Loricariinae (*i.e.*, about 27% of the total number of current known species within the subfamily; see FRICKE *et al.*, 2018a), plus six additional unidentified or undescribed taxa (identified at the genus level), totalizing 72 species/terminals as the ingroup, were analyzed. In addition, members of all the other subfamilies of the Loricariidae [*i.e.*, Delturinae, Hypoptopomatinae (including the Otothyridae; see SCHAEFER 1991, 1998; CRAMER *et al.*, 2011; LUJAN *et al.*, 2015), Hypostominae (including the Ancistrinae; see ARMBRUSTER, 1998, 2004), Lithogeninae, Neoplecostominae and Rhinelepidinae; see FRICKE *et al.*, 2018a, b; including 33 genera and 50 species], as well as other members of Siluriformes [including another four families (Astroblepidae, Callichthyidae, Pimelodidae and Pseudopimelodidae), five genera and seven species], totalizing 56 species as the outgroup, were analyzed; the final data set consisted of a total of 129 taxa. The list of the material examined is provided in the Appendix A totalizing more than 300 specimens (mostly adults, in order to avoid the potentially confusing effects of developmental changes; see HUBER & RYLANDER, 1992; ANGULO & LANGEANI, 2017). Data from species not listed in the material examined were obtained from the literature (see below). The current taxonomic status and classification of the species cited and evaluated in the present work follows Fricke *et al.* (2018b), except for members of the Otothyridae which were placed in the Hypoptopomatinae following CRAMER *et al.* (2011), MARTINS *et al.* (2014), LUJAN *et al.* (2015) and PEREIRA & REIS (2017).

4.4.2. Character sampling

The character (char.) sampling was intended to capture as much brain morphological variation as possible. Brains were dissected and removed as described in the Chapter one (also see ANGULO & LANGEANI, 2017). Characters (chars.) were examined directly from brains (when available; see material examined) using a stereomicroscope, from brain photographs (see Chapters one and two and

ANGULO & LANGEANI, 2017) and/or from brain descriptions and illustrations available in the literature (*i.e.*, PUPO, 2011, 2015; ABRAHÃO, 2013; PEREIRA, 2014; ROSA, 2015), as detailed in the Chapters one and two and in ANGULO & LANGEANI (2017). The list of the 89 characters analyzed is provided in the Appendix B; the resulting data matrix is provided in the Appendix D (see chars. 0 to 88). Most characters were described and discussed in previous studies, *i.e.*, PUPO (2011, 2015), ABRAHÃO (2013), PEREIRA (2014), ROSA (2015); also see the Chapter two. In the data matrix (see Appendix D; chars. 0 to 88), the characters for which published information was in conflict with the data herein generated were coded as polymorphic (*e.g.*, “0&1”); missing or unverifiable information, as well as non-applicable characters, were coded as “?”.

4.4.3. Cladistic methodology and phylogenetic analysis

The phylogenetic analysis was performed by parsimony, following the methods described by HENNIG (1966) and developed by FARRIS (*e.g.*, 1969, 1970, 1983), among others, using the software TNT 1.1 (GOLOBOFF *et al.*, 2008). All characters were considered as unordered, binary or multistate, non-additive and received equal weights. The most parsimonious trees were obtained through a heuristic search using new technologies (GOLOBOFF *et al.*, 2008) under the following parameters: ratchet=200 iterations; drift=50 iterations, random sequence additions=1000 replicates; maximum retention=10000 trees. From the equally parsimonious trees a strict *consensus* tree was constructed using the respective function in TNT. Bremer support was calculated in TNT using suboptimal trees with up to 15 steps more than the fundamental trees. Homoplasy levels, for the tree and each character, were calculated in WinClada (NIXON, 2002) as consistency and retention indices (CI and RI, respectively; see ARCHIE, 1989; FARRIS, 1989). The analyses was rooted in *Pimelodus argenteus* Perugia, 1891 as a representative of the Pimelodidae (Siluroidei), considered as the sister group of the Loricarioidei (see DE PINNA, 1998; NELSON *et al.*, 2016).

4.4.4. Combined analysis

A total of 61 additional morphological, mainly osteological, characters (see Appendix E) defining the major clades of the Loricariidae (*sensu* SCHAEFER, 1987, 1991; RAPP PY-DANIEL, 1997; ARMBRUSTER, 2004; PAIXÃO & TOLEDO-PIZA, 2009; MARTINS *et al.*, 2014; LONDOÑO-BURDUANO & REIS, 2016; PEREIRA & REIS, 2017), were incorporated (and analyzed in conjunction) into (with) the matrix of neuroanatomical characters (see Appendix D, chars. 89 to 150). This information was obtained from various sources, including the aforementioned works, as well as the original descriptions of the species evaluated. Besides to their taxonomic importance, these 61 characters were selected, of the overall available in the literature, considering the availability of information for most (more than 50%) of the terminal taxa herein analyzed. The combined analyses was performed in order to: (1) improve the detection of “more reliable” phylogenetic groups, by giving a greater descriptive and explanatory power to the analysis derived exclusively from neuroanatomical characters; and (2) understand the “behavioral patterns” of the neuroanatomical characters, throughout the phylogenetic analysis, as well as the possible support that these characters could give to the pre-existing phylogenetic arrangements. The character sampling and the phylogenetic analysis for the combined matrix of 150 characters (Appendix D), followed the same guidelines and methodology established and detailed above.

4.5. RESULTS

4.5.1. Neuroanatomical analysis

The phylogenetic analysis of the unordered, non-additive and unweighted neuroanatomical data matrix yielded ten equally parsimonious trees (overall length 1287 steps; CI=0.09; RI=0.66). The resulting strict *consensus* tree is presented in the Figures 13 and 14; the list of synapomorphies for each clade and autapomorphies for each terminal taxon is provided in the Appendix F. The superfamily Loricarioidea, represented in the analysis by members of the Astroblepidae, Callichthyidae and Loricariidae was recovered as a monophyletic group (clade 135), being supported by a total of seven synapomorphies: (1) width of the *corpus cerebelli* shorter than the width of the *tecta mesencephali* (char. 54: 1→0); (2) length of the *lobus vestibulolateralis* less than half the length of the *corpus cerebelli* (char. 67: 1→0); (3)

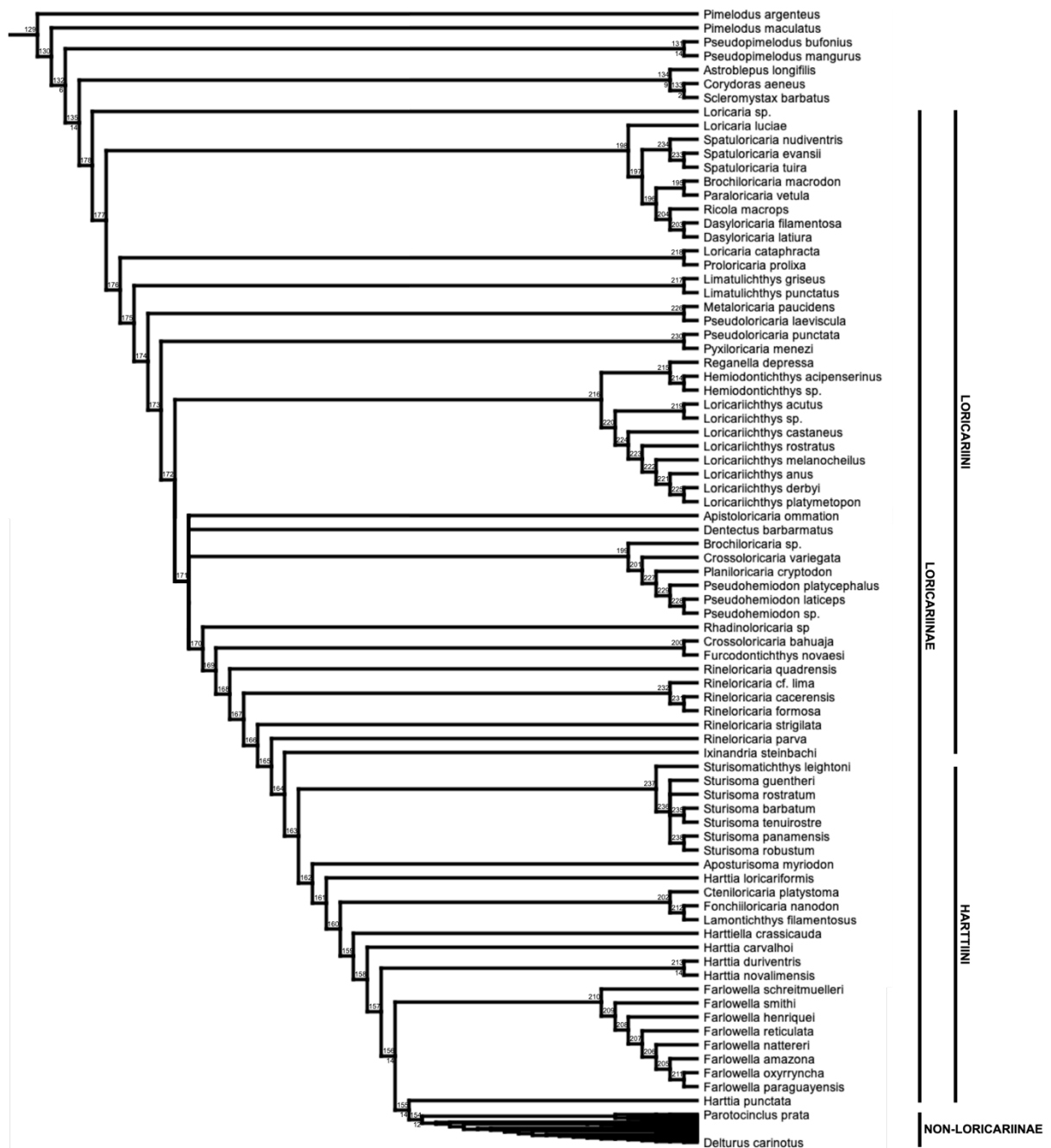


Figure 13. Strict consensus of ten maximally parsimonious trees (1154 steps; CI=0.10; RI=0.66), showing the interrelationships among members of the Loricariinae and Loricariidae (gross brain morphology); see part of the consensus tree (i.e., non-Loricariinae members of the Loricariidae) in Fig. 14. Numbers above branches indicate the number of the clade and those below the branches correspond to the Bremer support values (in those clades in which no number is indicated the Bremer support value was equal or greater than 15).

both portions of the *lobi facialis* not in contact (char. 74: 1→0); (4) angulation between both *lobi facialis* 90° or more (char. 75: 0→1); (5) contact between both *lobi vagi* only between its postero-lateral portions (char. 80: 1→0); (6) angulation between both *lobi vagi* more than 0° and less than 90° (char. 81: 0→1); (7) length of the *lobus vagi* larger than, or similar to, the length of the *eminentia granularis* (char. 82: 0→1). Within the Loricarioidea, the families Callichthyidae and Loricariidae were recovered as monophyletic groups, with the Callichthyidae (clade 133) supported by a total of seven synapomorphies [(1) margin lateral of the *telencephalon* continuous, without invagination(s) evident (char. 23: 1→0); (2) optic nerves oriented transversal to the anteroposterior axis of the encephalon, starting almost parallel to opposite sides (char. 27: 0→1); (3) anterior margin of the *lobus inferior hypothalami* not expanded anteriorly, in line with or not surpassing the anterior margin of the *tectum mesencephali* (char. 32: 1→0); (4) Height of the *corpus cerebelli* larger than the height of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi*, *corpus cerebelli* expanded dorsally (char. 63: 0→1); (5) *lobus facialis* inconspicuous, reduced or undetectable, not completely exposed, *i.e.*, located under the posterior portion of the *corpus cerebelli* (char. 70: 1→0); (6) volume of the *lobus facialis* shorter than, or similar to, the volume of the *lobus vagi* (char. 72: 1→0)] and the Loricariidae (clade 178) supported by a total of six synapomorphies [(1) olfactory organ almost circular or drop-shaped, *i.e.* anterior and/or posterior margins tapered (char. 0: 0→1); (2) lateral margin of the *lobus inferior hypothalami* continuous, without invagination(s) evident (char. 37: 0→1); (3) latero-posterior portion of the *lobus inferior hypothalami* ventrally expanded, surface discontinuous with the rest of the lobe (char. 39: 0→1); (4) volume of the *corpus cerebelli* larger than the volume of the *tecta mesencephali* (char. 56: 0→1); (5) posterior portion of the *lobus facialis* more voluminous than the anterior portion (char. 77: 0→1); and (6) *lobus vagi* very angled, anterior margins facing to the medial axis (char. 79: 1→2)].

Among the subfamilies of the Loricariidae, only the Delturinae, represented in the analysis by two genera and three species, was recovered as a monophyletic group (clade 137), being supported by five synapomorphies: (1) dorsal surface of the *telencephalon* not expanded ventrally, *i.e.*, ventral surface of the *telencephalon* completely exposed (char. 22: 2→0); (2) postero-mesial projection of the *telencephalon* absent or inconspicuous, surface concave or rectilinear (char. 24: 2→0); (3) lateral margin of the *lobus inferior hypothalami* not expanded posteriorly, in



Figure 14. Part of the strict consensus of ten maximally parsimonious trees (1154 steps; CI=0.10; RI=0.66), showing the interrelationships among members of the non-Loricariinae subfamilies of the Loricariidae (gross brain morphology); see the complete tree in Fig. 13. Numbers above branches indicate the number of the clade and those below the branches correspond to the Bremer support values (in those clades in which no number is indicated the Bremer support value was equal or greater than 15).

line with, or not surpassing, the lateral margin of the lateral portion of the *hypothalamus* (char. 35: 1→0); (4) length of the *tectum mesencephali* shorter than, or similar to, its height, *i.e.*, vertically elongated in shape in lateral view (char. 46: 1→0); and (5) posterior margin of the *corpus cerebelli* expanded on the *lobi facialis* or reaching the anterior margin of the lobes (char. 62: 2→1). Members of the Loricariinae (Loricariini) were recovered in a basal position as the sister group of the remaining members of the family.

Among the genera of the Loricariinae, represented in the analysis by more than one species, *Dasyloricaria* Isbrücker & Nijssen, 1979 (two species; clade 203), *Farlowella* Eigenmann & Eigenmann, 1889 (eight species; clade 210), *Hemiodontichthys* Bleeker, 1862 (two species; clade 214), *Limatulichthys* Isbrücker & Nijssen, 1979 (two species; clade 217), *Loricariichthys* Bleeker, 1862 (eight species; clade 220), *Pseudohemiodon* Bleeker, 1862 (three species; clade 229), *Spatuloricaria* Schultz, 1944 (three species; clade 234) and *Sturisoma* Swainson, 1838 (six species; clade 236) were recovered as monophyletic, being supported by four to seven synapomorphies (see Appendix F); contrary, the genera *Harttia* Steindachner, 1877, *Crossoloricaria* Isbrücker, 1979, *Loricaria* Linnaeus, 1758, *Pseudoloricaria* Bleeker, 1862 and *Rineloricaria* Bleeker, 1862 were not recovered as monophyletic. The non-Loricariinae genera *Delturus* Eigenmann & Eigenmann, 1889 (Delturinae; two species; clade 136), *Kronichthys* Miranda Ribeiro, 1908 (Neoplecostominae; two species; clade 240), *Neoplecostomus* Eigenmann & Eigenmann, 1888 (Neoplecostominae; six species; clade 242) and *Otothyris* Myers, 1927 (Hypoptopomatinae; two species; clade 244) also were recovered as monophyletic, being supported by three to seven synapomorphies (see Appendix F). Other non-Loricariinae genera, including *Hisonotus* Eigenmann & Eigenmann, 1889 (Hypoptopomatinae; two species), *Hypostomus* Lacepède, 1803 (Hypostominae; four species), *Pareiorhaphis* Miranda Ribeiro, 1918 (Neoplecostominae; two species) and *Pareiorhina* Gosline, 1947 (Neoplecostominae; two species), were not recovered as monophyletic.

4.5.2. Combined analysis

The phylogenetic analysis of the unordered, non-additive and unweighted combined data matrix yielded ten equally parsimonious trees (overall length 1544

steps; CI=0.13; RI=0.71); the resulting strict consensus tree is presented in the Figures 15 and 16; the list of synapomorphies for each clade and autapomorphies for each terminal taxon is provided in the Appendix G. The superfamily Loricarioidea was recovered as a monophyletic group (clade 150), being supported by a total of 14 synapomorphies, ten of them of neuroanatomical origin: (1) width of the *corpus cerebelli* shorter than the width of the *tecta mesencephali* (char. 54: 1→0); (2) margin anterior of the *corpus cerebelli* expanded on the *tecta mesencephali* but not surpassing its anterior margin (char. 58: 2→1); (3) margin anterior of the *corpus cerebelli* Not expanded on the *telencephalon*, the distance between the anterior margin of the *corpus cerebelli* and the posterior margin of the *telencephalon* is shorter than the minimum width of the *telencephalon* (char. 59: 2→1); (4) height of the *corpus cerebelli* shorter than, or similar to, the height of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi*, *corpus cerebelli* not expanded dorsally (char. 64: 1→0); (5) length of the *lobus vestibulolateralis* less than half the length of the *corpus cerebelli* (char. 67: 1→0); (6) no contact between both *lobi facialis* (char. 74: 1→0); (7) angulation between both *lobi facialis* 90° or more (char. 75: 0→1); (8) contact between both *lobi vagi* only between its postero-lateral portions (char. 80: 1→0); (9) angulation between both *lobi vagi* more than 0° and less than 90° (char. 81: 0→1); and (10) length of the *lobus vagi* larger than, or similar to, the length of the *eminentia granularis* (char. 82: 0→1). Within the Loricarioidea, the families Callichthyidae and Loricariidae were recovered as monophyletic groups, with the Callichthyidae (clade 182) supported by a total of nine synapomorphies, seven of them of neuroanatomical origin: [(1) less than 20 lamellae on the olfactory organ (char. 2: 1→0); (2) lamellae of the olfactory organ asymmetrical, posterior lamellae noticeably more elongated and thicker (char. 4: 0→1); (3) dorsal projections in the lamellae of the olfactory organ located on the posterior portion of the lamellae (char. 6: 0→1); (4) *nervus olfactorius* inserted in the mesial portion of the olfactory organ, with the fibers oriented obliquely towards the *bulbus olfactorius* (char. 7: 0→1); (5) width of the *nervus olfactorius* shorter than, or similar to, the width of a single olfactory lamella (char. 10: 2→0); (6) margin anterior of the *lobus inferior hypothalami* expanded anteriorly, clearly surpassing the anterior margin of the lateral portion of the *hypothalamus* (char. 33: 0→1); and (7) height of the *corpus cerebelli* larger than the height of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi*, *corpus cerebelli* expanded dorsally (char. 63: 0→1)] and the

Loricariidae (clade 148) supported by a total of eleven synapomorphies, ten of them of neuroanatomical origin: [(1) *telencephalon* rounded or reniform to semicircular (char. 14: 1→2); (2) *telencephalon* wider in its medial portion in dorsal view (char. 16: 0→1); (3) lateral projection of the *telencephalon* present, surface convex (char. 20: 0→1); (4) groove/furrow between the lateral and postero-mesial projections of the *telencephalon* present and, usually, very conspicuous (char. 25: 0→1); (5) width of the *diencephalon* shorter than, or similar to, the width of the *telencephalon* (char. 31: 1→0); (6) posterior margin of the *lobus inferior hypothalami* expanded posteriorly, surpassing the postero-mesial margin of the *hypothalamus*, with the posterior portions of each lobe not very close (char. 34: 3→2); (7) width of the *lobus facialis* about equal to half the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (char. 73: 2→1); (8) swelling of the *nervus facialis* evident, forming a small callosity on the wall facing to the ventricle (char. 78: 0→1); (9) height of the *lobus vagi* shorter than the height of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (char. 83: 1→0); and (10) width of the *lobus vagi* larger than, or similar to, half the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (char. 84: 1→0).

Among the subfamilies of the Loricariidae, the Delturiinae, Hypoptopomatinae *sensu lato*, Hypostominae, Loricariinae and Neoplecostominae, as usually defined (see below), were recovered as monophyletic groups. The Delturinae (clade 193) was supported by four synapomorphies, two of them of neuroanatomical origin: (1) lateral margin of the *lobus inferior hypothalami* not expanded posteriorly, in line with, or not surpassing, the lateral margin of the lateral portion of the *hypothalamus* (char. 35: 1→0); and (2) contact between both lobes of the *tectum mesencephali* present only between the anteriormost portion of lobes (char. 46: 1→0). The Hypoptopomatinae *sensu lato* (clade 144) was supported by seven synapomorphies, two of them of neuroanatomical origin: (1) length of the *nervus olfactorius* shorter than the length of the *bulbus olfactorius*, not visible dorsally (char. 9: 0→1); and (2) mesial portion of the *hypothalamus* not ventrally expanded, at the same level of the ventral surface of the *lobus inferior hypothalami* (char. 41: 1→0). The Hypostominae *sensu stricto* (clade 155) was supported by two synapomorphies, none of them of neuroanatomical origin; however, the species *Rhinelepis aspera* Spix & Agassiz 1829 (the single evaluated representative of the Rhinelepinae) was recovered as the

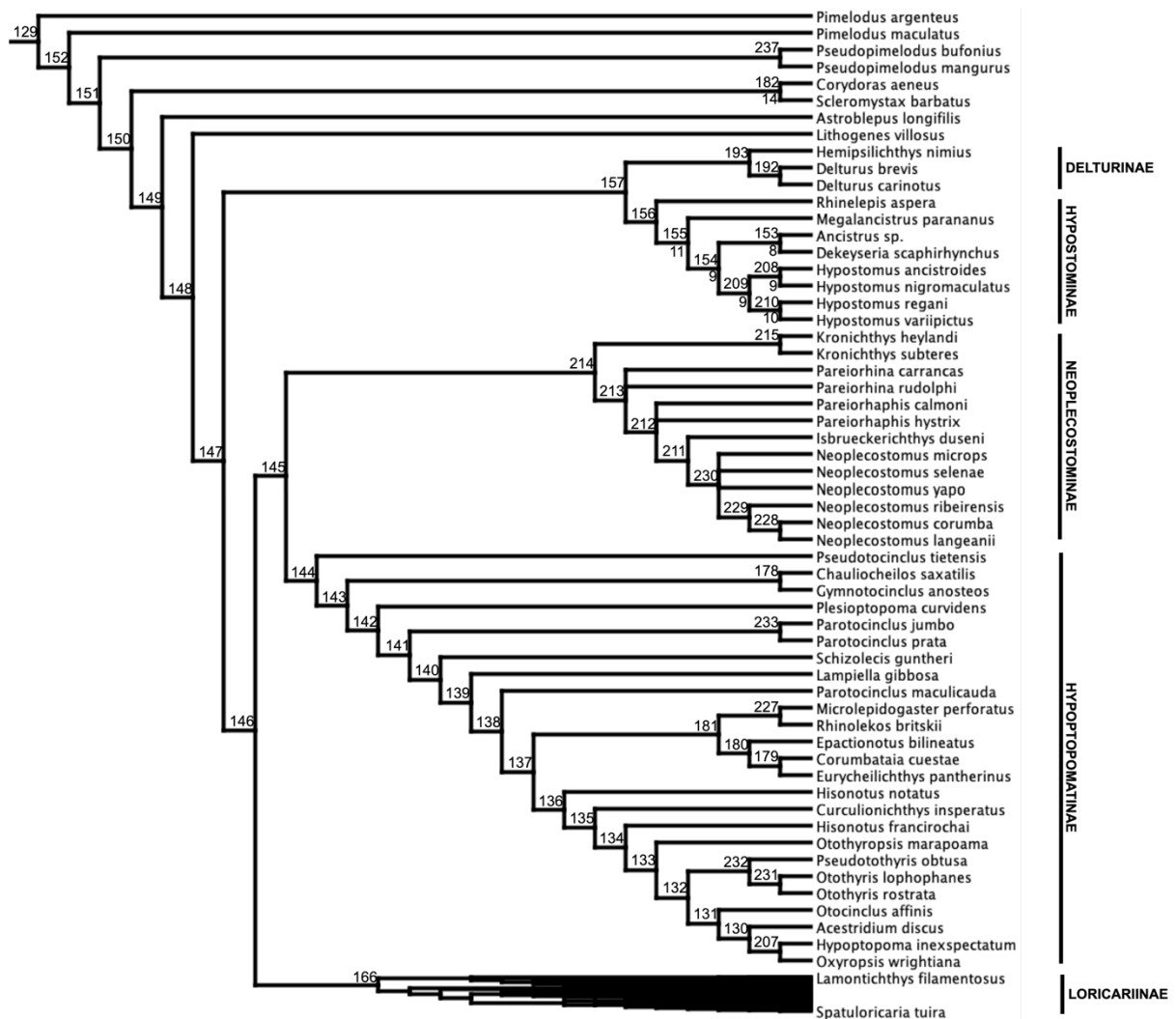


Figure 15. Strict consensus of ten maximally parsimonious trees (1459 steps; CI=0.13; RI=0.71), showing the interrelationships among members of the Loricariidae (combined analysis); see part of the consensus tree (i.e., members of the Loricariinae) in Fig. 16. Numbers above branches indicate the number of the clade and those below the branches correspond to the Bremer support values (in those clades in which no number is indicated the Bremer support value was equal or greater than 15).

sister group of the Hypostominae, sharing with the other six representatives of the subfamily (clade 156) a total of six synapomorphies, four of them of neuroanatomical origin: (1) fibers of the *nervus olfactorius* Inserted in the posterior portion of the olfactory organ and oriented posteriorly towards the *bulbus olfactorius* (char. 7: 0→1); (2) dorsal surface of the *telencephalon* fully expanded, covering totally the

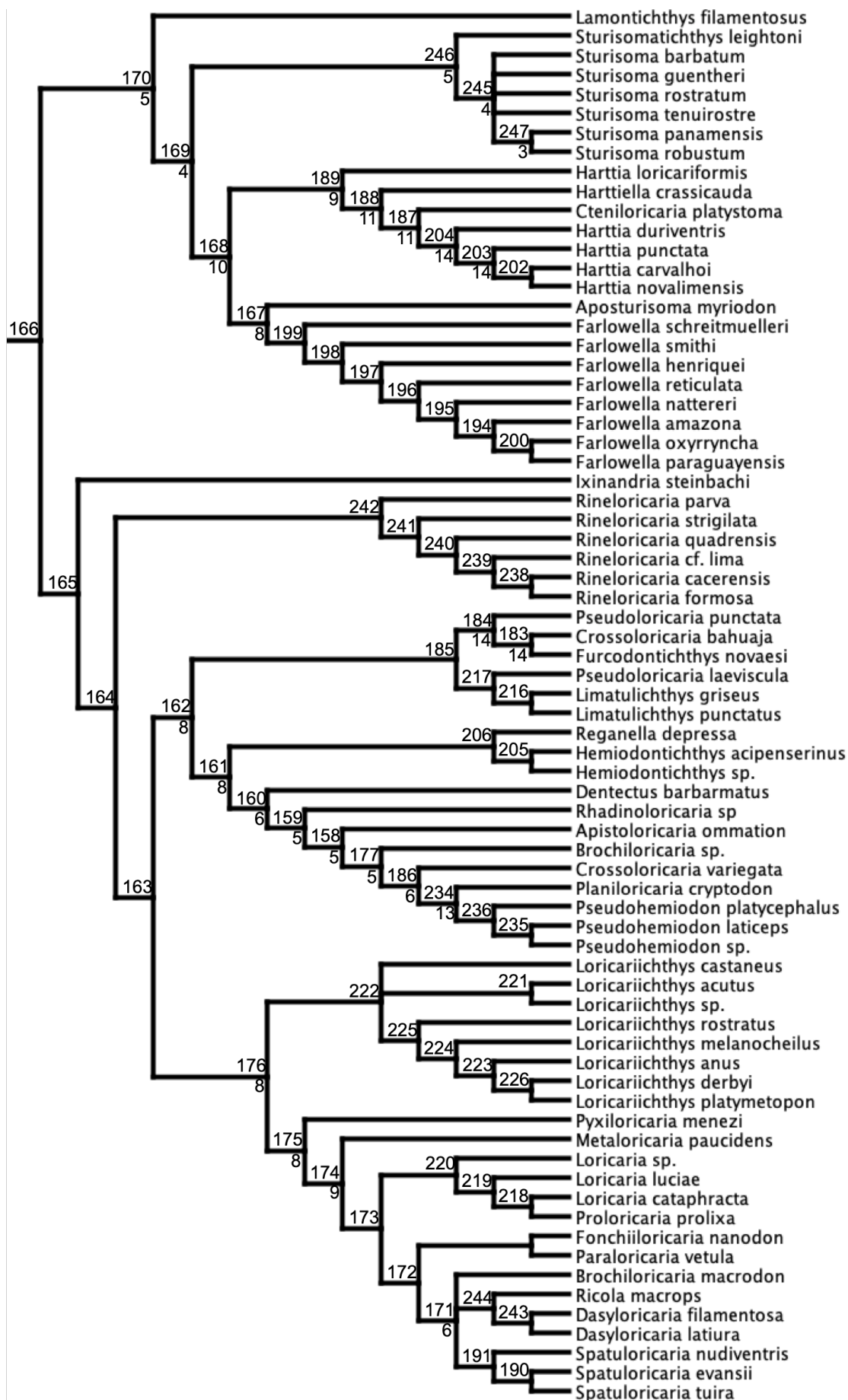


Figure 16. Part of the strict consensus of ten maximally parsimonious trees (1459 steps; CI=0.13; RI=0.71), showing the interrelationships among members of the Loricariinae (combined analysis); see the complete tree in Fig. 15. Numbers above branches indicate the number of the clade and those below the branches correspond to the Bremer support values (in those clades in which no number is indicated the Bremer support value was equal or greater than 15).

ventral surface of the *telencephalon* (char. 22: 0→2); (3) ventral overhang in the antero-medial portion of the *truncus cerebri* absent, ventral surface almost rectilinear, (char. 51: 1→0); and (4) anterior portion of the *lobus facialis* more voluminous than the posterior portion (char. 77: 0→2). The Loricariinae (clade 166; Fig. 4) was supported by nine synapomorphies, six of them of neuroanatomical origin: (1) dorsal projections in the lamellae of the olfactory organ located on the mesial portion of the lamellae, *i.e.*, subterminal (char. 6: 0→1); (2) length of the *telencephalon* shorter than, or similar to, the length of the *tectum mesencephali* (char. 15: 1→0); (3) dorsal surface of the *telencephalon* partially expanded, covering only the anterior portion of the ventral surface of the *telencephalon* (char. 22: 0→1); (4) length of *rhombencephalon* larger than the rest of the brain (char. 49: 1→0); (5) swelling of the *nervus facialis* not evident, wall facing to the ventricle concave (char. 78: 1→0); and (6) width of the *lobus vagi* larger than, or similar to, half the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (char. 84: 0→1). The Neoplecostominae (clade 214) was supported by seven synapomorphies, all of them of neuroanatomical origin: (1) length of the *telencephalon* larger than the length of the *tectum mesencephali* (char. 15: 0→1); (2) antero-mesial projection of the *telencephalon* absent or inconspicuous, surface concave or rectilinear (char. 19: 1→0); (3) postero-mesial projection of the *telencephalon* absent or inconspicuous, surface concave or rectilinear (char. 24: 1→0); (4) posterior margin of the *lobus inferior hypothalami* expanded posteriorly, surpassing the postero-mesial margin of the *hypothalamus*, with the posterior portions of each lobe not very close (char. 34: 3→2); (5) length of the *tectum mesencephali* larger than the length of the *corpus cerebelli* (char. 47: 0→1); (6) volume of the *tectum mesencephali* shorter than, or similar to, the volume of the *telencephalon* (char. 48: 1→0); and (7) length of *rhombencephalon* shorter than, or similar to, the length of the rest of the brain, *i.e.*,

mesencephalon, *diencephalon* and *telencephalon*, excluding the *nervus tractus olfactorius* and the olfactory bulbs (char. 49: 1→0).

Within the Loricariinae, the Harttiini, as traditionally defined (see Discussion), was recovered as a paraphyletic sequence of lineages, including the monophyletic: (1) *Aposturisoma* Isbrücker, Britski, Nijssen & Ortega, 1983 + *Farlowella* (*i.e.*, the subtribe Farlowellina *sensu* RAPP PY-DANIEL, 1997; clade 167); (2) *Cteniloricaria* + *Harttia* + *Harttiella* (clade 189, *i.e.*, the tribe Harttiini *sensu* COVAIN *et al.*, 2016); and (3) *Sturisoma* + *Sturisomatichthys* (clade 246), with the species *Lamontichthys filamentosus* in a basal position; being the sister group of a monophyletic Loricariini (clade 165) *sensu* RAPP PY-DANIEL (1997). The Loricariini (clade 165) was supported by eleven synapomorphies, six of them of neuroanatomical origin: (1) optic nerves oriented oblique to the anteroposterior axis of the encephalon, nerves directed anteriorly, intersecting each other in the form of a “X” (char. 27: 1→0); (2) anterior margin of the *lobus inferior hypothalami* expanded anteriorly, clearly surpassing the anterior margin of the lateral portion of the *hypothalamus* (char. 33: 0→1); (3) lateral margin of the *lobus inferior hypothalami* continuous, without invagination(s) evident (char. 37: 0→1); (4) volume of the *tectum mesencephali* larger than the volume of the *telencephalon* (char. 48: 0→1); (5) dorsal margin of the *corpus cerebelli* mostly rectilinear (char. 64: 0→1); and (6) *lobus vagi* very angled, anterior margins facing to the medial axis (char. 79: 1→2). Moreover, most genera of the Loricariini represented in the analysis by more than one species [*i.e.*, *Dasylicaria* (clade 190), *Hemiodontichthys* (clade 205), *Limatulichthys* (clade 216), *Loricaria* (clade 220), *Loricariichthys* (clade 222), *Pseudohemiodon* (clade 235), *Rineloricaria* Bleeker, 1862 (clade 242), and *Spatuloricaria* (clade 244)] were recovered as monophyletic, being supported by two to eleven synapomorphies (see Appendix G). Most non-Loricariinae genera, represented in the analysis by more than one species, including *Delturus* (clade 192), *Hypostomus* (clade 209), *Kronichthys* (clade 215), *Neoplecostomus* (clade 230) and *Otothyris* (clade 231), also were recovered as monophyletic, being supported by one to twelve synapomorphies (see Appendix G).

4.6. DISCUSSION

This discussion will be based on the tree generated from the combined analysis (Figs. 15 and 16) given that the tree generated from the analysis of (exclusively) neuroanatomical data (Figs. 13 and 14) did not present a clear resolution between groups. For a discussion of the neuroanatomical characters and states used in this study please refer to the Chapter two and the Appendix B.

The results of this study, considering both analyses, support the monophyly of the Loricariidae corroborating previous morphological (e.g., ARMBRUSTER, 2004, 2008) and molecular studies (e.g., LUJAN *et al.*, 2015; COVAIN *et al.*, 2016; ROXO *et al.*, 2019). The deeper nodes in the phylogenetic hypothesis were strongly supported and recovered the species *Lithogenes villosus* as the first diverging lineage within the family, being the sister taxon of the remaining members of the Loricariidae. These relationships were already suggested by SCHAEFER (1987) and LUJAN *et al.* (2015), among other authors, who discussed the position of the Lithogeninae, in the phylogeny of the Loricariidae, based on the analysis, as in the present study, of a single species, *i.e.*, *L. villosus*. The second lineage to diverge within the Loricariidae was the clade formed by the subfamilies Delturinae + Rhinelepinae + Hypostominae (clade 157), which was supported by four synapomorphies (all of them of neuroanatomical origin; see Appendix G), being the sister group of the clade formed by the remaining members of the family [*i.e.*, the clade formed by the subfamilies Neoplecostominae + Hypoptopomatinae *sensu lato* (*i.e.*, the Hypoptopomatinae *sensu* LUJAN *et al.*, 2015 and ROXO *et al.*, 2019, among others; clade 145; supported by thirteen synapomorphies, nine of them of neuroanatomical origin; see Appendix G) and the Loricariinae (clade 166)]. These results are, in part, incongruent with most current hypotheses based on morphological (e.g., ARMBRUSTER, 2004) and molecular data (e.g., LUJAN *et al.*, 2015; ROXO *et al.*, 2019), which suggest these groups (e.g., Rhinelepinae + Hypostominae and Hypoptopomatinae *sensu lato* + Loricariinae) as independent and not close related subfamily-level clades.

The subfamily Delturinae, specifically, was recovered as monophyletic and as the sister group of the clade formed by the Hypostominae + Rhinelepinae. These results are, in part, incongruent with the results of previous authors (e.g., MONTOYA-BURGOS *et al.*, 1998; MONTOYA-BURGOS, 2001; ARMBRUSTER, 2004; REIS *et al.*, 2006; CHIACHIO *et al.* 2008; LUJAN *et al.*, 2015; among others), who recovered

the Delturinae in a basal position within the Loricariidae, as the sister group of the clade formed by the remaining subfamilies, except the Lithogeninae. Within the Delturinae, the genus *Delturus*, represented in the analysis by two species; *i.e.*, *D. carinotus* (La Monte, 1933) and *D. brevis* Reis & Pereira, 2006, was recovered as monophyletic and received strong support, agreeing with the results of previous studies (*e.g.*, REIS & PEREIRA, 2006). Phylogenetic relationships of members of the Delturinae were examined and discussed by ARMBURSTER (1998, 2004), REIS *et al.* (2006) and LUJAN *et al.* (2015), among others.

The subfamily Hypostominae *sensu stricto* (see LUJAN *et al.*, 2015 and ROXO *et al.*, 2019), including here representatives of the tribes Ancistrini and Hypostomini *sensu* ISBRÜCKER (1980), SCHAEFER (1986, 1987) and ARMBURSTER (2004), among others (see ARMBURSTER, 1998, 2004), also was recovered as monophyletic and as the sister group of the Rhinelepinae (*sensu* LUJAN *et al.*, 2015). The phylogeny of the Hypostominae was examined and discussed by several authors including SCHAEFER (1986, 1987), ARMBURSTER (1998, 2004), MONTOYA-BURGOS (2001) and LUJAN *et al.* (2015), among others, with results slightly divergent regarding the conformation of the different groups and subgroups as well as in some inter-clade relationship. The results of this study agree, in general terms, with previous morphological-based hypotheses (*e.g.*, ARMBURSTER, 1998, 2004), which recovered the genera *Ancistrus* Kner, 1854, *Dekeyseria* Rapp Py-Daniel, 1985, *Megalancistrus* Isbrücker 1980 (members of the Ancistrinae *sensu* ISBRÜCKER, 1980 and SCHAEFER, 1986, 1987), *Hypostomus* (member of the Hypostomini *sensu* ISBRÜCKER, 1980 and SCHAEFER, 1986, 1987) and *Rhinelepis* (member of the Rhinelepinae *sensu* LUJAN *et al.*, 2015), within a monophyletic Hypostominae *sensu lato* (clade 156; see ARMBURSTER, 2004, among others); however, the suprageneric relations herein recovered, besides being limited given the restricted number of analyzed taxa, are not comparable with those proposed in previous studies. Moreover, recent molecular studies (*e.g.*, LUJAN *et al.*, 2015; ROXO *et al.*, 2019) recovered the Rhinelepinae in a basal position as the sister group of the clade formed by the remaining subfamilies of the Loricariidae, except the Lithogeninae and Delturinae, hypothesis not supported by the results of this study.

The subfamily Neoplecostominae, as traditionally defined (see PEREIRA & REIS, 2017), was recovered as monophyletic (clade 157) and as the sister group of the clade formed by members of the Hypoptopomatinae (including the Otothyridae;

see CHIACHIO *et al.*, 2008; clade 144). Previous studies, based on the analysis of morphological (e.g., ARMBRUSTER, 2004; Gauger & Buckup, 2005; LEHMANN, 2006; MARTINS *et al.*, 2014; PEREIRA & REIS, 2017; among others) and molecular data (e.g., CHIACHIO *et al.*, 2008; CRAMER *et al.*, 2011; LUJAN *et al.*, 2015; ROXO *et al.*, 2019; among others), also found a close relationship between these two groups (Hypoptopomatinae and Neoplecostominae), agreeing partially with the results of this study. Moreover, recent molecular studies (e.g., CRAMER *et al.*, 2011; LUJAN *et al.*, 2015; and ROXO *et al.*, 2019; among others) have suggested the inclusion of members of the Neoplecostominae in a broadly circumscribed Hypoptopomatinae, hypothesis not supported by the results of this study. Within the Neoplecostominae, properly, the clade formed by the genera *Isbrueckerichthys* [represented in the analysis by a single species; i.e., *I. duseni* (Miranda Ribeiro, 1907)] + *Neoplecostomus* (clade 211), as well as the genera *Kronichthys* (clade 215) and *Neoplecostomus* (clade 230), were recovered as monophyletic and received strong support; results congruent with the findings of previous morphological studies (e.g., PEREIRA & REIS, 2017).

The phylogeny of the Hypoptopomatinae *sensu lato* (including the Otothyriinae) was examined and discussed by several authors, including SCHAEFER (1991, 1998), GAUGER & BUCKUP (2005), LEHMANN (2006), CHIACHIO *et al.* (2008), CRAMER *et al.* (2011) and MARTINS *et al.* (2014), among others, with results divergent regarding the conformation of the different groups and subgroups as well as in the inter-clade relationship. The “traditional” division of the subfamily into the tribes Hypoptopomatini and Otothyriini (see SCHAEFER 1991, 1998; among others) was first challenged by GAUGER & BUCKUP (2005), who recovered the Otothyriini as a paraphyletic sequence of lineages sister of a monophyletic Hypoptopomatini; posteriorly, CHIACHIO *et al.* (2008), based on the analysis of molecular characters, found the Otothyriini to be more closely related to the Neoplecostominae, while the Hypoptopomatini was recovered as the sister group of that clade; based on such results, the tribes Hypoptopomatini and Otothyriini were elevated to the rank of subfamily. CRAMER *et al.* (2011) and LUJAN *et al.* (2015), based on the analysis of molecular characters, found a largely unresolved combination of taxa of the Hypoptopomatini and Otothyriini at the base of a clade composed by the remaining Otothyriini and Neoplecostominae, concluding that the elevation of these tribes to the rank of subfamily was unnecessary. The results of this

study corroborate the monophyly of the Hypoptopomatinae, as usually defined in recent studies (e.g., CRAMER *et al.*, 2011; MARTINS *et al.*, 2014; LUJAN *et al.*, 2015; PEREIRA & REIS, 2017; among others) and including the Otothyriinae, but do not support its division into these two groups (*i.e.*, the Hypoptopomatini and Otothyriini), as proposed by previous authors (e.g., CHIACHIO *et al.*, 2008). The results of this study (regarding to the members of the Hypoptopomatinae and Neoplecostominae) also are comparable to those obtained by ROSA (2015), who analyzed a set of 60 neuroanatomical characters; a more detailed discussion on the interrelationships of members of these two subfamilies can be found in that study.

The phylogeny of the Loricariinae, as detailed above, was examined and discussed by several authors. RAPP PY-DANIEL (1997) was the first to examine all existing genera within the subfamily dividing it into two tribes, the Harttiini and the Loricariini. After the work of RAPP PY-DANIEL, the composition and inter-generic relationships of these two tribes have been reexamined in more than a dozen works, including four morphological and nine molecular studies (see LUJAN *et al.*, 2015; COVAIN *et al.*, 2016, for more details). ARMBRUSTER (2004), for example, obtained results comparable to those obtained by RAPP PY-DANIEL (1997), recovering both the Harttiini and the Loricariini as monophyletic groups. Subsequent morphological analysis, however, only recovered the Loricariini as a monophyletic group, with the Harttiini being either a paraphyletic group successively removed from the Loricariini (see PAIXÃO & TOLEDO-PIZA, 2009) or distributed across an unresolved polytomy inclusive of the Loricariini (see PROVENZANO, 2011). Then, LUJAN *et al.* (2015) obtained results comparable, to some extent, to those obtained by previous authors (e.g., MONTOYA-BURGOS *et al.*, 1998; COVAIN *et al.*, 2008; RODRIGUEZ *et al.*, 2011), recovering the Loricariini, *sensu* RAPP PY-DANIEL (1997), as a monophyletic group, with only those genera of the Harttiini excluding "*Harttia*" being monophyletic (and as the sister group the Loricariini), and the genus "*Harttia*" as the successive sister group of all other members of the Loricariinae. The results of this study agree, in general terms, with these previous studies recovering the Harttiini as paraphyletic, being the sister group of a monophyletic Loricariini, but disagree partially, since some of the inter-generic relationships herein recovered [except for the clade formed by the *Aposturisoma* Isbrücker, Britski, Nijssen & Ortega, 1983 + *Farlowella*, *i.e.*, the subtribe Farlowellina (in part) *sensu* RAPP PY-DANIEL, 1997] are not equivalent or comparable with those proposed in most of these previous studies. More recently,

COVAIN *et al.* (2016), restricted the Harttiini to the genera *Cteniloricaria* + *Harttia* + *Harttiella* and divided the Loricariini into two subtribes: (1) the Farlowellina, including the genera *Aposturisoma* + *Farlowella* + *Lamontichthys* Miranda Ribeiro, 1939 + *Pterosturisoma* + *Sturisoma* + *Sturisomaticthys* Isbrücker & Nijssen, 1979; and (2) the Loricariina, including the remaining genera of the Loricariinae. The Harttiini *sensu* COVAIN *et al.* (2016) was herein recovered as monophyletic, contrary, the Farlowellina was recovered as paraphyletic (including the Harttiini); on the other hand, the Loricariina, as defined by these authors, also was recovered as monophyletic, with the genera *Ixinandria* and the monophyletic *Rineloricaria* (the first placed in synonymy with *Rineloricaria* by COVAIN *et al.*, 2016 - forming the *Rineloricaria* group) in a basal position, being the successive sister groups of the remaining members of the Loricariinae; which also agree, in part, with the results of previous authors, *e.g.*, RAPP PY-DANIEL (1997; see Figure 50). Within the Loricariina none of the suprageneric groups as proposed by previous authors, *e.g.*, the Hemiodontichthyina or the Planiloricariina of RAPP PY-DANIEL (1997) nor the *Loricariichthys* or the *Loricaria-Pseudohemiodon* of COVAIN *et al.* (2016), among others (see Table 1 in LUJAN *et al.*, 2015), were herein recovered as monophyletic.

Despite some contradictions with previous phylogenetic hypothesis, this work provides considerable additional data to the evolutionary tree of one of the most diversified families of vertebrates, highlighting the needing of more studies integrating information from different anatomical systems in a phylogenetic context. Moreover, this work could be a basis for further investigations on the relationships between brain anatomy and the ecology of members of the Loricariinae, Loricariidae and Siluriformes in a phylogenetic frame.

5. GENERAL CONCLUSIONS

The results obtained in this study suggest that the relative size, volume and shape of the different brain structures examined, in members of the Loricariinae and Loricariidae, varies mostly with feeding behaviour and preferred environment; including changes possibly related to a ontogenetic shift in the habitat/resources use. Furthermore, when analyzed in conjunction with hypotheses of phylogenetic relationships, the results of this study also can be considered as empirical evidence supporting the fact that brain diversity in current members of the subfamily and family could be the result of both phylogenetic niche conservatism and repeated adaptive radiation. This work also provides considerable additional data to the evolutionary tree of the subfamily and family, highlighting the needing of further studies integrating information from different anatomical systems in a phylogenetic context. This work could be a basis for further investigations on the relationships between brain anatomy and the ecology of members of the subfamily, family and order in a phylogenetic frame.

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APPENDIXES

APPENDIX A. Material examined. Species are listed in alphabetical order; for each species, the following information is provided: lot(s) number(s) [institutional abbreviations follow Sabaj (2016); collection data can be accessed through the “Species link” online database site (<http://splink.cria.org.br/>)], number of specimens examined by lot, sex and standard length. The taxonomic status of the species follows Fricke *et al.* (2018b).

Subfamily Delturinae: *Delturus brevis* Reis & Pereira, 2006: NUP 015446, 1, male, 137.66 mm SL. *Delturus carinotus* (La Monte, 1933): MCP 28037, 1, male, 153.08 mm SL. *Hemipsilichthys nimius* Pereira, Reis, Souza & Lazzarotto, 2003: DZSJRP 13916, 1, female, 89.20 mm SL.

Subfamily Hypoptopomatinae: *Acestridium discus* Haseman, 1911: MZUSP 085321, 2, 1 male, 53.40 mm SL, 1 female, 44.30 mm SL. *Chauliocheilos saxatilis* Martins, Andrade, Rosa & Langeani, 2014: DZSJRP 019158, 1, female, 40.80 mm SL. *Corumbataia cuestae* Britski, 1997: DZSJRP 008027, 1, female, 29.30 mm SL. *Curculionichthys insperatus* (Britski & Garavello, 2003): DZSJRP 014381, 1, female, 32.30 mm SL; DZSJRP 018211, 1, male, 23.20 mm SL. *Epactionotus bilineatus* Reis & Schaefer, 1998: UFRGS 006564, 1, male, 35.50 mm SL. *Eurycheilichthys pantherinus* (Reis & Schaefer, 1992): MCP 025590, 1, female, 30.90 mm SL. *Gymnotocinclus anosteos* Carvalho, Lehmann A. & Reis, 2008: UFRGS 011296, 1, male, 42.80 mm SL. *Hisonotus francirochai* (Ihering, 1928): DZSJRP 01599, 1, female, 25.700 mm SL. *Hisonotus notatus* Eigenmann & Eigenmann, 1889: DZSJRP 013852, 1, female, 27.40 mm SL. *Hypoptopoma inexpectatum* (Holmberg, 1893): NUP 010773, 1, female, 70.70 mm SL; NUP 010663, 1, male, 64.40 mm SL. *Lampiella gibbosa* (Miranda Ribeiro, 1908): LBP 007430, 2, 1 male (24.90 mm SL), 1 female (26.60 mm SL). *Microlepidogaster perforata* Eigenmann & Eigenmann, 1889: DZSJRP 016171, 1, female, 27.60 mm SL. *Otocinclus affinis* Steindachner, 1877: DZSJRP 007610, 1, female, 26.00 mm SL. *Otothyris lophophanes* (Eigenmann & Eigenmann, 1889): 013069, 2, 1 male (18.00 mm SL), 1 female (26.30 mm SL). *Otothyris rostrata* Garavello, Britski & Schaefer, 1998: UFRGS 008659, 1, female, 33.70 mm SL. *Otothyropsis marapoama* Ribeiro, Carvalho & Melo, 2005: DZSJRP 014108, 1, female, 27.20 mm SL. *Oxyropsis wrightiana* Eigenmann & Eigenmann, 1889: MCP 034503, 1, female, 44.00 mm SL. *Parotocinclus jumbo* Britski & Garavello, 2002: MCP 031456, 1, female, 32.30 mm SL. *Parotocinclus maculicauda* (Steindachner, 1877): DZSJRP 013853, 2, 1 male (29.90 mm SL), 1 female (36.10 mm SL). *Parotocinclus prata* Ribeiro, Melo & Pereira, 2002: DZSJRP 014248, 1, female, 42.10 mm SL; DZSJRP 014264, 1, male, 54.90 mm SL. *Plesioptopoma curvidens* Reis, Pereira & Lehmann A., 2012: DZSJRP 016133, 1, female, 58.50 mm SL. *Pseudotocinclus tietensis* (Ihering, 1907): DZSJRP 018764, 2, 1 male (48.00 mm SL), 1 female (54.50 mm SL). *Pseudotothyris obtusa* (Miranda Ribeiro, 1911): MZUSP 083024, 2, 1 male (20.7 mm SL), 1 female (26.90 mm SL). *Rhinolekos britskii* Martins, Langeani & Costa, 2011: DZSJRP 005622, 1, female, 33.30 mm SL. *Schizolecis guentheri* (Miranda Ribeiro, 1918): DZSJRP 012490, 1, female, 36.30 mm SL.

Subfamily Hypostominae: *Ancistrus* sp.: DZSJRP 011949, 1, female, 53.8 mm SL. *Dekeyseria scaphirhynchus* (Kner, 1854): INPA-ICT 000414, 1, male, 159.23 mm SL; INPA-ICT 036022, 1, male, 85.17 mm SL. *Hypostomus ancistroides* (Ihering, 1911): DZSJRP 017662, 1, female, 102.00 mm SL. *Hypostomus nigromaculatus* (Schubart, 1964): DZSJRP 016103, 1, male, 63.30 mm SL. *Hypostomus regani* (Ihering, 1905): DZSJRP 016049, 1, female, 123.00 mm SL. *Hypostomus variipictus* (Ihering, 1911): DZSJRP 017664, 1, male, 123.30 mm SL. *Megalancistrus parananus* (Peters, 1881): DZSJRP 004845, 1, female, 129.00 mm SL.

Subfamily Loricariinae: *Apistoloricaria* (= *Rhadinoloricaria*) *ommation* (Nijssen & Isbrücker, 1988): ANSP 192893, 1, male, 84.03 mm SL; ANSP 192903, 1, male, 84.03 mm SL. *Aposturisoma myriodon* Isbrücker, Britski, Nijssen & Ortega, 1983: MHNG 002584.029, 1, male, 167.00 mm SL. *Brochiloricaria macrodon* (Kner, 1853): NUP 002248, 1, male, 262.00 mm SL. *Brochiloricaria* sp.: DZSJRP 018858, 1, male, 83.88 mm SL. *Crossoloricaria* (= *Rhadinoloricaria*) *bahuaja* (Chang & Castro, 1999): MHNG 002710.084, 1, male, 52.92 mm SL. *Crossoloricaria variegata* (Steindachner, 1879): MZUSP 103055, 2, males, 92.98–99.13 mm SL. *Cteniloricaria platystoma* (Günther, 1868): ANSP 190521, 2, females, 116.71–130.38 mm SL. *Dasylicaria filamentosa* (Steindachner, 1878): USNM 121085, 1, male, 256 mm SL. *Dasylicaria latiura* (Eigenmann & Vance, 1912): USNM 293168, 1, male, 242 mm SL. *Dentectus barbarmatus* Martín Salazar, Isbrücker & Nijssen, 1982: ANSP 131631, 1, female, 80.57 mm SL; ANSP 198883, 1, male, 100.52 mm SL. *Farlowella amazonum* (Günther, 1864): INPA-ICT 042067, 2, females, 85.08–98.48 mm SL. *Farlowella henriquei* Miranda Ribeiro, 1918: MZUSP 14408, 1, male, 120.62 mm SL. *Farlowella nattereri* Steindachner, 1910: MZUSP 057234, 1, male, 86.29 mm SL; MZUSP 116570, 1, female, 105.10 mm SL. *Farlowella oxyrryncha* (Kner, 1853): DZSJRP 014920, 2, 1 male (121.00 mm SL), 1 female (124.00 mm SL); DZSJRP 017180, 3, 2 males (127.00–145.00 mm SL), 1 female (118.00 mm SL). *Farlowella paraguayensis* Retzer & Page, 1997: DZSJRP 018106, 5, 2 males (108.27–115.43 mm SL), 3 females (97.68–109.35 mm SL). *Farlowella reticulata* Boeseman, 1971: MZUSP 101676, 1, male, 136.67 mm SL. *Farlowella schreitmuelleri* Ahl, 1937: MZUSP 88997, 1, male, 120.25 mm SL. *Farlowella smithi* Fowler, 1913: MZUSP 116572, 1, female, 89.05 mm SL. *Fonchiiloricaria nanodon* Rodríguez, Ortega & Covain, 2011: MUSM 032153, 3, 1 male (167.98 mm SL), 2 female (160.28–166.27 mm SL). *Furcodontichthys novaesi* Rapp Py-Daniel, 1981: INPA-ICT 032376, 1, male, 78.38 mm SL; MZUSP 057726, 1, male, 126.38 mm SL. *Harttia carvalhoi* Miranda Ribeiro, 1939: MZUSP 047590, 1, female, 68.45 mm SL. *Harttia duriventris* Rapp Py-Daniel & Oliveira, 2001: NUP 008234, 1, male, 25.45 mm SL; NUP 008716, 2, 1 male (57.62 mm SL), 1 female (44.85 mm SL). *Harttia loricariformis* Steindachner, 1877: MZUSP 049263, 1, female, 121.72 mm SL. *Harttia novalimensis* Oyakawa, 1993: DZSJRP 011456, 2, females, 99.23–106.56 mm SL; DZSJRP 011522, 2, females, 53.10–54.61 mm SL; DZSJRP 011632, 2, 102.53–105.48 mm SL; DZSJRP 01644, 1, male, 102.53 mm SL. *Harttia punctata* Rapp Py-Daniel & Oliveira, 2001: MZUSP 96172, 1, male, 75.61 mm SL. *Harttiella crassicauda* (Boeseman, 1953): AUM 050392, 2, males, 36.00–36.65 mm SL. *Hemiodontichthys acipenserinus* (Kner, 1853): INPA-ICT 032082, 3, 2 males (85.01–92.34 mm SL), 1 female (87.23 mm SL); MZUSP 089474, 1, male, 66.94 mm SL. *Hemiodontichthys* sp.: MZUSP 24102, 1, male, 103.14 mm SL. *Ixinandria* (= *Rineloricaria*) *steinbachi* (Regan, 1906): MCP 041303, 3, 2 males (48.8–69.96 mm SL), 1 female (69.11 mm SL). *Lamontichthys filamentosus* (La Monte, 1935): LBP 000162, 2, males, 167–184 mm SL. *Limatulichthys griseus*

(Eigenmann, 1909): INPA-ICT 006477, 1, female, 90.95 mm SL; INPA-ICT 025869, 1, male, 95.71 mm SL; MCP 036574, 2, undefined sex, 41.99–46.62 mm SL; NUP 015220, 1, female, 110.89 mm SL. *Limatulichthys petleyi* (Fowler, 1940): MZUSP 023259, 1, male, 118.94 mm SL; MZUSP 073995, 1, male, 94.65 mm SL; MZUSP 34537, 1, male, 75.05 mm SL. *Loricaria cataphracta* Linnaeus, 1758: DZSJRP 014499, 2, males, 135.5–104.0 mm SL; INPA 032046, 1, male, 138.00 mm SL; MZUSP 014106, 1, male, 114.7 mm SL; NUP 008130, 1, undefined sex, 34.55 mm SL. *Loricaria luciae* Thomas, Rodriguez, Carvallaro, Froehlich & Castro, 2013: ZUFMS-PIS 003213, 2, male, 120.33–124.47 mm SL. *Loricaria* sp.: MZUSP 089708, 1, female, 133.80 mm SL. *Loricariichthys acutus* (Valenciennes, 1840): INPA-ICT 025860, 1, female, 162.36 mm SL; MZUSP 035074, 1, male, 126.52 mm SL. *Loricariichthys anus* (Valenciennes, 1835), DZSJRP 010987, 4, 3 males (141.55–213.00 mm SL), 1 female (158.00 mm SL). *Loricariichthys castaneus* (Castelnau, 1855): NUP 015042, 1, female, 221.8 mm SL; NUP 015410, 1, female, 192.21 mm SL. *Loricariichthys derbyi* Fowler, 1915: MCP 023379, 1, female, 146.84 mm SL. *Loricariichthys melanocheilus* Reis & Pereira, 2000: MCP 011755, 2, 1 male (193.80 mm SL), 1 female (179.84 mm SL). *Loricariichthys platymetopon* Isbrücker & Nijssen, 1979: DZSJRP 004393, 2, females, 261.00–291.00 mm SL; MZUSP 025081, 1, male, 153.00 mm SL. *Loricariichthys rostratus* Reis & Pereira, 2000: 2, males, 141.01–144.38 mm SL. *Loricariichthys* sp.: MZUSP 8544, 1, female, 132.33 mm SL. *Metaloricaria paucidens* Isbrücker, 1975: MHNG 002589, 1, male, 214.00 mm SL. *Paraloricaria vetula* (Valenciennes, 1835): 2, 1 male (226.58 mm SL), 1 female (320.10 mm SL); ZVCP 14036, 1, male, 217.00 mm SL. *Planiloricaria cryptodon* (Isbrücker, 1971): MHNG 002677.038, 1, male, 199.00 mm SL. *Proloricaria proluxa* (Isbrücker & Nijssen, 1978): DZSJRP 006312, 1, female, 104.51 mm SL; ZUFMS-PIS 005015, 1, female, 187.9 mm SL. *Pseudohemiodon laticeps* (Regan, 1904): NUP 003462, 2, 1 male (144.13 mm SL), 1 female (146.38 mm SL). *Pseudohemiodon platycephalus* (Kner, 1853): ZUFMS-PIS 000440, 1, female, 136.26 mm SL. *Pseudohemiodon* sp.: ANSP 198948, 1, male, 153.22 mm SL. *Pseudoloricaria laeviscula* (Valenciennes, 1840): INPA-ICT 021988, 1, male, 171.9 mm SL; MZUSP 044020, 1, male, 220.00 mm SL. *Pseudoloricaria punctata* (Kner, 1854): MZUSP 073995, 1, male, 94.65 mm SL; MZUSP 34537, 1, male, 75.05 mm SL. *Pyxiloricaria menezesi* Isbrücker & Nijssen, 1984: ZUFMS-PIS 003998, 1, male, 97.74 mm SL. *Reganella depressa* (Kner, 1853): INPA-ICT 038107, 1, female, 128.46 mm SL; MZUSP 057936, 1, male, 139.97 mm SL; MZUSP 57729, 1, female, 140.83 mm SL. *Rhadinoloricaria* sp.: ANSP 198974, 1, female, 104.13 mm SL. *Ricola macrops* (Regan, 1904): ZVCP 14035, 1, male, 221.00 mm SL. *Rineloricaria* (=Fonchiichthys) *uracantha* (Kner, 1863): UCR 000452, 2, 1 male (129.08 mm SL), 1 female (102.23 mm SL). *Rineloricaria* (=Hemiloricaria) *aurata* (Knaack, 2002): MCP 036535, 1, male, 63.69 mm SL; MCP 036541, 2, undefined sex, 49.72–50.76 mm SL; NUP 000963, 3, 1 male (48.82 mm SL), 2 females (40.86–47.7 mm SL); NUP 005416, 2, undefined sex, 23.67–24.02 mm SL. *Rineloricaria aequalicuspis* Reis & Cardoso, 2001: MCP 010617, 3, 2 males (69.39–135.19 mm SL), 1 female (114.53 mm SL). *Rineloricaria baliola* Rodriguez & Reis, 2008: UFRGS 005815, 1, male, 204.95 mm SL; UFRGS 019983, 2, females, 138.85–156.95 mm SL. *Rineloricaria cacerensis* (Miranda Ribeiro, 1912): DZSJRP 012919, 1, female, 67.92 mm SL. *Rineloricaria cadeae* (Hensel, 1868): MCP 009782, 2, males, 123.08–129.48 mm SL; MCP 011235, 1, male, 114.93 mm SL; UFRGS 006652, 1, female, 89.83 mm SL; UFRGS 008611, 2, males, 94.54–109.05 mm SL. *Rineloricaria* cf. *kronei* (Miranda Ribeiro, 1911): DZSJRP 013625, 4, 3 males (67.70–80.23 mm SL), 1 female (70.43 mm SL).

Rineloricaria cf. *lima* (Kner, 1853): MZUSP 050731, 1, female, 133.99 mm SL. *Rineloricaria cubataonis* (Steindachner, 1907): DZSJRP 003269, 6, 4 males (85.44–110.32 mm SL), 2 females (104.53–110.87 mm SL). *Rineloricaria formosa* Isbrücker & Nijssen, 1979: IMCN 6616, 1, male, 92.29 mm SL. *Rineloricaria hasemani* Isbrücker & Nijssen, 1979: DZSJRP 019798, 2, 1 male (86.69 mm SL), 1 female (83.22 mm SL). *Rineloricaria heteroptera* Isbrücker & Nijssen, 1976: DZSJRP 014427, 1, female, 67.86 mm SL; DZSJRP 017182, 3, 1 male (79.62 mm SL), 2 females (71.41–78.90 mm SL). *Rineloricaria jubata* (Boulenger, 1902): IMCN 0146, 1, male, 138.82 mm SL. *Rineloricaria lanceolata* (Günther 1868): DZSJRP 012408, 1, female, 63.00 mm SL. *Rineloricaria latirostris* (Boulenger 1900): DZSJRP 017682, 1, male, 107.40 mm SL. *Rineloricaria malabarbai* Rodriguez & Reis, 2008: MCP 049479, 1, male, 79.37 mm SL; MCP 049503, 2, males, 69.97–103.16 mm SL. *Rineloricaria maquinensis* Reis & Cardoso, 2001: UFRGS 003294, 2, 1 male (88.82 mm SL), 1 female (81.13 mm SL). *Rineloricaria microlepidogaster* (Regan, 1904): MCP 011220, 2, 1 male (153.38 mm SL), 1 female (141.93 mm SL). *Rineloricaria parva* (Boulenger, 1895): NUP 000202, 1, male, 80.11 mm SL; NUP 014346, 1, female, 89.12 mm SL. *Rineloricaria pentamaculata* Langeani & de Araujo, 1994: NUP 016079, 2, males, 44.10–46.31 mm SL. *Rineloricaria quadrensis* Reis, 1983: MCP 011039, 2, males, 71.29–94.43 mm SL. *Rineloricaria* sp.: IMCN 006617, 1, male, 117.86 mm SL. *Rineloricaria strigilata* (Hensel, 1868): MCP 014987, 1, female, 70.22 mm SL; MCP 015378, 2, females, 82.69–88.61 mm SL. *Rineloricaria zaina* Ghazzi, 2008: MCP 016784, 1, male, 91.96 mm SL; MCP 040053, 2, 1 male (44.01 mm SL), 1 female (68.03 mm SL). *Spatuloricaria evansii* (Boulenger, 1892): MZUSP 24141, 1, male, 87.83 mm SL; NUP 002260, 1, male, 87.02 mm SL. *Spatuloricaria nudiventris* (Valenciennes, 1840): INPA-ICT 001258, female, 57.13 mm SL. *Spatuloricaria taira* Fichberg, Oyakawa & de Pinna, 2014: MZUSP 094853, 1, male, 124.70 mm SL. *Sturisoma barbatum* (Kner, 1853): NUP 003282, 2, males, 204.59–222.89 mm SL. *Sturisoma guentheri* (Regan, 1904): INPA-ICT 032041, 1, female, 158.72 mm SL. *Sturisoma panamensis* (Eigenmann & Eigenmann, 1889): IMCN 0922, 1, male, 208.12 mm SL. *Sturisoma robustum* (Regan, 1904): DZSJRP 004255, 1, male, 113.19 mm SL. *Sturisoma rostratum* (Spix & Agassiz, 1829): MZUSP 105389, 2, 1 male (201.00 mm SL), 1 female (204.73 mm SL). *Sturisoma tenuirostre* (Steindachner, 1910): ANSP 166914, 2, 1 male (266.00 mm SL), 1 female (204.00 mm SL). *Sturisomatichthys leightoni* (Regan, 1912): ANSP 084177, 2, 1 male (118.26 mm SL), 1 female (82.77 mm SL); IMCN 3386, 1, female, 90.96 mm SL.

Subfamily Neoplecostominae: *Isbrueckerichthys duseni* (Miranda Ribeiro, 1907): MCP 012564, 1, female, 70.90 mm SL. *Kronichthys heylandi* (Boulenger, 1900): DZSJRP 015352, 2, 1 male (71.60 mm SL), 1 female (73.80 mm SL). *Kronichthys subteres* Miranda Ribeiro, 1908: MCP 020152, 1, female, 64.10 mm SL. *Neoplecostomus corumba* Zawadzki, Pavanelli & Langeani, 2008: DZSJRP 070031, female, 64.10 mm SL. *Neoplecostomus langeanii* Roxo, Oliveira & Zawadzki, 2012: DZSJRP 014049, 1, female, 59.10 mm SL. *Neoplecostomus microps* (Steindachner, 1877): DZSJRP 013908, 1, female, 74.10 mm SL. *Neoplecostomus ribeirensis* Langeani, 1990: DZSJRP 013662, 1, female, 46.90 mm SL. *Neoplecostomus selenae* Zawadzki, Pavanelli & Langeani, 2008: DZSJRP 015331, 1, male, 78.30 mm SL. *Neoplecostomus yapo* Zawadzki, Pavanelli & Langeani, 2008: DZSJRP 013651, 1, female, 74.90 mm SL. *Pareiorhaphis cameroni* (Steindachner, 1907): MCP 011542, 1, female, 35.80 mm SL. *Pareiorhaphis hystrix* (Pereira & Reis, 2002): MCP 018741, 1, male, 81.90 mm SL. *Pareiorhina carrancas* Bockmann & Ribeiro, 2003:

DZSJRP 016154, 1, female, 37.50 mm SL. *Pareiorhina rudolphi* (Miranda Ribeiro, 1911): MCP 020147, 1, female, 50.00 mm SL.

Subfamily Rhinelepininae: *Rhinelepis aspera* Spix & Agassiz, 1829: DZSJRP 004779, 1, male, 149.00 mm SL.

APPENDIX B. List of characters analyzed (gross brain morphology). Most characters used (78/89) were described and discussed in previous studies, e.g., Pupo (2011, 2015), Abrahão (2013), Pereira (2014) and Rosa (2015); the number of each character in the cited paper, when pertinent, is provided between brackets after the character name; cases in which character names, definitions and/or states were modified from its original description are denoted with a “modified—” immediately before the original description citation. Figures in the original paper illustrating the different characters states, when available, are listed between parentheses after each character state. Characters are listed in the antero-posterior axis direction, and separated by major brains subdivisions according to the scheme implemented by Abrahão & Shibatta (2015) and Pereira & Castro (2016), as presented in Angulo & Langeani (2017). In paired structures only the left lobe or left counterpart is considered, unless otherwise stated. Nomenclature of brain subdivisions follows Nieuwenhuys (1982), Meek & Nieuwenhuys (1998) and Butler & Hodos (2005).

Olfactory organ

0. **Shape of the olfactory organ, dorsal view [modified—Pupo 2011, char. 19; modified—Pereira 2014, char. 23; Rosa 2015, char. 52];** $CI_1=0.50$, $RI_1=0.90$, $CI_2=0.50$, $RI_2=0.90$: 0 Oval, horizontally elongated (Fig. 17A; Pupo 2011, Fig. 9; Pereira 2014, Fig. 54; Rosa 2015, Fig. 56A); 1 Almost circular or drop-shaped, i.e. anterior and/or posterior margins tapered (Figs. 17B, 17C; Rosa 2015, Fig. 15A).

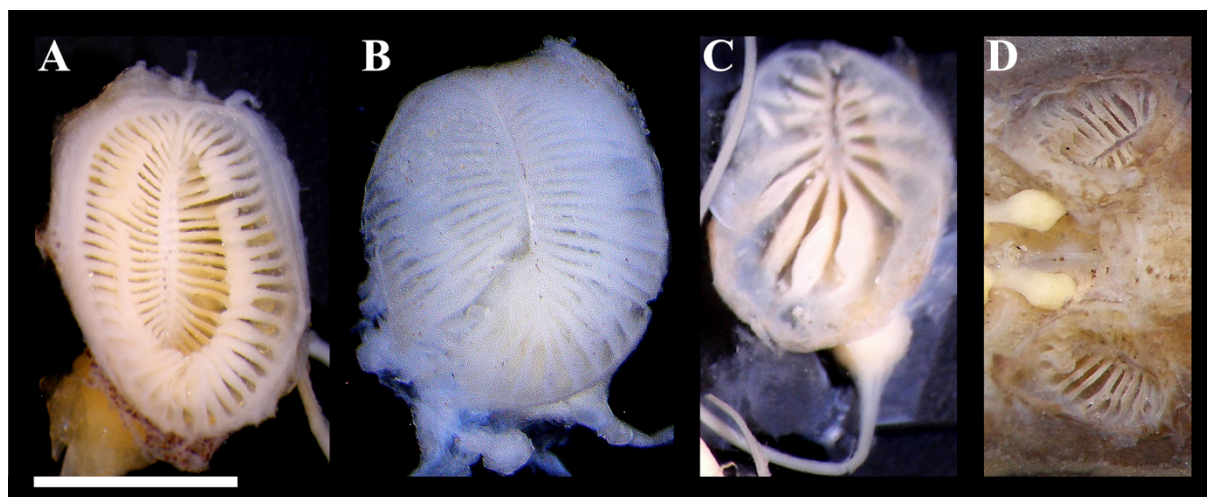


Figure 17. Detail of the olfactory organs and olfactory bulbs of selected species of the Loricariidae, dorsal view. (A) *Delturus brevis*, NUP 015446, male, 137.66 mm SL; (B) *Lamontichthys filamentosus*, LBP 000162, male, 184.00 mm SL; (C) *Loricariichthys anus*, DZSJRP 010987; female, 158.00 mm SL; (D) *Farlowella oxyrryncha*, DZSJRP 017180, male, 127.00 mm SL. Scale bar=2 mm.

1. **Sexual dimorphism on olfactory organ size and lamellae count, dorsal**

view [Rosa 2015, char. 55]; $CI_1=0.28$, $RI_1=0.61$, $CI_2=0.25$, $RI_2=0.50$: 0 Absent (Rosa 2015, Figs. 12A, 12C); 1 Present, males with larger olfactory organs and/or greater number of lamellae (Rosa 2015, Figs. 45A, 57A); 2 Present, females with larger olfactory organs and/or greater number of lamellae (Rosa 2015, Fig. 31).

2. Number of lamellae on the olfactory organ, dorsal view, females [modified—Pupo 2011, char. 20; modified—Pereira 2014, char. 25; modified—Rosa 2015, char. 56]; $CI_1=0.13$, $RI_1=0.59$, $CI_2=0.13$, $RI_2=0.59$: 0 Less than 20 (Rosa 2015, Figs. 12A, 12C); 1 From 20 to 40 (Rosa 2015, Fig. 41A); 2 From 41 to 100 (Rosa 2015, Fig. 28A); 3 More than 100 (Rosa 2015, Fig. 56A).

3. Symmetry of the lamellae of the olfactory organ 1, dorsal view [modified—Rosa 2015, char. 53]; $CI_1=0.11$, $RI_1=0.50$, $CI_2=0.10$, $RI_2=0.43$: 0 Absent, lamellae of the external side longer (Fig. 17D; Rosa 2015, Fig. 18A); 1 Present, lamellae on both external and internal sides of the same length (Figs. 17A, 17B, 17C; Rosa 2015, Fig. 29A).

4. Symmetry of the lamellae of the olfactory organ 2, dorsal view [modified—Pereira 2014, char. 42; modified—Rosa 2015, char. 54]; $CI_1=0.05$, $RI_1=0.57$, $CI_2=0.08$, $RI_2=0.53$: 0 Absent, posterior lamellae noticeably more elongated (Fig. 17D; Rosa 2015, Fig. 65); 1 Absent, posterior lamellae noticeably more elongated and thicker (Fig. 17C; Rosa 2015, Fig. 26A); 2 Present, posterior lamellae undifferentiated, all lamellae of similar size and thickness (Figs. 17A, 17B; Pereira 2014, Fig. 54B; Rosa 2015, Fig. 39A).

5. Presence and distribution of dorsal projections in the lamellae of the olfactory organ, dorsal view, females [modified—Rosa 2015, char. 57]; $CI_1=0.07$, $RI_1=0.72$, $CI_2=0.07$, $RI_2=0.71$: 0 Present, only in the posterior lamellae (Fig. 17C; Rosa 2015, Fig. 45A); 1 Present, in almost all lamellae (Fig. 17A; Rosa 2015, Fig. 15A).

6. Location of the dorsal projections in the lamellae of the olfactory organ, dorsal view, females [Rosa 2015, char. 58]; $CI_1=0.10$, $RI_1=0.74$, $CI_2=0.09$, $RI_2=0.71$: 0 Subterminal, located on the mesial portion of the lamellae (Fig. 17A; Rosa 2015, Fig. 30A); 1 Terminal, located on the posterior portion of the lamellae (Fig. 17C; Rosa 2015, Figs. 55A, 55C).

Telencephalon

7. Insertion of the *nervus olfactorius* in the olfactory organ and orientation of its fibers, ventral view [Rosa 2015, char. 48]; $CI_1=0.25$, $RI_1=0.57$, $CI_2=0.25$, $RI_2=0.53$: 0 Inserted in the posterior portion of the olfactory organ, with the fibers oriented posteriorly towards the *bulbus olfactorius* (Fig. 18A; Rosa 2015, Fig. 53B); 1 Inserted in the mesial portion of the olfactory organ, with the fibers oriented obliquely towards the *bulbus olfactorius* (Fig. 18B; Rosa 2015, Fig. 66B); 2 Inserted in the anterior portion of the olfactory organ, with the fibers oriented anteriorly towards the *bulbus olfactorius* (Fig. 18C; Rosa 2015, Fig. 13B).

8. Ramification of the fibers of the *nervus olfactorius* at their insertion into the olfactory organ, ventral view [modified—Rosa 2015, char. 50]; $CI_1=0.04$,

RI₁=0.54, CI₂=0.04, RI₂=0.54: 0 Diffuse, without principal branches (Figs. 18B, 18C; Rosa 2015, Figs. 16B, 67B); 1 Longitudinal, with two main branches (Fig. 18A; Rosa 2015, Figs. 42B, 67A).

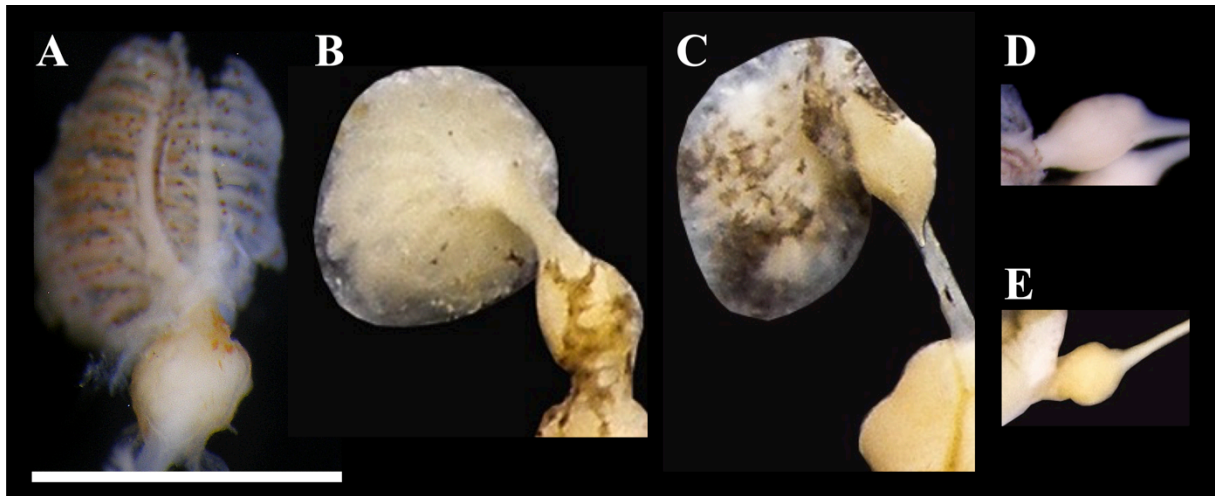


Figure 18. Detail of the olfactory organs and olfactory bulbs of selected species of the Loricariidae, ventral and lateral views. (A) *Farlowella henriquei*, MZUSP 014408, male, 120.62 mm SL; (B) *Scleromystax barbatus*, DZSJRP 005726, female, 63.70 mm SL; (C) *Ancistrus* sp., DZSJRP 011949, female, 53.80 mm SL; (D) *Dentectus barbarmatus*, ANSP 198883, male, 100.52 mm SL; (E) *Delturus carinotus*, MCP 028037, male, 153.10 mm SL. Scale bar=2 mm.

9. **Length of the *nervus olfactorius*, ventral view, females [Rosa 2015, char. 49]; CI₁=0.11, RI₁=0.46, CI₂=0.13, RI₂=0.45:** 0 Shorter than the length of the *bulbus olfactorius*, not visible dorsally (Fig. 18A; Rosa 2015, Fig. 21A); 1 Shorter than, or similar to, the length of the *bulbus olfactorius*, visibly dorsally (Fig. 18B; Rosa 2015, Fig. 44A); 2 Larger than the length of the *bulbus olfactorius* (Fig. 18C; Rosa 2015, Fig. 25A).

10. **Width of the *nervus olfactorius*, dorsal view, females [modified—Pupo 2011, char. 18; modified—Rosa 2015, char. 51]; CI₁=0.11, RI₁=0.50, CI₂=0.11, RI₂=0.46:** 0 Shorter than, or similar to, the width of a single olfactory lamella (Pupo 2011, Fig. 7; Rosa 2015, Fig. 60B); 1 Larger than the width of a single olfactory lamella but shorter than the width of three olfactory lamellae (Pupo 2011, Fig. 7; Rosa 2015, Fig. 38B); 2 Three times or more larger than the width of a single olfactory lamella (Rosa 2015, Fig. 57B).

11. **Shape of the *bulbus olfactorius*, lateral view [Rosa 2015, char. 46]; CI₁=0.07, RI₁=0.50, CI₂=0.09, RI₂=0.58:** 0 Elongated or drop-shaped, tapered at the ends (Fig. 18D; Rosa 2015, Fig. 17B); 1 Rounded, not tapered at the ends (Fig. 18E; Rosa 2015, Fig. 33C).

12. **Sexual dimorphism in the volume of the *bulbus olfactorius* [Rosa 2015, char. 47]; CI₁=0.40, RI₁=0.40, CI₂=0.50, RI₂=0.50:** 0 Absent (Rosa 2015, Fig. 14); 1 Present, males with *bulbus olfactorius* more voluminous (Rosa 2015, Fig. 45); 2 Present, females with *bulbus olfactorius* more voluminous (Rosa 2015, Fig. 12).

13. **Positioning of the *bulbus olfactorius*, dorsal view** [modified—Pupo 2011, char. 17; modified—Pereira 2014, char. 21; modified—Rosa 2015, char. 45]; $CI_1=0.10$, $RI_1=0.77$, $CI_2=0.10$, $RI_2=0.66$: 0 Sessile, inserted directly into the *telencephalon* (Fig. 19A; Pupo 2011, Fig. 8; Pereira 2014, Figs. 1, 13; Rosa 2015, Fig. 59); 1 Pedunculated, attached to the *telencephalon* by a *tractus olfactorius* short, *i.e.*, shorter than, or similar to, the length of the *bulbus olfactorius* (Fig. 18B; Pupo 2011, Fig. 8; Rosa 2015, Fig. 31); 2 Pedunculated, attached to the *telencephalon* by a *tractus olfactorius* long, *i.e.*, larger than the length of the *bulbus olfactorius* (Fig. 19B; Pupo 2011, Fig. 8; Pereira 2014, Figs. 48, 49; Rosa 2015, Fig. 61).

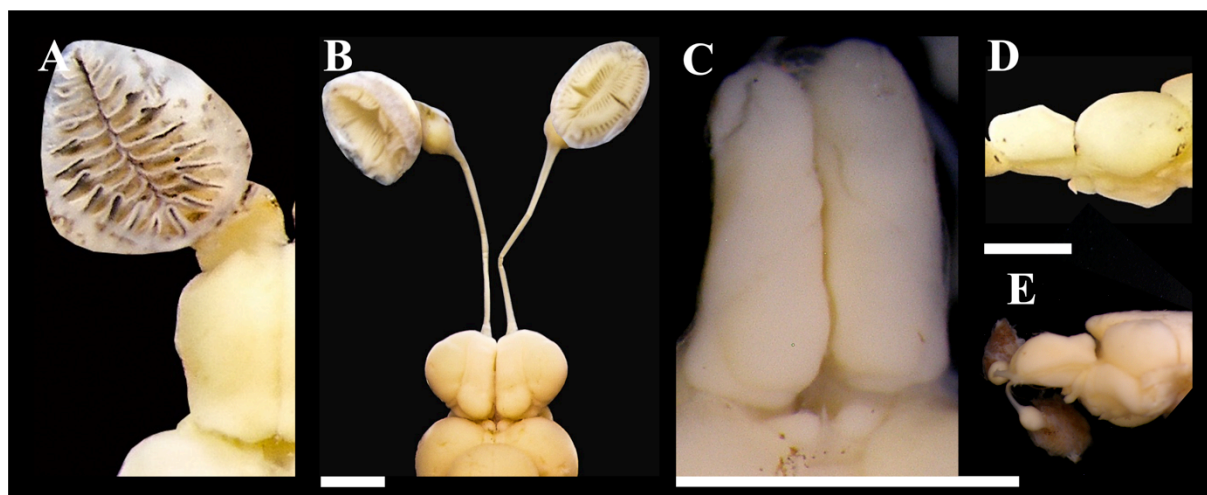


Figure 19. Brain of selected species of the Loricariidae; detail of the olfactory organs, olfactory bulbs and the anterior portion of the brain (*telencephalon* and *mesencephalon*), dorsal and lateral views. (A) *Corumbataia cuestae*, DZSJRP 008027, female, 29.30 mm SL; (B) *Megalancistrus parananus*, DZSJRP 004845, female, 129.00 mm SL; (C) *Limatulichthys petleyi*, MZUSP 073995, male, 94.65 mm SL; (D) *Loricaria cataphracta*, DZSJRP 014499, male, 130.13 mm SL; (E) *Otocinclus affinis*, DZSJRP 007610, female, 26.00 mm SL. Scale bar=2 mm.

14. **Shape of the *telencephalon* 1, dorsal view** [modified—Pupo 2011, char. 15; modified—Pereira 2014, char. 19]; $CI_1=0.05$, $RI_1=0.58$, $CI_2=0.06$, $RI_2=0.55$: 0 Oval or rectangular, horizontally elongated (Fig. 19A); 1 Oval, vertically elongated (Fig. 19C; Pupo 2011, Fig. 3; Pereira 2014, Figs. 8, 9 and 10); 2 Rounded or reniform to semicircular (Fig. 19B; Pupo 2011, Fig. 3; Pereira 2014, Fig. 51).

15. **Length of the *telencephalon*, lateral view**; $CI_1=0.03$, $RI_1=0.53$, $CI_2=0.03$, $RI_2=0.55$: 0 Shorter than, or similar to, the length of the *tectum mesencephali* (Fig. 19D); 1 Larger than the length of the *tectum mesencephali* (Fig. 19E).

16. **Shape of the *telencephalon* 2, dorsal view** [modified—Pupo 2011, char. 16; modified—Abrahão 2013, char. 30; Rosa 2015, char. 39]; $CI_1=0.09$, $RI_1=0.56$, $CI_2=0.09$, $RI_2=0.55$: 0 Wider in its posterior-most portion (Abrahão 2013, Figs. 3A, 3E, 3F, 4A, 4C, 4F; Rosa 2015, Fig. 56A); 1 Wider in its medial portion (Figs. 19A, 19B; Pupo 2011, Fig. 3; Rosa 2015, Fig. 14A); 2 Wider in its anterior-most portion (Figs. 19C, 20A; Abrahão 2013, Fig. 3D; Rosa 2015, Figs. 33A, 33D); 3 Uniform along most of its entire length (Fig. 20B; Abrahão 2013, Figs. 3B, 3C, 4B, 4E; Rosa 2015, Fig. 16A).

17. **Sexual dimorphism in the shape of the anterior margin of the telencephalon, dorsal view [modified—Rosa 2015, char. 36]; $CI_1=0.25$, $RI_1=0$, $CI_2=0.25$, $RI_2=0$:** 0 Absent (Rosa 2015, Fig. 14A); 1 Present, males and females exhibiting different shapes, *i.e.*, finished in tip (tapered), straight or circular (Rosa 2015, Fig. 23A).

18. **Shape of the anterior margin of the telencephalon, dorsal view, females [Pupo 2011, char. 16; modified—Pereira 2014, char. 20; modified—Rosa 2015, char. 36]; $CI_1=0.06$, $RI_1=0.48$, $CI_2=0.05$, $RI_2=0.41$:** 0 Tapered (Fig. 20A; Pupo 2011, Fig. 3; Pereira 2014, Figs. 49, 50; Rosa 2015, Fig. 58A, 58B); 1 Not tapered, straight or circular (Figs. 19B, 20B; Pereira 2014, Fig. 4; Rosa 2015, Figs. 14A, 60A).

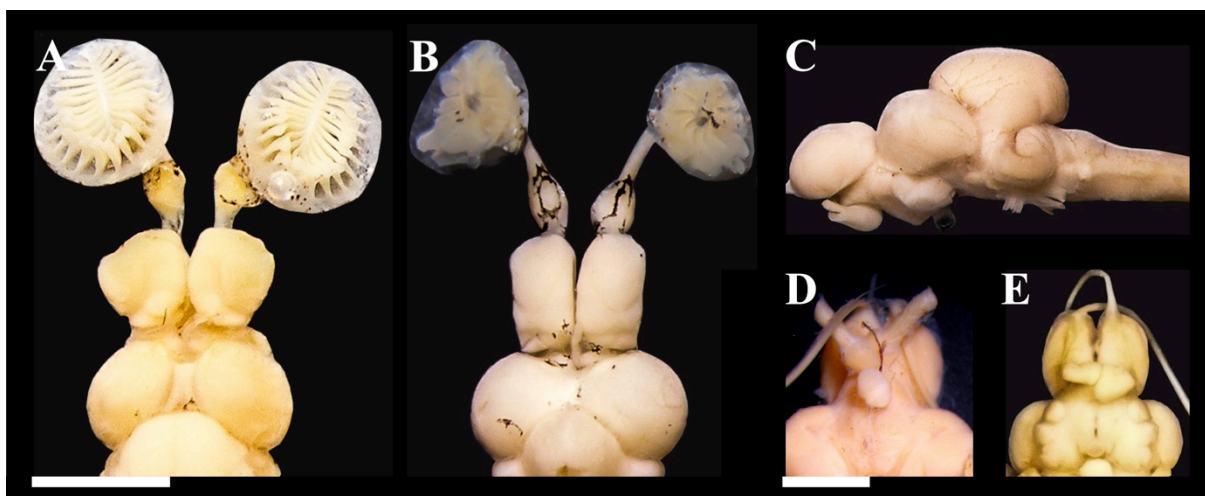


Figure 20. Brain of selected species of the Loricarioidea; detail of the antero-medial portion of the brain (*telencephalon*, *diencephalon* and *mesencephalon*), dorsal and lateral views. (A) *Kronichthys subteres*, MCP 020152, female, 64.10 mm SL; (B) *Corydoras aeneus*, DZSJRP 015193, female, 44.80 mm SL; (C) *Hypostomus regani*, DZSJRP 016049, female, 123.00 mm SL, lateral view; (D) *Dasylicaria latiura*, USNM 293168, male, 242.00 mm SL; (E) *Delturus carinotus*, MCP 028037, male, 153.10 mm SL. Scale bar=2 mm.

19. **Antero-mesial projection of the telencephalon, dorsal view [modified—Rosa 2015, char. 43]; $CI_1=0.11$, $RI_1=0.61$, $CI_2=0.11$, $RI_2=0.61$:** 0 Absent or inconspicuous, surface concave or rectilinear (Fig. 20A; Rosa 2015, Fig. 17A); 1 Present, conspicuous, surface convex (Figs. 19B, 20B; Rosa 2015, Fig. 21A); 2 Present, very conspicuous, surface extremely convex and expanded anteriorly (Rosa 2015, Fig. 38A).

20. **Lateral projection of the telencephalon, dorsal view [modified—Pereira 2014, char. 18; Rosa 2015, char. 37]; $CI_1=0.07$, $RI_1=0.75$, $CI_2=0.07$, $RI_2=0.71$:** 0 Absent or inconspicuous, surface concave or rectilinear (Figs. 19A, 19C, 20B; Pereira 2014, Figs. 49, 50; Rosa 2015, Fig. 46A); 1 Present, surface convex (Figs. 19B, 20A; Pereira 2014, Figs. 8, 9, 10; Rosa 2015, Fig. 32A).

21. **Grooves/furrows that delimits the lateral projections of the both telencephalic lobes, dorsal view [modified—Rosa 2015, char. 37]; $CI_1=0.07$,**

RI₁=0.73, CI₂=0.06, RI₂=0.71: 0 Not converging anteriorly, parallel to the longitudinal axis of the respective lobe (Figs. 19B, 20A; Rosa 2015, Fig. 36A); 1 Converging anteriorly, towards the mesial region of the respective lobe (Fig. 20B; Rosa 2015, Fig. 17A).

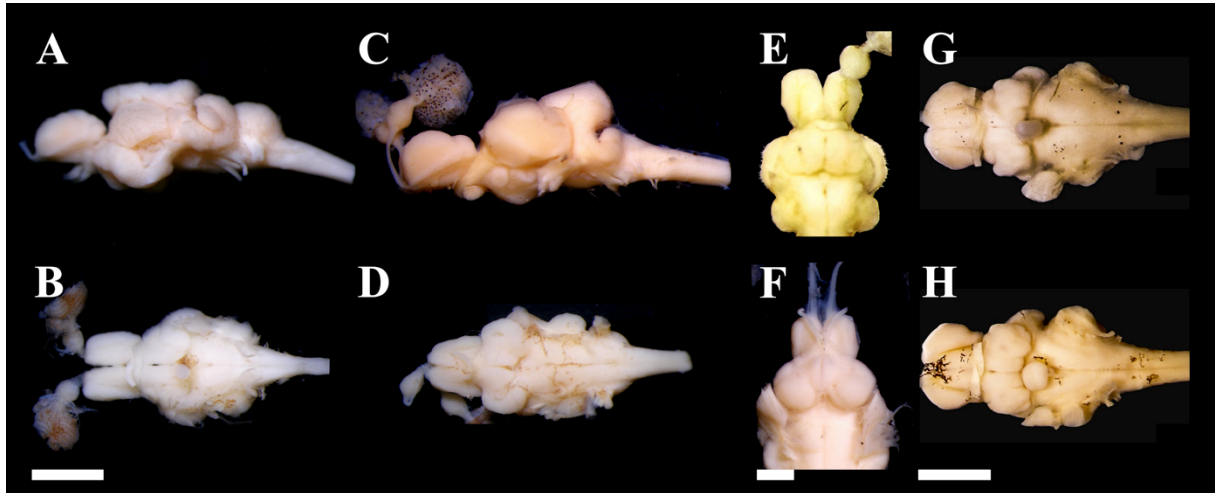


Figure 21. Brain of selected species of the Loricariidae, lateral and ventral views. (A) *Loricaria cataphracta*, MZUSP 014106, male, 114.70 mm SL; (B) *Farlowella paraguayensis*, DZSJRP 018794, female, 99.55 mm SL; (C) *Cteniloricaria platystoma*, ANSP 190521, female, 116.71 mm SL; (D) *Hemiodontichthys acipenserinus*, INPA-ICT 032082, male, 92.34 mm SL; (E) *Otothyropsis marapoama*, DZSJRP 014108, female, 27.20 mm SL; (F) *Paraloricaria vetula*, ZVCP 14036, male, 217.00 mm SL; (G) *Neoplecostomus selenae*, DZSJRP 015331, male, 78.30 mm SL; (H) *Neoplecostomus yapo*, DZSJRP 013651, female, 74.90 mm SL. Scale bar=2 mm.

22. Ventral expansion of the dorsal surface of the telencephalon, lateral view [Rosa 2015, char. 40]; CI₁=0.08, RI₁=0.68, CI₂=0.07, RI₂=0.58: 0 Not expanded, ventral surface of the telencephalon completely exposed (Fig. 19C; Rosa 2015, Fig. 47C); 1 Partially expanded, covering only the anterior portion of the ventral surface of the telencephalon (Fig. 19D; Rosa 2015, Fig. 12D); 2 Fully expanded, covering totally the ventral surface of the telencephalon (Fig. 20C; Rosa 2015, Fig. 28C).

23. Lateral margin of the telencephalon, dorsal view [Rosa 2015, char. 41]; CI₁=0.50, RI₁=0.66, CI₂=0.50, RI₂=0.66: 0 Not continuous, with invagination(s) evident (Fig. 20B; Rosa 2015, Fig. 57C); 1 Continuous, without invagination(s) evident (Fig. 19B; Rosa 2015, Fig. 19C).

24. Postero-mesial projection of the telencephalon, dorsal view [modified—Rosa 2015, char. 42]; CI₁=0.05, RI₁=0.54, CI₂=0.06, RI₂=0.60: 0 Absent or inconspicuous, surface concave or rectilinear (Fig. 19A; Rosa 2015, Fig. 52A); 1 Present, surface moderately convex, only the posterior margin well delimited (Fig. 20A; Rosa 2015, Fig. 32A); 2 Present, conspicuous, surface convex, circular contour well delimited (Fig. 19B; Rosa 2015, Fig. 61A).

25. Groove/furrow between the lateral and postero-mesial projections of the telencephalon, dorsal view [Rosa 2015, char. 44]; CI₁=0.05, RI₁=0.63, CI₂=0.05,

RI₂=0.63: 0 Absent or inconspicuous (Fig. 19A; Rosa 2015, Fig. 40A); 1 Present and, usually, very conspicuous (Figs. 20A, 19B; Rosa 2015, Fig. 55C).

Chiasma opticum and nervus opticus

26. **Fibers of the *nervus opticus* at the *quiasma opticum*, ventral view [Rosa 2015, char. 35]; CI₁=0.50, RI₁=0.50, CI₂=0.33, RI₂=0:** 0 Not mixtured, both left and right optic nerves noticeably individualized (Fig. 20D; Rosa 2015, Fig. 36B); 1 Mixtured, nerves united, not visibly individualized (Fig. 20E; Rosa 2015, Figs. 17B, 21B).

27. **Orientation of both left and right optic nerves at the *quiasma opticum*, ventral view [Rosa 2015, char. 33]; CI₁=0.16, RI₁=0.92, CI₂=0.12, RI₂=0.88:** 0 Oblique to the anteroposterior axis of the encephalon, nerves directed anteriorly, intersecting each other in the form of a “X” (Fig. 20D; Rosa 2015, Fig. 35B); 1 Transversal to the anteroposterior axis of the encephalon, nerves starting almost parallel to opposite sides (Fig. 20E; Rosa 2015, Fig. 38B).

28. **Bulging at the base of the *nervus opticus* anterior to the *quiasma opticum*, ventral view; CI₁=1, RI₁=1, CI₂=1, RI₂=1:** 0 Absent (Fig. 20E); 1 Present, conspicuous (Fig. 20D).

29. **Thickness of the *nervus opticus*, ventral view [modified—Pereira 2014, char. 22; Rosa 2015, char. 34]; CI₁=0.11, RI₁=0.70, CI₂=0.11, RI₂=0.68:** 0 Shorter than the thickness of the *nervus olfactorius* (Pereira 2014, Fig. 50; Rosa 2015, Fig. 30B); 1 Slightly larger than, or similar to, the thickness of the *nervus olfactorius* (Fig. 20D; Pereira 2014, Fig. 48; Rosa 2015, Fig. 48B); 2 Visibly larger (1.5 times or more) than the thickness of the *nervus olfactorius* (Fig. 20E; Pereira 2014, Fig. 16; Rosa 2015, Fig. 21B).

Diencephalon

30. **Length of the *diencephalon*, lateral view; CI₁=0.07, RI₁=0.61, CI₂=0.08, RI₂=0.64:** 0 Shorter than, or similar to, the length of the *tectum mesencephali* (Fig. 20C); 1 Larger than the length of the *tectum mesencephali* (Fig. 21A).

31. **Width of the *diencephalon*, ventral view [modified—Rosa 2015, char. 21]; CI₁=0.04, RI₁=0.64, CI₂=0.05, RI₂=0.68:** 0 Shorter than, or similar to, the width of the *telencephalon* (Fig. 21B; Rosa 2015, Fig. 18C); 1 Larger than the width of the *telencephalon* (Fig. 20E; Rosa 2015, Fig. 30C).

32. **Anterior margin of the *lobus inferior hypothalami* 1, lateral view [Rosa 2015, char. 22]; CI₁=0.09, RI₁=0.44, CI₂=0.10, RI₂=0.50:** 0 Not expanded anteriorly, in line with or not surpassing the anterior margin of the *tectum mesencephali* (Fig. 21C; Rosa 2015, Fig. 44B); 1 Expanded anteriorly, clearly surpassing the anterior margin of the *tectum mesencephali* (Fig. 21A; Rosa 2015, Fig. 34F).

33. **Anterior margin of the *lobus inferior hypothalami* 2, ventral view [Rosa 2015, char. 24]; CI₁=0.11, RI₁=0.82, CI₂=0.14, RI₂=0.86:** 0 Not expanded anteriorly, in line with or not surpassing the anterior margin of the lateral portion of the

hypothalamus (Fig. 20D; Rosa 2015, Fig. 32B); 1 Expanded anteriorly, clearly surpassing the anterior margin of the lateral portion of the *hypothalamus* (Fig. 21D; Rosa 2015, Fig. 63B).

34. **Posterior margin of the *lobus inferior hypothalami* 1, ventral view [modified—Rosa 2015, char. 25]; $CI_1=0.23$, $RI_1=0.86$, $CI_2=0.21$, $RI_2=0.84$:** 0 Not expanded posteriorly, not surpassing the postero-mesial margin of the *hypothalamus* (Fig. 21E; Rosa 2015, Fig. 48B); 1 Not expanded posteriorly, in line with the postero-mesial margin of the *hypothalamus* (Fig. 21B; Rosa 2015, Fig. 33E); 2 Expanded posteriorly, surpassing the postero-mesial margin of the *hypothalamus*, with the posterior portions of each lobe not very close (Fig. 21D; Rosa 2015, Fig. 36B); 3 Expanded posteriorly, clearly surpassing the postero-mesial margin of the *hypothalamus*, with the posterior portions of each lobe very close or in contact (Fig. 21F; Rosa 2015, Fig. 57B).

35. **Lateral margin of the *lobus inferior hypothalami* 1, ventral view [modified—Rosa 2015, char. 23]; $CI_1=0.14$, $RI_1=0.60$, $CI_2=0.12$, $RI_2=0.53$:** 0 Not expanded posteriorly, in line with, or not surpassing, the lateral margin of the lateral portion of the *hypothalamus* (Fig. 21E; Rosa 2015, Fig. 51B); 1 Expanded laterally, clearly surpassing the lateral margin of the lateral portion of the *hypothalamus* (Fig. 21F; Rosa 2015, Fig. 38B).

36. **Shape of the *lobus inferior hypothalami*, ventral view; $CI_1=0.12$, $RI_1=0.80$, $CI_2=0.14$, $RI_2=0.83$:** 0 Semicircular to bean-shaped (Fig. 21F); 1 Squarish or almost rectangular (Fig. 21E).

37. **Lateral margin of the *lobus inferior hypothalami* 2, ventral view [modified—Pupo 2011, char. 14; Rosa 2015, char. 29]; $CI_1=0.06$, $RI_1=0.76$, $CI_2=0.08$, $RI_2=0.81$:** 0 Not continuous, with invagination(s) evident (Fig. 21E; Pupo 2011, Fig. 7; Rosa 2015, Fig. 20B); 1 Continuous, without invagination(s) evident (Fig. 21F; Pupo 2011, Fig. 7; Rosa 2015, Fig. 34B).

38. **Latero-posterior portion of the *lobus inferior hypothalami* 1, ventral view [Rosa 2015, char. 26]; $CI_1=0.14$, $RI_1=0.62$, $CI_2=0.16$, $RI_2=0.68$:** 0 Not flattened, surface continuous with the rest of the lobe (Figs. 21E, 21F; Rosa 2015, Fig. 28B); 1 Flattened, surface discontinuous with the rest of the lobe (Fig. 21G; Rosa 2015, Fig. 38B).

39. **Latero-posterior portion of the *lobus inferior hypothalami* 2, lateral view [Rosa 2015, char. 27]; $CI_1=0.33$, $RI_1=0.95$, $CI_2=1$, $RI_2=1$:** 0 Not ventrally expanded, surface continuous with the rest of the lobe (Fig. 21C; Rosa 2015, Fig. 32C); 1 Ventrally expanded, surface discontinuous with the rest of the lobe (Fig. 21A; Rosa 2015, Fig. 35C).

40. **Posterior margin of the *lobus inferior hypothalami* 2, ventral view [modified—Pupo 2011, char. 14; modified—Pereira 2014, char. 17; modified—Rosa Rosa 2015, char. 28]; $CI_1=0.06$, $RI_1=0.55$, $CI_2=0.06$, $RI_2=0.55$:** 0 Not continuous, with invagination(s) evident (Figs. 21G, 21H; Pupo 2011, Fig. 7; Pereira 2014, Figs. 4, 28; Rosa 2015, Fig. 27B); 1 Continuous, without invagination(s) evident (Fig. 21F; Pupo 2011, Fig. 7; Pereira 2014, Fig. 35; Rosa 2015, Fig. 24B).

41. **Mesial portion of the *hypothalamus*, lateral view [Rosa 2015, char. 30]; $CI_1=0.06$, $RI_1=0.60$, $CI_2=0.05$, $RI_2=0.57$:** 0 Not ventrally expanded, at the same level of the ventral surface of the *lobus inferior hypothalami* (Fig. 22A; Rosa 2015, Fig. 40C); 1 Ventrally expanded, visibly differentiated from the ventral surface of the *lobus inferior hypothalami* (Figs. 21A, 21C; Rosa 2015, Fig. 45C).
42. **Aperture of the third ventricle, ventral view [Rosa 2015, char. 31]; $CI_1=0.03$, $RI_1=0.45$, $CI_2=0.03$, $RI_2=0.47$:** 0 Not dilated (Fig. 20D; Rosa 2015, Fig. 62B); 1 Dilated (Fig. 20E; Rosa 2015, Fig. 50B).
43. **Shape of the *hypophysis*, lateral view [modified—Rosa 2015, char. 32]; $CI_1=0.05$, $RI_1=0.56$, $CI_2=0.04$, $RI_2=0.48$:** 1 Not flattened, ovate or circular (Fig. 22A; Rosa 2015, Fig. 26C); 1 Flattened (Fig. 22B; Rosa 2015, Fig. 19C).

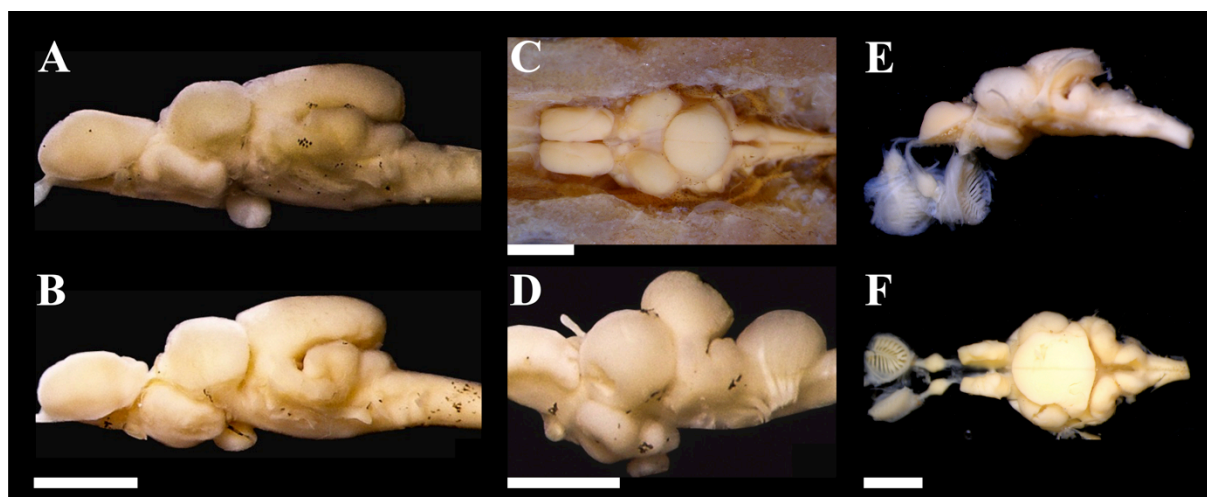


Figure 22. Brain of selected species of the Loricarioidea, detail of the anterior and medial portions of the brain (*telencephalon*, *mesencephalon* and *corpus cerebelli*), dorsal and lateral views. (A) *Neoplecostomus selenae*, DZSJRP 015331, male, 78.30 mm SL; (B) *Neoplecostomus yapo*, DZSJRP 013651, female, 74.90 mm SL; (C) *Rineloricaria cadeae*, MCP 009782, male, 123.08 mm SL; (D) *Corydoras aeneus*, DZSJRP 015193, female, 44.80 mm SL; (E) *Harttia novalimensis*, DZSJRP 011644, male, 102.53 mm SL; (F) *Proloricaria proluxa*, DZSJRP 006312, female, 104.51 mm SL. Scale bar=2 mm.

Mesencephalon

44. **Shape of the *tectum mesencephali*, dorsal view; $CI_1=0.06$, $RI_1=0.34$, $CI_2=0.07$, $RI_2=0.41$:** 0 Oval, horizontally elongated (Fig. 22C); 1 Oval, vertically elongated (Fig. 20A); 2 Circular or rounded (Fig. 20B).
45. **Contact between both lobes of the *tectum mesencephali*, dorsal view; $CI_1=0.33$, $RI_1=0$, $CI_2=0.33$, $RI_2=0$:** 0 Absent, both lobes not in contact (Fig. 20A); 1 Present only between the anteriormost portion of lobes; 2 Present along the entire lateral margin of the lobes (Fig. 20B).
46. **Length of the *tectum mesencephali* 1, lateral view [modified—Pereira**

2014, char. 35]; $CI_1=0.25$, $RI_1=0.40$, $CI_2=0.25$, $RI_2=0.40$: 0 Shorter than, or similar to, its height, *i.e.*, vertically elongated in shape (Fig. 22D); 1 Larger than its height, *i.e.*, horizontally elongated in shape (Figs. 22A, 22B).

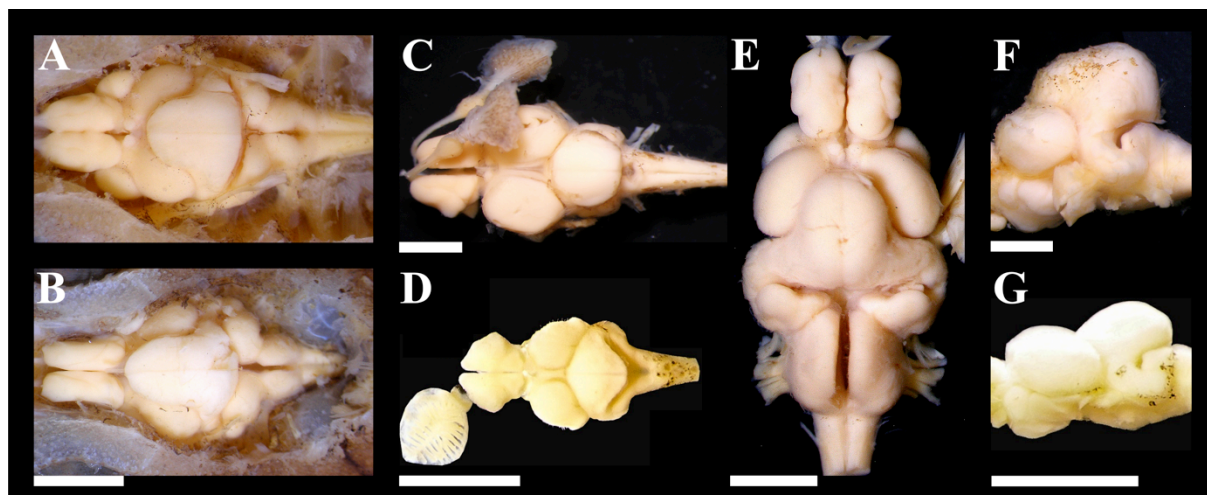


Figure 23. Brain of selected species of the Loricariidae, dorsal and lateral views. (A) *Pseudohemiodon platycephalus*, ZUFMS-PIS 000440, female, 136.26 mm SL; (B) *Loricaria luciae*, ZUFMS-PIS 003215, male, 120.33 mm SL; (C) *Dekeyseria scaphirhynchus*, INPA-ICT 036022, male, 85.17 mm SL; (D) *Hisonotus insperatus*, DZSJRP, 018211, male, 23.20 mm SL; (E) *Loricariichthys platymetopon*, DZSJRP 004395, female, 241.00 mm SL; (F) *Delturus brevis*, NUP 015446, male, 137.66 mm SL; (G) *Hisonotus insperatus*, DZSJRP, 014381, female, 32.30 mm SL. Scale bar=2 mm.

47. **Length of the *tectum mesencephali* 2, lateral view; $CI_1=0.06$, $RI_1=0.56$, $CI_2=0.07$, $RI_2=0.62$:** 0 Shorter than, or similar to, the length of the *corpus cerebelli* (Figs. 22A, 22B); 1 Larger than the length of the *corpus cerebelli* (Fig. 22D).

48. **Volume of the *tectum mesencephali* [modified—Abrahão 2013, char. 31; modified—Pereira 2014, char. 29]; $CI_1=0.03$, $RI_1=0.56$, $CI_2=0.03$, $RI_2=0.53$:** 0 Shorter than, or similar to, the volume of the *telencephalon* (Figs. 22A, 22B; Pereira 2014, Figs. 34, 38); 1 Larger than the volume of the *telencephalon* (Fig. 22D; Pereira 2014, Fig. 36).

Rhombencephalon

49. **Length of *rhombencephalon*, lateral view; $CI_1=0.07$, $RI_1=0.62$, $CI_2=0.06$, $RI_2=0.60$:** 0 Shorter than, or similar to, the length of the rest of the brain, *i.e.*, *mesencephalon*, *diencephalon* and *telencephalon*, excluding the *nervus tractus olfactorius* and the olfactory bulbs (Fig. 22E); 1 Larger than the rest of the brain (Figs. 22A, 22B).

50. **Width of the *rhombencephalon*, dorsal view [Rosa 2015, char. 1]; $CI_1=0.14$, $RI_1=0.57$, $CI_2=0.14$, $RI_2=0.57$:** 0 Shorter than, or similar to, the width of the *tecta mesencephali* (Fig. 22C; Rosa 2015, Figs. 12C, 19A); 1 Larger than the width of the *tecta mesencephali* (Fig. 22F; Rosa 2015, Fig. 15A).

51. **Ventral overhang in the antero-medial portion of the *truncus cerebri*, lateral view** [modified—Rosa 2015, char. 0]; $CI_1=0.07$, $RI_1=0.59$, $CI_2=0.07$, $RI_2=0.62$: 0 Absent, ventral surface of *rhombencephalon* almost rectilinear (Fig. 22E; Rosa 2015, Fig. 26C); 1 Present, ventral surface of the *rhombencephalon* swollen, non-rectilinear (Figs. 22A, 22B; Rosa 2015, Figs. 33C, 37C).
52. **Shape of the *corpus cerebelli*, dorsal view** [modified—Abrahão 2013, char. 23; modified—Pereira 2014, char. 32]; $CI_1=0.06$, $RI_1=0.46$, $CI_2=0.10$, $RI_2=0.44$: 0 Oval, horizontally elongated, triangular or rhomboid (Fig. 22C); 1 Hat-shaped, elongated vertically on its posterior portion (Fig. 23A); 2 Oval, vertically elongated (Fig. 23B); 3 Circular or rounded (Fig. 23C; Pereira 2014, Fig. 48).
53. **Length of the *corpus cerebelli*, dorsal view** [modified—Abrahão 2013, char. 26; Rosa 2015, char. 17]; $CI_1=0.07$, $RI_1=0.60$, $CI_2=0.06$, $RI_2=0.53$: 0 Shorter than, or similar to, its width, *i.e.*, horizontally elongated in shape (Figs. 23A, 23C); 1 Larger than its width, *i.e.*, vertically elongated in shape (Fig. 23A).
54. **Width of the *corpus cerebelli* 1, dorsal view** [modified—Pupo 2011, char. 13; modified—Pereira 2014, char. 16]; $CI_1=0.11$, $RI_1=0.65$, $CI_2=0.11$, $RI_2=0.65$: 0 Shorter than the width of the *tecta mesencephali* (Figs. 22C, 23C; Pupo 2011, Fig. 3; Pereira 2014, Figs. 38, 39); 1 Larger than, or similar to, the width of the *tecta mesencephali* (Figs. 22F, 23A; Pupo 2011, Fig. 3; Pereira 2014, Figs. 51, 52).
55. **Width of the *corpus cerebelli* 2, dorsal view** [modified—Rosa 2015, char. 18]; $CI_1=0.07$, $RI_1=0.76$, $CI_2=0.06$, $RI_2=0.74$: 0 Less than twice the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (Fig. 23C; Rosa 2015, Fig. 22A); 1 More than twice the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (Fig. 22F; Rosa 2015, Fig. 21A).
56. **Volume of the *corpus cerebelli*** [modified—Pereira 2014, char. 28]; $CI_1=0.12$, $RI_1=0.66$, $CI_2=0.16$, $RI_2=0.76$: 0 Shorter than, or similar to, the volume of the *tecta mesencephali* (Fig. 22D; Pereira 2014, Figs. 2, 32); 1 Larger than the volume of the *tecta mesencephali* (Figs. 22A, 22B; Pereira 2014, Fig. 17).
57. **Shape of the anterior margin of the *corpus cerebelli*, dorsal view** [modified—Abrahão 2013, char. 20; modified—Rosa 2015, char. 17]; $CI_1=0.08$, $RI_1=0.71$, $CI_2=0.07$, $RI_2=0.65$: 0 Not rounded, arrow-shaped, *i.e.*, tipped (Fig. 23D; Abrahão 2013, Figs. 4A, 4B; Rosa 2015, Fig. 49A); 1 Circular or rounded, convex (Figs. 22F, 23A, 23C; Abrahão 2013, Figs. 2, 3; Rosa 2015, Fig. 53A).
58. **Anterior margin of the *corpus cerebelli* 1, dorsal view** [modified—Pupo 2011, char. 12; modified—Rosa 2015, char. 16]; $CI_1=0.22$, $RI_1=0.87$, $CI_2=0.22$, $RI_2=0.87$: 0 Not expanded on the *tecta mesencephali* (Figs. 23C, 23D; Rosa 2015, Fig. 20A); 1 Expanded on the *tecta mesencephali* but not surpassing its anterior margin (Figs. 22C, 23A; Rosa 2015, Fig. 17A); 2 Expanded on the *tecta mesencephali* and surpassing its anterior margin (Figs. 22F, 23B; Rosa 2015, Fig. 57A).
59. **Anterior margin of the *corpus cerebelli* 2, dorsal view** [modified—Pupo

2011, char. 12; modified—Abrahão 2013, char. 24; modified—Pereira 2014, char. 15]; $CI_1=0.10$, $RI_1=0.70$, $CI_2=0.09$, $RI_2=0.60$: 0 Not expanded on the *telencephalon*, the distance between the anterior margin of the *corpus cerebelli* and the posterior margin of the *telencephalon* is greater than, or similar to, the minimum width of the *telencephalon* (Fig. 23D; Pupo 2011, Fig. 3; Pereira 2014, Figs. 45, 46, 47); 1 Not expanded on the *telencephalon*, the distance between the anterior margin of the *corpus cerebelli* and the posterior margin of the *telencephalon* is shorter than the minimum width of the *telencephalon* (Fig. 23A; Pereira 2014, Figs. 50, 51, 52); 2 Expanded on the *telencephalon* (Fig. 23B; Pupo 2011, Fig. 3).

60. Shape of the posterior margin of the *corpus cerebelli*, dorsal view [modified—Pupo 2011, char. 9; modified—Pereira 2014, char. 10; modified—Rosa 2015, char. 15]; $CI_1=0.05$, $RI_1=0.61$, $CI_2=0.05$, $RI_2=0.61$: 0 Not rounded, arrow-shaped, *i.e.*, tipped (Fig. 23D; Pupo 2011, Fig. 3; Pereira 2014, Figs. 32, 49; Rosa 2015, Fig. 30A); 1 Circular or rounded, convex (Figs. 23A, 23B; Pupo 2011, Fig. 3; Pereira 2014, Figs. 40, 41; Rosa 2015, Fig. 14A).

61. Posterior margin of the *corpus cerebelli* 1, dorsal view [modified—Abrahão 2013, char. 12; modified—Pereira 2014, char. 14]; $CI_1=0.05$, $RI_1=0.58$, $CI_2=0.05$, $RI_2=0.68$: 0 Not expanded on the *lobi facialis* (Fig. 23E; Abrahão 2013, Figs. 3–4; Pereira 2014, Figs. 49, 50); 1 Expanded on the *lobi facialis* or reaching the anterior margin of the lobes (Figs. 23A, 23B, 23C, 23D; Abrahão 2013, Fig. 4D; Pereira 2014, Figs. 26).

62. Posterior margin of the *corpus cerebelli* 2, dorsal view [modified—Pupo 2011, char. 9; modified—Pereira 2014, char. 10; modified—Rosa 2015, char. 14]; $CI_1=0.08$, $RI_1=0.61$, $RI_1=0.58$, $CI_2=0.08$, $RI_2=0.59$: 0 Not expanded on the forth ventricle (Fig. 22F; Pupo 2011, Fig. 3; Pereira 2014, Figs. 40, 41; Rosa 2015, Fig. 45A); 1 Expanded on the forth ventricle, not reaching the anterior margin of the *lobi vagi* (Fig. 23E; Pupo 2011, Fig. 3; Pereira 2014, Figs. 32, 49; Rosa 2015, Fig. 52A); 2 Expanded on the forth ventricle, reaching or surpassing the anterior margin of the *lobi vagi* (Fig. 23C; Pupo 2011, Fig. 3; Rosa 2015, Fig. 42A).

63. Height of the *corpus cerebelli*, lateral view [modified—Rosa 2015, char. 19]; $CI_1=0.07$, $RI_1=0.58$, $CI_2=0.06$, $RI_2=0.48$: 0 Shorter than, or similar to, the height of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi*, *corpus cerebelli* not expanded dorsally (Fig. 21C; Rosa 2015, Fig. 40C); 1 Larger than the height of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi*, *corpus cerebelli* expanded dorsally (Figs. 20C, 21C; Rosa 2015, Fig. 36C).

64. Shape of the dorsal margin of the *corpus cerebelli*, lateral view [modified—Pupo 2011, char. 10; modified—Pereira 2014, char. 9]; $CI_1=0.04$, $RI_1=0.47$, $CI_2=0.04$, $RI_2=0.47$: 0 Curved, mostly convex (Figs. 20C, 22D; Pupo 2011, Fig. 6; Pereira 2014, Figs. 4, 18, 48, 49); 1 Mostly rectilinear (Figs. 21A, 22A, 22B; Pupo 2011, Fig. 6; Pereira 2014, Figs. 3, 17, 51, 52).

65. Shape of the *corpus cerebelli*, lateral view [Pupo 2011, char. 11; Pereira 2014, char. 13]; $CI_1=0.50$, $RI_1=0.50$, $CI_2=0.50$, $RI_2=0.50$: 0 Oval, horizontally

elongated, or flattened (Figs. 22A, 22B, 22E; Pupo 2011, Fig. 6); 1 Almost circular or vertically elongated (Fig. 23F; Pupo 2011, Fig. 6).

66. ***Valvula cerebelli*** [modified—Rosa 2015, char. 20]; $CI_1=0.33$, $RI_1=0.87$, $CI_2=0.33$, $RI_2=0.87$: 0 Inconspicuous, not visibly dorsally (Rosa 2015, Fig. 47A); 1 Not very conspicuous, extended to approximately the half the length of the *tecta mesencephali* (Rosa 2015, Fig. 30A); 2 Very conspicuous, expanded beyond the half the length of the *tecta mesencephali* (Rosa 2015, Figs. 56A, 57A).

67. **Length of the *lobus vestibulolateralis* 1, lateral view**; $CI_1=0.07$, $RI_1=0.73$, $CI_2=0.06$, $RI_2=0.66$: 0 Less than half the length of the *corpus cerebelli* (Figs. 23F, 22D); 1 More than, or similar to, half the length of the *corpus cerebelli* (Fig. 22E).

68. **Height of the *lobus vestibulolateralis*, lateral view** [Rosa 2015, char. 13]; $CI_1=0.05$, $RI_1=0.37$, $CI_2=0.05$, $RI_2=0.33$: 0 Shorter than the height of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (Fig. 23G; Rosa 2015, Fig. 12D); 1 Larger than, or similar to, the height of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (Fig. 23F; Rosa 2015, Fig. 44C).

69. **Length of the *lobus vestibulolateralis* 2, lateral view** [Rosa 2015, char. 12]; $CI_1=0.10$, $RI_1=0.46$, $CI_2=0.11$, $RI_2=0.53$: 0 Shorter than, or similar to, its height (Fig. 22D; Rosa 2015, Fig. 33C); 1 Larger than its height, less than twice (Figs. 23F, 23G; Rosa 2015, Fig. 32C); 2 Larger than its height, more than twice (Figs. 22A, 22B; Rosa 2015, Fig. 35C).

70. ***Lobus facialis* 1, dorsal view** [Pupo 2011, char. 5; modified—Pereira 2014, char. 5; Rosa 2015, char. 7]; $CI_1=0.12$, $RI_1=0.61$, $CI_2=0.12$, $RI_2=0.61$: 0 Inconspicuous, reduced or undetectable, not completely exposed, *i.e.*, located under the posterior portion of the *corpus cerebelli* (Fig. 23C; Pupo 2011, Fig. 3; Pereira 2014, Figs. 18, 19, 20; Rosa 2015, Fig. 13A); 1 Conspicuous, completely exposed (Figs. 22C, 22F, 23A, 23B, 23D, 23E; Pupo 2011, Fig. 3; Pereira 2014, Fig. 31; Rosa 2015, Fig. 15A).

71. ***Lobus facialis* 2, dorsal view** [Rosa 2015, char. 10]; $CI_1=0.10$, $RI_1=0.52$, $CI_2=0.09$, $RI_2=0.47$: 0 Contained within the boundaries of the *rhombencephalon*, not exceeding its lateral margins (Fig. 23E; Rosa 2015, Fig. 45A); 1 Externalized, exceeding the lateral margins of the *rhombencephalon* (Fig. 24A; Rosa 2015, Fig. 63A).

72. **Volume of the *lobus fascialis*** [modified—Abrahão 2013, char. 7; Pereira 2014, char. 8]; $CI_1=0.09$, $RI_1=0.80$, $CI_2=0.08$, $RI_2=0.78$: 0 Shorter than, or similar to, the volume of the *lobus vagi* (Figs. 23A, 23C, 23D, 23E); 1 Larger than the volume of the *lobus vagi* (Fig. 23B; Pereira 2014, Fig. 31).

73. **Width of the *lobus facialis*, dorsal view** [modified—Pupo 2011, char. 2; modified—Pereira 2014, char. 4; modified—Rosa 2015, char. 6]; $CI_1=0.11$, $RI_1=0.82$, $CI_2=0.10$, $RI_2=0.76$: 0 Shorter than half the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (Figs. 23C, 23D; Pupo 2011, Fig. 3; Pereira 2014, Figs. 18, 19, 20; Rosa 2015, Fig. 12A); 1 About equal to

half the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (Fig. 24B; Pereira 2014, Fig. 17; Rosa 2015, Fig. 41A); 2 Larger than half the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (Figs. 23A, 23B, 23E; Pupo 2011, Fig. 3; Pereira 2014, Fig. 17; Rosa 2015, Fig. 16A).

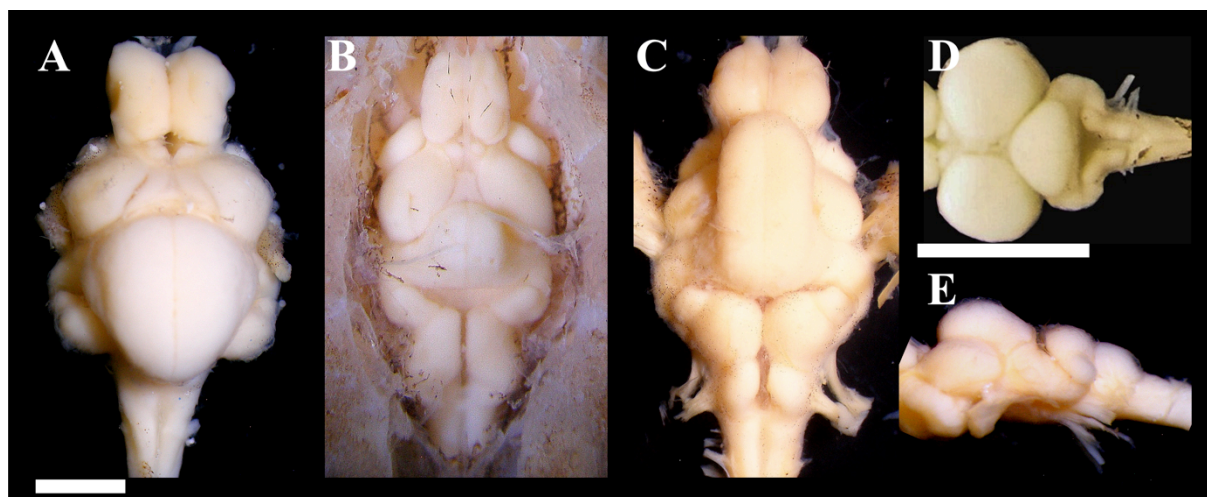


Figure 24. Brain of selected species of the Loricariidae, dorsal and lateral views. (A) *Fonchiiloricaria nanodon*, MUSM 032153, female, 166.27 mm SL; (B) *Reganella depressa*, MZUSP 057936, male, 139.97 mm SL; (C) *Brochiloricaria macrodon*, NUP 002248, male, 262.00 mm SL; (D) *Oxyropsis wrighthiana*, MCP 034503, female, 44.00 mm SL; (E) *Furcodontichthys novaesi*, MZUSP 057726, male, 126.38, mm SL. Scale bar=2 mm.

74. **Contact between both *lobi facialis*, dorsal view [Abrahão 2013, char. 8];** $CI_1=0.50$, $RI_1=0.80$, $CI_2=0.33$, $RI_2=0.60$: 0 Absent, lobes not in contact (Figs. 23A, 23B, 23C, 23D, 23E, 24A, 24B; Abrahão 2014, Fig. 4); 1 Present, lobes in contact (Fig. 24A; Abrahão 2014, Figs. 2, 3).

75. **Angulation between both *lobi facialis*, dorsal view [modified—Abrahão 2013, char. 11];** $CI_1=0.10$, $RI_1=0.35$, $CI_2=0.10$, $RI_2=0.35$: 0 Less than 90° (Fig. 24D; Abrahão 2013, Figs. 3, 4); 1 90° or more (Figs. 24B, 24C; Abrahão 2013, Fig. 3F).

76. **Segmentation of the *lobus facialis* 1, dorsal view [modified—Pupo 2011, char. 4; Rosa 2015, char. 8];** $CI_1=0.50$, $RI_1=0.85$, $CI_2=0.50$, $RI_2=0.85$: 0 Absent, lobe without visible subdivisions (Fig. 24D; Pupo 2011, Fig. 3; Rosa 2015, Fig. 12A); 1 Present, lobe with both anterior and posterior portions well differentiated (Figs. 24B, 24C; Pupo 2011, Fig. 3; Rosa 2015, Fig. 20A).

77. **Segmentation of the *lobus facialis* 2, dorsal view [modified—Rosa 2015, char. 9];** $CI_1=0.07$, $RI_1=0.73$, $CI_2=0.10$, $RI_2=0.71$: 0 Anterior and posterior portions not well differentiated or, if differentiated, both anterior and posterior portions of about the same volume (Fig. 23A; Rosa 2015, Fig. 39A); 1 Posterior portion more voluminous (Fig. 24C; Rosa 2015, Figs. 34A, 34D); 2 Anterior portion more voluminous (Fig. 23E; Rosa 2015, Fig. 15A).

78. **Swelling of the *nervus facialis*, dorsal view [Rosa 2015, char. 11];**

CI₁=0.25, RI₁=0.81, CI₂=0.22, RI₂=0.79: 0 Not evident, wall facing to the ventricle concave (Rosa 2015, Fig. 19A); 1 Evident, forming a small callosity on the wall facing to the ventricle (Rosa 2015, Fig. 12C); 2 Very evident, forming a bulky callosity on the wall facing to the ventricle and occupying much of the ventricle (Rosa 2015, Fig. 14A).

79. **Shape of the *lobus vagi*, dorsal view [modified—Rosa 2015, char. 4]; CI₁=0.11, RI₁=0.82, CI₂=0.14, RI₂=0.78:** 0 Straight, without angulation (Figs. 23D, 24D; Rosa 2015, Fig. 48A); 1 Angled, boomerang-shaped, anterior margins facing to the sides (Rosa 2015, Fig. 58A); 2 Very angled, anterior margins facing to the medial axis (Figs. 23A, 23B; Rosa 2015, Fig. 61A).

80. **Contact between both *lobi vagi*, dorsal view Abrahão 2013, char. 2]; CI₁=0.25, RI₁=0.50, CI₂=0.25, RI₂=0.50:** 0 Only between its postero-lateral portions (Figs. 23A, 23B; Abrahão 2013, Figs. 3, 4); 1 Along its entire lateral portions, practically forming a single structure (Fig. 23E; Abrahão 2013, Fig. 4D).

81. **Angulation between both *lobi vagi*, dorsal view [modified—Abrahão 2013, char. 5]; CI₁=0.10, RI₁=0.59, CI₂=0.12, RI₂=0.66:** 0 No angulation, *i.e.*, 0° (Fig. 23E; Abrahão 2013, Fig. 4D); 1 More than 0° and less than 90° (Figs. 23A, 23B; Abrahão 2013, Figs. 2, 4); 2 90° or more (Abrahão 2013, Fig. 3E).

82. **Length of the *lobus vagi*, lateral view [modified—Abrahão 2013, char. 3]; CI₁=0.10, RI₁=0.75, CI₂=0.10, RI₂=0.75:** 0 Shorter than the length of the *eminencia granularis* (Figs. 22A, 22B, 22E; Abrahão 2013, Fig. 4F); 1 Larger than, or similar to, the length of the *eminencia granularis* (Fig. 24E).

83. **Height of the *lobus vagi*, lateral view [modified—Rosa 2015, char. 5]; CI₁=0.16, RI₁=0.89, CI₂=0.14, RI₂=0.84:** 0 Shorter than the height of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (Figs. 22A, 22B; Rosa 2015, Fig. 55C); 1 Larger than, or similar to, the height of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (Fig. 24E; Rosa 2015, Fig. 66C).

84. **Width of the *lobus vagi*, dorsal view [modified—Pupo 2011, char. 2; modified—Pereira 2014, char 1; modified—Rosa 2015, char. 2]; CI₁=0.20, RI₁=0.93, CI₂=0.14, RI₂=0.89:** 0 Shorter than half the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (Fig. 23C; Pupo 2011, Fig. 3; Pereira 2014, Fig. 12; Rosa 2015, Fig. 22A); 1 Larger than, or similar to, half the width of the *medulla oblongata*, measured immediately posterior to the end of the *lobi vagi* (Figs. 23A, 23B; 23E, 24B; Pupo 2011, Fig. 3; Pereira 2014, Fig. 7; Rosa 2015, Fig. 35A).

85. **Angulation between the *lobus vagi* and the *lobus facialis*, dorsal view [modified—Rosa 2015, char. 3]; CI₁=0.12, RI₁=0.76, CI₂=0.16, RI₂=0.70:** 0 No angulation, set rectilinear (Rosa 2015, Fig. 52A); 1 Less than or about 90° (Fig. 23E; Rosa 2015, Fig. 34D); 2 More than 90° (Figs. 24B, 24C; Rosa 2015, Fig. 47A).

Other brain structures/areas

86. **Posterior margin of the *lobus vagi*, dorsal view [Pupo 2011, char. 1];** **CI₁=0.33, RI₁=0, CI₂=0.33, RI₂=0:** 0 Not reaching the anterior margin of the swim bladder (Figs. 22C, 24B; Pupo 2011, Fig. 4); 1 In contact with or surpassing the anterior margin of the swim bladder (Fig. 23B; Pupo 2011, Fig. 4).

87. **Opening of the *ductus endolymphatici*, dorsal view; CI₁=0.13, RI₁=0.71, CI₂=0.14, RI₂=0.62:** 0 Located anterior to the anterior margin of the eye; 1 Located in line with the anterior margin of the eye; 2 Located posterior to the anterior margin of the eye.

88. **Filaments on the surface of the brain, dorsal view [Rosa 2015, char. 59];** **CI₁=0.04, RI₁=0.48, CI₂=0.06, RI₂=0.40:** 0 Absent (Rosa 2015, Fig. 66); 1 Present in low abundance (Rosa 2015, Fig. 39B); 2 Present and numerous (Rosa 2015, Fig. 20A).

APPENDIX C. Data matrix used for the PCoA. Question marks (?) designate not only unknown states, but also polymorphisms and inapplicable characters. Abbreviations: De=Delturinae; Hp=Hypoptopomatinae; Hy=Hypostominae; LF=Loricariinae, Loricarini, Farlowellina; LH=Loricariinae, Harttiini; Li=Lithogeninae; LL=Loricariinae, Loricarini, Loricarina; Ne=Neoplecostominae; and Rh=Rhinelepidinae. Species are listed in alphabetical order.

***Acestridium discus* Haseman, 1911 (Hp):**

VV1001001101 012010?01? ?011000100 0?00101100 1101201111 0100000000
1010100002 1000010?11 020002??0

***Ancistrus* sp. (Hy):**

100101020? ??0201??11 102121010? 0110211010 011010?000 002100010?
0121001011 00000?1212 0?0002??2

***Apistoloricaria ommation* Nijssen & Isbrücker, 1988 (LL):**

1?010??01? ?1?2?01??1 01111?000? 0111211101 1001101001 0100010010
0100101111 1012011102 011112121

***Aposturisoma myriodon* Isbrücker, Britski, Nijssen & Ortega, 1983 (LF):**

1???01?01? ?1?2001??1 1101210002 0011211000 0110201110 0120010110
1111101111 1011011001 0100021?2

***Brochiloricaria macrodon* (Kner, 1853) (LL):**

1?2121001? ?1?2011??1 0111100001 1110310101 1010101001 0021001122
1110101012 1012111102 011112122

***Brochiloricaria* sp. (LL):**

1?0121101? ?0?2111??1 0101100001 1110211101 1011201011 0120010010
0100101002 1002001102 011112122

***Chauliocheilos saxatilis* Martins, Andrade, Rosa & Langeani, 2014 (Hp):**

1100010001 1000211011 10110?0100 10?0111100 1001101001 0?00000101
1120001001 0002010?20 010002??1

***Corumbataia cuestae* Britski, 1997 (Hp):**

101?210000 210000??00 0001000100 1110111100 11?1201011 1100110000
0020000000 1000011200 010000??1

***Crossoloricaria* (= *Rhadinoloricaria*) *bahuaja* Chang & Castro, 1999 (LL):**

1??121?00? ?1?0102??0 0111000002 0111211101 1001001111 0110010010
1000101010 1112011100 0111111?1

***Crossoloricaria variegata* (Steindachner, 1879) (LL):**

1?010??01? ?1?2011??1 0111100001 1110211101 1001101001 0100010111
0110101011 1012011102 0011121?2

***Cteniloricaria platystoma* (Günther, 1868) (LH):**

1?11211010 11?2?02?00 1111000102 0000211?00 1111?01110 0000010111
1111?01111 1011011201 011002102

***Curculionichthys insperatus* (Britski & Garavello, 2003) (Hp):**

1110?10010 110020?10? 1011010100 00?0??1100 1101?01101 01000?0000
?1?0000001 ?0000112?0 010000??2

***Dasylicaria filamentosa* (Steindachner, 1878) (LL):**

1?1100101? ?1?2012??1 0111110011 0110310101 1100101001 0010011111
1111101112 1001011002 011112??2

***Dasylicaria latiura* (Eigenmann & Vance, 1912) (LL):**

1?1100101? ?1?2011??1 0111110011 0110210101 1100101001 0021011111
1111101112 1001011102 011112??2

***Dekeyseria scaphirhynchus* (Kner, 1854) (Hy):**

10?1?10010 20020?2?11 1021210?02 0010211010 0111101011 0?30000101
0121001011 0000011212 010002?02

***Delturus brevis* Reis & Pereira, 2006 (De):**

0??12??01? ?1?2011??0 1101000102 0110201000 0110200011 0130011111
1111011011 00000110?2 010002?02

***Delturus carinotus* (La Monte, 1933) (De):**

0??????0?? ?1?2111??0 1101001102 0110201000 0110100011 0101011111
1111011011 00000110?2 010002?02

***Dentectus barbarmatus* Martín Salazar, Isbrücker & Nijssen, 1982 (LL):**

10?1011010 1002101001 01011?0001 0111211101 1?11101010 0100010110
1010101111 1012011102 011112122

***Epactionotus bilineatus* Reis & Schaefer, 1998 (Hp):**

1100010000 1100001?00 1011000100 0010101000 0001201011 0100000001
0120000001 1000011200 020000??1

***Eurycheilichthys pantherinus* (Reis & Schaefer, 1992) (Hp):**

??10010000 01?0111?10 0011000100 0100101100 1001201000 0100000000
0010100001 1000011200 010000??1

***Farlowella amazonum* (Günther, 1864) (LF):**

10??00000? 1101102010 0001000101 0010111000 1001201000 0100010010
0010101011 1012011002 010002102

***Farlowella henriquei* Miranda Ribeiro, 1918 (LF):**

1???2??01? ?1?1112??0 1001200101 0010111000 10?1201000 0100010100
1010101001 1011011002 010002102

***Farlowella nattereri* Steindachner, 1910 (LF):**

1???2??00? ?1?1001??0 00?1000101 0010111000 1001201000 0100010110
0010101011 1011011002 010002102

***Farlowella oxyrryncha* (Kner, 1853) (LF):**

101?000000 1101002000 0001200101 0000111000 1101101110 0100010000
0010101011 1012011002 010002102

***Farlowella paraguayensis* Retzer & Page, 1997 (LF):**

10??000000 1101002000 0001200101 0010111000 1101101110 0100010000
0010101011 1011011002 010002102

***Farlowella reticulata* Boeseman, 1971 (LF):**

1???2??00? ?1?2002??0 0001010101 0010111000 1111201000 0?00010110
1010101011 1011011002 010002102

***Farlowella schreitmuelleri* Ahl, 1937 (LF):**

1???2??01? ?1?1001??0 1001210101 0010111000 1101201010 0100010010
0010101011 1011011002 020002102

***Farlowella smithi* Fowler, 1913 (LF):**

1?0?20001? 11?1001?10 1001200101 0010111000 1001201110 0100010010
1010101011 1011011002 010002102

***Fonchiiloricaria nanodon* Rodriguez, Ortega & Covain, 2011 (LL):**

1011210010 2102012001 1011100001 0111310101 1101200000 0120011100
1121101112 1111011101 0100021?1

***Furcodontichthys novaesi* Rapp Py-Daniel, 1981 (LL):**

1??12??00? ?1?2100??0 0101000001 0111211101 1011101110 1110010?10
1000101111 1112011200 011111112

***Gymnotocinclus anosteos* Carvalho, Lehmann A. & Reis, 2008 (Hp):**

1101210001 1000201?11 1011010100 00?0111000 ?001101001 0100000001
0120100001 1000011211 0?0000??2

***Harttia carvalhoi* Miranda Ribeiro, 1939 (LH):**

1???011000 11?1002011 1001100101 0010211100 1111101010 0130010110
0110101111 1011011201 020002102

***Harttia duriventris* Rapp Py-Daniel & Oliveira, 2001 (LH):**

1?11011010 11?1101011 1001100101 0000211100 111?201110 0100000010
1110101111 1011011201 020002101

***Harttia loricariformis* Steindachner, 1877 (LH):**

1?11011000 11?2001011 1111210101 0010211100 1110201010 0130000110
1111101111 1011011201 020002102

***Harttia novalimensis* Oyakawa, 1993 (LH):**

1011011010 1102001011 1001100101 0000211100 1111101010 00?0000010
0110101111 1012011201 020002102

***Harttia punctata* Rapp Py-Daniel & Oliveira, 2001 (LH):**

1?1101101? ?1?1001??1 1001210101 0000211000 01112?1110 0100010010
0110100001 1010011201 0200021?2

***Harttiella crassicauda* (Boeseman, 1953) (LH):**

1?0101101? ?1?0011??1 1111100001 0010211100 1101201000 0100010110
1110101011 1011011201 020102121

***Hemiodontichthys acipenserinus* (Kner, 1853) (LL):**

1001001011 1102111??0 0101000001 0?11210101 1001201100 0010010110
1000101111 100?011202 011112122

***Hemiodontichthys* sp. (LL):**

1??11??010 11?2110??0 0101000001 0011210101 1001101100 0010010110
1010101111 1001011202 011112122

***Hemipsilichthys nimius* Pereira, Reis, Souza & Lazzarotto, 2003 (De):**

0?11010010 21?2212??1 1001011102 1010201000 0110100001 0121011111
1111001011 00010?1012 010002??0

***Hisonotus francirochai* (Ihering, 1928) (Hp):**

1100011010 1100213?10 1011000100 00?01?1100 1101201111 0100000000
0110000001 1000011211 010000??2

***Hisonotus notatus* Eigenmann & Eigenmann, 1889 (Hp):**

1101011010 110020??10 ?011000100 0000101000 1??1101110 0100000000
0110100001 1000011210 010000??2

***Hypoptopoma inexpectatum* (Holmberg, 1893) (Hp):**

1010001102 1001011100 0011010002 00001?1000 11?01?1111 0100000?00
1000000012 1000000?11 000002??0

***Hypostomus ancistroides* (Ihering, 1911) (Hy):**

10?111010? 2002201?11 1021210102 0110211000 ?110101001 0000000111
00?1001011 ?000011212 010002??1

***Hypostomus nigromaculatus* (Schubart, 1964) (Hy):**

1021010100 2001202??1 0011210101 0110?11000 0111101011 0?01000110
0121001011 00010?1212 0?0002??1

***Hypostomus regani* (Ihering, 1905) (Hy):**

1021010100 2002202?11 1021210102 0010211000 0110101011 0021000111
0021001011 0000001212 010002??0

***Hypostomus variipictus* (Ihering, 1911) (Hy):**

1021010100 2002202?11 1021210102 0010211000 0110101011 0021000111
0121001011 0000001212 010002??0

***Isbrueckerichthys duseni* (Miranda Ribeiro, 1907) (Ne):**

???12??01? ???1102??0 0001010100 0111211010 0111101010 0101010000
0121101012 1000011200 020000??1

***Ixinandria steinbachi* (Regan, 1906) (LL):**

10?10?1010 2101101001 1011110001 0011211100 1110101110 0100010110
0110101011 1001011002 010012122

***Kronichthys heylandi* (Boulenger, 1900) (Ne):**

1210110?10 2001212001 1011110101 00?01110?0 0111101111 0100000100
1010100001 100001121? 020002??1

***Kronichthys subteres* Miranda Ribeiro, 1908 (Ne):**

1011010000 1001202?01 1011110100 00?0101010 1101101110 0100000100
1011000011 1000001210 02000??1

***Lamontichthys filamentosus* (La Monte, 1935) (LF):**

??112??01? ?1?2002??1 1011200101 011?211000 0111101000 0100000110
1111001011 1102011101 0200121?2

***Lampiella gibbosa* (Miranda Ribeiro, 1908) (Hp):**

1111011000 2100202001 0001100100 0000101100 0101101110 0100000001
0110100010 0000011210 020000??0

***Limatulichthys griseus* (Eigenmann, 1909) (LL):**

1001001000 1102100001 010110000? 0111310101 1100101011 0110010110
1101001011 1112011202 001112112

***Limatulichthys petleyi* (Regan, 1904) (LL):**

1??10??01? ?1?2100??1 0101100001 0111310101 1100101011 1100010110
1101001011 1012011202 001112112

***Lithogenes villosus* Eigenmann, 1909 (Li):**

01????????? ???1211??1 1121211102 1010211100 110?101001 0121011011
1120100001 1111001110 021000?20

***Loricaria cataphracta* Linnaeus, 1758 (LL):**

1??100?01? ?1?2110??1 0011100001 1111310101 1111101001 1101111022
0100101011 1012011102 011112112

***Loricaria luciae* Thomas, Rodriguez, Carvallaro, Froehlich & Castro, 2013 (LL):**

1?1100101? ?1?2110??1 0001100001 1111310101 1?10101001 0021001122
1110101001 1012011102 0111121?2

***Loricaria* sp. (LL):**

1011001000 2112110010 1101200001 1111310101 1101101001 0?11011122
?00?101012 1012011102 011111110

***Loricariichthys acutus* (Valenciennes, 1840) (LL):**

1001101010 1102001001 ?011200001 0111310101 1000?01011 0?10010?11
1010101011 1002011202 011112121

***Loricariichthys anus* (Valenciennes, 1835) (LL):**

1001101010 2102002011 1011100001 0111310101 1100101011 1010010111
1100101112 1002011202 011111122

***Loricariichthys castaneus* (Castelnau, 1855) (LL):**

1?01101010 11?2101?11 ?1111?0001 0111310101 1010201011 0030000111
1111101101 1002011002 011112122

***Loricariichthys derbyi* Fowler, 1915 (LL):**

1?01101010 21?2101?11 ?001100001 0011310101 11?0001001 1?10110111
101?001111 1002011202 011111121

***Loricariichthys melanocheilus* Reis & Pereira, 2000 (LL):**

1001101010 1102002011 10111?0001 0111310101 1110201001 0110010111
1100001112 1002011202 011112122

***Loricariichthys platymetopon* Isbrücker & Nijssen, 1979 (LL):**

1?11101010 21?2002??1 1011200002 0111310101 1100101001 1010110111
100?101112 1002011202 101111?20

***Loricariichthys rostratus* Reis & Pereira, 2000 (LL):**

1?0110101? ???2102??1 10111?000? 0111310101 111?201011 001001011?
1000101111 1002011002 01111?122

***Loricariichthys* sp. (LL):**

1?01101011 11?2101?01 001121000? 0011310101 1110101011 001001011?
1110101111 1002011200 111112122

***Megalancistrus parananus* (Peters, 1881) (Hy):**

1021010110 2?02211?11 1021210102 00102?10?0 0110101001 0021000111
?121001?11 00010?1212 0?0002??1

***Metaloricaria paucidens* Isbrücker, 1975 (LL):**

1??12??01? ?1?2100??1 1101100002 0111310101 1110101011 0021011111
1120101012 1102011102 011112122

***Microlepidogaster perforata* Eigenmann & Eigenmann, 1889 (Hp):**

1100001000 1100201?01 1011000100 0010111110 1001101001 0100000000
0010100011 1000011210 02000???2

***Neoplecostomus corumba* Zawadzki, Pavanelli & Langeani, 2008 (Ne):**

?01?210001 1?01211?12 1011210100 1011211010 0001101001 11?1101000
0120101012 1101011000 020000??1

***Neoplecostomus langeanii* Roxo, Oliveira & Zawadzki, 2012 (Ne):**

1011210001 1101211?12 1001010100 1011211010 0001101001 1100101000
01201010?2 1101011000 020000??1

***Neoplecostomus microps* (Steindachner, 1877) (Ne):**

1111210001 2001011?10 1011000100 1111211010 0011101001 1100101000
0120101012 1100011100 020000??0

***Neoplecostomus ribeirensis* Langeani, 1990 (Ne):**

1011210000 1?01201?12 1001?00100 1111211010 0001101001 1100101000
0120101012 1101011000 020000??2

***Neoplecostomus selenae* Zawadzki, Pavanelli & Langeani, 2008 (Ne):**

1011210010 2001212?10 0001010100 1111211000 0000101001 1101101001
?120101012 1100011100 020000??0

***Neoplecostomus yapo* Zawadzki, Pavanelli & Langeani, 2008 (Ne):**

1011210000 200101??10 1011010100 1011211010 0001101001 1101101000
0120101012 11000110?0 020000??2

***Otocinclus affinis* Steindachner, 1877 (Hp):**

1000001011 1100002?11 ?001?00101 0000001000 0101001111 0100000000
1010000010 0000010?10 010002??0

***Otothyris lophophanes* (Eigenmann & Eigenmann, 1889) (Hp):**

1110001001 1?10012111 0001100100 0010011100 1101001110 0100000100
1000000011 1000010?00 010002??0

***Otothyris rostrata* Garavello, Britski & Schaefer, 1998 (Hp):**

1110001011 1110012?10 0001100100 0010011100 11?1001100 0100000101
1000000010 1000000?10 010002???

***Otothyropsis marapoama* Ribeiro, Carvalho & Melo, 2005 (Hp):**

1000011010 1100002?10 0001000100 0000001000 1101001111 0100000000
1010000011 1000010?10 010002??2

***Oxyropsis wrightiana* Eigenmann & Eigenmann, 1889 (Hp):**

1001001102 0000201?10 0011010101 0000001000 11?1001111 0100000?00
1000100012 1000000?10 010002??0

***Paraloricaria vetula* (Valenciennes, 1835) (LL):**

1011101010 1102000011 1011100001 0111310101 1101201001 0021111122
1110101012 1012111102 010112??2

***Pareiorhaphis cameroni* (Steindachner, 1907) (Ne):**

1011210000 20?0012?11 ?001110100 0110201010 0101101011 0100100000
0120100011 1000001200 020000??2

***Pareiorhaphis hystrix* (Pereira & Reis, 2002) (Ne):**

1011210000 200?012?11 1001110100 11102?1010 0111101011 0100100000
012100?111 00000?121? 020000??2

***Pareiorhina carrancas* Bockmann & Ribeiro, 2003 (Ne):**

1000211101 0100012?00 1001010100 0010101010 1101101011 ?100100000
0010000011 1000011210 020000??2

***Pareiorhina rudolphi* (Miranda Ribeiro, 1911) (Ne):**

1011010000 1100002?00 1001010100 0010101010 1111101011 0100100000
1010000001 1000011200 020000??2

***Parotocinclus jumbo* Britski & Garavello, 2002 (Hp):**

1000001011 0001?02?10 0001100100 0110111000 1111101111 0100000?00
0010000010 1000011211 020000??2

***Parotocinclus maculicauda* (Steindachner, 1877) (Hp):**

1111211010 1110002000 ?0010?0101 0100101110 1001001111 0100?00000
0010100011 1000011200 020000??2

***Parotocinclus prata* Ribeiro, Melo & Pereira, 2002 (Hp):**

1010011011 1001002000 1001?10100 01?0111000 1?11?01111 0100000000
1010100011 1000011211 020002??2

***Planiloricaria cryptodon* (Isbrücker, 1971) (LL):**

1?110??01? ?1?2111??1 0101110001 1110210101 1000101001 0011010111
0100101011 1012011102 011112122

***Plesioptopoma curvidens* Reis, Pereira & Lehmann A., 2012 (Hp):**

1?00010001 10?1202?01 1?01010100 0100111000 0011101011 0100000100
1010100011 1000011211 020002??0

***Proloricaria prolixa* (Isbrücker & Nijssen, 1978) (LL):**

1?01001000 11?2110?01 0011100001 1111310101 1111101011 1101111121
0100101011 1012011102 010111??2

***Pseudohemiodon laticeps* (Regan, 1904) (LL):**

1011011010 1?02111001 0101110001 1110210101 101?101001 0010100111
1100101001 1002011002 011112?22

***Pseudohemiodon platycephalus* (Kner, 1853) (LL):**

1?11011010 11?2111?11 01011?0001 1110?10101 1000101001 0010110111
1100101111 1002011002 011112?22

***Pseudohemiodon* sp. (LL):**

1?1101101? ?1?2011??1 0101110001 1110210101 1011201001 0010100111
1100101111 1002011002 011112?22

***Pseudoloricaria laeviscula* (Valenciennes, 1840) (LL):**

1??10??01? ?1?2110??1 0101000002 0111310101 1010101011 0101010111
1110101011 1102011102 101112?12

***Pseudoloricaria punctata* (Kner, 1854) (LL):**

1?010??01? ?1?2100??0 0101000001 0111?10101 1111101111 0100010110
1110101111 110201120? 011112011

***Pseudotocinclus tietensis* (Ihering, 1907) (Hp):**

1011001001 1100212100 1001110100 0010111010 1011?01001 0100000100
11?0000011 0000011211 020002??0

***Pseudotothyris obtusa* (Miranda Ribeiro, 1911) (Hp):**

?1010011?2 011000?010 0001?00100 0?10011100 11?1001101 0100000?01
1010100010 100001??10 010002??0

***Pyxiloricaria menezesi* Isbrücker & Nijssen, 1984 (LL):**

1??10??01? ?1?2100??1 1101100001 1111310101 1101101101 0000010110
0110101102 1002011102 010112?11

***Reganella depressa* (Kner, 1853) (LL):**

10010010?0 ??02101?01 0101100000 0111310101 1001111011 0020010?10
1000101111 1001011202 011112020

***Rhadinoloricaria* sp. (LL):**

1?01001011 11?2111?00 01?1100001 0111211101 1001101001 0120010110
1110101111 1112011102 010012?20

***Rhinelepis aspera* Spix & Agassiz, 1829 (Rh):**

1??10??10? ?1?2211??1 1021210002 0010211000 0100101001 0000001111
1021011011 0001011212 010012??0

***Rhinolekos britskii* Martins, Langeani & Costa, 2011 (Hp):**

1000011001 1100?11?01 1?11000100 0?10111010 1001101001 0100000?01
0010100001 1000011210 020000??2

***Ricola macrops* (Regan, 1904) (LL):**

1?1101101? ?1?2111??1 00?1110001 0110310101 1010101001 0111011122
1111101102 1012011102 010112022

***Rineloricaria* (=Fonchiiichthys) uracantha (Kner, 1863) (LL):**

1001001010 1102002?00 1111200001 0011210101 1101101000 0120010110
1100101111 1112011002 0110121?2

***Rineloricaria* (=Hemiloricaria) aurata (Knaack, 2002) (LL):**

1001001111 1100102011 11110?0001 0111210101 1101001110 0100010?10
1110101101 1111011202 020012112

***Rineloricaria aequalicuspis* Reis & Cardoso, 2001 (LL):**

1011001010 1102102011 1111210001 0111210101 1101101010 0120010110
0110101111 1111011202 020012?22

***Rineloricaria baliola* Rodriguez & Reis, 2008 (LL):**

10?1001010 1102101011 1111110001 0111210101 1100101001 0000010110
1101101102 1112011002 010112?22

***Rineloricaria cacerensis* (Miranda Ribeiro, 1912) (LL):**

1001001011 11??112?10 1111000001 0111210101 1101101?00 0100010110
0110101101 1011011002 010112?11

***Rineloricaria cadeae* (Hensel, 1868) (LL):**

1001001?10 1100112011 1111110001 011121?101 1100001000 0000010110
1110101101 1111011002 0100120?2

***Rineloricaria cf. kronei* (Miranda Ribeiro, 1911) (LL):**

10010?1010 1102002001 1111200?01 1111210101 1101101011 0120010110
0110101111 1112011002 0100121?2

***Rineloricaria cf. lima* (Kner, 1853) (LL):**

1001001011 11?2010010 1111000001 111121?101 1100101001 01?0010110
1110101111 1112011002 020112?11

***Rineloricaria cubataonis* (Steindachner, 1907) (LL):**

10010?1010 1102002001 ?101000001 1111210101 110110100? 01?0010110
0110101111 1112011002 020012??0

***Rineloricaria formosa* Isbrücker & Nijssen, 1979 (LL):**

1??10??01? ?1?1112??0 1111200001 ?01121?101 1101101000 0000010110
1100101101 1012011202 010012?21

***Rineloricaria hasemani* Isbrücker & Nijssen, 1979 (LL):**

1011000010 1102102001 1111000001 1011210101 1111101000 01?0010110
1110101111 1112011002 0100121?2

***Rineloricaria heteroptera* Isbrücker & Nijssen, 1976 (LL):**

10?10?1010 11020020?1 ?111000001 1011210101 110110100? 01?0010110
1110101111 1112011002 0100121??

***Rineloricaria jubata* (Boulenger, 1902) (LL):**

1??11??01? ?1?2101??1 1101210001 0011210101 1111?01000 0000010110
1010101111 1011011002 020012?22

***Rineloricaria lanceolata* (Günther 1868) (LL):**

10010?0010 1102012?01 1111000?01 1111210101 1101101011 0100010111
0010101111 1111011002 010012???

***Rineloricaria latirostris* (Boulenger 1900) (LL):**

10?10?101? 1102012?11 1111100001 111121?101 1101101011 0100010110
0010101111 1112011002 010112??2

***Rineloricaria malabarbai* Rodriguez & Reis, 2008 (LL):**

1??10??01? ?1?2000??1 ?011210001 001?210101 10?1?01010 0?20010110
1?0101111 1112011002 010012112

***Rineloricaria maquinensis* Reis & Cardoso, 2001 (LL):**

10010?1010 1101101011 1011110001 0011211101 1101001011 0120010110
0110101111 1112011002 010012112

***Rineloricaria microlepidogaster* (Regan, 1904) (LL):**

1011101010 2102101011 ?011010001 0111211101 1101101011 0100010110
1110101101 1112011002 0100121?2

***Rineloricaria parva* (Boulenger, 1895) (LL):**

1001001011 110?10101? 1111100001 0111210101 1110001010 0100010110
1110101111 1011011002 010112?11

***Rineloricaria pentamaculata* Langeani & de Araujo, 1994 (LL):**

1??10??01? ?1?2102??1 1011200001 0011210101 1101101010 0?20010110
1111101101 1112011002 0100121?2

***Rineloricaria quadrensis* Reis, 1983 (LL):**

1?010??01? ?1?2102??? 11110?0001 0111?11101 1101?01010 0100010110
0110101111 111?011102 010112122

***Rineloricaria* sp. (LL):**

1??10??01? ?1?2111??1 1101200001 0011210101 1111?01010 0100010110
1100101101 1111011002 010012?21

***Rineloricaria strigilata* (Hensel, 1868) (LL):**

1?0100101? 11?2?02?1? 10?1100001 0111?10101 1?11101010 0100010110
0110101111 1112011002 010112112

***Rineloricaria zaina* Ghazzi, 2008 (LL):**

10011?1010 1?01101011 ?011000001 0011210101 1101101010 0100010110
0110101111 1112011002 010012112

***Schizolecis guentheri* (Miranda Ribeiro, 1918) (Hp):**

1001011110 010021??11 ?011100100 1010111100 1111201101 0100000000
0010100011 1000011210 020002??2

***Spatuloricaria evansii* (Boulenger, 1892) (LL):**

1?1120001? ?1?2111??1 0101100001 0110311101 1110101011 010?010111
0100101001 1012011102 010012102

***Spatuloricaria nudiventris* (Valenciennes, 1840) (LL):**

1011200000 ?102001011 0101100001 0110210101 1100101001 0?11110121
0110101001 1012011102 010012112

***Spatuloricaria tui* Fichberg, Oyakawa & de Pinna, 2014 (LL):**

1?112??01? ???1110??? 0101000001 0110211101 1?11101011 0011010121
0110101001 1?12011102 010012112

***Sturisoma barbatum* (Kner, 1853) (LF):**

1?1100101? ?1?2011??? 11111?000? 0010111000 0100201001 0?10010110
1101001111 101?011002 010012122

***Sturisoma guentheri* (Regan, 1904) (LF):**

1?1?00?010 11?2001??? 1011210001 0010111000 1101201001 0000010110
1100101111 1011011002 010012112

***Sturisoma panamensis* (Eigenmann & Eigenmann, 1889) (LF):**

1??10??01? ?1?2001??? 1011210002 0110111000 0110101001 0000010110
1100101111 1011001002 010012??2

***Sturisoma robustum* (Regan, 1904) (LF):**

1?110??01? ???2001??? 10111?0001 0110111000 0110?01011 0?00010110
1100101111 1011011002 010012112

***Sturisoma rostratum* (Spix & Agassiz, 1829) (LF):**

1?11001010 11?2001?11 101121?002 0010111000 1110101001 0010010110
1101001111 10110?1002 010012??2

***Sturisoma tenuirostre* (Steindachner, 1910) (LF):**

1011001010 1102011011 1111210001 0010111000 1101101001 0?10010110
1100001112 1011001002 010002102

***Sturisomatichthys leightoni* (Regan, 1912) (LF):**

1001201010 1102002011 11?1210001 0011?11000 0111101001 0000010110
1110001111 1012011002 010012???

APPENDIX D. Data matrix used for the parsimony analyses. A=0&1; B=0&2;
C=1&2; D=1&3; E=2&3; “?”=Missing data/non applicable characters. Species are
listed in alphabetical order.

***Acestridium discus* Haseman, 1911:**

1001001101 012010D01A A011000100 0A00101100 1101201111 0100000000
1010100002 000010?11 20002??01 1111120000 C0?A00?000 ?1A100A100
A00121001 111?000121 211000A20A

***Ancistrus* sp.:**

100101020A CA0201C?11 102121010C 0110211010 011010A000 002100010A
0121001011 0000?1212 ?0002??2A 101?010010 C211200A11 01120A1021
20012A100 0001011101 A0110?A100

***Apistoloricaria ommation* Nijssen & Isbrücker, 1988:**

1?010??01? ?1?2B01??1 01111A000A 0111211101 1001101001 0100010010
0100101111 012011102 111121211 1121?10110 0111010111 1110010020
00?001000 0001?00111 1010000101

***Aposturisoma myriodon* Isbrücker Britski Nijssen & Ortega, 1983:**

1??A01?01? ?1?2001??1 1101210002 0011211000 0110201110 0120010110
1111101111 011011001 100021?2? 1112?10010 2110201101 1011000021
00?011000 0001?11121 201001C201

***Astroblepus longifilis* (Steindachner, 1882):**

0????????? ??2110??1 010110000? 1110311000 0101110001 1121000110
0120001010 112011001 11112??00 1001010000 021010?100 ?110100022
?11121010 0?01100101 001000?000

***Brochiloricaria macrodon* (Kner, 1853):**

1?2121001? ?1?2011??1 0111100001 1110310101 1010101001 0021001122
1110101012 012111102 11112122? 1????10??0 ??1???0111 11100???20
00?001000 0001??0121 1010000101

***Brochiloricaria* sp.:**

1?0121101? ?0?2111??1 0101100001 1110211101 1011201011 0120010010
0100101002 002001102 11112122? 1????10??0 ??1???0111 11100???20
00?001000 0001??0121 1010000101

***Chauliocheilos saxatilis* Martins, Andrade, Rosa & Langeani, 2014:**

1100010001 1000211011 10110?0100 10A0111100 1001101001 0?00000101
1120001001 002010?20 10002??1? 1????20?00 ????????01 ?1?200?100
10?121001 111???0121 A?1000A200

***Corumbataia cuestae* Britski, 1997:**

101A210000 210000C?00 0001000100 1110111100 11A1201011 1100110000
0020000000 000011200 10000??1? 11?1110?00 22?121?101 ?1?201A10?
10?121001 111??10121 011000A200

***Corydoras aeneus* (Gill, 1858):**

0001101102 0000113?11 0100000101 1101311000 0101210111 0A31000111
1001001010 002011001 111111?00 0?0?00?000 021011?101 1110100022
210111010 010?000100 000010A000

***Crossoloricaria* (=Rhadinoloricaria) bahuaja Chang & Castro, 1999:**

A1??121?00? ?1?0102??0 0111000002 0111211101 1001001111 0110010010
1000101010 112011100 111111?1A 1111010A10 A111000111 11100A0020
00?001000 0001?00111 1010000101

***Crossoloricaria variegata* (Steindachner, 1879):**

A1?010??01? ?1?2011??1 0111100001 1110211101 1001101001 0100010111
0110101011 012011102 011121?2A 1111010A10 1111000111 11100A0020
00?001000 0001?00111 1010000101

***Cteniloricaria platystoma* (Günther, 1868):**

A1?11211010 11?2A02?00 1111000102 0000211A00 1111C01110 0000010111
 1111A01111 011011201 11002102? 1????10??1 C?1??00111 1111010021
 00?011000 0001??0101 1010012201

***Curculionichthys insperatus* (Britski & Garavello, 2003):**

1110B10010 110020C10A 1011010100 00A0CA1100 1101B01101 01000A0000
 A1C0000001 0000112A0 10000??20 11?1110000 21?121?1AA ?10100A100
 00?121001 111??10121 A110000200

***Dasylicaria filamentosa* (Steindachner, 1878):**

A1?1100101? ?1?2012??1 0111110011 0110310101 1100101001 0010011111
 1111101112 001011002 11112??21 1??2?101?0 1?1?2?0111 11100???20
 00?001000 0001??0121 1010000101

***Dasylicaria latiura* (Eigenmann & Vance, 1912):**

A1?1100101? ?1?2011??1 0111110011 0110210101 1100101001 0021011111
 1111101112 001011102 11112??21 1??2?101?0 1?1?2?0111 11100???20
 00?001000 0001??0121 1010000101

***Dekeyseria scaphirhynchus* (Kner, 1854):**

10?1A10010 20020A2?11 1021210A02 0010211010 0111101011 0A30000101
 0121001011 000011212 10002?02A 101?010010 C211210111 01120A1021
 20012A100 0001011101 00110?A100

***Delturus brevis* Reis & Pereira, 2006:**

0??12??01? ?1?2011??0 1101000102 0110201000 0110200011 0130011111
 1111011011 0000110?2 10002?021 1011010020 A100C10111 011100102A
 210121000 0001000101 0010001010

***Delturus carinotus* (La Monte, 1933):**

0??????0?? ?1?2111??0 1101001102 0110201000 0110100011 0101011111
 1111011011 0000110?2 10002?021 1011010020 A100110111 011100102A
 210121000 0001000101 0010001010

***Dentectus barbarmatus* Martín Salazar Isbrücker & Nijssen, 1982:**

10A1011010 1002101001 01011A0001 0111211101 1A11101010 0100010110
 1010101111 012011102 111121221 1120?10110 0211110111 1110010020
 00?001000 0001?00121 10100A0101

***Epactionotus bilineatus* Reis & Schaefer, 1998:**

1100010000 1100001?00 1011000100 0010101000 0001201011 0100000001
 0120000001 000011200 20000??1? 11?1110?00 22?111?101 ?1?201A100
 10?021001 111??00111 A11000A200

***Eurycheilichthys pantherinus* (Reis & Schaefer, 1992):**

A?10010000 01?0111?10 0011000100 0100101100 1001201000 0100000000
 0010100001 000011200 10000??10 1011110?00 221111?100 010200A10?
 A0?0210A1 111??00111 0A1000A200

***Farlowella amazonum* (Günther, 1864):**

A10AA00000A 1101102010 0001000101 0010111000 1001201000 0100010010
 0010101011 012011002 100021021 111201001A 2111201101 1011000020
 00?010000 0001?1?121 2010011201

***Farlowella henriquei* Miranda Ribeiro, 1918:**

1??A2??01? ?1?1112??0 1001200101 0010111000 10A1201000 0100010100
 1010101001 011011002 100021021 1112010011 2111201101 1011000020
 00?010000 0001?1?121 2010011201

***Farlowella nattereri* Steindachner, 1910:**

1??A2??00? ?1?1001??0 00A1000101 0010111000 1001201000 0100010110
 0010101011 011011002 100021021 1112010011 2211201101 1011000020
 00?010000 0001?1?121 2010011201

***Farlowella oxyrryncha* (Kner, 1853):**

A101A000000 1101002000 0001200101 0000111000 1101101110 0100010000
 0010101011 012011002 100021021 1112010011 2211201101 1011000020
 00?010000 0001?1?121 2010011201

***Farlowella paraguayensis* Retzer & Page, 1997:**

10AA000000 1101002000 0001200101 0010111000 1101101110 0100010000
 0010101011 011011002 100021021 1112010011 2211201101 1011000020
 00?010000 0001?1?121 2010011201

***Farlowella reticulata* Boeseman, 1971:**

A1??A2??00? ?1?2002??0 0001010101 0010111000 1111201000 0A00010110
 1010101011 011011002 100021021 1112010011 2C11201101 1011000020
 00?010000 0001?1?121 2010011201

***Farlowella schreitmuelleri* Ahl, 1937:**

1??A2??01? ?1?1001??0 1001210101 0010111000 1101201010 0100010010
 0010101011 011011002 200021021 1112010011 2211201101 1011000020
 00?010000 0001?1?121 2010011201

***Farlowella smithi* Fowler, 1913:**

1?0A20001A 11?1001?10 1001200101 0010111000 1001201110 0100010010
 1010101011 011011002 100021021 1112010011 2211201101 1011000020
 00?010000 0001?1?121 2010011201

***Fonchiiloricaria nanodon* Rodriguez, Ortega & Covain, 2011:**

1011210010 2102012001 1011100001 0111310101 1101200000 0120011100
 1121101112 111011101 100021?1? 1????10??0 ??1???0111 11100???20
 00?001000 0001???121 1010000101

***Furcodontichthys novaesi* Rapp Py-Daniel, 1981:**

1??12??00? ?1?2100??0 0101000001 0111211101 1011101110 1110010A10
 1000101111 112011200 111111121 1121?10110 1111010111 1110000020
 00?001000 0001?11121 101000A101

***Gymnotocinclus anosteos* Carvalho, Lehmann A. & Reis, 2008:**

1101210001 1000201?11 1011010100 00A0111000 A001101001 0100000001
 0120100001 000011211 ?0000??2? 11?1A20?00 22?021?10A ?1?200A100
 10?121001 1111?00121 101000A200

***Harttia carvalhoi* Miranda Ribeiro, 1939:**

1?AA011000 11?1002011 1001100101 0010211100 1111101010 0130010110
 0110101111 011011201 200021020 1111010011 221AC01111 111201AA21
 000011000 000101?101 A010012201

***Harttia duriventris* Rapp Py-Daniel & Oliveira, 2001:**

1?11011010 11?1101011 1001100101 0000211100 111A201110 0100000010
 1110101111 011011201 200021010 1111010011 2210201111 1112010A21
 000011000 00010??101 1010012201

***Harttia loricariformis* Steindachner, 1877:**

1?11011000 11?2001011 1111210101 0010211100 1110201010 0130000110
 1111101111 011011201 200021020 1111A10011 2C1AC0111A 11120A0A21
 000011000 000100?101 1010012201

***Harttia novalimensis* Oyakawa, 1993:**

1011011010 1102001011 1001100101 0000211100 1111101010 00E0000010
 0110101111 012011201 200021020 1111010011 2210C01111 1112010A21
 000011000 00010??101 1010012201

***Harttia punctata* Rapp Py-Daniel & Oliveira, 2001:**

A1?1101101? ?1?1001??1 1001210101 0000211000 01112A1110 0100010010
 0110100001 010011201 200021?20 1111A10011 221A?01111 1112010A21
 A00011000 00010??101 1010012201

***Harttiella crassicauda* (Boeseman, 1953):**

A1?0101101? ?1?0011??1 1111100001 0010211100 1101201000 0100010110
 1110101011 011011201 201021210 111?010011 2?10?01111 1111010021
 000011000 00010??101 1010012201

***Hemiodontichthys acipenserinus* (Kner, 1853):**

1001001011 1102111??0 0101000001 0A11210101 1001201100 0010010110
 1000101111 00A011202 111121221 1111?10110 A010C00111 1110000020
 00?001000 0001??0121 2010000101

***Hemiodontichthys* sp.:**

1??11??010 11?2110??0 0101000001 0011210101 1001101100 0010010110
 1010101111 001011202 111121221 1?11?10110 0010100111 1110000020
 00?001000 0001??0121 2010000101

***Hemipsilichthys nimius* Pereira, Reis, Souza & Lazzarotto, 2003:**

0?11010010 21?2212?11 1001011102 1010201000 0110100001 0121011111
 1111001011 0010?1012 10002??01 1021010020 C21AC1011A 011C0A102A
 210121000 0001000101 0010001110

***Hisonotus francirochai* (Ihering, 1928):**

1100011010 1100213?10 1011000100 00A01A1100 1101201111 0100000000
 0110000001 000011211 10000??20 11?1111000 22?111?10A ?10101A100
 100021001 111?000111 A110000200

***Hisonotus notatus* Eigenmann & Eigenmann, 1889:**

1101011010 110020C?10 A011000100 0000101000 1AA1101110 0100000000
 0110100001 000011210 10000??20 11?1110000 21?111?10A ?101011100
 100021001 111?000121 A110000200

***Hypoptopoma inexpectatum* (Holmberg, 1893):**

1010001102 1001011100 0011010002 00001A1000 11A01A1111 0100000A00
 1000000012 000000?11 00002??00 11?CAC0000 CC?A00?10A ?1A2001A00
 A00121001 111?010121 A11000A200

***Hypostomus ancistroides* (Ihering, 1911):**

10C111010A 2002201?11 1021210102 0110211000 A110101001 0000000111
 00C1001011 000011212 10002??10 101?010010 C211210111 0112001021
 200120100 0001011121 A01001A100

***Hypostomus nigromaculatus* (Schubart, 1964):**

1021010100 2001202??1 0011210101 0110C11000 0111101011 0A01000110
 0121001011 0010?1212 ?0002??10 101?010010 C211210111 0112001021
 200120100 0001011121 001001A100

***Hypostomus regani* (Ihering, 1905):**

1021010100 2002202?11 1021210102 0010211000 0110101011 0021000111
 0021001011 000001212 10002??00 101?010010 C211210111 0112001021
 200120100 0001011121 001001A100

***Hypostomus variipictus* (Ihering, 1911):**

1021010100 2002202?11 1021210102 0010211000 0110101011 0021000111
 0121001011 000001212 10002??00 101?010010 C211210111 0112001021
 200120100 0001011121 001001A100

***Isbrueckerichthys duseni* (Miranda Ribeiro, 1907):**

A??12??01? ?A?1102??0 0001010100 0111211010 0111101010 0101010000
 0121101012 000011200 20000??10 112?110010 C210C1011A 011C0AA111
 000021000 0010010111 001000A300

***Ixinandria steinbachi* (Regan, 1906):**

10A10A1010 2101101001 1011110001 0011211100 1110101110 0100010110
 0110101011 001011002 100121220 1?22010010 A110A?0111 1110000021
 000001000 0001000111 1010000201

***Kronichthys heylandi* (Boulenger, 1900):**

1210110A10 2001212001 1011110101 00A01110A0 0111101111 0100000100
 1010100001 00001121A 20002??10 1012A10000 C21ACA011A 010C001111
 100121000 0010000101 001000A200

***Kronichthys subteres* Miranda Ribeiro, 1908:**

1011010000 1001202?01 1011110100 00A0101010 1101101110 0100000100
 1011000011 000001210 2000B??10 1012110000 2C1ACA0A1A 01A10A1111
 100121000 0010000101 001000A200

***Lamontichthys filamentosus* (La Monte, 1935):**

A?112??01? ?1?2002??1 1011200101 011A211000 0111101000 0100000110
 1111001011 102011101 200121?20 1111A10011 C21A101111 1111000021
 100011010 0001010121 1010012201

***Lampiella gibbosa* (Miranda Ribeiro, 1908):**

A1111011000 2100202001 0001100100 0000101100 0101101110 0100000001
 0110100010 000011210 20000??0? 11?11C0?00 22?121?101 ?1?200A100
 10?121001 1111?00111 111000A200

***Limatulichthys griseus* (Eigenmann, 1909):**

1001001000 1102100001 010110000C 0111310101 1100101011 0110010110
 1101001011 112011202 011121121 1?20A10110 1?1?110111 1110000020
 00?001000 0001?11121 1010000101

***Limatulichthys petleyi* (Regan, 1904):**

1??10??01? ?1?2100??1 0101100001 0111310101 1100101011 1100010110
 1101001011 012011202 011121121 1?20?10110 1110110111 1110000020
 00?001000 0001?11121 1010000101

***Lithogenes villosus* Eigenmann, 1909:**

0????????? ???1211??1 1121211102 1010211100 110?101001 0121011011
 1120100001 111001110 21000?200 1011010000 02101??100 ?11010002?
 011???0?? ?00100101 001000?000

***Loricaria cataphracta* Linnaeus 1758:**

A1??100?01? ?1?2110??1 0011100001 1111310101 1111101001 1101111022
 0100101011 012011102 11112112A 1A2?0?0A10 1110010111 1110000020
 000001000 0001010121 1010000101

***Loricaria luciae* Thomas, Rodriguez, Carvallaro, Froehlich & Castro, 2013:**

1?1100101? ?1?2110??1 0001100001 1111310101 1A10101001 0021001122
 1110101001 012011102 111121C21 11200?0A10 1110110111 1110000020
 000001000 0001010121 1010000101

***Loricaria* sp.:**

1011001000 2112110010 1101200001 1111310101 1101101001 0A11011122
 A00A101012 012011102 111111101 11200?0A10 1110110111 1110000020
 000001000 0001010121 1010000101

***Loricariichthys acutus* (Valenciennes, 1840):**

1001101010 1102001001 A011200001 0111310101 1000C01011 0A10010A11
 1010101011 002011202 111121211 1120010A10 111A110111 1110000020
 000001000 0001011121 101000A101

***Loricariichthys anus* (Valenciennes, 1835):**

1001101010 2102002011 1011100001 0111310101 1100101011 1010010111
 1100101112 002011202 111111221 1120010110 C110210111 1110000020
 000001000 0001011121 101000A101

***Loricariichthys castaneus* (Castelnau, 1855):**

1?01101010 11?2101?11 A1111A0001 0111310101 1010201011 0030000111
 1111101101 002011002 111121221 1120010110 1110110111 1110000020
 000001000 0001011121 101000A101

***Loricariichthys derbyi* Fowler, 1915:**

1?01101010 21?2101?11 A001100001 0011310101 11A0001001 1A10110111
 101A001111 002011202 111111211 1120010110 A110110111 1110000020
 000001000 0001011121 101000A101

***Loricariichthys melanocheilus* Reis & Pereira, 2000:**

1001101010 1102002011 10111AA001 0111310101 1110201001 0110010111
 1100001112 002011202 111121221 1120010110 A110110111 1110000020
 000001000 0001011121 101000A101

***Loricariichthys platymetopon* Isbrücker & Nijssen, 1979:**

1?11101010 21?2002?A1 1011200002 0111310101 1100101001 1010110111
 100A101112 002011202 01111A201 1020010110 111A110111 1110000020
 000001000 0001011121 101000A101

***Loricariichthys rostratus* Reis & Pereira, 2000:**

1?0110101? ?A?2102??1 10111A000C 0111310101 111A201011 001001011A
 1000101111 002011002 1111C1221 1120010110 A110110111 1110000020
 000001000 0001011121 101000A101

***Loricariichthys* sp.:**

1?01101011 11?2101?01 001121000C 0011310101 1110101011 001001011A
 1110101111 002011200 111121221 1120010110 A11??10111 1110000020
 000001000 0001011121 101000A101

***Megalancistrus parananus* (Peters, 1881):**

1021010110 2A02211?11 1021210102 00102A10A0 0110101001 0021000111
 A121001A11 0010?1212 ?0002??10 111?010010 C211210111 01120A1021
 20012A100 0001011111 00100?A100

***Metaloricaria paucidens* Isbrücker, 1975:**

1??12??01? ?1?2100??1 1101100002 0111310101 1110101011 0021011111
 1120101012 102011102 111121221 11????0??0 ??10??0111 11100??020
 00?011000 0001??0121 1010000101

***Microlepidogaster perforata* Eigenmann & Eigenmann, 1889:**

1100001000 1100201?01 1011000100 0010111110 1001101001 0100000000
 0010100011 000011210 2000B??2? 1121111000 22?1A1?10A ?1?201A10A
 10?021001 110??00121 0110000200

***Neoplecostomus corumba* Zawadzki, Pavanelli & Langeani, 2008:**

AA01A210001 1A01211?12 1011210100 1011211010 0001101001 11B1101000
0120101012 101011000 20000??10 1011010000 ??1?21011A 0111011111
100121000 0010011121 0010000200

***Neoplecostomus langeanii* Roxo, Oliveira & Zawadzki, 2012:**

1011210001 1101211?12 1001010100 1011211010 0001101001 1100101000
01201010A2 101011000 20000??10 101?010000 ??1?21011A 0111011111
100121000 0010011121 0010000200

***Neoplecostomus microps* (Steindachner, 1877):**

1111210001 2001011?10 1011000100 1111211010 0011101001 1100101000
0120101012 100011100 20000??00 1011010000 A21021011A 01110A1111
100121000 0010011121 0010000200

***Neoplecostomus ribeirensis* Langeani, 1990:**

1011210000 1A01201?12 1001B00100 1111211010 0001101001 1100101000
0120101012 101011000 20000??20 1011010000 ??1021011A 0111011111
A00121000 0010011121 0010000200

***Neoplecostomus selenae* Zawadzki, Pavanelli & Langeani, 2008:**

1011210010 2001212?10 0001010100 1111211000 0000101001 1101101001
A120101012 100011100 20000??00 1011010000 ??1?21011A 0111011111
100121000 0010011121 0010000200

***Neoplecostomus yapo* Zawadzki, Pavanelli & Langeani, 2008:**

1011210000 200101C?10 1011010100 1011211010 0001101001 1101101000
0120101012 1000110A0 20000??20 101?010000 ??1?21011A 0111011111
100121000 0010011121 0010000200

***Otocinclus affinis* Steindachner, 1877:**

1000001011 1100002?11 A001A00101 0000001000 0101001111 0100000000
1010000010 000010?10 10002??01 10121C0000 A20100?00A 01A2001100
C00021001 111?010121 A110000200

***Otothyris lophophanes* (Eigenmann & Eigenmann, 1889):**

1110001001 1A10012111 0001100100 0010011100 1101001110 0100000100
1000000011 000010?00 10002??0? 10?1121?00 21?121?A01 ?1?10A1100
10?0C1001 111??00111 011000A200

***Otothyris rostrata* Garavello Britski & Schaefer, 1998:**

A1110001011 1110012?10 0001100100 0010011100 11A1001100 0100000101
1000000010 000000?10 10002??B? 10?1121?00 22?A21?101 ?1?1011100
10?0C1001 111??00111 011000A200

***Otothyropsis marapoama* Ribeiro Carvalho & Melo, 2005:**

A1000011010 1100002?10 0001000100 0000001000 1101001111 0100000000
1010000011 000010?10 10002??2? 11?1121?00 21?1A1?101 ?1?10A1100
10?021001 111??00121 011000A200

***Oxyropsis wrightiana* Eigenmann & Eigenmann, 1889:**

A1001001102 0000201?10 0011010101 0000001000 11A1001111 0100000A00
 1000100012 000000?10 10002??00 11?C120000 1??000?00A ?11C0AAA00
 A0?121001 111??10101 111000A20A

***Paraloricaria vetula* (Valenciennes, 1835):**

A1011101010 1102000011 1011100001 0111310101 1101201001 0021111122
 1110101012 012111102 10112?221 11????0??0 ?110??0111 11100??020
 00?001000 0001??0111 1010000101

***Pareiorhaphis cameroni* (Steindachner, 1907):**

1011210000 20?0012?11 A001110100 0110201010 0101101011 0100100000
 0120100011 000001200 20000??2? 1111110000 2?0?21011A 011C011111
 A00121000 0010010101 001000A300

***Pareiorhaphis hystrix* (Pereira & Reis, 2002):**

1011210000 200C012?11 1001110100 11102A1010 0111101011 0100100000
 012100A111 0000?121A 20000??21 1111110000 220021011A 011201A111
 100121000 0010010101 001000A300

***Pareiorhina carrancas* Bockmann & Ribeiro, 2003:**

1000211101 0100012?00 1001010100 0010101010 1101101011 A100100000
 0010000011 000011210 20000??2A 1111110000 2?1A2101AA 0111001111
 100021000 0010010101 001000A300

***Pareiorhina rudolphi* (Miranda Ribeiro, 1911):**

1011010000 1100002?00 1001010100 0010101010 1111101011 0100100000
 1010000001 000011200 20000??2A 1111110000 C21AC101AA 01AC0AA111
 A00021000 00100A0101 001000A300

***Parotocinclus jumbo* Britski & Garavello, 2002:**

1000001011 0001A02?10 0001100100 0110111000 1111101111 0100000A00
 0010000010 000011211 20000??20 1021110000 221011?10A 01AC001100
 00012100A 111?010111 0A1000A200

***Parotocinclus maculicauda* (Steindachner, 1877):**

A1111211010 1110002000 A0010A0101 0100101110 1001001111 0100A00000
 0010100011 000011200 20000??20 1A111C0000 221111?10A 010C001100
 100121001 111?000121 011000A200

***Parotocinclus prata* Ribeiro Melo & Pereira, 2002:**

A1010011011 1001002000 1001A10100 01A0111000 1A11A01111 0100000000
 1010100011 000011211 20002??20 1A211C0000 210A11?10A 01AC0A1100
 100121001 111?010101 011000A200

***Pimelodus argenteus* Perugia, 1891:**

0?31010010 20?2110?01 0100100001 1100310000 1011101001 0121110122
 1010102111 012101001 00111??0? ?????????? ?????0????0 ?2?01????2
 20?121?10 0???????000 0000102?00

***Pimelodus maculatus* Lacepède, 1803:**

0?31010010 20?2110?01 0100100001 1100310000 1001101001 0121110122
 1011102111 012101001 00111???0? ?????????? ?????0???0 ?2?01????2
 20?121?10 0???????000 0000102?00

***Planiloricaria cryptodon* (Isbrücker, 1971):**

1?110??01? ?1?2111??1 0101110001 1110210101 1000101001 0011010111
 0100101011 012011102 111121221 1120?10110 1211010111 1110010021
 00?001000 0001?00111 0010000101

***Plesioptopoma curvidens* Reis, Pereira & Lehmann A., 2012:**

1?00010001 10?1202?01 1A01010100 0100111000 0011101011 0100000100
 1010100011 000011211 20002??00 101?1C0?00 221021?101 0112001100
 10?121001 111??A01C1 001000A200

***Proloricaria prolixa* (Isbrücker & Nijssen, 1978):**

A1?01001000 11?2110?01 0011100001 1111310101 1111101011 1101111121
 0100101011 012011102 10111??21 11220?0A10 1110010111 1110000020
 00?001000 0001?10121 1010000101

***Pseudohemiodon laticeps* (Regan, 1904):**

1011011010 1A02111001 0101110001 1110210101 101A101001 0010100111
 1100101001 002011002 11112?221 1110?10A10 A211010111 1110010020
 00?001000 0001?00121 1010000101

***Pseudohemiodon platycephalus* (Kner, 1853):**

1?11011010 11?2111?11 01011A0001 1110E10101 1000101001 0010110111
 1100101111 002011002 11112?221 1110?10A10 0211010111 1110010020
 00?001000 0001?00121 1010000101

***Pseudohemiodon* sp.:**

1?1101101? ?1?2011??1 0101110001 1110210101 1011201001 0010100111
 1100101111 002011002 11112?221 1110?10A10 1C11010111 1110010020
 00?001000 0001?00121 1010000101

***Pseudoloricaria laeviscula* (Valenciennes, 1840):**

A1???10??01? ?1?2110??1 0101000002 0111310101 1010101011 0101010111
 1110101011 102011102 01112?121 1A10010010 A111A10111 1110000020
 00?001000 0001?11121 1010000101

***Pseudoloricaria punctata* (Kner, 1854):**

A1?010??01? ?1?2100??0 0101000001 0111E10101 1111101111 0100010110
 1110101111 10201120C 111120111 1120010110 1110010111 1110000020
 00?001000 0001?11121 1010000101

***Pseudopimelodus bufonius* (Valenciennes, 1840):**

0?112??0?? ?1?2B10??1 0111010001 1010311000 0110201001 0121100122
 1100101101 000101201 00000??0? ?????????? ?????0???0 ?2?00????2
 20?121?10 0???????000 0000102?00

***Pseudopimelodus mangurus* (Valenciennes, 1835):**

0?112??0?? ?1?2B11??1 0121010001 1010311000 0110201001 0121100122
 1100101101 000101201 00000??0? ?????????? ?????0???0 ?2?00????2
 20?121?10 0???????000 0000102?00

***Pseudotocinclus tietensis* (Ihering, 1907):**

1011001001 1100212100 1001110100 0010111010 1011A01001 0100000100
 11C0000011 000011211 20002??01 11?C1C0?00 221A21?101 01120AA10A
 A0?121001 111??001C1 A01000A200

***Pseudotothyris obtusa* (Miranda Ribeiro, 1911):**

AA1010011A2 011000E010 0001A00100 0A10011100 11A1001101 0100000A01
 1010100010 00001A?10 10002??0? 11??121100 21?021?101 ?1?1011100
 00?021001 111??00111 011000A200

***Pyxiloricaria menezesi* Isbrücker & Nijssen, 1984:**

1??10??01? ?1?2100??1 1101100001 1111310101 1101101101 0000010110
 0110101102 002011102 10112?111 1?????0??0 ?110??0111 11100?0020
 00?001000 0001??0121 1010000101

***Reganella depressa* (Kner, 1853):**

A10010010?0 ?A02101?01 0101100000 0111310101 1001111011 0020010A10
 1000101111 001011202 111120201 1120?10110 0111010111 11100??020
 00?001000 0001?10121 2010000101

***Rhadinoloricaria* sp.:**

1?01001011 11?2111?00 01A1100001 0111211101 1001101001 0120010110
 1110101111 112011102 10012?201 111??10110 0111100111 1110010020
 00?001000 0001?00111 2010000101

***Rhinelepis aspera* Spix & Agassiz, 1829:**

A1??10??10? ?1?2211??1 1021210002 0010211000 0100101001 0000001111
 1021011011 001011212 10012??01 1?1?011010 2210??0?1A ?11?0011?0
 200021100 0001001111 0A100?C300

***Rhinolekos britskii* Martins, Langeani & Costa, 2011:**

1000011001 1100B11?01 1A11000100 0A10111010 1001101001 0100000A01
 0010100001 000011210 20000??2? 11?1111?00 22?111?101 ?1?201110A
 10?021001 111??00121 0A1000A200

***Ricola macrops* (Regan, 1904):**

1?1101101? ?1?2111??1 00?1110001 0110310101 1010101001 0111011122
 1111101102 012011102 101120221 1?????0??0 ?110??0111 11100??02?
 00?001000 0001??0121 1010000201

***Rineloricaria cacerensis* (Miranda Ribeiro, 1912):**

1001001011 11?C112?10 1111000001 0111210101 1101101A00 0100010110
 0110101101 011011002 10112?111 1?2??10?10 0110??0111 1110000020
 100001000 0001010121 1010000201

***Rineloricaria cf. lima* (Kner, 1853):**

A1001001011 11?2010010 1111000001 111121A101 1100101001 01B0010110
 1110101111 112011002 20112?111 1?22?10010 1110200111 1110000020
 100001000 0001010121 1010000201

***Rineloricaria formosa* Isbrücker & Nijssen, 1979:**

A1???10???01? ?1?1112???0 1111200001 A01121A101 1101101000 0000010110
 1100101101 012011202 10012?211 1122?10110 0110100111 1110000020
 100001000 0001010121 1010000201

***Rineloricaria parva* (Boulenger, 1895):**

A1001001011 110C10101A 1111100001 0111210101 1110001010 0100010110
 1110101111 011011002 10112?111 1?2???10??? ?110???0111 1110000020
 100001000 0001010121 1010000201

***Rineloricaria quadrensis* Reis, 1983:**

1?010???01? ?1?2102???A 11110A0001 0111E11101 1101A01010 0100010110
 0110101111 11C011102 101121221 1?2???10??? ?110???0111 1110000020
 100001000 0001010121 1010000201

***Rineloricaria strigilata* (Hensel, 1868):**

A1?0100101A 11?2A02?1A 10A1100001 0111E10101 1A11101010 0100010110
 0110101111 112011002 101121121 1122010110 1110C?0111 111000A020
 100001000 0001010121 1010000201

***Schizolecis guentheri* (Miranda Ribeiro, 1918):**

1001011110 010021C?11 A011100100 1010111100 1111201101 0100000000
 0010100011 000011210 20002???20 11?111A000 22?AC1?10A ?10C0A1100
 000021001 111?000121 0A1000A200

***Scleromystax barbatus* (Quoy & Gaimard, 1824):**

0001111101 0001000?11 0100100101 1101311000 110?101001 01A0010111
 1001001010 002011001 111111?10 0?0?00?000 021011?101 1110100022
 210111010 010?000100 000010A000

***Spatuloricaria evansii* (Boulenger, 1892):**

1?1120001? ?1?2111???1 0101100001 0110311101 1110101011 010A010111
 0100101001 012011102 100121021 102C?10110 121010011A 1110000020
 00?001000 0001?10111 1010000201

***Spatuloricaria nudiventris* (Valenciennes, 1840):**

1011200000 ?102001011 0101100001 0110210101 1100101001 0A11110121
 0110101001 012011102 100121121 102C?101?0 1210100111 1110000020
 00?001000 0001?10111 1010000201

***Spatuloricaria tuira* Fichberg, Oyakawa & de Pinna, 2014:**

A1?112???01? ?A?1110???1 0101000001 0110211101 1A11101011 0011010121
 0110101001 A12011102 100121121 1022?101?0 1210200111 1110000020
 00?001000 0001?10111 1010000201

***Sturisoma barbatum* (Kner, 1853):**

1?1100101? ?1?2011??1 11111A000C 0010111000 0100201001 0A10010110
1101001111 01C011002 100121220 1111A10011 211A201111 111100002A
100011000 00010?1121 2010011201

***Sturisoma guentheri* (Regan, 1904):**

1?1A00A010 11?2001??1 1011210001 0010111000 1101201001 0000010110
1100101111 011011002 100121120 1111A10011 211A201111 111100002A
100011000 00010?1121 2010011201

***Sturisoma panamensis* (Eigenmann & Eigenmann, 1889):**

1??10??01? ?1?2001??1 1011210002 0110111000 0110101001 0000010110
1100101111 011001002 10012??20 1111?10011 2110201111 111100002A
100011000 00010?1121 2010011201

***Sturisoma robustum* (Regan, 1904):**

1?110??01? ?A?2001??1 10111A0001 0110111000 0110B01011 0A00010110
1100101111 011011002 100121120 1111010011 2C1A201111 1111000021
100011000 00010?1121 2010011201

***Sturisoma rostratum* (Spix & Agassiz, 1829):**

1?11001010 11?2001?11 101121A002 0010111000 1110101001 0010010110
1101001111 0110A1002 10012??20 1111A10011 2C11201111 1111000021
100011000 00010?1121 2010011201

***Sturisoma tenuirostre* (Steindachner, 1910):**

1011001010 1102011011 1111210001 0010111000 1101101001 0A10010110
1100001112 011001002 100021020 1111A10011 2?1A201111 111100002A
100011000 00010?1121 2010011201

***Sturisomatichthys leightoni* (Regan, 1912):**

1001201010 1102002011 11A1210001 0011E11000 0111101001 0000010110
1110001111 012011002 10012??C0 1111010011 221A201111 1111000020
100011000 0001011121 1010012201

APPENDIX E. List of characters analyzed (osteology and other external characters). All characters (52) were described, illustrated and discussed in previous studies, e.g., Schaefer, (1987, 1991), Py-Daniel (1997), Armbruster (2004), Paixão & Toledo-Piza (2009), Martins *et al.* (2014), Londoño-Burduano & Reis (2016), Pereira & Reis (2017), among others; the respective reference(s), for each character, is/are cited, between parenthesis, after the respective list of character states.

Mesethmoid

89. **Anterolateral expansion of the mesethmoid; $CI_2=0.12$, $RI_2=0.83$:** 0 Absent; 1 Present (Schaefer, 1987, 1991; Armbruster, 2004; Martins *et al.*, 2014; Rodriguez *et al.*, 2015; Londoño-Burduano & Reis, 2016; Pereira & Reis, 2017).

90. **Ventral condyle of the mesethmoid (mesethmoid disk); $CI_2=1$, $RI_2=1$:** 0 Absent; 1 Present (Schaefer, 1987, 1991; Py-Daniel, 1997; Armbruster, 2004; Rodriguez *et al.*, 2015).

91. **Position of the mesethmoid disk in relation to the anterior margin of the mesethmoid; $CI_2=0.09$, $RI_2=0.64$:** 0 Terminal, anterior; 1 Subterminal, nonterminal, posterior or remote (Schaefer, 1991; Py-Daniel, 1997; Armbruster, 2004; Paixão & Toledo-Piza, 2009; Martins *et al.*, 2014; Pereira & Reis, 2017).

92. **Type of articulation between the metapterygoid and the lateral ethmoid; $CI_2=0.16$, $RI_2=0.72$:** 0 Absent, no articulation (*i.e.*, the metapterygoid does not contact the lateral ethmoid); 1 Via condyle, via a simple contact along its dorsal margin, or only along the posterodorsal region through an articulation surface; 2 Sutural (Schaefer, 1991; Py-Daniel, 1997; Pereira & Reis, 2017).

Lateral ethmoid

93. **Dorsolateral process of the lateral ethmoid; $CI_2=0.18$, $RI_2=0.76$:** 0 Absent; 1 Present, moderately developed, strut or spike; 2 Present, well developed, large wings (Schaefer, 1987, 1991; Py-Daniel, 1997; Martins *et al.*, 2014; Londoño-Burduano & Reis, 2016).

94. **Nasal capsule; $CI_2=0.50$, $RI_2=0.96$:** 0 Completely encased ventrally by the lateral ethmoid; 1 Open ventrally (Schaefer, 1998; Armbruster, 2004; Martins *et al.*, 2014; Rodriguez *et al.*, 2015; Pereira & Reis, 2017).

Compound pterotic

95. **Perforations of the compound pterotic; $CI_2=0.66$, $RI_2=0.87$:** 0 Absent; 1 Present, uniformly small; 2 Present, distinctly large, particularly towards the lateral margin of the bone (Schaefer, 1987, 1991; Py-Daniel, 1997; Armbruster, 2004; Martins *et al.*, 2014; Pereira & Reis, 2017).

Parietosupraoccipital

96. **Parietosupraoccipital; $CI_2=0.25$, $RI_2=0.57$:** 0 Not contributing to the dorsal portion of the swimbladder capsule; 1 Forming part of the dorsal wall of the swimbladder capsule (Schaefer, 1991; Ribeiro *et al.*, 2005; Martins *et al.*, 2014).

97. **Parietosupraoccipital crests; $CI_2=0.25$, $RI_2=0.88$:** 0 Absent or broad and rounded; 1 Present, tall and narrow (Py-Daniel, 1997; Armbruster, 2004; Martins *et al.*, 2014; Londoño-Burduano & Reis, 2016).

Infraorbitals

98. **Infraorbitals; $CI_2=0.50$, $RI_2=0.95$:** 0 Less than 6; 1 6; 2 More than 6 (Py-Daniel, 1997; Armbruster, 2004; Martins *et al.*, 2014).

Mandibular arc and jaw suspensorium

99. **Anterior process of the autopalatine; $CI_2=0.50$, $RI_2=0.95$:** 0 Absent; 1 Present (Py-Daniel, 1997; Martins *et al.*, 2014; Pereira & Reis, 2017).

100. **Metapterygoid channel; $CI_2=0.22$, $RI_2=0.84$:** 0 Absent; 1 Present, shallow, its depth much less than 50% of its length; 2 Present, deep, its depth about 50% of its length (Py-Daniel, 1997; Schaefer, 1998; Armbruster, 2004; Martins *et al.*, 2014; Londoño-Burduano & Reis, 2016).

101. **Suture/contact between the hyomandibula and the metapterygoid; $CI_2=0.12$, $RI_2=0.69$:** 0 Absent; 1 Present, small, contact between bones restricted, bones usually not contacting one another dorsally to suture; 2 Present, large, contact between bones complete, extending dorsally beyond the suture (Schaefer, 1987; Arratia, 1990; Py-Daniel, 1997; Martins *et al.*, 2014).

102. **Suture/contact between the hyomandibula and the prootic; $CI_2=0.20$, $RI_2=0.20$:** 0 Absent; 1 Present (Schaefer, 1998; Armbruster, 2004; Paixão & Toledo-Piza, 2009; Pereira & Reis, 2017).

103. **Suture/contact between the hyomandibula and the compound pterotic; $CI_2=0.10$, $RI_2=0.77$:** 0 Absent; 1 Present (Schaefer, 1987; Arratia, 1990; Py-Daniel, 1997; Armbruster, 2004; Paixão & Toledo-Piza, 2009; Martins *et al.*, 2014; Rodriguez *et al.*, 2015; Pereira & Reis, 2017).

104. **(Hyomandibula) Levator arcus palatini crest; $CI_2=0.11$, $RI_2=0.68$:** 0 Absent; 1 Present, short, low, poorly developed; 2 Present, tall, high, well-developed (Howes, 1983; Schaefer, 1991, 1998; Armbruster, 2004; Martins *et al.*, 2014; Rodriguez *et al.*, 2015; Londoño-Burduano & Reis, 2016; Pereira & Reis, 2017).

Opercular series

105. **Exposition of the preopercle; $CI_2=0.09$, $RI_2=0.76$:** 0 Not exposed; 1 Exposed, emergent to skin surface (Py-Daniel, 1997; Schaefer, 1997; Ribeiro *et al.*, 2005; Paixão & Toledo-Piza, 2009; Martins *et al.*, 2014).

106. **Ventral process of the preopercle; $CI_2=0.50$, $RI_2=0.95$:** 0 Absent or inconspicuous; 1 Present, well developed (Py-Daniel, 1997; Paixão & Toledo-Piza, 2009; Pereira & Reis, 2017).

107. **Preopercular canal; $CI_2=0.50$, $RI_2=0.50$:** 0 Absent; 1 Present (Schaefer, 1991; Py-Daniel, 1997; Martins *et al.*, 2014).

108. **Suprapreopercle; $CI_2=0.33$, $RI_2=0.94$:** 0 Absent; 1 Present (Py-Daniel, 1997; Armbruster, 2004; Martins *et al.*, 2014).

Hyoid arc and branchial skeleton

109. **Basibranchial 2; $CI_2=0.25$, $RI_2=0.57$:** 0 Absent or cartilaginous; 1 Present and ossified (Py-Daniel, 1997; Armbruster, 2004; Paixão & Toledo-Piza, 2009).

110. **Basibranchial 3; $CI_2=0.50$, $RI_2=0.96$:** 0 Absent or cartilaginous; 1 Present and ossified (Schaefer, 1987; Py-Daniel, 1997; Paixão & Toledo-Piza, 2009; Londoño-Burduano & Reis, 2016; Pereira & Reis, 2017).

111. **Branchiostegal rays; $CI_2=1$, $RI_2=1$** 1: 0 Less than 4; 1 4; 2 More than 4 (Py-Daniel, 1997; Armbruster, 2004).

112. **Interhyal; $CI_2=0.33$, $RI_2=0.66$** : 0 Absent; 1 Present (Py-Daniel, 1997; Armbruster, 2004; Rodriguez *et al.*, 2015; Pereira & Reis, 2017).

113. **Accessory process of the ceratobranchial 1; $CI_2=0.20$, $RI_2=0.88$** : 0 Absent; 1 Short, about 50% or less of the length of the ceratobranchial; 2 Long, more than 50% the length of the ceratobranchial, sometimes of the same length as the ceratobranchial (Schaefer, 1987; Py-Daniel, 1997; Armbruster, 2004; Martins *et al.*, 2014).

114. **Dorsal hypohyal; $CI_2=0.50$, $RI_2=0.80$** : 0 Absent or very reduced; 1 Present, well developed (Baskin, 1972; Reis, 1993; Py-Daniel, 1997).

Weberian apparatus and axial skeleton

115. **Ventral process of the complex centrum; $CI_2=0.14$, $RI_2=0.77$** : 0 Absent or short, not reaching the mesial tip of the rib of the sixth centrum; 1 Long, reaching the mesial tip of the rib of the sixth centrum (Armbruster, 2004; Martins *et al.*, 2014; Pereira & Reis, 2017).

116. **Bifid neural spines; $CI_2=0.50$, $RI_2=0.96$** : 0 Absent or reduced; 1 Present and well developed (Py-Daniel, 1997; Martins *et al.*, 2014; Pereira & Reis, 2017).

117. **Bifid hemal spines; $CI_2=0.50$, $RI_2=0.97$** : 0 Absent or reduced; 1 Present and well developed (Py-Daniel, 1997; Schaefer & Provenzano, 1998; Armbruster, 2004; Martins *et al.*, 2014; Rodriguez *et al.*, 2015; Pereira & Reis, 2017).

118. **Type of articulation between the pleural ribs posterior to the sixth centrum and the respective vertebral centra; $CI_2=1$, $RI_2=1$** : 0 Not directly articulated, ribs connected to the respective centra by means of a ligament; 1 Anteriormost ribs connected to the centra via a ligament, posteriormost ribs directly articulated to the centra; 2 (All ribs) Directly articulated to the centra (Pereira & Reis, 2017).

119. **Precaudal vertebrae; $CI_2=0.28$, $RI_2=0.86$** : 0 Less than 13; 1 13–16; 2 More than 16 (Schaefer, 1987; Py-Daniel, 1997; Paixão & Toledo-Piza, 2009; Londoño-Burduano & Reis, 2016; Pereira & Reis, 2017).

120. **Total vertebrae; $CI_2=0.33$, $RI_2=0.87$** : 0 Less than 30; 1 30 or more (Py-Daniel, 1997; Martins *et al.*, 2014; Pereira & Reis, 2017).

Median fins

121. **Spinelet; $CI_2=0.20$, $RI_2=0.85$** : 0 Absent; 1 Present, reduced, as a small plate; 2 Present and well developed (Schaefer, 1997; Py-Daniel, 1997; Armbruster, 1998, 2004; Martins *et al.*, 2014; Paixão & Toledo-Piza, 2009; Pereira & Reis, 2017).

122. **Number of dorsal-fin branched rays; $CI_2=0.33$, $RI_2=0.66$** : 0 Less than 8; 8

or more (Py-Daniel, 1997; Armbruster, 2004; Pereira & Reis, 2017).

123. **(Dorsal fin) Connecting bone/tendon; $CI_2=0.50$, $RI_2=0$:** 0 Absent, or, if present, flat (non-cylindrical); 1 Cylindrical (Armbruster, 2004).

124. **Adipose fin; $CI_2=0.10$, $RI_2=0.76$:** 0 Absent; 1 Present (Armbruster, 2004; Paixão & Toledo-Piza, 2009).

125. **Number of caudal-fin branched rays; $CI_2=0.50$, $RI_2=0.97$:** 0 10 or less; 1 12; 2 14 or more (Py-Daniel, 1997; Covain & Fish-Muller, 2007; Martins *et al.*, 2014; Pereira & Reis, 2017).

126. **Number of anal-fin branched rays; $CI_2=0.50$, $RI_2=0.90$:** 0 Less than 5; 1 5 or more (Py-Daniel, 1997; Armbruster, 2004; Pereira & Reis, 2017).

127. **Hypurals; $CI_2=1$, $RI_2=1$:** 0 Upper and lower lobes of the same length; 1 Lower lobe longer than the upper lobe (Py-Daniel, 1997; Armbruster, 2004).

Pectoral and pelvic girdle/fins

128. **Number of pectoral-fin branched rays; $CI_2=0.50$, $RI_2=0.85$:** 0 6 or less; 1 More than 6 (Py-Daniel, 1997; Covain & Fish-Muller, 2007; Pereira & Reis, 2017).

129. **Arrector fossae; $CI_2=1$, $RI_2=1$:** 0 Totally opened, arrector ventralis muscle totally exposed; 1 Partially or totally closed (Schaefer, 1998; Martins *et al.*, 2014).

130. **Exposition of the pectoral girdle; $CI_2=1$, $RI_2=1$:** 0 Not exposed; 1 Exposed (Schaefer, 1987; Py-Daniel, 1997; Martins *et al.*, 2014; Pereira & Reis, 2017).

131. **Shape of the posterior process of the coracoid; $CI_2=0.50$, $RI_2=0.96$:** 0 Straight and projected posteriorly; 1 Slightly curved and slightly projected dorsally (Armbruster, 2004; Pereira & Reis, 2017).

132. **Posterior expansion on the ventromesial process of the pelvic-fin spine; $CI_2=0.50$, $RI_2=0.97$:** 0 Absent; 1 Present (Pereira & Reis, 2017).

133. **Shape of the pelvic-fin spine in cross-section; $CI_2=0.50$, $RI_2=0.92$:** 0 Triangular; 1 Rounded (Pereira & Reis, 2017).

134. **Two rows of the first pelvic-fin ray; $CI_2=0.50$, $RI_2=0$:** 0 Fused; 1 Separated (Armbruster, 2004).

135. **Basipterygium; $CI_2=0.08$, $RI_2=0.69$:** 0 Anteriorly solid, without fenestrae; 1 Anteriorly opened, presence of fenestrae posterior to the anterior margin (Schaefer, 1991, 1998; Py-Daniel, 1997; Martins *et al.*, 2014; Pereira & Reis, 2017).

136. **Posteroventral ridge of the basipterygium; $CI_2=0.14$, $RI_2=0.82$:** 0 Absent; 1 Present (Armbruster, 2004).

Dermal bony plates and other external characters

137. **Body plates; $CI_2=1$, $RI_2=1$:** 0 Absent; 1 Present (Schaefer, 1987).
138. **Abdominal plates; $CI_2=0.08$, $RI_2=0.55$:** 0 Absent; 1 Present, abdomen partially covered by dermal plates, with naked areas; 2 Present, abdomen completely covered by dermal plates (Py-Daniel, 1997; Covain & Fish-Muller, 2007; Martins *et al.*, 2014; Pereira & Reis, 2017).
139. **Integumentary teeth; $CI_2=1$, $RI_2=1$:** 0 Absent; 1 Present (Reis, 1998, 2003; Reis *et al.* 2003; Garg *et al.*, 2010; Geerinckx *et al.*, 2011).
140. **Shape of the snout; $CI_2=0.20$, $RI_2=0.87$:** 0 Rounded; 1 Not rounded, triangular to somewhat rectangular; 2 Not rounded, prolonged (Py-Daniel, 1997; Pereira & Reis, 2017).
141. **Anterodorsal portion of the snout; $CI_2=1$, $RI_2=1$:** 0 Naked or bearing numerous small plates; 1 With 1–4 (or more) long plates (Schaefer, 1991, 1998; Martins *et al.*, 2014).
142. **Ventral oral disk; $CI_2=1$, $RI_2=1$:** 0 Absent; 1 Present (Reis, 1998, 2003; Reis *et al.* 2003; Garg *et al.*, 2010; Geerinckx *et al.*, 2011).
143. **Fleshy tentacles on snout; $CI_2=1$, $RI_2=1$:** 0 Absent; 1 Present (Armbruster, 2004).
144. **Barbels; $CI_2=1$, $RI_2=1$:** 0 One, 1 Two or more (Armbruster, 2004).
145. **Lips; $CI_2=0.50$, $RI_2=0.96$:** 0 Without bony plates; 1 With bony plates (Py-Daniel, 1997; Paixão & Toledo-Piza, 2009).
146. **Number of jaw teeth (each premaxillary or dentary); $CI_2=0.40$, $RI_2=0.90$:** 0 Less than 20; 1 20–50; 2 More than 50 (Boeseman, 1971; Schaefer, 1987; Py-Daniel, 1997; Armbruster, 1998; Reis *et al.*, 2006; Paixão & Toledo-Piza, 2009).
147. **Canal plate $CI_2=0.33$, $RI_2=0.88$:** 0 Absent, 1 Present, one, small; 2 Present, one, large; 3 Present, two (Armbruster, 2004).
148. **Postdorsal (preadipose) ridge; $CI_2=1$, $RI_2=1$:** 0 Absent; 1 Present (Armbruster, 2004; Pereira & Reis, 2017).
149. **Shape of the caudal peduncle; $CI_2=1$, $RI_2=1$:** 0 Compressed, round to oval; 1 Depressed, rectangular (Schaefer, 1987; Py-Daniel, 1997; Armbruster, 2004; Pereira & Reis, 2017).

APPENDIX F. List of synapomorphies and autapomorphies for each clade and terminal taxon, respectively (gross brain morphology). Species are listed in alphabetical order.

***Acestridium discus*:**
Char. 12: 0→2

Char. 14: 0→1
Char. 37: 0→1

Char. 44: 0→2
 Char. 68: 1→0
 Char. 81: 1→2

Ancistrus sp.:

Char. 48: 1→0
 Char. 49: 1→0

Apistoloricaria ommation:

Char. 14: 1→02
 Char. 22: 0→1
 Char. 48: 1→0
 Char. 57: 1→0
 Char. 60: 1→0
 Char. 62: 1→0
 Char. 88: 2→1

Aposturisoma myriodon:

Char. 22: 1→0
 Char. 29: 1→2
 Char. 40: 1→0
 Char. 47: 0→1
 Char. 52: 0→2

Astroblepus longifilis:

Char. 50: 0→1
 Char. 60: 1→0
 Char. 62: 0→2
 Char. 71: 0→1
 Char. 85: 1→2

Brochiloricaria macrodon:

Char. 2: 1→2
 Char. 5: 0→1
 Char. 6: 1→0
 Char. 30: 0→1
 Char. 41: 1→0
 Char. 55: 1→0

Brochiloricaria sp.:

Char. 4: 0→2
 Char. 11: 1→0
 Char. 44: 1→2
 Char. 52: 0→2
 Char. 57: 1→0
 Char. 68: 1→0
 Char. 69: 1→2
 Char. 72: 1→0

Char. 75: 1→0

Chauliocheilos saxatilis:

Char. 15: 0→1
 Char. 30: 0→1
 Char. 57: 0→1
 Char. 60: 0→1
 Char. 66: 0→1
 Char. 70: 1→0
 Char. 73: 0→2
 Char. 76: 1→0
 Char. 85: 0→2

Corumbataia cuestae:

Char. 20: 1→0
 Char. 25: 1→0
 Char. 30: 0→1
 Char. 37: 0→1
 Char. 38: 1→0
 Char. 44: 1→2
 Char. 50: 0→1
 Char. 55: 0→1
 Char. 69: 1→0
 Char. 81: 2→1

Corydoras aeneus:

Char. 16: 0→3
 Char. 24: 1→0
 Char. 44: 1→2
 Char. 47: 0→1
 Char. 48: 0→1

Crossoloricaria bahuaja:

Char. 13: 2→0
 Char. 29: 1→2
 Char. 44: 1→0
 Char. 67: 1→0
 Char. 69: 1→0
 Char. 88: 2→1

Crossoloricaria variegata:

Char. 14: 1→0
 Char. 22: 0→1
 Char. 81: 1→0

Cteniloricaria platystoma:

Char. 19: 1→0
 Char. 24: 12→0

Char. 29: 1→2
 Char. 32: 1→0
 Char. 47: 0→1
 Char. 51: 1→0
 Char. 59: 0→1
 Char. 82: 0→1

Curculionichthys insperatus:

Char. 17: 0→1
 Char. 18: 1→0
 Char. 25: 0→1

Dasylicaria filamentosa:

Char. 16: 1→2
 Char. 53: 1→0
 Char. 77: 1→0

Dasylicaria latiura:

Char. 34: 3→2

Dekeyseria scaphirhynchus:

Char. 8: 0→1
 Char. 31: 1→0

Delturus brevis:

Char. 26: 1→0
 Char. 44: 1→2
 Char. 53: 1→0

Delturus carinotus:

No autapomorphies

Dentectus barbarmatus:

Char. 11: 1→0
 Char. 49: 1→0
 Char. 61: 1→0

Epactionotus bilineatus:

Char. 14: 2→0
 Char. 18: 1→0
 Char. 40: 1→0
 Char. 48: 0→1

Eurycheilichthys pantherinus:

Char. 10: 1→0
 Char. 14: 2→1
 Char. 15: 0→1
 Char. 20: 1→0

Char. 31: 0→1
 Char. 49: 1→0
 Char. 61: 1→0
 Char. 64: 0→1

Farlowella amazona:

Char. 14: 0→1

Farlowella henriquei:

Char. 14: 0→1
 Char. 15: 0→1
 Char. 58: 1→0
 Char. 68: 1→0

Farlowella nattereri:

Char. 16: 2→1

Farlowella oxyrryncha:

Char. 32: 1→0

Farlowella paraguayensis:

No autapomorphies

Farlowella reticulata:

Char. 13: 1→2
 Char. 25: 0→1
 Char. 41: 0→1
 Char. 42: 0→1

Farlowella schreitmuelleri:

Char. 25: 0→1

Farlowella smithi:

Char. 2: 1→0
 Char. 47: 0→1

Fonchiiloricaria nanodon:

Char. 15: 0→1
 Char. 27: 1→0
 Char. 34: 2→3
 Char. 36: 1→0
 Char. 39: 0→1
 Char. 42: 1→0
 Char. 46: 1→0
 Char. 52: 0→2
 Char. 56: 0→1
 Char. 58: 1→0
 Char. 62: 1→2

Char. 69: 1→2

Char. 88: 2→1

Furcodontichthys novaesi:

Char. 16: 2→0

Char. 42: 0→1

Char. 50: 0→1

Char. 77: 1→2

Gymnotocinclus anosteos:

Char. 3: 0→1

Char. 4: 0→2

Char. 25: 0→1

Char. 79: 0→1

Harttia carvalhoi:

Char. 8: 1→0

Char. 16: 1→2

Char. 44: 2→1

Char. 52: 0→3

Harttia duriventris:

Char. 14: 0→1

Char. 47: 0→1

Char. 60: 0→1

Char. 88: 2→1

Harttia loricariformis:

Char. 8: 1→0

Char. 52: 0→3

Char. 55: 1→0

Harttia novalimensis:

Char. 13: 1→2

Char. 44: 2→1

Char. 51: 1→0

Char. 52: 0→23

Char. 73: 1→2

Harttia punctata:

Char. 25: 0→1

Char. 32: 1→0

Char. 40: 1→0

Char. 68: 1→0

Harttiella crassicauda:

Char. 2: 1→0

Char. 15: 0→1

Char. 27: 1→0

Char. 42: 1→0

Char. 48: 1→0

Char. 67: 1→0

Char. 83: 0→1

Char. 87: 0→2

Char. 88: 2→1

Hemiodontichthys

acipenserinus:

Char. 9: 0→1

Char. 44: 1→2

Hemiodontichthys sp.:

Char. 4: 0→1

Char. 16: 1→0

Hemipsilichthys nimius:

Char. 16: 1→2

Hisonotus francirochai:

Char. 15: 0→1

Char. 79: 0→1

Hisonotus notatus:

Char. 37: 1→0

Char. 49: 1→0

Hypoptopoma inexpectatum:

Char. 2: 0→1

Char. 13: 0→1

Char. 15: 0→1

Char. 18: 1→0

Char. 27: 1→0

Char. 43: 1→0

Char. 44: 0→1

Char. 81: 1→0

Hypostomus ancistroides:

Char. 4: 0→1

Char. 53: 1→0

Char. 61: 1→0

Hypostomus nigromaculatus:

Char. 13: 2→1

Char. 20: 1→0

Char. 22: 2→1

Char. 29: 2→1

Char. 43: 0→1

Char. 59: 1→0

Char. 73: 0→1

Hypostomus regani:

Char. 61: 1→0

Hypostomus variipictus:

No autapomorphies

Isbrueckerichthys duseni:

Char. 8: 0→1

Char. 14: 0→1

Char. 20: 1→0

Char. 49: 1→0

Char. 54: 1→0

Char. 55: 0→1

Char. 63: 0→1

Ixinandria steinbachi:

Char. 10: 1→2

Char. 13: 2→1

Char. 18: 1→0

Char. 21: 1→0

Char. 47: 0→1

Char. 60: 1→0

Char. 67: 1→0

Char. 72: 1→0

Char. 87: 1→2

Kronichthys heylandi:

Char. 1: 0→2

Char. 4: 0→1

Char. 8: 0→1

Char. 10: 1→2

Char. 15: 0→1

Char. 29: 0→1

Char. 40: 1→0

Char. 68: 1→0

Kronichthys subteres:

Char. 3: 0→1

Char. 35: 1→0

Char. 42: 1→0

Char. 49: 1→0

Char. 63: 0→1

Char. 64: 1→0

Char. 75: 1→0

Lamontichthys filamentosus:

Char. 37: 1→0

Char. 40: 1→0

Char. 44: 2→1

Char. 55: 1→0

Char. 64: 1→0

Char. 67: 1→0

Char. 72: 1→0

Char. 73: 1→2

Char. 84: 0→1

Lampiella gibbosa:

Char. 8: 1→0

Char. 10: 1→2

Char. 20: 1→0

Char. 40: 1→0

Char. 49: 1→0

Char. 59: 0→1

Char. 69: 1→0

Char. 70: 1→0

Char. 88: 2→0

Limatulichthys griseus:

Char. 8: 1→0

Char. 52: 0→1

Char. 71: 0→1

Limatulichthys petleyi:

Char. 50: 0→1

Lithogenes villosus:

Char. 13: 2→1

Char. 37: 0→1

Char. 40: 0→1

Char. 42: 1→0

Char. 57: 1→0

Char. 63: 1→0

Char. 64: 0→1

Char. 66: 1→0

Char. 68: 1→0

Char. 70: 0→1

Char. 71: 0→1

Char. 72: 0→1

Char. 75: 1→0

Char. 79: 2→0

Char. 81: 1→2

Char. 82: 0→1

Char. 85: 2→0

Char. 87: 0→2

Loricaria cataphracta:

Char. 57: 1→0

Loricaria luciae:

Char. 21: 1→0

Char. 55: 1→0

Loricaria sp.:

Char. 12: 0→1

Char. 19: 1→0

Char. 20: 0→1

Char. 24: 1→2

Char. 69: 1→2

Loricariichthys acutus:

Char. 14: 1→0

Char. 61: 1→0

Char. 67: 1→0

Char. 88: 2→1

Loricariichthys anus:

No autapomorphies

Loricariichthys castaneus:

Char. 52: 1→3

Char. 55: 1→0

Char. 63: 0→1

Char. 68: 1→0

Loricariichthys derbyi:

Char. 14: 0→1

Char. 16: 2→1

Char. 22: 1→0

Char. 31: 1→0

Char. 44: 1→0

Char. 62: 0→1

Char. 64: 1→0

Char. 69: 2→1

Loricariichthys melanocheilus:

Char. 51: 0→1

Char. 64: 1→0

Loricariichthys platymetopon:

Char. 2: 0→1

Char. 24: 1→2

Char. 29: 1→2

Char. 80: 0→1

Char. 81: 1→0

Loricariichthys rostratus:

Char. 61: 1→0

Loricariichthys sp.:

Char. 9: 0→1

Char. 25: 0→1

Char. 31: 1→0

Char. 41: 0→1

Char. 79: 2→0

Char. 80: 0→1

Megalancistrus parananus:

No autapomorphies

Metaloricaria paucidens:

Char. 4: 0→2

Char. 20: 0→1

Char. 51: 1→0

Char. 52: 0→2

Char. 56: 0→1

Char. 62: 1→2

Char. 69: 1→2

Char. 87: 1→2

Microlepidogaster perforatus:

Char. 5: 1→0

Char. 9: 1→0

Char. 59: 1→0

Char. 68: 0→1

Neoplecostomus corumba:

Char. 22: 0→1

Char. 24: 0→2

Neoplecostomus langeanii:

No autapomorphies

Neoplecostomus microps:

Char. 1: 0→1

Char. 9: 0→1

Char. 22: 0→1

Char. 25: 1→0

Char. 42: 0→1

Neoplecostomus ribeirensis:

Char. 15: 1→0

Char. 25: 1→0

Neoplecostomus selenae:

Char. 8: 0→1

Char. 14: 0→2

Char. 20: 1→0

Char. 38: 1→0

Char. 43: 1→0

Char. 59: 0→1

Neoplecostomus yapo:

Char. 22: 0→1

Char. 31: 1→0

Otocinclus affinis:

Char. 19: 0→1

Char. 29: 0→1

Char. 40: 1→0

Char. 70: 1→0

Otothyris lophophanes:

Char. 8: 1→0

Char. 19: 0→1

Char. 69: 0→1

Char. 78: 1→0

Otothyris rostrata:

Char. 75: 1→0

Otothyropsis marapoama:

Char. 5: 0→1

Char. 9: 1→0

Char. 69: 0→1

Char. 88: 0→2

Oxyropsis wrightiana:

Char. 14: 0→2

Paraloricaria vetula:

Char. 15: 1→0

Char. 16: 1→0

Char. 20: 0→1

Char. 21: 1→0

Char. 33: 0→1

Char. 43: 0→1

Char. 44: 1→2

Char. 54: 0→1

Pareiorhaphis cameroni:

Char. 35: 1→0

Char. 75: 1→0

Pareiorhaphis hystrix:

Char. 30: 0→1

Char. 67: 0→1

Pareiorhina carrancas:

Char. 2: 1→0

Char. 3: 1→0

Char. 7: 0→1

Char. 9: 0→1

Char. 10: 1→0

Char. 15: 0→1

Pareiorhina rudolphi:

Char. 4: 2→0

Char. 60: 0→1

Parotocinclus jumbo:

Char. 10: 1→0

Char. 31: 0→1

Char. 85: 2→0

Parotocinclus maculicauda:

Char. 12: 0→1

Char. 29: 0→1

Char. 31: 0→1

Char. 41: 1→0

Char. 44: 1→0

Parotocinclus prata:

Char. 31: 0→1

Pimelodus argenteus:

No autapomorphies

Pimelodus maculatus:

Char. 63: 0→1

Planiloricaria cryptodon:

Char. 53: 0→1

Plesioptopoma curvidens:

Char. 2: 1→0
 Char. 24: 1→0
 Char. 31: 0→1
 Char. 32: 1→0
 Char. 40: 1→0

Proloricaria prolixa:

Char. 8: 1→0
 Char. 59: 2→1
 Char. 82: 1→0
 Char. 85: 2→1

Pseudohemiodon laticeps:

Char. 68: 1→0

Pseudohemiodon platycephalus:

Char. 18: 0→1

Pseudohemiodon sp.:

Char. 14: 1→0
 Char. 44: 1→2

Pseudoloricaria laeviscula:

Char. 15: 0→1
 Char. 24: 1→0
 Char. 41: 1→0
 Char. 80: 0→1
 Char. 81: 1→0

Pseudoloricaria punctata:

Char. 19: 1→0
 Char. 24: 1→0
 Char. 71: 0→1
 Char. 77: 1→2

Pseudopimelodus bufonius:

No autapomorphies

Pseudopimelodus mangurus:

Char. 16: 0→1

Pseudotocinclus tietensis:

Char. 3: 0→1
 Char. 5: 1→0
 Char. 11: 0→1
 Char. 13: 1→0
 Char. 15: 0→1

Char. 17: 0→1
 Char. 48: 1→0
 Char. 61: 0→1
 Char. 64: 1→0
 Char. 70: 1→0

Pseudotothyris obtusa:

Char. 3: 0→1
 Char. 7: 0→1
 Char. 9: 1→2
 Char. 10: 1→0
 Char. 64: 0→1

Pyxiloricaria menezii:

Char. 20: 0→1
 Char. 30: 0→1
 Char. 48: 1→0
 Char. 51: 1→0
 Char. 60: 1→0
 Char. 68: 1→0
 Char. 69: 1→2
 Char. 82: 1→0

Reganella depressa:

Char. 29: 1→0
 Char. 45: 0→1
 Char. 52: 1→2
 Char. 86: 1→0
 Char. 88: 2→0

Rhadinoloricaria sp.:

Char. 15: 0→1
 Char. 48: 1→0
 Char. 52: 0→2
 Char. 83: 1→0
 Char. 88: 2→0

Rhinelepis aspera:

Char. 27: 1→0
 Char. 42: 1→0
 Char. 53: 1→0
 Char. 61: 1→0
 Char. 65: 0→1
 Char. 84: 0→1

Rhinolekos britskii:

Char. 1: 1→0
 Char. 15: 0→1

Ricola macrops:

Char. 5: 0→1
 Char. 21: 1→0
 Char. 41: 1→0
 Char. 51: 0→1

Rineloricaria cacerensis:

Char. 60: 1→0
 Char. 73: 2→1

Rineloricaria cf. lima:

Char. 14: 1→0
 Char. 16: 2→0
 Char. 30: 0→1
 Char. 43: 1→0
 Char. 49: 0→1
 Char. 81: 1→2

Rineloricaria formosa:

Char. 24: 0→2
 Char. 31: 1→0
 Char. 51: 1→0
 Char. 62: 1→0
 Char. 77: 0→2
 Char. 83: 1→0
 Char. 87: 1→2

Rineloricaria parva:

Char. 44: 1→0
 Char. 88: 2→1

Rineloricaria quadrensis:

Char. 60: 1→0

Rineloricaria strigilata:

Char. 21: 1→0
 Char. 60: 1→0

Schizolecis guntheri:

Char. 2: 1→0
 Char. 7: 0→1
 Char. 10: 1→0
 Char. 15: 0→1
 Char. 22: 0→1
 Char. 30: 0→1
 Char. 48: 1→0

Scleromystax barbatus:

Char. 14: 1→0
 Char. 15: 1→0
 Char. 53: 1→0
 Char. 88: 0→1

Spatuloricaria evansii:

Char. 51: 0→1
 Char. 52: 1→0
 Char. 58: 2→1
 Char. 62: 1→0
 Char. 87: 1→0

Spatuloricaria nudiventris:

Char. 8: 1→0
 Char. 15: 1→0
 Char. 54: 0→1

Spatuloricaria tuiara:

Char. 13: 2→1
 Char. 16: 1→0
 Char. 24: 1→0
 Char. 43: 0→1

Sturisoma barbatum:

Char. 24: 2→1
 Char. 40: 1→0
 Char. 44: 1→2
 Char. 63: 0→1

Sturisoma guentheri:

Char. 42: 1→0
 Char. 43: 0→1
 Char. 44: 1→2

Sturisoma panamensis:

Char. 29: 1→2
 Char. 75: 1→0

Sturisoma robustum:

Char. 24: 2→1
 Char. 44: 1→0
 Char. 48: 0→1

Sturisoma rostratum:

Char. 29: 1→2
 Char. 52: 0→1
 Char. 63: 0→1

Sturisoma tenuirostre:

Char. 43: 0→1
 Char. 69: 1→2
 Char. 75: 1→0
 Char. 84: 1→0

Sturisomatichthys leightoni:

Char. 4: 0→2
 Char. 16: 1→2
 Char. 40: 1→0
 Char. 43: 0→1
 Char. 73: 1→2

Clade 130:

No synapomorphies

Clade 131:

Char. 4: 0→2
 Char. 14: 1→02
 Char. 24: 1→0
 Char. 25: 0→1
 Char. 31: 1→0
 Char. 43: 1→0
 Char. 44: 1→2
 Char. 68: 1→0
 Char. 72: 1→0
 Char. 73: 2→0
 Char. 77: 0→2
 Char. 83: 1→0
 Char. 84: 1→0
 Char. 85: 1→0

Clade 132:

Char. 2: 3→1
 Char. 23: 0→1
 Char. 32: 0→1
 Char. 41: 0→1
 Char. 62: 1→0
 Char. 66: 2→1
 Char. 70: 0→1

Clade 133:

Char. 23: 1→0
 Char. 27: 0→1
 Char. 32: 1→0
 Char. 63: 0→1
 Char. 70: 1→0

Char. 72: 1→0

Clade 134:

Char. 58: 2→1
 Char. 64: 1→0
 Char. 69: 1→0

Clade 135:

Char. 54: 1→0
 Char. 67: 1→0
 Char. 74: 1→0
 Char. 75: 0→1
 Char. 80: 1→0
 Char. 81: 0→1
 Char. 82: 0→1

Clade 136:

Char. 19: 1→0
 Char. 25: 1→0
 Char. 31: 0→1
 Char. 48: 0→1
 Char. 65: 0→1
 Char. 73: 1→0
 Char. 88: 0→2

Clade 137:

Char. 22: 2→0
 Char. 24: 2→0
 Char. 35: 1→0
 Char. 46: 1→0
 Char. 62: 2→1

Clade 138:

Char. 0: 1→0
 Char. 26: 0→1
 Char. 51: 0→1
 Char. 55: 0→1

Clade 139:

Char. 11: 0→1
 Char. 15: 0→1
 Char. 31: 1→0
 Char. 60: 0→1
 Char. 73: 0→1

Clade 140:

Char. 16: 2→1
 Char. 48: 1→0

Clade 141:

Char. 14: 0→2
 Char. 15: 1→0
 Char. 38: 1→0
 Char. 58: 0→1
 Char. 88: 2→01

Clade 142:

Char. 43: 1→0
 Char. 53: 0→1

Clade 143:

Char. 4: 2→0
 Char. 22: 0→2
 Char. 24: 1→2
 Char. 29: 0→2
 Char. 54: 1→0
 Char. 57: 0→1
 Char. 59: 0→1
 Char. 79: 0→2
 Char. 81: 2→1
 Char. 85: 0→2

Clade 144:

Char. 13: 0→2
 Char. 63: 0→1
 Char. 70: 1→0
 Char. 78: 0→1

Clade 145:

Char. 19: 0→1
 Char. 24: 0→1

Clade 146:

Char. 11: 1→0
 Char. 18: 0→1
 Char. 34: 1→2
 Char. 40: 1→0
 Char. 61: 0→1

Clade 147:

Char. 10: 1→2
 Char. 31: 0→1
 Char. 35: 0→1
 Char. 62: 1→2

Clade 148:

Char. 6: 1→0

Clade 149:

Char. 1: 1→0
 Char. 8: 1→0
 Char. 32: 0→1
 Char. 37: 1→0
 Char. 47: 1→0
 Char. 64: 1→0

Clade 150:

Char. 4: 0→2
 Char. 14: 2→0
 Char. 38: 0→1

Clade 151:

Char. 19: 1→0
 Char. 24: 1→0

Clade 152:

Char. 1: 0→1
 Char. 32: 1→0
 Char. 35: 1→0
 Char. 42: 1→0
 Char. 85: 2→0

Clade 153:

Char. 13: 1→0
 Char. 14: 0→2
 Char. 37: 0→1
 Char. 79: 1→0

Clade 154:

Char. 16: 1→2
 Char. 29: 1→0
 Char. 49: 0→1
 Char. 55: 1→0
 Char. 58: 1→0
 Char. 72: 1→0
 Char. 78: 0→1

Clade 155:

Char. 47: 0→1
 Char. 66: 1→0
 Char. 73: 1→0

Clade 156:

Char. 37: 1→0

Char. 67: 1→0

Clade 157:

Char. 57: 1→0

Clade 158:

Char. 21: 1→0

Char. 22: 1→0

Char. 60: 1→0

Clade 159:

Char. 63: 1→0

Clade 160:

Char. 25: 1→0

Char. 43: 0→1

Clade 161:

Char. 27: 0→1

Char. 33: 1→0

Char. 77: 0→2

Clade 162:

Char. 5: 0→1

Char. 44: 1→2

Char. 63: 0→1

Char. 79: 2→1

Char. 84: 1→0

Clade 163:

Char. 14: 1→0

Char. 24: 1→2

Clade 164:

Char. 9: 1→0

Char. 25: 0→1

Char. 31: 1→0

Char. 36: 0→1

Char. 39: 1→0

Char. 83: 1→0

Clade 165:

Char. 16: 2→1

Char. 43: 1→0

Char. 71: 1→0

Char. 73: 2→1

Clade 166:

Char. 24: 0→1

Char. 42: 0→1

Clade 167:

Char. 36: 1→0

Char. 77: 1→0

Clade 168:

Char. 20: 0→1

Char. 41: 0→1

Clade 169:

Char. 16: 1→2

Char. 24: 1→0

Clade 170:

Char. 9: 0→1

Char. 19: 1→0

Char. 71: 0→1

Clade 171:

Char. 34: 3→2

Char. 36: 0→1

Char. 72: 0→1

Clade 172:

Char. 16: 0→1

Char. 41: 1→0

Char. 87: 1→2

Clade 173:

Char. 67: 0→1

Clade 174:

Char. 62: 0→1

Char. 72: 1→0

Clade 175:

Char. 15: 1→0

Char. 30: 1→0

Char. 56: 1→0

Char. 58: 2→1

Char. 59: 2→0

Clade 176:

Char. 2: 1→0

Char. 18: 1→0

Char. 52: 12→0

Clade 177:

Char. 10: 2→1
 Char. 85: 1→2
 Char. 88: 0→2

Clade 178:

Char. 0: 0→1
 Char. 37: 0→1
 Char. 39: 0→1
 Char. 56: 0→1
 Char. 77: 0→1
 Char. 79: 1→2

Clade 179:

Char. 7: 0→1
 Char. 8: 1→0
 Char. 16: 2→1
 Char. 22: 0→1
 Char. 69: 0→2

Clade 180:

Char. 24: 1→0
 Char. 32: 1→0
 Char. 35: 1→0

Clade 181:

Char. 13: 1→0
 Char. 34: 1→0
 Char. 42: 1→0
 Char. 44: 1→0
 Char. 76: 1→0
 Char. 79: 1→0
 Char. 81: 2→1
 Char. 88: 2→0

Clade 182:

Char. 2: 1→0
 Char. 5: 1→0
 Char. 20: 1→0
 Char. 64: 1→0
 Char. 69: 1→0

Clade 183:

Char. 3: 1→0
 Char. 9: 0→1

Clade 184:

Char. 9: 0→1
 Char. 19: 0→1
 Char. 35: 0→1
 Char. 44: 2→1

Clade 185:

Char. 32: 0→1
 Char. 59: 0→1
 Char. 62: 1→2

Clade 186:

Char. 8: 1→0
 Char. 41: 1→0
 Char. 47: 1→0
 Char. 88: 2→1

Clade 187:

Char. 6: 1→0
 Char. 48: 1→0

Clade 188:

Char. 3: 1→0
 Char. 44: 1→2
 Char. 64: 1→0

Clade 189:

Char. 22: 0→1
 Char. 68: 1→0
 Char. 81: 2→1

Clade 190:

Char. 64: 0→1
 Char. 88: 1→2

Clade 191:

Char. 9: 1→2
 Char. 11: 1→0
 Char. 25: 0→1
 Char. 62: 1→0
 Char. 75: 1→0

Clade 192:

Char. 8: 1→0
 Char. 14: 0→2
 Char. 57: 0→1
 Char. 88: 2→0

Clade 193:

Char. 18: 1→0
Char. 25: 0→1

Clade 194:

Char. 31: 1→0
Char. 75: 1→0

Clade 195:

Char. 74: 0→1

Clade 196:

Char. 22: 0→1
Char. 69: 1→2
Char. 87: 1→2

Clade 197:

Char. 16: 0→1
Char. 30: 1→0
Char. 33: 1→0

Clade 198:

Char. 51: 1→0
Char. 62: 0→1

Clade 199:

Char. 15: 0→1
Char. 30: 0→1
Char. 33: 1→0
Char. 60: 1→0
Char. 67: 1→0

Clade 200:

Char. 4: 0→2
Char. 8: 1→0
Char. 47: 0→1
Char. 52: 0→1
Char. 61: 1→0
Char. 62: 1→0
Char. 79: 2→0
Char. 85: 2→1

Clade 201:

Char. 48: 1→0
Char. 59: 0→1

Clade 202:

Char. 4: 0→2
Char. 16: 1→2

Char. 18: 1→0

Clade 203:

Char. 28: 0→1
Char. 58: 2→1
Char. 59: 2→1
Char. 72: 1→0
Char. 73: 2→1

Clade 204:

Char. 25: 0→1
Char. 63: 0→1
Char. 67: 0→1

Clade 205:

Char. 4: 2→0
Char. 57: 1→0

Clade 206:

Char. 60: 1→0

Clade 207:

Char. 8: 1→0
Char. 20: 1→0
Char. 24: 2→0

Clade 208:

Char. 16: 1→2
Char. 48: 1→0
Char. 57: 0→1

Clade 209:

Char. 41: 1→0
Char. 60: 0→1
Char. 81: 2→1

Clade 210:

Char. 4: 0→2
Char. 19: 1→0
Char. 42: 1→0
Char. 77: 2→0
Char. 79: 1→2

Clade 211:

Char. 18: 1→0
Char. 24: 0→2
Char. 41: 0→1
Char. 44: 2→1

Char. 47: 0→1
 Char. 48: 0→1
 Char. 58: 1→0

Clade 212:

Char. 21: 1→0
 Char. 31: 0→1
 Char. 48: 1→0
 Char. 71: 0→1
 Char. 77: 2→1

Clade 213:

Char. 32: 1→0
 Char. 55: 1→0

Clade 214:

Char. 15: 0→1
 Char. 19: 1→0
 Char. 24: 1→0
 Char. 34: 3→2
 Char. 47: 0→1
 Char. 48: 1→0
 Char. 49: 1→0

Clade 215:

Char. 61: 1→0
 Char. 73: 2→1

Clade 216:

Char. 51: 1→0
 Char. 52: 0→1
 Char. 77: 1→2

Clade 217:

Char. 63: 0→1
 Char. 64: 1→0
 Char. 77: 1→2
 Char. 81: 1→0

Clade 218:

Char. 21: 1→0
 Char. 22: 0→1
 Char. 50: 0→1
 Char. 54: 0→1
 Char. 60: 1→0

Clade 219:

Char. 24: 1→2

Clade 220:

Char. 4: 0→1
 Char. 22: 0→1
 Char. 43: 1→0
 Char. 59: 0→1

Clade 221:

Char. 10: 1→2
 Char. 42: 1→0
 Char. 44: 2→1
 Char. 50: 0→1
 Char. 85: 2→1

Clade 222:

Char. 14: 1→0
 Char. 69: 1→2

Clade 223:

Char. 16: 1→2
 Char. 41: 0→1
 Char. 62: 1→0

Clade 224:

Char. 18: 0→1
 Char. 44: 1→2

Clade 225:

Char. 54: 0→1
 Char. 61: 1→0

Clade 226:

Char. 29: 1→2
 Char. 59: 0→1
 Char. 71: 0→1

Clade 227:

Char. 2: 0→1
 Char. 25: 0→1
 Char. 36: 1→0
 Char. 51: 1→0
 Char. 52: 0→1

Clade 228:

Char. 42: 0→1
 Char. 55: 1→0

Clade 229:

Char. 54: 0→1
 Char. 60: 0→1
 Char. 72: 1→0
 Char. 77: 1→0

Clade 230:

Char. 47: 0→1
 Char. 88: 2→1

Clade 231:

Char. 68: 1→0
 Char. 71: 1→0

Clade 232:

Char. 15: 0→1
 Char. 48: 1→0
 Char. 88: 2→1

Clade 233:

Char. 36: 0→1
 Char. 48: 0→1

Clade 234:

Char. 6: 1→0
 Char. 56: 1→0
 Char. 59: 2→1
 Char. 60: 1→0
 Char. 83: 1→0

Clade 235:

Char. 15: 0→1
 Char. 21: 0→1
 Char. 42: 1→0
 Char. 52: 0→1

Clade 236:

Char. 21: 1→0
 Char. 33: 1→0
 Char. 34: 2→1
 Char. 62: 1→0

Clade 237:

Char. 48: 1→0
 Char. 49: 0→1
 Char. 51: 1→0

Clade 238:

Char. 31: 0→1
 Char. 40: 1→0

Clade 239:

Char. 13: 0→1
 Char. 33: 0→1
 Char. 69: 1→2

Clade 240:

Char. 9: 1→0
 Char. 22: 0→1
 Char. 88: 0→1

Clade 241:

Char. 10: 2→1
 Char. 14: 0→2
 Char. 19: 0→2
 Char. 73: 0→1

Clade 242:

Char. 30: 0→1
 Char. 41: 1→0
 Char. 48: 1→0
 Char. 50: 0→1
 Char. 56: 0→1
 Char. 71: 0→1
 Char. 77: 2→0

Clade 243:

Char. 6: 0→1
 Char. 18: 1→0
 Char. 38: 0→1
 Char. 61: 1→0
 Char. 62: 2→1

Clade 244:

Char. 2: 0→1
 Char. 15: 0→1
 Char. 49: 1→0
 Char. 62: 1→0

Clade 245:

Char. 1: 0→1
 Char. 12: 0→1
 Char. 37: 0→1

APPENDIX G. List of synapomorphies and autapomorphies for each

clade and terminal taxon, respectively (combined analysis).

Acestridium discus:

Char. 12: 0→2
Char. 14: 0→1
Char. 44: 0→2
Char. 68: 1→0
Char. 81: 1→2
Char. 101: 12→0

Ancistrus sp.:

Char. 31: 0→1
Char. 49: 1→0
Char. 105: 1→0

Apistoloricaria ommation:

Char. 14: 1→02
Char. 22: 0→1
Char. 88: 2→1

Aposturisoma myriodon:

Char. 27: 1→0
Char. 29: 1→2
Char. 33: 0→1
Char. 40: 1→0
Char. 43: 1→0
Char. 47: 0→1
Char. 52: 0→2
Char. 63: 0→1
Char. 99: 1→0
Char. 101: 2→1

Astroblepus longifilis:

Char. 45: 0→1
Char. 46: 1→0
Char. 50: 0→1
Char. 59: 1→0
Char. 60: 1→0

Brochiloricaria macrodon:

Char. 2: 1→2
Char. 5: 0→1
Char. 30: 0→1
Char. 41: 1→0
Char. 55: 1→0
Char. 74: 0→1

Brochiloricaria sp.:

Char. 4: 0→2
Char. 11: 1→0
Char. 42: 0→1
Char. 44: 1→2
Char. 48: 0→1
Char. 52: 0→2
Char. 68: 1→0
Char. 69: 1→2
Char. 72: 1→0
Char. 75: 1→0
Char. 138: 1→2

Chauliocheilos saxatilis:

Char. 30: 0→1
Char. 37: 0→1
Char. 66: 0→1
Char. 70: 1→0
Char. 73: 0→2
Char. 76: 1→0
Char. 78: 1→2
Char. 79: 1→0
Char. 88: 2→1

Corumbataia cuestae:

Char. 4: 0→2
Char. 22: 1→0
Char. 30: 0→1
Char. 35: 0→1
Char. 41: 0→1
Char. 50: 0→1
Char. 54: 0→1
Char. 55: 0→1
Char. 69: 1→0
Char. 104: 1→2
Char. 124: 0→1
Char. 135: 0→1

Corydoras aeneus:

Char. 5: 1→0
Char. 16: 0→3
Char. 24: 1→0
Char. 44: 1→2
Char. 45: 0→1
Char. 46: 1→0
Char. 47: 0→1
Char. 48: 0→1

Crossoloricaria bahuaja:

Char. 13: 2→0
 Char. 16: 0→2
 Char. 22: 0→1
 Char. 29: 1→2
 Char. 42: 1→0
 Char. 44: 1→0
 Char. 67: 1→0
 Char. 69: 1→0
 Char. 77: 2→1
 Char. 92: 2→1
 Char. 105: 1→0
 Char. 135: 1→0
 Char. 136: 1→0
 Char. 138: 2→1

Crossoloricaria variegata:

Char. 14: 1→0
 Char. 22: 0→1
 Char. 62: 0→1
 Char. 81: 1→0
 Char. 105: 1→0

Cteniloricaria platystoma:

Char. 4: 0→2
 Char. 16: 1→2
 Char. 18: 1→0
 Char. 19: 1→0
 Char. 24: 1→0
 Char. 29: 1→2
 Char. 51: 1→0
 Char. 59: 0→1
 Char. 63: 0→1
 Char. 81: 2→1
 Char. 82: 0→1
 Char. 106: 1→0

Curculionichthys insperatus:

Char. 2: 0→1
 Char. 6: 1→0
 Char. 25: 0→1
 Char. 48: 1→0
 Char. 104: 1→2
 Char. 115: 1→0
 Char. 121: 1→0
 Char. 124: 0→1
 Char. 135: 0→1

Dasylicaria filamentosa:

Char. 16: 1→2
 Char. 53: 1→0
 Char. 77: 1→0

Dasylicaria latiura:

Char. 34: 3→2

Dekeyseria scaphirhynchus:

Char. 43: 0→1
 Char. 52: 2→3
 Char. 53: 1→0

Delturus brevis:

Char. 44: 1→2
 Char. 53: 1→0

Delturus carinotus:

No autapomorphies

Dentectus barbarmatus:

Char. 11: 1→0
 Char. 49: 1→0
 Char. 101: 1→2

Epactionotus bilineatus:

Char. 37: 1→0
 Char. 40: 1→0
 Char. 59: 0→1
 Char. 61: 0→1

Eurycheilichthys pantherinus:

Char. 14: 0→1
 Char. 15: 0→1
 Char. 18: 0→1
 Char. 32: 1→0
 Char. 48: 1→0
 Char. 49: 1→0
 Char. 91: 1→0
 Char. 109: 1→0
 Char. 115: 1→0

Farlowella amazona:

Char. 14: 0→1
 Char. 101: 2→1

Farlowella henriquei:

Char. 14: 0→1
 Char. 15: 0→1
 Char. 58: 1→0
 Char. 68: 1→0
 Char. 101: 2→1

Farlowella nattereri:

Char. 16: 2→1

Farlowella oxyrryncha:

Char. 32: 1→0

Farlowella paraguayensis:

No autapomorphies

Farlowella reticulata:

Char. 13: 1→2
 Char. 25: 0→1
 Char. 41: 0→1
 Char. 42: 0→1

Farlowella schreitmuelleri:

Char. 60: 1→0
 Char. 81: 1→2

Farlowella smithi:

Char. 2: 1→0
 Char. 47: 0→1

Fonchiiloricaria nanodon:

Char. 5: 0→1
 Char. 10: 1→2
 Char. 16: 0→2
 Char. 18: 1→0
 Char. 46: 1→0
 Char. 49: 1→0
 Char. 51: 0→1
 Char. 53: 1→0
 Char. 58: 2→0
 Char. 59: 2→0
 Char. 62: 1→2
 Char. 63: 0→1
 Char. 67: 0→1
 Char. 71: 0→1
 Char. 73: 2→1
 Char. 79: 2→1
 Char. 83: 1→0
 Char. 84: 1→0

Char. 88: 2→1

Furcodontichthys novaesi:

Char. 49: 1→0
 Char. 50: 0→1

Gymnotocinclus anosteos:

Char. 4: 0→2
 Char. 57: 1→0
 Char. 60: 1→0
 Char. 85: 2→0

Harttia carvalhoi:

Char. 8: 1→0
 Char. 16: 1→2
 Char. 32: 0→1
 Char. 57: 0→1

Harttia duriventris:

Char. 14: 0→1
 Char. 55: 1→0
 Char. 88: 2→1

Harttia loricariformis:

Char. 8: 1→0
 Char. 43: 1→0
 Char. 52: 0→3
 Char. 55: 1→0
 Char. 63: 0→1
 Char. 113: 1→2
 Char. 135: 1→0

Harttia novalimensis:

Char. 13: 1→2
 Char. 51: 1→0
 Char. 55: 1→0
 Char. 73: 1→2

Harttia punctata:

Char. 24: 1→2
 Char. 25: 0→1
 Char. 37: 1→0
 Char. 40: 1→0
 Char. 66: 1→0
 Char. 67: 1→0
 Char. 68: 1→0
 Char. 73: 1→0

Harttiella crassicauda:

Char. 2: 1→0
 Char. 13: 2→0
 Char. 15: 0→1
 Char. 27: 1→0
 Char. 42: 1→0
 Char. 48: 1→0
 Char. 67: 1→0
 Char. 83: 0→1
 Char. 87: 0→2
 Char. 88: 2→1

Hemiodontichthys acipenserinus:

Char. 9: 0→1
 Char. 44: 1→2

Hemiodontichthys sp.:

Char. 4: 0→1
 Char. 16: 1→0

Hemipsilichthys nimius:

Char. 16: 1→2
 Char. 30: 0→1
 Char. 92: 1→2

Hisonotus francirochai:

Char. 15: 0→1
 Char. 16: 2→3
 Char. 79: 0→1
 Char. 101: 1→2
 Char. 138: 2→1

Hisonotus notatus:

Char. 37: 1→0
 Char. 49: 1→0

Hypoptopoma inexpectatum:

Char. 2: 0→1
 Char. 13: 0→1
 Char. 15: 0→1
 Char. 18: 1→0
 Char. 27: 1→0
 Char. 43: 1→0
 Char. 44: 0→1
 Char. 81: 1→0
 Char. 107: 0→1

Hypostomus ancistroides:

Char. 4: 0→1
 Char. 16: 2→1
 Char. 53: 1→0
 Char. 61: 1→0

Hypostomus nigromaculatus:

Char. 13: 2→1
 Char. 20: 1→0
 Char. 22: 2→1
 Char. 29: 2→1
 Char. 43: 0→1
 Char. 59: 1→0
 Char. 73: 0→1

Hypostomus regani:

Char. 61: 1→0

Hypostomus variipictus:

No autapomorphies

Isbrueckerichthys duseni:

Char. 8: 0→1
 Char. 14: 0→1
 Char. 15: 1→0
 Char. 20: 1→0
 Char. 49: 1→0
 Char. 54: 1→0
 Char. 55: 0→1
 Char. 63: 0→1
 Char. 88: 2→1
 Char. 92: 1→2
 Char. 98: 0→1
 Char. 121: 1→0
 Char. 124: 1→0

Ixinandria steinbachi:

Char. 10: 1→2
 Char. 13: 2→1
 Char. 18: 1→0
 Char. 43: 1→0
 Char. 47: 0→1
 Char. 60: 1→0
 Char. 138: 2→1

Kronichthys heylandi:

Char. 1: 0→2
 Char. 3: 1→0

Char. 4: 0→1
 Char. 8: 0→1
 Char. 10: 1→2
 Char. 29: 0→1
 Char. 40: 1→0
 Char. 64: 0→1
 Char. 68: 1→0

Kronichthys subteres:

Char. 15: 1→0
 Char. 42: 1→0
 Char. 49: 1→0
 Char. 63: 0→1
 Char. 75: 1→0

Lamontichthys filamentosus:

Char. 4: 0→2
 Char. 16: 1→2
 Char. 25: 1→0
 Char. 31: 0→1
 Char. 40: 1→0
 Char. 63: 0→1
 Char. 71: 0→1
 Char. 73: 1→2
 Char. 77: 0→1
 Char. 81: 1→2
 Char. 128: 0→1

Lampiella gibbosa:

Char. 8: 1→0
 Char. 10: 1→2
 Char. 20: 1→0
 Char. 40: 1→0
 Char. 49: 1→0
 Char. 59: 0→1
 Char. 61: 0→1
 Char. 69: 1→0
 Char. 70: 1→0
 Char. 88: 2→0
 Char. 138: 2→1
 Char. 140: 0→1

Limatulichthys griseus:

Char. 8: 1→0
 Char. 52: 0→1

Limatulichthys petleyi:

Char. 50: 0→1

Char. 71: 1→0

Lithogenes villosus:

Char. 13: 2→1
 Char. 22: 0→2
 Char. 26: 0→1
 Char. 37: 0→1
 Char. 57: 1→0
 Char. 64: 0→1
 Char. 66: 1→0
 Char. 68: 1→0
 Char. 75: 1→0
 Char. 77: 0→1
 Char. 79: 1→0
 Char. 81: 1→2
 Char. 85: 2→0
 Char. 121: 2→0
 Char. 133: 1→0

Loricaria cataphracta:

Char. 57: 1→0

Loricaria luciae:

Char. 43: 1→0
 Char. 55: 1→0
 Char. 68: 1→0

Loricaria sp.:

Char. 8: 1→0
 Char. 10: 1→2
 Char. 19: 1→0
 Char. 24: 1→2
 Char. 42: 1→0
 Char. 52: 2→1
 Char. 61: 1→0
 Char. 85: 2→1
 Char. 88: 2→0

Loricariichthys acutus:

Char. 14: 1→0
 Char. 41: 1→0
 Char. 42: 1→0
 Char. 61: 1→0
 Char. 67: 1→0
 Char. 88: 2→1

Loricariichthys anus:

Char. 104: 1→2

Loricariichthys castaneus:

Char. 41: 1→0
 Char. 52: 1→3
 Char. 55: 1→0
 Char. 63: 0→1
 Char. 68: 1→0

Loricariichthys derbyi:

Char. 14: 0→1
 Char. 16: 2→1
 Char. 22: 1→0
 Char. 31: 1→0
 Char. 44: 1→0
 Char. 62: 0→1
 Char. 64: 1→0
 Char. 69: 2→1

Loricariichthys melanocheilus:

Char. 51: 0→1
 Char. 64: 1→0

Loricariichthys platymetopon:

Char. 2: 0→1
 Char. 24: 1→2
 Char. 29: 1→2
 Char. 80: 0→1
 Char. 81: 1→0
 Char. 91: 1→0

Loricariichthys rostratus:

Char. 61: 1→0

Loricariichthys sp.:

Char. 9: 0→1
 Char. 25: 0→1
 Char. 31: 1→0
 Char. 79: 2→0
 Char. 80: 0→1

Megalancistrus parananus:

Char. 91: 0→1

Metaloricaria paucidens:

Char. 29: 1→2
 Char. 43: 1→0
 Char. 62: 1→2
 Char. 71: 0→1

Char. 125: 0→1

Microlepidogaster perforatus:

Char. 5: 1→0
 Char. 68: 0→1
 Char. 132: 1→0

Neoplecostomus corumba:

Char. 22: 0→1
 Char. 24: 0→2

Neoplecostomus langeanii:

No autapomorphies

Neoplecostomus microps:

Char. 1: 0→1
 Char. 9: 0→1
 Char. 22: 0→1
 Char. 25: 1→0
 Char. 42: 0→1
 Char. 88: 2→0

Neoplecostomus ribeirensis:

Char. 15: 1→0
 Char. 25: 1→0

Neoplecostomus selenae:

Char. 8: 0→1
 Char. 14: 0→2
 Char. 20: 1→0
 Char. 38: 1→0
 Char. 43: 1→0
 Char. 59: 0→1
 Char. 88: 2→0

Neoplecostomus yapo:

Char. 22: 0→1
 Char. 31: 1→0

Otocinclus affinis:

Char. 19: 0→1
 Char. 40: 1→0
 Char. 70: 1→0
 Char. 91: 1→0
 Char. 93: 1→2

Otothyris lophophanes:

Char. 8: 1→0

Char. 19: 0→1
 Char. 69: 0→1
 Char. 78: 1→0

Otothyris rostrata:

Char. 75: 1→0
 Char. 101: 1→2

Otothyropsis marapoama:

No autapomorphies

Oxyropsis wrightiana:

Char. 14: 0→2
 Char. 138: 2→0

Paraloricaria vetula:

Char. 4: 2→1
 Char. 15: 1→0
 Char. 54: 0→1
 Char. 74: 0→1
 Char. 138: 2→1

Pareiorhaphis cameroni:

Char. 42: 1→0
 Char. 75: 1→0

Pareiorhaphis hystrix:

Char. 30: 0→1
 Char. 63: 0→1
 Char. 67: 0→1
 Char. 70: 1→0
 Char. 89: 0→1
 Char. 113: 1→2

Pareiorhina carrancas:

Char. 2: 1→0
 Char. 3: 1→0
 Char. 6: 0→1
 Char. 7: 0→1
 Char. 9: 0→1
 Char. 10: 1→0
 Char. 42: 1→0

Pareiorhina rudolphi:

Char. 15: 1→0
 Char. 68: 1→0

Parotocinclus jumbo:

Char. 5: 1→0
 Char. 10: 1→0
 Char. 18: 0→1
 Char. 20: 1→0
 Char. 64: 1→0
 Char. 69: 1→0
 Char. 85: 2→0
 Char. 121: 1→0

Parotocinclus maculicauda:

Char. 4: 0→2
 Char. 12: 0→1
 Char. 14: 2→0
 Char. 29: 0→1
 Char. 31: 0→1
 Char. 38: 0→1
 Char. 44: 1→0
 Char. 78: 1→0

Parotocinclus prata:

Char. 2: 0→1
 Char. 101: 2→1
 Char. 102: 1→0

Pimelodus argenteus:

No autapomorphies

Pimelodus maculatus:

Char. 63: 0→1

Planiloricaria cryptodon:

Char. 53: 0→1
 Char. 119: 0→1
 Char. 140: 1→0

Plesioptopoma curvidens:

Char. 32: 1→0
 Char. 40: 1→0
 Char. 88: 2→0

Proloricaria prolixa:

Char. 8: 1→0
 Char. 48: 0→1
 Char. 59: 2→1
 Char. 82: 1→0
 Char. 85: 2→1

Pseudohemiodon laticeps:

Char. 68: 1→0

***Pseudohemiodon
platycephalus:***

Char. 18: 0→1
Char. 100: 1→0

Pseudohemiodon sp.:

Char. 14: 1→0
Char. 44: 1→2

Pseudoloricaria laeviscula:

Char. 15: 0→1
Char. 29: 1→2
Char. 53: 0→1
Char. 59: 0→1
Char. 77: 2→1
Char. 80: 0→1
Char. 92: 2→1
Char. 97: 1→0

Pseudoloricaria punctata:

Char. 86: 1→0

Pseudopimelodus bufonius:

No autapomorphies

Pseudopimelodus mangurus:

Char. 16: 0→1

Pseudotocinclus tietensis:

Char. 5: 1→0
Char. 6: 0→1
Char. 17: 0→1
Char. 19: 1→0
Char. 70: 1→0
Char. 88: 2→0
Char. 89: 0→1

Pseudotothyris obtusa:

Char. 3: 0→1
Char. 7: 0→1
Char. 9: 1→2
Char. 10: 1→0
Char. 64: 0→1
Char. 103: 1→0
Char. 121: 1→0

Pyxiloricaria menezis:

Char. 30: 0→1
Char. 42: 1→0
Char. 47: 0→1
Char. 60: 1→0
Char. 68: 1→0
Char. 82: 1→0
Char. 87: 2→1
Char. 88: 2→1

Reganella depressa:

Char. 29: 1→0
Char. 34: 2→3
Char. 45: 0→1
Char. 86: 1→0
Char. 88: 2→0
Char. 104: 1→0

Rhadinoloricaria sp:

Char. 9: 0→1
Char. 19: 1→0
Char. 52: 0→2
Char. 71: 0→1
Char. 82: 1→0
Char. 83: 1→0
Char. 88: 2→0
Char. 105: 1→0
Char. 140: 1→2

Rhinelepis aspera:

Char. 27: 1→0
Char. 42: 1→0
Char. 53: 1→0
Char. 61: 1→0
Char. 65: 0→1
Char. 84: 0→1
Char. 96: 0→1
Char. 117: 0→1
Char. 119: 1→0
Char. 124: 1→0

Rhinolekos britskii:

Char. 1: 1→0
Char. 9: 0→1
Char. 15: 0→1
Char. 37: 1→0
Char. 59: 0→1

Ricola macrops:

Char. 5: 0→1
 Char. 14: 0→1
 Char. 21: 1→0
 Char. 41: 1→0
 Char. 51: 0→1
 Char. 68: 1→0
 Char. 147: 1→2

Rineloricaria cacerensis:

Char. 73: 2→1

Rineloricaria cf. lima:

Char. 14: 1→0
 Char. 16: 2→0
 Char. 30: 0→1
 Char. 43: 1→0
 Char. 49: 0→1
 Char. 81: 1→2
 Char. 97: 1→0
 Char. 104: 1→2

Rineloricaria formosa:

Char. 24: 0→2
 Char. 31: 1→0
 Char. 51: 1→0
 Char. 62: 1→0
 Char. 77: 0→2
 Char. 83: 1→0
 Char. 87: 1→2

Rineloricaria parva:

Char. 43: 1→0
 Char. 44: 1→0
 Char. 88: 2→1

Rineloricaria quadrensis:

Char. 36: 0→1
 Char. 77: 0→1
 Char. 87: 1→2

Rineloricaria strigilata:

Char. 21: 1→0

Schizolecis guntheri:

Char. 7: 0→1
 Char. 10: 1→0
 Char. 15: 0→1

Char. 18: 0→1
 Char. 22: 0→1
 Char. 30: 0→1
 Char. 44: 1→2
 Char. 48: 1→0
 Char. 121: 1→0
 Char. 124: 1→0

Scleromystax barbatus:

Char. 14: 1→0
 Char. 15: 1→0
 Char. 53: 1→0
 Char. 88: 0→1

Spatuloricaria evansii:

Char. 51: 0→1
 Char. 52: 1→0
 Char. 58: 2→1
 Char. 62: 1→0
 Char. 87: 1→0

Spatuloricaria nudiventris:

Char. 8: 1→0
 Char. 15: 1→0
 Char. 42: 1→0
 Char. 54: 0→1

Spatuloricaria tuira:

Char. 13: 2→1
 Char. 16: 1→0
 Char. 24: 1→0
 Char. 43: 0→1
 Char. 104: 1→2

Sturisoma barbatum:

Char. 15: 0→1
 Char. 24: 2→1
 Char. 40: 1→0
 Char. 44: 1→2
 Char. 63: 0→1

Sturisoma guentheri:

Char. 44: 1→2
 Char. 64: 0→1

Sturisoma panamensis:

Char. 29: 1→2
 Char. 75: 1→0

Sturisoma robustum:

Char. 24: 2→1
 Char. 44: 1→02
 Char. 48: 0→1

Sturisoma rostratum:

Char. 29: 1→2
 Char. 63: 0→1
 Char. 103: 0→1

Sturisoma tenuirostre:

Char. 15: 0→1
 Char. 69: 1→2
 Char. 75: 1→0
 Char. 84: 1→0

Sturisomatichthys leightoni:

Char. 2: 1→0
 Char. 4: 0→2
 Char. 16: 1→2
 Char. 33: 0→1
 Char. 40: 1→0
 Char. 73: 1→2
 Char. 119: 1→0

Clade 130:

Char. 7: 0→1
 Char. 8: 1→0
 Char. 16: 2→1
 Char. 22: 0→1
 Char. 69: 0→2
 Char. 124: 0→1

Clade 131:

Char. 96: 1→0
 Char. 100: 2→1
 Char. 105: 1→0
 Char. 107: 1→0
 Char. 115: 1→0

Clade 132:

Char. 5: 1→0
 Char. 9: 0→1
 Char. 69: 1→0
 Char. 88: 2→0

Clade 133:

Char. 14: 2→0
 Char. 20: 1→0
 Char. 22: 1→0
 Char. 34: 1→0
 Char. 60: 0→1
 Char. 61: 1→0
 Char. 68: 0→1
 Char. 76: 1→0
 Char. 85: 0→2
 Char. 95: 1→2

Clade 134:

Char. 96: 0→1

Clade 135:

Char. 44: 1→02
 Char. 64: 1→0

Clade 136:

Char. 61: 0→1
 Char. 81: 2→1
 Char. 101: 2→1
 Char. 113: 2→1

Clade 137:

Char. 22: 0→1
 Char. 68: 1→0
 Char. 115: 0→1
 Char. 124: 1→0

Clade 138:

Char. 19: 1→0
 Char. 24: 1→0

Clade 139:

Char. 1: 0→1
 Char. 32: 1→0
 Char. 35: 1→0
 Char. 42: 1→0
 Char. 85: 2→0

Clade 140:

Char. 9: 1→0
 Char. 11: 0→1
 Char. 37: 0→1
 Char. 79: 1→0

Clade 141:

Char. 6: 0→1
 Char. 8: 0→1
 Char. 41: 0→1
 Char. 47: 0→1
 Char. 57: 1→0
 Char. 141: 0→1

Clade 142:

Char. 48: 0→1
 Char. 61: 1→0

Clade 143:

Char. 2: 1→0
 Char. 11: 1→0

Clade 144:

Char. 9: 0→1
 Char. 41: 1→0
 Char. 108: 1→0
 Char. 113: 1→2
 Char. 129: 0→1
 Char. 130: 0→1
 Char. 131: 0→1

Clade 145:

Char. 13: 2→0
 Char. 16: 1→2
 Char. 18: 1→0
 Char. 34: 2→1
 Char. 58: 1→0
 Char. 66: 1→0
 Char. 73: 1→0
 Char. 77: 0→2
 Char. 81: 1→2
 Char. 94: 0→1
 Char. 104: 1→2
 Char. 117: 0→1
 Char. 132: 0→1

Clade 146:

Char. 10: 2→1
 Char. 53: 1→0
 Char. 59: 1→0
 Char. 88: 0→2
 Char. 91: 0→1
 Char. 121: 2→1

Clade 147:

Char. 21: 1→0
 Char. 30: 1→0
 Char. 42: 0→1
 Char. 82: 1→0
 Char. 100: 0→2
 Char. 108: 0→1
 Char. 109: 0→1
 Char. 113: 0→1
 Char. 114: 1→0

Clade 148:

Char. 14: 1→2
 Char. 16: 0→1
 Char. 20: 0→1
 Char. 25: 0→1
 Char. 31: 1→0
 Char. 34: 3→2
 Char. 73: 2→1
 Char. 78: 0→1
 Char. 83: 1→0
 Char. 84: 1→0
 Char. 92: 0→1

Clade 149:

Char. 62: 0→2
 Char. 85: 1→2
 Char. 139: 0→1
 Char. 142: 0→1
 Char. 144: 1→0

Clade 150:

Char. 54: 1→0
 Char. 58: 2→1
 Char. 59: 2→1
 Char. 64: 1→0
 Char. 67: 1→0
 Char. 74: 1→0
 Char. 75: 0→1
 Char. 80: 1→0
 Char. 81: 0→1
 Char. 82: 0→1
 Char. 111: 2→1
 Char. 122: 0→1
 Char. 137: 0→1
 Char. 146: 2→01

Clade 151:

Char. 2: 3→1

Char. 36: 0→1
 Char. 41: 0→1
 Char. 62: 1→0
 Char. 66: 2→1

Clade 152:
 No synapomorphies

Clade 153:
 Char. 14: 2→0
 Char. 38: 0→1
 Char. 58: 1→0
 Char. 88: 01→2
 Char. 143: 0→1

Clade 154:
 Char. 16: 1→2
 Char. 73: 1→0

Clade 155:
 Char. 103: 0→1
 Char. 135: 0→1

Clade 156:
 Char. 7: 0→1
 Char. 22: 0→2
 Char. 51: 1→0
 Char. 77: 0→2
 Char. 127: 0→1
 Char. 136: 0→1

Clade 157:
 Char. 43: 1→0
 Char. 63: 0→1
 Char. 70: 1→0
 Char. 79: 1→2

Clade 158:
 Char. 60: 1→0
 Char. 62: 1→0
 Char. 104: 1→0

Clade 159:
 Char. 48: 1→0
 Char. 138: 2→1

Clade 160:
 Char. 36: 0→1

Char. 72: 0→1
 Char. 77: 2→1
 Char. 115: 0→1
 Char. 135: 1→0

Clade 161:
 Char. 100: 1→0

Clade 162:
 Char. 18: 1→0
 Char. 20: 1→0

Clade 163:
 Char. 49: 0→1
 Char. 82: 0→1
 Char. 93: 2→0
 Char. 147: 2→1

Clade 164:
 Char. 21: 0→1
 Char. 25: 1→0
 Char. 31: 0→1
 Char. 36: 1→0
 Char. 39: 0→1
 Char. 67: 0→1
 Char. 83: 0→1
 Char. 89: 0→1
 Char. 97: 0→1
 Char. 119: 1→0

Clade 165:
 Char. 27: 1→0
 Char. 33: 0→1
 Char. 37: 0→1
 Char. 48: 0→1
 Char. 64: 0→1
 Char. 79: 1→2
 Char. 92: 1→2
 Char. 93: 1→2
 Char. 100: 2→1
 Char. 101: 2→1
 Char. 113: 1→0

Clade 166:
 Char. 6: 0→1
 Char. 15: 1→0
 Char. 22: 0→1
 Char. 49: 1→0

Char. 78: 1→0
 Char. 84: 0→1
 Char. 124: 1→0
 Char. 140: 0→1
 Char. 149: 0→1

Clade 167:

Char. 22: 1→0
 Char. 93: 1→2
 Char. 108: 1→0
 Char. 111: 1→0
 Char. 140: 1→2

Clade 168:

Char. 44: 1→2
 Char. 48: 0→1
 Char. 64: 0→1
 Char. 84: 1→0
 Char. 121: 1→0

Clade 169:

Char. 67: 0→1
 Char. 72: 0→1
 Char. 104: 1→2

Clade 170:

Char. 99: 0→1
 Char. 106: 0→1
 Char. 145: 0→1
 Char. 146: 0→2

Clade 171:

Char. 16: 0→1
 Char. 20: 1→0
 Char. 33: 1→0
 Char. 43: 1→0

Clade 172:

Char. 14: 1→0
 Char. 22: 0→1

Clade 173:

Char. 15: 0→1
 Char. 58: 1→2
 Char. 72: 0→1

Clade 174:

Char. 52: 0→2

Char. 53: 0→1
 Char. 56: 0→1
 Char. 67: 1→0

Clade 175:

Char. 16: 1→0
 Char. 69: 1→2
 Char. 77: 02→1

Clade 176:

Char. 34: 2→3
 Char. 51: 1→0

Clade 177:

Char. 30: 0→1
 Char. 33: 1→0
 Char. 67: 1→0

Clade 178:

Char. 1: 0→1
 Char. 16: 2→1
 Char. 18: 0→1
 Char. 22: 0→1
 Char. 42: 1→0
 Char. 59: 0→1
 Char. 62: 1→2
 Char. 68: 1→0
 Char. 95: 1→2

Clade 179:

Char. 2: 0→1
 Char. 20: 1→0
 Char. 31: 0→1
 Char. 81: 2→1

Clade 180:

Char. 6: 1→0
 Char. 14: 2→0
 Char. 44: 1→2
 Char. 78: 1→0
 Char. 88: 2→1

Clade 181:

Char. 8: 1→0
 Char. 16: 2→1
 Char. 32: 0→1
 Char. 47: 1→0

Clade 182:

Char. 2: 1→0
 Char. 4: 0→1
 Char. 6: 0→1
 Char. 7: 0→1
 Char. 10: 2→0
 Char. 33: 0→1
 Char. 63: 0→1
 Char. 109: 0→1
 Char. 125: 2→1

Clade 183:

Char. 4: 0→2
 Char. 8: 1→0
 Char. 36: 0→1
 Char. 52: 0→1
 Char. 61: 1→0
 Char. 62: 1→0
 Char. 72: 0→1
 Char. 79: 2→0
 Char. 85: 2→1
 Char. 93: 0→1

Clade 184:

Char. 19: 1→0
 Char. 47: 0→1
 Char. 104: 1→0

Clade 185:

Char. 16: 1→0
 Char. 71: 0→1
 Char. 87: 2→1
 Char. 136: 0→1

Clade 186:

Char. 59: 0→1

Clade 187:

Char. 32: 1→0
 Char. 47: 0→1

Clade 188:

Char. 24: 2→1
 Char. 25: 1→0

Clade 189:

Char. 37: 0→1
 Char. 77: 0→2

Char. 81: 1→2
 Char. 138: 2→0

Clade 190:

Char. 28: 0→1
 Char. 42: 1→0
 Char. 58: 2→1
 Char. 59: 2→1
 Char. 72: 1→0
 Char. 73: 2→1

Clade 191:

Char. 4: 2→0
 Char. 25: 0→1
 Char. 63: 0→1
 Char. 67: 0→1

Clade 192:

Char. 19: 1→0
 Char. 21: 0→1
 Char. 25: 1→0
 Char. 31: 0→1
 Char. 48: 0→1
 Char. 65: 0→1
 Char. 73: 1→0
 Char. 88: 0→2
 Char. 101: 2→1
 Char. 102: 1→0

Clade 193:

Char. 35: 1→0
 Char. 46: 1→0
 Char. 120: 1→0
 Char. 148: 0→1

Clade 194:

Char. 4: 2→0
 Char. 57: 1→0

Clade 195:

Char. 60: 1→0

Clade 196:

Char. 8: 1→0
 Char. 20: 1→0
 Char. 24: 2→0

Clade 197:

Char. 16: 1→2

Char. 48: 1→0

Clade 198:

Char. 25: 1→0

Char. 41: 1→0

Clade 199:

Char. 4: 0→2

Char. 13: 2→1

Char. 19: 1→0

Char. 34: 2→1

Char. 42: 1→0

Char. 61: 1→0

Char. 67: 1→0

Char. 79: 1→2

Char. 103: 0→1

Char. 119: 1→0

Char. 126: 1→0

Clade 200:

Char. 18: 1→0

Char. 24: 0→2

Char. 41: 0→1

Char. 44: 2→1

Char. 47: 0→1

Char. 48: 0→1

Char. 58: 1→0

Clade 201:

Char. 21: 1→0

Char. 42: 1→0

Char. 44: 1→2

Clade 202:

Char. 44: 2→1

Char. 47: 1→0

Char. 52: 0→3

Clade 203:

Char. 60: 1→0

Clade 204:

Char. 13: 2→1

Char. 21: 1→0

Char. 22: 1→0

Char. 57: 1→0

Char. 113: 1→2

Clade 205:

Char. 15: 0→1

Char. 19: 1→0

Char. 24: 1→0

Char. 47: 0→1

Char. 48: 1→0

Char. 49: 1→0

Char. 92: 2→1

Char. 93: 0→1

Char. 101: 1→0

Char. 105: 1→0

Clade 206:

Char. 51: 1→0

Char. 73: 2→1

Char. 140: 1→2

Clade 207:

Char. 9: 1→2

Char. 11: 1→0

Char. 25: 0→1

Char. 62: 1→0

Char. 75: 1→0

Clade 208:

Char. 31: 0→1

Char. 52: 2→0

Clade 209:

Char. 15: 1→0

Clade 210:

Char. 75: 1→0

Clade 211:

Char. 33: 0→1

Char. 35: 0→1

Char. 66: 0→1

Char. 69: 1→2

Clade 212:

Char. 10: 1→2

Char. 11: 1→0

Char. 18: 0→1

Char. 31: 0→1

Char. 34: 1→2

Char. 40: 1→0

Char. 61: 0→1
 Char. 62: 1→2
 Char. 115: 0→1

Clade 213:

Char. 14: 2→0
 Char. 54: 0→1
 Char. 57: 1→0
 Char. 85: 2→0
 Char. 135: 0→1
 Char. 147: 2→3

Clade 214:

Char. 48: 0→1
 Char. 61: 1→0
 Char. 79: 1→0
 Char. 133: 1→0

Clade 215:

Char. 11: 1→0
 Char. 13: 0→1
 Char. 22: 0→1
 Char. 47: 0→1
 Char. 88: 2→1
 Char. 91: 1→0
 Char. 93: 1→2
 Char. 120: 1→0

Clade 216:

Char. 42: 1→0
 Char. 62: 1→0
 Char. 63: 0→1
 Char. 64: 1→0
 Char. 72: 0→1

Clade 217:

Char. 34: 2→3
 Char. 43: 1→0
 Char. 67: 1→0
 Char. 81: 1→0

Clade 218:

Char. 22: 0→1
 Char. 50: 0→1
 Char. 51: 0→1
 Char. 52: 2→0
 Char. 54: 0→1
 Char. 60: 1→0

Char. 104: 1→0

Clade 219:

Char. 20: 1→0
 Char. 21: 1→0
 Char. 69: 2→1

Clade 220:

Char. 30: 0→1
 Char. 87: 2→1

Clade 221:

Char. 18: 1→0
 Char. 24: 1→2

Clade 222:

Char. 4: 0→1
 Char. 43: 1→0
 Char. 52: 0→1
 Char. 136: 0→1

Clade 223:

Char. 10: 1→2
 Char. 42: 1→0
 Char. 50: 0→1
 Char. 85: 2→1

Clade 224:

Char. 14: 1→0
 Char. 69: 1→2

Clade 225:

Char. 16: 1→2
 Char. 62: 1→0

Clade 226:

Char. 54: 0→1
 Char. 61: 1→0

Clade 227:

Char. 19: 0→1
 Char. 35: 0→1
 Char. 38: 0→1
 Char. 48: 1→0
 Char. 96: 0→1

Clade 228:

Char. 9: 0→1

Char. 31: 1→0
Char. 88: 2→1

Clade 229:

Char. 10: 2→1
Char. 14: 0→2
Char. 19: 0→2
Char. 73: 0→1

Clade 230:

Char. 30: 0→1
Char. 41: 1→0
Char. 42: 1→0
Char. 48: 1→0
Char. 50: 0→1
Char. 56: 0→1
Char. 71: 0→1
Char. 77: 2→0
Char. 91: 1→0
Char. 94: 1→0
Char. 136: 0→1
Char. 147: 3→2

Clade 231:

Char. 2: 0→1
Char. 15: 0→1
Char. 49: 1→0
Char. 62: 1→0
Char. 91: 1→0

Clade 232:

Char. 12: 0→1
Char. 32: 0→1
Char. 35: 0→1
Char. 138: 2→1

Clade 233:

Char. 14: 2→0
Char. 19: 1→0
Char. 92: 1→2
Char. 135: 0→1

Clade 234:

Char. 2: 0→1
Char. 25: 0→1
Char. 36: 1→0
Char. 51: 1→0
Char. 52: 0→1

Char. 101: 1→2

Clade 235:

Char. 42: 0→1
Char. 55: 1→0

Clade 236:

Char. 54: 0→1
Char. 60: 0→1
Char. 72: 1→0
Char. 77: 1→0
Char. 138: 1→2

Clade 237:

Char. 4: 0→2
Char. 14: 1→0
Char. 24: 1→0
Char. 25: 0→1
Char. 31: 1→0
Char. 43: 1→0
Char. 44: 1→2
Char. 68: 1→0
Char. 73: 2→0
Char. 77: 0→2
Char. 83: 1→0
Char. 84: 1→0
Char. 85: 1→0
Char. 114: 1→0

Clade 238:

Char. 68: 1→0
Char. 71: 1→0
Char. 100: 1→0

Clade 239:

Char. 15: 0→1
Char. 48: 1→0
Char. 88: 2→1

Clade 240:

Char. 24: 1→0
Char. 42: 1→0

Clade 241:

Char. 16: 1→2
Char. 71: 0→1

Clade 242:

Char. 9: 0→1
Char. 72: 0→1
Char. 87: 2→1

Clade 243:

Char. 14: 0→1
Char. 36: 0→1
Char. 48: 0→1

Clade 244:

Char. 22: 1→0
Char. 56: 1→0
Char. 59: 2→1
Char. 60: 1→0
Char. 68: 1→0
Char. 69: 2→1
Char. 83: 1→0
Char. 87: 2→1
Char. 101: 1→2
Char. 138: 2→1

Char. 147: 1→2

Clade 245:

Char. 34: 2→1
Char. 62: 1→0
Char. 101: 2→1
Char. 140: 1→2
Char. 146: 2→1

Clade 246:

Char. 27: 1→0
Char. 49: 0→1
Char. 51: 1→0
Char. 79: 1→2

Clade 247:

Char. 31: 0→1
Char. 40: 1→0
Char. 64: 0→1

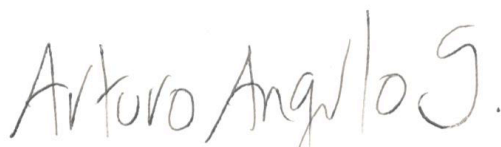


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