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

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

São José do Rio Preto
2019

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

Orientador: Prof. Dr. Francisco Langeani Neto

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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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São José do Rio Preto
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 Rodriguez (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 Rhinelepinae)] 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, "Otothyrinae" and Rhinelepinae)] 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 needing 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	*Adenohypophysis*
Ce	*Corpus cerebelli*
Ch	*Chiasma opticum*
Char	Character
De	Delturinae
EG	E*minentia granularis*
Hp	*Adenohypophysis/*Hypoptopomatinae
Hy	Hypothalamus/Hypostominae
I	*Nervus olfatorius*
II	*Nervus opticus*
III	*Nervus oculomotorius*
IV	*Nervus trochlearis*
IX	*Nervus glossopharyngeus*
La	Ofactory lamella
LF	Loricariinae, Loricarini, Farlowellina
LH	L*obus inferior hypothalami/*Loricariinae, Harttiini
Li	Lithogeninae
LL	Loricariinae, Loricarini, Loricarina
LLA	*Nervus linea lateralis anterior*
LLP	*Nervus linea lateralis posterior*
LobVII	*Lobus facialis*
LobX	*Lobus vagi*
MO	Alar portion of the *medulla oblongata*
Me	*Medulla spinalis*
Ne	Neoplecostominae
OB	Olfactory bulbs
Of	Olfactory organ
OT	Optic tectum
Rh	Rhinelepinae
TC	*Truncus cerebri*
SL	Standard length
Te	Telencephalon

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

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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, Neartic 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 andevaluate 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).

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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