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Critical review and mapping of the distribution of species of the *Hoplias* genus in South America

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Abstract

This study aimed to understand the biogeographic distribution and taxonomic diversity of the *Hoplias* genus, with special emphasis on the *Hoplias malabaricus* species. The research was carried out based on bibliographies referring to small river basins along the east coast of South America, with a focus on the Brazilian territory. Thus, the data collection was conducted through a literature review. Therefore, the main taxonomic studies indicated that *H. malabaricus* represents a complex group, exhibiting significant osteological and karyotypic variability, especially in regions of smaller basins. On the other hand, the biogeographic analysis methods showed significant segregation among species of the *Hoplias* genus among populations from different regions. Thus, a high taxonomic diversity and biogeographic patterns were revealed. Where the main conclusion points to the need for additional research to explore the geographic distribution and the microevolutionary processes involved, aiming to reduce knowledge gaps and promote a deeper understanding of the diversity of these species.

Keys world: phylogeography, cryptodiversity, ecology, systematics, genetic variability.

Resumo - Revisão crítica e mapeamento da distribuição de espécies do gênero *Hoplias* na América do Sul

Este estudo teve como objetivo compreender a distribuição biogeográfica e a diversidade taxonômica do gênero *Hoplias*, com ênfase especial na espécie *Hoplias malabaricus*. A pesquisa foi realizada baseada em bibliografias que se referem às pequenas bacias hidrográficas ao longo da costa leste da América do Sul, com foco principal no território brasileiro. Deste modo, o levantamento de dados foi conduzido através de uma revisão da literatura. Portanto, os principais estudos taxonômicos indicaram que *H. malabaricus* representa um grupo complexo, exibindo uma expressiva variabilidade osteológica e cariotípica, especialmente em regiões de bacias menores. Por outro lado, os métodos de análise biogeográfica mostraram uma significativa segregação entre espécies do gênero *Hoplias* entre populações de diferentes regiões. Sendo assim, revelou-se uma alta diversidade taxonômica e padrões biogeográficos. Onde, a principal conclusão aponta para a necessidade de pesquisas adicionais para explorar a distribuição geográfica e os processos microevolutivos envolvidos, visando reduzir lacunas no conhecimento e promover uma compreensão mais profunda da diversidade dessas espécies.

Palavras-chave: filogeografia, criptodiversidade, ecologia; sistemática, variabilidade genética.

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Resumen - Revisión crítica y mapeo de la distribución de especies del género Hoplias en América del Sur

Este estudio tuvo como objetivo comprender la distribución biogeográfica y la diversidad taxonómica del género *Hoplias*, con especial énfasis en la especie *Hoplias malabaricus*. La investigación se realizó con base en bibliografías que hacen referencia a pequeñas cuencas hidrográficas a lo largo de la costa este de América del Sur, con foco principal en el territorio brasileño. Así, la recolección de datos se realizó a través de una revisión de la literatura. Por lo tanto, los principales estudios taxonómicos indicaron que *H. malabaricus* representa un grupo complejo, que exhibe una variabilidad osteológica y cariotípica significativa, especialmente en regiones con cuencas más pequeñas. Por otra parte, los métodos de análisis biogeográfico mostraron una segregación significativa entre especies del género *Hoplias* entre poblaciones de diferentes regiones. De esta forma se reveló una alta diversidad taxonómica y patrones biogeográficos. Donde, la principal conclusión apunta a la necesidad de investigación adicional para explorar la distribución geográfica y los procesos microevolutivos involucrados, con el objetivo de reducir las brechas en el conocimiento y promover una comprensión más profunda de la diversidad de estas especies.

Palabras clave: Filogeografía; Criptodiversidad; Ecología; Sistemático; Variabilidad genética.

Introdução

The *Hoplias* genus is a main member of the Erythrinidae family, which in turn belongs to the Characiformes order, and was described by Theodore Gill in 1903. The fish belonging to this taxonomic grouping are notable for their predatory nature and wide distribution in South American freshwater environments. They include specimens known vernacularly as wolf fishes or trahiras, and giant wolf fishes (Oyakawa & Mattox 2009; Guimarães et al. 2021a). They have ecological importance as a predator, often indisputable in some watercourses (Rosso et al. 2018). They make up the assembly of these complex hydrographic systems, including rivers, waterfalls, lakes and reservoirs (Sassi et al. 2021). Therefore, it also has great economic importance, whether for fish farming, as animal protein, or for sport fishing or aquarium hobby, as there are many enthusiasts who greatly appreciate its aggressiveness and the large size of some specimens (Saviato et al. 2024a). It has a wide distribution, both natural and artificial, in several regions of the South American Shield, including waterways in North America (Albert et al. 2020).

These animals have morphological characteristics that make them clearly distinguishable from other groups of continental fish, even from closely related families. However, the attributes within the *Hoplias* genus are very acute, making identification at a specific level difficult for careless eyes (Rosso et al. 2018). And with the improvement of field and laboratory work, it has given new directions to the understanding of the identification of taxonomic entities and their distribution (Albert et al. 2020)

In this context, we can segregate the *Hoplias* genus into 3 (three) distinct groups, the *H. aimara* group, derived from the following group due to unique characteristics and large body size, the *H. lacerdae* group and finally the *H. malabaricus* group. The *H.* lacerdae group, in turn, described by Oyakawa (1990), proposes a discernible grouping based on specific morphological characteristics, having a more stable genetic pattern (Sassi et al. 2021). However, revisiting this taxonomic set, and considering the recent additions, it is possible to identify that there is a geographic expansion, manifested by the addition of specimens in ichthyological collections over time, attesting to the need for a more refined review (Ferreira et al. 2021).

Furthermore, the other organisms of the Erythrinidae family, which include the *Hoplias* genus, *Hoplerythrinus* and *Erythrinus*, cannot be separated, as they are equally important (Iaeger et al. 2022). However, the *Hoplias* genus stands out, with special emphasis on the Southeast region of Brazil, two distinct groups emerge, *H. malabaricus* and *H. lacerdae*, exhibiting notable karyotypic disparities (Pires et al. 2020, Guimarães et al. 2022). However, the taxonomic complexity is much higher in *H. malabaricus*, consecrated as a "species complex" due to its karyotypic multiplicity, morphological similarity and territorial overlap, while *H. lacerdae* presents itself as the holder of only 9 (nine) singular entities in some hydrographic basins of Brazil (Oyakawa & Mattox 2009; Sassi et al. 2021).

Thus, the American water systems harbor an unparalleled diversity of life, where the *Hoplias* genus presents itself as a striking protagonist in this scenario (Diniz et al. 2023). Where the species of this group occupy extensive areas of freshwater in the Neotropical region (Estrada et al. 2021). Among them, we can highlight the species present in the Western Amazon of the *H. aimara* group, those present in the Eastern Amazon and Paraná-Paraguay Basins, of the *H. lacerdae* group, and finally the trahira of the most complex and diverse

group, *H. malabaricus* (Saviato et al. 2024b). The latter, however, behind its apparent homogeneity, reveals intricate genetic nuances that instigate a deep questioning about the biogeographic reality of this fish (Sharpe et al. 2023).

Therefore, given its morphological, karyotypic and sympatric diversity, the *H. malabaricus* complex is an intricate web of almost indistinguishable unknowns (Sproul et al. 2020). Where the variations that extend from karyotyped populations to large territorial coverages reveal numerous distinct karyomorphic organisms, suggesting the existence of a complex of species or paraspecies (Takagui et al. 2020). And so, even with a more incisive analysis, it is possible to affirm that they are still quite identical to each other (Moraes et al. 2023).

Recently, some studies have highlighted a notable heterogeneity in the sampled species, contrasting among themselves by these aspects including behavioral appearance (Winemiller et al. 2021). Such divergences, associated with distinct patterns of biogeography and the presence of cryptic or sympatric specimens in this heteromorphic mosaic, point to a complex evolutionary history shaped by the geological dynamics of each region (Barby et al. 2019).

Several authors indicate that genetic analyses corroborate the hypothesis that this group dispersed in the late Miocene. And that during the Last Glacial Maximum (LGM), the geographic distribution of this taxonomic complex was restricted to the North and Northeast of South America, and in the Anthropocene, there was a reduction in potential areas. Indicating that the drainages of the eastern portion of the Amazon basin and the coastal drainages of the western basin of the Northeast Atlantic played crucial roles in the routes of population dispersals (Carrillo-Briceño et al. 2021). This suggests that, while many taxa already have their profile well known, other groups, such as the *H. malabaricus* complex, represent a more recent and less derived condition (Souza et al. 2020; Sassi et al. 2021). From this perspective, it offers a unique window, still little explored, to understand not only the evolution of this group, but also its complex geographic distribution in the South American region (Araújo-Flores et al. 2021).

Therefore, by interposing the results of genetic and morphological studies with geological history, it is possible to correlate and unravel the intricate complexity of this taxonomic group (Rosso et al. 2018). Thus, contributing to a broader understanding of the evolution and diversity of Neotropical species (Casatti et al., 2020; Ibagón et al. 2020). Thus, this study stands as a treatise, outlining a summarized overview of the prominent role of the *Hoplias* genus in Neotropical ichthyology, aiming to provide substantial contributions to the understanding of the diversity and biogeography of these organisms in South America.

Materials and methods

Theoretical basis

The scientific exploration of South American ichthyofauna has led to a foray into the past, recovering data from well-founded theoretical and conceptual strategies, combined with a detailed characterization of the regional hydrographic network. Thus, such studies on the South American continent spanned three distinct historical eras. Between 1750 and 1866, European naturalists played a seminal role in cataloging specimens of commercial importance. The period from 1866 to 1930 witnessed the prominence of European and North American ichthyologists, marked by comprehensive descriptions of species from various groups (Böhlke et al. 1978). The continuity in cataloging has lasted from 1930 to the present day, with contributions coming from North America, Europe and South America. However, even with these efforts, approximately 30 to 40% of the South American freshwater fish fauna remains awaiting taxonomic cataloging (Kavalco & Pazza 2007, Veiga & Melki 2022).

And in a broader scope, South America includes freshwater fish that make up approximately 40% of vertebrate species (Saviato et al. 2020), this Neotropical region stands out for being home to one third of the global ichthyofauna (Buckup 2021). The orders Characiformes, Siluriformes and Gymnotiformes stand out, while analyses of paleogeography (Demétrio et al. 2022), especially in the Amazon region, provide crucial insights into the historical conditions that shaped the exuberant biodiversity (Ferreira et al. 2021). However, this data set is less explored in the coastal areas of northeastern Brazil (Nascimento et al. 2021).

The scarcity of sources, with the lack of museum specimens for pertinent comparisons, and the scarce production of faunal studies in different areas pose significant challenges for ichthyologists and fisheries biologists in South America (Dopazo et al. 2023). There is an urgent need to scrutinize and rediscover species cataloged before 1870, as well as to carry out contemporary taxonomic revisions for most groupings of South American freshwater fishes (Castro 2021).

In the biogeographic context of this genus, sculpted by millions of years of evolution and shaped by geographic and climatic adversities in South America, it serves as a setting for more refined analyses (Dal Negro et al. 2022). Where the suggestion of revalidation of nomenclatures for some species highlights the urgency of more in-depth investigations, using additional markers, to address possible gaps in the ordering of lineages (Gallo et al. 2021). As well as the real geographic distribution of the species already identified and correctly cataloged, facilitating the understanding of new researchers who want to explore these groups (Figueiredo et al. 2022).

Therefore, specific research on river basins aims to discern biogeographic events, elucidating their impact on the dispersal, extinction and speciation of freshwater fish species (Gallo et al. 2021). Using geomorphological data, these studies highlight the significant influence of sea level variation events on the composition and distribution of species, highlighting the need to understand such events to interpret the incessant evolution of fish communities in this macroregion (Becker & Camana 2021).

In this scope, some groups whose relevance in fishing activities in the main South American river basins motivates a more pronounced approach, integrating with molecular studies to elucidate their phylogeny and systematics (Buckup 2021). Thus, molecular phylogenetic analysis, using specific genes, was conducted through models that combined or diverged certain past groupings, such as the *Hoplias* genus, more specifically the *H. malabaricus* group (Guimarães et al. 2021b). However, a more incisive approach regarding biological diversity and its territorial allocation is still incipient and deserves more attention (Saviato et al., 2024b).

In general, comprehensive reviews on the distribution of these organisms reveal a recent increase in academic production, especially regarding the study of the feeding habits of these fish and ecotoxicity (Dias et al. 2021). However, terminological and conceptual inconsistencies have been identified, signaling the urgency of more comprehensive debates about this taxonomic group specifically (Monteiro 2022). Therefore, this scenario points to a promising field of growth for research, enriching the understanding mainly about biogeography and the correct classificatory correlation for such organisms (Anghinoni et al. 2020; Saviato et al., 2024b).

Data collection

This study is configured as a meticulous literature review, with an approach that resembles a biogeographical analysis. The main objective was to explore and assimilate the existing knowledge on the topic in question. To this end, the adopted methodology involved a comprehensive and diverse collection of sources, starting with a search in indexed databases such as PubMed, Scopus and Web of Science, Google Scholar, as well as virtual libraries and specialized academic repositories. The choice of these sources was guided by rigorous criteria of relevance, quality and timeliness of the information, ensuring that the review was based on pertinent and reliable material (Saviato et al., 2024b).

Therefore, the data were then organized and classified in a structured manner, grouping them according to themes, methodologies and results of the reviewed studies. This organizational process allowed us to identify patterns and trends within existing literature. The analysis involved a synthesis of the findings, providing a cohesive view of the current knowledge on the topic. The interpretation of the data considered the main conclusions of the studies, the areas of consensus, as well as possible controversies or gaps in the literature.

This theoretical approach incorporated a biogeographical perspective, examining how environmental variables can influence the distribution and diversity of the groups studied. This helped to contextualize the data in a geographic and ecological framework. To maintain accuracy and relevance, a scientific-temporal systematic approach was followed, ensuring that the sources were updated and that any evolution in knowledge was considered.

Finally, to minimize theoretical and classificatory divergences, the study employed cross-validation techniques, comparing different studies to achieve a more robust and consensual understanding. The information was continually adjusted and reassessed to reduce bias or inconsistencies, ensuring that the analysis was objective and evidence-based.

Construction and data distribution

This approach included primary studies, systematic reviews and meta-analyses, each contributing as a unique element. The analysis of these data resulted in the construction of thematic maps on the biogeographic distribution of the biota corresponding to the *Hoplias* genus, categorizing information according to themes and territorial nuances. Thus, this critical analysis identified divergences and convergences of data, while the theoretical approach integrated findings, contributing to the mapping of interconnected habitats. And through this methodology, we sought not only to review, but also to contribute to the development of knowledge on the biogeography and territorial distribution of species of the *Hoplias* genus.

Results and Discussion

This study reviewed previous research on the *Hoplias* genus Gill 1903, notable for its endemic distribution in freshwaters of South America. The analysis covers the diversity of species of this genus, which extends throughout South America and part of Central America, and introduced into North America, distributed in several hydrographic systems. A total of at least 27 taxonomic entities were identified, divided into three functional groups: *H. aimara* group, *H. lacerdae* group and the *H. malabaricus* complex group.

Recent advances in taxonomic and cytogenetic studies, as indicated by Rosso et al. (2018), reflect the natural evolution of these analyses. The significant increase in the number of specimens in ichthyological collections as well as the number of publications for the group over time indicates that there has been a significant intellectual investment, although still with a necessary increase, as highlighted by Ferreira et al. (2021).

Thus, the approach to the *H. malabaricus* Complex reveals the presence of polymorphic taxonomic entities with significant osteological and karyotypic variability, according to Iaeger et al. (2022). The organisms of this complex, found in the small basins on the eastern side of South America, have greater habitat complexity and greater likelihood of similarities than those in inland regions, as pointed out by Sember et al. (2018). In Brazil, the diversity of *H. malabaricus* in the South, Southeast, and Northeast regions highlights important karyotypic disparities, corroborated by Guimarães et al. (2022b), and confirms the taxonomic complexity of this group, according to Pires et al. (2021).

Therefore, studies on *H. malabaricus* focus mainly on bioaccumulation, ecotoxicology, genetics, and taxonomy. In contrast, studies on the geographic distribution of these organisms, specifically, are less frequent, indicating that there is a predominance with less attention to biogeography, despite the growing scientific interest. Therefore, a peak in publications has also been observed in recent decades, with national and international contributions (Saviato et al., 2024) (Figure 1).

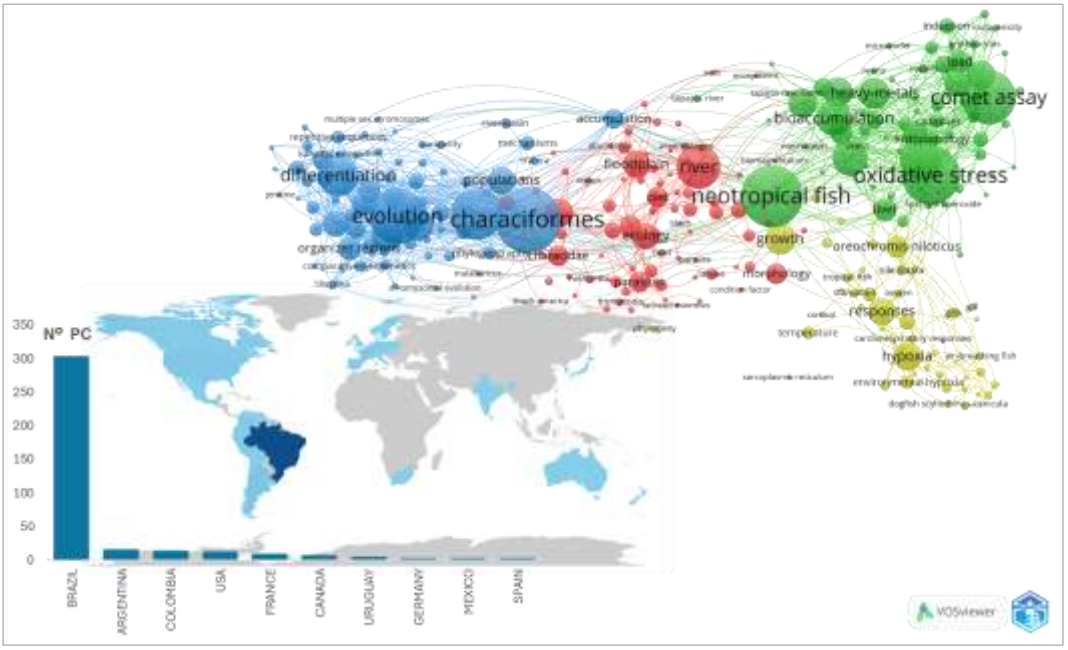

Figure 1. Quantifications of scientific research on the *Hoplias* genus, presenting the main countries involved and their contributions, as well as the most widely discussed topics. (Source: VOSviewer x Bibliometrix, adapted from Saviato et al., 2024b).

In this sense, Neotropical waters, coastal or in large continental basins in South America, appear as promising terrain for the study of the diversity of the *Hoplias* genus (Cardoso et al. 2018). Furthermore, emphasizing its ecological and taxonomic importance, especially the *H. malabaricus* complex, due to its apparent wide distribution, being contained in most of the South American drainage basins (Sharpe et al. 2023). It emerges as the protagonist of most taxonomic and cytogenetic studies in Neotropical fishes today (Albert et al. 2020).

Therefore, due to this diversity, we can highlight that despite some theoretical divergences, the *H.* aimara group, in this study, was considered to have 2 (two) species, the *H.* lacerdae group contains 9 (nine) species and the *H. malabaricus* group complex constitutes the largest set of species with almost indistinguishable

genetic and morphological proximity, totaling 16 taxonomic entities (Rosso et al. 2018, Sproul et al. 2020, Guimarães et al. 2021a, _ 2021b, _ 2022). Therefore, these disparities between populations reveal a profound heterogeneity of karyomorphic organisms, suggesting the possibility of a larger complex due to its marked hydrogeographic homogeneity (Moraes et al. 2023).

It is important to mention that the segregation of the *H.* aimara taxon into two distinct entities for this study is due to its unique geographic distribution. We would like to call them *H.* aimara north and *H.* aimara south, since this species is in the Western Amazon Basin, which is part of the Amazon River drainage system (Sassi et al. 2021). While *H. macrophthalmus* is distributed throughout the basin complex that makes up the Essequibo-Orinoco region and others in its subjacent areas, located in the northern part of the Amazon region (Ferreira et al., 2021; Correa et al., 2023; Lima-Corrêa et al., 2023).

However, biogeographically they are separated by the Guianas Shield Mountain range, which is characterized by its tepui formations, where the iconic Mount Roraima is located. And thus, it is an ancient geological impediment to gene flow between populations of this taxonomic group. Likewise, *H.* aimara and *H. macrophthalmus* were recently mentioned for the same taxon. The main reason for the separation between them is their distribution between antagonistic hydrographic basins, which is why it was decided to present the form of two different taxa for this study.

However, in the case of the *H. malabaricus* group, according to Bifi et al. (2013), it indicates the existence of 4 morphotypes present in the drainages of the Plata basin, the sympatric species *H. argentinensis* (Rosso et al. 2018), *H. mbigua* (Azpelicueta et al. 2015) and *H. misionera* (Rosso et al. 2016), and thus, we list possible divergences between these taxonomic units, while still maintaining possible new entities. In the same way, we segregate *H.* aimara from *H. macrophthalmus*, as already justified, because there is divergence regarding its regrouping into just one taxonomic entity, and because they are distinctly allocated in hydrographic basins that do not have current interconnections.

And from analyses inferred by Escobar (2019), it was possible to verify the existence of 3 more isolated karyotypic groupings for southeastern Brazil, distant from the other drainages already pointed out. Such as the discrepancies presented for the *H. malabaricus* ABZ3047 grouping, pointed out by Guimarães et al. (2022), as possible new species for the group. These results from this critical analysis of these bibliographies correlated and grouped the entities concisely, forming a set of all taxa pertinent to the *Hoplias* genus. And thus, with special attention to the complex grouping of *H. malabaricus* (Table 1).

Table 1. Taxonomic units cited by the bibliographies visited, segregated by phylogenetic proximity grouping and their respective geographic distribution locations, or the type of location of their collection and identification.

Taxonomic unit	Locality	Reference
***Hoplias aimara* group**		
H. aimara (Valenciennes 1847).	Middle and lower Amazon basin, Trombetas, Jari, Tapajós, Xingu, Tocantins rivers (Araguari and Amapá rivers - doubtful)	Mattox et al. 2006
H. macrophthalmus (Pellegrin, 1907)	Orinoco River and coastal basins of French Guiana and Suriname	
***H. lacerdae* group**		
H. australis Oyakawa & Mattox 2009	Misiones region Uruguay River basin	
H. brasiliensis (Spix & Agassiz 1829)	Coastal drainages in Northeast Brazil	
H. curupira Oyakawa & Mattox 2009	Araguaia-Tocantins and Xingu rivers and other drainages of the middle Amazon basin	
H. intermedius (Günther 1864)	São Francisco River drainages of the Rio Doce	
H. lacerdae Miranda Ribeiro 1908	Uruguay river basin (Uruguay and Argentina)	
H. microcephalus (Agassiz 1829)	São Francisco River, Brazil	
H. microlepis (Günther 1864)	Central American basins on the Pacific slope	
H. patana (Valenciennes 1847)	Atlantic drainages of French Guiana	
H. teres (Valenciennes 1847)	Lake Maracaibo river basin, Venezuela	

Table 1 (Cont.)

***Hoplias malabaricus* group**		
H. argentinensis Rosso, González-Castro, Bogan, Cardoso, Mabragaña, Delpiani et al. 2018	Paraná-Paraguay basin	
H. auri Guimarães, Rosso, González-Castro, Souza, Díaz de Astarloa & Rodrigues 2021	Crepori River, Amazon basin	
H. malabaricus (Bloch 1794)	South America	
H. mbigua Azpelicueta, Benítez, Aichino & Mendez 2015	Lower Paraná River (Yabebiry, Nemesio Parma, Corpus, Garupá, Puerto Maní in the province of Misiones and Ituzaingó in the province of Corrientes)	
H. misionera Rosso, Mabragaña, González-Castro, Delpiani, Avigliano, Schenone et al. 2016	Province of Misiones	
H. sp.1 (Sul)	Lower La Plata Basin	Gasparetto Bifi 2013
H. sp.2 (Sul)	Lower La Plata Basin	Gasparetto Bifi 2013
Hoplias sp.3 (Sul)	Lower La Plata Basin	Gasparetto Bifi 2013
Hoplias sp.4 (Sul)	Tapajós River Basin	Gasparetto Bifi 2013
Hoplias sp.5 ABZ3047 (SPOP6)	São Francisco River/East Atlantic/Eastern Northeast Atlantic/Parnaíba/Itapecuru Basins	Gasparetto Bifi 2013
Hoplias sp.6 ABZ3047 (SPOP3)	Lower Amazon River/Xingu River/Rupununi River Conferences	Guimarães et al. 2022
Hoplias sp.7 ABZ3047 (SPOP1)	Drainages of the Guiana Shields	Guimarães et al. 2022
Hoplias sp.8 ABZ3047 (SPOP4)	Southeast - Abrolhos - Eastern Basins	Pereira et al 2012
Hoplias sp.9 (Southeast)	Southeast - Abrolhos - Northeast Basins	Pereira et al 2012
Hoplias sp.10 (Southeast)	Southeast - Cabo Frio - Southeast Basins	Pereira et al 2012
Hoplias sp.11 (Southeast)	Middle and lower Amazon basin, Trombetas, Jari, Tapajós, Xingu, Tocantins rivers (Araguari and Amapá rivers - doubtful)	Guimarães et al. 2022

Source: Prepared by the author

The detailed analysis of the results obtained, including the precise delimitation of the hydrographic basins and watersheds that represent geological barriers to the dispersion of freshwater fish species, was fundamental for the preparation of the distribution maps. These maps were constructed from the integration of bibliographic data with geomorphological and hydrographic information specific to each region. The detailed consideration of these factors allowed a more precise representation of the areas of occurrence of the species and the limitations imposed by the geological elements, providing a solid basis for understanding the dynamics of the distribution of the species in relation to the local environmental and geographic characteristics.

In this regard, the species listed for the *H. aimara* group presented distinct distributions, being separated by the mountainous massif of the Guiana Shield region. Another important observation is that the species of the Lacerdae group have little to no overlap with the *H. aimara* group, being more concentrated in the channels of the Eastern Amazon and in the complex basins that flow into eastern Brazil, as well as the Paraná-Paraguay basins. On the other hand, two taxa, *H. microlepis* and *H. teres*, are separated from the majority being in the trans-Andean region towards Central America (

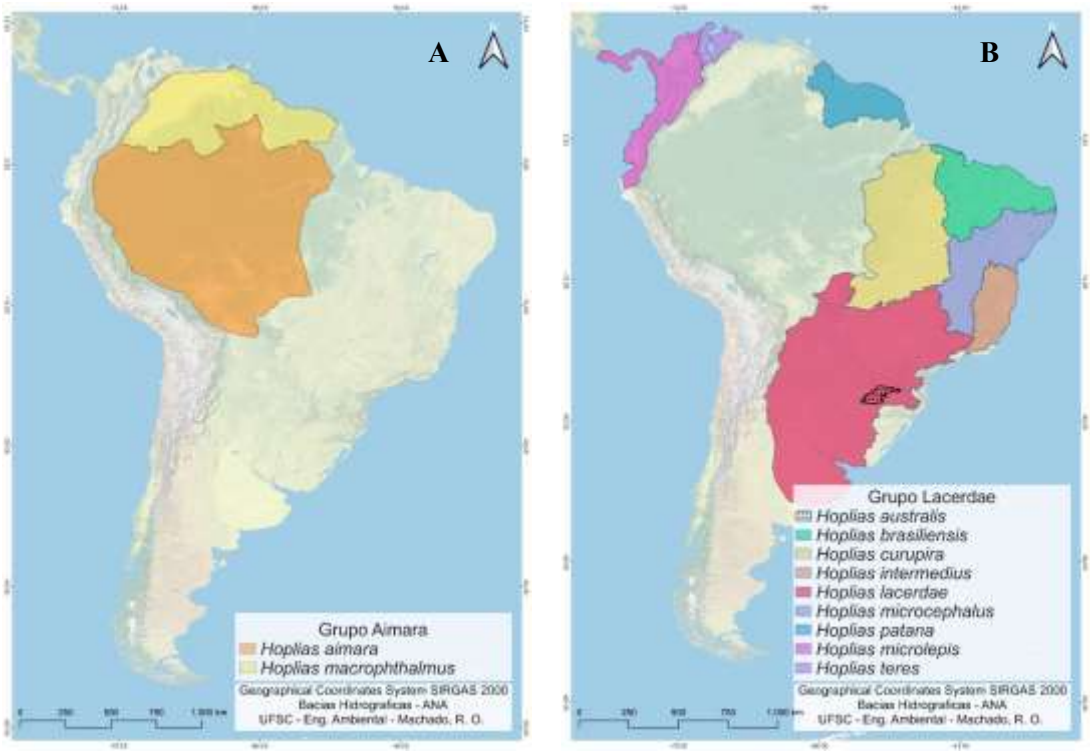

Figure 2. Distribution of the genus *Holplias* of the *Aymara* and *Lacerdae* groups, and their official and unofficial taxonomic units, in the South American continent (Source: Prepared by the author).

On the other hand, the divergences between the species of the *H. malabaricus* Complex attested to a more pronounced derivation of the species distributed along the South American shield. Thus, the mapping of the data outlined a summarized panorama of the geographic distribution of the taxa of this group in the Neotropical region. Where the largest taxonomic grouping is cited for the southeast and northeast coast. In contrast, the smallest number of bibliographies on the group is in the same region where there are fewer identified taxonomic entities. Even so, unlike *H. lacerdae*, this group does not have trans-Andean entities (Figure 3).

The taxonomic uncertainty surrounding the *Hoplias* genus, especially the *H. malabaricus* complex, has been intensively researched (Guimarães et al. 2022). This uncertainty is exacerbated by the difficulty in accurately discriminating species in the field, due to high genetic heterogeneity, morphological similarity, and limited taxonomic knowledge, which hinders assertiveness (Sassi et al. 2021). Furthermore, the evolutionary trajectory of H. malabaricus and other taxonomic groups, such as the H. aimara group, is still confined to distinct and disconnected river basins, such as the Essequibo-Orinoco basin and the Amazon basin (Guimarães et al. 2022).

In this context, the inclusion of the species *H. aimara* and *H. macrophthalmus*, still debated by some experts, highlights the need for in-depth studies to understand their evolutionary relationships. The controversial division between these species may reflect similar patterns to those observed in the *H. malabaricus* group, where genetic complexity and conservation issues are relevant, since the lack of connection between river basins promotes genetic isolation and, consequently, speciation after the Miocene (Carrillo-Briceño et al. 2021). This study, however, does not seek to argue or define the segregation between these taxa, but to draw attention to the taxonomic proximity between the species of the *H. malabaricus* group, which complicates the understanding of their actual geographic distribution, due to genetic complexity and the presence of sympatric and cryptic species.

The results of this study offer an in-depth understanding of the distribution of these species, representing a significant update in relation to previous taxonomic knowledge (Cardoso et al. 2018; Dias 2021). The meticulous integration of geological data and taxonomic distribution frameworks enabled a more accurate identification of taxonomic entities in the different hydrographic regions (Figueiredo et al. 2022). Species identification and delimitation were improved by detailed analysis of geological features, resulting in a better understanding of natural barriers and factors influencing species dispersal, considering sea level fluctuations during the Anthropocene (Carrillo-Briceño et al. 2021).

Figure 3. Distribution of species of the *Holplias malabaricus* complex, and their official and unofficial taxonomic units, in the South American continent (Source: Prepared by the author).

Compared to previous studies, which often relied on less detailed data or more general analyses, this study stands out for the accuracy and depth of data integration. Previous studies, such as those carried out by Castro (2021), often did not fully consider the geological and geomorphological aspects of the regions studied (Gallo et al. 2021), limiting the understanding of natural constraints on species dispersal (Figueiredo et al. 2022). The combination of bibliographic data with precise geomorphological and hydrological information offered a more robust approach to defining taxonomic distribution patterns. Previous studies, such as those by Ibagón et al. (2020), were based on broader and less specific data, resulting in a less accurate representation of the actual distributions of species.

Therefore, the implications of these results are significant for the conservation biology of species. Where the precise identification of geological barriers and the delimitation of the areas of occurrence of species allowed a more effective display of the specific distribution amplitude adapted to the characteristics of each hydrographic region (Albert et al. 2020; Demétrio et al. 2022). Therefore, these inferences are crucial for the development of studies with greater precision and assertiveness on the studied entities. The fusion between biogeography and the revelations of biological, genetic and morphological studies highlights the *H. malabaricus* complex, which instigates reflections on its distribution and underlines its importance in South American aquatic environments (Pires et al. 2020).

Considerations

This study made it possible to integrate and present the detailed classification based on geological, geomorphological and bibliographic data, allowing a precise delimitation of the areas of occurrence and dispersion of the species. Thus, the results indicated that the *H. malabaricus* group is quite diverse, with 16 taxonomic entities, reflecting the great heterogeneity and environmental complexity, mainly in the Southeast and Northeast regions of Brazil. Thus, it allowed a more precise representation of the distributions of these species and the limitations imposed by natural factors. When compared to previous studies, it offered a more robust and detailed view of the biogeography of the *Hoplias* genus. This not only improved the existing taxonomic understanding but also provided a solid basis for future research on these species. On the other hand, the implications of these results are significant for conservation biology and species management, highlighting the importance of considering geological barriers and biogeographic aspects in the conservation of aquatic species. Where the precise identification of the areas of occurrence allows the development of strategies adapted to the specific characteristics of each hydrographic region.

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