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Review

Biodiversity, Systematics, and Taxonomy of Ostariophysi (Osteichthyes, Actinopterygii): What We Know Today After Three Decades of Integration of Morphological and Molecular Data

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Abstract: Ostariophysi is the second largest superorder of fishes, formed almost exclusively by freshwater species, with 102 families, 1372 genera, and 11,883 species, thus containing approximately 30% of the known fish species in the world and almost 70% of the freshwater species. Despite the great richness of species and, therefore, its great scientific and economic importance, there are still many problems related to the relationships among the internal groups of the superorder (and consequently in its classification), as well as doubts about its diversification processes and historical distribution. The group has been studied for centuries using morphological approaches that permitted the solution or proposal of several hypotheses about the origin, constitution, and distribution of the species of the group, but in the last three decades, new approaches using molecular data, including phylogenomics, have allowed the testing of hypotheses made with morphological data and, more importantly, the proposition of new hypotheses. The present study aims to review the current state of knowledge about the biodiversity, systematics, and taxonomy of the various groups of the superorder Ostariophysi, highlighting the advances achieved in recent years and discussing the problems still existing in the group.

Keywords: evolution; fishes; ichthyology; phylogeny

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1. Main Text

Fish belong to a large monophyletic group: the phylum Chordata. Within this group we find the group called Osteichthyes, composed of ray-finned bony fishes (subclass Actinopterygii) and lobe-finned bony fishes plus tetrapods (subclass Sarcopterygii) [1]. Within the Actinopterygii, one of the most diverse groups is the Teleostei subdivision, which, among several very large fish groups, houses the Otocephala cohort with the superorders Clupeomorpha, Alepocephali, and Ostariophysi [1] (Figure 1).

Ostariophysi is one of the largest superorder of fishes, formed almost exclusively by freshwater fish, with 102 families, 1372 genera, and 11,883 species [2], thus containing approximately 30% of the known fish in the world and almost 70% of the freshwater species [1]. The size range among Ostariophysi is remarkably diverse, ranging from tiny species such as *Paedocypris progenetica* (Kottelat, Britz, Tan & Witte, 2006), with an adult length of 7.9–10.3 mm, medium-sized species (the vast majority) such as *Paracheirodon axelrodi* (Schultz, 1956), with an adult length of 2–20 cm, to very large species such as *Brachyplatystoma filamentosum* (Valenciennes, 1840), with an adult length reaching 3.6 m. Ostariophysi are present throughout the world, except in Antarctica, from where only

fossils are known [1]. Diversity studies in the group have been very frequent, with the description, in the last 10 years, of more than 1600 species [2], which represents more than 1 new species every two days!

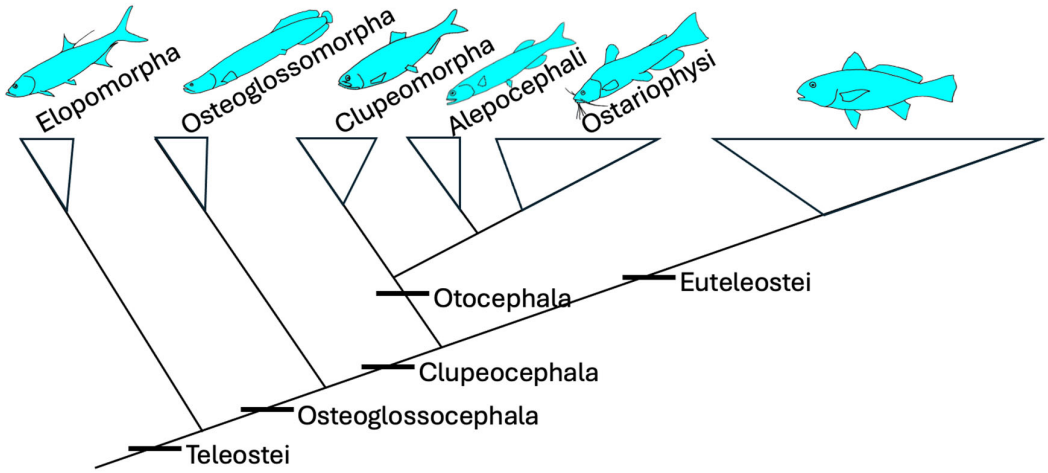

Figure 1. Phylogenetic relationships among the main groups of Teleostei (modified from Nelson et al. [1]).

Members of this group include important fish for the food industry, sport fishing, and aquariums, among others. Due to its great representativeness and scientific and economic importance, there are many old and recent studies with different hypotheses about the relationships between families and orders, but despite all these studies, problems in understanding the relationships among the internal groups of the superorder and, consequently, in their classification still persist [1], as well as doubts regarding its diversification processes and geographic distribution, which need to be addressed with modern and resolutive methodologies (i.e., macroevolutionary models and parametric biogeography).

The development of molecular approaches and the combination of morphological and molecular data have provided strong evidence of a close relationship between Clupeomorpha and Ostariophysi [3–7]. However, recent studies, based on both morphological and molecular data, suggest that the superorder Alepocephali (previously placed within the order Argentiniformes) may be the sister group of Ostariophysi [6–11] (Figure 1). These three groups have been recognized as cohort Otocephala [1,12,13] or Otomorpha [14]. This hypothesis was analyzed by Arratia [14] with the search for morphological characters, and her results show that many of the characteristics that could be synapomorphies for this group are in fact homoplasies, at some level, with the possible exception of the fusion of the haemal arches with their respective vertebral centers anterior to pleural center 2, which would probably be an unequivocal synapomorphy of the clade. The author emphasizes in the work the need for more in-depth work to better understand the relationships among these groups.

The oldest Otocephala fossil is a species of †*Tischlingerichthys viohli* (Arratia, 1997) that was found in Upper Jurassic, Upper Tithonian (i.e., ca. 145 million years old) marine sediments from the Mörnsheim Formation, Bavaria, Germany [15,16]. Currently extant Otocephala are mainly freshwater fishes, including most Otophysi, most Gonorynchiformes (ca. 80%), and some Clupeomorpha (ca. 10%), showing great diversification in the neotropics [14]. On the other hand, a study on the origin of Otochephala using mitochondrial DNA sequences and the molecular clock technique suggested that this group originated approximately 282 million years ago, during the Permian [17], which would double the age of origin of the group, established with the fossil cited above. These results should be interpreted with caution as issues such as saturation may negatively impact the accuracy of

divergence estimates, particularly for deep evolutionary nodes. In a more recent study using exon markers, Mu et al. [18] found that Otocephala may have originated more recently in the Lower–Upper Jurassic, showing that these data are still under debate.

In terms of composition, the superorder Clupeomorpha includes two orders: Ellimmichthyiformes, which includes only fossil species [1,14], and Clupeiformes, which includes fossil and current species and is composed of 10 families, 83 genera, and 455 species [2]. Half of these species are from the Indo-Pacific, approximately a quarter from the western Atlantic, and approximately 80 species occur primarily in freshwater [1]. There is an extensive fossil record of this group, dating back to the beginning of the Cretaceous [1,14].

The superorder Alepocephali contains a single order, Alepocephaliformes, two families, 33 genera, and 143 species [2], many of which inhabit mesopelagic or bathypelagic environments [1]. According to Arratia [14], compared to Clupeomorpha and Ostariophysi, the fossil record of Alepocephali is more recent (Cenozoic) and sparse, being represented by †*Carpathichthys polonicus* (Jerzmanska, 1979) from the Miocene–Oligocene, between approximately 30 and 23 Ma, and otoliths from the Mediterranean Basin, Quaternary of Italy [14]. Extensive studies of relationships among members of Alepocephaliformes using mitochondrial DNA data were published by Lavoué et al. [19], Poulsen et al. [20], and Fujihara et al. [21] who corroborated the hypothesis of its close relationship with Ostariophysi. The monophyly of the family Platytroctidae has been confirmed in all studies [19–22]; on the other hand, the monophyly of Alepocephalidae was observed in the studies of Lavoué et al. [19] and Poulsen et al. [20], but more recent studies with more specimens and data show the family Alepocephalidae as polyphyletic [21,22].

The superorder Ostariophysi is divided into two series (Anotophysi and Otophysi), as proposed by Fink and Fink [23] and corroborated by Fink and Fink [24] (Figure 2), and formed almost exclusively by freshwater fish with only about 120 marine species among the 11,883 species known [1,2]. The update of these numbers, according to Fricke et al. [2], shows that Ostariophysi currently has 11,039 species, of which 1709 (15.5%) were described in the last 10 years. Ostariophysi are present on all continents and major land masses except Antarctica and Greenland, with Australia having some catfishes secondarily derived from marine groups [1].

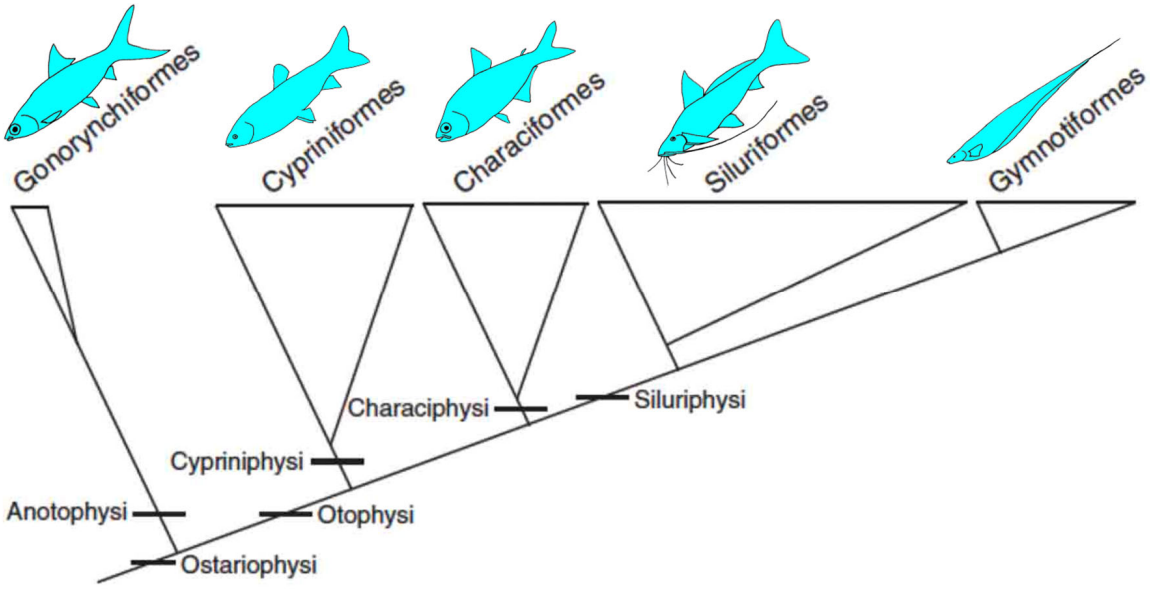

Figure 2. Phylogenetic relationships of the superorder Ostariophysi according to Fink and Fink [23,24] based on morphological data.

The monophyly of Ostariophysi was proposed by Fink and Fink [23] and more extensively analyzed by Fink and Fink [24]. This monophyly was corroborated in all subsequent studies, including phylogenomic approaches [7]. An interesting feature of this group is the presence of an alarm substance (Schreckstoff). This substance was first documented by Karl von Frisch in 1938 (according to Pfeiffer [25]) and described in detail by Pfeiffer [25]. This alarm substance is a pheromone produced by epidermal cells identified as 'club' cells, which are released when the skin is injured. This pheromone, once released, causes a startle (flight) reaction in nearby members of the same species (or sometimes even in other species), serving as a group defense mechanism. According to Nelson et al. [1], although widely distributed among Ostariophysi, this pheromone is not present in all Ostariophysi. Furthermore, some members of the superorder lack the startle response but possess an alarm substance (e.g., Serrasalmidae), while others have neither the alarm substance nor the startle response to alarm substances of other species (e.g., Loricariidae and Gymnotiformes) [1].

Gonorhynchiformes (Anotophysi series) is the sister group of Otophysi, that is, of all other Ostariophysi (Figure 2). The monophyly of Gonorhynchiformes was demonstrated through morphological [23,26] and molecular data [10,27]. Nelson et al. [1] recognize three families in the order, while Fricke et al. [2] recognize four, the difference being related to the recognition or not of the family Phractolaemidae, considered a subfamily of Kneriidae by Near et al. [27] and Nelson et al. [1]. There are a large number of fossils described for the order, such as forms from the Lower Cretaceous of Spain (†*Gordichthys*, Poyato-Ariza, 1994 and †*Rubiesichthys*, Wenz, 1984), Belgium (†*Aethalionopsis* (Traquair, 1911)), Equatorial Guinea and Brazil (†*Dastilbe crandalli* (Jordan, 1910)), Gabon (†*Parachanos aethiopicus*, Cuvier, 1829), and Brazil (†*Dastilbe*, †*Nanaichthys fariai*, Schultz, 1944, †*Tharrhias arcuatus*, Eigenmann, 1907), including a recently described species from Mexico (†*Sapperichthys bifurcus*, Broughton, Bloom & Wiley, 2013) considered the most primitive Gonorhynchiformes [1].

Although the monophyly of the order is not in doubt, the relationships between its families are not yet well understood since analyses using morphological data [23,26] strongly support a sister-group relationship between Gonorynchidae and Kneriidae, but molecular and molecular plus morphological analyses support a sister-group relationship between Chanidae and Kneriidae [10,27,28] (Figure 3). The other divergent point is the recognition of Phractolaemidae as a family [2] or as a subfamily [1,27].

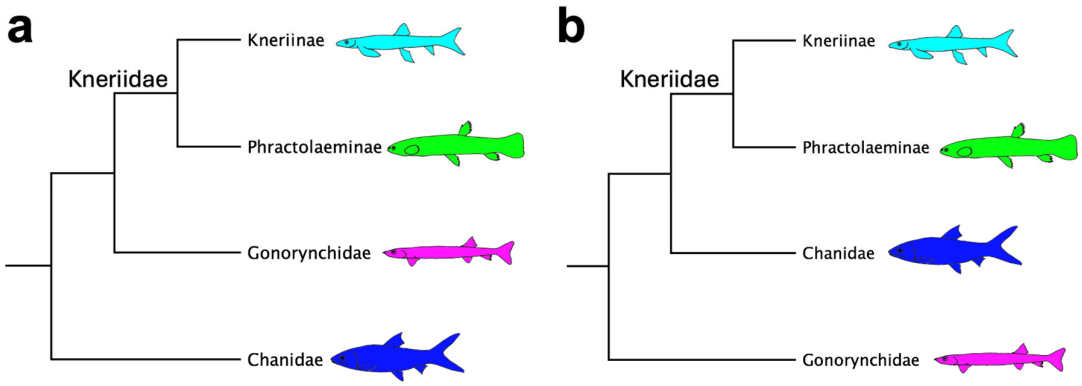

Figure 3. Trees showing putative relationships among Gonorhynchiformes. (**a**) Morphological data [26]; (**b**) total evidence (morphological + molecular) data [27].

Fishes of the series Otophysi are diagnosed, among other characteristics, by the presence of a Weber apparatus [1]. Ancient fossils (from the Early Cretaceous) that may be stem otophysans include †*Chanoides macropoma* (Agassiz, 1844), †*Lusitanichthys* (Figueiredo, Gallo & Carvalho, 2021), †*Nardonoides* (Mayrink, Brito & Otero, 2014), and †*Santanichthys*

(Brito, 1997) [29,30]. Many fossils require revision, and, for example, the genus †*Salminops* (Gayet, 1985), initially considered an Ostariophysi, was revised and is now considered Teleostei incertae sedis [30]. Others had their position in Gonorynchiformes corroborated and even resolved in detail, such as †*Dastilbe* (Ribeiro et al., 2018).

The monophyly of Otophysi was strongly supported in the study of Fink and Fink [23,24]. A later study by Dimmick and Larson [31] combining molecular data (160 phylogenetically informative nuclear ribosomal RNA sites and 208 phylogenetically informative mitochondrial ribosomal and transfer RNA genes) and 85 morphological characters corroborated the hypothesis of Fink and Fink [23] (Figure 4a). Several studies, carried out later, with molecular data, corroborate the hypothesis of the monophyly of Otophysi but refute the initial hypothesis of the relationship between its orders (see review in Chen et al. [32]), pointing out alternative hypotheses (Figure 4b). Arcila et al. [33] carried out an extensive literature review on studies of relationships between the orders Cypriniformes, Siluriformes, Gymnotiformes, and Characiformes (considering their two main lineages: Citharinoidei and Characoidei) and, with partial sequence data from 1051 exon loci of 225 species, in a total of 45 analytical approaches, constructed 15 possible tree hypotheses. Their results showed that Characiformes is monophyletic in 3 of the 15 resulting topologies. A more concise analysis (with 231 genes), using a methodology called Gene Genealogy Interrogation (GGI), showed that the tree with the highest probability of occurrence is identical to that proposed by Fink and Fink [23], constructed with morphological data (Figure 4a). Although the data presented represent a great contribution to the knowledge of the group, Arcila et al. [33] report that in only three of the fifteen possible hypotheses tested, Characiformes is monophyletic and obtaining a monophyly using the GGI methodology may be biased since other researchers reanalyzing the same data did not obtain the same results [34]. In a study with ultraconserved elements (UCEs) using 34 species and 567 loci (50% matrix) and morphological data, carried out by Chakrabarty et al. [35], the order Characiformes was found to be polyphyletic. Dai et al. [36] analyzed 22 Otochephala transcriptome datasets and found that Gymnotiformes are most closely related to Characiformes (Figure 4c), as proposed by Ortí and Mayer [37], and that Characiformes form a possible paraphyletic group, once again refuting part of the initial hypothesis of Fink and Fink [23].

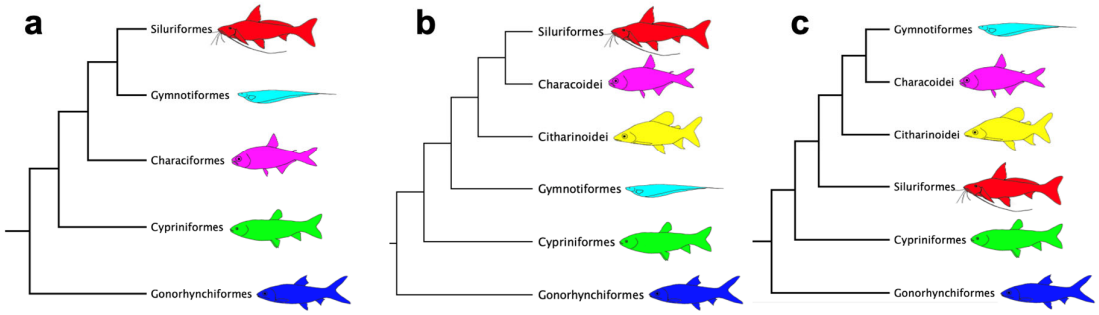

Figure 4. Hypotheses of relationships between orders of Ostariophysi. (**a**) Hypothesis based on morphological [23,24] and molecular (exon markers) [33] data; (**b**) hypothesis based on molecular (mitochondrial, nuclear, and UCEs) data [32,34,35] and total evidence (morphological and mitochondrial and nuclear) data [38]; (**c**) hypothesis based on molecular (mitochondrial, nuclear, and genomic) data [36,37].

Among the Otophysi, the order Cypriniformes is the group with the largest number of species, with 23 families, 526 genera, and 4909 species [2] distributed in freshwater environments around the world, except for South America, Australia, and Antarctica [1]. This group has been the subject of several systematic studies [39] that have significantly altered its composition and thus resulted in the recognition of many new species: 623 in the last

10 years [2]. Recently, Tan and Armbruster [39] published a taxonomic review of the order and divided it into four suborders: Cyprinoidei (12 families), Catostomoidei (1 family), Cobitoidei (9 families), and Gyrinocheiloidei (1 family). Two recent molecular phylogenetic studies have focused on broader relationships in Cypriniformes: a phylogenomic study using 219 loci and 172 species [40] and a phylogenetic study based on six nuclear loci and using 81 species [41] (Figure 5). The latter expands on previous phylogenetic studies based on these same loci in the Cypriniformes Tree of Life project [42–44] and explores the effect of particular gene selection on phylogenetic reconstruction. The results of the two studies (Figure 5) are quite divergent, which is aggravated by the different composition of groups between the two studies. As an example, in Stout et al. [40], Gyrinocheilidae is a sister group to all other Cypriniformes, while in Hirt et al. [41], Gyrinocheilidae is a sister group to a group of Cypriniformes excluding Catostomidae and Cyprinoidea (Figure 5). The same observation is valid for the large family Cyprinidae, one of the most species-rich families of teleosts, where the relationships among subfamilies are different among the studies and in the study of Hirt et al. [41], the subfamilies Cyprininae, Labeoninae, and Torinae are not monophyletic (Figure 6).

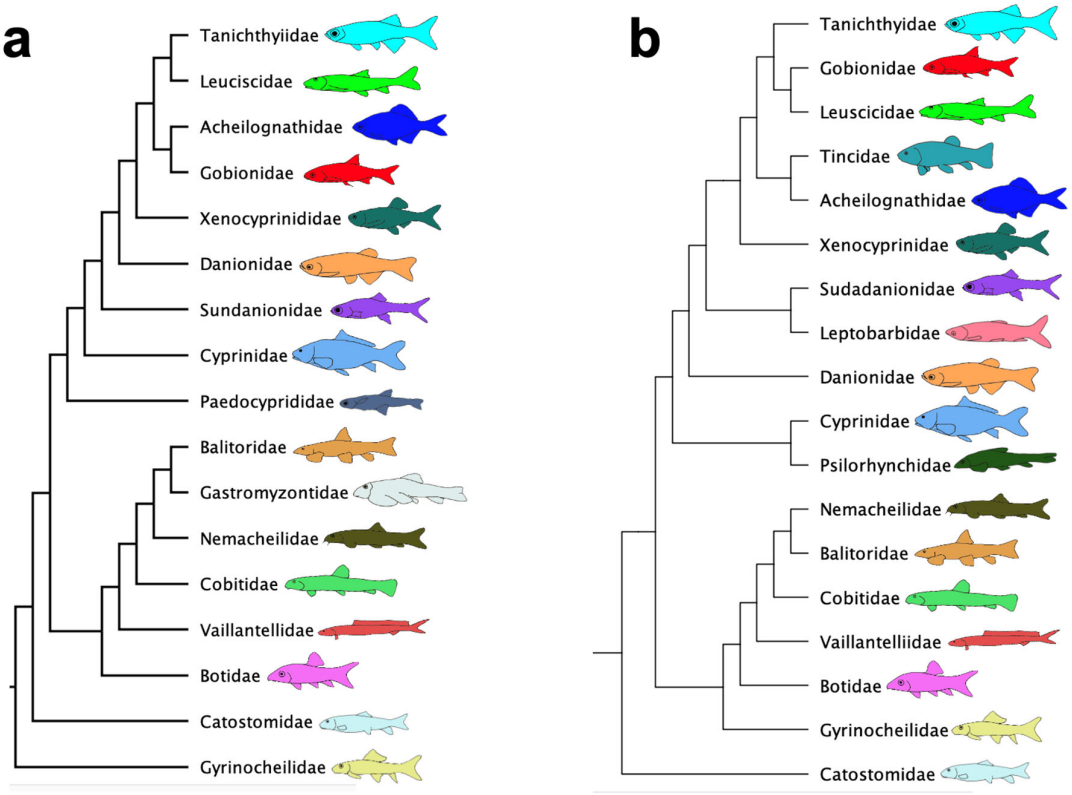

Figure 5. Phylogenetic hypotheses for Cypriniformes. (**a**) A phylogenomic study using 219 loci and 172 species [40]; (**b**) phylogenetic study based on six nuclear loci and using 81 species [41].

Another large group in Otophysi is the order Characiformes, excluding the families Citharinidae and Distichodontidae, now placed in Cithariniformes [38]. This order includes 26 families, 263 genera, and 2243 species [2] and is also an intensively studied group, with the description of 297 new species in the last 10 years. Two families were recently described: Tarumaniidae [45] and Lepidarchidae [46]. All members of Characiformes are freshwater species occurring in Africa, the southern United States, and Central and South America. Fossils assigned to the order Characiformes include †*Paleohoplias* (Bocquentin & Negri, 2003) and †*Tiupampichthys* (Gayet & Meunier, 1998) from South America, †*Mahengecharax* (Taverne & Bienvenu, 2022) (possibly sister to Alestidae) from Africa, and †*Sorbinicharax*

(Taverne, 2003) (family †Sorbinicharacidae) from the Cretaceous of Europe [1]. A partial mandible from a Late Cretaceous specimen from Canada has also been identified as a Characiformes [1], but as with many other fossils, this identification requires confirmation [29]. There are also more recent fossils (Eocene–Oligocene–Miocene) attributed to recent or extinct genera such as †*Leporinus scalabrinii* (Ameghino, 1898), †*Cyphocharax mosesi* (Travassos & Santos, 1955), †*Brycon avus* (Woodward, 1898), †*Megacheirodon unicus* (Travassos & Santos, 1955), †*Lignobrycon ligniticus* (Woodward, 1898), and †*Paleotetra entrecorregos* (Weiss, Malabarba & Malabarba, 2010), among others [29,47,48].

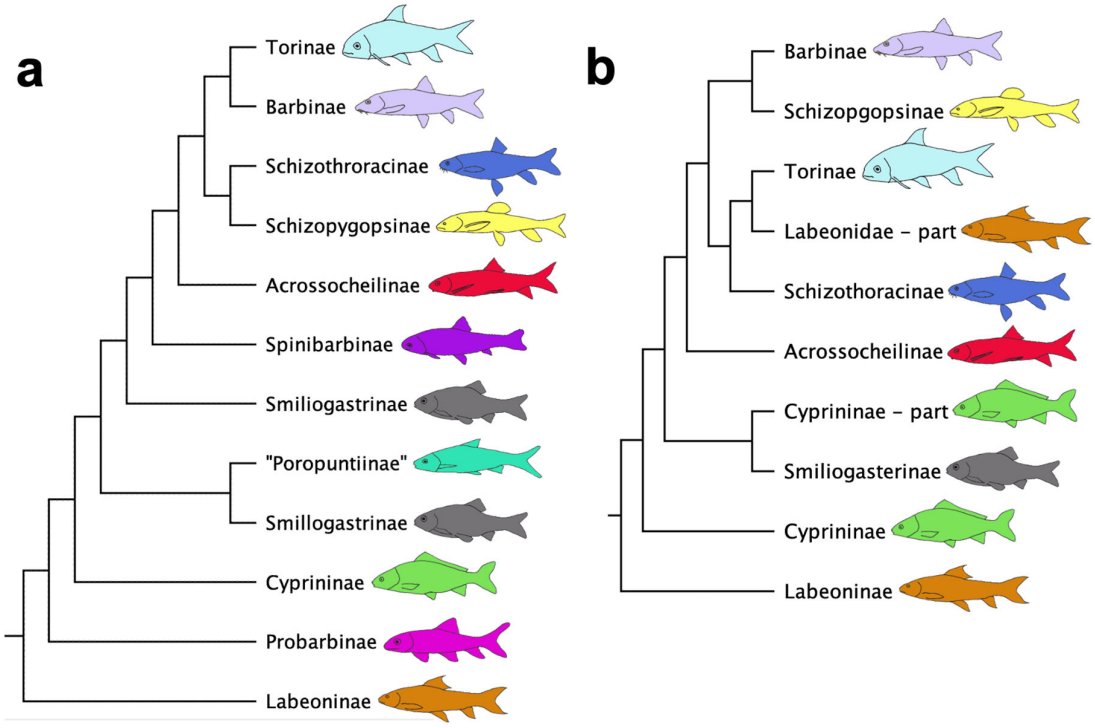

Figure 6. Phylogenetic hypotheses for the family Cyprinidae. (**a**) A phylogenomic study using 219 loci and 172 species [40]; (**b**) phylogenetic study based on six nuclear loci and using 81 species [41].

The first molecular phylogeny for Characiformes using representatives of all families, except for the recently described Tarumaniidae and Lepidarchidae, was published by Oliveira et al. [49] and represented a significant step in our knowledge, identifying all currently recognized families, such as Bryconidae, Acestrorhynchidae, Triportheidae, Chalceidae, Iguanodectidae, which were part of a large group previously identified only as Characidae. Arcila et al. [33] published a phylogeny of Ostariophysi using genomic data, where all families of Characiformes were sampled and found the same arrangement as that observed by Oliveira et al. [49] and solved some relationships unresolved in this paper. A more recent phylogeny published for the order, using genomic data from exon sequences with a larger set of Characiformes species than that used by Oliveira et al. [49] and Arcila et al. [33], corroborated the hypothesis of the monophyly of Characiformes [50], as well as the families identified in Oliveira et al. [49] and the relationships observed by Arcila et al. [33]). Melo et al. [51] published a new phylogeny for Characiformes using sequences of UCEs of 293 species, representing 79% of the genera of the order, using different analytical approaches, and found the same pattern of relationships among families. The position of the family Tarumaniidae was tested by Arcila et al. [52] and Melo et al. [53], who corroborated the initial hypothesis of de Pinna et al. [45] that this family is closed related to Erythrinidae. The position of the family Lepidarchidae was tested by Melo and Stiassny [46], who found it more related to Hepsetidae (Figure 7).

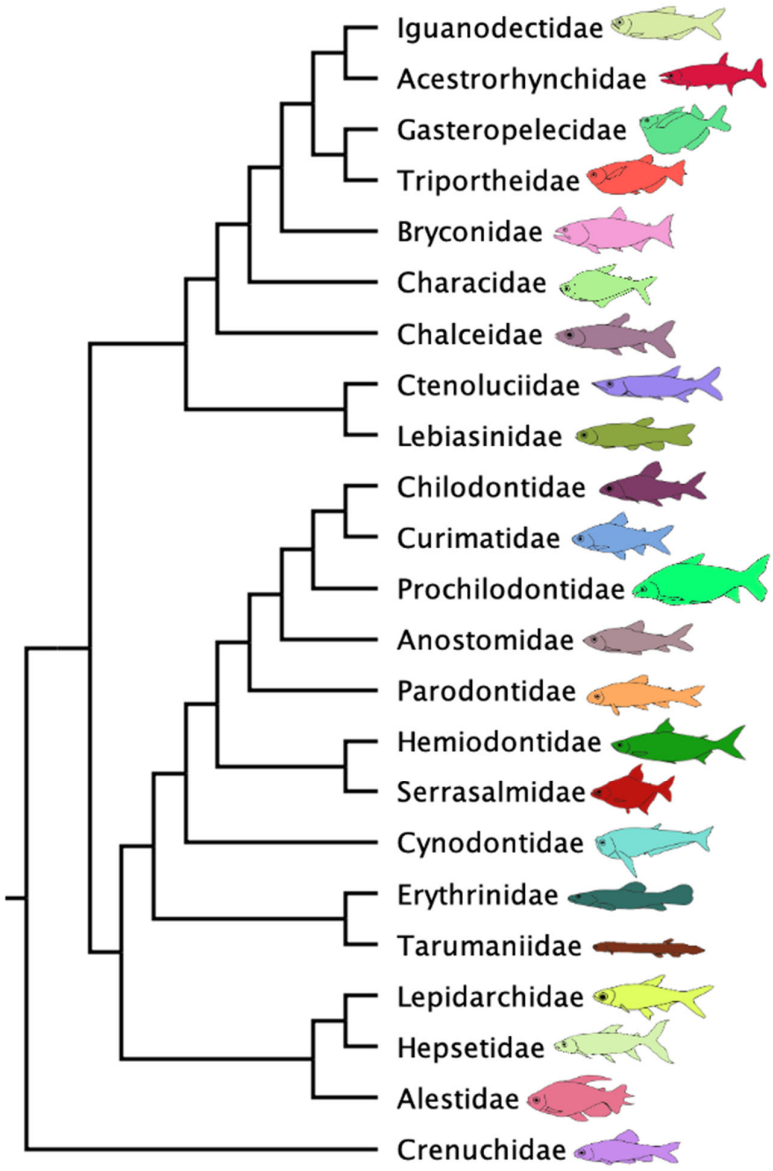

Figure 7. Phylogeny of Characiformes based on the studies of Melo et al. [51] and Melo and Stiassny [46], based on UCE loci.

Melo et al. [51] corroborate the hypothesis that Citharinifformes is the sister group to a larger clade formed by the Siluriformes and Characiformes, with this split having occurred in the Jurassic, approximately 170 million years ago, long before the breakup of Gondwana. The ancestors of at least five other modern Characiformes lineages also existed before this date. Subsequent diversification in the Cretaceous resulted in 17 of the 23 modern Characiformes families, most of which originated in South America. Although the reasons for the greater taxonomic diversification of Characiformes in the Neotropics than in the Ethiopian region are not entirely clear, a diversification analysis shows higher rates in the Neotropical families Anostomidae, Serrasalmidae, and Characidae, which may provide an answer to this question.

Several molecular studies within Characiformes families have been published recently, such as with Anostomidae [53–55], Bryconidae [56], Chilodontidae [57], Curimatidae [58], Crenuchidae [59], Gasteropelecidae [60], Hemiodontidae [61], Prochilodontidae [62], Serrasalmidae [63,64], and Triportheidae [65]. Many studies on molecular systematics have also been published within Characidae, such as in Aphyocharacinae [66], Characinae [67], Cheirodontinae [68], and Tetragonopterinae [69].

More recently, Melo et al. [70] published a phylogenomic study of Characidae sampling 575 specimens of 494 species and 123 genera, and generating data of 1348 UCE loci (538,472 bp) and corroborate the hypothesis of Oliveira et al. [49] that this family was composed by four monophyletic groups that were classified at the family level: (1) Spintherobolidae; (2) Stevardiidae (with nine subfamilies: Landoninae, Xenurobryconinae, Glandulocaudinae, Argopleurinae, Hemibryconinae, Stevardiinae, Planaltininae, Creagrutinae, and Diapominae); (3) Characidae (with five subfamilies: Aphyocharacinae, Cheirodontinae, Exodontinae, Tetragonopterinae, and Characinae); and (4) Acestrorhamphidae (with 14 subfamilies: Oxybryconinae, Trochilocharacinae, Stygichthyinae, Megalamphodinae, Stichonodontinae, Stethaprioninae, Pristellinae, Jupiabinae, Tyttobryconinae, Hyphessobryconinae, Thayeriinae, Rhoadsiinae, Grundulinae, and Acestrorhamphinae). This study (Figure 8) represents an enormous advance in the knowledge of Neotropical characids and opens many new doors to study several very complex groups.

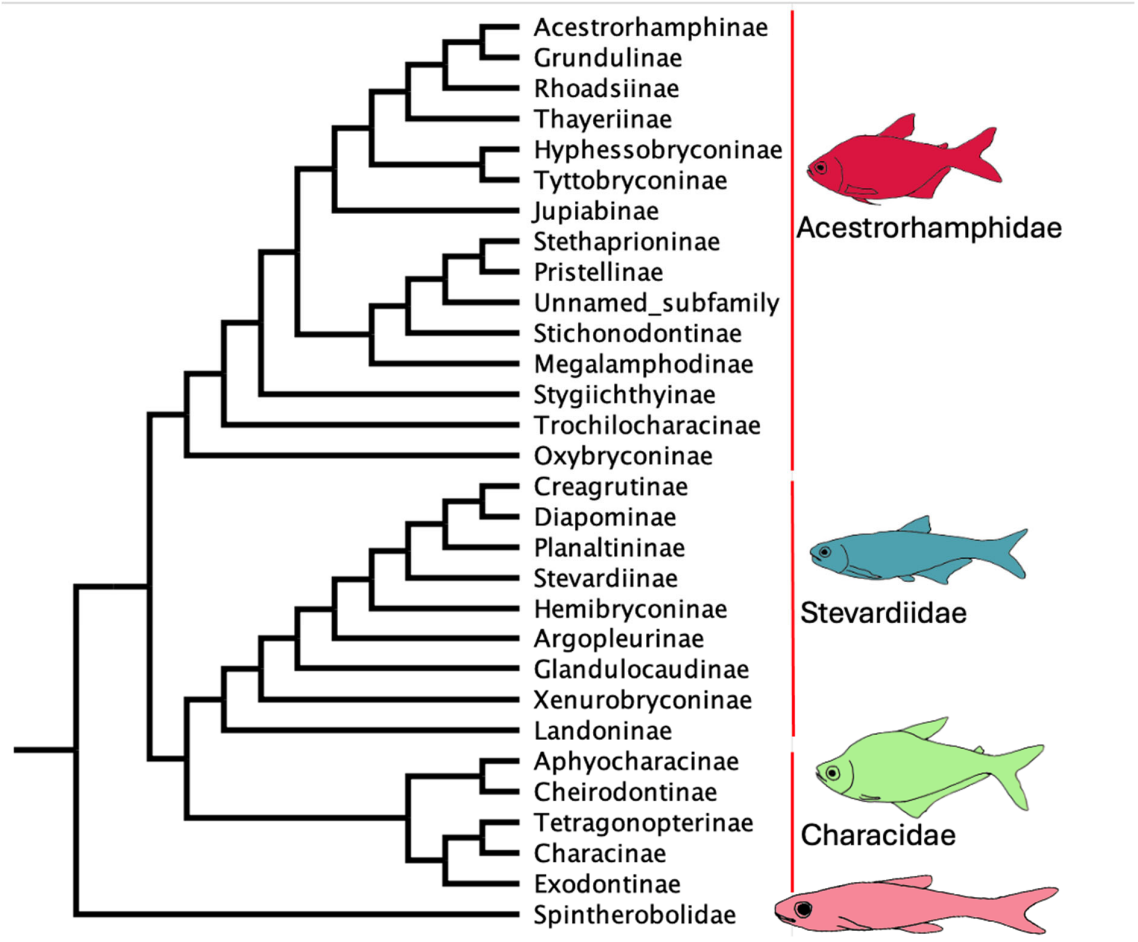

Figure 8. Phylogeny of characids, now divided into four families according to Melo et al. [70], based on UCE loci.

The families Citharinidae and Distichodontidae belong now to the order Cithariniformes [38]. This order includes two families, 19 genera, and 118 species [2]. Vari [71] found fourteen characters supporting the monophyly Citharinidae plus Distichodontidae. All members of Cithariniformes are freshwater species occurring in Africa. An Eocene fossil from Tanzania, named †*Eocitharinus macrognathus* was described by Murray [72].

The order Siluriformes is monophyletic and a sister group to Gymnotiformes [23,24], but there is still controversy on this last point. The order has 41 families, 513 genera, and 4291 species [2]. Many taxonomic studies have been carried out in the group, which

resulted in the description of 620 species in the last 10 years [2]. Two families have predominantly marine species, Ariidae and Plotosidae, but have representatives that are frequently found in brackish and coastal waters and sometimes in freshwater [1], such as the genus *Paragenidens* (Marceniuk & Oliveira, 2019) [73]. Other catfish families are freshwater, although some have species that can invade brackish water [1]. The fossil record of Siluriformes is quite vast, with forms known from all continents except for Australia, and quite old, with species identified from the Late Cretaceous [1]. Some families that present only fossil forms have been described, such as Andinichthyidae (Late Cretaceous to Paleocene, Bolivia), Bachmanniidae (Eocene, South America), and Hypsidoridae (Eocene, North America) [1]. Considering the fossils from the Eocene or Oligocene of Antarctica, Siluriformes are known on all continents [1].

Given the great diversity of siluriform species distributed across most continents of the globe, morphological and molecular studies have focused on the relationship among family groups within this order, such as Doradoidea [74], Loricarioidea [75,76], Pimelodoidea [77–82], and Sisoroidea [83,84]. Other phylogenetic studies have densely sampled species from specific families, such as Ariidae [85,86], Aspredinidae [87], Auchenipteridae [88], Austroglanididae [89], Cetopsidae [90,91], Clariidae [92,93], Doradidae [94], Ictaluridae [95,96], Loricariidae [97–100], Mochokidae [89], Pangasiidae [101], Pimelodidae [102,103], Pseudopimelodidae [104], Siluridae [105], Sisoridae [84,106], and Trichomycteridae [107,108]. However, despite recent progress in our understanding of the pattern of relationships between families, genera, and species, most relationships among families of Siluriformes are not sufficiently resolved, and we are far from proposing a classification for the Siluriformes order as a whole or even allowing mapping of morphological characteristics or precise biogeographic and macroevolutionary inferences, in order to understand the evolutionary processes responsible for the great diversity of this group.

Several new discoveries have revealed our limited knowledge of the group. For example, a new family of catfishes was described by Rodiles-Hernandez et al. [109], Lacantuniidae, known from a single species from southern Mexico. A phylogenetic and biogeographic study by Lundberg et al. [110] concluded that *Lacantunia* (Rodiles-Hernández, Hendrickson & Lundberg, 2005) in fact belongs to a separate family and, surprisingly, is more closely related to Claroteidae and some other African catfishes. *Kryptoglanis shajii* (Vincent & Thomas, 2011), another unusual Siluriformes that lives in groundwater in western India, was recently described by Vincent and Thomas [111] and presents a developmentally truncated morphology [112]. This species was assigned to a new family, Kryptoglanidae, by Britz et al. [113], but there is a hypothesis that the taxon is actually a member of Siluridae [112]. In Brazil, two enigmatic genera, *Conorhynchos* (Bleeker, 1858), endemic to the São Francisco and Paraguaçu river basins, and *Phreatobius* (Goeldi, 1905), which live in groundwater in the Amazon basin, were studied by Sullivan et al. [82], who hypothesized that *Conorhynchus* is a sister group to the other Heptapteridae and *Phreatobius* is a sister group to Pseudopimelodidae + Pimelodidae, possibly representing a new family.

The phylogenetic relationships of Siluriformes families are still debated. From a morphological point of view, de Pinna [81] highlighted those historical processes such as convergence, parallel adaptation to similar habitats, and reversion (such as that which occurred in subterranean fish) may be frequent in the group. According to Diogo [114], such frequency of changes in historical processes raises serious problems for correctly inferring the relationship between catfish groups from all continents. Diogo [114] presented and discussed the morphological phylogeny studies for Siluriformes and presented a hypothesis based on 440 osteological and myological characters of 87 genera and 32 recent families (Figure 9). This phylogeny is very similar (or in several points identical) to other previously published morphological data [114].

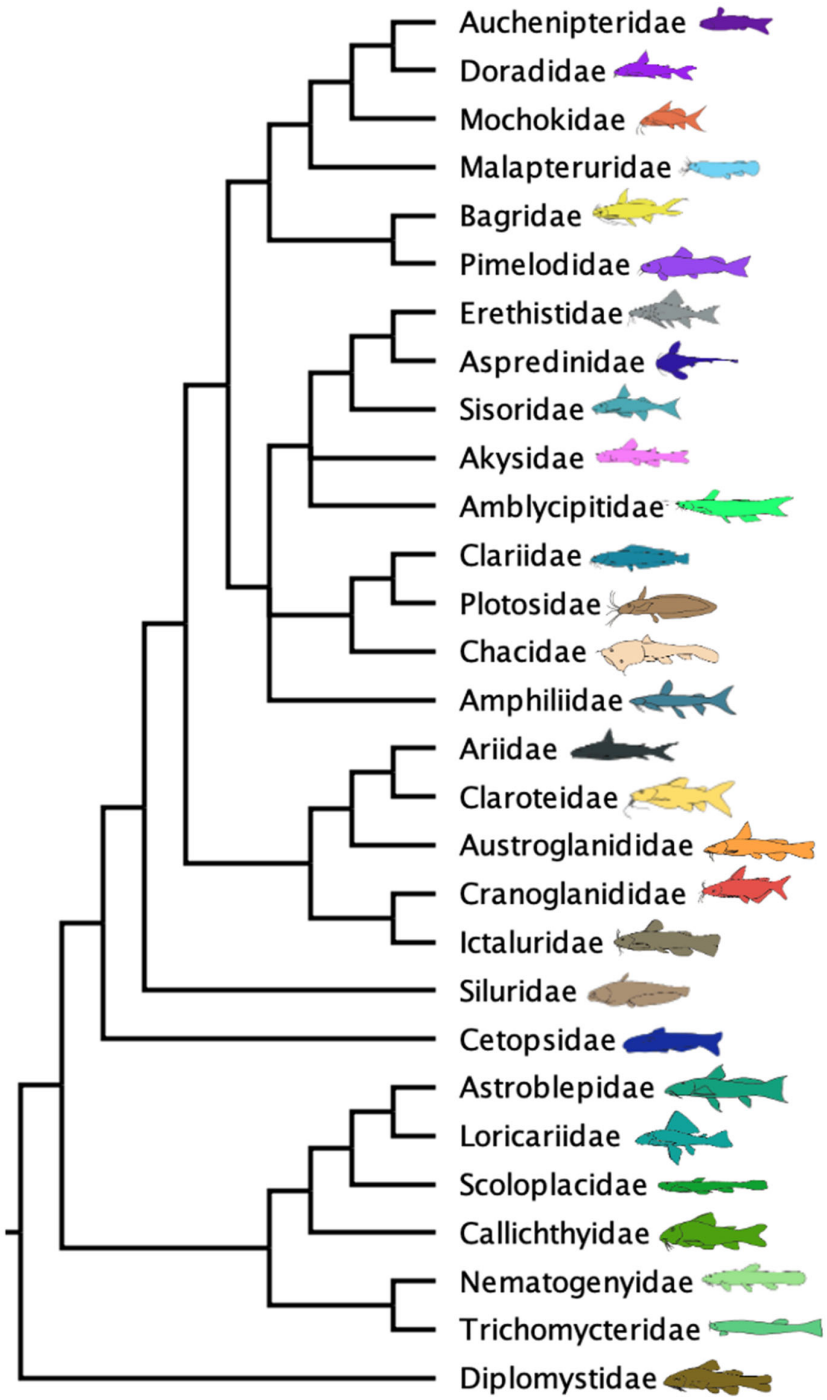

Figure 9. Phylogeny of Siluriformes, based on morphological data, proposed by Diogo [114].

In the first broad molecular study published for siluriforms, Sullivan et al. [115] presented a very different hypothesis, which shows, for example, Diplomystidae as a sister group to Siluroidei, among other issues, but whose interfamilial resolution is very low or nonexistent (Figure 10). The results also corroborate the monophyly of some large groups such as Pimelodoidea and showed that some families also form monophyletic lineages identified as 'Big Asia' and 'Big Africa'.

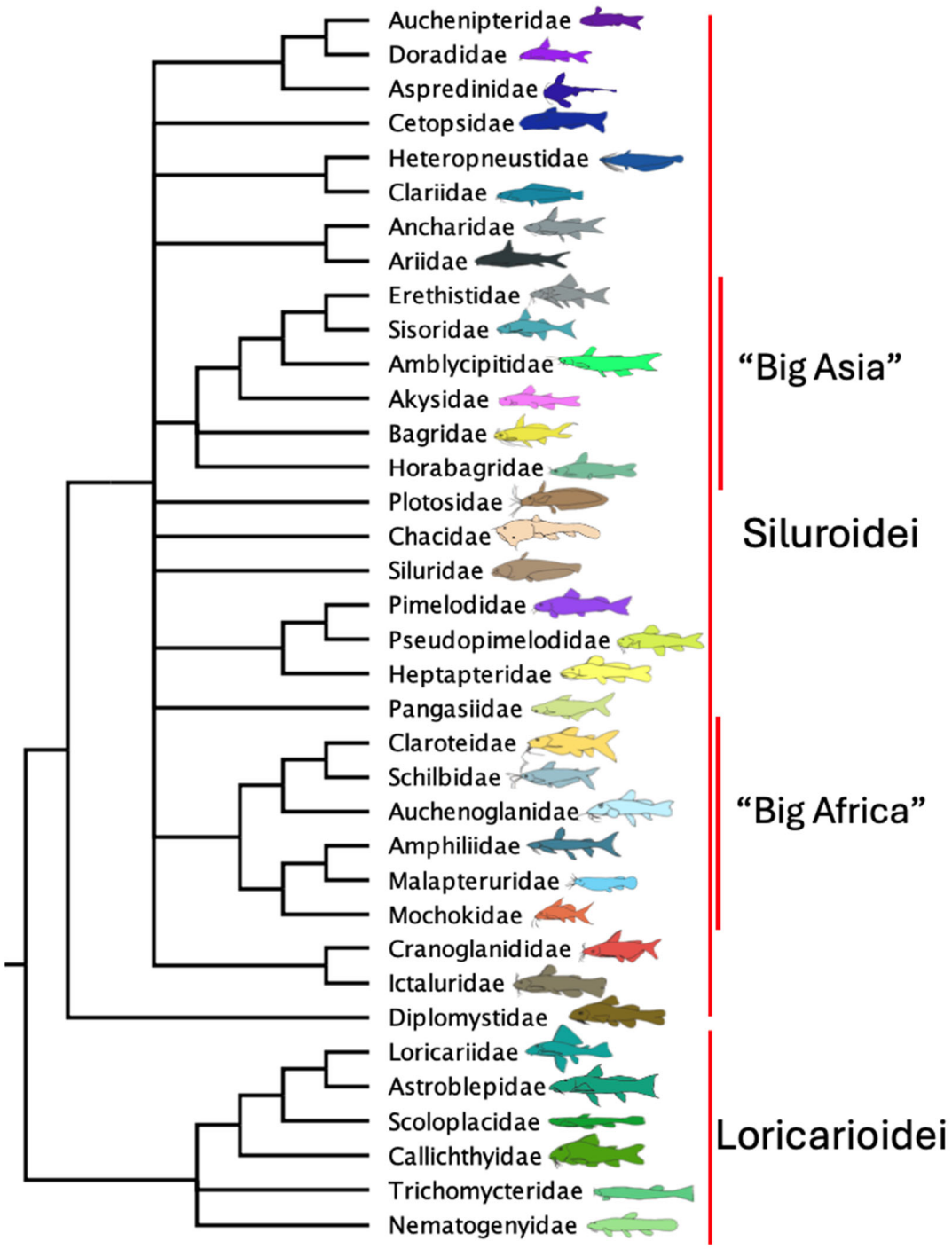

Figure 10. Phylogeny of Siluriformes, proposed by Sullivan et al. [115] based on partial sequences of the Rag1 and Rag2 genes.

Nakatani et al. [116] and Kappas et al. [117] published siluriforms phylogenies based on complete mitogenome sequences and obtained phylogenies like that of Sullivan et al. [115]. The phylogeny of Arcila et al. [33], using exons, also corroborates the hypothesis that Diplomystidae is the sister group of all Siluriformes except Loricarioidei. Rivera-Rivera and Montoya-Burgos [118] analyzed, by maximum likelihood, 54 siluriform taxa using partial sequences of 10 genes (mitochondrial and nuclear), and the results were initially like those obtained by Sullivan et al. [115] (Figure 10). However, when they applied a different method to reduce evolutionary rate heterogeneity among lineages, they found Diplomystidae as a sister group of all other siluriforms, as suggested by morphological data

(Figure 11b). Schedel et al. [89] published a phylogenetic study including all mitochondrial protein-coding genes of 239 catfish species representing 33 of the 39 families recognized at that time (Figure 12). The results also corroborate the hypotheses that Diplomystidae is the sister group of all Siluriformes except Loricarioidei (Figure 11). The results also corroborate the hypotheses that groups identified as 'Big Asia' and 'Big Africa', proposed by Sullivan et al. [115], are monophyletic and determinate that Austroglanididae are close related to Pangasiidae, Ictaluridae, and Ariidae.

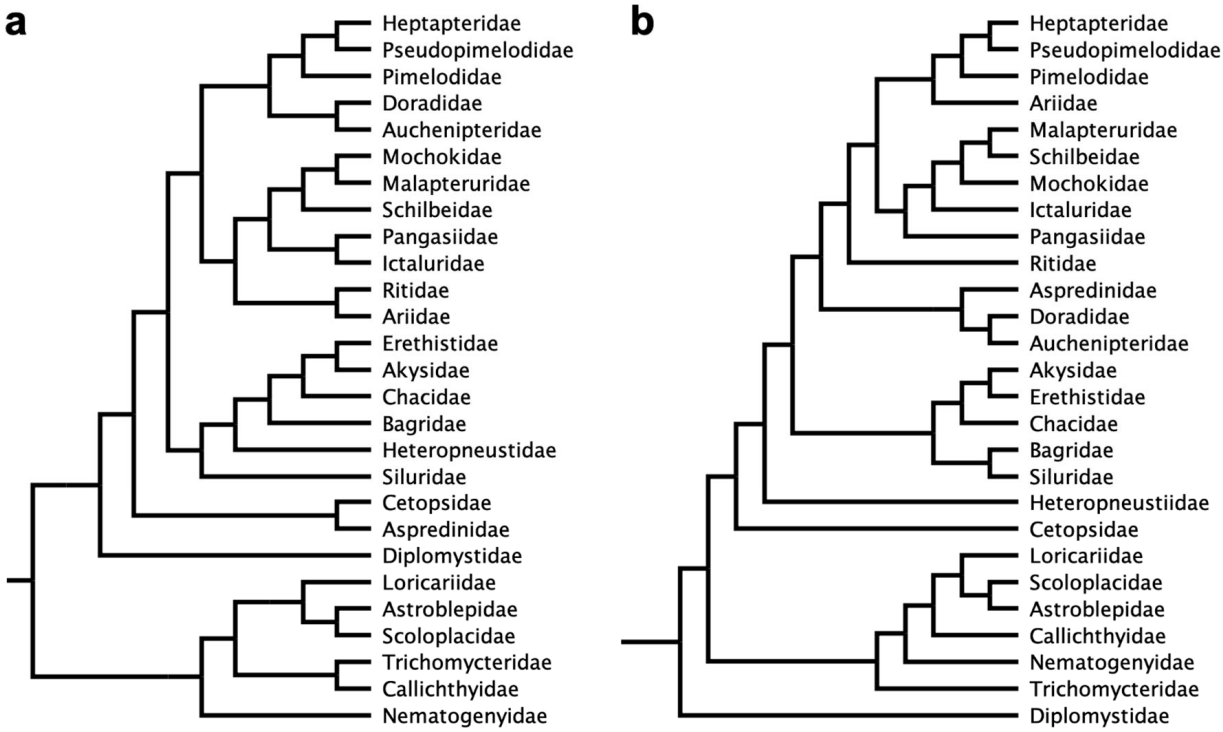

Figure 11. Siluriformes phylogenies proposed by Rivera-Rivera and Montoya-Burgos [118]. (**a**) ML tree using full 10 genes dataset. (**b**) ML tree using the LS4 data subsampling algorithm in order to reduce evolutionary rate heterogeneity among lineages.

The order Gymnotiformes is monophyletic and a sister group to Siluriformes [23,24], but there is still controversy on this point (see Figure 4). The order has five families, 36 genera, and 275 species [2]. Many taxonomic studies have been carried out in the group, resulting in the description of 60 species, almost half of the total species in the order, in the last 10 years [2]. Fish in this order are characterized by having an anguilliform body with extremely long anal fins that allow them to move forward and backward and by having electrical organs derived from muscle cells in most groups (myogenic) or from nerve cells in adult Apteronotidae (neurogenic) [1]. The only known fossil of Gymnotiformes is †*Humboldtichthys kirschbaumi* (Gayet & Meunier, 2000) from the Late Miocene of Bolivia [1].

The relationships among members of the order Gymnotiformes have been investigated in several studies summarized in Albert and Crampton [119] (Figure 13). Tagliacollo et al. [120] published a study combining morphological data (223 characters) with molecular data (5277 base pairs) for 120 species and 34 of the 35 known genera, and the results corroborate the hypothesis of Albert and Crampton [119]. The study by Arcila et al. [33] suggested that Apteronotidae was a sister group to all other Gymnotiformes, a result different from that found by Tagliacollo et al. [120].

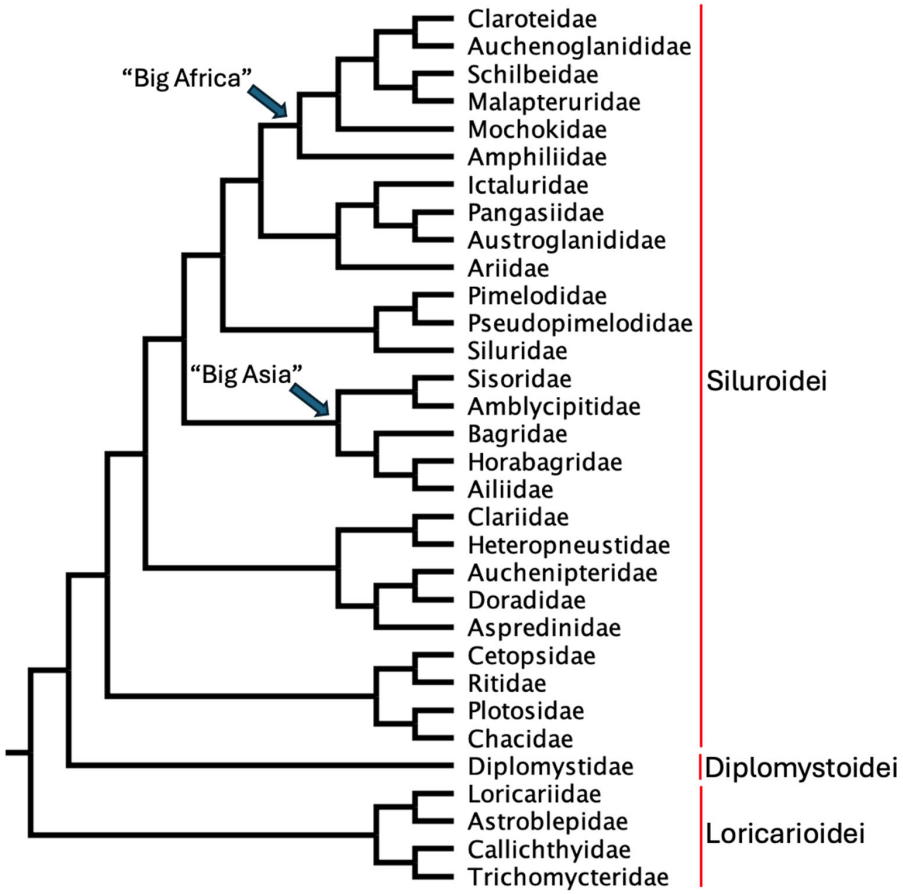

Figure 12. Siluriformes phylogeny proposed by Schedel et al. [89] including all mitochondrial protein-coding genes of representatives of 33 families.

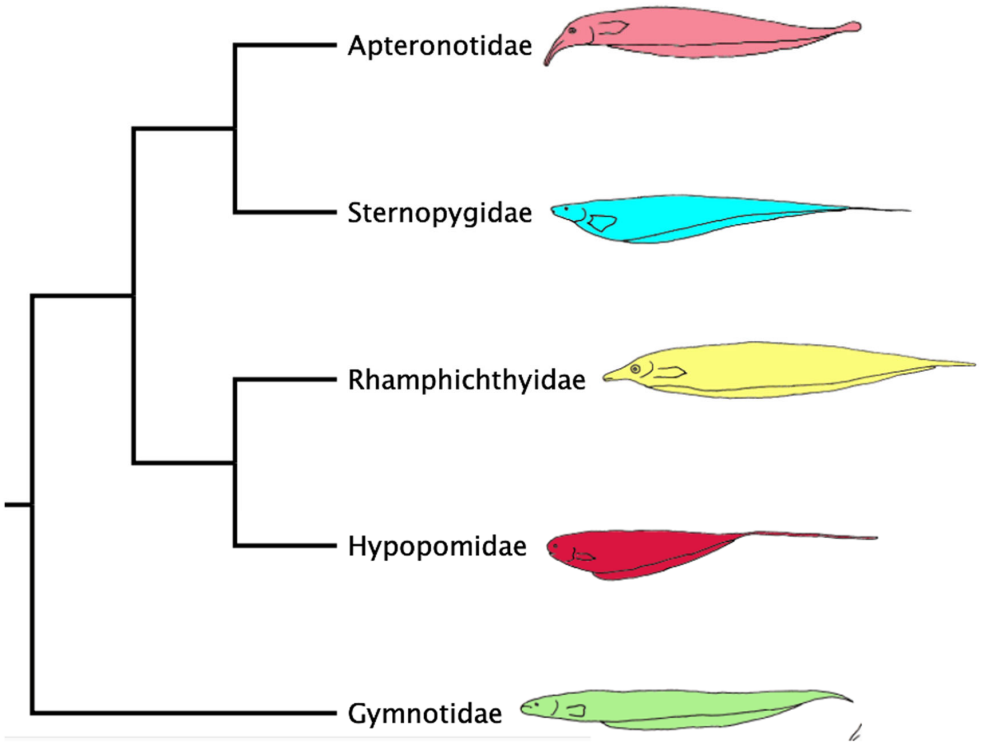

Figure 13. Composite phylogenetic hypothesis of interrelationships among families of Gymnotiformes according to Albert and Crampton [119].

In a more recent study, Alda et al. [121] sequenced 2681 UCE loci for 44 Gymnotiformes samples. After applying filters to remove regions with more than 25% missing data, the authors assembled a matrix with 966 loci (376,533 bp) that was analyzed in a comparative manner using several statistical methods, and the results are summarized in Figure 14. The authors found two different results when different analytical methods were used. Thus, when the data were analyzed after concatenation, Apteronotidae was found as a sister group to the other families of the order (Figure 14a). In contrast, the analysis by coalescent methods suggested a new hypothesis, where the families that have species that generate pulse-type electric currents (Pulseoidea: Gymnotidae, Hypopomidae, and Rhamphichthyidae) and wave-type electric currents (Sinusoidea: Apteronotidae and Sternopygidae) were recovered as monophyletic groups (Figure 14b). The comparative analyses showed that, for the analyzed data set, the coalescent approach was less susceptible to noise resulting from ILS (incomplete lineage sorting). Although these new data are consistent with the idea that the wave-producing system emerged only once, a matrix with new data needs to be analyzed so that this hypothesis can be tested.

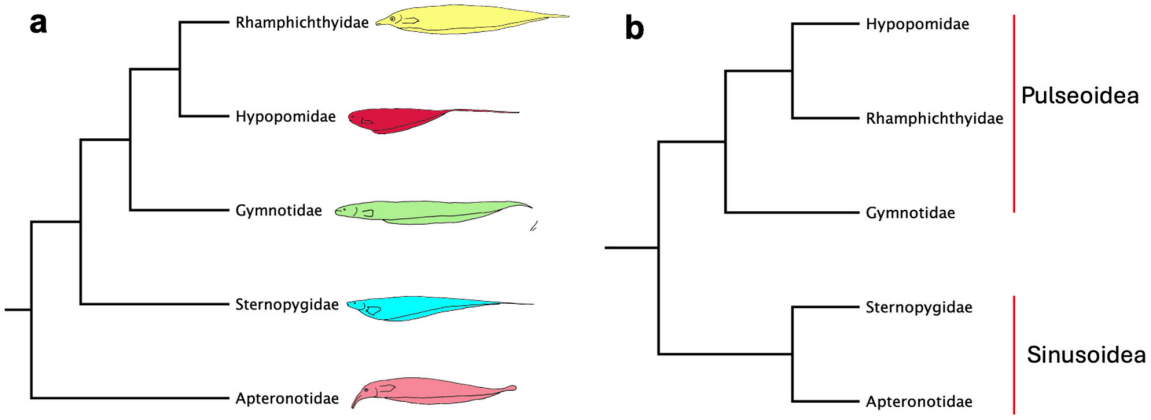

Figure 14. Gymnotiformes phylogenies proposed by Alda et al. [121]. (**a**) Phylogeny obtained by the maximum likelihood method with samples of 966 concatenated UCE loci. (**b**) Cladogram constructed from species trees based on a reduced matrix.

2. Conclusions

After three decades of investigations, combining morphological and molecular data, including phylogenomics, we have today a much more resolutive view of the composition and interrelationships of Ostariophysi groups. However, the group is composed of a very large number of recent and fossil species, and only recently the studies have included a representative number of species in the comparative studies. This increase in representativity, the use of more precise morphological data, and mainly the use of genomic data have permitted the proposition of more robust hypotheses about the relationships among many clades. Thus, thinking in further studies, we still must investigate the relationships among families of Gonorhynchiformes, Cypriniformes, Siluriformes, some Characiformes, and Gymnotiformes since the controversial proposed available as discussed in the text. In these cases, the main problem is possibly related rapid diversification processes, difficult to quantify from a molecular point of view and due to morphological convergence problems due to similar life habits in different regions of the world. The relationship among genera and species is also incipient for many families, mainly those very large ones, and will need additional studies, including more representatives of each genus or family and additional morphological and molecular data. All these efforts will increase our knowledge about a fascinating fish group and will also permit the development of other research lines such as biogeography, evolution, ecology, ethology, physiology, and genetics, among others.

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