Higher-level Phylogeny of Siluriformes—An Overview

Rui Diogo*

The Siluriformes, or catfishes, with approximately 416 genera and over 2500 species, represent about 32% of all freshwater fishes (Teugels, 1996). According to Ferraris and de Pinna (1999), 35 catfish families can be recognised. However, it is commonly accepted at present that the Pimelodidae is not a monophyletic group, but instead an unnatural group containing three distinguishable monophyletic units that are not closely related (see, e.g. de Pinna, 1998, for more details on this subject). Therefore, the number of catfish families should, very likely, be increased from 35 to 37.

The relationships among the various catfish families have long been studied. However, the number of studies focused on this subject has increased considerably in the last three decades due to the renewed impetus provided by the advent of cladistics in the second half of the last century (de Pinna, 1998). The principal aim of this chapter is to provide an overview of those cladistic studies published in these last decades.

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dealing with the higher-level phylogeny of Siluriformes, as a foundation for an overall discussion on the state-of-the-art of catfish phylogeny.

**INTRARELATIONSHIPS AND MONOPHYLY OF VARIOUS CATFISH FAMILIES**

As noted above, the main purpose of this chapter is to discuss the phylogenetic relationships among the various catfish families. However, I consider it convenient to present here a brief overview (Table 12.1) of the principal published cladistic studies providing relevant information on the autapomorphies of these families, as well as on the relationships among their genera. Before commencing analysis of Table 12.1, it should be noted that in this Table, as well as in the rest of the chapter, I treat each of the three subfamilies of so-called ‘Pimelodidae’ as a separate family. Therefore, I shall refer to 37 catfish families, that is, the 35 families listed by Ferraris and de Pinna (1999) plus Pseudopimelodidae and Heptapteridae (see above). It should also be noted that in Table 12.1, as well as in the rest of this chapter, when I refer to phylogenetic studies dealing either with relationships among the genera of these 37 families or with the relationships among these families, I refer only to published cladistic studies. Among the several reasons for following this procedure, one of the most important is to decrease the confusion associated with such a puzzling issue, i.e., the phylogeny of Siluriformes. In fact, many of the “precladistic” (see de Pinna, 1998) studies dealing with the relationships among catfishes are highly confusing, grouping certain taxa due to the presence of both plesiomorphic and highly homoplastic characters, or simply (several times) without giving a clear explanation for doing so. Moreover, it is somewhat complicated, and also highly confusing, to compare in a clear and objective way the conclusions of those studies using such “pre-cladistic” methodologies with the phylogenetic results of those studies following a cladistic methodology. Furthermore, recent cladistic works have pointed out that the conclusions of most of the “precladistic” studies (e.g. placement of the present Cetopsidae as a subfamily of Trichomycteridae; grouping of the present Bagridae, Claroteidae and Austroglanididae in the ‘Bagridae’; placement of the present Helogeninae as a subfamily of the Schilbeidae; etc.: see de Pinna, 1998) are highly questionable, which is understandable given the inappropriate phylogenetic methodologies used. It should be noted, however, that this does not mean that all the “precladistic” studies should be ignored but rather that, in the specific case of this chapter, the author
Table 12.1  List of the principal cladistic studies published to date providing relevant information concerning the phylogenetic relationships among the genera and/or the autapomorphies of the various catfish families. A (p) after the reference of a certain study indicates that the respective study only provides information about the relationships among part of the family (see text).

<table>
<thead>
<tr>
<th>Family</th>
<th>Relationships among the different genera of the family</th>
<th>Autapomorphies to support monophyly of the family</th>
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<tbody>
<tr>
<td>Akysidae</td>
<td>de Pinna, 1996</td>
<td>Mo, 1991; de Pinna, 1996</td>
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<tr>
<td>Amblycipitidae</td>
<td>Chen and Lundberg, 1994</td>
<td>Mo, 1991; Chen and Lundberg, 1994; de Pinna, 1996</td>
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<td>Amphiliidae</td>
<td>He et al., 1999; Diogo, this volume</td>
<td>Diogo, this volume</td>
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<td>Andinichthyidae</td>
<td>Family with only a single genus</td>
<td>Gayet, 1988</td>
</tr>
<tr>
<td>Ariidae</td>
<td><em>Not available</em></td>
<td>Mo, 1991; de Oliveira et al., in press</td>
</tr>
<tr>
<td>Aspredinidae</td>
<td>de Pinna, 1998</td>
<td>de Pinna, 1996; Diogo et al., 2001</td>
</tr>
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<td>Astroblepidae</td>
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<td>Schaefer and Lauder, 1986; Schaefer, 1990; Howes, 1983; de Pinna, 1998</td>
</tr>
<tr>
<td>Austroglanidida</td>
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<td>Mo, 1991</td>
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<td>Bagridae</td>
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<td>Mo, 1991; Diogo et al., 1999</td>
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<td>Callichthyidae</td>
<td>Reis, 1998</td>
<td>Schaefer, 1990; Reis, 1998</td>
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<td>de Pinna and Vari, 1995</td>
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<td>Chacidae</td>
<td>Family with only a single genus</td>
<td>Brown and Ferraris, 1988</td>
</tr>
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<td>Claridae</td>
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<td><em>Not available</em></td>
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<tr>
<td>Cranoglanidida</td>
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<td>Diogo et al., 2002</td>
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<tr>
<th>Family</th>
<th>Authors</th>
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<td>Erethistidae</td>
<td>de Pinna, 1996</td>
<td>de Pinna, 1996</td>
</tr>
<tr>
<td>Heptapteridae</td>
<td>Ferraris, 1988 (p); Lundberg et al., 1991a; Bockmann, 1994 (p)</td>
<td>Lundberg and McDade, 1986; Ferraris, 1988; Lundberg et al., 1988, 1991a; de Pinna, 1998</td>
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<td>Grande, 1987; Arratia, 1992 (but see Mo, 1991: 195; Grande and de Pinna, 1998: 471)</td>
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<td>Ploptidae</td>
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<td>de Oliveira et al., 2001</td>
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<td>Lundberg et al., 1991a; de Pinna, 1998</td>
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<td>Scoloplacidae</td>
<td>Family with only a single genus</td>
<td>Schaefer et al., 1989; Schaefer, 1990</td>
</tr>
<tr>
<td>Sisoridae</td>
<td>de Pinna, 1996 (p); He, 1996 (p)</td>
<td>de Pinna, 1996</td>
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</table>
considers it more appropriate to present a more detailed overview of all the cladistic studies published to date on the relationships among the genera of each of the 37 catfish families (Table 12.1) and/or among these families (next section) (for a recent, detailed overview of the most important "precladistic" works on the taxonomy and classification of siluriforms, see de Pinna, 1998).

From analysis of Table 12.1, a pronounced imbalance is apparent between the number of phylogenetic studies dedicated to the intrarelationships of New World families (although a phylogenetic analysis of the intrarelationships of Cetopsidae and Pseudopimelodidae is still lacking) and Old World taxa (intrarelationships of Mochokidae, Clariidae and Schilbeidae for example, have never been the subject of phylogenetic analysis). Furthermore, analysis of Table 12.1 indicates that little attention has been given to intrarelationships of those families formed largely of marine catfishes, i.e., Plotosidae and Ariidae. With respect to the autapomorphic characters that support the monophyly of the various catfish families, there is also a pronounced unbalance between studies dedicated to New versus Old World families. In fact, all the five families for which there are no available, well-defined autapomorphies published to date are from the Old World: Anchariidae, Heteropneustidae, Claridae, Pangasiidae and Schilbeidae (Table 12.1). Even if the lack of autapomorphies to support the monophyly of Anchariidae and Heteropneustidae is not, in a certain sense, highly problematic (both families are monogeneric, each including only two species: Teugels, 1996), the same cannot be said about the lack of autapomorphies to support the monophyly of the multigeneric families Claridae, Pangasiidae and Schilbeidae. In particular, the phylogenetic situation of the Schilbeidae, a family with 13 genera and about 51 species (Teugels, 1996) that is probably polyphyletic (Mo, 1991: 195-196) and has never been studied phylogenetically (Table 12.1), is especially problematic and, as emphasized by Teugels (1996: 15), “a detailed phylogenetic study of the schilbeidae is absolutely necessary”.

**HIGHER-LEVEL PHYLOGENY OF SILURIFORMES: AN HISTORICAL ACCOUNT**

Among all cladistic works published to date on catfish phylogeny, the vast majority were dedicated to the study of intrarelationships of either a part or the entirety of a particular catfish family (Table 12.1). The only
published cladistic studies presenting original, explicit cladograms on the interfamilial relationships of either a part or the whole of the order Siluriformes, are those of Howes (1983), Grande (1987), Schaefer (1990), Mo (1991), Arratia (1992), de Pinna (1992), Lundberg (1993), de Pinna (1996), de Pinna (1998) and He et al. (1999). A brief description of each of these studies follows.

**Howes, 1983 (Fig. 12.1)**

In his fig. 22, Howes presented a hypothesis on loricarioid relationships (Fig. 12.1), based both on his own observations and an unpublished thesis of Baskin, 1972 (Howes, 1983: 341-342). According to this hypothesis, Astroblepidae and the Loricariidae form a clade that is the sister-group of Scoloplacidae, with these three families being, in turn, the sister-group of Callichthyidae. Also, according to this hypothesis the clade formed by these four families is the sister-group of Trichomycteridae, with Nematogenyidae being the next sister-group and consequently, the more basal of the six loricarioid families. In order to support the phylogenetic hypothesis illustrated in Figure 12.1, Howes (1983: 342) advanced several derived morphological characters (involving mainly the osteology, myology and external morphology of the cephalic region, the Weberian apparatus and the caudal fin) to support its different nodes. The clade including all six loricaroid families is diagnosed by “swim-bladder encapsuled, divided into separate vesicles; some part of the cranium contributing to encapsulation”. The clade including all loricaroid families excluding Nematogenyidae is defined by “claustrum and intercalarium lacking from the Weberian vertebral series”. The characters uniting Callichthyidae, Scoloplacidae, Loricariidae and Astroblepidae are: “post-
temporal contributing to distal portion of swim-bladder capsule; derived hypural fusion pattern; low number of principal caudal fin rays”. Finally, Scoloplacidae, Loricariidae and Astroblepidae are united due to the presence of a “connecting bone between the 1st rib and the 2nd pterygophore”, with the latter two families grouped into a monophyletic clade by the presence of a retractor premaxillae muscle, medial division of the protractor hyoideus, as well as the “reverted lip; lateropterygium; 6 fused anterior centra”.

However, Howes called attention to some derived characters that conflict with this phylogenetic hypothesis. The single derived character defining the clade including all non-nematogenyid loricarioids (see above), for example, conflicts with the “lateral insertion of the dilatator operculi muscle”, a derived character shared by both Nematogenyidae and Trichomycteridae (Howes, 1983: 341-342).

Grande, 1987 (Fig. 12.2)

In 1987, Grande, based on his own osteological observations of a fossil catfish from the Eocene Green River Formation of Wyoming originally described by Lundberg and Case (1970), Hypsidoris farsonensis, as well as on his own comparisons between this fossil and other catfishes, proposed an original hypothesis on the higher-level phylogeny of the Siluriformes (Fig. 12.2). According to this hypothesis, the fossil catfish family Hypsidoridae is the sister-group of all other non-diplomystid catfish families (= Siluroidea), with the clade formed by the latter plus Hypsidoridae (= Siluroidei) being the sister-group of Diplomystidae (Fig. 12.2). Grande (1987: 48) listed three characters to diagnose the suborder Siluroidei, namely: (1) 17 or fewer principal caudal rays; (2) extension of lamellar bone over the ventral surface of the fifth centrum; (3) fifth centrum joined closely to the complex centrum. Grande (1987: 48) listed five characters to diagnose the superfamily Siluroidea, namely: 1) loss of maxillary teeth; (2) loss or reduction of distal expansion of the maxilla;

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Diplomystidae (Diplomyistoidei)

- Hypsidoridae (Siluroidei, Hypsidoroidei)
- All other families (Siluroidei, Siluroidea)

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Fig. 12.2 Hypothetical relationships among the Diplomystidae, Hypsidoridae and other catfish families (Grande, 1987).
Grande’s hypothesis (1987) contradicts the phylogenetic hypothesis formulated in the original description of *Hypsiporus farsonensis*, in which this fossil species was described as a member of family Ictaluridae (Lundberg and Case, 1970: 451-456).

**Schaefer, 1990 (Fig. 12.3)**

Schaefer (1990) undertook a phylogenetic analysis to infer the relationships among loricarioid families (Fig. 12.3) and also among the various scoloplacid species. This study was based on osteological, myological and arthrological structures of the cephalic region, as well as on osteological structures of the axial and caudal fins. The numerical analysis (using PAUP) of a data matrix of 72 characters − 9 terminal taxa, which did not include autapomorphic characters, resulted in a single, most parsimonious cladogram with 77 steps and a CI = 0.842. Concerning the interrelationships among Loricariidae, Astroblepidae, Scoloplacidae and Callichthyidae, this cladogram (Fig. 12.3) is similar to that of Howes (1983). The synapomorphies listed by Schaefer (1990: 204) to diagnose the clade including these four families were: (1) loss of mesethmoid lateral cornua; (2) fusion of the pterotic and supracleithrum; (3) loss of canal in the lacrimal-antorbital; (4) loss of tight attachment of the premaxillae with the neurocranium; (5) four or fewer branchiostegal rays; (6) dorsal hypurals fused with compound caudal centrum; (7) presence of mesethmoid-maxillary ligament; (8) presence of mesethmoid-premaxillary ligament; (9) presence of retractor tentaculi muscle. Synapomorphies listed by Schaefer (1990: 204) to define the clade formed by astroblepids, loricariids and scoloplacids included: (1) loss of open cranial fontanels; (2) loss of cranial aperture which receives the cleithral

![Fig. 12.3](image-url) Hypothetical relationships among loricarioid families (Schaefer, 1990).
dorsal process; (3) presence of bifid jaw teeth; (4) loss of interopercle; (5) ventrolateral shift in articulation of the rib on the sixth centrum; (6) presence of a lateral bone; (7) loss of the pterygoethmoid ligament; (8) loss of cranial attachment; (9) loss of interoperculomandibular ligament; (10) shift in origin of the retractor tentaculi muscle; (11) bifurcation of hyohyoideus muscles. Finally, the synapomorphies listed by Schaefer (1990: 204) to support the sister-group relationship between loricariids and astroblepids included: (1) loss of contact of the mesethmoid posterior process with the frontals; (2) presence of a hyomandibula-metapterygoid suture; (3) ventromedial rotation of the mandibles; (4) ankylosis or suture between the sixth centrum and Weberian complex centra; (5) loss of vertebral parapophyses; (6) presence of expanded transverse shelf on the first anal fin; (7) geniohyoideus bilaterally subdivided; (8) presence of an expanded oral disc; (9) right and left sides of lower jaws not tightly associated at the midline; (10) presence of intermandibular cartilage; (11) presence of juxtaposed nostrils.

The most significant difference between Schaefer’s (1990) and Howes’ (1983) studies is that Schaefer (1990) did not place Trichomycteridae as the sister-group of the clade formed by these four families, but instead in an unresolved trichotomy including that clade, Trichomycteridae and Nematogenyidae (Fig. 12.3). However, it should be noted that, as emphasized by Schaefer (1990: 174), such an unresolved trichotomy was not the consequence of his own phylogenetic results but, instead, of considering the relationships between nematogenyids, trichomycterids and the remaining loricarioids as ‘unresolved a priori’.

Mo, 1991 (Fig. 12.4)

One year after the publication of Schaefer’s 1990 paper, Mo (1991) published a study dealing mainly with the phylogenetic relationships of Bagridae, including a generic-level revision and phylogeny of the family. In addition, Mo (1991) included a somewhat brief (46 pages in a total of 216 plus 63 unnumbered figures) analysis of the higher-level phylogeny of siluriforms. This analysis, based on osteological characters of the cephalic region, the Weberian apparatus, pectoral girdle and various fins, but also on a few soft and/or myological characters, resulted in two considerably different cladograms. One (Fig. 12.4A), based on an “unweighted” numerical analysis (using the Hennig 86 computer program) of a data
matrix of 126 characters (40 terminal taxa (which did not include autapomorphic characters), had 602 steps, CI = 0.31, RI = 0.64 and was only poorly resolved. The other (Fig. 12.4B), based on a "weighted" numerical analysis (also using Hennig 86) of the same data matrix in which one of the 126 characters ("number of vertebrae united to the complex vertebra") was given a phylogenetic weight 4 times that of the other characters, had 549 steps, CI = 0.36, RI = 0.72 and, apart from two trichotomies, was completely resolved. According to Mo (1991: 193), this

Fig. 12.4 Hypothetical relationships among major groups of Siluriformes (Mo, 1991). A. Cladogram produced from numerical analysis of 126 unweighted characters. B. Cladogram produced from numerical analysis of 126 characters with a weighting (4) on one of them, namely, "number of vertebrae united to the complex vertebra" (Mo, 1991: 193).
“weighting” was due to the “morphological stability and consistent distribution of this character compared with those conflicting features”.

One of the main conclusions of Mo’s (1991) work was the separation of ‘Bagridae’ into three monophyletic units, namely Bagridae (sensu Mo, 1991), Claroteidae and Astroglanididae, which, according to Mo, are more closely related with other catfish families than with each other (Fig. 12.4).

Another important conclusion of this work is the suggestion that Cetopsidae occupies a markedly basal position in the order Siluriformes (although the ‘Helogeneidae’, ‘Cetopsidae’ and ‘Hemicetopsis’ of Mo were not, as commonly accepted today, grouped into a single monophyletic taxon; they were placed in a rather basal position among Siluriformes in both of Mo’s cladograms). In Mo’s cladogram I (clearly preferred by him), the cetopsids and diplomystids are separated from all other siluriforms by the presence in the latter of two characters: (1) interdigital union of the two coracoids; (2) ramus mandibularis nerve runs inside the hyomandibular for a distance (Mo, 1991: 204). Of these two characters, only the latter is listed in Mo’s cladogram II to diagnose the clade composed by all non-diplomystid, non-cetopsid catfishes.

Another important, but confusing, conclusion of Mo (1991) is the phylogenetic position of the fossil catfish Hypsidoris. In Mo’s cladogram II (Fig. 12.4B), Hypsidoris is placed in a far more derived position than in Grande’s 1987 cladogram (Fig. 12.2). However, in Mo’s cladogram I (Fig. 12.4A), Hypsidoris is placed in an unresolved polychotomy, with the phylogenetic position of this genus thus uncertain.

With respect to the other catfish groups, their phylogenetic position is also, with only a few exceptions, quite uncertain, not only as a consequence of the poor resolution of Mo’s cladogram I (Fig. 12.4A), but primarily due to the significant differences between this cladogram and Mo’s cladogram II (Fig. 12.4B). These few exceptions are discussed below.

One exception concerns the relationships among loricarioid families, essentially similar to those proposed by Howes (1983) and Schaefer (1990), with the only difference being that in Mo’s cladograms, Trichomycteridae and Nematogenyidae are considered sister-groups (Fig. 12.4). This sister-group relationship is supported, according to Mo (1991: 204, 208), by the fact that trichomycterids and nematogenyids, contrary to other loricarioids, have “nasal barbels situated at the anterior nostrils”.

In both the cladograms of Mo (1991) the loricarioids and amphiliids are grouped in a clade closely related to Sisoridae, Akyssidae,
Amblycipitidae, Claridae, Heteropneustidae, Aspredinidae and Chacidae (Fig. 12.4). In Mo’s cladogram I the clade including Amphiliidae and Loricarioidei is diagnosed by “posterior portion of the palatine reduced into a bony lamina or short spine-like process without distal cartilage” (Mo, 1991: 204), while in his cladogram II no character defines this clade. In Mo’s cladogram I the clade including loricarioids, amphiliids, sisorids, aksyids, amblycipitids, clarids, heteropneustids, aspredinids and chacids is justified by a “computer generated node (Mo, 1991: 204), while in his cladogram II the clade including all these groups is diagnosed by the “absence of extrascapular” (Mo, 1991: 207).

Both Mo’s cladograms suggest a monophyletic clade comprising Auchenipteridae, Doradidae, Mochokidae, Ariidae, Hypophthalmidae and Pimelodidae (although the ‘Auchenipteridae’, ‘Ageneiosidae’ and ‘Centromochlidae’ of Mo were not, as is commonly accepted, grouped in family Auchenipteridae, these three groups were placed in this clade in both of Mo’s cladograms). In Mo’s cladogram I this clade is defined by a single character, namely, “anteriorly thickened and rounded or convex mesethmoid” (Mo, 1991: 204). In Mo’s cladogram II this clade is defined not only by this character, but also another two—the presence of “four infraorbitals” and the “enclosed aortic canal in the complex vertebra” (Mo, 1991: 208).

**De Pinna, 1992 (Fig. 12.5)**

One year after the publication of Mo’s work, de Pinna (1992) described a new subfamily of the Neotropical catfish family Trichomycteridae, theCopionodontinae. In the same work, de Pinna provided a phylogenetic analysis of the interrelationships among trichomycterids, as well as among them and other loricarioids. The 27 characters included in that analysis consisted mainly of osteological characters of the cephalic region, Weberian apparatus, dorsal fin, pelvic fin and pectoral girdle, but also a few

![Fig. 12.5](image_url) Hypothetical relationships among trichomycterids, as well as among these fishes and other loricarioids (de Pinna, 1992).
soft and/or myological characters. A hand-made comparison of these characters resulted in a fully resolved cladogram with a CI (autapomorphic characters not included) = 0.78, that like both of Mo’s previous cladograms (1991), suggested a sister-group relationship between Trichomycteridae and Nematogenyidae. However, it should be noted that de Pinna’s 1992 phylogenetic analysis was completely independent from that of Mo (1991) (when de Pinna was writing his paper, he was unaware of Mo’s results). In fact, the main reason that led de Pinna to propose a sister-group relationship between Trichomycteridae and Nematogenyidae was “to a major extent induced by the inclusion of copionodontines and Trichogenes in the analysis of lower loricarioid relationships” (de Pinna, 1992: 175). According to de Pinna (1992: fig. 23), this inclusion indicated that, of the four derived characters traditionally used to support a sister-group relationship between the trichomycterids and the other non-nematogenyid loricarioids, only one (“transformator process of tripus absent”) indeed represented the plesiomorphic situation for trichomycterids. The other three (“intercalarium absent”, “ductus pneumaticus absent” and “superficial ossification covering ventral surface of articulation between complex vertebrae and basioccipital”) represented, on the other hand, an apomorphic configuration exclusively present in a restricted group of derived trichomycterids (Fig. 12.5: Remaining trichomycterids). Consequently, grouping of all non-nematogenyid loricarioid families that could no longer be supported by a single derived character, was parsimoniously discarded by de Pinna (1992) in favour of a sister-group relationship between Trichomycteridae and Nematogenyidae, supported by three derived characters. These three characters are: (1) mesial juncture between scapulo-coracoids without interdigitations; (2) first dorsal-fin pterygophore inserted posterior to neural spine of ninth free vertebra; (3) absence of dorsal-fin spine and locking mechanism (de Pinna, 1992: fig. 23).

Arratia, 1992 (Fig. 12.6)

Arratia’s 1992 work is a detailed, extensive study dedicated to the development, morphological variation and homologies of the suspensorium of certain siluriform and non-siluriform ostariophysans. It also provides an analysis based on the suspensorial features examined as well as on some other characters described previously in other studies (e.g., Fink and Fink, 1981; Arratia, 1987; Grande, 1987), of the phylogenetic
relationships among the various ostariophysan orders and also among certain catfish groups. With respect to the relationships among certain siluriforms, Arratia’s (1992) analysis resulted in four practically identical cladograms, the only difference concerning the relationships among diplomystids. As this section is essentially dedicated to the inter-familial relationships of the Siluriformes, I shall only refer to the cladogram illustrated in Arratia’s (1992) figure 46A (for a detailed explanation of the methodology followed to produce the other three cladograms, as well as for a discussion on the differences between them, see Arratia, 1992: 126-129).

This cladogram (Fig. 12.6), based on an numerical analysis (using PAUP) of a data matrix of 75 characters 15 terminal taxa, in which 69 characters were ordered and 6 unordered, corresponds to the consensus of two equally parsimonious threes (CI = 0.672) with 137 steps. It supports Grande’s (1987) hypothesis, according to which the fossil catfish Hypsidoris occupies a rather basal position within the Siluriformes. Arratia (1992: fig. 46) listed eight uniquely derived characters and two homoplastic ones to diagnose the clade constituted by all non-diplomystid, non-hypsidorid catfishes examined in her study. These characters are: (1) maxilla without long anterior process; (2) maxilla rudimentary; (3) articulation between autopalatine and maxilla double, lateroventrally oriented; (4) absence of autopalatine extension dorsal to the dermal entopterygoid; (5) absence of a dermal ectopterygoid; (6) absence of a
dermal entopterygoid; (7) presence of a link between the 'entopterygoid' and the vomer (homoplastic); (8) loss of notch separating the processus basalis and the posterodorsal part of the metapterygoid (homoplastic); (9) presence of three or four pairs of barbels; (10) absence of a supraneural bone above the Weberian apparatus in adults.

Arratia’s cladogram (Fig. 12.6) also supports Mo’s (1991) phylogenetic results, according to which the ariids are somewhat closely related to the pimelodids. The six characters uniting Parapimelodus and the two ariid genera, Bagre and Galeichthys, in Arratia’s cladogram (Fig. 12.6) are: (1) presence of a sesamoid ectopterygoid joining the autopalatine and ‘entopterygoid’; (2) presence of ectopterygoid process of metapterygoid (homoplastic); (3) blood vessels running in a tube-like lamellar formation ventral to the Weberian apparatus (homoplastic); (5) fusion of hypurals 1 and 2 (homoplastic); (6) branched sensory canals (homoplastic).

However, Arratia’s cladogram (Fig. 12.6) attributes a rather basal position to Nematogenyidae and Trichomycteridae, two families that occupy a rather derived position in Mo’s (1991) cladograms (Fig. 12.4). Indeed, Arratia (1992: fig. 46) listed nine derived characters to separate the diplomystids, hypsidorids, nematogenyids and trichomycterids from all the other catfishes represented in her cladogram. These characters are: (1) presence of a rod-like autopalatine; (2) no articulation between autopalatine and vomer (homoplastic); (3) presence of a ligament and/or connective tissue between ‘entopterygoid’ and lateral ethmoid (homoplastic); (4) presence of a metapterygoid-‘entopterygoid’ ligament (homoplastic); (5) hyomandibula articulating with autosphenotic; (6) absence of prootic in the hyomandibular fossa; (7) presence of bony extension over the ventral surface of the fifth centrum (homoplastic); (8) presence of suture between pterosphenoid and parasphenoid (homoplastic); (9) blood vessels in a groove partially surrounded by lamellar walls in the ventral part of the Weberian apparatus (homoplastic).

Another significant aspect of Arratia’s cladogram is the fact that the heptapterid genus Rhamdia appears more closely related to the clade formed by Parapimelodus (Pimelodidae), Bagre (Ariidae) and Galeichthys (Ariidae) than to the heptapterid genus Heptapterus. The characters listed by Arratia (1992: fig. 46) to unite genera Galeichthys, Bagre, Parapimelodus and Rhamdia, and thus to separate these genera from Heptapterus are: (1) fusion of abdominal centra 2-6 or more; (2) presence of a small, elongate pharyngobranchial attached to the epibranchial and the medial aspect of the hyomandibula (homoplastic).
Lundberg, 1993 (Fig. 12.7)

In an overview of certain clades formed by African and South American freshwater fishes, and their respective implications in the continental drift theory, Lundberg (1993) provided a phylogenetic hypothesis (Fig. 12.7) concerning the relationships among some catfish taxa. This hypothesis was based on a hand-made analysis of 12 osteological and myological characters of the cephalic region, dorsal fin and Weberian apparatus, previously described by other authors and/or personally observed by Lundberg (Lundberg, 1993: 180). Lundberg’s hypothesis (Fig. 12.7) is practically identical to that of Mo (Fig. 12.4), with the addition of the Eocene fossil catfish ‘Titanoglanis’ as the sister-group of the clade constituted by the Mochokidae, Auchenipteridae and Doradidae (the ‘Auchenipteridae’ and the ‘Ageneiosidae’ of Lundberg correspond to the Auchenipteridae of this work). It should be noted, however, that Lundberg (1993) was seemingly unaware of Mo’s study, since this latter paper was not cited by him. The two characters listed by Lundberg (1993: 180) to support the sister-group relationship between ‘Titanoglanis’ and the clade including the Mochokidae, Auchenipteridae and Doradidae were: (1) posterior edge of supraoccipital truncated, not drawn out to form a process; (2) middle nuchal plate with anterolateral processes contacting post-temporal-epioccipital region of skull.

Fig. 12.7 Hypothetical relationships among certain catfish taxa (Lundberg, 1993).

De Pinna, 1996 (Fig. 12.8)

Based on a phylogenetic comparison of a considerable number of characters of the cephalic region, Weberian apparatus, pectoral fins and girdle, vertebrae, dorsal fin, pelvic fins and girdle and caudal fin, de Pinna (1996) provided a hypothesis on the relationships among the Asiatic Amblycipitidae, Akysidae, Sisoridae and Erethistidae and the South-American Aspredinidae, as well as among certain genera of these families.
De Pinna's numerical analysis (using Hennig 86) of a data matrix, which had 112 characters 21 terminal taxa, resulted in a single, completely resolved, most parsimonious cladogram (Fig. 12.8) with 167 steps, CI = 0.70 (autapomorphic characters included) and RI = 0.79.

One of the most significant conclusions of de Pinna's work was that the Sisoridae of previous authors was a paraphyletic assemblage, with a subunit of it (subsequently named Erethistidae by de Pinna) being more closely related to Neotropical Aspredinidae than to the remaining taxa previously assigned to Sisoridae (Fig. 12.8). Five synapomorphies were listed by de Pinna (1996: 64) to diagnose the clade constituted by Erethistidae and Aspredinidae, of which only the last is non-homoplastic: (1) mandibular laterosensory canal absent; (2) second hypobranchial unossified; (3) anterior margin of pectoral spine with serrations; (4) internal support for pectoral fin rays small in size; (5) anterior portion of lateral line running closely in parallel to lateral margin of Weberian lamina. In turn, ten synapomorphies were listed by de Pinna (1993: 61) to diagnose the clade formed by these two families plus the Sisoridae sensu stricto, eight of which are homoplastic: (1) posterior portion of supracleithrum ankylosed to margin of Weberian lamina (homoplastic);
(2) parapophysis of fifth vertebra strongly flattened and expanded (homoplastic); (3) parapophysis of fifth vertebra long, almost or quite reaching lateral surface of body wall; (4) humeral process or region around it connected to anterior portion of vertebral column by well-defined ligament-state 3' (homoplastic); (5) posterior part of Weberian lamina extensively contacting parapophysis of fifth vertebra; (6) (reversal of) anterior half of segments of pectoral fin spine elongate, almost parallel to axis of spine (homoplastic); (7) coracoid with ventral anterior process (homoplastic); (8) (reversal of) second dorsal fin spine with medial ridge along its anterior surface, forming bilateral longitudinal pouches (homoplastic); (9) ventral arms of first dorsal fin spine with posterior subprocesses attached dorsal to their tip (homoplastic); (10) basipterygium with ventral longitudinal keel, anteriorly extending alongside internal arm (homoplastic).

In addition, de Pinna’s (1996) work suggested the existence of a monophyletic clade formed by Sisoridae, Erethistidae, Aspredinidae and Akysidae which, in turn, together with family Amblycipitidae formed the superfamily Sisoroidea (Fig. 12.8). Three synapomorphies were listed to define the clade including Sisoridae, Erethistidae, Aspredinidae and Akysidae, namely: (1) supratemporal fossae present (homoplastic); (2) supracleithrum strongly attached to skull; (3) posterior nuchal plate with anterior process forming facet for articulation with anterior nuchal plate (de Pinna, 1996: 60). With respect to superfamily Sisoroidea, de Pinna (1996: 59-60) listed seven synapomorphies, namely: (1) posterior centre of ossification of palatine compressed and expanded vertically (homoplastic); (2) articular region of lateral ethmoid elongated as a process, with articular facet for palatine at tip; (3) parapophysis of fifth vertebra strong and attached to ventral side of centrum, directed directly transverse to centrum; (4) humeral process or soft tissue around it connected to anterior portion of vertebral column by well-defined ligament; (5) segments of pectoral fin spine very oblique, almost parallel to axis of spine, not evident (homoplastic); (6) the dorsal spine with medial ridges along its anterior surface, forming bilateral longitudinal pouches (homoplastic); (7) ventral tip of first dorsal fin pterygophore and corresponding neural spines with contacting facets.

**De Pinna, 1998 (Fig. 12.9)**

Two years after the publication of his (1996) work, de Pinna published an overview on the phylogenetic relationships of Neotropical Siluriformes,
which included a not completely resolved cladogram expressing the relationships among the major groups of the whole order (Fig. 12.9). As explained by de Pinna (1998: 289-290), this cladogram was mainly derived from his 1993 unpublished thesis, “with some resolution added on the sisoroid-aspredinidid part of the tree based on the results of de Pinna (1996), the “position of Ariiidae from Lundberg (1993)” and position of Hypsidoridae left unresolved.

Fig. 12.9 Hypothetical relationships among major groups of Siluriformes (de Pinna, 1998).
One of the most remarkable aspects of de Pinna's 1998 cladogram is the fact that, although it is mainly derived from an unpublished thesis (de Pinna, 1993) of which the great part was realised parallelly and thus independent of that of Mo (1991), several points of this cladogram coincide with Mo's phylogenetic results. In fact, small differences excepted, both de Pinna (1998) and Mo (1991) agree upon: (1) rather basal position of the Cetopsidae within the siluriforms; (2) relationships among the different loricarioid families and a close relationship between these families and Sisoridae (sensu lato), Akysidae, Aspredinidae and Amblycipitidae; and (3) relationships among the Mochokidae, Auchenipteridae, Doradidae and Ariidae (however the position of Ariidae in de Pinna's 1998 cladogram is based on Lundberg's 1993 paper).

But there are also some significant differences between the cladogram of de Pinna (1998) and the phylogenetic results of Mo (1991), of which one of the most notable is de Pinna's suggestion that both Bagridae and Claroteidae sensu Mo (1991) are, in fact, polyphyletic groups.

Another important aspect of de Pinna's 1998 cladogram (Fig. 12.9) is that it constitutes the first published cladogram providing an explicit hypothesis about the phylogenetic position of the three Pimelodidae, groups, i.e., the Pseudopimelodidae (de Pinna's Pseudopimelodinae), Pimelodidae (de Pinna's Pimelodidae) and the Heptapteridae (de Pinna's Heptapterinae). In de Pinna's 1998 cladogram, the pseudopimelodids form, together with the loricarioids and sisoroids, a monophyletic unit that is the sister-group of a clade with the heptapterids and some bagrids as its more basal taxa (Fig. 12.9). With respect to the pimelodids, de Pinna suggests a sister-group relationship between these catfishes and some bagrids, with the clade formed by these two groups being included, together with the claroteins (see above), schilbeids, pangasiids, *Horabagrus* and austroglanidids, in a clad included in a large, unresolved pentatomy (Fig. 12.9).

Unfortunately, de Pinna's 1998 cladogram is mainly based on his 1993 unpublished results and except for the interrelationships among the loricarioid families, as well as some other specific cases, his 1998 paper does not directly provide the phylogenetic characters that support the interfamilial relationships illustrated in that cladogram (these characters are, however, provided in his 1993 unpublished thesis). Consequently, neither the characters concerning the polyphyly of Bagridae and Claroteidae sensu Mo (1991) nor the characters concerning the
phylogenetic position of both the Pimelodidae, Pseudopimelodidae and Heptapteridae, within the Siluriformes are included in his 1998 paper.

**He et al., 1999 (Fig. 12.10)**

The He et al.’s (1999) study is dedicated mainly to the phylogeny of the African family Amphiliidae, but also includes an analysis of the relationships between this family and some other taxa, namely Diplomystidae, Amblycipitidae, Hypsoridae, Bagridae, Sisoridae and *Leptoglanis* (the phylogenetic position of this genus, which was transferred from Bagridae to Amphiliidae in Bailey and Stewart’s 1984 paper, was considered uncertain a priori by He et al.). The characters used in this study are osteological characters of the cephalic region, Weberian apparatus, vertebrae, pectoral girdle, dorsal fin, caudal skeleton and pelvic girdle. This phylogenetic study of He et al. (1999), based on a numerical analysis (using PAUP) of a data matrix with 73 characters including 14 terminal taxa, resulted in a single most parsimonious cladogram with 190 steps and CI = 0.616 (0.603 excluding autapomorphic characters).

According to this cladogram (Fig. 12.10), neither Amphiliidae nor Sisoridae are monophyletic groups, with the doumein amphiliids more closely related to *Leptoglanis* and the sisorid *Glyptothorax* than to either the sisorid *Euchiloglanis* or the amphiliin amphiliids (Fig. 12.10). The

![Diagram](image-url)

**Fig. 12.10** Hypothetical relationships among amphiliid genera, as well as among these genera and some non-amphiliid taxa (He et al., 1999).
characters listed by He et al. (indirectly given in their table 1 to support the clade composed by the doumein, amphiliids, *Leptoglanis* and sisorid *Glyptothorax* are: (1) no posterior [frontal] fontanel (homoplastic); (2) posterodorsal process of supraoccipital short, slightly forked at its posterior end (homoplastic); (3) short maxillary without enlarged fan-like or forked posterior part; (4) fourth and fifth parapophyses of Weberian apparatus partly fused, thin and long (homoplastic); (5) proximal [radials] 1 and 2 of dorsal fin with [?] independent nuchal plates; (6) all units of second dorsal spine fused.

Another interesting aspect of the He et al. (1999) study is the placement of Amblycipitidae in an unresolved trichotomy leading to this family, the Diplomyistidae, and a clade constituted by the remaining catfishes examined, including the fossil catfish family Hypsidoridae (Fig. 12.10).

Higher-level Phylogeny of Siluriformes: Consensus, Contradictions and Perspectives

After presenting the phylogenetic hypotheses of Howes (1983), Grande (1987), Schaefer (1990), Mo (1991), de Pinna (1992), Arratia (1992), Lundberg (1993), de Pinna (1996), de Pinna (1998) and He et al. (1999), it is opportune to provide here a discussion on the consensus and contradictions between these phylogenetic hypotheses.

An overall analysis of these hypotheses reveals, indeed, some general consensus between them concerning the relationships and/or phylogenetic position of certain catfish families, which are described below.

Sister-group relationship between Diplomyistidae and all other Siluriformes. All the studies presented above dealing with the phylogenetic position of Diplomyistidae (Grande, 1987; Mo, 1991; Arratia, 1992; de Pinna, 1998; He et al., 1999) place the diplomystids as the sister-group of all other catfishes (Figs. 12.2, 12.4, 12.6, 12.9, 12.10). However, the general consensus on the basal position of Diplomyistidae within Siluriformes contrasts with the contradictions concerning the characters listed in these studies to support this position. For example, one of the characters listed by Grande (1987) and Arratia (1992) as a synapomorphy of the non-diplomystid catfishes (Siluroidei) is the ankylosis between the fifth centrum and the complex centrum of the Weberian apparatus. However, according to the phylogenetic results of Mo (1991: 207), this character does not constitute a synapomorphy of Siluroidei but instead, is a
synapomorphy uniting all non-helogenin siluroids. In turn, some characters listed by Mo to diagnose the Siluroidei, as e.g., the “T-shaped vomer” (Mo, 1991: 203), are contradicted by other authors, such as Arratia (1992: 122) and de Pinna (1998: 291). In reality, the only character that is commonly accepted in the aforesaid studies as an unambiguous synapomorphy of non-diplomystid siluriforms is the “17 or fewer principal caudal rays (vs. 18 or more in Diplomystes and other primitive teleosts)” (Grande, 1987: 48).

**Basal position of Cetopsidae and Hypsidoridae within Siluriformes.** The two studies presented in the section dealing with the phylogenetic position of Cetopsidae (Mo, 1991; de Pinna, 1998) place this family in a markedly basal position within the non-diplomystid Siluriformes (Figs. 12.4, 12.9). De Pinna (1998: 292) stated that cetopsids “lack some synapomorphies of all other catfishes except for diplomystids and in some instances also hypsidorids” but did not specify which synapomorphies. Mo (1991: 204) listed two derived characters not present in cetopsid and diplomystid catfishes, to support the rather basal position of Cetopsidae: (1) ramus mandibularis nerve runs inside hyomandibular for a distance (according to both cladograms of Mo); (2) interdigital union of the two coracoids (according to Mo’s cladogram I). With respect to the fossil hypsidorids, there is a general, but not strict, consensus concerning their phylogenetic position. In fact, of the six cladograms presenting an hypothesis concerning the phylogenetic relationships of these fossil catfishes, two (Mo’s 1991 cladogram II and He et al.’s 1999 cladogram) place them in a somewhat derived position, one (Mo’s 1991 cladogram I) leaves their phylogenetic position unresolved, and only three (Grande’s 1987, Arratia’s 1992 and de Pinna’s 1998) place them in a markedly basal position within Siluriformes. However, it should be noted that the phylogenetic hypotheses represented on both cladogram II of Mo (1991) and the cladogram of He et al. (1999) are strongly contested by some authors (e.g., de Pinna and Ferraris, 1992; de Pinna, 1993, 1998; Diogo, Chapter 14, this volume; M. Chardon, pers. comm.) and thus the phylogenetic position of Hypsidoridae on these cladograms should be regarded with some reservation. With respect to the three studies suggesting a markedly basal position of hypsidorids, i.e., Grande (1987), Arratia (1992) and de Pinna (1998), only the first two papers listed characters to support this basal position, with Grande (1987) listing five characters and Arratia (1992) adding a series of characters to Grande’s list (see above). However, it should be noted that one of the characters listed
by Grande (1987) as a synapomorphy of the non-hypsiderid siluroids, the absence of maxillary teeth, was questioned by Arratia (1992: 108-109), since, according to her, the absence of maxillary teeth constitutes a catfish plesiomorphy.

Sister-group relationship between heteropneustids and clariids. The two studies dealing with the interrelationships of these two groups (Mo, 1991; de Pinna, 1998) clearly suggest a sister-group relationship between them, with de Pinna (1998) going so far as to include heteropneustids in family Clariidae. However, of these two studies, only one, namely that of Mo (1991: 204, 207), provided a list of derived characters to support the close relationship between heteropneustids and clariids. These characters are: (1) pterotic sutured with the frontal on the cranial roof; (2) accessory respiratory organ; (3) enlarged laminar last infraorbital; (4) rib on the 6th vertebra vestigial.

Close relationship among aspredinids, erethistids, sisorids, akysids and amblycipitids. The three studies dealing with the interrelationships of Aspredinidae (Mo, 1991; de Pinna, 1996, 1998) suggest a close relationship between that Neotropical family and the Asiatic families Erethistidae, Sisoridae, Akysidae and Amblycipitidae. Mo (1991) suggested a somewhat close, but highly unresolved (Fig. 12.4), relationship among these families (see above). These five families were later the subject of a detailed phylogenetic analysis by de Pinna (1996), which provided seven synapomorphies to support their inclusion in a monophyletic clade (Sisoroidea) (see above), with the relationships within this clade being (Amblycipitidae + (Akysidae + (Sisoridae + (Aspredinidae + Erethistidae)))). This phylogenetic hypothesis was subsequently strengthened by de Pinna (1998: 319), who provided one additional character (development of the second ural centrum) to support the relationships between aspredinids and Asiatic sisoroids.

Close relationship among auchenipterids, doradids, mochokids and ariids. Mo’s 1991, Lundberg’s 1993 and de Pinna’s 1993 studies suggest a close relationship between the cosmopolitan family Ariidae and a clade (Doradoidea) including the African family Mochokidae and the Neotropical sister-groups Doradidae and Auchenipteridae. However, grouping the latter three families in superfamily Doradoidea is clearly more consensal than is the sister-group relationship between Ariidae and this superfamily, since the close relationship of ariids with doradoids suggested by de Pinna’s 1998 cladogram is based on the studies of Mo (1991) and Lundberg (1993), and not on his own phylogenetic results (see above).
The elastic spring apparatus is one of the characters most commonly mentioned to support a clade including Ariidae and Doradoidea (see Lundberg, 1993). This character, present in other catfish families, such as Malapteruridae and Pangasiidae, and also Cranoglanididae (Diogo et al., in press), was, however, questioned by Mo (1991: 197-198). In fact, according to Mo (1991) the only unambiguous characters supporting a close relationship between Ariidae and Doradoidea are: (1) prominent posterior process of the epioccipital; (2) ossified Baudelot ligament sutured proximally with the basioccipital; (3) absence of ascending portion of the intercalarium; (4) absence of ascending portion of the scaphium; (5) absence of mesocoracoid loop. The first two characters were corroborated by Lundberg (1993) (see above).

Phylogenetic relationships among different loricarioid families. There is a strict consensus in Howes’ 1983, Schaefer’s 1990, Mo’s 1991 and both de Pinna studies 1992 and 1998 concerning the relationships among Astroblepidae, Loricariidae, Scoloplacidae and Callichthyidae. Indeed, all these studies suggest that Scoloplacidae is the sister-group of a monophyletic unit including Loricariidae and Astroblepidae, with the clade formed by these three families being, in turn, the sister-group of Callichthyidae (Figs. 12.1, 12.3, 12.4, 12.5, 12.9). With respect to the relationships of Nematogenyidae and Trichomycteridae, although there is no strict consensus in these five studies, it can be said that it is somewhat agreed at present that these families are sister-groups, constituting a monophyletic unit that is the sister-group of all other loricarioid families. In fact, although Howes (1983) suggested that nematogenyids are probably the sister-group of all other loricarioids (Fig. 12.1), he clearly emphasised that this hypothesis was weakly supported, and even contradicted by some derived features present in both Trichomycteridae and Nematogenyidae (see above). Schaefer (1990) was fully aware of this problem and thus preferred to consider the relationships of Trichomycteridae and Nematogenyidae as unresolved a priori (see above). Mo (1991) analysed this problem and concluded that nematogenyids and trichomycterids are probably sister-groups, with the clade formed by these two groups being the sister-group of all other loricarioids (Fig. 12.4). This hypothesis was subsequently strongly supported by de Pinna (1992), who included in his analysis a new, undescribed group of trichomycterids, the Copionodontinae, which was proposed to be the most plesiomorphic taxa within Trichomycteridae. De Pinna’s (1992) phylogenetic analysis pointed out that some of the characters commonly used to place the
trichomycterids as the sister-group of all the remaining non-nematogenyid loricarioids were, in reality, plesiomorphically absent in the family Trichomycteridae (see above). The sister-group relationship between Nematogenyidae and Trichomycteridae was further supported by de Pinna (1998), who provided some new data to support that hypothesis (de Pinna, 1998: 296-297). Therefore, it can be said that there is a general consensus concerning the relationships among families of Loricaroidae, these being (((Nematogenyidae + Trichomycteridae) + (Callichthyidae + (Scoloplacidae + (Loricariidae + Astroblepidae))))). A splendid, extensive compilation of the numerous characters supporting the different clades within the Loricaroidea was recently provided by de Pinna (1998: fig. 6).

Close relationship between sisoroids and amphiliids. Although there are some important differences concerning the relationships of Sisoroidea and Amphiliidae in the studies of Mo (1991), de Pinna (1998) and He et al. (1999), all these studies suggest a close relationship between these two groups. In both cladograms of Mo (1991) the sisoroids and amphiliids were included in a monophyletic clade that also included the loricarioids, clariids and heteropneustids (Fig. 12.4). De Pinna (1998) included the sisoroids and amphiliids in a monophyletic clade that also included the loricarioids, but not the clariids and heteropneustids (Fig. 12.9). A close relationship between Amphiliidae and Sisoroidea is only partially supported by the rather confusing cladogram of He et al. (1999). In fact, according to He et al.’s (1999) cladogram (Fig. 12.10), the superfamily Sisoroidea, as well as families Amphiliidae and Sisoridae, are not monophyletic: the Amblycipitidae are, together with the Diplomystidae, the sister-groups of all the other catfishes represented in the cladogram (including the fossil hypsidorids); the sisorid Euchiloglanis is the sister-group of a clade formed by the sisorid Glyptothorax, the amphiliid Leptoglanis and the amphiliid doumeins. Although Mo’s 1991, de Pinna’s 1998 and He et al.’s 1999 studies suggest a close relationship between Sisoroidea and Amphiliidae, it is not possible, due to the important differences between these studies mentioned above, to list even a single consensual character supporting such a close relationship.

There is thus some general consensus concerning the phylogenetic position and/or interrelationships of certain catfish groups among those cladistic studies dealing with the higher-level phylogeny of Siluriformes. However, despite recent progress in catfish phylogeny, much remains to be done on this area. In fact, within the different cladistic studies referred to
above, the phylogenetic position of families such as Austroglanididae, Bagridae, Chacidae, Claroteidae, Cranoglanididae, Anchariidae, Heptapteridae, Ictaluridae, Andinichthyidae, Pseudopimelodidae, Malapteruridae, Pangasiidae, Pimelodidae, Plotosidae, Schilbeidae and Siluridae is rather unclear (cf. Figs. 12.4A,B, 12.6, 12.9, 12.10). Moreover, although there is general consensus concerning the interrelationships among the different families of Loricarioidea, Doradoidea and Sisoroidea (see above), the phylogenetic position of these major groups within the order Siluriformes is also unclear.

But one of most problematic issues concerning catfish phylogeny is surely the fact that a major fundamental question, with important implications not only for the choice of outgroups, but also for decisions regarding the polarity and/or evolutionary transformations of certain characters, remains unanswered: which is the most basal taxon within the suborder Siluroidei, that is, within the non-diplomystid taxa? According to Grande (1987), the most basal non-diplomystid taxon is the fossil family Hypsidoridae (see above). However, this hypothesis was contradicted by Mo's 1991 study, according to which the most plesiomorphic non-diplomystid catfishes are the cetopsids (see above). Arratia's 1992 phylogenetic analysis, which did not include cetopsids, pointed out that not only the hypsidoridae, but also the nematogenyid and trichomycterid loricarioids, probably occupy a rather basal position within the non-diplomystid catfishes (see above). De Pinna (1998) considered the most plesiomorphic non-diplomystid taxa to be Cetopsidae and Hypsidoridae, but did not specify which of these two taxa is, in fact, the most basal taxon within suborder Siluroidei (see above). The results of a preliminary, still unpublished phylogenetic analysis by the author, which did not include fossil hypsidoridae, partially agrees with the hypothesis of Arratia (1992) and partially contradicts those of Mo (1991) and de Pinna (1998). These results strongly support a markedly basal position of the nematogenyid loricarioids within Siluriformes, with the nematogenyids appearing, together with the cetopsids, as the most basal non-diplomystid catfishes.

The examples provided above clearly illustrate that much remains to be done in order to attain a satisfactory knowledge of catfish phylogeny. But the increasing number of new researchers working on Siluriformes, and particularly with siluriform phylogeny, as well as the increasing cooperation between them, associated with the more and more efficient computer techniques available to undertake phylogenetic analyses, seem to augur a promising future for this area of research. One of the simplest
ways of clarifying the uncertainties involving catfish phylogeny cited above would be to simply include more characters in studies dealing with this subject. For example, morphological features that could eventually reveal useful information to clarify the relationships of Siluriformes, such as, e.g., the musculature of the branchial apparatus, or the musculature associated with the caudal skeleton, have never been included in analyses of catfish phylogeny. Molecular characters are also rarely included in such analyses and when they are (e.g., Montoya-Burgos et al., 1997, 1998; Pouyaud et al., 2000), are often used to study the relationships among specific catfish groups and not the higher-level phylogeny of Siluriformes. A combination of both morphological and molecular data could also play an important role in clarifying catfish phylogeny. Knowledge in this area could be augmented by the inclusion of more taxa in future phylogenetic studies, as was elegantly demonstrated by de Pinna (1992). Also important would be to combine, either in different matrices or in a single one (see Kitching et al., 1998), all the data provided by the various studies dealing with the interfamilial relationships of catfishes, in order to establish a more robust and embracing hypothesis on the higher-level phylogeny of Siluriformes.

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