

Monophyly, affinities, and subfamilial clades of sea catfishes (Siluriformes: Ariidae)

Arturo Acero P.^{*,***} and Ricardo Betancur-R.^{**,***}

Abstract

The sea catfish family Ariidae is a natural group defined by four anatomical synapomorphies: lapillus otolith extraordinarily developed, bones of the otic capsules (prootic, pterotic, exoccipital, and epioccipital) profoundly inflated, presence of a well-developed ventral process of basioccipital, and male mouthbrooding of eggs and embryos. Recent studies, based on molecular and morphological evidence, agree that the sister group to ariids is the freshwater family Anchariidae from Madagascar; however, there is no consensus about the phylogenetic relationships of the Ariidae + Anchariidae clade among other siluroid families. The family Ariidae can be divided into two monophyletic lineages. Galeichthyinae, new subfamily, including one genus and four species, is defined by one derived morphological state: postcleithral process fused to the posterior dorsal process of cleithrum, forming a fan-shaped lamina. The subfamily Ariinae, including the remaining ariids, is characterized by four anatomical synapomorphies: posterior process of epioccipital produced and connected to the sustentaculum of Weberian apparatus, ventral process of basioccipital and ventral ossification of complex vertebra forming an aortic tunnel, presence of anterodorsal bony block of the orbitosphenoids, and absence of anterior nuchal plate. Additionally, mitochondrial and nuclear evidence strongly support the monophyly of the Ariidae (three amino acid synapomorphies) and its subfamilies (Galeichthyinae, six amino acid autapomorphies of *Galeichthys peruvianus*; Ariinae, four amino acid synapomorphies).

Resumen

La familia de bagres marinos Ariidae es un grupo natural definido por cuatro sinapomorfías anatómicas: otolito lápilo extraordinariamente desarrollado, huesos de las cápsulas óticas (proótico, pterótico, exoccipital y epioccipital) profundamente inflados, presencia de un proceso ventral del basioccipital bien desarrollado e incubación oral por parte de los machos de los huevos y embriones. Estudios recientes, basados en evidencia molecular y morfológica, coinciden en que el grupo hermano de los ariidos es la familia dulceacuícola Anchariidae, conocida de Madagascar; sin embargo, no hay consenso acerca de las relaciones filogenéticas del clado Ariidae + Anchariidae con respecto a otras familias de siluroideos. La familia Ariidae puede ser dividida en dos linajes monofiléticos. Galeichthyinae nueva subfamilia, con un género y cuatro especies, se halla definida por un estado derivado: proceso postcleitral fusionado al proceso posterior dorsal del cleitro, formando una lámina a modo de abanico. La subfamilia Ariinae, que incluye a los ariidos restantes, se caracteriza por cuatro sinapomorfías: proceso posterior del epioccipital pronunciado y conectado al sustentáculo del aparato de Weber, proceso ventral del basioccipital y osificación ventral de la vértebra compleja formando un túnel aórtico, presencia de un bloque

* Universidad Nacional de Colombia (Instituto de Ciencias Naturales), Cerro Punta Betín, A.A. 1016 (INVE-MAR), Santa Marta, Colombia. E-mail: aacero@invemar.org.co

** Department of Biological Sciences, Auburn University, 331 Funchess Hall, Auburn, AL 36849, USA. E-mail: betanri@auburn.edu

*** Both authors have contributed equally to the work, authorship in alphabetical order.

óseo anterodorsal del orbitosfenoides y ausencia de placa nugal anterior. Adicionalmente, la evidencia mitocondrial y nuclear respalda fuertemente la monofilia de Ariidae (tres sinapomorfías aminoacídicas) y de sus subfamilias (Galeichthyinae, seis autapomorfías aminoacídicas de *Galeichthys peruvianus*; Ariinae, cuatro sinapomorfías aminoacídicas).

Otophysan fishes include four orders and at least 67 families of teleosts widely distributed and diverse in world freshwaters (Ng & Sparks, 2005; Rodiles-Hernández et al., 2005; Nelson, 2006). Only two families of the catfish order Siluriformes are well represented in marine waters (Baras & Laleye, 2003): the Plotosidae, restricted to the Indian and western Pacific oceans, and the Ariidae. Ariids, also known as sea catfishes, are widespread in the tropical and subtropical continental shelves of the Atlantic, Indian and Pacific oceans. The species inhabit mainly brackish estuaries and lagoons, but some are confined to freshwaters and others occur only in totally marine environments.

The number of valid ariid species is uncertain and recent estimates range from 120 to 200 (Acero P., 2003; Teugels, 2003; Kailola, 2004). In the last decades several authors have attempted to solve the intrafamilial relationships of ariids on a regional or global basis (Kailola, 1991, 2004; Betancur-R., 2003; Acero P., 2004; Betancur-R. et al., 2004); however, a clear and consistent view of the suprageneric clades of ariids is still lacking. The aim of this paper is to discuss the monophyly of the Ariidae and its interfamilial relationships, and provide a suprageneric classification within the family, including the description of a new subfamily.

Names for skeletal structures follow Arratia (2003a,b). Institutional abbreviations for material illustrated are as in Leviton et al. (1985), with the modification of INVEMAR to INVEMAR-PEC. Molecular evidence is based on ariid sequences from Betancur-R. (2003) [cytochrome *b* (*cyt b*), 49 species; recombination activation gene 2 (*rag2*), 25 species] and other catfish sequences (one per family or major lineage) from Hardman (2005) (*cyt b*, 31 species) and Sullivan et al. (in press) (*rag2*, 37 species). Positions for amino acid synapomorphies are referenced from the start codon as compared to *Danio rerio* for *rag2* (GenBank accession no. NM 131385) and to *Ictalurus punctatus* for *cyt b* (GenBank accession no. AF482987). Unambiguous amino acid transformations are given in bold.

Monophyly of the Ariidae

Ariidae, originally described by Bleeker (1862) as Arii, was hypothesized to be primitive by Regan (1911), in his pioneering systematic study of catfishes. Further studies, such as Bhimachar (1933), Merriman (1940), Tilak (1965), Higuchi (1982), and Rao & Lakshmi (1984) made important contributions on the comparative anatomy of the group. Kailola (1991), Mo (1991), and de Pinna (1993) were the first authors that claimed the monophyly of ariids, based mainly on osteological evidence. Oliveira et al. (2002) reported two myological peculiarities of sea catfishes that might be synapomorphies. Kailola (2004) proposed several synapomorphies of the family and discussed other diagnostic features. Diogo (2005) presented additional corroboration of the monophyly of ariids based on osteological and myological characters. Hardman (2002, 2005), Betancur-R. (2003), and Sullivan et al. (2006) provided support of ariid monophyly using molecular data.

Corroborated synapomorphies. (1) Lapillus (= utricular) otolith extraordinarily developed (Fig. 1). In catfishes the three pairs of otoliths are minute, the lapillus is confined to the central area of the prootic and is usually larger than the other two (the saccular otolith or sagitta and the lagenar otolith or asteriscus) (Chardon, 1968; Higuchi, 1982; Mo, 1991; de Pinna, 1993; Oliveira et al., 2001). In three unrelated catfish lineages, ariids, plotosids, and the incertae sedis *Horabagrus*, the lapillus otolith is enlarged and occupies an area corresponding to several bones of the otic region (Oliveira et al., 2001). The lapillus of sea catfishes is larger than the lapillus of plotosids and *Horabagrus* (Oliveira et al., 2001; Diogo, 2005). In the Malagasy anchariids, considered sister to the Ariidae (Diogo, 2005; Ng & Sparks, 2005; Sullivan et al., 2006), the lapillus is reduced (Kailola, 2004; Diogo, 2005). The lapillus otolith of ariids is oval, conchoidal, and biconvex (Higuchi, 1982; Nolf, 1985; Betancur-R. et al., 2004).

The lapilli of sea catfishes are so distinctive that they have been widely noted in the fossil record (Frizzell, 1965; Nolf, 1976; Nolf & Aguilera, 1998). At least 23 fossil sea catfish species have been described based on their lapillus otolith (Weiler, 1968; Nolf, 1985). Apparently, the best known siluriform fossil described from lapillus material is *Vorhisia vulpes*, quoted as “genus Siluriformorum” *vulpes* by Nolf (1985) and as “genus Ariidarum” *vulpes* by Nolf & Stringer (1996). This species, found at the Upper Cretaceous of South Dakota and Maryland, is among the oldest catfish fossils recorded (see Hardman, 2005: fig. 3). *Vorhisia vulpes* has been reported as living in an estuarine-deltaic environment, not entering freshwater (Frizzell & Koenig, 1973; Nolf & Stringer, 1996). The shape of *Vorhisia*'s lapillus is relatively similar to that of *Galeichthys* (see Hecht & Hecht, 1981) and other neotropical sea catfishes (Acero P., 2004; Betancur-R. et al., 2004). Based on the shape and size of the lapillus and the environment that *V. vulpes* inhabited, it seems possible that it is a fossil ariid, as was hypothesized by Nolf & Stringer (1996).

(2) Otic capsules or bulla acoustico utricularis swollen: prootic, pterotic, exoccipital, and epioccipital profoundly inflated (Fig. 2) (Higuchi, 1982; Betancur-R. et al., 2004; Diogo, 2005). The extraordinarily development of otic capsules in ariids is likely related to the size of lapillus. In other catfish groups with enlarged lapillus (i.e. plotosids and *Horabagrus*), the otic capsules are also inflated, but only the prootic and the pterotic are involved (Oliveira et al., 2001; Diogo, 2005), prob-

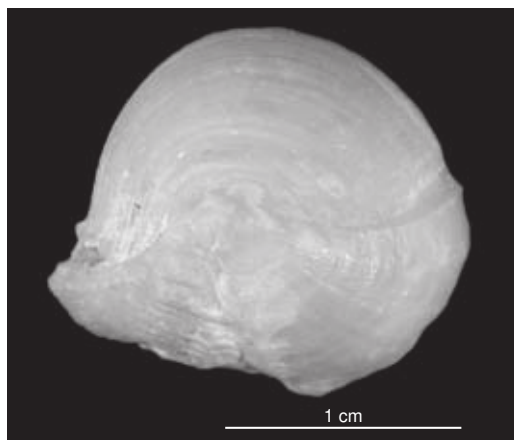


Fig. 1. *Potamarius nelsoni*, UMMZ 198713-S, 480 mm SL, lapillus (= utricular) otolith.

ably because their lapilli are smaller than in sea catfishes.

(3) Presence of well-developed ventral process of basioccipital, forming a cone-shaped projection (Fig. 3). The union between the basioccipital and the first vertebra is expressed externally by a toothed suture and by the subvertebral process, which is absent in other catfish families (Tilak, 1965; Higuchi, 1982; Rao & Lakshmi, 1984; Kailola, 1991, 2004).

(4) Male mouthbrooding of eggs and embryos (Rimmer & Merrick, 1983; Betancur-R. et al., 2004; Kailola, 2004). This trait has been found in all ariid species with known life histories, including *Galeichthys feliceps* (Tilney & Hecht, 1993).

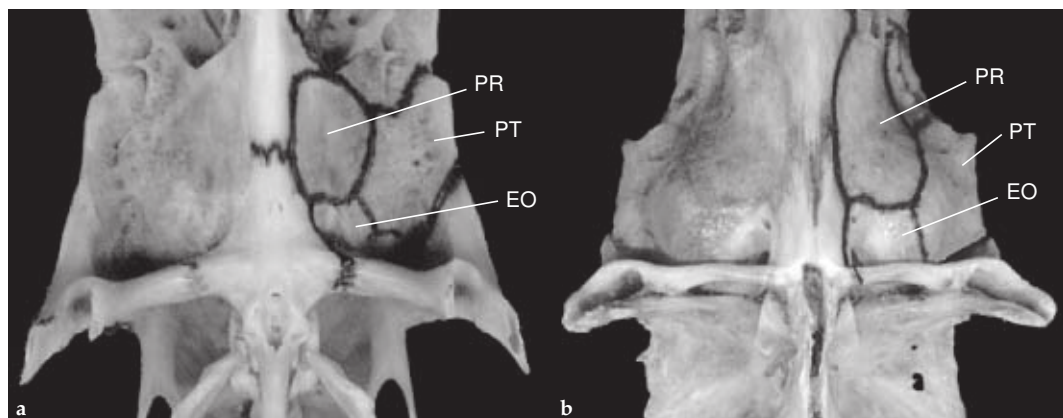


Fig. 2. Ventral view of posterior portion of cranium of: a, *Trachelyopterus insignis* (Auchenipteridae), INVEMAR PEC 6819, 171 mm SL; and b, *Galeichthys ater*, INVEMAR PEC 6799, 239 mm SL. EO, exoccipital; PR, prootic; PT, pterotic.



Fig. 3. *Notarius kessleri*, INVEMAR PEC 6785, 281 mm SL; lateral view of cranium. VPB, ventral process of basioccipital.

Mouthbrooding has not been reported in other catfish families, with the exception of males and females of the claroteid *Phyllonemus typus* (Ochi et al., 2000). The multiple occurrence of this feature in non-closely related teleost lineages will be discussed elsewhere.

The monophyly of sea catfishes is also strongly supported by evidence derived from mitochondrial (*cyt b*, ATP synthase 8/6, ribosomal 12S and 16S) and nuclear (*rag1* and *rag2*) sequences (Hardman, 2002, 2005; Betancur-R., 2003; Sullivan et al., 2006). Amino acid synapomorphies of the Ariidae are: *rag2*, 116: cysteine → serine, 118: arginine → lysine; *cyt b*, 305: leucine → methionine.

Other putative synapomorphies. Oliveira et al. (2002) and Diogo (2005) reported two myological peculiarities of ariids: the adductor arcus palatini muscle inserting on the mesial margin of the suspensorium and on a significant part of the lateral surface of this complex structure, and the adductor mandibulae Aw or A3" obliquely oriented with its posterodorsal fibers significantly dorsal to the upper edge of the coronoid process.

Kailola (2004) proposed that the possession of strong pelvic musculature, unique epidermal mucous secretions, and the maximal consolidation of the anterior vertebrae may also support the monophyly of the family. Sea catfishes are also characterized by lacking larvae, males mouth-brood eggs and embryos, releasing batches as juveniles much longer than one centimeter (Tilney & Hecht, 1993); this feature was named precocial larvae by Kailola (2004). She also commented that high DNA complement per cell (LeGrande, 1980) and chromosome number and arm length (Fitzsimmons et al., 1988) might be unique features of ariids. We also hypothesize that sexually dimorphic pelvic fins (i.e. larger in females than in males) might be a derived condition of the Ariidae (Fig. 4), but this feature needs corroboration in several taxa.

Other diagnostic characters. Fossa between dorsomedial limb of posttemporo-supracleithrum, extrascapular, and pterotic (= temporal fossa) remarkably developed in most ariids (Fig. 5b). The fossa is absent in most catfish

families, such as doradids and auchenipterids (Fig. 5a), or present but less developed in claroteids, schilbeids, pangasiids, ictalurids, and *Ancharius* (Diogo, 2005). Mesocoracoid arch reduced or absent from the pectoral girdle (condition shared with anchariids, akysids, aspredinids, bagrids, bunoccephalins, and doradoids) (Kailola, 2004; Diogo, 2005). Lateral ethmoid and frontal bones usually articulated through two facets (vs. single facet in the remaining siluriforms except pangasiids) (Kailola, 2004).

Interfamilial relationships

The phylogenetic position of sea catfishes within the order Siluriformes is under debate. Mo (1991) first proposed that the Ariidae is the sister family of a clade including the African Mochokidae and the neotropical doradoids (Doradidae and Auchenipteridae). Arratia (1992), in her analysis of the suspensorium of catfishes, suggested that ariids are closely related to pimelodids and more distantly to heptapterids. Lundberg's (1993) hypothesis is similar to that of Mo (1991), with the addition of the undescribed "titanoglanis", a coastal Eocene fossil from Arkansas. Lundberg (1993) provisionally placed ariids, mochokids, doradoids, and "titanoglanis" in the arioid group, which was supported by six skeletal synapomorphies. Such relationship was not supported by de

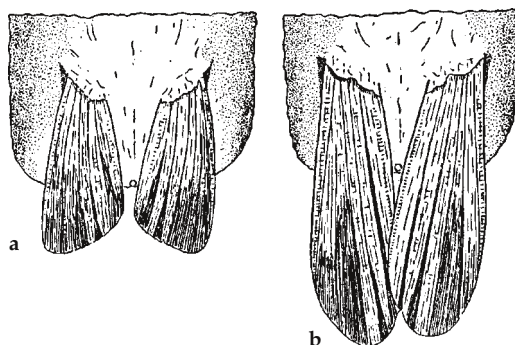


Fig. 4. Pelvic fins of (a) males and (b) females of *Bagre marinus* (after Merriman, 1940).

Pinna (1993), who considered the Ariidae (including *Ancharius*) the sister group to the African Claroteidae, and that clade the sister group to the Schilbeidae plus Pangasiidae, both from the Old World. In a later work de Pinna (1998) adopted an eclectic point of view, accepting a doradoid clade that includes Mochokidae, Doradidae, and Auchenipteridae, plus Ariidae, the African Malapteruridae, the Asian Pangasiidae, and the African and Asian Schilbeidae. De Pinna (1998)'s doradoid clade is diagnosed by the presence of an elastic spring mechanism associated to the Weberian complex; however, the condition may not be homologous in all those families (de Pinna, 1998; Diogo, 2005).

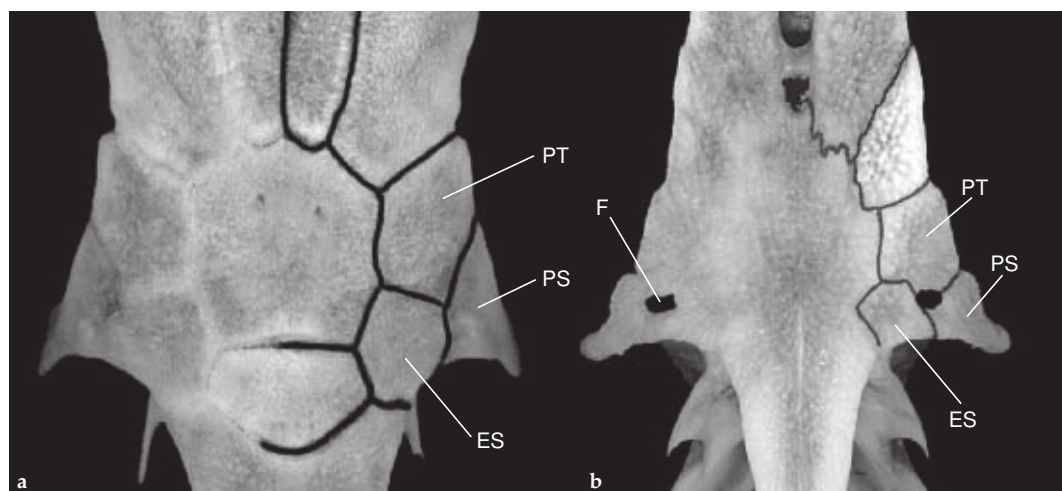


Fig. 5. Dorsal view of posterior portion of cranium of: a, *Trachelyopterus insignis* (Auchenipteridae), INVEMAR PEC 6819, 171 mm SL; and b, *Notarius kessleri*, INVEMAR PEC 6785, 328 mm SL. ES, extrascapular; F, fossa; PS, posttemporo-supracleithrum; PT, pterotic.

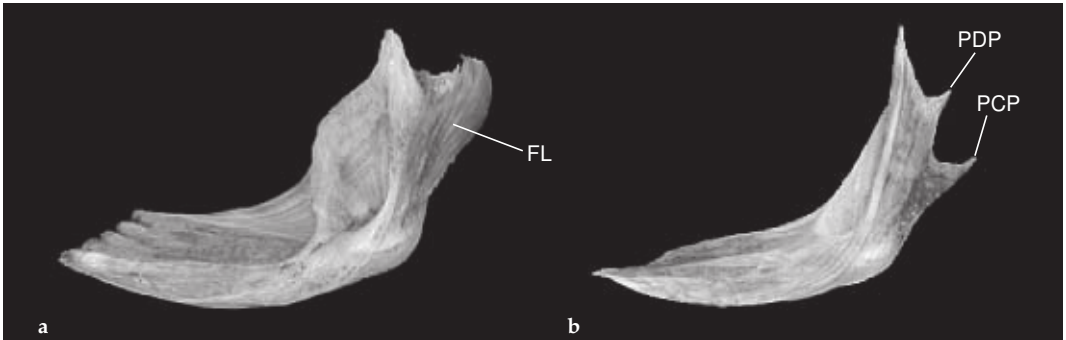


Fig. 6. Cleithrum of: **a**, *Galeichthys ater*, INVEMAR PEC 6799, 239 mm SL; and **b**, '*Arius*' *platypogon*, INVEMAR PEC 6802, 261 mm SL. FL, fan-shaped lamina; PCP, postcleithral process; PDP, posterior dorsal process.

Diogo et al. (2002) discussed four derived states from the cephalic region muscles shared by ariids, claroteids, and cranoglanidids. Diogo (2005) did a fairly complete analysis of the phylogeny of siluriforms based on morphological information. He concluded that ariids (including *Ancharius*) are the sister group to claroteids, and that clade plus the African Austroglanididae are sister to a clade including Cranoglanididae and Ictaluridae. According to Diogo (2005), those five families plus schilbeids and pangasiids form a monophyletic group.

Recent molecular evidence also reveals incongruence regarding the affinities of ariids to other siluriform groups. Hardman (2002) hypothesized the relationships of 22 catfish families using different reconstruction criteria on *cyt b* and *rag2* sequences. Ariids were often recovered close to ictalurids and sometimes close to the neotropical doradoids, or to schilbeids and pangasiids, or to the Asiatic chacids. In most topologies, however, the nodes relating ariids to those families were weakly supported. Hardman (2005) expanded to 29 families his catfish sampling (anchariids not included) using only *cyt b* sequences. He found a poorly supported relationship between ariids and schilbeids, ictalurids, cranoglanidids, mochokids, claroteids, and pangasiids. Sullivan et al. (2006), based on *rag1* and *rag2* sequences of 35 catfish families, reevaluated the phylogenetic relationships of siluriforms. They recovered the anchariid genus *Gogo* sister to five ariid genera and placed both lineages in the superfamily Arioidea, but failed to resolve the phylogenetic position of the arioid clade among other siluroid groups. Our comparison of the amino acid data reveals two arioid synapomorphies for *rag2*, **346:**

phenylalanine → **leucine** and 214: aspartic acid → asparagine.

The familial status of anchariids, a freshwater lineage endemic to Madagascar, has been controversial. The genus *Ancharius* has been traditionally treated as an ariid, but also placed within its own family (Stiassny & Raminosa, 1994) or in the family Mochokidae (Mo, 1991; Ng & Sparks in Sparks & Stiassny, 2003; Kailola, 2004; Nelson, 2006). Diogo (2005) supported de Pinna's (1993) hypothesis that *Ancharius* is the sister taxa of the remaining ariids. Diogo (2005) provided five ambiguous synapomorphies placing *Ancharius* as the sister taxa to '*Arius*' *heudelotii* + *Genidens genidens*. He also gave reasons to reject a close relationship between *Ancharius* and mochokids and stated that *Ancharius* should not be placed in its own family, but could be recognized as the ariid subfamily Anchariinae. The recent revision of anchariids by Ng & Sparks (2005) brought a new perspective to this controversy. Ng & Sparks (2005) described a new anchariid genus (*Gogo*) and diagnosed the group based on two putative apomorphic states, providing support for its familial status. We concur that anchariids are not sea catfishes. Despite the fact that some ariids are confined to freshwaters (e.g. *Potamarius* spp.), the family is originally a marine group and the freshwater restriction condition in some species implies secondarily acquisition and reversion to the primitive state in Otophysi (Betancur-R., 2003). Sullivan et al. (2006) argued that there is insufficient information to hypothesize the habitat preferences (i.e. coastal marine or freshwater) of the arioid ancestor. The position of the Anchariidae in their siluriform tree would parsimoniously imply that it retains the plesiomorphic

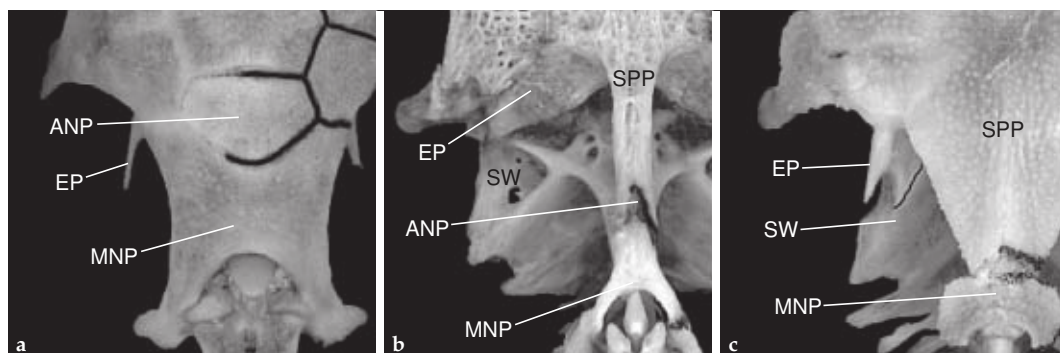


Fig. 7. Dorsal view of posterior portion of cranium of: **a**, *Trachelyopterus insignis* (Auchenipteridae), INVEMAR PEC 6819, 171 mm SL; **b**, *Galeichthys ater*, INVEMAR PEC 6799, 239 mm SL; and **c**, *Ariopsis* sp., INVEMAR PEC 6781, 274 mm SL. ANP, anterior nuchal plate; EP, epioccipital; MNP, middle nuchal plate; SPP, supraoccipital process; SW, sustentaculum of the Weberian apparatus.

Otophysi condition (i.e. freshwater confinement).

Suprageneric systematics of the Ariidae

The results obtained by Betancur-R. (2003), Betancur-R. et al. (2004), and Acero P. (2004), based on mitochondrial, nuclear, and morphological evidence, suggest that the Ariidae can be divided into two clades. These two clades are diagnosed below.

Subfamily Galeichthyinae new subfamily

Type genus. *Galeichthys* Valenciennes.

Diagnosis. The subfamily Galeichthyinae is distinguished from the other catfishes by a uniquely derived state: postcleithral (= humero-cubital *sensu* Arratia, 2003b) process fused to posterior dorsal process of cleithrum, forming a fan-shaped lamina (Fig. 6a). Primitively in other catfishes, including ariines (Fig. 6b) and anchariids, the postcleithral process is produced and distinct from the posterior dorsal process. Additionally, the new subfamily is characterized by having a long and narrow supraoccipital process, usually grooved along its entire extension (Fig. 7b). The polarization of this feature is, however, equivocal because the supraoccipital process of ariines (Fig. 7c) and other catfishes, if present, is widely variable in shape and size (Arratia, 2003a). Amino acid autapomorphies of *Galeichthys peru-*

vianus (only galeichthyine species sequenced) are: *rag2*, 214: asparagine → serine; *cyt b*, 37: leucine → methionine, 171: asparagine → serine, 232: isoleucine → alanine, 245: serine → tryptophan, 355: isoleucine → threonine.

Genus and species included. *Galeichthys*: *G. feliceps* Valenciennes (type species), *G. ater* Castelnau, *G. peruvianus* Lütken. The genus also includes an undescribed species from South Africa (Kulongowski, 2001).

Distribution and habitat. *Galeichthys* occurs in subtropical and temperate waters with three species in southern Africa and one in the Eastern Pacific in Perú. The biogeographic implications of the disjunct distribution of galeichthyines will be discussed elsewhere (see also Betancur-R., 2003; Acero P., 2004). The species inhabit coastal marine and estuarine waters, suggesting that the invasion of marine waters by ariids predated subfamilial cladogenesis.

Subfamily Ariinae Bleeker

Type genus. *Arius* Valenciennes.

Diagnosis. The subfamily Ariinae is diagnosed by four synapomorphies. (1) Posterior process of epioccipital (= epiotic *sensu* Higuchi, 1982; Rao & Lakshmi, 1984; Arratia, 2003a) produced and connected to the sustentaculum of Weberian apparatus (Fig. 7c). In galeichthyines the posterior process of epioccipital does not contact the sus-

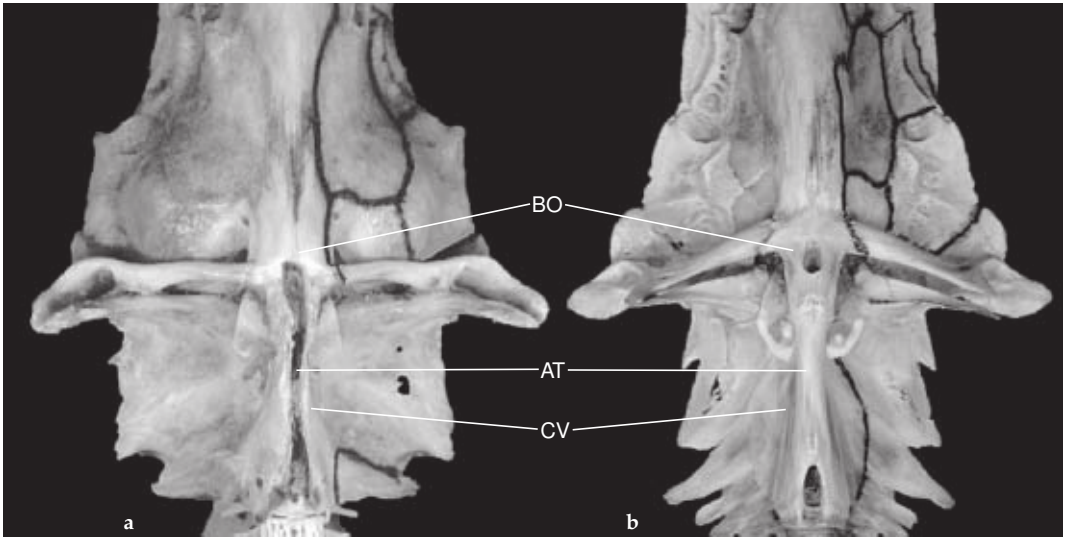


Fig. 8. Ventral view of posterior portion of cranium of: **a**, *Galeichthys ater*, INVEMAR PEC 6799, 239 mm SL; and **b**, *Sciades dowii*, INVEMAR PEC 6803, 296 mm SL. AT, aortic tunnel; BO, basioccipital; CV, complex vertebra.

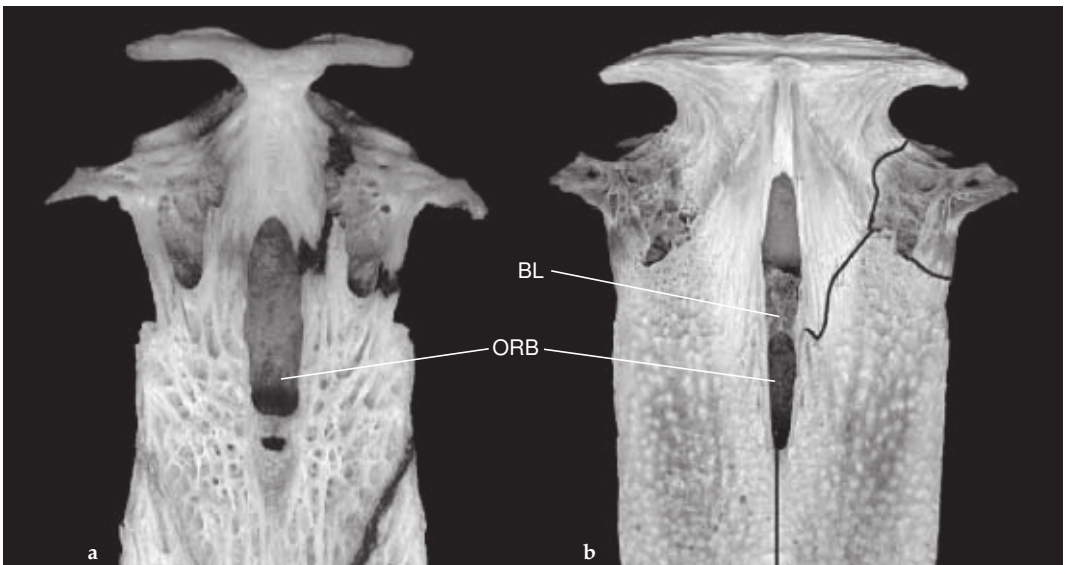


Fig. 9. Dorsal view of anterior portion of cranium of: **a**, *Galeichthys ater*, INVEMAR PEC 6799, 239 mm SL; and **b**, *Sciades proops*, INVEMAR PEC 6809, 377 mm SL. BL, block; ORB, orbitosphenoids.

tentaculum (Fig. 7b). Primitively in other catfish families, including anchariids, the posterior extension of the epioccipital is absent, except for auchenipterids, doradids, pangasiids, and schilbeids, in which the extension is not considered homologous to that of ariids (Fig. 7a) (Kailola, 2004; Diogo, 2005). (2) Ventral process of basioc-

cipital and ventral ossification of complex vertebra mesially closed forming an aortic tunnel (Fig. 8b). The basioccipital and the complex vertebra in galeichthyines are mesially opened, producing an incomplete aortic tunnel (Fig. 8a). The basioccipital and the ventral ossification of the complex centrum do not form an aortic tunnel

in anchariids or in other catfish families (Diogo, 2005). (3) Presence of antero-dorsal bony block of the orbitosphenoids (Fig. 9b). This block is present homoplasically in some pimelodoids (J. G. Lundberg, pers. comm.), but it is absent in galeichthyines (Fig. 9a) and anchariids (Ng & Sparks, 2005: fig. 14b). (4) Anterior nuchal plate absent (Fig. 7c). In galeichthyines the plate is reduced but distinct from the middle nuchal plate (= predorsal plate) (Fig. 7b). In many catfish groups (Fig. 7a), including anchariids (Ng & Sparks, 2005: fig. 14b), both plates are well developed. Amino acid ariine synapomorphies are: *rag2*, **147: ser-**

ine → **asparagine**, 108: isoleucine → valine; *cyt b*, 45: leucine → methionine, 344: histidine → aspartic acid.

Genera included. All non-*Galeichthys* sea catfishes; genera currently recognized are listed in Table 1. There are several undescribed and *incertae sedis* taxa not included in Table 1, such as the ariid fauna of the eastern Atlantic (at least four species, Acero P. & Betancur-R., in press), which generic affinities are unclear.

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Table 1. List of ariine genera. Classification of New World genera is based on Betancur-R. (2003) and Acero P. (2004) except for *Genidens* which follows Marceñiuk & Ferraris (2003). Classification of Old World genera is based on Kailola (2004), excluding Old World species from *Ariopsis* (otherwise treated as '*Ariopsis*') and New World species from *Hemiaris*. EI, eastern Indian; EP, eastern Pacific; M, Madagascar; SA, Sahul Shelf; SU, Sunda Shelf; WA, western Atlantic; WI, western Indian; B, brackish waters; F, freshwaters; M, marine waters.

	approx. number of species	distribution	habitat
New World			
<i>Ariopsis</i>	5	EP, WA	B, F, M
<i>Bagre</i>	4	EP, WA	B, M
<i>Cathorops</i>	15	EP, WA	B, F, M
<i>Genidens</i>	4	WA	B, F, M
<i>Notarius</i>	15	EP, WA	B, F, M
<i>Potamarius</i>	3	WA	F
<i>Sciades</i>	6	EP, WA	B, F, M
Old World			
<i>Amisidens</i>	1	SA	B, M
' <i>Ariopsis</i> '	11-14	SA, M?	B, F, M
<i>Arius</i>	16	EI, SU	B, F, M
<i>Batrachocephalus</i>	1	EI, SU	B, F, M
<i>Brustiarius</i>	2	SA	F
<i>Cephalocassis</i>	2	SU	F
<i>Cinetodus</i>	3-4	SA	B, F, M
<i>Cochlefelis</i>	3	EI, SA, SU	B, F
<i>Cryptarius</i>	2	EI, SU	B, F, M
<i>Hemiaris</i>	5	EI, SA, SU	B, F, M
<i>Hexanematichthys</i>	2	EI, SA, SU	B, M
<i>Ketengus</i>	1	EI, SU	B, M
<i>Nedystoma</i>	2	SA	B, F
<i>Nemapteryx</i>	6	EI, SA, SU	B, M
<i>Netuma</i>	3	WI, EI, SA, SU	B, M
<i>Osteogeneiosus</i>	1	EI, SU	B, F?, M
<i>Plicofollis</i>	7	WI, EI, SA, SU	B, F, M

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